

**A REVIEW OF *MELOE* (*TAPHROMELOE*), INCLUDING A DESCRIPTION
OF THE FIRST-INSTAR LARVA OF *M. (T.) ERYTHROCNEMUS* AND
COMMENTS ON THE CLASSIFICATION OF THE TRIBE MELOINI
(COLEOPTERA: MELOIDAE)**

MARCO A. BOLOGNA AND JOHN D. PINTO

(MAB) Università degli Studi dell'Aquila, Dipartimento di Scienze Ambientali, 67100 L'Aquila, Italy; (JDP) Department of Entomology, University of California, Riverside, California 92521, USA.

Abstract.—The first-instar larva of *Meloe* (*Taphromeloe*) *erythrocnemus* Pallas is described and compared to larvae of other components of the genus. The bionomics, distribution and taxonomy of this subgenus are reviewed. Larvae of *Taphromeloe* are similar to those of the subgenus *Meloegonius*. The intermediacy of several traits in these subgenera between the nominate subgenus and *Eurymeloe* questions the validity of the latter as a distinct genus. The recent expansion of the Meloini by Selander (1985, 1987, 1988) to include genera in addition to *Meloe* is only tentatively adopted because of its reliance solely on traits associated with larval phoresy.

Key Words: Meloidae, *Meloe*, *Taphromeloe*, systematics, first-instar larvae, phoresy

Meloe is a large genus of wingless and brachyelytrous blister beetles with phoretic first-instar larvae. Seventeen subgenera of *Meloe* are currently recognized based primarily on adult phenetic similarities (Bologna 1991). All occur in the Old World with two extending into North America. *Taphromeloe* Reitter (1911) is an exclusively Old World subgenus containing two species. Included are *M. erythrocnemus* Pallas (1782), a Turanian-Mediterranean species, and the poorly known *M. foveolatus* Guérin de Méneville (1842), distributed primarily in northwestern Africa. The latter has been considered either as a variety of *M. erythrocnemus* (Cros 1935, Mařan 1942, Iablokoff-Khnzorian 1983) or as a distinct species (Peyerimhoff 1949, Pinto and Selander 1970, Bologna 1991). A third nominal species, *M. roubali*, described and added to *Taphromeloe* by Mařan (1942), was

recently synonymized with *M. foveolatus* by Bologna (1991).

The primary purpose of this paper is to describe the first-instar larva of *M. (Taphromeloe) erythrocnemus*, and to compare it with larvae of other *Meloe* subgenera. Bionomic, distributional and taxonomic characteristics of *Taphromeloe* also are summarized. Certain features of *Taphromeloe* larvae intermediate to the nominate subgenus and the subgenus *Eurymeloe* question the validity of the most recent classification of the Meloini presented by Selander (1985, 1987, 1988). Our concerns with this classification are summarized.

FIRST-INSTAR LARVA OF
MELOE ERYTHROCNEMUS

Twelve slide-mounted specimens hatching from the same egg mass and numerous individuals in alcohol were examined for

this description. Quantitative data reported below represent means or ranges taken from three randomly selected individuals.

Color golden brown, head and legs slightly darker. Cuticle, including that of head, reticulate; reticulae about as broad as long on head, thorax and abdomen. Membranous areas of thoracic venter pebbled, microspinose adjacent to sternites. Line of dehiscence present on pro- and mesonotum, present at extreme apex of metanotum or entirely absent, absent on abdominal tergite I.

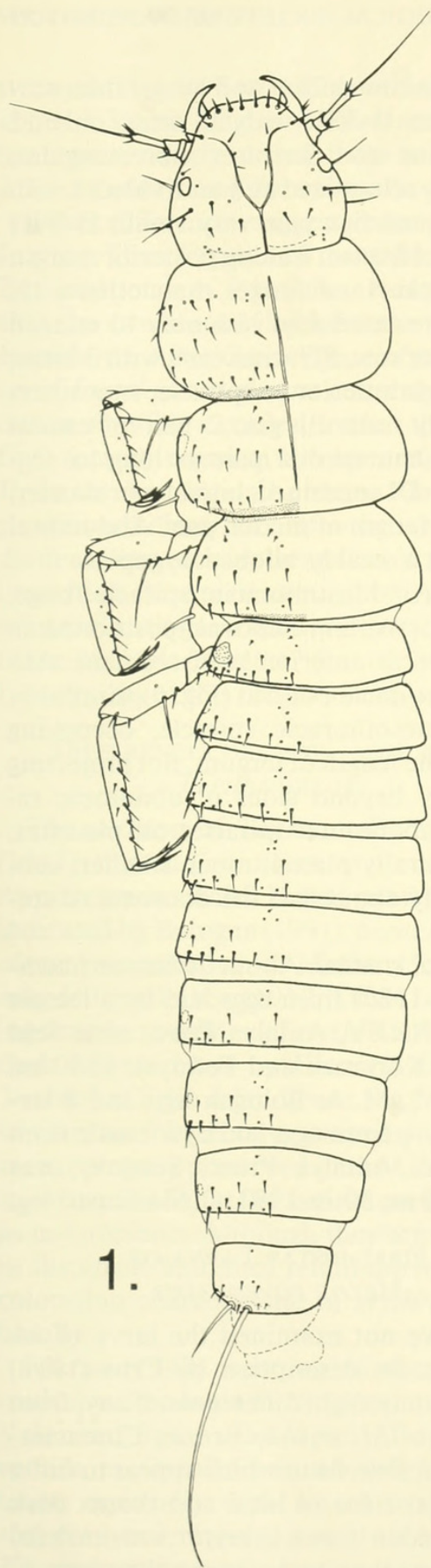
Body length 1.9–2.0 mm (slide-mounted specimens); length of longest pair of caudal setae 0.45–0.48 mm.

Head 0.9 as long as wide, widest at point about half the distance from eyes to base of head; sides arcuate posterior to antennae, straight and convergent anterior to eyes, anterior margin of head truncate; basal elevation absent but posterior margin of head thickened internally; epicranial suture with lateral arms weakly divergent at base, subparallel to level of antennae, then curved strongly laterad, not attaining antennal base; basal stem of epicranial suture elongate, 0.3 length of head and 0.4 length of entire suture. Eye large, strongly protuberant, diameter about $1.2\times$ greatest width of antennal segment II. Epicranial setation as in Fig. 1; major ocular seta distinctly longer than other setae, spiniform, $1.2\times$ the length of antenna, positioned well behind eye. Labrum transverse, not visible dorsally, a distinct clypeolabral suture present (Fig. 4). Gula well differentiated, anterior margin notched at center, gular setae subequal in length to antenna, positioned at anterior margin. Antenna (Fig. 3) with length/width of segments I, II and III $11/25$, $24/20$, $42/10$, respectively; terminal seta about $3.5\times$ length of segment III; segment II not widened apically but asymmetrical, longer along dorsal margin, its apex oblique; sensory organ disk-like (Fig. 5), its surface slightly convex, positioned at apex of II ventral to insertion of segment III. Mandible with base

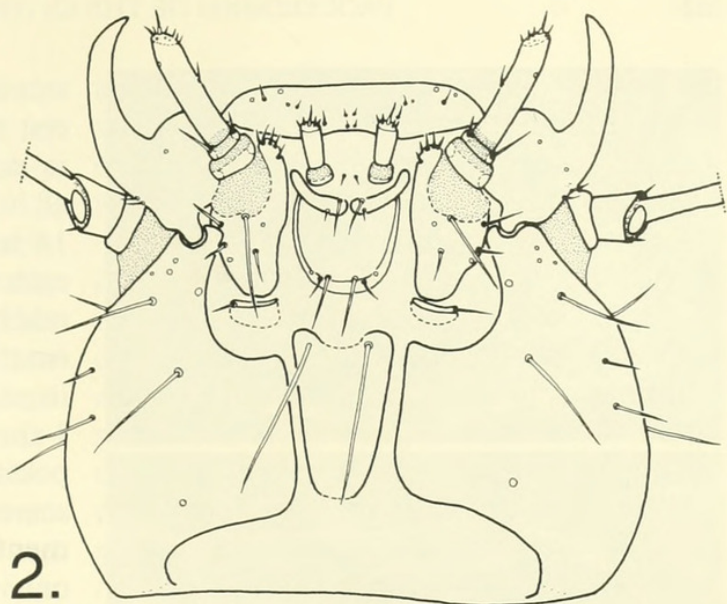
broad, apical half abruptly narrower, inner margin smooth, posterior condyle large, mandible moving in an obliquely vertical plane. Maxilla (Fig. 2) with mala simple; stipes with one long seta, three shorter setae and two sensory pits; palpi directed laterally, segments I and II short, subequal in length, I broader than II, III elongate, subcylindrical, about $7\times$ the length of II and slightly narrower, subequal in length to antennal segment III, apex of III slightly obliquely truncate with a prominent 2-segmented sensory appendix and several shorter papillae. Labial palpi elongate; apical segment subequal in length to antennal segment II, its apex with a prominent 2-segmented sensory appendix and several shorter papillae, sensory appendix about half the length of apical segment.

Thorax: Thoracic segments broader than head. Pronotum subrectangular, 0.6 as long as wide, $1.2\times$ width of head, broader at basal half, considerably membranous apically, with 40 setae. Mesonotum subequal in width to pronotum, almost twice as broad as long, with 28 moderately long setae and 4 minute anterior setae; base membranous. Metanotum slightly broader and shorter than mesonotum, with 26 elongate setae and 4 minute anterior setae. Prosternite with 3 (rarely 4) pair of setae; meso- and metasternite with 4 pair; anterior pair of setae on meso- and metasternite much shorter than others, posterior pair longer than second and third pair. Meso- and metasternites occupying entire length of segment, well developed; prosternite poorly sclerotized, confined to area between legs.

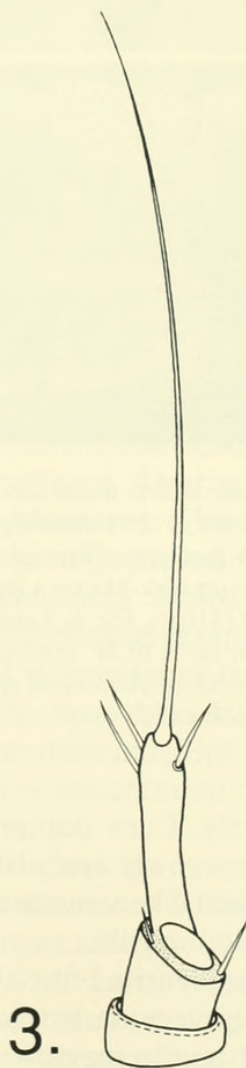
Legs with only profemur slightly swollen; width to length ratio of pro-, meso- and metafemur 0.38, 0.35, 0.30, respectively. Tibiae moderately tapered, with apical width about $\frac{3}{4}$ maximum width near base. Femora each with a long ventral seta at basal third, seta about twice maximum width of femora; setae on tibiae moderately long, length of longest tibial seta relative to tibial width 0.75, 1.0, 1.2 on pro-, meso- and



1.

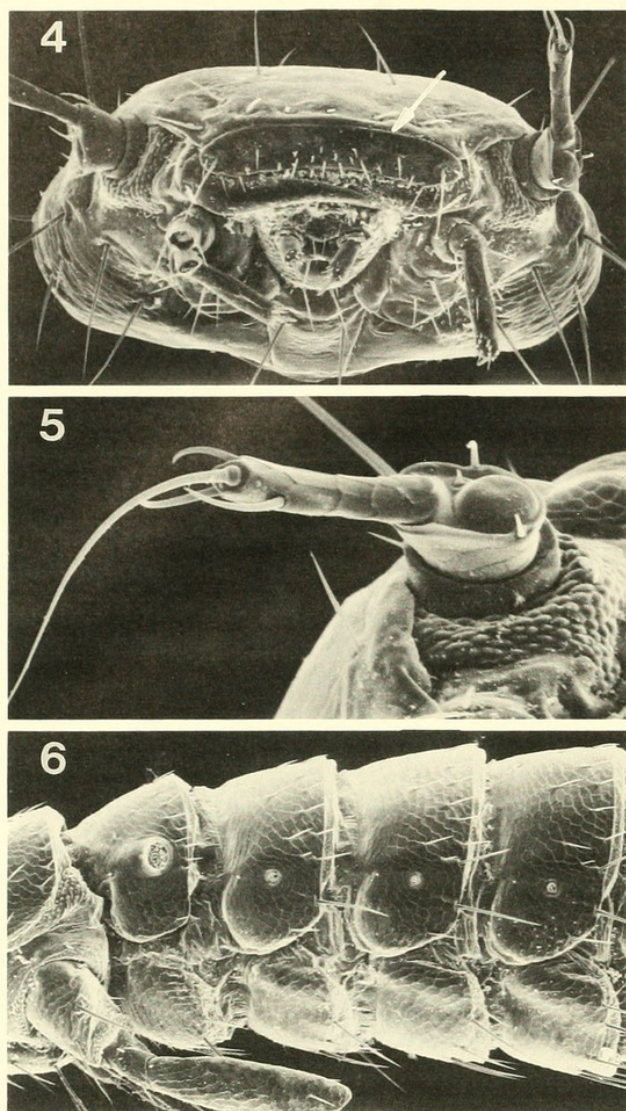


2.



3.

Figs. 1-3. Fig. 1. First-instar larva of *Meloe (Taphromeloe) erythrocnemus*. Dorsal view. Fig. 2. Head of first-instar larva of *M. erythrocnemus*. Ventral view. Fig. 3. Antenna of first-instar larva of *M. erythrocnemus* (ventral view).



Figs. 4-6. Fig. 4. Head of first-instar larva of *M. erythrocnemus* (anterior view, 372 \times). Arrow points to clypeolabral suture. Fig. 5. Antenna of first-instar larva of *M. erythrocnemus* showing disk-like sensory appendix at apex of segment II (810 \times). Fig. 6. Lateral view of abdomen in first-instar larva of *M. erythrocnemus* showing dorsal displacement of abdominal spiracle I relative to those which follow (203 \times).

metatibia, respectively. Claw compressed; basal pair of setae narrowly spatulate, together forming a trident-like structure; hind leg with claw 0.4 length of tibia.

Abdomen fusiform; pleurite I fused to tergite I, other pleurites very narrowly separated from adjacent tergite (narrow membranous line between tergite and pleurite visible in cleared specimens). Tergite I with 28 setae, 14 in posterior row, lateralmost

seta in this row thicker and longer than others; tergites II-VIII with 22 setae, only 12 in posterior row. Sternites subrectangular, all heavily sclerotized and undivided; I with 14 setae, anterior pair very small; II-VIII each with 12 setae, 8 along posterior margin much thicker and longer than others; IX emarginate anteriorly, with only 10 setae, 6 in posterior row. Pleurites each with 3 setae, 1 short seta anterior to spiracle, two others posteriorly near margin. 2 pair of caudal setae present, medial pair as long as segments VI-IX combined, lateral pair shorter, only 0.25 length of medial pair. Abdominal apex with a weakly bilobed pygopod.

Spiracles: Mesothoracic spiracle large, lateral in position, suboval, positioned in membrane at anterior $\frac{1}{3}$ of segment. Abdominal spiracle I dorsal (Fig. 6), similar in size to mesothoracic spiracle, occupying about $\frac{1}{3}$ the length of tergum, not projecting noticeably beyond sides of abdomen; remaining abdominal spiracles on pleurites, more ventrally placed, much smaller, subequal, only about half the diameter of spiracle I.

Material studied: About 70 larvae hatching (31-v-1982) from eggs laid by a female from TURKEY, Antalya Prov., near Seki (between Korkuteli and Fethiye), 1350 m, 30-iv-1982, M. A. Bologna leg.; and 3 larvae hatching from eggs laid by a female from TURKEY, Antalya Prov., Songuk, near Seki, 1400 m, 30-iv-1982, C. Manicasteri leg.

FIRST-INSTAR LARVA OF *MELOE FOVEOLATUS*

We have not examined the larva of *M. foveolatus*. Its description by Cros (1918) indicates only slight differences, if any, from the larva of *M. erythrocnemus*. Characteristics of *M. foveolatus* which appear to differ include: (a) color of head and thorax dark brown (golden brown in *erythrocnemus*); (b) head longer than wide (wider than long in *erythrocnemus*); (c) antennal segment II only slightly longer than I (twice as long as I in *erythrocnemus*); (d) antennal segment III

twice as long as I and II combined (only about $1.3 \times$ as long in *erythrocnemus*); (e) pronotum clearly wider than head (only $1.2 \times$ as wide in *erythrocnemus*).

Other differences suggested are probably in error. Thus, Cros states that there are only 2 caudal setae in *foveolatus*. It is probable that the two shorter lateral setae were not considered. Also, Cros's figure of the antenna of *foveolatus* is almost certainly erroneous in showing a conical (rather than disk-like) sensory organ at the apex of segment II. In his description he states "Je n'ai pas pu arriver à discerner nettement à la surface du deuxième article, en arrière et à côté de l'insertion du troisième segment un organe sensoriel analogue à celui qui existe sur l'antenne du *Meloe tucius*" (i.e. of the conical type typical of the subgenus *Eurymeloe*).

DIFFERENCES BETWEEN ADULTS OF *TAPHROMELOE*

The revision of *Taphromeloe* by Mařan (1942) treated *foveolatus* as a variety of *erythrocnemus* which lacked red femora. As indicated by Bologna (1991), however, *foveolatus* was unknown to Mařan. He mistakenly followed Cros (1918, 1935) in assuming that the specimen of *erythrocnemus* with dark femora cited by Leoni (1907) from Tuscany (Giglio Island) was the *foveolatus* of Guérin. We have examined this specimen, currently preserved in the Genoa Museum, and find that the femora are not black as in *foveolatus*. Although they are dark red in the apical half, they retain the bright red coloration characteristic of *erythrocnemus* basally.

Mařan (1942) went on to describe *M. roubali* on the basis of two specimens from Valencia, Spain. His description corresponds to *foveolatus* in all differentiating traits, especially with regard to pronotal shape, elytral rugosity and male genitalia. The examination of a syntype of *roubali* in the Prague National Museum of Natural History, its comparison to topotypic material of *foveolatus* from Tripoli and to spec-

imens from other Maghrebian localities, as well as the correspondence of *roubali* to the original description of *foveolatus*, confirm their synonymy.

Adults of *M. erythrocnemus* and *M. foveolatus* were recently redescribed, and distinguished by Bologna (1991). Briefly, they can be separated as follows: *M. erythrocnemus*—femora red, black only at apex; pronotum with medial incision of basal margin broadly arcuate; elytra deeply and coarsely punctate; male genitalia with fused gonostyli medially impressed. *M. foveolatus*—femora entirely black; pronotum with medial incision of basal margin more narrowly arcuate; elytra shallowly punctate; male genitalia with fused gonostyli not medially impressed.

DISTRIBUTION AND BIONOMICS OF *TAPHROMELOE*

A detailed account of geographic distribution and bionomic data is given by Bologna (1991). *M. erythrocnemus* is broadly distributed in the southern Palaearctic from the Tien Shan Mts. in western China, west through Turkey, Greece, and western Yugoslavia to central and southern Italy, Sicily, and northwestern Africa (northern Tunisia, northern Algeria, and northern and central Morocco). The range of *M. foveolatus* is more restricted. It occurs primarily in northwestern Africa [Libya (Tripolitania), northern and central Tunisia, northern Algeria], where it may be sympatric with *M. erythrocnemus*. Also, it is apparently relictual in southeastern Spain and southeastern Italy. It is uncommonly collected throughout its range.

Specific locality records of *M. foveolatus* based on material in the Paris, Prague and M. Bologna collections are as follows: ALGERIA: Mascara. ITALY: Brindisi. LIBYA: Tarabulus (= Tripoli) (type locality). SPAIN: "Arragon" or "Arragou" (Caceres Prov.?); Valencia (type locality of *roubali* Mařan). TUNISIA: Gafsa; Mahdia; Nabeul; El Skihrra; Sfax.

The bionomics and ontogeny are similar in both species of *Taphromeloe*. Adults are active primarily in spring, from March (rarely February) to May. Both species are diurnal, although *M. foveolatus* probably is also active at night. The eggs are similar in form but differ in color (yellow in *foveolatus*, white in *erythrocnemus*). In *M. erythrocnemus*, summer is probably passed in the sixth instar (= coarctate); adults apparently overwinter (De Stefani Perez 1885, Grandi 1934, Bologna 1991). Cros (1918, 1920b) described the larval instars and the pupa of *M. foveolatus*. Grandi (1934, 1961) and Cros (1935) discussed characters of the second and sixth larval instars and the pupa in *M. erythrocnemus* but didn't describe them.

Taphromeloe adults are known to feed on a variety of plants. *Meloe erythrocnemus* has been recorded from species of Asteraceae and Apiaceae; *M. foveolatus* has been associated with Resedaceae, Poaceae, and, questionably, Asteraceae. Both species are parasites of Apoidea (Megachilidae) as larvae. *Meloe erythrocnemus* has been associated only with *Chalicodoma muraria* Fabricius (Frauenfeld 1861, De Stefani Perez 1885, Leoni 1909, Grandi 1934, 1961, Bologna 1991). *Osmia saundersi* Vachal is a host of *M. foveolatus* (Cros 1918).

Sexual behavior of *M. foveolatus* was described by Cros (1918), and that of *M. erythrocnemus* was recently studied by Bologna and Marangoni (1986). Courtship is relatively simple in both and only minor differences occur in the dorsal and genital phases (Bologna and Marangoni 1986).

CHARACTERISTICS OF *TAPHROMELOE*

First-instar larvae: Moderately large, ca. 2.5 mm in length. Head with anterior margin truncate; antennal segment II twice as long as I (*erythrocnemus*) or subequal in length to I (*foveolatus*), and much shorter than III; apex of II oblique and with a disk-like, slightly convex sensory organ ventrally. Femora subcylindrical, slightly swollen at most; tibiae moderately tapered; tarsun-

gulus compressed, basal pair of setae narrowly spatulate, together forming a trident-like claw. Abdominal sternites completely sclerotized and undivided; abdominal spiracle I on tergite, not projecting beyond sides of segment; four caudal setae, medial pair much longer.

Adults: Body completely black, or with femora red in part; surface shiny; setation black, short, extremely sparse on head, pronotum and elytra; vestiture not noticeable macroscopically. Head subtriangular, broadest at tempora; without a longitudinal depression behind eyes; frons longitudinally impressed; coarsely, deeply, moderately densely punctate; interpunctal areas shagreened; eyes small. Antennae short, subclavate, segments submoniliform, V–VIII not noticeably modified in male. Pronotum transverse; sides parallel or convergent posteriorly, rounded anterolaterally to apex, subperpendicular to base; basal margin with a broad, arcuate incision at middle, narrowly bordered; disk relatively flat but with three distinct longitudinal furrows, two shorter ones laterally and a medial furrow usually extending entire length of disk; punctation as on head. Elytra coarsely, deeply rugose; punctures larger than on head and pronotum but not as distinct, confluent in part. Abdominal tergites broad, well sclerotized. Male genitalia with gonostyli very narrow apically.

The larva of *Taphromeloe* is similar to that of *Meloegonius* Reitter (1911). The latter includes only two species, *M. cicatricosus* Leach and *M. rufiventris* Germar. The first instar of what, according to Selander (1989), was almost certainly *M. cicatricosus* was first described by Zakhvatkin (1932) as an unidentified species. It was recently re-described by Selander (1989). This larva can be separated from those of *Taphromeloe* primarily by the structure of the first abdominal spiracle. According to Selander, in *Meloegonius* this spiracle is "transversely oval, projecting beyond sides of abdominal segment." In *Taphromeloe* the spiracle is

enlarged and suboval as in all *Meloe*, but it does not project beyond the sides of its segment. Also, in *Meloegonius*, several of the epicranial setae are lengthened and thickened, and antennal segment II is symmetrical. In *Taphromeloe*, only the major ocular setae are noticeably modified, and antennal segment II is oblique. Fig. 1 in Selander (1989) also indicates that the sensory organ at the apex of antennal segment II is more prominent in *Meloegonius* than in *Taphromeloe*.

Adults of *Taphromeloe* are separable from those of *Meloegonius* by traits associated with the antenna, pronotum and genitalia. *Meloegonius* lacks the arcuate basal emargination and discal furrows on the pronotum. Also the sides of the pronotum are distinctly angulate anterolaterally in *Meloegonius*, not rounded as in *Taphromeloe*. The antenna is somewhat longer in *Meloegonius* and is not subclavate as in *Taphromeloe*. In *Meloegonius* the gonostyli of the male genitalia are robust and not as narrow as in *Taphromeloe*.

COMMENTS ON THE CLASSIFICATION OF THE MELOINI

The larvae of *Taphromeloe* force a reexamination of the current classification of the Meloini, one of the tribes in the subfamily Meloinae (Selander 1964, Bologna 1991). The group is delimited from other Meloinae by first-instar larval traits presumably associated with phoresy primarily on adult Apoidea. The primary traits defining the tribe as listed by Selander (1985) include the following: clypeus not distinct from frons; labrum not visible from above, closely appressed to venter of head capsule; mandibles moving in an oblique dorsoventral plane; presence of an extrusible pygopod at apex of abdomen. The latter trait is associated with locomotion on smooth plant surfaces before larvae attach to their host. The head characters are believed to aid larvae to grasp the vestiture of hosts with their mandibles.

Studies by Pinto and Selander (1970), and Selander (1985, 1986, 1989) considerably modified the limits of the tribe. As defined by MacSwain (1956) and Selander (1964), the Meloini consisted only of *Meloe*, an apterous genus, and the only taxon of Meloinae known prior to 1970 to be phoretic as first-instar larvae. The discovery by Pinto and Selander that the North American and alate *Spastonyx* had larval traits that, in *Meloe*, are associated with phoresy, prompted its transfer to the Meloini. More recently, Selander (1985, 1987, 1988) treated the South American *Spastomeloe* and *Lyttomeloe*, and the Old World *Cyaneolytta* as Meloini upon discovering that their larvae also possessed phoretic traits. Bologna et al. (1990) followed this classification in their description of *Cyaneolytta* larvae which are phoretic on carabid beetles. There are no adult characters that can convincingly argue for these tribal assignments. *Spastonyx* and *Cyaneolytta* were previously assumed to be Lyttini (Selander 1964) and *Lyttomeloe* was either placed in the Lyttini (Denier 1920) or tentatively assigned to the Meloini (Kaszab 1969).

The expansion of the Meloini prompted Selander (1985) to redefine *Meloe*. Because the larvae of *Spastomeloe* and *Meloe* (*Eurymeloe*) (the more primitive type I larva of Selander) were more similar to one another than either was to the more derived larvae of other *Meloe* subgenera (type II larva of Selander), he considered the genus polyphyletic and thus elevated *Eurymeloe* (including *Coelomeloe* as a synonym) to generic status. The type II larva of *Spastonyx* provided further support for this change since it resembled nominate *Meloe* and related subgenera more than *Eurymeloe* did.

Eurymeloe was recently reviewed by Bologna (1988) and Bologna et al. (1989). Those studies, as we do here, continue to treat the group as a subgenus of *Meloe* and to tentatively recognize *Coelomeloe* as a distinct subgenus. We consider the elevation of *Eurymeloe* to genus to be premature for two

reasons. First, as more larvae of this group (see Bologna et al. 1989) and other elements of *Meloe* (such as those of *Taphromeloe*) become known, the gap between types I and II larvae is narrowing. Secondly, we are not convinced that the larval characters now defining the Meloini, i.e. those which forced the elevation of *Eurymeloe* in the first place, are homologous, and not simply homoplasies motored by the independent acquisition of phoresy in two or more of the genera now included in the tribe.

The two types of larvae in the Meloini were first recognized by Cros (1920a) and were recently characterized as follows by Selander (1985): Type I larvae—Antenna: segment II subequal in length to I, much shorter than III; sensory organ of segment II conical, prominent. Thoracic line of dehiscence absent from metanotum. Abdominal sternites entire. Two elongate caudal setae. Femora not swollen; tibiae tapered with elongate setae. Claw normal in shape, conicofalcate, with basal pair of setae setiform. Type II larvae—Antenna: segment II much longer than I, at least as long as III; sensory organ of antenna hemispherical or disk-like. Line of dehiscence partially developed on metanotum; 2–4 elongate caudal setae. Femora swollen; tibiae cylindrical, with very short setae. Claw and two basal setae flat, spatulate forming a trident-like structure.

According to Selander (1985, 1987, 1988) and Bologna et al. (1990), type I larvae occur in *Eurymeloe*, *Spastomeloe* and *Cyaneolytta*; type II larvae occur in *Meloe*, *Lyttomeloe* and *Spastonyx*. However, the larvae of several species bridge these original distinctions. *Cyaneolytta* larvae vary with regard to the length of antennal segment II. In *C. fryi* it is elongate, as in type II larvae (Selander 1987). In other species it is considerably shorter (Bologna et al. 1990). Also, in certain *Cyaneolytta* the thoracic line of dehiscence is present on the metanotum (Bologna et al. 1990). In his recent description of the larva of *M. (Meloegonius) cicatricosus*, Selander (1989) does not assign the

larva to type, noting that it is intermediate to *Meloe* and *Eurymeloe* with respect to the length of the antennal segments, but similar to *Meloe* based on claw and leg structure, and in the form of the antennal sensory organ. The larvae of *Taphromeloe* and *Meloegonius* have traits of both types, and those of the former are perhaps more clearly intermediate. Type I traits include the virtual absence of a line of dehiscence on the metanotum, the undivided abdominal sternites, and elongate tibial setae. Type II traits include the trident-like tarsungulus, 4 long caudal setae, and the disk-like sensory organ of the antenna. Traits intermediate to the two types include the only slightly swollen femora, the moderately tapered tibiae, and the intermediate length of antennal segment II. Obviously, the original definitions of types I and II larvae are not useful predictors of variation in this group of Meloinae.

The intermediacy of *Taphromeloe* larvae cloud the distinction between *Eurymeloe* and *Meloe* as defined by Selander. Only on the basis of tarsungulus structure can it clearly be assigned to *Meloe*. In addition to the problem of intermediacy, we are unaware of a single derived trait that can be used to define *Eurymeloe* as a monophyletic taxon at any level. For this reason also, we prefer to retain the group within *Meloe* at least until relationships are better resolved.

As defined here, *Meloe* includes, as before, all wingless and brachyelytrous Meloinae with phoretic larvae. We note that the larvae of all species (including those in *Eurymeloe*) have at least one derived trait lacking in *Cyaneolytta*, *Spastomeloe*, *Lyttomeloe*, and *Spastonyx*. This is the position of the first abdominal spiracle. In *Meloe* this spiracle is more dorsal than the other abdominal spiracles (Fig. 6) and is positioned on the tergite. In the other genera the spiracle is more ventrally placed and either positioned on the pleurite or on the membrane between the tergite and pleurite.

Returning *Eurymeloe* to *Meloe* resurrects the problem of extreme larval heterogeneity within *Meloe*. This posed no problem be-

fore the discovery of larvae of the other four genera now residing in the Meloini, and it is a concern now only if we assume the phoresy-correlated characters in *Meloe* and these other genera are homologous. We note that perhaps similar heterogeneity also occurs in *Cyaneolytta* (Bologna et al. 1990). Clearly, a detailed character analysis is called for. We are now in the early stages of such a study and thus only tentatively follow Selander's definition of the tribe.

We believe that the presumed monophyly of the Meloini should be validated by derived traits that are not associated with phoresy. This has not been done. All of the derived anatomical and behavioral characters currently used to argue the monophyly of the tribe are believed to be associated with phoresy (Selander 1988). It should be noted that several of these features also occur in larvae of the Nemognathinae (tentatively including the Tetraonycini), a very distinct meloid subfamily consisting entirely of phoretic species (MacSwain 1956). For example, the very distinctive trident-like "claw," the only clearly derived trait available to define *Meloe* (*sensu* Selander 1985), occurs in some species of *Nemognatha* (e.g. Blochtein and Wittmann 1988) and in *Stenoria* (Cros 1940). The head shows similar modifications in the Meloini and Nemognathinae, and an extrusible pygopod occurs in both groups. Of course the phylogenetic distance between the Meloini and Nemognathinae is sufficiently great that these similarities can easily be attributed to homoplasy. We suggest that homoplasy may also have resulted in the striking similarity among larvae of genera now placed in the Meloini but that it is not as easily detected owing to the relative phylogenetic proximity of these taxa. In our opinion, only non-phoretic characters can convincingly test the monophyly of the tribe.

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