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Immature Stages of Lithurgine Bees with Descriptions of the Megachilidae and Fideliidae Based on Mature Larvae (Hymenoptera, Apoidea)

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ABSTRACT

Mature larvae of *Lithurge*, *sensu stricto*, *Lithurge* (*Lithurgopsis*), and *Trichothurgus* are described as is the pupal exuviae of *Trichothurgus*. An account is given of the nests of *Trichothurgus dubius*. The mature larvae of the Lithurginae are quite homogeneous and are very similar to those of the other megachilid subfamily, the Megachilinae. Appended is a taxonomic description of the Megachilidae and a comparative taxonomic description of the Fideliidae; both descriptions are based on the mature larvae.

I demonstrated (Rozen, 1970 and 1973) that the mature fideliid larvae share numerous characters with the larvae of the Megachilinae, a situation that suggested a close relationship between these two groups. Whereas many genera of megachiline larvae had been studied (see for example Michener, 1953), larvae of the Lithurginae, the smaller of the two megachilid subfamilies, had been only superficially described (Claude-Joseph, 1926; Cros, 1939). The question remained if an analysis of the mature larvae of the Lithurginae would shed additional light on the relationships of the two families. The present paper attempts to answer that

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question by describing in detail larvae of lithurgines and by comparing and contrasting them with those of the Megachilinae and the Fideliidae. This paper also includes the following: (1) a brief description of the cast pupal exuviae of *Trichothurgus* because no pupa of the Lithurginae has been described; (2) a note on the nesting habits of *Trichothurgus* because much is yet to be learned about the biology of the lithurgines; and (3) an appendix giving taxonomic descriptions of the families Megachilidae and Fideiidae based on the mature larvae.

The Lithurginae is a small subfamily containing only three genera—*Lithurge*, widely distributed over the world, and *Trichothurgus* and *Lithurgomma*, both in Chile. Moure (1949) placed the last two genera in a separate tribe, the Trichothurgini.

This paper was possible because of the excellent cooperation of a number of people who, through special effort, collected or sent larvae to me: Dr. Terry F. Houston, Curator of Reptiles and Amphibians, The South Australian Museum, South Australia, provided the larvae of *Lithurge atratiformis*; larvae of the Philippine *Lithurge* were lent by Dr. Paul D. Hurd, Jr., National Museum of Natural History, Smithsonian Institution, Washington, D.C.; Dr. Frank D. Parker, United States Department of Agriculture, Logan, Utah, collected and sent larvae of *Lithurge* (*Lithurgopsis*) *apicalis*. Other megachilid larvae examined for this study came not only from the collection of the American Museum of Natural History but also from the immature bee collections of the California Insect Survey and the University of Kansas. The last two collections are on long-term loan to the American Museum of Natural History. Miss Liliane Floge carefully prepared the illustrations. The National Science Foundation supported the research under Grant GB-32193.

MATURE LARVA OF *Lithurge* (*Lithurge*) *atratisformis* COCKERELL

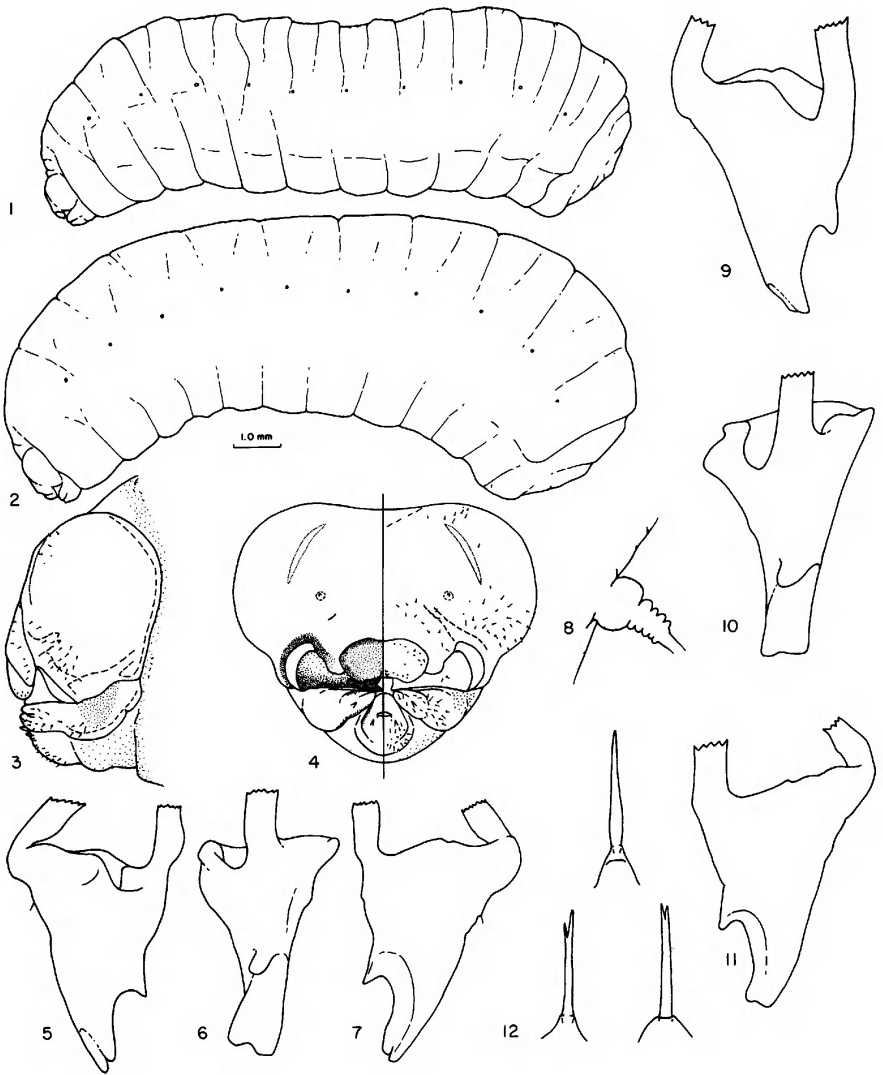
Figures 1–8

DIAGNOSIS: The smooth integument of the head capsule of *Lithurge*, *sensu stricto*, distinguishes the mature larvae from those of *Lithurge* (*Lithurgopsis*) *apicalis* and *Trichothurgus dubius*. The diagnosis of *L. (Lithurge)* species gives features separating it from *L. atratisformis*.

HEAD (FIGS. 3, 4): As seen from front, head capsule very wide in relation to labiomaxillary region. Integument smooth (i.e. not shagreened), with numerous scattered setae; hypopharynx indistinctly spiculate; lateral part of maxilla and base of labium spiculate; pigmentation as in figure 4. Tentorium incomplete on head capsules of two larvae that had been in cocoons; however, tentorium complete and well developed on young ultimate or penultimate larva; hence incomplete condition on other larvae

presumably indication of approaching pupation; posterior tentorial pits in normal position, although superficially appearing below hypostomal ridge because of posterior modifications of ridge as discussed below; posterior thickening of head capsule and pleurostomal ridge well developed; hypostomal ridge greatly developed and strongly inflected; anterior part serving as an extra strong ventral articulation for mandible; posterior part divided, with conspicuous, well-developed dorsal ramus continuing straight back nearly to posterior thickening of head capsule and with weak inconspicuous ventral ramus curving slightly down toward posterior tentorial pit; epistomal ridge well developed laterad of anterior tentorial pits, scarcely developed mesiad of pits; longitudinal thickening of head capsule indistinct; parietal bands moderately distinct. Antennal papilla minute but well formed, somewhat shorter than basal diameter; each papilla not arising from basal prominence and bearing approximately three or four sensilla. Labrum without paired tubercles, broadly but shallowly emarginate apically. Mandible (figs. 5-7) moderately massive and apically bidentate, with teeth subequal in length but with ventral tooth slightly wider than dorsal one; teeth on fully mature larvae strongly abraded and, therefore, truncate; on young ultimate or penultimate larva teeth pointed; apical concavity smooth and well defined, with large simple adoral tooth arising at base. Labiomaxillary region strongly produced (probably more strongly so than indicated in drawing of specimen, which had been encased in cocoon). Maxilla elongate, with apex bent mesiad so that palpus subapical in position; cardo and stipes somewhat sclerotic; palpus more than twice as long as basal diameter; galea not evident. Labium divided into prementum and postmentum and bearing salivary opening at apex; salivary opening a moderately narrow transverse slit with strongly projecting lips; palpus subequal to labial palpus. Hypopharynx protruding somewhat more laterally than medially although not distinctly bilobed.

BODY (FIGS. 1, 2): Form robust with posterior part more robust than anterior part; most body segments divided dorsally into cephalic and caudal annulets which, at least on larvae taken from cocoons, are of about same height; middorsal tubercles not evident; lateral tubercles (below spiracles) moderately low. Integument of quiescent form moderately soft, spiculate, and with widely scattered, very fine, inconspicuous setae (not shown in illustration), which are not restricted to caudal or cephalic annulets; spicules becoming less dense toward posterior end of body but even dorsum of abdominal tergum eight moderately spiculate. Spiracle (fig. 8) moderate in size; atrium projecting above body wall, atrial wall with scattered very small denticles; peritreme narrow, flat to concave;



FIGS. 1-8. Postdefecating larva of *Lithurge (Lithurge) atratiformis*. 1. Larva, lateral view; specimen somewhat shrunken. 2. Same except specimen somewhat bloated. 3. Head, lateral view. 4. Head, frontal view, left side of diagram showing pattern of pigmentation, right side showing spicules and setae. 5-7. Right mandible, dorsal, inner, and ventral views respectively. 8. Spiracle, side view.

FIGS. 9-11. *Lithurge (Lithurge)* sp., right mandible of mature larva, dorsal, inner, and ventral views, respectively.

FIGS. 12. *Trichothurgus dubius*, setae from dorsal surface of mesosoma of pupa. Scale refers to figures 1 and 2.

primary tracheal opening without distinct collar, without spines; subatrium moderately short with approximately five distinct chambers. Ninth and tenth abdominal segments appearing very short on larvae taken from cocoons, but probably not short on larvae not yet encased in cocoons; tenth segment apparently with no special elevations or modifications; anus terminal, being neither dorsal nor ventral. Imaginal disc of male genitalia a median somewhat elongate (probably paired) body lying between abdominal segments nine and 10 and accompanied by distinct integumental scar; imaginal discs of female not observed.

MATERIAL STUDIED: Two postdefecating larvae, 6 miles south of Noosa Heads, Queensland, Australia, September 15, 1957, ex cocoons in *Banksia* stump (T. F. Houston); two postdefecating larvae and one predefecating ultimate or penultimate instar, same except January 17-18, 1969, no ecological data.

MATURE LARVA OF *Lithurge* (*Lithurge*) SPECIES

Figures 9-11

DIAGNOSIS: The slight differences in shape of the mandible and possibly in the length of the setae on the head in conjunction with the fact that *L. atratiformis* is not known from the Philippine Islands suggests that the following larvae are not *L. atratiformis*. At the same time it must be realized that these larvae and those of *L. atratiformis* are in other respects remarkably similar and, furthermore, that members of this genus easily cross water barriers (Michener, 1965). Hence, when the systematics of the genus are eventually worked out, these larvae might be found to belong to *L. atratiformis*.

HEAD: As described for *Lithurge atratiformis*, except for following: Setae perhaps shorter and less numerous although this condition probably results from wear; tentorium complete on head capsules of two larvae taken from cocoons; mandibles (figs. 9-11) essentially same as those of *L. atratiformis* except apex almost truncate.

BODY: As described for *Lithurge atratiformis* except for following: Imaginal disc of female genitalia pared, paramedian, circular, subcuticular bodies on venter of abdominal segments seven, eight, and nine.

MATERIAL STUDIED: Five postdefecating larvae, Philippine Islands, nest in board, P.Q.-San Francisco 13158; presumably all larvae taken from cocoons.

REMARKS: A single cocoon of this species preserved with these larvae does not differ significantly from that described for *Lithurge atratiformis* by Houston (1971).

MATURE LARVA OF *Lithurge (Lithurgopsis) apicalis* (Cresson)¹

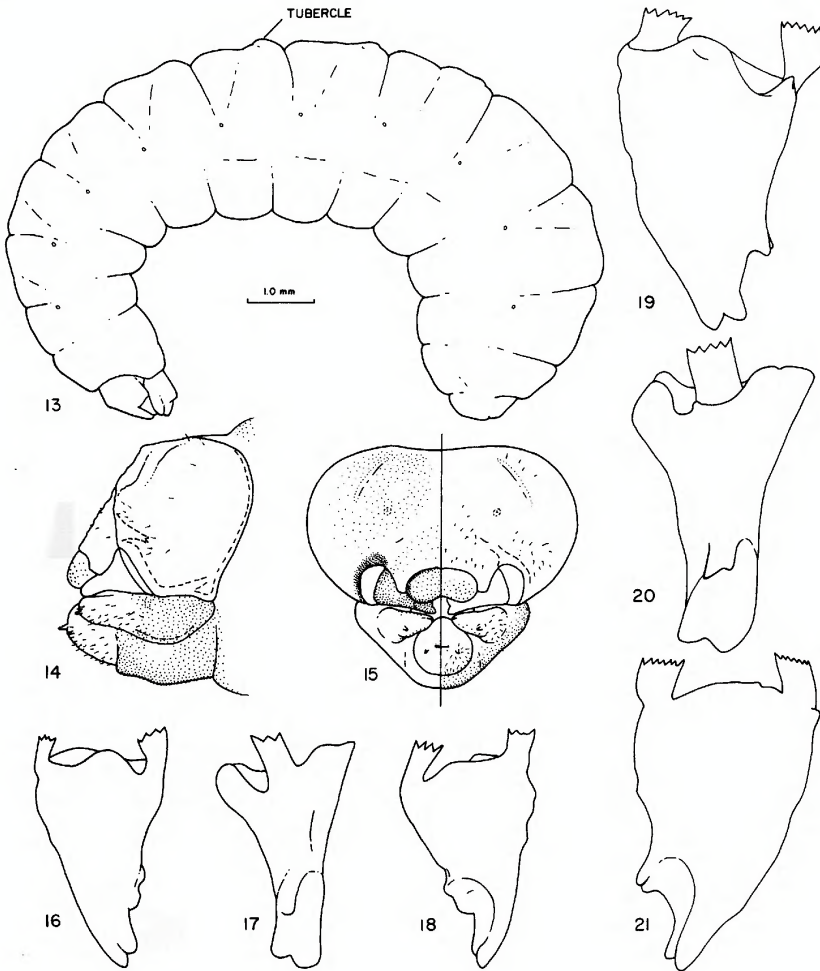
Figures 13-18

DIAGNOSIS: Because of the crinkled condition of the integument of the head capsule, these larvae can be distinguished from those of *Lithurge*, *sensu stricto*. Mandibular shape and spiculation of labiomaxillary region are diagnostic features that can be used to separate larvae of *Lithurgopsis* from those of both *Lithurge*, *sensu stricto*, and *Trichothurgus*.

HEAD (FIGS. 14, 15): As seen from front, head capsule moderately wide but not nearly so wide as that of *L. atratiformis*. Integument crinkled, almost rugosely so, especially on paramedian areas in the vicinity of and above the antennae; crinkling somewhat similar to, but more exaggerated than, shagreened condition found in *Trichothurgus dubius*; certain areas, such as that above each antennae, not crinkled; integument with numerous scattered setae; hypopharynx distinctly spiculate laterally but not medially; lateral part of maxilla and base of labium more extensively spiculate than those areas in *L. atratiformis*; pigmentation as indicated in figure 15; crinkled areas tending to be somewhat more heavily pigmented than rest of capsule. Tentorium well developed and complete; posterior tentorial pits, posterior thickening of head capsule; pleurostomal ridge, hypostomal ridge, epistomal ridge, and longitudinal thickening of head capsule as described for *L. atratiformis*; parietal bands very distinct, deeply incised in crinkled integument. Antenna and labrum as described for *L. atratiformis*. Mandible (figs. 16-18) moderately massive and apically bidentate with ventral tooth somewhat longer than dorsal one; apical teeth rounded; apical concavity well defined, somewhat sculptured and with large indistinctly bilobed adoral tooth arising at base. Labiomaxillary region, maxilla, labium, and hypopharynx as described for *L. atratiformis*.

BODY: As described for *L. atratiformis*, except for following: Form (fig. 13) moderately robust; low inconspicuous middorsal tubercles present on caudal annulets of abdominal segments three to five and also perhaps on other segments as well. Integument densely spiculate in most areas but middorsal tubercles smooth; spiracular atrium without denticles; ninth and tenth abdominal segments normal in size; anus slightly more dorsal than ventral; imaginal discs of genitalia not observed.

¹ After I completed the present manuscript, Philip F. Torchio, Bee Biology and Systematics Laboratory, United States Department of Agriculture, Logan, Utah, kindly sent me several mature larvae of *Lithurge (Lithurgopsis) echinocacti* (Cockerell) collected 4 miles west of Safford, Graham County, Arizona, June 15, 1962 (P. Torchio). These larvae were virtually identical to those of *L. apicalis* except that the middorsal tubercles on the body were not visible and the bilobed condition of the adoral tooth at the base of the apical concavity of the mandible was slightly more pronounced.



FIGS. 13-18. Postdefecating larva of *Lithurge (Lithurgopsis) apicalis*. 13. Well-preserved larva, lateral view. 14. Head, lateral view. 15. Head, frontal view, left side of diagram showing pattern of pigmentation, right side showing spicules and setae. 16-18. Right mandible, dorsal, inner, and ventral views, respectively.

FIGS. 19-21. Mature larva of *Trichothurgus dubius*, right mandible, dorsal, inner, and ventral views.

Scale refers to figure 13.

MATERIAL STUDIED: Five postdefecating larvae, near Vernal, Uintah County, Utah, late summer 1972, from nest in cottonwood log (F. D. Parker).

REMARKS: Frank D. Parker may describe the nesting habits of this species.

The crinkled condition of the head capsule is markedly different from the smooth integument of *Lithurge*, *sensu stricto*, and would support the separation of *Lithurgopsis* from *Lithurge* at the generic level. The crinkled condition almost certainly is a derived character; if it proves to be homologous with the shagreened integument of *Trichothurgus*, then *Lithurgopsis* and the Trichothurgini would seem to be closely related and therefore Moure's (1949) division of the Lithurginae into the Trichothurgini and Lithurgini would be questionable. The fact that adult males of *Lithurgopsis* and of the Trichothurgini have arolia, whereas males of *Lithurge*, *sensu stricto*, do not, supports the possible close relationship of *Lithurgopsis* with the Trichothurgini.

MATURE LARVA OF *Trichothurgus dubius* (SICHEL)

Figures 19-21

The following is incomplete because the description is based on cast larval skins. Claude-Joseph (1926) provided a brief verbal account of the species that augments the information available from the cast skins.

DIAGNOSIS: So far as can be determined, larvae of this species are essentially similar to those of other lithurgines. *Trichothurgus dubius* is unquestionably larger than the others and the bidentate condition of the adoral tooth at the base of the apical mandibular concavity contrasts with the simple condition of that tooth in *Lithurge*, *sensu stricto*, and the indistinctly bilobed adoral tooth in *Lithurgopsis*.

HEAD: Width of head unknown. Integument of much of head capsule shagreened, with numerous scattered setae; hypopharynx apparently nonspiculate; lateral part of maxilla and base of labium distinctly spiculate; pigmentation probably much as in *Lithurge atratiformis*. Tentorium not studied, but probably as in *L. atratiformis*; posterior tentorial pits in normal position; posterior thickening of head capsule probably well developed; hypostomal ridge greatly developed and strongly inflected and as otherwise described for *L. atratiformis*; pleurostomal ridge well developed; condition of epistomal ridge, longitudinal thickening of head capsule, and parietal bands not known. Antennal papilla small but not so minute as that of *L. atratiformis*, well formed, approximately as long as basal diameter; each papilla not arising from basal prominence and bearing approximately three or four sensilla. Labrum without tubercles broadly but shallowly emarginate apically. Mandible (figs. 19-21) in general similar to that of *L. atratiformis* but somewhat more massive; mandible apically bidentate, with teeth subequal in length but with ventral

tooth wider than dorsal one; apical concavity smooth and well defined with large adoral tooth rising at base; this tooth bidentate apically unlike that of *L. atratiformis*. Labiomaxillary region undoubtedly strongly produced. Maxilla elongate, with apex bent mesiad so that palpus subapical in position; cardo and stipes sclerotic; palpus approximately three times length of basal diameter; galea not evident. Labium divided into prementum and postmentum and bearing salivary opening at apex; salivary opening a moderate transverse slit with strongly projecting lips; palpus apparently slightly shorter than labial palpus. Hypopharynx probably much as described for that of *L. atratiformis*.

BODY: Form unknown, but according to Claude-Joseph (1926) "with posterior segments more dilated than anterior ones." Integument strongly spiculate, having scattered setae. Spiracle moderate in size, same as that described for *L. atratiformis*, except atrial wall apparently without denticles, presence or absence of collar on primary tracheal opening not known but without spines, and number of chambers to subatrium not known although subatrium short, hence number of chambers must be few. Ninth and tenth abdominal segments and features of imaginal discs not known.

MATERIAL STUDIED: Two cast larval skins from cells containing adults, Quebrada San Carlos, Coquimbo Province, Chile, October 17, 1971, from nest in cactus (*Eulychnia* or *Trichocereus*) (J. G. Rozen and L. Peña).

PUPA OF *Trichothurgus dubius* (SICHEL)

Figure 12

A pupal skin of this species was removed from one cell. Although pupal tubercles and spurs were not visible on the skin, some observations were made on the integument itself. The most noteworthy feature is the presence of large, stout, somewhat pigmented setae, which are simple, bifurcate, or even trifurcate (fig. 12). These setae are well developed on the dorsal surface of the mesosoma and are also well developed and arranged in linear bands on many of the metasomal terga. Some pieces of exuviae, apparently representing parts of the legs, have setae although they tend to be smaller than the others. The vertex of the pupa could not be identified. Areas of the integument definitely lacking setae include the wings, the ventral part of the metasoma and all but the dorsal surface of the mesosoma.

BIOLOGICAL NOTES

The nesting biology of lithurgine bees has been described in some detail by a number of workers, including Claude-Joseph (1926), Cros (1939), Houston (1971), and Malyshev (1930) (see their work for other references).

Houston's work refers to *Lithurge atratiformis*, the larva of which is described here, and Claude-Joseph's paper deals with *Trichothurgus dubius* (as *Lithurgus dubius* Herbst). In spite of rather numerous observations, many questions regarding choice of nesting site, nest materials, shape of pollen mass, and egg deposition need further review.

The following brief notes are presented in the hope that they will contribute toward a more comprehensive understanding of these matters. In October, 1971, at Quebrada San Carlos, near Vicuña, Chile, I noticed a number of large vacated bee cocoons in a fallen decayed cactus. The cactus was a large (6 to 10 feet high) arborescent form with long spines, belonging to *Eulychina* or *Trichocereus*; several specimens of the cactus are illustrated in Rozen (1973, fig. 1). Because the size of these cocoons suggested that they might have been spun by the larvae of *Trichothurgus*, Luis Peña, who accompanied me, searched the area for dead but still standing cacti with holes that might represent nest entrances of these bees. He returned with a number of nests only one of which was still occupied. The nest was taken from a dead, standing cactus and contained four cocoons arranged in linear fashion. Each cocoon contained a single, newly emerged adult bee (three females, one male) of *T. dubius*; another adult male was found in the nest entrance. One of the males had badly frayed wings, whereas the wings of the others were not worn. The elongate oval cocoons (fig. 22), slightly wider at one end than the other, were arranged end to end (although they were separated by loose frass) and were surrounded by considerable frasslike debris. Material external to the nest, such as soil and plant tissue, had not been used to line the nest. The cocoons measured 16 to 19 mm. by 9 to 11 mm. wide (outside dimensions). The outer surface (shown in fig. 22) of each was covered with a rough cemented layer of cactus tissue, feces, and some pollen grains. The fecal material in the layer



FIG. 22. Cocoon of *Trichothurgus dubius*.

and also loose in the nest was unusual in that each pellet appeared as a slightly flattened cylinder 0.5 to 1 mm. in length; the pellet was truncate at each end as if it had been broken, and its surface had a resinous luster. [Similar pellets were also observed attached to the cocoon of *Lithurge (Lithurgopsis) apicalis*.] Individual pollen grains could not be observed in a pellet until it had been soaked in water. Claude-Joseph (1926), indicating that the cells of this species were formed from "resinous particles mixed with wood" probably observed these feces. The rough outer layer completely covered and hid the inner part of the cocoon.

The inner layer consisting solely of silk was pressed to the outer one, although they could be rather easily separated with a forceps. The inner layer was evenly thin, brownish, semitransparent, continuous (no fenestrations), and parchment-like. Its outer face was somewhat fuzzy because of individual strands of silk, but the inner surface was smooth and shiny. Although normally less than 1 mm., the thickness of the two layers of the cocoon together was variable because of the variability of the outer layer.

DISCUSSION AND CONCLUSIONS

This study indicates that the Lithurginae, as larvae, are quite homogeneous and that, in answer to the question posed in the Introduction, the larval Lithurginae are not markedly different from the Megachilinae. Consequently, the family Megachilidae represented both by the Megachilinae and the Lithurginae is similar to the Fideliidae, as was concluded previously (Rozen, 1970, 1973) on the basis of larval megachilines alone.

The members of the Megachilinae, as mature larvae, are surprisingly homogeneous. Even the parasitic forms such as *Stelis (sensu lato)* (Rozen, 1966), *Dioxys* (Rozen, 1967), and *Coelioxys* (Baker, 1971) seem not to have strayed far from the basic type larvae, although earlier instars have become highly modified in some cases. The only diagnostic difference between the Megachilinae and Lithurginae seems to be that the lithurgines possess a large and pronounced adoral tooth at the base of the apical concavity on the mandible. The salivary lips of lithurgines may be narrower than those of the Megachilinae. Available lithurgines have relatively few body setae but there are some megachilines that have even fewer (e.g., some *Ashmeadiella*).

APPENDIX

DESCRIPTION OF THE MEGACHILIDAE BASED ON MATURE LARVAE

With the new information regarding the lithurgine larvae, it is now possible to

provide a preliminary description of the family Megachilidae pertaining to the mature larvae. The following is based on Michener (1953), Rozen (1966, 1967), the present study on lithurgines, and firsthand examination of larvae of a total of 14 megachilid genera.

DIAGNOSIS: Among mature larvae of bees only those of the Megachilidae, Fideliidae, and the anthophorid tribe Ceratinini (some *Allodape* and their relatives) have conspicuous body setae. Unlike the Megachilidae and Fideliidae, ceratinines do not spin cocoons. As a consequence, the labiomaxillary region of the mature larva is not modified for spinning, that is, it is recessed and protruding salivary lips are lacking. Larvae of the Megachilinae, one of the two subfamilies of the Megachilidae, can be distinguished from those of the Fideliidae because the former lack an adoral tooth at the base of the mandibular apical concavity. The Lithurginae have such a tooth and therefore cannot be separated from the Fideliidae on that basis. A distinguishing feature between the Lithurginae and the Fideliidae is the presence in the former of the distinctly divided condition of the posterior area of the hypostomal ridge, as seen in lateral view.

DESCRIPTION: Head with numerous long (compared with other groups of bee larvae) setae especially pronounced at the apexes of the maxillae and labium but also scattered over head capsule. Tentorium almost certainly complete and well developed, at least before cocoon spinning; posterior tentorial pit in normal position; posterior thickening of head capsule, hypostomal ridge, pleurostomal ridge, and epistomal ridge at least laterad of anterior tentorial pit well developed; hypostomal ridge often divided posteriorly into two branches, the dorsal one extending straight backward and the ventral one curving downward toward posterior tentorial pit; this feature far less pronounced in Anthidiini than in Megachilini and Lithurginae, but even in some Megachilini (e.g. *Coelioxys*) dorsal branch not developed. Antennal papilla distinct but varying between being minute (*Lithurge*, fig. 4) to being extremely large (*Dioxys*, Rozen, 1967, figs. 8, 15); papilla in most cases not arising from prominence. Labrum without tubercles but emarginate apically. Mandible in most cases robust but attenuate in some *Stelis* (i.e. *Microstelis*, Michener, 1953, figs. 115, 116) and in *Dioxys* (Rozen, 1967, figs. 3-5, 11-13); apex in most specimens bidentate and often with ventral tooth somewhat longer or larger than dorsal one; in *Trachusa* (Michener, 1953, fig. 112) apex truncate apically; in some *Stelis* (*Microstelis*, Michener, 1953, fig. 115) mandible apically simple; apical concavity normally large and well defined but absent in some *Stelis* (i.e. *Microstelis*, Michener, 1953, figs. 115, 116) and in *Dioxys* (Rozen, 1967, figs. 3-5, 11-13); concavity with large adoral tooth at base in Lithurginae but without such a tooth in Megachilinae. Labiomaxillary region strongly produced as is characteristic of larvae that can spin cocoons. Maxilla elongate with apex bent mesiad so that palpus subapical in position; cardo and stipes sclerotic; palpus elongate, normally much longer than basal diameter; galea not evident. Labium divided into prementum and postmentum, bearing salivary opening at apex; salivary opening with elongate lips that are wide at least in most Megachilinae but tending to be narrow in Lithurginae.

Body form moderately robust, often with posterior part of body more robust than anterior part; most body segments divided into cephalic and caudal annulets; body without distinct dorsolateral tubercles but some species with middorsal tubercles. Integument spiculate or not, but typically with conspicuous setae on many areas of body; on some species setae extremely numerous, on others some-

what reduced; on some (but not all) *Ashmeadiella* setae so reduced in number that only anterior body segments with few scattered setae.

DESCRIPTION OF THE FIDELIIDAE BASED ON MATURE LARVAE

Now that a formal description of the Megachilidae based on the mature larvae has been presented it is possible to provide a comparative taxonomic description of the Fideliidae. This description is based on previous studies of *Fidelia villosa* Brauns (Rozen, 1970) and *Neofidelia profuga* Moure and Michener (Rozen, 1973).

DIAGNOSIS: Same as for the Megachilidae.

DESCRIPTION: As described for the Megachilidae except for following: Hypostomal ridge not distinctly divided posteriorly so that dorsal branch not evident; antennal papilla moderately small; mandible moderately robust, apically bidentate and with more (*Neofidelia*, Rozen, 1973, figs. 15–17) or less (*Fidelia*, Rozen, 1970, figs. 18–20) well-developed adoral tooth at base of apical concavity (also characteristic of the Lithurginae); salivary lips strongly protruding but narrow (Rozen, 1970, fig. 15; 1973, fig. 12).

REMARKS: The presence of the adoral mandibular tooth in both the Fideliidae and the Lithurginae might suggest that these two taxa may be more closely related to each other than either is to the Megachilinae; however, it cannot be determined now whether this toothed condition is primitive or derived. The apparently somewhat narrow condition of the salivary lips in the Lithurginae also seems to place this subfamily more closely with the Fideliidae than with the other megachilids.

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