Observations on the Functions and Structure of the Reproductive Organs in the *Primulaceæ*. By Mr. JOHN SCOTT, Royal Botanic Gardens, Edinburgh. Communicated by CHARLES DARWIN, Esq., F.R.S. & L.S.

[Read Feb. 4, 1864.]

IN the paper which I have the honour to submit to the Society, my principal object is to give an account of a few experiments, made chiefly in the course of the present year, on several of the "*dimorphic*" and "*non-dimorphic*" species of *Primula*, the remarkable sexual relations of which were entirely unknown until Mr. Darwin laid before this Society his interesting paper on the subject. I have also, with the view of more completely elucidating the subject of dimorphism in the Primulas, prefixed to these a brief account of the structure and indications of the resultant functions in a few other genera of the order, which may not be uninteresting, as apparently showing that those sexual relations manifested in the genus *Primula* are common to other genera of the order*.

1. The genus *Hottonia* presents dimorphic characteristics in at least its solitary British representative, the common Water-Violet, *H. palustris*. Of this plant I can say little from personal observations, but, through the kindness of Mr. Darwin, who obligingly sent me his manuscript account of it, I am enabled to add, from his observations, the following interesting account of its structural dimorphism:—"Various authors have remarked that the *Hottonia palustris* presents two forms. Fresh specimens sent to me from North Wales were grandly dimorphic. In the long-styled form the pistil is more than twice as long as in the other form, and projects far out of the flower; the stigma is smaller and rougher than that of the short-styled, and the anthers lie within the tube of the corolla. In the short-styled form the

* I will here take the opportunity to acknowledge my great obligations to Mr. M'Nab for the privilege I have, under him, enjoyed in carrying on the experiments which I am now about to detail, the majority of which were performed upon plants in the Royal Botanic Gardens here.

I am also in the present instance, as in many others, particularly indebted to Mr. Sterling, of Stockbridge, Edinburgh, for the facilities he has afforded me in the following out my experiments, by placing at my disposal his fine collection of plants.

anthers project far out of the flower, and correspond in height with the projecting stigma of the other form, as does the short pistil with the short stamens of the long-styled form. But the most remarkable difference is in the size of the pollen-grains: those from the short-styled flowers, when distended with water, are $\frac{14}{14000}$ of an inch in diameter; those from the long-styled (and therefore from the shorter stamens) are $\frac{9}{14000}$ in diameter. Spheres differing in the proportion of 14 to 9 in diameter presented under the microscope a most remarkable contrast. The contents of the larger pollen-grains seemed to be coarser-grained and of a browner colour."

To these structural observations of Mr. Darwin I may add a few experiments which I have lately had an opportunity of making upon a "short-styled" plant of this species, which, though worth little, afford more than a negative presumption that the above-described morphological peculiarities are also, as in the genus *Primula*, connected with remarkable functional relations. My experiments were limited to two racemes. In one I fertilized twelve flowers with own pollen; these yielded six capsules, *five* of which were good, and contained in all *thirty-seven* seeds. The other raceme I fertilized with pollen sent me of a long-styled form. The results from eight flowers thus fertilized were, *five good capsules*, and *one hundred and fifty-four seeds.* Thus, in the "*homomorphic unions*"—or union with own-form pollen—the average production of seeds per capsule is about *seven*, while in the "*heteromorphic union*"—or that resulting from the union of the two forms—we find the average of seeds per capsule increased to thirty and upwards.

Before passing from this genus, I may state that the *H. inflata* of North America does not present structurally dimorphic characteristics, however it may be as respects function. In specimens which I have examined, I found the style very short, and reaching the base of the anthers; the pollen-grains very similar as respects size, *i. e.* judging from dried specimens, to those of the "long-styled" form of *H. palustris.*

2. The genus *Primula* has, along with a great majority of truly "dimorphic" species, others in which I have observed the one form only; also a few with stamens and pistils of an equal length—"*non-dimorphic.*" In the following list I have enumerated all the species of *Primula* which I have had an opportunity of examining, and arranged them in accordance with my observations on the structure of their sexual organs. The first list

comprises the truly "dimorphic" species. They are as follows:—

No. 1. *Dimorphic Species.*

Primula Altaica, *Lehm.*
—— amœna, *Bieb.*
—— aretioides, *Lehm.*
—— Auricula, *Linn.*
—— capitata, *Hook.*
—— Carniolica, *Jacq.*
—— cortusoides, *Linn.*
—— denticulata, *Smith.*
—— elatior, *Jacq.*
—— farinosa, *Linn.*
—— Finmarchica, *Jacq.*
—— glaucescens, *Morett.*
—— glutinosa, *Linn.*
—— Helvetica, *Don.*
—— hirsuta, *Dec.*
—— integrifolia, *Linn.*
—— involucrata, *Walk.*
—— latifolia, *Lapeyr.*
Primula macrocalyx, *Bunge.*
—— marginata, *Curt.*
—— minima, *Linn.*
—— Pallinurii, *Petagn.*
—— Pedemontana, *Thom.*
—— petiolaris, *Wall.*
—— pubescens, *Jacq.*
—— purpurea?
—— Sibirica, *Jacq.*
—— Sikkimensis, *Hook.*
—— Sinensis, *Lindl.*
—— Stuartii, *Wall.*
—— stricta, *Horn.*
—— venusta, *Hook.*
—— veris, *Linn.*
—— villosa, *Jacq.*
—— viscosa, *All.*
—— vulgaris, *Smith.*

No. 2. *Short-styled Species.*

Primula floribunda, *Wall.*
—— Pallindhm?
—— pusilla, *Goldie.*
—— rosea, *Bot. Mag.*
Primula saxifragifolia, *Lehm.*
—— rupestris?
—— nivalis, *Pall.*

No. 3. *Long-styled Species.*

Primula intermedia, *Curt.*
—— Flœrkeana, *Schr.*
—— longifolia, *Curt.*
Primula Mistassinica, *Mich.*
—— Pallasii, *Lehm.*
—— pulverulenta?

No. 4. *Non-Dimorphic Species.*

Primula elata, *Hook.*
—— longiflora, *All.*
—— mollis, *Hook.*
Primula Scotica, *Hook.*
—— Sibirica, var. β, *Bot. Mag.*
—— verticillata, *Forsk.*

The first of the above lists comprises all the species of *Primula* in which I have observed the dimorphic characteristics in full; the two following are respectively enumerations of those species presenting, first, the *short-styled*, and second, the *long-styled* form only; but this may be due to my limited researches, and perhaps those who have an opportunity for more extensive researches will find them truly dimorphic likewise. Space will not permit, nor indeed is it requisite, that I should enter into details as to the relative structure of the sexual organs of these species, and this the more especially because a few of them will come under special treatment in the sequel. I will here, therefore, simply remark, that the individual characteristics of all the above species, with two exceptions, were so decided as to leave no doubt as to which form they should be referred. The species which presented the exceptions were the *P. pusilla* and *P. floribunda*, in both of which along with normal "short-styled" forms I have observed an individual with stamens and pistils of an equal length. I have only seen six specimens of *P. pusilla*, five of which had the anthers surrounding the mouth of the corolla-tube, the pistil about half the length of the latter. In the other specimen the anthers were similarly attached, but in this case the stigma reached their base. The case of *P. floribunda* is exactly similar, one specimen having the stamens and pistils of an equal length; the others were "short-styled"—the anthers reaching the mouth of the corolla-tube, the pistils about half the length of the latter.

These lists then show us that "*dimorphism*" is a very general characteristic of the sexual organs of the species of *Primula*; it is not, however, *universal*, as Mr. Darwin informs me Prof. Treviranus has stated (Bot. Zeit. 1863, p. 4) on the authority of Koch and Tausch. This will be seen by referring to the fourth of the above lists, where the names are given of those species presenting, from personal observations, no structural dimorphism, stamens and pistils being of an equal length. I had no intention of entering into special details as to the relative structure of the sexual organs in these species; since the above diametrically opposite assertion, however, has been made, I cannot thus summarily pass them over. I will therefore give a brief account of the relations of the anthers and stigmas in each.

First, *Primula elata.*—Of this species a single specimen only has come under my observation. In it the stamens are attached immediately below the mouth of the corolla-tube, anthers included; the stigmas in a number of the flowers reach the middle, in the others the base of the anthers.

Second, *Primula longiflora.*—In this species the anthers invariably surround the mouth of the corolla-tube, the stigmas either very slightly exserted, or more frequently of an equal length with the anthers.

Third.—*Primula mollis* differs from its immediate allies the *P. Sinensis* and *P. cortusoides* (truly dimorphic species) in presenting an equality in the length of the sexual organs. The anthers are attached to the tube of the corolla about one-third below its mouth, and closely surround the flattened disk-shaped stigma, which usually reaches their apices.

Fourth.—*Primula Scotica* affords us an indigenous illustration of the "non-dimorphic" structure. In native specimens I find the anthers usually surround the mouth of the corolla-tube, while in cultivated specimens I have in general found them attached about one-third below its mouth; in either case, however, the length of the style varies similarly, the stigmas in both being closely appressed by the anthers.

Fifth, *Primula Sibirica.*—Of this species two varieties are known, one with oblong entire leaves, the other with ovate crenated leaves. I have examined a number of native specimens of the former variety, all of which were truly dimorphic; of the latter I have seen cultivated specimens only, which, on the other hand, had stamens and pistils of an equal length. Whether native specimens of the latter are similarly characterized I know not; but it is not at all improbable that the "non-dimorphic" structure in the cultivated specimens is due to an abnormal development, as I have frequently observed flowers on distinct plants with the anthers assuming a petaloid form. Mr. Darwin in his paper above referred to (p. 81) mentions a case of non-dimorphism also in this species; he suggests, however, that it may possibly be due to an abnormal development of the anthers. Until further evidence is afforded of the structural condition of the *P. Sibirica*, var. β, from native specimens, I will therefore place it provisionally amongst the non-dimorphic species.

Sixth.—*Primula verticillata* is the last species which I have to notice as presenting the non-dimorphic structure. In wild and cultivated specimens I find exactly similar relations between the anthers and stigmas—the former attached to the upper third of the corolla-tube, and included, usually closely appressed to the stigma. I may state, however, that the length of the style is slightly variable (an occurrence which gives it a theoretical interest from its intimate affinity with the *P. floribunda* already noticed as a "*dimorphic*" species occasionally presenting individuals with a non-dimorphic structure); and though, as I have just stated, the stigma usually stands at an equal height with the anthers, it occasionally rises above them, or even becomes slightly exserted beyond the mouth of the corolla-tube.

These five species, then, with the variety of *Primula Sibirica* ?, are non-dimorphic so far as structure is concerned: in respect to their functional performances, I will here merely remark that, from my experience, two of the above species, viz. *P. mollis* and *Scotica*, seem to be perfectly self-fertile; in respect to a third, *P. verticillata*, this is very doubtfully the case, as the experiments which I will give in a subsequent part of my paper will show. In the genus *Primula*, then, as in that of *Linum* already illustrated by Mr. Darwin, we have species structurally and functionally hermaphrodite, as well as species which, though hermaphrodite as to structure, have undergone such differentiations in their male and female sexual elements as to render their mutual functional action so highly imperfect, that they have been aptly designated "*subdiœcious hermaphrodites.*" How the former of these, the "non-dimorphic," should have escaped the notice of such excellent observers as Koch and Tausch, I fail to understand; but I feel convinced that a careful re-examination of the species will certainly induce them to cancel the above statement, if indeed the evidence which I have already adduced and that which I have yet to lay before the Society is not sufficiently demonstrative.

3. *Gregoria* presents at least one structurally "dimorphic" species, *G. Vitaliana*: respecting the others I am in perfect ignorance, never having seen specimens. In the "stort-styled" form of *G. Vitaliana* the anthers reach the mouth of the corolla-tube, while the pistil is about half the length of the latter. In the "long-styled" plants the anthers are attached about one-third below the mouth of the corolla-tube, the pistil in this case being exserted beyond the latter and fully twice as long as in the "short-styled" form. The pollen-grains in both forms are very similar—of an ovoid or oblong shape: the stigmas likewise are nearly of the same shape in both forms, apparently rougher in the "long-styled"; but I cannot speak confidently as to this, having only had dried specimens of the latter form to judge from. In respect to the reciprocal functional relations of these forms, I have no knowledge; but I think the following experiments on the "short-styled" form fully justify us in predicating the existence of a functional dimorphism. Three plants on which I had an opportunity of experimenting produced in the course of the season twenty-one flowers, which I treated in the following manner: five were left to natural agencies; eight were fertilized with own pollen; the remainder (eight) were fertilized with pollen from one of the other plants. The results were the complete abortion of every capsule of the two former, while in the latter case two cap-

sules were produced, but these did not contain a single good seed. I may also state that, after inquiring of various cultivators of alpine plants, I cannot hear that this plant ever produces seed. In Primulas, Mr. Darwin has shown that the pollen of the "short-styled" form, relatively to its own stigma, is considerably more sterile than the "long-styled" by its own-form pollen: may we not, then, in the "short-styled" forms of *Gregoria Vitaliana* have analogous relations of the sexual elements? Anyhow, the above experiments render it highly probable that for the production of perfect fertility the conjunction of the two forms is absolutely necessary.

4. The genus *Cortusa* is remarkable, though not peculiarly so, in apparently presenting the structure of the "long-styled" form only. I have at least failed in discovering the other form after a careful examination of the fine suite of specimens contained in the Edinburgh University Herbarium, as well as those in a few private herbaria. I find it to be the case also with cultivated plants of the *C. Matthioli*, the only representative of the genus; and in the generic definition by Linnæus "*stylus filiformis, exsertus*" also occurs, so that it is highly probable that the one form only exists. I will now briefly describe the floral structure of the genus in so far as connected with the economy of fertilization. The corolla-tube is short, with the limb expanding upwards in a campanulate manner; the filaments short, scarcely half the length of the obcordately-acuminated, excurrent anthers; the style is nearly three times the length of the stamens, and projects beyond the corolla. A plant which I protected from insects, when in flower, did not produce a single seed: those, on the other hand, which I artificially fertilized were perfectly fertile. I may further state, from the experience of others, as well as my own, that the plants of this species cultivated in our gardens, and left to the casual agencies of nature, produce in general a very small quantity of seed,—a consequence, perhaps, of their being less attractive to insects under cultivation than in their native haunts; for, undoubtedly, perfect fertilization can only be effected by some such agencies.

5. I have already stated that the structural relations of the sexual organs in *Cortusa* are not peculiar to it. In the allied genera *Dodecatheon* and *Soldanella* very similar relations are exhibited between the anthers and stigmas, the latter projecting considerably, in the majority of the species, beyond the former,—an occurrence which, considering the systematic affinities of the three

genera, favours the opinion that *Cortusa* has the structure of the one form only. *Dodecatheon* and *Soldanella* are also perfectly fertile when artificially fertilized: neither, however, in general, produce much seed in our gardens when fertilization is left to the agencies of nature. *Dodecatheon* is particularly deceptive in this respect, and ofttimes dupes the inexperienced collector of its seeds in our gardens by producing a profusion of well-formed and apparently good capsules destitute of all but the merest rudiments of seeds. In passing, I may remark that these genera (*Cortusa, Dodecatheon,* and *Soldanella*) afford excellent illustrations of a fact particularly emphasized by Mr.Darwin (*vide* Linn. Journ. vol. vii. p. 77), viz., that the fertilization of plants is not indifferently dependent on the agencies of insects or the action of the wind, inasmuch as they show that in the absence of the insects which visit them in their native habitats, or their non-attractiveness to those which frequent their new habitats, the mere action of the wind effects little in the economy of their fertilization.

6. The other genera of the Primulaceæ which I have had an opportunity of examining have stamens and pistils of an equal length, though occasional specific exceptions are certainly found. The *Lysimachia nutans* (a species referred to the genus *Lubinia* by Link and Otto) I would more particularly refer to in illustration of this, and, indeed, as possibly presenting both forms. In the single specimen which I have examined, the pistil was included within the tube of the corolla; the stamens *exserted* fully one-third beyond the latter! This relative inequality in the length of stamens and pistils is remarkable in a twofold manner—first, on considering the very general if not universal equality of the length of these organs in the other species of the genus, and secondly, from the circumstance that in this instance the *stamens* are the projecting organs; whereas in all the other representatives of the order (which I have examined) exhibiting differences in the length of stamens and pistils, I have invariably found that the latter organ was the more projected—excepting of course the genus *Primula,* though I strongly suspect that here all the dimorphic species are reciprocally so.

I have now briefly noticed those genera of Primulaceæ in which dimorphism has been observed—*Hottonia, Primula,* and *Gregoria.* These, singularly enough, are arranged by authors in the foregoing sequence from recognized structural relations—are thus seen to have innate bonds of affinity as manifested by those remarkable functional relations of the male and female sexual elements,—coincidences certainly not without an interest from a theoretical point of view. I have also noticed a few other genera, which, though not reciprocally dimorphic in structure, nevertheless present such relative inequalities in the length of their stamens and pistils, that certain external agents are absolutely necessary to induce anything like perfect fertility. In this arrangement of the sexual organs, then, it is evident that a better chance is afforded for the crossing of individuals than is the case in that arrangement where an equality in the length of the latter organs is observed. Thus nature presents us, as it were, with one of her simplest plans for effecting what Mr. Darwin on a thoroughly philosophical basis regards as one of the great ends gained by that more complex and novel plan in which she so differentiates the sexual elements of individual hermaphrodites, that the conjunction of these from distinct individuals is rendered imperative for the accomplishment of perfect fertility. In respect to the other genera of the order which I have examined, I observed nothing in the structural relations of the sexual organs worthy of special notice; this, however, is exclusive of the following genera, of which I know nothing—*Lubinia, Apochoris, Pelletiera, Asterolinum, Euparea*, and *Micropyxis*.

I will now give in detail my observations and experiments on several "*dimorphic*" and "*non-dimorphic*" species of *Primula*. The former of these, as previously stated, has been specially treated by Mr. Darwin, who, as might be expected, has left little for subsequent elucidation. This, indeed, is so much the case, that I fear my observations will do little more than show that the dimorphism manifested by those species to which Mr. Darwin's observations were directed is common to many more. It is, therefore, with no pretensions to originality that I venture to lay the following observations before this Society. However, as the phenomena of reciprocal dimorphism is comparatively new to science, further elucidations of it will not, I trust, be deemed superfluous.

Primula Auricula.—The dimorphic structure of this species has been fully described by Mr. Darwin, and we might anticipate, from the results of the few experiments he has made on this species, a functional dimorphism similar to that he has so ably illustrated in *Primula vulgaris, veris*, and *Sinensis*. I therefore had no intention of giving in detail the results of my experiments on the unions of the two forms of this species. My attention, however, has been lately directed to a tacit implication of the absolute sterility of the long-styled form. As this view is certainly erroneous, I will give, for the satisfaction of those who have had no means of testing the point at issue, the results of my own experience. The following are the results from plants growing together in a bed and freely exposed to the visits of insects*.

	Number of plants.	Number of umbels produced.	Number of capsules produced.	Number of seeds produced.	Number of umbels.	Number of seeds.
Short-styled Auriculas	10	33	287	2734	50	4142
Long-styled Auriculas	10	41	323	1816	50	2215

Again, in the following table the results are given from plants carefully protected from insects; though in no way effecting their fertility, as I proved by artificial fertilization.

	Number of plants.	Number of umbels produced.	Number of flowers produced.	Number of seeds produced.
Short-styled Auriculas	6	26	263	104
Long-styled Auriculas	6	22	272	8

If we compare the seed-results in the former of the above tables, we see that the short-styled are the more fertile—exceeding the long-styled in about the proportion of two to one. Again, in the latter table we see that the short-styled forms are also the more productive, though, comparatively with the results from the exposed plants, extremely sterile, showing us clearly how much these plants are dependent for their fertilization on insects or other mechanical agencies. This is more especially the case in the long-styled plants whose stigma stands high above the stamens, so that pollen cannot possibly reach the stigma without mechanical aid. The seed-results of this form in my table were the product of a single umbel infested with aphides; and which I have no doubt were the fertilizing agents, as not a single seed was produced upon any of the others. In the case of the short-styled plants, on the other hand, a low degree of fertility may be pretty regularly effected: the stamens surrounding the mouth of the corolla-tube are more or less inclined inwards, so that the anthers

* This and the succeeding Tables are arranged after the manner of Mr. Darwin (*loc. cit.*). It will be observed, however, that instead of giving the weight of the seeds, as he has done, I have given their number. This alteration has been made at the suggestion of Mr. Darwin, who considers that greater exa ctitude is thereby attained.

lie over though high above the nearly sessile stigma, thus affording a great facility for the pollen falling upon it. Indeed, but for the coherent nature of the pollen-grains, which do not readily fall from the anthers, these short-styled Auriculas would very regularly yield an amount of seed equal to an ordinary homomorphic union.

I may here notice a fact with which I have only lately become acquainted, though I understand it has been long known to cultivators of the Auricula, viz. that if "alpine" Auriculas* are grown amongst other varieties, the seeds saved from the latter produce plants the majority of which present the characteristics of the "alpine" variety. So that the pollen of this variety apparently exercises a prepotent influence over that of the other varieties, as shown by its superior power of impressing likeness on the offspring. It would be interesting to know if the female element possesses a like prepotency in transmitting likeness when treated with the pollen of the others, or whether, as is more frequently the case in the crossing of species, this power runs more strongly in the one sex than in the other. Irrespective of this, however, we see—and the fact is highly interesting from its bearings on one of the alleged physiological differences between species and varieties—that varieties like species when crossed have occasionally an individual prepotency in transmitting likeness. To recur to our more immediate subject: in ignorance of the above knowledge respecting the dispersion of the pollen of "alpine" Auriculas, I was much surprised at the great fertility of a somewhat isolated long-styled "self"-Auricula†, the nearest to it being a short-styled "alpine" variety about four yards distant. The former of these plants produced a single umbel, every capsule of which was full of seed; and thus presented a marked contrast with the results I had previously got from long- and short-styled plants growing together in a bed. I have now no doubt, though I have not proved it by sowing the seed, that the increased fertility of the above plant was due to fertilization by pollen of the neighbouring "alpine" plant.

In the following table I have given the results of several artificial "homomorphic" and "heteromorphic unions" of yellow-

* A term applied by florists to those varieties of Auricula which have that portion of the flower immediately around the stamens of a yellow, and that exterior to this of different colours.

† The term "self" is applied by the florist to those varieties which have a circle of white surrounding the stamens, exterior to which is a broad single coloured border.

flowered varieties of *Primula Auricula* approaching closely the normal form of the species.

TABLE I.—*Primula Auricula.*

	Number of flowers fertilized.	Number of capsules produced.	Number of seeds produced.
Long-styled by own-form pollen (homomorphic union)	16	13	153
Long-styled by pollen of short-styled (heteromorphic union)	18	17	1245
Short-styled by own-form pollen (homomorphic union)	16	12	169
Short-styled by pollen of long-styled (heteromorphic union)	18	18	1764
SUMMARY.			
The two homomorphic unions	32	25	322
The two heteromorphic unions	36	35	3009

By reducing the figures of the two homomorphic and the two heteromorphic unions, we get the following proportions:—

	Number of flowers fertilized.	Good capsules produced.	Number of seeds produced.	Good capsules.	Seeds.
The two homomorphic unions	100	78	1004	100	1288
The two heteromorphic unions	100	97	8339	100	8597

This comparative tabulation of the different unions shows that the flowers of the two heteromorphic unions produce a greater number of good capsules and seeds than the flowers of the two homomorphic unions. The good capsules of the two heteromorphic unions yield more seed, in about the proportion of seven to one, than those from the two homomorphic unions! Again, if we refer to the different unions of the two forms given separately in the upper table, we see that the short-styled forms produce the most seed in both homomorphic and heteromorphic unions. Thus, taking the two homomorphic unions, we see that the average of seeds per capsule from the short-styled unions is fourteen, that from the long-styled unions scarcely twelve, or as seven to six. In the heteromorphic unions these proportions are increased, the short-styled forms averaging 98, the long-styled 73 seeds per capsule,—that is, nearly as eight to six. These results, though clearly showing that the short-styled unions in every case yield the greatest amount of seed, are nevertheless far from lending any support to the opinion which I have already alluded to, *i. e.* the absolute sterility of the long-styled unions. This view seems to be entertained by Professor Treviranus, who states (Bot. Zeit. 1863, p. 6) that he found a plant of the long-styled *Primula Auricula* growing near a short-styled form, yet not one of the numerous flowers of the former produced a seed-capsule. We now know the absolute necessity for insect-agency in the fertilization of the long-styled form; hence, as I think, the observation of Professor Treviranus simply permits the inference that no insects had visited the plant. As all my results, however, have been obtained from less or more modified varieties of the *Primula Auricula*, whereas the observation of Professor Treviranus may possibly refer to the normal form of the species, objections may thence be taken to my regarding the former as correctly indicating the possible results of the latter. In view of such an objection, I can only add, that I have never had an opportunity of performing a single experiment on either form of the normal *P. Auricula*; but I can aver, from the examination of native specimens in herbaria, that the long-styled form *does produce capsules containing good seeds.*

As bearing upon this point, however, I may state that I never succeeded in getting a single good seed from homomorphic unions of the long-styled form of *Primula denticulata**. I had also a few flowers sent of the short-styled form of this species, with which I fertilized a single umbel of the former; but in this case also, though a few capsules swelled, every seed was abortive. I do not, however, wish to be understood as positively inculcating the absolute sterility of this form; though, certainly, I can assign good reasons for so regarding cultivated plants under *homomorphic* treatment. Thus, in the Royal Botanic Gardens of Edinburgh there are at present a few dozens of plants of the *P. denticulata*, consisting exclusively of the long-styled form. Mr. M'Nab informs me that a varying number of these have been cultivated in the Gardens for upwards of eighteen years, yet, though affording annually a profusion of flowers, he has never known them to produce a single seed. This evidence is of course open to the objection that sterility in this case (as in that previously noticed) may

* This species presents the two forms; their long salver-shaped corollas exhibiting very marked differences from the positional changes in the attachment of the anthers. These are accompanied with other differences: the pistil in the long-styled form is fully four times as long as that of the short-styled; the stigma is also twice as long, and rougher; the pollen-grains smaller, but of a similar triangular shape in both forms.

be due to the absence of insects; but it is to be remembered that we have here, as already stated, experimental observations affording similar evidence. These, conjointly with the long-continued observations of Mr. M'Nab, fully justify our suspicions respecting the sterility of the long-styled form under cultivation. The phenomena of sterility, however, are truly so capricious, that but for the remarkable sexual relations of the dimorphic species of *Primula* (including, as some suppose, a possible tendency to the diœcious structure), such observations were entirely superfluous; and this the more especially, as I am now aware, from observations on native specimens in the Edinburgh University Herbarium, that the long-styled forms do produce seed. Those who believe that dimorphism is a step towards diœciousness, instead of attributing sterility in the present case to certain unnatural conditions, will naturally be inclined to suppose that by man's artificial treatment the development of the plan of nature has been accelerated, the phenomena of reciprocal dimorphism exhausted by the functional impotence of the female element of the hypothetical male, and the final step made to the complete separation of the sexes.

I have hitherto spoken of two forms only of the *Primula Auricula*, viz. the long- and short-styled; occasionally, however, in this as in other truly dimorphic species, a third form occurs with stamens and pistils of an equal length. This trifling structural difference of the latter is connected with very important functional differences, as we find it yields much more seed when self-fertilized than either homomorphic union. In the following table I will illustrate this by giving the results from a self-fertilized umbel of an equal-stamened and -styled form; besides these, I have also given the results from unions between the latter and the long- and short-styled forms.

TABLE II.—*Primula Auricula.*

	Flowers fertilized.	Number of capsules.	Number of seeds.
Equal-stamened and -styled form by own pollen	14	9	272
Short-styled union—pollen from the above	12	7	59
Long-styled union—pollen from the above	12	9	47

The sexual powers of this equal-stamened and -styled form have a twofold interest: first, when viewed comparatively with the pure homomorphic unions of the other forms; and secondly, when the mutual sexual relations existing between it and the latter are taken into consideration. For the sake of illustrating these important points we will enter into a few comparative details. First, then, if we compare the results given in Table II. from the equal-stamened and -styled form when self-fertilized, with the most fertile of the homomorphic unions given in Table I., we see that the former produces more seed than the latter, the proportions being fully as two to one. Secondly, the results in Table II., from the short-styled form by the application of pollen from the form with stamens and styles of an equal length, afford an average of eight seeds per capsule, which is six seeds per capsule below the average homomorphic union of this form. Again, from the union of the long-styled form with the equal-stamened and -styled form, the average is reduced to five seeds per capsule, which is seven below the average produce of this form's homomorphic union. The lowest average of seeds is thus seen to be produced by the union of the equal-stamened and -styled with the long-styled form. This result I had partly anticipated from observations on the pollen-grains of the equal-stamened and -styled form, as I found that they agreed very closely with those characteristic of the long-styled form, and decidedly less than those of the short-styled form. From these results and observations, then, we may justifiably conclude, as Mr. Darwin has done from observations on a similar form (*loc. cit.* p. 80), that the equality in the length of the stamens and pistils was due to an abnormal development of the stamens, as shown by the relatively small grains of pollen they produced. We are thus afforded a tolerably satisfactory explanation for the decreased fertility remarked upon above, between the unions of this form and the long- and short-styled forms, in comparison with the homomorphic unions of the latter. There is yet, however, a most interesting fact, for which I can offer no explanation, namely, the high relative fertility of the equal-stamened and -styled form when fertilized with own pollen. We have seen that this form differs structurally from the long-styled form only in the place of attachment of the anthers, agreeing with it in the more important characteristics of the size of pollen-grains and stigma: physiologically, however, there is a marked divergence—an important functional adaptation in the relation of its own pollen to its own stigma.

No one has hitherto tested the influence of *dimorphism* on *hybridism*; and now, having done with the individual and reciprocal relations of the sexual powers in the different forms of *Pri-*

mula Auricula, I will, by way of illustrating the above phenomena, give the results of several experiments on the hybridization of ***P. Auricula***. These are as follows :—

TABLE III.—Hybrid unions of *Primula Auricula*.

	Number of flowers fertilized.	Total number of capsules produced.	Number of good capsules.	Number of seeds produced.	Average number of seeds per capsule.
Primula Pallinurii, long-styled, by pollen of long-styled *P. Auricula**	6	4	4	265	66
P. Auricula, short-styled, by pollen of short-styled *P. viscosa*	8	4	2	165	82
P. Auricula, long-styled, by pollen of short-styled *P. hirsuta*	8	4	3	168	56
P. Auricula, short-styled, by pollen of short-styled *P. hirsuta*	8	3	2	84	42
P. Auricula, long-styled, by pollen of the non-dimorphic *P. verticillata*	10	7	4	59	15

For the clear appreciation of the degree of sterility of the union of distinct species with the ***P. Auricula***, relatively to the lessened fertility of the pure homomorphic unions as compared with the pure heteromorphic unions of the latter, I have made the following comparative tabulation (see Table IV. p. 94) of the results given in the Table of the hybrid unions, with those from the summary of the different unions of ***P. Auricula*** in Table I. :—

In the second column of the table, the calculated number of seeds is given of the hybrid unions of ***P. Auricula*** relatively to the hundred seeds produced by the pure heteromorphic unions of that species given in the first column. The fourth column contains a similar estimate of number of seeds by the homomorphic unions of ***P. Auricula*** relatively to the hundred by the hybrid unions given in the third column. If we compare the results, we see that the decreased fertility of the homomorphic unions rela-

* The scape of *Primula Pallinurii* met with an injury which prevented the perfect maturing of the seeds; nevertheless, from an examination of a number of them, I believe the above is a fair estimate of the good embryonated seeds. I may here state, as worthy a passing notice, that while the above long-styled plant of *P. Pallinurii* produced both a large percentage of good capsules and seeds when fertilized by pollen of *P. Auricula*, every capsule aborted of twenty-two flowers fertilized by own pollen, though the pollen-tubes freely penetrated the stigmatic tissue. We thus see—and the fact is most interesting—that while the female element of a long-styled *Primula* has become impotent to its own male element, it is yet susceptible of fertilization by the male element of a distinct species.

tively to the heteromorphic unions in *P. Auricula* exceeds more or less that of each of the four hybrid unions of that species. These are most formidable facts for those who look upon sterility as a special endowment to prevent the blending of organic forms. Utterly irreconcileable, indeed, with such an idea, they, on the other hand, plainly show "that sterility is not a specially-acquired or endowed quality, but is incidental on other acquired and little-known differences," as Mr. Darwin has very properly urged.

TABLE IV.—Pure and hybrid unions of *P. Auricula.*

	Number of seeds produced by the heteromorphic unions of *P. Auricula.*	Number of seeds produced by the hybrid unions of *P. Auricula.*	Number of seeds produced by the hybrid unions of *P. Auricula.*	Number of seeds produced by the homomorphic unions of *P. Auricula.*
The heteromorphic unions relatively to the homomorphic unions of *P. Auricula*	100	...	...	15
The short-styled homomorphic union of *P. Auricula* by pollen of *P. viscosa* relatively to the pure unions of the former	100	96	100	16
The long-styled heteromorphic union of *P. Auricula* by pollen of *P. hirsuta* relatively to the pure unions of the former	100	65	100	23
The short-styled homomorphic union of *P. Auricula* by pollen of *P. hirsuta* relatively to the pure unions of the former	100	49	100	31
The union of long-styled *P. Auricula* by pollen of the non-dimorphic *P. verticillata* relatively to the pure unions of the former	100	17	100	87

In Table III. I have given the results of all my ***successful*** experiments on the hybridization of *Primula Auricula*: it is necessary, however, for the more complete elucidation of the influence of dimorphism on hybridism, that I also subjoin a few instances of my unsuccessful trials, in so far as connected with the reciprocal unions of those already given. First, then, by referring to Table IV. we see that the short-styled homomorphic unions of *P. Auricula* by pollen of *P. viscosa* are highly fertile; nevertheless I have completely failed to fertilize reciprocally *P. viscosa* by pollen of *P. Auricula.* I also failed to effect an heteromorphic union between these species: my experiments, however, in this case were limited to the long-styled *P. Auricula* by pollen of short-styled *P. viscosa.* Again, secondly, the long-styled heteromorphic and short-styled homomorphic unions of *P. Auricula* by pollen of *P.*

hirsuta are given in the table; but I have failed by either form pollen to effect the converse unions, *i. e.* fertilize the short-styled *P. hirsuta* by either form pollen of the *P. Auricula.* In the case of the long-styled form of *P. hirsuta* I utterly failed to effect a single union, though I tried it homomorphically and heteromorphically by the two-form pollens of *P. Auricula*, and also conversely by applying the pollen of the long-styled *P. hirsuta* to the two forms of *P. Auricula**. These few details then will enable us to consider, in part, the amount of parallelism existing between certain of the phenomena of hybridism in normal hermaphrodite species, and the hybridism of dimorphic species. In the fertilization of hermaphrodite species, several cases occur in which the male element of the one, A, for example, fertilizes the female element of the other, B, while the male element of B will not fertilize the female element of A: so in the hybridism of dimorphic species, with the important appanage of an increased complication of the conjunctive powers, we find analogous cases. Thus, let A *l* and A *s* and B *l* and B *s* respectively represent the long- and short-styled forms of the *P. Auricula* and *P. hirsuta* given above, then while the male element of A *s* fertilizes the respective female elements of B *l* and B *s*, that of A *l* cannot fertilize either of the latter; again, there is a mutual impotence between the male elements of B *l* and B *s* and the female elements of A *l* and A *s*. We thus see that a close parallelism exists between those remarkable phenomena occasionally observed in the reciprocal crossing of species on the one hand, and those observed in the reciprocal crossing of the two sexual individuals of a dimorphic species with those of a distinct dimorphic species on the other. In the latter case, as compared with the former, there is of course a greater complexity in the functional relations—eight crosses being possible between dimorphic species,—and so it is

* It may be advisable to state the number of flowers fertilized in each of the subjoined experiments:—First series, *P. Auricula* and *P. viscosa*: I fertilized eight flowers of the short-styled *P. viscosa* by pollen of the short-styled *P. Auricula*, and ten flowers of the long-styled *P. Auricula* by pollen of the short-styled *P. viscosa*. Second series, *P. Auricula* and *P. hirsuta*: of sixteen flowers of the short-styled *P. hirsuta*, one-half were fertilized by pollen of the long-styled, and the other by that of the short-styled *P. Auricula*; again, of the long-styled *P. hirsuta*, five flowers were fertilized by pollen of the long-styled, and five by that of the short-styled *P. Auricula*; in the converse unions of these, ten long-styled and ten short-styled flowers of the *P. Auricula* were fertilized by pollen of the long-styled *P. hirsuta*. Thus, including the three successful unions of these species given in Table III., we find that the above phenomena are the results of eighty-eight flowers, in each case carefully fertilized.

with the results, which are certainly most astounding; inasmuch as each of the sexual forms of a species manifest in their respective powers for conjunctions with those of another species, physiological peculiarities which might well entitle them, by the criterion of fertility, to specific distinction.

There is another interesting point illustrated by the above experiments upon which I will venture a few remarks—subject to the reservation, however, of their being modified by more numerous experiments. It is now perfectly well known that the two forms of several species of Primulas have their sexual powers so correlated, that while very imperfect fertility results from the fertilization of either form by own-pollen (a homomorphic union), perfect fertility results from the application of the pollen of the one form to the stigma of the other (a heteromorphic union). In the present instance, then, we are naturally led to inquire whether these correlations of the sexual powers in the two forms of a species extend in parallel lines to the two forms of a distinct species when hybridized? or are they limited in their operation to the individual forms of the species? In other words, in the hybridizing of dimorphic species, is the heteromorphic definitely more fertile than the homomorphic union? or is the alternative innately variable? Let us again, for a moment, recur to the above details and Table of hybrid unions for a little enlightenment on these queries. First, we see the short-styled *homomorphic union* of *P. Auricula* by pollen of *P. viscosa, highly fertile*; while of the other three unions tried between these species (*two heteromorphic* and *one homomorphic*), not one flower produced a seed-capsule! Again, secondly, successful results are derived from the long-styled *heteromorphic* and the short-styled *homomorphic* unions of *P. Auricula* by pollen of *P. hirsuta*,—the *heteromorphic* yielding more seed than the *homomorphic* in the proportion of 4 to 3. The other possible unions of these forms (three *heteromorphic* and three *homomorphic*) were also tried; but they did not produce a *single seed-capsule*! What now do these several experiments teach us respecting the points at issue? Looking to the successful experiments alone, we might be inclined to suppose, from the result of *P. Auricula* and *P. hirsuta*, that in the hybrid unions, as well as in the cross-unions of the two forms of a species, the *heteromorphic* were the more fertile,—even with the *remarkable fertility* of the *short-styled homomorphic unions* of *P. Auricula* and *P. viscosa* staring us in the face. On the other hand, if we take a general view of the evidence, and carefully balance and reflect on the results, I think we are all but forced to conclude that the parallelism noticed above is accidental*, and that, even as the greatest capricity and uncertainty is manifested in the sexual conjunctions of the respective forms, so is there a like capricity and uncertainty in the degree of fertility thereby induced. In fine, as there is a general indefiniteness in the results of the reciprocal unions of normal hermaphrodite species, so I believe (as above indicated) we shall find similar irregularities in the results of the reciprocal unions of the two forms of dimorphic species.

Primula vulgaris and the var. *alba* present both forms; of the *P. vulgaris*, var. *rubra*, I have seen the long-styled form alone. I instituted a series of experiments on these forms, with the view of determining the results of their reciprocal unions. Certain of these are so remarkable, that I hesitate not a little in bringing them forward until I have had again an opportunity of repeating my experiments. From their bearings, however, on certain highly important points in theoretical natural science, I will (subject to the above reservation) venture to lay the results before the Society, and thus directing the attention of those interested in such phenomena to subjects well worthy a careful experimental examination, show also that my results, remarkable though they undoubtedly are, have a basis sufficiently extensive to justify me in regarding them as at least an approximation to the true functional relations of these plants.

In the following Table I have given the results of my experiments on several plants of the above varieties, growing in pots and subjected to exactly similar treatment:—

* The necessity for further experimentation on this point, however, is shown by the following cases mentioned by Mr. Darwin, 'Origin of Species,' 3rd edit. p. 293, on the authority of Gärtner: "namely, that yellow and white varieties of the same species of *Verbascum* when intercrossed produce less seed than do either coloured varieties when fertilized with pollen from their own coloured flowers." Again, "that when yellow and white varieties of one species are crossed with yellow and white varieties of a DISTINCT species, more seed is produced by the crosses between the similarly coloured flowers than between those which are differently coloured." We thus see that the functional relations of varieties of a species MAY extend to, and similarly correlate the varieties of DISTINCT species!

TABLE V.—*Primula vulgaris*, and vars. *alba* and *rubra*.

	Number of flowers fertilized.	Total number of capsules produced.	Total number of good capsules produced.	Number of seeds produced.	Average number of seeds per capsule.
Primula vulgaris, var. *alba*, short-styled unions:—					
Homomorphic unions	14	10	8	106	13
Heteromorphic unions	12	10	10	206	21
Primula vulgaris, var. *alba*, long-styled unions:—					
Homomorphic unions	10	8	5	56	11
Heteromorphic unions	10	9	8	155	19
Primula vulgaris, var. *alba*, by pollen of *P. vulgaris*, short-styled unions:—					
Homomorphic unions	10	8	6	27	4
Heteromorphic unions	10	7	7	103	14
Primula vulgaris, var. *alba*, by pollen of *P. vulgaris*, long-styled unions:—					
Homomorphic unions	8	6	5	24	5
Heteromorphic unions	8	6	6	112	17
Primula vulgaris, by pollen of *P. vulgaris*, var. *alba*, short-styled unions:—					
Homomorphic unions	10	8	7	35	5
Heteromorphic unions	10	7	7	116	17
Primula vulgaris, by pollen of *P. vulgaris*, var. *alba*, long-styled unions:—					
Homomorphic unions	10	8	6	28	5
Heteromorphic unions	10	9	8	150	19
Primula vulgaris, var. *rubra*, long-styled union:—					
Homomorphic union	14	11	11	159	14
Primula vulgaris, var. *rubra*, long-styled, by pollen of *P. vulgaris*:—					
Homomorphic union	12	0			
Heteromorphic union	12	0			
Primula vulgaris, var. *rubra*, long-styled, by pollen of *P. vulgaris*:—					
Homomorphic union	8	0			
Heteromorphic union	8	0			

It may perhaps be desirable that the Society should have a detailed account of my experiments on effecting unions between the *P. vulgaris*, var. *rubra*, and the others, viz. *P. vulgaris*, and var. *alba*. As in that above given, the remarkable results are alone stated—the absolute zero of fertility, apparently, attained between undoubted varieties of a species!* By way of a preliminary to the

* The pure descent of the red and white Primrose from the common yellow has been questioned, and a hybrid origin from the Cowslip and Primrose (*P. veris* and *P. vulgaris*) ascribed to them. To my mind, the latter view is negatived by the results given in the above table. It is there shown that both (red and white) forms are, relatively to the results of similar unions with the common

special account of experiments, it is necessary to state that the red Primrose rarely ever, in its own natural state, produces a single seed—a peculiarity possessed in common with the above-mentioned white variety. Both of these varieties, Mr. M'Nab informs me, have been cultivated in the Botanic Gardens of Edinburgh for a number of years; yet, previous to this season, he has not known them to produce a single seed. With the view of satisfying myself as to the absolute sterility of these plants, I instituted a series of experiments, the results of which show that this is only partly correct,—certain individuals being perfectly fertile, others absolutely sterile, pollen being carefully applied to both. This is shown by the following experiments:—First, I selected a few fine vigorous-growing plants of the red and white varieties, and continued for some time regularly fertilizing the flowers as they were successively developed. I feel certain that I thus fertilized upwards of two hundred flowers without getting a single seed! Secondly, I directed my experiments to those plants which, with a less vigorous habit, produced a greater profusion of blooms. These I found to be alone productive—at least when artificially fertilized—for they seem to be equally as sterile as the others when fertilization is left to natural agencies: perhaps they are less sought after by insects than the common yellow Primrose. Anyhow, I have failed to detect a single seed on those plants in the Botanic Gardens of Edinburgh, which had proved fertile by artificial treatment, on leaving them to the agencies of nature. Those plants of the red and white Primrose, stated in the above table to yield such remarkable results, were also proved *susceptible of artificial fertilization* with *own pollen, both before and after I had repeatedly failed in effecting good results from cross-unions between them*, and also between *them* and the *common Primrose: every capsule thus treated*, singularly enough, *proved abortive*! However these results then may be modified by future experimentation, the following important conclusion will remain unaffected, namely, that plants of the *P. vulgaris*, var. *rubra*, characterized, as we have already shown, by the most capricious and uncertain performance of their sexual functions, nevertheless *proved fertile when treated with own pollen*; AT THE SAME TIME that *similar ex-*

Primrose, perfectly fertile *inter se*; whereas by their unions with the latter we see in the one case a relatively decreased fertility, in the other absolute sterility resulting! How utterly inconsistent, then, are such results with the idea of hybridity! In consonance with a hybrid origin, an increased instead of a decreased fertility ought to have resulted from the latter unions.

perimentations upon them with the *pollen* of the *parental form* (*P. vulgaris*), and likewise *that* of the other *modified descendant* (*P. vulgaris*, var. *alba*) *resulted in the abortion of every seed*! Such then are the experimental data from which the remarkable results stated in the latter part of Table V. were derived. That they are not sufficiently numerous to demonstrate the *unconditional* existence of an absolute sterility between two modified descendants from a common parent, and also between the latter and one of the former, I have already admitted; nevertheless I think they clearly demonstrate the *conditional* existence of physiological divergences sufficient in extent to induce complete sterility. How, I ask, on any other grounds than by the admission of the conditional existence of such physiological divergences can we explain the phenomena in question,—namely, the existence of plants *perfectly fertile* when their flowers are *fertilized* by *own pollen*, and yet, at the same time, yielding naught but abortive results from those flowers fertilized by the pollen of the other variety and by that of their common parent?

I will now reduce, for the sake of comparison, the figures of the different unions given in Table V.; first of the long- and short-styled homomorphic unions, and second, of the long- and short-styled heteromorphic unions.

TABLE A.—*Primula vulgaris* and vars. *alba* and *rubra*.

	Number of flowers fertilized.	Number of good capsules.	Number of seeds.	Number of good capsules.	Number of seeds.
LONG-STYLED HOMOMORPHIC UNIONS.					
P. vulgaris, var. *rubra*, by own-form pollen...	100	78	1124	100	1445
P. vulgaris, var. *alba*, by own-form pollen ...	100	50	560	100	1120
P. vulgaris, var. *alba*, by pollen of *P. vulgaris*	100	62	297	100	480
P. vulgaris by pollen of *P. vulgaris*, var. *alba*	100	60	280	100	466
SHORT-STYLED HOMOMORPHIC UNIONS.					
P. vulgaris, var. *alba*, by own-form pollen ...	100	57	755	100	1325
P. vulgaris, var. *alba*, by pollen of *P. vulgaris*	100	60	270	100	450
P. vulgaris by pollen of *P. vulgaris*, var. *alba*.	100	70	350	100	500

TABLE B.—*Primula vulgaris* and var. *alba*.

LONG-STYLED HETEROMORPHIC UNIONS.					
P. vulgaris, var. *alba*, by own-form pollen ...	100	80	1550	100	1937
P. vulgaris, var. *alba*, by pollen of *P. vulgaris*	100	75	1400	100	1866
P. vulgaris by pollen of *P. vulgaris*, var. *alba*	100	80	1500	100	1875
SHORT-STYLED HETEROMORPHIC UNIONS.					
P. vulgaris, var. *alba*, by own-form pollen ...	100	83	1709	100	2060
P. vulgaris, var. *alba*, by pollen of *P. vulgaris*	100	70	1030	100	1471
P. vulgaris by pollen of *P. vulgaris*, var. *alba*	100	70	1160	100	1657

In the comparative tabulation of the long-styled homomorphic unions (Table A.), I have assumed, in the first column, that 100 flowers were fertilized, and in the two columns to the right of this, given the relatively increased proportions of capsules and seeds; again, the right-hand column gives the calculated results from an assumed 100 of good capsules. If we compare the results, we see, first, that the short-styled form of *P. vulgaris*, var. *alba*, yields more seed, in about the proportion of 13 to 11 seeds per capsule, than those of the long-styled form, while the long-styled *P. vulgaris*, var. *rubra*, again exceeds the former in about the proportion of 14 to 13 seeds per capsule. In the reciprocal homomorphic unions of *P. vulgaris* and the variety *alba* we see some little discordance in the results: thus, the most productive union is the short-styled homomorphic union of *P. vulgaris* by pollen of *P. vulgaris alba*, whereas the least productive of the four is the converse union of these forms. Again, in the long-styled homomorphic unions most is yielded from the unions of *P. vulgaris alba* by pollen of *P. vulgaris*; so that the *most fertile* of the *long-* and *short-styled crosses* are thus seen to *result from converse unions*, namely in the former case from *P. vulgaris alba* by pollen of *P. vulgaris*, in the latter from *P. vulgaris* by pollen of *P. vulgaris alba*!

In the comparative tabulation of the long-styled heteromorphic unions (Table B.) a similar arrangement is observed to that in Table A. The calculated results of these unions also show that the short-styled form of *P. vulgaris alba* when fertilized by own pollen is the more fertile, exceeding the similar long-styled union in the proportion of 20 to 19 seeds per capsule: compared with the short-styled *homomorphic* the proportions are as 20 to 13 seeds per capsule, or as 4 to 3 in favour of the long-styled *heteromorphic*. This relative accordance of the degrees of fertility resulting from similar homomorphic and heteromorphic unions when these are *treated* by *own pollen* does not extend itself to the *cross-unions* of the different forms, the relative degree of fertility of the similar homomorphic and heteromorphic *cross-unions* being very irregular. Thus, in Table B., the *long-styled heteromorphic cross* of *P. vulgaris* by pollen of *P. vulgaris alba* yields more seed than that of the *similar* short-styled heteromorphic cross, in nearly the proportion of 19 to 17 seeds per capsule. In the converse unions of these, the long-styled heteromorphic cross of *P. vulgaris alba* also exceeds the similar short-styled heteromorphic cross, in about the proportion of 19 to 15. Again, in Table A. we see the highest degree of fertility resulting from the converse union of that in Table B., namely the short-styled homomorphic cross of *P. vulgaris* by pollen of *P. vulgaris alba*. In the long-styled homomorphic as compared with the long-styled heteromorphic unions, the highest degree of fertility is also the result of the converse unions of *P. vulgaris* and *P. vulgaris alba*! This discordance in the results of the different crosses surprised me much, though perhaps, after all, I had no right to expect perfect accordance or definite results from the reciprocal unions of normal individuals of a species, which consequently had a long-acquired morphological *status*, and of those from incipient or unestablished forms.

There is another point in the above tables to which I wish particularly to draw attention, namely the decreased proportion of seeds resulting from the cross-unions of *P. vulgaris* and *P. vulgaris alba*, relatively to the pure unions of either form. Thus, if we look to the short-styled heteromorphic unions, we find the *P. vulgaris alba* yielding with its own pollen above 20 seeds per capsule, while with the pollen of *P. vulgaris* it scarcely yields 15 seeds per capsule—that is, nearly as 2 to 3! Again, in the corresponding table of the homomorphic unions we find these proportions increased,—namely, *P. vulgaris alba* by own pollen yielding about 11 seeds per capsule, and by pollen of the *P. vulgaris* about 5 seeds per capsule, thus giving the proportions of 2 to 1! Such results as these from plants presenting no other appreciable difference than that of colour well exposes the slippery foundation of that dogma of natural science which would have us believe that nature had specially endowed organic beings with sterility to prevent the blending of specific types. These illustrations of sterility, in conjunction with those remarkable revelations of dimorphism, in which the sexual organs of a hermaphrodite individual undergo such great differentiations with respect to their mutual action, might certainly suffice to show that sterility is not a special endowment, but a necessary result of secondary causes, which have no connexion whatever with special ends in the development of the classifying principle.

With my experiments in crossing *P. vulgaris* with *P. veris* I was most unfortunate; all my experimental plants met with an accident, and thus provokingly disappointed me of the results of my work. But for the kindness of Mr. Darwin, who, when I made him aware of my misfortune, obligingly sent me the following table, comprising the results of his experiments on the crossing of these species, I should have been entirely unable to illustrate this important part of my subject. With the exception, then, of the two first unions (the few results derived from my own experiments), all the others in the following table have been afforded me by Mr. Darwin.

TABLE VI.—Cross-unions of Primroses, Cowslips, and Polyanthuses.

	Number of flowers fertilized.	Total number of capsules.	Number of seeds.	Average number of seeds per capsule.	By calculation.	
					Good capsules.	Number of seeds.
Long-styled Cowslip by pollen of Primrose:						
Homomorphic union	8	3	33	11	50	550
Heteromorphic union	8	0	0	0		
Long-styled Primrose by pollen of Cowslip:						
Homomorphic union	3	2	20	10	50	500
Heteromorphic union	3	0	0	0		
Long-styled Primrose by pollen of Polyanthus:						
Homomorphic union	5	0	0	0		
Heteromorphic union	5	2	53	26	50	1325
Short-styled Primrose by pollen of Cowslip:						
Homomorphic union	3	0	0	0		
Heteromorphic union	3	3	142	47	50	2366
Short-styled Primrose by pollen of Polyanthus:						
Homomorphic union	4	2	32	16	50	800
Heteromorphic union	4	1	28	28	50	1400

The results of certain unions in this table are most interesting in their bearings on the general phenomena of sterility, and particularly from the excellent illustrations they afford of the extraordinary complexity of the laws of hybridism. We shall best appreciate their bearings on these phenomena, however, by the following comparative details of the results given in the table. In the first place we shall see, as to the relative degrees of fertility resulting from the homomorphic and heteromorphic unions in each of the crosses:—1. In the ***homomorphic unions*** of the long-styled Cowslip by pollen of the common Primrose the results are 11 seeds per capsule, whereas from an equal number of flowers fertilized HETEROMORPHICALLY every seed-capsule aborted! 2. In the converse unions of these (the long-styled Primrose by pollen of the Cowslip) the results are singularly accordant, the ***homomorphic unions*** yielding an average of 10 seeds per capsule, while in the HETEROMORPHIC *unions* every seed-capsule is *again abortive*! 3. The *heteromorphic unions* of the long-styled Primrose by pollen of the Polyanthus yield an average of 26 seeds per capsule, and the *homomorphic unions* are utterly sterile. 4. Both unions of the short-styled Primrosè by pollen of the Polyanthus are *highly fertile*; the *heteromorphic* also exceeding the *homomorphic unions* in the proportion of 28 to 16 seeds per capsule—that is, as 5 to 3 *. 5. And, lastly, we find that the *heteromorphic unions* of the short-styled Primrose by pollen of the Cowslip are remarkably fertile, yielding an average of 49 seeds per capsule; the *homomorphic unions*, on the other hand, do not yield a single seed!

We have already adduced a few illustrations of the functional relations of the two forms of one species with those of another species, and also expressed our belief, from the teachings of those illustrations, that the RELATIVE *sexual powers* of the two forms of a species did not extend to, or govern the *results* of *unions* between the *respective forms* of two distinct species. How fully, then, are we supported in this view by the results given in the above table! how unequivocally do they show us that functional dimorphism is limited in its operations to the *individuals* of a species! † It is curious to observe how this is borne out by our experiments on the *P. vulgaris* and its modified descendants. Thus, in the above reciprocal unions of Primroses and Polyanthuses, the *heteromorphic unions* in *both* cases exceed

* Mr. Darwin, in his letter to me accompanying the above results, remarks that the seeds of this short-styled Primrose were very small; so that we may perhaps suspect a number of them unfit for germination.

† It is highly probable indeed, from the results of the red Primrose (*vide* Table V.), that we may yet have illustrations of the fertile unions of the modified descendants of a species in which the laws of dimorphism may not be observed, and thus have cause to give *it* even a more restricted field of operation.

the *homomorphic unions*; and so we find it to be in all the unions of the common Primrose with the white variety given in Table V. Though there are certainly great irregularities as to the *grade* of fertility of the different unions, we have still extending through all, the important parallelism that the *heteromorphic* unions in every case exceed the *homomorphic* unions. We thus see (and the fact is most interesting) that though the *Polyanthus* and *White Primrose* have been greatly differentiated with respect to their sexual relations with their common parent, *P. vulgaris*, it is yet insufficient to derange the operations of the laws of dimorphism by rendering the heteromorphic and homomorphic unions indifferently the more fertile. By comparing the relative fertility of the different cross-unions of these forms, however, we are forcibly impressed with the occasional unimportance of structural differences on the functional correlations of distinct forms. Who, for example, in absence of proof, would have suspected that unions between the Polyanthus and the common yellow Primrose would afford a higher grade of fertility than those of the latter (the common Primrose) with the red and white Primroses, which, so far as can be discerned, differ from each other in colour alone? Nevertheless such is the case: we have shown that the red Primrose will not unite with *either* the yellow or white Primrose, and that a very imperfect fertility results from the unions of the two latter forms,—the *united heteromorphic unions* of the common Primrose by pollen of the Polyanthus producing more seed than the *similar unions* of the *former* by pollen of the white Primrose, in about the proportion of twenty-seven to eighteen seeds per capsule, or as three to two!

I have previously stated that individuals of truly dimorphic species occasionally appear with stamens and pistils of an equal length; and also gave an instance of the occurrence of such an individual in *P. Auricula*, with the results of experiments illustrating the effects of such a structure on the functions of reproduction. I will now give an additional and much more remarkable illustration of this from my observations on *P. veris*. Amongst a number of seedling Cowslips I observed an individual with stamens and pistils of an equal length, both reaching the mouth of the corolla-tube. On examination, however, I found it to differ importantly from the non-dimorphic individual of *P. Auricula*. The pollen-grains were as large as, or even larger than, those of normal short-styled plants: the stigma globular, and rough with papillæ,—in fact, a perfect *fac-simile* of that characteristic of the long-styled form! These remarkable relative transpositions in the structure of the sexual organs are, as I will almost immediately show, connected with equally remarkable changes in the functions of reproduction. This will be seen by consulting the following table, comprising the results of nine distinct unions between the three sexual forms.

TABLE VII.—The Three Sexual Forms of *Primula veris*.

	Number of flowers fertilized.	Total number of capsules produced.	Number of good capsules.	Number of seeds.	Average of seeds per capsule.	By calculation. Good capsules.	By calculation. Number of seeds.
Red Cowslip, non-dimorphic form, 21 flowers self-fertilized	...	16	13	447	34	50	1719
Red Cowslip, non-dimorphic form, by pollen of long-styled Cowslip	5	3	2	15	7	50	375
Red Cowslip, non-dimorphic form, by pollen of short-styled Cowslip	4	3	3	27	9	50	450
Long-styled Cowslip by pollen of non-dimorphic Red Cowslip	5	5	4	22	5	50	275
Short-styled Cowslip by pollen of non-dimorphic Red Cowslip	5	4	4	16	4	50	200
Long-styled Cowslip, homomorphic union	10	6	5	83	16	50	830
Long-styled Cowslip, heteromorphic union	10	9	7	196	28	50	1400
Short-styled Cowslip, homomorphic union	7	5	5	58	11	50	580
Short-styled Cowslip, heteromorphic union	7	7	7	145	20	50	1035

In the first line of the above table the results are given of twenty-one flowers naturally fertilized of the equally-stamened and -styled Cowslip; the second to fifth, inclusive, give the results of the reciprocal crosses of the preceding form with the long- and short-styled forms. I have also added, for the sake of comparison, the results of the homomorphic and heteromorphic unions of the latter forms of *P. veris*. If we examine the results given in the fifth column of the table (in which the average of seeds per capsule is shown), we shall see that the highest grade of fertility results from the *self-union* of the *form* with *stamens* and *styles* of an equal length; thus, relatively to the most highly fertile of the other unions given in the table, viz. the long-styled heteromorphic union, we see that the average excess in favour of the former is thirty-four to twenty-eight seeds per capsule, or as five to four! * A most remarkable contrast is afforded when we compare the fertility of the form with stamens and styles of an equal length with that resulting from the homomorphic unions; thus, taking the long-styled as the more fertile of the homomorphic unions, we see that the average excess of seeds per capsule in favour of the former is eighteen, affording the proportions of two to one! In the four reciprocal unions of the *long-* and *short-styled* forms with the *non-dimorphic* form, the results are remarkably complicated. Thus, the *non-dimorphic* form by pollen of the *long-styled* form yields an average of seven seeds per capsule; and by the converse union, *i. e.* pollen of the former applied to the stigma of the latter form, the average of seeds per capsule is reduced to five, or as four to three. Again, the *non-dimorphic* form by pollen of the *short-styled* form yields an average of nine seeds per capsule, whereas from the converse union the average is only four seeds per capsule—that is, as two to one! In these illustrations we clearly see that a complete derangement of the normal dimorphic relations of the two forms in their converse unions has been effected; thus the short-styled form used as female with the non-dimorphic form yields the lowest grade of fertility—four seeds per capsule, whereas used as male with the non-dimorphic form the highest grade of fertility is afforded—nine seeds per capsule! It is also worthy of notice that the *non-dimorphic* in *both unions* as *female*, with the long- and short-styled forms, exceeds in fertility the converse unions in about the proportion of two to one! The fertility of all these cross-unions, relatively to the pure unions of the long- and short-styled forms, is greatly decreased. Thus the *united short-styled* pure *homomorphic* and *heteromorphic unions* yield more seed, in about the proportion of *three* to *one*, than those from the *united cross-unions* of the *long-styled* and *non-dimorphic form*! Again, we find a great increase in the proportions by making a similar comparison of the pure *long-styled homomorphic and heteromorphic unions* with the *cross-unions* of the *long-styled* and *non-dimorphic* form, the average in this case being as *five* to *one*!

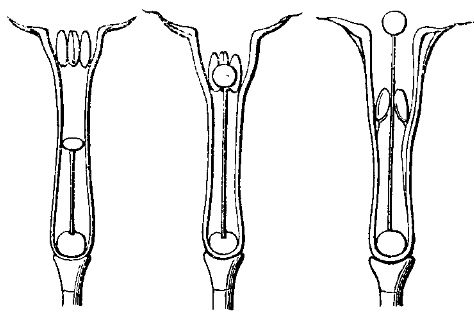
We thus see that the above Cowslip, structurally characterized, as I have previously stated, by an equality in the length of the stamens and styles, and in the resemblance of the pollen-grains and stigmas to those respectively characteristic of the long- and

* Mr. Darwin informs me those individuals of the *P. Sinensis* which have stamens and styles of an equal length are also more fertile with own pollen than a heteromorphic union!

short-styled forms, has also such functional characteristics as render it a normal hermaphrodite representative of the species! We also see that the pollen-grains and stigmas of this non-dimorphic form have become so differentiated with respect to their reciprocal action with those of the long- and short-styled forms, that a *grade* of *sterility* is induced greatly in excess of that which results from the homomorphic relatively to the heteromorphic unions of the latter forms! Now, Mr. Darwin has shown (and my experiments fully confirm it, *vide* Table IV.) that this lessened relative fertility of the homomorphic unions exceeds that resulting from the hybridism of several distinct species relatively to the pure union of those species. In view of such evidence, I think I am fully justified in adding that this *non-dimorphic* form is, in fact, judged by the physiological test so much insisted on by Prof. Huxley, *a new and distinct species.* Here we have an individual differing in colour, and likewise in important points of structure, from either of the forms which at present represent the species. Again, judged by the physiological test, we find a higher degree of sterility resulting from its unions with the two normal forms of the species, than that which results from the unions of other distinct species of Primulas! Certainly then, structurally and physiologically considered, this individual is perfectly entitled to specific honours. One class of naturalists would, indeed, readily admit the validity of such a claim if they had evidence of a constant recurrence of these characteristics; but there is another class which consider ignorance of origin a necessary appanage to this claim!

The foregoing experiments and observations on the non-dimorphic plant were made during its first or spring-flowering period, throughout which, as I have previously stated, a very constant equality was observed in the relative lengths of stamens and pistils in the flowers produced. A similar equality was observed in the relative lengths of these organs in the few flowers produced in its second or autumnal flowering; lately, however, it has produced an umbel in which the relative lengths of these organs in the respective flowers are so singularly variable that I have thought it worth while to give the measurements of each, as well as sketches of a few of the most distinct; thus:—

Number of flowers.	Length of stamens, in lines.	Length of pistils, in lines.
1	8	5
2	8	$8\frac{1}{4}$
3	$7\frac{1}{4}$	7
4	6	8
5	7	$8\frac{1}{4}$
6	6	7



1. 3. 4.

The numbers attached to the sketches correspond with those in the table of measurements. In the first case (No. 1) the structure is normally short-styled—stamens reaching the mouth of the corolla, pollen-grains large. In the second case (No. 3) the length of the stamens and pistils is nearly equal, and in this respect present the normal non-dimorphic characteristics of the plant, differing from it, however, in both (organs) being shorter than the tube of the corolla, and likewise in the greater variability of the size of the pollen-grains, which, upon the whole, are smaller than those produced by normally structured flowers. Again, in No. 4 we have an approximation to the long-styled structure—the stamens attached somewhat above the middle of the corolla-tube, while the stigma slightly projects from its mouth. The pollen-grains of this flower were plainly smaller than those from any of the other flowers, though undoubtedly more variable in size than those characteristic of the normal long-styled form.

In respect to the functional results of these flowers by fertilization with own pollen I cannot as yet speak, the capsules not being sufficiently matured. Nevertheless I think it will be admitted by all who believe in the gradual modification of organic beings, that, irrespective of any knowledge as to the subsistence of diverse functional correlations between the sexual elements of the individual flowers, the mere structural differences suffice to show us the manner by which the at present normally characteristic "subdiœcious hermaphrodism" of the *P. veris*—and, of course, of all the other dimorphic species of Primalus—has been attained, and, furthermore, take us back to that period in its genealogy when non-dimorphism or perfect hermaphrodism was the genital characteristic of its line. Here, as I believe, we are afforded an instance of variability perfectly analogous to, though certainly less remarkable than, the *Catasetum* case, so ably elucidated by Mr. Darwin. And just as *Catasetum* and *Monochanthus* occasionally produce each other and likewise the hermaphrodite *Myanthus*, thus inducing us to regard the former sexual forms as the modified descendants of the latter, so in the case of the non-dimorphic plant of the Cowslip, we see first the original condition in those flowers whose stamens and pistils are of an equal length, and a mutual adaptation subsisting between their male and female sexual elements, and secondly, the earliest indications of a divergence from that condition and a tendency to the dimorphic in those flowers with stamens and pistils of different lengths.

In the two forms of *Primula Sikkimensis* the stigmas differ little in shape or roughness, but greatly as respects the length of their styles, that of the long-styled being fully four times longer than that of the short-styled form. The stamens in the long-styled form rise little above the ovarium; in the short-styled form they are attached halfway up the corolla-tube; so that the relative differences in the length of these organs in the two forms are much less marked than those of their styles. There are also very marked differences in the pollen-grains of 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 shape.

In respect to the relative fertility of the two forms, I may state that when carefully protected from insects they rarely produce a single seed. The long-styled form I have indeed found perfectly sterile when thus protected, while the short-styled form under similar treatment occasionally produces a few seeds. This slightly greater self-productiveness of the latter form is readily explained when we take into consideration the relations of its anthers and stigmas, these being relatively so disposed that it is scarcely possible for the dehiscence of the anthers to take place without a few of the pollen-grains falling upon the stigma. In the long-styled form, on the other hand, where the stigma rises high above the anthers, such a result can only be effected by insects or other external agencies. When both forms, however, are artificially fertilized with their own pollen, we find that the long-styled unions are much the more fertile, exceeding the short-styled in about the proportion of two to one! This I have indeed found to be the case, in a more or less marked degree, in all the dimorphic species on which I have experimented, with the exception of the *P. Auricula* and the *P. vulgaris alba*, as may be seen by referring to the tables previously given of those plants. Mr. Darwin notices (*loc. cit.* p. 92) this relatively decreased grade of fertility in the short-styled homomorphic unions, and very naturally regards it as a quality specially acquired for the counteraction of the greater facilities presented by this form than the other for self-fertilization. Thus, by an increased differentiation of pollen and stigma with respect to their mutual action, Nature renders the short-styled forms equally dependent with the long-styled forms on external agencies for the production of aught above the lowest grade of fertility. And thus, as Mr. Darwin has forcibly urged, one of the great ends of reciprocal dimorphism is more perfectly effected—the greatest facilities afforded for the intercrossing of individuals.

The following table gives the results of my experiments on the two forms of *Primula Sikkimensis*:—

TABLE VIII.—*Primula Sikkimensis.*

	Number of flowers fertilized.	Number of good capsules produced.	Number of seeds produced.	Average of seeds per capsule.
Long-styled homomorphic union......	24	17	248	14
Long-styled heteromorphic union ...	12	8	285	35
Short-styled homomorphic union ...	14	8	64	8
Short-styled heteromorphic union ...	12	10	419	42
SUMMARY.				
The two homomorphic unions.........	35	25	312	12
The two heteromorphic unions	24	18	704	39

In the two forms of *Primula cortusoides* the pistil is about three times as long in the one as in the other, the anthers being situated about the middle of the corolla-tube in the long-styled form, and surrounding its mouth in the short-styled form. The longitudinal axis of the long-styled stigmas is double that of the short-styled stigmas, and the stigmatic papillæ of the former are about three times longer than those of the latter. Again, the pollen-grains of the short-styled plants are larger, less transparent, and more bluntly triangular than those from the long-styled plants.

In the following table I have given the results of my experiments on this species:—

TABLE IX.—*Primula cortusoides.*

	Number of flowers fertilized.	Number of good capsules produced.	Number of seeds produced.	Average of seeds per capsule.
Long-styled homomorphic union......	10	7	287	41
Long-styled heteromorphic union ...	8	6	343	51
Short-styled homomorphic union ...	10	6	228	38
Short-styled heteromorphic union ...	8	8	487	61
SUMMARY.				
The two homomorphic unions.........	20	13	515	39
The two heteromorphic unions	16	14	830	59

I tried repeatedly to reciprocally hybridize the two forms of *P. cortusoides* with those of *P. Sinensis*, but though I was led to anticipate favourable results from the swelling of several of the capsules, I was ultimately disappointed, as they did not contain a *single good seed.* I was more successful, however, in a similar series of experiments with the *P. cortusoides* and *P. mollis*; the latter, as I have previously stated, is characterized by an equality in the length of the stamens and styles. The results are given in the table beneath. If we compare the results with the pure unions of *P. cortusoides* in Table IX., and with those of *P. mollis*, we shall see that the fertility of both species is greatly decreased; we shall also see that there is still no regularity as to the degree of fertility resulting from the converse unions. Thus, the pure *long-styled homomorphic unions* of *P. cortusoides* yield an average of forty-one seeds per capsule, while by its union with *P. mollis* —the latter being used as male—the average is reduced to five seeds per capsule—that is, as eight to one. The short-styled *P. cortusoides* by pollen of *P. mollis* did not *yield* a *single seed*, though several of the capsules swelled. Higher grades of fertility are seen to result from *P. mollis* as female. Thus, by pollen of the long-styled *P. cortusoides* it yields an average of fifty-one seeds per capsule; by pollen of the short-styled *P. cortusoides* the results are sixty-seven seeds per capsule. Now, from the pure unions of

P. mollis the average of seeds per capsule is 165. So that the decreased fertility of the cross-unions relatively to the pure unions of the latter is in the former case as 1 to 3·23, in the latter as 1 to 2·46. Respecting the irregular fertilities of the converse unions we will simply refer to the fact, by way of further supporting our previous remarks on this point, that though the short-styled *P. cortusoides* when used as female with the *P. mollis* is utterly sterile, yet by the converse union of these the highest grade of fertility, relatively to any of the other unions given in the table, is produced. I may also, in passing, notice that the seeds produced upon the long-styled form of *P. cortusoides* were very fine, though the average per capsule is low. Those, on the other hand, produced by *P. mollis*, in its different unions with the long- and short-styled forms of *P. cortusoides*, were so very small, that I entertain little hopes of any of them germinating.

In the following table we have the results of these unions of *P. cortusoides* with *P. mollis*.

TABLE X.—Hybrid unions of *P. cortusoides* with *P. mollis*.

	Number of flowers fertilized.	Total number of capsules produced.	Number of good capsules.	Number of seeds produced.	Average of seeds per capsule.
Long-styled *P. cortusoides* by pollen of *P. mollis* ...	12	7	5	27	5
Short-styled *P. cortusoides* by pollen of *P. mollis* ...	12	5	0	0	0
P. mollis by pollen of long-styled *P. cortusoides*......	10	6	4	205	51
P. mollis by pollen of short-styled *P. cortusoides*......	10	8	5	336	67

In the two forms of *Primula involucrata* the pistil is about three times longer in the one form than in the other. The stigma of the long-styled form reaches the mouth of the corolla-tube, and the anthers are situated halfway down the tube: in the short-styled form the converse of this takes place, namely, the style is half the length of the corolla-tube, the anthers reaching its mouth. The stigma of the long-styled form is of a globular shape, and closely beset with long papillæ; that of the short-styled form is smooth and depressed on the apex: the pollen-grains of the latter are also larger and less transparent than those of the other form; in both, however, they are of a similar (spherical) shape.

Amongst many failures in my experiments on effecting unions between the *P. involucrata* and other species, I succeeded in getting a few capsules containing good seeds by application of the pollen of the short-styled form of *P. Sibirica* to the long-styled *P. involucrata*; I had also successful results by applying the pollen of the short-styled form of *P. farinosa* to the short-styled *P. involucrata.* I have utterly failed, however, to effect unions by the converse experiments of the above, *i. e.* by applying pollen of the two forms of *P. involucrata* to those of the *P. Sibirica* and the *P. farinosa.* The results of the successful unions were as follows:—1. From the long-styled *heteromorphic unions* of *P. involucrata* by pollen of *P. Sibirica* I got four capsules, which yielded an average of ten seeds each. 2. From the short-styled *homomorphic unions* of *P. involucrata* by pollen of *P. farinosa* I had three capsules, and, in all, seventeen seeds; so that the average in this case is reduced to about six seeds per capsule. If we compare these results with those given in the summary of the united homomorphic unions of *P. involucrata* in the following table, we see that these unions yield more seed, in about the proportion of *three to one*, than those from the heteromorphic union of *P. involucrata* with *P. Sibirica*, and as *five to one* relatively to its homomorphic unions with *P. farinosa.*

TABLE XI.—*Primula involucrata.*

	Number of flowers fertilized.	Number of good capsules produced.	Number of seeds produced.	Average of seeds per capsule.
Long-styled homomorphic union......	10	6	230	38
Long-styled heteromorphic union ...	6	4	263	66
Short-styled homomorphic union......	14	7	195	28
Short-styled heteromorphic union ...	6	5	347	69
SUMMARY.				
The two homomorphic unions.........	24	13	425	32
The two heteromorphic unions	12	9	610	68

In the *Primula farinosa* the pistil of the long-styled form is about twice as long as that of the short-styled form, and elevates the stigma slightly above the mouth of the corolla-tube, while the anthers are attached halfway down the latter. In the short-styled form there is a converse arrangement of these organs observed, the stamens corresponding, or nearly, in length with the pistils of the long-styled form, and the pistils with the stamens of the latter form. The stigmas of the two forms differ little in shape or size, but that of the short-styled form is evidently rougher. The pollen-grains are also of a similar (bluntly triangular) shape in both forms, those of the short-styled being the larger. Besides these two forms, however, characterized as we have seen by a relative inequality in the length of the stamens and pistils, it is not at all uncommon to find individual plants with these organs of an equal length, and reaching the mouth of the corolla-tube. From an examination of specimens, however, from various localities, I have no doubt, from the relatively small size of the pollen-grains as compared with those of the normal long-styled form, that these relations are due to an abnormal development of the stamens. This view is furthermore supported by the functional performances of these organs, as I find, from a few experiments on an equal-stamened and -styled plant in the Botanic Gardens of Edinburgh, that less seed results from its union with the long-styled than with those of the short-styled. The non-dimorphic form of *P. Auricula* (*vide* Table II.) affords an analogous illustration in so far as concerns its functional relations with the long- and short-styled forms of the species. But there is one important difference between the two cases, namely, that the non-dimorphic form of *P. Auricula* is perfectly fertile with own-pollen, whereas the like form of *P. farinosa* is very imperfectly fertile when thus treated! indeed much less so than either homomorphic union. This is seen by referring to the table beneath, where we find that the united homomorphic unions yield more seed, in about the proportion of *two to one*, than those of the equal-stamened and -styled form by own pollen.

In the following table I have given, first, the unions with the equal-stamened and -styled form by own pollen, and secondly, the reciprocal unions of the long- and short-styled forms.

TABLE XII.—*Primula farinosa.*

	Number of flowers fertilized.	Number of good capsules produced.	Number of seeds produced.	Average of seeds per capsule.
Form with stamens and pistils of an equal length by own pollen	12	5	62	12
Long-styled homomorphic union......	14	7	210	30
Long-styled heteromorphic union ...	8	5	264	52
Short-styled homomorphic union ...	14	8	150	19
Short-styled heteromorphic union ...	8	7	380	56
SUMMARY.				
The two homomorphic unions.........	28	15	360	24
The two heteromorphic unions	16	12	644	54

To the above notice of the pure unions of *P. farinosa* I will now add the results of my experiments on the fertilizing it with the pollen of other species; these were chiefly confined to the *P. Scotica*, *Sibirica*, and *involucrata*. In my previous notice of the latter species, I have shown that the short-styled form of *P. farinosa* is capable of fertilizing the short-styled form of *P. involucrata*, and I also stated that I had utterly failed in effecting the converse union of these forms. The latter failures are included in the following experiments on four fine umbels of the long-styled and three of the short-styled form of *P. farinosa.* I carefully fertilized sixty flowers, one half with the long-styled and the other with the short-styled form of *P. involucrata*, yet, though several capsules swelled, they did not contain a single good seed! I also tried reciprocal unions between the two forms of *P. farinosa* and the long-styled form of *P. Sibirica*, but these unions, like the preceding, resulted in the complete abortion of every seed. With *P. farinosa* by pollen of *P. Scotica* I have had a little more success: thus, from twelve flowers of short-styled *P. farinosa* fertilized by pollen of *P. Scotica* I got seven capsules; three of these contained no good seed; the other four yielded in all 91 seeds, which gives an average of nearly 23 seeds per capsule. Now if we refer to the above table of the different unions of *P. farinosa*, we shall see that the fertility of the united homomorphic unions is 24 seeds per capsule, so that these pure unions only exceed the above hybrid unions of the species in the proportion of 100 to 95 ; *i. e.*, for every hundred seeds yielded by the pure homomorphic unions of *P. farinosa*, 95 are yielded by its hybrid unions with *P. Scotica.* From these results of the *short-styled hybrid* unions, I naturally anticipated, from the evident structural affinities of the two species, somewhat similar results from the *long-styled* unions. In this, however, I was completely wrong; for, after a number of careful experiments, I have failed to get a single seed from the *long-styled P. farinosa* by pollen of *P. Scotica.* How clearly do such cases show us that sterility does not strictly follow systematic affinity. On the other hand, how forcibly do they urge, as Mr. Darwin has well remarked on certain analogous cases, "that the capacity of two species to cross is often connected with constitutional differences imperceptible by us, and confined to the reproductive system."*

We have seen that *dimorphism,* as applied to the structure of the reproductive organs, is a very general, though not, as has been asserted, a universal characteristic of the genus *Primula,* but that several of the species presenting structurally no such relations have, on the other hand, their stamens and pistils of an equal length. Seeing then that the dimorphic structure, in the case of the Primulas, is so invariably correlated with distinctive physiological characteristics, we are naturally led to consider the nature of the reproductive powers of those species which are structurally non-dimorphic, *i. e.* those which have stamens and pistils of an equal length, and see whether or not these structural dissimilarities are connected with any alteration in the functional characteristics of the species. With the view then of illustrating the latter point, I will give the results of a few experiments on three of the latter (non-dimorphic) species.

1. *Primula Scotica.*—The length of the stamens and pistils of this non-dimorphic species varies slightly, as I have already stated, under cultivation: there being a regular correlation, however, observed, in this variation of the sexual organs, the non-dimorphic structure remains unaffected,—the *stigma,* in every case which has come under my observation, being *closely appressed* by the surrounding *anthers.* From this intimate relation of anthers and stigmas, we are naturally inclined to suppose that, after the dehiscence of the anthers, the stigmas will be liberally supplied with pollen. This is not strictly true; the cohesive nature of the pollen-grains still retains them within the open lobes, so that if the flowers be carefully guarded from external disturbance, the *apices* of the stigmas, even in their last stages of decay, are generally found destitute of pollen-grains.

* 'Origin of Species,' 3rd edit., p. 280.

Even under these conditions, however, an imperfect fertility is induced; as by the dehiscence of the anthers, which closely surround the stigmas, the pollen-grains are brought into immediate contact with the exterior or circumference of the stigma, into which they protrude their tubes, and thus induce a variable though usually a low grade of fertility. This will be seen by an examination of the table beneath, which gives the results from four plants of the *P. Scotica* under the following treatment:—Two of the plants were placed under a shaded bell-glass, and had their flowers artificially fertilized; a third was placed under similar conditions, so as to guard against the aid of all external agencies in the fertilization of the flowers—each of the latter in this case being left to its own innate means; in the fourth, and last, the plant was freely exposed, so as to favour, as far as possible, the action of insects or other agents employed in the fertilization of the flowers.

In Table XIII. the results of the protected and artificially fertilized plants are given in distinct lines, as one of them was very weak and produced two poor umbels, the products of which, united with the other, would give a very unfair idea of the normal average of seeds produced by these plants under the above treatment. If we compare the results, then, of the artificially fertilized flowers in the second line alone with those in the first line, carefully protected from all external fertilizing agencies, we see that the latter, though equally as productive of capsules as the former, nevertheless falls far below it in the *average* of *seeds* per capsule, the proportion in favour of the former being as 2·24 to 1. Again, if we compare the results of the protected and unartificially fertilized flowers with those from the unprotected flowers, given in the fourth line, we see that the latter also exceeds the former in the average of seeds per capsule, in the proportion of 1·87 to 1. Lastly, by comparing the results of the artificially fertilized flowers, in the first line of the table, with those of the unprotected flowers, in the fourth line, we see that the average fertility of the former relatively to the latter is as 1·11 to 1.

We thus see that the *Primula Scotica is* capable of self-fertilization; but, from its extremely imperfect nature, we are rather inclined to regard it as a mere provision against absolute sterility, than to suppose that the plant is habitually dependent on such manifestly imperfect means for its fertilization; that, in fact, in this species, as in the truly dimorphic, fertilization is largely aided by insect or other mechanical agencies; so that, as one of the grand ends of sexual dimorphism is the crossing of distinct individuals, we have, in this imperfect self-fertility, indications of a desire in nature to facilitate similar conjunctions in this non-dimorphic species. As it might be supposed, however, that this imperfect self-fertility was due to a differentiation of a flower's own pollen to its own stigma, I may expressly state that the complete fertility of the artificially fertilized flowers was the result of fertilization in every instance by the flower's own pollen. There can be no doubt, therefore, that the imperfect fertility of the unartificially fertilized flowers was simply owing to the stigmas being insufficiently supplied with pollen. As further supporting this, I may also state, that in my tables where the amount of seeds produced by each capsule is stated separately, much less variation in the amount is presented by those artificially than those naturally fertilized.

TABLE XIII.—*Primula Scotica.*

	Number of flowers.	Number of flowers fertilized.	Number of capsules produced.	Number of seeds produced.	Average of seeds per capsule.
Flowers carefully protected from all external fertilizing agencies	10	...	6	568	95
Flowers protected from insects, and artificially fertilized	...	6	4	852	213
Flowers protected from insects, and artificially fertilized	...	14	9	1249	139
Flowers unprotected, and freely exposed to insect and other agencies	...	13	8	1426	178

2. *Primula mollis.*—The relations of anthers and stigmas in this species, as in the preceding, are highly favourable to self-fertilization, the latter organs being closely surrounded by the former, and included within the tube of the corolla. In respect to its regular self-fertility, it greatly exceeds all the other species with which I have any acquaintance, inasmuch as nearly every flower produces a capsule *filled* with *good seed*; whereas in the other non-dimorphic species which have come under my observation there is very generally a high percentage of abortive capsules, together with a great variability in the number of seeds contained in those that do set. Though I had never seen the flowers of

this species (*P. mollis*) frequented by insects, I carefully protected a few plants, in case this regularly complete fertility might be due in part to such agencies. The seed-produce, however, from these plants was in no way affected; the average of capsules, and of seed per capsule, was quite equal to those from the unprotected plants. The following are the results from a single scape of a protected plant, which I believe affords a fair idea of the average fertility of this species in a cultivated state:—

	Number of verticils.	Number of flowers.	Total number of capsules.	Number of good capsules.	Number of seeds.	Average of seeds per capsule.
Primula mollis	4	17	17	14	2306	165

3. We have thus seen, then, that the Primulas *Scotica* and *mollis*, in *function* as in *structure*, are alike *non-dimorphic*. This, however, does not appear to be the case with the following species, *P. verticillata*, which apparently presents an *imperfect functional dimorphism* in conjunction with a non-dimorphic structure! As I have already stated, the anthers in this species are attached to the upper third of the corolla-tube, and in general closely surround the stigma; occasionally, however, the latter rises above the anthers, and even becomes slightly exserted beyond the corolla-tube. In such relations, then, of anthers and stigma as occur in the latter case, it is at once evident that sterility may be simply due to the pollen not reaching the stigma. Anyhow, the existence of plants producing flowers of the latter description renders all but valueless the few observations I had made on the self-sterility of this species under cultivation, previous to the publication of Mr. Darwin's paper on Primula-dimorphism, inasmuch as I was then utterly ignorant of such singular sexual relations, and therefore paid no regard to the relative lengths of the stamens and pistils of those plants which came under my observation. In respect to these I will therefore simply state that for two successive seasons I failed to get a single seed from a fine healthy plant of this species, though each season it produced a profusion of flowers. I have also received a nearly similar testimony from the observations of others, namely, that they rarely ever succeeded in getting seed from *solitary plants* of this species, though they have frequently gathered it when a few plants were growing together. But for the existence,

then, of the form with the stigma rising above the anthers, which I only observed in a *cultivated* state this season, such testimony would have rendered highly probable the view I have taken as to the existence of a functional dimorphism in this species; and this the more especially on taking into consideration the results of the few experiments I have lately had an opportunity of making. It is, indeed, only from the accordance of the latter with my previous observations that I have ventured to refer sterility in this case to a dimorphism in function; and I think I am fully justified in so doing; for how, I ask, can an explanation otherwise be afforded for the low fertility of the hermaphrodite conjunctions and the high fertility of the diœcious conjunctions? That such phenomena are presented by the individuals of this species I will now show by the following details of my experiments.

In the summer of 1862 I examined every flower upon a fine scape of *P. verticillata*, and observed a very general equality in the length of the stamens and pistils. On a subsequent examination I observed more or less pollen on the stigmas of seventeen out of the twenty-three flowers borne upon the scape. The remaining six I therefore artificially fertilized with own pollen. The results, however, were in no respect different from those previously alluded to; a high percentage of the capsules were utterly abortive, and the few which did swell contained *no good seed.*

The results of my experiments this summer (1863) have somewhat modified those of 1862, inasmuch as certain of the flowers fertilized by own pollen have yielded a considerable amount of seed; this will be seen by consulting the following table:—

TABLE XIV.—*Primula verticillata.*

	Number of flowers fertilized.	Total number of capsules produced.	Number of good capsules.	Number of seeds produced.	Average per capsule.
Flowers fertilized by own pollen	18	8	3	769	256
Flowers fertilized by pollen from a distinct plant	8	5	5	1245	249
Flowers fertilized by pollen from a distinct plant	10	8	7	1957	279
SUMMARY.					
Flowers fertilized by own pollen	18	8	3	769	256
Flowers fertilized by pollen from a distinct plant	18	13	12	3202	267

In the first line of the above table I have given the results from a single scape, each flower of which was artificially fertilized by own pollen; in the second and third lines we have the results of the reciprocal crossings of flowers on distinct individuals; and lastly, for the sake of comparison, I have simply restated the results of the unions with own pollen, and given the united results of the reciprocal unions. If we compare the average of seeds per capsule, we see that the unions with own pollen give an average of four seeds per capsule over those in the second line of the table—fertilized by pollen from a distinct individual; the scape, however, which yielded the latter was very weak, so that it affords a very unfair estimate of the normal fertility of the species under the above treatment. A more just idea of the relative fertility of flowers fertilized by own pollen and those fertilized by that from a distinct individual may be formed by comparing the results of the first and third line of the table, these being the results of two equally healthy scapes. Now, in this case we see that those flowers fertilized by pollen from a distinct individual give an average of twenty-six seeds per capsule over those fertilized by own pollen. The most important fact, however, shown in the above table is the increase in the number of good capsules produced by those flowers fertilized by other's pollen as compared with those fertilized by own pollen. Thus, from eighteen flowers of the latter, treated by own pollen, eight capsules set, but of these only *three* contained good seeds; whereas from the same number of flowers of the former, treated by other's pollen, thirteen capsules set, twelve of which were well filled with good seeds: so that the treating with other's pollen exceeds that by own pollen in the proportion of *four* to *one*!

He who will carefully study these observations and experiments on *P. verticillata* will see those conditional peculiarities of the generative system which I have ascribed to a functional dimorphic quality. He will also see, however, by comparing the results of experiments in 1862 with those of 1863, that the individual and reciprocal—*i. e.* hermaphrodite and diœcious—functional relations of the male and female organs are much too capricious to permit of their assignment to any definite law; they are yet, as it were, mere tracings, or, rather, indications of a tendency to become functionally dimorphic. Apart from the evidence afforded by the low percentage of good capsules produced from fertilization by own pollen relatively to that from the reciprocal fertilization of distinct individuals, this, I think, is clearly shown by the relatively increased percentage of seeds resulting from the latter conjunctions. This relative increase in the percentage of seeds by the reciprocal unions, though certainly much under those usually resulting from a comparison of the homomorphic and heteromorphic unions of Primulas, is nevertheless sufficient to affect importantly the number of the individual representatives; and this the more especially if, as Mr. Darwin forcibly urges, close-breeding has a tendency to weaken the progeny.

Connected with these functional peculiarities there is another point worthy of a passing notice—namely, the variability in the length of the pistil. As I have previously stated, this organ is generally of an equal length with the stamens; occasionally, however, flowers occur in which the stigmas rise above the stamens and project beyond the mouth of the corolla-tube; and again there are others in which it does not even reach the stamens, while the latter in every case observed by me retain a definite position around the mouth of the corolla-tube. The intimate systematic affinities, already alluded to, of the present species with the *P. floribunda* give the above variabilities an additional interest. In respect to the latter species we have stated that along with normally short-styled plants, others occur in which the stamens and pistils are of an equal length. Guided by analogy, then, we may suppose that as the *P. floribunda* has not as yet attained the, at least provisional, equilibrium of dimorphism, as shown by a percentage of non-dimorphic forms, so these functional and structural peculiarities of the *P. verticillata* are presumptive indications of an ulterior dimorphic tendency.

Summary.—The species of *Primula* are variously estimated by authors, many of the forms reputed specific by one being considered as mere varieties by another. Steudel, for example, in his 'Enumeratio Plantarum,' admits 85 species, whereas DeCandolle ('Prodromus') gives only 61—a difference of 24 doubtful forms. Of these varieties or species, then, I have given the sexual characteristics of 54:—36 of which are truly dimorphic, presenting both long- and short-styled forms; 13 in which the long- or short-styled forms, respectively, have alone been observed by me; and 5 species and one variety with non-dimorphic characteristics, *i. e.* presenting stamens and pistils of an equal length.

The allied genera *Hottonia* and *Aretia* have also truly dimorphic species; whereas other allied genera—*Dodecatheon*, *Soldanella*, and

Cortusa—are very generally characterized by species presenting the structural characteristics of the long-styled form only, without, however, any decreased fertility arising from their hermaphrodite conjunctions.

The general differences of the two sexual forms may be thus briefly summed up:—First, the long-styled forms have pistils equalling in length the tube of the corolla; stigmas usually larger and rougher; stamens attached to, or frequently below the middle of the corolla-tube, whose diameter is thus expanded upwards; pollen-grains generally smaller and more transparent. Secondly, in the short-styled form the pistil is short, not rising above halfway up the corolla-tube; stigma generally smoother and depressed on the summit; stamens attached to the mouth of the corolla-tube, causing an abrupt expansion; pollen-grains generally larger and more opaque. According to all the trials, these structural differences are accompanied by equally remarkable functional differences,—the pollen of the long stamens being alone adapted to fertilize the long pistils, and the pollen of the short stamens to fertilize the short pistils. By applying, on the other hand, either form pollen to own form stigma, *i. e.* effecting a homomorphic union, the degree of fertility relatively to the above, or heteromorphic union, is greatly decreased. Analogous, though less striking, functional differences, however, occur without any appreciable change of structure, as shown by the *P. verticillata*, *e. g.*, yielding a much higher grade of fertility by its diœcious than its hermaphrodite conjunctions. Such an instance from a genus whose members are so generally characterized by a sexual dimorphism, naturally leads me to regard it as indicative of the acquirement of similar characteristics. An objection to this view may be urged from the occurrence of species which, having no immediate affinity with any structurally dimorphic species, nevertheless present individuals incapable of fertilization by own pollen, though perfectly susceptible to reciprocal fertilization, either with another individual of the same species, or one of a distinct species. To this category, at least, those who disbelieve in the genetic affinities of organic beings will no doubt refer the case of *P. verticillata*, and simply regard it as further illustrative of our ignorance of the conditions upon which sterility, in its varied grades, depends. Those, on the other hand, who believe in the existence of these genetic relations will look with an intelligent interest upon these functional peculiarities of the *P. verticillata*, and regard them, mayhap, as the primary indications of a tendency to assume those remarkable sexual characteristics of the correlated species, and thus presenting an illustration of incipient dimorphism.

The usual differences in the fertility of the heteromorphic and homomorphic unions will be best appreciated by giving the mean results from the unions of several species. Thus, taking the five heteromorphic and homomorphic unions given above, namely, *P. Auricula*, *Sikkimensis*, *cortusoides*, *involucrata*, and *farinosa*, we see, from the mean results of their combined products, that for every 100 seeds yielded by the heteromorphic unions, only twenty-four are yielded by the homomorphic unions,—the heteromorphic thus exceeding the homomorphic unions in about the proportion of five to three! I have also shown the remarkable fact that the pollen of a distinct species will produce a much higher grade of fertility than an ordinary homomorphic union, *i. e.* a flower's own pollen!

It is well known that A will fertilize B, and B will not fertilize A. I have given instances of this law with Primulas. I have also shown the new and remarkable fact, that of the two forms of the same species the pollen of the one, but not of the other, will fertilize a distinct species! For example, the long-styled *P. Pallinurii* can be fertilized readily by pollen of the long-styled *P. Auricula*; yet, after numerous trials, I have failed to effect a single union between the long-styled form of the *P. Pallinurii* and the short-styled *P. Auricula.* How utterly inconsistent, then, are such facts with the teachings of those who would have us believe that an absolute causal relation exists between the sterility from hybridism and systematic affinity! On the other hand, how unequivocally do these cases show us that the greater or less facility of one species to unite with another is, as Mr. Darwin has sagaciously argued, "incidental on inappreciable differences in their reproductive systems. And that there is no more reason to think that species have been specially endowed with various degrees of sterility to prevent them crossing and blending in nature, than to think that trees have been specially endowed with various and somewhat analogous degrees of difficulty in being grafted together in order to prevent them becoming inarched in our forests."*

Probably the most remarkable result from my observations is that when the dimorphic species cease to be dimorphic, their reproductive functions are greatly modified. Thus, in the case of the Cowslip, for example, we have seen that an ordinary homomorphic union yields about fourteen seeds per capsule, the hetero-

* 'Origin of Species,' 3rd edit. p. 299.

morphic about twenty-four seeds per capsule, whereas the form with stamens and pistils of an equal length yields, when fertilized with its own pollen, thirty-four seeds per capsule! Thus the non-dimorphic form by own pollen exceeds, first, the homomorphic unions in the proportion of 5 to 2, and secondly, the heteromorphic in the proportion of 3 to 2! Again, from the four different unions of the long- and short-styled forms with the non-dimorphic form, the seed-results in each case fall considerably below an ordinary homomorphic union: thus the mean results of the unions of the non-dimorphic with long- and short-styled are six seeds per capsule, whereas the pure homomorphic unions of the latter give an average of thirteen seeds per capsule—that is, as two to one!

Connected with these are the remarkable changes in the fertility of the coloured varieties of the Primrose, the red variety yielding no seed when fertilized by pollen of either yellow or white varieties: the reciprocal crosses of these, *i. e.* the pollen of the red variety applied to the stigmas of the yellow and white, are also absolutely sterile! On the other hand, fertile unions may be effected by the reciprocal crossing of the yellow and white varieties, though in every case we have found that the average seed-result of such unions is considerably under that of the pure unions of these forms.

Whether or not the ultimate tendency of dimorphism is a complete separation of the sexes, I think we have the clearest testimony that dimorphism has not always been a genealogical characteristic; and furthermore, that the two forms did not *per saltum* assume these structural and physiological characteristics. I here allude to the evidence afforded by the non-dimorphic Cowslip—namely, the resumption of perfect hermaphrodism, and the occasional production of intermediate stages between this and the normally dimorphic. These, taking us back in the genealogical line, show us an original non-dimorphic progenitor, and the graduated plan by which it gave rise to a dimorphically characterized race.