

Fig. 4. The same, in section. R. Rostellum; P. Pollinia.

5. The same at a later stage, the pollinia having become recurved into the stigma.
6. A later stage. The stelidia have curved over so as to overlap and press the pollinia into the stigma.
7. The same, side view.
8. The same stage, in section. *Gl.* Disc of pollinia.
9. Later stage. The pollen is now entirely plunged in the stigma and is almost absorbed.
10. Flower of *Ecceoclades maculata*, Lindl., from the side; nat. size.
11. The same, with the petals and sepals removed; enlarged.
12. Column, showing the pollinia falling forward.
13. Front view of column, with the pollinia still hanging from the clinandrium by the disc, but in contact with the stigma.
14. Pollinia, enlarged.

On the Fertilization of *Cattleya labiata*, var. *Mossiae*, Lindl.

By HARRY JAMES VEITCH, F.L.S.

[Read 2nd February, 1888.]

EVER since Darwin conclusively showed how the pollinia of certain orchids were conveyed to the stigmatic surface by insect agency, the subject of orchid-fertilization has been of special and even growing interest, not only to science through its further elucidation by the discovery of many new and interesting facts, but also to horticulture as serving to explain, at least in part, how it is that so many anomalous forms having the appearance of hybrids have made their way into European gardens. But while the observations of Darwin and those who followed him in the same track have been directed chiefly to the simple act of pollination by insect agency, the investigation of the process that follows appears to have received but a limited amount of attention. With the view, therefore, of adding, if possible, somewhat to the small stock of information already possessed, and also of deducing therefrom some practical results that may help to guide the operations of the hybridist, I and my assistant, with the aid of an able draughtsman, were induced to undertake the series of observations I am now about to bring under the Society's notice. Our purpose was to note the progress of the pollentubes during their course through the conducting-tissues of the column into the ovary; to detect, if possible, the act of fertiliza-

tion of the ovules, and to determine the time that elapses between pollination and that event; and, finally, to trace the development of the ovules after fertilization into perfect seeds.

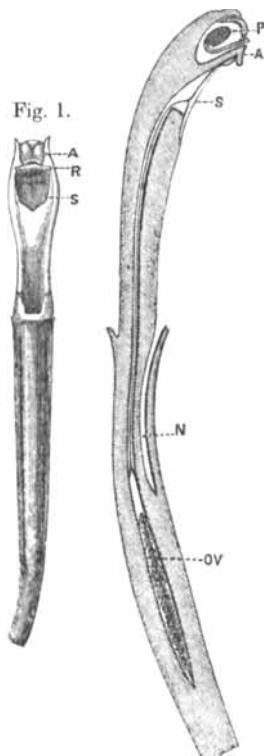
Before giving a *résumé* of our observations, it is necessary to state that we worked under the serious disadvantage of being confined, for such work, to a low microscopic power; that, with the exception of a little glycerine, we used no chemical reagents in preparing materials for examination; and therefore very many details of the minute structure of the parts examined are necessarily omitted. It is also necessary to premise that these observations were undertaken and made before we became aware of the fact that the subject had been partially investigated many years ago by Dr. Hildebrand in the Botanic Garden at Bonn, the results of whose observations were published in Mohl and Schlechtendal's 'Botanische Zeitung' for October 30 and November 6, 1863. Dr. Hildebrand there tells us that, incited by Darwin's most interesting researches, he was induced, during the winter and spring months of 1863, to undertake a series of observations on some cultivated and also on some native orchids, with the object of ascertaining the time that elapses between the pollination of the flower and the fertilization of the ovule, an investigation that appeared to him to be pregnant with unexpected results, seeing that the sexual apparatus of orchids differs so greatly from that of the great majority of other Phanerogams. For the results of these investigations I must refer to the memoirs quoted. Much of the ground, therefore, having been previously travelled over by Dr. Hildebrand, I am afraid that the simple facts I am about to bring before the Society have not altogether the merit of novelty to recommend them; yet they may prove to be of *some* interest, and serve to revive the subject of the fertilization of orchids, which still offers a wide field for investigation.

The subject selected for our object was the well-known *Cattleya labiata*, var. *Mossia*, Lindl., because we could command a good many plants for investigation, and because also in this *Cattleya* the column and its parts are among the largest to be found in the Orchidæ; we hoped that the probability of our being able to prosecute our search with some chance of obtaining results would thence be the greater. The chief characteristics of the column of a *Cattleya* of the *labiata* group are sufficiently familiar to most botanists. The column of one of the members of the group, apparently of the same that forms our present subject,

is well represented in Darwin's 'Fertilization of Orchids' at p. 161, where also some structural details are given. In the series of drawings made for illustration, fig. 1 represents the front view of the column and ovary of *Cattleya labiata*, var. *Mossiae*, two thirds natural size, a few days after the expansion of the flower. From the apex or top of the pollinary apparatus to the base of the ovary it is about 3 inches long; although shown upright in the figure, it slightly arches forward from below the stigma to the apex, the part so bent is thence parallel with the labellum, which is, in fact, appressed to it, and enfolds it with its side lobes, a circumstance that immensely facilitates the pollination of the stigma by insect agency. The stigmatic cavity is separated from the anther by a tongue-shaped rostellum; the stigmatic surface is coated with a thick layer of transparent viscid matter which holds the pollinia when applied to it with extraordinary tenacity. The pollinia are four in number, each pollinium, or pollen-mass as we are more accustomed to call it, is a waxy flattened disk, neither strictly oval nor strictly circular, but something between the two, or nearly the shape of an artist's palette, and is furnished with a semitransparent ribbon-like caudicle, which is also covered with numerous pollen-grains. The ovary is cylindric, and is traversed longitudinally by three equidistant sunk lines. Fig. 2 represents a longitudinal section of the column and ovary, one fourth larger than natural size, in which the positions of the anther, rostellum, and stigma are shown by the letters P, A, and S respectively; there is a duct or canal leading from the stigma to the ovary, down which the pollen-tubes pass. This canal in transverse section has the form of a W-shaped curve extending through the central part of the column where it is thickest, as shown in fig. 4; it is filled throughout with con-

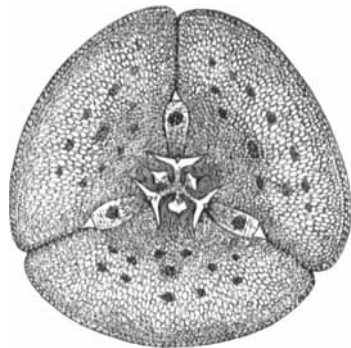
Fig. 2.

Fig. 1.



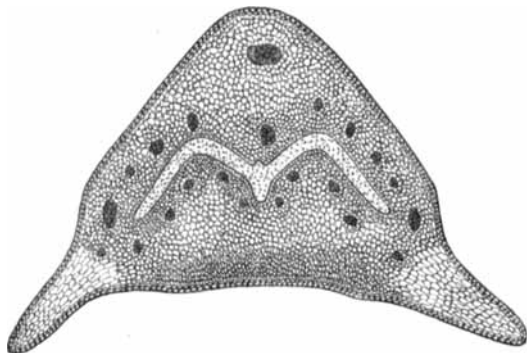
ducting-tissue which is of a very loose consistency, and formed of greatly elongated cells generally overlapping at their ends. The narrow slit at N (fig. 2) shows the nectary that penetrates into the ovary, and in which honey is freely secreted; OV is the immature ovary, of which, for the purpose of showing the parts more distinctly, an enlarged transverse section is given in fig. 3, where it is plainly shown to consist of three divisions or lobes, from each of which, where they approach at the centre, springs a placenta. Each placenta at this early stage consists of two thickened plates with their edges turned towards each other, and almost meeting, and thence almost enclosing a quadrangular space; the rudimentary ovules, or rather the

Fig. 3.



papillæ that are subsequently developed into ovules, are placed along the projecting angles of these plates. We shall see that this position of parts of the ovary is considerably modified as the process of fertilization goes on. Fig. 4 shows a similar enlargement of the column in transverse section. Although only eight times enlarged, it indicates sufficiently the parenchymatous tissue of the column and the position of the fibro-vascular bundles.

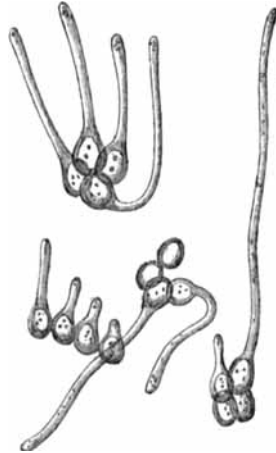
Fig. 4.



We are now in a position to trace the process of fertilization from the time of pollination to the impregnation of the ovules. On the 1st of June, 1885, forty-five flowers of plants of the same age

of *Cattleya labiata*, var. *Mossia*, were selected for pollination: the flowers were divided into three equal sets of fifteen each, of which one set was fertilized with their own pollen; a second set with the pollen of different flowers but of the same variety; the third set was fertilized with the pollen of flowers of a different species (*Lalia purpurata*, Lindl.), the whole of the pollinia being applied in every case. The object of so varying the circumstances was to ascertain whether the fertilization of the ovules and subsequent ripening of the seed would be in any way differently influenced or affected thereby. We shall see in the sequel that no material differences were observable, or at least, when any were noticed, they were of too trivial a nature to be taken into account. At the time the operation was performed the weather was fine and bright, and continued so for several days afterwards. Two days afterwards the flowers were examined, and one from each group was cut. The floral segments had already become flaccid, and showed signs of rapidly withering. Under the usual cultural treatment, the flowers of a *Cattleya* of the *labiata* group retain their freshness after expansion for upwards of three weeks, and even a month in cloudy weather; hence the effect of pollination on the floral segments is here made perceptible within a few hours. The pollinia in each case were found to be in course of disintegration, forming, with the viscid secretion from the stigma, a gelatinous mass that quite filled up the stigmatic cavity. On examination under the microscope, it was found in all three cases that the pollinia were breaking up into groups, generally of four granules, from some of which short tubes had already protruded; in the case, however, of the flower fertilized with the pollen of *Lalia purpurata* only a few such groups could be detected, and from these the tubes had but just started. In fig. 5 four of these groups of granules, with their tubes, are represented, as seen under the highest power at our disposal, that is, magnified 170 times.

Fig. 5.



Two days later we again examined a flower from each set. The column was found to be slightly

enlarged at and over the stigmatic chamber, and a change of colour, owing to their full exposure to the light, was perceptible in the epiderm. Nectar had freely exuded from the base of the column, and had spread itself over the ovary; the disintegration of the pollinia was seen to have advanced considerably, and pollen-tubes had pushed down into the canal to about a quarter of an inch below the stigmatic chamber. The flower fertilized with the *Lælia*-pollen was somewhat less advanced than the other two. An interval of four days was then allowed to elapse before a further examination was made. By that time the floral segments had become quite withered, and the change of colour in the epiderm of the column had become more manifest; at first, the ridge along the top was dull purple, but the sides were pale green. Transverse and longitudinal sections of the column and ovary showed that the tubes emitted from the pollen-granules had increased immensely in numbers, and the foremost of them could be traced as far as the base of the column. Fig. 6 represents roughly the state of affairs at this epoch; the pollen-tubes, as observed under a magnifying-power of about 75 diameters, are here seen passing downwards among the elongated cells of the conducting-tissue in vast numbers.

Four more days were again allowed to elapse before a further examination was made (June 9-12); the weather in the mean time having been clear and warm and the pollinated flowers having been fully exposed to direct sunlight, we expected to find that the process of fertilization had considerably advanced. The columns had now become much harder in texture and green in colour; the gelatinous mass in the stigmatic chamber had parted with much of its viscosity, and was changing to a rusty-brown colour; the ovaries were perceptibly enlarged, and pollen-tubes could be clearly traced to their entrance, and a few of the more advanced

Fig. 6.



had reached the apex of the placenta. The flowers in the three sets were now equally advanced; and from this time up to the conclusion of the observations scarcely any perceptible difference in condition was noticeable between them. From these and the previous observations, it now became very evident that the time which must elapse between the pollination of the flower and the impregnation of the ovules would be considerably longer than we anticipated.

It is now time to turn to the ovary itself, and to take note of the changes that took place there from the time of pollination till the impregnation of the ovules. The very rudimentary state of these at the epoch of the expansion of the flowers has been already mentioned. Fig. 7 shows transverse sections, natural size, in three different and successive stages of development—(A) shortly after the expansion of the flower and before pollination: (B) a fortnight after pollination; the change of form that had taken place in this short interval is very striking; the outline had changed from circular to triangular; the simple sunk lines of the earlier stage had widened into wedge-shaped clefts, dividing the whole into three well-marked carpellary lobes; each lobe has attained an almost triangular form by the enlargement of the placenta, and by the thickening of the walls of the ovary itself: (C) shows the further development about a month after pollination; the placenta and rudimentary ovules had then begun to assume a more definite form, although no signs of impregnation of the latter could be detected. On the day the last-mentioned section was made the pollen-tubes were found to have entered the ovary, and were pushing downwards along the sides of the placentas among the ovules. The condition of the ovules themselves

at the same date is represented in fig. 8, where an enlarged view of a minute section is given; it is there shown that they

Fig. 7.

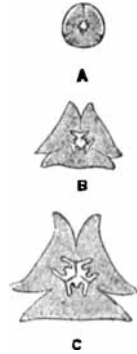
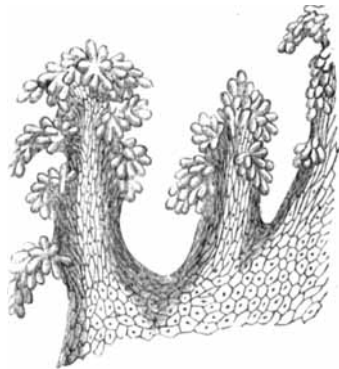


Fig. 8.



are grouped in clusters of no very definite form and outline; each ovule has the appearance of a single cell of ovoid form, but so minute are they at this stage, that no differentiation of parts could be made out under the low power to which we were restricted, although a faint reticulation was observable in some of the most advanced; but this may have been an optical effect. It was, however, evident that the actual impregnation of the ovules by the pollen-tubes, which we were anxious to detect, was yet remote, or at least it was apparent that that event would not immediately occur. In fact, we were up to this time simply groping our way towards trying to ascertain what we hoped would prove to be a most interesting scientific fact, but with the road to which we were very imperfectly acquainted indeed.

Our next examination was made fifty-five days after pollination; but, to our surprise, although the pollen-tubes had penetrated the ovary in countless numbers, and had completely choked up the canal leading from the stigmatic chamber to it, so that they had there taken the form of a bundle of fibres, minute as are the individuals composing it, and could be pulled away bodily in a coherent string, no actual impregnation of the ovules could be detected; the tubes lay along the sides of the placentas and among the ovules, and had reached as far as the bottom of the ovary. Moreover, all this while, and for some weeks afterwards, the summer weather was, for our climate, very favourable for the development of the impregnated flowers, the number of bright clear days being rather above the average. We waited 17 days longer before making a further examination; we then found that the ovules were not only enlarged, but were also undergoing a change in form—a fact that induced us to believe that the long sought-for event was at hand, and we accordingly made a further examination three days later, but no perceptible advance could be detected. We therefore desisted from further trial for another fortnight, that is till 90 days after pollination, when, at length we were able to understand with tolerable certainty the process by which the impregnation of the ovules is effected, and to get an idea of the space of time required for its accomplishment.

This will be best understood by reference to the diagrams. In fig. 9 are represented, two thirds natural size, two transverse sections of the ovary—D 55 days and E 72 days after the pollination of the flower; in fig. 10 a transverse section 90 days

after pollination, also two thirds natural size: these, with the drawings in fig. 7, form a series. The development of the ovules

Fig. 9.

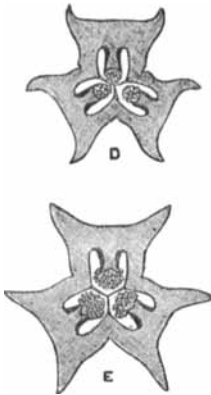


Fig. 10.

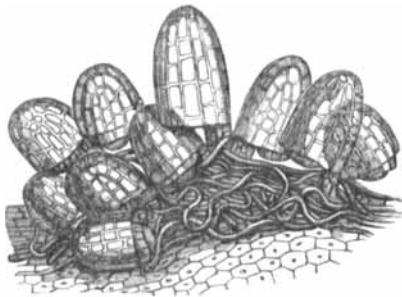


themselves is represented at five different stages in fig. 12, and four later in fig. 13, all greatly enlarged, thus:—

A, the ovule rudiment before pollination.

B,	„	„	30	days	after	the	pollination	of	the	flower.
C,	„	„	55	„	„	„	„	„	„	„
D,	„	„	66	„	„	„	„	„	„	„
E,	„	„	72	„	„	„	„	„	„	„
F,	„	„	75	„	„	„	„	„	„	„
G,	„	„	90	„	„	„	„	„	„	„
H,	„	„	120	„	„	„	„	„	„	„
I,	„	„	150	„	„	„	„	„	„	„

Fig. 11.



The series A–F simply shows the development of the rudiment into the perfectly anatropous ovule; it is at this stage that

impregnation takes place. That the pollen-tubes then come into contact with the true apex of the ovules is certain, but this was

Fig. 12.

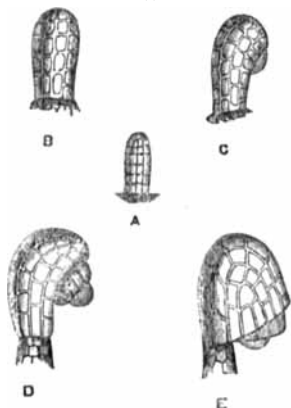
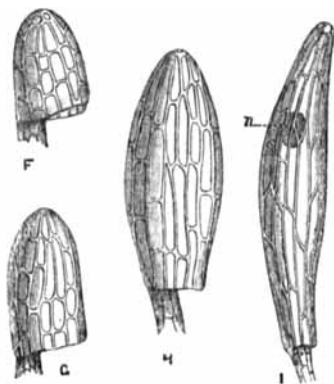


Fig. 13.



all we could detect. In no case could we find that the tubes actually penetrated the ovules; nor could we detect any embryo-sac or other differentiation of parts in the ovule itself under the low power we were constrained to use, and owing to the minuteness of the ovules even at this stage; but our failure to discover these parts by no means excludes the supposition of their existence, either in the form in which they occur in other monocotyledonous plants, or in some modification of that form.

But to return to observed facts. The pollen-tubes push down into the ovary in countless numbers, and make their way along the placentas and among the protuberances of it that bear the groups of ovules in the manner shown in fig. 11. The form of the ovule at this stage may be regarded as nearly cylindric, being slightly contracted at the apex. It will be noticed that this form differs considerably from the elongated spindle-shaped mature seed; and having still some materials left, we were desirous of observing one or two intermediate stages of the development of the former into the latter; we therefore cut one of the remaining capsules about four months after the pollination of the flower, and found the supposed impregnated ovules had attained the form represented by H in fig. 13. As this showed but a very slow development, we waited another month before examining another

capsule; by this time the ovules, or seeds as we should perhaps now call them, had become elongated in one direction and contracted in the other, as shown by I in fig. 13. A group of ovules at this stage, magnified 45 times, is shown in fig. 14.

It was now clear that the impregnated ovules had attained their mature form and size, although, from our experience in hybridizing orchids, we were sure the seed would not be ripe for some months to come. As the days at this period of our investigation were getting short and cold, and artificial heat alone had to be depended on to maintain the plants in health, we desisted from further



examination; and the few remaining capsules were left on the plants to mature their seeds or to fall, as the case might be, the latter being quite a common occurrence under the artificial conditions tropical orchids are cultivated in this country. When I say fall, the expression is not literally correct; the peduncle shrivels and withers, and the capsule dehisces before the contained seeds are mature, a cause due probably more to the murky condition of the atmosphere of London during the winter months than to any other I can suggest. It happened in the present instance that two of the remaining capsules failed in this way to mature their seed, and split early in March; the contents were examined, but showed nothing more than the shrivelling that would naturally be expected under the circumstances. The remaining two matured their seed and dehisced towards the end of May, or about twelve months after pollination. A number of the seeds were examined with the aid of the microscope; about one half were found to be plump; they may therefore be assumed to have been good; the other half consisted of mere dust and shrivelled ovules. The question at once suggested itself, Had these apparently abortive ovules ever been impregnated by the pollen-tubes? I think not; for on the same day the ovules were found in the condition represented in fig. 14, and

where numberless pollen-tubes were observed in the position there shown; in another section made from the same capsule no tubes could be detected, although the ovules had enlarged in the same way.

From the foregoing series of observations, we are enabled to deduce the following general statements :—

The impregnation of the ovules of *Cattleya labiata*, var. *Mossiae*, under glass in the climate of London takes place from 75 to 90 days after the pollination of the flower, the length of time being doubtless influenced by the state of the weather during the interval, and especially by the amount of direct sunlight the plants receive; the more direct sunlight, the shorter the interval, and *vice versâ*.

A proportion of the ovules only are fertilized; but how great that proportion is it is not possible to determine with certainty; it is never probably much less than one half; it probably varies from a little less to a little more than one half. It is certain also that of the seeds which are apparently mature and good, a greater or less proportion of them failed to germinate under artificial conditions.

It takes about twelve months, under the same conditions, to effect the maturation of the capsules; it being highly probable that during the winter months, when the temperature in which the plants are kept is comparatively low, and the amount of direct sunlight and sun-heat is at the minimum, there is a cessation of growth which is renewed as the summer months are approached.

In bringing my notes to a close, permit me to say that I have simply endeavoured to bring before the Society at least some of the phenomena that occur in the fertilization of orchids, which, so far as I am aware, have not previously been observed; and if in so doing I have added ever so little to our knowledge of the wonderful processes by which Nature effects the reproduction of these remarkable plants, I shall feel amply repaid for the time given to the investigation.
