

# Phylogenetic analysis of Geotrupidae (Coleoptera, Scarabaeoidea) based on larvae

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**Abstract.** Thirty-eight characters derived from the larvae of Geotrupidae (Scarabaeoidea, Coleoptera) were analysed using parsimony and Bayesian inference. Trees were rooted with two Trogidae species and one species of Pleocomidae as outgroups. The monophyly of Geotrupidae (including Bolboceratinae) is supported by four autapomorphies: abdominal segments 3–7 with two dorsal annulets, chaetoparia and acanthoparia of the epipharynx not prominent, glossa and hypopharynx fused and without sclerome, trochanter and femur without fossorial setae. Bolboceratinae showed notable differences with Pleocomidae, being more related to Geotrupinae than to other groups. *Odonteus* species (Bolboceratinae s.str.) appear to constitute the closest sister group to Geotrupinae. Polyphyly of Bolboceratinae is implied by the following apomorphic characters observed in the ‘*Odonteus* lineage’: anterior and posterior epitormae of epipharynx developed, tormae of epipharynx fused, oncyli of hypopharynx developed, tarsal claws reduced or absent, plectrum and pars stridens of legs well developed and apex of antennal segment 2 with a unique sensorium. A ‘*Bolbelasmus* lineage’ is supported by the autapomorphic presence of various sensoria on the apex of the antennal segment, and the subtriangular labrum (except *Eucanthus*). This group constituted by *Bolbelasmus*, *Bolbocerosoma* and *Eucanthus* is the first evidence for a close relationship among genera, but more characters should be analysed to test the support for the clade. A preliminary classification at tribe level of Geotrupinae is suggested as follows: Chromogeotrupini (type genus *Chromogeotrupes*), Lethrini (type genus *Lethrus*), Taurocerastini (type genus *Taurocerastes*) and Geotrupini (type genus *Geotrupes*). Some ecological facts of Geotrupidae evolution could also be explained by the present results, such as those related to diet and nesting behaviour. Both coprophagy and male–female co-operation in nesting appear as derived traits.

## Introduction

Geotrupidae include sixty-eight genera and about 620 species distributed in temperate, subtropical and Asian-tropical regions. It is classified into three subfamilies (*sensu* Lawrence & Newton, 1995). The Geotrupinae are distributed mainly in the Holarctic region. The Lethrinae are distributed

predominantly in Eastern Europe and Asia. The Bolboceratinae (= Bolboceratidae *sensu* Scholtz & Browne, 1996; including Bolboceratini and Athyreini) occur in Australia, Africa, Europe and South America. Some authors (e.g. Zunino, 1984a, b) include the southern South American Taurocerastinae at subfamily level.

Many authors have considered Geotrupidae to be monophyletic (e.g. Crowson, 1954, 1960, 1981; Paulian, 1959; Balthasar, 1963; Howden, 1964; Medvedev, 1976; Iablokoff-Khnzorian, 1977; Scholtz, 1990; Lawrence & Newton, 1995). Nevertheless, Scholtz & Browne (1996) described the family Bolboceratidae as an independent lineage more

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closely related to Pleocomidae. Morphological studies on immature stages have suggested a probable polyphyly in the Bolboceratinae group (Verdú *et al.*, 1998), as *Bolbelasmus* and *Odonteus* features differ considerably. Some authors (Davis, 1935; Paulian, 1941; Ritcher, 1947) have included the genus *Pleocoma* in the Geotrupidae, although *Pleocoma* species differ from the geotrupids on many adult and larval characters (e.g. Browne & Scholtz, 1999). On the basis of morphological and biological characters, Howden (1982) hypothesized that the Geotrupinae (including Geotrupini, Athyreini, Bolboceratini, and Lethrini) form a monophyletic lineage closely related to the Pleocomidae (=Pleocominae *sensu* Howden, 1982). Conversely, other authors (Browne & Scholtz, 1995, 1999; Scholtz & Chown, 1995; Scholtz & Browne, 1996) suggested that geotrupids constitute a polyphyletic group with Bolboceratidae being a part of a lineage which includes Pleocomidae, Trogidae, Glaphyridae, Passalidae, Lucanidae, and Diphylostomatidae, whereas Geotrupidae (including Geotrupinae, Taurocerastinae, and Lethrinae) are part of a different lineage which includes Ochodaëidae, Ceratocanthidae and Hybosoridae.

Crowson (1954) suggested that speculation on the systematic placement of *Taurocerastes* and *Frickius* should be delayed until the larvae were known, inferring that adult characters were not sufficient. Nevertheless the systematic position of these genera has been discussed by taxonomists, with allocation to either Geotrupinae (Geotrupini *sensu* Howden, 1982) at tribe level (Ritcher, 1968, 1969; Howden, 1982) or with Taurocerastinae at subfamily level (e.g. Zunino, 1984a, b).

In most papers dealing with the phylogeny of Coleoptera, adult characters are the rule, mainly because larval material is mostly missing or has been very poorly compared with adult character sets. In the previous classifications dealing with adults in Geotrupidae (Zunino, 1984a; Browne & Scholtz, 1995, 1999), polytomies and inconsistency between phylogenetic trees were obtained. On the other hand, in the previous analyses which combined adult and larval characters (Howden, 1982; Browne & Scholtz, 1999), the set of larval characters was too reduced to provide significant effects on the results. Moreover, in these studies, several mistakes have been noticed in the structure of larval respiratory spiracles and the morphology of endoskeletal figure (nomenclature *sensu* Ritcher, 1966) of anal lobes (see the reinterpretation in the present paper).

In Coleoptera, many apomorphic larval characters were crucial to elucidate phylogenetic relationships at the highest taxonomic levels in spite of the conservative nature of some characters (e.g. Crowson, 1954; Ritcher, 1966; Chown & Scholtz, 1990; Scholtz & Peck, 1990; Ashe & Newton, 1993; Beutel, 1993, 1999; Pinto *et al.*, 1996; Archangelsky, 1998; Beutel *et al.*, 1999; Beutel & Hörnschemeyer, 2002). For example, in Hydrophiloidea, a combined analysis at the family level showed that larvae were most informative deeper in the phylogeny, compared with adults which were more informative at the apex of the tree (Archangelsky, 1998). Also, in several larval studies of Scarabaeoidea, as expected, larval characters appeared to be more conserva-

tive than those of adults, but allowed elucidation of small monogeneric or paucigeneric groups (Hayes, 1949; Ritcher, 1966; Paulian & Lumaret, 1974, 1982; Verdú *et al.*, 1998; Verdú & Galante, 2001). In the present study, we hypothesize that the use of larval characters may provide powerful information to enlighten the phylogenetic history of Geotrupidae. All geotrupid larvae develop subterranean nests, a buffered system (stability of microclimatic conditions) protected from competition for food and space (individual brood masses). Conversely to larvae, the adults have to compete for reproduction and for food (both for themselves and the provisioning of the nest) against other geotrupids and all dung beetles present inside dung pats. In some species, adults have developed thoracic horns in males (e.g. *Typhaeus*, *Taurocerastes*) which could have orientated selection in the mating system, as observed in males of *Onthophagus* with cephalic horns (Moczek & Emlen, 2000; Emlen, 2001). In dung beetles, larvae have primitive mandibles compared with adults, whose mandibles differ according to the food regime or behaviour (Cambefort, 1991). Mouthparts of larvae of Anomalini (Scarabaeidae: Rutelinae) are very uniform in contrast to those observed in adults (Murayama, 1931; Ritcher, 1966). Adult beetles associated with rabbit pellets as food show morphological convergence of the epipharynx, as in several species of *Aphodius* and *Onthophagus* (Verdú & Galante, 2004). The specialization on dry excrements (such as rabbit pellets) also led to modifications in the shape of the hypopharynx and the mandibles of *Thorectes* adults (Verdú & Galante, 2004). In Lethrinae, adults are equipped with very large, chisel-shaped mandibles with which they cut young leaves. Afterwards, cut leaves are chewed by the female and packed into burrows in the shape of a sausage, similar to those of Geotrupinae (Popovici-Bazosanu, 1932; Nikolaiev, 1966). More generally, particular trophic habits and morphological adaptations in adults are more frequent and recent than in larvae.

Using only larval characters, we expect that in geotrupids these characters could be more informative than adult ones deeper in the phylogeny, with less background noise than for adult characters.

Our contribution presents a study of the larval morphology of representatives of all families, subfamilies and tribes classified historically into Geotrupidae (*sensu lato*); only the Athyreini are excluded here because their larvae are unknown.

Four main questions will be considered: (1) the monophyly or polyphyly of the Geotrupidae; (2) the phylogenetic relationships between the Bolboceratinae (or Bolboceratidae, *sensu* Scholtz & Browne, 1996) and the Pleocomidae; (3) the possible polyphyly of the Bolboceratinae group; and (4) the systematic position of the Taurocerastinae.

## Materials and methods

### *Taxa studied*

For this study, larvae were obtained either by breeding adults in the laboratory or by collecting larvae in the field.

Field-caught larvae were kept in the laboratory throughout their larval development in order to obtain the final instar and adults for identification. This material has been deposited at the Entomological Collections of the Universidad de Alicante, Spain and the Université Paul Valéry, Montpellier, France. Other taxa were obtained from museum collections: Oregon State University; the Canadian Museum of Nature, Instituto de Ecología de Xalapa, México; or borrowed from Dr V. Grebennikov. A list of taxa studied is shown in Table 1.

Data on the larvae of *Odonteus liebecki* (Wallis, 1928), *O. simi* (Wallis, 1928), *Bolbocerosoma tumefactum* (Palisot de Beauvois, 1805), *Anoplotrupes stercorosus* (Scriba, 1790), *Ceratophyus gopherinus* Cartwright, 1966, and *C. polyceros* Pallas, 1771, were taken from the literature (van Emden, 1941; Ritcher, 1947, 1966; Howden, 1955; Ritcher & Duff, 1971; Nikolaiev, 1975).

Nomenclatural note: After the controversial comments about the precedence of *Bolboceras* Kirby, or *Odonteus* Samouelle made by Jameson & Howden (2002) and Krell *et al.* (2003), we considered more appropriate the precedence of *Odonteus* over *Bolboceras* according to arguments of Krell *et al.* (2003).

#### Specimen preparation and study

Dissections of larval skins were made with a stereomicroscope (magnification up to 40×), and separated parts were studied on temporary slides under a microscope using magnifications of 100 and 200×. Drawings were made using a FSA 25 PE tube (Leica<sup>®</sup>). Light micrographs of respiratory spiracles were recorded on Ektachrome 64T (Kodak<sup>®</sup>) film with a photomicroscope (Leitz DM-RB, Leica<sup>®</sup>) using interference contrast. Scanning electron microscopy of mandibles and respiratory spiracles was carried out using a scanning microscope (JSM-840, Jeol<sup>®</sup>). Mouthparts and spiracles were first cleaned with ether–alcohol (1:1) and ultrasound and then coated with gold for 4 min. Anatomical terminology follows Jerath (1960) and Ritcher (1966).

#### Characters and character states used in the analysis

1. *General body shape*: (0) broadly C-shaped (Figs 1, 2); (1) strongly curved at the level of fourth or fifth abdominal segments (Fig. 3).
2. *Last abdominal segment*: (0) rounded and narrowed apically (Fig. 1); (1) obliquely flattened (Figs 2, 3).
3. *Sclerotized plate of prothorax*: (0) strongly sclerotized; (1) slightly sclerotized.
4. *Abdominal segments 3–7*: (0) with four dorsal annulets (Fig. 4); (1) with three dorsal annulets (Fig. 5); (2) with two dorsal annulets (Figs 1–3).
5. *Clypeo-frontal suture*: (0) present (Fig. 6); (1) absent (Figs 7, 8).

6. *Epicranial suture*: (0) not extending between frontal suture (Figs 6, 8a); (1) extending between frontal suture (Fig. 7).
7. *Frontal suture*: (0) V-shaped (Figs 6, 8a); (1) U-shaped (Fig. 7).
8. *Clypeus*: (0) symmetric (Figs 6, 8a); (1) asymmetric (Fig. 7).
9. *Stemmata*: (0) present (Fig. 8b); (1) absent.
10. *Antenna*: (0) with three segments (Figs 9–11); (1) with two segments (Fig. 12).
11. *Apex of antennal segment 2*: (0) with various sensoria (Fig. 9); (1) with a unique sensorium (Figs 10–12).

Based on more than 100 species of Scarabaeoidea studied, we have observed in several taxa (e.g. Aphodiidae and Geotrupidae) that only the number of larval sensoria shows phylogenetic information at the high taxa level. The shape of sensoria is very variable (e.g. conical, disklike, flattened) at the specific level, as observed between species of *Aphodius* subgenera (Verdú & Galante, 1997) and also in *Geotrupes* genus (unpublished data).

12. *Labrum shape*: (0) subspherical (Figs 13, 15); (1) subtriangular not trilobed (Fig. 14); (2) trilobed (Figs 16–18).
13. *Anterior epitoria of epipharynx*: (0) absent (Figs 13–15); (1) slightly developed (Fig. 16); (2) well developed (Figs 17, 18).
14. *Posterior epitoria of epipharynx*: (0) absent (Figs 13–15); (1) slightly developed (Figs 16, 17); (2) well developed (Fig. 18).
15. *Sclerotized plates of epipharynx*: (0) present (Fig. 15); (1) absent.
16. *Tormae of epipharynx*: (0) not fused in middle (Figs 13, 14); (1) fused (Figs 15–18).
17. *Crepis of epipharynx*: (0) posterior to the tormae (Fig. 13); (1) inserted and aligned to the tormae (Figs 15–18).
18. *Macrosensillae of epipharynx*: (0) not aligned with protophoba (Figs 13–16); (1) aligned (Figs 17, 18).
19. *Plegmatia of epipharynx*: (0) present (Fig. 13); (1) absent.
20. *Hapterum of epipharynx*: (0) with heli (Fig. 13); (1) without heli.
21. *Chaetoparia and acanthoparia of epipharynx*: (0) prominent; (1) not prominent.
22. *Oncyli of hypopharynx*: (0) absent (Fig. 19); (1) with symmetric oncyli (Fig. 20); (2) with asymmetric oncyli (Figs 21, 22).
23. *Glossa and hypopharynx*: (0) separated by a transverse sclerome (Fig. 19); (1) fused, without sclerome (Figs 20–22).
24. *Lacinia of maxillae*: (0) with bidentate apex; (1) with tridentate apex.
25. *Retinaculum of mandibles*: (0) absent (Figs 23, 26); (1) slightly developed (Figs 24, 25); (2) well developed (Fig. 27).
26. *Molar region of mandibles*: (0) poorly developed, molar surface simple (Figs 24, 25); (1) well developed, molar surface asperate or ridged (Figs 23, 26, 27).
27. *Respiratory spiracles*: (0) biforous (Fig. 28); (1) cribriform oligoforous (Figs 29–31); (2) cribriform multiforous (Figs 32–34).

**Table 1.** Taxa and larval material examined.

Taxa	Material studied	Collections
<b>Pleocomidae</b>		
<i>Pleocoma</i> Le Conte, 1856		
<i>Pleocoma linsleyi</i> Hovore, 1971 <sup>a</sup>	Penultimate-instar larva	XAL
<b>Trogidae</b>		
<i>Polynoncus</i> Burmeister, 1876		
<i>Polynoncus aeger</i> (Guérin, 1844) <sup>a</sup>	Four final-instar, two second-instar larvae	CEUA
<i>Trox</i> Fabricius, 1775		
<i>Trox cricetulus</i> Adám, 1994 <sup>a</sup>	Seven final-instar larvae	CEUA
<b>Geotrupidae</b>		
<i>Anoplotrupes</i> Jekel, 1866		
<i>Anoplotrupes horni</i> (Blanchard, 1888) <sup>b</sup>	One final-instar larva	CMN
<i>Bolbelasmus</i> Boucomont, 1910		
<i>Bolbelasmus bocchus</i> (Erichson, 1841) <sup>c</sup>	One final-instar larva	CEUA
<i>Bolbelasmus gallicus</i> (Mulsant, 1842) <sup>a</sup>	One final-instar larva	CEUA
<i>Ceratophyus</i> Fischer de Waldheim, 1823		
<i>Ceratophyus hoffmannseggii</i> Fairmaire, 1856 <sup>d</sup>	Three final-instar, two final-instar larvae	UPV CEUA
<i>Ceratotrupes</i> Jekel, 1865		
<i>Ceratotrupes bolivari</i> Halffter & Martínez, 1962 <sup>e</sup>	One final-instar larva	CMN
<i>Cnemotrupes</i> Jekel, 1865		
<i>Cnemotrupes blackburnii</i> (Fabricius, 1781) <sup>f</sup>	Three final-instar, four second-instar, two final-instar larvae	Ore
<i>Cnemotrupes semiopacus</i> (Jekel, 1866) <sup>b</sup>	One final-instar larva	CMN
<i>Cnemotrupes splendidulus</i> (Fabricius, 1775) <sup>b</sup>	One final-instar larva	CMN
<i>Cnemotrupes ulkei</i> (Blanchard, 1888) <sup>f</sup>	One second-instar larva	CMN
<i>Eucanthus</i> Westwood, 1852		
<i>Eucanthus lazarus</i> (Fabricius, 1775) <sup>f</sup>	One final-instar larva	Ore
<i>Frickius</i> Germain, 1897		
<i>Frickius variolosus</i> Germain, 1897 <sup>g</sup>	One final-instar larva	CMN
<i>Geohowdenius</i> Zunino, 1984		
<i>Geohowdenius egeriei</i> (Germar, 1824) <sup>b</sup>	One final-instar larva	CMN
<i>Geohowdenius opacus</i> (Haldeman, 1853) <sup>h</sup>	One final-instar larva	CMN
<i>Geotrupes</i> Latreille, 1796		
<i>Geotrupes ibericus</i> Baraud, 1958 <sup>a</sup>	Three final-instar larvae	CEUA
<i>Geotrupes mutator</i> (Marsham, 1802) <sup>i</sup>	Two second-instar larvae	CEUA
<i>Geotrupes puncticollis</i> (Malinowsky, 1811) <sup>i</sup>	Three final-instar, two second-instar, one final-instar larvae	CEUA UPV Ore
<i>Geotrupes stercorarius</i> (Linnaeus, 1758) <sup>i</sup>	One final-instar larva	Ore
<i>Lethrus</i> Scopoli, 1777		
<i>Lethrus (Abrognathus) tuberculifrons</i> Ballion, 1870 <sup>a</sup>	Three second-instar larvae	Ore
<i>Lethrus (Lethrus) apterus</i> Laxman, 1870 <sup>j</sup>	One second-instar, two first-instar larvae	V. Grebennikov
<i>Mycotrupes</i> Le Conte, 1866		
<i>Mycotrupes gaigei</i> Olson & Hubbell, 1954 <sup>k</sup>	One final-instar larva	CMN
<i>Odonteus</i> Samouelle, 1819		
<i>Odonteus armiger</i> (Scopoli, 1772) <sup>j</sup>	One final-instar larva	V. Grebennikov
<i>Odonteus darlingtoni</i> (Wallis, 1928) <sup>b</sup>	One final-instar larva one second-instar larva	CMN Ore
<i>Odonteus obesus</i> (Le Conte, 1859) <sup>l</sup>	One final-instar larva	Ore
<i>Peltotrupes</i> Blanchard, 1888		
<i>Peltotrupes youngi</i> Howden, 1955 <sup>b</sup>	Three final-instar, one final-instar larvae	Ore CMN
<i>Sericotrupes</i> Zunino, 1984		
<i>Sericotrupes niger</i> (Marsham, 1802) <sup>a</sup>	Ten final-instar, three second-instar, one first-instar larvae	UPV
<i>Taurocerastes</i> Philippi, 1866		

<i>Taurocerastes patagonicus</i> Philippi, 1866 <sup>m</sup>	One final-instar larva	CMN
<i>Thorectes</i> Mulsant, 1842		
<i>Thorectes (Jekelius) albarracinus</i> (Wagner, 1928) <sup>a</sup>	Six final-instar larvae	CEUA
<i>Thorectes (Jekelius) intermedius</i> (O.G. Costa, 1827) <sup>a</sup>	Three final-instar larvae	CEUA
<i>Thorectes (Jekelius) punctatolineatus</i> (François, 1904) <sup>a</sup>	Three final-instar, two second-instar larvae	CEUA
<i>Thorectes (Jekelius) sericeus</i> (Jekel, 1865) <sup>a</sup>	Two final-instar larvae	UPV
<i>Thorectes (Thorectes) baraudi</i> López-Colón, 1981 <sup>a</sup>	Four final-instar larvae	CEUA
<i>Thorectes (Thorectes) laevigatus lusitanicus</i> (Jekel, 1866) <sup>a</sup>	Twenty final-instar larvae	CEUA
<i>Thorectes (Thorectes) valencianus</i> (Baraud, 1966) <sup>a</sup>	Four final-instar, two second-instar larvae	CEUA
<i>Trypocopriss</i> Motschulsky, 1858		
<i>Trypocopriss pyrenaicus</i> (Charpentier, 1825) <sup>a</sup>	Two second-instar larvae	UPV
<i>Typhaeus</i> Leach, 1815		
<i>Typhaeus typhoeus</i> (Linnaeus, 1758) <sup>f</sup>	Two final-instar larvae	UPV

CEUA, Entomological Collections of the Universidad de Alicante, Spain; UPV, Université Paul Valéry, Montpellier, France; Ore, Oregon State University; CMN, Canadian Museum of Nature; XAL, Instituto de Ecología de Xalapa, México

<sup>a</sup>First published data on their larval morphology.

<sup>b</sup>Previously published by Howden (1955).

<sup>c</sup>Previously published by Verdú *et al.* (1998).

<sup>d</sup>Previously published by Lumaret (1984).

<sup>e</sup>Previously published by Howden (1967).

<sup>f</sup>Previously published by Ritcher (1947).

<sup>g</sup>Previously published by Howden (1982).

<sup>h</sup>Previously published by Howden (1964).

<sup>i</sup>Previously published by van Emden (1941).

<sup>j</sup>Previously published by Panin (1957).

<sup>k</sup>Previously published by Olson *et al.* (1954).

<sup>l</sup>Previously published by Ritcher (1966).

<sup>m</sup>Previously published by Howden & Peck (1987).

Biforous spiracles are found in larvae of Trogidae. Cribriform (oligoforous) spiracles, considered by Ritcher (1966), Scholtz & Browne (1996), and Browne & Scholtz (1999) as 'not biforous', are present in the Bolboceratinae group. Cribriform multiforous spiracles, described by Howden (1982) as 'not cribriform', are present in Lethrinae, Geotrupinae and Taurocerastinae.

28. *Legs*: (0) equal or subequal in length (Figs 35–39); (1) metathoracic leg reduced (Fig. 40).

29. *Trochanter and femur*: (0) with fossorial setae; (1) without fossorial setae.

30. *Metathoracic leg*: (0) four-segmented (Fig. 35); (1) three-segmented (Figs 36–40).

Within Bolboceratinae, the metathoracic legs of *Bolbocerosoma* Schaeffer, 1906 and *Bolbelasmus* are four-segmented (Ritcher, 1966; Verdú *et al.*, 1998). Moreover, the metathoracic legs of *Odonteus* species are not two-segmented as indicated by Ritcher (1966), Howden (1982) and Browne & Scholtz (1999). A reduced tibiotarsus is shown in Fig. 38.

31. *Plectrum of mesothoracic leg*: (0) absent (Figs 35–37); (1) well developed (Figs 38a–40a).

32. *Pars stridens of metathoracic leg*: (0) absent; (1) well developed (Figs 38b–40b).

33. *Tarsal claws*: (0) well developed (Figs 35–37); (1) reduced or absent (Figs 38–40).

34. *Lateral anal lobe*: (0) absent (Figs 41–42); (1) developed (Figs 43–49).

35. *Ventral anal lobes*: (0) not fused (Fig. 48); (1) fused (Fig. 49).

36. *Lateral anal lobes*: (0) without dorso-exterior indentation (e.g. Fig. 45); (1) with deep dorso-exterior indentation (Fig. 46).

37. *Ventral anal lobes*: (0) without exterior indentation (e.g. Fig. 46); (1) with deep exterior indentation (Figs 45, 47).

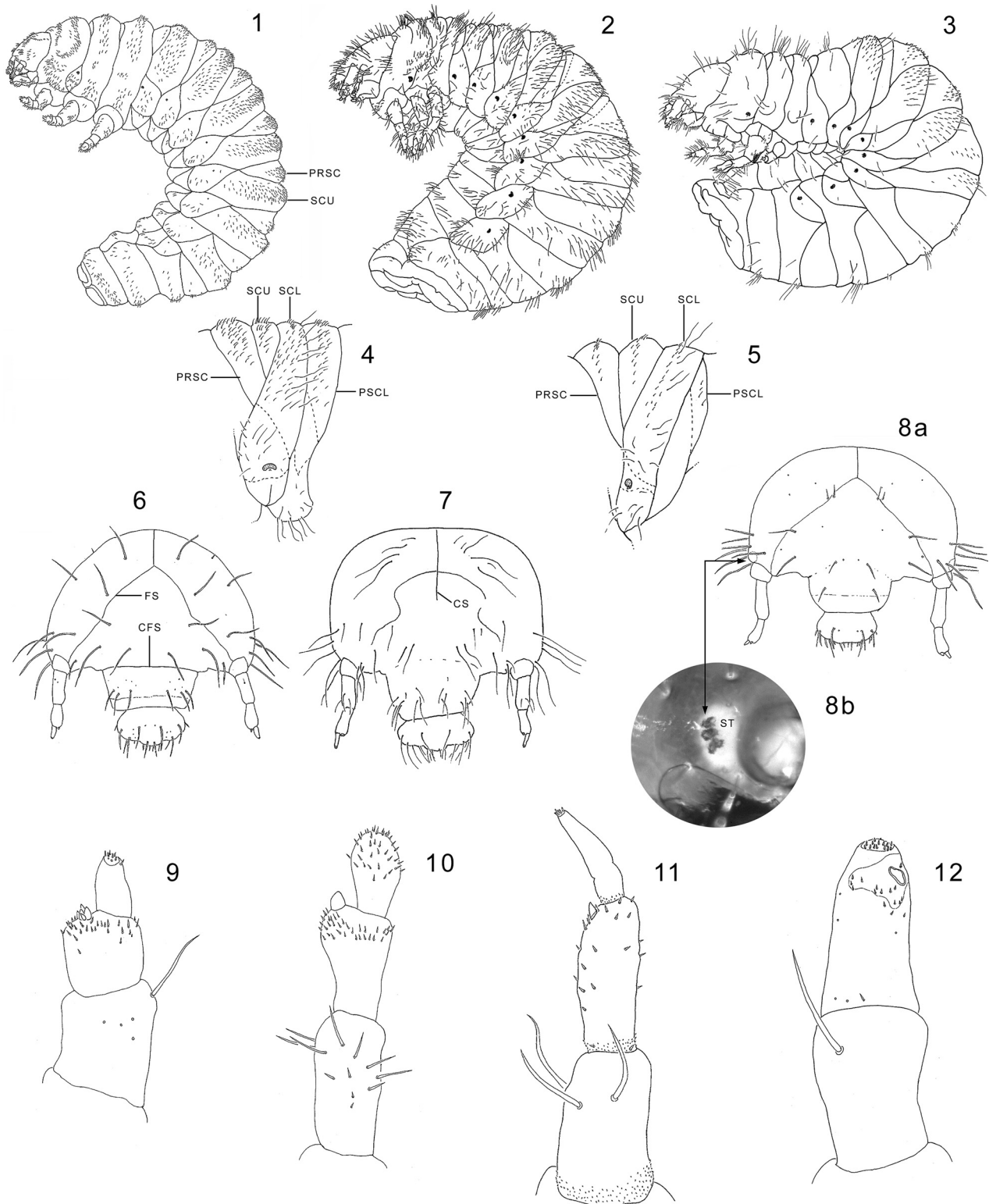
38. *Lateral anal lobes*: (0) without dorso-interior indentation (e.g. Fig. 46); (1) with deep dorso-interior indentation (Fig. 47).

#### Cladistic analysis

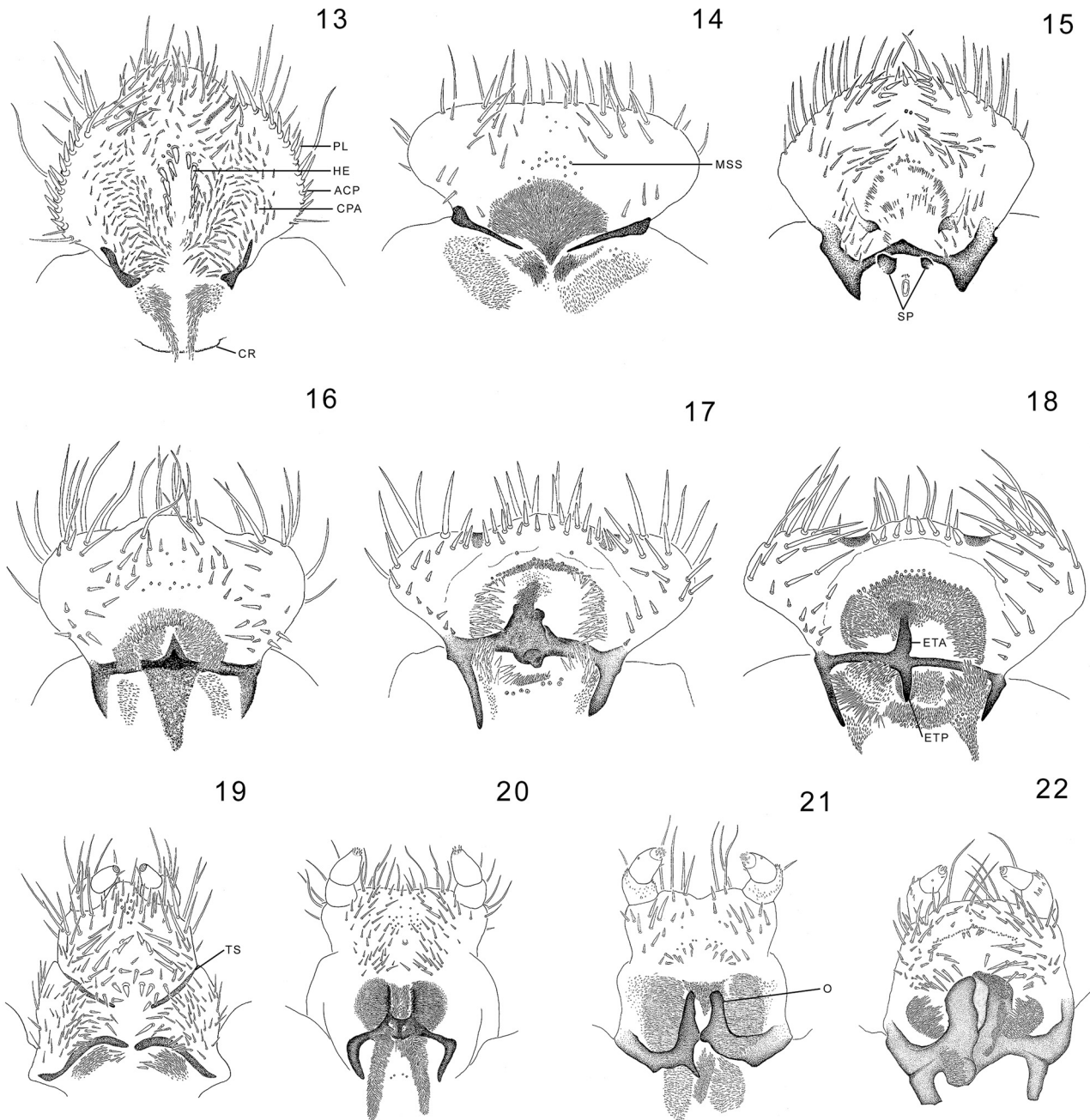
The phylogenetic analyses of the Geotrupidae included thirty-eight larval characters and twenty-two genera (forty-four species in total). *Trox cricetus*, *Polynoncus aeger* and *Pleocoma linsleyi* were used as outgroup taxa. The data matrix used in the analysis is shown in Table 2.

Three analyses are presented here; first, a heuristic parsimony analysis was performed with 1000 random stepwise additions of taxa (TBR branch swapping, MulTrees option in effect). These phylogenetic analyses were performed in PAUP\* version 4.0 (Swofford, 1998), under the Fitch criterion (Fitch, 1971). Characters were of equal weight. A heuristic search was then performed with TBR. All characters were unordered. Bootstrap values for clades were calculated in 500 replicates using a single heuristic search.

The second analysis, a ratchet parsimony analysis (Nixon, 1999), was carried out with WINCLADA 1.00.08 (Nixon, 2002), in order to find the most parsimonious tree



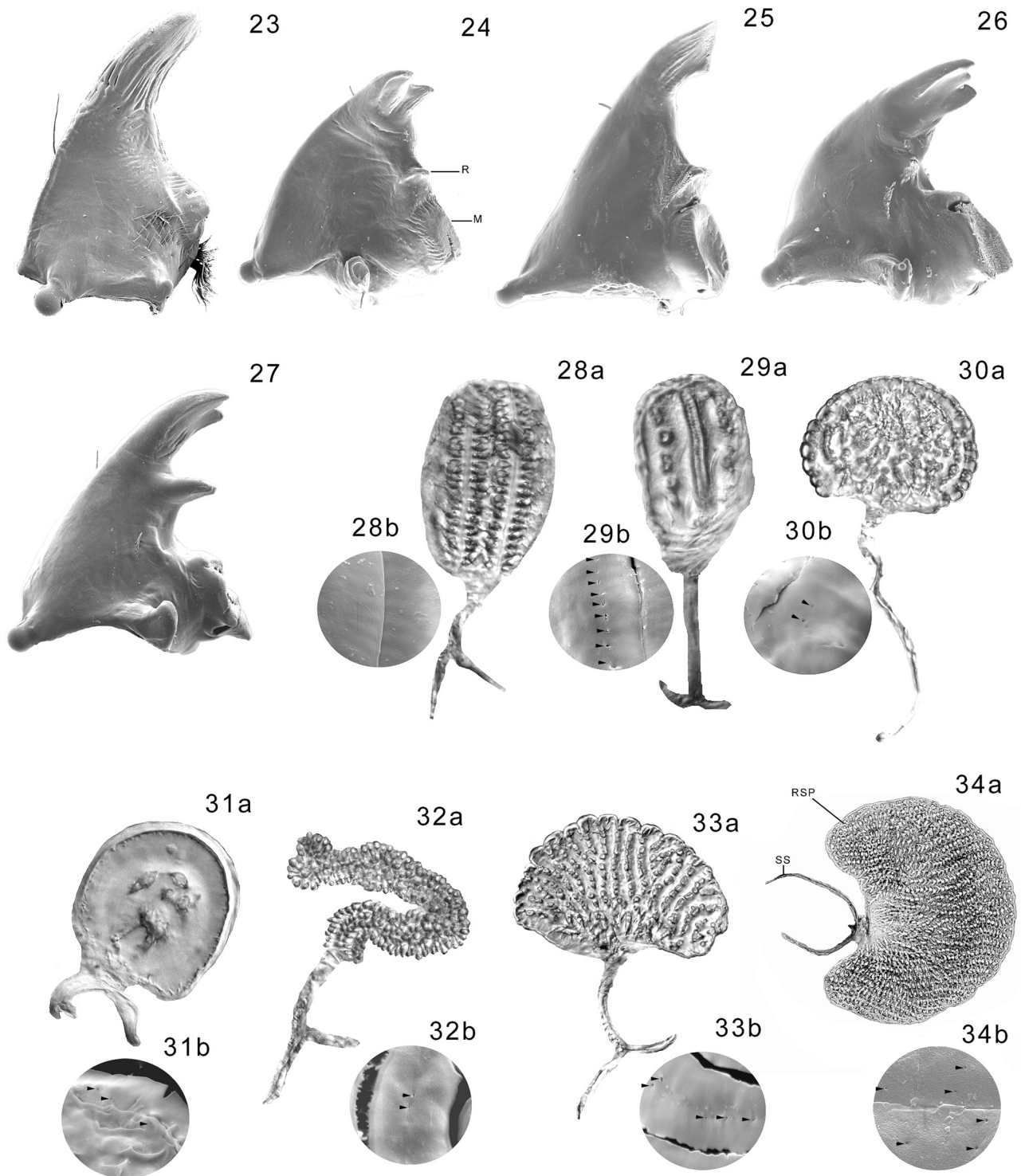
**Figs 1–12.** General body shape: 1, *Bolbelasmus bocchus* (from Verdú et al., 1998); 2, *Typhaeus typhoeus*; 3, *Thorectes valencianus*. Abdominal segments: 4, *Pleocoma linsleyi*; 5, *Polynoncus aeger*. Head: 6, *Frickius variolosus*; 7, *Thorectes punctatolineatus*; 8, *Trox cricetulus*. Antennae: 9, *Bolbelasmus gallicus*; 10, *Odonteus armiger*; 11, *Thorectes punctatolineatus*; 12, *Ceratophyus hoffmanseggi*. PRSC = prescutum; SCU = scutum; SCL = scutellum; PSCL = postscutellum; FS = frontal suture; CFS = clypeo-frontal suture; CS = coronal suture; ST = stemmata.



**Figs 13–22.** Epipharynx: 13, *Pleocoma linsleyi*; 14, *Bolbelasmus gallicus*; 15, *Polynoncus aeger*; 16, *Odonteus armiger*; 17, *Typhaeus typhoeus*; 18, *Thorectes intermedius*. Hypopharynx: 19, *Pleocoma linsleyi*; 20, *Bolbelasmus bocchus* (from Verdú *et al.*, 1998); 21, *Odonteus armiger*; 22, *Thorectes intermedius*. PL = plegmatium; HE = heli; ACP = acanthoparia; CPA = chaetoparia; MSS = macrosensillae; SP = sclerotized plate; ETA = anterior epitorma; ETP = posterior epitorma; TS = transversal sclerome; O = oncly.

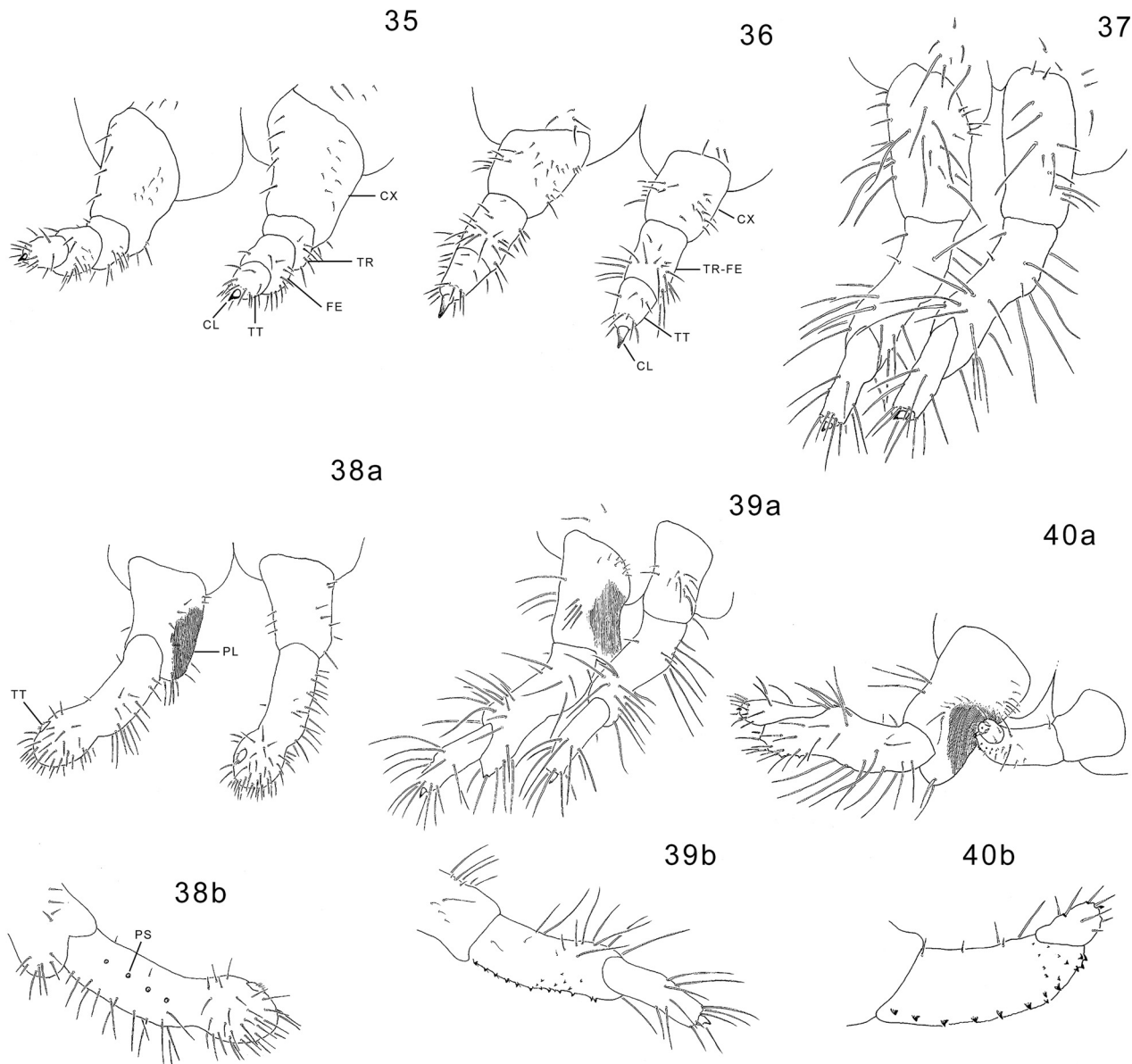
(MP tree; characters codified as nonadditive; Fitch, 1971; heuristic searches with 10 000 iterations/replication, one tree to hold/iteration, four characters to sample). The robustness of the resulting MP tree was tested by means of bootstrapping with 1000 pseudoreplications, as implemented in WINCLADA.

The third analysis, a Bayesian inference of phylogeny (Huelsenbeck & Ronquist, 2001), was performed with MRBAYES 3.0 (Huelsenbeck & Ronquist, 2002) by Metropolis coupled Markov chain Monte Carlo (MC3) sampling for 1 000 000 generations (four simultaneous MC chains, sample frequency 100, burnin=0) under the Mkv model



**Figs 23–34.** Scanning electron micrographs of mandibles: 23, *Pleocoma linsleyi*; 24, *Bolbelasmus gallicus*; 25, *Eucanthus lazarus*; 26, *Lethrus tuberculifrons*; 27, *Geotrupes ibericus*. Light (a) and scanning electron (b) micrographs of respiratory spiracles: 28, *Trox cricetus*; 29, *Eucanthus lazarus*; 30, *Bolbelasmus gallicus*; 31, *Odonteus darlingtoni*; 32, *Frickius variolosus*; 33, *Lethrus tuberculifrons*; 34, *Thorectes punctatolineatus* (respiratory holes are indicated by arrows). R = retinaculum; M = molar area; RSP = respiratory plate; SS = spiracular slit.





**Figs 35–40.** Meso- and metathoracic legs: 35, *Bolbelasmus gallicus*; 36, *Lethrus tuberculifrons*; 37, *Typhaeus typhoeus*; 38, *Odonteus armiger*, general view (a); metathoracic leg, anterior view (b); 39, *Ceratophyus hoffmannseggi*, general view (a); metathoracic leg, anterior view (b); 40, *Geotrupes ibericus*, general view (a); metathoracic leg, anterior view (b). CX = coxa; TR = trochanter; FE = femur; TT = tibiotalpus; CL = claw; PL = plectrum; PS = pars stridens.

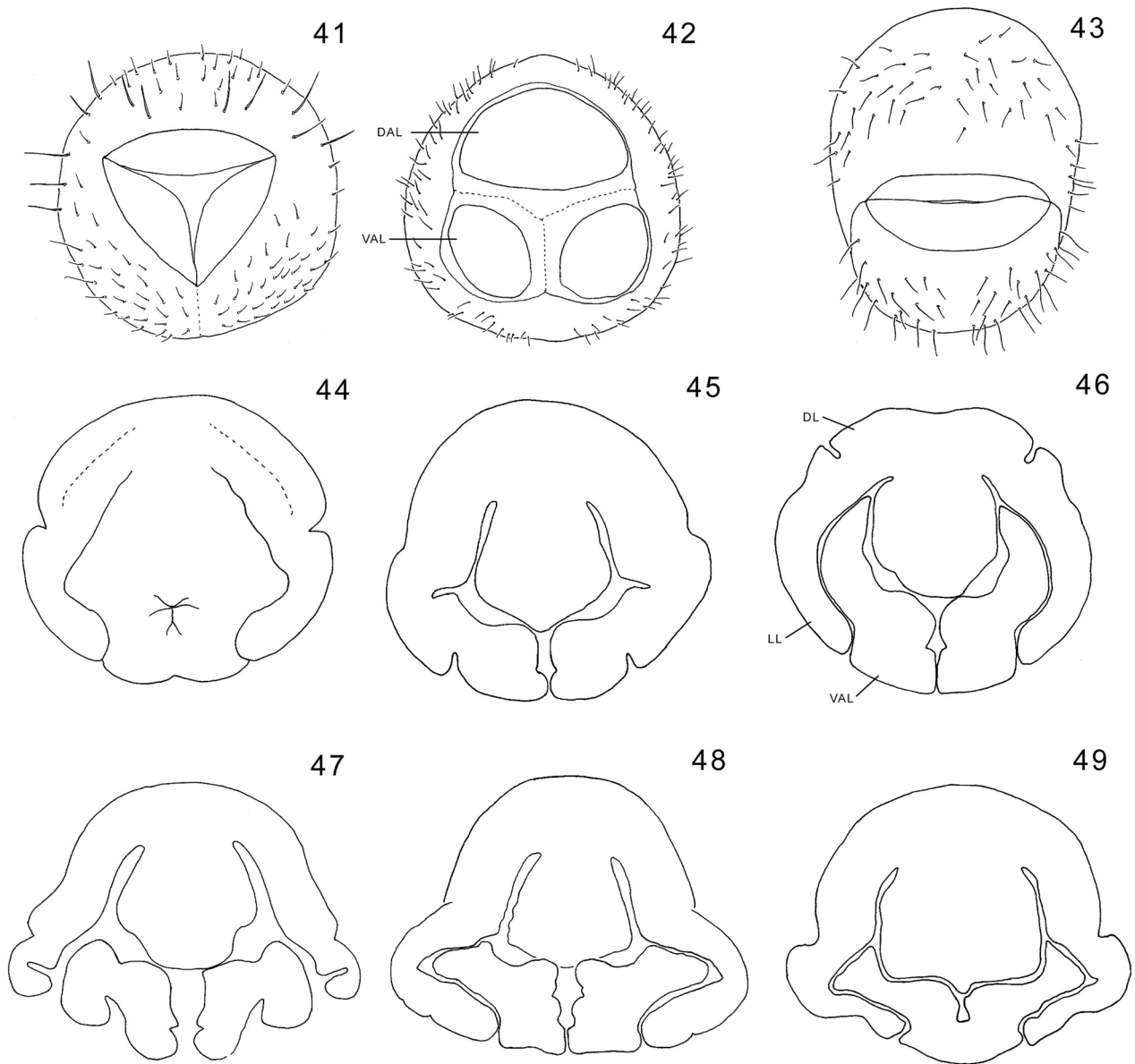
(Lewis, 2001) with a default gamma correction for rate heterogeneity ( $\alpha=0.075$ ).

## Results and discussion

### Parsimony analysis

The heuristic analysis resulted in three MP trees (length = 65, consistency index (CI) = 0.69, retention index

(RI) = 0.86; Fig. 50). The ratchet parsimony inference also resulted in three MP trees (length = 66, CI = 0.68, RI = 0.84; Fig. 50). These MP trees are only differentiated by the position of *Eucanthus* and the relationship between *Bolbelasmus* and *Bolbocerosoma*. So, *Eucanthus* could be closely related to the clade composed of *Bolbelasmus* and *Bolbocerosoma*, or at the base of the remaining Geotrupidae genera. On the other hand, *Bolbelasmus* and *Bolbocerosoma* could constitute a monophyletic clade or a polytomy together with the group composed of the other Geotrupidae genera.

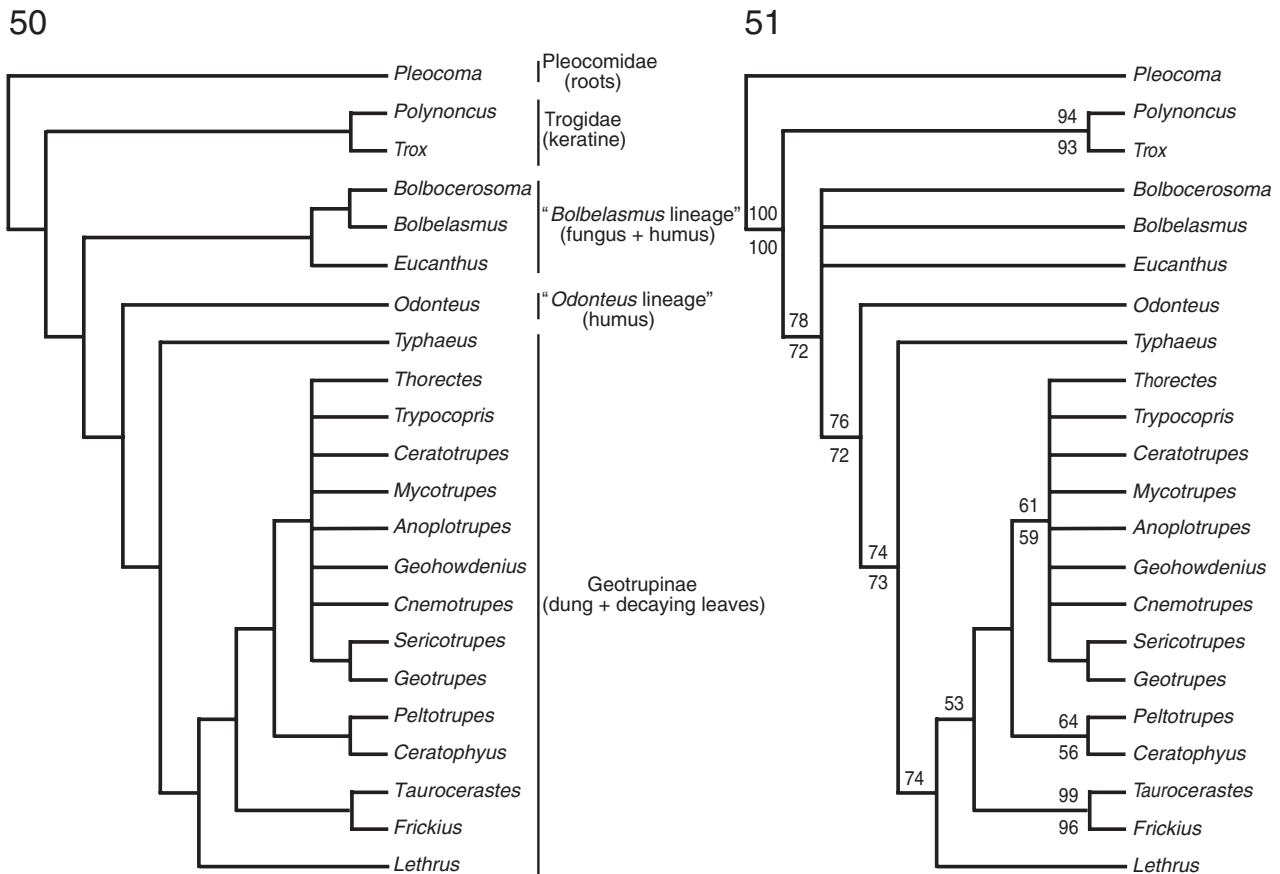


**Figs 41–49.** Anal lobes: 41, *Eucanthus lazarus*; 42, *Bolbelasmus bocchus* (from Verdú et al., 1998); 43, *Odonteus armiger*; 44, *Lethrus apterus*; 45, *Ceratophyus hoffmannseggi*; 46, *Typhaeus typhoeus*; 47, *Frickius variolosus*; 48, *Thorectes valencianus*; 49, *Geotrupes puncticollis*. DAL = dorsal anal lobe; VAL = ventral anal lobe; LL = lateral lobe.

The strict consensus tree for the three MPs of each analysis is shown in Fig. 51; bootstrapping values over 50% are also represented for both analyses. *Bolbelasmus*, *Bolbocerosoma* and *Eucanthus* genera appear close to the outgroup and their distinction from the rest is relatively well supported. Other supported groups within the remaining Geotrupidae are *Odonteus* and the clade composed of *Frickius* and *Taurocerastes*. Although there seems to be some kind of topological structure within the tree, as shown by strict consensus, most terminal taxa have negligible support or are not supported at all.

#### Bayesian inference

A Bayesian inference based on the morphological dataset arrived at a similar and congruent consensus tree (Fig. 52). This analysis recovered the clade of *Bolbelasmus* and *Bolbocerosoma* as sister to the remaining Geotrupidae. The next clade might be *Eucanthus*, but this clade and its position are not sufficiently supported. Again, *Odonteus* and the group constituted by *Frickius* and *Taurocerastes* are also significantly differentiated, as well as the *Ceratophyus* and *Pelto- trupes* clade. However, the relationships between the



**Figs 50–51.** Phylogenetic parsimony inferences: 50, Phylogenetic hypothesis preferred among the most parsimonious (MP) trees obtained through the heuristic search and the ratchet procedure. Feeding preferences of larvae are shown in parentheses (Howden, 1955; Ritcher, 1966; Cambefort, 1991; Scholtz & Chown, 1995; Verdú *et al.*, 1998; personal observations); 51, Strict consensus tree in both MP inferences. The numbers refer to bootstrapping values (over 50%) of both heuristic (up) and ratchet (down) analyses.

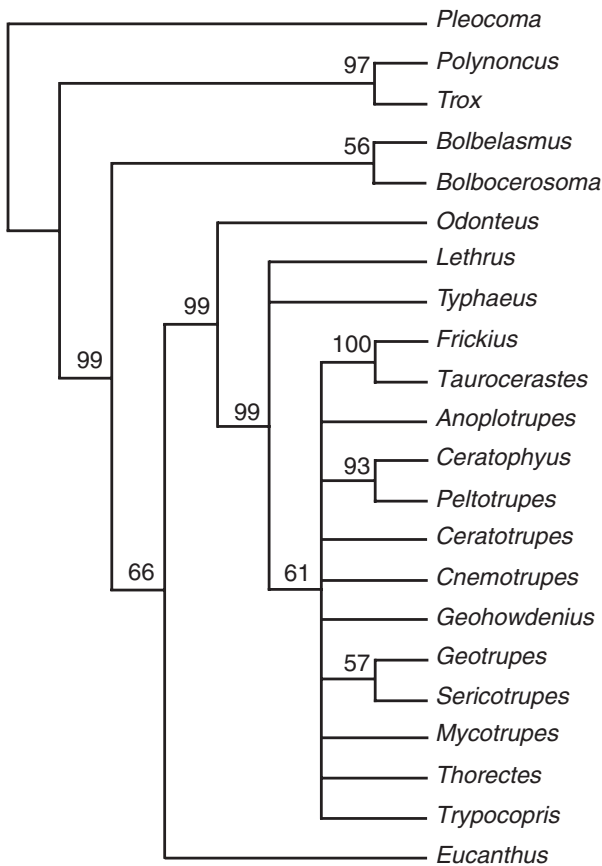
remaining taxa are not specified or must be taken with caution as nodes are supported by posterior probabilities below 95%. Nevertheless, phylogenetic relationships within Geotrupidae appear slightly better resolved and supported in the Bayesian tree than in the MP strict consensus.

#### Monophyly of Geotrupidae

Monophyly of Geotrupidae is well supported in both parsimony and Bayesian analyses (Figs 50–52). Bolboceratinae (*sensu lato*) show notable differences from Pleocomidae, and are the sister group to the rest of Geotrupidae. The close phylogenetic relationship between Pleocomidae and Bolboceratinae (-idae) proposed by Browne & Scholtz (1999) is not supported; the following larval apomorphies reject their hypothesis: abdominal segments 3–7 with two dorsal annulets (nonhomoplasious character; character 4), clypeo-frontal suture absent (except for *Taurocerastes* and *Frickius*; character 5), labrum subtriangular or trilobed

(character 12), chaetoparia and acanthoparia of the epipharynx not prominent (nonhomoplasious character; character 21), glossa and hypopharynx fused, without sclerome (nonhomoplasious character; character 23), trochanter and femur without fossorial setae (character 29) and metathoracic legs three-segmented (except for *Bolbelasmus* and *Bolbocerosoma*; character 30).

From a biological viewpoint, adults of most species of Geotrupinae provision larvae in earthen burrows with decaying organic matter (dead leaves, fungus, dung, or humus) (e.g. Howden, 1955). Larvae of the ‘*Odonteus* lineage’ can be characterized as decaying vegetable matter consumers, concretely humus. Adults of *Odonteus darlingtoni* and *O. liebecki* were found to provide finely divided surface humus for their larvae, which they pack into the bottom of their burrows (Howden, 1955). ‘*Bolbelasmus* lineage’ species have been characterized as fungus and humus consumers, concretely for the larval stages (Howden, 1955; González-Peña, 1979; Verdú *et al.*, 1998). However, adults of Pleocomidae do not feed and larvae are phytophagous, concretely root feeders (Ritcher, 1966) (summarized in Fig. 50).



**Fig. 52.** A strict consensus tree in Bayesian inference of phylogeny. The numbers refer to percentages of stabilized posterior probabilities (and higher than 50%) obtained for each clade through a MC3 procedure.

#### *Polyphyly of the Bolboceratinae group*

Bolboceratinae (-idae; s.l.) is clearly not monophyletic. Our results show that the Bolboceratinae group is divided into two lineages. The closest group to Geotrupinae is constituted by *Odonteus* species ('*Odonteus* lineage') and the second group by *Bolbelasmus*, *Bolbocerosoma*, and *Eucanthus* ('*Bolbelasmus* lineage').

The apomorphic character states supporting the '*Odonteus* lineage' are: apex of antennal segment 2 with a unique sensorium (character 11), anterior and posterior epitormae of epipharynx developed (characters 13, 14), tormae of epipharynx fused (character 16), oncyli of hypopharynx developed (character 22), tarsal claws reduced or absent (character 33), and plectrum and pars stridens of legs well developed (characters 31, 32). The '*Bolbelasmus* lineage' is supported by two apomorphies: apex of antennal segment with various sensoria (autapomorphy; character 11), and labrum subtriangular (excluding *Eucanthus*; character 12).

#### *Phylogenetic relationships within Geotrupinae*

The following apomorphic characters support the monophyly of Geotrupinae: last abdominal segment obliquely flattened (unique within Geotrupidae; character 2), anterior epitormae of epipharynx well developed (unique within Geotrupidae; character 13), macrosensillae of epipharynx forming an alignment with protophoba (unique within Geotrupidae; character 18), molar region of mandibles well developed and respiratory spiracles cribriform multiforous (character 26).

Within Geotrupinae, four groups are included: Chromogeotrupini (type genus *Chromogeotrupes*; represented by *Typhaeus* in the analysis) characterized by the presence of the posterior epitormae of the epipharynx slightly developed (character 14) and lateral anal lobes with a deep dorso-exterior indentation (character 36); Lethrini (type genus *Lethrus*) characterized by the presence of tarsal claws well developed (character 33) and the absence of plectrum of mesothoracic legs and pars stridens of metathoracic legs (characters 31, 32, including *Typhaeus*); Taurocerastini (type genus *Taurocerastes*) are included within Geotrupinae, which was also suggested by Howden (1982; fig. 15), and characterized by some apomorphies such as the reduction of the metathoracic legs (character 28) and the presence of well-developed stridulatory organs (character 32); Geotrupini (type genus *Geotrupes*) are characterized by a strongly curved body shape at the level of the fourth or fifth abdominal segment (nonhomoplasious character; character 1; excluding *Ceratophyus* and *Peltotrupes*) and the presence of a well-developed retinaculum of the mandibles (character 25; including *Typhaeus*). Moreover, the results suggested closer phylogenetic relationships between *Ceratophyus* and *Peltotrupes*, supported by some apomorphies such as the reduction of antennal segments (nonhomoplasious character; character 10) and the subtriangular not trilobed labrum shape (character 12), but to confirm this possible group as a new tribe, more characters should be analysed.

#### *Evolutionary specialization: the quality of food and the nesting behaviour*

A tendency to coprophagy is evident in several Scarabaeoidea families associated with dung, and in Geotrupidae in particular. The diet of the larvae of the most primitive geotrupids, such as the '*Odonteus* lineage' and the '*Bolbelasmus* lineage', is based on humus and fungi, whereas many Geotrupinae show coprophagous habits, with modification of mouthparts, particularly in adults (Halffter & Matthews, 1966; Cambefort, 1991). A similar evolutionary polarity regarding nesting behaviour can be seen. Primitive geotrupids construct simple burrows; adults pack surface humus and divide it into fine pieces to fill the nest. A single egg is laid in a small cavity just beyond the packed humus (Howden, 1955). In 'intermediate' geotrupids, such as Lethrini and Chromogeotrupini, adults construct burrows

**Table 2.** Data matrix showing the characters and character states used for the cladistic analysis.

	1		2		3		12345	678
	12345	67890	12345	67890	12345	67890		
<i>Pleocomma</i>	00100	00010	10001	00000	00010	12000	11000	000
<i>Polynoncus</i>	00010	00000	10000	11011	01001	12000	00000	000
<i>Trox</i>	00011	00000	10000	11011	01001	10000	00000	000
<i>Anoplotrupes</i>	11121	10110	12221	11111	12112	12111	11110	000
<i>Bolbelasmus</i>	00121	00010	01001	01011	11111	01010	00000	000
<i>Bolbocerosoma</i>	00121	00010	01001	01011	11111	01000	00000	000
<i>Ceratophyus</i>	01121	11111	11221	11111	12112	12011	11110	010
<i>Ceratotrupes</i>	11121	10110	12221	11111	12112	12111	11110	000
<i>Cnemotrupes</i>	11121	10110	12221	11111	12112	12111	11110	000
<i>Eucanthus</i>	00121	00010	02001	01011	11111	01001	00000	000
<i>Frickius</i>	01120	00010	12221	11111	12110	12111	11110	011
<i>Geohowdenius</i>	11121	10110	12221	11111	12112	12111	11110	000
<i>Geotrupes</i>	11121	11110	12221	11111	12112	12111	11111	000
<i>Lethrus</i>	01121	10010	12221	11111	12110	12011	00010	000
<i>Mycotrupes</i>	11121	10110	12221	11111	12112	12111	11110	000
<i>Odonteus</i>	00121	10010	12111	11011	12111	01001	11111	000
<i>Peltotrupes</i>	01121	10111	11221	11111	12112	12111	11110	000
<i>Sericotrupes</i>	11121	10110	12221	11111	12112	12111	11111	000
<i>Taurocerastes</i>	01120	00010	12221	11111	12110	12111	11110	011
<i>Thorectes</i>	11121	10110	12221	11111	12112	12111	11110	000
<i>Trypocopriss</i>	11121	10110	12221	11111	12112	12111	11110	000
<i>Typhaeus</i>	01121	10110	12211	11111	12112	12011	00110	100

with compact 'sausages' of dead leaves and dung. The eggs are still deposited singly in a small cell in the sand outside the food (Howden, 1955; Brussaard, 1983). In 'modern' geotrupids, such as Geotrupini, dung is generally used as food. In some cases, dead leaves can be used, as in some *Cnemotrupes* Jekel, 1865 species (Howden, 1955). In this group, male–female co-operation is frequent and the egg is laid in a small cell in the food mass, as also occurs in modern Scarabaeinae (Howden, 1955; Halffter & Matthews, 1966; Klemperer, 1979; personal observations). The high diversity of the nesting architecture observed in this group has been considered a possible taxonomic character at generic and subgeneric levels (Howden, 1955).

#### Taxonomic arrangements

The present results have confirmed the existence of two different lineages within Bolboceratinae s.l. The *Odonteus* lineage constitutes the sister group to Geotrupinae. The second lineage is constituted by *Bolbelasmus*, *Bolbocerosoma*, and *Eucanthus*; this is the first evidence of the close relationship among these genera, but to confirm this group as a well-supported clade, more characters should be analysed. Within Geotrupinae, the analysis of the larval morphology suggests a preliminary classification at tribal level into Lethrini, Chromogeotrupini, Geotrupini and Taurocerastini.

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