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Source: American Museum Novitates, 2016(3863) : 1-16

Published By: American Museum of Natural History

URL: <https://doi.org/10.1206/3863.1>

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Larval Diversity in the Bee Genus *Megachile* (Hymenoptera: Apoidea: Megachilidae)

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ABSTRACT

Mature larvae of five species representing each of the three principal groups within the genus *Megachile* sensu lato (i.e., including *Creightonella* and *Chalicodoma*, which are often recognized at generic rank) are described and are revealed to be quite similar to one another. On the basis of their descriptions a larval description of the genus is formulated. This, in turn, is compared with and found quite similar to a previously published Preliminary Description of Mature Larvae of the Megachilini based on study of larval representatives of the three genera in the tribe: *Megachile*, all species of which are pollen-collecting, and *Coelioxys* and *Radoszkowskiana*, both of which are cleptoparasitic, usually with *Megachile* hosts.

INTRODUCTION

Here we describe the last larval instar of four leaf-cutter bee species belonging to the enormous genus *Megachile* (sensu Michener, 2007): *Megachile* (*Eutricharaea*) *minutissima* Radoszkowski, *Megachile* (*Creightonella*) *atrata* Smith, and *M. (C.) frontalis* (Fabricius), and redescribe the larva of the dauber bee *Megachile* (*Chalicodoma*) *nigripes* Spinola. They were selected for this study because they represent the three major groups of the genus *Megachile* sensu lato as identified by Michener (2007), often recognized at generic rank, and therefore may provide a

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measure of the range of larval anatomical diversity within the genus as defined therein. Two of the species (*M. minutissima* and *M. nigripes*) are well represented by material on hand because of the rearing efforts in Egypt of S.M.K. The larva of *M. nigripes* was described and fully illustrated by Rozen and Kamel (2007) in connection with a study of species of the cleptoparasitic megachiline genera *Coelioxys* and *Radoszkowskiana*, and it is redescribed here for comparison with the larvae of *M. minutissima*, *M. atrata*, and *M. frontalis*. Rozen and Kamel (2007: figs. 89–91) also presented SEM micrographs of the larva of *M. minutissima*.

In addition to these four taxa, we also included the mature larva of *Megachile* (*Chelostomoides*) *prospididis* Cockerell because a phylogenetic study using morphological characters by Gonzalez (2008) placed *Chelostomoides* in a lineage divergent from other *Megachile* with known larvae.

Mature larvae and adults of *M. frontalis* were collected in eastern Papua New Guinea by R.G. Zweifel and G. Sluder more than 50 years ago and were donated to the entomology collection at the American Museum. C.D. Michener identified this species on the basis of associated adults. As explained below, these larval specimens, though in poor condition, were fully described and illustrated as they were thought to be the only available ones belonging to the subgenus *Creightonella*. At the end of the study, we received Singaporean specimens of the closely related *M. atrata* in excellent condition, enabling their inclusion in the study. The larval specimens of *M. atrata* were vouchers from a final year undergraduate project on *Megachile* nesting and life history by Eunice J.Y. Soh of the National University of Singapore, supervised by J.S.A. (Soh, 2014; see also Ascher et al., 2016).

As Michener (2007) explained, the genus *Megachile* sensu lato is complex, enormous, and in need of additional revisionary and phylogenetic study. He refrained from partitioning the genus due in part to problems involved in doing so, especially with regard to reliably delimiting his Group 2, i.e., *Chalicodoma* sensu lato, which “appears to have no unique synapomorphies, is highly diverse, and should eventually be divided into several genera” (Michener, 2007: 551). Subsequent phylogenetic studies of Megachilini and related tribes based on both adult morphology (Gonzalez, 2008; Gonzalez et al., 2012) and DNA sequence data (Litman et al., 2011, 2013) have clarified certain matters; for example, both datasets establish that *Creightonella* falls within the other leaf-cutting *Megachile* with cutting edges on their mandibles, and the result is that Michener’s Group 3 renders his Group 1 paraphyletic. However, some taxonomic placements, especially for obscure mud- and resin-using lineages of *Chalicodoma* sensu lato (Group 2), are still not conclusively resolved due in part to incongruence between analyses. In addition to taxonomic uncertainty within *Megachile*, adult morphology (Gonzalez, 2008) and various DNA studies (e.g., Litman et al., 2013) have also reached widely divergent conclusions regarding the placement of the parasitic megachiline genera *Coelioxys* and *Radoszkowskiana* with respect to nonparasitic *Megachile*. Whereas *Radoszkowskiana* was treated as congeneric with *Coelioxys* by Gonzalez (2008), these genera were widely separated in the molecular phylogeny of Litman et al. (2013). Given remaining uncertainty about phylogeny, the practical difficulties of identifying many lineages in the absence of comprehensive and user-friendly diagnostic keys for the partitioned genera, nomenclatural problems arising from transfer of specific epithets

from *Megachile* to *Chalicodoma*, and phenotypic similarity between phylogenetically divergent lineages, partition of *Megachile* into multiple genera has not been generally accepted. We wish to understand the extent of larval diversity in the tribe Megachilini so that we can use these independent data to evaluate phylogenetic and morphological diversity within the tribe, in comparison to other tribes within the subfamily Megachilinae. This study should be considered an early attempt to fulfill that purpose, with improved but still limited taxon sampling.

Larvae of a good many species of *Megachile* sensu lato have been described in the past, as documented by McGinley's (1989) listing of immatures of more than two dozen named taxa and additional unidentified morphospecies. Many of these were single descriptions, sometimes noncomparative or incomplete, although Michener (1953) attempted to interpret the older ones in a broader context. After McGinley's publication appeared, Torres and Gayubo (2001) presented larval description of several other megachilines. The existing descriptions represent many of the subgenera of *Megachile*, including typical leaf-cutter bees in Group 1 (*Megachile* sensu stricto) and dauber/resin bees in Group 2 (*Chalicodoma* sensu lato). Larvae of genus *Creightonella* (i.e., Group 3, incorrectly cited as *Creightoniella*) were cited as unknown by McGinley (1989), but *Megachile albisecta* (Klug), included on the list based on studies by Grandi (1931, 1961) and Michener (1953), actually belongs to this taxon. This same European species was subsequently illustrated, as *Creightonella albisecta*, by Banaszak and Romasenko (2001), and was included in a key to megachilid prepupae. Descriptions of the larvae of two additional species of *Creightonella*, the closely related *M. atrata* and *M. frontalis* from the Indo-Australian region, are presented here for the first time.

METHODS

With all four species, specimens were removed from storage containers, examined, and then illustrated with use of camera lucida and stereomicroscope. Each was then cleared as follows: head removed from body and both parts boiled in aqueous solution of sodium hydroxide until all opaque tissue removed, transferred to 75% ethanol, stained with Chlorazol Black E, and finally placed in glycerin on well slide for study and eventual storage. Illustrations were augmented after examination of cleared specimens and necessary microphotographs taken of spiracles and other important features. In diagrams, setae are represented only in diagrams of heads in lateral view. All scale bars = 1.0 mm and refer to lateral views of larvae. ATP = anterior tentorial pit.

In the following descriptions, the structures called *spicules* are sharply pointed cuticular projections of the integument that do not rise from alveoli and that can be detected with the aid of a stereomicroscope. At the very end of the study while taking pictures of the spiracle of *M. minutissima* with a compound microscope, we observed a faint patterning of the integument of fine, regularly spaced, buttonlike projections shown in figure 10. This may be an important discovery in that, as discussed, below, larvae not only of *Megachile* but of all other members of the tribe as well as a number of genera of Osmiini are believed to lack spicules. The occurrence of this minute integumental patterning will need further study and evaluation. While it seems almost certain

that these are unicellular projections of the cuticle and therefore would qualify as spicules if they were sharply pointed, we propose to call them cryptospicules here until they can be fully evaluated. So far, they have been detected only on *M. minutissima*.

In an earlier version of this manuscript, it was stated that the sex characters of none of the larvae are known, but as one of the reviewers pointed out, Nielsen and Bohart (1967) had demonstrated that larval sex characters could be identified on many bees, including *Megachile rotundata* (Fabricius). These characters pertain primarily to the so-called secondary sex characters on the venter of abdominal segment 9. They vary somewhat from one species to another and are often more evident in one sex than the other. They appear as cuticular scars on the venter of cleared, stained specimens and often require confirmation through preparation and examination of a series of specimens. Although they sometimes provide reliable information (e.g., see Rozen, 2008), attempts to identify them on a series of larval *M. nigripes* was unsuccessful despite the fact that this species is relatively large bodied, and one of the two here represented by many available specimens. It was concluded, therefore, not to explore further larval sex characters in the current investigation.

DESCRIPTIONS

DIAGNOSIS: The five larvae described below can be distinguished on the basis of the following: The larger size of the mature larvae of *M. nigripes* (fig. 11), *M. atrata* (fig. 15), *M. frontalis* (fig. 16), and *M. prosopidis* (fig. 20) distinguishes them from the larva of *M. minutissima* (fig. 1), as does the shape of their heads in frontal view, which are narrower than the extremely broad head capsule of *M. minutissima* (fig. 3). The length of the antennal papilla of these same four larger species (figs. 13, 18, 22; Rozen and Kamel, 2007: fig. 63) is at least about twice the length as the basal diameter whereas the antennal papilla length of *M. minutissima* (fig. 4; Rozen and Kamel, 2007: fig. 89) is only about the same as its basal diameter.

Interestingly, representatives of these four subgenera (and thus the three major numbered groups) can be distinguished on the basis of their spiracles. Whereas the atrial wall of *M. atrata* (fig. 7) and *M. frontalis* (fig. 8) consists of densely spiculate concentric atrial ridges, those of *M. minutissima* (fig. 5) and *M. prosopidis* (fig. 9) are nonspiculate, and those of *M. nigripes* (fig. 6) are nonspiculate except for the outermost ridges, which are more finely so. Unlike any others, the subatrium of *M. prosopidis* (fig. 9) is indistinctly divided into chambers because of weak cuticular strength. The internal coronal ridge of *M. nigripes* (fig. 13) is not developed, that of *M. atrata* and *M. frontalis* (fig. 18) extends to the level of the antennae in frontal view and that of *M. minutissima* (fig. 3) and *M. prosopidis* (fig. 21) extends less than halfway there.

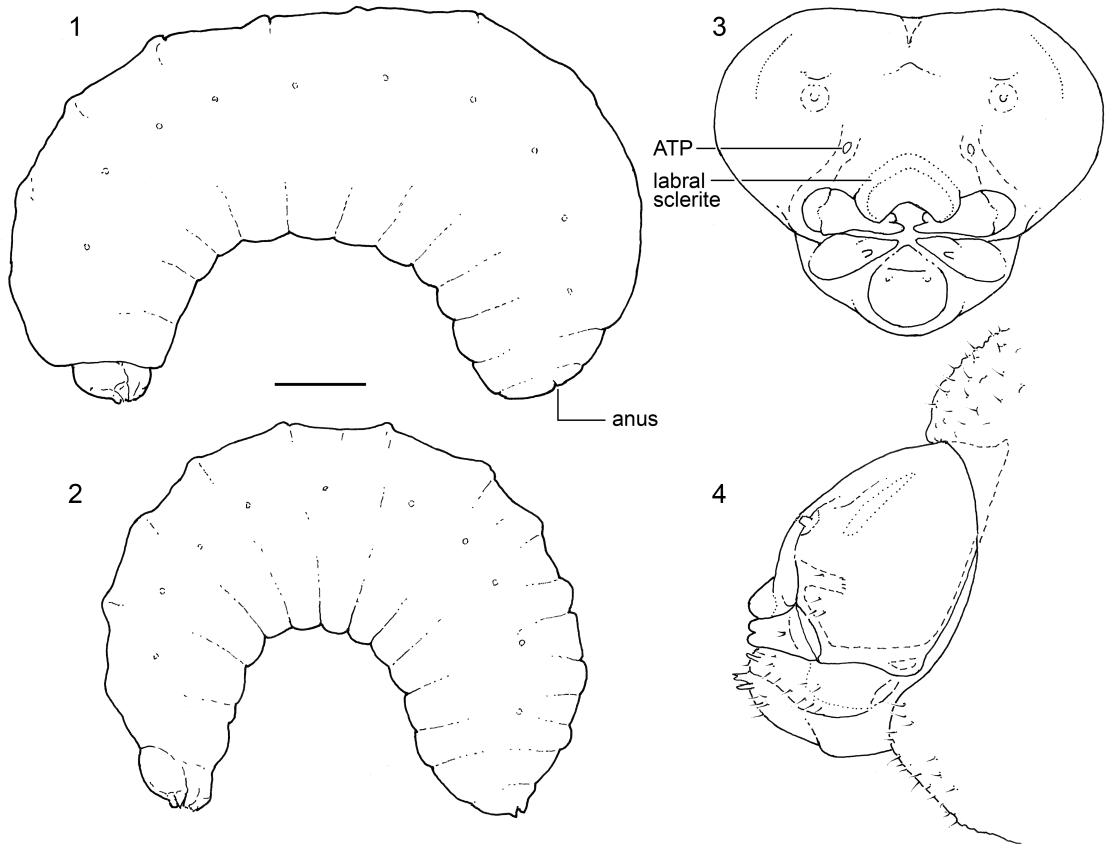
The brood cells of representatives of these four subgenera differ in that those of *M. minutissima* are lined with neatly cut leaves. Those of *M. nigripes* are lined with mud alone. Examination of cells originally stored in ethanol that had later dried revealed that cell walls of *M. frontalis* consist of an inner and outer lining of leaves sandwiching a layer of fine fibers representing the residue of masticated leaves. The closure, though not completely understood, was much thicker and certainly consisted of an inner lining composed of one or two

leaves, beyond which was a layer certainly composed of rather consolidated soil with inclusion of hard minerals but also possibly mixed with some fine plant fibers. Exterior to it was a very thick mass consisting of fine fibers. In another closure, the thickness of the closure was about 8 mm encircled by the outer layer of leaves at the front end of the cell. Those of *M. atrata* are similar to *M. frontalis* in that the middle lining of the cell wall is said to be of masticated leaves (Soh, 2014). Banaszak and Romansenko (2001: 131), based on their experience with *M. albisecta*, described the cells of *Creightonella* as “complex, constructed from pieces of leaves, but some African species use a mixture of resin and foliage mastic.” Michener (2007: 571]) reported that the native resin bees of North America in subgenus *Chelostomoides* often nested in beetle holes in stems or wood, partitioned into cells with resin and that the entrance closures were highly variable within and among species, with those of *M. prosopidis* [= *M. occidentalis* auct.] “particularly variable, consisting of layers of sand (or sand mixed with resin), pebbles (often mixed with bits of wood, stones, etc.), chewed leaves, etc.”

Mature Larvae of *Megachile* (*Eutricharaea*) *minutissima* Radoszkowski

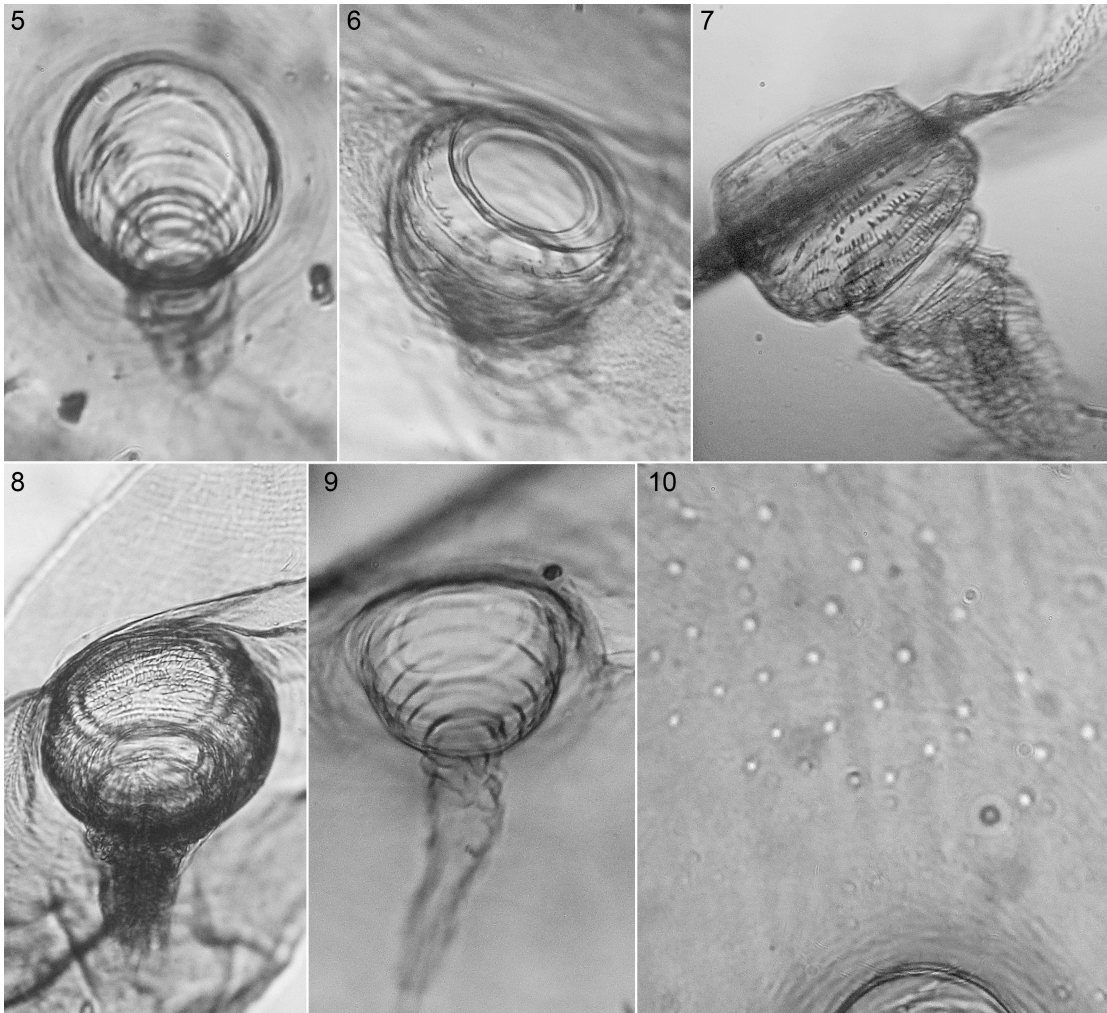
Figures 1–5, 10; also see Rozen and Kamel (2007: figs. 89–91)

DESCRIPTION: Head: Head size moderately small in relation to body size (figs. 1, 2); head of postdefecating larva slightly embedded in prothorax. Setae moderately long on sides of head but sparse and reduced in size on front of head capsule; those of maxillary and labial apices tending to be large, curved, abundant, and conspicuous with large conspicuous alveoli. Head capsule pigmentation limited to points of articulation of mandibles and head capsule, mandibular apices, labral sclerite, and surface of labrum including transverse sclerite; premental bridge, articulating arm of stipes, and stipital rod as well as premental sclerite also somewhat pigmented; slight pigmentation on leading surfaces of other mouthparts including salivary lips. Integumental spiculation reduced except for outer surfaces of hypopharyngeal lobes. Internal head ridges: coronal ridge present only near top of head, only briefly evident in frontal view; postoccipital ridge well developed, bending forward somewhat toward median line on top of head; hypostomal ridge well developed, giving rise to pronounced dorsal ramus that extends directly backward from frontal part of hypostomal ridge to join postoccipital ridge; thinner posterior part of hypostomal ridge curving mesad to join postoccipital ridge at deeply recessed posterior tentorial pit; pleurostomal ridge present; epistomal ridge well developed from anterior mandibular articulation to anterior tentorial pit; from pit, ridge extending vertically immediately mesad of antennal papilla and fading out above antenna, hence not extending across to opposite side of head. Tentorium complete, well developed. Parietal band weakly evident. In lateral view, clypeus not projecting much beyond frons, antenna in most cases arising from low prominence, and labrum normally not extending much beyond clypeus. Antennal papilla tapering, slightly longer than basal diameter. Lower margin of clypeus weakly sclerotized, so that midpoint of margin cannot be determined relative to level of anterior tentorial pits. Labrum broadly emarginated apically; labral sclerite transverse, well defined because of pigmentation.



FIGURES 1–4. Diagrams of mature larvae of mature larvae of *Megachile (Eutricharaea) minutissima*. 1, 2. Post- and predefecating larvae, lateral view, respectively. Predefecating larva, lateral view. 3, 4. Head, frontal and lateral views, respectively.

Mandible moderately robust; apex darkly pigmented, bidentate with ventral tooth longer than dorsal tooth; teeth tending to be apically rounded, but lower tooth more acutely rounded especially when viewed in maximum profile; teeth broad thereby forming broad apical concavity to entire inner surface of mandibular apex: this inner surface smooth, without teeth or denticles and thin in cross section; outer surface of mandible usually with one or two conspicuous setae. Maxillary apex strongly bent mesad in frontal view, so that maxillary palpus subapical in position; apex beyond palpus tapering, its outer surface bearing small cluster of 4–6 short sensilla, possibly representing galea; cardo distinct especially when stained; stipes consisting of conspicuously long stipital rod that is sometimes pigmented and is darkly stained by dye; at posterior end, rod articulating with cardo, and, at anterior end, rod broadening and branching to form somewhat pigmented articulating arm of stipes; other arm of branch circling orally around outer side of mound of hypopharynx; maxillary and labial palpi elongate, probably usually more than two times basal diameters. Labium divided into prementum and postmentum; apex usually moderate in width in frontal view; premental sclerite perhaps faintly evident, but border between pre- and postmentum distinctly incised; prementum projecting dorsally at midline forming pointed projection



FIGURES 5–10. Microphotographs of mature larvae of *Megachile*. 5. Spiracles of *M. minutissima*. 6. Spiracle of *M. nigripes*. 7. Spiracle of *M. atrata*. 8. Spiracle of *M. frontalis*. 9. Spiracle of *M. prosopidis* from inside larva, showing poorly formed subatrium and distinct ridges on atrial wall. 10. Spiracular area of *M. minutissima* showing patterning of cryptospicules.

behind which surface somewhat sclerotized and pigmented, forming dorsal bridge of prementum that extends in front of articulating arms of stipes and bridges the area between the dorsal end of the premental sclerite. Salivary opening broad with thin, strongly projecting, transverse lips that extend as far as distance between centers of labial palpi. Hypopharynx consisting of transverse pair of dorsally projecting finely spiculate mounds.

Body: Vestiture consisting of moderately short to short setae, which densely cover dorsal and lateral surfaces and sparsely cover ventral surfaces; each seta rising from small swelling of integument, which when stained, seem to be thicker than integument between swellings; these swellings imparting pebbled surface to integument; in vicinity of spiracles integument with cryptospicules (fig. 10, see discussion in Methods); only dorsal surface of abdominal segment

10 extremely finely spiculate.⁴ Body form of postdefecating larva moderately robust in lateral view (fig. 1), with thickest part of larva posterior to midbody and with only slight distinction between cephalic and caudal annulets; predefecating larva (fig. 3) with caudal annulets more distinctive particularly toward posterior part of abdomen; middorsal swellings between caudal annulet and following cephalic annulet moderately pronounced; head size relative to body moderately small; venter of abdominal segment 9 not produced; segment 10 attached to approximate middle of segment 9 in lateral view; anus positioned toward top of segment 10. Abdominal segment 10 without modification. Spiracles (fig. 5) unpigmented, subequal in diameter; atrium globular with width usually greater than depth, projecting only slightly beyond body wall, rim faintly present; atrial inner surface with coarse ridges concentric with primary spiracle opening without spicules; primary tracheal opening with collar; subatrium short consisting of about eight chambers that decrease in width away from body surface.

MATERIAL EXAMINED: Fifty-plus postdefecating larvae: Egypt: Tel el Kebir, XII-20-2005 (S.M. Kamel). Five predefecating larvae: Ismailia Experiment Station, no date (J.G. Rozen, S.M. Kamel).

Mature Larvae of *Megachile (Chalicodoma) nigripes* Spinola

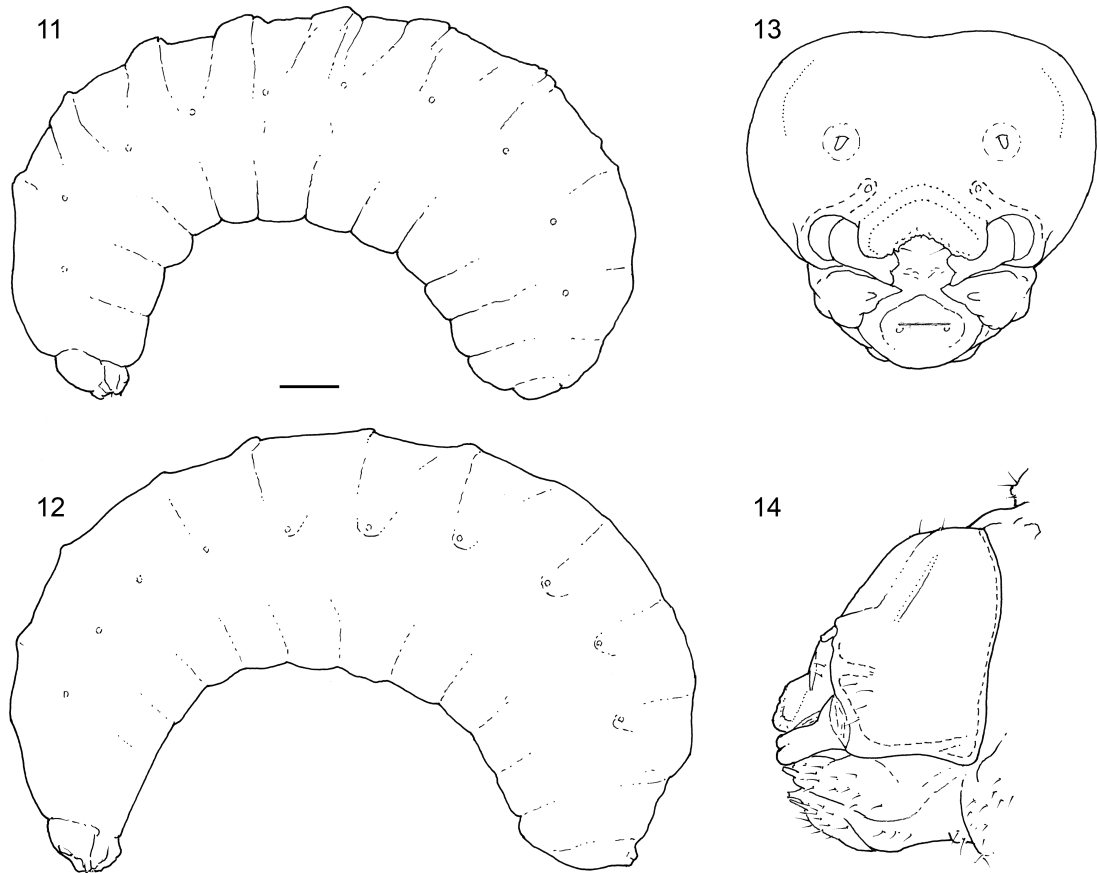
Figures 6, 11–14; also see Rozen and Kamel (2007: figs 41, 42, 52, 92–98)

DESCRIPTION: Head: Head size and position as described above for *M. minutissima*. Setae about as described for *M. minutissima* but somewhat less abundant and conspicuous. Head capsule pigmentation about as described for *M. minutissima* but somewhat more extensive in that apex of antennal papilla faintly pigmented as are internal ridges of mandible and mandibular apodemes; labral sclerite tending to be less pigmented than in *M. minutissima*. Integumental spiculation reduced as in *M. minutissima*. Internal head ridges: coronal ridge absent; other head ridges as in *M. minutissima* except dorsal ramus of hypostomal ridge fading before reaching postoccipital ridge. Tentorium and other head features as described for *M. minutissima*. Antennal papilla somewhat tapering toward rounded apex, elongate, length more than two times basal diameter. Lower margin of clypeus, labral shape, and labral sclerite as described for *M. minutissima*.

Mouthparts as described for *M. minutissima*.

Body: Vestiture consisting of uniformly very short, fine-pointed setae, which densely cover dorsal and upper-lateral surfaces and sparsely cover ventral surfaces; each seta rising from small integumental swelling as in *M. minutissima*; only dorsal surface of abdominal segments 9 and 10 perhaps finely roughened or spiculate. Body form of postdefecating larva (fig. 11) as described for *M. minutissima* although distinction between cephalic and caudal annulets somewhat more pronounced. Spiracles (fig. 6) as described for *M. minutissima* except outer atrial rings with fine spicules though more inner rings nonspiculate.

⁴ Spiculation restricted to the dorsal surface of abdominal segment 10 is considered a different character from general body spiculation that forms part of the body vestiture found on most if not all postcephalic body segments in many mature larvae of certain Megachilidae.



FIGURES 11–14. Diagrams of mature larvae of *Megachile (Chalicodoma) nigripes*. **11, 12.** Post- and predefecating larvae, lateral view, respectively. **13, 14.** Head, frontal and lateral views, respectively.

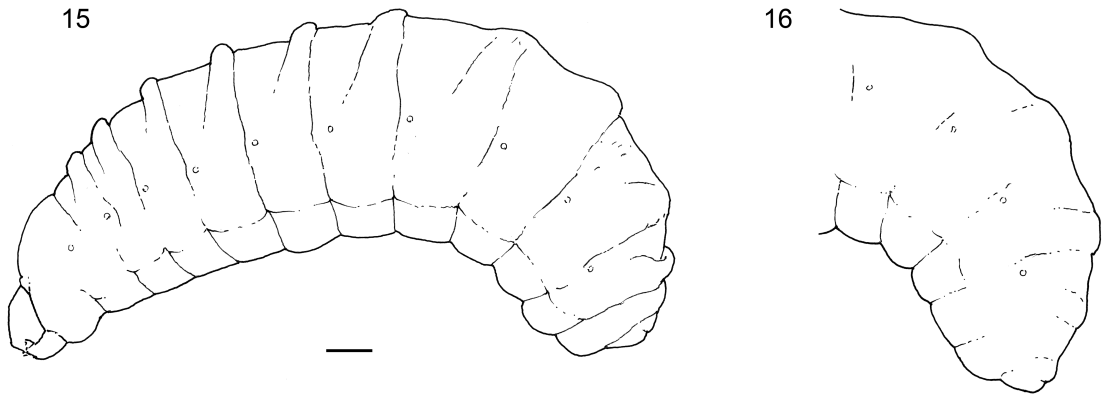
MATERIAL EXAMINED: Fifty-plus postdefecating larvae: Egypt: Ismailia Governorte: Tel el Kebir, II-12-2005 (S.M. Kamel). 6 predefecating larvae: same locality, N 30°32'02", E 32°49'48", V-19-04, (J.G. Rozen, S.M. Kamel).

Larva of *Megachile (Creightonella) atrata* Smith

Figures 7, 15, 16

The postdefecating larva of this species described and illustrated here was in excellent condition but was not cleared and stained as is customary because the predefecating larva had been damaged when collected by being cut open at midsection. The predefecating specimen alone was cleared and stained after its undamaged posterior section was diagramed (fig. 16).

The predefecating larva of *M. atrata* is probably almost identical to that of *M. frontalis*, as the adults of these two species are known to differ only in trivial characters such as wing color and are often treated as conspecific, i.e., *M. atrata* has been considered to be merely a subspecies of *M. frontalis*. The difference in the appearance of figures 16 and 17 most likely results



FIGURES 15, 16. Diagrams of mature larvae *Megachile (Creightonella) atrata*, lateral views. **15.** Entire post-defecating larva. **16.** Posterior part of predefecating larva.

from the fact that the larva of *M. frontalis* (fig. 17) had died and became mummified in its cell before being collected.

DESCRIPTION: Head: As described and illustrated for *M. frontalis*, although tentorium complete, well developed. Significant features: head width not expanded like that of *M. minutissima*; coronal ridge extending downward to level of antennae, postmental sclerites present, labial palpus longer than maxillary palpus, all as in *M. frontalis*.

Body: Vestiture as described for *M. frontalis*. Body form of postdefecating larva moderately robust in lateral view (fig. 15), with thickest part of larva posterior to midbody; caudal annulets tending to be considerably higher and more pronounced than cephalic annulets at front end of body; this distinction diminishing toward posterior end; predefecating larva (fig. 16) with caudal annulets about as distinctive as those of postdefecating larva (fig. 15) toward posterior part of abdomen; middorsal swellings between caudal annulet and following cephalic annulet faintly evident; dorsal surface of abdominal segment 10 minutely uneven, without spicules; other body features about as described for other taxa treated here. Spiracles (fig. 7) as described for *M. frontalis* with subatrium extremely short consisting of about 2 or 3 chambers.

MATERIAL STUDIED: One postdefecating larva: SINGAPORE: Pasir Ris Park, back mangroves, 1.39273, 103.952218, 3 Jun. 2014 (J.S. Ascher, J.X.Q. Lee et al. [S.X. Chui, E.J.Y. Soh] [nest 3, cell 5]). One fully fed predefecating larva, same data except [nest 3, cell 7].

Predefecating Larva of *Megachile (Creightonella) frontalis* (Fabricius)

Figures 8, 17–19

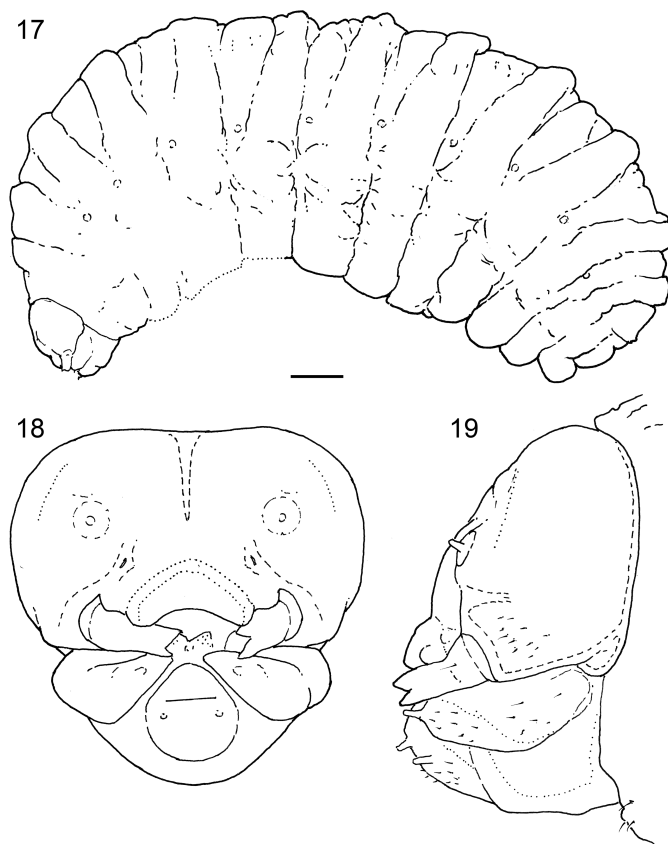
The single specimen of the larva described below probably had died well before being collected, judging by hardened body contents that did not respond to long periods of boiling in an aqueous solution of sodium hydroxide. When diagramed, its larval stage was recognized by the well-developed salivary lips and other head features. It was deemed a predefecating form when, after being cleared, the specimen was found to have a well-filled alimentary tract. While certainly the last larval instar, it probably was not fully grown as determined by the quantity

of gut contents and its reduced body size compared with associated pupae and adults. Likely, the heavily wrinkled body integument resulted from mummification of the less ridged integument of a predefecating larva. More uncertain are the strongly pronounced caudal annulets, as illustrated (fig. 17). However, the more sclerotized head capsule and spiracles seem quite normal.

DESCRIPTION: Head: Head size seemingly moderately small in relation to body size (fig. 17). Setae moderately short and inconspicuous on sides of head and sparse and reduced in size on front of head capsule (setae indicated only on fig. 19); those of maxillary and labial apices tending to be somewhat larger. Head capsule pigmentation and head spiculation about as described for *M. minutissima*. Internal head ridges: coronal ridge from top of head to level of antennae in frontal view (fig. 18); other head ridges as described of *M. minutissima*. Most of tentorium missing presumably from postmortem damage. Parietal band weakly evident. Lateral head profile approximately as described for *M. minutissima*. Antennal papilla tapering to rounded apex, length about two times basal diameter. Lower margin of clypeus and labrum as described for *M. minutissima*.

Mandible and maxilla as described for *M. minutissima* except maxillary palpus about twice as long as basal diameter and labial palpus slender, longer than maxillary palpus, and about three times basal diameters. Labium, salivary lips, and hypopharynx as described for *M. minutissima*, except premental sclerite extensively expressed and postmentum with large sclerites on each side (fig. 19).

Body: Vestiture consisting of very short setae, which densely cover dorsal surfaces but sparsely cover lateral surfaces; each seta rising from small integumental swelling as in *M. minutissima*; dorsal surface of abdominal segment 10 questionably without spicules. Body form of predefecating larva robust in lateral view (fig. 17), with thickest part of larva posterior to midbody;



FIGURES 17–19. Diagrams of predefecating larva of *Megachile (Creightonella) frontalis*. 17. Entire larva, lateral view. 18, 19. Head, frontal and lateral views, respectively.

as discussed above, caudal annulets appearing quite distinct compared with cephalic annulets; middorsal swellings between caudal annulet and following cephalic annulet more or less distinct; head size moderately small compared with massive body; other body features as described for *M. minutissima*. Spiracles (fig. 8) pigmented, subequal in diameter; atrium globular with width greater than depth, projecting beyond body wall, rim evident; atrial inner surface with pronounced ridges concentric with primary spiracle opening bearing fine elongate, linearly arranged spicules; primary tracheal opening with collar; subatrium extremely short consisting of approximately three chambers, which decrease in width away from body surface.

MATERIAL STUDIED: One larva: PAPUA NEW GUINEA: Oro Province [as Terr. Papua]: Kokoda, 24 July 1964 (R. Zweifel and G. Sluder).

REMARKS: This material included adult specimens as well as perhaps 6–8 leaf-covered cells, at least three containing pupae, and two with larvae. The cells and their contents had been preserved in ethanol. The second larva was severely distorted because of poor preservation. Another jar containing preserved cells from this locality had dried out, permitting partial examination of cell structure. The cell wall consisted of two layers of large pieces (some more than 10 mm long) of leaves between which was a layer consisting of fine-grained material, possibly of plant origin and also clearly soil as evidenced by sand grains of various sizes.

Postdefecating Larva of *Megachile (Chelostomoides) prosopidis* Cockerell

Figures 9, 20–22

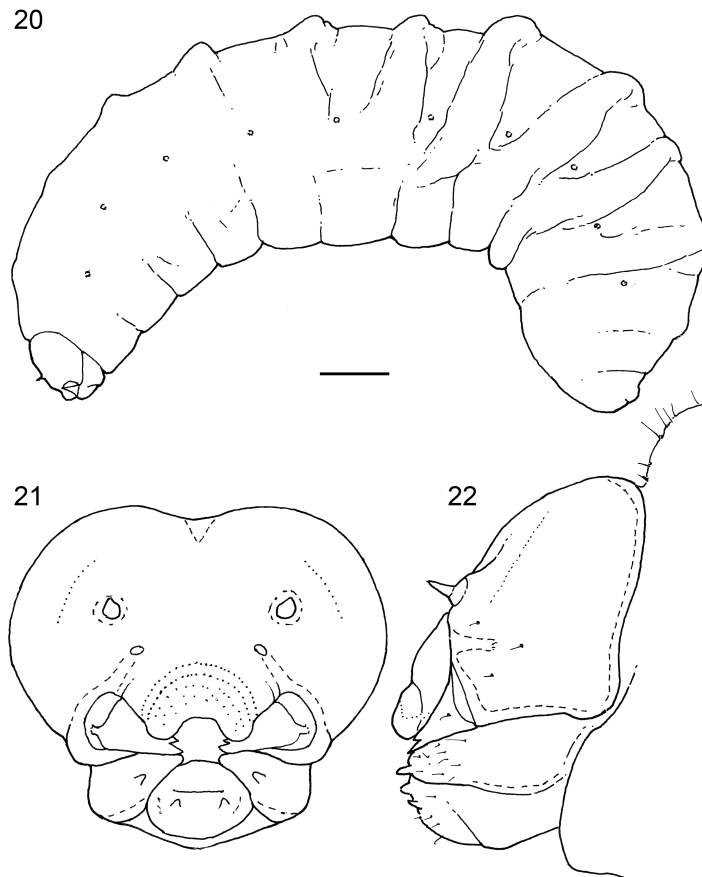
DESCRIPTION: Head: All features as described for *Megachile minutissima* except for following: Head setae sparse, moderate in size similar to those of labiomaxillary region. Dorsal ramus scarcely evident, not reaching postoccipital ridge. Tentorium incomplete, presumably because of impending ecdysis. Antennal papilla (fig. 22) conical, tapering apically, more than two times basal diameter.

Mouthparts as described for *M. minutissima*, except premental sclerite faintly but distinctly evident.

Body: Vestiture consisting of moderately short to short setae, which densely cover dorsal and lateral surfaces and sparsely cover ventral surfaces; each seta rising from conspicuous socket. Body form of postdefecating larva as described for *M. minutissima* except caudal annulets tending to be more pronounced and midbody tubercles particularly of first 5–6 abdominal segments involving posterior part of caudal annulet and anterior part of following cephalic annulet more pronounced (fig. 20); predefecating larva unknown. Spiracles (fig. 9) as described for *M. minutissima* except subatrial cuticle weak so that chambers poorly formed and of uncertain number.

MATERIAL STUDIED: Two postdefecating larvae and associated meloid: USA: CA: Riverside County: 15 mi N Blythe, 1972 (P.F. Torchio). “In *Megachile concinna* trap-nest preserved.”

REMARKS: An adult male preserved with these specimens was kindly identified as *M. prosopidis* Cockerell by Terry Griswold. Note that *Megachile occidentalis* sensu auct. (not Fox, which is restricted to Lower California, i.e., the Baja California Peninsula) pertains to *M. prosopidis* (see Snelling, 1990; the identity of the bee depicted as *M. occidentalis* Fox in Michener, 2007: fig. 84-9, requires clarification).



FIGURES 20–22. Diagrams of postdefecating larva of *Megachile (Chelostomoides) prosopidis*. **20.** Entire larva, lateral view. **21, 22.** Head, frontal and lateral views, respectively.

DISCUSSION

On the basis of the four selected species representing all three of Michener's (2007) major groups of *Megachile* sensu lato, and of another species belonging to the subgenus *Chelostomoides* and thus potentially belonging to a lineage separate from others in Group 2 of Michener (see Gonzalez, 2008), the following is the description of *Megachile* based on diverse larval features.

Preliminary Description of Genus *Megachile* Based on Mature Larvae

DESCRIPTION: Head: Head size moderately small in relation to body size; head of postdefecating larva slightly embedded in prothorax. Setae moderately long on sides of head but sparse and reduced in size on front of head capsule; those of maxillary and labial apices tending to be large, curved, abundant, and conspicuous, often with large conspicuous alveoli. Head capsule pigmentation variable but limited to points of articulation of mandibles, mandibular apices, labral sclerite and surface of labrum including transverse sclerite; premental bridge, articulating arm of stipes, and stipital rod as well as premental sclerite also somewhat pigmented; slight

pigmentation on leading surfaces of other mouthparts including salivary lips. Integumental spiculation reduced except for outer surfaces of hypopharyngeal lobes. Internal head ridges: coronal ridge usually only briefly evident near top of head in frontal view except in *M. frontalis* (fig. 18) and *M. atrata* ridge extending to level of antennae; postoccipital ridge well developed, bending forward somewhat toward median line on top of head; hypostomal ridge well developed and, except in *Chelostomoides*, giving rise to pronounced dorsal ramus that extends directly backward from frontal part of hypostomal ridge sometimes to join postoccipital ridge; thinner posterior part of hypostomal ridge curving mesad to join postoccipital ridge at deeply recessed posterior tentorial pit; pleurostomal ridge present; epistomal ridge well developed from anterior mandibular articulation to anterior tentorial pit; from pit, ridge extending vertically immediately mesad of antennal papilla and fading out above antenna, hence not extending across to opposite side of head. Tentorium complete, well developed. Parietal band weakly evident. In lateral view, clypeus not projecting much beyond frons, antenna in most cases arising from low prominence, and labrum normally not extending much beyond clypeus. Antennal papilla tapering, as long as basal diameter but variable in length. Lower margin of clypeus weakly sclerotized, so that midpoint of margin cannot be determined relative to level of anterior tentorial pits. Labrum broadly emarginated apically; labral sclerite transverse, well defined.

Mandible moderately robust; apex darkly pigmented, apically bidentate with ventral tooth longer than dorsal tooth; teeth tending to be apically rounded, but lower tooth more acutely rounded especially when viewed in maximum profile; teeth broad, thereby forming broad apical concavity to entire inner surface of mandibular apex (Rozen and Kamel, 2007: fig. 42); this inner surface smooth, without teeth or denticles and thin in cross section; outer surface of mandible usually with one or two conspicuous setae. Maxillary apex strongly bent mesad in frontal view, so that maxillary palpus subapical in position; apex beyond palpus tapering, its outer surface bearing small cluster of 4–6 short sensilla, probably representing galea; cardo distinct especially when stained; stipes consisting of conspicuously long stipital rod that is sometimes pigmented and is darkly stained by dye; at posterior end, rod articulating with cardo, and, at anterior end, rod broadening and branching to form somewhat pigmented articulating arm of stipes; other arm of branch circling orally around outer side of mound of hypopharynx; maxillary and labial palpi elongate, probably usually more than two times basal diameters. Labium divided into prementum and postmentum; apex usually moderate in width in frontal view; premental sclerite more or less faintly evident, but border between pre- and postmentum distinctly incised; prementum projecting dorsally at midline forming pointed projection behind which surface somewhat sclerotized and pigmented, forming dorsal bridge of prementum that extends in front of articulating arms of stipes and bridges area between the dorsal ends of the premental sclerite. Salivary opening broad with thin, strongly projecting, transverse lips, which extend as far as distance between centers of labial palpi. Hypopharynx consisting of transverse pair of dorsally projecting finely spiculate mounds.

Body: Vestiture consisting of moderately short to short setae, which densely cover dorsal and lateral surfaces and sparsely cover ventral surfaces. Body form of postdefecating larva moderately robust in lateral view (unknown but almost certain for *M. frontalis*), with thickest part of larva

posterior to midbody and usually with only slight distinction between cephalic and caudal annulets except in *M. prosopidis* (fig. 20), with caudal annulets tending to be more pronounced; mid-dorsal swellings between caudal annulet and following cephalic annulet moderately pronounced; venter of abdominal segment 9 not produced; segment 10 attached to approximate middle of segment 9 in lateral view; anus positioned toward top of segment 10. Abdominal segment 10 rarely with fine spiculation dorsally. Spiracles unpigmented to pigmented, subequal in diameter; atrium globular with width usually greater than depth, projecting only slightly beyond body wall, rim faintly present; atrial inner surface with coarse ridges concentric with primary spiracle opening with abundant fine spicules to without spicules; primary tracheal opening with collar; subatrium short to very short, decreasing in width away from body surface.

REMARKS: The above description of the mature larvae of *Megachile* can be compared with the Preliminary Description of the Mature Larvae of the Megachilini (Rozen and Kamel, 2007), which was based on representatives of *Coelioxys* and *Radoszkowskiana* as well as *M. nigripes*. The addition of cleptoparasitic genera provides little anatomical diversity⁵ to the entire group. Thus, the above description of the genus *Megachile* sensu lato based on material from its major lineages varies little from that previously provided for the tribe. The evolution into a cleptoparasitic life style has not modified the fundamental anatomy of the mature larva despite modifications into hospicial larval forms of earlier instars as identified in Rozen and Kamel (2007). Perhaps that should not be surprising since the last larval instar of all taxa, cleptoparasitic or not, performs the same functions: to finish feeding on provisions and to move about the cell in order to spin a cocoon and defecate.

On the basis of this limited sampling, *Megachile* larvae are found to be too uniform for their morphology to provide evidence for recognizing any of Michener's (2007) three major groups at generic rank. Definitive conclusions about the utility of larval data for studies of Megachilini will require discovery of immature stages for additional distinctive members of *Megachile* sensu lato such as *Matangapis*, which was treated as a separate genus by Gonzalez (2008).

ACKNOWLEDGMENTS

The authors thank Terry Griswold, USDA ARS Bee Biology & Systematics Laboratory, for identifying the male of *Megachile prosopidis* and for loaning the larval specimens of the same species. We also acknowledge that assistance of Stephen Thurston, Senior Scientific Assistant, AMNH, in composing all illustrative material used here. Eunice Jia Yu Soh of Singapore obtained the larva of *M. atrata* studied here and shared unpublished information on nests of this species. Corey Smith, Curatorial Assistant, AMNH, proofread the manuscript. We extend our thanks to two anonymous reviewers for their suggestions and corrections. Corey Smith's participation was supported by a donation from Robert G. Goelet, Chairman Emeritus, Board of Trustees, American Museum of Natural History.

⁵ In Rozen and Kamel (2007) it was stated that the hypopharynges of the treated taxa lacked spicules. This was an error; reexamination of all taxa revealed that outer surfaces of the paired hypopharyngeal mounds are spiculate.

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