A new aquatic beetle family, Meruidae, from Venezuela (Coleoptera: Adephaga)

PAUL J. SPANGLER and WARREN E. STEINER JR

Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

Abstract. An unknown beetle collected in the Territorio Federal Amazonas, Venezuela, and designated as belonging to a new family, is described (as *Meru phyllisae* **gen.n.**, **sp.n.**) and illustrated by line drawings and scanning electron micrographs. The new family, Meruidae, is diagnosed and assigned to the suborder Adephaga with a discussion of some characters and likely phylogenetic affinities. With a body length of 0.85–0.9 mm, *M. phyllisae* is the smallest known member of aquatic Adephaga. Based on the observed skeletal and behavioural characters to date, the taxon appears to represent the sister clade to the remaining families of Dytiscoidea, but also has features suggesting a close relationship among Noteridae and/or Haliplidae. A description and photographs of the habitat are included, with a list of other associated water beetle taxa. Some observations on the behaviour of captive beetles are given. The minute 'comb-clawed cascade beetles' are known only from the type locality, El Tobogán, where streams flow among exposed areas of bedrock in the geologically ancient Guyana Shield region.

Introduction

It was during a stopover en route to study the biota of the Venezuelan Cerro de la Neblina Tepui that the first specimens of the beetle species, genus and family described in this paper were collected. On 21 January 1985 we visited El Tobogán, near Puerto Ayacucho, in the Federal Territory of Amazonas, Venezuela, and found it so interesting that it warranted a second visit the next day, and several return trips in years to follow. The site is named after the natural 'water slide' where a stream, the Rio Coromoto, flows from tropical forest over a slope of granitic bedrock, naturally exposed and free of vegetation, then continues into a forested valley. The site lies on the 'ancient core' of northern South America, the Guyana Shield. Habitats for aquatic beetles included the swift to meandering stream over rock and sandy bed, both sunlit and shaded, the film of water

with wet leaves adhering to the rock face, and rivulets draining onto the bedrock from adjacent hillsides.

Field notes (WS) refer to our discovery of 'a few tiny pale tan beetles less than 1 mm long – look dytiscoid but carabid-like – not sure what family'. We also considered them to possibly be a new genus of Torridincolidae. These were taken by seining stirred substrate in the stream margin pool below the granite slide. It was not until our return to the museum 7 weeks later, after some dissection and examination of the specimens under a microscope, that we realized the beetles may represent a new family of Adephaga.

Only eight adults of the unknown taxon were collected in 1985; Spangler and others (see specimen data following description) returned to El Tobogán in 1986, 1987, and 1989 to search for additional specimens and, if possible, to find larvae or pupae that could be associated or reared. During those trips, more adults were collected, but no tiny larvae that could be those of the new taxon were found. Although the description of the new family would benefit from the inclusion of larval and pupal characters, we do not see any time soon when the immature stages may be discovered. Realizing that the taxon represents a crucial discovery and contribution towards the understanding of adephagan evolution, we offer the following description.

Correspondence: W. E. Steiner, Department of Entomology, NHB-187, Smithsonian Institution, Washington, DC 20560-0187, U.S.A. E-mail: steinerw@si.edu

Unpublished for the purposes of zoological nomenclature (Art. 8.2. ICZN)

Meru gen.n.

*Type species. Meru phyllisae*, **sp.n.**

Description. Size very small, length 0.85–0.9 mm; width 0.38–0.41 mm. Body form generally ovate, convex dorsally, less so ventrally (Fig. 1), widest at basal quarter of elytra; prothorax broadly attached to mesothorax and elytral base (Fig. 2A–I). Colour generally dark brown to yellowish brown. Most surfaces of body bearing flat, wrinkled 'setae' (possibly membranous papillae; see comments below) arising from the anterior side of large, shallow punctures.

Head (Figs 2A, B, D, E, 3A, B) prognathous, slightly longer than wide, with retracted neck region; eyes lateral, broadly elliptic, prominent; ommatidia numbering five by nine across axes of eye. Frons smooth, slightly convex, with reticulate microsculpture; laterally and basally with scattered shallow punctures and fine setae; frontoclypeal suture obscure; labroclypeal suture nearly straight. Labrum trapezoidal, with scalelike microsculpture; front edge with a

Fig. 1. *Meru phyllisae*, scanning electron micrograph, lateral habitus.
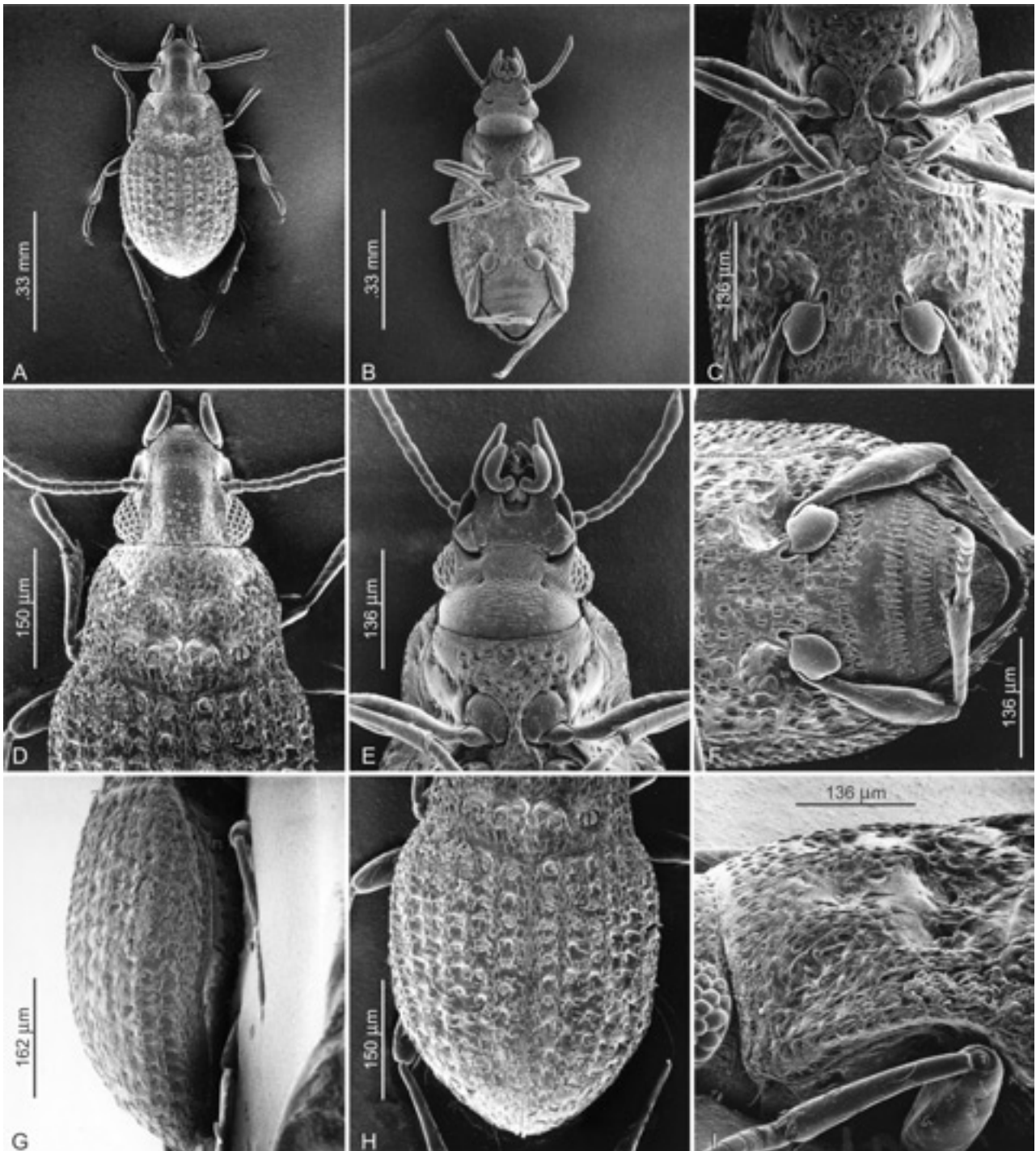
Fig. 2. *Meru phyllisae*. Scanning electron micrographs. A, Habitus, dorsal view; B, habitus, ventral view; C, thoracic sterna; D, head, pronotum and bases of elytra; E, head and prosternal area; F, metasternum and abdomen; G, right elytron; H, pronotal and elytral bases; I, pronotum, lateral view.

shallow median notch covered by opposing, overlapping, spatulate setae (Fig. 3E) and with three tapered setae originating from small pits lateral to base of spatulate seta; a pair of small, flat, toothlike setae imbedded in the anterior margin of the notch. Antenna (Fig. 4A–F1) longer than head, filiform, glabrous, eleven-segmented; scapus very short and nearly hidden; pedicellus almost globular, urn-shaped, bearing a few slender setae; antennomere III as

Fig. 3. *Meru phyllisae*. A, Head, lateral view; B, head, anterior view; C, mouthparts, ventral view; D, labial palpal bases; E, head, anterior view, detail of mouth; F, right maxillary and labial palpi, ventral view; G, right maxillary palpus, apex; H, left maxillary palpus, apex; I, right labial palpus, apex.

long as pedicellus but more narrow, nearly twice as long as wide, subcylindrical, thickest towards apex; antennomeres IV–X of similar form, but V, VII and IX longer and thicker than the adjacent ones; antennomeres VII and IX bearing a platelike sensorial patch ventrally; antennomere XI longer than the preceding two combined, thickest at middle and obliquely tapering to a narrow apex, with two platelike sensorial patches near apex on ventral side. Mandibles
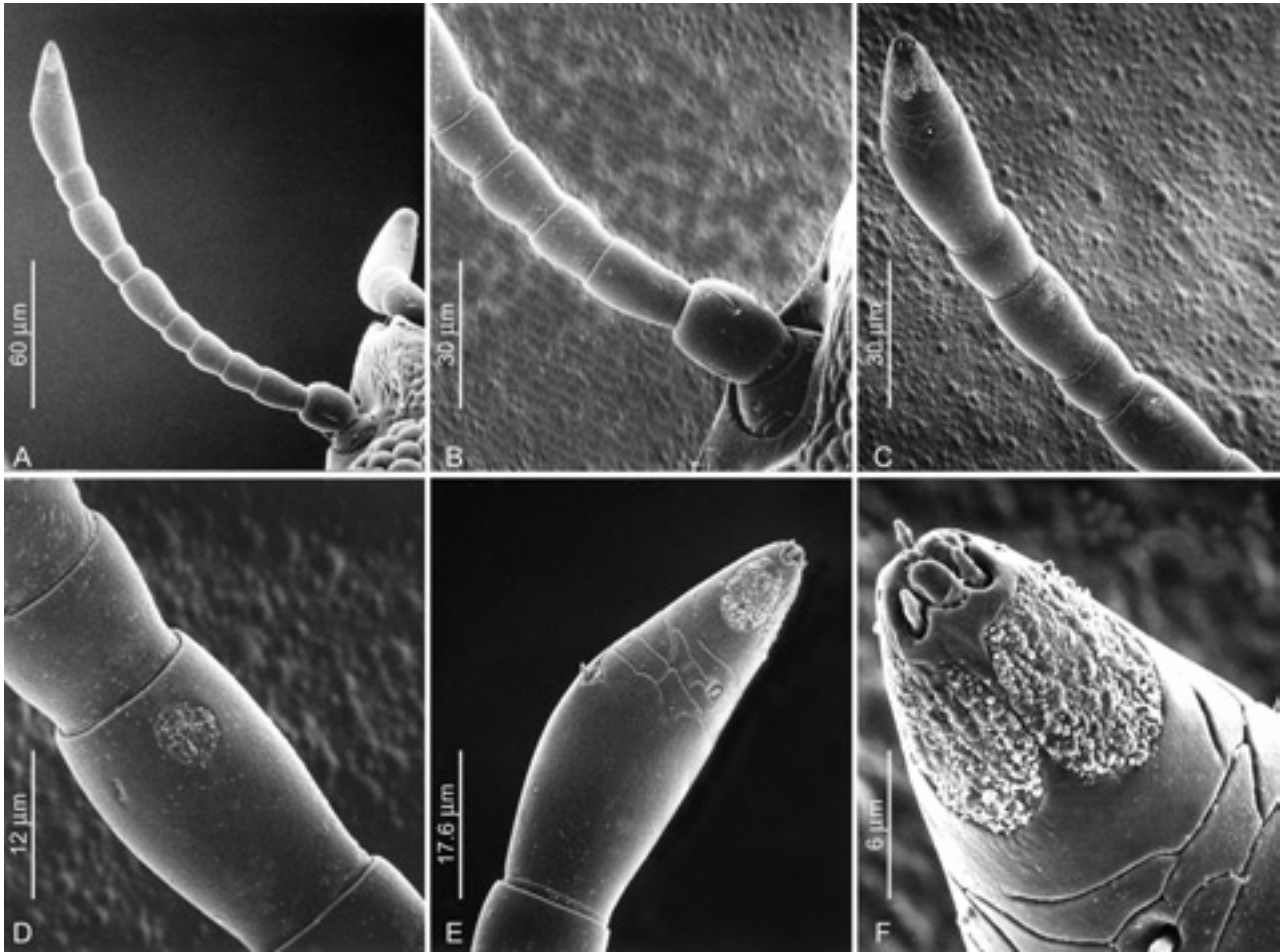
Fig. 4. *Meru phyllisae*, antennae. A, Left, dorsal view; B, right, segments 1–7, ventral view; C, right, segments 7–11, ventral view, showing sensorial patches on segments 7, 9 and 11; D, right, segments 6–8, ventral view, showing sensorial patch on segment 7; E, left, lateral view, apical (eleventh) segment with sensorial patches; F, right, ventral view, apical (eleventh) segment with sensorial patches.

(Fig. 7A) nearly twice as long as wide, with a single, blunt, falcate, apical incisor and median terebral tooth; brushes of trichiae, molar teeth, and retinaculum absent. Left mandible slightly longer than right, terebral tooth broadly angular; inferior terebral ridge with one or two minute teeth. Right mandible with terebral tooth truncate and closer to apex than that of left mandible; basal face with several small wrinkles. Maxilla (Fig. 7B) with cardo small, wedge-shaped; stipes and lacinia fused; lacinia stout, elongate, glabrous, with a curved, robust apical spine and seven setae on inner side; galea simple, two-segmented, shorter than lacinia, with apical segment elongate, cylindrical, smoothly rounded at apex; palpus four-segmented; apical segment slightly longer than combined length of segments 1–3, with sensory structures on the distal part (Fig. 3F–H). Submentum broad, with distinct tentorial pit at basolateral corner (Figs 2E, 3C); mentum flat, smooth, slightly more than half as wide as head, with two long setae on each side at approximately middle; prementum recessed, inserted between anterolateral rounded lobes of men-

tum; base of palpifer with a single small seta; ligula moderately extended and rounded apicomedially, with twelve to fourteen apical setae (Fig. 3C, D); labial palpus three-segmented; apical segment swollen and slightly longer than combined length of segments 1 and 2, with apical sensory structures (Fig. 3C, F, I) similar to those of maxillary palpus.

Prothorax (Figs 2D, E, I, 8A) about four-fifths as wide as elytra; pronotum widest at base, slightly wider than long, lateral margin sinuate, not beaded; anterior margin straight, anterior corners narrowly rounded; posterior corners angled; posterior margin nearly straight between corner and middle, tightly fitted against base of elytron and forming an angle of about 125° with other side at middle; disk evenly convex, surface with four shallow depressions on each side; surface coarsely, densely punctate; each puncture with a long, robust, flattened and wrinkled seta, pleated at base, arising from anterior edge of puncture and recumbent across it; length of seta about twice the diameter of a puncture; scattered, hairlike setae also

present, arising from smooth areas between the large punctures. Thoracic sternites with a similar combination of setae and punctures, but larger and more sparsely placed laterally. Prosternum (Figs 2E, 8A) with notopleural and pleurosternal sutures visible; propleuron large, extending behind coxa; procoxal cavity closed internally. Cervical sclerite absent. Anterior margin of prosternum evenly arcuate with a fine fringe of microsetae along edge and on each side with one large, anteriorly directed, club-shaped seta, with apex flattened and toothed, brushlike (Fig. 2E). Prosternal process very narrow between procoxae but wider and truncate behind them (Fig. 8A). Mesosternite, metasternite and lateral part of metacoxae fused, with sutures not discernible laterally (Fig. 8B); mesosternite with pentagonal depression partly covered by (articulated with) prosternal process. Transverse ridge of metaventrite absent. Metacoxal plates small, not covering base of trochanter, with lateral margins indistinct anteriorly; median lamina of metacoxae not distinctly separated from lateral part; posterior margin straight, with a small median emargination and deep incisions for trochantinal articulations

(Figs 2C, F, 8B). Metendosternal process slender, median ridge (metacoxal septum) attached to the metasternite for two-thirds of its length, ending with a slender-armed, Y-shaped metafurca anteriorly (Figs 9, 10A, B).

Scutellum not visible. Elytron convex, twice as wide as long, dorsally with setae and punctures like those on pronotum (Fig. 5A, B) in addition to rows of large, deep, strial punctures that do not bear setae; sutural stria absent and sutural edge not beaded; lateral margin arcuate in lateral view (Fig. 5A); epipleuron indistinct; inner surface smooth, laterally with a large, locking pit at about midlength and a round patch of granular surface (presumably for wing folding) anterior to it (Fig. 5C, D). Hind wings dimorphic (Fig. 11A, B), either fully developed with venation moderately developed and distal half folded (Figs 11B, 12), or brachypterous, as long as elytron, with venation very reduced and distal half appearing shrunken (Fig. 11A); margins with a fringe of long setae; subcubital binding patch absent; oblongum cell not discernible. Procoxa and mesocoxa globular; trochanters smooth, unmodified. Metatrochanter large, about twice the size of pro- and
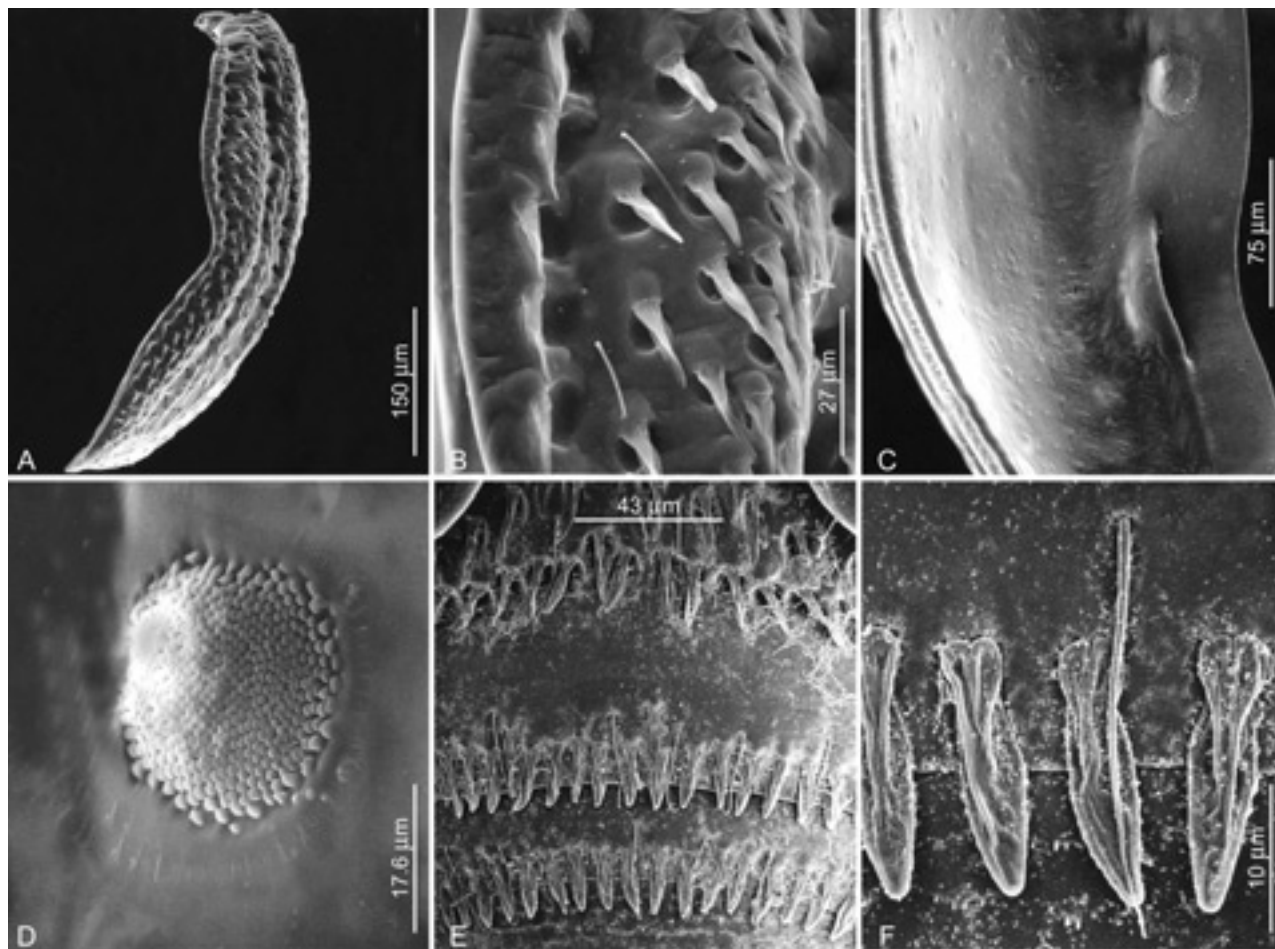
Fig. 5. *Meru phyllisae*. A, Left elytron, lateral view; B, left elytron, detail of margin; C, left elytron, inner surface; D, left elytron, wing-folding patch on inner surface; E, abdominal sternites, detail of posterior margins of 1–3; F, abdominal sternite 3, detail of posterior margin.

mesotrochanter, globular, swollen posteriorly; junction with metafemur oblique and sinuate. Femora smooth, club-shaped, widest at about apical third, with scattered sparse hairlike setae, some brush-tipped, and a row of five to seven thick, branched setae on dorsal surface. Metafemur very slender basally, attached dorsolaterally to trochanter; distal two-thirds swollen. Tibiae simple, straight, gradually thickening from base to near apex, with sparse hairlike
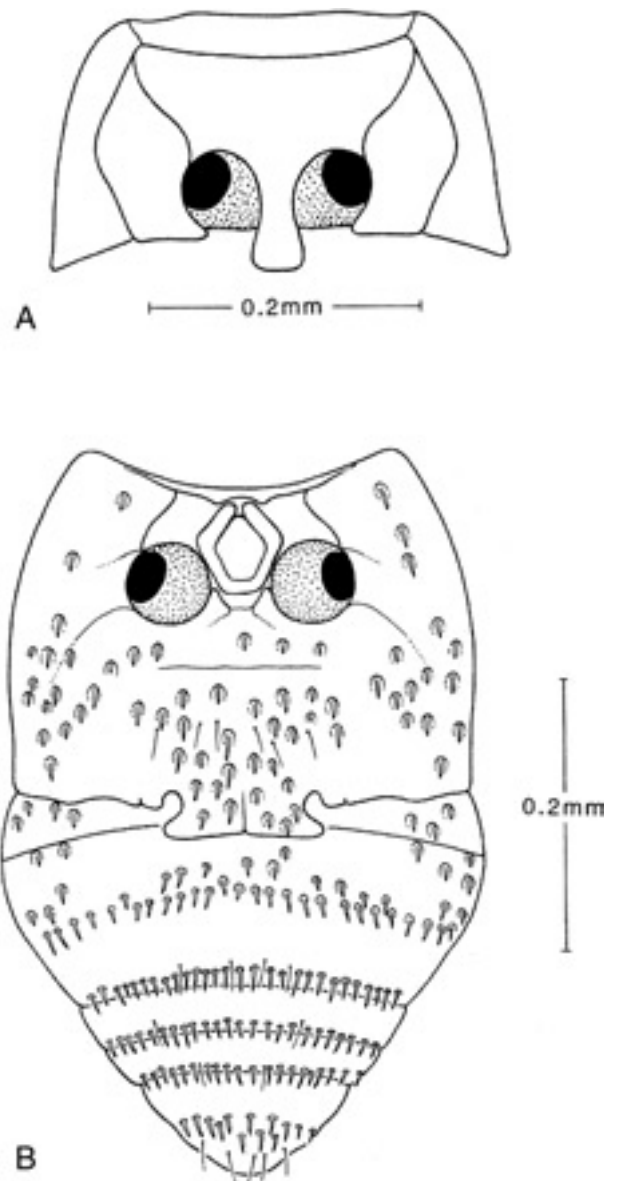

Fig. 6. *Meru phyllisae*. A, Front and mid legs, left, anterior view; B, front and mid legs, right, posterior view; C, D, mesotibia, right, apex; E, hind tarsus, left, ventral view; F, hind tarsus, left, posterior view; G, claws, right mesotarsal, lateral view; H, claws, left metatarsal, oblique view; I, claws, right metatarsal, ventral view.
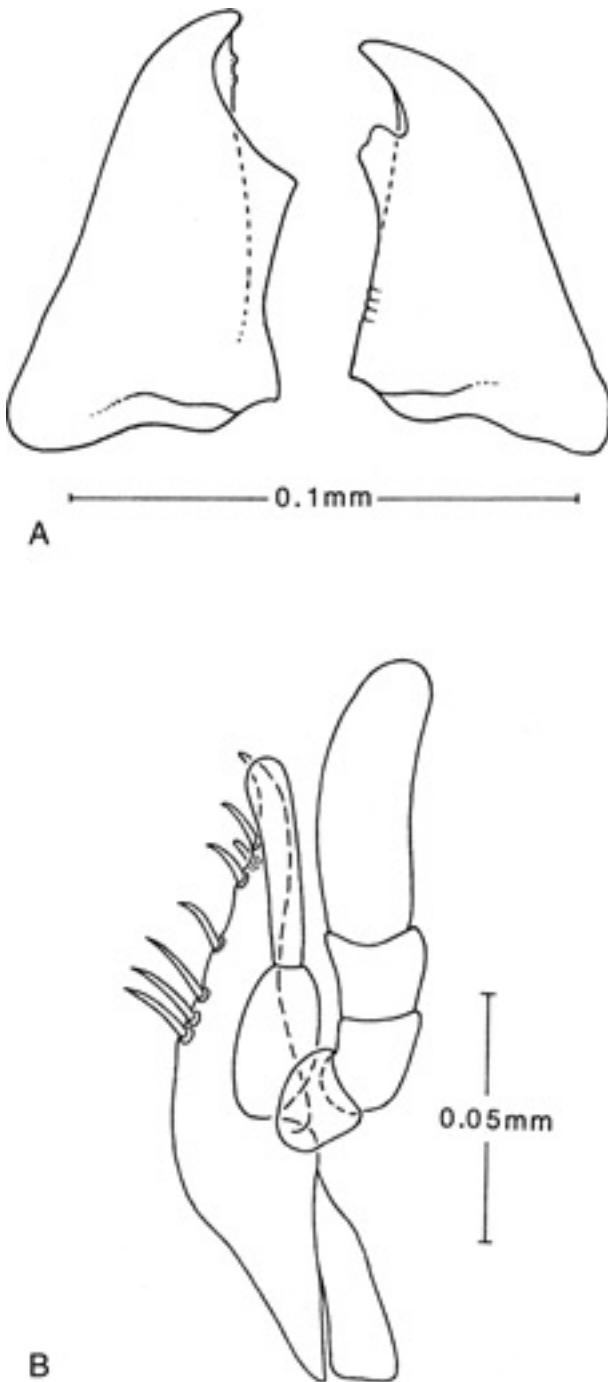
Fig. 7. *Meru phyllisae*. A, Mandibles, dorsal view; B, maxilla, left, ventral view.

Fig. 8. *Meru phyllisae*, sterna. A, Outline of prothorax; B, hind body.

setae, irregularly distributed, becoming more stout towards apex of tibia; each tibia bearing a pair of toothed apical spurs, both trident on pro- and mesotibia, one trident and one laterally pectinate on metatibia (Fig. 6A–F). Tarsal formula 5-5-5; last tarsomeres longer than combined lengths of the preceding two; tarsomeres 1 and 2 each with four stout, ventral setae, 3 and 4 with two setae, and 5 with one seta; hind tarsus with basal tarsomere longest; length equals combined length of tarsomeres 2–4. Tarsal claws large, pectinate, with four to five teeth (Fig. 6G–I). Empodium small, smooth, padlike.

Abdomen with six visible sternites (morphological sterna II–VII); visible sternites 1, 2 and 3 completely fused, with sutures indistinct (positions marked by row of setae); first visible sternite deeply and broadly divided medially for reception of metacoxal processes (Fig. 13), internally with a heavily sclerotized, transverse septum along posterior margin; posterior margins of sterna 1–5 bearing a comblike row of robust, flattened and grooved setae and forming a fringe along with fewer hairlike setae (Figs 2F, 5E, F, 8B); sternites 1 and 2 with punctures bearing robust wrinkled setae scattered over surface; the flat pleated setae on sternites 3–5
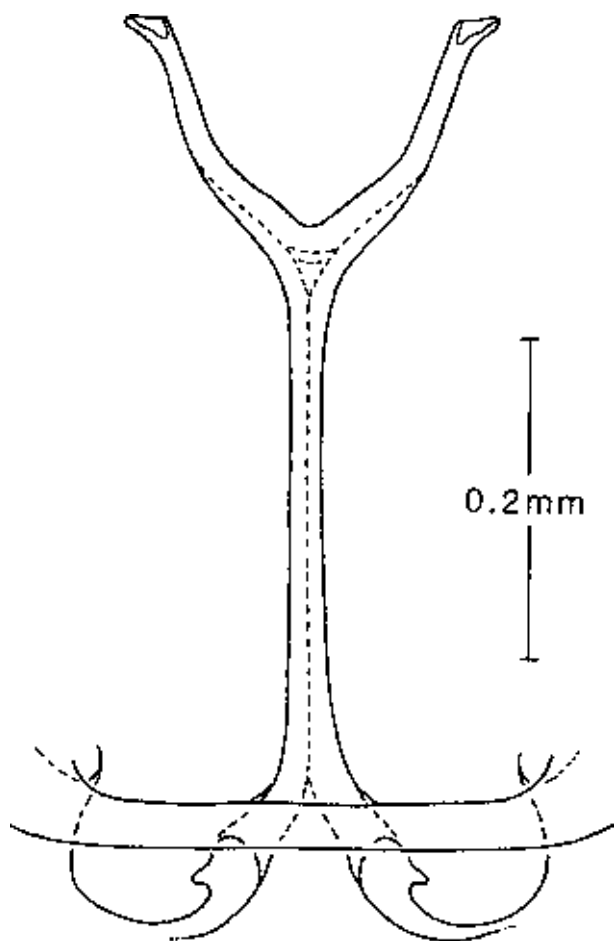
Fig. 9. *Meru phyllisae*, metendosternite, dorsal view.

without associated punctures (unlike others elsewhere on body); apical (sixth) sternite wider than long, apical margin rounded; surface bearing an irregular transverse band of flattened and grooved setae and fewer hairlike setae (Fig. 8B).

Male genitalia (Fig. 14A) asymmetric; basal piece absent (or fused with apical piece); median lobe with a curved, tubular base, becoming more straight, dorsoventrally flattened and tapered towards apex; parameres vestigial, scalelike, left paramere more rounded, laterally positioned at base of median lobe; right paramere smaller, more narrow, positioned on ventral side of base of median lobe. Aedeagus with only slight torsion in repose. Ring sclerite (ninth sternum) complete (Fig. 14B). Female genitalia lacking sclerotized structures except for reduced short gonocoxae, each bearing a few small apical setae (Fig. 15).

Proventriculus (Fig. 16) with four larger plates smooth, each with single median acuminate and serrulate flap that appears to be capable of folding against the base; smaller four plates vase-shaped in side view, smooth, with a fringe of fine hairs.

Wing dimorphism. Of twelve specimens that were fully dissected, ten possessed atrophied wings and two had the fully developed condition.

Wrinkled flat setae on the body. These appear to be membranous papillae, very different from the normal, fine setae among them. It is possible that these structures may have a respiratory function, but determining their connection to the tracheal system was beyond the scope of this study. On dry beetles examined under the scanning electron microscope, broken examples of the papillae have been seen and they are hollow, but details of the basal attachment have not been clearly viewed; no opening to the cuticle was observed.

*Etymology*. 'Meru' means 'waterfall' in the language of the Pemon people of the tepui region of Venezuela.

Meru phyllisae sp.n.

Description. Holotype, male, length 0.85 mm; width 0.39 mm. Wing condition undetermined. Other characters are as described for the genus.

Etymology. The specific name honours Phyllis M. Spangler who assisted in the discovery of this beetle and has been of great service to the study of aquatic Coleoptera for many years.

Type data and material examined. Holotype ♂, labelled 'VENEZUELA: Amazonas, Puerto Ayacucho (40 km S) at Tobogan, 22 January 1985/Seine of sunlit stream, slow water over sand & gravel, P. J. & P. M. Spangler, R. Faitoute, W. Steiner' and 7 paratypes, same data. Other paratypes, 8, same data except '23 February 1986, sandy margins, P. J. Spangler, Colln. # 10'; 1, same data except 'leaf packs, Colln. # 12, 24 February 1986, P. J. Spangler'; 1, same data except '26 February 1986, rootlets at shore edge, P. J. Spangler, Colln. # 19'; 7, same data except '27 February 1986, P. J. Spangler, Colln. # 20'; 19, same data except '28 February 1986, stream between cascades, P. J. Spangler, Colln. # 21'; 2, VENEZUELA, T. F. Amazonas, Puerto Ayacucho (40 km S) at Tobogán, 14 November 1987, Colln. # 1, P. J. Spangler & R. A. Faitoute'; 77, same data except '16 November 1987, Colln. # 7, P. J. Spangler & R. A. Faitoute'; 9, same data except '17 November 1987, Colln. # 11, P. J. Spangler & R. A. Faitoute'; 1, same data except '18 November 1987, Colln. # 13, P. J. Spangler & R. A. Faitoute//Collected by pouring water over stream bank & washing riparian insects into seine'; 3, 'VENEZUELA, T. F. Amazonas, Puerto Ayacucho (40 km S), El Tobogán, Caño Coromoto, 18 January 1989, P. J. Spangler, R. A. Faitoute & C. B. Barr//Collected at night with head lamp at upper shelter'; 2, same data except '20 January 1989, upper seep'; 1, same data except '20 January 1989, seined, at upper seep'; 1, same data except '23 January 1989, seined, stream between cascades'; 14, same data except 'January 1989 – reared'.
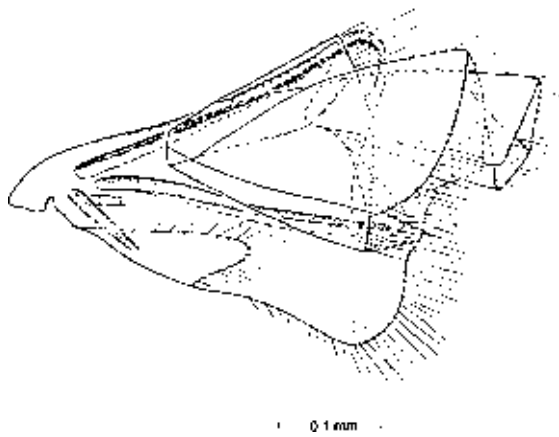
The holotype (and some paratypes from each of the labelled lots above) are deposited in the National Museum
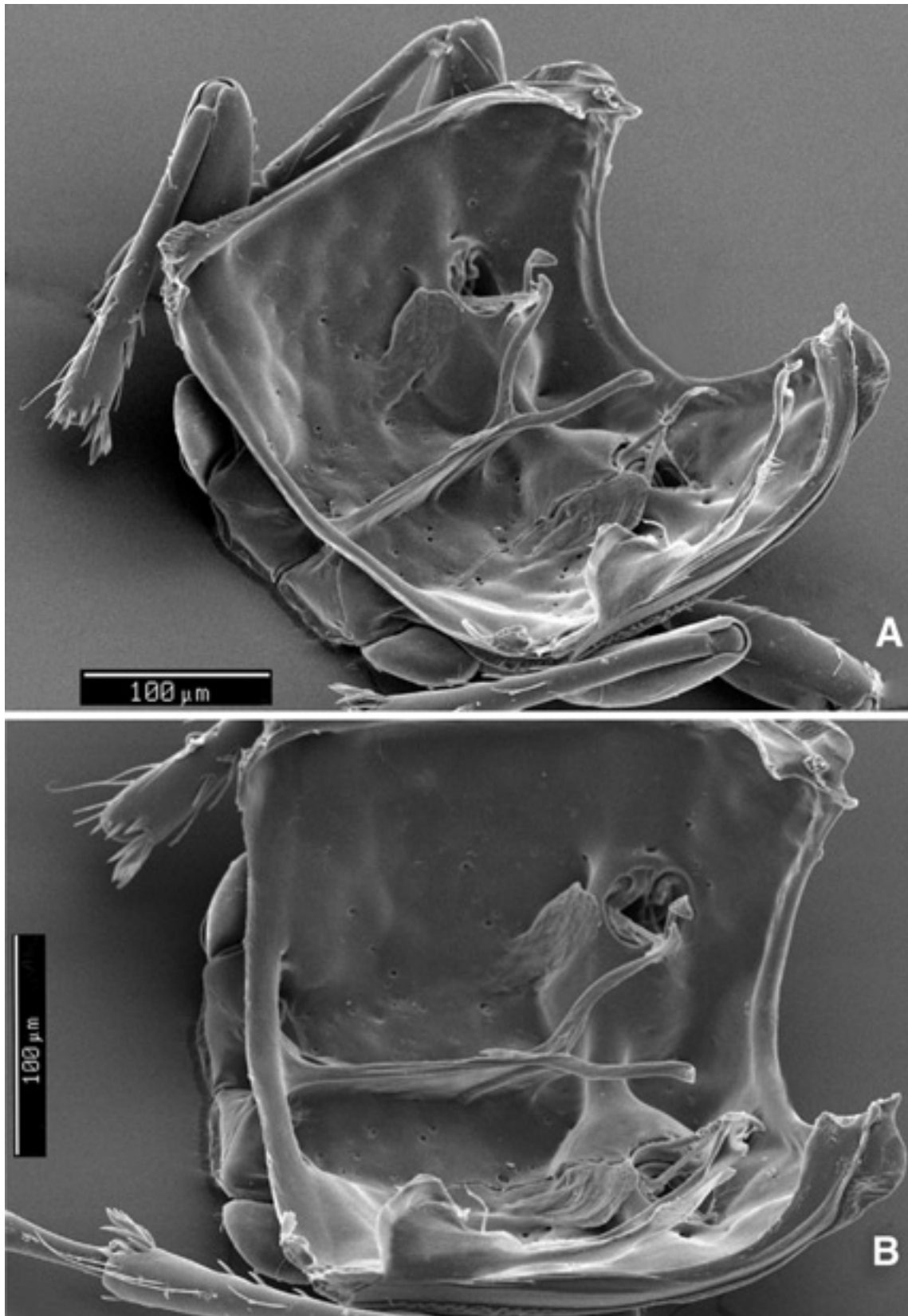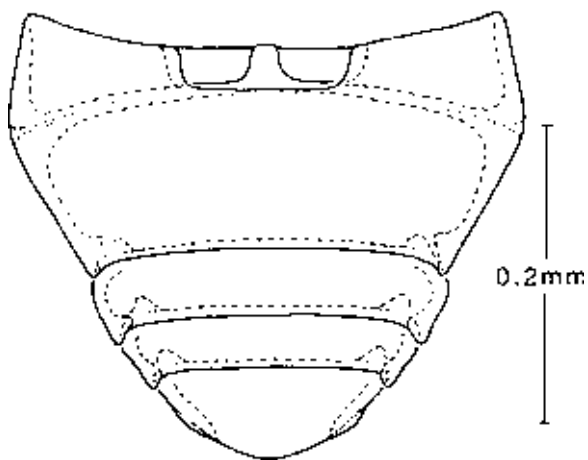
Fig. 10. *Meru phyllisae*, metendosternite, scanning electron micrographs. A, Oblique dorsolateral view; B, dorsolateral view.
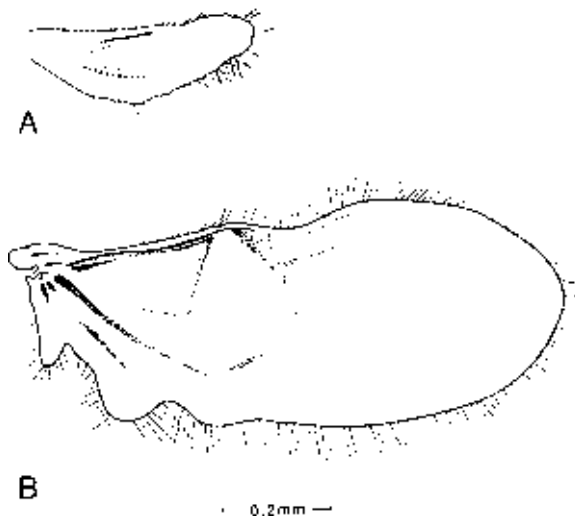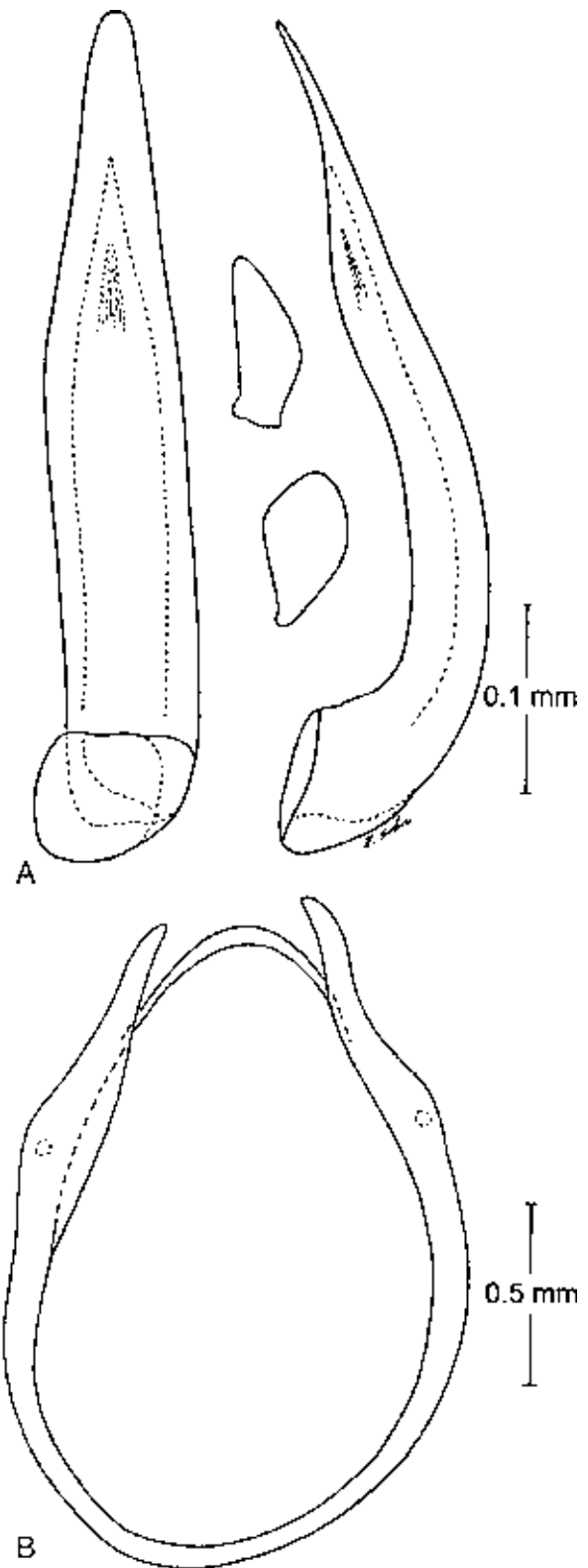
Fig. 11. *Meru phyllisae*, hind wing. A, Brachypterous condition; B, macropterous condition.

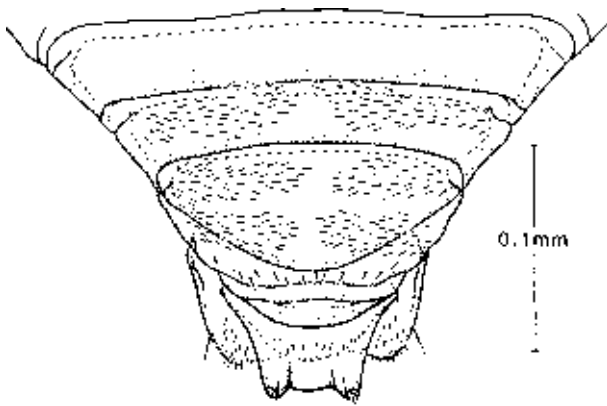**Fig. 12.** *Meru phyllisae*, hind wing, macropterous condition, in folded position.

Fig. 13. *Meru phyllisae*, visible abdominal sterna.

Fig. 14. *Meru phyllisae*, male genitalia. A, Median lobe, dorsal (left) and lateral (right) views, with parameres (centre), right (upper) and left (lower); B, ring sclerite (ninth sternite).

Fig. 15. *Meru phyllisae*, female genitalia and apical abdominal terga, dorsal view.

of Natural History, Smithsonian Institution, Washington, DC, U.S.A.; other paratypes are deposited in the following institutions: The Natural History Museum, London; Museum of Comparative Zoology, Harvard University, Cambridge; California Academy of Sciences, San Francisco; University of Arizona, Tucson; Canadian National Collection, Ottawa; Museo Argentino de Ciencias Naturales, Buenos Aires; Instituto de Zoologia Agricola, Maracay; Museum National d'Histoire Naturelle, Paris; Institut Royal des Sciences Naturelles de Belgique, Bruxelles; Naturhistorisches Museum, Wien; Zoologische Sammlung des Bayerischen Staates, Munich; Institut für Spezielle Zoologie und Evolutionsbiologie, Jena; Australian National Insect Collection, CSIRO, Canberra; Entomological Laboratory, Kyushu University, Fukuoka, Japan.

Type locality. VENEZUELA: District of Amazonas, at El Tobogán; 40 km south of Puerto Ayacucho, 2°14′N 63°45′W.

Habitats and collecting at the type locality

Various aquatic microhabitats were sampled at El Tobogán and yielded a rich assemblage of water beetle species. The cascade over the open bedrock (Figs 17A, B, E, H) was fed by an attractive white-water stream, the Rio (Caño) Coromoto, which originated in the mountains above. The stream emerged from the densely shaded jungle and flowed rapidly downhill through the forest for several hundred metres before the gradient flattened out as it reached an opening at a moderately deep, natural pool where the stream divided into two branches. Upon leaving the pool, the main water course flowed rapidly into a well-worn channel (Figs 17A, E) along the base of an adjacent hill. By contrast, the second branch fanned out and covered the broad expanse of granite bedrock with a shallow (3–5 mm) cover of slowly flowing water (Fig. 17C) with fallen leaves adhering to the wet rock. This broad area outlined the uppermost level of the entire cascade, which consisted of an upper

and lower level; each about equal in length but the upper level was much broader and had a moderate gradient. The bedrock was obviously scoured from eons of periodic flooding and occasionally had an uncharacteristic deep pothole in its midst. The rock cascade emptied into a small, natural pool somewhat altered in past years by a man-made cement dam (Fig. 17E). Below the dam, the stream changed to a nearly level and narrower stretch of 30–35 m as it flowed through a tree-shaded area (Figs 17F, G) to the crest of a lower cascade. The stream was about 3 m wide, 0.3 m deep, and flowing about 1–1.5 m s^{-1} when the photographs (Fig. 17G, H) were taken. The substrate between the upper and lower cascades was rocky and sandy before the water tumbled over the narrower, steeper, and faster flowing lower cascade. The lower level was accessible on one side over an area of scoured granite bedrock. The opposite side of the stream was essentially inaccessible because of the dense jungle, deep channel, steeper gradient, and extremely fast current. Consequently, our collecting was conducted primarily on the broad, shallow surface and margins of the upper level, to and including the slower flowing area between the two cascade levels. Water analysis of the Caño Coromoto provided the following data: pH 5; oxygen 12 p.p.m.; hardness, 0. The water temperature was 28 °C when most of the specimens were collected.

The following aquatic beetle taxa were also collected in and along the matted seepage areas that drained into the upper level of the cascade: Dytiscidae: *Copelatus* Erichson, *Laccodytes* Régimbart, *Desmopachria* Babington, various genera of Bidessini; Noteridae: *Notomicrus* Sharp, and a new genus; Elmidae: *Cylloepus* Erichson, *Gyrelmis* Hinton, *Heterelmis* Sharp, *Austrelmis* Brown, *Microcylloepus* Hinton, *Neoelmis* Musgrave, *Pagelmis* Spangler, *Pilielmis* Hinton, *Phanocerus* Sharp, *Hintonelmis* Spangler, *Stegoelmis* Hinton, *Stenhelmoides* Grouvelle, *Tyletelmis* Hinton, *Xenelmis* Hinton; Hydraenidae: *Adelphydraena orchymonti* Perkins, *Hydraena* Kugelann; Hydrophilidae: *Anacaena* Thomson, *Berosus* Leach, *Chaetarthria* Stephens, *Notionotus* Spangler, *Oocyclus* Sharp, *Phaenonotum* Sharp; Hydroscaphidae: *Scaphydra* Reichardt; Sphaeriusidae: *Sphaerius* Waltl; Torridincolidae: *Hintonia* Reichardt.

The majority of the elmids were obtained from the rocky and shaded stream before it emerged from the jungle or the shaded part that connected the upper and lower halves of the cascade. Other specimens, including some *M. phyllisae*, were taken by collecting the leaves containing beetles from the seepage areas into a fine-mesh dip-net or seine. Partly submerged root mats that held decaying leaves, sticks and other debris at the edges of the open or semishaded stream margins (Figs 17D, F, G) were the main source of the specimens of *Meru*.

Observations on captive beetles

Live specimens of *M. phyllisae* collected 24 January 1989 were brought back to the laboratory and placed in a large

glass finger bowl along with some decaying leaves. Daily observations were made and, from time to time, a search for eggs was conducted. Unfortunately, no eggs were found and no larvae appeared. The beetles spent most of their time sitting still or crawling about on the dead leaves. They were not observed feeding unless it was what appeared to be grazing over the leaf surfaces. Very rarely, a beetle would walk off a leaf into deeper water and simply float, posterior end uppermost, to the water surface. After floating against the surface film, it would turn over so that its venter was facing the surface and walk along under the surface film, as has been observed in Hydraenidae and some small Hydrophilidae. To submerge, the beetles would turn over with their head directed downwards and awkwardly 'kick' (with an alternating leg motion as in walking) their way downwards until finding a foothold on the substrate; if a beetle stopped 'kicking' on the way down, it would immediately float back to the surface, then start another descent. While the beetles were moving about, a silvery bubblelike area seemed to be present under each elytron; this was difficult to confirm because of the tiny size of the beetles.

No mortality was noted until almost 4 months after their capture, when two dead beetles were found on 24 May. After that, the following were found dead: one, 12 June; five, 11 July; two, 15 August. The last two specimens lived in the finger bowl for 196 days.
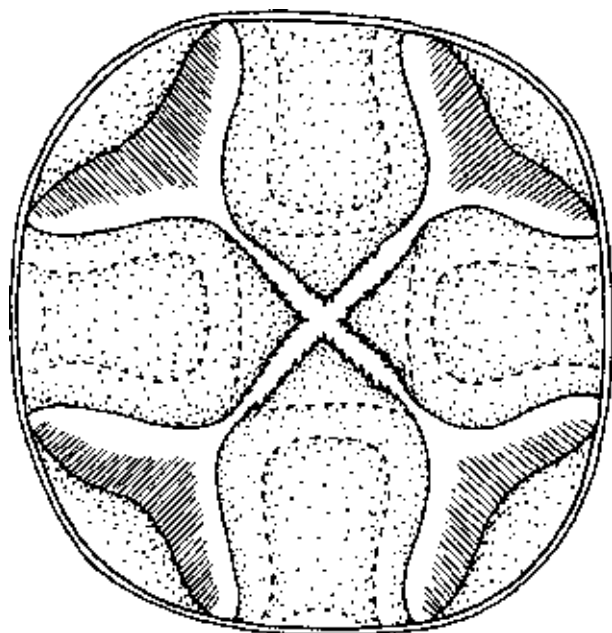
Fig. 16. *Meru phyllisae*, proventriculus, end view.

Meruidae fam. nov.

Systematic placement

The combination of skeletal characters, habits and minute size in *M. phyllisae* has offered a perplexing challenge for its classification. With the fusion of the hind coxae and metaventrite, the division of the first (of six) visible abdominal sternite (ventrite II divided by metacoxae) and fusion of visible sternites 1–3 (ventrites II–IV), the large propleuron and visible notopleural and pleurosternal sutures, the broad, lobed mentum, and glabrous palpiform two-segmented galea, suggest placement of *Meru* in the suborder Adephaga, according to the adult synapomorphies summarized by recent phylogenetic studies (Beutel, 1995, 1997; Beutel & Haas, 2000). Glabrous antennomeres place it among the Hydradephaga, an aquatic adephagan beetle assemblage for which monophyly is still open to question (Beutel, 1997; Ribera *et al.*, 2002a,b). For reasons discussed below, however, it has not been possible to place the genus in any known family taxon. We propose that it be placed in a new family, Meruidae, the 'comb-clawed cascade beetles', based on *M. phyllisae* **gen.** et **sp.n.**

Diagnosis

Meruidae can readily be identified by the following combination of characters:

1. Very small adephagan species.
2. Habitus resembling a minute haliplid.
3. Rough body sculpture with flat, wrinkled setae (possibly respiratory structures).
4. Pectinate tarsal claws.
5. Trident tibial spurs (inner metatibial spur serrate).
6. Pair of overlapping spatulate setae on the labrum.
7. Lack of swimming hairs on the legs.
8. Small, rounded scapus.
9. Alternating large and small segments of the antennal flagellum.

In the most recent key to adephagan families (Balke *et al.*, 2003), *M. phyllisae* runs to couplet 11, Dytiscidae, having obsolete metacoxal plates, but in *Meru*, the anterior extension of the metacoxae is obscured by complete fusion. Insertion of a couplet '11a' at this point would separate Meruidae:

11a. Beetles less than 1 mm long. Tarsal claws pectinate .... Meruidae
– Beetles larger than 1 mm long. Tarsal claws simple......11

Being less than 1 mm in length, *M. phyllisae* is among the smallest known members of Adephaga. Some *Notomicrus* (Noteridae) species are barely longer than 1 mm, as are the smallest Carabidae, e.g. members of *Geocharidius* Jeannel.

Characters of Hydradephaga coded for Meruidae

In their placement of the newly proposed family Aspidytidae, Ribera *et al.* (2002b) listed forty adult morphological characters used in analyses to hypothesize relationships among the family taxa of Hydradephaga. Although a full cladistic analysis to determine the sister group of Meruidae is beyond the scope of this paper (but will be the subject of ongoing and future studies), coding these characters at this point will assist in supporting the exclusion of *Meru* from other adephagan families, and point out some character systems that need additional scrutiny among many taxa. We were able to score most of these characters for Meruidae using character states defined by Ribera *et al.* (2002b), as follows, with (0) being plesiomorphic:

Character 1, body shape: with distinct pronoto-elytral angle (0); 2, head shape: not shortened and laterally rounded, eyes protruding (0); 3, compound eyes: undivided (0); 4, shape of scapus: strongly shortened but without enlarged globular part (3); 5, pedicellus: not enlarged, not strongly shortened or enclosed by scapus (0); 6, flagellomeres of males: antennomeres 5 and more than one of the following segments distinctly broadened (2); 7, galea: two-segmented (0); 8, elongate sensorial field of distal labial palpomere: absent (0); 9, sensorial field on a protuberance of the dorsal side of the distal labial palpomere: absent (0); 10, shape of the prosternal process: strongly broadened and apically truncate (3); 11, ventral procoxal joint: with distinct coxal condyle (0); 12, profemoral cleaning device: absent (0); 13, protibial burrowing spur: absent (0); 14, row of flattened thorns on apical part of protibia: absent (0); 15, outer edge of protibia: not rounded (0); 16, tibial groove or concavity for reception of protibial burrowing spur: absent (0); 17, curved spurs on ventral side of protarsomeres 1–3: absent (0); 18, prothoracic defence gland: (0, probably; needs further study); 19, mesoventrite: short, with hexagonal groove and anterolateral grooves for reception of procoxae (0); 20, mesocoxae: globular (1); 21, mesocoxal cavity: laterally bordered by mesepimeron and metathoracic anepisternum (1, but difficult to interpret with certainty due to extensive fusion); 22, proximal pro- and mesotarsomeres: not elongated and broadened (0); 23, middle and hind legs: elongate (0); 24,

Fig. 17. Biotope at El Tobogán, the type locality of *Meru phyllisae*. A, The upper cascade looking upstream from the dam; B, the upper cascade looking downstream from the upper edge. C, The edge of the upper cascade showing the wet rock face and stream edge; D, the stream edge at the upper cascade where the root mat habitat was sampled; E, Biotope at El Tobogán, the type locality of *Meru phyllisae*. A, The dam and pool below the upper cascade looking upstream; F, the pool and forested stream below the cascade looking downstream; G, Section of forested stream below the cascade, looking downstream; H, the open rock surface and edge of a rapid section of the cascade.
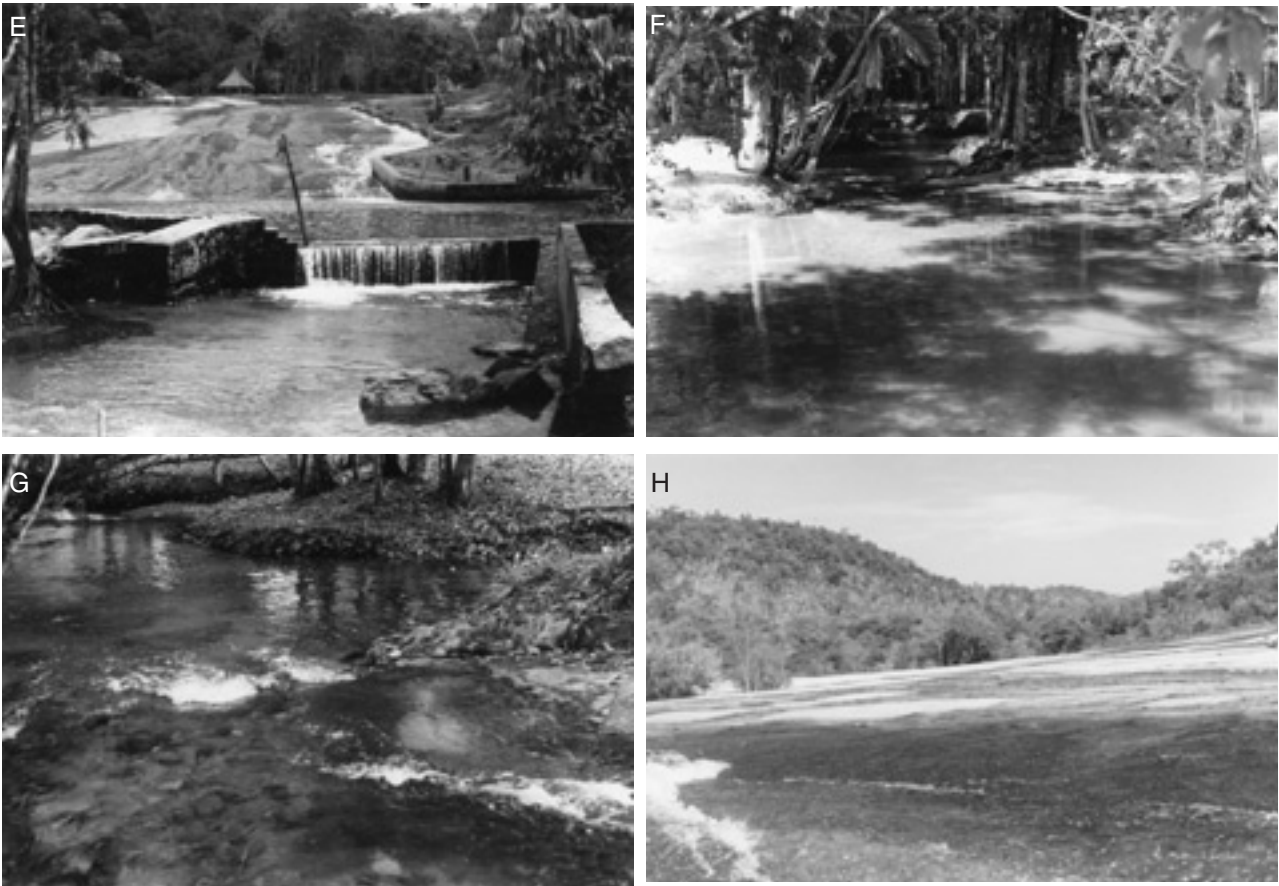
Fig. 17, *Continued.*

swimming hairs on meso- and metathoracic legs: absent (0); 25, noterid platform of metaventrite: absent (0); 26, transverse ridge of metaventrite: absent (2); 27, contact between pro- and metasternal process: present (1); 28, metafurca: originates from intercoxal septum (1); 29, size of metafurca: narrow, with reduced lateral arms (1); 30, mesal walls of metacoxae: with extensive contact area and intercoxal septum (3); 31, anterior margin of metacoxa: undetermined due to extensive fusion; 32, metacoxal plates: largely reduced (4); 33, lateral margin of metacoxal plates: indistinct anteriorly (4); 34–35, muscle characters (not studied); 36, abdominal segments III and IV: completely fused (1); 37, bulges on anterior abdominal sternites: absent (0); 38, gonocoxosterna VIII: not exposed (0); 39–40, ramen and laterotergite: (unsclerotized; not observed).

Exclusion from other hydradephagan families

Although *Meru* keys to Dytiscidae, it must be excluded from that family because of the undifferentiated legs, lack of swimming fringes, and alternating leg movement during swimming (Ribera *et al.*, 2002b). The oarlike hind legs and often highly streamlined body of 'diving beetles' separate

Meruidae and other aquatic taxa that are less equipped for rapid and evasive swimming. Roughley & Larson (2001) reviewed the characters, classification and literature on the Dytiscidae; Miller (2001) provided the most recent analysis of morphology and phylogeny.

Apomorphic features of Gyrinidae (Steiner & Anderson, 1981; Beutel & Roughley, 1988; Beutel, 1990, 1995; Roughley, 2001a) include divided eyes (for surface swimming), highly modified legs for swimming, stout and highly specialized antennae, and a single protibial spur. *Meru* shares none of these features but has synapomorphies with the remaining families of Adephaga, e.g. the short mesosternite, form of the male genitalia (curved asymmetric base, torsion) and other characters that would exclude it from Gyrinidae (Beutel, 1995, 1997).

Meru phyllisae is the 'undescribed adephagan from South America' mentioned by Lawrence & Newton (1995) as having haliplidlike features. The general body form is reminiscent of Haliplidae, but the very small size, surface sculpture and setae of the body, the pectinate claws, the lack of expanded coxal plates, the legs lacking swimming hairs, the differing shape of the hind femur (Kavanaugh, 1986) and trochanter, and the lack of a specialized ovipositor,

readily separate Meruidae from Haliplidae. Most of these characters are autapomorphies for one or the other taxon; the greatly expanded hind coxal plates are unique to Haliplidae, not known from any other extant group of beetles (Beutel & Ruhnau, 1990; Beutel, 1995; Roughley, 2001b).

In Noteridae, the smooth, streamlined body form and modified legs are highly specialized (except in *Phreatodytes* Uéno) for swimming and burrowing. Other derived features of the clade (Beutel & Roughley, 1987; Beutel, 1995, 1997; Roughley, 2001c) include the form of the scape, with a short globular base and more slender distal part, dilation of antennomeres V, VII and IX, presence of a profemoral excavation and antenna cleaning organ, metacoxal platform and anterior paramedian angles. *Meru* shares the characters of the antennal flagellum only, but does share a derived feature with *Notomicrus*, considered to be sister to most remaining noterids: complete fusion of the metacoxae with the metasternum (Beutel & Roughley, 1987). The absence of a sutural stria is also shared between Noteridae and *Meru*.

Although the body form of *Meru* is somewhat similar to that of an *Amphizoa*, the latter are very much larger, and the apomorphic features of Amphizoidae (absence of mental suture, one-segmented galea, and strongly reduced metafurca) preclude any close relationship. In Amphizoidae, legs are relatively unmodified for swimming and natatory abilities are poor (Kavanaugh, 1986; Beutel, 1995; Philips & Weiping Xie, 2001) but vestigial swimming hairs are present. Hygrobiidae are also much larger, have long fringes of swimming hairs on the legs, and several unique autapomorphies as listed by Beutel (1995, 1997) that are not found in *Meru*. Members of the recently described family Aspidytidae (Ribera *et al.*, 2002b; Balke *et al.*, 2003), also lacking swimming hairs (considered to be derived through loss) on the legs, have a smooth, noteridlike body form and unusual scapus and pedicellus very different from those of *Meru*. The carabidlike terrestrial Trachypachidae (Ball, 2001) have few similarities to Meruidae except for the groundplan adephagan features. *Meru* lacks the protibial antennal cleaner of Trachypachidae. Relationships with this group and aquatic Adephaga have been the subject of many studies (Bell, 1966; Roughley, 1981; Beutel & Belkaceme, 1986; Shull *et al.*, 2001). Lastly, the characters of known fossil taxa, as discussed by Balke *et al.* (2003), also rule out inclusion of *Meru* in any of these families.

Comments and conclusions

The overall body form of *Meru*, with rough surfaces, protruding eyes, and unmodified legs, is typical of aquatic beetles that are weaker swimmers of lentic water, or shallow marginal stream habitats, e.g. Haliplidae and Amphizoidae, and several nonadephagan groups that have acquired aquatic habits. For aquatic Adephaga, these characters are considered to be primitive, relative to the streamlined body and specialized swimming legs and methods of Dytiscidae, Noteridae, and Gyrinidae (Ribera *et al.*, 2002b). *Meru* has features of a beetle that has perhaps recently invaded the aquatic realm and/or has retained these primitive states, and this is in keeping with the postulated habitats of the earliest Adephaga (Beutel, 1995,1997) at the margins of ponds or rivers, from which multiple invasions of aquatic and terrestrial to arboreal habitats may have occurred.

The observed wing dimorphism, with atrophied wings in the majority of specimens, is not a common condition in aquatic beetles (Spangler, 1979) and also not typical of obligate streamside lowland species of Carabidae (Darlington, 1936, 1943). Maintenance of both wing forms in a population is probably advantageous for a small aquatic beetle in a habitat subject to fluctuation or sudden changes, such as flooding or drying of the stream margin habitat.

The unique apomorphic features of Meruidae are an enigmatic assemblage: the pectinate tarsal claws, the possibly respiratory structures covering the body, the odd leaflike setae of the labrum, and the trifid tibial spurs. The very small size of these beetles, also considered to be derived (Beutel & Haas, 1998) may be a contributing factor to the assemblage of other unusual characters of this taxon. Miniaturization in Coleoptera results in alteration of other characters via fusion, reduction and loss. In *Meru*, fusion of thoracic sclerites, loss of the oblongum cell and binding patch in the hind wing, reduced and membranous ovipositor, and probable loss of pygidial and prothracic defence glands, etc., can probably be attributed to miniaturization; similar conclusions have been drawn for other small-sized members of other beetle taxa, e.g. *Spanglerogyrus* in the Gyrinidae (Steiner & Anderson, 1981).

The folding pattern of the fully developed wing of *M. phyllisae* (Fig. 12) is of the adephagan type (Kavanaugh, 1986; Kukalová-Peck & Lawrence, 1993; Lawrence & Britton, 1994; Beutel & Haas, 2000), although with the reduced venation and marginal fringe, the wing is more similar to that seen in members of Myxophaga. Similarities in the wing to that of myxophagan beetles, all of which are relatively small, may be the result of convergence, but a sister-group relationship between Myxophaga and Adephaga has been suggested by wing characters (Kukalová-Peck & Lawrence, 1993).

Serrate tibial spurs are found in most Noteridae, especially the larger (inner) metatibial spur, which is also serrate in *M. phyllisae*. Some Haliplidae also bear serrations on this spur. Whether this represents any synapomorphy among these families should be a subject of future study.

The leaflike setae on the labrum, which oppose each other and overlap above a median emargination, along with the toothlike setae medial to these, may be related to a feeding specialization. The diet of these beetles is uncertain; observations on captive *M. phyllisae* suggest that they may be eating decaying leaf tissue or perhaps more likely, algal filaments and/or fungal hyphae growing on submerged leaves. The fact that captive beetles survived for nearly 200 days on decaying leaves, without any predatory or cannibalistic behaviour being observed during that time, supports this idea. Ancestral Adephaga were probably predators (Beutel, 1995) as are most extant

members, but predatory habits in *Meru* are doubtful, as it is not an agile or rapid swimmer. Although the head is prognathous, the mandibles are rather stout, less suitable for predation, but the terebral ridges and teeth in *Meru* mandibles would serve for cutting (Acorn & Ball, 1991). Haliplid adults have stout mandibles and are known to be more omnivorous (Seeger, 1971), whereas the larvae are algal specialists. *Meru phyllisae* could also be categorized as omnivorous, and if also an occasional predator, this would probably involve only small, perhaps sessile, prey species. Further comparisons of mandibular morphology, with scanning electron microscopy of the surfaces, will probably provide more information.

The labrum in adult haliplids (Beutel & Ruhnau, 1990) is also distinctly emarginate and with a fringe of flattened, blunt to tapered setae directed anteromedially. There are also similarities in the labrum of some Myxophaga, which are also small animals that feed on filaments of algae, e.g. the larva of *Hydroscapha* (Beutel & Haas, 1998: fig. 2A) and adult Torridincolidae (Spangler, 1980: figs 4, 5).

Antennal characters of *Meru* are intriguing and show similarities to both Haliplidae and Noteridae. The globular, short scape has been considered a derived feature of haliplids, and the condition in *M. phyllisae* seems to be even more reduced (derived) in that there is no separate distal portion; in haliplids, there is a slight constriction between basal and distal halves. The pseudo-two-segmented state in Noteridae and Aspidytidae appears to be intermediate in form and reduction between the scape in Haliplidae and that of other Adephaga, which have the distal portion generally longer than wide.

Modification of antennomeres V, VII and IX has been considered unique to Noteridae (Beutel, 1997). Increased size and sensory fields of the same alternating antennomeres among the two taxa would have a very remote chance of being a result of convergence, so this appears to be a synapomorphy with Meruidae. Perhaps the miniaturization (possibly an adaptation to the stream margin habitat) of *M. phyllisae* has resulted in the loss of sensoria on antennomeres and reduction of the number to single organs on antennomeres VII and IX. Some Haliplidae possess vestiges of this pattern, but this character system needs more comparative studies among many taxa in order to draw conclusions on possible relationships.

The two brush-tipped setae of the anterior margin of the prosternum deserve mention, as we find similar setae in a number of Noteridae, greater in number, but with the same general form. In *Notomicrus traili* Sharp, twelve such brush-tipped setae occur in a row along the margin; fewer are seen in the related *Speonoterus* (Spangler, 1996: fig. 58). Other larger noterids, e.g. *Hydrocanthus iricolor* (Say) generally have a fringe of these setae. Their function is unknown, but the distinctive form and placement are similar in Meruidae and Noteridae. Setae that line the prosternal margin in the haliplids examined appear to be of the simple, tapered form.

The hidden scutellum is a feature common to all known Haliplidae and Noteridae except *Phreatodytes* (Beutel,

1997), *Speonoterus* Spangler (1996), and *Notomicrus* species (Spangler, 1996); the latter have an exposed, but very small, scutellum, but according to Beutel (1997), concealed. Several unrelated tribes of smaller-sized Dytiscidae also have the scutellum concealed; the character may have arisen independently in some cases and may be another feature of convergence, related to the reduction in body size.

The form of the proventriculus, with its eight lobes of alternating large and small size, is typical for all Adephaga (Balfour-Browne, 1944; Smrž, 1982) but the backward pointing fringe of hairs on the smaller lobes is considered to be derived. If a proventriculus with lobes bearing sclerotized teeth is primitive compared with the purely hair filter type (Balfour-Browne, 1944), *Meru* shares the derived state with Gyrinidae, Noteridae, Haliplidae, and some hydroporine Dytiscidae.

The simple, membranous ovipositor with reduced gonocoxae in *M. phyllisae* indicates that these beetles are probably depositing eggs on surfaces rather than inserting them in plant tissue, as is the case for some Haliplidae (Beutel & Ruhnau, 1990; Roughley, 2001b) and Noteridae (Beutel, 1995). This appears to be the result of reductions of the sclerotized gonocoxae and setose appendages seen in most hydradephagan taxa.

We believe that the dytiscoid type of metacoxal fusion and metafurca, along with the other synapomorphies with Noteridae, suggest a sister-group relationship between Meruidae + Noteridae + the remaining Dytiscoidea. The globular antennal scape in Meruidae and Haliplidae, along with the nonpredatory feeding and associated features, could also indicate some relationship among these two taxa. A working hypothesis of a relationship among Haliplidae, Noteridae and Meruidae needs consideration. The position of Haliplidae among the other families of Adephaga has long been controversial and we hope that the discovery of Meruidae will lead to clarification of this. The results of molecular analyses in progress, using fresh material of *M. phyllisae* (M. Balke, pers. comm.), are eagerly awaited.

Early aquatic Adephaga were probably nonswimming forms that lived at the edges of rivers or ponds (Beutel, 1995). Hygropetric habitats have existed as 'edges' for millennia, as the exposed bedrock has never been under forest canopy, perpetuating the sunlit microhabitats for surface algal growth and the assemblage of often relictual insects associated with them. The recently discovered 'cliff water beetles', Aspidytidae, demonstrate other unusual taxa to be found at these sites (Ribera *et al.*, 2002b; Balke *et al.*, 2003). If there was a common ancestor to the modern aquatic Adephaga (excluding Gyrinidae), it probably had the general appearance of *Meru*, lacking modifications for swimming, but was probably larger, perhaps resembling an *Amphizoa*. From this form radiated the diverse and independent adaptations for different swimming, feeding and oviposition strategies. Future studies on additional characters of *M. phyllisae* (parsimony analysis including musculature, presence of defence glands via thin sectioning, molecular data, etc.) and the discovery of the elusive larval stages will further clarify these notions.

Acknowledgements

References

Acorn, J.H. & Ball, G.E. (1991) The mandibles of some ground beetles: structure, function, and the evolution of herbivory (Coleoptera: Carabidae). *Canadian Journal of Zoology*, **69**, 638–650.

Balfour-Browne, F. (1944) The proventriculus of the Coleoptera (Adephaga) and other insects, a study in evolution. *Journal of the Royal Microscopical Society*, **64**, 68–117.

Balke, M., Ribera, I. & Beutel, R.G. (2003) Aspidytidae: on the discovery of a new beetle family: detailed morphological analysis, description of a second species, and a key to fossil and extant adephagan families. *Water Beetles of China*, III (ed. by M. A. Jäch

and L. Ji), pp. 53–66. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Vienna.

Ball, G.E. (2001) Trachypachidae C. G. Thompson, 1857. *American Beetles*, Vol. 1 (ed. by R. H. Arnett, Jr and M. C. Thomas), pp. 144–146. CRC Press, Boca Raton, Florida.

Bell, R.T. (1966) *Trachypachus* and the origin of the Hydradephaga (Coleoptera). *Coleopterists Bulletin*, **20**, 107–112.

Beutel, R.G. (1990) Phylogenetic analysis of the family Gyrinidae (Coleoptera) based on meso- and metathoracic characters. *Quaestiones Entomologicae*, **26**, 163–191.

Beutel, R.G. (1995) The Adephaga (Coleoptera): phylogeny and evolutionary history. *Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson* (ed. by J. Pakaluk and S. A. Ślipiński), pp. 503–539. Muzeum i Instytut Zoologii PAN, Warszawa.

Beutel, R. (1997) Über Phylogenese und Evolution der Coleoptera (Insecta), insbesondere der Adephaga. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)*, **31**, 1–164.

Beutel, R. & Belkaceme, T. (1986) Comparative studies on the metathorax of Hydradephaga and Trachypachidae. *Entomologica Basiliensia*, **11**, 221–229.

Beutel, R.G. & Haas, A. (1998) Larval head of *Hydroscapha natans* LeConte, 1874 (Coleoptera, Myxophaga, Hydroscaphidae) with special reference to miniaturization. *Zoomorphology*, **18**, 103–116.

Beutel, R.G. & Haas, A. (2000) Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics*, **16**, 103–141.

Beutel, R.G. & Roughley, R.E. (1987) On the systematic position of the genus *Notomicrus* Sharp (Hydradephaga, Coleoptera). *Canadian Journal of Zoology*, **65**, 1898–1905.

Beutel, R.G. & Roughley, R.E. (1988) On the systematic position of the family Gyrinidae (Coleoptera: Adephaga). *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **26**, 380–400.

Beutel, R.G. & Ruhnau, S. (1990) Phylogenetic analysis of the genera of Haliplidae (Coleoptera) based on characters of adults. *Aquatic Insects*, **12**, 1–17.

Darlington, P.J. (1936) Variation of flying wings of carabid beetles (Coleoptera). *Annals of the Entomological Society of America*, **29**, 136–179.

Darlington, P.J. (1943) Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. *Ecological Monographs*, **13**, 37–61.

Kavanaugh, D.H. (1986) A systematic review of amphizoid beetles (Amphizoidae: Coleoptera) and their phylogenetic relationships to other Adephaga. *Proceedings of the California Academy of Sciences*, **44**, 67–109.

Kukalová-Peck, J. & Lawrence, J.F. (1993) Evolution of the hind wing in Coleoptera. *Canadian Entomologist*, **125**, 181–258.

Lawrence, J.F. & Britton, E.B. (1994) *Australian Beetles*. Melbourne University Press, Melbourne.

Lawrence, J.F. & Newton, A.F. Jr (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). *Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson* (ed. by J. Pakaluk and S. A. Ślipiński), pp. 779–1006. Muzeum i Instytut Zoologii PAN, Warszawa.

Miller, K.B. (2001) On the phylogeny of the Dytiscidae (Insecta: Coleoptera) with emphasis on the morphology of the female reproductive system. *Insect Systematics and Evolution*, **32**, 45–92.

Philips, T.K. & Weiping Xie (2001) Amphizoidae LeConte, 1853. *American Beetles*, Vol. 1 (ed. by R. H. Arnett, Jr and M. C. Thomas), pp. 153–155. CRC Press, Boca Raton, Florida.

Ribera, I., Beutel, R.G., Balke, M. & Vogler, A.P. (2002b) Discovery of Aspidytidae, a new family of aquatic Coleoptera. *Proceedings of the Royal Society of London (B)*, **269**, 2351–2356.

Ribera, I., Hogan, J.E. & Vogler, A.P. (2002a) Phylogeny of hydradephagan water beetles inferred from 18S rRNA sequences. *Molecular Phylogenetics and Evolution*, **23**, 43–62.

Roughley, R.E. (1981) Trachypachidae and Hydradephaga (Coleoptera): a monophyletic unit? *Pan-Pacific Entomologist*, **57**, 272–285.

Roughley, R.E. (2001a) Gyrinidae Latreille, 1810. *American Beetles*, Vol. 1 (ed. by R. H. Arnett, Jr and M. C. Thomas), pp. 133–137. CRC Press, Boca Raton, Florida.

Roughley, R.E. (2001b) Haliplidae Aubé, 1836. *American Beetles*, Vol. 1 (ed. by R. H. Arnett, Jr and M. C. Thomas), pp. 138–143. CRC Press, Boca Raton, Florida.

Roughley, R.E. (2001c) Noteridae C.G. Thompson, 1857. *American Beetles*, Vol. 1 (ed. by R. H. Arnett, Jr and M. C. Thomas), pp. 147–152. CRC Press, Boca Raton, Florida.

Roughley, R.E. & Larson, J.D. (2001) Dytiscidae Leach, 1815. *American Beetles*, Vol. 1 (ed. by R. H. Arnett, Jr and M. C. Thomas), pp. 156–186. CRC Press, Boca Raton, Florida.

Seeger, W. (1971) Morphologie, Bionomie und Ethologie von Halipliden, unter besonderer Berücksichtigung funktionsmorphologischer Gesichtspunkte (Haliplidae; Coleoptera). *Archiv für Hydrobiologie*, **68**, 400–435.

Shull, V.L., Vogler, A.P., Baker, M.D., Maddison, D.R. & Hammond, P.M. (2001) Sequence alignment of 18S ribosomal RNA and the basal relationships of Adephagan beetles: evidence for monophyly of aquatic families and the placement of Trachypachidae. *Systematic Biology*, **50**, 945–969.

Smrž, J. (1982) Comparative anatomy of proventriculus and intraelytral structure of the suborder Adephaga. *Acta Universitatis Carolinae Biologica*, **1980**, 213–296.

Spangler, P.J. (1979) A new genus of water beetle from austral South America (Coleoptera: Hydrophilidae). *Proceedings of the Biology Society of Washington*, **92**, 697–718.

Spangler, P.J. (1980) A new species of Ytu from Brazil (Coleoptera: Torridincolidae). *Coleopterists Bulletin*, **34**, 145–158.

Spangler, P.J. (1996) Four new stygobiontic beetles (Coleoptera: Dytiscidae; Noteridae; Elmidae). *Insecta Mundi*, **10**, 241–259.

Steiner, W.E. Jr & Anderson, J.J. (1981) Notes on the natural history of *Spanglerogyrus albiventris* Folkerts, with a new distribution record (Coleoptera: Gyrinidae). *Pan-Pacific Entomologist*, **57**, 124–132.