

American Museum **Novitates**

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2233

SEPTEMBER 10, 1965

The Larvae of the Anthophoridae (Hymenoptera, Apoidea) Part 1. Introduction, Eucerini, and Centridini (Anthophorinae)

BY JEROME G. ROZEN, JR.¹

INTRODUCTION

The present paper is the first of a series on the larvae of the bee family Anthophoridae. The series, though limited to a single family, should be considered as an expanded sequel to Michener's paper (1953) on the anatomy and taxonomy of bee larvae. Although little more than 10 years have elapsed since the publication of his work, the present investigation seems appropriate at this time because the larvae of many taxa have recently become available and shed new light on the phylogeny and higher classification of the family. The main purpose of the series, then, will be to clarify further the higher classification and phylogeny of the Anthophoridae. Sufficient larvae are not as yet on hand to permit an extensive treatment of the evolutionary relationship of the lower categories, though, as nests are studied and their inhabitants preserved, further refinements will become possible.

The Anthophoridae are one of the largest families of bees and have an essentially worldwide distribution. Although considered by Michener (1944) as a subfamily of the Apidae, they have subsequently been ac-

¹Chairman and Associate Curator, Department of Entomology, the American Museum of Natural History.

corded family status by most specialists, including Michener. Hurd and Moure (1963) have recently expanded the concept of the family by adding the Xylocopinae (Ceratinini and Xylocopini). On the basis of a superficial examination of all material on hand, I am tentatively recognizing three subfamilies, namely, Anthophorinae, Nomadinae, and Xylocopinae. However, when this study is completed, this classification may have to be modified. The family consists primarily of solitary bees, although numerous cleptoparasitic forms are also included and a few of the Ceratinini are social.

As with other taxonomic works on bee larvae, the fully fed, last-stage larva, or mature larva, will be treated for the most part. When available, first instars will be described because of their potential usefulness as a taxonomic aid. Typically, bee larvae defecate only after they have consumed the provisions in the cell. As a consequence, the mature larva, after voiding the meconial mass, appears quite different from the more robust form that has not defecated, even though they both represent the same instar. The postdefecating larva of many bees enters a state of diapause during which it may estivate or hibernate or, with spring- or fall-flying univoltine bees, do both. A few bees, for example, *Xylocopa* and *Diadasia*, begin defecating before the feeding has ended, but the terms "predefecating" and "postdefecating" seem necessary and desirable when the larvae of most bees are discussed.

The presentation of the series will be as follows: Each section will provide a taxonomic description of one or more tribes based on the mature larvae. The tribal description will be followed by descriptions of the larvae of the included species, and keys to the larvae within each tribe or subfamily will be presented. The final section will contain such elements as a key to the subfamilies and tribes, diagnoses and comparisons of these taxa, and, most importantly, a review of the classification and phylogeny of the higher categories in light of the information presented in the series.

To the best of my knowledge, there is no entirely satisfactory fixative and preservative for bee larvae. Best results are obtained with Kahle's solution or one of its numerous modifications. However, to avoid post-mortem changes, the larva should be illustrated, if possible, while still alive or, if active, it should be depicted immediately after it has succumbed to the fixative. Both the predefecating larva and the postdefecating larva should be drawn because of differences in the body shape. I (Rozen, 1958) have argued that the postdefecating form seems the better one to illustrate because it has a longer duration in the bee's life cycle and hence it is more likely to be encountered. However, with some bees, for example, the Eucerini, the postdefecating forms shrink badly in

fixative, whereas good preservation is quite possible with the predefecating forms. This fact and because some bees do not undergo diapause during the last larval instar suggest the advisability of treating both forms. In other respects the study techniques are the same as those used by Michener (1953). The general form of Michener's descriptions and presentation of illustrations have been adopted, although they are modified to incorporate new information that now seems important.

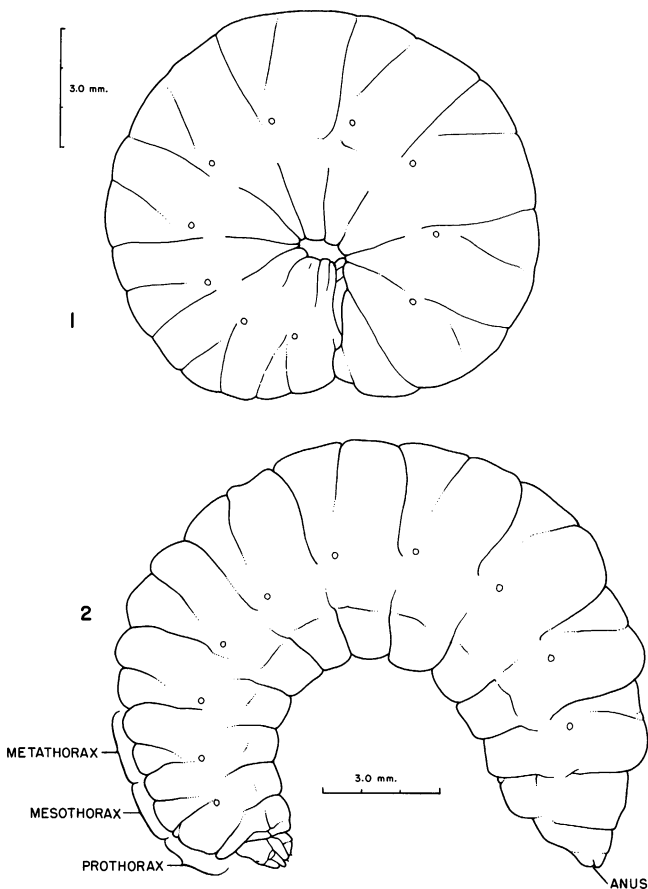
The research resulting in this series has been supported in part by National Science Foundation Grant G-14854. I wish to thank the following people for loans or gifts of specimens used in this part: Dr. George E. Bohart, Entomology Research Division, United States Department of Agriculture, Logan, Utah; Dr. Mont A. Cazier, Arizona State University, Tempe; Dr. Paul D. Hurd, Jr., and Dr. Robbin W. Thorp, University of California, Berkeley; and Dr. Charles D. Michener, University of Kansas, Lawrence. An expression of appreciation is due both to Mrs. Rose Ismay for her careful typing and editing of the manuscript, and to my wife, Barbara L. Rozen, for preparing the illustrations.

EUCERINI

Although this tribe is large and wide-ranging, Michener (1953) had available for study the larvae of only the genus *Melissodes*. Since then, Rozen (1964) described both the first- and last-stage larvae of *Svastra obliqua obliqua* (Say); and Grandi (1961), the last larval instar of *Tetralonia malvae* (Rossi). Two other genera, *Xenoglossa* and *Peponapis*, are treated here, bringing to five the total number of genera of which the larvae are reasonably adequately known. The following characterization is based on the mature larvae of seven species in four genera. Although the larva of *Tetralonia malvae* is excluded, Grandi's description and drawings depicted it as a typical eucerine form, and it probably fits the characterization in most, if not all, respects. Unfortunately these four genera may be closely related (Hurd and Linsley, 1964; Moure and Michener, 1955; Michener, 1944) so that the following characterization may have to be modified after the larvae of other generic groupings are discovered. The fact that these larvae are so similar would seem to contradict Moure and Michener's tentative hypothesis (1955) that *Peponapis*, *Svastra*, and *Melissodes* arose from different groups within the tribe.

DESCRIPTION OF THE EUCERINI BASED ON THE MATURE LARVAE

HEAD: Integument with a few scattered sensilla; dorsal surface of labrum with numerous hairlike spicules; dorsal apex of maxillae and



FIGS. 1, 2. *Xenoglossa angustior* Cockerell. 1. Postdefecating larva, lateral view. 2. Mature, predefecating larva, lateral view.

areas on epipharyngeal surface of labrum also with similar spicules; hypopharynx not spiculate; apices of mandibles darkly pigmented. Tentorium complete and well developed; 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 and usually evident mesiad of pits; longitudinal thickening of head capsule pronounced at least dorsally and often extending to epistomal thickening. Antennal prominences low; each papilla shorter than its basal diameter and bearing several sensilla. Labrum short and

broad; widely spaced paired labral tubercles rather small but evident; labral apex appearing faintly trilobed in anterior view. Mandibles massive though moderately narrow in adoral view; dorsal surface of mandible with numerous hairlike spicules; dorsal inner edge of apical concavity (fig. 6) projecting adorally much farther than ventral inner edge (fig. 8); concavity divided longitudinally by ridge (fig. 7); dorsal plane of concavity usually very narrow and with small denticles; mandibular apex bidentate, with both teeth sharp pointed and with dorsal one larger than ventral one. Each maxilla (fig. 21) as seen in dorsal view with apex subtruncate; inner apical angle spiculate and in some species (e.g., *Svastra obliqua obliqua*) produced adorally; galea¹ (fig. 21) evident but considerably less than length of palpus; palpus elongate; cardo and stipes somewhat sclerotic. Hypopharynx non-protuberant. Labium strongly projecting, divided into prementum and postmentum, and bearing transverse, slitlike opening of salivary gland at apex; opening wide and bearing projecting lips which are not armed with large teeth as indicated by Michener (1953); labial palpi nearly as large as those of maxillae.

BODY: Form moderately robust; most segments divided dorsally into cephalic and caudal annulations; low transverse dorsal tubercles occasionally present on caudal annulations of thoracic segments (*Melissodes*). Integument without spicules and setae but in some species with faint, paired, unpigmented or slightly pigmented, dorsal sclerites on caudal annulations of thoracic segments. Spiracular atrium and usually subatrium with large to small denticles; atrium projecting slightly to not at all above body wall; peritreme large; primary tracheal opening without collar or with, at most, indistinct one; subatrium (fig. 5) divided into outer wide section (outer subatrium) and inner narrow section (inner subatrium). Tenth abdominal segment small, apically pointed and bearing anus somewhat dorsally in at least predefecating forms of *Xenoglossa angustior* and *strenua*, *Peponapis fervens*, and *Svastra obliqua obliqua*; in *Melissodes* sp.? (fig. 33) and *robustior* (fig. 34) tenth segment somewhat modified.

The known larvae of the Eucerini seem to be remarkably similar, although so many genera are still not represented that the homogeneity may not be characteristic of the tribe. The most obvious differences between the taxa relate to various structures of the mandible and the shape of the last two abdominal segments. There is also some variation in the degree of denticulation of the atrium and subatrium, a character difficult

¹ Grandi (1961) does not believe this structure to be the galea in *Tetralonia malvae*.

to use for diagnostic purposes. The following key to mature larvae should be considered tentative.

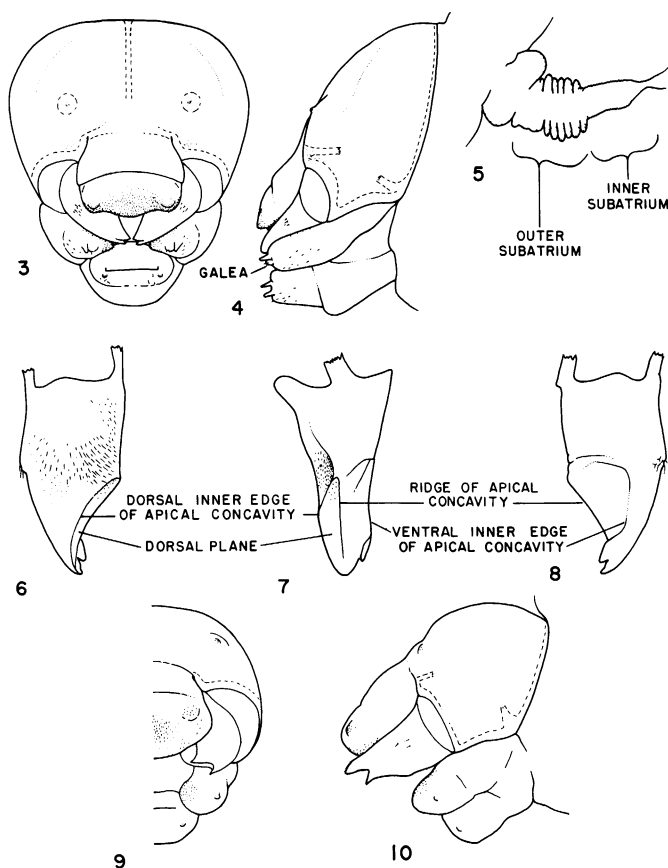
KEY TO THE MATURE LARVAE OF THE EUCERINI

1. Mandible in ventral view (fig. 32) with hairlike spicules visible along inner edge 2
 Mandible in ventral view (figs. 8, 27) with hairlike spicules not visible along inner edge 3
2. Mandible (figs. 30-32) with dorsal inner edge of apical concavity extending farther adorally than ridge of concavity, so that most of ridge cannot be seen in dorsal view (fig. 30); tenth abdominal segment (figs. 33, 34) more rounded, with anus more or less apical
 Melissodes pallidesignata Cockerell; *Melissodes* sp.?; *Melissodes robustior* Cockerell
 Mandible with ridge of apical concavity extending farther adorally than dorsal inner edge, so that ridge can be seen in dorsal view (Rozen, 1964, fig. 9); tenth abdominal segment (*ibid.*, fig. 7) of predefecating larvae more pointed, with anus dorsal *Svastra obliqua obliqua* (Say)
3. Mandible (fig. 7) with dorsal plane of apical concavity wider
 *Xenoglossa angustior* Cockerell
 Mandible (figs. 14, 19, 26) with dorsal plane of apical concavity narrower
 Xenoglossa fulva Smith; *Xenoglossa strenua* (Cresson); *Peponapis fervens* (Smith)

MATURE LARVA OF *Xenoglossa angustior* COCKERELL

Figures 1-8

HEAD: (FIGS. 3, 4): Integument with a few scattered setae; apex of maxilla and much of dorsal and epipharyngeal surfaces of labrum with numerous hairlike spicules; hypostomal ridges and mandibular articulations faintly pigmented; apices of mandibles darkly pigmented. Tentorium complete and thick; 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 clearly evident only near pits; longitudinal thickening of head capsule pronounced but becoming weaker anteriorly where it seems to join epistomal ridge; parietal bands very weak. Each antennal prominence low; papilla somewhat shorter than basal diameter, and bearing several sensilla. Labral tubercles moderately small and arising from lateral angles of short, broad labrum; apical margin of labrum trilobed in anterior view. Each mandible (figs. 6-8), seen from above or below, with large quadrate base and triangular apical section; oblique declivity forming basal boundary of apical concavity not so well defined as in *Melissodes* or *Svastra obliqua obliqua*; as seen in adoral view (fig. 7), concavity with ridge extending from base nearly to apex; surface of concavity dorsal to ridge (dorsal plane of apical concavity) with scattered denticles basally; this surface homologous to curved plane on upper



FIGS. 3-10. *Xenoglossa angustior* Cockerell. 3. Head capsule of mature larva, frontal view. 4. Same, lateral view. 5. Spiracle of same. 6-8. Right mandible of same, dorsal inner, and ventral views. 9. Head capsule of first-stage larva, frontal view. 10. Same, lateral view.

apical margin of *Svastra obliqua obliqua* (Rozen, 1964) as evidenced by mandibles of other eucerine larvae described here; dorsal surface of mandible with numerous hairlike spicules similar to, but more widely distributed than, those of *Melissodes* sp.? and *Svastra obliqua obliqua*; mandibular apex conspicuously bidentate. Maxillae with apices subtruncate and produced adorally but not so much so as in *Svastra obliqua obliqua*; galea present mesiad of palpus; palpi elongate; cardo and stipes somewhat sclerotic. Labium strongly projecting, divided into prementum and postmentum, and bearing salivary opening at apex; salivary opening a

wide slit, bearing projecting lips; labial palpi almost as long as maxillary palpi.

BODY: Form (figs. 1, 2) moderately robust as in *Svastra obliqua obliqua* and *Melissodes* sp.?; in all postdefecating larvae found in cocoon, body (fig. 2) looped so that head pressed into, and therefore obscured by, terminal abdominal segments. Integument of quiescent, postdefecating form soft and pliable. Body annulations as illustrated, and similar to those of other eucerines. Integument without spicules, apparently without setae, and apparently without distinct dorsal sclerites on thorax. Spiracular atrium and subatrium (fig. 5) with small denticles which become larger and more sharp pointed near inner subatrium; atrium projecting at most indistinctly above body wall and without rim; peritreme large; primary tracheal opening without collar; outer subatrium short as in other eucerine larvae; inner subatrium dense and not understood anatomically though filled with numerous sharp-pointed denticles (not illustrated). Tenth abdominal segment small, apically pointed, and with anus situated dorsally, all as in *Svastra obliqua obliqua*.

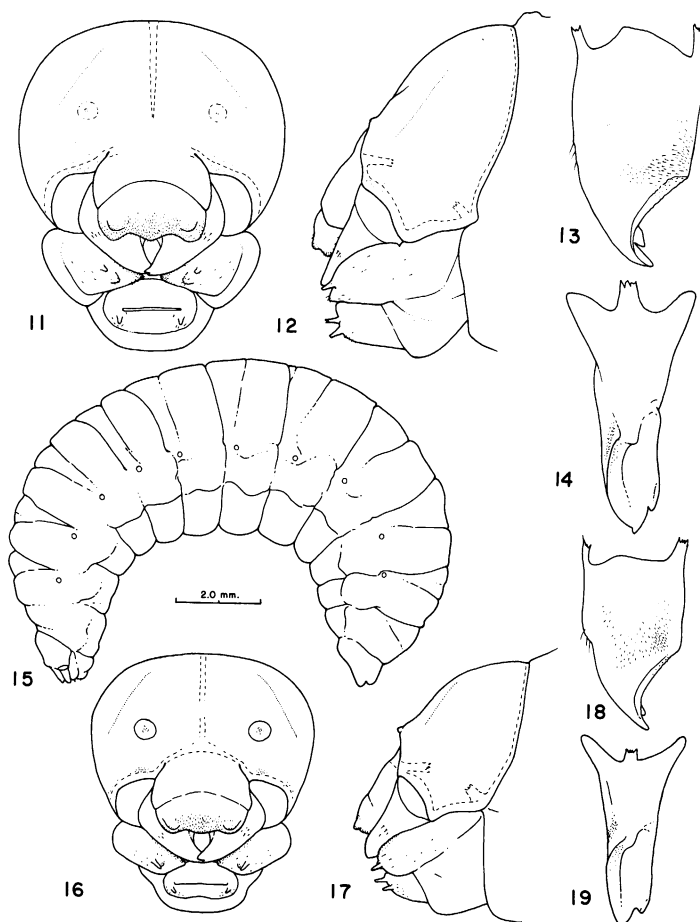
MATERIAL STUDIED: Numerous predefecating and four postdefecating mature larvae, Portal, Cochise County, Arizona, September 6 and 7, 1963 (M. A. Cazier and M. Mortenson), in the collection of the American Museum of Natural History.

FIRST-STAGE LARVA OF *Xenoglossa angustior* COCKERELL

Figures 9, 10

The following description is comparative with those of *Svastra obliqua obliqua* (Say) (Rozen, 1964) and *Exomalopsis chionura* Cockerell (Rozen, 1957). The marked similarities between the first instar of this species and that of *S. obliqua obliqua* are obvious from the following.

HEAD (FIGS. 9, 10): Capsule and mouth parts with few widely scattered sensilla; tentorium complete (though dorsal arm may be absent) and moderately weak. Posterior thickening of head capsule weak; hypostomal thickening moderately well developed and somewhat pigmented; pleurostomal thickening somewhat pigmented but rather obscure except near mandibular articulations; epistomal thickening moderately well developed laterally but absent between anterior tentorial pits; longitudinal median thickening of head capsule scarcely evident even dorsally. Parietal bands apparently absent. Antennae very low and bearing several sensilla. Labrum but not clypeus large and protuberant; moderately small labral tubercles present; labrum bearing elongate, fine spicules apically, laterally, and on epipharyngeal surface.



FIGS. 11–14. Mature larva of *Xenoglossa fulva* Smith. 11. Head capsule, frontal view. 12. Same, lateral view. 13, 14. Right mandible, dorsal and inner views.

FIGS. 15–19. Mature larva of *Xenoglossa strenua* (Cresson). 15. Predefecating larva, lateral view. 16. Head capsule, frontal view. 17. Same, lateral view. 18, 19. Right mandible, dorsal and inner views. Scale refers to figure 15.

Mandibular corium non-spiculate; mandibles stout, sharp pointed apically, with upper and lower apical edges sharply serrate; lower edge bearing very large (larger than that of *S. obliqua obliqua*) tooth subapically, so that mandibles appear apically bidentate; mandibles, with exception of linear series of sharp-pointed spicules on dorsal and ventral apical edges, without denticles or spicules. Maxillae with apices bearing long, fine spicules; apices not bent mesiad but palpi subapical in position.

Labium not protuberant and with palpi somewhat smaller than those of maxillae; salivary opening an elongate transverse slit without lips.

BODY: Form elongate cylindrical as illustrated for *S. obliqua obliqua* (Rozen, 1964, fig. 8). Integument non-setose but bearing patches of minute spicules; anal area without spines. Spiracles of equal size.

MATERIAL STUDIED: Two first-stage larvae, Portal, Cochise County, Arizona, September 6, 7, 1963 (M. A. Cazier, E. G. Linsley, M. Mortenson), in the collection of the American Museum of Natural History.

MATURE LARVA OF *Xenoglossa fulva* SMITH

Figures 11-14

As can be seen from the following description, the mature larva of this species, the type of the genus, is very similar to that of *X. angustior*.

HEAD (FIGS. 11, 12): Like that of *X. angustior* except mandible, as seen in dorsal view (fig. 13), somewhat more robust; with apical concavity more concave, and with dorsal plane of apical concavity narrower in adoral view (fig. 14), galea-like protuberance on maxilla more pronounced, and salivary lips broader.

BODY: Form (known only from single, imperfect, postdefecating specimen) apparently as in *X. angustior*, and with head apparently pressed into terminal abdominal segment; body annulations and integument as in *X. angustior*. Spiracles as in *X. angustior* except denticles perhaps slightly more pronounced. Tenth abdominal segment small and with anus dorsally situated.

MATERIAL STUDIED: One postdefecating larva, 11 miles southwest of Acambaro, Guanajuato, Mexico, August 18, 1954 (E. G. Linsley, J. W. MacSwain, and Ray F. Smith), in the collection of the California Insect Survey, Berkeley. Dr. Charles D. Michener identified the adults for a paper (Linsley, MacSwain, and Smith, 1955) treating the biology of the species.

MATURE LARVA OF *Xenoglossa strenua* (CRESSON)

Figures 15-19

Although Bohart (1964) recently illustrated and briefly described the larva of this species, it is treated here for comparison with other species of the genus. The material examined is the same as that used by Bohart.

HEAD (FIGS. 16, 17): Like that of *X. angustior* except for following: Epistomal ridge more strongly developed between anterior tentorial pits. Antennal papilla, like that of *X. angustior*, somewhat shorter than basal

diameter and not elongate as depicted by Bohart (1964). Mandible (figs. 18, 19) as described for *X. fulva*.

BODY: Both predefecating (fig. 19) and postdefecating forms as described for *X. angustior*. Spiracles as in *X. angustior* except denticles of atrium and subatrium less pronounced.

MATERIAL STUDIED: One postdefecating larva and three predefecating larvae, Beltsville, Maryland, August, 1957 (G. E. Bohart), in the collection of G. E. Bohart. Bohart (1964) described the biology of this species.

MATURE LARVA OF *Peponapis fervens* (SMITH)

Figures 20–27

HEAD (FIGS. 22, 23): As described for *Xenoglossa angustior* except for following: Epistomal ridge between anterior tentorial pits somewhat better developed. Mandible (figs. 25–27) similar to those of *X. fulva*. Inner apical angle of maxilla scarcely produced.

BODY: Form of predefecating larva (fig. 20) like that of *X. angustior*. Body without setae but with paired, very faint sclerites dorsally on caudal annulations of thoracic segments. Spiracles (fig. 24) similar to those of *X. angustior* except denticles of uniform size, atrium not projecting above body wall, primary tracheal opening with moderately distinct collar, and denticles (not illustrated) of inner subatrium not so dense.

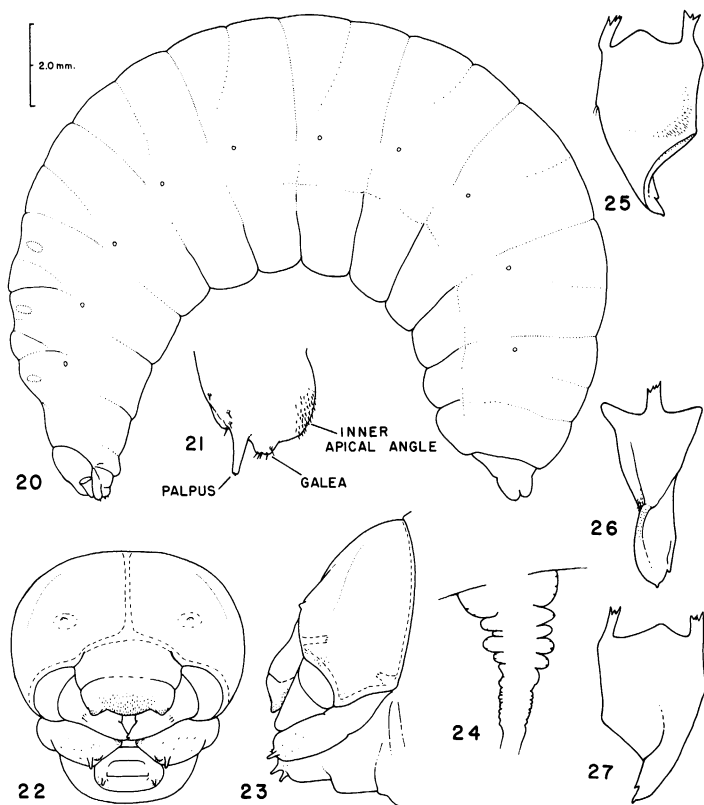
MATERIAL STUDIED: Two predefecating larvae, Curitiba, Paraná, Brazil, February 16–21, 1956 (C. D. Michener and R. B. Lange), in the collection of the University of Kansas. The nesting site from which these larvae were taken was described, with notes on the biology of the species, by Michener and Lange (1958).

MATURE LARVA OF *Melissodes* (*Eumelissodes*) *pallidesignata* COCKERELL

Figures 28–32

HEAD (FIGS. 28, 29): As described for *Xenoglossa angustior* except for following: Epistomal ridge evident mesiad of anterior tentorial pits. Mandible (figs. 30–32) with dorsal inner edge of apical concavity extending farther adorally than ridge of concavity, so that ridge not visible in dorsal view; spiculations of dorsal surface as in *Melissodes* sp.? (Contrary to Michener's drawing, 1953, fig. 202, the mandible of *Melissodes* sp.? possesses a distinct ridge in the apical concavity; the mandibles of the three *Melissodes* treated here are essentially identical.)

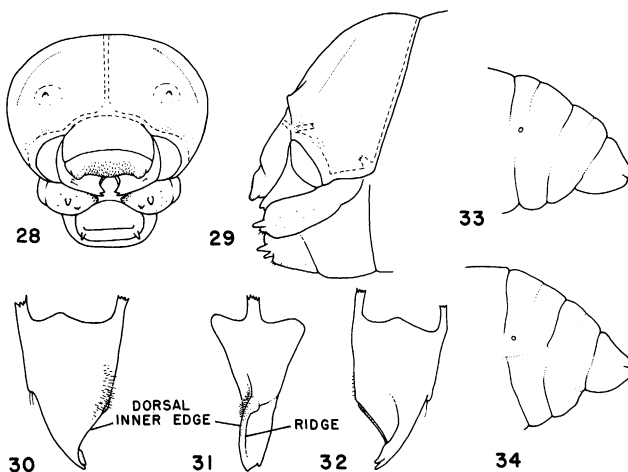
BODY: The specimens used in this study were poorly preserved but



FIGS. 20-27. Mature larva of *Peponapis fervens* (Smith). 20. Predefecating larva, lateral view. 21. Apex of right maxilla, dorsal view. 22. Head, frontal view. 23. Same, lateral view. 24. Spiracle. 25-27. Right mandible, dorsal, inner, and ventral views. Scale refers to figure 20.

seemed to resemble other eucerines in most respects; unfortunately the tip of the abdomen could not be contrasted with that of the other two *Melissodes* because it was misshapen. Caudal annulations of thoracic segments with paired low transverse dorsal tubercles which are somewhat sclerotized; tubercles similar to those of *Melissodes robustior* and sp.? (Michener, 1953, fig. 199). Spiracles as described for *Xenoglossa angustior* except atrium with larger and more numerous denticles, as in *Melissodes* sp.? (*ibid.*, fig. 205), and outer subatrium with very small denticles.

MATERIAL STUDIED: Two mature larvae, Rockaway Beach, near Pacifica, San Mateo County, California, July 11, 1963 (R. W. Thorp), in the collection of R. W. Thorp.



FIGS. 28-32. Mature larva of *Melissodes pallidesignata* Cockerell. 28. Head, frontal view. 29. Same, lateral view. 30-32. Right mandible, dorsal, inner, and ventral views.

FIG. 33. *Melissodes* sp.?, apex of abdomen of mature larva, lateral view.

FIG. 34. *Melissodes robustior* Cockerell, same.

MATURE LARVA OF *Melissodes* (*Eumelissodes*) *robustior* COCKERELL

Figure 34

HEAD: As described and illustrated for *Melissodes pallidesignata*.

BODY: Poorly preserved but apparently similar to that of *Xenoglossa angustior* except caudal annulations of thoracic segments with paired low transverse dorsal sclerites which are somewhat sclerotized; tubercles similar to those of *Melissodes pallidesignata* and *Melissodes* sp.? (Michener, 1953, fig. 199.) Spiracles as in *M. pallidesignata* and *Melissodes* sp.? except outer subatrium apparently without denticles. Ninth abdominal segment (fig. 34) short ventrally; tenth abdominal segment (fig. 34) narrow in basal diameter but rather long and rounded, and bearing anus almost apically, as in *Melissodes* sp.? (fig. 33).

MATERIAL STUDIED: Eight postdefecating larvae, Marsh Creek Canyon, Contra Costa County, California, November 4, 1954 (J. W. MacSwain and P. D. Hurd, Jr.), in the collection of the California Insect Survey, Berkeley.

CENTRIDINI

Although Claude-Joseph (1926) described and illustrated the larva

of *Centris* (*Wagenknechtia*) *cineraria* (Smith), there have been no satisfactory descriptions of the immature stages of any member of this subfamily. Primarily confined to the Neotropical Region, the Centridini are composed of two genera, *Epicharis* and *Centris*; representatives of both are treated below.

DESCRIPTION OF THE CENTRIDINI BASED
ON THE MATURE LARVAE

HEAD: Integument with scattered sensilla; dorsal surface of labrum without spicules though with sensilla; dorsal surface of maxillae and areas on epipharyngeal surface of labrum with non-hairlike spicules except for the epipharyngeal surface of *Epicharis* which has some hairlike spicules apically; hypopharynx spiculate (*Epicharis*) or smooth (*Centris*); apices of mandibles darkly pigmented. Tentorium complete and well developed; 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 of anterior tentorial pits and also usually mesiad of pits; longitudinal thickening of head capsule well developed dorsally. Antennal prominences absent or extremely low; papillae at most as high as basal diameter and bearing several sensilla. Labrum of moderate width and length; labral tubercles absent; labral apex bilobed. Mandibles massive; dorsal surface either without spicules or with non-hairlike spicules; dorsal inner edge of apical concavity usually with a number of teeth; this edge projecting adorally slightly more than ventral inner edge; apical concavity scooplike and not divided longitudinally by ridge; concavity smooth (*Centris*) or with pits and small spines (*Epicharis*); mandibular apex broadly rounded and with rounded ventral tooth. Each maxilla (fig. 39), as seen in dorsal view, with apex truncate (*Centris*) to moderately rounded (*Epicharis fasciata*); inner apical angle spiculate and not or only slightly produced mesiad; galea pronounced though shorter than palpus (*Centris*) to scarcely noticeable (*Epicharis*); maxillary palpus elongate (*Centris*) to very short (*Epicharis*); cardo and stipes somewhat sclerotic. Hypopharynx protuberant (*Epicharis*) or non-protuberant (*Centris*). Labium strongly projecting (*Centris*) or recessed (*Epicharis*), divided into prementum and postmentum, and bearing transverse, slitlike opening to salivary gland at apex; opening moderate in width (*Centris*) to narrow (*Epicharis*) and with lips large (*Centris*) or reduced (*Epicharis*); lips not armed with teeth; labial palpus elongate (*Centris*) or short (*Epicharis*).

BODY: Form moderately elongate to robust; most segments divided

dorsally into cephalic and caudal annulations; low transverse dorsal tubercles more or less evident on caudal annulations of thoracic and first abdominal segments of some *Centris* but not of *Epicharis*. Integument without spicules but in *Epicharis* with row of spines on some body segments; integument usually with very fine, widely scattered setae; paired faint dorsal sclerites present (*Centris*) or absent (*Epicharis*) on caudal annulations of some anterior segments. Spiracular atrium with ridges, denticles, or spines; atrium projecting slightly or not at all above body wall; peritreme present; primary tracheal opening with or without collar; subatrium long or short, thin walled, appearing much like trachea, and not divided into outer and inner parts. Tenth abdominal segment very short, not pointed apically, and bearing anus dorsally.

There are numerous similarities between *Centris* and *Bombus*, as is apparent when this description is compared with that of *Bombus* (Michener, 1953). The significance of these shared characters and of those held in common by the Apidae and the Centridini in general is difficult to understand at this time. This matter can perhaps be discussed in the final paper of the series.

It is obvious from the above description that the larvae of *Epicharis* and *Centris* are dissimilar, a fact suggesting that they have not recently evolved from a common ancestor. However, certain specialized characteristics such as the bilobed labrum, absence of labral tubercles, and the scoop-shaped mandible indicate that the Centridini are monophyletic. Some, though not all, of the differences between the larvae of these two genera relate to the fact that *Centris* spins a cocoon, whereas *Epicharis* does not. The short palpi, receding labiomaxillary region, reduced salivary lips, and minute galeae all reflect the fact that *Epicharis* does not produce a cocoon.

KEY TO THE MATURE LARVAE OF THE CENTRIDINI

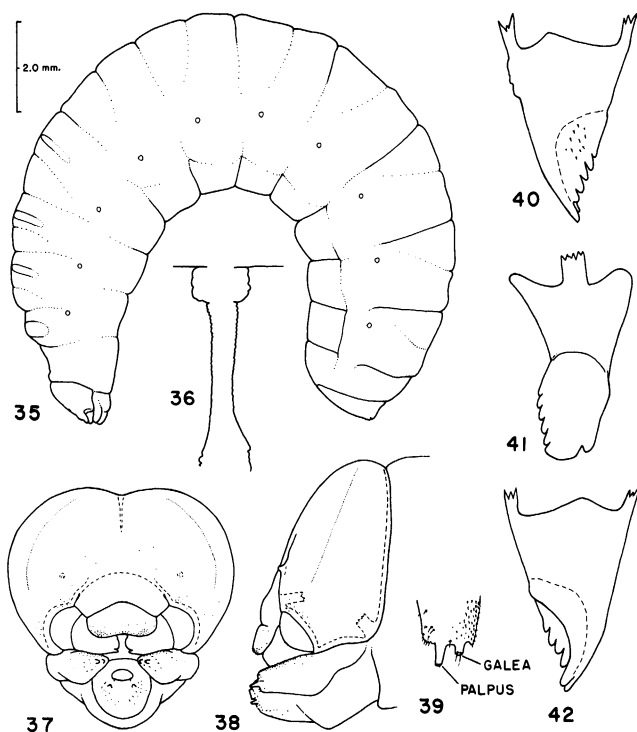
- 1. Labiomaxillary region (fig. 64) recessed; palpi (fig. 64) very short; abdominal segments II through VII or VIII (figs. 60, 61) each with row of darkly pigmented spines on dorsum. *Epicharis*, 2
- Labiomaxillary region (figs. 38, 46) protruding; apical concavity of mandible (figs. 41, 50) smooth; palpi (figs. 38, 46) elongate: abdomen (figs. 35, 54) without spines. *Centris*, 3
- 2. Scoop-shaped concavity of mandible (fig. 67) with numerous teeth and pits but without distinct transverse dentate ridge; abdominal segments (fig. 60) with spines longer; abdominal segment VIII without spines *Epicharis fasciata* Lepeletier and Serville
- Scoop-shaped concavity of mandible (fig. 70) with only a few teeth apicad of transverse dentate ridge; abdominal segment (fig. 69) with spines shorter; abdominal segment VIII with spines *Epicharis rustica* (Olivier)

3. Mandible (fig. 58) with outer surface having conspicuous longitudinal ridges
 *Centris rufosuffusa* Cockerell
- Mandible (figs. 40, 48) with outer surface smooth or nearly so 4
4. Dorsal labial sensilla (figs. 37, 45) tending to be restricted to apex of labium;
 primary tracheal opening (figs. 36, 44) without distinct collar 5
- Labial sensilla (fig. 51) occurring over much of dorsal surface; primary tracheal
 opening (fig. 53) with distinct collar *Centris derasa* Lepeletier
5. Teeth along dorsal inner edge of mandible (figs. 41, 42) larger; subatrium (fig.
 36) elongate *Centris lanipes* (Fabricius)
- Teeth along dorsal inner edge of mandible smaller (figs. 47, 48); subatrium (fig.
 44) short *Centris aenea* Lepeletier

MATURE LARVA OF *Centris* (*Hemisiella*)
lanipes (FABRICIUS)

Figures 35–42

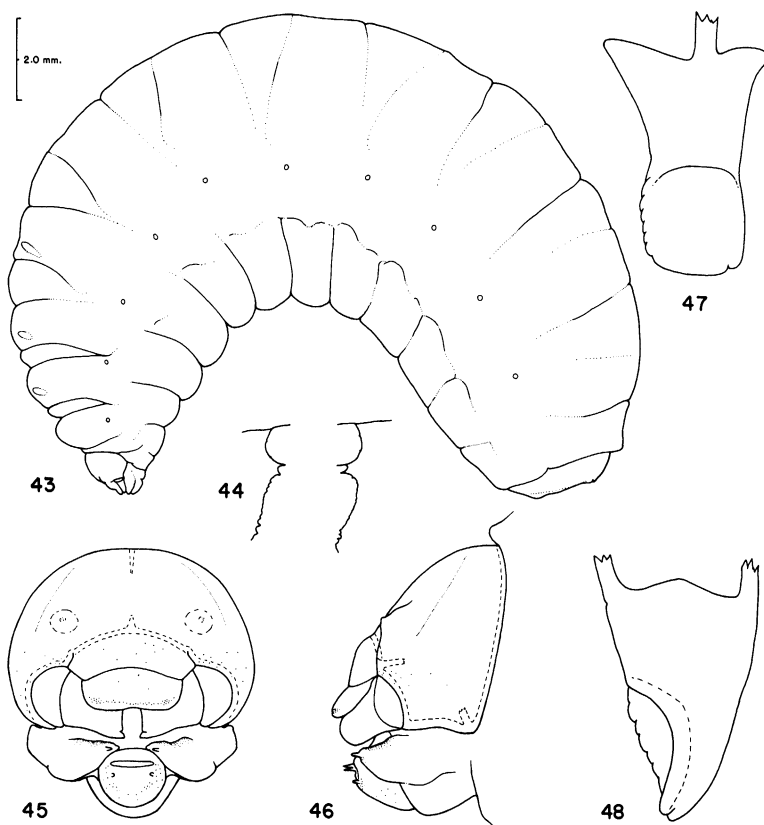
HEAD (FIGS. 37, 38): Integument with a few scattered setae; dorsal surface of maxilla with large, non-hairlike spicules; dorsal surface of labium without spicules; epipharyngeal surface with moderately thin, sharp-pointed spicules which also are not hairlike; hypopharynx without spicules; mandibular articulations and apices of mandibles pigmented. Tentorium complete and thick; posterior thickening of head capsule and hypostomal and pleurostomal ridges well developed; epistomal ridge and sulcus well developed laterad of anterior tentorial pits but absent mesiad of them except for faint cuticular thickening; longitudinal thickening of head capsule pronounced only dorsally; parietal band moderately expressed. Antennal papillae not on prominences; each papilla small, about as high as basal diameter, and bearing three or four sensilla. Labral tubercles absent; anterior margin of labrum bilobed in anterior view. Each mandible (figs. 40–42) massive, broadly rounded apically (on one specimen rounded apex with several very small, sharp-pointed, secondary teeth), with pronounced inner apical, scoop-shaped concavity; dorsal edge of concavity with approximately five rounded teeth and ventral edge with single rounded tooth subapical in position; concavity without spines or pits; mandibles with fine spicules on dorsal surface. Maxillae (fig. 39) with apices not produced mesiad; galea distinct; palpus elongate; cardo faintly sclerotic; stipes (labiomaxillary rod of Michener, 1953) somewhat more pronounced than cardo. Labium strongly projecting, divided into prementum and postmentum, and bearing salivary opening at apex; salivary opening in most specimens examined extruding dark-colored substance in form of thick thread (which dissolved in solution of potassium hydroxide); consequently salivary opening oval in outline and with projecting lips also oval; in one specimen



FIGS. 35-42. Mature larva of *Centris lanipes* (Fabricius). 35. Predefecating larva, lateral view. 36. Spiracle. 37. Head, frontal view. 38. Same, lateral view. 39. Apex of right maxilla, dorsal view. 40-42. Right mandible, dorsal, inner, and ventral views. Scale refers to figure 35.

which apparently had not finished eating, the salivary opening is a short slit with strongly projecting lips that are similar to those of the Eucerini; salivary duct on mature specimens extremely thick and branching in postmentum (the fact that the salivary opening is extruding while the digestive tract contains pollen indicates that the species spins its cocoon either before defecating or while defecating); labial palpi almost as long as maxillary palpi.

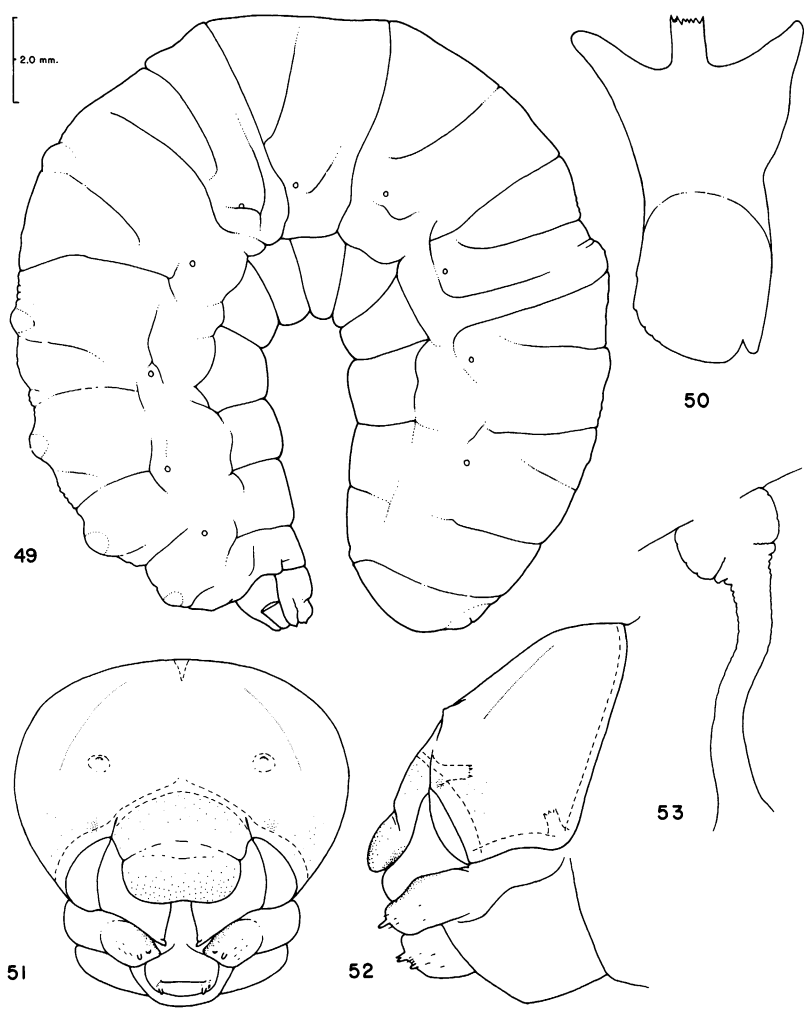
BODY: Form (fig. 35) moderately elongate. Body annulations as illustrated. Integument without spicules but with extremely fine, short setae (too small to illustrate in fig. 35) dorsally, particularly toward tip of abdomen and around anus; faint paired dorsal sclerites on each thoracic segment and on first abdominal segment. Spiracular atrium (fig. 36) with ridges; atrium not projecting above body wall and therefore not



FIGS. 43-48. Mature larva of *Centris aenea* Lepeletier. 43. Predefecating larva, lateral view. 44. Spiracle. 45. Head, frontal view. 46. Same, lateral view. 47, 48. Right mandible, inner and ventral views. Scale refers to figure 43.

provided with rim; peritreme present; primary tracheal opening without distinct collar; subatrium broad, poorly differentiated from trachea and not divided into outer and inner sections. Tenth abdominal segment short, with anus situated dorsally.

MATERIAL STUDIED: Five predefecating mature larvae, Caiobá, Paraná, Brazil, recovered from cells December 5, 1955 (J. S. Moure), in the collection of the University of Kansas. Michener and Lange (1958) discussed the nests from which these specimens were collected.

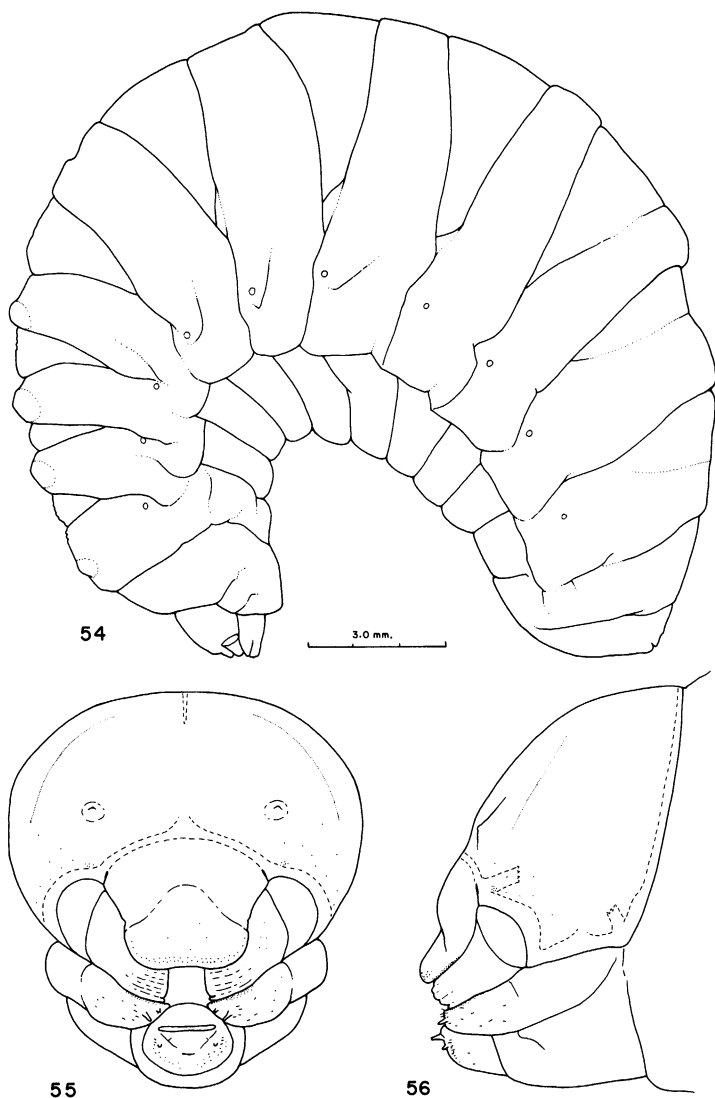


FIGS. 49-53. Mature larva of *Centris derasa* Lepeletier. 49. Predefecating larva, lateral view. 50. Right mandible, inner view. 51. Head, frontal view. 52. Head, lateral view. 53. Spiracle. Scale refers to figure 49.

MATURE LARVA OF *Centris* (*Centris*) *aenea* LEPELETIER

Figures 43-48

HEAD (FIGS. 45, 46): As described for *C. lanipes* except for following: Epistomal ridge well developed mesiad of anterior tentorial pits. Anten-

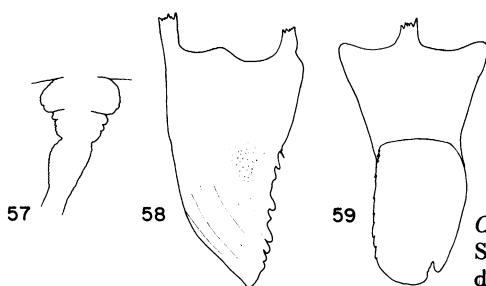


FIGS. 54-56. Mature larva of *Centris rufosuffusa* Cockerell. 54. Predefecating larva, lateral view. 55. Head, frontal view. 56. Head, lateral view. Scale refers to figure 54.

nal papillae on low prominences. Each mandible (figs. 47, 48) more truncate apically and teeth on dorsal inner edge less pronounced than in *C. lanipes* and apparently without spicules on dorsal surface. Maxillae with apices produced slightly mesiad; cardo and stipes moderately

sclerotic. Salivary opening slitlike and with lips projecting and wider than in *C. lanipes* (although these lips were projecting before the specimen was cleared in hot potassium hydroxide, they were not evident after treatment presumably because the prementum expanded; this fact suggests that lips may be retractile on live individuals); labial palpi more widely separated than in *C. lanipes*.

BODY: As in *C. lanipes* except for following: Form (fig. 43) robust. Integument without setae and with paired dorsal sclerites apparently on second and third thoracic segments and first abdominal segment. Spiracle (fig. 44) similar to that of *C. lanipes* except atrium shallower and with



FIGS. 57-59. Mature larva of *Centris rufosuffusa* Cockerell. 57. Spiracle. 58, 59. Right mandible, dorsal and inner views.

ridges of definite dotlike denticles and subatrium shorter and expanded (though this may be an artifact).

MATERIAL STUDIED: One predefecating larva, Porto Atlantida, Mato Grosso, Brazil, July, 1954 (W. E. Kerr), in the collection of the University of Kansas. Michener and Lange (1958) briefly described the nesting site from which this larva was taken.

MATURE LARVA OF *Centris* (*Ptilotopus*) *derasa* LEPELETIER

Figures 49-53

HEAD (FIGS. 51, 52): As described for *C. lanipes* except for following: Dorsal surface of maxilla with spicules smaller and more widely distributed than in *C. lanipes*; labrum pigmented. Epistomal ridge well developed mesiad of anterior tentorial pits. Mandible (fig. 50) as described for *C. aenea* except teeth on dorsal inner edge of apical concavity somewhat less pronounced. Maxillae with apices produced slightly mesiad. Salivary opening a slit with projecting lips.

BODY: As in *C. lanipes* except for following: Form (fig. 49) robust, similar to that of *C. aenea*. Spiracular atrium perhaps projecting slightly above body wall; primary tracheal opening with collar (fig. 53).

MATERIAL STUDIED: Two predefecating larvae, Curepe, Trinidad, the West Indies, March, 1964, from nest of *Microceratermes arboreus* Emerson (F. D. Bennett), in the collection of the American Museum of Natural History. Vesey-FitzGerald (1939) and Bennett (1964) briefly described the nesting activity of this form.

MATURE LARVA OF *Centris* (*Melanocentris*) *rufosuffusa* COCKERELL

Figures 54–59

HEAD (FIGS. 55, 56): As described for *C. lanipes* except for following: Dorsal surface of maxilla with fine spicules; epistomal ridge well developed mesiad of anterior tentorial pits. Outer surface of mandible (figs. 58, 59) with longitudinal ridges.

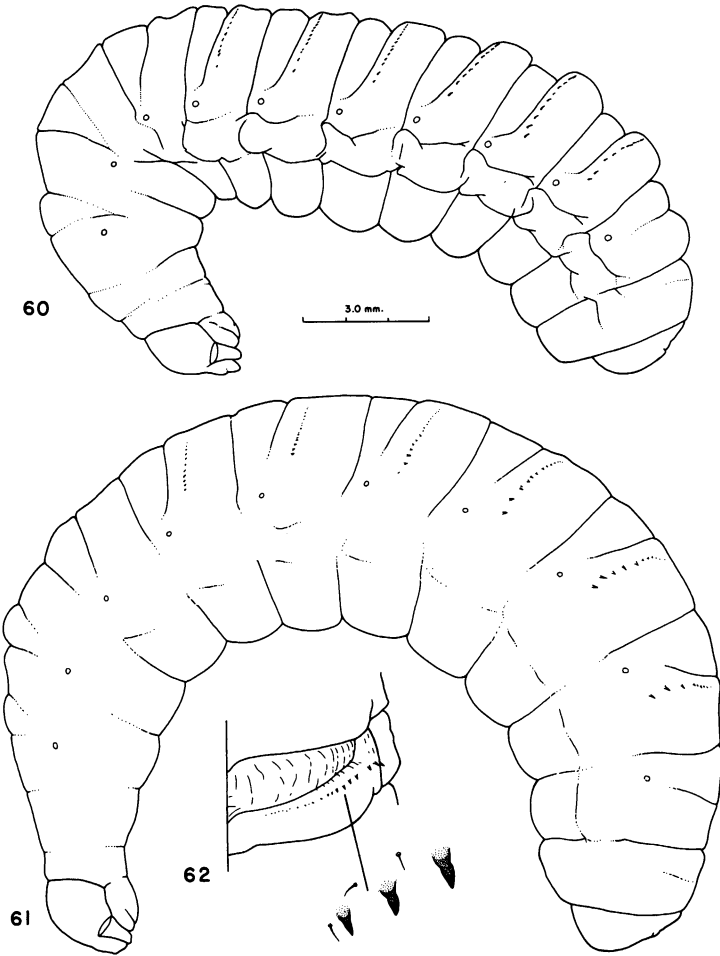
BODY: As in *C. lanipes* except for following: Form (fig. 54) robust. Spiracles (fig. 57) with primary tracheal opening having nearly flat collar.

MATERIAL STUDIED: Four postdefecating larvae, Nariva Swamp, Mayaro, Trinidad, the West Indies, April 8, 1964 (F. D. Bennett); four postdefecating and two predefecating larvae, same locality, February, 1964 (F. D. Bennett); both lots in the collection of the American Museum of Natural History. Information concerning the nesting of this species was given by Vesey-FitzGerald (1939).

MATURE LARVA OF *Epicharis* (*Hoplepicharis*) *fasciata*
LEPELETIER AND SERVILLE

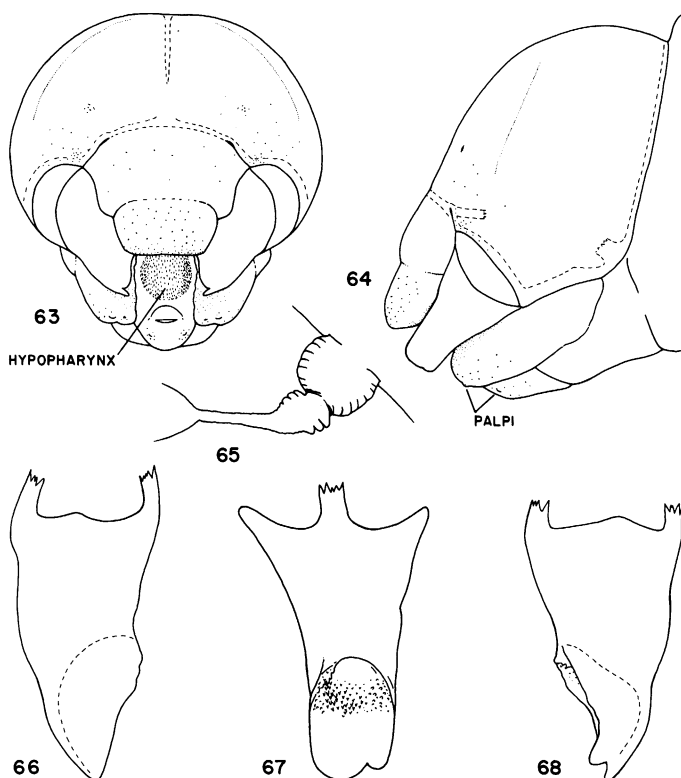
Figures 60–68

HEAD (FIGS. 63, 64): Integument with a few scattered sensilla; dorsal surface of maxilla with non-hairlike spicules; dorsal surface of labium without spicules; epipharyngeal surface with sharp-pointed spicules, most of which are non-hairlike; hypopharynx, unlike that of other known pollen-collecting anthophorids, with hairlike spicules; mandibular articulations and apices of mandibles pigmented. Tentorium complete and well developed; posterior thickening of head capsule and hypostomal and pleurostomal ridges well developed; epistomal ridge well developed laterad of anterior tentorial pits and moderately well developed mesiad of them; longitudinal thickening of head capsule conspicuous dorsally on cleared specimen; parietal bands evident. Antennal papillae not on prominences; each papilla scarcely evident and bearing three or four sensilla. Labral tubercles absent though labrum distinctly bilobed when viewed from above. Each mandible (figs. 66–68) massive,



FIGS. 60–62. Mature larva of *Epicharis fasciata* Lepeletier and Serville. 60. Live, postdefecating larva, lateral view. 61. Predefecating larva, lateral view. 62. Right half of fifth abdominal segment of live, postdefecating larva, dorsal view. Scale refers to figures 60 and 61.

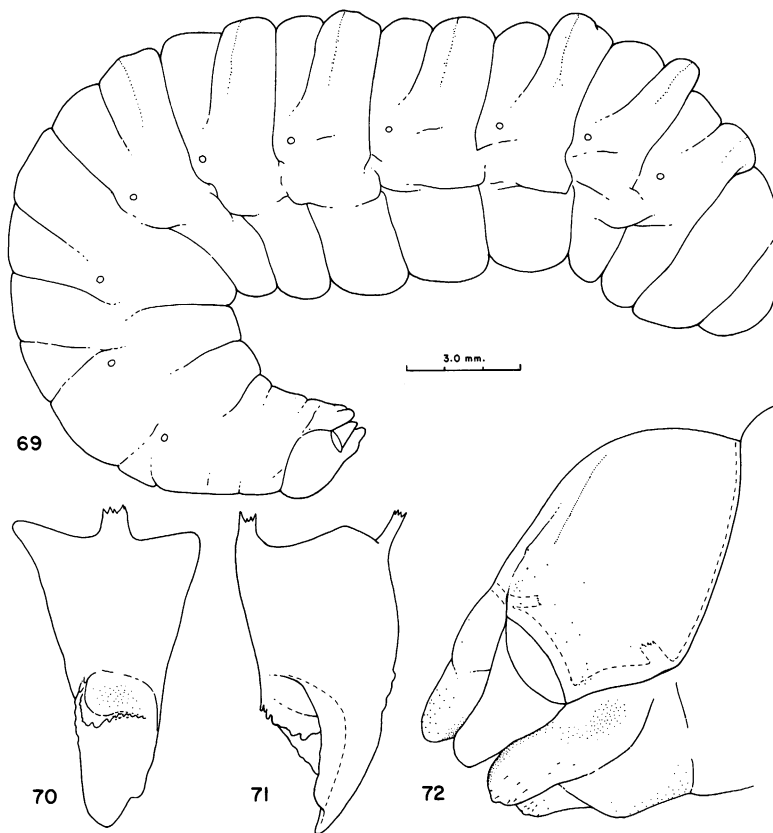
more or less broadly rounded apically, and with pronounced inner apical scoop-shaped concavity; dorsal edge of concavity somewhat sinuate in outline but without teeth; ventral edge with single rounded subapical tooth; concavity with numerous spines and pits basally; mandibles without spicules. Maxillae with apices not produced mesiad; galea only faintly distinguishable; palpus very short; cardo and stipes faintly



FIGS. 63–68. Mature larva of *Epicharis fasciata* Lapeletier and Serville. 63. Head, frontal view. 64. Head, lateral view. 65. Spiracle. 66–68. Right mandible, dorsal, inner, and ventral views.

sclerotic. Labium recessed but divided into prementum and postmentum and bearing salivary opening apically; salivary opening a short slit, with rather small sclerotic lips (the reduced salivary opening, the recessed labium, and perhaps the short palpi and antennae reflect the fact that this species does not spin a cocoon); hypopharynx, unlike that of other known pollen-collecting anthophorids, protruding in addition to being covered with spicules; labial palpus very short.

Body: Form (figs. 60, 61) moderately elongate. Body annulations as illustrated. Unlike those of other bee larvae, abdominal segments II through VII each with row of darkly pigmented spines dorsally along anterior part of caudal annulations; these spines (fig. 62) largest laterally and becoming smaller mesially before they disappear near median line;



FIGS. 69-72. Mature larva of *Epicharis rustica* (Olivier). 69. Live, postdefecating larva, lateral view. 70, 71. Mandible, inner and ventral views. 72. Head, lateral view. Scale refers to figure 69.

spines on second segment smallest, with those of each successive segment becoming somewhat larger; integument with fine scattered setae among spines and on anterior part of caudal annulation of segments VIII and IX (these setae too fine to be illustrated in figs. 60, 61). Spiracular atrium (fig. 65) with elongate spines (large denticles) arising from ridges; atrium projecting above body wall and with slight rim; peritreme distinct; primary tracheal opening without a collar though guarded by numerous spines; subatrium largest near atrium, tapering inwardly. Tenth abdominal segment short and anus situated dorsally.

MATERIAL STUDIED: Nineteen postdefecating larvae and three predefecating larvae, Nariva Swamp, Mayaro, Trinidad, the West Indies,

December 28, 1963 (D. Bharath), in the collection of the American Museum of Natural History. Brief data on the nesting activities were given by Vesey-FitzGerald (1939).

MATURE LARVA OF *Epicharis* (*Epicharana*) *rustica* (OLIVIER)

Figures 69–72

HEAD (FIG. 72): As described for *Epicharis fasciata* except for following: Lateral surface of maxilla with spicules; mandible rather variable apically but bilobed; scoop-shaped concavity of mandible with pronounced transverse dentate ridge as seen in adoral view (fig. 70), with only minute denticles basad of ridge and with a few teeth immediately apical of ridge; maxillary apices produced slightly mesiad.

BODY: As in *Epicharis fasciata* except for following: Size slightly larger; abdominal segment VIII (fig. 69) like preceding segments, with darkly pigmented spines; spines on all segments smaller than those of *Epicharis fasciata*; spines on caudal segments only very slightly larger than those of anterior segments.

MATERIAL STUDIED: Numerous postdefecating larvae, Maracas Valley, Trinidad, the West Indies, January 16, 1965 (F. D. Bennett), in the collection of the American Museum of Natural History. Vesey-FitzGerald (1939) briefly described the nesting habits of this species at another locality in Trinidad.

BIBLIOGRAPHY

BENNETT, FRED D.

1964. Notes on the nesting site of *Centris derasa* (Hymenoptera: Apoidea). Pan-Pacific Ent., vol. 40, pp. 125–128.

BOHART, GEORGE E.

1964. Notes on the biology and larval morphology of *Xenoglossa strenua* (Hymenoptera: Apoidea). Pan-Pacific Ent., vol. 40, pp. 174–182, figs. 1–17.

CLAUDE-JOSEPH, F.

1926. Recherches biologiques sur les hyménoptères du Chili (mellifères). Ann. Sci. Nat., Zool., ser. 10, vol. 9, pp. 113–268, figs. 1–97.

GRANDI, GUIDO

1961. Studi di un entomologo sugli imenotteri superiori. Boll. Ist. Ent. Univ. Bologna, vol. 25, pp. 1–661, 414 figs.

HURD, PAUL D., JR., AND E. GORTON LINSLEY

1964. The squash and gourd bees—genera *Peponapis* Robertson and *Xenoglossa* Smith—inhabiting America north of Mexico (Hymenoptera: Apoidea). Hilgardia, vol. 35, no. 15, pp. 375–477, figs. 1–18.

HURD, PAUL D., JR., AND J. S. MOURE, C.M.F.

1963. A classification of the large carpenter bees (Xylocopini) (Hymenoptera:

- Apoidea). Univ. California Publ. Ent., vol. 29, pp. 1-365, figs. 1-244.
- LINSLEY, E. G., J. W. MACSWAIN, AND RAY F. SMITH
1955. Biological observations on *Xenoglossa fulva* Smith with some generalizations on biological characters of other eucerine bees (Hymenoptera, Anthophoridae). Bull. Southern California Acad. Sci., vol. 54, pt. 3, pp. 128-141.
- MICHENER, CHARLES D.
1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Amer. Mus. Nat. Hist., vol. 82, art. 6, pp. 151-326, text figs. 1-246, diagrams 1-13.
1953. Comparative morphological and systematic studies of bee larvae with a key to the families of hymenopterous larvae. Univ. Kansas Sci. Bull., vol. 35, pp. 987-1102, figs. 1-287.
- MICHENER, CHARLES D., AND RUDOLF B. LANGE
1958. Observations on the ethology of Neotropical anthophorine bees (Hymenoptera: Apoidea). Univ. Kansas Sci. Bull., vol. 39, pp. 69-96, figs. 1-24.
- MOURE, J. S., AND C. D. MICHENER
1955. A contribution toward the classification of Neotropical Eucerini (Hymenoptera, Apoidea). Dusenía, vol. 6, pp. 239-331, figs. 1-35.
- ROZEN, JEROME G., JR.
1957. External morphological description of the larva of *Exomalopsis chionura* Cockerell, including a comparison with other anthophorids (Hymenoptera: Apoidea). Ann. Ent. Soc. Amer., vol. 50, pp. 469-475.
1958. Monographic study of the genus *Nomadopsis* Ashmead (Hymenoptera: Andrenidae). Univ. California Publ. Ent., vol. 15, pp. 1-202, 218 text figs., 17 maps.
1964. The biology of *Svastra obliqua obliqua* (Say), with a taxonomic description of its larvae (Apoidea, Anthophoridae). Amer. Mus. Novitates, no. 2170, pp. 1-13.
- VESEY-FITZGERALD, D.
1939. Observations on bees (Hym.: Apoidea) in Trinidad, B. W. I. Proc. Roy. Ent. Soc. London, ser. A, vol. 14, pp. 107-110.

