

REVIEWS.

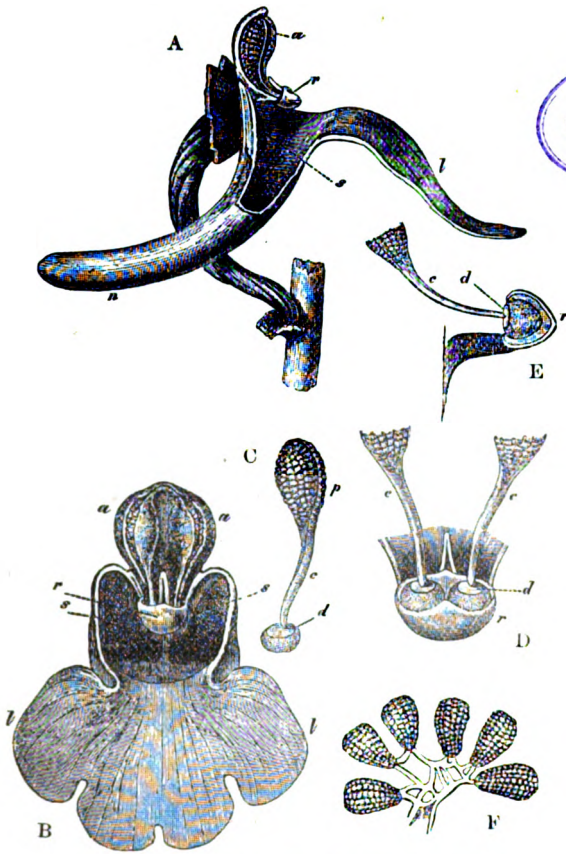
THE FERTILIZATION OF ORCHIDS.*

AMONG the points raised by Mr. Darwin in his celebrated work "On the Origin of Species" was the doctrine of the necessity of frequent or occasional cross-fertilization in the case even of plants whose flowers contain both stamens and pistils within the same set of envelopes. Several interesting cases in illustration of this principle were subsequently brought forward by Mr. Darwin himself; and in our last number we called attention to the publication by him of a most important series of observations in which the beneficial effects of such intercrossing, usually effected in nature by insects, were demonstrated beyond a doubt; but the first independent work in which the subject was treated by Mr. Darwin, was his treatise on the fertilization of orchids published in 1862, a second edition of which, embracing the later researches of the author, and the results obtained by many other observers, has lately appeared. Although this is only a second edition, the interest attaching to the subject, and the length of time that has elapsed since the appearance of the first edition, induce us to give a somewhat lengthened notice of it.

Whilst there was much *à priori* probability in the assumption that the occasional cross-fertilization of hermaphrodite flowers was a law of nature, a probability which received strong support from the observations of Mr. Darwin and others upon various plants, and the part played in the process by insects was not very doubtful, seeing that in most cases the influence of the wind could hardly be involved, and it is a matter of daily experience that flower-haunting insects are constantly dusted with pollen which they must necessarily convey from one flower to another, it was still a matter of considerable interest to find some plants in which this method of fecundation was a demonstrable necessity. Curiously enough the absolute evidence required was first obtained by the study of a group of plants in which the flowers are so singularly constructed that the stamens and pistils appear to form a single organ, and in which therefore the conditions for self-impregnation might at the first glance be supposed to be especially secured. In the orchids, in fact, the two cells of the usually single anther are imbedded in a portion of the pistil which stands up above the effective stigma, the whole

* "The Various Contrivances by which Orchids are fertilised by Insects." By Charles Darwin, M.A., F.R.S. A Second Edition, revised. Sm. 8vo. London: John Murray. 1877.

FIG. 1.



STRUCTURE OF THE FLOWER IN ORCHIS MASCULA.

The small letters throughout indicate the same parts, viz.—*a*, anther; *r*, rostellum; *s*, stigma; *l*, labellum; *n*, nectary; *p*, pollinium or pollen-mass; *c*, caudicle of pollinium; *d*, viscid disc of pollinium.

- A. Side view of flower, with all the petals and sepals cut off except the labellum, of which the near half is cut away, as well as the upper portion of the near side of the nectary.
- B. Front view of flower, with all the sepals and petals removed, except the labellum.
- C. A single pollinium or pollen-mass, showing the packets of pollen grains (*p*), the caudicle (*c*), and viscid disc (*d*).
- D. Front view of the discs and caudicles of both pollinia within the rostellum, with its lip depressed.
- E. Section through one side of the rostellum in a direction from front to back of the flower, with the included disc and the caudicle of one pollinium.
- F. Packets of pollen-grains, bound together by elastic threads, which are here shown as stretched.

*** For the use of these and the following illustrations we are indebted to the kindness of Mr. John Murray.

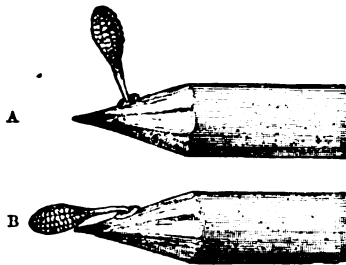
forming a body which received from the older botanists the name of the "column," and although, in some cases, these flowers are self-impregnating, fertilization is always effected by the escape of the contents of the anther cells from the cavities in which they were imbedded, before their contact with the stigmatic surface. This, indeed, was understood by Sprengel and some other old botanists, but it was reserved for Mr. Darwin to demonstrate clearly the process by which the fecundation is performed. The description of what takes place in the common orchis (*Orchis mascula*) will serve to explain the general nature of these curious phenomena.

In *Orchis mascula*, the well-known Purple Orchis of our meadows, the stigma is a bilobed viscid surface situated on the front of the pistil (*s*, in fig. 1), immediately beneath a projecting, pouch-like process (*r*) called the "rostellum," above which is the anther (*a*) consisting of two separate cells, each containing a coherent mass (*p*) of pollen, or "pollinium." The pollinia, which, when mature, are exposed by a longitudinal slit in the cells containing them, are composed of a number of wedge-shaped packets of pollen-grains, united by exceedingly elastic, thin threads (see fig. 1, *r*), which combine towards the lower part of each pollinium, to form a straight elastic stalk (*c*), the "caudicle." The lower extremity of each caudicle is attached to a small disc of membrane (*d*) forming part of the superior and posterior covering of the rostellum. The latter is a nearly spherical projection, which, at an early period of its growth, consists of a mass of polygonal cells, which soon become converted into two balls of extremely viscid, semi-fluid matter, destitute of all structure, lying quite freely within the rostellum, except at the back, where each of them adheres to one of the small, membranous discs (*d*), already mentioned as having the caudicles of the pollinia attached to them on their upper surface. These discs are at first continuous with the rest of the membrane enclosing the rostellum, but the slightest touch suffices to cause this membrane to split in certain definite lines, when, if the membrane of the front of the rostellum is pushed down, the two viscid balls which it enclosed are at once exposed.

This is the mechanism; its mode of action is as follows:—"Suppose an insect," says Mr. Darwin, "to alight on the labellum, which forms a good landing place, and to push its head into the chamber at the back of which lies the stigma, in order to reach with its proboscis the end of the nectary. Owing to the pouch-formed rostellum projecting into the gangway of the nectary, it is scarcely possible that any object can be pushed into it without the rostellum being touched. The exterior membrane of the rostellum then ruptures in the proper lines, and the lip or pouch is easily depressed. When this is effected, one or both of the viscid balls will almost infallibly touch the intruding body. So viscid are these balls that whatever they touch they firmly stick to. Moreover the viscid matter has the peculiar chemical quality of setting, hard and dry, in a few minutes' time." The same effects may be produced by pushing the pointed end of a pencil in the direction of the nectary; the viscid balls immediately adhere to it, and as the anther-cells are already open in front, the withdrawal of the pencil or of the insect's head, at once removes one or both of the pollinia, which may be pulled out, firmly cemented to the object and sticking up from it like horns (fig. 2, *A*), and owing to the position which they occupied in their cells, they diverge a little from each other when thus extricated. It is clear that if an insect after

plundering the nectary of one flower, flies away to visit another, it will insert the pollinium or pollinia that it may have extracted from the first into the corresponding part of the second, and, as Mr. Darwin remarks, the attached pollinium would simply be pushed into its old position, entirely avoiding the stigma, which is situated immediately below. To get over this difficulty one of the most remarkable "contrivances" of the whole series comes into play. It is described as follows by Mr. Darwin:—"Though the viscid surface," he says, "remains immovably affixed, the apparently insignificant and minute disc of membrane to which the caudicle adheres is endowed with a remarkable power of contraction, which causes the pollinium to sweep through an angle of about ninety degrees, always in one direction, viz., towards the apex of the proboscis or pencil, in the course of thirty seconds on an average. The position of the pollinium after the movement is shown at B in fig. 2. After this movement, completed in an

FIG. 2.



POINT OF A PENCIL WITH POLLINIUM OF ORCHIS MASCULA ATTACHED TO IT,
IN TWO POSITIONS.

- A. The position of the pollen-mass when first attached.
B. Its position after the act of depression.

interval of time which would allow an insect to fly to another plant, it will be seen by turning to the diagram (fig. 1, A), that if the pencil be inserted into the nectary the thick end of the pollinium now exactly strikes the stigmatic surface." The viscosity of the surface of the stigma causes the pollinia to adhere to it; but the peculiar composition of the latter, consisting as they do of numerous packets of pollen-grains held together only by slender threads,* renders the breaking up of the pollinium an easy matter. Hence only a small quantity of the pollen-grains remains attached to the stigma, and thus a pollinium attached to the head of an insect may be applied successively to several stigmas and fertilize them all. Mr. Darwin says that he has often seen the remains of the pollinia of another species of *Orchis* "adhering to the proboscis of a moth, with the stump-like caudicles alone left, all the packets of pollen having been left glued to the stigmas of the successively visited flowers."

Of the reality of this process no doubt can be entertained. The actual phenomena of the removal of the pollinia may be produced experimentally,

* It is evidently to the degree of coherence of the pollinia, and not, as Mr. Darwin seems to think, to the degree of viscosity of the stigma, that the breaking up of the former is to be ascribed.

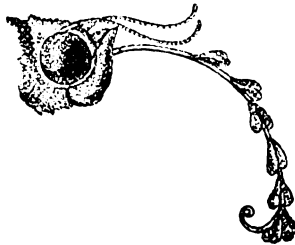
as already indicated, by the insertion of some suitable pointed object into the orifice of the nectary in the common purple orchis; after their removal the change of position may be directly observed; the fact that the whole of these operations are effected in nature by the agency of insects, is demonstrated by the frequent presence upon their heads and proboscides of the pollinia of various species of orchids; and these facts, coupled with the position assumed by the pollinia when thus attached, adapting them for being brought into direct contact with the stigmas of other flowers, and with the impossibility in most species of the pollen reaching the stigma by any other means, may be regarded as furnishing an irrefragable body of evidence, from which we may with no great difficulty infer that the whole of these contrivances, so wonderfully correlated as they are, are directed to one special object, namely the fecundation of one plant by the pollen of another. For the advantages gained by the intercrossing of distinct individuals of plants, the reader may consult Mr. Darwin's book, "On Cross and Self-fertilization," noticed in our last number, in which one side of the question at all events is thrown into high relief; perhaps the broadest and most general effect of this intercrossing of individuals of the same species is to keep the species "true," by its tendency to efface indifferent individual variations.

But whatever opinion we may form as to the purpose in nature of this apparent necessity for at least an occasional intercrossing of individuals of the same species of plants, there can be no doubt that in nearly all the orchids we find what may be called most careful provisions made to secure that the fertilization of the ovules in a given ovary shall not be effected by the pollen of the same flower, nor in a general way, by that of the same plant. The number of known self-fertilizing species is very small; they will be found referred to in Mr. Darwin's book. In all the rest the flower shows "contrivances," as Mr. Darwin calls them, for securing the removal of the pollinia by insects visiting the flowers, although the precise nature of these arrangements is by no means the same in all.

Several species of *Orchis* show the same arrangements as *Orchis mascula* just described, and it would appear that bees, humble-bees, and flies are the chief agents in transporting the pollinia of these species. In the Pyramidal Orchis (*O. pyramidalis*) the general arrangement of the parts is very similar to that which occurs in *O. mascula*, but the caudicles of the pollinia, instead of being attached to two separate membranous discs separated from the upper and posterior surface of the rostellum, are affixed to a single saddle-like piece, representing the two discs above mentioned united, and this, which is also strongly viscid beneath, not only adheres by its under surface to the object that sets it free by pushing down the pouch of the rostellum, but actually clasps and embraces the object, which, in nature, is usually the proboscis of some moth or butterfly. This clasping not only aids in fixing the pollinia to their means of transport, but also serves to produce a divergence of the pollinia, which, by this means and by the subsequent contraction of the membrane (as in *O. mascula*), are brought into a proper position for contact with the stigma of another flower. The moths and butterflies which frequent these flowers, are actually compelled to insert the proboscis into the nectary in such a direction as will bring them into contact with the rostellum, by means of certain guiding plates placed on the labellum, and in

this way as they go from flower to flower, they often accumulate two or three or even more pairs of pollinia. One specimen of a noctuid moth (*Acontia luctuosa*) had no fewer than seven (see fig. 3), and a specimen of a *Caradrina* eleven pairs of pollinia attached to the proboscis. "The proboscis of this latter moth," says Mr. Darwin, "presented an extraordinary arborescent appearance. The saddle-formed discs, each bearing a pair of pollinia, adhered to the proboscis, one before the other, with perfect symmetry; and this follows from the moth having always inserted its proboscis into the nectary in exactly the same manner, owing to the presence of the guiding plates on the labellum. The unfortunate *Caradrina*, with its proboscis thus encumbered, could hardly have reached the extremity of the nectary, and

FIG. 3.



HEAD AND PROBOSCIS OF *ACONTIA LUCTUOSA*, WITH SEVEN PAIRS OF THE POLLINIA OF *ORCHIS PYRAMIDALIS* ATTACHED TO THE PROBOSCIS.

would soon have been starved to death. Both these moths must have sucked many more than the seven and eleven flowers, of which they bore the trophies, for the earlier attached pollinia had lost much of their pollen, showing that they had touched many viscid stigmas."

From the examples furnished by these common British orchids, the reader may understand the general principle upon which the fertilization of the seeds is effected in the plants of that family. The process throughout is the same, modified in certain details, but always, except in the few species known or supposed to be self-fecundating, involving the attachment of a disc, forming part of the rostellum and bearing pollinia, to some part of the head of an insect, which thus conveys the fertilizing agents to other flowers. We shall not attempt, nor indeed would our space permit us to follow Mr. Darwin through his description of the details of the process in the various groups of orchids; for while any such attempt could only prove a failure, it might also have the effect of inducing our readers to avoid the perusal of one of the most charming natural history books that ever issued from the press. Otherwise we should have liked to give some account of the case of *Catasetum*, one of the most curious and interesting of the whole, in which the pollinia, attached to a common pedicel, which in its turn is attached to a viscid disc, are actually, as it were, shot out, disc forwards, as soon as any object comes in contact with the tentacle-like organs which here represent the rostellum. The whole of that portion of Mr. Darwin's book which is devoted to the description of the observed phenomena will be read with the greatest pleasure by everyone possessing some taste for

natural-history studies, and its perusal will open up a treasury of fresh interest for those who have the opportunity of practically following out the course of observations detailed in it.

The volume, moreover, contains dissertations upon various questions which arise naturally from the consideration of the phenomena to which we have briefly and very imperfectly called attention, questions which must possess great interest for the scientific botanist, such as the actual homological explanation of the structure of the flowers in the group of Orchids, the gradations in the mode of development of their various organs, the effects of the recognition of these gradations upon the phylogeny of the group, and the mechanism by which the peculiar phenomena of their fecundation are brought about. To enter upon any detailed exposition of the results of Mr. Darwin's investigations in these various directions would occupy much more space than we have at our disposal, and we must therefore refer the botanical reader to the book itself, which is certainly one of the most fascinating volumes that it has ever been our lot to study.

This second edition has received very considerable additions, not only arising out of the author's own observations, but also derived from the very numerous memoirs which have been published on the subject since Mr. Darwin first called attention to the curious facts revealed by the investigation of the orchids, some fifteen years ago. The illustrations, which are nearly the same as those printed in the first edition, have received some few additions; they are very carefully selected and executed, and serve to render all the details most readily intelligible.

THOMÉ'S TEXT-BOOK OF BOTANY.*

PROFESSOR THOMÉ'S "Text-book of Botany," which, as the Editor, Mr. Bennett, tells us, is the recognized book in use in the technical schools of Germany, will no doubt meet with great and well-deserved success in its English dress. Its descriptions of structure are exceedingly clear and intelligible, and the arrangement of the subject will be found to conduce greatly to a ready understanding of the internal and external anatomy of plants, in which the student will find further assistance in the very numerous and excellent illustrations. In this and the physiological section, Mr. Bennett has closely followed the German original, appending new additional information in the form of footnotes. But in the succeeding chapter, which treats of the morphology of plants, and the classification founded upon it, the Editor has departed from this rule, and while retaining his author's treatment of the Cryptogamia, he has introduced a classification of the flowering plants in accordance with the system most generally accepted in this country. The sections on Palæophytology, and on the geographical distribution of plants, although brief, are good; and the latter is illustrated by a coloured map.

* "Text-book of Structural and Physiological Botany." By Otto W. Thomé. Translated and Edited by A. W. Bennett, M.A., &c. Small 8vo. London: Longmans. 1877.