ing sown to poison birds.—Mr. H. C. E. on this matter. Mr. V. H. Miller stated 1 had ever sold seed for such a purpose.

### **EXHIBITS**

oral Fish, Whale Barnacle (Chromodoris, ven valves.

Calanthe veratrefolia, Pimelia decussata,

all garden-grown. series of the various forms of the mineral

## BACKED SPIDER

the March meeting was a glass tank conbacked spiders (Latrodectus hasseltii), the rarer male, very small by comparison, large number of baby spiderlings. This some time for purposes of photography, ith insects through a safety aperture in The spiders were exhibited primarily to ral untidy appearance of the web nest, and coloration of the dangerous female, aroused by another death (of a man in the bite of this small spider.

alize quite how fortunate they were in During the night, after they had been pparently completed their nuptial cereing the male was found dead and sucked to tank—obviously killed by his spouse, emale constructed another egg sac, which om of the tank to the top (apparently for distance of nine inches. From these it appears that most of the activities of night.

a more detailed note will be contributed

## ERRATA

The Victorian Naturalist, Vol. LVI, No. 11,

lonned" should read "had donned". Page 180, ld read "A. scoparia". Page 180, line 14: "var. ar. purpurascens". Page 180, line 27: "(Maiden Maiden & Blakely)". Page 180, line 43: "Alpine e localities". Page 180, line 44: "tree, Richea" Page 181, line 43: "Dicheclachne crimita" should

April 1940

# GARNET, Observations on the Pollination of Orchids

# OBSERVATIONS ON THE POLLINATION OF ORCHIDS By J. Ros. Garnet, Melbourne

The observations I am about to record concern the pollination, by a tiny fly, of a group of four species of the relatively large genus of Australian terrestrial Orchid, *Prasophyllum*, R. Brown.

The four species, Pr. Morrisii, Nicholls, Pr. Archeri, Hooker f., Pr. nigricans, R.Br., and Pr. despectans, Hk.f., have been in cultivation for several years and my interest in the progress of the plants from year to year was soon coupled with an interest in the process of pollination that went on in the flowers.

A point that was soon noticed was that the pollinia of a number of flowers of each of the species was missing when I came to examine them. Occasionally the missing pollen was traced to a stigma, where its presence was recognized by the altered appearance of the stigmatic surface. Normally smooth and glistening, it becomes rough and frosted after pollen absorption and no trace of the original pigment of the pollen remains.

As an explanation of this pollen transference it was thought that, as the plants were growing in small pots out of doors, agitation by wind may have caused the pollinia to spring from the anther in the manner not unusual with some of the larger members of this genus. Further agitation during transference of the plants to a place suitable for further examination may then have dislodged the pollen masses and caused their fortuitous deposition on the stigma.

That this conclusion was improbable was demonstrated later, when it was seen that several flowers on plants of each of three species which were, at that time, in cultivation, and which had not been cut, began to exhibit fruits. These, in course of time, dehisced and produced fertile seed. Thus it seemed that some external agency was responsible for the fertilization of the flowers.

In the following autumn a careful watch was kept to determine the identity of the mysterious agent. Prasophyllum Morrisii was the first of the group to bloom—a sturdy specimen with fourteen flowers. With all the satisfaction of one who has induced profuse bloom in a shy exotic Orchid, I was wont to stand and admire this bewhiskered Prasophyllum with its comically tremulous labellum; and one crisp sunny morning in March, 1934, I had the satisfaction of having the problem of the plants' pollination solved for me.

Several tiny flies appeared to be greatly attracted by the flowers, climbing over them, and often some, evidently more daring than others, made their way on to the labellum, where they appeared to browse in a leisurely fashion. Once on the surface of the labellum they seemed to lose interest in the outside world,

and the pot containing the plant could be lifted up and inverted to permit of examination with a hand-lens of their further manoeuvres. It was then seen that the flies became more eager the further they progressed, until, reaching the dead-end of the column, they settled themselves for two or three minutes, evidently feeding on the glandular excretions that occur at the base of the labellum. Here they assume a position similar to that shown in Fig. O, Plate XVIII.

After satisfying myself that this was not merely a chance occurrence, a large test tube was lowered over the flower-spike, and in due course three flies, each of which had pollen adhering to the dorsum of the thorax, were collected and subsequently

examined.

During the ensuing fortnight these visitations were frequently observed, until the several anthers of the plant were bereft of their pollen. Two flowers, evidently pollinated, were removed and examined under the microscope, and it was seen that the stigma of each showed the characteristic signs of pollen absorption.

Later in March, and during the first half of April, Pr. Archeri and Pr. despectans bloomed, together with other plants of Pr. Morrisii. It being Easter, there occurred ample opportunity for keeping them under observation, and it was found that the flies established a definite order of preference of one species of flower to another, the order of favour being Morrisii, Archeri, despectans. It seemed that only when the feeding grounds on the first two were exhausted did they visit despectans. In 1934, I saw no flies visit the latter; nevertheless, in two plants which were permitted to die a natural death, pollination had occurred in 8 of the 10 and 4 of the 15 flowers, respectively. In two plants of Pr. Archeri pollination had been effected in 14 of the 15 and 4 of the 5 flowers a quite high percentage! The popular Pr. Morrisii, despite the marked hospitality it afforded its visitors, gave a relatively low yield of fruits. For the two plants which were not cut and pressed the results were 6 of the 10 and 3 of the 11 flowers pollinated.

It is interesting to note here that the fruits are observed to take just over two months to ripen and dehisce. This is an average period and naturally the process of ripening is governed to a large extent by weather conditions. A further point of interest is that seed dispersal thus takes place in the late autumn or, in general, during the frosty weather and before the onset of the

winter rains.

In the autumn of 1935 the same set of Prasophylls was again kept under observation, and as *Pr. migricans* had been added to the collection in 1934, flowering plants of this species were also available for study. One specimen bloomed early in March—almost a fortnight in advance of plants of the three other species

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ALCALM MANAGEMENT

Plate XVII

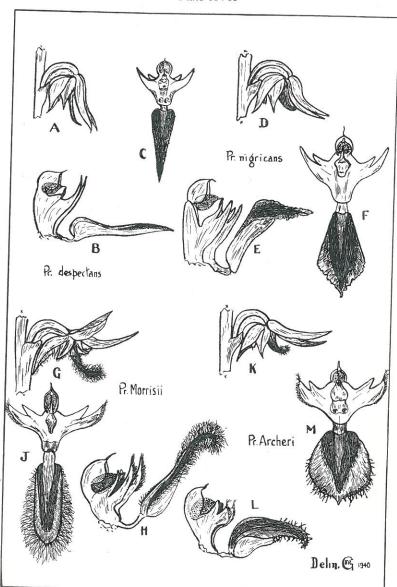
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For Key see page 197

-and it was seen that this species also attracted the tiny flies. In seven days the twelve flowers had expanded and two fruits had set, and when the plant was cut and examined at the end of this period it was seen that all but three of the anthers were bereft

of their pollen.

Later in March and during April, as representatives of the three other species flowered, it was again seen that Pr. Morrisii was first, while Pr. Archeri and Pr. nigricans seemed to share the honours for second place. During this season the flies were observed to enter the somewhat smaller flowers of Pr. despectans. and that pollination was effected was soon evident by the swelling fruits of 4 of the 23 flowers on one sturdy plant. The smaller and narrower opening to the inner structure made observation of the progress of the flies rather difficult, but it was seen that much the same course was followed as in the other three speciestentative browsing at the entrance and on the lamina of the labellum, followed by a more determined penetration into the interior, where a short stay occurred, the fly finally backing out with pollinia adhering to the dorsum of its thorax.

While carrying out these studies I realized the significance of the column appendages and the hinged labellum. Reference to the figures in Plate XVIII will show that one of the differentiating features of the four species is the shape and structure of the column appendage. It is easy to imagine that the characteristic shape of these processes has been evolved to meet a definite contingency, and if one compares flowers of each of the four species under discussion it will be seen that the angle of the sinus formed by the margins of the petals and dorsal sepals varies from species to species, being from 60 to 70 degrees in Pr. Morrisii and Pr. Archeri from 45 to 55 degrees in Pr. nigricans, and quite acutefrom 30 to 40 degrees—in Pr. despectans. In each type the appendage to the column is modified in such a way as to prevent lateral movements and egress through this sinus by a visiting

insect.

As part of the marvellously contrived mechanism the labellum plays its important part. In each of the species the callus plateof the labellum is represented by two parallel elongated glands arising at and occupying almost the whole of the proximal end and extending in decreasing width to the distal apex, near which they fuse and merge with the non-glandular lamina. These raised lines of the callus plate evidently constitute the preliminary feedinggrounds of the visiting insects. Experiment showed that a tiny drop of fluid exuded whenever the plates were stabbed with a fine needle, and it was also seen that the labella of freshly expanded flowers were liberally bedewed with minute drops of glandular exudate arising from the elongated gland.

Further examination of the labella showed that at the base of each there is a smooth, somewhat glistening and roughly triangular depression between the two raised lines. This area is connected to the hinge-like claw and it is possible that pressure on this area assists in maintaining the labellum in a rigid position when the visiting insect is properly installed on it. This is mere supposition, but the observable fact is that the labellum swings down on its hinge as the fly penetrates into the flower and while feeding at



Microphotograph of dipteran responsible for pollination of Prasophyllum Archeri Hk. f. Pollinarium of orchid attached to dorsum of thorax of fly.

Photo. by J. Ros. Garnet.

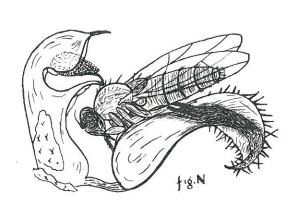
the base of the labellum the segment remains poised rigidly in a position that appears actually to confine the fly, the dorsum of its thorax being in contact with the rostellum. The few short bristles on the thorax are directed backwards and the slightest movement on the part of the visitor suffices to rupture the membrane covering the viscid disc of the rostellum. The exuding fluid adheres to the thoracic surface and when the fly finally backs out of the flower it carries with it the pollinarium firmly attached.

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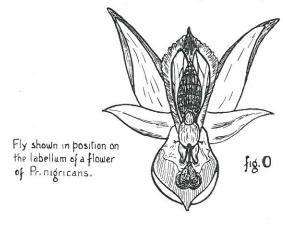


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Column & labellum of Pr. Archeri with lateral appendages of column removed to show position of rostellum in relation to the dorsum of the thorax of the fly.



Delin. & 1940.

The accompanying microphotograph shows two flies, both of the same family, collected from the flowers of *Pr. nigricans*; the larger one, to which is attached the pollinarium of the Orchid,

being actually 2 millimetres long.

From curiosity, an attempt was made to weigh the fly; however, the sensitivity of the balance at my disposal was such that I could only estimate its weight to be of the order 1/20th of a milligrame (i.e., 0.00005 gramme). This is a point of interest when considering the possible mechanical effect of the weight of the small dipteran on the balance of the labellum. When the flower is open to visitors the labellum is invitingly directed upwards, and it swings down towards the dorsal sepal only after the fly has passed into the interior of the flower. Whether this movement of the labellum is due entirely to the weight of the insect or to irritation of the basal triangular depression to which I have previously referred, is a matter for speculation. It is possible that the proboscis of the fly brings about an effect on the claw of the labellum in much the same manner as the claw of the labella of the genus Pterostylis is affected by the visitors to the flowers of that genus (vide O. H. Sargent, Vic. Naturalist, 1934, li, 82).

It is difficult to imagine what, in the first instance, attracts the flies to the flowers of these four Prasophylls. To the human eye the general appearance is far from showy, the colours being subdued tones of red and green, the red component ranging from maroon to purplish black. It may be mentioned in passing that Pr. despectans evidently occurs in two varietal forms, distinguishable mainly by their general aspect as being green or purplish-black. Of the four species under discussion, Pr. despectans alone appears to emit perfume, and it is interesting to note that, in my experience, the green form of that species is more noticeably fragrant than the dusky variety. Both forms have been in cultivation in the same pot over a period of more than six years, and although there have been variations from year to year in robustness, slenderness, size and the number of flowers on the spike, the characteristic hue of the flowers has remained constant.

Since the possession of colour and perfume are features that are not shared alike by the four species, it is safe to assume that the attraction for these little flies does not lie therein. Such characteristics, more obvious to our senses, may serve their purpose by attracting other insects (for visits by other insects do certainly occur). During March, 1937, I came across a robust specimen of *Pr. Morrisii*, near Heathmont (Victoria), in one flower of which a small dipteran was found evidently stupified, in which condition it remained for sometime afterwards. This fly, somewhat larger and sturdier than the usual visitants, was easily withdrawn with a pair of forceps. Having removed the insect, I was rather dis-

appointed to find that no pollinarium was attached to it. It may, of course, have been a mere chance visit by this insect, which was subsequently identified by Mr. J. Clark of the National Museum (Melbourne) as a species of *Drosophila*, commonly known as "ferment flies."

The identification of the flies that definitely pollinated the flowers of the four Prasophylls proved rather difficult. The late Mr. A. L. Tonnoir, of the C.S.I.R. (Canberra) examined a number of specimens which I had submitted to him, and he stated that there were "four species (perhaps five), three genera and two families represented in the series." It appeared that the flies so frequently observed on the plants included Caviceps flavipes Malloch, Oscinosoma subpilosa Beck, and an as yet undescribed species of Oscinosoma, all of the family Chloropidae.

That the visits of *Oscinosoma* are no mere chance is evident by the regularity and frequency of the occurrence and by the fact that they have been observed in districts as much apart as East Malvern and West Brunswick, in which places most of the observations I have recorded were made; and much further afield at Bayswater, where, in the autumn of last year (1939), a number were collected from the numerous specimens of *Pr. Morrissii* and *Pr. Archeri* that

grew in the district.

No reference has as yet been made to the mechanism of pollen transference. The minuteness of the flowers makes observation of the process impracticable, but with the aid of the microscope the course of events can be deduced with reasonable certitude. Without unduly reiterating the points stressed by Edith Coleman in her several papers on the pollination of our native terrestrial orchids, emphasis must again be laid on the importance of the caudicle in the process. Careful examination suggests that the pollinia is partly withdrawn from the anther while the flower is expanding or immediately after it has opened. The effect is facilitated by the contraction of the stigma-rostellum structure, which bends forward slightly. As the flower ages the beak of the rostellum describes a larger arc and the almost muscular action of the caudicle comes into play, with the frequently observed result that the pollinia are "sprung," i.e., rotated through an angle of more than 90° until poised either above or in front of the column. Once this stage is reached, removal of the pollinarium by insect agency becomes unlikely—a supposition supported by the observation that freshly expanded flowers prove the most attractive to the diptera, and one which explains the fact that on those occasions when I waited until the whole raceme of flowers had opened, nearly all but the terminal flowers had lost their pollinia.

The fly, having withdrawn from the flower burdened with its load of pollen, appears to be in no way daunted nor satiated, for almost directly it has been observed to commence browsing on

another f quite shor pollina att first almo pollen ma: to the hea the microlection of poised for This proce

Among in genus, auto fertilization autumn-flor invites spectamong them is produced myself and as hybrids, four species. In such circular, hybridization

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A, D, G & K.-

C, F, J & M.—

B, E, H & L.—

Dr. H. Fleck R. E. Painter, Mr. Painter Flora, Vol. 4, b plants (those ca belong to the sa April 1940

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another flower and following the same procedure. During the quite short interval between exit and re-entry the caudicle of the pollina attached to the fly functions in a remarkable manner. At first almost erect, it quickly collapses, with the result that the pollen mass is rotated so that it lies almost horizontal in relation to the head and thorax of the fly. This aspect is illustrated in the micro-photograph, which was taken some long time after collection of the specimen. In this position the pollen is correctly poised for implantation on the stigma of the flowers next visited. This process is illustrated in Fig. N, Plate XVIII.

Among multi-flowered species, such as those of the Prasophyllum genus, autopollination may be taken as the most common form of fertilization, and the fact that pollination of at least four of the autumn-flowering species is occasioned by the same type of insect invites speculation as to the likelihood of cross-pollination occurring among them. If such does happen it seems doubtful that fertile seed is produced. Field observations have not, in the experience of myself and others, revealed any plant forms that could be regarded as hybrids, although in a number of localities two or three of the four species mentioned are sometimes found growing together. In such circumstances one might expect to find some evidence of hybridization should it chance to occur.

The pollination of four autumn-flowering species of *Prasophyllum*—a genus of terrestrial Orchid—by various small acalyptratae Diptera of the family *Chloropidae* and especially of the genus *Oscinosoma*, is reported, and attention is drawn to the significance of certain structural features of the flowers in relation to the mode of pollination.

## EXPLANATION OF PLATE XVII

- A, D, G & K.—Flowers of Pr. despectans, Hook. f., Pr. nigricans, R.Br., Pr. Morrisii, Nicholls and Pr. Archeri, Hook. f., in profile.

  (Approx. × 4.)
- C, F, J & M.—Column and labellum (extended) of each of the above four species showing the characteristic shape of the lateral appendages to the column and the peculiarities of the lamina and glands of the labellum. (× 5.)

  Column and labellum of each of the same four species showing
- B, E, H & L.the relation of the labellum to the lateral appendages, rostellum, pollinia and anther, in profile. ( $\times$  5.)

## PITCHER PLANTS

Dr. H. Flecker, of Cairns, sends the following correction to a note, by R. E. Painter, on page 87, of the September issue of *The Naturalist*:—

Mr. Painter lists some eight species of Pitcher Plants from *Queensland Flora*, Vol. 4, by F. M. Bailey. However, it should be stated that all supports of those called Pitcher Plants in Australia) have since been shown to plants (those called Pitcher Plants in Australia) have since been shown to belong to the same species, namely N. mirabilis of Druce.