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A Taxonomic Key to Mature Larvae of Cleptoparasitic Bees (Hymenoptera: Apoidea)

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ABSTRACT

A taxonomic key is presented for the identification of mature larvae of cleptoparasitic bees to family, subfamily, tribe, and genus/subgenus. A total of 39 genera/subgenera are treated. All taxonomically important characters are illustrated. A table cites references to mature larvae described since the appearance of "A catalog and review of immature Apoidea (Hymenoptera)" (R. J. McGinley, 1989, *Smithson. Contrib. Zool.* 494: 24 pp.). Other tables list the known or strongly suspected cleptoparasite/host associations at the tribal, subfamilial, and familial levels. A final table lists the genera/subgenera of cleptoparasitic bees whose mature larvae have yet to be found and studied.

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INTRODUCTION

This paper is intended for bee biologists and others interested in identifying mature larvae of cleptoparasitic bees (Apoidea) to family, subfamily, tribe, and genus. It is an outgrowth of a recent phylogenetic study of the genera of the Nomadinae (Apidae) (Roz-en, 1996b), expanded to encompass all cleptoparasitic genera insofar as their larvae are known. Cleptoparasitism has evolved many times among bees. Recently, considerable attention has been directed toward interpreting the variable details of known cleptoparasitic life histories from an ecological and evolutionary perspective. (See, for example, Wcislo and Cane, 1996, and references therein.) Hopefully, the key presented here will assist in gathering additional information about these bees and further stimulate interpretation of their biologies and host relationships.

A cleptoparasitic bee (or cuckoo bee) is one in which the adult female enters the nest of a nonconspecific bee, oviposits in a cell, and then, in most cases, departs from the nest. Depending on the taxon, either the cleptoparasitic larva kills the host egg (or larva) or the cleptoparasitic female destroys the host egg before she oviposits. The larval cleptoparasite matures on the provisions stored for the host's larva. Thus, following Wcislo (1987), a distinction is made between cleptoparasites and social parasites.

This paper does not deal with socially parasitic bees. The reader should be aware that social parasites attack nests of social bees and that there are relatively few lineages of socially parasitic bees: *Bombus* (*Psithyrus*) are social parasites of other *Bombus*; the parasitic allodapines parasitize nests of other members of the Allodapini, all of which are social; and parasitic Halictini attack the nests of social Halictini as well as those of various solitary taxa. Hence, when a person recovers parasitic larvae from a nest of *Bombus* or an allodapine, these larvae cannot be identified using this paper. However, parasitic Halictini present a problem in that their halictine hosts (but not their other hosts) are a mixture of solitary and social forms. Furthermore, some of the social halictines may be attacked by cleptoparasites as well as by social parasites. For these reasons, the key distinguishes *Mi-*

crosphecodes, at least one species of which appears to be a social parasite, from clepto-parasitic *Sphecodes*.²

Larvae of many different holometabolous insects, especially those of Coleoptera and Hymenoptera, might be encountered in a bee nest because of the parasitoid habits of certain taxa. "Immature Insects" (Stehr, 1987, 1991) will enable identification of a parasitoid larva to order and family, although the user should be aware that familial classification of the Apoidea has undergone modification since the publication of the first volume. Most notably, Apidae is now generally recognized (Roig-Alsina and Michener, 1993) to include both the Anthophoridae and Apidae as used by Stehr (1987). A larva known to be that of a bee can be keyed to family in that work, and, if suspected of being a cleptoparasite, may be further identified by use of the key presented here. Alternatively, any larva known to be that of a cleptoparasitic bee should key to family here with the exception of Colletidae. (See comments in introduction to key.) Most larvae that run to Apidae (couplets 5, 8) can also probably be identified correctly to tribe and even to genus, because larval representatives of this family are now quite well-known (despite certain troublesome gaps). Although larvae of certain common and widely distributed cleptoparasites in the Halictidae (e.g., *Sphecodes*) and Megachilidae (e.g., *Coelioxys*, *Dioxys*, and *Stelis*) have been studied, many others are unknown. As a result, the key may be less useful for these families.

Most cleptoparasitic Apidae are known to have hospicidal first or second instars, that is, the instar is equipped with unusually long, sharply pointed mandibles, strongly sclerotized head capsules, special ambulatory fea-

² Our knowledge of *Sphecodes* biology is limited. Some species may actually be socially parasitic, and perhaps not all *Microsphecodes* are social parasites. Indeed, the distinction between cleptoparasitism and social parasitism in the Halictini may simply rest upon whether the parasite departs immediately after ovipositing or remains in the nest to attack other cells. If we define cleptoparasitism and social parasitism this way, we may have trouble categorizing parasitic bees that are associated with communally nesting, nonsocial bees, such as those Brachynomadini (Apidae: Nomadinae) that are parasites of Exomalopsini (Apidae), and *Psaenythia* (Andrenidae).

tures, and, often, attenuate or enlarged sensory structures (Rozen, 1991). These specialized features, adaptations for seeking and killing host immatures, are usually lost in subsequent instars. The loss is gradual from one instar to the next, and the last instar bears little resemblance to the first or second. This key is intended for the identification of only the last instar, although it might be usable for some of the earlier instars as well. Any larva that has finished defecating or cocoon spinning is a last instar; larvae that have completed half or more of their provisions are also probably last instars.

Among the cleptoparasitic Megachilidae there is considerable diversity regarding which larval instar (*Coelioxys*, *Dioxys*, *Stelis*) (Baker, 1971; Rozen and Favreau, 1967; Rozen, 1987), if any (*Hoplostelis*) (Bennett, 1966), eliminates the host competitor even among the few genera that have been studied. The key will be successful for the last instar whether or not it is hospicial. For the Halictidae, only characters of mature larval *Sphecodes* and *Microsphecodes* were used in preparing the key. These features are the general ones of the Halictinae, and it is unknown to what extent they fit earlier instars. In any event, there is no hospicial larval stage of any halictine known to date.

Predefecating and postdefecating last instars of a species may appear quite different, the former being pale with a seemingly thin, colorless integument and distended body because of ingested food, the latter often (but not invariably) darkly tinted, sometimes (especially with noncocoon-spinning larvae) with a firm integument and a more slender body. Nonetheless, either form should key successfully. Predefecating forms are active, capable of feeding and moving their bodies; postdefecating forms are completely quiescent.

The classification of Roig-Alsina and Michener (1993) is followed for long-tongued bees with the exception that the Dioxyini are considered distinct from the Anthidiini, following Michener and Griswold (1994). References to descriptions of the larvae in the key below can be found in McGinley (1989). References to larval descriptions appearing subsequent to that publication are listed in table 1. An alphabetical

index to species illustrated in this paper, with their authors identified, is given at the end.

Tables 2 and 3 represent another approach to identifying a cleptoparasite larva associated with an identified host. They list known or strongly suspected³ cleptoparasite/host associations at the tribal, subfamilial, and familial levels, and are based primarily on the following references: Celary (1989); Engel (2000), Garófalo et al. (1993); Lieftinck (1972); Mavromoustakis (1954); Michener (1978); Roig-Alsina (1989); Roig-Alsina and Rozen (1994); Rozen (1969, 1994); Rozen and McGinley (1974b); Roubik (1989); Snelling and Brooks (1985); Vicens et al. (1993); and Warncke (1983). The associations have been kindly augmented by Drs. Donald B. Baker, Charles D. Michener, and William T. Wcislo (personal commun.). Tables 2 and 3 will also serve as a quick reference for determining if an unusual new association (extension of host range) has been discovered.

These tables demonstrate that most major groups of solitary bees host one or more cleptoparasitic groups. Table 2 shows that halictid cleptoparasites attack nests of only Colletidae, Andrenidae, Halictidae, and Melitidae, and that megachilid cleptoparasites are restricted to the nests of long-tongued bees (Megachilidae and Apidae). The apid cleptoparasites (table 3) form the largest assemblage of cuckoo-bee taxa within a family; they have by far the greatest array of host taxa and attack taxa within all major bee families except for the Megachilidae.

Table 4 lists the cleptoparasitic genera of bees whose larvae have not been collected and studied.

METHODS

Many characters of taxonomic value used in the following key can be seen in specimens that have not been treated or dissected, but other features (such as the internal cranial ridges, mandibular shape and dentition, and integumental spiculation) are best observed

³ The associations of *Temnosoma* and other augochlorine cleptoparasites with augochlorine hosts and of *Townsendiella* with *Conanthalictus* (Rophitinae), though strongly suspected, have yet to be confirmed by recovering immatures from host nests.

TABLE 1

Mature Cleptoparasitic Bee Larvae Described Since Publication of McGinley (1989)

(Classification of Roig-Alsina and Michener, 1993. Characters of taxa referenced below to Rozen, 1996b, were presented in table 1 of that study. Also presented were the characters of all other larval Nomadinae described up to that time.)

Genus	Species and (reference)
Apidae: Nomadinae	
Ammobatoidini	
<i>Holcopasites</i>	<i>H. eamia</i> (Cockerell)(Rozen, 1996b) <i>H. minimus</i> (Linsley)(Rozen, 1996b) <i>H. ruthae</i> Cooper (Rozen, 1996b)
Biastrini	
<i>Rhopalolemma</i>	<i>R. rotundiceps</i> Roig-Alsina (Rozen, et al., 1997)
Brachynomadini	
<i>Brachynomada</i>	<i>B. roigi</i> Rozen (Rozen, 1994)
<i>Kelita</i>	<i>K. toroi</i> Ehrenfeld and Rozen (Rozen, 1994) <i>K. tuberculata</i> Ehrenfeld and Rozen (Rozen, 1994)
Caenoprosopidini	
<i>Caenoprosopis</i>	<i>C. crabronina</i> Holmberg (Rozen and Roig-Alsina, 1991)
<i>Caenoprosopina</i>	<i>C. holmbergi</i> Roig-Alsina (Rozen and Roig-Alsina, 1991)
Epeolini	
<i>Thalestria</i>	<i>T. species</i> (Rozen, 1996b)
Hexepeolini	
<i>Hexepeolus</i>	<i>H. rhodogyne</i> Linsley and Michener (Rozen, 1996a)
Neolarrini	
<i>Neolarra</i>	<i>N. californica</i> Michener (Rozen, 1996b) <i>N. verbesinae</i> (Cockerell)(Rozen, 1996b) <i>N. vigilans</i> (Cockerell)(Rozen, 1996b) <i>N. species</i> (Rozen, 1996b)
Nomadini	
<i>Nomada</i>	<i>N. gutierreziae</i> (Cockerell)(Rozen, 1996b)
Townsendiellini	
<i>Townsendiella</i>	<i>T. pulchra</i> Crawford (Rozen and McGinley, 1991)
Apinae	
Ericrocidini	
<i>Ericrocis</i>	<i>E. lata</i> (Cresson)(Rozen and Buchmann, 1990)
Protepeolini	
<i>Leiopodus</i> (= <i>Protepeolus</i>) ^a	<i>L. lacertinus</i> Smith (Roig-Alsina and Rozen, 1994) <i>L. abnormis</i> (Jørgensen)(Roig-Alsina and Rozen, 1994)
Isepeolini	
<i>Melectoides</i>	<i>M. bellus</i> (Jørgensen)(Michelette et al., 2000)
Tetrapediini	
<i>Coelioxoides</i>	<i>C. waltheriae</i> Duce (description to be published later)
Euglossini	
<i>Exaerete</i>	<i>E. smaragdina</i> (Guérin-Méneville)(description to be published later)

^a *Protepeolus* is now a junior synonym of *Leiopodus* (Roig-Alsina and Rozen, 1994). The mature larva of *L. singularis* had already been described as *Protepeolus singularis* Linsley and Michener before 1989.

in specimens that have been cleared in a 10% solution of sodium hydroxide (NaOH) and dissected. To clear, sever the head capsule from the rest of the body, and heat the head in the NaOH solution until the tissue is re-

moved. Tease the trachea from the capsule but avoid tearing the tentorium in the process. When mandibular features need to be observed, a mandible can usually be removed from its articulations with forceps and

TABLE 2

Associations of Cleptoparasitic Colletidae, Halictidae, Megachilidae with Tribe, Subfamily, or Family of Host

(Taxa in boldface totally cleptoparasitic; for further explanation, see text. Classification modified from Alexander and Michener, 1995, and Roig-Alsina and Michener, 1993.)

Cleptoparasite	Host	Family		
COLLETIDAE	Colletinae	COLLETIDAE		
	Diphaglossinae			
	Hylaeinae			
	Xeromelissinae			
	Euryglossinae			
HALICTIDAE	STENOTRITIDAE			
	Andreninae	ANDRENIDAE		
	Oxaeinae			
	Liphanthus			
	Protandrenini			
	Anthemurgini			
	Austropanurgini			
	Panurgini			
	Melitturgini			
	Perditini			
	Protomelitturgini			
	Calliopsini			
	Augochlorini	Nomiinae	HALICTIDAE	
		Rophitinae		
		Nomioidinae		
Halictini				
Augochlorini				
MELITTIDAE	Melittinae	MELITTIDAE		
	Meganomiinae			
	Dasypodainae			
MEGACHILIDAE	Pararhophitini	MEGACHILIDAE		
	Fidelliini			
	Lithurgini			
	Anthidiini			
	Osmiini			
	Megachilini			
	APIDAE		Xylocopinae	APIDAE
			Tetrapediini	
			Euglossini	
			Bombini	
Apini				
Meliponini				
Centridini				
Anthophorini				
Exomalopsini				
Ancyliini				
Eucerini				
Emphorini				
Ctenoplectrini				
Tapinotaspidini				

TABLE 3

Associations of Cleptoparasitic Apidae with Tribe, or Subfamily, or Family of Host

(Taxa in boldface totally cleptoparasitic; for further explanation, see text. Classification modified from Alexander and Michener, 1995, and Roig-Alsina and Michener, 1993.)

Cleptoparasite	Host	Family
NOMADINAE	Colletinae Diphaglossinae Hylaeinae Xeromelissinae Euryglossinae	COLLETIDAE
Ammobatini		
Caenoprosopidini		
Neolarrini		
Townsendiellini		
Nomadini		
Biastini		
Hexepeolini		
Ammobatoidini		
Brachynomadini		
Epeolini		
	STENOTRITIDAE	
	Andreninae Oxaeinae Liphanthus Protandrenini Anthemurgini Austropanurgini Panurgini Melitturgini Perditini Protomelitturgini Calliopsini	ANDRENIDAE
	Nomiinae Rophitinae Nomioidinae Halictini Augochlorini	HALICTIDAE
	Melittinae Meganomiinae Dasypodainae	MELITTIDAE
	Pararhophitini Fidelliini Lithurgini Anthidiini Osmiini Megachilini	MEGACHILIDAE
	Xylocopinae Tetrapediini Euglossini Bombini Apini Meliponini Centridini Anthophorini Exomalopsini Ancylini Eucerini Emphorini Ctenoplectrini Tapinotaspidini	APIDAE
Tetrapediini		
Rhathymini		
Euglossini		
Ericrocidini		
Melectini		
Osirini		
Protepeolini		
Isepeolini		
Ctenoplectrini		

TABLE 4

Genera/Subgenera of Cleptoparasitic Bees with Unknown Mature Larvae

(Classification of Roig-Alsina and Michener, 1993; Eardley, 1994. No cleptoparasitic larvae known for any subfamilies/tribes in boldface. Asterisk [*] indicates that not all species in the taxon are cleptoparasitic.)

COLLETIDAE	APIDAE
Hylaeinae	Epeolini
<i>Hylaeus</i> (<i>Nesoprosopis</i>)*	<i>Doeringiella</i> (described by Claude-Joseph, 1926, but needs redescription)
HALICTIDAE	<i>Rhogepeolus</i>
Halictini	<i>Rhinepeolus</i>
<i>Echthralictus</i>	<i>Trophocleptria</i>
<i>Parathrincostruma</i>	Ammobatini
<i>Lasioglossum</i> (<i>Paradialictus</i>)	<i>Melanempis</i>
<i>Lasioglossum</i> (<i>Dialictus</i>)*	<i>Spinopasites</i>
<i>Ptilocleptis</i>	Blastini
<i>Eupetersia</i>	<i>Biastes</i>
<i>Halictus</i> (<i>Paraseladonia</i>)	Ammobatoidini
Augochlorini	<i>Aethammobates</i>
<i>Temnosoma</i>	<i>Ammobatoides</i>
<i>Cleptommation</i>	<i>Schmiedeknechtia</i>
<i>Noctoraptor</i>	Apinae
MEGACHILIDAE	Ctenoplectrini
Osmiini	<i>Ctenoplectrina</i>
<i>Hoplitis</i> (<i>Bytinskia</i>)	Ericrocidini
Anthidiini	<i>Abromelissa</i>
<i>Afrostelis</i>	<i>Aglaomelissa</i>
<i>Euaspsis</i>	<i>Ctenioschelus</i>
<i>Larinostelis</i>	<i>Hopliphora</i>
Dioxyini	<i>Mesocheira</i>
<i>Ensliniana</i>	<i>Mesonychium</i>
<i>Eudioxys</i>	Euglossini
<i>Prodiioxys</i>	<i>Aglae</i>
<i>Paradiioxys</i>	Osirini
<i>Allodioxys</i>	<i>Ecclitodes</i>
<i>Metadiioxys</i>	<i>Epeoloides</i>
<i>Aglaeoapis</i>	<i>Osiris</i>
	<i>Parepeolus</i>

a fine pin after the capsule has been cleared, although this should be avoided if the desired mandibular feature is already visible. Removing the mandible of a small larva can be difficult and may distort the head shape. If mandibular removal is necessary, the right mandible is conventionally dissected so that the left side of the head capsule can be observed intact afterwards.

Spiracular features can be observed if a segment of the body wall with one or more spiracles is removed and cleared in the NaOH solution. However, when dealing with postdefecating larvae with a rigid body integument, you may wish to clear the entire

body after the head has been removed. Not only are the spiracles visible, but features of body shape and spiculation are more easily seen. Such treatment of the postcephalic region of predefecating larvae may cause the body wall to collapse, so that body features other than the spiracles are difficult to interpret. Cleared specimens can be examined and stored in ethanol or glycerin.

MORPHOLOGY

The anatomy of mature larvae of cleptoparasitic bees is fundamentally the same as that of non-cleptoparasitic taxa. Most of the

following terminology is adopted from Michener (1953). See that work, Rozen and McGinley (1974a), and Rozen and Michener (1988) for additional terminology applicable to bee larvae. To illustrate the structures below, larvae of two morphologically contrasting species have been used: *Coelioxys* sp. (figs. 1–6), which spins a cocoon; and *Triepeolus kathrynae* (figs. 7–13), which does not spin a cocoon. Larvae that spin cocoons, such as *Coelioxys*, tend to have well-developed internal head ridges, a robust tentorium, and a labiomaxillary region that projects forward. Larvae that have lost the cocoon-spinning ability, such as *Triepeolus*, have weak internal head ridges, a reduced (thin) tentorium, and a labiomaxillary region that is reduced in size and recessed.

The head (figs. 1, 2, 7, 8) of the larva consists of a weakly but distinctly sclerotized and often pigmented *cranium*, each side of which is called a *parietal*. Internally, the cranium is braced by a number of ridges and the tentorium, although the degree of development of the tentorium and the ridges varies greatly according to taxon. The internal ridge that defines the posterior boundary of the cranium of most taxa is the *postoccipital ridge*. It usually bears the *posterior tentorial pit* at the lowest point on each side, although in some Nomadinae these pits become weak and their position may shift from the ridge. The *hypostomal ridge* is an anterior extension of the ventral extremity of the postoccipital ridge and runs to the *posterior* (or *ventral*) *mandibular articulation*. It thus forms the ventral boundary of the parietal. Then the ridge, now termed the *pleurostomal ridge*, curves around the mandibular corium to the *anterior* (or *dorsal*) *mandibular articulation*. After this point, the ridge, now on the front of the cranium, is termed the *epistomal ridge*, and may be evidenced externally as a suture, the *epistomal suture*. The epistomal ridge and suture are usually apparent between the anterior mandibular articulation and the *anterior tentorial pit* (although al-

most lost in fig. 8), but are usually lost or obscure between the anterior tentorial pits (figs. 2, 8). Extent of the development of the larval *tentorium* varies greatly among bee taxa.

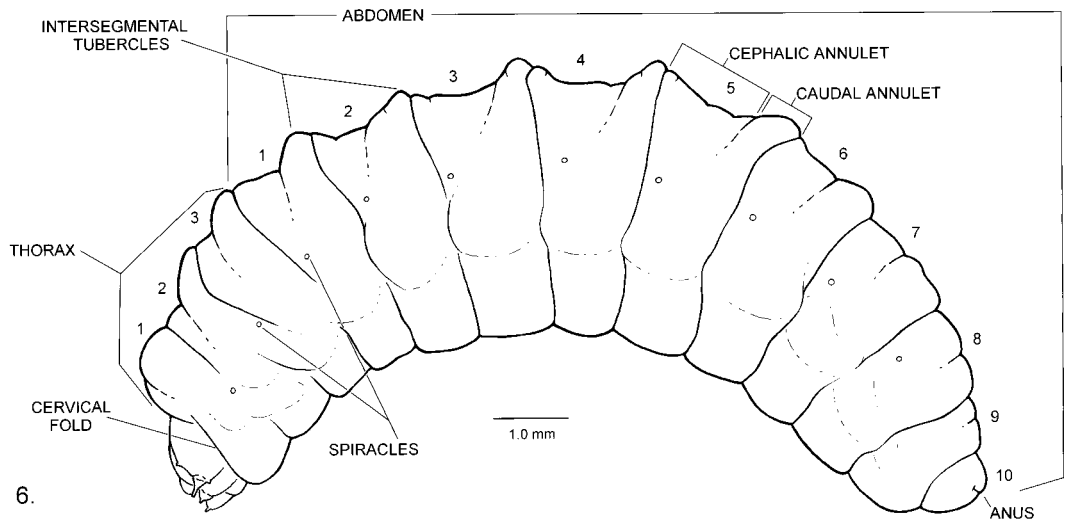
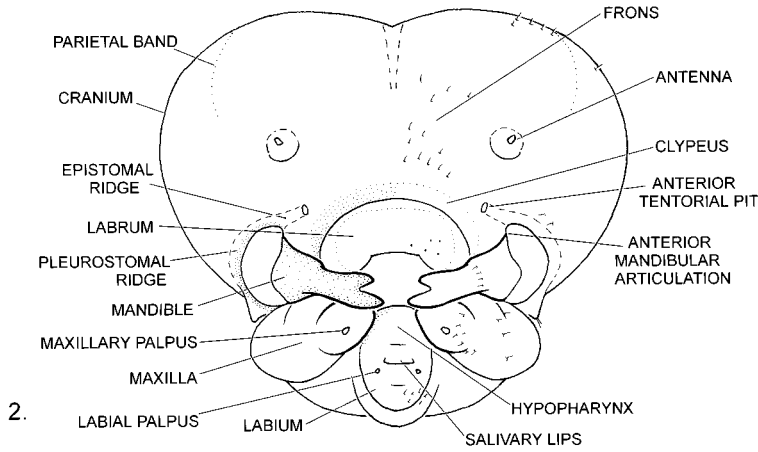
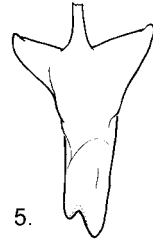
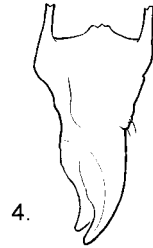
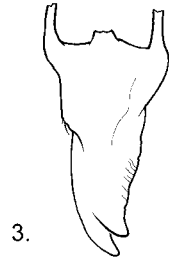
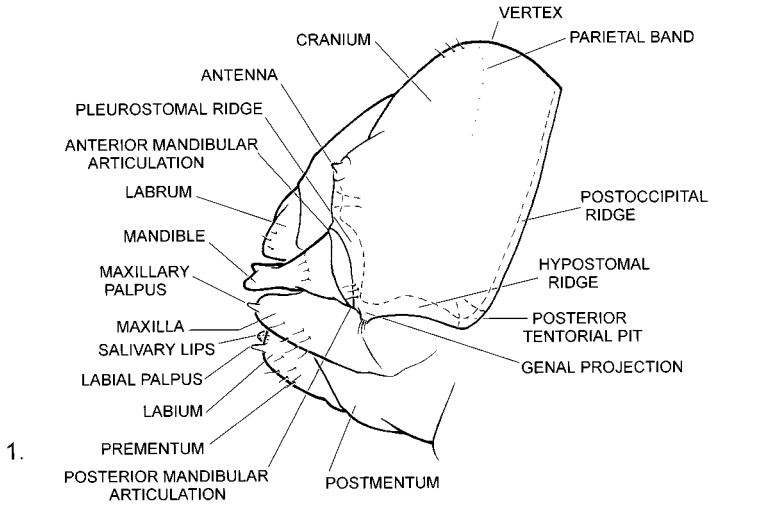
Areas of the cranium (figs. 1, 2, 7, 8) include the *vertex* (the top of the head capsule), the *frons* (the front of the head down to the epistomal ridge), and the *clypeus* (the area between the epistomal suture and the base of the labrum as seen in fig. 34). In the absence of the median part of the epistomal ridge (figs. 2, 8), the boundary between the clypeus and frons is indefinite, as is always the case with the demarcation between the vertex and frons.

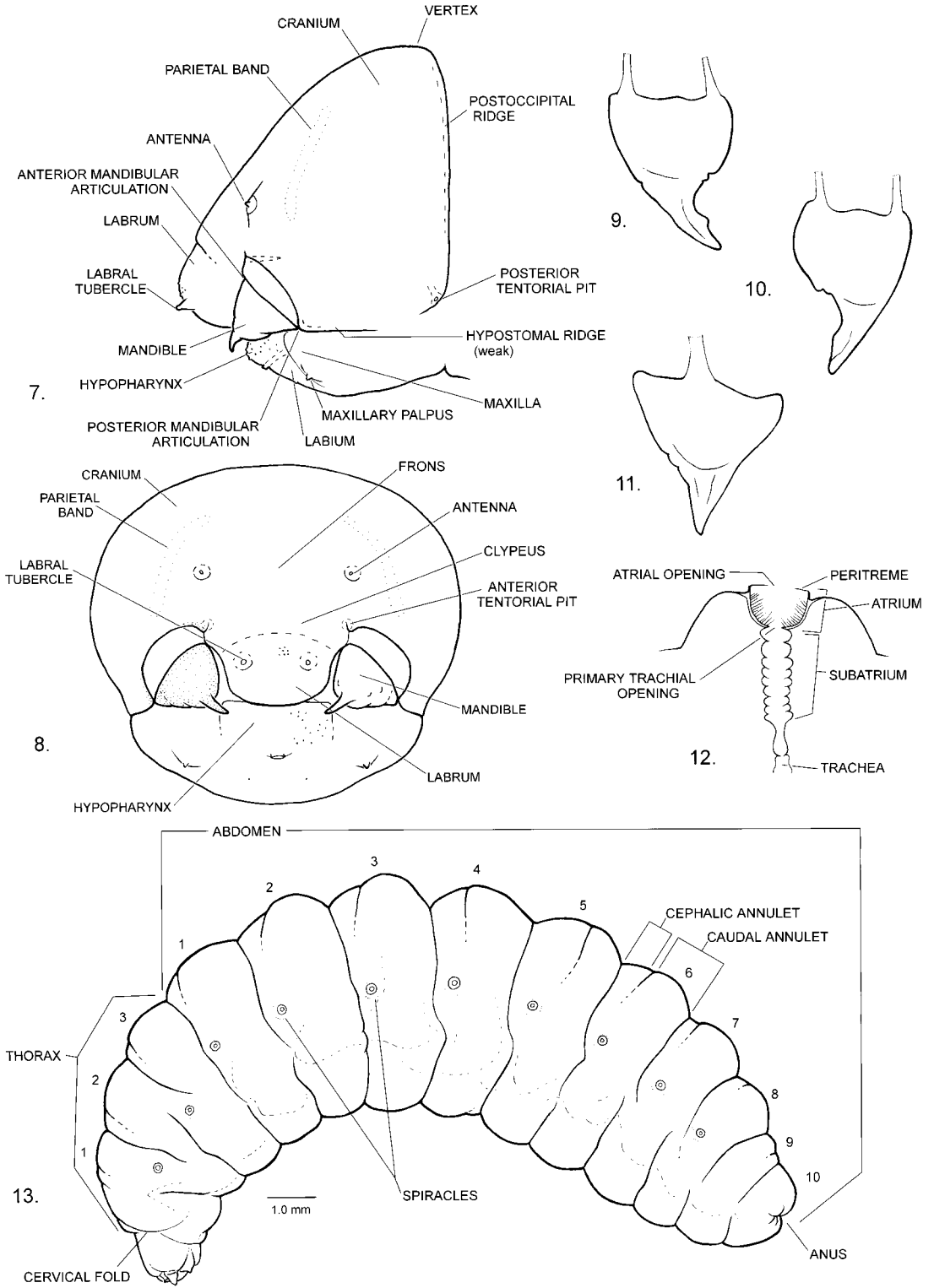
The larval head is without obvious compound and simple eyes, although the usually evident *parietal band* on each side of the cranium may be the external evidence of the imaginal disc that gives rise to the pupal/adult compound eye. A pair of *antennae* is almost always present on the front of the cranium above and slightly laterad of the anterior tentorial pits. The antenna is usually a small blisterlike swelling consisting of a basal *disc* and an apical, sensilla-bearing *papilla*. On a few taxa (fig. 19), the papilla is pronounced.

The *labrum*, subtending the clypeus, is typically flaplike, although it is lobelike in some cleptoparasitic larvae. It often features a pair of sensilla-bearing tubercles (figs. 7, 8). However, in a few taxa there is only a single median tubercle (fig. 29); in others the tubercles are absent and the entire labral apex is arrayed with sensilla (fig. 2). Paired tubercles vary in position; in some larvae they are apical and in others they arise from the disc. The *mandibles* (figs. 3–5, 9–11) are usually a dominant feature of the larval head, because they tend to be conspicuously sclerotized and apically pigmented. They vary greatly in shape, length, and dentition among taxa. The *mouth* is found behind the labrum and between the bases of the mandibles. Between the mouth and the base of the labium

→

Figs. 1–6. Mature larva of *Coelioxys* species. **1, 2.** Head, lateral and frontal views, respectively. **3–5.** Right mandible, dorsal, ventral, and inner views, respectively. **6.** Entire larva, lateral view. Scale refers to fig. 6.





exists the *hypopharynx*, often a distinct lobe separated from the labium by an integumental fold, the *hypopharyngeal groove* (fig. 43). Among some cleptoparasitic bees this groove is lost, so the demarcation between the labium and hypopharynx becomes uncertain (figs. 2, 8).

The *maxillae* and *labium* tend (but not invariably) to be weakly sclerotized. These structures in cocoon-spinning larvae (figs. 1, 2) are more pronounced and distinct from one another than they are on most noncocoon-spinning larvae (figs. 7, 8). On more heavily sclerotized taxa, the maxilla often consists of a discernibly sclerotized *cardo* and *stipes* (fig. 14) and almost always a pronounced, apical *maxillary palpus*. On these larvae (fig. 1), the labium is divided into a basal *postmentum* and an apical *prementum*, and the apex of the prementum bears a pair of transverse, projecting *salivary lips* at the opening of the salivary duct. Below and laterad of the lips can be found the paired *labial palpi*.

On most larvae that do not spin cocoons (figs. 7, 8), the maxillae and labium tend to be reduced and fused into a recessed *labiomaxillary region* (no doubt because the component parts on cocoon-spinning larvae are adaptive for spinning). On such noncocoon-spinning larvae as those of the *Nomadinae*, not only are the sclerotized *cardo* and *stipes* absent, but the maxillary and labial palpi are greatly reduced and recessed, with each labial palpus represented by a single sensilla (fig. 88). The salivary opening, though always present, is inconspicuous, usually as a small circular or transverse opening without lips.

The *cervical fold* (figs. 6, 13) is the boundary between the head and the rest of the body. The body (figs. 6, 13) is composed of a three-segmented *thorax* followed by a ten-segmented *abdomen*. Depending upon the taxon, most of the body segments may be divided dorsally into a *cephalic annulet* and a *caudal annulet*. The *anus* is situated, usu-

ally apically, on abdominal segment 10. Also depending on the taxon, the body segments may bear various tubercles, especially dorsolaterally.

Laterally (rarely nearly dorsally), the thorax bears two pairs of *spiracles*, and each of the first eight abdominal segments also possesses a pair of spiracles. With most bee larvae, a spiracle (fig. 12) consists of a large outer chamber, the *atrium*, that usually projects beyond the body surface, so that its periphery creates a circular *rim*. The atrium is normally covered by a flat plate (the *peritreme*) with a central circular hole (the *atrial opening*). The *atrial wall* may be smooth or variously ornamented with denticles (figs. 89, 90), spines (fig. 12), or fine ridges. The *primary tracheal opening*, usually provided with a *collar* (fig. 90), connects the atrium to the *subatrium* that, in turn, connects to the trachea.

KEY TO CLEPTOPARASITIC BEES, BASED ON KNOWN MATURE LARVAE

This key (pp. 12–24) is to the genera of cleptoparasitic bees whose larvae have been described. Because the mature larva of *Coeioxoides* (Tetrapediini) became available while this study was in progress, it is included, although its description will appear in a later publication. Similarly, the mature larva of *Exaerete* (Euglossini) became available after the manuscript had been accepted for publication. The manuscript was retrieved from the editor so that the key could be expanded and figure 113 added. The larva will be fully described later.

The key also identifies higher taxa containing, in whole or part, cleptoparasitic genera, with two exceptions: 1) Perkins (Perkins and Forel, 1899) identified five species of Hawaiian *Hylaeus* (*Nesoprosopis*) as being “parasitic”. This association appears authentic in that he even reported the host species of three of them. The assumption is that they are cleptoparasites because the hosts are

←

Figs. 7–13. Mature larva of *Tripeolus kathrynae*. **7, 8.** Head, lateral and frontal views, respectively. **9–11.** Right mandible, dorsal, ventral, and inner views, respectively. **12.** Spiracle, side view. **13.** Entire larva, lateral view. Scale refers to fig. 13.

members of the same subgenus; their larvae are unknown as are the larvae of any *Nesoprosopis*. (There seems to be little value in burdening the key with general characters of *Hylaeus* larvae.) 2) The following tribes containing cleptoparasites are not included because cleptoparasitic larvae have yet to be collected and studied: Augochlorini (*Temnosoma*, *Megommation* [*Cleptommmation*], and *Megalopta* [*Noctoraptor*]), Ctenoplectrini (*Ctenoplectrina*), and Osirini (*Ecclitodes*, *Epeoloides*, *Osiris*, and *Parepeolus*). Similarly, among the included tribes, many cleptoparasitic genera are omitted because their larvae are also unknown (table 4).

In the key, North America refers to the region north of Panama; South America, to the region south of Panama.

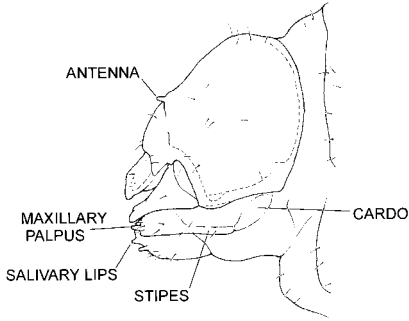
The reader should be mindful that this key is tentative; it is the first attempt to encourage identification of mature larvae of all genera of cleptoparasitic bees. Larvae of many have yet to be discovered; some taxa are represented by a single species, even by a single specimen. This key will certainly be modified after more taxa are found and studied.

- 1. Integument of head and at least anterior body segments with elongate setae (figs. 14, 15, 17); labral sclerite (fig. 15) pigmented (at least in postdefecating larvae) and crescentic as seen in anterior view; salivary opening (figs. 14, 19) with projecting, transverse lips (spinneret); intersegmental midline dorsal tubercles (figs. 6, 17) often evident on abdomen. MEGACHILIDAE 2
- Integument of head with only minute setae (figs. 21, 23); that of body usually without apparent setae, but in Ericrocidini with very fine, short setae; labral sclerite usually unpigmented, not distinguishable from rest of labrum, but, if present (*Coelioxoides*), then salivary opening small, not projecting, and without lips; salivary opening with or without transverse lips; intersegmental, midline dorsal tubercles absent, although paired intrasegmental dorsolateral tubercles often evident (figs. 22, 110) 5
- 2(1). *Either* mandible with more than three setae on outer surface, *or* gena (fig. 1) with pronounced, downward-directed projection (called *pleurostomal thickening* by Baker, 1971) immediately behind posterior mandibular articulation, *or* both characters present. MEGACHILINI *Coelioxys*

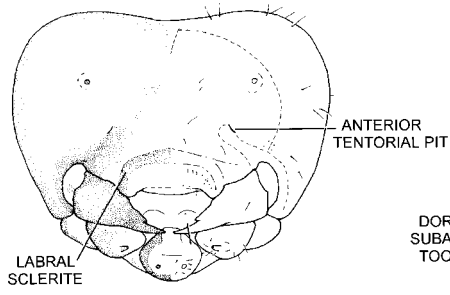
- Mandible with at most one or two setae; gena (figs. 14, 19 without projection) 3
- 3(2). Antennal papilla (fig. 19) elongate, longer and more robust than maxillary palpus;⁴ basal part of maxilla (fig. 19) enlarged. DIOXYINI *Dioxys*
- Antennal papilla (fig. 14) at most subequal in length to maxillary palpus; basal part of maxilla (fig. 14) normal in size. ANTHIDIINI 4
- 4(3). Mandibular apex in adoral view (fig. 16) elongate, sharply pointed, nonserrate, with or without subapical tooth *Stelis*
- Mandibular apex in adoral view (fig. 18) obliquely truncate, irregularly serrate *Hoplostelis*
- 5(1). Pigmented labral sclerite conspicuous (as in fig. 15); thoracic segments without paired sharp pigmented projections; labral tubercle(s) absent; dorsolateral body tubercles absent (fig. 20); abdominal segment 10 less than one-half maximum diameter of segment 9 and positioned apically on segment 9 (fig. 20). APIDAE: APINAE (in part; for other part, see couplet 8): TETRAPEDIINI *Coelioxoides*
- Pigmented labral sclerite absent (fig. 23) or, if faintly present (*Exaerete*), then thoracic segments dorsally with paired, sharp, pigmented projections (fig. 113); paired labral tubercles (fig. 55) or single median tubercle (fig. 29) often present; dorsolateral body tubercles present (figs. 22, 110) or absent (figs. 33, 67); abdominal segment 10 not unusually small (fig. 22), positioned variably 6
- 6(5). Maxillary palpus very broad relative to length, apex of maxilla thus appearing rounded or broadly pointed in lateral view (fig. 24), with contour of palpus little differentiated from maxillary apex; antennal papilla broad relative to length, and disc diameter large, antenna thus appearing as large, low blister (figs. 23, 24); dorsolateral body tubercles on anterior part of body (fig. 22) strongly transverse (best observed on postdefecating larva); salivary opening a narrow entrance, without projecting lips. HALICTIDAE:⁵ HALICTINI 7

⁴ This character may not apply to *Dioxys cincta* (Jurine) (see Rozen, 1967: 238).

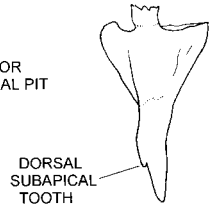
⁵ Presumably the mature larva of cleptoparasitic Augochlorini will also run to here, as larvae of the subfamily are quite uniform.



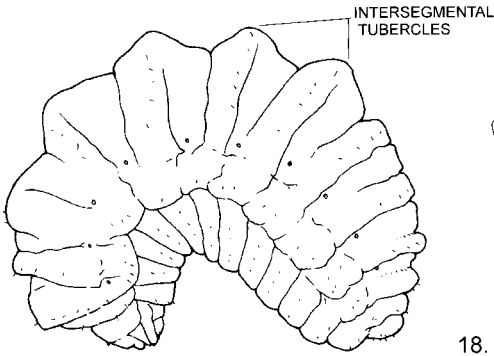
14. *Stelis elongativentris*



15. *Stelis elongativentris*



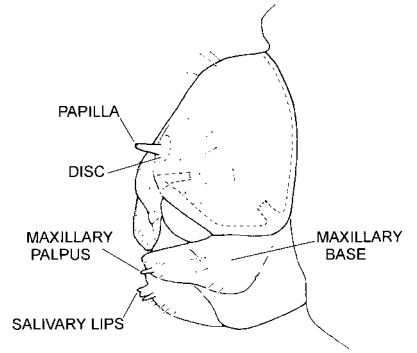
16. *Stelis elongativentris*



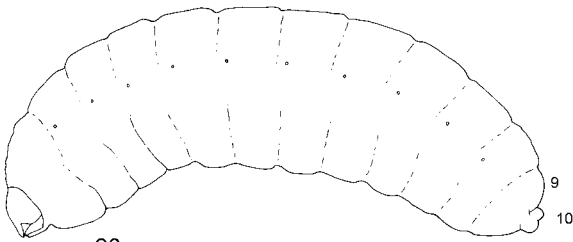
17. *Stelis elongativentris*



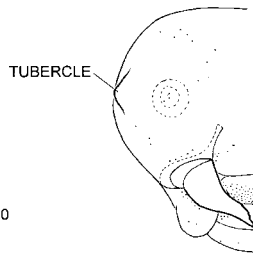
18. *Hoplostelis bilineolata*



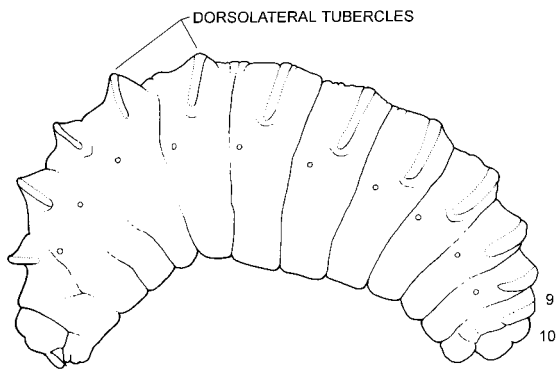
19. *Dioxys pomonae pomonae*



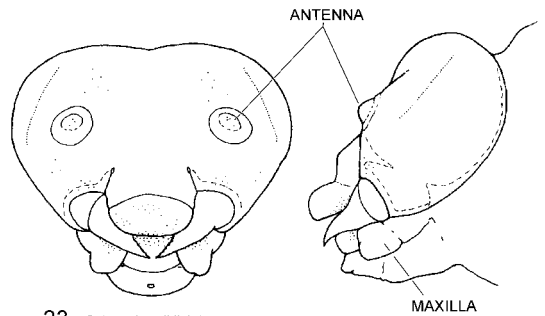
20. *Coelioxoides waltheriae*



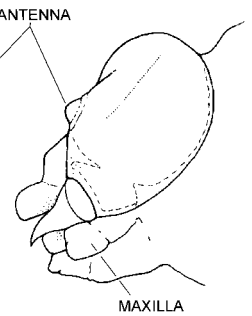
21. *Microsphecodes kathleenae*



22. *Sphecodes albilabris*



23. *Sphecodes albilabris*



24. *Sphecodes albilabris*

Figs. 14–24.

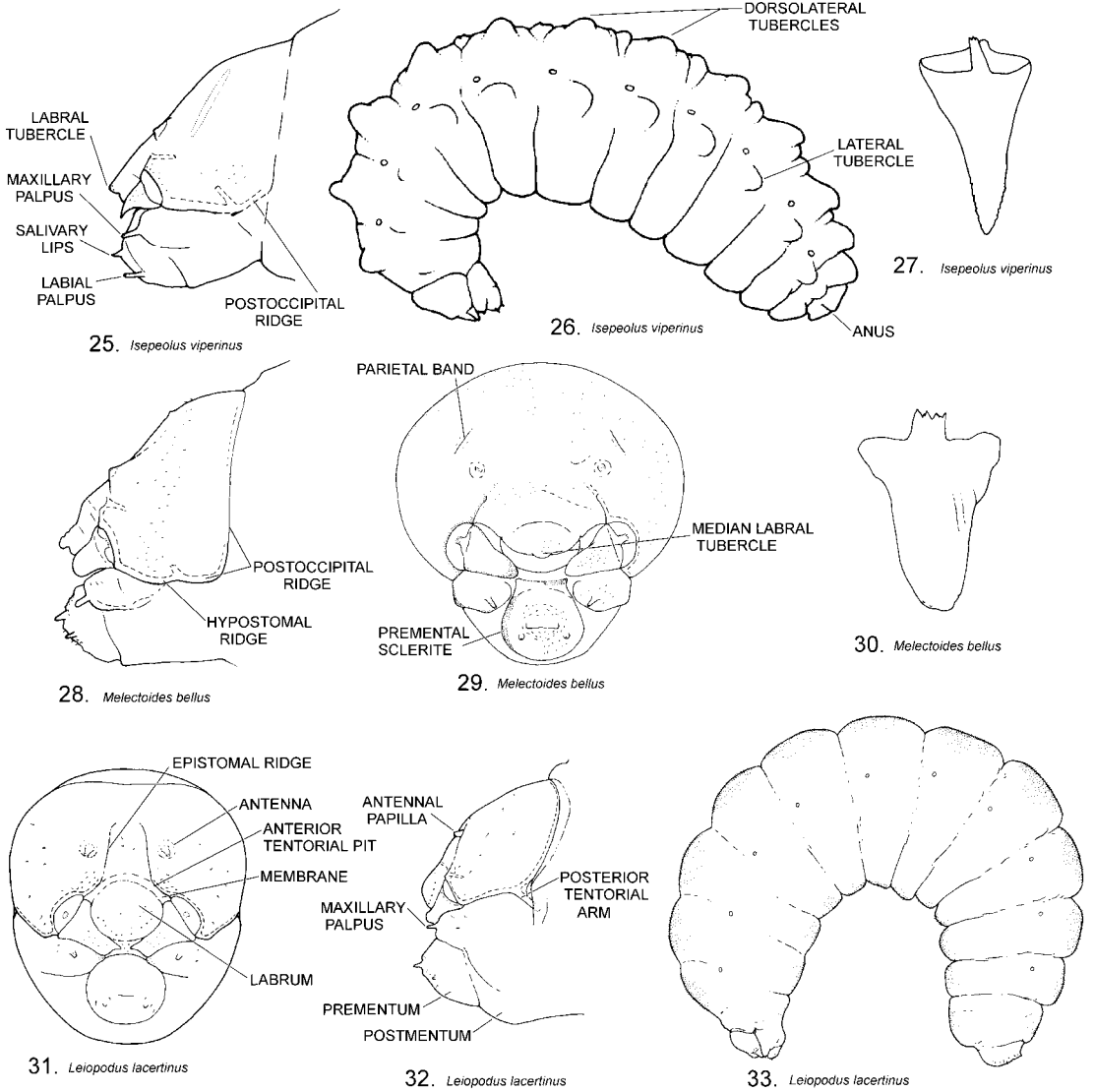
- Maxillary palpus elongate or small, but always projecting as distinct papilla beyond maxillary apex in lateral view (figs. 25, 46, 64); antennal papilla and disk small (figs. 31, 57), not combined as large blister; dorsolateral body tubercles present or absent, but if present (figs. 26, 110), not usually strongly transverse; projecting transverse salivary lips present or absent. APIDAE (in part; see couplet 5 for other part) . . . 8
- 7(6). Head in frontal view (fig. 23) evenly round on each side, without large tubercle *Sphecodes*⁶
- Head in frontal view (fig. 21) with large tubercle on each side, about at level of antenna *Microsphecodes*
- 8(6). Labial palpus (figs. 25, 35, 44, 46) evident as distinct papilla; labium divided into pre- and postmentum (figs. 32, 40, 44), except in several melectine genera; head capsule deeply inflexed at posterior tentorial pits (like that of cocoon-spinning solitary apines, fig. 52), except in Protepeolini, which lacks labral tubercles; labral tubercles, when present, variable, but rarely acutely pointed, usually arising from apex of labrum. APINAE (in part; for other part see couplet 5) . . . 9
- Labial palpus (figs. 54, 57, 68, 92) greatly reduced, not a distinct papilla; labium (figs. 58, 64, 100) not divided into pre- and postmentum; head capsule (fig. 51) not inflexed at posterior tentorial pits; labral tubercles (figs. 58, 68, 82, 111) invariably present, paired, acutely pointed, forward projecting, arising from disc of labrum. NOMADINAE 19
- 9(8). Abdomen (fig. 26) with rounded tubercles below spiracles; labrum (fig. 29) with single median tubercle. ISEPEOLINI 10
- Abdomen (fig. 33) without tubercles below spiracles; labrum with paired tubercles (fig. 34, 50) or without tubercles (fig. 31), but without single median tubercle⁷ 11
- 10(9). Postoccipital ridge, as seen in lateral view

- (fig. 28), gradually curving forward, thus anterior end a linear extension of hypostomal ridge; upper and lower apical edge of mandible with a few small, indistinct points (fig. 30) *Melectoides*
- Postoccipital ridge, as seen in lateral view (fig. 25), angling upward immediately behind posterior tentorial pit; upper and lower apical edges of mandible dentate (fig. 27) *Isepeolus*
- 11(9). Upper margin of labrum extending to level of anterior tentorial pits in frontal view (fig. 31);⁸ lower margin of labrum evenly rounded, without paired tubercles; labrum subcircular (fig. 31); maxilla strongly projecting in lateral view (fig. 32); posterior tentorial arm (fig. 32) appearing as external posterior extension of hypostomal ridge; most body segments conspicuously spiculate dorsally and ventrally (fig. 33). PROTEPEOLINI *Leiopodus*
- Upper margin of labrum well below level of anterior tentorial pits in frontal view (fig. 34); lower margin of labrum often showing paired tubercles so as to appear angled in frontal view (fig. 34); labrum generally transverse and quadrate or trapezoidal (fig. 34); if labrum circular to narrowly rounded and without tubercles (*Zacosmia*, fig. 38), then maxilla (fig. 39) greatly recessed, thus its apex is in line with posterior mandibular articulation in lateral view; posterior tentorial arm normal, at right angle to hypostomal ridge and not visible externally; integumental body spiculation inconspicuous if present 12
- 12(11). Each thoracic segment dorsally with pair of pigmented, small, sharply pointed projections (fig. 113). EUGLOSSINI *Exaerete*
- Thoracic segments without pigmented projections 13
- 13(12). Labiomaxillary region tending to be recessed, labroclypeal area thus extending beyond labiomaxillary region in lateral profile (figs. 35, 39, 40); labiomaxillary region not enlarged as in Ericroidini and Rhathymini. MELECTINI 14
- Labiomaxillary region greatly enlarged

⁶ Other cleptoparasitic Halictini whose larvae have yet to be collected, such as the cleptoparasitic *Lasioglossum (Dialictus)*, may also key here, as the characters used to reach the Halictini are broadly applicable to the tribe.

⁷ The narrowly rounded labral apex of *Zacosmia maculata* (fig. 36) could be interpreted as a median tubercle, although it does not project (fig. 37). This monotypic genus from the western United States and Mexico is far removed from the range of the South American Isepeolini.

⁸ The peculiar anatomy of the labrum and clypeus of mature larvae of *Leiopodus* is further described by Roig-Alsina and Rozen (1994).



Figs. 25–33.

and projecting; this region produced as far as, or farther than, labroclypeal area in lateral profile (figs. 44, 46, 49)17

14(13). Labrum (fig. 34) bilobed or bituberculate, as seen in frontal view; adoral surface of mandible apically broad (figs. 36, 41, 42); maxilla moderately long, its apex clearly exceeding posterior mandibular articulation in lateral view (figs. 35, 40) 15

– Labrum (fig. 38) narrowing to rounded point, as seen in frontal view; adoral

surface of mandible greatly narrowed apically (fig. 37); maxilla short, its apex approximately in line with posterior mandibular articulation in lateral view (fig. 39) *Zacoscia*

15(14). Labium (fig. 40) divided into prementum and postmentum; hypopharynx not projecting forward beyond base of salivary lips in lateral view (fig. 40)16

– Labium (fig. 35) not divided into prementum and postmentum; hypopharynx projecting forward beyond base

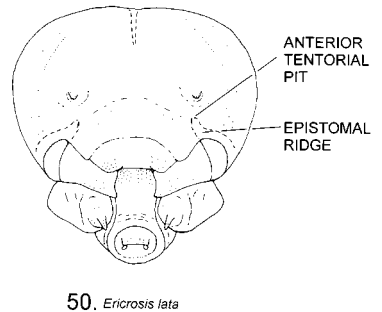
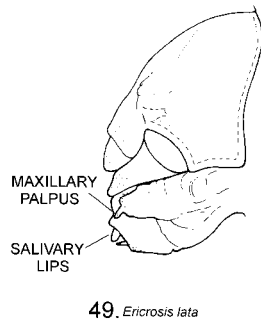
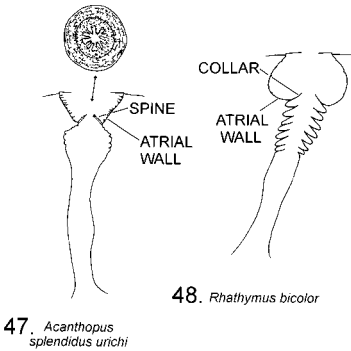
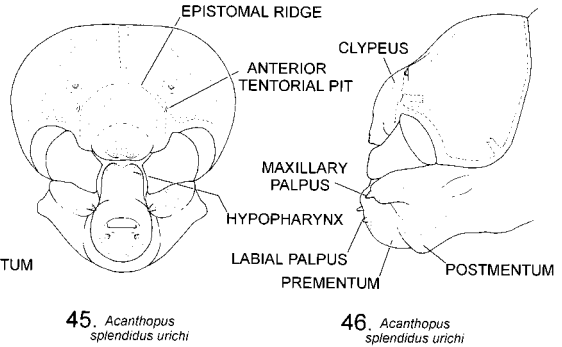
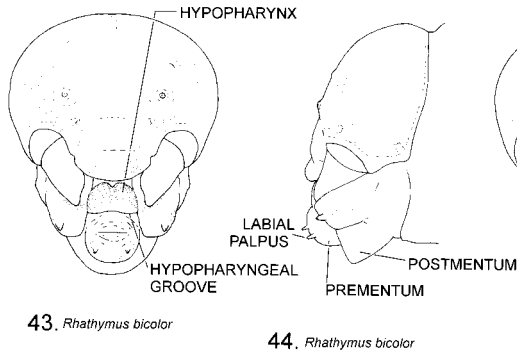
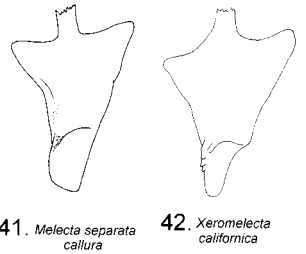
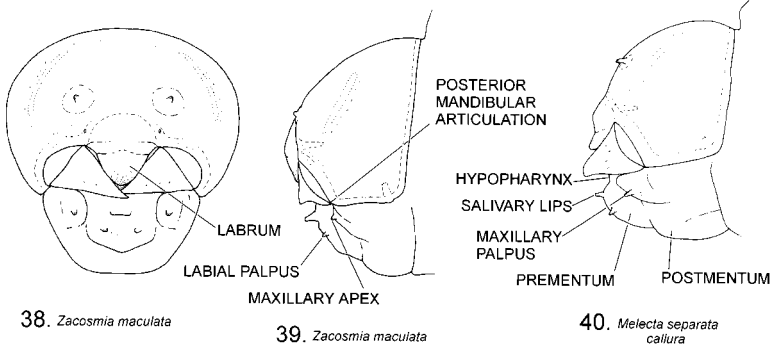
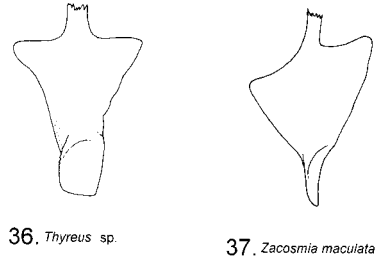
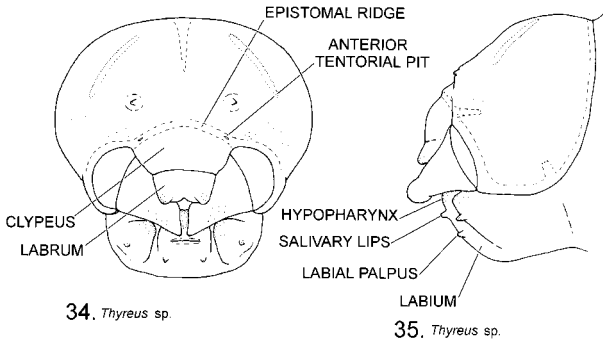
- of salivary lips in lateral view (fig. 35) *Thyreus*
- 16(15). Adoral surface of mandible narrowly truncate apically (fig. 41)
 *Melecta*
- Adoral surface of mandible acutely rounded apically (fig. 42)
 *Xeromelecta*
- 17(13). Hypopharyngeal groove (fig. 43) deep and distinct, separating lobelike hypopharynx from labium; primary tracheal opening (fig. 48) with collar, without spines. RHATHYMINI *Rhathymus*
- Hypopharyngeal groove absent or only weakly developed laterally (figs. 45, 50), separating elongate hypopharynx from labium; primary tracheal opening (fig. 47) guarded by spines, without collar. ERICROCIDINI⁹ 18
- 18(17). Epistomal ridge (fig. 45) extending between anterior tentorial pits; maxillary palpus (fig. 46) more robust, length about 1.25 times basal diameter
 *Acanthopus*
- Epistomal ridge (fig. 50) interrupted medially between anterior tentorial pits; maxillary palpus (fig. 49) more attenuate, length about 1.75 times basal diameter *Ericrocis*
- 19(8). Frontal area normal, not so strongly produced that it extends beyond labrum in lateral view (figs. 54, 64); except in *Paranomada*, labrum normally long, length greater than one-half width 20
- Frontal area (or combined frontoclypeal area) bulging, thus it extends well beyond labrum, which appears small and recessed in lateral view (figs. 104, 108, 112); labrum transverse, its length one-half to less than one-half its width (figs. 106, 107) except in *Neolarra*; North America 37
- 20(19). Hypopharynx (figs. 63, 68) spiculate dorsally or completely 21
- Hypopharynx (fig. 82) totally nonspiculate 30
- 21(20). Mandibles¹⁰ (fig. 53) elongate, with api-

- ces downcurved (except in *Triopasites*); head capsule (figs. 54, 58) bearing more or less evident wrinkled swelling above each antennal prominence. BRACHYNOMADINI, except for *Kelita* 22
- Mandibles short to very short, with apices that curve normally toward mouth; head capsule evenly curved above antennae (fig. 64), without wrinkled swellings 25
- 22(21). Mandibular apex acute (fig. 53) 23
- Mandibular apex more broadly rounded (fig. 60) *Triopasites*
- 23(22). Labral tubercles (fig. 57) separated by less than their basal diameter; prothoracic dorsolateral tubercles (fig. 59) larger than those of mesothorax
 *Brachynomada (Brachynomada)*¹¹
- Labral tubercles (figs. 55, 61) separated by about their basal diameter or more widely spaced; prothoracic dorsolateral tubercles (figs. 56, 62) subequal to or smaller than those of mesothorax 24
- 24(23). Head capsule (fig. 61) very wide as seen in frontal view; dorsolateral thoracic tubercles (fig. 62) relatively large
 *Paranomada*
- Head capsule (fig. 55) not abnormally wide; dorsolateral thoracic tubercles (fig. 56) scarcely noticeable
 *Brachynomada (Melanomada)*¹¹
- 25(21). Posterior tentorial pit at posterior boundary of head, adjacent to cervical fold as seen in lateral view (fig. 64); salivary opening well separated from spiculate part of hypopharynx as seen in frontal view (fig. 63); mandibular apex broadly rounded (fig. 65); abdominal segment 9 appearing produced ventrally because segment 10 attached dorsally to 9 (fig. 66); abdominal segment 10 dorsally with median transverse sulcus about one-third distance from segment 9 to anus (fig. 66). HEXEPEOLINI
 *Hexepeolus*
- Posterior tentorial pit anterior to cervical

⁹ The mature larva of *Mesoplia*, known only from a cast skin, presumably will run to here, but it cannot be further differentiated from other genera in the tribe.

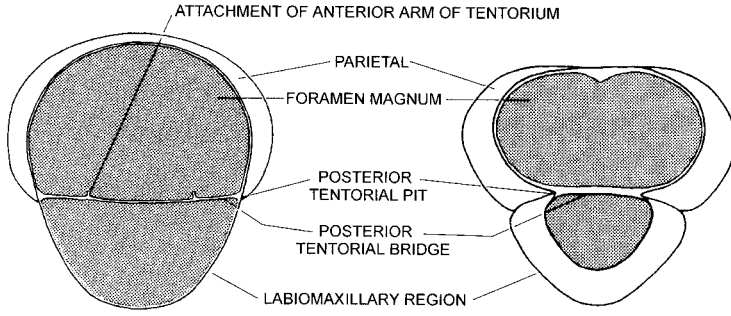
¹⁰ The original description of the larva of *Triopasites penniger* (Rozen, 1977) was based on two poorly preserved specimens that seemed to have relatively short, apically rounded mandibles, the apices of which were not certainly downcurved. Recently collected specimens that are well preserved show that the mandibles, though still apically blunt, are somewhat more elongate, although perhaps not so elongate as those of the typical brachynomadines (i.e., exclusive of *Kelita*). The mandibular apices were clearly downcurved.

¹¹ Michener (1996) synonymized *Melanomada* with *Brachynomada*, but pointed out that they might be considered subgenera because of the thornlike projection at the base of the male hind femur of species assigned to *Melanomada*. They are here regarded as subgenera because of this character and also because the metasomal sternum 8 of these males (Snelling and Rozen, 1987: figs. 8, 10, 12, 14 [sic, error in figure caption]; Rozen, 1994: fig. 29) is not produced into an elongate apical process as in at least some *Brachynomada* sensu stricto (Rozen, 1994: figs. 24, 25).



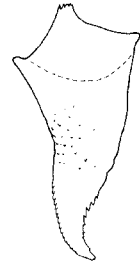
Figs. 34–50.

- fold as seen in lateral view (fig. 69); salivary opening adjacent to spiculate part of hypopharynx as seen in frontal view (fig. 68); mandibular apex (fig. 71) sharply pointed; abdominal segment 9 (fig. 67) not produced ventrally; segment 10 (fig. 67) not attached dorsally to 9; abdominal segment 10 either without median transverse sulcus or with sulcus much closer to anus than to segment 9, forming upper anal lip 26
- 26(25). Mandible with dorsal and adoral surfaces spiculate (fig. 71); spiracular atrium (fig. 70) smooth or with very short denticles; spiracles of postdefecating larva (fig. 70) not on pigmented tubercles; labrum (fig. 68) lacking median cluster of large sensilla near base. NOMADINI *Nomada*
- Mandible with dorsal and adoral surfaces (figs. 74, 77) without spicules, though often irregularly roughened; spiracular atrium (fig. 79) with elongate denticles that may extend to peritreme; spiracles of postdefecating larvae (fig. 13) usually on pigmented tubercles; labrum (fig. 78) with median cluster of large sensilla near base. EPEOLINI 27
- 27(26). Mandible (fig. 73) with elongate, sharp tooth arising from outer surface apically; maxilla spiculate beneath hypostomal sulcus (fig. 72) *Odyneropsis*
- Mandible (figs. 74, 76, 77) apically simple, normal, without elongate tooth arising from outer surface apically; maxilla nonspiculate 28
- 28(27). Mandibular apex broad, bladelike (fig. 74); upper and lower apical edges (fig. 74) toothed with very fine, sharply pointed denticles; inner surface with more (fig. 74) or less strongly projecting acute lobe; labral tubercles separated by about their basal diameter *Thalestria*
- Either mandible of normal breadth apically (fig. 76) and labral tubercles (fig. 75) closer than their basal diameter, or mandible abruptly narrowed apically, apex fanglike (fig. 77) and labral tubercles separated by their basal diameter or more (fig. 80); upper and lower apical edges of mandible with or without fine denticles 29
- 29(28). Labral tubercles (fig. 75) nearly contiguous, separated by less than their basal diameter; mandibular apices (fig. 76) tapering evenly *Epeolus*
- Labral tubercles (fig. 80) separated by distance as great as or greater than basal diameter; mandible (fig. 77) abruptly narrowed toward apex; apex parallel sided and fanglike *Triepeolus*
- 30(20). Salivary opening situated well behind maxillary apices in ventral view (i.e., specimen oriented so that line of sight is at right angle to plane of hypostomal ridges) (fig. 88); labrum strongly projecting, most anterior part well beyond lower edge of clypeus in lateral view (fig. 86). AMMOBATINI 31
- Salivary opening approximately in line with or anterior to maxillary apices in ventral view (fig. 94); labrum projecting normally (fig. 93) beyond lower edge of clypeus or even unusually recessed, so that most anterior part recessed behind lower edge of clypeus in lateral view (figs. 100, 104) 34
- 31(30). Posterior tentorial pit nearly equidistant from posterior mandibular articulation and apparent posterior margin of head capsule as seen in lateral view (fig. 81); labral tubercles not apically attenuate, separated by about basal diameter; southern Africa *Sphecodopsis*
- Posterior tentorial pit clearly closer to apparent posterior margin of head capsule than to posterior mandibular articulation as seen in lateral view (fig. 83); labral tubercles usually separated by more than basal diameter, but if close set (some *Oreopasites*), then tubercles apically attenuate 32
- 32(31). Hypopharynx (fig. 82) well-defined and strongly projecting; maxillary palpus larger than labral tubercle (figs. 82, 83); vertex (fig. 83) with median rounded swelling; postdefecating larva in dorsal view (fig. 84) with intersegmental lines not incised; Old World *Ammobates*
- Hypopharynx (fig. 87) poorly defined and weakly projecting; maxillary palpus smaller than labral tubercle; vertex (fig. 86) without median, rounded swelling; postdefecating larva in dorsal view (fig. 85) with intersegmental lines moderately to deeply incised 33
- 33(32). Spiracular atria (fig. 89) subquadrate; abdominal segments dorsally evenly curved in cross-section, without dorsolateral elevations; Old World *Pasites*
- Spiracular atria (fig. 90) subglobular; most abdominal segments, at least of

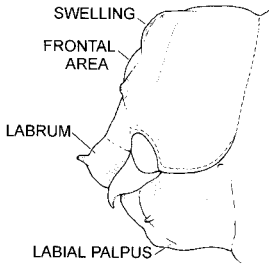


51. *Brachynomada (Melanomada) sidaefloris*

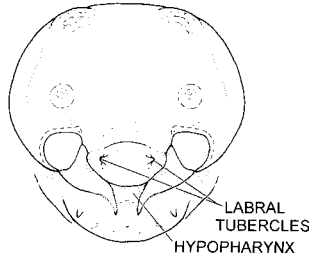
52. *Ancyloscelis apiformis*



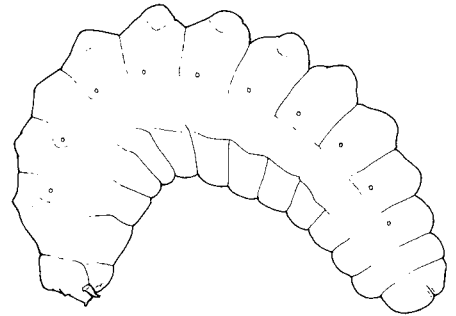
53. *Brachynomada (Melanomada) sidaefloris*



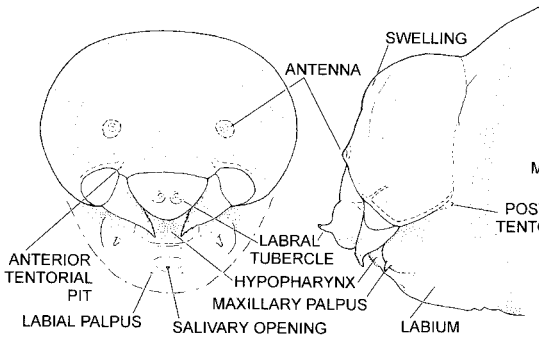
54. *Brachynomada (Melanomada) sidaefloris*



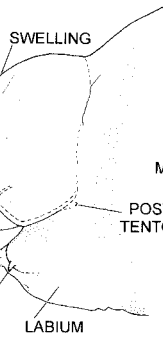
55. *Brachynomada (Melanomada) sidaefloris*



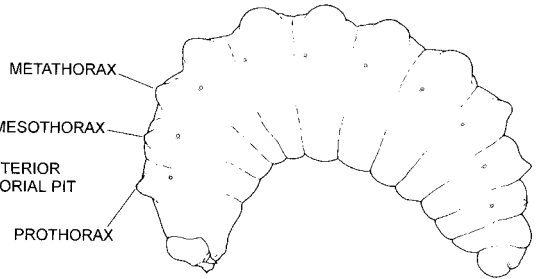
56. *Brachynomada (Melanomada) sidaefloris*



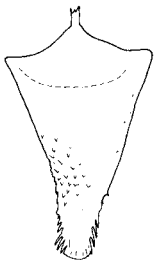
57. *Brachynomada (Brachynomada) roigi*



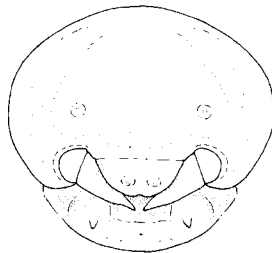
58. *Brachynomada (Brachynomada) roigi*



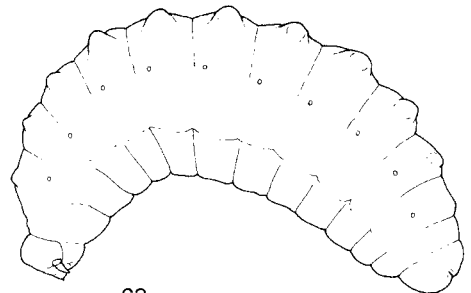
59. *Brachynomada (Brachynomada) roigi*



60. *Triopasites penniger*

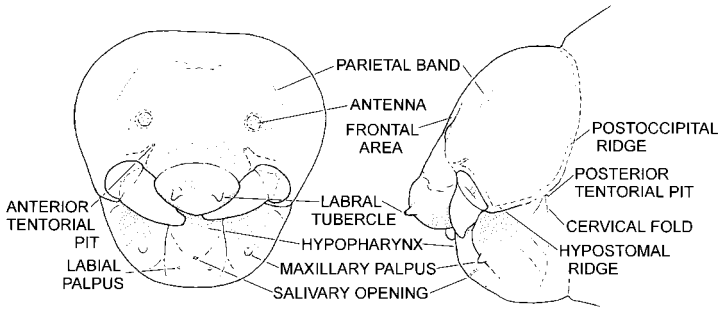


61. *Paranomada velutina*



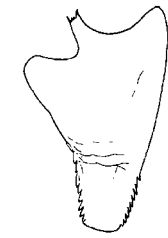
62. *Paranomada velutina*

Figs. 51–62.

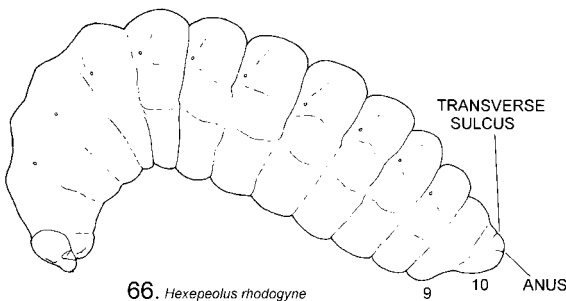


63. *Hexepeolus rhodogyne*

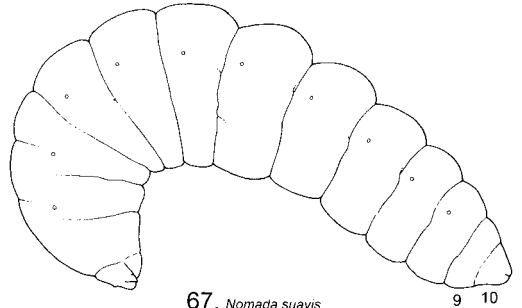
64. *Hexepeolus rhodogyne*



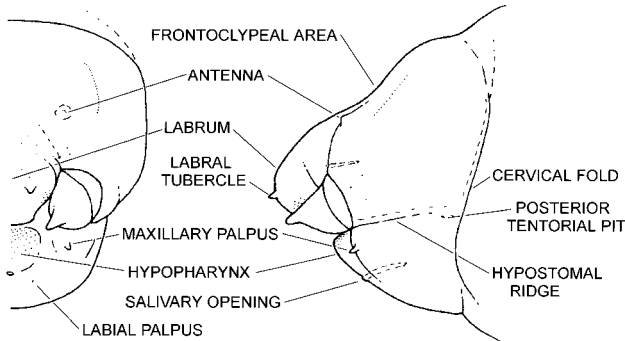
65. *Hexepeolus rhodogyne*



66. *Hexepeolus rhodogyne*

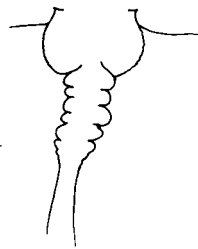


67. *Nomada suavis*

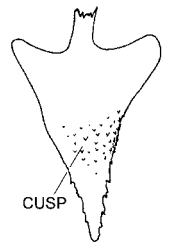


68. *Nomada fowleri*

69. *Nomada fowleri*



70. *Nomada suavis*

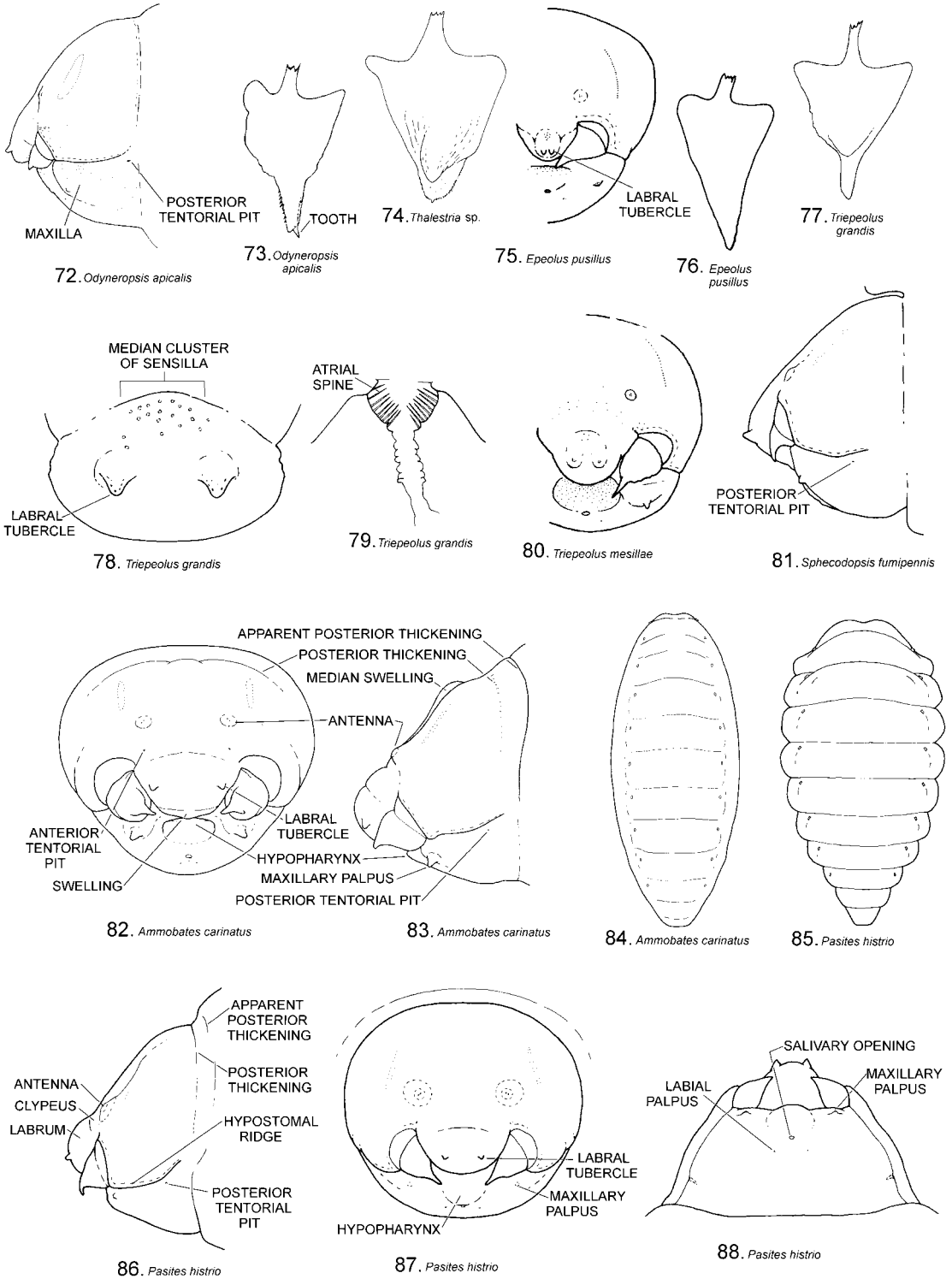


71. *Nomada suavis*

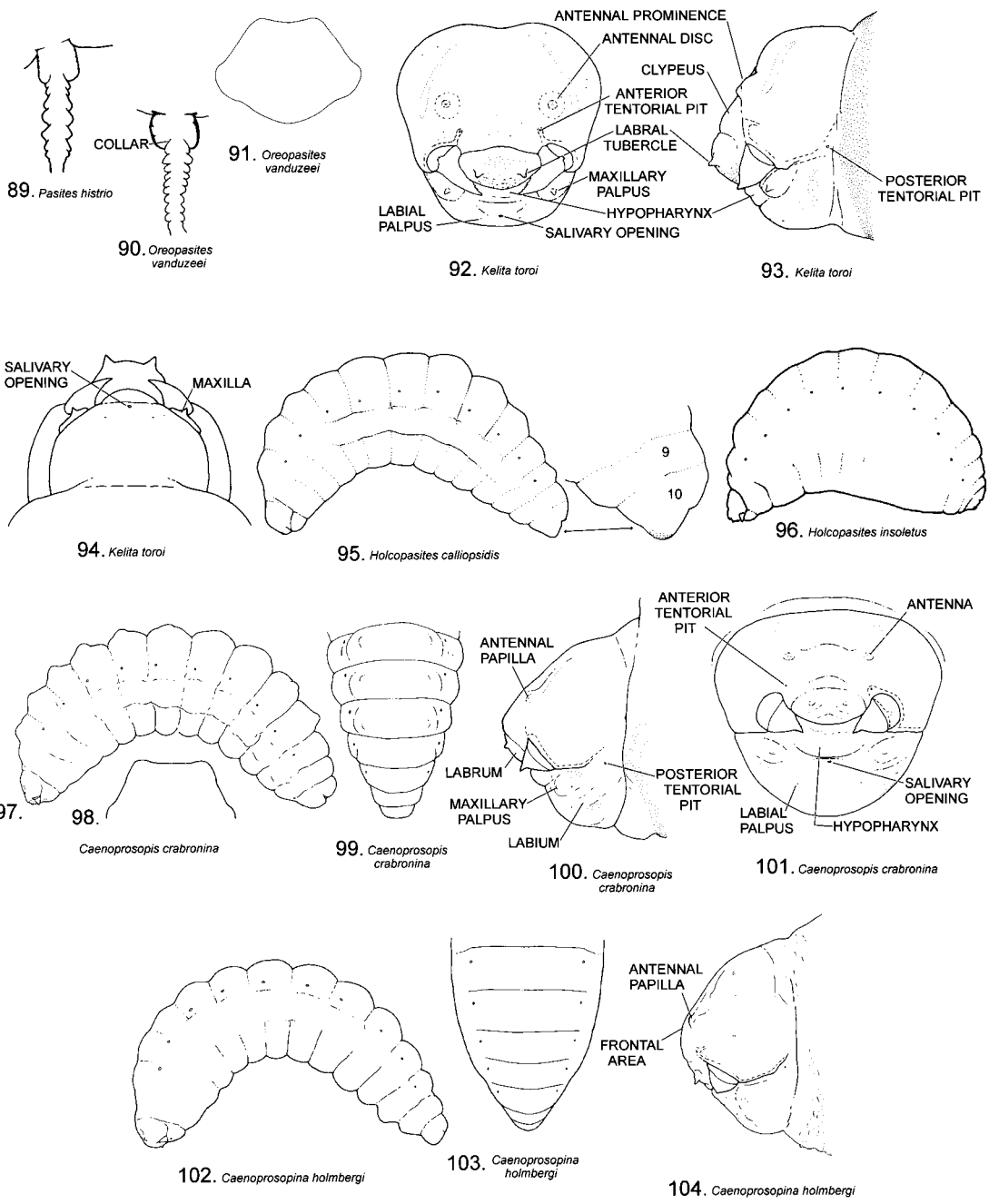
Figs. 63-71.

postdefecating larva, with dorsolateral elevations, thus cross section through these elevations appears angled (fig. 91); North America . . . *Oreopasites* 34(30). Anterior tentorial pit (fig. 92) about halfway between anterior mandibular articulation and antennal disc; maxillary palpus about as long as basal diameter; labrum projecting beyond lower edge of clypeus in lateral view (fig. 93); South America. BRACHYNOMADINI

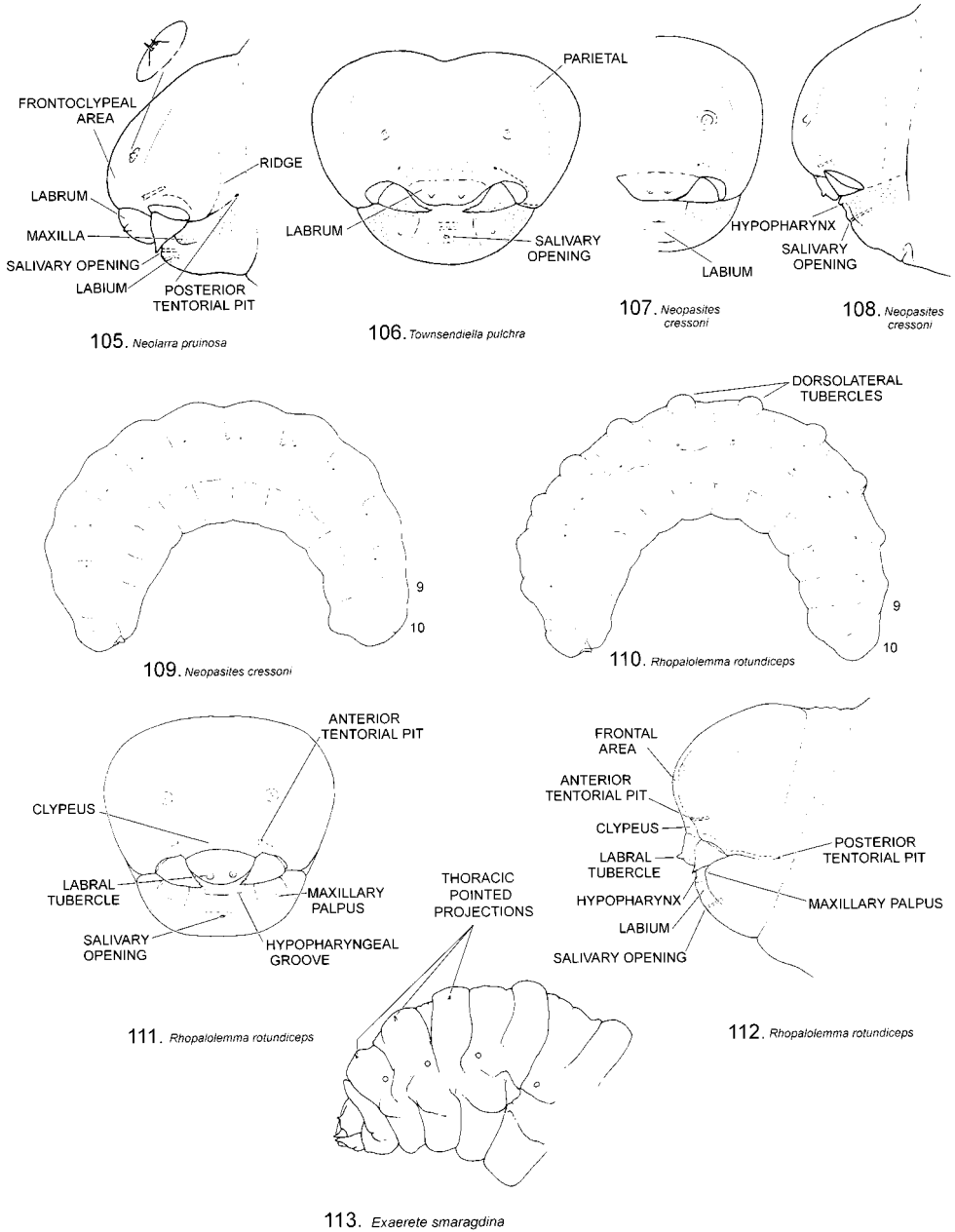
(in part; for other part see couplet 21) *Kelita*
 - Anterior tentorial pit (fig. 101) low on face, much closer to anterior mandibular articulation than to antennal disc; maxillary palpus greatly reduced to virtually absent, shorter than basal diameter (fig. 100); most anterior part of labrum approximately in line with lower edge of clypeus or more recessed in lateral view (figs. 100, 104) 35



Figs. 72–88.



Figs. 89-104.



Figs. 105–113.

35(34). Abdominal segment 10 (fig. 95) spiculate posteroventrally, these spicules larger than other body spicules; segment 10 (fig. 95) tending to be more or less produced posteroventrally; predefecating larva (fig. 96) extremely robust; North

America. AMMOBATOIDINI
 *Holcopasites*
 - Abdominal segment 10 (fig. 97) nonspiculate posteroventrally or if spiculate, spicules like those on other body segments; segment 10 protruding or not

- protruding ventrally; predefecating larva (where known) not extremely robust; South America. CAENOPROSOPIDINI 36
- 36(35). Labiomaxillary region (fig. 100) bearing spicules in some areas; venter of abdominal segment 10 (fig. 97) not protruding; postdefecating larva with produced dorsolateral swellings on most body segments as seen in cross-section (fig. 98) and deeply incised intersegmental lines on lateral body swelling as seen from above (fig. 99) *Caenoprosopis*
- Labiomaxillary region (fig. 104) nonspiculate; venter of abdominal segment 10 (fig. 102) produced posteroventrally; postdefecating larva without dorsolateral swellings on body segments and lateral body outline smooth as viewed from above (fig. 103) because intersegmental lines not invading lateral body swellings *Caenoprosopina*
- 37(19). Salivary opening projecting as far as or farther than hypopharynx in lateral view (fig. 105); labial apex spiculate; salivary opening anterior to maxillary palpi in lateral view (fig. 105). NEOLARRINI *Neolarra*
- Hypopharynx exceeding salivary opening in lateral view (figs. 108, 112); labium nonspiculate; salivary opening in line with maxillary apices in lateral view (figs. 108, 112) (character state unknown for *Townsendiella*) 38
- 38(37). Head capsule with parietals expanded laterally, thus head unusually broad and posterior margin with median indentation as seen in frontal view (fig. 106). TOWNSENDIELLINI *Townsendiella*
- Head capsule normally narrow, thus that dorsal margin of head forming continuous curve as seen in frontal view (figs. 107, 111). BIASTINI 39
- 39(38). Hypopharynx nonspiculate (fig. 107); dorsolateral body tubercles absent (fig. 109) *Neopasites*
- Hypopharynx spiculate (fig. 111); dorsolateral body tubercles present (fig. 110) *Rhopalolemma*

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Many of the specimens used in this study are in the collection of the American Museum of Natural History and are available to qualified researchers. A more complete understanding of immature social, solitary, and cleptoparasitic bees can come about only if specimens of additional taxa are preserved. Melittologists who encounter eggs, larvae, and/or pupae, but do not wish to retain them, are urged to deposit them in this museum so that specimens are available for study by others.

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