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(Darwin
Japan)

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NOTES

ON

THE FERTILIZATION OF ORCHIDS.

BY

CHARLES DARWIN, M.A., F.R.S.

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, corrections of some serious errors into which I had fallen, and, on the other hand, confirmations of many of my statements. I have also been able to add, from my own observations and those of others, a few new facts of interest. A heading is given to each note, which will show the nature of the correction or addition, without any reference to my book; but I have added in a parenthesis the page to which the note ought to be appended.

Gentlemen,
Your obedient Servant,
Charles Darwin.

Down, Beckenham, Kent.
July 23, 1869.

Orchis or *Anacamptis pyramidalis* (p. 20).—The late Prof. Treviranus has confirmed (Botanische Zeitung, 1863, p. 241) my observations on this remarkable species; but he differs from me in one or two minor points.

On the kinds of Insects which habitually visit and fertilize some of the common British species of Orchis (p. 35).—I believe

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 specimens of a fly (*Empis livida*) inserting their proboscides into the nectary; and subsequently I saw the same occurrence. He brought home six specimens of this *Empis*, with pollinia attached to their spherical eyes, on a level with the bases of the antennæ. The pollinia had undergone the movement of depression, and stood a little above and parallel to the proboscis: hence they were in a position excellently adapted to strike the stigma. Six pollinia were thus attached to one specimen, and three to another. My son also saw another and smaller species (*Empis pennipes*) inserting its proboscis into the nectary; but this species did not act so well or so regularly as the other in fertilizing the flowers. One specimen of this latter *Empis* had five pollinia, and a second had three pollinia, attached to the dorsal surface of the convex thorax.

On nectar being secreted and contained between the outer and inner membranes of the nectary in several species of Orchis (p. 51).—I have repeated my observations on the nectaries of some of our common species, and especially on those of *Orchis morio*, *at the time when various bees were continually visiting*

the flowers; but I could never see the minutest drop of nectar within the nectary. Each bee remained a considerable time with its proboscis in constant movement whilst inserted into the nectary. I observed the same fact with *Empis* in the case 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* both pollinia are attached to the same viscid disk; when first withdrawn, they are bent backwards, but soon afterwards move forwards and downwards in the usual manner. As the stigmatic cavity is narrow, the pollinia are guided into it by two guiding plates.

Mr. Moggridge sent me from Northern Italy living plants of *Orchis* or *Neotinea intacta*, together with excellent drawings and a full account of the structure of the flower. He informed me that this species is remarkable for producing seed without the aid of insects; and I ascertained that when insects were carefully excluded, almost all the flowers produced capsules. Their fertilization follows from the pollen being extremely incoherent, and spontaneously falling on the stigma. Nevertheless a short nectary is present, the pollinia possess

small viscid disks, and all the parts are so arranged that, if insects were to visit the flowers, the pollen-masses would probably be removed and then carried to another flower, but not so effectually as with most other orchids. We shall hereafter 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.

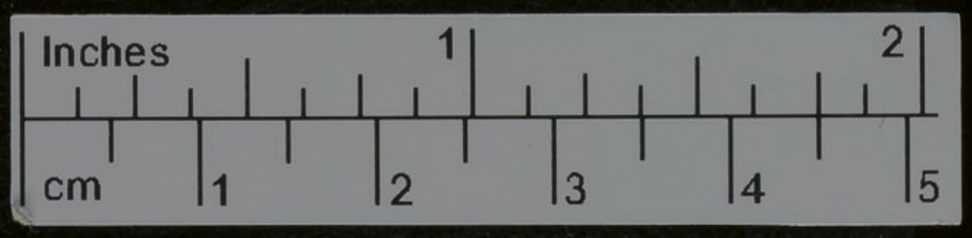
On the movement of the pollinia of Ophrys muscifera (p. 56).—Mr. T. H. Farrer, who has lately been attending to the fertilization of various plants, has convinced me that I have erred, and that the pollinia of this *Ophrys* do undergo a movement of depression. Hence my remarks on the correlation of the 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 led to suspect that they puncture or gnaw the small lustrous prominences beneath the viscid disks, which, I may add, are likewise present in several allied species. I have observed very minute punctures on these prominences, but I could not decide whether these had been made by insects or whether superficial cells had spontaneously burst.

Ophrys aranifera (p. 63).—F. Delpino states (Fecondazione nelle Piante &c., Firenze, 1867, p. 19) that he has examined in Italy thousands of specimens of this *Ophrys*, and that it seldom produces capsules. It does not secrete any nectar. Although he never saw an insect on the flowers (excepting once a green locust), nevertheless they are fertilized by insects; for he found pollen on the stigmas of some flowers, which had their own pollinia still within the anther-cases. The pollinia never

Spiranthes autumnalis (p. 123).—As in the case of the *Goodyera*, Prof. Gray feels confident that it is the column which moves from the labellum as the flower grows older, and not, as I had supposed, the labellum which moves from the column. He adds that this change of position, which plays so important

the stigma, which was penetrated by the pollen-tubes. Hence, if insects should fail to remove the pollinia by causing the explosion of the rostellum, this orchid certainly seems capable of occasional self-fertilization. But the scattering of the incoherent pollen was largely aided by, and perhaps wholly depended on, the presence of *Thrips*—insects so minute that they could not be excluded by any net.

Listera cordata (p. 152).—Prof. Dickie has been so good as

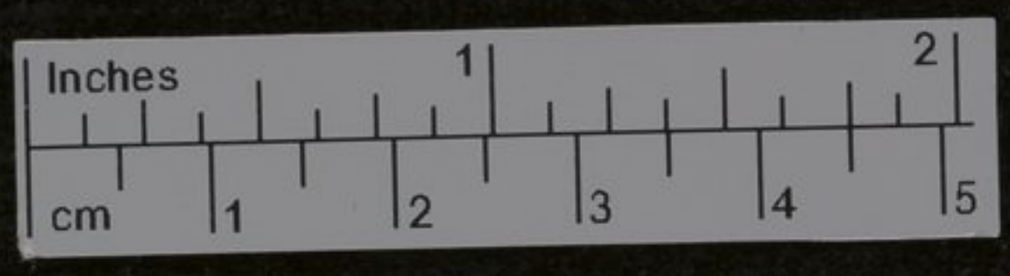


uncovered plants. I may here add that I detected on the crest of the rostellum some minute rough points, which seemed *particularly* sensitive in causing the rostellum to explode.

Dr. H. Müller, of Lippstadt, informs me that he has seen Diptera sucking the nectar and removing the pollinia of this plant

'Cottage Gardener,' 1863, p. 206) that with him the flowers of *Dendrobium cretaceum* never expand, and yet produce capsules with plenty of seed, which, when examined by me, was found to be perfectly good. These orchids make a near approach to those dimorphic plants (as *Oxalis*, *Ononis*, and *Viola*) which habitually produce open and perfect, as well as closed and imperfect flowers.

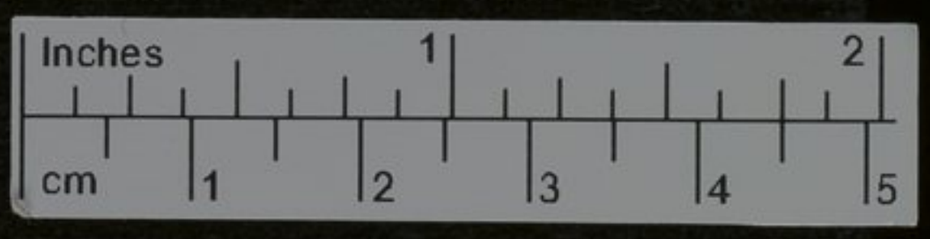
On the slow movement of the pollinia in Oncidium (p. 189).



German translation of this work (1862, p. 221), gives a description of the structure and manner of fertilization of *Stanhopea devoniensis*. 113

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 part, from being bathed by the stigmatic fluid, swells, and the whole pollen-mass is thus gradually drawn into the stigmatic entrance. But, from observations which I have made on *Acropera* and *Stanhopea* in my own hot-house, I suspect that, with many of these orchids, the pedicel with the narrow end 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



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 diœcious 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-tubes! This appears to me a very curious instance of the slow and gradual manner in which structures are modified; for the female pollen-masses, included within an anther which never opens, are seen still partially to retain their former powers and function.

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

are asymmetrical to an extraordinary degree, the right-hand and left-hand sides differing much in shape.

Cycnoches ventricosum (p. 265).—The plant described in my work as a second species of *Mormodes* proves to be *Cycnoches ventricosum*. I first received from Mr. Veitch some flower-buds, from which the section (fig. xxx.) was taken; but subsequently he sent me some perfect flowers. The yellowish-green petals and sepals are reflexed; the thick labellum is singularly shaped, with its upper surface convex, like a shallow basin turned upside down. The thin column is of extraordinary length, and arches like the neck of a swan over the labellum; so that the whole flower presents a very singular appearance. In the section of the flower, given in my work, we see the elastic pedicel of the pollinium bowed, as in *Catasetum* or *Mormodes*; but at the period of growth represented in the figure the pedicel was still united to the rostellum, the future line of separation being shown by a layer of hyaline tissue indistinct towards the upper end of the disk. The disk is of gigantic size, and its lower end is produced into a great fringed curtain, which hangs in front of the stigmatic chamber. The viscid matter of the disk sets hard very quickly, and changes colour. The disk adheres to any object with surprising strength. The anther is very different in shape from that of *Catasetum* or *Mormodes*, and apparently would retain the pollen-masses with greater force. A part of the filament of the anther, lying between two little leaf-like appendages, is sensitive; and when this part is touched, the pollinium is swung upwards, as in *Mormodes*, and with sufficient force, if no object stands in the way, to throw it to the distance of an inch. An insect of large size alights probably on the labellum, for the sake of gnawing the convex surface, or perhaps on the extremity of the arched and depending column, and then, by touching the sensitive point, causes the ejection of the pollen-masses, which are affixed to its body and thus transported to another flower or plant.

Fertilization of the Arethuseæ (p. 269).—*Epipogium Gmelini* has been the subject of an admirable memoir (Ueber den Blüthenbau, &c., Göttingen, 1866) by Dr. P. Rohrbach, who has shown how the flowers are fertilized by *Bombus lucorum*. With respect to another genus belonging to this same tribe, namely *Pogonia*, Dr. Scudder of the United States has described (Proc. Boston Nat. Hist. Soc. vol. ix. 1863, p. 182) the manner in which it is fertilized by the aid of insects.

Cypripedium (p. 274).—Prof. Asa Gray, after examining several American species of *Cypripedium*, wrote to me (see also Amer. Journ. of Science, vol. xxxiv. 1862, p. 427) that

he was convinced that I was in error, and that the flowers are fertilized by small insects entering the labellum through the large opening on the upper surface, and crawling out by one of the two small orifices close to either anther and the stigma. Accordingly I caught a very small bee which seemed of about the right size, namely the *Andrena parvula* (and this by a strange chance proved, as we shall presently see, to be the right genus), and placed it in the labellum through the upper large opening. The bee vainly endeavoured to crawl out again the same way, but always fell backwards, owing to the margins being inflected. The labellum thus acts like one of those conical traps with the edges turned inwards, which are sold to catch beetles and cockroaches in the London kitchens. Ultimately the little bee forced its way out through one of the small orifices close to one of the anthers, and was found when caught to be smeared with the glutinous pollen. I then again put the same bee into the labellum; and again it crawled out through one of the small orifices. I repeated the operation five times, always with the same result. I then cut away the labellum, so as to examine the stigma, and found it well smeared over with pollen. Delpino (Fecondazione &c. 1867, p. 20) with much sagacity foresaw that some insect would be discovered to act in the manner just described; for he argued that if an insect were to insert its proboscis, as I had supposed, from the outside through one of the small orifices close to one of the anthers, the stigma would be fertilized by the plant's own pollen; and in this he did not believe, from having confidence in what I have often insisted on—namely, that all the contrivances for fertilization are arranged so that the stigma shall receive pollen from a distinct flower or plant. But these speculations are now all superfluous; for, owing to the admirable observations of Dr. H. Müller, of Lippstadt (Verh. d. Nat. Ver. Jahrg. xxv. III. Folge, v. Bd. p. 1), we actually know that *Cypripedium calceolus* in a state of nature is fertilized by two species of *Andrena*, in the manner above supposed.

On the relation between the more or less viscid condition of the pollen and stigma in Cypripedium (p. 276).—The relation between the state of the pollen and stigma, which I have pointed out in my work, is strongly confirmed by Prof. Gray's statement (Amer. Journ. of Science, vol. xxxiv. 1862, p. 428), namely, that in *C. acaule* the pollen is much more granular or less viscid than in other American species of the genus, and in this species alone the stigma is slightly concave and viscid! Dr. Gray adds that in most of the species the broad stigma presents another remarkable peculiarity, "in being closely

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 witnessed humble-bees of the genus *Euglossa* gnawing the labellum of *Catasetum*, *Coryanthes*, *Gongora*, and *Stanhopea*; and Fritz Müller has repeatedly found, in South Brazil, the prominences on the labellum of *Oncidium* gnawed. We are thus enabled to understand the meaning of the various extraordinary crests and projections on the labellum of various exotic orchids; for they invariably stand in such a position that insects, whilst gnawing them, will be almost sure to touch the viscid disks of the pollinia, and thus remove them.

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 under the microscope, nearly 100 compound grains; and each compound grain is formed of four grains. By multiplying these figures together, the product for a single flower is about 120,000 pollen-grains. Now we have seen that in the allied *O. maculata* a single capsule produced about 6,200 seeds; so that there are nearly twenty pollen-grains for each ovule or seed. As a single flower of a *Maxillaria* produced 1,756,000 seeds, it would produce, according to the above ratio, nearly 34 million pollen-grains, each of which, no doubt, includes 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