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Bionomics of the Bee *Stenotritus greavesi* and Ethological Characteristics of Stenotritidae (Hymenoptera)

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Abstract

A nest aggregation of *S. greavesi* in south-western Australia is described. Females nested individually in bare ground. Nests were very shallow but essentially like those described for other stenotritids and particularly *Ctenocolletes ordensis*. Additional data on adult behaviour, flower preferences, phenology and parasitoids (Meloidae and Mutillidae) are included. Dormant post-defaecating larvae had unusually tough integuments that were coated with an apparently secreted film. Known habits of Stenotritidae are discussed and the ancestral and derived ethological characteristics of the family postulated.

Introduction

The genera *Stenotritus* Smith and *Ctenocolletes* Cockerell comprise the endemic Australian family Stenotritidae. Details of the bionomics of stenotritids have become available only comparatively recently (Houston 1975, 1984). Nests have been described only for *S. pubescens* (Smith) and *C. ordensis* Michener. These species are essentially solitary and ground-nesting. While their nests are basically similar, some differences were noted. The cell closures of *ordensis* were more elaborate and the question arose (Houston 1984) whether some details of construction may have been overlooked in *pubescens* nests. If not, were the differences of specific or generic significance?

An opportunity to investigate the habits of stenotritids further arose with discovery of an active nest aggregation of another *Stenotritus* species at Boorabbin Rock, about 93 km east of Southern Cross, Western Australia, on 8 October 1981. On that occasion and the following day we excavated several nests and observed adult activity at and near the nest site. One of us (TFH) revisited the site and made further excavations on 21 January 1982 and obtained additional data from specimens in the Western Australian Museum, Perth (WAM).

In this paper we present our observations and compare the nests and habits of *S. greavesi* with those of previously studied stenotritid species.

The genus *Stenotritus* is much in need of revision and includes several undescribed species. Identification of our Boorabbin Rock species followed a check of all species descriptions and a comparison of specimens with the holotype of *S. greavesi* (Rayment, 1930). Adult and immature specimens taken during the course of our study are lodged in WAM. Additional adults are deposited in the Bohart Museum of Entomology, University of California, Davis.

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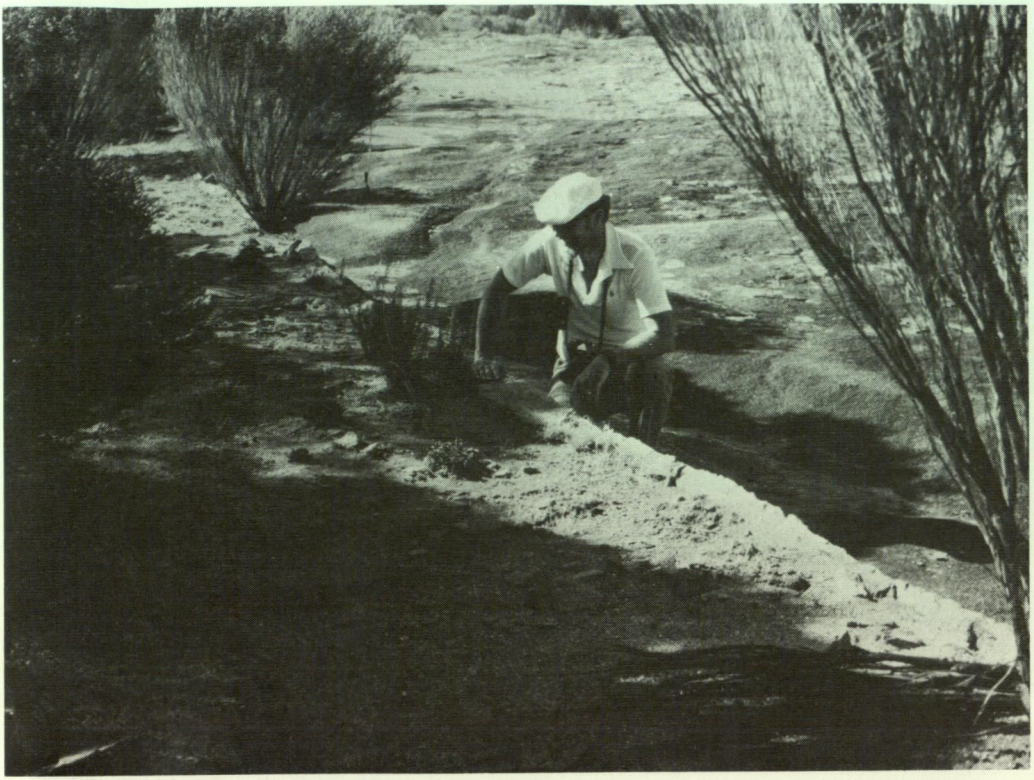


Figure 1 Nest site of *Stenotritus greavesi* at Boorabbin Rock, W.A. Burrows occurred in foreground within 1 m of the rock wall.

Observations

Nest Site

Female bees were found entering and leaving burrows in an area of bare level ground at the edge of the Boorabbin Rock granite exposure (Figure 1). The area was margined on the rock side by a stone and concrete retaining wall forming part of a rainwater catchment system and on the other side by 2-3 m tall shrubs (*Thryptomene tuberculata*). Burrows were confined to a 3.5 m long, 1 m wide strip near the wall and about 35 entrances were randomly scattered there. The sandy loam soil overlay a granite rock basement to a depth of about 43 cm and was riddled with roots and termite galleries. The top 13 cm or so was dry and powdery while the deeper soil was moist and firmer.

Nest Architecture

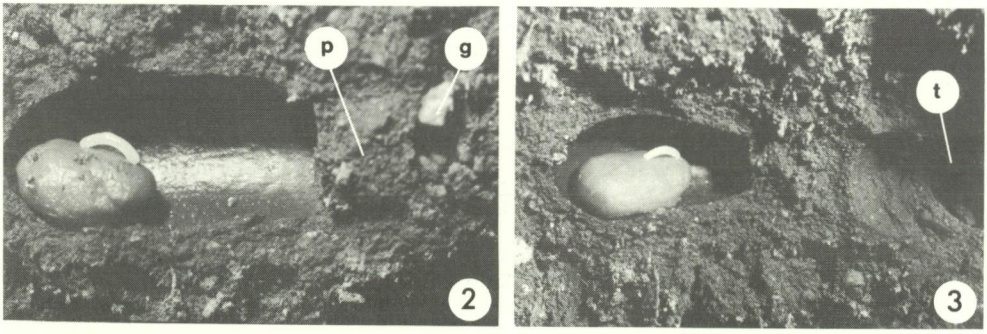
Burrow entrances were simple irregular holes with neither turrets nor conspicuous tumuli (a few had a little loose soil cast to one side). Some occurred in the open and others beneath the edges of stones and exposed roots. Shafts descended at angles of 45° or less to the horizontal (Figures 4, 5) and bent laterally irregularly, some turning through more than 90°.

They were circular in cross section, 9 mm in diameter and extended an average of 35 cm (but not exceeding a depth of 16 cm). Their walls were mostly unworked but, in a few nests, portions had clearly been cemented-in where the shaft passed through soil that was very soft or honeycombed with termite galleries.

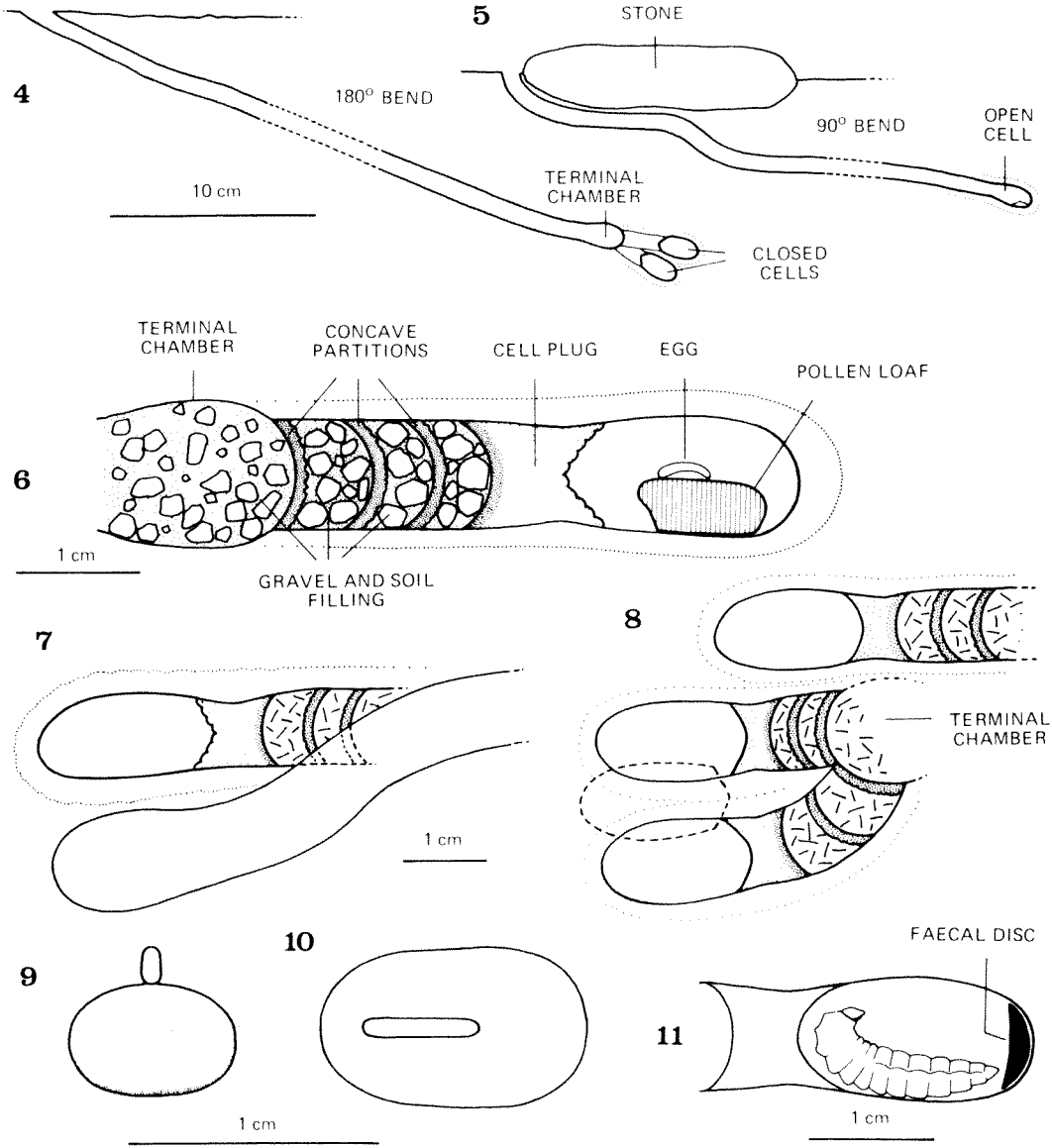
Brood cells occurred at and near the ends of shafts (Figures 4, 5, 7, 8) 9-16 cm below the surface and chiefly above the moist soil zone. Five nests still under construction in October had one or two cells. Completed nests (judging from a few that were inhabited and several that were vacated) may have from 1-4 cells but most had two. In all cases where there was more than one per nest, cells were side by side or one above the other, never end to end. Long axes of cells were mostly horizontal or nearly so; only one was steeply dipped.

The earthen walls of cells were continuous with those of their access burrows (Figure 6) and much firmer than the surrounding soil. Consequently, cells were easily detectable during excavation and could be removed intact. Internally, they were rather ovoid (slightly flatter on their lower side and truncated at the plug end) (Figures 2, 3, 6), 9 mm in diameter and about 18 mm long. Their inner walls were extremely smooth, chocolate-brown, shiny and water-proofed as far as their necks. The water-proofing material was generally inseparable from the earthen wall but in one cell a small portion had lifted and could be peeled away like a stiff plastic film. When a portion of a cell was soaked overnight in water and detergent, a delicate transparent brownish membrane separated within it. Under the microscope the membrane appeared amorphous (having no fibrous inclusions as do colletid membranes; Batra 1972). It was insoluble in xylene and turpentine and did not melt when heated. Probably, it was a laminester film (*sensu* Hefetz, *et al.* 1979).

The inner walls of cells are evidently built in. In one open active nest examined, the shaft terminated in a rough-walled ovoid chamber, 12 mm in diameter, adjacent to a freshly completed cell (Figure 7). The chamber was probably a roughed-out cell and, given a 1.5 mm thick coating, its diameter would reduce to 9 mm (the observed diameter of completed cells). However, since the solidified walls of cells are mostly about 3 mm thick, it seems likely that the bees also impregnate the soil with some cementing liquid.



Figures 2-3 Newly completed brood cells opened from side showing pollen loaves with eggs, cell plug (p), gravel filling (g) and terminal chamber (t).



Figures 4-11 Nests and provisions of *Stenotritus greavesi* (dotted lines define cemented earthen walls of cells and access burrows): (4 and 5) profiles of incomplete nests (drawn as if in one vertical plane but burrows bent laterally as indicated by broken lines); (6) sagittal section of freshly completed cell, access burrow and terminal chamber of shaft; (7) shaft ending in simple chamber (roughed-out cell?) adjacent to newly completed cell; (8) cluster of four cells from nest of previous season (contained pupae) (to same scale as 7; detail to right side lost in excavation); (9 & 10) end and top views of pollen loaf bearing egg; (11) sagittal section of cell with post-defaecating larva and faecal disc (solid black).

Cells were closed by earthen plugs and access burrows filled with soil. A cursory inspection may reveal no more than a solid earth barricade in the access burrow but the closures were quite elaborate (Figures 2, 6). The plug in the cell neck consisted of compacted fine soil and showed a spiral pattern on its concave inner (cell-side) surface. Its outer surface was cemented, concave and very smooth like the inner end of a cell (except that it was not varnished, shiny and waterproof). Following this in the access burrow were usually two further 'false cell-base' septa separated by 1-4 mm. The chambers so formed were packed with gravel and soil, incorporating particles up to 4 mm in maximum width.

In some nests, an ovoid chamber 12 mm in diameter was found where the access burrows of two or more cells joined the shaft (Figures 3, 4, 8). Its end wall was smoothly concave and cemented. In closed nests the chamber was filled with gravel and soil.

Provisions

Several freshly provisioned and closed cells were obtained in October. The provisions consisted of a solid moist pollen loaf of characteristic shape (Figures 2, 3, 6, 9, 10) but no free liquid. The loaves were dull yellow, uniformly moist throughout, uncoated and moderately variable in size (dimensions in mm of four samples were length 8.2-11.0, width 5.6-6.7, height 4.5-4.9). One open cell being provisioned contained an amorphous heap of moist pollen indicating that formation of the loaf occurs at the end of provisioning.

The composition of some of the pollen loaves is discussed below under Food Plants and Foraging.

Immatures

Eggs were deposited atop the pollen loaves, each resting on its ends and situated nearer the cell mouth end (Figures 2, 3, 6, 9, 10).

No larvae were encountered in October but, in January, 18 mature post-defaecating larvae were obtained (Figure 12). They were not enclosed in cocoons but rested with their heads towards the cell plugs and were in dormant condition. They were unusual for Hymenoptera larvae in having stiff creamy brown integuments. This condition is attributable (at least in part) to a thin transparent amorphous film overlying the body integument but not the head. The film was not noticed on live larvae but was detected in spirit-preserved specimens in which it had separated from the underlying integument. It appears to be a secreted coating.

In the base of cells with dormant larvae were hard blackish brown faecal discs moulded to the shape of the walls (Figure 11). The plugs of such cells, too, had been altered, their inner surfaces being smoothed and concave (Figures 8, 11) with no trace of a spiral pattern and some of their soil being smeared over adjacent portions of the cell wall. Presumably mature larvae writhe about, compressing loose faeces into solid discs and, at the same time, abraiding their cell plugs.

Several larvae were kept at room temperature in vials but only one developed, pupating on 25 September and becoming adult on 14 November, 1982. The remaining larvae gradually shrivelled despite being placed on moist tissues during September.

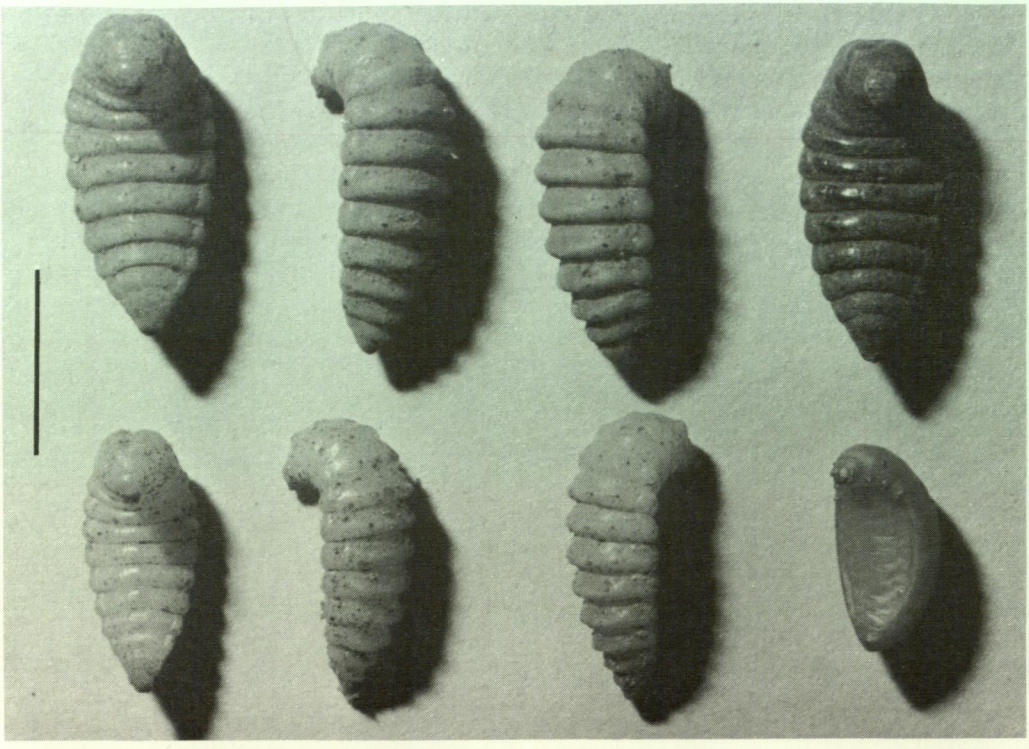


Figure 12 Dormant post-defaecating larvae of *S. greavesi* and coarctate larva of meloid beetle (bottom right) taken from brood cells in January. Scale line = 1 cm.

Associated Organisms

Two kinds of parasitoids were obtained from cells. In October, a triungulin (Coleoptera: Meloidae) was found crawling on the pollen loaf of a newly completed cell and a coarctate larva of the same family was taken from a cell in January (Figure 12). The latter specimen was kept at room temperature but had not developed at the time of writing (June 1983). In October, several cells containing cocoons were encountered. A few cocoons were old and vacated but three were occupied and yielded adult Mutillidae (Hymenoptera) of both sexes in late November 1981. These specimens were identified as '*Ephutomorpha*' sp. near *morosa* (Westwood) (D.J. Brothers pers. comm.). In the base of each cell outside the cocoons were the usual faecal discs so the mutillids must have developed on post-defaecating host larvae. The cocoons consisted of an outer delicate papery membrane applied to the cell walls (this was very incomplete in some cases) and a thick inner capsule spun of dull golden silk and suspended in a lattice-work of the same fibres.

No adult parasitoids were observed active at the nest site on either visit and no signs of gasteruptiid wasp infestation (as observed in nests of other stenotritids) were noted.

Adult Behaviour

Adults were active at the nest site only on the October visit. On that occasion, adults were still emerging from brood cells of the previous generation as pharate and newly emerged individuals were present in some of them. Several females were observed hovering over the nest area as if searching for suitable places to burrow. Others were returning laden with pollen: they hovered in as they orientated towards their burrows and, when about 15 cm above them, plummetted swiftly into the entrances. Departing females left their burrows rapidly and without warning. Some burrow entrances were blocked by their occupants pushing up soil from below but mostly they were left open. Entrances of most active burrows were blocked overnight after females made their last return. Of 16 plugged entrances, 11 were opened between 9:15 and 11:21 on 9 October by females pushing the loose soil inward. Females often positioned themselves just inside the entrance moving back into the tunnel if disturbed by movements of the observer.

A few males were observed in nest burrows. One male appeared at 9:30 on 9 October just within and facing out of an unplugged burrow where it had spent the night. A small net was placed over the entrance and the male was captured as it exited at 11:43. During the middle portion of the day, many more hovered persistently along the bank of *Thryptomene* shrubs facing the nest area. Each male hovered almost stationary with its fore and mid legs tucked beneath its body and its hind legs projecting slightly outward and rearward. Males periodically darted off in pursuit of a neighbouring male or some passing insect or occasionally patrolled a section of shrubbery usually returning to its original hovering post as if defending a territory. Similar behaviour in solitary males was observed (by TFH) on 27 October 1978, 3.5 km south of Yellowdine, W.A. One male hovered near a flowerless shrub and two others in spaces between flowering bushes of *Verticordia chrysantha*. Although males at Boorabbin Rock were occasionally observed to swoop down after females arriving at their nests, no matings were observed.

First observations of activity at and near the nest site were made on 8 October at about 13:30 when males were patrolling and females were entering and leaving nests. By 14:40 only one male was seen flying and some marked nests which were earlier open and active were plugged with soil just within the entrances. From 15:00 to 17:00, while we excavated nests, we saw no males in flight and three females that returned without pollen and were apparently confused by disturbance of landmarks, were the only ones active.

Adults were not active at the site when we arrived on 9 October at 8:15 (temperature 14°C). The first female appeared just inside the entrance after unplugging her burrow at 9:15 (16°C). The first female leaving a burrow did so by 10:00 (19°C) by which time there had appeared heads of three females at the entrances of burrows blocked overnight and two more females and the male noted above in unplugged burrows. The first female with a pollen load returned at 11:04. Males were active in their territories by 10:48. Although difficult to observe due to their rapidity of egress and entry, durations of trips from and to nests and times in nests between trips were measured for several females between 10:00 to 11:57. Females returning with pollen averaged 22.7 ($\pm$ SE 5.85) minutes (N = 7) for foraging trips and 6.5 ($\pm$ SE 2.12) minutes (N = 2) in the nest between trips. Females returning without

pollen loads averaged 25.7 (± SE 18.77) minutes (N = 3) away from the nest and 11.7 (± SE 11.24) minutes (N = 3) between trips. (The high variance for females without pollen loads is not just a function of small sample size but reflects the greater range in times for activities in contrast to the rather regular timing of pollen foraging. It may be that females without pollen loads were each engaged in quite different activities such as nectar foraging or orientation.) One female unplugged her burrow at 10:07, left at 10:35, returned unobserved and replugged her burrow at 11:19 and reopened it at 11:57 when observations ceased. Of 16 burrows plugged when observations began, only 11 were opened and active during the morning. In addition, 4 of 19 open burrows were active during this time. Three of these had females, all of which foraged for pollen, and one contained a male which had spent the night.

Food Plants and Foraging

The recorded food plants of the species based on WAM specimens are listed in Table 1. Also shown in the table are the pollens identified in scopal loads on nine females. Additional data on pollen sources were obtained by microscopic examination of samples from five fresh pollen loaves. Four of the latter consisted entirely of myrtaceous pollen (matching that of *Melaleuca scabra*) and one was composed of 75% of this same pollen mixed with an unidentified myrtaceous species.

The data suggest that *Melaleuca scabra* is the favoured pollen source with *Cheiranthera filifolia* and *Hakea* (or perhaps *Grevillea*) providing lesser amounts. *Verticordia chrysantha* evidently serves as a nectar source. Females must at times visit more than one plant species during a single foraging trip as evidenced by the mixed loads of four individuals. However, in only one case were the two pollens sufficiently well represented to suggest active collection of both had occurred. In the others, the additional pollens may represent contaminants from grooming following nectar visits.

Females worked feverishly while collecting pollen and scurried through the dense stamens of *Melaleuca scabra* flower heads. Flowers of *Cheiranthera filifolia* have large, yellow, apically porose anthers and the female observed working this species emitted readily audible sounds as she clutched the anthers and vibrated her thorax in the manner well known for bees (Buchmann 1983). Pollen was carried on the hind tibiae and basitarsi in large amounts that were moistened towards the end of foraging trips.

Table 1 Flowers visited and pollens carried by adults of *Stenotritus greavesi*. Relative amounts of pollen (as % total volume) were estimated visually from microscope slide preparations. M = pollen matches that of flower species visited; U = unidentified species.

Flowers visited	Numbers of bees	Pollens carried on scopae	No. of females
Baeckea ?leptospermoides	1♀	–	
Cheiranthera filifolia	1♀	*Cheiranthera* (M, 75%), *?Hakea* + Myrtaceae (equal)	1
Melaleuca scabra	11♀	Myrtaceae (M, 100%)	5
		Myrtaceae (M, 98%) + *?Hakea*	1
		Cheiranthera (95%), Myrtaceae (M) + U_1 + U_2 (equal)	2
Verticordia chrysantha	10♂ 3♀		

Phenology

Collection dates for 22 females in WAM range from 4 October to 8 December. However, most of these females and all ten males were collected in October. A further six females collected at New Norcia on 1 January may belong to *S. greavesi* but differ from the bulk of specimens in some details of pubescence. On 8-9 October 1981, the Boorabbin colony was in the early throes of nesting. The following January, no adults were present and larvae lay dormant in their cells. These data strongly suggest that *S. greavesi* is a univoltine vernal species.

Discussion

In terms of infrageneric relationships, *Stenotritus greavesi* and *S. pubescens* are distantly related and representative of two species groups. Their phylogenetic separation is reflected by differences in their biologies and nest architecture (although some apparent differences may not be real as will be discussed below). Characteristics of *greavesi* that differ from those of *pubescens* (given in parentheses) are as follows: nests shallow, not deeper than 16 cm (up to 32 cm deep); shafts oblique (more or less vertical) and simple (with blind diverticulae); cells constructed in dry loose soil (cells constructed in compact moist soil); all cells on separate access burrows (some cells recorded as being in linear series but this is now in doubt – see below); cell closure incorporating 'false cell-base' septa and gravel-filled chambers (cell closure and access burrow barricade recorded as solid fill but this, too, is in doubt – see below); closed nests with ovoid chamber at junction of shaft and access burrows incorporating 'false cell-base' (not observed); moulded pollen loaf bilaterally symmetrical with dissimilar ends (more or less radially symmetrical about long axis with similar ends); no free liquid in cells (clear liquid around base of pollen loaf); larvae coated with secreted film (absent); larval faeces compacted into solid disc in end of cell (deposited as separate streaks on ceiling of cell); univoltine and vernal (apparently bivoltine, summer flight season).

We alluded above to some possibly erroneous observations recorded for *pubescens*. 'False cell-bases' were not recorded in nests of that species (Houston 1975) but (as they are very inconspicuous amongst the compacted soil-filling of *greavesi* burrows) they could easily have escaped attention. It is quite possible that had a false cell-base been observed in an access burrow of *pubescens* it might have been identified as the base of one cell in series with another. Hence, the report of linear cell pairs is brought into question. This matter can only be settled with further, more critical examination of *S. pubescens* nests.

In terms of ethology and particularly nest architecture and provisions, *S. greavesi* seems to resemble *Ctenocolletes ordensis* more than *S. pubescens*. The most notable differences are that *S. greavesi* has shallower nests lacking entrance pits and gravel coats on cell walls, constructs more false cell-bases in its cell closures, constructs a chamber with false-cell base in the shaft of advanced nests, moulds narrower pollen loaves and its final instar larvae construct solid faecal discs and are coated with an apparently secreted film.

Each species probably has its own derived characteristics but features shared by *Stenotritus* and *Ctenocolletes* species may be deemed to be ancestral for the family Stenotritidae. Such are the following: essentially solitary habits although nests are aggre-

gated and males form sleeping clusters; nests in ground; entrances without turrets or conspicuous tumuli; shafts simple, occasionally with partial built-in walls; cells few per nest, each on its own access burrow, more or less horizontal, with built-in earthen walls continuous with those of access burrows, varnished internally with thin, waterproof (possibly laminester) membrane which is not readily separable from earthen wall; cell closure consisting of spiral earthen plug, smoothed, concave and cemented externally, and followed in access burrow by one or more gravel-filled chambers closed by false cell-base septa; provisions consisting of firm, uniformly moist, uncoated, moulded, bilaterally symmetrical pollen loaf with a projection at cell plug end; egg with both ends placed on cell plug end of pollen loaf; larval faeces deposited as streaks on cell wall; no larval cocoon; univoltine, vernal, with dormancy occurring in post-defaecating larvae; pollen sources limited to few plant genera but more than one family; pollen and nectar sources often separate; mixed pollen loads sometimes collected; pollen carried on hairs of hind tibiae and basitarsi and forming large firm moist masses towards end of foraging trips; females work feverishly while pollen-collecting and are capable of employing buzzing technique to extract pollen from anthers with apical pores; males frequently establish and hover in territories; males roost singly or gregariously on foliage.

The separation of Stenotritidae from Colletidae (McGinley 1980) is supported by what is now known of stenotritid habits which seem more to resemble those of Andrenidae. Stenotritid nests differ most notably from those of colletids in the absence of cellophane-like membranes, in having built-in walls in access burrows and cells, false cell-bases and concentrations of gravel in cell closures, and bilaterally symmetrical pollen loaves (all but the first of these features also distinguish stenotritid from andrenid nests and can be regarded as stenotritid synapomorphies). Although Andrenidae are not known to construct concave partitions, some species (Panurginae) form cell plugs with smooth concave external surfaces (see Houston 1984: 167).

The films covering post-defaecating larvae of *S. greavesi* are unusual and may be an adaptation to aid water conservation necessitated by the very shallow, dry-soil nests. Rozen (1967: 14) records that the integument of post-defaecating larvae of panurgine bees (Andrenidae) is tough and apparently coated with a waterproof secretion. Probably the films arose independently in the two families.

Acknowledgements

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