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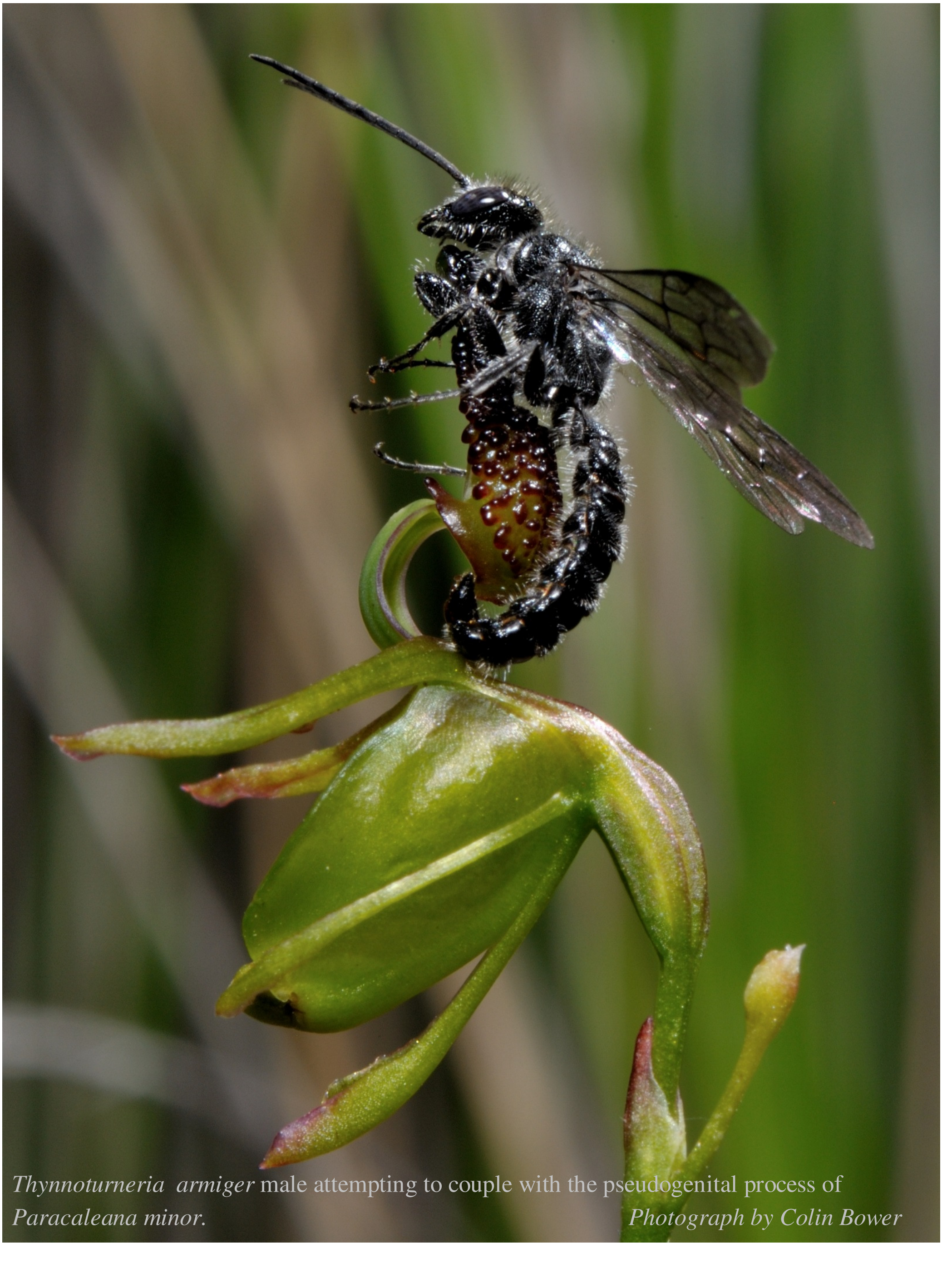

Thynnoturneria armiger male attempting to couple with the pseudogenital process of *Paracaleana minor*. *Photograph by Colin Bower*

Pollination of the Small Duck Orchid, *Paracaleana minor*: Flower Structure and Function.

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Abstract

The peculiar duck-shaped flowers of the Small Flying Duck Orchid, *Paracaleana minor* (R.Br.) Blaxell*,* are oddities among orchids. The structure and function of *C. minor* flowers in pollination is described and illustrated by photographs. *C. minor* is pollinated by sexually deceived males of the Thynnid wasp, *Thynnoturneria armiger* Turner, on the Central Tablelands of NSW. Attracted males attempt to couple with the female-mimicking duck 'head', causing it to spring over, trapping them upside down against the column in the bowl of the duck 'body'. The labellum of *C. minor* mimics key aspects of the shape of a Thynnid female, including the female genitalia, that are critical for correctly orienting the male for successful pollination. The mechanism of the rapid labellum movement is described and illustrated.

Key words

Paracaleana minor, *Thynnoturneria armiger*, Orchidaceae, Diurideae, Drakaeinae, pollination, sexual deception, pseudocopulation.

Introduction

Orchids fascinate us with an extraordinary variety of colour and form, all built on the very simple template of a column, three petals and three sepals. Some 30,000 species have evolved by the astonishing diversification of these seven floral segments. The ventral petal, or labellum, is usually the most elaborately modified part, but all segments show extreme plasticity, far exceeding that of any other plant family. Some orchids are so bizarrely contorted as to be scarcely recognisable as flowers at all.

The often complex structures of orchid flowers are adaptations for attracting, guiding and manipulating pollinators. Generally, the more elaborate the flower, the more specialised is the pollination mechanism, and the more likely that the orchid species has evolved to exploit a particular insect or group of closely related insects. Accordingly, there is a close relationship between flower structure and function for pollination. In this paper I will explore the detailed structure and function of the peculiar duck-shaped flowers of the Small Duck Orchid, *Paracaleana minor* (R.Br.) Blaxell (Figure 1).

Structure

Small Duck Orchids have the following structural features:

- Flowers are resupinate (reversed) with the column oriented downwards.
- A long column foot extends horizontally from the base of the inverted column.
- The sepals and lateral petals are reduced in size compared to the labellum and column which dominate the flower.
- The dorsal sepal and petals are attached at the base of the column, but the lateral sepals attach to the end of the column foot.
- Large wings extend outwards from the column and column foot forming a deep concave bowl, the duck 'body' (Figures 1 and 2).
- The duck 'neck', a broad, laterally concave, strap-like claw is bent into a C-shape and holds the labellum aloft from the end of the column foot.
- Shiny dark maroon to black warty glands cover the upper surface of the labellum (duck 'head') which is vaguely insect-like; broad at the base (the 'abdomen') before narrowing into a neck (the 'thorax') and expanding into a narrow bi-lobed head at the apex (Figure 3).

Figure 1. *Paracaleana major*

Figure 2. Column bowl of *C. minor* formed by column wings.

Previous studies

It is well known that if the tip of the labellum is gently pushed downwards in *Paracaleana* and the closely related Flying Duck Orchid, *Caleana major* R.Br., it will trigger the rapid rotation of the labellum into the column bowl. According to Rica Erickson (1965), it was Western Australian plant collector James Drummond who, in 1838, first reported the motion of the labellum in *Paracaleana nigrita* (J.Drumm. ex Lindl.) Blaxell. Erickson quotes Drummond as saying the labellum *'makes a prisoner of any small insect which the pouch will hold. When it catches an insect it remains shut while the insect continues to move about, but if the insect be not caught the box soon opens again.'* The venerable RD Fitzgerald wrote at length in 1880 on the same phenomenon in the *C. major*. He concluded that the flower functioned as a trap for insects, but was unable to ascertain the insects responsible for pollination.

Cady (1965) made the first modern field observation of pollination in Duck Orchids at Narooma in NSW. He saw a male sawfly, *Lophyrotoma leachii* Kirby, land on the labellum of *C. major* only to be instantly flipped violently into the column bowl and held there for a minute and a half until it could free itself. In the process, the orchid pollinia were attached to the

Figure 3. Insect-like labellum decoy of *P. minor.*

middle of insect's thorax. Bates (1989) made similar observations on *C. major* near Wauchope, NSW and published an excellent photograph of the event in *The Orchids of South Australia* (Bates and Weber, 1990) showing a sawfly identified as *Pterygophorus* sp.) '*jammed head first between the labellum and column*' with only its abdomen and wings projecting beyond the labellum. Beardsell and Bernhardt (1982) and Bates (1989) suggested male sawflies may be attracted to *C. major* by sexual deception. However, the numbers observed are very low and there is no evidence of attempted pseudocopulation to support this conjecture.

Published observations of pollination in *Paracaleana* are also limited. Although *P. nigrita* is generally considered to be pollinated by sexually deceived males of a Thynnid wasp in the genus *Eirone* (misspelt as *Erione*) (Hoffman and Brown, 1992; Hopper and Brown, 2006), all reports are based on personal communications or personal observations without corroborating evidence. As part of a review of *Caleana* pollination (Bower, 2001a), the author summarised observations he made on *P. minor* using the pollinator-baiting technique (Stoutamire, 1983) at three locations in the Bathurst-Orange area of NSW in 1988. Three attracted insects were identified by GR Brown as males of the Thynnid wasp, *Thynnoturneria armiger* Turner.

The author also photographed the interaction between *T. armiger* and translocated flowers of *P. minor* in the Mullion Range State Forest, approximately 15 km north east of Mullion Creek, NSW. These photos were the basis of the description of *P. minor* pollination published in Bower (2001a), but were lost in a house fire. In November 2013, the author rephotographed the pollination of *P. minor* at the same location. This paper provides a more detailed account of the pollination of *P. minor* illustrated by the new images.

Pseudocopulation in *C. minor*

Males of *T. armiger* fly upwind to *P. minor* bait flowers as if following an odour trail (Bower, 2001a). They alight directly on the labellum, grappling it with their forelegs around the narrow 'neck' (Figure 4). The male then arches his abdomen and probes with the terminal genitalia in an attempt to mate with the labellum (Figure 5 and front cover). The image on the Front Cover shows the expanded male

Figure 4. Male of *Thynnoturneria armiger* grappling the narrow thoracic region of the decoy with his forelegs.

Figure 5. *T. armiger* probing with his genitalia on the labellum of *P. minor*

genitalia clasping a small triangular process at the base of the labellum. This process is clearly visible in Figure 1 and most likely represents pseudo female genitalia and is termed here the pseudogenital process.

This behaviour is characteristic of Thynnid males when picking up their wingless females from ground cover vegetation. Prior to being picked up, females 'call' for males by emitting species specific sex pheromone odours to which males respond rapidly. A responding male will couple immediately with the female once he has grasped her behind the head, around her narrow neck-like thorax (Bower, 2001b). Coupling may occur at the point of pick up or after a short flight to nearby vegetation. The male then carries the female in copula to a flowering shrub or tree where he assists her to feed on nectar.

The pollination syndrome in *P. minor* is clearly based on the sexual deception of *T. armiger* males. The insect-like labellum is an elegantly crafted pseudo-female wasp. Critical structural features are:

- The length and colour of the decoy is likely to be similar to the real female.
- The 'abdominal' width of the decoy is greater than expected for Thynnid females. This may provide additional stimulus (supernormal stimulus) to attracted males.
- The presence of a pseudogenital process.
- The head region of the decoy is the correct size and shape to fit behind the male's head and between his forelegs into a cavity below the thorax which is adapted for carriage of females in flight. [Some male Thynnids have concave expanded forecoxae on their forelegs to cradle females]. This fit of the decoy's 'head' and 'thorax' to the male puts him into the correct position to couple with the pseudogenital process (front cover).
- It is likely that the warty glands on the labellum emit a faithful mimic of the sex pheromone odour used by female *T. armiger* to attract males for mating.

The above features ensure correct orientation of the male for pollination of the orchid.

Trigger mechanism

The following account of the explosive mechanism of labellum closure is amended and expanded from Bower (2001a).

The strap-like labellum claw of *P. minor* has cable-like thickenings running down the sides of the thinner, broad, flexible lamina. In the resting position the lamina has a side to side concavity and the claw is curved upwards. Slight pressure on the labellum apex bends the strap outwards causing the concavity to suddenly pop out, or reverse, bending the claw rapidly downwards. This process was first described by Fitzgerald (1880).

Although labellum closure occurs in the blink of an eye, resetting is slow, taking 15 to 20 minutes (Bates, 1989; personal observations). Even when the labellum has returned to its upright position, it is insensitive to touch for some time.

The accompanying photographs were obtained by taking a flower that, unbeknownst to the author, had not fully reset after closure, and using it to attract wasps. The result was that rather than closing abruptly when a wasp landed, the labellum closed quite slowly. This allowed different stages in the mechanism to be observed and photographed.

Triggering the labellum takes place in two stages (Bower, 2001a). Reversal of the claw begins at its outer end, where it joins the labellum, and proceeds rapidly to the basal end. Reversal in the outermost part of the claw tips the labellum under and closely parallel to the claw (Figure 6). When the concavity of the claw is half reversed, the body of the wasp is suspended horizontally upside down with its head in the column bowl (Figure 7). Finally, when the claw is fully reversed, the wasp is head up in the bowl with its wings pointing downwards (Figure 8). This double action ensures the tip of the labellum, and the wasp, clear the column apex.

Discussion

C. minor is an elegant example of the strikingly close relationship between structure and function that occurs frequently in the most physically complex orchids. The *P. minor* labellum decoy is an excellent mimic of a flightless female Thynnid wasp, albeit exaggerated in width, most probably to maximise attractiveness to males.

The two key physical features of the decoy for orienting male *T. armiger* are the 'neck' which the male grasps with his forelegs and the pseudogenital process, with which the male attempts to couple. All other genera in the Drakaeinae, including *Chiloglottis*, *Drakaea*, *Spiculaea* and *Arthrochilus* have labellum decoys with analogous distinct head and neck regions for orientation of Thynnid males (Bower, 2001b). Several species in the genus *Caladenia* (Caladeniinae) that are pollinated by Thynnid wasps (Phillips *et al*. 2009) also have decoys with similar structures.

The mechanism of the labellum claw exhibits remarkable complexity with its elegant two stage movement. Rapid closure of the labellum appears to be a mechanical action brought on by the weight of the wasp overtipping the labellum. By contrast, the slow resetting suggests that physiological processes re-establish the critical unstable equilibrium and provide the potential energy for the sudden mechanical discharge.

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Figure 6. Labellum of *P. minor* bent against the labellum claw.

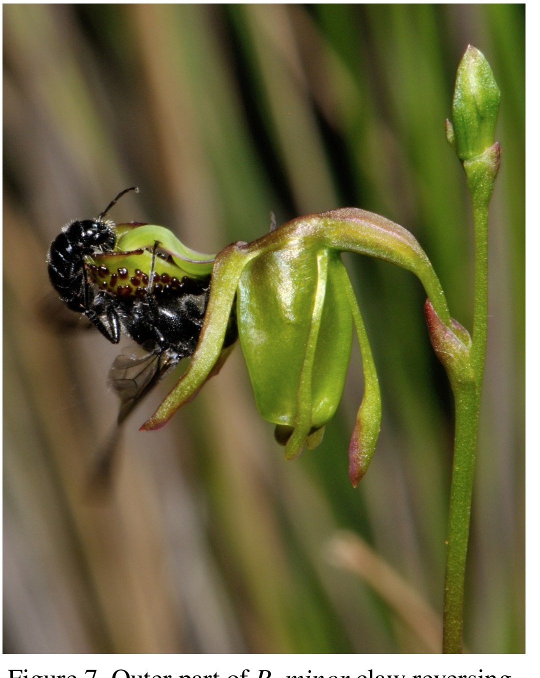

Figure 7. Outer part of *P. minor* claw reversing concavity.

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Figure 8. Male *T. armiger* trapped between *P. minor* labellum and the column.