REVIEWS AND NOTICES OF BOOKS.

On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects, and on the good Effects of Intercrossing. By CHARLES DARWIN, M.A., F.R.S., &c. John Murray, London, 1862. 8vo, pp. 366.

The object of this work is to point out that the contrivances by which Orchids are fertilized are as varied, and almost as perfect, as any of the most beautiful adaptations in the animal kingdom; and, *secondly*, to show that these contrivances have for their main object the fertilization of each flower by the pollen of another flower. This latter statement bears on the author's views, as given in his work "On the Origin of Species," that it is a universal law of nature that organic beings require an occasional cross with another individual, or, which is about the same thing, that no hermaphrodite fertilizes itself for a perpetuity of generations. In treating of the subject, the author enters into interesting details in regard to the structure of Orchids, the arrangement of the parts of their flowers, their homologies, and the varied adaptations which have been observed in their organs. He has produced a most fascinating volume, which ought to be perused by every one who wishes to understand the nature of Orchids. This extensive family embraces at least 433 genera and about 1000 species. "These wonderful, and often beautiful productions, are unlike common flowers in their many adaptations, in having parts capable of movement, and others endowed with something like, though no doubt really different from, sensibility. The flowers of Orchids, in their strange and endless diversity of shape, may be compared with the great Vertebrate class of Fish, or, still more appropriately, with tropical Homopterous insects, which seem to us, in our ignorance, as if modelled by the wildest caprice."

The author states, that his "treatise affords an opportunity of attempting to show that the study of organised beings may be as interesting to an observer who is fully convinced that the structure of such is due to secondary laws, as to one who views every trifling detail of structure as the result of a direct interposition of the Creator." In this passage he seems to us to mistake the views of those who believe that everything, however minute, must be under the direction of the Creator; that not a sparrow, nor a hair of the head, falls to the ground without God. No one doubts the existence of what are called secondary laws, or, in other words, that the Creator chooses to work by certain great laws

which He has made and upholds every moment. These laws are but the expression of the way in which the Creator works; but it is clear that they have no independent existence; they are not self-acting, and they cannot operate except by the continued superintendence of the Lawgiver. We think that no one who reads God's Word aright can look upon the world as a mechanism set a-going by the Creator in the first instance, and then left to work out its wonders without Him; or can believe that the Creator, like a human engineer, retires from the scene, and leaves the machine to go on of itself. This is the view apparently maintained by some, and it is one which we consider irreconcilable with the statements of Holy Writ.

The parts of the flower of an Orchid are arranged in five rows, each of which consists of three parts. There are, normally, three stigmas, two of which are usually confluent, and one is modified into the rostellum; six stamens in two rows, the inner row of these (two of which are fertile in Cypripedium) usually abortive, and modified to form the clinandrium; the outer row of three, one being fertile and two abortive, combined with the lower petal, forming the labellum; the fourth row consists of three petals, and the fifth or outermost of three sepals. Darwin finds that there are fifteen groups of spiral vessels corresponding to these fifteen parts. An Orchid flower, according to him, "consists of five simple parts—three sepals and two petals; and of two compound parts, namely, the column and labellum. The column is formed of three pistils, and generally of four stamens, all completely confluent. The labellum is formed of one petal and two petaloid stamens of the outer whorl, likewise completely confluent. This view of the labellum explains its large size, its frequently tripartite form, and especially its manner of cohesion to the column." Such are the homologies of Orchids, and in this manner the arrangement and forms of their curiously moulded organs are explained.

The subject of Orchid fertilization has engaged the attention of many eminent botanists, such as Sprengel and Robert Brown. The nature of the pollen-masses and of their appendages, as well as the formation of pollen-tubes, and the general agency of insects, are facts which have been already recorded in various works; but it remained for Darwin to ascertain fully the mode in which insects act in the process of fertilization, as well as to show the true structure of the pollinia, and the way in which they are applied to the stigma. He has done this in a most masterly and convincing manner. His experiments are reported with great clearness and candour, and the reader is made acquainted with the difficulties which he encountered and the mode in which they were overcome. The whole is the work of a philosophic naturalist, having powers of observation of no ordinary kind, and a

wonderful facility of communicating scientific facts in an attractive and popular manner.

The phenomena of fertilization have been examined in fourteen genera of British Orchids—viz., *Orchis*, *Aceras*, *Ophrys*, *Herminium*, *Peristylus*, *Gymnadenia*, *Habenaria*, *Epipactis*, *Cephalanthera*, *Goodyera*, *Spiranthes*, *Malaxis*, *Listera*, and *Neottia*; and in forty-three exotic genera, including, among others, *Cattleya*, *Epidendrum*, *Masdevallia*, *Bolbophyllum*, *Dendrobium*, *Oncidium*, *Stanhopea*, *Calanthe*, *Angræcum*, *Acropera*, *Catasetum*. The chief facts recorded are illustrated by characteristic woodcuts.

According to the author, all the British species of Orchis require absolutely the aid of insects for their fertilization. This is obvious from the fact that the pollinia are so closely embedded in the anther-cells, and the disc with its ball of viscid matter in the pouch-formed rostellum, that they cannot be shaken out by violence. A list is given of twenty-three Lepidoptera which were found with the pollinia of an Orchis attached to their probosces. The viscid matter secreted in the disc at the foot of the pollinia adheres easily to any body with which it comes into contact, and it has the power of becoming hard during drying, so as to be firmly fixed in its position. Various means are adopted for securing the withdrawal of the pollen-masses. In some Orchids, nectar secreted in the spur of the corolla is easily obtained by moths; in such cases the pollinia are at the same time withdrawn, and their viscid disc adheres at once to the probosces. In other instances nectar is secreted between the two membranes of the spur, and in order to reach it the moth must rupture the delicate inner membrane. These phenomena seem to be connected with a difference in the viscidity and setting of the discs. In those cases where the viscid matter requires time to set and grow hard, the moths are delayed in getting nectar, so as to allow the discs to adhere to their probosces. This is a singular case of adaptation. Remarkable movements are manifested by Orchids in various parts of their flowers. The labellum of *Bolbophyllum barbigerum* is furnished with a beard of fine hairs, which causes the labellum to be in constant motion from any breath of air. In Acropera the labellum is articulated to the base of the column by a thin strap, so elastic and flexible that a breath of wind sets it vibrating. The Australian genus Calæna has a remarkably irritable labellum. When an insect lights on this labellum, it suddenly shuts up against the column, and encloses its prey as it were in a box. In *Stelis racemiflora* the little flowers are widely expanded; but after a time the three sepals close with perfect exactness, and shut up the flower, so as to appear like a bud. It is thus difficult to distinguish an old flower from a bud. The closed flower opens under water. Numerous are the movements shown by the pollinia. In *Dendrobium chrysanthum* the anther has a peculiar spring-

ing action, by which it scoops the pollen-mass out of the concave clinandrium, and pushes it up in the air with exactly the right force, so as to fall in the middle of the viscid stigma, where it sticks. In many Vandeæ the pedicel of the rostellum has a strong natural elastic tendency to spring up at right angles to the disc; in other cases, hygrometric movements are seen. As regard the movements of the pollinia in British Ophreæ, these are "due to the nicely regulated combination of that small portion of membrane (together with the pedicel in the case of Habenaria) lying between the layer or ball of adhesive matter and the extremity of the caudicle. In most of the species of Orchis the stigma lies directly beneath the anther-cells, and the pollinia simply move vertically downwards. In *Orchis pyramidalis* and in Gymnadenia there are two lateral and inferior stigmas, and the pollinia move downwards and outwards, diverging at the proper angle (by a different mechanism in the two cases), so as to strike the two lateral stigmas. In Habenaria the stigmatic surface lies beneath and between the two widely-separated anther-cells, and the pollinia here again move downwards, but at the same time converge."

The mode in which insects act in the case of *Orchis pyramidalis*, is thus described:—"Let a moth insert its proboscis between the guiding ridges of the labellum, or insert a fine bristle, and it is surely conducted to the minute orifice of the nectary, and can hardly fail to depress the tip of the rostellum; this being effected, the bristle comes into contact with the now naked and sticky under-surface of the suspended saddle-formed disc. When the bristle is removed, the saddle with the attached pollinia is removed. Almost instantly, as soon as the saddle is exposed to the air, a rapid movement takes place, and the two flaps curl inwards and embrace the bristle. When the pollinia are pulled out by their caudicles, by a pair of pincers, so that the saddle has nothing to clasp, I observed that the tips curled inwards, so as to touch each other in nine seconds; and in nine more seconds, the saddle was converted, by curling still more inwards, into an apparently solid ball. The probosces of the many moths which I have examined, with the pollinia of the Orchis attached to them, were so thin, that the tips of the saddle just met on the other side. This rapid clasping movement helps to fix the saddle with its pollinia upright on the proboscis; but the viscid matter rapidly setting hard would probably suffice for this end, and the real object gained is the divergence of the pollinia. The pollinia being attached to the flat tip or seat of the saddle, project at first straight up, and are nearly parallel to each other; but as the flat top curls round the cylindrical and thin proboscis, or round a bristle, the pollinia necessarily diverge. As soon as the saddle has clasped the bristle, and the pollinia have diverged, a second movement commences; which

action, like the last, is exclusively due to the contraction of the saddle-shaped disc of membrane. The second movement causes the divergent pollinia, which at first projected at right angles, to the needle or bristle, to sweep through nearly 90 degrees towards the tip of the needle, so as to seem depressed and finally to lie in the same plane with the needle. This second movement was often effected in thirty or thirty-four seconds after the removal of the pollinia from the anther-cells. The object of this double movement seems to be, to allow the ends of the pollinia to touch the double stigmatic surface, when the proboscis of the insect is pushed between the guiding ridges of the labellum into the nectary of the same or another flower. These stigmas are so viscid, that they rupture the elastic threads by which the packets of pollen are bound together; and some dark-green grains will be seen, even by the naked eye, remaining on the two white stigmatic surfaces."

The phenomena connected with the fertilization of *Listera ovata* may be given as another illustration. They are thus summed up:—"The anther-cells open early, leaving the pollen-masses quite loose, with their tips resting on the concave crest of the rostellum. The rostellum then slowly curves over the stigmatic surface, so that its explosive crest stands at a little distance from the anther; and this is very necessary, otherwise the anther would be caught by the viscid matter, and the pollen for ever locked up. This curvature of the rostellum over the stigma or base of the labellum is excellently well adapted to favour an insect striking the crest when it raises its head, after having crawled up the labellum, and licked up the last drop of nectar at its base. The labellum becomes narrower where it joins the rostellum, so that there is no risk of the insect going too much to either side. The crest of the rostellum is so exquisitely sensitive, that a touch from a most minute insect causes it to rupture at two points, and instantaneously two drops of viscid fluid are expelled, which coalesce. This viscid fluid sets hard in so wonderfully rapid a manner, that it rarely fails to cement the tips of the pollinia, nicely laid on the crest of the rostellum, to the insect's forehead. As soon as the rostellum has exploded, it suddenly curves downwards till it projects at right angles over the stigma, protecting it in its early state from impregnation, in the same manner as the stigma of Spiranthes is protected by the labellum clasping the column. But as in Spiranthes the labellum after a time moves from the column, leaving a free passage for the introduction of the pollinia, so here the rostellum moves back, and not only recovers its former arched position, but stands upright, leaving the stigmatic surface, now become more viscid, perfectly free for pollen to be left on it. The pollen-masses, when once cemented to an insect's forehead, will generally remain firmly attached to it,

until the viscid stigma of a mature flower removes these encumbrances from the insect, by rupturing the weak elastic threads by which the grains are tied together, receiving at the same time the benefit of fertilization."

In the case of another genus, Catasetum, the author points out a series of remarkable phenomena. In these plants, some mechanical aid is required to remove the pollen-masses from the receptacle, and to carry them to the stigmatic surface. Some of the species, such as *Catasetum tridentatum*, *C. saccatum*, and *C. callosum*, are unisexual, and require that the pollen-masses should be transported to the female plant, in order that seed may be produced. *Catasetum tridentatum* presents three forms—1. The ordinary male form; 2. The female form, which has been named *Monacanthus viridis;* 3. The hermaphrodite form, called *Myanthus barbatus*. These three sexual forms are borne on separate plants, but sometimes they are mingled together, so that the plant becomes Polygamous. The three forms are wonderfully different from each other. In the male and hermaphrodite flowers, irritable antennæ (tubular horn-like processes, formed by prolongations of the anterior face of the rostellum) are present, which are specially adapted to receive and convey the effects of a touch to the disc of the pollinium; causing the membrane to rupture, and the whole pollinium to be ejected by its elasticity. If we required further proof, nature has afforded it in the case of the so-called genus Monacanthus, which is the female plant of *Catasetum tridentatum*, and has no pollinia to eject—and here the antennæ are entirely absent.

"When the left-hand antenna of *Catasetum saccatum* (or either antenna of *C. tridentatum* and *C. callosum*) is touched, the edges of the upper membrane of the disc, which are continuously united to the surrounding surface, instantaneously rupture, and the disc is set free. The highly elastic pedicel then instantly flirts the heavy disc out of the stigmatic chamber with such force that the whole pollinium is ejected, bringing away with it the two balls of pollen, and tearing the loosely attached spike-like anther from the top of the column. The pollinium is always ejected with the viscid disc foremost." The pollen-mass is sent out with considerable force, sometimes even to the distance of two or three feet. The viscid matter sets hard, and firmly fixes the winged pedicel to the insect's body. The insect then flies from flower to flower till at last it visits a female or hermaphrodite plant; it then inserts one of the masses of pollen into the stigmatic cavity. When the insect flies away, the elastic caudicle, made weak enough to yield to the viscidity of the stigmatic surface, breaks, and leaves behind the pollen-mass; then the pollen-tubes slowly protrude, penetrate the stigmatic canal, and the act of fertilization is completed. How interesting and surprising are these complex and admirable arrangements.

Self-fertilization is a rare event with Orchids. In *Cephalanthera grandiflora* it occurs, but in a very imperfect degree, and the early penetration of the stigma by the flower's own pollen-tubes seems to be fully as much determined by the support thus given to the pillars of pollen, as by the production of a small proportion of seed; certainly the fertilization of this orchid is favoured by insects. In some species of Dendrobium self-fertilization apparently occurs; but only if insects accidentally fail to remove the flower's own single pollen-mass. In Cypripedium, the Frog Orchis, and perhaps in a few other cases, it will depend on the manner (at present unknown) in which insects first insert their probosces by the one or the other entrance, whether the flower's own pollen, or that of another flower, is habitually placed on the stigma; but in these cases there will assuredly always be a good chance of the stigma being fertilized by pollen brought from another flower. In the *Ophrys apifera* alone there are special and perfectly efficient contrivances for self-fertilization. "In this Orchid the caudicles are very slender; the mother-cells naturally open, and the masses of pollen, from their weight, slowly fall down to the exact level of the stigmatic surface, and are thus made to vibrate to and fro by the slightest breath of wind, till the stigma is struck. This phenomenon seems to be plainly adapted in this instance for self-fertilization. Hence, in this species, all the capsules are frequently perfected. At the same time there are manifest adaptations in this Orchid for the occasional transport by insects of the pollinia from one flower to another, as in the other species of the same genus." Darwin thinks that Nature tells us in the most emphatic manner that she opposes perpetual self-fertilization. He has endeavoured to prove this in the case of many other plants besides Orchids, and even in plants which are hermaphrodite, such as species of Primula. The conclusion at which he thus arrives is considered by him of vast importance, and as justifying the ample details given in this volume. "For may we not infer as probable," he says, "in accordance with the belief of the vast majority of the breeders of our domestic productions, that marriage between near relations is likewise in some way injurious; that some unknown great good is derived from the union of individuals which have been kept distinct for many generations?"

In reviewing all the variations which occur in the flowers of Orchids, the author thinks that "the simple and intelligible view is, that all Orchids owe what they have in common to descent from some monocotyledonous plant, which, like so many other plants of the same division, possessed 15 organs, arranged alternately 3 within 3, in five whorls; and that the now wonderfully changed structure of the flower is due to a long course of slow modification,—each modification having been preserved which was useful to each plant during the incessant changes to which the

organic and the inorganic world have been exposed." If we had every Orchid which has ever existed throughout the world, he supposes that "every gap in the existing chain, and every gap in many lost chains, would be amply filled up by a series of easy transitions." The more he studies nature, the more he is convinced of the correctness of his conclusion, "that the contrivances and beautiful adaptations are slowly acquired through each part occasionally varying in a slight degree, but in many ways, with the preservation or natural selection of those varieties which are beneficial to the organism under the complex and ever-varying conditions of life."

The connection between certain tribes of insects and orchids is well shown in the case of the beautiful Madagascar plant called *Angræcum sesquipedale*. This plant has a whip-like green nectary, 11 or 12 inches long, with the lower part only filled with nectar, and requiring visits from insects with very long probosces. In collecting the nectar, the insect requires to insert its proboscis up to the very base through the cleft of the rostellum, and by this means provision is made for the attachment of the pollinia to the proboscis during its withdrawal. The author remarks that, if the Angræcum in its native forests has its nectary filled more than in the specimens he examined, then small moths might obtain their share of the nectar, but the pollinia would not be moved, and thus fertilization would not be effected. The pollen-masses can only be withdrawn by means of an insect with a wonderfully long proboscis, trying to drain the last drop of nectar. "If such great moths were to become extinct in Madagascar, assuredly the Angræcum would become extinct. On the other hand, as the nectar, at least in the lower part of the nectary, is stored safe from depredation by other insects, the extinction of the Angræcum would probably be a serious loss to these moths. We can thus partially understand how the astonishing length of the nectary may have been acquired by successive modifications. As certain moths of Madagascar became larger through natural selection in relation to their general conditions of life, either in the larval or mature state, or as the proboscis alone was lengthened to obtain honey from the Angræcum, and other deep tubular flowers, those individual plants of the Angræcum which had the longest nectaries, and which consequently compelled the moths to insert their probosces up to the very base, would be best fertilized. These plants would yield much seed, and the seedlings would generally inherit longer nectaries; and so it would be in successive generations of the plant and moth. Thus it would appear that there has been a race in gaining strength between the nectary of the Angræcum and the proboscis of certain moths; but the Angræcum has triumphed, for it flourishes and abounds in the forests of Madagascar, and still troubles each moth to insert its

proboscis as far as possible, in order to drain the last drop of nectar."

In these passages we see the bearing of the facts of Orchid fertilization on the production of new forms, as propounded by the author in his work on the "Origin of Species." He traces all modifications through successive generation, and thinks that this is a better view of the case than to suppose that the Creator at once called into existence the varied forms of the present flora. He thinks that if we could trace back floral forms from generation to generation for long epochs, extending it may be over millions of years, we would be able to account for all variations in a more philosophic manner than by referring them to one creative fiat of the Almighty. He deprecates the idea of M'Cosh and others, that in these modified forms of great types the Creator displayed the plan and order of His work, and that in the abnormalities in the forms of organs and their gradation God has shown the principles of His arrangement, and has developed the workings of His all-creative mind. For our own part, we do not see the great superiority of the Darwin view over this latter hypothesis. Both are no doubt theoretical. The obstacles to the reception of Darwin's hypothesis in its full extent are great. To believe that all the forms of animals and vegetables spring from a cell, which through countless millions of ages has undergone an infinite series of transformations by natural selection, correlation of growth, struggle for life, &c., is certainly not an easy thing for the mind, more especially when *man* is included in the category. Here it is that the difficulty occurs; and it is precisely at this latter stage that the opponents of Darwin's views have a sure foundation to rest upon. For here Revelation steps in, to tell us of man's creation, of his relation to the Deity, of his present fallen condition, and of his future prospects, and speaks in such terms as to preclude the possibility of our adopting the Huxleyan view that, as the lowest ape, in the conformation of its skeleton, differs as much from the highest ape as the latter does from man, therefore we are merely transformed apes.

In his work on Orchids, however, Darwin does not stretch his view to this limit. He details facts with the utmost candour, and then very plausibly shows how they might be accounted for on his view of transmission by generation. Setting aside all theory, and looking at the work in itself, we have no hesitation in saying, that it is one of the deepest interest, well worthy of being studied; that it presents forms and functions to us under new aspects; illustrates in no ordinary degree the beautiful adaptations which are seen in plants, and is calculated to exalt our ideas of the wonder-working Jehovah.