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ABSTRACT

The mature larvae of the Melittinae (*Melitta*), Macropidinae (*Macropis*), and Dasypodinae (*Dasypoda, Capicola,* and *Hesperapis*) (larvae of the Ctenoplectrinae are still unknown) are described and illustrated; keys and diagnoses for their identification are provided. A lengthy diagnosis and taxonomic description of the family based upon the larvae is presented. An analysis of the phylogeny of the family on the basis of mature larvae indicates that larvae of *Melitta* and *Macropis* are primitive (and similar) and that the Dasypodinae have undergone extensive evolutionary diversification. Taxonomic descriptions and illustrations of the pupae of *Melitta* and *Macropis* are appended.

INTRODUCTION

The mature larvae of bees of the Melittidae have been less studied than those of any other family of bees. This systematic treatment therefore provides taxonomic descriptions, keys, and illustrations of larvae and also addresses the phylogeny of the Melittidae as revealed by the larvae and the evolutionary relationships of the family with other groups of bees. Taxonomic descriptions and illustrations of the pupae of *Melitta* and *Macropis* are appended.

The small family contains 10 to 12 genera. These genera, in the adult stage, show considerable diversity and are accordingly grouped into four subfamilies: Melittinae, Dasypodinae, Macropidinae, and Ctenoplectrinae. We demonstrate that the mature larvae also reveal a great range of variation. Until now, larvae of only *Hesperapis* (Dasypodinae) have been reasonably well described (Michener, 1953; Burdick and Torchio, 1959). We treat here all subfamilies except the Ctenoplectrinae, for which immature stages are still unknown.

Larval melittids are uncommon in collections, and this paper would not have been possible without the excellent cooperation of a number of persons. Dr. M. A. Lieftinck, "Kalliste," Rhenen, Netherlands, provided the only collection of *Macropis* larvae. Dr. Gerald I. Stage, The University of Connecticut, Storrs, turned over to us his extensive collections of larval *Hesperapis*. Dr. Philip F. Torchio, United States Department of Agriculture, Agricultural Research Service, Bee Biology and Systematics Laboratory, Utah State University, Logan, sent us specimens of *Hesperapis* and, more importantly, of *Melitta* that had been collected by Siavosh Tirgari in France. Dr. M. Münster-Swendsen, Zoological Institute, Royal Veterinary and Agricultural University, Copenhagen, Denmark, donated the specimens of *Dasypoda.* Other specimens were from the collections of the California Insect Survey, University of California, Berkeley, and the American Museum of Natural History.

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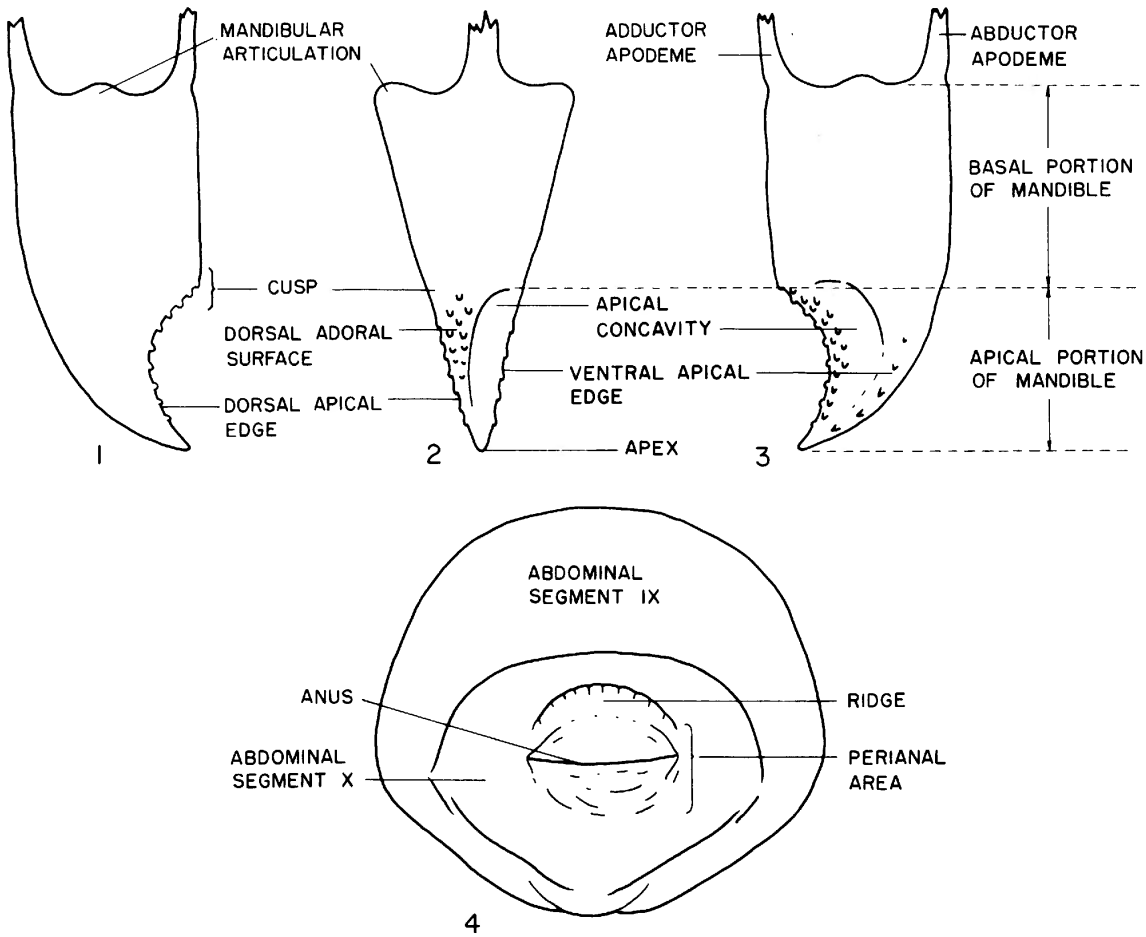
TECHNIQUES

The techniques and methods used in studying the material for the present investigation are the same as those that have been used by the first author in most of his studies on larval bees and differ little from the practices employed by Michener (1953) for his base-line study of bee larvae. Entire larvae are first illustrated in lateral view under a dissecting microscope. Preferably they are drawn while alive or just freshly killed so that there is as little distortion as possible. Next the head is drawn in frontal and lateral views, dissected from the body, and treated in a gently boiling solution of potassium hydroxide (KOH) until cleared. After being neutralized in acidulated water, the cleared head capsule is immersed in glycerine on a micro culture slide. Illustrations of the head are then modified so that internal ridges (dashed lines) are depicted and fine details of spiculation and sensilla added with the aid of both compound and dissecting microscopes. Afterward the right mandible is pried from the head capsule with a fine needle inserted into the mandibular chorion, and it is drawn in three views with the apodemes used as a point of reference. One or two spiracles and surrounding chorion are cut from the right side of the larva, cleared in boiling KOH, neutralized,



FIGS. 1-3. Generalized right mandible of bee larva, dorsal, inner, and ventral views.
FIG. 4. *Dasypoda plumipes*. Posterior view of terminal abdominal segments.

and kept on the same micro culture slide with the head capsule and mandible. Special features of the anal areas are drawn from preserved, untreated specimens.

ANATOMY

External structures on larval bees have been identified by numerous workers, the most comprehensive treatment being that of Michener (1953). We have used his interpretations and terms in the present study, and in the following paragraphs discuss only those structures that need further explanation.

Mandible. Mandibles of bee larvae exhibit considerable variation important for classification and for interpreting phylogenetic trends throughout the Apoidea. The following account, which applies not only to the Melittidae but to all groups of bee larvae, is presented because the anatomical areas of the mandible need to be more precisely defined so that this variation can be discussed and analyzed.

The mandible of a bee (figs. 1-3) like that of most insects articulates at two points—the anterior and posterior mandibular articulations—and has attached to it opposing apodemes to which the abductor and adductor mandibular muscles attach. Mandibles vary among the Apoidea from being very robust (e.g. *Fidelia*, Rozen, 1970b; *Centris*, Rozen, 1965b) to being slender and attenuate (e.g. *Psaenythia*, Rozen, 1970a; *Sphecodes*, Rozen, 1965a). The basal portion of the

mandible exhibits little variation. The apical portion tapers to the *apex* which may be sharp-pointed (*Dasypoda*, fig. 31), broadly rounded (*Centris*), bidentate (*Fidelia*), or modified in many other ways. The demarcation between the basal and apical portions is often defined on the adoral surface by the cusp, which is either a swelling or the region where the apical narrowing of the mandible begins. The cusp in some instances (e.g. *Isepeolus*, Rozen, 1966a) is impossible to demonstrate, but in those bees where the cuspal area is not produced (e.g. *Pseudopanurgus*, Rozen, 1966b) it may often be identified by a group of teeth (cuspal teeth).

The apical portion of the mandible is usually somewhat flat adorally and the flattened surface (dorsal adoral surface) possesses a dorsal apical edge and a ventral apical edge. These edges on some groups of bees (e.g. most Melittidae and Andrenidae) are dentate (or serrate) but on other groups (e.g. Melectini, Ericrocini, and Rhathymini, Rozen, 1969) are not dentate. Whereas the dorsal edge is usually sharply defined (Mellittidae, figs. 12, 13, 49, 50), the ventral edge often is less well defined (*Dasypoda*, figs. 31, 32; and *Hesperapis*, figs. 50, 51) and at times is so rounded as to be indistinguishable. The dorsal apical edge when seen from above or below assumes various configurations—curving in (*Capicola*, fig. 37), straight (*Macropis*, fig. 12), or curving out (*Rhathymus*). The adoral surface may be dentate, smooth, or modified in a variety of ways. Many larvae exhibit on this surface a sharply defined scooplike concavity, the apical concavity (e.g. *Macropis*, fig. 13; *Centris*, Rozen, 1965b). This concavity may be sharply set off from the rest of the adoral surface of the apical portion of the mandible because of a sharp declivity (fig. 2) or even a carina (Eucerini, Rozen, 1965b). When the apical concavity occupies a somewhat ventral position on the apical adoral surface, the dorsal part of the adoral surface can be sharply defined (fig. 2) or even further modified (some Eucerini). When the concavity is adoral in position, it may occupy the entire apical part of the mandible (*Centris*). The concavity is by no means present in all larvae and may be poorly defined in others (*Hesperapis*, fig. 50; *Capicola*, fig. 38; or *Dasypoda*, fig. 31).

Our knowledge of the functional significance of the different mandibular types is rudimentary at best. We can only assume that various configurations are adaptive in nature, accommodating both the structural peculiarities of the other mouthparts and the special characteristics of the provisions upon which the larvae feed.

Galea. Galeae are evident on the maxillary apexes of a number of groups of bees including some apids (Michener, 1953), Eucerini (Rozen, 1965b), and Centridini (*ibid.*). On these bees the galea is expressed as a slightly sclerotic tubercle mesiad of the maxillary palpus and bears a number of sensilla. Because of its position and shape, the small tubercle mesiad of the maxillary palpus of *Melitta* and *Macropis* (fig. 16) is thought to be the galea; it bears a single apical setiform sensillum.

Posterior Tentorial Pit. The posterior tentorial pits of melittid larvae are normal in position, but in *Capicola* and *Hesperapis* the pits tend to appear posterior to their normal position. In these two genera an internal ridge has developed that connects the posterior thickening of the head capsule with the hypostomal ridge. This special ridge lies immediately in front of the posterior tentorial pit. In certain species such as *H. carinata* the small subtriangular sclerite defined by the ridge, the posterior thickening of the head capsule, and the hypostomal ridge is slightly swollen and is therefore conspicuous at least on cleared specimens (figs. 35, 64).

Terminal Abdominal Segments. Abdominal segments IX and X exhibit considerable variation within the Melittidae. The primitive condition as discussed in the section on phylogeny is for abdominal segment X to be attached medially to IX as exhibited by *Melitta* (fig. 17) and *Macropis* (figs. 7, 8). The ventral attachment found in *Dasypoda* is accentuated by the fact that the ventral intersegmental line between IX and X is not incised (fig. 25). The dorsal attachment, characteristic of *Capicola* and *Hesperapis* (figs. 34, 43) is accompanied by a tendency for the abdominal tip to become attenuate. In *Hesperapis*, where the attenuation is greatest, the venter of segment IX and, in some cases, all of segment X become elongate. Furthermore, in *Hesperapis* there appears a ventral intrasegmental line on both segment IX and segment X (fig. 54). In some species of *Hesperapis* the intersegmental line separating

IX and X apparently is obsolete ventrally. The intrasegmental lines may be associated with muscle attachment or at least with the folding of the integument and therefore may be evidence of a special activity of the abdominal tip for feces deposition or for ambulation. It is of interest that some of the modifications of the abdominal apex found in *Capicola* and *Hesperapis* seem to have convergent counterparts in certain of the Exomalopsini and Emphorini, as do the special perianal features discussed below.

An unusual source of taxonomic characters in the Melittidae is found on the integument above the perianal area and on the perianal area (fig. 4). A distinct transverse ridge occurs along the top of the perianal area in *Melitta* (fig. 18) and a less distinct one in *Macropis* (fig. 15). A pronounced transverse ridge is found just anterior to the perianal area in *Dasypoda* (figs. 4, 26) and is here tentatively considered homologous with that of *Melitta* and of *Macropis*. Observations on additional species will be needed to confirm this homology. The integument above the ridge in *Macropis* is faintly spiculate and conspicuously spiculate in *Melitta*. The perianal area in *Hesperapis* (figs. 48, 63, 66, 75) and perhaps *Capicola* (fig. 41) varies considerably both in the characteristic folding of the integument and also apparently in the width to height ratio of the area as seen in caudal view. Analogous modifications have been reported for the Emphorini (Linsley, MacSwain, and Smith, 1956).

PHYLOGENY

Method of Deducing Phylogeny. In developing the phylogenetic schemes of the family we used the following approach: 1) The alternative states of 22 major taxonomic characters (e.g., galea present-galea absent) were listed. 2) Where possible, they were then classified as to which state was primitive and which specialized on the basis of the reasoning presented in the following paragraphs. Fifteen of these characters (table 1) could be so classified (a priori) with a good degree of probability. 3) We then hypothesized the two most likely phylogenetic schemes on the basis of these 15 characters assuming a) as few multiple origins of derived states as possible, and b) that features tend to be lost more easily than regained. 4) As is more fully discussed below, we were then able to define (a posteriori) the primitive and derived states of a number of other major taxonomic characters (table 2) on the basis of these schemes and incorporate them into the schemes. Figure 5 depicts what we believe to be the most likely phylogeny for the family. Large numbers refer to the 15 characters whose primitive or derived states were identified a priori.

TABLE 1
Characters Used in Developing an Understanding of the Phylogeny of the Melittidae

Primitive	Derived
1. Maxillae and labium separated	Fused
2. Palpi long	Short
3. Cardines sclerotic	Unsclerotized
4. Labium divided into prementum and postmentum	Not divided
5. Salivary lips broad, strongly projecting	Narrow, weakly or not projecting
6. Maxillary apex bent slightly mesiad	Bent strongly, or not bent mesiad
7. Galea present	Absent
8. Mandible normally long	Short
9. Mandible bifid	Simple
10. Front of head somewhat flat in lateral profile	Broadly rounded and projecting beyond labrum
11. Head sensilla setiform	Reduced to minute pegs or cones
12. Antennal papilla a moderate convexity	Nearly flat
13. Ventral intersegmental line between abdominal segments IX and X incised	Not incised
14. Abdominal sterna IX and X without intrasegmental lines	With such lines
15. Spiracular subatrium with normal annulations	With annulations in shape of atrium

TABLE 2
Primitive and Derived Character States Based on the Hypothesized Phylogeny of the Melittidae

Primitive	Derived
16. Antennal protuberances present	Absent
17. Head moderately wide, elongate	Wide, moderately short
18. Epistomal ridge complete	Incomplete
19. Paired dorsal body tubercles present	Absent
20. Abdominal segment X central in attachment to IX	Dorsal or ventral in attachment
21. Dorsum of abdominal segment X spiculate	Nonspiculate
22. Abdominal segment X with transverse ridge above anus	Without ridge

Small numbers cover the characters whose states were deduced a posteriori. Figure 6 is the second most probable phylogeny.

The numerous characters associated with cocoon spinning are thought to be primitive because cocoon spinning is widely encountered throughout the Hymenoptera and because it is highly improbable that the ability to spin cocoons once lost would evolve again in a phyletic line. Features involved with cocoon spinning are: a broad transverse opening of the salivary gland with projecting lips; the salivary opening at the apex of the labium; labium projecting strongly forward and divided into a distinct prementum and postmentum, presumably a modification permitting it to be extended and retracted; maxillae well separated apically from the labium; sclerotic cardines which are perhaps important for either retracting the maxillae or positioning them during silk deposition; head sensilla in the form of setae; antennal protuberances and papillae that are at least somewhat produced; and palpi elongate.

The derived condition, that of not being able to spin a cocoon, has evolved numerous times among bee larvae and indeed there are even some species, e.g., *Exomalopsis chionura* Cockerell (Rozen and MacNeill, 1957), in which some individuals spin cocoons and others do not. Larvae that no longer spin cocoons tend to exhibit the following features: the salivary opening reduced to a small curved or straight aperture with or without slightly projecting lips; labium short, recessed by comparison with the rest of the head capsule and weakly, if at all, divided into prementum and postmentum; cardines at most weakly developed; maxillae more or less fused with labium; palpi, antennae, and sensilla tending to be short.

The apically bifid condition of the mandible in contrast to a simple apex is considered primitive because this feature is found among many groups of wasps, from which bees arose; however, the bifid condition, once lost, could arise again in view of the fact that the mandibular shape and dentition exhibit considerable evolutionary plasticity among bee larvae.

Maxillary apexes bent mesiad are found in many groups of bees and wasps and this condition is therefore probably primitive. So far as is known it has not evolved anew in any groups of bees. The fact that the maxillary apex of *Dasypoda* is more strongly bent in than are those of *Melitta* or *Macropis* is interesting. The condition in *Dasypoda* is here considered to be a derivative of the *Macropis-Melitta* maxilla because the maxilla of *Macropis* and *Melitta* is associated with a galea (almost certainly a primitive characteristic), whereas galeae are absent in *Dasypoda*. One hypothetical scheme (fig. 5) of the phylogeny of the Melittidae is based on the assumption that the maxillary apex as found in *Melitta* and *Macropis* is primitive and the other (fig. 6) on the assumption that the condition found in *Dasypoda* is primitive.

Galeae are a primitive feature in wasp and bee larvae, and a structure once lost is not likely to evolve again. However, one must not overlook the fact that the genetic basis for galeae is preserved in the genotype of the bee, in that galeae are expressed in the phenotype of pupae and adults. If it is assumed that the genetic control for the development of the galea of the adult is the same as that for the galea of the larva, then the *de novo* origin of such a feature in the larva of a holometabolous insect is probably not so unlikely as that of a feature whose genetic basis

is not in the genotype. To the best of our knowledge this theoretical consideration has not been discussed before; in general it may apply to all animals that undergo a marked metamorphosis. Nonetheless, for the purpose of this analysis the presence of galeae is deemed primitive, as it is still more likely to be primitive than the absence of galeae.

The following features are considered primitive because they are widely found among bees: mandibles long; frontal area of head flat in lateral profile; intrasegmental lines of sterna IX and X absent; ventral intersegmental line between abdominal segments IX and X incised; and chambers of the spiracular subatrium unlike atrium in shape. The derived states are: mandibles short; frontal area rounded; intrasegmental lines of sterna IX and X present; ventral intersegmental line between abdominal segments IX and X not incised; and subatrial chambers appearing like atrium.

All other character states (table 2) used in developing the phylogenies presented in the next section were judged to be primitive or specialized on the basis of the phylogenetic scheme present in figure 5. For example, a moderately wide, elongate head (character 17) was thought to be primitive because if the wide condition were primitive then the narrow condition arose independently on a number of occasions. Two characters (16 and 21) in table 2 could not be so evaluated if the phylogenies in figure 6 were assumed correct. In the phylogeny depicted by figure 6, it is just as unlikely that antennal protuberances (16) evolved from the absent condition as that the absent condition evolved from the protuberant state. The same reasoning applies to character 21.

Phylogeny of Melittidae. For reasons discussed above, the following narrative of the phylogeny of the family (figure 5) is based on the assumption that the primitive condition of the maxillary apexes was for them to be slightly bent mesiad, as in *Melitta* and *Macropis*. Numbers in parentheses below refer to characters presented in tables 1 and 2 and in figure 5.

The ancestral type of melittid larva possess all the primitive characteristic states identified in tables 1 and 2. Larvae of both *Macropis* and *Melitta* evolved little from the primitive form; the mandible (8) of *Macropis* became shorter than those of the original melittid and each subatrial chamber (15) of *Melitta* assumed the shape of the atrium. Hence, larvae of *Melitta* and *Macropis* look very much alike and indicate that most of the evolution with respect to these two genera assigned to separate subfamilies is expressed in the adult stage. In contrast, evolutionary diversification in larval Dasypodinae was extensive, whereas that of the adults was much more conservative.

The lineage that gave rise to the Dasypodinae (*Dasypoda, Capicola,* and *Hesperapis*) underwent considerable evolutionary change. Some modifications were associated with the loss of cocoon spinning: reduction in palpal length (2), in salivary lips (5), in length of head capsule (17), and perhaps in antennal papilla (12), and antennal protuberances (16). But other changes also occurred; galeae were lost (7), the epistomal ridge became interrupted medially (18), and the dorsum of abdominal segment X lost spiculation (21).

Dasypoda split from the lineage that gave rise to *Capicola* and *Hesperapis* in that its maxillary apexes became strongly bent mesiad (6′), abdominal segment X developed a ventral attachment to IX (as seen in lateral profile) (20′), the intrasegmental line between segments IX and X was no longer deeply incised (13), and the paired dorsal tubercles were lost (19).

However, in some respects *Dasypoda* retained the characteristics of its ancestors. Certain features generally associated with the ability of a larva to produce a cocoon are still evident in *Dasypoda* but were lost from the lineage leading to *Capicola* and *Hesperapis* after the *Dasypoda* stock branched off. As a consequence *Dasypoda* presents anatomical features halfway between the cocoon spinning and the noncocoon spinning conditions. The primitive cocoon spinning features retained by *Dasypoda* are: maxillae well separated from labium (1), cardines still sclerotic (3), and labium divided into prementum and postmentum (4).

After the development of the *Dasypoda* branch, the lineage giving rise to *Capicola* and *Hesperapis* underwent considerable modification: maxillae and labium became greatly fused (1); the cardines lost their sclerotization (3); the mentum and prementum fused (4); maxillary apexes were no longer bent mesiad (6′) or were only slightly

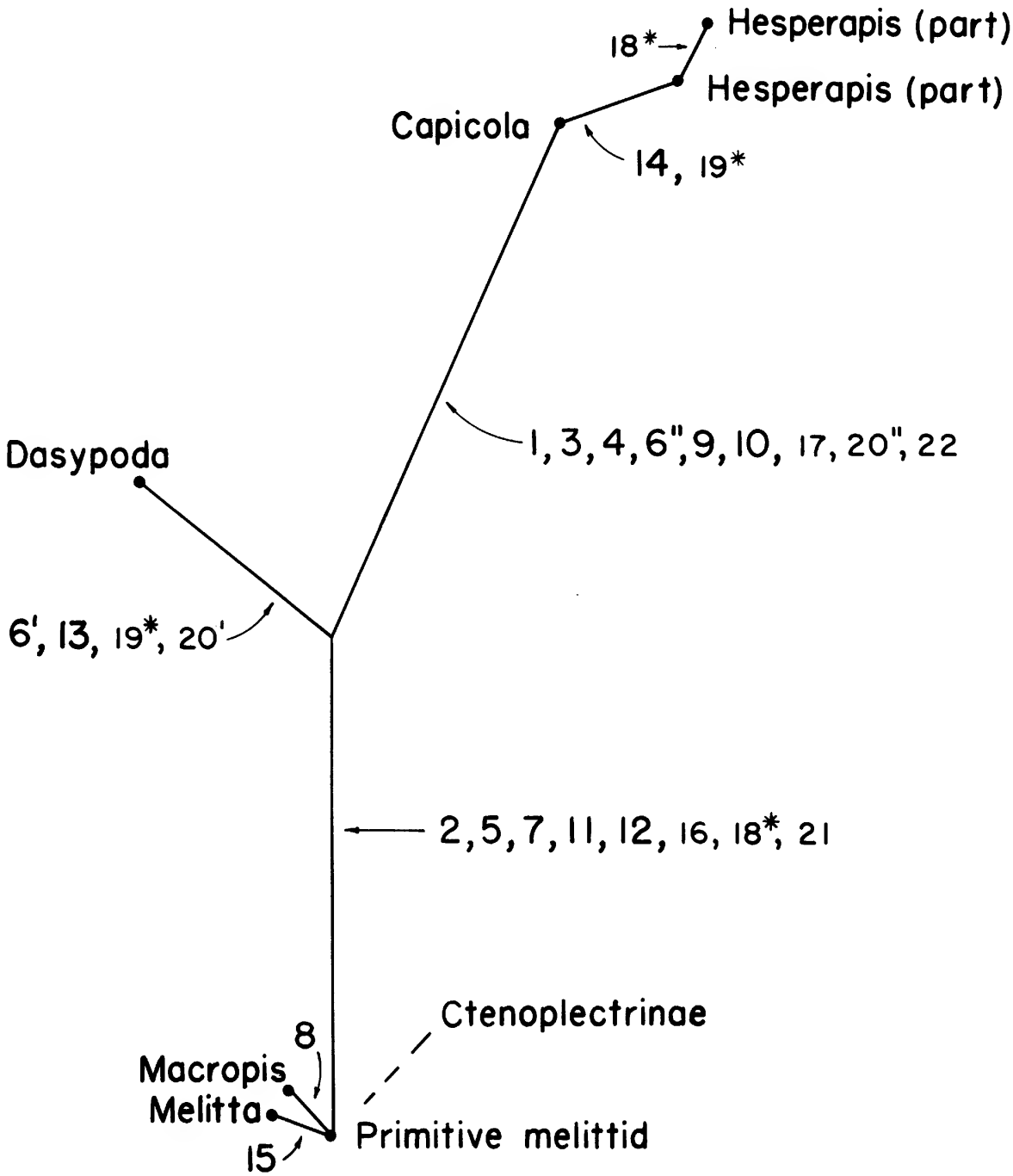


FIG. 5. Hypothesized phylogeny of the Melittidae based on characters in tables 1 and 2 and assuming the condition of the maxillary apex as found in *Mellitta* and *Macropis* is primitive. This is judged to be the most probable phylogeny. Length of lines indicates approximate amount of character change, but size of angle has no meaning. Number followed by asterisk indicates feature of multiple origin or a reversal of character state. Prime and double prime numbers refer to characters that have three, rather than two, states. For a further explanation see text.

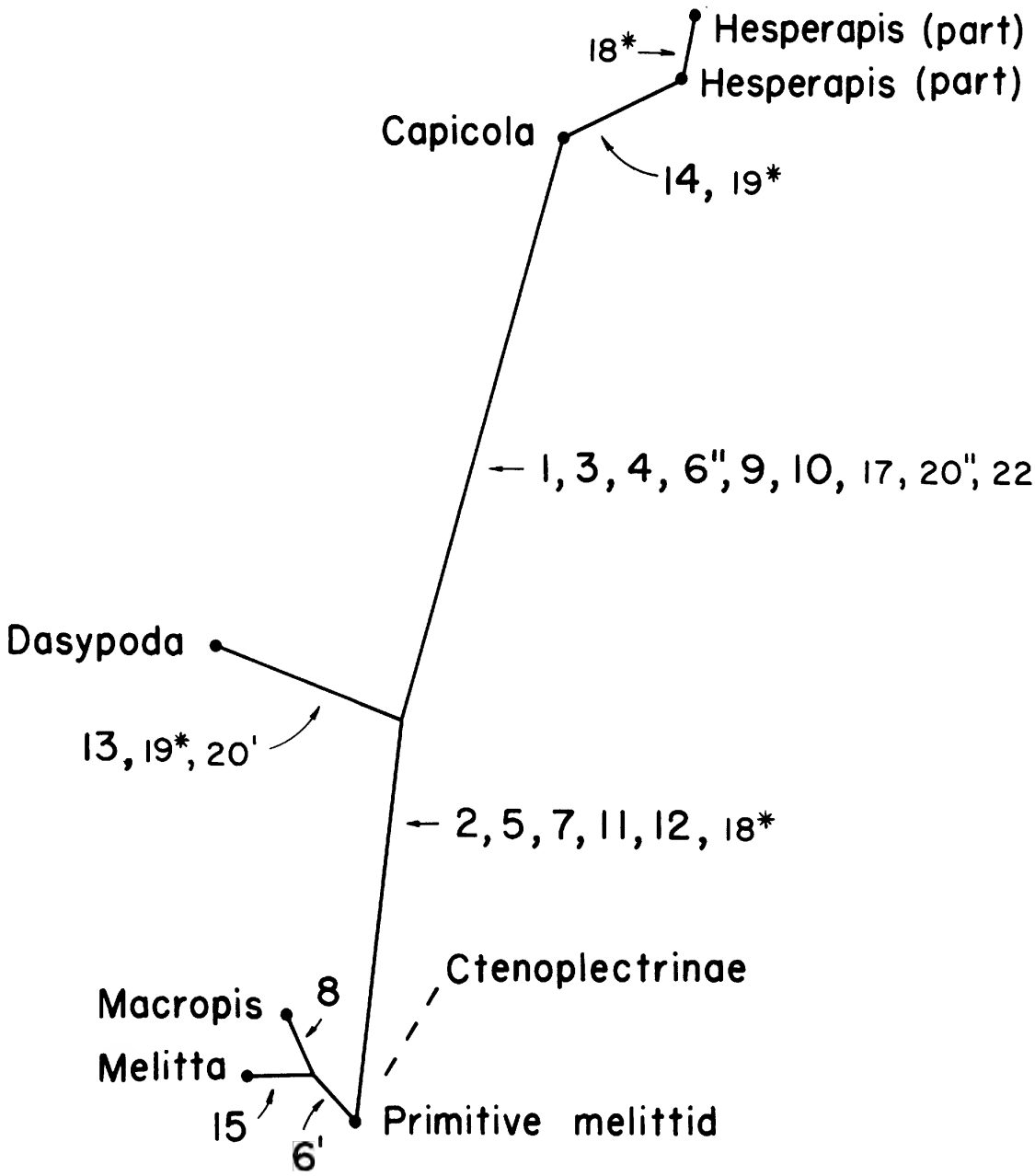


FIG. 6. Hypothesized phylogeny of the Melittidae based on characters in tables 1 and 2 and assuming the condition of the maxillary apex as found in *Dasypoda* is primitive. This is judged to be the second most likely phylogeny. For a further explanation see figure 5.

so (*Capicola*); mandibular apexes became simple (9); the head became somewhat shorter and wider (17); the profile of the head in the lateral view became rounded (10); abdominal segment X developed a dorsal attachment to IX (20"); and the ridge above the anus (22) was lost.

The larva of *Capicola*, although highly specialized in relation to other melittid larvae, is directly in line as the ancestor to *Hesperapis*. *Hesperapis* larvae differ from *Capicola* in having intrasegmental lines on abdominal sterna IX and X (14). Furthermore, paired dorsal tubercles (19)

were lost before *Hesperapis* developed, a condition that repeated in the line that gave rise to *Dasypoda*. Within *Hesperapis* there occurred a reversal of character state in that some *Hesperapis* possess complete epistomal sutures (18).

Nothing is known of the larvae of the Ctenoplectrinae beyond the fact that they spin cocoons (Williams, 1928). We assume that it is unlikely therefore that the Ctenoplectrinae evolved from the Dasypodinae but we cannot ascertain its evolutionary origin with respect to the Melittinae and Macropidinae.

SYSTEMATICS

Description of Melittidae

The mature larvae of many groups of bees have not been studied. The following diagnosis is therefore not complete and probably will prove unnecessarily lengthy when diagnostic features of other families and subfamilies have been worked out. Larvae of all nonmelittid genera discussed below have been examined by us firsthand or, if so indicated, by recent authors.

Diagnosis. Larval melittids can be separated from the larvae of both Fideliidae (*Fidelia*, Rozen, 1970b; *Neofidelia*, Rozen, 1973b) and Megachilidae (numerous genera, Rozen, 1973b) because melittids lack setae on the body. The slender, apically pointed mandibles and more slender body also serve to distinguish melittids from fideliids and megachilids.

Because the larvae of the Colletidae have not been studied as a family, it is difficult to give diagnostic characteristics by which the melittids can be distinguished from them. Larvae of the Colletini (*Colletes*), Euryglossinae (*Euryglossa*), Hylaeinae (*Meroglossa*; *Hylaeus*, Michener, 1953), and Chilicolinae (undescribed genus; *Chilicola*, Eickwort, 1967) all have antennae low on face and an epistomal suture that arcs upward from the anterior pits so that the median part of the suture (and ridge) is essentially at the same level as the antennae (in *Meroglossa* the median part of the ridge is absent). Furthermore, the antennal papillae of these groups are large in diameter. Hence these colletids differ from melittids which have rather small antennae and an epistomal ridge[1] that is usually well below the antennae. The Diphaglossinae (*Ptiloglossa*; *Caupolicana*, Michener, 1953; *Policana*, *ibid.*) are unique among all bees in that the salivary opening is at the tip of a spoutlike projection (Michener, 1953, figs. 37, 40, 41). Larvae of the Paracolletini (*Leioproctus, Lonchopria, Scrapter*) differ from the other colletids and agree with the melittids in having the antennal papillae small in diameter and the median section of the epistomal suture well below the antennae. Preliminary studies of the Paracollitini indicate that the strongly produced clypeus and labrum of this group may serve to distinguish them from melittids in which the labroclypeal region is relatively flat. Larval Paracollitini, however, show great morphological diversification, and recognition of additional diagnostic characters will have to await a more detailed study of this group.

The larva of the Oxaeidae (*Protoxaea*, Rozen, 1964) has a darkly pigmented head capsule, a labrum cleft apically and bearing two distinct tubercles, a greatly recessed labiomaxillary region (far more so than in any melittid), and spiracles beset with numerous hairlike atrial spines having a slitlike primary tracheal opening. As can be seen in the following description none of these features is found in the Melittidae.

In the Andrenidae, larval Panurginae can be distinguished from melittids because all panurgines possess paired labral tubercles, whereas melittids do not. Antennae of the Andreninae (*Andrena*, Michener, 1953; Rozen, 1973a) have antennae on pronounced protuberances, whereas antennae of larval melittids are not on protuberances or on slight protuberances (*Macropis* and *Melitta*).

Halictid larvae can be separated from those of the melittids in most cases. All known Halictinae (*Halictus*, *Lasioglossum sensu lato*, *Augochlora*, Michener, 1953; *Agapostemon*; *Sphecodes*, Rozen, 1965a) are characterized by having antennal papillae that are very broad in diameter and maxillary and labial palpi represented as extremely broad, vaguely defined areas that seem to blend with the apex of the maxillae and the labium. As a consequence, palpi appear com-

[1] In *Hesperapis* species b the epistomal suture does arc upward. In all other respects this species is a typical *Hesperapis*, with the peculiar head shape and unique modifications of the ventral part of the abdominal apex.

pletely absent. Antennae of melittids are normal in size, and palpi are long or short but never wide and are always evident. Both the Halictinae and the Nomiinae (*Nomia*, Michener, 1953) possess a distinct sensilla-bearing tubercle on the outer surface of the mandible at about the level of the cusp. Such mandibular tubercles are absent in the Melittidae, although there are a number of sensilla in the same position. Larvae of the Dufoureinae (*Dufourea*, *Rophites*, and *Systropha*) spin cocoons and therefore have the labiomaxillary region produced as is characteristic of all cocoon-spinning larvae. Consequently they can be confused only with *Melitta* and *Macropis* among the Melittidae. Dufoureine larvae have dorsal body tubercles, but these tubercles are conical and apparently the prothorax tubercles although distinct are noticeably smaller than the other paired tubercles; the prothoracic tubercles of *Macropis* and *Melitta* are subequal to the other dorsal tubercles and all tubercles are transverse. Dufoureine larvae also apparently possess paired ventral tubercles on many of the body segments; these tubercles are more noticeable on intermediate larvae than on last stage forms but can be detected, at least in some cases, on mature larvae. No melittids have such tubercles.

Among the Anthophoridae, larvae of Nomadinae (numerous genera, Rozen, 1966a) have distinct paired labral tubercles except for the larva of *Isepeolus* which has a single median labral tubercle. Larvae of melittids lack labral tubercles. In the Melectini (Rozen, 1969), *Melecta* and *Thyreus* possess broadly rounded mandibles in contrast to the pointed mandibles of melittids. The melectine *Zacosmia* possesses apically pointed mandibles but its peculiar, small labrum, which is produced apically into a rounded point, is unlike that of any melittid. Rhathymini (*Rhathymus*) and Ericrocini (*Acanthopus*, Rozen, 1969) have massively developed labiomaxillary regions nowhere encountered in the Melittidae. Among the nonparasitic anthophorids, the Eucerini possess paired labral tubercles and mandibles that are very differently shaped from those of melittids. The Centridini all have mandibles broadly rounded apically. Larvae of the Exomalopsini and Emphorini apparently can be distinguished from those of the Melittidae because the exomalopsines and emphorines have strongly protruding abdominal sterna IX, and their bodies tend to be extremely elongate. Larvae of some Xylocopinae (*Xylocopa* and *Ceratina*, Michener, 1953) have apically bidentate mandibles similar to those of *Melitta*. However, Xylocopinae do not have a labiomaxillary region modified for cocoon spinning as is the case with *Melitta*. Other xylocopines may not have bidentate mandibles and consequently this subfamily must be studied further before a reliable diagnosis can be presented to separate it from other Melittidae.

All apid larvae (Michener, 1953) spin cocoons and as a consequence possess strongly protruding salivary lips, a character shared only by *Melitta* and *Macropis* (and presumably also *Ctenoplectra*) among the Melittidae. So far as can be determined the mandibles of apids (*Bombus*, *Eulaema*, *Psithyrus*, *Melipona*, *Trigona*, and *Apis*), although varying from genus to genus, are all quite distinct from those of *Melitta* and *Macropis*.

Description. Head with scattered sensilla which are distinct setae only in *Macropis* and *Melitta*; in *Macropis* and *Melitta* these setae very short by comparison with those of Megachilidae and Fideliidae. Tentorium probably complete and moderately well developed in all forms before development of adult features; posterior tentorial pit in normal position, i.e., at juncture of posterior thickening of head capsule and hypostomal ridge; in *Capicola* and some species of *Hesperapis* area of capsule immediately behind junction modified as described in anatomy section; posterior thickening of head capsule, hypostomal ridge, pleurostomal ridge, and epistomal ridge below anterior tentorial pits well developed; epistomal ridge complete or fading medially, well developed laterad of anterior pits; hypostomal ridge either indistinctly branched or if more distinctly branched (fig. 29) then division almost at juncture of posterior thickening of head capsule and ridge; hence in lateral view hypostomal ridge very different in appearance from that of most Megachilidae. Antennal papilla moderately small, nearly flat to moderately well produced; papilla not arising from prominences (*Dasypoda*, fig. 29; *Capicola*, fig. 35; and *Hesperapis*, fig. 46) or arising from very low prominences (*Macropis*, fig. 11; *Melitta*, fig. 20); papilla bearing three to five sensilla. Labrum without tubercles although apical lateral angles tending to be somewhat swollen; apical edge varying from being somewhat emarginate to truncate to rounded. Mandibles

moderately slender to slender; apex bifid (*Melitta*, figs. 23, 24) to acute; mandible short (*Macropis*, figs. 12-14) or moderate in length; cusp moderately defined, dentate; apical concavity in *Macropis* (fig. 13), and *Melitta* (fig. 23), well expressed, in others poorly so; only in *Melitta*, concavity with low tooth-bearing projection (fig. 23). Labiomaxillary region varying from being moderately strongly produced (*Macropis*, fig. 11; *Melitta*, fig. 20) to being greatly recessed (*Capicola*, fig. 35; *Hesperapis*, fig. 46); maxilla and labium varying from being well defined to greatly fused. Maxilla, with apex varying from being strongly bent mesiad (*Dasypoda*, fig. 28) to being not bent mesiad (fig. 44); apparent galea present only on *Melitta* and *Macropis* (fig. 16); cardo and stipes moderately weakly sclerotic to not sclerotic; palpus long (*Macropis*, *Melitta*) to very short (*Hesperapis*). Labium divided or not divided into distinct prementum and postmentum; salivary opening varying from transverse slit with strongly projecting lips (*Macropis*, figs. 10, 11; *Melitta*, figs. 20, 21) to being narrow and without lips (*Capicola*, figs. 35, 36).

Body form moderately slender with anterior part of body somewhat more robust than posterior part; except in *Capicola* most body segments weakly divided into cephalic and caudal annulets; body with (*Macropis*, fig. 8; *Capicola*, fig. 34; *Melitta*, fig. 17) or without (*Dasypoda*, fig. 25; *Hesperapis*, fig. 43) dorsal tubercles on most segments; middorsal tubercles absent. Integument with spicules or without; setae absent. Spiracular atrium with rim and produced above body surface; atrial wall smooth or with low ridges but without denticles or spines; primary tracheal opening with collar; subatrium short to long.

KEY TO GENERA

1. Labium not recessed, subequal to or exceeding maxillae in lateral view (figs. 11, 20); maxillary and labial palpi long (length at least twice the basal diameter); apparent galea present (figs. 10, 16, 21); salivary lips well developed (figs. 11, 20); body with dorsal transverse tubercles (figs. 8, 17); abdominal segment X central in attachment to segment IX (figs. 8, 17) 2

   Labium recessed, exceeded by maxillae in lateral view (figs. 29, 46); maxillary and labial palpi short (length subequal to or less than basal diameter); galea absent; salivary lips reduced (fig. 29) or absent; body with (fig. 34) or without (figs. 25, 43) dorsal tubercles; abdominal segment X dorsal (figs. 34, 43) or ventral (fig. 25) in attachment to segment IX 3

2(1). Venter of abdominal segment X produced posteriorly (fig. 8); dorsum of abdominal segment X faintly spiculate; annulations of spiracular subatrium numerous, narrow, without tapered appearance (fig. 9); labrum evenly rounded laterally, nearly truncate apically (fig. 10); mandibular apical concavity without tooth-bearing projection (fig. 13); subapical teeth of mandible small or absent (figs. 12-14 . . . . . *Macropis*

   Venter of abdominal segment X not produced posteriorly (fig. 17); dorsum of abdominal segment X conspicuously spiculate; annulations of spiracular subatrium few in number, in shape of atrial chamber, tapering to trachea (fig. 19); labrum irregularly curved laterally, moderately emarginate apically (fig. 21); mandibular apical concavity with tooth-bearing projection (fig. 23); subapical tooth large and conspicuous (figs. 23, 24) . . . . . *Melitta*

3(1). Maxillae and labium not greatly fused, at least apical third of maxillae distinct (fig. 29); labium clearly divided into prementum and postmentum (fig. 29); salivary slit transverse with weakly projecting lips (figs. 28, 29); ventral intersegmental line between abdominal segments IX and X not incised (fig. 25); abdominal segment X ventral in attachment to segment IX (fig. 25) . . . . . *Dasypoda*

   Maxillae and labium greatly fused (figs. 35, 46); labium not clearly divided into prementum and postmentum (figs. 35, 46); salivary slit small, flat-circular in shape, with lips absent or present as a low surrounding rim (figs. 36, 44); ventral intersegmental line between abdominal segments IX and X normally incised (figs. 34, 43); abdominal segment X dorsal in attachment to segment IX (figs. 34, 43) 4

4(3). Body with moderately low paired dorsal tubercles (figs. 33, 34); intrasegmental

lines on abdominal sterna IX and X absent; venter of abdomen spiculate . . . . . *Capicola*

Body without dorsal tubercles (figs. 42, 43); intrasegmental lines on abdominal sterna IX and X present (figs. 43, 54); venter of abdomen nonspiculate. . . . . *Hesperapis*

MACROPIS KLUG

Diagnosis. The well-produced labium (fig. 11), large labial and maxillary palpi, strongly projecting salivary lips, and presence of galeae (figs. 10, 16) readily distinguish the larval *Macropis* described below from all other known immature melittids except *Melitta*, from which it differs by spiracular structure (fig. 9), produced venter of abdominal segment X (fig. 8), and the absence of a tooth-bearing projection on mandibular apical concavity.

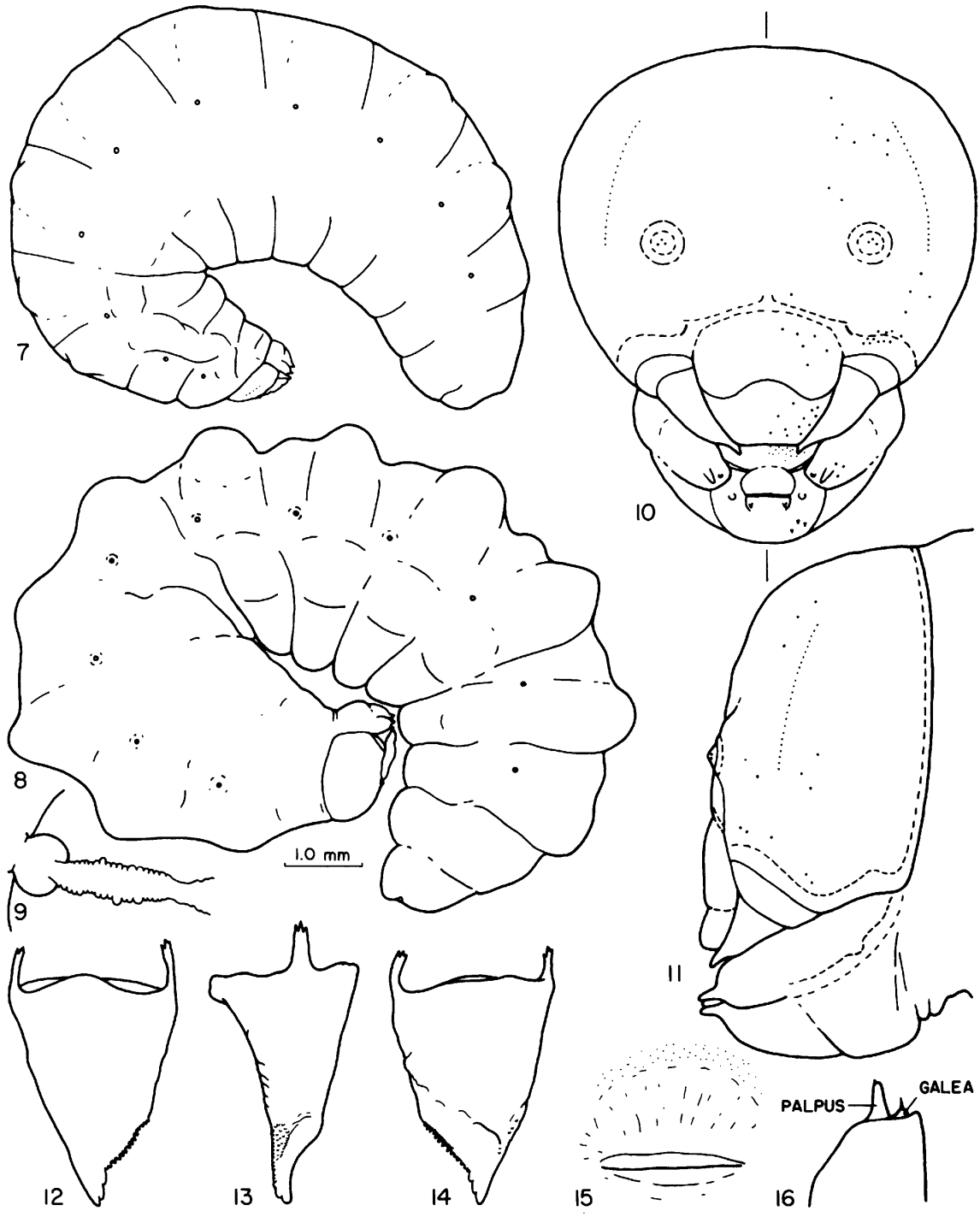
Macropis europaea Weke

Figures 7-16

Diagnosis. See that of genus.

Head (figs. 10, 11). Integument with scattered sensilla; some of those on labrum, maxillae, and labium in form of short or even moderately long setae; epipharynx and upper part of hypopharynx finely spiculate, spicules smaller and less dense than those of *Hesperapis*, *Dasypoda*; pigmentation clearly evident only on mandibular articulations and apodemes, apex of mandible, anterior tentorial pit, and narrow band along ventrolateral margin of hypopharynx. Head somewhat elongate, length (top of vertex to base of labium) greater than greatest width; supraclypeal area flat in lateral view (fig. 11), not projecting forward beyond labrum as that of *Hesperapis*. Tentorium complete and well developed; anterior tentorial pit in upper part of epistomal ridge; posterior pit in normal position, i.e., at junction of hypostomal ridge and posterior thickening of head, area immediately behind junction not swollen; posterior thickening of head capsule, hypostomal and pleurostomal ridges well developed; epistomal ridge well developed and complete; longitudinal thickening of head vestigially present near epistomal ridge; parietal band faint (much weaker than that of *Hesperapis*, *Dasypoda*). Antenna arising from very slight elevation (fig. 11), situated low on face; antennal papilla a moderate convexity (more pronounced than those of other melittids) bearing three sensilla. Clypeus somewhat narrow as seen in frontal view (fig. 10), narrowest of all melittids studied; apical margin emarginate. Labrum moderately small, with apex nearly truncate; apicolateral angles slightly swollen, but labral tubercles absent. Mandible (figs. 12-14) relatively short, moderately robust at base, tapering to simple apex; two weakly defined subapical teeth present on some specimens but nearly absent on others; cusp moderately well defined, with many small teeth extending apically along dorsal adoral surface; dorsal inner edge well defined, nearly straight when viewed dorsally or ventrally, and with many short, slender teeth; ventral edge weakly formed, with a few minute teeth; apical concavity well expressed, directed somewhat ventrally. Labiomaxillary region protruding moderately strongly; maxillae and labium not greatly fused, so that apical third of maxilla distinct from labium. Maxilla, in lateral view (fig. 11), not produced beyond labium; apex bent only slightly mesiad but inner apical angle rather sharp (fig. 16); cardo moderately sclerotized, more so than that of *Dasypoda* but unpigmented; palpus large, length twice the basal diameter; galea present and bearing large seta, length of galea and seta more than one-half length of palpus (fig. 16). Labium divided into prementum and postmentum, but division not so pronounced as that of larvae of many other cocoon-spinning groups; palpus large, subequal in size to maxillary palpus. Salivary opening broad, straight transverse slit with strongly projected lips; salivary lips slightly higher than labial palpus (fig. 10). Hypopharynx protruding about as far as labium; hypopharyngeal groove distinct laterally but less so mesially.

Body. Integument nonspiculate, except for patch of faint spicules on dorsum of segment X, without setae. Form (figs. 7, 8) moderately robust; intersegmental lines present, moderately incised on postdefecating larva; well-defined but moderately low paired transverse dorsal tubercles present on most caudal annulets of postdefecated form (fig. 8); these tubercles similar to those of *Andrena* (Rozen, 1973a); on predefecating larva, tubercles appearing as inconspicuous rounded swellings (fig. 7); lateral swellings below spiracles present but very weak; dorsal intrasegmental lines present; because of tubercles, caudal annu-



FIGS. 7-16. *Macropis europaea*. 7. Predefecating larva, lateral view. 8. Live postdefecating larva, lateral view. 9. Spiracle. 10. Head, frontal view, right side showing distribution of spicules and sensilla. 11. Head, lateral view. 12-14. Right mandible, dorsal, inner, and ventral views. 15. Perianal area, caudal view. 16. Right maxillary apex, ventral view.

Scale refers to figure 8.

lets distinctly higher than cephalic annulets; abdominal segment IX with venter normal in length; ventral intersegmental line between segments IX and X normally incised; abdominal sterna IX and X without intrasegmental lines; segment X central in attachment to IX (figs. 7, 8), not elongate but with venter distinctly produced posteriorly as figured (segment X on predefecating specimen abnormally compressed in preservation); anus more or less apical in position; anus distinctly transverse; perianal area not puckered, with faint wrinkles (fig. 15); faint transverse ridge along top of perianal area much less distinct than that of *Melitta*. Spiracles (fig. 9) on low elevations; atrial rim present and produced above body surface, although not so pronounced as that of *Dasypoda*; peritreme present; atrial wall without spines or ridges; primary tracheal opening with long collar; subatrium long with many annulations. Male with distinct median transverse cuticular invagination of abdominal sternum IX approximately one-fourth distance from posterior end of segment. Female with paired imaginal discs on segments VII, VIII, and IX; discs on segment IX near middle of segment, discs on segments VIII and VII approximately one-third distance from posterior end of segment; discs of segment VII farthest apart and those of segment IX closest together, being approximately 1.5 disc diameters apart; cuticular scars evident beneath each disc; median transverse scar on segment IX absent.

Material Studied. Three live and one preserved postdefecating larvae, one preserved predefecating larva, Rhenen (Utrecht), Netherlands (M. A. Lieftinck).

MELITTA KIRBY

Diagnosis. The well-produced labium (fig. 20), the large and strongly projecting labial and maxillary palpi and salivary lips, and the presence of galeae (fig. 21) distinguish *Melitta* from all other known larval forms of melittids with the exception of *Macropis*. *Melitta* differs from *Macropis* in its characteristic spiracular structure (fig. 19), nonproduced venter of abdominal segment X (fig. 17), and presence of a tooth-bearing projection on mandibular apical concavity (figs. 23, 24).

Melitta leporina (Panzer)
Figures 17-24

Diagnosis. See that of genus.

Head (*figs.* 20, 21). As described for *Macropis europaea* except for following: longitudinal thickening of head capsule completely absent; antennal elevations and papillae slightly more projecting; antennal papillae with 3-5 sensilla; labrum moderately emarginate apically (fig. 21); mandible (figs. 22-24) longer and more robust basally; one large and conspicuous subapical tooth present; dorsal inner edge curved inward when viewed dorsally or ventrally with teeth longer and more acutely pointed; apical concavity with tooth-bearing projection; labial palpus slightly shorter than maxillary palpus (fig. 20).

Body. As described for *Macropis europaea* except for following: integument spiculate anteroventrally, conspicuous spiculation present on dorsum of abdominal segment X; venter of segment X not produced posteriorly (fig. 17); distinct transverse ridge present along top of perianal area (fig. 18), much more distinct than that of *Macropis*; spiracular atrium (fig. 19) less globular, more elongate and narrow apically; subatrium with few annulations, in shape of atrial chamber and tapering to trachea.

Material Studied. Eleven postdefecating larvae, France, 1964 (S. Tirgari).

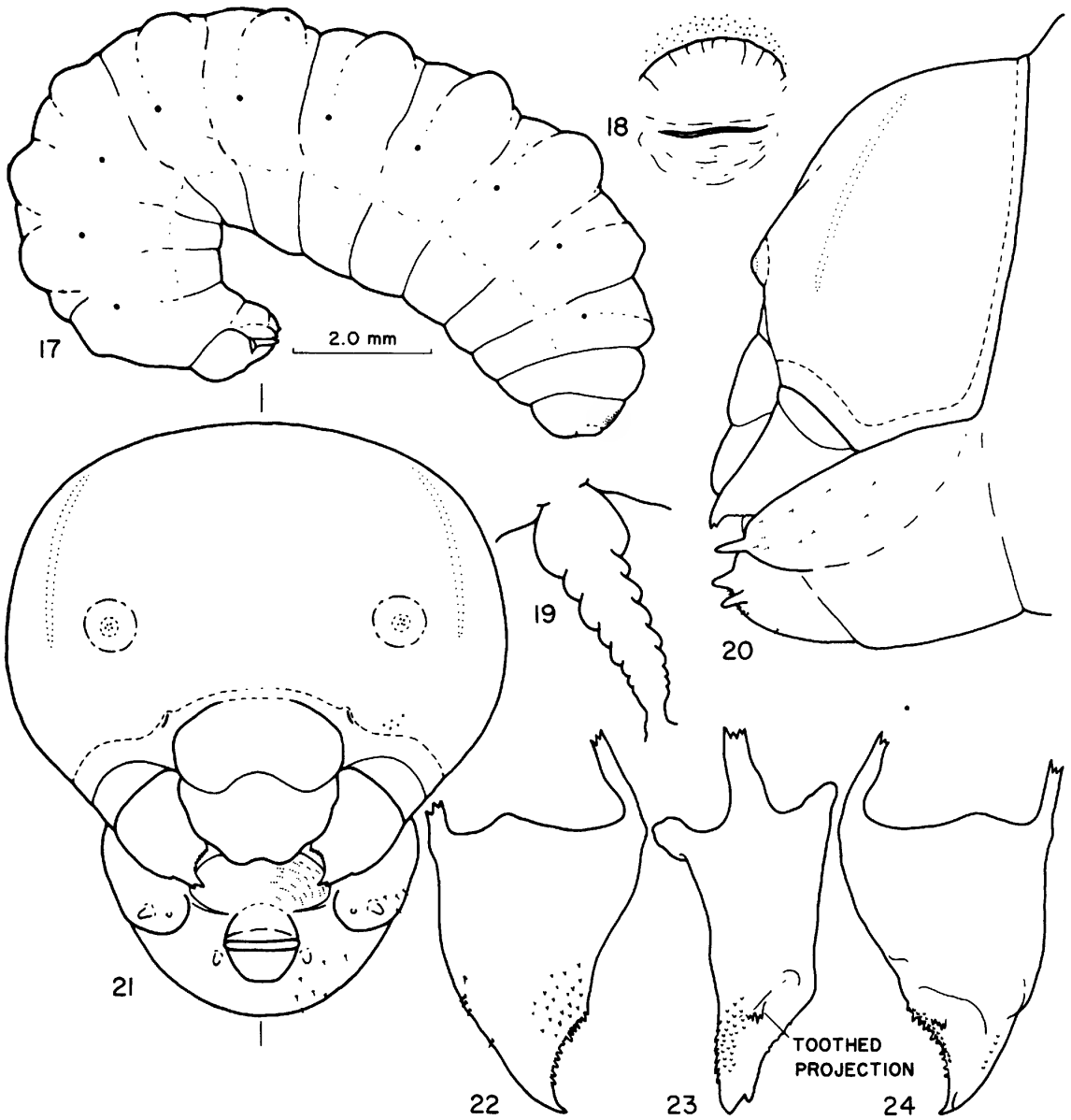
DASYPODA LATREILLE

Diagnosis. The distinct and well-produced maxillae in combination with the recessed labium (fig. 29), small maxillary and labial palpi, and weakly projecting salivary lips distinguish the larval *Dasypoda* described below from other known immature melittids. Also diagnostic is the unusually large labrum (fig. 28), lack of abdominal dorsal tubercles, produced sternum of abdominal segment IX (fig. 25), and the ventral attachment of abdominal segment X to segment IX.

Dasypoda plumipes Panzer
Figures 25-32

Diagnosis. See that of genus.

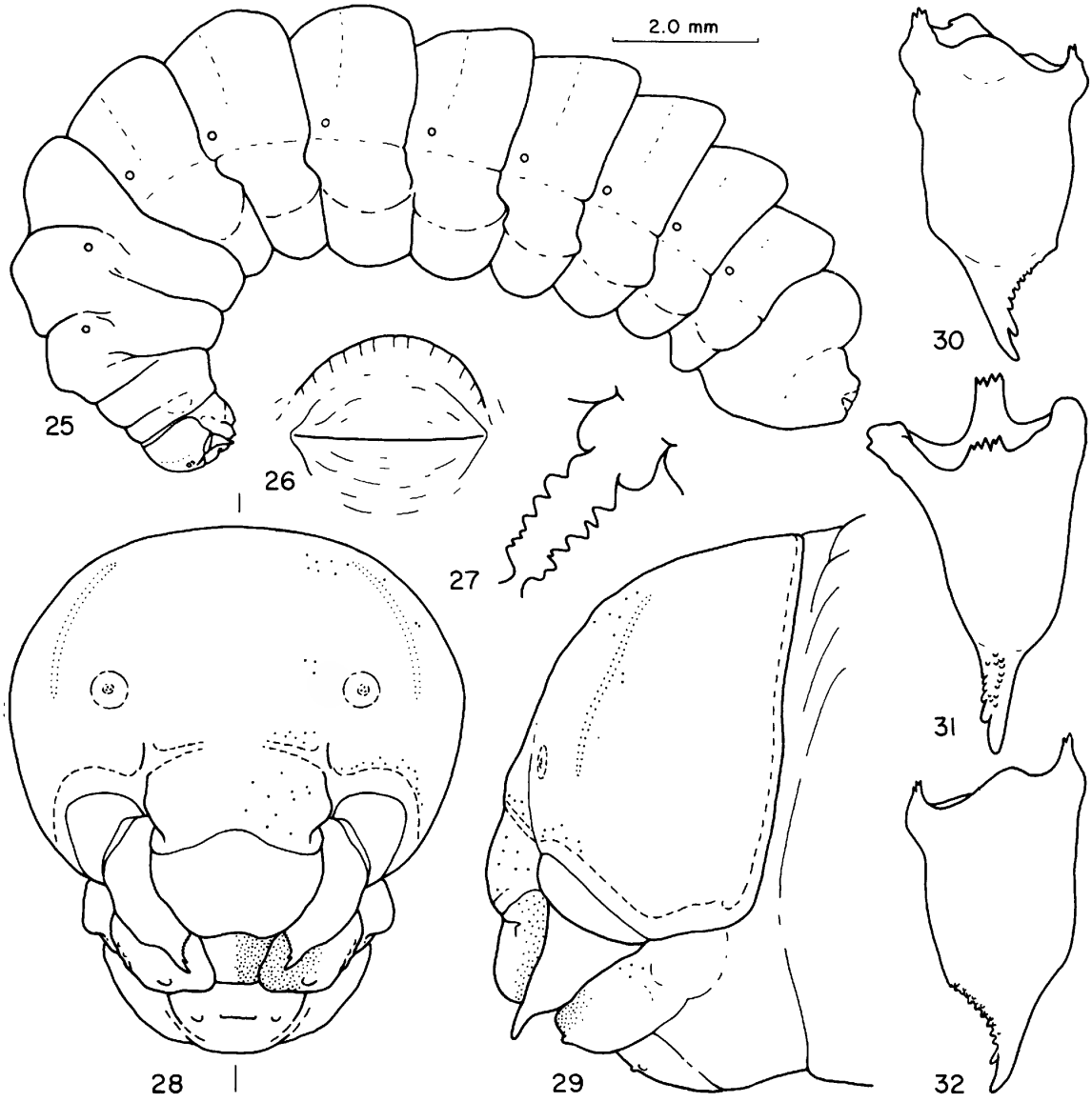
Head (*figs.* 28, 29). Integument without setae but with scattered sensilla; epipharynx, hypopharynx, dorsal and apical surface of maxilla,



FIGS. 17-24. *Mellitta leporina*. 17. Postdefecating larva, lateral view. 18. Perianal area, caudal view. 19. Spiracle. 20. Head, lateral view. 21. Head, frontal view, right side showing distribution of spicules and sensilla. 22-24. Right mandible, dorsal, inner, and ventral views.
Scale refers to figure 17.

lateral surface of labrum, and apical portion of prementum (above salivary slit) spiculate to densely spiculate; pigmentation moderate, darker than those of other melittids. Head elongate, length (top of vertex to base of labium) greater than greatest width; in lateral view (fig. 29), vertex evenly rounded, supraclypeal area flattened. Tentorium complete and well developed; anterior tentorial pit situated immediately above epistomal ridge; posterior pit at junction of hypostomal ridge and posterior thickening of head; area of capsule immediately behind junction not swollen; posterior thickening of head capsule, hypostomal ridge, and pleurostomal ridge well devel-

oped; epistomal ridge fading somewhat toward median line of head; longitudinal thickening of head absent; parietal band well expressed. Antenna not arising from protuberance, low on face; antennal papilla a low convexity bearing three sensilla. Clypeus moderately wide as seen in frontal view (fig. 28), intermediate in width between wide clypeus of most *Hesperapis* and narrow clypeus of *Macropis*; apical margin moderately emarginate. Labrum unusually large, longer than clypeus; apical margin moderately emarginate; apicolateral swellings well developed but distinct labral tubercles absent. Mandibles (figs. 30-32) moderate in length, moderately robust at base but becoming suddenly slender apically so that base appears swollen, apex



FIGS. 25-32. *Dasypoda plumipes*. 25. Postdefecating larva, lateral view. 26. Perianal area, caudal view. 27. Spiracle. 28. Head, frontal view, right side showing distribution of spicules and sensilla. 29. Head, lateral view. 30-32. Right mandible, dorsal, inner, and ventral views.
Scale refers to figure 25.

simple; moderately small dorsal subapical tooth present; cusp well produced with a conspicuous row of teeth extending apically along ventral edge of dorsal adoral surface but with few teeth present on surface itself; dorsal inner edge well defined, curved inward when viewed dorsally or ventrally and with numerous well-formed teeth; ventral edge poorly defined, without teeth; apical concavity poorly defined. Labiomaxillary region moderately recessed, but not so much as that of *Hesperapis*; maxillae and labium not greatly fused. Maxilla, as seen in lateral view (fig. 29), produced well beyond apex of labium, apex bent strongly mesiad, inner apical angle sharply produced; cardo only slightly sclerotic but quite distinct because of dark pigmentation; palpus small, its length subequal to basal diameter; all signs of galea absent. Labium divided into prementum and postmentum, but this division not greatly pronounced; palpus very small, smaller than maxillary palpus (length shorter than basal diameter). Salivary opening moderately narrow, straight, transverse slit on only very weakly projecting lips; salivary lips in same, or only slightly higher, horizontal plane as labial palpi (fig. 28). Hypopharynx protruding beyond labium, distinctly separated from labium by deep hypopharyngeal groove.

Body. Integument spiculate anteroventrally, dorsum of abdominal segment X nonspiculate, setae absent. Form (fig. 25) moderately robust, abdomen not tapering greatly; intersegmental lines of postdefecating form deeply incised; paired dorsal tubercles absent; lateral swellings below spiracles well defined; dorsal intrasegmental lines weak but evident on most body segments so that cephalic and caudal annulets poorly differentiated; caudal annulets somewhat elevated above cephalic annulets; abdominal segment IX with venter elongate; ventral intersegmental line between IX and X not incised; sterna IX and X without intrasegmental lines; segment X ventral in attachment to IX, not elongate, venter not produced posteriorly; anus apical; anus a broad, straight, transverse, pigmented slit (fig. 26); perianal area not puckered; pronounced transverse ridge just anterior to perianal area present (fig. 26), giving segment truncate appearance in lateral view. Spiracles (fig. 27) on low elevations; atria produced above body surface; atrial wall with low ridges but without spines or denticles; rim and peritreme present; primary tracheal opening with short but distinct collar; subatrium somewhat short in length with relatively few annulations. Male with distinct median transverse cuticular invagination of abdominal sternum IX approximately one-fourth distance from posterior end of segment; female with paired imaginal discs on segments VII, VIII, and IX; these discs halfway between intersegmental lines; discs of segment VII farthest apart and those of segment IX closest together, being approximately two disc diameters apart; cuticular scars evident beneath each disc; faint median transverse scar apparently present on segment IX in same position as invagination of male.

Material Studied. Two postdefecating larvae, "Hojbakkegard," Tastrup, 15 km. west of Copenhagen, Denmark, May 24, 1969 (Mikael Münster-Swendsen).

CAPICOLA FRIESE

Diagnosis. When viewed laterally (fig. 35), the broadly rounded and projecting clypeus and supraclypeal area, fusion of maxillae and labium, and the dorsal attachment of abdominal segment X to segment IX (figs. 33, 34) distinguish the larval *Capicola* described below from other known immature melittids except *Hesperapis*. The presence of paired dorsal tubercles and the absence of intrasegmental lines on abdominal sterna IX and X separate *Capicola* from *Hesperapis*.

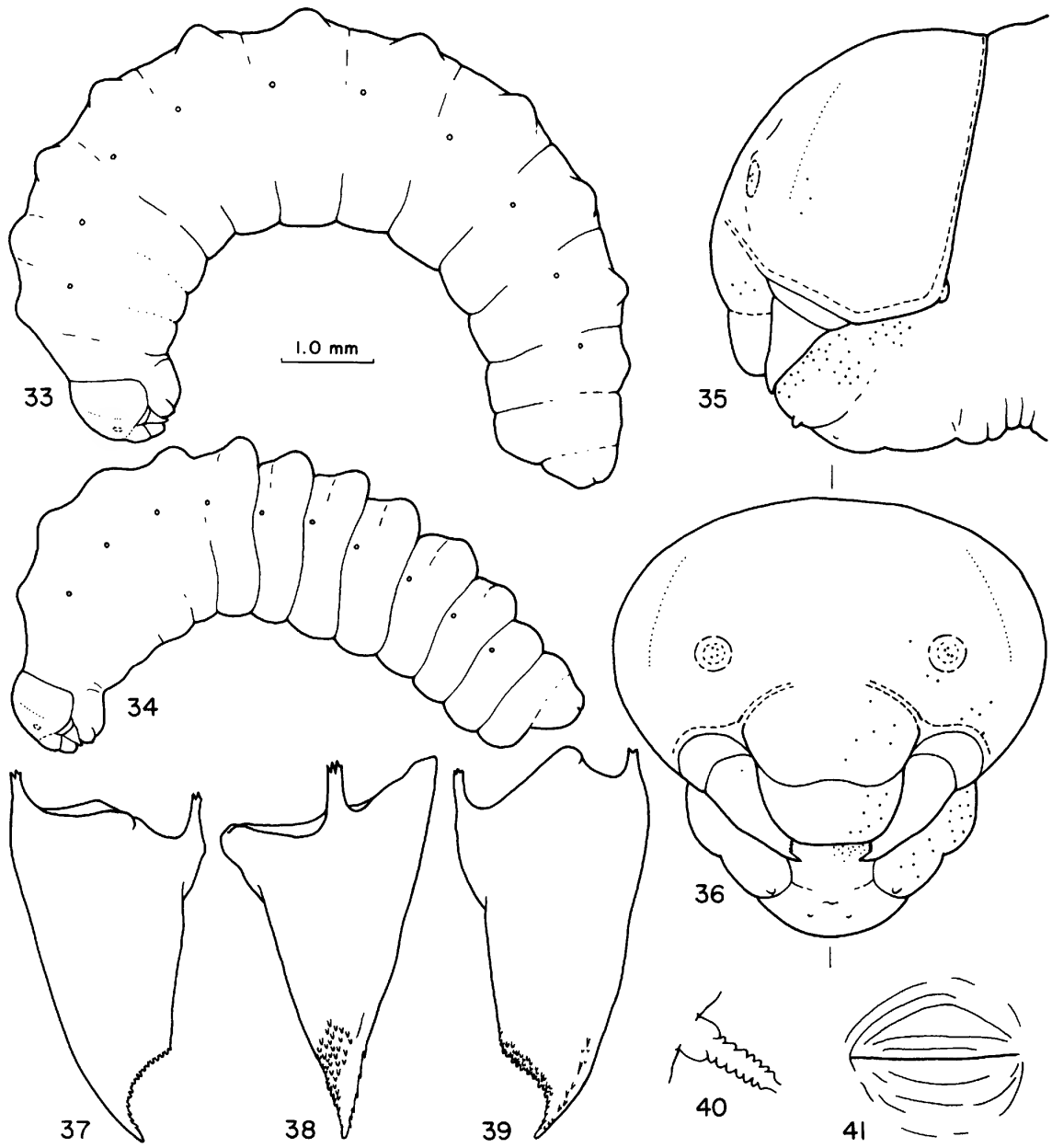
Capicola braunsiana Friese[1]

Figures 33-41

Diagnosis. See that of genus.

Head (figs. 35, 36). Integument without setae but with sensilla present on head capsule, clypeus, labrum, maxillae, and labium (sensilla somewhat dense on lateral side of maxilla, sparse on labium); epipharynx moderately spiculate; hypopharynx weakly spiculate; pigmentation clearly evident only at mandibular articulations and apex. Head broad (fig. 36), length (top of vertex to base of labium) subequal to greatest width; clypeus, supraclypeal area, and vertex broadly, evenly rounded in lateral view (fig. 35) as in *Hesperapis*. Tentorium incomplete, possibly due

[1] Adults kindly identified by Dr. Gerald I. Stage.



FIGS. 33-41. *Capicola* species. 33. Predefecating larva, lateral view. 34. Postdefecating larva, lateral view. 35. Head, lateral view. 36. Head, frontal view, right side showing distribution of spicules and sensilla. 37-39. Right mandible, dorsal, inner, and ventral views. 40. Spiracle. 41. Perianal area, caudal view.

Scale refers to figures 33 and 34.

to nearness of specimen to pupation; anterior tentorial pit on upper part of epistomal ridge; posterior pit at junction of hypostomal ridge and posterior thickening of head; area immediately posterior to junction modified as described in anatomy section; posterior thickening of head capsule, hypostomal and pleurostomal ridges present but somewhat thin; epistomal ridge

present but fading and becoming absent near midline of head; longitudinal thickening of head absent; parietal band extremely faint. Antenna not arising from protuberance; antennal papilla broad, nearly flat convexity bearing three to four sensilla. Clypeus moderately wide as seen in frontal view (fig. 36), intermediate in width between wide clypeus of most *Hesperapis* and narrow clypeus of *Macropis*; apical margin shallowly emarginate but more so than that of *Hesperapis*. Labrum moderate in size with apex nearly truncate, although apicolateral angles more rounded than those of *Macropis*; apicolateral angles slightly swollen but distinct labral tubercles absent. Mandible (figs. 37-39) relatively long, moderately robust at base, tapering to simple apex; large subapical teeth absent; cusp well produced and with numerous well-defined teeth, extending apically along dorsal adoral surface; ventral apical edge weakly formed but with distinct row of long slender teeth; apical concavity poorly expressed. Labiomaxillary region recessed; maxillae and labium greatly fused. Maxilla, in lateral view (fig. 35), produced beyond labium; apex bent very slightly mesiad, inner apical angle not produced; cardo not sclerotized or pigmented; palpus small, length subequal or slightly longer than basal diameter; galea absent. Labium faintly divided into prementum and postmentum by depression on ventral surface; palpus extremely small, much smaller than maxillary palpus (fig. 35). Salivary opening poorly developed, transverse slit without lips; opening well above labial palpi (fig. 36). Hypopharynx protruding about as far as labium; hypopharyngeal groove indistinct.

Body. Integument spiculate ventrally, dorsum of abdominal segment X nonspiculate; setae absent. Form (figs. 34, 35) moderately slender; intersegmental lines well incised on postdefecating larva; well-defined but moderately low paired dorsal tubercles present on caudal annulets of postdefecating form (fig. 34); unlike those of *Macropis*, these tubercles only indistinctly transverse; on predefecating larva, these tubercles present as conspicuous rounded swellings (fig. 33); lateral swellings below spiracles not clearly defined; dorsal intrasegmental lines absent; because of tubercles, caudel annulets distinctly higher than cephalic annulets; abdominal segment IX with venter normal in length; ventral intersegmental line between segments IX and X normally incised; unlike those of *Hesperapis*, abdominal sterna IX and X without intrasegmental lines; segment X dorsal in attachment to IX (figs. 33, 34), not elongate; anus slightly dorsal in position, distinctly transverse; perianal area faintly ridged by nearly concentric grooves (fig. 41); perianal area and dorsum just anterior to perianal area without ridges. Spiracles (fig. 40) not on elevations; atrial rim present and only slightly produced above body surface; peritreme present; atrial wall without spines or ridges; primary tracheal opening present, moderate in length; subatrium relatively short with few annulations. Male with distinct, dumbbell-shaped, pigmented, median cuticular invagination of abdominal sternum IX approximately one-third distance from posterior end of segment; imaginal discs of female genitalia already developing on specimens; position approximately as described for *Hesperapis pellucida*; cuticular scar on sternum IX apparently absent.

Material Studied. Two postdefecating larvae, two predefecating larvae, 67 km. east of Port Nolloth, Cape Province, South Africa, October 17, 1972 (J. G. Rozen, Jr., F. C. Thompson, R. J. McGinley).

HESPERAPIS COCKERELL

Diagnosis. As in *Capicola*, the broadly rounded and projecting clypeus and supraclypeal area (figs. 46, 53, 64, 73) as well as the dorsal attachment of abdominal segment X to segment IX (figs. 42, 43, 54, 62, 65, 74) distinguish the larvae of *Hesperapis* from other known immature melittids. The absence of paired dorsal tubercles and presence of intrasegmental lines on abdominal sterna IX and X (fig. 54) distinguish *Hesperapis* from *Capicola*.

Head. Integument without setae but with scattered sensilla; epipharynx, hypopharynx, dorsal and apical surface of maxilla, and lateral surface sparsely to moderately spiculate; pigmentation clearly evident only on apical portion of mandible; head moderately wide to wide, length (top of vertex to base of labium) at most subequal to greatest width; clypeus, supraclypeal area, and vertex usually broadly, evenly rounded in lateral view (figs. 46, 64, 73) and projecting beyond labrum or with supraclypeal area some-

what depressed (fig. 53). Tentorium including dorsal arms, complete but thin (not quite so strong as that of *Dasypoda*); anterior tentorial pit on or slightly above (fig. 44) epistomal ridge; posterior pit at junction of hypostomal ridge and posterior thickening of head capsule; area of capsule immediately behind junction unmodified to distinctly swollen (fig. 64); posterior thickening of head capsule and pleurostomal ridge well developed; hypostomal ridge well developed but short; epistomal ridge well developed and complete or fading toward median line of head; longitudinal thickening of head absent; parietal band well expressed. Antenna low on face, not arising from protuberance or from very slight, roughened elevation, e.g., *H. carinata* (fig. 64); antennal papilla small, well produced to flat, bearing three to five sensilla. Clypeus wide to moderately wide as seen in frontal view; apical margin emarginate to only slightly emarginate. Labrum not unusually large; apical margin evenly rounded to shallowly emarginate; apicolateral swellings absent to moderately well developed; labral tubercles absent. Mandible (figs. 49-51, 67-72) moderate in length, moderately robust at base, gradually tapering to slender, simple apex; spiculation present on basal dorsal surface, extending to basal adoral surface or apparently absent; enlarged subapical tooth absent; cusp poorly to well defined, with numerous small teeth extending apically along dorsal adoral surface (figs. 57, 60, 68, 71) or teeth apparently absent, e.g., *H.* species b (fig. 77); dorsal inner edge well defined, curved inward to various degrees when viewed dorsally or ventrally and with numerous teeth of variable length and sharpness or with few, relatively large teeth (fig. 77); ventral edge poorly defined and with or without minute teeth; apical concavity weakly produced. Labiomaxillary region recessed; maxillae and labrum nearly completely fused basally. Maxilla, in lateral view (figs. 46, 53, 64, 73), produced well beyond apex of labium, maxillary apex not bent mesiad, inner apical angle not produced; cardo not sclerotized or pigmented; palpus very small, length less than basal diameter; galea absent. Labium with prementum and postmentum indicated by ventral depression; palpus minute, smaller than maxillary palpus. Salivary opening small and narrow, dorsomesiad to labial palpi (fig. 44); lips minute, scarcely visible or present as low, surrounding circular rim. Hypopharynx protruding about as far as labium; hypopharyngeal groove faint.

Body. Integument mostly smooth and nonspiculate, without setae. Form (figs. 42, 43) moderately slender to moderately robust; intersegmental lines clearly evident but not so strongly incised as those of *Dasypoda*; paired dorsal tubercles absent; lateral swellings below spiracles present but not so well defined as those of *Dasypoda*; dorsal intrasegmental lines weak but present on most body segments so that cephalic and caudal annulets poorly differentiated; caudal annulets only indistinctly elevated above cephalic annulets; abdominal segment IX with venter somewhat elongate (figs. 43, 54) to greatly elongate (figs. 62, 65); ventral intersegmental line between segments IX and X normally incised; abdominal sterna IX and X with transverse intrasegmental lines (fig. 54); segment X dorsal in attachment to IX (figs. 54, 67, 74), elongate (figs. 62, 65, 74) or not elongate (figs. 43, 54); anus apical or perhaps slightly dorsal; anus distinctly to indistinctly transverse and with perianal area nearly circular and puckered (fig. 48) to flattened and wrinkled (fig. 66); perianal area and dorsum just anterior to perianal area without ridges. Spiracles (fig. 47) on distinct elevations, although elevations may not be apparent on predefecating forms; atria with rim and produced above body surface; atrial wall smooth, without spines, ridges or denticles; peritreme present; primary tracheal opening with moderately long and narrow collar; subatrium moderately long, with numerous annulations. Male with distinct median, transverse cuticular invagination on abdominal segment IX in posterior half of segment; female with paired imaginal discs on segments VII, VIII, and IX; these discs (visible only on predefecating larvae) halfway between intersegmental lines; discs of segment VII farthest apart and those of segment IX closest together, being approximately two disc diameters apart; cuticular scar evident beneath each disc; faint median transverse scar apparently present on segment IX in same position as invagination of male.

KEY TO MATURE LARVAE OF *HESPERAPIS*

In the following, we have used the subgeneric groupings as kindly supplied by Dr. Gerald I.

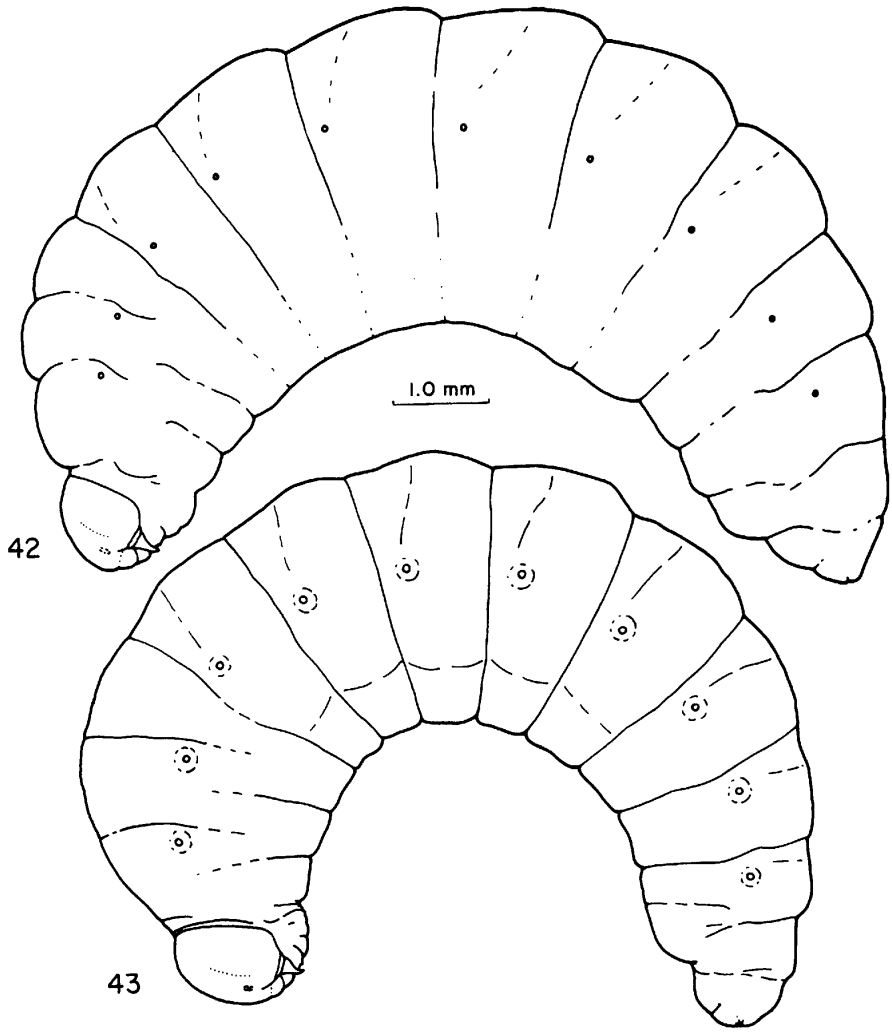
Stage (*in litt.*). Characteristics of the larvae agree with his groupings.

1. Epistomal ridge complete (fig. 44); abdominal segments IX and X short (figs. 43, 54). (*Panurgomia* Viereck) 2
   Epistomal ridge incomplete, fading medially; abdominal segments IX and X short or elongate (figs. 62, 65, 74) ...4
2(1). Antennal papillae nearly flat convexities (fig. 55) ..... *regularis* (Cresson)
   Antennal papillae, though small, well-produced convexities (figs. 45, 52) 3
3(2). Supraclypeal area depressed as seen in lateral view (fig. 53); antennal papillae moderately produced (fig. 52); teeth along dorsal inner edge very short..... ..... *nitidula* Cockrell
   Supraclypeal area broadly rounded as seen in lateral view (fig. 46); antennal papillae strongly produced (fig. 45); teeth along dorsal inner edge moderately long (figs. 49-51) .....*pellucida* Cockerell
4(1). Area immediately behind junction of hypostomal ridge and posterior thickening of head capsule swollen (fig. 64); abdominal segments IX and X elongate (figs. 62, 65); large forms, mature larvae at least 1.5 cm. in length (subgenus I). .5
   Area immediately behind junction of hypostomal ridge and posterior thickening of head capsule not swollen; abdominal segments IX and X short or elongate; smaller forms, mature larvae well under 1.5 cm. in length 6
5(4). Dorsum of abdominal segment X rounded in lateral outline (fig. 62); swelling behind junction of hypostomal ridge and posterior thickening of head capsule large and conspicuous (fig. 64); basal portion of mandible tapering toward apex as seen in dorsal or ventral view (figs. 59, 61) ..... *carinata* Stevens
   Dorsum of abdominal segment X straight in lateral outline (fig. 65); swelling behind junction of hypostomal ridge and posterior thickening of head capsule small and somewhat inconspicuous; basal portion of mandible nearly parallel-sided as seen in dorsal or ventral view (figs. 67, 69) .....species a
6(4). Clypeus wide, as seen in frontal view, combined length of clypeus and labrum less than greatest width of clypeus; teeth along dorsal inner edge small, rather inconspicuous; anterior portion of head capsule, as seen in lateral view (fig. 73) depressed. (*Zacesta* Ashmead). . ..... *rufipes* (Ashmead)
   Clypeus moderately wide, as seen in frontal view, combined length of clypeus and labrum subequal to greatest width of clypeus; teeth along dorsal inner edge elongate and conspicuous (figs. 70-72, 76-78); anterior portion of head capsule, as seen in lateral view, broadly rounded 7
7(6). Epistomal ridge broadly rounded, not reaching level of antennae; dorsal inner edge of mandible with many slender, sharply pointed teeth (figs. 70-72). (*Amblyapis* Cockerell) ....*ilicifoliae* (Cockerell)
   Epistomal ridge arcing dorsally, reaching level of antennae; dorsal inner edge of mandible with approximately five enlarged, blunt teeth (figs. 76-78). (*Hesperapis*).....species b

Hesperapis pellucida Cockerell
Figures 42-51

Diagnosis. See key.

Head (figs. 44, 46). Head capsule moderately wide as seen in frontal view (fig. 44); supraclypeal area, as seen in lateral view (fig. 46), broadly rounded. Area of capsule immediately behind junction of hypostomal ridge and posterior thickening of head capsule only slightly swollen; epistomal ridge well developed and complete, not reaching level of antennae (fig. 44). Antenna not arising from protuberance; antennal papilla small but strongly produced (fig. 45). Clypeus moderately wide, as seen in frontal view (fig. 44), as seen in lateral view (fig. 46) not greatly projecting beyond labrum. Apical margin of labrum only slightly emarginate; apicolateral swellings of labrum absent. Mandible (figs. 49-51) as seen in dorsal or ventral view, with only slight basal swelling on outer margin; sides of basal portion of mandible distinctly tapering apically as seen in dorsal or ventral view; sparse spiculation present on basal, dorsal, and adoral surfaces; cusp poorly defined with numerous small teeth extending apically along dorsal adoral surface; dorsal inner edge curved inward only apically when viewed dorsally or ventrally and with numerous long, slender teeth; ventral edge with minute teeth although these teeth may be obscured in post-



FIGS. 42, 43. *Hesperapis pellucida*. 42. Predefecating larva, lateral view. 43. Postdefecating larva, lateral view.

Scale refers to figures 42 and 43.

defecating forms. Salivary lips minute, scarcely visible.

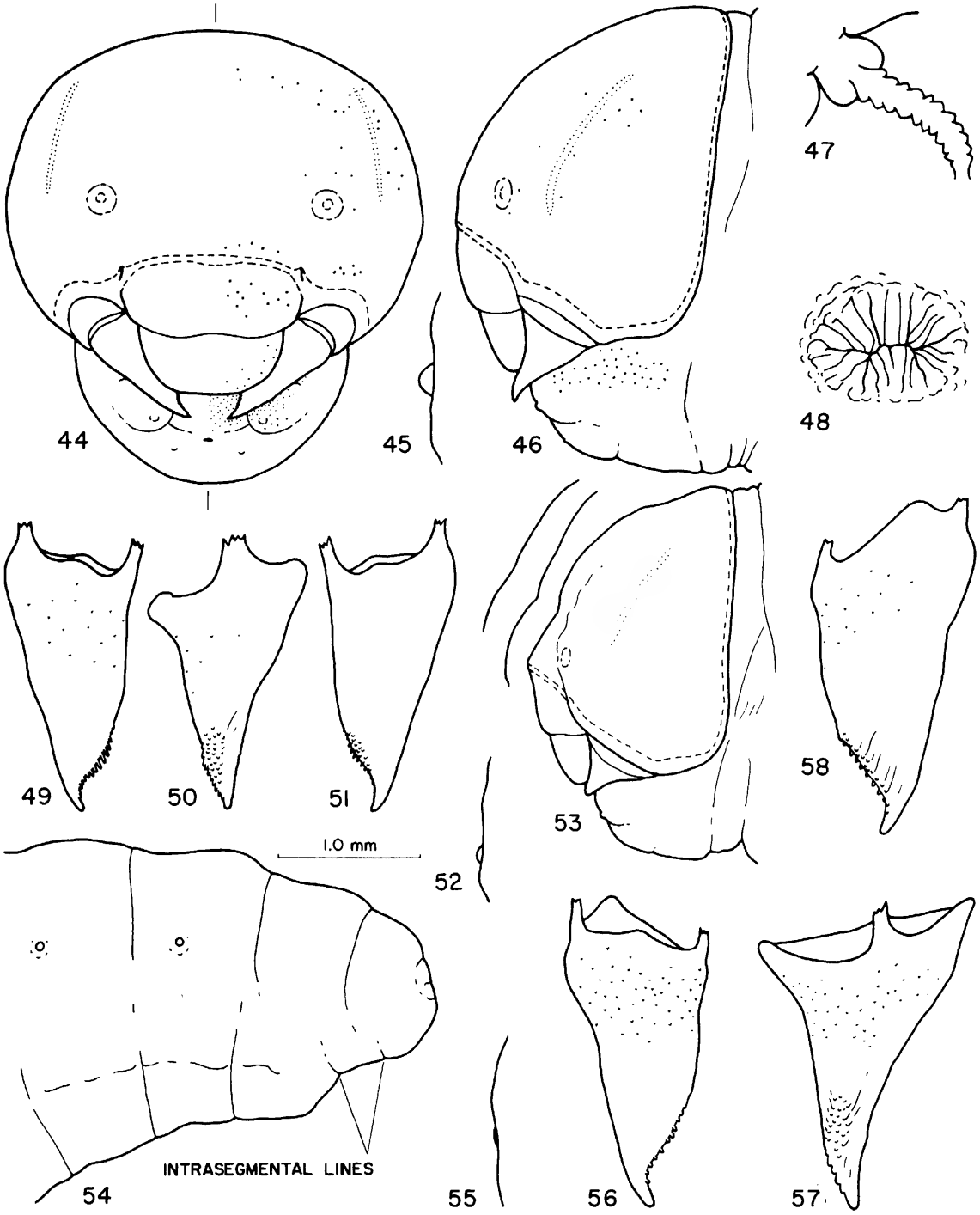
Body. Form (figs. 42, 43) moderately slender; abdominal segment IX with venter perhaps somewhat elongate as in *H. regularis* (fig. 54) but not greatly elongate as in *H. carinata* (fig. 62) and *peninsularis* (fig. 65); segment X not elongate; anus indistinctly transverse and with perianal area nearly circular and puckered (fig. 48).

Material Studied. Three postdefecating and three predefecating larvae, Lobos Creek, San Francisco, California, June 14, 1963 (G.I. Stage).

Hesperapis nitidula Cockerell
Figures 52, 53

Diagnosis. See key.

Head (fig. 53). As described for *H. pellucida* except for following: supraclypeal area, as seen in lateral view (fig. 53), depressed, varying in degree with each specimen observed; antennal papillae moderately produced (fig. 52); apical labral margin nearly rounded to moderately emarginate; apicolateral swellings of labrum slightly developed or absent; mandible somewhat shorter; teeth along dorsal inner edge short.



FIGS. 44-51. *Hesperapis pellucida*. 44. Head, frontal view, right side showing distribution of spicules and sensilla. 45. Right antenna, ventrolateral view. 46. Head, lateral view. 47. Spiracle. 48. Perianal area, caudal view. 49-51. Right mandible, dorsal, inner, and ventral views.

FIGS. 52, 53. *Hesperapis nitidula*. 52. Right antenna, ventrolateral view. 53. Head, lateral view, showing varying degrees of supraclypeal depression.

FIGS. 54-58. *Hesperapis regularis*. 54. Terminal abdominal segments, lateral view. 55. Right antenna, ventrolateral view. 56-58. Right mandible, dorsal, inner, and ventral views.

Scale refers to figure 54.

Body. As described for *H. pellucida.*

Material Studied. One postdefecating and three predefecating mature larvae, Eaton Canyon, San Gabriel Mountains, Los Angeles County, California, June 6, 1963 (G. I. Stage).

Hesperapis regularis (Cresson)
Figures 54-58

Diagnosis. See key.

Head. As described for *H. pellucida* except for following: head capsule wider as seen in frontal view, labrum shallowly emarginate apically; antennal papillae small, very low convexities (fig. 55), much less projecting than those of *H. pellucida* or *H. nitidula*; mandible (figs. 56-58) robust basally, basal outer surface of mandible, viewed dorsally, usually more swollen than that of *H. pellucida*; moderately dense spiculation present on basal dorsal and adoral surfaces of mandible, becoming sparse on ventral surface; teeth along dorsal inner edge of mandible shorter (on some specimens dorsal teeth may be very sharp, apex very acute, and ventral teeth distinct and sharp, as illustrated by Burdick and Torchio, 1959).

Body. As described for *H. pellucida.*

Material Studied. Two mature predefecating larvae, Antioch, Contra Costa County, California, April 2, 1963 (G. I. Stage); two postdefecating larvae, Arroyo Seco, Monterey County, California, April 15, 1958 (P. F. Torchio).

Hesperapis carinata Stevens
Figures 59-64

Diagnosis. See key.

Head (fig. 64). As described for *H. pellucida* except for following: head capsule somewhat wider, roughly sculptured; area immediately behind junction of posterior thickening of head and hypostomal ridge distinctly swollen as seen in lateral view (fig. 64); epistomal ridge fading somewhat toward median line of head; antenna arising from very slight, roughened elevation; antennal papilla poorly produced; clypeus, as seen in lateral view, projecting far beyond labrum; apical margin of labrum shallowly to moderately emarginate; apicolateral swellings of labrum moderately developed; mandible (figs. 59-61) roughly sculptured and ridged; teeth on dorsal adoral surface small and less numerous; teeth on dorsal inner edge less numerous; salivary lips although minute, more distinct.

Body. As described for *H. pellucida* except for following: form moderately robust, more elongate; abdominal segment IX with venter greatly elongate (fig. 62), more so than in *H. pellucida* and allies; abdominal segment X elongate, dorsum rounded in lateral outline and thereby differing from that of *peninsularis* which is straight (fig. 65); anus transverse with perianal area flat-elliptical with some ridging but without distinct puckered condition (fig. 63).

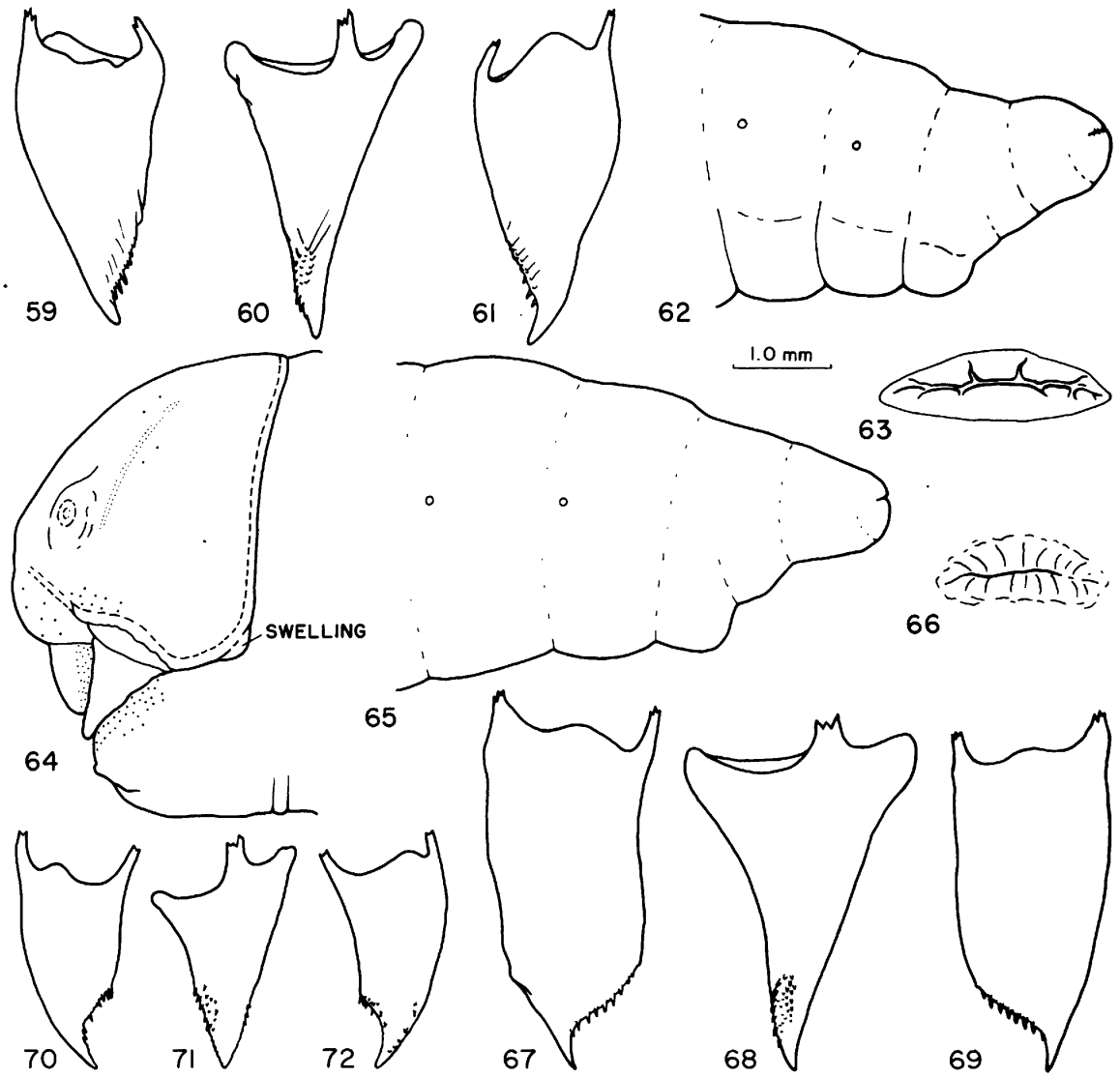
Material Studied. Two mature predefecating larvae, three postdefecating larvae, 2 miles north of Smith, Lyon County, Nevada, September 10, 1965 (G. I. Stage); two predefecating mature larvae, Cornish, Cache County, Utah, August 20, 1959 (G. E. Bohart).

Hesperapis species a
Figures 65-69

Diagnosis. See key.

Head. As described for *H. pellucida* except for following: as seen in frontal view, head capsule wider; area immediately behind junction of posterior thickening of head and hypostomal ridge swollen, but not so conspicuous as that of *H. carinata*; epistomal ridge fading somewhat toward median line of head; antennal papilla poorly produced; clypeus, as seen in lateral view, projecting far beyond labrum; apical margin of labrum shallowly emarginate; apicolateral swellings of labrum moderately developed; mandible (figs. 67-69) more robust; basal portion of mandible nearly parallel-sided when viewed dorsally or ventrally; cusp moderately well defined with teeth on dorsal adoral surface less numerous; dorsal inner edge sharply curved inward, teeth well separated and somewhat regularly spaced; salivary opening, as seen in ventral view, in distinct depression; salivary lips evident as a low circular rim.

Body. As described for *H. pellucida* except for following: form moderately robust, more elongate; abdominal segment IX with venter greatly elongate (fig. 65), more so than in *H. pellucida*; abdominal segment X elongate, dor-



FIGS. 59-64. *Hesperapis carinata*. 59-61. Right mandible, dorsal, inner, and ventral views. 62. Terminal abdominal segments, lateral view. 63. Perianal area, caudal view. 64. Head, lateral view.

FIGS. 65-69. *Hesperapis* species a. 65. Terminal abdominal segments. 66. Perianal area. 67-69. Right mandible, dorsal, inner, and ventral views.

FIGS. 70-72. *Hesperapis ilicifoliae*. Right mandible, dorsal, inner, and ventral views.

sum straight in lateral outline, unlike rounded dorsum of *H. carinata* (fig. 62); anus transverse with perianal area flat-elliptical in outline (fig. 66), not greatly wrinkled or puckered.

Material Studied. Two mature predefecating larvae, San Felipe, Baja California, Mexico, March 26, 1963, nest no. 2 (G. I. Stage).

Hesperapis ilicifoliae (Cockerell)
Figures 70-72

Diagnosis. See key.

Head. As described for *H. pellucida* except for following: head capsule wider in frontal view; epistomal ridge nearly complete, fading slightly toward median line of head; antennal papilla

nearly flat; clypeus, as seen in frontal view, not so wide; apical margin of labrum broadly rounded, not emarginate; mandible (figs. 70-72) relatively short; cusp moderately well defined; dorsal inner edge curved inward from cusp, with teeth more acute than those of *H. pellucida*; ventral edge with conspicuous row of teeth, teeth small and blunt apically, longer and acute basally; orientation of mandible slightly different from other *Hesperapis* in that, when viewed adorally, with apodemes overlapping, mandible appears much wider apically with cusp directed slightly dorsally (in other *Hesperapis* cusp is adoral in orientation); salivary lips virtually absent.

Body. Study of terminal abdominal segments not possible owing to poor condition of the one specimen available.

Material Studied. One postdefecating larva, Diablo Range, 4 miles east of Walnut Creek, Contra Costa County, California, June 19, 1963 (G. I. Stage).

Hesperapis rufipes (Ashmead)
Figure 73

Diagnosis. See key.

Head (fig. 73). As described for *H. pellucida* except for following: head depressed anteriorly, as seen in lateral view (fig. 73); epistomal ridge incomplete; antennal papillae flat; mandible more robust with short dorsal teeth, well-defined ventral teeth, strongly produced cusp and narrow dorsal adoral surface (Michener, 1953, figs. 281-287).

Body. As described for *H. pellucida* except study of terminal abdominal segments not possible because specimen damaged. The illustrations of the terminal abdominal segments presented by Michener, 1953, may be inaccurate, as judged by other *Hesperapis* now available for study.

Material Studied. One postdefecating larva, Tanbark Flat, San Gabriel Mountains, Los Angeles County, California, July 16, 1952 (J. W. MacSwain).

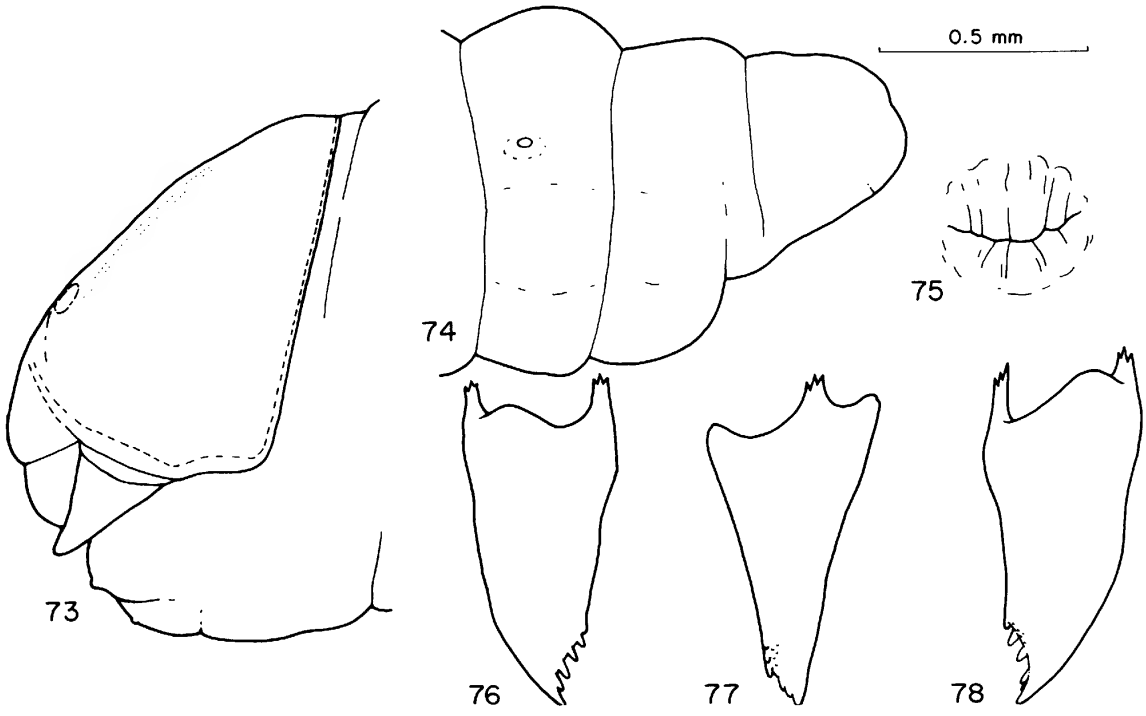


FIG. 73. *Hesperapis rufipes*. Head, lateral view.

FIGS. 74-78. *Hesperapis* species b. 74. Terminal abdominal segments, lateral view. 75. Perianal area. 76-78. Right mandible, dorsal, inner, and ventral views.

Scale refers to figure 74.

The specimen available for this study differed from that of Michener's by its more depressed head capsule and by the presence of an incomplete epistomal ridge.

Hesperapis species b
Figures 74-78

Diagnosis. See key.

Head. As described for *H. pellucida* except for following: head capsule wider, cuticle crinkled and roughly textured; epistomal ridge incomplete, fading medially but arcing upward so that meeting point of ridge, if extended, would be nearly in line with lower margin of antennae; antennal papilla nearly flat; clypeus much narrower than that of *H. pellucida*; apical margin of labrum broadly rounded, not emarginate; mandible (figs. 76-78) with cusp moderately well defined with only very few teeth extending apically along dorsal adoral surface; dorsal inner edge curved inward from cusp when viewed dorsally or ventrally and with only few, enlarged teeth; ventral teeth absent; apical concavity moderately produced.

Body. As described for *H. pellucida* except for following: abdominal segment IX with venter elongate (fig. 74), approaching condition of *H. carinata*; segment X elongate, with slight swelling present at base of dorsum; perianal area nearly circular in outline, similar to that of *H. pellucida*, but not distinctly puckered (fig. 75).

Material Studied. Three postdefecating larvae, 2.8 miles west of Wadsworth, Washop County, Nevada, June 30, 1963 (G. I. Stage).

APPENDIX
Pupae of Melittidae

Because no melittid pupa has been described taxonomically, at least in recent times, we offer the following two accounts.

Melitta leporina (Panzer)
Figures 79, 80

Diagnosis. Knowledge of bee pupae is still so incomplete that satisfactory diagnoses are not possible. However, the pupa of *Melitta leporina* can be separated from pupae of the Panurginae by the fact that most of the Panurginae have a tubercle at the base of the hind tibia. The absence of a tubercle on the outer surface of the fore wing will presumably separate *M. leporina* from halictids, and the absence of body setae will separate *M. leporina* from most, if not all, the Megachilidae. In general, the arrangement of body tubercles and the very elongate pronotal, genal, and leg tubercles will probably be useful in separating this pupa from pupae of other taxa.

Head. Integument without setae or spicules. Scape, frons, and vertex without tubercles; pedicle with at most weakly developed tubercle; gena with elongate spine parallel to mandible; mandible simple (not bifid as that of adult) with tubercle on ventral surface.

Mesasoma. Integument without setae or spicules. Lateral angles of pronotum strongly produced as spines; posterior lobe of pronotum strongly produced, acutely pointed posteriorly; mesepisternum without tubercles; mesoscutum without tubercles; axilla not produced and otherwise undifferentiated; scutellum with pair of moderately large, broad, anteriorly projecting tubercles; metanotum with pair of anteriorly directed tubercles which are apparently more elongate in male than in female; propodeum without protuberances. Tegula without tubercles; wing without tubercle. Each coxa with long spine; each trochanter with long spines, extremely long on fore trochanters; fore femur with extremely long broad spine; midfemur of female with long basal spine (absent in males); apex of hind femur with small tubercle on inner surface; this tubercle visible in lateral view on male but somewhat smaller and visible only in dorsal view (fig. 80) on female; apex of hind tibia with broad protuberance.

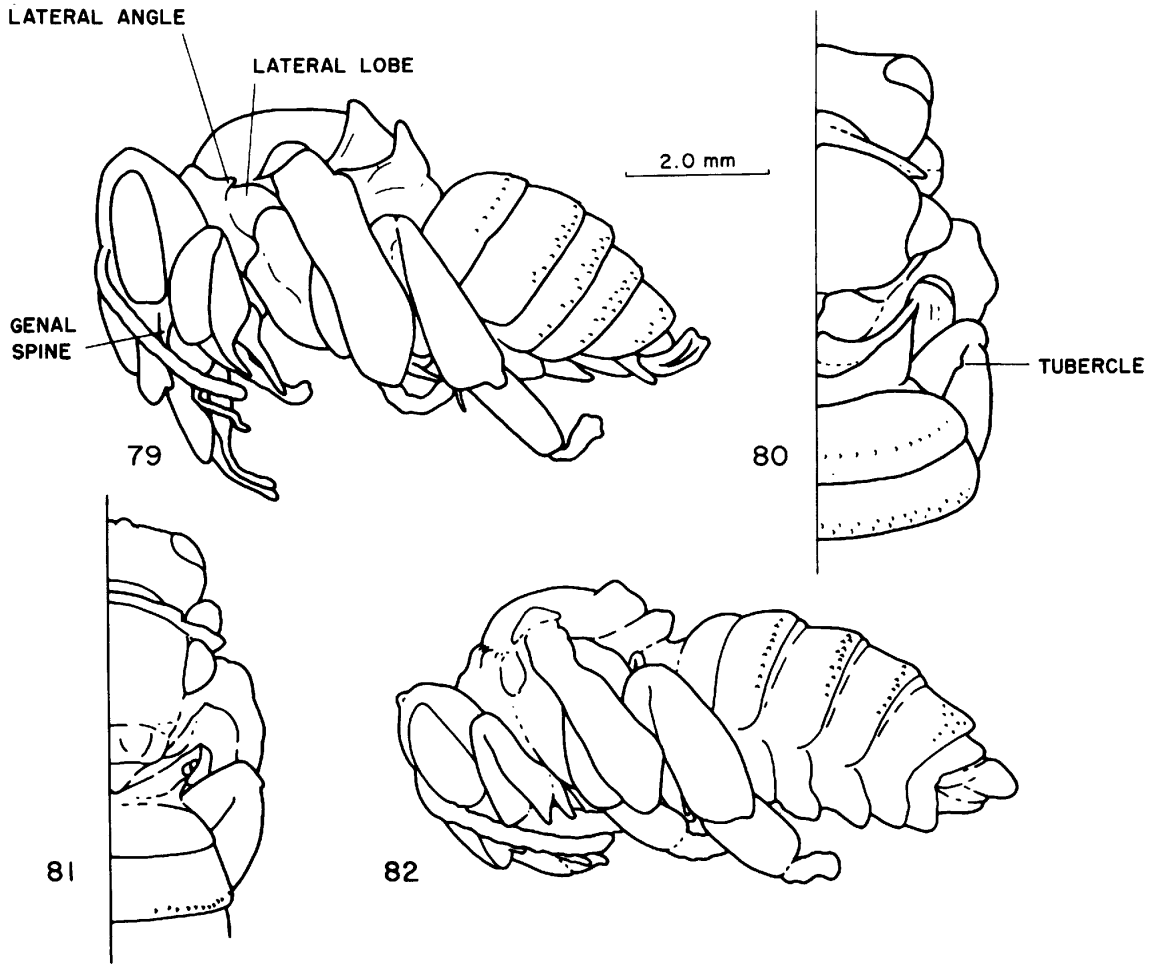
Metasoma. Integument without setae. Tergum I with single row of small tubercles; terga II-V (female) and II-VI (male) with two irregular rows of small tubercles; sterna apparently without tubercles; terminal spine short, broadly rounded, deeply ridged laterally.

Material Studied. One female, two males, France, 1964 (S. Tirgari).

Macropis europaea Weke
Figures 81, 82

Diagnosis. The pupa of *Macropis europaea* differs from other known apoid pupae by the diagnostic characters given for *Melitta leporina* and differs from the pupa of *Melitta leporina* by the presence of tubercles on the vertex, by the absence of genal and metanotal spines and of tubercles on metasomal tergum I, by the lateral orientation of lateral lobes of the pronotum, and by the much shorter spines of the leg segments.

Head. As described for *Melitta leporina* ex-



FIGS. 79, 80. Pupa of female *Melitta leporina*. 79. Lateral view. 80. Dorsal view.
FIGS. 81, 82. Pupa of female *Macropis europaea*. 81. Dorsal view. 82. Lateral view.
Scale refers to figures 79 to 82.

cept for following: pedicel with small, well-formed tubercle on posterior side strongly formed in male; vertex with two rounded tubercles just mesiad of lateral ocelli; gena with broadly rounded swelling but spine absent; ventral mandibular tubercle more slender and attenuate than that of *Melitta leporina*.

Mesosoma. As described for *Melitta leporina* except for following: lateral angles of pronotum not produced as spines but rounded and only moderately produced; posterior lobe of pronotum strongly produced, differing from that of *Melitta* by less acute, attenuate apex and conspicuous lateral orientation (posteriorly directed in *Melitta*); scutellum with pair of broad, narrowly rounded tubercles, not so acute or so anteriorly directed as those of *Melitta*; metanotum slightly produced with shallow, median cleft, lacking distinct tubercles. Fore coxa each with long, attenuate spine; midcoxa each with moderately long narrowly rounded spine; hind coxa each with apically truncate spine, subequal in length to midcoxal spine; each trochanter with two spines; fore and midtrochanter each with small, rounded basal spine and moderately long, pointed apical spine; hind trochanter each with well-developed, narrowly rounded basal spine and thin, short apical spine; fore femur with basal spine moderately long, pointed; midfemur with spine faintly indicated; hind femora without spine; apexes of femora and tibiae without tubercles or protuberances.

Metasoma. Integument without setae. Unlike *Melitta leporina*, tergum I without tubercles; terga II-V (female) and II-VI (male) with irregular row of small tubercles; tubercles on female tergum V very small and widely spaced; sterna without tubercles; terminal spine moderately short, rounded apically, ridged laterally.

Material Studied. One female, two males, Rhenen (Utrecht), Netherlands, pupated in laboratory March 8, 14, 21, 1974 (M. A. Lieftinck).

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