



Plate 1. Ant-like labellum glands of *Myrmechila formicifera*, which in fact mimic a female thynnine wasp.

The Wasp, Ant and Bird Orchids of the *Chiloglottis* Alliance

– A General Overview

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Abstract

Taxonomic research on the genus *Chiloglottis sensu lato* over the last twenty years has resulted in the description of some eighteen new species and the splitting of the genus into three segregate genera. As well as the taxonomic work, there is a major ongoing research effort aimed at understanding the pollination and evolution of the genus, which has implications for the taxonomy. The published information on the *Chiloglottis* alliance is scattered in many reports and scientific papers. This is the first in a series of articles that collate information on distribution, habitats, pollination biology and morphological differences among the species of the *Chiloglottis* alliance. This introductory article provides a general overview of the group.

Introduction

Wasp, Ant and Bird Orchids of the *Chiloglottis* alliance, are common, but rarely noticed denizens of moist forests, sheltered slopes, damp shady gullies, grassy montane habitats and sphagnum hummocks in the forests and woodlands of eastern Australia. Cryptic and inconspicuous, the small maroon, pale green or brownish flowers blend into the background, escaping the attention of the casual observer. The most obvious signs of these orchids are the twin opposite ground-hugging leaves, usually in massed colonies. In most years flowering is sparse and one must search the colonies for the occasional thin stem arising between the paired leaves. Often, it is only after finding a stem that the single small flower materialises at its apex.

The Wasp and Ant Orchids are named for the remarkable resemblance of their labellum calli to hymenopterous insects. Indeed, R.D. Fitzgerald (1877) named *Chiloglottis formicifera* (now *Myrmechila formicifera*) 'from the likeness of the glands on the labellum to an ant' (family Formicidae) (Plate 1). *Chiloglottis reflexa* (Labill.) Druce has a similarly insectiform labellum, which is missing from the type specimen. It is thought the original collector, Labillardiere, removed the labellum thinking it was an insect stuck to

the specimen(!) (M.A. Clements, personal communication).

Dockrill (1956) was the first to discover the function of the insect-like labellum glands when he observed black wasps attempting to copulate (pseudocopulation) with the labellum of *C. formicifera* (now *Myrmechila platyptera*) at Barrington Tops in November 1954. He interpreted the ant-like labellum glands as mimicking a female wasp, which he mistook for an ichneumonid. Giles (1964) correctly reported that wasps he observed pseudocopulating on *Chiloglottis reflexa* at Batlow (probably plants currently known as *C. trilabra*) belonged to the family Thynnidae (Plate 2). Since that time all studies of pollination in the *Chiloglottis* alliance have reported male Thynnine wasps (now Tiphiidae subfamily Thynninae) as the pollinators.

Plant Habit and Flower Structure

The unifying characteristic of *Chiloglottis* alliance species is the pair of equal prostrate oblong or ovate leaves that usually lie opposite each other on the substrate (Plate 3), but may be erect if the plant is pushing up through dense growth. All species have a single flower, either almost sessile between the leaves, or borne on an erect stem to about 15 cm high, which elongates after fertilisation to

aid wind borne seed dispersal.

There are two main plant types in the *Chiloglottis* alliance. The so-called 'gunnii' group (now *Simpliglottis*) has broad ovate to circular, somewhat leathery leaves with straight margins and relatively large sessile or short-stalked flowers. By contrast, the 'reflexa' group (now *Myrmechila* and *Chiloglottis*) has narrower oblong leaves of thin texture, often with undulating or wrinkled margins. Flowers of the 'reflexa' group are small and borne on stalks much longer than the flower.

Flower morphology of the two groups is quite divergent. The labellum of 'gunnii' type flowers is concave, heart-shaped, rotates passively on a flexible hinge to form a tight fit against the column and has loosely clustered non insect-like calli. The lateral sepals are thin and project forward below the labellum, which may rest on them, while the petals are broader, spreading horizontally or curved upwards to partially cover the gap between the resting labellum and the column (Plate 4). 'Reflexa' type flowers are much more open, the petals being reflexed against the ovary, and the flat trapezoid or rhomboid labellum held horizontally, or erect in some species, to display the dense cluster of wasp-mimicking calli (Plate 1). The two flower types suggest two distinct pollination mechanisms have evolved in the *Chiloglottis* alliance.

The large crowded colonies often associated with the *Chiloglottis* alliance are mainly the result of vegetative reproduction (Plate 5). Plants have a small globular or ovoid tuber from one to seven or more centimeters below the surface depending on the substrate. Each season after a period of dormancy, a vertical stem from the tuber ascends to the surface forming few to many lateral roots. The stem shoots at the surface giving rise to the twin leaves. During the growing period, a replacement tuber is produced next to the parent tuber. Two

daughter tubers are also formed at the ends of lateral roots arising from the stem just below the soil surface. The daughter tubers may be as far as 20 cm from the parent plant and are responsible for colony extension (Plate 6). Daughter plants are clones of the parent and genetic analysis has shown that large colonies may contain only one or a few genetically distinct clones comprising hundreds or thousands of leaves extending over several meters (R. Peakall, personal communication).

The long lateral roots with daughter tubers perform an important function in the *Chiloglottis* alliance. Overexploitation of soil resources is likely in the very crowded colonies often formed by these species, which may explain why flowering is so sparse. The lateral roots provide a means for some plants to migrate to fresh unexploited sites. This is equivalent to repotting the tubers into new soil as a means of maintaining flowering, which is necessary every one to two years for *Chiloglottis* alliance species in cultivation (Jones 2006a).

Brief Taxonomic History of the *Chiloglottis* Alliance

Robert Brown described the genus *Chiloglottis* in 1810, with *C. diphylla* as type species. However, Labillardiere in 1806 had previously incorrectly described a collection of *Chiloglottis reflexa* from Tasmania in the European genus *Epipactus*. This mistake was not corrected until 1917 by Druce. The next species described were *C. gunnii* in 1840 and *C. cornuta* in 1844 by John Lindley and J.D. Hooker, respectively. The first resident Australian orchidologist, Robert Fitzgerald, described three species, *C. formicifera*, *C. trapeziformis* and *C. trilabra* in his monumental folio work, 'Australian Orchids' in 1877. In 1918, R.S. Rogers added *C. pescottiana*, which is now recognised as a natural hybrid between *C. valida* and *C. trapeziformis*. *C. dockrillii*, described by the Reverend Herman Rupp in 1953, is now a synonym of *C. trilabra*.



Plate 2. Typical female thynnine wasp as mimicked by orchids of the *Chiloglottis* alliance.



Plate 3. Paired opposite leaves characteristic of the *Chiloglottis* alliance (*Simpliglottis turfosa*).



Plate 4. Flower of *Simpliglottis gunnii*.

The preceding account is summarised from Clements (1989).

The modern era in *Chiloglottis* taxonomy began with the description of *Chiloglottis truncata* and *C. sylvestris* by David Jones and Mark Clements in 1987, which brought the number of species in the *Chiloglottis* alliance to nine and one hybrid. 1991 was a watershed year in which thirteen species were described including two from Tasmania, *C. grammata* and *C. platychila*, by Geoff Carr (1991) and eleven in one publication by David Jones (1991) as follows; *C. anaticeps*, *C. chlorantha*, *C. longiclavata*, *C. palachila*, *C. platyptera*, *C. pluricallata*, *C. seminuda*, *C. sphyrnoides*, *C. trullata*, *C. turfosa* and *C. valida*. *C. platychila* Carr was subsequently synonymised with *C. gunnii* Lindl. by Jones (1998). Over the last ten years a further three species have been added, *C. jeanesii* (Jones 1997), *C. triceratops* (Jones 1998) and *C. sphaerula* (Jones 2006b), bringing the total number of described species to twenty four and one hybrid (Jones 2006a, b).

The first step in splitting *Chiloglottis* into three segregate genera was the erection of the genus *Simpliglottis* (Szlachetko 2001) to accommodate the distinctive large flowered *Chiloglottis gunnii* group. For a short time *Simpliglottis* was reduced to subgeneric status within 'The *Chiloglottis* Alliance' (Jones 2002), but was maintained as a genus by Jeanes (2002) who also named the hybrid genus *xChilosimpliglottis* to accommodate *C. pescottiana*, whose parents are now in different genera. Detailed molecular genetic studies on fifteen species (Mant *et al.* 2002) showed there are at least three genetically distinct and coherent groups within the *Chiloglottis* alliance. These are the *C. gunnii* group (*Simpliglottis*), the late summer / autumn flowering *C. reflexa* group and the spring flowering *C. formicifera* group. The *C. reflexa* and *C. formicifera* groups are also consistently different in their lateral sepals; the former

being much shorter with shorter apical clubs than the latter. Jones and Clements (2005) erected the genus *Myrmechila* for the 'formicifera' group.

Pollination Mechanism

Apart from *Simpliglottis cornuta*, which is self-pollinating, most *Chiloglottis* alliance species so far tested are pollinated by sexual deception of male thynnine wasps of the genus *Neozeleboria* or closely related genera (Bower 1992, 1996; Bower and Brown 1997; Peakall *et al.* 1997, 2002; Mant *et al.* 2005a, b). The exception is *Simpliglottis grammata* in Tasmania which is pollinated by a species of the distantly related thynnine genus *Eirone* (Mant *et al.* 2005a). The orchids mimic not only the shape and colour of a female thynnine, but also the wind-borne sex pheromone odour she uses to attract males from a distance. The imitation pheromone, or allomone, is emitted from glands (osmophores) on the labellum calli and sepal clubs of the orchid. Downwind males detect the odour and follow the scent trail upwind to the flower. A recent breakthrough has been the chemical identification of the allomone of *Myrmechila trapeziformis* (*Chiloglottis trapeziformis*) and confirmation that it is identical to the sex pheromone of its pollinator, *Neozeleboria cryptoides* (Schiestl *et al.* 2003). The chemical, a cyclic diketone, has the common name, chiloglottone.

Males attracted to *Myrmechila* and *Chiloglottis* flowers may zig zag in front of the flower or circle around it before landing near it, or on the stem, or directly on the labellum or sepal clubs. Wasps landing near the flower may walk to the stem and climb up, or fly again and land on or near the labellum. Peakall and Handel (1993) suggest that males are attracted from the distance by the allomone, and use visual cues to find the female at close range. Occasionally, males may attempt to mate with the sepal clubs, rather than the insectiform labellum, indicating that even at close range chemical cues can be more

important that visual ones.

Males crawl over the labellum calli seeking the head and thorax region of the 'female', while probing the calli or labellum margin with the genital claspers at the tip of the abdomen in an attempt to couple (Plate 7). Males that orient 'correctly' on the decoy, will grasp it with the forelegs just behind the head region, as they would a female (Plate 7), and attempt to lift it and fly away. This action brings the male's thorax into contact with the overhanging column (Plate 8) allowing any attached pollinia to pollinate the sticky stigma. After failing to move the female, males may move backwards receiving a coating of glue on the thorax from the rostellum before pushing open the anther flaps and removing one or both pollinia. However, pollinia removal or pollination can also occur by males simply moving over the 'head' region of the 'female' and squeezing below the column.

Pollination in *Simpliglottis* differs in several ways from *Myrmecophila* and *Chiloglottis*. The initial approach by wasps to flowers is the same in all three genera. However, the sepal clubs of *Simpliglottis* are very small and unattractive to incoming males, which walk or fly straight onto the labellum. While probing with the abdomen, males move over the calli towards the tall knobbed central callus at the base (Plate 9). Known as the major proximal callus (Jones 1991), it is inclined towards the labellum apex. Males generally move between the callus and the column while attempting to mount and grapple it with their forelegs below the apical knob; in the process tipping the finely balanced labellum against the column. Trapped between the concave labellum and the column, the male must move upwards over the labellum calli to escape. The male's weight holds the labellum closed forcing it's thorax to contact the stigma, rostellum and anthers in that order, first pollinating the flower, if it is carrying pollinia, then picking up additional pollinia on its departure (Plate 10).

Pollinator Specificity

A key feature of pollination by sexual deception of male insects is that each orchid species has a single unique pollinator (Table 1). This characteristic of sexual deception has been exhaustively tested by the author for most species in the *Chiloglottis* alliance by using pollinator choice tests in the field (Bower 1996, 2006, Bower and Brown 1997). Experiments have been carried out through much of eastern Australia from the Blackdown Tableland in Queensland to Portland in western Victoria and Tasmania. Pollinator choice tests are a rigorous method for determining the degree of pollinator specificity in sexually deceptive orchids (Plates 11 and 12). Several sets of flowers from different *Chiloglottis* alliance species, populations or geographical areas can be compared for their attraction to populations of particular wasp species. For example, a population of the known pollinator of *Myrmecophila trapeziformis* can be exposed in a choice test to several other orchid species to see if any of them are attractive to it, and hence may have the same or a functionally similar allomone. When *Chiloglottis* alliance species that occur in the same geographical region in the wild, and flower at the same time, are tested together in their normal range and habitats, different wasps are always attracted to each species.

However, a complication is that some orchid and wasp species appear to have similar allomones to other species, but only if they are separated by geography or altitude. For example, *Myrmecophila trapeziformis* and *Simpliglottis valida* have the same allomone (Schiestl and Peakall 2005), but different pollinators, and are usually separated by altitude. Where there is occasional overlap in distribution, the hybrid *Chiloglottis* x *pescottiana* (x*Chilosimpliglottis pescottiana*) may be produced (Peakall et al. 2002). The apparent sharing of similar attractant chemicals by different *Chiloglottis* alliance orchid and pollinator species across



Plate 5. Colony of *Myrmechila trapeziformis* plants.

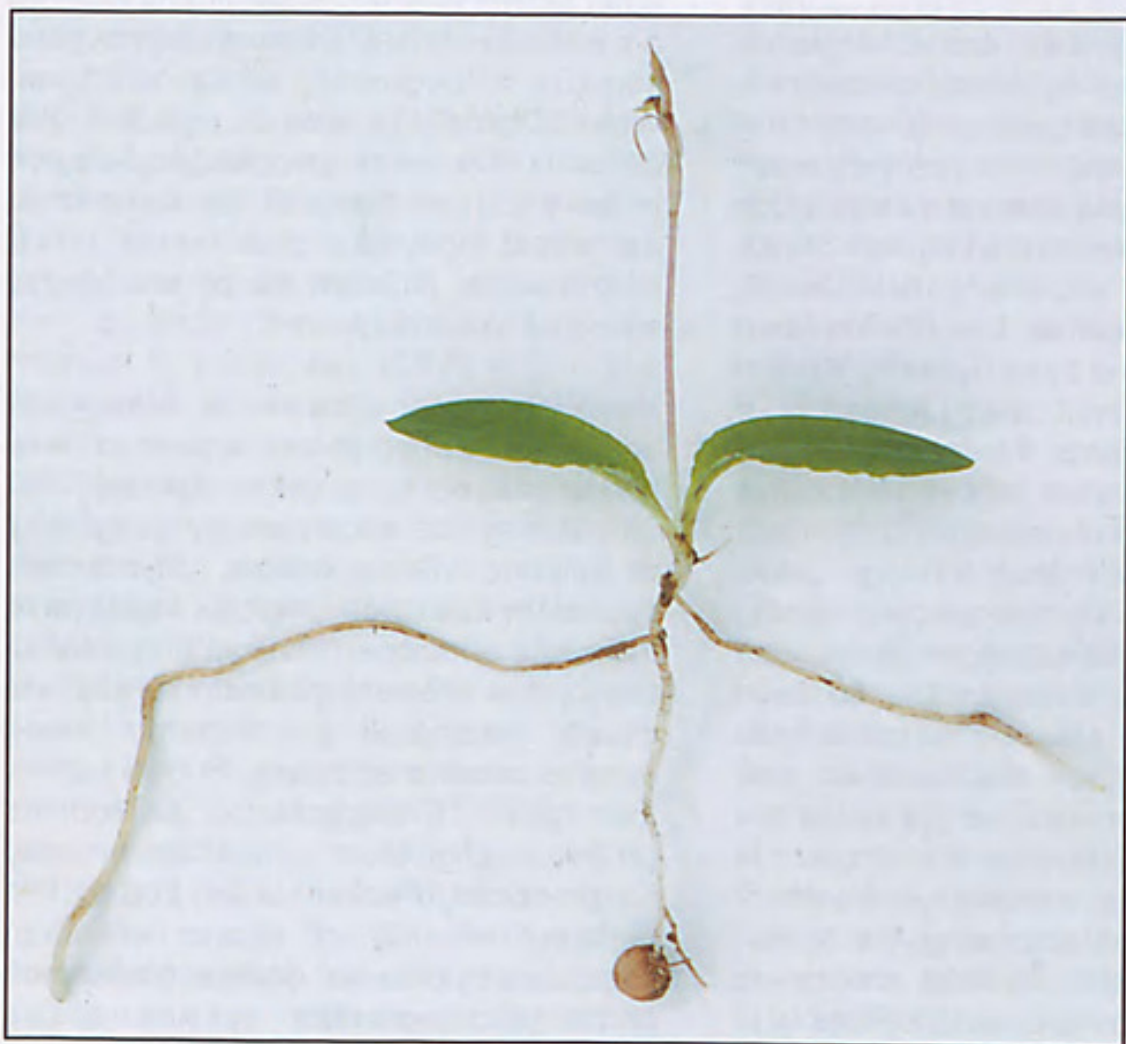


Plate 6. Plant of *Chiloglottis seminuda* showing the parent tuber below the leaves and flower stem, and two lateral roots which will later form the daughter tubers.



late 7. Male *Neozeleboria* species 45 pseudocopulating on the labellum of *Myrmechila* aff. *formicifera* 1. The wasp's forelegs are holding the decoy behind the head region while the genital claspers grip the labellum apex.

geographical and altitudinal boundaries is relatively common. However, despite some allomone sharing, in all known cases each orchid species has its own unique pollinator.

The knowledge that thynnine-pollinated sexually deceptive orchids typically have a single specific pollinator has been used to support the description of several new *Chiloglottis* alliance species, e.g. Carr (1991) used the findings of Stoutamire (1975) to support the description of *Chiloglottis grammata* (now *Simpliglottis grammata*). Similarly, Jones (1991) used pollinator information generated by the author to support the description of *Chiloglottis platyptera* (now *Myrmechila platyptera*), *C. pluricallata* (now *Simpliglottis pluricallata*), *C. seminuda* (now *M. seminuda*) and *C. valida* (now *S. valida*), as well as *C. jeanesii* (now *S. jeanesii*) (Jones 1997). In addition to having different pollinators, all these species, on close examination, are quite distinct morphologically and readily identifiable in the field.

The pollinators of eighteen of the twenty four described species in the *Chiloglottis* alliance have been collected and identified (Table 1). In addition, another eight undescribed species of *Chiloglottis* alliance orchids have been identified by virtue of their unique pollinators (Table 1). Some implications of the data in Table 1 are:

- Fifteen of the wasp species are unnamed, illustrating the enormous job still confronting entomologists to document Australia's insect diversity.
- Most of the pollinators belong to the thynnine genus *Neozeleboria* onto which the *Chiloglottis* alliance has radiated (Mant *et al.* 2005).
- *Chiloglottis diphylla* has attracted two species of *Arthrothynnus* in apparent contradiction of pollinator specificity. However, further investigation is needed to determine if the two wasp

taxa are variants of the same species, or there are two cryptic orchid species within *C. diphylla* (see below).

- *Chiloglottis reflexa sensu stricto* from Tasmania has the same pollinator, *Neozeleboria proxima*, as mainland *C. trilabra* and is the same biological species. Mainland plants currently called *C. reflexa* have a different pollinator, *Neozeleboria* sp. 30, and are an undescribed species.

Cryptic Species

Although the eight undescribed orchid taxa in Table 1 consistently attract different pollinator species, many of them lack any morphological differences to reliably identify them in the field, or which can form the basis of a formal description. However, the pollinator evidence indicates they are separate entities that will not interbreed with others in the field. The absolute lack of genetic interchange that this implies is sufficient evidence to regard them as separate species. Such entities are referred to as cryptic species. There are two well-documented examples among the taxa in Table 1.

1. ***Myrmechila* aff. *formicifera* 1 and *M.* aff. *formicifera* 2.** These two taxa in the *Myrmechila formicifera* complex occur in mixed colonies in sheltered gullies and on shady slopes in the Stanthorpe to Tenterfield area of the Granite Belt on the NSW / Qld. border. Tests with identical looking flowers from near Bald Rock in NSW and Wyberba in Qld showed both populations contained flowers that attracted one or the other of two different wasp species as pollinators, but never both. The two taxa, designated *M.* aff. *formicifera* 1 and 2, are pollinated by *Neozeleboria* new species 45 and *N.* near new species 40, respectively. However, when translocated to the habitats of *M. formicifera*, *M.* aff. *formicifera* 1 attracts the *M. formicifera* pollinator, *N.* new species 41, which is closely

related to, and appears to have the same or similar attractant odours to, *N. new species* 45.

2. ***Simpliglottis valida*, *S. aff. valida* 1 and *S. aff. valida* 2.** Flowers from thirty eight different populations thought to be *Simpliglottis valida* from southern NSW and across Victoria were found to attract four different species of thynnine wasps in pollinator choice tests (Bower 2006). The tests showed the orchids and pollinators belonged to two odour types, with two wasps in each type. The two wasps in each odour type were separated spatially by altitude, so that one wasp of each type occurred above about 1000 m with the other pair below 1000 m. There were two cryptic orchid taxa above 1000 m pollinated by the two high altitude wasps, which themselves were cryptic species within *Neozeleboria monticola*. The two high altitude orchids and wasps cannot be reliably distinguished morphologically in the field. It was only apparent that two different odour types were involved when the high altitude orchids were tested at low altitudes and attracted morphologically distinct wasps which shared the same or similar pheromones as the high altitude species. The study revealed three cryptic species within *S. valida*; true *S. valida* pollinated by *N. monticola*, which mainly occurs at medium to high altitudes, *S. aff. valida* 2 pollinated by *N. near monticola*, at altitudes of above 1000 m, and *S. aff. valida* 1, pollinated by *N. near impatiens* at altitudes below about 1000 m. *N. near monticola* and *N. near impatiens* have the same or very similar sex pheromones, as do *S. aff. valida* 1 and *S. aff. valida* 2.

These scenarios show the kind of complexity that is unfolding in sexually deceptive pollination systems.

Subsequent articles will discuss each of the *Chiloglottis* alliance species, including the undescribed ones, with one article for each of the three genera currently recognised.

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Plate 8. Male *Neozeleboria usitatum* thorax in contact with the stigma of *Chiloglottis truncata* while grasping the decoy's 'thorax' with its forelegs.



Plate 9. Male *Eirone* sp. attempting to couple with the labellum of *Simpliglottis grammata*.



Plate 10. Male *Neozeleboria monticola* emerging with pollinia from between the labellum and column of *Simpliglottis valida*.

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Table 1
Pollinators of Taxa in the *Chiloglottis* Alliance

Orchid taxon	Confirmed pollinator	Probable pollinator
<i>Chiloglottis</i>		
<i>C. anaticeps</i>		<i>N. ? sp.</i> 33
<i>C. diphylla</i>	<i>Arthrothynnus latus</i> <i>A. angustus</i>	
<i>C. palachila</i>	<i>Chilothynnus palachilus</i>	
<i>C. reflexa</i> s.s. (Tas.)	<i>Neozeleboria proxima</i>	
<i>C. aff. reflexa</i> (mainland)	<i>N. sp.</i> 30	
<i>C. seminuda</i>	<i>N. sp.</i> 29	
<i>C. sphyrnoides</i>	<i>N. sp.</i> 3	
<i>C. sylvestris</i>		<i>N. sp.</i> 50
<i>C. trilabra</i>	<i>N. proxima</i>	
<i>Myrmechila</i>		
<i>M. formicifera</i>	<i>N. sp.</i> 41	
<i>M. aff. formicifera</i> 1	<i>N. sp.</i> 45	
<i>M. aff. formicifera</i> 2	<i>N. sp.</i> near 40	
<i>M. platyptera</i>		<i>N. sp.</i> 40
<i>M. trapeziformis</i>	<i>N. cryptoides</i>	
<i>M. truncata</i>		<i>N. usitatum</i>
<i>Simpliglottis</i>		
<i>S. grammata</i>	<i>Eirone leai</i>	
<i>S. jeansii</i>	<i>N. nr. impatiens</i> 2	
<i>S. pluricallata</i> s.s.		<i>N. sp.</i> near 41
<i>S. aff. pluricallata</i> 1	<i>N. tabulata</i>	
<i>S. aff. pluricallata</i> 2	<i>N. nr. monticola</i> 2	
<i>S. aff. pluricallata</i> 3		<i>N. impatiens</i>
<i>S. triceratops</i>	<i>N. carinicollis</i>	
<i>S. turfosa</i>	<i>N. nr. monticola</i> 1	
<i>S. valida</i>	<i>N. monticola</i>	
<i>S. aff. valida</i> 1	<i>N. nr. impatiens</i> 3	
<i>S. aff. valida</i> 2	<i>N. nr. monticola</i> 3	

AUSTRALIAN ORCHID RESEARCH
Volume 5. 2006

New Taxa of Australasian Orchidaceae.
by David L. Jones and Mark A. Clements *et al*
Published by the Australian Orchid Foundation 2006.
ISBN 0-9595384-8-8.

Price: \$40.00 plus postage.
Available through the Australian Orchid Foundation
107 Roberts St Essendon Vic. 3040 Australia.
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Plate 11. Samples of *Simpliglottis* flowers in vials of water placed on the ground to attract pollinators.



Plate 12. The author conducting a pollinator choice test.



Bower, Colin C. 2007. "The Wasp, Ant and Bird Orchids of the Chiloglottis Alliance – A General Overview." *The Orchadian* 15(9), 402–416.

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