Larval Morphology of Meruidae (Coleoptera: Adephaga) and Its Phylogenetic Implications

YVES ALARIE,[1] ANDREW E. Z. SHORT,[2] MAURICIO GARCIA,[3] AND LUIS JOLY[4]

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ABSTRACT Meruidae, or comb-clawed cascade beetles, are a recently discovered monotypic family of Adephaga endemic to Venezuela. The larvae of Meruidae are described for the first time, based on material of *Meru phyllisae* Spangler & Steiner, 2005, collected together with adults in southern Venezuela. External morphological features, including chaetotaxy, are reported for the mature larva and an assessment made of the polarity of larval characters of phylogenetic utility in Adephaga. Larvae of Meruidae possess a mixture of primitive and derived character states, and they are unique within the Adephaga in that here the mandibles are asymmetrical, the respiratory system is comprised of only two pairs of spiracles (=oligopneustic), the claws are pectinate, and the abdominal sternite VIII is prolonged overlapping the abdominal sternite IX. A parsimony analysis based on 18 informative larval characteristics was conducted with the program PAUP*. The most parsimonious trees confirm Meruidae as a relatively basal lineage within the Dytiscoidea. Both *Meru* Spangler & Steiner and Noteridae are hypothesized to have diverged anterior to Amphizoidae, Aspidytidae, Hygrobiidae, and Dytiscidae.

KEY WORDS *Meru phyllisae*, phylogeny, chaetotaxy, Adephaga, comb-clawed cascade beetles

Meruidae or comb-clawed cascade beetles are a monotypic adephagan family described recently from a series of specimens collected in shallow films of moving waters in Venezuela (Spangler and Steiner 2005). With an adult body length of 0.85–0.90 mm, these beetles are the smallest known members of aquatic Adephaga. On the basis of adult morphology and molecular data, Beutel et al. (2006) and Balke et al. (2008) postulated that the family belongs to the Dytiscoidea, showing affinities with the Noteridae.

In September 2007, larvae of *Meru phyllisae* Spangler & Steiner, 2005 were collected in association with adults at its type locality in southern Venezuela, allowing the larvae of these adephagans to be described here for the first time, together with observations on their ecology, and consideration of larval characters of potential phylogenetic value. In the current study, an emphasis is put on chaetotaxy because detailed investigation of larval chaetotaxy has shown it is a source of abundant characters useful for phylogenetic inference (e.g., Carabidae: Bousquet and Goulet 1984; Dytiscidae: Alarie 1991, 1995, 1998; Alarie and Harper 1990; Alarie et al. 1990; Hygrobiidae: Alarie et al. 2004; Aspidytidae: Alarie and Bilton 2005).

The objectives of this article are 1) to describe the larvae of *M. phyllisae* and 2) to test whether external morphological larval characters confirm the placement of the family Meruidae within the suborder Adephaga in the same position as based on molecules and adult morphology.

Materials and Methods

Material Examined. Larvae of *M. phyllisae* were collected together with adults from the following locality: Venezuela, Amazonas state, El Tobogán de la Selva, 100 m, 5° 23,309′ N, 67° 37,045′ W, 12–13-IX-2007. M. Garcia, L. Joly & A.E.Z. Short leg. It should be noted that the latitude and longitude for the type locality provided by Spangler and Steiner (2005) are erroneous.

These larvae were evidently adephagans but differed significantly in morphology from those of all previously described families and possessed the identical unique "combed claws" found in the adults that give the family their common name. Larvae were determined as third instars based upon larval size relative to adult size and presence of functional spiracles. Voucher specimens are deposited in the research larval collection of Y.A (Department of Biology, Laurentian University, Sudbury, ON, Canada), A.S. (Department of Ecology and Evolutionary Biology University of Kansas, Lawrence, KS), M.G. (Museo de Arthropodos, Universidad del Zulia, Es-

[1] Corresponding author: Department of Biology, Laurentian University, Sudbury, ON, Canada P3E 2C6 (e-mail: yalarie@laurentian.ca).

[2] Department of Ecology and Evolutionary Biology, University of Kansas, 1501 Crestline Dr., Suite 140, Lawrence, KS 66049.

[3] Centro de Investigacions Biológicas, Facultad de Humanidades y Educación, Universidad del Zulia, Apdo. 526, Maracaibo 4011-A, Estado Zulia, Venezuela.

[4] Museo del Instituto de Zoologia Agricola, Facultad de Agronomia, Universidad Central de Venezuela, Apdo. 4579, Maracay 2101-A, Estado Aragua, Venezuela.

tado Zulia, Venezuela), and L.J. (Museo del Instituto de Zoologia Agricola, Universidad Central de Venezuela, Estado Aragua, Venezuela).

Study of External Features. Specimens representing the mature larva were disarticulated and mounted on standard glass slides with Hoyer's medium.

Morphometric Analysis. All measurements were made with a compound microscope equipped with an eyepiece graticule. The part to be measured was adjusted so that it was, as near as possible, parallel to the plane of the objective.

The following measures were taken. Head length (HL): total head length including the frontoclypeus, measured medially. Head width (HW): maximum head width. Length of antenna (A), maxillary (MP) and labial (LP) palpi were derived by adding the lengths of the individual segments; each segment is denoted by the corresponding letter(s) followed by a number (e.g., A1: first antennomere). A3′ is used as an abbreviation for the apical lateroventral process of third antennomere. Length of leg (L) including the longest claw was derived by adding the lengths of the individual segments; each leg is denoted by the letter L followed by a number (e.g., L1: prothoracic leg). Dorsal and ventral lengths of last two abdominal segments: measured along midline from anterior to posterior margin. Length of urogomphus (U) measured along outer margin including the tergum IX. The individual measurements defined above were used in calculating several ratios aiming at characterizing the body shape.

Chaetotaxic Analysis. Primary setae and pores were distinguished on the head capsule, legs and urogomphi assuming that no secondary (those added during ontogenetic development) are found in Meruidae. The setae and pores were coded according to the system developed for other Adephaga families: Bousquet and Goulet (1984) (Carabidae); Alarie et al. (2004) (Hygrobiidae); Alarie and Bilton (2005) (Aspidytidae); and Alarie et al. (1990), Alarie and Harper (1990), Alarie (1991), Alarie and Michat (2007), and Nilsson (1988) (Dytiscidae). Setae are coded by two capital letters corresponding to the first two letters of the name of the structure on which the seta is located (e.g., CO, coxa; FE, femur; FR, frontoclypeolabrum, PA, parietale; TA, tarsus; TI, tibia; TR, trochanter; UR, urogomphus) and a number. Pores are coded in a similar manner except that the number is replaced by a lower case letter. The position of the sensilla is described by adding the following abbreviations: A, anterior; AV, anteroventral; D, dorsal; Di, distal; Pr, proximal; and PV, posteroventral.

Color. Description of color is given from ethanol-preserved specimens.

Cladistic Analysis. To examine the phylogenetic signal of the characters observed on the larvae of Meruidae and test the relationship of the family with other Adephaga, a cladistic analysis was conducted rooting the cladogram with the family Gyrinidae as it has been suggested as the sister-group of all other Adephaga (Beutel 1993).

Fig. 1. *M. phyllisae*, third-instar larva habitus (scanning electron micrograph). (A) Dorsal view. (B) Ventral view. (C) Lateral view. Scale bar = 0.50 mm.

PAUP* version 4.0b10 (Swofford 2002) and MacClade 4 (Maddison and Maddison 2000) software packages were used for parsimony searches, character editing, and cladogram examinations. The analyses included only informative characters. All characters were treated as unordered and equally weighted. A heuristic search strategy was used to find minimum-length trees. Search was conducted with 100 random-addition replicates (tree bisection-reconnection [TBR]). The data were bootstrapped with 100 replicates to assess branch support. The consistency index (CI) (Kluge and Farris 1969) and retention index (RI) (Farris 1989) are given.

Systematics

Description of Third-Instar Larva of *M. phyllisae*

(Figs. 1–9)

Diagnosis. Meruidae larvae may be distinguished from other Dytiscoidea larvae (i.e., Aspidytidae, Hygrobiidae, Noteridae, Dytiscidae, and Amphizoidae) by the following combination of characters: small size, body length of mature larva = 1.60–1.80 mm; body fusiform; mandibles asymmetrical, right mandible not channeled with a retinaculum (Fig. 1B), left mandible channeled lacking a retinaculum (Fig. 1A); short legs; abdomen nine-segmented (Fig. 1A), abdominal sternite VIII elongate, covering the abdominal sternite IX (Fig. 8B); oligopneustic, with a pair of spiracles on abdominal segments one and eight (Fig. 8D and E).

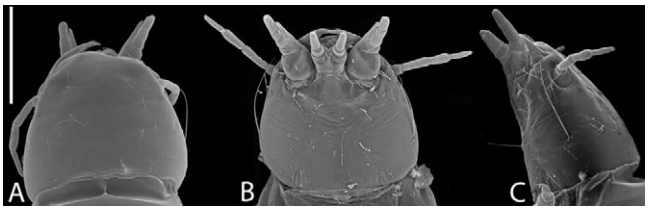

Fig. 2. *M. phyllisae*, third-instar larva, head capsule (scanning electron micrograph). (A) Dorsal aspect. (B) Ventral aspect. (C) Lateral aspect. Scale bar = 0.10 mm.

Description. Body subcylindrical; maximum body width at level of posterior margin of metathorax and first abdominal segment (measurements, $n = 5$; Fig. 1); body length = 1.60–1.70 mm.

Color. Body uniformly brown.

Head. HL = 0.16–0.17 mm (mean = 0.16 mm); HW = 0.17–0.18 mm (mean = 0.17 mm) (Figs. 2–5). Cephalic capsule (Figs. 2 and 3) partially retracted into pronotum (Fig. 1A), sagittate to globose, prognathous, slightly broader than long (HL/HW = 0.91–0.94), narrower than prothorax, without neck constriction; foramen occipitale broad and oval in outline; ecdysial suture well developed, coronal suture lacking (Fig. 3A); occipital carina lacking; posterior margin with a narrow postocciput, which is bordered by a distinct postoccipital suture (Fig. 3A). Frontoclypeolabrum elongate, about as long as HL; anterior margin with rounded lateral lobes (=adnasalia), produced medially into a faint nasale (Fig. 3A); anterior margin sinuate mesally. *Parietale.* Parietal plates meeting along ventral midline; gular suture not developed, tentorial pits visible ventrally on each side of median

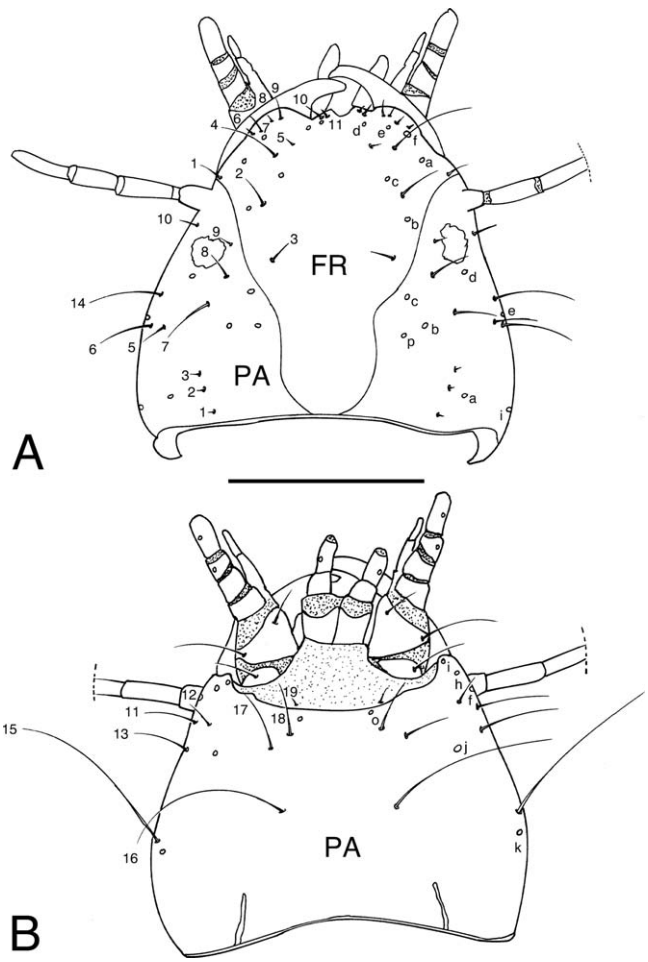

Fig. 3. *M. phyllisae*, third-instar larva, head capsule. (A) Dorsal aspect. (B) Ventral aspect. FR, frontoclypeus; PA, parietale. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.10 mm.

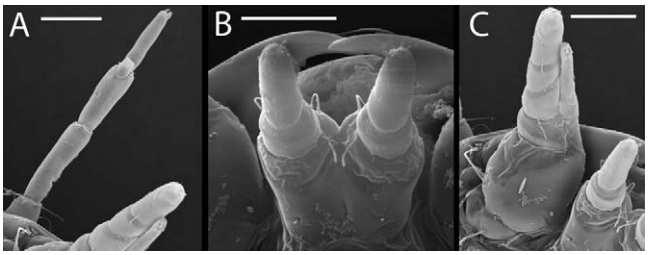

Fig. 4. *M. phyllisae*, third-instar larva, cephalic appendages (scanning electron micrograph). (A) Antenna, dorsal aspect. (B) Labium, ventral aspect. (C) Maxilla, ventral aspect. Scale bar = 0.02 mm.

line at about midlength (Figs. 2B and 3B); occipital foramen slightly sinuate ventrally; ventral surface with a short plica on each side posteriorly (Fig. 3B); ocularium present, with at least five well developed stemmata present posterior to antennal insertion, arranged in two vertical rows (we were unable to determine the presence of a sixth stemma owing to small size and deterioration on the stemmata in the mounting medium). *Antenna* (Fig. 4A). Four-segmented, shorter than HL (A/ HL = 0.53–0.57); A4 = A2 > A3 > A1, A3/A2 = 0.72–0.95, A4/A3 = 1.21–1.43; A3 with an accessory bulbous segment (A3′), A3′/A4 = 0.18–0.35. *Labium* (Figs. 3B and 4B). Prementum arising from a membranous mentum, short, fully sclerotized, divided into two parts by a medial suture; ligula absent; palpus two-segmented, inserted on the anterolateral edges of the prementum, shorter than maxillary palpus (MP/LP = 1.31–1.55), palpomeres subcylindrical, LP2/LP1 = 1.90–1.91. *Maxilla* (Figs. 3B and 4C) short; cardo represented by a small ovate sclerite; galea one-segmented, inserted on a large palpiger, inserted on stipes; lacinia absent; stipes broad, subtrapezoidal; palpus three-segmented, inserted on broad palpifer similar to a palpomere, shorter than antenna (A/MP = 2.04–2.33); MP1 < MP2 < MP3; MP1 and MP2 subtrapezoidal, MP3 subcylindrical; MP2/MP1 = 1.10–1.30, MP3/MP2 = 1.70–2.40. Mandible (Fig. 5) falciform, short, asymmetrical, right mandible not channeled with a retinaculum (Fig. 5B), left mandible channeled lacking a retinaculum (Fig. 5A); prostheca, penicillum and mola absent. *Chaetotaxy* (Fig. 3). Forty-seven sensilla (29 setae and 18 pores) are coded on the head capsule. Sensilla located along the anterior margin of the frontoclypeolabrum were very difficult to locate owing to small larval size and therefore some sensilla could have been missed. The sensilla observed are illustrated in Fig. 3, and they are listed with their positions in Table 1. Frontoclypeolabrum. Eleven setae (FR1–FR11) and six pores (FRa–FRf) compose the number of primary sensilla on the frontoclypeolabrum. *Parietale.* Eighteen setae and 12 pores compose the number of primary sensilla on the parietale. The basal half of the sclerite bears six setae (PA1–PA3, PA5–PA7) and six pores (PAa–PAc, PAe, PAi, and PAp) dorsally and two setae (PA15 and PA16) and one pore (PAk) ventrally. The distal portion of the parietale bears four setae (PA8–PA10, PA14) and two pores dorsally (PAd–PAe) and six setae (P11–PA13, PA17–PA19) and five pores (PAf, PAi–PAj, PAn, PAo) ventrally.

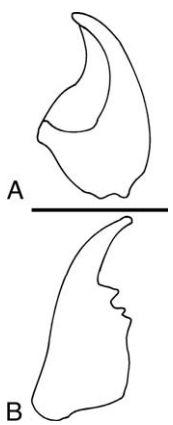

Fig. 5. *M. phyllisae*, third-instar larva. (A) Left mandible , dorsal aspect. (B) Right mandible, dorsal aspect. Scale bar = 0.05 mm.

Thorax. (Fig. 6A). Pro-, meso-, and metathoracic terga well sclerotized dorsally; pronotum subtrapezoidal, approximately twice as long as mesonotum; meso- and metanota divided medially by an ecdysial line; metanotum subequal to mesonotum in length; mesonotum subrectangular, as broad as posterior margin of pronotum; metanotum subtrapezoidal, posterior margin broader than pro- and mesonota; thoracic venter membranous; spiracular openings absent.

Legs. Six-segmented (sensu Lawrence 1991) (Figs. 6B–D; 7); L1 = 0.34–0.35 mm (mean = 0.35 mm); L3 = 0.40 mm, L3/L1 = 1.15–1.17; L3/HW = 2.30–2.34; coxa > trochanter = femur > tibia = tarsus; trochanter lacking a trochanteral annulus (Figs. 6B and 7); pretarsus with two claws, each claw with well-developed spinulae along inner margin (Fig. 6C and D). *Chaetotaxy* (Fig. 7; Table 2). Forty-four setae and nine pores are coded on the leg. Coxa with 17 setae (CO1–CO10, CO12–CO18) and one pore (COa). Trochanter with six setae (TR1, TR3–TR7) and six pores (TRa, TRc–TRg). Femur with six setae (FE1–FE6). Tibia with seven setae (TI7–TI7) and one pore (TIa). Tarsus with six setae (TA2–TA7) (TA4 and TA5 pore-like) and one pore (TAb). Pretarsus with two short spiniform setae (PT1–PT2). Sensilla located along the apical margin of the tarsi were very difficult to locate

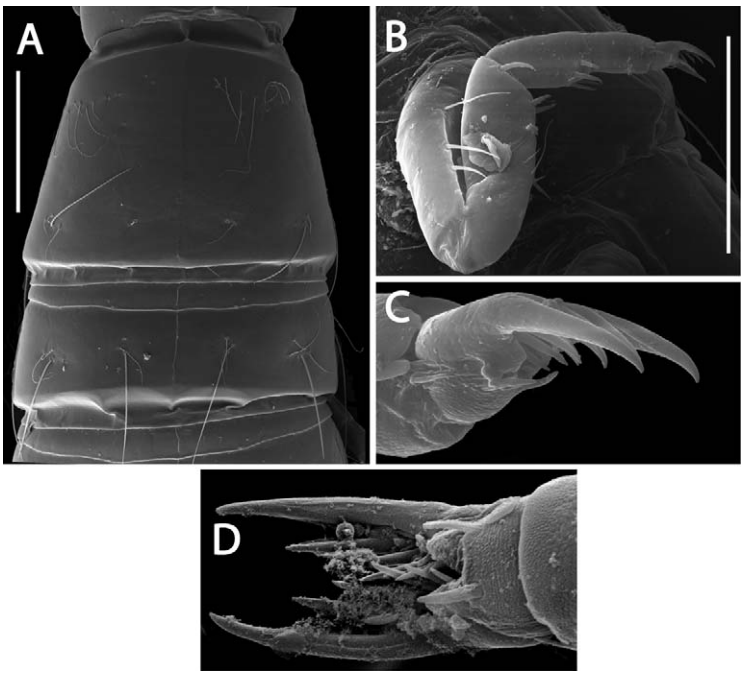

Fig. 6. *M. phyllisae*, third-instar larva, thorax and legs (scanning electron micrograph). (A) Dorsal surface. (B) Metathoracic legs, anterior surface. (C) Metathoracic claws, lateral aspect. (D) Metathoracic claws, ventral aspect. Scale bar = 0.01 mm.

owing to small larval size and therefore some sensilla could have been missed.

Abdomen. Nine-segmented (Figs. 1; 8, and 9), fully sclerotized (Fig. 1C); segments gradually decreasing in width posteriorly; abdominal sternite VIII extended posteriorly forming a nonarticulated operculum covering segment IX, suggesting an eight-segmented abdomen (Figs. 1B, 8A–C, and 9A and C); A8 = 0.07–0.08 mm dorsally (mean = 0.08 mm), 0.12–0.15 mm ventrally (mean = 0.14 mm); A9 (including urogomphi) = 0.06–0.08 mm (mean = 0.07 mm).

Urogomphus. (Figs. 8F and G; 9B). One-segmented, very small but prominent, fused with tergum IX posterolaterally (Figs. 8G and 9B). *Chaetotaxy* (Fig. 9B; Table 3). Seven setae (UR2–UR8) and two pores (URf–URg) are coded on the urogomphus. The sensilla articulated on the urogomphi were extremely difficult to identify owing to the very reduced size.

Spiracles. Annular, present near dorsolateral margin of segments 1 and 8 (Fig. 8D and E).

Ecology of *M. phyllisae*. Spangler and Steiner (2005) provide a very detailed account of the type locality of Tobogan de la Selva. The ecological complexity in terms of number of apparent aquatic habitats present, and more specifically how the beetle taxa are partitioned within these various situations, is difficult to overstate. For example, the site contains isolated forest pools and small detrial streams, a larger primary river that flows both through dense forest and exposed bedrock and over various substrates, and isolated seepage habitats that are disconnected from other waters sources. Although dubbed "comb-clawed cascade beetles," most specimens collected previously were from marginal root mats and detritus (Spangler and Steiner 2005) and not in the iconic rock-slide that is the primary hydrologic feature that gives the site its name. Indeed, we and others (M. Balke, personal communication) failed to find a single specimen of *Meru* (adult or larvae) in the main or marginal regions of the cascade. Rather, we found them in rock seepages originating from surrounding forested or woodland areas (e.g., Fig. 10A). Seepages with *Meru* were repeatedly characterized as shallow, barely flowing, and usually fully exposed in the sun with extensive algal growth on the granite. These seepages are usually only present during the wet season (e.g., May–November), and not during the early to mid dry season in January and February when nearly all prior collecting took place. It was on these side seepages that we encountered *Meru* larvae.

We collected these larvae by placing a fine-mesh sheet down current of the seepage, and brushing and scraping the water film and surface detritus and algae into the fabric; essentially, creating a micro-seine (Fig. 10B). We spread the sheets out on the bare rock and examined them for moving beetles. When high densities of *Meru* were found, we repeated this process and collected ≈1 liter of concentrated algae scrapings, which was subsequently examined in the lab. From approximately 10 m^2 of rock seepage surface, we extracted >900 adult and 50 larval *Meru* specimens. Similar efforts in other habitats (e.g., the main cascade) resulted in few, if any, adult *Meru* (we did not collect or pick algae from other habitats for larvae). Similar

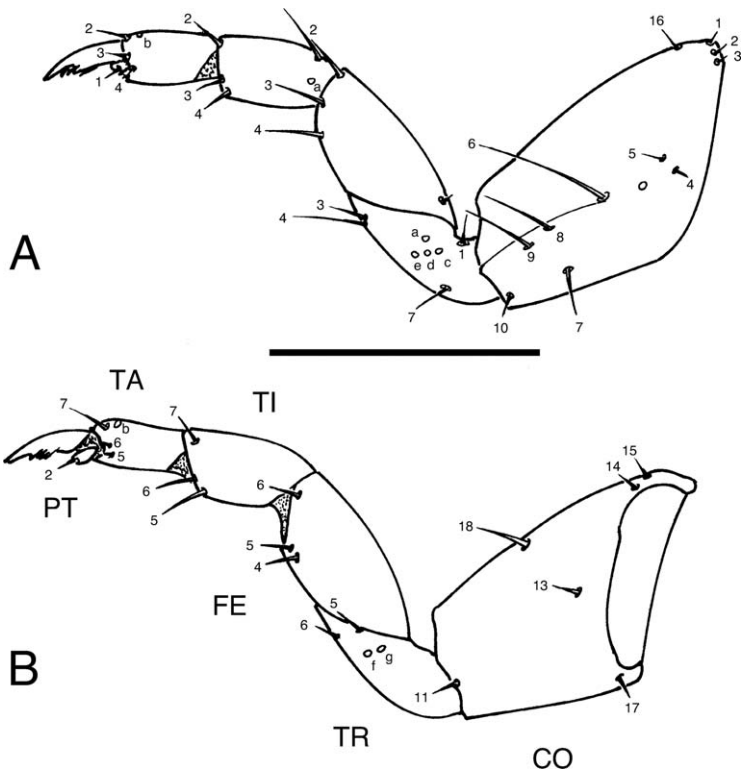

Fig. 7. *M. phyllisae*, third-instar larva, metathoracic leg. (A) Anterior surface. (B) Posterior surface. CO, coxa; FE, femur; PT, pretarsus; TA, tarsus; TI, tibia; TR, trochanter. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.10 mm.

efforts in subsequent dry seasons did not result in any mass-collections of *Meru* adults or larvae, suggesting it is a seasonally abundant species, and primarily (if not exclusively) breeds during the wet season when its preferred habitat is abundant. The collection of (comparatively few) adult specimens in root mats or along the primary cascades along the main river in the dry season may be incidental rather than representing a preferred habitat.

Results

Here, we provide a list of larval morphological characters used for phylogenetic analysis. The polarity rationale in the list of characters (Table 3) presented below is based on the outgroup comparison method (Watrous and Wheeler 1981). It is carried out individually for each character. The states are coded to reflect the hypothesized polarity, i.e., the presumptive plesiomorphic condition is scored as (0). The outgroup comprises all nondytiscoid adephagan families (Gyrinidae, Haliplidae, Trachypachidae, and Carabidae) and character states found in larvae of Geadephaga and at least one of the presumably basal groups Gyrinidae and Haliplidae (Beutel 1995) are considered as plesiomorphic.

Head Capsule

1. Egg-bursters, instar I: (0) absent; (1) present (Beutel et al. 2006). Absent in larvae of Gyrinidae, Noteridae, and Haliplidae. Present in Aspidytidae (Alarie and Bilton 2005), Hygrobiidae (Alarie et al. 2004), and Dytiscidae and larvae of most groups of Carabidae. Cannot be determined for Meruidae as no first-instar larvae were available for study.

2. Egg-bursters, instar II: (0) absent; (1) present. Larvae of Aspidytae are unique among the Adephaga in that here the egg-bursters are preserved in the second instar, apparently representing an autapomorphy of the family (Alarie and Bilton 2005).

3. Pore PAe: (0) absent; (1) present. The parietale of Meruidae, Aspidytidae, most Dytiscidae, Amphizoidae, and apparently Noteridae (observation based on instar II of *Hydrocanthus*) are characterized by the presence of the primary pore PAe, which is located close to the primary seta PA13 (Fig. 3). Primary pore PAe is not recorded in Carabidae, *Trachypachus* (Bousquet and Goulet 1984) and Gyrinidae and Hygrobiidae (Alarie et al. 2004). We were unable to determine the condition of primary pore PAe in Haliplidae because of the bad quality of the specimens studied.

4. Anteromesoventral region of parietale: (0) with three primary setae; (1) with two primary setae. The

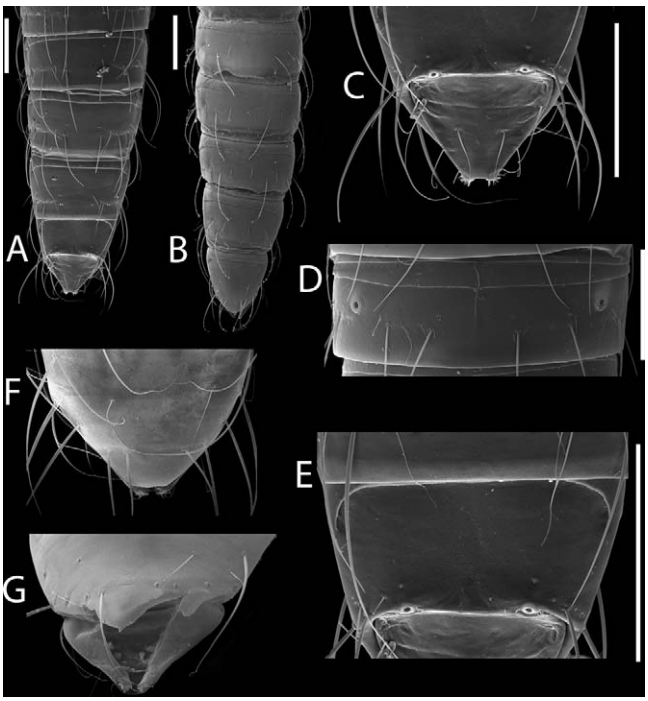

Fig. 8. *M. phyllisae*, third-instar larva, abdomen (scanning electron micrograph). (A) Segments 4–9, dorsal aspect. (B) Segments 4–8, ventral aspect. (C) Segments 8 and 9, dorsal aspect. (D) Segment 1 with spiracles, dorsal aspect. (E) Segment 8 with spiracles, dorsal aspect. (F) Segment 8 and urogomphus, ventral aspect. (G) Segment 9 and urogomphus, ventral aspect. Scale bar = 0.10 mm (A–E), 0.50 mm (F and G).

parietale of larval Adephaga including Meruidae show three primary setae (PA17, PA18, and PA19) anteromesoventrally (Fig. 3B). These setae are included in the ground plan condition of the suborder. Larvae of the Dytiscidae differ in that here one seta is lacking (Alarie 1991, 1998). It is not possible to determine which of setae PA17 and PA18 this is, because of the difficulty in establishing homology of each of them independently across taxa.

5. Adnasalia: (0) present; (1) absent. The anterior margin of the frontoclypeolabrum of larvae of Meruidae is characterized by the presence of adnasalia (=lateral lobes) (Fig. 3A). Presence of adnasalia is generally observed in most Adephaga. Hygrobiidae, and Noteridae (*Hydrocanthus*) lack adnasalia.

Head Appendages

6. Mandible: (0) symmetrical; (1) asymmetrical. Larvae of Meruidae are unique among Adephaga by the presence of asymmetrical mandibles (Fig. 5).

7. Right Mandible: (0) retinaculum present; (1) retinaculum absent. Larvae of Meruidae are characterized by the presence of a retinaculum on the mesal side of the right mandible (Fig. 5B). The presence of a retinaculum is postulated to be part of the ground plan condition of the larval mandible of Adephaga (Beutel 1993). The retinaculum is absent in larvae of Hygrobiidae and Dytiscidae and in some larvae of Noteridae (e.g., *Hydrocanthus, Suphis, Canthydrus;* Beutel et al. 2006). We believe that the mandibular retinaculum is also present in Amphizoidae and Haliplidae albeit in a reduced condition.

8. Left mesal mandibular edge in mature larvae: (0) one cutting edge; (1) two cutting edges delimiting a mesal groove; (2) mandibular sucking channel (Beutel et al. 2006). A mandible with one mesal edge is found in mature larvae of Carabidae and Hygrobiidae Larvae of Aspidytidae, Trachypachidae, Noteridae (partim; e.g., *Noterus*), and Amphizoidae (Ruhnau 1986, Beutel 1993) are characterized by a mandible with two mesal mandibular cutting edges delimiting a mesal groove, which is similar to the condition observed on the left mandible of Meruidae (Fig. 5A). Closed mandibular channels formed by fusion of two mesal edges are present in larvae of Gyrinidae (Beutel and Roughley 1994), Haliplidae (Jaboulet 1960, Beutel 1986), Noteridae (partim; e.g., *Hydrocanthus*), Dytiscidae (excl. Copelatinae and *Hydrotrupes;* De Marzo 1976, Ruhnau 1986, Beutel 1994).

9. Galea: (0) present; (1) absent.

The maxilla of Meruidae is characterized by the presence of a one-segmented galea articulated on a large palpiger (Fig. 4C). Presence of a galea is a ground plan condition of Adephaga. The galea was probably lost independently in Hygrobiidae (Alarie et al. 2004) and most members of the dytiscid subfamily Hydroporinae (Alarie and Michat 2007).

10. Lacinia: (0) present; (1) absent. Presence of a lacinia is probably a ground plan feature of Adephaga

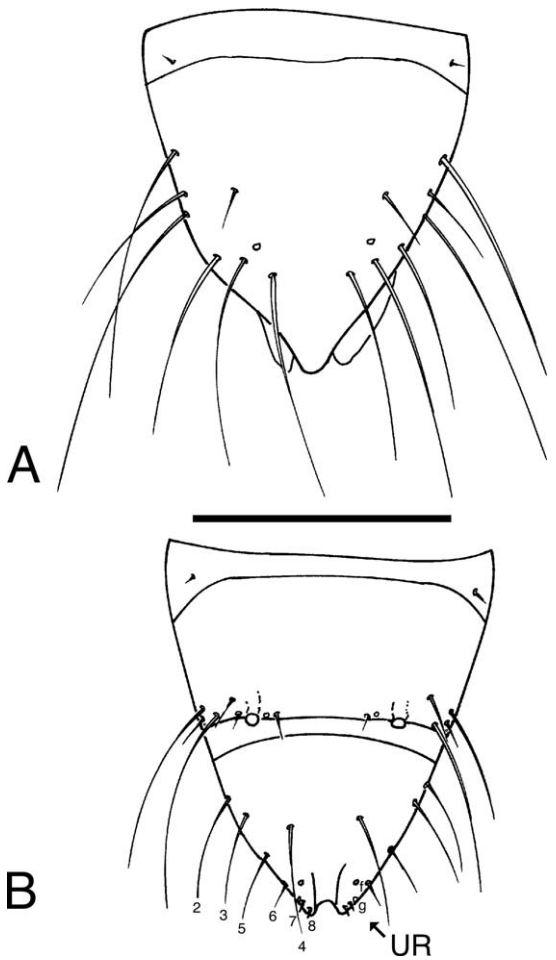

Fig. 9. *M. phyllisae*, third-instar larva, abdomen. (A) Segment 8, ventral aspect. (B) Segments 8 and 9, dorsal aspect. UR, urogomphus. Numbers and lowercase letters refer to primary setae and pores, respectively. Scale bar = 0.10 mm.

(Beutel 1991, 1993). A lacinia is present in Gyrinidae, Haliplidae and most members of the Carabidae. It is lacking in Meruidae, Trachypachidae, Aspidytidae, Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae.

11. Cardo: (0) present; (1) absent. A cardo is present in most Adephaga, including Meruidae (Fig. 1B). The cardo is absent or completely fused with stipes in larvae of Hygrobiidae (Alarie et al. 2004).

12. Antennomere IV: (0) well-developed; (1) reduced. Antennomere IV is well developed in Meruidae, which is considered as an adephagan ground plan character state. Antennomere IV is extremely reduced in larvae of Amphizoidae.

13. Sensorial appendage on antennomere III (A3′): (0) present; (1) absent. Larvae of Meruidae have a bulge-like sensorial appendage on antennomere III identified as A3′ (Fig. 4A). A sensory appendage is present in most Adephaga, although sometimes in a reduced form (e.g., Aspidytidae), which probably represent a ground plan character state. A sensorial appendage is lacking in Gyrinidae and is also apparently lacking in Noteridae. Finally, contrary to a statement by Beutel (1993), a sensory appendage is present in Amphizoidae albeit in a reduced form (bulge-like).

Table 1. Position of ancestral setae and pores on the head capsule of Meruidae

Setae or pores[a]	Position[b]	Setae or pores[a]	Position[b]
FR1	DL	PA9	DPM
FR2	DL	PA10	DAL
FR3	DM	PA11	VAL
FR4	DAp	PA12	VAL
FR5	DAp	PA13	VL
FR6	DAp	PA14	DL
FR7	DAp	PA15	VL
FR8	DAp	PA16	VM
FR9	DAp	PA17	VAM
FR10	DAp	PA18	VAM
FR11	DAp	PA19	VAM
FRa	DL	PAa	DPL
FRb	DM	PAb	DM
FRc	DAp	PAc	DM
FRd	DAp	PAd	DAL
FRe	DAp	PAe	AL
FRf	DAp	PAf	VAL
PA1	DPL	PAh	VApL
PA2	DPL	PAi	VApL
PA3	DPL	PAj	VAL
PA5	DL	PAk	VPL
PA6	DL	PAm	DMP
PA7	DM	PAo	VAp
PA8	DM		

[a] Setae/pores: FR, frontoclypeolabrum; PA, parietale.
[b] Position: A, anterior; Ap, apical; D, dorsal; M, medial; L, lateral; P, posterior; V, ventral.

14. Prementum: (0) undivided; (1) with distinct anteromedian incision; (2) completely divided longitudinally. The prementum of larvae of Meruidae characterized by the presence of a deep anteromedian incision (Fig. 1B), which is similar to the condition observed in the known larvae of Noteridae (Beutel et al. 2006). Whereas undivided in most Adephaga, the prementum is completely divided in larvae of Gyrinidae.

Legs

15. Primary seta CO18: (0) present; (1) absent. The ground plan condition of the larval leg in Adephaga includes the presence of the primary seta CO18, which is articulated dorsoproximally on the coxa (Bousquet and Goulet 1984, Alarie et al. 1990, Alarie 1995). Seta CO18 is present in Meruidae (Fig. 7). It is lacking in Hygrobiidae (Alarie et al. 2004).

16. Primary pore COc: (0) absent; (1) present. Coxa of larval Carabidae and Trachypachidae is characterized by the presence of five primary pores (COa–COe) (Bousquet and Goulet 1984). Of these pores, the primary pore COc does not occur in other Adephaga, including Meruidae (Fig. 7) (not determined for Haliplidae).

17. Trochanteral annulus: (0) absent; (1) present. The trochanter of larvae of Hygrobiidae and Dytiscidae is subdivided by an annular line (Alarie et al. 1990,

Table 2. Position of ancestral setae and pores on legs and urogomphi of the family Meruidae

Setae/pores[a]	Position[b]	Setae/pores[a]	Position[b]	Setae/pores[a]	Position[b]	Setae/pores[a]	Position[b]	Setae/pores[a]	Position[b]	Setae/pores[a]	Position[b]
CO1	DPr	CO13	PPr	TR6	PDi	FE4	PVDi	TA2	ADDi	UR4	DM
CO2	ADPr	CO14	PDPr	TR7	VPr	FE5	PDDi	TA3	ADi	UR5	LDi
CO3	ADPr	CO15	PDPr	TRa	ADDi	FE6	DDi	TA4*	AVDi	UR6	LDi
CO4	APr	CO16	DPr	TRc	AD	TI1	DPr	TA5	PVDi	UR7	DAp
CO5	APr	CO17	AVPr	TRd	A	TI2	ADDi	TA6	PDi	UR8	DAp
CO6	ADi	CO18	PD	TRe	A	TI3	AVDi	TA7*	PDDi	URf	DAp
CO7	AVPr	COa	APr	TRf	PV	TI4	AVDi	TAb	DAp	URg	DAp
CO8	ADi	TR1	D	TRg	P	TI5	PVDi	PT1	AVDi		
CO9	ADi	TR2	AVDi	FE1	DPr	TI6	PVDi	PT2	PVDi		
CO10	AVDi	TR4	VDi	FE2	ADDi	TI7	PDDi	UR2	LP		
CO11	PVDi	TR5	PVDi	FE3	ADDi	TIa	APr	UR3	LP		

[a] Setae/pores: CO, coxa; FE, femur; PT, pretarsus; TA, tarsus; TI, tibia; TR, trochanter; UR, urogomphus.
[b] Position: A, anterior; D, dorsal; Di, distal; P, posterior; Pr, proximal; V, ventral. *, pore-like.

2004; Alarie 1995). A trochanteral annulus is lacking in larvae of every other Adephaga including the Meruidae (Fig. 7). Despite thorough efforts, it was not possible to distinguish a trochanteral annulus in *Amphizoa*, which is contrary to the observation made by Ruhnau (1986), although it was stated that the annulus was present in a reduced form. Absence of a trochanteral annulus in the dytiscid genera *Batrachomatus* Clark and *Allomatus* Mouchamps (Matinae) is deemed to represent a secondary loss (Alarie et al. 2001, Alarie and Butera 2003, Alarie and Watts 2003).

18. Trochanter: (0) with six or seven primary setae; (1) with eight primary setae. The rationale for the polarity of this character is similar to that made for character 14. The larval trochanter of Carabidae and Trachypachidae has eight primary setae (Bousquet and Goulet 1984). Of these, the seta TR8 is lacking among other families of Adephaga including Meruidae (Fig. 7A).

19. Primary setae FE7–FE10: (0) absent; (1) present. Larvae of Aspidytidae, Hygrobiidae, Dytiscidae, and Amphizoidae (assuming that those setae are represented among the several additional setae occurring on the femur of amphizoids) are characterized by the presence of the primary setae FE7, FE8, FE9, and FE10, which articulate along the ventral margin of femur (Alarie and Bilton 2005). These setae are lacking in every other adephagan family including Meruidae (Fig. 7A).

20. Anterodistal additional pore on tibia: (0) absent; (1) present. Within Adephaga, larvae of Aspidytidae and Amphizoidae are distinguished by the presence of an additional pore on the anterior surface (Alarie and Bilton 2005). That pore is lacking in Meruidae (Fig. 7A) and other Adephaga.

21. Seta TA1: (0) present; (1) absent. The larval ground plan of the tarsus of Adephaga includes one hair-like seta (TA1) which is located along the dorsal margin (Bousquet and Goulet 1984, Nilsson 1988, Alarie et al. 1990, Alarie 1995). The primary seta TA1 is lacking in Meruidae (Fig. 7), Amphizoidae and some Gyrinidae (*Dineutus*) and Noteridae (*Hydrocanthus*).

22. Tarsal claws: (0) not pectinate; (1) pectinate. Larvae of *M. phyllisae* are unique among Adephaga in that the tarsal claws are pectinate ventrally.

Abdomen

23. Abdominal segment IX: (0) well developed; (1) reduced and visible; (2) reduced and not visible. The abdominal segment IX is well developed in larvae of Meruidae (Fig. 1A) albeit not visible ventrally (Fig. 1B). The abdominal segment nine is visible in Gyrinidae, Haliplidae (Jaboulet 1960), and Geadephaga

Table 3. Character state matrix

Taxon	01	02	03	04*	05	06	07	08	09	10	11	12*	13	14	15*	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Meru	?	?	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1
Gyrinus	0	0	0	0	0	0	0	2	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0
Dineutus	0	0	0	0	0	0	1	2	0	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	—	0
Haliplus	0	0	?	?	0	0	0	2	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0
Carabidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0		
Trachypachus	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0		
Aspidytes	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	2	0	0			
Amphizoa	1	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	1	0	0	2	1	0	2	?	0			
Hydrocanthus	?	0	1	?	1	0	1	2	0	1	0	0	1	1	0	0	0	0	0	1	0	1	2	1	0	2	1	0			
Noterus	0	0	?	?	1	0	0	1	0	1	0	0	?	1	0	0	0	0	0	?	0	0	2	1	0	2	1	0			
Hygrobia	1	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	1	0	1	0	0	0	2	1	0	2	1	0			
Dytiscidae	1	0	1	1	0	0	1	2	0	1	0	0	0	0	0	0	1	0	1	0	0	0	2	1	0	2	1	0			

Symbols: plesiomorphic character state, 0; apomorphic character states, 1, 2; —, not applicable; ?, not determined; *, uninformative characters, not retained for the parsimony analysis.

Fig. 10. Larval habitat of *M. phyllisae.* (A) Large wet rock seepage on rock outcropping at Tobogan de la Selva, Venezuela, the type locality for Meruidae where the larvae were collected. (B) Same locality, showing collecting method of scrapping the rock surface into a fine mesh fabric. (Online figure in color.)

(e.g., Beutel 1995) but distinctly reduced in Aspidytidae (Alarie and Bilton 2005). Segment IX is not visible in Hygrobiidae, Amphizoidae, Noteridae, and Dytiscidae.

24. Segment X: (0) well developed, pygopod-like; (1) absent or extremely reduced. The abdominal segment X is well developed and pygopod-shaped in larvae of Gyrinidae, Haliplidae (*Brychius* and *Haliplus;* Jaboulet 1960), and Geadephaga but extremely reduced or absent in larvae of other Adephaga, including Meruidae (Figs. 1; 8A and C).

25. Spiracles: (0) polypneustic; (1) oligopneustic. The adephagan respiratory system has multiple pairs of spiracles (=polypneustic). Meruidae are unique in that here the respiratory system is comprised of only two pairs of spiracles (=oligopneustic) (Figs. 1A and 8A).

26. Urogomphi: (0) absent; (1) present, articulated; (2) present, fixed. The urogomphi are generally present in Adephaga. either fixed in most Carabidae, Meruidae (Figs. 8F and G; 9B), and Trachypachidae or articulated as in Dytiscoidea; they are absent in Gyrinidae (possibly transformed into gills), Haliplidae (excluding Peltodytes; Jaboulet 1960) and few Carabidae.

27. Primary seta UR9, primary pores URd, URe, URf: (0) present; (1) absent. The ground plan pattern of setae and pores of the urogomphi of both Carabidae and Aspidytidae includes nine primary setae and seven pores (Alarie and Bilton 2005). This is postulated to represent the ground plan condition of the ancestor of Carabidae + Dytiscoidea. The primary seta UR9 and the primary pores URd, URe, and URf are lacking on the urogomphus of Hygrobiidae (Alarie et al. 2004), Dytiscidae (Alarie and Harper 1990, Alarie 1995) and probably Meruidae (Figs. 8F and 9B) and Noteridae, although the reduced shape of urogomphi in these taxa does not allow a decisive conclusion. This character cannot be studied in Gyrinidae and Haliplidae owing to the absence of urogomphi in these taxa as well as in Amphizoidae because of the presence of numerous additional sensillae.

28. Abdominal sternite 8: (0) not covering abdominal venter IX; (1) covering abdominal venter IX. Larvae of *Meru phyllisae* are unique among Adephaga in that here the abdominal sternite VIII is elongated posteriorly covering the abdominal segment IX. As a result of this, the abdomen is seen as comprised of eight segments ventrally, whereas nine segments are fully developed (Figs. 1; 8A and B).

Discussion

The mature larva of *M. phyllisae* was described and documented in detail in this contribution, and this species has turned out to be characterized by three unique larval character states: the presence of asymmetrical mandibles (character 6; Fig. 5), the presence of pectinate claws (character 22; Figs. 6C and 7); the presence of only two pairs of spiracles on abdominal segments I and VIII, respectively (character 25; Fig. 1A), and the posterior elongation of the abdominal sternite VIII, which overlaps the abdominal sternite IX (character 28; Figs. 8B and 9B). All these features indicate that Meruidae are very distinctive within Adephaga, which warrant a placement in a separate family.

The phylogenetic relationships of the aquatic adephagan families were analyzed recently based on morphology and DNA sequence data (Ribera et al. 2002a,b; Alarie and Bilton 2005; Balke et al. 2005, 2008; Beutel et al. 2006). These studies, however, did not include larval *M. phyllisae*, which is described here. Heuristic search with random-addition sequence replicates found minimal length topologies of 38 steps from the data matrix presented in this study (Table 3). TBR swapping of minimal-length trees from 1,000 random-addition replicates led to three trees (CI = 0.58; RI = 0.69). The bootstrap consensus tree of the three most parsimonious trees reconstructed is shown in Fig. 11.

A placement of Meruidae within the Dytiscoidea (Noteridae, Amphizoidae, Aspidytidae, Hygtobiidae, and Dytiscidae) seems rather clear based on external larval morphology (Fig. 10, bootstrap value = 0.80).

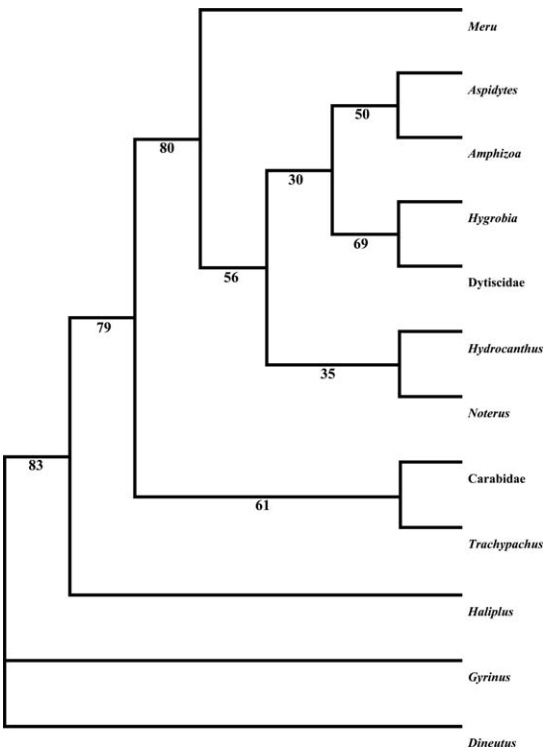

Fig. 11. Bootstrap consensus tree of three most parsimonious trees reconstructed (18 larval informative characters of 12 taxa); bootstrap support values are indicated above branches.

Larvae of *M. phyllisae* share with other members of this superfamily a reduction of the abdominal segment X (character 24; Fig. 1) and the absence of the primary seta UR9 and of the primary pores URd, URe and URf (character 27; Fig. 9B). Like other Dytiscoidea, larvae of Meruidae characterized also by the presence of the primary pore PAe (character 3; Fig. 2A), (secondary loss in Hygrobiidae) and the absence of a lacinia (character 10) (putative synapomorphy of Trachypachidae + Dytiscoidea according to Beutel 1998). Inclusion of Meruidae within the Dytiscoidea based on larval morphology therefore reinforces the hypothesis formulated in previous studies based on adult morphology and DNA sequence data (Beutel et al. 2006, Balke et al. 2008).

On the basis of larval morphology, *Meru* seems to have retained two plesiomorphic character states, which would argue in favor of a more basal position of this group within the Dytiscoidea. Indeed, larvae of Meruidae have retained a fully developed abdominal segment IX (character 23; Fig. 1A) as well as fixed urogomphi (character 26; Fig. 9B). The hypothesis of sister-group relationship of Meruidae with other Dytiscoidea (Fig. 10) cannot be seen as strongly supported, however, owing to the low bootstrap value obtained (50).

Our study is also in agreement with the hypothesis of a sister-group relationship of Amphizoidae +Aspidytidae + Hygrobiidae + Dytiscidae with *Meru* and Noteridae, which is supported by the shared presence of the primary setae FE7, FE8, FE9, and FE10 on femur (character 19) and the absence of an anteromedian incision on the prementum (character 14) among those taxa. This is once again in agreement with recent studies based on adult morphology and DNA sequence data (Beutel et al. 2006, Balke et al. 2008).

The absence of a trochanteral annulus (character 17; Fig. 7) exclude Meruidae, Noteridae, Aspidytidae, Amphizoidae, and Geadephaga from Dytiscidae and Hygrobiidae. We suggest that the presence of a trochanteral annulus represents an evolutionary novelty within Adephaga likely to have a direct functional relationship to swimming ability. Indeed, because legs probably enhance the swimming propensity upon contraction of the body (similar to rows), the presence of a broken line at the level of the narrowest portion of leg (i.e., trochanter) would have provided greater leg flexibility and resistance to an aquatic larva. It is noteworthy that larvae of both hygrobiids and dytiscids characterized by the presence of a more or less large number of secondary setae on legs. Hair-bearing appendages along with size and shape of the legs may have a direct functional relationship to swimming ability (Loudon et al. 1994, Vogel 1994). Like Aspidytidae, Meruidae do not add secondary setae throughout their ontogenetic development (Aspidytae only have two to three secondary setae; cf. Alarie and Bilton 2005). It is therefore postulated that a reduced number of setae on legs allied to the absence of a trochanteral annulus would indicate that their larvae are not adapted for swimming, which could also argue in favor of a transitional stage from a fully terrestrial to a fully aquatic condition within the Dytiscoidea.

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