

XXXV.—ON THE VARIOUS CONTRIVANCES BY WHICH BRITISH AND FOREIGN ORCHIDS ARE FERTILIZED BY INSECTS, AND ON THE GOOD EFFECTS OF INTERCROSSING. By Charles Darwin, M.A., F.R.S., &c. With illustrations.

AMONGST the prominent differences between the animal and vegetable kingdoms, there is one which, though never taught in schools and seldom alluded to in books, cannot fail to occur to the reflecting Naturalist; it is this, that whereas unisexuality is the rule amongst the highest orders of animals, and hermaphroditism becomes more frequent as we descend in the scale, the contrary is the case with plants. It is not our purpose here to discuss this curious contrast, of the significance of which in a scientific point of view we have hitherto been absolutely ignorant; it is enough to say that the results arrived at in the work whose title heads this article, show that amongst many plants apparent and real hermaphroditism are totally different things, and that before reasoning further on the subject, we must begin again not only to observe, but also to experiment.

But our future observations will be of very little use if they are to comprise nothing more than the circumstances of the presence of both sexes in one plant, or on one individual; observations, to lead to any good results, must not only be systematically and carefully, but intelligently made; they must, in fact, be suggested by some previous idea, and collected for the support or the contrary, of some possible or probable truth; and the wider the application of that truth, the more fruitful and suggestive will be the accumulated observations directed to its elucidation.

In the present work Mr. Darwin has given the results of observations made for the purpose of trying his theory, "that no hermaphrodite fertilizes itself for a perpetuity of generations;" his ulterior hypothesis, of the origin of species by natural selection, is, as enunciated by himself, untenable if the contrary were demonstrable. Now one of the most obvious objections to this position lies in the fact that the higher plants are structurally hermaphrodite, and that not only is it the apparent design of that condition to ensure the fertilization of each flower by its own pollen, but that a multitude of minor points in the structure of the flower appear to be as many contrivances to render self-fecundation doubly sure. To controvert this view was a bold idea, under any circumstances; and to show, as Mr. Darwin has done, that in one very large Natural Order of plants, and in that very Order in which the contrivances seemed most directed to ensure self-fertilization, all our previous notions were wrong, and most of our observations faulty, is a great triumph, that cannot fail to secure to its author a more attentive hearing for his ulterior views than these have hitherto gained. Nay further, had Mr. Darwin not investigated this point he would have had no secure foundation for his great hypothesis, for, as we have observed already,

this question of structural hermaphroditism is a fundamental one; and the rule that the more perfect plants are so constructed must occur to every one as a notable and insuperable objection to cross-fertilization, in default of its being shown that first impressions are in this, as in so many other cases, utterly fallacious; or, in other words, that we have utterly misinterpreted the phenomena we have hitherto recorded.

In his introductory pages the author indeed states that the primary object of his work is "to show that the contrivances by which Orchids are fertilized are as varied and almost as perfect as any of the most beautiful adaptations of the animal kingdom;" and such, no doubt, was his primary object in publishing his observations in the form of a separate treatise, addressed to the general reader; but the real primary object of the investigation, and therefore, in its best sense, of the work too, is involved in his secondary object, "to show that these contrivances have for their main object the fertilization of each flower by the pollen of another flower." It is under this last point of view that we shall notice its contents, confining ourselves mainly to an endeavour to make them and their importance clear to the readers of the *Natural History Review*, assuming that they, like ourselves, were previously very insufficiently acquainted with the whole subject of the structure of Orchid flowers and the functions of their parts. We must however, *in limine* say, that without an accurate knowledge of many Orchids, the whole subject is not intelligible, and that to understand it thoroughly requires a practised botanist. The key to the whole lies in the right comprehension of the exact structure, position, and relations of the rostellum to the other parts of the flower in every species commented on: and when we add that this rostellum is usually a very minute organ; that it is a compound and highly differentiated body; that the figures it assumes are seldom comprehensible from descriptions; that it alters much in form during development and suddenly changes its aspect after fertilization; that its homologies are obscure and its functions often intricate and always dependent on external agencies for their exercise;—it will be obvious that Mr. Darwin's is no work for the general reader and our task one of unusual difficulty. To put the matter more plainly, we do not believe that any student can, after his three months course of botany as usually taught in Europe, describe accurately the rostellum of any British genus of Orchids; and yet we must assume that our readers can. Such being the case, it may be wondered why Mr. Darwin chose the popular form for his treatise; for his many and good reasons we must refer to his introduction, adding, that for other reasons we are glad that he has done so, amongst them, because Mr. Darwin's writings afford the best specimen in English biological literature, of rigidly accurate descriptions expressed in perfectly simple language; of a style and language, in short, that are equally admirable and charming; we are glad too that the public should have in an available form the means of seeing

how varied are the accomplishments, how laborious the investigations, and how sharpened become the faculties of a working naturalist with a theory to establish, and how subservient the latter may always be kept to the sternest demands of facts and their teachings.

The book opens with a brief description of the structure of Orchid flowers, and of the terms applied to their organs, and is divisible into three parts, of which the first is devoted to British Orchids, the second to exotic forms, and the third to general considerations on the structure, morphology and physiology of Orchids. Such at least would be our division of the work, but the author has disposed of the whole matter in seven chapters, without concise headings, somewhat arbitrarily, as if the conception of putting forth the treatise as a separate work were an after-thought; an arrangement that does not recommend itself to the general reader, who thus loses sight of the grand divisions of the Order as well as of the subject.

The general results obtained from all Orchids then are—1. That the structural obstacles to self-fertilization are almost insuperable. 2. That the adaptation of all parts of Orchid flowers is for cross impregnation of one flower by the pollen of *another of the same species only*. 3. That insects are the agents of fertilization almost invariably. 4. That the labellum is the landing place of the insects, and contains the object of attraction to them in the shape of a honey-bearing spur, or sweet pulpy excrescences, or nectar-distilling hairs. 5. That the relative position of the labellum to the reproductive organs is such, that an insect to reach the attractive object in the former, places head or thorax in contact with the latter. 6. That an insect on its first visit to a hitherto unvisited flower, must in its search for honey usually so place itself as to close the stigmatic cavity, while at the same time it removes the pollen. 7. That in numerous cases, so long as the insect remains on the plant whose flowers it has sucked, the pollen retains such a direction as that it cannot reach the stigma of any flower it visits; and that, as owing to its unerring instinct it never visits the same flower twice, it cannot reach the stigma of that from which the pollen was taken. 8. That in many cases, after a certain period, generally longer than that spent by the insect in one flower or plant, the pollen spontaneously assumes such a direction that it is infallibly applied by the insect to the stigma of another flower of the same species as that from which it took the pollen. Bearing these points in mind we shall now very briefly review the principal modifications in structure and method of fertilization presented by the British genera of Orchids examined by Mr. Darwin.

*Orchis mascula, morio, fusca, maculata, latifolia*, and *Aceras anthropophora*. In these an insect alights on the labellum, and pushing its head into the cavity at the base of the labellum, the rostellum is touched, its membranes ruptured along definite lines, and the viscid balls at the base of the pollinia consequently cement themselves to the insect's head or proboscis, with the pollinia erect. In this position the pollinia cannot touch the stigma of a flower subsequently

visited; but they do not retain this position, they gradually become depressed and point forwards, and assume such a position that they infallibly strike the stigma of the next flower visited. The viscid stigmatic surface is not adhesive enough to overcome the attachment of the whole pollinium to the insect's head, but is adhesive enough to overcome the cohesion of the pollen grains, *inter se*, which are consequently detached in masses, and one pollinium may therefore fertilize many flowers. There are many other beautiful little contrivances noticed by Mr. Darwin which are brought into play in this operation, of which we have given an outline only.

*Orchis pyramidalis* differs considerably from its allies; the most curious point connected with it being the union of the viscid balls of the pollinia into the form of a single saddle-shaped disc, which clasps the antennæ of moths in a most rapid and remarkable manner, causing a divergence of the pollinia: but for this divergence, and their succeeding depression, they could not reach the stigmatic surfaces of subsequently visited flowers. *O. ustulata* presents many points in common with *O. pyramidalis*. A catalogue is given of twenty-three species of Lepidoptera which were found to have pollinia of *O. pyramidalis* attached to their probosces, one of which bore seven pair.

*Ophrys muscifera*. In this plant the pollinia have doubly-bent caudicles, the effect of which seems to be the same as that of the movement of depression in *Orchis*.

*Ophrys aranifera*. The caudicles here are nearly straight, and a movement of depression is hence necessitated.

In *O. apifera* the method of fertilization differs, not only from all others of its genus, but from all other Orchids. The greatest structural difference is in the caudicles, which are so slender as to be flexible with the weight of the pollen itself. The consequence is, that the pollinia hang out of their pouches, and are blown by the wind against the stigmatic surface, and *self-impregnation ensues almost infallibly*. Mr. Darwin finds it almost impossible to escape the conclusion that self-fecundation is here absolute: his discussion of the case is most ingenious, but he can do no more than show that crossing is possible.

*O. arachnites*. The principal point established regarding this is, that it is certainly not, as supposed by some, a variety of *O. apifera*, but more closely allied to *O. aranifera*, with which it agrees in its method of fecundation.

*Herminium Monorchis* has flowers highly attractive to insects, and seems adapted to a similar mode of fertilization as *Orchis*.

*Habenaria viridis*. There is no movement of depression in the pollinia, and it is not apparent at first how the latter can strike the stigma. The explanation is most curious and unique. There are three nectarial spots, and an insect bearing the pollen must, to reach the two lateral of these, so move its head that the pollinia strike the stigmata; the supplementary nectaries thus replacing the power of movement of the caudicles and disc.

*Gymnadenia conopsea* and *albida* differ in detail only from *Orchis*.

*Habenaria chlorantha* has a drum-like viscid disc of great functional importance, but its structure and action are far too complicated to be abridged here.

*H. bifolia* is found to differ in so many characters from *H. chlorantha* as to be considered an undoubtedly good species, and further it is fertilized in a totally different manner.

*Epipactis palustris*. The labellum is of peculiar structure, the distal half being hinged on the other so lightly that a fly depresses it. An insect entering the flower depresses the distal portion (which closes after it), and reaches the nectarial cavity without touching the rostellum; but, in backing out, the action of raising the said distal portion forces the insect against the rostellum, when it removes the pollen. There is no movement of depression required; for, on the entrance of the insect in another flower, the pollinia it bears are brought into immediate contact with its stigmatic surface. In *E. latifolia*, the distal portion of the lip is not flexible, and the operation is more simple.

*Cephalanthera grandiflora* presents the all but unique case of an Orchid wanting the rostellum (*Cypripedium* being the only other); its pollen grains are separate and spherical. Here perpetual self-fertilization is *imperfectly* secured by the friable pollen grains reaching the stigma at a very early period indeed; but the structure of the flower and relations of the parts are such that insects must help, so that the flowers are partially fertilized by their own pollen and partly by that of other flowers. The details are very intricate, and the discussion highly interesting and curious.

*Goodyera repens* is one of the most interesting British Orchids, as connecting several distinct forms; in the development of a caudicle and cohesion of the pollen grains, it approaches the tribe *Ophreæ*; in other respects it is allied to *Epipactis*, *Spiranthes*, and *Orchis*.

*Spiranthes autumnalis*. The rostellum here bears an erect boat-shaped disc, filled with a viscid fluid, and decked with a membrane endowed with the power of fissuring on the slightest stimulus (but not spontaneously). The pollinia consist each of two brittle, leaf-like laminae, and are exposed by a contraction of the anther case. The lip, at an early period, moves away from the rostellum, leaving a narrow passage to the nectary. The flowers are visited by bees, which touch the rostellum with their proboscis, causing the boat's deck to burst and expose the viscid fluid which attaches the pollinia to their proboscis. But at the period when the flower is open enough to allow of bees removing the pollinia, the aperture is not sufficiently wide to allow this to be applied to the stigma. The flower thereafter opens wider by the further movement of the labellum; hence it happens that fully expanded flowers are fertilized by newly expanded ones. The analysis of the whole operation is most graphically given by Mr. Darwin.

*Malaxis paludosa* has flowers with the lip turned upwards, owing

to a greater than usual twist of the ovary, and the upper sepal and petal are reflexed instead of protecting the flower. The pollen-masses are almost wholly exposed, and so placed that an insect must withdraw them on visiting the flower, and carry them off lying parallel to its proboscis, and in the proper position for being applied to the stigmatic cavity of the next flower visited.

*Listera ovata*. The rostellum is here exceedingly curious, being divided internally into loculi, a structure found in no other Orchid but *Neottia*. It is exquisitely sensitive, rupturing suddenly with a touch of the finest human hair, and ejecting a ball of viscid matter at its apex. The pollinia, which lie free and are very friable, have their bases so close to the apex of the rostellum, as to be invariably entangled in the expelled viscid mass. The long lip presents a longitudinal nectarial ridge. Insects visit this, crawl upwards, touch the apex of the rostellum, when the viscid matter shoots out, carrying the pollen masses by their entangled lower ends, and glueing them to the insect's head. The insect visits other flowers, and masses of the friable pollen are left on their stigmatic surfaces.

*Listera cordata* and *Neottia nidus-avis* present essentially the same structure and method of fertilization as *L. ovata*.

To complete this extremely brief and incomplete account of the phenomena in British Orchids we should by right allude to *Cypripedium*, of which genus however only exotic species were examined. This genus, as is well known, differs from all other Orchids in having three confluent stigmata (hence no rostellum), the anther of other Orchids represented by a shield-like body, two fertile anthers, and in the pollen grains being glutinous. Fertilization seems here to take place by insects visiting the flower to extract the sweet fluid from the glandular hairs within the labellum; to effect this they insert their proboscis into a narrow chink which leads to the anthers, the sticky grains of which attach themselves to their proboscis, and are conveyed to other flowers. *Cypripedium* is thus the only genus in which the pollen grains attach themselves not only to the insect's proboscis but to the stigmatic surface, which is not viscid.

We have preferred thus giving a rather extended resumé of Mr. Darwin's observations on British Orchids to reviewing the very extensive and intricate chapters devoted to foreign Orchids, the homologies of Orchid flowers, and general considerations; both because they may be repeated by any observer and extended by many, and because this procedure of ours gives a better idea of the completeness of the work than a more sporadic selection of his observations and experiments, results and conclusions, could have. Those other chapters are however by far the more interesting and important, and to them we shall at some future time recur, if opportunity offer. It remains to add that the work is copiously illustrated with most useful and in general very clear woodcuts, which would, however, have been greatly increased in value had the insects been introduced, in position, on the flowers.