AMERICAN MUSEUM NOVITATES

Number 3989, 15 pages

June 28, 2022

Descriptions of the Mature Larvae of Three Australian Ground-Nesting Bees(Hymenoptera: Colletidae: Diphaglossinae and Neopasiphaeinae)

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ABSTRACT

Fully fed larvae of three Australian bee species formerly classified as Colletidae: Paracolletini are described and compared in light of recent phylogenetic studies. Two of these species, *Leioproctus* (*Goniocolletes*) *wanni* (Leijs and Hogendoorn) and *Trichocolletes orientalis* Batley and Houston, belong in the Neopasiphaeinae, while the third, *Paracolletes crassipes* Smith, belongs in Diphaglossinae: Paracolletini (sensu Almeida et al., 2019). We find that larval characters support the separation of *Paracolletes* from the neopasiphaeines, in particular the spoutlike salivary gland opening associated with cocoon spinning. In addition, we suggest that nest architecture of *P. crassipes* includes a feature that prevents flooding of open brood cells, a feature common to a number of other large ground-nesting bees.

INTRODUCTION

Herein we describe the external morphology of mature larvae of three Australian colletid bees, two belonging to the subfamily Neopasiphaeinae and one to the subfamily Diphaglossinae, tribe Paracolletini (sensu Almeida et al., 2012, 2019). These three taxa were previously classified as Colletinae: Paracolletini by Michener (1965, 2007). Phylogenetic studies by Almeida and Danforth (2009) revealed that *Paracolletes crassipes* Smith, the type species of *Paracolletes*, aligned more closely with the Diphaglossinae of the Americas than with other

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"paracolletines." Almeida et al. (2012) placed *Paracolletes* as incertae sedis within the Colletidae and resurrected the name Neopasiphaeinae Cockerell, 1930, for the bulk of the former "Paracolletini." Subsequently, Almeida et al. (2019) formally transferred *Paracolletes* to Diphaglossinae: Paracolletini.

Details of the nesting biology and life history of *Paracolletes crassipes* were first made available by Houston (2020c) and they tend to corroborate the species' placement in Diphaglossinae. The construction of cocoons by late-stage larvae was particularly significant. Here, we describe the mature larva of *P. crassipes* for the first time. In addition, we describe mature larvae of *Leioproctus* (*Goniocolletes*) wanni (Leijs and Hogendoorn) and *Trichocolletes orientalis* Batley and Houston.

Larvae of the Neopasiphaeinae treated here for the first time were collected in Australia by the second author, enabling us to gain a better understanding of known larvae of the entire subfamily. Members of this subfamily occur in Australia and South America. In his masterful early study of the larvae of Colletidae, McGinley (1981) described larvae of four species of "Paracolletini," genus "Leioproctus." All four species have been subject to taxonomic and nomenclatural changes (table 1) and only one (which is Australian) remains in *Leioproctus*. The other three are South American.

McGinley (1981), under the heading "Paracolletini," also described the larvae of a species of *Callomelitta*, now in the Callomelittinae, and *Scrapter longula* (Friese) now in the Scrapterinae. Thus, larvae described below augment our understanding of the larval anatomy of the Neopasiphaeinae by adding one more subgeneric representative of *Leioproctus* (i.e., *Goniocolletes*) and one additional genus (i.e., *Trichocolletes*).

METHODS

Specimens selected for detailed examination and illustration were first drawn using a stereomicroscope and camera lucida. Afterwards, with head capsules severed from the postcephalic region, both body parts were cleared of internal tissue by being boiled in an aqueous solution of KOH, thus allowing fine structures to be examined and imaged with stereo- and compound microscope. After clearing many specimens were stained with Chlorazol Black-E to further reveal structural details.

Figure 1A identifies the major anatomical features on the frontal view of the head of *Leio-proctus wanni* to aid interpretation of these features on subsequent diagrams and SEM micrographs herein.

In the following descriptions of larvae, the original label orthographies associated with the specimens are presented under Material Examined. Length of scale bars associated with diagrams of entire larvae in lateral view (figs. 1B, 9, 14) = 2 mm.

Many of the scanning electronic micrographs presented herein unfortunately are less than ideal (note, for example, the flaking and fibrous surfaces on figs. 4, 17–19). The number of specimens of all treated taxa was extremely limited, so that experimentation with ways to improve them was thought unwise. Careful labeling of anatomical structures should help offset confusion.

Names Used by McGinley (1981)	Current Name	Authority
Leioproctus (Lonchopria) zonalis (Reed)	Lonchopria zonalis	Michener (2007)
Leioproctus (Ctenosibyne) cingulatus (Moure)	Lonchopria (Ctenosibyne) cingulata	Michener (2007)
Leioproctus (Belopria) zonatus (Moure)	L. (Perditomorpha) zonata	Michener (2007)
Leioproctus (Leioproctus) species A, near semipurpureus (Cockerell)	Leioproctus (Leioproctus) species A, near amabilis (Smith)	Maynard (2013)

TABLE 1. Four species of Neopasiphaeinae for which larvae were described by McGinley (1981).

SUBFAMILY NEOPASIPHAEINAE

Leioproctus (Goniocolletes) wanni (Leijs and Hogendoorn)

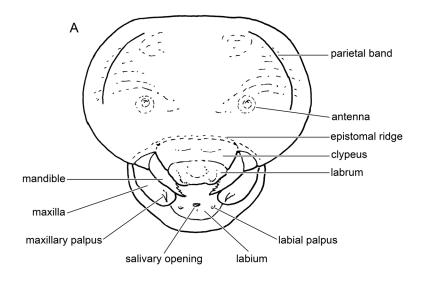
Figures 1A, B-3

DIAGNOSIS: The larva of *Leioproctus wanni* is similar to those of the four neopasiphaeine species described by McGinley (1981) in not spinning a cocoon; labium recessed in lateral view; salivary opening (fig. 6) small, at most only slightly protruding and oval but capable of closing as dorsal edge curves downward; labral tubercles small. Distinguished from those same four species in frons being broadly depressed between mounds mesad of parietal bands, antennal mounds and projecting clypeus.

The following description of the larva of *L. wanni* is based on four specimens, all postdefecating.

HEAD: Unusually small compared with body size (fig. 1B) as seems to be characteristic of most larval Colletidae illustrated by McGinley (1981).3 Integument thick, faintly translucent amber where not pigmented, with outer surface strongly, minutely wrinkled, thereby providing rigidity to surface of head capsule. On cleared head capsule, posterior thickening of capsule narrow but distinct, pleurostomal and epistomal ridges evident; median coronal ridge not evident; parietal bands distinctly impressed (figs. 2, 4); integument mesad of each band produced as a mound (figs. 2-5) below each of which occurs large antennal mound (figs. 2-5); epistomal ridge in frontal view (figs. 2, 4) curving slightly upward between anterior tentorial pits but remaining well below level of antennae; anterior surface of clypeus sharply bending forward from epistomal ridge in lateral view (figs. 3, 5), hence front of face in frontal view (fig. 4) of mature larva dominated by large depression created by mounds mesad of parietal bands and antennal mounds and above projecting clypeus. Labrum small, bearing pair of moderately small apical tubercles (fig. 3). Mandibular apex sharply pointed, pigmented, rather short but broadening quickly approaching broad inner surface of cusp; apical dorsal edge with numerous fine teeth; ventral apical edge well defined but without teeth at extreme apex; broad cuspal area surface densely covered with fine, darkly pigmented denticles. Maxillae (fig. 5) moderately large, each with tapering elongate palpus that is pigmented. Labium recessed, short in lateral view (fig. 3) with scarcely projecting, unpigmented palpi. Salivary opening (fig. 6) small, at

³ Although McGinley (1981) referred to the heads of some colletid larvae as moderate in size, now—40 years later—they are more accurately described as small headed relative to body size, based on our current, more inclusive understanding of head-size range among a larger sampling of mature bee larvae.



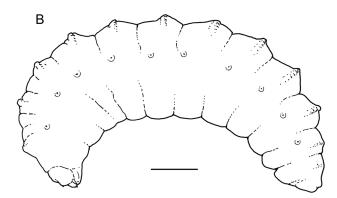
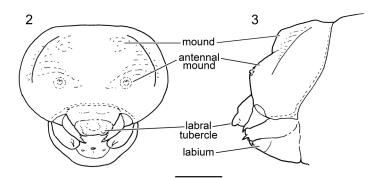


FIGURE 1. **A.** Enlarged diagram of head of mature larva of *Leioproctus wanni*, frontal view, identifying major anatomical features of head capsules of bee larvae. **B.** Diagrams of mature larva of *Leioproctus wanni*. Fullbody lateral view. Scale bar = 2 cm.



FIGURES 2, 3. Diagrams of mature larva of *Leioproctus wanni*. Head, frontal and lateral views. Scale bar = 2 cm.

most only slightly protruding and oval, but capable of closing as dorsal edge curves downward, all as in *Trichocolletes orientalis*.

Body: In lateral views of mature larva (figs. 1B, 7), body segments 1–4+5 increasing in size posteriorly, and segments posterior to segment 5 gradually, evenly tapering in size toward posterior end; terminal segment as illustrated (fig. 1B). Most body segments clearly divided dorsally into anterior and posterior annulets. Each posterior annulet with dorsolateral transverse linear series of low rounded projections on each side that diminish laterally well before reaching level of spiracles; linear series of projections on body segments interrupted along body midline; specimen cleared and treated with ethanol solution of Chlorazol Black E with paired ridges scarcely staining. Spiracular peritremes, though not tuberculate, projecting somewhat from body surface (figs. 7, 8); see Discussion below.

MATERIAL EXAMINED: Four postdefecating larvae: *Leiopr.* (*Goniocolletes*) wanni. Corackerup Creek, c. 44 km SSW of Jerramungup, W.A. 34.2932° S, 118.6998° E, 26 September 2019, T.F. Houston 1567-1.

DISCUSSION: One of us (T.F.H., 2020a) provided both a detailed description of the nesting site and nests with more or less horizontal cells from which larval specimens of *Leioproctus wanni* were gathered. Mature larvae were clearly not enclosed in cocoons.

The two mounds each mesad of the parietal bands of this species (figs. 2, 3) are unusual features but somewhat similar mounds occur in Xeromelissinae sp. A (McGinley, 1981: figs. 80, 81).

Spiracles of postdefecating larvae are small and questionably understood. The atrium is darkly pigmented, very possibly but not certainly spiculate as in *T. orientalis*, described below, but the apparent spiculation on the single specimen cleared for study may also have been an artifact of fine particle contamination.

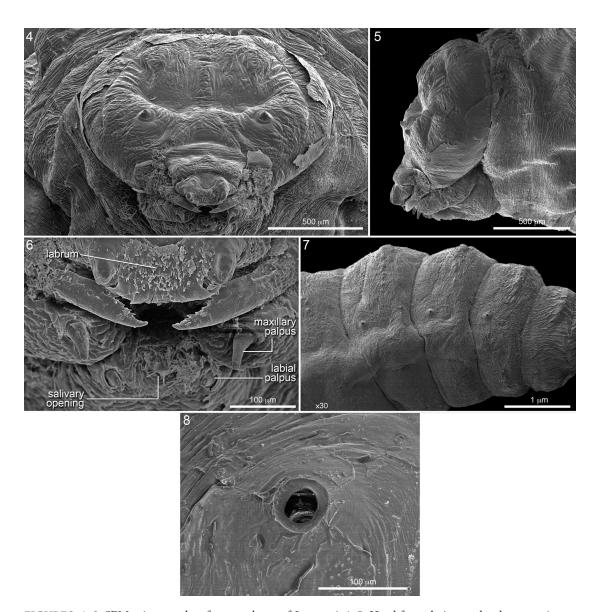
Trichocolletes orientalis Batley and Houston

Figures 9-13

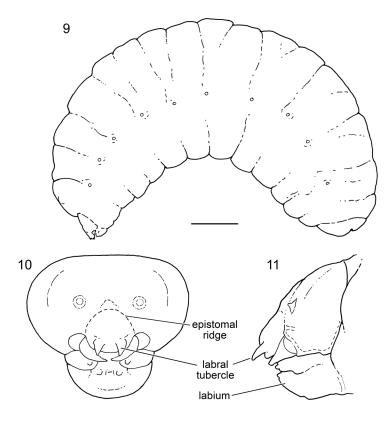
DIAGNOSIS: Larva similar to known Neopasiphaeinae in not spinning a cocoon; labium recessed in lateral view; salivary opening small, at most only slightly protruding and oval. Unique in labrum bearing pair of extremely large, down-curved apical tubercles (figs 12, 13). Unlike *Leioproctus wanni* in frons being convex, not broadly depressed.

All four available larvae of this species were predefecating, characterized by their seemingly bloated body (fig. 9) and thinner and more transparent cuticle than in most postdefecating larvae of other bees. These specimens were collected by T.F.H., who also reported on their biology (Houston, 2020b).

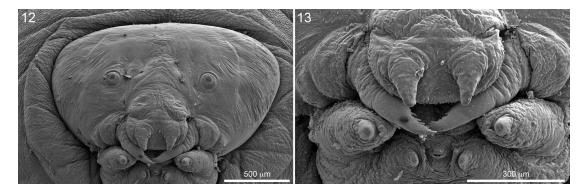
HEAD: Very small relative to bloated predefecating body (fig. 9). Integument of cleared head capsule translucent, not strongly wrinkled as in specimen of *L. wanni* described above, but difference possibly due to developmental stage. On cleared, stained head capsule, posterior thickening of head capsule narrow but distinct; pleurostomal and epistomal ridges faintly evident; median coronal ridge not evident; parietal bands only moderately impressed (fig. 12); in



FIGURES. 4–8. SEM micrographs of mature larva of *L. wanni*. **4**, **5**. Head frontal view and only approximate lateral view (note both left and right antennae visible). **6**. Frontal view of mouthparts showing: (a) conspicuous pattern of spicules on labrum between labral tubercles; (b) elongate maxillary palpi; (c) recessed labial palpi; and (d) recessed and somewhat obscure salivary opening lacking lips. **7**. SEM micrograph of left side of metasomal segments 5–9, showing projecting spiracles of segments 6–8. **8**. Close-up of projecting spiracle.



FIGURES 9–11. Diagrams of predefecating larva of *Trichocolletes orientalis* Batley and Houston. **9.** Entire larva, lateral view. Scale bar = 2 cm. **10, 11.** Head, frontal and lateral views.



FIGURES 12, 13. SEM micrographs of predefecating larva of *Trichocolletes orientalis*. 12. Front of head. 13. Close-up of mouthparts, noting huge down-curved labral tubercles and uncertain arrangement of spicules on maxilla as well as clear arrangement of labial palpi laterad of only slightly projecting salivary opening.

lateral view (fig. 11), profile of integument mesad of parietal band normally curved and antennal mound only moderately produced, hence profile of clypeus and frons above, not eclipsed by moderate antennal mound (fig. 11). Epistomal ridge arching upward from anterior tentorial pits to near level of antenna in frontal view (figs. 10, 12). Because of these features, surface of face in frontal view of mature larva (fig. 12) not dominated by large depression created by mounds mesad of parietal bands, large antennal mounds, and short clypeus, all as pictured for *L. wanni* (fig. 4). Labrum bearing pair of extremely large, down-curved apical tubercles (figs 10–13). Mandible elongate, ending in darkly pigmented, sclerotized, sharply pointed apex, with cuspal area weakly produced, and dorsal apical edge with linear row of 7 or 8 strongly developed, sharply pointed teeth; ventral apical edge apparently without teeth. Maxillae moderately large, with tapering palpi somewhat shorter than those of *L. wanni*. Labium recessed, short in lateral view (fig. 11) with scarcely projecting, unpigmented palpi. Salivary opening faintly projecting, probably oval when open, but capable of closing when dorsal edge curves downward (fig. 13).

Body: In lateral view (fig. 9) body segments of mature larva enlarged and intersegmental constrictions much reduced because of predefecating condition; terminal abdominal segment as illustrated and most body segments at most weakly subdivided dorsally into anterior and posterior annulets. Posterior annulets without dorsolateral projections or ridges. Atrial surfaces densely spiculate. Because of predefecating condition, dark content of alimentary tract of preserved larva vaguely evident at some intersegmental constrictions.

MATERIAL EXAMINED: Four predefecating, mature larvae: *Trichocolletes orientalis*, ex brood cell 3/xii/2020, Yanchep National Park, Western Australia, 31.5431° S, 115.6895° E, T.F. Houston 1598-1.

DISCUSSION: Houston's (2020b) treatment of the nesting biology and larva of *T. orientalis* provides a wealth of information about that species. It also offers some biological insight regarding *Trichocolletes venustus* (Smith), *T. dowerinensis* Rayment, and *T.* species indeterminate.

The salivary opening and small labial tubercles of larvae of both *T. orientalis* and *L. wanni* are similar and contrast strongly with the elongate spoutlike salivary opening with associated elongate labial palpi of *P. crassipes*, below.

SUBFAMILY DIPHAGLOSSINAE

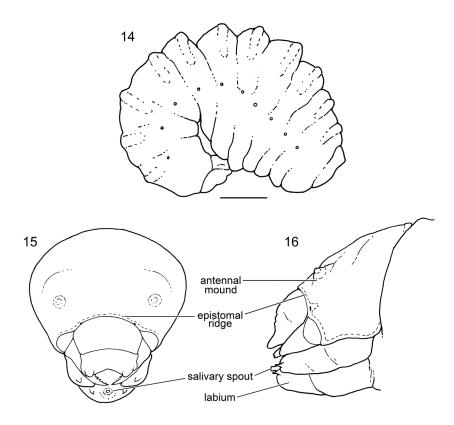
TRIBE PARACOLLETINI

Paracolletes crassipes Smith

Figures 14-22

DIAGNOSIS: Like most Diphaglossinae (and unlike all Neopasiphaeinae) in having labium extending forward to front of head and bearing a projecting salivary spout with circular, apical opening (figs 15–19); epistomal ridge (figs. 15, 16) strongly expressed.

HEAD: Small compared with body (figs. 14, 21). Posterior margin of head capsule distinct on cleared and stained specimen; external impression of epistomal ridge not strong but inter-

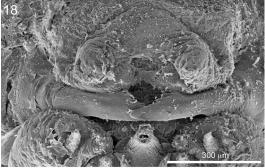


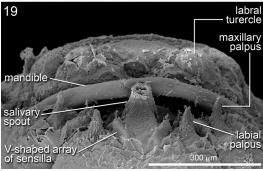
FIGURES 14–16. Diagrams of postdefecating larva of *Paracolletes crassipes* Smith. **14.** Full body, lateral view. **15, 16.** Head, frontal and approximate lateral views.

nally ridge extremely well developed as seen on cleared head capsule (figs. 15, 16); this ridge thick, long, curving slightly upward between widely separated anterior tentorial pits but remaining somewhat below level of antennae (fig. 15); median coronal ridge absent; parietal bands only moderately impressed (figs. 15); integument mesad of each band not produced as mound; antennal mounds weakly expressed (fig. 16); anterior surface of clypeus in lateral view (fig. 16) continuing slope of frons. Labrum moderate in size, bearing pair of moderately sized, widely separated, apical tubercles (fig. 15). Mandibular apex elongate, darkly pigmented, gradually tapering to narrowly rounded apex; apical dorsal edge with numerous sharp teeth; ventral apical edge smooth, without teeth. Maxillae (fig. 18) moderately large, each with tapering elongate pigmented palpus. Labium large, projecting (figs. 16, 22) with paired, pigmented palpi that are almost as large as maxillary palpi. Circular salivary opening apically positioned on large, conspicuous, projecting spout (figs. 16–19); outer surface of spout translucent, seemingly pigmented because of internal, darkly infuscate salivary duct. Labial apex and salivary opening forming complicated structure described in further detail in Discussion section, below.

BODY: As explained below, general body form of postdefecating larva impossible to generalize because of various deformities presumably imposed by cocoon constraints. In lateral view (fig.







FIGURES 17–19. SEM micrograph of mouthparts of postdefecating larva of *Paracolletes crassipes*. 17. Oral view. 18. Close-up of labium and surrounding structures. 19. Ventral view.

14) body segmentation accentuated but intrasegmental subdivisions much reduced with posterior annulets projecting farthest and each bearing slightly elevated modified integument forming transverse band on each side of segments. When stained with ethanol solution of Chlorazol Black E, these transverse bands on each side of body becoming much more distinctive.

MATERIAL EXAMINED: Four postdefecating larvae: ex cocoon January 2021, excavated Dec. 29–32/i/20-20, 10 km ENE of Waroona, W.A. 32.9705° S, 116.0099° E, T.F. Houston 1578-7.

DISCUSSION: The inclusion of this species in the Diphaglossinae is supported by the fact that its mature larva spins a cocoon (Houston 2020c) while larvae of other colletid subfamilies (with one exception) are not known to do so. Moreover, the anatomical features associated with cocoon-spinning in this species are characteristic of the subfamily: namely the projecting labium with its salivary spout and circular, ringed, apical opening (figs 16–20).

With most other cocoon-spinning bees the larval salivary opening is a transverse slit formed by projecting transverse lips (as found on divergently related bee larvae (e.g., *Melitta* (Rozen and McGinley, 1974, figs. 20, 21); *Dioxys* (Rozen, 1967. figs. 6–8); and *Xenoglossa* and *Centris* (Rozen, 1965, figs. 11, 12, 55, 56).

Early on, Michener (1953) pointed out and illustrated spoutlike salivary openings on mature larvae both of *Policana herbsti* Friese (now *Cadeguala albopilosa* (Spinola))

(Michener, 1953: figs. 37, 38) and *Caupolicana gayi* (Spinola) (Michener, 1953: figs. 40, 41). More than a quarter century later McGinley (1981) expanded the listing with *Ptiloglossa fulvopilosa* Cameron, *P. guinnae* Roberts, and *P. jonesi* Timberlake. He allowed that *Policana herbsti* belonged to this group in spite of the fact that its salivary opening was "flattened and transverse." However, as clearly shown by illustrations of the larva of this species (Michener, 1953: figs. 37, 38), the labium strongly projects and the salivary opening is a spout.

In cocoon spinning *P. crassipes*, the spout projects, but in others that are nonspinners, like *Trichocolletes orientalis* (figs. 12, 13) above, the external salivary opening is thought to be a simple circular hole on the labial apex that closes when its upper edge bends down reducing the aperture to a small, curved slit.

Each of the four preserved specimens of *P. crassipes* (fig. 20) was anatomically strongly curved, contrasting with the uniformly elongate linear posture of preserved postdefecating larvae of the other subfamilies (e.g., figs. 1, 9). The variously bent, physogastric shapes of larval *P. crassipes* (figs. 20, 21) presumably resulted from their being physically confined by their cocoons. On cleared, stained specimens, the strongly expressed internal epistomal ridge (figs. 15, 16) immediately separates this species from those of known Neopasiphaeinae.



FIGURE 20. Microphotograph of the four preserved postdefecating larvae of *Paracolletes crassipes* showing body distortion attributed to being confined by their cocoons when first preserved, contrasting with shape of postdefecating larvae of *Leioproctus wanni* (fig. 1) and of predefecating larva of *Trichocolletes orientalis* (fig. 9).

The labial apex of larval *P. crassipes* consists of a number of elements that require description because they differ from those of noncocoon spinners of other colletid subfamilies. In *P. crassipes* (figs. 17, 19) the paired labial palpi are tapering and elongate, nearly as long as the maxillary palpi. Centered between them is the protruding, slender, tapering, unpigmented, and therefore nearly transparent salivary tubercle housing a long inner, parallel-sided, more or less darkly infuscate duct of the salivary gland, features not revealed in figures 17–19 because they are opaque SEM micrographs. The nearly transparent salivary outer tubercle and inner duct of the salivary gland join apically forming a conspicuous circular hole, i.e., the opening of the salivary spout (fig. 19) where they provide a ringed circular apex. Although the SEM micrograph (figs. 17–19) gives the impression of two openings, one above the other, a careful reexamination of the apex on an untreated specimen clearly reveals only a single aperture, thus indicating that the lower, apparent opening on the micrographs is an accidental artifact. This same round, ringed opening to the salivary gland was observed in the case of *Trichocolletes orientalis* and perhaps *Leioproctus wanni* suggesting a similar internal structuring but without the projecting shape.

In addition to the pronounced labial tubercles and protruding salivary opening of *P. crassipes*, a highly magnified view of the apex of the labium (figs. 18, 19) also reveals more, though smaller projections. These are seemingly tipped with sensilla, perhaps raising interesting but unanswered questions about their function and/or consistency of the food material.



FIGURES 21, 22. Microphotograph of head and body, lateral views, of a live postdefecating larva of *Paracolletes crassipes*, revealing texture and color as well as shape of integument.

Presumed Function of Nest Architecture of Paracolletes crassipes Smith

One of us (Houston, 2020c) provided significant detailed information on the in-ground nest structure of *P. crassipes* that explains not only how the particular architecture functions for this species, but also how it serves other taxa as well. As he pointed out, the descending main burrow of the nest is not lined with a coating that provides a water repellent surface, nor do the laterals leading to cells have such a complete lining. However, with certain taxa, before each lateral reaches a cell, it curves upward and then bends downward to connect to the cell. Significantly, the surface of the bending lateral is lined and airtight as is the lining of the cell wall to which it connects. If heavy rains occur during the active nesting period, water flowing along the ground surface that reaches a nest entrance will flow into the main descending nest burrow and possibly into laterals leading to cells. However, when reaching the lined upward bend at the far end of a lateral, flowing rainwater will be blocked from entering the cell by the trapped chambered air in the upward bend and connecting cell. The amount of air thus trapped in a cell during a rain is likely sufficient to sustain the preemerged bee until the passageway to the cells is no longer flooded.

It is here proposed that air trapped in the upswing of a lined lateral where it connects to a cell may be a mechanism that allows the inhabitant of the cell to survive during periods of severe precipitation during the nesting season. Although Roberts (1971: fig. 3) correctly and fully diagramed the cell and its coated inverted U-shaped connection to the lateral tunnel in the nest of *Ptiloglossa guinnae* Roberts, neither he nor anybody else has explained the mode of action of the system, namely, the air enclosed in the cell and its airtight, lined, inverted U-shaped connection to the lateral is blocked from escaping, barred by the water- and airtight lining of the cell and its connecting upward loop to the lateral. Examples of the possible use of this mechanism revealed from J.G.R.'s research are listed in table 2. Based on research by Sarzetti et al. (2013, 2014) it is likely that this mechanism has been extensively employed by the Diphaglossinae.

Although the listings in table 2 contain only a few examples, the examples seem to include mostly large-bodied taxa with large burrow diameters. This may suggest that small-bodied taxa using small burrow diameters may be at less risk, perhaps because burrow entrances smaller in diameter do not accommodate as much runoff water compared with the length of tunnel surface available to absorb the runoff before it reaches the cell entrance. Furthermore, with bees nesting in unconsolidated porous ground, falling water will tend to be absorbed by the soft earth rather than forced to channel over the surface and thereby pour into encountered nest entrances. In addition, nest entrances on vertical surfaces are shielded from surface water runoff and even entrances on sloping surfaces are somewhat protected, especially if the entrance burrow is horizontal as it extends into the ground.

Table 2 lists published descriptions of bee nests that display tunnels leading to cell entrances that routinely rise and then turn downward before connecting to cell entrances. They therefore possibly protect the cell from flooding, a prediction that can be confirmed if the bend in the tunnel proves to be airtight.

TABLE 2. References to ground-nesting bee taxa in which nest laterals are either suspected of blocking or known to block rainwater from flowing into brood cells.

Family, Subfamily, Tribe	Genus, Species	References
COLLETIDAE		
Diphaglossinae		
Caupolicanini	Caupolicana ocellata Michener	Rozen and Rozen, 1986
	Caupolicana yarrow (Cresson)	Rozen et al., 2019
ANDRENIDAE.		
Oxaeinae	Oxaea flavescens Klug	Rozen, 2018
	Protoxaea gloriosa (Fox)	Rozen, 2018
APIDAE		
Tapinotaspidini	Tapinotaspis tucumana (Vachal)	Rozen, 1984
Eucerini	Peponapis utahensis (Cockerell)	Rozen and Ayala, 1987
	Thygater analis (Lepeletier)	Rozen, 1974

ACKNOWLEDGMENTS

We extend our appreciation to Corey Smith, Senior Museum Specialist, for his diligent contributions to this project as well as for the preparation of SEM micrographs. Figures were arranged and labeled by Stephen Thurston.

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