

## THE FLOWER GARDEN.

### MR. DARWIN ON PRIMROSES, COWSLIPS, AND OXLIPS.

As much confusion still exists among cultivators as to the relationship of these plants and the forms of hybrids that spring from them, we have thought it well to reprint from the *Journal of the Linnean Society* the more important points in Mr. Darwin's remarkable essay on the subject, in the hope that it may serve to clear up a matter on which many of our correspondents seem to be interested.

The claim (says Mr. Darwin) of the above three forms (namely, the common Cowslip, Primrose, and Bardfield Oxlip) to be ranked as distinct species has been discussed at greater length than that of almost any other plants. Linnæus considered them varieties, as do some of the most distinguished botanists at the present day; whilst others who have carefully studied these plants do not doubt that they deserve to be ranked as distinct species. The following observations show, I think, that the latter view is correct; and they further show that the common Oxlip, which is found in most parts of England, is a hybrid between *P. veris* and *vulgaris*. The Cowslip differs so conspicuously in general appearance from the Primrose, that nothing need here be said with respect to their external characters. But some less obvious differences deserve notice. As both species are dimorphic, their complete fertilisation depends on insects. They emit a different odour. The Primrose, when legitimately fertilised, produces on an average many more seeds than the Cowslip, namely, in about the proportion of 100 to 55. It is a more important distinction that both the long-styled and short-styled forms of the Primrose, when illegitimately fertilised with their own pollen, are much more fertile than the corresponding forms of the Cowslip when similarly treated. When long-styled plants of the Cowslip are protected by a net, so that they cannot be visited by insects, they yield no seed, as I found to be the case with no less than eighteen plants; and the short-styled form is only a little less sterile. The long-styled Primrose, on the other hand, when similarly protected, produces a considerable number of capsules, of which twenty-three contained on an average 19·2 seeds: the short-styled form produces under these circumstances fewer capsules, of which fourteen contained on an average only 6·2 seeds. This great difference in the fertility of the Cowslip and Primrose, when all insects which are capable of exclusion are excluded, depends in part on the Primrose being innately much more self-fertile than the Cowslip, and in part on the former being much frequented by thrips, which, dusted with pollen, may often be seen crawling within the flowers.

The Primrose, as everyone knows, flowers a little earlier in the spring than the Cowslip, and inhabits slightly different stations and districts. The Primrose generally grows on banks or in woods, whilst the Cowslip is found in more open places. The geographical range of the two forms is different. Dr. Bromfield remarks that "the Primrose is absent from all the interior region of northern Europe, where the Cowslip is indigenous." In Norway, however, both plants range to the same degree of northern latitude. The Cowslip and Primrose, when reciprocally crossed, are far from fertile. Gartner crossed twenty-seven flowers of *P. vulgaris* with pollen of *P. veris*, and obtained sixteen capsules; but these did not contain any good seed. He also crossed twenty-one flowers of *P. veris* with pollen of *P. vulgaris*; and now he got only five capsules, containing seed in a still less perfect condition. Gartner knew nothing about dimorphism; and his complete failure may perhaps be accounted for by his having crossed together the same form of the Cowslip and Primrose; for this would have been an illegitimate as well as a hybrid union, and would consequently have been sterile in the highest degree. I was rather more fortunate in my trials: I crossed legitimately three flowers on the long-styled and three on the short-styled Cowslip, with pollen from the opposite form of the Primrose, and obtained one capsule containing the large number of forty-eight apparently good seeds. I crossed on the same plant six flowers illegitimately, with pollen from the corresponding form of the Primrose, and obtained three capsules, containing seeds so poor that there was no chance of their germination. I likewise fertilised twelve flowers of the Primrose, consisting of both forms, with pollen from both forms of the Cowslip, and eighteen flowers in the same manner with pollen of the Polyanthus. I should here state that the Polyanthus is a variety of the Cowslip, as I infer from their mongrel offspring being perfectly fertile *inter se*; and as there seems to be no essential difference in the action of Cowslip and Polyanthus-pollen on the Primrose, the results are here run together. Eight long-styled and seven short-styled flowers of the Primrose were legitimately crossed with pollen of the Cowslip and Polyanthus, and, together, they yielded six capsules, containing on an average thirty-seven

seeds, some of fine quality and some only moderately good. The pure Primrose, when legitimately fertilised by pollen from the Primrose, yields an average of almost exactly double this number of seeds, viz., seventy-one. Lastly, eight long-styled and seven short-styled flowers of the Primrose were illegitimately fertilised by pollen of the Cowslip and Polyanthus, and, together, they yielded only four capsules, containing on an average only thirteen seeds, some good and some poor. The Primrose, when illegitimately fertilised by pollen from the Primrose, yields an average of about forty-four seeds. We thus see that a cross between the same forms of the Primrose and Cowslip is far more sterile than a cross between the opposite forms. The Primrose, especially the short-styled form, when fertilised by the Cowslip, is less sterile, as Gartner likewise observed, than the Cowslip when reciprocally fertilised by the Primrose. I sowed the seeds produced from the several foregoing crosses; but none germinated except those from the short-styled Primrose fertilised by the pollen of the Polyanthus; and these seeds were the finest of the whole lot. I thus raised six plants, and compared them with a group of wild Oxlips, evidently produced from the same capsule, which I had transplanted into my garden. One of these wild Oxlips produced slightly larger flowers than the others, and this one was identical in every character (in foliage, flower-peduncle, and flowers) with my six plants, excepting that the flowers in the latter were tinged of a dirty red colour.

We have now seen that the Cowslip and Primrose cannot be crossed either way except with considerable difficulty, that they differ conspicuously in external appearance, that they differ in certain curious physiological characters, that they inhabit slightly different stations, and range differently. Hence those botanists who rank these plants as varieties ought to be able to prove that they are not as well fixed in character as are most species; and the evidence in favour of such instability of character does appear at first very strong. It rests, first, on statements made by several competent observers that, from seeds of the same plant, they have raised Cowslips, Primroses, and Oxlips; and, secondly, on the frequent occurrence in a state of nature of plants presenting every intermediate gradation between the Cowslip and Primrose.

The evidence, however, on the first head is of little value; for, dimorphism not being formerly understood, the seed-bearing plants were in no instance protected from the visits of insects; and there would be almost as much risk of an isolated Cowslip, or of several Cowslips, if consisting of the same form, being crossed by a neighbouring Primrose and producing Oxlips, as of one sex of a dioecious plant, under similar circumstances, being crossed by the opposite sex of an allied and neighbouring species. Mr. H. C. Watson, a critical and most careful observer, made many experiments by sowing the seeds of Cowslips and of various kinds of Oxlips, and arrived at the following conclusion, namely, "that seeds of a Cowslip can produce Cowslips and Oxlips, and that seeds of an Oxlip can produce Cowslips, Oxlips, and Primroses." This conclusion harmonizes perfectly with the view that in all cases, when such results have been obtained, the unprotected Cowslips have been crossed by Primroses, and the unprotected Oxlips by either Cowslips or Primroses; for in this latter case we might expect, by the aid of reversion, which notoriously comes into powerful action with hybrids, that both parent forms in appearance pure, as well as many intermediate gradations, would be produced. Nevertheless the two following statements offer considerable difficulty. The Rev. Professor Henslow raised from seed of a Cowslip growing in his garden various kinds of Oxlips and one perfect Primrose; but a statement in the same paper, perhaps, throws light on this anomalous result. Professor Henslow had previously transplanted into his garden a Cowslip, which completely changed its appearance during the following year, and now resembled an Oxlip. Next year again it changed its character, and produced, in addition to umbels, a few single-flowered scapes, bearing flowers somewhat smaller and more deeply coloured than those of the common Primrose. From what I have myself observed with Oxlips, I cannot doubt that this plant was an Oxlip in a highly variable condition, almost like the famous *Cytisus Adami*. This variable plant was propagated by offsets, which were planted in different parts of the garden; and if Professor Henslow took, by mistake, seeds from one of these plants, especially if it had been accidentally crossed by a Primrose, the result would be quite intelligible. Another case is still more difficult to understand—Dr. Herbert raised, from seed of a highly-cultivated red Cowslip, Cowslips, Oxlips of various kinds, and a Primrose. This case, if accurately recorded, is explicable only on the improbable assumption that the red Cowslip was not of pure parentage. With plants of many kinds, when crossed, one species or variety is sometimes strongly prepotent over the other; and instances are known of one variety crossed by another producing offspring which in certain characters, as in colour, hairiness, &c., have proved identical with the pollen-bearing parent, and quite dissimilar to the mother-plant;

but I do not know of any good instance of the offspring of a cross perfectly resembling, in a number of important characters, the father alone. Hence we cannot admit that a pure Cowslip crossed by a Primrose would ever produce a Primrose in appearance pure. Although the facts given by Dr. Herbert and Professor Henslow are difficult to explain, yet until it can be shown that a Cowslip or a Primrose, carefully protected from insects, will occasionally give birth to at least Oxlips, the cases hitherto recorded have little weight in leading us to admit that the Cowslip and Primrose are varieties of one and the same species.

Negative evidence is of little value; but the following facts may be worth giving:—Some Cowslips which had been transplanted from the fields into a shrubbery were again transplanted into highly-manured land. In the following year they were protected from insects, artificially fertilised, and the seed thus procured was sown in a hotbed. The young plants were afterwards planted out, some in very rich soil, some in stiff poor clay, some in old peat, and some in pots in the greenhouse; so that these plants, 765 in number, as well as their parents, were subjected to diversified and unnatural treatment; but not one of them presented the least variation except in size—those in the peat growing to almost gigantic dimensions, and those in the clay being much dwarfed. I do not, of course, doubt that Cowslips exposed during several successive generations to changed conditions would vary, and that this would occasionally take place in a state of nature. Moreover, from the law of analogical variation, the varieties of any one species of *Primula* would probably in some cases resemble other species of the genus: thus I raised a red Primrose from seed from a protected plant, and the flowers, though still resembling those of the Primrose, were borne during one season on a long foot-stalk like that of a Cowslip.

With regard to the second class of facts in support of the Cowslip and Primrose being ranked as mere varieties (namely, the well-ascertained existence in a state of nature of numerous linking forms), if it can be shown that the common wild Oxlip, which stands exactly between the Cowslip and Primrose, resembles in sterility and other essential respects a hybrid plant; and if it can further be shown that the Oxlip, though in a high degree sterile, can be fertilised by the pure parent species, thus giving rise to still finer gradational links—then the presence of such forms in a state of nature ceases to be an argument of any weight in favour of the Cowslip and Primrose being varieties, and becomes, in fact, an argument on the other side. The hybrid origin of a plant in a state of nature can be recognised, first, by its occurrence only where both presumed parent forms exist, or have recently existed; and this holds good, as far as I can discover, with the Oxlip; but the *P. elatior* of Jacq., which, as we shall presently see, constitutes a distinct species, must not be confounded with the common Oxlip. Secondly, by the supposed hybrid plant being nearly intermediate in character between the two parent species, and especially by its resembling hybrids artificially made between the same two species. Now the Oxlip is intermediate in character, and is identical in every respect, except in the colour of the corolla, with hybrids artificially produced between the Primrose and the Polyanthus, which latter is a variety of the Cowslip. Thirdly, by the supposed hybrids being more or less sterile when crossed *inter se*: but, to try this fairly, two distinct plants of the same parentage should always be crossed; for some pure species are more or less sterile with pollen from the same individual plant; and, in the case of hybrid dimorphic plants, the opposite forms should be crossed. Fourthly and lastly, by the supposed hybrids being much more fertile when crossed with either pure parent-species than when crossed *inter se*, but still not as fully fertile as the parent species.

From having many experiments in hand, I did not sow the seed obtained by reciprocally crossing Primroses and Cowslips with the Oxlips, and I now regret this; but I ascertained a more interesting point, namely, the character of the offspring from Oxlips in a state of nature growing near both Primroses and Cowslips. The Oxlips were the same plants which were subsequently transplanted and experimented on. From seed thus obtained, eight plants were raised, which, when they flowered, might have been mistaken for pure Primroses; but on close comparison the eye in the centre of the corolla was seen to be of a darker yellow, and the peduncles more elongated. As the season advanced, one of these plants threw up two naked scapes, seven inches in height, which bore umbels of flowers of the same character as before. This fact led me to examine the other plants after they had flowered and were dug up; and I found in all that the flower-peduncles sprung from an extremely short common scape, of which no trace can be found in the pure Primrose. Hence these plants are beautifully intermediate between the Oxlip and the Primrose, inclining rather towards the latter; and we may safely conclude that the parent Oxlips had been fertilised by the surrounding Primroses.

From the various facts now given, there can be no doubt that

the common Oxlip is a hybrid between the Cowslip (*P. veris*, Brit. Fl.) and the Primrose (*P. vulgaris*, Brit. Fl.), as has been surmised by several botanists. It is probable that Oxlips may be produced either from the Cowslip or the Primrose as the seed-bearer, but oftentimes from the latter, as I judge from the nature of the stations in which Oxlips are generally found, and from the Primrose when crossed by the Cowslip being more fertile than the Cowslip by the Primrose. The hybrids themselves are also rather more fertile with the Primrose than with the Cowslip. Whether the Cowslip or the Primrose be the seed-bearing plant, it is probably fertilised by the opposite form of the other species; for we have seen that legitimate hybrid unions are more fertile than illegitimate hybrid unions. Moreover a friend in Surrey found that twenty-nine Oxlips which grow in the neighbourhood of his house consisted of thirteen long-styled and sixteen short-styled plants; now, if the parent plants had been illegitimately united, either the long or short-styled form would have greatly preponderated in number. The case of the Oxlip is interesting; for hardly any other instance is known of a hybrid spontaneously arising in such large numbers over so wide an extent of country. The common Oxlip (not the *P. elatior* of Jacq.) is found almost everywhere throughout England where the Cowslip and Primrose both grow. In some districts, as I have seen near Hartfield in Sussex and in parts of Surrey, specimens may be found on the borders of almost every field and small wood. In other districts the Oxlip is comparatively rare; near my own residence I have not seen during the last twenty-five years more than five or six plants or groups of plants. It is difficult to conjecture what is the cause of this difference in number. It is almost necessary that a single plant, or several plants of the same form, of one parent species should grow near the opposite form of the other species; and it is further necessary that both species should be frequented by the same kind of moth. It is possible that such moths do not everywhere abound.

Finally, as the Cowslip and Primrose differ in the various characters before specified, as they are in a high degree sterile when intercrossed, as there is no trustworthy evidence that either plant, when uncrossed, has given birth to the other plant or to any intermediate form, and as the intermediate forms which are often found in a state of nature have been shown to be more or less sterile hybrids of the first or second generation, we must for the future look at the Cowslip and Primrose as good and true species.

#### PRIMULA ELATIORE, JACQ., OR BARDFIELD OXLIPI.

This *Primula* is found in England only in two or three of the eastern counties; and on the continent it has a somewhat different range from that of the Cowslip and Primrose. It inhabits districts where neither of these species live. In general appearance it differs so much from the common Oxlip, that no one accustomed to see both in the living state would afterwards confound them; but there is scarcely more than a single character by which they can be distinctly defined, namely, the linear-oblong capsule equalling the calyx in length. The capsules, when mature, owing to their length, differ conspicuously from those of the Cowslip and Primrose. Plants propagated by seed in a garden during twenty-five years have kept constant, excepting that in some cases the flowers varied a little in tint and size. Nevertheless Mr. Hewett C. Watson and Dr. Bromfield state that "exceptional instances to all the characters, taken singly, by which this plant is distinguished from *P. vulgaris* and *veris*," may be occasionally detected; it remains to be discovered whether these intermediate forms are not hybrids between *P. elatior* and *veris*, which often grow together. With respect to differences in function, both the long and short-styled forms of *P. elatior* are more sterile when fertilised by their own pollen than the corresponding forms of the Cowslip and Primrose when similarly fertilised.

Mr. H. Doubleday, who I believe first called attention to the existence of the Bardfield Oxlip in England, kindly sent me several living plants, which I subjected to trial for the sake of ascertaining whether they differed in their reproductive power from the common Oxlip. I did not think it worth the time and labour to ascertain whether the Bardfield Oxlip, when crossed with the Cowslip and Primrose, behaved like a distinct species; for if it can be clearly proved not to be a hybrid, and if the Cowslip and Primrose are specifically distinct, I presume that no one will any longer doubt that the *P. elatior* is likewise distinct.

Finally, although we may feel confident that *Primula veris*, *vulgaris*, and *elatior*, as well as the other species of the genus, are all descended from some primordial form, yet, from the facts which have been given, we may conclude that they are now as fixed in character as are very many other forms which are universally ranked as species. Consequently they have as good a right to receive distinct specific names as have, for instance, the ass, quagga, and zebra.