

A second contribution to the biology of *Ctenocolletes* bees (Hymenoptera: Apoidea: Stenotritidae)

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Abstract

Field observations of adult behaviour (particularly foraging and mating) and nests of five species of *Ctenocolletes* are presented and compared with earlier observations. All studied species are solitary and ground-nesting. Nests are unusual in lacking tumuli and those of *C. albomarginatus* and *C. nicholsoni* are remarkably deep (2.7-3.2 m).

C. fulvescens is unusual in the genus in having a summer/autumn (rather than a winter/spring) flight season and in exhibiting matinal foraging in females and a bimodal flight pattern in males.

Conjugate flight of mating pairs and territorial hovering and darting flights of males are recorded for additional species. Meloidae (Coleoptera) are confirmed as cleptoparasites in nests of *C. nicholsoni* and a *Crassifoenus* species (Hymenoptera: Gasteruptiidae) is recorded from nests or nesting areas of four *Ctenocolletes* species.

Introduction

In a previous paper (Houston 1984), I recorded the first details of the bionomics of bees in the genus *Ctenocolletes*. Nests of only one species (*C. ordensis* Michener) were described and much of the information on adult behaviour was fragmentary, providing only a very incomplete picture of the bionomics of the genus as a whole.

The observations presented here were made opportunistically during field work at various Western Australian localities in 1983-1985 and are similarly fragmentary. Nevertheless, they augment and significantly extend earlier observations. Examination of the nests of several species has revealed some significant interspecific differences and discovery of the nests of *C. albomarginatus* Michener and *C. nicholsoni* Cockerell provided the first opportunity to study the life histories of acarid mites associated with the bees. The mite-bee symbiosis will be the subject of a forthcoming paper and the present paper provides the necessary background.

The nomenclature employed here follows Houston (1985). Specimens taken as vouchers in the course of my studies are lodged in the Western Australian Museum.

In respect of brood cells, I use the terms 'proximal' to mean near the opening (or cell plug) and 'distal' to mean near the closed (blind) end.

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Observations

Ctenocolletes albomarginatus Michener

Nests

A nesting area of this species adjacent to the eastern margin of East Yuna Nature Reserve (c. 34 km WNW of Mullewa) was examined first on 13-16 September 1984. It was on the crest of a sandy rise in a farm paddock that had lain fallow for some years. Areas of bare, wind-eroded sand were interspersed with areas of herbs and shrub regrowth and bordered on natural *Banksia* shrubland and heath in the reserve.

The persistent flight of *albomarginatus* males over an area of level bare sand attracted my attention initially and the arrival of pollen-laden females confirmed the presence of nests there. The females alighted at barely discernible pits in the ground and quickly burrowed out of sight through loose sand. About 10 burrows were thus revealed in an area about 7 x 15 m but more may have been present. Tumuli were totally absent from the nest entrances.

One burrow was excavated and was so deep and required so much time and effort to expose that I was unable to excavate more. The excavation pit went to a depth of 3.3 m through uniform but increasingly more compacted yellow sand. To a depth of 2.6 m the sand was soft and damp but below this it became dry and hard and near 3 m depth could only be chipped with a spade.

The entrance shaft extended at an angle of 13° below horizontal for 27 cm and near the entrance was filled with loose sand (Figure 1). At its lower end it turned vertically and descended to a depth of 295 cm. Here the shaft turned obliquely for 11 cm, made two lateral turns and terminated in an open empty cell at a depth of 305 cm (23 cm to one side of the vertical shaft line). The shaft was 8.5 mm in diameter, uncemented and unlined.

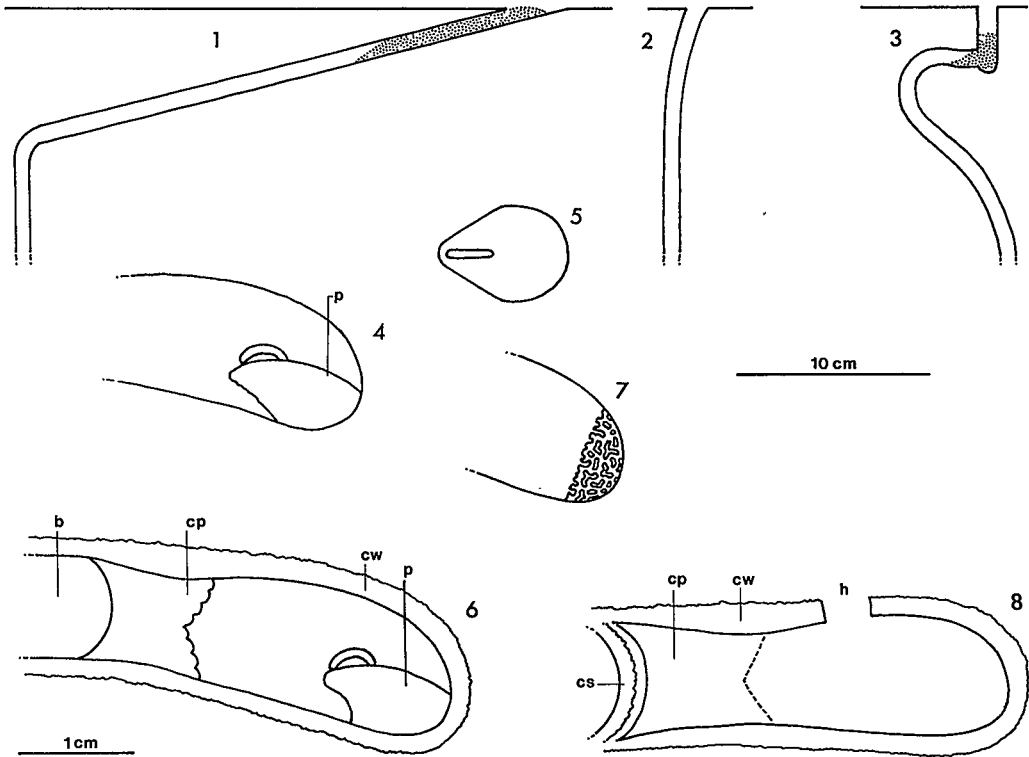
Three closed cells apparently associated with this nest were exposed at depths of 308-316 cm. They were 20-28 cm from the vertical shaft axis and spanned 100° of arc about it. All were cut through before they were discovered and no details of their closures were obtained. The internal shape of the cells was ovoid (although the lower side was flatter than the upper) and their long axes dipped about 30-45° below the horizontal. Their walls did not appear to be built-in nor any harder than the mortar-like matrix and were the same colour internally as the matrix. Only the distal half of each cell was varnished and waterproof; the walls nearer the cell plug readily absorbed droplets of water and the interstices between sand grains forming the walls there were seen to be open under the microscope.

Several old cells were cut through in the lower reaches of the excavation but they were compactly filled with sand and were difficult to detect.

The entrance shaft of a second nest was like that of the first but extended only 18 cm before turning vertically. It had an 8 cm barricade of loose sand

and fine litter within the entrance.

Each of the three closed cells from the nest fully excavated contained a pollen mass surmounted by an egg (Figure 4). The pollen provision was soft and moist and could not be handled without distortion.



Figures 1-8 Nest details of *Ctenocolletes* species. (1-3) Profiles of entrance galleries of (1) *C. albomarginatus*, (2) *C. nicholsoni* and (3) *C. smaragdinus* (loose soil stippled). (4, 5) *C. albomarginatus*: profile of brood cell (closure lost in excavation) and provision mass (4) and top view of provision mass and egg (5). (6, 7) *C. nicholsoni*: profile of brood cell and provision mass (6) and profile of faecal mass in distal end of cell (7). (8) Profile of old soil-filled brood cell of *C. smaragdinus* with hole in ceiling presumably made by an emerging parasite (original orientation of cell not shown). Upper scale line refers to Figures 1-3, lower to Figures 4-8.

Legend: b, soil barricade; cp, cell plug; cs, concave septum; cw, built-in cell wall; h, hole; p, provision mass surmounted by egg.

Associated organisms

All four cells contained 2-6 acarid mites or their exuviae and these will be discussed in a forthcoming paper. A few gasteruptiid wasps (*Crassifoenus* sp.) were observed searching the ground at the nesting area but none was seen to enter a nest.

Adult behaviour

On a brief visit to the East Yuna Reserve on 29 August 1984, I first noted males coursing over the bare sand (there were only two of them) and collected both sexes at flowers. On a return visit on 13-16 September 1984, more males (about 12 at any one time) were patrolling the nesting area. They flew erratically within 10 cm of the surface and their paths interwove. Occasionally two would engage in circling or chasing one another but there appeared to be no territoriality at the site. Some spots seemed to elicit more attention from males than others. Males would hover near them and almost alight. One spot (a tiny mound with an ant nest entrance hole to one side) received close attention from several males for over an hour but the reason was not apparent.

When a pollen-laden female flew in and approached her burrow 50 cm from this 'hot spot', the males immediately converged on her. She quickly became enveloped in a ball of grappling males that tumbled about on the ground while other males hovered about. After a few seconds the female mounted by a male struggled free and the pair flew conjugately up and over adjacent shrubbery out of sight. A similar sequence of events occurred when a second female approached her burrow. A third female that was pursued by a single male was netted. The pursuing male persisted about the net bag and followed as I moved it some metres. Males showed no response to flying insects other than their own species or to small objects flicked past or dangled near them.

Further observations of adult behaviour were made at the site on 24-26 August 1985. In mild overcast conditions, the males patrolled from about 11 am to 4.30 pm each day. They were more widely dispersed than previously and only about half of them flew close to the ground. The remainder flew rapidly 40-60 cm above it and frequently circled a patch of *Ricinocarpus* shrubs. On this visit I had hoped to observe females burrowing but only one female was seen entering the ground and she did not reappear. One mating as described above was observed at the site.

Ctenocolletes centralis Houston

Recent collection records of this species indicate that its chief forage plants are *Acacia* species and *Thryptomene maisonneuvei*. Pollen loads of five females collected at flowers of the latter plant proved to be composed of *Acacia* pollen in four cases and myrtaceous (probably *Thryptomene*) pollen in the fifth. *Thryptomene* apparently serves primarily as a nectar source. The only other plant genera visited are *Baeckea* and *Dicrastylis*.

Males have been observed at several localities engaging in fast wide-ranging flight over *Thryptomene maisonnewii* flowers. Numerous individuals crossed paths and there was no evidence of aggression. However, on 28 July 1983, at least 20 males were found defending territories amongst *Triodia* hummocks in a flat sandy interdune swale 17 km west of Wiluna. Males maintained hover stations about 20-50 cm above the ground and made frequent forays out from them. This activity was observed at midday in fine sunny conditions. No females were observed in the area, nor could I find any nest burrows. The area and surrounds were dry and flowerless.

Ctenocolletes fulvescens (Houston)

Recent collection records (Houston 1985) confirm that this species is unique in the genus in its adult activity being confined to late summer and early autumn (January-March). Of 21 males and four females collected on 26 February-4 March 1984, most showed little or no wing wear and few showed extensive emargination. The one female collected in January (21, 1970) had entire wing margins. This suggests that emergence of young adults may occur from late January through February.

All individuals collected or observed were at flowers of mallee (*Eucalyptus gracilis* and *E. oleosa*). Both sexes took nectar and females collected pollen (verified by microscopic examination of two pollen loads). Flowers of other plants such as *Amyema*, *Banksia* and *Melaleuca* were available but were not visited.

Females exhibited a matinal activity pattern and foraged from about 7.30-10.30 am (Western Standard Time) with a peak of activity between 8 and 9 am. Males exhibited a bimodal activity pattern, flying about the mallees from 6.55-11.45 am and 5.50-7.10 pm (sunrise 6.20-6.30 am; sunset 7.00-7.10 pm). The one female collected in January was flying at sunrise during extremely hot weather.

Males spent most of their time flying very rapidly from tree to tree and were difficult to net as they seldom alighted or hesitated. Occasional chases between males were noted but none was observed to hover in or defend a territory.

Several copulating pairs were encountered during morning. They flew conjugately and ponderously about the blossoms and settled intermittently. The females foraged and some carried pollen. Males were mounted above and behind the females much as described for *C. smaragdinus* (Houston, 1984: 159) but held their antennae erect. Initiation of copulation was observed twice: each time a male swooped in near a feeding female, hovered momentarily while orientating, then pounced on her. The pairs fell from the foliage, buzzing loudly but quickly took flight conjugately.

This species' habitat consists of mallee eucalypt woodland over sandy loam soil with calcrete outcrops.

Ctenocolletes nicholsoni Cockerell

Nests

A populous nesting colony of this species was discovered 13 km south of Wannoo (or about 209 km north of Geraldton) on 24 August 1984 and studied over the next three days. It was in a sandy flat between sand ridges which had been burnt at least two years previously. The vegetation consisted almost entirely of waist-high *Acacia* and *Grevillea* shrubs providing about 30 per cent ground cover. The ground surface was largely bare except for some leaf litter beneath the shrubs.

Nest entrances were simple holes in the ground and were identifiable only when females entered or departed. Hundreds were scattered irregularly over an area at least 50 m across (the full extent of the aggregation was not determined). Some were in open bare ground but most were partly concealed beneath shrubs or litter. Tumuli were completely absent and entrances were open, the galleries descending vertically or obliquely (Figure 2).

Only two nests were excavated. Their considerable depth and the amount of labour required to expose them precluded more being tackled. The soil was 'red' sand to a depth of 3 m where it gave way to gravel and stone. It was soft near the surface and increasingly more compacted with depth so that below 1.5-2.0 m it could be cut in blocks. It was damp to a depth of 2.7 m.

The first burrow excavated had an elliptical entrance 10 x 12 mm and descended vertically, narrowing to a diameter of 8.5 mm below about 20 cm. The unlined uncemented shaft descended vertically with only slight deviations. Eleven separate brood cells apparently associated with this shaft were exposed at depths of 2.4-2.7 m. Their access burrows were compactly soil-filled and untraceable. The cells were distributed around the shaft axis, 8-20 cm from it, except for one directly beneath the shaft. A few cells were in close proximity to one another but no cells were in linear sequence.

In general form, the cells resembled those described and figured for *C. ordensis* (Houston, 1984) but the following differences were noted: long axes of cells inclined from almost horizontal to almost vertical, most dipping steeply (distal ends lowermost); inner walls shiny and waterproof only in distal end, grading to matt and absorbent near plug; closures consisting only of soil plug and barricade of sand and fine gravel (no concave partitions although outer surface of plug was smooth and concave) (Figure 6). Cells were detectable during excavation by their hardened gritty walls.

The second nest excavated had an entrance hidden beneath litter, an oblique entrance gallery 5 cm long and, proceeding from this, a vertical shaft descending to a depth of 2.4 m. At the lower end of the shaft was a soil plug beneath which an open burrow extended obliquely for 30 cm then horizontally for a further 5 cm ending in an open cell. The cell contained mouldy amorphous pollen meal and had obviously been abandoned. Ten freshly closed cells were exposed at

depths of 2.4-2.7 m within 20 cm of the shaft axis. Not all need have been associated with the one nest for a second shaft ran parallel to and only 6 cm from the first. The structure and arrangement of the cells were essentially as for the first nest.

Over half of the cells found contained immatures on provisions. In each case the provision was a soft, very moist mass of pollen making broad contact with the lowest part of the cell and moulded to a peak facing the cell plug. Eggs, when present, rested atop the provision touching it only by their ends (Figure 6). Larvae from hatchlings to middle instars rested on the provisions, ventral surface down and head towards the cell plug, and fed on the peaked proximal surface. They thus appeared to be sedentary.

Two cells contained post-defaecating larvae and khaki faecal material formed hemispherical masses in the distal ends of the cells (Figure 7). These meconia were dry and firm and riddled with minute passages. Two fully fed defaecating larvae were also found and passed copious quantities of orange faecal material as long pasty extrusions which fused into a mass or were smeared about as the larvae writhed.

Almost all cells of nest 1 contained larvae ranging from newly hatched to post-defaecating. One damaged cell had probably contained an egg and another had an early stage meloid larva in place of the bee immature. Most cells of nest 2 contained provisions with either bee eggs (3 cells) or meloid larvae (5 cells); only one contained a post-defaecating bee larva. All post-defaecating larvae rested with their heads towards the cell plug, otherwise their orientation was not recorded.

Numerous old soil-filled cells were encountered at depths of 2.3-2.8 m while excavating the fresh cells. They were harder and more easily removed than the latter. None contained any conspicuous traces of faecal material.

Associated organisms

As mentioned above, at least six cells contained meloid larvae. One recently closed provisioned cell must have received two triungulins: when opened it contained a second instar meloid larva on a dead flaccid bee egg, a dead triungulin and a triungulin exuvium. Other cells contained older meloid larvae up to fully developed size.

Adult meloids were not obtained from the nests but some *Zonitis* adults were collected on bushes at the nesting area and on the forage plants. Triungulins attached to the bees' pubescence are commonplace (6 of 20 females collected at nests carried 1-3 triungulins and one female carried six on the metanotum and propodeum).

Numerous adults of both sexes of a *Crassifoenus* species (Hymenoptera: Gasteruptiidae) hovered close to the ground at the nesting area. Females occasionally inspected nest entrances but I saw none enter. However, a dead specimen was found in a burrow from a previous season.

All cells closely inspected contained at least some individuals of the acarid mite *Ctenocolletacarus longirostris* Fain. Details will appear in a forthcoming paper.

Several cells were returned to the laboratory in vials and microscopic examination of their inner walls revealed numerous tiny nematodes writhing in a film of moisture. Also, hundreds of minute black fungal bodies peppered the walls in a broad band around the proximal half of each cell. These were identified as pycnidia (spore bodies) of a *Sphaeronaema* species, form class Coelomycetes (R.N. Hilton, pers. comm.). Each spherical pycnidium, measuring 30-40 μ in diameter, was embedded in or situated beneath the secreted wall lining and extended a single bristle up to 0.3 mm long into the cell lumen. In some cases, heavy growths ruptured the wall lining but otherwise the fungus appeared to cause no harm to the bees or their provisions. Greenish globules of yeast also developed on the walls of these cells while they were kept moist.

Adult activity

One adult female bee was recovered from each of the excavated nests and no more than one female was observed at any other burrow. Clearly the species is solitary.

Adult activity was not closely monitored but following a cold night (min. temp. 2.5°C) and in sunny conditions, females began leaving their burrows at about 9.18 am (sunrise at 7.05 am, WST). They were heard returning to or leaving their burrows intermittently throughout the day and a peak of activity was noted from 4.30-6.00 pm as hundreds of females returned from their final foraging trip. Activity then trailed off to zero following sunset at about 6.05 pm. Females returning to their burrows did so swiftly and entered without hesitation. Departures were also swift and without warning.

Males were not encountered at the nests but, judging by sounds heard intermittently throughout the day, some patrolled the nesting area flying fast just above the tips of the foliage.

Twenty-five females collected as they returned to nests during my 1984 visit were rated as to the degree of wear of their wing margins and mandible apices as a guide to age of the population. Wing wear varied from moderate to heavy indicating that the population had been active for some weeks and was more or less in phase. Mandible wear was far more variable (from nil to heavy) and did not correlate as clearly with wing wear as would be expected if all females burrowed and foraged to the same extent during their lives: several females with moderate to heavy wing wear exhibited little or no mandible wear. This could be explained if some females in the population re-use burrows from an earlier generation or usurp those of other females and thereby avoid a major part of excavation work.

The nesting site was revisited twice in July and August 1985 in the hope of observing earlier stages of nesting activity. Conditions appeared to be conducive

to activity but none was observed on either visit nor were any burrows evident. Although adults were absent at the nesting area on the first visit (28 July-3 August), numerous freshly emerged males and a female were captured at flowers of *Grevillea* sp. and *Thryptomene* sp. 1.2 km away. Fewer more worn adults were present at the same plants on the second visit (21-23 August). Evidently the nesting site had either been abandoned by its population or had failed to produce an adult generation for the season.

Males favoured the *Hakea* flowers over the *Thryptomene* but patrolled and took nectar from both from c. 10 am-3 pm. No territorial behaviour was noted in several days of observation. Mating has not been observed for *nicholsoni* and only once did I see an encounter between sexes at Wannoo: a female taking nectar at *Hakea* flowers was approached several times in rapid succession by two flying males but she repelled them each time and they eventually desisted.

Ctenocolletes nigricans Houston

Nest

A solitary nest was found on 16 September 1984 about 100 m from the nesting area of *C. albomarginatus* at East Yuna Nature Reserve. A pollen-laden female entered a simple hole about 9 mm in diameter amongst twigs on largely bare, gently sloping sand. There was no tumulus and the female did not close the entrance. The nest was not excavated.

Adult activity

A flying conjugate pair was observed on 24 August 1984 at the *C. nicholsoni* nesting area south of Wannoo. The pair settled on a shrub stem and the male, mounted above and behind the female, made attempts to engage its genitalia with the female's. When netted, the bees remained *in copula* until placed in a killing jar.

Further observations of mating behaviour were made on 16 September 1984 adjacent to the nesting area of *C. albomarginatus* near East Yuna. Several males were encountered in mid afternoon patrolling and defending areas of bare or sparsely vegetated ground. Males hovered almost stationary within 50 cm of the ground or meandered about for several seconds before suddenly darting off on a rapid foray, then returned to their original position within 5-10 seconds. They darted after any flying insects including other males and butterflies that came near. They also chased small objects flicked over them and a 7 mm diameter plumb-bob swung on the end of a nylon line (the tone of their wing beats rising sharply as they did so). One male, which hovered near the nest mentioned above, darted after the female as she approached her entrance. She fled and he returned to hover as before.

Ctenocolletes smaragdinus (Smith)

Nests

Two burrows about 3 m apart were found on 26-27 October 1985 about 75

km east of Hyden. They were in gently sloping sandy ground sparsely vegetated with stunted heath. The simple round entrance holes amongst litter and wiry grass stems lacked tumuli and were most inconspicuous. They were revealed when the females entered them. One was also entered for several minutes prior to the bee's arrival by a gasteruptiid wasp (*Crassifoenus* sp.). As several of these wasps were observed patrolling the ground nearby (over an area of about ¼ hectare) and occasionally inspected holes, I suspect more nests than the two found occurred there.

The entrance galleries were vertical and plugged with loose sand through which the females burrowed as they entered. Careful excavation failed to reveal an open shaft beneath the first entrance except at a depth of 50-53 cm where the occupant female was turned up. Apparently the shaft above her was compactly soil-filled. There were no brood cells. The second burrow had an entrance gallery about 3 cm deep with a shaft 9 mm in diameter opening off one side near its lower end (Figure 3). The shaft curved around and descended more or less vertically into compacted sand; its lower end curved almost horizontally and ended at a depth of 172 cm and 15 cm from the vertical shaft axis. The burrow was open except for a loose soil barricade in the entry shaft and a plug and barricade in the lower section (the female was recovered below this closure). The walls of the upper section of shaft appeared to be cemented or at least consolidated and of a different colour from the surrounding sand but were not built-in. A short lateral burrow occurred at 52 cm depth.

There were no fresh cells with the second burrow but several old soil-filled cells occurred within a radius of about 25 cm of the shaft at depths of 168-186 cm. Their structure was very similar to that of cells of *ordensis* and *nicholsoni* and they were inclined at an angle of about 45° below horizontal. One such cell had an entire closure and a hole about 4 mm in diameter in the cell ceiling indicated a parasite (? *Crassifoenus*) had emerged there. The closure consisted of a plug with a smooth concave outer surface and a concave mud partition closely applied to it (Figure 8). Maximum internal diameters of cells were 10.5-11.0 mm. Inner surfaces of cells were very smooth, matt, similar in colour to the sand matrix (light yellow) and readily absorbed drops of water. No faecal deposits were noted.

Adult activity

The two females associated with the nests described above entered them without pollen in the early afternoon and did not reappear during the next hour despite suitable conditions for flight. Evidently they were extending their nest burrows and accumulating the loose soil in the shafts. Their wings showed only slight wear indicating that they were young and commencing their first nests.

Occasionally, males flew low over the nesting area but showed no interest in burrows. Instead, they patrolled flowering bushes of *Verticordia picta* scattered

through the heath. Several mating pairs were disturbed from stems of shrubs and others flew conjugately amongst the *Verticordia* flowers foraging.

Ctenocolletes tigris Houston

Two females were observed to enter burrows in bare level sandy ground on 24-28 August 1984 at and near the nesting area of *C. nicholsoni* 13 km south of Wannoo. The burrow entrances were simple holes about 9 or 10 mm wide and lacked tumuli. They were closed with loose sand through which the females burrowed as they entered at a shallow angle to the ground surface (entrance galleries were obviously oblique). The burrows were not excavated.

Males were not observed near the burrows but were abundant about flowers of *Teucrium* on a nearby sand ridge. They patrolled the flowers from morning to evening and several conjugate male/female pairs were encountered. No territorial hovering and darting behaviour was observed.

Discussion

Although our knowledge of the bionomics of *Ctenocolletes* species is far from complete, enough is now known to be able to make some generalisations with reasonable confidence. The species studied demonstrate considerable uniformity of behaviour and nest architecture and the list of ethological characteristics considered to be ancestral for Stenotritidae given by Houston and Thorp (1984) may stand virtually unaltered.

Notwithstanding this, significant interspecific differences occurred in nests in respect of depth, entrance gallery form, inclination of brood cells, presence or absence of concave partitions in cell closures, extent of varnishing in cells, consistency (firmness) of provisions and form of larval faecal deposits.

Nests of *albomarginatus* and *nicholsoni* are remarkable for their depth and surpass the 2.45 m deep nest of *Oxaea flavescens* (Oxaeidae) claimed by Roberts (1973) to be the deepest bee nest on record. Some *Leioproctus* (Colletidae) are known to burrow to depths of 1.8-3.5 m in sand (personal observation and R.W. Thorp, pers. comm.). However, the deepest bee nest ever recorded was one of an anthophorid, *Exomalopsis aureopilosa* which descended to 5.3 m (Zucchi 1973). It was inhabited by 44 females and may have been excavated co-operatively or progressively by more than one generation. While acknowledging that nest burrows of *Ctenocolletes* may be re-used, I believe that individual females burrow to the maximum depths recorded for their species and that nests are not progressively deepened over several generations. Were the latter so, old cells from previous generations would be shallower than new cells but observation has shown they occupy the same horizons. I have no ready explanation of why some species excavate such deep nests but clearly they must gain some survival advantage from doing so. It may be that their brood cells escape the extremes of temperature and humidity occurring nearer the surface and are therefore less susceptible to growths

of pathogenic fungi and micro-organisms. Certainly the soil of the cell horizons at all nesting sites described in this paper was comparatively dry, whereas that nearer the surface was conspicuously damp. Temperatures at a depth of 3 m may be expected to remain within a range of 2°C throughout the year and would approximate the mean annual temperatures at the surface. At Carnarvon this would mean a temperature of c. 25°C, at Geraldton 19.5°C and at Perth 18.3°C (R. Belford, pers. comm.).

A notable feature of *Ctenocolletes* (and other stenotritid) nests is the absence of tumuli at burrow entrances. Despite attempts to observe the method of soil disposal, it remains a mystery. I suspect females carry soil well away from their entrances.

Cells are bilaterally symmetrical with the floor flatter than the ceiling. The steep inclination of cells of *albomarginatus* and *nicholsoni* (and possibly also *smaragdinus*) compared with those of *ordensis* may be associated with much softer provisions. The reduced extent of their waterproof lining (confined to the distal end of the cell) may correlate with the more distal position of the provisions. Cell closures of *ordensis* and *smaragdinus*, but not *nicholsoni*, have a concave partition in close juxtaposition to the outer concave surface of the cell plug (no intact closures were found for *albomarginatus*). Gravel particles were consistently present in all access burrow barricades.

Species differences occur in the form of larval faecal deposits: streaks along the cell walls in *ordensis* and hemispherical masses in the distal ends of cells in *nicholsoni*. Both kinds of deposit are also recorded for *Stenotritus* and which is more primitive is now in doubt.

Some species differences in mate-seeking and mating behaviour were evident. While males of all species patrol the forage plants, only those of *albomarginatus* and *nigricans* are known to patrol nesting areas as well. Nesting areas of *ordensis*, *nicholsoni* and *smaragdinus* received no male attention. Territorial behaviour involving hovering and darting is recorded for three species but not in their closest relatives. Thus, it occurs in *centralis* but not *nicholsoni*, *nigricans* but not *albomarginatus* and *smaragdinus* but not *tigris*.

Rozen (1968) noted unusual sexual dimorphism in two species of Andrenidae and suggested it may be associated with the hovering and darting behaviour of their males. Males of *Meliturgula* and *Melitturga* exhibit (1) enlarged compound eyes which converge dorsally so that the upper part of the face is relatively narrow; (2) clubbed antennal flagella; and (3) hind wings which are broader relative to their length than those of females and which have an enlarged jugal lobe. Similar sexual dimorphism occurs amongst species of *Ctenocolletes* (and also *Stenotritus*) in respect of (1) and (3) above, but no species have clubbed antennal flagella. However, all stenotritid bees of both sexes have the first antennal segment greatly attenuated. The degree to which compound eyes converge and the jugal lobe is enlarged in males varies amongst the species of *Ctenocolletes* and yet does not seem to be correlated with whether males engage in territorial hovering

and darting. Males of *C. smaragdinus* hover and dart although they do not exhibit ocular convergence nor enlargement of the jugal lobe. The reverse is the case with *C. nicholsoni*. Seven of the 10 species of *Ctenocolletes* are now known to exhibit conjugate flight of male/female pairs (identification for two is dubious). Females in such pairs frequently forage for nectar and pollen. Mating has yet to be observed in *centralis*, *nicholsoni* and *rufescens*.

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