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The Larvae of the Anthophoridae (Hymenoptera, Apoidea) Part 3. The Melectini, Ericrocini, and Rhathymini

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Two assemblages of parasitic bees exist in the Anthophoridae. The mature larvae of the largest group, the Nomadinae, were described taxonomically and their phylogeny was discussed in the last paper of the present series (Rozen, 1966); the other group, consisting of the small tribes Melectini, Ericrocini, and Rhathymini, is treated similarly here.

I wish to express my special appreciation to the following people for providing, as indicated, the immature stages of these rare bees: Dr. Fred D. Bennett, Commonwealth Institute of Biological Control, Trinidad, the West Indies; Dr. Robbin W. Thorp, University of California, Davis; and Mr. P. F. Torchio, Entomology Research Division, United States Department of Agriculture, Logan, Utah. The present paper could not have been prepared without their co-operation. Mrs. Rose Ismay, with her customary care, typed and helped edit the manuscript, and my wife, Barbara L. Rozen, and Mrs. Marjorie Favreau carefully prepared the illustrations. The research was supported by National Science Foundation Grant GB-5407.

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EVOLUTIONARY CONSIDERATIONS

Apidologists have known for a long time on the basis of comparative adult anatomy that the nomadine complex of parasitic bees had a separate evolutionary origin from that of the Ericrocini, Rhathymini, and Melectini. The anatomy of the mature larvae of both groups corroborates this separate origin, for the two parasitic assemblages hold in common almost no derived features.

Michener (1944), studying adults, believed that the nomadines arose from exomalopsine stock. Although I deferred discussing the matter with respect to the larvae (Rozen, 1966), those that I investigated shared few derived features with exomalopsine larvae or with larvae of other non-parasitic anthophorids. However, subsequent to publishing my paper, I collected larvae of other nomadine genera that, when studied, may support Michener's conclusions; these larvae will be described in another paper of this series.

By undertaking an investigation of the larvae of the Melectini, Ericrocini, and Rhathymini, I hoped to find answers to two main problems regarding the phylogeny of these three tribes. First, did the tribes have a monophyletic origin or did each evolve from a separate unrelated group of non-parasitic bees, and, second, from what group or groups of non-parasitic bees did they arise? The total evidence does not provide conclusive answers to either question because there are too few characters and because some characters have arisen *de novo* more than once. Nonetheless, tentative conclusions, brought out in the following discussion, have been reached regarding the evolution of these three tribes.

Because some larval melectines, rhathymines, and ericrocines share certain features, I assume that the tribes evolved from ancestors that possessed the same characteristics, namely: tentorium well developed and complete; internal ridges of head capsule (although perhaps not the median segment of the epistomal ridge) strongly developed; antennal prominences very low; labral tubercles low; mandibles massive, broadly rounded apically, and with pronounced, inner apical, scoop-shaped cavity; labium divided into prementum and postmentum, strongly projecting, with salivary lips transverse and protruding (adaptations for cocoon spinning); hypopharynx large, spiculate, and bilobed; body form moderately robust and perhaps size large; body segments divided into caudal and cephalic annulets, with caudal annulets tending to be produced into paired, transverse, low tubercles dorsally; anus dorsal.

These characteristics are common to a number of the non-parasitic anthophorids and, for reasons as yet unknown, to *Bombus*. Therefore, such

features do not indicate precisely from what group or groups the three tribes may have evolved. However, it seems unlikely that these parasitic tribes could have arisen from the exomalopsines (as the Nomadinae may have done), the emphorines, or the eucerines because of the distinctive mandibles of these non-parasitic groups. Furthermore, the broad, spiculate clypeus of the eucerines and the tendency toward an extremely elongate body in the exomalopsines and emphorines are features without counterparts in the melectine complex of tribes. The broad scoop-shaped mandibles of the Melectini, Rhathymini, and Ericrocini are strikingly similar to those of the Anthophorini and Centridini, as are the other features listed above. For these reasons, I believe that the parasitic bees probably evolved from either the anthophorine lineage or the centridine lineage, or from both.

The melectines, ericrocines, and rhathymines share one specialized feature not found in the Centridini and the Anthophorini; they lack galeae. This fact suggests (1) that the three parasitic tribes evolved from a single ancestor that lacked galeae and (2) that, as a group, they are therefore monophyletic. The absence of a galea, however, has evolved in many unrelated groups of bees, and a conclusion derived from one character is hardly reliable, especially in the presence of the following contradictory evidence.

The melectines have a maxillary palpus that is preapical in position. The feature, not shared with the Rhathymini and Ericrocini, suggests that the melectines and their hosts, the anthophorines, may have evolved from a common ancestor somewhat different from the non-parasitic ancestor of the other two non-parasitic tribes. The melectine type of maxilla, although lacking an apex that bends inward, is probably derived from a maxilla in which the apex is strongly bent inward so that, as a consequence, the palpus is preapical in position. Such strongly bent maxillae with preapical palpi exist in the present-day Anthophorini (*Emphoropsis*, *Amegilla*, and *Anthophora*) and, presumably, in the ancestral stock that gave rise to the Anthophorini, Centridini, and the three tribes of parasitic bees discussed here (fig. 1). If the melectines and the anthophorines had a common ancestor (as indicated in fig. 1), it must have been a non-parasitic bee different from the existing anthophorines, in that it spun a cocoon and had a produced labium with protruding lips. Cocoon spinning, as found in *Melecta*, *Zacoscma*, and *Xeromelecta*, is assumed to be the primitive condition, whereas non-cocoon spinning (and associated modifications of the labium) is derived. This ancestor was also the progenitor of the centridine-ericrocine-rhathymine stock.

There is no reason to believe that the various melectine genera evolved

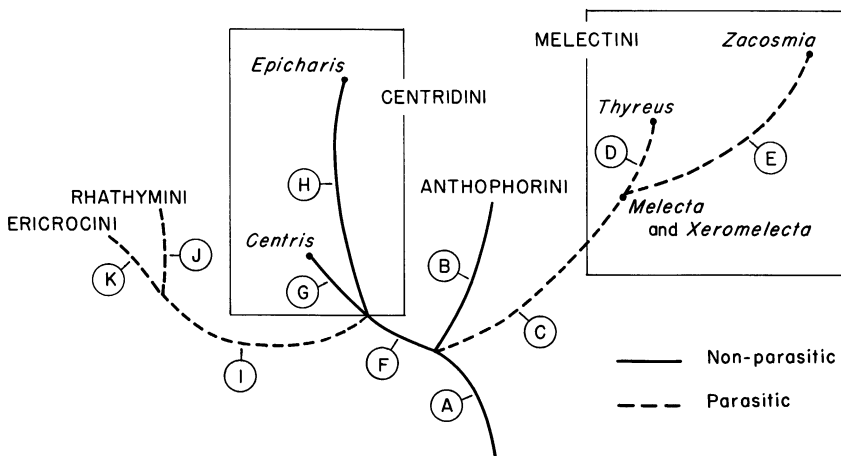


FIG. 1. Hypothesized phylogenetic relationships of the Anthophorini, Centridini, Melectini, Rhathymini, and Ericrocini as shown by mature larvae. A. Ancestral lineage of entire assemblage of tribes with these characteristics: non-parasitic; maxillae bending mesiad; maxillary palpi subapical; maxillae normal in size; galeae expressed; labiomaxillary region normally elongate for cocoon-spinning larva; mandible normally broad apically; labium projecting and adapted for cocoon spinning (i.e., divided into prementum and postmentum and salivary lips projecting strongly); labrum normally rounded apically; integument of body without spines; atrial wall smooth or with short denticles and primary tracheal opening with collar and without toothed spines. Evolutionary changes for each lineage, as follows: B. Cocoon-spinning adaptations lost; atrial wall with long denticles and primary tracheal opening spinose. C. Parasitic; galeae lost; maxillary apices not bent mesiad, although palpi still preapical. D. Cocoon-spinning adaptations lost. E. Labiomaxillary region recessed, although still adapted for cocoon spinning; mandible narrowed apically in adoral view; labium pointed apically. F. Maxillary apices not bent mesiad so that palpi apical. G. Spiculate, bilobed condition of hypopharynx lost. H. Cocoon-spinning adaptations lost; each abdominal segment with dorsal row of spines; atrial wall with long denticles and primary tracheal opening spinose. I. Parasitic; labiomaxillary region greatly elongate; galeae lost. J. Maxillae enlarged. K. Atrial wall with long denticles and primary tracheal opening spinose.

the parasitic of life independently, for the first instars on superficial examination are very similar one to another. Nonetheless, mature larvae of the melectines have undergone considerable evolutionary modification (fig. 1). The most primitive condition is found in *Melecta* and *Xeromelecta*, in which the mandibles are unmodified, the labium is still adapted for cocoon spinning, and the labrum is bilobed or has low tubercles. This kind of larva was ancestral to that of *Thyreus* which differs in having the labium more recessed and not divided into prementum and post-

mentum, modifications associated with the loss of cocoon spinning. The larva of *Thyreus*, in other respects, is *Melecta*-like. The *Melecta* type of larva also gave rise to the highly modified one of *Zacoscma* which still possesses a labium adapted for cocoon spinning, although the entire labiomaxillary region is recessed. The apical, as opposed to preapical, position of the maxillary palpi of *Zacoscma* seems to be a secondary modification resulting from the recession of the entire labiomaxillary region. The larva of *Zacoscma* is also distinctive in that the mandibles have become greatly narrowed apically so that in adoral view they resemble those of the Nomadinae. However, they retain the basic scoop-shaped apex as seen in other views. The highly modified labrum narrows to a simple, rounded point apically; it is thereby somewhat similar to the condition found in the nomadine *Isepeolus*.

Because maxillary palpi are apical in position in the Rhathymini and Ericrocini, these parasitic bees may have evolved from their hosts, the centridines (or from the immediate ancestors of the centridines). The condition in which the apices of the maxillae are bent mesiad and the palpi are therefore subapical is considered primitive because it is found widely in the non-parasitic tribes of the Anthophoridae. The apical condition of the maxillary palpi in the Rhathymini, Ericrocini, and Centridini is derived from the more primitive state. The Centridini contain only *Centris*, which has a labium modified for cocoon spinning but which has a non-spiculate, non-bilobed hypopharynx, and *Epicharis*, with a spiculate, bilobed hypopharynx but with a non-cocoon-spinning type of labium (Rozen, 1965). Because ericrocines and rhathymines possess both a spiculate, bilobed hypopharynx and a cocoon-spinning labium, they could not have arisen from either existing centridine genus but probably evolved from the lineage that gave rise to the two genera.

The Rhathymini and Ericrocini seem to have had a common parasitic ancestor, for both groups have a greatly elongate labiomaxillary region, a specialized character that is unlikely to have arisen twice. The strongly denticulate atrial wall and spinous primary tracheal opening of the ericrocines (not found in the rhathymines) are strikingly similar to the structures of the spiracles of the anthophorines and *Epicharis*. This condition must have arisen *de novo* in each case, if the above phylogenetic relationships are correct.

The hypothesized evolutionary relationships of the Anthophorini, Centridini, Melectini, Ericrocini, and Rhathymini are summarized and presented visually in figure 1 in order to aid future testing.

If the diphyletic origin of the ericrocine-rhathymine-melectine complex of tribes postulated above is correct, then the melectines evolved from

the same lineage as their hosts, the anthophorines, and likewise the rhathymines and ericrocines evolved from their hosts, the centridines. That many parasitic bees have arisen from the same stock as their hosts is true in many instances and is a matter of significant interest to the evolutionist delving into the relationships of bees. This phenomenon, sometimes referred to as Müller's law, was discussed in some detail a half-century ago by Wheeler (1919). It would be naive, however, to apply this rule *a priori* in order to deduce the origin of parasitic bees. This point is proved, for example, merely by the fact that the larvae of the anthophorid genus *Triepeolus* (Epeolini) have been recovered from the nests of bees representing four families (Colletidae, Oxaeidae, Anthophoridae, and Halictidae; Rozen, 1966).

KEY TO THE MATURE LARVAE OF THE MELECTINI, ERICROCINI, AND RHATHYMINI

To date, all members of the Melectini have been found in cells of anthophorine bees, whereas the other two tribes depredate the nests of Centridini. Larvae of the megachilid genus *Coelioxys* have been recovered from the nests of both non-parasitic tribes, but I know of no other parasitic bee that attacks anthophorines and centridines. *Coelioxys* larvae can be easily recognized by their conspicuously setose body in contrast to the non-setose integument of melectine and rhathymine larvae, and to the very finely setose integument of the ericrocines.

The following key includes not only species described in the present paper, but also *Xeromelecta californica* (Michener, 1953) and the Australian *Thyreus lugubrus* (Cardale, 1968). *Mesoplia rufipes* does not appear in the key because of the lack of definite information regarding its labiomaxillary region. I would be surprised, however, if it did not key to the related *Acanthopus splendidus urichi* from which it can be distinguished by the difference in size of the maxillary palpi (figs. 47, 52).

1. Labiomaxillary region, as seen in lateral view (figs. 32, 33, 46, 47), abnormally elongate and projecting 4
- Labiomaxillary region, as seen in lateral view (figs. 4, 11, 12, 18, 19), at most only moderately elongate and projecting, in some cases recessed. Melectini 2
- 2(1). Clypeus, as seen in lateral view (fig. 47), strongly projecting; atrial wall (figs. 48, 53) with elongate denticles and primary tracheal opening guarded by spines *Acanthopus splendidus urichi* Cockerell
- Clypeus, as seen in lateral view (figs. 33, 40), non-protuberant; atrial wall (fig. 34) with only minute denticles; primary tracheal opening with collar. *Rhathymus* 3
- 3(2). Head capsule with small protuberance above each antenna (fig. 33) ...

-*Rhathymus bicolor* Lepeletier
- Head capsule (fig. 40) without such protuberances
-*Rhathymus trinitatis* Cockerell
- 4(1). Labrum bilobed or bituberculate, as seen in frontal view (figs. 3, 11);
mandible (figs. 7, 15) broad at apex 5
- Labrum narrowing to a rounded point, as seen in frontal view (fig. 25);
mandible, as seen in adoral view (fig. 29), greatly narrowed apically
.....*Zacosmia maculata* (Cresson)
- 5(4). Labium divided into prementum and postmentum, an adaptation for co-
coon spinning (fig. 4; Michener, 1953, fig. 238)
-*Melecta separata callura* (Cockerell)
-*Xeromelecta californica* (Cresson)
- Labium not divided into prementum and postmentum (fig. 12)
-*Thyreus lieftincki* Rozen
-*Thyreus lugubrus* (Smith)
-*Thyreus* sp.

SYSTEMATICS

MELECTINI

Members of this tribe differ from the Ericrocini and Rhathymini most conspicuously in the much less well-developed labiomaxillary region, which, even in cocoon-spinning *Melecta* and *Xeromelecta*, is reduced compared with that of most cocoon-spinning bees. This region is greatly enlarged in the other two tribes. The subapical position of the maxillary palpi, also a diagnostic characteristic in the Melectini, suggests that the tribe shared a common ancestor with the Anthophorini.

HEAD: Integument with scattered sensilla; dorsal surface of labrum non-spiculate or with non-hairlike spicules at apex; epipharyngeal surface spiculate or non-spiculate; hypopharynx spiculate; maxillae partly spiculate or non-spiculate; apices of mandibles darkly pigmented. Tentorium in all cases complete and thick; tentorial pits well developed; posterior tentorial pits either at juncture of hypostomal ridge and posterior thickening of head capsule or slightly anterior to juncture; hypostomal and pleurostomal ridges well developed; epistomal ridge well developed below (laterad of) anterior tentorial pits; middle segment of epistomal ridge tending to become obsolete toward median line but still evident; longitudinal thickening of head capsule weak to moderately expressed. Antennal prominences absent; each papilla moderately small to moderately large and bearing variable number of sensilla. Clypeus non-protuberant. Labrum protruding moderately (*Thyreus*) to recessed (*Zacosmia*); labrum normal in size or small and with or without paired, well-developed tubercles; anterior margin of labrum emarginate, rounded, or pointed. Mandible normally long, massive, with broad scoop-shaped

concavity toward apex; in *Zacosmia* mandible, as seen in adoral view, tapering to point apically. Labiomaxillary region not greatly elongate as seen in *Ericrocini* and *Rhathymini*. Maxilla moderately recessed even in cocoon-spinning larvae; apex not bent mesiad but with palpus usually preapical in position (except in *Zacosmia*); galea not evident. Hypopharynx moderately large and usually protuberant, bilobed. Labium varying from being moderately projecting to being recessed; palpus moderately long; salivary opening a wide slit bearing projecting lips to a narrow slit with weakly developed lips.

BODY: Form moderately elongate but not especially slender; most body segments each divided into cephalic annulet and caudal annulet; in many cases caudal annulet produced on each side as low, flat, transverse tubercle. Integument without setae and spines and usually without spicules. Spiracles moderately large; atrium usually projecting moderately above body wall; peritreme conspicuous; primary tracheal opening with collar; atrial wall smooth or with concentric rows of very fine denticles; subatrium not divided. Tenth abdominal segment moderately short; anus dorsal.

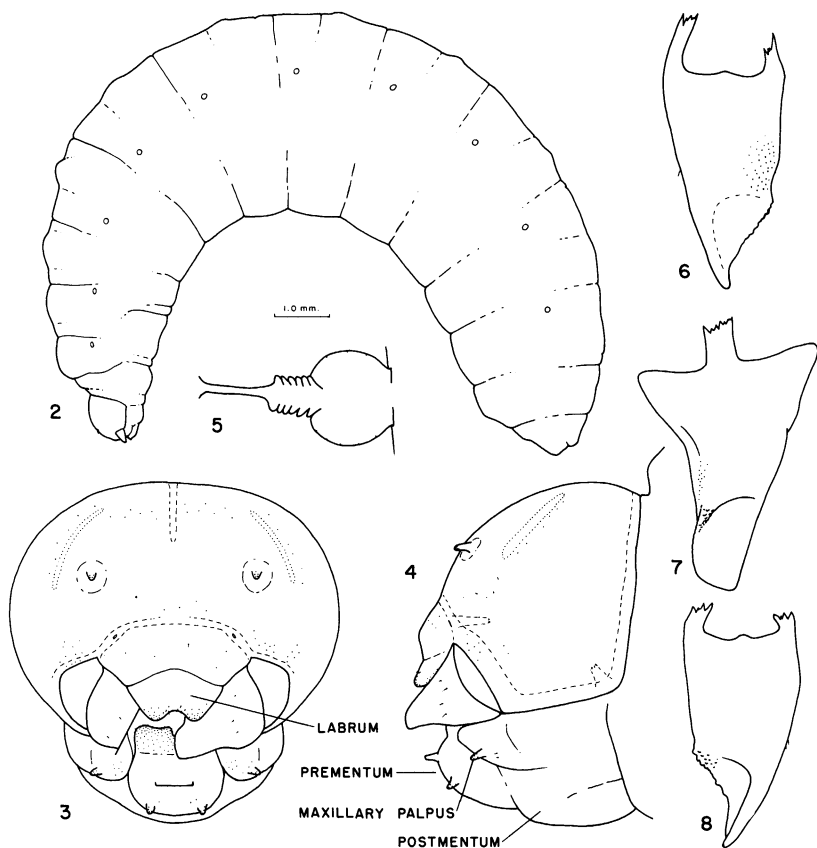
MELECTA LATREILLE

The larva of the species treated here does not seem to differ significantly from that of *Xeromelecta californica* (Cresson) (Michener, 1953). It can be readily distinguished, however, from the larvae of *Zacosmia* and *Thyreus* by the characteristics presented in the key.

Melecta (Melecta) separata callura (Cockerell)

Figures 2-8

HEAD (FIGS. 3, 4): Integument with scattered sensilla; dorsal surface of maxilla with only a few widely scattered, non-hairlike spicules; dorsal surface of labrum non-spiculate; epipharyngeal surface with non-hairlike spicules; hypopharynx with numerous non-hairlike, sharp-pointed spicules; mandibular articulations and apexes pigmented; antennae faintly pigmented. Tentorium complete and thick; each posterior tentorial pit at juncture of posterior thickening of head capsule and hypostomal ridge; posterior thickening of head capsule and hypostomal and pleurostomal ridges well developed; epistomal ridge well developed both laterad and mesiad of anterior tentorial pits except near median line of head; longitudinal thickening of head capsule pronounced dorsally; parietal bands moderately expressed. Antennal papillae not on prominences; each papilla moderately large, longer than basal diameter; each papilla bearing approximately 10 sensilla. Clypeus non-protuberant. Labrum moderately



FIGS. 2-8. *Melecta (Melecta) separata callura* (Cockerell). 2. Somewhat swollen postdefecating larva, lateral view. 3. Head, frontal view, right mandible partly cut away. 4. Head, lateral view. 5. Spiracle. 6-8. Right mandible, dorsal, inner, and ventral views. Scale refers to figure 2.

short; raised labral tubercles absent but anterior margin deeply emarginate medially, hence labrum bilobed apically; each lobe with numerous sensilla. Each mandible (figs. 6-8) massive, broadly rounded apically, with pronounced, deep, inner apical, scoop-shaped concavity; dorsal apical edge of concavity with small rounded teeth; ventral apical edge of concavity smooth; concavity with a few rounded small teeth at base near upper edge; mandible spiculate dorsally. Labiomaxillary region only moderately large and produced ventrally, much smaller than that of *Rhathymus* and of *Acanthopus*, hence head with only normal elongate

aspect of cocoon-spinning larva. Maxilla (fig. 4) of normal size, with apex not bent mesiad but with palpus preapical in position, as seen in lateral view; palpus moderately large and elongate; galea not evident; cardo and stipes faintly sclerotic. Labium projecting only moderately, divided into prementum and postmentum, and bearing salivary opening at apex; labial palpi slightly smaller than maxillary palpi. Hypopharynx large, bilobed. Salivary opening a wide slit bearing projecting lips.

BODY: Form (fig. 2) moderately elongate. Body annulations as illustrated; dorsolateral part of caudal annulets of anterior segments produced on each side into low tubercle. Integument without setae, spines, and apparently without spicules; paired dorsal tubercles of thorax not visibly sclerotized. Spiracular atrium (fig. 5) large, projecting above body wall, faintly pigmented, and with rim; peritreme present; atrial wall with rows of very fine, scarcely noticeable denticles; primary tracheal opening with distinct collar; subatrium annulate. Tenth abdominal segment moderately short, with anus situated dorsally.

MATERIAL STUDIED: Two postdefecating larvae, 14.5 miles north of Coalinga, Fresno County, California, June 12, 1963, in nesting site of *Anthophora edwardsii* Cresson; preserved July 25, 1963 (R. W. Thorp and J. W. MacSwain); one postdefecating larva, same, except November 19, 1963 (R. W. Thorp); all in the collection of R. W. Thorp.

XEROMELECTA LINSLEY

The larva of *X. (Melectomorpha) californica* (Cresson) described by Michener (1953) was not found for this study. Michener's complete description and illustrations, however, adequately indicate that the larva resembles closely that of *Melecta*.

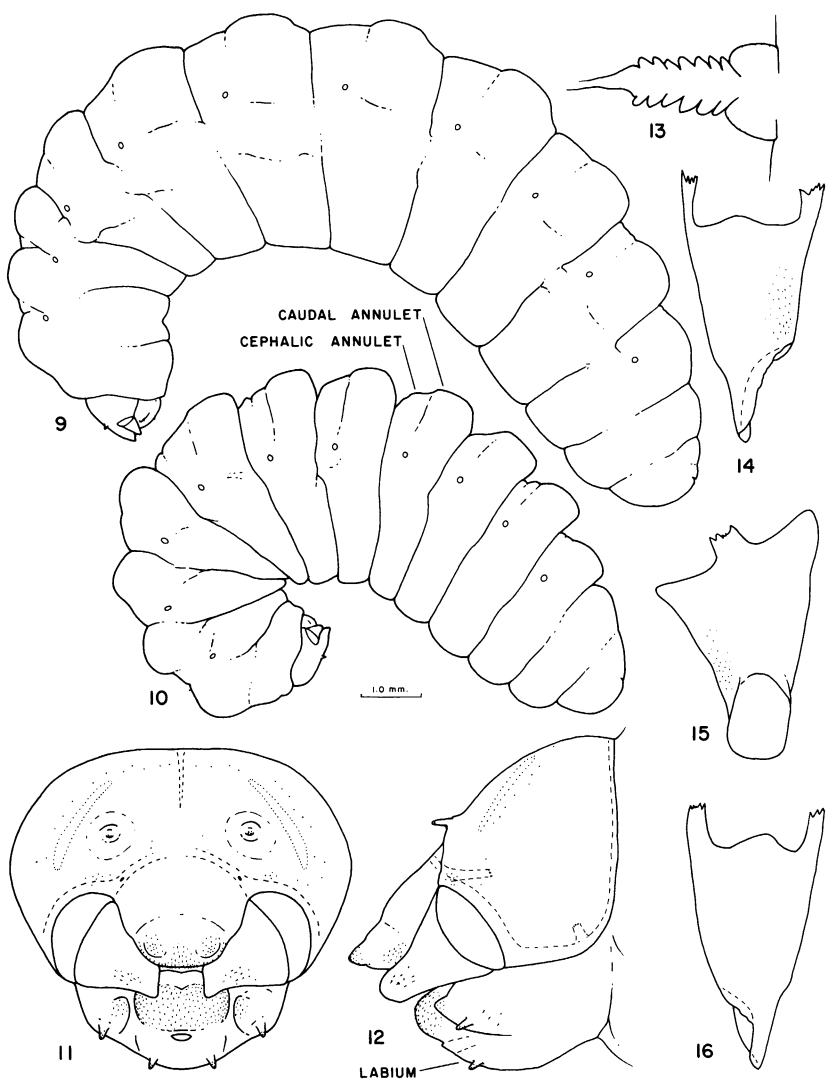
THYREUS PANZER

This is the only genus treated here in which the larvae do not spin cocoons; the recessed labium, which is not conspicuously divided into prementum and postmentum, is therefore diagnostic. Another species, *T. lugubrus* (Smith), was described and illustrated by Cardale (1968) and seems essentially the same as the species dealt with in the present paper.

Thyreus lieftincki Rozen

Figures 9-16

HEAD (FIGS. 11, 12): Integument with scattered sensilla; apex of maxilla, dorsal apex of labrum, epipharyngeal surface, hypopharyngeal surface, and dorsal surface of mandibles spiculate; spicules non-hairlike, sharp-pointed; mandibular articulations and apices pigmented. Tentorium



FIGS. 9-16. *Thyreus lieftincki* Rozen. 9. Predefecating larva, lateral view. 10. Freshly killed, postdefecating larva, lateral view. 11, 12. Head, frontal and lateral views. 13. Spiracle. 14-16. Right mandible, dorsal, inner, and ventral views. Scale refers to figures 9 and 10.

complete and thick; posterior thickening of head capsule bending forward below so that posterior tentorial pits slightly anterior in position;

posterior thickening of head capsule and hypostomal and pleurostomal ridges well developed; epistomal ridge well developed laterad of anterior tentorial pits; mesiad of pits ridge somewhat thinner and tending to become obscure near median line; longitudinal thickening of head capsule moderately developed above; parietal band moderately weakly expressed. Antennal papillae not on prominences; each papilla large and distinctly longer than basal diameter; number of sensilla on each papilla unknown. Clypeus non-protuberant. Labrum normal in size, with two well-developed tubercles, each bearing numerous sensilla apically. Each mandible (figs. 14–16) massive, broadly rounded apically, with pronounced, inner apical, scoop-shaped concavity; both dorsal and ventral apical edges somewhat irregular; concavity smooth, without teeth or pits; mandibles spiculate dorsally. Labiomaxillary region not produced ventrally and recessed. Maxilla (fig. 12) of normal size, with apex not produced mesiad but with palpus preapical in position as seen in lateral view; palpus moderately large and elongate; galea not evident; cardo and stipes not discernible. Labium recessed behind protruding hypopharynx, not distinctly divided into prementum and postmentum; labial palpi slightly smaller than maxillary palpi. Hypopharynx large and protruding, bilobed. Salivary opening moderately narrow, with non-sclerotized, weakly developed lips.

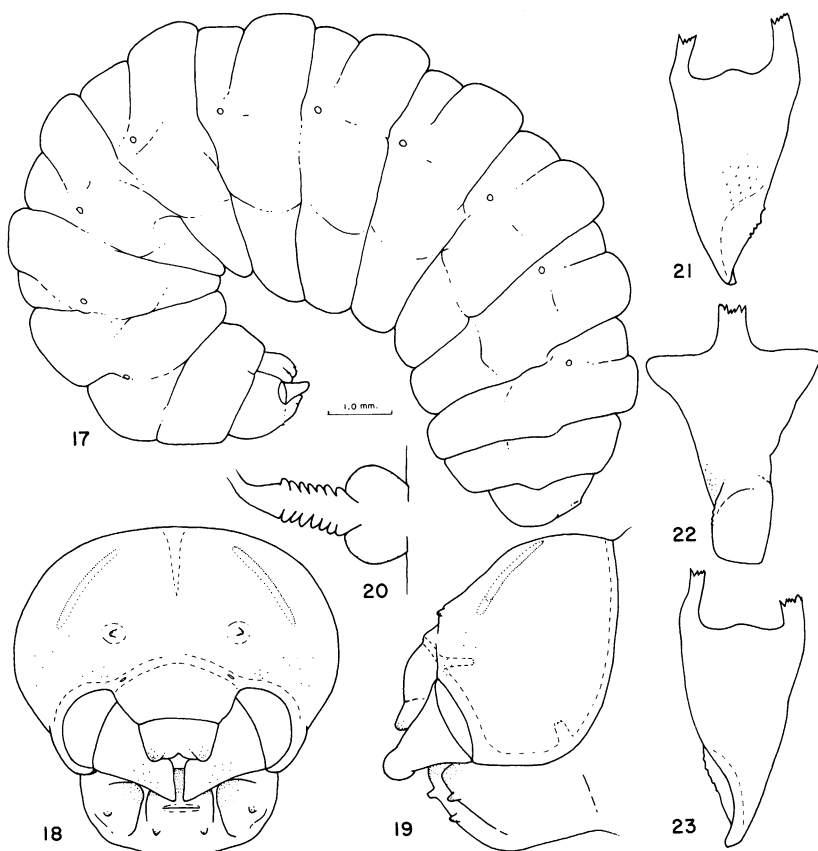
BODY: Form (figs. 9, 10) moderately elongate. Body annulations as illustrated; dorsolateral part of caudal annulets of most segments produced on each side into low, flat, transverse tubercle. Integument without setae, spines, or spicules; paired dorsal tubercles of thorax not visibly sclerotized. Spiracular atrium (fig. 13) projecting only slightly above body wall, unpigmented, and without rim; peritreme present; atrial wall with concentric rows of very fine denticles; primary tracheal opening with distinct collar; subatrium annulate. Tenth abdominal segment moderately short, with anus situated dorsally.

MATERIAL STUDIED: Three predefecating larvae, 3 miles south of Avontuur, Cape Province, Republic of South Africa, November 16, 1966, from nest of *Anthophora braunsiana* Friese (J. G. Rozen); one postdefecating larva, same, except preserved November 26, 1966; two postdefecating larvae, same, except preserved December, 1966; all specimens in the collection of the American Museum of Natural History. Rozen (in press) discussed the life history of this species of *Thyreus*.

Thyreus sp.

Figures 17–23

HEAD (FIGS. 18, 19): As described for *T. lieftincki* except for following:



FIGS. 17-23. *Thyreus* sp. 17. Postdefecating larva, lateral view. 18, 19. Head, frontal and lateral views. 20. Spiracle. 21-23. Right mandible, dorsal, inner, and ventral views. Scale refers to figure 17.

dorsal apex of labrum and epipharyngeal surface non-spiculate; parietal band darkly pigmented and more conspicuous; epistomal ridge more strongly developed near median line; antennal papillae apparently much smaller than those of *T. lieftincki*; dorsal apical edge of mandible with distinct teeth; ventral apical edge of mandible smooth; salivary opening non-sclerotized, but with lips seemingly more distinct than those of *T. lieftincki*.

BODY: As described for *T. lieftincki*.

MATERIAL STUDIED: One postdefecating larva, Sandgate, Queensland, Australia, November 30, 1958, collected with numerous larvae of *Ame-*

gilla salteri (Cockerell) (C. D. Michener), in the collection of the University of Kansas. Michener (1959) discussed the biology of the hosts and wondered if *Thyreus* attacked their nests.

ZACOSMIA ASHMEAD

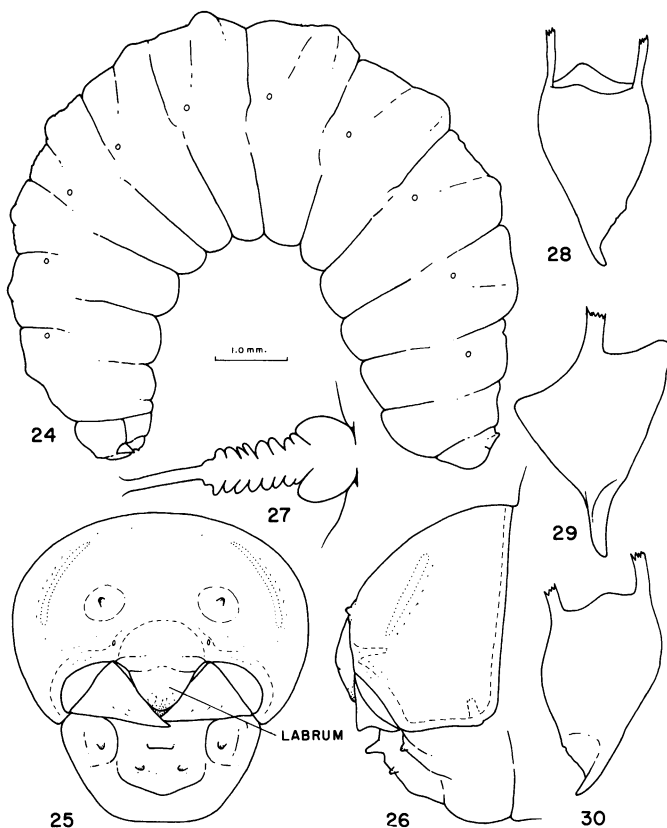
The larva of this genus is the most highly modified of the melectines. The apically pointed labrum is diagnostic.

Zacosmia maculata (Cresson)

Figures 24–30

HEAD (FIGS. 25, 26): Integument with scattered sensilla; dorsal surface of maxilla, dorsal surface of labrum non-spiculate, and epipharyngeal surface non-spiculate; hypopharynx with numerous non-hairlike, sharp-pointed spicules; mandibular articulations and apexes pigmented. Tentorium complete and moderately thick; each posterior tentorial pit slightly anterior to juncture of posterior thickening of head capsule and hypostomal ridge; posterior thickening of head capsule and hypostomal and pleurostomal ridges well developed; epistomal ridge well developed laterad of anterior tentorial pits, ridge fading near median line of head; longitudinal thickening of head capsule weak; parietal bands moderately expressed. Antennal papillae not on prominences; each papilla bearing approximately four or five sensilla. Clypeus non-protuberant. Labrum small, without tubercles, and forming a rounded point apically; apex with numerous sensilla. Each mandible (figs. 28–30) broad at base but, unlike mandibles of related forms, tapering nearly to a point apically when viewed in adoral aspect (fig. 29); inner apical, scoop-shaped concavity pronounced but narrow; dorsal apical edge of concavity irregular (possibly owing to wear); ventral apical edge of concavity smooth; concavity without teeth or pits; mandible non-spiculate dorsally. Labiomaxillary region weakly produced compared with this region in other cocoon-spinning melectine larvae. Maxilla (fig. 26) very short; apexes not produced mesiad and palpus apical in position (presumably a secondary modification, derived from preapical condition found in other melectines); galea not evident; cardo and stipes faintly sclerotic. Labium moderately recessed, divided into prementum and postmentum, and bearing salivary opening at apex; labial palpi subequal in length to maxillary palpi. Hypopharynx not so large as that of other melectines but evident and bilobed. Salivary opening a moderately wide slit bearing projecting lips.

BODY: Form (fig. 24) moderately elongate. Body annulations as illustrated; dorsolateral part of caudal annulets of most segments produced on each side into low transverse tubercle. Integument without setae,



FIGS. 24-30. *Zacosmia maculata* (Cresson). 24. Larva, lateral view. 25, 26. Head, frontal and lateral views. 27. Spiracle. 28-30. Right mandible, dorsal, inner, and ventral views. Scale refers to figure 24.

spines, or spicules; paired dorsal tubercles of thorax not visibly sclerotized. Spiracular atrium (fig. 27) projecting above body wall, faintly, if at all, pigmented, and with rim; peritreme present; atrial wall smooth; primary tracheal opening with distinct collar; subatrium annulate. Tenth abdominal segment moderately short, with anus situated dorsally.

MATERIAL STUDIED: Two postdefecating larvae, 16 miles south of Moab, San Juan County, Utah, October 13 to 17, 1965, host, *Anthophora* (*Micranthophora*) *flexipes* Cresson (P. F. Torchio and N. Youssef), in the collection of P. F. Torchio. Torchio and Youssef (1968) described the larva of this species and discussed its biology.

RHATHYMINI

This tribe contains only the genus *Rhathymus*.

HEAD: As described for the Melectini, except for following: dorsal surface of labrum non-spiculate; epipharyngeal surface, hypopharynx, and dorsal surfaces of maxillae spiculate; posterior tentorial pits at juncture of hypostomal ridge and posterior thickening of head capsule; median segment of epistomal ridge not expressed; each antennal papilla bearing approximately 10 sensilla; labrum rather small, without tubercles, and short; anterior margin curved; labiomaxillary region greatly elongate, hence like that of *Acanthopus* (Ericrocini); maxilla enlarged, projecting; palpus at tip of maxilla; hypopharynx large, protuberant, bilobed; labium strongly projecting; palpus moderately long; salivary opening a wide slit bearing strongly projecting lips.

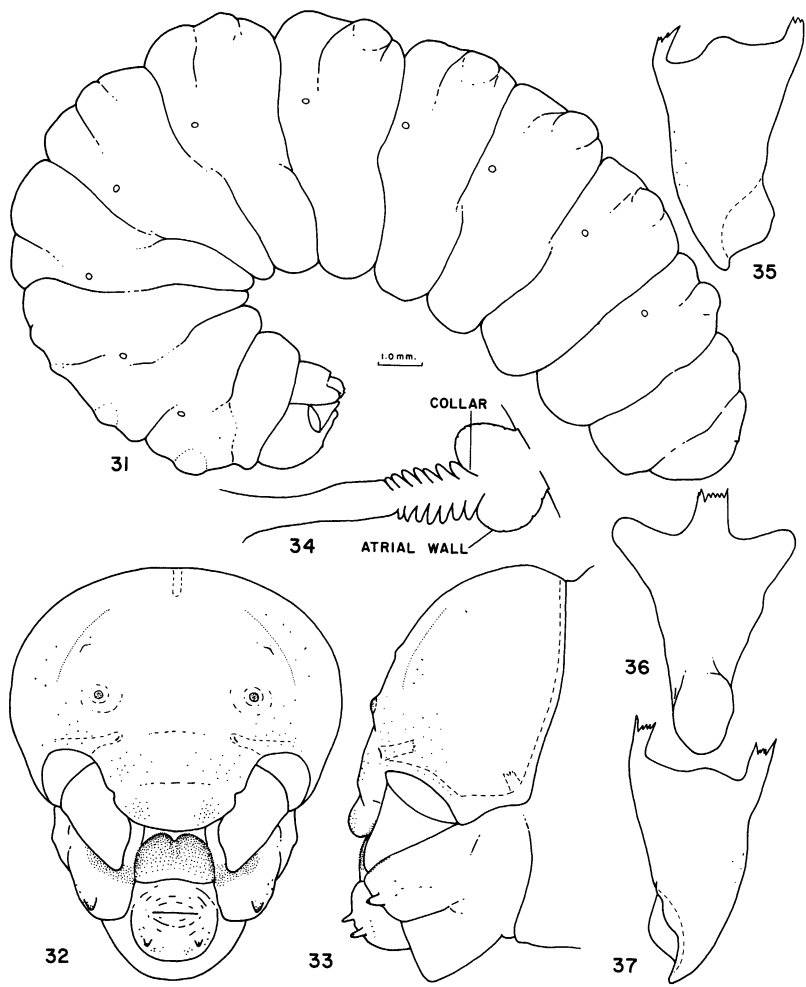
BODY: As described for Melectini except for following: atrial wall with concentric rows of very fine denticles.

RHATHYMUS LEPELETIER*Rhathymus bicolor* Lepeletier

Figures 31-37

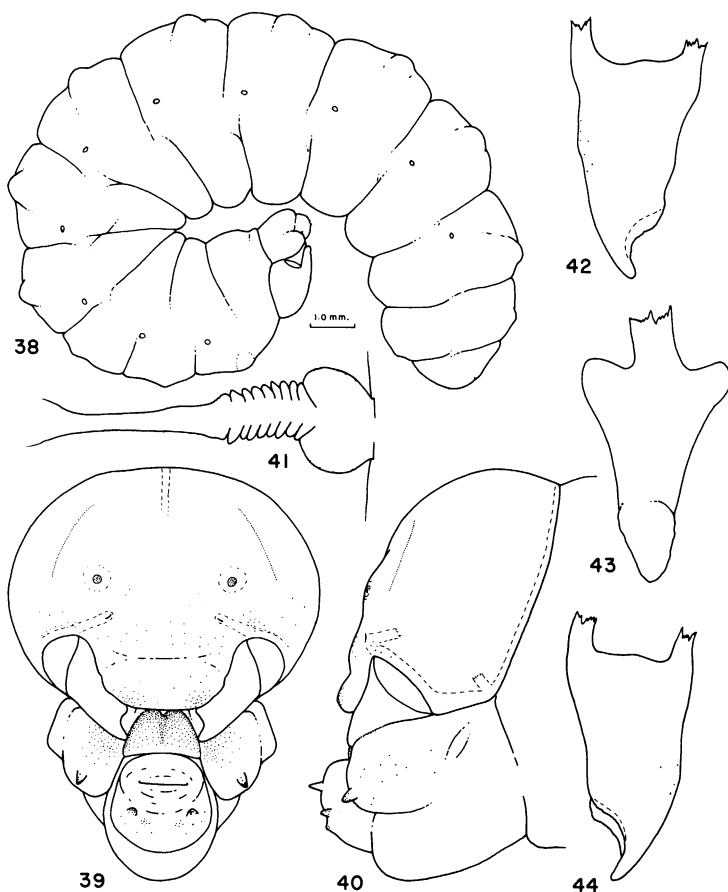
This species and *R. trinitatis* apparently can be distinguished on the basis of the presence or absence of a low irregular tubercle below each parietal band and by the ratio of head to body size. Mandibular differences between the two, although seemingly conspicuous, result from the wearing of the lamellate upper and lower edges rather than from genetic factors.

HEAD (FIGS. 32, 33): Integument with scattered sensilla; dorsal surface of maxilla with non-hairlike spicules; dorsal surface of labrum non-spiculate; epipharyngeal surface with non-hairlike spicules; hypopharynx with numerous non-hairlike, sharp-pointed spicules; mandibular articulations and apices pigmented. Tentorium complete and thick; each posterior tentorial pit at juncture of posterior thickening of head capsule and hypostomal ridge; posterior thickening of head capsule and hypostomal and pleurostomal ridges well developed; epistomal ridge well developed laterad of anterior tentorial pits but absent mesiad of pits; longitudinal thickening of head capsule pronounced dorsally; parietal bands moderately expressed; below each band, integument with low irregular tubercle which is slightly pigmented, at least in some cases. Antennal papillae not on prominences; each papilla small, not so high as basal diameter, and bearing approximately 10 sensilla. Clypeus non-protuberant. Labrum short; labral tubercles absent, although dorsal surface of



FIGS. 31–37. *Rhathymus bicolor* Lepeletier. 31. Live, postdefecating larva, lateral view. 32, 33. Head, frontal and lateral views. 34. Spiracle. 35–37. Right mandible, dorsal, inner, and ventral views. Scale refers to figure 31.

labrum slightly produced on each side; raised areas bearing numerous sensilla; anterior margin a continuous curve, not bilobed. Each mandible (figs. 35–37) massive, broadly rounded apically, with pronounced, inner apical, scoop-shaped concavity; both dorsal and ventral edges of concavity without teeth but each produced into thin lamella; on some specimens this lamella broken, giving mandibular apex somewhat dif-



FIGS. 38-44. *Rhathymus trinitatis* Cockerell. 38. Live, postdefecating larva, lateral view. 39, 40. Head, frontal and lateral views. 41. Spiracle. 42-44. Right mandible, dorsal, inner, and ventral views. Scale refers to figure 38.

ferent appearance; concavity without spines or pits; mandibles without spicules on dorsal surface although with scattered sensilla on outer surface. Labiomaxillary region large and produced ventrally, providing head with elongate aspect. Maxilla (fig. 33) extremely large, with apex not produced mesiad; galea not evident; palpus moderately large, elongate, and at apex of maxilla; cardo and stipes faintly sclerotic. Labium strongly projecting, divided into prementum and postmentum, and bearing salivary opening at apex; labial palpi approximately same length as, but somewhat less robust than, maxillary palpi. Hypopharynx large,

bilobed. Salivary opening a wide slit bearing projecting lips.

BODY: Form (fig. 31) moderately elongate; size large in comparison with head. Body annulations as illustrated; dorsolateral part of caudal annulets of most segments produced on each into low transverse tubercle. Integument without setae or spines but with minute spicules in some areas; faint, paired, dorsal sclerites on first thoracic segment and perhaps on second. Spiracular atrium (fig. 34) projecting above body wall, pigmented, with rim; peritreme present; atrial wall with scattered short denticles; primary tracheal opening with distinct collar; subatrium annulate. Tenth abdominal segment moderately short, with anus situated dorsally.

MATERIAL STUDIED: One predefecating mature larva, two postdefecating larvae, Maracas Valley, Trinidad, the West Indies, February 5, 1965, from cells of *Epicharis rustica* (Olivier) (F. D. Bennett and J. G. Rozen); one postdefecating larva, same, except January 19, 1966 (F. D. Bennett); two predefecating mature larvae, same, except April, 1965 (F. D. Bennett); all in the collection of the American Museum of Natural History.

Rhathymus trinitatis Cockerell

Figures 38-44

HEAD (FIGS. 39, 40): As described for *R. bicolor* except for following: each parietal band not subtended by low irregular tubercle; mandibles on all specimens examined appearing more acute apically, but this condition resulting from wearing away of dorsal and ventral edges.

BODY (FIG. 38): As described for *R. bicolor* except for following: size small in comparison with head.

MATERIAL STUDIED: Three postdefecating larvae, Maracas, Trinidad, the West Indies, January 19, 1964 (D. Bharath); nine postdefecating larvae, same, except April 11, 1964, from cells of *Epicharis fasciata* Lepeletier and Serville (F. D. Bennett); all in the collection of the American Museum of Natural History.

ERICROCINI

The following description is based only on the larva of *Acanthopus splendidus urichi*. Insofar as is known, the cast larval skin of *Mesoplia rufipes* agrees with this description.

HEAD: As described for that of Melectini except for following: dorsal surface of labrum, epipharyngeal surface non-spiculate; dorsal surface of maxilla and hypopharynx weakly spiculate; each posterior tentorial pit at juncture of posterior thickening of head capsule and hypostomal ridge; each antennal papilla bearing approximately 10 sensilla; clypeus

protuberant, at least in *Acanthopus*; labrum short, narrow, with paired, low, labral tubercles; anterior margin of labrum curved; labiomaxillary region greatly elongate; maxilla projecting but not enlarged as is that of *Rhathymus*; palpus at tip of maxilla; hypopharynx large, protuberant, bilobed; labium strongly projecting; palpus moderately large; salivary opening a wide slit bearing strongly projecting lips.

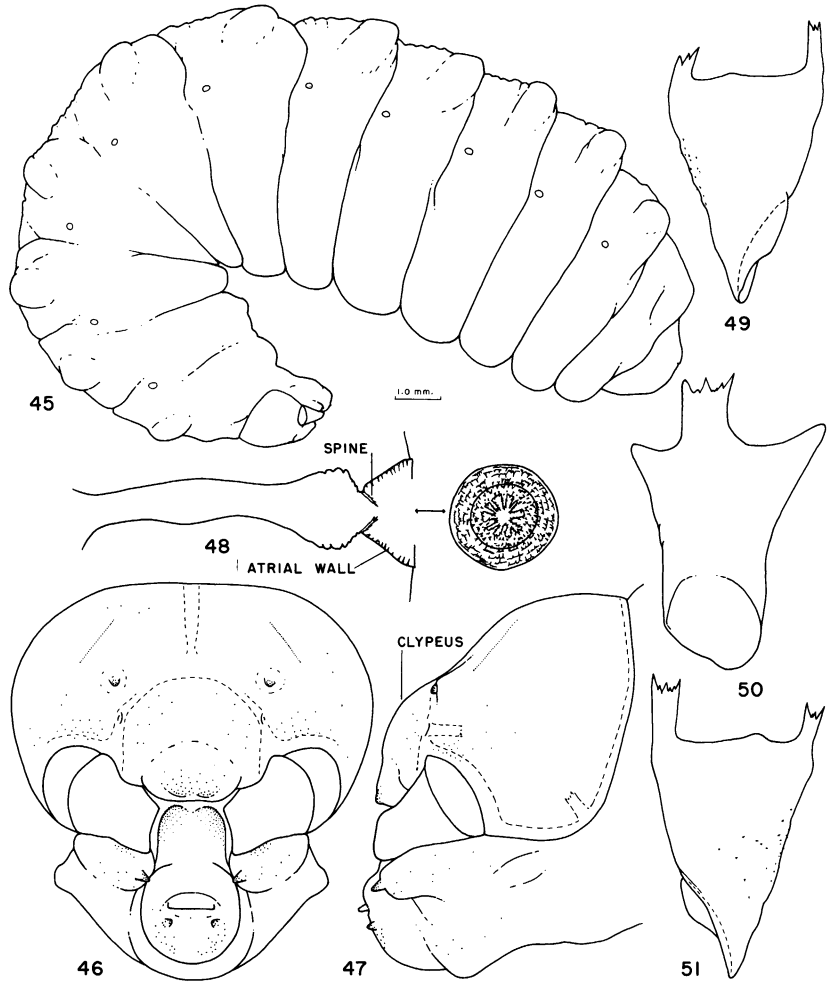
BODY: As described for Melectini except for following: integument with very fine setae; atrial wall with numerous elongate denticles which are not arranged in distinct rows; primary tracheal opening without collar but with toothed spines; subatrium weakly annulate.

ACANTHOPUS KLUG

Acanthopus splendidus urichi Cockerell

Figures 45-51

HEAD (FIGS. 46, 47): Integument with scattered sensilla; dorsal surface of labrum non-spiculate; epipharyngeal surface without spicules; dorsal surface of maxilla with scattered, non-hairlike spicules; hypopharynx with a few non-hairlike, sharp-pointed spicules; antennal papillae, mandibular articulations and apices, pleurostomal ridges, cardines, part of prementum, and various other areas pigmented. Tentorium complete and thick; each posterior tentorial pit at juncture of posterior thickening of head capsule and hypostomal ridge; posterior thickening of head capsule and hypostomal and pleurostomal ridges well developed; epistomal ridge exceedingly broad laterad of (below) anterior tentorial pits (fig. 46); mesiad of pits epistomal ridge evident but becoming weaker toward median line; longitudinal thickening of head capsule evident; parietal bands weakly expressed. Antennal papillae not on prominences; each papilla small, not so high as basal diameter, pointed downward (at least on single specimen available), and each bearing approximately 10 sensilla. Clypeus unlike that of *Rhathymus*, somewhat protuberant. Labrum short and rather narrow; paired labral tubercles represented by low swellings; anterior margin of labrum, at least when seen in view drawn, a continuous curve, not bilobed. Each mandible (figs. 49-51) extremely massive, broadly rounded (although on one cast skin apex more pointed) apically, with pronounced but shallow, inner apical, scoop-shaped concavity; dorsal and ventral edges of concavity without teeth and not produced into extremely thin lamellae as in *Rhathymus*; concavity without spines or pits; mandibles without spicules on dorsal surface, although with scattered sensilla in rather large pits on outer surface. Labiomaxillary region large and produced ventrally but not so



FIGS. 45-51. *Acanthopus splendidus urichi* Cockerell. 45. Live, postdefecating larva, lateral view. 46, 47. Head, frontal and lateral views. 48. Spiracle. 49-51. Right mandible, dorsal, inner, and ventral views. Scale refers to figure 45.

great as in *Rhathymus*. Maxilla (fig. 47) of normal size, smaller than that of *Rhathymus*; apex not produced mesiad; galea not evident; palpus moderately large, elongate, and at apex of maxilla; cardo and stipes distinctly sclerotic. Labium strongly projecting, divided into prementum and postmentum, and bearing salivary opening at apex; labial palpi slightly smaller than maxillary palpi. Hypopharynx large, bilobed. Salivary open-

ing a wide slit bearing projecting lips.

BODY: Form (fig. 45) robust. Body annulations as illustrated but intrasegmental lines obscured; dorsolateral part of caudal annulets of most segments produced on each side into low transverse tubercle. Integument of tubercles and also of anal area beset with very fine setae (too fine to appear in fig. 45) which arise from pigmented alveoli; integument with minute spicules in some areas; anterior tubercles apparently faintly sclerotized. Spiracular atrium (fig. 48) projecting above body wall, pigmented, with rim; peritreme present; atrial wall with numerous elongate denticles which are not arranged in distinct rows; primary tracheal opening without collar but with toothed spines; subatrium weakly annulate. Tenth abdominal segment moderately short, with anus situated dorsally.

MATERIAL STUDIED: One postdefecating mature larva, Curepe, Trinidad, the West Indies, from cell of *Centris derasa* Lepeletier, found in nest of *Microcerotermes arboreus* Emerson (F. D. Bennett and D. Bharath); one larval skin, same data except April, 1964 (F. D. Bennett); one larval skin, same, except January 13 and 16, 1965 (F. D. Bennett); all in the collection of the American Museum of Natural History.

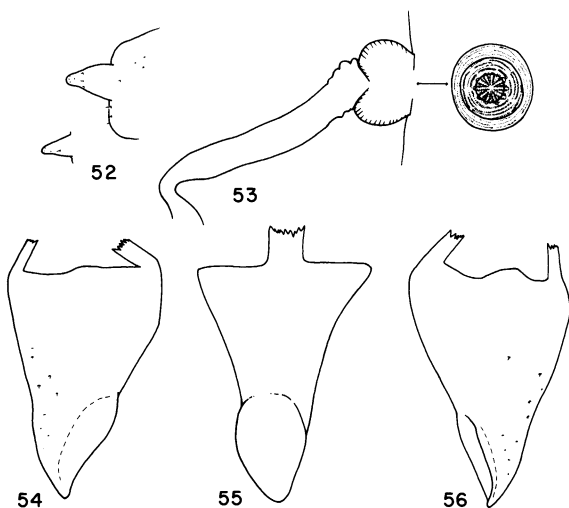
MESOPLIA LEPELETIER

Mesoplia rufipes (Perty)

Figures 52-56

Because the following description is based on cast larval skins, not all the important diagnostic features can be reported, but in most respects the skins seem to agree with the larva of *Acanthopus splendidus urichi*.

HEAD (FIG. 52): Integument with scattered sensilla; dorsal surface of maxilla with scattered, non-hairlike spicules; dorsal surface of labrum without spicules; epipharyngeal surface without spicules, as in *Acanthopus*; hypopharynx with sharp-pointed spicules more numerous than in *Acanthopus*; pigmentation difficult to see on cast skin. Most of tentorium missing on cast skin but trunks of both posterior and anterior arms thick, hence tentorium probably complete; each posterior tentorial pit at junction of posterior thickening of head capsule and hypostomal ridge; posterior thickening of head capsule very weak on cast skin; hypostomal and pleurostomal ridges apparently well developed; condition of epistomal ridge not evident on cast skin; longitudinal thickening of head capsule not evident on cast skin; parietal bands not evident on cast skin. Antennal prominences not evident; antennal papillae moderately small, not so high as basal diameter, and each bearing approximately eight sensilla. Clypeal protuberance cannot be determined from cast skin. Labral length and width unknown; paired low but distinct labral tu-



FIGS. 52-56. Cast larval skin of *Mesoplia rufipes* (Perty). 52. Apex of maxilla (upper) and labial palpus (lower), lateral view. 53. Spiracle. 54-56. Right mandible, dorsal, inner, and ventral views.

bercles present. Each mandible (figs. 54-56) massive, somewhat pointed apically, and with pronounced, inner apical, scoop-shaped concavity; dorsal and ventral edges of concavity without teeth and not produced into extremely thin lamellae; concavity without spines or pits; mandibles without spicules on dorsal surface, although with scattered sensilla arising from large pits on outer surface. Size of labiomaxillary region not evident from cast skin. Maxilla (fig. 52) apparently of normal size for cocoon-spinning larva; apex not produced mesiad; galea not evident; palpus apparently considerably larger than labial palpus and at apex of maxilla; sclerotized condition of cardo and stipes not known. Labium projecting, almost certainly divided into prementum and postmentum, and bearing salivary opening at apex; labial palpi of normal size for cocoon-spinning larva but apparently smaller than maxillary palpi. Hypopharynx large, bilobed. Salivary opening a very wide slit bearing projecting lips.

BODY: Form unknown. Presence of annulations unknown; dorso-lateral tubercles not visible but presumably as in *Acanthopus*. Integument of anal area and presumably of tubercles beset with very fine setae which arise from pigmented alveoli, as in *Acanthopus*; integument with minute spicules over most of surface. Spiracular atrium (fig. 53) projecting above body wall, with rim; peritreme present; atrial wall with numerous elongate denticles arranged in concentric rows; primary tracheal opening

without collar but with toothed spines; subatrium presumably annulate. Length of tenth abdominal segment unknown; position of anus unknown.

MATERIAL STUDIED: One cast larval skin, Curepe, Trinidad, the West Indies, April–May, 1966, from cells of *Centris carrikeri* (F. D. Bennett); one cast larval skin, St. Augustine, Trinidad, the West Indies, April 13, 1966, from cells of *Centris carrikeri* (F. D. Bennett); two cast larval skins, Hollis Reservoir, near Valencia, Trinidad, the West Indies, April, 1968, from cells of *Epicharis albofasciata* Smith (F. D. Bennett); all skins and associated pupae, adults, and cocoons in the collection of the American Museum of Natural History.

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