On the Inheritance of Heterostylism in Primula.

By W. Bateson, M.A., F.R.S., and R. P. Gregory, M.A.

(Received July 31, 1905.)

In view of the results obtained by Darwin,* Hildebrand and others, it seemed likely that the characters long-style and short-style, well known in Primulaceæ and other orders, might have a Mendelian inheritance. Our experiments have shown that this is the case in *P. sinensis*, the short style being dominant, the long recessive.

The inheritance is usually of the simplest type. In one case (p. 584) there was considerable divergence from the expected proportions, and it is no doubt possible that this case was one of real abnormality; but we incline to think that the irregularity was due to accident or error. But besides the cases which can be regarded as normal one individual short-styled plant gave an entirely aberrant result (p. 584); and as the offspring of this plant gave results similarly aberrant, there can be little question that we are here concerned with an inheritance of a special type. Further experiments with this family are in progress.

Another feature of interest was seen in the F_2 families raised from matings in which an *equal*-styled race was used, the phenomena well illustrating the mode of appearance of a new type by the recombination of the factors brought in by the pure parental types.

Horticultural experience as to the production of long- and short-styled offspring is in general harmony with our results. Fashion has decreed that *P. sinensis* shall be exhibited in the long-styled form alone. This being the recessive, breeds true, and short-styled plants are consequently absent from selected strains, being even difficult to procure at the present time. The florists' Auricula, on the contrary, must be exhibited in the short-styled or "thrum" form, but as this is the dominant, long-styled Auriculas continue abundant.

In the wild Primrose (*P. acaulis*, Jacq.) the two forms are about equally numerous in nature. Experiments with this species, now in progress, give indications that the inheritance of the two types follows the same rules. From the greater sterility of its illegitimate unions the Primrose is less easy to work with, and as might be expected from the same cause, all short-styled

* 'Forms of Flowers,' edit. 1884, giving references to the principal memoirs on the subject.

wild plants so far tested, have been found to be heterozygous in respect of style.

The experiments now to be described all relate to *P. sinensis*. The inheritance of flower-colour and other characters will be dealt with in a future communication. We take this opportunity of acknowledging our indebtedness to Messrs. Sutton and Sons, who have for some years placed their great collection of Primulas at our disposal, and have assisted us in many ways during the course of our inquiries.

I.—Normal Cases.

Long-styled × Long-styled.

Ten such crosses were made, from which 90 offspring were raised, all long-styled. In F_2 56 offspring, all long, were raised. Various extracted long-styled recessives, fertilised by self, and by pure longs, gave 85 plants, all long.*

Short-styled × Short-styled.

All the four short-styled plants originally obtained for use in these experiments proved to be heterozygous. From short-styled × short-styled, 26 short and 10 long were raised, the expectation being 3 : 1. Of the 26 short some were DD and others DR. One, on self-fertilisation, gave seven shorts. Two others, on self-fertilisation, gave 24 short, four long. Nine shorts raised in F_1 from long × short gave, on self-fertilisation, 120 shorts and 49 longs. The union DR × DR gave, therefore, a total of 144 short, 53 long; or, including the 36 raised between the original plants, 170 short, 63 long.

Darwin's† results from this form of union are valuable as indicating that he probably obtained a pure dominant. The parent short-styled plant, self-fertilised, gave eight plants, seven short, one long. The shorts, self-fertilised, gave only two plants which flowered (short), but the cross between short-styled and long-styled gave 15, all short.

Long ♀ × Short ♂, and Reciprocal Cross.

In the first instance these crosses were all R × DR or DR × R, which gave respectively 30 short, 24 long; and 14 short, 13 long. In F_2, crosses between DD and R gave 92 all short; and DR × R gave 40 short, 48 long.

Crosses with an Equal-styled Race.

Of late years a peculiar type of *P. sinensis* has been much grown, which is characterised by an extensive spreading of the central yellow eye. Instead

* *Cf.* Darwin, *loc. cit.*, pp. 213, 214.

† *Loc. cit.*, p. 215.

of forming a fairly sharp pentagon as in normal flowers, the eye in this type is produced as a yellow flush extending over about half of each petal. All the strains having this flush are in the condition called by Darwin "equal-styled." The anthers are at the same level as in the long-styled flowers, and the pollen grains are small and indistinguishable from those of the long-styled. The styles, however, are short and do not reach above the level of the anthers.* We at first supposed that the equal-styled plants corresponded to the mid-styled type seen in trimorphic species, but this is evidently a mistake, and the relations of the three types of trimorphic forms present much greater complexity than is met with in Primula.

Experiment shows that the yellow flush is an ordinary recessive character, the ordinary or non-flushed type being dominant. The flush is transmitted independently of the length of style or the size of the pollen grains, for it may be transferred to the true short-styled or "thrum" type. But when the flush is developed in plants which by gametic composition would be long-styled, the style does not pass through the anthers, and the equal-styled condition is produced. Why the development of the yellow flush in these flowers should entail the reduction of the style, we cannot in any way suggest.

From these considerations it follows that when the equal-styled race is crossed with the true short-styled type, two allelomorphic pairs are concerned, viz., short-style (D) and long-style (R); no yellow flush (D) and yellow flush (R). F_1 is, therefore, short-styled with no yellow flush. F_2 has four types, viz., short, non-flushed; short, flushed; long, non-flushed; long, flushed, which latter is the equal-styled, the ratio being 9 : 3 : 3 : 1. The long non-flushed, which appears as a new form in F_2, is, of course, made by the recombination of the parental characters, and the meeting of the "long" character from the equal-styled parent with the non-flushed eye derived from the short-styled parent.

Equal-styled × *Equal-styled.*

Four plants were raised by crossing equal-styled plants of the same race, and did not differ from their parents. From these were raised 14 more by self-fertilisation, again identical with their parents.

* Occasional flowers, in which the stigma is at the anther-level, may be seen on normal long-styled plants. They are usually first flowers, and are especially frequent in *P. acaulis* in early spring. We have never seen a genuine case of mixture of types on one plant.

Equal-styled × *Long-styled.*

The yellow flush being recessive, F_1 is here the normal non-flushed long style; 45 such plants were first raised, all long and without the flush. In the next year, 77 such plants were produced by similar matings.

Such F_1 plants gave by self-fertilisation 183 long, non-flushed, 51 equal-styled, with the flush, the expectation being 3 : 1. Crossed with the pure recessive, they gave 93 long, non-flushed, 107 equal-styled, with the flush, numerical equality being expected.

Equal-styled × *Short-styled.*

From such crosses, in which the short-styled parents were DR, 39 plants were raised, 19 long, 20 short, all without yellow flush. The pure short-styled plants raised in 1903, crossed with pure equal-styled plants, gave 41, all short-styled, without flush.

Such F_1 plants on self-fertilisation gave 247 plants, viz., 147 short, non-flushed, 35 short, flushed, 44 long, without flush, 21 equal flushed, the expectation being 138·9, 46·3, 46·3, 15·4.

Crossed with ordinary longs, the same F_1 plants gave 73 short, 76 long, all without flush, the expectation being equality.

The same F_1 plants, crossed with the pure equal-styled, gave 59 short, non-flushed, 39 short, flushed, 32 long, non-flushed, 24 long, flushed. This result, showing in each class a great excess of shorts, instead of numerical equality, is quite unexplained. The numbers can scarcely be taken as chance departures from equality. The same plants, however, gave recognisably normal results in both their other sets of matings, and the segregation was evidently quite normal. On the whole, it seems more likely that the aberration was due to accident, than that any novel phenomenon actually occurred in this case.

II.—Abnormal Cases.

With the exception just mentioned, all the cases hitherto dealt with gave fairly simple Mendelian results, but the entire series of crosses in which a certain short-styled plant (referred to as No. 6) was used showed a definite and consistent departure from normal expectation. No. 6 was a red thrum plant, obtained from a nurseryman, and we know nothing of its origin. By self-fertilisation it gave four shorts. Fertilised by a short-styled plant, which had been proved to be DR, it gave six shorts, three longs. No. 6 was used as male on both long- and equal-styled plants, giving 10, all short-styled; but

when fertilised with pollen of long- and equal-styled plants, No. 6 gave 14 short, 5 long.

The evidence so far is, therefore, that the *pollen* of No. 6 gave a mixture of longs and shorts, and consequently was carrying both characters, while all the plants raised from it as *female* were shorts. The numbers alone are of course too few to justify any conclusion, had it not been that a closely similar result appeared in the next generation.

By self-fertilisation No. 6 gave a short-styled plant, No. 37. This, on self-fertilisation, gave 22 shorts and no longs. Fertilised by pollen of long-styled plants, it gave 14 short, 24 long. But when used as a male parent, its pollen applied to long- and equal-styled plants gave 148 shorts and only 4 longs, of which one was recorded as "doubtful."*

Taking their offspring together, Nos. 6 and 37, when fertilised by long- and equal-styled, gave 29 long, 28 short; while when the same two plants were used as *males*, the total offspring were 184 shorts and 4 (? 3) longs. We have, therefore, the remarkable phenomenon of plants which, judged by the female gametes, were ordinary heterozygotes, while their male gametes were almost exclusively bearing the dominant character. Pending further investigation, we can offer no further comment on this singular case. It will be noted that, since the mixture was given by the *female* side, no hypothesis of parthenogenesis will meet the case.

Results of Double Pollination.

In addition to the experiments described above, an attempt was made to investigate another possibility respecting the consequences of legitimate and illegitimate unions. Darwin, and after him many others, proved that in Primula more seeds are produced when plants with styles of dissimilar types are united (legitimately) than when similars are united (illegitimately). Nevertheless, illegitimate unions are not necessarily sterile, but, especially in the case of *P. sinensis*, may produce a good deal of seed.

For examples we may refer to the average numbers given by Darwin.† Taking the average for legitimate unions at 100, the 13 illegitimate unions in the genus *Primula* give an average of 53 seeds per capsule, and we have found a similar proportion maintained with some constancy in our own fertilisations.

Some egg-cells (about half) are therefore fertilised by illegitimate pollen,

* The nature of the doubt is not recorded. Until the results were added and classified no special interest had been attached to this family. Each plant as it began to flower was recorded and thrown away to make room. Probably this individual was recorded before the flower completely matured.

† *Loc. cit.*, p. 246.

while the rest are not. This fact suggested that there may be a differentiation between egg-cells of the same plant, such that some are capable of illegitimate fertilisation, others incapable.

To test this possibility, we made a large number of trials with *P. acaulis* and *sinensis*, pollinating some flowers legitimately, some illegitimately, and others with pollen of both types. We anticipated that the double pollinations, in which pollen of both types was put on the same stigma, would produce a maximum number of seeds. In the case of *P. sinensis*, by making use of the fact that green stem and pinnate leaf are recessive to red stem and palmate leaf, it was possible to arrange these double pollinations in such a way that the paternity of each resulting seedling would be apparent, and thus the number of individuals derived from each set of pollen grains could be ascertained.

This series of experiments has, however, led to no definite conclusion. They were carried out through two seasons, and an enormous number of fertilisations were made, but the resulting figures were so discrepant that we are unable to give either a positive or a negative answer to the question proposed. These discrepancies are partly due to great individual differences between plants and between flowers of the same plant, but in all probability serious irregularities were also introduced in the actual operations owing to the difficulty of applying the two sorts of pollen equally to the same stigma under really uniform conditions. If these technical difficulties could be overcome, a valuable result might possibly follow from the experiment.