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A new genus of Osoriinae in the Neotropical region with a cladistic analysis of the tribe Thoracophorini (Insecta: Coleoptera: Staphylinidae)

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> Abstract

The new genus *Arborilispinus* from the Neotropical region is described. Although further undescribed species of this genus exist in South America, only two species, *A. longulus* and *A. mirabilis*, are here described based on male specimens from the Brazilian and Peruvian Amazon rainforest. According to the tarsal formula 4,4,4, *Arborilispinus* should be placed in the subtribe Glyptomina of the tribe Thoracophorini. A morphology-based cladistic analysis, however, contradicts the existing classification of Thoracophorini into subtribes. Alternative systematic relationships among the Neotropical genera of Glyptomina and Thoracophorina suggested by the cladistic analysis are discussed.

> Key words

New species, new genus, Neotropics, cladistic analysis.

1. Introduction

The subfamily Osoriinae of the family Staphylinidae shows a worldwide distribution; most species are small and poorly coloured (usually brown or black). They are likely close relatives of the Oxytelinae and Piestinae (see Thayer 2005). In contrast to all other staphylinid subfamilies, the lateral sclerites of the abdomen are absent in Osoriinae. Whereas in the tribe Osoriini most species have an elongate-cylindrical habitus, other tribes show an extreme dorso-ventral depression as adaptation to the under-bark habitat, e.g. Leptochirini and Eleusini. In the osoriine tribe Thoracophorini elongate-cylindrical and depressed species (but never as extreme as in Leptochirini and Eleusini) are included. The tribe Thoracophorini is distinguished from the tribe Osoriini by the absence of an emargination with comb-like structure on the protibia. It includes 33 genera with 694 species worldwide and 23 genera with 248 species in the Neotropical region.

Blackwelder (1942) was the first to present a modern concept of subtribe-level classification of Thoracophorini, which was largely accepted by Newton & Thayer (1992) and Herman (2001). In contrast to Blackwelder (1942), however, Eleusini are now treated as a separate tribe and no longer as a subtribe of Thoracophorini (Herman 2001). Blackwelder (1942) used the following characters to separate the four remaining subtribes: The anterior coxae are separated by a (prosternal) process in Lispinina and Glyptomina, while this process is absent in Clavilispinina and Thoracophorina. Gular sutures are absent, united or throughout approximate in Clavilispinina, while they are widely divergent in Thoracophorina. Glyptomina and Lispinina were separated according to the discreteness of the neck, the head being narrowed posteriorly in the former but not in the latter. Newton (1990) presented additional characters for the separation of genera and subtribes of Thoracophorini. Unfortunately, no detailed studies exist on the phylogenetic relationships between tribes, subtribes or genera of Osoriinae.

Within the collections from Central Amazonian inundation forests sampled by my colleague Prof. Joachim Adis (†), I found an osoriine species collected

in tree eclectors that could not be placed in any of the genera recorded previously from the Neotropical region or elsewhere. As three other species of the same new genus were found in the collections of the Natural History Museum, London, and in my own collection from Peru, it seems that this genus is widely distributed in South America.

This study will present the description of this new genus, including the description of two new species (those with males known), and a discussion of the placement of the new genus within Thoracophorini based on a preliminary cladistic analysis.

Material and methods

The types of the newly described species are deposited in my own collection (UIC), in the Natural History Museum, London, UK (BMNH), and in the Instituto National de Pesquisa da Amazônia (INPA), Manaus, Brazil. Material of the two additional undescribed species is deposited in the UIC and BMNH. Among the latter, one has reduced eyes and was found in the Peruvian Amazon (UIC); the other one is similar to the newly described *A. longulus* and originates from a terra firme rain forest near Manaus (BMNH). These two species are not described here because only females are known.

The lengths of various bodyparts were measured along their respective midlines, their widths at their widest parts. In the measurements of total length, the contribution of abdominal intersegmental membranes is deducted.

The cladistic analysis was performed using "past version 1.95", which is a freeware program supervised by O. Hammer, University of Oslo, D.A.T. Harper, Geological Museum Copenhagen, and P.D. Ryan (HAMMER et al. 2001). Heuristic search (SPR = subtree pruning and regrafting) was used in the parsimony analysis. The SPR algorithm is an elaborate branch swapping scheme: A subtree is cut off the tree, and regrafting onto all other branches of the tree is then attempted in order to find a shorter tree (KITCHING et al. 1988). This is done after each taxon has been added, and for all possible subtrees. SPR often finds shorter trees than the NNI (nearest neighbour interchange) algorithm does. FITCH was selected as character optimising criterion, because characters are reversible and unordered, meaning that all changes have equal cost. This criterion needs fewest assumptions, and is therefore generally preferable. Bootstrap replicates were set to 500. Consensus trees were developed on the basis of 'strict' rule. However, the authors warn that the "past" cladistics package, although being adequate for education and initial data exploration, is not intended for more 'serious' phylogenetic work. Unfortunately, more professional programs like for example "paup" were not available. At the same time, results for the selected characters and genera obtained by "past" seem reasonable to the best of the author's systematic experience, which suggests that the parsimony-based cladistic analysis performed here is accurate.

Description of new taxa

Arborilispinus n.gen.

Type species. *Arborilispinus longulus* n.sp. is here designated as the type species of the genus.

Description. *Length & habitus*: elongate, small species of about 1.5–2.5 mm. *Head*: without discrete neck; eyes present or absent, if present number of ommatids small (in described species about 17); with two supraocular setae; gular sutures absent. Antennae variable in length; increasing in width to apex; penultimate antennomeres more or less quadrate or transverse; 8th antennomere distinctly smaller and narrower than 7th and 9th. *Pronotum*: elongate or quadrate, not wider than head; finely margined; at front edge and sides with few setae; in front of posterior edge a central round depression. *Elytra*: length variable, either distinctly longer than pronotum or as long as pronotum; with few lateral setae. *Abdomen*: first four visible segments equal in length, 5th slightly longer than preceding ones. *Aedeagus*: central lobe divided in a dorsal and ventral sub-lobe. *Legs*: protibia without emargination and comb; all legs with 4 tarsomeres, 4th extremely long, longer than 1st–3rd together.

Diagnosis. The genus is unambiguously characterised by the combination of an elongate cylindrical shape of the body, 4 tarsomeres, gular sutures absent, 8th antennomere narrower than preceding and following antennomeres, and the presence of a ventral lobe of the aedeagus which seems to have a distinct shape in all species and which is absent in all other Thoracophorini. In its elongate shape *Arborilispinus* resembles *Clavilispinus* Bernhauer, 1926. However, the gular sutures are absent and not confluent along their total lengths as in *Clavilispinus* Bernhauer, 1926, and the head is much smaller and shorter considering the proportions between head and pronotum. In the overall shape of head, pronotum and elytra, *Arborilispinus* reminds of very small species of *Lispinus* Erichson, 1840 because a discrete neck is not developed. It also resembles the genera *Allotrochus* Fagel, 1955 and *Ge-*

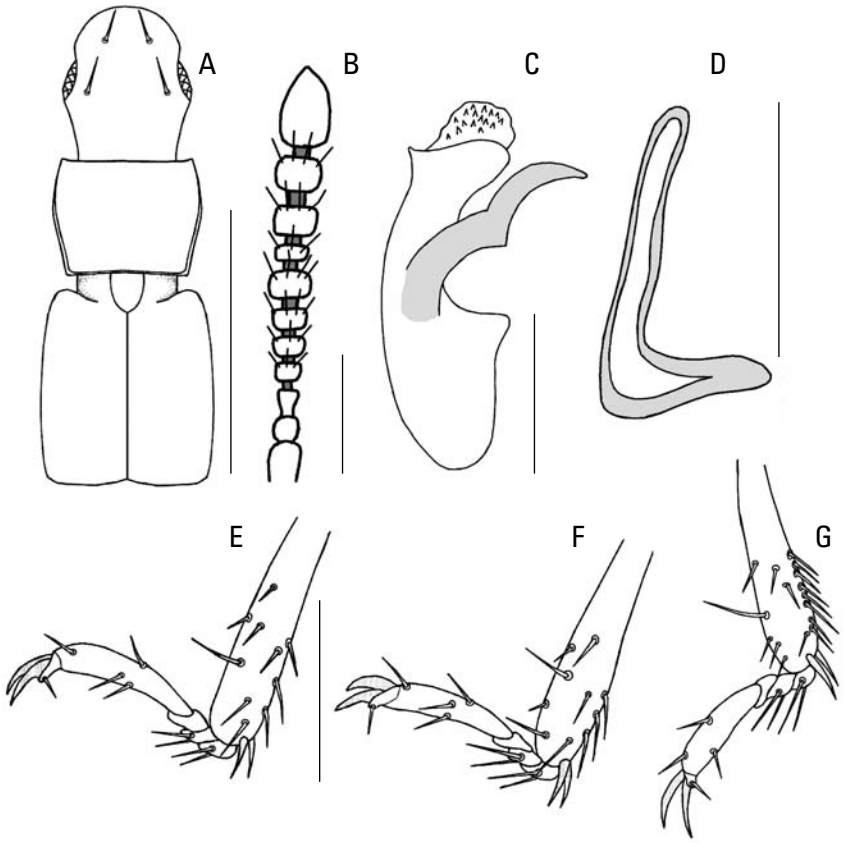

Fig. 1. *Arborilispinus longulus*, **A**: forebody, **B**: antenna, **C**: aedeagus, **D**: paramere, **E**: protarsus, **F**: mesotarsus, **G**: metatarsus (scale bars: A: 0.5 mm; B–G: 0.1 mm).

omitopsis Scheerpeltz, 1931 in its elongate-cylindrical habitus. As in *Geomitopsis* Scheerpeltz, 1931 and *Pseudespeson* Lecoq, 1994, the new genus has 4 tarsomeres. Compared to *Pseudespeson* Lecoq, 1994 and *Espeson* Schaufuß, 1882, the lateral sides of the pronotum are smoothly rounded and not distinctly emarginated in the posterior half. Eyes are developed in the newly described species, but there exists also a species without eyes (not yet described herein because only females are known), which otherwise is characteristic for the genus *Geomitopsis* Scheerpeltz, 1931. In comparison to *Geomitopsis*, *Arborilispinus* is much more elongate and narrower in its overall shape.

Etymology. The generic name is a combination of the Latin word *arbor* meaning tree and the generic name *Lispinus*, pointing to the similarity between this genus and the new one.

Arborilispinus longulus n.sp.

Figs. 1A–G, 3lA–C,D

Material. Holotype: ♂, Brazil: Amazonas, Manaus, 15 km SW, Ilha Marchantaria (59°58′W 03°15′S), inundation forest, 14.ix. 1981, collected by tree eclector #50C, leg. J. Adis (INPA). – Paratypes: 2 ♀♀ with same date as holotype, but 04.ii.1982 #50C and 14.iii.1981 #50A (INPA, UIC).

Description. *Length*: 1.8 mm. *Colour*: light brown; elytra, legs and antennae yellow. *Head*: 0.20 mm long, 0.25 mm wide; eyes not prominent, with 17 ommatids; temples evenly continued into broad neck; punctation moderately fine and sparse; average distance between punctures as wide as or wider than diameter of punctures; with a supraocular and a post-clypeal setiferous puncture; net-like microsculpture moderately deep; surface slightly shiny. *Antennae*: two basal antennomeres oval, 3rd antennomere conical; width of antennomeres increasing from 4th to 7th; 4th antennomere quadrate and 7th antennomere 1.5 times as wide as long; 8th antennomere distinctly smaller and narrower than preceding and following antennomeres, only half as wide as 7th antennomere; penultimate antennomeres 1.5 times as wide as long. *Pronotum*: 0.20 mm long, 0.27 mm wide; widest slightly in front of middle; slightly narrowed to anterior angles; distinctly narrowed to posterior angles; lateral, anterior, and posterior edges finely margined; punctation moderately deep and sparse; between normal punctures a sparse fine micropunctation; distance between normal punctures on average slightly shorter than diameter of punctures; a pair of larger punctures near the middle at anterior edge; another deep puncture medially in posterior third; net-like microsculpture as deep as on head; surface slightly shiny. *Elytra*: 0.37 mm long,

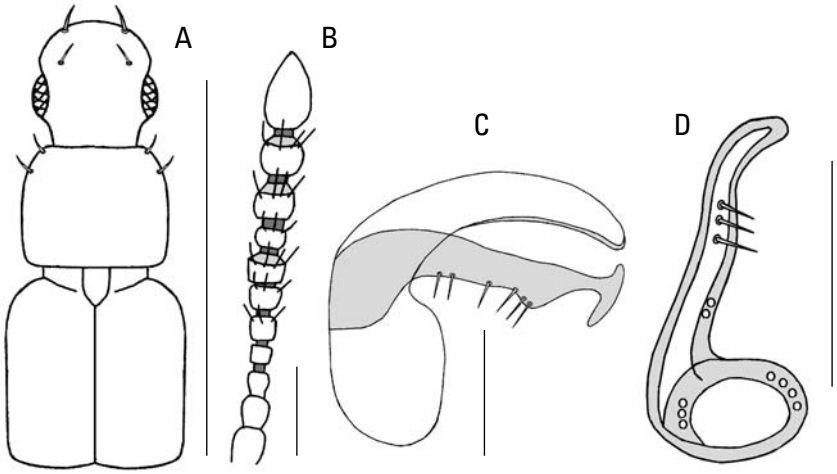

Fig. 2. *Arborilispinus mirabilis*, **A**: forebody, **B**: antenna, **C**: aedeagus, **D**: paramere (scale bars: A: 1 mm; B–D: 0.1 mm).

0.30 mm wide; with sparse and fine punctation; distance between punctures on average distinctly wider than diameter of punctures; microsculpture deeper than on pronotum; thus, surface less shiny. *Abdomen*: without punctation, but with distinct net-like microsculpture; surface as shiny as on elytra. *Male genitalia*: Aedeagus with simply shaped ventral sub-lobe, curved at apex, but without hook-like prominence; paramera straight, without setae or punctures and as long as aedeagus.

Diagnosis. See below: *A. mirabilis*.

Etymology. The specific name *longulus* is derived from the same Latin word meaning long and refers to the very elongate shape of the species.

Arborilispinus mirabilis n.sp.

Figs. 2A–D, 3mA–C

Material. Holotype: ♂, Amazon: Iquitos, lowland forest, Rio Napo – Rio Sucusari (73°15′49″W 3°96′46″S), xii.1997, leg. M.V.L. Barclay (BMNH{E} 2003-49).

Description. *Length*: 2.3 mm. *Colour*: light brown; tarsi yellow. *Head*: 0.25 mm long, 0.33 mm wide; eyes slightly prominent with 17 large ommatids; temples shortly narrowed to a broad neck; punctation distinct, but fine and moderately dense, denser at neck than on disc and clypeus; average distance between punctures as wide as, or slightly wider than, diameter of punctures; with a supraocular and a post-clypeal, deeply depressed setiferous puncture; two further setiferous punctures in the fine front margin of clypeus; net-like microsculpture fine, but distinct; surface moderately shiny. *Antennae*: two basal antennomeres oval, 3rd antennomere conical; width of antennomeres increasing from 4th to 7th; 4th antennomere quadrate and 7th antennomere 1.5 times as wide as long; 8th antennomere distinctly smaller and narrower than preceding and following antennomeres, only half as wide as 7th antennomere; penultimate antennomeres 1.5 times as wide as long. *Pronotum*: 0.33 mm long, 0.37 mm wide; widest in middle; smoothly narrowed to the obtuse anterior angles and straightly narrowed to obtuse posterior angles; lateral, anterior, and posterior edges finely margined; punctation distinctly coarser than on head; distance between punctures on average shorter than diameter of punctures; a large puncture near the middle at anterior edge on each side and a central circular depression in the posterior half; net-like microsculpture more distinct than on head; thus, surface slightly less shiny. *Elytra*: 0.50 mm long, 0.50 mm wide; with much finer and sparser punctation than on pronotum; punctation nearly invisible in the distinct net-like microsculpture; surface slightly shiny as on pronotum. *Abdomen*: without punctation, but with distinct net-like microsculpture; surface slightly shiny. *Male genitalia*: central lobe of aedeagus divided into a simply shaped dorsal sub-lobe and a ventral sub-lobe with a hook-like prominence at apex; paramera straight in their basal part but with slightly rounded top and with three setae and several punctures.

Diagnosis. The species can be separated from *A. longulus* by the larger eyes and the different shape of the pronotum. Sides of pronotum are evenly narrowed to the posterior angles, whereas they are slightly emarginate in *A. longulus*. Moreover, the ventral lobe of the aedeagus is distinctly different from the simple shape in *A. longulus*.

Etymology. The specific name *mirabilis* is derived from the same Latin word meaning peculiar and refers to the curious development of the aedeagus.

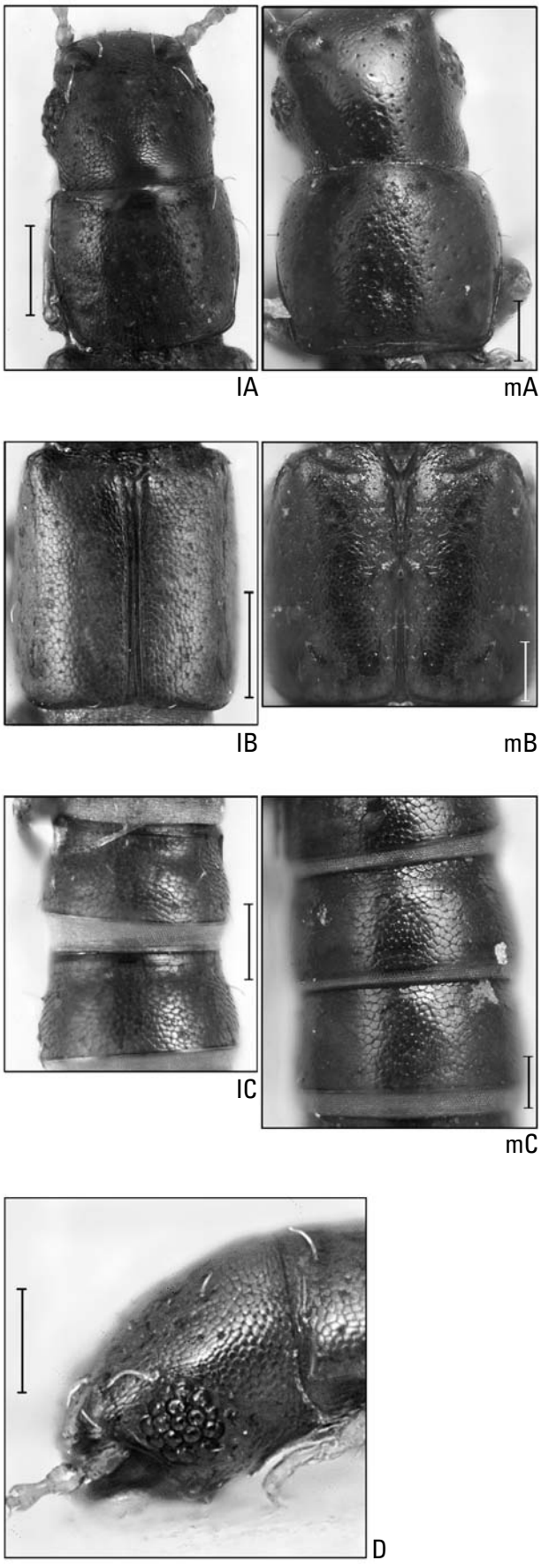

Fig. 3. Surface of head and pronotum (A), elytra (B) and abdomen (C) of *Arborilispinus longulus* (l) and *A. mirabilis* (m) in dorsal aspect and eyes of *A. longulus* in lateral aspect (D) (scale bars: 0.1 mm).

Cladistic analysis of Neotropical Thoracophorini and discussion

In order to analyse the placement of the new genus within the tribe Thoracophorini, morphological characters of all Neotropical genera of the tribe were studied. According to Herman (2001), the study genera are placed in the following subtribes:

Clavilispinina: *Allotrochus* Fagel, 1955, *Clavilispinus* Bernhauer, 1926, *Geomitopsis* Scheerpeltz, 1931.

Glyptomina: *Espeson* Schaufuß, 1882, *Glyptoma* Erichson, 1839, *Lispinodes* Sharp, 1880, *Pseudespeson* Lecoq, 1994.

Lispinina: *Liberiana* Blackwelder, 1942, *Lispinuncus* Irmler, 2005a, *Lispinus* Erichson, 1840, *Nacaeus* Blackwelder, 1942, *Neolosus* Blackwelder, 1942, *Tannea* Blackwelder, 1952.

Thoracophorina: *Aneucamptus* Sharp, 1880, *Thoracophorus* Motschulsky, 1837, *Rhopalopherus* Bernhauer, 1909, *Mesotrochus* Wasmann, 1890, *Euctenopsia* Bruch, 1942, *Pselaphomimus* Bruch, 1942, *Verhaaghiella* Irmler, 2005b, *Quadricephalus* Irmler, 2005b, *Pardirocephalus* Bruch, 1942, and *Dirocephalus* Silvestri, 1938.

The tribe Osoriini was selected as outgroup taxon because it provides the highest number of plesiomorphic characters compared to the other tribes Eleusini and Leptochirini. These are tarsal formula 5,5,5, elongate coxae and absence of a dorsoventrally depressed body shape. But in contrast to the tribe Osoriini, the protibial emargination with comb is absent in Thoracophorini (Newton 1990).

The following characters were included in the cladistic analysis and scored for the sampled genera (character matrix Tab. 1). The condition of the gular suture, taken as a main character to divide Clavilispinina from the other subtribes by Blackwelder (1942), was omitted as it was found to vary within several genera and it was difficult to decide whether sutures are throughout united or close but separated. In all species of all genera investigated gular sutures are at least united for a short distance.

Antennae

1. Change of relative width of antennomeres along entire antenna: continuously and quite uniformly increasing distally (0); equal width from base to apex (1) (Fig. 4B); three or five apical antennomeres forming a knob (2). State (0) is likely plesiomorphic as it is found in most Thoracophorini and Osoriini genera (Fig. 4A); states (1) and (2) are likely apomorphic as

they are present in specialised species living with ants (Fig. 4C–D).

2. Width of 8th antennomere relative to 7th and 9th: 8th not narrower than 7th and 9th (0); 8th narrower than 7th and 9th (1) (Figs. 4A, 1B; 2B). State (1) is likely apomorphic.

3. Shape of 3rd antennomere: conical (0) (Fig. 4A,C,D); oval (1) (Fig. 4B). The 2nd antennomere is oval throughout.

Head

4. Presence of a central dorsal elevation on the head: absent (0) (Fig. 4E); present (1) (Fig. 4G).

5. Presence and number of supraocular setae: absent (0) (Fig. 4G); two present (1) (Fig. 4E); more than ten present (2) (Fig. 4F).

6. Presence of subocular furrow on head: absent (0) (Fig. 4J); present (1) (Fig. 4K).

7. Presence of supraocular furrow on head: absent (0) (Fig. 4J); present (1) (Fig. 4L).

8. Presence of compound eyes: present (0); absent (1). State (1) is likely apomorphic.

9. Degree of separation of neck from remainder of head: neck not at all discrete (0) (Fig. 4E); neck "normally" separated by gradual and moderate narrowing of hind part of head (1) (Fig. 4F); neck deeply separated by abrupt and strong narrowing of hind part of head (2) (Fig. 4 G). State (2) is clearly apomorphic.

10. Presence of glandular hairs on head: absent (0) (Fig. 4E,F); present at least at posterior edge of vertex (1) (Fig. 4G). State (0) is likely plesiomorphic as it is usually found in Osorinae, whereas state (1) is an apomorphy only found in specialised species living with ants.

Pronotum

11. Lateral furrow on pronotum: absent (0) (Fig. 4H,I); present (1) (see IRMLER 2005b).

12. Distribution of margination on lateral sides of pronotum: along total length of pronotum (0) (Fig. 4H); only in anterior half of pronotum (1); only in posterior half of pronotum (2) (Fig. 4I); entirely absent (3).

13. Number of setiferous punctures on lateral margin of pronotum: 0 (0); 1–6 (1) (Fig. 4H); >10 (2) (Fig. 4I).

14. Presence of transverse depression in posterior half of pronotum: absent (0); present (1) (see IRMLER 2005b).

15. Carinate condition of prosternum: absent (0); distinctly present (1) (see IRMLER 2005b).

16. Presence of prosternal process: absent (0); present (1).

17. Presence of margination on prosternal process: absent (0); present (1). Not applicable to taxa lacking the prosternal process, which are scored (-1).

18. Presence of raised line on hypomeron: absent (0); present (1).

19. Interrelation between punctures on pronotum: individual punctures strongly confluent (0); individual punctures distinctly separated (1).

Elytra

20. Presence of carinae on elytra: absent (0); present, at least weak ones (1). State (1) is likely apomorphic.

21. Presence of lateral setiferous punctures on elytra: absent (0); present (1).

Abdomen

22. Combined lengths of visible abdominal segments 2 and 3: shorter than combined length of following segments (0); longer than combined length of following segments (1).

23. Presence of striae on abdominal sternites: absent (0); present (1).

24. Condition of microsculpture on abdominal tergites: without net-like microsculpture (0); with net-like microsculpture (1).

Spermatheca

25. Shape of bursa of spermatheca: globular (0) (Fig. 4M,O); oblong (1) (Fig. 4N).

26. Length and shape of sclerotic spermathecal ductus: ductus absent or extremely short (0) (Fig. 4M); ductus longer, straight and with margin (1) (Fig. 4N); ductus longer, hook-like (2) (Fig. 4O).

Aedeagus

27. Shape of endophallus: not spiral (0); spiral (1). Not applicable to parthenogenetic taxa lacking males (*Clavilispinus*), which are scored (-1).

28. Segmentation of paramera: absent (one-segmented) (0); present (bi-segmented) (1). Not applicable to parthenogenetic taxa lacking males (*Clavilispinus*), which are scored (-1).

29. Subdivision of central lobe of aedeagus: central lobe of aedeagus simple (0); central lobe of aedeagus divided into dorsal and ventral sub-lobe (1). Not applicable to parthenogenetic taxa lacking males (*Clavilispinus*), which are scored (-1).

Legs

30. Number of tarsomeres (all legs): 5 (0); 4 (1); 3 (2).

31. Shape of procoxae: elongate (0); globular (1).

32. Presence of emargination and comb on protibia: present (0); absent (1).

The results of this preliminary analysis (strict consensus tree in Fig. 5) suggest for Thoracophorini a basal sistergroup relationship between *Allotrochus* and all other genera. *Allotrochus* has been classified together with *Geomitopsis* and *Clavilispinus* to form

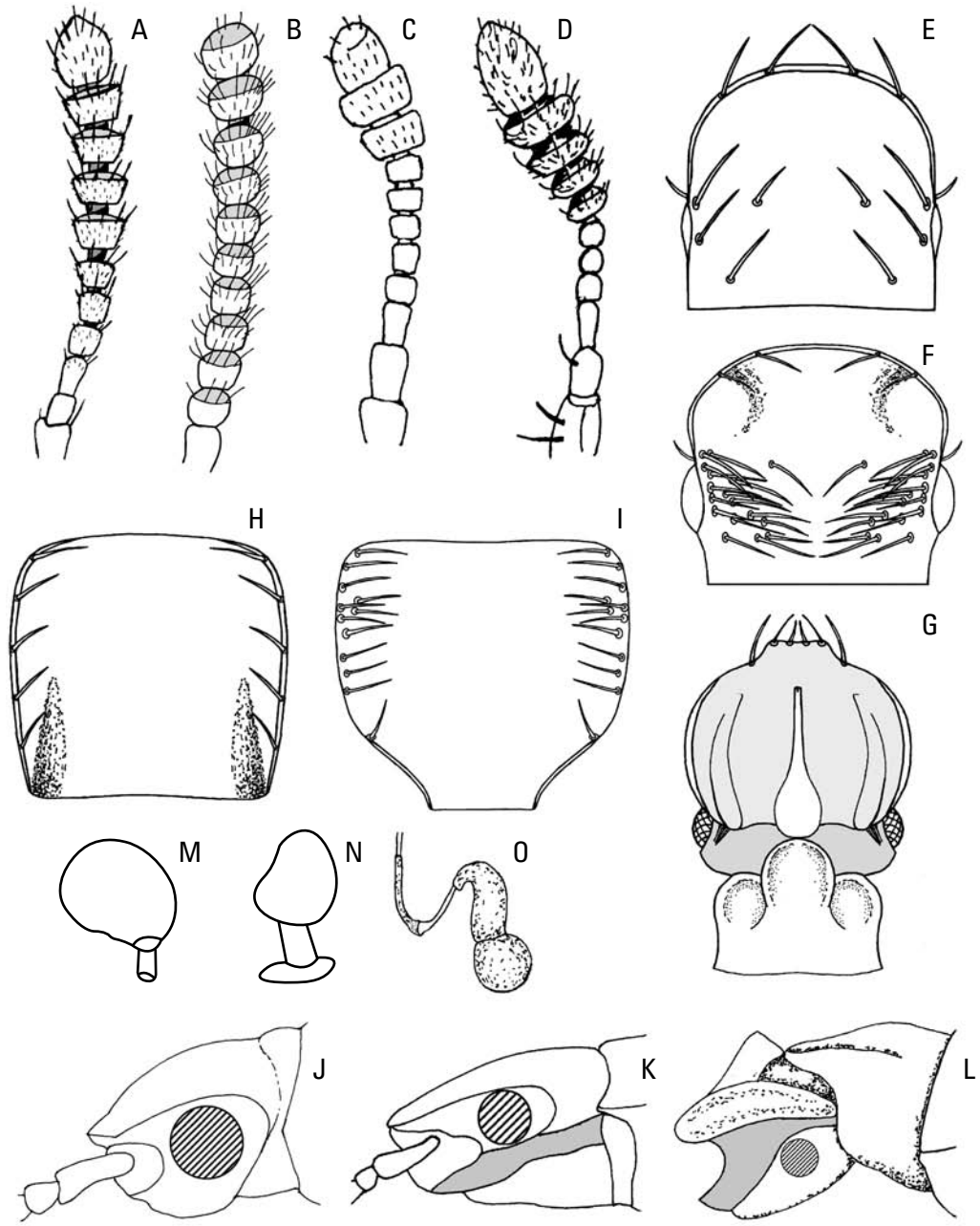

Fig. 4. Antennae of **A**: *Allotrochus marginatus* (Sharp, 1889); **B**: *Dirocephalus obtusus* Irmler, 2005; **C**: *Rhopalocerus magnipennis* Bernhauer, 1925; **D**: *Mesotrochus paradoxus* Wasmann, 1890. Dorsal aspect of head of **E**: *Lispinus catena* Sharp, 1876; **F**: *Lispinuncus pulcher* Irmler, 2005; **G**: *Dirocephalus mirabilis* Irmler, 2005. Dorsal aspect of pronotum of **H**: *Lispinus catena* Sharp, 1876; **I**: *Lispinuncus pulcher* Irmler, 2005. Lateral aspect of head of **J**: *Thoracophorus guadalupensis* Cameron, 1913; **K**: *Rhopalocerus magnipennis* Bernhauer, 1925; **L**: *Pselaphomimus amphiphilus* Bruch, 1942. Spermatheca of **M**: *Thoracophorus guadalupensis*; **N**: *Tannea mexicana* Irmler, 2005; **O**: *Lispinus catena* Sharp, 1876.

the tribe Clavilispinina ("C" in Fig. 5), which thus is an artificial grouping. The remaining Thoracophorini genera are placed in a large polytomy comprising the isolated genera *Espeson*, *Pseudespeson*, *Lispinodes*, *Geomitopsis*, *Clavilispinus*, and *Arborilispinus* as well as two clades composed of several genera each.

The first of these larger clades includes the genera *Lispinus*, *Lispinuncus*, *Liberiana*, *Neolosus*, *Tannea*, and *Nacaeus*. These are the taxa together classified as the subtribe Lispinina ("L" in Fig. 5), whose monophyly is thus supported. However, there is no discrete autapomorphy for this clade; yet its members can be recognised by a margined prosternal process (character 17 state 1 = Ch17-1; with the exception of *Neolosus*) and by a comparatively long spermathecal ductus (Ch26-1,2; not in the basal *Liberiana*), which is usually hook-like (Ch26-2). Within this clade, *Lispinus* and *Neolosus* share striae on abdominal sternites (Ch23-1), which is unique in the used sample of Thoracophorini.

Tab. 1. Matrix of characters included in the cladistic analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Osoriini	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	-1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0
Allotrochus	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	-1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1
Arborilispinus	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	-1	0	1	0	1	0	0	1	0	0	0	0	1	1	1	1
Clavilispinus	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	-1	0	1	0	1	0	0	1	0	0	-1	-1	-1	0	1	1
Geomitopsis	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	-1	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1
Espeson	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	-1	0	1	0	1	0	0	0	0	0	0	1	0	2	1	1
Pseudespeson	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1
Lispinodes	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	1	1
Rhopalopherus	2	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	-1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
Mesotrochus	2	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Thoracophorus	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	-1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
Aneucamptus	0	0	0	0	0	0	0	0	1	0	0	3	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
Glyptoma	1	0	1	0	0	0	0	0	1	0	0	3	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1
Verhaaghiella	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1
Quadricephalus	0	0	0	1	0	0	0	0	2	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1
Euctenopsia	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1
Pselaphomimus	1	0	1	1	0	0	1	0	2	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1
Pardirocephalus	1	0	1	1	0	0	1	0	2	0	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	2	1	1
Dirocephalus	1	0	1	1	0	0	1	0	2	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	2	1	1
Liberiana	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	0	0	0	0	0	1	0	0	0	1	1
Tannea	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	0	0	1	1	1	1	0	0	0	1	1
Nacaeus	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	0	0	1	0	2	1	0	0	0	1	1
Lispinuncus	0	0	0	0	2	0	0	0	0	0	0	2	2	0	0	1	1	0	1	0	1	0	0	0	0	2	1	0	0	0	1	1
Lispinus	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	0	1	0	0	2	1	0	0	0	1	1
Neolosus	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	0	1	0	0	2	1	0	0	0	1	1

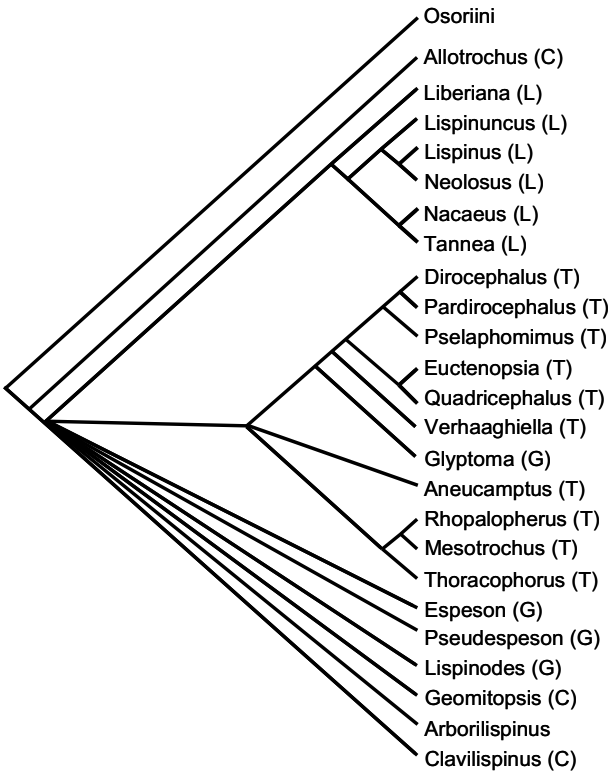

Fig. 5. Results of the cladistic analysis, strict consensus tree. Tree length = 61, CI = 0.66, RI = 0.86; characters in brackets indicate the placement of genera to subtribes according to HERMAN (2001) – (C): Clavilispinina, (L): Lispinina, (T): Thoracophorina, (G): Glyptomina.

The second larger clade includes *Dirocephalus*, *Pardirocephalus*, *Euctenopsia*, *Quadricephalus*, *Verhaaghiella*, *Glyptoma*, *Aneucamptus*, *Rhopalopherus*, *Mesotrochus* and *Thoracophorus*. This clade is congruent with the subtribe Thoracophorina ("T" in Fig. 5) – with the sole exception that *Glyptoma* is additionally included. The Thoracophorina + *Glyptoma* clade appears well supported by several apomorphies: absence of supraocular setae on head (Ch5-0), lack of setiferous punctures on pronotum (Ch13-0), confluent pronotal punctures (Ch19-0 – only *Glyptoma* with state 1), and carinate elytra (Ch20-0 – only *Mesotrochus* with state 1). The absence of lateral setiferous punctures on the elytra (Ch21-0) is also consistently found in this clade and also in *Pseudespeson*; this might suggest the latter genus to be most closely related to Thoracophorina. The same distribution across taxa is found for the presence of a neck (Ch9-1,2), but besides *Pseudespeson* the genus *Espeson* is additionally included. On the other hand, *Pseudespeson* shares with *Arborilispinus* the likely apomorphic narrowed antennomere 8 (Ch2-1). Within the Thoracophorina + *Glyptoma* clade, *Rhopalopherus* and *Mesotrochus* share a subocular furrow on the head (Ch6-1), and *Pselaphomimus*, *Pardirocephalus* and *Dirocephalus* share a supraocular furrow on the head (Ch7-1), both conditions being unique in the sample of Thoracophorini here used.

With regard to the subtribal classification of Thoracophorini, the phylogenetic analysis suggests the Lispinina to be a major monophyletic subgroup of this tribe – although its support by characters is weak. Thoracophorina is a group with considerable support, but only under inclusion of *Glyptoma*. In contrast, the Clavilispinina and Glyptomina are both para- or polyphyletic, being at least to some extent artificial groupings of 'basal' genera. If *Allotrochus* indeed is sister to the entire remaining Thoracophorini, it deserves to be ranked in a subtribe of its own. This genus shows plesiomorphic conditions in many characters, among which its elongate procoxae (Ch31-0) are unique in Thoracophorini, and it thus bears considerable resemblance to members of the Osoriini. This is also expressed by the fact that *Allotrochus marginatus* (Sharp, 1887) was first placed in Osoriini and described as *Holotrochus marginatus* by Sharp (1887). Consequently, it would appear adequate to eliminate subtribes Glyptomina and Clavilispinina, but this can only be done when further cladistic work on Osoriinae has led to a more inclusive and conclusive phylogenetic hypothesis for this taxon. In addition, the discovery of the new genus *Arborilispinus* shows that we are far away from knowing all genera and the entire range of morphological diversity of the Thoracophorini.

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