

## Biological Observations of Bees in the Genus *Ctenocolletes* (Hymenoptera: Stenotritidae)

Terry F. Houston\*

### Abstract

*Ctenocolletes* consists of chiefly vernal species which forage at plants in several families. Some species appear to prefer particular kinds of nectar and pollen but not necessarily of the same plant genera.

Males either patrol flowers in search of females or (in *C. smaragdinus*) hover in territories near flowers. Prolonged mating and conjugate flight were observed in three species. In *C. smaragdinus* and *C. tigris*, females mounted by males continued to forage and some gathered full loads of pollen.

Two roosting aggregations of *smaragdinus* males were observed to disperse in the mornings and re-form each evening at fixed sites on foliage. Males of *C. tigris* roosted solitarily.

Nests of *C. ordensis* were found loosely aggregated in level ground and each was tended by a single female. Details of the site, nest architecture, provisions, adult activity at nests and associated organisms are provided. Features of nests were their entrance pit and complex cell closure which incorporated a pair of 'false cell-base' partitions. Nests were frequented by gasteruptiid wasps of the genera *Crassifoenus* and *Hyptiogaster*.

Adults of *C. centralis*, *C. nicholsoni* and *C. tricolor* frequently carry hypopial mites (Acarina: Acaridae). On females the hypopi are normally secreted in unusual cavities beneath the lateral portions of two metasomal terga. *Triungulins* (Coleoptera: Meloidae) were found attached to adults.

### Introduction

This paper presents the first observations of the habits of bees in the primarily Western Australian genus *Ctenocolletes* Cockerell and adds significantly to our meagre knowledge of the biology of Stenotritidae as a whole. Previously, the only detailed behavioural information available for this small endemic Australian family concerned *Stenotritus pubescens* (Smith) and some of its congeners (Houston 1975). More information has been eagerly awaited in the hope that it might help elucidate the affinities of stenotritids whose place in the taxonomic hierarchy of Apoidea has long been subject to doubt.

The taxonomy of *Ctenocolletes* (at genus and species levels) has been dealt with by Houston (1983a, b).

---

\* Department of Entomology, Western Australian Museum, Francis Street, Perth, Western Australia 6000.

## Observations and Discussion

### Seasonality

Judging from collection data (Houston 1983a, b), *Ctenocolletes* are predominantly univoltine vernal bees. More northerly species such as *C. centralis* Houston and *C. nicholsoni* (Cockerell) may make their first appearance in July while more southerly ones such as *C. smaragdinus* (Smith) and *C. tricolor* Houston do not appear until September. The period of adult activity appears to be only about one month in *C. nicholsoni* but may extend over four months in *C. rufescens* Houston. The latter inhabits a far greater latitudinal range than the former and its activity at any one site may be shorter. Adults of *smaragdinus* have been observed at study sites from early September to late November. However, two collection records (a female in July and a male in February), if accurate, suggest that emergences may occur at other times.

A possible exception to the rule of vernal habits is *C. fulvescens* Houston which, although known only from a unique female, was collected in January.

### Flower Visiting and Foraging

Plant records for museum specimens of *Ctenocolletes* are comparatively few as are field observations. Consequently only tentative conclusions may be drawn regarding preferred nectar and pollen sources. The available information is presented in Table 1.

Some additional data on pollen preferences of *C. ordensis* Michener were obtained by analysis of food masses in eleven brood cells. Six kinds of pollen were distinguished and various combinations of these occurred in all but one cell. *Cassia charlesiana* pollen was present in all samples and formed about 40-100% of each. Pollen from *Acacia*, *Eucalyptus* (tentatively identified) and an unidentified source formed significant portions of about half the samples. *Scaevola spinescens* grains formed a minor fraction of two samples.

From the table it may be seen that, except perhaps for *C. fulvescens*, all species forage at flowers of two or more plant families. Myrtaceae are visited by all species. Other families visited (in order of popularity) are Mimosaceae, Proteaceae, Goodeniaceae, Caesalpiniaceae, Chloanthaceae and Solanaceae. Despite the variety of food plants visited, some species exhibit apparent preferences for certain pollens: *C. albomarginatus* Michener, *C. rufescens*, *C. smaragdinus*, *C. tigris* Houston and *C. tricolor* for certain Myrtaceae; *C. centralis* and *C. nicholsoni* for *Acacia*; and *C. ordensis* for *Cassia*. However, because these species sometimes visit and collect from plants of two or more families they cannot be strictly termed oligolectic.

Clearly, females often visit two or more kinds of plant while collecting pollen and gather mixed loads. On these same trips they may frequently visit other kinds for nectar alone. One cannot assume, therefore, that pollen-laden females are necessarily carrying pollen of the plant on which they were recorded. *Verticordia*,

for example, is primarily a nectar source for *C. smaragdinus* as are other myrta-ceous genera for *C. nicholsoni*.

*Ctenocolletes* species prefer certain food plants and are not merely limited by what is available to them. For *nicholsoni*, *ordensis*, *rufescens*, *smaragdinus* and *tigris*, at least, there are many good nectar and pollen sources available during their activity periods that they do not utilize.

Plants visited by *Ctenocolletes* vary in form from low shrubs to small trees and display a wide range of flower colours. This applies to the food plants of some species as well as the genus as a whole. However, a common characteristic of almost all pollen sources is that the flowers are small and clustered and/or have numerous erect stamens. Pollen collecting females work feverishly, running over the flower heads and seldom remaining alighted for more than a few seconds. They hover frequently to preen and transfer pollen to the scopa and on alighting do not usually fold the wings but retract them to a V-shape. Some females of *nicholsoni* even continue to beat their wings as they scurry over *Acacia* flowers. *C. ordensis* and *C. tigris* are the only species known to collect pollen from flowers with porose vibratile anthers and do so in the manner of many other bees by hunching over the anthers and vibrating their thoracic muscles with an audible buzz. Pollen is at first accumulated dry but (at least in four species) is moistened towards the end of foraging trips and forms smooth firm masses on the outer sides of the hind tibiae and basitarsi (Figure 1).

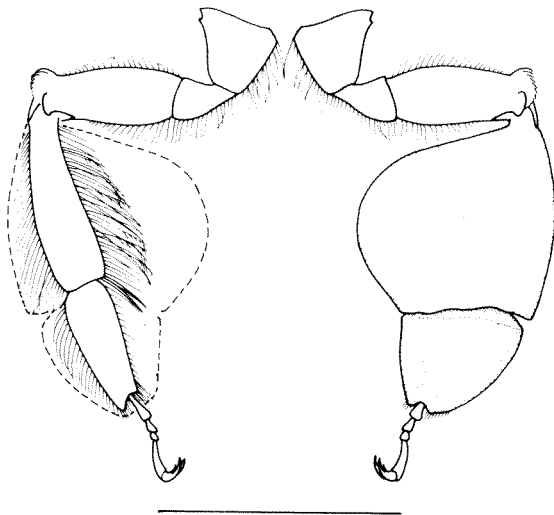


Figure 1 Hind legs of *Ctenocolletes ordensis* female (anterior view) showing full pollen load (right, stippled) in relation to tibial and basitarsal scopa (left; anterior setation omitted for simplicity). Scale line, 5 mm.

**Table 1** Records of flowers visited by adults of *Ctenocolletes* and pollens carried on the scopae of females. Sight records are distinguished by parentheses around numbers of specimens. Relative amounts of pollens in samples were estimated visually and are indicated by +, > and  $\gg$  (e.g. in a mixture of A and B these symbols mean that A represents 45-55%, 56-70% or 71-95% respectively). Amounts less than 5% may have represented flower contaminants and are ignored. Abbreviations: M, matches pollen of plant visited; N, many; NK, not known; NM, not matching pollen of plant visited; U, U<sub>1</sub>, U<sub>2</sub>, etc., unidentified species.

Species	Flowers visited	No. bees	Pollens carried by females	No. ♀	
<i>C. albomarginatus</i>	<i>Baeckea stowardii</i>	1 ♀	Myrtaceae <sub>1</sub> NM $\gg$ Myrtaceae <sub>2</sub> NM + U	1	
	<i>Eucalyptus oldfieldii</i>	1 ♂			
	<i>Hakea coriacea</i>	1 ♂			
	<i>Scholtzia spathulata</i>	2 ♂			
	<i>Wehlia thryptomenoides</i>	2 ♀	Myrtaceae M	2	
<i>C. centralis</i>	<i>Baeckea stowardii</i>	1 ♂			
	NK	4 ♀	Myrtaceae	4	
		2 ♀	nil	2	
<i>C. fulvescens</i>		5 ♀	<i>Acacia</i>	5	
	<i>Eucalyptus oleosa</i>	1 ♀	Myrtaceae M	1	
<i>C. nicholsoni</i>	<i>Acacia aneura</i>	1 ♀	<i>Acacia</i> > <i>Scaevola spinescens</i> > <i>Baeckea</i>	1	
	<i>Acacia blakelyi</i>	1 ♀	<i>Acacia</i>	1	
	<i>Acacia tetragonophylla</i>	3 ♀	<i>Acacia</i>	3	
	<i>Acacia</i> sp.	1 ♀	<i>Acacia</i>	1	
	<i>Baeckea pentagonatha</i>	2 ♂	6 ♀	<i>Acacia</i>	4
	<i>Calytrix oldfieldii</i>	1 ♂	1 ♀	U > <i>Acacia</i> $\gg$ <i>Calytrix</i>	1
	<i>Scholtzia drummondii</i>	2 ♂	5 ♀	nil	5
	<i>Wehlia thryptomenoides</i>	2 ♀	2 ♀	Myrtaceae M	2
	NK	10 ♀	<i>Acacia</i>	8	
			<i>Acacia</i> $\gg$ Myrtaceae	1	
		Myrtaceae $\gg$ <i>Acacia</i>	1		
<i>C. ordensis</i>	<i>Cassia charlesiana</i>	(1 ♀)			
	<i>Cassia chatelainiana</i>	1 ♂			

	<i>Scaevola spinescens</i>	2 ♂	1 ♀	nil	1
	NK (collected at nests)		6 ♀	<i>Cassia charlesiana</i>	1
				<i>Cassia</i> > Myrtaceae ≧ <i>Acacia</i>	1
				<i>Cassia</i> + Myrtaceae ≧ <i>Scaevola spinescens</i>	1
				<i>Cassia</i> ≧ U <sub>1</sub> + <i>Scaevola spinescens</i>	2
				<i>Scaevola spinescens</i> > Myrtaceae + U <sub>1</sub>	1
<i>C. rufescens</i>	<i>Eucalyptus oldfieldii</i>	2 ♂			
	<i>Grevillea ?pterosperma</i>		3 ♀	Myrtaceae NM	2
	<i>Hakea coriacea</i>	5 ♂			
	<i>Melaleuca scabra</i>		1 ♀	Myrtaceae M	1
	<i>Melaleuca uncinata</i>		1 ♀	Myrtaceae M	1
	<i>Scholtzia drummondii</i>	4 ♂			
	<i>Scholtzia spathulata</i>	14 ♂	1 ♀	nil	1
	<i>Wehlia thryptomenoides</i>		8 ♀	Myrtaceae M	4
	NK		2 ♀	Myrtaceae	1
				Myrtaceae ≧ <i>Acacia</i> + ? <i>Grevillea</i>	1
<i>C. smaragdinus</i>	<i>Baeckea ?leptospermoides</i>		1 ♀	nil	1
	<i>Beaufortia bracteosa</i>		(1 ♀)		
	<i>Grevillea biformis</i>	(N ♂)	1 ♀	<i>Grevillea</i> M	1
	<i>Leptospermum erubescens</i>	1 ♂	1 ♀	nil	1
	<i>Melaleuca leptospermoides</i>		1 ♀	Myrtaceae M ≧ <i>Grevillea</i>	1
	<i>Melaleuca microphylla</i>	1 ♂	1 ♀	Myrtaceae M	1
	<i>Melaleuca scabra</i>		1 ♀	Myrtaceae M	1
	<i>Verticordia chrysantha</i>	7 ♂	(3 ♀)		
	<i>Verticordia picta</i>	1 ♂	3 ♀	Myrtaceae NM ≧ <i>Grevillea</i>	1
				<i>Grevillea</i> > Myrtaceae NM ≧ U	1
<i>C. tigris</i>	<i>Baeckea stowardii</i>	1 ♂	1 ♀	nil	1
	<i>Dicrastylis exsuccosa</i>	7 ♂	4 ♀	<i>Dicrastylis</i> M	1
		(N ♂)			
	<i>Solanum</i> sp.		1 ♀	<i>Solanum</i> > <i>Dicrastylis</i>	1
	<i>Wehlia thryptomenoides</i>	3 ♂	3 ♀	Myrtaceae M	3
		(N ♂)			
<i>C. tricolor</i>	<i>Grevillea paradoxa</i>	1 ♂			
	<i>Grevillea ?pterosperma</i>	7 ♂			
	<i>Melaleuca scabra</i>		1 ♀	Myrtaceae M	1
	<i>Wehlia thryptomenoides</i>		1 ♀	Myrtaceae M	1

The majority of food plants have exposed or readily accessible nectaries as is to be expected in view of the bees' relatively short mouth parts.

Foraging in most species occurs from mid-morning to late afternoon. However, the type specimen of *fulvescens* was collected while foraging at sunrise in very hot weather.

Because *Ctenocolletes* mainly forage at plants of characteristically Australian genera with wide distributions in this continent, the distributions of food plants alone cannot determine those of the bees.

Up to five species of *Ctenocolletes* occur together in some localities (Houston 1983a) and, as they are active during more or less the same period, the question arises as to whether they compete for resources. In the neighbourhood of Sandstone, one finds *centralis*, *nicholsoni*, *albomarginatus*, *rufescens* and *ordensis*. The last-named is unique in being largely dependent on *Cassia* for pollen. Its nectar sources are not known with certainty but probably include *Scaevola spinescens*. The first two appear to rely largely on *Acacia* pollen while the remaining two rely largely on myrtaceous pollen. Probably all four utilize myrtaceous nectar. Thus, partition of food resources is partial. However, because the shared food plants usually flower prolifically (except in periods of drought), there is not normally likely to be serious interspecific competition.

### Male Patrolling and Territoriality

Males of all species but *C. fulvescens* have been observed in fast, patrolling flights over the food plants. Often their flight is so fast that the bees are heard rather than seen and they can be extremely difficult to net. Males of *C. nicholsoni* are particularly fast and noisy fliers. Males occasionally alight to take nectar but most of their time from mid-morning to late afternoon is spent in flight.

Because of their brilliant green iridescence, males of *C. smaragdinus* are easiest to identify in the field. They appear to follow fairly regular circuits passing clumps of flowering food plants over wide areas of heath. They seldom slacken their pace as they pass flowers. In open heaths their density is so low that encounters between them are few but at a bank of tall, heavily flowered *Melaleuca microphylla* shrubs, both sexes were abundant and contact between individuals was frequent. Many times males were observed to engage one another in bouts of circling and chasing.

A smaller number of *smaragdinus* males were observed in prolonged hovering flight near food plants. At the *Melaleuca* shrubs just mentioned several males hovered in gaps in the foliage at heights of 0.5 to 3.0 m above ground. For the most part they hovered almost stationary but frequently turned this way or that or moved a few centimetres. Most movement was confined to a space of about 50 cm diameter but occasional brief dashes were made to other parts of the shrub bank. In an area of low heath, several isolated males were observed hovering as low as 5 cm above ground in the lee of flowering *Melaleuca scabra* shrubs. Many

similar but untended shrubs were nearby and the basis of the bees' selection was not apparent.

Despite several hours of observation at localities where males of *nicholsoni*, *rufescens*, *tigris* and *tricolor* were numerous, no instances of territoriality were found. Males of *nicholsoni* occasionally paused momentarily in hovering flight near flowers but generally their flight seemed erratic and the flight paths of numerous individuals interwove.

### Mating and Conjugate Flight

The following observations of *C. smaragdinus* were made at Emu Rocks, 53 km east of Hyden, and at Boorabbin Rock, 93 km east of Southern Cross.

Initiation of mating was observed only once when a patrolling male dashed upon a female taking nectar at flowers of *Verticordia chrysantha*. The pair fell to the ground buzzing and struggled for a few seconds, then took flight conjugately, the male above the female, and flew laboriously out of sight.

Thirteen other male/female pairs of this species were observed over several days in mid-October and again (at the same locality) in mid-November; so pairing apparently occurs throughout the flight season. In all cases pairs consisted of a male mounted on the back of a female. A few of them rested on shrubbery and took flight as I brushed by. One such pair remained united when netted and even when handled. Unfortunately, the bees escaped before details of their coupling could be noted. A second disturbed pair resettled on a stem and close observation revealed that the genitalia were coupled and the male's metasoma was pulsating. The female carried no pollen and her unworn wings suggested she was newly emerged. The remaining pairs were observed on flowers. In eight of these where close inspection was possible the genitalia were definitely not coupled and three females carried pollen loads. One foraging pair was observed for 15 minutes, during which time the female gathered pollen from *Melaleuca scabra* and nectar from *Verticordia picta*. The pair settled intermittently on shrub stems while the female groomed herself and compacted her pollen load and, when the latter was moist and complete, flew rapidly out of sight.

In each pair which was closely inspected, the male gripped his partner as depicted in Figure 2. His fore tarsi gripped the bases of her wings near the tegulae, his mid legs grasped her body behind her wings and in front of her hind legs, and his hind legs wrapped around and under her metasoma. His antennae stretched forward over her thorax. When pairs took flight, both individuals beat their wings, the male apparently taking his cue from the female and probably sensing her wing vibrations through his fore tarsi. Pairs flew slower, more directly and more noisily than individuals.

Similar behaviour was observed for *C. tigris* in the Great Victoria Desert, Western Australia, in September 1982. Four pairs flying conjugately were captured at flowers of various food plants. In two cases the genitalia appeared to be coupled and the females were taking only nectar and not carrying pollen. In

the others, the females carried pollen loads but the coupling was not ascertained. Conjugate pairs were not troubled by other males even at one bush attended by about eight individuals. One difference from *C. smaragdinus* was that males in pairs carried their antennae erect.

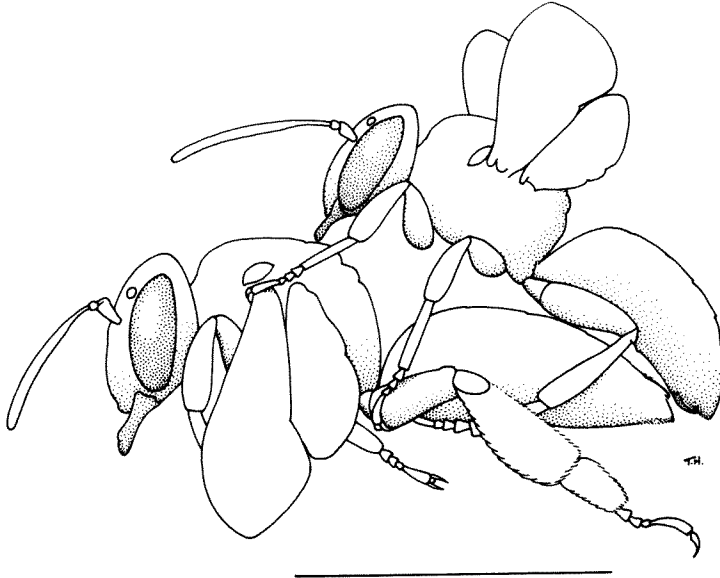


Figure 2 Sketch showing how *Ctenocolletes smaragdinus* male (above) grasps female during conjugate flight. Scale line, 1 cm.

Conjugate flight has also been observed in two other species. On 22 October 1974, about 8 km south of Yellowdine, I observed a pair of large bees hovering slowly through foliage before settling on a shrub stem. I was only able to note that a male was mounted on the back of a female before they were disturbed and flew off, still united. Males of *C. tricolor* were abundant in the near vicinity and I assumed that the pair was of this species. However, a few females of *C. rufescens* were also collected near the site. On 2 September 1981, Mr G.A. Holloway of the Australian Museum observed and collected large bees flying *in copula* near flowers of *Eucalyptus*, 28 km west of Yalgoo (pers. comm.). Two pairs of *C. ordensis* were amongst specimens collected by him on that occasion and his recollection was that they were the mating pairs (a male of *C. nicholsoni* was also collected). As mentioned later in this paper, females of *C. ordensis* arrived alone at their nests which were not frequented by males, so conjugate flight may be confined to the vicinity of food plants.

The prolonged sexual coupling and conjugate flight of *Ctenocolletes* are singular habits not observed in its sister genus *Stenotritus* despite some days of



observation of several species. Conjugate flight has seldom been reported for bees. It is known in certain species of the North American genus *Nomadopsis* (Andrenidae: Panurginae) (Rozen 1958, Alcock *et al.* 1978) and the non-Australian genus *Colletes* (Colletidae: Colletinae) (Batra 1980). Behaviour of *Colletes* differs markedly from that of *Ctenocolletes*: in *C. thoracicus* Smith and *C. cunicularius* (L.), pairs engage in nuptial flights of up to 2 minutes duration but males are carried horizontally behind females, coupled by their genitalia. Coupled females are mostly newly emerged and do not forage. *Nomadopsis* behaviour is rather more similar in that males ride facing forward above females often while the latter collect full pollen loads. However, two differences are that the genitalia are always coupled and males hold their mid and hind legs out away from females.

Alcock *et al.* (1978) supposed that protraction of mating in *Nomadopsis* may serve to shield foraging females from the disruptive attentions of other males. This may be so but, at least in *Ctenocolletes*, this advantage would seem to be offset by the slowing effect male jockeys exert on their partners.

The three species of *Ctenocolletes* definitely known to fly conjugately (*ordensis*, *smaragdinus*, *tigris*) form a discrete group but my observation of similar behaviour in a more distant species (either *rufescens* or *tricolor*) suggests that conjugate flight may be a generic trait.

### Male Roosting

In the second week of October 1979, on the crest of a low heath-covered rise 53 km east of Hyden, clusters of *C. smaragdinus* males were found gathering at evening in two low dense shrubs about 30 m apart. The bushes, one a *Chamaelaucium virgatum*, the other a *Casuarina* sp., were rotund, about 40 cm high and had fine foliage but neither was conspicuous amongst the surrounding vegetation. Attention was first drawn to them by males milling about in their near vicinity at 4.25 p.m. (W.S.T.). As some males arrived for a period of circling, others departed. Gradually, the number of males grew to dozens producing a hum audible many metres away. At around 5.15 p.m. males began settling and all had alighted by 6.00 p.m. (10 minutes before sunset). At 6.20 p.m. an inspection revealed three spherical clusters in one bush and a larger elongate cluster (c. 15 cm x 5 cm) in the other. Each bush held approximately 100 tightly packed males with their heads hidden within the groups.

At sunrise the morning after their discovery, the males were quite torpid and remained motionless when picked off into the hand. At 10.30 a.m., as the first rays of sunlight penetrated a cloud cover, only a few bees remained and these soon dispersed. Each evening the clusters re-formed in the same manner. Revisited a month later, one bush had a much diminished cluster while the other was deserted.

In September 1982, in the Great Victoria Desert, W.A., three males of *C. tigris* were found separately in torpid condition on various low shrubs at night or



Figure 3 Part of nesting area of *Ctenocolletes ordensis* on Anketell Station, W.A. Many nest entrances were in bare ground near excavation (right foreground).

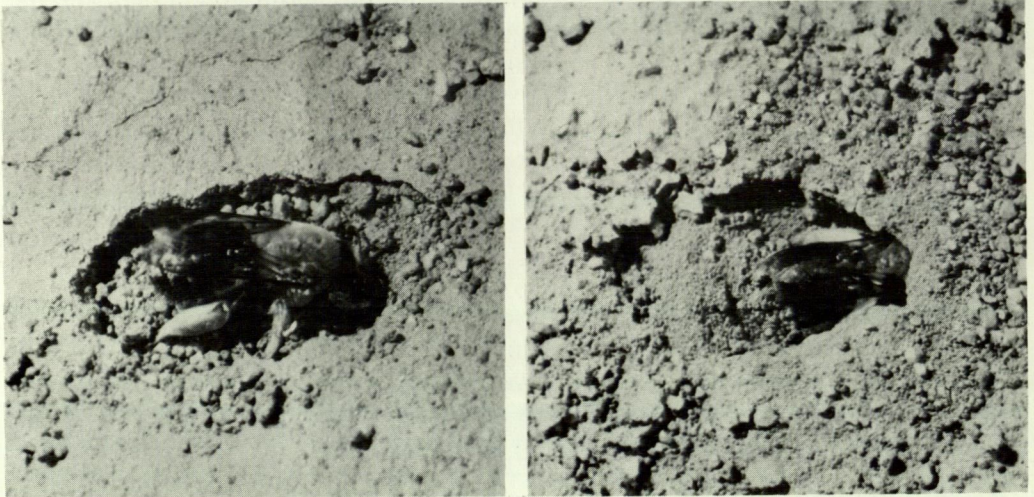


Figure 4 Pollen laden females of *Ctenocolletes ordensis* burrowing into loose soil in nest entrance pits.

early morning. Two clung to leaves and one to an *Acacia* flower using all legs. The antennae were held erect.

### **Nesting Biology of *Ctenocolletes ordensis***

This is the only species whose nests have been examined in detail.

A nesting population was discovered on Anketell Station between Mt Magnet and Sandstone on 3 September 1981 and was examined over the following two days. The area generally was one of dense mulga (*Acacia aneura*) shrubland but the nests occurred in disturbed ground adjacent to a road, on and near the path of a former (but now non-existent) railway. The reddish sandy loam soil was level and, near the road where it was relatively soft near the surface, bore medium dense regrowth. On the railway path it was compacted hard and its weathered surface was largely devoid of vegetation (Figure 3).

Females were observed entering and leaving burrows scattered irregularly in both hard and soft ground. At least 50 burrows occurred in an area 10 m x 30 m. They were not obviously aggregated but some were very close and six entrances were found within an area 40 cm wide. All were in bare ground.

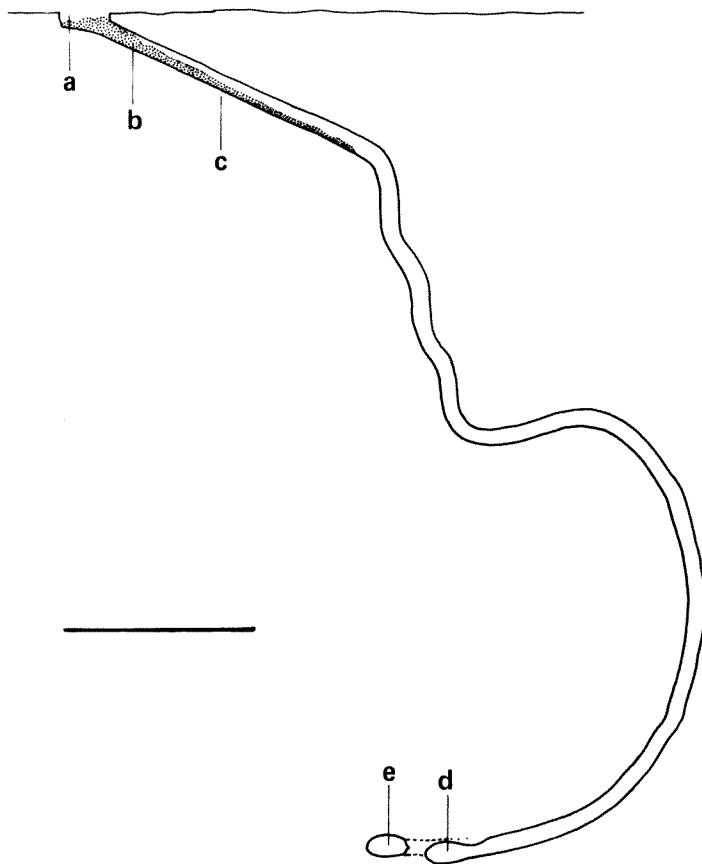
### *Nest Architecture, Provisions and Immatures*

Nests were characterized at the surface by roughly ovoid, sharp-edged pits (Figures 4, 5) varying in length from 15-30 mm. A shaft entrance was at one end of each pit. Tumuli were absent although a little loose soil was scattered about some pits and loose sand lay in the pit floors and blocked the burrow entrances.

Three separate excavations were made, one in the bare railway path and two in the softer vegetated zone. Altogether, seven active nests were exposed along with remains of several old, vacated nests. On the railway path the surface soil was so compacted to a depth of about 30 cm that it could only be chipped with a spade. Elsewhere the surface soil was more easily dug and below 30 cm the soil was everywhere much the same: moderately compacted, slightly moist, sandy loam containing patches of harder gravelly soil.

In each nest excavated the entry shaft extended laterally for 10-15 cm at an angle of only 10-20° to the horizontal and was partially filled with loose sand (Figure 5). Shafts then turned vertically and descended irregularly to depths of 30-60 cm where they turned more horizontally again and led to the cells. Shafts were circular in cross-section and 9 mm in diameter. Those through solid soil appeared to have unworked walls but some through soft soil were at least partially cemented.

Brood cells were encountered at depths of 45-77 cm. Some were open and being provisioned, some were closed and contained eggs on completed provisions, and the remainder were old vacated or failed cells from previous generations. Basically, cells were ovoid chambers at the ends of access burrows with built-in cemented earthen walls continuous with those of the burrows (Figure 6). The long axes of cells dipped to the rear and floors were flatter than ceilings.



**Figure 5** Nest of *Ctenocolletes ordensis* in profile: a, entrance pit; b, loose soil closing burrow; c, entrance shaft; d, open cell being provisioned; e, closed provisioned cell (access burrow soil-filled and connection with shaft obscure). Scale line, 10 cm.

During excavation, cells could be detected by their hardened gravelly outer coat which contrasted with the softer soil matrix and cells and their access burrows could be removed intact. The internal cell walls were composed of very fine gravel-free soil; it appears that the bees are able to separate finer and coarser grains as they build.

The inner surfaces of all cells were very smooth and shiny as if varnished. The gloss diminished slightly near the neck of each cell and was absent outside it. Drops of water placed on the inner walls of cells remained unabsorbed while others placed on the walls of access burrows or on the outer coats of cells were absorbed immediately. No lining could be peeled, scraped or flaked from the walls of untreated cells. However, when portion of a cell was soaked in water and detergent, a very delicate transparent membrane separated slightly from the

earthen wall. It was flexible like a plastic film and could be peeled away. It was insoluble in xylene and turpentine, did not melt when heated and appeared amorphous under the microscope. Clearly, it was not a wax film but more probably a laminester (*sensu* Hefetz *et al.* 1979).

Completed provisioned cells were closed by elaborate earthen plugs (Figure 6). Initial closure was effected by a plug of fine compacted soil in the cell neck. Its inner surface was concave with a spiral pattern and was uncemented. Its exterior was also concave but smooth and cemented to a depth of about 3 mm. Following this plug was a short cavity filled with gravel and soil, then a thin cemented earth partition about 1 mm thick, concave and smooth externally and rough internally. The concave surfaces of both plug and partition were 11 mm in diameter and since all open access burrows were only 10 mm, females must enlarge the cell antechambers as they build in the closure. Although both concave surfaces were smoothed and looked like cell bases, they were rather flatter and were not waterproofed. Beyond the concave partitions the access burrows were filled with loose soil and gravel.

Five nests excavated had one open and one closed cell but no more than two cells were found in close proximity anywhere during the September 1981 dig (nor subsequently — see below). Where cells occurred in pairs they and their access burrows were side by side (or at least in parallel, not sequentially arranged).

Each of the open cells examined contained an amorphous mass of moist pollen lying in the rear (Figure 5). In consistency, it resembled completed pollen loads carried on the scopae of females (see under Flower Visiting and Foraging). Closed cells each contained a characteristically shaped pollen mass surmounted by an egg (Figures 6-8). The masses were khaki, smooth, uncoated, and 10.5-13.0 mm in length. They were uniformly moist throughout but firm enough that they could be handled gently without distorting. No free liquid was present in cells.

Some pollen masses returned to the laboratory in their cells gradually liquefied and slumped, filling the lower portions of the cells. After some weeks they congealed again.

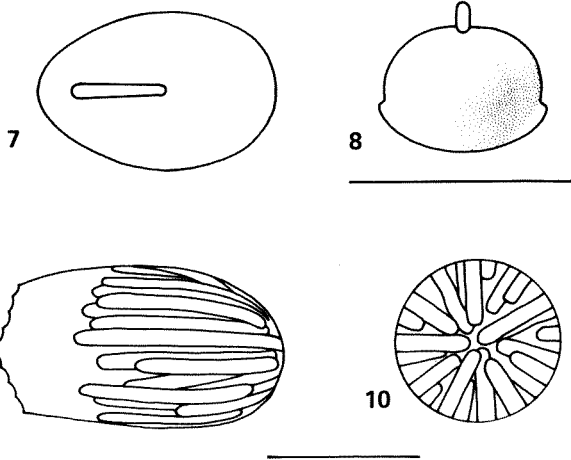
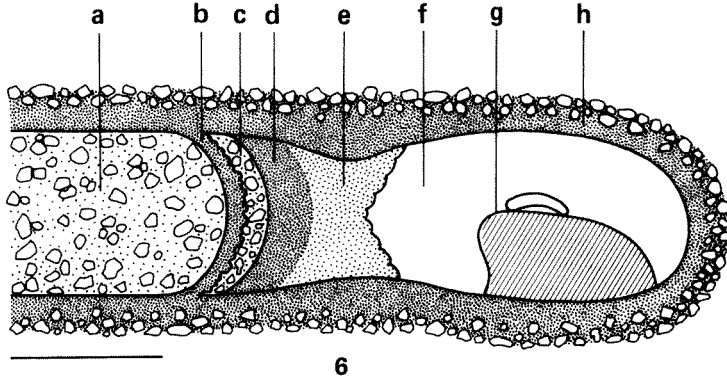
On the first visit no immatures other than eggs were found. However, the site was revisited on 15-16 March 1982 and one of the excavations was reopened and extended. Several further cells were encountered (singly or in pairs as before) and five post-defaecating larvae obtained. There were no cocoons and the soft white larvae rested with their heads towards the cell plugs (whose spiral patterns were still evident). The walls of the inner 3/5 of each cell were streaked with flaky whitish faecal deposits (Figures 9,10).

Evidently, the bees may reuse old nest shafts: four shafts of active nests excavated in September connected with soil-filled burrows leading to old vacated cells.

Nest closure was not studied extensively but it was clear that shafts and access burrows are filled with soil after cell completion. In one such closed shaft examined closely on my March visit, two thin cemented earth partitions 4.5 cm apart were located in its upper reaches a few centimetres below the oblique entry

shaft. They were virtually identical to the thin partitions forming part of cell closures.

In many respects, the nests of *C. ordensis* are like those described for *Stenotritus pubescens* (Houston 1975). Distinguishing features are the entrance pits, oblique sand-filled entry shafts, thicker built-in cell walls, smooth, cemented and concave outer surfaces of cell plugs, gravel-filled chambers outside cell plugs and



**Figures 6-10** *Ctenocolletes ordensis*: 6, schematic sagittal section of newly completed brood cell and adjacent portion of access burrow (a, access burrow occluded by compacted gravelly soil; b, 'false cell-base' partition; c, antechamber filled with compacted gravelly soil; d, cemented outer portion of cell plug with smooth concave outer surface; e, compacted uncemented portion of cell plug with spiral-patterned inner surface; f, cell chamber; g, pollen mass surmounted by egg; h, cemented earth wall of cell with gravelly outer coat); 7, 8, pollen mass and egg in top and end views, respectively; 9, 10, larval faecal deposits on cell wall in side and end views, respectively. Scale lines, 1 cm.

the cemented earthen partitions (like cell bases) forming part of cell and shaft closures.

Comparison of the cell closure of *C. ordensis* (which appears to be unusually elaborate) with those of other bee families is hampered by lack of data for more than a few species: many authors in describing nest structure have failed to note details of more than the inner surface of the cell plug. The other surface is usually obscured by the soil barricade and, as in the case of *ordensis*, it requires very careful examination to reveal any surfaces or cavities. A smoothed concave and cemented outer surface of the cell plug has been reported for some Panurginae (Andrenidae) by Malyshev (1936) and Rozen (1968, 1971), a melittid (Rozen 1974) and is typical of ground-nesting Anthophoridae (Linsley, MacSwain and Smith 1956; Cardale 1968*a, b*; Linsley, MacSwain and Michener 1980; and many other authors). The inclusion of gravel-filled cavities and cemented earthen partitions in cell and shaft closures has no parallel amongst other short-tongued bees as far as I am aware but anthophorid bees such as *Amegilla* make multiple cell closures and plug shafts with concave cemented earthen partitions (personal observations).

The elaborate structure of cells would necessitate a high labour input and may explain the presence of only two cells per nest. However, it was not ascertained whether females construct more than one nest each.

The provisions of *C. ordensis* are also much like those of *S. pubescens*, differing slightly in the shape of the pollen mass and in the absence of free liquid under or around it. In both species larvae deposit faeces as linear streaks on the cell walls but *C. ordensis* deposits them over more of the cell than *S. pubescens*. Absence of cocoons is common to both species.

#### *Adult Activity at Nests*

With the exception of a single male grooming itself on shrubbery, all adults observed at the nest site in September were females (no adult activity was evident in March).

Females returning to the nest area usually hovered for a few seconds while orientating towards their nests. Then, when about 15 cm from them, they dropped swiftly into the pits and began burrowing into the loose-fill. Once a female had gained access to her burrow she would intermittently back up with simultaneous kicking movements of her hind legs and shove loads of sand into the entrance until it was completely blocked. The successive loads formed ripples in the loose-fill.

Imminent departure of a female from a nest was usually heralded by one or more shrill chirps (presumably produced by vibration of the thorax and folded wings). As a female emerged into the entry pit she performed the same kind of soil-shoving movements described above (but in reverse direction) to close the burrow entrance. Brief grooming was followed by swift departure.

A few females did not block their entrances and made swift entries and departures. They were unladen, unlike the majority of females which arrived heavily laden with pollen.

One female was observed apparently making final closure of her burrow at about 8 a.m. She was in her entrance pit facing away from the burrow and, after breaking down part of the pit wall in front of her (thus lengthening the pit) she backed up with the characteristic rearward kicking movements of the hind legs and pushed the loosened soil towards the burrow entrance. Alternately biting and shoving, she extended the pit to a length of 8 cm and filled most of it with loose sand. She then took flight and, after briefly inspecting the pit, departed.

There appeared to be only one female to a nest. Females were largely unperturbed by the presence of an observer and exhibited no aggression even when their nests were disturbed.

Female traffic at nests was observed from 8.18 a.m. to 5.20 p.m. (W.S.T.) in temperatures of 15-28°C.

#### *Organisms Associated with Nests*

During my September visit, two kinds of parasitoid wasps were observed in association with the bee nests: a *Hyptiogaster* species and a *Crassifoenus* species (Hymenoptera: Gasteruptiidae). One to a few specimens of each were seen searching the ground of the nest area in slow hovering flight at most times of the day. Adults of the first species were much smaller than those of the second (which approximated the bees in bulk, though not dimensions). A pair of *Hyptiogaster* hovered together for several minutes at the entrance of an occupied nest with their faces and antennae directed towards it but eventually departed without entering. Females of *Crassifoenus* were twice observed to enter burrows in the absence of bee occupants and spend several minutes within (presumably ovipositing). However, none of the cells excavated from any nest showed clear evidence of the wasps (nor any other insects). A hard black partition across the lumen of one old cell, though, may have been composed of the characteristic larval excrement of a gasteruptiid.

A large neuropterous larva of the family Ithoniidae was taken from a burrow at a depth of 77 cm, very close to old soil-filled cells and not far from newly constructed ones. However, it was not clear whether the larva was in a bee burrow or one of its own.

#### **Nesting in Other Species**

Only a few minor observations are available but tend to confirm the ground-nesting habits of the genus.

On 7 September 1981, about 30 km west of Sandstone, a female of *C. albomarginatus* was observed alighting at a simple burrow in a graded road drain. It proceeded to perform motions similar to those described above for *C. ordensis* females when entering and closing their burrow entrances. The soil was soft and



sandy. No other burrows were evident and, as the female had not carried pollen and did not reappear, the burrow was not excavated.

Much time and effort has been expended searching for the nests of *C. smaragdinus* in areas where this species was both active and abundant but without success. Perhaps the bees nest solitarily or under cover. Some females were observed hovering close to the ground in an area of heath on white sand and especially near some very low prickly pincushion-like plants. One female began burrowing beneath the edge of such a tussock but abandoned its work after a few minutes.

### Associated Organisms

Some insects associated with nests of *C. ordensis* were discussed above. Here I report on those organisms found associated with adults of *Ctenocolletes*. A survey of all adult specimens available revealed two kinds of phoretic organisms: triungulins (Coleoptera: Meloidae) and mites (Acarina: Acaridae).

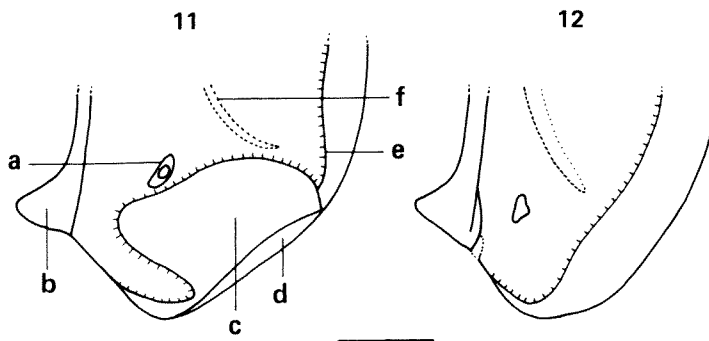
Solitary triungulins were found attached to hairs of the face, legs or propodeum of *C. nicholsoni* (1 ♂, 1 ♀), *C. rufescens* (1 ♀), and *C. smaragdinus* (1 ♀). This is a low incidence and carriage of triungulins is not proof that the bees' larvae are subject to meloid attack.

Three species of *Ctenocolletes* were found to carry hypopial mites: *albomarginatus*, *centralis* and *nicholsoni*. The incidence of mite infestation was quite high. With females, 17 of 20 *albomarginatus*, 25 of 28 *centralis* and 23 of 31 *nicholsoni* were carriers. The incidence on males was at least as high.

Specimens of hypopi were identified as Acaridae and represented (then) three undescribed species of an undescribed genus. The taxonomy and host relationships of the mites are dealt with in an accompanying paper (Fain 1984).

On female bees, mite hypopi were mainly found secreted in cavities (or pouches) beneath the lateral portions of the third and fourth metasomal terga. The cavities (which do not occur in mite-free species) are formed by invagination of the intersegmental membranes and convexity of the overlying cuticle (cf. Figures 11, 12). Up to 43 hypopi occupied each pouch and a total of 133 were carried by one female of *nicholsoni*. The hypopi are usually visible through the transparent integument. There are no conspicuous openings to the pouches and how the mites enter and leave them is not known but would seem to require some assistance from the bees. A few female bees also carried hypopi under the edges of other terga and scattered externally on the body. On males, hypopi occurred beneath the translucent lateral margins of the first to sixth metasomal terga and in the genital chamber.

Because no other function of the tergal pouches is apparent, their purpose may be to protect and transport mites. Hypopi are non-feeding, dispersal stage nymphs and do not harm adults carrying them. However, they may drop from adults in nests under construction, metamorphose into feeding nymphs and consume some material within brood cells. Some kinds of mites feed on bees' larval



Figures 11-12 Right lateral portions of fourth metasomal terga of *Ctenocolletes* females (inner views); 11, *C. nicholsoni* (a, spiracle; b, anterolateral apodeme; c, mite chamber; d, reflexed margin of tergum; e, line of attachment of intersegmental membrane; f, gradulus); 12, *C. ordensis*. Scale line, c. 1 mm.

food stores and immatures (Krombein 1962 and author's own unpublished observations of hylaeine and xylocopine bees). Such feeding activity is inimical to the bees' welfare and would not be favoured by natural selection of bee features. More likely, the mites associated with *Ctenocolletes* may feed in a beneficial manner, consuming larval faeces as occurs in nests of *Lithurge* (Houston 1971), thus reducing the chances of mould growth. Symbiotic relationships between mites and some vespoid wasps (which carry them in special pouches or acarinarium) have been reported by Krombein (1961).

Strepsiptera, commonly found as parasites of Colletidae and other bees, are not known from *Ctenocolletes*.

### Conclusion

The information gathered so far provides only a very incomplete picture of the habits of *Ctenocolletes* and much more is required before one could confidently distinguish generic from specific traits. Comparisons of stenotritid habits with those of other families of short-tongued bees is hampered further by our incomplete knowledge of the latter. For example, nothing at all is recorded of the habits of several genera of Colletidae. However, combined with what is known of *Stenotritus*, the *Ctenocolletes* data permit some tentative generalizations concerning Stenotritidae. The family appears to consist of solitary burrowing bees whose nest architecture most resembles that of Andrenidae and Melittidae (also some Paracolletini, Colletidae, except for absence of cellophane-like material). Male mate-seeking behaviour involves both fast patrolling of food plants and prolonged hovering in stationary territories.

Features which may be derived for (or within) *Ctenocolletes* are the conjugate flights of males and foraging females, the thick built-in walls of cells and access

burrows, incorporation of gravel in the latter and cell closures, and construction of 'false cell-base' partitions in cell and burrow closures.

Following my examination of *C. ordensis* nests I wonder now whether I did not overlook some details of cell arrangement and closure in nests of *Stenotritus pubescens* and further observations of *Stenotritus* nests are needed.

### Acknowledgements

I am most grateful to Dr A. Fain (Prince Leopold Institute of Tropical Medicine, Belgium) for identification of the mites, Mrs C.A. Houston for preparation of pollen samples and technical advice, Mr N.S. Lander (Western Australian Herbarium, Perth) for identification of many plants, Mr K.T. Richards (W.A. Department of Agriculture, Perth) for loan of bee specimens and Mr M.J. Tyler (University of Adelaide) for providing some of the literature.

### References

- Alcock, J., Barrows, E.M., Gordh, G., Hubbard, L.J., Kirkendall, L., Pyle, D.W., Ponder, T.L. and Zalom, F.G. (1978). The ecology and evolution of male reproductive behaviour in the bees and wasps. *Zool. J. Linn. Soc.* 64: 293-326.
- Batra, S.W.T. (1980). Ecology, behaviour, pheromones, parasites and management of the sympatric vernal bees *Colletes inequalis*, *C. thoracicus* and *C. validus*. *J. Kans. ent. Soc.* 53 (3): 509-538.
- Cardale, J.C. (1968a). Nests and nesting behaviour of *Amegilla (Amegilla) pulchra* (Smith) (Hymenoptera: Apoidea: Anthophorinae). *Aust. J. Zool.* 16: 689-707.
- Cardale, J.C. (1968b). Observations on nests and nesting behaviour of *Amegilla (Asaropoda)* sp. (Hymenoptera: Apoidea: Anthophorinae). *Aust. J. Zool.* 16: 709-713.
- Fain, A. (1984). A new genus and three new species of mites (Acari: Acaridae) phoretic on bees of the genus *Ctenocolletes* in Australia. *Rec. West. Aust. Mus.* 11 (2): 77-86.
- Hefetz, A., Fales, H.M. and Batra, S.W.T. (1979). Natural polyesters: Dufour's gland macrocyclic lactones form brood cell laminesters in *Colletes* bees. *Science, N.Y.* 204: 415-417.
- Houston, T.F. (1971). Notes on the biology of a lithurgine bee (Hymenoptera: Megachilidae) in Queensland. *J. Aust. ent. Soc.* 10: 31-36.
- Houston, T.F. (1975). Nests, behaviour and larvae of the bee *Stenotritus pubescens* (Smith) and behaviour of some related species (Hymenoptera: Apoidea: Stenotritinae). *J. Aust. ent. Soc.* 14: 145-154.
- Houston, T.F. (1983a). A revision of the bee genus *Ctenocolletes* (Hymenoptera: Stenotritidae). *Rec. West. Aust. Mus.* 10 (3): 269-306.
- Houston, T.F. (1983b). A new species of *Ctenocolletes* (Hymenoptera: Stenotritidae). *Rec. West. Aust. Mus.* 10 (4): 307-313.
- Krombein, K.V. (1961). Some symbiotic relations between saproglyphid mites and solitary vespid wasps. *J. Wash. Acad. Sci.* 51: 89-93.
- Krombein, K.V. (1962). Natural history of Plummers Island, Maryland. XVI. Biological notes on *Chaetodactylus krombeini* Baker, a parasitic mite of the megachilid bee, *Osmia (Osmia) lignaria* Say (Acarina: Chaetodactylidae). *Proc. biol. Soc. Wash.* 75: 237-249.

- Linsley, E.G., MacSwain, J.W. and Michener, C.D. (1980). Nesting biology and associates of *Melitoma* (Hymenoptera, Anthophoridae). *Univ. Calif. Publs Ent.* 90: i-vii, 1-45.
- Linsley, E.G., MacSwain, J.W. and Smith, R.F. (1956). Biological observations on *Ptilothrix sumichrasti* (Cresson) and some related groups of emphorine bees (Hymenoptera, Anthophoridae). *Bull. Sth Calif. Acad. Sci.* 55 (2): 83-101.
- Malyshev, S.I. (1936). The nesting habits of solitary bees. *Eos, Madr.* 11: 201-309.
- Rozen, J.G. (1958). Monographic study of the genus *Nomadopsis* Ashmead (Hymenoptera: Andrenidae). *Univ. Calif. Publs Ent.* 15: i-iv, 1-196.
- Rozen, J.G. (1968). Biology and immature stages of the aberrant bee genus *Meliturgula* (Hymenoptera, Andrenidae). *Am. Mus. Novit.* 2331: 1-18.
- Rozen, J.G. (1971). Biology and immature stages of Moroccan panurgine bees (Hymenoptera, Apoidea). *Am. Mus. Novit.* 2457: 1-37.
- Rozen, J.G. (1974). The biology of two African melittid bees (Hymenoptera, Apoidea). *Jl N.Y. ent. Soc.* 82: 6-13.