On the method of fertilization in Bulbophyllum macranthum, and allied Orchids.

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With Plate XXII. A.

ALL who have examined the flowers of any species of *Cirrhopetalum*, or *Bulbophyllum*, cannot fail to have remarked the singular arrangement of the lip, which is usually small and inconspicuous, especially when compared with the lateral sepals, and is so loosely articulated with the prolonged foot of the column as to be exceedingly mobile, frequently being kept in a constant state of vibration by every current of air. How this state of affairs conduced to insect fertilization was altogether obscure. Darwin, in the Fertilization of Orchids, p. 138, states, after examining several species of *Bulbophyllum*, e.g. *B. cupreum*, *B. cocoinum*, and *B. Rhizophorae*, that he was quite unable to conjecture the use of this extreme mobility of lip, unless it were to attract the attention of insects; adding that possibly in the case of *B. barbigerum* and a few other species in which the lip is decorated with tufts of very delicate clubbed hairs, this may play some part in calling the attention of the fertilizer. But I shall hope to show an entirely different reason for this arrangement, which, especially in the case of *B. macranthum*, is I think one of the most beautiful and marvellous among all those in the Order.

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B. macranthum, Lindl. In this species the following organs are concerned in the process of fertilization. The lip is very small in proportion to the sepals. It is a curved tongue-shaped fleshy organ, acute at the apex and squared at the base, where it has two little projecting angles or ears, and a central groove. It is light yellow, the apex speckled with red, and is not smooth and polished like the sepals. The squared base is notched and balanced upon the apex of the column-foot, so that it hangs half through the aperture between the two sepals. It is prevented from falling quite through by the little ears which rest on the inner edges of the two sepals. It moves easily backwards and forwards upon its hinge, but in whatever position the flower is held, the lip always remains in the normal position, as shown in Figs. 3, 4, the centre being 4 mm. from the column. But a certain amount of weight placed between the ears causes it to fall backwards towards and nearly to touch the column. The column is a little more than 5 mm. in height, stout, and rounded at the back. The stelidia are short triangular processes, rather thin in substance but stiff; they stand out towards the lip, but slightly converge together at the apices, which are 2 mm. apart.

The anther is sunk in the clinandrium, and turned on its back, so that the apex touches the back of the clinandrium and the pollen-disc is exposed between the two stelidia. The pollen-masses are two, rather large, bright yellow, semi-transparent, pyriform, curved, bilobed.

The column is yellow, with a fairly long up-curved foot, the apex of the anther is red. From the position of the foot, which is curved upwards nearly to the height of the stigma, the squared base of the lip stands a little above and at some distance (4 mm.) from the stigma and pollen.

The fertilizer of this orchid is a small and active fly (Dipteron); it is diurnal, and delights in bright sunshine. I have seen it invariably close by when this plant is in bloom, and it also makes its appearance when *Dendrobium superbum* and another smaller flowered Sestochilous *Bulbophyllum*, which I

[1] Bot. Reg., 1844, t. 13.

have not identified, are in flower. I have never seen it at other flowers of any kind, nor have I ever found it elsewhere, except on one or two occasions when I have taken it on the white ceiling of my verandah in the heat of the day. But in whatever part of the house or garden any of these plants are in blossom, there will always be seen one or more of these flies, unless the weather be too dark or wet for them. The three orchids I have mentioned have but little in common, but they have all a certain amount of deep red colour in the flowers, the little *Bulbophyllum* last mentioned being entirely dark speckled red, and the *Dendrobium* having two deep red eyes at the base of the lip. They also all possess a very strong scent; *B. macranthum* that of cloves, the others of Turkey rhubarb. I endeavoured to find out which was the most important of these characters, by scenting pieces of dark maroon leaves and other objects with oil of cloves, but the flies took no notice of them, although the two scents are, to my senses, very similar.

The insect usually commences by licking with its short tongue the upper part of the sepals, both back and front. It eventually settles down to the front of the lateral sepals, especially on their dark coloured grooved apices. As long as it is at work in the narrow upper part of the sepals, it can hold on to their edges, but when it gets to the broad part, it cannot reach across. Its feet slip from the glassy surface, and it clutches wildly at the lip. Immediately its weight falls upon the lip the latter suddenly drops back, pitching the insect stern first into the column between the stelidia, which have enough springiness in them to separate a little and then close tightly on the abdomen of the captive (Figs. 5, 6). The insect strikes the disc of the pollinia with the upper part of its abdomen and the pollinia become fixed with exact precision upon the first segment, the lower part of the abdomen generally adhering to the stigma; the lip, released by the astonished fly, instantly returns to its original position, and the insect is left struggling on its back in the arms of the column; soon, however, it extricates itself, and flies away with the pollen on its back. As the

insect generally begins at the tips of the sepals, by the time it has got into the position for fertilizing the flower it has licked the sepals quite clean; so it flies off to another one, where the same operation is repeated, and the pollen placed upon the stigma of the second flower. The fly with the pollen upon its back is less active than when free, the pollen apparently being an appreciable weight to it; and it seems to me probable that, owing to this extra weight, the fly may on a second visit fall off the lip more rapidly, and so, falling a little lower, strike the stigma with the part of its abdomen with which it struck the pollinia before: but this I have not been able definitely to prove, and indeed there is the less need for it, because it must be remembered that when the fly strikes the viscid disc of the pollinia, the latter are at right-angles to its body; but when they are extracted, they fall by their own weight and lie at full length upon the insect's abdomen, which they partially cover.

It is essential that the fly's whole weight should be thrown upon the lip; one or two of its legs will not do, and smaller insects, as an ant or a thrips, will not pull over the lip. And a considerable amount too of pressure upon the pollen is required. A fly wandering about the sepals often puts its wings into the stigma, or on the pollen-mass, but does not move it. In one form of the plant which I have seen, from Borneo, the flower is much smaller, and shorter. In this case the arrangement is less successful, because some of the flies can reach quite across the broadest part of the sepals and hold on by the edges, so that they do not slip at all. It is therefore a decided advantage to the plant to have the flowers of large size, but the small-flowered form has one advantage, and that is a saving of time; for there being so much less area of food-supply it takes a much shorter time for a fly to work over the sepals in this form than in the other. I watched one fly for over an hour before it got into a position for fertilizing the flower, and long before this occurred, a fly appeared from a neighbouring plant with smaller flowers with a pair of pollinia upon its back. I should state, however, that three or four flies

were at work upon the smaller flowers and were jostling each other in close proximity to the lip. This saving of time is of considerable importance. The flowers only last two days at the outside, and a heavy shower of rain may come at any minute and spoil them. Besides, the mechanism of the lip is liable to get out of order, and it will not move properly after the flower has been open some time, if it gets at all dry. Although the mechanism is so beautifully arranged it does not always succeed. I have seen a fly twice running thrown from the lip without striking the pollen-masses. This was because it managed to use its wings before it reached the column, and so flew off. But it returned each time, until on one occasion it was not quick enough and was caught.

I examined the sepals carefully with the microscope to see what it was the flies obtained, and made transverse and longitudinal sections of the upper portion. The upper surface of the sepals is covered with an exceedingly thin layer of delicate, rather narrow and elongate cells, quite transparent and apparently empty. Beneath these is a layer of thicker and broader cells full of granular matter, which readily escapes when a section is made of the sepals; below these again is a layer of coloured cells. There are no definite saccharine glands; but, as far as I was able to make out, there seems to be an exudation of nectar on the surface of the sepals, perhaps analogous to honeydew, which seems to come from the second layer of cells. I was unable to detect any sweetness of taste on the sepals, and they always appear to be quite dry. One cannot help being reminded of the shining black bosses at the base of the lip in *Ophrys muscifera*, which has been seen (Hermann Müller, Fertilization of Flowers, p. 535) to be visited by a species of Dipteron (*Sarcophaga*). And one may reasonably doubt whether these and similar bodies are really sham nectaries, as Sprengel, Darwin and Müller seem to have imagined; for we have in this *Bulbophyllum* a flower with no visible nectar regularly visited by a species of Dipteron only seen besides on two very similarly constructed flowers; and furthermore this insect is evidently not disappointed in its

search, for it spends hours licking this flower, and if driven away speedily returns, nor will it visit a flower which is beginning to wither.

It is interesting to note that *Dendrobium superbum* is not a native of these regions, and so cannot strictly speaking be known to the native Dipteron, yet the insect, although evidently very particular in its tastes, is very quickly attracted to it. Another point is worthy of note in connection with the *Bulbophyllum*. In most of the species of the genus the lip is darker coloured than the rest of the flower, or at least more conspicuously ornamented; but here the conspicuous colouring is transferred, so to say, to the sepals, which are the attractive portion, though there are traces of the red colouring of the lip still left upon the apex of the inconspicuous lip. I do not believe that there are very many *Bulbophylla* that are fertilized exactly in this way. Nearly all the species, including most at least of the *Sestochilus* section, have the ovary twisted, and the lateral sepals thus hang downwards instead of being turned up as they are in *B. macranthum*; and the closely allied *Cirrhopetala* and *Megaclinia* have the same arrangement.

The *Cirrhopetala* are very rarely fertilized even in their native haunts, although they flower well and constantly. Many of the smaller *Bulbophylla*, however, constantly fruit, and I recently found a small species in the act of being fertilized by a small red Dipteron. This, *B. striatellum* mihi, is a small creeping plant with very slender filiform scapes bearing solitary terminal flowers. The three sepals are all similar, lanceolate with a filiform apex, half an inch long, connivent, yellow with red stripes. The petals shorter, oblong-lanceolate, stiff with rounded apices, and similarly coloured. The lip is loosely articulated with the foot of the column, very small, dark red purple, tongue-shaped, curved and fleshy. It is quite invisible from the outside, from being shorter than the sepals, which conceal it. The column has the usual shape, but possesses two setiform erect stelidia. As I have seen only a single flower, I cannot

give so detailed a description of its fertilization as I could of the preceding species. It appears, however, that a minute fly enters the flower between the sepals, presumably in search of nectar, and climbs upon the nicely balanced lip, with its head towards the base of the lip. Its weight overbalances the lip, and it is thrown headfirst into the arms of the column (Figs. 7, 8). The stiff erect petals play the part assigned to the stelidia, preventing the insect's escaping on either side, and the pollinia are planted between its eyes (Fig. 9). In this plant the insect cannot use its wings on account of the sepals being too close together, so that when once it gets on the lip it must go headfirst into the column. In these small-flowered species it is absolutely essential that the lip should be very delicately balanced, on account of the very light weight of the small fertilizer, and this I believe is the reason of the extreme mobility of the lip. I do not think it plays any part in attracting insects, although it is true that the lip quivers more in the species with open flowers than in those with closed or partially closed ones. But in the latter case the insect cannot use its wings, so that, even if the motion of the lip is slow, it is quite sure, and the fly cannot avoid falling with its head on the column. On the other hand, in open-flowered plants like *Cirrhopetalum* the fertilizer must be taken by surprise, and be suddenly pitched off, or it would escape; and for this it is essential that the lip should be exquisitely balanced.

In the typical *Cirrhopetala*, e.g. *C. Cumingii*, the lateral sepals are connate for most of their length, and the lip hangs in the space between their bases. The sepals are the most conspicuous portion of the flower, and it is probable that they form the alighting place of the fertilizer. The lip is separated from the margin of the sepals in front by a considerable space, so that a small insect wishing to get at the nectar at the base of the lip cannot do so without getting upon it. There is a small-flowered species of *Cirrhopetalum* here which is of very remarkable structure, and is apparently undescribed, in which I have seen the fertilizer at work. This species has the

dorsal sepal and petals ciliate along the edges and ending in long points, the lateral sepals form a funnel-shaped body ending below in two very long setae; all are dark red, with a little yellow at base. The lip is violet, lighter in the centre, and very conspicuous against the dark red petals and sepals. It seems to be glutinous and shiny. After the flowers were opened I found a very small black Dipteron, resembling a minute *Musca*, upon the lip. It was seated on the apex of the lip with its head towards the column, and appeared to be licking the lip. Presently it moved towards the lip-base, and as it did so the lip suddenly went over, throwing the fly into the column, where it stuck, the lip remaining in the same position. I attempted to secure the fly, but it released itself, and escaped without removing the pollen, and the lip sprang back to its old position. Probably I had touched the lip and so set the insect free, and if it had been left to extricate itself, it would have received the pollen upon its head in its struggles to escape. Shortly before this, while watching another species of *Cirrhopetalum*, also undescribed, I saw a similar fly, this time upon the broad flattened lateral sepals, which it was carefully examining. In the latter species which is an ally of *C. Cumingii*, and much resembles *C. pulchrum*, N.E. Brown (figured in the Illustration Horticole), but is smaller, the lip is dark-coloured, while the rest of the flower is comparatively light-coloured. The attractive part here is certainly the sepals.

Now to compare the principles of fertilization of a typical *Bulbophyllum*, such as *B. adenopetalum* or *Medusae*, with that of a *Cirrhopetalum*. In the first case the flower is partially closed, and the lateral sepals only serve to narrow the apprasch to the column. In the second case they frequently perform the function usually allotted to the lip, i.e. of an attractive alighting place. They are of different colour and form to the dorsal sepal, and much larger. The petals seem to play the same part in both, they are more inconspicuous, smaller, stiff, often in the latter case armed with cilia; in *B. Epicrianthes* they are reduced to a tuft of cilia, and serve to prevent the

escape of the fertilizer, and also I believe to put an obstacle in the way of its obtaining the nectar on the lip from the side of the flower. The lip in both is conspicuously coloured, at least if the flower is at all coloured. The balancing principle is the same in both ; but in *Cirrhopetalum* it is more perfectly arranged, since being nowhere in apposition with any other part of the flower, it is necessary that the fertilizer should trust itself wholly to the lip in order to get at the nectar with its short tongue, and also, for the same reason, there is no risk of friction with the petals or lateral sepals, so that the mobility is not at all impaired.

The flowers, especially the thinner-textured ones, last from 24 to 48 hours only in a fertilizable state, after which the lip becomes stiff and does not work properly. It is, however, rare for any orchid flower to survive the second day in its native haunts here; under any circumstances it will be effete forty-eight hours after opening, and usually in a very much shorter time.

In conclusion, taking the whole group of Bulbophylleae, including *Cirrhopetalum*, I do not doubt but that they are intended altogether for Dipterous fertilization. There is always a tendency to that dark red colouring so much associated with plants attractive to flies, as *Amorphophallus*, *Rafflesia*, *Arum*. The nectar too is not placed in a sac or tube, but on an open flat body, and is exuded in small quantities, so as to be easily licked off by Diptera. The nearly allied genus *Dendrobium*, on the other hand, is adapted for Bee-fertilization, and consequently the arrangement, structure, and colouring of the flowers are quite different.

B. striatellum, nob. Planta pusilla, rhizomate filiformi tenui longe repente. Pseudobulbi curvi, conici, pallide virides, vix ½ unc. longi, ½ unc. dissiti. Folium erectum, lanceolatum, acutum, 2 unc. longum, ⅓ unc. latum, subtenue. Scapus filiformis, pseudobulbo vix superans, vaginis 1–2 ad basin. Flos terminalis, parvus, clausus, nutans, pedicello unciali rubro. Sepala similia, oblonga vel oblongo-lanceolata, caudata, flava carinis tribus rufis, semi-unc. longa. Petala

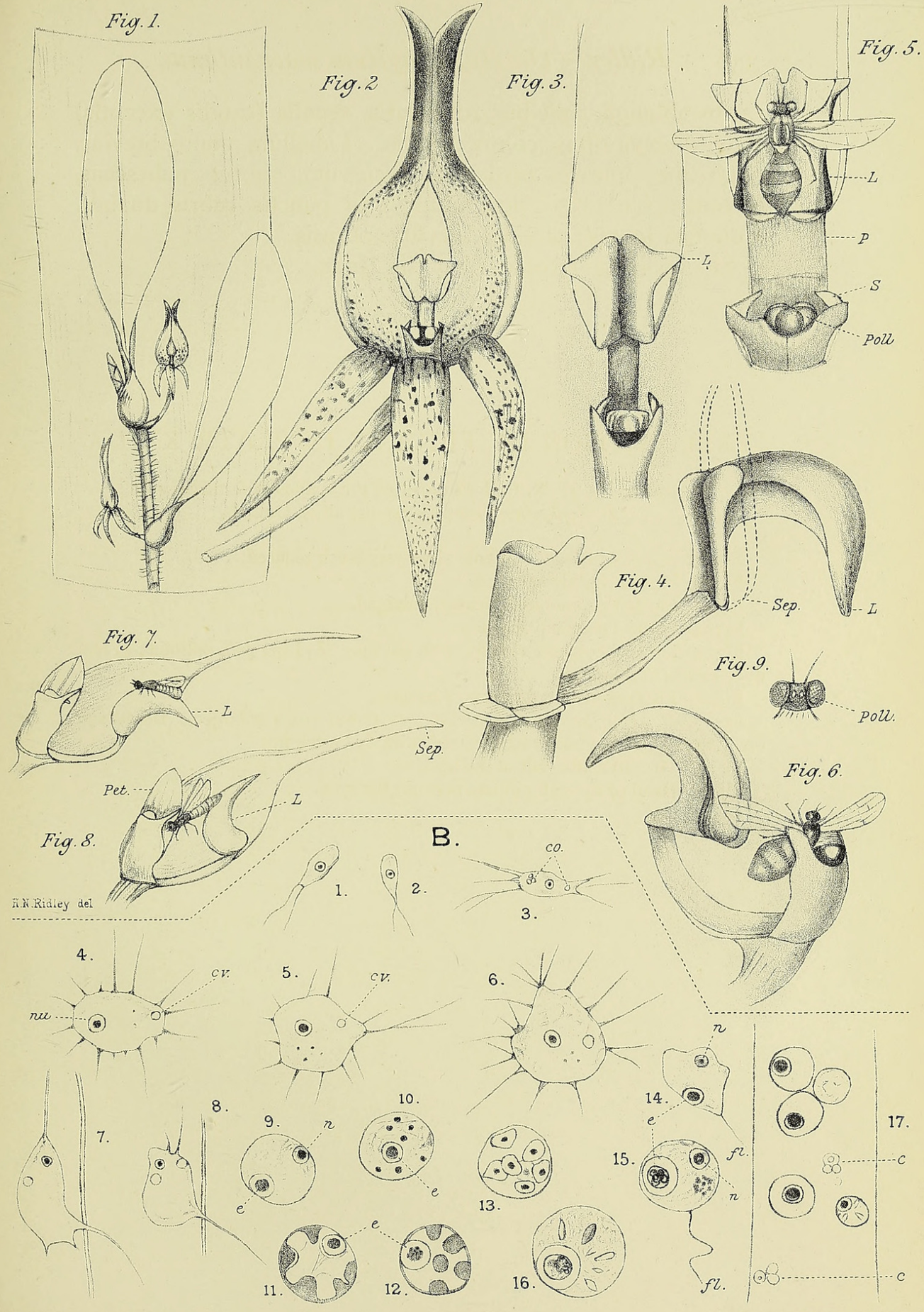
ovato-oblonga, apicibus rotundatis, sepalis (caudis exceptis) paullo brevioribus, colore similia. Labellum multo brevius, angustum, lineare, carnosum, recurvum, subtus pubescens, flavum apice rubro punctatum, basi punctis rubris duabus. Columna brevis; stelidiis brevibus obtusis.

Singapore, on trees at Char chu Rang.

EXPLANATION OF FIGURES IN PLATE XXII. A.

Illustrating Mr. H. N. Ridley's paper on the method of fertilization in *Bulbophyllum macranthum* and allied Orchids.

Fig. 1. *B. macranthum.* Whole plant very much reduced.
Fig. 2. Flower slightly enlarged.
Fig. 3. Lip and column from behind, enlarged.
Fig. 4. Lip and column, side view.
Fig. 5. Lip and column, with fly upon the lip. *L.* Lip; *poll.* pollinia; *p.* foot of column; *S.* stelidium.
Fig. 6. Fly thrown into the arms of column.
Fig. 7. *B. striatellum* mihi. Side view of flower much enlarged. Dorsal and one lateral sepal and one petal removed, with fly on the lip.
Fig. 8. The same after fall of the lip.
Fig. 9. Head of fly with pollinia between the eyes.



M.M.Hartog del.

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A. RIDLEY.—ON FERTILISATION IN BOLBOPHYLLUM.

B. HARTOG.—ON A PARASITIC MONADINE.