



The systematic position of Meruidae (Coleoptera, Adephaga) and the phylogeny of the smaller aquatic adephagan beetle families

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Abstract

A phylogenetic analysis of Adephaga is presented. It is based on 148 morphological characters of adults and larvae and focussed on a placement of the recently described Meruidae, and the genus-level phylogeny of the smaller aquatic families Gyrinidae, Haliplidae and Noteridae. We found a sister group relationship between Gyrinidae and the remaining adephagan families, as was found in previous studies using morphology. Haliplidae are either the sister group of Dytiscoidea or the sister group of a clade comprising Geadephaga and the dytiscoid families. Trachypachidae was placed as the sister group of the rhyssodid-carabid clade or of Dytiscoidea. The monophyly of Dytiscoidea including *Meru* is well supported. Autapomorphies are the extensive metathoracic intercoxal septum, the origin of the metafurca from this structure, the loss of *Mm. furcocalis* anterior and posterior, and possibly the presence of an elongated subcubital setal binding patch. Meruidae was placed as sister group of the Noteridae. Synapomorphies are the absence of the transverse ridge of the metaventrite, the fusion of abdominal segments III and IV, the shape of the strongly asymmetric parameres, and the enlargement of antennomeres 5, 7 and 9. The *Meru*-noterid clade is the sister group of the remaining Dytiscoidea. The exact position of *Aspidytes* within this clade remains ambiguous: it is either the sister group of Amphizoidea or the sister group of a clade comprising this family and Hygrobiidae + Dytiscidae. The sister group relationship between Spanglerogyrinae and Gyrininae was strongly supported. The two included genera of Gyrinini form a clade, and Enhydrini are the sister group of a monophylum comprising the remaining Enhydrini and Orectochilini. A branching pattern (*Pelodytes* + (*Brychius* + *Haliphus*)) within Haliplidae was confirmed. *Algophilus*, *Apteraliplus* and the *Haliphus*-subgenus *Liaphlus* form a clade. The generic status of the two former taxa is unjustified. The Phreatodytinae are the sister group of Noterinae, and *Notomicrus* (+ *Speonoterus*), *Hydrocoptus*, and *Pronoterus* branch off successively within this subfamily. The search for the larvae of *Meru* and a combined analysis of morphological and molecular data should have high priority.

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Meru phyllisae Spangler and Steiner (2005) was arguably one of the most exciting discoveries in adephagan studies of the past decades. The first individuals of this morphologically highly derived species were collected in 1985 from a small, clean river, partially running over a large granitic water slide in Venezuela, by Paul Spangler and co-workers. The “tiny pale tan beetles” are only about 0.8 mm long and are among or even the smallest adephagan

species. They were assigned to the newly described family Meruidae (Spangler and Steiner, 2005). These authors provided a detailed treatment of the morphological features of the adults with numerous illustrations and a discussion of possible phylogenetic affinities. However, a cladistic analysis was not carried out in that study. Consequently, the major goal of our contribution was to investigate the systematic position of Meruidae based on an analysis of a large sample of adephagan taxa and a comprehensive morphological data set. We also attempt to resolve the phylogeny of the smaller aquatic families (Gyrinidae, Haliplidae, Noteridae), as the phylogenetic hypotheses of earlier

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studies were not based on strictly cladistic character analyses (e.g., Beutel, 1989a,b, 1990; Beutel and Ruhnau 1990; Belkaceme, 1991).

Materials and methods

Nomenclature

The nomenclature of taxa is generally based on Lawrence and Newton (1995). Some of the higher categories introduced by Jeannel (1941–1942) are occasionally used for Carabidae. The terms Hydradephaga and Geadephaga are used for convenience of communication, but without implying monophyly.

List of ingroup taxa examined (taxa not included in the analysis are in square brackets)

Geadephaga

Carabidae: [*Gehringia olympiaca* Darlington (larvae* and adults [fixed in 70% ethanol = eth.] [* = used for microtome sections, see below]), *Metrius contractus* Eschscholtz (1st instar larvae* and adults [70% eth.]), *Omophron limbatum* Olivier (larvae* and adults [fixed in formol ethanol acetic acid = FAE]), *Nebria brevicollis* F. (larvae* and adults [FAE]), *Carabus* spp. (larvae* and adults [FAE]), *Bembidion* sp. (larvae* and adults [eth.]), [*Brachinus* sp. (adults [FAE])]

Rhysodidae: *Omoglymmius hamatus* LeConte (larvae* and adults [70% eth.]), [*Clinidium americanum* Dejean (larvae and adults [70% eth.])]

Trachypachidae: *Trachypachus holmbergi* Mannerheim (larvae* and adults* [70% eth.]), *Systolosoma breve* Solier (larvae and adults [70% eth.])

Hydradephaga

Gyrinidae: *Spanglerogyrus albiventris* Folkerts (adults* [FAE]), *Aulonogyrus concinnus* Klug (adults [FAE]), *Gyrinus argentinus* Mouchamps (larvae* and adults [FAE]), *Dineutus assimilis* Kirby (larvae and adults [FAE]), *Andogyrus colombicus* Régimart (adults [70% eth.]), *Orectochilus villosus* Müller (adults [FAE]), *Orectogyrus* spp. (adults [Bouin]), *Gyretes* sp. (adults [FAE]).

Haliplidae: *Peltodytes caesus* (Duftschmidt) (adults [FAE]), *Brychius elevatus* (Panzer) (larvae* and adults [FAE]), *Apteralipus parvulus* Roberts (larvae and adults [70% eth.]), *Halipus lineatocollis* (Marsham) (larvae* and adults [Dubosq brasil]), *Halipus mucronatus* Stephens (adults [FAE])

Hydradephaga: *Dytiscoidea.* **Amphizoidae:** *Amphizoa lecontei* Matthews (larvae and adults, [FAE]), *A. insolens* LeConte (adults [FAE])

Hygrobiidae: *Hygrobia hermanni* (F) (larvae [70% eth.], adults [FAE]), *H. australasiae* (larvae* [70% eth.])

Aspidytidae: *Aspidytes niobe* Ribera et al. (larvae* [all instars] and adults [90% eth.]), *A. wrasei* Balke, Ribera and Beutel (adults, dried specimen)

Dytiscidae: *Liopterus haemorrhoidalis* (F) (adults [FAE]), *Agabus* spp. (e.g., *A. bipustulatus* L., *A. guttatus* Paykull) (larvae and adults, [FAE]), *Dytiscus marginalis* L. (larvae* and adults, [FAE])

Meruidae: *Meru phyllisae* Spangler and Steiner (adults* [80% and 100% eth.])

Noteridae: *Notomicrus gracilipes* Sharp (adults [FAE]), *Hydrocoptus subvittulus* Motschulsky (adults [70% eth.]), *Pronoterus obscuripennis* Fleutiaux and Salle (adults [70% eth.]), *Synchortus sparsus* Sharp (adults [dried]), *Mesonoterus addendus* Blatchley (adults [70% eth.]), *Renotus deyrollei* (Sharp) (adults [dried]), *Noterus clavicornis* DeGeer (larvae* and adults, [FAE]), *N. crassicornis* Müller (adults [FAE]), *Siolius bicolor* J. Balfour-Browne (adults [dried]), *Suphis inflatus* (LeConte) (adults [70% eth.]), *Hydrocanthus* sp. (larvae* and adults [70% eth.]), *Canthydrus luctuosus* (Aubé) (larvae [70% eth.]), *Suphisellus bicolor* (Say) (adults* [70% eth.])

Ingroup taxon sampling

Emphasis was placed on presumably basal representatives of each family, e.g., *Spanglerogyrus* for Gyrinidae (Beutel, 1989a,b, 1990), *Phreatodytes* and *Notomicrus* for Noteridae (Belkaceme, 1991), and *Metrius* and *Omophron* for Carabidae. This increases the probability of a reliable reconstruction of the ancestral states (= ground plan *sensu* Hennig 1969, i.e., the sum of apomorphic and plesiomorphic characters of the last common ancestor of a clade) for the higher taxa. A broad taxon sampling (representatives of all genera) was attempted for all taxa with the exception of the large families Carabidae and Dytiscidae, their phylogeny not being one of the aims of the present investigation.

Outgroup

The outgroup comprises the archostematan family Cupedidae (*Priacma serrata* LeConte [adult characters], *Rhysideigma raffrayi* Fairmaire [larval characters]) and one representative of the polyphagan superfamily Staphylinioidea (*Catops* sp. [Leiodidae]). Two different taxa were chosen for the former group as detailed morphological data are only available for larvae of *Rhysideigma*.

Characters

This study is exclusively based on internal and external morphological characters. It has been demonstrated that larval character transformations have played an important role in aedeophagan evolution (e.g., Alarie, 1991; Arndt, 1993; Beutel, 1993). Therefore characters of immature stages were included even

though they are not available for *Meru* or some other important taxa (e.g., *Spanglerogyrus*, *Notomicrus*).

Morphological methods

Larval and/or adult representatives of species marked with an asterisk were embedded in Histoiresin, sectioned at 3 μm , and stained with methylene-blue and acid fuchsin. Drawings were made using an ocular grid or a camera lucida (cross sections). V. K  ler's (1963) muscular nomenclature is used in the text and the corresponding numbers are used in the illustrations. Scanning electronic microscopy was carried out with an FEI (Philips) XL 30 ESEM TMP. Specimens were critical point dried (larvae) and sputter coated.

Cladistic analysis

Cupedidae (see above), *Catops*, and adephagan genera or subgenera (Haliplidae) were used as terminal taxa. The present as well as previous investigations by the first author (e.g., Beutel, 1992a, 1993, 1997) suggest that the characters used do not or very rarely (e.g., anterior metacoxal margin in *Aspidytes*) show intrageneric variation. The data matrix (Table 1) was analyzed with the computer program PAUP version 4.0b10 (Swofford, 2002) (TBR heuristic searches, 200 random addition sequences, multrees in effect, amb-). All characters were equally weighted and characters 3, 25, 34 and 36 were treated as additive (see list of characters for rationale). Branch support values (Bremer, 1988) were calculated using TreeRot version 2c (Sorenson, 1996) in combination with PAUP. Parsimony jackknife replications (Farris et al., 1996) were based on 1000 replicates with 100 random addition sequences and deletion of 37% of the data and run in PAUP. Characters were mapped onto one of the randomly chosen parsimonious trees using Winclada (Nixon, 1999) and NONA (Goloboff, 1995).

Results

List of morphological characters used for phylogenetic analysis (see also Table 1).

Adults

1. Body shape: (0) pronoto-elytral angle present, distinct (120° or less); (1) present, weakly pronounced (more than 135°); (2) body laterally evenly rounded, streamlined. Body fully streamlined in Gyrinidae, most Haliplidae, Noteridae (excl. *Phreatodytes*), and most Dytiscidae. Pronoto-elytral angle present but fairly indistinct in *Meru* (Fig. 1; Spangler and Steiner, 2005), *Hygrobia* (coded as 1), and some *Haliphilus* spp. (coded as 1 for *H. lineatocollis* and 0&1 for *Haliphilus* [*Liaphilus*];

Franciscolo, 1979). Distinct in Geadephaga (Fig. 5A; with some exceptions: e.g., *Omophron*, *Brychius*, *Algophilus* (Beutel and Ruhnau, 1990), *Phreatodytes* (U  no, 1957, 1996), *Amphizoa* and Cupedidae).

2. Head shape: (0) not shortened and laterally rounded, eyes protruding (1) shortened, laterally rounded, eyes not protruding. Fairly elongate with moderately prominent eyes in *Meru* (Figs 1 and 2A; Spangler and Steiner, 2005), Haliplidae, *Hygrobia*, *Amphizoa*, Geadephaga (with few exceptions), and the outgroup taxa. Shortened and laterally rounded in Gyrinidae (Hatch, 1927; Beutel, 1989a), Noteridae (Belkaceme, 1991), *Aspidytes* (Fig. 2B; Ribera et al. 2002b; Balke et al., 2003), Dytiscidae (Franciscolo, 1979; Balke, 2005), and *Omophron*.

3. Compound eyes: (0) undivided; (1) divided by a narrow chitinous bridge; (2) divided by a broad chitinous bridge (e.g., Beutel, 1989a). Completely divided into upper and lower portion by a chitinous bridge in Gyrinidae (and †Coptoclauidae; Ponomarenko, 1977). Separating bridge narrow in *Spanglerogyrus* (Fig. 3A) but very broad in Gyrininae (Hatch, 1927; Honomichl, 1975; Folkerts, 1979; Beutel, 1989a). We treated this character as additive, assuming that state “1” is more similar to either “0” or “2” than the latter to each other, and suggest that convergent evolution in *Spanglerogyrus* and the rest of Gyrinidae is highly unlikely.

4. Secondary genal ridge: (0) absent; (1) present (Beutel and Ruhnau, 1990). Present in adults of the subgenus *Liaphilus* (*Haliphilus*), *Apteraliplus* (Fig. 3B), and *Algophilus*.

5. Rows of labral setae: (0) not arranged in three distinctly separated rows; (1) three distinct rows (Beutel, 1989a). Three distinct rows present in Gyrininae (Honomichl, 1975, fig. 9; Beutel, 1989a). One row in *Spanglerogyrus* (Fig. 3A) and representatives of other adephagan families (Fig. 3C).

6. Tactile supraorbital setae: (0) absent; (1) present. Present in Trachypachidae (Fig. 3C) and Carabidae.

7. Large epipharyngeal sensilla: (0) absent; (1) present. Large, sclerotized peg-like sensilla present in Dytiscidae (comparatively short but distinctly sclerotized in *Liopterus*), *Amphizoa* (Fig. 4B) and *Aspidytes* (Fig. 4A). Absent in *Meru*, in all dissected noterids (*Noterus*, *Hydrocanthus*, *Canthyrus*, *Suphisellus*), and in other groups of Adephaga.

8. Shape of scapus: (0) parallel-sided, longer than wide; (1) shortened, large globular basal part, cylindrical distal part; (2) hemispherical and extremely short; (3) basal and distal part globular; (4) strongly shortened but cylindrical, without enlarged globular part; (5) strongly enlarged, cup-shaped (see Ribera et al., 2002b). Usually parallel-sided and longer than wide (e.g., Geadephaga [Fig. 3C], *Amphizoa*, *Hygrobia*, Dytiscidae, Archostemata). Shortened, with a large globular basal part and cylindrical distal part in Noteridae (Beutel and Roughley, 1987, figs 4, 5; Belkaceme, 1991) and *Brychius*. Hemispherical and extremely short in *Meru* (Spangler and Steiner,

Table 1
Continued

		6	7	8	9	10	11
	0	0	0	0	0	0	0
Cupididae	0	0	0	0	0	0	0
Catops	0	0	0	0	0	0	0
Meru	0	1	0	0	0	0	0
Aspidytes	0	1	0	0	0	0	0
Spanglerogyrus	0	0	0	0	0	0	0
Gyrinus	1	0	0	0	0	0	0
Aulonogyrus	1	0	0	0	0	0	0
Enhydrus	1	0	1	0	0	0	0
Dineutus	1	0	1	0	0	0	0
Andogyrus	1	1	1	0	0	0	0
Macrogyrus	1	1	1	0	0	0	0
Orectochilus	1	1	1	0	0	0	0
Orectogyrus	1	1	1	0	0	0	0
Gyretes	1	1	1	0	0	0	0
Peltodytes	0	0	0	0	0	0	0
Brychius	0	0	0	0	0	0	0
Apteraliplus	0	0	0	0	0	0	0
Algophilus	0	0	0	0	0	0	0
Haliplus (Liaphl)	0	0	0	0	0	0	0
Haliplus (Neohal)	0	0	0	0	0	0	0
Phreatodytes	0	0	0	0	0	0	0
Notomicrus	0	0	0	0	0	0	0
Hydrocoptus	0	0	0	0	0	0	0
Pronoterus	0	0	0	0	0	0	0
Noterus	0	0	0	0	0	0	0
Synchortus	0	0	0	0	0	0	0
Mesonoterus	0	0	0	0	0	0	0
Renotus	0	0	0	0	0	0	0
Siolius	0	0	0	0	0	0	0
Suphis	0	0	0	0	0	0	0
Hydrocanthus	0	0	0	0	0	0	0
Canthydrus	0	0	0	0	0	0	0
Suphisellus	0	0	0	0	0	0	0
Amphizoia	0	0	0	0	0	0	0
Hygrobia	0	0	0	0	0	0	0
Liopterus	0	0	0	0	0	0	0
Agabus	0	0	0	0	0	0	0
Dytiscus	0	0	0	0	0	0	0
Omoglymmius	0	0	0	0	0	0	0
Trachypachus	0	0	0	0	0	0	0
Systolosoma	0	0	0	0	0	0	0
Metrius	0	0	0	0	0	0	0
Omophron	0	0	0	0	0	0	0
Carabus	0	0	0	0	0	0	0
Bembidion	0	0	0	0	0	0	0
Pterostichus	0	0	0	0	0	0	0

Aspidytes (antennomeres 4–11, without smaller intermediary antennomeres [Fig. 13]; Balke et al., 2003), and slightly expanded and distinctly longer than adjacent segments in *Meru*. It was pointed out in Spangler and Steiner (2005) that slightly expanded antennomeres do also occur in Haliplidae. However, this was not observed in the genera *Peltodytes*, *Brychius* (Beutel and Ruhbau, 1990), *Apteraliplus* and the different species of *Haliplus*

examined during this study (coded as 0). Modifications of flagellomeres do also occur in some representatives of Dytiscidae (e.g., few species of *Agabus* [Franciscolo, 1979; Larson et al., 2000], Copelatinae and Hydroporinae). However, enlarged flagellomeres are almost certainly neither part of the ground plan of the Dytiscidae nor of the genera where they occur. Therefore we coded this and the following two characters as 0 in the case of *Agabus*.

Table 1
Continued

	1	1	1	1	1
	1	2	3	4	4
	0	0	0	0	8
Cupididae	0	0	0	0	0
Catops	0	0	0	0	0
Meru	?	?	?	?	?
Aspidytes	2	1	4	0	1
Spanglerogyrus	?	?	?	?	?
Gyrinus	0	1	?	0	0
Aulonogyrus	0	1	?	0	0
Enhydrus	?	?	?	?	?
Dineutus	0	1	0	0	0
Andogyrus	0	1	?	0	0
Macrogyrus	0	?	?	0	0
Orectochilus	0	1	?	0	0
Orectogyrus	0	1	?	0	0
Gyretes	0	1	?	0	0
Peltodytes	0	2	0	1	0
Brychius	0	2	0	1	0
Apteralipus	?	?	?	?	?
Algophilus	?	?	?	?	?
Halipus (Liaphl)	0	2	0	1	0
Halipus (Neohal)	0	2	0	1	0
Phreatodytes	?	4	?	1	?
Notomicrus	?	?	?	?	?
Hydrocoptus	?	?	?	?	?
Pronoterus	?	?	?	?	?
Noterus	1	2	0	1	1
Synchortus	?	?	?	?	?
Mesonoterus	?	?	?	?	?
Renotus	?	?	?	?	?
Siolius	?	?	?	?	?
Suphis	?	?	?	?	?
Hydrocanthus	1	2	0	1	1
Canthydrus	?	?	?	?	?
Suphisellus	?	?	?	?	?
Amphizoa	2	0	0	0	1
Hygrobia	2	-	0	0	1
Liopterus	2	0	0	0	1
Agabus	2	0	0	0	1
Dytiscus	2	0	0	0	1
Omoglymmius	0	0	0	0	1
Trachypachus	1	1	0	0	2
Systolosoma	1	1	0	0	2
Metrius	0	1	1	0	0
Omophon	0	1	1	0	0
Carabus	0	1	1	0	0
Bembidion	0	1	1	0	0
Pterostichus	0	1	1	0	0

11. Expansion of antennomere 7 of males: (0) absent; (1) present (Belkaceme, 1991; Spangler and Steiner, 2005). Expanded in males of all genera of Noteridae (Belkaceme, 1991; Spangler, 1996) and also slightly expanded in *Aspidytes* (Fig. 13; see Character 10) and *Meru*.

12. Expansion of antennomere 9 of males: (0) absent; (1) present (Belkaceme, 1991; Spangler and Steiner, 2005). Expanded in most males of Noteridae (not

in *Noterus*, *Siolius*, *Suphis*; Belkaceme, 1991; Spangler, 1996) and slightly expanded in *Aspidytes* and *Meru*.

13. Dense pubescence of distal antennomeres (IV–XI): (0) absent; (1) present. Absent in *Meru* as in all other hydradephagan groups (Figs 3A, B and 13) and Trachypachidae (Fig. 3C). Rather sparse in *Gehringia* (miniaturization) and distinctly modified in Rhyso-



Fig. 1. *Meru phyllisae*, habitus, dorsal view.

didae (e.g., Bell and Bell, 1978; coded as 1). A distinctly different setation of the antennomeres is present in *Priacma* (coded as 0).

14. Number of galeomeres: (0) 2; (1) 1; (2) 0. Usually two (e.g., *Meru*; Spangler and Steiner, 2005, fig. 7B) but one in Amphizoidae (Beutel, 1988) and Gyrinini (Hatch, 1927; Honomichl, 1975). Galea absent in Orectochilini and Enhydrini (Hatch, 1927; Beutel, 1989a).

15. Lateral rounded lobes of mentum: (0) absent; (1) present, moderately sized; (2) present, large. Rounded lobes present in *Meru* (Fig. 2A; Spangler and Steiner, 2005, fig. 3C) and all other adults of Adephaga (Fig. 2B) with the exception of Rhysodidae (mentum strongly enlarged and fused with submentum, covering reduced prementum; see Characters 16–18). Very large in Gyrininae (Beutel, 1989a). Absent in non-adephagan beetles (e.g., Williams, 1938).

16. Fusion of palpiger with prementum: (0) absent; (1) present (Beutel, 1989a). Palpiger fused with prementum in Gyrininae. Free in *Meru* (Fig. 2A; Spangler and Steiner, 2005, fig. 3C) and other adephagans (Fig. 2B). Prementum strongly reduced in Rhysodidae, completely covered by mentum (coded as inapplicable).

17. Shape of terminal labial palpomere: (0) as large or large than penultimate segment; (1) small subulate. Subulate in adults of Haliplidae (excl. *Peltodytes*) (Fig. 3B), *Gehringia*, and *Bembidion*. Coded as inapplicable for Rhysodidae.

18. Elongate and narrow sensorial field on terminal labial palpomere: (0) absent; (1) present. Transverse, elongate and narrow sensorial field (“leistenförmiges Sinnesfeld”; Belkaceme, 1991) present on widened apex of distal labial palpomere in most noterid genera (not in *Phreatodytes*, *Notomicrus* and *Noterus*; see Belkaceme, 1991). A round field of sensorial structures is present in *Aspidytes* (coded as 0), and the entire apical part of the palpomere is wrinkled and covered with different sensilla in *Meru* (coded as 0; see Spangler and Steiner, 2005, fig. 3I).

19. Field of setae on lateral part of pronotum and elytra (Beutel, 1989b): (0) present; (1) absent (Beutel, 1989b). Present in *Spanglerogyrus* and Orectochilini.

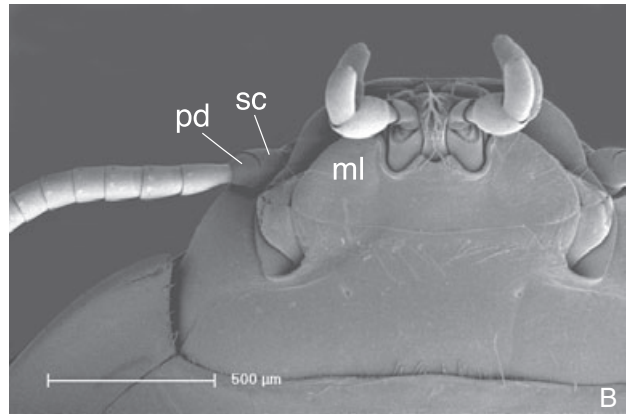
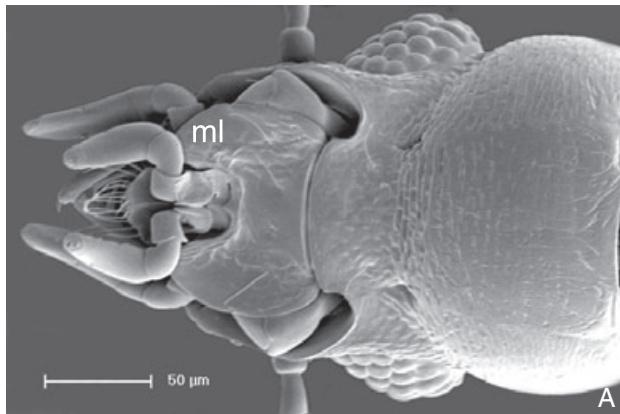


Fig. 2. Head of adults, ventral view (SEM). (A) *Meru phyllisae*; (B) *Aspidytes niobe*. Abbreviations: pd—pedicellus, ml—mental lobes, sc—scapus.

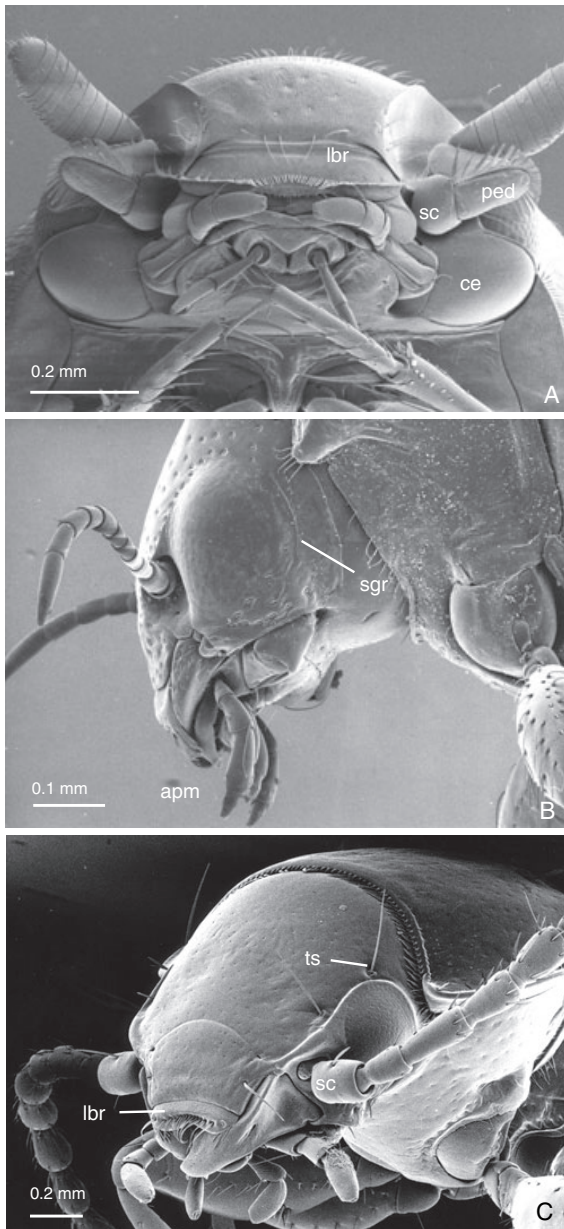


Fig. 3. Head of adults (SEM). (A) *Spanglerogyrus albiventris*, frontal view; (B) *Apteraliplus parvulus*, lateral view; (C) *Trachypachus holmbergi*, anterolateral view. Abbreviations: apm—apical maxillary palpomere, ce—compound eye, lbr—labrum, pd—pedicellus, sc—scapus, ts—tactile supraorbital setae.

20. Shape of prosternal process: (0) short and narrow; (1) longer and broader, converging towards apex; (2) long, apically broad and laterally rounded; (3) long, strongly broadened and apically truncate; (4) apex reduced, laterally fused with hypomeral process. Short and narrow in Gyrinidae (Fig. 10) and Cupedidae. Rounded posteriorly in *Meru*, *Aspidytes wrasei* (Balke et al., 2003, figs 2, 3), *Phreatodytes*, *Noterus*, *Synchor-tus*, *Mesonoterus*, *Amphizoa*, Trachypachidae (Fig. 5A)

and *Gehringia* (Beutel, 1992). The apex is nearly truncate in *Aspidytes niobe*, but the posterolateral edges are still rounded (Fig. 5B) (coded as 2). Strongly broadened and apically truncate in *Omophron* (Beutel, 1992), Haliplidae and several genera of Noteridae (*Siolius*, *Renotus*, *Suphis*, *Hydrocanthus* [Fig. 8D], *Canthydrus*, *Suphisellus*; Belkaceme, 1991). Distal part acuminate or at least converging in Dytiscidae, *Hygrobia*, few Noteridae (*Notomicrus*, *Hydrocoptus* [Fig. 8C]; Belkaceme, 1991, figs 63–66), and presumably basal representatives of Carabidae (e.g., *Metrius*, *Carabus*, Beutel, 1992). Apical part shortened and fused with hypomeral process in most Carabidae (external postcoxal bridge; see Character 20 and Beutel, 1992a).

21. External posterior procoxal bridge: (0) absent; (1) present (Beutel, 1992a). Present in Rhysodidae, Paus-sinae, Cicindelinae, *Omophron*, Elaphrini, Loricerini, Migadopini, and Caraboidea Limbata (Jeannel, 1941–1942). Absent in other adephagan groups (Figs 5A, B and 10).

22. Width of posterior procoxal bridge: (0) narrow; (1) broadened. Strongly broadened in Rhysodidae, Cicindel-idae and Scaritinae (Baehr, 1979; Beutel, 1992a).

23. Internal posterior procoxal bridge: (0) absent; (1) present. Present in *Meru* (Spangler and Steiner, 2005), Trachypachidae and Hydradephaga (Baehr, 1979; Beutel, 1992a).

24. Caudal process of profurca: (0) absent; (1) present, short; (2) present, elongated. Present in Gyrininae. Distinctly elongated in Enhydrini and Orectochilini (Baehr, 1979; Beutel, 1989b).

25. Prothoracic proprioceptive organ: (0) absent; (1) present, simple setae; (2) present, spatulate setae. Present on notal part of the posterior prothoracic wall in Gyrinidae (Larsén, 1966; Beutel, 1989b). Setae simple in *Spanglerogyrus*, but spatulate in Gyrininae (Larsén, 1966; Beutel, 1989b). This character was treated as additive as independent evolution of this organ in *Spanglerogyrus* and Gyrininae is very unlikely.

26. Prothoracic defensive gland: (0) absent; (1) present. Absent in *Meru* (pers. obs. Beutel). Present in *Hygrobia* and *Dytiscidae* (Forsyth, 1968, 1969).

27. Ventral procoxal joint: (0) absent; (1) with distinct coxal condyle; (2) strongly shortened. Absent in Gyrin-inae (well developed in *Spanglerogyrus*) and non-ade-phagan beetles, and largely reduced in adults of Dytiscidae (Baehr, 1979; Beutel, 1989b). Well developed in *Aspidytes* and other groups of Adephaga.

28. Profemoral antenna cleaning device: (0) absent; (1) present. Present in *Aspidytes*, adults of all noterid genera (Belkaceme, 1991, fig. 22; Spangler, 1996), and in some representatives of Dytiscidae (e.g., *Liopterus*, *Laccophi-lus*). Absent in *Meru* and adults of the other adephagan families.

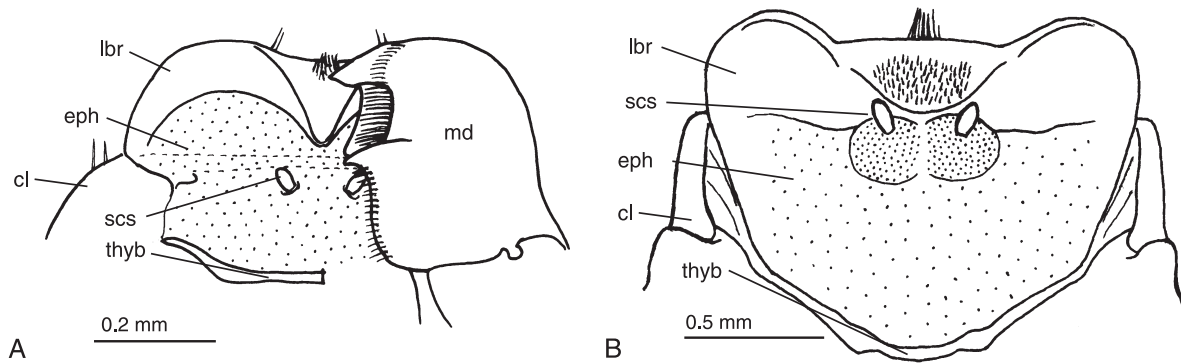


Fig. 4. Labrum, ventral view. (A) *Aspidytes niobe*; (B) *Amphizoa lecontei*. Abbreviations: cl—clypeus, eph—epipharynx, lbr—labrum, md—mandible, scs—sclerotized sensilla, thyb—transverse hypopharyngeal bar.

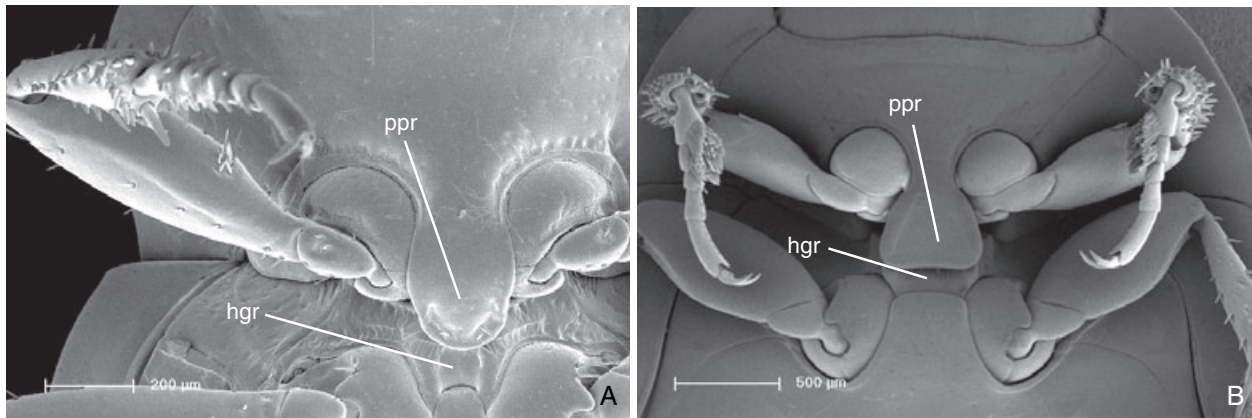


Fig. 5. Prothoracic structures of adults, ventral view (SEM), (A) *Trachypachus holmbergi*; (B) *Aspidytes niobe*. Abbreviations: hgr—hexagonal groove of mesoventrite, ppr—prosternal process.

29. Protibial antenna cleaning device: (0) absent; (1) present. Present in Geadephaga (Fig. 6; e.g., Beutel, 1997).

30. External protibial spur: (0) present; (1) absent. Absent in Gyrinidae (Beutel, 1989b) and Rhysodidae (Bell and Bell, 1978).

31. Position of external spur of the protibia: (0) apical; (1) subapical. Both spurs inserted apically in Hydradephaga (incl. *Meru*), Trachypachidae (Fig. 6A) and some Carabidae. Shifted in a more or less proximal position in most Carabidae (Anisochaeta [excl. *Carabus*; Jeannel, 1941–1942]).

32. External protibial spur: (0) not modified as burrowing spur; (1) modified as strong, curved burrowing spur (Beutel and Roughley, 1987). Modified as curved burrowing spur in Noterinae (Fig. 9A) excluding *Notomicrus*, *Hydrocoptus* and *Pronoterus*, and also in *Hygrobia* (Beutel, 1986a) and *Omophron* (both with two burrowing spurs).

33. Internal protibial spur: (0) present; (1) absent. Absent in Noterinae excluding *Notomicrus*, *Hydrocoptus*, *Pronoterus* and *Noterus* (Belkaceme, 1991), and in Rhysodidae (Bell and Bell, 1978) and Gyrininae.

34. Row of stout, flattened setae on apical part of protibia: (0) absent; (1) present, short; (2) present, extending to proximal part of tibia (Belkaceme, 1991). Regular row of flattened, ribbed setae present at outer apical tibial edge of Noterinae excluding *Notomicrus*, *Speonoterus*, *Hydrocoptus* and *Pronoterus* (Belkaceme, 1991; Spangler, 1996). Extended towards proximal part of tibia in *Hydrocanthus* (Fig. 9A), *Canthydrus* and *Suphisellus* (Belkaceme, 1991). Absent in *Meru*, *Aspidytes* and most other adepagan and non-adephan beetles (a similar condition occurs in the dytiscid genus *Hydaticus*; M. Balke, pers. obs.). We treated this character as additive as independent evolution of the row of thorns within Noteridae is very unlikely.

35. Outer edge of protibia: (0) not rounded; (1) rounded (Belkaceme, 1991). Rounded in adults of Noterinae excluding *Notomicrus*, *Speonoterus*, *Hydrocoptus* and *Pronoterus* (Belkaceme, 1991; Spangler, 1996).

36. Tibial groove or concavity for reception of burrowing spur: (0) absent; (1) present as furrow; (2) present as a pit (Belkaceme, 1991). Present in adults of Noterinae excluding *Notomicrus*, *Speonoterus*, *Hydrocoptus*, *Pronoterus* and *Noterus* (Belkaceme, 1991; Spangler, 1996).

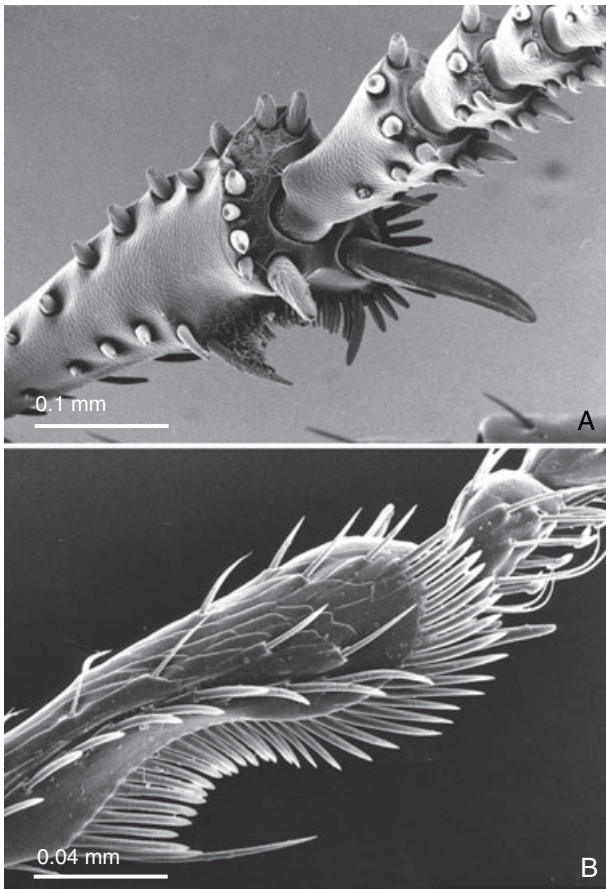


Fig. 6. Protibiae with antenna cleaning organs (SEM). (A) *Trachypachus holmbergi*; (B) *Gehringia olympiaca*.

Developed as a furrow in adults of *Synchortus* and *Mesonoterus*, and as a deep pit in the remaining genera (Fig. 9A; Belkaceme, 1991). We treated this character as additive as it is unlikely that the furrow or pit have evolved independently.

37. Curved spurs on ventral side of protarsomeres 1–3: (0) absent; (1) present (Belkaceme, 1991). Present on protarsomeres 1–3 in Noterinae excl. *Notomicrus* and *Speonoterus* (Fig. 9A; Belkaceme, 1991, figs 61, 70 and 71; Spangler, 1996).

38. Excavation for reception of prolegs: (0) absent; (1) absent (Larsén, 1966; Beutel, 1990). Present in Gyrininae. Absent in *Spanglerogyrus* (Fig. 10) and adults of all other groups of Adephaga.

39. Opening between anepisternum and elytron: (0) absent; (1) present (Larsén, 1966; Beutel, 1990). Present in Gyrininae.

40. Shape of mesoventrite (terminology: see Baehr, 1975; Beutel, 1986a; Belkaceme, 1991): (0) flat and extensive, without hexagonal groove and anterolateral grooves; (1) short, with hexagonal groove and anterolateral grooves for reception of the procoxae; (2) with rounded, horizontal anterior part and steeply ascending

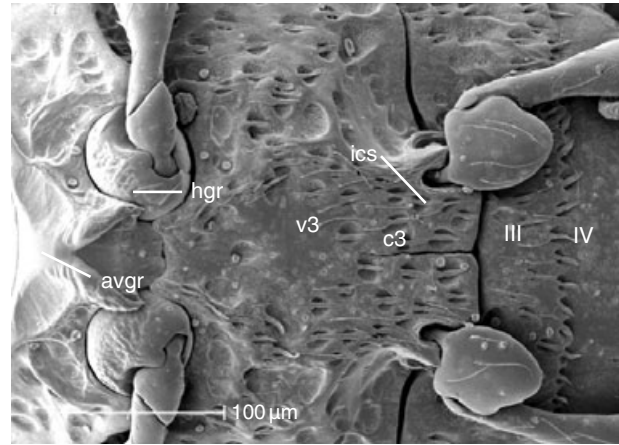


Fig. 7. *Meru phyllisae*, pterothorax, ventral view (SEM). Abbreviations: avgr—anteroventral groove of mesoventrite for reception of procoxae, c3, metacoxa, hgr—hexagonal groove of mesoventrite, ics—intercoxal septum, v3—metaventrite, III, IV—abdominal sternites III, IV.

posterior part. Flat and more or less extensive in Gyrinidae (Fig. 10), Cupedidae and some groups of Polyphaga (e.g., Hydraenidae, Leiodidae). Strongly shortened with characteristic hexagonal groove in *Meru* (Fig. 7), Trachypachidae (Fig. 5A), Haliplidae, Dytiscoidea, *Aspidytes* (Fig. 5B), and basal carabids (e.g., *Opisthius*, *Carabus*, *Nebria*; covered by the prosternal process in *Omophron*; Beutel, 1992a). With collar-like anterior margin, anterior part round in cross section and steeply ascending posterior part in most Carabidae (Beutel, 1992a).

41. Discrimen of mesoventrite: (0) absent; (1) present. Absent in *Meru* (Fig. 7) and most other nonarchostematan beetles. Present in Gyrininae (Beutel, 1990).

42. Contact between mesepimeron and mesocoxal cavity: (0) present; (1) absent (conjunct type) (Bell, 1967). No contact in Caraboidea Limbata excl. Scrobifera (Jeannel, 1941–1942) and few other carabids (Notiophilini, Paussini partim; Beutel, 1992a). Inapplicable for *Meru* (Fig. 7; mesanepisternum and mesepimeron fused with metaventrite).

43. Contact between metanepisternum and mesocoxal cavity: (0) absent; (1) present (complex type) (Bell, 1967). Contact present in †Eodromeinae (Trachypachidae) (Ponomarenko, 1977), *Aspidytes*, *Amphizoa*, and most Dytiscidae but not in Laccophilinae and Vatelini (Balke, 2005). Inapplicable for *Meru* (see Character 42).

44. Orientation of metepimeron: (0) elongate or triangular, not at right angle to longitudinal body axis; (1) parallel-sided, approximately at right angle to longitudinal body axis (Beutel, 1992a). Triangular in Trachypachidae and Hydradephaga. Parallel-sided (with or without lobe at posterior margin; see Character 52)

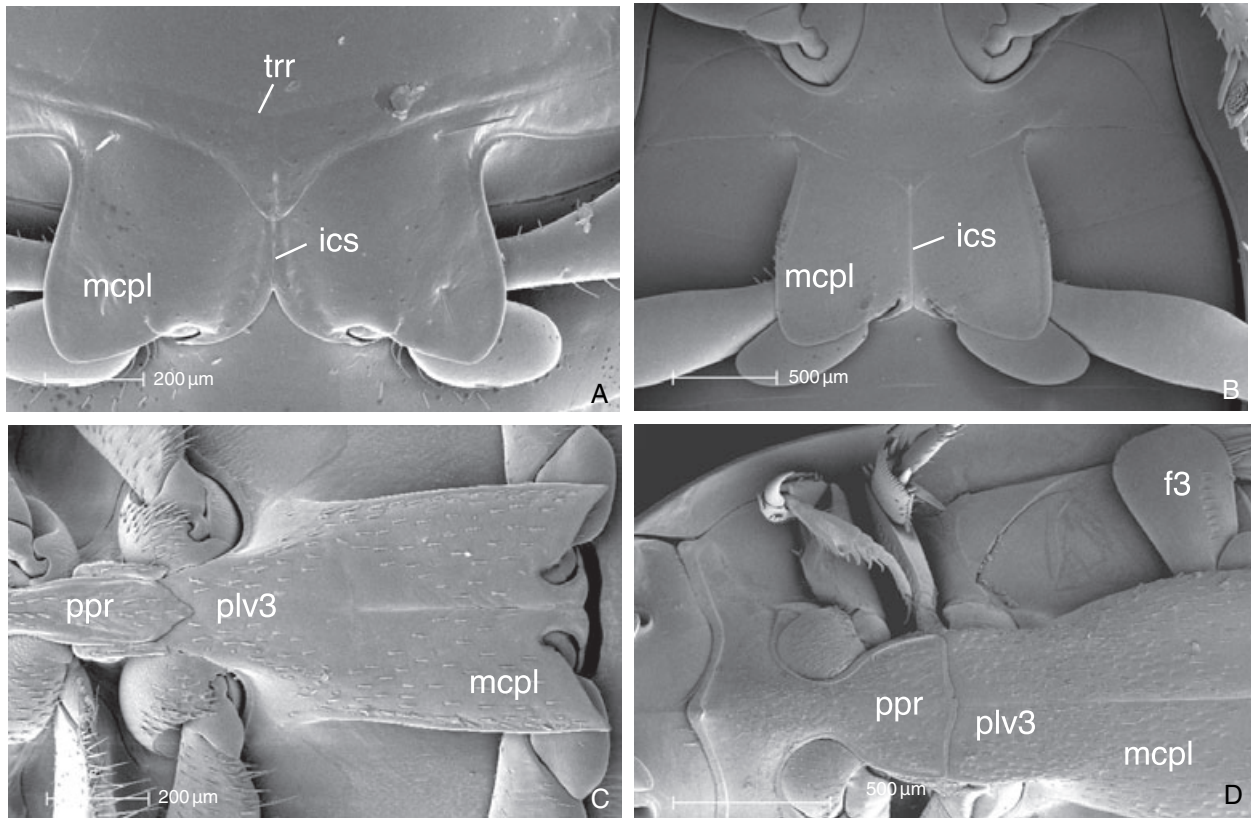


Fig. 8. Thoracic structures of adults, SEM, ventral view. (A) *Trachypachus holmbergi*; (B) *Aspidytes niobe*; (C) *Hydrocoptus bivittis*; (D) *Hydrocanthus iricolor*. Abbreviations: f3—metafemur, ics—intercoxal septum, mcpl—metacoxal plate, ppr—prosternal process, plv3—platform of metaventricle, trr—transverse ridge.

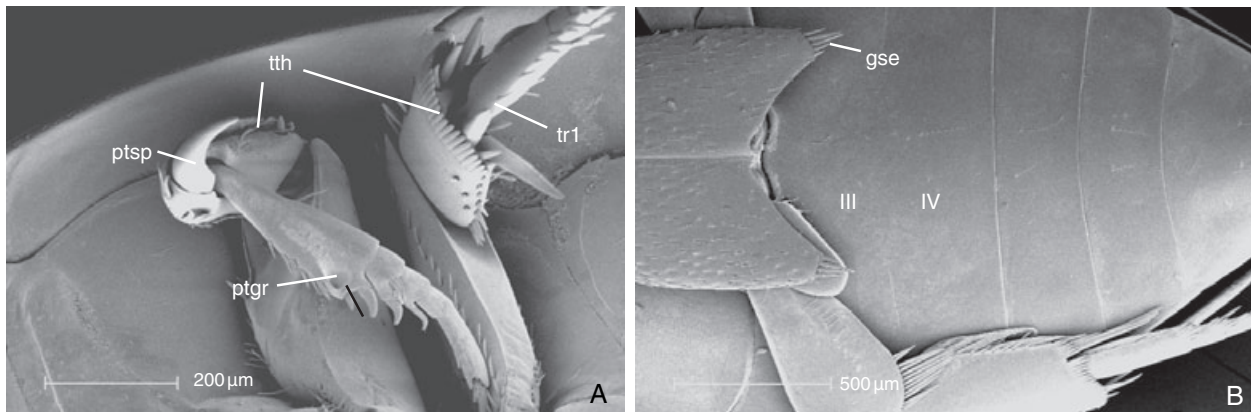


Fig. 9. Thoracic structures of adults, ventral view, *Hydrocanthus iricolor* (SEM). (A) fore- and middle legs; (B) Metacoxae and abdomen. Abbreviations: gse—group of setae, ptgr—protibial groove, ptsp—protibial spur, tr1—mesotarsomere 1, tth—stout flattened tibial setae, III, IV—abdominal sternites III, IV.

and approximately at right angle to the body axis in Rhysoidea and Carabidae. Elongate and parallel to longitudinal body axis in Archostemata (Baehr, 1975).

45. Lobe of hind margin of metepimeron: (0) absent; (1) present (e.g., Beutel, 1992a). Present in Hiletini, Harpalinae and Brachininae (Beutel, 1992a).

46. Elytral apex: (0) not truncate; (1) truncate (Beutel and Roughley, 1988). Truncate in all Gyrinidae (not covering tergite VIII and a small part of VII), *Gehringia* and Brachininae.

47. Shape of mesocoxae: (0) triangular; (1) rounded. Triangular in Archostemata and Gyrinidae (Fig. 10).

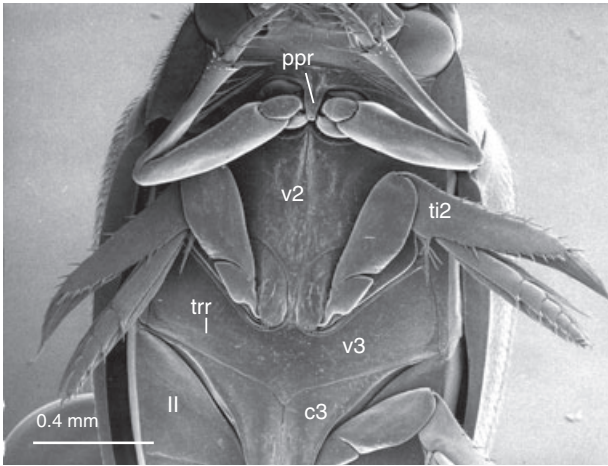


Fig. 10. *Spanglerogyrus albiventris*, thorax, ventral view. Abbreviations: c3—metacoxa, ppr—prosternal process, ti2—mesotibia, trr—transverse ridge of metaventricle, v2, 3—meso-, metaventricle, II—abdominal sternite II.

More or less globular in other groups of Adephaga (Figs 5B, 7, 9C, D).

48. Fusion of mesocoxa with mesoventrite: (0) absent; (1) present (Larsén, 1966; Beutel, 1990). Fused in *Orectochilus* and *Orectogyrus*.

49. Lateral internal process of mesocoxae: (0) absent; (1) not fused with anepisternum; (1) fused with anepisternum (Larsén, 1966; Beutel, 1990). Fused with anepisternum 2 in *Orectogyrus* and *Orectochilus*.

50. Proximal mesotarsomeres of males: (0) not distinctly elongated and broadened; (1) elongated and broadened. Elongated and distally broadened in Noterinae (Fig. 9A) excluding *Notomicrus* and *Hydrocoptus* (Belkaceme, 1991), and in *Hygrobia* and *Omophron* (Beutel and Roughley, 1987).

51. Middle legs: (0) unmodified walking leg or, if modified for swimming not strongly shortened; (1) strongly shortened, broad and paddle-like. Short and paddle-like in Gyrininae (Hatch, 1927; Larsén, 1966; Beutel, 1990), but not in *Spanglerogyrus* (Fig. 10).

52. Tarsomeres 4 and 5 of paddle-like middle legs: (0) not at right angle to proximal tarsomeres; (1) at right angle to proximal tarsomeres (Larsén, 1966; Beutel, 1990). At right angle to proximal tarsomeres in *Macrogyrus*, *Andogyrus* and *Orectochilini*.

53. Anterior and posterior wall of middle and hind femora: (0) not connected by cuticular columnae; (1) connected by cuticular columnae (Larsén, 1966; Beutel, 1990). Connected in Enhydrini and *Orectochilini*.

54. Swimming hairs on middle legs: (0) absent; (1) sparse fringe of very thin and fine hairs; (2) dense fringe of longer hairs; (3) lamellae; (4) fimbriate hairs. Absent in

Meru, *Aspidytes* and most non-adephagan beetles. Dense rows of hairs present in Haliplidae, *Hygrobia*, Dytiscidae, and Noterinae (Fig. 9B). Sparse fringe of very fine hairs present in *Amphizoa*. Middle- and hind legs of Gyrininae with swimming lamellae. Swimming hairs fimbriate in *Spanglerogyrus* (Fig. 10).

55. Shape of metanotum: (0) median part not or only moderately narrowed; (1) laterally more than twice as broad than medially (Beutel, 1990). Strongly narrowed medially in Enhydrini and *Orectochilini*.

56. Noterid platform of metaventricle: (0) absent; (1) present (Beutel and Roughley, 1987). Present in Noterinae (Fig. 9C, D) excl. *Notomicrus*, *Speonotus* (Spangler, 1996) and *Phreatodytes* (Uéno, 1957; Beutel and Roughley, 1987; Belkaceme, 1991).

57. Transverse ridge of metaventricle: (0) complete; (1) partly reduced; (2) absent. Partly reduced in *Aspidytes* (only visible internally; Ribera et al., 2002a; Balke et al., 2003; Fig. 8B), Trachypachidae (Fig. 8A), *Hygrobia* (Beutel, 1986a) and *Amphizoa* (Beutel, 1988). Absent in *Meru* (Fig. 7), Gyrininae (complete in *Spanglerogyrus*; fig. 10; Folkerts, 1979; Beutel, 1990), Noteridae (Fig. 8C, D) and Dytiscidae (e.g., Franciscolo, 1979; Beutel, 1995).

58. Contact between pro- and metasternal process: (0) absent; (1) present. Prosternal process distinctly overlaps with anterior part of metasternal process in Haliplidae (Baehr, 1979), Noterinae (Fig. 8C, D; Belkaceme, 1991; Spangler, 1996, fig. 59), *Hygrobia* and Dytiscidae (Beutel, 1986a). The apex of the prosternal process nearly reaches the anterior margin of the metasternal process in *Aspidytes* (Fig. 5b) but does not overlap with it.

59. Metapostnotum: (0) not inflected below scutellum; (1) inflected below scutellum (Beutel, 1990). Inflected in Gyrininae.

60. Metepimeron: (0) not at right angle to body axis; (1) parallel-sided and perpendicular to body axis. Parallel-sided and approximately perpendicular to body axis in Rhysodidae and Carabidae (Beutel, 1992a, figs 3–20, 24–27; Beutel and Haas, 1996). Triangular and more or less elongated along the body axis in the outgroup taxa and in Trachypachidae (Beutel, 1992a, fig. 23) and Hydradephaga. Not applicable for *Meru* due to fusion of sclerites (Character 153; Spangler and Steiner, 2005).

61. Origin of metafurca: (0) katapisternum; (1) intercoxal septum. Originates from the intercoxal septum in *Meru* (Spangler and Steiner, 2005, fig. 10; pers. obs. Beutel), *Aspidytes* and Dytiscoidea (e.g., Beutel, 1986a, 1988, 1995, 1997).

62. Lateral arms of metafurca: (0) present; (1) absent. Absent in *Meru* (Spangler and Steiner, 2005, fig. 10) and Gyrininae (not in *Spanglerogyrus*) (Beutel, 1990). Very small but present in Rhysodidae (coded as 0).

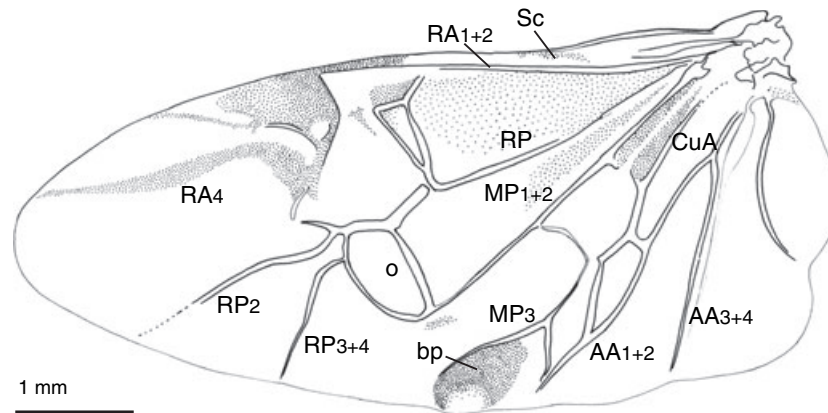


Fig. 11. Hind wing, *Aspidytes niobe*. Abbreviations: AA_(1+2, 3+4)—anal anterior, bp—binding patch, MP₁₊₂—Media posterior, RA_(1+2, 3, 3+4, 4)—radius anterior, RP_(2, 3+4), Sc—subcosta.

63. Subcubital setal binding patch: (0) absent; (1) present. Present in *Trachypachus* (not in *Systolosoma*; Beutel, 1994a), *Aspidytes* (Fig. 11), Noteridae, *Amphizoa* and Dytiscidae. Absent in alate specimens of *Meru* and in *Hygrobia* (Beutel, 1986a).

64. Position of RP3+4 (M_4 sensu Ward, 1979): (0) anterior to the middle of the oblongum cell; (1) at or posterior to the middle of the oblongum cell (Ward, 1979). Anterior in Hydradephaga (Ward, 1979; Kukulova-Peck and Lawrence, 1993, 2004) incl. *Aspidytes* (Fig. 11). Coded as inapplicable for *Meru* (oblongum absent; Spangler and Steiner, 2005).

65. Width of metacoxa: (0) distinctly broader than metaventricle; (1) not distinctly broader than metaventricle. Distinctly broader than metaventricle in Archostemata, Trachypachidae, and Hydradephaga (e.g., Beutel, 1992a) incl. *Meru* (as broad as metaventricle + fused pleural parts, reaching elytra laterally; Fig. 7).

66. Mesal walls of metacoxa: (0) free; (1) connected, contact area small; (2) connected along ventral edge; (3) connected, contact area extensive, intercoxal septum. Extensive intercoxal septum present in *Meru* (Fig. 7; Spangler and Steiner, 2005, fig. 10) and Dytiscoidea (Beutel, 1995). Attachment area small in *Trachypachus* (Fig. 8A). Only ventral edges connected in Gyrininae (not in *Spanglerogyrus*; Beutel, 1990).

67. Anterior margin of the metacoxa: (0) almost straight or slightly rounded anterolaterally; (1) with distinct angle; (2) rounded, strongly extended anteriorly; (3) oblique, strongly extended anteriorly, lateral part of metaventricle strongly reduced. Metacoxae of Noterinae with distinct anteromesal angle (Fig. 8D; Beutel and Roughley, 1987, figs 1, 2). Strongly extended anteriorly in adults of Dytiscidae, Gyrinini, Orectochilini, and Phreatodytinae (Uéno, 1957). Anterior margin rounded in Dytiscidae, but oblique in the latter taxa (Uéno, 1957). Metacoxae slightly extended anteriorly in *Amphizoa* (Beutel, 1988) and *Hygrobia* (Beutel, 1986a), with nearly straight or very slightly rounded anterior margin as in adults of

Trachypachidae and Carabidae. Very indistinct angle recognizable in *Aspidytes niobe* (Fig. 8B) but absent in *Aspidytes wrasei* (Balke et al., 2003, fig. 3) (coded as 0). Not applicable for *Meru* (anterior margin not recognizable; Fig. 7; Spangler and Steiner, 2005).

68. Metacoxal plates: (0) absent; (1) moderately sized; (2) mesal part of coxa prominent, but duplicature largely or completely reduced; (3) large. Absent in many non-adephagan beetles (e.g., Archostemata, Hydraenidae) and in Gyrinidae (incl. †*Triadogyrus*; Beutel and Roughley, 1988; Ponomarenko, 1977). Mesal part of coxa prominent in *Meru* (Fig. 7), *Hygrobia* (Beutel, 1986a) and Dytiscidae (and †Charonoscapinae; Ponomarenko, 1977), but without distinct duplicature. Very large in Haliplidae (and †Triaplidae; Ponomarenko, 1977), where they cover about half of the hindtibia and reach the epipleuron laterally to form a reservoir for air (Beier, 1929). Moderately sized in *Aspidytes* (Fig. 8B) and most other groups of Adephaga (Fig. 8A, C, D) where they cover parts of the trochanter and a small part of the metafemoral base.

69. Group of setae at posterolateral margin of metacoxal plates: (0) absent; (1) present (Belkaceme, 1991). Present in *Mesonoterus*, *Renotus*, *Siolius*, *Suphis*, *Hydrocanthus* (Fig. 9B), *Canthydrus* and *Suphisellus*.

70. Lateral margin of metacoxal plates: (0) reaching anterior margin of coxa at lateral edge; (1) slightly diverging anteriorly; (3) converging anteriorly, attaining anterior coxal margin; (3) very indistinct anteriorly. Lateral margin of metacoxal plates reaching anterior coxal margin at its lateral edge in adults of Haliplidae, Trachypachidae (Fig. 8A) and Carabidae. Slightly diverging in *Aspidytes* (Fig. 8B), *Phreatodytes*, *Amphizoa* (Beutel, 1988) and *Hygrobia* (Beutel, 1986a). Noterinae with clearly delimited lamina interna with anteriorly converging external margin (Fig. 8C, D). Very indistinct anteriorly in Dytiscidae. Not applicable for *Meru* (Fig. 7: lateral margin not recognizable; Spangler and Steiner, 2005).

71. Hind legs: (0) unmodified walking leg or, if modified for swimming not strongly shortened; (1) strongly shortened, broad and paddle-like. Short and paddle-like in Gyrininae (Hatch, 1927; Larsén, 1966; Beutel, 1990), but not in *Spanglerogyrus* (Fig. 10).

72. Swimming hairs of metatibiae: (0) absent; (1) present, sparse fringe; (2) present, dense fringe; (3) lamellae; (4) fimbriate. Unmodified hairs present in Haliplidae, Noteridae (sparse in *Notomicrus*, coded as 1), *Amphizoa* (sparse, coded as 1), *Hygrobia* (Beutel, 1986a), Dytiscidae (with few exceptions), and *Cicindis* (pers. obs. Steiner). Hind tibiae with fimbriate hairs in *Spanglerogyrus* (Fig. 10) and with lamellae in Gyrininae (Larsén, 1966; Beutel, 1990).

73. Distal tarsomeres of paddle-like hind legs: (0) not at right angle to proximal tarsomeres; (1) at right angle to proximal tarsomeres (Beutel, 1990). At right angle to proximal tarsomeres in Enhydrini (excl. *Enhydrus*) and Orectochilini.

74. Mm. furca-coxalis anterior: (0) present; (1) absent. Absent in *Meru*, *Aspidytes*, Dytiscoidea, and Gyrininae (Larsén, 1966; Beutel, 1990). Present in *Spanglerogyrus* (Beutel, 1990), Haliplidae (Belkaceme, 1986) and Geadephaga (Larsén, 1966; Beutel, 1992a).

75. Mm. furca-coxalis posterior: (0) present; (1) absent. Absent in *Meru*, *Aspidytes*, Dytiscoidea, and *Orectochilus* (Larsén, 1966; Baehr, 1975; Beutel, 1990; Beutel and Haas, 2000).

76. M. noto-trochanteralis: (0) present; (1) absent. Present in Gyrininae and *Priacma* (Larsén, 1966; Beutel and Roughley, 1988; Baehr, 1975).

77. Median piece of abdominal segment II: (0) absent; (1) present. Present in Rhysodidae, *Gehringia* and *Metrius*.

78. Abdominal sternites III and IV: (0) clearly separated; (1) largely or completely fused. Separating lines between abdominal sternites III and IV extremely indistinct or absent in *Meru* and Noteridae (Figs 7 and 9B; Uéno, 1957; Belkaceme, 1991, figs 63, 65–69). Present in *Aspidytes* (Ribera et al. 2002a; Balke et al., 2003, figs 2, 3) and other groups of Adepaga.

79. Sternal bulges of abdominal segments V–VII. (0) present; (1) absent (Beutel and Ruhnau, 1990). Present in Haliplidae (Fig. 12) excluding *Peltodytes* and *Brychius*.

80. Position of gonocoxosterna VIII: (0) not exposed; (1) exposed, sternite-like. Exposed in Gyrinidae (Beutel and Roughley, 1988; Burmeister, 1990).

81. Fusion of gonocoxosterna VIII: (0) absent; (1) present. Fused in Gyrininae.

82. Median row of setae on exposed gonocoxosterna VIII: (0) absent; (1) present. Present in Orectochilini (Larsén, 1966).

83. Subdivision of gonocoxa: (0) absent; (1) present (Bils, 1976). Usually subdivided in females of Geadephaga but undivided in *Metrius* (Bils, 1976), Trachypachidae, and Hydradephaga (Burmeister, 1976).

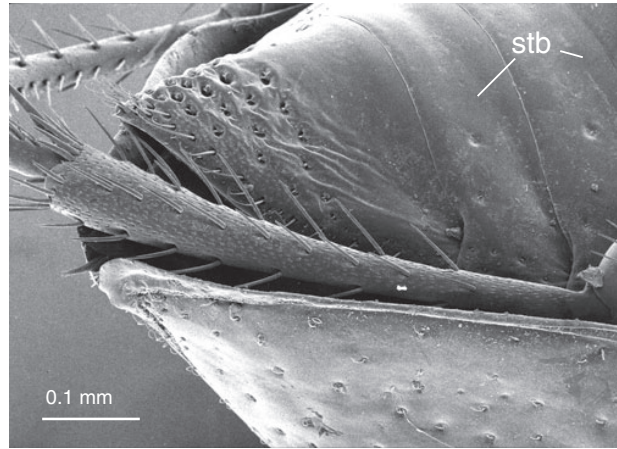


Fig. 12. *Apterallipus parvulus*, abdomen, lateral view. Abbreviations: stb—sternal bulges.

84. Laterotergite: (0) vertical orientation; (1) rod-like, cranial orientation; (2) rod-like, caudal orientation. Laterotergite IX (= tergal half IX in Burmeister, 1976) rod-like, with a caudal orientation and articulating with the cranial portion of the gonocoxa in *Notomicrus*, *Aspidytes*, *Amphizoa*, *Hygrobia*, and Dytiscidae. Rod-like and cranially oriented in Gyrinidae, Haliplidae and Noteridae (major part, e.g., *Hydrocanthus*) (Burmeister, 1976). Usually more or less vertically oriented in Geadephaga and not shaped as a more or less straight rod as in Hydradephaga (Bils, 1976, e.g., *Trachypachus*: fig. 6, *Cicindela*: fig. 4, *Omophron*: fig. 27, *Carabus*: fig. 27).

85. Torsion of aedeagus: (0) absent; (1) present (Beutel and Roughley, 1988). Torsion absent in Gyrinidae and most non-adephagan beetles. Less distinct in *Meru* (Spangler and Steiner, 2005) as compared to other groups of Adepaga (coded as 1).

86. Symmetry of parameres: (0) symmetric or only slightly asymmetric; (1) strongly asymmetric, left paramere shortened, triangular or “conchoid”. Slightly asymmetric in *Peltodytes* (Franciscolo, 1979) and many carabids (e.g., *Gehringia*, *Omophron*, *Carabus*) (Jeannel, 1941–42). Strongly asymmetrical with shortened triangular left paramere in the remaining Haliplidae, Rhysodidae (“conchoid type”), *Metrius*, Harpalinae, Brachininae (Jeannel, 1941–42; Deuve, 1988), and Lacophilinae (not included here).

87. Shape of distal part of parameres: (0) not abruptly narrowed; (1) abruptly narrowed. Abruptly narrowed with distinct incision in Trachypachidae. Strongly but not abruptly narrowed apically in *Aspidytes* (Balke et al., 2003) (coded as 0).

88. Digitus of parameres: (0) absent; (1) on left paramere; (2) on both parameres. Present on left paramere in *Algophilus*, *Apterallipus*, and the subgenera *Paraliaphlus* (partim) and *Liaphlus* (*Haliphus*) (Beutel

and Ruhnau, 1990), and on both parameres in *Liopterus* (Franciscolo, 1979).

89. Pygidial defensive glands: (0) absent; (1) present. Pygidial defensive glands are present in *Meru* (distinct on microtome sections) and all other groups of Adephaga (Forsyth, 1968, 1969).

Larvae

90. Egg bursters: (0) absent; (1) present. Absent in larvae of Gyrinidae, Noteridae (*Noterus* examined), Haliplidae, and *Brachinus* (Erwin, 1967; Ruhnau, 1985; Arndt, 1993; Beutel, 1993). Present in *Aspidytes niobe*, Hygrobiidae, Dytiscidae, and larvae of most groups of Carabidae (Arndt, 1993).

91. Orientation of head: (0) subprognathous; (1) prognathous; (2) hyperprognathous. Prognathous in almost all known larvae of Adephaga. Hyperprognathous in larvae of Cicindelinae and Paussinae.

92. Lateral tubercles of head capsule: (0) absent; (1) present. Conspicuous tubercles with apical setae are present posterior to the stemmata region in larvae of *Brychius* and *Haliphus* (Jaboulet, 1960, figs 6, 7, 9; Beutel, 1986b, 1997). Absent in *Peltodytes* (Jaboulet, 1960, fig. 8) and all other larvae examined.

93. Labrum: (0) free; (1) fused. Fused in all known adephagan larvae (Fig. 8A; Beutel, 1992b–d, 1993).

94. Nasal teeth: (0) absent; (1) present. Nasal teeth present in most larvae of Gyrininae (4) (absent in Orectochilini; Beutel and Roughley, 1994), larvae of most groups of Carabidae (e.g., *Metrius*, *Carabus*, *Nebria*; Thompson, 1979; Arndt, 1993; absent in Cicindelinae and Brachininae; Thompson, 1979), and in larvae of Trachypachidae (6–8). Absent in Rhysodidae and Haliplidae, and almost always absent in Dytiscoidea (present in first instar larvae of *Hydrotrupes*; Beutel and Roughley, 1994). Nasale distinct but without teeth in larvae of *Aspidytes niobe* (Fig. 13A, B).

95. Sensorial setae or pegs of anterior clypeolabral margin of 3rd instar larvae: (0) 6 or less; (1) 24 or more arranged in a transverse row. Twenty-four pointed sensorial setae present in 3rd instar larvae of Amphizoidae (Ruhnau, 1986; Beutel, 1991a), and 24 or more (= lamellae clypeales; Bertrand, 1972) in 3rd instar larvae of Hygrobiidae (Alarie et al., 2004) and Dytiscidae (Bertrand, 1972; De Marzo, 1976a,b,c; Ruhnau, 1986; Alarie et al., 1998). Sensilla (probably six) located in nasal region in *Aspidytes niobe*, difficult to identify within dense field of spines, not arranged in a transverse row (Fig. 13B).

96. Frontal suture: (0) straight or evenly curved; (1) with indistinct indentation; (2) sinuate; (3) reduced. Distinctly sinuate in larvae of Rhysodidae, Carabidae (with some exceptions, e.g., *Brachinus*; Erwin, 1967), Noterinae (obsolete in *Phreatodytes*: coded as 3), and most larvae of Hydroporinae (Bertrand, 1972; Alarie, 1991; Beutel, 1993). With indistinct indentation in larvae

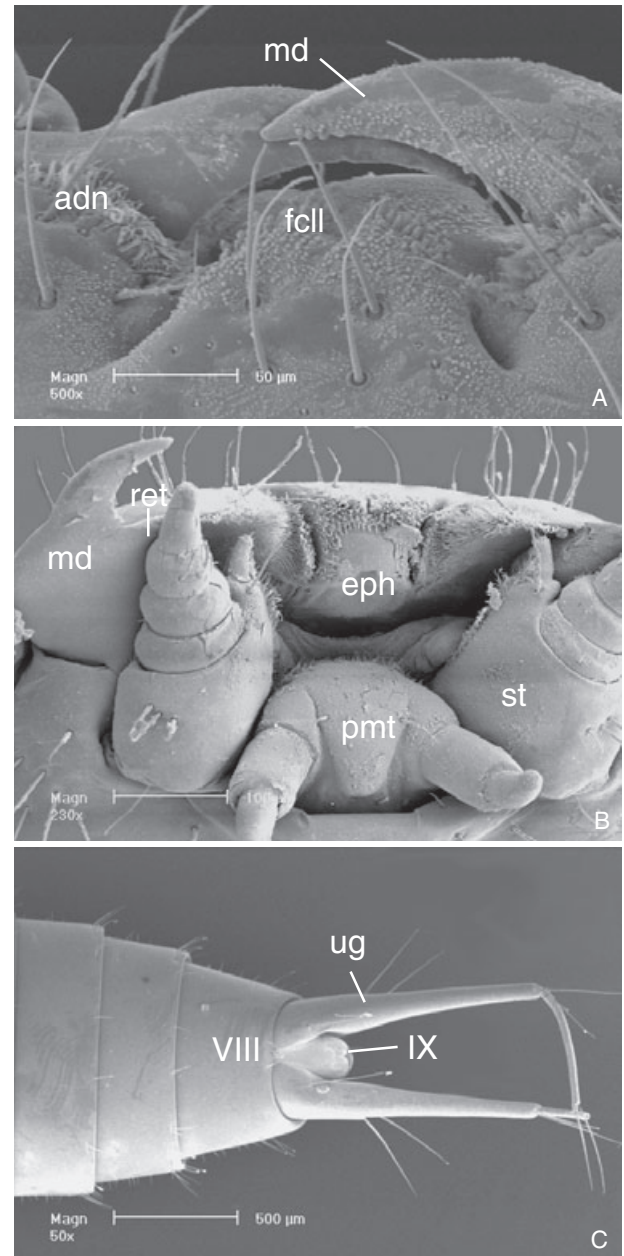


Fig. 13. Larva, *Aspidytes niobe* (SEM). (A) anterior head region, dorsal view; (B) epipharynx and mouthparts, frontal view; (C) Posterior abdomen. Abbreviations: adh—adnasalia, eph—epipharynx, fcll—frontoclypeolabrum, md—mandible, pmt—prementum, ret—retinaculum, st—stipes, ug—urogomphi, VIII, IX—abdominal segments VIII, IX.

of *Aspidytes niobe*. V- or U-shaped (*Liopterus*) and straight or evenly curved in larvae of Amphizoidae, Hygrobiidae, and Dytiscidae (Bertrand, 1972; Alarie, 1991; Alarie et al., 1998).

97. Cervical ridge (0) absent; (1) present (Beutel, 1993). Present in larvae of most genera of Caraboidea Limbata (e.g., Bembidiini, Pterostichini; Thompson, 1979; Arndt,

1993). Absent in larvae of Hydradephaga, Trachypachidae, Rhysodidae, basal groups of Carabidae (e.g., *Gehringia*, *Metrius*, *Carabus*, Cicindelinae), and in some tribes of “higher carabids” (e.g., Chlaeniini, Panagaeni, Brachiniinae, Pseudomorphini; Erwin, 1967; Thompson, 1979; Arndt, 1993).

98. Postocular ridge: (0) absent; (1) present (Beutel, 1993). Similar character state distribution as in Character 94. Vestigial or absent in Amarini (see Thompson, 1979; Arndt, 1993; Beutel, 1993).

99. Gula (0) not present as a sclerotized structure; (1) sclerotized, about as broad as long or broader; (2) not suture-like, less than half as broad as long; (3) narrow, suture-like; (4) sclerotized gular halves separated by semimembranous area. Strongly narrowed and suture-like in most adepghan larvae (e.g., Gyrininae, Trachypachidae, Carabidae [with few exceptions]). Moderately broad in larvae of Hygrobiidae, Amphizoidae and Dytiscidae (Beutel, 1991a; Alarie et al., 2004). As broad as long or broader in larvae of Haliplidae, Noteridae (condition in *Phreatodytes* unknown), *Aspidytes*, and some Carabidae (Arndt, 1993; Beutel, 1993). The gula is strongly modified in *Omoglymmius* (coded as 4) and apparently absent in *Clinidium* (Beutel, 1992b, figs 2 and 5).

100. Position of posterior tentorial grooves: (0) central region of ventral wall of head capsule; (1) posterior head region, at anterior margin of short gula or adjacent to foramen occipitale. Central region of head capsule in most adepghan larvae. Slightly shifted posteriorly in larvae of *Aspidytes niobe* (coded as 0), but adjacent with foramen occipitale in Noterinae (Bertrand, 1972; Ruhnau, 1985; Beutel, 1993; condition in *Phreatodytes* unknown), *Omoglymmius* (Beutel, 1992b), some groups of Carabidae (e.g., *Omophron*; Beutel, 1991b) and in many polyphagan larvae (e.g., Hydraenidae; Beutel and Molenda, 1997).

101. Caudal tentorial arm: (0) absent; (1) very short; (2) elongate and slender (Beutel, 1993); (3) thin arms dorsally attached to head capsule. Absent in most adepghan larvae. Short in larvae of *Trachypachus*, *Noterus* (Ruhnau, 1985; Beutel, 1993) and *Canthydrus*. Strongly elongated and slender and attached to the head capsule posteriorly in larvae of Amphizoidae (Beutel, 1991a, fig. 4), Hygrobiidae (Alarie et al., 2004), Dytiscidae (De Marzo, 1979; Ruhnau, 1986) and *Aspidytes niobe*. The somewhat extended base of the posterior tentorial arms in *Haliphus lineatocollis* (Beutel, 1986b) is different from the caudal tentorial arms (coded as 0). *Cicindela* (Breyer, 1989) with thin caudal arm dorsally attached to head capsule.

102. Shape of tentorial bridge: (0) straight; (1) U-shaped, posteriorly directed; (3) V-shaped anteriorly directed. Straight in most non-adephagan larvae (e.g., Leiodidae) and in larvae of Haliplidae (Jaboulet, 1960; Beutel, 1986b) and Rhysodidae (Beutel, 1992b). Usually

slender, U-shaped and posteriorly directed in geadephagan larvae (Beutel, 1992c,d, 1993). V-shaped and anteriorly directed in *Noterus* (Ruhnau, 1985) and *Hydrocanthus*.

103. Orientation of antennae: (0) anteriorly; (1) anterolaterally. Anteriorly directed with nearly parallel orientation in larvae of Carabidae and Rhysodidae (e.g., Thompson, 1979; Bell, 1991, fig. 34.71; Beutel, 1992b, 1993).

104. Shape of antennomeres 2–4: (0) less than 5 times as long as wide; (1) at least 7 times as long as wide. Extremely slender and elongate antennomeres 2–4 and palpomeres (not coded as separate characters) are characteristic for larvae of Enhydrini and Orectochilini (Beutel and Roughley, 1994).

105. Sensorial appendage: (0) present, distinctly convex; (1) absent; (2) present as a flattened sensorial field. Absent in larvae of Noteridae and Gyrininae (Beutel and Roughley, 1994). Present as a flattened sensorial field in larvae of Trachypachidae (coded as 2; Arndt and Beutel, 1995).

106. Three long apical antennal setae: (0) present; (1) absent. Present in Geadephaga (Vanin and Costa, 1978; Arndt, 1993; Arndt and Beutel, 1995) but absent in Hydradephaga incl. *Aspidytes niobe* (pers. obs. Beutel; Ruhnau, 1986).

107. Mola: (0) present; (1) absent. Absent in all adepghan larvae (Beutel, 1995).

108. Penicillus: (0) present; (1) absent. Present in larvae of anisochaetous carabids with the exception of *Omophron* and some other taxa (e.g., Bembidiini partim [coded as 1], Brachiniinae) (Arndt et al., 2005).

109. Retinaculum: (0) present; (1) vestigial or absent (Alarie and Bilton, 2005). Present in most larvae of Adepghaga (Fig. 13B), but absent in larvae of Orectochilini and Enhydrini (Beutel and Roughley, 1994), in some larvae of Noteridae (e.g., *Suphis*, *Hydrocanthus*, *Canthydrus*; Spangler, 1991), and in larvae of Dytiscidae and Hygrobiidae. Very small or vestigial in larvae of Haliplidae and Amphizoidae, but still recognizable (Alarie and Bilton, 2005) (coded as 1). Absent in Cupedidae (Beutel and Hörschemeyer, 2002a,b). Usually present in Leiodidae (Paulian, 1941, fig. 189; Newton, 1991, figs 34.147–34.149 and 34.151).

110. Mesal mandibular edge in mature larvae: (0) without distinct cutting edge; (1) one cutting edge; (2) two cutting edges delimiting a mesal groove; (3) mandibular sucking channel. With one mesal edge in mature larvae of Carabidae and Hygrobiidae (Ruhnau, 1986). An upper and a lower cutting edge is present in larvae of Trachypachidae (Arndt and Beutel, 1995), *Noterus* (Ruhnau, 1985; pers. obs. Beutel), *Amphizoa* (Beutel, 1991a, fig. 6) and *Aspidytes niobe*. Mandibular sucking channels are present in larvae of Gyrininae, Haliplidae, *Hydrocanthus* and *Canthydrus* (Ruhnau, 1986). The second cutting edge is usually absent in non-adephagan larvae.

111. Adductor tendon: (0) undivided; (1) divided into an upper and lower portion. Divided into an upper and a lower portion in larvae of Amphizoidae (Beutel, 1991a, fig. 6a), Hygrobiidae (Alarie et al., 2004), Dytiscidae (Ruhnau, 1986) and *Aspidytes niobe*. Upper and lower branch separated a strong lateral component of *M. verticopharyngalis* in Hygrobiidae and Dytiscidae.

112. Maxillary articulation: (0) retracted in deep maxillary group with exposed articulatory membrane; (1) slightly retracted, distinct oblique maxillary groove present; (2) slightly retracted, maxillary groove largely reduced, mesal maxillary base distinctly posterior to submento-mental border; (3) maxilla and labium form a retracted maxillolabial complex; (4) maxilla articulates at anterior margin of ventral wall of head capsule. Deep in larvae of Archostemata (Beutel and Hörnschemeyer, 2002a,b) and in many larvae of Polyphaga (e.g., Leiodidae; Beutel and Molenda, 1997). Slightly retracted in larvae of Gyrinidae and Haliplidae. Distinct oblique maxillary groove present in Gyrinidae (Beutel, 1993, fig. 6; Beutel and Roughley, 1994). Largely reduced in Haliplidae, but mesal base of maxilla distinctly posterior to submento-mental border (Jaboulet, 1960, figs 7 and 6; Beutel, 1993, fig. 7) (coded as 2). Maxilla and labium form a distinctly retracted complex in larvae of Rhysodidae (Beutel, 1992b, figs 2 and 5). Maxilla articulates at anterior margin of ventral wall of head capsule in other groups of Adephaga (Beutel, 1993, figs 8–10). The maxilla of gyrid and haliplid larvae is largely restricted to lateral movements, whereas movements in all directions are possible in the groups with the anterior articulation.

113. Exposure of maxillary base: (0) not covered by anterior margin of head capsule and mentum; (1) retracted, covered by anterior margin of head capsule and mentum. Maxillary base moderately retracted in larvae of Amphizoidae (Beutel, 1991a, fig. 2) and inserted into a deep pouch in larvae of Hygrobiidae (Alarie et al., 2004).

114. Intramaxillary moveability: (0) fully retained; (1) absent. The intramaxillary movability is fully retained in larvae of Archostemata, in many larvae of Polyphaga (e.g., Hydraenidae; Beutel and Molenda, 1997) and in larvae of Gyrinidae. It is largely reduced or absent in other adephagan larvae.

115. Width of cardo: (0) as broad as stipital base; (1) distinctly narrower than stipital base. About half as broad as stipes in larvae of Noteridae (Beutel, 1993, fig. 9), Amphizoidae (Beutel, 1991a, fig. 2), Dytiscidae (Bertrand, 1972) and *Aspidytes niobe* (scarcely visible due to vertical position of cardo; Fig. 13B). Absent or completely fused with stipes in larvae of Hygrobiidae (Alarie et al., 2004).

116. Subdivision of cardo into lateral and mesal sclerite: (0) absent; (1) present. Cardo represented by a mesal and

a lateral sclerite in most larvae of Carabidae (Beutel, 1992b,c,d, 1993, fig. 10). Apparently not subdivided in primary larvae of *Brachinus* (Erwin, 1967, fig. 2).

117. Lacinia: (0) present; (1) absent. Absent in larvae of Trachypachidae and Dytiscoidea (Fig. 13B), and in larvae of some groups of Carabidae (e.g., Brachininae; Erwin, 1967).

118. Shape of lacinia: (0) large, hook-shaped, broadly fused with stipes; (1) hook-shaped process of mesodistal stipital edge, not articulated; (2) hook-shaped, articulated; (3) small, peg-like; (4) strongly reduced and fused with stipes; (5) membranous. Large and hook-shaped in *Metrius*, *Omophron* and Gyrinidae (e.g., Beutel, 1991a,b, 1992c, 1993; Arndt, 1993). Articulated and moveable in the latter group. Peg-like in many carabid larvae (e.g., *Carabus*, *Pterostichus*; Thompson, 1979; Arndt, 1993). Absent in larvae of other carabid groups such as, e.g., Bembidiini or Brachininae (Thompson, 1979). Strongly reduced and fused with stipes in Haliplidae (with specialized sensilla in *Haliplus*; Jaboulet, 1960, figs 13 and 14) and strongly modified and unsclerotized in Rhysodidae (Beutel, 1992b).

119. Subdivision of galea: (0) 1-segmented; (1) 2-segmented. Usually 2-segmented in adephagan larvae but 1-segmented in larvae of Haliplidae (Jaboulet, 1960; Beutel, 1997). Composed of two segments in cupedid larvae (Beutel and Hörnschemeyer, 2002b). One-segmented in larvae of Leiodidae (Beutel and Molenda, 1997).

120. Shape of galea: (0) rounded and densely set with hairs; (1) slender, apically fimbriate; (2) palp-like, hairs largely or completely absent. Palp-like in all adephagan larvae with the exception of Haliplidae. More or less short, rounded and densely set with hairs in haliplid larvae and in larvae of Cupedidae (Beutel and Hörnschemeyer, 2002b). Slender and apically fimbriate in larvae of Leiodidae (Beutel and Molenda, 1997).

121. Stipitopalpal muscles: (0) two; (1) one. Usually one stipitopalpal muscle in Adephaga, but two antagonistic muscles present in larvae of Gyrinidae (Noars, 1956; Beutel, 1993).

122. Origin of *M. craniolacinalis*: (0) laterally on head capsule; (1) ventrally on head capsule between *M. craniocardinalis* and *Mm. tentoriocardinalis* and -stipitalis (= *M. craniostipitalis medialis sensu* Beutel, 1993). From lateral wall of head capsule in most non-adephagan larvae and in larvae of Gyrinidae and Haliplidae (Beutel, 1986b, 1993). Between *M. craniocardinalis* and *Mm. tentoriocardinalis* and -stipitalis in Dytiscoidea and Geadephaga (Beutel, 1993).

123. Insertion of *M. craniolacinalis*: (0) base of lacinia; (1) dorsal side of stipes. Dorsally on stipital base in most adephagan larvae, but on base of lacinia in larvae of Gyrinidae (Beutel, 1993, fig. 12) and most non-adephagan larvae. The cranial component of the

“adducteur du stipes” described by Noars (1956) is in fact a muscle of the lacinia. The very thin tendon attached to the lacinia was apparently overlooked.

124. Prementum: (0) undivided; (1) with distinct antero-medial incision; (2) completely divided longitudinally. With deep anteromedian incision in the known larvae of Noteridae (Uéno, 1957; Spangler, 1991; Dettner, 2005). Completely divided in larvae of Gyrininae (Noars, 1956; Beutel and Roughley, 1994).

125. Ligula: (0) distinctly developed as a median ligular node (Thompson, 1979); (1) not present as a well defined ligular node. Absent or fused with prementum in larvae of Hydradephaga (incl. *Aspidytes*: Fig. 13B), Trachypachidae (Beutel, 1993), Rhysodidae (Beutel, 1992b), *Gehringia* and *Brachinus* (Lindroth, 1960; Thompson, 1979; Beutel, 1993) (coded as inapplicable for Gyrinidae). Broad and setose in Cicindelinae (Thompson, 1979; coded as 1).

126. Prehypopharyngeal filter apparatus formed by long hairs: (0) absent; (1) present. Present in carabid larvae (Tröster, 1987, fig. 15; Beutel, 1992c,d, 1993). Absent in Rhysodidae (Beutel, 1992b), Trachypachidae (Beutel, 1993) and the aquatic groups (Fig. 13B).

127. Prepharyngeal filter apparatus formed by lamellae: (0) absent; (1) present (Beutel and Roughley, 1994). Present in larvae of Enhydrini (*Enhydrus?*) and Orectochilini (not verified for *Gyretes* and *Orectogyrus*).

128. M. tentoriohypopharyngalis medialis: (0) present, with origin from tentorial bridge; (1) absent (Beutel, 1993). Present in most hydradephagan larvae (absent or with atypical origin in Gyrinidae, coded as 1; Noars, 1956; Beutel, 1993), in larvae of *Trachypachus*, *Omo-glymmius* (Beutel, 1992c), *Metrius* and *Carabus* (Beutel, 1992d). Absent in *Cicindela* (Breyer (1989), and most other carabid larvae examined.

129. M. tentoriohypopharyngalis: (0) moderately sized or absent; (1) very strong, several bundles. Very strongly developed and composed of several bundles in larvae of Haliplidae (Beutel, 1986b), and all dytiscoid larvae examined (e.g., Beutel, 1993) including *A. niobe*.

130. M. verticopharyngalis: (0) present; (1) absent. Absent in larvae of Archostemata (Beutel and Hörnschemeyer, 2002a,b), Rhysodidae, Gyrinidae (partim; present in *Dineutus*), Haliplidae, Noteridae (examined in *Noterus* and *Canthydrus*; R.G. Beutel, pers. obs.) (Beutel, 1986b, 1993), and in many larvae of Carabidae (e.g., *Nebria*, *Pterostichus*, *Licinus*, *Panagaeus*; Tröster, 1987; Beutel, 1992b,c, 1993). Present in larvae of *Metrius*, *Cicindela* (Breyer (1989), *Omophron*, *Carabus*, *Trachypachus* and most hydradephagan larvae (strongly developed in Dytiscoidea excl. Noteridae) (Beutel, 1992c,d, 1993).

131. Position of cerebrum: (0) posterior part of head; (1) anterior part of head. Strongly shifted anteriorly in larvae of Dytiscidae (De Marzo, 1979) and *Hygrobia* (Alarie et al., 2004).

132. Clasp apparatus of prolegs: (0) absent (1) formed by claw and femur; (2) formed by claw and tibia. Formed by claw and tibia in *Haliplus* (partim: *Haliplinus*, *Neohaliplus*; Jaboulet, 1960; Seeger, 1971b) and *Peltodytes*, but by claw and femur in *Brychius* (Jaboulet, 1960).

133. Trochanteral annulus: (0) absent; (1) present (Alarie and Bilton, 2005). Present in larvae of Hygrobiidae and Dytiscidae.

134. Primary setae FE7-FE10: (0) absent; (1) present (Alarie and Bilton, 2005). Present in larvae of *A. niobe*, Hygrobiidae, Amphizoidae and Dytiscidae, but absent in larvae of the other groups of Adepaga.

135. Additional pore on tibia: (0) absent; (1) present (Alarie and Bilton, 2005). Present in larvae of *A. niobe* and Amphizoidae. Absent in larvae of the other groups of Adepaga.

136. Segment IX: (0) well developed; (1) small but distinct; (2) vestigial or absent (Alarie and Bilton, 2005). Small but still distinctly visible in dorsal view in larvae of *A. niobe* (Fig. 13C). Vestigial or absent in larvae of the other groups of Dytiscoidea.

137. Segment X: (0) present; (1) absent. Absent in the known larvae of Dytiscoidea (including *A. niobe*; Fig. 13C) and in larvae of *Peltodytes* (Jaboulet, 1960).

138. Hooks of segment X (pygopodium): (0) absent; (1) present. Present in the known larvae of Gyrinidae (Noars, 1956).

139. Spiracle VIII: (0) normally developed; (1) enlarged, terminal; (2) reduced; (3) small, shifted to dorsal side of segment VIII. Enlarged in larvae of Amphizoidae and Dytiscidae. Reduced in larvae of *Hygrobia* and very small and shifted to the dorsal side of tergite VIII in *A. niobe*. Terminal and large in larvae of Noteridae, but non-functional in 3rd instar larvae (Spangler, 1991; coded as 1).

140. Large terminal tracheal trunks: (0) absent; (1) present. Present in larvae of Noteridae (examined in *Noterus* and *Canthydrus*), Amphizoa, Dytiscidae and *A. niobe*. Absent in Hygrobiidae and other groups of Adepaga.

141. Microtracheal gills: (0) absent; (1) present. Present in larvae of *Brychius* and *Haliplus* (Jaboulet, 1960; Seeger, 1971b).

142. Long lateral tracheal gills: (0) absent; (1) present. Present in larvae of Gyrininae and *Coptotomus* (Dytiscidae; Larson et al. 2000).

143. Collar-like semimembranous connections between segments: (0) present; (1) absent. Present in larvae of *Aspidytes niobe* and Noteridae (examined in *Noterus* and *Canthydrus*; pers. obs. Beutel; Dettner, 2005).

144. Urogomphi: (0) absent; (1) present, articulated; (2) present, fixed. Generally present in Adepaga (Fig. 13C), but absent in Gyrinidae (possibly transformed into gills, coded as 0), Haliplidae (excl.

Peltodytes; Jaboulet, 1960), Rhysodidae, *Systolosoma* (partim; Arndt and Beutel, 1995), and few Carabidae (e.g., Cicindelinae). Articulated in Dytiscoidea (extremely short in Noteridae) and few larvae of Carabidae (e.g., *Metrius* [antler-shaped], *Nebria*, *Loricera*). Fixed in larvae of Trachypachidae (if present), *Gehringia*, *Omophon*, Carabini, Bembidiini, *Licinus*, *Brachinus*, and many other carabid subgroups (Thompson, 1979; Arndt, 1993). Articulation also absent in *Peltodytes* (Jaboulet, 1960).

145. Length of articulated urogomphi: (0) elongate, not shorter than abdominal segment I; (1) strongly shortened, shorter than segment I. Strongly shortened urogomphi are characteristic for Noteridae (Uéno, 1957; Spangler, 1991; Dettner, 2005). Moderately long in larvae of *Amphizoa*. Long and 2-segmented in *Aspidytes niobe* (Fig. 13C), and also elongated in *Hygrobia* (Alarie et al., 2004) and many dytiscid larvae (Bertrand, 1972).

146. Postanal prolongation (segment X) with paired process: (0) absent; (1) present. Present in *Brychius* and *Haliphus* (Jaboulet, 1960).

Pupae

147. Urogomphi: (0) present; (1) absent. Absent in Gyrinidae, Haliplidae, *Noterus*, Rhysodidae and Cicindelinae, but usually present in Dytiscoidea and Carabidae (Erwin, 1967; Ruhnau, 1986).

Eggs

148. Chorion: (0) distinctly developed, ribbed or honey-combed; (1) very thin (Beutel and Roughley, 1987). Distinctly developed in larvae of Archostemata and Gyrinidae (*Gyrinus*, *Dineutus*; Hinton, 1981), but strongly reduced in other groups (e.g., *Peltodytes*, *Haliphus*, *Noterus*, *Hygrobia*, *Agabus*, *Dytiscus*, *Cicindela*, *Carabus*, *Pterostichus*, *Brachinus*; Hinton, 1981; Dettner, 2005; [only taxa explicitly mentioned in these studies are coded]) and in Leiodidae (“smooth”; Newton, 2005).

Presumptive autapomorphies of *Meru* (unique within Adephaga unless otherwise noted, not included in the analysis):

149. Massive laminentorium. Laminentoria do also occur in *Spanglerogyrus* (Beutel, 1998) and some carabids (e.g., *Carabus*), but less strongly developed than in *Meru*.

150. Dorsal tentorial arms absent. Also absent in Gyrinidae (Hatch, 1927; Beutel, 1989a), likely due to convergence.

151. Tibial spurs tridentate (Spangler and Steiner, 2005).

152. Mesepimeron fused with mesanepisternum and metanepisternum (Spangler and Steiner, 2005).

153. Metepimeron fused with metaventrite (Spangler and Steiner, 2005).

154. Flat, wrinkled setae on posterior margin of abdominal sternites (Spangler and Steiner, 2005).

Characters not included in the analysis

—Sensorial fields on flagellomeres

Sensorial structures are present on flagellomeres of *Meru* (Spangler and Steiner, 2005, fig. 4D) *Noterus* (Belkaceme, 1991, fig. 5) and *Aspidytes* (Fig. 13). They are absent from several representatives of Noteridae examined (pers. obs. Balke). The variation of sensorial structures on the flagellomeres in the taxa included in this study causes uncertainties establishing primary homology.

—Shape of the mandibles

This character is highly variable and dependent on the habitat and preferred food source. Hydradephaga have shorter mandibles (Fig. 4A), sometimes without or with poorly developed setal brushes (e.g., Franciscolo, 1979; Beutel, 1986b, 1989a; Acorn and Ball, 1991, fig. 4E–G). The mandible of *Trachypachus* appears intermediate, whereas longer mandibles with well developed brushes are characteristic for Carabidae (Acorn and Ball, 1991). An evolutionary scenario for mandibular forms was outlined by Acorn and Ball (1991) (with the mandible of *Priacma* as hypothesized ancestral condition).

—Emarginate labrum with a fringe of flattened, blunt to tapered setae directed anteromedially (Spangler and Steiner, 2005, fig. 4D).

A similar condition, i.e., an emarginate labrum, is not only found in *Meru* and Haliplidae, but also in other groups of Adephaga such as *Spanglerogyrus* (Fig. 3A; Beutel, 1989a) and *Trachypachus* (Fig. 3C). An emarginate labrum is likely part of the adephagan ground plan, but many gradual modifications occur within the suborder.

—Group of spatulate setae on anterior prosternal margin

It was pointed out by Spangler and Steiner (2005) that this character may indicate affinities between Meruidae and Noteridae. However, as the character is very variable within the latter group (Belkaceme, 1991, figs 63–69), we excluded it from the analysis.

—Metatibial spurs

The presence of serrate metatibial spurs was considered as a potential synapomorphy of Meruidae and Noteridae or of a clade, which includes these families and also Haliplidae. The serration is absent in the haliplid genera *Peltodytes* and *Brychius*, in *Haliphus* excl. *Liaphlus* (Beutel and Ruhnau, 1990), and also in most representatives of Noteridae we examined (e.g., *Notomicrus*, *Noterus*, *Mesonoterus*, *Synchortus*, *Renotus*, *Suphisellus*). Besides this, the tibial spurs of *Meru* are highly specialized and differ strongly from those of other adephagans.

Results

We found 21 equally parsimonious trees of 347 steps (CI: 0.60; RI: 0.89), 145 characters were parsimony informative. One of these trees is shown in Fig. 15, with characters mapped onto the tree and the strict consensus tree is depicted in Fig. 16. The analysis of all characters coded as nonadditive revealed seven trees of 345 steps (CI: 0.60; RI: 0.89), the strict consensus of which is in general agreement with Fig. 16, except for minor differences within Noteridae: *Mesonoterus* and *Synchortus* were sister taxa and basal to (*Noterus* (*Suphis* (*Siolius* (*Renotus* (*Suphisellus* + *Hydrocanthus* + *Canthydrus*))))).

Apomorphies of major clades (only unambiguous changes, non-homoplastic changes in bold; L = larva):

Adephaga (BSV [= branch support value] 6): **15.1.** lateral lobes of mentum rounded; **23.1.** internal posterior procoxal bridge present; **89.1.** pygidial defence glands present; **93.1.** larval labrum fused; **100.1.** larval posterior tentorial grooves positioned on posterior head region, at anterior margin of short gula or adjacent to foramen occipitale; **107.1.** larval mola absent. Possession of these characters unambiguously places *Meru* in the Adephaga where it is part of Dytiscoidea (justification: see below).

Adephaga excluding Gyrinidae (BSV 3): 40.1. mesoventrite short, with hexagonal groove and anterolateral grooves for reception of the procoxae; **47.1.** mesocoxae globular, restricted to rotatory movements; **85.1.** torsion of aedeagus; **114.1.** intramaxillary moveability reduced in larvae (L); **121.1.** maxilla with only one stipitopalpal muscle (L); **123.1.** M. craniolacinalis attached to stipital base (L).

Gyrinidae (BSV 4): 2.1. head shortened and laterally rounded; **3.1.** compound eyes divided; **8.5.** scapus strongly enlarged, cup-shaped; **9.2.** pedicellus ear-shaped, with fringe of sensory hairs; **25.1.** prothoracic proprioceptive organ; 30.1. external protibial spur absent; **46.1.** elytral apex truncate; **80.1.** gonocoxosternites VIII exposed. No larval apomorphies (character states unknown for *Spanglerogyrus*).

Gyrininae (BSV 15): **3.2.** compound eyes widely separated; **5.1.** three rows of labral setae; **15.2.** lateral lobes of mentum enlarged; **16.1.** palpiger fused with prementum; **25.2.** prothoracic proprioceptive organ with spatulate setae; 33.1. internal protibial spur absent; **38.1.** excavations for prolegs present; 39.2. opening between anepisternum and elytron present; 41.1. discrimin of mesoventrite present; **51.1.** middle legs short and paddle-like; 57.2. transverse ridge of metaventricle absent; **59.1.** metapostnotum inflected below scutellum; 62.1. lateral arms of metafurca absent; **66.2.** mesal metacoxal walls ventrally fused; **71.1.** hind legs short and paddle-like; 74.1. M. furca coxalis absent; **81.1.**

gonocoxosternites VIII fused. No larval apomorphies (character states unknown for *Spanglerogyrus*).

Gyrinus + *Aulonogyrus* (Gyrinini [*Metagyrimus* and *Heterogyrus* not included in analysis]) (BSV 1): 67.3. anterior margin of metacoxae oblique, strongly extended anterolaterally (also in *Orectochilini*).

Enhydrini (*Enhydrus*, *Dineutus* + *Macrogyrus* + *Andogyrus* included in analysis) + *Orectochilini* (BSV 2): **53.1.** anterior and posterior wall of middle and hind femora connected by cuticular columnae; **55.1.** metanotum strongly narrowed medially. No larval apomorphies (unknown for *Enhydrus*).

Dineutus + *Macrogyrus* + *Andogyrus* + *Orectochilini* (BSV 1): **73.1.** Distal tarsomeres of paddle-like hind legs at right angle to proximal tarsomeres. No larval apomorphies (unknown for *Enhydrus*).

Macrogyrus + *Andogyrus* + *Orectochilini* (BSV 1): **52.1.** tarsomeres 4 and 5 of paddle-like middle legs at right angle to proximal tarsomeres.

Orectochilini (BSV 4): 19.1. field of setae on lateral part of pronotum and elytra (also in *Spanglerogyrus*); 67.3. anterior margin of metacoxae oblique, strongly extended anterolaterally (also in Gyrinini). 74.1. M. furcacoxalis posterior absent; **82.1.** median row of setae on fused gonocoxosterna VIII; 94.1. nasal teeth absent (L).

Orectochilus + *Orectogyrus* (BSV 1): **48.1.** mesocoxae fused with mesoventrite; **49.1.** lateral process of mesocoxa fused with anepisternum.

Haliplidae + Dytiscoidea (BSV 0): **58.1.** contact between pro- and metasternal process present; 94.1. nasal teeth absent (L); **99.1.** gula sclerotized and broad (L); **129.1.** M. tentoriopharyngalis strongly developed, composed of several bundles (L).

[alternative hypothesis: Adephaga excl. Gyrinidae and Haliplidae: **110.2.** maxillary groove absent (L); **122.1.** mesal origin of M. craniolacinalis (L).]

Haliplidae (BSV 6): **8.4.** scapus strongly shortened, cylindrical; 20.3. prosternal process broadened and apically truncate; 54.2. middle legs with dense rows of swimming hairs; **68.3.** metacoxal plates strongly enlarged; 72.2. hind legs with dense rows of swimming hairs; **112.2.** maxillary articulation slightly retracted, groove largely reduced (L).

Haliplidae excl. *Peltodytes* (BSV 5): 17.1. terminal labial palpomere subulate; 86.1. parameres strongly asymmetric; **141.1.** microtracheal gills (L); **146.1.** postanal prolongation (segment X) with paired process (L).

Haliplidae excl. *Peltodytes* and *Brychius* (BSV 1): **79.1.** sternal bulges of abdominal segments V–VII.

Liaphlus + *Algophilus* + *Apteraliplus* (BSV 2): **4.1.** secondary genal ridge; **88.1.** digitus of left paramere.

Geadephaga (BSV 1): 1.0. distinct pronto-elytral angle; **29.1.** protibial antenna cleaning device; 84.0. vertical orientation of laterotergite IX; 89.1. egg bursters present (L).

Trachypachidae (BSV 4): 57.1. transverse ridge of metaventrite partly reduced; **66.1.** mesal metacoxal walls fused, with small contact area; **87.1.** distal part of parameres abruptly narrowed; 101.1. short caudal tentorial arm (L); **105.2.** sensorial appendage of antennomere 3 present as a flattened sensorial field (L); 117.1. lacinia absent (L); 130.0. M. verticopharyngalis present (L) (?).

Rhysodidae + Carabidae (BSV 5): 13.1. dense pubescence of distal antennomeres (IV–XI); 20.4. prosternal process with apex reduced and laterally fused with hypomeral process (?); 21.1. external prothoracic postcoxal bridge present (?); 23.0. internal prothoracic postcoxal bridge absent; 40.2. mesoventrite with rounded, horizontal anterior part and steeply ascending posterior part (?); **44.1.** metepimeron parallel-sided, at right angle to longitudinal body axis; 65.1. metacoxae narrowed; 83.1. gonocoxae subdivided; 87.1. parameres strongly asymmetric; 96.2. frontal suture distinctly sinuate (L).

Carabidae (BSV 3): **103.1.** antennae anteriorly directed (L); **116.1.** cardo subdivided into mesal and lateral sclerite (L); 125.0. ligula distinctly developed (L) (?); **126.1.** hairy preoral filter (L); 144.2. fixed urogomphi (L) (?); 147.0. urogomphi present in pupae (?).

Dytiscoidea (including Aspidytidae and Meruidae) (BSV 8): **61.1.** origin of metafurca from intercoxal septum; **67.3.** extensive intercoxal septum; **70.1.** lateral margin of metacoxal plates slightly diverging anteriorly; 74.1. M. furcaxalis anterior absent; 75.1. M. furcaxalis posterior absent; **115.1.** cardo distinctly narrower than stipital base (L); 117.1. lacinia absent (L); 127.1. (anteriorly) M. tentoriopharyngalis strongly developed, composed of several bundles (L); **136.2.** segment IX vestigial or absent (L) (reversal in *Aspidytes?*); **140.1.** large terminal tracheal trunks (L); 144.1. urogomphi present, articulated (L) (?). All potential larval apomorphies are uncertain as larvae of *Meru* are unknown.

Meruidae + Noteridae (BSV 1): 10.1.–12.1. antennomeres 5, 7 and 9 enlarged; **78.1.** abdominal sternites III and IV fused; 86.1. parameres strongly asymmetric.

Noteridae (BSV 2): 2.1. head shortened and laterally rounded; 28.1. profemoral cleaning device.

Noterinae (BSV 2): **70.2.** lateral margins of metacoxal plates converging.

Noterinae excl. *Notomicrus* (BSV 2): **37.1.** curved spurs on ventral sides of protarsomeres 1–3; **56.1.** noterid platform of metaventrite.

Noterinae excl. *Notomicrus* and *Hydrocoptus* (BSV 1): 50.1. proximal mesotarsomeres of males elongated and broadened (parallelism in *Aspidytes*).

Noterinae excl. *Notomicrus*, *Hydrocoptus* and *Pro-noterus* (BSV 3): 32.1. external protibial spur modified as burrowing device; **34.1.** short row of stout, flattened setae on protibia; 36.1. outer edge of protibia rounded.

Noterinae excl. *Notomicrus*, *Hydrocoptus*, *Pronoterus* and *Noterus* (BSV 0): 33.1. internal protibial spur absent; **36.1.** tibial furrow for reception of protibial spur.

Mesonoterus, *Siolius*, *Renotus*, *Hydrocanthus*, *Canthydrus* and *Suphisellus* (BSV 0): **69.1.** group of setae at posterolateral margin of metacoxal plates.

Renotus, *Suphis*, *Siolius*, *Hydrocanthus*, *Canthydrus* and *Suphisellus* (BSV 1): 20.3. prosternal process broadened and apically truncate; **36.2.** tibial pit for reception of protibial spur.

Suphis + *Siolius*: 12.0. antennomere 9 not extended.

Hydrocanthus, *Canthydrus* and *Suphisellus* (BSV 2): 10.0. antennomere 5 not extended; 34.2. protibial row of stout, flattened setae extending to proximal part of tibia.

Aspidytidae + Amphizoidae + Hygrobiidae + Dytiscidae (BSV 3): **84.2.** laterotergite rod-like, caudal orientation; 90.1. egg bursters present (L); 99.2. gula not suture-like, less than half as broad as long (L); **111.1.** mandibular adductor tendon divided into upper and lower portion (L); 130.0. M. verticopharyngalis present (L) (?); **134.1.** Primary setae FE7–FE10 present (L).

Aspidytidae + Amphizoidae (BSV 0): 56.0. contact between pro- and metasternal process absent; **135.1.** additional pore on tibia (L).

[alternative hypothesis: Amphizoidae + Hygrobiidae + Dytiscidae: **95.1.** 24 or more sensorial setae or pegs of anterior clypeolabral margin (L); 99.2. moderately broad gula (L) (?).]

Hygrobiidae + Dytiscidae (BSV 5): 20.1. prosternal process converging towards apex (?); **26.1.** prothoracic defensive glands; 54.2., 72.2. dense fringes of swimming hairs on middle and hind legs; **131.1.** cerebrum shifted anteriorly (L); **133.1.** trochanteral annulus (L).

Dytiscidae (BSV 5): 2.1. head shortened and laterally rounded; **27.2.** ventral procoxal joint distinctly reduced; 56.2. transverse ridge of metaventrite absent; **67.2.** anterior margin of the metacoxa rounded, strongly extended anteriorly; 70.3. lateral margin of metacoxal plates very indistinct anteriorly.

Discussion (Figs 15 and 16)

The branching pattern we found is largely consistent with earlier studies based on morphology (Beutel and Roughley, 1988; Beutel, 1993, 1998; Beutel and Haas, 1996). The placement of Gyrinidae as sister group of the remaining adephagan families (Fig. 16) is in contrast to the results of analyses of full length 18S rRNA sequence data (Shull et al., 2001; Ribera et al., 2002b), which suggest the monophyly of Hydradephaga, Gyrinidae being the sister group of the remaining aquatic families. The placement of Gyrinidae in a clade Hydradephaga (five additional steps required), would imply that the following seemingly plesiomorphic character states of

different life stages have evolved secondarily in Gyrinidae: a very short and narrow prosternal process (20.0), a flat and extensive mesoventrite (40.0), triangular mesocoxae (47.0), absence of the torsion of the aedeagus (85.0), a deep larval maxillary groove (112.1), fully retained movability between cardo and stipes of larval maxilla (114.0), a hook-like and movable larval lacinia (118.2), two antagonistic stipitopalpal muscles in larvae (121.0), *M. craniolacinalis* attached to the base of the larval lacinia (123.0), and the presence of a distinct chorion (148.0). It is conceivable that the flattened mesoventrite of Gyrinidae is a result of reversal related to surface gliding habits. However, this is not very plausible for the other unusual characteristics of adults, and certainly not true for the plesiomorphic features of the larvae and egg. A basal position of Gyrinidae within Adephaga is also tentatively supported by the old age of the group, if an Upper Permian larva, which was described as a representative of Megaloptera (*Permosialis*; Sharov, 1953), does indeed belong to Gyrinidae as was suggested by Beutel and Roughley (1988) (see also Achtelig in Hennig, 1981).

It is apparent that more data are required for a full interpretation of the incongruence of the morphological and DNA sequence data. An analysis of the full set of protein coding genes (PCGs) from the mitochondrial genome, as well as conserved PCGs encoded in the nucleus, may help to solve this problem.

The Gyrinidae must have undergone rapid changes in their morphology and biology in the early evolution of the suborder, whether they are the sister group of the remaining Adephaga or of Haliplidae + Dytiscoidea. The larva of †*Permosialis* and an Upper Triassic adult (†*Triadogyrus*; Ponomarenko 1977) do not differ distinctly from extant representatives of the family. Adaptations to surface gliding habits such as the complete division of the compound eyes (3.1) and the extremely modified antennae (8.5, 9.2) must have evolved in the stem lineage of the family. However, the evolutionary scenario culminated later with the rise of Gyrininae and modifications of the locomotor apparatus, which are unique in the animal kingdom (51.1, 71.1) (see below). In the larval stage, among other apomorphies, Gyrinidae are characterized by mandibular sucking channels (110.3) and long abdominal tracheal gills (142.1). The former character guarantees efficient liquid feeding under water without a loss of digestive fluid and the latter enables them to live at greater depths than most hydradephagan larvae (Beutel, 1997).

The Haliplidae are placed as the sister group of Dytiscoidea in some of the trees, in contrast to earlier morphological studies (Beutel, 1993, 1998), but in agreement with Beutel and Haas (1996), Beutel (1997) and the results of analyses based on 18S rDNA sequence data (Shull et al., 2001; Ribera et al., 2002b). If the ancestral adephagan habit was terrestrial (riparian

habitats) as was suggested by Beutel (1995, 1997), this requires only two invasions of the aquatic environment by adephagan beetles instead of three as suggested by Beutel and Roughley (1988). On the other hand, a secondary terrestrial lifestyle of Geadephaga cannot be completely ruled out.

Potential synapomorphies of Haliplidae and Dytiscoidea are the contact between the pro- and mesosternal process (reversal in several groups) (58.1), the absence of nasal teeth in later instar larvae (94.0), the broadened, sclerotized larval gula (99.1), and the presence of a very strongly developed *M. tentoriopharyngalis* (129.1) (Beutel, 1986b, 1993). This placement of Haliplidae implies that the slightly retracted larval maxillae (112.2) and the lateral origin of the larval *M. craniolacinalis* (122.0) (Beutel, 1993) are secondarily derived features, and not plesiomorphies (see Beutel, 1993). The equally parsimonious alternative is a sistergroup relationship between Haliplidae and a clade comprising the dystycoid families and Geadephaga.

The aquatic †Triaplidae (Triassic) are characterized by strongly enlarged metacoxal plates (68.3), just like the extant Haliplidae (and some Triassic Eodromeinae; Ponomarenko, 1977). Nevertheless, they are probably not closely related to this family. A placement in the stem lineage of Adephaga excluding Gyrinidae was suggested by Beutel (1997). A presumably plesiomorphic feature is the extremely short prosternal process (long and broad in Haliplidae: 20.3) and possibly the presence of a longitudinal (and transverse) suture on the flat mesoventrite (Ponomarenko, 1977, fig. 2) (pentagonal groove present and sutures absent in Haliplidae). The position of this group remains uncertain. The orthognathous or hypognathous head clearly distinguishes it from all other groups of Adephaga. The only recognizable apomorphic feature that is shared with the remaining families of the suborder is the complete division of abdominal sternite II by the metacoxae.

The Trachypachidae were placed as the sister group of the rhyssodid-carabid-clade in some trees (Fig. 16), but as sister group of Dytiscoidea in others. The former placement is in agreement with Beutel and Haas (1996) and with the results of molecular analyses (18S rRNA; Shull et al. 2001; Ribera et al., 2002b), but in contrast to Beutel (1993, 1998). The main argument in support of a clade Geadephaga is the protibial antennal cleaning organ. This hypothesis implies that the fusion of the median metacoxal walls (66.1) has occurred independently in Trachypachidae (or is an ancestral character of Adephaga), and that the subcubital setal binding patch has evolved independently in the genus *Trachypachus* (63.1).

The monophyly of Dytiscoidea, including *Meru* and *Aspidytes*, is well supported (Figs 15 and 16). Apomorphies include the extensive metathoracic intercoxal septum (66.3) and the origin of the metafurca from this

structure (61.1). The losses of *Mm. furcaxialis* anterior and posterior (74.1, 75.1) are likely to be correlated with these modifications. Another potential apomorphy of the adults is the presence of an elongated subcubital setal binding patch (round in *Trachypachus*) (63.1). Its absence in *Meru* may be due to miniaturization, as it is also absent in other very small dytiscoids (e.g., *Notomicrus*). Potential larval apomorphies (larvae of *Meru* unknown) are the narrow cardo (115.1) and the reduction of abdominal segments IX and X (136.2, 137.1).

Even though fossils were not included in the analysis, some problems related with extinct adaphagan taxa may be briefly discussed in this context. The affinities of some Mesozoic taxa with Dytiscoidea were noted by Beutel (1997). Larvae of †*Stygeonectes* (†Coptoclavidae, †Necronectinae) share the reduced abdominal segments IX and X with the larvae of recent dytiscoid groups (136.2, 137.1). Very strongly sclerotized tergites, distinctly elongated legs, very small trochanters, forelegs with spines, middle and hind legs with swimming hairs, strongly developed, acuminate urogomphi, short mandibles, and a short and compact head (Ponomarenko, 1977, fig. 9) indicate a close relationship with †*Coptoclava* (Ponomarenko, 1977, fig. 13). This larva, however, was placed in a different subfamily, †Coptoclavinae by Ponomarenko (1977). The extensively fused metacoxae (with reduced plates) (66.3, 68.2) and the complete absence of the transverse suture of the metaventricle (57.2) suggest dytiscoid affinities of †*Exedia* (†Necronectinae), †*Charonoscapa*, †*Charonoscapidia* (†Charonoscapinae), and †*Coptoclava* (†Coptoclavinae) (Ponomarenko, 1977, figs 8, 10, 11, 13). In contrast, the presence of a complete transverse ridge (57.0) and narrow and separated metacoxae (66.0) (with large plates, 68.3) in †*Necronectus* (†Necronectinae) (Ponomarenko, 1977, figs 4, 5) suggest that this genus does not belong to Dytiscoidea as it lacks any shared characteristics with that group. It is evident that Coptoclavidae and Necronectinae are artificial, non-monophyletic units, and it was pointed out in Beutel (1997) that the use of these taxa in works on the fossil record may create confusion (see e.g., Ross and Jarzembowski, 1993; Labandeira, 1994).

Meruidae were placed as sister group of Noteridae, as was already suggested by Spangler and Steiner (2005). Synapomorphies of Noteridae and Meruidae are the absence of the transverse ridge of the metaventricle (57.2), the fusion of abdominal segments III and IV (78.1) and the shape of the strongly asymmetric parameres (86.1). Another potential synapomorphy is the enlargement of antennomeres 5, 7 and 9, as is found in males of *Meru* (Spangler and Steiner, 2005, fig. 4, antennomere 5 slightly enlarged, 7 and 9 strongly enlarged), Phreatodytinae (Uéno, 1957, fig. 1) and

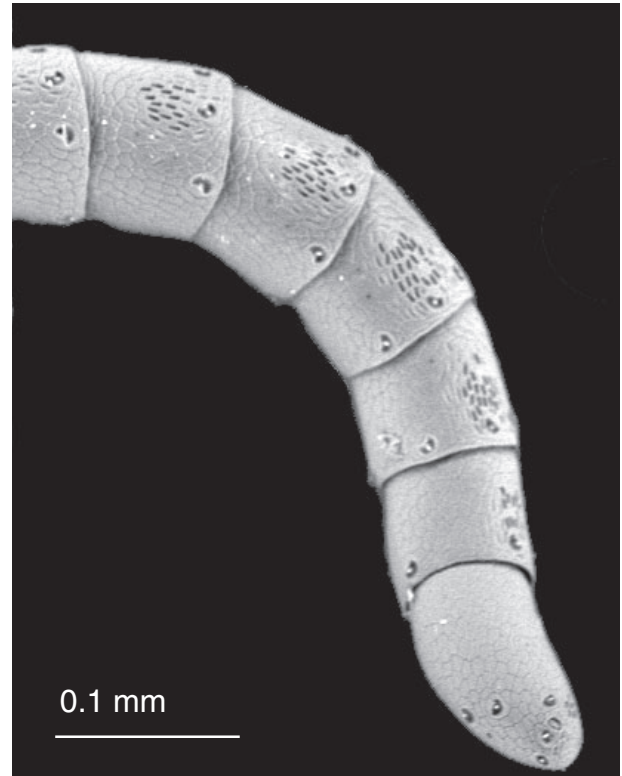


Fig. 14. *Aspidytes niobe*, adult, distal part of antenna with sensilla.

Noterinae (with some variation; Belkaceme, 1991). An enlargement of antennomeres does rarely occur within Dytiscidae (e.g., *Agabus serricornis* (Paykull); Franciscolo, 1979, p. 569) and occurs in males of *Aspidytes* (Fig. 14; Balke et al., 2003, fig. 2), but not in the characteristic pattern displayed by *Meru* and most noterid genera. The pattern of smaller and larger antennomeres is somewhat vague in some representatives of Noteridae (e.g., *Notomicrus*: Belkaceme, 1991, figs 63 and 64; pers. obs. Balke). Nevertheless, it appears reasonable to interpret a condition as it is found in *Meru* and *Phreatodytes* as a derived groundplan feature of the meruid-noterid clade. Even though a clade comprising Meruidae and Noteridae appears reasonably well supported, some uncertainty is caused by the lack of larval characters for *Meru* (and several basal genera of Noteridae). Finding (or rearing) the minute larvae of *Meru* may be considered a major challenge for beetle collectors.

The position of Noteridae (or the meruid-noterid clade), is in agreement with earlier studies of Beutel (1993, 1995, 1998). The placement of Noteridae as the sister group of Dytiscidae proposed by Miller (2001) could not be confirmed here and was also rejected by analyses of molecular data (Ribera et al., 2002a,b) as well as by a combined analysis (Balke et al., 2005). The exact placement of *Aspidytes* within Dytiscoidea

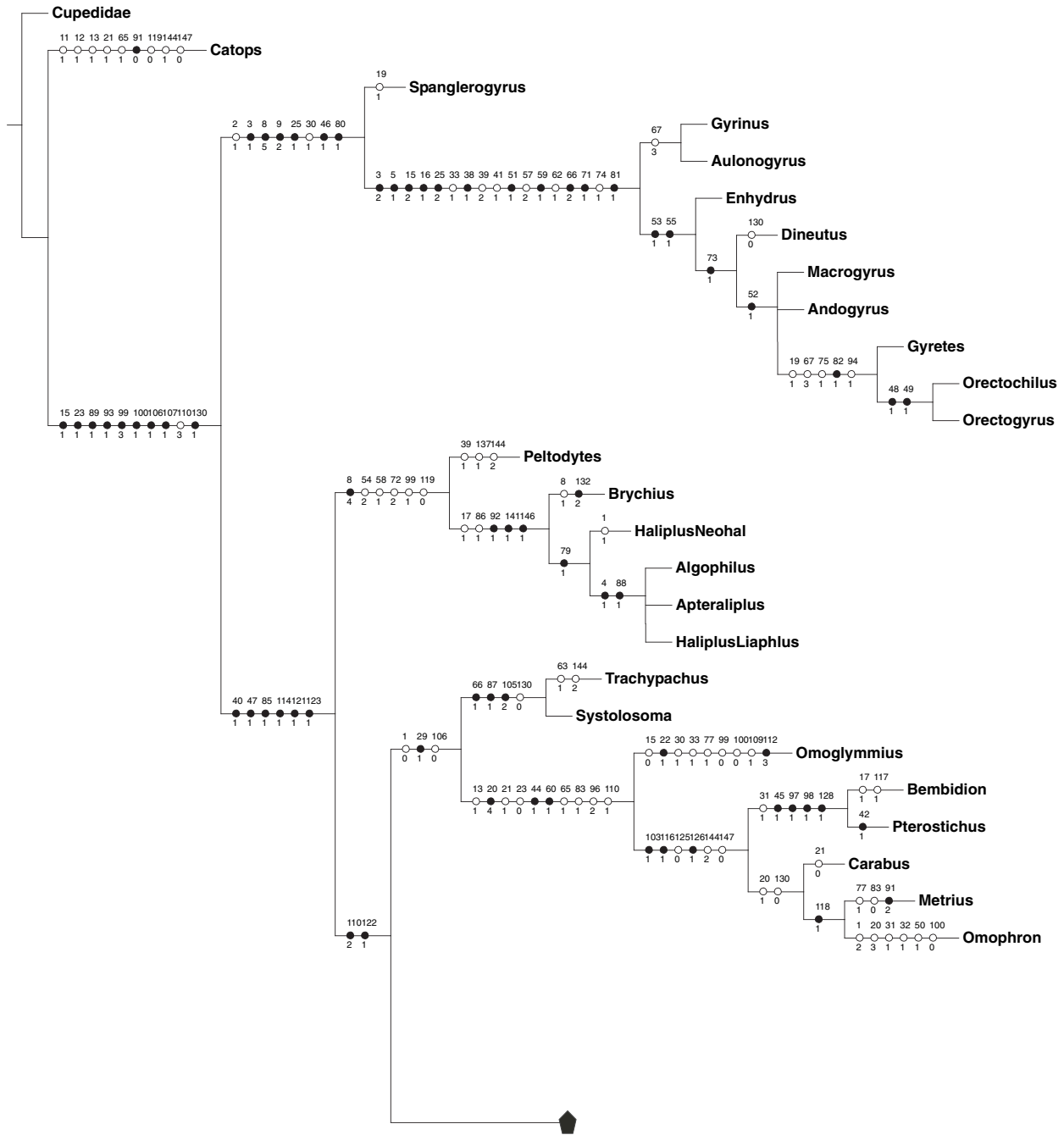
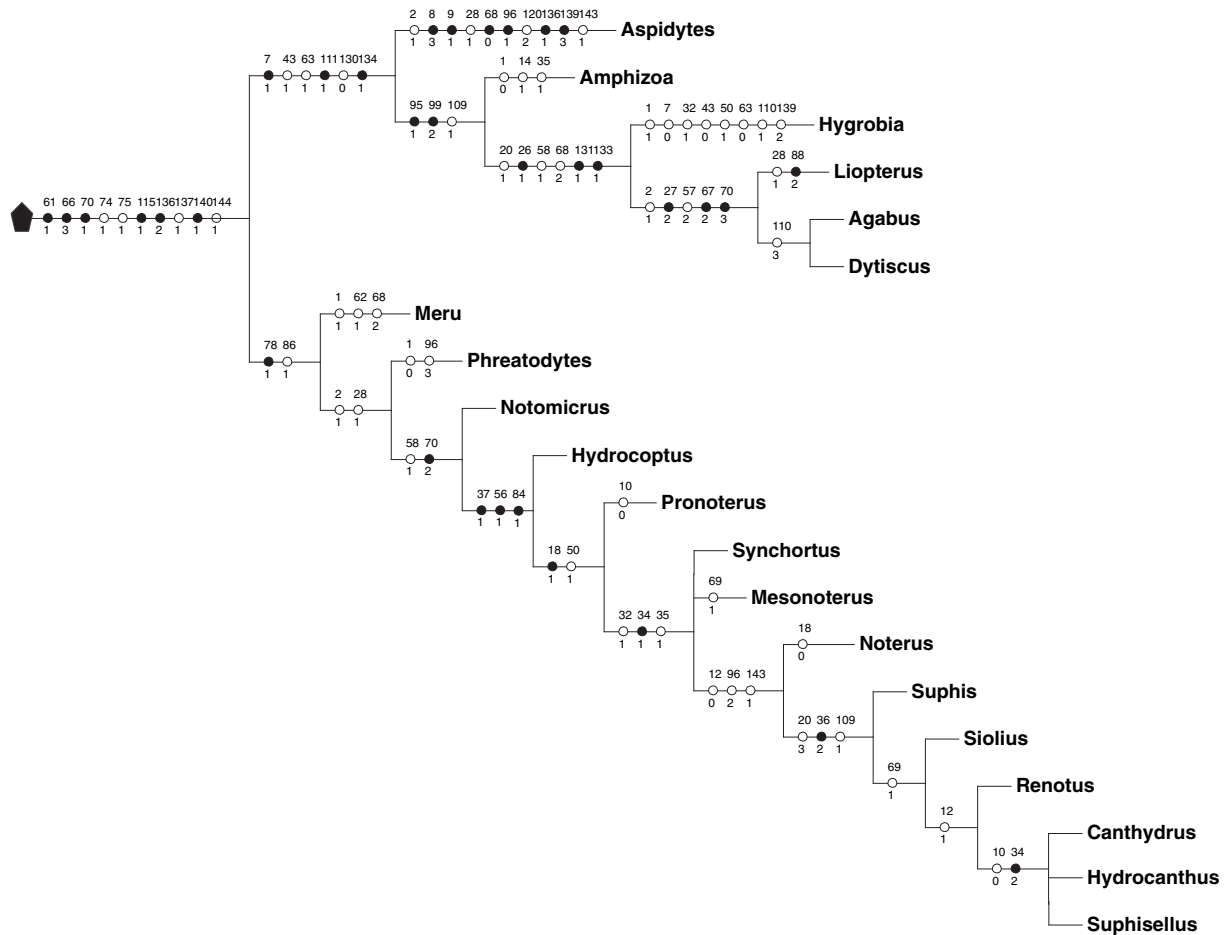


Fig. 15. One of 21 equally parsimonious trees (347 steps) with character distribution mapped onto the tree (continued next page).

remains uncertain (Fig. 16) despite considerable efforts to settle this question. The first analysis based on morphology and 18S rRNA, 16S rRNA and COI sequences (excluding 3rd codon positions of COI) suggested a sister group relationship with Dytiscidae + Hydrobiidae (Ribera et al., 2002a). Based on an extended morphological and molecular data set (Balke et al., 2005), the genus was placed as sister group of

Amphizoidae (see Fig. 15), and both taxa together either as sister group of Dytiscidae (molecular data/combined analysis) or a clade comprising Dytiscidae + Hydrobiidae (morphology only). Balke et al. (2005) found no evidence that would justify the exclusion or down-weighting of the 3rd codon positions of the PCGs analyzed, and thus the full dataset was used for the final analyses. Here, *Aspidytes* is placed either as

Fig. 15. *Continued*

the sister group of Amphizoidae or of a clade comprising Amphizoidae, Hygrobiidae and Dytiscidae.

The presence of a small but distinct larval abdominal segment IX (136.1) agrees with a basal placement of *Aspidytes* within Dytiscoidea, as suggested by Alarie and Bilton (2005). However, this is neither supported by other morphological data nor by molecular evidence. Within Dytiscoidea, we found a clade Hygrobiidae + Dytiscidae which was supported by the presence of prothoracic defensive glands (26.1) and other morphological features of adults and larvae (see also Alarie et al., 2004), but this was never supported by molecular data (Ribera et al., 2002a,b; Balke et al., 2005).

Among the smaller families, the sister group relationship between Spanglerogyrinae and Gyrininae (Folkerts, 1979; Beutel, 1989a,b, 1990) is strongly supported (BSV 15). The most interesting apomorphy is the unique locomotor system of the adults of the latter subfamily, which was treated in great detail by Nachtigall (1961) and Larsén (1966). It has been suggested by the species numbers (Spanglerogyrinae: 1, Gyrininae: > 500), that

the diversification of Gyrinidae was mainly triggered by the modification of the swimming apparatus, which, according to Nachtigall (1961), is the most efficient of all aquatic animals. A sister group relationship of the two included genera of Gyrinini and the monophyly of a group comprising Enhydrini and Orectochilini is well supported. Potential larval apomorphies of the latter clade (larvae of *Enhydrus* unknown) are the vestigial or absent retinaculum (109.1), the advanced mandibular sucking channel (110.3) (Noars, 1956; Beutel and Roughley, 1994), a specific lamellar prepharyngeal filter apparatus (127.1), and the extremely slender antennae (104.1) and palps (Beutel and Roughley, 1994). *Enhydrus* is the sistergroup of the the remaining enhydrine-orectochiline clade. This implies paraphyly of Enhydrini as already suggested by Beutel (1990) (Enhydrini appears to be a junior homonym of a tribe of otters, Lutrinae, including the genus *Enhydra*, and will need to be replaced in a separate study). The most advanced group within Gyrinidae is Orectochilini. Among other autapomorphic features, the adults are characterized by

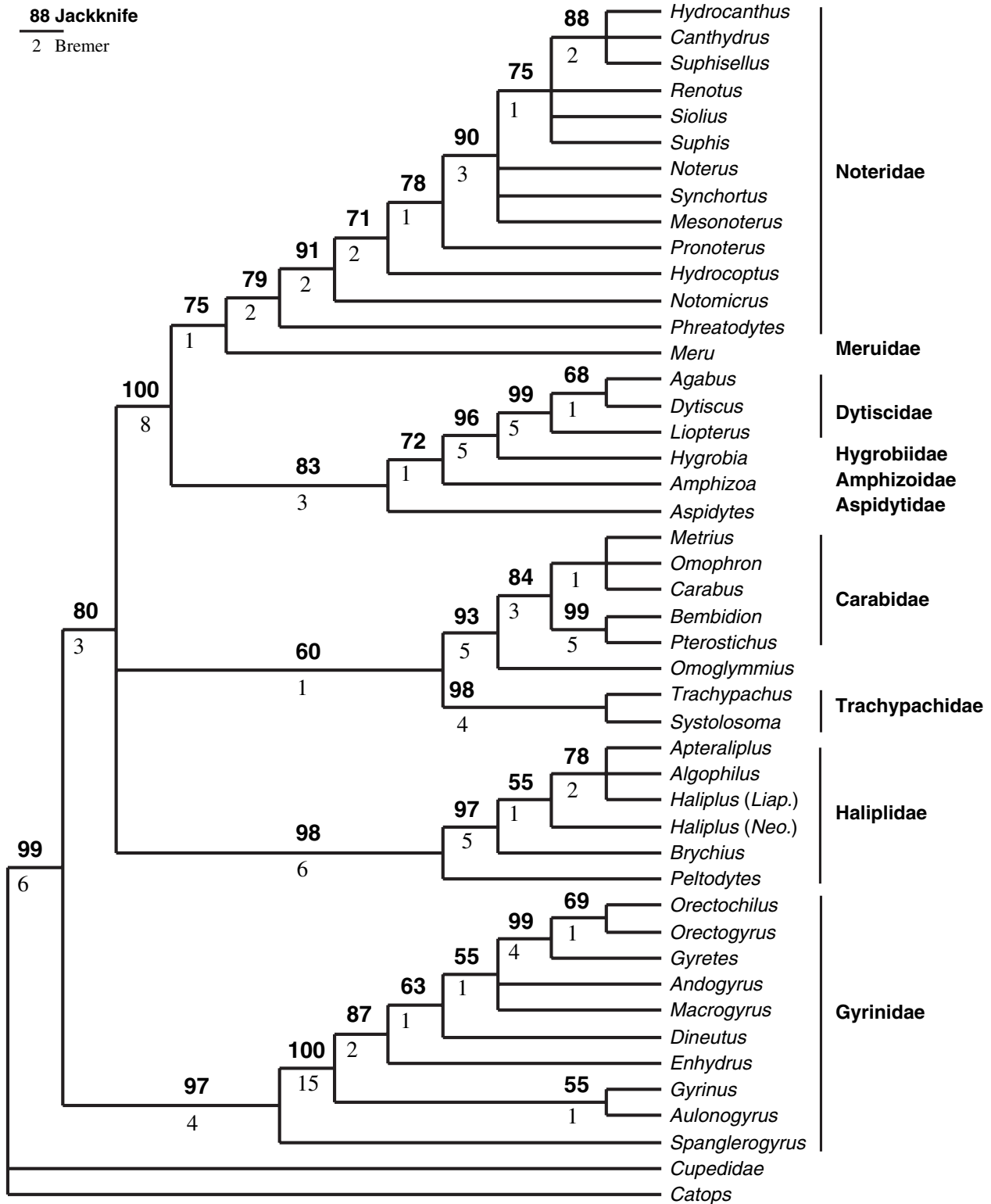


Fig. 16. Strict consensus of 21 equally parsimonious trees with branch support values.

laterally setose pronota and elytra (19.1) and a median row of hairs on the fused and exposed gonocoxosterna (82.1). The presence of the former character in *Span-*

glerogyrus is almost certainly due to parallelism and not to phylogenetic affinities with Orectochilini as suggested by Crowson (in litt.).

The monophyly of Haliplidae is also well supported (BSV 6). The most conspicuous feature of adults is the presence of greatly enlarged metacoxal plates (as in adults of †Triaplidae; Ponomarenko, 1977) (68.3), which provide additional storage space for breathing air (Beier, 1929). A characteristic set of larval characters is related with their algophagous habits (Seeger, 1971a,b), which is a highly unusual exception within the otherwise almost exclusively predacious adepagans. A unique type of mandibular sucking apparatus is present (Jaboulet, 1960; Seeger, 1971b; Beutel, 1986b), the apical part of the maxilla is strongly modified (119.0, 120.0), and the space between the short labial palps serves as guiding device for filamentous algae. A larval adaptation towards crawling among masses of algae is the presence of a clasping apparatus of the prolegs (132). Interestingly, two different conditions have evolved within the family, the protibia-claw-type in *Peltodytes* and most *Haliphilus* species, and the profemur-claw-type in *Brychius*. The absence in larvae of *Liaphilus* and *Haliphilus* s.str. is very likely the result of a secondary switch from filamentous algae (e.g., *Syprogyra*, *Cladophora*) to *Chara* (Seeger, 1971a; Beutel, 1997).

A branching pattern (*Peltodytes* + (*Brychius* + *Haliphilus*)) within Haliplidae (Beutel and Ruhnau, 1990) was confirmed. Haliplidae excl. *Peltodytes* were supported by the subulate apical labial palpomeres of adults (17.1), the strong asymmetry of the parameres (86.1), and by the unique microtracheal gills of larvae (141.1) (Seeger, 1971b). A clade comprising the genera *Algophilus* and *Apteraliphilus* and the *Haliphilus*-subgenus *Liaphilus* (and possibly *Paraliaphilus*) was confirmed by the presence of secondary genal ridges (4.1) (Fig. 3B) and the digitus of the left paramere (88.1) (Beutel and Ruhnau, 1990). This shows that the generic rank of *Algophilus* and *Apteraliphilus* is merely based on autapomorphies (related by wing reduction) and not justified phylogenetically (Beutel and Ruhnau, 1990).

The branching pattern within Noteridae is very similar to the cladogram of Belkaceme (1991, fig. 72), which was based on a manual character analysis. Phreatodytinae are the sister group of Noterinae, and *Notomicrus* (+ *Speonoterus* Spangler, 1996), *Hydrocoptus* and *Pronoterus* branch off successively within this subfamily. Modifications of the fore legs and metaventrite have obviously played an important role in the evolution of the group. As pointed out by Beutel and Roughley (1987) and Belkaceme (1991), the forelegs are gradually transformed into burrowing and grasping devices. The ventral side of the beetle is distinctly convex in the basal genera *Notomicrus* and *Speonoterus*, but flattened in the other groups (“noterid platform”). The beetles are usually found in debris, root mats, or crawling on vascular plants, and often burrow in the substrate (Dettner, 2005), and are apparently adapted to this environment. A

remarkable feature, which is likely to be unique within Adepagana, is their pupation underwater (Ruhnau, 1985; Dettner, 2005). However, this has only been documented for the genus *Noterus* so far. Whether ancestral noterids (and dytiscoids) were able to swim is doubtful, as swimming adaptations are completely lacking in *Meru* and Phreatodytinae (Uéno, 1957, 1996).

Future tasks we identified are to obtain the yet unknown larval stages of *Meru*, *Spanglerogyrus* and several noterid genera, as well as targeting a combined analysis adding DNA sequence data.

In summary, the recent discovery of the morphologically highly characteristic adepagan beetle species *Meru phyllisae* in Venezuela as well as the two species of Aspidytidae in South Africa and China underpin the importance of expert fieldwork to properly understand biological diversity on Earth.

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