

The basal phylogeny of Scarabaeoidea (Insecta: Coleoptera) inferred from larval morphology

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Abstract. Larvae of 60 genera representing the following families and subfamilies of Scarabaeoidea were studied and analysed phylogenetically: Lucanidae (Aesalinae, Nicaginae, Syndesinae, Lampriminae, Lucaninae), Passalidae (Passalinae, Aulacocyclinae), Trogidae, Pleocomidae, Geotrupidae (Taurocerastinae, Lethrinae, Geotrupinae), Bolboceratidae, Ceratocanthidae, Hybosoridae, Glaphyridae, Scarabaeidae (Aphodiinae, Scarabaeinae, Melolonthinae, Dynastinae, Cetoniinae). Seventy-eight larval morphological characters were employed in the analysis. Our data confirm that Dascillidae are not closely related to Scarabaeoidea. The monophyly of the superfamily is supported by 20 apomorphic character states, 18 of them unique. Monophyly of the following scarabaeoid clades is supported (with the number of larval synapomorphies followed by the bootstrap value in parentheses): Scarabaeoidea without Passalidae (6/67), Passalidae (9/100), Pleocomidae (11/93), Trogidae (8/93), Glaphyridae (10/96), Lucanidae (9/95), Ceratocanthidae + Hybosoridae (5/74), Scarabaeinae (9/98). The family Ceratocanthidae was found to be paraphyletic with respect to Hybosoridae. Monophyly of the family Scarabaeidae is not supported. The resolution of the basal parts of the strict consensus tree is higher when using Dascillidae + Eulichadidae v. Agyrtaeidae + Helophoridae as an outgroup, but the differences in topology become insignificant after bootstrapping. It is suggested that larval morphology alone is not an adequate tool to address basal relationships of Scarabaeoidea and a total evidence analysis should be performed.

Additional keywords: Bolboceratidae, Ceratocanthidae, Geotrupidae, Glaphyridae, Hybosoridae, Lucanidae, Passalidae, Pleocomidae, Scarabaeidae, Trogidae.

Introduction

The superfamily Scarabaeoidea is one of the largest subdivisions of beetles with an estimated 35,000 species worldwide. Unlike the majority of beetles, scarabaeoids are well known to most people due to their relatively large size, often bright colouration, significant economic importance and to the association of the genus *Scarabaeus* Linnaeus, 1758 with sacred symbols of ancient Egypt. Among enthusiastic beetle collectors specimens belonging to Scarabaeoidea are arguably amongst the most desired objects, particularly the vividly coloured, often metallic Rutelinae and Cetoniinae (Scarabaeidae) and horned males of Lucanidae and Dynastinae (Scarabaeidae).

Fourteen families constitute the superfamily Scarabaeoidea. The family Lucanidae (stag beetles) is a cosmopolitan group with ~95 genera and up to 1250 species (Moore and Cassis in Houston 1992) arranged in six subfamilies: Aesalinae, Nicaginae, Syndesinae, Lucaninae, Lampriminae

and Penichrolucaninae with larvae normally living in decaying logs (Lawrence 1981). The Passalidae is a widespread, mainly tropical family with 61 genera and 680 described species (Reyes-Castillo 2002). This family is divided into two subfamilies: Passalinae occurs throughout the family's distribution range and Aulacocyclinae from South-East Asia and Australia (Reyes-Castillo 1970). These beetles are remarkable for their subsocial behaviour, where adults feed their larvae and the latter are unable to finish their development without the parents (Schuster and Schuster 1985; Schuster and Reyes-Castillo 1990; Schuster 1992). The Trogidae is a small distinctive cosmopolitan family that consists of three genera: *Trox* Fabricius, 1775; *Omorgus* Erichson, 1847 and *Polynoncus* Burmeister, 1876, with ~300 species (Scholtz 1986). *Trox* has a Holarctic and Afrotropical distribution, *Omorgus* is widespread on the Gondwana continents and southern North America, whereas *Polynoncus* is a Neotropical endemic (Scholtz 1986).

Trogids are unique among the Scarabaeoidea since adults and larvae of all species feed primarily on keratin (Baker 1968). The family Glaresidae consists of a single widely distributed genus *Glaresis* Erichson, 1848 with ~50 species (it does not occur in Australia, New Zealand, or Japan; Scholtz 1983; Scholtz *et al.* 1987b). The family Pleocomidae is monogeneric, with the genus *Pleocoma* LeConte, 1856 including 26 species occurring in western North America (Hovore 2002). *Pleocoma* males usually fly during rain while the soil-dwelling larvae are unique in the superfamily in that they have more than three instars. The cosmopolitan family Bolboceratidae (*sensu* Scholtz and Browne 1996) comprises two distinct subfamilies Bolboceratinae and Athyreinae and ~40 genera and 350 species. The former subfamily includes the majority of taxa (Howden and Cooper 1977; Howden 1982, 1985, 1989, 1992; Verdú *et al.* 1998; Gussmann and Scholtz 2000, 2001), whereas the Athyreinae includes four genera and some 70 species from the Neotropical and Afrotropical Regions (Howden and Martínez 1963, 1978). The family Diphylostomatidae includes three species in the genus *Diphylostoma* Fall, 1901 endemic to the west coast of California (Holloway 1972; Jameson and Ratcliffe 2002). The family Geotrupidae comprises three distinct subfamilies: the mainly Holarctic Geotrupinae (25 genera and ~150 species; Howden 1955; Král *et al.* 2001); monogeneric Lethrinae with ~80 species of the genus *Lethrus* Scopoli, 1777 in eastern Europe and central Asia (Král and Olexa 1996); and the southern Neotropical Taurocerastinae with *Taurocerastes patagonicus* Philippi, 1886 from southern Argentina and Chile, and two species of *Frickius* Germain, 1897 from central Chile (Howden 1982; Zunino 1984; Howden and Peck 1987). The enigmatic family Belohinidae includes a single species, *Belohina inexpectata* Paulian, 1958 from southern Madagascar (Paulian 1958, 1979a) known only from the type series. The Ochodaeidae is divided into two subfamilies (Ochodaeinae and Chaetocanthinae) with 10 genera and ~80 species mainly in the Holarctic region, southern Africa and Madagascar (Carlson and Ritcher 1974; Paulian 1976; Scholtz and Evans 1987; Scholtz *et al.* 1988). The mainly pantropical family Ceratocanthidae includes ~320 species in ~40 genera (Paulian 1977, 1979b, 1982; Ballerio 1999, 2000a, b; Howden and Gill 2000; Grebennikov *et al.* 2002). The cosmopolitan family Hybosoridae includes ~30 genera and ~230 species (Allsopp 1984; Kuijten 1985, 1986; Scholtz *et al.* 1987a; Howden 2001; Ocampo 2002). The family Glaphyridae comprises two subfamilies (Holarctic Glaphyrinae and South American Lichninae) with eight genera and ~80 species (Chapin 1938; Baraud 1989; Mitter 1996; Carlson 2002). The family Scarabaeidae is by far the largest and most diverse group within the superfamily. It consists of several well defined subfamilies and several groups of uncertain status. There are ~1600 genera and 27,000 species

known in the family. Thirteen subfamilies are currently recognised: Aphodiinae (Tangelder and Krikken 1982; Stebnicka and Howden 1996; Stebnicka 1999; Dellacasa *et al.* 2001); Scarabaeinae (Ferreira 1972; Edmonds and Halfpter 1978; Hanski and Cambefort 1991; Montreuil 1998; Forgie *et al.* 2002; Philips *et al.* 2002, 2004); Pachypodinae (Crovetti 1969; Arnone and Sparacio 1990); Orphninae (Paulian 1984; Baraud 1991; Barbero and Palestini 1993); Allidiostomatinae (Ruiz 1924; Lawrence *et al.* 1999); Dynamopodinae (Lawrence *et al.* 1999); Aclopininae (Allsopp 1981, 1983; Lawrence *et al.* 1999); Euchirinae (Young 1989); Phaenomeridinae (Lawrence *et al.* 1999); Melolonthinae (Ratcliffe *et al.* 2002); Rutelinae (Jameson *et al.* 1994; Jameson 1998, 2000; Smith 2002); Dynastinae (Endrödi 1985; Ratcliffe *et al.* 2002) and Cetoniinae (Krikken 1984).

It might be expected that such an easily recognisable group of relatively large size such as Scarabaeoidea would have a well established phylogeny. However, although most currently recognised families have been considered monophyletic, relationships between them are far from being resolved.

A first attempt at a phylogenetic reconstruction of the higher taxa was done by Howden (1982) and focused on the phylogenetic position of Taurocerastinae (Geotrupidae) in relation to many other scarabaeoid taxa. Scholtz (1990) provided a comprehensive review of the available scarabaeoid data and literature. Browne and Scholtz (1995) studied the evolution and morphology of the hind wing articulation, base and venation; their resulting cladogram was based on a total of 73 characters. Scholtz *et al.* (1994) re-examined adult and larval characters and established a general ground plan for the characters, with special emphasis on the hind wing base, articulation and wing vein characters. Browne and Scholtz (1999) brought together all of the available data in the final paper of the series and proposed a phylogenetic classification of the superfamily consisting of two basal lineages: Glaresidae and the rest of the superfamily consisting of two lower level lineages: passalid and scarabaeid. The passalid lineage comprises a glaphyrid line (((Passalidae (Lucanidae Diphylostomatidae)) Trogidae) (Bolboceratidae Pleocomidae) Glaphyridae) and geotrupid line (Geotrupidae (Ochodaeidae (Ceratocanthidae Hybosoridae))). The scarabaeid lineage includes only the family Scarabaeidae. To date, this is the only work providing a classification of the superfamily based on a formal cladistic procedure.

The sister-group relationships of the superfamily Scarabaeoidea remain controversial. Böving (1929) and Böving and Craighead (1931), based on larval characters, proposed that the Scarabaeoidea is most closely related to the Dascillidae. Crowson (1955, 1960, 1981) followed Böving and Craighead (1931) and linked Dascilloidea and Scarabaeoidea as the two superfamilies in Scarabaeiformia based mainly on larval morphological characters. Later Crowson

(1995: 67) indicated six more possible larval synapomorphies between Scarabaeoidea and Dascilloidea in addition to general similarities in body shape: stemmata 0 or 1 on each side of cranium; mandible with well developed mola; maxillae with sharp, rather than finger-like galea; spiracles basically biforous; urogomphi, if present (*Dascillus cervinus* Linnaeus, 1858, *Sandalus* Knoch, 1801), small, inconspicuous, not articulated; distinct hypopharyngeal bracon present.

Adult morphology also provides some support to the Scarabaeoidea–Dascilloidea relationships. The supposedly homologous intersegmentalia associated with mesothoracic spiracles (Ritcher 1969); similarity in exocone ommatidium structure in dascilloids and Passalidae (Caveney 1986); similarity in trilobe male genitalia with a well defined genital capsule in some dascilloids and various basal scarabaeoids (e.g. Glaresidae), and close similarity between Dascilloidea and *Pleocoma* and *Diphyllostoma* in the subdivision of the median lobe of the aedeagus into dorsal and ventral lobe (d’Hotman and Scholtz 1990a, 1990b); mouthparts (Nel and Scholtz 1990); as well as open procoxal cavities, which are similar in *Dascillus* and Pleocomidae, lend support to the hypothesis that Dascilloidea is the sister-group of the Scarabaeoidea. Crowson (1981) and Scholtz (1990) favoured this possibility.

In contrast, Verhoeff (1923a: 59, 1923b: 123) combined the Dascillidae with the Scirtidae based on larval characters and listed differences and similarities between Lamellicornia (= Scarabaeoidea) and Dascillidae but did not link the two groups assuming that these similarities were insufficient evidence for relationship. Lawrence and Newton (1982) and Lawrence and Britton (1991) claimed similarities between dascillid and scarabaeoid larvae are either plesiomorphic or associated with soil-dwelling habits. Jeannel and Paulian (1944) proposed a classification of the Polyphaga based on the degree of regression of the basal abdominal sternites in adults and divided the Polyphaga into two groups, Haplogastra and Heterogastra (= Symphiogastra). Haplogastra (first proposed by Kolbe in 1908 and including Hydrophiloidea, Staphylinoidea, Histeroidea and Scarabaeoidea) is characterised by having sternite II visible only as a lateral rudiment and pleural sclerite whereas in Heterogastra (rest of the Polyphaga) it is usually complete though membranous. Evidence presented by Kukalová-Peck and Lawrence (1993, 2004), Scholtz *et al.* (1994) and Browne and Scholtz (1998) on the evolution of the hind wing in Coleoptera lends further strong support to a Haplogastra–Scarabaeoidea relationship and refutes close relationship between the latter and the Dascilloidea. Hansen (1995: 331; 1997: fig. 7), on the basis of combined analysis of larval and adult morphology, also indicated close relationship for Haplogastra–Scarabaeoidea. Lawrence and Newton (1982) and Lawrence and Britton (1991) stated that adult dascilloids share many more important features (such as the complex prothoracic

interlocking device) with elateriform taxa such as Callirhipidae and Ptilodactylidae than with scarabaeoids. This view was corroborated by Grebennikov and Scholtz (2003) after the study of larvae of four Dascillidae genera. They concluded that Dascillidae are probably most closely related to the dryopoid family Eulichadidae (for larval description of Eulichadidae, see Costa and Vanin 1998) and not to Scarabaeoidea. Moreover, known pupae of two species of Dascillidae (*D. cervinus* and *D. davidsoni*, see Verhoeff 1923a: 59; 1923b: 123; Grebennikov and Scholtz 2003) have seven functional abdominal spiracles, whereas those of Scarabaeoidea have not more than four (advanced stage; Alfred Newton, personal communication).

The primary aim of this study was to undertake a phylogenetic analysis of Scarabaeoidea based on the characters of larval morphology. Particular emphasis was on a search for larval synapomorphies of the superfamily and of each family included in the analysis. Second, we wished to address the most basal branching pattern within Scarabaeoidea based on larval characters and estimate its statistical robustness. In order to do so, we wished to critically re-evaluate the larval characters previously employed in higher classification of Scarabaeoidea (Ritcher 1966; Howden 1982; Browne and Scholtz 1999) and provide new ones. The final aim was to evaluate the resolution of the analysis based on larval characters, its ability to provide clearly defined clades within basal groups of Scarabaeoidea and usefulness of separate larval organs for such analysis. The concept of the superfamily Scarabaeoidea follows Lawrence and Newton (1995) and Browne and Scholtz (1999) with the later modifications by Scholtz and Grebennikov (in press).

Material and methods

Abbreviations

Larvae used in this study are housed in the following collections (curators and loan technicians in parentheses).

ABC	Alberto Ballerio collection, Brescia, Italy
ANIC	Australian National Insect Collection, Canberra, Australia (J. F. Lawrence, S. A. Ślipiński)
CMNC	Canadian Museum of Nature, Ottawa, Canada (H. F. Howden, R. S. Anderson)
FMNH	Field Museum of Natural History, Chicago, USA (M. K. Thayer, A. F. Newton)
MNHN	Muséum National d’Histoire Naturelle, Paris, France (S. Boucher)
NHML	The Natural History Museum, London, UK (S. Hine, M. Kerley)
NMNH	National Museum of Natural History, Washington DC, USA (D. G. Furth, N. Adams)
NZAC	New Zealand Arthropod Collection, Auckland, New Zealand (R. Leschen, B. Holloway)
OSUC	Oregon State Arthropod Collection, Corvallis, USA (D. Judd, A. Warren)
UPC	University of Pretoria collection, Pretoria, South Africa
ZISP	Zoological Institute, St. Petersburg, Russia (B. M. Kataev, G.S. Medvedev)

ZMHB Museum für Naturkunde, Humboldt-Universität, Berlin, Germany (H. Wendt, M. Uhlig)

Material preparation

At least one larva of each studied species (see Appendix 1) was disarticulated, cleaned in a hot solution of 2–5 % KOH in water, placed in glycerol and studied under dissecting and compound microscopes with magnification up to 900×. Drawings were made with the aid of a camera lucida. Morphological terms used in this work are those of Lawrence (1991: 147–177). ‘A’ means adult; ‘L3’ means third-instar larva; ‘P’ means pupa.

Sampled Scarabaeoidea taxa

Larvae of all families and subfamilies of Scarabaeoidea available were included in the analysis (see Appendix 1), although we had a rather restricted set of the diverse pleurostict Scarabaeidae (subfamilies Melolonthinae, Rutelinae, Dynastinae and Cetoniinae). Besides this, the most notable omissions in our analysis are the families Glaresidae, Belohinidae, and Diphylostomatidae, larvae of which are unknown. Larvae of the family Ochodaeidae are known for the genus *Pseudochodaeus* Carlson & Ritcher, 1974 only; a single specimen studied by these authors (Carlson and Ritcher 1974) was received by us as a loan from OSUC, but turned out to have deteriorated and to be unsuitable for character scoring. At the subfamily level, we were unable to study larvae of Penichrolucaninae (Lucanidae), Athyreinae (Bolboceratidae), Lichninae (Glaphyridae), Pachypodinae, Allidiostomatinae, Aclopiniae, Phaenomeridinae and Dynamopodinae (Scarabaeidae) since they are still unknown.

Phylogenetic analysis

In total, four analyses were run (see below). Three IBM-compatible phylogenetic analysis programmes were used: Hennig86 (Farris 1988), Nona (Goloboff 1993) and Winclada (Nixon 2002). The size of the dataset prevented us from using exhaustive searches when searching for the most parsimonious trees and, therefore, we used a heuristic method (command ‘mh*’ in Hennig86). A strict consensus tree was obtained using command ‘n’ (in Hennig86). No *a priori* or *a posteriori* character weighting was implemented and all multistate characters were coded as unordered (Appendix 2, Appendix 3). To measure the support for the individual clades on a cladogram in the first, third and fourth analyses (see below), a randomisation procedure was applied

(command ‘Bootstrap’ in Winclada 1.00.08) with 1000 replications (100 for the first analysis) and 10 searches per replication. Only unambiguous character changes are indicated on the cladograms.

The first analysis was designed to test the hypothesis of a sister-group relationship between the superfamily Scarabaeoidea and the family Dascillidae. It was recently suggested, based on larval morphology, that Dascillidae are closely related to the dryopoid family Eulichadidae (Grebennikov and Scholtz 2003) and not to Scarabaeoidea, as advocated by Crowson (1955, 1960, 1981, 1995). To address this question, the ingroup was combined to include all Scarabaeoidea taxa, three genera of Dascillidae (*Dascillus*, *Notodascillus* and *Pleolobus*) and the genus *Eulichas* (Eulichadidae; morphological data from Costa and Vanin 1998). The analysis was run against *Distocupes varians* (Lea, 1902) (Archostemata: Cupedidae) and *Pterostichus adstrictus* Eschscholtz, 1823 (Adephaga: Carabidae) used as outgroups; the former species was used as the outgroup for bootstrapping analysis. The choice of outgroup was based on the hypothesis of Beutel and Haas (2000) that Archostemata is the first branch of the Coleoptera clade, followed by Adephaga and then by a clade of Myxophaga and Polyphaga.

The second analysis was designed to test the monophyly of Scarabaeoidea and to find larval synapomorphies of the family. The ingroup included all Scarabaeoidea taxa, as well as *Necrophilus hydrophiloides* Guérin-Méneville, 1835 (Agyrtidae) and *Helophorus Fabricius*, 1775 (Hydrophilidae: Helophorinae). The analysis was run against *Distocupes varians* and *Pterostichus adstrictus* used as outgroups. Six uninformative characters were deactivated (18, 19, 26, 36, 40, 41).

The third analysis was aimed at determining branching pattern within Scarabaeoidea. The ingroup included all Scarabaeoidea taxa and the outgroup consisted of *Necrophilus hydrophiloides* and *Helophorus* sp. Eight uninformative characters were deactivated (13, 18, 19, 26, 36, 40, 52, 62). A strict consensus was created from the three most parsimonious trees resulting from the analysis. Bootstrapping was undertaken using only one outgroup, *Necrophilus hydrophiloides* (results in Fig. 4, with bootstrap values shown above the respective branches).

A fourth analysis was aimed at finding differences between Agyrtidae and Hydrophilidae against Eulichadidae and Dascillidae outgroup polarization. The ingroup included all Scarabaeoidea taxa and the outgroup consisted of the representatives of four genera of Eulichadidae and Dascillidae (see Appendix 1). Five most parsimonious trees resulted from the analysis and a strict consensus tree was constructed from them. Characters from one of the five most parsimonious trees were then mapped onto the consensus tree, showing only those characters at branches that were topologically identical between the two trees. Four uninformative characters were deactivated (11, 52, 62, 77). Bootstrapping was undertaken using only one outgroup, *Eulichas dudgeoni* Jäch, 1995 (results in Fig. 4, with bootstrap values shown below the respective branches).

Results and discussion

Analysis 1. Sister-group relationships between Scarabaeoidea and Dascillidae

The first analysis resulted in a single most parsimonious tree with length 214, *CI* 51, *RI* 85 (Fig. 1). This result supports the opinion expressed by Grebennikov and Scholtz (2003) that Dascillidae are more closely related to Eulichadidae than to Scarabaeoidea. There are six larval synapomorphies of Dascillidae and Eulichadidae: coronal suture absent and frontal sutures reaching posterior edge of the cranium (unique synapomorphy, character 18/1); apical antennomere

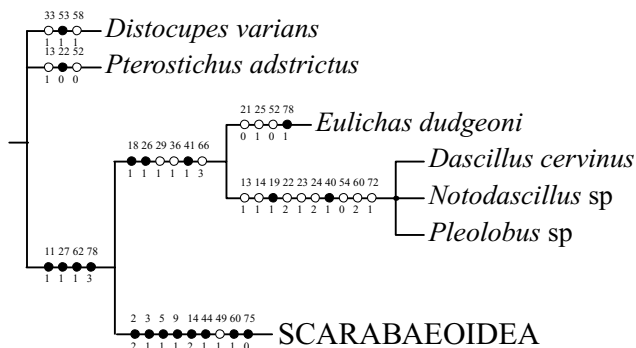


Fig. 1. Single most parsimonious tree (length 214, *CI* 50, *RI* 85) obtained as a result of the first analysis and reflecting the sister-group relationships between Eulichadidae (represented by the genus *Eulichas*) and Dascillidae (represented by the genera *Dascillus*, *Notodascillus* and *Pleolobus*). Black circles represent non-homoplasious characters; white circles indicate homoplasies. Numbers above circles represent characters, numbers below represent character states (see Appendix 2).

shifted laterally whereas sensorium located apically (unique synapomorphy, character 26/1); ultimate (third) antennomere $\sim 10\times$ shorter than penultimate (character 29/1); sensorium on penultimate antennomere located apically (character 36/1); mandibles with articulated process mesally (unique synapomorphy, character 41/1) and claws with more than four setae (character 66/3). This relationship is supported by a bootstrap value of 71 for the Dascillidae + Eulichadidae clade.

Our first analysis is an attempt to provide a formal cladistic background to the results recently obtained by Grebennikov and Scholtz (2003), who suggested that Dascillidae are more closely related to Eulichadidae than to Scarabaeoidea. Eulichadidae, like other members of the superfamily Dryopoidea, had never been proposed as close relatives of Scarabaeoidea. Consequently, this result leaves us with the hypothesis, advocated by Hansen (1997), that the origin of Scarabaeoidea lies within the Staphyliniformia beetles. It is, however, outside of the scope of the present work to challenge or support this opinion.

Analysis 2. Testing the monophyly of Scarabaeoidea

The second analysis resulted in four most parsimonious trees with length 202, *CI* 51 and *RI* 85. The strict consensus tree (not shown) supports the monophyly of the superfamily Scarabaeoidea with 20 apomorphic characters of which all, except 49 and 74, are unique. Scarabaeoidea apomorphies are: thorax and abdomen together C-shaped (character 2/2); dorsal part of body not flattened, nearly round in cross-section (character 3/1); thoracic and abdominal segments I–V dorsally and laterally clearly subdivided into 2–4 markedly developed folds (character 5/1); thoracic and abdominal segments I–V with three-folds (character 6/2); defined thoracic and abdominal sclerites absent, except on prothorax (character 9/1); larval chaetotaxy of highly advanced type (character 11/1); cranium hypognathous (character 14/2); cranium posteriorly rounded (character 16/1); frontoclypeal suture between dorsal mandibular articulation present over full length, clearly detectable (character 21/0); stemmata absent (character 22/2); frontal sutures absent or poorly visible, or not complete (character 25/1); markedly developed sclerotized antennifer is present, about as wide as long (character 27/1); mandibles markedly asymmetrical (character 42/1); ventral mandibular process on both mandibles present (character 44/1); stridulatory teeth on stipes present (character 49/1); hypopharyngeal dorsal armature present, setose or sclerotized (character 60/1/2); urogomphi on tergum IX absent (character 74/0); abdominal segment X not concealed ventrally under segment IX (character 75/0); mesothoracic spiracle located posteriorly on prothorax (character 77/1); spiracles cribriform (character 78/3).

The second analysis clearly supports the monophyly of the superfamily Scarabaeoidea and provides a string of

larval synapomorphies for the group. Although the monophyly of the superfamily was never seriously questioned, our analysis is the second (following Browne and Scholtz 1999) attempt to outline such synapomorphies for the superfamily using a formal cladistic procedure.

Analysis 3. Determining branching pattern within Scarabaeoidea using Agyrtidae + Helophoridae as outgroups

The third analysis resulted in six most parsimonious trees with length 190, *CI* 54 and *RI* 86. The strict consensus tree (Fig. 2) supports the monophyly of the family Passalidae with nine synapomorphic characters, four of them unique. Passalidae synapomorphies are: presence of characteristic membranous ventral collar (unique synapomorphy; character 4/1); presence of a set of markedly long, stout, straight and pigmented setae on head, thorax and abdomen (unique synapomorphy; character 7/1); sides of clypeus markedly divergent posteriorly (unique synapomorphy; character 24/0); antennal apex does not extend beyond level of clypeal apex (character 33/1); ultimate (3rd) and penultimate (2nd) antennomeres completely fused (character 34/1); sensorium flat (character 38/1); hind legs markedly reduced to one-segmented appendages (unique synapomorphy; character 65/2); sound-producing organ on middle and hind legs present (character 68/1); suture between trochanter and femur on fore and middle legs absent, segments completely fused (character 70/2). The monophyly of Passalidae is strongly supported with a bootstrap value of 100 (Fig. 4).

Monophyly of the family Pleocomidae is supported by 11 larval synapomorphic characters, two of which are unique. Pleocomid synapomorphies are: four folds on thoracic and abdominal segments I–V (unique synapomorphy; character 6/3); presence of one round, small, flat sensory ‘window’ in apical half of apical (third) antennomere (character 28/1); sensorium flat (character 38/1); mandibles symmetrical or slightly asymmetrical (character 42/0); galea with characteristic membranous subdivision at basal part (character 47/1); anterior edge of prementum between insertion of the palps markedly protruding forwards (character 56/0); hypopharyngeal armature setose (character 60/1); sound producing organ on middle and hind legs present (character 68/1); claws partly reduced (character 69/2); claw setae longer than claw (character 72/1); apices of middle and hind claws turned markedly forwards (unique synapomorphy; character 73/1). The monophyly of Pleocomidae is strongly supported with a bootstrap value of 99 (Fig. 4).

Monophyly of the family Trogidae is supported by eight synapomorphic characters, four of them unique. Trogidae synapomorphies are: long setae on body spiral-shaped (unique synapomorphy; character 8/1); cranium and prothoracic tergum markedly darker than rest of body, almost black (unique synapomorphy; character 17/1); cranium with 1–5 stemmata (character 22/1); frontal sutures clearly visible

over the complete length (character 25/0); galea with characteristic membranous subdivision at basal part (character 47/1); galea with membranous subdivision in apical part (unique synapomorphy; character 48/1); hypopharyngeal armature setose (character 60/1); basal labial palpomere with characteristic seta-like structures on dorsal surface (unique synapomorphy; character 61/1). The monophyly of Trogidae is strongly supported with a bootstrap value of 93 (Fig. 4).

Monophyly of the subfamily Glaphyrinae (family Glaphyridae) is supported by ten synapomorphic characters, six of them unique. Glaphyrinae synapomorphies are: defined thoracic and abdominal sclerites absent, including those on prothorax (character 9/2); head, body and all appendages covered with numerous setae and thus larvae appear setose (unique synapomorphy; character 10/0); sides of clypeus almost parallel, clypeus appears rectangular (unique synapomorphy; character 24/2); frontal sutures clearly visible over complete length (character 25/0); apical part of second (penultimate) antennomere with numerous pores (unique synapomorphy; character 35/1); sensorium flat (character 38/1); basal labial palpomere characteristically curved inwards and, therefore, apical palpomere directed mesally (unique synapomorphy; character 57/1); hypopharyngeal armature setose (character 60/1); claws with four setae (unique synapomorphy; character 66/2); claws markedly enlarged, ~80–120% of tibiotarsus length (unique synapomorphy; character 69/0). The monophyly of Glaphyrinae is strongly supported with a bootstrap value of 96 (Fig. 4).

Monophyly of the family Lucanidae is supported by nine synapomorphic characters, three of them unique. Lucanidae synapomorphies are: larval body viewed laterally with thorax straight and abdomen C-shaped (unique synapomorphy; character 2/1); thoracic and abdominal segments I–V dorsally and laterally subdivided into 2–4 poorly developed folds (character 5/2); cranium asymmetrical, with right side markedly larger (unique synapomorphy; character 20/1); three-segmented antenna with basal antennomere subdivided by membranous band (character 30/1); sensorium flat (character 38/1); stridulatory teeth on stipes absent (character 49/0); palpifer and basal maxillar palpomere dorsally with round membranous spots (unique synapomorphy; character 50/1); hypopharynx markedly asymmetrical with right dorsally pointed sclerotized projection (character 59/2); middle- and hind-legs with sound-producing organ (character 68/1). The monophyly of Lucanidae is strongly supported with a bootstrap value of 95 (Fig. 4).

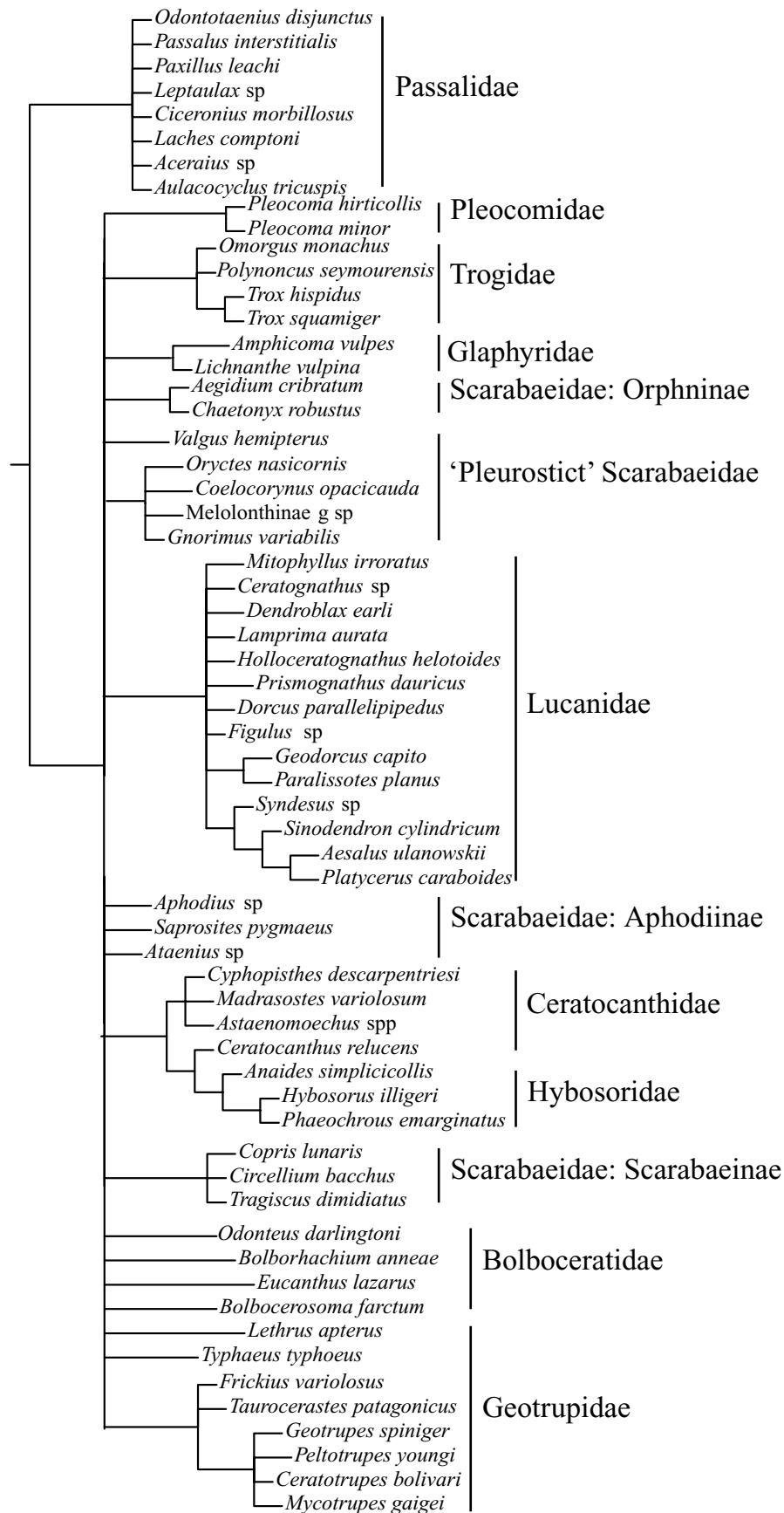
The third analysis indicates that the family Ceratocanthidae is a paraphyletic group with respect to Hybosoridae and that the apparent monophyly of the latter family is supported

by a single homoplasious character: mandibles with dorsal perpendicular keel (45/1). The bootstrap support for Hybosoridae is less than 50 (Fig. 4). Both of these families form a monophyletic unit supported by five synapomorphies, two of them unique: defined thoracic and abdominal sclerites absent, including those on prothorax (character 9/2); three-segmented antenna with basal antennomere subdivided by membranous band (character 30/1); apical antennomere with large sensory spot covering more than one-third of surface (character 31/1); molar base with 3–5 characteristic cuticular strips mesally (unique synapomorphy; character 46/1); suture between trochanter and femur on fore and middle legs present and incomplete, segments partly fused (unique synapomorphy; character 70/1). Bootstrap support for the clade of Ceratocanthidae and Hybosoridae is 74 (Fig. 4).

Ceratocanthidae + Hybosoridae is the only strongly supported clade above the family level (Fig. 4), whereas the former family appears as a paraphyletic unit with respect to the latter. This result, which indicates close relationships between the two families, supports the opinions expressed by Browne and Scholtz (1995, 1999), Nikolajev (1999), Howden and Gill (2000) and Grebennikov *et al.* (2004). In the last-named study, also based on larval morphology, it was demonstrated that Hybosoridae is paraphyletic with respect to Ceratocanthidae, which supported the opinion expressed by Nikolajev (1999).

Our third analysis supports neither the monophyly of the family Geotrupidae, nor that of the family Bolboceratidae (Fig. 2). In addition, the monophyly of the family Scarabaeidae is not supported. Instead, members of Scarabaeidae appear on the cladogram in six (Fig. 2) or in five (Fig. 4) different places. In the strict consensus of the most parsimonious trees (Fig. 2) the pleurostict Scarabaeidae form a monophyletic unit (without Valgini) supported by seven synapomorphies, one of them unique: frontal sutures clearly visible over the complete length (character 25/0); three-segmented antenna with basal antennomere subdivided by membranous band and its basal part widened apically (character 30/2); apical antennomere with 2–10 large sensory spots (32/1); sensorium flat (character 38/1); mandibles with ventral stridulatory area (unique synapomorphy, character 43/1); galea and lacinia completely fused forming a mala (53/2); hypopharynx markedly asymmetrical with right dorsally pointed sclerotized projection (character 59/2). The bootstrap value (Fig. 4) for pleurostict Scarabaeidae without Valgini is 74 and with Valgini 52. The subfamily Orphninae appears as a monophyletic group that is supported by five homoplasious characters: three-segmented antenna with basal antennomere subdivided by membranous band (char-

Fig. 2. Strict consensus tree of six most parsimonious trees (length 190, *CI* 54, *RI* 86) obtained as a result of the third analysis (outgroup: Agyrtidae + Helophoridae) and reflecting the hypothesised relationships within Scarabaeoidea based on larval morphology. Nine uninformative characters (13, 18, 19, 26, 36, 40, 52, 62) were deactivated.



acter 30/1); apical antennomere with a large sensory spot covering more than 1/3 of surface (character 31/1); sensorium flat (character 38/1); mandibles symmetrical or slightly asymmetrical (character 42/0); hypopharynx markedly asymmetrical with right dorsally pointed sclerotized projection (character 59/2). The bootstrap value for the Orphniinae clade is 59 (Fig. 4). The subfamily Scarabaeinae is supported by nine characters, one of them unique: body with characteristic dorsal hump (unique synapomorphy, character 1/1); body C-shaped, markedly curved at level of abdominal segments 4–5 (character 2/3); head, body and all appendages without long and medium-long setae, body appears glabrous (character 10/2); three-segmented antenna with basal antennomere subdivided by membranous band (character 30/1); claw markedly reduced or absent (character 69/3); suture between trochanter and femur on forelegs and middle legs absent, segments fused (character 70/2); suture between tibiotarsus and femur on forelegs and middle legs poorly developed or absent (character 71/1); claw setae longer than claws (character 72/1); last (X) abdominal segment obliquely flattened (character 76/1). The bootstrap value for Scarabaeinae clade is 98 (Fig. 4).

Three Aphodiinae taxa belonging to the tribes Aphodiini and Eupariini were studied. Their monophyly is not supported (Fig. 2).

Monophyly of the superfamily Scarabaeoidea without the family Passalidae is supported by six synapomorphic characters, all of them are unique. They are: body C-shaped (character 2/2); cranium hypognathous (character 14/2); antennal fossa not, or poorly, separated from mandibular fossa (character 15/0); mandibles markedly asymmetrical (character 42/1); mandibles with ventral process (character 44/1); anterior edge of prementum between insertion of the palps more or less straight (character 56/1). The bootstrap value for this branch is 67 (Fig. 4).

The most notable result of the third analysis is the fact that some of the families and subfamilies are clearly supported as monophyletic units (Figs 2, 4), whereas the relationships between other families (except two clades: Scarabaeoidea without Passalida and Hybosoridae + Ceratocanthidae) are not supported. This result is similar to the situation with the classification of Scarabaeoidea based on adult characters, where most of the present day family-level groups were recognised long ago, but their relationships are still uncertain.

Analysis 4. Determining branching pattern within Scarabaeoidea using Eulichadidae + Dascillidae as outgroups

Our fourth analysis aimed at finding differences in Scarabaeoidea internal topology using Eulichadidae + Dascillidae v. Agyrtidae + Hydrophilidae as an outgroup. This resulted in five most parsimonious trees with length 197, *CI* 52, *RI* 86. The strict consensus tree (Fig. 3) shows the branching

topology of Scarabaeoidea families and subfamilies. It differs from the tree obtained in the third analysis (Fig. 2), which used Agyrtidae + Helophoridae as the outgroup, in that its basal part is more resolved with Passalidae, then Pleocomidae, then Trogidae and then Glaphyrinae branching consecutively off from the rest of Scarabaeoidea.

Monophyly of the superfamily Scarabaeoidea without the family Passalidae is supported by three synapomorphic characters (Fig. 3), all of them unique: body C-shaped (character 2/2); cranium hypognathous (character 14/2); and mandibles with ventral process (character 44/1). Monophyly of the superfamily Scarabaeoidea without the families Passalidae and Pleocomidae is supported by two synapomorphic characters (Fig. 3), both of them unique: mandibles markedly asymmetrical (character 42/1); and anterior edge of prementum between insertion of the palps more or less straight (character 56/1). Monophyly of the superfamily Scarabaeoidea without the families Passalidae, Pleocomidae and Trogidae is supported by two synapomorphic characters (Fig. 3), both of them unique: three-segmented antenna with basal antennomere subdivided by membranous band and, therefore, antennae appear four-segmented (character 30/1); and presence of the markedly developed sclerotized ridge and apodeme connecting base of fore coxa and cranium (character 63/1). Monophyly of the superfamily Scarabaeoidea without the families Passalidae, Pleocomidae, Trogidae and Glaphyridae is supported by two synapomorphic characters (Fig. 3): hypopharynx markedly asymmetrical with right dorsally pointed sclerotized projection (unique synapomorphy; character 59/2); and hypopharynx with sclerotized armature (character 60/2). None of these branches withstands 50% bootstrapping (Fig. 4) and therefore they are not significantly supported.

A second difference of the fourth analysis is that Geotrupidae and Bolboceratidae form a weakly supported clade based on four reversal characters (Fig. 3), which corresponds to the results obtained by Verdú *et al.* (2004). This branch also collapses under 50% bootstrapping.

Position of Passalidae

The phylogenetic position of Passalidae within Scarabaeoidea is one of the main mysteries. For a long time their relatively straight larvae with body segments not subdivided into fleshy lobes were considered as plesiomorphic states and, therefore, the group was believed to be basal within the superfamily. In our study we adopted the view that the absence of fleshy lobes on the body segments in Passalidae (also in Lucanidae) is a superficial impression, whereas in fact, remnants of these lobes are present on the body segments and they are the result of secondary reduction. Our strict consensus tree (Fig. 2) shows Passalidae being a sister-group to the rest of the superfamily. However, this topology has relatively low bootstrap value 67 in our third analysis and below 50 in the fourth analysis (Fig. 4). Consequently,

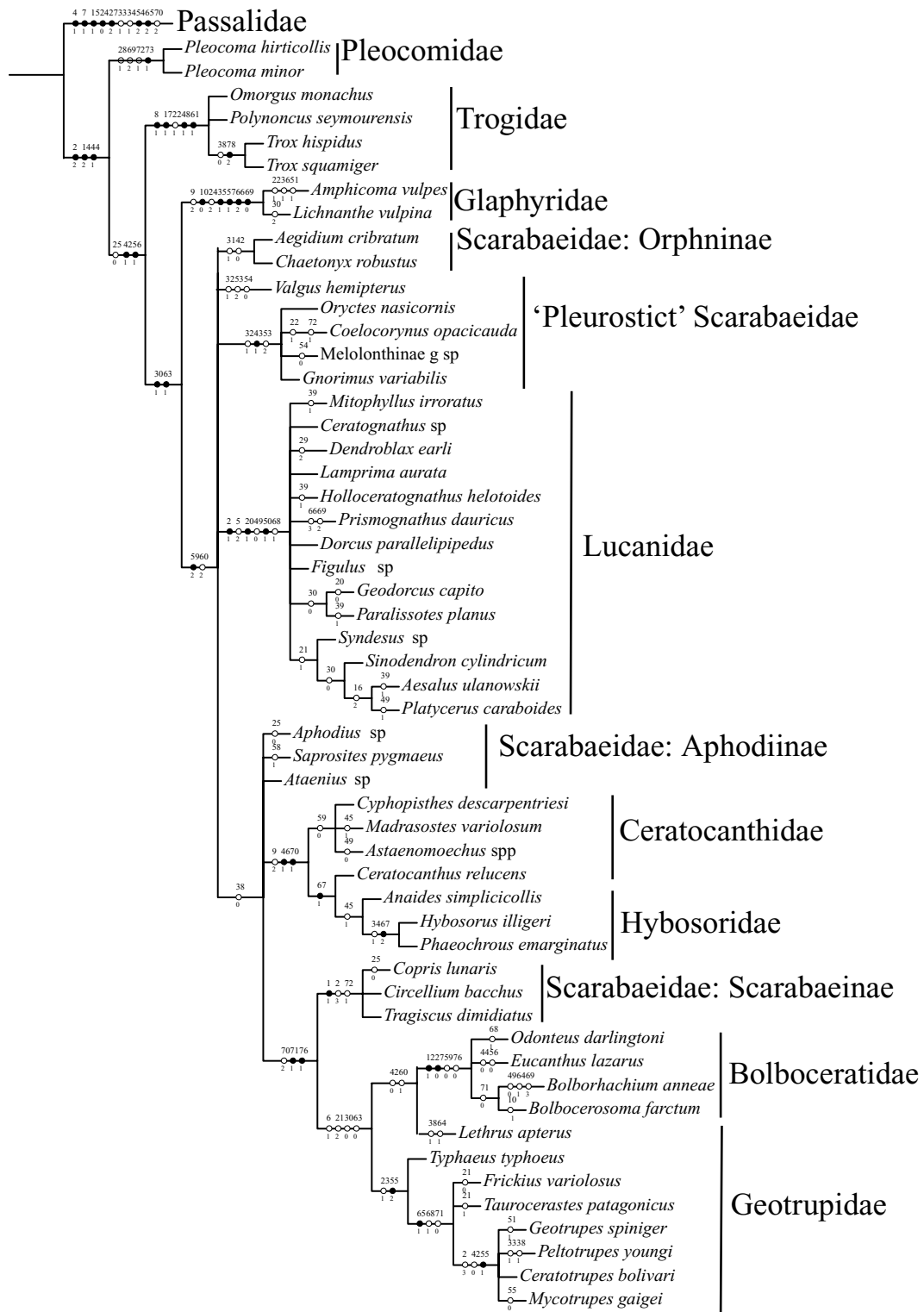


Fig. 3. Strict consensus tree of five most parsimonious trees (length 197, CI 52, RI 86) obtained as a result of the fourth analysis (outgroup: Eulichadidae + Dascillidae) and reflecting the hypothesised relationships within Scarabaeoidea based on larval morphology and character evolution (characters have been mapped on those branches which were topologically identical to one of the most parsimonious trees). Four uninformative characters (11, 52, 62, 77) were deactivated. Only unambiguous characters are indicated. Black circles represent non-homoplasious characters; white circles indicate homoplasies. Numbers above circles represent characters, numbers below represent character states (see Appendix 2).

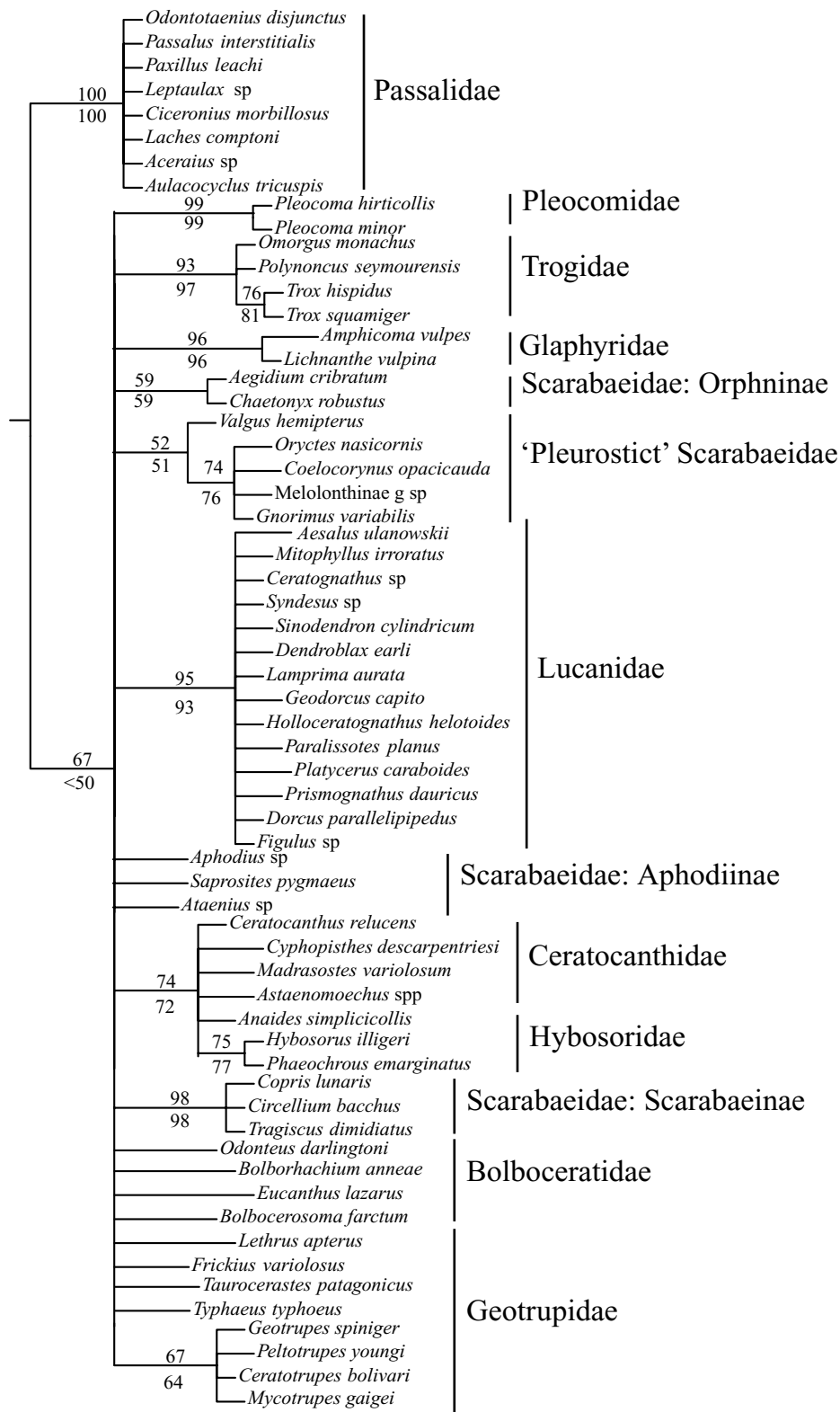


Fig. 4. Bootstrap 50% majority rule tree reflecting the hypothesised relationships within Scarabaeoidea. Bootstrap values for the third analysis (outgroup: Agyrtidae + Helophoridae) are indicated above the respective branches; those for the fourth analysis (outgroup: Eulichadidae + Dascillidae) are indicated below the branches. Branches with bootstrap support less than 50% have been collapsed.

we would consider that the relationships of Passalidae are far from being resolved.

Use of some morphological characters of Scarabaeoidea larvae for phylogenetic analysis

During the course of the present study we encountered difficulties in interpreting the morphology of certain larval structures for phylogenetic purposes. Larval descriptions of Scarabaeoidea would normally pay particular attention to the shape of the epipharynx (e.g. Ritcher 1966). However, when proposing the system for naming epipharyngeal structures, Böving (1936) was referring to the epipharynx on pleurostict scarabaeoids, particularly Melolonthinae and Rutelinae. It is noteworthy that none of these epipharyngeal characters were employed for the matrix we have constructed. The main reason for this is that we were unable to define independent characters on the epipharynx and, moreover, to designate discrete character states when observing modifications of some epipharyngeal structures. The epipharynx works in close conjunction with both mandibles and hypopharynx in the process of food consumption. Therefore, it seems plausible to assume that the shape modifications of these structures are closely associated and have direct adaptation value. We would emphasise that most of the usefulness of epipharyngeal structures should be utilised for the purpose of species discrimination between otherwise similar larvae of related taxa. In such cases a good drawing of the epipharynx helps significantly to find iconographic similarity and, therefore, identify the species. The usefulness of epipharyngeal structures declines markedly when it comes to the necessity to homologise their diversity across the superfamily and, additionally, to interpret independent characters and find their discrete stages. Consequently, we refrained from using them.

Rather similar difficulties arose with the use of the shape of cranium, mandibles, and abdominal apex for phylogenetic purposes. The main difficulty was to identify discrete character states and, moreover, to homologise complex three-dimensional structures across the superfamily. In many cases we were unable to find clear division between the number of apical teeth on mandibles in different taxa, or even to be certain about the homology of such teeth. The shape of the fleshy lobes and of the anus also proved to be impossible to homologise unambiguously across the superfamily. Moreover, another difficulty appeared owing to the fact that in many instance no homologous structures could be found in the outgroup and, therefore, it was impossible to identify character polarisation within Scarabaeoidea. Consequently, much of the morphological diversity within Scarabaeoidea larvae could not be utilised for the purpose of the present study.

There is another potentially useful set of morphological larval characters in coleopteran larvae that we were unable to employ within Scarabaeoidea. This is the pattern of larval

chaetotaxy, which has proved to be highly informative in several beetle groups such as Carabidae (Bousquet and Goulet 1984; Grebennikov and Maddison 2004), Staphylinidae (Ashe and Watrous 1984; Thayer 2000; Solodovnikov and Newton 2004), Leiodidae (Wheeler 1990; Kilian 1998), Histeridae (Kovarik and Passoa 1993), Hydraenidae (Delgado and Soler 1996, 1997), Dytiscidae (Alarie and Balke 1999), Ptiliidae (Grebennikov and Beutel 2002), Micromalthidae and Cupedidae (Grebennikov 2004a). During the course of this study we were unable to find a system of homologies between sensilla in scarabaeoid larvae throughout the superfamily similar to that proposed for the families mentioned above. Instead of the symmetrical set of a few and permanently located setae and pores (character 11/0), Scarabaeoidea larvae have thoracic and abdominal segments with fields of normally short and numerous setae without permanent position (character 11/1). In some scarabaeoid families a few recognisable and symmetrical setae were identified on the cephalic capsule (Trogidae, Scholtz and Peck 1990; Ceratocanthidae, Grebennikov *et al.* 2002), but to find homologies among these within the superfamily was not possible. The presence of sensilla that were relatively easy to fit in a system of homologies among larvae of the basal groups of Coleoptera (see above), as well as in some Neuroptera (Hoffman and Brushwein 1992; Grebennikov 2004b) makes it reasonable to assume that the high degree of chaetotaxy modification in larval Scarabaeoidea is in itself an advanced state.

Concluding remarks

We would suggest that the results of our analysis depicted in Figs 2 and 3 should be considered as preliminary, particularly in regard to the suprafamily assemblages. Although the monophyly of most of the families analysed, except Scarabaeidae, Geotrupidae and Bolboceratidae, appears well supported, we should be hesitant to propose any interfamily relationships, with the exception that all analysed taxa of Ceratocanthidae and Hybosoridae form a clade. This last result supports the analysis done by Grebennikov *et al.* (2004). However, in the study by Grebennikov *et al.* (2004), the family Hybosoridae was found to be paraphyletic with respect to Ceratocanthidae, whereas in the present work Ceratocanthidae appear paraphyletic with respect to Hybosoridae. Even the seemingly well supported basal position of Passalidae within the superfamily (Figs 2, 3) does not appear so after bootstrapping the tree that resulted from the fourth analysis (Fig. 4, bootstrap values indicated under respective clades). Moreover, larvae of some key families and subfamilies of Scarabaeoidea remain unknown, most notably those of Glaresidae, Penichrolucaninae (Lucanidae), Diphylostomatidae, Athyreinae (Bolboceratidae), Lichninae (Glaphyridae) and Dynamopodinae (Scarabaeidae or Hybosoridae). At this stage it would be highly desirable to undertake a total

evidence analysis of basal lineages of Scarabaeoidea, including all available data on biology, larval and adult morphology as well as DNA sequences. We would hope that our present work contributes towards this ultimate goal.

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Appendix 1. Larvae of Scarabaeoidea: material studied

Family/Subfamily	Genus and species	L1	L2	L3	Country	Source
Carabidae	<i>Pterostichus adstrictus</i> Eschscholtz, 1823			3	USA	UPC
Cupedidae	<i>Distocupes varians</i> (Lea, 1902)	2		3	Australia	ANIC
Eulichadidae	<i>Eulichas dudgeoni</i> Jäch, 1995			1	China	Costa & Vanin 1998
Dascillidae	<i>Dascillus cervinus</i> (Linnaeus, 1758)			2	Denmark	NHML
Dascillidae	<i>Notodascillus</i> sp.			1	Australia	ANIC
Dascillidae	<i>Pleolobus</i> sp.			1	Chile	ANIC
Agyrtidae	<i>Necrophilus hydrophiloides</i> Guérin-Ménéville, 1835	1	2	3	USA	FMNH
Hydrophilidae	<i>Helophorus</i> sp.	2			Russia	UPC
Lucanidae/Aesalinae	<i>Aesalus ulanowskii</i> Ganglbauer, 1887			4	Russia	UPC
Lucanidae/Nicaginae	<i>Mitophyllus irroratus</i> Parry, 1842			1	New Zealand	NZAC
Lucanidae/Nicaginae	<i>Mitophyllus parrianus</i> Westwood, 1863			1	New Zealand	NZAC
Lucanidae/Nicaginae	<i>Ceratognathus</i> sp.			4	Australia	ANIC
Lucanidae/Syndesinae	<i>Syndesus</i> sp.			2	Australia	ANIC
Lucanidae/Syndesinae	<i>Sinodendron cylindricum</i> (Linnaeus, 1758)			2	Russia	ZISP
Lucanidae/Lampriminae	<i>Dendroblox earli</i> White, 1846			1	New Zealand	NZAC
Lucanidae/Lampriminae	<i>Lamprima aurata</i> Latreille, 1817			2	Australia	ANIC
Lucanidae/Lucaninae	<i>Geodorcus capito</i> (Deyrolle, 1873)			1	New Zealand	NZAC
Lucanidae/Lucaninae	<i>Geodorcus philpotti</i> (Broun, 1914)			1	New Zealand	NZAC
Lucanidae/Lucaninae	<i>Holloceratognathus helotoides</i> (Thomson, 1862)			1	New Zealand	NZAC
Lucanidae/Lucaninae	<i>Paralissotes planus</i> (Broun, 1880)			1	New Zealand	NZAC
Lucanidae/Lucaninae	<i>Paralissotes reticulatus</i> (Westwood, 1844)			1	New Zealand	NZAC
Lucanidae/Lucaninae	<i>Platycerus caraboides</i> (Linnaeus, 1758)			2	Belarus	ZISP
Lucanidae/Lucaninae	<i>Prismognathus dauricus</i> Motschulsky, 1860			1	Russia	ZISP
Lucanidae/Lucaninae	<i>Dorcus parallelipipedus</i> (Linnaeus, 1758)			10	Russia	UPC
Lucanidae/Lucaninae	<i>Figulus</i> sp.			2	Australia	CMNC
Passalidae/Passalinae	<i>Odontotaenius disjunctus</i> (Illiger, 1801)		1	4	USA	TM
Passalidae/Passalinae	<i>Odontotaenius striatopunctatus</i> (Percheron, 1853)			2	Mexico	MNHN
Passalidae/Passalinae	<i>Passalus interstitialis</i> Eschscholtz, 1829			3	French Guyana	MNHN
Passalidae/Passalinae	<i>Paxillus leachi</i> (MacLeay, 1819)	1		2	Mexico	MNHN
Passalidae/Passalinae	<i>Leptaulax</i> sp.		1	1	Malaysia	MNHN
Passalidae/Passalinae	<i>Ciceronius morbillosus</i> Klug, 1832			3	Madagascar	MNHN
Passalidae/Passalinae	<i>Laches comptoni</i> (Kaup, 1868)		1	2	Sri Lanka	MNHN
Passalidae/Passalinae	<i>Aceraius</i> sp.	1			Malaysia	MNHN
Passalidae/Aulacocyclinae	<i>Aulacocyclus tricuspis</i> Kaup, 1868			3	New Caledonia	MNHN
Trogidae	<i>Omorgus monachus</i> (Herbst, 1790)			1	USA	NMNH
Trogidae	<i>Trox squamiger</i> Roth, 1885			1	South Africa	UPC
Trogidae	<i>Trox hispidus</i> Pontoppidan, 1763			2	France	UPC
Trogidae	<i>Polynoncus seymourensis</i> (Mutchler, 1925)			1	Ecuador	TM
Pleocomidae	<i>Pleocoma hirticollis</i> Schaufuss, 1870			1	USA	NMNH
Pleocomidae	<i>Pleocoma minor</i> Linsley 1938	2			USA	OSUC
Bolboceratidae/Bolboceratinae	<i>Odonteus darlingtoni</i> (Wallis, 1928)			1	USA	CMNC
Bolboceratidae/Bolboceratinae	<i>Bolborhachium anneae</i> Howden, 1985			2	Australia	ANIC
Bolboceratidae/Bolboceratinae	<i>Eucanthus lazarus</i> (Fabricius, 1775)			1	USA	CMNC
Bolboceratidae/Bolboceratinae	<i>Bolbocerosoma farctum</i> (Fabricius, 1775)				USA	CMNH
Geotrupidae/Geotrupinae	<i>Typhaeus typhoeus</i> (Linnaeus, 1758)		1	1	Germany	ZMHB
Geotrupidae/Geotrupinae	<i>Peltotrupes youngi</i> Howden, 1955			1	U.S.A	CMNC
Geotrupidae/Geotrupinae	<i>Ceratotrupes bolivari</i> Howden & Matrínez, 1962	1			Mexico	CMNC
Geotrupidae/Geotrupinae	<i>Mycotrupes gaigei</i> Olson & Hubbell, 1954			1	USA	CMNC
Geotrupidae/Lethrinae	<i>Lethrus apterus</i> Laxman, 1870	1	2		Russia	CMNC
Geotrupidae/Taurocarastinae	<i>Taurocerastes patagonicus</i> Philippi, 1866			1	Chile	CMNC
Geotrupidae/Taurocarastinae	<i>Frickius variolosus</i> Germain 1897			1	Chile	CMNC
Glaphyridae/Glaphyrinae	<i>Lichnanthe vulpina</i> Hentz, 1826			1	USA	NMNH
Glaphyridae/Glaphyrinae	<i>Amphicoma vulpes</i> Fabricius, 1792			1	Georgia	ZISP
Ceratocanthidae	<i>Ceratocanthus relucens</i> (Bates, 1887)			2	Mexico	ABC, UPC
Ceratocanthidae	<i>Cyphopisthes descarpentriasi</i> Paulian, 1977			3	Australia	ANIC
Ceratocanthidae	<i>Madrasostes variolosum</i> (Harold, 1874)			1	Malaysia	ABC, UPC
Ceratocanthidae	<i>Astaenomoechus</i> spp.			2	Ecuador, Cost Rica	NMNH, ZMHB
Hybosoridae	<i>Hybosorus illigeri</i> Reiche, 1853			2	USA	NMNH

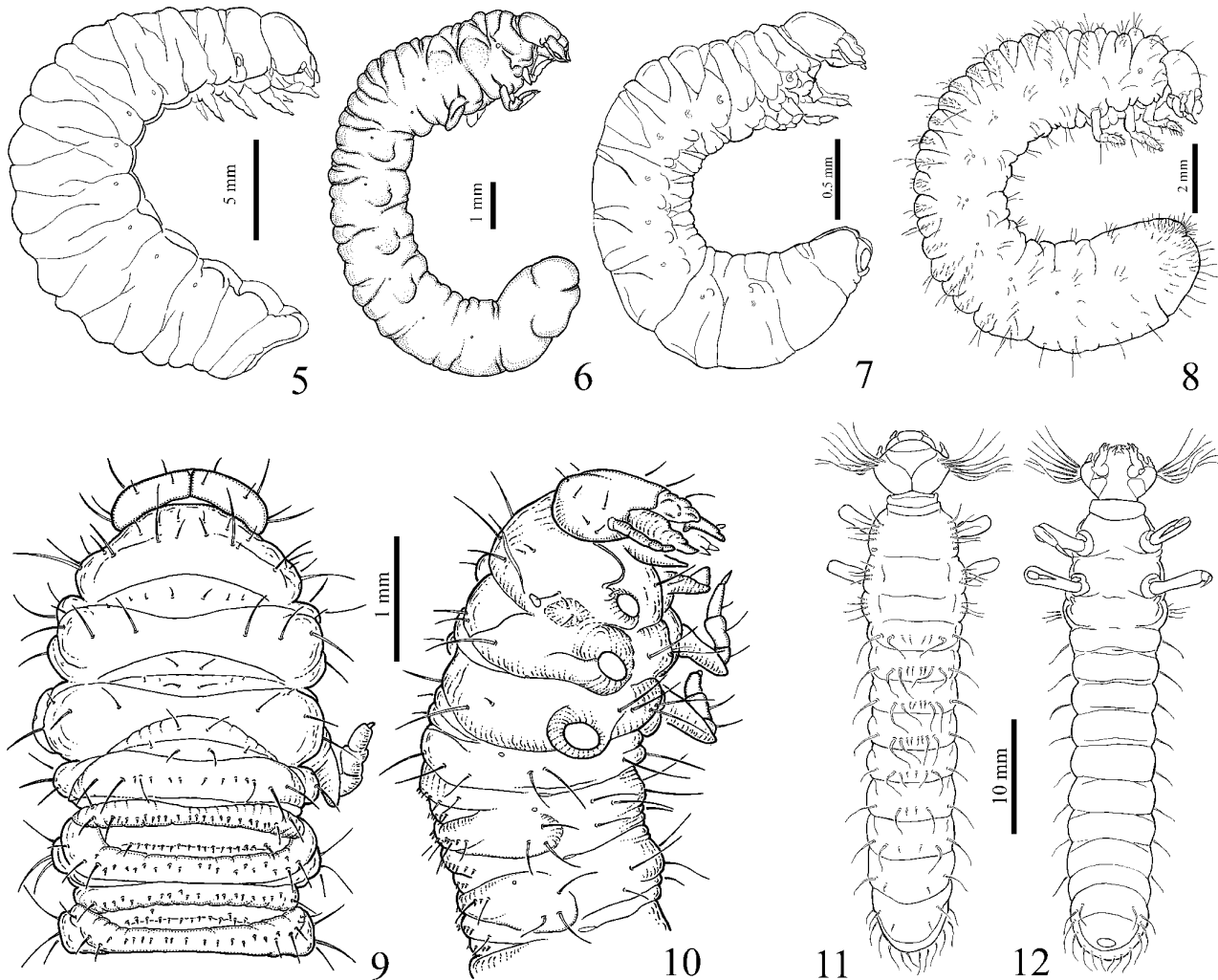
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Appendix 1. (continued)

Family/Subfamily	Genus and species	L1	L2	L3	Country	Source
Hybosoridae	<i>Phaeochrous emarginatus</i> Laporte, 1840			2	India	NMNH
Hybosoridae	<i>Anaides simplicicollis</i> Bates, 1887			2	Mexico	NMNH
Scarabaeidae/Scarabaeinae	<i>Circellium bacchus</i> Fabricius, 1985			2	South Africa	TM
Scarabaeidae/Scarabaeinae	<i>Tragiscus dimidiatus</i> Klug, 1955			2	South Africa	TM
Scarabaeidae/Scarabaeinae	<i>Copris lunaris</i> (Linnaeus, 1758)			1	France	TM
Scarabaeidae/Aphodiinae	<i>Saprosites pygmaeus</i> Harold, 1877			1	USA, Hawaii	NMNH
Scarabaeidae/Aphodiinae	<i>Ataenius</i> sp.			1	USA	NMNH
Scarabaeidae/Aphodiinae	<i>Aphodius</i> sp.			1	USA	NMNH
Scarabaeidae/Orphininae	<i>Chaetonyx robustus liguricus</i> Mariani, 1946		1	1	Italy	UPC
Scarabaeidae/Orphininae	<i>Aegidium cribratum</i> Bates, 1887			1	Mexico	UPC
Scarabaeidae/Melolonthinae	Melolonthinae gen, sp.			5	South Africa	UPC
Scarabaeidae/Dynastinae	<i>Oryctes nasicornis</i> (Linnaeus, 1758)			1	Russia	ZISP
Scarabaeidae/Dynastinae	<i>Coelocorynus opacicauda</i> Arrow, 1926	1			Kenya	UPC
Scarabaeidae/Cetoniinae	<i>Valgus hemipterus</i> (Linnaeus, 1758)			2	Russia	ZISP
Scarabaeidae/Cetoniinae	<i>Gnorimus variabilis</i> (Linnaeus, 1758)			1	Russia	ZISP

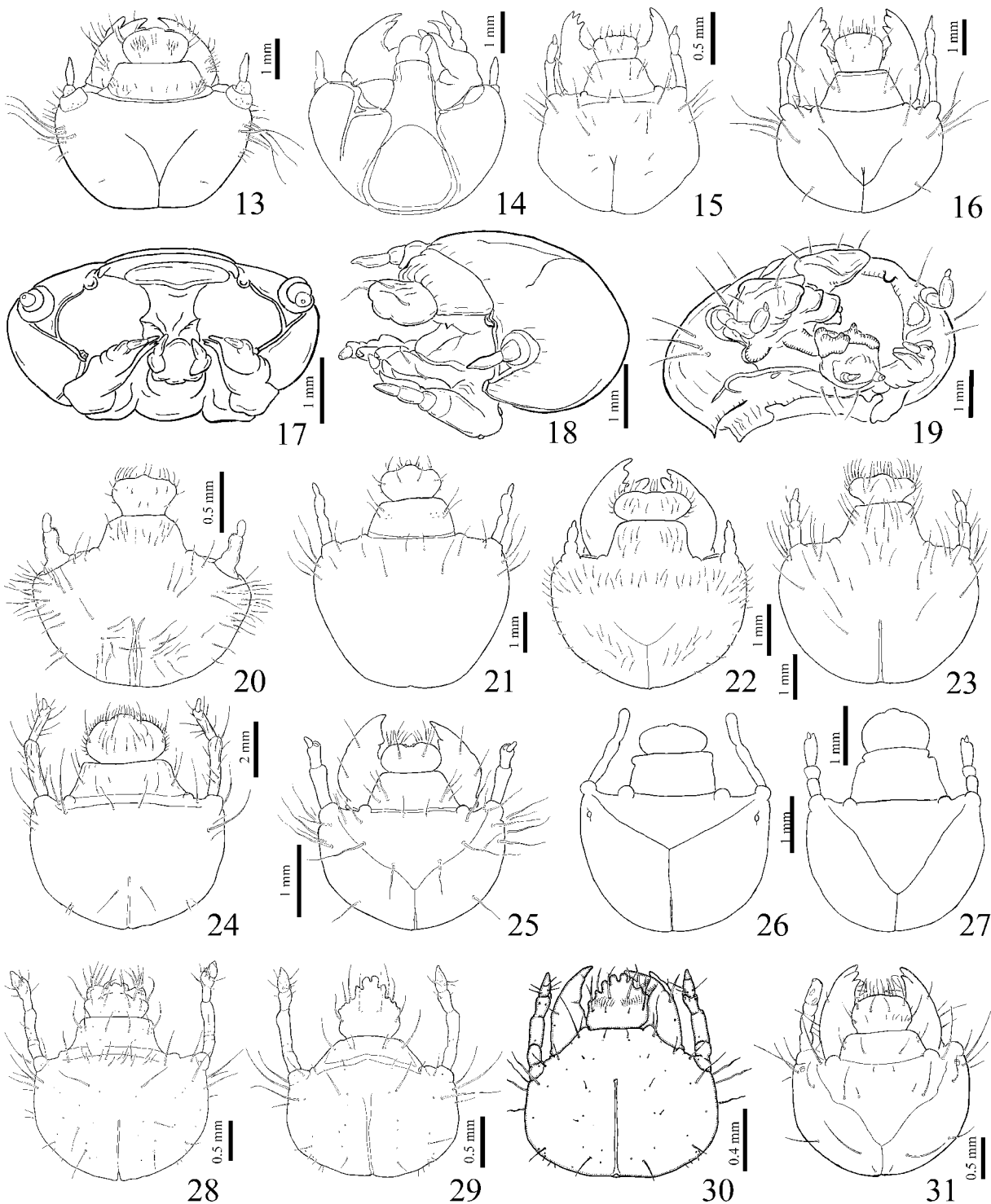
Appendix 2. Characters of Scarabaeoidea (Coleoptera) larvae and their states as coded in the matrix

1. Dorsal hump on abdomen
0: absent
1: present
2. Body shape
0: nearly straight, not or only slightly curved ventrally (Figs 11–12)
1: thorax straight, abdomen C-shaped (Fig. 7)
2: thorax and abdomen together C-shaped (Figs 5, 6, 8)
3: C-shaped, markedly curved at level of 4–5 abdominal segment
3. Dorsal part of body
0: flattened dorso-ventrally
1: not flattened, nearly round in cross-section (Fig. 10)
4. Characteristic ventral membranous collar
0: absent (Figs 5–8)
1: present (Figs 11–12)
5. Thoracic and abdominal segments I–V dorsally and laterally
0: complete, not subdivided into folds
1: clearly subdivided into 2–4 markedly developed folds (Figs 5–12)
2: subdivided into 2–4 poorly developed folds
6. Number of folds on thoracic and abdominal segments I–V
0: no folds; segment complete
1: 2-folds (Fig. 5)
2: 3-folds (Figs 6, 8)
3: 4-folds
7. Set of markedly long, stout, straight and pigmented setae on head, thorax and abdomen
0: absent (Figs 5–10)
1: present (Figs 11–12)
8. Long setae on head, thorax and abdomen
0: straight
1: spiral-shaped (Figs 25, 114)
9. Defined thoracic and abdominal sclerites
0: present
1: absent, except those on prothorax
2: absent, including those on prothorax (Figs 5–11)
10. Head, body and all appendages
0: covered with numerous setae and appearing setose
1: with a few long and medium long setae (Fig. 7)



Figs 5–12. Larvae of Scarabaeoidea. 5, *Lethrus apterus* (Geotrupidae: Lethrinae), habitus, lateral; 6, *Cyphopisthes descarpentriesi* (Ceratocanthidae), habitus, lateral; 7, *Dorcus parallelipedus*, habitus, lateral; 8, *Coelocorynus opacicauda* (Scarabaeidae: Dynastinae), habitus, lateral; 9–10, *Cyphopisthes descarpentriesi* (Ceratocanthidae), anterior part of body, dorsal (9) and latero-ventral (10); 11–12, *Odontotaenius disjunctus* (Passalidae: Passalinae), habitus, dorsal (11) and ventral (12). Figs 6, 9, 10 from Grebennikov *et al.* (2002).

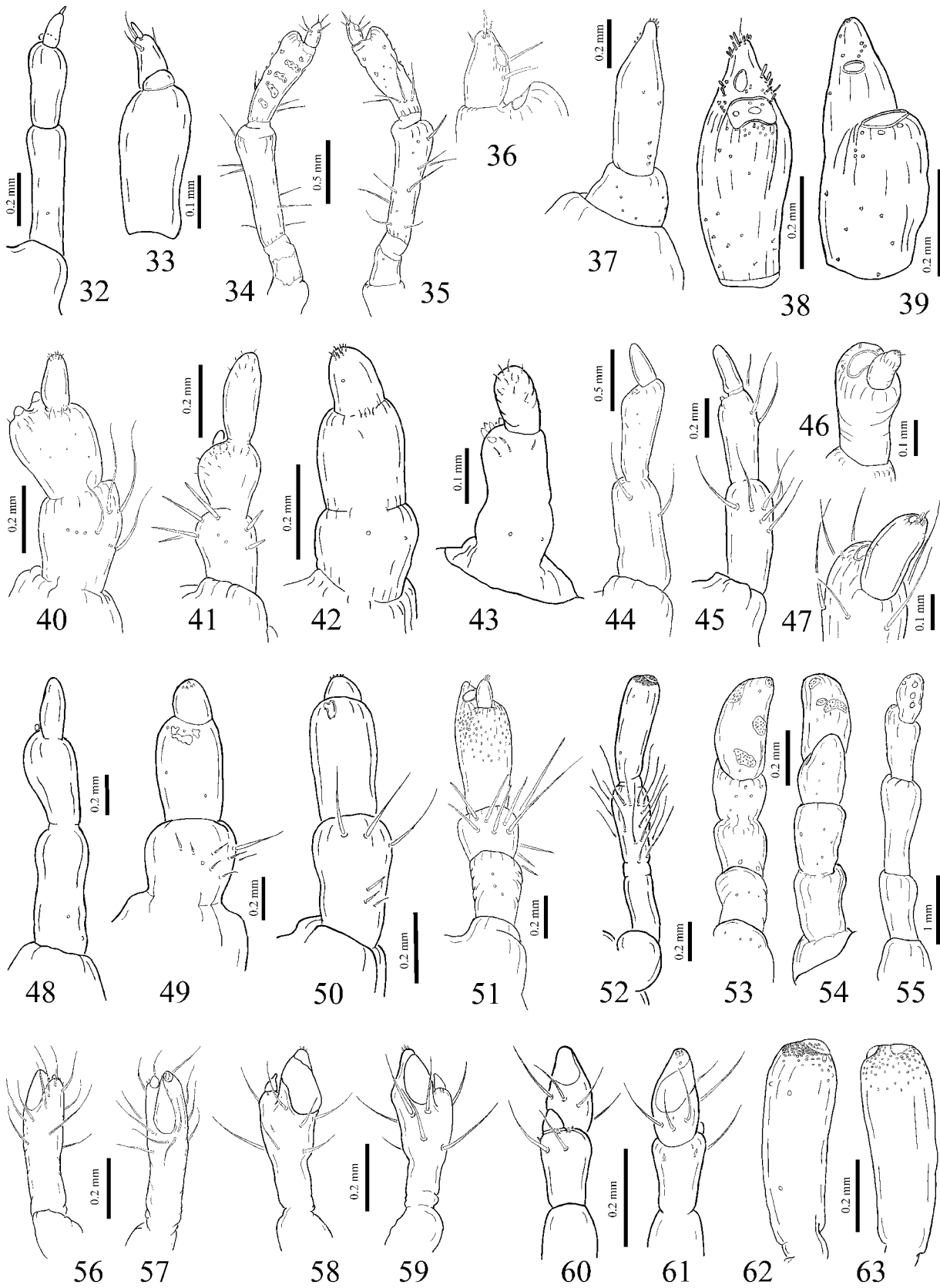
- 2: without long and medium-long setae, body appears glabrous (Fig. 8)
11. Larval chaetotaxy (for detailed definition see section: *Use of some morphological characters of Scarabaeoidea larvae for phylogenetic analysis*)
0: ancestral type
1: highly advanced type
12. Five apical abdominal segments
0: not markedly and progressively narrowing (Figs 5–8, 11–12)
1: markedly and progressively narrowing
13. Labrum
0: distinct, separated from clypeus with suture (Figs 13–31)
1: indistinct, fused with clypeus without suture
14. Cranium
0: prognathous
1: subprognathous (Figs 11–12)
2: hypognathous (Figs 5–10)
15. Antennal fossa
0: not or poorly separated from mandibular fossa (Fig. 19)
1: clearly separated from mandibular fossa by a sclerotized strip (Fig. 17)
16. Cranium posteriorly
0: straight
1: rounded (Figs 13–14, 16, 20–31)
2: round, with two obtuse and poorly developed angles (Fig. 15)
17. Cranium and prothoracic tergum
0: slightly darker than body
1: markedly darker, almost black
18. Coronal suture
0: present
1: absent, frontal sutures reach posterior edge of cranium
19. Markedly developed asymmetrical carina on left side of clypeus
0: absent
1: present
20. Cranium
0: symmetrical (Figs 13, 16, 20–31)
1: asymmetrical, with right side markedly larger (Fig. 15)
21. Frontoclypeal suture between dorsal mandibular articulation
0: present on all length, clearly detectable (Figs 13, 16, 24–29, 31)
1: weakly developed or present not on all length (Fig. 15)
2: absent (Figs 20, 22, 23, 30)
22. Number of stemmata
0: six
1: one to five (Figs 26, 31)
2: nil (Figs 13–24, 27–30)
23. Clypeus (or anterior part of cranium)
0: symmetrical (Figs 13, 25, 29)
1: asymmetrical (Fig. 23)
24. Clypeus (or front), sides
0: markedly divergent posteriorly (Fig. 13)
1: slightly divergent posteriorly (Figs 15, 16, 20–25)
2: almost parallel, clypeus appears rectangular (Figs 26, 27)
25. Frontal sutures
0: clearly visible over the complete length (Figs 25–28, 31)
1: absent or poorly visible, or not complete (Figs 20–24, 28–30)
26. Apical antennomere
0: located apically on penultimate antennomere (Figs 32–36, 40–58)
1: shifted laterally while sensorium located apically
27. Markedly developed sclerotized antennifer
0: absent
1: present, about as wide as long (Figs 15, 16, 21–31)
2: present, about twice as wide as long (Figs 13, 18)
28. One round small flat sensory ‘window’ in apical half of apical (third) antennomere
0: absent
1: present (Figs 36, 47)
29. Size of ultimate (third) antennomere
0: equal or up to 5× less than penultimate (Figs 32–36, 40–50)
1: ~10× less than penultimate
2: more than 20× less than penultimate, hardly visible (Figs 43, 62–63)
30. Three-segmented antenna with
0: basal antennomere not subdivided (Figs 40–42, 44–45, 48–50)
1: basal antennomere subdivided by membranous band (Figs 34, 35, 52)
2: basal antennomere subdivided by membranous band and its basal part widened apically looking like a true antennomere (Figs 51, 53–55)
31. Large sensory spot on apical antennomere covering more than 1/3 of surface
0: absent (Figs 33, 46, 47)
1: present (Figs 56–61)
32. Numerous (2–10) sensory spots on apical antennomere
0: absent
1: present (Figs 53–55)
33. Antennal apex
0: extends beyond the level of clypeal apex (Figs 15, 16, 24–31)
1: does not extend beyond the level of clypeal apex (Figs 13, 20, 22)
34. Ultimate (3rd) and penultimate (2nd) antennomeres
0: not fused (Figs 60–61)
1: completely fused (Figs 38, 39, 56–59)
35. Numerous pores on apical part of second (penultimate) antennomere
0: absent
1: present (Figs 51, 62, 63)
36. Sensorium on penultimate antennomere located
0: not apically
1: apically
37. Number of sensoria
0: none
1: one (Fig. 41)
2: two (Fig. 40)
3: three or more (Fig. 43)
38. Shape of sensorium
0: conical (Figs 32, 33, 40, 41, 57–61)
1: flat (Figs 38, 39, 46, 49–51)
39. Apical antennomere
0: without small apical sclerotized appendage
1: with small apical sclerotized appendage (Fig. 33)
40. Weakly sclerotised and partly transparent spot between articulated process and mola on mandible
0: absent
1: present
41. Articulated process on mandibles mesally
0: absent (Figs 64–81)
1: present
42. Mandibles
0: symmetrical or slightly asymmetrical
1: markedly asymmetrical (Figs 70–71)
43. Ventral stridulatory area on mandibles
0: absent (Fig. 77–79)
1: present (Fig. 81)
44. Ventral mandibular process on both mandibles
0: absent (Figs 66, 69)
1: present (Figs 70–75, 77–79, 81)
45. Dorsal perpendicular keel on both mandibles
0: absent (Figs 64, 67)
1: present (Fig. 80)



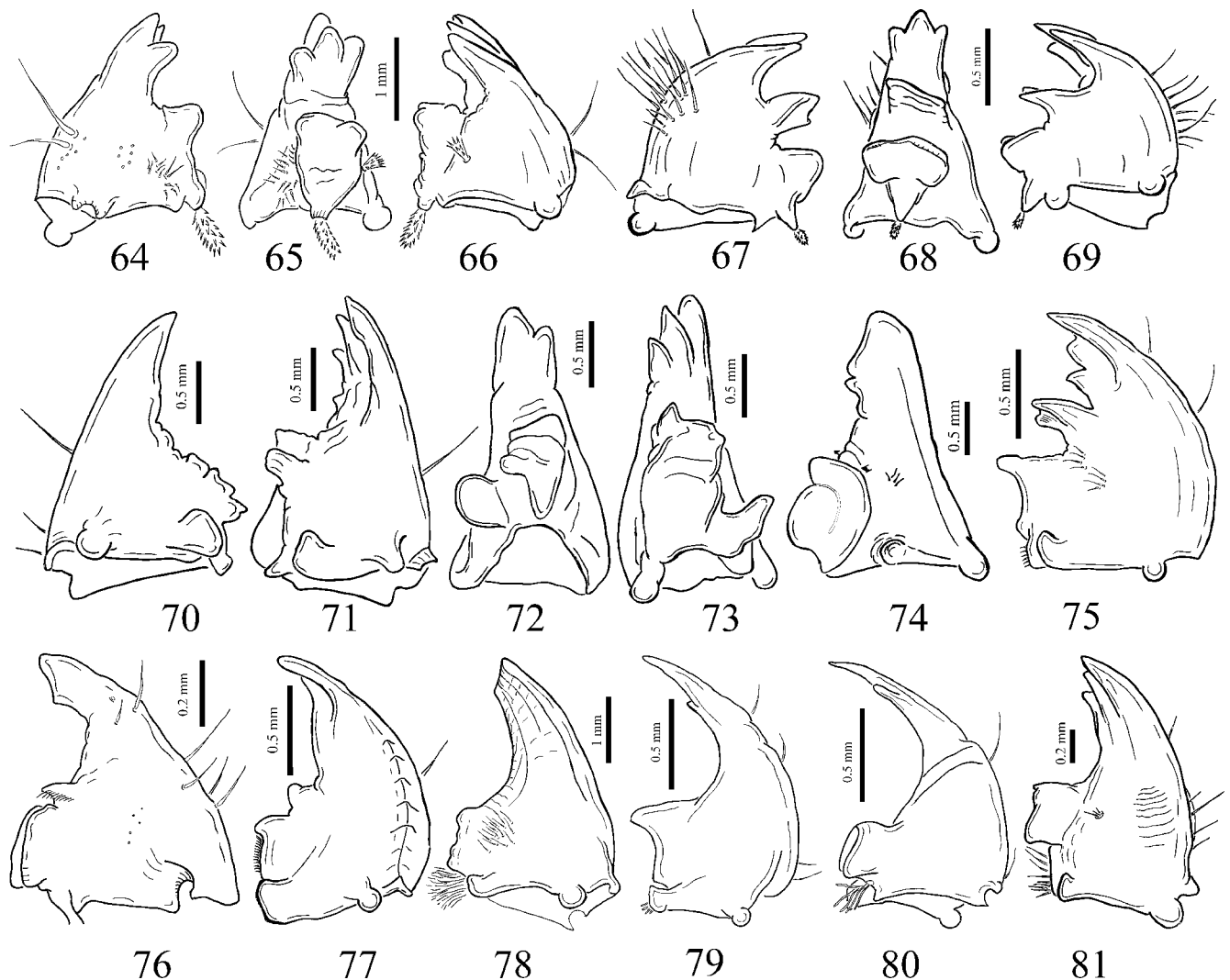
Figs 13–31. Heads of Scarabaeoidea larvae. 13, 15–16, 20–31, dorsal; 14, ventral; 17, 19, frontal view; 18, fronto-latero-dorsal. 17, 18, 19, 26, 27, setae omitted. 13–30, older instar; 31, first instar. 13, 14, 17, 18, *Odontotaenius disjunctus* (Passalidae: Passalinae); 15, *Aesalus ulanowskii* (Lucanidae: Aesalinae); 16, *Geodorcus philpotti* (Lucanidae: Lucaninae); 19, *Prismognathus dauricus* (Lucanidae: Lucanidae), note mandibulo-hypopharyngeal locking device; 20, *Eucanthus lazarus* (Bolboceratidae: Bolboceratinae); 21, *Frickius variolosus* (Geotrupidae: Taurocerastinae); 22, *Lethrus apterus* (Geotrupidae: Lethrinae); 23, *Typhaeus typhoeus* (Geotrupidae: Geotrupinae); 24, *Pleocomma hirticollos* (Pleocomidae); 25, *Omorgus monachus* (Trogidae); 26, *Amphicomma vulpes* (Glaphyridae: Glaphyrinae); 27, *Lichnanthe vulpina* (Glaphyridae: Glaphyrinae); 28, *Hybosorus illigeri* (Hybosoridae); 29, *Madrasostes variolosum* (Ceratocanthidae); 30, *Cyphopisthes descarpentriesi* (Ceratocanthidae); 31, *Coelocorynus opacicauda* (Scarabaeidae: Dynastinae). Fig. 30 from Grebannikov *et al.* (2002).

46. Characteristic 3–5 cuticular strips at molar base mesally
0: absent
1: present (Fig. 80)
47. Characteristic membranous subdivision at basal part of galea
0: absent (Figs 82–84, 86, 89–94)
1: present (Figs 87, 88)
48. Membranous subdivision in apical part of galea
0: absent (Figs 82–84, 86, 88–94)
1: present (Fig. 87)
49. Stridulatory teeth on stipes
0: absent (Fig. 44)
1: present (Figs 82, 84, 86, 88, 89, 92, 94)
50. Dorsal round membranous spots on palpifer and basal maxillar palpomere
0: absent (Figs 82, 88)
1: present (Fig. 83)
51. Lateral angles of the stipes-cardo joint
0: not markedly extended laterally (Fig. 87)
1: markedly extended laterally (Fig. 46)
52. Galea and lacinia
0: movably connected to stipes
1: fixed to stipes (Fig. 94)
53. Galea and lacinia
0: separate (Fig. 87)
1: partly fused
2: completely fused to form mala (Fig. 94)
54. Number of maxillar palpomeres (not counting basal palpifer)
0: three (all three palpomeres present), palpifer reduced or absent
1: three (all three palpomeres present), palpifer present (Fig. 85)
2: two (two basal palpomeres fused), palpifer present (Fig. 82)
55. Antero-ventral longitudinal apodema separating prementum between palps
0: absent (Fig. 87)
1: present, weakly developed
2: present, markedly developed (Fig. 86)
56. Anterior edge of prementum between insertion of the palps
0: markedly protruding forwards (Fig. 87)
1: more or less straight
2: with deep groove
57. Characteristic medial curvature of basal labial palpomere and medially directed apical palpomere
0: absent (Fig. 87)
1: present (Figs 90, 91)
58. Number of labial palpomeres
0: two (Fig. 93)
1: one
59. Hypopharynx
0: symmetrical (Fig. 87)
1: moderately asymmetrical (Fig. 89)
2: markedly asymmetrical with right dorsally pointed sclerotized projection (Figs 82, 94)
60. Hypopharyngeal armature
0: not or poorly developed
1: setose (Figs 82, 84, 88)
2: sclerotized (onculus) (Figs 83, 94)
61. Characteristic seta-like structures on dorsal surface of basal labial palp
0: absent (Fig. 93)
1: present (Fig. 87)
62. Tibia and tarsus
0: separate
1: fused (Fig. 95)
63. Markedly developed sclerotized ridge and apodema connecting base of fore coxa and cranium
0: absent
1: present (Fig. 10)
64. All three pairs of legs
0: normal, not reduced or only third pair reduced (Figs 6–8, 10–12)
1: all legs markedly reduced (Fig. 5)
65. Hind legs compared to fore legs and middle legs
0: not reduced
1: reduced, 3-segmented (Fig. 103)
2: reduced, 1-segmented (Figs 11, 12)
66. Number of claw setae
0: nil
1: two (Fig. 96)
2: four (Figs 115, 117)
3: five to nine (Fig. 97)
67. Sound producing organ on fore and middle legs
0: absent
1: present, mid-femur with micro-teeth (Fig. 119)
2: present, mid-femur with 5–7 large teeth (Fig. 121)
68. Sound producing organ on middle and hind legs
0: absent
1: present
69. Claw size
0: markedly enlarged (80–120% of tibiotarsus length) (Fig. 115)
1: not reduced (Figs 95, 96, 98, 104, 106, 114, 119–121)
2: partly reduced (Fig. 109, 110–112, 119)
3: highly reduced or absent (Figs 99–103, 107–109, 113)
70. Suture between trochanter and femur on forelegs and middle legs
0: present and complete, segments not fused (Figs 96, 114–116)

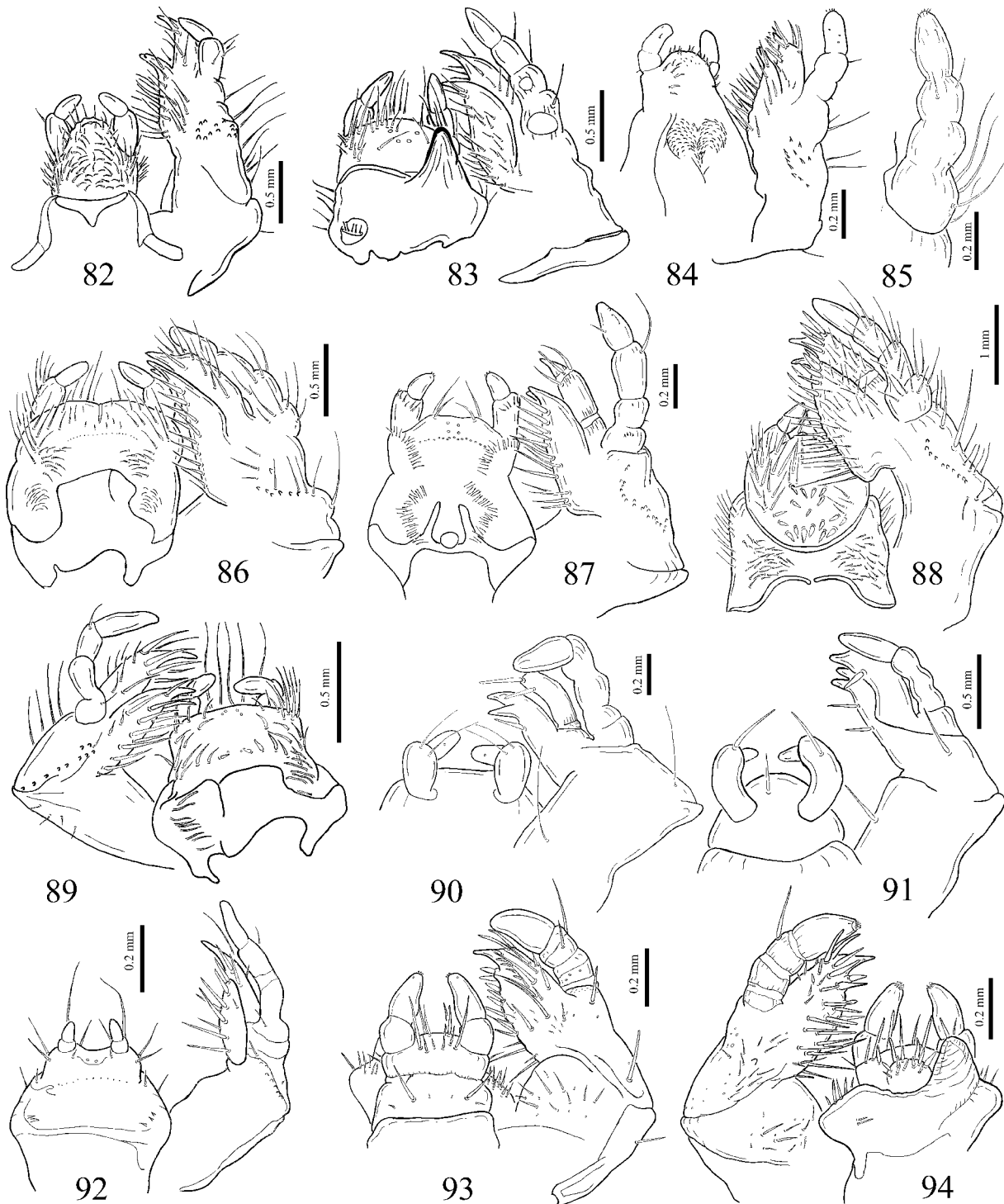
Figs 32–63. Antennae of Scarabaeoidea larvae. 32, 33, *Aesalus ulanowskii* (Lucanidae: Aesalinae), 32, left antenna, dorsal; 33, left antenna, two apical antennomeres, ventral; 34–36, *Dorcus parallelipedus* (Lucanidae: Lucaninae), 34, 35, right antenna, ventral (34) and dorsal (35); 36, apex of right antenna, dorsal; 37, *Odontotaenius disjunctus* (Passalidae: Passalinae), right antenna, dorsal; 38, *Odontotaenius striatopunctatus* (Passalidae: Passalinae), right apical antennomere, ventral; 39, *Aulacocyclus tricuspis* (Passalidae: Aulacocyclinae), right apical antennomere, ventral; 40, *Bolbocerosoma farctum* (Bolboceratidae: Bolboceratinae), right antenna, dorsal; 41, *Odonteus darlingtoni* (Bolboceratidae: Bolboceratinae), right antenna, dorsal; 42, *Bolborhachium annaea* (Bolboceratidae: Bolboceratinae) right antenna, dorsal; 43, *Eucanthus lazarus* (Bolboceratidae: Bolboceratinae), right antenna, dorsal; 44, *Geotrupes spiniger* (Geotrupidae: Geotrupinae), right antenna, dorsal; 45, *Typhaeus typhoeus* (Geotrupidae: Geotrupinae), right antenna, dorsal; 46, *Omorgus monachus* (Trogidae), two right apical antennomeres, dorsal; 47, *Pleocoma hirticollis* (Pleocomidae), apex of right antenna, dorsal; 48, *Frickius variolosus* (Geotrupidae: Taurocerastinae), right antenna, dorsal; 49, *Lethrus apterus* (Geotrupidae: Lethrinae), right antenna, dorsal; 50, *Peltotrupes youngi* (Geotrupidae: Geotrupinae), right antenna, dorsal; 51, *Lichnanthe vulpina* (Glaphyridae: Glaphyrinae), right antenna, dorsal; 52, *Amphicoma vulpes* (Glaphyridae: Glaphyrinae), right antenna, dorsal; 53, 54, *Coelocorynus opacicauda* (Scarabaeidae: Dynastinae), right antenna dorsal (53) and ventral (54); 55, *Oryctes nasicornis* (Scarabaeidae: Dynastinae), right antenna, dorsal; 56, 57, *Phaeochrous emarginatus* (Hybosoridae), two right fused apical antennomeres, ventral (56) and dorsal (57); 58, 59, *Hybosorus illigeri* (Hybosoridae), two left fused apical antennomeres, dorsal (58) and ventral (59); 60, 61, *Anaides* sp. (Hybosoridae), two right apical antennomeres, ventral (60) and dorsal (61); 62, 63, *Amphicoma vulpes* (Glaphyridae: Glaphyrinae), second and third, much reduced, antennomeres; dorsal (62) and ventral (63).



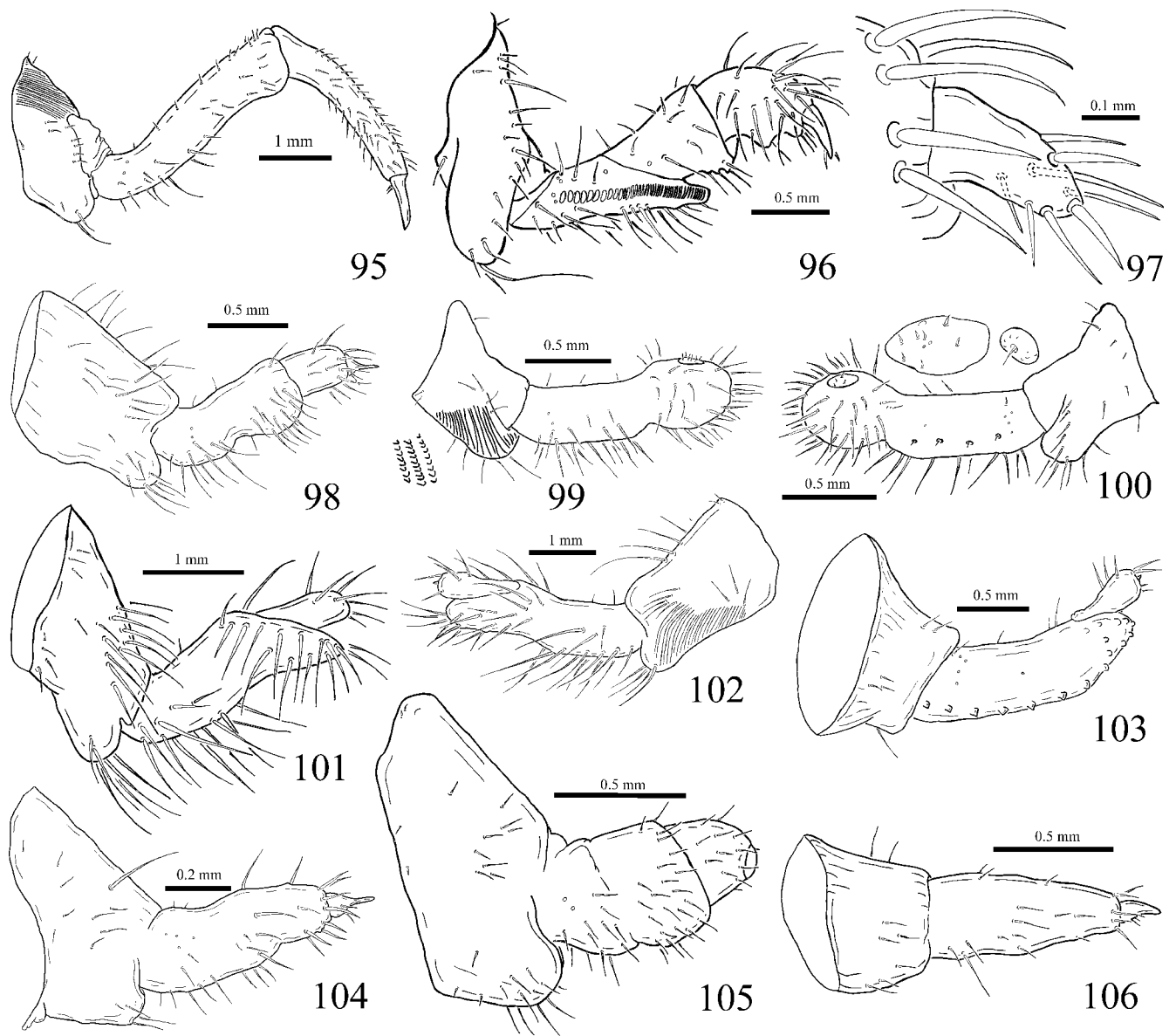
- 1: present but not complete, segments partly fused (Figs 95, 119–121)
 2: absent, segments fused (Figs 98–104, 106, 113)
71. Suture between tibiotarsus and femur on forelegs and middle legs
 0: present, clearly developed (Figs 95, 96, 114–116)
 1: poorly developed or absent (Figs 99, 100, 104, 106)
72. Claw setae
 0: not longer than claw (Fig. 114)
 1: longer than claw (Figs 120, 121)
73. Apices of middle and hind claws
 0: pointed laterad or slightly forwards (Fig. 114)
 1: turned markedly forwards (Figs 111, 112)
74. Urogomphi on tergum IX
 0: absent (Figs 5–8)
 1: present
75. Abdominal segment X
 0: not concealed ventrally under segment IX (Figs 5–8)
 1: at least partly concealed under segment IX
76. Last (X) abdominal segment
 0: not flattened (Figs 6–8)
 1: obliquely flattened (Fig. 5)
77. Mesothoracic spiracle located
 0: anteriorly on mesothorax
 1: posteriorly on prothorax (Fig. 10)
78. Spiracles
 0: annular
 1: annular-biforous
 2: biforous
 3: cribriform



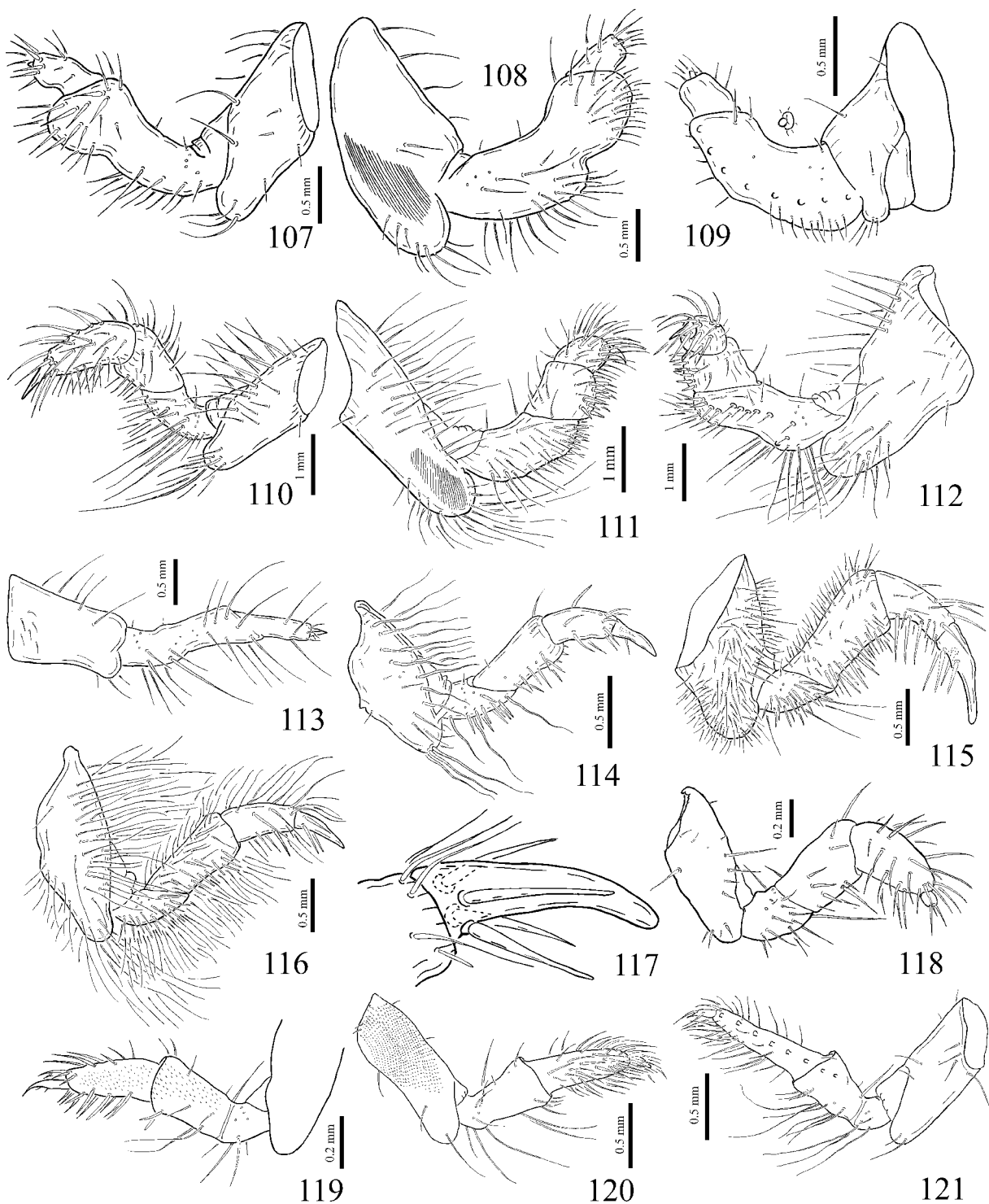
Figs 64–81. Mandibles of Scarabaeoidea larvae. 64–66, *Aceraius* sp. (Passalidae: Passalinae), left mandible, dorsal (64), mesal (65), ventral (66); 67–69, *Aulacocyclus tricuspis* (Passalidae: Aulacocyclinae), left mandible, dorsal (67), mesal (68), ventral (69); 70–73, *Dorcus parallepipipedus* (Lucanidae: Lucaninae), right mandible, ventral (70); left mandible, ventral (71); right mandible, mesal (72); left mandible, mesal (73); 74, *Frickius variolosus* (Geotrupidae: Taurocerastinae), left mandible, ventro-mesal; 75, *Peltotrupes youngi* (Geotrupidae: Geotrupinae), left mandible, ventral; 76, *Eucanthus lazarus* (Bolboceratidae: Bolboceratinae), left mandible, ventral; 77, *Omorgus manachus* (Trogidae), left mandible, ventral; 78, *Pleocoma hirticollis* (Pleocomidae), left mandible, ventral; 79–80, *Phaeochrous emarginatus* (Hybosoridae), left mandible, ventral (79) and right mandible, dorsal (80); 81, *Coelocorynus opacicauda* (Scarabaeidae: Dynastinae), left mandible, ventral.



Figs 82–94. Ventral mouthparts of Scarabaeoidea. 82, *Aulacocyclus tricuspis* (Passalidae: Aulacocyclinae), dorsal; 83, *Dorcus parallelipipedus* (Lucanidae: Lucaninae), dorsal; 84, *Eucanthus lazarus* (Bolboceratidae: Bolboceratinae), dorsal; 85, *Bolbocerosoma farctum* (Bolboceratidae: Bolboceratinae), right maxillar palp, dorsal; 86, *Typhaeus typhoeus* (Geotrupidae: Geotrupinae), dorsal; 87, *Trox squamiger* (Trogidae), dorsal; 88, *Pleocoma hirticollis* (Pleocomidae), dorsal; 89, *Phaeochrous emarginatus* (Hybosoridae), dorsal; 90, *Amphicoma vulpes* (Glaphyridae: Glaphyrinae), ventral, setae omitted; 91, *Lichnanthe vulpina* (Glaphyridae: Glaphyrinae), ventral, setae omitted; 92, *Madrasostes variolosum* (Ceratocanthidae), dorsal; 93, 94, *Coelocorynus opacicauda* (Scarabaeidae: Dynastinae), ventral (93) and dorsal (94).



Figs 95–106. Legs of Scarabaeoidea larvae. 95, *Odontotaenius disjunctus* (Passalidae: Passalinae), middle leg, posterior; 96, *Dorcus parallepipedus* (Lucanidae: Lucaninae), hind leg, anterior; 97, *Prismognathus dauricus* (Lucanidae: Lucaninae), fore claw, anterior; 98, *Bolbocerosoma farctum* (Bolboceratidae: Bolboceratinae), middle leg, anterior; 99, 100, *Odonteus darlingtoni* (Bolboceratidae: Bolboceratinae), middle leg, posterior (99), hind leg, anterior (100); 101–103, *Geotrupes spiniger* (Geotrupidae: Geotrupinae), fore leg, anterior (101), middle leg, posterior (102), hind leg, anterior (103); 104, *Eucanthus lazarus* (Bolboceratidae, Bolboceratinae), middle leg, anterior; 105, *Bolborhachium anneae* (Bolboceratidae: Bolboceratinae), middle leg, anterior; 106, *Lethrus apterus* (Geotrupidae: Lethrinae), middle leg, anterior.



Figs 107–121. Legs of Scarabaeoidea larvae. 107–109, *Frickius variolosus* (Geotrupidae: Taurocerastinae), fore leg, anterior (107), middle leg, posterior (108), hind leg, anterior (109); 110–112, *Pleocoma hirticollis* (Pleocomidae), fore leg, anterior (110), middle leg, posterior (111), hind leg, anterior (112); 113, *Typhaeus typhoeus* (Geotrupidae: Geotrupinae), middle leg, anterior; 114, *Trox squamiger* (Trogidae), middle leg, anterior; 115, *Lichnanthe vulpina* (Glaphyridae: Glaphytinae), middle leg, anterior; 116, 117, *Amphicoma vulpes* (Glaphyridae: Glaphyrinae), middle leg (116) and claw (117), anterior; 118, *Coelocorynus opacicauda* (Scarabaeidae: Dynastinae), fore leg, anterior; 119, *Anaides* sp. (Hybosoridae), middle leg, anterior; 120, 121, *Phaeochrous emarginatus* (Hybosoridae), fore leg, posterior (120), middle leg, anterior (121).

Appendix 3. Character matrix

Taxa	Character						
	10	20	30	40	50	60	70
<i>Distocupes varians</i>	0	0	0	0	0	0	0
<i>Pterostichus adstrictus</i>	0	0	0	0	0	0	0
<i>Necrophius hydrophiloides</i>	0	0	0	0	0	0	0
<i>Helophorus</i> sp.	0	0	0	0	0	0	0
<i>Eulichas dudgeoni</i>	0	0	0	0	0	0	0
<i>Dascillus cervinus</i>	0	0	0	0	0	0	0
<i>Notodascillus</i> sp.	0	0	0	0	0	0	0
<i>Pleolobus</i> sp.	0	0	0	0	0	0	0
<i>Aesalus ulanowskii</i>	0	1	1	0	0	0	0
<i>Mitophyllus irroratus</i>	0	1	1	0	0	0	0
<i>Ceratognathus</i> sp.	0	1	1	0	0	0	0
<i>Syndesus</i> sp.	0	1	1	0	0	0	0
<i>Sinodendron cylindricum</i>	0	1	1	0	0	0	0
<i>Dendroblax earli</i>	0	1	1	0	0	0	0
<i>Lamprima aurata</i>	0	1	1	0	0	0	0
<i>Geodorcus capito</i>	0	1	1	0	0	0	0
<i>Holloceratognathus helotoides</i>	0	1	1	0	0	0	0
<i>Paralissotes planus</i>	0	1	1	0	0	0	0
<i>Platycerus caraboides</i>	0	1	1	0	0	0	0
<i>Prismognathus dauricus</i>	0	1	1	0	0	0	0
<i>Dorcus parallelipipedus</i>	0	1	1	0	0	0	0
<i>Figulus</i> sp.	0	1	1	0	0	0	0
<i>Odontotaenius disjunctus</i>	0	1	1	0	0	0	0
<i>Passalus interstitialis</i>	0	1	1	0	0	0	0
<i>Paxillus leachi</i>	0	1	1	0	0	0	0
<i>Leptaulax</i> sp.	0	1	1	0	0	0	0
<i>Ciceronius morbillosus</i>	0	1	1	0	0	0	0
<i>Laches comptoni</i>	0	1	1	0	0	0	0
<i>Aceraius</i> sp.	0	1	1	0	0	0	0
<i>Aulacocycylus tricuspis</i>	0	1	1	0	0	0	0
<i>Trox hispidus</i>	0	2	1	0	0	0	0
<i>Trox squamiger</i>	0	2	1	0	0	0	0
<i>Omorgus monachus</i>	0	2	1	0	0	0	0
<i>Polynoncus seymourensis</i>	0	2	1	0	0	0	0
<i>Pleocoma hirticollis</i>	0	2	1	0	0	0	0
<i>Pleocoma minor</i>	0	2	1	0	0	0	0
<i>Odonteus darlingtoni</i>	0	2	1	0	0	0	0
<i>Bolborhachium anneae</i>	0	2	1	0	0	0	0
<i>Eucanthus lazarus</i>	0	2	1	0	0	0	0
<i>Bolbocerosoma farctum</i>	0	2	1	0	0	0	0
<i>Geotrupes spiniger</i>	0	3	1	0	0	0	0
<i>Peltotrupes youngi</i>	0	3	1	0	0	0	0
<i>Ceratotrupes bolivari</i>	0	3	1	0	0	0	0
<i>Mycotrupes gaigei</i>	0	3	1	0	0	0	0
<i>Lethrus apterus</i>	0	2	1	0	0	0	0
<i>Frickius variolosus</i>	0	2	1	0	0	0	0
<i>Taurocerastes patagonicus</i>	0	2	1	0	0	0	0
<i>Typhaeus typhoeus</i>	0	2	1	0	0	0	0
<i>Ceratocanthus relucens</i>	0	2	1	0	0	0	0
<i>Cyphopisthes descarpentriensi</i>	0	2	1	0	0	0	0
<i>Madrasostes variolosum</i>	0	2	1	0	0	0	0
<i>Astaenomoechus</i> spp.	0	2	1	0	0	0	0
<i>Hybosorus illigeri</i>	0	2	1	0	0	0	0
<i>Phaeochrous emarginatus</i>	0	2	1	0	0	0	0
<i>Anaides simplicicollis</i>	0	2	1	0	0	0	0
<i>Amphicomma vulpes</i>	0	2	1	0	0	0	0

(continued next page)

Appendix 3. (continued)

Taxa	Character						
	10	20	30	40	50	60	70
<i>Lichnanthe vulpine</i>	021012002010020100000202001012000010110001010000100101011001011002000000000013						
<i>Aphodius</i> sp.	021012001110020100000201001001100000100001010000100101010012011001001000000013						
<i>Saprosites pygmaeus</i>	021012001110020100000201101001100000100001010000100101010112011001001000000013						
<i>Ataenius</i> sp.	021012001110020100000201101001100000100001010000100101010012011001001000000013						
<i>Copris lunaris</i>	131012001210020100000201001001000000100001010000100101010012011001003211000113						
<i>Circellium bacchus</i>	131012001210020100000201101001000000100001010000100101010012011001003211000113						
<i>Tragiscus dimidiatus</i>	131012001210020100000201101001000000100001010000100101010012011001003211000113						
<i>Aegidium cribratum</i>	021012001110020100000201101001100000110000010000100101010022011001001000000013						
<i>Chaetonyx robustus</i>	021012001110020100000201101001100000110000010000100101010022011001001000000013						
<i>Oryctes nasicornis</i>	021012001110020100000201001002010000110001110000101121010022011001002000000013						
<i>Coelocorynus opacicauda</i>	021012001110020100000101001002010000110001110000100121010022011001002001000013						
<i>Melolonthinae</i> sp.	021012001110020100000201001002010000110001110000101120010022011001001000000013						
<i>Valgus hemipterus</i>	021012001110020100000201101001010000110001010000100120010012011001001000000013						
<i>Gnorimus variabilis</i>	021012001110020100000201001002010000110001110000100121010022011001001000000013						