Morphological Notes.

BY

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With Plates **XXI-XXIII.**
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IX. A KALANCHOE HYBRID.

WHEN two distinct species are crossed, one would expect, *a priori*, the offspring to exhibit a 'blend' of the parental characters. And this appears to correspond largely with experience. Thus Darwin states: 'As a general rule, crossed offspring in the first generation are nearly intermediate between their parents' (Variation of Animals and Plants, ii. 48).

Such cases occur in nature, and before their real origin was understood they were regarded as intermediate species. Thus *Geum intermedium* stands between *G. rivale* and *G. urbanum*. But Bell Salter by crossing these two species proved it to be a hybrid.

The rule is, however, by no means invariable, and Romanes, writing in 1881, remarks: 'Until recently the interest attaching to hybridism was almost entirely of a practical nature, and arose from the fact, which is of considerable importance in horticulture, that hybrids are often found to present characters somewhat different from those of either parent or species' (Encycl. Brit., xii. 422). Darwin states the same

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fact: 'When two races or species are crossed, there is the strongest tendency to the reappearance in the offspring of long-lost characters possessed by neither parent nor immediate progenitor' (loc. cit., ii. 48).

Though such facts are well known to cultivators and are of extreme interest, they have seldom been put on record with much exactness or in a form convenient for reference. It seemed to me, therefore, worth while to illustrate rather fully a striking case which has come under my own notice at Kew.

Kalanchoe is a genus of *Crassulaceae* with about fifty species which has its head quarters in Africa, from which, like many types of the African flora, it has spread eastward by way of Arabia and North-west India. Kew has had the good fortune to be able to add to science and to horticulture two striking new species, both of which have been well figured in the Botanical Magazine, and can therefore be readily studied.

K. flammea (B. M. 7595), so named from its brilliant orange-red flowers, was raised from seed collected in Somaliland by Mrs. Lort-Phillips and Miss Edith Cole. The flowering plant is about a foot high, with 'obovate or obovate-oblong, thickly fleshy, quite entire or obscurely crenulate' leaves.

K. Bentii (B. M. 7765) was raised from seeds collected by the late Mr. Theodore Bent in the Hadramaut district of Southern Arabia. The flowering plant is about three feet high, with thickly fleshy, recurved, 'dagger-shaped,' or rather stiletto-shaped, leaves; the flowers are white, but pinkish when unexpanded.

Both species happening to be in flower together, Mr. W. Watson, the Curator of the Royal Botanic Gardens, a skilful and intrepid hybridizer, attempted to cross them. This was done both ways in June, 1900, and in each case the result was successful.

The results were as remarkable as unexpected. I will briefly summarize them.

1. *K. flammea* ♀ × *K. Bentii* ♂. About fifty seedlings were raised and grew vigorously. The middle figure of Plate XXII represents a young seedling about fifteen months old. It will be noticed that the lower and earliest leaves are intermediate, as was to be expected, between those of the two parents. They are neither flat and obovate nor simply stiletto-shaped, but are thickly fleshy and oblanceolate. Plants of the two parents of about the same age are shown on the same plate, *K. flammea* on the left, *K. Bentii* on the right. The three figures tell their own story.

Very soon, however, the characters of the hybrid entirely changed. The leaves ceased to be entire, but became strongly pinnatisect with segments which were less and less flat and more and more stiletto-shaped. In these characters and in the mode of their development the whole batch of seedlings were absolutely uniform.

On Plate XXIII the details of the leaf-forms of the hybrid and its two parents are shown more in detail. It is to be observed that the earliest leaves of a shoot are always more or less rudimentary. And it is well known that rudimentary structures, not being immediately adaptive, often afford evidence of ancestral influence which is afterwards obliterated. In each case in the plate the rudimentary as well as the mature forms of the leaves are shown. In the case of *K. flammea* (Fig. 2) there is nothing that is not merely ordinary or which calls for remark. In the hybrid (Fig. 3) the earliest leaf may be thought to recall the crenulation of *K. flammea* exaggerated into teeth. But no crenulation will explain the pinnatisect forms into which the dentation is afterwards developed. In the case of *K. Bentii* (Fig. 1) it occasionally, though rarely, happens that one of the rudimentary leaves is strongly two-toothed. It seems possible, therefore, that the extraordinary character of the foliage of the hybrid derives from this parent, in which it was latent.

But I will pass on for the moment to the further development of the hybrid. The plants were grown on, and in their second year attained rapidly a height of about three feet,

rather less or more in individual cases. And they began to flower in May, 1902, when, therefore, about two years old. The appearance they then presented is shown in Plate XXI. This, however, gives only an imperfect idea of the singular appearance of the plants: the leaves were strictly decussate, i.e. each successive pair was set on the stem at right angles to those above and below. And the divisions were so uniform and symmetrical that they exactly corresponded when looked down upon from above.

The flowering of the hybrid was looked forward to with much interest, and when it occurred was a complete surprise. The majority of the plants flowered, and in every case the colour of the flowers was a clear rosy pink, recalling the tint of those of *Erythraea Centaurium*. In the case of a sudden variation or 'break' of this kind it is usual for the colour of the flowers to become highly variable. But in this case it seemed absolutely uniform, and I could not persuade myself that there was any difference between one individual and another.

I must confess that I was completely at a loss to explain how a bright pink could arise from a cross between an orange and a white. The explanation, however, occurred to my friend Dr. Lotsy, who, while staying at Kew, had been much interested in the hybrid. The orange colour of the flowers of *K. flammea* is due to deep yellow chromoplasts immersed in a pink cell-sap. In *K. Bentii* both chromoplasts and cell-sap are colourless. The hybrid has inherited the white chromoplasts of one parent and the coloured cell-sap of the other.

The foliage, however, exhibits in the adult plant no trace of the influence of *K. flammea*. But it is widely divergent from that of *K. Bentii*. *K. laciniata*, which extends from Tropical Africa through India to Java, has deeply pinnatifid leaves with sometimes linear segments. The leaves of *K. Schweinfurthii* from Abyssinia are also similarly divided. The conclusion seems irresistible that we have in the case of the hybrid a reversion to an ancestral character which

exists elsewhere in the genus but is latent in both parents. In attempting to explain how this comes about, I cannot better the theory of Delage: 'Il peut arriver qu'un caractère vraiment latent revienne au jour. Le croisement jette un grand trouble dans l'évolution de l'œuf, par ce rapport d'innombrables gemmules inattendues; certains caractères normaux sont aussi contrariés dans leur développement et des caractères anciens se développent à leur place' (Structure du Protoplasma, 580).

2. *K. Bentii* ♀ × *K. flammea* ♂. A number of seedlings were raised which at first differed in no appreciable character from seedlings of the same age of *K. Bentii* as represented in Plate XXII. All were exactly alike, and exhibited at first no trace of hybrid origin. But though raised at the same time and subjected to exactly the same treatment as the reverse cross described above (which may be called *K. kewensis*), they at once showed a marked constitutional difference in the extreme slowness of their growth. When *K. kewensis* was three feet high, the plants of the reverse cross had only attained six inches. It is, however, interesting to note that after cultivation for two years and a half they have begun to develop the same pinnatisect leaves which are so characteristic a feature in *K. kewensis*. As none of the plants have yet flowered, what will happen then can only be a matter of conjecture. It is probable, however, that they will resemble those of *K. kewensis*, for as Darwin observes: 'Hybrids raised from reciprocal crosses . . . rarely differ in external characters' (Origin, 6th ed., 244).

It is clear that in the reciprocal crosses the influence of *K. Bentii* has been prepotent. This is in agreement with the facts cited from Gärtner by Darwin in regard to *Nicotiana* (Variation of Animals and Plants, ii. 67).

But *K. kewensis* exhibits in the most striking way a character in the foliage which cannot be attributed to either parent. If I am right in attributing this to reversion, it presents a striking exception to the principle laid down by Gärtner and accepted by Darwin: 'Reversions rarely occur

with hybrid plants raised from species which have not been cultivated, while with those which have been long cultivated they are of frequent occurrence. . . . Max Wichura, who worked exclusively on willows, which had not been subjected to culture, never saw an instance of reversion' (Darwin, loc. cit., 50). I have already quoted Darwin's dictum that: 'As a general rule, crossed offspring in the first generation are nearly intermediate between their parents, but,' he adds, 'the grandchildren and succeeding generations continually revert, in a greater or less degree, to one or both of their progenitors.' It is to this fact, I suppose, that an attempt is made to give expression in what is called Mendel's law. It would have been very interesting to have seen what would have happened to *K. kewensis* in succeeding generations. Unfortunately, so far every attempt to raise seedlings from it has failed. The capsules form with every promise of fertility, but only contain shrivelled rudiments of seeds. But had this been otherwise, it by no means follows that its characters would have shown any dissociation. Wichura 'found in opposition to Naudin that the progeny of hybrid willows retains its hybrid character' (Romanes, loc. cit., 426).

While writing these lines the important paper by De Vries (Comptes rendus, 2 Fevr., 1903, pp. 321-3) comes into my hands. It confirms the suspicion which I have long entertained that Mendel's law is not of universal application. De Vries lays it down that: 'La loi de Mendel s'applique aux caractères dits de variété, tandis que les caractères spécifiques vrais donnent dans leurs croisements des caractères d'hybrides constants.' Such characters 'ne se disjoignent pas; ils restent les mêmes dans les générations successives. J'ai vérifié ce fait par quatre générations d'un hybride entre les *Oenothera muricata*, L., et *O. biennis*, L., et j'ai étudié à ce point de vue différents autres hybrides, notamment dans le même genre.'

The explanation depends probably on the principle of specific stability, on the importance of which I have elsewhere insisted. From this point of view a hybrid may carry

over the stability of its parents, though it may not necessarily do so. In other words, the resultant of the fused parental characters may be as stable as their components. But when a species is varying, i. e. producing varieties, its stability is for the time lost, and there is nothing to prevent the dissociation of the fused characters and of their constituents, or their recombination in every possible way.

And I am confirmed in this opinion by the statement of Bateson that there is 'one group of cases, definite though as yet not numerous, where we know that the Mendelian principles do not apply' (Principles of Heredity, pp. 34, 35). The remainder of the passage is too long to quote, but may be referred to with advantage by those who are disposed to pursue a fascinating subject.

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