

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

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

[Read March 19, 1868.]

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

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

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

serve notice. As both species are dimorphic, their complete fertilization depends on insects. They emit a different odour. The Cowslip is habitually visited during the day by humblebees (viz. *Bombus muscorum* and *hortorum*, and perhaps by other species) and at night by moths, as I have seen with the *Cucullia*. The Primrose is never visited (and I speak after many years' observation) by the larger humblebees, and only rarely by smaller kinds; hence its fertilization depends almost exclusively on moths. Consequently the nectar in these two plants must differ much; for there is nothing in the structure of the flowers which can determine the visits of different insects. The utmost difference in the colour of the corolla does not in the least prevent, as I have often observed, a bee from recognizing the varieties of any species which it may at the time be visiting. The Primrose, when legitimately fertilized, 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 fertilized 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,

* Phytologist, vol. iii. p. 694.

however, both plants range to the same degree of northern latitude*.

The Cowslip and Primrose, when reciprocally crossed, are far from fertile. Gärtner † crossed 27 flowers of *P. vulgaris* with pollen of *P. veris*, and obtained 16 capsules; but these did not contain any good seed. He also crossed 21 flowers of *P. veris* with pollen of *P. vulgaris*; and now he got only 5 capsules, containing seed in a still less perfect condition. Gärtner 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 48 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 fertilized 12 flowers of the Primrose, consisting of both forms, with pollen from both forms of the Cowslip, and 18 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-

* H. Lecoq, 'Géograph. Bot. de l'Europe,' tom. viii. (1858) pp. 141, 144. See also Ann. & Mag. of Nat. Hist. ix. (1842) pp. 156, 515. Also Boreau, 'Flore du centre de la France,' 1840, tom. ii. p. 376. With respect to the rarity of *P. veris* in western Scotland, see H. C. Watson, 'Cybele Britannica,' ii. p. 293.

† Bastarderzeugung, 1849, p. 721.

‡ Mr. Scott has discussed this subject (Proc. Linn. Soc. viii. Bot. (1864) p. 103) and has arrived at a different conclusion; but I do not think sufficient experiments were tried to justify his conclusions. The results of sterile crosses are always liable to much fluctuation. Pollen from the Cowslip at first appears rather more efficient on the Primrose than that of the Polyanthus; for 12 flowers of both forms of the Primrose, fertilized legitimately and illegitimately by the Cowslip, gave 5 capsules, containing 32.4 seeds; whilst 18 flowers similarly fertilized by Polyanthus-pollen yielded only 5 capsules, containing only 22.6 seeds. On the other hand, the seed produced by the Polyanthus-pollen was much the finest of the whole lot.

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 37 seeds, some of fine quality and some only moderately good. The pure Primrose, when legitimately fertilized by pollen from the Primrose, yields an average of almost exactly double this number of seeds, viz. 71. Lastly, eight long-styled and seven short-styled flowers of the Primrose were *illegitimately* fertilized by pollen of the Cowslip and Polyanthus, and, together, they yielded only four capsules, containing on an average only 13 seeds, some good and some poor. The Primrose, when *illegitimately* fertilized by pollen from the Primrose, yields an average of about 44 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 fertilized by the Cowslip, is less sterile, as Gärtner likewise observed, than the Cowslip when reciprocally fertilized by the Primrose.

I sowed the seeds produced from the several foregoing crosses; but none germinated except those from the short-styled Primrose fertilized 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 diœcious 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. Prof. 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. Prof. 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

* One author states in the 'Phytologist' (vol. iii. p. 703) that he covered with bell-glasses the Cowslips, Primroses, &c. on which he experimented. He specifies all the details of his experiment, but does not say that he artificially fertilized his plants; yet he obtained an abundance of seed, which is simply impossible. Hence there must have been some strange error in these experiments: possibly the bell-glasses may have been removed by some one during the night. The results of these experiments may be passed over as valueless.

† Phytologist, ii. pp. 217, 852; iii. p. 43.

‡ Loudon's Mag. of Nat. Hist. iii. (1830) p. 409.

garden; and if Prof. 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 explainable 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 Prof. 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 fertilized, 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

* Transact. Hort. Soc. iv. p. 19.

† I have given instances in my work 'On the Variation of Animals and Plants under Domestication,' vol. ii. p. 92.

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 fertilized 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 recognized, 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.

For the sake of ascertaining the two latter points, I transplanted the group of wild Oxlips before alluded to into my garden. They

* See an excellent article on this subject by Mr. H. C. Watson in the 'Phytologist,' vol. iii p. 43.

consisted of one long-styled and three short-styled plants, which, except in the corolla of one being slightly larger, resembled each other closely. The trials which were made, and the results which were obtained, are shown in the five following Tables. No less than twenty different crosses are necessary in order to ascertain fully the fertility of hybrid dimorphic plants, *inter se* and with their two parent species. In this instance 256 flowers were crossed in the course of four seasons. I may mention, as a mere curiosity, that if any one were to raise hybrids between two trimorphic species, he would have, in order to ascertain their fertility in all ways, to make 90 distinct unions; and as he would have to try at least 10 flowers in each case, he would be compelled to fertilize 900 flowers and count their seeds. This would probably exhaust the patience of the most patient man.

TABLE I.

Crosses *inter se* between the two forms of the common Oxlip.

<i>Illegitimate union.</i>	<i>Legitimate union.</i>	<i>Illegitimate union.</i>	<i>Legitimate union.</i>
Short-styled oxlip, by pollen of short-styled oxlip: 20 flowers fertilized, did not produce one capsule.	Short-styled oxlip, by pollen of long-styled oxlip: 10 flowers fertilized, did not produce one capsule.	Long-styled oxlip, by pollen of long-styled oxlip: 24 flowers fertilized, produced five capsules, containing 6, 10, 20, 8, and 14 seeds. Average 11.6.	Long-styled oxlip, by pollen of short-styled oxlip: 10 flowers fertilized, did not produce one capsule.

TABLE II.

Both forms of the Oxlip crossed with pollen of both forms of the Cowslip, *P. veris*.

<i>Illegitimate union.</i>	<i>Legitimate union.</i>	<i>Illegitimate union.</i>	<i>Legitimate union.</i>
Short-styled oxlip, by pollen of short-styled cowslip: 18 flowers fertilized, did not produce one capsule.	Short-styled oxlip by pollen of long-styled cowslip: 18 flowers fertilized, produced three capsules, containing 7, 3, and 3 wretched seeds, apparently incapable of germination.	Long-styled oxlip, by pollen of long-styled cowslip: 11 flowers fertilized, produced one capsule, containing 13 wretched seeds.	Long-styled oxlip, by pollen of short-styled cowslip: 5 flowers fertilized, produced two capsules, containing 21 and 28 very fine seeds.

TABLE III.

Both forms of the Oxlip crossed with pollen of both forms of the Primrose, *P. vulgaris*.

<i>Illegitimate union.</i>	<i>Legitimate union.</i>	<i>Illegitimate union.</i>	<i>Legitimate union.</i>
Short-styled oxlip, by pollen of short-styled primrose: 34 flowers fertilized, produced two capsules, containing 5 and 12 seeds.	Short-styled oxlip, by pollen of long-styled primrose: 26 flowers fertilized, produced six capsules, containing 16, 20, 5, 10, 19, and 24 seeds. Average 15.7. Many of the seeds very poor, some good.	Long-styled oxlip, by pollen of long-styled primrose: 11 flowers fertilized, produced four capsules, containing 10, 7, 5, and 6 wretched seeds.	Long-styled oxlip, by pollen of short-styled primrose: 5 flowers fertilized, produced five capsules, containing 26, 32, 23, 28, and 34 seeds. Average 28.6.

TABLE IV.

Both forms of the Cowslip crossed with pollen of both forms of the Oxlip.

<i>Illegitimate union.</i>	<i>Legitimate union.</i>	<i>Illegitimate union.</i>	<i>Legitimate union.</i>
Short-styled cowslip, by pollen of short-styled oxlip: 8 flowers fertilized, produced not one capsule.	Long-styled cowslip, by pollen of short-styled oxlip: 8 flowers fertilized, produced one capsule, containing 26 seeds.	Long-styled cowslip, by pollen of long-styled oxlip: 8 flowers fertilized, produced 3 capsules, containing 5, 6, and 14 seeds. Average 8.3.	Short-styled cowslip, by pollen of long-styled oxlip: 8 flowers fertilized, produced 8 capsules, containing 58, 38, 31, 44, 23, 26, 37, and 66 seeds. Average 40.4.

TABLE V.

Both forms of the Primrose crossed with pollen of both forms of the Oxlip.

<i>Illegitimate union.</i>	<i>Legitimate union.</i>	<i>Illegitimate union.</i>	<i>Legitimate union.</i>
Short-styled primrose, by pollen of short-styled oxlip: 8 flowers fertilized, produced not one capsule.	Long-styled primrose, by pollen of short-styled oxlip: 8 flowers fertilized, produced two capsules, containing 5 and 2 seeds.	Long-styled primrose, by pollen of long-styled oxlip: 8 flowers fertilized, produced eight capsules, containing 15, 7, 12, 20, 22, 7, 16, and 13 seeds. Average 14.0.	Short-styled primrose, by pollen of long-styled oxlip: 8 flowers fertilized, produced four capsules, containing 52, 52, 42, and 49 seeds, some good and some bad. Average 48.7.

We will first consider the results, as shown in the two left-hand compartments in the five Tables, obtained from the short-styled Oxlip when crossed with the long-styled Oxlip, and when crossed with both forms of the Cowslip and Primrose. I may premise that the pollen of two of the short-styled Oxlips consisted of nothing but minute aborted whitish cells; but in the third plant about one-fifth of the grains appeared in a sound condition. Hence it is not surprising that neither the short-styled nor the long-styled Oxlip produced a single seed when fertilized by this pollen. Nor did pure Cowslips or Primroses when illegitimately fertilized by it; but when legitimately fertilized they yielded a few good seeds. The female organs of the short-styled Oxlips, though greatly deteriorated in power, are in a rather better condition than the male organs; for though the short-styled plants yielded no seed when fertilized by the long-styled Oxlip, and hardly any when illegitimately fertilized by pure Cowslips or Primroses, yet when legitimately fertilized by these latter species, especially by the long-styled Primrose, they yielded a moderate supply of seed.

The long-styled Oxlip was more fertile than the short-styled, and about half the pollen-grains appeared sound. It bore no seed when legitimately fertilized by the short-styled Oxlip; but this no doubt was caused by the badness of the pollen of the latter; for when illegitimately fertilized (Table I.) by its own pollen it produced some good seeds, though much fewer in number than self-fertilized pure Cowslips or Primroses would have produced. The long-styled Oxlip likewise yielded a very low average of seed, as may be seen in the third compartments in the Tables, when illegitimately fertilized by, and when illegitimately fertilizing, pure Cowslips and Primroses. The four corresponding legitimate unions, however, were moderately fertile, and one (*viz.* that between a short-styled Cowslip and the long-styled Oxlip in Table IV.) was nearly as fertile as if both parents had been pure. A short-styled Primrose legitimately fertilized by the long-styled Oxlip (Table V.) also yielded a moderately good average, namely 48·7 seeds; but if the short-styled Primrose had been fertilized by a pure long-styled Primrose it would have yielded an average of seventy-seven seeds. In a previous part of this paper it was shown that a cross between the same forms of the Primrose and Cowslip is more sterile than a cross between the two opposite forms; and we now see in these latter Tables that the same rule almost invariably holds good with crosses between hybrids and the two pure parent species; so that

the same law prevails with the pure unions, the hybrid unions and the hybrid offspring of dimorphic species.

Seed from the long-styled Oxlip fertilized by its own pollen was sown, and three plants, which, according to the usual rule, were all long-styled, were raised. The first of these was identical in every character with its parent. The second bore rather smaller flowers, of a paler colour, almost like that of the Primrose; the scapes were at first single-flowered, but later in the season a tall thick scape, bearing many flowers, like that of the parent Oxlip, was thrown up. The third plant likewise produced at first only single-flowered scapes, with the flowers rather small and of a darker yellow; but it perished early; otherwise it would probably have thrown up an umbel. The second plant also died in September; and the first plant, though all three grew under very favourable conditions, looked very sickly. Hence we may infer that seedlings from a self-fertilized Oxlip would not be able to exist in a state of nature. I was surprised to find that all the pollen-grains in the first of these seedling Oxlips appeared sound; and in the second only a moderate number were bad. These two plants, however, did not reacquire the power of producing the proper number of seeds; for though left uncovered and surrounded by pure Primroses and Cowslips, the capsules were estimated to include an average of only from fifteen to twenty seeds.

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 fertilized 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 oftenest 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 fertilized 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 grew 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

* Godron has shown (Bull. Soc. Bot. de France, tom. x. (1863) p. 178) that *Primula variabilis* is a hybrid between *P. officinalis* (i.e. *P. veris*) and *P. grandiflora*.

† See also on this head Hardwicke's 'Science Gossip,' 1867, pp. 114, 137.

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 ELATIOR, Jacq., or Bardfield Oxlip.

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 equaling 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 fertilized by their own pollen than the corresponding forms of the Cowslip and Primrose when similarly fertilized.

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

* For England, see Hewett C. Watson, 'Cybele Britannica,' vol. ii. (1849) p. 292. For the Continent, see Lecoq. 'Géograph. Distrib. de l'Europe,' tom. viii. (1858) p. 142. For the Alps, see Ann. and Mag. Nat. Hist. vol. ix. (1842) pp. 156 & 515.

† Babington's 'Manual of British Botany,' 1851, p. 258.

‡ See Mr. H. Doubleday in the 'Gardeners' Chronicle,' 1867, p. 435, also Mr. W. Marshall, *ibid.* p. 462.

§ *Phytologist*, vol. i. p. 1001, and vol. iii. p. 695.

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. The following Table shows the fertility of the four unions between the two forms of this dimorphic species:—

Table VI.

Primula elatior or Bardfield Oxlip.

Nature of union.	Number of flowers fertilized.	Number of good capsules.	Average number of seeds per capsule.	Maximum number in any one capsule.	Minimum number in any one capsule.
Short-styled form, by pollen of long-styled. Legitimate union }	10	8	47·7	61	37
Long-styled form, by pollen of short-styled. Legitimate union }	10	6	46·5	62	34
Short-styled form, by own-form pollen. Illegitimate union	17	3	12·13	19	9
Long-styled form, by own-form pollen. Illegitimate union	20	4	27·7	49 & 40 *	2
* But these seeds were so poor and small that they could hardly have germinated.					

Both forms of this plant, when protected from insects, spontaneously produced a few capsules, some of which contained no seed, and the others, only six in number, included on an average only 7·8 seeds, many of which were bad. The foregoing Table clearly shows that *P. elatior* resembles in the nature of its fertility the many other species of *Primula* which have been experimented on by Mr. J. Scott † and myself. On the other hand, this plant differs almost as widely as is possible from the common Oxlip, both forms of which when legitimately fertilized (see Table I.) were absolutely barren, whereas the two forms of *P. elatior* when similarly fertilized yielded averages of 47·7 and 46·5 seeds. The pollen differs in condition in an equal degree; for in two out of the three short-styled plants of the common Oxlip all the grains, and

† "On the Functions of the Reproductive Organs in the Primulaceæ," Journ. Proc. Linn. Soc. vol. viii. (1864) p. 78.

in the third plant a large majority of the grains, were in an aborted condition, whilst in the short-styled *P. elatior* I could not detect a single bad grain. It may be seen in Table V. that eight long-styled flowers of the Primrose, fertilized by pollen from the long-styled common Oxlip, produced eight capsules, containing, however, only a low average of seeds; but the same number of flowers of the Primrose similarly fertilized by the long-styled Bardfield Oxlip produced only a single capsule. From these various facts it is manifest that *P. elatior* is not a hybrid, and that it differs fundamentally from the common Oxlip.

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.

Supplementary Note on some WILD HYBRID VERBASCUMS.

In a previous part of this paper I remarked that hardly any other instance could be given of a hybrid spontaneously arising in such large numbers, over so wide an extent of country, as that of the common Oxlip; but perhaps the number of well-ascertained cases of naturally produced hybrid Willows is equally great*. Numerous spontaneous hybrids between several species of *Cistus*, found near Narbonne, have been carefully described by M. Timbal-Lagrave †, and many hybrids between an *Aceras* and *Orchis* have been observed by Dr. Weddell‡. In the genus *Verbascum*, hybrids are supposed to have often originated§ in a state of nature; some of these undoubtedly are hybrids, and several hybrids have originated in gardens; but most of these cases require ||, as Gärtner remarks, verification. Hence the following case is worth recording. I transplanted a young wild plant into my garden for experimental purposes, and when it flowered it plainly differed from the three species of the genus which grow in this neighbourhood. I thought

* Max Wichura, 'Die Bastardbefruchtung.....der Weiden,' 1865.

† Mém. de l'Acad. des Sciences de Toulouse, 5^e série, tom. v. p. 28.

‡ Annales des Sc. Nat. 3rd series, Bot. tom. xviii. p. 6.

§ See, for instance, the 'English Flora,' by Sir J. E. Smith, 1824, vol. i. p. 307.

|| See Gärtner, 'Bastarderzeugung,' 1849, p. 590.

that it was a strange variety of *V. thapsus*. It attained the height (by measurement) of 8 feet! It was covered with a net; and most species of *Verbascum*, when thus treated, seed freely. Ten flowers were also carefully fertilized with pollen from the same plant; and later in the season, when uncovered, it was freely visited by bees; nevertheless, although many capsules were produced, not one contained a single seed. During the following year this same plant was left uncovered near plants of *V. thapsus* and *lychnitis*; but again it did not produce a single seed. Four flowers, however, which were repeatedly fertilized whilst the plant was under the net with pollen of *V. lychnitis*, produced four capsules, which contained five, one, two, and two seeds; at the same time three flowers were fertilized with pollen of *V. thapsus*, and these produced two, two, and three seeds. To show how unproductive these eight capsules were, I may state that a fine capsule from a plant of *V. thapsus* growing close by contained above 700 seeds. These facts led me to search the moderate-sized field whence the plant had been removed, and I found in it many plants of *V. thapsus* and *lychnitis* and of no other species, and thirty-three plants intermediate in character between these two species. These thirty-three plants differed much from each other. In the branching of the stem they more closely resembled *V. lychnitis* than *V. thapsus*, but in height the latter species. In the shape of their leaves they often closely approached *V. lychnitis*, but some had leaves extremely woolly on the upper surface and decurrent like those of *V. thapsus*; yet the degree of woolliness and of decurrency did not always go together. In the petals being flat and remaining open, and in the manner in which the anthers of the longer stamens were attached to the filaments, these plants all took more after *V. lychnitis* than *V. thapsus*. In the yellow colour of the corolla they all resembled the latter species. On the whole, these plants appeared to take rather more after *V. lychnitis* than *V. thapsus*. On the supposition that they are hybrids, it is not an anomalous circumstance that they all should have produced yellow flowers; for Gärtner crossed white- and yellow-flowered varieties of *Verbascum*, and the offspring thus produced never bore flowers of an intermediate tint, but either pure-white or pure-yellow flowers, generally of the latter colour*.

My observations were made in the autumn; so that I was able to collect some half-matured capsules from twenty of the thirty-three intermediate plants, and likewise capsules of the pure

* Bastarderzeugung, p. 307.

V. lychnitis and *thapsus* which grew in the same field. All the latter were charged with perfect but immature seeds, whilst the capsules of the twenty intermediate plants did not contain one single perfect seed. These plants, consequently, were absolutely barren. From this fact, from the one plant which was transplanted into my garden yielding when artificially fertilized with pollen from *V. lychnitis* and *thapsus* some seeds, though extremely few in number, from the fact of the two pure species growing in the same field, and from the intermediate character of the sterile plants, there can be no doubt that they are hybrids. Judging from the position in which they were chiefly found, I am inclined to believe they are descended from *V. thapsus* as the seed-bearer, and *V. lychnitis* as the pollen-bearer.

It is known that many species of *Verbascum*, when the stem is jarred or struck by a stick, cast off their flowers*. This is the case with *V. thapsus*, as I repeatedly observed. The corolla first separates from its attachment, and then the sepals spontaneously bend inwards so as to clasp the ovarium; and by this movement, in the course of two or three minutes, the corolla is pushed off. This does not occur with quite young flowers barely expanded. *Verbascum lychnitis* and, as I believe, *V. phœniceum* do not cast their corollas, however often and severely they may be struck. In this curious property the above-described hybrids take after *V. thapsus*; for I observed to my great surprise that when I pulled off the flower-buds surrounding the flowers round which I wished to tie threads as a mark, the slight jar invariably caused the corollas to fall off.

These hybrids are interesting under several points of view. First, from the number found in various parts of the same moderate-sized field. That the parent plants should be crossed so frequently is the more surprising, as the species of *Verbascum* do not secrete nectar; but they are frequented by pollen-gathering bees. Bees, though they devour much pollen, are beneficial to these plants, by crossing distinct individuals of the same species; for I have found on trial that plants raised from crossed seed are more vigorous than those from self-fertilized seed; on the other hand, as we now see, bees often bastardize and deteriorate the species. Secondly, these hybrids are highly remarkable from dif-

* This was first observed by Correa de Serra. See Sir J. E. Smith's 'English Flora,' 1824, vol. i. p. 311. Also 'Life of Sir J. E. Smith,' vol. ii. p. 210. I was guided to these references by the Rev. W. A. Leighton, who observed this same phenomenon in *V. virgatum*.

fering much from each other; for hybrids of the first generation, when raised from uncultivated plants, are generally uniform in character. That these wild plants belonged to the first generation we may safely conclude, from the absolute sterility of all those observed by me in a state of nature, and of the one plant in my garden, excepting when artificially and repeatedly fertilized with pure pollen; and then the number of seeds produced was extremely small. From these hybrids varying so much, an almost perfect series of forms connecting the two parent species, though these are widely distinct, could easily have been selected. This case, like that of the common Oxlip, shows that botanists ought to be cautious in inferring the specific identity of two forms from the presence of intermediate gradations; nor in the many cases in which hybrids are moderately fertile would it be easy to detect a slight degree of sterility in plants growing in a state of nature and liable to be fertilized by either parent species. Thirdly and lastly, these hybrids offer an excellent illustration of one of the many profound remarks made by that admirable observer Gärtner, namely, that although plants which can be crossed with ease generally produce moderately fertile offspring, yet well-pronounced exceptions to the rule occur; and here we have species of *Verbas-cum* which are evidently crossed with the greatest ease, but produce hybrids which are excessively sterile.