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Pupal Descriptions of Some Cleptoparasitic Bees (Apidae), with a Preliminary Generic Key to Pupae of Cleptoparasitic Bees (Apoidea)

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ABSTRACT

Pupae of the following cleptoparasitic Apidae are described and compared with pupae of other cleptoparasitic members in that family: *Neolarra (Neolarra) californica* Michener and *N. (Phileremulus) vigilans* (Cockerell) (Neolarrini); *Holcopasites (Trichopasites) insoletus* (Linsley) (Ammobatoidini); *Osiris pallidus* Smith? (Osirini); *Mesoplia (Mesoplia) rufipes* (Perty) and *M. (Eumelissa)* species (Ericrocidini); *Isepeolus viperinus* (Holmberg) (Isepeolini); and *Xeromelecta (Melectomorpha) californica* (Cresson) and *Thyreus* species? (Melectini). Pupae of the Neolarrini and Ammobatoidini have not been described before, nor has the pupa of *Mesoplia* although the pupa of the related *Ericrocis* is known. The pupa of *Isepeolus* was briefly described before but not illustrated. The pupa of *Xeromelecta californica* was illustrated earlier but not described. A preliminary generic key to known pupae of cleptoparasitic Apoidea exclusive of the Sphecidae is presented.

INTRODUCTION

To further our understanding of cleptoparasitic bee pupae, those of the following species are described: *Neolarra (Neolarra) californica* Michener and *N. (Phileremulus) vigilans* (Cockerell) (Neolarrini); *Holcopasites insoletus* (Linsley) (Ammobatoidini); *Osiris pallidus* Smith? (Osirini sensu Roig-Alsina, 1989); *Mesoplia (Mesoplia) rufipes* (Perty) and *M. (Eumelissa)* species (Ericrocidini); *Isepeolus viperinus* (Holmberg) (Isepeolini); and *Xeromelecta (Melectomorpha) californica* (Cresson) and *Thyreus* species? (Melectini). Pupae are rarely collected because of the short pupal stadium; those of cleptoparasitic bees are even less frequently encountered because cleptoparasites are normally less common than solitary and social bees. Pupal structures can shed light on phylogenetic/taxonomic relationships, and their anatomy is, therefore, worthy of documenting.

These species, all belonging to the Apidae, clearly represent a number of separate evolutionary origins of cleptoparasitism from nonparasitic lineages. The number of origins and the relationships of parasitic lineages to one another in the Apidae (and Apoidea) have long been unsettled matters of great interest (see for example: Grütte, 1935, and reference therein; Michener, 1944; Bohart, 1970; and Roig-Alsina and Michener, 1993). A study of pupae of cleptoparasitic apids by itself cannot address questions about relationships of cleptoparasitic lineages to nonparasitic ones since we know little about the pupae of the latter. However, distinctive pupal features identified in the descriptions below should prove useful in searching for derived characters shared by parasitic and nonparasitic lineages.

We can also start investigating pupal characters that indicate the monophyly of, or within, cleptoparasitic lines. For example, pupae of all Melectini exhibit a pair of peculiar, multispined mesoscutal tubercles, a feature not shared with any other cleptoparasitic bee. Known pupae of all Nomadinae, except for the Brachynomadini, possess scattered, sharply pointed tubercles on their vertexes and often on their mesoscuta (lack of these tubercles can be explained by the Brachynomadini being considered the most basal clade; see Rozen et al., 1997). The presence of sharply pointed tubercles on the vertex in the Melectini as well is tentatively considered a convergence since these two groups differ in so many ways. Pupae of *Leiopodus*, *Osiris*, and *Isepeolus* are quite distinct from one another and from the other parasitic lineages, which corroborates the assignment of these taxa to three separate tribes by Roig-Alsina and Michener (1993). Pupae of the Ericrocidini and Rhathymini, although easily separated, are perhaps less distinctive.

An interesting observation resulting from this study is that pupal characters of these bees apparently do not exhibit features that reflect a cleptoparasitic lifestyle. This contrasts with certain larval features (such as methods of crawling about the brood chamber in search of host offspring, elongate, sharply pointed mandibles for host killing, and special sensory devices presumably used in detecting host eggs or larvae) and with certain adult features associated with egg deposition in host cells. These features of larvae and adults are sometimes confusing be-

cause an investigator cannot always distinguish between synapomorphies and convergences. Thus it might be hoped that pupal features may eventually be found to reflect more accurately the true relationships of taxa.

The pupa of *Isepeolus viperinus* was described earlier by Michener (1957) but a more complete account, with illustrations, is presented here. A pupa of *Thyreus caeruleopunctatus* (Blanchard) was described but not illustrated by Cardale (1968). The other descriptions are the first for any species in their respective genera (although the pupa *Xeromelecta californica* had been illustrated, though not described, by Porter, 1951, as *Melecta californica miranda* [Fox]). Descriptions of pupal Neolarrini and Ammobatoidini (both Nomadinae) are the first for their tribes as is that of *Osiris* for the Osirini.

The key to genera and higher taxa, following the descriptions, is obviously tentative since it is based upon few taxa and upon published descriptions that often omit details. However, where pupae of more than one species are known for a genus (e.g., *Coelioxys*, *Leiopodus*, *Mesoplia*, *Neolarra*), they conform to the key characters and thus support the possible usefulness of the key for identifying other pupae yet to be collected. The key demonstrates that pupal characters can be used to group genera into higher categories and may aid identifications in certain situations. For example, occasionally nests are encountered with pupae of both host and cleptoparasite. If the pupa of the host can be recognized, then the cleptoparasite might be identified by use of the key.

TERMINOLOGY

T = metasomal tergum; S = metasomal sternum; hence T1 is the first metasomal tergum, S3 the third metasomal sternum, etc.

The term spicule as used here refers to the very fine integumental projections found on some pupae. Some authors (e.g., Michener, 1954; Baker et al., 1985) have used this term for the small, sharply pointed tubercles arranged in subapical transverse bands on metasomal terga. However, if the very fine projections described on pupae of *Neolarra* and *Holcopasites*, below, are spicules, then the much larger subapical tergal projections are probably better regarded as tubercles, particularly since there are similar tubercles on the heads of these and other Nomadinae and Melectini.

The distinction between spicule and seta with reference to pupae (and perhaps larvae as well) is ambiguous. It has generally been thought that the dorsal, elongate, hairlike structures on pupal Megachilidae (Baker et al., 1985; Michener, 1954; Rozen, 1966, 1967; Rust and Thorp, 1973; Thorp, 1966) are setae. However, on careful examination of pupae of at least *Coelioxys* and *Habrostelis*, I saw that these sclerotized, hairlike structures abruptly arose from very small tubercles. An alveolus was not detected separating the base of the hair from the tubercle under stereoscopic examination. However, the apparent lack of an alveolus may have resulted from the seta arising from a soft pupal integument rather than from a sclerite. If this is true then one has to question the anatomical distinction between a nonsensory seta (that is, one that is not a setiform sensilla) and a spicule. In the following descriptions the term ''fine (or minute) spicule'' probably correctly denotes integumental features that are spicules as usually defined. However, the terms, ''hair,'' ''spine,'' and ''setiform'' are used in descriptive senses only.

The term verruca (-ae, plural) (wartlike swelling) refers to a low, rounded swelling with an uneven surface that is too poorly defined to be termed a tubercle. In pupae of *Osiris* and certain other taxa, verrucae, often grouped into rows, appear on the head and body where the surface might come in contact with the cocoon wall or cell wall. They may protect the body surface from abrasion.

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I thank Dr. Carlos A. Garófalo, Universidade de São Paulo, Brazil, for the loan of pupae of *Osiris pallidus?* described below. Similarly, Dr. Charles D. Michener, University of Kansas, kindly loaned the pupa of *Isepeolus viperinus* redescribed here. All other pupae treated are in the collection of the American Museum of Natural History. I also express my appreciation to Dr. Chris Dietrich

and Mr. John K. Bouseman, both of the Illinois Natural History Survey, Champaign, IL, who invited me to join them on the expedition to Kyrgyzstan that led to the collection of the pupa of *Thyreus* species. The expedition was supported by a grant from the National Science Foundation, project number DEB-9870187 (Chris Dietrich, PI). My participation was made possible through the generosity of Mr. Robert G. Goelet, Chairman Emeritus, Board of Trustees, American Museum of Natural History.

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Molly Rightmyer and Eric Quinter, both in the Division of Invertebrate Zoology of the American Museum of Natural History, assisted in editing the manuscript.

APIDAE: NOMADINAE: NEOLARRINI

NEOLARRA ASHMEAD

Neolarra belongs to the monotypic tribe Neolarrini and is restricted to North America including Mexico. In her revision of the genus, Shanks (1977) recognized 14 species and two subgenera. She reported that all known hosts were species in the panurgine genus *Perdita* except for *N. hurdi* Shanks, which, she stated, parasitized nests of *Calliopsis (Micronomadopsis) larreae* (Timberlake). She attributed this later association to me presumably because I had reported (Rozen, 1958: 54) a single individual of *N. hurdi* examining a nest entrance of *C. larreae* 18 miles west of Blythe, Riverside Co., California. I had no other indication that the *Neolarra* individual was attacking *C. larreae*; no immatures of either presumed host or parasite were found. Rust (1988) reported no cleptoparasites in his study of the nesting biology of *C. larreae*, and recently, at the same site I had worked in the 1950s, I discovered a large nesting site of an unidentified *Perdita* around which numerous *N. hurdi* adults were searching the sand. Hence, I conclude that *Neolarra* is exclusively cleptoparasitic on species of *Perdita* so far as is now known.

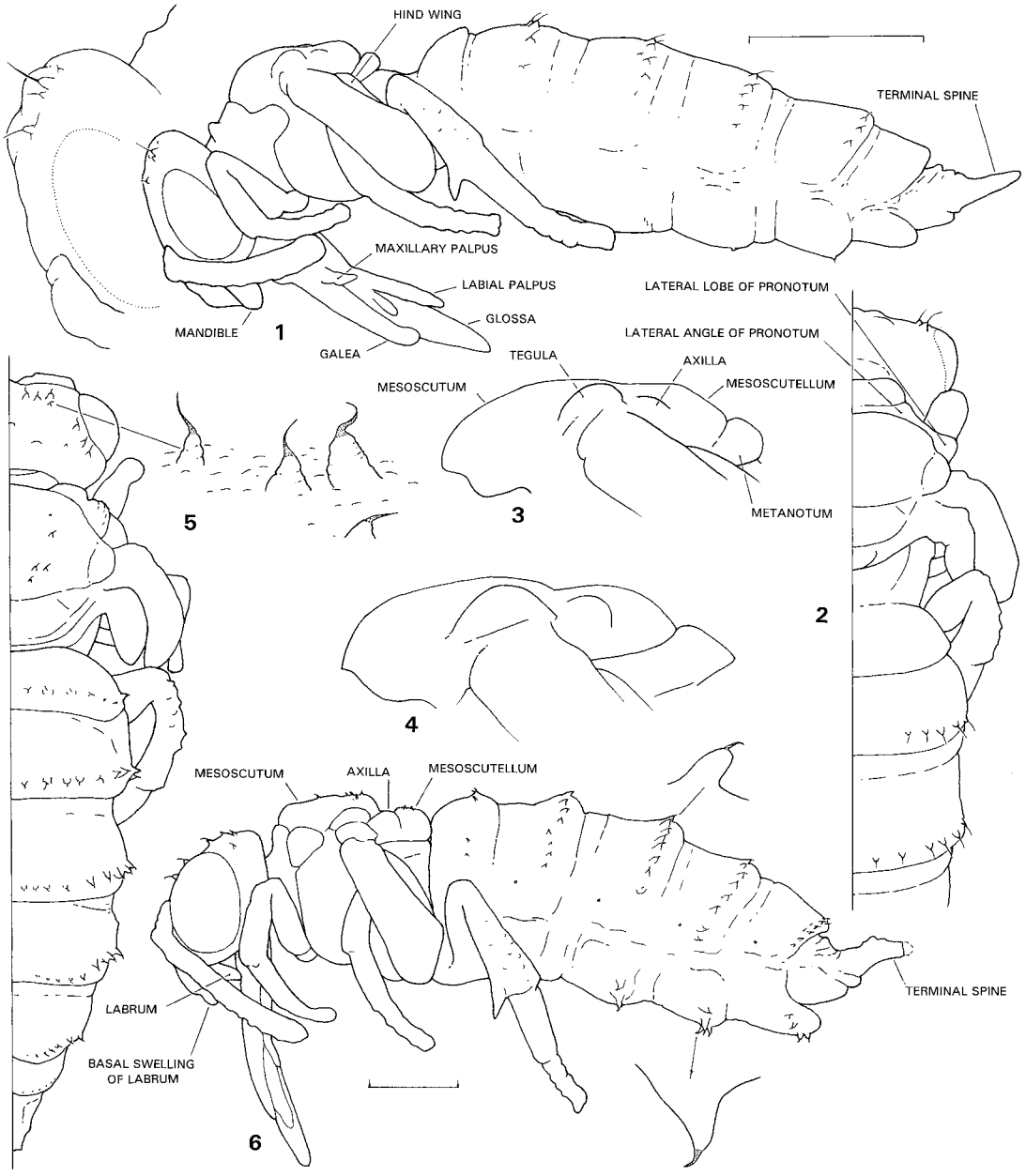
Neolarra (Neolarra) californica Michener

Figures 1–3

DIAGNOSIS: The pupae of the two species of *Neolarra* described here are nearly identical and can be separated only on the basis of slight differences in the production of their axillae and mesoscutellum. They are easily distinguished from pupae of other Nomadinae sensu lato because of the single, long, setalike apex of the larger tubercles on the vertex and on most of the metasomal terga. These hairlike structures are longer than the tubercles themselves in *Neolarra*. In most other known pupae of the Nomadinae, vertical (if present) and tergal tubercles are sharply pointed, without a setalike apex (see references in McGinley, 1989; Roig-Alsina and Rozen, 1994; Rozen, 1989, 1992, 1994, and 1997a). The pupa of *Holcopasites*, described below, also has some cephalic tubercles with elongate apices, but some of these are hooked or zigzagged (fig. 5), unlike the straight or gently curved ones of *Neolarra*. The lack of tubercles on the mesoscutum, mesoscutellum, and the first metasomal tergum is also helpful in separating the genus in the pupal stage from pupae of many other Nomadinae.

HEAD: Integument without setae but with series of two small and several very small tubercles on each side; these tubercles each with elongate, setalike apex (fig. 1); elsewhere integument without tubercles but with some obscure patches of fine spicules that are not so dense or long as to appear velvety. Apex of clypeus without rounded, downward-projecting swelling on each side of labrum as in Ammobatini; labrum somewhat shorter than maximum width, its apex narrowly curved in frontal view; pupal ocelli moderately defined but not tuberculate; flagellomere not distinctly swollen apically. Mandibles vaguely swollen subapically both adorally and medially.

MESOSOMA: Integument in many areas finely spiculate but spiculation not velvety; setae absent. Lateral angles and posterior lobes of pronotum moderately produced, corresponding to those of adult. Mesepisternum without tubercles; mesoscutum without rounded or sharp tubercles or even verrucae; axillae unmodified, not elevated; mesoscu-



Figs. 1–3. Pupa of *Neolarra (Neolarra) californica*. **1.** Body, lateral view, with vertex enlarged to show tubercles with elongate, setalike apices. **2.** Anterior part of body, right side, dorsal view. **3.** Dorsal surface of mesothorax and metathorax, enlarged, lateral view.

Fig. 4. Dorsal surface of mesothorax and metathorax, enlarged, lateral view, of pupa of *N. (Phileremulus) vigilans*.

Figs. 5, 6. Pupa of *Holcopasites insoletus*, right side, dorsal view, and entire body, lateral view, respectively, with sharply pointed tubercles of top of head and metasoma enlarged.

Scales (= 1.0 mm) refer to figs. 1 and 2, and to figs. 5 and 6, respectively.

tellum not produced, without tubercles; metanotum slightly produced, corresponding to that of adult. Tegula slightly produced, without tubercle(s); wings without tubercles. All coxae, trochanters, femora, and tarsi without tubercles; hind tibia with low, sharply pointed tubercles along outer surface.

METASOMA: Integument finely spiculate in some areas but spicules not long enough to be velvety; setae absent. T1 without transverse row of tubercles; T2–5 (female) and T2–6 (male) each with subapical row of tubercles, most of which bear single, elongate, setalike apex; T6 (female) and T7 (male) without tubercles. S3 and 4 (female) and S3–5 (male) with a few very small apical tubercles (figs. 1, 2). Apex of metasoma produced as tapering, apically rounded, terminal spine as seen from above, below, or side (fig. 1). Spiracles present but obscure.

MATERIAL STUDIED: 1 female pupa, Cienega, Hidalgo Co., New Mexico, V-16-1987 (J. G. Rozen); 1 male and 1 female pupa, same except V-14-1987, from nest of *Perdita luciae* Cockerell (NEW HOST RECORD). Identified by comparison with adults collected at the same time.

REMARKS: These three pupae are nearly identical, displaying little variation (except for sex differences). They are reasonably well-preserved, although their metasomas have become distended, as can be seen in figure 1.

Neolarra (Phileremulus) vigilans (Cockerell)

Figure 4

DIAGNOSIS: See Diagnosis for *Neolarra californica*, above.

HEAD, MESOSOMA, METASOMA: As described for *Neolarra californica* except for following: Labrum about as long as maximum width. Axillae produced as distinct lobes (accommodating pointed axillae of adult); mesoscutellum more produced relative to mesoscutum as seen in lateral profile (fig. 4), but without tubercles.

MATERIAL STUDIED: male, 1 female pupa, Fort Robinson, Dawes Co., Nebraska, VIII-12-1971 (J. G., B. L., and K. C. Rozen) from *Perdita zebrata* Cresson? nest area. Identified by adults collected at the same time and by features of the developing imago within the pupal exoskeleton.

AMMOBATOIDINI

Holcopasites insoletus (Linsley)

Figures 5, 6

DIAGNOSIS: Like the pupae of all Nomadinae except those of the Brachynomadini, the pupa of *Holcopasites* possesses sharply pointed head tubercles. The hooked and zigzagged form (fig. 5) of the apices are unknown elsewhere in the subfamily. The elongate labrum of the adult is also reflected in the pupa but might be difficult to interpret because the basal swelling of the labrum superficially resembles the entire labrum of other bees.

HEAD: Integument without setae but with series of approximately eight moderately small, variably sized tubercles on each side of vertex and frons, mesad of eye; apices of these tubercles drawn out into long, darkly pigmented points (fig. 5) that are straight, curved, hooked, and zigzag; some of these apices as long as tubercle base; elsewhere integument wrinkled and with minute, rounded spicules. Apex of clypeus without rounded, downward-projecting swelling on each side of labrum as in Ammobatini; labrum much longer than maximum width, its apex a simple curve in frontal view; pupal ocelli moderately defined but not tuberculate; flagellomere with swelling in inner aspect (hence swellings not visible in fig. 6). Mandibles without swellings or tubercles.

MESOSOMA: Integument wrinkled and with minute, rounded spicules; setae absent. Lateral angles and posterior lobes of pronotum moderately produced, corresponding to those of adult. Mesepisternum without tubercles; mesoscutum and mesoscutellum with scattered small tubercles bearing darkly pigmented, sharp apices; axillae unmodified, slightly elevated; metanotum not produced. Tegula slightly produced, without tubercle(s); wings without tubercles. All coxae, trochanters, femora, and tarsi without tubercles; hind tibia with scattered, low, mostly rounded tubercles along outer surface but some tubercles sharply pointed.

METASOMA: Integument with minute, rounded spicules; setae absent; T1–5 with

transverse row of apical tubercles, most of which bear single, darkly pigmented, sharply pointed apices that may be straight or hooked (fig. 6); T6 with apical row of small, almost indistinct tubercles. S3 (fig. 6) with pair of conspicuous tubercles laterally on each side along posterior margin, these tubercles bearing sharply pointed, darkly pigmented apices that are hooked and directed anteromesad; S4 and S5 each with four conspicuous tubercles laterally on each side along posterior margin with apices like those of S3 (fig. 6). Apex of metasoma produced as parallel-sided terminal spine, apex of which appeared invaginated because of accident of preservation but probably normally rounded. Spiracles evident.

MATERIAL STUDIED: 1 female pupa, Apache, Cochise Co., Arizona, VIII-19-1972 (J. G. Rozen) from nest of unknown bee.

APINAE: OSIRINI

Osiris pallidus Smith?

Figures 7–10

In the recent past (e.g., Hurd, 1979), *Osiris* was generally placed in the exclusively parasitic Nomadinae with a large array of other genera. More recently Roig-Alsina (1989) suggested that the genus and its close relatives did not belong to the Nomadinae, and Roig-Alsina and Michener (1993) subsequently placed it in the Apinae with several other parasitic tribes that had been included in the Nomadinae sensu lato. Sharply pointed tubercles on the pupal head are characteristic of the Nomadinae; their absence in *Osiris*, therefore, seems to support the removal of the genus from the Nomadinae. However, there are no pupal features that align the genus with other bee taxa to the extent pupal bees are now known.

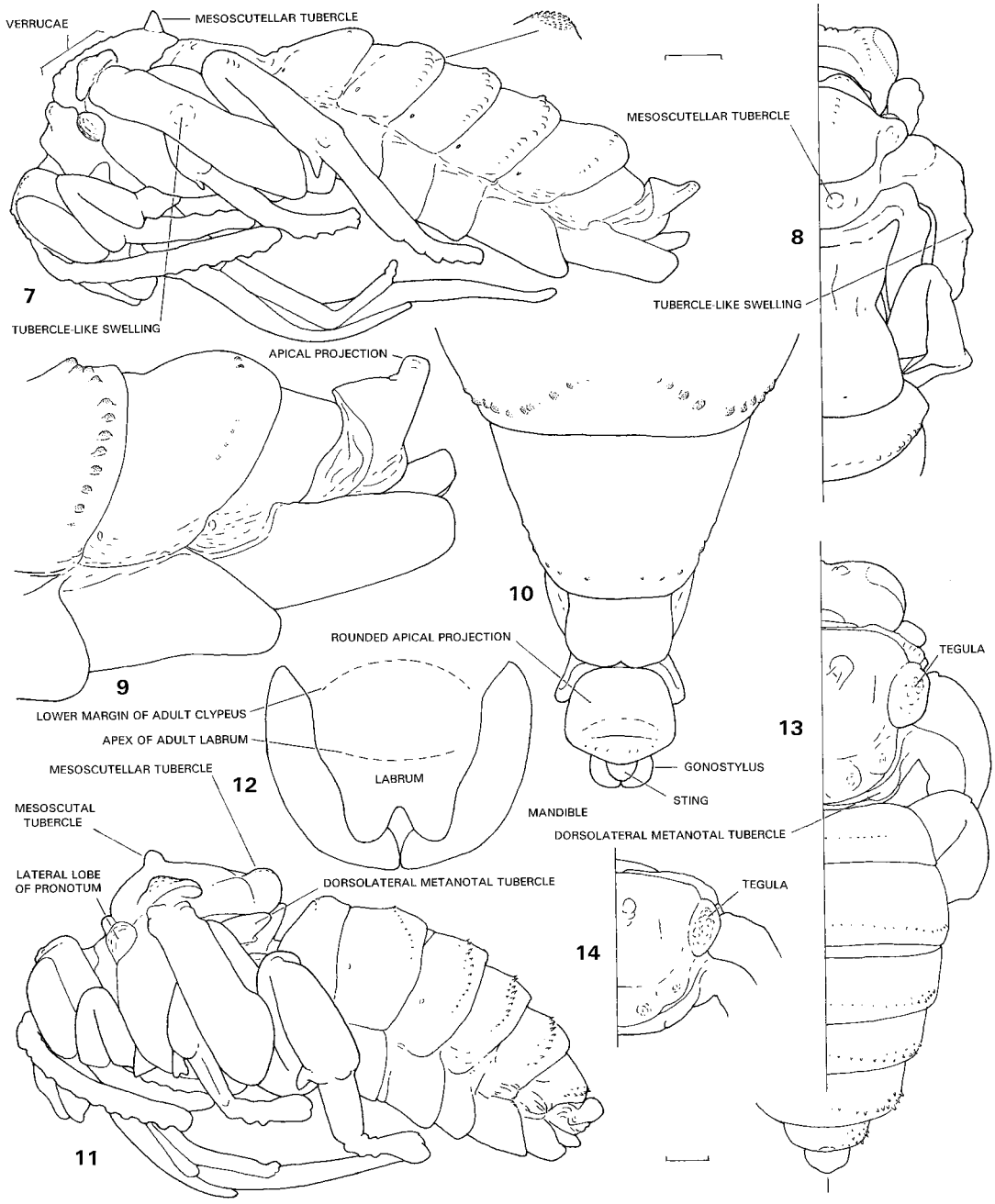
DIAGNOSIS: Among all of the cleptoparasitic Apidae, pupal *Osiris* can be recognized by the densely spiculated apical patch on each of the larger tergal tubercles (figs. 7, 9, 10). The erect, acutely pointed, paired mesoscutellar tubercles (figs. 7, 8) and the absence of mesoscutal tubercles are also helpful in distinguishing these pupae.

HEAD: Integument apparently nonspiculate, without either setae or sharply pointed tubercles, but with low, sometimes almost undetectable row of rounded verrucae above level of antennal sockets along inner orbit and another, even fainter series on vertex above and behind upper orbit. Apex of clypeus without rounded, downward-projecting swelling on each side of labrum as in Ammobatini; labrum about as long as wide, its apex a simple curve in frontal view; pupal ocelli strongly defined; each lateral ocellus with small, rounded tubercle immediately mesad; distal flagellomeres expanded on outer (lower) side. Mandibles strongly swollen posteriorly near apex.

MESOSOMA: Integument finely, inconspicuously spiculate in some areas; setae absent. Lateral angles of pronotum strongly produced, well elevated above lateral lobes, bearing low verrucae; posterior lobes of pronotum strongly produced. Mesepisternum without tubercles; mesoscutum without distinct paired tubercles but with paramedian row of verrucae on each side, anterior ones of which are larger than posterior ones; axillae unmodified, not elevated; mesoscutellum with pair of elevated, acutely pointed, paramedian tubercles; metanotum not produced. Tegula slightly produced, without tubercle(s), but apparently with low, poorly defined verrucae; wings with low, tuberclelike swelling about ⅓ way to apex. Coxae without tubercles; trochanters with apicoventral, angled expansion; femora somewhat expanded basoventrally; tibiae apically expanded into outer, angled, tuberclelike swelling, extreme apex of which often becomes pigmented; hind tibia also with basal verrucae on outer surface, without sharply pointed tubercles; tarsi without tubercles.

METASOMA: Integument finely, inconspicuously spiculate in some areas except apices of most tergal tubercles each with dense, conspicuously spiculate patch; setae absent. T1 with only one or two small subapical tubercles; T2–4 (female) with subapical row of rounded tubercles; T5 with tubercles small, indistinct; T6 without tubercles. Sterna without apical tubercles. Apex of metasoma produced into broadly rounded projection as seen from above (fig. 10), not as terminal spine. Spiracles evident.

MATERIAL STUDIED: 4 female pupae, Fazenda Santa Carlota, São Paulo, Brasil, preserved V-25-89 (E. Camillo, C. A. Garófalo).



Figs. 7–10. Pupa of *Osiris pallidus?* **7.** Entire body, lateral view, with tergal tubercle with spiculate apex enlarged. **8.** Anterior part of body, right side, dorsal view. **9, 10.** Apex of metasoma enlarged, lateral and dorsal views, respectively.

Figs. 11–13. Pupa of *Mesoplia (Mesoplia) rufipes*. **11.** Entire body, lateral view. **12.** Labrum and mandibles, frontal view, enlarged. **13.** Right side of body, frontal view.

Fig. 14. Pupal thorax of *Mesoplia (Eumelissa)* species?, dorsal view.

Scales (= 1.0 mm) refer to figs. 7, 8 and to 11, 13, and 14, respectively.

The determination of this species as *Osiris pallidus* was based on body size, shape of pygidial plate and hind basitarus, and most aspects of color pattern of a developing pharate female that was nearing eclosion. However, integumental texture was difficult to evaluate, and the metasoma became quite dark apically, a feature not recorded by Shanks (1986) or found on females in the collection of the American Museum of Natural History. Hence the specific identity of these specimens is questionable.

ERICROCIDINI

Mesoplia (Mesoplia) rufipes (Perty)

Figures 11–13

DIAGNOSIS: The bilobed labral apex of known ericrocidine pupae distinguishes the tribe from other cleptoparasitic Apidae except for the pupa of *Rhathymus* (Rhathymini) (Camargo et al., 1975). However, in contrast to the Ericrocidini, *Rhathymyus* does not possess paired mesoscutal tubercles. Pupae of *Ericrocis* (Rozen and Buchmann, 1990) and *Mesoplia* are similar although the tegular tubercles of *Ericrocis* are more prominent than those of *Mesoplia*.

The following description is based on a single, well-preserved female; reference is made to a poorly preserved male parenthetically.

HEAD: Integument nonspiculate, without either setae or sharply pointed tubercles, but with low, rounded verrucae in vicinity of lateral ocelli. Apex of clypeus without rounded, downward-projecting swelling on each side of labrum; labrum with maximum length about equal to maximum width, its apex downward deeply bituberculate in frontal view (fig. 12), its tubercles accommodating long, labral hairs of adult; pupal ocelli well defined; all except for first two flagellomeres with well-defined swelling along ventral surface as defined in figure 11. Mandibles swollen posteriorly subapically.

MESOSOMA: Integument nonspiculate; setae absent. Lateral angles of pronotum not strongly produced, not elevated far above lateral lobes, not bearing verrucae; posterior lobes of pronotum strongly produced. Mesepisternum without tubercles; mesoscutum with pair of elevated tubercles, which do not accommodate adult setae; axillae somewhat elevated, faintly verrucose; mesoscutellum with pair of pronounced, rounded tubercles bearing faint verrucae; metanotum with dorsolateral area strongly swollen, accommodating dorsolateral, metanotal, setal tufts of adult. Tegula somewhat produced and apically verrucose; wings without tubercles. Foreleg with coxa having small, apical tubercle; trochanter with ventral tubercle; femur swollen basally. Midleg with coxa bearing small, pronounced, basal tubercle ventrally; trochanter with ventroapical tubercle; tibial spur apically bifurcate; basitarsus with shallow, longitudinal groove on outside, posterior edge of which ends in small apical projection. Hind leg with coxae bearing very small, apical tubercle mesoventrally; trochanter with apical projection ventrally; femur with small, basal projection along posterior edge (this projection much enlarged in male); two tibial spurs (one in male).

METASOMA: Integument nonspiculate; setae absent. T1–6 with posterior row of small, sharply pointed, mostly apically pigmented tubercles; tubercles scarcely noticeable on T1 and T2 but more conspicuous on other terga. Sterna without apical tubercles. Apex of metasoma produced into short, broadly rounded projection as seen from above (fig. 13), not as elongate, terminal spine. Spiracles evident.

MATERIAL STUDIED: 1 female and 1 male pupa, Hollis Reservoir, Valencia, Trinidad, W.I., IV-1968 (F. D. Bennett) from cells of *Epicharis albofasciata* Smith.

Mesoplia (Eumelissa) species?

Figure 14

The above description of the pupa of *Mesoplia rufipes* fits almost exactly that of this species; however, they differ slightly in the extent of expression of certain features. In this species the verrucae associated with the ocelli are even less pronounced, the midtibial spur is less clearly bifurcate, and the midbasitarsus is scarcely grooved longitudinally. Also, the hind femur lacks a basal tubercle, and the pupal tegula (fig. 14) is more elliptical, corresponding to that of the adult. It is reasonable to assume the male pupa and adult have two hind tibial spurs.

MATERIAL STUDIED: 2 female pupae, Raco, Tucumán Prov., Argentina, XII-93 (J. G. Rozen) with larval skins, cocoons, from nest of *Centris*. Identified to subgenus on basis of elliptical tegulae and narrowly pointed, pygidial plate of pharate adult. The single adult female collected at the same nesting site corresponded to the description of *Eumelissa* presented by Snelling and Brooks (1985).

ISEPEOLINI

Isepeolus viperinus (Holmberg)

Figures 15, 16

DIAGNOSIS: The most notable features of the pupa of *Isepeolus* are the pronounced, rounded tubercles near the lateral ocelli, the paired, rounded, mesoscutal tubercles, the pair of low verrucae posterior to the mesoscutal tubercles, and the projecting axillae. The microscopically pointed apices (fig. 15) of some tergal tubercles are also unusual.

This pupa, on loan from the University of Kansas, is the same one briefly described by Michener (1957).

HEAD: Integument without setae or sharply pointed tubercles but with pair of rounded, elevated tubercles in vicinity of lateral ocelli (fig. 15); each of these tubercles accommodating adult hair tuft but tubercle larger than tuft; small, tuberclelike projection immediately laterad of this tubercle; upper anterior surface of compound eye with indistinct, verrucose patch. Apex of clypeus without rounded, downward-projecting swelling on each side of labrum; labral length two-thirds maximum width, its apex simple, rounded in frontal view; pupal ocelli obscured by tubercles; distal flagellomeres with well-defined, apical swelling. Mandible simple, without swellings.

MESOSOMA: Integument finely spiculate in some areas; setae absent. Lateral angles of pronotum not strongly produced, not elevated far above lateral lobes; posterior lobes of pronotum produced. Mesepisternum without tubercles; mesoscutum with pair of conspicuous, elevated, apically rounded tubercles (figs. 15, 16), which do not accommodate adult setae; mesoscutum also with pair of conspicuous verrucae between these tubercles and posterior margin; axillae strongly produced; mesoscutellum strongly bituberculate, apices of tubercles verrucose; metanotum evenly produced. Tegula without tubercle, scarcely produced, with apex faintly verrucose; wings without tubercle. Legs without spines, projections, or tubercles.

METASOMA: Integument nonspiculate; setae absent. T1–5 with subapical row of very small tubercles without apical patch of spicules, unlike that of *Osiris*; tubercles rounded apically and many without pigmented apex but largest ones with single, pigmented spot (fig. 16), presumably homologous with apical spines of other taxa; tubercles of T1 scarcely noticeable. Sterna without tubercles. Apex of metasoma without terminal spine. Spiracles evident.

MATERIAL STUDIED: 1 female pupa, Araucaria, Paraná, Brazil, I-13-1956 (C. D. Michener) #169M.

MELECTINI

Xeromelecta (Melectomorpha) californica (Cresson)

Figures 17–20

DIAGNOSIS: The paired, multispined, mesoscutal tubercles of known pupae of *Xeromelecta*, *Melecta* (Semichon, 1922; Thorp, 1969), *Thyreus* (Cardale, 1968), and *Zacosmia* (Torchio and Youssef, 1968) appear to be a unique diagnostic feature of pupal Melectini as has already been pointed out by Torchio and Youssef (ibid.) and Thorp (op. cit.).

The previously published descriptions (cited above) and those presented here demonstrate pupal features whereby some taxa included in the tribe can be distinguished. The extent of expression of the mesoscutellar tubercles varies from taxon to taxon and corresponds to the variability of the mesoscutellum in adults. Semichon's figure of the thorax of *Melecta albifrons albifrons* (as *armata* Panzer) shows two large, posteriorly directed, mesoscutellar tubercles (no doubt containing the pronounced adult mesoscutellar tubercles). Similarly, Thorp referred to the mesoscutellar tubercles of *Melecta separata callura* (Cockerell) as being ''large, erect protuberances each provided with several spicules.'' Hence, these species of *Melecta* have mesoscutellar tubercles more pronounced than those of *Xeromelecta (Melec-*

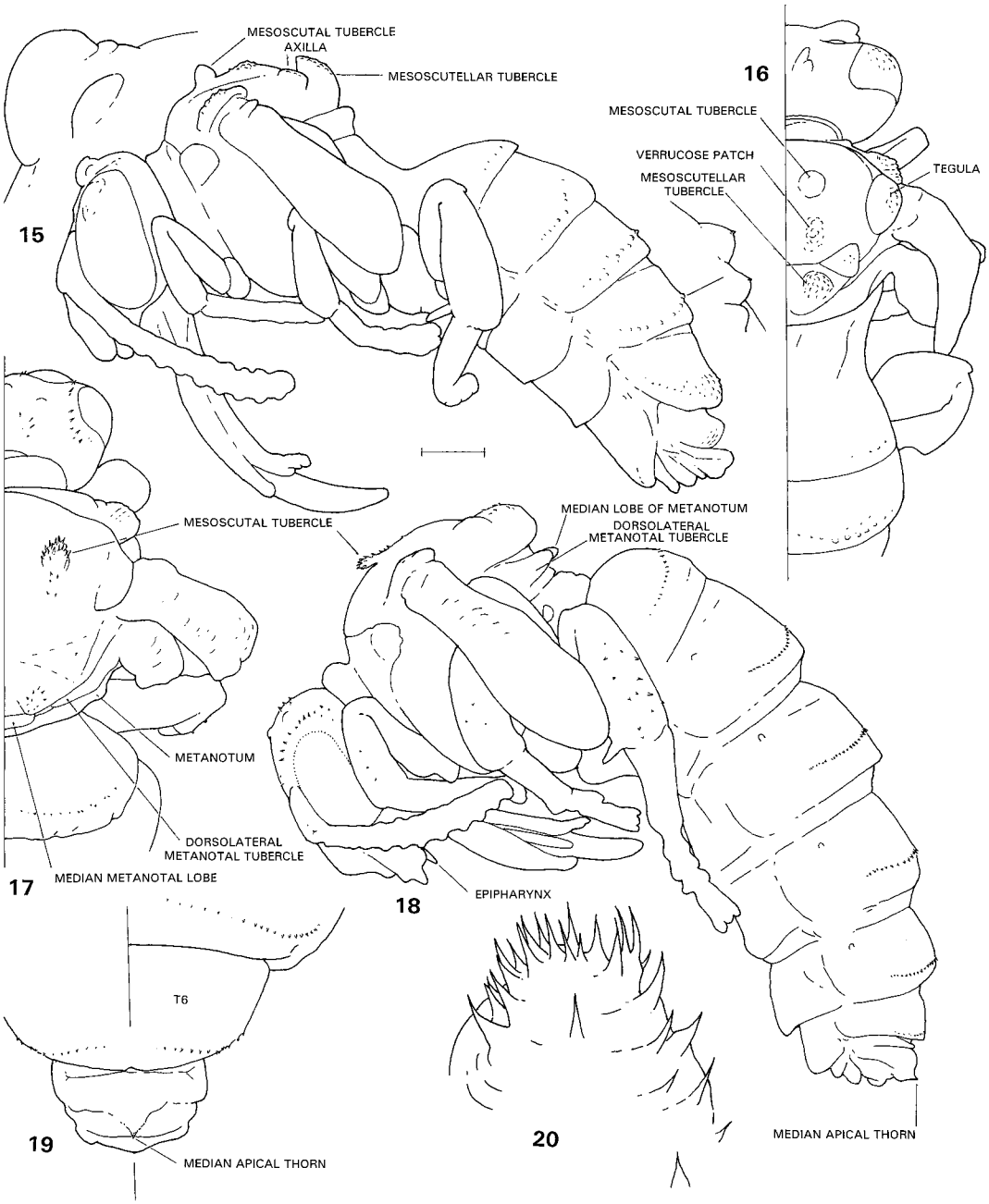


Fig. 15. Pupa of *Isepeolus viperinus*, entire body, lateral view with tubercles of vertex enlarged.

Fig. 16. Same, right side of anterior part of body, dorsal view.

Figs. 17–20. Pupa (female) of *Xeromelecta californica*. **17.** Right side of anterior part of body, dorsal view. **18.** Entire body, lateral view. **19.** Apex of metasoma, enlarged, dorsal view, showing median apical thorn. **20.** Left mesoscutellar tubercle, enlarged, seen from behind, maximum profile.

Scale (= 1.0 mm) refers to figs. 15–18.

tomorpha) californica. Adults of *Xeromelecta (Xeromelecta) larreae* (Cockerell) (a monotypic subgenus) lack mesoscutellar tubercles (Hurd and Linsley, 1951), and therefore its pupa will likely be distinguishable from those of *Melecta*. On the other hand, adults of all known species of *Xeromelecta (Nesomelecta)* have pronounced mesoscutellar tubercles (Michener, 1988), and their pupae will probably be similar to those species of *Melecta* whose pupae have been described.

Although not illustrated, the pupal mesoscutellum of *Thyreus caeruleopunctatus* is said by Cardale to be ''produced into two posterior angles as in adults, each with a tubercle.'' Hence, its pupal mesoscutellum is probably even more exaggerated than that of *Melecta*. However, the mesoscutellar tubercles of *Thyreus* species?, described below, are smaller than those of most pupal *Thyreus* because its entire adult scutellum is more like that of *Melecta* than that of most species of *Thyreus*. Because the pupa of *Thyreus* species? was not found in a cocoon, *Thyreus* remains the only known melectine genus with pupae not in cocoons (Cardale, 1968; Rozen, 1969).

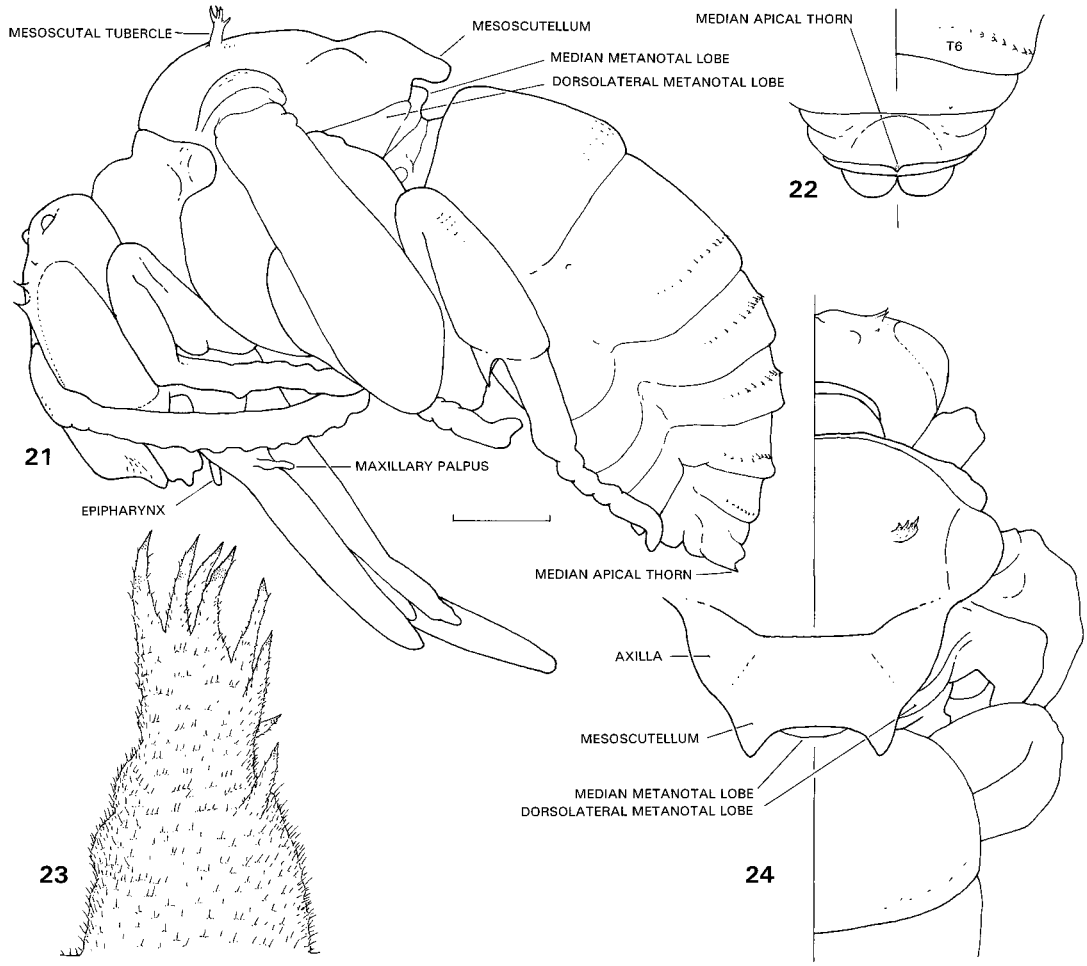
The mesoscutellum of the pupa of *Zacosmia* is said to have two ''weakly developed tubercles'' by Torchio and Youssef (1968), suggesting that its tubercles are even less pronounced than those of *Xeromelecta*. In any event, *Zacosmia* (ibid.: fig. 21) does not have the small but distinctive, median, apical thorn on the metasoma as depicted here (figs. 18, 19) and by Porter (1951: fig. 8) for *Xeromelecta*.

This apical metasomal thorn, not mentioned in any of the other accounts of melectine pupae, also occurs in *Thyreus* species? (figs. 21, 22) and suggests that the phylogenetic relationship of *Thyreus* and *Xeromelecta* should be explored.

HEAD: Integument without setae but with numerous small tubercles bearing sharply pointed, sclerotized apices; these tubercles on frons and vertex; scape with a few similar sharply pointed tubercles on outer apex; rounded tubercles and verrucae absent. Apex of clypeus without rounded, downward-projecting swelling on each side of labrum; labrum apparently nearly as long as maximum width, its apex simple, rounded in frontal view; pupal ocelli weakly defined; most flagellomeres with well-defined swelling along ventral surface, defined as oriented in figure 18. Mandibles markedly swollen anteriorly and posteriorly, subapically.

MESOSOMA: Integument microscopically spiculate in many areas and with small, spinelike, sclerotized projections described below; setae absent. Lateral angles of pronotum not strongly produced, not elevated far above lateral lobes, not bearing verrucae; posterior lobes of pronotum strongly produced. Mesepisternum without tubercles; mesoscutum with pair of conspicuous tubercles (figs. 17, 18, 20) that bear numerous, sharply pointed, pigmented, sclerotized, forward-projecting spines, these tubercles somewhat flattened anterior-posteriorly (hence flaplike) but actually positioned somewhat obliquely on mesoscutum; mesoscutum with several small tubercles each bearing similar spines immediately behind large tubercles, elsewhere mesoscutum with a few scattered, mostly forward-projecting spines; axilla weakly expressed; mesoscutellum with pair of low, rounded tubercles, apparently with verrucose summits and a few multidirectional spines like those of mesoscutum; these tubercles conforming to shape of adult mesoscutellum; metanotum with dorsolateral area swollen, no doubt accommodating dorsolateral, metanotal, setal tufts of adult, and with median, metanotal lobe. Tegula without tubercle, not produced, but with apex faintly verrucose; wings without tubercle but outer surface somewhat verrucose. All coxae with small, apically rounded tubercle on inside; each trochanter with ventroapical projection; all femora with scattered, very small, usually apically pigmented, sharply pointed tubercles on outer surface.

METASOMA: Integument microscopically spiculate; setae absent. T1–6 with subapical row of very small, sharply pointed, mostly apically pigmented and curved tubercles; these tubercles tending to be smaller on T1 than on other terga. Sterna without tubercles. Apex of metasoma produced into short, broadly rounded projection as seen from above (fig. 19), this projection armed with small, median, sclerotized, thornlike spine



Figs. 21–24. Pupa (male) of *Thyreus* species? **21.** Entire body, lateral view. **22.** Apex of metasoma, enlarged, dorsal view, showing median apical thorn. **23.** Left mesoscutellar tubercle, enlarged, seen from behind, maximum profile. **24.** Right side of anterior part of body except for axillae and scutellum, dorsal view.

Scale (= 1.0 mm) refers to figs. 21, 24.

and not with elongate, nonsclerotized apical spine. Spiracles evident.

MATERIAL STUDIED: 1 female pupa, Cedar Point Biological Station, 8 mi. north Ogallala, Keith Co., Nebraska (J. G. Rozen) collected as larva VII-16-1988, pupa preserved I-30-1989; from nest of small *Anthophora*.

Thyreus species?
Figures 21–24

DIAGNOSIS: The pupa of this species is similar to that of *Xeromelecta californica*, above, and is compared to other melectine pupae in the diagnosis of the latter. Character states in boldface, below, differentiate the pupa of *Thyreus* species? from that of *X. californica*.

HEAD: **Integument** without setae but **with approximately three tubercles with sharply pointed, sclerotized apices on each side of upper frons (figs. 21, 24) (but not on vertex as in *Xeromelecta californica*)**; scape without sharply pointed tubercles; rounded tubercles and verrucae absent. Apex of clypeus and labrum as described for *X. californica* except labrum as long as maximum

width; pupal ocelli well defined; most flagellomeres with well-defined swelling along ventral surface. Mandibles markedly swollen anteriorly and posteriorly, subapically; these swellings accommodating developing adult setae.

MESOSOMA: Integument spiculate in many areas; spicules especially long and conspicuous on mesoscutal tubercles (fig. 23); setae absent. Pronotum, mesepisternum, mesoscutal tubercles, and axillae as described for *Xeromelecta californica* except **paired, spine-bearing mesoscutal tubercles (figs. 21,23) much longer relative to basal width, with fewer spines, and nearly erect; mesoscutum without any other tubercles; mesoscutellar integument smooth, without spines; mesoscutellum with conspicuous pair of posteriorly directed tubercles overhanging metanotum (figs. 21, 24),** corresponding to scutellar spines of adult; metanotum and tegula as described for *X. californica*. Mid and hind coxae with small, apically rounded tubercle on inside; trochanters without ventroapical projection; all femora without tubercles on outer surface.

METASOMA: As described for *Xeromelecta californica* except T1 without subapical row of very small, sharply pointed, mostly apically pigmented tubercles (figs. 21, 14). As in *X. californica*, apex of metasoma produced into short, broadly rounded projection as seen from above (fig. 22), this projection armed with small, median, sclerotized, thornlike spine and not with elongate, unsclerotized apical spine. Spiracles faintly evident.

MATERIAL STUDIED: One male pupa, S shore Issyk Kul, 10 km E Kadshi-Saj, Issyk-Kul Region, Kyrgyzstan, 1675 m, 42°10′33″N 72°18′55″E, VII-5-1999 (J. G. Rozen) not in cocoon; from cell of *Anthophora (Petalosternon) albifascies* Alfken (kindly identified by Dr. Robert W. Brooks). Numerous adults (predominantly males) of this *Thyreus* were collected while patrolling the face of a vertical bank in which the host was nesting. These adults run to the distinctive ''Group of *Thyreus dimidiatapunctata* (Spinola)'' in Lieftinck's (1968) key to palearctic species and may represent an undescribed species near *T. dimidiatipunctus* or *T. bidentatus* (Kirby).

REMARKS: Although adults of this species lack maxillary palpi, the pupa possesses short, thin, distinct maxillary palpi (fig. 21).

GENERIC KEY TO PUPAE OF CLEPTOPARASITIC BEES

The following preliminary key is presented from published accounts and from the information presented above. For completeness, the undescribed pupa of *Coelioxoides* (couplet 1) is included; it will be described in a forthcoming paper in which it will be compared with that of its host, *Tetrapedia*. Table 1 lists the species that provided the information for this key and references to published accounts.

1. Vertex, mesoscutum, and terga without hairs or tubercles; labrum longer than maximum width; pupa without cocoon. APIDAE (in part): TETRAPEDIINI . . . . . *Coelioxoides*

   Vertex, mesoscutum, and terga either with fine hairs or at least some of these structures with tubercles; labral length variable; pupa with or without cocoon 2

2(1). Vertex, mesoscutum, and terga with fine hairs, longest of which are at least four to five times length of minute tubercles from which they arise;[2] these tubercles so minute that terga appear to lack subapical, transverse row of tubercles; labrum elongate, much more than twice maximum diameter in frontal view; pupae found in cocoons. MEGACHILIDAE 3

   Vertex, mesoscutum, and terga without fine hairs, sometimes with sharply pointed tubercles whose apices may be setiform but these setiform apices never much more than length of tubercles from which they arise; these tubercles large enough that most terga appear to have subapical, transverse row of tubercles (figs. 1, 2, 5, 6); labrum usually about as long as maximum width or shorter, but, if longer (*Holcopasites*, *Oreopasites*), then vertex, mesoscutum, and terga with more or less conspicu-

[2] This character may not hold for *Heterostelis*, since Thorp (1966) commented that the pupa of *H. hurdi* was ''apparently without long setae on'' these surfaces. Nonetheless, fine hairs on these areas are common on most megachilid pupae, and it would be surprising, therefore, if they were not present.

ous sharp tubercles; pupae with or without cocoons 6

3(2). Axillae produced (correspond to axillae of adult) (Baker et al., 1985: fig. 6) . . . . . *Coelioxys*

Axillae not produced 4

4(3). Mesoscutum not produced strongly posteriorly so that metanotum visible in dorsal view (Rozen, 1967: fig. 31); metanotum with single, median, rounded tubercle as seen from above (ibid.) . . . . . *Dioxys*

Mesoscutum projecting posteriorly so that metanotum scarcely if at all visible in dorsal view (Rozen, 1966: fig. 18); metanotum without median tubercle . . . 5

5(4). Median section of mesoscutellum swollen, so that division of mesoscutum and mesoscutellum forming transverse groove as seen in lateral view (Rozen, 1966: fig. 17) . . . . . *Habrostelis*

Median section of mesoscutellum apparently not swollen, so that profile of mesoscutum and mesoscutellum nearly continuous in lateral view (Rust and Thorp, 1973: fig. 15) . . . . . *Stelis*

6(2). Forewing with conspicuous tubercle midway to apex (Rozen, 1965: figs. 21, 22; Eickwort and Eickwort, 1972: fig. 7); subapical tubercles of terga rounded to acutely pointed but not bearing apical spine; hind tibia with large or small rounded tubercle at base; pupae without cocoons. HALICTIDAE[3] 7

Forewing either without tubercle or, if present, tubercle low and not situated halfway to apex; subapical, tergal tubercles sharp pointed, not rounded, except those of *Osiris* and *Isepeolus*, which occur in cocoons; hind tibia without basal rounded tubercle. APIDAE (in part) 8

7(6). Vertex with pair of large rounded tubercles in position of lateral ocelli, with pair of lower protuberances in front of upper end of compound eye, and with very low protuberance just above eye (Rozen, 1965: fig. 21) . . . . *Sphecodes*

Vertex with tubercles in position of lateral ocelli small, very small tubercle just laterad of ocellar tubercle, without tubercle in front of upper end of eye or at summit of eye (Eickwort and Eickwort, 1972: fig. 7) . . . . . *Microsphecodes*[4]

8(6). Mesoscutum with single pair of conspicuous tubercles, each bearing numerous sharp spines (figs. 17, 18, 20, 21, 23, 24); upper frons and/or vertex with fine, sharply pointed tubercles (figs. 17, 18, 21, 24). MELECTINI . . Included taxa differentiated in diagnosis of *Xeromelecta californica*

Mesoscutum with or without tubercles, but tubercles never bearing numerous spines; upper frons and vertex with or without sharply pointed tubercles . . 9

9(8). Tergal tubercles each with patch of dense spicules apically (figs. 7, 9, 10), without single, sharp point; mesoscutellum with pair of elevated, acutely pointed paramedian tubercles (fig. 17). OSIRINI . . . . . *Osiris*

Most tergal tubercles each with single, short or attenuated, sharp apex, always without apical patch of dense spicules; mesoscutellum with or without pair of tubercles, but tubercles apically rounded when present (figs. 11, 15) . . . 10

10(9). Labral apex bilobed as seen in frontal view (fig. 11) 11

Labral apex truncated, curved, or broadly pointed, not bilobed in frontal view 13

11(10). Mesoscutum without pair of rounded tubercles (Camargo et al. (1975: fig. 11); midtibial spur normal, tapering to apex. RHATHYMINI . . . . . *Rhathymus*

Mesoscutum with pair of rounded tubercles (fig. 11); midtibial spur truncate or bilobed (fig. 11), not tapering to pointed apex. ERICROCIDINI 12

12(11). Tegula with pronounced tubercle (Rozen and Buchmann, 1990: fig. 61) . . . . . *Ericrocis*

Tegula only slightly produced, without distinct tubercle (fig. 11) . . . *Mesoplia*

13(10). Tergal tubercles apparently without apically pointed tip under normal magnification but larger tubercles actually with tiny dotlike spine under high magnification (fig. 15); axillae strongly produced (fig. 15); tubercles in position of

[3] As Dr. Michael S. Engel (personal commun.) has pointed out after reviewing the manuscript, pupae of only some parasitic Halictini are known; immatures of cleptoparasitic Augochlorini (*Temnosoma, Cleptommation,* and *Noctoraptor*) are unknown. However, the characters presented in this couplet correspond to those of the nonparasitic *Augochlora pura* (Say) (Michener, 1954) of the Augochlorini and therefore are likely to apply to the cleptoparasitic taxa of that tribe as well.

[4] Although Eickwort and Eickwort (1972) pointed out that *Microsphecodes kathleenae* is a social parasite, other species in the genus may be cleptoparasites, and hence the genus is included.

lateral ocelli pronounced, rounded, without sharp apices (fig. 15). ISEPEOLINI . . . . . *Isepeolus*

Most tergal tubercles with distinct, sharply pointed apices under normal magnification; axillae usually not produced, but, if so (some Nomadinae), tubercles of head with pointed apices 14

14(13). Tegula without distinct tubercle **and** vertex without sharply pointed tubercles; mesoscutum with pair of tubercles that are rounded or apically verrucose and located in line with or in front of tegula in lateral view (Rozen et al., 1978: fig. 34; Roig-Alsina and Rozen, 1994: figs. 20, 24); pupa found in cocoon. PROTEPEOLINI . . . . . *Leiopodus*

Either tegular tubercle well developed (Rozen, 1977: figs. 21, 26; 1994: fig. 20; 1997b: fig. 25) **or** vertex with sharply pointed tubercles; mesoscutum with or without tubercles; if present, tubercles either sharply pointed or (in *Brachynomada*) somewhat posterior to tegula in lateral view (Rozen, 1994: fig. 20; 1997b: fig. 25); pupa without cocoon. NOMADINAE 15

15(14). Tegula with conspicuous tubercle (Rozen, 1977: figs. 21, 26; 1994: fig. 20; 1997b: fig. 25); vertex, mesoscutum, mesoscutellum without sharply pointed tubercles (see same figures); sterna without tubercles. BRACHYNOMADINI 16

Tegula without tubercle (figs. 1–4, 5, 6); usually vertex and often mesoscutum and mesoscutellum with sharply pointed tubercles (figs. 1, 2, 5, 6); if vertex without sharp tubercles (*Odyneropsis*), some sterna with apical row of sharp tubercles 18

16(15). Mesoscutum with pair of small, rounded tubercles (Rozen, 1994: fig. 20) . . . . . *Brachynomada*

Mesoscutum without tubercles (Rozen, 1977: figs. 21, 26) 17

17(16). Forewing with distinct, acutely rounded tubercle along anterior margin, approximately two-thirds way to apex (Rozen, 1977: fig. 26); vertex with tubercles somewhat more pronounced . . . . . *Melanomada*

Forewing with only vague swelling along anterior margin approximately two-thirds way to apex (Rozen, 1977: fig. 21); vertex with tubercles vaguely expressed . . . . . *Paranomada*

18(15). Apical lateral angle of clypeus with downward-directed tubercle (Rozen and McGinley, 1974: fig. 29); sterna without apical, sharply pointed tubercles. AMMOBATINI 19

Apical lateral angle of clypeus normal, without tubercle; some sterna with apical, sharply pointed tubercles (fig. 6) (these tubercles very small and easily overlooked in *Neolarra*, fig. 1) . . . 20

19(18). Terminal metasomal spine moderately long (Rozen and McGinley, 1974: fig. 26); mesoscutellum with sharply pointed tubercles (ibid.; Rozen, 1992: figs. 5, 8) . . . . . *Oreopasites*

Terminal metasomal spine small, short (Rozen and McGinley, 1974: figs. 32, 33); mesoscutellum without sharply pointed tubercles (ibid.) . . . . *Pasites*

20(18). Tubercles of vertex and most metasomal terga with apices produced as straight or curved, elongate hair, often as long a tubercle itself (fig. 1). NEOLARRINI . . . . . *Neolarra*

Tubercles of vertex and metasomal terga with sharp apices short, not hairlike; if somewhat elongate (*Holcopasites*), then apices hooked or zigzagged (figs. 5, 6) 20

20(19). Terminal spine not developed (Rozen, 1989: fig. 24), so that metasoma ending in short triangular projection in dorsal view; axillae often strongly projecting posteriorly. EPEOLINI 21

Terminal spine elongate (figs. 1, 6), about as broad as high; axillae not strongly projecting posteriorly (figs. 2, 5) . . 22

21(20). Vertex and mesoscutum[5] apparently without sharply pointed tubercles . . . . . *Odyneropsis*

Vertex and mesoscutum with numerous sharply pointed tubercles . . . . . *Epeolus, Triepeolus*

22(20). Labrum elongate, much longer than maximum width (labrum with basal swelling, fig. 6, that should not be confused with apex that is posterior to closed mandibles); tubercles of head and elsewhere with long apices some of which are kinked or zigzag. AMMOBATOIDINI . . . . . *Holcopasites*

Labrum somewhat shorter than maximum width, its apex just reaching closed mandibles (Rozen, 1997a: fig. 1); tubercles of head with apices that are at most hooked. BIASTINI . . . . . *Neopasites*

[5] Evaluated on the basis of a single, poorly preserved specimen.

TABLE 1

Taxa Used for the Generic Key to Pupae of Cleptoparasitic Bees

(References are to published descriptions of material examined. Early references taken in large part from the work of McGinley, 1989. AMNH = American Museum of Natural History.)

HALICTIDAE	
Sphecodes albilabris (Kirby)	Rozen (1965)
Microsphecodes kathleenae (Eickwort)	Eickwort & Eickwort (1972)
MEGACHILIDAE	
Stelis cholorocyanea (Cockerell)	Rust & Thorp (1973)
Heterostelis hurdi Thorp	Thorp (1966)
Hoplostelis bilineolata (Spinola)	Rozen (1966)
Dioxys pomonae pomonae (Cresson)	Rozen (1967)
Coelioxys sayi Robertson	Baker et al. (1985)
C. lativentris Friese	In AMNH collection
APINAE	
Ericrocis lara (Cresson)	Rozen & Buchmann (1990)
Mesoplia (*Mesoplia*) *rufipes* (Perty)	Present study
M. (*Eumelissa*) species	Present study
Rhathymus species	Camargo et al. (1975)
R. near *bicolor* Lepeletier	In AMNH collection
Leiopodus singularis (Linsley & Michener)	Rozen et al. (1978)
L. lacertinus Smith	Roig-Alsina & Rozen (1994)
L. abnormis (Jörgensen)	Roig-Alsina & Rozen (1994)
Isepeolus viperinus (Holmberg)	Michener (1957); present study
Osiris pallidus Smith?	Present study
Coelioxoides waltheriae Ducke	Description to be published elsewhere
Xeromelecta (*Melectomorpha*) *californica* (Cresson)	Porter (1951); present study
Thyreus caeruleopunctatus (Blanchard)	Cardale (1968)
T. dimidiatipuncta bidentatus (Kirby)?	Present study
Melecta (*Melecta*) *albifrons albifrons* (Foster) (as *M. armata* Panzer)	Semichon (1922)
M. (*Melecta*) *separata callura* (Cockerell)	Thorp (1969)
Zacosmia maculata (Cresson)	Torchio & Youssef (1968)
NOMADINAE	
Brachynomada scotti Rozen	Rozen (1997b)
B. roigi Rozen	Rozen (1994)
Paranomada velutina Linsley	Rozen (1977)
Melanoma sidaefloris (Cockerell)	Rozen (1977)
Triepeolus grandis (Friese)	Rozen (1989)
Epeolus tristis Smith	Mayet (1875)
E. pusillus Cresson	In AMNH collection
Odyneropsis species	In AMNH collection
Nomada imbricata Smith	Packard (1897)
N. japonica Smith	Masuda (1946)
N. pygmaea Cresson (as *N.* species)	Rozen (1977)
N. species	In AMNH collection
Pasites histrio (Gerstaecker) (as *Morgania h. transvaalensis* Bischoff)	Rozen & McGinley (1974)
Neopasites cressoni Crawford	Rozen (1997a)
Oreopasites vanduzeei Cockerell	Rozen & McGinley (1974)
O. favreauae Rozen	Rozen (1992)
Holcopasites insoletus (Linsley)	Present study
Neolarra (*Neolarra*) *californica* Michener	Present study
N. (*Phileremulus*) *vigilans* (Cockerell)	Present study

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