

THE
DIFFERENT FORMS OF FLOWERS
ON
PLANTS OF THE SAME SPECIES.

revised
BY CHARLES DARWIN, M.A., F.R.S.

WITH ILLUSTRATIONS.

NEW YORK:
D. APPLETON AND COMPANY,
549 AND 551 BROADWAY.

1877. *p*

TO
PROFESSOR ASA GRAY

This Volume is Dedicated

BY THE AUTHOR
AS A SMALL TRIBUTE OF RESPECT AND
AFFECTION.

CHAPTER I.

HETEROSTYLED DIMORPHIC PLANTS: PRIMULACEÆ.

Primula veris or the Cowslip—Differences in structure between the two forms—Their degrees of fertility when legitimately and illegitimately united—*P. elatior*, *vulgaris*, *Sinensis*, *auricula*, &c.—Summary on the fertility of the heterostyled species of *Primula*—Homostyled species of *Primula*—*Hottonia palustris*—*Androsace Vitalliana*.

It has long been known to botanists that the common Cowslip (*Primula veris*, Brit. Flora, var. *officinalis*, Lin.) exists under two forms, about equally numerous, which obviously differ from each other in the length of their pistils and stamens.* This difference has hitherto been looked at as a case of mere variability, but this view, as we shall presently see, is far from the true one. Florists who cultivate the *Polyanthus* and *Auricula* have long been aware of the two kinds of flowers, and they call the plants which display the globular stigma at the mouth of the corolla, "pin-headed" or "pin-eyed," and those which display the anthers, "thrum-eyed."† I will designate the two forms as the long-styled and short-styled.

The pistil in the long-styled form is almost exactly twice as long as that of the short-styled. The stigma

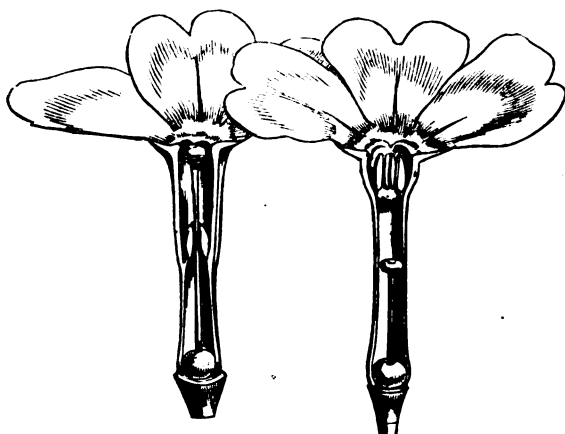
* This fact, according to von Mohl ('Bot. Zeitung,' 1863, p. 326) was first observed by Persoon in the year 1794.

† In Johnson's Dictionary, *thrum* is said to be the ends of weavers' threads; and I suppose

that some weaver who cultivated the *Polyanthus* invented this name, from being struck with some degree of resemblance between the cluster of anthers in the mouth of the corolla and the ends of his threads.

stands in the mouth of the corolla or projects just above it, and is thus externally visible. It stands high above the anthers, which are situated halfway down the tube and cannot be easily seen. In the short-styled form the anthers are attached near the mouth of the tube, and therefore stand above the stigma, which is seated in about the middle of the tubular corolla. The corolla itself is of a different

Fig. 1.



Long-styled form.

Short-styled form.

PRIMULA VERIS.

shape in the two forms; the throat or expanded portion above the attachment of the anthers being much longer in the long-styled than in the short-styled form. Village children notice this difference, as they can best make necklaces by threading and slipping the corollas of the long-styled flowers into one another. But there are much more important differences. The stigma in the long-styled form

is globular; in the short-styled it is depressed on the summit, so that the longitudinal axis of the former is sometimes nearly double that of the latter. Although somewhat variable in shape, one difference is persistent, namely, in roughness: in some specimens carefully compared, the papillæ which render the stigma rough were in the long-styled form from twice to thrice as long as in the short-styled. The anthers do not differ in size in the two forms, which I mention because this is the case with some heterostyled plants. The most remarkable difference is in the pollen-grains. I measured with the micrometer many specimens, both dry and wet, taken from plants growing in different situations, and always found a palpable difference. The grains distended with water from the short-styled flowers were about $\cdot 038$ mm. ($\frac{10-11}{7000}$ of an inch) in diameter, whilst those from the long-styled were about $\cdot 0254$ mm. ($\frac{7}{7000}$ of an inch), which is in the ratio of 100 to 67. The pollen-grains therefore from the longer stamens of the short-styled form are plainly larger than those from the shorter stamens of the long-styled. When examined dry, the smaller grains are seen under a low power to be more transparent than the larger grains, and apparently in a greater degree than can be accounted for by their less diameter. There is also a difference in shape, the grains from the short-styled plants being nearly spherical, those from the long-styled being oblong with the angles rounded; this difference disappears when the grains are distended with water. The long-styled plants generally tend to flower a little before the short-styled: for instance, I had twelve plants of each form growing in separate pots and treated in every respect alike; and at the time when only a single short-styled plant was in

flower, seven of the long-styled had expanded their flowers.

We shall, also, presently see that the short-styled plants produce more seed than the long-styled. It is remarkable, according to Prof. Oliver,* that the ovules in the unexpanded and unimpregnated flowers of the latter are considerably larger than those of the short-styled flowers; and this I suppose is connected with the long-styled flowers producing fewer seeds, so that the ovules have more space and nourishment for rapid development.

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

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

I have examined a large number of flowers; and though the shape of the stigma and the length of the pistil both vary, especially in the short-styled form, I have never met with any transitional states between the two forms in plants growing in a state of nature. There is never the slightest doubt under which form a plant ought to be classed. The two kinds of flowers are

* 'Nat. Hist. Review,' July 1862, p. 237.

never found on the same individual plant. I marked many Cowslips and Primroses, and on the following year all retained the same character, as did some in my garden which flowered out of their proper season in the autumn. Mr. W. Wooler, of Darlington, however, informs us that he has seen early blossoms on the *Polyanthus*,* which were not long-styled, but became so later in the season. Possibly in this case the pistils may not have been fully developed during the early spring. An excellent proof of the permanence of the two forms may be seen in nursery-gardens, where choice varieties of the *Polyanthus* are propagated by division; and I found whole beds of several varieties, each consisting exclusively of the one or the other form. The two forms exist in the wild state in about equal numbers: I collected 522 umbels from plants growing in several stations, taking a single umbel from each plant; and 241 were long-styled, and 281 short-styled. No difference in tint or size could be perceived in the two great masses of flowers.

We shall presently see that most of the species of *Primula* exist under two analogous forms; and it may be asked what is the meaning of the above-described important differences in their structure? The question seems well worthy of careful investigation, and I will give my observations on the cowslip in detail. The first idea which naturally occurred to me was, that this species was tending towards a dioecious condition; that the long-styled plants, with their longer pistils, rougher stigmas, and smaller pollen-grains, were more feminine in nature, and would produce more seed;—that the short-styled plants, with their shorter pistils, longer stamens and larger pol-

* I have proved by numerous experiments, hereafter to be given, that the *Polyanthus* is a variety of *Primula veris*.

len-grains, were more masculine in nature. Accordingly, in 1860, I marked a few cowslips of both forms growing in my garden, and others growing in an open field, and others in a shady wood, and gathered and weighed the seed. In all the lots the short-styled plants yielded, contrary to my expectation, most seed. Taking the lots together, the following is the result:—

TABLE 1.

—	Number of Plants.	Number of Umbels produced.	Number of Capsules produced.	Weight of Seed in grains.
Short-styled cowslips . . .	9	33	199	83
Long-styled cowslips . . .	13	51	261	91

If we compare the weight from an equal number of plants, and from an equal number of umbels, and from an equal number of capsules of the two forms, we get the following results:—

TABLE 2.

—	Number of Plants.	Weight of Seed in grains.	Number of Umbels.	Weight of Seed.	Number of Cap- sules.	Weight of Seed in grains.
Short-styled cowslips .	10	92	100	251	100	41
Long-styled cowslips .	10	70	100	178	100	34

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

In 1861 the trial was made in a fuller and fairer

manner. A number of wild plants had been transplanted during the previous autumn into a large bed in my garden, and all were treated alike; the result was—

TABLE 3.

—	Number of Plants.	Number of Umbels.	Weight of Seed in grains.
Short-styled cowslips . .	47	173	745
Long-styled cowslips . .	58	208	692

These figures give us the following proportions:—

TABLE 4.

—	Number of Plants.	Weight of Seed in grains.	Number of Umbels.	Weight of Seed in grains.
Short-styled cowslips . . .	100	1585	100	430
Long-styled cowslips . . .	100	1093	100	332

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

Looking to these trials made during two successive years on a large number of plants, we may safely conclude that the short-styled form is more productive than the long-styled form, and the same result holds

good with some other species of *Primula*. Consequently my anticipation that the plants with longer pistils, rougher stigmas, shorter stamens and smaller pollen-grains, would prove to be more feminine in nature, is exactly the reverse of the truth.

In 1860 a few umbels on some plants of both the long-styled and short-styled form, which had been covered by a net, did not produce any seed, though other umbels on the same plants, artificially fertilised, produced an abundance of seed; and this fact shows that the mere covering in itself was not injurious. Accordingly, in 1861, several plants were similarly covered just before they expanded their flowers; these turned out as follows:—

TABLE 5.

—	Number of Plants.	Number of Umbels produced.	Product of Seed.
Short-styled . . .	6	24	{ 1·3 grain weight of seed, or about 50 in number.
Long-styled . . .	18	74	
			Not one seed.

Judging from the exposed plants which grew all round in the same bed, and had been treated in the same manner, excepting that they had been exposed to the visits of insects, the above six short-styled plants ought to have produced 92 grains' weight of seed instead of only 1·3; and the eighteen long-styled plants, which produced not one seed, ought to have produced above 200 grains' weight. The production of a few seeds by the short-styled plants was probably due to the action of Thrips or of some other minute insect. It is scarcely necessary to give any additional evidence, but I may add that ten pots of polyanthuses and

cowslips of both forms, protected from insects in my greenhouse, did not set one pod, though artificially fertilised flowers in other pots produced an abundance. We thus see that the visits of insects are absolutely necessary for the fertilisation of *Primula veris*. If the corolla of the long-styled form had dropped off, instead of remaining attached in a withered state to the ovarium, the anthers attached to the lower part of the tube with some pollen still adhering to them would have been dragged over the stigma, and the flowers would have been partially self-fertilised, as is the case with *Primula Sinensis* through this means. It is a rather curious fact that so trifling a difference as the falling-off of the withered corolla, should make a very great difference in the number of seeds produced by a plant if its flowers are not visited by insects.

The flowers of the cowslip and of the other species of the genus secrete plenty of nectar; and I have often seen humble-bees, especially *B. hortorum* and *muscorum*, sucking the former in a proper manner,* though they sometimes bite holes through the corolla. No doubt moths likewise visit the flowers, as one of my sons caught *Cucullia verbasci* in the act. The pollen readily adheres to any thin object which is inserted into a flower. The anthers in the one form stand nearly, but not exactly, on a level with the stigma of the other; for the distance between the anthers and stigma in the short-styled form is greater than that in the long-styled, in the ratio of 100 to 90. This difference is the result of the anthers in the long-styled form standing rather higher in the tube than does the stigma in the short-styled, and this favours their

* H. Müller has also seen *Anthophora pilipes* and a *Bombylius*

sucking the flowers. 'Nature,' Dec. 10th, 1874, p. 111.

pollen being deposited on it. It follows from the position of the organs that if the proboscis of a dead humble-bee, or a thick bristle or rough needle, be pushed down the corolla, first of one form and then of the other, as an insect would do in visiting the two forms growing mingled together, pollen from the long-stamened form adheres round the base of the object, and is left with certainty on the stigma of the long-styled form; whilst pollen from the short stamens of the long-styled form adheres a little way above the extremity of the object, and some is generally left on the stigma of the other form. In accordance with this observation I found that the two kinds of pollen, which could easily be recognised under the microscope, adhered in this manner to the proboscides of the two species of humble-bees and of the moth, which were caught visiting the flowers; but some small grains were mingled with the larger grains round the base of the proboscis, and conversely some large grains with the small grains near the extremity of the proboscis. Thus pollen will be regularly carried from the one form to the other, and they will reciprocally fertilise one another. Nevertheless an insect in withdrawing its proboscis from the corolla of the long-styled form cannot fail occasionally to leave pollen from the same flower on the stigma; and in this case there might be self-fertilisation. But this will be much more likely to occur with the short-styled form; for when I inserted a bristle or other such object into the corolla of this form, and had, therefore, to pass it down between the anthers seated round the mouth of the corolla, some pollen was almost invariably carried down and left on the stigma. Minute insects, such as Thrips, which sometimes haunt the flowers, would

likewise be apt to cause the self-fertilisation of both forms.

The several foregoing facts led me to try the effects of the two kinds of pollen on the stigmas of the two forms. Four essentially different unions are possible; namely, the fertilisation of the stigma of the long-styled form by its own-form pollen, and by that of the short-styled; and the stigma of the short-styled form by its own-form pollen, and by that of the long-styled. The fertilisation of either form with pollen from the other form may be conveniently called a *legitimate union*, from reasons hereafter to be made clear; and that of either form with its own-form pollen an *illegitimate union*. I formerly applied the term "heteromorphic" to the legitimate unions, and "homomorphic" to the illegitimate unions; but after discovering the existence of trimorphic plants, in which many more unions are possible, these two terms ceased to be applicable. The illegitimate unions of both forms might have been tried in three ways; for a flower of either form may be fertilised with pollen from the same flower, or with that from another flower on the same plant, or with that from a distinct plant of the same form. But to make my experiments perfectly fair, and to avoid any evil result from self-fertilisation or too close interbreeding, I have invariably employed pollen from a distinct plant of the same form for the illegitimate unions of all the species; and therefore it may be observed that I have used the term "own-form pollen" in speaking of such unions. The several plants in all my experiments were treated in exactly the same manner, and were carefully protected by fine nets from the access of insects, excepting Thrips, which it is impossible to exclude. I performed all the manipulations myself, and weighed the seeds in a chemical balance; but during

many subsequent trials I followed the more accurate plan of counting the seeds. Some of the capsules contained no seeds, or only two or three, and these are excluded in the column headed "good capsules" in several of the following tables:—

TABLE 6.

Primula veris.

Nature of the Union.	Number of Flowers fertilised.	Total Number of Capsules produced.	Number of good Capsules.	Weight of Seed in grains.	Calculated Weight of Seed from 100 good Capsules.
Long-styled by pollen of short-styled. Legitimate union . . }	22	15	14	8·8	62
Long-styled by own-form pollen. Illegitimate union . . }	20	8	5	2·1	42
Short-styled by pollen of long-styled. Legitimate union . . }	13	12	11	4·9	44
Short-styled by own-form pollen. Illegitimate union . . }	15	8	6	1·8	30
SUMMARY:					
The two legitimate unions }	35	27	25	13·7	54
The two illegitimate unions }	35	16	11	3·9	35

The results may be given in another form (Table 7) by comparing, first, the number of capsules, whether good or bad, or of the good alone, produced by 100 flowers of both forms when legitimately and illegitimately fertilised; secondly, by comparing the weight of seed in 100 of these capsules, whether good or bad; or, thirdly, in 100 of the good capsules.

TABLE 7.

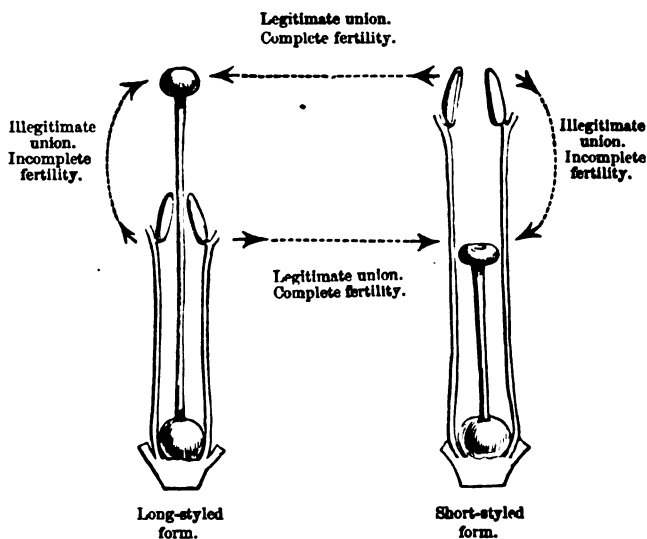
Nature of the Union.	Number of Flowers fertilised.	Number of Capsules.	Number of good Capsules.	Weight of Seed in grains.	Number of Capsules.	Weight of Seed in grains.	Number of good Capsules.	Weight of Seed in grains.
The two legitimate unions .	100	77	71	39	100	50	100	54
The two illegitimate unions .	100	45	31	11	100	24	100	35

We here see that the long-styled flowers fertilised with pollen from the short-styled yield more capsules, especially good ones (i.e. containing more than one or two seeds), and that these capsules contain a greater proportional weight of seeds than do the flowers of the long-styled when fertilised with pollen from a distinct plant of the same form. So it is with the short-styled flowers, if treated in an analogous manner. Therefore I have called the former method of fertilisation a legitimate union, and the latter, as it fails to yield the full complement of capsules and seeds, an illegitimate union. These two kinds of union are graphically represented in Fig. 2.

If we consider the results of the two legitimate unions taken together and the two illegitimate ones, as shown in Table 7, we see that the former compared with the latter yielded capsules, whether containing many seeds or only a few, in the proportion of 77 to 45, or as 100 to 58. But the inferiority of the illegitimate unions is here perhaps too great, for on a subsequent occasion 100 long-styled and short-styled flowers were illegitimately fertilised, and they together yielded 53 capsules: therefore the rate of 77 to 53, or as 100 to 69, is a fairer one than that of 100 to 58.

Returning to Table 7, if we consider only the good capsules, those from the two legitimate unions were to those from the two illegitimate in number as 71 to 31, or as 100 to 44. Again, if we take an equal number of capsules, whether good or bad, from the legitimately and illegitimately fertilised flowers, we find that the former contained seeds by weight compared with the latter as 50 to 24, or as 100 to 48; but if all the

Fig. 2.



poor capsules are rejected, of which many were produced by the illegitimately fertilised flowers, the proportion is 54 to 35, or as 100 to 65. In this and all other cases, the relative fertility of the two kinds of union can, I think, be judged of more truly by the average number of seeds per capsule than by the proportion of flowers which yield capsules. The two methods might

have been combined by giving the average number of seeds produced by all the flowers which were fertilised, whether they yielded capsules or not; but I have thought that it would be more instructive always to show separately the proportion of flowers which produced capsules, and the average number of apparently good seeds which the capsules contained.

Flowers legitimately fertilised set seeds under conditions which cause the almost complete failure of illegitimately fertilised flowers. Thus in the spring of 1862 forty flowers were fertilised at the same time in both ways. The plants were accidentally exposed in the greenhouse to too hot a sun, and a large number of umbels perished. Some, however, remained in moderately good health, and on these there were twelve flowers which had been fertilised legitimately, and eleven which had been fertilised illegitimately. The twelve legitimate unions yielded seven fine capsules, containing on an average each 57·3 good seeds; whilst the eleven illegitimate unions yielded only two capsules, of which one contained 39 seeds, but so poor, that I do not suppose one would have germinated, and the other contained 17 fairly good seeds.

From the facts now given the superiority of a legitimate over an illegitimate union admits of not the least doubt; and we have here a case to which no parallel exists in the vegetable or, indeed, in the animal kingdom. The individual plants of the present species, and as we shall see of several other species of *Primula*, are divided into two sets or bodies, which cannot be called distinct sexes, for both are hermaphrodites; yet they are to a certain extent sexually distinct, for they require reciprocal union for perfect fertility. As quadrupeds are divided into two nearly equal bodies of different sexes,

so here we have two bodies, approximately equal in number, differing in their sexual powers and related to each other like males and females. There are many hermaphrodite animals which cannot fertilise themselves, but must unite with another hermaphrodite. So it is with numerous plants; for the pollen is often mature and shed, or is mechanically protruded, before the flower's own stigma is ready; and such flowers absolutely require the presence of another hermaphrodite for sexual union. But with the cowslip and various other species of *Primula* there is this wide difference, that one individual, though it can fertilise itself imperfectly, must unite with another individual for full fertility; it cannot, however, unite with any other individual in the same manner as an hermaphrodite plant can unite with any other one of the same species; or as one snail or earth-worm can unite with any other hermaphrodite individual. On the contrary, an individual belonging to one form of the cowslip in order to be perfectly fertile must unite with one of the other form, just as a male quadruped must and can unite only with the female.

I have spoken of the legitimate unions as being fully fertile; and I am fully justified in doing so, for flowers artificially fertilised in this manner yielded rather more seeds than plants naturally fertilised in a state of nature. The excess may be attributed to the plants having been grown separately in good soil. With respect to the illegitimate unions, we shall best appreciate their degree of lessened fertility by the following facts. Gärtner estimated the sterility of the unions between distinct species,* in a manner which allows of a strict comparison with the results of the

* 'Versuche über die Bastarderzeugung,' 1849, p. 216.

legitimate and illegitimate unions of *Primula*. With *P. veris*, for every 100 seeds yielded by the two legitimate unions, only 64 were yielded by an equal number of good capsules from the two illegitimate unions. With *P. Sinensis*, as we shall hereafter see, the proportion was nearly the same—namely, as 100 to 62. Now Gärtner has shown that, on the calculation of *Verbascum lychnitis* yielding with its own pollen 100 seeds, it yielded when fertilised by the pollen of *V. Phoeniceum* 90 seeds; by the pollen of *V. nigrum*, 63 seeds; by that of *V. blattaria*, 62 seeds. So again, *Dianthus barbatus* fertilised by the pollen of *D. superbus* yielded 81 seeds, and by the pollen of *D. Japonicus* 66 seeds, relatively to the 100 seeds produced by its own pollen. We thus see—and the fact is highly remarkable—that with *Primula* the illegitimate unions relatively to the legitimate are more sterile than crosses between distinct species of other genera relatively to their pure unions. Mr. Scott has given* a still more striking illustration of the same fact: he crossed *Primula auricula* with pollen of four other species (*P. Palinuri*, *viscosa*, *hirsuta*, and *verticillata*), and these hybrid unions yielded a larger average number of seeds than did *P. auricula* when fertilised illegitimately with its own-form pollen.

The benefit which heterostyled dimorphic plants derive from the existence of the two forms is sufficiently obvious, namely, the intercrossing of distinct plants being thus ensured.† Nothing can be better adapted for this end than the relative positions of the anthers and stigmas in the two forms, as shown in Fig. 2; but to

* 'Journ. Linn. Soc. Bot.,' vol. viii. 1864, p. 93.

† I have shown in my work on the 'Effects of Cross and Self-

fertilisation' how greatly the offspring from intercrossed plants profit in height, vigour, and fertility.

this whole subject I shall recur. No doubt pollen will occasionally be placed by insects or fall on the stigma of the same flower; and if cross-fertilisation fails, such self-fertilisation will be advantageous to the plant, as it will thus be saved from complete barrenness. But the advantage is not so great as might at first be thought, for the seedlings from illegitimate unions do not generally consist of both forms, but all belong to the parent form; they are, moreover, in some degree weakly in constitution, as will be shown in a future chapter. If, however, a flower's own pollen should first be placed by insects or fall on the stigma, it by no means follows that cross-fertilisation will be thus prevented. It is well known that if pollen from a distinct species be placed on the stigma of a plant, and some hours afterwards its own pollen be placed on it, the latter will be prepotent and will quite obliterate any effect from the foreign pollen; and there can hardly be a doubt that with heterostyled dimorphic plants, pollen from the other form will obliterate the effects of pollen from the same form, even when this has been placed on the stigma a considerable time before. To test this belief, I placed on several stigmas of a long-styled cowslip plenty of pollen from the same plant, and after twenty-four hours added some from a short-styled dark-red polyanthus, which is a variety of the cowslip. From the flowers thus treated 30 seedlings were raised, and all these, without exception, bore reddish flowers; so that the effect of pollen from the same form, though placed on the stigmas twenty-four hours previously, was quite destroyed by that of pollen from a plant belonging to the other form.

Finally, I may remark that of the four kinds of unions, that of the short-styled illegitimately fertilised with its own-form pollen seems to be the most sterile of

all, as judged by the average number of seeds, which the capsules contained. A smaller proportion, also, of these seeds than of the others germinated, and they germinated more slowly. The sterility of this union is the more remarkable, as it has already been shown that the short-styled plants yield a larger number of seeds than the long-styled, when both forms are fertilised, either naturally or artificially, in a legitimate manner.

In a future chapter, when I treat of the offspring from heterostyled dimorphic and trimorphic plants illegitimately fertilised with their own-form pollen, I shall have occasion to show that with the present species and several others, equal-styled varieties sometimes appear.

PRIMULA ELATIOR, Jacq.

Bardfield Oxlip of English Authors.

This plant, as well as the last or Cowslip (*P. veris*, vel *officinalis*), and the Primrose (*P. vulgaris*, vel *acaulis*) have been considered by some botanists as varieties of the same species. But they are all three undoubtedly distinct, as will be shown in the next chapter. The present species resembles to a certain extent in general appearance the common oxlip, which is a hybrid between the cowslip and primrose. *Primula elatior* is found in England only in two or three of the eastern counties; and I was supplied with living plants by Mr. Doubleday, who, as I believe, first called attention to its existence in England. It is common in some parts of the Continent; and H. Müller* has seen several kinds of humble-bees and other bees, and Bombylius, visiting the flowers in North Germany.

* 'Die Befruchtung der Blumen,' p. 347.

The results of my trials on the relative fertility of the two forms, when legitimately and illegitimately fertilised, are given in the following table :—

TABLE 8.
Primula elatior.

Nature of Union.	Number of Flowers fertilised.	Number of good Capsules produced.	Maximum of Seeds in any one Capsule.	Minimum of Seeds in any one Capsule.	Average Number of Seeds per Capsule.
Long-styled form, by pollen of short-styled. } Legitimate union . . }	10	6	62	34	46·5
Long-styled form, by own-form pollen. Il- } legitimate union . . }	20	4	49*	2	27·7
Short-styled form, by pollen of long-styled. } Legitimate union . . }	10	8	61	37	47·7
Short-styled form, by own-form pollen. Il- } legitimate union . . }	17	3	19	9	12·1
The two legitimate unions together . . }	20	14	62	37	47·1
The two illegitimate unions together . . }	37	7	49*	2	35·5

* These seeds were so poor and small that they could hardly have germinated.

If we compare the fertility of the two legitimate unions taken together with that of the two illegitimate unions together, as judged by the proportional number of flowers which when fertilised in the two methods yielded capsules, the ratio is as 100 to 27; so that by this standard the present species is much more sterile than *P. veris*, when both species are illegitimately fertilised. If we judge of the relative fertility of the two kinds of unions by the average number of seeds per capsule, the ratio is as 100 to 75. But this latter

number is probably much too high, as many of the seeds produced by the illegitimately fertilised long-styled flowers were so small that they probably would not have germinated, and ought not to have been counted. Several long-styled and short-styled plants were protected from the access of insects, and must have been spontaneously self-fertilised. They yielded altogether only six capsules, containing any seeds; and their average number was only 7·8 per capsule. Some, moreover, of these seeds were so small that they could hardly have germinated.

Herr W. Breitenbach informs me that he examined, in two sites near the Lippe (a tributary of the Rhine), 894 flowers produced by 198 plants of this species; and he found 467 of these flowers to be long-styled, 411 short-styled, and 16 equal-styled. I have heard of no other instance with heterostyled plants of equal-styled flowers appearing in a state of nature, though far from rare with plants which have been long cultivated. It is still more remarkable that in eighteen cases the same plant produced both long-styled and short-styled, or long-styled and equal-styled flowers; and in two out of the eighteen cases, long-styled, short-styled, and equal-styled flowers. The long-styled flowers greatly preponderated on these eighteen plants,—61 consisting of this form, 15 of equal-styled, and 9 of the short-styled form.

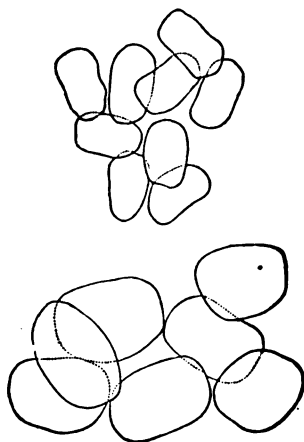
PRIMULA VULGARIS (var. *acaulis*, Linn.),

The Primrose of English Writers.

Mr. J. Scott examined 100 plants growing near Edinburgh, and found 44 to be long-styled, and 56 short-styled; and I took by chance 79 plants in Kent, of which 39 were long-styled and 40 short-styled; so

that the two lots together consisted of 83 long-styled and 96 short-styled plants. In the long-styled form the pistil is to that of the short-styled in length, from an average of five measurements, as 100 to 51. The stigma in the long-styled form is conspicuously more globose and much more papillose than in the short-styled, in which latter it is depressed on the summit;

Fig. 3.



Outlines of pollen-grains of *Primula vulgaris*, distended with water, much magnified and drawn under the camera lucida. The upper and smaller grains from the long-styled form; the lower and larger grains from the short-styled.

it is equally broad in the two forms. In both it stands nearly, but not exactly, on a level with the anthers of the opposite form; for it was found, from an average of 15 measurements, that the distance between the middle of the stigma and the middle of the anthers in the short-styled form is to that in the long-styled as 100 to 93. The anthers do not differ in size in the two forms. The pollen-grains from the short-styled

flowers before they were soaked in water were decidedly broader, in proportion to their length, than those from the long-styled ; after being soaked they were relatively to those from the long-styled as 100 to 71 in diameter, and more transparent. A large number of flowers from the two forms were compared, and 12 of the finest flowers from each lot were measured, but there was no sensible difference between them in size. Nine long-styled and eight short-styled plants growing together in a state of nature were marked, and their capsules collected after they had been naturally fertilised ; and the seeds from the short-styled weighed exactly twice as much as those from an equal number of long-styled plants. So that the primrose resembles the cowslip in the short-styled plants, being the more productive of the two forms. The results of my trials on the fertility of the two forms, when legitimately and illegitimately fertilised ; are given in Table 9.

We may infer from this table that the fertility of the two legitimate unions taken together is to that of the two illegitimate unions together, as judged by the proportional number of flowers which when fertilised in the two methods yielded capsules, as 100 to 60. If we judge by the average number of seeds per capsule produced by the two kinds of unions, the ratio is as 100 to 54 ; but this latter figure is perhaps rather too low. It is surprising how rarely insects can be seen during the day visiting the flowers, but I have occasionally observed small kinds of bees at work ; I suppose, therefore, that they are commonly fertilised by nocturnal Lepidoptera. The long-styled plants when protected from insects yield a considerable number of capsules, and they thus differ remarkably from the same form of the cowslip, which is quite sterile under the same circumstances. Twenty-three spontaneously self-fertilised capsules from

TABLE 9.
Primula vulgaris.

Nature of Union.	Number of Flowers fertilised.	Number of good Capsules produced.	Maximum Number of Seeds in any one Capsule.	Minimum Number of Seeds in any one Capsule.	Average Number of Seeds per Capsule.
Long-styled form, by pollen from short-styled. Legitimate union . . }	12	11	77	47	66·9
Long-styled form, by own-form pollen. Illegitimate union . . }	21	14	66	30	52·2
Short-styled form, by pollen from long-styled. Legitimate union . . }	8	7	75	48	65·0
Short-styled form, by own-form pollen. Illegitimate union . . }	18	7	43	5	18·8*
The two legitimate unions together . . }	20	18	77	47	66·0
The two illegitimate unions together . . }	39	21	66	5	35·5*

* This average is perhaps rather too low.

this form contained, on an average, 19·2 seeds. The short-styled plants produced fewer spontaneously self-fertilised capsules, and fourteen of them contained only 6·2 seeds per capsule. The self-fertilisation of both forms was probably aided by Thrips, which abounded within the flowers; but these minute insects could not have placed nearly sufficient pollen on the stigmas, as the spontaneously self-fertilised capsules contained much fewer seeds, on an average, than those (as may be seen in Table 9) which were artificially fertilised with their own-form pollen. But this difference may perhaps be attributed in part to the flowers in the table having been fertilised with pollen from a distinct plant be-

longing to the same form; whilst those which were spontaneously self-fertilised no doubt generally received their own pollen. In a future part of this volume some observations will be given on the fertility of a red-coloured variety of the primrose.

PRIMULA SINENSIS.

In the long-styled form the pistil is about twice as long as that of the short-styled, and the stamens differ in a corresponding, but reversed, manner. The stigma is considerably more elongated and rougher than that of the short-styled, which is smooth and almost spherical, being somewhat depressed on the summit; but the stigma varies much in all its characters, the result, probably, of cultivation. The pollen-grains of the short-styled form, according to Hildebrand,* are 7 divisions of the micrometer in length and 5 in breadth; whereas those of the long-styled are only 4 in length and 3 in breadth. The grains, therefore, of the short-styled are to those of the long-styled in length as 100 to 57. Hildebrand also remarked, as I had done in the case of *P. veris*, that the smaller grains from the long-styled are much more transparent than the larger ones from the short-styled form. We shall hereafter see that this cultivated plant varies much in its dimorphic condition and is often equal-styled. Some individuals may be said to be sub-heterostyled; thus in two white-flowered plants the pistil projected above the stamens, but in one of them

* After the appearance of my paper this author published some excellent observations on the present species ('Bot. Zeitung,' Jan. 1, 1864), and he shows

that I erred greatly about the size of the pollen-grains in the two forms. I suppose that by mistake I measured twice over pollen-grains from the same form.

it was longer and had a more elongated and rougher stigma, than in the other; and the pollen-grains from the latter were to those from the plant with a more elongated pistil only as 100 to 88 in diameter, instead of as 100 to 57. The corolla of the long-styled and short-styled form differs in shape, in the same manner as in *P. veris*. The long-styled plants tend to flower before the short-styled. When both forms were legitimately fertilised, the capsules from the short-styled plants contained, on an average, more seeds than those from the long-styled, in the ratio of 12·2 to 9·3 by weight, that is, as 100 to 78. In the following table we have the results of two sets of experiments tried at different periods.

TABLE 10.
Primula Sinensis.

Nature of Union.	Number of Flowers fertilised.	Number of good Capsules produced.	Average Weight of Seeds per Capsule.	Average Number of Seeds per Capsule, as ascertained on a subsequent occasion.
Long-styled form, by pollen of short-styled. Legitimate union }	24	16	0·58	50
Long-styled form, by own-form pollen. Illegitimate union }	20	13	0·45	35
Short-styled form, by pollen of long-styled. Legitimate union }	8	8	0·76	64
Short-styled form, by own-form pollen. Illegitimate union }	7	4	0·23	25
The two legitimate unions together }	32	24	0·64	57
The two illegitimate unions together }	27	17	0·40	30

The fertility, therefore, of the two legitimate unions together to that of the two illegitimate unions, as judged by the proportional number of flowers which yielded capsules, is as 100 to 84. Judging by the average weight of seeds per capsule produced by the two kinds of unions, the ratio is as 100 to 63. On another occasion a large number of flowers of both forms were fertilised in the same manner, but no account of their number was kept. The seeds, however, were carefully counted, and the averages are shown in the right-hand column. The ratio for the number of seeds produced by the two legitimate compared with the two illegitimate unions is here 100 to 53, which is probably more accurate than the foregoing one of 100 to 63.

Hildebrand in the paper above referred to gives the results of his experiments on the present species; and these are shown in a condensed form in the following table (11). Besides using for the illegitimate unions pollen from a distinct plant of the same form, as was always done by me, he tried, in addition, the effects of the plant's own pollen. He counted the seeds.

It is remarkable that here all the flowers which were fertilised legitimately, as well as those fertilised illegitimately with pollen from a distinct plant belonging to the same form, yielded capsules; and from this fact it might be inferred that the two forms were reciprocally much more fertile in his case than in mine. But his illegitimately fertilised capsules from both forms contained fewer seeds relatively to the legitimately fertilised capsules than in my experiments; for the ratio in his case is as 42 to 100, instead of, as in mine, as 53 to 100. Fertility is a very variable element with most plants, being determined by the conditions to which they are subjected, of which fact I have observed striking instances with the

TABLE 11.

Primula Sinensis (from Hildebrand).

Nature of Union.	Number of Flowers fertilised.	Number of good Capsules produced.	Average Number of Seeds per Capsule.
Long-styled form, by pollen of short-styled. Legitimate union }	14	14	41
Long-styled form, by own-form pollen, from a distinct plant. Illegitimate union . }	26	26	18
Long-styled form, by pollen from same flower. Illegitimate union }	27	21	17
Short-styled form, by pollen of long-styled. Legitimate union }	14	14	44
Short-styled form, by own-form pollen, from a distinct plant. Illegitimate union }	16	16	20
Short-styled, by pollen from the same flower. Illegitimate union }	21	11	8
The two legitimate unions together . .	28	28	43
The two illegitimate unions together (own-form pollen) }	42	42	18
The two illegitimate unions together (pollen from the same flower) }	48	32	13

present species; and this may account for the difference between my results and those of Hildebrand. His plants were kept in a room, and perhaps were grown in too small pots or under some other unfavourable conditions, for his capsules in almost every case contained a smaller number of seeds than mine, as may be seen by comparing the right-hand columns in Tables 10 and 11.

The most interesting point in Hildebrand's experiments is the difference in the effects of illegitimate fertilisation with a flower's own pollen, and with that

from a distinct plant of the same form. In the latter case all the flowers produced capsules, whilst only 67 out of 100 of those fertilised with their own pollen produced capsules. The self-fertilised capsules also contained seeds, as compared with capsules from flowers fertilised with pollen from a distinct plant of the same form, in the ratio of 72 to 100.

In order to ascertain how far the present species was spontaneously self-fertile, five long-styled plants were protected by me from insects; and they bore up to a given period 147 flowers which set 62 capsules; but many of these soon fell off, showing that they had not been properly fertilised. At the same time five short-styled plants were similarly treated, and they bore 116 flowers which ultimately produced only seven capsules. On another occasion 13 protected long-styled plants yielded by weight 25·9 grains of spontaneously self-fertilised seeds. At the same time seven protected short-styled plants yielded only half-a-grain weight of seeds. Therefore the long-styled plants yielded nearly 24 times as many spontaneously self-fertilised seeds as did the same number of short-styled plants. The chief cause of this great difference appears to be, that when the corolla of a long-styled plant falls off, the anthers, from being situated near the bottom of the tube are necessarily dragged over the stigma and leave pollen on it, as I saw when I hastened the fall of nearly withered flowers; whereas in the short-styled flowers, the stamens are seated at the mouth of the corolla, and in falling off do not brush over the lowly-seated stigmas. Hildebrand likewise protected some long-styled and short-styled plants, but neither ever yielded a single capsule. He thinks that the difference in our results may be accounted for by his plants having been kept in a room and never having been shaken;

but this explanation seems to me doubtful; his plants were in a less fertile condition than mine, as shown by the difference in the number of seeds produced, and it is highly probable that their lessened fertility would have interfered with especial force with their capacity for producing self-fertilised seeds.

PRIMULA AURICULA.*

This species is heterostyled, like the preceding ones; but amongst the varieties distributed by florists the long-styled form is rare, as it is not valued. There is a much greater relative inequality in the length of the pistil and stamens in the two forms of the auricula than in the cowslip; the pistil in the long-styled being nearly four times as long as that in the short-styled, in which it is barely longer than the ovarium. The stigma is nearly of the same shape in both forms, but is rougher in the long-styled, though the difference is not so great as between the two forms of the cowslip. In the long-styled plants the stamens are very short, rising but little above the ovarium. The pollen-grains of these short stamens, when distended with water, were barely $\frac{2}{100}$ of an inch in diameter, whereas those from the long stamens of the short-styled plants were barely $\frac{7}{100}$, showing a relative difference of about 71 to 100. The smaller grains of the long-styled plant are also much more transparent, and before distension with water more triangular in outline than those of the other form. Mr. Scott † compared ten plants of both forms growing under similar conditions, and found that, although the long-styled plant produced more umbels and more capsules than the short-styled, yet they yielded fewer seeds, in the ratio of 66 to 100. Three short-styled plants were protected by me from the

* According to Kerner our garden auriculas are descended from *P. pubescens*, Jacq., which is a hybrid between the true *P. auricula* and *hirsuta*. This hybrid has now been propagated for about 300 years, and produces, when legitimately fertilised, a large number of seeds; the long-styled forms yielding an average number of 73, and the

short-styled 98 seeds per capsule: see his "Geschichte der Aurikel," 'Zeitschr. des Deutschen und Oest. Alpen-Vereins,' Band vi. p. 52. Also 'Die Primulaceen-Bastarten,' 'Oest. Bot. Zeitschrift,' 1835, Nos. 3, 4, and 5.

† 'Journ. Linn. Soc. Bot.' vol. viii. 1864, p. 86.

access of insects, and they did not produce a single seed. Mr. Scott protected six plants of both forms, and found them excessively sterile. The pistil of the long-styled form stands so high above the anthers, that it is scarcely possible that pollen should reach the stigma without some aid; and one of Mr. Scott's long-styled plants which yielded a few seeds (only 18 in number) was infested by aphides, and he does not doubt that these had imperfectly fertilised it.

I tried a few experiments by reciprocally fertilising the two forms in the same manner as before, but my plants were unhealthy, so I will give, in a condensed form, the results of Mr. Scott's experiments. For fuller particulars with respect to this and the five following species, the paper lately referred to may be consulted. In each case the fertility of the two legitimate unions, taken together, is compared with that of the two illegitimate unions together, by the same two standards as before, namely, by the proportional number of flowers which produced good capsules, and by the average number of seeds per capsule. The fertility of the legitimate unions is always taken at 100.

By the first standard, the fertility of the two legitimate unions of the auricula is to that of the two illegitimate unions as 100 to 80; and by the second standard as 100 to 15.

PRIMULA SIKKIMENSIS.

According to Mr. Scott, the pistil of the long-styled form is fully four times as long as that of the short-styled, but their stigmas are nearly alike in shape and roughness. The stamens do not differ so much in relative length as the pistils. The pollen-grains differ in a marked manner in the two forms; "those of the long-styled plants are sharply triquetrous, smaller, and more transparent than those of the short-styled, which are of a bluntly triangular form." The fertility of the two legitimate unions to that of the two illegitimate unions is by the first standard as 100 to 95, and by the second standard as 100 to 31.

PRIMULA CORTUSOIDES.

The pistil of the long-styled form is about thrice as long as that of the short-styled, the stigma being double as long and covered with much longer papillæ. The pollen-grains of the short-

styled form are, as usual, "larger, less transparent, and more bluntly triangular than those from the long-styled plants." The fertility of the two legitimate unions to that of the two illegitimate unions is by the first standard as 100 to 74, and by the second standard as 100 to 66.

PRIMULA INVOLUCRATA.

The pistil of the long-styled form is about thrice as long as that of the short-styled; the stigma of the former is globular and closely beset with papillæ, whilst that of the short-styled is smooth and depressed on the apex. The pollen-grains of the two forms differ in size and transparency as before, but not in shape. The fertility of the two legitimate to that of the two illegitimate unions is by the first standard as 100 to 72; and by the second standard as 100 to 47.

PRIMULA FARINOSA.

According to Mr. Scott, the pistil of the long-styled form is only about twice as long as that of the short-styled. The stigmas of the two forms differ but little in shape. The pollen-grains differ in the usual manner in size, but not in form. The fertility of the two legitimate to that of the two illegitimate unions is by the first standard as 100 to 71, and by the second standard as 100 to 44.

Summary on the foregoing heterostyled species of Primula.—The fertility of the long and short-styled plants of the above species of *Primula*, when the two forms are fertilised legitimately, and illegitimately with pollen of the same form taken from a distinct plant, has now been given. The results are seen in the following table; the fertility being judged by two standards, namely, by that of the proportional number of flowers which yielded capsules, and by that of the average number of seeds per capsule. But for full accuracy many more observations, under varied conditions, would be requisite.

TABLE 12.

Summary on the Fertility of the two Legitimate Unions, compared with that of the two Illegitimate Unions, in the genus Primula. The former taken at 100.

Name of Species.	Illegitimate Unions.	
	Judged of by the Proportional Number of Flowers which produced Capsules.	Judged of by the Average Number (or Weight in some cases) of Seeds per Capsule.
<i>Primula veris</i>	69	65
<i>P. elatior</i>	27	75 { (Probably too high.)
<i>P. vulgaris</i>	60	54 { (Perhaps too low.)
<i>P. Sinensis</i>	84	63
„ (second trial)	?	53
„ (after Hildebrand)	100	42
<i>P. auricula</i> (Scott)	80	15
<i>P. Sikkimensis</i> (Scott)	95	31
<i>P. cortusoides</i> (Scott)	74	66
<i>P. involucrata</i> (Scott)	72	48
<i>P. farinosa</i> (Scott)	71	44
Average of the nine species	88.4	61.8

With plants of all kinds some flowers generally fail to produce capsules, from various accidental causes ; but this source of error has been eliminated, as far as possible, in all the previous cases, by the manner in which the calculations have been made. Supposing, for instance, that 20 flowers were fertilised legitimately and yielded 18 capsules, and that 30 flowers were fertilised illegitimately and yielded 15 capsules, we may assume that on an average an equal proportion of the flowers in both lots would fail to produce capsules from various accidental causes ; and the ratio of $\frac{18}{20}$ to $\frac{15}{30}$, or as 100 to 56 (in whole

numbers), would show the proportional number of capsules due to the two methods of fertilisation; and the number 56 would appear in the left-hand column of Table 12, and in my other tables. With respect to the average number of seeds per capsule hardly anything need be said: supposing that the legitimately fertilised capsules contained, on an average, 50 seeds, and the illegitimately fertilised capsules 25 seeds; then as 50 is to 25 so is 100 to 50; and the latter number would appear in the right-hand column.

It is impossible to look at the above table and doubt that the legitimate unions between the two forms of the above nine species of *Primula* are much more fertile than the illegitimate unions; although in the latter case pollen was always taken from a distinct plant of the same form. There is, however, no close correspondence in the two rows of figures, which give, according to the two standards, the difference of fertility between the legitimate and illegitimate unions. Thus all the flowers of *P. Sinensis* which were illegitimately fertilised by Hildebrand produced capsules; but these contained only 42 per cent. of the number of seeds yielded by the legitimately fertilised capsules. So again, 95 per cent. of the illegitimately fertilised flowers of *P. Sikkimensis* produced capsules; but these contained only 31 per cent. of the number of seeds in the legitimate capsules. On the other hand, with *P. elatior* only 27 per cent. of the illegitimately fertilised flowers yielded capsules; but these contained nearly 75 per cent. of the legitimate number of seeds. It appears that the setting of the flowers, that is, the production of capsules whether good or bad, is not so much influenced by legitimate and illegitimate fertilisation as is the number of seeds which the capsules

contain. For, as may be seen at the bottom of Table 12, 88·4 per cent. of the illegitimately fertilised flowers yielded capsules; but these contained only 61·8 per cent. of seeds, in comparison, in each case, with the legitimately fertilised flowers and capsules of the same species.

There is another point which deserves notice, namely, the relative degree of infertility in the several species of the long-styled and short-styled flowers, when both are illegitimately fertilised. The data may be found in the earlier tables, and in those given by Mr. Scott in the Paper already referred to. If we call the number of seeds per capsule produced by the illegitimately fertilised long-styled flowers 100, the seeds from the illegitimately fertilised short-styled flowers will be represented by the following numbers:—

Primula veris.	71		Primula auricula.	119
P. elatior . .	44	{(Probably too low.)	P. Sikkimensis . . .	57
P. vulgaris . .	36	{(Perhaps too low.)	P. cortusoides . . .	93
P. Sinensis . .	71		P. involucreta . . .	74
			P. farinosa	63

We thus see that, with the exception of *P. auricula*, the long-styled flowers of all nine species are more fertile than the short-styled flowers, when both forms are illegitimately fertilised. Whether *P. auricula* really differs from the other species in this respect I can form no opinion, as the result may have been accidental. The degree of self-fertility of a plant depends on two elements, namely, on the stigma receiving its own pollen and on its more or less efficient action when placed there. Now as the anthers of the short-styled flowers of several species of *Primula* stand directly above the stigma, their pollen is more likely to fall on it, or to be carried down to it by insects, than in the case of

the long-styled form. It appears probable, therefore, at first sight, that the lessened capacity of the short-styled flowers to be fertilised with their own pollen, is a special adaptation for counteracting their greater liability to receive their own pollen, and thus for checking self-fertilisation. But from facts with respect to other species hereafter to be given, this view can hardly be admitted. In accordance with the above liability, when some of the species of *Primula* were allowed to fertilise themselves spontaneously under a net, all insects being excluded, except such minute ones as Thrips, the short-styled flowers, notwithstanding their greater innate self-sterility, yielded more seed than did the long-styled. None of the species, however, when insects were excluded, made a near approach to full fertility. But the long-styled form of *P. Sinensis* gave, under these circumstances, a considerable number of seeds, as the corolla in falling off drags the anthers, which are seated low down in the tube, over the stigma, and thus leaves plenty of pollen on it.

Homostyled species of Primula.—It has now been shown that nine of the species in this genus exist under two forms, which differ not only in structure but in function. Besides these Mr. Scott enumerates 27 other species* which are heterostyled; and to these probably others will be hereafter added. Nevertheless, some species are homostyled; that is, they exist only under a single form; but much caution is necessary on this head, as several species when cultivated are apt to become equal-styled. Mr. Scott believes that *P. Scotica*, *verticillata*, a variety of *Sibirica*, *elata*, *mollis*, and

* H. Müller has given in 'Nature,' Dec. 10, 1874, p. 110, a drawing of one of these species,

viz. the Alpine *P. villosa*, and shows that it is fertilised exclusively by Lepidoptera.

longiflora,* are truly homostyled; and to these may be added, according to Axell, *P. stricta*. Mr. Scott experimented on *P. Scotica*, *mollis*, and *verticillata*, and found that their flowers yielded an abundance of seeds when fertilised with their own pollen. This shows that they are not heterostyled in function. *P. Scotica* is, however, only moderately fertile when insects are excluded, but this depends merely on the coherent pollen not readily falling on the stigma without their aid. Mr. Scott also found that the capsules of *P. verticillata* contained rather more seed when the flowers were fertilised with pollen from a distinct plant than when with their own pollen; and from this fact he infers that they are sub-heterostyled in function, though not in structure. But there is no evidence that two sets of individuals exist, which differ slightly in function and are adapted for reciprocal fertilisation; and this is the essence of heterostylism. The mere fact of a plant being more fertile with pollen from a distinct individual than with its own pollen, is common to very many species, as I have shown in my work 'On the Effects of Cross and Self-fertilisation.'

HOTTONIA PALUSTRIS.

This aquatic member of the Primulaceæ is conspicuously heterostyled, as the pistil of the long-styled form projects far out of the flower, the stamens being enclosed within the tube; whilst the stamens of the short-styled flower project far outwards, the pistil being enclosed. This difference between the two forms has attracted the attention of various botanists, and that

* Koch was aware that this species was homostyled: see "Treviranus über Dichogamie nach

Sprengel und Darwin," 'Bot. Zeitung,' Jan. 2, 1863, p. 4.

of Sprengel,* in 1793, who, with his usual sagacity, adds that he does not believe the existence of the two forms to be accidental, though he cannot explain their purpose. The pistil of the long-styled form is more than twice as long as that of the short-styled, with the stigma rather smaller, though rougher. H. Müllert† gives figures of the stigmatic papillæ of the two forms, and those of the long-styled are seen to be more than double the length, and much thicker than the papillæ of the short-styled form. The anthers in the one form do not stand exactly on a level with the stigma in the other form; for the distance between the organs is greater in the short-styled than in the long-styled flowers in the proportion of 100 to 71. In dried specimens soaked in water the anthers of the short-styled form are larger than those of the long-styled, in the ratio of 100 to 83. The pollen-grains, also, from the short-styled flowers are conspicuously larger than those from the long-styled; the ratio between the diameters of the moistened grains being as 100 to 64, according to my measurements, but according to the measurements of H. Müller as 100 to 61; and his are probably the more accurate of the two. The contents of the larger pollen-grains appear more coarsely granular and of a browner tint, than those in the smaller grains. The two forms of *Hottonia* thus agree closely in most respects with those of the heterostyled species of *Primula*. The flowers of *Hottonia* are cross-fertilised, according to Müller, chiefly by Diptera.

Mr. Scott‡ made a few trials on a short-styled plant, and found that the legitimate unions were in all ways more fertile than the illegitimate; but since the pub-

* 'Das entdeckte Geheimniss der Nature,' p. 103.

† 'Die Befruchtung,' &c., p. 350.

‡ 'Journ. Linn. Soc. Bot.' vol. viii. 1864, p. 79.

lication of his paper H. Müller has made much fuller experiments, and I give his results in the following table, drawn up in accordance with my usual plan:—

TABLE 13.

Hottonia palustris (from H. Müller).

Nature of Union.	Number of Capsules examined.	Average Number of Seeds per Capsule.
Long-styled form, by pollen of short-styled. Legitimate union }	34	91·4
Long-styled form, by own-form pollen, from a distinct plant. Illegitimate union . . . }	18	77·5
Short-styled form, by pollen of long-styled. Legitimate union }	30	66·2
Short-styled form, by own-form pollen, from a distinct plant. Illegitimate union . . . }	19	18·7
The two legitimate unions together . . .	64	78·8
The two illegitimate unions together . . .	37	48·1

The most remarkable point in this table is the small average number of seeds from the short-styled flowers when illegitimately fertilised, and the unusually large average number of seeds yielded by the illegitimately fertilised long-styled flowers, relatively in both cases to the product of the legitimately fertilised flowers.* The two legitimate unions compared with

* H. Müller says ('Die Befruchtung,' &c., p. 352) that the long-styled flowers, when illegitimately fertilised, yield as many seeds as when legitimately fertilised; but by adding up the number of seeds from all the capsules produced by the two methods of fertilisation, as given by him,

I arrive at the results shown in Table 13. The average number in the long-styled capsules, when legitimately fertilised, is 91·4, and when illegitimately fertilised, 77·5; or as 100 to 85. H. Müller agrees with me that this is the proper manner of viewing the case.

the two illegitimate together yield seeds in the ratio of 100 to 61.

H. Müller also tried the effects of illegitimately fertilising the long-styled and short-styled flowers with their own pollen, instead of with that from another plant of the same form; and the results are very striking. For the capsules from the long-styled flowers thus treated contained, on an average, only 15·7 seeds instead of 77·5; and those from the short-styled 6·5, instead of 18·7 seeds per capsule. The number 6·5 agrees closely with Mr. Scott's result from the same form similarly fertilised.

From some observations by Dr. Torrey, *Hottonia inflata*, an inhabitant of the United States, does not appear to be heterostyled, but is remarkable from producing cleistogamic flowers, as will be seen in the last chapter of this volume.

Besides the genera *Primula* and *Hottonia*, *Androsace* (vel *Gregoria*, vel *Aretia*) *vitalliana* is heterostyled. Mr. Scott* fertilised with their own pollen 21 flowers on three short-styled plants in the Edinburgh Botanic Gardens, and not one yielded a single seed; but eight of them which were fertilised with pollen from one of the other plants of the same form, set two empty capsules. He was able to examine only dried specimens of the long-styled forms. But the evidence seems sufficient to leave hardly a doubt that *Androsace* is heterostyled. Fritz Müller sent me from South Brazil dried flowers of a *Statice* which he believed to be heterostyled. In the one form the pistil was considerably longer and the stamens slightly shorter than the corresponding organs in the other form. But as in the shorter-styled form the stigmas reached up to the anthers

* See also Treviranus in 'Bot. Zeitung,' 1863, p. 6, on this plant being dimorphic.

of the same flower, and as I could not detect in the dried specimens of the two forms any difference in their stigmas, or in the size of their pollen-grains, I dare not rank this plant as heterostyled. From statements made by Vaucher I was led to think that *Soldanella alpina* was heterostyled, but it is impossible that Kerner, who has closely studied this plant, could have overlooked the fact. So again from other statements it appeared probable that *Pyrola* might be heterostyled, but H. Müller examined for me two species in North Germany, and found this not to be the case.

Letter 3468 Darwin to J. D. Hooker

7 Mar [1862]

Down Bromley Kent
March 7th

My dear Hooker.

I have thought you would like to see enclosed from Gray: without having seen mine, you will not perceive what nice little sneers it contains; & there is a slap at you.^{f2} I heartily wish I cd. sympathise more with so excellent a man. Some time, return the note to me.—

I will soon prepare & modify some extracts for Linn. Soc about the three Orchid forms; why I wrote again was because I did not think that you understood they would be chiefly mere extracts from my book.^{f3}

You will be disappointed in my little book: I have got to hate it, though the subject has fairly delighted me: I am an ass & always fancy at the time that others will care for what I care about: I am convinced its publication will be bad job for Murray. Well it won't be a big concern.—^{f4}

Your last note will be very useful when I come to reconsider your Arctic paper^{f5} (by the way I will never believe that naturalists are so dull, as not sooner or later to appreciate this paper); your notion of a preglacial centre of dispersal far north, seems good. I have often speculated that during eocene period, there could hardly have been any strictly Arctic Flora & Fauna; & consequently their curious poverty, from want of time for great modification in strictly Arctic genera.— Greenland is indeed very curious; I do not feel quite so sure as you (considering direction of currents of sea, & greater proximity of land far north) that chance migration would have brought to there *temperate* forms. I am more willing, considering Geolog. nature of Spitzbergen & Bear Isd. to admit a recent continental extension there than almost anywhere else.—^{f6}

“Link Die Urwelt & das Alterthum &c 1821. p. 102”,—on Alpine plants & change of climate.—^{f7}

I have had a most obliging letter from Mr. Crocker;^{f8} who offers & wishes to experiment, so I have given him some things to do;^{f9} it will be grand if he will work.— I am at work on Dimorphism; in *Primula* & am finding out some very odd & perplexing facts; including a third form in the Chinese Primrose;^{f10} & I am nearly sure that daylight is coming with respect to the *melastomas*.— Can you tell me whether anything is better than Spirits & Water to preserve flowers in, as I have to preserve all, as I cannot draw.—

Have you read Buckle's 2d. Vol: it has interested me greatly; I do not care whether his views are right or wrong; but I shd. Think they contained much truth.^{f11} There is a noble love of advancement & truth throughout; & to my taste he is the very best writer of the English Language that ever lived, let the other be who he may.—

Yours affect | C. Darwin

Footnotes

^{f1} The year is provided by the reference to CD's paper on the Linnean Society's trimorphic orchid specimen (see n. 3, below).

Freshman Seminar 24p: Getting to Know Darwin
Fall 2012 Harvard College/Professor William (Ned) Friedman

f2 See the letter from Asa Gray, 18 February 1862, which is a reply to the letter to Asa Gray, 22 January [1862].

f3 CD's letter has not been found, but see the letter from J. D. Hooker, 3 March 1862. CD's paper, 'Three sexual forms of *Catasetum tridentatum*', was read before the Linnean Society of London on 3 April 1862.

f4 CD's publisher, John Murray, issued 1500 copies of the first edition of *Orchids* on 15 May 1862. Although favourably reviewed, the book sold slowly. See letter to John Murray, 9 April [1862], and Freeman 1977, p. 112.

f5 J. D. Hooker 1861a. See letter from J. D. Hooker, 3 March 1862.

f6 See letter to J. D. Hooker, 25 February [1862], and letters from J. D. Hooker, 27 February 1862 and 3 March 1862.

f7 Link 1821. See letter from J. D. Hooker, 27 February 1862 and n. 5.

f8 See letter from C. W. Crocker, 17 February 1862.

f9 CD's letter has not been found. The letters from C. W. Crocker, [before 13 March 1862] and 13 March 1862 give an indication of the experiments Crocker agreed to carry out for CD.

f10 CD had carried out crossing experiments with the Chinese primrose, *Primula sinensis*, in 1861 ('Dimorphic condition in *Primula*', pp. 87–8; see also *Collected papers* 2: 54–6), and had subsequently raised plants from the resulting seeds. With this second generation of plants CD carried out a second series of crosses in late January and February 1862, some of the results of which were later given in 'Illegitimate offspring of dimorphic and trimorphic plants', pp. 410–18 (see also the experimental notes in DAR 108: 15–18, 26–8, 34–9). The experiments were designed to investigate further the connection between dimorphism and sterility (see 'Illegitimate offspring of dimorphic and trimorphic plants', pp. 431–7, letter to T. H. Huxley, 14 [January 1862] and n. 9, and *Correspondence* vol. 10, Appendix VI). See also letter to Alphonse de Candolle, 17 June [1862] and n. 2, letter to J. D. Hooker, 23 June [1862] and n. 4, and letter to John Scott, 11 December [1862]. In 'Illegitimate offspring of dimorphic and trimorphic plants', p. 414, CD reported that his attention was first drawn to the equal-styled variety of *Primula sinensis* in 1862 by observing some anomalous flowers in a long-styled plant derived from a self-fertilised long-styled parent. As a result, he reported (p. 415), he had examined the plants 'in several small collections', and had discovered that 'the equal-styled variety is not rare'. CD's notes from these observations and experiments, dated 27 February — 30 March, 24 April 1862, and 30 May 1862, are in DAR 108: 38 v., 56–66.

f11 CD had read and greatly admired the first volume of Henry Thomas Buckle's *History of civilization in England* (Buckle 1857–61) in 1858 (see *Correspondence* vol. 7, letter to J. D. Hooker, 23 February [1858]). In the second volume, published in 1861, Buckle used the examples of Spain and Scotland to defend his four leading propositions concerning the history of civilisation: first, that human progress depends on the prosecution and diffusion of science; second, that scientific investigation requires a prior 'spirit of scepticism', itself subsequently fostered by science; third, that the discoveries thus made increase the influence of intellectual as compared with moral truths; and, finally, that the 'great enemy' of such progress, and thus of civilisation, is 'the protective spirit' found in the constant interference of church and state in human affairs (Buckle 1857–61, 2: 1).

Letter 3515 Daniel Oliver to Darwin

23 Apr 1862

Kew.

Wednesday | 23. Apr. 1862

Dear Sir

Here are the flowers of *Oxalis* as requested. I do not perceive anything distinctly dimorphic.—^{f1}

My examining of the plant had reference chiefly to the aestival small flowers: they are very remarkable.— I altered a little the “definition” of the two groups of dimorphism in the paper which you so kindly looked over (& tho’t worth printing!).—^{f2} Making one group with the Dimorphism manifest in, primarily, a separation more or less of the sexual organs, accompanied or not by alteration in the outer whorls.— (Thus including all wholly or partially diclinous plants,—*Catsetum*, *Primula*, &c) & the other group marked primarily by alteration primarily in envelopes of the flower without separation of the sexes.

Of course this is only the *morphologl.* definition

After discussing their function &c. we may class them in corresponding group by other characters.

Very sincerely yours | Danl. Oliver

Footnotes

^{f1} See letter to Daniel Oliver, 20 [April 1862] and n. 2. There are observational notes relating to these specimens, dated 24 April 1862, in DAR 109 (ser. 2): 5. CD subsequently concluded that *Oxalis acetosella* was not dimorphic (see *Forms of flowers*, pp. 181–3).

^{f2} [Oliver] 1862c. See letter to Daniel Oliver, 15 April [1862].

Letter 3757 J. D. Hooker to Darwin

[12 Oct 1862]

Kew
Sunday

Dr. Darwin

There is an article in Bull. Bot. Soc. France VIII. 519 by A. de Lassus on irritability of leaves of *Aldrovanda* a kinsman of *Drosera*.^{f2}

Thanks for your long letter on *Linum* &c &c.^{f3} I sent you last Thursday a box with two good species of *Impatiens* flowers, & can send a third if you care for it. I shall be most curious to know what you make of the Floral whorls & their vasc. bundles^{f4}

Cassia is another genus that has different anthers in same flower. I have also thought of some *Comelyneæ* but am not sure.^{f5} Oliver^{f6} has brought in a Tray of *Drosera rotundifolia*, but I doubt either of us having time to look at it.

My wife went to Cambridge & enjoyed it—I stayed at home! (& enjoyed it) working away at *Welwitschia* every day & almost every night—^{f7} I entirely agree with you by the way, that after long working at a subject, & after making something out of it, one invariably finds that it all seems dull flat stale and unprofitable—^{f8} this feeling however you will observe only comes (most mercifully) after you *really* have made out something worth knowing—I feel as if every body must know more of *Welwitschia* than I do, & yet I cannot but believe I have (ill or well) expounded & faithfully recorded a heap of the most curious facts regarding a simple plant that have been brought to light for many years.

The whole thing is however a dry record of singular structures, & sinks down to the level of the dullest descriptive account of dead matter, beside your jolly dancing facts anent orchid life & bee-life. I have looked at an Orchid or two since reading the Orchid book & feel that I never should have made out one of your points, even had I limitless leisure zeal & material—I am a dull dog, a very dull dog.—I may content myself with the per contra reflection that you could not (be dull enough to) write a “*Genera plantarum*”, which is just about what I am best fitted for.—^{f9} I feel I have a call that way, & you the other.

The dismal fact you quote of hybrid transitions between *Verb. Thapsus* & *nigra* (or whichever two it was) & its bearing on my practice of lumping species through intermediate specimens, is a very horrible one; & would open my eyes to my own blindness if nothing else could.^{f10} I have long been prepared for such a case, though I once wrote much against its probability—^{f11} I feel tolerably sure I must have encountered many such, but have not the tact to discern them, when under my nose: & I hence feel as if all my vast experience in the field has been thrown away. Your Orchid book has pretty well convinced me that such cases must be abundant,^{f12} & they only tend further to disturb our ideas of physiological versus structural species.^{f13} Perhaps my intermediates between *Habenaria chlorantha* & *bifolia* (of which I retain a lively recollection) were of this hybrid nature.^{f14} Certain it is that I had only to look for Hybrid orchids at the in Switzerland to find *two* different sorts. & numerous specimens of one of them.^{f15}

Huxley seems to have made short work of Owen at Cambridge.^{f16} the latter H. says “trailed his coat”—^{f17} Otherwise the meeting seems to me to have been dull enough, but cheery & friendly as far as sociability goes

Ever Yours affec | J D Hooker

I don't think it can be worth while returning the *Melastomas* but will enquire.^{f18}

Footnotes

^{f1} The date is established by the relationship to the letter to J. D. Hooker, 6 October [1862], and by reference to a note in DAR 205.8: 4, dated 14 October 1862, which records some of the observations made in this letter (see n. 5, below); the intervening Sunday fell on 12 October.

^{f2} Augé de Lassus 1861. In his letter of 26 September [1862], CD had asked Hooker for his opinion concerning irritability in the insectivorous plant *Drosera*.

^{f3} Letter to J. D. Hooker, 6 October [1862].

^{f4} In his letter to Hooker of [18 September 1862], CD asked Hooker to send him '2 or 3 single Balsams', so that he could trace the vascular bundles as part of his study of the homologies of floral parts; 'balsam' is a common name for plants of the genus *Impatiens*.

^{f5} In his letter to Hooker of 22 [August 1862], CD requested information about species in which there were differently coloured sets of anthers or pollen. Hooker apparently refers to the Commelinaceae. There is a note in DAR 205.8: 4, dated 14 October 1862, which records Hooker's identification of two sets of stamens in *Cassia*.

^{f6} Daniel Oliver was librarian and assistant in the herbarium at the Royal Botanic Gardens, Kew.

^{f7} Hooker was preparing a monograph on the Angolan plant *Welwitschia mirabilis* (J. D. Hooker 1863a). In his letter of 16 September 1862, Hooker informed CD that he intended to display the plant at the 1862 meeting of the British Association for the Advancement of Science, held in Cambridge from 1 to 8 October, and that his wife, Frances Harriet Hooker, planned to accompany him.

^{f8} See letter to J. D. Hooker, 6 October [1862]. Hooker alludes to William Shakespeare's *Hamlet*, 1.2.133–4: 'How weary, stale, flat, and unprofitable Seem to me all the uses of this world!'

^{f9} For CD's concern at the amount of time Hooker spent in preparing *Genera plantarum* (Bentham and Hooker 1862–83), see the letter to J. D. Hooker, 9 February [1862], and the letter to Asa Gray, 21 April [1862].

^{f10} See letter to J. D. Hooker, 6 October [1862]. In a section of J. D. Hooker 1853, which is headed 'Species vary in a state of nature more than is usually supposed' (pp. xii–xvii), Hooker stated: The result of my observations is, that differences of habit, colour, hairiness, and outline of leaves, and minute characters drawn from other organs than those of reproduction, are generally fallacious as specific marks, as being attributable to external causes, and easily obliterated under cultivation. It has hence been my plan to group the individuals of a genus which I assume after careful examination to contain many species whose limits I cannot define, that the species shall have the same relative value as those have of allied genera whose specific characters are evident... with all, the tendency would be to regard dubious species as varieties, to take enlarged views of the range and variation of species, and to weigh characters not only *per se*, but with reference to those which prevail in the Order to which the species under consideration belong. Hooker employed this principle in his systematic work, and was inclined to combine in one species individuals previously considered to represent distinct species (see, for example, *Correspondence* vol. 5, letter from Asa Gray, 22 May 1855 and n.6).

f11 In Hooker 1853, p. xv, Hooker stated: Hybridization has been supposed by many to be an important element in confusing and masking species. Nature, however, seems effectually to have guarded against its extensive operation and its effects in a natural state, and as a general rule the genera most easily hybridized in gardens, are not those in which the species present the greatest difficulties. With regard to the facility with which hybrids are produced, the prevalent ideas on the subject are extremely erroneous.

f12 See, for example, *Orchids*, pp. 72 and 88–9, where CD questioned the classification by some botanical authorities of *Ophrys apifera* and *O. arachnites*, and of *Habenaria bifolia* and *H. chlorantha*, as two varieties of one species, rather than as separate species.

f13 In his review of *Origin*, Thomas Henry Huxley distinguished between what he termed 'morphological' species, 'distinctly definable from all others, by certain constant ... morphological peculiarities', and 'physiological' species ([T. H. Huxley] 1860, p. 543). He stated that the best way to distinguish between two true physiological species and two varieties was to attempt hybridisation: true species would either be infertile *inter se* or would produce infertile offspring, whereas two varieties would give rise to fertile progeny ([T. H. Huxley] 1860, pp. 552–3). However, CD had come to the conclusion, in view of the hybridisation experiments carried out on *Verbascum* by Karl Friedrich von Gärtner, and of his own crossing experiments with *Primula sinensis*, that 'the lessened fertility of the first union of the offspring of two forms is no sure criterion of specific distinctness' ('Illegitimate offspring of dimorphic and trimorphic plants', p. 436). See also *Correspondence* vol. 10, Appendix VI, letter to T. H. Huxley, 14 [January 1862], and letter to Asa Gray, 9 August [1862] and n. 13.

f14 See n. 12, above. See also letter to J. D. Hooker, 19 [July 1860] and n. 4 (*Correspondence* vol. 8).

f15 See letter from J. D. Hooker, [24 July 1862].

f16 Hooker refers to Thomas Henry Huxley and Richard Owen, who had engaged in intense debate concerning the differences in brain anatomy between humans and anthropoid apes, at the 1862 meeting of the British Association, held in Cambridge from 1 to 8 October. For Huxley's account of the exchanges, see his letter to CD of 9 October 1862.

f17 The phrase is used to describe one who seeks an argument (*OED*).

f18 See letter to J. D. Hooker, 6 October [1862].

Letter 4053 Darwin to Asa Gray

20 Mar [1863]

Down Bromley Kent
March 20th

My dear Gray.

I have very little to say, but will amuse myself by scribbling a few lines to thank you for information in last note of Feb. 9th^{f2} & to thank you in my dear little man's name for two precious stamps.^{f3} He told me with joyful triumph that in American stamps he equalled all other collections put together in the school. He exchanged a duplicate Blood's stamp for a whole lot of treasures.^{f4} He says there is an envelope of same value as the stamps you put on your letter, which would be of value to him.—

I have one request to make for myself, viz seed of *Campanula perfoliata*: I have tried in vain at Kew & elsewhere for some.—^{f5}

I am very glad you like Bates' paper;^{f6} I expect his Amazonian Travels will be good.^{f7} If you read Lyell's book, tell me what you think of it;^{f8} I (& Hooker) have told him that we regret much that he did not speak more boldly out about Species.^{f9} He answers that his belief in change fluctuates.—^{f10} His Book has made me reread your essay; & I admire it as much as ever.^{f11} What a dead hand you are in parrying a lounge & transfixing your adversary! You ask about Sprengel's "Dichogamy":^{f12} he means by this a plant in which each flower first matures & *sheds* its pollen & then has its stigma mature; & much more rarely matures its stigma first & subsequently its pollen: so that these plants are in function monoecious. I am sure his observations are to large extent correct, & the case is very common.^{f13} In the *Primula*-like cases the plants are in function Dioecious.—^{f14}

A couple of days ago I had an interesting letter from Dr. Cruger of Bot. Gardens of Trinidad,^{f15} & he tells me odd facts of native species (& only native species) of *Cattleya* &c which *never* open their flowers, & yet set seed-capsules. Happy man he has actually seen crowds of Bees flying round *Catasetum* with the pollinia sticking to their backs! I wrote to him to ask him to observe what insects did in flowers of *Melastomaceæ*;^{f16} he says not proper season yet, but that on one species a small Bee seemed busy about the horn-like appendages to the anthers. It will be too good luck if my study of the flowers in the green-house has led me to right interpretation of these queer appendages.^{f17} By the way, I have just built a hot-house & got some orchids, & it amuses me much.—^{f18} Some plants of *Amsinckia spectabilis*, at least the seed was so named (small dark orange flowers, elongated hairy leaves) have just begun to flower, & I find in two plants that stigma stands on exact level with anthers; hence I fear they cannot be dimorphic.—^{f19}

Your Mitchellas look healthy: I hope they will not flower very soon;^{f20} for my health (& that of my youngest Boy) has been of late so bad, that we have resolved all to go about middle of April for 6 or 8 weeks to Malvern for Water-Cure for me & change for my Boy.—^{f21} It breaks my heart: I shall never get my present Book on Variation under Domestication finished; yet it interests me much & I am now in middle of long chapter on Inheritance Reversion &c, giving results of my own & other Breeders' Experiments.—^{f22}

Good Night.— | My dear Gray | Yours most truly | Ch. Darwin

Many thanks for Pamphlet Chapters on History of war & newspaper just arrived.^{f23}

Footnotes

f1 The year is established by the relationship between this letter and the letter from Asa Gray, 13 April 1863.

f2 Gray's letter has not been found; however, a portion of the letter is quoted in CD's letter to H. W. Bates, 4 March [1863] (see n. 6, below).

f3 CD refers to his twelve-year-old son, Leonard Darwin; at CD's request, Gray had been sending United States postage stamps for Leonard's collection since the summer of 1862 (see *Correspondence* vol. 10).

f4 The reference is to a stamp issued by the Philadelphia carriers, D. O. Blood & Co. (see Sutton 1966, p. 41). See also letter to Asa Gray, 2 January [1863].

f5 *Campanula perfoliata* (also called *Specularia perfoliata*) is native to the eastern United States (Bailey and Bailey 1976). CD had been interested in the plant since learning from Gray that it bore unopened flowers in which self-pollination occurred, a phenomenon later known as cleistogamy (see, for example, *Correspondence* vol. 9, letter from Asa Gray, 11 October 1861, and *Correspondence* vol. 10, letters to Asa Gray, 10–20 June [1862] and 26[–7] November [1862], and letters from Asa Gray, 18–19 August 1862 and 29 December 1862).

f6 Gray evidently discussed Bates 1861 in a letter to CD written on 9 February 1863 that has not been found; CD quoted Gray's comments in a letter to Henry Walter Bates of 4 March [1863]. Bates sent a copy of his paper to Gray in January, after CD had persuaded Gray to attempt to have it reviewed in the *American Journal of Science and Arts*, of which he was one of the contributing editors (see letter to H. W. Bates, 12 January [1863], and letter from H. W. Bates, 17 January [1863]).

f7 Bates's account of his eleven years as a naturalist in the Amazon region of South America (Bates 1863) was published between 1 and 14 April 1863 (*Publishers' Circular* 26 (1863): 193).

f8 C. Lyell 1863a; see letter from Asa Gray, 20 April 1863.

f9 See letters to Charles Lyell, 6 March [1863] and 17 March [1863], and letter from J. D. Hooker, [15 March 1863].

f10 See letter from Charles Lyell, 11 March 1863. See also letter from Charles Lyell, 15 March 1863.

f11 A. Gray 1861a.

f12 See *Correspondence* vol. 10, letter from Asa Gray, 29 December 1862. The reference is to Sprengel 1793, in which the term 'dichogamie' was first used (Baillon *et al.* 1876–92).

f13 CD cited Sprengel 1793 extensively in *Orchids*, adding (p. 340 n.): I am aware that this author's curious work...has often been spoken lightly of. No doubt he was an enthusiast, and probably carried some of his ideas to an extreme length. I feel sure, from my own observations, that his work contains a large body of truth. Although little regarded by botanists, the work was notable for its statement of two related doctrines, namely, that flowers were generally adapted to be cross-pollinated, and that floral structures were often adapted for insect visitation (*DSB*). These doctrines related closely to CD's own belief that it was a 'law of nature...that no organic being self-fertilises itself for an eternity of generations; but that a cross with another individual is occasionally...indispensable' (*Origin*, p. 97).

f14 In his letter to Gray of 26[–7] November [1862] (*Correspondence* vol. 10), CD objected to Gray's use of the term 'Dioecio-dimorphism' to describe cases of flower dimorphism like those occurring in several species of *Primula*, on the grounds that he doubted the implied evolutionary transition between such dimorphism and dioeciousness. In his reply of 29 December 1862 (*Correspondence* vol. 10), Gray drew on CD's account of the functional similarity of dimorphic and dichogamous plants, suggesting that CD extend the meaning of the word 'dichogamy' to include such cases of dimorphism as that in *Primula*.

f15 Letter from Hermann Cruger, 23 February 1863.

f16 See letter to Hermann Cruger, 25 January [1863] and n. 2.

f17 See letter to Hermann Cruger, 25 January [1863] and n. 6.

f18 CD's new hothouse was completed by 15 February 1863 (see letter to J. D. Hooker, 15 February [1863] and n. 5); Joseph Dalton Hooker had sent CD orchids and other plants for cultivation from the Royal Botanic Gardens, Kew (see letter to J. D. Hooker, [21 February 1863]). See also Appendix VI.

f19 Gray had suggested that *Amsinckia spectabilis* might be dimorphic, a view CD endorsed, having seen dried specimens sent by Gray (see *Correspondence* vol. 9, letter from Asa Gray, 9 November 1861, and letter to J. D. Hooker, 18 [December 1861]). CD subsequently grew plants from seed in order to experiment on the species (see *Correspondence* vol. 10, letter to Asa Gray, 15 March [1862], and this volume, letter to Asa Gray, 2 January [1863]). He recorded his observations on these plants, and on one belonging to his neighbour, George Henry Turnbull, in notes dated 23 March and 1 April 1863 (DAR 110: B2), concluding that the plant was not dimorphic, but that the length of the stigma was very variable, and the first-formed flowers tended to have stamens somewhat arrested in development. See also *Forms of flowers*, pp. 110–11.

f20 Gray sent CD live specimens of the dimorphic plant *Mitchella repens* in December 1862, for use in crossing experiments (see *Correspondence* vol. 10, letter from Asa Gray, 9 December 1862, and this volume, letter to Asa Gray, 2 January [1863]). CD deferred his experiments until 1864, because the plants did not flower abundantly in 1863 (see letters to Asa Gray, 31 May [1863] and 26 June [1863], and *Forms of flowers*, p. 125).

f21 CD had been suffering ill health since the end of February (see, for example, letter to J. D. Hooker, 5 March [1863]). Horace Darwin had been ill for much of 1862 (see letter from G. V. Reed, 12 January 1863 and n. 2); on 17 March 1863, Emma Darwin recorded in her diary (DAR 242) that he was again unwell. CD refers to James Manby Gully's hydropathic establishment in Great Malvern, Worcestershire.

f22 According to his 'Journal' (see *Correspondence* vol. 11, Appendix II), CD wrote a draft of the section of *Variation* dealing with inheritance (*Variation* 2: 1–84) between 23 January and 1 April 1863, noting: 'took me 6½ weeks time lost by illness & London'. *Variation*, which CD began writing early in 1860, was not published until 1868.

f23 The pamphlet has not been identified. Gray periodically sent CD American newspapers, although CD told Hooker that he never read them (see *Correspondence* vol. 10, letter to J. D. Hooker, 29 [December 1862]).