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OBTAINED BY ARTIFICIAL FERTILISATION

BY GREGOR MENDEL.

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ON HIERACIUM-HYBRIDS OBTAINED BY ARTIFICIAL FERTILISATION

BY GREGOR MENDEL.

(Communicated to the meeting 9 June, 1869)

ALTHOUGH I HAVE ALREADY UNDERTAKEN many experiments in fertilisation between species of *Hieracium*, I have only succeeded in obtaining the following 6 hybrids, and only from one to three specimens of them:

H. Auricula ♀ × *H. aurantiacum*, ♂
H. Auricula ♀ × *H. Pilosella* ♂
H. Auricula ♀ × *H. pratense* ♂
*H. echioides*¹ ♀ × *H. aurantiacum*, ♂
H. praealtum ♀ × *H. flagellare* Rchb., ♂
H. praealtum ♀ × *H. aurantiacum*, ♂

The difficulty of obtaining a larger number of hybrids is due to the minuteness of the flowers and their peculiar structure. On account of this circumstance it was seldom possible to remove the anthers from the

¹ The plant used in this experiment is not exactly the typical *H. echioides*. It appears to belong to the series transitional to *W. praealtrum*, but approaches more nearly to *H. echioides* and for this reason was reckoned as belonging to the latter.

flowers chosen for fertilisation without either letting pollen get on to the stigma or injuring the pistil so that it withered away. As is well known, the anthers are united to form a tube, which closely embraces the pistil. As soon as the flower opens, the stigma, already covered with pollen, protrudes. In order to prevent self-fertilisation the anther-tube must be taken out before the flower opens, and for this purpose the bud must be slit up with a fine needle. If this operation is attempted at a time when the pollen is mature, which is the case two or three days before the flower opens, it is seldom possible to prevent self-fertilisation; for with every care it is not easily possible to prevent a few pollen grains getting scattered and communicated to the stigma. No better result has been obtained hitherto by removing the anthers at an earlier stage of development. Before the approach of maturity the tender pistil and stigma are exceedingly sensitive to injury, and even if they are not actually injured, they generally wither and dry up after a little time if deprived of their protecting investments. I hope to obviate this last misfortune by placing the plants after the operation for two or three days in the damp atmosphere of a greenhouse. An experiment lately made with *H. Auricula* treated in this way gave a good result.

To indicate the object with which these fertilisation experiments were undertaken, I venture to make some preliminary remarks respecting the genus *Hieracium*. This genus possesses such an extraordinary profusion of distinct forms that no other genus of plants can compare with it. Some of these forms are distinguished by special peculiarities and may be taken as type-forms of species, while all the rest represent intermediate and transitional forms by which the type-forms are connected together. The difficulty in the separation and delimitation of these forms has demanded the close attention of the experts. Regarding no other genus has so much been written or have so many and such fierce controversies arisen, without as yet coming to a definite conclusion. It is obvious that no general understanding can be arrived at, so long as the value and significance of the intermediate and transitional forms are unknown.

Regarding the question whether and to what extent hybridisation plays a part in the production of this wealth of forms, we find very various and conflicting views held by leading botanists. While some of them maintain that this phenomenon has a far-reaching influence, others, for example, Fries, will have nothing to do with hybrids in *Hieracia*. Others take up an intermediate position; and while granting that hybrids are not rarely formed between the species in a wild state, still maintain that no great importance is to be attached to the fact, on the ground that they are only of short duration. The [suggested] causes of this are partly their restricted fertility or complete sterility; partly

also the knowledge, obtained by experiment, that in hybrids self-fertilisation is always prevented if pollen of one of the parent-forms reaches the stigma. On these grounds it is regarded as inconceivable that *Hieracium* hybrids can constitute and maintain themselves as fully fertile and constant forms when growing near their progenitors.

The question of the origin of the numerous and constant intermediate forms has recently acquired no small interest since a famous *Hieracium* specialist has, in the spirit of the Darwinian teaching, defended the view that these forms are to be regarded as [arising] from the transmutation of lost or still existing species.

From the nature of the subject it is clear that without an exact knowledge of the structure and fertility of the hybrids and the condition of their offspring through several generations no one can undertake to determine the possible influence exercised by hybridisation over the multiplicity of intermediate forms in *Hieracium*. The condition of the *Hieracium* hybrids in the range we are concerned with must necessarily be determined by experiments; for we do not possess a complete theory of hybridisation, and we may be led into erroneous conclusions if we take rules deduced from observation of certain other hybrids to be Laws of hybridisation, and try to apply them to *Hieracium* without further consideration. If by the experimental method we can obtain a sufficient insight into the phenomenon of hybridisation in *Hieracium*, then by the help of the experience which has been collected respecting the structural relations of the wild forms, a satisfactory judgment in regard to this question may become possible.

Thus we may express the object which was sought after in these experiments. I venture now to relate the very slight results which I have as yet obtained with reference to this object.

1. Respecting the structure of the hybrids, we have to record the striking phenomenon that the forms hitherto obtained by similar fertilisation are not identical. The hybrids *H. praealtum* ♀ × *H. aurantiacum* ♂ and *H. Auricula* ♀ × *H. aurantiacum* ♂ are each represented by two, and *H. Auricula* ♀ × *H. pratense* ♂ by three individuals, while as to the remainder only one of each has been obtained.

If we compare the individual characters of the hybrids with the corresponding characters of the two parent types, we find that they sometimes present an intermediate structure, but are sometimes so near to one of the parent characters that the [corresponding] character of the other has receded considerably or almost evades observation. So, for instance, we see in one of the two forms of *H. Auricula* ♀ × *H. aurantiacum* ♂ pure yellow disc-florets; only the petals of the marginal florets are on the outside tinged with red to a scarcely noticeable

degree: in the other on the contrary the colour of these florets comes very near to *H. aurantiacum*, only in the centre of the disc the orange red passes into a deep golden-yellow. This difference is noteworthy, for the flower-colour in *Hieracium* has the value of a constant character. Other similar cases are to be found in the leaves, the peduncles, &c.

If the hybrids are compared with the parent types as regards the sum total of their characters, then the two forms of *H. praealtum* ♀ × *H. aurantiacum* ♂ constitute approximately intermediate forms which do not agree in certain characters. On the contrary in *H. Auricula* ♀ × *H. aurantiacum* ♂ and in *H. Auricula* ♀ × *H. pratense* ♂ we see the forms widely divergent, so that one of them is nearer to the one and the other to the other parental type, while in the case of the last-named hybrid there is still a third which is almost precisely intermediate between them.

The conviction is then forced on us that we have here only single terms in an unknown series which may be formed by the direct action of the pollen of one species on the egg-cells of another.

2. With a single exception the hybrids in question form seeds capable of germination. *H. echioides* ♀ × *H. aurantiacum* ♂ may be described as fully fertile; *H. praealtum* ♀ × *H. flagellare* ♂ as fertile; *H. praealtum* ♀ × *H. aurantiacum* ♂ and *H. Auricula* ♀ × *H. pratense* ♂ as partially fertile; *H. Auricula* ♀ × *H. Pilosella* ♂ as slightly fertile, and *H. Auricula* ♀ × *H. aurantiacum* ♂ as infertile. Of the two forms of the last-named hybrid, the red-flowered one was completely sterile, but from the yellow-flowered one a single well-formed seed was obtained. Moreover it must not pass unmentioned that among the seedlings of the partially fertile hybrid *H. praealtum* ♀ × *H. aurantiacum* there was one plant which possessed full fertility.

[3.] As yet the offspring produced by self-fertilisation of the hybrids have not varied, but agree in their characters both with each other and with the hybrid plant from which they were derived.

From *H. praealtum* ♀ × *H. flagellare* ♂ two generations have flowered; from *H. echioides* ♀ × *H. aurantiacum* ♂, *H. praealtum* ♀ × *H. aurantiacum* ♂, *H. Auricula* ♀ × *H. Pilosella* ♂ one generation in each case has flowered.

4. The fact must be declared that in the case of the fully fertile hybrid *H. echioides* ♀ × *H. aurantiacum* ♂ the pollen of the parent types was not able to prevent self-fertilisation, though it was applied in great quantity to the stigmas protruding through the anther-tubes when the flowers opened.

From two flower-heads treated in this way seedlings were produced resembling this hybrid plant. A very similar experiment, carried out this summer with the partially fertile *H. praealtum* ♀ × *H. aurantiacum* ♂ led to the conclusion that those flower-heads in which pollen of the parent type or of some other species had been applied to the stigmas, developed a notably larger number of seeds than those which had been left to self-fertilisation alone. The explanation of this result must only be sought in the circumstance that as a large part of the pollen-grains of the hybrid, examined microscopically, show a defective structure, a number of egg-cells capable of fertilisation do not become fertilised by their own pollen in the ordinary course of self-fertilisation.

It not rarely happens that in fully fertile species in the wild state the formation of the pollen fails, and in many anthers not a single good grain is developed. If in these cases seeds are nevertheless formed, such fertilisation must have been effected by foreign pollen. In this way hybrids may easily arise by reason of the fact that many forms of insects, notably the industrial Hymenoptera, visit the flowers of *Hieracia* with great zeal and are responsible for the pollen which easily sticks to their hairy bodies reaching the stigmas of neighbouring plants.

From the few facts that I am able to contribute it will be evident the work scarcely extends beyond its first inception. I must express some scruple in describing in this place an account of experiments just begun. But the conviction that the prosecution of the proposed experiments will demand a whole series of years, and the uncertainty whether it will be granted to me to bring the same to a conclusion have determined me to make the present communication. By the kindness of Dr Nägeli, the Munich Director, who was good enough to send me species which were wanting, especially from the Alps, I am in a position to include a larger number of forms in my experiments. I venture to hope even next year to be able to contribute something more by way of extension and confirmation of the present account.

If finally we compare the described result, still very uncertain, with those obtained by crosses made between forms of *Pisum*, which I had the honour of communicating in the year 1865, we find a very real distinction. In *Pisum* the hybrids, obtained from the immediate crossing of two forms, have in all cases the same type, but their posterity, on the contrary, are variable and follow a definite law in their variations. In *Hieracium* according to the present experiments the exactly opposite phenomenon seems to be exhibited. Already in describing the *Pisum* experiments it was remarked that there are also hybrids whose posterity do not vary, and that, for example, according to Wichura the hybrids of *Salix* reproduce themselves like pure species. In *Hieracium* we may

take it we have a similar case. Whether from this circumstance we may venture to draw the conclusion that the polymorphism of the genera *Salix* and *Hieracium* is connected with the special condition of their hybrids is still an open question, which may well be raised but not as yet answered.

Bateson: The discovery of Ostenfeld and Raunkiaer that *Hieracium* is frequently parthenogenetic, or apogamous, of course puts an entirely new construction on the results of these experiments.