

# THE LARVAE OF LEIESTINAE WITH NOTES ON THE PHYLOGENY OF ENDOMYCHIDAE (COLEOPTERA: CUCUJOIDEA)

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**Abstract.**— Larvae representing three genera of Leiestinae (Coleoptera, Endomychidae) are described and illustrated: *Leiestes seminiger* (Gyllenhal) (Poland, Białowieża National Park), *Phymaphora pulchella* Newman (USA, Virginia), and *Rhanidea unicolor* (Ziegler) (USA, New Jersey). The larval characters of Endomychidae and its subfamilies are discussed, and the key to the known genera is provided. The larval characters show only partial congruence with the recent family classification based on the adult data.



**Key words.**— Coleoptera, Endomychidae, Leiestinae, *Leiestes*, *Rhanidea*, *Phymaphora*, larvae, biology, mycophagy.

## INTRODUCTION

Because of the peculiar pseudotrimerous tarsi of most large and aposematic species of Endomychidae, the group has always been closely associated with Coccinellidae, and indeed some coccinellid genera were described as endomychids (e.g., *Mimolitoophilus* or *Monocoryna*) and vice versa (e.g., *Cyclotoma*). While most of the coccinellids are either predaceous or herbivorous, Endomychidae are primarily fungivorous (Lawrence 1991) with the notable exception of the predaceous larva of *Saula* described by Sasaji (1978a). Both families are currently classified within the superfamily Cucujoidea, and are recognized as members of the cerylonid series by Crowson (1960) and Ślipiński and Pakaluk (1991). Very little information is published on biology and immature stages of Endomychidae (Lawrence 1991). Of more than 120 currently recognized genera, larvae of 25 genera have been described so far, mostly from the northern hemisphere. In the recent classification of Endomychidae (Tomaszewska 2000b) twelve subfamilies have been recognized, of which larvae remain unknown for Eupsilobiinae (Pakaluk and Ślipiński 1990) and Danascelinae (Tomaszewska 2000b). The Australian genus *Periptyctus* Blackburn included in the subfamily Epipocinae (McHugh and Pakaluk 1977) belongs in the Corylophidae (Ślipiński and Tomaszewska, in prep.), and is not discussed further in this paper.

Leiestinae include 6 genera distributed in Europe, Japan and North America. Leiestinae adults are rather small beetles with distinctly clubbed antennae, simple tarsomeres, very narrow, bicarinate mesosternum, hidden antennal insertions, concealed mesotrochantin and

the procoxal cavity with narrow slit (Tomaszewska 2000a). Their larvae have not been described in detail. The larva of *Rhanidea unicolor* is illustrated in Lawrence (1991), while both *Phymaphora* and *Rhanidea* are jointly characterized in Lawrence (1999). Below we present descriptions and illustrations of the immature stages of *Leiestes seminiger* based on the larvae collected by the senior author in the Białowieża National Park, north eastern Poland, and supplementary descriptions of *Phymaphora* and *Rhanidea*.

Since the data of Tomaszewska (2000b) includes only adult characters, we also tried to summarize the available larval characters to investigate distribution of larval character states among the recognized subfamilies. To stimulate further interests in the endomychid natural history we consulted all papers containing larval descriptions of Endomychidae, and constructed a key to the genera based on these descriptions and our larval collection.

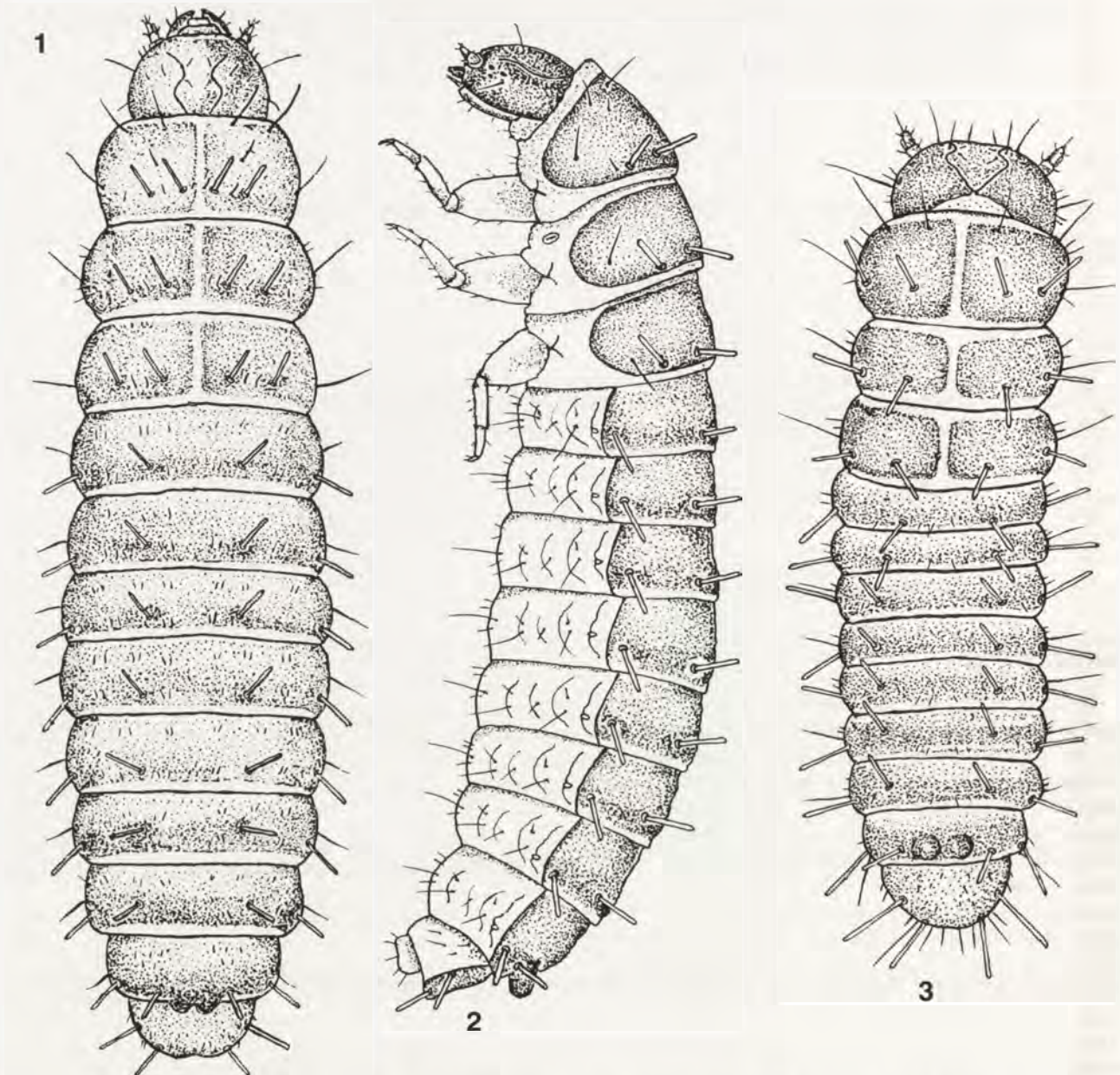
## LARVAE OF LEIESTINAE

*Leiestes seminiger* (Gyllenhal)  
(Figs 1–19)

**Diagnosis.** The larva of *Leiestes seminiger* is easily distinguished from all known endomychid larvae by the biforous spiracles and the peculiar tubercles on the eighth abdominal tergite.

**Measurements.** length 4.6 mm; head width 0.64 mm; pronotum width 0.9 mm; width of 9th abdominal segment 0.56 mm.

**Mature larva.** Body elongate, approaching fusiform (Fig. 1), widest at middle, subcylindrical, slightly flat-

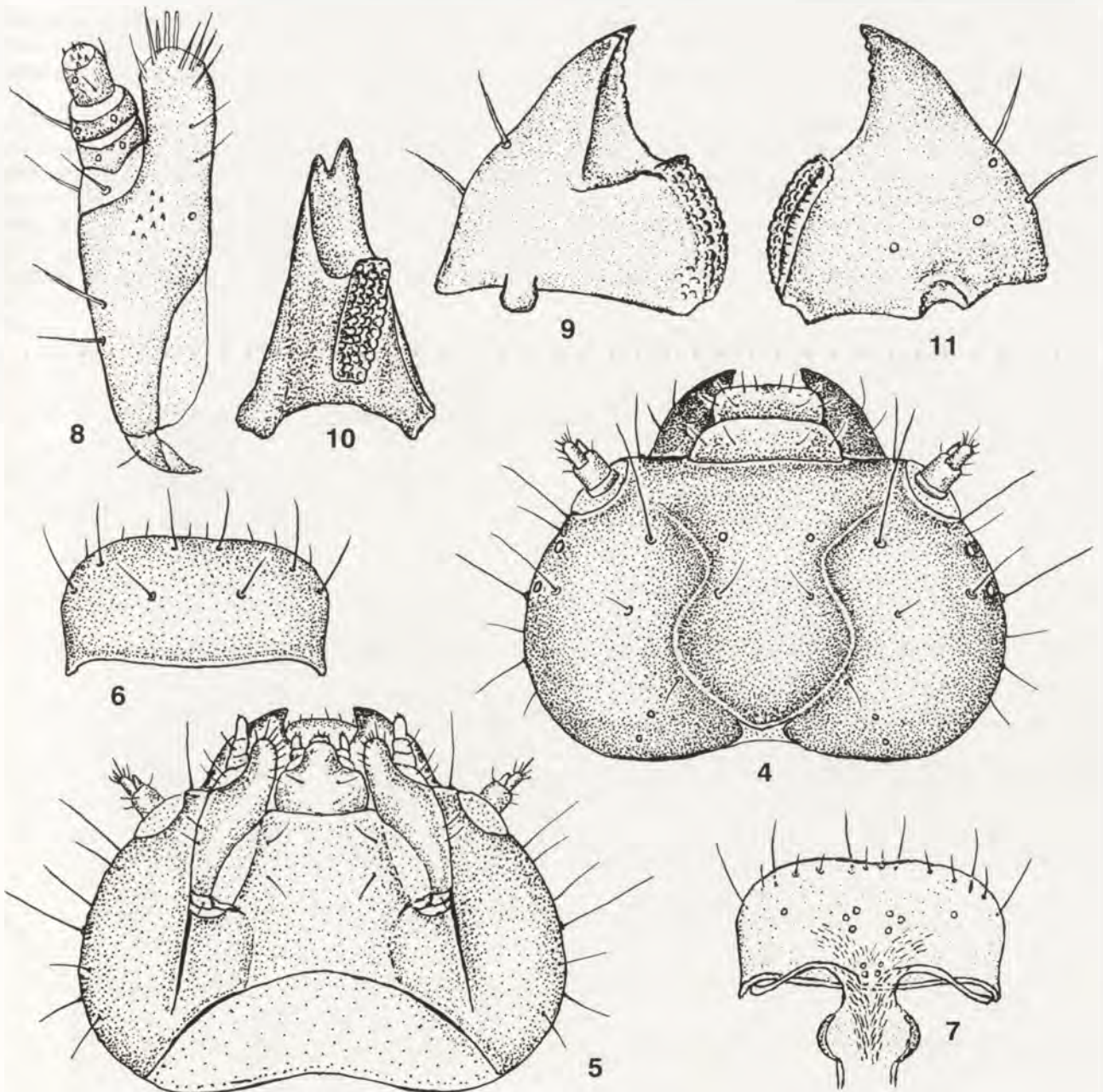


Figures 1-3. *Leistes seminiger*, larva. 1, 2. Mature larva: (1) dorsal; (2) lateral. 3. First-instar larva, dorsal.

tened dorsally, weakly constricted between segments, without urogomphi. Color ochreous, each tergite of thorax with two brownish patches; first eight abdominal tergites brownish posteriorly. Body feebly sclerotized except for head, mandibles, and tergites which are moderately strongly sclerotized. Cuticle of dorsal surfaces finely and rather densely microtuberculate, with transverse or oblique rows of asperities visible under  $100\times$  magnification (Fig. 18). Vestiture consists of scattered simple apically acute setae, and long, sparse stick-like setae on thoracic and abdominal tergites.

Head (Figs 4, 5) prognathous and protracted, depressed,  $0.6\times$  as long as wide, and  $0.7\times$  as wide as pro-

thorax; rim of occipital foramen distinctly thickened. Stemmata 3 on lateral side (Fig. 2) forming a triangle. Frontal sutures lyriform, almost complete anteriorly, meeting posteriorly; coronal suture absent. Frons broad, with 2 setae and 2 pores in front of middle; epistomal margin with 2 long setae near talus. Epicranium with one pair of long setae and two pairs of short setae near frontal suture, and seven pairs of setae on lateral sides. Frontoclypeal suture weak, indistinct. Clypeus trapezoidal, about  $0.3\times$  as wide as head capsule, with 2 pairs of setae. Labrum (Figs 6, 7) free,  $0.3\times$  as long as wide, with 4 pairs of setae near anterior margin and 2 setae on median area. Epipharynx (Fig. 7) membranous; anterior-



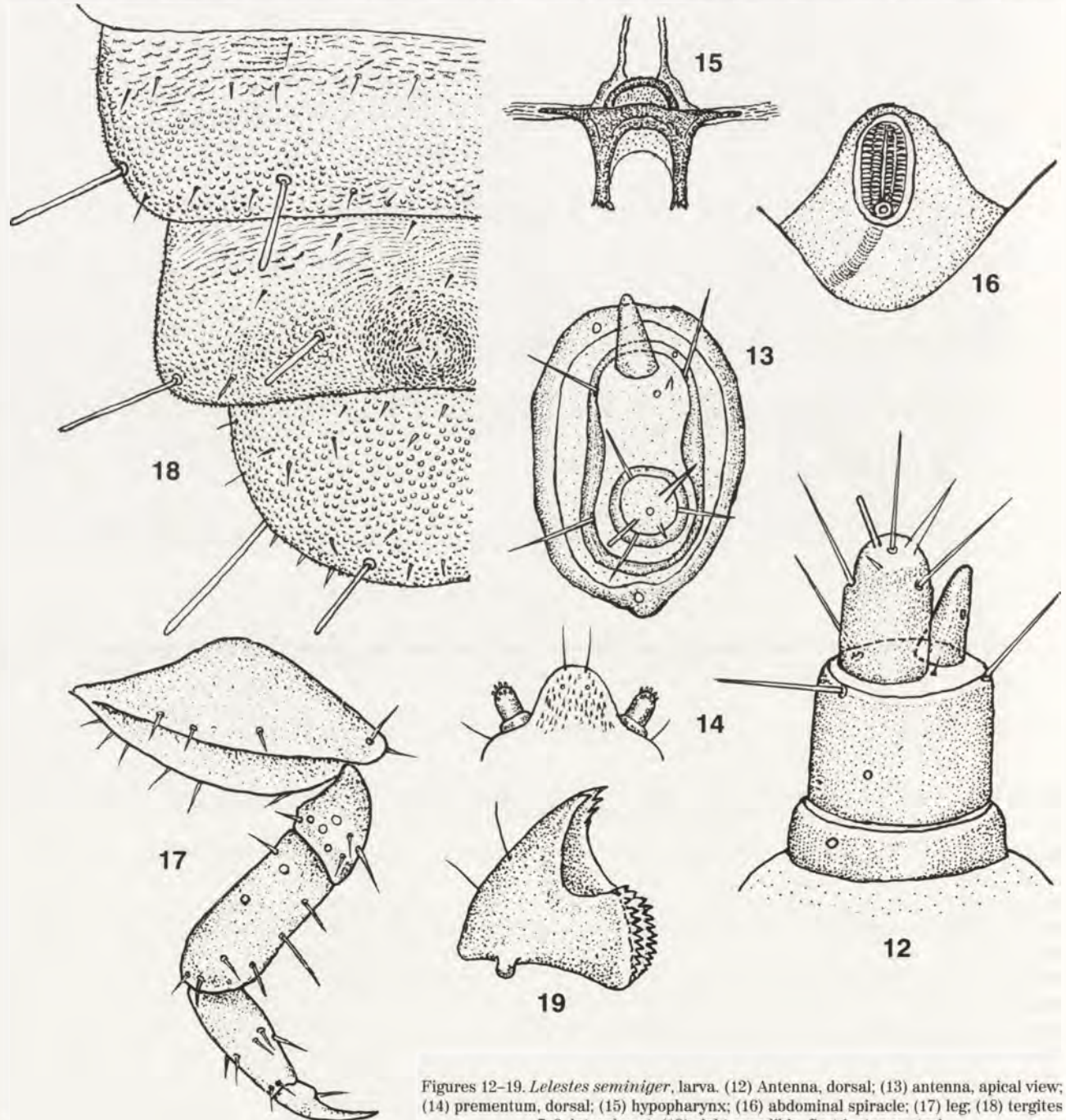
Figures 4–11. *Leiestes seminiger*, mature larva. (4) Head, dorsal; (5) head, ventral; (6) labrum, dorsal; (7) labrum-epipharynx, ventral; (8) maxilla; (9) right mandible, ventral; (10) same, mesal; (11) same, dorsal.

ly furnished with 8 placoid sensilla, posteromedian part with 2 clusters of numerous microtrichia obliquely directed to midline; 4 placoid sensilla at middle. Antenna (Figs 12, 13) short, 3-segmented, situated on circular membrane; insertion fairly close to mandibular articulations. Relative length of antennomeres as 1.0:2.5:3.0; sensory appendage about  $0.7 \times$  as long as antennomere 3. Antennomere 1 lacks setae but with 2 campaniform sensilla; 2nd with 3 long setae near apex, and conical sensory appendage situated ventro-laterally; antennomere 3 dome-shaped, with 3 long setae, 3 solenidia (1 styliform, 2 setiform), the longest solenidium thickened at base.

Mandible (Figs 9–11) subtriangular, bidentate apically; incisor edge serrate apically; external margin with 2 long setae; dorsal surface with 2 campaniform sensilla; mola narrow but well developed bearing transverse rows of blunt tubercles or ridges. Ventral mouthparts (Fig. 5) retracted, jointly about as long as wide. Maxilla (Fig. 8) slender, movable; cardo subtriangular bearing single seta, juxtacardo oblique; stipes with 2 setae at outer margin; mala  $2 \times$  as long as wide, rounded at apex, with numerous setae close to apical margin (2 of them blunt apically), and 2 setae along inner margin. Maxillary palp 3-segmented based on membranous palpifer bearing 2

setae; palpomere 1 with 2 pores, 2nd with single seta and 2 pores, the terminal segment bearing 2 short setae, single pore and a group of minute papillae at apex. Labium (Figs 5, 14) with mentum fused to submentum, with 4 setae; prementum well separated from mentum with 2 setae; labial palps 2-segmented, first palpomere short, the terminal one much longer, cone-shaped, bearing minute papillae at apex; ligula reduced to a small membranous protuberance bearing two rigid setae and numerous sensilla dorsally. Hypopharynx (Fig. 15) membranous anteriorly, limited posteriorly by dark hypopharyngeal sclerome bearing anterior membranous rods and posterior sclerotized processes; hypopharyngeal bracon alignentous. Hypostomal rods long, slightly diverging posteriorly (Fig. 5).

Thorax (Figs 1, 2) about  $0.3 \times$  as long as body length, each tergum transverse, sclerotized and divided by a pale longitudinal line. Prototum about  $0.5 \times$  as long as wide, widest at middle; anterior angles broadly rounded; each half of tergite bears 4 long and 2 short pointed setae, and 2 stick-like setae posteriorly arranged as in Fig. 1; surfaces granulose, especially near hind margin.



Figures 12-19. *Lelestes seminiger*, larva. (12) Antenna, dorsal; (13) antenna, apical view; (14) prementum, dorsal; (15) hypopharynx; (16) abdominal spiracle; (17) leg; (18) tergites 7-9, lateral part; (19) right mandible, first-instar, ventral.

Meso- and metathorax similar in size, each about  $0.4 \times$  as long as wide; half of each tergal plate bears 2 stick-like, 4B5 minute, and one long seta laterally; surfaces of terga granulose.

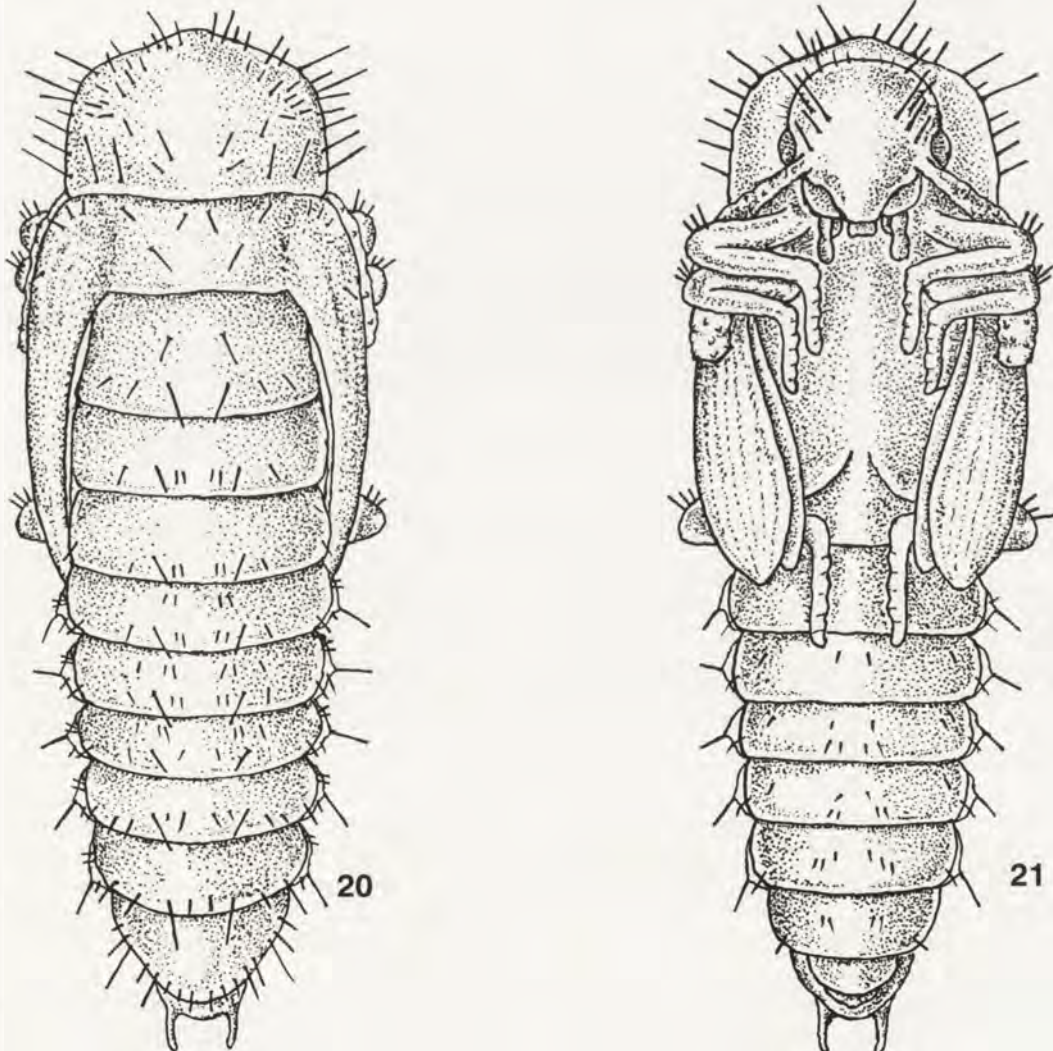
Legs (Fig. 17) slender, relatively short, not visible from above in normal position; all pairs subequal; coxae widely separated with short setae. Trochanter triangular with 1 long and 3 short setae and four setae; femur about  $2 \times$  as long as wide, dorsally with 1 seta and 2 pores, 4 setae ventrally and 2 short setae apically; tibiotarsus  $0.7 \times$  as long as femur with 5 setae medially and 2 short setae on antero-dorsal surface; claw broadened at base, bearing single seta.

Spiracles (Fig. 16) elliptical, biforous, with a median septum, set within a small oval peritreme, each situated in a membranous field. Spiracles of abdominal segments 1–8 located at apices of short integumental processes between fleshy furcate process above epipleura, their average length is 0.06 mm, width 0.03 mm. Thoracic spiracle similar, but larger and located at antero-lateral part

of mesothorax. The number of teeth or corrugations on either side of the orifice is about 24 in the thoracic spiracle, and 20 in the abdominal one.

Abdomen. Segments 1–7 subequal in length, each tergite with 4 stick-like setae, numerous minute setae and patches of granules and asperities (Fig. 18). Ventral surfaces weakly sclerotized, whitish; lateral side of each of segments 1–8 with protuberant epipleuron bearing 1 long and 1 short seta; hypopleuron with 1 long seta; laterosternum with 1 long and 1 minute seta and mediosternum with pair of long, and 3–4 pairs of short setae. Tergite VIII similar to the preceding one but bearing a pair of admedian protuberances covered with small granules and minute pointed apically setae (Figs 1, 2). Tergite IX short, uncolored, oval in outline with 4 stick-like setae; cuticle covered with minute hairs and granulations. Segment 10 very short and ring-like, oriented posteroventrally with a whorls of about 14–16 fine setae.

*First instar larva* (Figs 3, 19). Length 1.65 mm; maximum width 0.42 mm; head width 0.32 mm. This



Figures 20–21. *Leistes seminiger*, pupa: (20) dorsal; (21) ventral.

instar is very similar to the mature one described above and differs as follows: body more strongly flattened, less strongly sclerotized, the setae relatively longer, and with darker spots on thorax and abdominal tergites 1–8 (Fig. 3); mandible (Fig. 19) with the apical teeth sharp and pointed, the serration on incisor edge more apparent and the molar tubercles more prominent.

**Pupa** (Figs 20, 21). Length 3.7 mm, width 1.3 mm (across first abdominal segment, including elytra), pronotal width 0.9 mm. Body flattened dorsoventrally, about 4 – as long as wide. Cuticle whitish, weakly sclerotized; vestiture consists of sparse, apically blunt setae.

Head subglobular, strongly reflexed ventrally, not visible from above; disk with one pair of interocular setae, 3 pairs of frontal setae and 5–6 pairs of anterior and lateral setae. Labrum elongate, extending to apex of mandibles; maxillary and labial palps not well visible. Antenna short, claviform with apex extending ventrally slightly beyond midtibia; surfaces with sparse spines. Pronotum subpentagonal,  $0.7 \times$  as long as wide, widest at base with weak subbasal constriction; anterior and posterior margin rounded; dorsal and lateral setae arranged as in Fig. 20. Mesonotum  $0.67 \times$  as long as wide with 3 pairs of setae. Metanotum longer than mesonotum bearing 8 setae. Elytra and wings fitting obliquely at both sides of body; apices of them extending to second abdominal ventrite; basal part of elytron with 3–5 setae. Anterior and mid legs well visible, hind ones partially covered by wings and elytra; each femur with 3 short setae near apex; distal parts of midtarsi extending to middle of metasternum, those of hind tarsi to third abdominal ventrite. Abdomen dorsally convex,  $0.6 \times$  as long as total body length, composed of 9 segments. Tergites 1–7 similar, each with 1 pair of long and 3–8 pairs of short setae on each side; last tergite with two parallel urogomphi. Pleural zone protuberant, each with 1 long and 1 minute seta. Sternites with 2–5 pairs of minute setae.

**Material and rearing data.** Poland: Białowieża National Park, district 399, *Circaeo-Alnetum*, 17.v.1969, B. Burakowski, adults and mature larvae (some preserved in alcohol); moist and shady site, on surface of whitish-rotting damp, soft wood of stump and base of fallen trunk of *Populus tremula* L. Several adults and larvae were brought to the laboratory at room temperature, and two cultures have been established. Three larvae were transferred to individual glass tubes (15 – 80 mm) in two-thirds filled with small particles of soft decaying wood, stoppered with moistened cotton plugs. Larvae were observed moving and tunneling in galleries, feeding and making pupal chambers near the glass walls; pupae were visible on 26.vi (1 preserved), imago emerged on 11.vii.1969; specimens remained teneral for 4–8 weeks. The remaining specimens were transferred to a 0.5 litre jar, in two-thirds filled with moist substratum collected with the specimens. No copulation or ovipositing were observed. Four first-instar larvae mov-

ing slowly on surface of sap wood seen on 10.viii.1969 (2 preserved); further culture unsuccessful.

**Notes.** The larva of *Leiestes* is apparently adapted for tunneling in sapwood. It may easily move backwards in tunnels because of its subcylindrical form, protracted head, stout mandibles, relatively short legs, granulate and asperate abdominal terga, and protrusible tubercles on eight abdominal tergite. The mouth parts of larva are highly adapted for xylophagy. The labrum bears tormae, small spines and hairs which may help to sweep the food particles into the mouth. The mandibles having chisel-like apices are adapted for scooping the fibriles of sapwood then being masticated by the strongly tuberculate molar lobes.

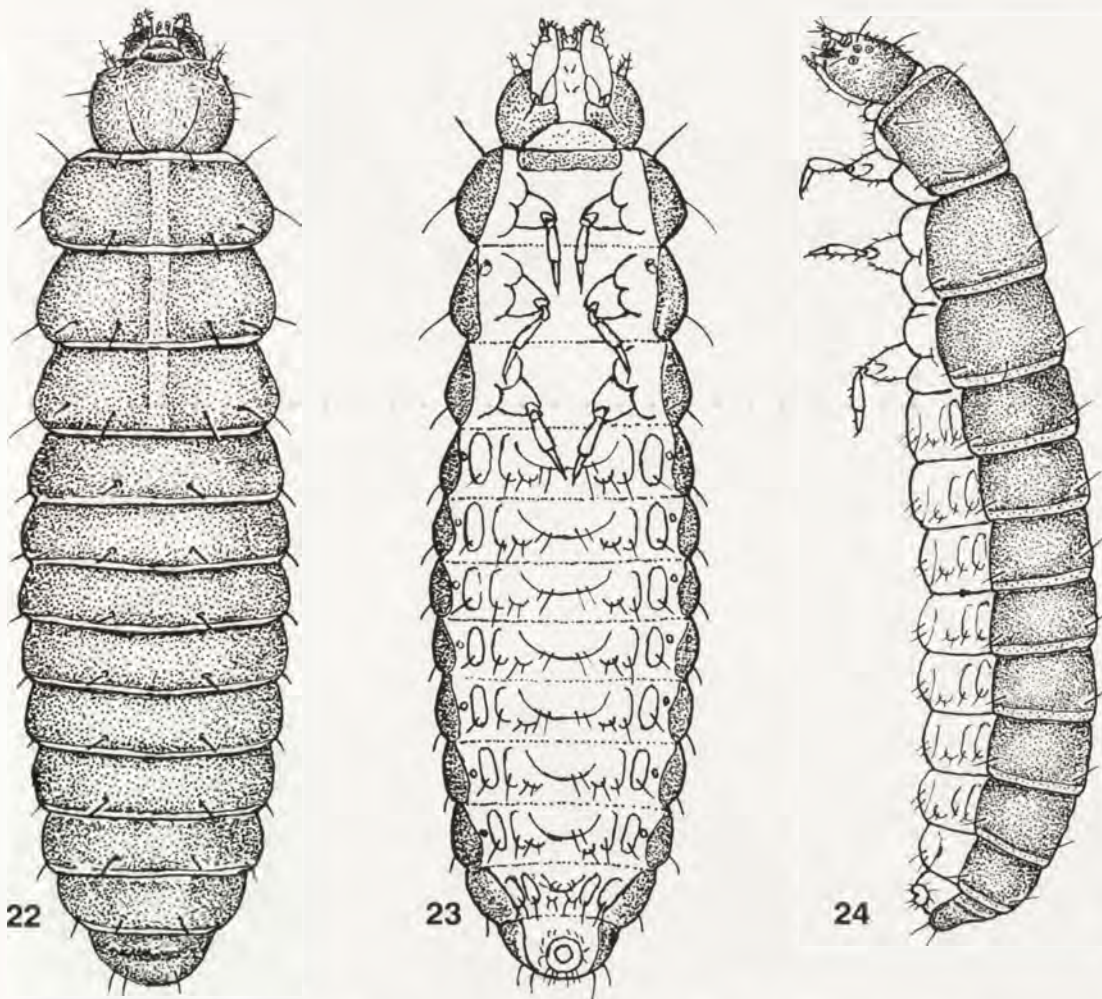
*Phymaphora pulchella* Newman  
(Figs 22–32, 40–44)

**Diagnosis.** This larva is very similar to *Rhanidea* but differs in having distinct frontoclypeal suture.

**Measurements.** Length 5.0 mm; head width 0.8 mm; pronotum width 1.2 mm.

**Description of mature larva.** Body elongate, subcylindrical (Figs 22–24), widest at middle, gradually narrowing posteriorly, slightly flattened, weakly constricted between segments, without urogomphi. Dorsum yellowish brown, well sclerotized, mola and mandibular tips brown; venter white, feebly sclerotized except for darker hypostomal rods and hypopharynx. Cuticle of dorsal surfaces apparently smooth but faint microserrate granules and asperities visible under  $150 \times$  magnification (Fig. 44). Dorsal vestiture sparse, consists of scattered long simple stout setae and more closely set short ones on thoracic and abdominal tergites.

Head (Figs 25–27) prognathous to weakly declined and protracted, slightly depressed, as long as wide, and  $0.6 \times$  as wide as prothorax. Stemmata 3 on lateral side, hemispherical with black additional spot ventrally (Fig. 27) positioned posteriorly to antennal insertion. Frontal arms lyriform, translucent, almost complete anteriorly, meeting posteriorly; epicranial stem and endocarinae absent. Frons broad, with 6 pairs of setae near epistomal margin. Epicranium with one pair of long setae and several short ones. Frontoclypeal suture distinct, weakly arcuate. Clypeus transverse, trapezoidal, about  $0.3 \times$  as wide as head capsule, with 6 long setae. Labrum (Fig. 42) free,  $0.5 \times$  as long as wide, with 9 stout inclined setae along margin and 2 on median area. Epipharynx membranous. Antenna (Figs 30–31) 3-segmented, situated on circular membrane, less than  $0.2 \times$  as long as head width; insertion close to mandibular articulations. Relative length of antennomeres as 1.0:2.5:2.5; sensory appendage about  $0.8 \times$  as long as antennomere 3. First antennomere lacks setae but with 2 pores; 2nd with 3 long setae near apex, and single pore and conical sensory appendage situated ventrally; antennomere 3 with three long setae and apical setiform sensillum. Mandible (Figs 28, 29) triangular, bidentate



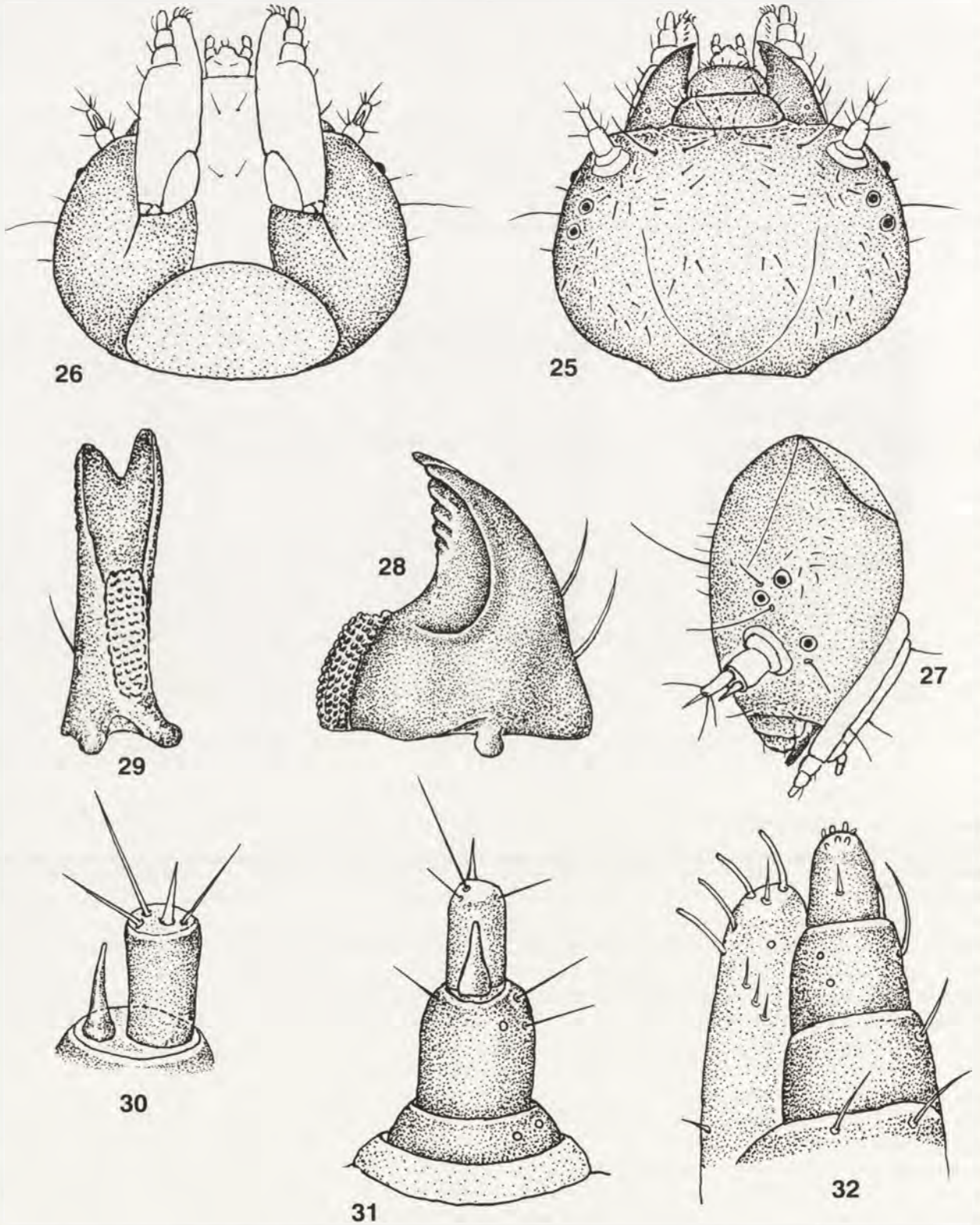
Figures 22–24. *Phymaphora pulchella*, mature larva: (22) dorsal; (23) ventral; (24) lateral.

apically; incisor edge bearing 4 teeth subapically; external margin with 2 long setae; dorsal surface with single campaniform sensillum; mola narrow but well-developed bearing transverse rows of asperities at edges merging to form grooves and serrate ridges. Ventral mouthparts (Fig. 26) protracted. Maxilla (Fig. 32) slender, movable; cardo small, divided, triangular bearing single seta; stipes elongate bearing 4 setae; mala  $2 \times$  as long as wide, rounded at apex, with 4 dorsally and a row of curved setae along apical margin. Maxillary palp 3-segmented; first palpomere with 1 seta, second with single curved seta and 2 pores, the terminal segment bearing 1 short seta and a group of minute papillae at apex. Labium (Fig. 26) with mentum fused to submentum, with 4 setae; prementum well separated from mentum with 2 setae; labial palps 2-segmented and broadly separated; ligula broad, arcuate distally bearing pair of setae at apex. Hypopharynx (Fig. 41) membranous anteriorly, limited posteriorly by dark hypopharyngeal sclerome bearing anterior membranous rods and posterior sclerotized bridges; maxillulae bidivided, lobe shaped; hypopharynx-

geal bracon aligementous. Hypostomal rods short, diverging posteriorly (Fig. 26).

Thorax (Fig. 22) about  $0.3 \times$  as long as body length, each tergum transverse, sclerotized and divided a pale longitudinal line. Prototum about  $0.5 \times$  as long as wide, widest behind middle; anterior angles broadly rounded; anterior and posterior margins bordered by narrow stripes of posteriorly directed spinules, each half of tergite bears 2 anterior, 2 median and 1 lateral setae; surfaces granulate; prosternum transverse with 2 median setae. Meso- and metathorax similar in size, each about  $0.4 \times$  as long as wide; half of each tergal plate bears 1 lateral and 2 median setae.

Legs (Fig. 40) slender, relatively long, all pairs of subequal lengths; coxa sessile, widely separated, broadest and longest part of a leg, emarginate at outer surface receiving coxa with numerous short setae and spines. Trochanter triangular with 1 long and 2 short setae and five pores; femur cylindrical weakly thickened apically with 5 setae and 1 pore; tibiotarsus as long as femur, narrowing distally with 5 long and 2 short setae; claw long broadened at base, bearing single seta.



Figures 25–32. *Phymaphora pulchella*, mature larva. (25) Head, dorsal; (26) head, ventral; (27) head, lateral; (28) mandible, ventral; (29) same, mesal; (30) antenna, apical part, lateral; (31) antenna, ventral; (32) maxilla, ventral.



Spiracles annular, small and hidden in folds between bases of tergal and hypopleural lobes. Thoracic spiracle similar, but larger and located at antero-lateral part of mesothorax.

Abdominal segments 1–8 subequal in length, terga protuberant laterally, posterior edge bordered by microspinules, each tergite with 4 long setae and numerous minute setae (Fig. 44). Ventral surfaces weakly sclerotized, whitish; hypopleuron protuberant with one long and one short seta; laterosternum suboval with long seta; mediosternum with circular posterior edge and 4 setae (Fig. 43); sternellum with 2 setae. Tergite 9 extending onto ventral surfaces, dorsum with transverse impression and protuberance bearing 2 pairs of long setae on posterior angles. Segment 10 short, ventral, ring-like with a whorls of fine setae.

**Material examined.** USA: Virginia: Fairfax Co., Springfield, 7.vi.1975, JFL lot 4036, ex *Donkia pulcherrima*? on *Fagus*, J. Doyen (3 larvae). Wisconsin: Sauk Co., Hemlock Draw, 30.v.1996, on white fungal mycelium in wood and beneath bark of *Populus* log; above the "Glade", D.K. Young (5 larvae).

*Rhanidea unicolor* (Ziegler)

(Figs 33–39)

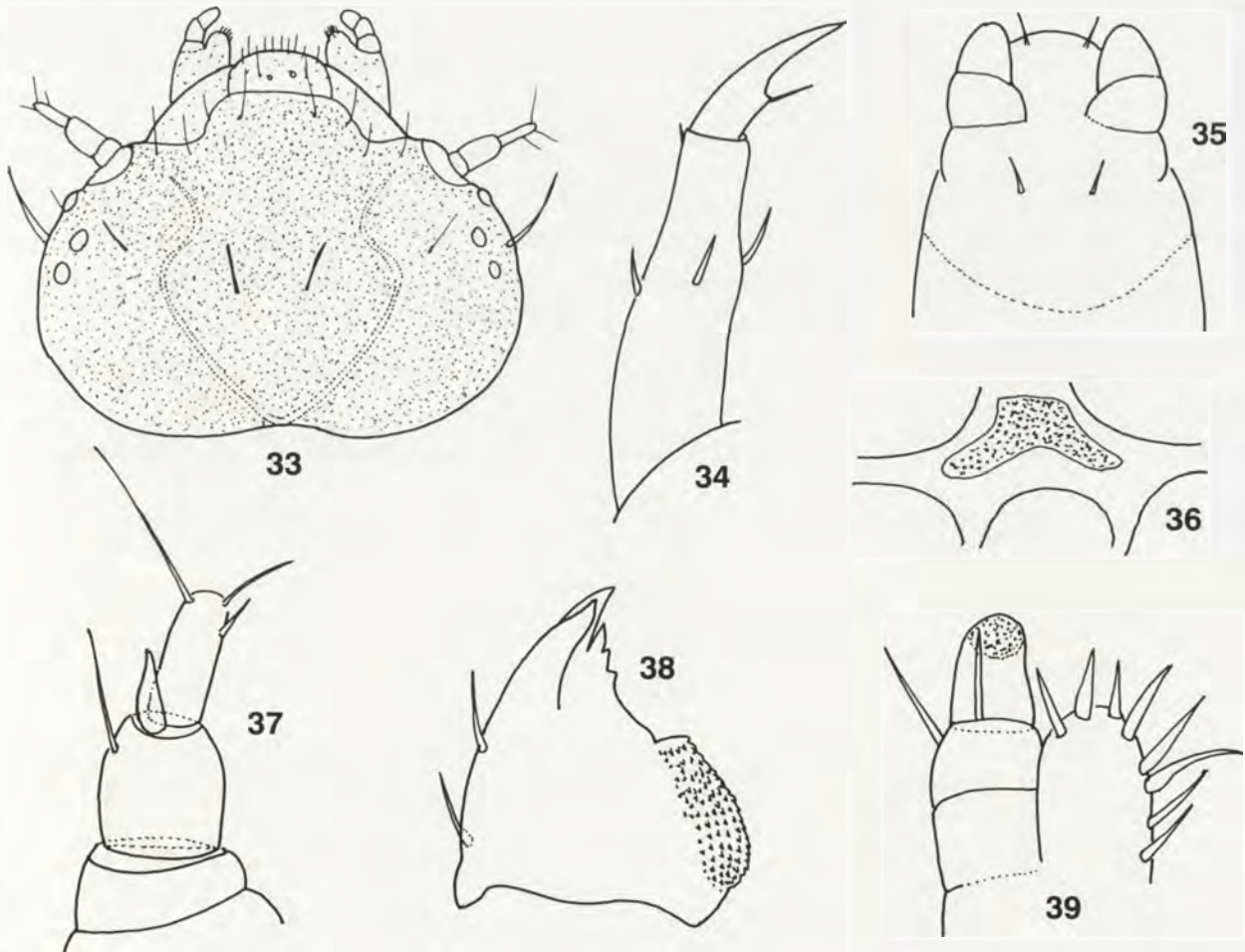
**Diagnosis.** Very similar to *Phymaphora* but distinguished by the absence of frontoclypeal suture.

**Measurements.** Length 3.7–4.5 mm; head width 0.7 mm; pronotum width 1.0–1.1 mm.

**Description of mature larva.** This larva is very similar to the larva of *Phymaphora pulchella* described above; it was also illustrated and described by Lawrence (1991, 1999), therefore in the diagnostic description below we quote, and illustrate the characters which differ as compared to the larva of *Phymaphora* or were not indicated in the descriptions cited above.

Dorsum creamy yellow, mola and mandibular tips brownish, venter white. Cuticle of dorsal surfaces apparently smooth but faint granules are traceable under 150× magnification. Dorsal vestiture sparse, consists of sparse long setae along margins and more closely set short ones on thoracic and abdominal tergites.

Head (Fig. 33) prognathous to weakly declined and protracted, slightly depressed, as long as wide, and



Figures 33–39. *Rhanidea unicolor*, mature larva. (33) Head, dorsal; (34) tibiotarsus and claw; (35) labium, ventral; (36) hypopharynx; (37) antenna, ventral; (38) mandible, ventral; (39) apical part of maxilla.

0.5–0.6 × as wide as prothorax. Stemmata 3 on lateral side, hemispherical with black additional spot ventrally, positioned posteriorly to antennal insertion. Frontal arms lyriform, translucent, almost complete anteriorly, meeting posteriorly; epicranial stem and endocarinae absent. Frontoclypeal suture absent. Clypeus transverse, trapezoidal, about 0.3 × as wide as head capsule, with 6 long setae. Labrum free, arcuate anteriorly, 0.3 × as long as wide. Antenna (Fig. 37) 3-segmented, situated on circular membrane, 0.2–0.25 × as long as head width; insertion close to mandibular articulations. Relative length of antennomeres as 1.0:2.4:2.3; sensory appendage about 0.6 × as long as antennomere 3. Mandible (Fig. 38) triangular, tridentate apically, because of very high subapical tooth; incisor edge bearing 3 teeth. Maxilla (Fig. 39) slender, movable; cardo indistinctly divided externally; mala 2 × as long as wide, rounded at apex, with a row of curved setae along apical margin. Maxillary palp 3-segmented; first palpomere with single seta, second with 2 setae, the terminal segment bearing a group of minute papillae at apex. Labium (Fig. 35) with mentum fused to submentum, with 4 setae; prementum well separated from mentum with 2 setae; labial palps 2-segmented and broadly separated; ligula broad, arcuate distally bearing pair of setae at apex. Hypostomal rods short, diverging posteriorly. Abdomen.

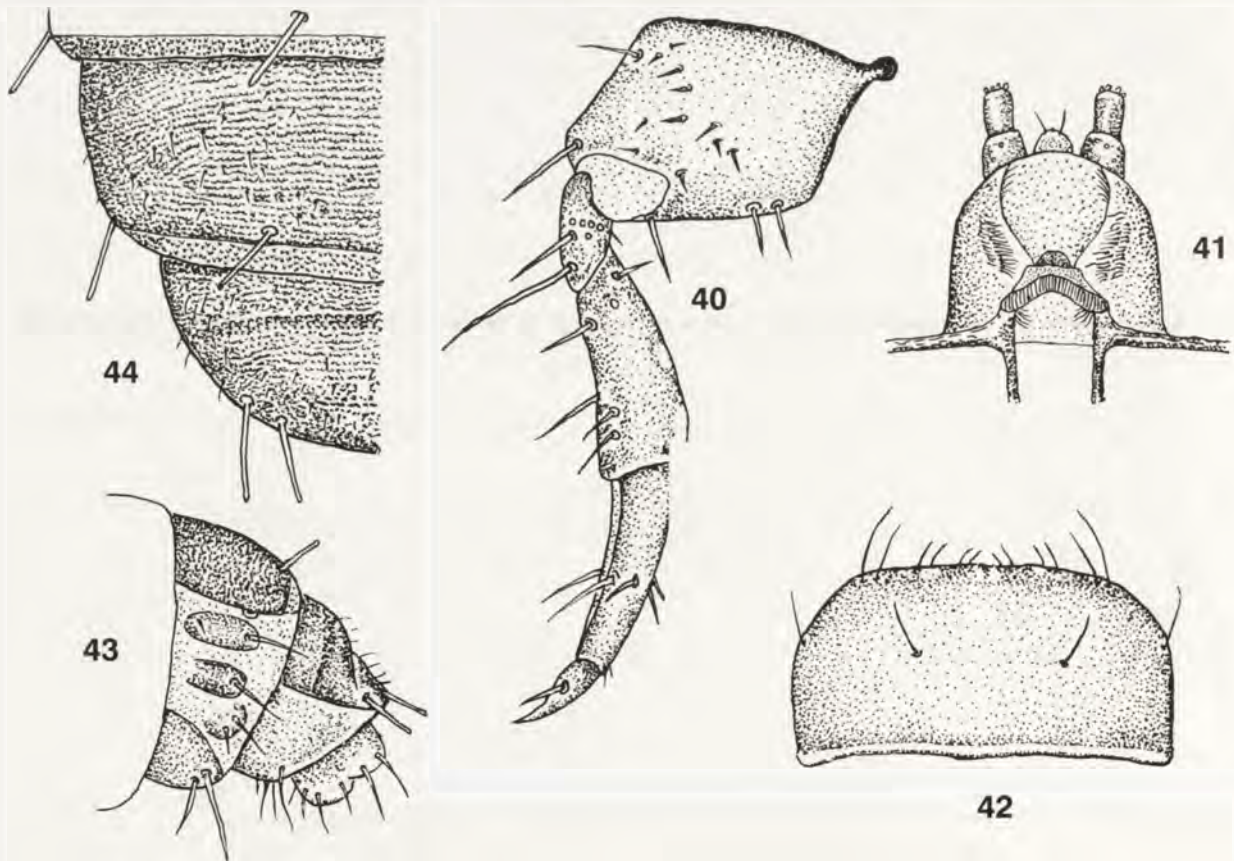
Segments 1–8 subequal in length, terga protuberant laterally, posterior edge bordered by microspinules, each tergite with 4 long setae and numerous minute setae. Tergite 9 extending onto ventral surfaces, dorsum with transverse impression and protuberance bearing 2 pairs of long setae on posterior angles. Segment 10 short, ventral, ring-like with a whorls of fine setae. Spiracles annular, small and hidden in folds between bases of tergal and hypopleural lobes. Thoracic spiracle similar, but larger and located at antero-lateral part of mesothorax.

**Material examined.** USA: New Jersey, Burlington Co., Rancocas, 31.v.1974, JFL lot 3556, ex. *Irpex tulipiferae*, A.F. Newton (2 larvae).

## IMMATURE STAGES AND THE PHYLOGENY OF ENDOMYCHIDAE

### Introduction

As noted by Lawrence (1991) endomychid larvae are highly variable in form, sculpture and vestiture and might be easily confused with a great number of other cucujoid larvae. This variability clearly exceeds that of the adult structures, which, with rare exceptions, allow specimens to be easily placed in their family.



Figures 40–44. *Phymaphora pulchella*, mature larva. (40) leg; (41) hypopharynx, dorsal; (42) labrum, dorsal; (43) tergites 7–9, lateral part.

Endomychidae (along with Alexiidae, Bothrideridae, Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae and Latridiidae) are classified in the cerylonid series of Cucujoidea, a group which is based on many reductions (adult tarsi and wing venation, larval stemmata or claw setae) and may be polyphyletic (Ślipiński and Pakaluk 1991). Already, the inclusion of Bothrideridae (Pal and Lawrence 1986) in the group questioned the validity of the wing characters (e.g., clearly visible radial cell and more complete venation in many Deretaphrinae), and here the *Leiestes* larva with its biforous spiracles contradicts the universal presence of annular ones throughout the series. It is beyond the scope of the present paper to discuss or propose the solution to phylogeny of the entire Cucujoidea (see Beutel and Ślipiński, in preparation), but we want to call the attention to problems that should be addressed by a further research.

The probable sister taxon of Endomychidae is the largest cucujoid family Coccinellidae, and both adults and larvae show many apparent similarities to each other. Endomychid adults are easily separated from the coccinellids in having distinct frontoclypeal suture and well developed mandibular mola in addition to the simple tegmen and less elongate and sclerotized median lobe (sipho). However the male genitalia of Eupsilobiinae (larvae unknown) approach the coccinellid condition (Pakaluk and Ślipiński 1990) with a sclerotized median lobe and expanded base (capsule). Although the study of Tomaszewska (2000b) confirms the monophyly of Coccinellidae and Endomychidae as separate sister clades based on the adult characters, the larval data shows some contradictions to her system (S.A. Ślipiński, unpublished).

#### Endomychidae

No single synapomorphy has been discovered for the endomychid larvae, which seem to have plesiomorphic features as compared to the larvae of Coccinellidae. Endomychidae are distinguished from Coccinellidae (Kamiya 1965; Lawrence 1982) by their larger and distinctly ridged mandibular mola (absent in *Endomychus*) and distinct prostheca (absent in Anamorphinae, Leiestinae and Merophysinae), primitively 4 stemmata (3 in Coccinellidae), separate cardo and maxillary stipes (fused in Coccinellidae), apex of tibiotarsus without specialized setae (present in *Mychothenus*) and the tarsal claw (pretarsus) slender as compared to short and basally toothed claw of most of Coccinellidae (indistinct in Sukunahikonini and Serangini). Some Coccinellidae (e.g., Chilocorini) have paired repugnatorial glands on abdominal terga and such structures have not been reported so far in Endomychidae. The undescribed larva of *Encymon* from New Guinea however has the first abdominal tergite with a lateral protuberance above the spiracle bearing a clear opening, which may be homologous to a repugnatory gland opening of Coccinellidae. The illustration of the *Eumorphus* larva (Bougnion 1909) shows the abdominal tergum 1 with small setose tubercles laterally above the pleural lobe which may represent similar structures to that discovered in *Encymon*.

#### Anamorphinae

Larvae of this group are very well characterized by their reduced mandibular apices, falcate mala and obliterated frontal arms - all apomorphic features as compared to Coccinellidae. Leschen and Carlton (1993) point to the three setae in the transverse row along the base of labrum as another potential character, but this needs to be confirmed in the remaining taxa. Larvae are external feeders; collected from polypore fungi and in rotting litter or logs, probably feeding on spores.

#### Endomychinae

Only *Endomychus* larva is known. It is distinguished from Coccinellidae and remaining Endomychidae in having the mandibular mola replaced by a hyaline process (but according to fig. 1 in Hayashi and Nakamura 1953 a distinct mola is present in *E. gorhami* - error?), and frontal arms distant at bases. Larvae are external feeders on Basidiomycetes of the families Schizophyllaceae (*Schizophyllum commune*) and Auriculariaceae (*Auricularia mesenterica*) (Leschen and Carlton 1988; Lawrence 1999).

#### Leiestinae

Larvae are internal feeders in basidiomycete fruiting bodies (*Donkia pulcherrima* and *Irpex tulipiferae*) and are characterized by subcylindrical body form and short appendages. This group appears to be monophyletic, and the 3 stemmata and the absence of a prostheca might serve as the larval synapomorphies (all homoplasious).

#### Merophysinae

The larvae of merophysinae are poorly known; they feed on molds in rotting logs and litter; some *Holoparamecus* occur in food stores and are cosmopolitan. The larvae share a subcylindrical body form and absent prostheca with Leiestinae, but differ in having no stemmata or dorsal sclerotization.

#### Mycetaeinae

The previously large and diverse group has been limited by Tomaszewska (2000b) to *Mycetaea* and *Agaricophilus*, the larvae of both have 2 stemmata, rigid mandibular prostheca and distinct frontoclypeal suture. Unfortunately the description of the unusual larva of *Agaricophilus* by Mamaev (1977) is very incomplete.

#### Xenomycetinae

This group includes the sole North American genus *Xenomycetes*, whose larvae were collected by Johnson (1986) feeding on sporocarps or mycelium of *Paxillus atrotomentosus* (Agaricales). The larva is characterized by the frontal arms U-shaped, 3 stemmata and annular-uniform spiracles.

#### Pleganophorinae

Of the three genera classified in this subfamily, the only larval description is that of *Trochoideus* by Kemner (1924), who reported the larvae occurring in the termite nests. The description is somewhat superficial, but the apparent characters of this larva are the 2 stemmata, short epicranial stem (error?), mandible multisetose

dorsally and peculiar comb of clubbed and hooked spines along the outer edge of mala.

#### Lycoperdininae

This is the largest subfamily of Endomychidae characterized by the presence in adults of the stridulatory file on the occiput and a corresponding membrane on the anterior margin of the pronotum. Larvae are very diverse morphologically and biologically, and no characters have been found to unite them. There are 4 major larval types within Lycoperdininae (Burakowski 1997): (1) the *Lycoperdina* itself whose larvae occur in puffballs (Lycoperdaceae), with double hypostomal rods, 1-segmented labial palps, paired acute processes on abdominal terga the last pair forming apparent urogomphi; (2) *Amphix*, with an odd, onisciform form without apparent dorsal vestiture and dorsal spiracles, that feeds on fungal material and lichens; (3) *Eumorphus*, *Ancylopus* and *Encymon* larvae, which are oval or elongate, have narrow, dehiscent processes along thoracic and abdominal edges, and they all may have repuganatorial gland openings on abdominal terga 1; (4) *Aphorista* and *Mycetina* with broad and not dehiscent lateral processes, and the dorsum with specialized setae.

#### Stenotarsinae and Epipocinae

Larvae of these groups are very similar to each other (McHugh and Pakaluk 1997) and to group 4 of Lycoperdininae. No characters are currently available to define Epipocinae and Stenotarsinae either separately or as a joint group. Biology of these taxa are virtually unknown, but *Saula japonica* is a predator on scale insects (Sasaji 1978b).

### KEY TO GENERA OF KNOWN LARVAE OF ENDOMYCHIDAE

We have found descriptions of 25 genera of Endomychid larvae and these, sometimes tentatively, are included in the key below. Some of the descriptions are fairly old or incomplete and need further revision to record the characters of high taxonomic value. The list below records all the described endomychid larvae, with descriptions at least partly allowing further identification and use for phylogenetic purposes (old incomplete descriptions are omitted). Additionally we examined larvae in our possession (indicated by an asterisk \*) while constructing the key and the discussions.

#### Anamorphinae

- Anagaricophilus* sp.: Pakaluk 1986: 313 (Madagascar).  
*Bystus decorator*\* Leschen and Carlton 1993: 39 (Peru).  
*Bystus* sp.: Lawrence 1991: 483, fig. 34.564 (Panama).  
*Idiophyes niponensis* (Gorham): Hayashi 1992: 119, fig. 12 (Japan).  
*Mychothenus asiaticus* Sasaji: Sasaji 1978a: 6 (Japan).  
*Rhymbus pallidus* Gerstaecker: Costa *et al.* 1988: 201, pl. 96 (Brazil).

*Rhymbus ulkei* Crotch: Böving and Craighead 1931: pl. 40 (USA).

#### Endomychinae

- Endomychus biguttatus*\* Say: Lawrence 1991: 484, fig. 34.568; Leschen and Carlton 1988 (USA).  
*Endomychus coccineus*\* (Linnaeus): Böving and Craighead 1931: pl. 40, 41 (Denmark).  
*Endomychus gorhami* (Lewis): Hayashi and Nakamura 1953: 28 (Japan).

#### Epipocinae

- Anidrytus* sp.: McHugh and Pakaluk 1997: 63 (Guyana, El Salvador).  
*Ephebus* sp.: McHugh and Pakaluk 1997: 65 (Honduras).  
*Epipocus* sp.: McHugh and Pakaluk 1997: 65 (Honduras, Mexico).  
*Saula japonica* Gorham: Sasaji 1978b: 24 (Japan).  
*Stenotarsus commodus* Blackburn: McHugh and Pakaluk 1997: 73 (Australia).

#### Merophysinae

- Colucera formicaria* Motschulsky: Silvestri 1912: 243 (Italy).  
*Holoparamecus*\* sp.: Lawrence 1991: 483, fig. 34.563 (USA, Florida).

#### Mycetaeinae

- Agaricophilus reflexus* Motschulsky: Mamaev 1977: 768 (Russia).  
*Mycetaea hirta*\* Marscham: Böving and Craighead 1931: pl. 39 (Denmark); Lawrence 1991: 484, fig. 34.567 (Scotland).

#### Leiestinae

- Leilestes seminiger*\* (Gyllenhal): present paper (Poland: Białowieża Nat. Park).  
*Rhanidea unicolor*\* (Ziegler): Lawrence 1991: 483, fig. 34.565 (USA: Vermont).  
*Phymaphora pulchella*\* Newman: Lawrence 1999: [descriptions file]; present paper (USA: Virginia).

#### Lycoperdininae

- Amphix*\* sp.: Costa *et al.* 1988: 199, pl. 95, 161 (Brazil).  
*Amphix laevigatus* (Gerstaecker): Böving and Craighead 1931: pl. 39 (Panama).  
*Ancylopus melanocephalus* (Olivier): Hayashi and Nakamura 1953: 29 (Japan).  
*Aphorista vittata* (Fabricius): Böving and Craighead 1931: pl. 39 (USA).  
*Aphorista morosa* LeConte: Lawrence 1991: 483, fig. 34.566 (USA: Arizona).  
*Eumorphus pulchripes* Gerstaecker: Bugnion 1909: 282 (Sri Lanka).  
*Lycoperdina mandarinea* Gerstaecker: Hayashi and Nakamura 1953: 30 (Japan).  
*Lycoperdina dux* Gorham: Hayashi and Nakamura 1953: 31 (Japan).  
*Lycoperdina succinta* (Linnaeus): Böving and Craighead 1931: pl. 40 (Denmark).  
*Lycoperdina ferruginea*\* LeConte: Böving and Craighead 1931: pl. 40 (USA); Pakaluk 1984 (USA);

- Lawrence 1988: 11, figs 15, 16; Lawrence 1991: 484, fig. 34.569 (USA: Michigan).
- Mycetina* sp.: Hayashi 1992: 119, fig. 12. (Japan).
- Mycetina cruciata*\* (Schaller): Burakowski 1997: 209 (Poland); Beutel *et al* 2000: 7–9 (Germany).
- Pleganophorinae**
- Trochoideus termitophilus* Roepke: Kemner 1924: 185 (Indonesia: Java).
1. Maxillary mala falcate or with inner spines; mandibular apex reduced or entirely missing; frontal arms indistinct; stemmata 0 or 1 (Anamorphinae) . . . . . **2**
  - Maxillary mala obtuse apically; mandibular apex always present; frontal arms distinct; stemmata usually 3 or 4 . . . . . **6**
  2. Number of stemmata 1 . . . . . *Rhymbus*
  - Number of stemmata 0 . . . . . **3**
  3. Tibial apex with 2 spatulate setae; antennomere 3 strongly reduced . . . . . *Mychothenus*
  - Tibial apex with simple setae; antennomere 3 distinct, about 2 length of the sensorium . . . . . **4**
  4. Antennomere 3 about as long as the sensorium; mala with modified, clubbed setae apically relatively broad with narrow spine . . . . . *Idiophyes*
  - Antennomere 3 distinctly shorter than the sensorium; mala narrower apically with two spines or dentate inner process, with simple setae only . . . . . **5**
  5. Mandible with single seta (error ?); apex of mandible missing and without membranous processes; inner part of mala with multi dentate process; antennomere 2 about 2 times as long as broad . . . *Anagaricophilus*
  - Mandible with 2 setae; apex of mandible with membranous processes; inner part of mala with 2 long spines; antennomere 2 very long, 4–5 times as long as broad . . . . . *Bystus*
  6. Mandibular mola replaced by a membranous lobe; frontal sutures; separated at base (Endomychinae ?) . . . . . *Endomychus*
  - Mandibular mola distinct, tuberculate; frontal sutures approximate at bases . . . . . **7**
  7. Abdominal terga 1B9 with dorsal, paired, acute processes; hypostomal rods paired . . . *Lycoperdina*
  - Abdominal terga without paired dorsal, acute processes, often with lateral processes in addition to the pleural lobes or processes; hypostomal rods single . . . . . **8**
  8. Mandibular prosthema absent (Fig.); body subcylindrical or slightly flattened, without tergal or pleural tubercles/processes; vestiture consisting of hairs or simple setae/spines; antennal socket always close to the mandibular articulation . . . . . **9**
  - Mandibular prosthema present; body usually flattened or onisciform with tergal and/or pleural lobes or processes; vestiture almost always consisting of modified setae; antennal socket very often shifted posteriorly due to the hypognathous, triangular head . . . . . **13**
  9. Stemmata absent; dorsal surfaces very lightly pigmented (Merophysiinae) . . . . . **10**
  - Stemmata 3; dorsal surfaces with distinctly sclerotized plates (Leiestinae) . . . . . **11**
  10. Frontal arms lyriform, distinct; antennomere 2 subquadrate or longer than broad . . . *Holoparamecus*
  - Frontal arms indistinct (error ?); antenna very short with antennomere 2 strongly reduced, transverse . . . . . *Coluocera*
  11. Tergite 8 with paired protuberances (Fig.); spiracles biforous . . . . . *Leiestes*
  - Tergite 8 simple; spiracles annular . . . . . **12**
  12. Frontoclypeal suture absent . . . . . *Rhanidea*
  - Frontoclypeal suture present . . . . . *Phymaphora*
  13. Antennomere 2 no more than 2.5 times as long as wide; head prognathous or slightly declined, rounded, widest near middle; antennal socket close to the mandibular articulation . . . . . **14**
  - Antennomere 2 at least 3.5 times as long as broad; head hypognathous, triangular broadest posteriorly; antennal socket distinctly posterior, far from the mandibular articulations . . . . . **16**
  14. Stemmata 3; spiracles annular-uniformous (Xenomycetinae) . . . . . *Xenomycetes*
  - Stemmata 2; spiracle annular (Mycetaeinae) . . . **15**
  15. Body broadly ovate, strongly flattened and disc-like; metathroacic and abdominal terga with lateral processes; frontal arms indistinct (error ?) . . . . . *Agaricophilus*
  - Body narrow and elongate, moderately convex; frontal arms distinct, V-shaped . . . . . *Mycetaea*
  16. Stemmata 2; mala with large comb of modified (clubbed) setae apically (Pleganophorinae) . . . . . *Trochoideus*
  - Stemmata 3 or 4; mala usually with spines or simple setae apically (Lycoperdinae, major part; Epipocinae, Stenotarsinae) . . . . . **17**
  17. Body broadly oval, onisciform, apparently glabrous; tergal and pleural lobes absent; all spiracles placed dorsally . . . . . *Amphix*
  - Body elongate-oval, usually with tergal and/or pleural lobes or parascoli; abdominal spiracles placed under tergal prominences, not visible from above; vestiture with modified setae . . . . . **18**
  18. Abdominal segments bearing a large lateral tergal and often pleural lobes, each lobe with area of highly modified multiply barbed or spinose setae (lobes often dehiscent) . . . . . **20**
  - Abdominal segments without large fleshy lobes, often with parascoli bearing simple setae (Stenotarsinae ?) . . . . . **19**
  19. Thoracic segments each bearing a parascolus near midpoint of lateral margin . . . . . *Saula*
  - Thoracic segments bearing setiferous tubercles at midpoint of lateral margin . . . . . *Stenotarsus*
  20. Thoracic and abdominal terga each bearing narrow, elongate and easily dehiscent setiferous process; mala somewhat falcate (?) . . . . . **21**

- Thoracic and abdominal terga with broad fleshy processes, than may or may not be dehiscant; mala blunt apically ..... 22
- 21. Head broadened behind the antennal fossae (error ?); lateral lobes blunt apically; antennomere 2 densely spinose in basal half ..... *Ancylopus*
- Head not distinctly bulged behind antennal fossae; lateral lobes pointed apically; antennomere 2 without spines (?) at base ..... *Eumorphus*
- 22. Labrum serrate along anterior margin .. *Mycetina*
- Labrum smooth anteriorly ..... 23
- 23. Labial palps 2-segmented; prostheca hyaline; mandibular ventral accessory process absent (?); head less transverse and the antennal sockets placed about mid length of head; antenna shorter ? ..... *Aphorista*
- Labial palps 1-segmented; prostheca with large tuft of setae in addition to the membrane; ventral accessory process of mandible present; head strongly transverse, and antennal articulations distinctly posterior; antenna longer ? ..... 24
- 24. Mesothorax and metathorax bearing a rounded tergal lobe and pleural lobe laterally ..... 25
- Mesothorax and metathorax bearing only large pleural lobe at lateral margin ..... *Epipocus*
- 25. Median line visible on thoracic and abdominal terga; abdominal lateral lobes large, directed laterad, completely concealing pleural lobes in dorsal view; abdominal terga with longitudinal pale ecdysial line ..... *Anidrytus*
- Median line not visible on abdominal terga; abdominal lateral tergal lobes smaller, directed dorsolaterad, pleural lobes visible in dorsal view; ecdysial line not visible on abdominal terga ..... *Ephebus*

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