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I. Notes on the Fertilisation of Orchids

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- I. *Notes on the Fertilisation of Orchids.* By WILLIAM RUTHERFORD, M.D., President of the Royal Medical Society, Resident Physician Royal Infirmary. (Being a portion of a thesis, for which a gold medal was awarded by the Medical Faculty of the University of Edinburgh at the Graduation in 1863.)

Mr Darwin, in the introduction to his admirable work on "The Fertilisation of Orchids," states, that his chief reason for writing the work was, "to show that the contrivances by which orchids are fertilised, have for their main object the fertilisation of each flower by the pollen of another flower;" and to show that, in his "Origin of Species," he had good grounds for expressing his belief in what he regards as an apparently universal law—viz., "That no hermaphrodite fertilises itself for a perpetuity of generations, an occasional cross with another individual being required." He, moreover, expresses the hope, that his researches may stimulate others to inquire into the habits of our native species.

During the past summer (1862), I spent some time in the examination of a considerable number of orchids, with a view to ascertain whether or not Mr Darwin's observations were accurate, and the conclusions at which he had arrived correct. The points which I especially wished to test, were, 1st, Is insect agency essential for their fertilisation? 2d, Is a flower fertilised by its own pollinia, or by those of other flowers? As regards the first of these, Mr Darwin says, that in every orchis, with the exception of the bee orchis and *Cephalanthera grandiflora*, insects are required to remove the pollinia, and apply them to the stigma; and with regard to the second point, he says,—that although in some cases the pollinia may be applied to the stigma of the flower from which they are taken, yet in all they may be—and most generally they are—applied to the stigmas of other flowers; farther, in some flowers—the marsh *Epipactis*, for

example—the pollinia are removed only when the insect retires from the flower.

Sprengel, in 1795, and Robert Brown, in 1833, though the latter was not without his doubts on the subject, both expressed their belief in the necessity for insect agency; and many others have concurred with the opinion; but Darwin was the first to show that the necessity for insects, which was previously considered to be confined to a few, is almost universal. My observations, so far as they have extended, have most thoroughly convinced me of the truth of Mr Darwin's statement. But I must here mention, to prevent any misunderstanding, that I have examined four species only,—for the district in which I resided contained only these four species, although they were severally represented by large numbers of individuals, so that I was able to make a pretty thorough examination of each species. I was staying in a part of Kent where *Orchis maculata* and *Cephalanthera grandiflora* were especially abundant; and *Gymnadenia conopsea*, and *Orchis pyramidalis*, to a lesser degree. I examined 1175 flowers of *Cephalanthera*, 1000 of *Orchis maculata*, 244 of *Gymnadenia conopsea*, and 60 of *Orchis pyramidalis*, in all 2479 flowers. This number may seem very large; but it must be remembered, that the flowers grew abundantly in the locality; and I had but little difficulty in procuring them. All the plants grew near, or in, woods, so that they were most favourably situated for visitation by insects. Mr Darwin says, that on one occasion only has he seen an insect capable of carrying away the pollinia visit an Orchis. I have been more fortunate; for I have repeatedly observed, especially on warm, cloudy days, lepidopterous insects paying their visits; and on one occasion I actually saw an insect remove the pollinia. Although Mr Darwin thinks that an insect does not confine its visitations to one particular species, but embraces several,—an opinion which he has shown to be true in the case of some one or two insects,—I must say that *Orchis maculata* and *Cephalanthera grandiflora*, although growing together, were visited by totally distinct insects, and either species was only visited by one kind of insect.

This fact is certain regarding the fertilisation of three

out of these four species,—*self-fertilisation is impossible*,—the pollinia must be removed from the flower and applied to the stigma of either the same or another flower. In by far the greater majority of the flowers, the pollinia, where these were single, were both removed, and in only a few of these were the ovaries non-fertilised. Sometimes I found the heads of pollinia sticking to the stigmas: this was rare, however; more frequently I found bundles broken off from the pollinia adhering to the stigma, and in some of these instances the pollinia remained in the same flower untouched, showing conclusively, that these flowers had been fertilised by the pollinia of other flowers. The flowers I examined were generally *old*, with the viscid discs and stigmas quite dry, so that no farther change could take place in the fertilisation of such flowers. Out of 1304 flowers, 953 had both pollinia removed, of which 895 were fertile and 58 were non-fertile. From this it appears, that although the pollinia may have been removed from the flowers, these were sometimes non-fertile. This is, because the insect has carried away the pollinia without pushing them against the stigma, and because the flowers have never been visited by insects having pollinia on their probosces. If such flowers could ever have become fertilised (most were old), it must have been by the pollinia of other flowers.

In 212, both pollinia were still remaining, although the flowers were mostly dry and shrivelled. Of these 119 were fertile, and 96 were non-fertile, so that although these flowers are incapable of self-fertilisation, the flowers are oftener fertilised than not. Insects with pollinia attached to their probosces visited the flowers and fertilised them, although they did not remove the pollinia. Had the flowers grown in a less wooded district, where insects are more scarce, many more of them would have had both pollinia remaining, and fewer of these would have been fertilised. Observe (*see the Table at the end*) how different is the case of *Cephalanthera grandiflora*, which is capable of self-fertilisation, although to a small degree: only 39 out of 1175 flowers had both pollinia remaining, and these, nevertheless, were *all* fertile; while of the 1128 which had both pollinia removed, only 8 were non-fertile. In the two other species which had the pollinia

separate, that is, unattached at the base to one another, the right pollinium was removed rather oftener than the left, a fact which would be difficult to explain. Of the 166 flowers which had only one pollinium removed, 142 were fertile and 24 non-fertile, showing that where only one pollinium is removed, the flower is not so certainly fertilised ; in short, the insects have not visited them so frequently.

It is unnecessary for me to comment further upon the following Table, but I may shortly state, that it fully bears out Mr Darwin's conclusions ; it establishes nothing new, but simply places beyond doubt very important opinions advanced by Darwin, among which the following are the most important :—1st, Insect agency is necessary for fertilisation ; 2d, Crossing of the individuals of a species is not only permitted, but all the arrangements seem especially adapted to bring about such a result.

One would suppose that hybrids ought to be very common if Mr Darwin's opinion were correct,—that one insect visits several species of orchids,—while it is well known that orchidaceous hybrids are extremely rare. From all that I have observed, I believe it to be the rule that each species has its special visitor, and that the same insect visits several species, to be the exception. I dare not, however, speak too positively on this point, for my observations have not been extensive.

Finally, it may seem superfluous for me to draw attention to the beautiful and laborious investigations contained in Mr Darwin's work on orchids ; but only those who have carried on such researches are able to estimate the severe and prolonged labour which they entail.

NAME.	Number of Flowers examined.	Both Pollinia remaining.		Both Pollinia removed.		One Pollinium removed.			
		Fertile.	Non-fertile.	Fertile.	Non-fertile.	The Right.		The Left.	
						Fertile.	Non-fertile.	Fertile.	Non-fertile.
<i>Orchis maculata</i> }	1000	50 2 of these young.	28 12 of these young.	765	47 15 of these young.	53	3	44	10
<i>Gynadenia conopsea</i> }	244	54	29	96	9	30	7	15	4
<i>Orchis pyramidalis</i> }	60	15	39	34	2	Pollinia attached to one another by their bases.			
TOTALS, {	1304	119	96	895	58	83	10	59	14
		215		953		93		73	
<i>Cephalanthera grandiflora</i> }	1175	39	None.	1128	8	Pollinia attached to one another by their bases.			