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NOTES

ON

THE FERTILIZATION OF ORCHIDS.

BY

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To the Editors of the Annals and Magazine of Natural History.

GENTLEMEN,

Having drawn up some notes for a French translation of my work 'On the various contrivances by which British and Foreign Orchids are Fertilized by Insects' (1862), it has appeared to me that these notes would be worth publishing in English. I have thus been able to bring up the literature of the subject to the present day, by giving references to, together with very brief abstracts of, all the papers published since my work appeared. These papers contain, on the one hand, cor-

that it may be safely predicated that orchids with very long nectaries, such as the *Anacamptis*, *Gymnadenia*, and *Platanthera*, are habitually fertilized by Lepidoptera, whilst those with only moderately long nectaries are fertilized by bees and Diptera—in short, that the length of the nectary is correlated with that of the proboscis of the insect which visits the plant. I have now seen *Orchis morio* fertilized by various kinds of bees, namely:—by the hive-bee (*Apis mellifica*), to some of which from ten to sixteen pollen-masses were attached; by *Bombus muscorum*, with several pollen-masses attached to the bare surface close above the mandibles; by *Eucera longicornis*, with eleven pollen-masses attached to its head; and by *Osmia rufa*. These bees, and the other Hymenoptera mentioned throughout these notes, have been named for me by our highest authority, Mr. Frederick Smith, of the British Museum. The Diptera have been named by Mr. F. Walker, of the same establishment. In Northern Germany, Dr. H. Müller of Lippstadt found pollen-masses of *Orchis morio* attached to *Bombus silvarum*, *lapidarius*, *confusus*, and *pratorum*. The same excellent observer found the pollen-masses of *Orchis latifolia* attached to a *Bombus*; but this orchis is also frequented by Diptera. A friend watched for me *Orchis mascula*, and saw several flowers visited by a *Bombus*, apparently *B. muscorum*; but it is surprising how seldom any insect can be seen visiting this common species. With respect to *Orchis maculata*, my son, Mr. George Darwin, has clearly made out the manner of its fertilization. He saw many

of *Orchis maculata*; and in this orchis I could occasionally detect minute brown specks, where punctures had been made. Hence the view suggested by me that insects puncture the inner lining of the nectary and suck the fluid contained between the two coats may be safely accepted. I have said in my work that this hypothesis was a bold one, as no instance was known of Lepidoptera penetrating with their delicate proboscides any membrane; but I now hear from Mr. R. Trimen that at the Cape of Good Hope moths and butterflies do much injury to peaches and plums by penetrating the skin, in parts which have not been in the least broken.

Since the appearance of my work, the following observations have been published on other species of Orchis *and on certain allied forms* (p. 53).—Mr. J. Traherne Moggridge has given (Journ. Linn. Soc. vol. viii. Botany, 1865, p. 256) a very interesting account of the structure and manner of fertilization of *Orchis* or *Aceras longibracteata*. Both pollinia, as in *Anacamptis pyramidalis*, are attached to the same viscid disk; but, differently from those in that species, after being removed from the anther-cases, they first converge and then undergo the movement of depression. But the most interesting peculiarity in this species is that insects suck nectar out of minute open cells in the honeycombed surface of the labellum. Mr. Moggridge saw this plant fertilized by a large bee, the *Xylocopa violacea*. He adds some observations on *Orchis hircina*, and describes the structure and manner of fertilization of *Serapias cordigera* by another bee, viz. the *Ceratina albilabris*. In this *Serapias*

find a few other cases of orchids which have structural peculiarities adapted both for self-fertilization and for crossing. I may here also refer to a paper by Mr. R. Trimen (Journ. Linn. Soc. vol. vii. Botany, 1863, p. 144) on the beautiful *Disa grandiflora* of the Cape of Good Hope. This orchid presents several remarkable characteristics, one of these being that the pollinia do not spontaneously undergo any movement of depression, the weight of the pollen-masses sufficing to bend the caudicle into the proper curvature for the act of fertilization. Another peculiarity is that the posterior sepal secretes nectar, and is developed into a spur-like nectary. Mr. Trimen informs me that he has seen a Dipterous insect, allied to *Bombylius*, frequenting the flowers. I may add that Mr. Trimen has sent me descriptions and specimens of various other South-African orchids, which confirm the general conclusions at which I have arrived in my work.

On the movement of the pollinia of Ophrys muscifera (p. 56). —Mr. T. H. Farrer, who has lately been attending to the fertilization of various plants, has convinced me that I have erred, and that the pollinia of this *Ophrys* do undergo a movement of depression. Hence my remarks on the correlation of the various parts of the flower are to a certain extent invalidated; but there can be no doubt that the naturally bent caudicle plays an important part in placing the pollen-mass in a proper position for striking the stigma. I have continued occasionally to watch the flowers of this species, but have never succeeded in seeing insects visit them; but I have been

spontaneously fall out. He appears to think that I infer that this *Ophrys* fertilizes itself, which is an error.

Ophrys apifera (p. 71).—Prof. Treviranus at first doubted (Botanische Zeitung, 1862, p. 11) the accuracy of my account of this *Ophrys*, and of the differences between it and *O. arachnites*; but he has subsequently (Bot. Zeit. 1863, p. 241) fully confirmed all that I have stated.

Ophrys arachnites (p. 72).—I have now examined several additional living specimens of this *Ophrys*, and can confirm my statement that the pollinia do not fall out of the anther-cases, even when the spikes are strongly shaken; nor do they fall out when the spikes are kept standing in water for a week. Mr. J. Moggridge has made (Journ. Linn. Soc., Bot. vol. viii. 1865, p. 258) a remarkable observation on *O. scolopax*, which is closely allied to *O. arachnites*,—namely, that at Mentone it never exhibits any tendency to self-fertilization, whilst at Cannes all the flowers fertilize themselves, owing to a slight modification in the curvature of the anther, which causes the pollinia to fall out. This botanist has given, in his 'Flora of Mentone,' a full description, with excellent figures, of *O. scolopax*, *arachnites*, *aranifera*, and *apifera*; and he believes, from the number of intermediate forms, that they must all be ranked as varieties of a single species, and that their differences are intimately connected with their period of flowering. It does not appear that these forms in England, judging from their distribution, are liable to pass into each other, within any moderate or observable period of time.

On the fertilization of Herminium monorchis (p. 74).—My son, Mr. George Darwin, has fully observed the manner of fertilization of this minute and rare orchis. It differs from that of any other genus known to me. He saw the flowers entered by various minute insects, and brought home no less than twenty-seven specimens with pollinia (generally with only one, but sometimes with two) attached to them. These insects consisted of minute Hymenoptera (of which *Tetrastichus diaphantus* was the commonest), of Diptera and Coleoptera, the latter being *Malthodes brevicollis*. The one indispensable point appears to be that the insect should be of very minute size, the largest being only the $\frac{1}{20}$ of an inch in length. It is an extraordinary fact that in all the specimens the pollinia were attached to the same peculiar spot, namely, to the outer side of one of the two front legs, to the projection formed by

of the labellum stands so close to the anther and stigma, that insects always enter the flower at one corner, between the margin of the labellum and one of the upper petals; they also almost always crawl in with their backs turned directly or obliquely towards the labellum. My son saw several which had begun to crawl into the flower in a different position; but they came out and changed their position. Thus, standing in either corner of the flower, with their backs turned towards the labellum, they inserted their heads and fore legs into the short nectary, which is seated between the two widely separated viscid disks. I ascertained that they stand in this position by finding three dead insects, which had been permanently glued to the disks. Whilst sucking the nectar, which occupies about two or three minutes, the projecting joint of the femur stands under the large helmet-like viscid disk on either side; and when the insect retreats, the disk exactly fits on, and is glued to, the prominent joint. The movement of depression in the caudicle then takes place, and the mass of pollen-grains projects just beyond the tibia; so that the insect, when entering another flower, can hardly fail to fertilize the stigma, which is situated directly beneath the disk on either side. I know of hardly any other case in which the whole structure of the flower is more beautifully correlated than in the *Herminium* for a most peculiar manner of fertilization.

On the movement of the pollinia in Peristylus viridis (p. 76).—Mr. T. H. Farrer informs me that the pollinia certainly undergo a movement of depression, but that this does not take place until twenty or thirty minutes have elapsed after their removal from the anther-cases. This length of time probably accounts for my oversight. He asserts that, after the movement of depression, the pollinia become much better adapted to strike the stigmatic surface. He suggests that insects may take a long time to lick up the nectar from the two naked spots on the labellum, and through the narrow slit-like opening into the nectary—and that during this time the pollinium becomes firmly attached, by the slow hardening of the viscid matter, to the insect's body, so as to be subsequently ready to fertilize another flower when visited by the same insect.

On the Lepidoptera which fertilize the Gymnadenia conopsea, *and on the divergence of the pollinia* (p. 82).—Mr. George

I may add that he caught the first-named moth, bearing the pollinia of this orchis, in my flower-garden, although more than a quarter of a mile distant from any spot where the plant grows. I state in my work that I do not understand the cause of the divergence of the pollinia so that they are enabled to strike the lateral stigmatic surfaces; but the explanation is simple. The upper margin of the nectary is arched, being formed on one side by the disk of one pollinium, and on the other side by the other disk. Now if a moth inserts its proboscis obliquely, and there are no guiding-ridges by which, as in *Anacamptis pyramidalis*, a moth is compelled to insert its proboscis directly in front, or if a bristle be inserted obliquely, one pollinium alone is removed. In this case the pollinium becomes attached a little on one side of the bristle or proboscis; and its extremity, after the vertical movement of depression, occupies a proper position for striking the lateral stigma on the same side.

On the Gymnadenia tridentata *of North America* (p. 83).—

disks do not stand far apart, have curious contrivances, such as a channelled labellum, lateral shields, &c., compelling moths to insert their proboscides directly in front. *Pl. Hookeri*, on the other hand (*ibid.* vol. xxxiv. 1862, p. 143), differs in a very interesting manner: the two viscid disks stand widely separated from each other; consequently a moth, unless of gigantic size, would be able to suck the copious nectar without touching either disk; but this risk is avoided in the following manner:—The central line of the stigma is prominent, and the labellum, instead of hanging down, as in most of the other species, is curved upwards, so that the front of the flower is made somewhat tubular and is divided into two halves. Thus a moth is compelled to go to one or the other side, and its face will almost certainly be brought into contact with one of the disks. The drum of the pollinium, when removed, contracts in the same manner as I have described under *Pl. chlorantha*. Prof. Gray has seen a butterfly from Canada with the pollinia of this species attached to each eye. In the case

do this; they always clung, whilst sucking the nectar, to the distal and hinged half of the labellum, which was thus pressed downwards. Owing to this part being elastic and tending to spring up, the bees, as they left the flowers, seemed to fly rather upwards; and this would favour, in the manner explained by me, the complete withdrawal of the pollen-masses, quite as well as an insect crawling out of the flower in an upward

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the experiment on nine additional flowers: of these, three did not produce seed-capsules; but this may have been accidental. Of six capsules which were produced, two contained about as many seeds as the capsules of unmutilated flowers on the same plant; but four capsules contained much fewer seeds. The seeds themselves were well-formed. These experiments, as far as they go, support the view that the distal part of the

labellum plays an important part in leading insects to enter and leave the flower in a proper manner for fertilization.

Fertilization of Epipactis latifolia (p. 104).—Although this orchis is not common in the vicinity of Down, by a fortunate chance several plants sprang up in a gravel walk close to my house, so that I have been able to observe them during several years, and have thus discovered how they are fertilized. Al-

Cephalanthera grandiflora (p. 108).—During the year 1862, the flowers of this orchis appeared to have been visited much less frequently by insects than during the previous years; for the masses of pollen were seldom broken down. Although I have repeatedly examined the flowers, I have never seen a trace of nectar; but some appearances lead me to suspect that the ridges within the base of the labellum are attractive to

On the self-fertilization of certain Epidendreæ (p. 166).—Dr. Crüger says (Journ. Linn. Soc. vol. viii. Botany, 1864, p. 131) that "we have in Trinidad three plants belonging to the Epidendreæ (a *Schomburgkia*, *Cattleya*, and *Epidendron*)

insects, and are gnawed by them, as in the case of many Vandeæ and other exotic orchids.

Goodyera repens (p. 114).—Mr. R. B. Thomson informs me that in the north of Scotland he saw many humble-bees visit-

matic surface; subsequently the rostellum rises and exposes

the stigma; so that everything here goes on as I have described under *Listera ovata*. The flowers are frequented by minute Diptera and Hymenoptera.

On the self-fertilization of Neottia nidus-avis, *and on the*

Manner of fertilization of various exotic Orchids (p. 189).

—I may here remark that Delpino (Fecondazione nelle Piante, Firenze, 1867, p. 19) says he has examined flowers of *Vanda*, *Epidendron*, *Phaius*, *Oncidium*, and *Dendrobium*, and confirms my general statements. The late Prof. Bronn, in his German translation of this work (1862, p. 221), gives a description of the structure and manner of fertilization of *Stanhopea devoniensis*.

Sexes of Acropera *not separated* (p. 206).—I have committed a great error about this genus, in supposing that the sexes were separate. Mr. J. Scott, of the Royal Botanic Garden of Edinburgh, soon convinced me that it was an hermaphrodite, by sending me capsules containing good seed, which he had obtained by fertilizing some flowers with pollen from the same plant. He succeeded in doing this by cutting open the stigmatic chamber, and inserting the pollen-masses. My error arose from my ignorance of the remarkable fact that, as shown by Dr. Hildebrand (Botanische Zeitung, 1863, Oct. 30 *et seq.*, and Aug. 4, 1865), "in many orchids the ovules are not developed until several weeks or even months after the pollen-tubes have penetrated the stigma." No doubt if I had examined the ovaria of *Acropera* some time after the flowers had withered, I should have found well-developed ovules. In many exotic orchids besides *Acropera* (namely, in *Gongora*, *Cirrhæa*, *Acineta*, *Stanhopea*, &c.), the entrance into the stigmatic chamber is so narrow that the pollen-masses cannot be inserted without the greatest difficulty. How fertilization is effected in these cases is not yet known. That insects are the agents there can be no doubt; for Dr. Crüger saw a bee (*Euglossa*) with a pollinium of a *Stanhopea* attached to its back; and bees of the same genus continually visit *Gongora*. Fritz Müller has observed, in the case of *Cirrhæa* (Bot. Zeitung, Sept. 1868, p. 630), that if one end of the pollen-mass be inserted into the narrow entrance of the stigmatic chamber, this

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of the pollinium, and not the broad end, is ordinarily inserted into the stigmatic chamber. By thus placing the pollinium, I have occasionally succeeded in fertilizing some of these orchids, and have obtained seed-capsules.

Structure and fertilization of the Vandeæ *&c. of Brazil* (p. 210).—Fritz Müller has sent me many letters containing an astonishing number of new and curious observations on the structure and manner of cross-fertilization of various orchids

inhabiting South Brazil. I much regret that I have not here space or time to give an abstract of his many discoveries, which support the general conclusions given in my work; but I hope that he will some day be induced to publish a full account of his observations.

Fertilization of Catasetum (p. 211).—It has been highly satisfactory to me that my observations and predictive conclusions in regard to *Catasetum* have been fully confirmed by the late Dr. Crüger, the Director of the Botanic Gardens of Trinidad, in letters to me and in his paper in the 'Journal of the Linnean Society' (vol. viii. Bot. 1864, p. 127). He sent me specimens of the bees, belonging to three species of *Euglossa*, which he saw gnawing the inside of the labellum. The pollinia, when ejected, become attached to, and lie flat on, the backs of the bees, on the hairy surface of the thorax. Dr. Crüger has also proved that I was correct in asserting that the sexes of *Catasetum* are separate, for he fertilized female flowers with pollen from the male plants; and Fritz Müller effected the same thing with *Catasetum mentosum* in South Brazil. Nevertheless, from two accounts which I have received, it appears that *Catasetum tridentatum*, though a male plant, occasionally produces seed-capsules; but every botanist knows that this occasionally occurs with the males of other dicœcious plants. Fritz Müller has given (Botanische Zeitung, Sept. 1868, p. 630) a most interesting account, agreeing with mine, of the state of the minute pollinia in the female plant: the anther never opens, and the pollen-masses are not attached to the viscid disks, so that they cannot be removed by any natural means. The pollen-grains, as so generally occurs with rudimentary organs, are extremely variable in size and shape. Nevertheless the grains of the rudimentary pollen-masses belonging to the female plant, when applied (which can never naturally occur) to the stigmatic surface, emitted their pollen-

Mormodes luxatum (p. 265).—I have now examined another species of *Mormodes*, the rare *M. luxatum*, and I find that the chief points of structure, and the action of the different parts, including the sensitiveness of the filament, are the same as in *M. ignea*. The cup of the labellum, however, is much larger, and is not pressed down firmly on the filament on the summit of the column. This cup probably serves to attract insects, and, as in *Catasetum*, is gnawed by them. The flowers

beset with minute, rigid, sharp-pointed papillæ, all directed forwards, which are excellently adapted to brush off the pollen from an insect's head or back."

The use of the copious fluid contained within the labellum of Coryanthes (p. 278).—The *Coryanthes macrantha* is perhaps the most wonderful of all known orchids, even more wonderful in structure and function than *Catasetum*. Its manner of fertilization has been described by Dr. Crüger in the 'Journal of the Linnean Society' (vol. viii. Bot. 1864, p. 130), and in letters to me. He sent me bees, belonging to the genus *Euglossa*, which he saw at work. The fluid in the bucket formed by the basal part of the labellum is not nectar and does not attract insects, but serves, by wetting their wings, to prevent them from crawling out except through the small passages close to the anther and stigma. Thus the secretion of fluid in this orchis serves exactly the same end as the inflected margins of the labellum in *Cypripedium*.

On the evidence that Insects visit many exotic Orchids in order to gnaw parts of the labellum, and not for the sake of nectar (p. 284).—It has been highly satisfactory to me that this hypothesis has been fully confirmed. In the West Indies, Dr. Crüger

Bonatea speciosa (p. 305).—The manner of fertilization of this extraordinary orchis has now been fully described by Mr. R. Trimen in the 'Journal of the Linnean Society' (vol. ix. Bot. 1865, p. 156). A projection rising from the base of the labellum is one of its most remarkable peculiarities, as an insect is thus compelled to insert its proboscis on one side, and thus to touch one of the two widely separated and projecting viscid disks. Mr. J. P. Mansel Weale has also published (*ibid.* vol. x. 1869, p. 470) analogous observations on a second species, viz. *Bonatea Darwinii*. Mr. Weale caught a skipper-butterfly (*Pyrgus elmo*) quite embarrassed by the number of pollinia belonging to this orchis which adhered to its sternum. I do not know of any other case in which the pollinia adhere to the sternum of a Lepidopterous insect.

On the nature of the contraction which causes the pollinia, after their removal from the anther, to change their position

(p. 338).—In *Orchis hircina*, I clearly saw, under the microscope, the whole front of the viscid disk become depressed as the two pollinia together underwent the movement of depression.

Number of seeds (p. 344).—The number of seeds produced by *Orchis maculata*, as given in my work, is small in comparison with that produced by some foreign species. I have shown (Variation of Animals and Plants under Domestication, vol. ii. 1868, p. 379), on the authority of Mr. Scott, that a single capsule of *Acropera* contained 371,250 seeds; and the species produces so many flowers and racemes, that a single plant probably sometimes produces as many as 74 millions of seeds in the course of a single year. Fritz Müller carefully estimated, by weighing, the number of seeds in a single capsule of a *Maxillaria* in South Brazil, and found the number 1,756,440. The same plant sometimes produces half-a-dozen capsules.

Number of pollen-grains (p. 355).—I have endeavoured to estimate the number of pollen-grains produced by a single flower of *Orchis mascula*. There are two pollen-masses; in one of these I counted 153 packets of pollen; each packet contains, as far as I could count, by carefully breaking it up

the elements for the reproduction of every single character in the mature plant!

Enumeration of the Orchideæ *which, as at present known, habitually fertilize themselves* (p. 358).—We have now seen that self-fertilization habitually occurs, in a more or less perfect manner, in one of the species of *Ophrys*, of *Neotinea*, *Gymnadenia*, *Platanthera*, *Epipactis*, *Cephalanthera*, *Neottia*, and in those *Epidendreæ* and in *Dendrobium* which often produce flowers that never expand. No doubt other cases will hereafter be discovered. Self-fertilization seems to be more perfectly secured in *Ophrys apifera* and in *Neotinea intacta* than in the other species. But it deserves especial notice that in all these orchids structures are still present, not in a rudimentary condition, which are manifestly adapted for the transport by insects of the pollen-masses from one flower to another. As I have elsewhere remarked, some plants, both indigenous

and naturalized, rarely or never bear flowers, or, if they do bear flowers, these never produce seed. But no one doubts that it is a general law of nature that phanerogamic plants should produce flowers, and that these flowers should produce seed. When they fail to do this, we believe that such plants would perform their proper functions under different conditions, or that they formerly did so and will do so again. On analogical grounds I believe that the few orchids which do not now intercross, either did formerly intercross (the means for effecting this being still retained) or that they will do so at some future period under different conditions, unless, indeed, they become extinct from the evil effects of long-continued close interbreeding.