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On the Fertilisation of Epipactis latifolia. By A. D.
WEBSTER, Llandegai, Penrhyn.

(Read 12th November 1885.)

Having during the past few years, but particularly the summer of 1885, devoted considerable attention to the above interesting subject, I have thought the following observations not unworthy of record, as contributing to a subject which, as yet, has received little investigation. In the woodlands of this county (Carnarvonshire), where the plant grows in unusual quantity, exceptional opportunities have been afforded me of studying it under various conditions as to soil, altitude, and situation.

All, or nearly all my observations tend to show (1) that *Epipactis latifolia* is very imperfectly fertilised; (2), that, although visited by insects, cross-fertilisation seldom takes place; and (3) that self-fertilisation by the pollen falling spontaneously on the stigma is not uncommon.

1. That the plant is very imperfectly fertilised is evident from the small quantity of seed produced. On examining nearly one hundred plants when the seeds were ripe in October, I was surprised at the small number of capsules produced. (The ovules of unfertilised flowers drop from the plant at an early date, thus affording an unerring guide as to the difference between barren and well-filled capsules.)

I examined nineteen plants growing in consecutive order in one wood, and out of a possible 492 capsules only 38 produced seed. Thinking that perhaps the density of foliage or maritime situation might account for this unusually small production of seed, I examined the plant in quantity in two other warm, shady woodlands, but with almost similar results. Sixteen plants, growing within a short distance of each other, produced only 32 capsules from 516 flowers; while in another wood similarly situated 26 were produced out of a total of 215. This small production of seed, in an unusually fine season like that of 1885, clearly proves that *Epipactis latifolia* is very imperfectly fertilised, and, as will be seen hereafter, that cross-fertilisation by insect agency seldom takes place.

The conclusions naturally arrived at are, that this orchid is more frequently self than cross-fertilised, but when the small production of seed is taken into account, very imperfectly by either method.

2. That, although visited by insects, cross-fertilisation seldom takes place, is proved by the following observations:—Amongst insects of sufficient size to remove the pollinia that I have seen visiting the flowers of this *Epipactis*, I may mention the red-tailed humble bee and our common wasp, the latter, however, but very rarely. On the other hand, the red-tailed humble bee visits the flowers of this plant frequently, but, owing to its peculiar method of sipping the nectar without entering the flower, never removes the pollinia. On August 21, 1885, being in a wood where beds of this plant were in full flower, I saw the above bee enter several flowers on two different plants growing side by side, without in any case removing the pollinia. On the 24th of the same month, and in the same wood, I saw a red-tailed humble bee visit successively no less than sixteen flowers on a spike of this *Epipactis* without removing any of the pollinia. In this case the spike of flowers was so dense that the bee crawled from one to the other in a spiral fashion from bottom to top without once bringing its head or proboscis in contact with the viscid disc at the base of the pollinia. After sucking the nectar from the last flower, it flew off for a few yards, but immediately returned and revisited three of the same flowers, but this time in a half discontented fashion, as if striving to improve on work that had been already well done. Again, on the 26th of the same month, I saw several visit the flowers of this plant (one visited most of the flowers on seven plants in succession) without removing the pollen, although, being near, I noticed them visit numerous flowers that contained the pollen masses. The bees hung on the distal portion of the labellum and inserted their long proboscis without the head coming in contact with the viscid disc. The evening was lovely, and I spent an hour watching the plants, but during that time, although wasps were flying about in number, not one visited a flower. (This certainly was the opposite of what I expected, as several

naturalists are under the belief that this *Epipactis* is constantly fertilised by this insect, one indeed going so far as to say that if wasps were becoming extinct in any locality, so, in all probability, would *Epipactis latifolia*.) On other occasions, however, I did see the common wasp visit several flowers, but the visits were short, and, if I may use the expression, heartless, as if it could derive little therefrom. Owing to their long narrow shape and short proboscis, wasps remove the pollen masses with ease, for I have caught them immediately after coming out of the flower with the pollinia attached to their head; but as these visits are few and far between, fertilisation by this way is of rare occurrence. In numerous instances, also, the pollen masses will be found glued to the upper sepal of the flower, which is done as follows:—The wasp on entering, particularly a newly-opened flower, gets the pollinia attached to its head when sucking the nectar; but immediately on entering another flower, the upper sepal is so situated that the sharp stiff edge comes in contact with the viscid substance, which, with the pollinia, is left attached to it. This, I have never seen take place, but repeated experiments bear out the statement. It is also readily illustrated with a pencil. In various other parts of the plants it is not uncommon to find the pollen masses attached as if the discs were not sufficiently viscid to retain their hold on the insect's head, and on more than one occasion I have found them unbroken, on their stigmatic surface. Small insects also visit the flowers in numbers, as I have watched them creeping about within the labellum and other parts; but in numerous instances many of those which come in contact with the viscid stigma are unable to free themselves, and so perish. The largest insect that I have seen killed in this way was $\frac{3}{16}$ of an inch in length. When the plants begin to wither, or immediately after fertilisation takes place, the distal portion of the labellum curves upwards, and effectually closes the entrance to the basal portion or nectary, but for what end I am unable to say.

3. That self-fertilisation by the pollen falling spontaneously on the stigma is not uncommon. I have frequently observed that the pollen masses in a few days,

or perhaps a week after the flowers open, become swollen, or the particles of pollen disunited so as to protrude slightly beyond the sharp upper edge of the stigma. At the same time, or later on, the pollen becomes remarkably friable, and before the plant withers, either spontaneously or by the action of the wind, falls on the stigma and other parts of the flower. The peculiar position of the pollen masses—hanging directly above the stigmatic surface—ensures this the more readily. That the pollen masses become detached and fall apart is beyond dispute, as I have on many occasions found the grains scattered over the leaves, flower, and stem of the plant, as well as, in one or two instances, noticed the pollen masses still within their cells, but with the corners broken off and lying on the stigmatic surface. This breaking up of the pollen masses may be spontaneous, but it is materially assisted by both wind and rain.

On examining numbers of the plant, I have found it a general rule that the entire pollinia, or a large part of them, have not been removed from such flowers as bear well-filled capsules. Now this of itself seems to me to indicate self-fertilisation by particles of the pollen falling on the stigma, for it is quite evident that if wasps (the only insect, so far as is known, that in this country does fertilise the plant) visited and impregnated the flower, they could hardly have avoided removing the pollinia. To make sure, I examined several withered flowers with swollen ovaries on different plants, and was surprised to find that in most cases remnants of the then musty pollen could be distinctly detected within the shrivelled anther.

After reading the above remarks, one is naturally led to ask:—Why, if *Epipactis latifolia* is so imperfectly fertilised, is the plant so abundant?

This I can only answer as follows:—(1) Nature, as if to make up for the small production of seed, has endowed this plant, unlike the generality of our native orchids, with special facilities for the perpetuation of its race. The original roots do not, as in most other orchids, die off annually, but serve for collecting nutriment for the

succeeding plant, the eye or bud of which is formed close to the old or last year's stem. At times the plant produces several of these eyes in one season; indeed, during the present summer, I counted sixteen and twenty-six flowering stems on two plants, and it is not at all uncommon for three or four stems to be found attached to the same plant. (2) Each capsule (judging by the number in the almost equally sized *Cephalanthera grandiflora*) will contain about 6000 seeds, so that even if one only were produced on each plant, it would be more than sufficient to keep up the stock.

In conclusion, one cannot but wonder how remarkable it is that the nectar of *Epipactis latifolia* should be so highly attractive to the red-tailed humble bee, that cannot fertilise the flower; while to the wasp, that can remove the pollen masses with ease, and thereby insure cross-fertilisation, it offers but little attraction, as is clearly shown by the almost total absence of its visits. I have mentioned above, that, under certain conditions, the roots of this plant produce eyes or buds, but, strange as it may appear, this is not the case in all, for I have examined numbers without any such means of reproduction. In many instances also, indeed it is the general rule in this district, that the plant in question is destitute of a rostellum, the viscid matter at the base of the pollinia being free or uncovered, thus imitating in structure the degraded and self-fertilised *Cephalanthera grandiflora*.

Now, can it be that *Epipactis latifolia*, from not being sufficiently attractive to insects, or from the want of proper insects in this country to fertilise it, is gradually becoming modified, and propagation by increase of the root slowly but surely taking the place of seed, or at least materially assisting to prevent the extinction of the plant, as would in all probability result from the present imperfect fertilisation and subsequent small production of seed? This is rendered all the more probable by the curious fact that, in most if not all of our native orchids that are either partially or wholly self-fertilised, nature, as if to make up for the small production of seed, has

endowed them with special facilities for perpetuation,—namely, by increase of the root.

Take the example of *Neottia nidus-avis*, which is very imperfectly cross-fertilised, but in which nearly all the rootlets produce young plants; also that of *Epipactis latifolia*, which, under certain circumstances, behaves in a similar manner. Again, *Ophrys apifera*, which is perhaps the most noted example of constant self-fertilisation in British Orchideæ, is well known to appear and disappear somewhat mysteriously from certain localities, by the young tubers increasing beneath ground until of a flowering size; *Cephalanthera grandiflora*, which is fertilised in the bud state by the emitting of tubes from the pollen grains, also increases by the root, but of this rare species I am able to give little original information.

Report on the Excursion of the Scottish Alpine Botanical Club to Killin and Loch Awe in 1885. By WILLIAM CRAIG, M.D., F.R.C.S.Ed., F.R.S.E.

(Read 11th March 1886.)

The annual excursion of the Scottish Alpine Botanical Club in 1885 was to Killin and Loch Awe. The following members were present during the whole or part of the time:—Professor Dickson, President; Mr W. B. Boyd, Vice-President; Rev. George Alison, Chaplain; Dr Aitken, Minstrel; Dr Craig, Secretary and Treasurer; Rev. David Paul, Dr Stuart, Mr Archibald Gibson, Mr G. H. Potts, Mr A. H. Evans, and Mr Robert Lindsay. There were also present as visitors at Loch Awe, Mr James B. Gibson, Glasgow, and Rev. W. W. Peyton, Broughty Ferry. The latter is an experienced alpine climber and an excellent geologist.

The Club arrived at Killin on Thursday, 30th July 1885, and took up their quarters as usual at Cameron's Bridge of Lochay Hotel, the favourite resort of botanists, and specially of the Scottish Alpine Botanica Club. The formation of the Club took place in this hote in 1870.