Notes on the anthecology of *Pterostylis curta* (Orchidaceae)

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Bernhardt, Peter[1] (National Herbarium of New South Wales, Royal Botanic Gardens, Sydney, Australia 2000) 1995. Notes on the anthecology of Pterostylis curta *(Orchidaceae).* Cunninghamia 4(1): 1–8. Field observations suggest that *P. curta* R.Br. is pollinated by male fungus gnats in the genus *Mycomya* (Diptera; Mycetophilidae). The viscidium is deposited dorsally on the gnat's thorax. The labellum is self-motile and irritable. Manipulations of *P. curta* under controlled temperatures show that the majority of labella reset and regained irritability (responsive to direct contact) two to three hours after they had been triggered the first time. Flowers of cultivated plants fail to self-pollinate. These three observations suggest that some populations of *P. curta* require cross-pollination by insect vectors.

Introduction

Pterostylis R.Br. (Orchidaceae) is a geophytic genus of about 120 species (Johns & Molloy 1985; Clements 1989) endemic to Australasia, reaching its centre of diversity through the wet temperate and coastal regions of south-eastern Australia, Tasmania and New Zealand (Bernhardt 1995). As in the Australasian genus *Caleana* (*sensu* Bernhardt 1994), *Pterostylis* species are usually characterised by 'spring trap' flowers (Dressler 1981). In a spring trap flower the labellum petal is both irritable and self-motile. Direct but slight pressure on the lamina causes the labellum to change position spontaneously and rapidly so it collides with the winged column.

In *Pterostylis* species, labellum movement should trap the prospective pollinator between the labellum lamina and the column wings and rostellum for 30–90 seconds until the labellum hinge begins to reset spontaneously. As the labellum begins to return to its original position the pollinator is released and can escape through a sinus formed by the inflated hood (galea) and the fused lateral sepals (Jones 1981).

Despite similarities in the floral mechanisms of *Caleana* and *Pterostylis,* the two genera have different flowering seasons and attract different pollinators. *Caleana* flowers appear from mid-spring through early summer. They appear to be pseudocopulatory systems pollinated exclusively by male sawflies (Cady 1965; Bates 1989).

In contrast, the floral phenology of *Pterostylis* species in south-eastern Australia peaks in late winter through mid-spring (August to early October). The pollination syndrome of *Pterostylis* has been open to several interpretations since the turn of this century (see review by Jones 1981).

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Pterostylis appears to belong to a guild of terrestrial, winter-early spring-flowering orchids (*Acianthus*, *Corybas*, *Rhizanthella*) that are pollinated exclusively by micro-dipterans in the families Culicidae, Phoridae and Mycetophilidae (George & Cook 1981; Jones 1981; Dafni & Bernhardt 1990). Species pollinated by mycetophilids (fungus gnats) tend to produce greenish to rusty to deep-iodine-coloured flowers that either lack a discernible fragrance or smell like carrion or ripe fungi (Vogel 1973). *Acianthus* flowers produce nectar, while nectarless *Corybas* species appear to mimic mushrooms and appear to be pollinated by ovipositing females (Dafni and Bernhardt 1990).

Pterostylis flowers are also nectarless. The pigmentation of a few species may suggest fungal or carrion mimesis (e.g. *P. pedunculata* R.Br.) but the majority of flowers in the genus are green or boldly striped with green. Jones (1981) suggested that some *Pterostylis* species are 'window flowers' and fungus gnats are attracted to the rays of light shining through translucent, dorsal portions of the inflated hood. However, the few gnats captured in the flowers have all been males, suggesting a pseudocopulatory syndrome (Beardsell & Bernhardt 1982; Jones 1988; Dafni & Bernhardt 1990).

The actual role of fungus gnats as agents of cross-pollination of the geophytes throughout the forests of the world remains uncertain. For example, although *Asarum* has been treated as a classic example of a gnat-pollinated genus, most seedset in *A. hartwegii* Wats. derives from mechnaical self-pollination (Mesler & Lu 1993). What-ever the mode of floral mimesis may be in *Pterostylis*, pollination appears to be vector-mediated in most species studied. In fact, mechanical, self-pollination has been recorded far less often in the tribe *Pterostylideae* (*sensu* Burns-Balogh & Funk 1986) than in any other tribe of terrestrial orchids in Australia (Dafni & Bernhardt 1990; Catling 1990).

Some degree of cross-pollination must occur in some species of *Pterostylis* since some uncommon taxa have had to be reclassified as recurrent hybrids (Clements 1989). Mycetophilids have been implicated in the recurrent production of *P. curta* X *P. pedunculata* where populations of the parent species are sympatric. However, Bates and Weber (1983) did not find the orchid gnats carrying pollinaria and did not identify the genera or gender of prospective pollinators.

Therefore, additional field and glasshouse observations on *Pterostylis curta* should be useful since published accounts of the floral biology in the genus remain so fragmentary. *Pterostylis curta* is one of the most widely distributed members of the genus through eastern Australia and natural clones are very floriferous (Woolcock & Woolcock 1984; Jones 1988). Therefore, brief observations on the floral biology of this species should help clarify some aspects of pollination mechanisms within a troublesome genus.

Materials and methods

Floral presentation, morphology and visitors

Flowering specimens for morphological studies were collected along Woola Track 2 of Royal National Park, New South Wales, from a population of about 30 flowering

shoots. The population of *Pterostylis curta* was found in wet, shady, sclerophyll forest, co-blooming with *Acianthus fornicatus* R.Br., *P. grandiflora* R.Br., *P. nutans* R.Br. and *P. longifolia* R.Br. Field observations were made between 7 July 1991 and 22 July 91. Dried vouchers and spirit collections of flowers were made by R. Coveny and deposited at the Royal Botanic Gardens Sydney (NSW). Insect vouchers were deposited at the CSIRO Division of Entomology in Canberra, ACT. A pollinarium carried by an insect was checked against the pollinarium morphology of other orchid genera flowering at the same time of year and from the columns of living flowers.

Labellum manipulations

The living collection of *P. curta* (910182, 910654) at the Missouri Botanical Garden consisted of a total of four pots, housed in Greenhouse B1 and maintained at day temperatures of 19–22 C and night temperatures of 11–13 C. A total of 22 living flowers were labeled and used to record the floral lifespan and response of labella to direct contact between 27 January 1993 and 13 March 1993. Flowers were considered open on the first day the bud showed both expansion of the opening of the floral sinus and labellum irritability. Flowers were recorded as dead when the lateral petals dried or collapsed, obscuring the sinus, and the labellum failed to move when provoked.

Sixty-three test manipulations were conducted over the flowering period of the greenhouse collection from 10 am to 3 pm. A flower's labellum was tapped gently with a probe to make it spring. If it did not spring after the third tap it was recorded as non-responsive. Flowers in which the labellum had 'tripped' were monitored hourly, and the time required for the labellum to reset was recorded. Once the labellum had returned to its original position it was recorded as reset. Hourly attempts were then made to retrigger the mechanism by tapping the labellum three times with the probe. Therefore, the labellum of any study flower could be triggered more than once during each day of experimental manipulations.

Results and discussion

Floral presentation and gross morphology

Jones (1981) subdivided floral presentation of *Pterostylis* species into two groups. In the first group, the fused lateral sepals are so relaxed or deflexed that the labellum lamina is completely visible outside the galea. The labellum lamina is short-truncated and highly sculptured with marginal hairs and papillae. This form of presentation was not employed by *P. curta*.

Pterostylis curta employs the second mode of presentation. The lateral sepals are erect-ascending and embrace the galea, narrowing the sinus dimensions. The labellum lamina is much longer than wide, and less than half of the lamina protrudes through the sinus, often contacting the median cleft formed by the fused lateral sepals. In *P. curta* the apical half of the lamina appears to twist to the right of the viewer (Fig. 1).
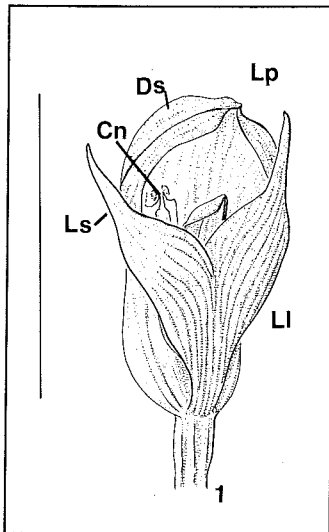
Fig. 1. Front view of the flower of *Pterostylis curta*. Cn = column; Ds = dorsal sepal; Ll = labellum lamina; Lp = lateral petal; Ls = lateral petal.
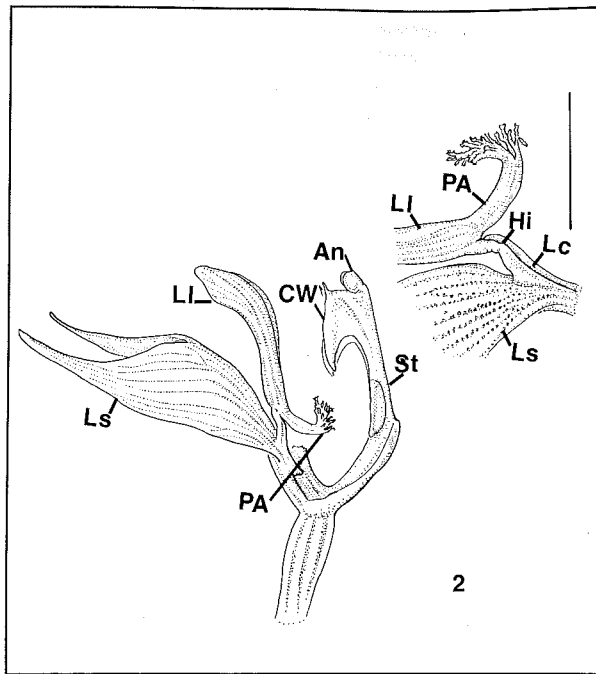
Fig. 2 (above right). Labellum and column details of *P. curta* (galea removed and lateral sepals spread). Abbreviations as in Fig. 1 including An = anther; CW = column wings; Hi = claw hinge; Lc = Lamina claw; PA = penicillate appendage; St = style.
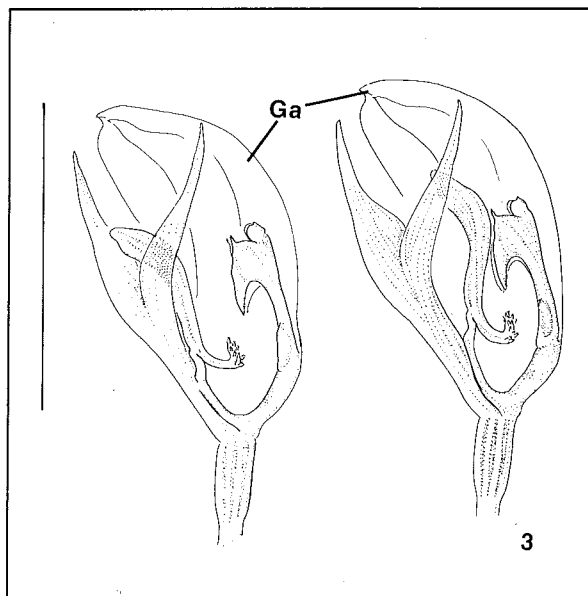
Fig. 3. Movement of the labellum lamina within the galea (Ga); Scale = 3 cm. Left = labellum lamina not triggered; Right = labellum lamina triggered (note that it contacts the column wings).
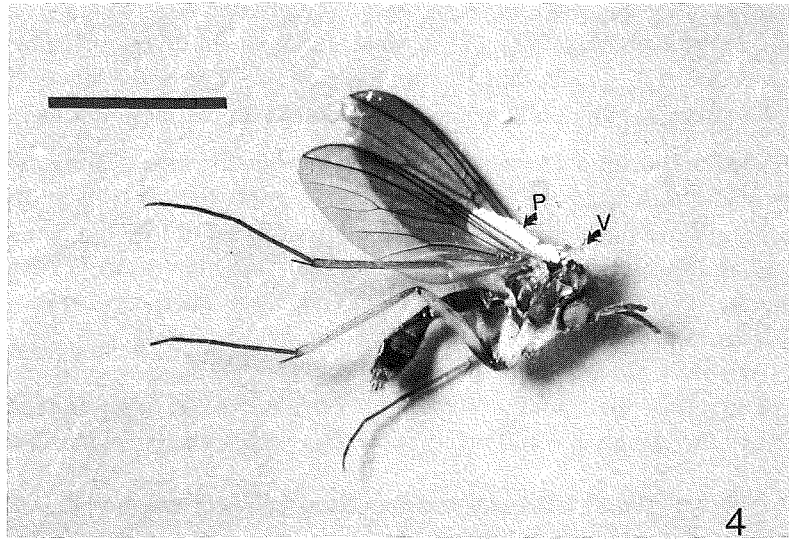
Fig. 4. Male *Mycomya* species carrying *P. curta* pollinarium (scale = 3 mm). P = pollinium; V = viscidium attached to mesonotum of insect.

As in most *Pterostylis* species within the second type of presentation the labellum lamina of *P. curta* is entire, longer than wide and its base bears a penicillate and vasculated appendage that is elongated, curved and terminates in an angled, fringed, brushlike crest of branched and webbed trichomes (Fig. 2). The lamina is connected to the claw by a flexible hinge. The claw is fused to the base of the lateral sepals (Figs. 2 & 3). When the spring mechanism is triggered the entire lamina is withdrawn completely into the inflated galea, contacting the expanded, hatchet-like wings of the column (Fig. 3).

Collection and observations of floral visitors

On 7 July 1991 examination of a *Pterostylis curta* flower at the study site located a dead gnat that had become attached to the outer surface of the galea. The anther in the flower was empty of pollinia, but a *Pterostylis* pollinarium was deposited dorsally on the mesonotum of the gnat's thorax (Fig. 4). The gnat had apparently died of exposure, as the visicidium of the pollinarium had welded the insect to the outer surface of the galea before it could fly away. Half an hour later a second gnat was found alive and fluttering inside the floral chamber of a second *P. curta*. The lamina of the labellum had not reset completely and one anther loculus lacked its pollinium. The entire flower was placed inside a plastic bag. The gnat crawled out of the flower via the sinus but the *Pterostylis* pollinia it had been carrying was knocked off against the side of the bag. Examination of the specimen under a dissecting microscope showed that the mesonotum had lost hairs and remaining hairs had been matted by viscidial residue. Both insects were identified as males of *Mycomya* species (Mycetophilidae). Both were less than 4 mm long.

The deposition of the pollinarium on the body of a gnat may be similar in different *Pterostylis* species. Colour photographs of unidentified, male mycetophilids collected in living flowers of *P. nutans* R.Br. (Jones 1981) and *P. furcata* R. Rogers (Bates & Weber 1990) also show the pollinarium fixed dorsally to the mesonotum.

Although each anther in a *Pterostylis curta* flower contains four pollinia, only one pollinium was attached to the body of the male gnat (Fig. 4). When dissecting needles, pin tips and the tips of needle forceps were inserted into the sinus of a *P. curta* flower and then withdrawn under the column, these instruments never withdrew more than one or two pollinia at a time. This observation concurred with the colour photographs of Jones (1981) and Bates and Weber (1990). Van der Pijl and Dodson (1966) were among the first to note that *Pterostylis* species were among the few orchids to release their pollinia separately. They suggested this was an adaptive feature since a tiny dipteran could not support the weight of four pollinaria in flight.

Floral lifespan and labellum sensitivity

Individual flowers of *P. curta* in the glasshouse collection survived and responded to probes for an average of three weeks. One flower responded to probes for five weeks. All flowers of cultivated plants wither without successful self-pollination. Labellum sensitivity appeared to be greatest during the first week after anthesis, when the labella of both wild and greenhouse plants proved so sensitive that the spring mechanism was activated by merely tapping the flower's peduncle. No flower of *P. curta* at Royal National Park was observed to reset its labellum within five hours after triggering. Field observations of labelled flowers indicated that under natural conditions, i.e. where daily temperatures fluctuated and were less than 19°C, flowers of *P. curta* did not reset labella fully for an average of 9–24 hours after the spring mechanism was triggered.

In contrast, experimental series showed that, under higher controlled temperatures, *P. curta* flowers reset much more rapidly, with the majority of flowers fully reset within two to three hours after the first triggering (Table 1). Restoration of labellum irritability peaked between two to three hours after initial triggering. However, no lamina was found to respond to the probe stimulus unless it had reset and protruded from the sepal cleft.

Over 40% of all labella that reset following experimental probing still failed to spring upwards the second time the lamina was tapped (Table 1). The labellum mechanism could be triggered a maximum of three times during two experimental series. Twenty-nine out of 63 tests recorded that the labellum had been triggered twice over a five hour period.

Experimental procedures suggested that the resting of the labellum often occurred independently of the actual restoration of irritability. Table 1 shows that the process of resetting the position of the lamina occurred more rapidly than the restoration of the irritability response. Since the resetting process is gradual but slow, a pollinator the size of a gnat would be able to escape from the floral chamber before the labellum begins to protrude from the sinus. This appeared to be the case for the second gnat collected.

Table 1. Response of labella to artificial manipulations over time

Time period	Labellum activity		
	No response or partial reset	Reset but not irritable	Reset and irritable[1]
1. End of first hour	59	28	10
2. End of second hour	23	29	41
3. End of third hour	6	4	29
4. End of fourth hour	1	3	10
5. End of fifth hour	2	0	0

[1] Refers to a labellum that reset and the spring mechanism responded to pressure.

It is still not understood why these insects entered the floral chamber in the first place and perched, one presumes, on the labellum lamina. As both were male, the pseudocopulatory explanation seems most likely. Jones (1981) suggested that the appendage at the base of the lamina functions as a counterweight to the tripping mechanisms. I will present a second hypothesis. The appendage has a crested tip resembling the stalked osmophores of other orchid taxa as depicted by Vogel (1990). Perhaps it is a dummy female and plays some role in the visual and/or olfactory deception of the male gnat.

Acknowledgements

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