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A few Notes on the Fecundation of Orchids and their Morphology.

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[PLATE IX.]

WHOEVER has read C. Darwin's remarkable work on the fecundation of Orchids must have regretted that the chapters on tropical and other foreign Orchids leave a certain amount of uncertainty on the mind of the reader until the observations and suppositions shall have been endorsed by actual facts observed in the native countries of these plants. To fill up, as far as lies in my power, this blank is the purpose of the following observations and notes, to which I have added some remarks which I hope will not be deemed out of place.

Of the larger-flowered *Catasetideæ* we have here in Trinidad three genera (defining the section somewhat differently from Dr. Lindley). These are *Catasetum*, *Coryanthes*, and *Stanhopea*. Of the first we have one species, *C. tridentatum*, very common, and in various varieties, of which some authors have thought proper to make species. It shows in this island both the extreme forms, which I do not hesitate to call male and female; very frequently intermediate forms may be seen. I may state at once that these latter are always sterile. The two principal forms have been described so often, and latterly so well by Darwin, that I may restrict myself to a very few words, bearing principally on the essential parts for fecundation.

The anther and pollen of the male flower are principally distinguished by size and quantity from the corresponding parts in the female flower; the microscopic character of the pollen-tetrades is the same in both. We shall see further on that it is not so with

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masses, &c., are in a much more considerable state of development, the deficiency is in the conducting tissue (*tela conductrix*), which is the true stigma of this and allied plants as far as function is concerned. While in the male flower there is only a thin layer of this tissue lining the stigmatic canal, it is very abundant in the

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female flower, mixed with a large quantity of sweetish mucosity. This secretion, while it probably causes the disaggregation of the cells of the conducting tissue, has the property of separating the pollen-cells when these latter are brought into contact with it. I could not, however, discover any difference in this respect between the pollinia of male and female flowers, for both were acted on in the same way; but there the resemblance ceases. Left a little longer in contact with this mucosity, the pollen-cells of the male push forth a vigorous vegetation of pollen-tubes, while from the pollen of the female only here and there a rudimentary tube may be seen.

I would here remark, that this action of the sweet mucosity on the cohering tissues of the pollen appears to me to belong to the phenomena of fermentation, in its wider sense. The same effect is produced by substances in a state of decomposition, and may be compared in some manner to the ripening of fruit. It must not, however, be confounded with the action of boiling on certain tissues of roots, where it is explained, according to recent researches, by the conversion of the outer layers of cells into pectose, which is rendered soft by boiling in water.

Although I have tried, like others before me, repeatedly to impregnate a male flower with its own pollen, I have always failed. The incomplete development of the conducting tissue explains this sufficiently. On the other hand, the operation never fails with the female flower when male pollen-masses are applied to it at the proper moment. The action of female pollen is at first not to be distinguished from that of male pollen, but until now I have not seen a case of complete success. The ovarium enlarges, the labellum &c. fade, pollen-tubes are emitted; but after a week or so the ovarium begins to fade, turns yellow, and finally drops, without bringing any seeds to perfection, or even without fecundation taking place.

Hildebrand has lately (Bot. Zeitung, 1863, Nos. 44 & 45) published detailed observations on this subject, without however stating anything not previously known. Does not the female pollen of *Catacetum* possess only one-half of the functions of the male pollen? In answering this question it should not be forgotten that both powers, although they admit of being considered separately, may be only consequences of the same physiological quality.

From the above it is made evident that the fecundation of the female flower must take place by means of the pollen of the male

flower, the pollinia are caught by the upper margin of the stigmatic cavity, which projects a little beyond the face of the column; and if the gland be then detached from the back of the insect, or the tissues which connect the pollinia with the caudicle, or this with the gland, break, fecundation takes place. I have been an eye-witness only of the first event; I conceive, however, the possibility of the other.

I have tried to represent the above by a sketch (Pl. IX. figs. 1, 2, 3). That the insects are attracted at first by the smell of the flower I take from the fact that the same insect visits *Coryanthes macrantha*, *Stanhopea grandiflora*, and *Gloxinia maculata*, all three of which have the same perfume. But the smell probably only gives notice to the insects; the substance they really come for, in the case of these Orchids, is the interior lining of the labellum, which they gnaw off with great industry, and for which there is a continual contest. The same substance is also very attractive to other insects, such as cockroaches, &c.

This same substance, *i. e.* some cellular tissue which these humble-bees gnaw off, exists also in the hypochil of *Coryanthes ma-*

I have not seen the fecundation of *Stanhopea*; it is visited by the same insect, and I have caught it with the pollen-mass of the plant on its back, but I do not see how it can insert the same into the stigma. The insect visits this flower again for the purpose of gnawing off some substance from the labellum; but the same is so far removed from the stigma, that it could hardly, in the fully-opened flower, perform the act of impregnation except in very rare cases and accidentally. I may say that *Stanhopea grandiflora* very rarely bears seeds.

The disposition of *Stanhopea*, and partly of *Catasetum*, where there is no stigmatic liquid substance secreted at the exterior of the column, and where consequently the pollinia have to be inserted into the stigmatic transverse cleft, is repeated in *Gongora maculata*, L. (figs. 4, 5, 6, magnified). This plant often bears fruit.

While in *Catasetum* one flower is always impregnated by pollen of another, the possibility of self-impregnation exists in the other three examples, and I have no doubt that it often happens. In *Epidendreæ* I have also noticed it many times; and I believe it is owing, in the latter cases, to the abundance of stigmatic viscosity on the face of the stigma, which is situated, in nearly all plants of this suborder, immediately below the pollen-bed. We have here in Trinidad three plants belonging to *Epidendreæ*—a *Schomburgkia*, a *Cattleya*, and an *Epidendrum*—which rarely open their flowers, and invariably are impregnated when they do not open them. In these cases it is easily seen that the pollen-masses have been acted upon by the stigmatic fluid, and that the pollen-tubes descend from the masses still *in situ* down into the ovarian canal. This has also been shown to be the case in a certain class of dimorphic flowers, as in *Viola* and *Oxalis*, where the pollen emits tubes from the anthers, which tubes enter the stigma and descend to the ovules (see H. v. Mohl, Bot. Zeitung, 1863, Nos. 42 & 43).

But, surrounded as we are by innumerable facts demonstrating that self-impregnation is, contrary to what was formerly supposed, *not* the rule, and *necessary* self-impregnation an extremely rare case, I must entirely demur to the conclusion that these few facts are destructive to the Darwinian theory, or, as Mohl has it, are of equal value to prove a contrary theory. Probabilities deduced from the number of observed facts must always enter for a large part into our theories, in sciences of a complex nature. It is true that a *complete* theory admits of no exceptions; but nobody will, I believe, maintain that the above theory has arrived at that state. A few residual facts will not disturb our admiration for it, and the harmony into which it has brought so many branches of natural history hitherto unconnected. As far as intercrossing, and the gradual variation and transformation arising therefrom especially are concerned, there is no necessity to represent to ourselves

('Linnæa,' xxii. 1849, translated by Henfrey in 'Scientific Memoirs,' part ii.) been acquainted with facts which support this idea. Subsequent studies, however, have modified my views on the subject, based principally on the development of the flower.

As long as the labellum of the Orchid flower is considered a complex organ, it separates the family from all those that might be compared with it—it stands quite alone. Besides, its degree of complexity is not fixed, as we have seen that Endlicher considers some of the "natura stylina" as entering into its composition. A most unphilosophic view has been taken of the various excrescences and lobes of the column and labellum, showing how the weeds of fantastic morphology will grow in the absence of guiding principles.

Writers like R. Brown and Darwin, who felt that simple fancies were insufficient in a matter of this importance, have thought that the distribution of the vascular cords in the axis at various heights would, if not decide the question, at least bring it near its solution. The result of their investigation has been favourable to the idea that the column consists of seven, and the labellum of three originally distinct organs.

The production and multiplication of vascular cords and their distribution belongs, however, to quite a different class of phenomena, and has only an indirect relation to what I should call morphologic tendencies or impulses. Like dehiscence, disarticulation, production of pollen, ovules, nectar, &c., it belongs to physiologic activity. Darwin accounts for the one by the genetic relation which exists between different beings and organs: for the other by adaptation, itself again consequent on natural selection, often giving by this happy idea the death-blow to the sterile and unhealthy principle of final causes. To persons who have dissected much, it must be evident that the transition of vascular cords into a given organ depends on their number principally, and on the relative space which the organ occupies on the axis at the time of its origin, and that their subsequent multiplication is equally dependent on the quantity of tissue which composes the organ in question.

If we look upon the labellum as a simple organ, the family is variously connected with the remainder of the Monocotyledons, and the labellum finds its analogue in various families of both great divisions of the vegetable kingdom (Phanerogams). At the same time the column must contain the nine interior organs of the flower, or, as I would express it, it is here where they partly have not made their appearance.

R. Brown, as is well known, first showed the great importance of organogenetic studies in questions of this kind. He was not led by them in this case, not perhaps admitting that these investigations are always decisive. Others, myself amongst the number, have tried to solve the question in this manner, and finished by owning that the decision was doubtful. Yet, if we consider how many other dark points have been settled by such research, I think the soberest course will always be to try our morphologic speculations on the touchstone of the same, and to accept nothing that has not been ratified by it.

It will be sufficient to describe shortly the development of the Orchid flower to bring out the important points which bear on the question at issue. I shall choose a common plant, *Catasetum tridentatum.* The three sepals appear at the same time, and are followed immediately by the two lateral petals. The labellum makes its appearance only after these, which accounts for its being generally partly covered by them. As the axis grows during this time, the labellum stands a little higher on it than the petals which theoretically belong to the same whorl. Nearly simultaneous with the appearance of the labellum is that of the anther, but the former occupies a larger space on the part of the flower where both are situated.

After this the flower becomes more hollow at the bottom, and the first traces of the ovarian cavity appear. The next organ which becomes visible is the anterior segment of the stigma, as a represented by the above little swellings, soon unite, in other plants (*Vanilla* e. g.) they remain divided. This state of things (*i. e.* a part of the stigma standing on the posterior side of the flower) lasts comparatively a long time; it is only late that, by an elongation of the axial part of the flower and a partial reversion, the stigmatic aperture is fixed on one side of the column, and a more or less considerable distance is created between its posterior lobe and the base of the labellum.

This is, I believe, the common mode of development; the bottom of the flower, marked by the undeveloped stigmata, is carried up nearly to the top of the column. In *Cypripedieæ* it is, as far as I can see, rather different, the parts of the stigma being more developed (fig. 16, *Selenipedium palmifolium*, Rchb. fil., column; fig. 17, the same very young) and more distinct from each other, even at a very early period. As this is the only plant of that section which grows wild here, I cannot contrast this with other species*.

The various appendages, excrescences, &c., which are observed on the full-grown column and labellum of so many Orchids are of very late origin, and prove their unessential nature in a morphological point of view, whatever their physiological importance may be.

From the above history of development I draw the following conclusions:—

The eccentric development of the Orchid flower begins with the labellum; and it explains why, when the other perigonial leaves are connected, it remains free, and also the frequent connexion of the same with the column. The successive appearance of the parts of the stigma is another consequence of the above eccentricity.

The part of the axis which bears the stigmata, and the organs immediately surrounding these, of which generally five, sometimes four, do not make their appearance, is afterwards considerably lengthened, and at the same time the eccentric development causes a partial reversal of its apex, and generally the bent or prostrate position of the anther, originally erect.

It is clear that the *Neottieæ*, in the later stages of their development, must have some differences.

As an example of an Orchid where the eccentric development of the flower is reduced to its lowest degree may be quoted *Thelychiton*, Endl. Iconogr. t. 29, where the stigma is central, surrounded by a six-lobed cup, bearing on one of its lobes the anther.

The only example that I am acquainted with of an Orchid flower in which all the stamens make their appearance, or nearly all, is a species of *Isochilus*, found here common enough, and in which this irregularity is very frequent. The flower is normally triandrous, but very often bears five anthers, with a filament proceeding from the front of the column just beneath the stigmatic cavity (fig. 18). If this filament should ever be found to bear an anther, we should have the Orchid flower restored.

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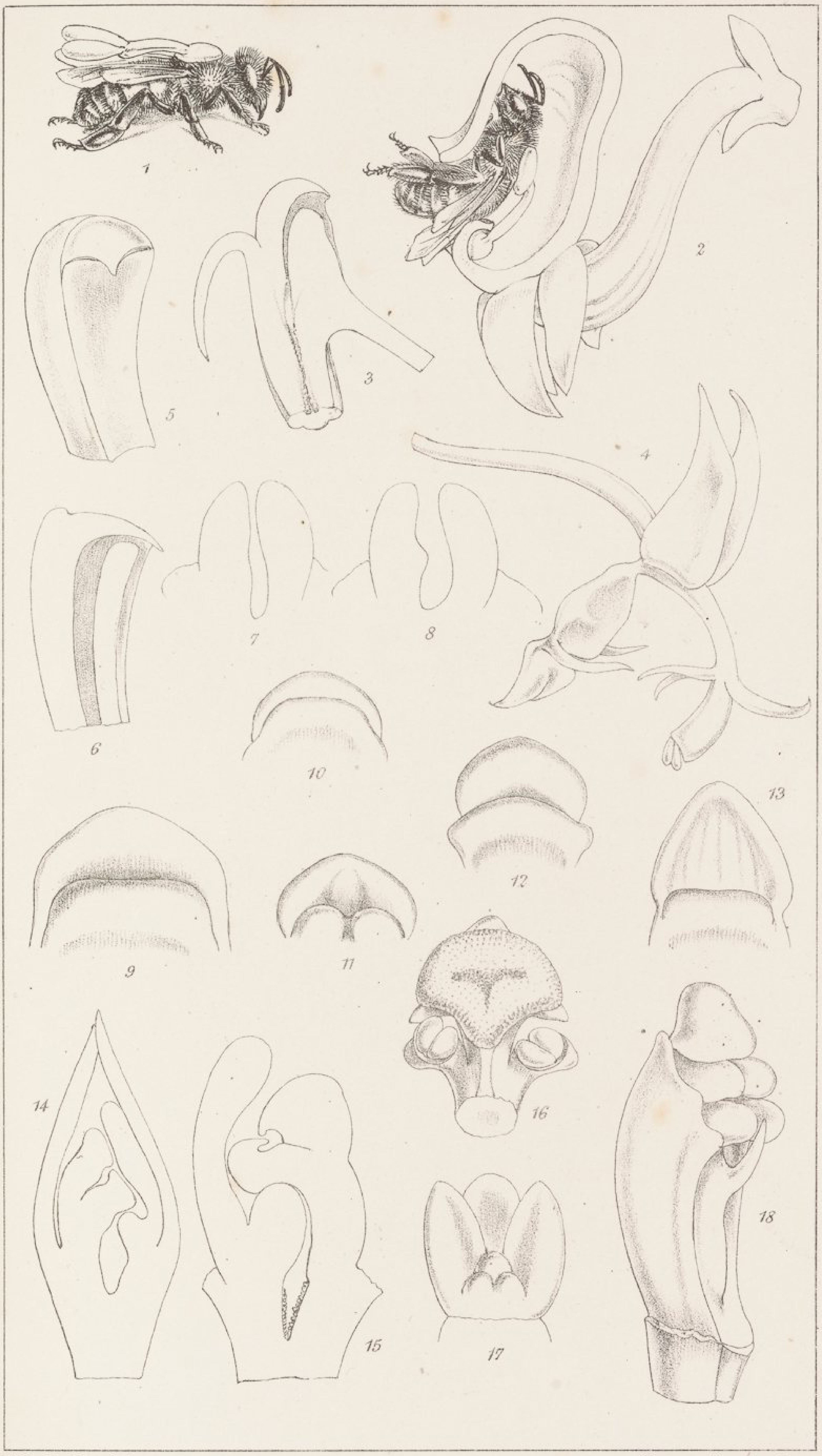

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