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A review of the Trogossitidae Part 2: Larval morphology, phylogeny and taxonomy (Coleoptera, Cleroidea)

by Jiří Kolibáč

Abstract. All the known larvae of Trogossitidae are reviewed, seven of them are figured and redescribed. Larval and adult characters of all trogossitid genera are analyzed, employing the NONA program. Two new tribes are established in the subfamily Peltinae: Ancyronini trib.nov. and Colydiopeltini trib.nov. All the other genera are also re-classified within newly defined tribes. The following phylogenetic system for the family Trogossitidae is proposed: [Trogossitinae (Calitini + ((Larinotini + Egoliini) + (Gymnochilini + Trogossitini)))] + [Peltinae (Colydiopeltini + Peltini + Thymalini) + (Decamerini + (Ancyronini + Lophocaterini))]. Three subfamilies are synonymized with the tribe Thymalini Léveillé, 1888: Rentoniinae Crowson, 1966 syn.nov., Protopeltinae Crowson, 1970 syn.nov. and the Mesozoic subfamily Meligethiellinae Kireitshuk et Ponomarenko, 1990 syn.nov. The tribe Lycoptini Casey, 1890 syn.nov. (Coleoptera: Colydiidae) is synonymized with the tribe Lophocaterini Crowson, 1964. Higher taxa of the family Trogossitidae are listed, together with their name-bearing types.

Key words. Coleoptera – Cleroidea – Trogossitidae – morphology of larvae – new tribes – synonymy – taxonomy – phylogeny

Introduction

The morphology of adults of the trogossitid genera was described and figured in the first part of this communication (KOLIBÁČ 2005). The main aim of the present work is to present an overview of the larval morphology, to analyze both larval and adult characters and to propose a higher system for the family Trogossitidae. The biogeography of, and keys to, the particular taxa will be addressed in a later communication.

Methods

Standard dissection methods were employed throughout. This communication has been around 10 years in the creation, so the drawing techniques have changed over time. Some of the illustrations were drawn through an ocular grid in a binocular microscope or a compound microscope, while the most recent illustrations were made using a camera lucida. Both drawings and photographs were made by the author.

The NONA program (GOLOBOFF 1999) in conjunction with WinClada (NIXON 1999–2002) software were used for a character analysis and construction of cladograms. The heuristic analysis (maximum trees to keep = 1000, number of replications = 10, multiple TBR+TBR) was used. The Matrix 1 was optimized by the accelerated optimization (ACCTRAN) and re-counted. Characters were not weighted; strict consensus was used. Tree 1 is a result. Because Tree 1 includes a large amount of homoplasies, both major branches (the subfamilies Trogossitinae and Peltinae) were once more analyzed separately. The uninformative characters were deleted first and

the both matrices were re-counted and re-optimized by ACCTRAN. Matrix 2 and Tree 2 are the results for the Trogossitinae, Matrix 3 and Tree 3 for the Peltinae (excl. the fully resolved cluster Colydiopeltini-Peltini-Thymalini). The Matrix 3 was re-weighted (weight = 10 for characters 2, 30, 31, 34) in view of a supposed paraphyly for the tribe Lophocaterini. The final Tree 4 better expresses monophyly of Ancyronini trib.nov. and Lophocaterini.

Overview of known larvae of the family Trogossitidae

***Acalanthis* Erichson, 1844**

Species: *Acalanthis* sp.: CROWSON (1964: 299) (supposed larva, described as *Phanodesta* Reitter, 1876).

See character matrices for description.

***Airora* Reitter, 1876**

Species: *Airora cylindrica* (Serville, 1828): BÖVING & CRAIGHEAD (1931: 273, Pl. 93).

See character matrices for description.

***Calitys* Thomson, 1859**

Species: *Calitys scabra* (Thunberg, 1784): BÖVING & CRAIGHEAD (1931: 275, Pl. 94); KLAUSNITZER (1996: 156).

See character matrices for description.

***Corticotomus* Sharp, 1891**

Species: *Corticotomus cylindricus* (Leconte, 1863): BÖVING & CRAIGHEAD (1931: 273, Pl. 93).

See character matrices for description.

***Diontolobus* Solier, 1849**

Species: *Diontolobus* sp.: CROWSON (1964: 291). (supposed larva)

See character matrices for description.

Egoliinae gen., sp.

(Pls 1–2)

Species: A mature larva from Tasmania described by SLIPINSKI (1992: 360), redescribed here.

Addendum to the matrices. Gula as long as half of capsule, with 2 long setae; hypostomal rods long, extending to base of capsule; mandible with medial tooth; mala bilobed, basal piece weakly sclerotized; cardo pigmented; prementum divided and

membraneous, probably partially coalescent with postmentum; postmentum as large as cardo and stipes together; epipharynx oval, without clavate sensillae; torma composed of rigid plate with 2 pigmented areas along lateral margins; abdominal segment IX with large, concave dorsal sclerite, bordered by raised rim; ampullae situated along urogomphi; spiracles annular; pubescence long and sparse.

Biology: Found “under bark and in rotten log”.

***Eronyx* Reitter, 1876**

Species: *Eronyx* *expansus* Van Dyke, 1916: TAIT *et al.* (1990: 13).

See character matrices for description.

***Grynocharis* Thomson, 1859**

Species: *Grynocharis oblonga* (Linnaeus, 1758): KLAUSNITZER (1996: 164).

Grynocharis pubescens (Erichson, 1844): MAMAEV (1976: 1656).

See character matrices for description.

***Grynomia* Sharp, 1877** (Pl. 30)

Species: *Grynomia varians* Broun, ?: CROWSON (1964: 299).

See character matrices for description.

***Larinotus* Carter et Zeck, 1937**

Species: *Larinotus umblicatus* Carter et Zeck, 1937: SLIPINSKI (1992: 455).

See character matrices for description.

***Leperina* Erichson, 1844**

Species: *Leperina squamulosa* (Gebler, 1830): MAMAEV (1976: 1651).

See character matrices for description.

***Lophocateres* Olliff, 1883** (Pls 3–4)

Species: *Lophocateres pusillus* (Klug, 1832): reared in laboratory.

Addendum to the matrices. Gula conspicuous, not divided, extending to 2/3 of capsule; paragular sclerites absent; hypostomal rods long, extending to base of capsule; mandible with medial tooth; maxillary palpi 3-segmented, short; mala membraneous, sparsely pubescent, with small sclerite at base; labial palpi cylindrical; prementum small, weak; postmentum indistinctly transversely divided, as large as cardo and stipes together;

epipharynx transverse, oval, without clavate sensillae; torma H-shaped, partially pigmented; median process between urogomphi with glandular opening; ampullae absent; spiracles annular; four malpighian glands observed; pubescence sparse, relatively long; body whittish.

Biology: in stored products, especially grains.

***Melambia* Erichson, 1844**

Species: *Melambia tekkensis* Koenig, 1889: MAMAEV (1976: 1650).

See character matrices for description.

***Nemozoma* Latreille, 1824**

Species: *Nemozoma elongatum* (Linnaeus, 1761): KLAUSNITZER (1996: 149); MAMAEV (1976: 1650); NIKITSKY (1974: 566); RUSSO (1938: 105).

Nemozoma caucasicum Ménétričs, 1832: MAMAEV (1976: 1653); NIKITSKY (1974: 566).

Nemozoma cornutum Sturm, 1826: MAMAEV (1976: 1654); NIKITSKY (1974: 566).

See character matrices for description.

***Paracalanthis* Crowson, 1970 (Pl. 1)**

Species: *Paracalanthis binnaburrense* Crowson, 1970: CROWSON (1970: 16) (supposed larva).

Partly redescribed here (Pl. 1 and the character matrices).

***Peltis* O. F. Müller, 1764 (Pls 5–6, 14)**

Species: *Peltis grossa* (Linnaeus, 1758): KLAUSNITZER (1996: 157); MAMAEV (1976: 1656).

Peltis ferruginea (Linnaeus, 1758): "Czechia, Šumava Mts.", redescribed here.

Addendum to the matrices. Frontal arms Y-shaped, not reaching base of capsule; gular sutures present but indistinct, weakly curved; three indistinct stemmata (1 posterior + 2 anterior); mandible with large medial tooth; lacinia mandibulae absent (extremely minute ciliation perhaps present in upper part of mola); mala with thick setae, with large pigmented (sclerotized) plate at base – this sclerite with protrusion from inner margin; cardo transverse, stipes relatively small but distinct; ligula with 2 longitudinal rows of setae; labial palpi cylindric; prementum soft, with pigmented middle part; postmentum membranous; epipharynx oval, with clavate sensillae; trochanter elongate, with armature at base; abdominal segment IX not sclerotized, not pigmented; urogomphi minute, dorsally situated; ampullae absent; spiracles annular; pubescence short, dense; body whittish.

Biology: in rotten wood of *Abies*, *Picea* and other old trees, including deciduous.

Note. The larva of *P. grossa* is nearly identical. It is another piece of evidence for synonymization of the former genus *Ostoma* Laicharting, 1781 (KOLIBÁČ 2005).

***Promanus* Sharp, 1877**

Species: *Promanus depressus* Sharp, 1877: CROWSON (1964: 298).

See character matrices for description.

***Protopeltis* Crowson, 1964**

Species: *Protopeltis viridescens* (Broun, 1886): CROWSON (1964: 290).

See character matrices for description.

Rentoniinae gen., sp.

Species: Rentoniini Crowson, 1966 (?*Rentonium daldinia* Crowson, 1966): CROWSON (1966: 123)
(supposed larva).

See character matrices for description.

***Temnoscheila* Westwood, 1830**

Species: *Temnoscheila caerulea* (Olivier, 1790): KLAUSNITZER (1996: 150); MAMAEV (1976: 1651).

Temnoscheila virescens (Fabricius, 1775): BÖVING & CRAIGHEAD (1931: 273, Pl. 93).

Temnoscheila japonica Reitter, 1875: MAMAEV (1976: 1650).

Temnoscheila sp.: COSTA *et al.* (1988: 177).

See character matrices for description.

***Tenebroides* Piller et Mitterpacher, 1783**

(Pls 7–10)

Species: *Tenebroides turkestanicus* Ballion, 1870: MAMAEV (1976: 1654).

Tenebroides nanus (Melsheimer, 1844): BÖVING & CRAIGHEAD (1931: 273).

Tenebroides mauritanicus (Linnaeus, 1758): “Czechia, Brno, found in bakery”, redescribed here
(Pls 7–8).

Tenebroides fuscus Goeze, 1777: KLAUSNITZER (1996: 151); a specimen from “SE Bulgaria,
Michurin, Khasekiyata, J. Kolibáč leg.” described here (Pls 9–10).

Addendum to the matrices (*Tenebroides mauritanicus*). Frontal arms V-shaped, straight; epicranial stem short, key “^”-like; gula as long as half of capsule; hypostomal rods extending beyond halfway along capsule; mandible with weak medial tooth; lacinia mandibulae composed of about 5 long, rigid spines; cutting edge convex; maxillary mala consisting of one part, with 2 pigmented plates, moderately pubescent; ligula conspicuous, sparsely pubescent; prementum distinct, with shallow notch in middle; postmentum as long as stipes; epipharynx oblong, lateral margins evenly rounded, with clavate sensillae; trochanter with distinct internal armature; abdominal segment IX dorsally sclerotized; ampullae absent; spiracles annular-biforous; six malpighian glands; body pubescence long, dense; body whitish.

Biology: in stored food (flour, grains).

Addendum to the matrices (*Tenebroides fuscus*). Frontal arms V-shaped, straight; epicranial stem very short; gula shorter than half of cranium, with 2 long setae; hypostomal rods extending to half of cranium; mandible with small medial tooth; lacinia mandibulae composed of about 5 long, rigid spines; cutting edge present, straight; pedunculate seta not observed – mala densely pubescent, perhaps seta not seen; labial palpi coniform; postmentum shorter than stipes; epipharynx oblong, without clavate sensillae; trochanter narrow, internal armature large; abdominal segment IX dorsally sclerotized; single ampulla situated at outer margin of each urogomphus; body pubescence long, sparse; body pink; body size 6 mm.

Biology: The larva was found on the bark of a dry oak branch, together with adults of *Clerus mutillarius* (Fabricius, 1775). Certainly predatory.

Note. The larva was not associated with adults. It possesses all the most significant trogossitine features and it is very similar to *T. mauritanicus*, although there are some differences between the species (see Pls 7–10). The larva does not belong to *Nemozoma* (all three European species have been described). The only possible other trogossitine species, possibly occurring in southeastern Bulgaria, is *Seidlitzella procera* Kraatz, 1858, of which the larva is unknown. The last European species of Trogossitidae with unknown larva is *Ancyrona japonica* Reitter, 1889, also recorded from Bulgaria. The species is classified within Peltinae, Ancyronini trib.nov. in this communication and the presence of trogossitine features (such as e.g. parangular sclerites) would be surprising. On the other hand, the habitat of this larva is characteristic for the species *A. japonica*.

Thymalus Latreille, 1802

(Pls 11–13)

Species: *Thymalus limbatus* Fabricius, 1802: KOLIBÁČ (2002: 55). A mature larva from “Czechia, Beskydy Mts., J. Kolibáč lgt.”, redescribed here.

Thymalus marginicollis Chevrolat, 1842: BÖVING & CRAIGHEAD (1931: 273).

Addendum to the matrices. Frontal arms V-shaped, slightly curved; remains of epicranial stem present; frontoclypeal suture present; gular sutures inconspicuous: weak and short sutures present only in anterior part of gula (*T. marginicollis* with gular sutures complete, strongly convergent); gula narrow, inconspicuously bordered by sutures, anteriorly with 2 large apodemes; mandible with ventral apical tooth small; medial tooth present; lacinia mandibulae inconspicuous or absent (single spine present in *T. marginicollis*); cutting edge straight; maxillary palpi weakly coniform; prementum oblong; epipharynx oblong, with evenly rounded lateral margins and with clavate sensillae; abdominal segment IX seemingly transversely divided; urogomphi large, tuberculate, with several projections; spiracles annular-biforous; pubescence long, sparse (shorter pubescence in *T. marginicollis*); body whitish. Body size ca. 9 mm.

Biology: Mature larva found on fir (*Abies alba*), under a scale of a bark. It may also live in rotten wood.

Character	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	
Taxon	1 2 3	4 5 6 7 8 9 0 1 2	3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1	2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1	2 3 4 5 6 7 8 9 0 1 2 3 4																					
<i>Acalanthis</i>	1 1 1	0 1 0 0 1 0 0 0 0	1 0 1 0 0 1 0 1 0 0 0 1 1 0 0 1 1 2 1	1 1 1 0 2 1 1 1 0 1 0 1 1 1 0 1 0 1 1 1	0 0 0																					
<i>Aiora</i>	1 1 1	0 1 0 0 1 3 0 1 2	0 0 0 1 1 1 0 0 0 0 0 0 1 1 0 0 2 1 3 0	1 1 1 0 1 1 1 0 0 0 0 0 1 1 1 0 0 1 1 1	0 0 0																					
<i>Alindria</i>	1 2 1	0 1 1 0 1 3 0 1 2	0 0 0 1 0 1 0 0 0 2 0 1 1 0 0 2 1 3 0	1 1 1 0 0 1 0 0 0 1 0 0 1 0 0 1 1 0 1 1	0 0 0																					
<i>Anacypta</i>	0 0 1	0 0 0 1 2 1 0 2 2	2 0 1 0 1 0 2 0 0 2 2 0 0 0 0 0 1 0 3 1	1 1 1 0 0 1 0 0 1 0 0 2 0 1 0 1 1 0 1 1	0 0 0																					
<i>Ancyrona</i>	0 1	[02]	0 1 0 0 1 1 0 2 0	1 0 0 0 0 2 2 0 2 2 0 0 0 0 1 0 0 2 1	2 0	0 1																				
<i>Calanthosoma</i>	1 1 1	0 1 1 0 1 0 0 0 1	2 1 1 0 1 0 0 0 1 0 1 0 1 0 3 0	1 1 1 0 2 1 1 1 0 1 0 1 0 0 0 0 0 0 0 0 0	0 0																					
<i>Calitys</i>	0 0 0	0 0 0 0 0 1 0 0 0 1	1 0 1 0 0 0 0 0 0 2 0 0 2 0 2 0 2 0	0 0 1 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0	0 1																					
<i>Colydiopeltis</i>	2 0 1	0 0 0 0 1 0 0 0 0	[01]	4 0 2 0 2 0 0 1 2 2 0 0 4 0 1 0 0 3	- 0 0 0 0 0 0 0 0 1 0 1 0 1 0 1 1 0 1 1	0 1																				
<i>Corticotomus</i>	1 1 1	0 0 0 0 1 0 0 1 2	0 1 0 1 0 1 0 0 0 2 0 1 1 1 0 0 1 0 1 0	1 1 1 0 1 1 1 0 0 0 0 1 0 0 1 1 0 1 1 0 1	0 0																					
<i>Decamerus</i>	0 0 0	0 0 0 0 0 1 0 2 2	0 0 1 0 0 0 0 0 2 0 2 0 5 0 1 0 1 2 1 2	2 0 0 0 0 0 0 0 0 2 0 0 0 0 0 2 0 1 0 0 2 0 1	1 0																					
<i>Diontobelus</i>	0 0 0	0 0 0 0 0 1 0 2 2	1 0 0 0 0 0 0 1 0 0 0 0 4 0 1 0 1 2 0	2 0 1 0 0 0 0 0 0 2 0 0 0 0 0 2 0 1 0 0 2 0 1	1 0																					
<i>Egolia</i>	1 1 1	0 0 0 1 0 0 0 0	1 0 1 0 0 0 0 1 0 0 0 1 1 0 0 1 2 1 2	1 1 1 0 2 1 1 1 0 0 1 0 0 1 1 0 1 1 0 1 1 0 0	0 0																					
<i>Eronyma</i>	0 0 0	0 0 0 0 0 1 0 0 0	4 0 0 0 0 0 0 0 2 0 0 0 5 0 1 0 1 0 0	0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 2 0 0 0 0 0 2 0 1	1 0																					
<i>Grynocharina</i>	0 0 0	0 0 0 0 1 1 0 0 3	1 0 0 0 0 2 2 0 1 2 0 0 4 0 1 0 0 2 2	2 0 0 0 0 0 0 0 0 2 0 0 0 0 0 2 0 0 0 0 0 2 0 0	0 0																					
<i>Grynocharis</i>	0 0 2	0 0 0 0 1 0 0 1 0	1 0 0 0 0 1 0 0 2 0 0 2 0 1 0 0 3 0	2 0 0 0 0 0 0 0 0 2 0 0 0 0 0 2 0 0 0 0 0 2 0 0	0 0																					
<i>Gynoma</i>	0 0 0	0 0 0 0 0 1 0 0 2	1 0 1 0 0 2 2 0 2 2 1 0 0 1 0 0 3 1	2 0 0 0 0 0 0 0 0 2 0 0 0 0 0 2 0 0 0 0 0 2 0 1	1 0																					
<i>Gymnochila</i>	1 2 1	0 0 1 1 1 2 1 1 2	2 0 2 1 2 0 0 0 2 1 0 1 0 0 0 0 0 0 0	1 1 1 0 0 1 1 0 2 1 1 0 0 0 0 0 0 0 0 0 0	0 1																					
<i>Indopeltis</i>	0 0 1	0 0 0 0 0 1 0 0 1	0 0 0 0 0 1 0 0 0 0 0 1 0 1 2 0	2 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0	0 0																					
<i>Larinotus</i>	2 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 1 0 2 2 0 0 2 0 0 0 3 2	0 0 1 0 0 0 1 1 1 0 0 0 3 2 0 0 0 0 0 0 0 0 0	0 0																					
<i>Latolaeva</i>	0 1 0	0 1 0 0 1 1 0 2 0	1 0 0 0 0 2 2 0 2 2 0 0 0 1 0 0 2 1	2 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0	0 0																					
<i>Leipaspis</i>	1 0 1	0 0 0 0 0 1 3 0 0 2	0 1 0 1 0 2 0 0 0 2 0 1 1 1 0 0 1 1 0 1 0	1 1 1 0 1 1 0 0 0 0 0 1 1 0 0 0 0 0 1 1 0 1 0	0 0																					
<i>Leperina</i>	1 0 1	0 1 0 0 1 2 0 1 2	2 0 2 0 0 1 0 0 2 2 0 2 1 1 0 0 0 3 0	1 1 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 0	0 1																					
<i>Leptonyxa</i>	0 0 1	0 1 0 0 0 1 0 2 2	0 0 2 0 0 2 1 1 0 2 1 0 0 0 0 0 0 0 0 1	2 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0	0 0																					
<i>Lophocateres</i>	0 0 2	0 0 0 0 0 1 0 0 3	1 0 0 0 0 0 1 0 2 0 0 4 0 1 0 0 3 0	2 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0	0 0																					
<i>Lycoptis</i>	0 0 2	0 0 0 0 0 1 0 0 3	0 0 1 0 0 0 1 0 2 0 0 4 0 1 0 0 3 0	- 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0	0 0																					
<i>Melambia</i>	1 2 1	0 0 1 0 1 3 0 0 2	2 0 2 1 1 2 0 0 0 0 0 1 1 0 0 1 1 0 0	1 1 1 0 0 1 0 0 0 0 0 1 1 0 0 1 0 2 1 0	0 0																					
<i>Narcisa</i>	0 1 1	0 0 0 0 1 2 1 2 2	2 0 2 0 1 2 2 0 0 0 0 2 1 1 0 0 1 0 0 0	1 1 1 0 0 1 0 0 0 0 0 1 1 0 0 1 0 0 0 1 1	0 1																					
<i>Neaspis</i>	0 0 1	0 0 0 0 0 0 0 2 2	1 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 2 1	0 0	0 1																					
<i>Necrobiopsis</i>	2 1 0	0 0 0 0 1 1 0 0 0	0 0 0 0 0 1 1 0 0 0 0 2 0 1 1 0 1 0 2 3	- 1 1 1 0 0 1 1 2 1 0	0 0																					
<i>Nemozoma</i>	1 0 1	1 1 0 0 1 3 0 0 2	0 1 2 0 1 2 1 0 0 0 0 1 0 1 1 0 1 0 0	[01] 1 1 1 0 1 1 0 0 0 0 0 1 1 0 0 1 0 2 1 1	0 0																					
<i>Parapeltis</i>	2 0 1	0 0 0 0 1 0 0 0 2	0 0 2 0 0 0 0 0 1 2 0 0 4 0 1 0 0 3	- 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0	0 1																					
<i>Peltis</i>	0 3 2	0 0 0 0 1 0 0 0 1	0 0 1 0 0 0 1 0 2 0 0 0 2 0 1 0 1 3 0	0 0	0 0																					
<i>Peltonyxa</i>	0 0 2	0 0 0 1 0 0 0 0 2	4 0 0 0 0 0 2 1 0 2 0 0 0 3 0 1 0 1 2 2	2 0	[01] 0 0																					
<i>Phanodesta</i>	1 2 1	0 1 0 0 0 1 3 0 1 2	2 0 2 0 1 1 0 0 0 2 0 1 1 0 0 2 0 0 0 0	1 1 1 0 0 1 0 0 0 2 0 1 1 0 0 1 0 0 0 1 1	0 0																					
<i>Promanus</i>	0 0 2	0 0 0 0 1 0 1 0 2 0	1 0 2 0 0 0 2 0 0 2 0 0 3 0 1 0 1 2 0	2 0	0 0																					
<i>Protopeltis</i>	0 3 1	0 0 0 0 0 1 0 1 0 3	0 0 0 0 0 1 1 0 0 0 0 2 0 1 1 2 0 1 0 0 0	- 0 1 0	0 0																					
<i>Rentonellum</i>	3 3 0	0 0 0 0 0 1 1 0 2 2	3 0 2 0 0 0 1 0 2 2 0 0 0 0 0 0 0 0 0 3 1	0 0 0 1 0 1 1 0 1 0 1 0 1 0 1 0 1 0 1 0 1 0 1	1 0																					
<i>Rentonium</i>	3 3 1	0 0 0 0 0 1 1 0 2 -	- - - 2 1 1 0 2 2 0 0 0 0 0 0 0 0 0 2 1	0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	- 2 0 1																					
<i>Seiditzella</i>	1 0 1	0 1 1 0 0 1 3 0 0 2	2 0 0 1 1 2 0 0 0 2 2 0 0 1 1 0 0 1 0 0 0	1 1 1 0 0 1 0 0 0 2 0 1 1 0 0 1 1 0 0 0 1 0 0	0 0																					
<i>Temnoscheila</i>	1 2 1	1 1 1 0 0 1 3 0 1 2	0 1 0 1 1 2 0 0 0 2 0 1 1 0 0 1 0 1 0 3 0	1 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0																					
<i>Tenebroides</i>	1 0 1	0 1 0 0 0 1 3 0 0 2	0 1 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0																					
<i>Thymalus</i>	2 3 1	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 1 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0	0 0																					
<i>Xenoglena</i>	1 1 1	0 0 0 1 1 2 1 2 2	2 0 2 0 1 1 2 0 2 0 1 1 0 0 0 0 0 0 0 0 0 0	1 1 1 0 0 1 0 0 2 1 1 0 0 0 0 0 0 0 0 0 0 0 0	0 1																					

Character	4	5	6	7	8
Taxon	5 6	7 8 9 0 1 2 3 4	5 6	7 8 9 0 1 2 3 4	

Phylogeny of the family Trogossitidae

List of characters for Matrix 1 (Trogossitidae)

Adult characters

01. **Body shape:** flat=0; elongate=1; convex (not conglobate)=2; conglobate=3. [nonadditive]
02. **Gular sutures:** wide, convergent at apex=0; narrow, subparallel at apex=1; reduced=2; wide, subparallel=3. [nonadditive]
03. **Frontoclypeal suture:** present=0; absent=1; broadly emarginate=2. [nonadditive]
04. **Frons - longitudinal groove or depression:** absent=0; present=1.
05. **Cranium ventrally - tufts of long setae at sides:** absent=0; present=1.
06. **Submentum of males - tuft of setae:** absent=0; present=1.
07. **Submentum - anterior margin with row of setae:** absent=0; present=1.
08. **Antennal groove:** absent=0; present=1. [deactivated]
09. **Eyes - size, position:** moderate=0; large, lateral=1; large, dorsal=2; flat=3. [nonadditive]
10. **Eyes - number:** 2=0; 4=1.
11. **Epicranial acumination:** moderate=0; deep=1; absent=2. [nonadditive] [deactivated]
12. **Lacinia - hooks:** 2=0; 1=1; 0=2; 3=3. [nonadditive] [deactivated]
13. **Galea - shape:** elongate=0; sub-clavate=1; clavate=2; partially fused with lacinia=3; very small=4. [nonadditive]
14. **Galea - ciliate setae:** absent=0; present=1.
15. **Mediostipes - lacinia:** not fused=0; partially fused=1; fused together=2. [additive] [deactivated]
16. **Palpifer - outer edge:** even=0; denticulate=1.
17. **Mandible, apical teeth - number, position:** 2 in horizontal axis=0; 2 in vertical axis=1; 1=2. [additive]
18. **Mola:** present=0; reduced but present=1; absent=2. [additive]
19. **Penicillus (at base):** present (fine, often membranous)=0; absent=1; long setae=2. [nonadditive]
20. **Pubescence above mola or cutting edge:** absent=0; present=1. [deactivated]
21. **Ventral ciliate furrow:** furrow ciliate=0; furrow not ciliate=1; absent=2. [additive] [deactivated]
22. **Basal notch:** moderate=0; deep=1; shallow or absent=2. [additive] [deactivated]
23. **Labrum - cranium:** not fused=0; fused=1.
24. **Epipharynx - sclerite:** absent=0; present=1.

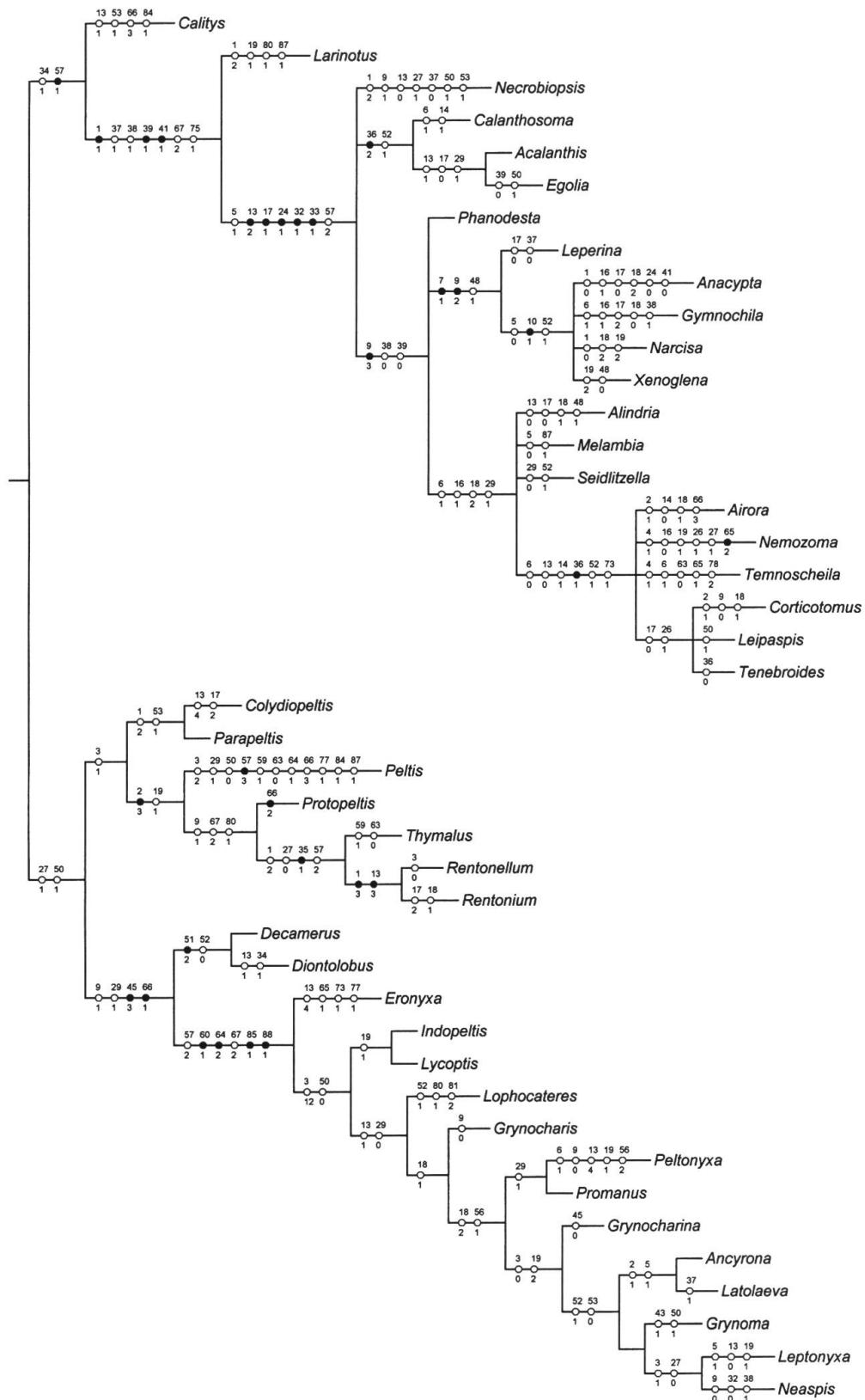
25. **Lateral tormal process - projection:** projection not developed=0; curved downwards, processes not connected (*Airora*)=1; curved downwards, processes with bridge (*Peltis*)=2; projection reduced or absent (*Pro manus*)=3; projection curved upwards (*Colydiopeltis*)=4; projections extending laterally and downwards (*Eronyx*)=5. [nonadditive] [deactivated]
26. **Ligula - ciliate setae:** absent=0; present=1.
27. **Ligula:** rigid=0; membranous=1.
28. **Ligula:** not retroflexed=0; weakly retroflexed=1; strongly retroflexed=2. [additive] [deactivated]
29. **Ligula - shape:** weakly emarginate=0; deeply emarginate=1.
30. **Hypopharyngeal sclerite:** absent=0; sickle shaped=1; H-shaped=2; 2 separate sclerites=3. [nonadditive] [deactivated]
31. **Antenna:** 11-segmented=0; 10-segmented=1; 9-segmented=2; 8-segmented=3; 7-segmented=4. [nonadditive] [deactivated]
32. **Antennal club:** symmetrical=0; asymmetrical=1; weakly asymmetrical=2. [nonadditive]
33. **Antenna - sensorial fields:** absent=0; present=1.
34. **Front coxal cavities externally:** open=0; closed=1.
35. **Front coxal cavities internally:** open=0; closed=1.
36. **Pronotum - shape:** transverse=0; elongate=1; cordate=2. [nonadditive]
37. **Prepectus:** present=0; absent=1.
38. **Middle coxal cavities:** open=0; closed=1.
39. **Elytra - long hairs:** absent=0; present=1.
40. **Epipleure:** moderate=0; wide=1; thin=2. [nonadditive] [deactivated]
41. **Elytral lock:¹⁾** absent=0; present=1.
42. **Elytra - carinae:** conspicuous=0; reduced=1. [deactivated]
43. **Elytra - punctuation:** regular=0; irregular=1.
44. **Elytra - scales:** absent=0; present=1. [deactivated]
45. **Wing - radial cell:** oblong (or reduced)=0; triangular=1; open (outer vein present)=2; cell moved down, often small=3. [nonadditive]
46. **Wing - wedge cell:** present=0; absent=1; small (*Peltis*)=2. [nonadditive] [deactivated]
47. **Wing - cross vein MP3-4:** present=0; absent=1. [deactivated]
48. **Wing - cross vein AA1+2-3+4:** absent=0; present=1.
49. **Front tibiae - spines along side:** moderate=0; large=1; reduced=2. [nonadditive] [deactivated]
50. **Front tibiae - hooked spur:** present=0; absent, apical spurs not hooked or weakly hooked=1.

¹⁾ The elytral lock is the widened edge of the elytral suture near an elytral apex. These widened edges of the both elytra mesh together and close the elytra even in dry (prepared) specimens.

51. **Claws - denticle:** absent=0; small=1; distinct=2. [nonadditive]
52. **Parasternites in sternites III-VII:** absent=0; one=1; two=2. [nonadditive]
53. **Spiculum gastrale (male sternite VIII):** absent=0; present=1.
54. **Tegmen - number of parts:** 3 parts=0; 2 parts=1; 1 part=2. [nonadditive] [deactivated]
55. **Coxitae:** divided=0; undivided=1. [deactivated]
56. **Biology:** herbivorous or fungivorous=0; predatory=1; floricolous=2. [nonadditive]

Larval characters

57. **Frontal arms:** curved (cucujoid)=0; weakly curved=1; V-shaped=2; Y-shaped=3. [nonadditive]
58. **Epicranial stem:** present=0; reduced=1; absent=2. [additive] [deactivated]
59. **Endocarina:** present=0; absent=1.
60. **Gular sutures:** conspicuous, parallel=0; conspicuous, convergent=1; inconspicuous=2. [nonadditive]
61. **Gula - anterior apodemes:** present=0; absent=1.
62. **Parangular sclerites:** absent=0; present=1.
63. **Hypostomal rods:** absent=0; present=1.
64. **Stemmata:** 5=0; 3=1; 2=2. [nonadditive]
65. **Mandible, apical teeth - number, position:** two, situated in horizontal axis=0; two, situated in horizontal or even vertical axes=1; one tooth=2. [additive]
66. **Lacinia mandibulae:** several small spines=0; plumose=1; tridentate=2; absent=3. [nonadditive]
67. **Mola:** present=0; reduced=1; absent=2. [additive]
68. **Maxillary palpi:** 3-segmented=0; 2-segmented=1. [deactivated]
69. **Palpifer:** present=0; absent=1.
70. **Pedunculate seta:** absent=0; present=1.
71. **Mala:** simple=0; bilobed=1. [deactivated]
72. **Mala - bidentate protrusion:** absent=0; present=1.
73. **Cardo - stipes:** not fused=0; partially fused=1.
74. **Cardo - size:** much smaller than stipes=0; nearly as large as stipes=1.
75. **Ligula:** present=0; absent=1.
76. **Labial palpi:** 2-segmented=0; 1-segmented=1. [deactivated]
77. **Prementum:** in single part=0; in two parts=1.
78. **Prementum - anterior margin:** even=0; with notch=1; projecting=2. [nonadditive]
79. **Torma:** single compact plate=0; two separate lateral sclerites=1; H-shaped=2. [nonadditive]



Tree 1. Trogossitidae (Matrix 1). Under equal weights: 25 characters deactivated, 2 deactivated characters uninformative (68, 76); number of characters = 88, activated = 63, nonadditive = 19, additive = 69. NONA: heuristic analysis; strict consensus of 48 trees, L = 287, Ci = 33, Ri = 64.

80. **Antenna:** joints 1-2 elongate=0; joints 1-2 transverse=1; 1st transverse, 2nd elongate=2. [nonadditive]
81. **Sensory appendix:** medium-sized (to half of joint 3)=0; very small=1; longer than half of joint 3=2. [nonadditive]
82. **Thoracic sclerites pattern (dorsally):** 1-2-2=0; 1-0-0=1; 0-0-0=2; 2-0-0=3. [nonadditive] [deactivated]
83. **Thoracic sclerites pattern (ventrally):** 3-1-1=0; 1-1-1=1; 1-0-0=2; 0-0-0=3; 2-0-0=4. [nonadditive] [deactivated]
84. **Trochanter:** triangular=0; oblong=1.
85. **Abdominal segment IX:** not divided=0; transversely divided=1.
86. **Tergite IX:** flat=0; depressed=1.
87. **Urogomphi:** present, hooked=0; minute=1.
88. **Urogomphi - median process:** absent=0; present=1.

Character	0	1	2	3	4
Taxon	1 2 3	4 5 6 7 8 9 0 1 2	3 4 5 6 7 8 9 0 1 2 3	4 5 6 7 8 9 0 1 2 3 4	2 3 4 5 6 7 8 9 0 1 2 3 4
<i>Antixoon</i>	0 - -	0 0 - 0 0 - 0 -	- - - - - 0 1 0 0 0 0	- - - - - - - - - -	0 0 1 - 0 - - 0 - - -
<i>Australiodes</i>	3 - -	0 0 - 0 - 0 - 2	3 0 2 - - - - - 0	- - - - - - - - - -	- - 0 1 0 - - 0 - - -
<i>Dupontiella</i>	- - -	- 0 - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -
<i>Elestora</i>	0 0 1	0 0 1 - 1 3 0 -	- - - - 2 - - - - 0 - - -	- - - - - - - - - - 0	1 1 1 0 3 1 0 0 0 1 0 0 0
<i>Eupycnus</i>	1 0 -	0 1 0 - 1 3 0 0	- - - - 1 2 - - - 0 - -	- - - - 1 0 0 0 3 0	1 1 1 0 0 1 0 0 0 1 1 0 0
<i>Euschaefferia</i>	1 - -	- 0 - - - - - -	- - - - - - - - - -	- - - - - - - - - -	1 - - - 1 - - 0 - - 1 1 0
<i>Paracalanthis</i>	1 - 1	0 - - - 1 0 0 -	- - - - - - - - - -	- - - - - - - - - -	1 - - 1 0 2 - - 1 1 2 - 1 0 0
<i>Parallelodera</i>	1 0 0	1 1 0 - 1 3 0 -	- - - - 1 - - - - - -	- - - - - - - - - - 0	1 1 1 0 0 1 0 0 2 1 1 0 0
<i>Parentonium</i>	3 3 0	0 0 0 - 1 1 0 2 2	3 0 2 1 - - - - - -	- - - - - - - - - -	- - 0 1 0 - - 0 1 0 - - 0
<i>Rentonidium</i>	3 - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -

Character	4	5	6	7	8
Taxon	5 6	7 8 9 0 1 2 3 4	5 6	7 8 9 0 1 2 3 4 5 6	7 8 9 0 1 2 3 4 5 6 7 8
<i>Antixoon</i>	- - -	- - - - 2 - - -	- 2	- - - - - - - - -	- - - - - - - - -
<i>Australiodes</i>	- - -	- - - - - - - -	- 2	- - - - - - - - -	- - - - - - - - -
<i>Dupontiella</i>	- - -	- - - - - - - -	- - - - - - - -	- - - - - - - - -	- - - - - - - - -
<i>Elestora</i>	0 0	0 1 0 1 0 - - -	- 1	- - - - - - - - -	- - - - - - - - -
<i>Eupycnus</i>	2 1	1 0 1 0 0 1 1 0	- 1	- - - - - - - - -	- - - - - - - - -
<i>Euschaefferia</i>	- -	- 2 0 0 - - -	- 1	- - - - - - - - -	- - - - - - - - -
<i>Paracalanthis</i>	- -	- 0 0 0 - - -	- -	- - - - - - - - -	- - - - - - - - -
<i>Parallelodera</i>	2 1	1 0 1 0 0 - - -	- 1	- - - - - - - - -	- - - - - - - - -
<i>Parentonium</i>	- -	- - 2 0 - - -	- 0	- - - - - - - - -	- - - - - - - - -
<i>Rentonidium</i>	- -	- - - - - - - -	- 0	- - - - - - - - -	- - - - - - - - -

Matrix 1 – Addendum. Character states matrix of poorly described genera which were not used in a phylogenetic analysis by NONA.

²⁾ Shortened catalogues mentioned *sub* higher taxa summarize selected important references only.

FAMILY TROGOSSITIDAE LATREILLE, 1802²⁾

Type genus: *Trogossita* Olivier, 1790 (= *Temnoscheila* Westwood, 1830)

Trogossitairii Latreille, 1802: 159.

Family Trogossitidae (= Trogositidae, Temnochilidae): HOPE (1840: 131), REITTER (1876: 1), LÉVEILLÉ (1910: 1), etc.

See BARRON (1971: 4) for a more detailed catalogue.

Remarks. In comparison with other families of Cleroidea, the Trogossitidae are generally characterized by the following character states: 1) adult body hardly sclerotized, eyes not emarginate, mandible with 2 apical teeth situated in horizontal axis, antenna clubbed (club more/less asymmetrical), empodium conspicuously projecting, prothorax with lateral edge, front coxae transverse, tibiae with spines along side and hooked spur at tibial apex, tarsomeres without lobes, elytra with carinae and regular punctuation, inverted tegmen in 2 or 3 parts, bursa copulatrix and vagina without sclerites; 2) larva with head capsule ventrally open (gular region shorter than half of capsular length), gula with paragular sclerites or two apodemes at anterior margin, conspicuous endocarina, V-shaped frontal arms (sometimes arms curved or angled), dorsally situated urogomphi.

The family Phlophilidae is a sister group.

Distribution. All continents including temperate areas (southern Argentina and Chile, Tasmania, New Zealand, Holarctic region), Madagascar, Oceania.

SUBFAMILY TROGOSSITINAE LATREILLE, 1802

Type genus: *Trogossita* Olivier, 1790 (= *Temnoscheila* Westwood, 1830)

Trogossitairii Latreille, 1802: 159.

Subfamily Trogossitinae (= Trogositinae, Temnochilinae): ERICHSON (1842: 150), LÉVEILLÉ (1910: 6), CROWSON (1955: 82), BARRON (1971: 14), SLIPINSKI (1992: 462), etc.

See BARRON (1971: 14) for a more detailed catalogue.

Diagnosis. Antennal club mostly strongly asymmetrical, apical joints with sensorial fields; front coxal cavities externally closed; larval capsule with distinct endocarina and mostly straight frontal arms; gular region with paragular sclerites. Mainly predatory.

The subfamily Peltinae is a sister group.

Distribution. Worldwide distribution.

Tribe Calityni Winkler, 1924

Type genus: *Calitys* C. G. Thomson, 1859

Tribus Calityni Winkler, 1924: 688.

Subfamily Calitiniae Crowson, 1970: 13; SLIPINSKI (1992: 460).

Remarks. The most primitive tribe of the Trogossitinae with a similar way of life to that of the primitive *Peltis* of the subfamily Peltinae (adults and larvae are fungivorous).

The most important synapomorphies shared with other trogossitines are externally closed front coxal cavities (adult) and presence of parangular sclerites (larva). Middle coxal cavities are almost closed. According to CROWSON (1970: 12), larval abdominal tergite IX has a raised rim (i.e. the sclerotized area of the tergite is concave) as in Egoliini. Most of other features of this genus are either autapomorphies or plesiomorphies (the absence of an elytral lock is especially important). Body shape and presence of wax scales can indicate affinities to the tribe Gymnochilini – *Calitys* could be a primitive member of the latter tribe. However, this question requires further study.

The genus was clear-sightedly classified with Gymnochilini (*sub* the names Leperini or Leperinae) by REITTER (1876) and his followers (e.g. LÉVEILLÉ 1910) then removed to Peltinae s.l. by various authors and again classified within Trogossitinae s.l. by CROWSON (1970). Since that time, various authors have again connected this enigmatic genus with Peltinae rather than Trogossitinae (e.g. BARRON 1971, KOLIBÁČ *et al.* 2005) because of similar body shape and biology with *Peltis* which lives in the same habitats.

The cluster (Larinotini + Egoliini) + (Gymnochilini + Trogossitini) is a sister group.

Distribution. A single genus with one species (two other species described from South Africa may not belong to Cleroidea) is widely distributed in Holarctic region.

Tribe Larinotini Slipinski, 1992 stat.nov.

Type genus: *Larinotus* Carter et Zeck, 1937

Subfamily Larinotinae Slipinski, 1992: 443.

Remarks. A single genus with one species that shows affinity with the tribe Egoliini. Perfectly closed middle coxal cavities (a unique synapomorphy within Trogossitidae), dorsal surface with long hairs and concave tergite IX are the most important common apomorphies of both tribes. On the other hand, the larva of *L. umblicatus* Carter et Zeck, 1937 is the single known trogossitine species without parangular sclerites and the adult tibiae have reduced apical spurs. These features convinced SLIPINSKI (1992) to connect *Larinotus* with Peltinae s.l. In spite of the cladogram (Tree 1), detailed study of the character state matrix (Matrix 1) shows that the tribe Larinotini is probably paraphyletic and it could be synonymized with the Egoliini. This question will be addressed in a separate study.

The genera *Colydiopeltis* and *Parapeltis* were classified together with *Larinotus* in the subfamily Larinotinae by SLIPINSKI (1992). Both genera are probably more related to Peltinae s.l. (see Tree 1) as discussed in the relevant section. The subfamily was based on reduction of the tibial spurs. However, the value of this character is rather low in view of similar tendencies in other groups of Trogossitidae and Cleroidea.

The tribe Egoliini is a sister group.

Distribution. A single genus with one rare species is distributed in Queensland (Australia).

Tribe Egoliini Lacordaire, 1854 stat.nov.

Type genus: *Egolia* Erichson, 1842

Egoliides Lacordaire, 1854: 334.

Subfamily Egoliinae Crowson, 1964: 287; CROWSON (1970: 13), SLIPINSKI (1992: 460).

Remarks. This tribe is based mainly on the following synapomorphies: front and middle coxal cavities closed, body surface with distinctly long hairs (excepting *Egolia*), frons with longitudinal wrinkles, larval tergite IX with raised rim (i.e. sclerotized area of tergite is concave). Several distinct character states (probably underlying synapomorphies) of *Calanthosoma* connect Egoliini with Trogossitini: galea with ciliate setae, shape of tormal processes and tuft of hairs in male prementum. There are also symplesiomorphies shared with some Peltinae (e.g. mandibles with remnants of mola) that show the ancestral position of Egoliini within Trogossitinae. This status is more conspicuous if Larinotini is considered a relative of the tribe Egoliini. The position of *Necrobiopsis* is somewhat weak and it is situated separately from the cluster *Calanthosoma-Acalanthis-Egolia* in some trees (Tree 2). Nevertheless, there are several important synapomorphies in, for example, wing, front and middle coxal cavities and dorsal body surface which justify classification within Egoliinae as it is depicted in Tree 1. This classification should be supported by character weighting, in similar fashion to the three tribes of Peltinae (see below).

The tribe Larinotini is a sister group.

Distribution. Australia, Tasmania, Argentina, Chile, Venezuela, Brazil, Antilles.

Tribe Gymnochilini Lacordaire, 1854 stat.nov.

Type genus: *Gymnochila* Klug in Erichson, 1844

Gymnochilides Lacordaire, 1854: 344.

Tribe Leperini Reitter, 1876: 29; LÉVEILLÉ (1888: 440, as Leperinini).

Subfamily Leperininae (*sic!*) Léveillé, 1910: 20.

Remarks. The tribe is clearly defined by body shape, way of life, wax scales, four eyes and hind legs appropriate to jumping in advanced genera. Some species of *Xenoglena* and *Gymnochila* show primitive character states such as, for example, the remnants of mandibular mola that support monophyly of the tribe in relation to Trogossitini. Earlier authors (e.g. REITTER 1876) connected Gymnochilini (*sub* the name Leperini) with the genus *Calitys* because of similar habitus and surface structures. This interesting idea requires further study. The classification of apterous *Phanodesta* is unclear. The genus shows interesting similarities with Gymnochilini and its isolation in the southern part of South America indicates a Laurasian origin for Gymnochilini and their dispersion around America in the late Cretaceous period (compare with the Baltic amber clerid species *Lemidia wachteli* Kolibáč et Gerstmeier, 1997). On the other hand, the position of *Phanodesta* is somewhat weak in the cladogram and further study may show relations of the genus with the tribe Trogossitini.

The tribe Trogossitini is a sister group.

Matrix 2. Character states matrix of the subfamily Trogossitinae.

Distribution. Tropical Africa, Siberia, China, southeastern Asia, Australia, Tasmania, Chile (incl. Juan Fernández Islands).

Tribe Trogossitini Latreille, 1802

Type genus: *Trogossita* Olivier, 1790 (= *Temnoscheila* Westwood, 1830)

Trogossitairii Latreille, 1802: 159.

Tribe Trogositini (*sic!*) Reitter, 1876: 17; LÉVEILLÉ (1888: 432, as Temnochilini).

Tribe Nemozomini Reitter, 1876: 7; LÉVEILLÉ (1888: 431, as Nemosomatini; 1910: 1, as Nemosomatinae).

Subfamily Temnochilinae (= *Trogossitinae*, *Trogositinae*) Léveillé, 1910: 20; CROWSON (1955: 82, 1964: 296).

BARRON (1971: 14), SLIPINSKI (1992: 462).

Remarks. The tribe is defined by bare body, mouthparts and body shape highly adapted for a predatory (clerid-like) way of life, characteristic shape of tormal processes, often presence of tuft of hairs in male prementum and absence of closed radial cell in advanced members. The Old World genera *Alindria*, *Melambia* and *Seidlitzella* can be considered primitive members with some symplesiomorphies (e.g. wing venation) shared with *Xenoglena* and *Gymnochila*, i.e. the primitive genera of Gymnochilini. The genera also distributed in the both Americas are more advanced (incl. the Canary Islands genus *Leipaspis*, which was probably derived from *Tenebroides* and the Oceanian genus

Parallelodera derived from *Temnoscheila* or *Airora*) although they largely have several Old World species as well. The genera *Temnoscheila* and *Tenebroides* are the richest in species of all Trogossitidae – the bulk of species of both genera is recently widespread in South America although the origin of the genera is probably Eurasian. It is interesting that wild populations of *T. mauritanicus* (syn. *T. fuscus* Goeze, 1777) are predatory, whereas the cosmopolitan synanthropous *T. mauritanicus* feeds on stored grains. Tree 2 shows the re-counted and re-optimized Matrix 2 – the positions of the genera *Alindria*, *Melambia*, *Seidlitzella* and *Airora* are fully resolved.

Four Jurassic and Cretaceous species of the genera *Cretocateres* Ponomarenko, 1986 and *Thoracotes* Handlirsch, 1906³⁾ were described from area of Baykal lake and Western Mongolia and classified within the former Lophocateridae (PONOMARENKO 1985, 1986, 1990). The genera are characteristic by conspicuously asymmetric 3-segmented antennal club, widened prosternal process, oblong (not arcuate or concave in anterior margin) pronotum and slender body. All these character states perfectly correspond with relatives of the genus *Temnoscheila*.

The tribe Gymnochilini is a sister group.

Distribution. All continents excluding Australia and New Zealand. One genus in Oceania (*Parallelodera*), one genus in Canary Islands (*Leipaspis*). Several species of *Temnoscheila* and *Tenebroides* tend to cosmopolitism.

List of characters for Matrix 2 (Trogossitinae)

Adult characters

01. **Body shape:** flat=0; elongate=1; convex (not conglobate)=2. [nonadditive]
02. **Gular sutures:** wide, convergent at apex=0; narrow, subparallel at apex=1; reduced=2. [nonadditive]
03. **Frontoclypeal suture:** present=0; absent=1.
04. **Frons - longitudinal groove or depression:** absent=0; present=1.
05. **Cranium ventrally - tufts of long setae at sides:** absent=0; present=1.
06. **Submentum of males - tuft of setae:** absent=0; present=1.
07. **Submentum - anterior margin with row of setae:** absent=0; present=1.
08. **Eyes - size, position:** moderate=0; large, lateral=1; large, dorsal=2; flat=3. [nonadditive]
09. **Eyes - number:** 2=0; 4=1.
10. **Epicranial acumination:** moderate=0; deep=1; absent=2. [nonadditive] [deactivated]

³⁾ Descriptions of two non-type species, *Thoracotes glabrus* Ponomarenko, 1990 and *T. sibiricus* Ponomarenko, 1985, were studied. The type species *T. dubius* Handlirsch, 1906 is unknown to me.

11. **Lacinia - hooks:** 2=0; 1=1; 0=2. [nonadditive] [deactivated]
12. **Galea - shape:** elongate=0; sub-clavate=1; clavate=2. [nonadditive]
13. **Galea - ciliate setae:** absent=0; present=1.
14. **Mediostipes - lacinia:** not fused=0; partially fused=1; fused together=2. [additive] [deactivated]
15. **Palpifer - outer edge:** even=0; denticulate=1.
16. **Mandible, apical teeth - number, position:** 2 in horizontal axis=0; 2 in vertical axis=1; 1=2. [additive]
17. **Mola:** present=0; present but reduced=1; absent=2. [additive]
18. **Penicillus (at base):** present (fine, often membranous)=0; absent=1; long setae=2. [nonadditive]
19. **Pubescence above mola or cutting edge:** absent=0; present=1. [deactivated]
20. **Ventral ciliate furrow:** furrow ciliate=0; furrow not ciliate=1; absent=2. [additive] [deactivated]
21. **Basal notch:** moderate=0; deep=1; shallow or absent=2. [additive] [deactivated]
22. **Epipharynx - sclerite:** absent=0; present=1.
23. **Lateral tormal process - projection:** projection not developed=0; curved downwards, processes not connected (*Airora*)=1; curved downwards, processes with bridge (*Peltis*)=2. [nonadditive] [deactivated]
24. **Ligula - ciliate setae:** absent=0; present=1.
25. **Ligula:** rigid=0; membranous=1.
26. **Ligula:** not retroflex=0; weakly retroflex=1; strongly retroflex=2. [additive] [deactivated]
27. **Ligula - shape:** weakly emarginate=0; deeply emarginate=1.
28. **Hypopharyngeal sclerite:** absent=0; sickle shaped=1; H-shaped=2; 2 separate sclerites=3. [nonadditive] [deactivated]
29. **Antenna:** 11-segmented=0; 10-segmented=1; 9-segmented=2; 8-segmented=3. [nonadditive] [deactivated]
30. **Antennal club:** symmetrical=0; asymmetrical=1.
31. **Antenna - sensorial fields:** absent=0; present=1.
32. **Pronotum - shape:** transverse=0; elongate=1; cordate=2. [nonadditive]
33. **Prepectus:** present=0; absent=1.
34. **Middle coxal cavities:** open=0; closed=1.
35. **Elytra - long hairs:** absent=0; present=1.
36. **Epipleure:** moderate=0; wide=1; thin=2. [nonadditive] [deactivated]
37. **Elytral lock:** absent=0; present=1.
38. **Elytra - carinae:** conspicuous=0; reduced=1. [deactivated]

39. Elytra - scales: absent=0; present=1. [deactivated]
40. Wing - radial cell: oblong (or reduced)=0; triangular=1; open (outer vein present)=2. [nonadditive]
41. Wing - wedge cell: present=0; absent=1; small (*Peltis*)=2. [nonadditive] [deactivated]
42. Wing - cross vein MP3-4: present=0; absent=1. [deactivated]
43. Wing - cross vein AA1+2-3+4: absent=0; present=1.
44. Front tibiae - spines along side: moderate=0; large=1; reduced=2. [nonadditive] [deactivated]
45. Front tibiae - hooked spur: present=0; absent, apical spurs not hooked or weakly hooked=1.



Tree 2. Trogossitinae (Matrix 2). Under equal weights: 20 characters deactivated, number of characters = 69, activated = 49, nonadditive = 15, additive = 54. NONA: heuristic analysis; strict consensus of 8 trees, L = 149, Ci = 43, Ri = 53.

46. **Parasternites in sternites III-VII:** absent=0; one=1; two=2.
[nonadditive]
47. **Spiculum gastrale (male sternite VIII):** absent=0; present=1.
48. **Tegmen - number of parts:** 3 parts=0; 2 parts=1. [deactivated]
49. **Coxitae:** divided=0; undivided=1. [deactivated]
50. **Biology:** herbivorous or fungivorous=0; predatory=1.

Larval characters

51. **Frontal arms:** curved (cucujoid)=0; weakly curved=1; V-shaped=2.
[nonadditive]
52. **Epicranial stem:** present=0; reduced=1; absent=2. [additive]
[deactivated]
53. **Gula - anterior apodemes:** present=0; absent=1.
54. **Parangular sclerites:** absent=0; present=1.
55. **Hypostomal rods:** absent=0; present=1.
56. **Mandible, apical teeth - number, position:** two, situated in horizontal axis=0; two, situated in horizontal or even vertical axes=1; one tooth=2. [additive]
57. **Lacinia mandibulæ:** several small spines=0; plumose=1; tridentate=2; absent=3. [nonadditive]
58. **Mola:** present=0; reduced=1; absent=2. [additive]
59. **Palpifer:** present=0; absent=1.
60. **Pedunculate seta:** absent=0; present=1.
61. **Cardo - stipes:** not fused=0; partially fused=1.
62. **Ligula:** present=0; absent=1.
63. **Prementum - anterior margin:** even=0; with notch=1; projecting=2.
[nonadditive]
64. **Torma:** single compact plate=0; two separate lateral sclerites=1.
65. **Sensory appendix:** medium sized (to half of joint 3)=0; very small=1; longer than half of joint 3=2. [nonadditive]
66. **Thoracic sclerites pattern (ventrally):** 3-1-1=0; 1-1-1=1; 1-0-0=2;
0-0-0=3. [nonadditive] [deactivated]
67. **Trochanter:** triangular=0; oblong=1.
68. **Tergite IX:** flat=0; depressed=1.
69. **Urogomphi:** present, hooked=0; minute=1.

SUBFAMILY PELTINAE KIRBY, 1837

Type genus: *Peltis* O. F. Müller, 1764

Family Peltidae. Peltidans Kirby, 1837: 104; CROWSON (1964: 285, 1970: 4).

Subfamily Peltinae (= Ostominae, Ostomatinae): LÉVEILLÉ (1910: 24); CROWSON (1955: 82), BARRON (1971: 11), SLIPINSKI (1992: 443), etc.

See BARRON (1971: 11) for a more detailed catalogue.

Diagnosis. Labium with membranous ligula, lacinia mostly with large spurs, antennae weakly asymmetrical or symmetrical, adult body flat, elytra mostly with carinae. Larvae with reduced hypostomal rods, gular sutures and endocarina; frontal arms sometimes curved (angled) as in Cucujoidea. Primitive members fungivorous or herbivorous, advanced floricolous and also predatory.

The subfamily Trogossitinae is a sister group.

Distribution. Worldwide distribution.

Tribe Peltini Kirby, 1837 stat.nov.

Type genus: *Peltis* O. F. Müller, 1764

Family Peltidae. Peltidans Kirby, 1837: 104.

Tribe Peltini Reitter, 1876: 44.

Subfamily Peltinae (= Ostominae, Ostomatinae): LÉVEILLÉ (1910: 24); CROWSON (1955: 82), BARRON (1971: 11), SLIPINSKI (1992: 443), etc.

Remarks. Several species of *Peltis*, the single genus of the tribe, are highly adapted for a fungivorous way of life under bark (adult) or in rotten wood (larva), but the general features of the genus are primitive. Autapomorphies of larva include a number of reductions (endocarina, frontal arms, thoracic sclerites, urogomphi). The position of *Peltis* in the cladogram (Tree 1) is rather weak but it must surely be related to other “peltines”. In some trees of a non-optimized cladogram, *Peltis* has also been associated with *Calitrys*. The reason may be found in the relative primitiveness of the both genera, i.e., the lack of synapomorphies. *Peltis* is therefore classified in an independent tribe here, rather than together with Thymalini.

A sister group is unclear. According to the cladogram (Tree 1), Peltini are more related to Thymalini than Colydiopeltini but this question requires further study. Some of trees also show an association with the last-mentioned tribe. The genus *Peltis* is so primitive but at the same time so highly adapted that it could also have a common ancestor with Colydiopeltini.

Distribution. Holarctic.

Tribe Thymalini Léveillé, 1888

Type genus: *Thymalus* Latreille, 1802

Tribe Thymalini Léveillé, 1888: 444.

Tribe Rentoniini Crowson, 1966: 120.

Tribe Protopeltini Crowson, 1966: 120.

Subfamily Rentoniinae Crowson, 1966: 120 (with the tribes Rentoniini + Protopeltini); SLIPINSKI (1992: 460). **syn.nov.**

Subfamily Protopeltinae Crowson, 1970: 5; SLIPINSKI (1992: 460). **syn.nov.**

Subfamily Meligethiellinae Kireitshuk & Ponomarenko, 1990: 79. **syn.nov.** (fossil)

Remarks. There are distinct relations between the two relict genera *Thymalus* and *Protopeltis* in both adults and larvae (see Matrix 1). The association of the both latter genera with the former subfamily Rentoniinae is very interesting and well-founded; however, it tends to be based on adult characters. The presumed larva of *Rentonium* shows several distinct apomorphies (shortened frontal arms, reduced number of palpal segments, minute urogomphi) but also plesiomorphies such as, for example, a complete endocarina. However, CROWSON (1966: 125) also speculated upon a common ancestor for *Protopeltis* and the former Rentoniinae and upon relations between *Protopeltis* and “Holarctic Peltinae”.

Three Mesozoic (Jurassic and Cretaceous) genera from Siberia and Central Asia were described by KIREITSHUK & PONOMARENKO (1990) and MEDVEDEV (1969). According to original descriptions and illustrations, the genera *Juralithinus*, *Meligethiella* and *Ostomalynus* can be classified within the subfamily Peltinae. They probably share the following common character states: wide, flat body, conspicuous antennal club, narrow front intercoxal process, front and middle coxae externally open, front coxae strongly transverse, elytral epipleure very wide for the whole length of elytra, five visible abdominal sternites. Excepting elytral epipleure, these character states occur in Thymalini and Peltini. On the basis of the wide epipleure, I suggest their classification within Thymalini.

The tribe Peltini is a sister group according to the cladogram (Tree 1) but further study may show also sistership of Thymalini with the cluster Peltini – Colydiopeltini.

Distribution. Holarctic (*Thymalus*), New Zealand, Chile, Brazil.

Tribe Colydiopeltini trib.nov.

Type genus: *Colydiopeltis* Slipinski, 1992

Remarks. Relations among the tribes Peltini, Thymalini and Colydiopeltini have already been mentioned above. The adults of the both genera of the tribe, *Colydiopeltis* and *Parapeltis*, are very small apterous creatures with thick setae on dorsal surface, compact antennal club, and reduced tibial spurs. They live in forest litter. Their mouthparts show relations to Peltini and Thymalini, other characters are more autapomorphic. There are also two interesting character states in *Parapeltis*: (1) externally closed front coxal cavities and (2) almost closed middle coxal cavities. The genus is the single member of the cluster Peltini-Thymalini-Colydiopeltini with the front coxal cavities closed. On the other hand, a tendency to close the front and middle coxal

cavities occurs often in all apterous Cleroidea. This feature may be connected with loss of the wings.

Recently, several habitually similar peltine species have been found in South Africa. Their study may help clarify relationships within the tribe.

The cluster Peltini-Thymalini is a sister group according to the cladogram. However, further study of the South African species mentioned may show closer a connection between Colydiopeltini and Peltini.

Distribution. Thailand (*Colydiopeltis*), Australia: Queensland (*Parapeltis*).

Tribe Decamerini Crowson, 1964 stat.nov.

Type genus: *Decamerus* Solier, 1849

Subfamily Decamerinae Crowson, 1964: 287; SLIPINSKI (1992: 460).

Remarks. Four floricolous genera were originally classified within the former sufamily Decamerinae: *Antixoon*, *Decamerus*, *Diontolobus* and *Eronyx*. J. Doyen in TAIT *et al.* (1990) described the larva of *Eronyx* *expansus* which shares distinct synapomorphies with the larva of *Lophocateres pusillus*. The adults of *Eronyx* do have not exhibit the most conspicuous synapomorphy of the other three genera – tarsal claws with denticle – as well as externally closed or nearly closed front coxal cavities (Pl. 14: 7–12). The presumed larva of *Diontolobus* shows more primitive “peltine” features than known larvae of Lophocaterini. Moreover, a floricolous way of life is also known in *Peltonyx* (= *Floricateres* Crowson, 1970) which belongs to Lophocaterini. These facts support monophyly of three genera of Decamerini and classification of *Eronyx* within Lophocaterini.

The cluster Lophocaterini-Ancyonini is a sister group.

Distribution. South and Central America.

Tribe Ancyonini trib.nov.

Type genus: *Ancyrona* Reitter, 1876

Remarks. The new tribe represents a distinct monophyletic group of predatory beetles. Adult Ancyonini are defined by synapomorphies of mouthparts (e.g. mandibular penicillus composed of tuft of long setae). The larvae of Ancyonini are not known, with the exception of the dubious “*Grynomia varians* Broun” mentioned by CROWSON (1964). The species is not listed in Coleopterorum Catalogus (LÉVEILLÉ 1910) and I have not studied it. CROWSON (1964: 299) classified the species within the subfamily Lophocaterinae, unfortunately without description of relevant characters. He only mentioned that the larva is probably predatory (insect fragments and detrital material found in the foregut) and figured its spiracles and epipharynx. The question is whether his *G. varians* is congeneric with *G. diluta*, type of the genus *Grynomia*. If so, sisterhood of the tribes Ancyonini and Lophocaterini would also be confirmed by larval characters.

The bulk of species is classified within *Ancyrona* and *Latolaeva*. Both the genera are morphologically very similar and, perhaps, they could be synonymized. However, a taxonomic revision of the both rich genera is required before this takes place. At the moment, naked African species (lacking pubescence or scales) are classified within *Latolaeva* and Old World species with pubescence or coloured wax scales belong to *Ancyrona*. The primitive Madagascan *Ancyrona* species *A. kosnovskorum* Kolibáč, 2005 (several other undescribed species occur in Madagascar) shows similarities with New Zealand *Grynomia* and Brazilian *Leptonyxa*. However, the latter genus, with monstrous male mandibles (Pl. 14: 6), is the most derived member of the tribe Ancyronini.

The tribe Lophocaterini is a sister group.

Distribution. Euroasia, Africa, New Zealand, Australia, tropical South America (Brazil).

Tribe Lophocaterini Crowson, 1964 stat.nov.

Type genus: *Lophocateres* Olliff, 1883

Subfamily Lophocaterinae Crowson, 1964: 297; SLIPINSKI (1992: 443).

Tribe Lycoptini Casey, 1890: 311, 494. **syn.nov.** (Coleoptera: Colydiidae). See also BARRON (1975).

Remarks. The tribe is well defined by larval synapomorphies (shape of gula, large cardo, divided abdominal tergite IX, median process between urogomphi). However, the larvae of only four genera out of eight are known. Adult morphology is not homogenous, and the ways of life vary. Some of members are fungivorous (*Grynocharis*, probably *Lycoptis*), others herbivorous (e.g. *Lophocateres*) or predatory (*Promanus*, *Eronyxa*).

The classification of *Eronyxa* and *Grynocharina* is complicated. Adults of *Eronyxa* have features of Decamerini and they might be considered primitive members of that tribe, whereas adults of *Grynocharina* possess several features of Ancyronini. Nevertheless, most of the character states of both latter genera show that their position in the tribe Lophocaterini is firm (see Tree 4).

Character	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2								
Taxon	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2									
<i>Ancyrona</i>	1	[02]	1	1	1	2	0	1	0	2	2	0	2	2	0	0	1	0	2	1	2	0	0	0	1	3	0	0	0	1	0	[01]	1	1	—						
<i>Decamerus</i>	0	0	0	1	2	2	0	1	0	0	0	0	2	0	5	1	1	2	1	2	2	1	1	0	3	1	1	2	0	0	2	—	2	—	—						
<i>Diontolobus</i>	0	0	0	1	2	2	1	0	0	1	0	0	4	1	1	2	0	2	2	1	1	0	3	1	1	2	0	0	0	—	2	0	0	0	0	2	0	0			
<i>Erynya</i>	0	0	0	0	1	0	4	0	0	0	2	0	0	5	1	1	0	0	0	2	1	1	1	0	3	0	1	0	2	0	1	0	2	2	1	2	2	1	1	1	
<i>Gynocharina</i>	0	0	0	1	1	0	3	1	0	2	2	0	1	2	0	4	1	0	2	2	2	2	0	0	0	1	0	0	2	1	0	—	—	—	—	—	—	—	—		
<i>Gynocharis</i>	0	2	0	1	0	1	0	1	0	1	0	0	1	2	0	2	1	0	3	0	2	0	0	0	3	1	0	0	2	1	0	—	0	2	—	2	2	0	1	1	
<i>Gynoma</i>	0	0	0	0	1	0	2	1	1	2	2	0	2	2	1	0	1	0	3	1	2	0	1	1	0	3	1	1	0	1	0	0	—	1	—	—	—	—	—	—	—
<i>Indopeltis</i>	0	1	0	—	1	0	1	0	0	0	1	1	0	0	0	1	1	2	0	2	0	0	0	0	3	1	0	0	—	1	0	—	—	—	—	—	—	—	—		
<i>Latolæva</i>	1	0	1	1	1	2	0	1	0	2	2	0	2	2	0	0	1	0	2	1	2	0	0	0	3	0	0	0	1	0	1	—	1	—	—	—	—	—	—		
<i>Leptonyxa</i>	0	1	0	1	2	2	0	2	2	1	1	0	2	1	0	0	0	1	2	0	0	0	0	0	3	1	0	0	0	0	0	0	1	1	—	—	—	—	—		
<i>Lophocateres</i>	0	2	0	1	1	0	3	1	0	0	0	1	2	0	0	4	1	0	3	0	2	0	0	0	0	3	1	0	0	1	0	0	1	0	2	1	2	2	2	1	1
<i>Lycoptis</i>	0	2	—	0	1	—	3	0	1	0	1	0	2	0	0	—	—	1	—	4	—	0	0	0	0	3	1	0	0	—	1	1	—	0	—	—	—	—	—		
<i>Neaspis</i>	0	1	0	0	0	2	2	1	0	2	2	0	2	0	0	0	2	1	0	0	1	0	1	0	1	3	1	0	0	—	0	0	1	—	—	—	—	—	—		
<i>Peltonyxa</i>	0	2	0	1	0	0	2	4	0	2	1	0	2	0	0	3	1	1	2	2	2	0	[01]	0	0	0	3	1	0	0	2	—	0	2	—	—	—	—	—	—	
<i>Promanus</i>	0	2	0	1	1	2	0	1	2	2	0	0	2	2	0	3	1	1	2	0	2	0	1	0	0	3	1	0	0	2	—	0	1	2	1	2	2	1	—	1	1

Matrix 3. Character states matrix of the subfamily Peltinae excluding the tribes Colydiopeltini, Peltini and Thymalini.

The Cretaceous genus *Peltocoleops* Ponomarenko, 1990 is characteristic by weakly asymmetric 3-segmented antennal club, wide (but not dilated) prosternal process and body shape which is more slender than that in Colydiopeltini-Peltini-Thymalini but wider than in *Thoracotes* (Trogossitini). All these characters allow to classify *Peltocoleops* within the cluster Decamerini-Acyronini-Lophocaterini. A classification within Lophocaterini is based on body shape, spinulose middle tibiae and shape of hind coxae.

The tribe Acyronini is a sister group.

Distribution. North America, Euroasia, Australia, New Zealand. One species of the originally Southeastern Asian genus *Lophocateres* is cosmopolitan (*L. pusillus*).

List of characters for Matrix 3 (Decamerini, Acyronini, Lophocaterini)

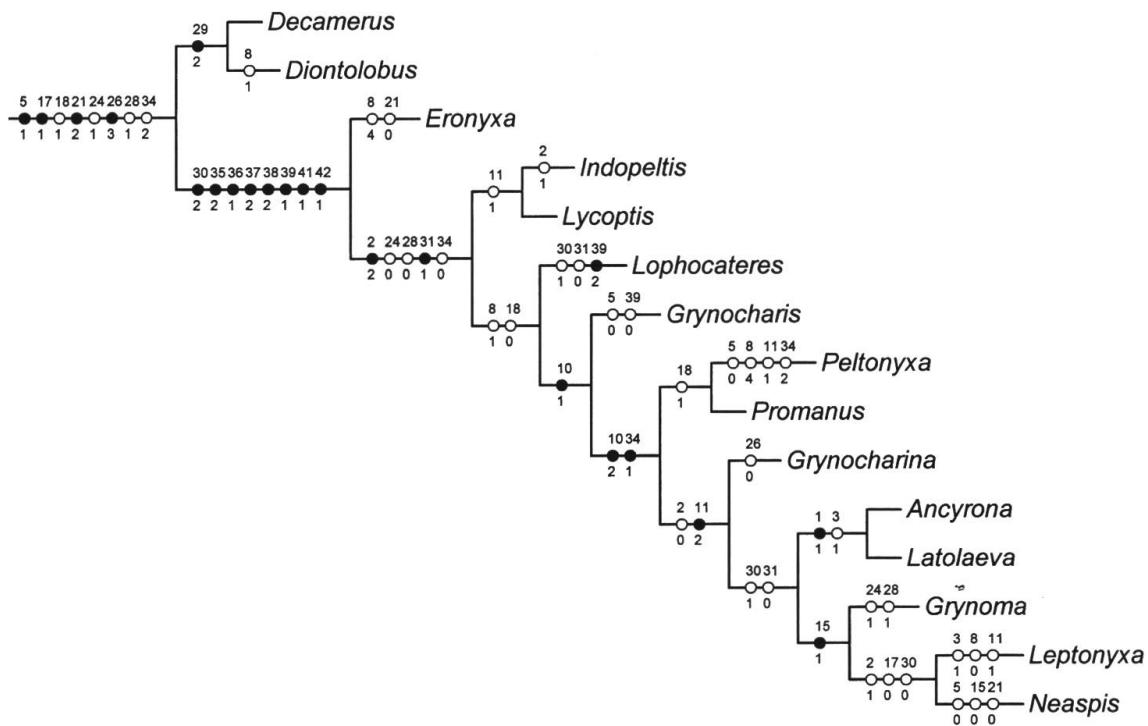
Adult characters

01. **Gular sutures:** wide, convergent at apex=0; narrow, subparallel at apex=1.
02. **Frontoclypeal suture:** present=0; absent=1; broadly emarginate=2. [nonadditive]
03. **Cranium ventrally - tufts of long setae at sides:** absent=0; present=1.
04. **Antennal groove:** absent=0; present=1. [deactivated]
05. **Eyes - size, position:** moderate=0; large, lateral=1.
06. **Epicranial acumination:** moderate=0; deep=1; absent=2. [nonadditive] [deactivated]
07. **Lacinia - hooks:** 2=0; 1=1; 0=2; 3=3. [nonadditive] [deactivated]
08. **Galea - shape:** elongate=0; sub-clavate=1; clavate=2; partially fused with lacinia=3; very small=4. [nonadditive]
09. **Mediostipes - lacinia:** not fused=0; partially fused=1; fused together=2. [additive] [deactivated]
10. **Mola:** present=0; reduced but present=1; absent=2. [additive]
11. **Penicillus (at base):** present (fine, often membranous)=0; absent=1; long setae=2. [nonadditive]
12. **Pubescence above mola or cutting edge:** absent=0; present=1. [deactivated]
13. **Ventral ciliate furrow:** furrow ciliate=0; furrow not ciliate=1; absent=2. [additive] [deactivated]
14. **Basal notch:** moderate=0; deep=1; shallow or absent=2. [additive] [deactivated]
15. **Labrum - cranium:** not fused=0; fused=1.
16. **Lateral tormal process - projection:** projection not developed=0; curved downwards, processes not connected (*Airora*)=1; curved downwards, processes with bridge (*Peltis*)=2; projection reduced or absent (*Promanus*)=3; projection curved upwards (*Colydiopeltis*)=4;

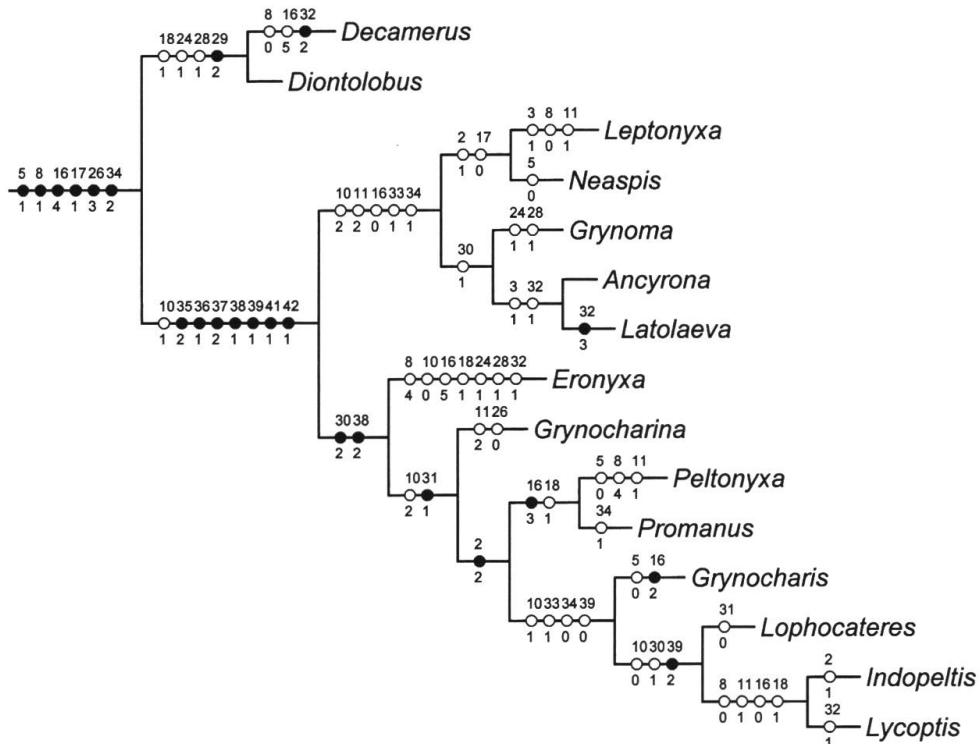
- projections extending laterally and downwards (*Eronyxa*)=5.
[nonadditive] [deactivated]
17. **Ligula:** rigid=0; membranous=1.
 18. **Ligula - shape:** weakly emarginate=0; deeply emarginate=1.
 19. **Hypopharyngeal sclerite:** absent=0; sickle-shaped=1; H-shaped=2; 2 separate sclerites=3. [nonadditive] [deactivated]
 20. **Antenna:** 11-segmented=0; 10-segmented=1; 9-segmented=2; 8-segmented=3; 7-segmented=4. [nonadditive] [deactivated]
 21. **Antennal club:** symmetrical=0; asymmetrical=1; weakly asymmetrical=2. [nonadditive]
 22. **Epipleure:** moderate=0; wide=1; thin=2. [nonadditive] [deactivated]
 23. **Elytra - carinae:** conspicuous=0; reduced=1. [deactivated]
 24. **Elytra - punctuation:** regular=0; irregular=1.
 25. **Elytra - scales:** absent=0; present=1. [deactivated]
 26. **Wing - radial cell:** oblong (or reduced)=0; triangular=1; open (outer vein present)=2; cell transferred downwards, often small=3. [nonadditive]
 27. **Wing - cross vein MP3-4:** present=0; absent=1. [deactivated]
 28. **Front tibiae - hooked spur:** present=0; absent, apical spurs not hooked or weakly hooked=1.
 29. **Claws - denticle:** absent=0; small=1; distinct=2. [nonadditive]
 30. **Parasternites in sternites III-VII:** absent=0; one=1; two=2. [nonadditive]
 31. **Spiculum gastrale (male sternite VIII):** absent=0; present=1.
 32. **Tegmen - number of parts:** 3 parts=0; 2 parts=1; 1 part=2. [nonadditive] [deactivated]
 33. **Coxitae:** divided=0; undivided=1. [deactivated]
 34. **Biology:** herbivorous or fungivorous=0; predatory=1; floricolous=2. [nonadditive]

Larval characters

35. **Frontal arms:** curved (cucujoid)=0; weakly curved=1; V-shaped=2. [nonadditive]
36. **Gular sutures:** conspicuous, parallel=0; conspicuous, convergent=1.
37. **Stemmata:** 5=0; 3=1; 2=2. [nonadditive]
38. **Mola:** present=0; reduced=1; absent=2. [additive]
39. **Sensory appendix:** medium-sized (to half of joint 3)=0; very small=1; longer than half of joint 3=2. [nonadditive]
40. **Thoracic sclerites pattern (dorsally):** 1-2-2=0; 1-0-0=1; 0-0-0=2. [nonadditive] [deactivated]
41. **Abdominal segment IX:** not divided=0; transversely divided=1.
42. **Urogomphi - median process:** absent=0; present=1.



Tree 3. Peltinae: Decamerini, Ancyronini, Lophocaterini (Matrix 3). As in Matrix 1 but all uninformative characters deleted. Under equal weights: 17 characters deactivated; number of characters = 42, activated = 25, nonadditive = 14, additive = 28. NONA: heuristic analysis; tree 1 of 1, L = 62, Ci = 51, Ri = 62.



Tree 4. Peltinae: Decamerini, Ancyronini, Lophocaterini (Matrix 3). ACCTRAN optimization of Tree 3. Weight = 10 for characters 2, 30, 31, 34. NONA: heuristic analysis; tree 1 of 1, L = 186, Ci = 49, Ri = 68.

System of the family Trogossitidae Latreille, 1802

[Genera are listed alphabetically. For their relationships see cladograms. Relations of genera not included in the Trees 1–4 are mentioned in footnotes.]

SUBFAMILY TROGOSSITINAE LATREILLE, 1802

Type genus: *Trogosita* Olivier, 1790 (= *Temnoscheila* Westwood, 1830)

Tribe Calityni Winkler, 1924

Type genus: *Calitys* C. G. Thomson, 1859

Genus *Calitys* Thomson, 1859

Type species: *Hispa scabra* Thunberg, 1784 (by original designation and monotypy)

Tribe Larinotini Slipinski, 1992 stat.nov.

Type genus: *Larinotus* Carter et Zeck, 1937

Genus *Larinotus* Carter et Zeck, 1937

Type species: *Larinotus umblicatus* Carter et Zeck, 1937 (by monotypy)

Tribe Egoliini Lacordaire, 1854 stat.nov.

Type genus: *Egolia* Erichson, 1842

Genus *Acalanthis* Erichson, 1844

Type species: *Acalanthis quadrisignata* Erichson, 1844 (by monotypy)

Genus *Calanthosoma* Reitter, 1876

Type species: *Calanthosoma flavomaculatum* Reitter, 1876 (by monotypy)

Genus *Egolia* Erichson, 1842

Type species: *Egolia variegata* Erichson, 1842 (by monotypy)

Genus *Necrobiopsis* Crowson, 1964

Type species: *Necrobiopsis tasmanicus* Crowson, 1964 (by monotypy and original designation)

Genus *Paracalanthis* Crowson, 1970

Type species: *Paracalanthis binnaburrense* Crowson, 1970 (by monotypy and original designation)

Tribe Gymnochilini Lacordaire, 1854 stat.nov.

Type genus: *Gymnochila* Klug in Erichson, 1844

Genus *Anacypta* Illiger, 1807

Type species: *Nitidula punctata* Fabricius, 1801 (by KOLIBÁČ 2005)

Genus *Gymnochila* Klug in Erichson, 1844

Type species: *Trogosita vestita* Griffith, 1832 (by monotypy) [= *Trogosita varia* Fabricius, 1801]

Genus *Leperina* Erichson, 1844

Type species: *Trogosita decorata* Erichson, 1844 (by KOLIBÁČ 2005)

Genus *Narcisa* Pascoe, 1863

Type species: *Narcisa decidua* Pascoe, 1863 (by monotypy)

Genus *Phanodesta* Reitter, 1876

Type species: *Phanodesta cordaticollis* Reitter, 1876 (by KOLIBÁČ 2005)

Genus *Xenoglena* Reitter, 1876

Type species: *Xenoglena deyrollei* Reitter, 1876 (by monotypy)

Tribe Trogossitini Latreille, 1802

Type genus: *Trogosita* Olivier, 1790 (=*Temnoscheila* Westwood, 1830)

Recent genera

Genus *Airora* Reitter, 1876

Type species: *Airora cylindrica* Serville, 1828 (by BARRON 1971)

Genus *Alindria* Erichson, 1844

Type species: *Trogosita grandis* Serville, 1828 (by KOLIBÁČ 2005)

Genus *Corticotomus* Sharp, 1891

Type species: *Corticotomus basalis* Sharp, 1891 (by BARRON 1971)

Genus *Dupontiella* Spinola, 1844⁴⁾

Type species: *Dupontiella ichneumonoides* Spinola, 1844 (by KOLIBÁČ 2005)

Genus *Elestora* Pascoe, 1868⁵⁾

Type species: *Elestora fulgorata* Pascoe, 1868 (by monotypy)

Genus *Eupycnus* Sharp, 1891⁶⁾

Type species: *Eupycnus latus* Sharp, 1891 (monotypy)

Genus *Euschaefferia* Leng, 1920⁷⁾

Type species: *Euschaefferia hectoriae* Schaeffer, 1918 (by monotypy and original designation)

Genus *Leipaspis* Wollaston, 1862

Type species: *Leipaspis lauricola* Wollaston, 1862 (by KOLIBÁČ 2005)

Genus *Melambia* Erichson, 1844

Type species: *Trogosita gigas* Fabricius, 1798 (by KOLIBÁČ 2005)

Genus *Nemozoma* Latreille, 1824

Type species: *Dermestes elongatus* Linnaeus, 1760 (by monotypy)

Genus *Parallelodera* Fairmaire, 1881⁸⁾

Type species: *Parallelodera quadraticollis* Fairmaire, 1881 (by monotypy)

Genus *Seidlitzella* Jacobs, 1915

Type species: *Peltis procera* Kraatz, 1858 (by monotypy)

⁴⁾ The genus is probably related to *Nemozoma*.

⁵⁾ The genus is related to *Melambia* and *Seidlitzella*. (See Pl. 14: 4, 5.)

⁶⁾ The genus is related to *Tenebroides*.

⁷⁾ The genus is related to *Corticotomus*.

⁸⁾ The genus is probably related to *Airora* and *Temnoscheila*.

Genus *Temnoscheila* Westwood, 1830

Type species: *Trogosita caerulea* Olivier, 1790 (by monotypy)

Genus *Tenebroides* Piller et Mitterpacher, 1783

Type species: *Tenebrio mauritanicus* Linnaeus, 1758 (by WESTWOOD 1838)

Mesozoic genera

Genus *Cretocateres* Ponomarenko, 1986

Type species: *Cretocateres mongolicus* Ponomarenko, 1986 (by monotypy)

Genus *Thoracotes* Handlirsch, 1906

Type species: *Thoracotes dubius* Handlirsch, 1906 (by monotypy)

SUBFAMILY PELTINAE KIRBY, 1837

Type genus: *Peltis* O. F. Müller, 1764

Tribe Peltini Kirby, 1837 stat.nov.

Type genus: *Peltis* O. F. Müller, 1764

Genus *Peltis* O. F. Müller, 1764

Type species: *Silpha grossa* Linnaeus, 1758 (by HOPE 1840)

Tribe Thymalini Léveillé, 1888

Type genus: *Thymalus* Latreille, 1802

Recent genera

Genus *Australiodes* Endrödy-Younga, 1960⁹⁾

Type species: *Clambus vestitus* Broun, 1886 (by monotypy)

Genus *Parentonium* Crowson, 1970¹⁰⁾

Type species: *Rentonium magnum* (Crowson, 1966) (by original designation)

Genus *Protopeltis* Crowson, 1964

Type species: *Grynomia viridescens* Broun, 1886 (by monotypy and original designation)

Genus *Rentonellum* Crowson, 1966

Type species: *Rentonellum apterum* Crowson, 1966 (by monotypy and original designation)

Genus *Rentonidium* Crowson, 1966¹¹⁾

Type species: *Rentonidium costiventris* Crowson, 1966 (by monotypy and original designation)

Genus *Rentonium* Crowson, 1966

Type species: *Rentonium daldiniaae* Crowson, 1966 (by original designation)

Genus *Thymalus* Latreille, 1802

Type species: *Peltis brunnea* Thunberg, 1794 (by monotypy and original designation)

⁹⁾ The genus genus is related to *Rentonium* and *Rentonidium*.

¹⁰⁾ The genus is related to *Rentonium*.

¹¹⁾ The genus genus is related to *Rentonium*.

Mesozoic genera

Genus *Juralithinus* Kireitshuk et Ponomarenko, 1990

Type species: *Juralithinus gracilidorsum* Kireitshuk et Ponomarenko, 1990
(by monotypy and original designation)

Genus *Meligethiella* Medvedev, 1969

Type species: *Meligethiella soroniiformis* Medvedev, 1969 (by monotypy and original designation)

Genus *Ostomalynus* Kireitshuk et Ponomarenko, 1990

Type species: *Ostomalynus ovalis* Kireitshuk et Ponomarenko, 1990 (by monotypy and original designation)

Tribe *Colydiopeltini* trib.nov.

Type genus: *Colydiopeltis* Slipinski, 1992

Genus *Colydiopeltis* Slipinski, 1992

Type species: *Colydiopeltis burckhardti* Slipinski, 1992 (by SLIPINSKI 1992)

Genus *Parapeltis* Slipinski, 1992

Type species: *Parapeltis australicum* Slipinski, 1992 (by monotypy and original designation)

Tribe *Decamerini* Crowson, 1964 stat.nov.

Type genus: *Decamerus* Solier, 1849

Genus *Antixoon* Gorham, 1886

Type species: *Antixoon cribripenne* Gorham, 1886 (by monotypy)

Genus *Decamerus* Solier, 1849

Type species: *Decamerus haemorrhoidalis* Solier, 1849 (by monotypy)

Genus *Diontolobus* Solier, 1849

Type species: *Diontolobus punctipennis* Solier, 1849 (by monotypy)

Tribe *Ancyonini* trib.nov.

Type genus: *Ancyrona* Reitter, 1876

Genus *Ancyrona* Reitter, 1876

Type species: *Ancyrona lewisi* Reitter, 1876 (by KOLIBÁČ 1993)

Genus *Grynomma* Sharp, 1877

Type species: *Grynomma diluta* Sharp, 1877 (by KOLIBÁČ 2005)

Genus *Latolaeva* Reitter, 1876

Type species: *Latolaeva ferrarii* Reitter, 1876 (by KOLIBÁČ 2005)

Genus *Leptonyxa* Reitter, 1876

Type species: *Leptonyxa brevicollis* Reitter, 1876 (by KOLIBÁČ 2005)

Genus *Neaspis* Pascoe, 1872

Type species: *Neaspis villosa* Pascoe, 1872 (by monotypy)

Genus *Peltonyxa* Reitter, 1876

Type species: *Peltonyxa deyrollei* Reitter, 1876 (by monotypy)

Genus *Pro manus* Sharp, 1877

Type species: *Pro manus depressus* Sharp, 1877 (by monotypy)

Tribe Lophocaterini Crowson, 1964 stat.nov.

Type genus: *Lophocateres* Olliff, 1883

Recent genera

Genus *Eronyxa* Reitter, 1876

Type species: *Eronyxa dohrni* Reitter, 1877 (by monotypy)

Genus *Grynocharina* Reitter, 1877

Type species: *Grynocharina peltiformis* Reitter, 1877 (by monotypy)

Genus *Grynocharis* Thomson, 1859

Type species: *Silpha oblonga* Linnaeus, 1758 (by monotypy and original designation)

Genus *Indopeltis* Crowson, 1966

Type species: *Indopeltis nilgiriensis* Crowson, 1966 (by monotypy and original designation)

Genus *Lophocateres* Olliff, 1883

Type species: *Lophocateres nanus* Olliff, 1883 (by monotypy)

Genus *Lycoptis* Casey, 1890

Type species: *Peltis americana* Motschoulsky, 1863 (by monotypy)

Mesozoic genera

Genus *Peltocoleops* Ponomarenko, 1990

Type species: *Peltocoleops onokhojensis* Ponomarenko, 1990 (by monotypy and original designation)

Fossils (incertae sedis)

[The following Mesozoic genera from China were not studied, nor were their comprehensible descriptions available to me. *Anhuistoma* Sin, 1985 was originally described in Trogossitidae, *Palaeoendomychus* Zhang, 1992 in Endomychidae and *Sinosoronia* Zhang, 1992 in Nitidulidae. Two latter genera have been recently classified within Trogossitidae by PONOMARENKO & KIREITSHUK (2005).]

Genus *Anhuistoma* Sin, 1985

Type species: *Anhuistoma hyla* Sin, 1985

Genus *Palaeoendomychus* Zhang, 1992

Type species: *Palaeoendomychus gymnus* Zhang, 1992

Genus *Sinosoronia* Zhang, 1992

Type species: *Sinosoronia longiantenna* Zhang, 1992

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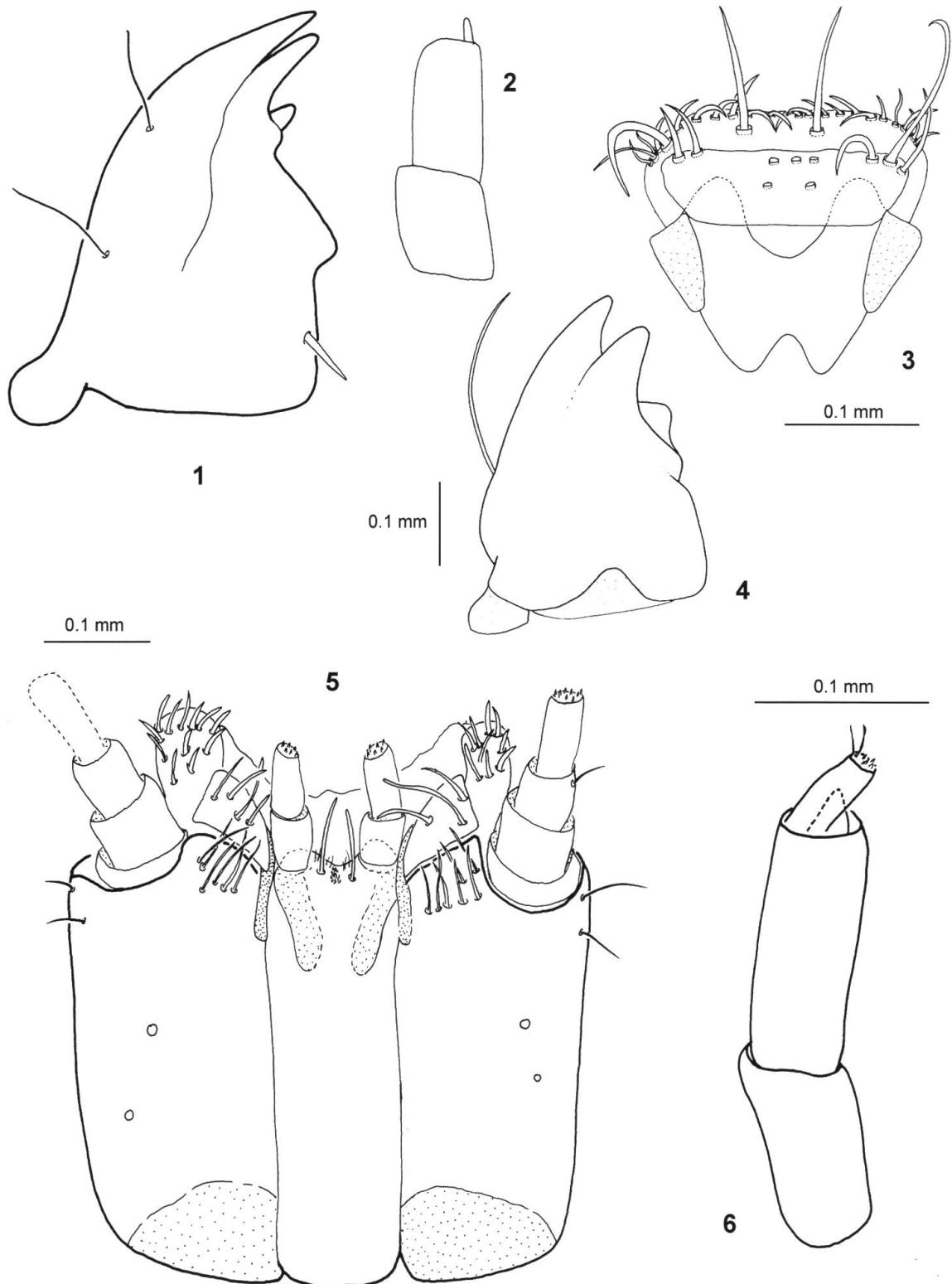
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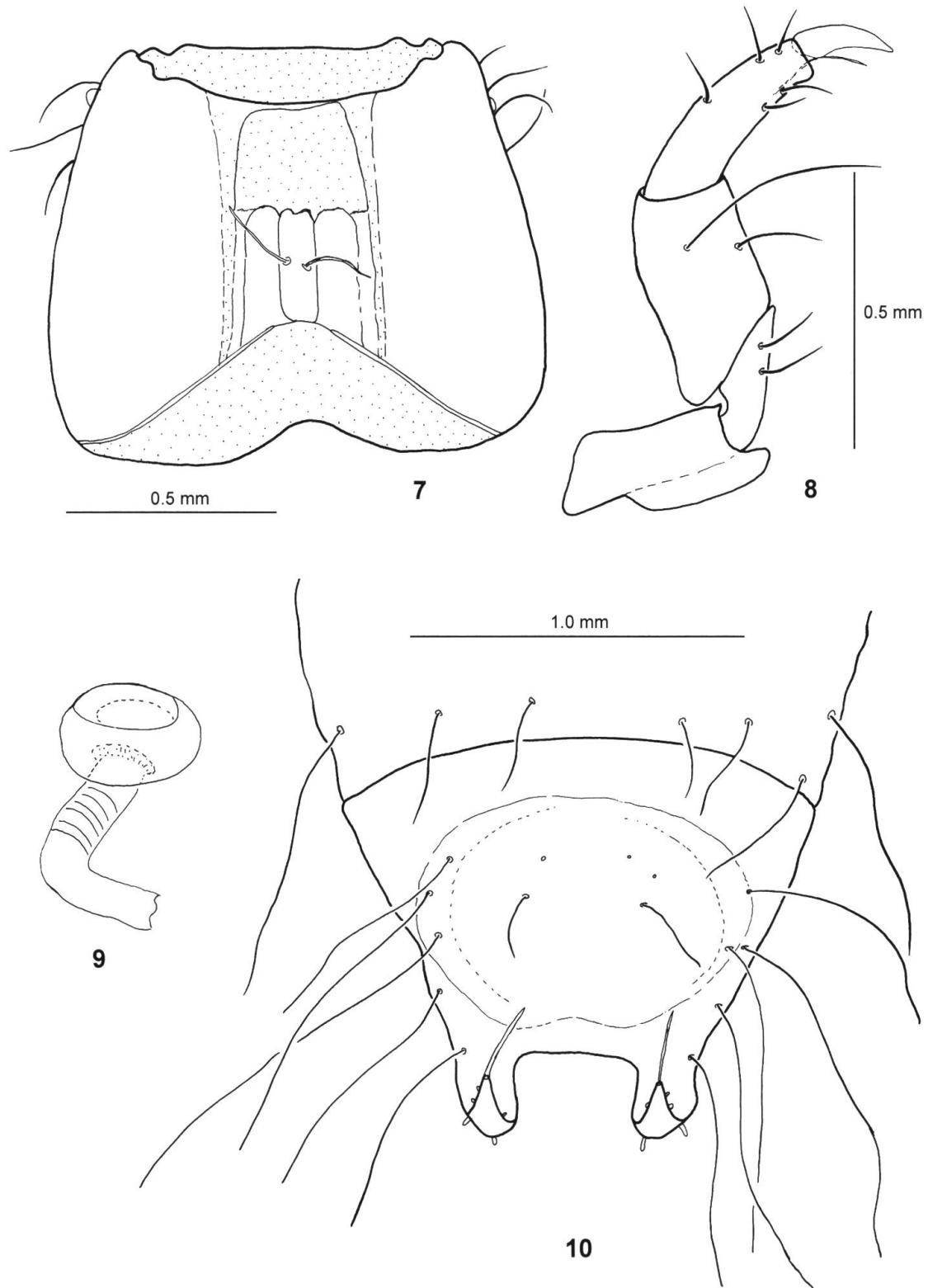
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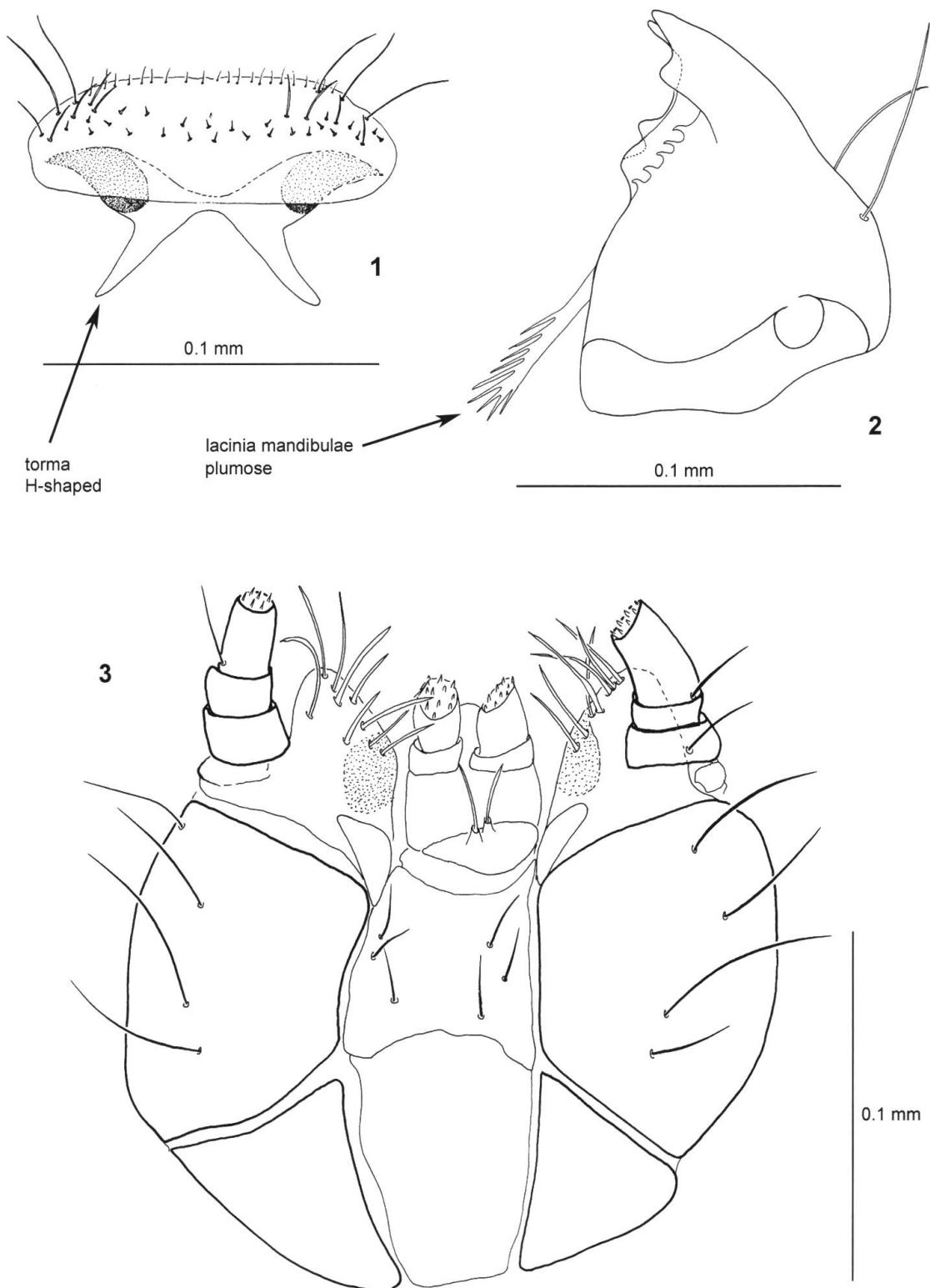
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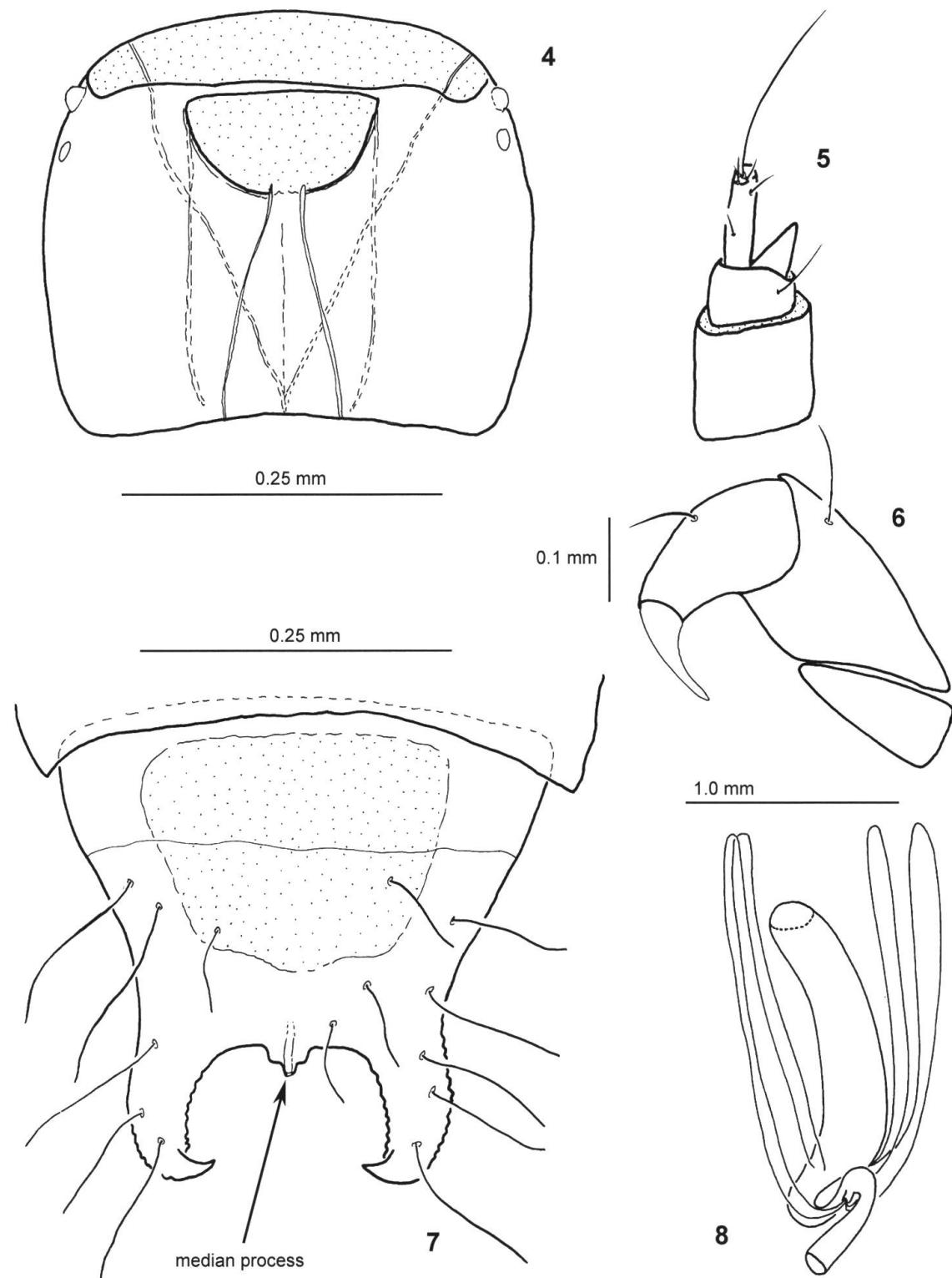
Pl. 1. *Paracalanthis binnaburrense* Crowson, larva: 1, mandible ventrally; 2, antenna. *Egoliinae* gen. sp., larva from Tasmania: 3, epipharynx; 4, mandible dorsally; 5, maxillolabial complex; 6, antenna. Figures 1, 2 without scales.



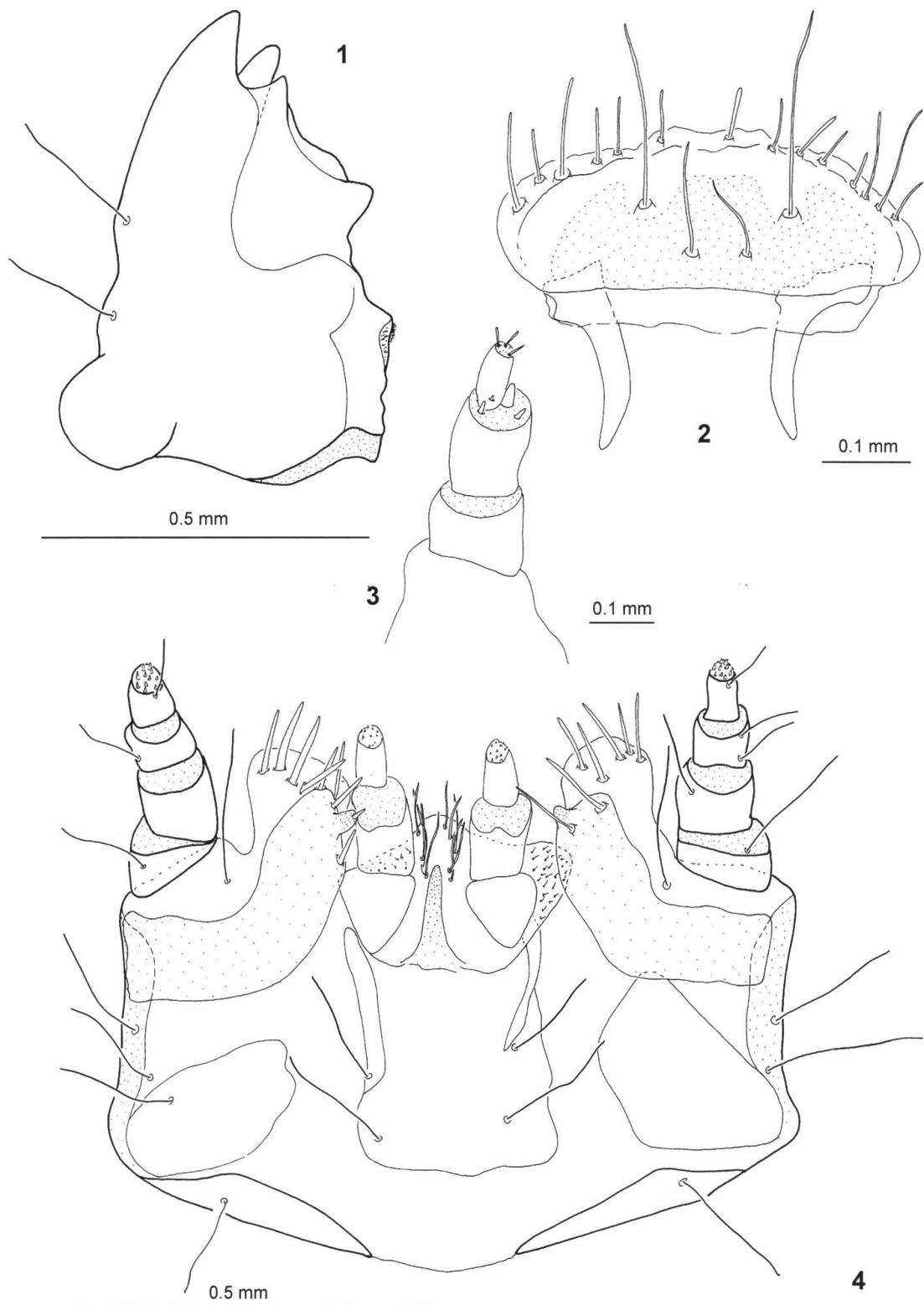
Pl. 2. *Egoliinae* gen.sp., larva from Tasmania: 7, head capsule ventrally; 8, front leg; 9, abdominal spiracle; 10, abdominal segments VIII, IX dorsally. Figure 9 schematically, without scale.



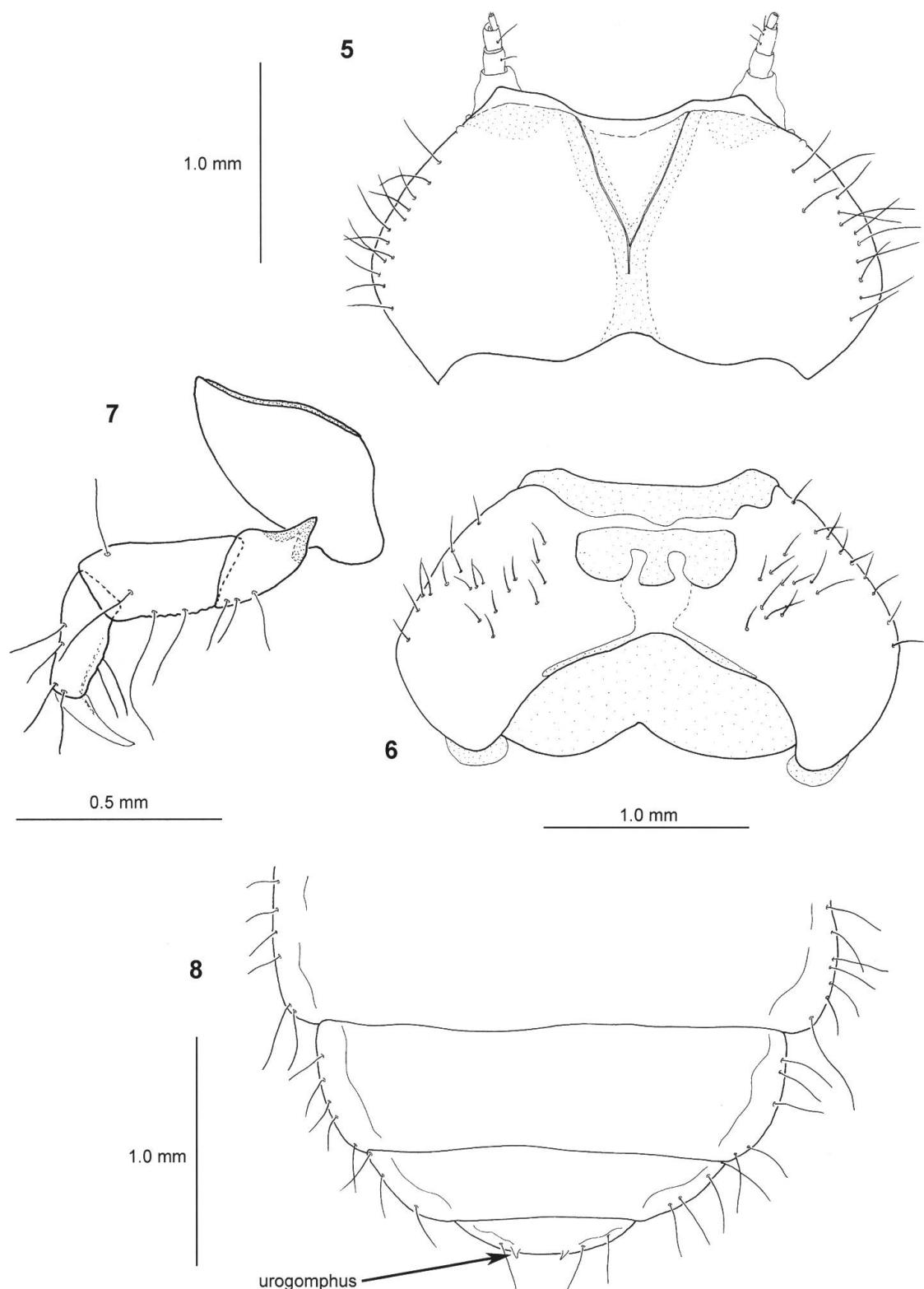
Pl. 3. *Lophocateres pusillus* Klug, larva: 1, epipharynx; 2, mandible ventrally; 3, maxillolabial complex.



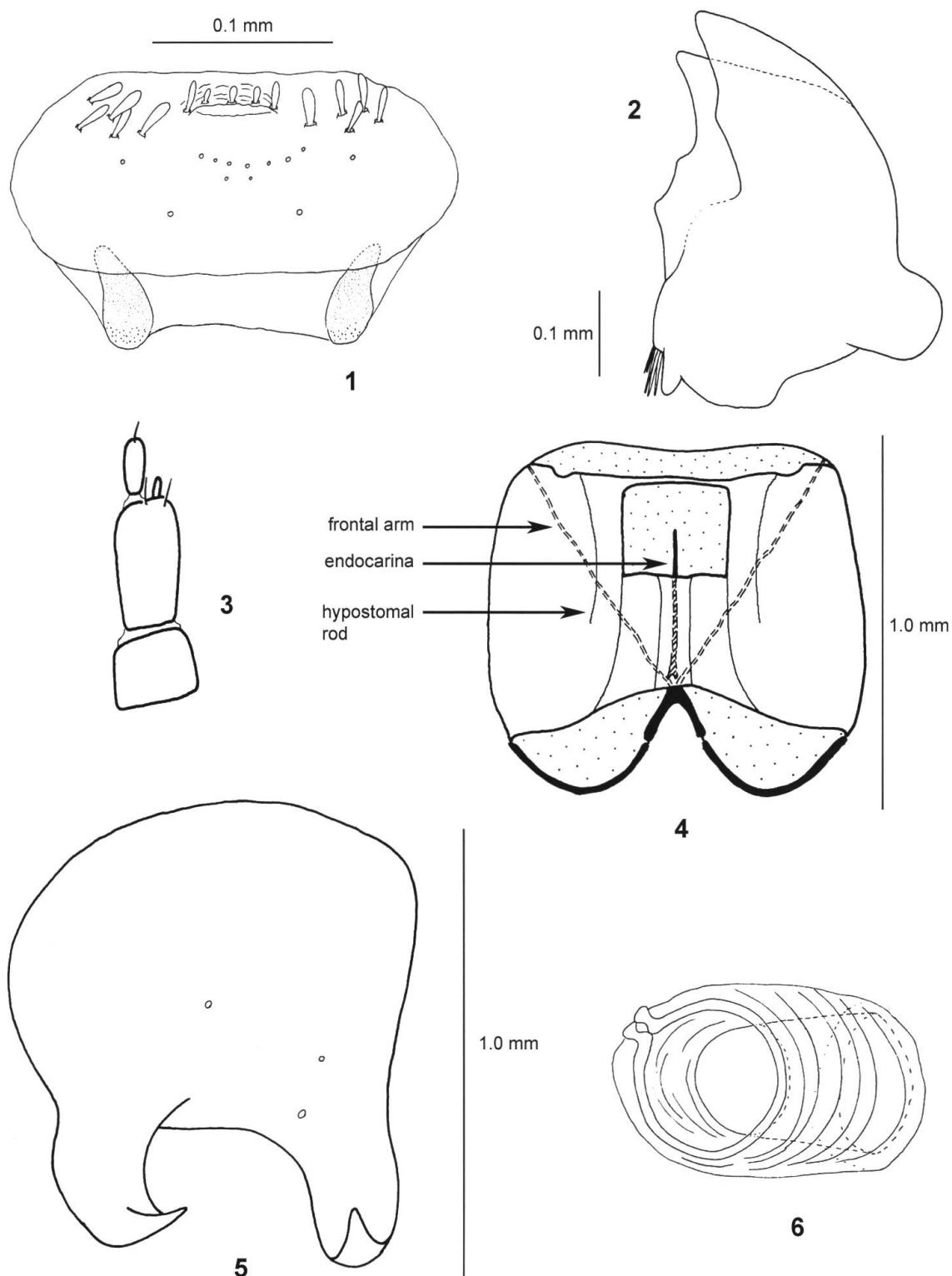
Pl. 4. *Lophocateres pusillus* Klug, larva: 4, head capsule ventrally (transparent view); 5, antenna; 6, front leg; 7, abdominal segment IX dorsally; 8, alimentary canal. Figure 5 without scale.



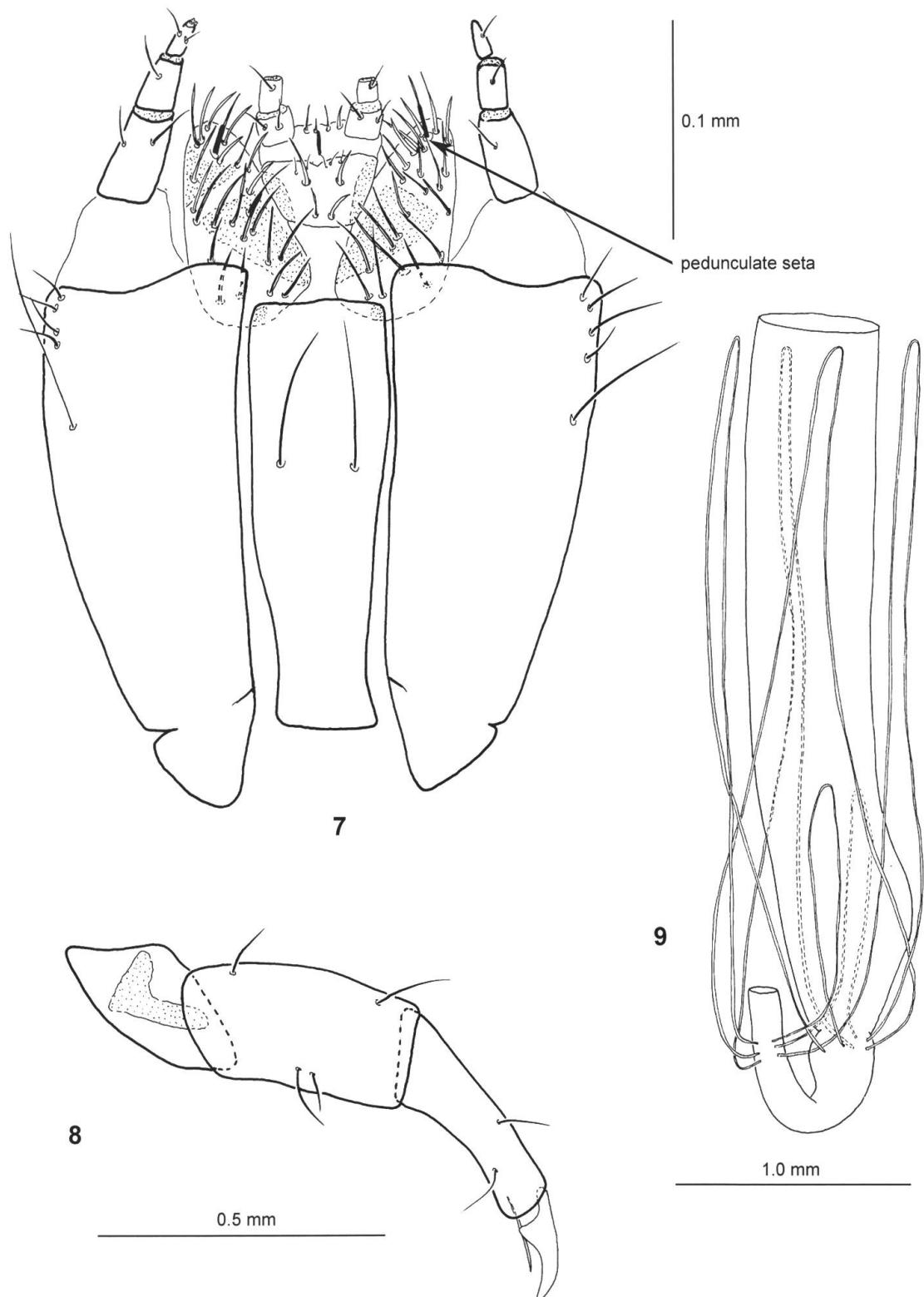
Pl. 5. *Peltis ferruginea* Linnaeus, larva: 1, mandible ventrally; 2, epipharynx; 3, antenna; 4, maxillolabial complex.



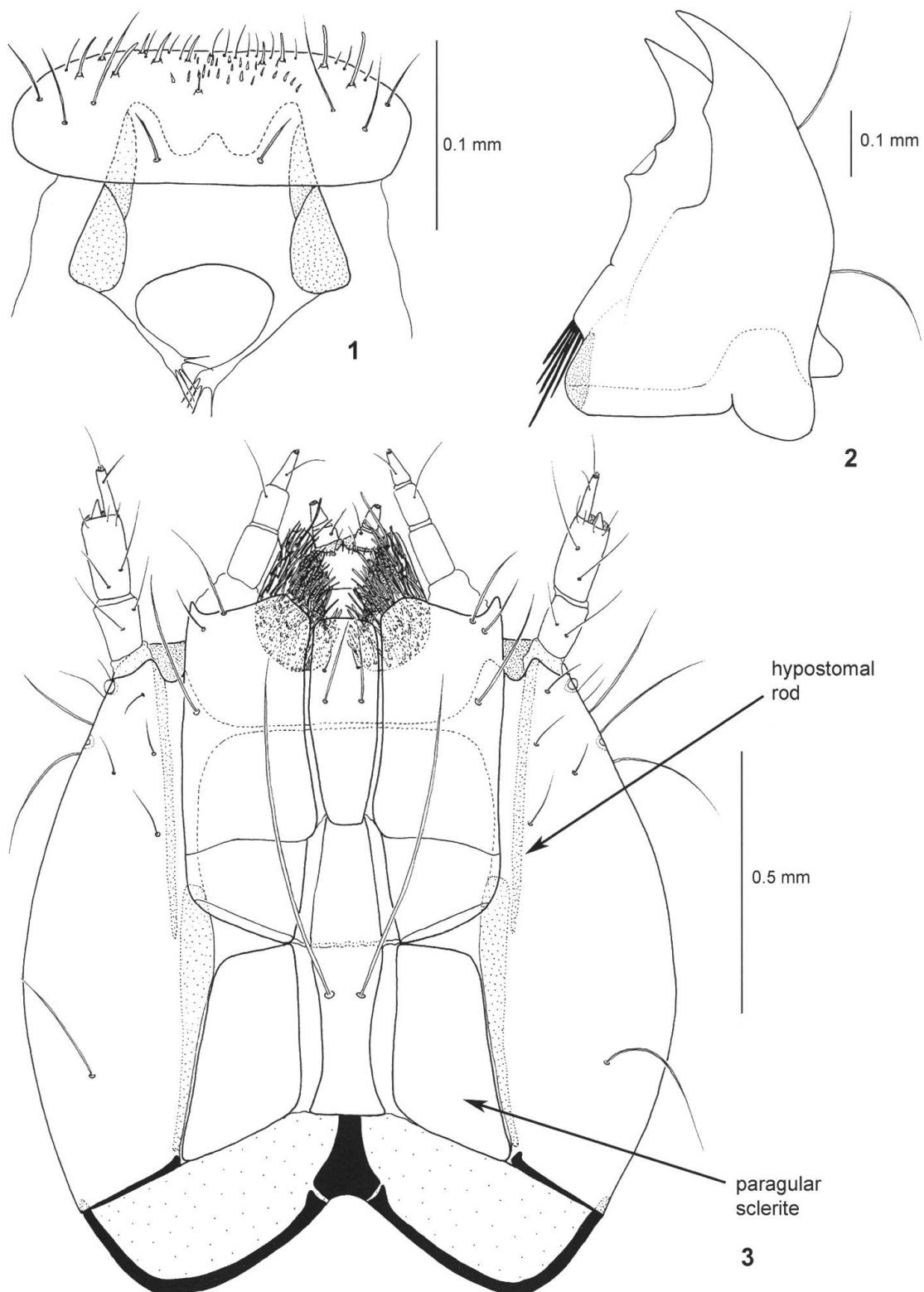
Pl. 6. *Peltis ferruginea* Linnaeus, larva: 5, head capsule dorsally; 6, head capsule ventrally; 7, hind leg; 8, abdominal segments VI–IX dorsally.



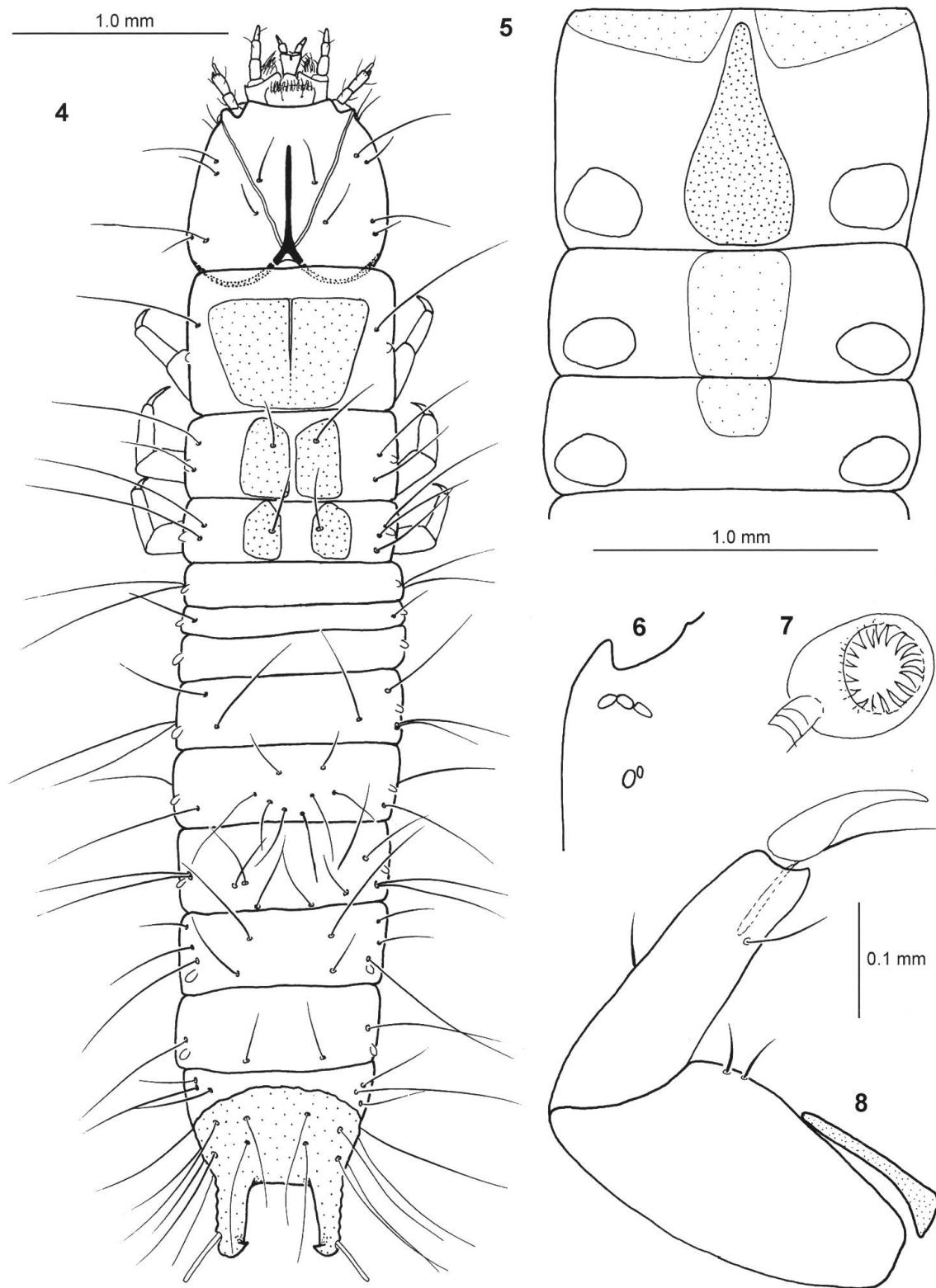
Pl. 7. *Tenebroides mauritanicus* Linnaeus, larva: 1, epipharynx; 2, mandible ventrally; 3, antenna; 4, head capsule ventrally (transparent view); 5, abdominal segment IX dorsolaterally; 6, abdominal spiracle. Figures 3, 6 without scales.



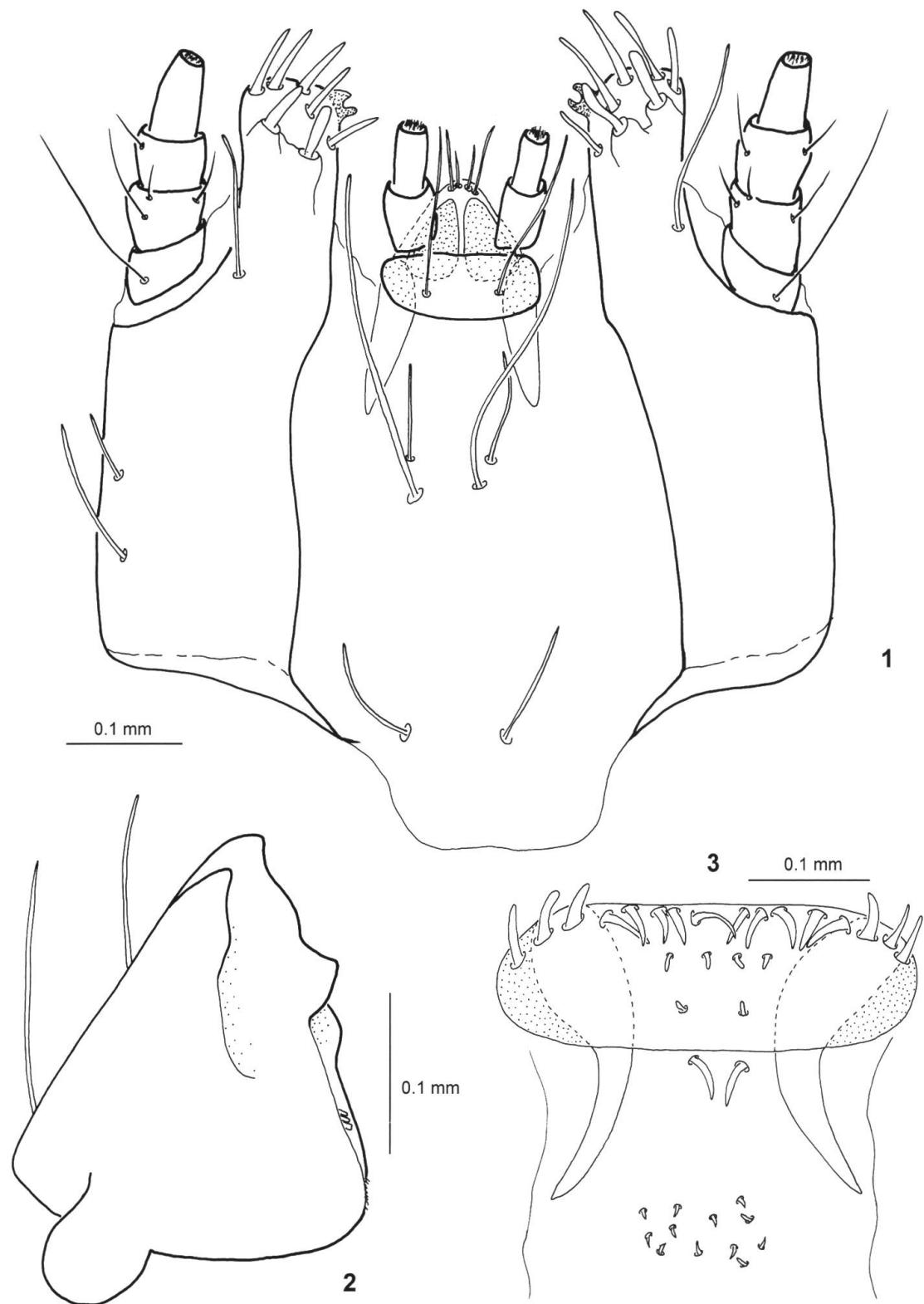
Pl. 8. *Tenebroides mauritanicus* Linnaeus, larva: 7, maxillolabial complex; 8, hind leg; 9, alimentary canal.



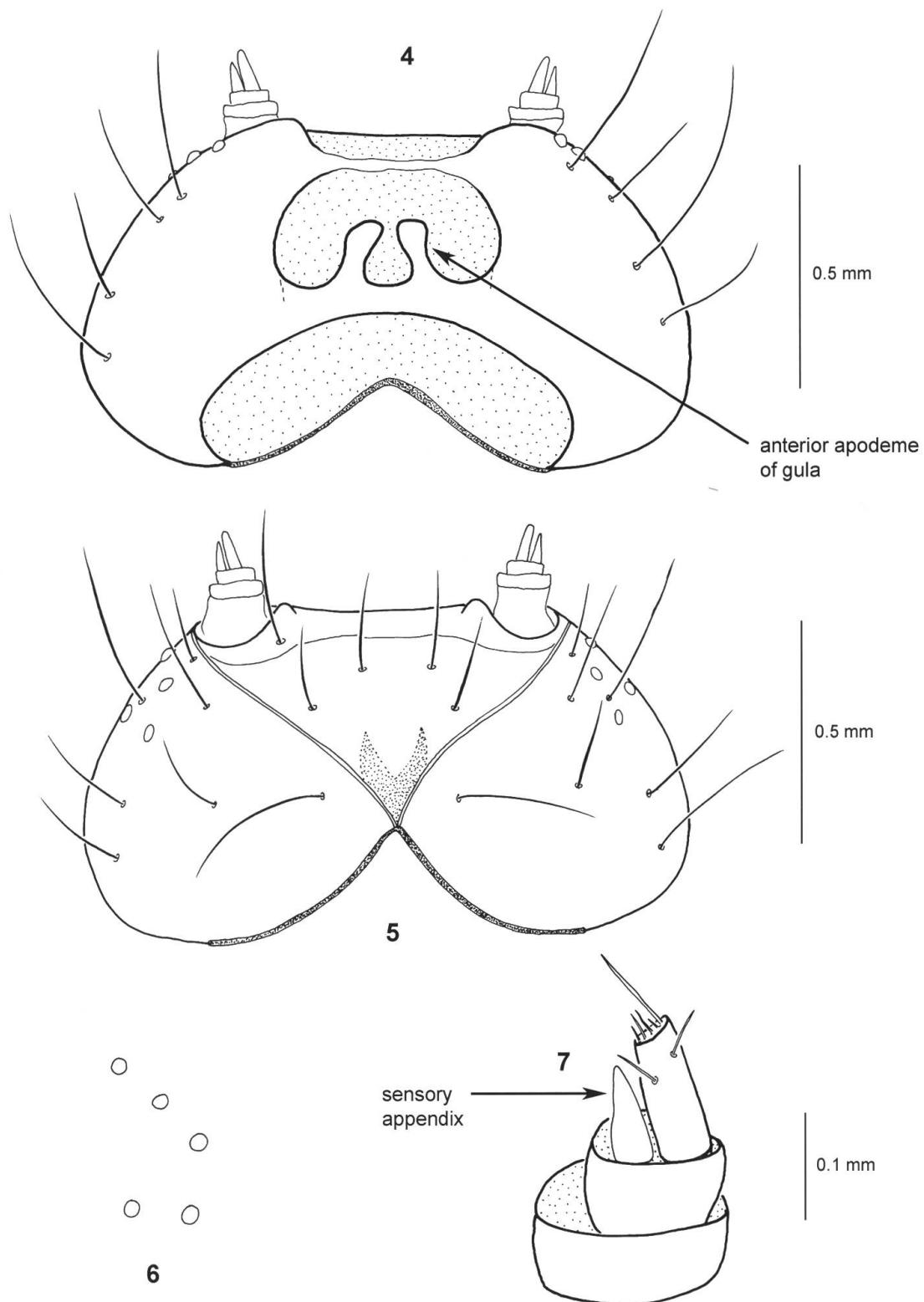
Pl. 9. *Tenebroides fuscus* Goeze, larva: 1, epipharynx; 2, mandible ventrally; 3, head ventrally.



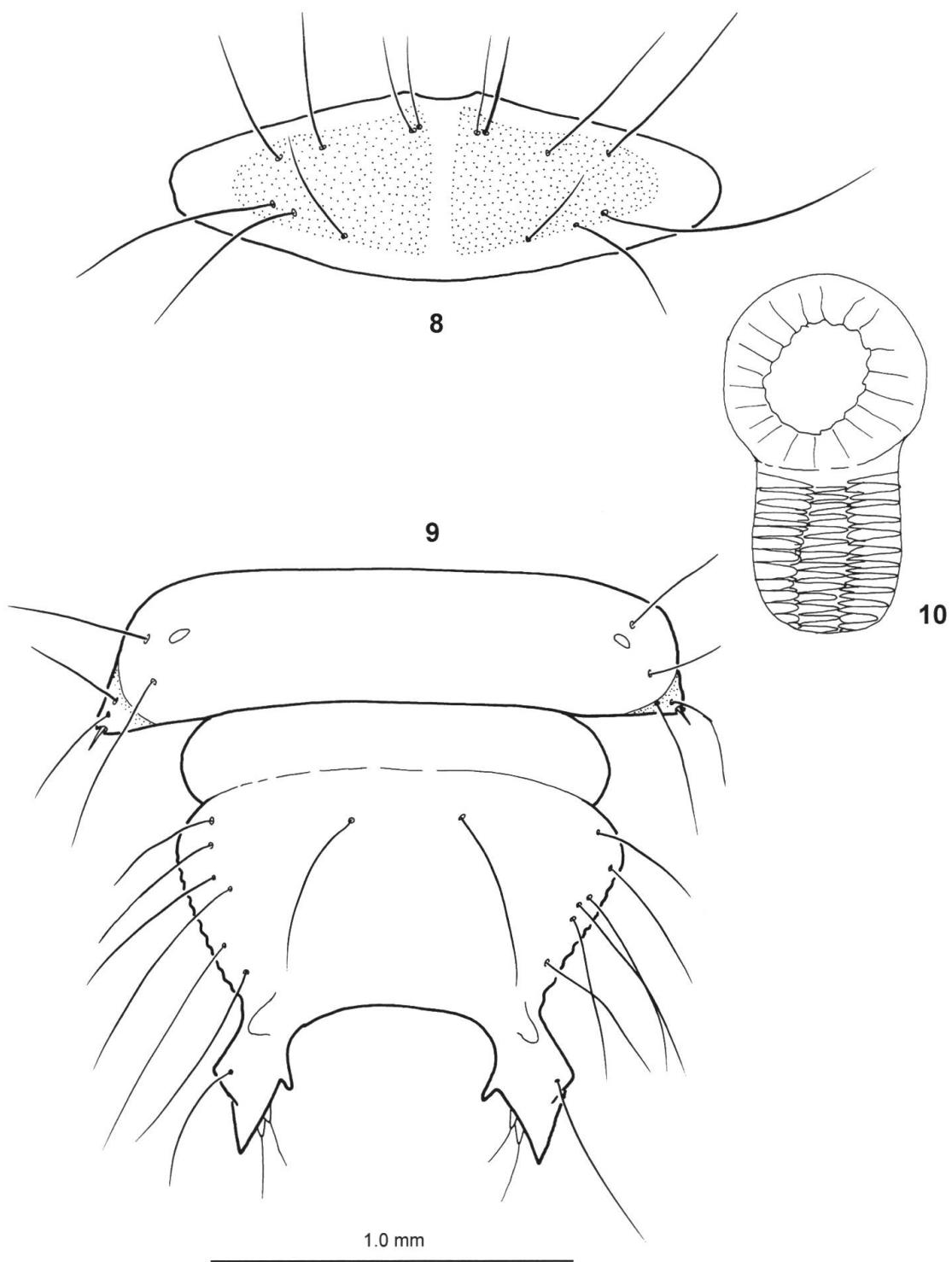
Pl. 10. *Tenebroides fuscus* Goeze, larva: 4, body dorsally; 5, thorax ventrally (legs removed); 6, stemmata; 7, abdominal spiracle; 8, front leg. Figures 6, 7 schematically, without scales.



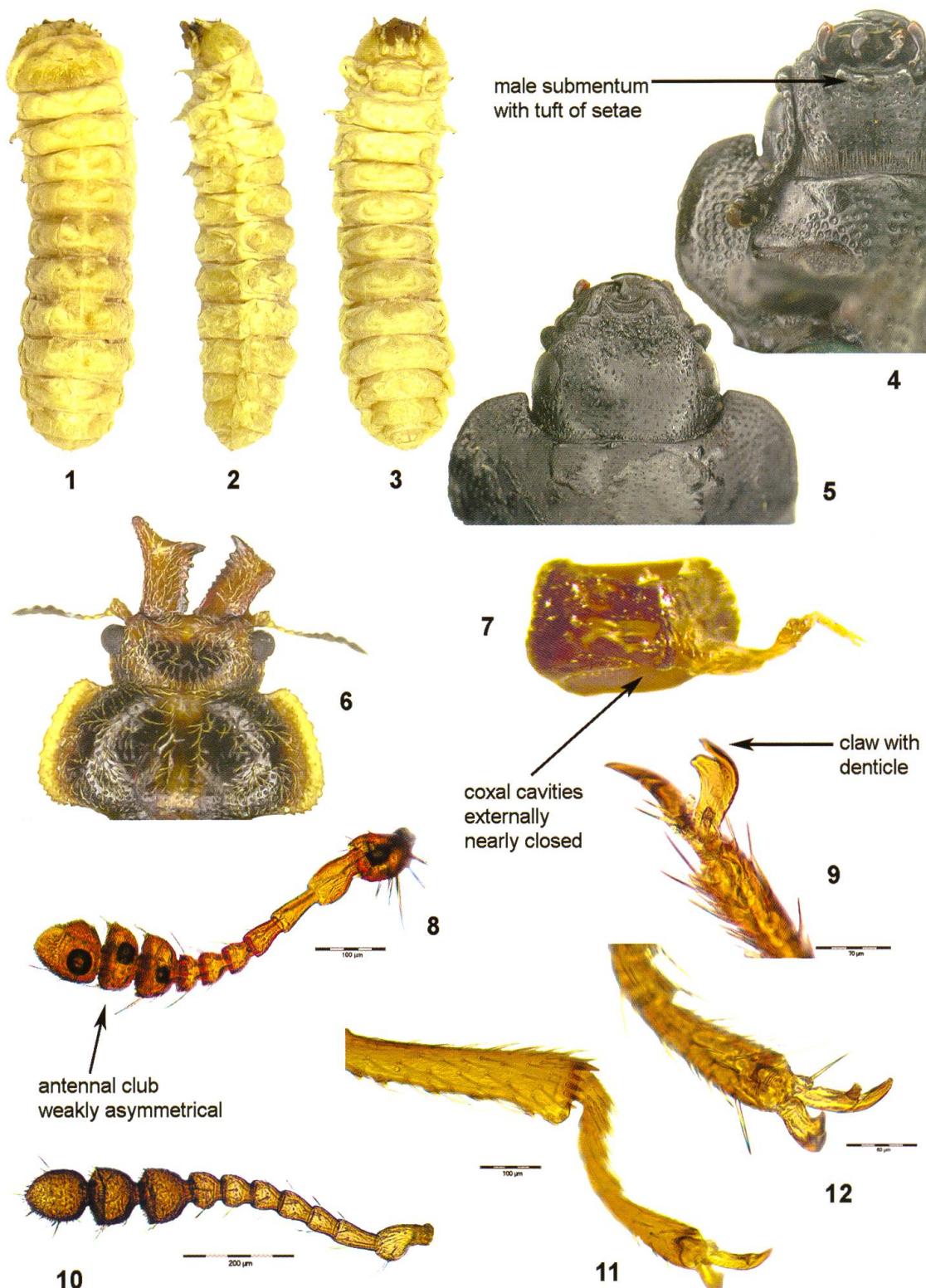
Pl. 11. *Thymalus limbatus* Fabricius, larva: 1, maxillolabial complex; 2, mandible ventrally; 3, epipharynx.



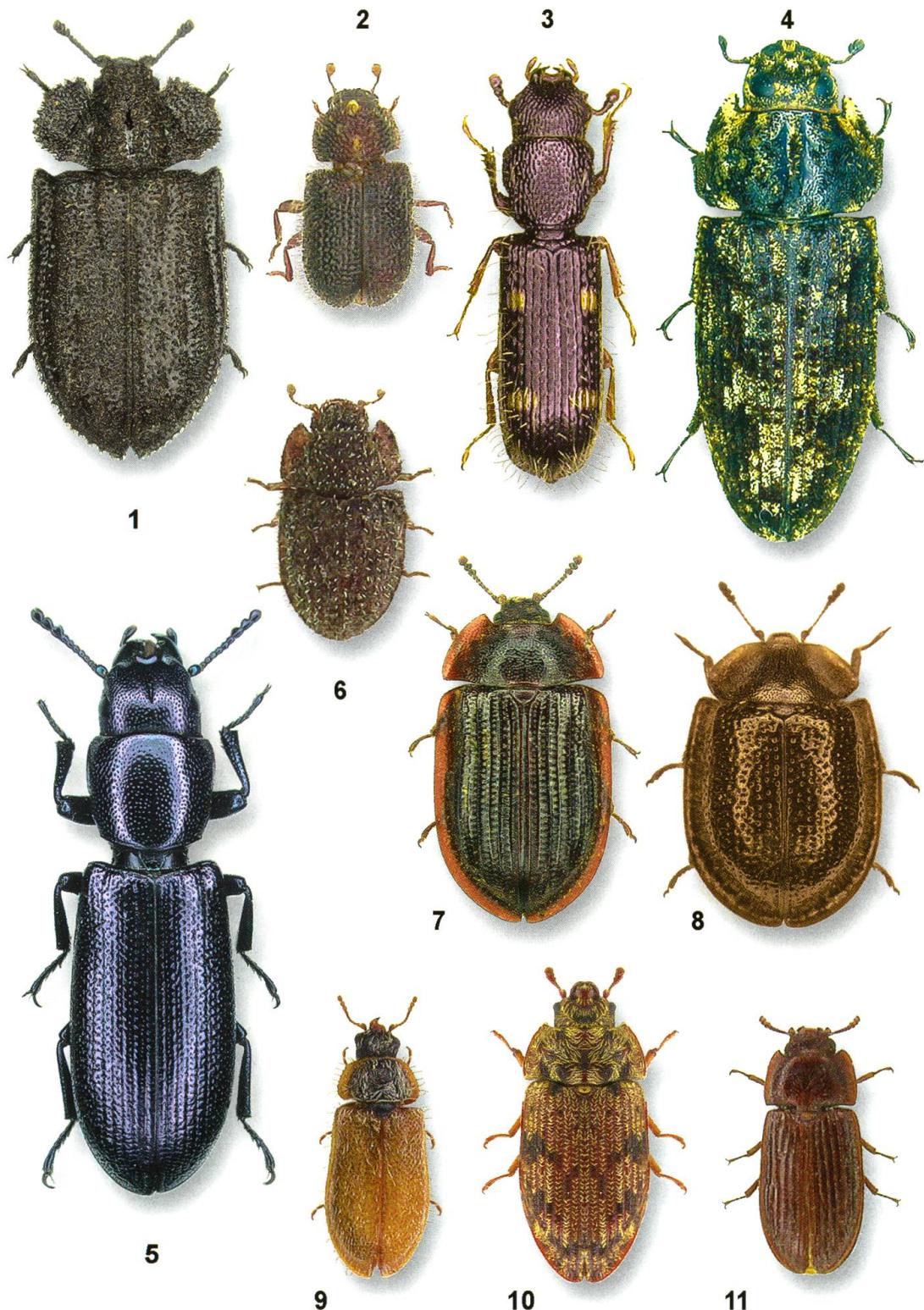
Pl. 12. *Thymalus limbatus* Fabricius, larva: 4, head capsule ventrally; 5, head capsule dorsally; 6, stellmata; 7, antenna. Figure 6 schematically, without scale.



Pl. 13. *Thymalus limbatus* Fabricius, larva: 8, pronotum; 9, abdominal segments VIII, IX dorsally; 10, abdominal spiracle. Figures 8, 10 without scale.



Pl. 14. *Peltis ferruginea* Linnaeus, larva: 1, dorsally; 2, laterally; 3, ventrally. *Elestora fulgorata* Pascoe, head and prothorax: 4, ventrally; 5, dorsally. 6, *Leptonyxa fairmairei* Léveillé: head and pronotum. *Decamerus haemorrhoidalis* Solier: 7, prothorax ventrally; 8, antenna; 9, tarsal claw with denticle. *Diontolobus punctatipennis* Solier: 10, antenna; 11, middle tibia and tarsus; 12, tarsal claws and empodium.



Pl. 15. Representatives of the tribes: 1, *Calitys scabra* Thunberg; 2, *Larinotus umblicatus* Carter et Zeck; 3, *Acalanthis quadrisignata* Erichson; 4, *Gymnochila varia* Fabricius; 5, *Temnoscheila caerulea* Olivier; 6, *Colydiopeltis compactum* Slipinski; 7, *Peltis ferruginea* Linnaeus; 8, *Thymalus limbatus* Fabricius; 9, *Decamerus haemorrhoidalis* Solier; 10, *Ancyrona kosnovskorum* Kolibáč; 11, *Lophocateres pusillus* Klug.

