THE

LONDON QUARTERLY REVIEW.

OCTOBER, 1899.

THE PRIMROSE AND DARWINISM.

1. *Cross and Self-Fertilisation of Plants.* By CHARLES DARWIN. (London: John Murray. 1891.)
2. *Different Forms of Flowers on Plants of the same Species.* By CHARLES DARWIN. (London: John Murray. 1892.)
3. *Darwinism.* By A. R. WALLACE. (London: Macmillan & Co. 1889.)
4. *Natural Selection.* By A. R. WALLACE. (London: Macmillan & Co. 1891.)
5. *British Wild Flowers considered in Relation to Insects.* By the Right Hon. SIR JOHN LUBBOCK. (London: Macmillan & Co. 1897.)
6. *Chapters on Popular Natural History.* By the Right Hon. SIR JOHN LUBBOCK. (London: National Society.)

PERHAPS some of the most elaborate experiments of Darwin in reference to the cross-fertilisation of flowers are found in connexion with the Order of the *Primulaceæ*, as given in his book, *The Different Forms of Flowers*

on Plants of the same Species. This Order contains the common and well-known flowers—the cowslips and primroses. To these we shall confine our remarks in our review of the books at the head of this article. Both Sir John Lubbock and Mr. Wallace in each of their books mentioned above adopt as to cross-fertilisation the opinion of Darwin on the above two flowers; they also accept the other conclusions of Darwin concerning cross-fertilisation of flowers generally, which he had himself arrived at from his system of experimenting. If the results of Darwin's experiments in regard to the cowslips and primroses are found unsatisfactory and untrustworthy, the result cannot but materially affect also the scientific value of Darwin's other experiments, conducted exactly on the same system, with respect to the other heterostyled dimorphic and trimorphic plants as well.

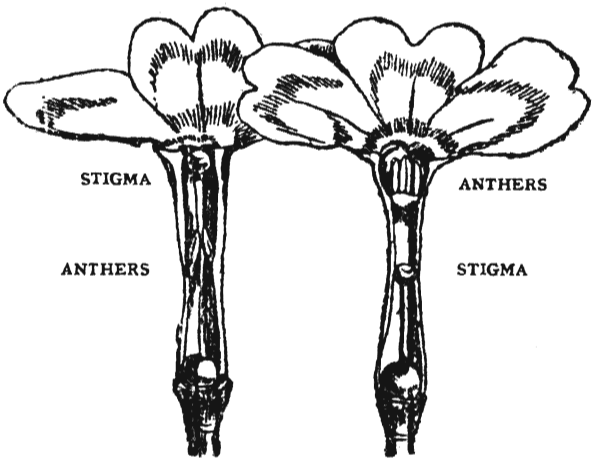
We may here explain one or two terms to the more general reader, which are technical terms, but which cannot well be completely avoided in such a subject.

The word "heterostyled," which will be met with in the following pages, means that flowers of one and the same species, as the common primrose and cowslip, have each their styles of different lengths in different flowers. These different forms grow on different roots. Such flowers are also called dimorphic—of two forms—as having flowers differing in the relative position or length of their styles and anthers. When there are three different kinds or lengths of styles and anthers in different flowers of the same species, such plants are said to be trimorphic or of three forms. The flowers generally of the primrose tribe *(Primulaceæ)* are heterostyled and dimorphic.

There are few observers of flowers but know that there are these two different forms in the primrose. Some of the flowers have their stigmas—which are the terminations of the styles—at the mouth of the corolla tube (these are commonly called "pin-eyed"), and their anthers midway down the tube. These are the long-styled flowers. Others, on the other hand, have their anthers at the mouth of the corolla tube (these are commonly called "thrum-eyed"), and their

stigmas half-way down the tube. These are the short-styled flowers. A few wild or garden primroses or primulas will immediately illustrate the difference between the two forms. Thus the chief difference between the two forms of flowers lies in the different lengths of their styles, and in the interchange of the relative position in the flowers of their stigmas and anthers. These two different kinds are found on different plants growing side by side with each other, and both forms are equally common.

Now Darwin found that when these two different forms grew naturally in the fields and woods, that those flowers



Long-Styled form of Cowslip and Primrose. Short-Styled form of Cowslip and Primrose.

which had short styles—styles ending with their stigmas half-way down the corolla—were much more productive as to weight or number of their seeds than those which had long styles. Darwin marked, as they were growing wild in spring, an equal number of each kind of flower of the cowslip and the primrose, and gathered these marked ones when fully ripe in the autumn.

We give first the following summary as to the weight of

seeds in the two different forms of the wild cowslip, the long-styled and the short-styled, as taken from Darwin's *Forms of Flowers* :—

TABLE II., p. 19.

	Number of plants.	Weight of seed in grains.	Number of umbels.	Weight of seed in grains.	Number of capsules	Weight of seed in grains.
Short-styled cowslip...	10	92	100	251	100	41
Long-styled „ ...	10	70	100	178	100	34

A similar experiment was repeated the following year. The wild plants were transplanted in the autumn into his own garden, into good soil, and all were treated alike. The result in the weight of the seeds of the two kinds was the following :—

TABLE IV., p. 20.

	Number of plants.	Weight of seed in grains.	Number of umbels.	Weight of seed in grains.
Short-styled cowslip ...	100	1585	100	430
Long-styled „ ...	100	1093	100	332

"In all these standards of comparison," Darwin says, "it is evident that the flowers containing the short styles, growing naturally, were the most productive. In the first case in the ratio of nearly 4 to 3. In the last case, where the plants were placed in better soil and not in a shady wood or struggling with other plants in the open field, the actual produce of the seeds was considerably larger. Nevertheless, there was the same relative result in favour of the short-styled plants (taking the fairest test, that of the umbels) as in the former case, nearly as 4 to 3." *

Now to carry out his experiments as to cross and self-fertilisation † of these flowers, Darwin was obliged, in order

* *Forms of Flowers*, p. 20.

† Self-fertilisation means that the pollen of its own flower, or of a flower on the same root, was allowed to fertilise its own stigma. Cross-fertilisation, on the other hand, means that pollen from a flower growing on a different root was applied to the stigma.

to prevent bees or other insects from carrying pollen from flower to flower, to cover the plants with a fine close-meshed net, "so that no insect but a thrips" (which is a very minute insect, so minute that the shank of the thinnest pin is thick in comparison to it, and so small that it is scarcely much more than noticeable to the naked eye) "could pass through the net."*

"In 1860," Darwin says, "a few umbels on some plants of both the long-styled and short-styled form, which had been covered by a net, did not produce any seed, though other umbels on the same plants, *artificially fertilised*, produced an abundance of seed, and the fact shows that the *mere covering of the net itself was not injurious.*" †

Now how Darwin could come to such a conclusion with the fact before him that all the plants, which were not artificially fertilised from seed naturally grown outside the net, produced no seed whatever, very much surprises us. On the contrary, we are very decidedly of opinion that the covering of a very close-meshed net was, for the following reasons, most injurious to the fertility of the flowers.

The influence of the solar rays would be greatly diminished in passing through a close-meshed net, and consequently they would be much debarred from exercising their maturing power on the anthers. Radiation would likewise be almost entirely prevented by the net, and the dew consequently would fail to fall on the anthers. ‡

The importance of this influence cannot be over estimated. In the mornings of early spring after clear nights we have frequently found the flowers of the primrose bedrenched with dew. Occasionally the dew deposited on the anthers, especially noticeable where the anthers are of the short-

---

* *Forms of Flowers*, p. 24.

† *Ibid*, p. 21.—The italics are ours.

‡ This test may be very easily made by placing any fine close-meshed net on any grass or lawn, or raised a few inches above it, and removing the net in the morning before the sun is on the grass. After a clear night in spring or summer the grass outside the net will be covered with dew, whilst that under the net will be almost entirely dewless.

styled position, has been so great as to lie upon the anthers, and entirely to fill the orifice of the corolla. Thus the anthers could not attain under such conditions their natural condition for fertilisation. The stigmas would likewise be affected. Moreover, in calm weather the covering would prevent the free access of the air, and so would prevent its freely distributing and applying the pollen. So close were the meshes of the net in order to exclude all insects except the tiny thrips, that Darwin tells us that in his experiments with the *Linum perenne* it required the wind to be high to pass through the net.* His words are, "they were covered by a rather coarse net, through which the wind, when high, passed." In that experiment there were one hundred meshes to the square inch. In the experiments with the primrose and cowslip the meshes were equally close.† "Fertility," as Darwin on several occasions tells us, "is a very variable element with most plants, being determined by the conditions to which they are subjected."‡ The withdrawal of such natural influences as those mentioned above was quite sufficient in many cases to sterilise the flowers. Such sterilisation was only overcome by *applying artificially pollen naturally grown*, and thus "those flowers to which it was applied produced abundance of seed."§ The rest were unproductive.

That such sterilisation arises from the use of the net is again conclusively shown by the following two experiments of Darwin's.

These two experiments, the one on the red, or purple, clover *(Trefolium pratense)*, the other on umbels of cowslips, amply suffice—though similar instances might be almost indefinitely multiplied—to prove that such sterilisation arose from the influence of the net.

"One hundred flower heads of the red clover," Darwin says, "on plants protected by a net, did not produce a single

---

* *Forms of Flowers*, p. 93.
† *Cross and Self-Fertilisation*, p. 11.
‡ *Forms of Flowers*, p. 40.
§ *Ibid*, p. 21.

seed, whilst a 100 heads on plants growing outside the net which were visited by bees, yielded 68 grains weight of seeds; and as 80 seeds weighed two grains, the 100 heads must have yielded 2,720 seeds. I have often watched this plant and have never seen hive bees sucking the flowers, except through holes bitten by humble bees. It is at least certain that humble bees are the chief fertilisers of the common red clover."*

Yet in contrast to this last sentence Darwin was fully aware how little humble bees—on account of the extreme length and narrowness of the tube of the corolla of the red clover—contribute to such fertilisation. Some pages further on in the same volume (pp. 428, 429) Darwin says, "I have already alluded to bees biting holes in the flowers for the sake of obtaining the nectar. The plants when the nectar is thus stolen from the outside there can be no cross-fertilisation. I have seen whole fields of red clover *(Trefolium pratense)* which had every flower perforated." Similar or closely similar treatment, we may conclude, would necessarily be applied to the "red clovers growing outside which were visited by bees."

Hence in the experiment above we have a 100 heads of flowers, generally beyond the influence of bees for fertilisation, but fully exposed to sun, dew, wind, and all other natural atmospheric influences, producing 2,720 seeds, whilst a 100 heads of the same flowers under the net *produce not a single seed.*

But we pass to one example more—Darwin's experiment with the umbels of cowslips.

In 1861, twenty-four umbels of short-styled cowslips and seventy-four umbels of long-styled ones were similarly covered "just before they expanded their flowers. † The result of this experiment—and here there was no artificial fertilisation introduced—was "that the 24 umbels produced but 1¼ grains weight of seed, and the 74 long-styled

---

* *Cross and Self-Fertilisation*, p. 36.

† *Ibid*, p. 21.

ones produced none at all." As the plants outside the net produced at the same time abundance of seed, Darwin accounts for the contrast between the produce of the flowers outside and under the net, by the presence of insects in the former case, and the absence of insects in the latter, and draws this conclusion: "We see thus that the visits of insects are absolutely necessary to the fertilisation of the cowslip *(Primula veris)*."*

But such an experiment, for the reasons given above and for others which will be adduced below from the primrose, proves in our opinion nothing of the kind; but on the contrary, that the presence of the net alone fully and adequately accounts for the non-fertilisation of the flowers. Minimise the sun, the dew, the wind, and other atmospheric influences, in such a way as practised in these experiments, and not all the insects in the world would have caused sound and full fertility.

Let us now turn to Darwin's experiments where the two different kinds of cowslips, the long-styled and the short-styled, are covered with a net, and where the two kinds are subjected to exactly similar treatment of intercrossing. In one set of flowers the long-styled stigmas are crossed with pollen from the short-styled ones, and the short-styled flowers are crossed with pollen from the long-styled.

The result is as follows:† Under the net one hundred capsules of

The long-styled
cowslip crossed by pollen of the short-styled produced 62 gr.;
The short-styled
cowslip crossed by pollen of the long-styled produced 44 gr.

Again, one set of flowers, the long-styled, are fertilised by their "own form" pollen, and the short-styled flowers are similarly fertilised by their "own form" pollen.‡

* *Cross and Self-Fertilisation*, p. 22.

† Table VI., *Forms of Flowers*, p. 25.

‡ The term "own form" pollen is used by Darwin to signify pollen taken not from its own flower, but from a flower with the same kind of style, growing on a different plant.

This result follows: Under the net one hundred capsules of

The long-styled
cowslip fertilised by "own form" pollen produced 42 grains;

The short-styled
cowslip fertilised by "own form" pollen produced 30 grains.

By this we see that in both the experiments above the long-styled cowslips are the more fertile of the two, in the proportion respectively of 3 to 2 and 4 to 3.

Thus we see that under Darwin's method of experimenting the natural productiveness of the two sets of cowslips is *completely reversed*. When naturally grown, we have seen from Darwin's tables that the short-styled were in productiveness to the long-styled as 4 to 3; but under the net the long-styled were superior to the short-styled, in one case of 3 to 2, in the other as 4 to 3.

Let us now take in the same way the case of the primrose.

The primrose, as the cowslip, has the two forms. Under the net, when the primrose was treated in exactly the same way as the cowslip above, it gave the following results as to the average number of seeds.*

The long-styled
primrose crossed by pollen from short-styled produced 66 seeds.

The short-styled
primrose crossed by pollen from long-styled produced 65 seeds.

And again

The long-styled
primrose fertilised by "own form" pollen produced 52 seeds;

The short-styled
primrose fertilised by "own form" pollen produced 18 seeds.

Now when Darwin gathered capsules from primroses growing together in their natural habitats he found that "the seeds from the short-styled weighed exactly *twice as*

* Table ix., p. 37

much as those from an equal number of long-styled plants. So that the primrose resembles the cowslip, in the short-styled forms being the more productive of the two forms." *

But here under the net in the first case they are placed on an equality, in the second case the long-styled in fertility is to the short-styled as 5 to 2. So that in both cases there is a *great reversion* under the net from what takes place under natural conditions.

Such a system of experiments, which actually *reversed* in both crossed and uncrossed flowers that found under nature, in both cowslips and primroses in weight and in number of seeds respectively, is evidently most untrustworthy as a scientific indicator of what takes place in these two flowers in a state of nature.

Let us now consider whether cross-fertilisation or self-fertilisation is most probable when the primrose grows wild in its natural habitat and with its natural surroundings.

Everybody is well aware that the tube of the corolla of the primrose is of very considerable length. It requires consequently an insect with a long tongue or proboscis to reach the nectar at the bottom of it. Such insects are chiefly the humble bees, moths and butterflies. Humble bees and hive bees are not in the habit of visiting the primroses. If such a case occurs it is most exceptional. Darwin, speaking of his own experience, says, "the primrose is never visited, and I speak after many years of observation, by the larger humble bees, and only rarely by the smaller kinds." † ‡

---

* *Forms of Flowers*, p. 36.

† *Ibid.*, p. 56.

‡ This rare visitation of the primrose by the smaller kinds of humble bees (*i.e.*, the workers)—irrespective of what is stated below—is very easily accounted for. The tubes of the corolla of the primrose (and also of the cowslip) average 12–14 millimetres in length (25 millimetres being the equivalent of an inch). The tongue of the smaller humble bees averages from 7–8½ millimetres. The only smaller humble bee that even approaches it would be that of the *Bombus hortorum*, whose tongue varies, according to its size, from 8–11, and ocasionally 12 millimetres. But strangely these smaller humble bees never appear until primroses

In all our experience we have never seen a humble bee, nor a hive bee, visiting the flowers, and only once a smaller bee, *Andræna nigroænea*; even this small bee was only sunning itself, as its proboscis was too short to reach the nectar. One insect and one insect only, and on one occasion only, with a long proboscis, have we seen visiting the primrose and probing for honey. This was a diptera, the two-winged Humble bee Fly *(Bombylius discolor)*. This single instance was when the season of the primroses was well on, past the middle of April. Darwin suggests that they are visited by the night-flying moths, but of this there is no evidence. On the contrary, neither butterflies, nor day-flying moths, are seen to visit them. It is therefore an equal probability that they are unvisited by night-flying moths at night.

To account for the absence of bees from primroses whilst they are accustomed to visit the cowslips, Darwin says, "they (the primroses) emit a different odour, and perhaps their nectar may have a different taste."* If so this condition would equally affect the night-flying moths, as it does the day-flying moths and the butterflies. The nectar which was distasteful to the one, would be equally so to the other; night or day would make no difference whatever in this respect.

Moreover, in March and in the early days of April, when the primroses bloom, preceding in this respect three or four weeks the cowslips, bees, butterflies, and moths are infinitely scarce, whilst the primroses in many situations are infinitely numerous. The clear nights of March and of early April are also very frequently frosty, and unfavourable for insects, even if they were existing in their imago form, being upon the wing at night.

Yet in spite of this negative relation in which the prim-

---

generally have been several weeks out of flower. The primulas of our gardens might possibly be alluded to by Darwin. All other bees, such as hive bees, whose tongue is only 6 millimetres long (*Flowers and Insects*, p. 61), are necessarily excluded.

* *Forms of Flowers*, p. 56.

roses stand to the bees, even according to Darwin's own experience, Sir John Lubbock applies to primroses in particular Darwin's ingenious exposition of the action of a bee in effecting cross-fertilisation, which Darwin had applied generally to the *Primulaceæ.** "An insect thrusting its proboscis down a *primrose*," Sir John says, "of the long-styled form would dust its proboscis at a part which, when it visited a short-styled flower, would come just opposite the head of the pistil, and could not fail to deposit some of the pollen on the stigma; and conversely, an insect visiting a short-styled plant, would dust its proboscis at a part further from the tip, which when it subsequently visited a long-styled flower, would again come just opposite to the head of the pistil. Hence we see by this beautiful arrangement insects must carry the pollen of the long-styled form to the short-styled, and *vice versâ*." † Mr. Wallace repeats the same exposition of the action "of bees and moths visiting the flowers" of the cowslip, and then adds, "the same thing was found to occur in the primrose." ‡

Now this beautiful arrangement in Sir John Lubbock's idea whereby insects "*must effect*" cross-fertilisation in the primrose might be true in the case of the cowslip, but cannot be true in any way in the case of the primrose, as unfortunately for such a theory, neither bees, nor butterflies, nor any insects generally with a proboscis long enough to reach the nectar, are accustomed, as we have seen, to visit the primrose.

We are thus driven in the case of the primroses to smaller insects: to insects which must pass up and down the corolla, such as the thrips, for their supposed cross-fertilisation. But even of insects generally Darwin says: "It is surprising how rarely insects can be seen during the day visiting the flowers." § With this observation every one

---

* *Forms of Flowers*, p. 22.
† LUBBOCK: *Flowers and Insects*, p. 39.
‡ *Natural Selection*, p. 465.
§ *Forms of Flowers*, p. 36.

who has at all carefully noticed and examined the primrose flowers will agree. It is not only rare, as Darwin says, but it is a remarkable exception to see any insect except a thrips present on a primrose. During one year we gathered very considerably over a thousand primroses from more than a thousand different roots, and in different situations, as woods, and open hedge rows, and road sides, from March 17 to considerably past the middle of April, which we opened and examined, and we found besides the thrips only one small beetle, and one beetle caterpillar. But besides these primroses we observed thousands upon thousands of ungathered primroses, and yet that was all the living insect life excepting the thrips, and the one short-tongued bee (*Andrœna*) and the *Bombylius* found or seen upon them. Cross-fertilisation could not in any way therefore be effected by insects in the primrose.

Moreover, the thrips is so minute an insect, that the pollen of a single flower, on which, as far as we have been able to observe, it chiefly feeds, would amply supply the wants of many of those insects. Darwin allows that even the amount of pollen which the thrips would convey could have very little influence in causing any effectual fertilisation of the stigma. "A cross of this kind" (from a thrips) "does not produce any effect, or at most only a slight one." * Even the little influence which it might exercise would necessarily arise from its conveying the pollen of the flower, down which, or up which, it passed, to that flower's own stigma, and so would contribute to the self-fertilisation of that flower. Darwin allows the fact of such insects causing the self-fertilisation of these flowers. "Minute insects, such as thrips, which sometimes haunt the flowers, would be apt to cause the self-fertilisation of both forms; and this self-fertilisation would be much more apt to occur when it was visiting a short-styled form." †

Darwin says that he has "more than once seen a minute

---

* *Cross and Self-Fertilisation*, p. 22.

† *Forms of Flowers*, p. 23.

thrips with pollen adhering to its body fly from one flower to another flower of the same kind." * We are not astonished at the rarity of the occasions, as his words "more than once" indicate, on which he witnessed the thrips in flight. Yet in his examination of the flowers he must have seen hundreds of these tiny insects. Darwin, too, must have had keen eyesight to have followed the thrips on its way at all. We have never seen it fly. We have frequently tried it on the palms of our hands in the woods, and have brought it back from the woods with us, and provoked it to fly with a piece of grass or primrose stalk, but have never succeeded on any single occasion. It would only give a very minute leap of about ⅛ of an inch. This seems to be, as far as our experience goes, its usual habit. This habit necessarily would confine it, as a rule, to a single root, and so to a single form of the primrose. It would debar it, except on rarest occasions, from being an agent in cross-fertilisation.

In the short-styled form the anthers—as the flower stalk is, whilst in flower, naturally erect—are placed above the stigmas, and when the flowers are shaken by the wind, or disturbed by an insect, as the thrips, passing down the flower, or more particularly when the thrips is feeding on the pollen above—for they are found when the flower is gathered chiefly among the stamens—some portion of the pollen would be dislodged, and would drop down upon the stigmas below. "These stigmas are eminently liable," Darwin says, "to receive their own pollen, for when I inserted a bristle or other such objects in the corolla of this form, some pollen was almost invariably carried down and left on the stigma." † ‡

---

* *Cross and Self-Fertilisation*, p. 420.

† *Forms of Flowers*, p. 23.

‡ There is a minute difference in the size of the pollen grains in the two forms when examined under a micrometer. Darwin, from the case of *Linum*, and of other flowers, says: "These cases seem to prove that the difference in size between the grains in the two forms is not determined by the length of the pistil down which the tubes of the pollen grains have to grow. That with plants in general there is no close relationship between the size of the pollen grains and the length of the

In examining very considerably over five hundred stigmas of each kind, both of the long and short-styled forms, we found as a rule the pollen in the short-styled deposited on the top and upper half of the stigma; on the other hand, in the long-styled the pollen was in most cases deposited on the bottom and the lower half of the stigma. So much so was this the case that we could almost without fail (when the pollen was shed) decide by the position of the deposited pollen to which form the stigma belonged. Such distinctive difference generally in the position of the pollen on their respective stigmas would not have been seen if it had been deposited by insects.* Moreover, the anthers in both forms, but more particularly so in the short-styled form, as in the long-styled they are pierced and kept apart by the style passing through them, curve inwardly at the top toward the centre of the corolla tube, and with their triangular apices they form in the short-styled, when the pollen is ripe, in very many cases, an almost perfectly closed roof over the tube of the corolla below, so that the corolla is almost a

---

pistil is manifest." (*Forms of Flowers*, p. 250.) Yet Sir J. Lubbock to subserve the theory of cross-fertilisation in these heterostyled plants, and in spite of these statements and conclusions of Darwin, and without affording any proof against their correctness, seems to adopt the opinion of their relationship as probable. "The importance of this difference is probably due to the fact that each grain has to give rise to a tube which penetrates the whole length of the style, and the tube which penetrates the long-styled stigma must therefore be nearly twice as long as in the other." (*Flowers and Insects*, p. 40.) It might with equal or rather greater probability, from the above observations and conclusions of Darwin against the former, be said that this minute distinction in size and consequently in weight is in each case exactly suited to the position in which the heavier and the lighter grains of pollen stand relatively to their respective stigmas, the heavier over its stigma, and the lighter under its, so as to effect more assuredly the self-fertilisation of each. Might not also the minute difference in size and form be attributable merely to the fact that the stamens of the larger pollen grains are found in the short-styled form, where they are from their position fully exposed —in contrast to the other kind—to the sun and other atmospheric influences?

* In making such examination care must be taken in removing the corolla that no pollen falls upon the stigmas.

closed box with its contained stigma within. This is a most noticeable feature in the short-styled primrose. It would consequently be most exceptional for any foreign pollen to pass from the outside into the corolla of the short-styled. The anthers open on their inner and under surface into the corolla tube, and into it discharge their pollen.

If there were any validity in the idea so strongly pressed by Sir John Lubbock * after Darwin's † that Nature has in many cases made arrangements that *self-fertilisation should be prevented*, such an idea in this case is singularly inapplicable. Nature, indeed, would seem to be acting in wanton waywardness to trap the corolla tube with a close covering of anthers, with their hard backs facing outside; to place these anthers directly overhanging the stigma; to arrange that the anthers should burst inwardly, and that the pollen grains should be the heaviest of their kind; and yet that, with all these arrangements for self-fertilisation, other pollen for the full fertilisation of the stigma below should have to come from another flower and from another root; that it should have to pass the block of its own stigma; to travel to, and to pass through, the covering of the close-trapped box formed by the short-styled anthers when the pollen and stigma are mature, before it could ever reach the stigma of the short-styled primrose at all. Moreover, to make the waywardness of Nature in this case more complete, such a necessity would tend to bring about, from any failure in the transmission of the pollen, the sterilisation, and so the ultimate extinction of the form itself, and that, too, after such guarded arrangements to ensure its fertilisation. Nature is scarcely open to the charge of being guilty in her *natural* course of such "fantastic contrariness."

From all the above considerations we cannot see how it could be concluded otherwise than that the *short-styled primrose is purely self-fertilised.*

---

* *Flowers and Insects*, pp. 36–38; *Popular Natural History*, p. 122.

† *Forms of Flowers*, p. 49.

These short-styled primroses, moreover, Darwin shows are when growing naturally the most productive of the two forms.*

In face of this superior fertility of the purely self-fertilised short-styled form of primrose, we think that Darwin had no evidence to support his statement, but rather strong evidence against it, "that one kind of primula must unite with the other kind in order to produce full fertility."†

These conclusions which Darwin arrived at so mislead those who adopted them after him, that Mr. Wallace could write in reference to the results of such experiments in the case of the primrose, the following sentence: "The meaning and use of these different forms was quite unknown until Darwin discovered first, that primroses are absolutely barren if insects are prevented from visiting them, and then, what is still more extraordinary, that each form is almost sterile when fertilised by its own pollen." ‡

Mr. Wallace then adopts the exposition of Darwin which we have already quoted above from Sir John Lubbock, and accounts for the superior fertility of the short-styled to the long, by saying that "whereas the long-styled plants might often be fertilised by their own form, the *short-styled* must be all fertilised by the pollen of the other." Now such an explanation is absolutely contradicted by the natural facts in reference to the short-styled flowers.

The long-styled primroses, on the other hand, though chiefly self-fertilised, as we have seen, by the general position of the pollen on the bottom and the lower half of their stigmas, would yet be slightly more exposed to cross-fertilisation by the wind on account of the exsertion of their stigma from the corolla tube by the pollen of the short-styled, whose anthers are also generally exserted from their corolla. The more papillose character of the long-styled form would also slightly conduce to such cross-fertilisation.

Whatever may be the cause of the superiority of the

---

* *Forms of Flowers*, p. 36. † *Ibid*, p. 29.
‡ *Darwinism*, p. 157.

short-styled form, as Darwin found in his examination of the flowers, in productiveness to the other in number of seeds, both kinds of primroses, whether short-styled or long-styled, though both are quite unvisited by bees or insects for cross-fertilisation, are each more productive than the cowslips, which are visited by humble and other bees, and so are in a measure subject to cross-fertilisation. "Both the long-styled and short-styled forms of primroses," Darwin says, "when naturally fertilised, on an average yield many more seeds per capsule than the cowslip, namely in the proportion of one hundred to fifty-five." *

Thus the cross-fertilised cowslip is surpassed by both kinds of primroses in productiveness, and still more surpassed by that form of primrose, the short-styled, which is least subject, if at all, to cross-fertilisation.

We see from the above instances that Darwin has no ground for his statement, as far at least as it bears upon the primrose, except that which his own misleading net experiments afforded him, "that the superiority of a 'legitimate' over an 'illegitimate (in Darwin's application of those terms) union' admits of not the least doubt." † ‡

---

* *Forms of Flowers*, p. 57.

† *Ibid*, p. 28.

‡ When a stigma is fertilised by its "own form" pollen, Darwin calls this union "illegitimate"; when fertilised by the pollen of a flower of a different form, he calls this union "legitimate." Surely when Nature herself unites pollen and stigma in the same corolla, that is Nature's "legitimate union." To call it "illegitimate union" is merely subserving an unproven theory. Moreover, the origin and application of these terms in this manner arose from Darwin's net experiments (*Forms of Flowers*, p. 26), by which he was misled; experiments which, like his own application of the above terms, traversed in their result the absolute arrangements of Nature. Nor have we perhaps arrived at that perfect and complete knowledge in this matter, as to venture to appear wiser than Nature herself, and so divorce what she has naturally and so "legitimately" joined together. Such forced transpositions in terminology of the arrangements of Nature should we think, for the sake of clearness and to avoid all appearance of subserving a theory, be most carefully eschewed. For Darwin to set up as judge in Nature's divorce court, and to give a decision for divorce, when the evidence against the legitimacy of the union of the occupants of the same corolla has not yet

Darwin's idea also that "the individual plants of the primrose and cowslip, and of the other members of the *Primulaceæ* are divided into two sets, which cannot be called distinct sexes (for they each have their stamens and pistils), yet they are to a certain extent severally distinct for they require reciprocal union for perfect fertility," * the short-styled primrose adequately and fully disproves.

We see thus that the *primrose* holds a *special position* in reference to several theories of Darwin about heterostyled plants, which except for it could scarcely be disproved, or shown to be built on misleading net experiments. The same could not be shown, as far as we are aware, by any other member of the *Primulaceæ*, nor by any other heterostyled flower.

The primrose disproves the following theories of Darwin: "that every known heterostyled plant depends on insects for fertilisation, and not on the wind" ;† that "heterostyled flowers need intercrossing between different forms for perfect fertility" ;‡ that "flowers which are self-fertilised are less productive than flowers of the same order subjected to cross-fertilisation" ;§ and, lastly, that "the heterostyled flowers stand in the reciprocal relation of different sexes to each other."‖

These cases of the cowslips and primroses support the eminent botanist Axell's opinion that cross-fertilisation under equal conditions in a state of nature is rather injurious than beneficial to the fertilisation of flowers. Axell allows the beneficial influence of cross-fertilisation by bees and insects as a secondary agency. Such secondary agency doubtless is constantly occurring. The pollen of a flower might be imperfectly developed and imperfectly matured from various causes; from the position of the flower in

---

been thoroughly sifted, much less established, and when many a primrose strongly testifies to the legitimacy of their union, transgresses a little, we think, the bounds of modesty.

* *Forms of Flowers*, p. 28.

† *Cross and Self-Fertilisation*, p. 250.

‡ *Forms of Flowers*, p. 28. § *Ibid*, p. 28. ‖ *Ibid*, p. 2.

field or hedge, on stem or branch, as being more exposed to injury from wind or weather; from its growing under any shade, and so deprived more or less of the solar rays or dew; from the character of the soil; or from the flower's own internal defective growth. From all these and many other accidental and natural causes this might constantly arise. In such cases pollen from flowers more favourably situated, and consequently more healthy and vigorous in growth, and so, with anthers more matured, would, by the conveyance of bees and other Hymenoptera and butterflies, most beneficially act. In such cases it would exert what Darwin called a "prepotent" influence over the legitimate influence of the pollen of its own flower, but its "prepotency" would be usually limited to such weaker cases amongst the flowers.*

---

* We do not ourselves believe that the floral world in its ordinary course is utterly dependent (as we have been assured by some writers) upon insects, but rather, that it is by the insects through their seeking for food, beneficially assisted. Such a statement as the following by Sir John Lubbock, "It is not too much to say that if, on the one hand, flowers are in many cases necessary to the existence of insects; insects, on the other hand, are still more indispensable to the very existence of flowers" (*Flowers and Insects*, p. 5), seems to us to diverge very far indeed from and to reverse the facts as found in Nature. All purely nectar-feeding insects, as bees, fossores (diggers), butterflies, and moths, which are the acknowledged chief agents in effecting cross-fertilisation, would die out in less than a single year if they had no food provided for them by the flowers. The inconspicuous flowers generally are acknowledged by all to be self-fertilised. Nor do we see any sufficient reason for placing the more conspicuous flowers—many of which, as well as the primroses, are quite unvisited by bees, and very many others only very partially visited by them—in a different category from the inconspicuous as to their general independence of insects for their existence. The reasons alleged, which we do not here enter upon, are in many cases very weak and very unconvincing. Moreover, Mr. Wallace tells us, "An immense variety of plants are habitually self-fertilised, and their numbers probably exceed those which are habitually cross-fertilised by insects." (*Darwinism*, p. 321.) Again, Mr. Wallace says: "As opposed to the theory that there is any absolute need for cross-fertilisation, it has been urged by Mr. Henslow and others that many self-fertilised plants are exceptionally vigorous, while most plants of world-wide distribution are self-fertilised." (*Darwinism*, p. 323.)

But it might be objected that Darwin, in his experiments detailed in his volume *Cross and Self-Fertilisation of Flowers*, has shown that seedlings from cross-fertilised flowers are more vigorous than seedlings raised from self-fertilised ones. On this subject we do not propose to enter at any length, as it is beyond the purpose of our present article, more than merely stating our reason for considering the method of Darwin's experiments there detailed, renders questionable or rather, in our opinion, vitiates, and renders untrustworthy the results and conclusions at which Darwin arrived.

Now, the objection in this case is not so much from the net itself, for the self-fertilised and the cross-fertilised were both under a net. It is in the method adopted in these experiments which, in our view, vitiates the results. "My experiments were tried in the following manner," Darwin says. "A single plant, if it produced a sufficiency of flowers, was placed under a net, stretched on a frame. On the plants thus protected several flowers were marked and were fertilised with their own pollen; and an equal number on the same plant were at the same time crossed with pollen from a distinct plant; the crossed flowers had not their anthers removed." In these experiments consequently the cross-fertilised flowers had a great advantage. The self-fertilised flowers had only their own pollen, and that developed under a net, to fertilise them; but the cross-fertilised had not only their own pollen—for, as we have seen above, their anthers were not removed—but pollen from another plant applied to them as well, and that too grown naturally outside the net, as Darwin wished by leaving the flowers their own pollen, and at the same time crossing them with other pollen naturally grown "to make the experiments as like as possible to what occurs under nature with plants fertilised by the aid of insects."*

The cross-fertilised had consequently two sets of pollen to choose between, and whichever happened to be most in its

* *Cross and Self-Fertilisation*, pp. 10-11.

prime that would exercise a "prepotent" influence in the fertilisation. But the self-fertilised flower had no other pollen but its own to depend upon, and none to choose between. It must be its own pollen, and that developed under a net, which must fertilise it, or none at all. Such a system of experiments evidently gave to the cross-fertilised flowers a very great advantage over the self-fertilised ones, and consequently a very great advantage to the healthy maturing of its seeds, and to the growth and vigour of the seedlings raised from them. It is no wonder under such conditions that the "seedlings of the self-fertilised" were in comparison with the others "somewhat weakly in constitution." It is this inequality of conditions under which the seeds, whence the seedlings were produced, which in our opinion vitiates, and renders scientifically untrustworthy the results which Darwin obtained.

We are therefore quite unable to accept Darwin's conclusions deduced from experiments conducted under such a method, as that expressed in his last chapter, "General Results," of *Cross and Self-Fertilisation of Plants*. "The first and most important of the conclusions which may be drawn from the observations given in this volume," Darwin says, "is that generally cross-fertilisation is beneficial, and self-fertilisation often injurious. The truth of these conclusions is shown by the difference in height, weight, constitutional vigour, and fertility of the offspring from crossed and self-fertilised flowers." *

Now the primrose singularly enough is actually never mentioned nor alluded to in this volume, though it occupies so important a position, as we have seen, in his *Forms of Flowers*. This is a very singular omission indeed, as not only the cowslip is introduced in these experiments, and in a dozen different allusions, but all the other principal primulas as well—as elatior, Sinensis, Scotica, &c.

But notwithstanding that omission Darwin in that volume makes this general assertion concerning the *Primulaceæ:*

---

* *Cross and Self-Fertilisation*, p. 439.

"The *Primulaceæ* seem eminently liable to suffer in fertility from self-fertilisation." * The primrose, as we have already seen, as a test flower, holds a special position in reference to the question of cross and self-fertilisation, and absolutely contravenes for itself, and equally in our opinion from their analogous formation contravenes for its Order, this aspersion upon their natural and independent productivity. Insects may visit them for their nectar, but that is no proof whatever, in face of the primrose, that any beneficial influence in fertilisation under ordinary conditions is derived from their visits. Doubtless had Darwin included the primrose among those which he experimented upon as recorded in his volume of *Cross and Self-Fertilisation*, he would have caused that flower, under the influence of the net (or greenhouse), to lose its natural virility, and would have formed the same conclusion about it as he does about the Order of *Primulaceæ*, "that it was eminently liable to suffer from self-fertilisation."

The unnatural results in the case of the cowslips and primroses under a close-meshed net as those given in the preceding pages—first, the long-styled flowers being more productive in seeds than the short-styled ones when they are each cross-fertilised; and, secondly, the same result occurring when they are each fertilised by their "own form" pollen; and next the short-styled being the most sterile of all, when so fertilised by its "own form" pollen, seem consequently quite to invalidate the value of experiments conducted under such a method, and to render all conclusions in respect to the heterostyled *Primulaceæ* drawn from such experiments eminently unsatisfactory and even scientifically untrustworthy. Nor can they fail to render similar conclusions drawn from exactly similarly conducted experiments on the other heterostyled dimorphic and trimorphic forms, such as *Lythrum salicaria*, equally questionable, and equally untrustworthy.

We are consequently very far indeed from accepting

* *Forms of Flowers*, p. 319.

Mr. Wallace's absolute dictum: "There is thus the clearest proof (!) that these complex arrangements" (in the trimorphic plants) "have the important end of securing a more abundant and more vigorous offspring."*

Why the two forms of the cowslip and primrose exist in nature is distinctly, by the above facts, not solved by the idea of Darwin, that it was "to ensure cross-fertilisation of distinct plants"; † nor is it solved by the alternative form in which Sir J. Lubbock expresses the same idea that "this condition of the heterostyled *Primulaceæ* is one of the principal modes by which self-fertilisation is prevented." ‡

The distinction of the two forms has been considered as Darwin allows "as a case of mere variability." § The probability that it is nothing more than a mere variation seems necessarily to arise from what has previously been said, and from the following additional facts.

First, equal-styled forms are found in species of Primulas; in such forms the anthers and styles are of equal lengths in the same flowers. Darwin says of the Primulas in general "some species are home-styled; that is, they exist only under a single form," ‖ and of the cowslip that "with this species and several others, equal-styled varieties sometimes appear." ¶ Mr. Scott, of Edinburgh, sent Darwin a cowslip where the stigma and anthers stood on the same level and "the flowers were highly self-fertile when insects were excluded." ** Of the primrose, from what Darwin met with in his experiments, he says, "It is therefore probable that an equal-styled form of the primrose might be found, and I have received two accounts of plants apparently in this condition." †† But in addition, the four following Primulas produce equal-styled forms: *P. Sinensis*, *auricula*, *farinosa*, and elatior (Oxlip). ‡‡ Of the first, *Sinensis*, Darwin says, "it is often equal-styled." §§

---

* *Natural Selection*, p. 466. † *Forms of Flowers*, p. 30.
‡ *Flowers and Insects*, pp. 36-38.
§ *Forms of Flowers*, p. 14. ‖ *Ibid*, p. 49. ¶ *Ibid*, p. 32.
** *Cross and Self-Fertilisation*, p. 235.
†† *Forms of Flowers*, p. 225. ‡‡ *Ibid*, p. 273. §§ *Ibid*, p. 38.

In our own examination of over five hundred flowers of the long-styled form of primrose, each gathered from a different root, we found styles of every variety of length. Some exceeding the length of the corolla tube, others halfway between the top of the tube and the anthers below; eight shortened styles touching the top of the anthers with the base of the stigmas, and eight perfectly healthy in style and ovarium actually below the anthers placed in the middle of the corolla. *

The same variation in the length of style was also found among five hundred specimens of the short-styled form, gathered from different roots. In six instances the stigmas all but touched the roots of the anthers at the corolla mouth. Every variation in length was found between such long ones, to, in one instance, an almost sessile stigma.

Secondly, the one form will produce the other form. "Seeds from the short-styled form of cowslip fertilised by pollen of the same form, produced 14 plants, which consisted of 9 short-styled and 5 long-styled plants."†

And again, 162 plants were raised from long-styled cowslips fertilised by their "own-form" pollen, and these consisted of 156 long-styled and 6 short-styled plants.‡ The Primula auricula produced from the short-styled form, fertilised from its "own-form" pollen, 25 long-styled and 75 short-styled offspring.§ "Dr. Hildebrand raised from the long-styled form of *P. Sinensis* fertilised by its 'own-

---

* In thirty-four instances we found the stigmas involved in the midst of the anthers; but in these cases both the style and ovarium were invariably discoloured and unhealthy. The latter—the ovarium—wrinkled and dark-coloured. The stigmas in these cases seem to have been arrested in their progression towards the top of the corolla by the anthers—which, as we have pointed out above, curve inwardly at their top—as these styles were generally bent and distorted. They occurred chiefly in the month of March, when perhaps the frosty nights affected them. We also found a few unhealthy stigmas and ovaria, as well as the above healthy ones, below the anthers placed in the middle of the corolla.

† *Forms of Flowers*, p. 228. ‡ *Ibid*, Table xxxvi., p. 269.

§ *Ibid*, p. 269.

form' pollen 17 plants, of which 14 were long-styled and 3 short-styled. From a short-styled plant similarly fertilised by its own pollen he raised 14 plants, of which 11 were short-styled and 3 long-styled."* †

Lastly, the two forms have been found on the same plant of a Primula, and even the three forms—long-styled, short-styled and equal-styled. Herr Breitenbach found on one hundred and ninety-eight plants of the Primula elatior (Jacq.)—the Oxslip—growing wild on the banks of the Lippe, a tributary of the Rhine, 894 flowers, of which "467 were long-styled flowers, 411 short-styled, and 16 equal-styled. In eighteen cases the same plant produced both long-styled and short-styled, or long-styled and equal-styled flowers; and in two out of the eighteen cases long-styled, short-styled, and equal-styled flowers."‡

From all the above facts it seems impossible to come to any other conclusion concerning the heterostyled *Primulaceæ* than that the two forms are mere variations. Nature, from the two last instances, markedly herself decides, we might say, the question. This being so, in the case of the *Primulaceæ*, we may assuredly infer by analogy, supported as it is by the facts quoted above in the last note concerning *Polygonum fagopyrum* and *Lythrum salicaria*, that it applies equally also to all the other heterostyled dimorphic and trimorphic plants as well.

---

* *Forms of Flowers*, p. 217.

† The production of one form by the other extends to other heterostyled dimorphic and trimorphic plants. The dimorphic *Polygonum fagopyrum* is a remarkable instance of it. The short-styled form fertilised by its "own form" pollen produced 13 long-styled offspring, and 20 short-styled ones (*Forms of Flowers*, Table xxxvi., p. 269). The mid-styled form of the trimorphic *Lythrum salicaria* fertilised by pollen from longest stamens of short-styled produced all three forms, 14 long-styled, 8 mid-styled, and 18 short-styled offspring (Table xxxvii., p. 270). From a short-styled form of *Lythrum salicaria*, grown in the open air, Darwin raised 12 plants, 1 long-styled, 4 mid-styled, and 7 short-styled. I will only add, Darwin says, "that any single plant of a trimorphic species in a state of nature produces all three forms" (*Forms of Flowers*, p. 372).

‡ *Forms of Flowers*, p. 34.

It is not possible from the above considerations in reference to the method of Darwin's experiments, and especially also from the above case of the primrose, to avoid the conclusion that Darwin has not established his theory that cross-fertilisation is necessary to the full fertility of flowers. On the contrary, we are of opinion that the primrose gives strong confirmatory evidence to Axell's view, that under *natural* and equal conditions self-fertilisation of flowers is both the *legitimate* fertilisation, and the most productive.

A FIELD NATURALIST.