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Morphology and Systematic Significance of First Instars of the Cleptoparasitic Bee Tribe Epeolini (Anthophoridae: Nomadinae)

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ABSTRACT

The highly modified first instars of *Triepeolus grandis* (Friese), *T. loomisorum* Rozen, *T. concavus* (Cresson), and *T. dacotensis* (Stevens), *Epeolus ilicis* Mitchell, *E. pusillus* Cresson, and *E. compactus* Cresson are compared and contrasted with one another and with first instars of non-epeoline cleptoparasitic bees known either from the literature or to the author. The morphology of the first and subsequent instars of *T. grandis* is examined in order to establish homologies with the structures of the last instar of this species and of other less modified bee larvae. A taxonomic key to these species is presented as are diagnoses and descriptions of each. The first instars of *Triepeolus* and *Epeolus* differ substantially from one species to the next, and, at least in the case of these limited representatives, the two genera can be distinguished on the basis of first instars. First instars of cuckoo bees possess many features that, when studied, should shed light on the phylogenetic relationships of the taxa.

INTRODUCTION

Past field investigations on the colletid bee genus *Ptiloglossa* (Rozen, 1984) yielded a series of first instars of the cuckoo bee *Triepeolus grandis* (Friese) preserved in the collection of the American Museum of Natural History. Because even short series of first-stage parasitic bees are rarely collected and because those of this species are unusually large, I prepared a taxonomic description of this larva. Such an endeavor seemed worthy because the scant literature pertaining to first-stage cuckoo bees hints of a storehouse of features to illuminate the phylogenetic relationships of the taxa to which these bees belong.

In preparing the description of *Triepeolus*

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grandis, I immediately recognized that the morphology of nomadine first instars was incompletely understood because these animals are so different from most solitary and social bee larvae. Intermediate-stage larvae of this species preserved with the first instars allowed me to homologize structures from one stage to the next and with the more typical last instar. The results of this morphological study are included in this paper as a basis for future taxonomic treatment of cleptoparasitic first instars in general.

After preparing the taxonomic description and anatomical study of *Triepeolus grandis,* I examined first instars of three other species in the genus: *loomisorum, concavus,* and *dacotensis.* The four species exhibit considerable interspecific variation. *T. loomisorum* especially differs from the others, far more than might be expected of a congener, and reinforces the assumption that, among cleptoparasitic taxa, first instars may be of primary importance in elucidating evolutionary relationships. I then studied and described first instars of *Epeolus* (*ilicis, pusillus,* and *compactus*). Although they too show substantial differences from one species to the next, they can be separated as a group from those of *Triepeolus.* Torchio and Burdick (1988) also recognized the potential value of first instar and other nonadult characteristics in phylogenetic studies of the Nomadinae.

The Epeolini, like all other Nomadinae, are composed solely of cleptoparasitic bees. With the exception of *Epeolus,* found in the Old World as well as North America, the other five commonly recognized epeoline genera are restricted to the New World. Their first instars, which exist for only a few days in the cells of the host bees, have not been systematically studied before because of their rarity. The larvae described here are the only ones in existing collections.

Acknowledgments

I wish to thank Philip F. Torchio, USDA Bee Biology and Systematics Laboratory, Logan, Utah, and Arturo Roig A., Department of Entomology, University of Kansas, Lawrence, for critically reviewing this manuscript. Eric Quinter, Scientific Assistant, American Museum of Natural History, proofread the manuscript and assisted in other ways in the study.

First instars of parasitic bees are difficult to collect because they are small, short-lived, and must be extricated from host brood cells in difficult-to-reach places. I therefore wish to acknowledge the kind cooperation of the following persons: Mont A. Cazier, Arizona State University, donated the specimen of *Triepeolus grandis* taken from the nest of *Ptiloglossa jonesi* Timberlake; George E. Bohart and Philip F. Torchio, both of the USDA Bee Biology and Systematics Laboratory, Logan, Utah, lent larvae of *T. dacotensis* as did Torchio, of *Epeolus compactus*; and Robert L. Minckley, Department of Entomology, University of Kansas, provided the single first instar of *T. concavus.* Their specimens contributed substantially to this study.

I collected larvae of *T. grandis* and *T. loomisorum* while I was in residence at the Southwestern Research Station (V. D. Roth and W. C. Sherbrooke, Resident Directors) of the American Museum of Natural History. I recovered first instars of *E. ilicis* while I visited St. Catherines Island (Royce Hayes, Superintendent) supported by the Edward J. Noble Foundation and the St. Catherines Island Foundation.

MORPHOLOGICAL STUDY OF LARVAL INSTARS OF *TRIEPEOLUS GRANDIS*

Anatomy of First Instar: Hospicidal[2] cuckoo bee larvae are highly modified compared with nonhospicidal larvae, and the first instars of the Nomadinae have evolved some of the most extreme modifications of any bee larvae. The small size of most nomadine first instars makes them difficult to study. However, the first-stage larva of *Triepeolus grandis* is large,[3] allowing investigation of its ex-

[2] From Latin: *hospes* = host; *caedo* = to cut down, to kill. Refers to those cleptoparasitic bee larvae that have special modifications (e.g., elongate, sickle-shaped mandibles) used to destroy the host larvae (or eggs). Antonym: nonhospicidal—referring to cleptoparasitic bee larvae without such modifications (e.g., in those taxa where the cleptoparasitic female destroys the host immature when she oviposits).

[3] The first instar (6.2–7.5 mm) is markedly longer than the host egg (3.9–4.6 mm) (Rozen, 1984). Although this

ternal and (because of its semitransparent integument) some aspects of its internal anatomy. The functions of some adaptations seem obvious, but other functions are more doubtful and are presented below as hypotheses for future testing.

For *Triepeolus grandis* and other nomadines, the alterations relate to the fact that the first instar must search out and battle for survival with the host larva and possibly with other *T. grandis* larvae if more than one cuckoo bee egg has been deposited. (First and perhaps subsequent instars of its hosts, two species of *Ptiloglossa,* may be capable of defending themselves as evidenced by their enlarged mandibles, Rozen, 1984. First instars of *Protoxaea gloriosa* Fox, which hosts *T. kathrynae* Rozen, also have elongate mandibles, Rozen, 1965.)

Two remarkable modifications of the head capsule of *T. grandis* are its prognathous, elongate condition and its heavy sclerotization accompanied by dark pigmentation (figs. 1, 2, 4–6), features shared with other *Triepeolus* and *Epeolus* species studied here. The elongation of the ventral area of the head positions the huge, sickle-shaped mandibles to reach out and seize rivals or host larvae. Heavy sclerotization serves the double function of protection from the sharp mandibles of other larvae and (probably more importantly) of providing a firm structure for attachment of mandibular muscles, which originate on much of the dorsal part of the parietals. The ventral mesial extension of the parietals and complete ringing of the postoccipital area give further strength to the head in that it becomes almost a cylinder. The head elongation is paralleled by the lengthening of the mandibular apodemes, which accommodate the large mandibular muscles.

Internal head ridges, which are important structural elements and significant anatomical landmarks for insects, are obscure—probably because the head is so heavily sclerotized that bracing structures are unnecessary. Hence, the epistomal ridge cannot be identified, and the anterior tentorial pits (fig. 4), normally associated with the ridge, lie in the featureless frontoclypeal area. Similarly, the pleurostomal and hypostomal ridges cannot be distinguished from the parietals. A peculiar feature on the ventromesial edge of each parietal is the hypostomal groove (fig. 2), a long external sulcus that runs from the base of the head forward to the posterior (ventral) mandibular articulation. Its position and the fact that the posterior tentorial pit lies in it indicate that the groove may be a homolog of the hypostomal suture (and ridge). However, its broad, troughlike appearance and its pebbled surface indicate some purpose other than that of a brace (the normal function of the hypostomal ridges of bee larvae) and therefore suggest a different evolutionary origin from that of the hypostomal ridge.

The mesial extension of the ventral sclerotization of the head capsule (fig. 2) probably gives further strength to the head capsule and reduces the amount of unprotected membrane on the undersurface of the head. The sclerotization curves around the maxillary palpus so that the palpi are not fixed to the head capsule. The anterior end of the sclerotization bends inward and upward around the base of the mandible before ending in a blunt, ridge-bearing process (the hypostomal process), discussed below in relation to the mandibles and the hypopharynx.

The antennae (fig. 1) appear dorsally on the anterior part of the head capsule as two inconspicuous, sensilla-bearing mounds. Their low profile (fig. 6) and position well behind the front of the head capsule suggest that they do not play an important role in locating the host, in contrast to the pronounced antennae of a number of other cuckoo bee taxa with hospicidal larvae (e.g., *Stelis,* Rust and Thorp, 1973, Rozen, 1987; *Dioxys,* Rozen, 1967; *Melecta,* Giordani-Soika, 1936, Torchio and Youssef, 1968, Bohart, 1970; *Thyreus,* new information; *Zacosmia,* Torchio and Yous-

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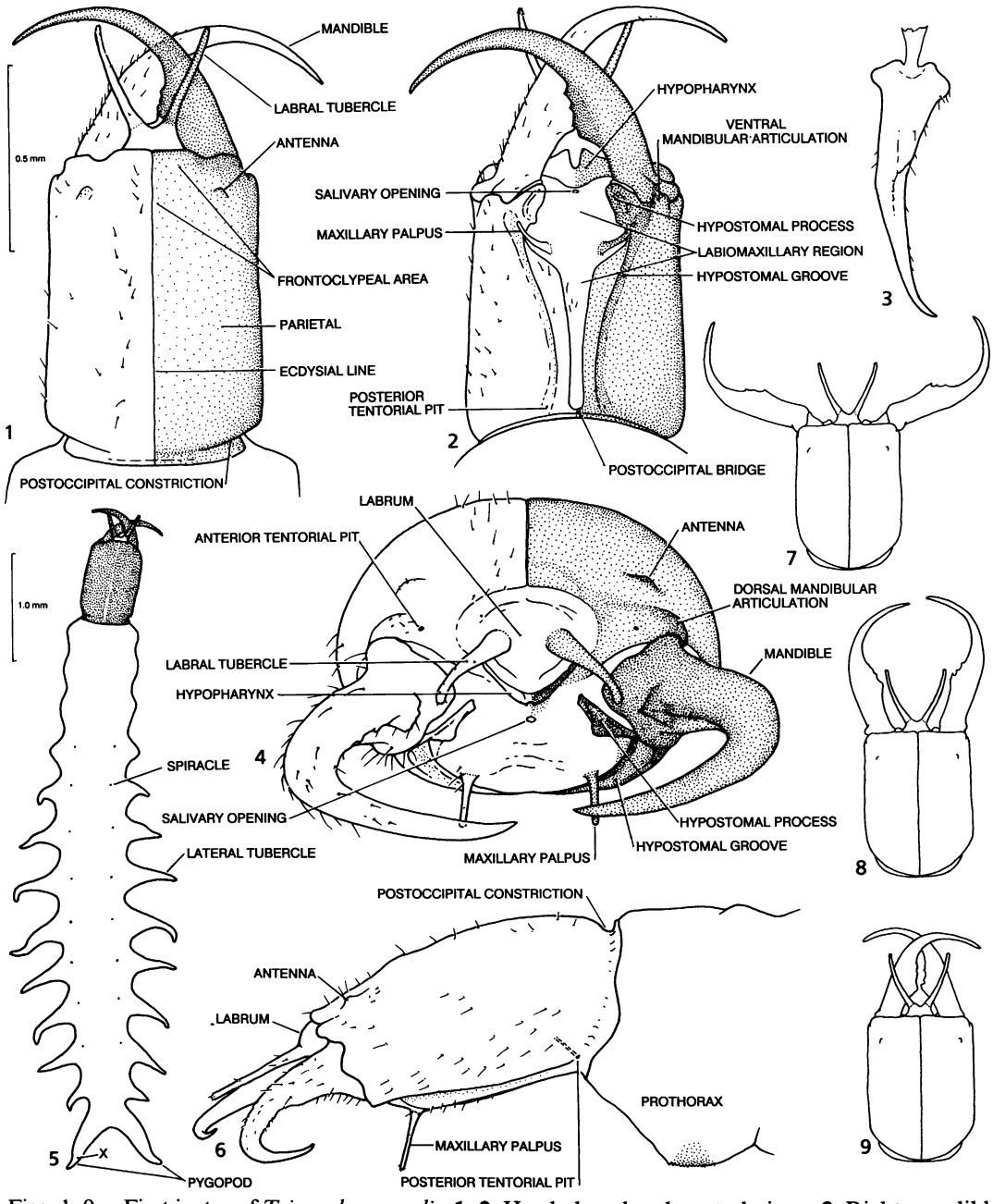
seemed to suggest that the egg of *Triepeolus grandis* would be found to be correspondingly large, a single egg actually measured only 2.4 mm (ibid.). Its relatively small size agrees with the observations of Alexander and Rozen (1987) that mature oocytes of cleptoparasitic bees tend to be small compared with those of solitary bees. However, the small size of the egg compared to the large first instar indicates that the newly hatched larva grows dramatically and quickly, increasing well over 2.5 times the length of the mature embryo in a very short time. Similar lengthening of the first instar of *Epeolus* at eclosion has been described in some detail by Torchio and Burdick (1988).



Figs. 1–9. First instar of *Triepeolus grandis*. **1, 2.** Head, dorsal and ventral views. **3.** Right mandible, inner view. **4.** Head, frontal view. **5.** Entire body, dorsal view. **6.** Head, lateral view. **7–9.** Head, dorsal view, showing various positions of mandibles. 0.5 mm scale refers to figures 1–3 and 6; 1.0 mm scale, to figure 5.

sef, 1968; *Mesoplia,* new information). So far as is known, all Nomadinae agree with *Triepeolus* in having low antennae, as is also true for the first instar of the unrelated *Rhathymus* (Camargo et al., 1975).

The frontoclypeal area (fig. 1), which is not separated from the rest of the head by a suture, can be defined as the area mesad of the antennae and extending somewhat posterior to them where the labral muscles find their

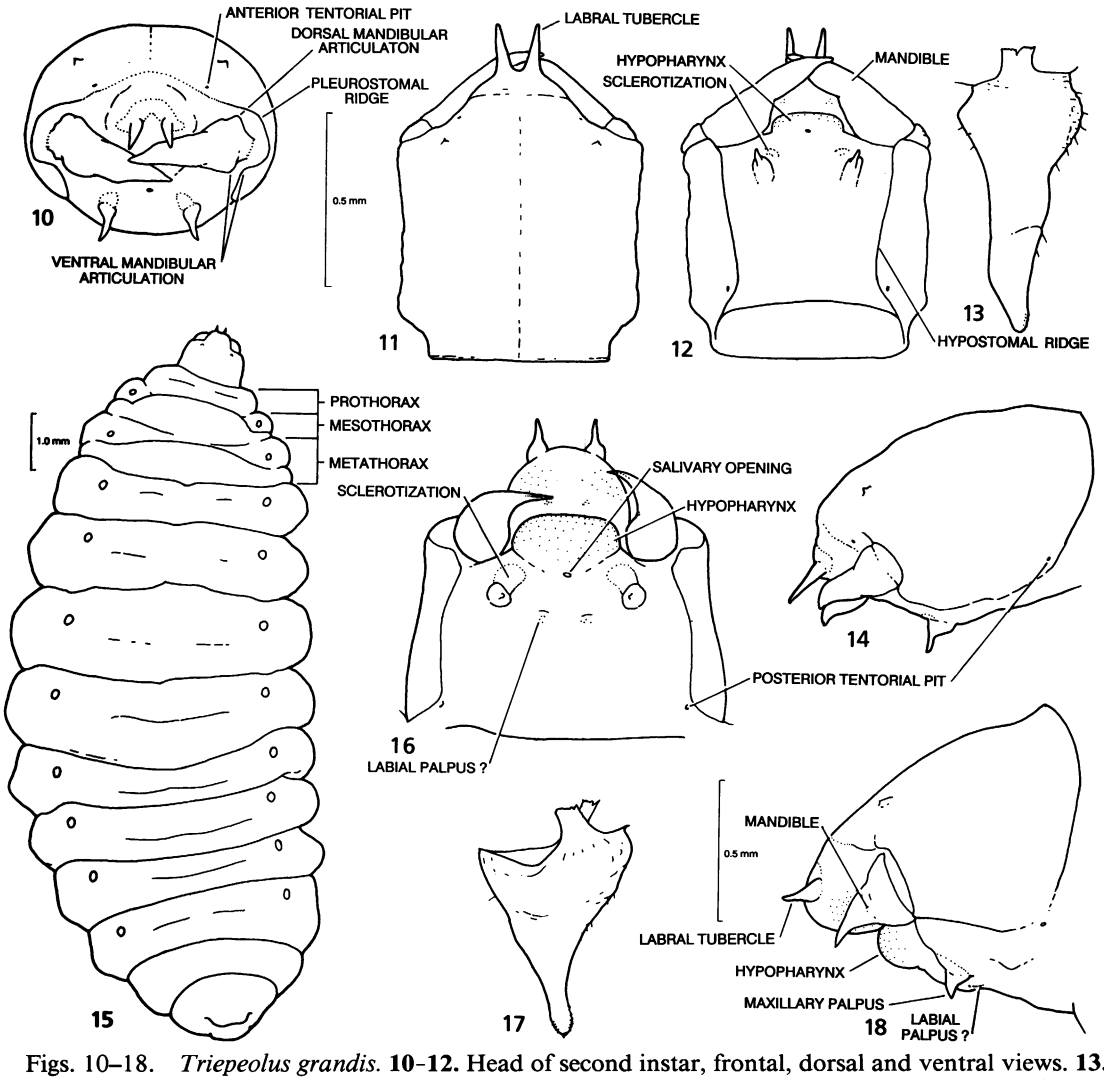
origin. The head capsule is abruptly constricted near its posterior margin. Immediately behind the constriction it flares outward before ending, to form a narrow rim. This rim can be considered the postocciput, for the muscles of the prothorax attach to it. On the venter, the two ends of the rim fuse and form the postoccipital bridge. The tentorial arms extend into the head capsule from inconspicuous external pits. Although these arms are so thin that they clearly do not brace the cranium, the tentorial armature may be complete although difficult to observe.

Like the head capsule, the mouthparts exhibit a number of conspicuous modifications associated with killing other immatures found in the host cell. Although the labrum (figs. 1, 2, 4, 6) is small, membranous, and unpigmented, it possesses a pair of elongate, sclerotized, pigmented, sensilla-bearing, diverging tubercles. These structures permit the larva to probe the area in front of its head and between its open mandibles (fig. 7). The fact that the labrum is membranous enables the tubercles to bend away from any larva or egg grasped in the closed mandibles. Paired labral tubercles, though seldom so elongate, are characteristic of first instars of the Nomadinae, and persist through all larval instars. *Isepeolus,* an exception, has only a single median labral tubercle both in the first instar (Michener, 1957; Oliveira, 1966) and in the last (Rozen, 1966a). The prognathous condition of its head suggests that the tubercle functions as do paired labral tubercles in other genera.

The greatly elongate mandibles of *Triepeolus grandis* open widely (fig. 7) so that the larva commands a large area. They apparently pose a series of threats to other immatures in that the tips are sufficiently sharp to pierce soft integument. In addition, an immature caught by the inner apical curve (rather than by the points as in fig. 8) of the mandibles will be forced against the opposing series of sharp, sawlike, irregular teeth on the inner surfaces as the mandibles close (as in fig. 9). Lastly, any caught immature escaping these teeth presumably will be forced against the anterior edge of the sclerotic hypopharynx when the mandibles are closed even farther (figs. 1, 2). The hypostomal processes at the base of the mandibles may also injure the immature at the same time. The reduction of these processes in *T. loomisorum* and in *Epeolus* suggests that they serve a function other than being simply armor protecting the mandibular bases in *T. grandis.* (The dissimilarities of the mandibles and the hypostomal areas immediately behind the mandibular bases of *T. loomisorum* may imply that it kills the host only by piercing with the tips of the mandibles rather than by the several ways described for *T. grandis.*) Torchio (personal commun.), in his comments after reviewing this manuscript, stated that he believed that the hypostomal process acts like the cocking of a gun trigger, enabling each mandible to snap shut rapidly (and presumably with force). He proposed that finding muscles attached to the process would be a test of the idea. I cannot identify such muscles on available specimens, nor can I detect a hinge that would permit the hypostomal process to bend in relation to the head capsule, a seeming requisite of a triggering mechanism. Indeed the external ridge of the process would seem to add additional rigidity in *T. grandis.* However, the external ridge is absent in *T. dacotensis,* and in any event such a possibility cannot be discounted without further study.

In spite of its unusual appearance the hypopharynx (figs. 2, 4) can be identified easily because it lies below the mouth (best observed on a cleared specimen) and anterior to the small, but evident, median salivary opening (fig. 2). The sides of the hypopharynx are firmly attached to the sides of the frontoclypeal area (fig. 4) so that an immature being squeezed against it will encounter an unyielding jagged edge. At the same time, the soft labrum of *Triepeolus* is retracted or pushed out of the way.

The membranous area on the venter of the head behind the hypopharynx is the labiomaxillary region. The hypopharyngeal groove is not evident, but the boundary of the labium and hypopharynx is undoubtedly the posterior edge of the sclerotic hypopharynx where the salivary opening is also found. Hence the salivary opening is situated in a position characteristic of most insects rather than at the tip of the labium as seems characteristic of mature cocoon-spinning Hymenoptera larvae (Rozen and Michener, 1988). It is a single, circular opening without lips, to which is attached the salivary duct, visible on a cleared specimen.



Figs. 10–18. *Triepeolus grandis.* **10–12.** Head of second instar, frontal, dorsal and ventral views. **13.** Right mandible of same, inner view. **14.** Head of same, lateral view. **15.** Entire body of third instar, dorsal view. **16.** Head of same, ventral view. **17.** Right mandible of same, inner view. **18.** Head of same, lateral view. Two 0.5 mm scales refer respectively to figures 10–12 and 14 and to figures 16 and 18; 1.0 mm scale, to figure 15.

Except for a pair of elongate, sclerotized maxillary palpi (fig. 2), the labiomaxillary region has no notable features in that the separate elements of the labium and maxilla are indistinguishable. The region extends posteriorly as a narrow V until it ends at the postoccipital bridge. Its integument bears scattered setae, some of which may be the sensilla of the labial palpi. The maxillary palpi can be recognized as such by observing them through the ontogenetic transformation series (figs. 2, 4, 6, 10, 12, 14, 16, 18). They were correctly identified by Torchio (1986) in the embryo of *Triepeolus dacotensis* but misinterpreted by others in the first instar of *T. remigatus* (Fabricius) as being the labial palpi (Bohart, 1966; Stephen et al., 1969). Stephen et al. (1969, fig. 104) also misidentified other parts on the ventral surface of the head if my interpretation is correct. Their "maxilla" corresponds to the hypostomal groove containing the posterior tentorial pit;

their "prementum (?)," to the mesial extension of the parietal; and their "labium," to the labiomaxillary region.

The body of the first instar (fig. 5) is less modified than the head with two major exceptions. The lateral tapering abdominal tubercles, characteristic of many but not all *Triepeolus* and at least one *Epeolus* (as revealed by this study), are pronounced features that may stabilize the larva in combat, particularly on the liquid food surface where it is usually found (Rozen, 1984). (However, *T. loomisorum* lacks such tapering tubercles even though it too was on the surface of wet provisions. Further, the tubercles of *T. dacotensis* are rounded and not long and tapering even though its provisions are liquid. Do first instars of species of *Triepeolus* on solid provisions, e.g., those in *Nomia* nests, have lateral abdominal tubercles, tapering or rounded?) The tubercles do not assist locomotion in that they have no muscle attachments, in contrast to the forked pygopod on abdominal segment 10. Torchio (personal commun.) states that each pair of tubercles of *T. dacotensis* on eclosion expand laterally when they are freed from the egg capsule and thereby anchor the larva in the interim period as the pygopod is brought forward in preparation for another push.

The second major specialization is the pygopod itself, seemingly but actually not homologous to the lateral tubercles, in that muscles attach to each ramus subapically (fig. 5, point x) (also the case with the other *Triepeolus* and *Epeolus* species). Hence the pygopod is eversible by muscle contraction and by body fluid eversion and probably helps push the larva as it crawls over the cell wall after eclosion. Because of its large size (a feature of all known *Triepeolus* and *Epeolus* species), the pygopod probably also improves larval stability as do the lateral tubercles. Pygopods probably represent a synapomorphy of first instar Nomadinae since they have been observed in very different taxa (*Protepeolus,* Rozen et al., 1978; *Neopasites,* Torchio et al., 1967; *Nomada,* Linsley and MacSwain, 1955; *Pseudodichroa,* Rozen and Michener, 1968; *Pasites,* Rozen, 1986; *Epeolus,* Rozen and Favreau, 1968, Torchio and Burdick, 1988; *Triepeolus,* Bohart, 1966, Stephen et al., 1969, Torchio, 1986). However, they are not reported for *Isepeolus* (Michener, 1957; Oliveira, 1966). The pygopod of *Nomada,* instead of being forked as in other genera, bears a median lobe so that it is trilobed (Linsley and MacSwain, 1955).

So little is known about first instars of bees that I cannot interpret the meaning of the missing thoracic spiracles (fig. 5) of *Triepeolus grandis* and of the other species of *Triepeolus* and *Epeolus.* However, in *Stelis elongativentris* Parker (Rozen, 1987) the thoracic spiracles are also missing, and the last two pairs of abdominal spiracles are rudimentary. All ten pairs of spiracles are present and of equal size in *Stelis montana* Cresson, according to Torchio (personal commun.). In *Dioxys pomonae pomonae* Cockerell all ten pairs of spiracles are present in the first instar, but the second pair is reduced in size (Rozen, 1967). All spiracles are present and uniform in size in *Protepeolus* first instars (Rozen et al., 1978). Clearly more data need to be recorded on this matter for first instars of parasitic and nonparasitic bees alike. The spiracles of *Triepeolus grandis* assume a nearly dorsal position on the abdomen because of the lateral tubercles which lie below them. As a consequence spiracles on both sides of the body are fully exposed in the air in contrast to the situation in the host larva which feeds on its side so that the spiracles on its lower side are submerged in the liquid provisions (Rozen, 1984).

Although first instars of *Triepeolus grandis* have a straight and slender aspect upon eclosion (fig. 5), the body gradually becomes fusiform as the larva ingests provisions. Just before molting, the first instar appears navicular with the dorsal region tending to be nearly flat and the venter bowing into the provisions. This shape is carried over to the next instar.

MATERIAL STUDIED: See listing of specimens in description of first instar of this species.

ANATOMY OF SECOND INSTAR: The head capsule (figs. 10–12, 14) of this instar differs from that of the first in a number of substantial ways. It is now weakly sclerotized, scarcely pigmented, and has an uneven surface. Although its length is about equal to that of the first instar, it is wider and assumes a more quadrate appearance from

above or below (figs. 11, 12). The internal head ridges continue to be poorly defined, but now because of weak sclerotization of the whole head capsule rather than heavy sclerotization. The epistomal ridge is the leading edge of the parietals and bears the small anterior tentorial pits (fig. 10). The pleurostomal ridge is a vague, pigmented thickening of the integument that arches above the mandibular corium on each side. The hypostomal ridge (fig. 12), though weak, is pigmented and extends from the posterior mandibular articulation to the posterior tentorial pit. The pronounced hypostomal groove of the first instar is completely absent, as are the hypostomal processes at the bases of the mandibles and the mesial ventral extensions of the parietal. The labiomaxillary region is no longer a narrow V but a broad expanse of membrane running between the two hypostomal ridges. The sides of the head are constricted immediately anterior to the posterior margin, but there is no longer a postoccipital bridge ventrally; the membrane of the labiomaxillary region is a continuum with the membranous venter of the prothorax. The tentorium is slightly thicker, and the antennae appear as small but more acute mounds in this instar.

The mouthparts have also changed. The labrum now bears a weak apical sclerotization to which the relatively short labral tubercles are affixed. The mandibles (figs. 12, 13) are substantially shorter but still sufficiently long that, when closed, they cross. No longer sickle-shaped, they consist of (1) an apical part that tapers to a narrowly rounded, adorally flattened apex bearing indistinct marginal serrations and (2) a somewhat larger basal part (fig. 12). There are no teeth or ridges on the inner surface.

The salivary opening (figs. 10, 12) continues to be a well defined, small oval opening posterior to the now completely membranous, unpigmented, spiculate, somewhat bulbous hypopharynx. The maxillary palpi are still sclerotic and elongate, but the basal part of each is expanded and a weak patch of sclerotization is visible in front of each. There is as yet no indication of the features of the labium as separate from the labiomaxillary region.

These changes probably signify that the second instar cannot effectively battle host or rival *Triepeolus* larvae. The head capsule has lost its rigidity and therefore the mandibles, their strength. Further, the mandibles are no longer armed with sharp points or inner teeth, and the sharp processes at the front of the head (hypostomal processes and sharp-edged hypopharynx) are missing. The function of the mandibles is unclear. Although the mandibles are still long and seemingly capable of pushing provisions into the mouth, the mandibular articulating points on the head are weakly sclerotized, suggesting that the mandibles are not functional for feeding, as seems to be the case for the extremely short mandibles of the last instar. If this is true then their length in the second instar may merely represent a step in their gradual reduction from one instar to the next. Microscopic examination of a feeding larva should resolve this matter.

The postcephalic region of the second instar retains the lateral abdominal tubercles although they are not as long or tapering. The eversible, bifurcate pygopod also apparently persists but was inverted at time of specimen preservation and therefore difficult to assess. In this instar the thoracic spiracles appear, but are only half the diameter of those on the first abdominal segment. Abdominal segments are subdivided into cephalic and caudal annulets. The anus is now clearly visible as a small median transverse slit between the rami of the pygopod.

Bohart's (1966) account of the second instar of *Triepeolus remigatus* seems to agree with the above description of *T. grandis.*

Material Studied: 1 second instar, Portal, Cochise Co., Arizona, September 1, 1983 (J. G. Rozen) from cell of *Ptiloglossa arizonensis* Timberlake.

ANATOMY OF SUBSEQUENT LARVAL INSTARS: Although I have usually thought that bees have five larval instars, these larvae and the several cast skins associated with them indicate only four distinct morphological types. Hence *Triepeolus grandis* may have only four instars, the same number that Bohart (1966) reported for *T. remigatus.*

Changes in the anatomy (other than body size) are relatively gradual after the second instar (see figs. 10–14 for second instar; figs. 15–18 for third instar; and Rozen, 1966a, figs. 8–14 for last instar). The shift from prog-

nathous to hypognathous head, already evident in the second instar, continues so that, by the last instar, the head position is normal for bee larvae in general. The labral tubercles also shorten from one instar to the next. Reduction in mandibular size is dramatic not only because of the huge mandibles of the first instar but also because those of the last are abnormally short compared with those of most bees. The tips of the closed mandibles of the third instar just reach the midline of the head (fig. 16), and those of the last instar do not reach the midline. Mandibular apexes become slender relative to their bases in the third (fig. 17) and last instar (Rozen, 1966a, figs. 12–14). Apical marginal serrations are evident in the third instar (fig. 17) but are nearly lost in the last (Rozen, 1966a). Although the mandibles continue to be one of the most heavily sclerotized and darkly pigmented body parts, they appear to take on additional sclerotization and pigmentation in the last instar. This feature coupled with the very thin, fanglike apex (Rozen, 1966a, figs. 12–14) suggests a function of defense (or attack) in the last instar, although I have not seen live last instars in a position of having to defend themselves. It seems clear from its shortness and lack of a broad apex that the mandible of the last instar is functionless for eating.

The maxillary palpi (figs. 14, 18) are always evident from one instar to the next even though they become shorter. The sclerotized area in front of each, first seen in the second instar, persists in the third, but is scarcely evident in the last. The labial palpi, fundamental anatomical features of most bee larvae, are not clearly developed in any larval instar of *Triepeolus grandis* (indeed, they tend to be missing or greatly reduced in almost all Nomadinae). However, a pair of vague, slightly sclerotized swellings mesad of and posterior to the maxillary palpi are seen in the third instar. Their position and their sensilla reasonably establish them as the labial palpi. After its dramatic change from the first to second instar, the hypopharynx remains almost the same from the second to last instar, increasing only in protrusion. The salivary opening, always a lipless oval slit, remains immediately below (behind) it.

Several changes take place within the last stadium. The predefecating body is now extremely large and rounded. After defecation the body becomes much more tapering, especially posteriorly, and the quiescent, overwintering larva has a strongly curved anterior end (Rozen, 1966a: fig. 8) that is characteristic of many Nomadinae. Although spiracular sclerites are not evident in predefecating last instars and are also absent in early postdefecating ones, distinct, darkly pigmented sclerotized rings appear around the spiracles as the body integument darkens and the larva enters deep diapause. The sclerites, once developed, cause the spiracles to project above the body surface. Development of a distinct sclerite within a larval stadium is an unusual feature to say the least, and is unique in my experience with respect to bee larvae (although it may be found to be characteristic of *Triepeolus* and some other epeolines).

MATERIAL STUDIED: 1 third instar (with cast skin of second instar), Portal, Cochise Co., Arizona, August 23, 1983 (J. G. Rozen) from nest of *Ptiloglossa arizonensis*; 1 predefecating last instar, same except September 1, 1982; 3 predefecating and 1 postdefecating last instars (one with skin of previous instar partly shed), same except August 14 to September 2, 1983 (J. G. Rozen and M. Favreau); 4 postdefecating last instars, same except September 1, 1983 (J. G. Rozen); 1 postdefecating last instar, same except September 6, 1982.

COMPARISON OF FIRST INSTARS OF THE EPEOLINI WITH THOSE OF OTHER CLEPTOPARASITIC BEES

A precise diagnosis of the first instar Epeolini permitting the tribe to be distinguished from other cleptoparasitic groups is not yet possible because representatives of this stadium are infrequently collected and studied. However, there are sufficient accounts in the literature and additional taxa (at least of the non-Nomadinae) in the collections of the American Museum of Natural History (AMNH) to present some preliminary comparisons. I hope these comparisons will encourage further investigations not only of the systematics of first instar parasitic bees, but also of the behavioral-ecological role played by the peculiar and distinctive structures of these highly modified animals.

Among other Nomadinae, first instars of *Oreopasites* (Rozen, 1954) and *Kelita* (Ehrenfeld and Rozen, 1977) are also prognathous, but the labral tubercles and maxillary palpi are much shorter than in epeolines. *Isepeolus* (Michener, 1957; Oliveira, 1966) is immediately distinguishable from all other Nomadinae in that it has a single median labral tubercle (rather than paired tubercles) at the front of its strongly prognathous head. The first instar of *Protepeolus* (Rozen et al., 1978) can be separated from all other known Nomadinae including *Triepeolus* and *Epeolus* because of its hypognathous head, multituberculate labrum, padlike maxillae, and setaform spicules on much of its body. There are as yet no descriptions of the first instars of the widespread *Nomada,* the North American *Holcopasites,* and some other rarer Nomadinae beyond brief references to the fact that observed first instars are linear, often exhibit pigmented, prognathus head capsules, possess unusually elongate, curved, sharp-pointed mandibles, and ambulate by pushing with the tip of the abdomen (see section on morphology for details).

First instars of many non-nomadine cleptoparasitic bees are hypognathous and therefore easily separated from *Triepeolus* and *Epeolus,* including *Dioxys* (Rozen, 1967), *Stelis* (Rust and Thorp, 1973; Rozen, 1987), and *Rhathymus* (Camargo et al., 1975). Others are prognathous but, because of their well-developed antennae, can easily be distinguished from the Nomadinae. These genera include: *Melecta* (Giordani-Soika, 1936), *Zacosmia* (Torchio and Youssef, 1968), *Xeromelecta* (Torchio and Trostle, 1986), *Thyreus* (new information), *Mesoplia* (new information), and *Aglaomelissa* (new information). Second and third instars of *Coelioxys* possess heavily sclerotized, prognathous head capsules and elongate mandibles and therefore superficially resemble Nomadinae. However, their elongate antennae, lack of labral tubercles, and presence of maxillary and labial palpi and genal tubercles (pleurostomal thickenings of Baker, 1971) immediately set them apart. Not included in this comparison are those taxa (such as *Sphecodes,* Bohart, 1966, and *Hoplostelis,* Rozen, 1966b) in which the adult cleptoparasite removes the host immature; larvae of these taxa do not have elongate mandibles and other special modifications in any stadium.

FIRST INSTAR EPEOLINI

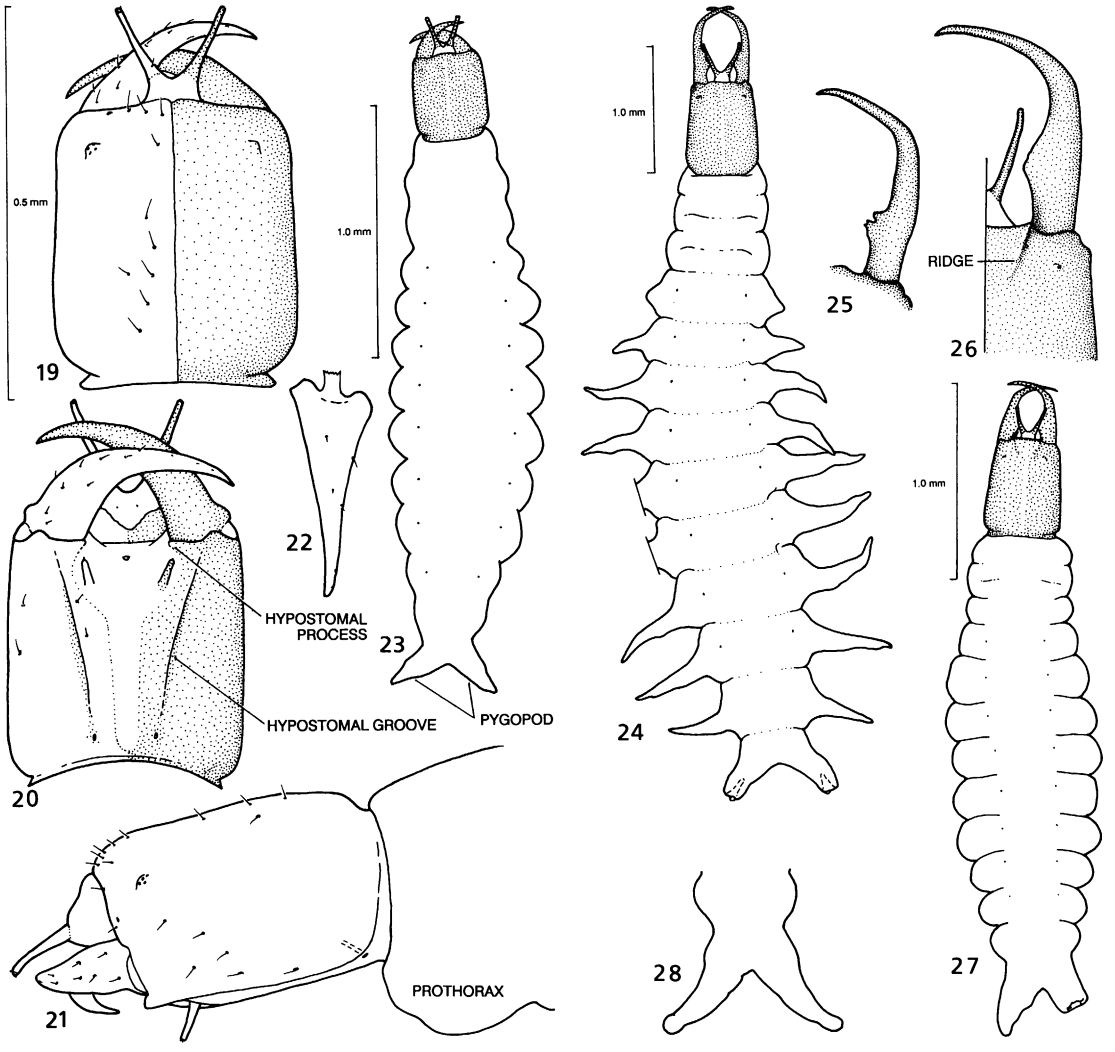
Triepeolus and *Epeolus* (the only epeoline genera whose first instars have been collected) can be distinguished from one another on the basis of the shape of their head capsules. In *Triepeolus* the postoccipital constriction is greater so that its height as seen in lateral view (figs. 6, 21) is considerably less than the maximum height of the head. In *Epeolus* (figs. 31, 35, 37) the postoccipital constriction is more nearly the same height as the maximum height of the head. If one views the head capsules of cleared specimens internally, the vertical and horizontal diameters of the constriction of *Triepeolus* are shorter in relation to the maximum vertical and horizontal diameters of the capsule than is the case in *Epeolus.* Consequently, as seen in lateral view the top of the head of *Triepeolus* (figs. 6, 21) curves downward to the constriction more than in *Epeolus* (figs. 33, 35, 37).

Although this suite of features apparently consistently separates these two genera, it is difficult to use. The following key, not based on these characters, will help to separate the species treated here. In addition to the anatomical features for distinguishing the two genera, host preferences remain diagnostic: *Triepeolus* first instars have been recovered from the nests of many taxa of bees (*Ptiloglossa, Protoxaea, Nomia, Melissodes, Svastra, Peponapis, Xenoglossa, Xenoglossodes, Anthophora*) but not from nests of *Colletes,* whereas *Epeolus* larvae have been associated only with *Colletes.*

KEY TO SPECIES OF *TRIEPEOLUS* AND *EPEOLUS* BASED ON FIRST INSTARS

1. Inner surface of mandible (figs. 1–4, 25, 26) with midsection produced and forming sharp edge that is irregularly toothed, serrate, or straight depending upon species (all *Triepeolus* except *loomisorum*) ... 2
   Inner surface of mandible (figs. 19, 20, 22, 31, 32, 36, 40) rounded, not produced, although in some species surface is irregular (*Epeolus* and *T. loomisorum*) ... 4

2(1). Abdomen (figs. 5, 24) with elongate tapering



Figs. 19–23. First instar of *Triepeolus loomisorum*. **19-21.** Head, dorsal, ventral, and lateral views. **22.** Mandible, inner view. **23.** Entire body, dorsal view.

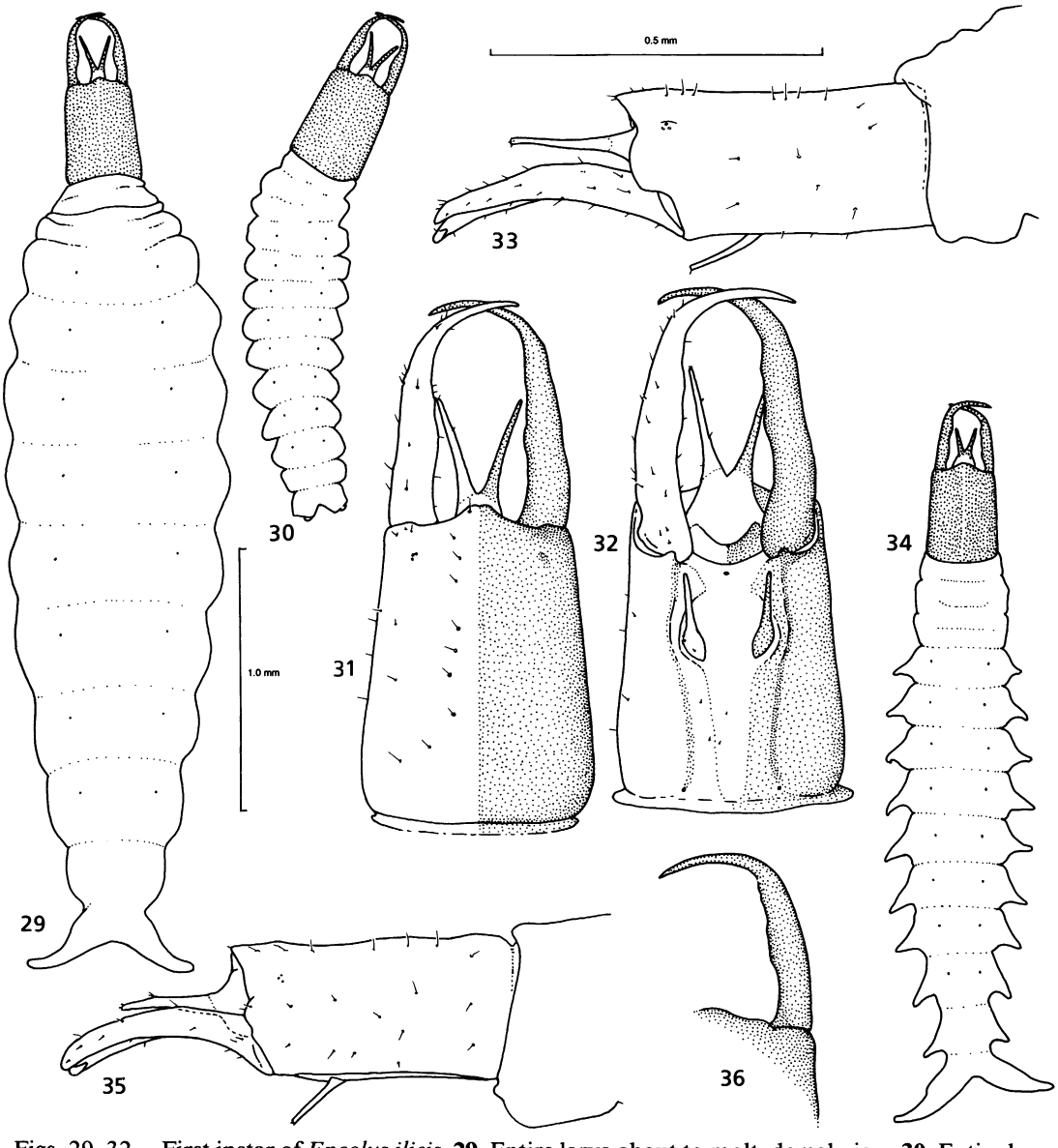
Figs. 24, 25. First instar of *Triepeolus concavus*. **24.** Entire body, dorsal view. **25.** Right mandible, dorsal view.

Figs. 26–28. First instar of *Triepeolus dacotensis*. **26.** Right mandible and right half of labrum and of anterior part of head capsule, dorsal view, showing frontoclypeal ridge. **27.** Entire larva, dorsal view, with pygopod partly retracted. **28.** Apex of abdomen, dorsal view, the pygopod mostly extended. 0.5 mm scale refers to figures 19–22; three 1.0 mm scales refer respectively to figure 23, to figure 24, and to figures 27 and 28.

lateral tubercles; frontoclypeal area (figs. 1, 4) without pair of ridges 3
Abdomen (fig. 27) with lateral tubercles rounded, not elongate; frontoclypeal area (fig. 26) with pair of anteriorly diverging, seta-bearing ridges ..... *T. dacotensis*

3(2). Head capsule, as seen from above (figs. 1, 5), nearly parallel-sided; mandible (fig. 2) with inner teeth extending along inner edge for greater distance ..... *T. grandis*
Head capsule (fig. 24) with sides converging anteriorly; mandible (fig. 25) with teeth confined to short distance .. *T. concavus*

4(1). Mandible (figs. 31, 32, 36, 40) slender, basal part nearly straight, apical part strongly curved; head capsule (figs. 31, 32, 35, 37)



Figs. 29–32. First instar of *Epeolus ilicis*. **29.** Entire larva about to molt, dorsal view. **30.** Entire larva just having eclosed, dorsal view, pygopod mostly retracted. **31, 32, 33.** Head capsule, dorsal, ventral, and lateral views, respectively.

Figs. 34–36. First instar of *Epeolus compactus*. **34.** Entire larva, dorsal view. **35.** Head capsule, lateral view. **36.** Right mandible, dorsal view. 1.0 mm scale refers to figures 29, 30, and 34; 0.5 mm scale, to all other figures.

elongate; abdomen with or without lateral tubercles 5

Mandible (figs. 19, 20, 22) relatively short, stout, evenly curved; head capsule (figs. 19, 20, 21) not so greatly elongate; abdomen without lateral tubercles .... *T. loomisorum*

5(4). Frontoclypeal area in profile (figs. 33, 35) nearly straight, continuous with rear of head capsule; mandible slender (figs. 31, 36); abdomen with or without lateral tubercles but without ventral tubercles .. 6

Frontoclypeal area in profile (fig. 37) more curved; mandible (fig. 40) stouter; abdo-

men (figs. 38, 39) without lateral tubercles but with low rounded paired ventral tubercles ..... *E. pusillus*

6(5). Abdomen (fig. 34) with elongate tapering lateral tubercles ..... *E. compactus*

Abdomen (figs. 29, 30) without lateral tubercles ..... *E. ilicis*

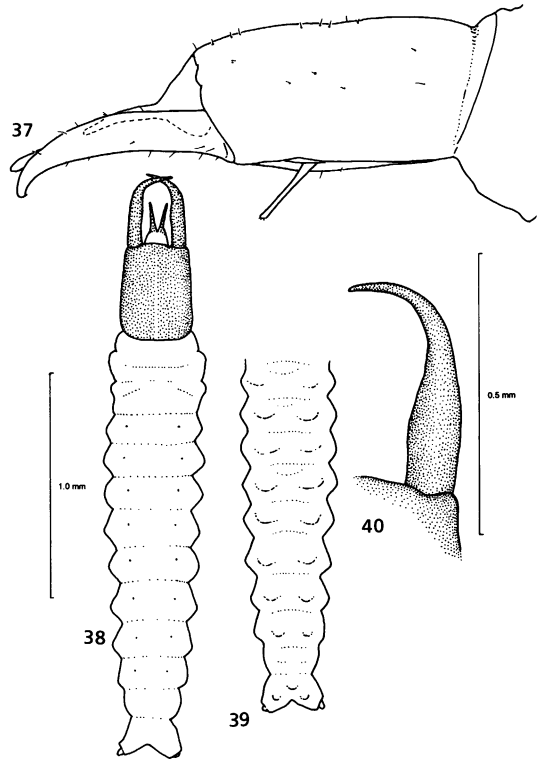
TRIEPEOLUS GRANDIS (FRIESE)

Figures 1–9

DIAGNOSIS: The first instar of this species shares with *Triepeolus concavus* a large body and conspicuous tapering lateral abdominal tubercles, but can be recognized by its more parallel-sided head capsule and more curved mandibles. The other two species of *Triepeolus* treated here lack long tapering body tubercles, are much smaller, and have features of the head capsule and mandibles that readily separate them from *T. grandis* (see their diagnoses). The first instar of *T. remigatus* (Bohart, 1966) appears to agree with *T. grandis* in body shape but probably is smaller, as judged by adult size. Among *Epeolus* species, only *E. compactus* (fig. 34) bears tapering lateral abdominal tubercles, but its smaller size, differently shaped mandibles, and other features of the head capsule immediately distinguish it from *T. grandis* and *T. concavus*.

LENGTH: Mean = 6.8 mm; range = 6.2–7.5 mm (N = 6).

HEAD (figs. 1, 2, 4, 6): Shape strongly prognathous, dorsoventrally flattened and elongate; seen from above or below, nearly parallel-sided; frontoclypeal area smooth, without pair of oblique seta-bearing ridges as described for *Triepeolus dacotensis*; head capsule constricted immediately in front of posterior margin (postoccipital constriction); posterior rim of head capsule slightly flared; its ventral ends fusing along ventral midline to form postoccipital bridge and thus a complete ring around posterior end of head. Integument with moderately abundant, fine, and inconspicuous setae, especially on head capsule and mandibles; integument of head capsule, mandibles, labral tubercles, hypopharynx, and maxillary palpi sclerotized and brown to dark brown, in sharp contrast to nonsclerotized, unpigmented areas of head and rest of body. Tentorium very fine and possibly complete; anterior tentorial pits very small, between dorsal (anterior) mandibular articulations and labrum (fig. 4); posterior tentorial pits in hypostomal grooves on ventral side of head immediately anterior to postoccipital bridge; hypostomal ridge difficult to define (see following section) but distinct broad hypostomal groove (fig. 2) extending forward from each posterior tentorial pit to ventral mandibular articulation; integument in groove pebbled in contrast to smooth sclerotized surface of rest of capsule; mesial edge of groove pronounced and sclerotization of capsule continuing mesad of groove (fig. 2); membranous median area between these extensions narrowly V-shaped, part of labiomaxillary region; at base of mandible, hypostomal area projecting inward and upward close to mandibular base and bearing sharp ridge and thus forming hypostomal process (fig. 2); pleurostomal and epistomal



Figs. 37–40. First instar of *Epeolus pusillus*. **37.** Head capsule, lateral view. **38.** Entire larva, dorsal view, pygopod retracted. **39.** Abdomen, ventral view. **40.** Right mandible, dorsal view. 0.5 mm scale refers to figures 37 and 40; 1.0 mm scale, to figures 38 and 39.

ridges not defined presumably because of heavy sclerotization of head capsule; therefore anterior tentorial pits not associated with external suture or internal ridge; distinct pale median dorsal ecdysial line extending from posterior edge of head capsule to front edge of frontoclypeal area (i.e., to membranous labrum); parietal bands not evident. Each antenna (figs. 1, 4, 6) a small protrusion of integument posterior to dorsal mandibular articulation, not a distinct papilla separated from a basal disk as typical of mature larvae; each antenna with approximately five sensilla. Labrum (figs. 4, 6) nonsclerotized, bearing two elongate sclerotized tubercles which project about as far as closed mandibles. Mandible (figs. 1–4) extremely elongate, much longer than width of head capsule, slender, curved, tapering to sharp-pointed apex; inner edge with linear series of sharp, irregular projections extending one-quarter to one-half distance from base to apex of mandible. Labiomaxillary region entirely membranous except for elongate maxillary palpi (figs. 2, 4, 6); region featureless except for these palpi and scattered setae (cardo, stipes, prementum, and postmentum indistinguishable); maxillary palpi greatly elongate, sclerotized, nonsegmented, similar to but somewhat smaller than labral tubercles; labial palpi presumably absent but possibly represented by sensilla. Salivary opening (fig. 2) evident but small and circular, without lips, immediately behind pigmented, sclerotized hypopharynx (fig. 2); hypopharynx a transverse bladelike structure with sharp, somewhat irregular front edge bearing narrow median notch (as seen in ventral view, fig. 2); hypopharynx fusing laterally with head capsule between mandibular bases and labrum.

BODY: Form (fig. 5) elongate, slender, straight; three thoracic segments without tubercles but venter of prothorax (fig. 6) projecting medially; abdominal segment 1 with lateral projection on each side below level of spiracle; segment 2 with similar but more pronounced conical lateral projection on each side; abdominal segments 3–8 each with pair of elongate, tapering lateral tubercles (lengths as depicted in fig. 5) below spiracular level; segment 9 with similar but somewhat smaller pair of tubercles; abdominal segment 10 with two eversible, posterolaterally projecting processes (the pygopod), which are as long as longest lateral tubercles. Integument without setae, with patches of fine, inconspicuous spicules on some areas including venter of most segments; these spicules most conspicuous on prothoracic ventral projection (fig. 6). Thoracic spiracles absent although anlage evident; tracheae leading to anlage tapering before ending as seen in cleared specimen; spiracles on abdominal segments 1–8 dorsal in position, above lateral tubercles, approximately equal in size. Anus not evident on either cleared or uncleared specimens.

MATERIALS STUDIED: 1 larva, Portal, Cochise Co., Arizona, August 25, 1983 (J. G. Rozen) from cell of *Ptiloglossa arizonensis*; 2 larvae, same except September 2, 1982; 3 larvae, same except September 1, 1983; 2 larvae, same except September 2, 1983; 1 larva, same except August 14–September 2, 1983 (J. G. Rozen and M. Favreau); 1 larva, same except August 1, 1964 (M. A. Cazier and M. Mortenson) from nest of *Ptiloglossa jonesi.*

REMARKS: Activities of this first instar were described by Rozen (1984).

TRIEPEOLUS LOOMISORUM ROZEN

Figures 19–23

DIAGNOSIS: This first instar can be distinguished from *Triepeolus grandis* and *T. concavus* on the basis of its lack of tapering lateral abdominal tubercles (fig. 23), its shorter head (figs. 19–21), relatively short mandible (fig. 20), nondentate inner surface of the mandible (figs. 20, 22), and a relatively unmodified hypostomal area, as well as its much smaller size. The same mandibular and hypostomal features will separate it from *T. dacotensis.* The absence of lateral abdominal tubercles separates it from *Epeolus compactus* but not from *E. pusillus* and *E. ilicis.* However, all three *Epeolus* species have more elongate mandibles which are abruptly curved apically (as seen in dorsal or ventral views, figs. 31, 36, 40) in contrast to the more evenly curved mandibles of *T. loomisorum* (figs. 19, 20).

LENGTH: 2.5 mm (N = 1).

HEAD (figs. 19–21): Shape as described for first instar of *Triepeolus grandis* except not so strongly flattened dorsoventrally and somewhat shorter in relation to width. Integument as described for *T. grandis.* Ten-

torium as described for *T. grandis*; hypostomal ridge as described for *T. grandis* except hypostomal groove (fig. 20) less distinct, its integument not so distinctly pebbled; mesial edge of groove very pronounced; sclerotization of head capsule (fig. 20) continuing mesad of groove as in *T. grandis* but mesial edge of extension not sharply delineated from narrow median V-shaped part of labiomaxillary region; at base of mandible hypostomal process (fig. 20) fading into ventral median membranous area and not bearing sharp ridge characteristic of *T. grandis*; rest of head capsule as described for *T. grandis*. Antenna as described for *T. grandis*. Labrum as described for *T. grandis* but tubercles shorter. Mandible (figs. 20, 22) elongate, about as long as width of head capsule, tapering to sharp-pointed apex, but not as slender as that of *T. grandis*; inner edge, unlike that of *T. grandis*, without linear series of sharp-pointed projections; labiomaxillary region as described for *T. grandis* except maxillary palpi slightly shorter though still elongate. Salivary opening as in *T. grandis*; hypopharynx as described for *T. grandis* except perhaps less heavily sclerotized; front edge irregular, with broad median notch.

BODY (fig. 23): As described for *T. grandis* except abdominal segments lacking long tapering lateral projection on each side, but abdominal segment 10 with eversible, posterolaterally projecting, long processes, similar (including muscle attachments) to those of *T. grandis*. Integument without setae; dorsal integument of abdomen with sharp-pointed, fine spicules; spicules laterad of spiracles less conspicuous; integument of thorax and venter of abdomen apparently completely nonspiculate; prothoracic ventral projection nonspiculate. Thoracic spiracles absent; abdominal spiracles on segments 1–8, dorsal in position. Anus not evident on cleared specimen.

MATERIAL STUDIED: 1 larva, 13 mi southwest of Apache, Cochise Co., Arizona, August 31, 1988 (J. G. Rozen) from cell of *Xenoglossodes eriocarpi* (Cockerell).

REMARKS: The diagnosis of this species reflects the many conspicuous differences between it and the other *Triepeolus*. Although the meaning of such large dissimilarities is conjectural, it seemingly relates to different behavioral patterns on the part of the first instars and/or to different environments in host brood cells.

I referred to this larva in the description of the species (Rozen, 1989).

TRIEPEOLUS CONCAVUS (CRESSON)

Figures 24, 25

DIAGNOSIS: This species is similar to *Triepeolus grandis* in size and most other attributes, including tapering lateral abdominal tubercles. It differs in the shape of the head capsule and in the mandibular characteristics presented below. The tapering abdominal tubercles and mandibular features readily distinguish it from all other species treated here except for *Epeolus compactus*. Its large size, hypostomal ridges, and numerous other features distinguish it from *E. compactus*.

LENGTH: 6.4 mm (N = 1).

HEAD (figs. 24, 25): As in *Triepeolus grandis* except: Shape, as seen from above, slightly more elongate and sides converging anteriorly; frontoclypeal ridges (as described in *T. dacotensis*) at most faintly represented. Tentorium not examined but presumably as in *T. grandis*. Antenna slightly more protuberant (sensilla not examined). Mandible (fig. 25) with basal two-thirds straighter and apical one-third more distinctly angled in contrast to more curved mandible of *T. grandis*; irregular, sharp-pointed projections on inner edge not extending as far out on mandible and mandible slightly swollen on outside opposite projections.

BODY: Form (fig. 24) as described for *Triepeolus grandis* except: Venter of prothorax with median protrusion anteriorly as small but distinct median tubercle (this structure needs to be examined on live material to be verified).

MATERIAL STUDIED: 1 larva associated with adult bearing following data: 15 km east Lawrence, Douglas Co., Kansas, September 4, 1988 (R. L. Minckley, University of Kansas), from nest of *Svastra obliqua*.

TRIEPEOLUS DACOTENSIS (STEVENS)

Figures 26–28

DIAGNOSIS: This larva is half the size of the first instars of *Triepeolus grandis* and *T. concavus* and lacks their long tapering lateral abdominal tubercles. Like them but unlike *T.*

loomisorum or any *Epeolus,* it possesses a produced sharp inner mandibular edge. Its lateral abdominal tubercles are broadly rounded, a unique feature for the known epeolines, and, unlike any of the other species, its head capsule bears a pair of oblique, seta-bearing frontoclypeal ridges.

LENGTH: 2.4–3.3 mm (N = 3).

HEAD (figs. 26, 27): As described for *Triepeolus grandis* except: As seen from above, sides of head capsule converging anteriorly, as in *T. concavus*; frontoclypeal area (fig. 26) bearing low but distinct ridge on each side of midline; each ridge starting from point behind level of antennae, running obliquely to front edge of head capsule and bearing approximately five seta-bearing prominences. Tentorium not studied; hypostomal process well developed but without ridge. Antennae as described for *T. grandis* but perhaps even less conspicuous. Mandible with basal two-thirds straight and not swollen and apical one-third more distinctly angled (much like in *T. concavus*); inner edge with projecting sharp ridge more knifelike than toothed (as in *T. grandis* and *concavus*).

BODY: Form (figs. 27, 28) as described for *Triepeolus grandis* except: Lateral abdominal tubercles rounded (fig. 27; Bohart, 1970: fig. 22), not long and tapering. Integument generally spiculate, but spiculation of venter of prothorax not pronounced. Spiracles very small, those of abdominal segment 8 apparently smaller than those of preceding segments.

MATERIAL STUDIED: 2 larvae, 1 cast skin, Logan, Utah, 1983 (P. F. Torchio, USDA Bee Biology and Systematics Laboratory), from nest of *Anthophora occidentalis*; 2 larvae B. S. Fork, Utah, August 1962 (G. E. Bohart, USDA Bee Biology and Systematics Laboratory).

REMARKS: Torchio (1986) reported on the late embryogenesis and eclosion of this larva.

EPEOLUS ILICIS MITCHELL

Figures 29–32

DIAGNOSIS: The lack of either tapering or rounded lateral abdominal tubercles separates this species and *Epeolus pusillus* from most known *Triepeolus* species and from *E. compactus.* Although *T. loomisorum* also lacks tubercles, its evenly curved, stout mandibles (fig. 20) cannot be confused with the mandibles (figs. 31, 32, 36, 40) of known *Epeolus* species, which are long, slender, and nearly straight basally and short and strongly curved apically as seen in dorsal or ventral views. *Epeolus pusillus,* in contrast to *E. ilicis,* has a differently shaped mandible as seen from above (fig. 40), a more sloping frontoclypeal area as seen in lateral view (fig. 37), and ventral abdominal tubercles (fig. 39).

LENGTH: 2.25 mm (newly eclosed larva), 3.6 mm (larva soon to molt) (N = 2).

HEAD (figs. 31, 32, 35): As described for *Triepeolus grandis* except: Head capsule, as seen from above or below, with sides converging anteriorly; frontoclypeal region, like that of *Epeolus compactus,* projecting dorsally so that in profile dorsal and ventral surfaces of head nearly parallel (fig. 33), not converging anteriorly as in *T. grandis*; head capsule not so strongly constricted in front of posterior margin (a character shared with other *Epeolus* and distinguishing *Epeolus* from all known *Triepeolus*). Hypostomal groove (fig. 32) not so pronounced, but pebbled (grainy) surface clearly evident; boundary between mesial extensions of head capsule and membranous V-shaped labiomaxillary region not sharply defined except around bases of maxillary palpi; hypostomal process weakly defined and lacking ridge found in *T. grandis.* Each antenna very low, even less pronounced than in *T. grandis,* recognizable primarily by tight grouping of approximately three sensilla. Mandible (figs. 31, 32) elongate; basal part nearly straight (gently curved); apical part bending sharply; inner surface rounded, irregular, without distinct protrusions.

BODY: As described for *Triepeolus grandis* except for following: Form elongate, slender, straight at first (fig. 30), becoming navicular (fig. 29) after feeding so that dorsum becomes relatively flat while venter bows outward; venter of prothorax (fig. 35) apparently not projecting medially; abdomen without tapering lateral tubercles. Integumental spiculation reduced.

MATERIAL STUDIED: 2 larvae, St. Catherines Island, Liberty Co., Georgia, April 27, 1982 (J. G. Rozen), from nest of *Colletes brimleyi* Mitchell.

EPEOLUS COMPACTUS CRESSON

Figures 34–36

DIAGNOSIS: See diagnosis of *Epeolus ilicis.*

LENGTH: 1.5–6.2 mm (N = 20).

HEAD (figs. 35, 36): As described for *Triepeolus grandis* except for following: Head capsule, as seen from above or below with sides converging anteriorly; frontoclypeal region, like that of *Epeolus ilicis,* projecting dorsally so that in profile dorsal and ventral margins of head nearly parallel (fig. 35); head capsule not so constricted in front of posterior margin. Hypostomal groove, hypostomal process, other ventral features of head, and antenna as described for *E. ilicis.* Mandible (fig. 36) elongate, similar to that of *E. ilicis*; basal part nearly straight; apical part bending sharply; inner surface rounded, irregular, without distinct protrusions.

BODY: As described for *Triepeolus grandis* except for following: Abdominal segments 1–9 each bearing paired lateral tubercles that are smaller than those of *T. grandis.* Integument of thorax including protruding venter of prothorax nonspiculate; that of abdomen spiculate in many areas.

MATERIAL STUDIED: 20 larvae, Bonny Doon, Santa Cruz Co., California, June 1985 (P. F. Torchio), from nests of *Colletes kincaidii* Cockerell.

REMARKS: Torchio and Burdick (1988) gave information on eclosion of the first instar and other aspects of the natural history of this species of cuckoo bee.

EPEOLUS PUSILLUS CRESSON

Figures 37–40

DIAGNOSIS: See diagnosis of *Epeolus ilicis.*

LENGTH: 2.9 mm (N = 1).

HEAD (figs. 37, 40): As described for *Triepeolus grandis* except for following: Head capsule as seen from above or below with sides converging anteriorly; capsule, like that of other *Epeolus* species, not so strongly constricted in front of posterior margin of head. Hypostomal groove, other aspects of ventral surface of head, and antennae as described for *E. ilicis.* Mandible (fig. 40) elongate but stouter than that of *E. ilicis* and *E. compactus*; basal part nearly straight; apical part strongly curved; inner surface rounded, without protrusions, and smoother in outline than that of *E. ilicis.*

BODY: As described for *Triepeolus grandis* except for following: Abdomen (figs. 38, 39) without long tapering lateral tubercles but with low paired ventral tubercles on each segment and on pygopod (these tubercles were not noticed on the rather poorly preserved specimen until after the abdomen was cleared in a solution of potassium hydroxide; hence their exact shape needs to be confirmed on a live or freshly killed specimen). Integumental spiculation less pronounced on protruding venter of prothorax but elsewhere spiculation well developed, especially on paired ventral abdominal tubercles (hence this species differing substantially from *E. ilicis*).

MATERIAL STUDIED: 1 larva, Lewisboro, Westchester Co., New York, October 5, 1967 (M. Favreau), from cell of *Colletes compactus compactus* Cresson.

REMARKS: The activities of this larva were described by Rozen and Favreau (1968).

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