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XVI.—*Notes on the Fertilization of Orchids.*

By CHARLES DARWIN, M.A., F.R.S., &c.

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,

Down, Beckenham, Kent.
July 23, 1869.

Your obedient Servant,
CHARLES DARWIN.

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

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 the articulation of the femur with the coxa. In one instance alone a pollinium was attached to the outside of the femur a little beneath the articulation. The cause of this peculiar manner of attachment is sufficiently clear: the middle part

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 Darwin went at night to a bank where this species grows plentifully, and soon caught *Plusia chrysitis* with six pollinia, *P. gamma* with three, *Anaitis plagiata* with five, and *Triphœna pronuba* with seven pollinia attached to their proboscides.

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).—Prof. Asa Gray has published (American Journal of Science, vol. xxxiv. 1862, p. 426, and footnote p. 260; and vol. xxxvi. 1863, p. 293) some interesting notes on the *Gymnadenia tridentata*. The anther opens in the bud, and some of the pollen invariably falls on the naked cellular tip of the rostellum; and this part, strange to say, is penetrated by the pollen-tubes, so that the flowers are self-fertilized. Nevertheless "all the arrangements for the removal of the pollinia by insects (including the movement of depression) are as perfect as in the species which depend upon insect aid." Hence there can be little doubt that this species is occasionally crossed.

Habenaria or *Platanthera bifolia* (p. 88).—According to Dr. H. Müller, of Lippstadt, *Pl. bifolia* of English authors is the *Pl. solstitialis* of Boenninghausen; and he fully agrees with me that it must be ranked as specifically distinct from *Pl. chlorantha*. Dr. Müller states that this latter species is connected by a series of gradations with another form which in Germany is called *Pl. bifolia*. He gives a very full and valuable account of the variability of these species of *Platanthera* and of their structure in relation to their manner of fertilization. (See Verhandl. d. Nat. Verein. Jahrg. xxv. III. Folge, v. Bd. pp. 36–38.)

American species of Platanthera (p. 91).—Prof. Asa Gray has described (American Journal of Science, vol. xxxiv. 1862, pp. 143, 259, & 424, and vol. xxxvi. 1863, p. 292) the structure of ten American species of *Platanthera*. Most of these resemble in their manner of fertilization the two British species described by me; but some of them, in which the viscid

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 of *Platanthera flava* (American Journal of Science, vol. xxxvi. 1863, p. 292), moths are compelled in a different manner to enter the nectary on one side. A narrow but strong protuberance, rising from the base of the labellum, projects upwards and backwards, so as almost to touch the column; thus the moth, being forced to go to either side, is almost sure to withdraw one of the viscid disks. In the allied and wonderful *Bonatea speciosa* of the Cape of Good Hope there is a similar contrivance for the same purpose.

Platanthera hyperborea and *dilatata* have been regarded by some botanists as varieties of the same species; and Prof. Asa Gray says (Amer. Journ. of Science, vol. xxxiv. 1862, pp. 259 & 425) that he has often been tempted to come to the same conclusion; but now, on closer examination, he finds, besides other characters, a remarkable physiological difference, namely, that *Pl. dilatata*, like its congeners, requires insect aid and cannot fertilize itself; whilst in *Pl. hyperborea* the pollen-masses commonly fall out of the anther-cells whilst the flower is very young or in bud, and thus the stigma is self-fertilized. Nevertheless the various structures adapted for crossing are still present.

Fertilization of Epipactis palustris (p. 102).—My son, Mr. W. E. Darwin, has carefully observed for me this plant in the Isle of Wight. Hive-bees seem to be the chief agents in fertilization; for he saw about a score of flowers visited by these insects, many of which had pollen-masses attached to their foreheads, just above the mandibles. I had supposed that insects crawled into the flowers; but hive-bees are too large to

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 direction. Perhaps, however, this upward movement may not be so necessary as I had supposed; for, judging from the point at which the pollen-masses were attached to the bees, the back part of the head would press against, and thus lift up, the blunt, solid, upper end of the anther, thus freeing the pollen-masses.

Various other insects besides hive-bees visit this *Epipactis*. My son saw several large flies (*Sarcophaga carnosa*) haunting the flowers; but they did not enter in so neat and regular a manner as the hive-bees; nevertheless two had pollen-masses attached to their foreheads. Several smaller flies (*Cœlopa frigida*) were also seen entering and leaving the flowers, with pollen-masses adhering rather irregularly to the dorsal surface of the thorax. Three or four distinct kinds of Hymenoptera (one of small size being *Crabro brevis*) likewise visited the flowers; and three of these Hymenoptera had pollen-masses attached to their backs. Other still more minute Diptera, Coleoptera, and ants were seen sucking the nectar; but these insects appeared to be too small to transport the pollen-masses. It is remarkable that some of the foregoing insects should visit these flowers; for Mr. F. Walker informs me that the *Sarcophaga* frequents decaying animal matter, and the *Cœlopa* haunts seaweed, occasionally settling on flowers; the *Crabro* also, as I hear from Mr. F. Smith, collects small beetles (*Halticæ*) for provisioning its nest. It is equally remarkable, seeing how many kinds of insects visit this *Epipactis*, that, although my son watched for some hours on three occasions hundreds of plants, not a single humble-bee alighted on a flower, though many were flying about. In a footnote I have given the results of experiments made by Mr. More, by cutting off the distal and hinged half of the labellum, in order to ascertain how far this part is important. He has now repeated 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. Although hive-bees and humble-bees of many kinds were constantly flying over the plants, I never saw a bee or any Dipterous insect visit the flowers; whilst, on the other hand, I repeatedly observed each year the common wasp (*Vespa sylvestris*) sucking the nectar out of the open cup-shaped labellum. I thus saw the act of fertilization effected by the pollen-masses being removed and carried on the foreheads of the wasps to other flowers. Mr. Oxenden also informs me that a large bed of *E. purpurata* (which is considered by some botanists a distinct species, and by others a variety) was frequented by "swarms of wasps." It is very remarkable that the sweet nectar of this *Epipactis* should not be attractive to any kind of bee. If wasps were to become extinct in any district, so would the *Epipactis latifolia*.

Dr. H. Müller of Lippstadt has published (Verhandl. d. Nat. Ver. Jahrg. xxv. III. Folge, v. Bd. pp. 7–36) some very important observations on the differences in structure and in the manner of fertilization, as well as on the connecting gradations, between *Epipactis rubiginosa*, *microphylla*, and *viridiflora*. The latter species is highly remarkable by the absence of a rostellum, and by being regularly self-fertilized. This latter circumstance follows from the incoherent pollen of the lower part of the pollen-masses emitting, whilst still within the anther-cells, pollen-tubes, which penetrate the stigma; and this occurred even in the bud state. This species, however, is probably visited by insects, and occasionally crossed; for the labellum contains nectar. *E. microphylla* is equally remarkable, by being intermediate in structure between *E. latifolia*, which is always fertilized by the aid of insects, and *E. viridiflora*, which does not necessarily require any such aid. The whole of this memoir by Dr. H. Müller deserves to be attentively studied.

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

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 visiting the flowers and removing the pollen-masses, which were attached to their proboscides. The bee sent was *Bombus pratorum*. This species grows also in the United States; and Prof. Gray (Amer. Journ. of Science, vol. xxxiv. 1862, p. 427) confirms my account of its structure and manner of fertilization, which is likewise applicable to another and very distinct species, namely, *Goodyera pubescens*. Prof. Gray states that the passage into the flower, which is at first very narrow, becomes, as I suspected, more open during its older state. Prof. Gray believes, however, that it is the column, and not the labellum, which changes its position.

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 a part in the fertilization of the flower, "is so striking that we wonder how we overlooked it" (Amer. Journ. of Science, vol. xxxiv. p. 427).

On the rostellum of Listera ovata *not exploding spontaneously* (p. 149).—I have covered up some additional plants, and found that the rostellum lost its power of explosion in about four days, the viscid matter then turning brown within the loculi of the rostellum. The weather at the time was unusually hot, and this may have hastened the process. After the four days had elapsed, the pollen had become very incoherent and some had fallen on the two corners, or even over the whole surface, of 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 to observe the flowers on living plants. He informs me that, when the pollen is mature, the crest of the rostellum is directed towards the labellum, and that, as soon as touched, the viscid matter explodes, the pollinia becoming attached to the touching object; after the explosion, the rostellum bends downwards and spreads out, thus protecting the virgin stigmatic 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 rostellum not exploding spontaneously* (p. 153).—I covered up with a net several plants, and after four days found that the rostellum had not spontaneously exploded, and had already almost lost this power. The pollen had become incoherent, and in all the flowers much had fallen on the stigmatic surfaces, which were penetrated by pollen-tubes. The spreading of the pollen seemed to be in part caused by the presence of *Thrips*, many of which minute insects were crawling about dusted all over with pollen. The covered-up plants produced plenty of capsules, but these were much smaller and contained much fewer seeds than the capsules produced by the adjoining 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.

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*) which rarely open their flowers, and are invariably impregnated when they do open them. In these cases it is easily seen that the pollen-masses have been acted on by the stigmatic fluid, and that the pollen-tubes descend from the pollen-masses *in situ* down into the ovarian canal." Mr. Anderson, a skilful cultivator of orchids in Scotland, informs me (see also '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).—Mr. Charles Wright, in a letter to Prof. Asa Gray, states that he observed in Cuba a pollinium of an *Oncidium* attached to a *Bombus*, and he concluded at first that I was completely mistaken about the movement of depression; but after several hours the pollinium moved into the proper position for fertilizing the flower.

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 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

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 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

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.

XVII.—*Note on* Hyponome Sarsi, *a recent Cystidean.*

By S. Lovén*.

The general appearance of this very remarkable Echinoderm is that of a small starfish or a Euryalid. It has a disk, convex on the ventral surface, flattened on the dorsal, and five short and broad rays; each of these is divided into two short dichotomous branches, terminating in four very short rounded lobes. As in the recent genera *Antedon* and *Pentacrinus*, a large, conical, proboscis-like funnel rises in one of the interradial spaces of the ventral surface of the disk; and from a point situated a little before the centre of the same surface five narrow channels, protected by marginal scales, radiate and, bifurcating thrice, run out on the rays and their branches, giving off short branchlets to certain sacculate protuberances placed at regular distances. No pinnulæ. On the protuberances and on the rays the channels are open; but upon the disk, between their first bifurcation and their common starting-point, their marginal scales close over them, forming a vault, so that the five channels are converted into covered ducts, converging into a common subcentral aperture, concealed beneath the integument, and not visible from the outside. In the covered parts of the channels I found masses, consisting of microscopic Crustacea, larval bivalves, and other remains of the food of the animal, apparently taken through the ends and open parts of the channels, and on its way, through their covered parts, to the concealed mouth. On the rays, near their tips, are seen some few pores, perhaps indicating the existence of retractile organs. The ventral surface is clothed with rather small, thick-set,

* We are indebted to the Author for the communication of this translation from 'Forhandlinger ved de Skandinaviske Naturforskeres tiende Möde, i Christiania,' July 1868.