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Morphology, taxonomy and phylogeny of *Phloiophilus edwardsi* Stephens, 1830 (Coleoptera, Cleroidea)

by **Jiří Kolibáč**

Abstract. *Phloiophilus edwardsi* Stephens, 1830 (Coleoptera, Cleroidea) is redescribed and its character states inserted into a character matrix of ten families of Coleoptera and into a matrix of Trogossitidae genera. The matrices are analyzed by NONA. The resulting trees reveal relations of *P. edwardsi* to Cleroidea and to the tribes Thymalini and Colydiopeltini (Trogossitidae) and support its classification within Peltinae. It is therefore suggested that the former family Phloiophilidae should be re-classified as the tribe Phloiophilini Kiesenwetter, 1863 stat.nov. in Trogossitidae, Peltinae. Remarks on a classification and phylogeny of Trogossitidae are provided.

Key words: Coleoptera – Derodontoidea – Cucujoidea – Cleroidea – *Phloiophilus edwardsi* Stephens – Phloiophilidae – Phloiophilini – Trogossitidae – Peltinae

Introduction

The superfamily Cleroidea was established by Böving & Craighead (1931) exclusively on larval features. It contained all present taxa, Ciidae and Dermestidae. Trogossitidae (as Ostomatidae), formerly classified within "Clavicornia", was also included in Cleroidea in the same source. Crowson (1955) later defined Cleroidea in its modern form, Trogossitidae as a basal member of the superfamily. The classification of the family Trogossitidae itself has undergone several changes in the past 50 years. It evolved from Reitter's (1876) system of four groups (Nemozomini, Trogositini, Leperini, Peltini) which were later used as subfamilies (e.g. Léveillé 1910). Böving & Craighead (1931) had used a more simple system with two subfamilies, Tenebroidinae (= modern Trogossitinae) and Ostominae (= modern Peltinae). The latter system was also followed, for example, by Crowson (1955), Barron (1971), and Kolibáč *et al.* (2005). The second approach used in modern publications is that of Crowson some years later, who established two independent families, Trogossitidae and Peltidae (Crowson 1964a). He went on to add the third family Lophocateridae (Crowson 1970). This system, in its most atomized form, is as follows: Trogossitidae (Calitinae, Egoliinae, Trogossitinae), Peltidae (Decamerinae, Peltinae, Protopeltinae, Rentoniinae) and Lophocateridae. Since that time, two more subfamilies of Trogossitidae *sensu lato* have been established by Kireichuk & Ponomarenko (1990, Mesozoic Meligethiellinae) and Slipinski (1992, Larinotinae). The latter author also classified all nine recent subfamilies within the single family Trogossitidae. Such a classification was used by Lawrence & Newton (1995) and also in several important compendia and handbooks, including those by Lawrence *et al.* (1993, 1999ab) which contain comprehensive information on the morphology and biology of both larvae and adults. More valuable information on larvae is included in Lawrence (1991a) and Foster & Lawrence (1991). The most recent publications on the morphology, phylogeny and classification of Trogossitidae are those by Kolibáč (2005, 2006). The resulting system again contains only two subfamilies, but they are divided into a number of tribes: Trogossitinae (Calityni, Egoliini, Gymnochilini, Larinotini, Trogossitini) and Peltinae (Ancyronini, Colydiopeltini, Decamerini, Lophocaterini, Peltini, Thymalini). Information on the biology, distribution and identification of particular species of Trogossitidae is included in various handbooks, such as Arnett *et al.* (2002), Barron (1971), Klausnitzer (1996), Kolibáč (2007), Kolibáč *et al.* (2005), Vogt (1967).

Phloiophilus edwardsi Stephens, 1830 is an enigmatic species of European beetle. It has been classified within Dasytidae or Melyridae *sensu lato* (Reitter 1911, Lohse 1979) or as a part of an independent family, i.e. Phloiophilidae Kiesenwetter, 1863 (= Phloeophilidae), in conjunction with the genera *Xerasia* Lewis (now Byturidae) and *Acanthocnemus* Perris (Pic 1926). The latter genus is now classified in the monotypic family Acanthocnemidae Crowson, 1970 within the melyrid branch of Cleroidea, whereas Phloiophilidae is generally considered a relative of Trogossitidae (Crowson 1964a, Kolibáč 2004, Klausnitzer 1996, Lawrence *et al.* 1993, 1999ab, Majer 1994). Recently, Hunt *et al.* (2007) published a comprehensive study based exclusively on molecular data, according to which *Phloiophilus edwardsi* is related to Biphyllidae and Byturidae. Both the families are situated in a basal position at Cleroidea, near to Trogossitidae.

The biology of adults and larvae was described by Crowson (1964b), morphology for example by Crowson (1964a), Klausnitzer (1996), Lawrence (1982, 1991b), Lawrence *et al.* (1993, 1999ab), Lohse (1979). Details on distribution in Central Europe are mentioned, for example, by Horion (1953), Kolibáč *et al.* (2005) and Majer (1986). The Palaearctic distribution is described by Mayor (2007) and Lawrence *et al.* (1999a).

Herein, the relationship of *P. edwardsi* to Trogossitidae and other relevant families is evaluated on the basis of adult and larval morphology.

Material

The following taxa were studied:

Derodontidae	(*Derodontus maculatus* Melsheimer): Lawrence & Hlavac (1979), Ge *et al.* (2007), Böving & Craighead (1931), author's observation.
Phloeostichidae	(*Hymaea magna* Sen Gupta et Crowson): Leschen *et al.* (2005), Sen Gupta & Crowson (1966, 1969).
Cucujidae	(*Cucujus cinnaberinus* Scopoli): author's observation.
Cerylonidae	(*Cerylon* spp.): Lawrence & Stephan (1975), Lawrence *et al.* (1999ab).
Endomychidae	(*Endomychus coccineus* Linnaeus): Lawrence *et al.* (1999ab), Klausnitzer (1999), author's observation.
Coccinelidae	(*Psyllobora vigintiduopunctata* Linnaeus): author's observation.
Byturidae	(*Byturus tomentosus* DeGeer): Kolibáč (2008); author's observation.
Dasytidae	(*Haplamaurus suturalis* Kirsch): Majer (1994) and author's observation.
Malachiidae	(*Malachius aeneus* Linnaeus): Klausnitzer & Constantin (1996), author's observation.
Cleridae	Clerinae (*Clerus mutillarius* Fabricius), Korynetinae (*Necrobia violacea* Linnaeus): author's observation.

The representatives of the families listed above were selected with reference to data in the literature (especially LAWRENCE & NEWTON 1982, BEUTEL & POLLOCK 2000, LESCHEN *et al.* 2005, HUNT *et al.* 2007) and their availability. Derodontidae are generally considered a primitive polyphagan family. The 'cerylonid series' (represented by Coccinellidae, Endomychidae, Cerylonidae) are considered relatives of Cleroidea (HUNT *et al.* 2007) which are represented by the three largest groups (Dasytidae, Cleridae, Malachiidae). The remainder of the material includes representatives of Phloeostichidae and Cucujidae (LESCHEN *et al.* 2005). Trogossitidae are represented by three major groups: Trogossitinae (*Tenebroides mauritanicus* Linnaeus), Peltinae (*Thymalus limbatus* Fabricius), and former Lophocaterinae or the cluster Decamerini-Lophocaterini-Ancyronini (*Lophocateres pusillus* Klug).

Representatives (mostly type species) of nearly all trogossitid genera had already been gathered and examined for previous work on the morphology and phylogeny of the family (KOLIBÁČ 2002b, 2005, 2006).

Numerous specimens of adult *P. edwardsi* were available (locality labels "Germania, Arnstadt Thür., 26.10.18, W. Liebmann"). Larval features were extracted from literature, especially CROWSON (1964a) and LAWRENCE *et al.* (1993, 1999b).

Methods

NONA® (GOLOBOFF 1999), in conjunction with WinClada® (NIXON 1999–2002), was used for character analysis and construction of cladograms. Characters were unweighted and strict consensus techniques employed. A heuristic analysis (maximum trees ('hold') = 1000, number of replications ('mult*') = 100, multiple TBR+TBR ('mult*max*')) was used. The trees were rooted by the first taxon in the matrix (*Derodontus* in Derodontidae/ Cucujoidea/ Cleroidea matrix, a hypothetical ancestor in *Phloiophilus*/ Trogossitidae matrix). Tree support was calculated with a bootstrap (1000 replications, option 'mult*100; hold/100'), and Bremer support ('bsupport 1000').

In the first step, 31 morphological characters (16 adult and 15 larval) of 15 representatives of 10 beetle families were analyzed and selected using accelerated optimization (ACCTRAN) which favours acquisition of a character, with subsequent homoplasy accounted for by reversals (KITCHING *et al.* 1998). (For an ancient group, the frequency of reversals might be high, therefore this optimization was favored against DELTRAN.) Six multistate characters (with more than 2 states) were switched as nonadditive because their states did not form linear transformations. The character matrix was then counted by NONA to find a position for *P. edwardsi*. Because this species showed the nearest relation with *Thymalus limbatus* (Trogossitidae, Peltinae) and the cleroid branch, the character states of *P. edwardsi* were included in a matrix for Trogossitidae assembled by KOLIBÁČ (2006). The latest taxonomic changes in the tribe Ancyronini (KOLIBÁČ 2007) were adopted into the matrix: *Latolaeva* Reitter, 1876 was synonymized with *Ancyrona* Reitter, 1876 and *Afrocyrona* Kolibáč, 2007 was described. The matrix by KOLIBÁČ (2006) was changed as follows: *Ancyrona*, character 45: 0.3 instead of 45: 3; row with *Latolaeva* deleted and row for *Afrocyrona* character states added. A complete matrix of 43 trogossitid genera [1] with 88 characters (56 adult, 32 larval) was optimized by accelerated optimization (ACCTRAN) (see Kolibáč 2006). Optimization was checked again while preparing this communication because of the mentioned changes. The characters marked as uninformative (27 characters; see List of characters) were not used for construction of trees but they are kept in the matrix. They can serve as reference for the morphology of particular genera and as a complement to the description of *P. edwardsi*. From the remaining 61 informative characters, all multistate characters were switched as nonadditive (none of them forms a linear transformation) but for characters 17, 18. Unknown character states (especially those of unknown larvae) were marked by the question mark (“?”). These characters were mostly switched off during optimization.

Standard dissection methods were employed throughout. This communication has been several years in the creation, and ink 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.

Abbreviations

labium (Fig. 1)

hpb	hypopharyngeal bar
lg	ligula
ma	mental apodeme
mt	mentum
pm	prementum

mandible (Fig. 2)

bn	basal notch
dat	dorsal apical tooth
mt	medial tooth
pc	penicillus
pt	prostheca
vat	ventral apical tooth

maxilla (Fig. 3)

bs	basistipes
hls	hook-like spines (lacinia)
lc	lacinia
ms	mediostipes
pf	palpifer

labrum (Fig. 4)

ltp	lateral tormal process
mtp	median tormal process
pltp	projection of lateral tormal process

cranium (Fig. 5)

gs	gular suture
tb	tentorial bridge

prothorax (Fig. 6)

psp	prosternal process

meso- and metathorax (Fig. 7)

aes	anepisternum
aet	anepisternum of metathorax
dl	discriminal line
mf	mesosternal furca (mesendosternite)
pcs	paracoxal suture
pp	prepectus

leg (Figs 7, 8)

aps	apical spines in tibiae
em	empodium
tr	trochanter

metendosternite (Fig. 12)

at	anterior tendons
lm	lamina
st	stalk

male abdominal segment IX (Fig. 14)

st IX	sternite IX
tg IX	tergite IX
sp IX	spiculum of sternite IX

ovipositor (Figs 17, 18)

cx	coxita
cxs	coxital stylus

female internal reproductive organs (Fig. 19)

bcx	bursa copulatrix
sg	spermathecal gland
spt	spermatheca
vg	vagina
gt	gut

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1) Trogossitidae comprise 52 recent genera. Morphological data on ten of them are poor and could not be used in analysis. For a list of them and a description of their known characters see Kolibáč (2005, 2006).

Results

Analysis of the matrix (Tab. 1) resulted in six most parsimonious trees. A strict consensus tree is shown in Tree 1 (L = 75, Ci = 49, Ri = 63). There are four monophyletic groups, all of them supported by more than 50% probability (bootstrap support – BO, Bremer support – BR): (1) *Derodontus*, (2) *Hymaea* (BO = 100), (3) other 'Cucujoidea' (BO = 51, BR = 1), (4) Cleroidea (BO = 53, BR = 2). *Byturus* is situated among *Psyllobora*, *Endomychus*, *Cucujus* and *Cerylon*. *Phloiophilus* is a part of the Cleroid clade. The taxa representing three major groups of Trogossitidae (two tribal clusters of Peltinae or former Lophocaterinae, Peltinae; Trogossitinae) form separate clades in Cleroidea. Sister groups *Haplamaurus* – *Malachius* and *Clerus* – *Necrobia* are highly supported (BO = 98, BR = 12; BO = 74, BR = 13).

In the second step, *Phloiophilus edwardsi* was studied together with representatives of 43 genera of Trogossitidae. Analysis of the matrix (Tab. 2) resulted in 48 most parsimonious trees. A strict consensus tree is shown in Tree 2 (L = 286, Ci = 31, Ri = 65). There are three major branches: Peltinae *sensu stricto* (the cluster Peltini-*Phloiophilus*-Colydiopeltini-Thymalini), Trogossitinae and former Lophocaterinae (the tribe Decamerini, Lophocaterini, Ancyronini). Approximately two-thirds of the trees (32 total) support a sister-group relationship between the latter group and Peltini-*Phloiophilus*-Colydiopeltini-Thymalini. Only 16 trees support a sister-group relationship between Decamerini-Lophocaterini-Ancyronini and the subfamily Trogossitinae. Moreover, the latter relation is based on a only single character state in all those 16 trees – absence of the anterior apodemes in the larval gula. *P. edwardsi* is situated in the vicinity of Colydiopeltini and Thymalini (BR = 5). Bootstrap values are relatively low in this cluster, only the clades *Colydiopeltis*-*Parapeltis* and *Rentonellum*-*Rentonium* are supported with values higher than 50 (BS = 60 and BS = 64, respectively).

Character list (Cleroidea, outgroups)

Adult characters

01. **Clypeus (exposed, distinct):** present = 0; absent = 1.
Presence of the exposed clypeus is widespread among Cucujoidea. It is considered a plesiomorphy because of its presence in Derodontidae.

02. **Eyes emarginate near antennal insertion:** no = 0; yes = 1.

03. **Antennal club:** present = 0; absent = 1.

04. **Mandibular mola:** present = 0; absent = 1.

05. **Mandible – number of apical teeth:** 2 teeth = 0; 1 tooth = 1.
Two apical teeth are considered a plesiomorphic state because of their presence in basal groups of Cucujoidea and Cleroidea, mostly fungivorous. Unidentate mandibles often occur in predacious groups (Cleridae, some Trogossitidae).

06. **Mandible – prostheca:** present = 0; absent = 1.

07. **Maxilla – lacinia:** apex with hook-like spines = 0; apex without hook-like spines = 1.
See for example Kolibáč (2005: pl. 47, 3; pl. 51, 3).

08. **Front coxae:** transverse = 0; rounded = 1.

09. **Front coxae:** projecting = 0; not projecting = 1.
The front coxae are coded as projecting when the projection is approximately as long as the horizontal length of the coxa.

10. **Middle coxal cavities:** not widely separated = 0; widely separated = 1.
The middle coxal cavities are coded as widely separated when the space between the coxae is approximately as wide as a diameter of the coxa.

11. **Middle and hind coxae:** projecting = 0; not projecting = 1.
The middle coxae are coded similarly to the front ones (character 8). Projections of the hind coxae are approximately as long as the width of the coxa.

12. **Wing – medial (sub-cubital) fleck:** absent = 0; present = 1.

13. **Tarsomeres (excluding the last one):** without lobes = 0; with lobes = 1.

14. **Tarsal claw – appendages:** absent = 0; present = 1.
This refers to membranous appendages between the tarsal claws. They are typical of the Melyrid branch of Cleroidea (Majer 1994). Some membranes also occur in Hydnocerinae (Cleridae) (Kolibáč 1998).

15. **Male abdominal segment IX:** present = 0; absent = 1.
Segment IX is either well developed (i.e. sternite, tergite and spiculae are present) or tergite and sternite are absent and only a spicular fork (spiculum) remains.

16. **Aedeagus:** uninverted = 0; inverted = 1.
The phallobase is dorsally open in the uninverted aedeagus, ventrally open in the inverted one. An orifice in the apical (parameral) part of the tegmen is usually situated on the opposite surface to that in the basal part.

Larval characters

17. **Frontal arms:** curved = 0; straight = 1; reduced or absent = 2. [nonadditive].
This character is coded as nonadditive because an absence of the frontal arms can be derived from state 0 or even state 1.

18. **Epicranial stem:** absent = 0; present = 1.

19. **Endocarina:** absent = 0; present = 1.

20. **Stemmata:** 6 = 0; 5 or less = 1.

21. **Cranium – anterior hypostomal margin:** connected (if gula same as, or shorter than, half of cranium) = 0; disconnected (if gula same as, or shorter than, half of cranium) = 1; disconnected, (if gula as long as cranium) = 2; absent = 3. [nonadditive].
The character is probably not homologous with an endoskeletal structure called the hypopharyngeal bracon (Lawrence 1991). See Kolibáč (2006: pl. 4, 4 and all other figures of larval head) for state 0. This state also occurs in Lymexylidae (Kolibáč 2002) and is considered plesiomorphic. State 1 means absence of the hypostomal (anterior) margin of the cranium – it is ventrally open after removal of the maxillolabial complex. If the gula is as long as the ventral surface of the cranium, the hypostomal margin is absent and the cranium is open; the character state is derived regarding 21(0) and 21(1). The ventral surface of the cranium is highly modified in Cerylonidae and the state is coded as 'absent' (3). The state is unknown to me in *Derodontus* and *Hymaea*.

22. **Clypeus (exposed, distinct):** yes = 0; no = 1.

23. **Gula:** shorter than half of cranium = 0; longer than half of cranium = 1; absent = 2. [nonadditive].

    See character 21. The ventral surface of the cranium is highly modified in Cerylonidae and the state is coded as 'absent'.

24. **Gula – anterior apodemes:** present (tentorium rooted in apodemes) = 0; absent (tentorium rooted in gular sutures) = 1; gula absent = 2. [nonadditive].

    State 0 also occurs in Lymexylidae (Kolibáč 2002) and is considered plesiomorphic.

25. **Antenna – sensory appendix:** shorter than half of segment 3 = 0; nearly as long as segment 3 = 1.

26. **Mandible – prostheca (lacinia mandibulae):** absent = 0; present = 1.

27. **Lacinia or mala – pedunculate seta:** absent = 0; present = 1.

28. **Lacinia or mala – apical spines or bidentate protrusion:** present = 0; absent = 1.

    See Kolibáč (2006: pl. 11, 1), Crowson (1966: Fig. 15) for state 0.

29. **Number of pretarsal setae:** 2 = 0; 1 = 1; 0 = 2. [nonadditive].

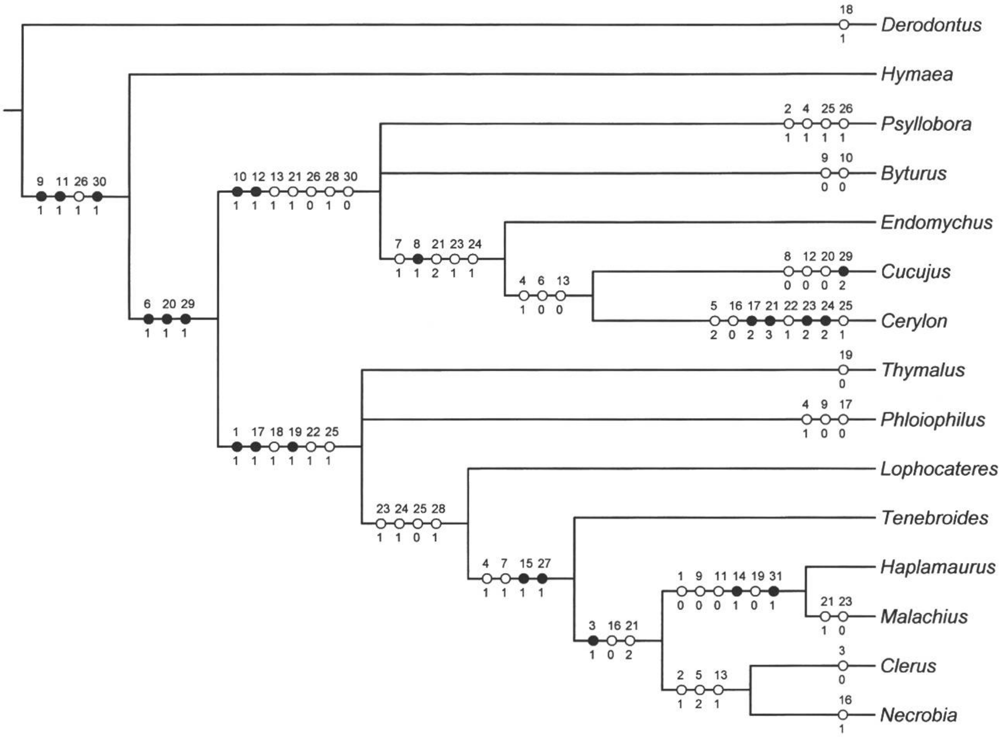
30. **Abdominal sclerites (dorsal):** longitudinal line present = 0; longitudinal line absent = 1.

31. **Ventriculus – structure:** smooth or undulate = 0; net-like = 1.

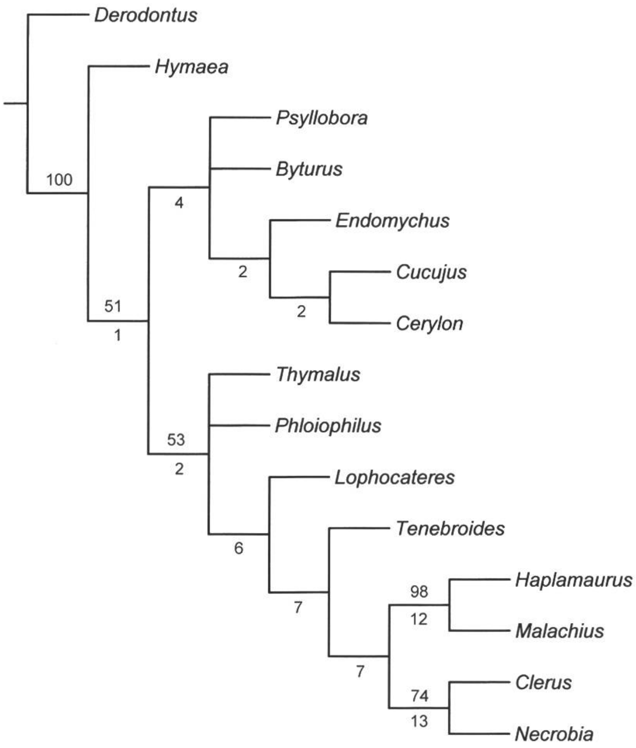
    State 1 is typical of the Melyrid branch of Cleroidea (Kolibáč 1999). Leschen & Carlton (1988) illustrated the alimentary canal of *Endomychus biguttatus* Say with perhaps a similar structure.

CHARACTER TAXON	01	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	20	1	2	3	4	5	6	7	8	9	30	1
Derodontus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	?	0	0	?	0	0	0	0	0	0	0
Hymaea	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	?	0	0	?	0	1	0	0	0	1	0
Cucujus	0	0	0	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	2	0	1	1	0	0	0	1	2	0	0
Cerylon	0	0	0	1	1	0	1	1	1	1	1	1	0	0	–	0	2	0	0	1	3	1	1	2	1	0	0	1	1	0	0
Endomychus	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	0	0	0	1	2	0	1	1	0	0	0	1	1	0	0
Psyllobora	0	1	0	1	0	1	?	0	1	1	1	1	1	0	?	1	0	0	0	1	1	0	0	?	1	1	?	1	1	0	0
Byturus	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	1	1	0	0	0	1	0	0	1	1	0	0
Thymalus	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	1	1	0	1	0	1	0	0	1	1	0	0	1	1	0
Lophocateres	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	0
Tenebroides	1	0	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	0
Clerus	1	1	0	1	1	1	1	0	1	0	1	0	1	0	1	0	1	1	1	1	2	1	1	1	0	1	1	1	1	1	0
Necrobia	1	1	1	1	1	1	1	0	1	0	1	0	1	0	1	1	1	1	1	1	2	1	1	1	0	1	1	1	1	1	0
Haplamaurus	0	0	1	1	0	1	1	0	0	0	0	0	0	1	1	0	1	1	0	1	2	1	1	1	0	1	1	1	1	1	1
Malachius	0	0	1	1	0	1	1	0	0	0	0	0	0	1	1	0	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1
Phloiophilus	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	1	1	0

Tab. 1. Character state matrix for 15 taxa of Cleroidea and outgroups.



Tree 1a. Strict consensus tree of 6 equally parsimonious trees computed from Tab. 1. L = 75, Ci = 49, Ri = 63.



Tree 1b. Bootstrap values above 50 (numbers above branches) and Bremer support values (numbers below branches) for Tree 1a.

Character list (Trogossitidae, *Phloiophilus edwardsi*)

[incl. characters deactivated after optimization]

Adult characters

01. **Body shape:** flat, oval = 0; elongate = 1; oval, weakly convex (not conglobate) = 2; oval, conglobate = 3. [nonadditive]
States 1, 2 are derived from 0; state 3 could be derived from 2. Therefore the character is coded as nonadditive.

02. **Gular sutures:** widely separated at base, convergent at apex = 0; narrowly separated at base, subparallel = 1; reduced in length = 2; widely separated at base, subparallel = 3. [nonadditive]
States 1, 2, 3 may be independently derived from 0. The character is therefore coded as nonadditive.

03. **Frontoclypeal suture:** present, straight = 0; absent = 1; broadly emarginate (curved posteriad) = 2. [nonadditive]
States 1, 2 are independently derived from 0. For an illustration of state 2 see Kolibáč (2005: pl. 58, 3).

04. **Frons – longitudinal groove or depression:** absent = 0; present = 1.

05. **Cranium in ventral view – lateral tufts of long setae:** absent = 0; present = 1.

06. **Submentum of males – tuft of setae:** absent = 0; present = 1.
See Kolibáč (2006: pl. 14, 4) for state 1.

07. **Submentum – anterior margin with row of setae:** absent = 0; present = 1.

08. **Antennal groove:** absent = 0; present = 1. [deactivated]
The antennal groove is situated in the ventral surface of the head. About three to eight antennal segments may fit into the groove.

09. **Eyes – size:** moderate (space between eyes about twice eye diameter) = 0; large (space between eyes narrower than eye diameter), eyes laterally situated = 1; large (space between eyes narrower than eye diameter), eyes dorsolaterally situated = 2; small and flat (space between eyes more than twice eye diameter) = 3. [nonadditive]

10. **Eyes – number:** 2 = 0; 4 = 1.
The eyes of some Gymnochilini are horizontally divided. Smaller ventral eyes are situated near the antennal sockets.

11. **Epicranial acumination:** moderate = 0; deep = 1; absent = 2. [nonadditive] [deactivated]
See Kolibáč (2005: pl. 67, 6) for state 0.

12. **Lacinia – number of hook-like spines at apex:** 2 = 0; 1 = 1; 0 = 2; 3 = 3. [nonadditive] [deactivated]

13. **Galea – shape:** elongate = 0; subclavate = 1; clavate = 2; partially fused with lacinia = 3; very small = 4. [nonadditive]
See Fig. 3 and Kolibáč (2005: pl. 1, 1) for state 1. See Kolibáč (2005: pl. 7, 6) for state 2.

14. **Galea – ciliate setae:** absent = 0; present = 1.

Setae in maxilla and rarely also labium are 'ciliate' in some Trogossitinae – the setae bear minute denticles or very fine pubescence (KOLIBÁČ 2005: pl. 13, 3; pl. 49, 4).

15. **Mediostipes – Lacinia:** `not fused = 0; partially fused = 1; completely fused = 2. [additive]`

16. **Palpifer – outer edge:** `smooth = 0; denticulate = 1.`

17. **Mandible – number of apical teeth:** `2 teeth situated in horizontal axis = 0; 2 teeth situated in vertical axis = 1; 1 tooth present = 2. [additive]`
    The apical teeth form a linear transformation series in Trogossitidae: bidentate mandible (0) with teeth situated "one next to the other" (or in horizontal axis) are primitive (see character 5 in the previous character list); dorsal tooth moved down and apical teeth situated "one above the other" (or in vertical axis) – former ventral teeth is apical, former dorsal teeth below it (1); former dorsal or subapical tooth more or less reduced to absent (2) and mandible is unidentate.

18. **Mandibular mola:** `present = 0; reduced but remnant of mola present = 1; absent = 2. [additive]`
    See KOLIBÁČ (2005: pl. 5, 9) for state 1. There are genera (e.g. *Gymnochila*) of which the species possess, or do not have, remnants of the mola. The character states form a linear transformation series and are coded as additive.

19. **Mandible – penicillus (at mandibular base):** `membrane with fine pubescence = 0; membrane and pubescence absent = 1; only long setae present, membrane absent = 2. [nonadditive]`
    The penicillus is considered the pubescent, mostly membranous, piece situated below the cutting edge or mola.

20. **Mandible – pubescence above mola or cutting edge (prostheca):** `absent = 0; present = 1. [deactivated]`

21. **Mandible – ventral ciliate furrow:** `furrow ciliate = 0; furrow not ciliate = 1; absent = 2. [additive][deactivated]`

22. **Mandible – basal notch:** `moderate = 0; deep (reaching about 1/3 of mandible) = 1; shallow or absent = 2. [additive] [deactivated]`

23. **Labrum – Cranium:** `not fused = 0; fused = 1.`

24. **Labrum – sclerite in epipharynx:** `absent = 0; present = 1.`
    See KOLIBÁČ (2005: pl. 66, 1) for state 1.

25. **Labrum – projection of lateral tormal process:** projection not developed (all remaining genera) = 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]

26. **Ligula – ciliate setae:** `absent = 0; present = 1.`
    See character 14 for explanation. Figured by KOLIBÁČ (2005: pl. 49, 1).

27. **Ligula:** `rigid = 0; membranous = 1.`

28. **Ligula:** `not retroflex = 0; weakly retroflex = 1; strongly retroflex = 2. [additive][deactivated]`

The ligula is a complex, 3-dimensional formation in Trogossitinae. It is mostly sclerotized (rigid) and retroflexed to inner (hypopharyngeal) side. It is schematically illustrated e.g. in Kolibáč (2005: pl. 3, 2).

29. **Ligula – shape:** weakly emarginate = 0; deeply emarginate = 1.
30. **Labium – hypopharyngeal sclerite:** absent = 0; sickle-shaped = 1; H-shaped = 2; 2 separate sclerites = 3. [nonadditive] [deactivated]

    States 1, 2 are derived from 0. State 3 is probably derived from 2. The character is therefore nonadditive.
31. **Antenna:** 11-segmented = 0; 10-segmented = 1; 9-segmented = 2; 8-segmented = 3; 7-segmented = 4. [nonadditive] [deactivated]

    States 0 to 4 as appear to be a linear transformation series. However, the states occur in unrelated genera (*a posteriori* principle). The character is nonadditive.
32. **Antennal club:** symmetrical = 0; strongly asymmetrical, joints 9, 10 triangular = 1; weakly asymmetrical, apical joints oval = 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. **Mesothorax – prepectus:** present = 0; absent = 1.
38. **Middle coxal cavities:** open = 0; closed = 1.
39. **Elytra – long hairs:** absent = 0; present = 1.
40. **Elytral epipleure:** moderate (wide along humerus, continuously contracting towards apex) = 0; wide (same width along whole length) = 1; thin along whole length beyond humerus = 2. [nonadditive] [deactivated]
41. **Elytral lock:** absent = 0; present = 1.

    The elytral lock is a tongue-like apodeme situated in the apical part of the both elytra, on the inner side of the elytral suture.
42. **Elytra – carinae:** conspicuous = 0; inconspicuous (absent) = 1. [deactivated]
43. **Elytra – punctation:** regular, in rows = 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, slender (spines fine, much longer than wide at base) = 0; large (spine robust, about as long as width at base) = 1; reduced (absent) = 2. [nonadditive] [deactivated]

50. **Front tibiae – hooked spur:** present (well-developed) = 0; absent (apical spurs fine, not hooked) = 1.

51. **Tarsal claws – denticle:** absent = 0; small (only base of claw roundly thickened) = 1; well-developed (claw with distinct denticle) = 2. [nonadditive]

52. **Parasternites in abdominal sternites III–VII:** absent = 0; one = 1; two = 2. [nonadditive] [deactivated]

53. **Male abdominal sternite VIII – spiculum gastrale:** absent = 0; present = 1. [deactivated]

54. **Aedeagus – number of parts of tegmen:** 3 parts = 0; 2 parts = 1; 1 part = 2. [nonadditive] [deactivated]

55. **Ovipositor – coxitae:** divided = 0; undivided = 1. [deactivated]

56. **Biology:** fungivorous = 0; predatory = 1; floricolous = 2. [nonadditive]

Larval characters

57. **Cranium – frontal arms:** strongly curved (cucujoid) = 0; weakly curved (e.g. *Larinotus*) = 1; V-shaped = 2; Y-shaped = 3. [nonadditive]

58. **Cranium – epicranial stem:** present = 0; reduced (shorter than 1/5 of cranium) = 1; absent = 2. [additive] [deactivated]

59. **Cranium – endocarina:** present = 0; absent = 1.

60. **Cranium – gular sutures:** conspicuous, parallel = 0; conspicuous, convergent = 1; reduced, inconspicuous = 2. [nonadditive]
    State 1 is derived from 0, state 2 may be derived either from 0 or 1 (only in *Peltis* and *Thymalus*).

61. **Gula – anterior apodemes:** present = 0; absent = 1.
    State 0 also occurs in Lymexylidae (KOLIBÁČ 2002) and is considered plesiomorphic. (See also the previous character list to Cleroidea and outgroups.)

62. **Cranium – paragular sclerites:** absent = 0; present = 1.
    The terminology follows BÖVING & CRAIGHEAD (1931). The character has been omitted by CROWSON (1964a, 1966, 1970) and many modern authors.

63. **Cranium – hypostomal rods:** absent = 0; present = 1.

64. **Cranium – stemmata:** 5 = 0; 3 = 1; 2 = 2. [nonadditive]

65. **Mandible – apical teeth:** two, horizontally situated = 0; two, horizontally and vertically situated = 1; one tooth = 2. [additive] [deactivated]
    The character is explained in detail above (character 17, mandibles of adults).

66. **Mandible – prostheca (lacinia mandibulae):** several small spines = 0; plumose = 1; tridentate = 2; absent = 3. [nonadditive]

67. **Mandibular mola:** present = 0; reduced = 1; absent = 2. [nonadditive]
    The transformation of the mola is explained in the relevant section above (character 18). Too few larvae of Trogossitidae are known, so it is uncertain if the transformation is linear. The character is coded as nonadditive.

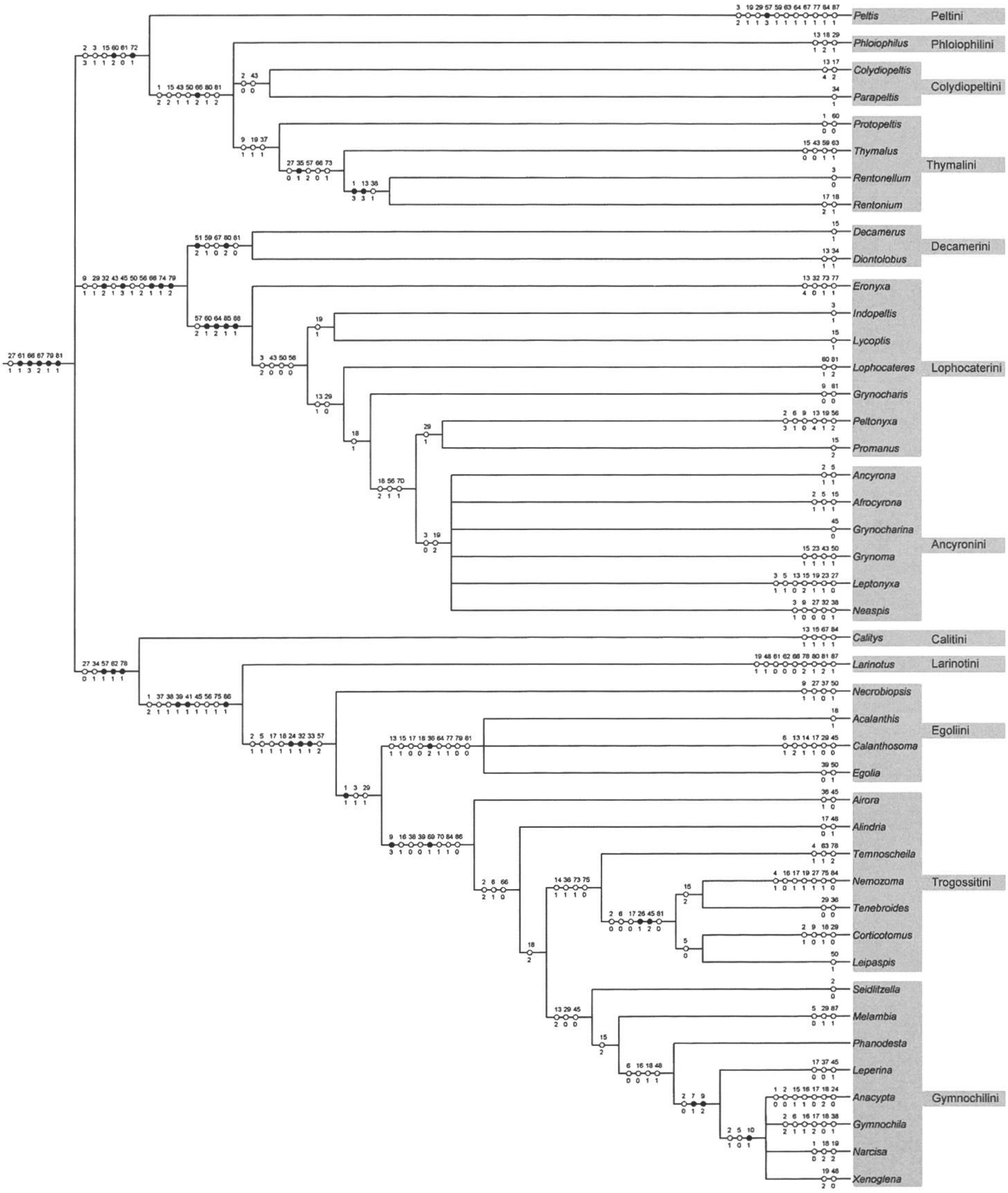
68. **Maxillary palpi:** 3-segmented = 0; 2-segmented = 1. [deactivated]
    State 1 is an autapomorphy of the presumed *Rentonium* larva. Uninformative character deactivated.
69. **Palpifer:** present = 0; absent = 1.
70. **Lacinia or mala – pedunculate seta:** absent = 0; present = 1.
71. **Lacinia or mala:** simple = 0; bilobed = 1. [deactivated]
72. **Lacinia or mala – apical spines or bidentate protrusion:** absent = 0; present = 1.
    See Kolibáč (2006: pl. 11, 1), Crowson (1966: Fig. 15) for state 0.
73. **Cardo – stipes:** not fused = 0; partially fused = 1.
74. **Cardo:** 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]
    State 1 is an autapomorphy of the presumed *Rentonium* larva. Uninformative character deactivated.
77. **Prementum:** in single part = 0; in two parts = 1.
78. **Prementum – anterior margin:** even = 0; with notch = 1; projecting = 2. [nonadditive]
79. **Labrum – torma:** single compact plate = 0; two separate lateral sclerites = 1; H-shaped = 2. [nonadditive]
80. **Antenna:** joints 1, 2 elongate = 0; joints 1, 2 transverse = 1; 1st transverse, 2nd elongate = 2. [nonadditive]
81. **Antenna – 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. **Abdominal tergite IX:** flat = 0; depressed (concave) = 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	5	6	7	8	9	0	1	2	3	4
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phloiophilus	2	3	1	0	0	0	0	0	0	0	2	0	1	0	2	0	0	2	0	1	2	2	0	0	4	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	0	1	1	0
Acalanthis	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	1	0	0
Airora	1	1	1	0	1	0	0	1	3	0	1	2	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	2	1	3	0	1	1	1	0	1	1	0	0	0	1	1	0	0
Alindria	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	1	0	0
Anacypta	0	0	1	0	0	0	1	1	2	1	0	2	2	0	1	1	0	2	0	0	2	2	0	0	0	0	0	1	0	3	1	1	1	1	0	0	1	0	0	2	1	1	0	0
Ancyrona	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	0	0	0	0	0	0	0	0	0	1
Afrocyrona	0	1	0	0	1	0	0	1	1	0	2	0	1	0	1	0	0	2	2	0	2	2	0	0	0	0	1	0	0	2	[01]	2	0	0	0	0	0	0	0	0	0	0	0	1
Calanthosoma	1	1	1	0	1	1	0	1	0	0	0	1	2	1	1	0	1	0	0	0	1	0	0	1	1	0	0	1	0	3	0	1	1	1	0	2	1	1	1	0	1	0	0	0
Calitys	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	2	0	0	2	0	0	2	0	2	0	0	0	1	0	0	0	0	0	1	0	0	0	1
Colydiopeltis	2	0	1	0	0	0	0	1	0	0	0	[01]	4	0	2	0	2	0	0	1	2	2	0	0	4	0	1	0	0	0	3	?	0	0	0	0	0	0	0	1	0	1	0	1
Corticotomus	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	0	1	0	1	1	1	0	1	1	0	0	0	1	1	0	0
Decamerus	0	0	0	0	0	0	0	0	1	0	2	2	0	0	1	0	0	0	0	0	0	2	0	0	5	0	1	0	1	2	1	2	0	0	0	0	0	0	0	2	0	1	1	0
Diontolobus	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	2	0	1	1	0
Egolia	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	1	2	1	1	1	1	0	2	1	1	0	0	1	1	0	0
Eronyxa	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	2	0	1	1	0
Grynocharina	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	2	0	0	0	0
Grynocharis	0	0	2	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	2	0	0	2	0	1	0	0	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Grynoma	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	0	1	0	0	3	1	2	0	0	0	0	0	0	0	0	0	1	1	0
Gymnochila	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	1
Indopeltis	0	0	1	0	0	0	0	?	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	2	0	2	0	0	0	0	?	0	0	0	0	0	0	0
Larinotus	2	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	0	3	2	0	0	1	0	0	1	1	1	0	1	1	0	0
Leipaspis	1	0	1	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	1	1	0	1	1	0	0	0	1	1	0	0
Leperina	1	0	1	0	1	0	1	1	2	0	1	2	2	0	2	0	0	1	0	0	2	2	0	1	1	0	0	0	0	3	0	1	1	1	0	0	0	0	0	0	1	0	0	1
Leptonyxa	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	1	2	0	0	0	0	0	0	0	0	0	0	0	0
Lophocateres	0	0	2	0	0	0	0	1	1	0	0	3	1	0	0	0	0	0	0	1	2	0	0	0	4	0	1	0	0	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Lycoptis	0	0	2	0	?	0	0	0	1	0	?	3	0	0	1	0	0	0	1	0	2	0	0	?	?	0	?	0	1	?	4	?	0	0	0	0	?	?	0	0	0	0	0	0
Melambia	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	2	1	0	0	0
Narcisa	0	1	1	0	0	0	1	1	2	1	2	2	2	0	2	0	1	2	2	0	2	2	0	1	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	1	1	0	1
Neaspis	0	0	1	0	0	0	0	0	0	0	2	2	1	0	0	0	0	2	2	0	2	2	0	0	0	0	0	0	0	2	1	0	0	0	0	0	?	1	0	0	0	1	0	1
Necrobiopsis	2	1	0	0	?	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	2	0	1	1	0	1	0	0	2	3	?	1	1	0	0	0	1	1	2	1	0	0	0
Nemozoma	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	[01]	1	1	1	0	1	1	0	0	2	1	1	0	0
Parapeltis	2	0	1	0	0	0	0	1	0	0	0	2	0	0	2	0	0	0	?	1	2	0	0	0	4	0	1	0	0	0	3	?	0	1	0	0	0	0	0	0	0	0	0	1
Peltis	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	0	0	0	0	0	0	0	0	0
Peltonyxa	0	3	2	0	0	1	0	1	0	0	0	2	4	0	0	0	0	2	1	0	2	0	0	0	3	0	1	0	1	2	2	2	0	0	0	0	0	0	0	0	0	[01]	0	0
Phanodesta	1	2	1	0	1	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	1	1	1	0	0	1	0	0	0	1	1	0	0
Promanus	0	0	2	0	0	0	0	1	1	0	2	0	1	0	2	0	0	2	0	0	2	2	0	0	3	0	1	0	1	2	0	2	0	0	0	0	0	0	0	0	0	1	0	0
Protopeltis	0	3	1	0	0	0	0	1	1	0	?	3	0	0	?	0	0	0	1	1	0	0	0	?	?	0	1	0	?	?	0	0	0	0	0	0	?	0	0	0	0	1	1	0
Rentonellum	3	3	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	3	1	0	0	0	1	0	1	1	0	1	0	1	1	0
Rentonium	3	3	1	0	0	0	0	1	1	0	2	?	?	?	?	?	2	1	1	0	2	2	0	0	0	0	0	0	0	2	1	0	0	0	1	0	?	?	?	2	0	1	1	0
Seidlitzella	1	0	1	0	1	1	0	1	3	0	0	2	2	0	0	1	1	2	0	0	2	2	0	1	1	0	0	1	0	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0
Temnoscheila	1	2	1	1	1	1	0	1	3	0	1	2	0	1	0	1	1	2	0	0	0	2	0	1	1	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	1	1	0	0
Tenebroides	1	0	1	0	1	0	0	1	3	0	0	2	0	1	2	1	0	2	0	0	0	0	0	1	1	1	0	1	0	3	0	1	1	1	0	0	1	0	0	0	1	1	0	0
Thymalus	2	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	1	0	0	1	0	1	0	0
Xenoglena	1	1	1	0	0	0	1	1	2	1	2	2	2	0	2	0	1	1	2	0	2	2	0	1	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	2	1	1	0	1

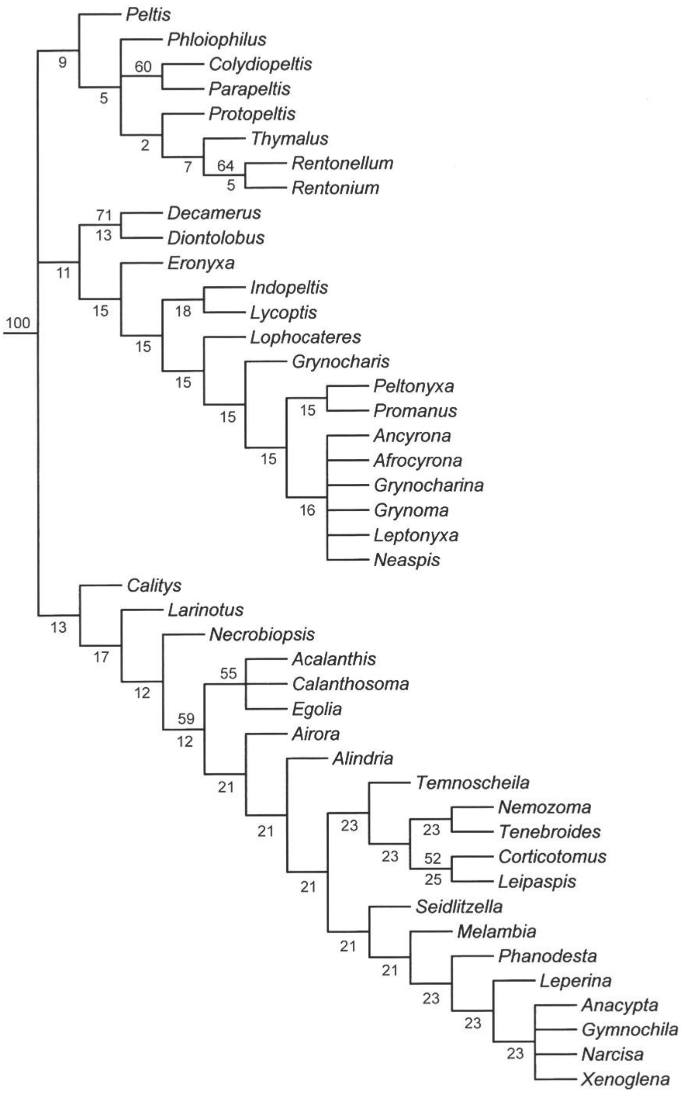
Tab. 2a. Character state matrix for Trogossitidae. Characters 1 to 44.

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	9	0	1	2	3	4	5	6	7	8
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phloiophilus	0	0	0	0	2	1	0	?	?	2	0	0	0	1	0	2	0	0	0	0	1	2	2	0	?	0	0	1	?	?	0	0	?	?	?	1	2	1	1	?	0	0	0	0
Acalanthis	1	0	0	0	0	0	0	1	0	0	1	1	2	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	0	?	0	?	?	?	1	0	0
Airora	0	0	0	0	1	0	0	1	0	1	1	1	2	1	0	0	1	1	0	0	0	3	2	0	?	?	?	?	?	0	?	0	0	?	?	0	1	0	0	?	0	0	0	0
Alindria	1	0	0	1	1	0	0	2	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Anacypta	0	1	1	1	2	0	0	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ancyrona	[03]	1	0	0	0	0	0	1	0	[01]	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Afrocyrona	[03]	1	0	0	0	0	0	1	0	1	0	[01]	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Calanthosoma	0	0	0	0	0	0	0	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Calitys	0	2	0	0	0	0	0	2	1	0	?	0	1	2	0	0	1	1	0	0	0	3	1	0	?	?	?	?	0	0	0	0	?	?	?	0	1	0	3	1	0	0	0	0
Colydiopeltis	?	?	?	?	2	1	0	2	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Corticotomus	2	1	1	0	1	0	0	?	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Decamerus	3	1	1	0	0	1	2	0	0	2	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Diontolobus	3	1	1	0	0	1	2	0	0	0	?	2	0	2	1	0	?	0	0	0	0	1	0	0	?	0	0	?	0	?	0	0	0	?	?	2	0	2	?	?	0	0	0	0
Egolia	1	0	0	0	2	1	0	1	0	0	?	1	2	2	0	0	1	1	0	1	0	3	2	0	0	0	1	0	0	0	1	0	1	?	0	0	0	0	?	0	0	1	0	0
Eronyxa	3	1	0	0	1	1	0	2	0	1	0	2	2	2	0	1	?	0	0	2	1	1	2	0	0	0	0	0	1	?	0	0	1	?	2	0	1	1	2	0	1	0	0	1
Grynocharina	0	1	1	0	0	0	0	2	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Grynocharis	3	1	1	0	0	0	0	2	1	0	?	0	2	2	0	?	?	?	?	2	0	1	2	0	?	0	0	0	0	1	0	0	0	?	?	0	0	0	?	?	1	0	0	1
Grynoma	3	1	1	0	0	1	0	1	0	0	?	1	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	2	?	?	?	?	?	1	0	0	1
Gymnochila	0	0	0	1	0	0	0	1	0	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Indopeltis	3	1	1	0	0	0	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Larinotus	1	0	1	1	2	0	0	?	0	1	?	?	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	2	1	1	2	2	3	0	0	1	1	0
Leipaspis	?	?	?	?	2	1	0	1	0	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Leperina	1	0	0	1	0	0	0	2	0	0	?	[01]	2	1	0	?	?	?	?	?	0	0	2	0	?	?	?	0	?	0	1	0	0	?	?	0	?	0	?	?	0	0	0	0
Leptonyxa	3	1	1	0	0	0	0	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lophocateres	3	1	1	0	0	0	0	1	0	0	1	0	2	2	0	1	1	0	0	2	0	1	2	0	0	0	0	0	0	1	0	0	0	0	2	1	2	2	4	0	1	0	0	1
Lycoptis	3	1	1	0	0	0	0	?	1	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Melambia	0	0	0	0	0	0	0	2	0	[01]	?	1	2	0	0	?	?	?	?	0	?	?	?	0	1	?	0	0	0	0	1	0	0	1	?	?	3	?	?	0	0	1	0	
Narcisa	0	0	0	1	2	0	0	1	0	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Neaspis	3	1	1	0	0	0	0	?	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Necrobiopsis	1	1	0	0	2	1	0	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nemozoma	2	1	0	0	1	0	0	1	0	0	1	1	2	1	0	0	1	1	?	0	2	0	2	0	1	1	0	0	?	0	1	0	0	1	?	0	0	0	0	0	0	0	0	0
Parapeltis	?	?	?	?	2	1	0	?	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Peltis	0	2	0	0	0	0	0	?	0	0	0	0	3	0	1	2	0	0	1	1	0	3	1	0	0	0	0	1	0	0	0	0	1	0	1	0	1	2	3	1	0	0	1	0
Peltonyxa	3	1	1	0	0	0	0	?	1	0	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Phanodesta	?	?	?	?	0	0	0	2	0	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Promanus	3	1	1	0	0	0	0	2	?	?	0	1	2	2	0	1	1	0	0	2	0	1	2	0	?	1	?	0	0	1	?	0	0	0	?	0	1	?	?	?	1	0	0	1
Protopeltis	0	1	1	0	0	?	0	?	?	1	?	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	1	0	0	?	0	0	0	?	1	2	0	2	0	0	0	0	0
Rentonellum	?	?	?	?	2	1	0	1	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rentonium	0	1	1	0	0	1	0	?	1	2	?	0	2	2	0	?	?	?	0	0	0	0	2	1	?	?	?	?	?	?	?	1	?	?	1	1	2	0	?	?	0	0	0	0
Seidlitzella	0	[01]	0	0	0	0	0	1	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Temnoscheila	1	0	0	0	0	0	0	1	?	?	1	1	2	1	0	0	1	1	1	0	1	0	2	0	1	1	0	0	1	0	0	0	0	2	1	0	1	0	0	1	0	0	0	0
Tenebroides	2	1	1	0	0	0	0	?	0	0	1	1	2	1	0	0	1	1	0	0	0	0	2	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0
Thymalus	0	0	0	0	2	1	0	1	0	0	?	0	2	1	1	2	0	0	1	0	0	0	2	0	0	0	0	1	1	0	0	0	0	0	1	1	2	3	3	0	0	0	0	0
Xenoglena	0	1	0	0	2	0	0	1	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Tab. 2b. Character state matrix for Trogossitidae. Characters 45 to 88.



Tree 2a. Strict consensus tree of 48 equally parsimonious trees computed from Tabs 2a, 2b (27 characters deactivated after ACCTRAN optimization; see character list). L = 287, Ci = 31, Ri = 65.



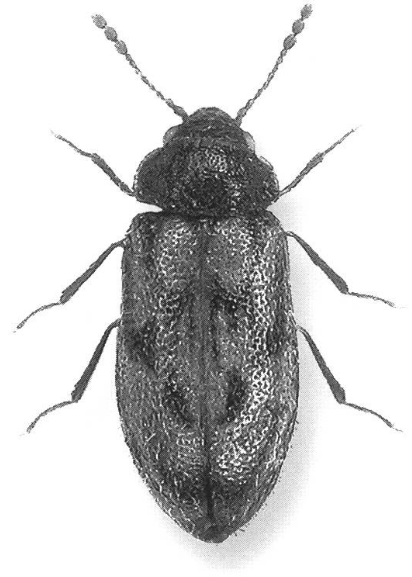
Tree 2b. Bootstrap values above 50 (numbers above branches) and Bremer support values (numbers below branches) for Tree 2a.

Redescription of *Phloiophilus edwardsi* Stephens, 1830

Adult.

Body oval, weakly convex; dorsal surface yellowish with brown pattern on elytra; whole body including antennae and legs densely pubescent; head, pronotum and elytra densely and irregularly punctate. Body length: ~3 mm.

Cranium (Fig. 5): gular sutures widely separated, extending to middle of cranium, weakly convergent or subparallel; frontoclypeal suture absent; frons without



Phloiophilus edwardsi Stephens. (Photo by the author.)

longitudinal groove; antennal grooves absent; antennal sockets visible from above; two eyes present, moderate in size (space between them about twice as wide as eye diameter), distinctly elevated, not emarginate; epicranial acumination absent; tentorial bridge with two distinct apodemes; ventral and lateral side of cranium without long setae.

Maxilla (Fig. 3): lacinia narrow, elongate, with two dark, hook-like spines at apex; basigalea present but weakly sclerotized; galea weakly clavate, with spines and two pigmented spurs; without ciliate setae; mediostipes completely fused with lacinia, suture inconspicuous; basistipes rhomboid; palpifer not denticulate along outer margin; maxillary palps 4-segmented, terminal joint conical, elongate.

Mandible (Fig. 2): with two apical teeth, one situated next to and very slightly above the other (thus in vertical, and very slightly horizontal, axes); medial tooth small; mola absent; penicillus formed by a small, membranous, finely-pubescencent appendage at base; prostheca formed by a larger, membranous, finely- pubescencent appendage along the "cutting edge"; ventral ciliate furrow absent; cutting edge concave; basal notch weak and shallow.

Labrum (Fig. 4): free (not fused with cranium); oblong, weakly emarginate; epipharynx without sclerite; projection of lateral tormal processes ("connecting tormal process") curved upwards but not connected at middle; median tormal process present.

Labium (Fig. 1): submentum without tuft of setae; mentum large, trapezoidal; prementum with deep notch or divided into two parts; ligula membranous, deeply emarginate, without ciliate setae, not retroflexed; mental apodeme composed of fused pair of sclerites; hypopharyngeal bar present; hypopharyngeal sclerite absent; terminal joint of labial palps short, conical.

Antennae (Fig. 5): 11-segmented; antennal club 3-segmented, loose; antennal joints symmetrical, without sensorial fields; antennae extend backwards to base of elytra.

Prothorax (Figs 6, 20): pronotum transverse, oval, lateral margins excavate; lateral edge present; prosternal process slender; procoxal cavities externally and internally open; trochantin indistinct.

Mesothorax (Figs 6, 9): prepectus present in anterior margin of anepisternum only, absent in mesosternum; mesocoxal cavities externally open, internally closed; trochantin indistinct; mesonotum wide (Fig. 9).

Metathorax (Figs 7, 10–12, 22, 23): metasternum flat and wide, weakly narrowed towards anterior portion; discriminal line present; paracoxal sutures well-demarcated, parallel with coxae; anepisternum weakly triangular; metanotum narrowed anteriad, with weak constriction at half of length (Fig. 11); metendosternite with broad stalk, laminae obliquely directed, anterior tendons rather widely separated (Fig. 12); elytra irregularly punctate, with narrow epipleure (Fig. 23); elytral locking mechanism absent, elytral carinae absent (Fig. 22); wing with radial cell present, trapezoidal, not displaced ventrally; pigmented fleck (below Rc) small, inconspicuous; medial (sub-cubital) fleck absent; wedge cell present, large; medial field with all four veins, cross veins MP3–4 and AA1+2–3+4 present (Fig. 10).

Legs (Figs 6–8, 20, 21, 24, 25): procoxae distinctly projecting (Fig. 21); mesocoxae oval, metacoxae normal (Fig. 7); weakly transverse; trochanters relatively small, triangular; femora not clavate; tibiae without denticles or spines along margin; apical spine pattern 2–2–2; hooked spurs absent; tarsomere 1 small but conspicuous in all pairs of legs; tarsomere 5 as long as, or subequal to, 1–4 combined; tarsal lobes absent (Fig. 8); claws without denticles (Fig. 24); empodium projecting, bisetose (Figs 24, 25); tarsomere 5 ventrally with apodeme – empodium partially retracted in ventral view; tarsal formula 5–5–5.

Abdomen (Figs 13–20): 5–6 sternites visible in dry specimens of both sexes (Fig. 20): sternite VIII visible or retracted in sternite VII; male sternite VIII without spiculum gastrale; male segments IX–X complete (Fig. 14); tegmen composed of single part, inverted (Fig. 16); phallobasic apodeme absent (or fused with dorsal part of phallobase); tegmenal struts absent; phallus slender, about twice as long as tegmen (Fig. 15) and about as long as three final visible apical sternites together; ovipositor relatively short, coxitae in two parts (Figs 17, 18); bursa copulatrix present; spermatheca oval, large (Fig. 19); vaginal sclerites absent.

Larva (Crowson 1964a, Lawrence 1982, Lawrence *et al.* 1999b).

Larva elongate, slightly flattened, lightly sclerotized except for head and tergite IX. Body whitish, moderately pubescent. Body length: ~4–4.5 mm.

Head prognathous, cranium transverse, strongly rounded; frontal arms strongly curved (lyriform), cucujoid; epicranial stem extremely short, nearly absent; endocarina complete to distinct frontoclypeal suture; gular sutures inconspicuous; gula with anterior apodemes; paragular sutures absent; hypostomal rods distinct, weakly convergent; five ocelli (stemmata) in cleroid pattern.

Mandible symmetrical; two apical teeth, one situated next to and above the other (or in both horizontal and vertical axes); one medial tooth present; prostheca (lacinia mandibulae) formed by tridentate projection growing from cutting edge; mola absent.

Maxilla: palpi short, 3-segmented, segments 1–2 transverse, segment 3 nearly twice as long as wide and slightly narrowed to apex; palpifer distinct; mala simple, blunt, with spines but without pedunculate seta, with bidentate protrusion near middle of inner side of mala; cardo transverse, articulating area well marked; stipes elongate.

Labium with broad obtuse ligula; insertion of palpi widely separated; prementum transverse, narrowed to base; mentum less transverse, somewhat widened to base; palpi 2-segmented, segment 1 transverse, segment 2 elongate; prementum, mentum and postmentum each with pair of long ventral setae.

Labrum free, small, transverse, oval, anterior margin rounded; epipharynx with about six clavate sensillae; torma composed of two relatively long lateral processes.

Antenna: 3-segmented, segments 1–2 wider than long (transverse); sensory appendix large, as long as segment 3.

Thorax: weakly sclerotized, pattern of thoracic sclerites 1–0–0 dorsally, 1–1–1 ventrally; pronotal sclerite divided by median line, bearing 4 pairs of large setae along front margin and 3 pairs along hind margin; prosternum with single pair of setae; meso- and metasternum sclerotized, each with single pair of setae; hind coxae more widely separated than front coxae; tarsungulus claw-like, with one ventral seta.

Abdomen: segments I–VIII without tergal sclerites and without distinct ampullae, with regularly arranged setae; segment IX not transversely divided, flat; urogomphi present, hooked; one small tubercle present at lateral side of each urogomphus; dorsal ampullae at segment IX absent; spiracles annular-biforous.

Biology. Described in detail by CROWSON (1964b). Adult and larva fungivorous, larvae feed beneath the thin and fleshy fruiting bodies of the basidiomycete *Phlebia radiata* Fr. from Meruliaceae (Crowson referred to it under the synonym *P. merismoides* Fr.) that occurs on dead wood of various deciduous trees (oak, beech, hazel), occasionally also conifers (pine). Adults are active in the warm days of autumn and winter (approx. from late September to March). They have not been observed outside that period (*P. radiata* can also be found only in that period. They can be collected by sweeping from dry or decaying branches. Larvae can be found at all seasons, under fruiting bodies of the fungus or under bark in spring and summer.

Distribution. Central and western Europe: Austria, Belgium, Czech Republic, Denmark, France, Great Britain, Germany, Hungary, Ireland, The Netherlands, Poland, Slovakia, Sweden, Switzerland (HORION 1955, MAYOR 2007). According to LAWRENCE *et al.* (1999a), *P. edwardsi* also lives in the North Africa.

Phloiophilus edwardsi was commonly recorded in the first half of the 20th century. In recent decades, it has been found sporadically at isolated sites (although the fungus *P. radiata* is still common). The last Central European record known to me is from Austria, about 70 km east of Vienna, on young decaying trees of *Pinus sylvestris* L. The species probably lives in the temperate Atlantic climatic zone from lowlands to the middle altitudes of mountains, and not in dry, warm areas or those that are too cold.

Tribe Phloiophilini Kiesenwetter, 1863 stat.nov.

Type genus: *Phloiophilus* Stephens, 1830 (type species: *P. edwardsi* Stephens, 1830 by monotypy)

Phloiophilidae Kiesenwetter, 1863 (selected references): PIC (1926), CROWSON (1955, 1964a, 1970), SLIPINSKI (1992), LAWRENCE *et al.* (1999a, b), KOLIBÁČ (2004).

Following the results of the character analysis, a classification of the former family Phloiophilidae as the tribe Phloiophilini stat.nov. in the subfamily Peltinae (Trogossitidae) is suggested. The tribes Thymalini and Colydiopeltini are sister groups.

Diagnosis. *P. edwardsi* differs from other Trogossitidae in having procoxae distinctly projecting (somewhat transverse in Trogossitidae). This character state should be considered a plesiomorphy in consideration of the general occurrence of the state within the outgroup taxa (Derodontidae, Cucujidae, and the clerid and melyrid branches of

Cleroidea). The apomorphies of *P. edwardsi* cited by Crowson (1964a: 283) are reductions that are also common in other Trogossitidae and Cleroidea. In particular, these consist of absence of spines and hooked spurs on the front tibiae (also in related Colydiopeltini, Thymalini), absence of mandibular mola in the adult (also in *Rentonium* Crowson and Ancyronini) and larva (also in Ancyronini, Lophocaterini, Thymalini).

Discussion

Crowson (1964a) first mentioned similarities between adults and larvae of the New Zealand species *Protopeltis viridescens* Broun (Peltinae: former Protopeltini or Protopeltinae, recently Thymalini; see Kolibáč 2006) and *P. edwardsi*. He also offered insights into the relations between *Protopeltis* Crowson and the former subfamily Rentoniinae (*Rentonium* Crowson) (Crowson 1966). Similarities between *Protopeltis* and the Holarctic genus *Thymalus* Latreille were proposed by Kolibáč (2004). All these relations have been variously demonstrated (Kolibáč 2005, 2006) and herein.

Recently, Hunt *et al.* (2007) published a phylogenetic tree of Coleoptera at the subfamily level based exclusively on molecular data. The families Byturidae and Biphyllidae are included in Cleroidea, while Phloiophilidae was shown to be a sister group of those two families. The 'cerylonid series' is a sister group of Cleroidea and both the groups are related to Tenebrionoidea and Lymexyloidea rather than to other traditional Cucujoidea. A close relationship between Cleroidea and Lymexyloidea (Lawrence & Newton 1982) was refuted by Beutel & Pollock (2000) and their conclusion confirmed by Hunt *et al.* (2007). On the other hand, Beutel & Slipinski (2001) show a close relationship of a representative sample of monophyletic Cleroidea with traditional Cucujoidea (paraphyletic in their cladograms). Lymexyloidea and Tenebrionoidea are distinguished from that cluster. The results of the latter authors are different of those of Hunt *et al.* (2007) and are more similar to the conclusions presented herein.

Byturidae (*Xerasia* Lewis) and Biphyllidae (*Anchorius* Casey) have also been studied by Leschen *et al.* (2005). In that paper, Byturidae are in a relationship with Boganiidae (*Paracucujus* Sen Gupta et Crowson) and Peltinae (*Thymalus* Latreille, *Eronyxa* Reitter) while Biphyllidae are placed near Erotylidae (*Pharaxonotha* Reitter). Adult *Byturus tomentosus* has aedeagus, mouth parts, meso- and metathorax very similar to those in primitive Cleridae or some Trogossitidae; the most conspicuous differences shown by *B. tomentosus* are in the presence of the medial (sub-cubital) fleck in the wings and the exposed clypeus. On the other hand, its larva is very different to all cleroid larvae known to me and resembles, for example, the larvae of some Endomychidae (e.g. *Leistes seminiger* Gyllenhal; Burakowski & Slipinski 2000). Further, particular cladograms based on larval and adult characters (Leschen *et al.* 2005) show differences in the classification of the taxa studied.

With regard to the different results in Hunt *et al.* (2007), the tribal rank for *Phloiophilus edwardsi* is a suggestion only; this topic requires further analysis of both molecular and morphological datasets.

The subfamilies and genera of Trogossitidae proposed by KOLIBÁČ (2006) only constitute a skeleton of the system; detailed classification of some genera has been unclear to date. The positions of the primitive (or 'basal') taxa are the most problematic. Here are some conclusions figured from the present communication (compare Tree 2a and relevant trees in KOLIBÁČ 2006) and critical remarks on the system of 2006:

(1) The genera *Seidlitzella* Jakobson and *Melambia* Erichson, formerly classified within Trogossitini, may be primitive members of Gymnochilini (Trogossitinae) as also mentioned by KOLIBÁČ (2006). This requires study of additional characters. Also the positions of *Necrobiopsis* Crowson (Egoliini) and *Airora* Reitter, *Alindria* Erichson (Trogossitini) are weak and the genera need further study (see KOLIBÁČ 2006 for details).

(2) The cluster Decamerini-Lophocaterini-Ancyronini is different from the content of the former subfamily Lophocaterinae (CROWSON 1964, 1966), which was identical with the present tribe Lophocaterini (KOLIBÁČ 2006). Although that cluster forms a tritomy together with Trogossitinae and the cluster Peltini-Colydiopeltini-Thymalini-suggested Phloiophilini in the consensus tree (Tree 2a), it is probably a sister group of the latter cluster (see the "Results" above and conclusions of HUNT *et al.* 2007). However, both the mentioned clusters of tribes form monophyletic groups; the separate subfamily names Lophocaterinae and Peltinae could therefore be used for them.

(3) Lophocaterini appears to be paraphyletic group in Tree 2a, ancestral with reference to Ancyronini. However, Lophocaterini are well defined by larval synapomorphies (characters 85, 88), the shape of the frontoclypeal suture (character 3) is a distinct synapomorphy in adults. Ancyronini are well defined by a number of derived characters in their mouthparts and their aedeagus. They are adapted to a predacious way of life.

(4) The position of *Grynocharina* Reitter is unclear. Only one specimen of *G. peltiformis* Reitter is known to date. This needs further study.

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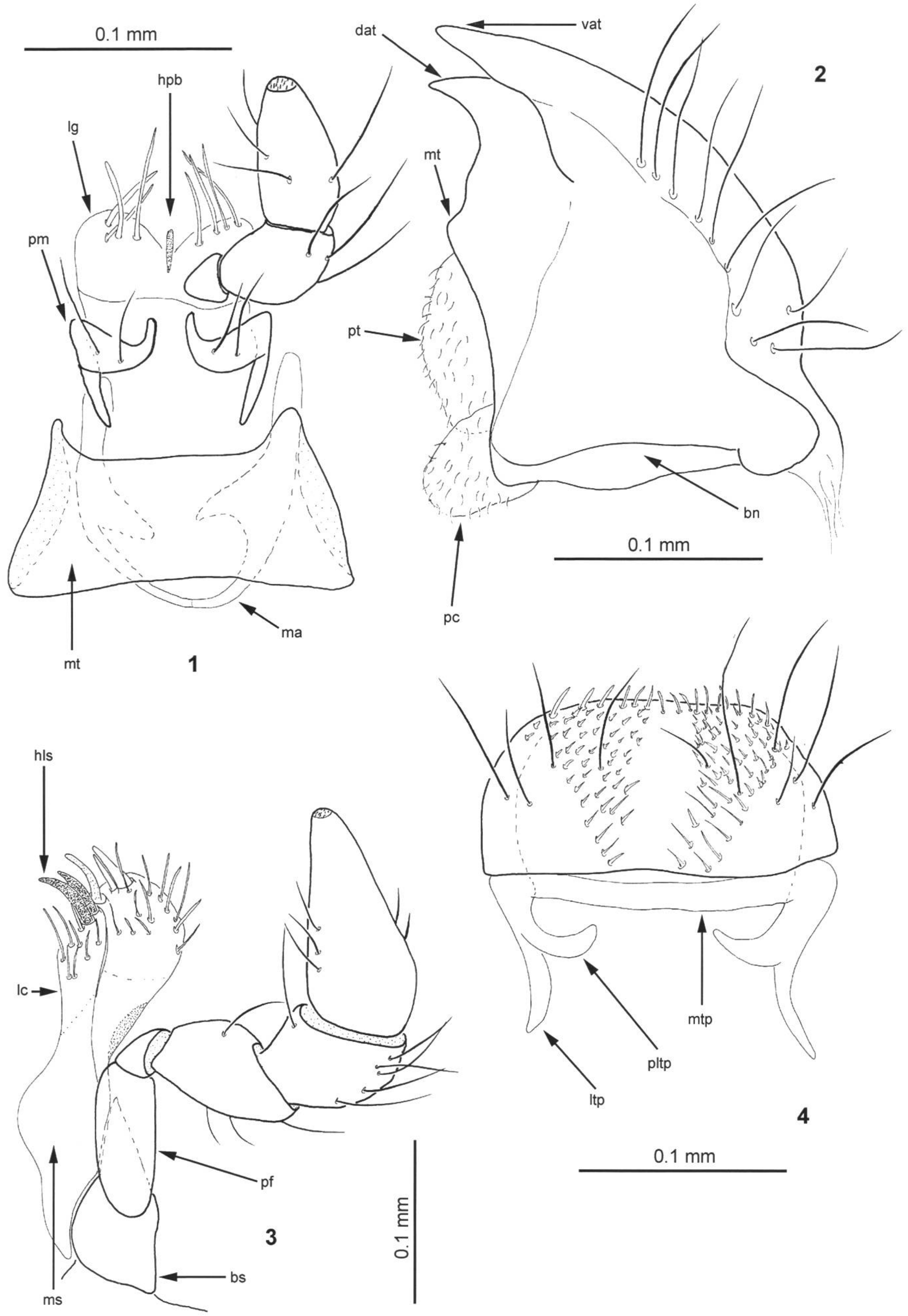
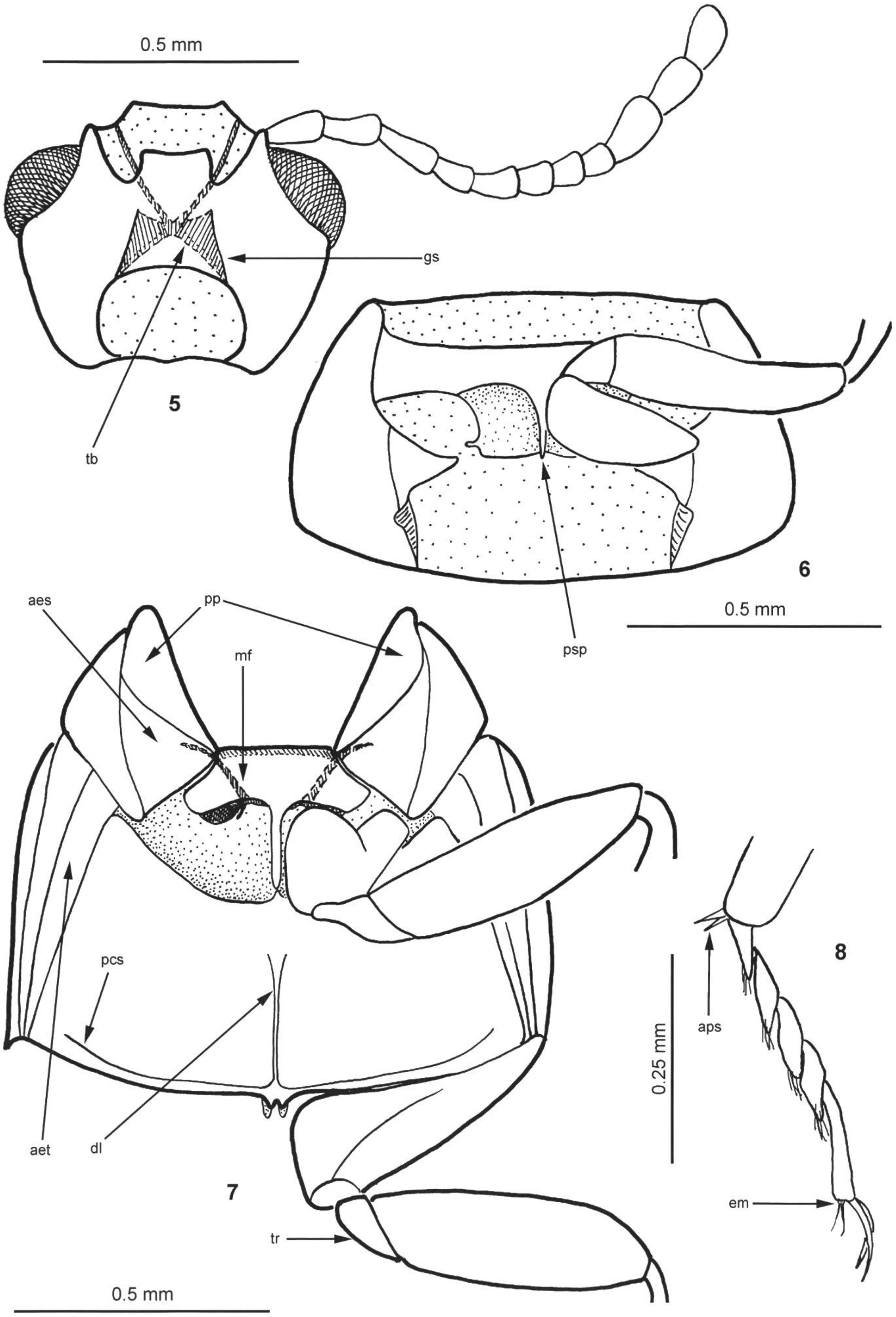
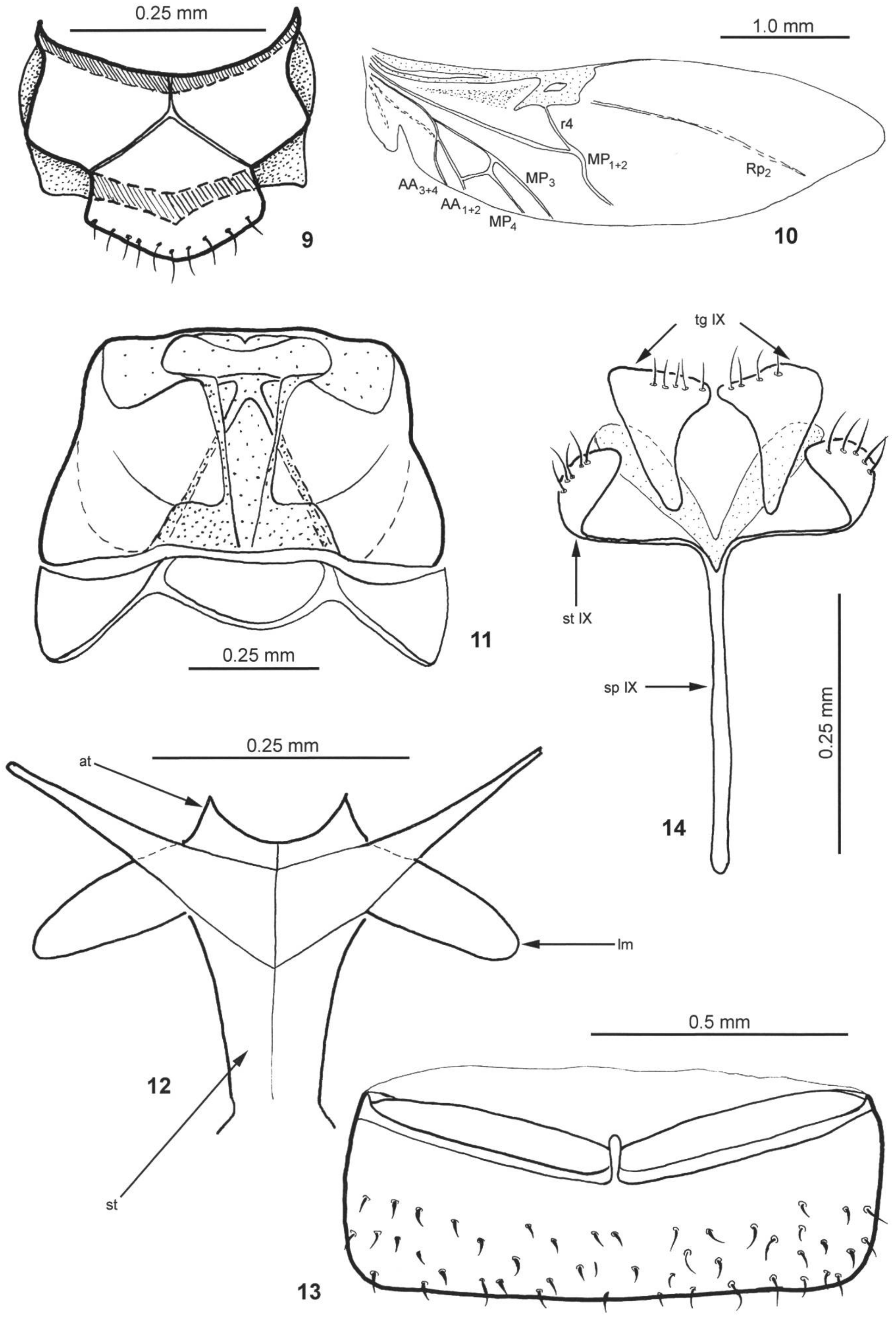


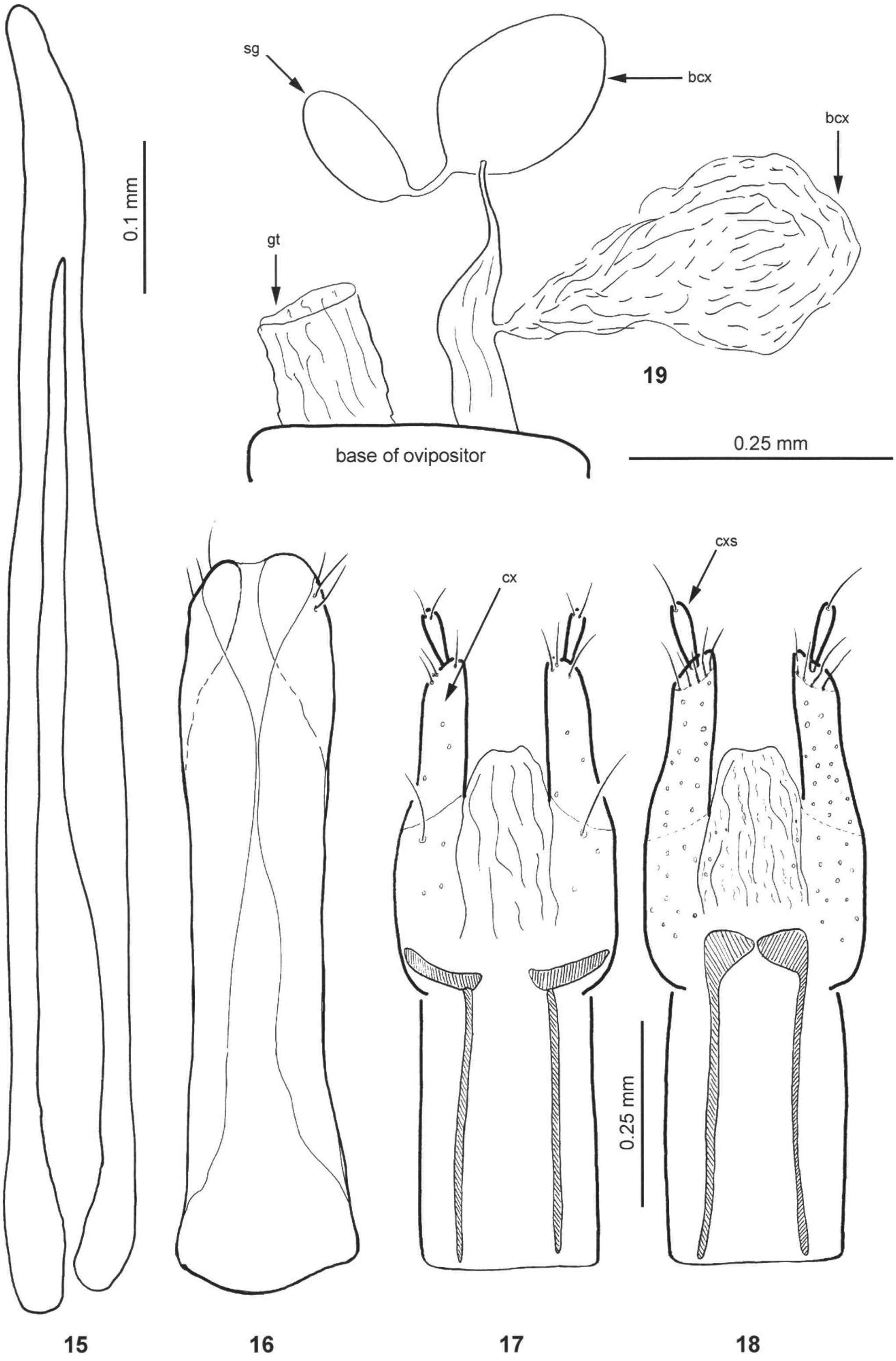
Figs 1–4. *Phloiophilus edwardsi*: 1 – labium, 2 – mandible ventrally, 3 – maxilla, 4 – labrum (transparent view).



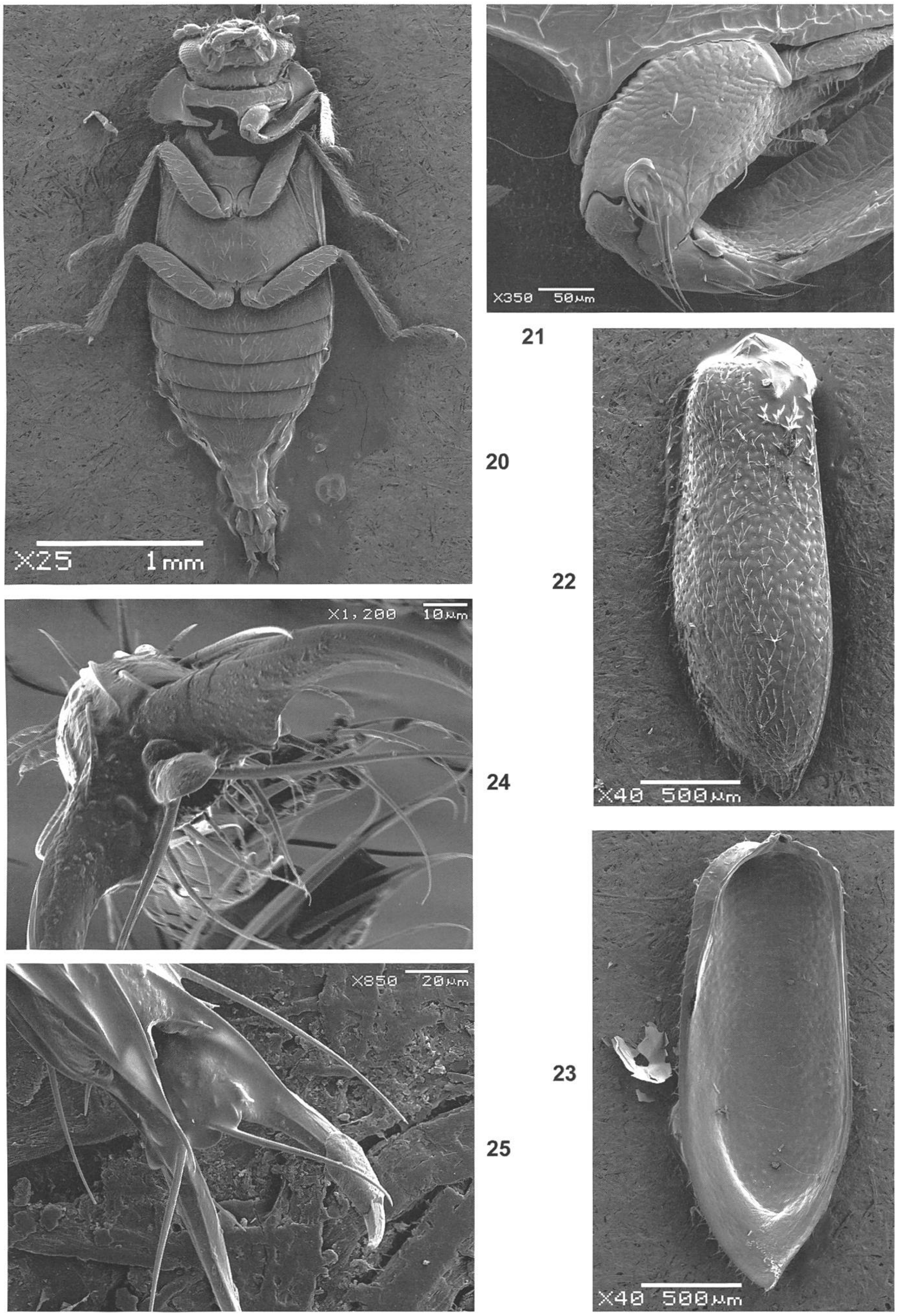
Figs 5–8. *Phloiophilus edwardsi*: 5 – head ventrally (mouth parts removed) with transparent view on tentorium, 6 – prothorax ventrally (right leg removed), 7 – meso- and metathorax ventrally (right legs removed), 8 – middle tarsus.



Figs 9–14. *Phloiophilus edwardsi*: 9 – mesonotum, 10 – wing, 11 – metanotum, 12 – metendosternite, 13 – first visible abdominal sternite (= sternites I+II+III), 14 – last abdominal segments ("spicular fork") of male.



Figs 15–19. *Phloiophilus edwardsi*: 15 – phallus, 16 – tegmen ventrally (transparent view), 17 – ovipositor ventrally, 18 – ovipositor dorsally, 19 – female internal reproductive organs (oviducts and ovaries removed, gut cut off).



Figs 20–25. *Phloiophilus edwardsi*: 20 – ventral view, 21 – detail of procoxa and prosternal process, 22 – left elytron dorsally, 23 – right elytron ventrally, 24 – tarsal claws and empodium of hind leg, 25 – tarsal claws and empodium of middle leg.