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PHYLOGENETICS AND DIVERSIFICATION OF WHIRLIGIG BEETLES (COLEOPTERA, GYRINIDAE)

by

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B.S. Biology, The University of Kansas, 2010

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ABSTRACT

Whirligig beetles are a family of aquatic beetles with an estimated 1,000 species distributed globally. Phylogenetic analysis incorporating molecular data has only recently been conducted on the family and many genera have never received modern taxonomic revision. The first chapter of the dissertation provides a taxonomic revision of the Southeast Asian whirligig beetle genus *Porrorhynchus*, finding the genus to contain 5 species, and no support for the numerous proposed subspecies. For the second chapter a phylogenetic analysis utilizing the most novel phylogenetic reconstructions methods incorporating the new Fossilized Birth-Death macroevolutionary model implemented in the program MrBayes 3.2.6 was conducted on the whirligig beetle tribe Dineutini. The analysis finds strong support for the monophyly of the tribe, and 4 out of 5 of the proposed genera. The numerous subgenera proposed for the genera *Dineutus* and *Macrogyrus* are unsupported, with most synonymized, and the remaining subgenera provided with new diagnoses and constituent species. The second chapter also includes a biogeographic analysis reconstructing the historical biogeography of the Dineutini. The third chapter utilizes the same phylogenetic methods as the second chapter, however, the analysis was performed at the family level, combining the dataset from a previous study as well taxa sampled in chapter two. The analysis reveals the whirligig beetles to be an ancient beetle

group with Triassic origins, and the two currently monotypic subfamilies as the sole survivors of dominant clades from the Mesozoic.

Introduction

Phylogenetic study of the family Gyrinidae utilizing molecular data has only just begun. A 2012 study analyzed the family in an attempt to primarily elucidate the subfamilial, tribal, and generic relationships. This study proposed a new classification scheme and found strong support for the monophyly of most genera. However, within the tribe Dineutini, three out of the five recognized subgenera had their monophyly in question. Because of this, the tribe Dineutini is the focus of the first and second chapters of the dissertation. Chapter one, *Revision of the Southeast Asian whirligig beetle genus Porrorhynchus Laporte, 1835 (Gyrinidae: Gyrininae: Dineutini)* investigated the species level diversity within this dineutine genus that has never before received a modern taxonomic revision. This also allows assessment of species-level taxon sampling for the phylogenetic analysis in chapter two. Chapter two, *Systematics and evolution of the whirligig beetle tribe Dineutini (Coleoptera, Gyrininae, Gyrinidae)* inferred the phylogenetic relationships of the dineutine whirligig beetles from both morphological and molecular datasets using Bayesian and maximum likelihood analyses. This chapter provides a reconstruction of the historical biogeography of the dineutines, during their diversification, to assess the proposed Gondwanan relationships among the genera, as well as an explanation for the genus *Dineutus*' interesting biogeography. Chapter three, *Relicts of early Mesozoic whirligig beetle clades persist in biodiversity hotspots* provides a timeframe for the origins and diversification of the family Gyrinidae using a total-evidence fossil calibration approach and the most recent version of the phylogenetic software MrBayes 3.2.6 to provide a time calibrated phylogeny of the whirligig beetles.

TABLE OF CONTENTS

CHAPTER 1. Revision of the Southeast Asian whirligig beetle genus *Porrorhynchus* Laporte, 1835 (Gyrinidae: Gyrininae: Dineutini) …………………………………………. 1

1.1 Text ………... 1

1.2 References ……………………………………………………………………….. 37

1.3 Figure captions ………………………………………………………………... 41

1.2 Figures ………..………………………………………………………………….. 44

CHAPTER 2. Systematics and evolution of the whirligig beetle tribe Dineutini (Coleoptera, Gyrininae, Gyrinidae) ………………………………………………………………… 61

2.1 Text ……………………………………………………………………….…... 61

2.2 Figure captions ………………………………………………………………... 82

2.3 References ……………………………………………………………………….. 85

2.4 Appendix ………………………………………………………………………… 91

2.2 Supporting information ………………………………………………………….. 98

2.3 Figures ………………………………………………………………………..… 103

2.4 Supporting figures ……………………...…………………………………………. 117

CHAPTER 3. Relicts of early Mesozoic whirligig beetle clades persist in biodiversity hotspots ………………………………………………………………………………. 131

3.1 Text ……………………………………………………………………….. 131

3.2 Figure captions ………………………………………………………………… 136

3.3 Methods ………………………………………………………………………… 138

3.4 References ……………………………………………………………………… 139

3.5 Author contributions …………………………………………………………………… 141

3.6 Extended data ……………………………………………………………………….. 142

3.7 Supplementary information ………………………………………………………. 149

3.8 Figures ……………………………………………………………………………. 179

Revision of the Southeast Asian whirligig beetle genus *Porrorhynchus* Laporte, 1835 (Gyrinidae: Gyrininae: Dineutini)

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Abstract The Southeast Asian whirligig beetle genus *Porrorhynchus* Laporte, 1835 is revised. The genus is found to be composed of five species, *P. depressus* Régimbart, 1892, *P. indicans* (Walker, 1858), *P. landaisi* Régimbart, 1892, *P. marginatus* Laporte, 1835, and *P. misoolensis* (Ochs, 1955) **new status**, and two subgenera the *Porrorhynchus s. s.tr*. subgenus and *Rhomborhynchus* Ochs, 1926. The characters uniting the species within the two subgenera are discussed, as is their relation to the genus *Dineutus* Macleay, 1825. Many new synonyms are established: *Ceylorhynchus* Brinck, 1955, **new synonymy**, is synonymized with the s. str. subgenus**,** *P. barthelemyi* Régimbart, 1907 **new synonymy** and *P. landaisi latilimbus* Ochs, 1926 **new synonymy** are synonymized with *P. landaisi, P. marginatus mjoebergi* Ochs, **new synonymy** is synonymized with *P. marginatus,* and *D.* (*R.*) *depressus jamurensis* Ochs, 1955 **new synonymy,** *D.* (*R.*) *depressus versteegi* Ochs, 1955: **new synonymy**; *D.* (*R.*) *depressus moszkowskii* Ochs, 1955 **new synonymy** are synonymized with *P.* (*R.*) *depressus. Porrorhynchus misoolensis* (Ochs, 1955) is elevated to full species status. Lectotypes are designated for *P. brevirostris* Régimbart, 1877, *P. tenuirostris* Régimbart, 1877, *P. landaisi* Régimbart, 1892, *P. barthelemyi* Régimbart, 1907, *P. marginatus mjoebergi* Ochs, 1926, and *P. landaisi latilimbus* Ochs, 1926. Each species has the dorsal habitus imaged, male and female genitalia illustrated, important morphology illustrated, a complete catalog of associated names and their use, distribution mapped, common name proposed, and discussion section. A key to the species is included, as is a checklist of the species including synonyms and common names.

Key words: aquatic beetles, identification keys, morphology, taxonomy

Introduction

The genus *Porrorhynchus* Laporte, 1835 contains the largest species of whirligig beetle known (*P. landaisi* Régimbart, 1892) and some of the most charismatic members within the family Gyrinidae. The genus is widely distributed throughout much of Southeast Asia and New Guinea, where they inhabit streams. Most of the species have been implicated as being of potential use as water quality indicators, appearing restricted to fast-flowing, clean, forested streams (Brinck 1980; Ochs 1927b; Polhemus 2011), increasing the need for their accurate identification. Several water beetle workers have also noticed the need for a revision of the genus and its highly variable species (Balke et al. 2004; Miller and Bergsten 2012). Despite this, the genus has never received a modern taxonomic revision.

Porrorhynchus was original erected by Laporte (1835) for a single characteristic species from Java. Subsequently several other species were added by Régimbart (1892a; b; 1907), as well as another lesser known species originally described by Walker (1858) in the genus *Dineutus* Macleay, 1825. Since these early descriptions, numerous subspecies have been added by the works of Georg Ochs (Ochs 1926; 1955). The genus was also carved up into three subgenera by Brinck (1955), and its relationship with the genus *Dineutus* has been questioned several times, and remains unclear (Brinck 1955; Miller and Bergsten 2012; Ochs 1926).

The purpose of this paper is to revise the species originally proposed to be in the genus and supported by the majority of gyrinid workers (Brinck 1955; Guignot 1950; Miller and Bergsten 2012; Régimbart 1902). Some of the morphological characters supporting the different species' grouping into subgenera and their relationship to the genus *Dineutus* will be discussed. However, the goal of this paper is to determine how many species are present within this group, while the final consensus on its status as a genus proper in relation to *Dineutus* and its constituents will be resolved in a forthcoming phylogenetic analysis of the tribe Dineutini.

The common name of "snout whirligig" has been proposed for the genus *Porrorhynchus* (Jäch and Ji 1998). We here continue to use this common name for the genus, but emend it to "snouted whirligig", as snouted is a more appropriate adjective for the descriptive common name. We propose common names for all the species of *Porrorhynchus* in order aid future attempts at protection status for these whirligig species of potential conservation concern.

The complete life history has never been described for any of the species of *Porrorhynchus* and only the imago stage is known. Larvae and pupae remain to be discovered and described. It is likely the larvae are similar in habit to those of the closely related *Dineutus*, being found in stream bottoms (Hatch 1927), and that pupation takes place on land in a pupal chamber under nearby cover such as rocks or logs, as is done in *Dineutus* (Wilson 1923).

Materials and methods

A total of 1362 specimens were examined in this study.

Measurements were taken using a Cen-Tech 4 inch Digital Caliper (ITEM 47256).
Total body lengths were measured from the anterolateral margin of the clypeus to the apex of the elytral apices. These areas were chosen for the boundaries of lengths since they are more fixed than other possible boundaries. For example, the labrum may be depressed thereby making it a poor choice as an anterior boundary, and the abdomen may be more or less protruding making it an unsuitable posterior boundary. Width was taken from the widest point of the body, typically just posteriad to the mid-length of the elytra. For each taxon an attempt was made to measure the largest and smallest specimens available for each sex.

Specimens for dissections and imaging were relaxed by placing them in lightly boiling water. The aedeagus was then dissected from relaxed males and placed in warm 10% KOH for about 5 minutes. Following removal from KOH the aedeagus was placed in vinegar to neutralize the base and washed in water. Female dissection follows Miller (2001). Genitalia were drawn while in water and kept in glycerin, allowing the genitalia to dry causes them to become distorted and brittle. After dissection and/or illustration, aedeagi, female reproductive tracts, and abdomens were placed in microvials attached to the pin with the original specimens.

Illustrations were first drawn via camera lucida attached to a Zeiss Discovery V8 stereo microscope, then scanned and traced in Adobe Illustrator CS5.

Dorsal and ventral habitus were taken using a Visionary Digital BK+ light imaging system as well as a Passport imaging system (www.visionarydigital.com, R. Larimer).

Habitus images were then edited using Adobe Photoshop CS5 to add scale bars and improve clarity and color.

Distribution maps were created using Arc GIS.

Handwriting on type labels was identified using Horn et al. (1990).

Terminology of dineutine structures follows Gustafson and Miller (2015).

For each species a taxonomic history is provided. The family-group name classification follows Gustafson and Miller (2013).

Depository abbreviations:

BMNH	The Natural History Museum, London, United Kingdom (C. Taylor)
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA (S. Myers)
CNC	Canadian National Collection of Insects, Ottawa, Ontario, Canada (P. Bouchard)
DAPC	Dan A. Polhemus Collection
ICRI	Research Institute of Entomology, Sun Yat-Sen University, Zhonghan, Guangzhou, Guangdong, China (F. Jia)
IRSB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (W. Dekoninck)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (P. Perkins)
MNHN	Musée National d'Histoire Naturelle, Paris, France (A. Mantilleri)
MSBA	Museum of Southwestern Biology Arthropod Division, The University of New Mexico, Albuquerque, New Mexico, USA (K. Miller)
MSNG	Museo Civico di Storia Naturale, Genoa, Italy (M. Tavano)
MVMA	Museum Victoria, Abbortsford, Victoria, Australia (S. Hinkley)
MZLU	Museum of Zoology, Lund University, Lund, Sweden (R. Danielson)
NHMW	Naturhistorisches Museum Wien, Vienna, Austria (M. Jäch)
NMPC	National Museum, Prague, Czech Republic (J. Hájek)
ROME	Royal Ontario Museum, Toronto, Ontario, Canada (D. Currie)
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main, Germany (D. Kovac)
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor, Michigan, USA (P
UMRM	Enns Entomology Museum, University of Missouri, Columbia, Missouri, USA (R. Sites)
ZMUC	Zoological Museum, University of Copenhagen, Denmark (A. Solodovnikov)

Species concept utilized

The evolutionary species concept sensu Wiley (1978) is the preferred definition for a species utilized in this study, defining a species as "… a single lineage of ancestral descendant populations of organisms which maintains its identity form other such lineages and which has it own evolutionary tendencies and historical fate." Our requirement for species level taxa is evidence from morphology, that the individuals studied exhibit features warranting their membership within a lineage distinct from other such populations, and maintenance of that lineage's ***unique*** identity, as inferred through exclusive combinations of morphological characters.

Structures of taxonomic importance

Antennal flagellomere number: The number of antennomeres in the flagellum of the antenna for *Porrorhynchus* has been reported previously several times (Brinck 1980; Hatch 1925; 1926; Miller and Bergsten 2012), however, it was found that the number of antennomeres differs between most of the species and some reports were in error. Hatch (1925; 1926) reported *P. landaisi* as having 8 flagellomeres, however, we found that *P.* (*P.*) *landaisi* had two different antennomere counts between the posterior and anterior faces of the flagellum, 8 posterior, 7 normally on the anterior (Fig. 2A). The anterior face of the flagellum of *P.* (*P.*) *landaisi* often varied in degree of the appearance of the 8th, with some specimens having it strongly effaced, while in others it was fairly distinguishable. *Porrorhynchus* (*P.*) *indicans* was reported by Brinck (1980) as having 8 antennomeres in the flagellum, however, it actually has 7 on both faces (Fig. 2B). Miller and Bergsten (2012) reported *Porrorhynchus* as having 6 antennomeres in the flagellum, having only examined *P. marginatus*. We concur that *P.* (*P.*) *marginatus* has 6 flagellomeres (Fig. 2C) but as stated above this is not true of the whole genus. *Porrorhynchus* (*R.*) *depressus* similarly has 6 flagellomeres (Fig. 2D).

Labrum shape: The labra of species of *Porrorhynchus* are relatively elongate (being at least ca. 1/2 as long as wide), especially in comparison to most members of *Dineutus*, and vary in shape among the species. Of the species, *P.* (*P.*) *indicans* and *P.* (*P.*) *landaisi* have relatively short, sub-triangular labra, while those of *P.* (*P.*) *marginatus* and *P.* (*R.*) *depressus* are more triangular in shape. In *P.* (*P.*) *marginatus* the labrum is in the form of an isosceles triangle and is the longest among the species of *Porrorhynchus*. The labrum of *P.* (*R.*) *depressus* is in the form of a near equilateral triangle and relatively short in relation to body size.

Labral setation: The setation of the ventral surface of the labrum differs between the two subgenera of *Porrorhynchus*. Member of the *sensu stricto* subgenus have the labral setation similar to that of *Dineutus* with two transverse rows of setae, while *Rhomborhynchus* has an additional row of setae situated paramedially running longitudinally down the labrum. This character appears to be unique to *Rhomborhynchus*.

Interorbital ridge coloration: The lateral canthus of the dorsal and ventral eyes, dubbed the interorbital ridge by Brinck (1955), has a character that distinguishes *P.* (*P.*) *marginatus* from all other members of *Porrorhynchus*. In *P.* (*P.*) *marginatus* the yellow margin exhibited on the elytra and pronotum is extended onto the lateral margin of the interorbital ridge. In all other species of *Porrorhynchus* the interorbital ridge is similarly colored as the frons and vertex.

Labial and maxillary palpi: Within *Porrorhynchus* the ultimate maxillary palpomere is truncate apically and quadrate in shape. The ultimate labial palpomere on the other hand is different among the species. In *P.* (*P.*) *indicans* and *P.* (*P.*) *landaisi* the ultimate labial palpomere differs in shape from that of the maxillary by being more elongate in form and apically subtruncate to weakly rounded (Figs. 6C,G,N). In *P.* (*P.*) *marginatus* and *P.* (*R.*) *depressus* the ultimate labial palpomere is similar in form to that of the maxillary palps (Fig. 8I,N,S,X,BB). In *P.* (*R.*) *depressus* the palps are hatchet-form being short and quadrate with a relatively large highly truncate apical surface (Fig. 11C,G,K,O).

Pronotal transverse impressed line: The pronotum has a transverse impressed line, just removed from the anterior margin and is variously developed in different groups of whirligig beetles (Hatch 1926; Oygur and Wolfe 1991). Within *Porrorhynchus* this character divides the two subgenera, being absent in the *s. str.* group of species but present in *Rhomborhynchus*.

Yellow lateral margin of elytra: The lateral margin of the elytra is yellow in color and variable in its extent, width, and whether it is interrupted in its basal 1/3, among the species. In *P.* (*P.*) *indicans* (Fig. 1C) the yellow margin typically only extends up to the basal half of the elytra and is reduced to variable degrees in width and extension among individuals. In *P.* (*P.*) *landaisi* (Fig. 1B) the yellow margin is well developed, extending most of the elytral length, ending just before the apex, being replaced by a blue reflective spot, and is interrupted at its basal 1/3 by a constriction of its width. This constriction is associated with a swelling resulting from a cavity formed for pro-leg reception. In *P.* (*P.*) *marginatus* (Fig. 1A), *P.* (*R.*) *depressus* (Fig. 1D), and *P.* (*R.*) *misoolensis* (Fig. 1E), the yellow lateral margin of the elytra is complete, reaching the apicolateral margin of the elytral apex. *Porrorhynchus* (*P.*) *marginatus* differs in having the yellow margin interrupted at its basal 1/3 by a dark spot of coloration as well as a darkly colored apicolateral margin of variable length. The dark spot is associated with the swelling created by the cavity for pro-leg reception and is highly variable in size among individuals, as is the apicolateral marginal dark spot.

Dorsal punctation: The dorsal punctation differs greatly between the two subgenera. In the *s. str.* subgenus the dorsal punctation is well evident and composed of fairly large well-impressed punctures. In *Rhomborhynchus* punctation is present, but the punctures are finer, mostly obscured by the dense microreticulation covering the dorsum. Between the different species of the *s. str.* subgenus the distance between punctures varies considerably, with *P.* (*P.*) *landaisi* having the largest and densest dorsal punctation.

Elytral apices: The elytral apices differ among each species and are critical for identification. *Porrorhynchus* (*P.*) *indicans* differs from all other species having non-spinose elytral apices, instead having two large parasutural points, forming a large triangle between the sutural and epipleural angles (Fig. 1C). Both *P.* (*P.*) *landaisi* and *P.* (*P.*) *marginatus* have saw-tooth-like serration, consisting of large triangular spinose cuticle extensions, running the apicolateral margin of the elytra. The saw-tooth serration becomes larger distally and the final extension is greatly expanded into a spine at the epipleural angle. In additional to this, *P.* (*P.*) *landaisi* has the sutural angle produced and two parasutural spines (Fig. 1B). *Porrorhynchus* (*P.*) *marginatus* similarly has the sutural angle produced but only has a single large parasutural spine, as well as having a larger epipleural spine (Fig.1A). *Porrorhynchus* (*P.*) *depressus* has the elytral apices very similar to *P.* (*P.*) *marginatus*, but lacks any saw-tooth-serration (Fig. 1D).

Setose furrow of ultimate female protarsomere: The ultimate protarsomere of females of most species have a setose furrow located on its posterolateral face running for most its length (Brinck

1980). This character divides the subgenera, being present in the *s. str.* subgenus, but completely absent in *Rhomborhynchus*.

Protrochanteric setose patch: The protrochanter of males of the *s. str.* subgenus possess a small patch of setae (Fig.3B) that appear to be recessed in a pit on the ventral face of the protrochanter (Fig. 3A). This sexually dimorphic character has previously been overlooked in the past and appears to constitute a synapomorphy for the *s. str.* subgenus. The position of this setose patch varies among the species. In *P.* (*P.*) *marginatus* and *P.* (*P.*) *indicans* it is located in the apicolateral corner, while being situated paramedially in *P.* (*P.*) *landaisi*. The Protrochanteric setose patch is not found in members of the subgenus *Rhomborhynchus*.

Profemoral setation pattern: The profemoral setation is another character dividing the two subgenera. In the *sensu stricto* subgenus the profemur possesses two rows of setae clustered together into large tufts along the anterior and posterior margins of the ventral surface, becoming more closely clustered and larger as they proceed distally (Fig. 4). The subgenus *Rhomborhynchus* has only three to four small, narrow clusters of setae situated on the posterior margin of the ventral surface and 4 – 5 setigerous punctures on the anterior face, similar to species of *Dineutus*. These two characters are discussed more in the broader conclusions section.

Protarsus: The shape of the protarsus varies between the different species, being much broader in *P.* (*P.*) *landaisi* and *P.* (*P.*) *indicans* (Fig. 6A,E,I,L), and more narrow in *P.* (*P.*) *marginatus* and *P.* (*R.*) *depressus* (Fig. 8A,F,K,P,U,Y, Fig. 11 A,E,I). There are also differences in the relative proportions of the protarsomeres between some of the species.

Metacoxal process: The form of the metacoxal process varies among most the species. In general the species have a slight production of the distolateral corner of the apex of the metacoxal process. Which is weakly produced in all the species (Fig. 6B,F,J,M), except for *P.* (*P.*) *marginatus* in which the process is clearly produced and spinose in most populations (Fig. 8B,G,L,Q,V,Z).

Aedeagus: The aedeagus also shows a major division between the subgenera especially in the form of the parameres. In *Porrorhynchus* s. str. the parameres all have the setae restricted to their apical 1/4, while in *Rhomborhynchus* the setae is located in the apical 1/3. The parameres also articulate broadly with the median lobe in the *s. str.* subgenus, while in *Rhomborhynchus* they are much more narrowly articulated. The form of the aedeagus differs between all the species and as such, the aedeagus is a good indicator of species boundary.

Female reproductive tract: The gonocoxae of the female RT can distinguish most the species. All species have the female RT (Fig. 13) with a long tubiform spermatheca and relatively long, narrow laterotergites, and the vaginal shield (Brinck 1980) bordered by a strongly developed sclerotized region anteriorly.

Key to the adults of the known species of *Porrorhynchus* Laporte, 1835

1 Elytral apices spinose, distinct parasutural spine(s) present. Yellow margin of elytra complete or nearly so, normally extending well beyond half the elytral length. ……………………………………………………………………………...…. **2**

— Elytral apices not spinose, instead with large parasutural point forming broad triangle between the sutural and epipleural angles. Yellow margin of elytra incomplete and normally strongly reduced, only reaching basal 1/2 to 1/3 of the elytral. Known only from Sri Lanka……………………...…..… ***Porrorhynchus* (*Porrorhynchus*) *indicans***

2 Elytra apicolaterally with saw-tooth-like serration. Yellow margin of elytra normally interrupted in basal 1/3 by constriction of margin's width or darkly pigmented spot. Pronotal transverse impressed lines absent. Distributed in Southeast Asia, west of Wallace's line ………..……………………………………………………...…… **3**

— Elytra apicolaterally without saw-tooth-like serration of any kind. Yellow margin of elytra never interrupted in basal 1/3. Pronotal transverse impressed line present. Known only from east of Wallace's line in West Papua, and New Guinea …….……...……….. **4**

3 Yellow lateral margin continued onto interorbital ridge. One large parasutural spine present on elytral apex. Elytral yellow margin normally interrupted by darkly pigmented spot in basal 1/3. Labrum highly elongate, in the form of an isosceles triangle. Widely distributed in Southeast Asia, west of Wallace's line. More commonly encountered species. …………………………...…... ***Porrorhynchus* (*Porrorhynchus*) *marginatus***

— Yellow lateral margin not continued onto interorbital ridge. Two parasutural spines of similar size present on elytral apex. Elytral yellow margin interrupted by constriction of its width in basal 1/3. Labrum shorter, sub-triangular in shape. Known from mainland Southeast Asia, primarily in the northeast, and southern China. …………………………………...…….. ***Porrorhynchus* (*Porrorhynchus*) *landaisi***

4 Length 9.5 – 11.6 mm; body form of most populations broader, especially broad at mid-length. Metacoxal process with lateral margins less sinuate, less strongly constricted apically. Aedeagus with median lobe as- or nearly as long as parameres, apex not laterally expanded, parallel sided then narrowed in apical 1/6. Labrum larger. Widespread in New Guinea. ………………………………………….. ***Porrorhynchus* (*Rhomborhynchus*) *depressus***

— Length 9.4 – 10.1 mm; body form more narrow, broadest just anteriad to mid-length. Metacoxal process with lateral margins more strongly sinuate, more constricted apically. Aedeagus with median lobe shorter than parameres, apex briefly laterally expanded, with lateral margins broadly rounded towards apex. Labrum smaller. Only known from Misool Island. …………...................... ***Porrorhynchus* (*Rhomborhynchus*) *misoolensis* n. stat.**

Taxonomy

Genus *Porrorhynchus* Laporte, 1835

Type species: *Porrorhynchus marginatus* Laporte, 1835: 108 by monotypy.

Trigonocheilus Dejean, 1833: 59 [manuscript name and *nomen nudum*, synonymy by Aubé, 1838a: 406]; *Trigonochilus rostratus*: Agassiz 1846: 377 [unjustified emendation of *Trigonocheilus rostratus*, *nomen nudum*]; ***Porrorhynchus* Laporte, 1835**: 108 [original description]; *Porrhorhynchus*: Régimbart 1877: 105 [misspelling]; *Porrhorrhynchus*: Régimbart 1886: 250 [misspelling]; ***Dineutus* (*Porrorhynchus*): Ochs 1926:** 64 [new status]; ***Porrorhynchus*: Guignot 1950**: 124 [change in status]; ***Dineutus* (*Porrorhynchus*): Ochs 1955**: 130 [change in status]; ***Porrorhynchus*: Brinck 1955**: 103 [change in status].

Diagnosis: Medium to very large whirligig beetles size: 9 – 26 mm. Body form elongate oval to teardrop-shaped. Antennal flagellum with 6 – 7 antennomeres, ultimate flagellomere trapezoidal in shape and ca. at least 2x as long as every other flagellomere. Labrum large, elongate, and more or less triangular in shape. Pronotum and elytra with yellow-margins, often for entirety of their length, but at least in the basal half of the elytra. Protibia with distolateral margin spinose. Venter lightly colored.

Description:

Head. Vertex and frons with punctation present, reticulation composed of round to ovoid sculpticells. Dorsal eye smaller than ventral eye, anterior margin of ventral eye situated posteriad of anterior margin of dorsal eye; orbital furrow of dorsal eye complete, becoming narrowest anteromedially; exoculata suture well defined. Antenna with cup-like scape; pedicel broad, laterally expanded, dorsoventrally flattened, trapezoidal in form, lateral face with fringe of long fine setae; flagellum with 6 – 8 flagellomeres, flagellomere I stalked, triangular in form, ultimate flagellomere trapezoidal in form, at least 2x longer than flagellomeres II – V or VI, flagellomeres II – V or VI similar in size and shape. Frontal ridge length at least 1.5 – 2x width of clypeus at midlength, frontoclypeal suture well developed, posterior margin flat, lateral margins meeting posterior margin at ca. 100 – 110° angle. Clypeus weakly to fairly strongly emarginate medially, with reticulation compose of round sculpticells, punctation present, clypealium with long fine setae ventrolaterally. Labrum large, elongate, more or less triangular in shape, densely punctate, with reticulation composed of round sculpticells, ventral margins fringed with long fine setae. Maxilla without galea, maxillary palp 4 segmented, ultimate palpomere ca. as long as proximal three combined, apically truncate. Labial palp 3 segmented with ultimate palpomere as long as all proximal palpomeres combined, apically truncate to subtruncate. Gula well developed, T-shaped with tentorial pits evident, series of long fine setae present anteriad to lateral arms of gular suture.

Thorax. Pronotum with punctation present, reticulation consisting of round sculpticells, lateral margins yellow with fairly broad marginal depressed area, posterolateral corners with several setae. Prosternum with well differentiated prosternal process, prosternal process narrow and paralleled sided for entirety. Prolegs with procoxal process round to lobiform; protrochanter fusiform, posterior face with short field of curved stout setae; profemur nearly parallel sided for most its length, only weakly tapered apically, weakly expanded basally; protibia club-shaped with distolateral marginal apex produced to a more-or-less acute spine, anterior face with

paramedial linear to arcuate series of setigerous punctures in distal half, proximal lateral margin with long grove running distal half of protibiae to distal apex with golden hair-like setae, distomedial apex encircled with short, stout, pointed setae, continuing to posterior face, ventral face of protibia with setose groove running near entire length, setae become larger, more brush-like towards distal apex, setae at distal apex projecting beyond apex's medial process, posterior face of protibia with brush of golden setae in distal 1/5; protarsus 5 segmented, protarsomeres I – IV ventral face with long projecting setose patch located in the proximomedial corner, protarsomere V of female with short series of brush-like setae running near entire length of ventral surface, posterior surface of protarsus highly sexually dimorphic, protarsal claws similar between the sexes. Elytra without sutural border, punctation present, reticulation consisting of round sculpticells, lateral margins yellow at least basally. Mesoventrite with well developed cavity for proleg reception; mesoventrite bordered anteriorly, border complete, thinly so at anteromedial projection between procoxae, projection with long setae basolaterally, large shallow punctures present anterolaterally on mesoventral body, mesoventral discrimen well developed, running ca. 1/2 mesoventrite's length; mesepimeron narrow, strap-like. Mesolegs with mesocoxa possessing, shallow setose pit posteromedially; mesotrochanter lobiform; mesofemur broad, stout in distal half, distal apex very flatly rounded, proximal apex strongly attenuate towards trochanter, mesotibia triangular in form, dorsal surface with long natatory setae, distolateral angle of dorsal surface with series of short stout setae, distomedial surface with similar short stout setae, adorned with two spines, anterior shorter, posterior longer, ventral face of mesotibia also with short stout spines for its entire length; mesotarsus 5 segmented, mesotarsomere I in the form of equilateral triangle, 5 times length of mesotarsomere II, mesotarsomere III similar in size and form of II, all with ventral face with short stout setae running their entire length, mesotarsomere IV elongate and narrow, V ovoid with ventrodistal margin produced to spine before claws, both with long natatory setae; mesotarsal claws larger than metatarsal claws, sexually dimorphic in shape. Metaventrite with well developed cavity for proleg reception; metanepisternum lobiform; metacoxal process with posteromedial shallow setose pit, metacoxal process with circular pit anterolaterally, metatrochanter trapezoidal in shape, remainder of leg similar in form to mesoleg except metatarsal claws of both sexes smaller than mesotarsal claw, similar in form.
Abdomen. Abdominal tergites VI-VIII strongly pubescent with long fine setae covering most their surface, medially darkly pigmented, lateral margins lighter yellow in color, reticulation present, composed of round sculpticells, tergite VIII with two types of punctation distinctly present, smaller well impressed punctation covering most of darkly pigmented area, second type consisting of very large, shallowly impressed crater-like punctation situated basomedially extending half its length; abdominal sternite II+III ca. 2x length of sternite IV, sternite IV ca. 2x length of sternite V, sternites V,VI,VII, similar in size, sternite VIII triangular in form, nearly 2x length of sternite VII, emarginate apicomedially, faintly impressed reticulation present over abdominal sternites, composed of ovoid sculpticells. Female reproductive tract with tubiform spermatheca; fertilization duct weakly differentiated; vaginal shield with anterior margin bounded by highly sclerotized bridge.

Sexual dimorphism: Protarsus of male laterally expanded with dense covering of uniform suction cup setae occupying near entirety of posterior surface, missing only from proximomedial corner of protarsomere I. Protarsus of female not laterally expanded, without suction cup setae on posterior surface, instead posterior surface of at least protarsomeres I – IV with smaller patches of setae located at distal margins. Mesotarsal claws of male more strongly curved ventrally. Female mesotarsal claws less strongly curved, more similar in form to metatarsal claws.

Subgenus *Porrorhynchus* Laporte, 1835

Type species: same as for genus.

Trigonocheilus Dejean, 1833: 59 [manuscript name and *nomen nudum*, synonymy by Aubé, 1838a: 406 *Trigonochilus* Agassiz, 1846 (*nomen nudum*); *Porrhorhynchus*: Régimbart 1877: 105 [misspelling]; *Porrhorrhynchus*: Régimbart 1886: 250 [misspelling]; ***Dineutus* (*Porrorhynchus*)**: Ochs 1926: 64 [description]; ***Porrorhynchus* (*Ceylorhynchus*) Brinck, 1955**: 103 **new synonymy.**

Diagnosis: Large to very large whirligig beetles, size: 12 – 26 mm. Most species with 7 antennal flagellomeres. Gular suture incomplete. Pronotum without transverse impressed line. Elytral lateral margin with swelling at mid-length associated with proleg reception. Males with protrochanteric setose patch. Profemora with unique setation pattern consisting of large clusters of setae arranged along the anterior and posterior margins of the ventral femoral face, becoming larger and more closely clustered apically.

Description:
Head. Antenna of most species with 7 antennal flagellomeres; pedicel narrow, trapezoidal in form, mildly to noticeably narrowed apically. Labrum ventrally with two transverse linear setose rows in basal 1/2. Gular suture incomplete, lateral arms of gular suture effaced before meeting anterolateral margin of ventral epicranium, posteriad to submentum.
Thorax. Pronotum without transverse impressed line. Elytral lateral margin with swelling at midlength associated with depressed pro-leg reception cavity in meso- and metaventrite. Proleg with protrochanter of male possessing setose patch located paramedially or apicolaterally on posterior face, absent in female; profemur ventrally with two linear rows of setose clusters running entirety of length, clusters consists of long fine golden setae, clusters fairly evenly spaced along most series, becoming longer, larger, more clustered in apical 1/4 of profemur, longest setose cluster ca. 1/2 width of profemur, setose clusters smaller in basal 1/4, anterior face of profemur with sinuate ventral margin, ventral margin of anterior face similar but to lesser degree, posterior face covered with short stout setae in recessed pits, dorsal face similar but to lesser degree, absent on posterior/ventral faces; protarsomere V of female protarsus with setose furrow running near entirety of posterior face. Metasternal wing in form of near equilateral triangle. Metacoxal wing laterally transverse, most species with metacoxal wing ending at apex of metepisternum.
Abdomen. Abdominal sternite VIII deeply emarginate medially. Male genitalia with median lobe of aedeagus broadly articulating basomedially with parameres, lateral proximal longitudinal lists meeting median list, forming trident-shape. Female reproductive tract with medial apodeme extended anteriorly forming continuous, strongly sclerotized bridge forming anterior to lateral boundaries of vaginal shield.

Sexual dimorphism: Males noticeably larger in size in many populations, much more broad in body form being laterally expanded at elytral mid-length. Protibia of very large males often with weak to very strong sinuation. Females with similar but much smaller and sparser profemoral setation. Female elytra without swelling associated with proleg reception.

***Porrorhynchus* (*Porrorhynchus*) *indicans* (Walker, 1858)**

***Dineutes indicans* Walker, 1858**: 205 [original description]; ***Porrhorhynchus brevirostris* Régimbart, 1877**: 113, Pl. 6 fig. 5 [original description, dorsal habitus, synonymy by Régimbart, 1886: 250]; *Porrhorhynchus brevirostris*: Régimbart 1882: 429, pl. 11 fig. 50 [redescription, elytron]; *Porrhorhynchus brevirostris*: Régimbart 1884: 471 [checklist]; *Porrhorrhynchus brevirostris*: Régimbart 1886: 250 [misspelling]; ***Porrhorrhynchus indicans*: Régimbart 1886**: 250 [new status]; *Porrhorrhynchus indicans*: Régimbart 1892a: 740 [checklist]; *Porrhorrhynchus indicans*: Régimbart 1902: 5 [distribution]; ***Dineutus* (*Porrorhynchus*) *indicans:* Ochs 1926**:139 [checklist]; *Dineutus* (*Porrorhynchus*) *indicans*: Ochs 1929a: 248 [distribution]; ***Porrorhynchus* (*Ceylorhynchus*) *indicans*: Brinck 1955**: 103 [new status]; *Porrorhynchus indicans*: Vazirani 1969: 403 [distribution]; *Porrorhynchus* (*Ceylorhynchus*) *indicans*: Brinck 1980: 106, Fig. 2 - 6 [description, morphology]

Type material examined: *Dineutes indicans* Walker, 1858: Holotype by monotypy (1 ♂ pinned, Fig. 16B) “Type [beige disc, typed black ink, red circle around font]// Ceylon [blue disc, handwritten in black ink, handwriting unknown]// indicans Walker/ Ann. Nat Hist (Type) [blue label, handwritten in black ink, handwriting unknown]// *indicans* [beige label, handwritten in black ink, handwriting unknown]// No 464/ examined by/ Prof. Thaxer for/ Laboulbeniaceae. [beige label, typed black ink, except for 464 handwritten in black ink]//” (BMNH).

***Porrorhynchus brevirostris* Régimbart, 1877 lectotype here designated** (1 ♂ pinned, Fig. 16A) “Ceylan [beige label, handwritten in black ink, handwriting unknown]// MUSEUM PARIS/ COLL MAURICE REGIMBART/ 1908 [beige label with thin black border, typed in black ink]// TYPE [red label, typed black ink]// LECTOTYPE [red label, typed black ink]” (1 ex. MNHN); **paralectotype here designated** (1 ♀ pinned, missing right proleg after femur) “Java [beige label, handwritten in black ink, handwriting unknown]// MUSEUM PARIS/ COLL MAURICE REGIMBART/ 1908 [beige label with thin black border, typed in black ink]// TYPE [red label, typed black ink]// PARALECTOTYPE [red label, typed black ink]” (1 ex. MNHN).

Type designation: Régimbart’s (1877) original description of *P. brevirostris* indicates that there were 4 specimens used in the description, 2 from “Ceylan” which were stated to be in the Fairmaire and Deyrolle collections, while the other 2 were stated as being from Java (in error) in the Jekel and Régimbart collection. Only two specimens could be located in the MNHN, one with the locality label of Java and the other with Ceylan, both indicated as being from Régimbart’s collection, now in the general collection of the MNHN. After searching for the other 2 specimens in the MNHN, they are now presumed lost. Therefore, these two specimens are considered to be part of the syntype series, and the male specimen with the label “Ceylan” is here designated as the lectotype, as *P. indicans* is truly found in Sri Lanka. Given that Régimbart himself synonymized his own name, this designation seems quite sound. The specimen from Java is here designated as a paralectotype.

Additional material examined:
SRI LANKA ("Ceylonia"): "Mus: Brents" (1 ex. ZMUC); **"Ceylon"**: (2 ex. BMNH), Sharp Collection 1905-313 (1 ex. BMNH), "Mus./ Hauschild/ 12-9-1914" (2 ex. ZMUC), "Mus./ Westerm" (1 ex. ZMUC); "Niemer" (1 ex. BMNH), "Niemer" "Fry Collection/ 1905-100" (1 ex. BMNH); leg. P. Brinck, ZML.2010/ 332 (1 ex. MZLU), leg. Lewis, Sharp Collection 1905-313 (1 ex. BMNH), leg. G. Lewis, ZML.2010/ 331 (1 ex. MZLU), leg. G. Lewis, Sharp Collection 1905-313 (2 ex. BMNH); 1910, leg. G. Lewis, -320, (4 ex. BMNH); [illegible addition], "Coll.Mus./ Vindob." (3 ex. NHMW); [illegible addition], l"M. Doh", "Coll.Mus./ Vindob." (1 ex. NHMW); **Colombo**: Sharp Collection 1905-313 (1 ex. BMNH).
No locality information: Sharp Collection 1905-313 (3 ex. BMNH); "Jekyl" (1 ex. BMNH); "6756" (1 ex. BMNH).

Diagnosis: Labrum ovoid and shorter relative to other *Porrorhynchus* species. Antenna with 7 flagellomeres. Yellow lateral margins incomplete on elytra, extending normally only to the basal 1/3. Elytral apices with blunt parasutural point, without spines.

Description: *Size*: ♂ L: 16.6 – 19.2 mm, W: 9.4 – 11.2 mm; ♀ L: 15.1 – 17.0 mm, W 8.2 – 9.5 mm.
Habitus. Medium sized member of genus; body form elongate oval, attenuated anteriorly in male, female nearly parallel sided in appearance; in lateral view weakly convex, only slightly humped in scutellar region, in general dorsoventrally depressed relative to other species.
Coloration. Dorsally head, pronotum, elytra olive green, pronotum, basal 1/3 of elytra with yellow lateral margins; venter yellowish to reddish orange, ultimate maxillary palpomere black, except for apex; prolegs often slightly darker in coloration, tibia black in proximal 1/2.
Head. Dorsally vertex with sparse weakly impressed punctures; interorbital ridge without yellow margin, similarly colored as vertex; frons with weakly impressed punctures separated by 2x to 3x diameter of one puncture, fronto-lateral margins lightly wrinkled, frontoclypeal suture with posterior margin nearly straight, lateral margins nearly straight, meeting posterior margin at ca. 110° angle; clypeus with punctation most evident at anterior margin, punctures separated by ca. 2x to 3x diameter of one puncture; antennal flagellum with 7 flagellomeres (Fig. 2B); labrum ovoid in shape, punctation nearly absent basomedially, strongly present apically, punctation well impressed, dense, separated by 1.5x to 2x diameter of one puncture; maxillary/labial palpi somewhat dissimilar in shape, maxillary palps broader with asymmetrical dorsal/ventral margins, ventral margin more strongly curved than dorsal margin, labial palps with anterior/posterior margins more similar, anterior margin nearly straight, posterior margin weakly curved
Thorax. Pronotum with shallow weakly impressed wrinkles medially on disc, shallow transverse depression also often present medially, reticulation effaced on medial disc, weakly impressed sparse punctation present, laterally reticulation well impressed, punctation weakly impressed, nearly imperceptible, widely spaced, distance between nearest punctures up to 4x to 5x diameter of single puncture, lateral marginal depression present; Protrochanteric setose patch situated apicolaterally; protibial spine projecting forward; male protarsi wide, dorsally convex, shape as in Fig. 6L, male ultimate protarsomere ca. >2x as long as wide; ultimate protarsomere of female ca. 2.5x length of penultimate; elytra with reticulation effaced in scutellar/sutural regions,

reticulation present apically/laterally, most strongly impressed marginally, elytral disc with even covering of weakly impressed, fine punctation, distance between nearest punctures ca. 2x to 3x diameter of single puncture; lateral marginal depression narrow, of similar length throughout, yellow lateral margin incomplete, typically ending in basal 1/3, when longer never reaching epipleural angle, apicolateral margins of elytra without triangular saw-tooth-like spines, elytral apices (Fig. 1C) not spinose, with parasutural points in form of broad triangle, created by lateral obliquely truncate margin, with rounded inner margin, sutural angle often produced; mesosternal apex not noticeably acuminate; mesocoxae/metacoxae dissimilar, mesocoxae without posteriorly projecting process, mesocoxal process broadly rounded; male mesotarsal claws as in Fig. 6O with ventral margin broadly rounded, anterior claw apically narrowed; metacoxal process as in Fig. 6M with distinct apicolateral corners, weakly sinuate lateral margins.

Genitalia. Aedeagus (Fig. 5) with median lobe nearly as long as parameres, parallel sided for most its length, strongly acuminate in apical 1/5, apex broadly rounded, in lateral view (Fig. 5B) apex briefly weakly curved dorsally; parameres in dorsal view laterally expanded in apical 1/3, rounded apically, medially reflexed basally; in lateral view ventral margin of parameres evenly curved anteriorly to posteriorly. Female reproductive tract (Fig.13B) with large broad tubiform spermatheca; gonocoxae with lateral sinuation, apically acuminate.

Sexual dimorphism. Females are smaller in size and much more parallel sided in body form.

Differential diagnosis: *Porrorhynchus indicans* can be distinguished from all other species of *Porrorhynchus* by the incomplete yellow lateral margins of the elytra, as well as the elytral apices possessing large, triangular, parasutural points, rather than spines.

Distribution: Fig. 14. This species is only known from Sri Lanka. Within the country Brinck (1980) found the species to be primarily known from the southern central region of the island. For this study almost none of the material had specific locality information, aside from the island of Sri Lanka. One specimen indicated it was collected from Colombo, see Brinck (1980) for more precise locality and distribution data.

Biology: Brinck (1980) demonstrated that *P. indicans* is restricted to intact (what he calls “primeval”) montane forest. After searching previously known localities, Brinck (1980) was only able to recollect the species from two streams in sheltered ravines within such forests, with water temperatures below 20ºC, and at elevations above 1,200 m. Within the streams the species was mainly found in regions sheltered from the main current (Brinck 1980).

Discussion: Given the few known exact localities from Brinck (1980), the difficulty in re-collecting the species in 1980, and imperiled with future potential habitats loss, *P. indicans* is certainly warranting formal protection status. Future investigation into the distribution and status of this species on the island is highly desirable.

We here propose the common name of the Sri Lankan Snouted Whirligig for *P. indicans*.

***Porrorhynchus* (*Porrorhynchus*) *landaisi* Régimbart, 1892**

***Porrhorrhynchus landaisi* Régimbart, 1892a**: 667, 740 [original description, checklist]; *Porrhorrhynchus barthelemyi* Régimbart, 1902: 5 [*nomen nudum*]; *Porrhorrhynchus landaisi*: Régimbart 1902: 5, fig. 12 [distribution, partial dorsal habitus]; ***Porrhorrhynchus barthelemyi* Régimbart, 1907**: 153 [original description] **new synonymy**; *Porrhorrhynchus landaisi*: Régimbart 1907: 152 [description of habitat, collection information] ; *Porrhorrhynchus landaisi*: Peschet, 1923: 123 [review]; *Porrhorrhynchus landaisi*: Hatch 1925: 437, 450 [size, minor description]; *Porrhorrhynchus landaisi*: Hatch 1926: 311, Pl. XX 3, 9, 16, 17, 21, Pl. XXI 29, 41, Pl. XXII 47, 60, 64, Pl. XXIII 80, Pl. XXIV 90, 98 [morphology]; *Dineutus* (*Porrorhynchus*) *barthelemyi*: Ochs 1926: 139 [cheklist]; *Dineutus* (*Porrorhynchus*) *landaisi*: Ochs 1926: 139 [checklist]; *Dineutus* (*Porrorhynchus*) *landaisi latilimbus*: Ochs 1926: 139 [*nomen nudum* in checklist]; ***Dineutus* (*Porrorhynchus*) *landaisi latilimbus* Ochs, 1926**: 193 [original description] **new synonymy**; *Dineutus* (*Porrorhynchus*) *landaisi*: Ochs 1929b: 719 [distribution]; *Dineutus* (*Porrorhynchus*) *landaisi latilimbus*: Ochs 1929b: 719 [distribution]; *Dineutus* (*Porrorhynchus*) *barthelemyi*: Ochs 1930: 15 [catalog]; *Dineutus* (*Porrorhynchus*) *landaisi*: Ochs 1930: 16 [catalog]; *Dineutus* (*Porrorhynchus*) *landaisi latilimbus*: Ochs 1930: 16 [catalog]; *Dineutus* (*Porrorhynchus*) *landaisi:* Wu 1931: 71 [distribution]; *Dineutus* (*Porrorhynchus*) *landaisi latilimbus*: Wu 1931: 71 [distribution]; *Dineutus* (*Porrorhynchus*) *landaisi*: Cheo 1934: 222, Pl.1 Fig. 12, 13 [redescription, elytra]; *Dineutus* (*Porrorhynchus*) *landaisi latilimbus*: Cheo 1934: 223 [diagnosis] *Dineutus landaisi latilimbus*: Kamiya 1936: 14, fig. 19 [description, dorsal habitus]; *Dineutus* (*Porrorhynchus*) *landaisi latilimbus*: Ochs 1942: 206 [holdings]; *Porrorhynchus landaisi landaisi*: Mazzoldi 1995: 162 [distribution]; *Porrorhynchus landaisi latilimbus*: Mazzoldi 1995: 162 [distribution]. Snout Whirligig, *Porrorhynchus landaisi latilimbus*: Jäch & Li 1998: foreword [notes on distribution]. *Porrorhynchus* sp.: Jäch et al. 2012: 66 [distribution].

Type material examined:
***Porrorhynchus landaisi* Régimbart, 1892 lectotype here designated** (1 ♀ pinned, Fig. 16C) “Environs de/ Cao-Bang./ Tonkin Landais [white label, handwritten in black ink, handwriting appears to be Régimbart’s]/ MUSEUM PARIS COLL MAURICE REGIMBART/ 1908 [white label with thin black border, type black ink]// LECTOTYPE [red label, typed black ink]//” (1 ex. MNHN). **Paralectotype** (1 ♂ pinned [prothorax clearly glue back on, head glue back on): “Tonkin, Hanoi/ Landais [white label, handwritten in black ink, handwriting appears to be Régimbart’s]// MUSEUM PARIS/ COLL MAURICE REGIMBART/ 1908 [white label with thin black border, typed black ink]// TYPE [red label, typed black ink]// PARALECTOTYPE [red label, typed black ink]//” (1 ex. MNHN); **paralectotype** (1 ♀ pinned) “ Hanoi/ Landais [white label, handwritten in black ink, handwriting appears to be Régimbart’s]// MUSEUM PARIS COLL MAURICE REGIMBART/ 1908 [white label with thin black border, type black ink]// PARALECTOTYPE [red label, typed black ink]//” (1 ex. MNHN).

***Porrorhynchus barthelemyi* Régimbart, 1907 lectotype here designated** (1 ♂ pinned, aedeagus dissected on point, Fig. 16E) “ MUSEUM PARIS/ ANNAM/ ~~DÉCION DE QUANG NAM~~/ ~~AU NHA TRANG~~/ C^{te} DE BARTHÉLEMY 1899 [brown label, typed black in]// Dans le Aroyos/ des Mois/ à 17000 m. d’altitude [brown label, handwritten in black ink, unknown handwriting]// MUSEUM PARIS/ Annam/ C^{te} Barthelemy/ 1899 [brown label, MUSEUM PARIS printed in black ink, rest handwritten, unknown handwriting]// MUSEUM PARIS/ COLL MAURICE REGIMBART/ 1908 [white label with thin black border, typed black ink]//

LECTOTYPE [red label, typed black ink]//" (1 ex. MNHN); **paralectotype** (1 ♀ pinned) same labels as previous except without the final two MUSEUM PARIS labels and with "TYPE [red label, typed black ink]// PARALECTOTYPE [red label, typed black ink]//" (1 ex. MNHN).

***Dineutus* (*Porrorhynchus*) *landaisi latilimbus* Ochs, 1926 lectotype here designated** (1 ♂ pinned, Fig. 16D): " ♂ [white label, printed black ink]// China/ Insel Hainan/ 10.-25.III.09/ H.Schoede S.G. [beige label, typed black ink, except date which is handwritten in black ink]// Coll./ G.Ochs [white label, typed black ink]// Para-/ typoid [red label with black border, typed black ink]// latilimbus Ochs [beige label with black border, handwritten in ink, handwriting appears to be Ochs']// LECTOTYPE [red label typed black ink]" (1 ex. SMF); **paralectotype (**1 ♀ pinned) same as previous except with ♀ label and without latilimbus Ochs label and "PARALECTOTYPE [red label, typed black ink] (1 ex. SMF).

Type designation: Régimbart in his original description of *P. landaisi* mentions having examined 3 specimens (1 male and 2 females) from Tonkin, collected by M. A. Landais (Régimbart 1892a). The exact locality given by Régimbart (1892a) is Ban-Khau, to the south of Cao-bang. Of the material examined in the MNHN Régimbart collection there are 4 specimens with handwritten labels by Régimbart with Landais listed as the collector. Three are listed as being from Tonkin (1 male with a glued head and thorax and 2 intact female specimens), the other specimen has only Tuyen Quan as the locality. Therefore, we consider the 3 specimens with Tonkin on the label as the original syntype series. As the only specific locality provided by Régimbart mentions Cao-Bang, we here designate the female specimen with Cao-Bang as the locality and Landais as collector, the lectotype. This specimen is also completely intact. The male specimen from the syntype series, while carrying a type label, is heavily damaged and has not been formerly designated as a lectotype. For this reason we consider the male and the second female specimen as paralectotypes.

Ochs (1926) in his original description of *P. l. latilimbus* does not specify how many specimens were examined, but does describe both a male and female, implying more than a single specimen involved. Since no specimen was explicitly designated as the holotype the series must be regarded as syntypes. We here designate the large male specimen as the lectotype for *P. l. latilimbus* and the remaining specimens from the syntype series as paralectotypes. A lectotype was also designated for *P. barthelemyi* in order to stabilize the nomenclature. The male with its aedeagus dissected and available for study was selected as the lectotype.

Additional material examined:
CHINA: leg. G. Liu (1 ex. MCZ); **Hainan Island**: leg. J Whitehead (1 ex. BMNH), Kiung-ah an Dist., Mt. ran go, 21-22.v.1935, leg. P. K. To (2 ex. BPBM), 5 km NE Tian Chi, Jianfeng mtns, 800m, 22.i.1996, leg. Jäch (4 ex. NHMW), same as previous except: leg. Ji & Wang (1 ex. NHMW), Jianfengling, 8.ix.1938, leg. "Protector" (1 ex. ICRI), same locality as previous except: 8.xii.1981, leg. B.R. Li (1 ex. ICRI), same as previous except: 22.ii.1982, leg. R.L. Pan (1 ex. ICRI), same as previous except: leg. H.Q. Chen (2 ex. ICRI), Jianfengling Mts., Tiachi Lake env., BiSHU VILLA, 18º44'40"N, 108º50'41"E, 950m, 9-11.v.2011, leg. M. Fikáček, V. Kubeček & L. Li , at light (4 ex. NMPC); **Tibet**: Zayu co., Xiachayu, vii.2011, leg. Li Jingke (1 ex. NHMW); **Yunnan**: Kunming ("Yunnanfou"), ZML. 2010/ 336 (1 ex. MZLU). **VIETNAM**: "Annam": 1895, leg. Barthélemy, coll. C.L. Legros (1 ex. MNHN) "Tonkin": (4 ex. NHMW), "Tonkin": ZML. 2010/ 341 (1 ex. MZLU); **Bac Kan** ("Backan"): viii.1907, leg. P. Lemée,

Oberthur Coll./ 1909-159. (8 ex. BMNH); same as previous except: Oberthür Coll. (1 ex. MNHN), same as previous except: ZML. 2010/ 337-340 (5 ex. MZLU); **Bắc Quang:** "Bac-Quang", "Entre Hagiang et Vinh-Tuy", "Vallées de la Haute Riv. Claire", 1908, leg. J. de Retz (2 ex. MNHN); "Thatkhé", coll. R. Peschet (2 ex. MNHN). **Kon Tum**: ca. 20 km NE Ngoc Linh, 1-4m trib. of Ngoc Mi River, , 15º08'23.5"N 107º54'40.2"E, 980m, 10.ix.1998, leg. B. Hubley, D.C. Currie, & M. Tseng, 2º tropical forest, ROM 982314, (2 ex. ROME); **Lào Cai**: ("Laokay"), in WNW part, 12-13.viii.1934, leg. Ernest R. Tinkham (1 ex. ICRI), Bao Hà ("Bao-Ha"), 24.x.1923, leg. H. Stevens, Sladen-Goodman/ Trust Exped./ B.M.1924-329. (2 ex. BMNH); **Nghệ An**: Pu Mat ntl. Prk. Moi River, 18º57.085'N 104º48.746'E, 241m, 13.vii.2007, leg. Sites & Trung, rocky stream, L-1014, (6 ex. UMRM), W of Con Cuong, Khe Moi Forestry Camp, Keh Moi River, 18º56'N 104º49'E, 308m, 27.x.1994, leg. DC Currie, tropical forest, ROM 946108, ROMEnt Spec. No. 17526 - 17528 (3 ex. ROME), ca. 25 km SW of Con Cuông, Khe Moi River Forestry Camp, 18º56'N 104º49'E, 308m, 4.vi.1995, leg. B. Hubley, pool in Khe Moi River, ROM 956157, ROMEnt Spec. No. 2145, 4595, 4607, 4619, 4643 (7 ex. 5 ROME, 2 CNC); **Quảng Ngãi**: "Vie Klong", 97 km NE of Kon Tum ("Kontum"), 1140m, 10.vi.1960, leg. R.E. Leech (1 ex. BPBM) **Tuyên Quang** "Tuyen quan": "Ruiss. Affluents de la Rivieu Claire", leg. Capc A. Landais (1 ex. MNHN); **Uncertain locality within Vietnam:** "Haut Tonkin": "Rég de Bac Ken Ha-Giang, Quan-Ba et Yen-Minh": 1918, leg. F. de Broissia (3 ex. MNHN). **Uncertain localities:** "Kouy-Tchéo": 1909, leg. P. Cavalerie (2 ex. MNHN), "Kouy-Tchéo": "Rég. de Pin-Fa", 1909, leg. P. Cavalerie (23 ex. MNHN), same as previous except: coll. R. Peschet (3 ex. MNHN); same as previous except: coll. C.L. Legros (10 ex. MNHN).

Diagnosis: Labrum elongate and subtriangular. Antenna with 7 complete flagellomeres and an 8th typically only complete along its posterior face. Yellow lateral margins nearly complete on elytra, extending to just anteriad of elytral apices, interrupted in basal 1/3 by mediad constriction of yellow margin, associated in males with swelling for proleg reception. Elytral apices spinose, apicolaterally with saw-tooth-like serration, sutural angle produced to a short point, two parasutural spines of similar size, last saw-tooth-like spine at the epipleural angle larger and more projecting than rest.

Description: *Size*: ♂ L: 19.3 – 26.0 mm, W: 11.0 – 14.1 mm; ♀ L: 17.9 – 21.2 mm, W 10.5 – 11.9 mm.
Habitus. Largest member of genus; most specimens normally elongate oval in body form, attenuated anteriorly in large males; in lateral view strongly convex, greatly humped in scutellar region, depressed posteriorly; in anterior/posterior view very steeply sloped towards lateral margins from strongly humped scutellar region.
Coloration. Dorsally head, pronotum, elytra olive green; base of labrum yellow basomedially; pronotum, elytra with yellow lateral margins; turquoise blue reflections apicolaterally just posteriad to end of yellow lateral margins; venter yellow to yellowish orange; ultimate maxillary palpomere black, except for apex; prolegs with tibia black in proximal 1/2, profemur anteriorly with black ventral border for most its length.
Head. Dorsally vertex with even covering of weakly impressed punctures, separated from nearest puncture by ca. 2x to 3x diameter of single puncture; interorbital ridge without yellow margin, similarly colored as vertex; frons similarly punctate as vertex, fronto-lateral margins lightly wrinkled, frontoclypeal suture with posterior margin nearly straight, lateral margins nearly straight, meeting posterior margin at ca 120° angle; clypeus with punctation most evident at

anterior margin, punctures separated from nearest puncture by ca. 2x to 3x diameter of one puncture, becoming more densely spaced anteriorly; antennal flagellum with 7 complete flagellomeres, 8th incomplete suture present on posterior face; labrum sub-triangular, punctation absent basomedially in association with yellow coloration, strongly present apically, punctation well impressed, dense, separated by 1.5x to 2x diameter of single puncture; maxillary/labial palpi dissimilar in shape, maxillary palps broader, shorter with asymetrical dorsal/ventral margins, ventral margin more strongly curved than dorsal margin, labial palps narrower, more elongate with anterior/posterior margins more similar, anterior margin nearly straight, posterior margin weakly curved.

Thorax. Pronotum densely punctate, punctation consists of medium sized, well impressed punctures separated from nearest puncture by <1x to 2x diameter of single puncture, reticulation less impressed medially, becoming more well impressed laterally, very shallow transverse depression often present medially, lateral marginal depression present; Protrochanteric setose patch situated paramedially; protibial spine projecting anterolaterally; male protarsi wide, fairly dorsally convex, shape as in Fig. 6A, ultimate protarsomere of male ca. < 2x as long as wide; ultimate protarsomere of female ca. 2.5x length of penultimate; elytra with reticulation effaced in scutellar region/along elytral suture, reticulation present apically/laterally, being most strongly impressed marginally, elytral disc with even covering of well impressed, medium sized punctation, distance between nearest punctures ca. 1x – 2x diameter of one puncture; lateral marginal depression broad, expanded posteriad to humeral region; yellow lateral margin nearly complete, ending just anteriad to elytral apices, interrupted in basal 1/3 by constriction, in males associated with swelling created by cavity for proleg reception, apicolateral margins of elytra with triangular saw-tooth-like spines, final spine at epipleural angle elongate, elytral apices (Fig. 1B) spinose, with 2 parasutural spines, sutural angle produced; mesosternal apex noticeably acuminate; mesocoxae/metacoxae similar, mesocoxal process broadly rounded, without projecting process; male mesotarsal claws as in Fig. 6D,ventral margin broadly rounded, anterior claw apically narrowed; metacoxal process as in Fig. 6B, without distinct apicolateral corners, without sinuate lateral margins.

Genitalia. Aedeagus (Fig. 7A – C, E – G, I – K) with median lobe shorter than parameres, running ca. 5/6 their length, weakly to moderate laterally expanded in apical 1/3, strongly acuminate in apical 1/6, apex truncate, in lateral view apex briefly strongly curved dorsally; parameres in dorsal view weakly laterally expanded in apical 1/2, narrowly rounded, medially reflexed after apical 1/4, basally strongly constricted; in lateral view ventral margin of parameres strongly curved anteriorly to posteriorly after basal 1/3. Female reproductive tract (Fig. 13A) with large tubiform spermatheca; gonocoxae with lateral margin straightly angled towards apex, apex obliquely truncate.

Sexual dimorphism. Males tend to be larger in size than females, some males exhibit a broader body form, having their outline laterally expanded posteriad to elytral midlength, giving large males a more attenuated feel, whereas females are more evenly narrowed anteriorly and posteriorly. The spines of the elytral apices tended to be longer and more pronounced in females, whereas in very large males they tended to be smaller and more blunt.

Variation. There a considerable amount of size variation in this species in terms of body form (Fig. 7D,H,L). Several populations had very large males, especially those from Vietnam (Fig.

7H), while some like those from Hainan Island, China, had very small and narrow males (Fig. 7D), but also some of the largest. Body form tended to change along with size as noted above. The male aedeagus also showed some variation, which is discussed in the discussion section below.

Differential diagnosis: *Porrorhynchus landaisi* can be distinguished from all other species of *Porrorhynchus* being dorsally olive green with nearly complete yellow lateral margins of the elytra, ending just anteriad to elytral apex, being interrupted in basal third by a mediad constriction, and in the form of the spinose elytral apices with two parasutural spines.

Distribution: Fig. 14. Known primarily from southern China and northern Vietnam; found as far west as Zayü Co. Tibet in China (*Porrorhynchus* sp. in (Jäch et al. 2012), through southern China, Vietnam as far south as the Central Highlands, and east to Hainan Island, China.

Biology: This species is lotic, being known from forested streams based on the label data.

Discussion: This is the largest species of gyrinid known, approaching 30 mm in length! The largest specimen examined during this study was ca. 29.5 mm's from the MNHN in the Legro's collection, including labrum and abdomen. The next largest species of gyrinid known is *Dineutus macrochirus* Régimbart, 1899 reaching 22.9 mm (without the abdomen) from New Guinea (Brinck 1984).

Porrorhynchus barthelemyi (Fig. 16E) was described from specimens from the Central Highlands region of Vietnam, inhabited by the Degar indigenous ethnic group, called the "mois" by the French. These specimens are more elongate and narrow in dorsal habitus and the dorsal punctation is larger and denser than other populations of *P. landaisi*. However these are the only characters with which these specimens differ from others of *P. landaisi*, thus the name is here synonymized as it represents variation in a more southern population. Furthermore the variation of a narrow body form is exhibited in other populations of *P. landaisi*. The ventral surface of the "*barthelemyi*" specimens appears to have become unnaturally discolored in certain sclerites (Fig. 16E). *Porrorhynchus landaisi latilimbus* was described by Ochs from Hainan island, however there is absolutely no distinguishable morphological differences between the Hainan populations (Fig. 6A,B,C,D and Fig. 7A,B,C) and those from the mainland, thus this subspecies is here synonymized.

A very uniquely broad specimen (Fig. 7L) was recently collected from Tibet, collected at a light trap (Jäch et al. 2012). The specimen unfortunately is damaged, missing its labrum and was the only one of its kind collected (Fig. 7L), preventing further access of the populational variation from this area. Aside from the broader habitus the other morphological features are within the variation (Fig. 6I,J,K), including the aedeagus (Fig. 7I, J,K). This extends the known range of the species much further west than previously known.

This species has a very unique antennomere count for gyrinids, having seven distinct, but an 8th noticeable along its posterior face, most other genera having either 9 or 6, with only *Enhydrus* previously known to possess seven (Miller and Bergsten 2012).

No information is available on this species potential for sensitivity to water quality, but given all other species of *Porrorhynchus* are, it is also likely sensitive as well. This species has a more northeastern distribution in Southeast Asia (Fig. 14) and one that is considerably smaller than that of *P. marginatus*.

We propose the common name of the Splendid Snouted Whirligig for *P. landaisi*.

***Porrorhynchus* (*Porrorhynchus*) *marginatus* Laporte, 1835**

Trigonocheilus rostratus: Dejean 1833: 59 [manuscript name and *nomen nudum*, synonymy by Aubé, 1838a: 406], ***Porrorhynchus marginatus* Laporte, 1835**: 108; *Porrorhynchus marginatus*: Laporte 1835: 108 [redescription]; *Porrorhynchus marginatus*: Aubé 1838a: 406, Pl. 46 fig. 4 [redescription and habitus image]; *Trigonocheilus rostratus*: Dejean 1836: 67 [manuscript name and *nomen nudum*, synonymy by Aubé, 1838a: 406]; *Porrorhynchus marginatus*: Aubé 1838b: 759 [redescription]; *Porrorhynchus marginatus*: Hope 1838: 145 [list of type species]; *Porrorhynchus marginatus*: Laporte 1840: 170 [redescription]; *Trigonochilus rostratus*: Agassiz 1846: 377 [unjustified emendation of *Trigonocheilus rostratus*, *nomen nudum*]; *Porrorhynchus marginatus*: Newman 1847: 48 [specimen holdings]; *Porrorhynchus marginatus*: Desmarest 1851: 224, fig. 399 [redescription and dorsal habitus]; *Porrorhynchus marginatus*: Lacordaire 1854: 440 [minor description]; *Porrorhynchus marginatus*: Wood 1874: 69, fig. 28 [redescription, illustration]; *Porrhorhynchus marginatus*: Régimbart 1877: 110, Pl. 6 fig. 3 [revision, elytron]; ***Porrhorhynchus tenuirostris* Régimbart, 1877**: 110, fig. 4 [description, dorsal habitus]; *Porrhorhynchus marginatus*: Régimbart 1882: 427, Pl. 12, fig.49, fig. 49a [redescription, range extension, elytron, foreleg]; *Porrhorhynchus marginatus* var. *tenuirostris*: Régimbart 1882: 428 [new status, redescription]; *Porrhorhynchus marginatus*: Régimbart 1884: 270 [checklist]; *Porrhorhynchus marginatus* var. *tenuirostris*: Régimbart 1884: 470 [checklist]; *Porrorhynchus marginatus*: Hagen 1890: 228 [checklist]; *Porrorhynchus marginatus*: Duncan 1891: 311 [minor description]; *Porrhorrhynchus marginatus*: Régimbart 1892a: 740 [checklist]; *Porrhorrhynchus* var. *tenuirostris*: Régimbart 1892a: 740 [checklist]; *Porrhorrhynchus marginatus*: Régimbart 1902: 5 [distribution]; *Porrhorrhynchus marginatus*: Régimbart 1907: 152 [distribution]; *Porrorhynchus marginatus*: Laporte 1910: 170 [redescription]; *Porrhorrhynchus marginatus*: Zimmermann 1917: 139 [locality and holdings information]; *Porrhorrhynchus marginatus*: Peschet, 1923: 122 [review] *Porrorrhynchus marginatus*: Hatch 1925: 450 [minor description]; ***Dineutus* (*Porrorhynchus*) *marginatus*: Ochs 1926**: 139 [new status, checklist]; ***Dineutus* (*Porrorhynchus marginatus tenuirostris*: Ochs 1926**: 139 [new status, checklist]; *Dineutus* (*Porrorhynchus*) *marginatus mjöbergi*: Ochs 1926: 139 [*nomen nudum,* checklist]; *Dineutus* **(*Porrorhynchus*) *marginatus mjöbergi* Ochs, 1926**: 193 [original description] **new synonymy**; *Dineutus* (*Porrorhynchus*) *marginatus*: Ochs 1927b: 242 [distribution, habitat note]; *Dineutus* (*Porrorhynchus*) *marginatus*: Ochs 1927a: 116 [distribution]; *Dineutus* (*Porrorhynchus*) *marginatus*: Ochs 1928: 44 [distribution]; *Dineutus* (*Porrorhynchus*) *marginatus mjöbergi*: Ochs 1928: 44 [redescription]; *Dineutus* (*Porrorhynchus*) *marginatus*: Ochs 1929a: 248 [distribution]; *Dineutus* (*Porrorhynchus*) *marginatus*: Ochs 1930: 16 [catalog]; *Dineutus* (*Porrorhynchus*) *marginatus mjöbergi*: Ochs 1930: 17 [catalog]; *Dineutus* (*Porrorhynchus*) *marginatus tenuirostris*: Ochs 1930: 17 [catalog]; *Dineutus* (*Porrorhynchus*) *marginatus*: Ochs 1931: 472 [distribution]; *Dineutus* (*Porrorhynchus*) *marginatus*: Ochs 1937: 111 [locality data]; *Dineutus* (*Porrorhynchus*) *marginatus*: Ochs 1940b: 33 [distribution, habitat, variation]; *Dineutus* (*Porrorhynchus*) *marginatus*: Ochs 1940a: 5 [locality data]; *Dineutus* (*Porrorhynchus*) *marginatus*: Ochs 1953: 220 [locality data]; *Porrorhynchus* (*Porrorhynchus*) *marginatus*: Brinck 1955: 103 [new status]; *Porrorhynchus marginatus*: Balke et al. 2004: 570, Fig. 5A [distribution, dorsal habitus]; *Porrorhynchus marginatus*: Jäch et al. 2012: 66 [distribution]. *Porrorhynchus marginatus*: Miller and Bergsten 2012: figs. 9D, 12B, 15D, 16A, 20B [morphology].

Type material examined: *Porrorhynchus marginatus* Laporte, 1835: Holotype by monotypy (1 ♀ card mounted, Fig. 17A) “Rostratus/ (Java.) [handwritten black ink on card mount base, handwriting unknown]//” (1 ex. MVMA).

***Porrorhynchus tenuirostris* Régimbart, 1877 lectotype here designated** (1♂ pinned, Fig. 17D) “MUSEUM PARIS/ COCHINCHINE/ *HARMAND 1876* [white label, printed black ink]// yellow disk [underneath is handwritten 9/668 in black ink]// 7 [handwritten in black ink on small beige square]// MUSEUM PARIS/ MUSEUM PARIS COLL MAURICE REGIMBART/ 1908 [white label with thin black border, type black ink]// TYPE [red label, black ink]// LECTOTYPE [red label, black ink]//” (1 ex. MNHN); **paralectotypes here designated (**3: 1 ♂ pinned, 2 ♀ pinned) same labels as previous except without yellow disk or beige square and with “PARALECTOTYPE [red label, black type]//” (3 ex. MNHN).

***Dineutus* (*Porrorhynchus*) *marginatus mjoebergi* Ochs, 1926 lectotype here designated (**1 ♂ pinned, with aedeagus on point, Fig. 17G) “♂ [white label, typed black ink]// Mt. Dulit/ 3,500 f. [beige label, typed black ink]// Coll./ G.Ochs [white label, typed black ink]// Cotypus [red label with black borders, typed black ink]// P. marginatus/ subsp. mjobergi/ Type! Ochs/ 1924 [beige label, handwritten in ink, handwriting appears to be Ochs’]// mjobergi Ochs [beige label with black border, handwritten in ink, handwriting appears to be Och’s]// LECTOTYPE [red label, typed black ink]//” (1 ex. SMF); **paralectotype here designated** (1 ♂ pinned) same as previous except ♀ symbol label and without mjobergi Ochs label and with “PARALECTOTYPE [red label, typed black ink] (1 ex. SMF). **Nomenclatural note.** According to article 32.5.2.1 of *The Code* (ICZN 1999), the name *mjöbergi* must be emended to *mjoebergi*, so it is here emended.

Type designation. Régimbart (1877) mentions having many examples from Cochinchine from Dr. Harmand, with Phu-Quoc in quotes. In the MNHN collection there are numerous specimens collected by Harmand, however, only 4 specifically state Cochinchine on the label and as being collected in 1876. There are many more specimens in the Régimbart collection collected by Harmand, but these have Lakhon as the locality and the collection date as 1878. Given that the publication date is 1877, only those aforementioned 4 specimens are here considered as part of the syntype series. The specimen selected as the lectotype (Fig. 17D) is a male specimen already possessing a label that says “TYPE”.

Additional material examined:
INDONESIA: **"Borneo"**: (3 ex. NMPC), "Borneo": Coll. Mus. Vindob. (1 ex. NHMW), "Borneo/ Sunda Isl." (2 ex. UMRM), "Borneo": 1891, leg. Chaper (4 ex. MNHN), same as previous except: 1926, leg. E. Mjöberg, (5 ex. MCZ), "Bivang Riv.", 1926, leg. E. Mjöberg (67 ex. MCZ), "Riv. Mandar", 1897, leg. Fr. Buffat, Coll. MAURICE REGIMBART 1908 (1 ex. MNHN), same as previous except: 7.xi.1897, Coll. MAURICE REGIMBART 1908 (9 ex. MNHN), "Bohac" (1 ex. NMPC); **East Kalimantan**: Kac. Pujungan, Kayan-Mentarang Nat. Reserve, 2º52'N 115º49'E, 378m, 20.ii.-4.iii.1993, leg. D.C. Darling, lowland diptero. Forest/

WWF station, Lalut Birai/ rocky stream (Nggeng), IIS 930003, ROMEnt Spec. No. 1739, 3150 (4 ex. 2 ROME, 2CNC), same as previous except: 6.vi.1993, leg. D.C. Darling & Rosichon U., lowland diptero. Forest/ WWF station, Lalut Birai/ small stream above Nggeng River, IIS 930330, ROMEnt Spec. No. 3098, 3141 (3 ex. ROME); **West Kalimantan** (“Borneo”): "Riv. Sambey", near Ngabang ("pres Ngabang"), 1897, leg. J.B. Ledru, ZML. 2010/ 342-344 (3 ex. MZLU); **Java**: (1 ex. NMPC), Java: Coll. MAURICE REGIMBART 1908 (1 ex. MNHN), Java: leg. O. Koechlin (1 ex. NMPC), "Jiansberge", Coll. M. SÉDILLOT (2 ex. MNHN); **"Sumatra"**: Coll. MAURICE REGIMBART 1908 (1 ex. MNHN), "Sumatra": "Balighe", x.90-iii.91, leg. E. Modigliani (8 ex. ZMUC), same as previous except: ZML. 2010/ 345,346,347,354 (4 ex. MZLU), same as previous except: Coll. MAURICE REGIMBART 1908 (1 ex. MNHN), "Sumatra": "Palembang", coll. R. Peschet (7 ex. MNHN),"Sumatra": "Manna" (likely the Manna River), 1901, leg. M. Knappert, Coll. Mus. Vindob. (1 ex. NHMW), same as previous except 1902, Coll. Mus. Vindob. (1 ex. NHMW), "Sumatra": "Indrapoera", Coll. MAURICE REGIMBART 1908 (1 ex. MNHN); **North Sumatra**: "Ober Langkat", "Sumatra/ Sunda Isl.", "ix-x" (2 ex. UMRM), Bohorok, vi.1975, leg. P. Blum (1 ex. NHMW), Nias, "Hili Madjedja", N. Nias, "4 de trim".1895, leg. I.Z. Kannegieter, ZML.2010/ 348-350 (3 ex. MZLU), Gunung Leuser Ntl. Prk., Bukit Lavang env., 26.iv.2004, leg. D. Trávníček, Jiří Hájek Collection (2 ex. NMPC); **West Sumatra**: "NSG Lemba Harau", 15km NE Payakumbuh ("Payakumbu"), 11.ii.1991, leg. Jäch, , 12b, (3 ex. NHMW), Siberut Island, Salappa vill. Env., Labuan Bajau, ii.2006, leg. St. Jakl, Jiří Hájek Collection (2 ex. NMPC), same as previous except: xii.2005, leg. St. Jakl, Jiří Hájek Collection (2 ex. NMPC), Siberut Island, "Toteburu-Bakeuluk, 17.ii.1991, leg. Schödl, 22 (13 ex. NHMW), same as previous except: leg. Jäch, 22 (26 ex. NHMW), Siberut Island, "Toteburu", "W Muarasiberut", 16.ii.1991, leg. Jäch, 21 (2 ex. NHMW).

LAOS: **Champasak**: Ban Houei Khong ("Houei Kong"), iii.1965, J.A. Rondon Collection (5 ex. BPBM), Muang Paxong, Ban Thongvay, Bolaven plateau, 15º14.398'N 106º31.806'E, 1000-1200m, 7-16.vi.2008, leg. A. Solodovnikov & J. Pedersen, disturbed primary rainforest (2 ex. ZMUC); **Khammouane**: Phon Tiou, 11-12.vi.1965, J.A. Rondon Collection (3 ex. BPBM), Ban Khoun Nguen env., 18º07'N 104º29'E, 250m, 4-16, 25-30.xi.2000, leg. E. Jendek & P. Pacholátko (227 ex. NMW); **Luang Namtha**: "Nam Youan", 7km N of Ban Muangsing, 21º14'N 101º8'E, 1.v.1997, leg. W.J. Rainboth & S. Virawong (2 ex. UMMZ), 10-20km NW Luang Namtha, 600m, 17.vi.1996, leg. Schillhammer, 29, (2 ex. NHMW); **Luang Prabang**: "A THENG", 1888, leg. A. Pavie (12 ex. MNHN), Houay Houp ("Houay Houn"), ca. 16km upstream from mouth at Nam Ou, 3.iii.1998, leg. W.J. Rainboth & K.P. Bounkhamvongsa (2 ex. UMMZ); **Sainyabuli** ("Sayaboury"): 18.viii.1966, leg. "Native Collector" (1 ex. BPBM), Sainyabuli ("Sayaboury"), 29.iii.1966, leg. "Native Collector" (5 ex. BPBM), same as previous except: 20.v.1966 (3 ex. BPBM); **Vientiane**: "Ban Van Eue", 15.vii.1965, leg. "Native Collector" (2 ex. BPBM), same as previous except: 1-15.ix.1965 (2 ex. BPBM), same as previous except: 30.ix.1965 (7 ex. BPBM), same as previous except: 30.xi.1965 (5 ex. BPBM), same as previous except: 30.i.1966 (1 ex. BPBM), same as previous except: 15.ii.1966 (1 ex. BPBM), same as previous except: 16.iii.1966 (2 ex. BPBM), same as previous except: 15.v.1966 (1 ex. BPBM), same as previous except: 31.v.1966 (22 ex. BPBM), same as previous except: 30.xi.1966 (1 ex. BPBM), same as previous except: 15.xii.1966 (2 ex. BPBM), same as previous except: 30.iii.1967 (1 ex. BPBM), same as previous except: 30.viii.1967 (1 ex. BPBM), same as previous except: 1-15.ix.1967 (1 ex. BPBM), Phou Khao Khouay ("Phou Kou Khouei"), 15.ii.1966, leg. "Native Collector" (8 ex. BPBM), same as previous except: 15.iv.1966, leg. (3 ex. BPBM), Phou Khao Khouay, 18º20.369'N 102º48.523'E, 700-800m, 26-31.v.2008, leg. A.

Solodovnikov & J. Pedersen, strongly disturbed primary rainforest (1 ex. ZMUC), Phou Khao Khouay Ntl. Pr. env., Tad Luek Waterfall, 200m, 1-8.vi.1996, leg. Schillhammer, 15 (1 ex. NHMW), same as previous except: 300m, 16 (4 ex. NHMW); **Xiangkhouang** "Xieng Khouang": 21.iii.1915, leg. Vitalis, coll. R. Peschet (1 ex. MNHN); **uncertain locality within Loas:** "Bas-Laos": ii.1900, leg. Barthélemy (1 ex. MNHN); "Lakhon", 1878, leg. Harmand, Coll. MAURICE REGIMBART 1908 (13 ex. MNHN); "Tonkin" 1886, leg. Langue (4 ex. MNHN),"Tonkin", "central", 1911, leg. A. Krempf (1 ex. MNHN), "Tonkin", "region de Chim-Hua et de Tuyen-Quan", 1901, leg. A. Weiss (2 ex. MNHN); "Tonpheng", 29.v.1966, leg. "Native Collector" (1 ex. BPBM), same as previous except: 16.xii.1966 (1 ex. BPBM).
MALAYSIA: **Melacca**: leg. de Morgan (1 ex. MNHN); **Pahang**: 4 km W Rompin, "Selendang", 29.iv-6.v.1993, leg. I. Jenis (3 ex. NHMW), same as previous except: leg. Strba (5 ex. NHMW), Pahang: Taman Negara Ntl. Prk., 3º36'52"N 102º29'11"E, 21.viii.2003, leg. G. Svenson, GJS21080301 (5 ex. MSBA); **Perak**: Kwala-Kangsar, Coll. MAURICE REGIMBART 1908 (2 ex. MNHN), Kwala-Kangsar, 1902, leg. Grubauer, Coll. Mus. Vindob. (3 ex. NHMW); **Sabah**: Tawau Hills, Tawau River, 7-10.vi.1998, leg. J. Kodada & F. Ciampor (20 ex. NHMW); **Sarawak**: "Baram", 1910, leg. H.W. Smith (1 ex. MCZ), "Tuba", 18.i.1979, leg. Gärdenfors, Hall, Hansson, & Samuelsson (15 ex. MZLU). Kapit, ca. 40km SE Kapit, iii.1994, leg. J. Kodada (9 ex. NHMW), Kapit, "Rumah Ugap vill.", Slut riv., 3-9.iii.1994, leg. J. Horák (12 ex. NHMW), same as previous except: leg. J. Horák, Jiří Hájek Collection (3 ex. NMPC), Kuching, 80km S Kuching, Kampung Ana Rais, 18.ii.1993, leg. M. Jäch (1 ex. NHMW), Miri, 8 km NE Bario, stream in jungle, 24.vi.2003, leg. D. Trávníček, Jiří Hájek Collection (1 ex. NMPC), Miri, Kelabit Hi., 6km E Bario, Pa Ukat, 1000m, 27.ii.1993, leg. M. Jäch, 15 (1 ex. NHMW), Miri, Gunung Mulu Ntl. Prk. ("Mulu N.P."), Long iman, 4.iii.1993, leg. M. Jäch, 20 (1 ex. NHMW), same as previous except: 3-5.iii.1993, leg. Zettel, (14 e) (1 ex. NHMW), same as previous except: small stream, 4º0.207'N 114º49.267'E, 20.x.2006, leg. K.B. Miller, KBM20100601 (5 ex. MSBA), Miri, Sungai Kelimau, "ca. 1.3 km above mouth", 3º24'36"N 114º3'00"E, 12.ix.1980, leg. M.H. Ang, Acc. 4302-3 (EN-0002) (2 ex. ROME), Sri Aman, Batang Ai Ntl. Prk., Engkari riv., "E Bandar Sri Amman", 19-20.ii.1993, leg. Zettel, 7 (3 ex. NHMW).
MYANMAR: **Mandalay**: 8km E Pyin Oo Lwin, "Pwe Kauk Wf.", 22º03.523'N 96º31.956'E, 1070m, 19.x.1998, leg. Schillhammer, 20 (1 ex. NHMW); **Tanintharyi**: "Tenasserim", Mus. Westerm (1 ex. ZMUC), same as previous except: leg. Helfer (14 ex. NMPC).
THAILAND: "Siam": Coll. MAURICE REGIMBART 1908 (1 ex. MNHN); THAILAND: viii.1984 (3 ex. ZMUC); **Chaiyaphum**: Phu Khieo Wildlife Sanctuary, "Nam Prom", 4.iv.1994, leg. W. Shephard, WDS A 1053 (7 ex. NHMW); **Chanthaburi**: 15km E Chanthaburi City, stream at Philiu Waterfall, 29.i.1995, leg. P.P. Chen (1 ex. NHMW); **Chiang Mai**: "Soppong-Pai", 1800m, 1-8.v.1993, leg. Pacholatko & Dembicky (1 ex. NHMW); **Chumphon**: Khun Mae Yam Oum Wildlife Sanct., Haew Lome Waterfall water surf., 09º43'N 98º40'E, 122m, 22.v.2005, leg. Sites, Vitheepradit, & Prommi, L-785b (2 ex. UMRM); **Kanchanaburi**: Amphur Sangkhla Buri, Heuy Kob, 15º13'N 98º22'E, 289m, 13.iv.2002, leg. UMC and CMU teams, gravel stream, L-339 (11 ex. UMRM), Amphur Sai Yok, Thong Pha Phum Reforestation Station, Mae Nam Noi, 14º31'N 98º37'E, 204m, 12.iv.2002, leg. UMC and CMU teams, L-335 (9 ex. UMRM), 30km N Thong Pha Phum, sm. Mount. Riv., sec. veget, neustic, 14º58'11"N 98º38'35"E, 160m, 13.xii.2010, leg. Freitag, 22b (1 ex. NHMW); **Loei**: Dan Sai, "Lomie Mt.", 1.iii.1955, leg. R.E. Elbel, ZML. 2010/ 356 (1 ex. MZLU), Na Haeo, river bank, 15.v.2003, leg. P. Grootaert, J. Constant, & K. Smets, Light trap (3 ex. IRSB), Phu Luang Wildlife Sanctuary, 700-900m, 8-14.x.1984, leg. Karsholt, Lomholdt, & Nielsen (8 ex. ZMUC), Phu Rua Nat. Prk.,

Nam Tok Huay Pai, waterfall, 10.vi.1998, leg. Sites, Simpson, & Vitheepradit, L-175 (1 ex. UMRM); **Mae Hong Son**: "Ban Si Lang", 19 19'N 97 59'E, 1200m, 23-31.v.1991, leg. Dembicky (1 ex. NHMW), Huai Sua Tao, v.1992, leg. Dembicky (1 ex. NHMW); **Mukdahan**: Phu Pa Yon Ntl. Prk., Keang Pho Waterfall, 16º45.368'N 104º14.736'E, 314m, 23.iv.2004, leg. A. Vitheepradit, margin, L-634 (9 ex. UMRM); **Nakhon Nayok**: Khao Yai Ntl. Prk., ca. 700m, 29.ix-6.x.1984, leg. Karsholt, Lomholdt, & Nielsen (6 ex. ZMUC); **Nakhon Ratchasima**: Khao Yai Ntl. Prk., 14º20'N 101º30'E, 1000m, 26.iii.1992, leg. E. Hüttinger (10 ex. NHMW), Khao Yai N. D., 700-800m, 31.iv.1990, leg. E. Fuller (3 ex. NHMW); **Nan**: Ban Pha Khap, 15-20.v.1992, leg. P. Pecholatko (2 ex. NHMW), Mae Charim Ntl. Prk., Nam Wa River, 18º36'N 100º59'E, 335m, 13.iii.2002, leg. CMU Team (2 ex. UMRM); **Phang Nga**: Amphur Khura Buri, Tumbon Bang Won, 08º59'N 98º26'E, 45m, 27.iv.2002, leg. Vitheepradit & Kirawanich, gravel stream, L-375 (23 ex. UMRM), Khao Lak surr., 10.i.2003, leg. H. Forster (6 ex. NHMW), Khura Buri , "Baan Tumnang", W of Si Phang Nga Ntl. Prk., 29.xi.2006, leg. H. Zettel, 48 (4 ex. NHMW); **Phetchabun**: 5 km E Sila, "Mae Nam Pa Sak", 2.iii.1994, leg. W. Shephard, WDS A 1025 (1 ex. NHMW), Khao Kor Non-Hunting Area, Sridit Waterfall, 16º37'N 100º56'E, 702m, 11.v.2004, leg. Vitheepradit & Prommi, water surface, L-677 (1 ex. UMRM); **Rayong**: Khao Chamao-Khao Ntl. Prk. ("Khao Chamao NP"), 12.xii.1990, leg. Jäch, 14 (1 ex. NHMW); **Sakon Nakhon**: "Keek poo", 9.xi.1954, leg. R.E. Elbel ZML.2010/ 357 (1 ex. MZLU), "11 km NE Kham Poem", "Huai Ya", 5.iii.1994, leg. W. Shephard, WDS A 1027 (4 ex. NHMW); **Saraburi**: Khao Yai Ntl. Prk., Lamtok Khlong, 2.i.2008, leg. R.W. Sites, L-1025 (9 ex. UMRM); **Songkhla**: Ton Nga Chang Ntl. Prk., stream at Buddhist temple, 30.i.1995, leg. B.J. Nichols, L-81 (3 ex. UMRM), same as previous except: 6.vii.1997, leg. R.W. Sites, L-127 (24 ex. UMRM), same as previous except: 9.vi.2001, L-236 (54 ex. UMRM), Khoa Nam Khang ("Khao Nam Chang"), SW Na Thawi ("SW Nathawee"), 13.i.1995, leg. R. Sites & B. Nichols (5 ex. UMRM), 102 km SE Amphur Hat Yai, Amphur Na Tawee, Khao Nam Khang Ntl. Prk., 6º36'N 100º36'E, 100m, 15.vi.2001, leg. R.W. Sites, L-246 (5 ex. UMRM); **Surat Thani**: Khao Sok Ntl. Prk., 5-9.vi.1999, leg. D. Šanc, Jiří Hájek Collection (5 ex. NMPC), same as previous except: 15.1.2003, leg. H. Forster (5 ex. NHMW); **Yala**: Betong, "Gunung Cang dun vill.", 25.iii-22.iv.1993, leg. J. Strnad (1 ex. NHMW); **uncertain locality within Thailand**: Khao Yai Ntl. Prk., 14.xi.1988, leg. Jäch, 2 (3 ex. NHMW).

VIETNAM: **Đắk Lắk**: ca. 2km SE Ban Don, Yok Don Ntl. Prk. H.Q.,12º53'N 107º48'E, 22-31.v.1997, leg. D.C. Darling & D.C.Currie, UV/MV light, ROM 974004 (3 ex. ROME), same as previous except: leg. D.C. Darling, D.C. Currie, & A. Guidotti, MV light, ROM 974019 (1 ex. ROME), 8km SW Ban Don, Yok Don Ntl. Prk., Dak Ken R., 12º53'N 107º48'E, 16-22.vi.1997, leg. B. Hubley, Dipterocarp forest, ROM 974105 (40 ex. ROME); **Gia Lai**: 20 km N of Pleiku, 650m, 9.v.1960, leg. L.W. Quate (1 ex. BPBM), 25 km SW of Pleiku, 400m, 12.v.1960, leg. L.W. Quate (1 ex. BPBM), 40 km NW An Khe, Buon Luoi, 14º10'N 108º30'E, 620-750m, 28.iii-12.iv.1995, leg. Pacholatko & Dembicky (47 ex. NHMW), An Khe Dist., Tram Lap. Azun R., 2km NW on trail from forestry building, 14º27'N 108º33'E, 18.vi.1996, leg. B. Hubley & D.C. Currie, 1º rainforest edge/ coffee plantation, ROM 961059 (8 ex. ROME), An Khe Dist., 5.2km NE Tram Lap on forest road, Dacklest River, 14º24'N 108º33'E, 900m, 22-23.vi.1996, leg. B. Hubley & D.C. Currie, 200m upstream bridge/ stream margin/ deep pools, ROM 961086, ROMEnt Spec. No. 17529-17536 (8 ex. ROME), An Khe Dist., 3km E. Buoenloy, small stream 6km on logging road past Cha River, 25.vi.1996, leg. N. Orlov, ROM 961093 (1 ex. ROME); **Hòa Bình** ("Hoa Binh"): 1919, leg. R.P.A. de Cooman, ZML.2010/ 355 (1 ex. MZLU); **Lâm Đồng**: Fyan, 900-1000m, 11.vii-9.viii.1961, leg. N.R. Spencer (5 ex. BPBM),15km SW Bảo

Lộc, 11º27'N 107º43'E, 900m, 22-24.iv.1995, leg. Pacholatko & Dembicky (8 ex. NHMW); **M'Đrăk**: E of Buon Ma Thuot ("BanMeThuot"), 400-600m, 8-19.xii.1960, leg. C.M. Yoshimoto (5 ex. BPBM); **Nghệ An**: Phúc Sơn ("Phuc-Son"), xi-xii, leg. H Fruhstorfer, ZML.2010/ 353 (1 ex. MZLU), same as previous except: Coll. MAURICE REGIMBART 1908 (1 ex. MNHN); **Ninh Thuận**: Phan Rang ("Pha-Rang"), leg. H. Fruhstorfer, (1 ex. NHMW), same as previous except: ZML.2010/ 351-352 (2 ex. MZLU); **Quảng Trị**: "Cua Tung", H.C. Fall Collection (1 ex. MCZ), Da Krong Nature Reserve, 16º37'N 106º47'E, 5-10.vii.2011, leg. J. Constant & J. Bresseel, day collecting, I.G.:31.933 (4 ex. IRSB), same as previous except: 16º37'N 106º47'E, Light trap, I.G.:31.933 (1 ex. IRSB); **uncertain locality within Vietnam:** "Houtabo", "Se-Souk", 1897, leg. J.M. Bel (1 ex. MNHN); "Karyu Danar": , 200m, 13-28.ii.1961, leg. N.R. Spencer (10 ex. BPBM).
Uncertain locality: "Inde, Bellary, ou Ceylan", 1896, leg. De Morgan (3 ex. MNHN); "Indes Or.", "Marc 1196-36" (1 ex. MNHN); "Cochinchine", 1878, leg. Pierre (2 ex. MNHN); "Cochinchine", ii.1900, leg. Barthélemy (1 ex. MNHN); "Muang You", 26.v, coll. R. Peschet (1 ex. MNHN).
No locality information: "Patra Ignota" (1 ex. MNHN); [illegible handwriting in ink] (1 ex. NMPC); [illegible handwriting in ink], coll. R. Peschet (1 ex. MNHN); ZML. 2010/ 359 (1 ex. MZLU); 334, ZML.2010/ 358 (1 ex. MZLU); leg. Plason, Coll. Mus. Vindob. (1 ex. NHMW); 1871, "Fieber/ Mulmeir", Coll. Mus. Vindob. (1 ex. NHMW); Mus. Westerm (2 ex. ZMUC); [illegible handwriting in pencil] (1 ex. ZMUC).

Diagnosis: Interorbital ridge with yellow lateral margins, labrum highly elongate and in the form of an isosceles triangular. Antenna with 6 flagellomeres. Dorsally olive green to bronzy-brown, yellow lateral margins complete on elytra, extending to elytral apices, nearly always interrupted in basal 1/3 by a dark spot, associated in males with swelling for proleg reception. Elytral apices spinose, apicolaterally with saw-tooth-like spines, sutural angle produced to a short point, one large parasutural spine, last saw-tooth-like spine at the epipleural angle larger and more projecting than the rest, often strongly produced and spinose.

Description: *Size*: ♂ L: 13.7 – 18.1 mm, W: 7.6 – 10.8 mm; ♀ L: 12.2 – 15.1 mm, W 7.1 – 8.7 mm.
Habitus. Medium to very large members of genus; body form often tear dropped shaped, broadest posteriad to middle, attenuated anteriorly, especially in large males, other populations elongate oval, evenly attenuated anteriorly to posteriorly, especially in females; in lateral view convex, strongly humped in scutellar region, depressed posteriorly/anteriorly; in anterior and posterior view steeply sloped towards lateral margins from strongly humped scutellar region.
Coloration. Dorsally head, pronotum, elytra olive green to bronzy brown in color; labrum yellow basomedially; pronotum/elytra with yellow lateral margins; elytral margin apicolaterally darkly colored, turquoise blue reflections apicolaterally mediad to end of yellow lateral margins in some individuals; venter yellow; ultimate maxillary palpomere, not darkened in color; prolegs with tibia black in proximal 1/2, profemora black apically.
Head. Dorsally vertex with even covering of lightly impressed punctures, separated from nearest puncture by ca. 2x to 3x diameter of a single puncture; interorbital ridge with yellow margin; frons similarly punctate as vertex, punctures mostly concentrated apicomedially, fronto-lateral margins very lightly wrinkled to non-wrinkled, frontoclypeal suture with posterior margin nearly straight, lateral margins nearly straight, meeting posterior margin at ca 120° angle; clypeus with

punctation most evident at anterior margin, punctures separated from nearest puncture by ca. 2x to 3x diameter of one puncture, becoming more densely spaced anteriorly; antennal flagellum with 6 complete flagellomeres, ultimate flagellomere at least 2x longer than penultimate, trapezoidal in shape; labrum in form of isosceles triangle, punctation absent basomedially, in association with yellow coloration, strongly present apically, punctation well impressed and dense, separated from nearest puncture by .5x to 1.5x diameter of one puncture; maxillary and labial palpi similar in shape, both hatchet-form with anterior margin of maxillary palp/ventral margin of labial palp weakly curved, posterior margin of maxillary palp/dorsal margin of labial palp more strongly curved, apex of both truncate.
Thorax. Pronotum with even covering of punctation, punctation consists of finer, weakly impressed punctures separated from nearest puncture by 2x to 3x diameter of single puncture, reticulation less impressed medially, becoming very well impressed laterally, very shallow transverse depression often present medially, lateral marginal depression present; Protrochanteric setose patch situated apicolaterally; protibial spine projecting forward; male protarsi not laterally broadened, not noticeably dorsally convex, shape as in Fig. 8A, ultimate male protarsomere ca. 2x as long as wide; ultimate protarsomere of female ca. 1.5x length of penultimate; elytra with reticulation effaced in scutellar and sutural region, reticulation present apically/laterally, being very strongly impressed marginally, elytral discs with even covering of finely impressed, punctation, distance between nearest punctures ca. 2x – 3x diameter of single puncture; lateral marginal depression broad, strongly expanded posteriad to humeral region; yellow lateral margin complete, ending apicolaterally at elytral apices, nearly always interrupted in basal 1/3 by darkly colored spot, in males associated with swelling created by cavity for proleg reception, apicolateral margins of elytra with triangular saw-tooth-like spines, final spine at the epipleural angle often strongly elongate, spine-like, elytral apices (Fig. 1A) spinose, with single parasutural spine, sutural angle produced; mesosternal apex not noticeably acuminate, evenly narrowed basally to apically; mesocoxae and metacoxae similar, mesocoxae with posteriorly projecting process, processes strongly acuminate, almost spine-like (Fig. 8C); male mesotarsal claws as in Fig. 8E with ventral margin flatly rounded, anterior claw not significantly narrowed apically.

Genitalia. Aedeagus (Fig. 10) with median lobe shorter than parameres, running ca. 5/6 their length, parallel sided in basal 1/2, some populations with medial constriction, moderately laterally expanded in apical 1/2, acuminate in apical 1/4, apex truncate, in lateral view apex briefly and strongly curved dorsally; parameres in dorsal view with lateral margins briefly expanded in apical 1/3, setose in apical 1/5, apex with apicomedial margin straight to oblique reflexed in apical 1/5, medial margin arcuately reflexed after apical 1/5 until basal 1/2; lateral margins often constricted in basal 1/5; in lateral view ventral margin of parameres often evenly curved anteriorly to posteriorly. Female reproductive tract (Fig. 13C) with narrow, elongate, tubiform spermatheca; gonocoxae short, lateral margin straightly angled towards apex, apex obliquely truncate.

Sexual dimorphism. Males tend to be larger in size than females, some males exhibit a broader body form, having their outline laterally expanded posteriad to elytral midlength, giving large males a more attenuated feel anteriorly. Females tend to be much more elongate in appearance, being evenly attenuated posteriorly and apically.

Variation. This widely spread species is highly variable in terms of body form and size. Specimens examined from more northern mainland latitudes tend to be more elongate and narrowly oval in overall body form, with a much more acute labrum (Fig. 9B,C,D), with some larger specimens reaching some fairly long body lengths (Fig. 9B). Specimens from along the Malay Peninsula tended to be smaller in overall body length, with a more evenly oval body form, with a broader labrum (Fig. 9F,G,H). Borneo had specimens that ran the gamut of body forms but was notable for having a unique race containing very large and broad males (described as a formal subspecies *P. mjoebergi*, Fig. 9O). The largest specimens of *P. marginatus* came from East Kalimantan (Fig. 9O). These specimens also have relatively blunt metacoxal processes relative to other populations (Fig. 8Q).

Differential diagnosis: *Porrorhynchus marginatus* can be distinguished from all other species of the genus in having the interorbital ridge with yellow margins, and elytral apices with a single parasutural spine and buzz-saw-like serration apicolaterally. The species most similar to *P. marginatus* is *P. depressus*, however these two species drastically differ in size (with *P. marginatus* normally being much larger), the shape of the labrum (with that of *P. marginatus* being much more elongate and acuminate, and in the form of an isosceles triangle), and finally the distribution's of the two species should easily separate the two.

Distribution: Fig. 14. The most widely distributed species in the genus. Found throughout most of Southeast Asia from as far northwest as Zayü county China (Jäch et al. 2012), east to Vietnam and south to Java, including Borneo, but notably absent from the Philippines and east of Wallace's line.

Biology: Label data support the previous observation (Ochs 1927b) that *P. marginatus* is found in smaller forested streams, often above 100 m and up to 1,000 m. This species has been implicated as sensitive to water quality, being found only in streams in the Malay peninsula not contaminated by tailings from tin mines (Ochs 1927b).

Discussion: This species exhibits great variation in body form (Fig. 9), however, similar variation was not exhibited elsewhere in external morphology (Fig. 8). The northern populations exhibiting a more narrow body form, formally described by Régimbart as *P. tenuirostris* 1877, exhibit no other significant variation. Régimbart (1882) identified his "*tenuirostris*' as being mere variation and synonymized himself. Only later would the name be re-instated by the Ochs (1926). Given this name was only based on variation in outline, with other southern populations having a narrow outline (i.e. Fig. 9I) this name is formally synonymized here again.

The aedeagus shows considerable variation (Fig. 10). Most populations have a narrow elongate median lobe, that is weakly constricted medially and strongly acuminate apically. Populations from Sumatra (Fig. 10 I,J,K) have a shorter and broader aedeagus, with a thicker median lobe. However, all populations, including the Sumatran, exhibit the same general form of the median lobe, being laterally expanded in their apical 1/2, then acuminate in the apical 1/4 with a truncate apex, and having the same length to paramere proportions, being just shorter than the parameres. Importantly in lateral view all medial lobes have the apex curved dorsally. The greatest degree in variation was exhibited by the apex of the parameres. Specimens from Sumatra have broad and mostly rounded apices to the parameres (Fig. 10J,K), while other populations have strongly truncate apices (Fig. 10D,E,H,I), and many with the apex more-or-less evenly rounded (Fig. 10A,F,L,M,N). However all the parameres had a consistent obliquely truncate medial margin to the apex, and a lateral expansion in their apical 1/3. Furthermore the difference in parameres morphology could not be attributed to any single region. The broader median lobe of the Sumatran populations, were the only consistent morphological differences exhibited among the aedeagi of the *P. marginatus* specimens examined. However, this does not correspond to any formally described subspecies.

Porrorhynchus marginatus mjoebergi was described from very large specimens collected from Borneo's Mount Dulit. Other specimens from Borneo were similarly robust and among the largest specimens examined. However the broad body size was not consistent among specimens from Borneo. Specimens from East Kalimantan matched *P. m. mjoebergi* well and did exhibit a minor unique morphology apart from the more robust dorsal habitus of males. The metacoxal apex Fig. 8Q had broader and more rounded apices. The labrum of the specimen was also broader and rounder than those of other populations. The aedeagus however, exhibited no substantial difference from other populations (Fig. 10N). Given the potential isolation of the population to the mountains of central Borneo and some of the unique features exhibited, *P. m. mjoebergi* may be deserving of subspecies status pending a phylogenetic analysis. However, morphologically, there is nothing to merit continuing this distinction as a formally named taxon, until phylogenetic evidence gives credence to its distinction.

While the species has been suggested to be sensitive to water quality it has a very large range, unlike the two other members of the *sensu stricto* subgenus. Given its large range and common occurrence in museums, it is not likely of conservation concern currently.

We propose the common name of the Margined Snouted Whirligig for *P. marginatus*.

Subgenus *Rhomborhynchus* Ochs, 1926

Type species: *Porrorhynchus depressus* Régimbart, 1902 by original designation of Ochs, 1926: 65.

Dineutus (*Rhomborhynchus*) Ochs, 1926: 65 [original description]; ***Porrorhynchus* (*Rhomborhynchus*): Guignot 1950**: 124 [new status]; ***Dineutus* (*Rhomborhynchus*)**: Ochs 1955: 130; ***Porrorhynchus* (*Rhomborhynchus*): Brinck 1955**: 103 [change status]; *Porrorhynchus* (*Rhomborhynchus*): Polhemus 2011: 52 [minor description, habitat]

Diagnosis: Medium sized whirligig beetles: 9 – 11 mm. Antennal flagellum with 6 flagellomeres. Labrum ventrally with longitudinal line of setae paramedially. Dorsal eye situated posteriorly with posterior margin located in plane with that of ventral eye. Gular suture complete. Pronotum with transverse impressed line. Elytral margin without significant swelling associated with proleg reception. Males without Protrochanteric setose patch. Profemur without two linear series of large setose clusters, only with a single linear series of small setose clusters on posterior margin of ventral face, anterior face of profemur with setigerous punctures. Posterior face of protibia with golden setose brush limited to distal 1/10. Posterior face of ultimate protarsomere in female without setose furrow, completely glabrous.

Description:

Head. Antenna with 6 flagellomeres; pedicel broad, nearly rectangular in form. Labrum ventrally with two transverse linear setose rows in basal 1/2, and an additional longitudinal row anteriad to two basal transverse rows, running near entire length of labrum, situated paramedially. Gular suture complete, lateral arms of gular suture meeting anterolateral margin of ventral epicranium posteriad to submentum.

Thorax. Pronotum with transverse impressed line, situated close to anterior margin of pronotum, running parallel with it, nearly meeting anteromedially, weakly effaced medially. Elytral lateral margin without significant swelling at midlength associated with depressed cavity in meso- and metaventrite which receives proleg, elytra evenly deflexed throughout. Protrochanter of male without setose patch, posterior face completely glabrous, ventral face of males and females with linear series of short sharp setae in distal third; profemur ventrally with linear series of small setose clusters on anterior margin only, running only basal 1/3 to 1/2 of profemur, setose patches composed of one to few long setae, ventral surface with excavation apically for reception of protibia, anterior and posterior margins of ventral surface with series of knobs, especially apically, posterior face covered with short stout setae in recessed pits, as well as linear series of setigerous punctures (4 – 6), seta of setigerous punctures long and narrow, ventral margin of anterior face basally with series of short setae in basal 1/2, posterior face with warty bumps situated basally and towards ventral margin, mostly glabrous; posterior face of protibiae with setose brush limited to distal ca. 1/10 length of tibia; posterior face of protarsomere V of female protarsus without setose furrow, posterior face entirely glabrous. Elytra with elytral striae very faintly visible. Metasternal wing in the form of isosceles triangle. Metacoxal wing obliquely transverse, evenly arcuate, metacoxal wing ending at apical 1/9 of metepisternum length.

Abdomen. Abdominal sternite VIII weakly emarginate medially. Male genitalia with median lobe of aedeagus not broadly articulating basomedially with the parameres, parameres with narrow basal bridge, longitudinal lists of medial lob very narrow, lateral lists not meeting medial list.

Sexual dimorphism: No significant size or habitus dimorphism evident. Profemoral setation sexually dimorphic, males often with 2 to 3 tufts of setae, whereas females tend to have 4 or more.

Porrorhynchus (*Rhomborhynchus*) *depressus* Régimbart, 1892

***Porrhorrhynchus depressus* Régimbart, 1892b**: 996 [original description]; *Porrhorrhynchus depressus*: Régimbart 1902: 5 [distribution]; *Dineutus* (*Rhomborhynchus*) *depressus*: Ochs 1929c: 200 [holdings]; *Dineutus* (*Rhomborhynchus*) *depressus*: Ochs 1955: 133 [redescription]; ***Dineutus* (*Rhomborhynchus*) *depressus jamurensis* Ochs, 1955**: 133 [original description] **new synonymy**; ***Dineutus* (*Rhomborhynchus*) *depressus versteegi* Ochs, 1955**: 134 [original description] **new synonymy**; ***Dineutus* (*Rhomborhynchus*) *depressus moszkowskii* Ochs, 1955**: 134 [original description] **new synonymy**; ***Porrorhynchus* (*Rhomborhynchus*) *depressus*: Brinck 1955**: 103 [new status]; *Porrorhynchus* (*Rhomborhynchus*) *depressus depressus*: Polhemus 2011: 52 [locality and habitat]

Type material examined: *Porrorhynchus depressus* Régimbart, 1892: Holotype (♂ card mounted, with aedeagus glued to card, missing labrum, Fig. 17B) “N. Guinea/ Dilo/ Loria Vi.VII.90 [beige label, typed black ink with black border]// Typus [beige label, typed red ink with red border]// “Porrhorrhynch./ depressus/ Reg. n.sp. [beige label, handwritten in black ink, handwriting appears to be Régimbart’s]// *depressus*/ Rég. [beige card label, handwritten in black ink, unknown handwriting, black border]// Porrhorhynch./ depressus/ typus! Rég. [yellow label, handwritten in black ink, unknown handwriting]// Museo Civico/ di Genova [beige label, typed black ink]// Dineutus/ (Rhomborhynchus)/ depressus Rég./ vid. Ochs 1954 [beige label, typed black ink]// Vidit P. Brinck,/ 1982-2006 [white label, typed black ink]// HOLOTYPUS/ Porrorhynchus/ depressus/ Regimbart, 1832 [red label, HOLOTYPUS typed in black ink, rest handwritten in black ink, handwriting unknown]//” (MSNG).

***Dineutus* (*Rhomborhynchus*) *depressus jamurensis* Ochs, 1955: Paratype** (♂ pinned, with aedeagus on point, Fig. 17C) “♂ [white label, black typed ink]// B Jamoer/ 4 VIII 1903 [white label, handwritten in ink, handwriting unkown]// Coll./ G.Ochs [white label, typed black ink]// Para-/ typoid [red label with black border, typed black ink; underneath handwritten in black ink SMF C 9535]// jamurensis/ Ochs [beige label with black border, handwritten in blue ink, handwriting appears to be Ochs’]//” (SMF); **paratype** (♀ pinned) same as previous except with ♀ label and underneath Para-typoid label handwritten in black ink SMF C 9536, without jamurensis Ochs label (SMF).

***Dineutus* (*Rhomborhynchus*) *depressus moszkowskii* Ochs, 1955: Holotype** (*♂ pinned, with aedeagus on point, Fig. 17E) “♂ **[**white label, typed black ink]// Holl. N.-Guinea/ Zentralgeb. Ende XII.10/ Moszkowski S.G. [gray label, typed in black ink, except Zentralgeb. Ende XII.10 handwritten, handwriting uknown]// 94915 [beige label, handwritten in black ink, handwriting unknown]// Coll./ G.Ochs [white label, typed black ink]// Typus [red label with black border, typed black ink; underneath handwritten in black ink SMF C 9538]// moszkowskii/ Ochs [beige label with black border, handwritten in blue ink, handwriting appears to be Ochs’]//” (SMF); **paratype (Allotype)** (♀ pinned) same label data as holotype except with ♀ label and “Allo- /typus [red label with black border, Allo- hand written in black ink, rest typed black ink; underneath handwritten in black in SMF C 9539]//” (SMF).

***Dineutus* (*Rhomborhynchus*) *depressus versteegi* Ochs, 1955: Holotype** (♂ pinned, with aedeagus on point, Fig. 17F) “♂ [white label, type black ink]// Z. NieuwGuinea/ Versteeg 1912.13/ Beaufort. II [white label, typed black ink, except Beaufort. II handwritten in black ink]// [blue label, underneath typed in black ink 1919, plus some illegible scribble in pencil]// Museum/ Dresden/ leg. 1928. [white label with thin black border, typed black ink]// Coll./ G.Ochs [white black, typed black ink]// Typus [red label with thick black border, typed black ink; underneath handwritten in black ink SMF C 9537]// versteegi Ochs [beig label with black border, handwritten in blue ink, handwriting appears to be Ochs’]//” (SMF); **paratype** (♀ pinned) same locality label as previous, except with ♀ label, as well as “Para-/ typoid [red label with black border, typed black ink; underneath handwritten in black ink SMF C 11258]// det. K.M.HELLER 1915/ Porrorhynchus/ depressus Rég. [beige label, typed black ink, except 15 handwritten in black ink]//” and without blue label and versteegi Ochs label (SMF).

Type material notes. Upon initial receipt of the type specimens of *P. d. moszkowskii* from SMF close examination revealed that what had been indicated as the male holotype based on the type labels (SMF C 9538), as well as having the male symbol label and pointed aedeagus, was in fact a female specimen. The specimen with the Allotype label (SMF C 9539) and female symbol label, was the actual male specimen and whose abdomen was propped open, indicative of dissection. It appears at some point during a past examination all the male holotype labels, including the dissected genitalia, were removed, as were those of the female allotype's, at which point they were subsequently switched upon being returned to the specimens. Ochs (Ochs 1955) was explicit when he designated a male as the holotype. Therefore, since it is clear that the male specimen received from SMF was previously dissected, and carrying allotype labels, being likely switched with the present female holding the holotype labels, the holotype labels were returned to the dissected male specimen and the allotype label's were placed back on the female specimen received.

Additional material examined:
INDONESIA: **West Papua** ("Irian Jaya"): Nabire, 30km S. Nabire, Kali Cemara, 150m, 15.viii.1998, leg. M. Balke, CE 1 (29 ex. NHMW), Nabire, rd. Nabire-Ilaga, Km 35 Kali Cemara, 100m, 27.ix.1997, leg. M. Balke, IRS97#6 (41 ex. NHMW), Nabire, rd. Nabire-Ilaga, Km 63, 8.x.1997, leg. M. Balke, IRS97#9 (62 ex. NHMW), Danau Yamur ("B Jamer"), 4.viii.1905, Coll. MAURICE REGIMBART 1908 (1 ex. MNHN), same as previous except: coll. C.L. Legros (1 ex. MNHN), "Nelle Guinea Limmena", Danau Yamur ("B Jamer"), 4.viii.1905, Coll. MAURICE REGIMBART 1908 (2 ex. MNHN).
PAPUA NEW GUINEA: : 1912-1913, leg. Versteeg, ZML.2010/ 334,335 (2 ex. MZLU); **Central Province**: "Astrolabe Geb.", leg. E. Weiske, ZML.2010/ 333 (1 ex. MZLU); **Gulf Province**: Omo River, at Omo, 6°58'41"S 144°18'15"E, 40m, 28.ii.1995, leg. D.A. Polhemus, CL 7001 (6 ex. DAPC).

Diagnosis: Labrum elongate and in the form of a near equilateral triangular. Antenna with 6 flagellomeres. Dorsally bronzy-brown, with pronotal yellow lateral margins broad, completely reaching lateral boundary of pronotum. Yellow lateral margins complete on elytra, extending to elytral apices, never interrupted in basal 1/3 by a dark spot, elytra without swelling associated with proleg reception in males. Elytral broadest at midlength, apices spinose, apicolaterally without saw-tooth-like spines, sutural angle produced to a short point, one large parasutural spine, epipleural angle with a large spine.

Description: *Size*: ♂ L: 9.5 – 11.5 mm, W: 5.5 – 7.0 mm; ♀ L: 9.6 – 11.6 mm, W 5.2 – 7.1 mm.
Habitus. Small member of genus; body form often tear dropped shaped, broadest posteriad to middle, attenuated anteriorly, and posteriorly, other populations elongate oval, evenly attenuated anteriorly to posteriorly; in lateral view fairly depressed, weakly humped in scutellar region, depressed posteriorly and anteriorly; in anterior and posterior view weakly sloped towards lateral margins, lateral margins explanate.
Coloration. Dorsally head, pronotum, elytral bronzy brown in color; labrum of uniform color, similar to head; pronotum/elytra with yellow lateral margins; elytral margin of uniform yellow color, only darkened at epipleural spine; venter yellow; ultimate maxillary palpomere, not darkened in color; prolegs with tibia somewhat darker in color in proximal 1/2, profemora shortly darker apically.
Head. Dorsally vertex with fairly even covering of lightly impressed, fine punctures, often obscured by strongly reticulation, most readily visible in lateral view, separated from nearest puncture by ca. 2x to 3x diameter of single puncture; interorbital ridge without yellow margin; frons punctation similar to vertex, more sparse, punctures sparsest apicomedially, fronto-lateral

margins lightly wrinkled, frontoclypeal suture with posterior margin nearly straight, lateral margins shallowly arced, meeting posterior margin at ca 130° angle; clypeus with punctation most evident at anterior margin, sparsest medially, punctures separated from nearest puncture by ca. 3x to 4x diameter of single puncture, becoming more densely spaced anteriorly and laterally; antennal flagellum with 6 complete flagellomeres, ultimate flagellomere ca. 3x longer than penultimate, trapezoidal in shape; labrum in form of equilateral triangle, punctation absent basomedially, in association with strong reticulation, strongly present apically, punctation more strongly impressed, separated from nearest puncture by 1x to 2x diameter of single puncture; maxillary and labial palpi similar in shape, strongly hatchet-form. anterior margin of maxillary palp/ventral margin of labial palp evenly curved, posterior margin of maxillary palp/dorsal margin of labial palp more strongly curved proximally, nearly straight apically, apex of both truncate.
Thorax. Pronotum with even covering of punctation, punctation consists of fine, weakly impressed punctures, most evident medially, nearly imperceptible laterally, punctures separated from nearest puncture by 1x to 2x diameter of single puncture, reticulation less impressed medially, becoming very well impressed laterally, shallow transverse depression often present medially, lateral marginal depression absent; protibial spine projecting anterolaterally; male protarsi narrow, somewhat dorsally convex, shape as in Fig. 11A, ultimate protarsomere of male ca. 2x as long as wide, penultimate protarsomere slightly larger than previous three; ultimate protarsomere of female ca. .5x longer than length of penultimate; elytra with uniform reticulation, elytral discs with even covering of very weakly impressed, fine punctation, nearly imperceptible, distance between nearest punctures ca. 4x – 5x diameter of a single puncture, punctures more closely spaced at suture; lateral marginal depression absent, elytral margins evenly sloped, weakly explanate; yellow lateral margin complete, ending apicolaterally at epipleural spine, never interrupted in basal 1/3 by darkly colored spot, males without swelling associated with cavity for proleg reception, apicolateral margins of elytra without triangular saw-tooth-like spines, the epipleural angle produced to spine, elytral apices spinose (Fig. 1D), with 1 parasutural spine, sutural angle produced; mesosternal apex shortly acuminate with broad apex; mesocoxae/metacoxae dissimilar, mesocoxae without posteriorly projecting process; metacoxal process with without distinct lobes (Fig. 11B); male mesotarsal claws as in Fig. 11L with ventral margin strongly arched, anterior claw not significantly narrowed apically.

Genitalia. Aedeagus (Fig.12 A – C, E – G, I – K) with median lobe, nearly as long as parameres, just shorter in some populations, parallel sided for 4/5 length, narrowed towards apex in apical 1/5 with straight apicolateral margins, carinate in apical 1/6, apex in lateral view subtruncate, median lobe evenly arced dorsally; parameres in dorsal view narrow, setose in apical 1/2, weakly laterally expanded in apical 1/2, shallowly arced towards apex, apex flatly rounded, basally with narrow basal bridge, in lateral view ventral margin of parameres very weakly curved anteriorly to posteriorly. Female reproductive tract (Fig. 13D) with narrow, elongate, tubiform spermatheca; gonocoxae elgonate and narrow, apically narrowly rounded.

Sexual dimorphism. No sexual dimorphism appears evident, only differences are those mentioned in the description of the subgenus.

Variation. This species is variable in the extent of lateral expansion of the elytra. Specimens from more eastern regions exhibit a broader dorsal habitus (Fig. 12D, H) from the greater lateral expansion of the elytra, while those from the western part of the range are more narrow, with only slightly laterally expanded elytra (Fig. 12L).

Differential diagnosis: *Porrorhynchus depressus* can be distinguished from all other species of the genus in having spinose elytral apices without apicolateral triangular saw-tooth-like spines and from *P. misoolensis* in the form of the aedeagus and gonocoxae of the female RT. The aedeagus of *P. d. depressus* is parallel-sided for 4/5 its length, straightly narrowed towards apex in apical 1/5 and nearly as long as the narrow parameres, which are narrow, whereas that of *P. misoolensis* is shortly laterally expanded in apical 3/4, then roundly narrowed towards apex in apical 1/4, and distinctly shorter than the broader parameres. The gonocoxae of *P. depressus* are narrower, and more elongate in appearance, with their apex narrowly rounded, compared to those of *P. misoolensis* which has broader, less elongate gonocoxae. In general *P. depressus* is larger in body size and has a broader dorsal habitus, with elytral that are typically much more laterally expanded. The lateral expansion of the elytra occurs near mid-length, as opposed to just anteriad to it, as in *P. misoolensis*.

Distribution: Fig. 15. Found infrequently across New Guinea.

Biology: This species is known primarily from rivers, and one locality is described in detail by Polhemus (2011). Older records also include the lake, Danau Yamur, but it is unclear if *P. depressus* was collected on the lake or from streams near or feeding the lake, the latter being more likely.

Discussion: Several subspecies of *P. depressus* were described of by Ochs (1955), all from very few specimens, from disparate localities across New Guinea. The subspecies *jamurensis* was described from Danau Yamur in northwestern New Guinea and based upon minor variation in the yellow lateral margins of the elytra and parameres of the aedeagus. The subspecies *versteegi* was described from the "Beaufort River", described by Ochs (1955) as a tributary of the Lorentz River, distinguished as being slightly larger and broader than the nominal species, also associated with minor aedeagal variation. Finally *moszkowskii*, described from the Van Daalen River, was separated by Ochs (1955), due to its smaller size and narrower body form. This minor variation in body size, outline, and parameres served as the basis for separating these subspecies from the typical form from southeastern New Guinea.

As can be seen from Fig. 12D,H,L there is considerable variation in degree of lateral expansion to the elytra, creating relatively broader and narrow dorsal habitus among populations. Newly examined specimens from Nabire are considerably narrower than the southeastern populations, more so than any other previously described subspecies, but similar significant variation is not exhibited in other morphological features (Fig. 11 A – L). As seen with other *Porrorhynchus* species, the parameres tend to vary considerably among populations (i.e. *P. marginatus*), but the median lobes tend to be fairly conserved. The most noticeably variation among the median lobes is exhibited in the degree of acumination in the apex. Specimens from Nabire (Fig. 12I) were more weakly constricted, relative to typical specimens (Fig. 12A), while those from the Lorentz River (corresponding to *versteegi*,Fig. 12E) were more strongly acuminate. However, all the median lobes of all populations are similarly proportioned, being nearly as long as the parameres, with similar features being mostly parallel-sided for nearly their entire length, acuminate in the apical 1/5, and with a carinate apex. For this reason all the former subspecies are here synonymized, being based on simple populational variation.

This species has not yet been implemented as being sensitive to water quality. However, it is apparently infrequently encountered, suggesting it may be relatively rare compared to other New Guinean gyrinid fauna (Polhemus 2011).

We here propose the common name of Flat Snouted Whirligig for *P. depressus*.

***Porrorhychus* (*Rhomborhynchus*) *misoolensis* (Ochs, 1955), new status**

***Dineutus* (*Rhomborhynchus*) *depressus misoolensis* Ochs, 1955**: 135 [original description]; *Porrorhynchus* (*Rhomborhynchus*) *depressus misoolensis*: Polhemus 2011: 53 [locality and habitat information]

Type material examined: Paratype (♂ pinned, with aedeagus pointed, Fig. 17H) "♂ [white label, typed black ink]// MISOOL Id. (W.)/ 0 – 75m. Fakal./ 8.ix – 20.x.1948./ M.A. Lieftinck [beige label, typed black ink, except Fakal handwritten in black ink]// Coll./ G.Ochs [white label, typed black ink]// Para-/ typoid [red label with thick black border, typed black ink; underneath handwritten in black ink SMF C 9540]// misoolensis/ Ochs [beige label with black border, handwritten in blue ink, handwriting appears to be Ochs']//" (SMF); **paratype** (♀ pinned) same as previous except with ♀ label and underneath Para-typoid label handwriting reads SMF C 9541, and without misoolensis Ochs label (SMF).

Additional material examined:
INDONESIA: **West Papua** ("Irian Jaya"): **Misool Island**: Tama River, SE of old Fakal village site, 1°51'38.1"S 129°55'24.1"E, 60m, 22.iv.1999, leg. D.A. Polhemus, CL 7110 (4 ex. DAPC).

Diagnosis: Labrum elongate and in the form of a near equilateral triangular. Antenna with 6 flagellomeres. Dorsally bronzy-brown, with pronotal yellow lateral margins broad, completely reaching lateral boundary of pronotum. Yellow lateral margins complete on elytra, extending to elytral apices, never interrupted in basal 1/3 by a dark spot, elytra without swelling associated with proleg reception in males. Elytra broadest just anteriad to midlenth, apices spinose, apicolaterally without saw-tooth-like spines, sutural angle produced to a short point, one large parasutural spine, epipleural angle with a large spine.

Description: *Size*: ♂ L: 9.4 – 10.1 mm, W: 5.6 – 5.8 mm; ♀ L: 9.9 – 10.1 mm, W 5.6 – 5.8 mm. *Habitus*. Smallest member of genus; body form elongate oval, evenly attenuated anteriorly and posteriorly; in lateral view depressed, weakly humped in scutellar region, depressed posteriorly and anteriorly; in anterior and posterior view weakly sloped towards lateral margins, lateral margins explanate.
Coloration. Dorsally head, pronotum, elytra bronzy brown in color; labrum of uniform color, similar to head; pronotum, elytra with yellow lateral margins; elytral margin of uniform yellow color, only darkened at epipleural spine; venter yellow; ultimate maxillary palpomere, not darkened in color; prolegs with tibia darker in color in proximal 1/2, profemora shortly darker apically.

Head. Dorsally vertex with even covering of lightly impressed, fine punctures, often obscured by the strong reticulation, most readily visible in lateral view, separated from nearest puncture by ca. 1.5x to 2x diameter of single puncture; interorbital ridge without yellow margin; frons punctation similar to vertex, more sparse, punctures sparsest apicomedially, separated from nearest puncture by ca. 2x to 3x diameter of single puncture, fronto-lateral margins very lightly wrinkled, frontoclypeal suture with posterior margin nearly straight, lateral margins shallowly arced, meeting posterior margin at ca 130° angle; clypeus with punctation most evident at anterior margin, sparsest medially, punctures separated from nearest puncture by ca. 1.5x to 2x diameter of single puncture, becoming more densely spaced anteriorly/laterally; antennal flagellum with 6 complete flagellomeres, ultimate flagellomere ca. 3x longer than penultimate, trapezoidal in shape; labrum in form of equilateral triangle, punctation absent basomedially, strongly present apically, punctation more strongly impressed than remainder of head, separated from nearest puncture by 1x to 1.5x diameter of single puncture; maxillary and labial palpi similar in shape, both strongly hatchet-form with anterior margin of maxillary palp/ventral margin of labial palp evenly curved, posterior margin of maxillary palp/dorsal margin of labial palp more strongly curved proximally, nearly straight apically, apex of both truncate.
Thorax. Pronotum with even covering of punctation, punctation consists of fine, weakly impressed punctures, most evident medially, nearly imperceptible laterally, punctures separated from nearest puncture by 1x to 1.5x diameter of single puncture, reticulation less impressed medially, very well impressed laterally, shallow transverse depression often present medially, lateral marginal depression absent; protibial spine projecting anterolaterally; male protarsi narrow, somewhat dorsally convex, shape as in Fig. 11M, ultimate protarsomere of male ca. 2x as long as wide, penultimate protarsomere slightly larger than previous three; ultimate protarsomere of female ca. .5x length of the penultimate; elytra with uniform reticulation, elytral discs with even covering of weakly impressed, fine punctation, nearly imperceptible, distance between nearest punctures on average ca. 5x to 6x diameter of single puncture, punctures more closely spaced in suture; lateral marginal depression absent, elytral margins evenly sloped, explanate; yellow lateral margin complete, ending apicolaterally at epipleural spine, never interrupted in basal 1/3 by darkly colored spot, males without swelling associated with cavity for proleg reception, apicolateral margins of elytra without triangular saw-tooth-like spines, epipleural angle produced to spine, elytral apices spinose (Fig. 1E), with 1 parasutural spine, sutural angle produced; mesosternal apex shortly acuminate with broad apex; mesocoxae/metacoxae dissimilar, mesocoxae without posteriorly projecting process (Fig._); metacoxal process without distinct lobes (Fig. 11N); male mesotarsal claws as in Fig. 11P with ventral margin strongly arched, anterior claw not significantly narrowed apically.

Genitalia. Aedeagus (Fig. 12M – O) with median lobe, shorter than parameres, running ca. 5/6 their length, parallel sided in basal 3/4, then laterally expanded, apically arcuately narrowed towards apex in apical 1/4, apex carinate, narrowly rounded, in lateral view apex subtruncate, median lobe weakly arced dorsally; parameres broad, setose in apical 1/2, in dorsal view, laterally expanded in apical 1/2, apically narrowly rounded; in lateral view ventral margin of parameres very weakly curved anteriorly to posteriorly. Female reproductive tract (Fig. 13E) with narrow, elongate, tubiform spermatheca; gonocoxae broad, lateral margin straightly angled towards apex, apex truncate.

Sexual dimorphism. No sexual dimorphism appears evident, only differences are those mentioned in the description of the subgenus.

Variation. Very little variation observed, but only a small number of individuals were available for study.

Differential diagnosis: *Porrorhynchus misoolensis* can be distinguished from all other species of the genus in having spinose elytral apices without apicolateral triangular saw-tooth-like spines and from *P. depressus* in the form of the aedeagus and female RT. See differential diagnosis under *P. depressus* for further details. Distribution can also be used to separate *P. misoolensis* as it is only known from Misool Island.

Distribution: Fig. 15. Known only from Misool Island, West Papua.

Biology: This species has only been collected once after its original description from a upland forested stream (Polhemus 2011). The habitat is described in detail by Polhemus (2011) who suggested this species may be influenced by stream water chemistry and substrate characteristics.

Discussion: *Porrorhynchus misoolensis* was only collected from a single locality during sampling of many streams on Misool island by Polhemus in 1999 (Polhemus 2011). This coupled with the species, limited distribution, and potential sensitivity to water chemistry suggests *P. misoolensis* may be of conservation concern. Further investigations into the species distribution on the island and its sensitivity to water quality and chemistry would be beneficial.

We here propose the common name of the Misool Snouted Whirligig for *P. misoolensis*.

Conclusions

Few features unite all the species currently recognized within *Porrorhynchus,* they are: 1) an elongate labrum that is at least 1/2 as long as wide; 2) a spinose distolateral angle of the protibia; 3) an elongate tubiform spermatheca associated with a vaginal shield. These, however, could simply be symplesiomorphies as members of *Rhombodineutus* also have elongate labra and elongate spermathecae, and members of *Andogyrus* have an expanded distolateral angle to their protibia forming a blunt spine (Brinck 1983; Hatch 1925). Members of *Porrorhynchus sensu stricto* on the other hand present at least three potential synapomorphies: 1) the presence of a protrochanteric setose patch in males; 2) loss of the pronotal transverse impressed line; 3) setation of the ventral face of the profemora consisting of two longitudinal lines of clusters of large setae, progressively becoming denser apically. These features separate members of *Porrorhynchus sensu stricto* from all other gyrinid genera and may, in fact, represent excellent apomorphies for the true genus *Porrorhynchus*. Brinck's *Ceylorhynchus* was erected for *P. indicans* and diagnosed by small setae present at the apicolateral angle of the protibia, but these setae are present on many gyrinid species, and the separation of *P. indicans* from the members of the sensu stricto group seems unjustified given the aforementioned shared features.

Rhomborhynchus on the other hand shares numerous features with the genus *Dineutus*, these are: 1) profemora with setigerous punctures, 2) setation of the ventral face of profemora composed of small clusters of setae, 3) narrow protibia that are not strongly laterally expanded,

4) median lobe of aedeagus narrowly articulating with parameres. Given these shared features, it is understandable why Ochs (1926; 1955) considered *Rhomborhynchus* a subgenus of *Dineutus*. Whether *Rhomborhynchus* is sister to the rest of *Dineutus* retaining features from a common ancestor with *Porrorhynchus*, sister to *Porrorhynchus sensu stricto* retaining features from a common ancestor with *Dineutus*, or forming a grade into *Dineutus* from *Porrorhynchus* will need to be clarified via phylogenetic analysis.

Checklist of species

The Sri Lankan Snouted Whirligig	
Porrorhynchus (*Porrorhynchus*) *indicans* (Walker, 1858)	**Sri Lanka**
= *Porrorhynchus brevirostris* Régimbart, 1877	
The Splendid Snouted Whirligig	
Porrorhynchus (*Porrorhynchus*) *landaisi* Régimbart, 1892	**China, Vietnam**
= *Porrorhynchus barthelemyi* Régimbart, 1907	
= *Dineutus* (*Porrorhynchus*) *landaisi latilimbus* Ochs, 1926	
The Margined Snouted Whirligig	
Porrorhynchus (*Porrorhynchus*) *marginatus* Laporte, 1835	**Borneo, China, Java, Laos, the Malay Peninsula, Myanmar, Sumatra, Thailand, Vietnam**
= *Porrorhynchus tenuirostris* Régimbart, 1877	
= *Dineutus* (*Porrorhynchus*) *mjoebergi* Ochs, 1926	
The Flat Snouted Whirligig	
Porrorhynchus (*Rhomborhynchus*) *depressus* Régimbart, 1907	**New Guinea**
= *Dineutus* (*Rhomborhynchus*) *depressus jamurensis* Ochs, 1955	
= *Dineutus* (*Rhomborhynchus*) *depressus moszkowskii* Ochs, 1955	
= *Dineutus* (*Rhomborhynchus*) *depressus versteegi* Ochs, 1955	
The Misool Snouted Whirligig	
Porrorhynchus (*Rhomborhynchus*) *misoolensis* Ochs, 1955 **new status**	**Misool Island**

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Hainan Island. Thanks to Fenglong Jia (ICRI) for loaning of Chinese specimens. Further thanks are due to Christine Taylor for loan extensions. Very special thanks to Dan Polhemus for loaning material of the very uncommon *P. depressus* and *P. misoolensis* from his personal collection. The first author wishes to thank Nathan Lord for helpful comments early on during this project, and for providing images of specimens held in the MNHN. Thanks to Andrew Short for SEM images and to Heather Shinogle for assistance with the SEM. SEM images were made possible by the KU Microscopy and Analytical Imaging Laboratory. Johannes Bergsten and Joe Cook are thanked for edits and suggestions on an early form of the manuscript. Travel for examination of type material within the MNHN was funded by the MCZ Ernst Mayr Travel Grants in Animal Systematics awarded to GTG. This research was partially funded the Alvin R. and Caroline G. Grove Research Scholarship, University of New Mexico.

References Cited

Agassiz, L. 1846. Nomenclatoris Zoologici. Index Universalis, continens Nomina Systematica Classum, Ordinum, Familiarum et Generum Animalium Omnium. . Jent et Gassmann, Soloduri.

Balke, M., M. Jäch, and L. Hendrich. 2004. Insecta: Coleoptera. [pp. 555 - 609]. In: C. M. Yule and H. S. Yong (editors), Freshwater Invertebrates of the Malaysian Region. Academy of Sciences Malaysia, Kuala Lumpur. 555 - 609 pp.

Brinck, P. 1955. A revision of the Gyrinidae (Coleoptera) of the Ethiopian region. I. Acta Universitatis Lundensis. Nova Series 51(16):1 – 144.

Brinck, P. 1980. *Porrorhynchus indicans* Walker (Coleoptera: Gyrinidae). A representative of the relict montane forest ecosystem in Sri Lanka. . P.E.P. Deraniyagala Commemoration Volume (Sri Lanka 1980):103-108.

Brinck, P. 1983. A revision of *Rhombodineutus* Ochs in New Guinea (Coleoptera: Gyrinidae). Entomologica Scandinavica 14(2):205-233.

Brinck, P. 1984. Evolutionary trends and specific differentiation in *Merodineutus* (Coleoptera: Gyrinidae). International Journal of Entomology 26(3):175-189.

Dejean, P. F. M. A. 1833. Catalogue des Coléoptères de la collection de M. le comte Dejean. Chez Mélquignon-Marvis Père et fils, Paris. 433 p.

Desmarest, E. 1851. Coléoptères. Cicindélètes, carabiques, dytisciens, hydrophiliens, sylphaes et nitidulaires. Encyclopédie d'histoire naturelle ou traité complet de cette science d'après les travaux des naturalistes le plus éminents de tous les pays et de toutes les époques Buffon, Daubenton, Lacépède, G Cuvier, F Cuvier, Geoffroy Saint-Hilarie, Latreille, de Jussieu, Brongniart, etc, etc, Ouvrage résumant les observations de auteurs anciens et comprenant toutes les découvertes modernes jusqu'à nos jours. Marescq & Compagnie, Paris. [2] + 312 pp. 328 pls. p.

Duncan, P. M. 1890. Cassell's Natural History. Vol. II. [p. 360 pp.]. Cassell & Company Limited, London, Paris, Melbourne. 360 pp. p.

Guignot, F. 1950. Sur la systematique des *Dineutus* (Col. Gyrinidae). Bulletin Mensuel de la Société Linnéenne de Lyon 19:124 – 127.

Gustafson, G. T., and K. B. Miller. 2013. On the family- and genus-series nomina in Gyrinidae Latreille, 1810 (Coleoptera, Adephaga). Zootaxa 3731(1):077 – 105.

Gustafson, G. T., and K. B. Miller. 2015. The New World whirligig beetles of the genus *Dineutus* Macleay, 1825 (Coleoptera, Gyrinidae, Gyrininae, Dineutini). Zookeys 476:1 - 135.
Hagen, B. 1890. Die Pflanzen- und Theirwelt von Deli auf der Ostküste Sumatra's. Naturwissenschaftliche skizzen und beiträge. [p. 240 pp.]. E. J. Brill, Leiden. 240 pp. p.
Hatch, M. H. 1925. The phylogeny and phylogenetic tendencies of Gyrinidae. Papers of the Michigan Academy of Science, Arts and Letters V:429 – 467.
Hatch, M. H. 1926. The morphology of Gyrinidae. Papers of the Michigan Academy of Science, Arts and Letters 7:311 – 350.
Hatch, M. H. 1927. Notes on the biology of *Dineutus* (Gyrinidae). Bulletin of the Brooklyn Entomological Society 22(1):27 – 28.
Hope, F. W. 1838. Coleopterist's Manual, Part the Second, containing the predacious land and water beetles of Linneus and Fabricius. Henry G. Bohn, York Street, Covent Garden, London. 168 p.
Horn, W., I. Kahle, G. Friese, and R. Gaedike. 1990. Collectiones Entomologicae A Compendium of the Locations of the World's Entomological Collections Up To 1960. Part I A to K and Part II L to Z. Akademie der Landwirtschaftswissenschaften der Deutschen Demokratischen Republik, Berlin, Germany. 220 pp. (Part I); 353 pp (Part II) p.
ICZN. 1999. International Code of Zoological Nomenclature, Fourth Edition, adopted by the International Union of Biological Sciences. International Trust for Zoological Nomenclature, London. xxix + 306 p.
Jäch, M., and L. Ji. 1998. Foreword. [p. Foreward]. In: M. Jäch and L. Ji (editors), The Water Beetles of China. Vol. II. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. Foreward p.
Jäch, M., J. Li, X. Zhang, and M. Gao. 2012. A remarkable collection of aquatic and riparian beetles from Xiachayu, Zayü County, southeastern Tibet (Coleoptera: Gyrinidae, Noteridae, Dytiscidae, Spercheidae, Hydrophilidae, Heteroceridae, Limnichidae). Koleopterologische Rundschau 82:65-69.
Kamiya, K. 1936. Family Gyrinidae, Family Haliplidae. Fauna Nipponica 10((8(6))):1—55.
Lacordaire, M. T. 1854. Histoire Naturelle des Insectes. Genera des Coléoptères. Vol. 1. . Librairie Encyclopédique de Roret, Paris. 486 p.
Laporte, F. L. d. 1834 - 1835. Études entomologiques, ou description d'insectes nouveaux et observations sur leur synonymie. Par F. L. de Laporte Comte de Castelnau. Coléoptères. Première partie. Carnassiers. Méquignon-Marvis Père et Fils, Paris. 1 - 94, 1834; 1895 - 1159, 1835 pp.
Laporte, F. L. d. 1840. Histoire naturelle des insectes Coléoptères; avec une introduction renfermant l'anatomie et la physiologie des animaux articulés, par M. Brullé. Tome premier. Histoire naturelle des animaux articulés, annelides, crustacés, arachnides, myriapodes et insectes Tome troisième. [p. cxxv + 324pp. + 319pls.]. P. Duménil, Paris. cxxv + 324pp. + 319pls. p.
Macleay, W. S. 1825. Annulosa javanica, or an attempt to illustrate the natural affinities and analogies of the insects collected in Java by Thomas Horsfield and deposited by him in the Museum of the Honourable East-India Company. Kingsbury, Parbury and Allen, London. xii + 150pp. p.
Mazzoldi, P. 1995. Gyrinidae: Catalogue of Chinese Gyrinidae (Coleoptera), pp. 155-172. In M. A. Jäch and L. Ji, eds. Waterbeetles of China. Zoologisch-Botanische Gesellschaft, Vienna.

Miller, K. B. 2001. Descriptions of new species of *Desmopachria* Babington (Coleoptera: Dytiscidae: Hydroporinae: Hyphydrini) with a reassessment of the subgenera and species groups and a synopsis of the species. The Coleopterists Bulletin 55(2):219 – 240.

Miller, K. B., and J. Bergsten. 2012. Phylogeny and classficiation of whirligig beetles (Coleoptera: Gyrinidae): relaxed-clock model outperforms parsimony and time-free Bayesian analyses. Systematic Entomology 37:705 – 746.

Ochs, G. 1926. Die Dineutini. 2. Tribus der Unterfamilien Enhydrinae Fam. Gyrinidae (Col). A. Aligemeiner Teil. Entomologische Zeitschrift 40:(3/4): 61 – 74; (65): 112 – 126; (116): 129 – 140; (118): 190 – 197.

Ochs, G. 1927a. Fauna sumatrensis. (Beitrag Nr. 43). Gyrinidae (Col.). Supplementa Entomologica/ Deutsches Entomologisches Museum 15:114 – 122.

Ochs, G. 1927b. XII. Papers on Malayan aquatic biology. iv. On the Gyrinidae of the Malay Peninsula. Journal of the Federated Malay States Museums 13(4):242 – 245.

Ochs, G. 1928. Über die Gyriniden Borneo's. Entomologische Blatter 24(1-2):41-45, 78-85, 93-103.

Ochs, G. 1929a. On the Gyrinidae of the Nerbudda River. Records of the Indian Museum 31(3):241 – 249.

Ochs, G. 1929b. The present status of knowledge about Chinese Gyrinidae. Lingnan Science Journal 7(715 – 720).

Ochs, G. 1929c. Über einige neue und bemerkenswerte Gyriniden vorzüglich aus dem Dresdener Museum. Entomologische Blatter 25(4):197 – 200.

Ochs, G. 1930. Gyrinoidea. Catalogue of Indian Insects 19:1 – 39.

Ochs, G. 1931. Über die Gyriniden-Ausbeute der Deutschen Limnologischen Sunda-Expedition mit einer Übersicht über die Gyriniden-Fauna Javas und Larvenbeschreibungen. Archiv für Hydrobiologie 8:461 – 485.

Ochs, G. 1937. Nachtrag zur Gyriniden-Fauna Javas und der benachbarten Sunda-Inseln nebst Beschreibung einiger Verwandten des *Orectochilus spiniger* Rég. aus Hinter-Indien und Ceylon. Archiv für Hydrobiologie 15:109 – 118.

Ochs, G. 1940a. Entomological results from the Swedish Expedition 1934 to Burma and British India. Coleoptera: Gyrinidae, gesammelt von René Malaise. Arkiv för Zoologi 32A(14):1 – 22.

Ochs, G. 1940b. Erganzende Mitteilungen zür Kenntnis der Gyriniden-Fauna der grossen Sunda-Inseln. Arbeiten über morphologische und taxonomische Entomologie aus Berlin-Dahlem 7(1):33 – 50.

Ochs, G. 1942. Über die von Herrn J. Klapperich in China 1937-38 gesammelten Gyriniden. (Col.). Mitteilungen der Münchner Entomologischen Gesellschaft 32(1):201 – 207.

Ochs, G. 1953. Die Sunda-Gyriniden des Museum Zoologicum Bogoriense (Col., Gyrinidae). Treubia 22(1):217 – 223.

Ochs, G. 1955. Die Gyriniden-fauna von Neuguinea nach dem derzeitigen stand userer kenntnisse (Coleoptera, Gyrinidae). Nova Guinea 6(1):87 – 154.

Oygur, S., and G. W. Wolfe. 1991. Classification, distribution, and phylogeny of North American north of Mexico species of *Gyrinus* Müller (Coleoptera: Gyrinidae). Bulletin of the American Museum of Natural History 207:1-97.

Peschet, R. 1923. Fauna Entomologique de l'Indochine, Gyrinidae. Opuscules de l'Institut Scientifique de l'Indochine, Saigon 1:1-18.

Polhemus, D. 2011. New distributional records for Gyrinidae (Insecta: Coleoptera) on New Guinea and nearby islands, with a checklist of the New Guinea species. Zootaxa 2900:51-68.
Régimbart, M. 1877. Monographie du genre *Enhydrus* Casteln. (groupe des *Epinectes* Eschsch.) et du genre *Porrhorhynchus* Castelnau. Annales de la Société entomologique de France 46:105 – 114.
Régimbart, M. 1882. Essai monographique de la famille des Gyrinidae. 1e partie. Annales de la Société entomologique de France (6) (2):379 – 458 + 373 pls.
Régimbart, M. 1884. Essai monographique de la famille des Gyrinidae. 3e partie. Annales de la Société entomologique de France 6(3):381– 482 + 384pl.
Régimbart, M. 1886. Essai monographique de la famille des Gyrinidae (1er supplément). Annales de la Société entomologique de France 6(6):247–272.
Régimbart, M. 1892a. Essai monographique de la famille des Gyrinidae. 2e Supplément. Annales de la Société entomologique de France 60:663 – 752.
Régimbart, M. 1892b. Viaggio di Lamberto Loria, Nelia Papuasia Orientale. IV. Haliplidae, Dytiscidae, et Gyrinidae. Annali del Museo Civico di Storia Naturale di Genova 2(10):978 – 997.
Régimbart, M. 1902. Fascicules I: Coleoptera. Family Gyrinidae. Verteneuil & Desmet, Bruxelles. 13 p.
Régimbart, M. 1907. Essai monographique de la famille des Gyrinidae. 3e supplément. Annales de la Société entomologique de France 76:137 – 245.
Vazirani, T. G. 1969. Two new species and notes on other species of aquatic Coleoptera from Ceylon. Spolia Zeylanica 31(2):399-403.
Walker, F. 1858. Charaters of some apparently undescribed Ceylon Insects. Annals and Magazine of Natural History 2:202-209.
White. 1847. Nomenclature of Coleopterous Insects in the collection of the British Museum. Part II. Hydrocanthari. [p. 59 pp.]. Edward Newman, London. 59 pp. p.
Wiley, E. O. 1978. The Evolutionary Species Concept Reconsidered. Systematic Zoology 27(1):17-26.
Wilson, C. B. 1923. Water beetles in relation to pondfish culture, with life histories of thsoe found in fishponds of Fairport, Iowa. Bulletin of the Bureau of Fisheries 39:231—345.
Wood, J. G. 1874. Insects abroad. Being a popular account of foreign insects, their structure, habits, and transformations. [p. 780 pp.]. Longmans, Green, and Co., London. 780 pp. p.
Wu, C. F. 1931. Catalogue of Chinese Gyrinidae. Peking Natural History Bulletin 6(3):63—73.
Zimmermann, A. 1917. Der derzeitige Bestand der Gyrinidensammlung des Deutschen Entomologischen Museums in Berlin-Dahlem und die wissenschaftlichen Ergebnisse ihrer Durcharbeitung (Col.). Entomologische Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museum Hamburg 6:135 – 170.

Fig. 1. Dorsal habitus of *Porrorhynchus* species. A) *P.* (*P.*) *marginatus*, B) *P.* (*P.*) *landaisi*, C) *P.* (*P.*) *indicans*, D) *P.* (*R.*) *depressus*, E) *P.* (*R.*) *misoolensis*. Scale bar = 5 mm.

Fig. 2. Right antenna of species of *Porrorhynchus*. For each, above anterior view, below posterior view, scale bars 0.5 mm. A) *P.* (*P.*) *landaisi,* B) *P.*(*P.*) *indicans*, C) *P.* (*P.*) *marginatus*, D) *P.* (*R.*) *depressus*.

Fig. 3. Scanning electron microscope image of male *P.* (*P.*) *marginatus*. A) Protrochanter, marked area shows protrochanteric setose patch, scale bar = 400 µm, B) Protrochanteric setose patch, scale bar = 50 µm.

Fig. 4. Scanning electron microscope image of male *P.* (*P.*) *marginatus* profemur. Scale bar = 1mm.

Fig. 5. Aedeagus of *P.* (*P.*) *indicans*. A) Dorsal view, B) Lateral view, C) Ventral view. Scale bar = 1mm.

Fig. 6. Morphology of *P.* (*P.*) *landaisi* [A – K] and *P.* (*P.*) *indicans* [L – O]. A – D specimen from Hainan island. A) Protarsus, scale bar = 1 mm, B) Metacoxal apex, scale bar = 0.5 mm, C) Maxillary palps above, labial palps below, scale bar = 0.5 mm, D) Mesotarsal claws, scale bar = 0.5 mm. E – H specimen from Vietnam. E) Protarsus, scale bar = 1 mm, F) Metacoxal apex, scale bar = 0.5 mm, G) Maxillary palps above, labial palps below, scale bar = 0.5 mm, H) Mesotarsal claws, scale bar = 0.5 mm. I – K specimen from Tibet, China. I) Protarsus, scale bar = 1 mm, J) Metacoxal apex, scale bar = 0.5 mm, K) Mesotarsal claws, scale bar = 0.5 mm. L – O *P.* (*P.*) *indicans*. L) Protarsus, scale bar = 1 mm, M) Metacoxal apex, scale bar = 0.5 mm, N) Maxillary palps above, labial palps below, scale bar = 0.5 mm, O) Mesotarsal claws, scale bar = 0.5 mm.

Fig. 7. Aedeagus [A – C, E – G, I – K] and dorsal habitus [D, H, L] of *P.* (*P.*) *landaisi.* A – D specimen from Hainan Island. A) Dorsal view, scale bar = 1 mm, B) Ventral view, C) Lateral view, D) Dorsal habitus, scale bar = 5 mm. E – H specimen from Vietnam. E) Dorsal view, scale bar = 1 m, F) Ventral view, G) Lateral view, H) Dorsal habitus, scale bar = 5 mm. I – L specimen from Tibet, China. I) Dorsal view, J) Ventral view, K) Lateral view, L) Dorsal habitus, scale bar = 5 mm.

Fig. 8. Morphology of *P.* (*P.*) *marginatus*. A – E specimen from Chumphon, Thailand. A) Protarsus, scale bar = 1 mm, B) Metacoxal apex, scale bar = 0.5 mm, C) Mesocoxal apex, scale bar 0.5 mm, D) Maxillary palp above, labial palp below, scale bar = 0.5 mm, E) Mesotarsal claws, scale bar = 0.5 mm. F – J specimen from Khammouane, Laos. F) Protarsus, scale bar = 1 mm, G) Metacoxal apex, scale bar = 0.5 mm, H) Mesocoxal apex, scale bar 0.5 mm, I) Maxillary palp above, labial palp below, scale bar = 0.5 mm, J) Mesotarsal claws, scale bar = 0.5 mm. K –

O specimen from Dac Lac, Vietnam. K) Protarsus, scale bar = 1 mm, L) Metacoxal apex, scale bar = 0.5 mm, M) Mesocoxal apex, scale bar 0.5 mm, N) Maxillary palp above, labial palp below, scale bar = 0.5 mm, O) Mesotarsal claws, scale bar = 0.5 mm. P – T specimen from East Kalimantan, Malaysia. P) Protarsus, scale bar = 1 mm, Q) Metacoxal apex, scale bar = 0.5 mm, R) Mesocoxal apex, scale bar 0.5 mm, S) Maxillary palp above, labial palp below, scale bar = 0.5 mm, T) Mesotarsal claws, scale bar = 0.5 mm. U – X specimen from Manna, Sumatra. U) Protarsus, scale bar = 1 mm, V) Metacoxal apex, scale bar = 0.5 mm, W) Mesocoxal apex, scale bar 0.5 mm, X) Maxillary palp above, labial palp below, scale bar = 0.5 mm. Y – C2 specimen from Java. Y) Protarsus, scale bar = 1 mm, Z) Metacoxal apex, scale bar = 0.5 mm, A2) Mesocoxal apex, scale bar 0.5 mm, B2) Maxillary palp above, labial palp below, scale bar = 0.5 mm, C2) Mesotarsal claws, scale bar = 0.5 mm.

Fig. 9. Dorsal habitus of *P.* (*P.*) *marginatus*, populational variation. Scale bar = 5 mm. A) Mandalay Dist., Myanmar, B) Loei Prov., Thailand, C) Khammouane Prov., Laos, D) Đắk Lắk Prov., Vietnam, E) Saraburi Prov., Thailand, F) Chumphon Prov., Thailand, G) Songkhla Prov., Thailand, H) Pahang, Malaysia, I) Gunung Leuser, Sumatra, J) West Sumatra, Sumatra, K) Siberut Island, Sumatra, L) Manna, Sumatra, M) Java, N) Kapit Distr., Sarawak, Malaysia, O) East Kalimantan, Indonesia.

Fig. 10. Aedeagus of *P.* (*P.*) *marginatus*, lateral and dorsal view, populational variation. Scale bar = 1 mm. A) Mandalay Dist., Myanmar, B) Loei Prov., Thailand, C) Khammouane Prov., Laos, D) Đắk Lắk Prov., Vietnam, E) Saraburi Prov., Thailand, F) Chumphon Prov., Thailand, G) Songkhla Prov., Thailand, H) Pahang, Malaysia, I) Gunung Leuser, Sumatra, J) Siberut Island, Sumatra, K) Manna, Sumatra, L) Java, M) Kapit Distr., Sarawak, Malaysia, N) East Kalimantan, Indonesia.

Fig. 11. Morphology of *P.* (*R.*) *depressus* [A – L] and *P.* (*R.*) *misoolensis* [M – P], all scale = 0.5 mm. A – D specimen from Gulf Prov. Papua New Guinea. A) Protarsus, scale B) Metacoxal apex, C) Maxillary palp above, labial palp below, D) Mesotarsal claw. E – H specimen from the Lorentz River, southwestern Irian Jaya. E) Protarsus, F) Metacoxal apex, G) Maxillary palp above, labial palp below, H) Mesotarsal claw. I – L specimen from Nabire, western Irian Jaya. I) Protarsus, J) Metacoxal apex, K) Mesotarsal claws. L – O *P.* (*R.*) *misoolensis*. L) Protarsus, M) Metacoxal apex, N) Maxillary palp above, labial palp below, O) Mesotarsal claws.

Fig. 12. Aedeagus [A – C, E – G, I – K, M – O] and dorsal habitus [D, H, L, P] of *P.* (*R.*) *depressus* [A – L] and *P.* (*R.*) *misoolensis* [M – P]. A – D specimen from Omo River, Gulf Prov., Papua New Guinea. A) Dorsal view, scale bar = 1 mm, B) Ventral view, C) Lateral view, D) Dorsal habitus, scale bar = 5 mm. E – H specimen from Lorentz River, southwestern Irian Jaya. E) Dorsal view, scale bar = 1 m, F) Ventral view, G) Lateral view, H) Dorsal habitus, scale bar = 5 mm. I – L specimen from Nabire, western Irian Jaya. I) Dorsal view, scale bar = 1mm, J) Ventral view, K) Lateral view, L) Dorsal habitus, scale bar = 5 mm. M – P *P.* (*R.*) *misoolensis.* M) Dorsal view, scale bar = 1mm, N) Ventral view, O) Lateral view, P) Dorsal habitus, scale bar = 5 mm.

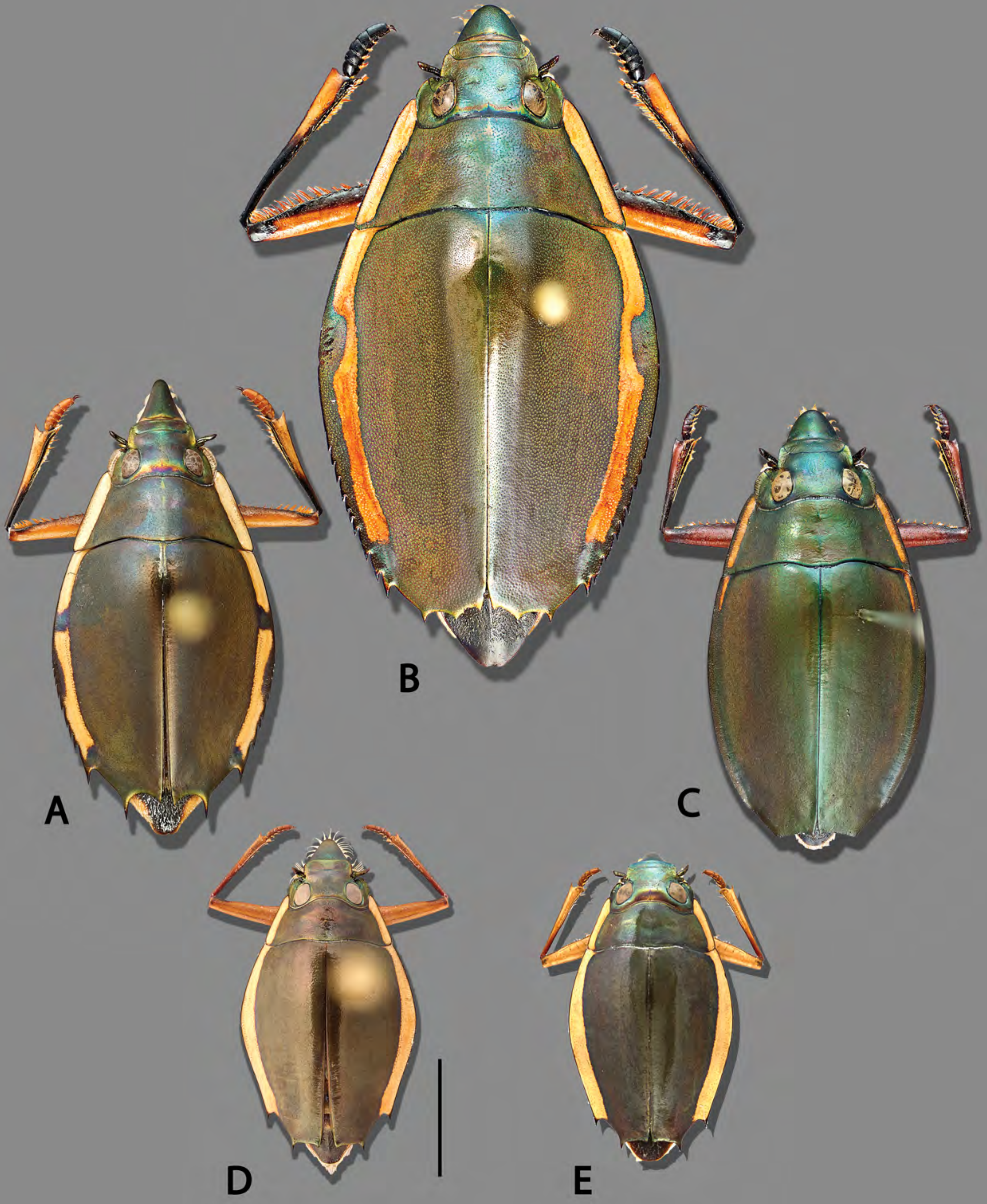
Fig. 13. Female reproductive tracts of *Porrorhynchus* species, scale bars = 1 mm. More heavily sclerotized areas indicated in gray. A) *P.* (*P.*) *landaisi,* B) *P.* (*P.*) *indicans*, C) *P.* (*P.*) *marginatus*, D) *P.* (*R.*) *depressus*, D*) P.* (*R.*) *misoolensis*.

Fig. 14. Map showing distribution of *Porrorhynchus sensu stricto* species. Triangles = *P.* (*P.*) *landaisi*, Circles = *P.* (*P.*) *marginatus*, Square = *P.* (*P.*) *indicans*.

Fig. 15. Map showing distribution of species in the subgenus *Rhomborhynchus*. Triangles = *P.* (*R.*) *depressus*, Circle = *P.* (*R.*) *misoolensis*.

Fig. 16. Type specimens. A) *Porrorhynchus brevirostris* Régimbart, 1877, lectotype, B) *Dineutes indicans* Walker, 1858, holotype C) *Porrorhynchus landaisi* Régimbart, 1892, lectotype, D) *Dineutus* (*Porrorhynchus*) *landaisi latilimbus* Ochs, 1926, lectotype E) *Porrorhynchus barthelemyi* Régimbart, 1907, lectotype.

Fig. 17. Type specimens. A) *Porrorhynchus marginatus* Laporte, 1835, holotype B) *Porrorhynchus depressus* Régimbart, 1892, holotype C) *Dineutus* (*Rhomborhynchus*) *depressus jamurensis* Ochs, 1955, paratype, D) *Porrorhynchus tenuirostris* Régimbart, 1877, lectotype E) *Dineutus* (*Rhomborhynchus*) *depressus moszkowskii* Ochs, 1955, holotype, F) *Dineutus* (*Rhomborhynchus*) *depressus versteegi* Ochs, 1955, holotype, G) *Dineutus* (*Porrorhynchus*) *marginatus mjoebergi* Ochs, 1926, lectotype, H) *Dineutus* (*Rhomborhynchus*) *depressus misoolensis* Ochs, 1955, paratype.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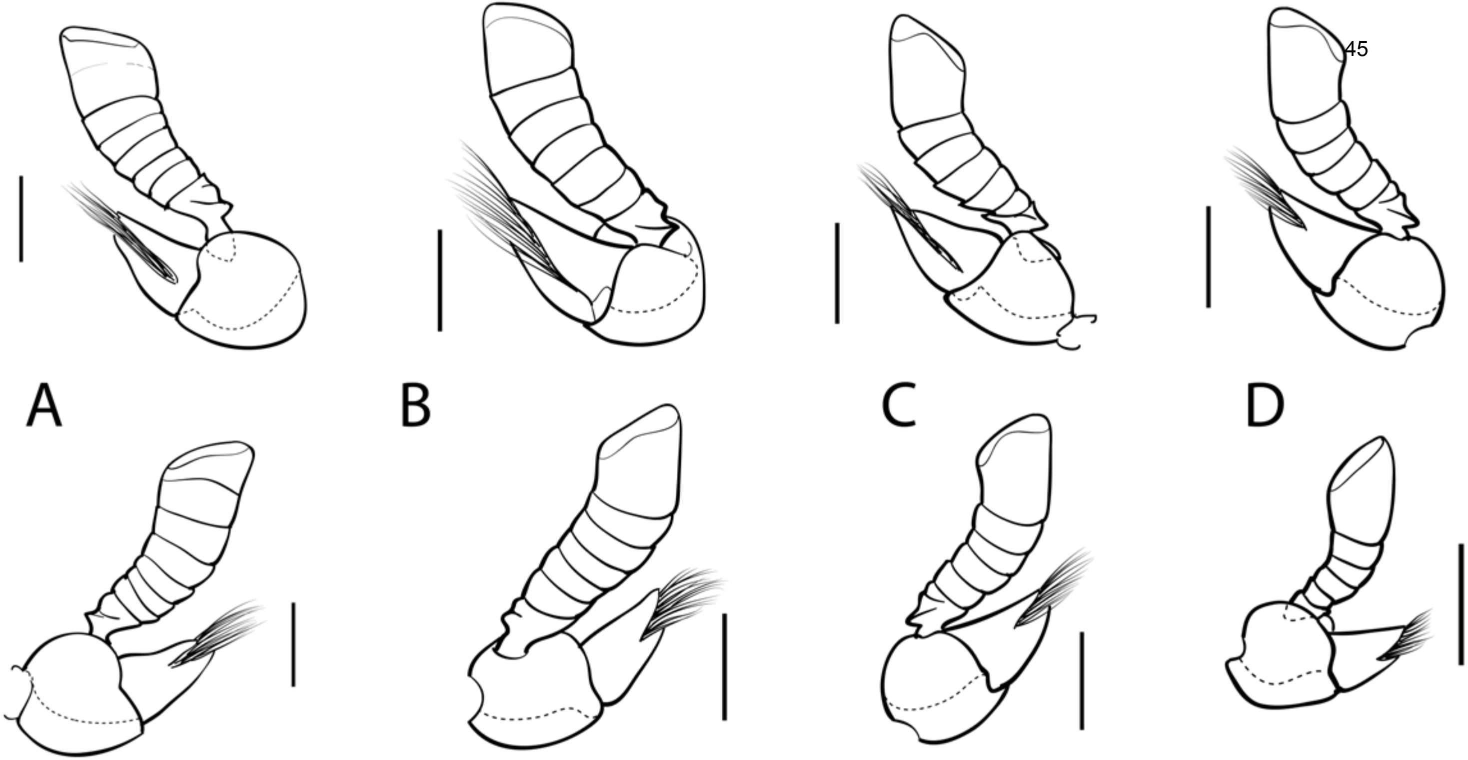
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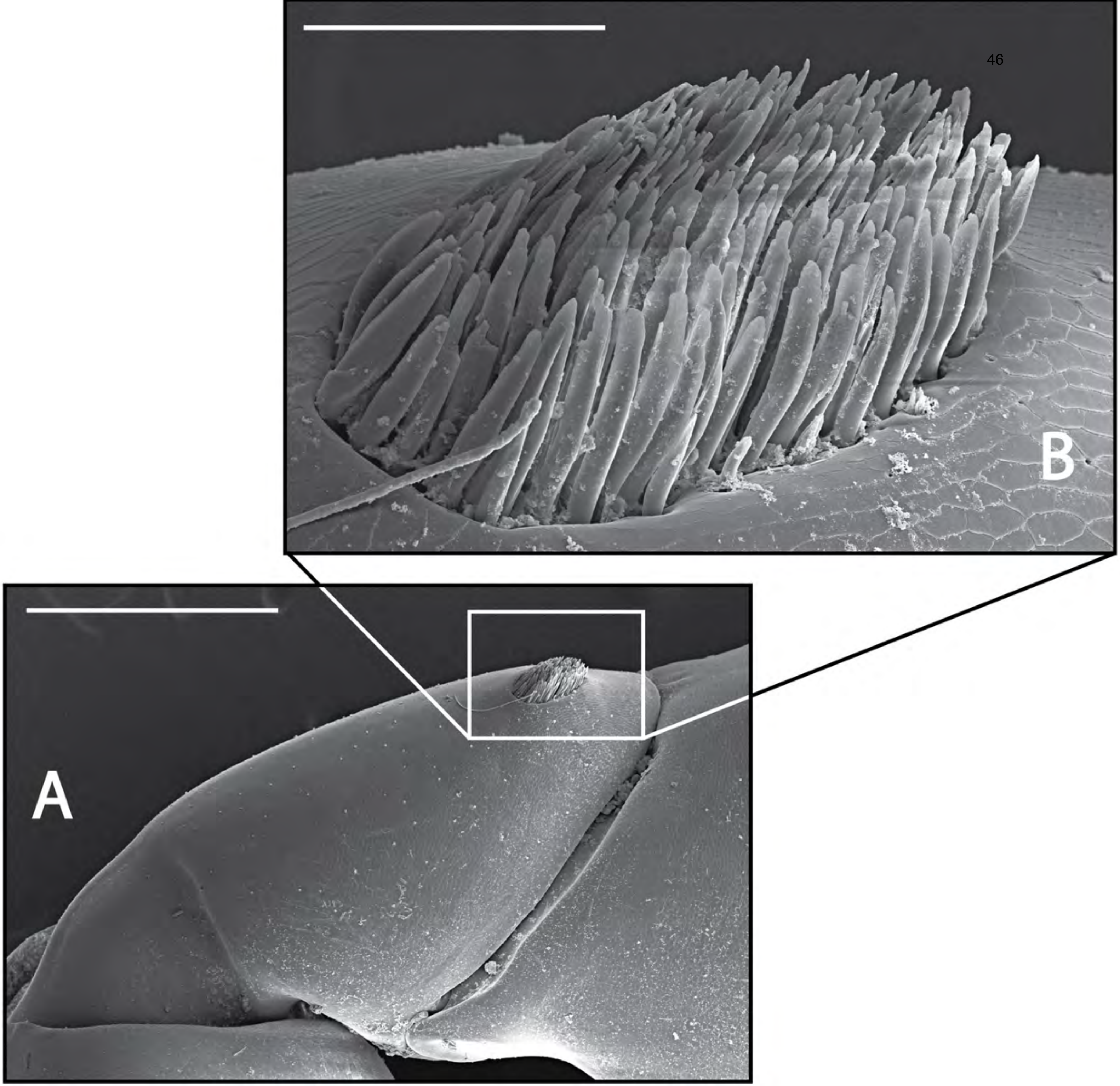
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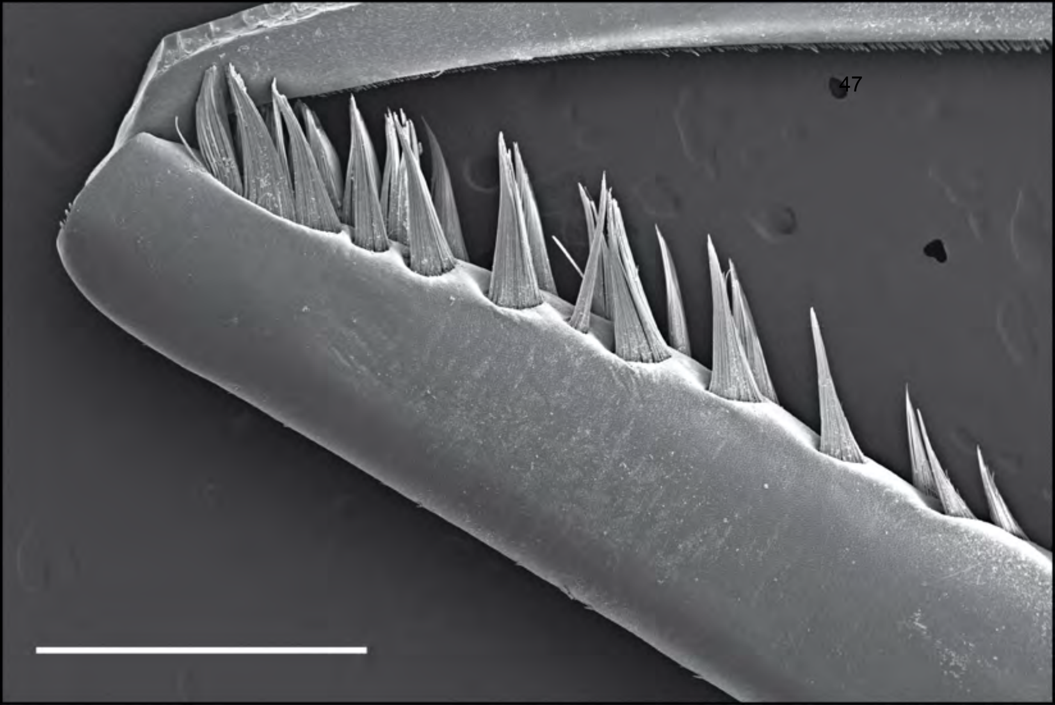
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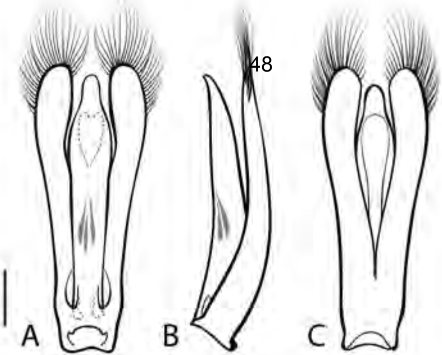

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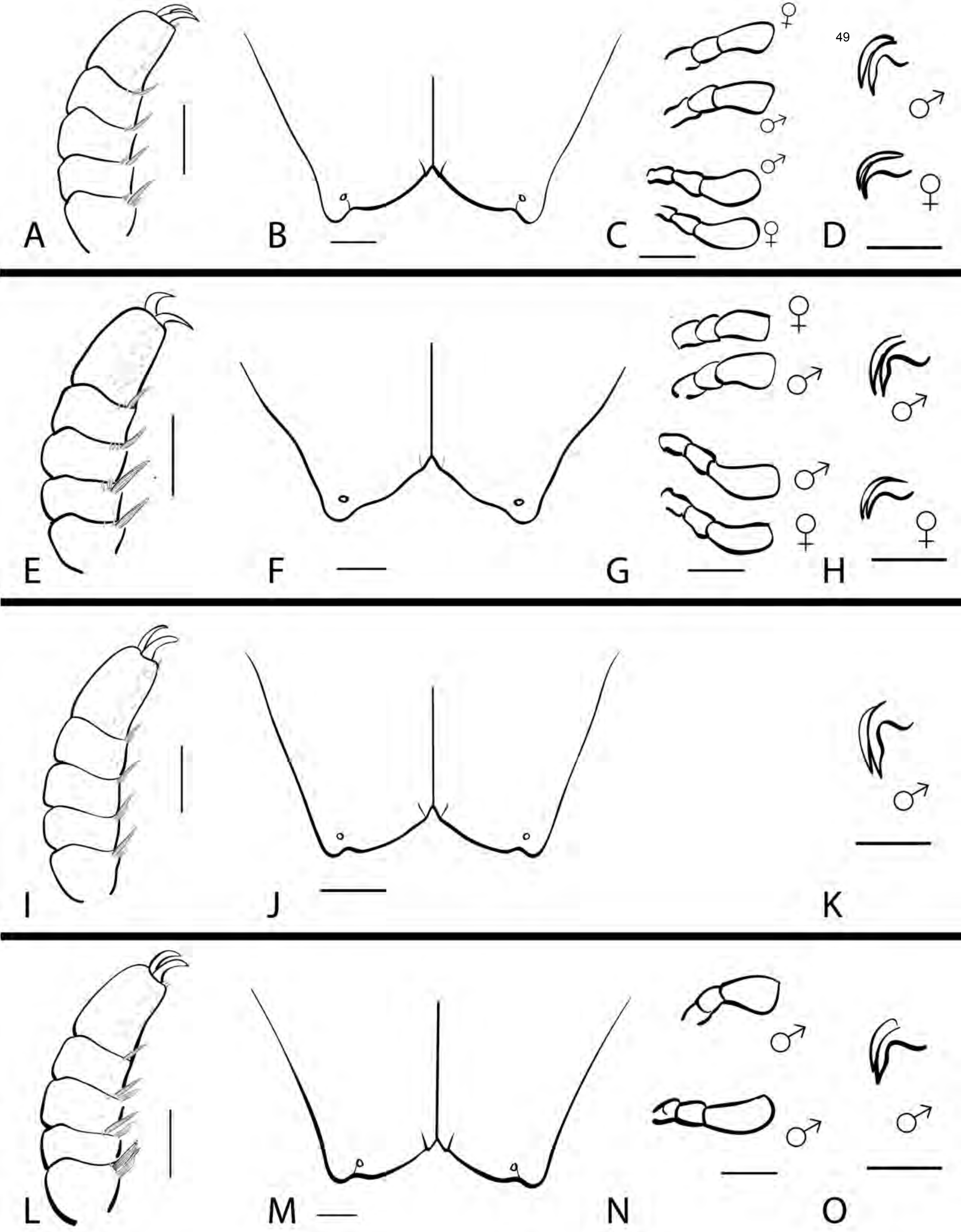
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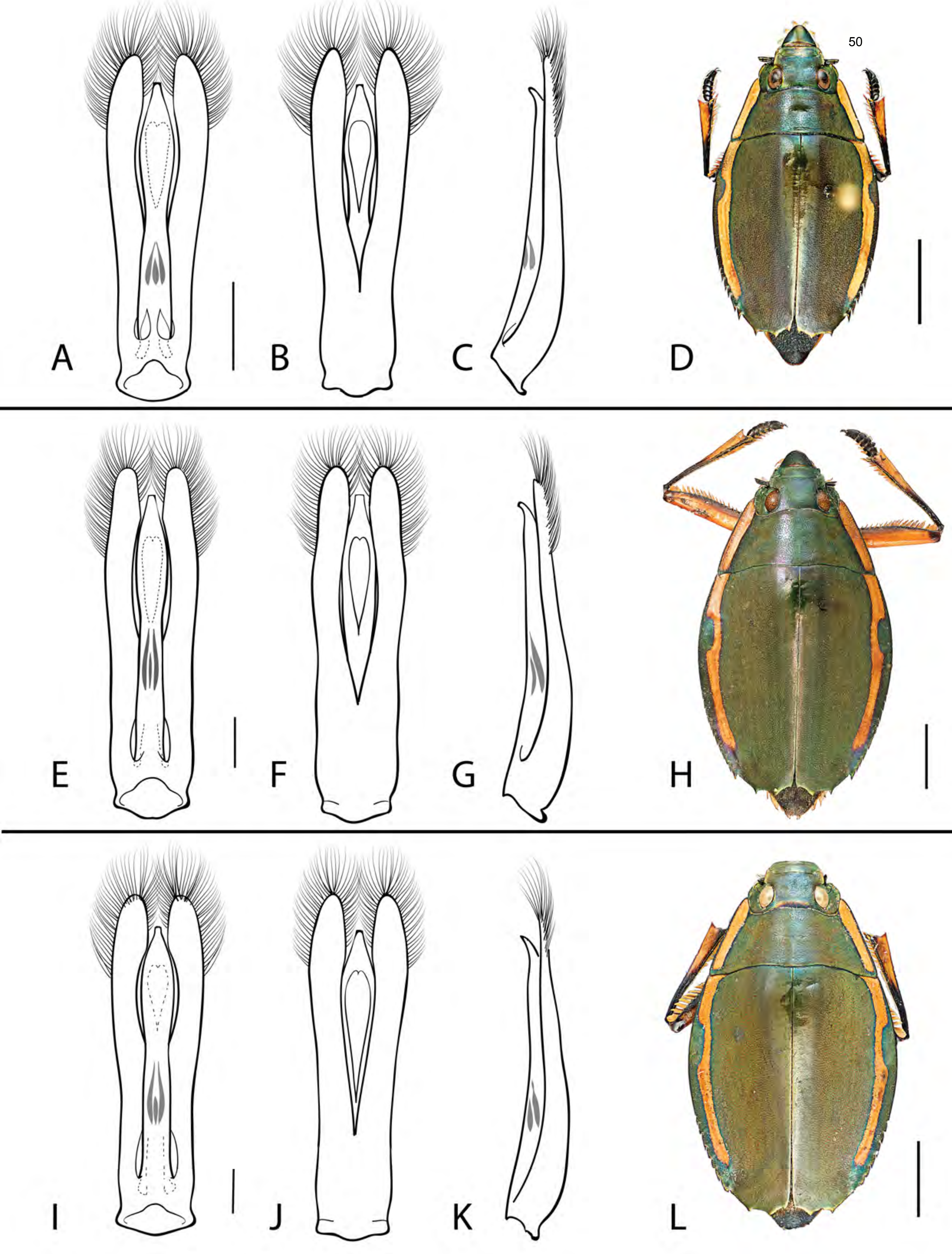
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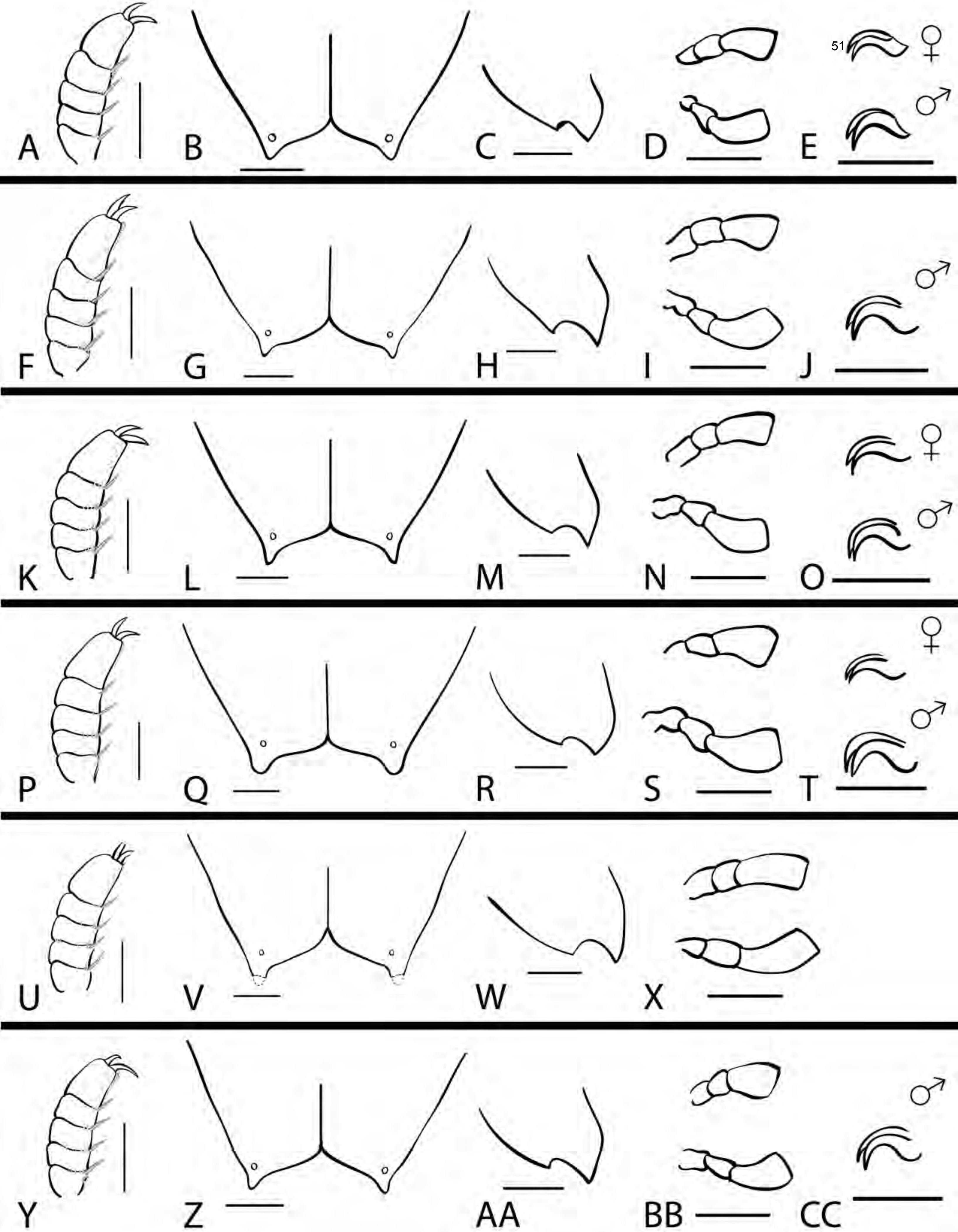
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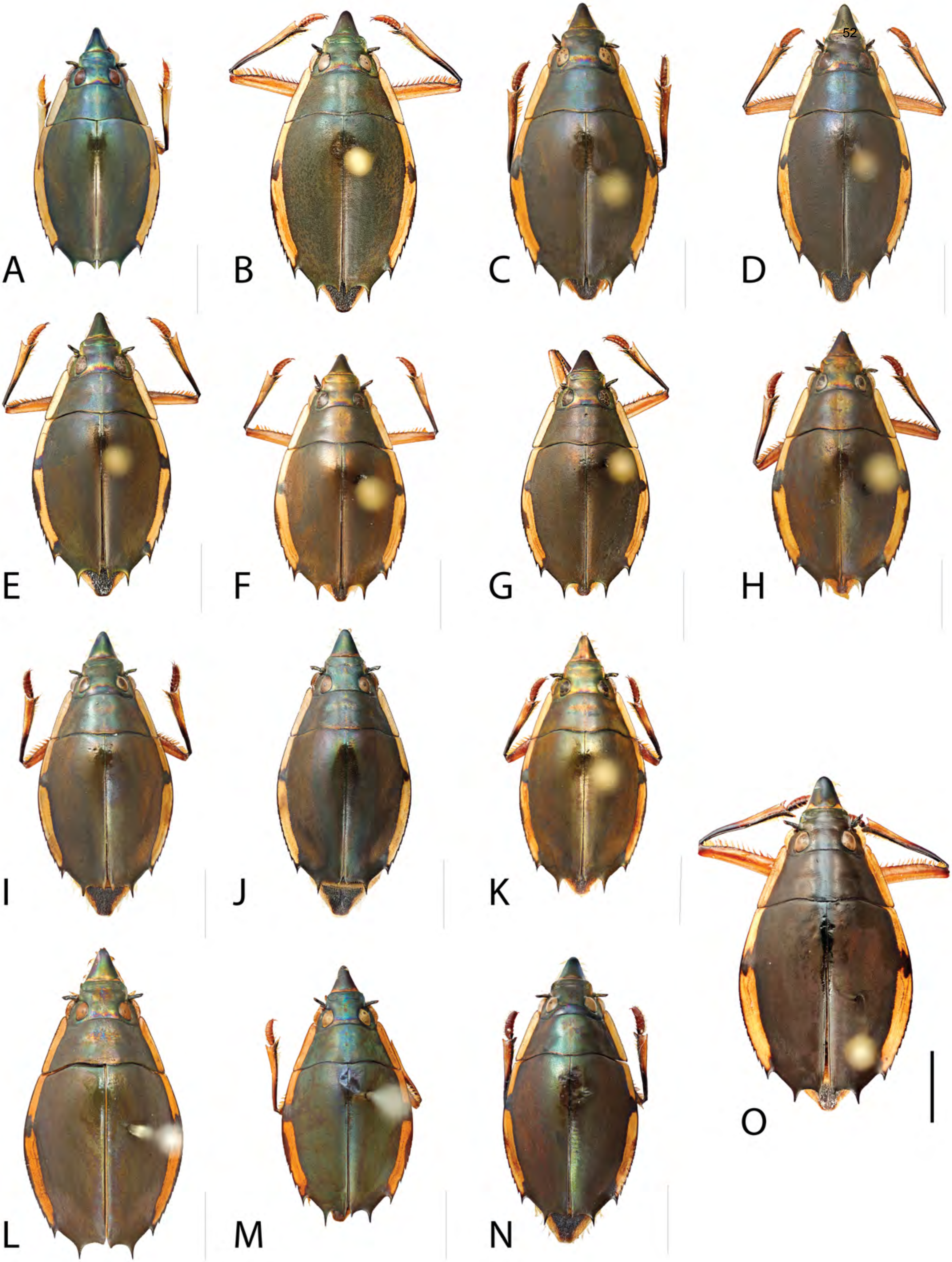
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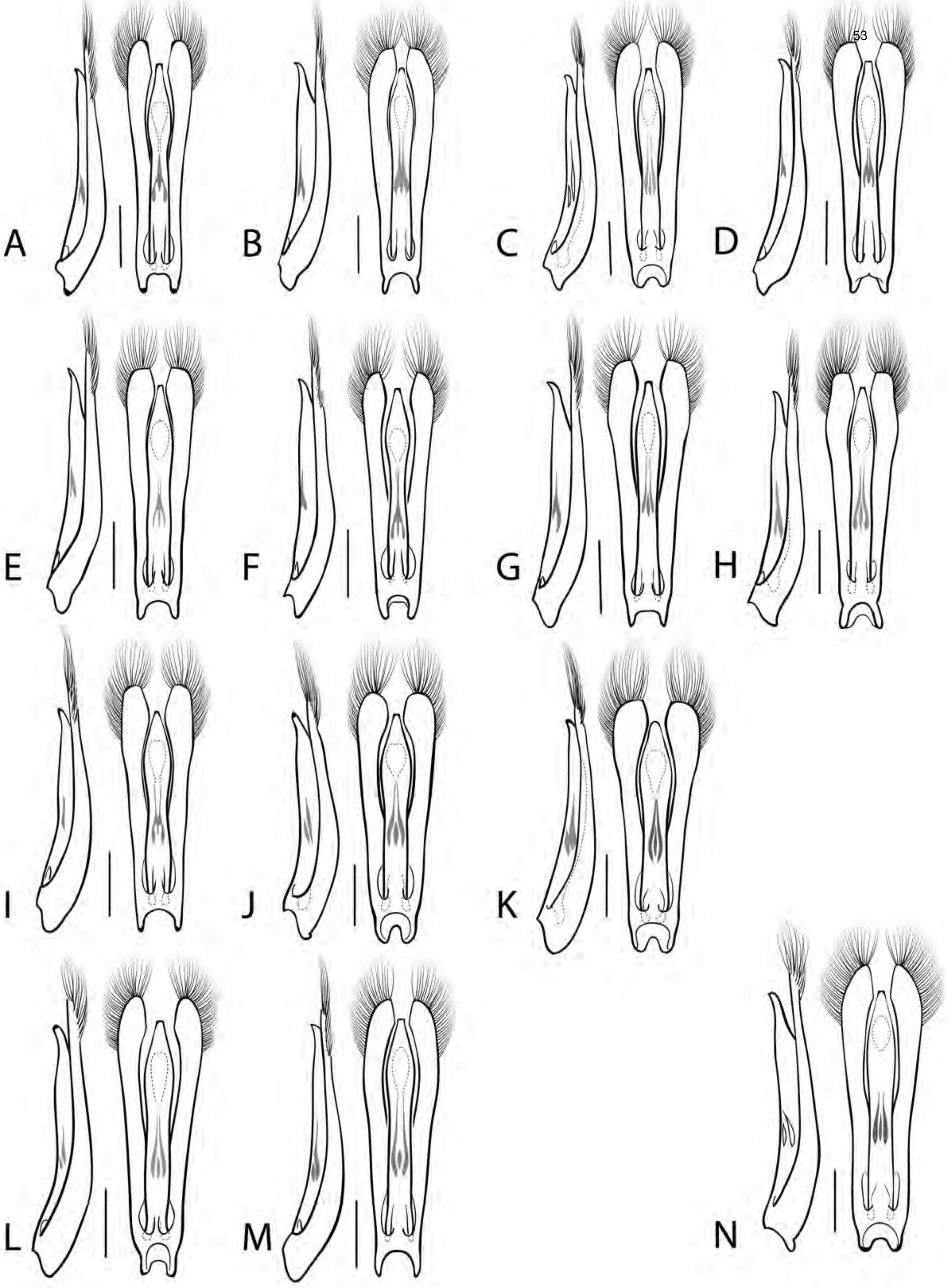
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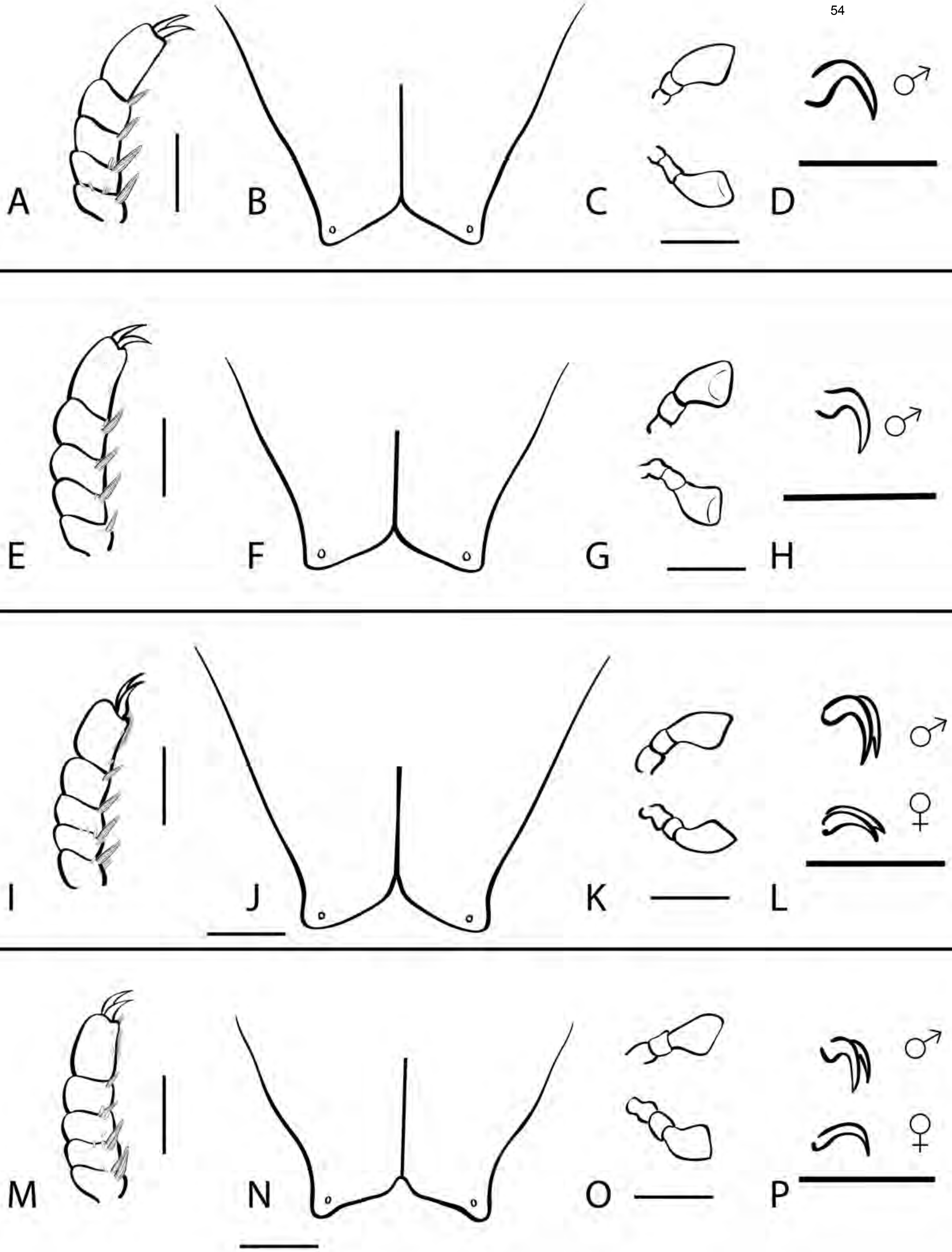
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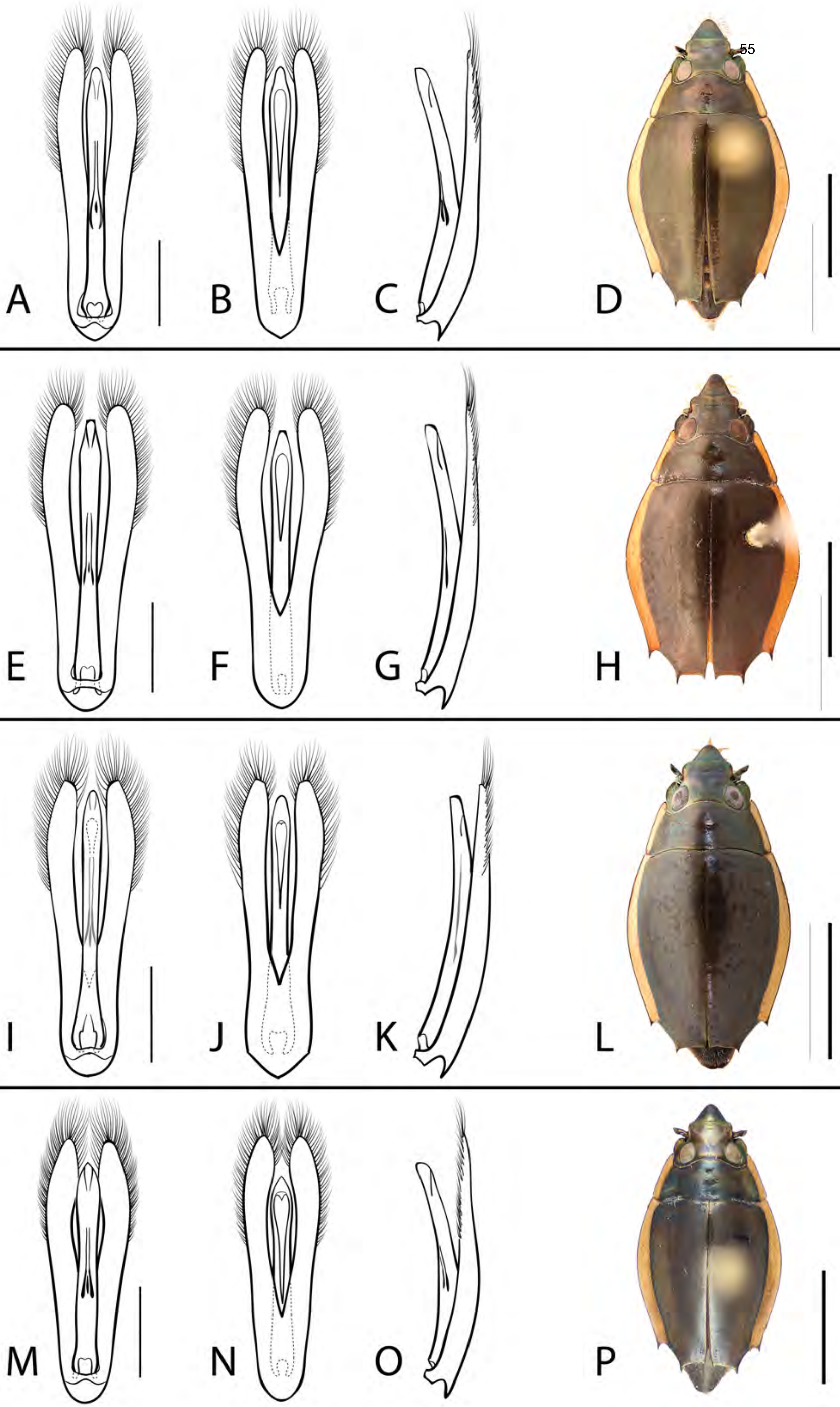
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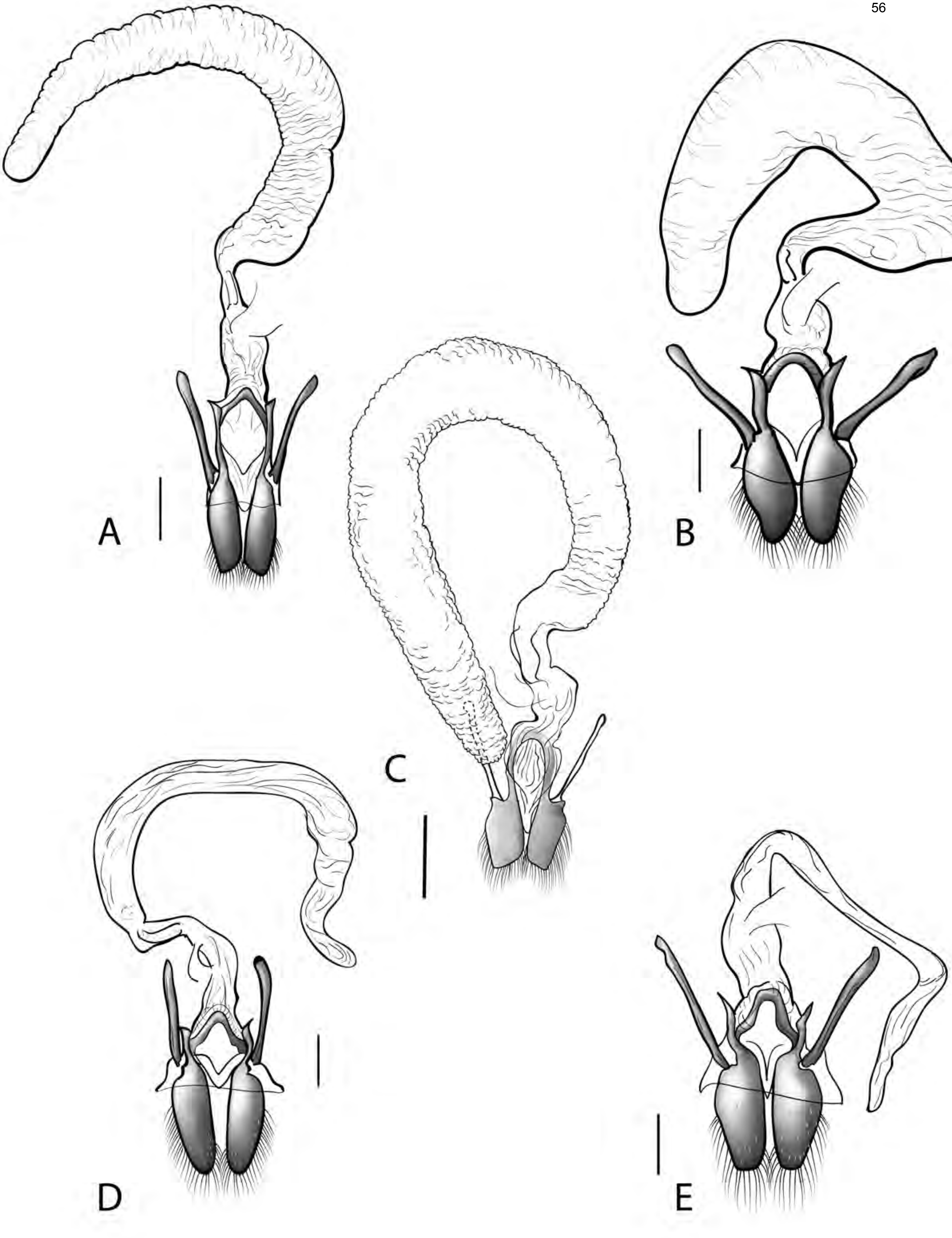
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Ceylan

MUSEUM PARIS
COLL MAURICE RÉGIMBART
1908

LECTOTYPE

Environ de
Cao-Bang,
Tonkin Lamdaï

MUSEUM PARIS
COLL MAURICE REGIMBART
1908

LECTOTYPE

♂

China
Insel Hainan
70.-25.III.09
H.Schoede S.G.

Coll.
G.Ochs

Para-
typoid

latolimbus Ochs

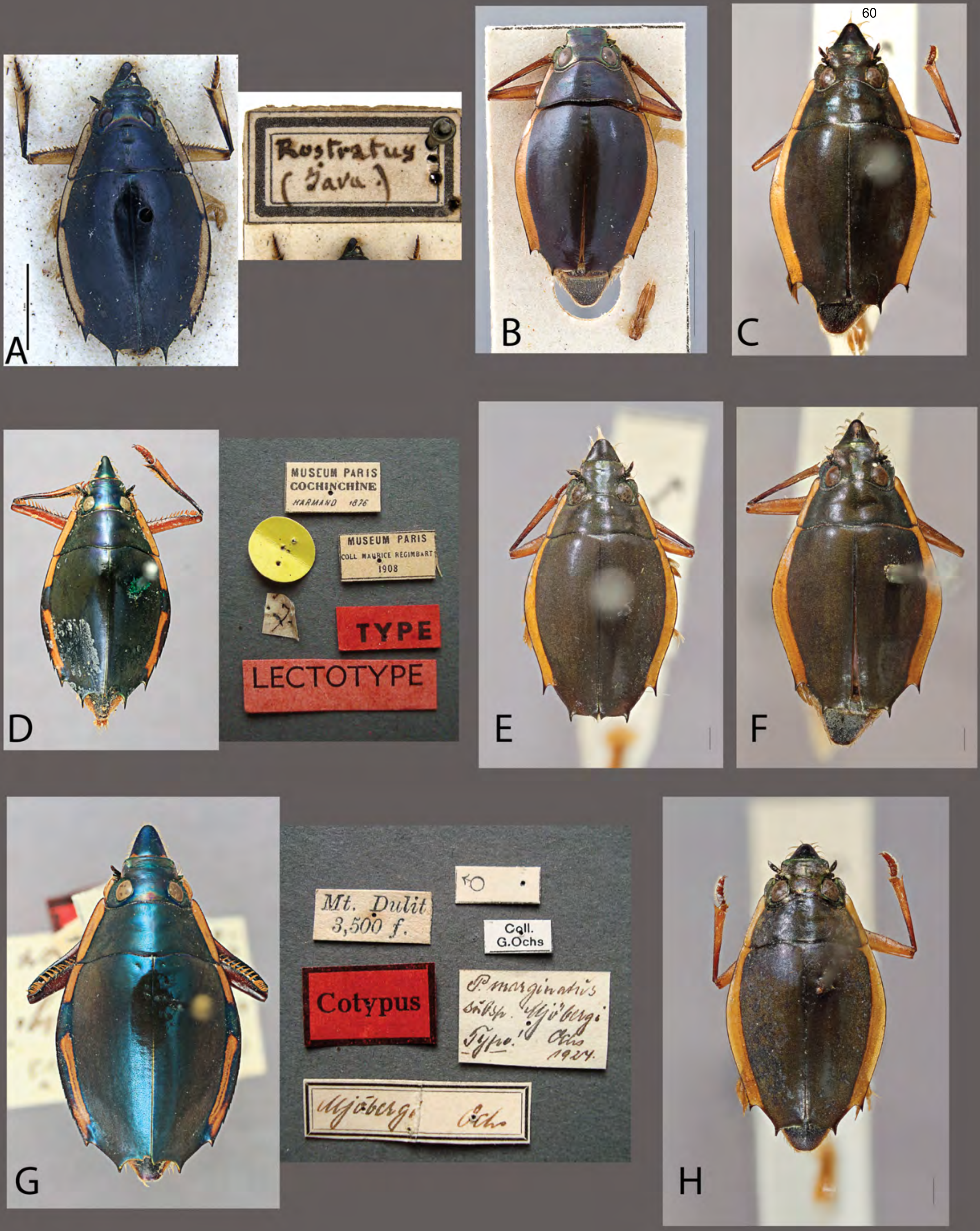
MUSEUM PARIS
ANNAM
~~RÉGION DE QUANG NAM~~
~~AU NHA TRANG~~
Cte DE BARTHÉLEMY 1899

Dans les Aroyos
des Moïs
à 1700 m. d'altitude

MUSEUM PARIS
Annam
Cte Barthélemy
1899

MUSEUM PARIS
COLL MAURICE REGIMBART
1908

LECTOTYPE


A
Rostratus
(Java)
B
C
D
MUSEUM PARIS
COCHINCHINE
HARMAND 1876
MUSEUM PARIS
COLL MAURICE REGIMBART
1908
TYPE
LECTOTYPE
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Mt. Dulit
3,500 f.
♂
Coll.
G.Ochs
Cotypus
P. marginatus
subsp. Mjöbergi
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Systematics and evolution of the whirligig beetle tribe Dineutini (Coleoptera, Gyrininae, Gyrinidae)

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Abstract. The phylogeny and evolutionary history of the whirligig beetle tribe Dineutini are inferred from analysis of 56 morphological characters and DNA sequence data from the mitochondrial genes COI, COII, and 12S, and the nuclear genes H3 and *arginine kinase*. Bayesian and maximum likelihood analyses were performed. A Bayesian total-evidence approach was taken to provide a time calibrated phylogenetic tree incorporating fossil taxa. Seventy-one species of extant Gyrinidae were included in the analysis, as well as two fossil taxa, representing all dineutine genera and all proposed, non-monotypic subgenera. The resulting trees strongly support the monophyly of the Dineutini and the genera *Dineutus*, *Macrogyrus*, *Porrorhynchus*, and *Enhydrus*. The results do not support the distinction of *Andogyrus* as a separate genus, nor do they support the majority of proposed subgenera. A new classification is presented here requiring the following taxonomic changes: *Andogyrus* **stat. n.** is relegated to a subgenus of *Macrogyrus*; the following subgenera are synonymized with *Macrogyrus* sensu stricto **sensu n.**: *Australogyrus* Ochs, 1949 **syn. n.**, *Ballogyrus* Ochs, 1949 **syn. n.**, *Clarkogyrus* Ochs, 1949 **syn. n.**, *Megalogyrus* Ochs, 1949 **syn. n.**, *Orectomimus* Ochs, 1930 **syn. n.**, *Tribologyrus* Ochs, 1949 **syn n.**; the subgenus *Stephanogyrus* Ochs, 1955 **syn. n.** is synonymized with the subgenus *Cyclomimus*; the genus *Dineutus* now includes two subgenera *Cyclous* **sensu n.** and the *Dineutus* sensu stricto subgenus **sensu n.;** the following subgenera are synonymized with the subgenus *Cyclous*: *Callistodineutus* Ochs, 1926 **syn. n.**, *Cyclinus* Kirby, 1837 **syn. n.**, *Paracyclous* Ochs, 1926 **syn. n.**, *Protodineutus* Ochs, 1926 **syn. n.**, *Spinosodineutes* Hatch, 1925 **syn. n.**; the following subgenera are synonymized with the *Dineutus* sensu stricto subgenus: *Rhombodineutus* Ochs, 1926 **syn. n.**, *Merodineutus* Ochs, 1955 **syn n.** The subgenus *Rhomborhynchus* **incert. s.** is tentatively moved to the genus *Dineutus*, without phylogenetic placement. The analysis confirms *Mesodineutes*† is a member of the Dineutini. Each genus and subgenus reviewed in detail with (i) a morphological diagnosis, (ii) its taxonomic circumscription, including the placement of species not included in the analysis, (iii) known distribution, and (iv) relevant discussion. A new identification key to the extant genera and subgenera of the Dineutini is provided. Finally a biogeographic analysis reconstructing ancestral ranges was conducted revealing the historical biogeography of the tribe.

Introduction

The tribe Dineutini contains the most conspicuous members of the whirligig beetles, (Coleoptera, Gyrinidae), being large in size (commonly ≥ 10 mm in length) (Brinck, 1984; Gustafson & Miller, 2015) and with a near global distribution (Miller & Bergsten, 2012). Most species are lotic (Balfour-Browne & Brinck, 1961; Brinck, 1977, 1983, 1984; Gustafson & Miller, 2015), but a few are primarily lentic, or found in a variety of freshwater habitats (Brinck, 1955a; Gustafson & Miller, 2015). Despite their large size and conspicuous nature, new species are still being discovered, even in well explored regions such as the U.S.A. (Gustafson & Sites, 2016), and the vast majority of species lack formal descriptions of immature stages and life history. Furthermore, the tribe itself has never specifically been the focus of a phylogenetic analysis.

Régimbart (1882) was the first to formally diagnosis and describe the tribe Dineutini (see the Classification section for more details) who recognized within it four genera, *Macrogyrus* Régimbart, 1882, *Porrorhynchus* Laporte, 1835, *Enhydrus* Laporte, 1835, and *Dineutus* Macleay, 1825. The genus *Dineutus* was first to be split into subgenera by Hatch (1925), then extensively split into many subgenera, along with the genus *Macrogyrus*, by the work of Ochs (1926, 1949, 1955). Ochs (1924) would also erect a new genus within the tribe, *Andogyrus* Ochs, 1924. The problematic nature of these subgenera has long been recognized (Brinck, 1955b) as has the distinction of *Andogyrus* from *Macrogyrus* (Brinck, 1977). The monophyly of the tribe has also been called into question (Beutel, 1990). The first phylogenetic analysis of the family Gyrinidae using molecular and morphological data, provided support for the monophyly of the tribe (Miller & Bergsten, 2012), but sampling was not extensive enough to strongly test the monophyly of the genera *Enhydrus, Andogyrus* and *Porrorhynchus,* nor the numerous subgenera erected within *Dineutus* and *Macrogyrus*.

The interesting distribution of the tribe has resulted in hypotheses about the biogeography and origins of the group. Of particular interest are the genera *Macrogyrus, Andogyrus* and *Dineutus*. *Andogyrus* is distributed widely in South America along the Andes (Brinck, 1977) and appears closely related to *Macrogyrus* found in Australia, New Guinea, and Wallacea (Ochs, 1949). Gondwanan vicariance origins have been invoked to explain this distribution (Hatch, 1925; Ochs, 1949). Furthermore, classic gyrinid taxonomists have debated whether *Macrogyrus* is descended from a South American (Hatch, 1925) or Australian common ancestor (Ochs, 1949). *Dineutus* shows a very peculiar distribution, found in Southeast Asia, the Austral regions, throughout Africa, the North American continent, and eastern Palearctic in Korea (Lee & Ahn, 2015) and the Ryukyu Islands (Satô, 1962), but is absent from South America (Gustafson & Miller, 2015). There are two possible explanations for this distribution: 1) local extinction within the continent, 2) *Dineutus* has yet to disperse to South America.

The purpose of this study is to provide the first phylogenetic analysis of the tribe Dineutini to (i) assess the monophyly of the currently proposed genera and numerous subgenera, to improve and stabilize classification; (ii) construct a time calibrated phylogenetic tree to understand the relationships of dineutine species and the timing of their evolution; and (iii) reconstruct the historical biogeography of the group to test the proposed Gondwanan relationship of *Macrogyrus* and *Andogyrus*, and provide an explanation to the absence of *Dineutus* in South America.

Materials and Methods

Data

Taxon sampling

Seventy-three species of Gyrinidae were included in the main time calibrated analysis (Table S1). Ten outgroup species were selected: *Heterogyrus milloti* for Heterogyrinae, four species from the tribe Gyrinini, four from Orectochilini, and *Gyretes giganteus*† for a fossil outgroup member. Within the Dineutini an attempt was made to include at least two members from all currently recognized subgenera. This was mostly attained with the exception of the following monotypic subgenera not sampled for the analysis: *Dineutus* (*Paracyclous*) *ritsemai* (only known from the type series from Sulawesi); *Macrogyrus* (*Ballogyrus*) *leopoldi* (only known from the holotype specimen from New Guinea); *Macrogyrus* (*Stephanogyrus*) *caledonicus* (known from New Caledonia). The subgenus *Rhomborhynchus* (two species of contentious placement within *Porrorhynchus*) was represented by a single specimen only coded for morphological data, no molecular grade specimens were available for analysis. The fossil *Mesodineutes amurensis*† was utilized as the fossil ingroup member. Non-time calibrated analyses utilized a subset of taxa, excluding those available only for morphology and *Heterogyrus milloti* (Fig. S1, S2).

Ingroup taxa sampled were identifiable from the genera *Dineutus, Andogyrus, Enhydrus*, and *Porrorhynchus* to species and subspecies were applicable. The genus *Macrogyrus* has never received a comprehensive revision. The species from Australia are readily identifiable, thanks to the work of Watts & Hamon (2010); however, the species from New Guinea and the Lesser Sunda Islands are a major issue for identification. Numerous subspecies have been described by Ochs (1955) based on only a few specimens, with characters primarily relating to general body-form, providing no illustrations, and poorly constructed identification keys. Therefore many species sampled from New Guinea and the surrounding area cannot be identified reliably beyond the subgeneric level.

Morphology

Female genitalia were prepared following the methods outlined in Miller & Bergsten (2012). The genitalia were illustrated in water using a Camera Lucida attached to a Zeiss Discovery.V8 SteREO microscope. Illustrations were then scanned and traced using Adobe Illustrator CS5. Other morphology illustrated were drawn under the camera lucida, scanned, and traced using the same methods. Scanning electron microscope images were taken at the KU Microscopy and Analytical Imaging Laboratory, University of Kansas, Lawrence, KS, U.S.A.

Dorsal and ventral habitus were taken using a Visionary Digital BK+ light imaging system as well as a Passport imaging system (www.visionarydigital.com, R. Larimer). Habitus images were then edited using Adobe Photoshop CS5 to add scale bars and improve clarity and color.

Sperm has been found to be phylogenetically informative (Jamieson, 1987) and the sperm of *Dineutus* species was found to exhibit a very unique conjugation form (Breland & Simmons, 1970). For these reasons sperm was examined from several dineutine species and the conjugation type exhibited included as a morphological character in the analysis. Sperm specimens were harvested from the seminal vesicles of specimens in the field. A portion of seminal vesicle was removed from the specimen while in Phosphate Buffer Solution (PBS) then moved to a slide with an additional drop of PBS. The seminal vesicle was then agitated to free sperm. The slide was then allowed to dry and the original specimen was given a unique identifier (SVSK #) and kept as a voucher deposited in the Museum of Southwestern Biology, Division of Arthropods (MSBA), at the University of New Mexico. The slide was then DAPI stained and mounted with a slide cover. Sperm slides were visualized using a Zeiss AXIO Imager A2 compound microscope with attached Axiocam 506 mono camera.

Fifty-six morphological characters were coded from all body regions, the female RT, male genitalia, and sperm morphology. Full description of morphological characters (Appendix) and coding of morphological characters from (Table S2) is availalbe. Morphology was coded in MacClade 4.08 (Maddison & Maddison, 2005). Terminology for dineutine external morphology follows Gustafson & Miller (2015) and Miller & Bergsten (2012) for female RT, unless otherwise cited.

DNA

DNA was extracted using a Qiagen DNEasy kit (Valencia, California, USA) and the protocol for animal tissue. Thoracic muscle tissue was extracted from a lateral incision via fine forceps. The remaining specimen was retained and given a unique voucher identifier attached to the specimen via a label. Original DNA extractions are deposited at MSBA, as are the voucher specimens, unless indicated otherwise (Table S1).

Portions of five genes were used in the phylogenetic analysis, and a sixth only for some *Dineutus* specimens used previously in the analysis by Miller & Bergsten (2012). The six genes are: *cytochrome c oxidase* subunit I (COI, 1317 bp aligned), *cytochrome c oxidase* subunit II (COII, 740 bp aligned), *12S rRNA* (12S, 359 bp aligned), *histone III* (H3, 328 bp aligned), *arginine kinase* (AK, 712 bp aligned), and *elongation factor 1 alpha* (EF1α, 348 bp aligned). Standard PCR protocols were used for amplification and sequencing following Miller & Bergsten (2012). Primers and their sources, used for amplification and sequencing are available in Table S3. Gene coverage for each taxon analyzed is available in Table S1. Sequences were edited using Sequencher 4.8 (Gene Codes, 1999). Sequences were aligned using MUSCLE (Edgar, 2004) via EMBL-EBI's website (EMBL-EBI, 2015). Concatenation and clean up implemented in Mesquite 3.01 (Maddison & Maddison, 2015).

Partitioning

The dataset broadly overlaps that used by Miller & Bergsten (2012), and for this reason we used the same partitioning scheme, with codon-position specific nuclear and mitochondrial partitions. This partitioning scheme was previously tested and found to be preferred by a Bayes Factor test over gene-specific partitions (Miller *et al.*, 2009).

Analyses

Phylogenetic, Bayesian

Bayesian analysis was implemented using MPI version of MrBayes 3.2.6 (Ronquist *et al.*, 2011; Zhang *et al.*, 2015). No substitution model was selected *a priori*, instead the reversible-jump MCMC method with gamma rate variation across sites was used to test the probability of different models *a posteriori* during analysis (Huelsenbeck *et al.*, 2004; Ronquist *et al.*, 2011; Miller & Bergsten, 2012). A total-evidence approached was taken for time-calibration (Ronquist *et al.*, 2012). This technique is desirable as it incorporates inherent uncertainty regarding placement of fossils during phylogenetic reconstruction, treating fossil taxa as terminals, as opposed to node-based calibration in which fossils are forced to stem positions (Ronquist *et al.*, 2012).

To infer the substitution rate the methods outlined by Ronquist *et al.* (2012) were followed with the mean age of the fossil *Angarogyrus minimus* (178 Ma) used to calculate median rate, and the mean age of *Mesogyrus antiquus* (161 Ma) for the standard deviation. The Fossilization-Birth-Death macroevolutionary model (Heath *et al.*, 2014) was employed using the methods outlined by Zhang *et al.* (2015). The sampling strategy was set to diversity, with a sample probability of 0.06 as there are 153 known species of Dineutini, the ingroup for the analysis. Fossils were given a uniform age prior based on the age of the fossil. The tree age was given an offset exponential prior based on the age of *Mesogyrus antiquus,* a likely heterogyrine fossil, as *Heterogyrus milloti* was used as the furthest outgroup member. A relaxed clock model was used, with the branch length clock prior set to fossilization to use the FBD model, and the clock rate variance prior set to igr. The analysis was run for 10 million generations, using four chains (three heated, one cold), with swap number set to two, and a temperature of 0.1 for the heated chains. MCMC convergence was monitored using Tracer v.1.6 (Rambaut *et al.*, 2013).

Additional analyses using only mitochondrial and nuclear gene data were performed to check their data sets influence on the final total evidence topology (Figs. S1,S2). Certain problematic species were also removed from analyses to test effects on phylogenetic reconstruction (Fig. S4, S5).

Phylogenetic, Maximum Likelihood

A maximum likelihood analysis was also performed (Figure S6) as a form of reciprocal illumination (Hennig, 1966). The maximum likelihood analysis was implemented using the Hybrid MPI RAxML ver. 8 (Stamatakis, 2014). Model choice for the different genes was tested *a priori* using jModelTest (Posada, 2008). The GTR+G model was implemented as it was selected as the primary or secondary model for the majority of codon positions for the majority of genes. Each gene was analyzed individually. The genes were then combined to construct a multi-locus species tree using ASTRAL-II (Mirarab *et al.*, 2014; Mirarab & Warnow, 2015). One hundred replicates of multi-locus bootstrap support (Seo, 2008) were then performed in ASTRAL-II. Morphology was not included in the maximum likelihood analysis. All phylogenetic analyses were run on the super computer cluster Ulam at the Center for Advanced Research Computing, University of New Mexico.

Biogeographic, Ancestral Range Estimation

The time-calibrated consensus tree from the Bayesian total evidence analysis was used for the biogeographic analysis, with outgroup and fossil taxa pruned, as well as AyTs832 (*Macrogyrus albertisi*) to remove a polytomy. The analysis was performed using the program R and the package BioGeoBEARS (Matzke, 2013b, a) to estimate the ancestral range of the Dineutini across their entire distribution. The program offers several models and statistical comparison of model fit. Analyses were run under the DEC (Ree *et al.*, 2005; Ree & Smith, 2008) and DIVALIKE (Ronquist, 1997) models both with and without the +j found-event speciation parameter (Matzke, 2014). Following completion of analyses model fit was compared statistically within BioGeoBEARS.

For the biogeographic regions in the analysis the following abbreviations were used: A, Australia; M, Melanesia, New Guinea and surrounding islands; W, Wallacea; O, Oriental; P, Palearctic; E, Ethiopean region; N, Nearctic; C, Central America; I, West Indies (Fig. 3). Coding of taxa for biogeography is available in Table S1. The maximum distribution allowed for a species was 5.

Four time strata (TS) were established for the time stratification, these were: TS1, 120 – 90 Ma; TS2, 90 – 50 Ma; TS3, 50 – 20 Ma; TS4, 20 – Present. TS1 represents the early stages of the final Gondwanan break-up with the rifting of South American and Africa, and the initial break-up of East Gondwana (Storey, 1995). This point also represents the origins of the Dineutini. For this time slice the following areas were made unavailable based on paleogeographic data: Central America (Iturralde-Vinent, 2006), the West Indies (Iturralde-Vinent, 2006), Melanesia (Toussaint *et al.*, 2014), and Wallacea (Hall, 2001, 2002, 2013). TS2 represents the final stages of the Gondwanan break-up with drifting of South America, Antarctica, Australia (Storey, 1995), and their subsequent final separation (Livermore *et al.*, 2005; Lawver *et al.*, 2011; Reguero *et al.*, 2014). During TS2 the same areas were unavailable, except Central America was made available (Iturralde-Vinent, 2006). TS3 represents the isolation of South America, Antarctica, and Australia (Lawver & Gahagan, 2003; Lawver *et al.*, 2011); and the first potential emergence of the Caribbean (Iturralde-Vinent, 2006). New Guinea likely had little available land before 25 Ma (Toussaint *et al.*, 2014), but an orogenic event around 35 Ma (van Ufford & Cloos, 2005) likely created a small island, which persisted to form the oldest regions of the New Guinea (Baldwin *et al.*, 2012). At this point the West Indies, as well as the Melanesia area, are available, but the latter with low dispersal rate multipliers. TS4 represents the appearance of Wallacea (Hall, 2013) and major formation of the terrestrial New Guinean area (Toussaint *et al.*, 2014) with biotic interchange between the regions. At this point Wallacea areas is allowed. The dispersal rate coding followed that of Toussaint *et al.* (2016), based on the above paleogeographic evidence reference for each time slice.

Results

Phylogenetic

The Bayesian analysis (Figs. 1, 2, S1, S2) strongly supports a monophyletic Dineutini (posterior probability, pp = 0.99) with a Late Cretaceous origin (95% highest probability density, hpd = 75.75 – 113.93 Ma, median of hpd, m = 94.24 Ma). Within the Dineutini there are two clades, one comprising *Dineutus, Porrorhynchus* and the extinct genus *Mesodineutes*†; the other with *Macrogyrus* and *Enhydrus*. As *Mesodineutes*† only had few characters available it introduced uncertainty into the analysis, resulting in lower pp for the clades. Removing *Mesodineutes*† resulted in significantly higher support (Fig. S4) for the two clades (pp = 1.00 for the *Porrorhynchus* + *Dineutus* clade and pp = 0.86 for *Enhydrus* + *Macrogyrus*). Both are similar in age with Late Cretaceous origins (hpd = 67.38–101.44 Ma, m = 83 Ma and hpd = 67.31–105.32 Ma, m = 85 Ma respectively). The genera *Porrorhynchus* and *Enhydrus* are monophyletic with strong support (pp = 1.00); both are long branches, and sister to the much larger genera *Dineutus* and *Macrogyrus* respectively. *Mesodineutes*† originated around 83 Ma, and is placed as sister to the extant genera *Porrorhynchus* and *Dineutus*, having gone extinct around 64 Ma. While this placement for *Mesodineutes*† is weakly supported (pp = 0.51), the little morphology available is considerably more suggestive of this placement, than with *Enhydrus* and *Macrogyrus* (see *Mesodineutes*† discussion section under classification).

The clade *Macrogyrus* + *Andogyrus* (here after referred to as the genus *Macrogyrus* **sensu n.**) is strongly supported as monophyletic (pp = 1.00) with Paleocene origins (hpd = 45.95

– 72.73 Ma, m = 59.22 Ma). The earliest diverging lineage within *Macrogyrus*, are Neotropical species representing the subgenus *Andogyrus*, which is strongly supported as a monophyletic group (pp = 1.00), sister to the remaining non-South American species. The next branch is a clade of New Guinean species, representing the subgenus *Cyclomimus*, which is similarly strongly supported as being monophyletic (pp = 1.00), diverging in the Eocene (hpd = 40.30 – 65.81 Ma, m = 51.97 Ma). Above this branch are species of *Macrogyrus* from Australia, grading into New Guinean and Wallacean species. This group represents the subgenus *Macrogyrus* sensu stricto. *Macrogyrus striolatus* is recovered as sister to the remaining species of the *Macrogyrus* sensu stricto, but with weak support (pp = 0.50). The Australian species *M. oblongus*, *M. rivularis*, and *M. reichei* form a strongly supported clade (pp = 1.00), but interestingly *M. oblongus* and *M. rivularis* are not recovered as sisters, instead *M. rivularis* is placed as sister to *M. reichei* (pp = 1.00) with *M. oblongus* sister to both (pp = 1.00). *Macrogyrus howittii* is placed in an isolated position as sister to the more derived species found in Australia, as well as those from New Guinea and Indonesia, with strong support (pp = 1.00). The widespread Australian species *Macrogyrus australis* is found to be among the youngest (originating around 7 Ma) and most derived members of *Macrogyrus* with strong support (pp = 0.96).

The genus *Dineutus* is strongly supported as monophyletic (pp = 1.00) with Eocene origins (hpd = 40.23 – 63.16 Ma, m = 50.31 Ma). Within *Dineutus* there is a major split between primarily New Guinean and Southeast Asian species and those found mostly in Africa and North America. This clade is fairly well supported (pp = 0.79) and represents the new sensu stricto subgenus as it includes species related to the type species. The other major clade sports the majority of *Dineutus* species and has strong support for monophyly (pp = 0.99), this is the newly defined subgenus *Cyclous* **sensu n.** Within the subgenus *Cyclous* there are two groups, a strongly supported (pp = 0.97) North American clade and a mostly African clade, with slightly less support (pp = 0.87). The origin of the two subgenera and the major clades within *Cyclous* are place within the late Eocene (between 44 – 38 Ma).

Within the North American *Cyclous* clade there are two groups of species, a strongly monophyletic (pp = 0.96) Nearctic only clade, and a weakly supported widely distributed (pp = 0.68) clade consisting of mostly Central American species, the Caribbean species, and some Nearctic species. The Nearctic only clade includes some of the largest and the most widely distributed species within North America (e.g. *D. ciliatus*, *D. discolor,* and *D. robertsi*) (Gustafson & Miller, 2015). Interestingly despite exceptionally similar morphology, *D. ciliatus* and *D. robertsi* are not recovered as sister species. Instead *D. ciliatus* is strongly supported (pp = 0.96) as sister to a clade comprising *D. serrulatus* (*D. discolor* + *D. shorti*). The newly described *D. shorti* (Gustafson & Sites, 2016) is recovered as sister to the more widely distributed *D. discolor* (pp = 1.00), having diverged from a common ancestor around 7 Ma. The earliest diverging lineage holds the large Central American species, *D. truncatus* and *D. mexicanus* which are strongly supported as sisters (pp = 1.00) with the Caribbean *D. longimanus* strongly supported as sister to both (pp = 1.00). The next branch has weakly supported placement (pp = 0.59) and consists of two species that are strongly supported as sisters (pp = 1.00), *D. pagdeni* and *D. fairmairei,* known from the Solomon Islands and Fiji respectively. Sister to these island species is a strongly supported monophyletic group (pp = 0.97) with Nearctic and Central America species. *Dineutus sublineatus* is recovered as sister to the remaining members of this clade (pp = 0.97). Interestingly another Central American species, *D. solitarius* is also recovered in a isolated position, as sister to a clade of species with a primarily Nearctic distribution (pp = 1.00).

The primarily African clade similarly exhibits a large divide between members of the subgenus *Protodineutus* and those of species placed in the subgenus *Spinosodineutes*. *Spinosodineutes* as currently defined is strongly paraphyletic within the analysis. *Dineutus australis* the type species of the subgenus *Cyclous* is strongly supported (pp = 1.00) as sister to the African species *D. fauveli* and *D. subspinosus*, both members of *Spinosodineutes.* Interestingly the other member of *Spinosodineutes* included in the analysis, *D. striatus* is strongly supported (pp = 1.00) as sister to the large widespread Malagasy species, *D. proximus.* The clade containing the members of *Protodineutus* (including *D. striatus* of *Spinosodineutes*) is strongly supported as monophyletic (pp = 1.00). Interestingly the Malagasy species *D. sinuosipennis* is recovered as the earliest diverging lineage (m = 34 Ma) and sister to all the species within group (pp = 1.00). The other Malagasy species *D. proximus* is distantly related, nested well within a clade or primarily mainland Africa species.

The maximum likelihood (ML) analysis (Figure S5) generally supported the broader conclusions of the analysis. Importantly the ML analysis strongly supports monophyly of the Dineutini (bootstrap support, bt = 96). There is similarly strong support for the monophyly of *Dineutus* (bt = 97.4) and *Macrogyrus* (bt = 97.6). Within *Macrogyrus* there is strong support for the subgenera *Andogyrus* (bt = 97.6) and *Cyclomimus* (bt = 100). *Enhydrus* and *Porrorhynchus* are each strongly monophyletic (bt = 99) but are sister to one another, within a clade with the Gyrinini outgroup members. However, this is clearly a case of long branch attraction occurring in the analysis, known to effect ML analysis, despite selection of correct substitution model (Kück *et al.*, 2012).

Biogeographic

For the ancestral state estimation the DEC models fit the data significantly better than both DIVALIKE models (Table S4). The DEC +j model, including founder event speciation (Matzke, 2014), had a similar log-likelihood to the DEC model, but the Akaike weights identify this model as the overall best fit for the data (Table S4). Despite the difference in log-likelihood the DEC and DIVALIKE models recovered nearly identical ancestral state reconstructions (Figs. S7 – 14). The differences in estimation primarily relate to the ancestral ranges of the common ancestor of all Dineutini and the common ancestor of *Dineutus* subgenus *Cyclous*, however, with so many possible states the ancestral range is ambiguous for both (Figs. S7 – S14). The models either suggest slightly high possibility for a Nearctic *Cyclous* common ancestor in the DEC +j model, or an Ethiopian and Nearctic ancestral range in the DEC and DIVALIKE models (Figs. S7 – S14). For the common ancestor of all Dineutini, the DIVALIKE models suggest higher likelihood for a common ancestor distributed in both Southeast Asia and South America (Figs. S11 – S14).

The ancestor of both *Enhydrus* and *Macrogyrus* is recovered as being distributed in South America (Fig. 3). The ancestral state reconstruction supports an origin for *Macrogyrus* in the Paleocene of South America with subsequent dispersal to Australia around the early Eocene, coinciding with the Early Eocene Climatic Optimum (Fig. 3). The ancestral reconstruction then reveals numerous subsequent dispersal events out of Australia to the Melanesian area around the late Oligocene and early Miocene (Fig. 3). Dispersal to Less Sunda Islands in Wallacea happened most recently around the mid-Miocene.

In the *Porrorhynchus* and *Dineutus* clade, the common ancestor is estimated to have been distributed in the Oriental region during the Late Cretaceous (Fig. 3). The common ancestor of

Dineutus likely originated similarly in the Oriental region in the early Eocene, around the Early Eocene Climatic Optimum. In the *Dineutus* sensu stricto subgenus the common ancestor likely arose in the Oriental region, with subsequent dispersal to Papua New Guinea around the late Eocene (Fig. 3). There is considerable ambiguity related to the ancestral range of the common ancestor of the *Dineutus* subgenus *Cyclous* (Figs. S7 – S14) preventing any conclusions about its location. The primarily North American clade within *Cyclous* is estimated to have had a Nearctic ancestor, and the primarily African clade an Ethiopian ancestor (Fig. 3). Given the isolated positions of African and North American at this time, these likely represent two different dispersal events. Within the North American clade dispersal to Central America occurred around the end Eocene (Fig. 3). Several dispersal events out of Central America are then inferred around the early Miocene and late Miocene (Fig. 3).

Discussion

Origins of Macrogyrus and the importance of Antarctica

The final stages of the breakup of Gondwana around 100 Ma, involved South America rifting from Africa moving west, while Antarctica and Australia migrated south remaining in close proximity with New Zealand rifting away from Antarctica around 80 Ma (Storey, 1995; Blakey, 2008). However, during the Late Cretaceous the southern tip of South America remained closely associated with western Antarctica into the early Paleogene (Reguero *et al.*, 2014). Data from the Antarctic Peninsula and the southern tip of South America support a continuous land-mass connecting South America to Antarctica during the Early Paleogene (Lawver *et al.*, 2011). This landmass, dubbed the Wedellian Isthmus (Reguero *et al.*, 2014), is proposed to have served as a land bridge, allowing faunal exchange between Patagonia and west Antarctica until around 57 Ma (Reguero *et al.*, 2014). During this time (60 – 50 Ma) the ancestral state reconstruction (Fig. 3) suggests the common ancestor of the *Cyclomimus* subgenus dispersed from South America, across a cool-temperate Antarctica (Pross *et al.*, 2012) to Australia. In support of this scenario, Patagonia is currently occupied by a single species *M.* (*Andogyrus*) *seriatopunctatus* (Brinck, 1977), which our analysis shows to be earlier diverging than its more northerly Andean sisters, *M.* (*Andogyrus*) *zimmermanni* in Peru and *M.* (*Andogyrus*) *colombicus* in Venezuela and Colombia (Fig. 2).

At around 50 Ma the Drake's passage opened (Fig. 3, DPO), severing the Wedellian Isthmus, separating South America from western Antarctica (Lawver & Gahagan, 2003; Livermore *et al.*, 2005) and opening of the Tasmanian Gateway to ocean currents cut Antarctic ties with Australia, leading to thermal isolation of Antarctica and global cooling (Bijl *et al.*, 2013) and representing the final breakup of Gondwana (Blakey, 2008). While the ancestral state reconstruction does not support a Gondwanan vicariant origin for the subgenus *Andogyrus*, the isolation of this subgenus is associated with the final breakup of Gondwana and the dispersal event to Australia was possible via the last remaining Gondwanan connections of South America, Antarctica, and Australia. Antarctica clearly played a critical role in the evolution of *Macrogyrus* by facilitating dispersal to Australia. Antarctica likely supported a very unique *Macrogyrus* fauna given its near tropical warmth during the Eocene, until its glaciation around 30 Ma (Pross *et al.*, 2012).

Origins of Dineutus and its absence from South America

The common ancestor of *Dineutus* is reconstructed as arising within the Oriental region during the early Eocene (Fig. 3). Subsequent to this dispersal into the Nearctic and the Ethiopian regions likely occurred during the Mid-Eocene Climatic Optimum (Fig. 3). This period of time is way to recent for dispersal to the western hemisphere have occurred over the transatlantic De Geer Route or Thulean Route (Brikiatis, 2014). The most likely route to the Nearctic was through the Beringia, which during the Eocene was a lush swamp forest occupied by such thermophilic species as primates, tapirs, and alligators (Eberle & Greenwood, 2011). Following the Eocene during the cooling of the Oligocene, dispersal to Central America occurred (Fig. 3). From here subsequent dispersals to the Caribbean occurred either directly, or through the Nearctic during the Miocene (Fig.3). All this data strongly suggest that the absence of *Dineutus* in South America is because the genus has yet to disperse there. The *Dineutus* species of the western hemisphere likely dispersed to the western hemisphere through Beringia into North America and have yet to spread further south than Panama.

Interestingly, the species located in the Solomon Islands and Fiji are reconstructed as having diverged from Central American ancestors around the Oligocene (Fig. 3). A transpacific dispersal even out of Central America seems highly unlikely. More probable is a second dispersal back across Beringia to the Palearctic, into the Oriental region and southward to the Melanesian area. A likely critical taxon for reconstructing this path is *D. ritsemai*, a species known only from Sulawesi. *Dineutus ritsemai* appears to be closely related to *D. pagdeni* and *D. fairairei* in that these three species all share a relatively rare morphological feature, the profemoral sub-apicoventral tooth being located on the anterior margin of the profemur's ventral face.

Broader conclusions

Future sampling in Southeast Asia and the Sunda Islands for *Dineutus* species will greatly aid in reconstructing the region occupied by the common ancestor of the subgenus *Cyclous*. However, the reason for *Dineutus* species' absence from South America seems clear given the young age of the group and the estimated Oriental ancestral range of the common ancestor of *Dineutus*. The phylogenetic position of *Porrorhynchus indicans* may also effect the biogeographic reconstruction for the common ancestor of *Porrorhynchus* and *Dineutus*, being located in Sri Lanka. Sri Lanka may have held a central position at the heart of Gondwana along with Madagascar (Dissanayake & Chandrajith, 1999). Given the age and phylogenetic position of *P. indicans*, its presence in Sri Lanka may be exceptionally important for the biogeographic reconstruction and origins of the common ancestor of the Dineutini. The only taxon with a unique distribution missing from the analysis for *Macrogyrus* is *M. caledonicus* from New Caledonia. However, this area is unlikely to alter the recovered biogeographic reconstruction.

Classification

Tribe DINEUTINI Desmarest, 1851

Dineutini Desmarest (1851): 225. Type genus *Dineutus* Macleay, 1825 by original designation.

Synonyms: Enhydrini Régimbart, 1882; Dineutini Ochs, 1926; Prothydrinae Guignot (1954); Enhydrusini ICZN (2012)

Diagnosis. Within the Gyrinidae the Dineutini can be diagnosed by having the following combination of characters: 1) maxilla without galea, 2) elytron possessing nine elytral striae without accompanying sutural border, 3) metaventral wings (Hatch, 1925) in the form of a more-or-less equilateral triangle (Fig. 6) (Régimbart, 1882), 4) lobiform metanepisternum, 5) transverse metacoxae (Fig. 6), 6) female RT with greatly expanded, sac-like spermatheca without a well differentiated fertilization duct (Fig. 11, 12) (Miller & Bergsten, 2012) 7) primary conjugation of sperm via the spermostyle (Fig. 13). The dineutine diagnosable traits are most similar to traits found in *Heterogyrus*, which also has nine elytral striae, the lateral wing of the metaventrite in the form of an equilateral triangle, and a lobiform metanepisternum. However, the elytra of *Heterogyrus* have sutural borders, which are absent in all dineutines, and the metacoxae of *Heterogyrus* are oblique, not transverse as in the dineutines. In regards to the female reproductive tract, the dineutines are most similar to the orectochiline genera *Orectochilus* and *Orectogyrus.* The dineutines however, never have the fertilization duct well differentiated or expanded. In *Orectochilus* the fertilization duct is well differentiated and somewhat removed from the bursa (Miller & Bergsten, 2012). Most species of *Orectogyrus* have the fertilization duct greatly expanded, curled, and sclerotized, often forming a snail-shell shape (Brinck, 1956; Miller & Bergsten, 2012). The lack of maxillary galea is an additional trait shared with orectochilines. Transverse metacoxae are also found in *Spanglerogyrus*, however, the metacoxae of *Spanglerogyrus* are weakly developed, and *Spanglerogyrus* does not have triangular metaventral wings. Some larger *Patrus* species have transverse metacoxae as well.

Taxonomy. The first formal description and diagnosis of the tribe was by Régimbart (1882). Régimbart (1882) did an excellent job providing potential morphological synapomorphies for the tribe and its constituent genera. Unfortunately an earlier division of the family Gyrinidae was proposed by Desmarest (1851) including some of the genera which Régimbart united in his seemingly new tribe Enhydrini, rendering it a junior synonym of Desmarest's Dineutini. The rediscovery of Desmarest's early name by Bouchard *et al.* (2011) was quite welcome, however, given the nomenclatural difficulty associated with Régimbart's proposed name for the tribe (Gustafson & Miller, 2013). The constituent genera were greatly subdivided by the work of Georg Ochs (1924, 1926, 1949), the vast majority of which are not supported by the results of this analysis. A great testament to the outstanding work of Régimbart, we here return to the classification originally proposed by him in 1882 for the Dineutini, with only minor revision. The valid constituent species of the tribe Dineutini have not changed considerably since Régimbart's (1882) work, only growing in number following the taxonomic works of proceeding gyrinid experts.

Distribution. Members of the Dineutini have a global distribution, missing only from more northern latitudes and the arctic regions (Fig. 14).

Discussion. The sperm of *Dineutus* (Fig. 13D) was first described by Breland & Simmons (1970), in which they discovered these species had primary conjugation via spermatodesma (as defined by Higginson & Pitnick (2011)), they dubbed spermatostyles. Because sperm has been found to be phylogenetic informative (Baccetti, 1987), and sperm conjugation is relatively rare phenomenon (Pitnick *et al.*, 2009) the sperm of the dineutine genera were sampled. The study revealed that all *Enhydrus* (Fig. 13 A – C), *Porrorhynchus* (Fig. 13F), and *Macrogyrus* (Fig. 13E) all exhibit primary sperm conjugation via spermatostyles.

Genus *Dineutus* Macleay, 1825

(Figs 1, 4C, 5E, 6D, 7A – D, 8C, 9E, 9G, 11B – D, 13D)
Dineutus Macleay, 1825: 30, type species *Dineutus politus* Macleay, 1825.
Synonyms: *Necticus* Laporte, 1835, *Dineutes* Régimbart, 1882.

Diagnosis. The genus *Dineutus* can be diagnosed within the Dineutini by the following combination of characters: 1) Gular suture complete, 2) frons without lateral bead (Fig. 4C), 3) antennal flagellum with 6 – 7 flagellomeres (Fig. 5E), 4) pronotal transverse impressed line present, 5) scutellar shield invisible with elytra closed, 6) protibia and male protarsi narrow (Fig. 9E), 7) mesotarsal claws sexually dimorphic, 8) metaventrite medially triangular in shape (Fig. 6D) and narrow, 9) female RT with vaginal shield (Fig. 11B, C, D) (Brinck, 1980, 1983, 1984). The genus *Dineutus* lacks a single distinct autapomorphy among gyrinid genera. A character that comes close are sexually dimorphic mesotarsal claws, but this character is a synapomorphy shared with *Porrorhynchus*, however, the sexual dimorphism is most pronounced among species of *Dineutus*. The other synapomorphies with *Porrorhynchus* include the invisible scutellar shield and most noticeably the female RT possessing a vaginal shield. *Dineutus* can be readily distinguished from all other dineutine genera by the narrowed protibia, which is likely the sole apomorphy separating this genus from *Porrorhynchus*. *Dineutus* can be furthered distinguished from *Porrorhynchus* in having a complete gular suture and the pronotal transverse impressed line present.

Taxonomy. The genus was monotypic when originally erected by Macleay (1825). Régimbart subsequently treated the genus several times, revising it and adding many species (Régimbart, 1882, 1886, 1892, 1907). Hatch (1925) was the first author to divide the genus into subgenera, based primarily on overall body-shape. Georg Ochs (1926, 1955) subsequently erected numerous subgenera, including subsuming *Porrorhynchus* as one of the subgenera. Since Ochs' work, no new subgenera have been proposed, but the composition of the subgenera has been re-arranged by Guignot (1950), and most recently by Brinck (1955b), who attempted to provide distinct morphological traits identifying each subgenus, unsuccessfully.

There are currently 92 species within the genus *Dineutus*, making it easily the largest genus within the Dineutini.

Distribution. *Dineutus* has a near global distribution, missing from Europe, and most notably from South America (Fig. 14D) (Mouchamps, 1949b; Brinck, 1955b; Satô, 1962; Brinck, 1976; Mazzoldi, 1995; Watts & Hamon, 2010; Hájek, 2011; Gustafson & Miller, 2015; Lee & Ahn, 2015). Currently the highest diversity is in the Austral region, primarily in New Guinea, but this likely reflect bias due to recent taxonomic work on species in this region (i.e. Brinck (1976, 1981, 1983, 1984). The second highest diversity is found in tropical Africa.

Discussion. This is the largest and most widely distributed genus within the Dineutini.

Subgenus *Dineutus* sensu novo

(Figs. 1, 7C, 9E, 11B)
Type species: *Dineutus politus* Macleay, 1825.

Synonyms: *Rhombodineutus* Ochs, 1926 **new synonymy**, *Merodineutus* Ochs, 1955 **new synonymy**

Diagnosis. Within *Dineutus* the sensu stricto subgenus can be diagnosed by the following characters: 1) head capsule of most species with a frons to clypeus ratio less than or equal to 1.5, 2) a transverse, rounded labrum, 3) distolateral angle of protibia without spine, 4) protrochanter glabrous (Fig. 7C) –without setae apically on ventral face, 5) mesotarsal claws distinctly sexually dimorphic. The *Dineutus* sensu stricto subgenus contains the largest members of the genus (e.g. *Dineutus macrochirus*) (Brinck, 1984). Most species exhibit little to no distinguishable sexual dimorphism in terms of elytral shape. The mesotarsal claws are distinctly sexually dimorphic, but not nearly as well developed as those of the *Cyclous* subgenus.

Taxonomy. There are now 23 species within the sensu stricto subgenus, containing members of the former subgenera *Merodineutus* and *Rhombodineutus*. The species of this group were last treated by Mouchamps (1949b) (the original sensu stricto species), Brinck (1983) (the *Rhombodineutus* species), and Brinck (1984) (*Merodineutus* species).

Distribution. Primarily distributed in New Guinea and Southeast Asia. One species, *D. insularis* extends into the far eastern Palearctic being found on the Ryukyu islands.

Discussion. The distinction of *Merodineutus* from *Dineutus* was tenuous, based primarily on elytral sculpture, protarsus, and protibial modifications (Brinck, 1984). Brinck (1984) even predicted the derivation of *Merodineutus* from *Dineutus* sensu stricto. The subgenus *Rhombodineutus* was similarly based on elytral modifications resulting in a rhomboid body outline, and a more elongate labrum than other species of *Dineutus* (Brinck, 1983). Many *Dineutus* species show unique modifications to the elytral apices and protibial modifications as exhibited by the diversity of North American *Dineutus* (Gustafson & Miller, 2015). The large glabrous protrochanters within *Dineutus* are unique to this clade. For this reason, the other subgenera are synonymized with the *Dineutus* sensu stricto subgenus.

The close relation found here between *Rhombodineutus* and *Merodineutus* is novel. A phylogenetic analysis of the species of this area, including *Rhomborhynchus*, would prove quite interesting in elucidating directionality of colonization of New Guinea and validity of the numerous described species and subspecies (Brinck, 1983, 1984).

Subgenus *Cyclous* Dejean, 1833 sensu novo

(Figs 1, 4C, 5E, 6D, 7A – B, 7D, 8C, 9G, 11C,13D)
Type species: *Dineutus australis* (Fabricius, 1775).
Synonyms: *Callistodineutus* Ochs, 1926 **new synonymy**, *Cyclinus* Kirby, 1837 **new synonymy**, *Gyrinodineutus* Ochs, 1926, *Paracyclous* Ochs, 1926 **new synonymy**, *Protodineutus* Ochs, 1926 **new synonymy**, *Spinosodineutes* Hatch, 1925 **new synonymy**.

Diagnosis. Within *Dineutus* the *Cyclous* subgenus can be diagnosed by the following characters: 1) Head capsule with a frons to clypeus ratio less than or equal to 1.5, 2) a transverse, rounded labrum, 3) distolateral angle of protibia without spine, 4) ventral face of protrochanter apically with series of stout setae (Fig. 8C), 5) mesotarsal claws strongly sexually dimorphic 6) spermatheca not tubiform, less elongate and more rounded. Many species are strongly sexually dimorphic in elytral shape. This group exhibits the most strongly sexually dimorphic mesotarsal claws.

Taxonomy. This is the largest subgenus, now with 67 species. The species were treated taxonomically most recently by Mouchamps (1949a) (the *Spinosodineutes* species), Brinck (1955b) (African species), Brinck (1976) (the *Callistodineutus* species), and Gustafson & Miller (2015) (the North American species).

Distribution. Widely distributed, found in North America, Africa, Asia, and Australia.

Discussion. The numerous subgenera of *Dineutus* have long been a source of conflict among gyrinid workers (Hatch, 1925; Ochs, 1926; Guignot, 1950; Brinck, 1955b; Ochs, 1955). The first division of *Dineutus* into subgenera was proposed by Hatch (1925), but the majority of subgenera was erected by Ochs (1926) during his pre-cladistic systematic treatment of the species of *Dineutus* (and *Porrorhynchus*, see below). The subgenera have nearly all been diagnosed in the past by body form, modification to the elytral apex, and/or elytra reticulation. These characters are highly variable among the numerous *Dineutus* species, and typically not unique to any one subgenus, causing much of the disagreement between constituent species.

The only authority to attempt to propose discrete morphological characters for the subgenera was Brinck (1955b), but was unsuccessful, resorting to the distinction of African species and American species for the subgenera *Protodineutus* and *Cyclinus* respectively. However, our analysis shows *Callistodineutus* to be nested within the North American species, despite a proposed distinct morphological character, suggesting those utilized by Brinck (1955b) were unsuccessful in identifying large natural groups of species. The distinct character of the ventral face of the protrochanter with a series of short stout setae apically, in combination with the other diagnostic features successfully recognizes a large monophyletic group within *Dineutus*. While *D. ritsemai* was not included in the phylogenetic study, the taxon was studied for morphology. *Dineutus ritsemai* has well-developed sexually dimorphic mesotarsal claws, and resembles closely members of the former subgenus *Callistodineutus* having a single profemoral sub-apicoventral tooth on the anterior face only. Given the former species are nested within the North American members, including this species and synonymizing *Paracylous* with *Cyclous* is justified. For this reason we here synonymous the former subgenera. The oldest available name for this grouping is *Cyclous* initially proposed by Dejean, 1833 for *Dineutus australis*, one of the most widespread species of *Dineutus* (Ochs, 1949).

This subgenus is notable for having numerous sexually dimorphic traits. Many species have sexually dimorphic elytral apices, often with one sex having thorn-like productions. This is exhibited in several North American species (Gustafson & Miller, 2015). This group also exhibits sexually dimorphic modification to the protrochanter, such as the strange waxy region of male *Dineutus proximus* (Fig. 7B), and most notably the setose brush of *D. australis* males (Fig. 7A). The male mesotarsal claws are also strongly sexually dimorphic in this group. The North American species exhibit species-specific sexually dimorphic claws, with the claws of *D. nigrior* being the most extremely dimorphic known (Gustafson & Miller, 2015). The median lobe of the aedeagus of members of the subgenus *Cyclous* also present a wide diversity of forms, not seen elsewhere within Dineutini. No other dineutine group exhibits such a suite of sexually selected traits.

Subgenus *Rhomborhynchus* Ochs, 1926 incertae sedis

(Figs 11D, S5)
Rhomborhynchus Ochs, 1926: 65
Type species: *Porrorhynchus depressus* Régimbart, 1907.

Diagnosis. Within *Dineutus* the subgenus *Rhomborhynchus* can be diagnosed by the following characters: 1) head capsule with a frons to clypeus ratio of greater than or equal to 1.5, 2) labrum elongate and triangular, 3) labrum with a longitudinal paired row of setae, and one transverse row, 4) spinose distolateral corner of the protibia, 5) ventral face of protrochanter apically with series of stout setae, 6) mesotarsal claws weakly sexually dimorphic, 7) female RT with tubiform spermatheca. These species are most similar to members of the former subgenus *Rhombodineutus* having relatively elongate labra and a greatly elongate spermatheca (Fig. 11D). But can be distinguished by the spinose distolateral corner of the protibia, the more strongly triangular labrum, and the presence of setae apically on the ventral face of the protrochanter.

Taxonomy. Two species, *D. depressus* and *D. misoolensis*.

Distribution. Known from New Guinea and the neighboring island of Misool. Widespread within New Guinea.

Discussion. *Rhomborhynchus* was originally erected as a subgenus of *Dineutus*, however the type species *D. depressus* has mostly been considered a member of *Porrorhynchus* for much of its history (Régimbart, 1907; Guignot, 1950; Brinck, 1955b). Ochs (1926) was the first to recognize the different features of *D. depressus* relative to the members of *Porrorhynchus* and provided a discussion of why this taxon and several others proposed by him should be considered members of *Dineutus* (Ochs, 1955). However, Ochs (1926) did not recognize the unique autapomorphies of the other *Porrorhynchus* species in relation to *Dineutus*.

This subgenus exhibits numerous similarities to members of the former subgenus *Rhombodineutus*, such as 1) elongate labra, 2) a more longitudinal orientation to the labral setation, 3) rhomboid body-outline. "*Rhombodineutus"* species also have a relatively elongate spermatheca (Fig. 11B) compared to other *Dineutus* members. However, *Rhomborhynchus* species have setae situation apically on the ventral face of the protrochanter, suggesting placement outside of the *Dineutus* sensu stricto subgenus and away from the species of the former subgenus *Rhombodineutus*. The lack of sexually dimorphic traits and weakly sexually dimorphic mesotarsal claws also suggest *Rhomborhynchus* is not a member of the subgenus *Cyclous*. *Rhomborhynchus* species also lack all the synapomorphic characters of *Porrorhynchus* sharing only seemingly plesiomorphic features like the elongate labrum and the tubiform spermatheca.

Unfortunately, no molecular-grade specimens of *Rhomborhynchus* were available for this study and analysis only used morphological characters. The Bayesian analysis placed *Rhomborhynchus* well within *Dineutus* (*Cyclous*) in a polytomy with the Malagasy species *Dineutus sinuosipennis* (Fig. S5), which seems highly unlikely. As the analysis placed the subgenus well within *Dineutus* and its lack of synapomorphic characters shared with members of *Porrorhynchus*, it seems safe to tentatively transfer the species to this genus for the time being, but with an incertae sedis in relation to the other *Dineutus* subgenera. The final placement of this subgenus is clearly still in question. Future phylogenetic analyses including molecular grade *Rhomborhynchus* specimens will be necessary to resolve its phylogenetic position.

Genus *Enhydrus* Laporte, 1835

(Figs 2, 4A, 5D, 6A, 9F, 12F – G, 13A – C)
Type species: *Enhydrus sulcatus* (Wiedemann, 1821).
Synonyms: *Epinectus* Aubé, 1838, *Epinectes* Régimbart, 1877, *Prothydrus* Guignot, 1954

Diagnosis. Within the tribe Dineutini *Enhydrus* can be diagnosed by the following combination of characters: 1) antenna of most species with 7 flagellomeres (Fig. 5D) –one with 6, 2) fons with lateral bead (Fig. 4A), 3) pronotal transverse impressed line present, 4) elytral striae present as strongly impressed lines, 5) scutellar shield visible with elytra closed, 6) protibia laterally expanded apically (as in Fig. 8A), 7) broad, compact male protarsi (Fig. 9F), protarsi of both sexes often with fused segments and large protarsal claws, 8) metaventrite medially pentagonal in shape (Fig. 6A), 9) suture of abdominal sternite II present, 10) female RT without vagina shield, gonocoxae short and stout (Fig. 12G).

Taxonomy. There are four known species in the genus. The species of *Enhydrus* were last treated taxonomically by Brinck (1978).

Distribution. Disparately distributed in South American and extreme southeastern Central America (Fig. 14C) (Brinck, 1977).

Discussion. The genus *Enhydrus* lacks a single autapomorphy, however, retention of a fully developed suture to abdominal sternite II is unique to this genus. Fusion of the protarsomeres is unique to *Enhydrus* as well, but not all species exhibit protarsomere fusion (*E. tibialis* does not have fused protarsomeres). Molecular data (Fig. S4) however strongly support *Enhydrus* is a distinct monophyletic group and in general morphology species strongly resemble one another, despite lacking a distinct synapomorphy.

Genus *Macrogyrus* Régimbart, 1882

(Figs 2, 4B, 4D, 4E, 5A – B, 6B, 7F, 8A, 8D, 9A – C, 10, 12A – E, 13E)
Type species: *Macrogyrus howittii* (Clark, 1866).

Diagnosis. Within the tribe Dineutini, *Macrogyrus* can be diagnosed by the following combination of characters: 1) antennae with 9 flagellomeres (Fig. 5A – B), 2) frons with lateral bead (Fig. 4B, 4D, 4E), 3) pronotal transverse impressed line present, 4) scutellar shield visible with elytra closed, 5) protibia laterally expanded apically (Fig. 8A), 6) protarsus of male broad, discus present ventrally on protarsomere I (described blow) (Fig. 9A – C), 7) metacoxal process bordered posterolaterally (Fig. 6B), 8) female RT without vaginal shield, gonocoxae elongate (Fig. 13B).

Taxonomy. There are now 54 species of *Macrogyrus* with the inclusion of the former genus *Andogyrus*. This genus has never received a comprehensive revision.

Distribution. Found in South America, Australia, New Caledonia, New Guinea and surrounding islands, and Lesser Sunda Islands (Fig. 14D) (Ochs, 1949, 1953, 1955; Brinck, 1976, 1977; Watts & Hamon, 2010).

Discussion. This genus exhibits an excellent autapomorphy: the male protarsus has protarsomere I with a recessed pit possessing adhesive setae with a different suction cup morphology than the remaining adhesive setae (Fig. 9 A – C, di). This character was first described by Régimbart (1882: 433) and dubbed the discus. This feature is a synapomorphy uniting all the *Macrogyrus* species.

Subgenus *Andogyrus* Ochs, 1924 new status

(Figs 2, 4D, 5B, 6B, 8A, 8D, 9A, 12A)
Type species: *Andogyrus ellipticus* (Brullé, 1836).
Synonyms: *Proteogyrus* Mouchamps, 1951.

Diagnosis. Within the genus *Macrogyrus*, *Andogyrus* can be diagnosed by the following combination of characters: 1) clypeus narrow, 2) elytra without canaliculate microsculpture 3) metaventrite medially pentagonal in form (Fig. 6B), 4) metaventral discrimen with elongate transverse sulcus ancestrally (as in Fig. 10A). The elongate transverse sulcus of the metaventral discrimen is lost in many species of the subgenus *Andogyrus*, but its presence in *M. seriatopunctatus* suggest the absence to be a secondary loss, given its phylogenetic position (Fig. 2).

Taxonomy. This subgenus has twenty known species. The species of this subgenus were last treated by Brinck (1977).

Distribution. Found along the Andes of South America, from Venezuela to Argentina (Brinck, 1977).

Discussion. The separation of *Andogyrus* from *Macrogyrus* was based primarily on distribution (Ochs, 1924) and Hatch (1925) would prove quite correct in asserting that the Australian *Macrogyrus* were derived from a common ancestor similar to *Andogyrus*. As can be seen from the phylogeny (Fig. 2) *Andogyrus* is far too similar to *Macrogyrus* to be regarded as a genus distinct from the latter. Instead *Andogyrus* should be regarded as an early diverging lineage within *Macrogyrus*. Especially given the very distinct synapomorphy of the male protarsal discus. Separating these two groups into formal genera would also suggest *Cyclous* and *Dineutus sensu stricto* deserve separation into distinct genera, using similar phylogenetic logic.

Subgenus *Cyclomimus* Ochs, 1949 sensu novo

(Figs 2, 4F)
Type species: *Macrogyrus purpurascens* Régimbart, 1882.
Synonyms: *Stephanogyrus* Ochs, 1955 **new synonymy**

Diagnosis. Within the genus *Macrogyrus*, *Cyclomimus* can be diagnosed by the following combination of characters: 1) clypeus considerably enlarged (Fig. 4F), 2) elytra without canaliculate microsculpture 3) metaventral discrimen without transverse sulcus. Some of the

New Guinean species exhibit unique modification to the adhesive setae of the male protarsus. The discus still retains a relatively normal amount of setae, however outside the discus the adhesive setae are reduced in number, nearly absent from the ventral face of the ultimate protarsomere, and have very large suction cups. The species within this group are smaller in body size than most other members of *Macrogyrus*, but not all.

Taxonomy. Five known species, and the subgenus is returned to its original sense as initially proposed by Ochs (1949). The species were most recently treated by Ochs (1955) (for the New Guinea species) and by Mazzoldi (2010) (for *M. caledonicus*).

Distribution. Primarily found in New Guinea (fours species) (Ochs, 1955) where it appears widespread, with one species from Grande Terre, New Caledonia (Mazzoldi, 2010).

Discussion. The subgenus *Stephanogyrus* was erected for the single species *M. caledonicus* by Ochs (1954) based only on modifications to the elytra. While this species was not included in the formal phylogenetic analysis, specimens were studied and found to exhibit the diagnostic features uniting the monophyletic group of species from New Guinea. Furthermore, this returns *Cyclomimus* to its original sense, prior to splitting of a single isolated species from New Caledonia.

Subgenus *Macrogyrus* sensu novo

(Figs 2, 4B, 5A, 7F, 9B – C, 10, 12D – E, 13F)
Type species: *Macrogyrus howittii* (Clark, 1866).

Synonyms: *Australogyrus* Ochs, 1949 **new synonymy**, *Ballogyrus* Ochs, 1949 **new synonymy**, *Clarkogyrus* Ochs, 1949 **new synonymy**, *Megalogyrus* Ochs, 1949 **new synonymy**, *Orectomimus* Ochs, 1930 **new synonymy**, *Tribologyrus* Ochs, 1949 **new synonymy**, *Tribolomimus* Ochs, 1949.

Diagnosis. Within the genus *Macrogyrus*, the sensu stricto subgenus, can be diagnosed by the following combination of character: 1) clypeus neither narrow nor considerably enlarged (Fig. 4B), 2) elytra with unique canaliculate microsculpture (Fig. 10B – C), 3) metaventral discrimen of most species with well developed transverse sulcus (Fig. 10A). The unique canaliculate microsculpture (Fig. 10B – C) is an excellent autapomorphy for the sensu stricto subgenus. This character is strongly reduced in one species *M. sumbawae* (Fig. 2), but is still faintly evident apically on the elytra.

Taxonomy. There are now 29 species within this subgenus, a massive increase from the former classification, in which the subgenus only contained the type species, *M. howittii* (Ochs, 1949). The Australian species are the most well known (Ochs, 1949, 1956) and were recently treated by Watts & Hamon (2010), making their identification possible. The New Guinean fauna and those of the surrounding islands are in desperate need of revision following the work of Ochs (1955), in which the few known species were divided into numerous subspecies, from disparate locations in New Guinea, based on few specimens. The work of Ochs (1955), including no illustrations, non-discrete morphological characters, and excessive splitting of species, has made the identification of New Guinean specimens exceptionally difficult. For this reason, most species in the analysis were unable to be identified reliably.

Distribution. Primarily known from Australia and New Guinea, also found in the islands surrounding New Guinea, and the Lesser Sunda Islands (Ochs, 1949, 1955).

Discussion. The new definition of the sensu stricto subgenus is based on the earliest diverging taxon suggesting a common ancestor with canaliculate microsculpture (Fig. 10B – C), which in this analysis is *M. striolatus*. However, the placement of *M. striolatus* is weakly supported (Fig. S3, S4). It is possible that the subgenus *Cyclomimus* is nested within the sensu stricto subgenus, as examination of the .t tree files from the Bayesian analysis show the placement of *M. striolatus* fluctuating between a position above or below the *Cyclomimus* clade. In the case *M. striolatus* is truly earlier diverging than the *Cyclomimus* clade, the putative synapomorphic character of the sensu stricto subgenus still stands, with an inferred subsequent loss of the canaliculate microsculpture in *Cyclomimus*. Reduction of the canaliculate microsculpture is seen in the more derived members of the sensu stricto subgenus, e.g. *M. sumbawae* (Fig. 2) and other species found in Wallacea. The species of *Cyclomimus* show their other highly derived characters (e.g. the reduction in number and expansion in size of adhesive setae of the male protarsus; a largely expanded clypeus, reduction of the transverse sulcus of the metaventral discrimen). Therefore, a convergent derived loss of the canaliculate microsculpture is certainly plausible. Because of the strong support for the monophyly of the *Cyclomimus* subgenus in the analysis is currently retained as a valid subgenus separate from the sensu stricto, but the definition of the *Macrogyrus* sensu stricto subject to change in future phylogenetic analyses depending upon the placement of *M. striolatus*.

Genus *Mesodineutes*† Ponomarenko, 1977

(Figs. 6E)
Type species *Mesodineutes amurensis* Ponomarenko, 1977

Diagnosis. Within the tribe Dineutini *Mesodineutes* can be diagnosed by the following combination of characters: 1) elytral striae present as punctures, 2) elytral apex rounded, without apicolateral sinuation or other modification, 3) metaventrite medially triangular in shape (Fig. 6E) and broad, 4) metacoxal process without border posterolaterally (Fig. 6E).

Taxonomy. This fossil genus is monotypic.

Distribution. Described from the Paleocene of southeastern Russian Federation (Ponomarenko, 1977).

Discussion. While the support for the phylogenetic placement of this species was not strong (Fig. S3), the available morphological information and its distribution strongly support its placement with *Porrorhynchus* and *Dineutus*. Similar to *Porrorhynchus* and *Dineutus*, *Mesodineutes* has a triangular shaped medial expanse to the metaventrite (Fig. 6 C – E), while *Enhydrus* and *Macrogyrus* have a more pentagonal shape (Fig. 6 A – F). *Mesodineutes* can further be separated from a close relation with *Macrogyrus* in that it lacks a border to the posterolateral margin of the metacoxae (Fig. 6E compared to 6B). Importantly this species is found in the Palearctic of the Paleocene, which according to the biogeographic analysis suggests it does not belong in the clade with *Enhydrus* + *Macrogyrus* whose ancestors evolved in or near Australia. Importantly it also supports the biogeographic reconstruction that the ancestor of *Porrorhynchus* + *Dineutus* was likely found in or near the Oriental region (Fig. 3).

Genus *Porrorhynchus* Laporte, 1835

(Figs. 1, 4E, 5C, 6C, 7E, 8B, 9D, 11A, 13F)
Type species: *Porrorhynchus marginatus* Laporte, 1835
Synonyms: *Ceylorhynchus* Brinck, 1955

Diagnosis. Within the tribe Dineutini *Porrorhynchus* can be diagnosed by the following combination of characters: 1) Labrum elongate and triangular in form (Fig. 4E), 2) gular suture incomplete, 3) frons without lateral bead (Fig. 4E), 4) antennal flagellum with 6 – 8 flagellomeres (Fig. 5C), 4) pronotal transverse impressed line absent, 5) scutellar shield invisible with elytra closed, 5) male protrochanter with setose patch (Fig. 7E), 6) male protarsi narrow (Fig. 9D), 7) protibia expanded distolaterally (8B), 8) ventral face of profemur with two rows of setae arranged into large clusters, progressively becoming denser apically, 9) mesotarsal claws weakly sexually dimorphic, 8) metaventrite medially triangular in shape (Fig. 6C) and narrow, 9) female RT with vaginal shield (Fig.11A). Diagnostic characters (5) and (8) appear apomorphic among all Gyrinidae.

Taxonomy. There are now three species within the genus, following removal of the former subgenus *Rhomborhynchus*.

Distribution. Widely distributed in Southeast Asia west of Wallace's line, as far northwest as southeastern Tibet (Jäch *et al.*, 2012) and east through southern China (Fig. 14B). One species, *P. indicans,* known from Sri Lanka (Brinck, 1980).

Discussion. This genus contains the largest known species of whirligig beetle (*P. landaisi*) and species apparently very sensitive to water quality (Ochs, 1927; Brinck, 1980). Among the *Porrorhynchus* species, *P. indicans* is of the most concern in terms of conservation, found to already be uncommonly encountered and limited in distribution in 1980's due to deforestation of preferred habitat montane forests within Sri Lanka (Brinck, 1980). This is especially concerning given the unique information *P. indicans* can potentially provide for future analyses (see Discussion).

Key to the extant genera of the Dineutini

1. Scutellar shield invisible with elytra closed; sexually dimorphic mesotarsal claws (even if weakly so). Female RT with vaginal shield (Fig. 11C, vs). ……………………..………………… 2

—Scutellar shield visible with elytra closed; mesotarsal claws not sexually dimorphic. Female RT without vaginal shield (Fig. 12). …………………………………………………...…………... 4

2. Pronotum without transverse impressed line; ventral face of profemur with two rows of setae arranged in large clusters, becoming denser apically; protrochanter of male with setose patch (Fig. 7E); mesotarsal claws weakly sexually dimorphic ……………….……..……. ***Porrorhynchus***

— Pronotum with transverse impressed line; setae of ventral face of profemur not arranged into large cluster becoming denser apically; protrochanter of male without setose patch, variously modified or not; mesotarsal claws sexually dimorphic, often strongly so. …………..… ***Dineutus***

4. Elytra with striae in the form of well impressed lines; protarsus (male and female) compressed often with fused segments; male protarsus ventrally without discus (Fig. 9F). ……..…. ***Enhydrus***

— Elytra with striae in the form of punctures or weakly impressed lines, never as well impressed lines; protarsus without compressed or fused segments; male protarsus ventrally with discus (Fig. 9 A – C). …………………………..……………………………………………. ***Macrogyrus***

Key to the subgenera of *Dineutus*

1. Labrum elongate and strongly triangular in form; distolateral corner of protibia produced into a spine. …………………………………………………………..………. ***Rhomborhynchus***

— Labrum most often not elongate, strongly rounded, never triangular in form; distolateral corner of protibia not produced into a spine. …………………………………………………… 2

2. Protrochanter of both sexes glabrous (Fig. 7C); species without strongly sexually dimorphic elytra. ……………………………………………………………..... ***Dineutus* sensu stricto**

— Protrochanter of both sexes with setae situated apically on ventral face (Fig. 7D), males of some species with modification (i.e. brushes); many species sexually dimorphic in elytral modification.
………………………………………………………………………………………. ***Cyclous***

Key to the subgenera of *Macrogyrus*

1. Elytra with canaliculate microsculpture presenting themselves as distinct "scratches" (Fig. 10B); if scratches barely present or even absent, then species large (ca. 10 mm), clypeus neither narrow, nor exceptionally large, and without strongly pentagonal medial expanse of the metaventrite (Fig. 10A). ………………..……………….................… ***Macrogyrus* sensu stricto**

— Elytra without canaliculate microsculpture. ……………………………………….... 2

2. Clypeus narrow (Fig. 4D); elytral apices unmodified (i.e. without apicolateral sinuation and/or productions); most species very large (i.e. ≥ 10 mm). Only found in South America. ***Andogyrus***

— Clypeus wide and greatly enlarged (Fig. 4F); elytral apices modified, with apicolateral sinuation and truncate apex. Most species with males having the adhesive setae of the ventral face of the protarsus modified into fewer and larger cups. New Guinea and New Caledonia.
………………………………………………………………………………..… ***Cyclomimus***

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Figure captions

Figure 1. Phylogeny of the Dineutini based on Bayesian total-evidence analysis Part 1. Labels at node denote median age, blue bars indicate 95% hpd for age, and asterisks above node indicates pp of $\geq$0.95.The blue clades indicate members of *Dineutus*, with lighter blue showing the subgenus *Cyclous* **sensu n.** and the dark blue the sensu stricto subgenus. Purple indicates the genus *Porrorhynchus*. Species are approximately to relative scale.

Figure 2. Phylogeny of the Dineutini based on Bayesian total-evidence analysis Part 2. Labels at node denote median age, blue bars indicate 95% hpd for age, and asterisks above node indicates pp of $\geq$0.95.The green clades indicate members of *Macrogyrus*, with the lightest green showing the sensu stricto subgenus, the next darkest members of the subgenus *Cyclomimus*, and the darkest green showing the subgenus *Andogyrus* **stat. n.**. Orange indicates the genus *Enhydrus*. Species are approximately to relative scale.

Figure 3. Historical biogeography of the dineutine whirligig beetles. The Bayesian total-evidence chronogram is plotted as used in the biogeographic analysis. Blue bars indicate 95% hpd for age. The circle at the node shows the preferred ancestral state reconstruction from the BioGeoBears results (Figs. S6 – S9). The following abbreviations are used: DG R, De Geers route; Th R, Thulean route; EECO, Early Eocene Climatic Optimum; DPO, Drake's Passage opening; MECO, Mid-Eocene Climatic Optimum. The map legend just below the tree shows the color key for the ancestral state reconstructed. The paleogeographic maps below © Colorado Plateau Geosystems used with permission, show continental positions in the major time slices (Blakey, 2008).

Figure 4. Head capsules of dineutine species, anterior view, scale bars = 1 mm, abbreviations: lbr = labrum, cly = clypeus, frb = frontolateral bead. (A) *Enhydrus sulcatus*; (B) *Macrogyrus* (*Macrogyrus*) *australis*; (C) *Dineutus* (*Cyclous*) *australis*; (D) *M.* (*Andogyrus*) *seriatopunctatus*; (E) *Porrorhynchus landaisi*; (F) *M.* (*Cyclomimus*) *purpurascens.*

Figure 5. Antennae of dineutine species, above anterior view, below posterior, scale bar = 0.5 mm. (A) *Macrogyrus* (*Macrogyrus*) *australis*; (B) *M.* (*Andogyrus*) *zimmermanni*; (C) *Porrorhynchus landaisi*; (D) *Enhydrus tibialis*;
(E) *Dineutus* (*Cyclous*) *australis*.

Figure 6. Meso- and meta-ventrites of dineutine species and a gyrinine species, ventral view, scale bars = 1 mm, except (F). (A) *Enhydrus sulcatus*: (B) *Macrogyrus* (*Andogyrus*) *colombicus*, (C) *Porrorhynchus marginatus*; (D) *Dineutus* (*Cyclous*) *carolinus*: (E) *Mesodineutes amurensis*†: (F) *Gyrinus maculiventris*, scale bar = 0.5 mm.

Figure 7. Prtrochanters of male dineutine species, ventral view, abbreviations: ts = protrochanteric setae, wx = waxy spot, pt = protrochanteric setose patch. (A) *Dineutus* (*Cyclous*) *australis*, scale bar = 200 µm, pb = protrochanteric brush; (B) *D.* (*Cyclous*) *proximus*, scale bar = 500 µm; (C) *D.* (*Dineutus*) n. sp., scale bar = 300 µm; (D) *D.* (*Cyclous*) *serrulatus analis*, scale bar = 300 µm, (E) *Porrorhynchus marginatus,* scale bar = 400 µm; (F) *Macrogyrus* (*Macrogyrus*) *albertisii,* scale bar = 500 µm.

Figure 8. Prolegs of male dineutine species, abbreviations: sb = setose brush, asr = anterior row of profemoral setae, psr = posterior row of profemoral setae, sp = setigerous puncture. (A) *Macrogyrus* (*Andogyrus*) *zimmermanni* protibial apex, posterior view, scale bar = 400 µm; (B) *Porrorhynchus marginatus* protibia, posterior view, scale bar = 500 µm; (C) *Dineutus* (*Cyclous*) *australis* protrochanter and profemur, ventral view, scale bar = 500 µm; (D) *M.* (*A.*) *zimmermanni* protrochanter and profemur, ventral view, scale bar = 1 mm.

Figure 9. Protarsus of male dineutine species, abbreviations: di = protarsal discus, sb = setose brush. (A) *Macrogyrus* (*Andogyrus*) *zimmermanni,* scale bar = 500 µm; (B) *M.* (*Macrogyrus*) sp., scale bar = 500 µm; (C) *M.* (*M.*) *albertisi*, scale bar = 500 µm; (D) *Porrorhynchus marginatus,* scale bar = 1 mm; (E) *Dineutus* (*Dineutus*) n sp, scale bar = 1 mm; (E) *Enhydrus atratus*, scale bar = 2 mm; (G) *D.* (*Cyclous*) *australis*, scale bar = 500 µm.

Figure 10. Sculpture of *Macrogyrus* (*Macrogyrus*) *albertisi*. (A) metaventrite showing, md = metaventral discrimen, tvs = transverse sulcus, scale bar = 1 mm; (B) elytra with canliculate microsculpture, scale bar = 300 µm; (C) canaliculate microsculpture, scale bar = 40 µm.

Figure 11. Female reproductive tracts, ventral view, abbreviations: sp = spermatheca, fd = fertilization duct, ov = common oviduct, bu = bursa, lt = laterotergite, vs = vaginal shield, mp = medial apodeme of gonocoxa, gc = gonocoxa; scale bars = 1 mm. (A) *Porrorhynchus landaisi;* (B) *Dineutus* (*Dineutus*) *tetracanthus;* (C) *D.* (*Cyclous*) *discolor*; (D) *D.* (*Rhomborhynchus*) *depressus*.

Figure 12. Female reproductive tracts, abbreviations: bg = bursal gland; scale bars = 1 mm. (A) *Macrogyrus* (*Andogyrus*) *seriatopunctatus,* ventral view; (B) gonocoxa of the same; (C) lateral view of the same; (D) *M.* (*Macrogyrus*) *gouldii*, ventral view; (E) gonocoxa of the same; (F) *Enhydrus tibialis*, ventral view; (G) gonocoxa of the same.

Figure 13. Sperm of dineutine species, exhibiting primary conjugation via spermatostyles. (A) *Enhydrus atratus*, scale bar = 300 µm; (B) the same, scale bar = 50 µm; (C) the same with single sperm, scale bar = 20 µm; (D) *Dineutus emarginatus*, scale bar = 50 µm; (E) *Macrogyrus* (*Macrogyrus*) *rivularis,* scale bar = 100 µm; (F) *Porrorhynchus marginatus*, scale bar = 100 µm.

Figure 14. General distribution maps of dineutine genera. (A) *Dineutus*; (B) *Porrorhynchus*); (C) *Enhydrus*; (D) *Macrogyrus*.

Supporting information

Figure S1 Bayesian analysis of mitochondrial genes only (COI, COII, 12S). Using a codon position specific partitioning scheme. Run using the reverse jump technique described in methods section with an invariant gamma distribution and a non-clock model, 16 chains were run, swap number set to 4, temperature set to 0.2. Number at nodes indicates posterior probability.

Figure S2 Bayesian analysis of nuclear genes only (H3, AK). Using same settings as those described in Figure S1. Number at nodes indicates posterior probability.

Figure S3 Bayesian total-evidence calibration analysis results including *Mesodineutes amurensis*. Settings for analysis described in methods. Number at nodes indicate posterior probability.

Figure S4 Bayesian total-evidence calibration analysis results excluding *Mesodineutes amurensis*. Number at nodes indicate posterior probability.

Figure S5 Bayesian total-evidence calibration analysis results including *P.* (*Rhomborhynchus*) *depressus*. Settings for analysis described in methods. Numbers at nodes indicate posterior probability.

Figure S6 Maximum likelihood tree. Analysis settings outlined in methods section. Numbers at nodes indicate boot strap support.

Figure S7 Ancestral state reconstruction results using DEC model. Label at node indicates probable state.

Figure S8 Ancestral state reconstruction results using DEC model. Pie chart at node indicates probable state.

Figure S9 Ancestral state reconstruction results using DEC +j model. Label at node indicates probable state.

Figure S10 Ancestral state reconstruction results using DEC +j model. Pie chart at node shows probable ancestral states.

Figure S11 Ancestral state reconstruction results using DIVALIKE model. Label at node indicates probable state.

Figure S12 Ancestral state reconstruction results using DIVALIKE model. Pie chart at node shows probable ancestral states.

Figure S13 Ancestral state reconstruction results using DIVALIKE +j model. Label at node indicates probable state.

Figure S14 Ancestral state reconstruction results using DIVALIKE +j model. Pie chart at node shows probable ancestral states.

Appendix Description of morphological characters and coding.

Table S1 Taxa included in the phylogenetic and biogeographic analyses of the Dineutini. Gene coverage for molecular character dataset is indicated for each taxon as is geographical coding used for the biogeographic analysis.

Table S2. Character coding for morphological dataset.

Table S3. Primers used for amplification and sequencing.

Table S4 Statistical comparison of the DEC, DEC +j, DIVALIKE, and DIVALIKE +j model fit.

References

Baccetti, B. (1987) News on phylogenetical and taxonomical spermatology. *New Horizons in Sperm Cell Research*, (ed. by H. Mohri), 333–348. Gordon and Breach Scientific Publishing, New York.

Baldwin, S. L., Fitzgerald, P. G. & Webb, L. E. (2012) Tectonics of the New Guinea region. *Annual Review of Earth and Planetary Sciences*, **40**, 495-520. 10.1146/annurev-earth-040809-152540.

Balfour-Browne, J. & Brinck, P. (1961) *Enhdrus* Castelnau, 1834 (Insecta, Coleoptera): proposed validation under the plenary powers. *The Bulletin of Zoological Nomenclature*, **18**, 137 – 139.

Beutel, R. G. (1990) Phylogenetic analysis of the family Gyrinidae (Coleoptera) based on mesothoracic and metathoracic characters. *Quaestiones Entomologicae*, **26**, 163-192.

Bijl, P. K., Bendle, J. A. P., Bohaty, S. M., Pross, J., Schouten, S., Tauxe, L., Stickley, C. E., McKay, R. M., Röhl, U., Olney, M., Sluijs, A., Escutia, C., Brinkhuis, H. & Expedition 318

Scientists (2013) Eocene cooling linked to early flow across the Tasmanian Gateway. *Proceedings of the National Academy of Sciences*, **110**, 9645-9650. 10.1073/pnas.1220872110.

Blakey, R. C. (2008) Gondwana paleogeography from assembly to breakup— A 500 m.y. odyssey. *The Geological Society of America*, **Special Paper 441**, 1 - 28

Bouchard, P., Bousquet, Y., Davies, A. E., Alonso-Zarazaga, M. A., Lawrence, J. F., Lyal, C. H. C., Newton, A. F., Reid, C. A. M., Schmitt, M., Ślipiński, S. A. & Smith, A. B. T. (2011) Family-group names in Coleoptera (Insecta). *Zookeys*, **88**, 1 – 972.

Breland, O. P. & Simmons, E. (1970) Preliminary studies of the spermatozoa and the male reproductive system of some whirligig beetles (Coleoptera: Gyrinidae). *Entomological News*, **81**, 101–110.

Brikiatis, L. (2014) The De Geer, Thulean and Beringia routes: key concepts for understanding early Cenozoic biogeography. *Journal of Biogeography*, **2014**, 1036-1054. 10.1111/jbi.12310.

Brinck, P. (1955a) A monograph of the whirligig beetles of southern Africa. *South African Animal Life,* 1 (ed. by B. Hanström, P. Brink and G. Rudebeck), 329 – 518. Almqvist Wiksel, Stockholm.

Brinck, P. (1955b) A revision of the Gyrinidae (Coleoptera) of the Ethiopian region. I. *Acta Universitatis Lundensis. Nova Series*, **51**, 1 – 144.

Brinck, P. (1956) A revision of the Gyrinidae (Coleoptera) of the Ethiopian region. II. *Acta Universitatis Lundensis. Nova Series*, **52**, 1 – 190.

Brinck, P. (1976) The Gyrinidae of the Bismarck Archipalago and the Solomon Islands (Coleoptera: Gyrinidae). *Entomologica Scandinavica*, **7**, 81-90.

Brinck, P. (1977) Evolution and taxonomy of *Andogyrus* Ochs (Coleoptera: Gyrinidae). *Entomologica Scandinavica*, **8**, 241-270.

Brinck, P. (1978) Derivation, taxonomy and history of distribution of whirligig beetle genus *Enhydrus* (Coleoptera - Gyrinidae). *Entomologica Germanica*, **4**, 317 – 326.

Brinck, P. (1980) *Porrorhynchus indicans* Walker (Coleoptera: Gyrinidae). A representative of the relict montane forest ecosystem in Sri Lanka. . *P.E.P. Deraniyagala Commemoration Volume (Sri Lanka 1980)*, 103-108.

Brinck, P. (1981) *Spinosodineutes* (Coleoptera: Gyrinidae) in New Guinea and adjacent islands. *Entomologica Scandinavica Supplement*, **15**, 353-364.

Brinck, P. (1983) A revision of *Rhombodineutus* Ochs in New Guinea (Coleoptera: Gyrinidae). *Entomologica Scandinavica*, **14**, 205-233.

Brinck, P. (1984) Evolutionary trends and specific differentiation in *Merodineutus* (Coleoptera: Gyrinidae). *International Journal of Entomology*, **26**, 175-189.

Desmarest, E. (1851) *Coléoptères. Cicindélètes, carabiques, dytisciens, hydrophiliens, sylphaes et nitidulaires. Encyclopédie d'histoire naturelle ou traité complet de cette science d'après les travaux des naturalistes le plus éminents de tous les pays et de toutes les époques Buffon, Daubenton, Lacépède, G Cuvier, F Cuvier, Geoffroy Saint-Hilarie, Latreille, de Jussieu, Brongniart, etc, etc, Ouvrage résumant les observations de auteurs anciens et comprenant toutes les découvertes modernes jusqu'à nos jours.*, [2] + 312 pp. 28 pls. Marescq & Compagnie, Paris.

Dissanayake, C. B. & Chandrajith, R. (1999) Sri Lanka—Madagascar Gondwana Linkage: Evidence for a Pan-African Mineral Belt. *The Journal of Geology*, **107**, 223-235.

Eberle, J. & Greenwood, D. R. (2011) Life at the top of the greenhouse Eocene world— A review of the Eocene flora and vertebrate fauna from Canada's High Arctic. *Geological Society of America Bulletin*, **124**, 3 - 23. 10.1130/B30571.1.

Edgar, R. C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acid Research*, **32**, 1792-1797.

EMBL-EBI (2015) *Multiple Sequence Alignment*. http://www.ebi.ac.uk/Tools/msa/muscle/ [accessed on,

Gene Codes (1999) *Sequencher ® Version 4.8 Sequence Analysis Software*. http://www.genecodes.com

Guignot, F. (1950) Sur la systematique des *Dineutus* (Col. Gyrinidae). *Bulletin Mensuel de la Société Linnéenne de Lyon*, **19**, 124 – 127.

Guignot, F. (1954) Quarantième note sur les Hydrocanthares. *Bulletin et annales de la Société entomologique de Belgique*, **90**, 40 – 45.

Gustafson, G. T. & Miller, K. B. (2013) On the family- and genus-series nomina in Gyrinidae Latreille, 1810 (Coleoptera, Adephaga). *Zootaxa*, **3731**, 077 – 105. http://dx.doi.org/10.11646/zootaxa.3731.1.3.

Gustafson, G. T. & Miller, K. B. (2015) The New World whirligig beetles of the genus *Dineutus* Macleay, 1825 (Coleoptera, Gyrinidae, Gyrininae, Dineutini). *Zookeys*, **476**, 1 - 135. 10.3897/zookeys.476.8630.

Gustafson, G. T. & Sites, R. W. (2016) A North American biodiversity hotspots gets richer: A new species of whirligig beetle (Coleoptera: Gyrinidae) from the Southeastern Coastal Plain of the United States. *Annals of the Entomological Society of America*, **109**, 42 - 48. 10.1093/aesa/sav100.

Hájek, J. (2011) Order Coleoptera, Family Gyrinidae. *The Arthropod fauna of the United Arab Emirates*, **4**, 123-125.

Hall, R. (2001) Cenozoic reconstructions of SE Asia and the SW Pacific: Changing patterns of land and sea. *Faunal and Floral Migrations and Evolution in SE Asia-Australasia*, (ed. by I. Metcalfe, J. M. B. Smith, M. Morwood and I. D. Davidson), 35-56. Swets and Zeitlinger, Lisse.

Hall, R. (2002) Cenozoic gelogical and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Eartch Sciences*, **20**,

Hall, R. (2013) The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *Journal of Limnology*, **72**, 1-17. 10.408/jlimnol.2013.s2.el.

Hatch, M. H. (1925) The phylogeny and phylogenetic tendencies of Gyrinidae. *Papers of the Michigan Academy of Science, Arts and Letters*, **V**, 429 – 467.

Heath, T. A., Huelsenbeck, J. P. & Stadler, T. (2014) The fossilized birth-death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences*, 10.1073/pnas.1319091111E2957-E2966. 10.1073/pnas.1319091111.

Hennig, W. (1966) *Phylogenetic Systematics*, University of Illinois Press, Urbana, IL.

Higginson, D. M. & Pitnick, S. (2011) Evolution of intra-ejaculate sperm interactions: do sperm cooperate? *Biological Reviews*, **86**, 249–270.

Huelsenbeck, J. P., Larget, B. & Alfaro, M. E. (2004) Bayesian phylogenetic model selection using reversible jump Markov Chain Monte Carlo. *Molecular Biology and Evolution*, **21**, 1123-1133.

ICZN (2012) Opinion 2297 (Case 3514). Enhydrini Régimbart, 1882 (Insecta, Coleoptera): spelling emended to Enhydrusini to remove homonymy with Enhydrini Gray, 1825 (Mammalia, Mustelidae). *Bulletin of Zoological Nomenclature*, **69**, 145 - 146.

Iturralde-Vinent, M. A. (2006) Meso-Cenozoic Caribbean Paleogeography: Implications for the historical biogeography of the region. *International Geology Review*, **48**, 791-827. 10.2747/0020-6814.48.9.791.

Jäch, M., Li, J., Zhang, X. & Gao, M. (2012) A remarkable collection of aquatic and riparian beetles from Xiachayu, Zayü County, southeastern Tibet (Coleoptera: Gyrinidae, Noteridae, Dytiscidae, Spercheidae, Hydrophilidae, Heteroceridae, Limnichidae). *Koleopterologische Rundschau*, **82**, 65-69.

Jamieson, B.G.M. (1987) A biological classification of sperm types, with special reference to annelids and mollusks, and an example of spermiocladistics. *New Horizons in Sperm Cell Research* (ed. by H. Mohri), 311-332. Gordon and Breach Scientific Publishing, New York.

Kück, P., Mayer, C., Wägele, J.-W. & Misof, B. (2012) Long branch effects distort Maximum Likelihood phylogenies in simulations despite selection of the correct model. *PLoS ONE*, **7**, e36593. 10.1371/journal.pone.0036593.

Laporte, F. L. d. (1834 - 1835) *Études entomologiques, ou description d'insectes nouveaux et observations sur leur synonymie. Par F. L. de Laporte Comte de Castelnau. Coléoptères. Première partie. Carnassiers.*, 1 - 94, 1834; 95 - 159, 1835 Méquignon-Marvis Père et Fils, Paris.

Lawver, L. A. & Gahagan, L. M. (2003) Evolution of Cenozoic seaways in the circum-Antarctic region. *Paleogeography, Paleoclimatology, Paleoecology*, **198**, 11-37. 10.1016/S0031-0182(03)00392-4.

Lawver, L. A., Gahagan, L. M. & Dalziel, I. W. D. (2011) A different look at gateways: Drake Passage and Australia/Antarctica. *Tectonic, Climatic, and Cryospheric Evolution of the Antarctic Peninsula*, (ed. by J. B. Anderson and J. S. Wellner), 5-33. AGU, Washington, D.C.

Lee, D.-H. & Ahn, K.-J. (2015) A taxonomic review of the Gyrinidae (Coleoptera) in Korea. *Zookeys*, **509**, 87-107. 10.3897/zookeys.509.9442.

Livermore, R., Nankivell, A., Eagles, G. & Morris, P. (2005) Paleogene opening of Drake Passage. *Earth and Planetary Science Letters*, **236**, 459-470. 10.1016/j.epsl.2005.03.027.

Macleay, W. S. (1825) *Annulosa javanica, or an attempt to illustrate the natural affinities and analogies of the insects collected in Java by Thomas Horsfield and deposited by him in the Museum of the Honourable East-India Company.*, xii + 150pp. Kingsbury, Parbury and Allen, London.

Maddison, D. R. & Maddison, W. P. (2005) *MacClade 4: Analysis of phylogeny and character evolution.* http://macclade.org

Maddison, W. P. & Maddison, D. R. (2015) Mesquite: a modular system for evolutionary analysis. Version 3.04. http://mesquiteproject.org.

Matzke, N. J. (2013a) *BioGeoBears: BioGeography with Bayesian (and Likelihood) Evolutionary Analysis in R Scripts. R package, version 0.2.1*. http://CRAN.R-project.org/package=BioGeoBEARS

Matzke, N. J. (2013b) Probabilistic historical biogeography: new models for founder-even speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Frontiers of Biogeography*, **5**, 242-248.

Matzke, N. J. (2014) Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology*, **63**, 951-970. 10.1093/sysbio/syu056.

Mazzoldi, P. (1995) Gyrinidae: Catalogue of Chinese Gyrinidae (Coleoptera), pp. 155-172. In M. A. Jäch and L. Ji, eds. Waterbeetles of China. *Zoologisch-Botanische Gesellschaft, Vienna.*,

Mazzoldi, P. (2010) Gyrinidae (Coleoptera). *Water beetles of New Caledonia Part 1*, (ed. by M. Jäch and M. Balke), 31—43. Zoologisch-Botanische Gesellschaft, Section of Entomology, Vienna.

Miller, K. B. & Bergsten, J. (2012) Phylogeny and classficiation of whirligig beetles (Coleoptera: Gyrinidae): relaxed-clock model outperforms parsimony and time-free Bayesian analyses. *Systematic Entomology*, **37**, 705 – 746.

Miller, K. B., Bergsten, J. & Whiting, M. F. (2009) Phylogeny and classification of the tribe Hydaticini (Coleoptera: Dytiscidae): partition choice for Bayesian analysis with multiple nuclear and mitochondrial protein-coding genes. *Zoologica Scripta*, **38**, 591-615.

Mirarab, S., Reaz, R., Bayzid, M. S., Zimmermann, T., Swenson, M. S. & Warnow, T. (2014) ASTRAL: Genome-scale colescent-based species tree estimation. *Bioinformatics*, **30**, i541-i548. 10.1093/bioinformatics/btu462.

Mirarab, S. & Warnow, T. (2015) ASTRAL-II: coleasecent-based species tree estimation with many hundreds of taxa and thousands of genes. *Bioinformatics*, **31**, i44-i52. 10.1093/bioinformatics/btv234.

Mouchamps, R. (1949a) Contribution a la systématique des Coléoptères Gyrinides I. *Dineutus* (*Spinosodineutes*) Hatch. *Bulletin et annales de la Société entomologique de Belgique*, **85**, 216 - 264.

Mouchamps, R. (1949b) Notes sur quelques *Dineutus* M.L. (Coléoptères Gyrinides) interessants du British Museum (Londres). *The Annals and Magazine of Natural History*, **12**, 660 - 679.

Mouchamps, R. (1951) Contribution a la systématique des Coléoptères Gyrinides (4e note). *Bulletin et annales de la Société entomologique de Belgique*, **87**, 229 - 234.

Ochs, G. (1924) Über neue und interessante Gyriniden aus dem British Museum in London. . *Entomologische Blätter*, **20**, 228 – 244.

Ochs, G. (1926) Die Dineutini. 2. Tribus der Unterfamilien Enhydrinae Fam. Gyrinidae (Col). A. Aligemeiner Teil. *Entomologische Zeitschrift*, **40**, (3/4): 61 – 74; (5): 112 – 126; (6): 129 – 140; (8): 190 – 197.

Ochs, G. (1927) XII. Papers on Malayan aquatic biology. iv. On the Gyrinidae of the Malay Peninsula. *Journal of the Federated Malay States Museums*, **13**, 242 – 245.

Ochs, G. (1930) Über einige neue und bemerkenswerte Gyriniden, vorzüglich aus dem Dresdener Museum. *Entomologische Blätter*, **26**, 14 – 18.

Ochs, G. (1949) A revision of the Australian Gyrinidae. *Records of the Australian Museum*, **22**, 171 – 199.

Ochs, G. (1953) Die Sunda-Gyriniden des Museum Zoologicum Bogoriense (Col., Gyrinidae). *Treubia*, **22**, 217 – 223.

Ochs, G. (1954) Die Gyriniden Perus un der übrigen südamerikanischen Kordilleren. *Beiträge zur Fauna Perus nach der Ausbeute der Hamburger Südperu-Expedition 1936, anderer Sammlungen, wie auch auf Grund von Literaturangaben*, **4**, 116 – 155.

Ochs, G. (1955) Die Gyriniden-fauna von Neuguinea nach dem derzeitigen stand userer kenntnisse (Coleoptera, Gyrinidae). *Nova Guinea*, **6**, 87 – 154.

Ochs, G. (1956) Additional remarks on Australian Gyrinidae. *Records of the Australian Museum*, **24**, 31-35.

Pitnick, S., Hosken, D. J. & Birkhead, T. R. (2009) Sperm morphological diversity. *Sperm Biology: An Evolutionary Perspective*, (ed. by T. R. Birkhead, D. J. Hosken and S. Pitnick), 69–149. Academy Press, San Diego, CA.

Ponomarenko, A. G. (1977) [Mesozoic Coleoptera. Description of new taxa]. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, **161**, 17-96.

Posada, D. (2008) jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, **25**, 1253-1256. 10.1093/molbev/msn083.

Pross, J., Contreras, L., Bijl, P. K., Greenwood, D. R., Bohaty, S. M., Schouten, S., Bendle, A., Röhl, U., Tauxe, L., Raine, J. I., Huck, C. E., van de Flierdt, T., Jamieson, S. S. R., Stickley, C. E., van de Schootbrugge, B., Escutia, C., Brinkhuis, H. & Integrated Ocean Drilling Program Expedition 318 Scients (2012) Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch. *Nature*, **488**, 73-77. 10.1038/nature11300.

Rambaut, A., Suchard, M. & Drummon, A. (2013) *Tracer v1.6*. http://tree.bio.ed.ac.uk/software/tracer/ [accessed on Nov. 10, 2015]

Ree, R. H., Moore, B. R., Webb, C. O. & Donoghue, M. J. (2005) A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution*, **59**, 2299-2311.

Ree, R. H. & Smith, S. A. (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogensis. *Systematic Biology*, **57**, 4-14.

Régimbart, M. (1882) Essai monographique de la famille des Gyrinidae. 1e partie. *Annales de la Société entomologique de France*, **(6)** 379 – 458 + 3 pls.

Régimbart, M. (1886) Essai monographique de la famille des Gyrinidae (1er supplément). *Annales de la Société Entomologique de France*, **6**, 247–272.

Régimbart, M. (1892) Essai monographique de la famille des Gyrinidae. 2e Supplément. *Annales de la Société Entomologique de France*, **60**, 663 – 752.

Régimbart, M. (1907) Essai monographique de la famille des Gyrinidae. 3e supplément. *Annales de la Société entomologique de France*, **76**, 137 – 245.

Reguero, M. A., Gelfo, J. N., López, G. M., Bond, M., Abello, A., Santillana, S. N. & Marenssi, S. A. (2014) Final Gondwana breakup: The Paleogene South American native ungulates and the demise of the South America-Antarctica land connection. *Global and Planetary Change*, **123**, 400-413. 10.1016/j.gloplacha.2014.07.016.

Ronquist, F. (1997) Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, **46**, 195-203.

Ronquist, F., Klopfstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D. L. & Rasnitsyn, A. P. (2012) A total-evidence approach to dating with fossils, applied to the early radiation of Hymenoptera. *Systematic Biology*, **61**, 973-999.

Ronquist, F., Teslenko, M., Mark, P. & al., e. (2011) MrBayes version 3.2: efficient Bayesian phylogenetic inference and model choice, across a large model space. *Systematic Biology*, **61**, 539-542. http://mrbayes.sourceforge.net/index.php.

Satô, M. (1962) The gyrinid-beetles from Toku-no-shima of the Ryukyu Islands. *Konchugaku hyoron*, **14**, 23 - 25 + pl. 5.

Seo, K-T (2008) Calculating bootstrap probabilities using multilocus sequence data. *Molecular Biology and Evolution*, **25**, 960-971.

Stamatakis, A. (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, **30**, 1312-1313. 10.1093/bioinformatics/btu033.

Storey, B. C. (1995) The role of mantle plumes in continental breakup: case histories from Gondwanaland. *Nature*, **377**, 301-308.

Toussaint, E. F. A., Hall, R., Monaghan, M. T., Sagata, K., Ibalim, S., Shaverdo, H. V., Vogler, A. P., Pons, J. & Balke, M. (2014) The towering orogeny of New Guinea as a trigger for arthropod megadiversity. *Nature Communications*, **5**, 4001. 10.1038/ncomms5001.

Toussaint, E. F. A., Hendrich, L., Hájek, J., Michat, M., Panjaitan, R., Short, A. E. Z. & Balke, M. (2016) Evolution of Pacific Rim diving beetles sheds light on Amphi-Pacific biogeography. *Ecography*, 10.1111/ecog.0219510.1111/ecog.02195.

van Ufford, A. Q. & Cloos, M. (2005) Cenozoic tectonics of New Guinea. *American Association of Petroleum Geologists*, **89**, 119-140. 10.1306/08300403073.

Zhang, C., Stadler, T., Klopfstein, S., Heath, T. A. & Ronquist, F. (2015) Total-evidence dating under the fossilized birth-death process. *Systematic Biology*, **00**, 1-22. 10.1093/sysbio/syv080.

Appendix

Morphological characters

Head

1. Maxillary galea. (0) absent; (1) present, one segmented; (2) present, two segmented. The maxillary galea is completely absent in members of the Dineutini and Orectochilini. The Gyrinini have a maxillary galea with a single segment and the Heterogyrinae have a two segmented maxillary galea. This character is treated as ordered in the analyses.
2. Number of antennomeres in scape. (0) nine segments; (1) eight segments; (2) seven segments; (3) six segments. Nine segments are present in the scape of *Heterogyrus*, gyrinine species, *Orectochilus*, and all *Macrogyrus* species. Eight segments are unique to *Porrorhynchus landaisi*. Seven segments are present in the *Enhydrus* species. Six segments are present in *Porrorhynchus marginatus*, nearly all the *Dineutus*, and all *Patrus* and *Orectogyrus* species. This character is treated as ordered in the analyses.
3. Ratio of the frontolateral margin to the width of the clypeus at mid-length. (0) nearly equal or less than one; (1) frontolateral margin at least 1.5 times the longer than the medial clypeal width. The frontolateral margin appears elongate in *Heterogyrus*, in many orectochilines, in *Porrorhynchus*, some *Dineutus* and most *Macrogyrus*. A reduction of the frons length

is seen in the gyrinines and *Dineutus*. Several *Macrogyrus* species in the subgenus *Cyclomimus* have a greatly enlarged clypeus (Fig. 4F) but not an apparent reduction in the frontolateral margin.

4. Lateral margin of frons with a well developed bead. (0) absent; (1) present. Within the dineutines the bead is absent in *Porrorhynchus* and *Dineutus*. A strong frontal bead is present in *Macrogyrus* and *Enhydrus* (Fig. 4A, 4B, 4D, 4F). This character is also present in *Heterogyrus* and the gyrinines. This character cannot be scored for the orectochilines as the lateral margin of the frons is modified into the pseudofrontal ridge (Hatch, 1925).
5. Labral shape. (0) transverse; (1) elongate. A transverse labrum is very common within the Gyrinidae and in these analyses a labrum is coded as being transverse if it is less than half as long as wide. Most species of Gyrinidae have a transverse labrum. An elongate labrum is defined as being at least half as long as wide. An elongate labrum (Fig. 4E) is present in *Orectochilus*, *Orectogyrus*, *Porrorhynchus*, and the *Dineutus* subgenus *Rhomborhynchus*.
6. Labral basoventral setation. (0) composed of two transverse rows of setae; (1) composed of one transverse and one longitudinal paired row. This character helps separate the *Dineutus* subgenus *Rhomborhycnhus* from *Porrorhynchus* and the remaining *Dineutus*.
7. Gular suture. (0) complete, reaching anterior margin; (1) incomplete, effaced prior to anterior margin. An incomplete gular suture unites the species of *Porrorhynchus*.
8. Clypealium setation. (0) mostly glabrous, only a few sparse setae present basally; (1) strongly setose. The clypealium of gyrinines is mostly glabrous with only setae present basally. The dineutines and orectochilines have a strongly setose clypealium, often with a row of dense long setae medially. *Heterogyrus* has a setose clypealium, much more setose than the gyrinines, but not as well developed as that of the dineutines and the orectochilines.

Prothorax

9. Pronotal transverse impressed line. (0) absent; (1) present. The pronotal transverse impressed line (Oygur and Wolfe, 1991) is absent in members of *Porrorhynchus* and *Orectochilus*. It is present in all other gyrinid species studied.
10. Prosternal process. (0) not well differentiated; (1) well differentiated and strongly elevated from the remained of the prosternum. In *Macrogyrus* and *Enhydrus* the medium portion of the prosternum is not well differentiated into a prosternal process, the posterior margin remains in nearly the same plane as the rest of the prosternum. In *Dineutus* and *Porrorhynchus* the prosternum is medially elevated and well differentiated into a distinct often bullet-shaped prosternal process. A similar prosternal process is found in the gyrinines. *Heterogyrus* and the orectochilines have a different sternum shape that is more cushion like, not comparable to the well differentiated prosternal process discussed previously.
11. Prosternal anteromedial sulcus. (0) absent; (1) present. There is a anteromedial sulcus present on the prosternum in *Enhydrus* and some *Macrogyrus* that is absent in *Dineutus* and *Porrorhynchus*.

Foreleg

12. Protrochanteric ventral face setation. (0) absent, completely glabrous; (1) present, a short series of short stout setae present apically. These setae are absent in the gyrinines, *Heterogyrus*, *Orectochilus*, *Porrorhynchus* and the *Dineutus* s. str. subgenus. These setae are present in *Orectogyrus*, in most of the *Dineutus*, and present in *Macrogyrus* only in *M.* (*Andogyrus*) *seriatopunctatus*. The setae are often most easily seen in females of the species.
13. Protrochanteric setose patch. (0) absent; (1) present. The protrochanteric setose patch (Fig. 7E, pt) is present in species of *Porrorhynchus*.
14. Protrochanteric setose brush. (0) absent; (1) present. The protrochanteric setose brush (Fig. 7A, pb) is unique to *Dineutus australis*.
15. Profemoral sub-apicoventral tooth/teeth. (0) absent; (1) present. These teeth are unique to the males of certain species of *Dineutus* (Gustafson & Miller, 2015). They are present subapically on the ventral margin of the profemur. As many as two teeth may be present on both the anterior and posterior margins, but many species have only a single tooth present on either margin. Two teeth is a common state for many of the *Dineutus* s. str. subgenus and the African species of *Dineutus.*
16. Profemoral sub-apicoventral tooth on anterior margin. (0) absent; (1) present. This feature unites *Dineutus fairmairei* and *D. pagdeni*. It is also present in *D. ritsemai* suggesting this species may also be closely related to the aforementioned two.
17. Profemoral sub-apicoventral tooth on posterior margin. (0) absent; (1) present. This character is present in most of the North American *Dineutus* species.
18. Setigerous punctures of the anterior face of the profemur. (0) absent; (1) present. A series of setigerous punctures are present on the anterior face of the profemur medially (Fig. 8C – D, sp). These punctures are absent in members of *Porrorhynchus* and *Enhydrus* but present in all other species examined.
19. Lines of setae of ventral face of profemur. (0) absent; (1) one present on posterior margin (Fig. 8C – D, psr); (2) two present on both posterior and anterior margin (Fig. 8 C – D, psr, asr). Within the Gyrininae at least one line of setae is present on the posterior margin. Two are present in all *Porrorhynchus* and most *Dineutus.*
20. Setation of ventral face of profemur. (0) without setation composed of large clumps of setae becoming denser distally; (1) with setation composed of large clumps of setae become denser distally. Profemoral setation composed of two series of large clumps of setae becoming denser distally are present in species of *Porrorhynchus*.
21. Setose brush of posterior face of protibia. (0) present, not noticeably reduced (Fig. 8B, sb); (1) present but strongly reduced (Fig. 8A, sb); (2) absent indistinguishable from apical setae. A protibial brush is present and not reduced in *Heterogyrus*, *Orectogyrus*, *Porrorhynchus*, and *Dineutus*. It is absent in *Enhydrus*, the gyrinines, *Orectochilus*, *Patrus*, and some *Macrogyrus*. The strongly reduced state (Fig. 8A, sb) is seen most often in *Macrogyrus* species. This character is most variable in *Macrogyrus*. This character is treated as ordered in the analyses.
22. Protibia apically. (0) not laterally expanded (Fig. 9G); (1) expanded laterally (Fig. 8A – B). The protibia of *Enhydrus*, *Macrogyrus*, *Porrorhynchus, Orectogyrus*, and *Patrus* is laterally expanded. The protibia is not laterally expanded in all *Dineutus*, the gyrinines, *Orectochilus*, and *Heterogyrus*.
23. Adhesive setose palette of posterior face of male protarsus. (0) completely covered in adhesive setae; (1) adhesive setae reduced to half palette along outer margin. Nearly all

gyrinids have a complete setose palette, the reduced half palette condition (Fig. 9C) was only observed in three species studied. A half palette is present in *D. pagdeni* and *D. fairmairei* uniting this two species. A convergent condition is exhibited in *Macrogyrus albertisii*.

24. Male protarsomere I with recessed pit possessing differently sized adhesive setae. (0) absent; (1) present. The "discus" of Régimbart (1882) (Fig. 9A – C, di), is present in all species of *Macrogyrus*, absent in all other gyrinid species (Fig. 9 D – G).
25. Posterior face of female protarsomere V with setae. (0) present in well developed furrow; (1) present but without furrow; (2) absent or reduced to a small patch. A well developed furrow is present in *Porrorhynchus*, and some *Dineutus*. The large majority of species studied have setae present without a furrow, or largely reduced to absent. This character is ordered in the analyses.

Metaventrite I

26. Metanepisternum overall shape. (0) not lobiform; (1) lobiform. The metanepisternum of the dineutines and heterogyrines is lobiform (Fig. 6 A – D). The metanepisternum of the orectochilines is neither lobiform nor strongly triangular.
27. Metanepisternum overall shape. (0) not triangular; (1) triangular. The metanepisternum of the gyrinines is strongly triangular (Fig. 6F).

Mesoventrite

28. Scutellar shield. (0) not visible when elytra closed; (1) visible when elytra closed. Among the species studied only members of *Dineutus* and *Patrus* had the scutellar shield not visible when the elytra rae closed.
29. Elytral setation. (0) absent; (1) present. The elytra has fields of setae in *Heterogyrus* and the orectochlines. The gyrinines and dineutines completely lack setae on the elytra.
30. Elytral serial striae. (0) none evident; (1) 11 striae evident; (2) 9 striae evident. The orectochilines exhibit no serial striae, while gyrinines have 11, and 9 striae are present in heterogyrines and dineutines.
31. Elytral strial appearance. (0) punctures; (1) well impressed lines; (2) weakly impressed lines. The elytral striae appear as punctures in the gyrinines, as well as in *M.* (*Andogyrus*) *seriatopunctatus* and the fossil *Meiodineutes amurensis*, suggesting that dineutines ancestrally possessed punctate elytral striae. Strongly impressed lines are evident in *Heterogyrus* and *Enhydrus*. Weakly impressed lines are present primarily in *Dineutus* and *Macrogyrus*. This character is treated as ordered as several gyrinine species exhibit intermediate stages between punctate to strongly impressed lines, suggesting a trend from punctures to strongly impressed lines, with weakly impressed lines as a step towards loss of impressed lines and elytral striae in general.
32. Elytral sutural border. (0) absent; (1) present. The elytra in many species of whirligigs is bordered (Brinck, 1955b), at least apically. A sutural border to the elytral is present in *Heterogyrus*, many orectochilines, and gyrinines. It is absent in the dineutines.

33. Elytral apex modification. (0) absent; (1) present. Unmodified elytra are attenuated toward the apex, where the apex is regularly rounded. Most gyrinid species exhibit some sort of elytral modification. Unmodified elytra are mostly found in *Dineutus* and *Gyrinus*.
34. Elytral apex with sutural production. (0) absent; (1) present. The sutural angle of the elytra is produced in many North American *Dineutus* (Gustafson and Miller, 2015), the majority of *Macrogyrus* species, and all *Porrorhynchus*.
35. Elytral apex with parasutural production. (0) absent; (1) present. The elytra of many dineutines has a production between the sutural and epipleural angles.
36. Elytral apex with epipleural production. (0) absent; (1) present. The epipleural angle has a production in most *Macrogyrus*, many orectochilines, and *Porrorhynchus*. This angle is not producted in *Dineutus*, *Enhydrus*, and the gyrinines.
37. Elytral apices truncate. (0) absent; (1) present. The elytral apices are truncate in the orectochilines, some *Macrogyrus*, and only two *Dineutus*.
38. Elytral apices with serration and irregularities. (0) absent; (1) present. The elytral apices may have serration and irregularities (Gustafson and Miller, 2015). This character is most commonly present in the North American and African *Dineutus*. It is absent in most other species studied.
39. Elytral apicolateral margins with strongly developed buzz-saw shaped serration. (0) absent; (1) present. This serration is most evident in members of *Porrorhynchus*. One *Dineutus* species also presents this serration, *Dineutus micans*, but it is variously developed among the different subspecies (Brinck, 1955a).
40. Elytral postscutellar pits. (0) absent; (1) present. A pair of postscutellar pits are present in the males of species of the former subgenus *Rhombodineutus* (Brinck, 1983).
41. Elytra with canalicuate micorsculpture. (0) absent; (1) present. Canaliculated microsculpture (Fig. 10B – C) is present in the *Macrogyrus* s. str. subgenus, creating a “scratch-like” appearance on the elytra under the dissecting scope. This microsculpture is present only in the *Macrogyrus* s. str. subgenus with some *Macrogyrus* species like *M. sumbawae* exhibiting very strong reduction.

Mid-leg

42. Male mesotarsal claw sexual dimorphism. (0) absent; (1) present but weakly developed; (2) present strongly developed. The male mesotarsal claws of *Dineutus* species are strongly sexually dimorphic (Gustafson and Miller, 2015). The claws of *Porrorhynchus* are also sexually dimorphic but more weakly so, compared to those of *Dineutus*. No other gyrinid species studied have sexually dimorphic mesotarsal claws. This character is treated as ordered

Metaventrite II

43. Lateral wings of metaventrite strap-like. (0) not strap-like in form; (1) strap-like in form. The gyrinines have a narrow and strap-like metaventral wing (Fig. 6F), a similarly formed metaventral wing is exhibited in many orectochilines.

44. Lateral wings of metaventrite triangular in form. (0) not triangular in form; (1) triangular in form. The dineutines exhibit a strongly triangular lateral wing of the metaventrite (Fig. 6A – E), this character is also shared with the heterogyrines.

45. Discrimen of metaventrite with transverse suture. (0) absent; (1) present. The discrimen of the metaventrite has a transverse suture (Fig. 10A, tvs) in some Gyrinidae (Beutel and Roughley, 1988; Beutel, 1990; Miller and Bergsten, 2012). This character was thought to only be present in *Spanglerogyrus* and *Heterogyrus* however it is here also found in some members of *Macrogyrus* (Fig. 10A).

Hind-leg

46. Anterior margin of lateral wings of metacoxal plate. (0) running more obliquely; (1) running more transversely. The anterior margin of the metacoxal plate is much more oblique (Hatch, 1925) in the dineutines and some *Patrus* species. In most other gyrinid species the anterior margin of the metacoxal plate is much more obliquely situated.

47. Posterolateral margin of metacoxal plate. (0) without border; (1) bordered. The posterolateral margin of the metacoxal plate exhibits a thick border (Fig. 6B) in species of orectochilines, gyrinines and *Macrogyrus* species. This border is absent (Fig. 6A, 6C, 6D – E) in *Enhydrus*, *Dineutus*, *Porrorhynchus*, and heterogyrines.

Abdomen

48. Suture of abdominal sternite II. (0) absent; (1) present. Abdominal sternite II still exhibits a suture in species of *Enhydrus* (Hatch, 1926; Brinck, 1978), this suture is effaced in all other species studied for the analysis.

49. Overall shape of abdomen. (0) not-cylindrical, broadly rounded; (1) strongly cylindrical. The abdomen of orectochilines is strongly constricted and cylindrical in shape. All other gyrinid species have an overall rounded appearance to the abdomen.
50. Abdominal sternites VII & VIII with linear series of setae. (0) absent; (1) present. The orectochiline in addition to the constricted cylindrical shape of the abdominal have a linear series of setae postermedially on abdominal sternites VII & VIII for a sort of "rudder". These setae are not present in any other species studied.
51. Venter coloration. (0) darkly colored; (1) lightly colored. The venter of many species is darkly colored, dark reddish brown to black. Other species have light red to yellowish white.

Female reproductive tract

52. Spermathecal form. (0) not elongate and sac-like; (1) greatly elongate and sac-like in form. The spermatheca of dineutines and species of *Orectochilus* and *Orectogyrus* are greatly elongate and sac-like in form (Miller and Bergsten, 2012). Those of *Patrus*, gyrinines, and *Heterogyrus* are not greatly elongate and sac-like.

53. Bursal accessory gland. (0) absent; (1) present. There is an accessory gland (Fig. 12, bg) associated with the bursa of species of *Macrogyrus*, *Enhydrus*, and *Orectogyrus* species (Miller and Bergsten, 2012). This accessory gland is lacking in *Dineutus* and *Porrorhynchus*, as well as in gyrinines.

54. Vaginal shield. (0) absent; (1) present. The vaginal shield (Fig. 11C, vs) was first described by Brinck (1980) in *Porrorhynchus indicans*, then later described again for several *Dineutus* species (Brinck, 1983, 1984), it is formed by anterior circular bursal sclerites (again described in Miller and Bergsten, 2012) and a posteromedial cone-like projection enclosed in more strongly sclerotized bursal cuticle. This character is present in *Dineutus* and *Porrorhynchus* and absent in all other species studied.

Aedeagus

55. Paramere articulation with median lobe. (0) broadly; (1) narrowly. The aedeagus of *Porrorhynchus* species broadly articulates with the median lobe via a broad sclerotized basal region, whereas other species of dineutines the median lobe and parameres articulate via a narrow sclerotized bridge. The orectochilines and gyrinines were not coded for this character.

Sperm

56. Spermatostyle primary conjugation (Fig. 13). (0) absent; (1) present. The sperm of *Orectogyrus*, *Orectochilus*, and all dineutines is conjugated via a unique spermatostyle (Breland & Simmons, 1970).

References

Beutel, R. G. (1990) Phylogenetic analysis of the family Gyrinidae (Coleoptera) based on mesothoracic and metathoracic characters. *Quaestiones Entomologicae*, **26**, 163-192.

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

Breland, O. P. & Simmons, E. (1970) Preliminary studies of the spermatozoa and the male reproductive system of some whirligig beetles (Coleoptera: Gyrinidae). *Entomological News*, **81**, 101–110.

Brinck, P. (1980) *Porrorhynchus indicans* Walker (Coleoptera: Gyrinidae). A representative of the relict montane forest ecosystem in Sri Lanka. . *P.E.P. Deraniyagala Commemoration Volume (Sri Lanka 1980)*, 103-108.

Brinck, P. (1983) A revision of *Rhombodineutus* Ochs in New Guinea (Coleoptera: Gyrinidae). *Entomologica Scandinavica*, **14**, 205-233.

Brinck, P. (1984) Evolutionary trends and specific differentiation in *Merodineutus* (Coleoptera: Gyrinidae). *International Journal of Entomology*, **26**, 175-189.

Gustafson, G. T. & Miller, K. B. (2015) The New World whirligig beetles of the genus *Dineutus* Macleay, 1825 (Coleoptera, Gyrinidae, Gyrininae, Dineutini). *Zookeys*, **476**, 1 - 135. 10.3897/zookeys.476.8630.

Hatch, M. H. (1925) The phylogeny and phylogenetic tendencies of Gyrinidae. *Papers of the Michigan Academy of Science, Arts and Letters*, **V**, 429 – 467.

Miller, K. B. & Bergsten, J. (2012) Phylogeny and classficiation of whirligig beetles (Coleoptera: Gyrinidae): relaxed-clock model outperforms parsimony and time-free Bayesian analyses. *Systematic Entomology*, **37**, 705 – 746.

Oygur, S. & Wolfe, G. W. (1991) Classification, distribution, and phylogeny of North American north of Mexico species of *Gyrinus* Müller (Coleoptera: Gyrinidae). *Bulletin of the American Museum of Natural History*, **207**, 1-97.

Régimbart, M. (1882) Essai monographique de la famille des Gyrinidae. 1e partie. *Annales de la Société entomologique de France*, **(6)** 379 – 458 + 3 pls.

Supporting information Table S1. Taxa included in the phylogenetic and biogeographic analyses of the Dineutini. Gene coverage for molecular character dataset is indicated for each taxon as is geographical coding used for the biogeographic analysis.

Genus	Subgenus	species	voucher #	collection data	**Geo**	**COI**	**COII**	**12S**	**H3**	**AK**	**Efa**
Andogyrus		colombicus	Adco828	VENEZUELA: Merida State 8°38.006'N, 71°09.762'W, 2037 m Monte Zerpa area; 20.vii.2009 leg. Short, Sites, Gustafson, Camacho; stream margin/pools VZ09-0720-01A/L-1098 ABTC-01476. MSBA	S	X	X	X	X	X	-
Andogyrus		seriatopunctatus	Adsr886	Argentina. MSBA	S	X	X	X	X	X	-
Andogyrus		zimmermanni	Adsp648	see Miller & Bergsten, 2012	S	X	X	X	X	-	-
Aulonogyrus	Aulonogyrus	striatus	Aost469	see Miller & Bergsten, 2012	-	X	X	X	X	X	-
Dineutus	Callistodineutus	fairmairei	DiCf916	Fiji03. ZSM	M	-	X	X	X	-	-
Dineutus	Callistodineutus	pagdeni	DiCp918	SOLOMON ISLANDS: Guadal-canal ca. 4.5 km S of Barana vill. Forest nr. "Japanese Camp" & Moka riv. 9°30.3'S 159°58.9'E, 27m. 5-6.xii.2013 leg. Jiří Hájek. MSBA	M	X	X	X	X	X	-
Dineutus	Cyclinus	americanus	Diam850	Cuba: Holguín, river/ near Biological Station of PN La Mensura-/ Piloto, 657 m, 11.v.2013, 20.48640N 75.79134W, A. Deler-Hernández. NMPC	I	X	X	X	X	X	-
Dineutus	Cyclinus	assimilis	Dias819	USA: KS: Osage Co. pond off hwy 69 nr milemark 54. 38.031° -94.705° 254m 17.vi.2013 leg. CK Faris & GT Gustafson GTG06171301. MSBA	N	X	X	-	X	X	-
Dineutus	Cyclinus	carolinus	Dica821	USA: TX: Hardin Co. Big Thicket Pres. 30.260° -94.525° 20m 28.vi.2013 colr. CK Faris & GT Gustafson. Mud bottomed bayou GTG06281301. MSBA	I,N	X	X	X	X	X	-
Dineutus	Cyclinus	ciliatus	Dici474	see Miller & Bergsten, 2012	N	X	X	X	X	X	X
Dineutus	Cyclinus	discolor	Didi473	see Miller & Bergsten, 2012	N	X	X	X	X	X	X
Dineutus	Cyclinus	emarginatus	Diem820	USA: AL: Conecuh Co. nr. Evergreen. 31.291° -86.931° 82m 25.vi.2013. leg. CK Faris & GT Gustafson. Slow mud/sand bottom strm GTG06251302. MSBA	N	X	X	-	X	X	-
Dineutus	Cyclinus	longimanus longimanus	Dilo818	DOMINICAN REP.: Pedernales Prov. W of Pedernales on rd. to border with Haiti; roadside sweeping in dry for. & sec. veg. 15 May 2010 18.154° -71.7582° colr. G. J. Svenson. MSBA	I	X	X	X	X	X	-
Dineutus	Cyclinus	mexicanus	Dimx822	MÉXICO: Michoacán: Coalcoma, La Nuez, cañada el colorin. 15.ix.2003. col. R Novelo. MSBA	C	X	X	X	X	X	-
Dineutus	Cyclinus	productus	Dipd844	USA: KS: Elk Co. Elk River S of Longton 37.36960° -96.07873 265m 22.vi.2014 leg. C.Maier, C.Faris, S.Baca, G.Gustafson Muddy riv. Nr falls. GTG062214A. MSBA	C,N	X	X	X	-	X	-
Dineutus	Cyclinus	robertsi	Diro913	USA: Georgia: Warwoman Wld Mgmt Area. Tuckaluge Cr. 34.90155°N 83.30015°W. 533 m. 11July2012. KB Miller colr. KBM11071201. MSBA	N	X	X	X	X	X	-
Dineutus	Cyclinus	serrulatus analis	Disa843	USA: KS: Bourbon Co. Marmaton River, NE Ft. Scott 37.866°, -94.675° 237m 21.vi.2014 leg. C.Maier, C.Faris, S.Baca, G.Gustafson GTG062114A. MSBA	N	X	X	X	-	X	-
Dineutus	Cyclinus	shorti	Dish895	USA: AL: Covington Co. Conecuh Nat. For., trib. Of YellowRiv. 31.0929°, -86.5183° 43 m 27.iv.2015, leg. G.Gustafson & S.M.Baca GGSB042715C1	N	X	-	X	X	-	-
Dineutus	Cyclinus	solitarius	Diso605	see Miller & Bergsten, 2012	C	X	X	X	X	X	X
Dineutus	Cyclinus	sublineatus	Disu505	see Miller & Bergsten, 2012	C	X	X	X	X	X	X
Dineutus	Cyclinus	truncatus	Ditr726	Panama: Ngäbe-Buglé Comarca, small stream nr Soloy. 8°36.554'N, 82°07.814'W. 06July2009. Leg K.B. Miller KBM07060903	C	X	X	X	X	X	-
Dineutus	Cyclous	australis	Diau911	AUSTRALIA: QLD. 19°41.153'S 145°49.536'E 14.Mar.2011. colr. KB Miller KBM14031102. MSBA	P,O,W,M,A	X	X	X	X	-	-
Dineutus	Dineutus	fulgidus	DiDf915	INDONESIA: Sumatra Barat, Solok, Alahan Panjank Road. 1190 m. 0°56.345'S 100°46.411'E. ZSM	O	X	X	X	X	X	-

Dineutus	Dineutus	n sp	DiDn865	BALI: Telaga Forest, BLI07. ZSM	O	X	X	X	X	X	-
Dineutus	Merodineutus	macrochirus	DiMm919	PAPUA NEW GUINEA: Central Prov. Kokoda Trek. 9°00.338'S 147°44.252'E. 1390 m. i.2008. leg. Posman (PNG 173). ZSM	M	-	X	X	X	-	-
Dineutus	Merodineutus	priscus	DiMp917	PAPUA NEW GUINEA: S Highlands Prov. Sopulkul, 30-35 km NE Mendi. 6°2.944'S 143°46.485'E. 2679 m. 16.vi.2006. Leg. John ex swamp into stream (PNG 79). ZSM	M	-	X	X	X	X	-
Dineutus	Protodineutus	aereus	Disp481	see Miller & Bergsten, 2012	E	X	X	X	X	X	-
Dineutus	Protodineutus	grossus abyssinicus	Digr855	CONGO (DRC): Bas Congo Prov. Nduizi River. 5°44.446'S 13°44.385'E 266 m. 6Aug 2012. coll: Sites, Shephard, Pwema L-1439. MSBA	E	X	X	X	X	X	-
Dineutus	Protodineutus	grossus angolensis	Diga826	TANZANIA: Kagera Reg. ca. 5 km E of Bhiaramulo 2°38.159'S 31°20.789'E 1427 m. 26Jul2010. coll: R.W. Sites & A. Mbogho L-1154. MSBA	E	X	X	X	X	X	-
Dineutus	Protodineutus	indicus	Diin482	see Miller & Bergsten, 2012	O	X	X	X	X	X	X
Dineutus	Protodineutus	micans	Disp577	see Miller & Bergsten, 2012	E	X	X	X	X	X	X
Dineutus	Protodineutus	proximus	Dipx515	see Miller & Bergsten, 2012	E	X	X	X	-	X	X
Dineutus	Protodineutus	sinuosipennis	Disn516	see Miller & Bergsten, 2012	E	X	X	X	X	-	X
Dineutus	Protodineutus	staudingeri	Dist825	TANZANIA: Arusha Reg. Sanaware River at Arusha 3°21.549'S 36°41.619'E 1442 m. 11Aug2010. coll. R.W. Sites & A. Mbogho L-1239. MSBA	E	X	X	X	X	X	-
Dineutus	Rhombodineutus	pectoralis	Disp507	see Miller & Bergsten, 2012	M	X	X	X	X	X	-
Dineutus	Rhombodineutus	tetracanthus	DiRt908	PAPUA NEW GUINEA: Madang Prov. Wannang, 5°15.458'S 145°2.389'E 270 m. 31.x.2008. leg. Posman (PNG187) ZSM.	M	X	X	X	X	X	-
Dineutus	Spinosodineutes	fauveli	Difa485	see Miller & Bergsten, 2012	E	X	X	X	X	X	-
Dineutus	Spinosodineutes	striatus	Disp576	see Miller & Bergsten, 2012	E	X	X	X	X	X	X
Dineutus	Spinosodineutes	subspinosus	Disu484	see Miller & Bergsten, 2012	E	X	X	X	X	X	X
Enhydrus		atratus	Ehas646	see Miller & Bergsten, 2012	C,S	X	X	X	X	-	-
Enhydrus		sulcatus	Ehsu856	BRAZIL: Rio de Janeiro: Cachoei Ras de Macacu - Regua. 01.vi.2013. Ponto do Ganesh (Parte Alta) col. Equipe Coleoptera. MSBA	S	X	X	X	X	X	-
Macrogyrus	Australogyrus	oblongus	AyAo857	AUSTRALIA: QLD. Broken River. 21° 10.077'S 148° 30.386'E. 713m. 17Mar2011. Coll: KB Miller. KBM1703110D. MSBA	A	X	X	X	X	X	-
Macrogyrus	Australogyrus	rivularis	AyAr909	AUSTRALIA: VIC. Off Old Coast Rd, -37.73667, 148.95166. 30 m. 12.i.2015 leg. G.Gustafson, K.Miller. Small strm in forest. GTG01122015A. MSBA	A	X	X	X	-	X	-
Macrogyrus	Clarkogyrus	reichei	Ayre912	AUSTRALIA: VIC. Glenelg River nr. Dergholm, -37.36686, 141.2428. 75 m. 13.i.2015. Leg G.Gustafson. MSBA	A	X	X	X	-	-	-
Macrogyrus	Cyclomimus	purpurascens	AyCs841	PAPUA NEW GUINEA: Morobe Prov. Pindiu. 6°27.147'S 147°29.574'E, 1470 m. 12.x.2009 leg. Inaho (PNG206). ZSM	M	X	X	X	X	X	-
Macrogyrus	Cyclomimus	sp	AyCs831	PAPUA NEW GUINEA: Sandaun Prov. Mianmin 4°54.570'S 141°35.490'E 990 m. 23.x.2008. leg. Ibalim (PNG193). ZSM	M	X	X	X	X	-	-
Macrogyrus	Cyclomimus	toxopeusi	AyCs829	INDONESIA: Papua: Poga 3°48.382'S, 138°34.780'E 2285-2330 m. ZSM	M	X	X	X	X	X	-
Macrogyrus	Macrogyrus	howittii	Ayhw887	AUSTRALIA: Tasmania. Franklin Beach, Lake St. Clair. 10.i.2015 CHS Watts. MSBA	A	X	-	X	X	X	-
Macrogyrus	Megalogyrus	striolatus	Ayst882	AUSTRALIA: NSW. Megalong Valley, -36.65629, 150.27377, 861 m. 04.i.2015. leg. G.Gustafson Forested strm GTG01042015A. MSBA	A	X	X	X	X	X	-
Macrogyrus	Orectomimus	paradoxus	Aypa817	AUSTRALIA: QLD. Cardstone. 17°46.650'S 145°39.015'E. 19Mar2011 KB Miller colr. KBM19031102. MSBA	A	X	X	X	X	X	-
Macrogyrus	Tribologyrus	albertisi	AyTs832	Papua New Guinea: Sanduan. Toricelli Mts. 2h walk fr Sibilanga Stm. 350 m, 19.iv.2006, 03°39.121'S 142°29.991'E. Balke (PNG 44). ZSM	-	X	-	-	X	X	-
Macrogyrus	Tribologyrus	australis	Ayau910	AUSTRALIA: Frog's Hollow Creek off Princes HWY, -36.74363, 149.81474. 35 m. 07.i.2015. leg. G.Gustafson. Small strm in open grassland. GTG01072015B. MSBA	A	X	X	X	X	-	-
Macrogyrus	Tribologyrus	gouldi	Aygo501	see Miller & Bergsten, 2012	A	X	X	X	X	X	-
Macrogyrus	Tribologyrus	sexangularis	AyTs835	PAPUA NEW GUINEA: Herowane. ZSM	M	X	X	X	X	X	-
Macrogyrus	Tribologyrus	sp	Aysp861	INDONESIA: Timor: Mt. Mutis, creeks and streams. 1580 m. 9°38.124'S 124°12.800'E (TIM04). ZSM	O	X	X	X	X	X	-
Macrogyrus	Tribologyrus	sp	Aysp863	INDONESIA: Lombok: Senaru area. 834 m. 8°19.326'S 116°24.989'E (LOM004). ZSM	O	X	X	X	X	X	-
Macrogyrus	Tribologyrus	sp	AyTs833	PAPUA NEW GUINEA: Central Prov. Woitape. 08°31.290'S 147°13.684'E 1700 m. i.2008 leg. Posman (PNG166). ZSM	M	X	X	X	X	X	-
Macrogyrus	Tribologyrus	sp nr. blanchardii	AyTs830	PAPUA NEW GUINEA: Bougainville Isl.: Kieta 06°12.955'S 155°29.755'E 520 m. 12.vi.2008. leg. Posman (PNG180). ZSM	M	X	X	X	X	-	-

Macrogyrus	Tribologyrus	sp nr. blanchardii	AyTs834	PAPUA NEW GUINEA: E Highlands Prov. Onerunka, small creek, redsoil rock 6°20.936'S 145°46.874'E 1700 m. 21.v.2006 leg. John & Balke (PNG71). ZSM	M	X	X	X	X	X	-
Macrogyrus	Tribologyrus	sumbawae	Aysp860	INDONESIA: Sumba: dry forest stream in limestone. 370 m 9°49.474'S 120°20.856'E (SUA08). ZSM	O	X	X	X	X	X	-
Mesodineutes		amurensis	Meamure	Arkhara, Amur Oblast, Russia (49.4°N, 130.1°E: paleocoordinates 52.1°N, 118.2°E). Darmakan formation, Danian (66.0 - 51.7 mya) Paleocene. PIN	-	-	-	-	-	-	-
Porrorhynchus	Porrorhynchus	landaisi	Prla852	CHINA: Hainan Isl. Jianfengling Mts. Tiachi Lake rd. from Taichi village to 'Sector 5' 18°43.6-44.1'N 820-950m, 108°52.1-52.5'E 10.v.2011. M.Fikáček & Sh. Zhao lgt. Small slow-flowing stony river in the primary forest. MSBA	O	X	X	X	X	X	-
Porrorhynchus	Porrorhynchus	marginatus	Prma779	THAILAND: Kanchanaburi Prov. Huay Ou Long at Ban Ou Long. N14°35.177' W98°34.921' 1Jun2011. 274m col. R.W. Sites. Gravel bottom stream. MSBA	O	X	X	X	-	X	-
Porrorhynchus	Rhomborhynchus	misoolensis	Prdepre	INDONESIA: West Papua: Misool Island: Tama River, SE of old Fakal village site, 1°51'38.1"S 129°55'24.1"E, 60m, 22.iv.1999. leg. D.A. Polhemus, CL7110. DAPC.	-	-	-	-	-	-	-
Gyretes		giganteus	Gegigan	Auvergne, France (46.1°N, 2.9°E: paleocoordinates 40.6°N, 0.6°E). Menat formation, Thanetian (58.7 - 55.8 mya), Paleocene. MNHN.	-	-	-	-	-	-	-
Gyrinus	Gyrinus	sericeolimbatus	Gysp840	PAPUA NEW GUINEA: Morobe Prov. Pindiu. 6°27.147'S 147°29.574'E, 1470 m. 12.x.2009 leg. Inaho (PNG206). ZSM	-	X	X	X	X	X	-
Gyrinus		maculiventris	Gysp837	USA: New Mexico, Cibola Co., Zuni Mountains. 18.v.2013. leg. S. Baca. 180513-A. MSBA	-	X	X	X		X	-
Gyrinus	Oreogyrinus	dimorphus	Gysp839	USA: New Mexico, Cibola Co., Zuni Mtns, 35.40178°N, 108.44956°W. 30.v.2013. leg. G.Gustafson & S.Baca. GGSB053013C. MSBA	-	X	X	X	X	X	-
Mesogyrus		antiquus	Msantiq	Karatau-Mikhailovka, Chimkent, Kazakhstan (42.9ºN, 70.0ºE: paleocoordinates 41.6ºN, 73.7ºE), lacustrine, siltstone in the Karabastau Formation, Callovian/Oxfordian (157.3 – 166.1 Ma), Upper Jurassic. PIN	-	-	-	-	-	-	-
Orectochilus		villosus	Orvi527	see Miller & Bergsten, 2012	-	X	X	X	X	-	-
Orectogyrus	Orectogyrus	madagascariensis	Ogmd601	see Miller & Bergsten, 2012	-	X	X	X	X	X	-
Orectogyrus		sp	Ogsp564	see Miller & Bergsten, 2012	-	X	X	X	X	X	-
Patrus		productus	Orpr487	see Miller & Bergsten, 2012	-	X	X	X	X	X	-

Supporting information Table S2. Character coding for morphological dataset.

```
            1      6      11     16     21     26     31     36     41     46     51   56
            |      |      |      |      |      |      |      |      |      |      |    |
Hsmi596     20110  0011-  -0000  00110  0000?  10112  11100  01000  00011  00000  1010-0
Orvi527     001-1  -0101  12000  00010  20002  01110  -1100  01000  00100  01011  1110-1
Orpr487     031-0  -0100  02000  00010  21002  01010  -1100  11000  00100  01011  0010-?
Ogmd601     031-1  10100  01000  00120  01001  01110  -1100  11000  00100  01011  01?0-1
Ogsp564     031-1  10100  01000  00120  01001  01110  -1100  11000  00100  01011  11?0-1
Gegigan     ????0  ?????  ?????  ?????  ?????  ?????  ??100  01000  ?????  ???1?  ??????
Gysp837     10010  00011  10000  00120  20002  01101  01000  00000  00100  01000  0000-0
Gysp839     10000  00011  10000  00120  20002  01101  01000  00000  00100  01000  0000-0
Gysp840     11010  00011  10000  00120  20002  01101  01000  00000  00100  01000  0000-0
Aost469     11000  00010  00000  00120  10002  01101  01000  00000  00100  01000  0000-0
Diau911     03000  00111  01010  00120  00001  10002  20100  10100  01010  10000  010111
Ehas646     03100  00110  10000  00010  11002  10102  10000  01000  00010  10100  011011
Ehsu856     02100  00110  10000  00010  11002  10102  10000  00000  00010  10100  011011
Ayhw887     00110  00110  02000  00120  11012  10102  20100  01000  10011  11000  011011
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Ayre912     00100  00110  10000  00010  01011  10102  20100  10100  10011  11000  011011
Ayst882     00110  00110  00000  00110  11012  10102  20100  01000  10011  11000  011011
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AyTs834     00110  00110  00000  00120  1101?  10102  20111  10000  10011  11000  011011
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Aygo501	00110	00110	00000	00110	11011	10102	21111	10000	10011	11000	111011
Aypa817	00110	00110	10000	00110	1101?	10102	20110	10000	10011	11000	111011
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Difa485	03000	00110	01000	00120	00001	10002	20111	10100	01010	10000	110111
Disp507	03100	00111	00000	00110	00000	10002	20100	10001	01010	10000	110111
DiRt908	02100	00111	00000	00120	00001	10002	20101	10001	01010	10000	010111
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Dipx515	03000	00111	01000	00120	00002	10002	20000	00000	01010	10000	010111
Dilo818	03000	00111	01001	01110	00002	10002	20111	00100	01010	10000	110111
Ditr726	03000	00111	01001	01120	00002	10002	20100	01100	01010	10000	010111
Dimx822	03000	00111	01001	01120	00002	10002	20100	01100	01010	10000	010111
Disa843	03000	00111	01001	01120	00002	10002	20110	00100	01010	10000	110111
Disp576	03000	00111	01000	00120	00002	10002	20110	10100	01010	10000	110111
DiCp918	03000	00111	00001	10110	00101	10002	20000	00000	01010	10000	110111
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Diso605	03000	00111	01001	01120	00002	10002	20000	00000	01010	10000	010111
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Diin482	03000	00111	01001	01120	00002	10002	20000	00000	01010	10000	010111
Dici474	03000	00111	01000	00120	00002	10002	20000	00000	01010	10000	010111
Diro913	03000	00111	01000	00120	00002	10002	20000	00000	01010	10000	110111
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Dish895	03000	00111	01000	00120	00002	10002	20000	00000	01010	10000	110111
Disp577	03000	00111	01000	00120	00002	10002	20100	00110	01010	10000	010111
Digr855	03000	00111	01000	00120	00002	10002	20000	00000	01010	10000	010111
Diga826	03000	00111	01000	00120	00002	10002	20000	00000	01010	10000	010111
Dist825	03000	00111	01000	00120	00002	10002	20000	00000	01010	10000	010111
Prla852	01101	01101	00100	00021	01000	10000	-0111	10110	01010	10000	110101
Prma779	03101	01101	00100	00021	01000	10000	-0111	10110	01010	10000	110101
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Meamure	?????	?????	?????	?????	?????	10?02	00000	00000	0?01?	10000	??????
Prdepre	03101	10111	01000	00120	10002	10002	20111	10000	01010	10000	110111

Supporting information Table S3. Primers used for amplification and sequencing.

Gene	Forward primer (5'-3')	Reverse primer (5'-3')	Reference
COI	Jerry, CAACATTTATTTTGATTTTTTGG	Pat, TCCAATGCACTAATCTGCCATATTA	Simon *et al.* 1994
COII	F-leu, TCTAATATGGCAGATTAGTGC	R-lys, GAGACCAGTACTTGCTTTCAGTCATC	Whiting 2002
12S	12Sai, AAACTACGATTAGATACCCTATTAT	12Sbi, AAGAGCGACGGGCGATGTGT	Svenson & Whiting 2004
H3	HexAF, ATGGCTCGTACCAAGCAGACGGC	HexAR,, ATATCCTTGGGCATGATGGTGAC	Colgan et al. 1998
AK	AK183F, GATTCTGGAGTCGGNATYTAYGCNCCYGAYGC	AK939R, GCCNCCYTCRGCYTCRGTGTGYTC	Wild & Maddison, 2008
AK	DinAKF1, CCGNCYTGTTCGACCCCRT	DinAKR1, ARYTTRGCCYTGTTRGMRG	This study

For difficult taxa internal primers were designed for AK183F and AK939R, these are DinAKF1 and DinAKR1. Nested PCR was performed using these primers to amplify Arginine kinase in difficult specimens.

References

Colgan, D. J., McLauchlan, A., Wilson, G. D. F., Livingston, S. P., Edgecombe, G. D., Macaranas, J. & et al. (1998) Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. *Australian Journal of Zoology*, **46**, 419-437.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P. (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, **87**, 651-701.

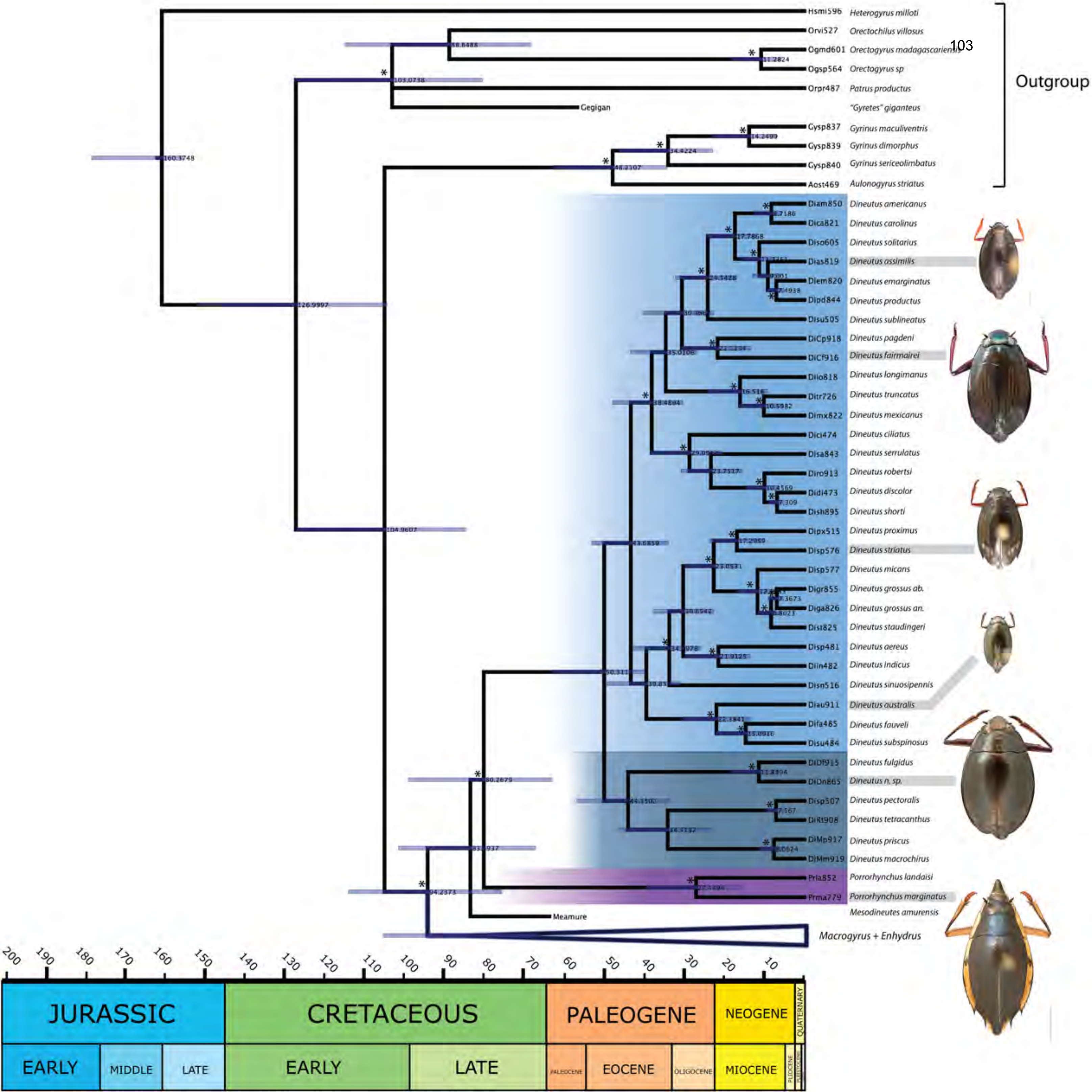
Svenson, G. J. & Whiting, M. F. (2004) Phylogeny of Mantodea based on molecular data: Evolution of a charismatic predator. *Systematic Entomology*, **29**, 359-370.

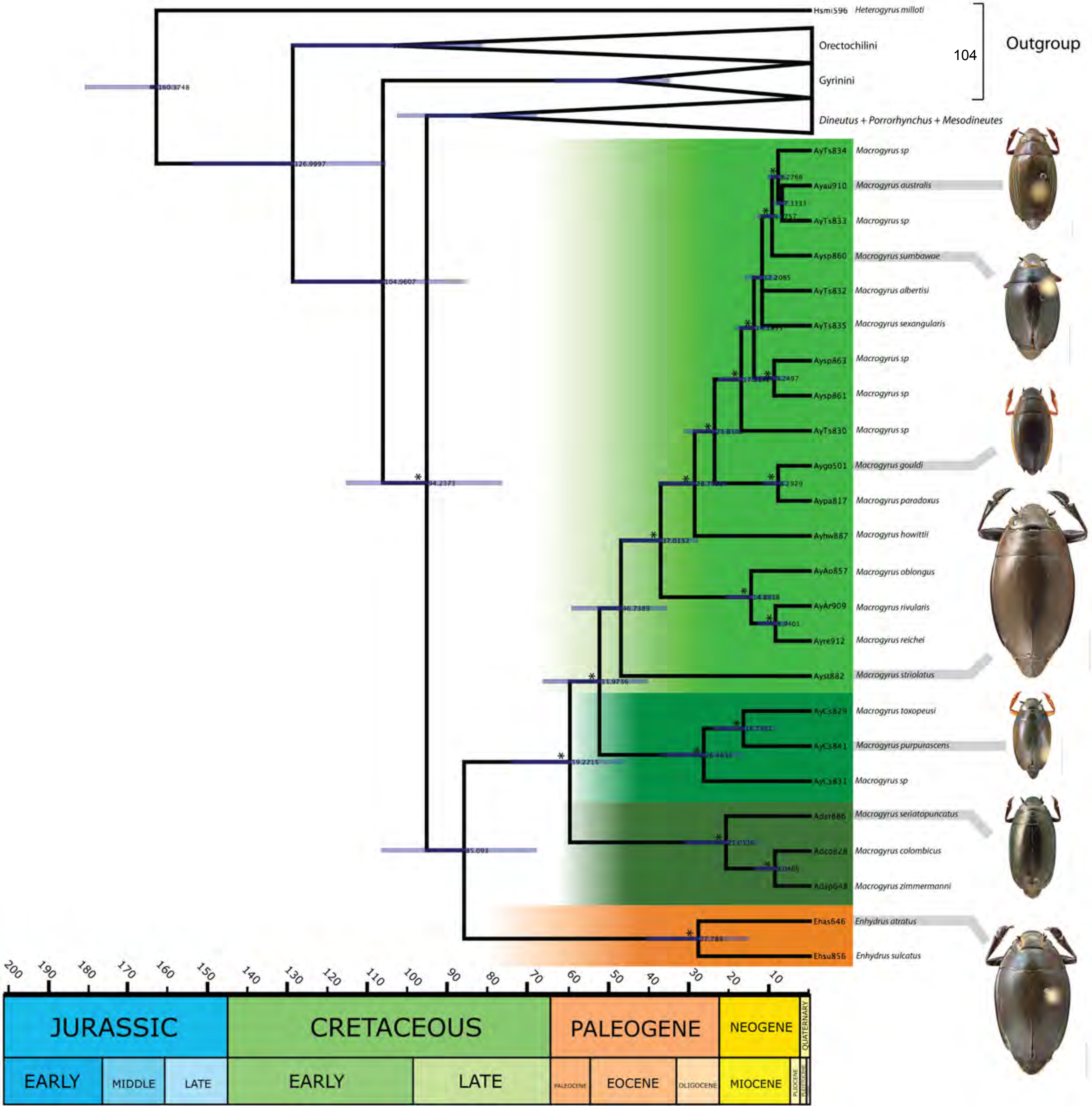
Whiting, M. F. (2002) Mecoptera is paraphyletic: multiple genes and phylogeny of Mecoptera and Siphonapter. *Zoologica Scripta*, **31**, 93-104.

Wild, A. L. & Maddison, D. R. (2008) Evaluating nuclear protein-coding genes for phylogenetic utility in beetles. *Molecular Phylogenetics and Evolution*, **48**, 877-891. 10.1016/j.ympev.2008.05.023.

Supporting information Table S4. Statistical comparison of the DEC, DEC +j, DIVALIKE, and DIVALIKE +j model fit.

	LnL	param #	d	e	j	AIC	AIC_wt
DEC	-99.9	2	0.012	0.16	0	203.8	0.25
DEC+J	-97.78	3	0.0056	0.065	0.052	201.6	0.75
DIVALIKE	-103.7	2	0.0029	0.0007	0.061	213.5	0.0019
DIVALIKE+J	-103.8	3	0.003	0.0011	0.064	213.7	0.0018


Hsmi596 Heterogyrus milloti
Orvi527 Orectochilus villosus
Ogmd601 Orectogyrus madagascariensis
Ogsp564 Orectogyrus sp
Orpr487 Patrus productus
Gegigan "Gyretes" giganteus
Gysp837 Gyrinus maculiventris
Gysp839 Gyrinus dimorphus
Gysp840 Gyrinus sericeolimbatus
Aost469 Aulonogyrus striatus
Outgroup
Diam850 Dineutus americanus
Dica821 Dineutus carolinus
Diso605 Dineutus solitarius
Dias819 Dineutus assimilis
Diem820 Dineutus emarginatus
Dipd844 Dineutus productus
Disu505 Dineutus sublineatus
DiCp918 Dineutus pagdeni
DiCf916 Dineutus fairmairei
Dilo818 Dineutus longimanus
Ditr726 Dineutus truncatus
Dimx822 Dineutus mexicanus
Dici474 Dineutus ciliatus
Disa843 Dineutus serrulatus
Diro913 Dineutus robertsi
Didi473 Dineutus discolor
Dish895 Dineutus shorti
Dipx515 Dineutus proximus
Disp576 Dineutus striatus
Disp577 Dineutus micans
Digr855 Dineutus grossus ab.
Diga826 Dineutus grossus an.
Dist825 Dineutus staudingeri
Disp481 Dineutus aereus
Diin482 Dineutus indicus
Disn516 Dineutus sinuosipennis
Diau911 Dineutus australis
Difa485 Dineutus fauveli
Disu484 Dineutus subspinosus
DiDf915 Dineutus fulgidus
DiDn865 Dineutus n. sp.
Disp507 Dineutus pectoralis
DiRt908 Dineutus tetracanthus
DiMp917 Dineutus priscus
DiMm919 Dineutus macrochirus
Prla852 Porrorhynchus landaisi
Prma779 Porrorhynchus marginatus
Meamure Mesodineutes amurensis
Macrogyrus + Enhydrus
160.3748
126.9997
104.9607
103.0738
88.8486
11.2824
48.2107
34.4224
14.2499
17.7868
24.5428
35.0106
38.4884
16.516
10.5982
23.7517
10.4569
7.309
43.6859
17.2959
23.0531
30.6542
21.9125
22.1841
15.0916
11.8304
7.567
8.0624
80.2679
94.2373
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
JURASSIC
CRETACEOUS
PALEOGENE
NEOGENE
QUATERNARY
EARLY
MIDDLE
LATE
EARLY
LATE
PALEOCENE
EOCENE
OLIGOCENE
MIOCENE
PLIOCENE
PLEISTOCENE


Hsmi596 Heterogyrus milloti
Orectochilini
Gyrinini
Dineutus + Porrorhynchus + Mesodineutes
Outgroup
160.3748
126.9997
104.9607
94.2373
85.093
AyTs834 Macrogyrus sp
Ayau910 Macrogyrus australis
AyTs833 Macrogyrus sp
Aysp860 Macrogyrus sumbawae
AyTs832 Macrogyrus albertisi
AyTs835 Macrogyrus sexangularis
Aysp863 Macrogyrus sp
Aysp861 Macrogyrus sp
AyTs830 Macrogyrus sp
Aygo501 Macrogyrus gouldi
Aypa817 Macrogyrus paradoxus
Ayhw887 Macrogyrus howittii
AyAo857 Macrogyrus oblongus
AyAr909 Macrogyrus rivularis
Ayre912 Macrogyrus reichei
Ayst882 Macrogyrus striolatus
AyCs829 Macrogyrus toxopeusi
AyCs841 Macrogyrus purpurascens
AyCs831 Macrogyrus sp
Adsr886 Macrogyrus seriatopuncatus
Adco828 Macrogyrus colombicus
Adap648 Macrogyrus zimmermanni
Ehas646 Enhydrus atratus
Ehsu856 Enhydrus sulcatus
7.3333
12.2085
23.830
28.7
37.0152
14.8918
46.7389
51.9736
59.2215
26.4613
21.0936
27.786
*
200 190 180 170 160 150 140 130 120 110 100 90 80 70 60 50 40 30 20 10
JURASSIC
CRETACEOUS
PALEOGENE
NEOGENE
QUATERNARY
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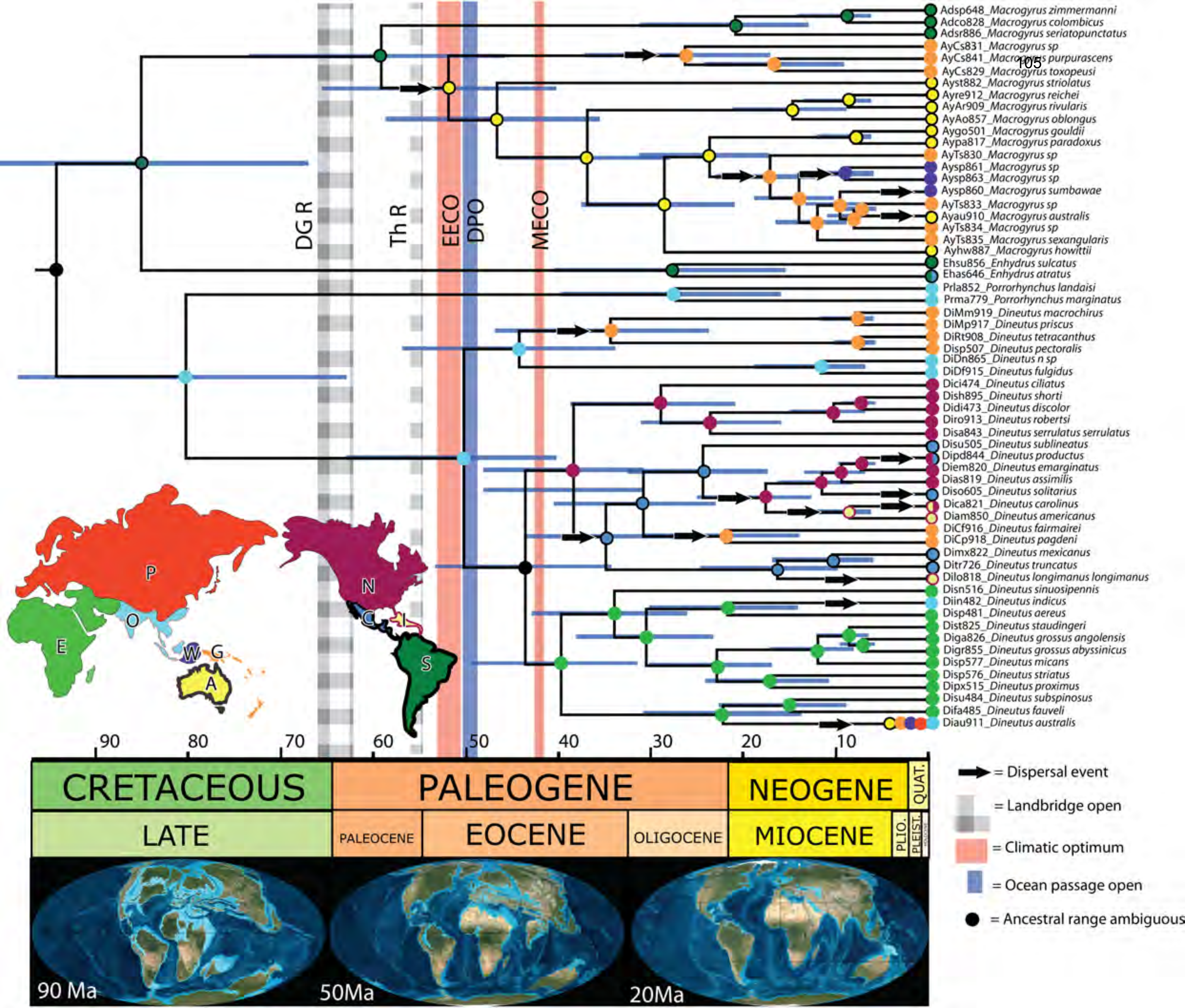
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AyCs831_Macrogyrus sp
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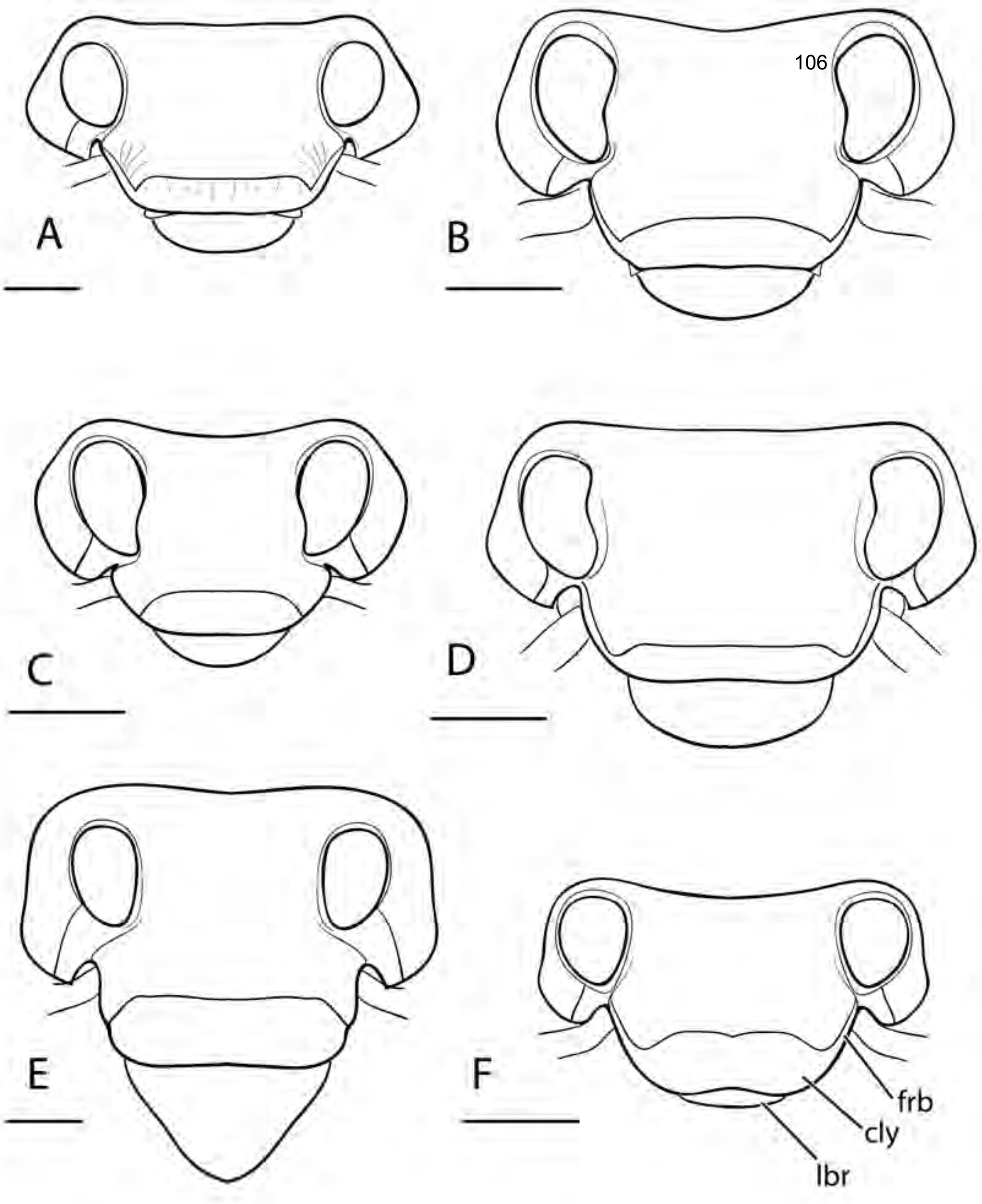
AyCs829_Macrogyrus toxopeusi
Ayst882_Macrogyrus striolatus
Ayre912_Macrogyrus reichei
AyAr909_Macrogyrus rivularis
AyAo857_Macrogyrus oblongus
Aygo501_Macrogyrus gouldii
Aypa817_Macrogyrus paradoxus
AyTs830_Macrogyrus sp
Aysp861_Macrogyrus sp
Aysp863_Macrogyrus sp
Aysp860_Macrogyrus sumbawae
AyTs833_Macrogyrus sp
Ayau910_Macrogyrus australis
AyTs834_Macrogyrus sp
AyTs835_Macrogyrus sexangularis
Ayhw887_Macrogyrus howittii
Ehsu856_Enhydrus sulcatus
Ehas646_Enhydrus atratus
Prla852_Porrorhynchus landaisi
Prma779_Porrorhynchus marginatus
DiMm919_Dineutus macrochirus
DiMp917_Dineutus priscus
DiRt908_Dineutus tetracanthus
Disp507_Dineutus pectoralis
DiDn865_Dineutus n sp
DiDf915_Dineutus fulgidus
Dici474_Dineutus ciliatus
Dish895_Dineutus shorti
Didi473_Dineutus discolor
Diro913_Dineutus robertsi
Disa843_Dineutus serrulatus serrulatus
Disu505_Dineutus sublineatus
Dipd844_Dineutus productus
Diem820_Dineutus emarginatus
Dias819_Dineutus assimilis
Diso605_Dineutus solitarius
Dica821_Dineutus carolinus
Diam850_Dineutus americanus
DiCf916_Dineutus fairmairei
DiCp918_Dineutus pagdeni
Dimx822_Dineutus mexicanus
Ditr726_Dineutus truncatus
Dilo818_Dineutus longimanus longimanus
Disn516_Dineutus sinuosipennis
Diin482_Dineutus indicus
Disp481_Dineutus aereus
Dist825_Dineutus staudingeri
Diga826_Dineutus grossus angolensis
Digr855_Dineutus grossus abyssinicus
Disp577_Dineutus micans
Disp576_Dineutus striatus
Dipx515_Dineutus proximus
Disu484_Dineutus subspinosus
Difa485_Dineutus fauveli
Diau911_Dineutus australis
DG R
Th R
EECO
DPO
MECO
P
N
E
O
C
I
W
G
S
A
90
80
70
60
50
40
30
20
10
CRETACEOUS
PALEOGENE
NEOGENE
QUAT.
LATE
PALEOCENE
EOCENE
OLIGOCENE
MIOCENE
PLIO.
PLEIST.
90 Ma
50Ma
20Ma
= Dispersal event
= Landbridge open
= Climatic optimum
= Ocean passage open
= Ancestral range ambiguous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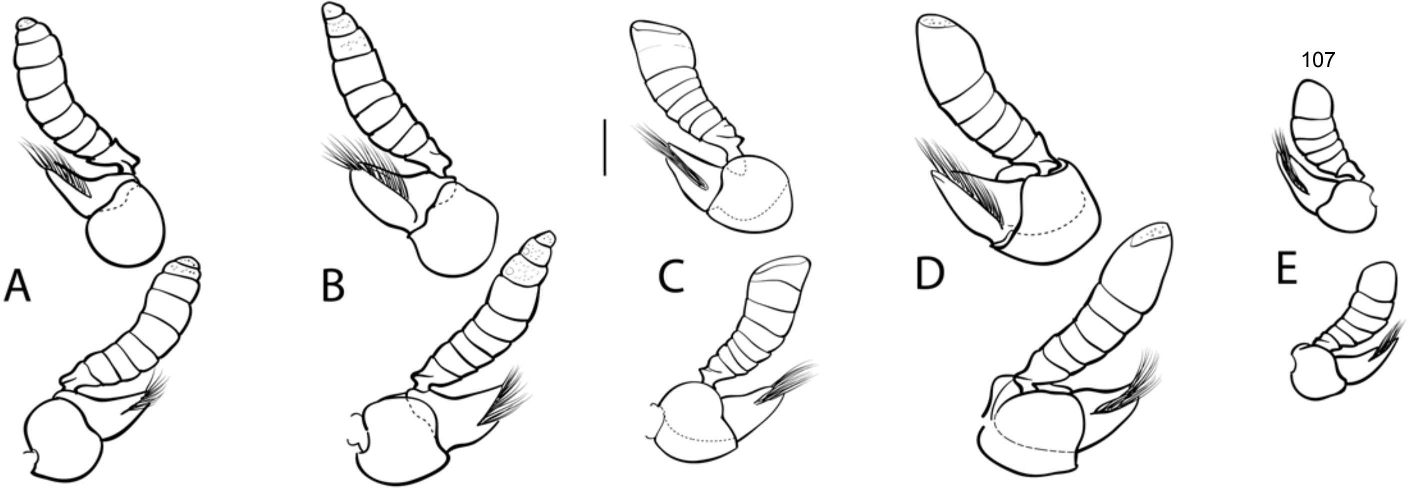
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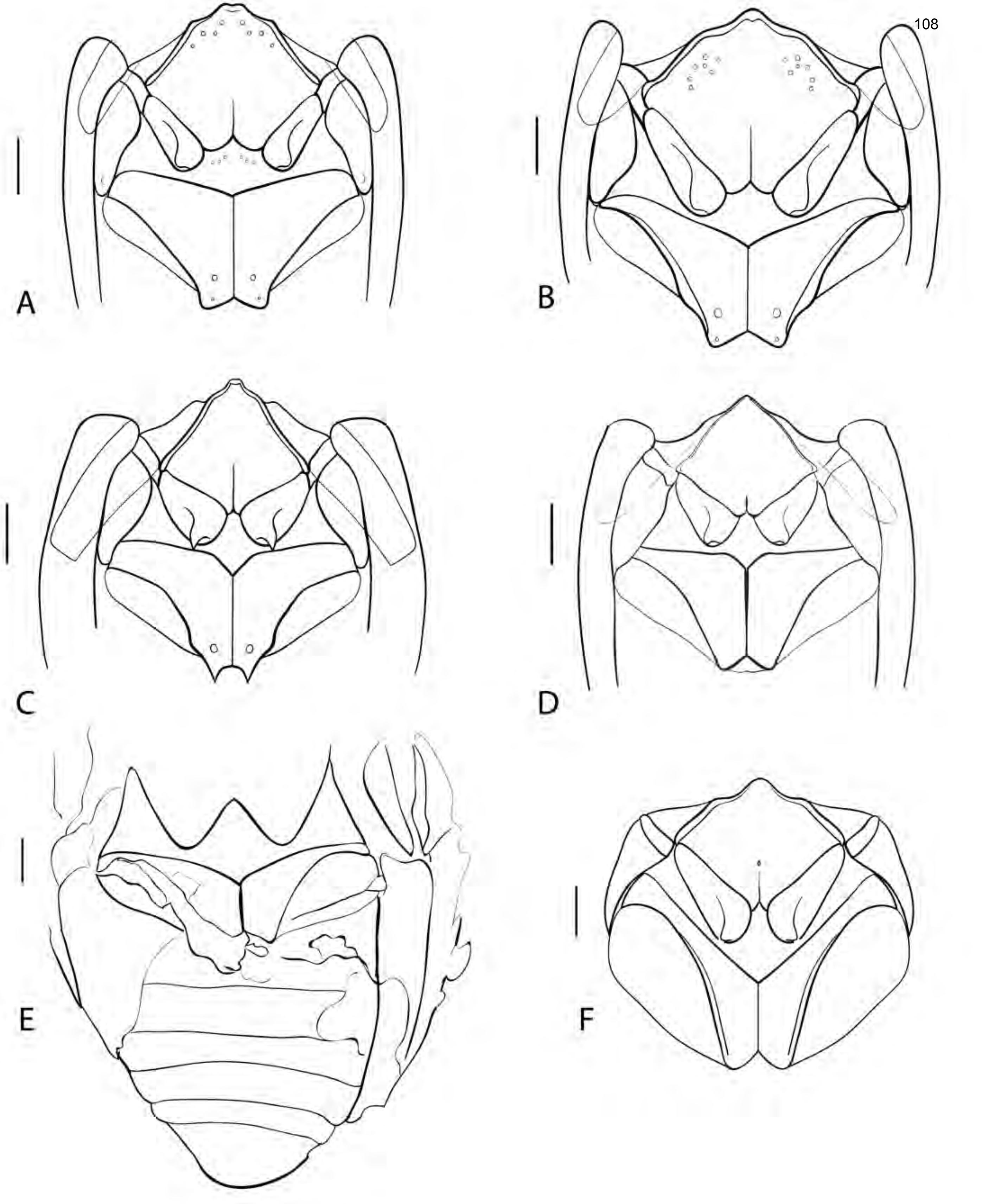
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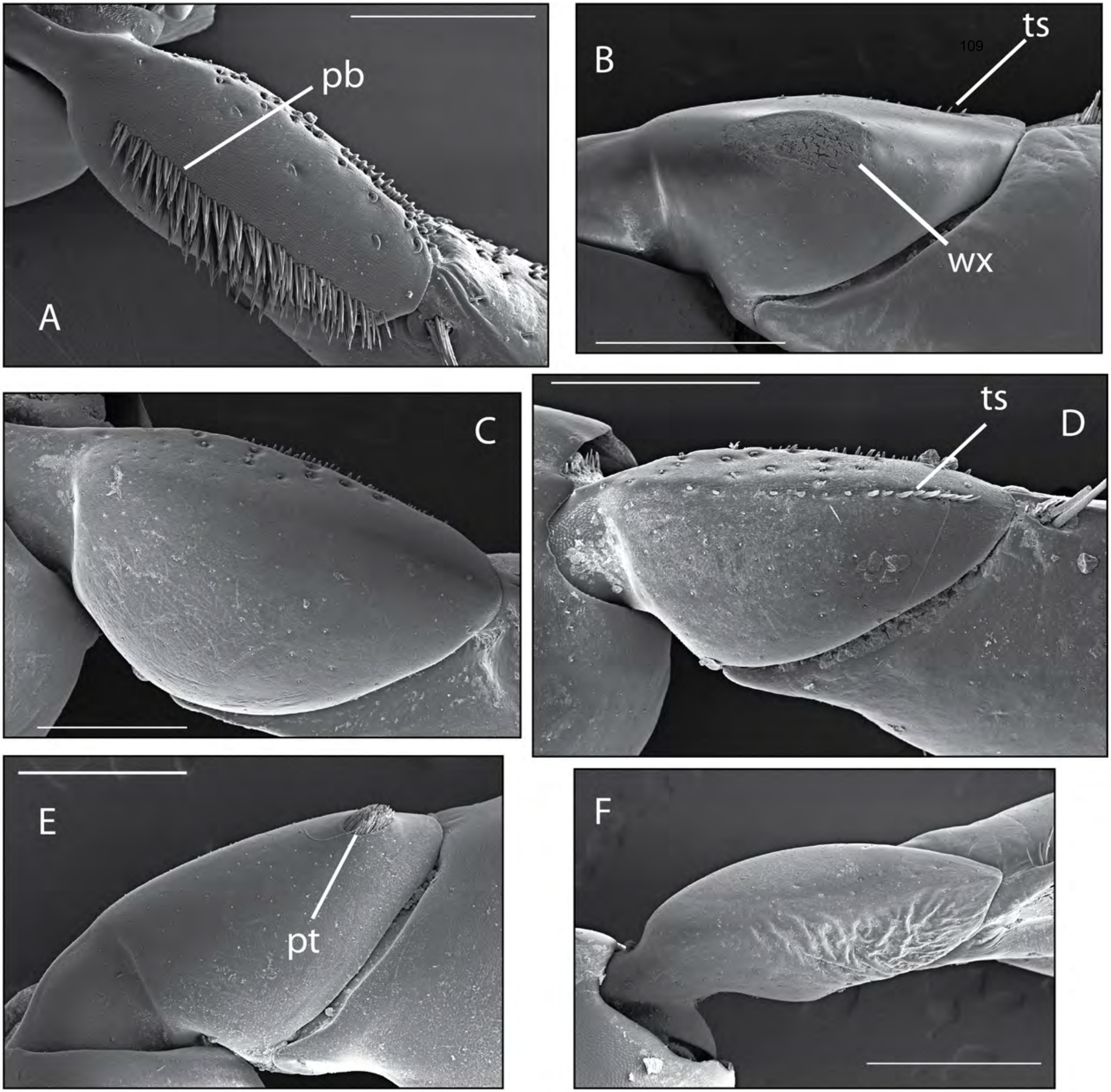
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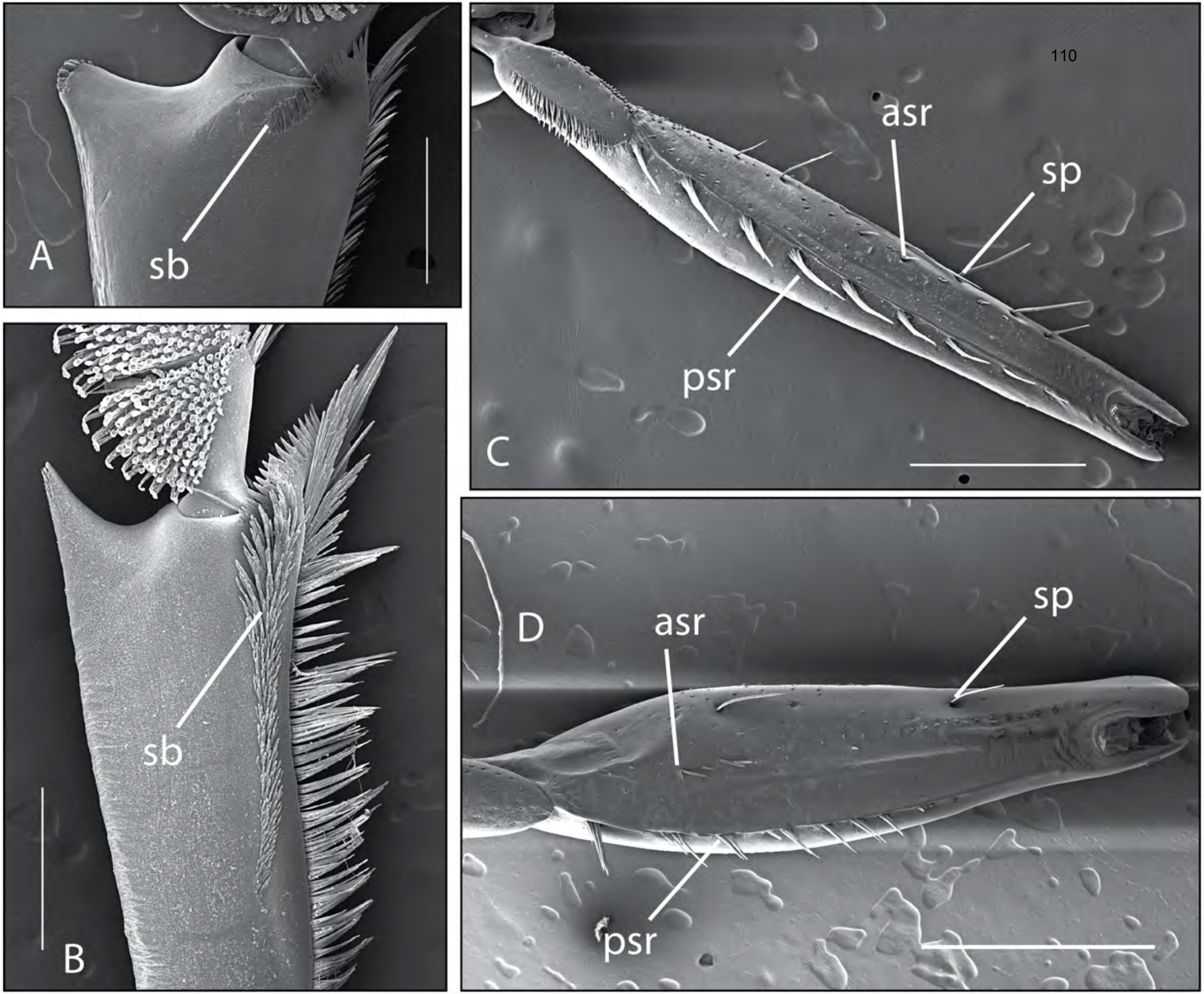
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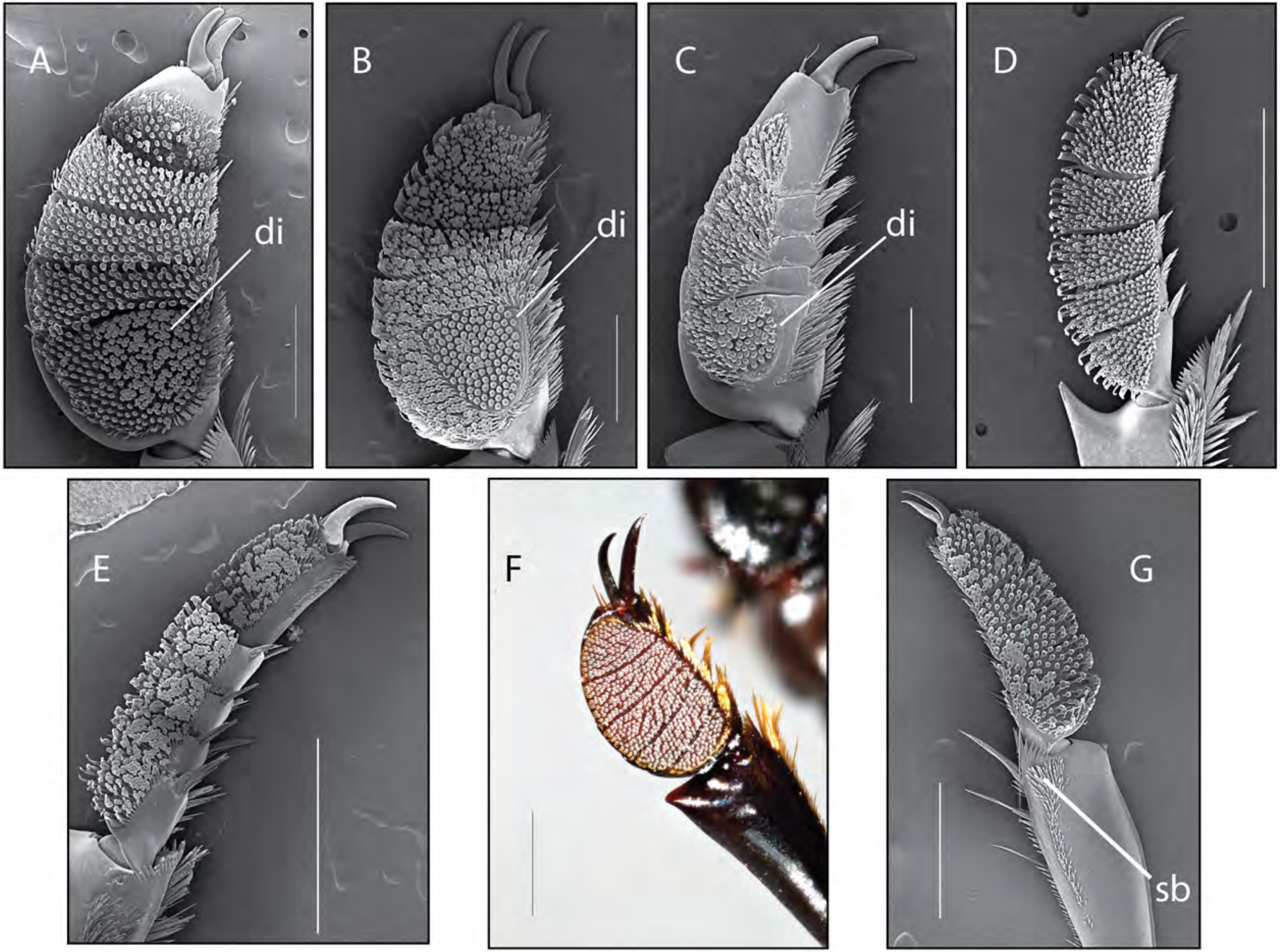
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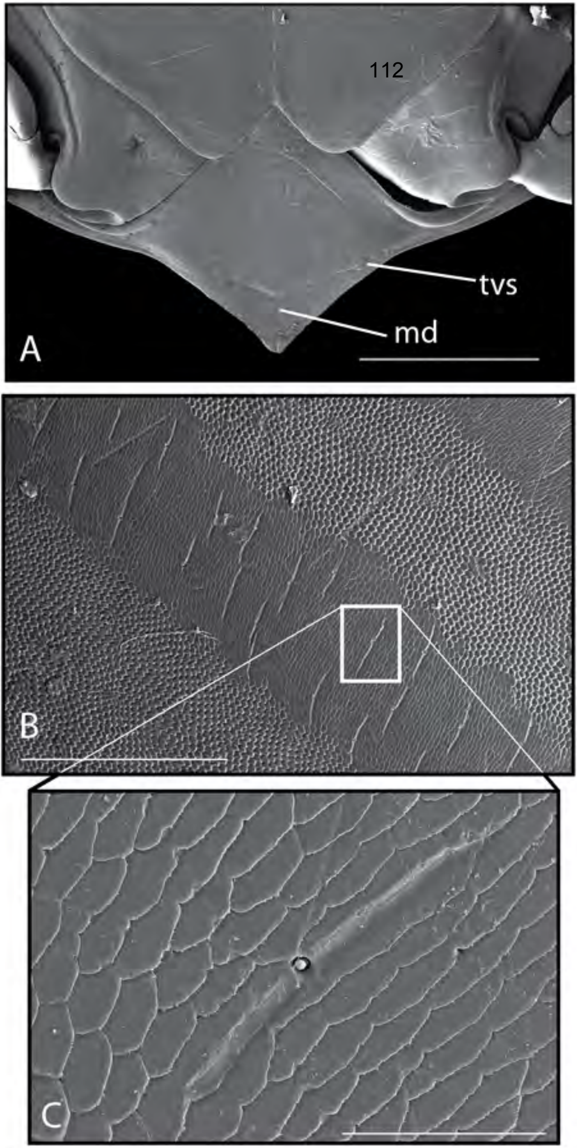
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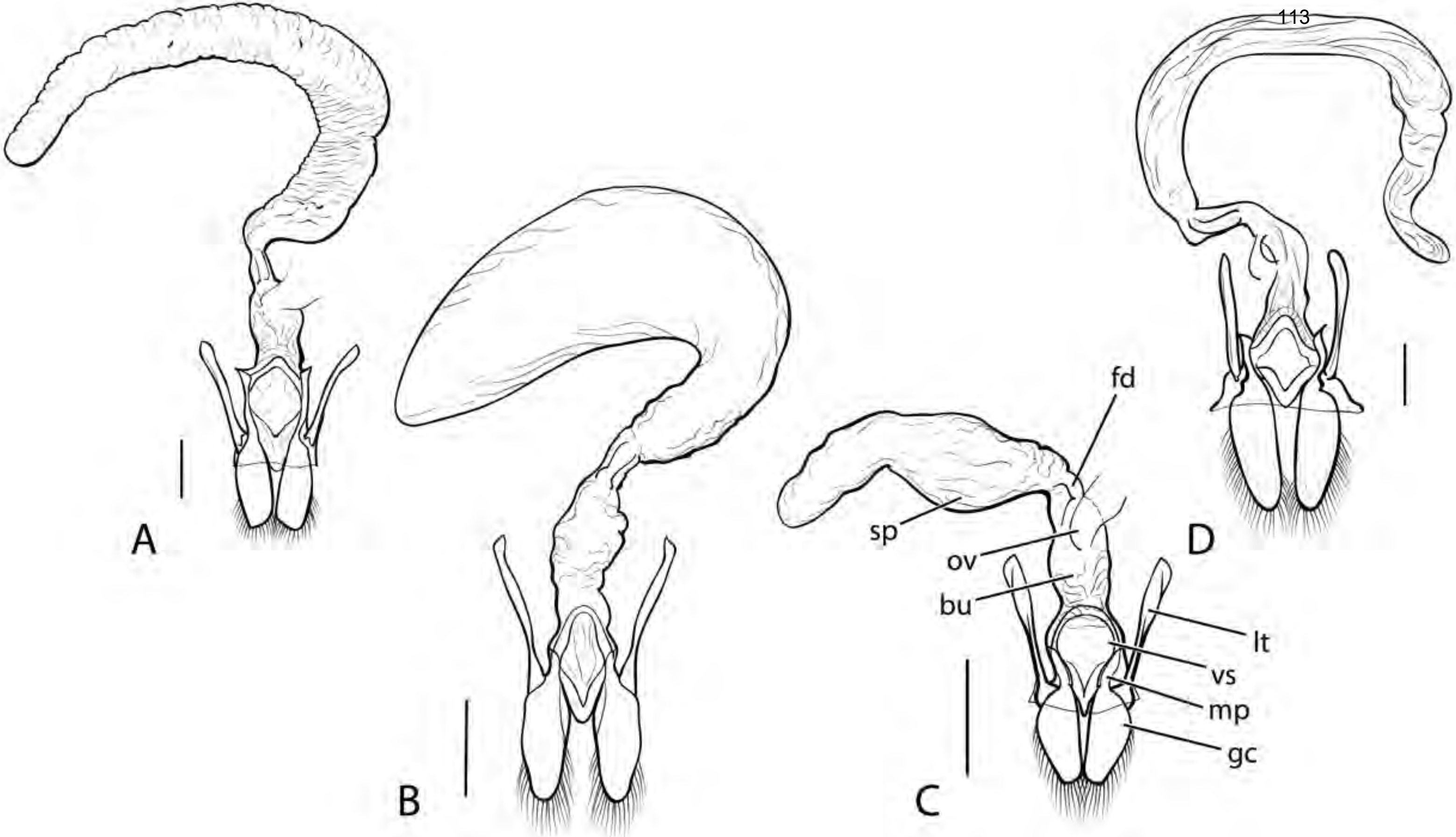
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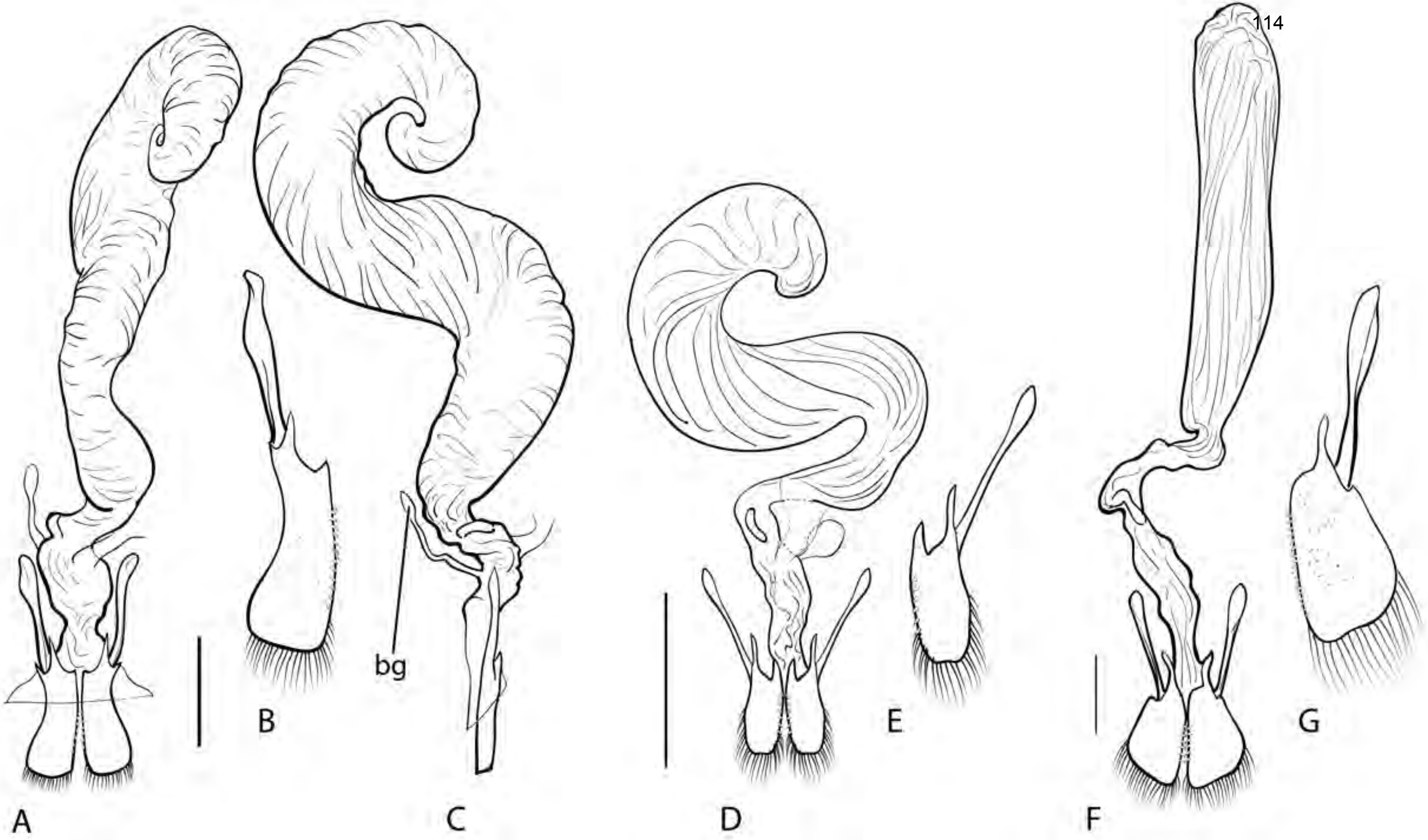
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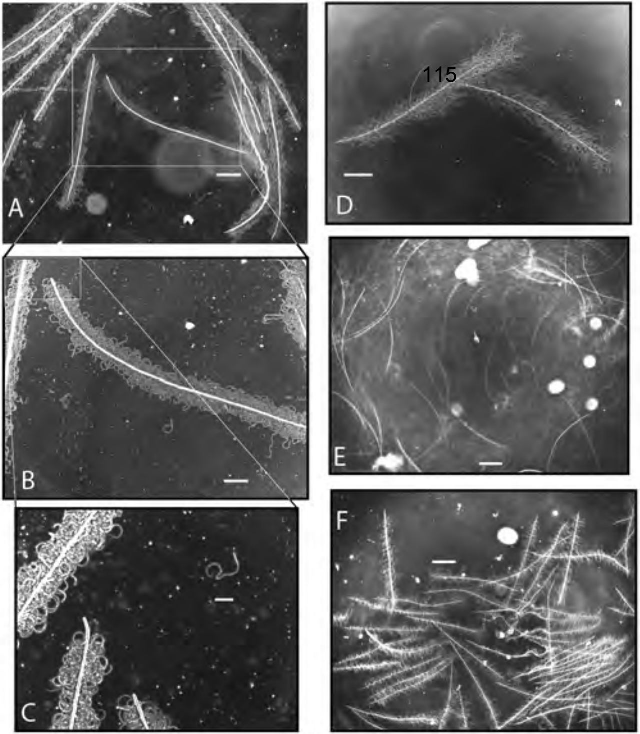
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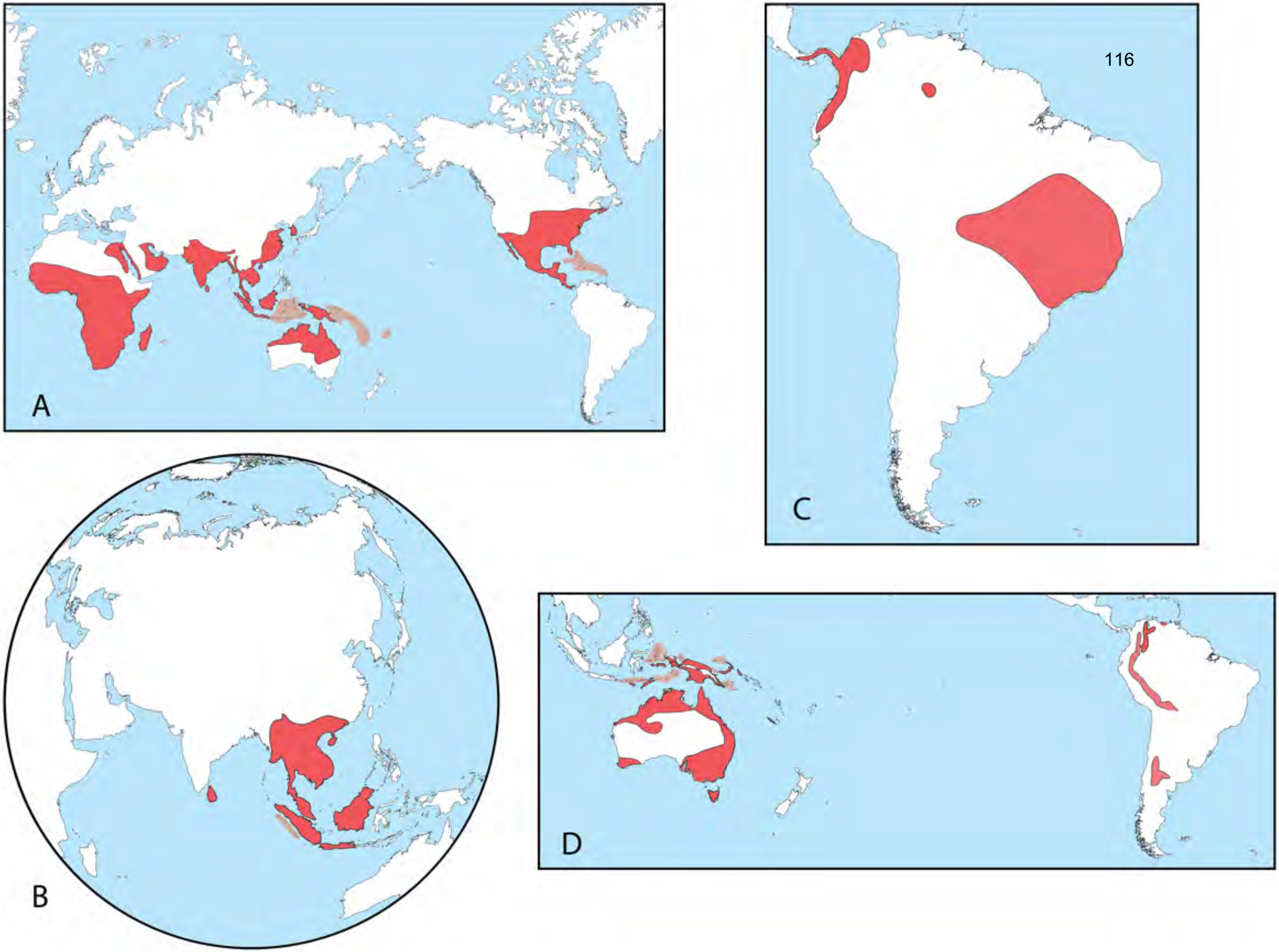
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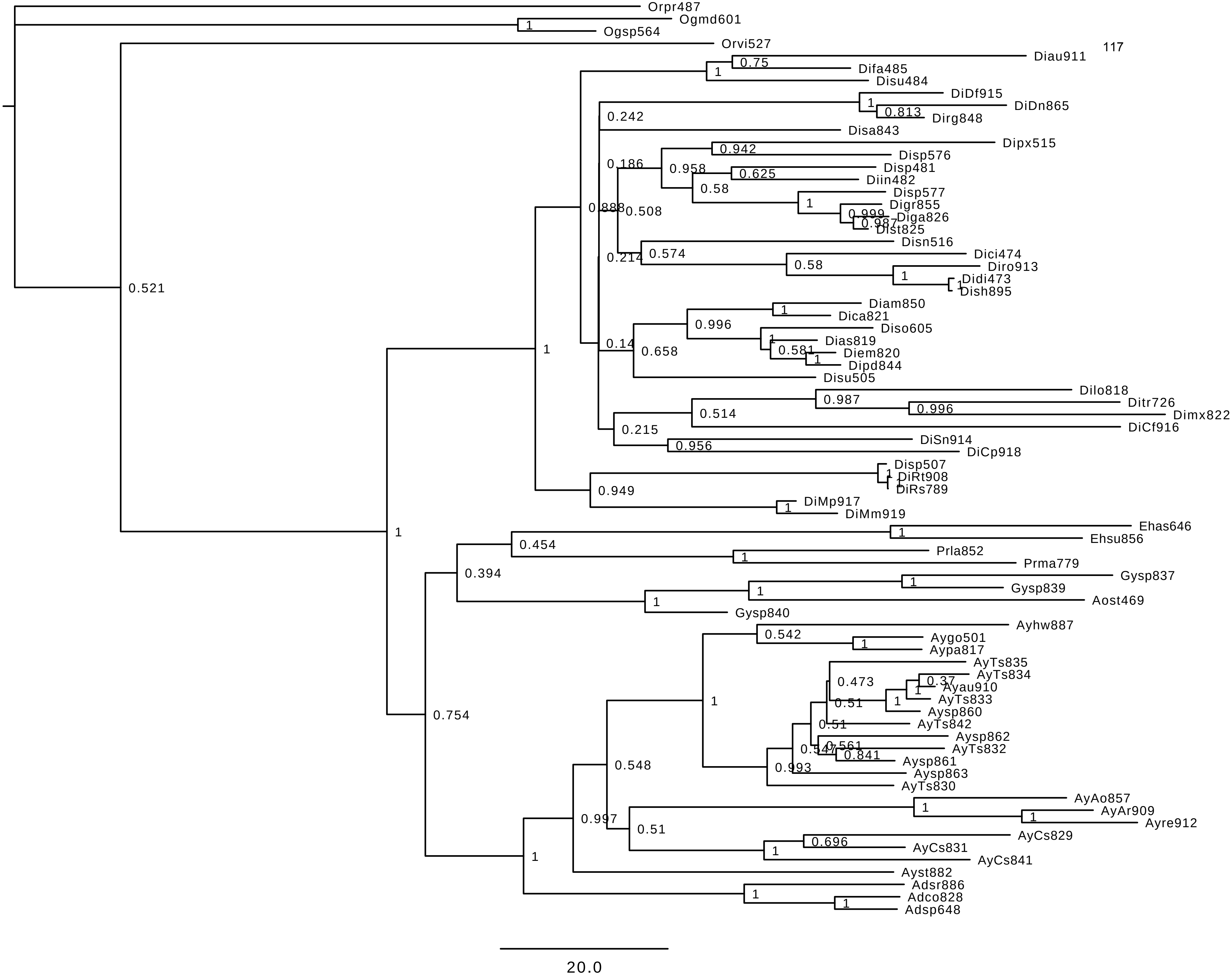
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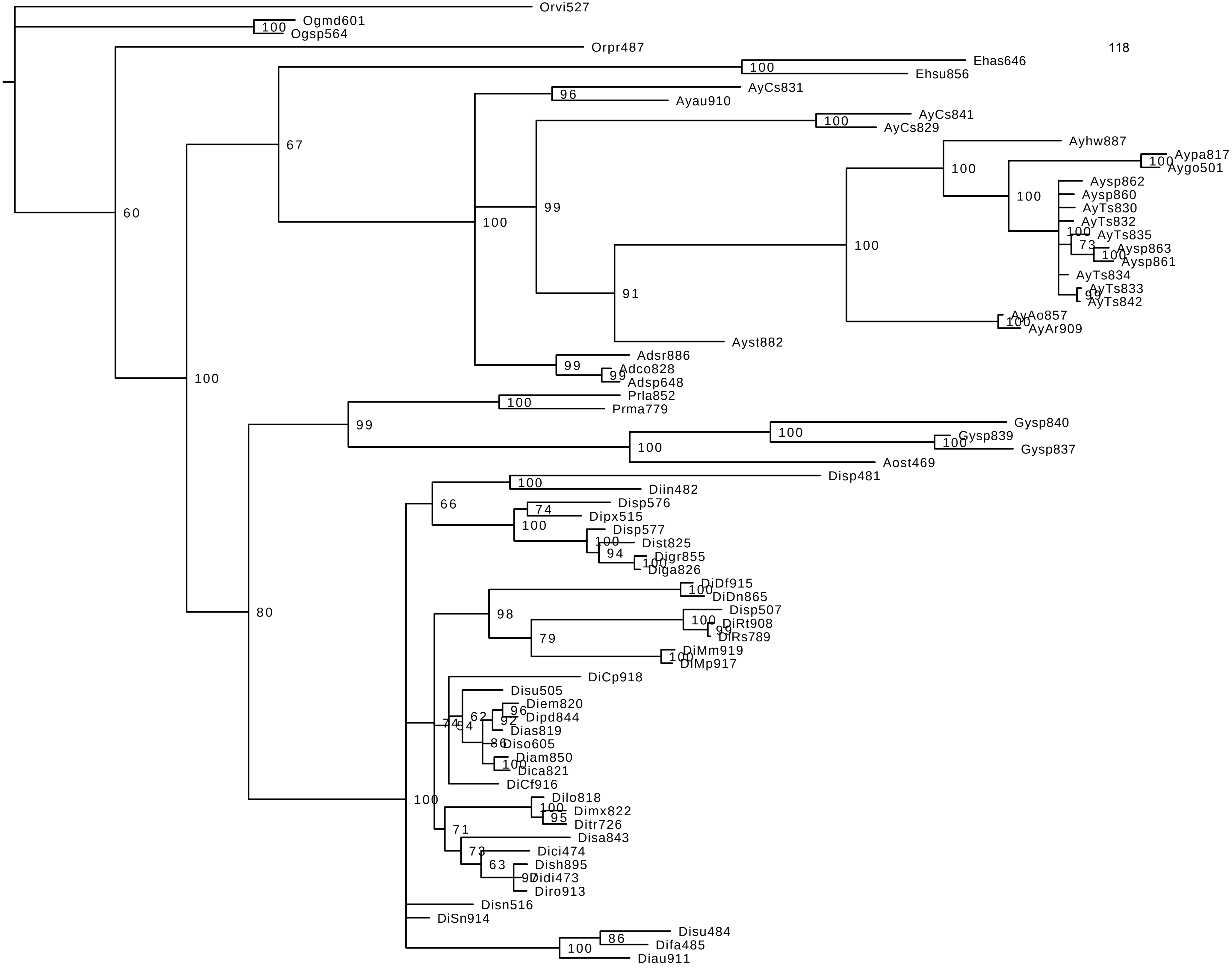
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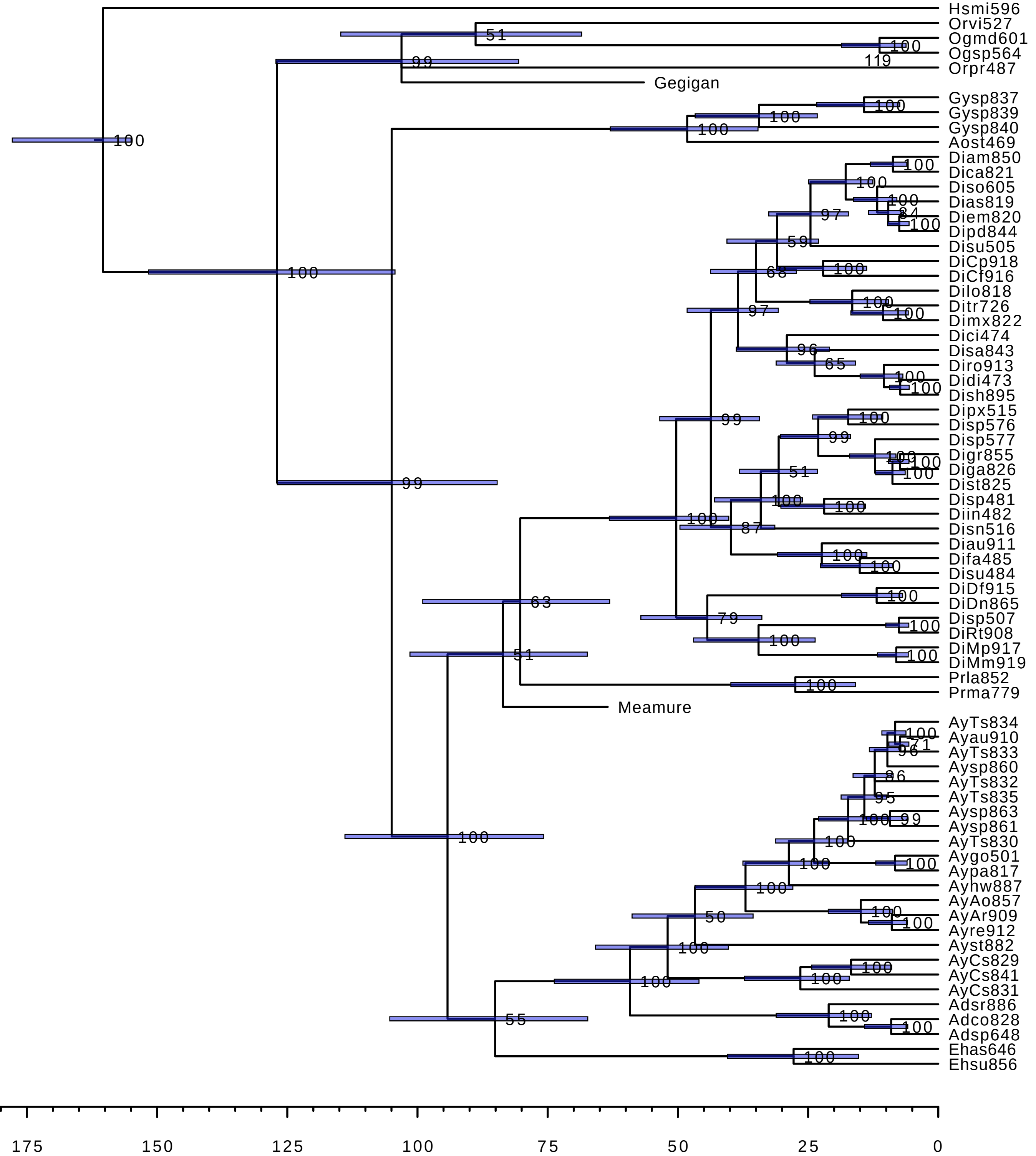
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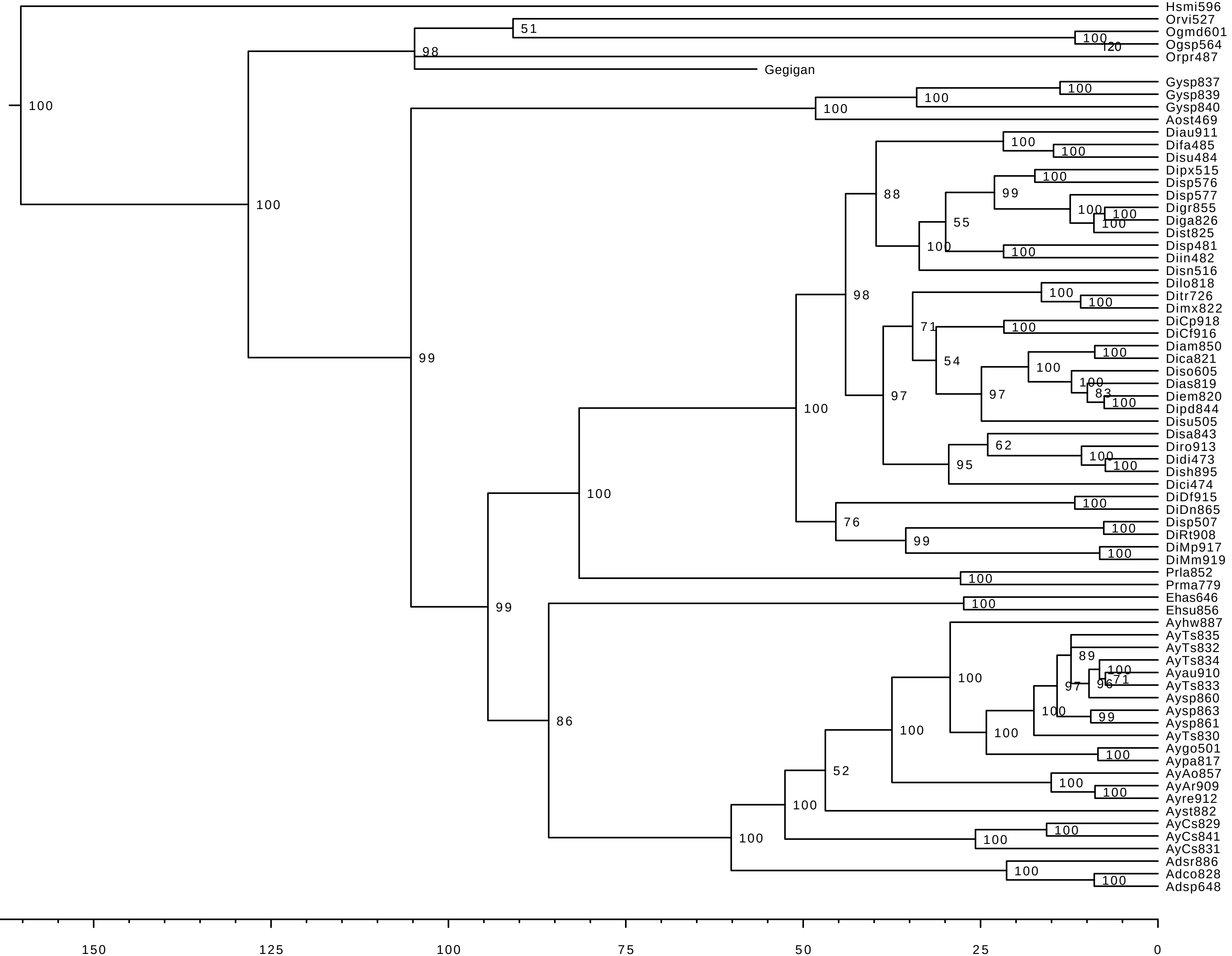
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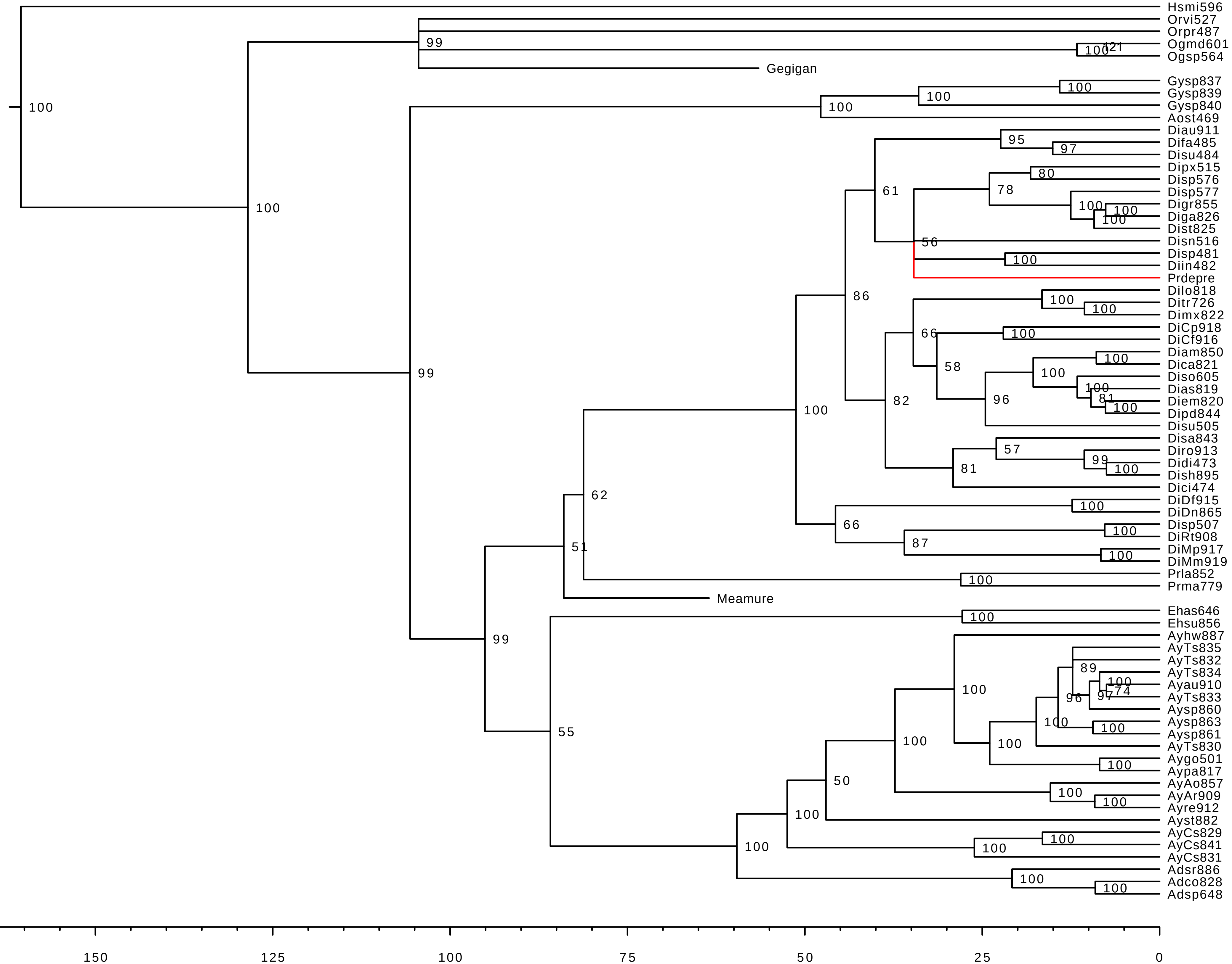
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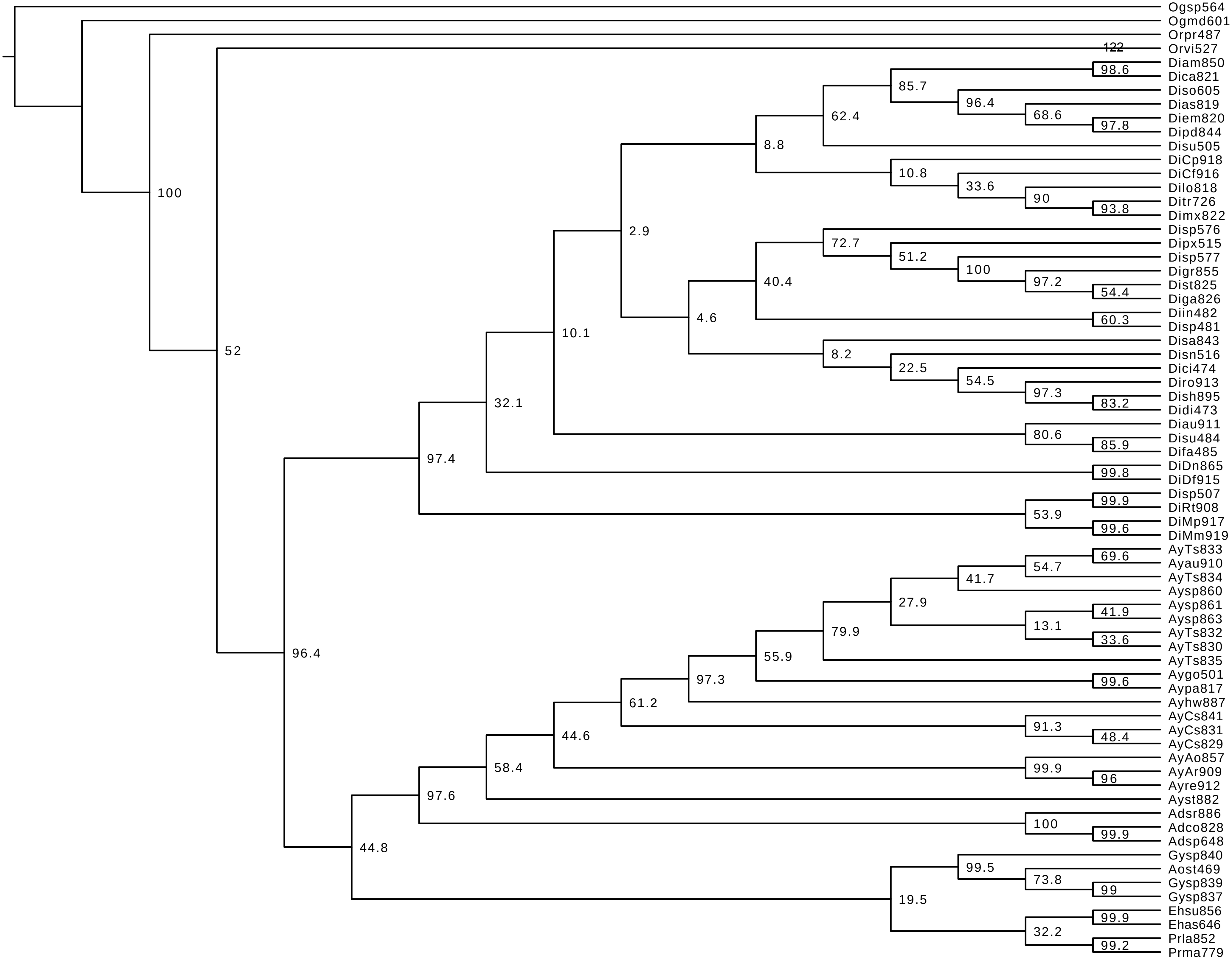
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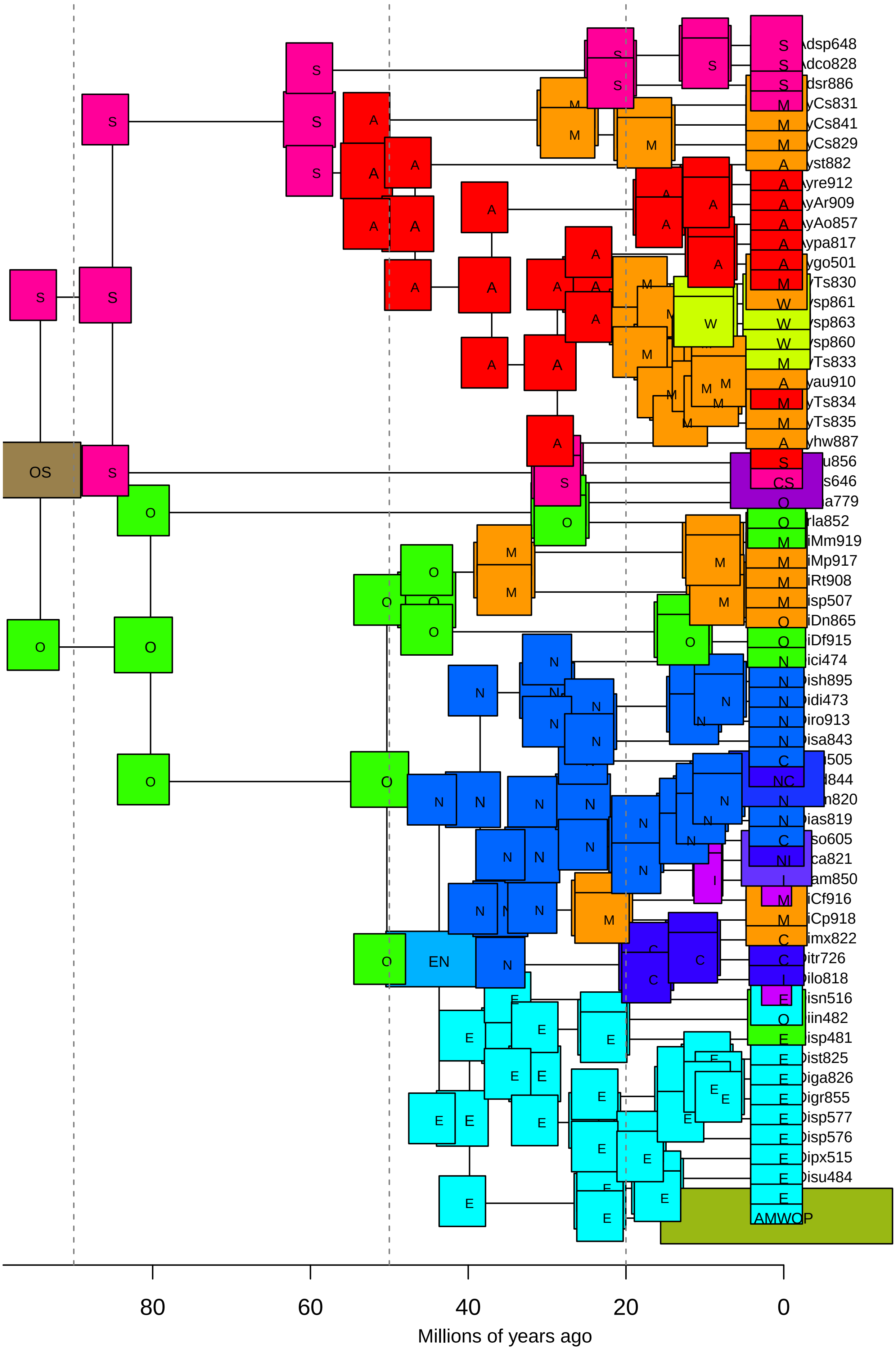

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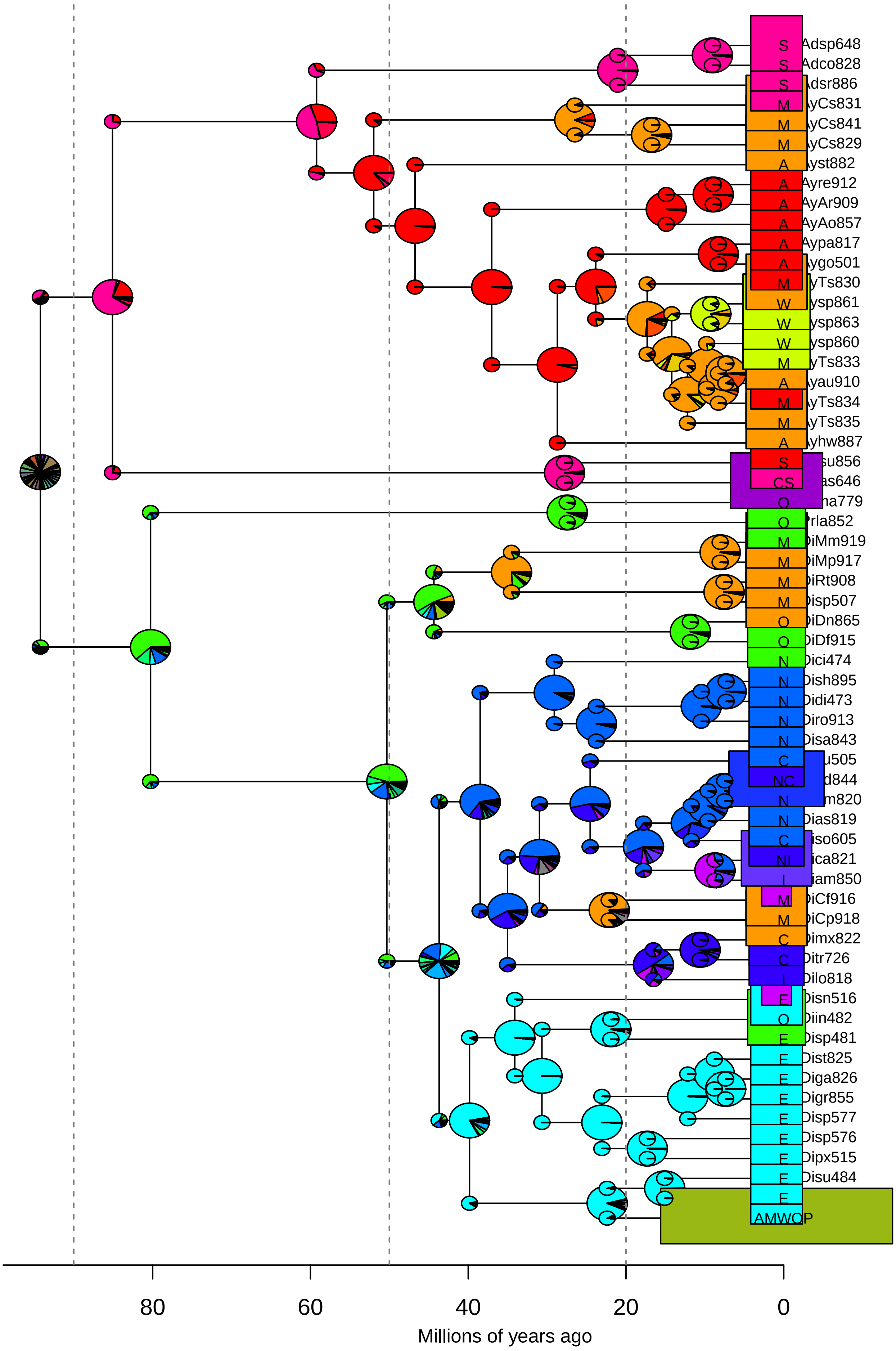

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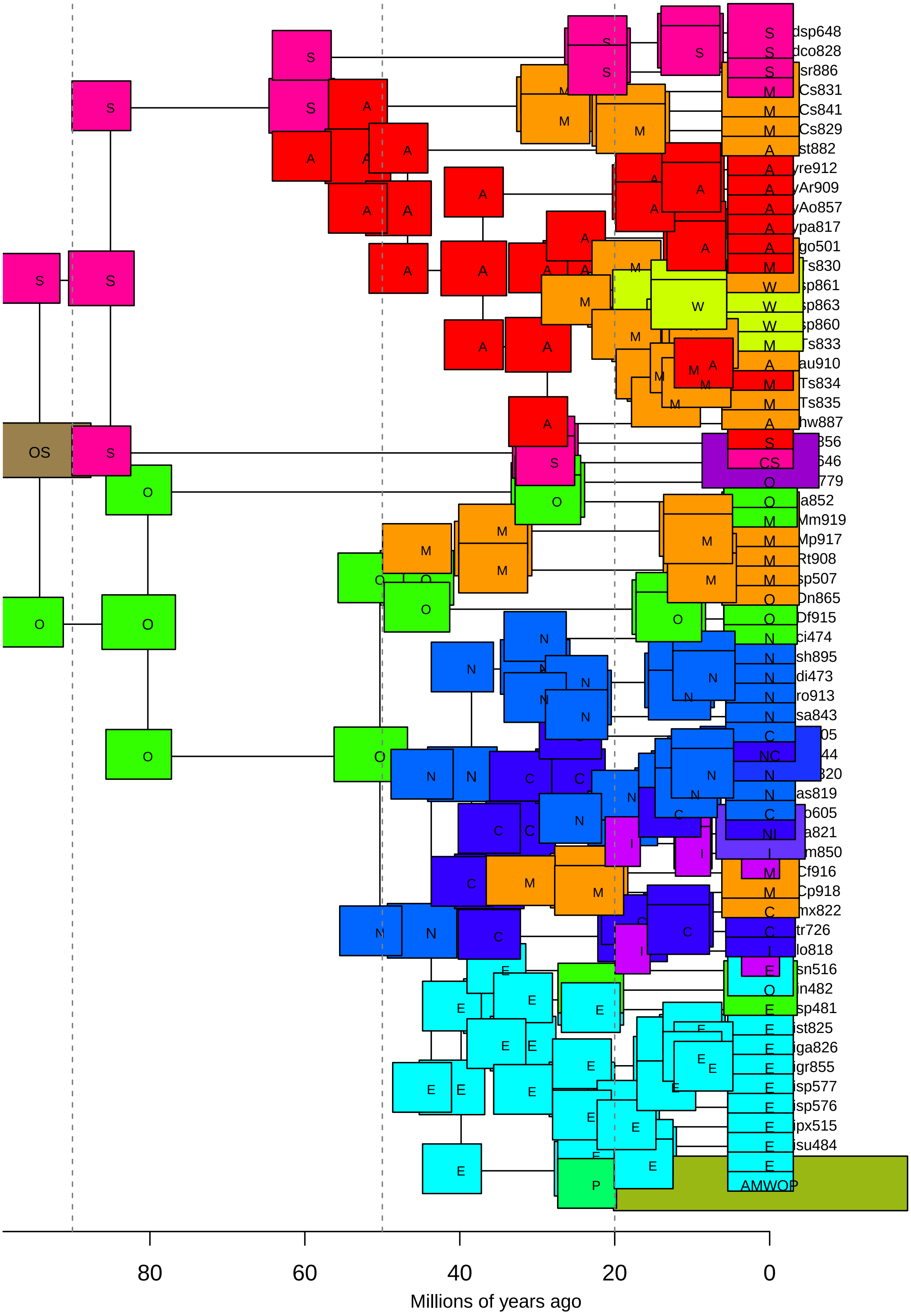

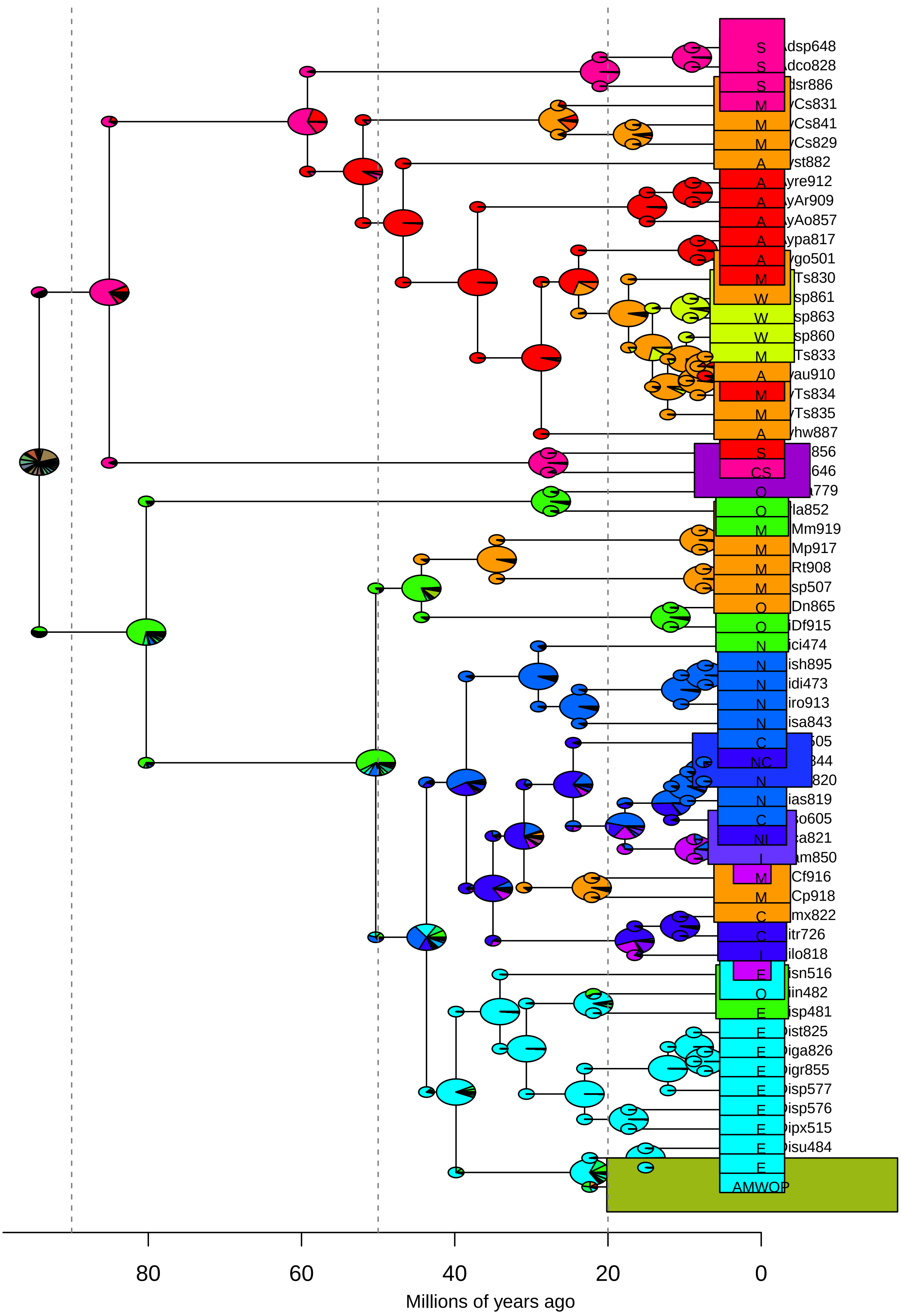
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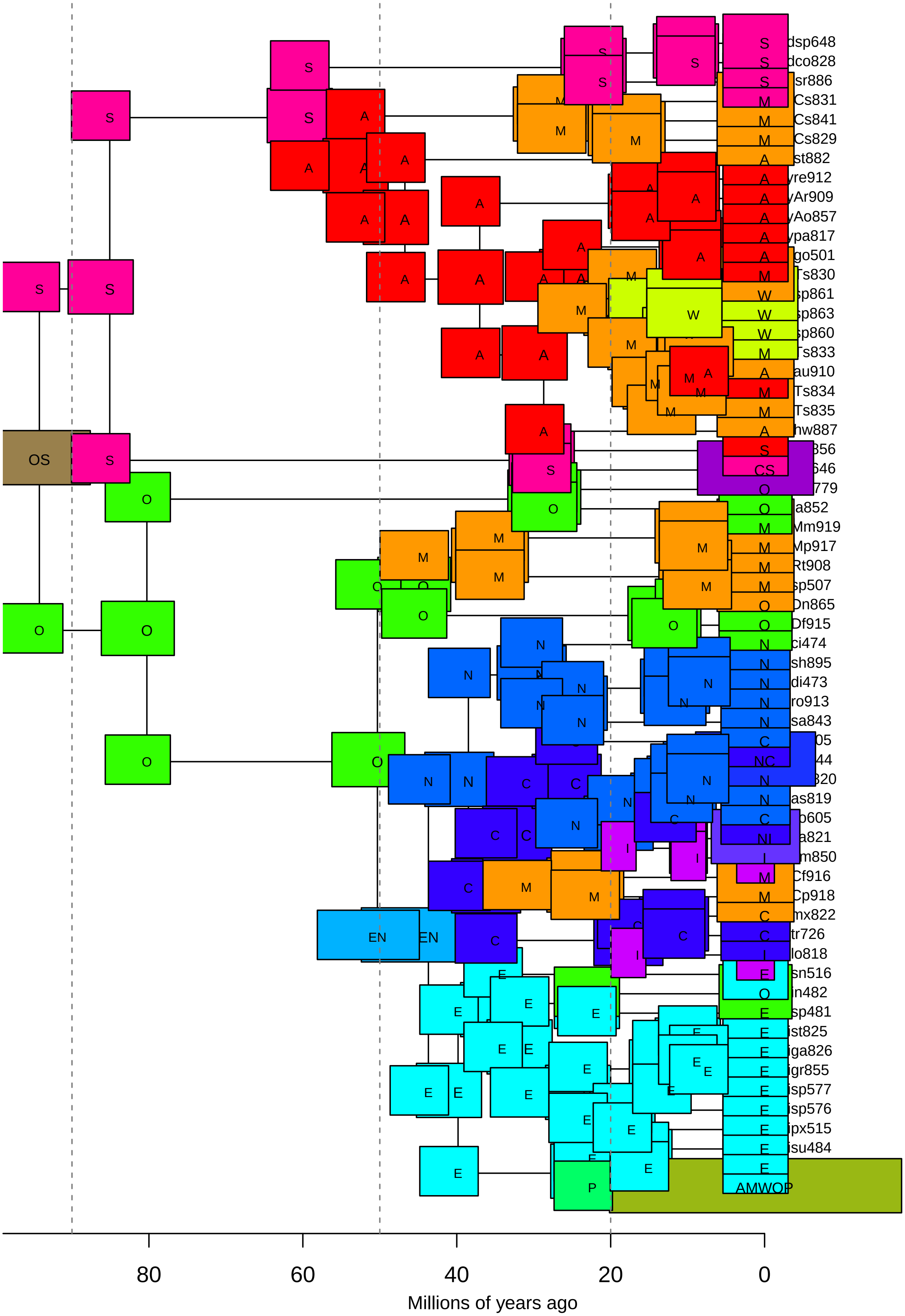

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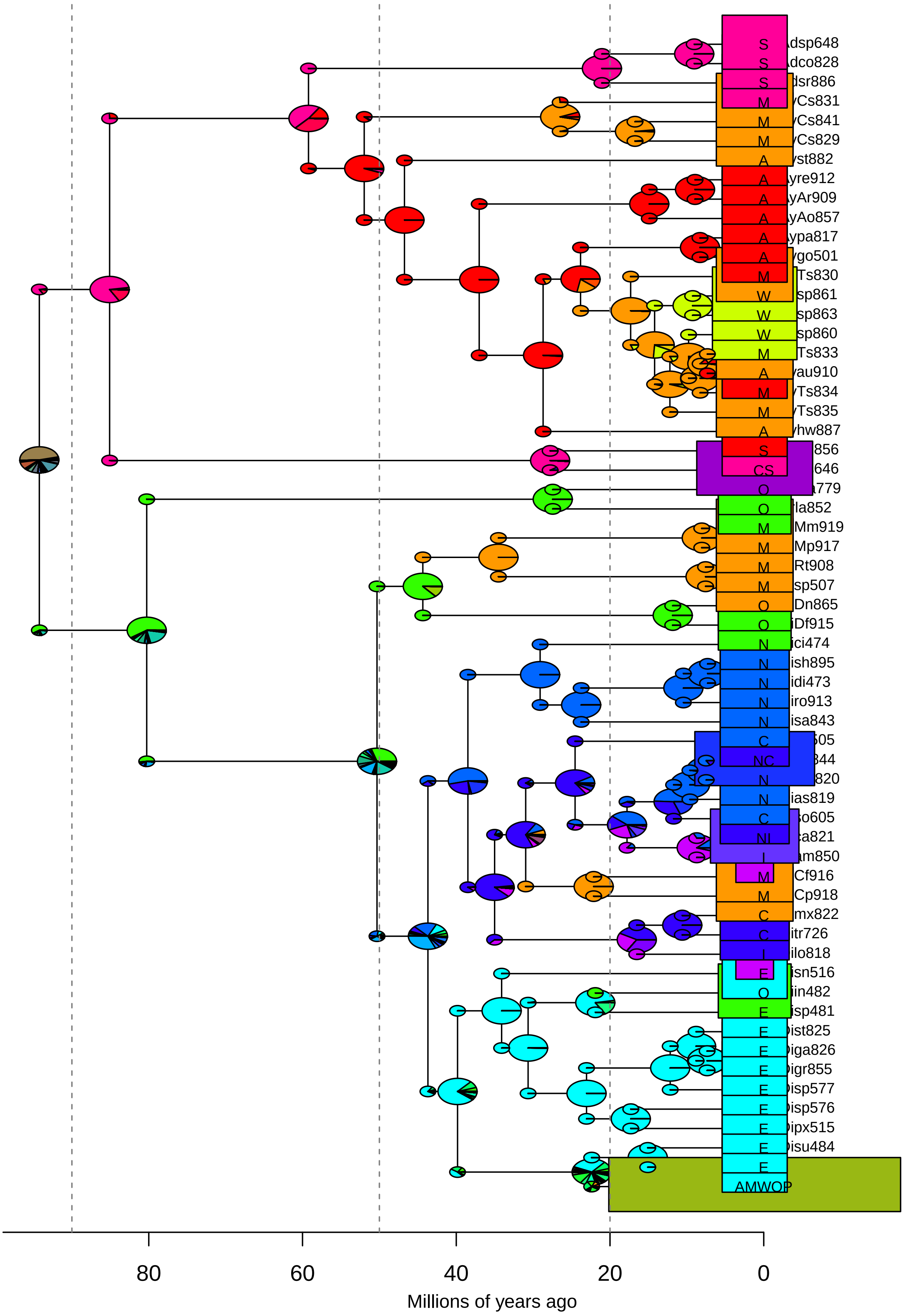

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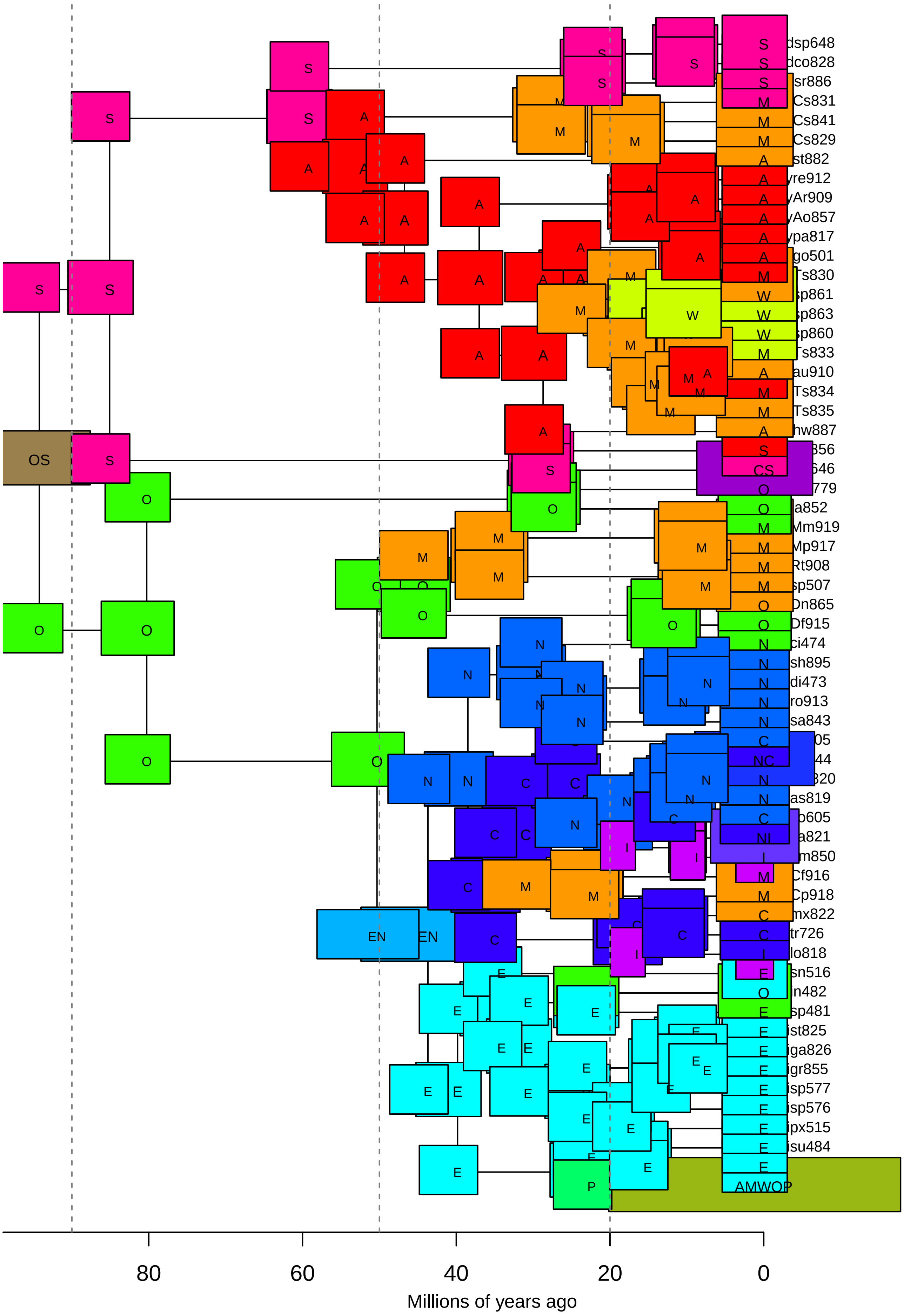

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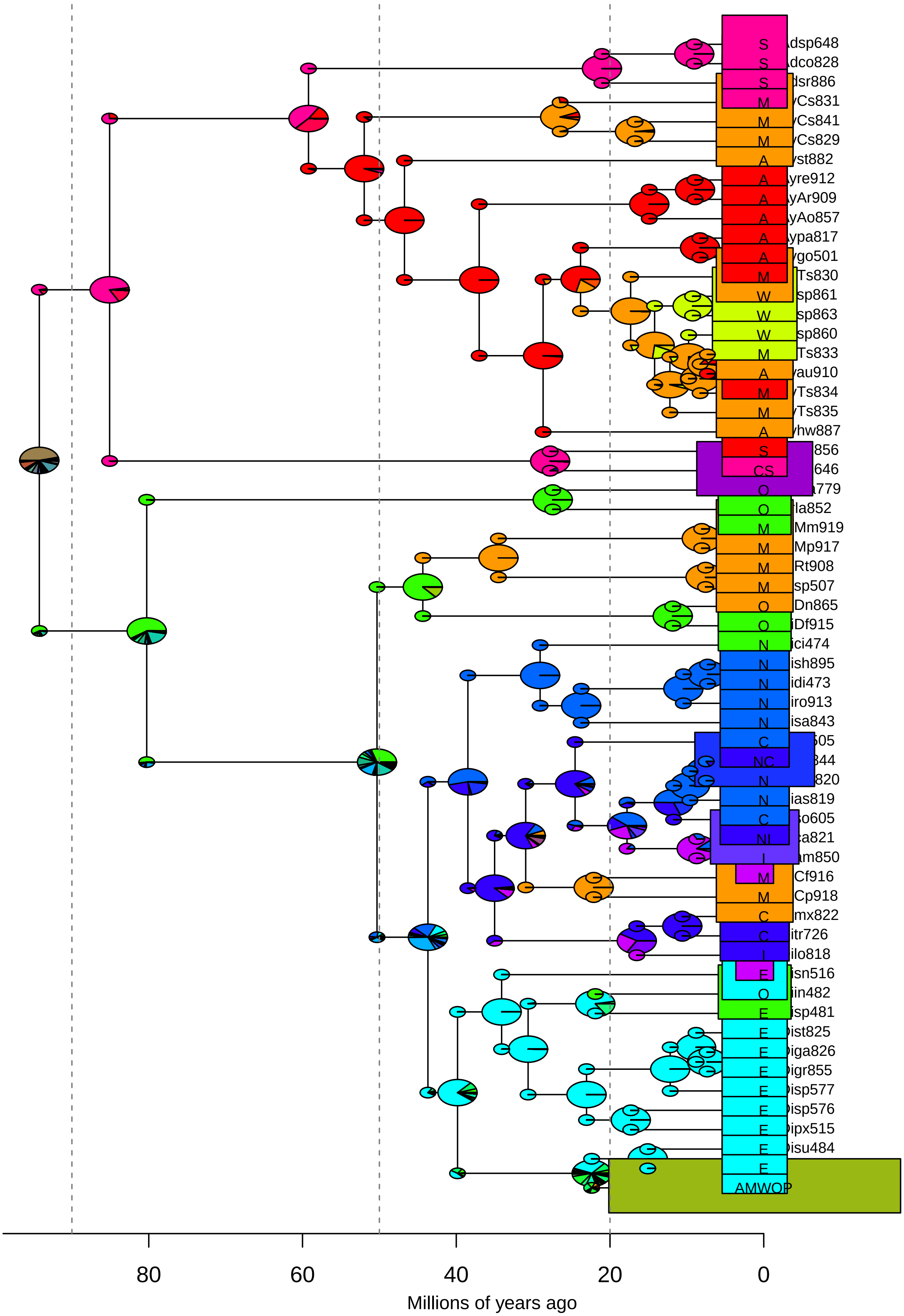

Relicts of early Mesozoic whirligig beetle clades persist in biodiversity hotspots

Grey T. Gustafson[1], Alexander A. Prokin[2], Rasa Bukontaite, Kelly B. Miller[1], Johannes Bergsten[3]

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Madagascar's distinctive fauna has long fascinated biologists; its unique geologic history including an extensive period of isolation following the break up Gondwana[1], has been proposed to account for its unique biodiversity[2]. However, most of Madagascar's extant fauna is found to have originated recently during the Cenozoic[2-4]. Whirligig beetles (Coleoptera, Gyrinidae) are a common aquatic insect group, with a global distribution[5], and numerous endemic Malagasy taxa[6,7]. Here we present the first time-calibrated phylogenetic analysis of the family using novel dating techniques and show a Late Triassic origin, significantly older than the most recent estimate of Middle Jurassic[8]. The Malagasy striped whirligig beetle, *Heterogyrus milloti*, is found to be the sole surviving lineage of the Heterogyrinae, the dominant gyrinid fauna of the Mesozoic era. The origin of the Heterogyrinae is dated to a median age of 196 million years ago making *Heterogyrus* the oldest endemic animal lineage known from Madagascar. The other currently monotypic subfamily, Spanglerogyrinae, has its origin in the Late Triassic. *Spanglerogyrus albiventris* is known only from the North American Coastal Plain, another global biodiversity hotspot[9]. Our findings show a once widespread Mesozoic taxon isolated on Madagascar, which served as a refugium for the last surviving heterogyrine species. The monotypic relictual gyrinid lineages dated to the Early Jurassic provide further evidence of the

persistence of coleopteran lineages and new precedence for invertebrate specific conservation in biodiversity hotspots.

The fauna of Madagascar is among the most unique and threatened biodiversity on the planet[10]. The origin of the island's fauna is of great interest given its central position in Gondwana and extensive isolation following separation from India[1,2]. Few studies, however, have revealed taxa with truly Gondwanan relationships or ancient origins[2]. The most iconic fauna, the lemurs, tenrecs, and unique carnivorans rafted to the island[11] from Africa within the past sixty million years[3,4,12]. A primarily Cenozoic origin is similarly shared among most of the island's other extant endemic vertebrate fauna[3,4]. Few notable exceptions include oplurine iquanids, podocnemidid turtles, mantellid frogs, and cichlid fish, which show Mesozoic origins[3,4]. Invertebrate groups similarly show mostly Cenozoic origins, but among the dated analyses, also contain some of the oldest endemic lineages currently known (Extended Data Tab. 1).

The whirligig beetle fauna of Madagascar is highly endemic, similar to other aquatic invertebrates[13], with 25 of the 26 known species found nowhere else[6,7]. Notable among the Malagasy fauna is *Heterogyrus milloti*, the Malagasy striped whirligig beetle, for its intriguing morphology uniting it with several groups of Gyrinidae[7]. Molecular data have only recently been utilized for phylogenetic analysis of the Gyrinidae[5]. This previous study placed the monotypic *Heterogyrus* in its own subfamily, as sister to the Gyrininae, containing the vast majority of species, but without strong support[5]. The family has also never received a time-calibrated phylogenetic reconstruction, preventing timing of diversification from being known.

Phylogenetic analyses employing novel Bayesian total-evidence fossil calibration[14] were performed on nine fossil and 128 extant gyrinid taxa. Total-evidence calibration constructs a time-calibrated tree, while simultaneously placing fossil taxa within the phylogeny during analysis[14]. This calibration technique is desirable to node-based methods as it incorporates inherent uncertainty regarding fossil taxa's relationship to extant diversity[14]. Previous iterations of these analyses implemented in MrBayes 3.2.5 were found to give suspiciously old ages for clades lacking fossils[15]. For this reason a novel Fossilization-Birth-Death (FBD) model[16] was introduced in MrBayes 3.2.6 to improve dating accuracy[15].

Origins of the family Gyrinidae are dated to the Late Triassic (95% highest probability density (hpd) 203 – 259 Ma, median 95% hpd (m) 228 Ma). This age is significantly older than the most recent estimate for the family[8], and while closer to prior estimates[17,18] is still older. The earliest diverging lineage, Spanglerogyrinae, is found to have originated in the Early Jurassic (hpd 175 – 200 Ma, m 185 Ma) and the fossil genus *Angarogyrus* is now a member of this subfamily (Fig. 1), rendering it no longer monotypic. Reexamination of the *Angarogyrus* fossils reveals remarkable similarity to the extant genus *Spanglerogyrus* (Fig. 3). Both have a unique quadrate frons, with the frontolateral margins continued posteriorly over the dorsal eye (Fig. 3a', c', d), a pronotum with a strong medial lobe projecting anteriorly onto the head capsule (Fig. 3a', c', d), and a very small in body size (Fig 3a,b,c). An exceptionally well-preserved elytron of *Angarogyrus minimus* shows similar coloration to the extant *Spanglerogyrus albiventris* and covering of setae (Fig. 3e,f). *Spanglerogyrus* is clearly an exceptionally relictual taxon, exhibiting little morphological change since the Early Jurassic.

The analyses unequivocally support placement of *Heterogyrus* as sister to the Gyrininae (Fig. 1). Several morphological characters shared with *Spanglerogyrus* (Extended Data Fig. 1) strongly support this distinction, including the medially divided labrum (Extended Data Fig. 1a, b), retention of the medial spur of the protibia, (Extended Data Fig. 1c, d), and the pronotum with a well-developed median lobe (Fig. 3d, 4e). The subfamily Heterogyrinae is no longer monotypic. The extinct genera *Baissogyrus* (Fig. 4c, c'), *Cretotortor* (Fig 4a, a'), and *Mesogyrus* are placed within the Heterogyrinae with strong support (Fig. 1). The origin of the Heterogyrinae is placed in the Mid- to Early Jurassic (hpd 157 – 188 Ma, m 170Ma). The fossil record shows the heterogyrine genera were widely distributed and found throughout the Mesozoic (Fig. 2), clearly forming the dominant gyrinid fauna. Morphology of the exceptionally preserved fossil *Mesogyrus antiquus* (Fig. 4g, g') from the well-known Karatau deposits[19], compared to that of the extant Malagasy *Heterogyus milloti* (Fig. 4b, d, e, f), shows morphologically heterogyrines have changed very little throughout their evolutionary history. The Karatau deposits are the remains of a large, stable, freshwater, Jurassic lake[20], indicating *M. antiquus* was lentic, compared to the extant *H. milloti* known only from small trickling mountain streams[5], suggesting increased ecological diversity in the past.

No insect fossils have been described from Madagascar, limiting our inference of Mesozoic Malagasy fauna to the well studied fossil vertebrates[21]. The fossil vertebrate fauna at the end Cretaceous of Madagascar is composed of widespread Gondwanan lineages, such as sauropod, non-avian therapod dinosaurs, crocodyliforms, anurans, and snakes[22]. These widespread lineages likely became isolated on Madagascar following Gondwana's breakup, given many were not good dispersers (i.e. therapod and sauropod dinosaurs) and the unlikelihood of a land bridge[22]. The fossil evidence (Fig. 2) shows the Heterogyrinae were widespread across Laurasia, but given both the age of the estimated most recent common ancestor (Fig. 1) and the only extant member being found in Madagascar, were probably similarly distributed in Gondwana. The current Laurasian-only-distribution is very likely a result of sampling bias as the vast majority of known Jurassic insect deposits are Palearctic, with exceptionally few

Gondwanan Jurassic insect fossils known primarily from deposits in Antarctica[19]. The heterogyrine lineage leading to *Heterogyrus* most likely arrived similarly to other Mesozoic fauna of the time, having become isolated from relatives in Africa or South America following the break up of Gondwana[22]. The phylogeny (Fig. 1) has *Heterogyrus* diverging from *Cretotortor archarensis* between 138 Ma – 90 Ma (hpd) (m = 109 Ma), but this estimate is unreliable given the Laurasian distribution of *Cretotortor archarensis,* the isolated position of Madagascar at this time, the low posterior probability associated with the node, and likely is an artifact of the limited available sampling.

A distinct transition is seen in the fossil record of the Gyrinidae following the K-T boundary (Fig. 2), where the Heterogyrinae are replaced by the Gyrininae as the dominant whirligig beetle fauna. Madagascar appears to have served as a refugium for the last heterogyrine lineage, having been isolated since the break up of Gondwana, while heterogyrines went extinct elsewhere. In Madagascar, the extant *Heterogyrus milloti* has a very limited distribution, known only from two localities in the southeast with old geologic origins: the mountains near mount Andringitra[6,23], whose origins date to the Permian; and the other in the nearby mountainous cloud forests of Ranomafana[5]. Here *Heterogyrus* is only encountered in small trickling streams, where no other gyrinids are found. A variety of gyrinine species are found on the larger streams and ponds in the surrounding area at lower elevations. Fossils of heterogyrines are known from a variety of habitats such as large lakes (Fig. 2) (i.e. *Mesogyrus antiquus* known from the Karabastau formation and *M. elongates* from the Sharteg formation[24]) as well as fluvial deposits (*Cretotortor zherichini* from the Kzyl-Zhar deposits), similar to modern Gyrininae, suggesting the current unique habitat of *Heterogyrus milloti* represents a final stronghold for this relictual species.

The other Malagasy gyrinid fauna, members of the Gyrininae, exhibit a more typical pattern, diverging from African sister taxa, within the Cenozoic (Fig. 1). The notable exception being *Orectogyrus cyanicollis* and *O. hastatus*, which show a Late Cretaceous divergence (hpd 66 Ma – 99 Ma, m 83 Ma) from their African sister taxa (Fig. 1). The late arrival of the gyrinines lends further support for an early arrival of the ancestor of *H. milloti*, as gyrinines appear to have replaced heterogyrines elsewhere. The heterogyrine lineage extant today was able to persist via isolation on Madagascar following the break up of Gondwana, and remaining isolated in a unique habitat in an isolated mountain chain, to become the oldest endemic animal lineage on Madagascar.

The Spanglerogyrinae and Heterogyrinae serve as exemplars of the persistence of coleopteran lineages contributing to the diversity of the group [18], and the unique nature of the fauna of Madagascar. Our findings of two currently monotypic gyrinid subfamilies representing the sole surviving lineages of the Mesozoic fauna are remarkable. Importantly both species are only known from very few localities, within threatened biodiversity hotspots. Given the exceptionally unique evolutionary story arthropod lineages tell, greater consideration should be given to arthropod inclusive conservation[25] to protect these last remaining Mesozoic gyrinid lineages, and other unique arthropod lineages.

Figure legends

Figure 1. **Phylogenetic relationships of the Gyrinidae**. Tree from Bayesian analysis using the FBD macroevolutionary model[15,16]. Blue bars show 95% highest posterior density age range (hpd), dates at select nodes represent median (m) age from the hpd. The asterisk above select nodes indicates high support (≥ 95% posterior probability). Red branches denote Malagasy

lineages. Gray triangles show selected fossils' phylogenetic placement as terminals, unique to the total evidence approach[14]. Fossils and dineutine exemplar not to scale.

Figure 2. Table of known gyrinid fossils. Green indicates heterogyrine fossil species, teal gyrinine fossil species, and yellow spanglerogyrine fossil species.

Figure 3. Spanglerogyrine species. Arrows indicate important morphological features, abbreviations pro = pronotum, frs = frons, frl = frons lateral margin. **a**, *Angarogyrus mongolicus* fossil no. 3149/970 (**a'**) line drawing of specimen. **b**, *Spanglerogyrus albiventris* dorsal habitus, scale bar = 1 mm. **c**, *Angarogyrus minimus* fossil no. 1670/385, scale bar = 1 mm (**c'**) line drawing of specimen. **d**, scanning electron microscope (SEM) of *Spanglerogyrus albiventris* pronotum and head, scale bar = 500 µm. **e**, *Spanglerogyrus albiventris* lateral habitus to scale with **b**. **f**, *Angarogyrus minimus* elytron fossil no. 1670/385 scale bar = 1 mm.

Figure 4. Heterogyrine species. Arrows indicate important morphological features. **a**, *Cretotortor zherichini* elytron fossil no. 3149/970 (**a'**) line drawing of specimen. **b**, *Heterogyrus milloti* elytron SEM, scale bar = 1 mm. **c**, *Baissogyrus savilovi* holotype fossil no. 1668/1787, scale bar = 1 mm (**c'**) line drawing of specimen. **d**, the Malagasy striped whirligig beetle, *H. milloti* dorsal habitus, scale bar 2 mm. **e**, pronotum of *H. milloti*. **f**, thorax and abdomen of *H. milloti* ventral view, scale bar = 2 mm. **g**, *Mesogyrus antiquus* fossil no. 2997/1846, scale bar = 2 mm, (**g'**) line drawing of specimen.

Methods

No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assement.

Phylogenetic analysis.

The entire phylogenetic dataset from Miller & Bergsten, 2012 was utilized, with the exception of the morphological portion. Thirty-three additional ingroup gyrinid taxa and one outgroup taxon, *Haliplus lineatocollis*, were added to the analysis (Extended Data Tab. 2). Additional taxa included sequences for all genes except EF1α which was found to have multiple copies in Gyrinidae[5]. Thirteen fossil taxa were included, four outgroup taxa, and five ingroup (Extended Data Tab. 3). The fossil *Coptoclava longipoda* was originally included in the dataset but was removed for the analysis. In total taxon sampling for the analysis included ten outgroup Hydradephaga species and 128 gyrinid taxa.

The same genes and primers were used as in Miller & Bergsten, 2012. A novel morphological character set of 120 characters was established (Supplementary Data 1) and taxa were coded as in Supplementary Data Table 1. This brought the total character number up from that of Miller & Bergsten, 2012 to 3438. The same partitioning scheme was used in Miller & Bergsten, 2012.

Bayesian phylogenetic analysis was implemented using MPI version of MrBayes 3.2.6 [15,26] and were run on the super computer cluster 'Ulam' at the Center for Advanced Research Computing (CARC), University of New Mexico. No substitution model was selected *a priori*, instead the reversible-jump MCMC method with gamma rate variation across sites was used to test the probability of different models *a posteriori* during analysis [5,26,27]. To infer the substitution rate the methods outlined by Ronquest et al. 2012 were followed with the mean age of the fossil *Moravocoleus permianus* (293 Ma), the oldest known Coleopteran[28], used to calculate median rate, and the mean age of *Triaplus sibiricus* (253 Ma), the oldest known aquatic Adephagan[28], for the standard deviation. The Fossilization-Birth-Death macroevolutionary model [16] was employed using the methods outlined by Zhange et al. 2015. The sampling strategy was set to diversity, with a sample probability of 0.01 as there are an estimated 1000 species of Gyrinidae[29]. Fossils were given a uniform age prior based on the age of the fossil. The tree root was constrained and with a calibration point given a uniform prior with the minimum age based on the age of *T. sibiricus* and the maximum on *M. permianus*. The analysis was run for 10 million generations, using four chains (three heated, one cold), with swap number set to two, and a temperature of 0.1 for the heated chains. MCMC convergence was monitored using Tracer v.1.6 [30].

References

1 Briggs, J. C. The biogeographic and tectonic history of Inida. *Journal of Biogeography* **30**, 381-388 (2003).

2 Yoder, A. D. & Nowak, M. D. Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annual Review of Ecology, Evolution, and Systematics* **37**, 405-431, doi:10.1146/annurev.ecolsys.37.091305.110239 (2006).

3 Crottini, A. *et al.* Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K-T boundary in Madagascar. *Proceedings of the National Academy of Sciences* **109**, 5358-5363 (2012).

4 Samonds, K. E. *et al.* Imperfect isolation: factors and filters shaping Madagascar's extant vertebrate fauna. *PLoS ONE* **8**, e62086, doi:10.1371/journal.pone.0062086 (2014).

5 Miller, K. B. & Bergsten, J. Phylogeny and classficiation of whirligig beetles (Coleoptera: Gyrinidae): relaxed-clock model outperforms parsimony and time-free Bayesian analyses. *Systematic Entomology* **37**, 705 – 746 (2012).

6 Brinck, P. A revision of the Gyrinidae (Coleoptera) of the Ethiopian region. I. *Acta Universitatis Lundensis. Nova Series* **51**, 1 – 144 (1955).

7 Brinck, P. A revision of the Gyrinidae (Coleoptera) of the Ethiopian region. II. *Acta Universitatis Lundensis. Nova Series* **52**, 1 – 190 (1956).

8 McKenna, D. D., Wild, A. L., Kanda, K. & al., e. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology* **40**, 835-880 (2015).

9 Noss, R. *Annoucing the world's 36th biodiversity hotspot: the North American Coastal Plain*, <http://www.cepf.net/news/top_stories/Pages/Announcing-the-Worlds-36th-Biodiversity-Hotspot.aspx> (2016).

10 Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M. & Gascon, C. in *Biodiversity hotspots: distribution and protection of conservation priority areas* (eds F.E. Zachos & J.C. Habel) Ch. 1, 3 - 22 (Springer, 2011).

11 Ali, J. R. & Huber, M. Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* **463**, 653-656, doi:10.1038/nature08706 (2010).

12 Poux, C. *et al.* Asynchronous colonizations of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from Nuclear genes. *Systematic Biology* **54**, 719-730 (2005).

13 Benstead, J. P. *et al.* Conserving Madagascar's Freshwater Biodiversity. *BioScience* **53**, 1101-1111 (2003).

14 Ronquist, F. *et al.* A total-evidence approach to dating with fossils, applied to the early radiation of Hymenoptera. *Systematic Biology* **61**, 973-999 (2012).

15 Zhang, C., Stadler, T., Klopfstein, S., Heath, T. A. & Ronquist, F. Total-evidence dating under the fossilized birth-death process. *Systematic Biology* **00**, 1-22, doi:10.1093/sysbio/syv080 (2015).

16 Heath, T. A., Huelsenbeck, J. P. & Stadler, T. The fossilized birth-death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences*, E2957-E2966, doi:10.1073/pnas.1319091111 (2014).

17 McKenna, D. D. & Farrell, B. D. in *The Timetree of Life* (eds S.B. Hedges & S. Kumar) 278-289 (Oxford University Press, 2009).

18 Hunt, T. *et al.* A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* **318**, 1913-1916 (2007).

19 Grimaldi, D. & Engel, M. S. *The Evolution of Insects*. 755 pp. (Cambridge University Press, 2005).

20 Dzik, J., Sulej, T. & Niedźwiedzki, G. Possible link connecting reptilian scales with avian feathers from the early Late Jurassic of Kazakstan. *Historical Biology* **22**, 394-402 (2010).

21 Krause, D. W. *et al.* Late Cretaceous terrestrial vertebrates from Madagascar: implications for Latin American biogeography. *Annals of the Missouri Botanical Garden* **93**, 178-208 (2006).

22 Ali, J. R. & Krause, D. W. Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: refutation of the Gunnerus Ridge causeway hypothesis. *Journal of Biogeography* **38**, 1855-1872 (2011).

23 Legros, C. Un gyrinide nouveau de Madagascar (Coeloptera). *Naturaliste Malgache* **V**, 63 – 67 (1953).

24 Ponomarenko, A. G. *et al.* Upper Jurassic lagerstätte Shar Teg, southwestern Mongolia. *Paleontological Journal* **48**, 1573-1682 (2014).

25 Jenkins, C. N., Guénard, B., Diamond, S. E., Weiser, M. D. & Dunn, R. R. Conservation implications of divergent global patterns of ant and vertebrate diversity. *Diversity and Distributions* **19**, 1084-1092, doi:DOI: 10.1111/ddi.12090 (2013).

26 Ronquist, F., Teslenko, M., Mark, P. & al., e. MrBayes version 3.2: efficient Bayesian phylogenetic inference and model choice, across a large model space. *Systematic Biology* **61**, 539-542 (2011).
27 Huelsenbeck, J. P., Larget, B. & Alfaro, M. E. Bayesian phylogenetic model selection using reversible jump Markov Chain Monte Carlo. *Molecular Biology and Evolution* **21**, 1123-1133 (2004).
28 Ponomarenko, A. G. & Prokin, A. A. Review of paleontological data on the evolution of aquatic beetles (Coleoptera). *Paleontological Journal* **49**, 1383-1412 (2015).
29 Jäch, M. & Balke, M. Global diversity of water beetles (Coleoptera) in freshwater. *Hydrobiologia* **595**, 419—442 (2008).
30 Rambaut, A., Suchard, M. & Drummon, A. *Tracer v1.6*, <http://tree.bio.ed.ac.uk/software/tracer/> (2013).

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Author contributions

G.T.G and J.B.S designed the study. J.B.S. aided in analysis, contributed data, and aid in the field. G.T.G. performed the analyses, constructed morphological data set, coded characters, constructed figures, and wrote the paper. A.A.P. selected outgroup fossil taxa, provided images of fossils, and character coding suggestions. R.B. performed literature review and constructed dated Malagasy lineage table. K.B.M. provided data, specimens, and aid in field work.

Extended Data

Extended Data Table 1. Dated Malagasy lineages.

group	Taxa or clade	taxon	age	min	max	method	genes	reference	doi or ISBN
Birds	vangas	Malagasy vangas	**20**	**n/p**	**n/p**	rate	mt	Reddy, S., et al. 2012	10.1098/rspb.2011.2380
	sunbirds	Souimanga	**0.0258**			clEn	mt	Warren et al. 2003.	10.1016/S1055-7903(03)00063-0
	sunbirds	Souimanga	**0.484**			clEn	mt	Warren et al. 2003.	10.1016/S1055-7903(03)00063-0
	sunbirds	Souimanga	**0.657**			clEn	mt	Warren et al. 2003.	10.1016/S1055-7903(03)00063-0
	sunbirds	Souimanga	**0.779**			clEn	mt	Warren et al. 2003.	10.1016/S1055-7903(03)00063-0
	sunbirds	Souimanga	**0.506**			PL	mt	Warren et al. 2003.	10.1016/S1055-7903(03)00063-0
	sunbirds	Souimanga	**0.935**			PL	mt	Warren et al. 2003.	10.1016/S1055-7903(03)00063-0
	sunbirds	Souimanga	**0.688**			PL	mt	Warren et al. 2003.	10.1016/S1055-7903(03)00063-0
	parrots	Malagasy parrots (*Caracopsis*)	**67#**	**58#**	**77#**	rmc	mt	Wright et al. 2008	10.1093/molbev/msn160
	songbirds	Malagasy/other Megalurines	**25.2**	**21.4**	**31.7**	rmc	mt&nc	Beresford et al. 2005	10.1098/rspb.2004.2997
	owl	*Otus rutilus/Otus mayottensis*	**3.6**	**n/p**	**n/p**	rmc	mt&nc	Fuchs et al. 2008	10.1186/1471-2148-8-197
	wagtails	*Motacilla flaviventris /M. clara + capensis*	**4.5**			mc	mt	Voelker G 2002	9780643065116
	Vangidae	colonization of Madagascar	**28.9**			Brc	mt	Fuchs et al 2006	10.1111/j.1463-6409.2006.00238.x
		Coracina cinerea	**2.23**	**1.78**	**2.70**	Brc	mt	Fuchs et al. 2007	10.1016/j.ympev.2006.10.014
	Vangidae	Malagasy Vangas	**3.72**	**3.15**	**4.26**	Brc	mt	Fuchs et al. 2007	10.1016/j.ympev.2006.10.014
	Songbirds	*H. m. madagascariensis*	**n/p**	**0.4**	**1.8**	mc	mt	Warren et al. 2005	10.1111/j.1095-8312.2005.00492.x
	Songbirds	*Z. m. maderaspatanus*	**0.5**			mc	mt	Warren et al. 2005	10.1111/j.1365-294X.2006.03058.x
	parrots	Malagasy parrots (*Caracopsis*)	**42#**	**35#**	**49#**	rmc	mt	Wright et al. 2008	10.1093/molbev/msn160
Centipedes		Scutigerinae (Madagascar)	**159#**	**113#**	**200#**	Brc	mt&nc	Giribet & Edgecombe 2013	10.1071/IS13019
		Lassophora	**135#**	**100#**	**160#**	Brc	mt&nc	Giribet & Edgecombe 2013	10.1071/IS13019
Decapods	crayfish	*Astacoides*	**147**	**122**	**169**	rmc	mt&nc	Toon et al. 2010	10.1111/j.1365-2699.2010.02374
	freshwater crab	Malagasy Potamonautidae	**n/p**	**73.13**	**76.22**	rmc	mt	Daniels et al. 2006	10.1016/j.ympev.2006.02.022
Fish	cichlid	P. maculatus/S.America+ Africa	**n/p**	**112**	**145**	rmc	mt	Azuma et al 2008	10.1186/1471-2148-8-215
	cichlid	Malagasy P*aretroplus* /Indian *Etroplus*	**27**	**5**	**43**	mc	mt&nc	Vences et al. 2001	10.1046/j.1365-2699.2001.00624.x

		bedotiidae						2012	
	Bedotiidae	Madagascar bedotiidae	**51**	**26**	**82**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Aplocheilidae	Madagascar Aplocheilidae	**41**	**24**	**65**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Aplocheilidae	Madagascar Aplocheilidae	**53**	**28**	**82**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Cichlidae	Madagascar Cichlidae	**58**	**38**	**86**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Cichlidae	Madagascar Cichlidae	**76**	**46**	**103**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
Frogs	frogs	Madagascar mentallidea	**73#**	**60#**	**75#**	rmc	nc	Van Bocxlaer et al. 2006	10.1371/journal.pone.0000074
	frogs	Madagascar dyscophinea	**70#**	**65#**	**73#**	rmc	nc	Van Bocxlaer et al. 2006	10.1371/journal.pone.0000074
	frogs	Madagascar cophylinea	**62#**	**55#**	**70#**	rmc	nc	Van Bocxlaer et al. 2006	10.1371/journal.pone.0000074
	frogs	Madagascar Phrynomantis	**75#**	**68#**	**80#**	rmc	nc	Van Bocxlaer et al. 2006	10.1371/journal.pone.0000074
	frogs	Malagasy *Heterixalus/ Seychellean Tachycnemis*					mt&rRNA	Vences et al. 2003	10.1046/j.1439-0469.2003.00205.x
	frog	Malagasy mentallidea/Rhacophoridae	**73.1**	**51.6**	**100.1**	mDiv	nc	van der Meijden et al. 2005	10.1016/j.ympev.2005.05.001
	frog	Malagasy hyperoliids	**22.05**	**n/p**	**n/p**	rate	nc	Vences et al. 2003	10.1098/rspb.2003.2516
	frog	Malagasy hyperoliids	**26.55**	**n/p**	**n/p**	rate	nc	Vences et al. 2003	10.1098/rspb.2003.2516
	toads	Discophinae/ Microhylinae	**55**	**39**	**76**	mDiv	nc	van der Meijden et al. 2007	10.1016/j.ympev.2007.02.008
	toads	Scaphiophryninea+Cophylinae	**53***	**38***	**74***	mDiv	nc	van der Meijden et al. 2007	10.1016/j.ympev.2007.02.008
	Frog	Mantellinae	**82.7**	**58.5**	**111.8**	mc	mt&nc	Bossuyt et al. 2006	10.1080/10635150600812551
	Frog	Mantellinae	**76**	**50**	**108**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Frog	Mantellinae	**87**	**55**	**122**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Microhylidae	Cophylinae/ Scaphiophryninae	**77**	**49**	**114**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Microhylidae	Cophylinae/ Scaphiophryninae	**92**	**63**	**123**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Microhylidae	Dyscophinae	**62**	**37**	**94**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Microhylidae	Dyscophinae	**65**	**38**	**95**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Hyperoliidae	**57**	**30**	**94**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Hyperoliidae	**53**	**25**	**85**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Ptychadenidae	**8**	**2**	**20**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Ptychadenidae	**13**	**4**	**24**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
Insects	dung beetles	Helictopleurini	**44**	**29**	**64**	Brc	mt	Wirta et al. 2008	10.1016/j.ympev.2008.03.010
	dung beetles	Helictopleurini	**28**	**18**	**39**	Brc	mt	Wirta et al. 2008	10.1016/j.ympev.2008.03.010

Allodapine bees	*Hasinamelisa*	**38#**			PL	mt&nc	Chenoweth & Schwarz 2011	10.1111/j.1365-2699.2011.02488.x
Carpenter bees	*Hirashima*	**23**	**14**	**32**	PL	mt&nc	Sandra et al. 2010	doi:10.1016/j.ympev.2010.01.011
Carpenter bees	*Hirashima*	**15**	**6**	**24**	Brc	mt&nc	Sandra et al. 2010	doi:10.1016/j.ympev.2010.01.011
Carpenter bees	*Malgatina*	**25**	**17**	**33**	PL	mt&nc	Sandra et al. 2010	doi:10.1016/j.ympev.2010.01.011
Carpenter bees	*Malgatina*	**19**	**4**	**36**	Brc	mt&nc	Sandra et al. 2010	doi:10.1016/j.ympev.2010.01.011
Allodapine Bees	*Halterapis*	**43**	**27**	**60**	Brc	mt&nc	Schwarz et al. 2006	10.1080/10635150500431148
Allodapine Bees	*Halterapis*	**31**	**28**	**44**	PL	mt&nc	Schwarz et al. 2006	10.1080/10635150500431148
dung beetles	*Epactoides*	**38.03**	**20.18**	**62.75**	Brc	mt	Wirta et al. 2010	10.1016/j.ympev.2010.08.013
dung beetles	*Epactoides*	**23.76**	**12.61**	**39.15**	Brc	mt	Wirta et al. 2010	10.1016/j.ympev.2010.08.013
dung beetles	*Arachnodes* and *Epilissus*	**40.04**	**25.74**	**55.08**	Brc	mt	Wirta et al. 2010	10.1016/j.ympev.2010.08.013
dung beetles	*Arachnodes* and *Epilissus*	**64.04**	**43.59**	**85.97**	Brc	mt	Wirta et al. 2010	10.1016/j.ympev.2010.08.013
dung beetles	*Apotolamprus* and *Nanos*	**23.52**	**14.45**	**35.8**	Brc	mt	Wirta et al. 2010	10.1016/j.ympev.2010.08.013
dung beetles	*Apotolamprus* and Nanos	**14.7**	**8.96**	**22.26**	Brc	mt	Wirta et al. 2010	10.1016/j.ympev.2010.08.013
dung beetles	Madagascar Scarabaeini	**15.18**	**11.89**	**18.78**	Brc	mt	Sole et al. 2011	10.1163/187631211X552800
dung beetles	Madagascar Scarabaeini	**24.15**	**18.87**	**29.83**	Brc	mt	Sole et al. 2011	10.1163/187631211X552800
termites	Malagasy *Microtermes*	**13.18**	**n/p**	**n/p**	PL	mt&nc	Nobre et al. 2010	10.1098/rspb.2009.1373
butterfly	*Euxanthe madagascariensis*	**4***	**1.5***	**5,5***	Brc	mt&nc	Aduse-Poku et al. 2009	10.1016/j.ympev.2009.06.021
butterfly	*Charaxes antamboulou*	**4***	**2***	**5,5***	Brc	mt&nc	Aduse-Poku et al. 2009	10.1016/j.ympev.2009.06.021
butterfly	*Papilio meriones*	**0.5***	**n/p**	**n/p**	PL	mt&nc	Clark R. & Vogler 2009	10.1111/j.1365-294X.2009.04259.x
Cascade beetles	*Tritonus* cascade beetles	**91.56**	**63.7**	**126.82**	Brc	mt nc	Toussaint et al. 2016	10.1111/bij.12791
ants	*Adetomyrna*	**49**	**-**	**-**	PL	nc	Brady S.G. et al. 2006	10.1073/pnas.0605858103
ants	*Adetomyrna*	**43**	**-**	**-**	PL	nc	Brady S.G. et al. 2006	10.1073/pnas.0605858103
waterbeetles	*Hydaticus ornatus*	**10**	**5**	**16**	Brc	mt&nc	Bukontaite et al. 2015	10.1371/journal.pone.0120777
waterbeetles	*Hydaticus lineatus*	**29**	**19**	**39**	Brc	mt&nc	Bukontaite et al. 2015	10.1371/journal.pone.0120777
waterbeetles	*Hydaticus kolbei*	**8**	**6**	**11**	Brc	mt&nc	Bukontaite et al. 2015	10.1371/journal.pone.0120777
waterbeetles	*Hydaticus sobrinus*	**23**	**17**	**29**	Brc	mt&nc	Bukontaite et al. 2015	10.1371/journal.pone.0120777
waterbeetles	*Hydaticus nigrotaeniatus*	**31**	**23**	**42**	Brc	mt&nc	Bukontaite et al. 2015	10.1371/journal.pone.0120777
waterbeetles	*Hydaticus petiti*	**23**	**17**	**30**	Brc	mt&nc	Bukontaite et al. 2015	10.1371/journal.pone.0120777
waterbeetles	*Hydaticus madagascariensis*	**6**	**3**	**9**	Brc	mt&nc	Bukontaite et al. 2015	10.1371/journal.pone.0120777
waterbeetles	*Cybister guignoti*	**10**	**5**	**16**	Brc	mt&nc	Bukontaite et al. 2015	10.1371/journal.pone.0120777
waterbeetles	*Cybister tibialis*	**16**	**10**	**23**	Brc	mt&nc	Bukontaite et al. 2015	10.1371/journal.pone.0120777
waterbeetles	*Cybister operosus*	**29**	**20**	**39**	Brc	mt&nc	Bukontaite et al. 2015	10.1371/journal.pone.0120777
whirligig beetle	Heterogyrinae	**170**	**156**	**188**	Brc	mt&nc	this study	

	lemurs	Malagasy lemuriforms	**66**	**55**	**75**	Brc	mt&nc	Yoder et al. 2003	10.1038/nature01303
	lemurs	Malagasy Lemura/Lorisiformes	**60.4**	**51.6**	**69.6**	Brc	nc	Poux et al. 2005	10.1080/10635150500234534
	carnivoran	Malagasy carnivorans	**20**	**15**	**26**	Brc	mt&nc	Yoder et al. 2003	10.1038/nature01303
	carnivoran	Malagasy carnivorans /suricata	**25.9**	**20.1**	**32.5**	Brc	nc	Poux et al. 2005	10.1080/10635150500234534
	tenrec	Malagasy tenrecs/ Potamogalines	**41.8**	**34.1**	**50.3**	Brc	nc	Poux et al. 2005	10.1080/10635150500234534
	tenrec	Malagasy tenrecs/ (*Oryzorictinae-Tenrecinae split)*	**53¤**	**51¤**	**55¤**	mc	mt&nc	Doudy et al. 2002	10.1006/mpev.2001.1055
	tenrecs	Malagasy tenrecs/Potamogalinae	**47**	**40**	**55**	mdRc	nc	Poux et al. 2008	10.1186/1471-2148-8-102
	tenrecs	Malagasy tenrecs/Potamogalinae	**45**	**37**	**54**	mdRc	nc	Poux et al. 2008	10.1186/1471-2148-8-102
	lemurs	Lemuriformes/Lorisiformes	**75**	**66.9**	**84.4**	Brc	BAC seq	Horvath et al. 2008	10.1101/gr.7265208
	bat	Myzopoda	**52**	**46**	**57**	Brc	nt	Teeling et al. 2005	10.1126/science.1105113
	bat	*Triaenops*	**2.25**	**1.7**	**3.5**	coal	mt	Russell et al. 2008	10.1111/j.1365-2699.2008.01891.x
	rodents	Nesomyine rodents[1]		**18.2**	**29.6**	Brc	nc	Poux et al. 2005	10.1080/10635150500234534
	lemurs	Strepsirhini	**71**	**51**	**94**	rmc		Crottini et al. 2012	10.1073/pnas.1112487109
		Strepsirhini	**73**	**46**	**103**	rmc		Crottini et al. 2012	10.1073/pnas.1112487109
		Tenrecidae	**60**	**40**	**84**	rmc		Crottini et al. 2012	10.1073/pnas.1112487109
		Tenrecidae	**101**	**62**	**142**	rmc		Crottini et al. 2012	10.1073/pnas.1112487109
	Muridae	Nesomyinae	**28**	**17**	**42**	rmc		Crottini et al. 2012	10.1073/pnas.1112487109
	Muridae	Nesomyinae	**47**	**26**	**71**	rmc		Crottini et al. 2012	10.1073/pnas.1112487109
		Eupleridae	**26**	**16**	**38**	rmc		Crottini et al. 2012	10.1073/pnas.1112487109
		Eupleridae	**26**	**14**	**39**	rmc		Crottini et al. 2012	10.1073/pnas.1112487109
Plants		ChrysophyllumFenerivense/ C. Roxburghii	**12#**			Brc		Bartish et al. 2011	10.1111/j.1365-2699.2010.02389.x
		Sonerilae	**n/p**	**18**	**20**	Brc	cpDNA	Renner 2004	10.3732/ajb.91.9.1427
		Medinilla	**n/p**	**15**	**17**	Brc	cpDNA	Renner 2005	10.3732/ajb.91.9.1427
		Malagasy *Dichaetanthera*	**11.5**			rmc	cpDNA	Renner & Meyer 2001	10.1111/j.0014-3820.2001.tb00654.x
		C.necandolleana	**5***	**n/p**	**n/p**	Brc	cpDNA	Strijk et al. 2012	10.1371/journal.pone.0042932
		Psiadia (Madagascar)	**10***			Brc	cpDNA	Strijk et al. 2012	10.1371/journal.pone.0042932
		Malagasy *Dichaetanthera*	**10.7**			PL	cpDNA	Janssen et al. 2008	10.1111/j.1558-5646.2008.00408.x
		Madagascar bipinnate	**30.3**			PL	cpDNA	Janssen et al. 2008	10.1111/j.1558-5646.2008.00408.x
		Madaascar Tripinnate	**19.52**			PL	cpDNA	Janssen et al. 2008	10.1111/j.1558-5646.2008.00408.x
		Gymnosphera	**13.38**			PL	cpDNA	Janssen et al. 2008	10.1111/j.1558-5646.2008.00408.x
		Megistohibiscus	**n/p**	**11.45**	**14.5**	PL	cpDNA	Koopman & Baum 2008	10.1600/036364408784571653
		Euhibiscus	**n/p**	**3.7**	**4.9**	PL	cpDNA	Koopman & Baum 2008	10.1600/036364408784571653

		Tambourissa	**17**	**11**	**23**	Brc	cpDNA	Renner et al. 2010	10.1111/j.1365-2699.2010.02319.x
		Tambourissa	**24**	**14**	**34**	Brc	cpDNA	Renner et al. 2010	10.1111/j.1365-2699.2010.02319.x
		Xerosicyos	**49**	**40**	**57**	rmc	cpDNA	Schaefer et al. 2009	10.1098/rspb.2002.1447
		Ampelosicyos	**29**	**19**	**39**	rmc	cpDNA	Schaefer et al. 2009	10.1098/rspb.2002.1447
		Muellerargia	**12**	**7**	**18**	rmc	cpDNA	Schaefer et al. 2009	10.1098/rspb.2002.1447
		Chrysophyllum boivinianum	**68#**			Brc	cDNA	Bartish et al. 2011	10.1111/j.1365-2699.2010.02389.x
Reptiles	turtles	Erymnochelys/Podocnemis (Madagascar/S.America)	**85.74**			Brc	mt&nc	Vargas-Ramirez et al. 2008	10.1016/j.ode.2008.10.001
	turtles	Podocnemidae	**76**	**66**	**96**	Brc	mt&nc	Noonan & Chippindale 2006	10.1016/j.ympev.2006.03.009
	snakes	Boidae[2]	**72**	**61**	**85**	Brc	mt&nc	Noonan & Chippindale 2006	10.1016/j.ympev.2006.03.010
	snakes	Boidea[3]	**77**	**68**	**89**	Brc	mt&nc	Noonan & Chippindale 2006	10.1016/j.ympev.2006.03.011
	snakes	Malagasy *Mimophis/ Psammophis*	**12.9**	**8.2**	**29.5**	rate	mt&nc	Nagy et al. 2003	10.1098/rspb.2003.2547
	snakes	Malagasy Pseudoxyrhophiinae/Ditypophis	**30.8**	**21.5**	**75.9**	rate	mt&nc	Nagy et al. 2003	10.1098/rspb.2003.2547
	snakes	Malagasy *Xenotyphlops*	**99**			Brc	nc	Vidal et al. 2010	10.1098/rsbl.2010.0220
	snakes	Malagasy *Typholps*	**59**	**46**	**74**	Brc	nc	Vidal et al. 2010	10.1098/rsbl.2010.0220
	zonosaurus	Zonosaurinae	**66**	**53**	**85**	Brc	mt&nc	Raselimanana et al. 2009	10.1016/j.ympev.2008.10.004
	geckos	Uroplatus/Phelsuma	**40.5**	**29.75**	**52.5**	rmc	mt&nc	Raxworthy et al. 2008	10.1111/j.1469-7998.2008.00460.x
	lizards	Oplurinae	**162**	**147**	**178**	mc	mt	Okajima & Kumazawa 2009	10.1016/j.gene.2008.06.011
	Iguans	Iguanidae	**90**	**67**	**118**	Brc	mt&nc	Noonan & Chippindale 2006	10.1016/j.ympev.2006.03.010
		Xenotyphlopidae	**61**	**42**	**82**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Xenotyphlopidae	**66**	**43**	**90**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Typhlopidae	**54**	**36**	**74**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Typhlopidae	**39**	**21**	**59**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Boidae	**61**	**48**	**75**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Boidae	**47**	**22**	**74**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Lamprophiidae	Pseudoxyrhophiinae	**24**	**14**	**37**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Lamprophiidae	Pseudoxyrhophiinae	**28**	**15**	**41**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Lamprophiidae	Psammophiinae	**19**	**10**	**31**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Lamprophiidae	Psammophiinae	**22**	**10**	**37**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Opluridae	**90**	**62**	**120**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Opluridae	**72**	**32**	**117**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109

		Chamaeleonidae	**54**	**34**	**77**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Chamaeleonidae	**54**	**34**	**75**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Gerrhosauridae	**61**	**32**	**96**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Gerrhosauridae	**37**	**17**	**63**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Scincidae	*Trachylepis*	**1**	**9**	**37**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Scincidae	*Trachylepis*	**24**	**10**	**39**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Scincidae	Scincinae	**65**	**39**	**96**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Scincidae	Scincinae	**47**	**23**	**70**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Phelsuma*	**62**	**39**	**91**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Phelsuma*	**49**	**34**	**65**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Lygodactylus*	**62**	**39**	**91**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Lygodactylus*	**49**	**34**	**65**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Blaesodactylus*	**42**	**23**	**68**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Blaesodactylus*	**27**	**10**	**45**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Paroedura*	**57**	**34**	**86**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Paroedura*	**43**	**27**	**60**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Uroplatus*	**51**	**29**	**78**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Uroplatus*	**38**	**20**	**58**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Hemidactylus*	**4**	**1**	**10**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Gekkonidae	*Hemidactylus*	**6**	**1**	**11**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
	Tortoise	*Geochelone*	**n/p**	**11,5***	**17,5***	seqdivR		Palkovacs et al. 2002	doi:10.1016/S1055-7903(02)00211-7
	Tortoise	*Pyxis*	**n/p**	**9.5***	**14.5***	seqdivR		Palkovacs et al. 2003	doi:10.1016/S1055-7903(02)00211-7
	Tortoise	*Geochelone*	**n/p**	**14**	**22**	seqdivR	mt	Caccone et al. 1998	doi:10.1006/mpev.1998.0594
	Tortoise	*Pyxis*	**n/p**	**8***	**12***	seqdivR	mt	Caccone et al. 1999	doi:10.1006/mpev.1998.0594
		Podocnemididae	**112**	**73**	**159**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Podocnemididae	**87**	**65**	**111**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Testudinidae	**79**	**33**	**134**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Testudinidae	**16**	**6**	**30**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Crocodylidae	**5**	**0**	**20**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
		Crocodylidae	**1**	**0**	**2**	rmc	nc	Crottini et al. 2012	10.1073/pnas.1112487109
Spiders	orb weaver spider	*Nephila* spiders	**2.46**	**0.6**	**5.3**	Brc	mt&nc	Kuntner & Agnarsson 2011	10.1186/1471-2148-11-119
	spider	Madagascar *Nephilengys*	**1.9**	**n/p**	**7.4**	Brc	mt&nc	Kuntner & Agnarsson 2011a	doi:10.1016/j.ympev.2011.02.002
	assasin spiders	*Eriauchenius*	**154**	**115**	**191**	Brc	mt&nc	Wood et al. 2015	10.1111/evo.12578

Snails	snail	*Madagasikara/Pachychilus*	**15.6**	**20.3**	**31.5**	smc	mt	Köhler & Glaubrecht 2012	10.1111/j.1095-8312.2009.01390.x
Flat-worms	flatworms	*Madapolystoma/ Eupolystoma*	**116.2**	**95.6**	**134.6**	mdiv	rRNA	Verneau et al. 2010	10.1098/rspb.2008.1530

* - only the crown age provided
\# - the age is not provided.
¤ -approximate

Abbreviations for methods
Brc – Bayesian relaxed clock
clEn – clock enforced
coal – coalescence
mc – molecular clock
mDiv – multidivtime
rate – rate smoothing
rmc – relaxed molecular clock
smc – strict molecular clock
mdRc – multidivtime relaxed clock
clEn – clock enforced
PL – penalized likelihood
seqdivR – sequence divergence rate

Abbreviations for genes
mt – mitochondrial
nc – nuclear
rRNA – ribosomal RNA
cpDNA – chloroplast DNA
cDNA – complimentary DNA
BACseq – Bacterial artificial chromosome sequence

Highlighted taxa indicate lineages predating the Cenozoic.

Extended Data Figure 1. Characters shared between *Spanglerogyrus* and *Heterogyrus*. a, SEM of *S. albiventris* anterior view, arrow indicates setose furrow dividing labrum, scale bar = 200 µm. **b**, the same feature on *H. milloti*, scale bar = 500 µm. **c**, prolegs of *S. albiventris*, arrow indicates medial protibial spur, scale bar = 200 µm. **d**, the same on *H. milloti* scale bar = 300 µm.

Extended Data Figure 2. Phylogenetic tree. Bayesian consensus tree resulting from analysis, from which Figure 1 was constructed. Number at nodes indicate posterior probabilities. Bars at node denote 95% highest probability density interval for age. Scale access in millions of years.

Supplementary information

Supplementary Data 1. Description of morphological chracters.

Morphology

First number indicates the character number in the morphology matrix only. Numbers given in parentheses correspond to character numbers in total-evidence matrix found in the Nexus file.

Head

1 (3319). Head capsule shape excluding labrum. (0) elongate, longer than wide; (1) broad, wider than long. The head capsule of *Haliplus* and *Hygrobia* species are distinctly elongate, while those of the remaining species studied are clearly broad.

2 (3320). Divided eyes. (0) absent; (1) present. The eyes of two aquatic beetle families are clearly divided into a dorsal and ventral pair, the Coptoclavidae[1] and the Gyrinidae. All other species studied exhibit non-divided eyes.

3. (3321) Eyes. (0) bulging; (1) in contour with head. The eyes of most hydradephagans are in contour with the headcapsule. Bulging eyes not in-line the contour of the headcapsule are present in *Haliplus* and *Hygrobria* species.

4 (3322). Eye division. (0) narrowly divided by thin canthus; (1) widely divided with well developed ocular ridge. *Spanglerogyrus* exhibits narrowly divided eyes separated by a thin canthus[2], while the remaining gyrinid species have widely divided eyes separated by a well-developed interorbital ridge[3,4].

5 (3323). Antennal form. (0) scape elongate and flagellum filiform; (1) compact flagellum, with an expanded pedicel and cup-like scape. The second character state describes the antennae unique to the family Gyrinidae.

6 (3324). Number of antennomeres in flagellum. (0) more than nine; (1) nine antennomeres; (2) eight antennomeres; (3) seven antennomeres; (4) six antennomeres.

7 (3325). Antennal flagellum apex with long setae. (0) absent; (1) present. *Spanglerogyrus* and *Heterogyrus* have antennal scape apices with long setae. These setae are absent in the remaining Gyrinidae and the other Hydradephaga.

8 (3326). Posterior margin of clypeus. (0) complete; (1) incomplete. *Hygrobia* and the Gyrinidae have a complete posterior margin of the clypeus. In the other hydradephaga studied the clypeal posterior suture is partially effaced.

9 (3327). Ratio of the frontolateral margin to the width of the clypeus at mid-length. (0) frontolateral margin at least 1.5 times the longer than the medial clypeal width; (1) nearly equal or less than one. The frontolateral margin character is specific to the Gyrinidae studied. The frontolateral margin is elongate in *Spanglerogyrus*, *Heterogyrus*, in many orectochilines and dineutines. A reduction of the frons length is seen independently in several gyrinid such as the gyrinines, *Dineutus*, and Gyretes and some *Patrus*.

10 (3328). Lateral margin of frons with a well developed bead. (0) absent; (1) present. This bead appears in some Gyrinidae such as *Heterogyrus*, *Enhydrus*, *Macrogyrus*, and *Gyrinus*.

11 (3329). Frons swollen and quadrate with frontolateral ridge continued dorsally to caudal third of dorsal eye[5]. (0) absent, fronts not swollen in appearance, frontolateral ridge not continued dorsally to caudal third of dorsal eye; (1) present. The distinctly swollen, quadrate frons[2] with the frontolateral margins continue dorsally to caudal third of dorsal eye[5] are unique to *Spanglerogyrus* and *Angarogyrus*.

12 (3330). Pseudofrontal ridge. (0) absent; (1) present, but narrow and weakly developed; (2) present and well developed, broad and often setose. The frons of orectochiline species has an additional lateral, depressed ridge, the pseudofrontal ridge[6]. This ridge is unique to this tribe of whirligig beetles.

13 (3331). Labral shape. (0) transverse; (1) elongate. A transverse labrum is very common within the Hydradephaga and in these analyses a labrum is coded as being transverse if it is less than half as long as wide. An elongate labrum is defined as being at least half as long as wide. An elongate labrum (Fig._) is present in *Orectochilus*, *Orectogyrus*, *Porrorhynchus*.

14 (3332). Labral form. (0) quadrate; (1) rounded, including triangular; (2) emarginate. The *Spanglerogyrus* and *Angarogyrus* possess a strongly quadrate labrum, all other gyrinid species have a rounded labrum, as well as *Noterus clavicornis*. An emarginate labrum is seen in most of the other dytiscoid species.

15 (3333) Labrum basally. (0) with transverse setose division, ventrad to division lightly colored cuticle present, dorsad to division cuticle darkly colored; (1) entire, no division evident. The labrum of *Angarogyrus, Spanglerogyrus*, and *Heterogyrus* exhibit a unique basal transverse division. All other species studied had the labrum entire.

16 (3334) Labrum dorsally with setae. (0) absent (1) present. The labrum of *Spanglerogyrus*, *Heterogyrus*, and oretochiline species exhibit dorsal setae. These setae are not present in any of the other species studied.

17 (3335) Maxillary galea. (0) two segment; (1) one segmented; (2) absent. The out-group hydradephagan species all have two segmented maxillary galea. Within the Gyrinidae, *Spanglerogyrus* and *Heterogyrus* have two segmented maxillary galea, the gyrinines have maxillary galea with a single segment, and the orectochilines and dineutines have the maxillary galea totally absent[5-7]. This character is treated as ordered in the analysis.

18 (3336) Palpi. (0) narrow and elongate; (1) broadened and shortened. Within the Gyrinidae, *Spanglerogyrus* and *Heterogyrus* have narrow and elongate labial and maxillary palpi. The other gyrinines have the palpi broadened and relatively shortened.

19 (3337) Palpigers. (0) free, not fused to mentum; (1) palpigers fused to mentum. The out-group hydradephagan species all have free, un-fused palpigers. Within the Gyrinidae, *Spanglerogyrus*[5] and *Heterogyrus* also have free palpigers, while the remaining gyrinid species have the labial palpigers fused to the mentum.

20 (3338) Mentum. (0) weakly tri-lobed; (1) strongly tri-lobed. *Heterogyrus milloti* and *Cretotortor striatus* have a mentum with a well developed medial lobe, giving the mentum a strongly tri-lobed appearance. All other species studied have a weakly tri-lobed mentum.

21 (3339) Mental lateral lobe. (0) not strongly expanded; (1) strongly expanded. The lateral mental lobes are greatly expanded in the Gyrinidae[5].

22 (3340) Clypealium. (0) mostly glabrous, few sparse setae, especially basally; (1) setose with row of long fine setae. The Orectochilini and Dineutini have a strongly setose clypealium. Character not coded for non-gyrinid taxa.

Prothorax

23 (3341) Pronotum with largely expanded medial lobe. (0) absent; (1) present. The pronotum of *Angarogyrus*, *Spanglerogyrus*, *Heterogyrus*, and *Mesogyus* has a strong medial lobe. Other pronotum examined did not exhibit such an expanded medial region to the pronotum.

24 (3342) Expanse of lateral margin of pronotum. (0) not reaching anteriad to medial expanse of pronotum; (1) reaching at least equally anteriad to the medial expanse of pronotum, if not beyond. The lateral margins of the pronotum of *Spanglerogyrus* and *Angarogyrus* do not reach the medial lobe of the pronotum. In *Heterogyrus* and *Mesogyrus* the pronotal lateral margins extend to at least the length of the medial lobe. In the remaining Gyrinidae for which the pronotum is known, the medial lobe of the pronotum is lost and the lateral margins typically extend further anteriad than the medial expanse of the pronotum. Not coded for non-gyrinid taxa

25 (3343) Pronotal lateral bead. (0) absent; (1) present. Some Hydradephaga have a distinct lateral bead to the pronotum.

26 (3344) Pronotal transverse impressed line. (0) absent; (1) present. Most Gyrinidae have a transverse impressed line following the anterolateral margin of the pronotum[8]. This line is absent in *Orectochilus* and *Porrorhynchus* species.

27 (3345) Pronotum dorsally with transverse crease. (0) absent; (1) present. Species of *Gyrinus* exhibit a transverse crease dorsally on the pronotum[7,8].

28 (3346) Pronotum with basolateral plicae. (0) absent: (1) present. Species of *Haliplus* exhibit strongly plicae basolaterally on the pronotum[9].

29 (3347) Pronotal setation. (0) absent; (1) present. *Spanglerogyrus*, *Heterogyrus*, and the orectochiline species exhibit setation on the pronotum.

30 (3348) Prosternal medially expanded ventrad and differentiated. (0) Prosternum weakly expanded ventrally relative to lateral margins, weakly differentiated; (1) Prosternum strongly expanded ventrally relative to lateral expanse, medially clearly differentiated. In *Spanglerogyrus* the Prosternum is weakly humped, but not strongly ventrally expanded relative to the lateral margins. Other Hydradephagan species have the Prosternum strongly differentiated, either expanded ventrally or modified into a prosternal process.

31 (3349) Prosternal differentiation. (0) not cushion shaped; (1) cushion shaped. In *Heterogyrus*, *Mesogyrus striatus*, and the orectochilines, the Prosternum is medially expanded into a cushion shape[4], whose medial region is variously modified.

32 (3350) Prosternal cushion[4] medially. (0) with depression; (1) entire; (2) with elevated process. In *Heterogyrus* and *Mesogyrus striatus* the prosternal cushion has a medial depression. In many orectochilines the prosternal cushion is entire, without a medial depression or elevated process. In some orectochiline species, such as *Orectochilus villosus*, the prosternal cushion has a medial elevated process.

33 (3351) Prosternum medially. (0) without distinct process; (1) with well differentiated process. The genera *Gyrinus* and *Dineutus* have a well differentiated prosternal process as do the out-group hydradephagans studied. Members of *Aulonogyrus* and *Macrogyrus* have neither a well differentiated prosternal process, nor a prosternal cushion. However, their

prosterna medially are strongly expanded ventrally, becoming strongly differentiated from the lateral expanse, different from the situation in *Spanglerogyrus*.

34 (3352) Prosternal process extent. (0) ending at or prior to posterior margin of procoxae; (1) extending just beyond posterior margin of the procoxae; (2) extending between the mesocoxae. The Gyrinidae to not have the prosternal process extending beyond the posterior margin of the procoxae. *Coptoclava longipoda* and *Liadytes longus* have the prosternal process extending just beyond the procoxae[1]. The remainder of the out-group hydradephagan species have the procoxae extending between the mesocoxae.

35 (3353) Prosternal process form. (0) not strongly raised and plat-form-like, without truncate posterior margin; (1) strongly raised and plat-form-like, posterior margin truncate. The Haliplidae have strongly raised, plat-form-like prosternal process with a truncate posterior margin[10].

36 (3354) Pronotum with lateral explanate margin. (0) absent; (1) present. The pronotum of many gyrinid species have a lateral explanat margin to the pronotum.

37 (3355) Pronotum lateral explanate margin color. (0) lightly colored, normally yellow; (1) darkly colored. The lateral explanate margin of most gyrinid species is lightly colored, in some it is darkly colored, as in *Enhydrus* species.

Foreleg

38 (3356) Natatory setae. (0) absent; (1) present. Natatory setae is present on the foreleg of out-group hydradephaga species, with the exception of *Coptoclava longipoda*.

39 (3357) Protibial medial spur number. (0) absent; (1) one spur; (2) two spurs. The species of the subfamily Gyrininae lack protibial spurs. *Heterogyrus* and *Spanglerogyrus* both have a single spur. All the out-group hydradephagans have two medial protibial spurs, with the exception of *Noterus clavicornis*.

40 (3358) Protibial medial spur modification. (0) unmodified; (1) modified for digging; (2) modified raptorially. *Coptoclava longipoda* has the protibial medial spurs modified raptorially[1], being elongate and sharp. *Hygrobia* and *Noterus* have the protibial medial spurs modified for digging[11,12]. All other species studied with protibial medial spurs unmodified.

41 (3359) Fringe of setae along dorsal and anterior protibial margins. (0) absent; (1) present. *Hygrobia* and *Noterus* have a fringe of short stout setae along the dorsal and anterior apical margins of their protibia[13].

42 (3360) Protrochanter ventral face. (0) without series of short stout setae; (1) with series of short stout setae apically; (2) with series of short stout setae extending nearly the entire length of the ventral face. The protrochanters of certain dineutines and orectochilines have a series of short stout setae along their ventral face, either limited apically or extending most the protrochanters length.

43 (3361) Protrochanteric setose patch. (0) absent; (1) present. The protrochanters of *Porrorhynchus* have a distinct setose patch (Gustafson and Miller, TBA).

44 (3362) Profemoral sub-apicoventral tooth/teeth. (0) absent; (1) present. Certain species of *Dineutus* have a profemoral sub-apicoventral tooth (Gustafson and Miller, 2015).

45 (3363) Setigerous punctures of anterior face of profemur. (0) absent; (1) present. Most species of gyrinid have at least one or more setigerous punctures present on the anterior face of the profemur[14].

46 (3364) Ventral face of profemur. (0) without lines of setae on either anterior or posterior margin; (1) with one line of setae present on posterior margin only; (2) with two lines of setae on the posterior and anterior margin. *Spanglerogyrus* lacks lines of setae of the ventral face of the profemur, *Heterogyrus* has one line of setae along the posterior margin, and nearly all Gyrininae species have either two lines of setae on or at least one.

47 (3365) Setation of ventral face of profemur. (0) not composed of think tufts of setae; (1) composed of thick tufts of setae becoming distally. *Porrorhynchus* species have the two lines of setae of the ventral face of the profemur modified into thick tufts of setae that becoming denser distally.

48 (3366) Setose brush of posterior face of protibia. (0) absent; (1) reduced; (2) fully present. The protibia of most gyrinid species has some sort. In many species the setose brush is reduced to a small patch at the protibial apex, sometimes continue posteriorly by a very narrow strip of setae. The fully present state is a large triangular brush of setae beginning apically on the protibia and continue down the protibia. Most *Dineutus* have a fully present setose brush, as do *Aulonogyrus* species and some *Orectogyrus*. This character is treated as ordered.

49 (3367) Distolateral corner of protibia. (0) not expanded laterally; (1) expanded laterally. The protibia of orectochiline species and those of most dineutines, except *Dineutus* species, have the distolateral corner of the protibia laterally expanded and triangular in form, if not pointed. This character is also exhibited in *Coptoclava longipoda*.

50 (3368) Male protarsomere I posterior face. (0) without recessed pit; (1) with recessed pit containing differently shaped sucker-disc setae. The males of *Macrogyrus* species possess a recessed pit containing differently shaped sucker-disc setae[15].

51 (3369) Female protarsomere V posterior face with setae. (0) absent; (1) present but reduced to small patch; (2) present as a line of numerous setae. This character is absent in gyrinines and *Spanglerogyrus*. But appears variously developed within dineutine and orectochilines[4]. Line of setae is fully present on the posterior face of female protarsomere V in *Heterogyrus*.

Mesoventrite

52 (3370) Modification for proleg reception. (0) absent; (1) present. The mesoventrite of all gyrinids except *Spanglerogyrus* has recessed areas for receiving the prolegs[7,16].

53 (3371) Mesoventrite size. (0) smaller than metaventirte; (1) larger than metaventrite. The Gyrinidae have a modified and greatly enlarged metaventrite. The out-group hydradephagan species all have the metaventrite much larger than the mesoventrite.

54 (3372) Mesoventrite with recessed hexagonal area for reception of prosternal process. (0) absent; (1) present. Most of the out-group hydradephagan species have the mesoventrite with a hexagonal recessed area for reception of the prosternal process[10-12], with the exception of *Coptoclava longipoda*.

55 (3373) Mesoventrite shape. (0) not triangular; (1) triangular and extensive, often shaped similar to the bow of a ship. All gyrinid species with the exception of *Spanglerogyrus* have the mesoventrite triangular and extensive, shaped similarly to the bow of a ship.

56 (3374) Mesoventral discrimen. (0) absent; (1) present. A medial discrimen of the mesoventirte is present in all Gyrinidae except for *Spanglerogyrus*.

57 (3375) Mesoventrite with paramedical ridges. (0) absent; (1) present. The fossil gyrinid *Baissogyrus savilovi* has distinct paramedical ridges on the mesoventrite.

58 (3376) Mesoventral pit. (0) absent; (1) present. Some *Gyrinus* species have a the mesoventrite basomedially with a distinct pit.

59 (3377) Scutellar shield. (0) visible with elytra close; (1) invisible with elytra closed. The scutellar shield is variously invisible with the elytra closed of the species studied.

60 (3378) Scutellar shield shape. (0) more evenly triangular; (1) transversely triangular. The scutellar shield of *Metagyrinus* is transversely triangular[17] and used as a character to distinguish it form *Aulonogyrus*.

61 (3379) Elytral length. (0) not covering abdominal apex; (1) covering abdominal apex. The elytra cover the apex of the abdomen in most of the hydradephagan out-group taxa. The abdominal apex is not covered in the Gyrinidae and in some out-group taxa.

62 (3380) Elytral setation. (0) absent; (1) present but with distinct glabrous regions to the elytra; (2) present, elytra nearly entirely pubescent. Within Gyrinidae the elytra are glabrous in the gyrinines and the dineutines. Pubescence is present on the elytra but with distinct glabrous regions in *Spanglerogyrus*, *Heterogyrus*, *Orectogyrus*, *Patrus*, and most *Gyretes*. Completely pubescent elytra is found in *Orectochilus* and some *Gyretes* like *Gyretes sericeus.*

63 (3381) Elytral explanate lateral margin. (0) absent; (1) present. Many gyrinid species exhibit a broad explanate lateral margin to the elytra.

64 (3382) Elytral explanate lateral margin color. (0) lightly colored, yellow often; (1) darkly colored. Most gyrinids with an explanate latera margin have the margin lightly colored, normally yellow. Rarely is the lateral margin darkly colored, similar in color to the elytral disc, as in *Enhydrus* species.

65 (3383) Ten or more primary punctures accompanied by numerous secondary punctures. (0) absent; (1) present. Species of *Haliplus* have distinctly punctate elytra, with ten or more primary punctures associated with numerous secondary punctures[9,10].

66 (3384) Serial striae number. (0) none evident; (1) nine visible; (2) eleven visible. Within the Gyrinidae the orectochilines have no visible elytral striae, at least dorsally, similarly with *Spanglerogyrus*, *Angarogyrus*, and *Porrorhynchus*. *Heterogyrus*, *Mesogyrus*, *Cretotortor* and most the dineutines, with the exception of *Porrorhynchus,* have nine elytral striae visible. The Gyrinini all have eleven elytral striae.

67 (3385) Elytral strial appearance. (0) punctures; (1) well impressed lines; (2) faintly evident lines. The elytral striae appear as punctures in the gyrinines, as well as in *M.* (*Andogyrus*) *seriatopunctatus* and the fossil *Meiodineutes amurensis*, suggesting that dineutines. Strongly impressed lines are evident in *Heterogyrus*, *Mesogyrus*, *Cretotortor*, *Metagyrinus* and *Enhydrus*. Weakly impressed lines are present primarily in *Dineutus* and *Macrogyrus*. This character is treated as ordered as several *Aulonogyrus* and *Gyrinus* species exhibit intermediate stages between punctate to strongly impressed lines, suggesting a trend from punctures to strongly impressed lines, with weakly impressed lines as a step towards loss of impressed lines and elytral striae in general.

68 (3386) Elytral sutural border. (0) absent; (1) present. The elytra is bordered by an additional, non-serial striae (Brinck, 1955). This border is present in most gyrinid species, being completely lost in dineutines, and lost in some orectochilines.

69 (3387) Elytral lateral plica. (0) absent; (1) present. The two species of *Angarogyrus* studied have a distinct longitudinal plica laterally on the elytra. This character is unique to *Angarogyrus*.

70 (3388) Elytral apices. (0) unmodified; (1) modified. Unmodified elytra, those that are regularly rounded and attenuated towards the apex are common in the out-group hydradephagans studied, but relatively rare in the Gyrinidae. Unmodified elytra are primarily found in *Dineutus* and some *Gyrinus*.

71 (3389) Elytral apex with sutural production. (0) absent; (1) present. The sutural angle of the elytra has a production[18] in many species of Gyrinidae. Importantly a sutural production is present in both *Spanglerogyrus* and *Angarogyrus*.

72 (3390) Elytral apex with parasutural production. (0) absent; (1) present. The elytral apex may have a production between the sutural and epipleural angles, the parasutural production. This is present in dineutine species in members of *Dineutus*, *Porrorhynchus*, and *Macrogyrus*.

73 (3391) Elytral apex with epipleural angle modified. (0) absent; (1) present as prominence; (2) present, spinose. The epipleural angle is modified as a strong spine in many orectochilines and some dineutines. The epipleural prominence is variously present among gyrinid species.

74 (3392) Elytral apices with straight truncation. (0) absent; (1) present. In many gyrinid species the elytral apex has a straightly truncate margin. This is common in many orectochilines and dineutines.

75 (3393) Elytral apices with oblique truncation. (0) absent; (1) present. An oblique truncation to the apex of the elytra is less common within Gyrinidae. *Heterogyrus*, *Mesogyrus*, and *Cretotortor* exhibit this type of truncation, as do some oretochilines and very few dineutines.

76 (3394) Elytral apices with serrations/irregularities. (0) absent; (1) present. Some *Dineutus* species exhibit serration and/or irregularities to the elytral apices (Gustafson and Miller, 2015).

77 (3395) Elytral apicolateral margins with buzz-saw shaped serration. (0) absent; (1) present. Most species of *Porrorhynchus* exhibit this time of elytral modification. It is also present in *Dineutus micans*.

78 (3396) Elytral with canaliculated microsculpture. (0) absent; (1) present. This microsculpture appears as minute “scratch-like” sculpturing of the elytra. It is present on the elytra of the *Macrogyrus* s. str. species.

Mid-legs

79 (3397) Mid-legs. (0) not broadened nor flattened; (1) not broadened but dorsoventrally flattened with expanded mesotibia; (2) broadened and flattened dorsoventrally; (3) broadened, flattened dorsoventrally, but also shortened and paddle-like. Most of the out-group hydradephagan species have mid-legs that are not broadened or flattened. *Spanglerogyrus* has mid-legs that are not broadened but are dorsoventrally flattened with an expanded mesotibia. The fossil *Angarogyrus mongolicus* has the mid-legs visible, these are interpreted as being similar to those of *Spanglerogyrus* given the majority of other similarities the species share in morphology. The legs appear slightly broader than the totally unmodified legs of the out-group taxa, but certainly not broadened like those

of *Coptoclava longipoda* nor of the other gyrinid species. State (2) is unique in the analysis to *Coptoclava longipoda* which exhibits broad and flattened midlegs. State (3) is unique to all Gyrinidae except *Spanglerogyrus* and *Angarogyrus mongolicus*.

80 (3398) Mesocoxal shape. (0) rounded; (1) triangular and strongly transverse. Triangular and strongly transverse mesocoxae are unique to the Gyrinidae[19].

81 (3399) Mesocoxae separation[6]. (0) narrowly separated; (1) broadly separated. The mesocoxae are broadly separated in the dineutines, and most of the orectochiline genera *Patrus* and *Gyretes*.

82 (3400) Meso- and metatibial medial spurs. (0) both spurs large, greater than or nearly equal to half the length of the first tarsomere; (1) both spurs small, less than half the length of the first tarsomere; (2) the metatibia with the posterior spur larger than or nearly equal to half the length of the first metatarsomere; (3) both the meso- and metatibia with the posterior spur larger than or nearly equal to half the first tarsomere. In the out-group hydradephagan species as well as in *Spanglerogyrus*[5] and *Heterogyrus* the meso- and metatibial medial spurs are both large. In the majority of the Gyrinidae both spurs are short. In some *Gyrinus* species and orectochiline species the metatibia has the posterior spur large and the anterior spur small. Only in *Macrogyrus howittii* and in one *Gyretes* species was a large posterior spur observed in both the meso- and metatibia.

83 (3401) Mesotarsal claws. (0) not sexually dimorphic; (1) weakly sexually dimorphic; (2) strongly sexually dimorphic. The male mesotarsal claws of *Dineutus* species are strongly sexually dimorphic[18]. Within *Porrorhynchus* the mesotarsal claws are weakly sexually dimorphic. In the remaining Gyrinidae the mesotarsal claws are not sexually dimorphic.

Metaventrite

84 (3402) Mesoventrite with anteromedial process. (0) absent; (1) present, receiving posterior expansion of prosternal process. Most of the out-group hydradephagan species have the mesoventrite with an anteromedial process that receives the posterior expansion of the prosternal process, with the exception of *Liadytes longus* and *Coptoclava longipoda*[1].

85 (3403) Metaventrite. (0) not largely expanded anteriorly; (1) largely expanded anterior. *Haliplus* species have the metaventrite largely expanded anteriorly[10].

86 (3404) Metaventrite paramedially. (0) not constricted; (1) weakly constricted; (2) distinctly constricted. In the out-group hydradephaga species the metaventrite is not noticeably constricted paramedially by the mesocoxae with the exception of *Coptoclava longipoda*, which has a weak constriction. Within the Gyrinidae only *Spanglerogyrus* has the metaventrite weakly constricted paramedially by the mesocoxae, all the remaining Gyrinidae have the metaventrite distinctly constricted, resulting in the formation of “metaventral wings”[6].

87 (3405) Metaventral wings. (0) absent; (1) in the form of a near equilateral triangle; (2) narrowed and strap-like. The out-group hydradephagan species and *Spanglerogyrus* lack metaventral wings like other gyrinid species, as per the above character. *Heterogyrus*, *Mesogyrus*, *Mesodineutes*, and the dineutines have the metaventral wings in the form of a near equilateral triangle. The gyrinines and the orectochilines have the metaventral wings strap-like, strongly narrowed medially then gradually broadened laterally.

88 (3406) Medial expanse of metaventrite. (0) relatively narrower and diamond shaped; (1) very broad and pentagonal shaped. The species of *Enhydrus* have a very broad medial expanse

of the metaventrite (the area medial to the mesocoxae) that is strongly pentagonal shape with a nearly straight posterior margin. Some *Macrogyrus* species in the subgenus *Andogyrus* come close to have a similarly shaped medial expanse, however, the posterior margin is not nearly as straight.

89 (3407) Discrimen of metaventrite with transverse sulcus. (0) present and long; (1) present but short; (2) absent. Some of the out-group hydradephagan taxa retain a long transverse sulcus associated with the metaventral discrimen, as does *Spanglerogyrus* and interesting many *Macrogyrus* species. An intermediate stage is present in the Gyrinidae, where a transverse sulcus is present but is greatly shortened[7]. This character is present in *Heterogyrus*, *Mesogyrus antiquus*, and *Baissogyrus*.

90 (3408). Metepisternal ostiole. (0) absent; (1) present. The metepsternum of *Gyrinus* species has an ostiole that is variously developed[8].

91 (3409). Metanepisternum shape. (0) largely triangular; (1) lobiform; (2) narrow and trapezoidal in form. The out-group hydradephaga have a largely triangular metanepisternum, as do *Spanglerogyrus*, the gyrinines, and a few *Patrus* species. A lobiform Metanepisternum is found in *Heterogyrus*, *Mesogyrus*, *Mesodineutes*, and the dineutines. A strongly narrowed and trapezoidal shaped Metanepisternum is unique to most of the orectochilines, with the exception of a few *Patrus*.

92 (3410). Metanepisternum reaching coxal cavities. (0) absent, ending prior to coxal cavities; (1) present. This character is found in some of the out-group hydradephagan taxa, but is never present in the Gyrinidae.

93 (3411). Noterid platform. (0) absent; (1) present. The distinct "noterid platform" is found only in *Noterus clavicornis*.

Hind legs

94 (3412). Hind legs. (0) narrow; (1) narrow and weakly dorsoventrally flattened with expanded metatibia; (2) broadened for swimming, but not dorsovenrally flattened; (3) broadened and significantly dorsoventrally flattened; (4) broadened, significantly dorsoventrally flattened, and shortened to a paddle-like form. Unmodified narrow hind legs are found in the hydradephagan out-group species of *Hygrobia*, *Haliplus*, and *Liadytes*. Narrow and weakly dorsoventrally flattened hindlegs with expanded metatibia are found in *Spanglerogyrus*, the hind legs of *Angarogyrus mongolicus* are treated similarly as justified for the mid-legs. Hind legs that are broadened for swimming, but not dorsoventrally flattened, are found in the Dytiscidae and *Noterus* species examined. The broadened and significantly dorsoventrally flattened hind-legs, that are not shortened, are found in *Coptoclava longipoda*. Finally the majority of gyrinid species exhibit the paddle-like leg form, with hid legs that are expanded, dorsoventrally flattened, and shortened.

95 (3413). Anterior margin of metacoxae. (0) more transverse; (1) distinctly oblique to very strongly oblique. Most of the hydradephagan out-group species studied (with the exception of the Dytiscidae), *Spanglerogyrus*, the dineutines, and a few orectochilines have a more transverse anterior margin to the metacoxae. In *Heterogyrus*, *Mesogyrus*, the gyrinines, and most of the orectochilines have a distinctly more oblique anterior margin to the metacoxae.

96 (3414). Posterolateral margin of metacoxae. (0) without border; (1) bordered. Many gyrinid species have the posterolateral margin of the metacoxae bordered. *Heterogyrus*, *Mesogyrus*, *Aulonogyrus*, *Orectochilus, Porrorhynchus*, and *Dineutus* do not have a border along the posterolateral margin of the metacoxae.

97 (3415). Metacoxae. (0) not expanded anteriorly; (1) greatly expanded anteriorly. The Dysticidae have the metacoxae greatly expanded anteriorly.

98 (3416). Metacoxal plate (sensu Lawrence et al. 2011). (0) present as large plates concealing the basal portion of leg and part of abdomen; (1) present, not concealing leg and abdomen, but continued laterally along anterior margin of metacoxae, (2) strongly reduced present only medially. As Lawrence et al. 2011 defines metacoxal plates: "the excavation of the metacoxae to form at least weak coxal plates", we consider the medial raised region of the metacoxae to be reduced coxal plates, which in the out-group hydradephagan species studied are present only medially, with the exception of *Haliplus* and *Triaplus* species[1], which have large metacoxal plates covering the basal portion of the hind legs[10]. In the Gyrinidae the metacoxal plates are present medially but also continued laterally along the anterior margin of the metacoxae.

99 (3417). Metacoxal plate secondary reduction in Gyrinidae. (0) absent, metacoxal plate region largely triangular; (1) present, metacoxal plate medially rectangular in form with a narrow anterior bridge or with bridge totally reduced. Within the Gyrinidae the dineutines and *Spanglerogyrus* have large broadly triangular metacoxal plates. Within the orectochilines and gyrinines the metacoxal plates are consricted to a medial rectangular area, with a narrow anterior bridge continued laterally or with the anterior bridge totally reduced in some taxa. This character is associated with more oblique metacoxae.

100 (3418). Metacoxal process apex. (0) straightly truncate; (1) obliquely truncate; (2) rounded and lobiform. The metacoxal process apex of Gyrinidae is most often obliquely truncate. Many orectochilines have this apex straightly truncate, with many *Orectogyrus* having a rounded or lobiform metacoxal process apex.

Abdomen

101 (3419). Suture of abdominal sternite II. (0) totally or mostly obliterated; (1) present. The species of *Enhydrus* still have the suture of abdominal sternite II present[3,21].

102 (3420). Overal shape of abdominal apex. (0) not cylindrical, clearly broadly rounded; (1) distinctly cylindrical and strongly narrowed apically. The orectochilines have a strongly cylindrical and stinctly narrowed abdominal apex.

103 (3421). Abdominal sternites VII & VIII. (0) glabrous; (1) with row of long fine setae. The orectochilines have a row of long fine setae posteromedially on abdominal sternites VII & VIII forming a 'keel'[7].

104 (3422). Abdominal sternite VIII. (0) apically longitudinally divided; (1) apically bi-emarginate; (2) entire. This character is discussed in Miller and Bergsten, 2012 and treated as ordered in the analysis.

105 (3423). Posterior margin of penultimate abdominal tergite. (0) not trilobed; (1) weakly trilobed; (2) strongly trilobed. This character is discussed in Miller and Bergsten, 2012.

106 (3424). Tergite VIII divided medially in half. (0) absent, tergite VIII entire; (1) present. The out-group hydradephagan species have tergite VIII divided medially in half.

107 (3425). Venter coloration. (0) entirely lightly colored; (1) distinctly infuscate; (2) entirely darkly colored. Most gyrinid species have either light (ranging from light red, orange, yellow, and even white) or darkly colored venters (dark reddish brown, brown, to black). Some gyrinine and *Orectogyrus* species exhibit distinctly infuscate venters.

Female reproductive tract

108 (3426). Spermatheca. (0) not largely expanded nor sac-like; (1) largely expanded and sac-like. The spermatheca of dineutines and *Orectochilus* and *Orectogyrus* are largely expanded and sac-like to varying degrees. The spermathecae of other gyrinidea are not nearly as expanded or sac-like.

109 (3427). Spermathecal accessory gland. (0) absent; (1) present. An accessory gland attached to the spermatheca is present in *Spanglerogyrus*, *Heterogyrus*, and the gyrinines.

110 (3428). Bursal accessory gland. (0) absent; (1) present. An accessory gland attached to the bursa is present in *Heterogyrus*, the orectochilines, and *Enhydrus* and *Macrogyrus*.

111 (3429). Vaginal shield. (0) absent; (1) present. The vaginal shield[22-24] is present in *Porrorhynchus* and *Dineutus*.

112 (3430). Fertilization duct expansion. (0) absent; (1) weakly expanded; (2) strongly expanded. Most orectochilines have the fertilization duct weakly to strongly expanded. The remaining gyrinid species typically do not have the fertilization duct expanded[7]. This character is treated as ordered in the analysis.

113 (3431). Fertilization duct convolution. (0) absent; (1) randomly convoluted; (2) cork-screw shaped convolution. The fertilizaiton duct of orectochilines is often convoluted with random twists and turns. In certain *Gyretes* species the convolutions are arranged serially into a cork-screw shape[7]. This character is treated as ordered in the analysis.

114 (3432). Fertilization duct curling. (0) absent: (1) weakly curled; (2) strongly curled. The fertilization duct of *Orectochilus* and *Orectogyrus* species are curled. In *Orectochilus* this curling is weakly, with only a single turn back into itself, similarly with some *Orectogyrus* species. Many *Orectogyrus* species of the *s. str.* subgenus have the fertilization duct strongly curled, with numerous recurves, creating a snail-shell shape. Other gyrinids do not have the fertilization duct curled. This character is treated as ordered in the analysis.

115 (3433). Gonocoxae with medial apodeme. (0) absent; (1) present. This character is described by Miller and Bergsten, 2012.

Aedeagus

116 (3434). Orientation of aedeagus in repose. (0) no rotated; (1) rotated. The aedeagus of Gyrinidae is not rotated in repose, unlike other hydradephaga.

117 (3435). Basal piece. (0) distinctly present; (1) present but fused to parameres; (2) absent/indistinguishable. *Spanglerogyrus* has a distinct basal piece[5] which was reconfirmed in this study. *Heterogyrus* has a distinct additional segment fused to the parameres, which is interpreted here as the basal piece. The remained of the Gyrinidae and the out-group hydradephaga species no longer have a distinguishable basal piece. This character is treated as ordered in the analysis.

118 (3436). Paramere position. (0) ventral to median lobe; (1) lateral to median lobe. The genus *Orectogyrus* has parameres that are situated lateral to the median lobe. All other gyrinid psecies have the parameres situated ventral to the medial lobe.

119 (3437). Parameres with ventromedial project. (0) absent; (1) present. The gyrinines have a distinct ventromedial projection extending off the parameres. This projection is in a serially homologous postion to the fused basal piece of *Heterogyrus*. This character is coded here are a distinct character, but it seems reasonable that this character could be interpreted as a transformation series step, and supports the position of the gyrinines as sister to Dineutini + Orectochilini, where this medially project is reduced, representing the total loss of the basal piece.

Sperm

120 (3438). Spermostyle type sperm conjugation. (0) absent; (1) present. The dineutines and *Orectogyrus* and *Orectochilus* have sperm conjugation utilizing a specialized structure, the spermostyle[25]. This type of sperm conjugation appears associated with female reproductive tracts that have a large sac-like spermatheca.

References

1 Ponomarenko, A. G. [Mesozoic Coleoptera. Description of new taxa]. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR* **161**, 17-96 (1977).

2 Folkerts, G. W. *Spanglerogyrus albiventris*, a primitive new genus and species of Gyrinidae (Coleoptera) from Alabama. *The Coleopterists Bulletin* **33**, 1-8 (1979).

3 Hatch, M. H. The morphology of Gyrinidae. *Papers of the Michigan Academy of Science, Arts and Letters* **7**, 311 – 350 (1926).

4 Brinck, P. A revision of the Gyrinidae (Coleoptera) of the Ethiopian region. I. *Acta Universitatis Lundensis. Nova Series* **51**, 1 – 144 (1955).

5 Beutel, R. G. & Roughley, R. E. in *Handbuch der Zoologi/ Handbook of Zoology* Vol. 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim) (eds R.G Beutel & R.A.B. Leschen) 55-64 (Walter de Gruyter, inc., 2005).

6 Hatch, M. H. The phylogeny and phylogenetic tendencies of Gyrinidae. *Papers of the Michigan Academy of Science, Arts and Letters* **V**, 429 – 467 (1925).

7 Miller, K. B. & Bergsten, J. Phylogeny and classficiation of whirligig beetles (Coleoptera: Gyrinidae): relaxed-clock model outperforms parsimony and time-free Bayesian analyses. *Systematic Entomology* **37**, 705 – 746 (2012).

8 Oygur, S. & Wolfe, G. W. Classification, distribution, and phylogeny of North American north of Mexico species of *Gyrinus* Müller (Coleoptera: Gyrinidae). *Bulletin of the American Museum of Natural History* **207**, 1-97 (1991).

9 Holmen, M. The aquatic Adephaga (Coleoptera) of Fennoscandia and Denmark. I. Gyrinidae, Haliplidae, Hygrobiidae and Noteridae. *Fauna Entomologica Scandinavica* **20**, 1-168 (1987).

10 van Vondel, B. J. in *Handbook of Zoology* Vol. 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim) (eds R.G Beutel & R.A.B. Leschen) 64-71 (Walter de Gruyter, Inc., 2005).

11 Dettner, K. in *Handbook of Zoology* Vol. Vol 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim) (eds R.G Beutel & R.A.B. Leschen) 72-79 (Walter de Gruyter, Inc., 2005).

12 Dettner, K. in *Handbook of Zoology* Vol. Vol 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim) (eds R.G Beutel & R.A.B. Leschen) 85-89 (Walter de Gruyter, Inc., 2005).

13 Miller, K. B. On the systematics of Noteridae (Coleoptera: Adephaga: Hydradephaga): Phylogeny, description of new tribe, genus and species, and survey of female genital morphology. *Systematics and Biodiversity* **7**, 191-214 (2009).

14 Ochs, G. On the West Indian Gyrinidae and a new species of *Gyretes* from northern Brazil. *American Museum Novitates* **125**, 1– 8 (1924).

15 Régimbart, M. Essai monographique de la famille des Gyrinidae. 1e partie. *Annales de la Société entomologique de France* **(6)** 379 – 458 + 373 pls. (1882).

16 Beutel, R. G. Phylogenetic analysis of the family Gyrinidae (Coleoptera) based on mesothoracic and metathoracic characters. *Quaestiones Entomologicae* **26**, 163-192 (1990).

17 Mazzoldi, P. & Jäch, M. A. in *Water Beetles of China Vol. III* (eds M.A. Jäch & L. Ji) 43-47 (Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, 2003).

18 Gustafson, G. T. & Miller, K. B. The New World whirligig beetles of the genus *Dineutus* Macleay, 1825 (Coleoptera, Gyrinidae, Gyrininae, Dineutini). *Zookeys* **476**, 1 - 135, doi:10.3897/zookeys.476.8630 (2015).

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

20 Lawrence, J. F. *et al.* Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici* **61**, 1—217 (2011).

21 Brinck, P. Derivation, taxonomy and history of distribution of whirligig beetle genus *Enhydrus* (Coleoptera - Gyrinidae). *Entomologica Germanica* **4**, 317 – 326 (1978).

22 Brinck, P. *Porrorhynchus indicans* Walker (Coleoptera: Gyrinidae). A representative of the relict montane forest ecosystem in Sri Lanka. . *P.E.P. Deraniyagala Commemoration Volume (Sri Lanka 1980)*, 103-108 (1980).

23 Brinck, P. A revision of *Rhombodineutus* Ochs in New Guinea (Coleoptera: Gyrinidae). *Entomologica Scandinavica* **14**, 205-233 (1983).

24 Brinck, P. Evolutionary trends and specific differentiation in *Merodineutus* (Coleoptera: Gyrinidae). *International Journal of Entomology* **26**, 175-189 (1984).

25 Breland, O. P. & Simmons, E. Preliminary studies of the spermatozoa and the male reproductive system of some whirligig beetles (Coleoptera: Gyrinidae). *Entomological News* **81**, 101–110 (1970).

Supplementary Data Table 1. Character coding for morphology dataset.

Character #	**1**	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**
	|	|	|	|	|	|	|	|	|

Trlati Triaplus laticoxa	101-	0???-	?000?	?????	0?-0-	?000?	00-00	00-??	????
Nocl503 Noterus clavicornis	101-	0001-	00001	10010	00-0-	10000	10-12	00-11	1100
Haho504 Hygrobia hermanni	000-	0000-	00002	10010	00-0-	00000	10-02	00-12	1100
Mabi2 Matus bicarinatus	101-	0001-	00002	10000	00-0-	10000	10-02	00-12	0000
Plde130 Platynectes decemaculatus	101-	0001-	00002	10010	00-0-	10000	10-02	00-12	0000
Lcla91 Lancetes lanceolatus	101-	0001-	00002	10000	00-0-	10000	10-02	00-12	0000
Hali Haliplus lineatocollis	000-	0001-	00002	100-0	00-0-	10010	10-02	10-12	0000
Hacr Haliplus cretaceus	????	?????	?????	1????	??-0?	?0000	10-12	1????	????
Colg Coptoclava longipoda	011?	?????	000??	1????	00-0-	00000	10-01	00-02	20??
Lilo Liadytes longus	101-	010?-	00002	1??00	00-0-	10000	10-01	00-12	00??
Mdrh Mesodytes rhantoides	101-	0??1-	00002	10???	??-0-	10000	10-12	00-??	????
Spal472 Spanglerogyrus albiventris	1110	11100	01000	01000	01010	11001	00-00	00-01	0000
Hsmi596 Heterogyrus milloti	1111	11100	10001	01000	11011	01001	110-0	01001	0000
Aoal525 Aulonogyrus alternatus	1111	11001	00001	10111	01001	01000	10-00	01000	-000
Aoma523 Aulonogyrus marginatus	????	?????	?????	?????	?????	?????	?????	?????	????
Aocr519 Aulonogyrus cristatus	????	?????	?????	?????	?????	?????	?????	?????	????
Aoca604 Aulonogyrus carinipennis	1111	11001	10001	10111	01001	01000	10-00	01000	-000
Aosp569 Aulonogyrus sp	1111	11001	10001	10111	01001	01000	10-00	01000	-000
Aobe493 Aulonogyrus bedeli	1111	11001	10001	10111	01001	01000	10-00	01100	-000
Aoca540 Aulonogyrus caffer	1111	11001	10001	10111	01001	01000	10-00	00-00	-000
Aost469 Aulonogyrus striatus	1111	11001	00001	10111	01001	01000	10-00	01000	-000
Aogo529 Aulonogyrus goudoti	1111	11001	00001	10111	01001	01000	10-00	00-00	-000
Berg1 Metagyrinus sinensis	1111	1??01	?0001	10???	?1001	??000	?????	?1000	-0??
Gyig598 Gyrinus ignitus	1111	11001	10001	10111	01001	01100	10-10	00-00	-000
Aost687 Aulonogyrus strigosus	1111	11001	10001	10111	01001	01000	10-00	01000	-000
Gymi526 Gyrinus minutus	1111	11101	00001	10111	01001	01100	10-00	00-00	-000
Gymd597 Gyrinus madagascariensis	1111	11001	10001	10111	01001	01100	10-10	00-00	-000
Gyna539 Gyrinus natalensis	1111	11001	10001	10111	01001	01100	10-10	00-00	-000
Gypl495 Gyrinus plicifer	1111	11001	10001	10111	01001	01100	10-10	00-00	-000

Gygi496 Gyrinus gibber	1111	11001	10001	10111	01001	01100	10-10	00-00	-000
Gyel494 Gyrinus elevatus	1111	11001	10001	10111	01001	01100	10-10	00-00	-000
Gysp492 Gyrinus sp	1111	11001	00001	10111	01001	01100	10-10	00-00	-000
Gysp628 Gyrinus amazonicus	1111	11001	00001	10111	01001	01100	10-10	00-00	-000
Difv672 Dineutus fauveli	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Disp507 Dineutus pectoralis	1111	14001	00001	10211	01101	01000	10-10	00-00	-000
Disu484 Dineutus subspinosus	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Diso605 Dineutus solitarius	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Dipx515 Dineutus proximus	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Disp576 Dineutus striatus	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Dici474 Dineutus ciliatus	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Didi473 Dineutus discolor	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Disn516 Dineutus sinuosipennis	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Disp481 Dineutus aereus	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Disu505 Dineutus sublineatus	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Diin482 Dineutus indicus	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Disp577 Dineutus micans	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Ayau483 Macrogyrus oblongus	1111	11000	10001	10211	01101	01000	10-00	00-00	-000
Aygo501 Macrogyrus gouldi	1111	11000	10001	10211	01101	01000	10-00	01000	-000
Ayan502 Macrogyrus australis	1111	11000	10001	10211	01101	01000	10-00	00-00	-000
Aysp506 Macrogyrus albertisi	1111	11000	10001	10211	01101	01000	10-10	00-00	-000
Ehas646 Enhydrus atratus	1111	13000	10001	10211	01101	01000	10-10	01100	-000
Adsp648 Andogyrus zimmermanni	1111	11000	10001	10211	01101	01000	10-00	00-00	-000
Prte497 Porrorhynchus marginatus	1111	14000	00011	10211	01101	00000	10-10	01000	-001
Ogca666 Orectogyrus camerunensis	1111	14000	-0211	11211	01101	01001	111-0	01000	-020
Gesp615 Gyretes sericeus	1111	11000	10001	11211	01101	01002	112-0	00-00	-000
Ogsp566 Orectogyrus noctuabundis	1111	14000	-0201	11211	01101	01001	111-0	01000	-000
Orvi527 Orectochilus villosus	1111	11000	10011	11211	01101	00002	112-0	00-00	-000
Berg2 Orectochilus bellieri	1111	11000	10011	11211	01101	00002	112-0	00-00	-000

Ogcy520 Orectogyrus cyanicollis	1111	14000	-0211	11211	01101	01001	111-0	01000	-020
Ogha600 Orectogyrus hastatus	1111	14000	-0211	11211	01101	01001	111-0	01000	-000
Orpr487 Patrus productus	1111	14000	-0101	11211	01101	01001	111-0	01000	-000
Ordi488 Patrus discifer	1111	14001	10001	11211	01101	01001	111-0	01000	-000
Orsp499 Patrus sp	1111	14000	-0101	11211	01101	00001	112-0	00-00	-020
Oran486 Patrus andamanicus	1111	14001	-0101	11211	01101	01001	111-0	01000	-010
Orvo489 Patrus volubilis	1111	14001	-0101	11211	01101	01001	111-0	01000	-010
Orsp500 Patrus sp	1111	14001	-0101	11211	01101	00001	111-0	00-00	-020
Orsp677 Patrus sp	1111	14000	-0101	11211	01101	00001	111-0	00-00	-020
Ogar669 Orectogyrus argenteovittatus	1111	14000	-0201	11211	01101	01001	111-0	01000	-000
Ogsj671 Orectogyrus sjostedti	1111	14001	-0211	11211	01101	01001	112-0	01000	-020
Ogpi665 Orectogyrus pictimanus	1111	14000	-0101	11211	01101	01001	111-0	01000	-020
Ogde524 Orectogyrus dedalus	1111	14000	-0211	11211	01101	01001	111-0	01000	-000
Ogdi491 Orectogyrus discors	1111	14000	-0101	11211	01101	01001	111-0	01000	-020
Ogos667 Orectogyrus oscari	1111	14000	-0211	11211	01101	01001	111-0	01000	-020
Ogpl662 Orectogyrus prolongatus	1111	14001	-0211	11211	01101	01001	111-0	01000	-010
Ogdy664 Orectogyrus demeryi	1111	14000	-0101	11211	01101	01001	111-0	01000	-020
Ogsp565 Orectogyrus specularis	1111	14000	-0211	11211	01101	01001	111-0	01000	-020
Ogms670 Orectogyrus masculinus	1111	14000	-0211	11211	01101	01001	111-0	01000	-020
Ogsp663 Orectogyrus sp	1111	14000	-0211	11211	01101	01001	111-0	01000	-020
Ogmd601 Orectogyrus madagascariensis	1111	14000	-0211	11211	01101	01001	111-0	01000	-010
Ogdo517 Orectogyrus dorsiger	1111	14000	-0211	11211	01101	01001	111-0	01000	-020
Ogsp490 Orectogyrus posticalis	????	?????	?????	?????	?????	?????	?????	?????	????
Ogsp564 Orectogyrus wittei	1111	14000	-0211	11211	01101	01001	111-0	01000	-020
Ogbd661 Orectogyrus bedeli	1111	14000	-0201	11211	01101	01001	111-0	01000	-020
Ogsp567 Orectogyrus specularis	1111	14000	-0211	11211	01101	01001	111-0	01000	-020
Ogsp668 Orectogyrus sp	????	?????	?????	?????	?????	?????	?????	?????	????
Ogob595 Orectogyrus oberthuri	1111	14000	-0211	11211	01101	01001	111-0	01000	-020
Ogse521 Orectogyrus sedilloti	1111	14000	-0201	11211	01101	01001	111-0	01000	-000
Ogve522 Orectogyrus	1111	14000	-0211	11211	01101	01001	111-0	01000	-020

vestitus									
Gesp626 Gyretes sp	1111	11001	-0101	11211	01101	01001	112-0	01000	-010
Gesp619 Gyretes sp	1111	11001	-0101	11211	01101	01001	111-0	01000	-010
Gesp616 Gyretes quadrispinosus	1111	11001	-0101	11211	01101	01001	112-0	01000	-010
Gesp624 Gyretes sp	1111	11001	-0101	11211	01101	01001	111-0	00-00	-010
Geir470 Gyretes iricolor	1111	11001	-0101	11211	01101	01001	111-0	00-00	-010
Gysp686 Gyretes boucardi	1111	11001	-0101	11211	01101	01001	111-0	00-00	-010
Gysp685 Gyretes acutangulus	1111	11001	-0101	11211	01101	01001	112-0	00-00	-010
Gesp617 Gyretes sp	1111	11001	-0101	11211	01101	01001	112-0	00-00	-010
Gesp614 Gyretes sp	1111	11001	-0101	11211	01101	01001	112-0	00-00	-010
Ayhw887 Macrogyrus howittii	1111	11000	10001	10211	01101	01000	10-00	00-00	-000
Ayre912 Macrogyrus reichei	1111	11000	10001	10211	01101	01000	10-00	00-00	-000
Ayst882 Macrogyrus striolatus	1111	11000	10001	10211	01101	01000	10-00	00-00	-000
Adsr886 Andogyrus seriatopunctatus	1111	11000	10001	10211	01101	01000	10-00	00-00	-010
Adco828 Andogyrus colombicus	1111	11000	10001	10211	01101	01000	10-00	00-00	-000
AyCs829 Macrogyrus toxopeusi	1111	11001	10001	10211	01101	01000	10-00	00-00	-000
AyCs841 Macrogyrus purpurascens	1111	11001	10001	10211	01101	01000	10-00	00-00	-000
Aysp863 Macrogyrus sumbawae	1111	11000	10001	10211	01101	01000	10-00	00-00	-000
AyTs834 Macrogyrus sp	1111	11000	10001	10211	01101	01000	10-00	00-00	-000
AyTs833 Macrogyrus sp	1111	11000	10001	10211	01101	01000	10-00	00-00	-000
AyCs831 Macrogyrus sp	1111	11001	10001	10211	01101	01000	10-00	00-00	-000
DiDf915 Dineutus fulgidus	1111	14001	00001	10211	01101	01000	10-10	00-00	-000
DiDn865 Dineutus n sp	1111	14001	00001	10211	01101	01000	10-10	00-00	-000
DiRt908 Dineutus tetracanthus	1111	14001	00001	10211	01101	01000	10-10	00-00	-000
Dilo818 Dineutus longimanus	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
DiCp918 Dineutus pagdeni	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Dica821 Dineutus carolinus	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Dias819 Dineutus assimilis	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Diro913 Dineutus robertsi	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
Prla852 Porrorhynchus landaisi	1111	12000	00011	10211	01101	00000	10-10	01000	-001
Ehsu856 Enhydrus sulcatus	1111	13000	10001	10211	01101	01000	10-00	01100	-000
DiCf916 Dineutus	1111	14001	00001	10211	01101	01000	10-10	00-00	-010

fairmairei									
Diau911 Dineutus australis	1111	14001	00001	10211	01101	01000	10-10	00-00	-010
DiMp917 Dineutus priscus	1111	14001	00001	10211	01101	01000	10-10	00-00	-000
DiMm919 Dineutus macrochirus	1111	13001	00001	10211	01101	01000	10-10	00-00	-000
Ogor901 Orectogyrs ornaticollis	1111	14000	-0201	11211	01101	01001	111-0	01000	-000
Oghe900 Orectogyrus heros	1111	14000	-0211	11211	01101	01001	111-0	01000	-020
Pasp897 Patrus sp	1111	14000	-0101	11211	01101	00001	111-0	01000	-020
Pasp896 Patrus sp	1111	14000	-0101	11211	01101	00001	111-0	01000	-000
Pasp898 Patrus sp	1111	14000	-0101	11211	01101	00001	111-0	01000	-010
Gysp840 Gyrinus sericeolimbatus	1111	11001	10001	10111	01001	01100	10-10	00-00	-000
Gysp839 Gyrinus dimorphus	1111	11001	10001	10111	01001	01100	10-10	00-00	-000
Gysp837 Gyrinus maculiventris	1111	11001	10001	10111	01001	01100	10-10	00-00	?000
Agmo Angarogyrus mongolicus	111?	?????	01000	0????	???10	?????	?????	?????	????
Agmi Angarogyrus minimus	111?	?????	?1?00	?????	?????	?????	?????	?????	????
Basa Baissogyrus savilovi	????	?????	?????	?????	?????	?????	?????	?????	????
Mgan Mesogyrus antiquus	111?	?????	?0?01	?????	???11	0100?	?????	?????	????
Mgst Mesogyrus striatus	111?	?????	???01	?????	11???	?????	110-0	0????	????
Crzh Cretotortor zherichini	111?	?????	???01	?????	???11	?????	?????	?????	????
Meam Mesodineutes amurensis	????	?????	?????	?????	?????	?????	?????	?????	????
Gegi Gyretes giganteus	1111	???00	-0101	11???	???01	?????	?????	?????	????
Miin Miodineutes insignis	111?	?????	?0?01	11???	???01	?????	?????	?????	????
Cresp Cretotortor sp	111?	?????	10001	?????	?1?1?	0?00?	110-0	0????	????

Character #	**44**	**50**	**55**	**60**	**65**	**70**	**75**	**80**	**85**
Trlati Triaplus laticoxa	??????	??000	0-000	0??0-	00-10	00000	00000	0-??0	00
Nocl503 Noterus clavicornis	000-00	00001	0-001	-100-	00-00	00000	00000	0-001	00
Haho504 Hygrobia hermanni	000-00	00001	0-000	0000-	00-00	00000	00000	0-001	00
Mabi2 Matus bicarinatus	000-00	00001	0-000	0100-	00-00	00000	00000	0-001	00
Plde130 Platynectes decemaculatus	000-00	00001	0-000	0100-	00-00	00000	00000	0-001	00
Lcla91 Lancetes lanceolatus	000-00	00001	0-000	0000-	00-00	10001	00000	0-001	00
Hali Haliplus lineatocollis	000-00	00001	0-001	-100-	1--00	00000	00000	0-001	10

Hacr Haliplus cretaceus	??????	???00	????1	-100-	1--00	00000	0000?	0-??0	10
Colg Coptoclava longipoda	0????1	??000	00000	0100-	00-00	00000	00002	0-000	01
Lilo Liadytes longus	0????0	0?00?	0?0?0	0100-	00-00	?????	????0	0-0?0	00
Mdrh Mesodytes rhantoides	0?????	??001	0-000	0000-	00-00	10001	0000?	0-??1	00
Spal472 Spanglerogyrus albiventris	000-00	00010	00000	0010-	00-10	11000	00001	10000	01
Hsmi596 Heterogyrus milloti	011010	02110	11000	00110	01110	10010	10003	10000	02
Aoal525 Aulonogyrus alternatus	012020	0?110	11000	00010	02010	10001	00003	10100	02
Aoma523 Aulonogyrus marginatus	??????	?????	?????	?????	?????	?????	?????	?????	??
Aocr519 Aulonogyrus cristatus	??????	?????	?????	?????	?????	?????	?????	?????	??
Aoca604 Aulonogyrus carinipennis	012020	00110	11000	00010	02110	10001	00003	10100	02
Aosp569 Aulonogyrus sp	012020	0?110	11000	00010	02010	10001	00003	10100	02
Aobe493 Aulonogyrus bedeli	012010	00110	11000	00011	02010	10001	00003	10100	02
Aoca540 Aulonogyrus caffer	012020	00110	11000	0000-	02010	10001	00003	10100	02
Aost469 Aulonogyrus striatus	012020	00110	11000	00010	02010	10001	00003	10100	02
Aogo529 Aulonogyrus goudoti	012020	00110	11000	0000-	02110	10001	00003	10100	02
Berg1 Metagyrinus sinensis	?????0	??110	1?0?0	10010	021?0	10001	00003	1?10?	?2
Gyig598 Gyrinus ignitus	012010	00110	11010	0000-	02010	10001	00003	10100	02
Aost687 Aulonogyrus strigosus	012020	00110	11000	00010	02010	10001	00003	10100	02
Gymi526 Gyrinus minutus	012010	00110	11000	0000-	02010	10001	00003	10100	02
Gymd597 Gyrinus madagascariensis	012010	00110	11010	0000-	02010	00000	00003	10100	02
Gyna539 Gyrinus natalensis	012010	00110	11000	0000-	02010	10001	00003	10100	02
Gypl495 Gyrinus plicifer	012010	00110	11010	0000-	02010	00000	00003	10100	02
Gygi496 Gyrinus gibber	012010	00110	11010	0000-	02010	00000	00003	10100	02
Gyel494 Gyrinus elevatus	012010	00110	11010	0000-	02010	00000	00003	10100	02
Gysp492 Gyrinus sp	012010	00110	11000	0000-	02010	10011	00003	10200	02
Gysp628 Gyrinus amazonicus	012010	00110	11000	0000-	02010	00000	00003	10200	02
Difv672 Dineutus favareli	012010	02110	11001	-000-	01200	11120	01003	11120	02
Disp507 Dineutus pectoralis	011020	02110	11001	-000-	01200	10010	10003	11120	02
Disu484 Dineutus subspinosus	012010	02110	11001	-000-	01200	10020	11003	11120	02
Diso605 Dineutus	112020	00110	11001	-000-	01200	00000	00003	11120	02

solitarius									
Dipx515 Dineutus proximus	012020	00110	11001	-000-	01200	00000	00003	11120	02
Disp576 Dineutus striatus	012020	00110	11001	-000-	01200	11021	01003	11120	02
Dici474 Dineutus ciliatus	012020	00110	11001	-000-	01200	00000	00003	11120	02
Didi473 Dineutus discolor	112020	00110	11001	-000-	01200	11000	00003	11120	02
Disn516 Dineutus sinuosipennis	012020	00110	11001	-000-	01200	11100	00003	11120	02
Disp481 Dineutus aereus	112020	00110	11001	-000-	01200	11000	01003	11120	02
Disu505 Dineutus sublineatus	112020	00110	11001	-000-	01200	00000	00003	11120	02
Diin482 Dineutus indicus	112020	00110	11001	-000-	01200	00000	00003	11120	02
Disp577 Dineutus micans	012020	00110	11001	-000-	01200	10000	01103	11120	02
Ayau483 Macrogyrus oblongus	011021	12110	11000	00011	01200	11110	00013	11100	02
Aygo501 Macrogyrus gouldi	011011	12110	11000	00010	01210	11120	00013	11100	02
Ayan502 Macrogyrus australis	011011	11110	11000	0000-	01200	11120	00013	11100	02
Aysp506 Macrogyrus albertisi	011011	12110	11000	00010	01200	11120	00013	11100	02
Ehas646 Enhydrus atratus	001001	00110	11000	00010	01100	10001	00003	11100	02
Adsp648 Andogyrus zimmermanni	012001	10110	11000	0000-	00-00	00000	00003	11100	02
Prte497 Porrorhynchus marginatus	002121	02110	11001	-0010	01200	11110	01103	11110	02
Ogca666 Orectogyrus camerunensis	011021	02110	11000	00110	00-10	11021	00003	10100	02
Gesp615 Gyretes sericeus	011001	00110	11001	-020-	00-00	10020	10003	11100	02
Ogsp566 Orectogyrus noctuabundis	001001	00110	11000	00110	00-00	10001	00003	10100	02
Orvi527 Orectochilus villosus	001001	00110	11000	0020-	00-10	00000	00003	10100	02
Berg2 Orectochilus bellieri	001001	00110	11000	0020-	00-10	00000	00003	10100	02
Ogcy520 Orectogyrus cyanicollis	011021	02110	11000	00110	00-10	10010	00003	10100	02
Ogha600 Orectogyrus hastatus	011021	01110	11000	00110	00-10	10011	00003	10100	02
Orpr487 Patrus productus	011001	01110	11001	-0110	00-00	10021	00003	11100	02
Ordi488 Patrus discifer	011001	00110	11000	00110	00-00	10011	00003	11200	02
Orsp499 Patrus sp	001011	02110	11000	00111	00-00	10010	10003	11200	02
Oran486 Patrus andamanicus	011001	00110	11001	-0110	00-00	10021	00003	11100	02
Orvo489 Patrus volubilis	011001	00110	11000	00110	00-00	10021	00003	11100	02
Orsp500 Patrus sp	011001	00110	11000	00111	00-00	10011	00003	11200	02

Orsp677 Patrus sp	011011	01110	11000	00110	00-00	10001	00003	11200	02
Ogar669 Orectogyrus argenteovittatus	001011	00110	11000	00110	00-00	10000	10003	10100	02
Ogsj671 Orectogyrus sjostedti	011021	02110	11000	00110	00-10	10011	00003	10100	02
Ogpi665 Orectogyrus pictimanus	011011	02110	11000	00110	00-00	10010	10003	10100	02
Ogde524 Orectogyrus dedalus	001011	00110	11000	00110	00-00	111-0	00003	10100	02
Ogdi491 Orectogyrus discors	001011	01110	11000	00110	00-00	10010	10003	10100	02
Ogos667 Orectogyrus oscari	001001	01110	11000	00110	00-00	10020	00003	10100	02
Ogpl662 Orectogyrus prolongatus	001011	0?110	11000	00110	00-10	10011	00003	10100	02
Ogdy664 Orectogyrus demeryi	011011	01110	11000	00110	00-00	00000	00003	10100	02
Ogsp565 Orectogyrus specularis	011021	02110	11000	00110	00-10	10021	00003	10100	02
Ogms670 Orectogyrus masculinus	011011	02110	11000	00110	00-10	10021	00003	10100	02
Ogsp663 Orectogyrus sp	011021	0?110	11000	00110	00-10	10021	00003	10100	02
Ogmd601 Orectogyrus madagascariensis	011021	02110	11000	00110	00-10	10021	00003	10100	02
Ogdo517 Orectogyrus dorsiger	011021	02110	11000	00110	00-10	10020	00003	10100	02
Ogsp490 Orectogyrus posticalis	??????	?????	?????	?????	?????	?????	?????	?????	??
Ogsp564 Orectogyrus wittei	011021	02110	11000	00110	00-10	10021	00003	10100	02
Ogbd661 Orectogyrus bedeli	011021	02110	11000	00110	00-10	10021	00003	10100	02
Ogsp567 Orectogyrus specularis	011021	02110	11000	00110	00-10	10021	00003	10100	02
Ogsp668 Orectogyrus sp	??????	?????	?????	?????	?????	?????	?????	?????	??
Ogob595 Orectogyrus oberthuri	001021	02110	11000	00110	00-10	10011	00003	10100	02
Ogse521 Orectogyrus sedilloti	001011	01110	11000	00110	00-10	10011	00003	10100	02
Ogve522 Orectogyrus vestitus	001021	0?110	11000	00110	00-10	10011	00003	10100	02
Gesp626 Gyretes sp	011001	00110	11001	-0110	00-00	10011	00003	11300	02
Gesp619 Gyretes sp	011001	0?110	11001	-0110	00-00	10011	00003	11100	02
Gesp616 Gyretes quadrispinosus	011001	02110	11001	-0110	00-00	11020	00003	11200	02
Gesp624 Gyretes sp	011001	00110	11001	-010-	00-00	00000	00003	11100	02
Geir470 Gyretes iricolor	011001	00110	11001	-010-	00-10	00000	00003	11100	02
Gysp686 Gyretes boucardi	011001	00110	11001	-010-	00-00	10001	00003	11100	02
Gysp685 Gyretes acutangulus	011001	00110	11001	-010-	00-00	10001	00003	11200	02
Gesp617 Gyretes sp	011001	00110	11001	-010-	00-00	10001	00003	11200	02

Gesp614 Gyretes sp	011001	00110	11001	-010-	00-00	10001	00003	11200	02
Ayhw887 Macrogyrus howittii	012001	11110	11000	0000-	01200	10011	00013	11300	02
Ayre912 Macrogyrus reichei	001021	11110	11000	00011	01200	10010	01013	11100	02
Ayst882 Macrogyrus striolatus	011011	11110	11000	00011	01200	10011	00013	11100	02
Adsr886 Andogyrus seriatopunctatus	012001	10110	11000	0000-	01000	10011	00003	11100	02
Adco828 Andogyrus colombicus	012001	10110	11000	0000-	01200	00000	00003	11100	02
AyCs829 Macrogyrus toxopeusi	011001	10110	11000	0000-	01200	11110	00003	11100	02
AyCs841 Macrogyrus purpurascens	012001	1?110	11000	0000-	01200	11110	00003	11200	02
Aysp863 Macrogyrus sumbawae	011011	11110	11000	0000-	01200	11011	00013	11100	02
AyTs834 Macrogyrus sp	011011	1?110	11000	00011	01200	10110	00013	11100	02
AyTs833 Macrogyrus sp	011011	1?110	11000	00011	01200	11110	00013	11200	02
AyCs831 Macrogyrus sp	012001	10110	11000	0000-	01200	11110	00003	11200	02
DiDf915 Dineutus fulgidus	111020	02110	11001	-000-	01200	00000	00003	11120	02
DiDn865 Dineutus n sp	111020	02110	11001	-000-	01200	00000	00003	11120	02
DiRt908 Dineutus tetracanthus	011020	02110	11001	-000-	01200	10120	00003	11120	02
Dilo818 Dineutus longimanus	111020	00110	11001	-000-	01200	11100	01003	11120	02
DiCp918 Dineutus pagdeni	111020	01110	11001	-000-	01200	00000	00003	11120	02
Dica821 Dineutus carolinus	112020	00110	11001	-000-	01200	10000	01003	11120	02
Dias819 Dineutus assimilis	012020	00110	11001	-000-	01200	11000	00003	11120	02
Diro913 Dineutus robertsi	012020	00110	11001	-000-	01200	00000	00003	11120	02
Prla852 Porrorhynchus landaisi	002121	02110	11001	-0010	00-00	11120	00103	11110	02
Ehsu856 Enhydrus sulcatus	000011	00110	11000	00011	01100	00000	00003	11100	02
DiCf916 Dineutus fairmairei	011020	01110	11001	-000-	01200	00000	00003	11120	02
Diau911 Dineutus australis	012020	02110	11001	-000-	01200	10011	01003	11120	02
DiMp917 Dineutus priscus	011020	02110	11001	-000-	01200	00000	00003	11120	02
DiMm919 Dineutus macrochirus	011020	02110	11001	-000-	01200	00000	00003	11120	02
Ogor901 Orectogyrs ornaticollis	011011	0?110	11000	00110	00-10	10011	00003	10100	02
Oghe900 Orectogyrus heros	011021	02110	11000	00110	00-10	10010	10003	10100	02
Pasp897 Patrus sp	001001	0?110	11000	00110	00-00	10001	00003	10100	02

Pasp896 Patrus sp	001001	00110	11000	00110	00-00	10001	00003	10100	02
Pasp898 Patrus sp	001001	0?110	11000	00110	00-00	10021	00003	10100	02
Gysp840 Gyrinus sericeolimbatus	012010	00110	11010	0000-	02010	10001	00003	10100	02
Gysp839 Gyrinus dimorphus	012010	00110	11010	0000-	02010	10001	00003	10200	02
Gysp837 Gyrinus maculiventris	012010	00110	11010	0000-	02010	00000	00003	10100	02
Agmo Angarogyrus mongolicus	??????	?????	????0	00?0-	00-11	11000	00001	?????	??
Agmi Angarogyrus minimus	??????	?????	?????	??10-	00-11	11000	0000?	?????	??
Basa Baissogyrus savilovi	??????	??110	1110?	?????	?????	?????	?????	10??0	02
Mgan Mesogyrus antiquus	??????	??110	11?00	00?10	01110	10010	1000?	10??0	02
Mgst Mesogyrus striatus	??????	?????	?????	?????	?????	1???1	0????	10??0	02
Crzh Cretotortor zherichini	??????	?????	????0	0??10	01110	10000	1000?	10???	??
Meam Mesodineutes amurensis	??????	??110	11???	?0?0-	01000	00000	0000?	11??0	02
Gegi Gyretes giganteus	??????	?????	????0	00?10	00-10	10011	0000?	?????	??
Miin Miodineutes insignis	??????	?????	?????	?????	00-?0	10001	0000?	?????	??
Cresp Cretotortor sp	??????	?????	????0	00?10	01010	10010	1000?	?????	??

	87	95	100	105	110	115	120
Trlati Triaplus laticoxa	0-000100	0?00-	-10?2	0????	?????	?????	?
Nocl503 Noterus clavicornis	0-000112	0002-	-0002	0?0--	-----	-12-_	-
Haho504 Hygrobia hermanni	0-000000	0002-	-0002	011--	-----	-12--	-
Mabi2 Matus bicarinatus	0-200102	1012-	-0002	010--	-----	-12--	-
Plde130 Platynectes decemaculatus	0-200102	1012-	-0002	012--	-----	-12--	-
Lcla91 Lancetes lanceolatus	0-200102	1012-	-0002	010--	-----	-12--	-
Hali Haliplus lineatocollis	0-000000	0000-	-0002	010--	-----	-12--	-
Hacr Haliplus cretaceus	0-0?0000	0000-	-?002	01???	?????	?????	?
Colg Coptoclava longipoda	00200003	0002-	-0002	01???	?????	?????	?
Lilo Liadytes longus	0-000100	0012-	?????	?????	?????	?12--	?
Mdrh Mesodytes rhantoides	0-200100	1012?	??0?2	01???	?????	?12--	?
Spal472 Spanglerogyrus albiventris	00000001	01010	10000	00001	00000	00000	0
Hsmi596 Heterogyrus milloti	10101004	00011	10001	00001	10000	00100	0
Aoal525 Aulonogyrus alternatus	20200004	10011	10002	20101	00000	00201	?

Aoma523 Aulonogyrus marginatus	????????	?????	?????	?????	?????	?????	?
Aocr519 Aulonogyrus cristatus	????????	?????	?????	?????	?????	?????	?
Aoca604 Aulonogyrus carinipennis	20200004	10011	10002	20001	00000	00201	?
Aosp569 Aulonogyrus sp	20200004	10011	10002	20001	00000	00201	?
Aobe493 Aulonogyrus bedeli	20200004	10011	10002	20101	00000	00201	?
Aoca540 Aulonogyrus caffer	20200004	10011	10002	20101	00000	00201	?
Aost469 Aulonogyrus striatus	20200004	10011	10002	20201	00000	00201	?
Aogo529 Aulonogyrus goudoti	20200004	11011	10002	20201	00000	00201	0
Berg1 Metagyrinus sinensis	??????04	1?0??	??002	10?01	00000	0020?	?
Gyig598 Gyrinus ignitus	20210004	11011	00002	00201	00000	00201	0
Aost687 Aulonogyrus strigosus	20200004	11011	10002	20201	00000	00201	0
Gymi526 Gyrinus minutus	20200004	11011	10002	00101	00000	00201	?
Gymd597 Gyrinus madagascariensis	20210004	11011	00002	00201	00000	00201	0
Gyna539 Gyrinus natalensis	20210004	10011	00002	00201	00000	00201	?
Gypl495 Gyrinus plicifer	20210004	11011	10002	00201	00000	00201	0
Gygi496 Gyrinus gibber	20210004	11011	10002	00201	00000	00201	0
Gyel494 Gyrinus elevatus	20210004	11011	10002	00201	00000	00201	?
Gysp492 Gyrinus sp	20200004	11011	10002	00001	00000	00201	?
Gysp628 Gyrinus amazonicus	20200004	11011	00002	00001	00000	00201	?
Difv672 Dineutus favareli	10201004	00010	10002	00010	01000	10200	?
Disp507 Dineutus pectoralis	10201004	00010	10002	00110	01000	10200	?
Disu484 Dineutus subspinosus	10201004	00010	10002	00210	01000	10200	?
Diso605 Dineutus solitarius	10201004	00010	10002	00210	01000	10200	?
Dipx515 Dineutus proximus	10201004	00010	10002	00210	01000	10200	1
Disp576 Dineutus striatus	10201004	00010	10002	00010	01000	10200	?
Dici474 Dineutus ciliatus	10201004	00010	10002	00010	01000	10200	1
Didi473 Dineutus discolor	10201004	00010	10002	00210	01000	10200	1
Disn516 Dineutus sinuosipennis	10201004	00010	10002	00210	01000	10200	1
Disp481 Dineutus aereus	10201004	00010	10002	00210	01000	10200	?
Disu505 Dineutus	10201004	00010	10002	00210	01000	10200	1

sublineatus							
Diin482 Dineutus indicus	10201004	00010	10002	00210	01000	10200	?
Disp577 Dineutus micans	10201004	00010	10002	00210	01000	10200	?
Ayau483 Macrogyrus oblongus	10001004	01010	10002	00210	10000	10200	1
Aygo501 Macrogyrus gouldi	10001004	01010	10002	00010	10000	10200	?
Ayan502 Macrogyrus australis	10001004	01010	10002	00210	10000	10200	?
Aysp506 Macrogyrus albertisi	10001004	01010	10002	00210	10000	10200	?
Ehas646 Enhydrus atratus	11201004	00010	11002	00210	10000	10200	1
Adsp648 Andogyrus zimmermanni	10201004	01010	10002	00210	10000	10200	?
Prte497 Porrorhynchus marginatus	10201004	00010	10002	00010	01000	10200	1
Ogca666 Orectogyrus camerunensis	20202004	11011	10112	00010	10202	10210	?
Gesp615 Gyretes sericeus	20202004	11011	00112	00200	10110	10200	?
Ogsp566 Orectogyrus noctuabundis	20202004	11011	00112	00010	10101	10210	?
Orvi527 Orectochilus villosus	20202004	10011	00112	00010	10101	10200	1
Berg2 Orectochilus bellieri	20202004	10011	00112	000??	?????	?????	?
Ogcy520 Orectogyrus cyanicollis	20202004	11011	00112	00210	10201	10210	?
Ogha600 Orectogyrus hastatus	20202004	11011	00112	00110	10201	10210	?
Orpr487 Patrus productus	20202004	11011	20112	00200	10010	10200	?
Ordi488 Patrus discifer	20200004	11011	00112	00100	10010	10200	?
Orsp499 Patrus sp	20200004	01011	00112	00200	10210	10200	?
Oran486 Patrus andamanicus	20202004	11011	00112	00200	10210	10200	?
Orvo489 Patrus volubilis	20202004	01011	00112	00200	10210	10200	?
Orsp500 Patrus sp	20202004	11011	00112	00200	10???	10200	?
Orsp677 Patrus sp	20202004	01011	00112	00200	10???	10200	?
Ogar669 Orectogyrus argenteovittatus	20202004	11011	00112	00010	10201	10210	?
Ogsj671 Orectogyrus sjostedti	20202004	11011	10112	00110	10202	10210	?
Ogpi665 Orectogyrus pictimanus	20202004	11011	00112	00010	10201	10210	?
Ogde524 Orectogyrus dedalus	20202004	11011	00112	00010	10101	10210	?
Ogdi491 Orectogyrus discors	20202004	11011	20112	00010	10101	10210	?
Ogos667 Orectogyrus	20202004	11011	20112	00010	10202	10210	?

oscari							
Ogpl662 Orectogyrus prolongatus	20202004	11011	20112	00010	10???	10210	?
Ogdy664 Orectogyrus demeryi	20202004	11011	20112	00010	10202	10210	?
Ogsp565 Orectogyrus specularis	20202004	11011	20112	00110	10202	10210	?
Ogms670 Orectogyrus masculinus	20202004	11011	20112	00010	10202	10210	?
Ogsp663 Orectogyrus sp	20202004	11011	20112	00010	10???	10210	?
Ogmd601 Orectogyrus madagascariensis	20202004	11011	20112	00110	10202	10210	1
Ogdo517 Orectogyrus dorsiger	20202004	11011	20112	00210	10202	10210	?
Ogsp490 Orectogyrus posticalis	????????	?????	?????	?????	?????	?????	?
Ogsp564 Orectogyrus wittei	20202004	11011	20112	00010	10202	10210	?
Ogbd661 Orectogyrus bedeli	20202004	11011	20112	00110	10202	10210	?
Ogsp567 Orectogyrus specularis	20202004	11011	20112	00110	10202	10210	?
Ogsp668 Orectogyrus sp	????????	?????	?????	?????	?????	?????	?
Ogob595 Orectogyrus oberthuri	20202004	11011	20112	00010	10202	10210	?
Ogse521 Orectogyrus sedilloti	20202004	11011	20112	00110	10202	10210	1
Ogve522 Orectogyrus vestitus	20202004	11011	10112	00110	10202	10210	?
Gesp626 Gyretes sp	20202004	11011	00112	00200	10???	10200	?
Gesp619 Gyretes sp	20202004	11011	00112	00200	10???	10200	?
Gesp616 Gyretes quadrispinosus	20202004	11011	20112	00200	10110	10200	?
Gesp624 Gyretes sp	20202004	11011	00112	00200	10???	10200	?
Geir470 Gyretes iricolor	20202004	11011	00112	00200	10220	10200	0
Gysp686 Gyretes boucardi	20202004	11011	00112	00200	10220	10200	?
Gysp685 Gyretes acutangulus	20202004	11011	00112	00200	10220	10200	?
Gesp617 Gyretes sp	20202004	11011	00112	00200	10???	10200	?
Gesp614 Gyretes sp	20202004	11011	00112	00200	10???	10200	?
Ayhw887 Macrogyrus howittii	10001004	01010	10002	00210	10000	10200	?
Ayre912 Macrogyrus reichei	10001004	01010	10002	00210	10000	10200	1
Ayst882 Macrogyrus striolatus	10001004	01010	10002	00210	10000	10200	1
Adsr886 Andogyrus seriatopunctatus	10001004	01010	10002	00210	10000	10200	?
Adco828 Andogyrus colombicus	10201004	01010	10002	00210	10000	10200	?
AyCs829 Macrogyrus	10201004	01010	10002	00210	10000	10200	?

toxopeusi							
AyCs841 Macrogyrus purpurascens	10201004	01010	10002	00010	10000	10200	?
Aysp863 Macrogyrus sumbawae	10001004	01010	10002	00210	10000	10200	?
AyTs834 Macrogyrus sp	10001004	01010	10002	00210	10000	10200	?
AyTs833 Macrogyrus sp	10001004	01010	10002	00210	10000	10200	?
AyCs831 Macrogyrus sp	10201004	01010	10002	00010	10000	10200	?
DiDf915 Dineutus fulgidus	10201004	00010	10002	00210	01000	10200	?
DiDn865 Dineutus n sp	10201004	00010	10002	00210	01000	10200	?
DiRt908 Dineutus tetracanthus	10201004	00010	10002	00210	01000	10200	?
Dilo818 Dineutus longimanus	10201004	00010	10002	00010	01000	10200	?
DiCp918 Dineutus pagdeni	10201004	00010	10002	00010	01000	10200	?
Dica821 Dineutus carolinus	10201004	00010	10002	00210	01000	10200	1
Dias819 Dineutus assimilis	10201004	00010	10002	00210	01000	10200	1
Diro913 Dineutus robertsi	10201004	00010	10002	00010	01000	10200	?
Prla852 Porrorhynchus landaisi	10201004	00010	10002	00010	01000	10200	?
Ehsu856 Enhydrus sulcatus	11201004	00010	11002	00210	10000	10200	?
DiCf916 Dineutus fairmairei	10201004	00010	10002	00010	01000	10200	?
Diau911 Dineutus australis	10201004	00010	10002	00210	01000	10200	?
DiMp917 Dineutus priscus	10201004	00010	10002	00210	01000	10200	?
DiMm919 Dineutus macrochirus	10201004	00010	10002	00210	01000	10200	?
Ogor901 Orectogyrs ornaticollis	20202004	11011	20112	00110	10202	10210	1
Oghe900 Orectogyrus heros	20202004	11011	20112	00110	10202	10210	1
Pasp897 Patrus sp	20202004	11011	20112	0020?	?????	?????	0
Pasp896 Patrus sp	20202004	10011	20112	0020?	?????	?????	0
Pasp898 Patrus sp	20202004	11011	20112	0010?	?????	?????	0
Gysp840 Gyrinus sericeolimbatus	202?0004	11011	10002	00201	00000	00201	?
Gysp839 Gyrinus dimorphus	20210004	11011	10002	00201	00000	00201	?
Gysp837 Gyrinus maculiventris	20210004	11011	10002	00101	00000	00201	?
Agmo Angarogyrus mongolicus	???????1	?????	??0??	?0???	?????	?????	?
Agmi Angarogyrus minimus	????????	?????	??0??	?????	?????	?????	?

Basa Baissogyrus savilovi	101?100?	00011	1000?	??0??	?????	?????	?
Mgan Mesogyrus antiquus	1010100?	00011	1000?	??0??	?????	?????	?
Mgst Mesogyrus striatus	10??100?	0?011	1?0??	?????	?????	?????	?
Crzh Cretotortor zherichini	????????	?????	?????	?????	?????	?????	?
Meam Mesodineutes amurensis	1000100?	00010	10002	00???	?????	?????	?
Gegi Gyretes giganteus	????????	?????	??1??	00???	?????	?????	?
Miin Miodineutes insignis	????????	?????	??1??	00???	?????	?????	?
Cresp Cretotortor sp	????????	?????	??0??	?0???	?????	?????	?

Supplementary Data Table 2. Additional taxa added to dataset.

Genus	species	voucher #	Collection data	COI	COII	12S	H3
Haliplus	lineatocollis	Hali	GenBank	X	-	X	X
Macrogyrus	howittii	Ayhw887	AUSTRALIA: Tasmania. Franklin Beach, Lake St. Clair. 10.i.2015 CHS Watts. MSBA	X	-	X	X
Macrogyrus	reichei	Ayre912	AUSTRALIA: VIC. Glenelg River nr. Dergholm, -37.36686, 141.2428. 75 m. 13.i.2015. Leg G.Gustafson. MSBA	X	X	X	-
Macrogyrus	striolatus	Ayst882	AUSTRALIA: NSW. Megalong Valley, -36.65629, 150.27377, 861 m. 04.i.2015. leg. G.Gustafson Forested strm GTG01042015A. MSBA	X	X	X	X
Andogyrus	seriatopunctatus	Adsr886	Argentina. MSBA	X	X	X	X
Andogyrus	colombicus	Adco828	VENEZUELA: Merida State 8°38.006'N, 71°09.762'W, 2037 m Monte Zerpa area; 20.vii.2009 leg. Short, Sites, Gustafson, Camacho; stream margin/pools VZ09-0720-01A/L-1098 ABTC-01476. MSBA	X	X	X	X
Macrogyrus	toxopeusi	AyCs829	INDONESIA: Papua: Poga 3°48.382'S, 138°34.780'E 2285-2330 m. ZSM	X	X	X	X
Macrogyrus	purpurascens	AyCs841	PAPUA NEW GUINEA: Morobe Prov. Pindiu. 6°27.147'S 147°29.574'E, 1470 m. 12.x.2009 leg. Inaho (PNG206). ZSM	X	X	X	X
Macrogyrus	sumbawae	Aysp860	INDONESIA: Sumba: dry forest stream in limestone. 370 m 9°49.474'S 120°20.856'E (SUA08). ZSM	X	X	X	X
Macrogyrus	sp nr. blanchardii	AyTs834	PAPUA NEW GUINEA: E Highlands Prov. Onerunka, small creek, redsoil rock 6°20.936'S 145°46.874'E 1700 m. 21.v.2006 leg. John & Balke (PNG71). ZSM	X	X	X	X
Macrogyrus	sp	AyTs833	PAPUA NEW GUINEA: Central Prov. Woitape. 08°31.290'S 147°13.684'E 1700 m. i.2008 leg. Posman (PNG166). ZSM	X	X	X	X
Macrogyrus	sp	AyCs831	PAPUA NEW GUINEA: Sandaun Prov. Mianmin 4°54.570'S 141°35.490'E 990 m. 23.x.2008. leg. Ibalim (PNG193). ZSM	X	X	X	X
Dineutus	fulgidus	DiDf915	INDONESIA: Sumatra Barat, Solok, Alahan Panjank Road. 1190 m. 0°56.345'S 100°46.411'E. ZSM	X	X	X	X
Dineutus	n sp	DiDn865	BALI: Telaga Forest, BLI07. ZSM	X	X	X	X
Dineutus	tetracanthus	DiRt908	PAPUA NEW GUINEA: Madang Prov. Wannang, 5°15.458'S 145°2.389'E 270 m. 31.x.2008. leg. Posman (PNG187) ZSM.	X	X	X	X
Dineutus	longimanus longimanus	Dilo818	DOMINICAN REP.: Pedernales Prov. W of Pedernales on rd. to border with Haiti; roadside sweeping in dry for. & sec. veg. 15 May 2010 18.154° -71.7582° colr. G. J. Svenson. MSBA	X	X	X	X

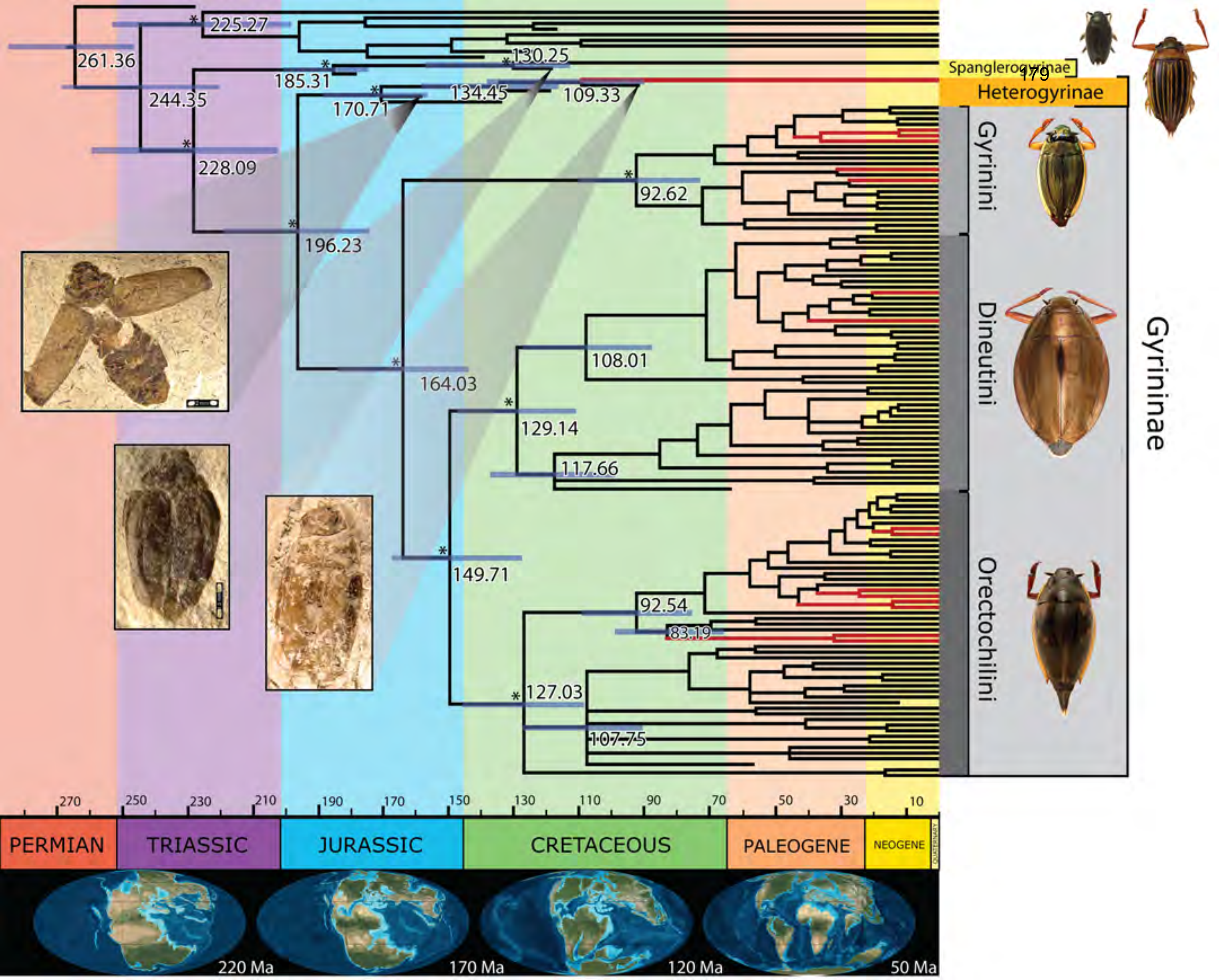
Dineutus	pagdeni	DiCp918	SOLOMON ISLANDS: Guadal-canal ca. 4.5 km S of Barana vill. Forest nr. "Japanese Camp" & Moka riv. 9°30.3'S 159°58.9'E, 27m. 5-6.xii.2013 leg. Jiří Hájek. MSBA	X	X	X	X
Dineutus	carolinus	Dica821	USA: TX: Hardin Co. Big Thicket Pres. 30.260° -94.525° 20m 28.vi.2013 colr. CK Faris & GT Gustafson. Mud bottomed bayou GTG06281301. MSBA	X	X	X	X
Dineutus	assimilis	Dias819	USA: KS: Osage Co. pond off hwy 69 nr milemark 54. 38.031° -94.705° 254m 17.vi.2013 leg. CK Faris & GT Gustafson GTG06171301. MSBA	X	X	-	X
Dineutus	robertsi	Diro913	USA: Georgia: Warwoman Wld Mgmt Area. Tuckaluge Cr. 34.90155°N 83.30015°W. 533 m. 11July2012. KB Miller colr. KBM11071201. MSBA	X	X	X	X
Porrorhynchus	landaisi	Prla852	CHINA: Hainan Isl. Jianfengling Mts. Tiachi Lake rd. from Taichi village to 'Sector 5' 18°43.6-44.1'N 820-950m, 108°52.1-52.5'E 10.v.2011. M.Fikáček & Sh. Zhao lgt. Small slow-flowing stony river in the primary forest. MSBA	X	X	X	X
Enhydrus	sulcatus	Ehsu856	BRAZIL: Rio de Janeiro: Cachoei Ras de Macacu - Regua. 01.vi.2013. Ponto do Ganesh (Parte Alta) col. Equipe Coleoptera. MSBA	X	X	X	X
Dineutus	fairmairei	DiCf916	Fiji03. ZSM	-	X	X	X
Dineutus	australis	Diau911	AUSTRALIA: QLD. 19°41.153'S 145°49.536'E 14.Mar.2011. colr. KB Miller KBM14031102. MSBA	X	X	X	X
Dineutus	macrochirus	DiMm919	PAPUA NEW GUINEA: Central Prov. Kokoda Trek. 9°00.338'S 147°44.252'E. 1390 m. i.2008. leg. Posman (PNG 173). ZSM	-	X	X	X
Dineutus	priscus	DiMp917	PAPUA NEW GUINEA: S Highlands Prov. Sopulkul, 30-35 km NE Mendi. 6°2.944'S 143°46.485'E. 2679 m. 16.vi.2006. Leg. John ex swamp into stream (PNG 79). ZSM	-	X	X	X
Orectogyrus	ornaticollis	Ogor901	MADAGASCAR: Analamanga Reg. Ankazobe dist. Ambohitantely Res. -18.1808°, 47.2901°, 1340 m. 22.xi.2014 leg. G. Gustafson. MAD14-76. MSBA	X	-	X	-
Orectogyrus	heros	Oghe900	MADAGASCAR: Analamanga Reg. Ankazobe dist. Ambohitantely Res. -18.1808°, 47.2901°, 1340 m. 22.xi.2014 leg. G. Gustafson. MAD14-76. MSBA	X	X	X	-
Patrus	sp	Pasp897	THAILAND: Kanchanaburi Prov. Huey Ka Yaeng at Ban Pracham Mai 16°21.0277'N, 101°19.541'E 428 m. 19.i.2015. gravel streams leg G.Gustafson. MSBA	X	X	X	X
Patrus	sp	Pasp896	THAILAND: Kanchanaburi Prov. Heuy Ou Long, opposite Keong Ka Wia Reforestation Station 14°33.199'N, 98°34.238'E 326 m. 19.i.2015. gravel streams leg G.Gustafson. MSBA	X	X	X	-
Patrus	sp	Pasp898	THAILAND: Kanchanaburi Prov. Huey Ka Yaeng at Ban Pracham Mai 16°21.0277'N, 101°19.541'E 428 m. 19.i.2015. gravel streams leg G.Gustafson. MSBA	X	X	X	X
Gyrinus	sericeolimbatus	Gysp840	PAPUA NEW GUINEA: Morobe Prov. Pindiu. 6°27.147'S 147°29.574'E, 1470 m. 12.x.2009 leg. Inaho (PNG206). ZSM	X	X	X	X
Gyrinus	maculiventris	Gysp837	USA: New Mexico, Cibola Co., Zuni Mountains. 18.v.2013. leg. S. Baca. 180513-A. MSBA	X	X	X	-
Gyrinus	dimorphus	Gysp839	USA: New Mexico, Cibola Co., Zuni Mtns, 35.40178°N, 108.44956°W. 30.v.2013. leg. G.Gustafson & S.Baca. GGSB053013C. MSBA	X	X	X	X

Depository abbreviations:
MSBA: Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM, USA.
ZSM: Zoologische Staatssammlung München, Munich, Germany

Supplementary Data Table 2. Fossil taxa examined.

group	Genus	species	Age Ma	Locality of deposit	Depository
Out-	*Triaplus*	*laticoxa*	221 - 235	Madygen area, Batken Region,Osh Oblast, Kyrgyzstan	PIN
Out-	*Haliplus*	*cretaceus*	112 - 125	Bon-Tsagan, outcrop 87.8, Bayankhongor Province, Mongolia	PIN
Out-	*Liadytes*	*longus*	125 - 150	Daya settlement, Glushkovo Formation, Russian Federation	PIN
Out-	*Mesodytes*	*rhantoides*	122 - 125	Yixian Formation, Liutiaogou, China	NIG
In-	*Angarogyrus*	*mongolicus*	112 - 125	Gurvan-Eren Formation, Govi-Altai, Mongolia	PIN
In-	*Angarogyrus*	*minimus*	175 - 183	Cheremkhovskaya Formation, Irkutsk, Russian Federation	PIN
In-	*Baissogyrus*	*savilovi*	112 - 125	Zaza Formation, Buryatia, Russian Federation	PIN
In-	*Mesogyrus*	*antiquus*	155 - 164	Karabastau Formation, Karatau-Mikhailovka, Kazakhstan	PIN
In-	*Mesogyrus*	*striatus*	122 - 150	Turga Formation, Undurga River, Russian Federation	PIN
In-	*Cretotortor*	*zherichini*	89 - 94	Kzyl-Zhar deposits, Northeastern Karatau Range, Kazakhstan	PIN
In-	*Mesodineutes*	*amurensis*	61 - 66	Arkhara site, Darmakan Formation, Russian Federation	PIN
In-	*Gyretes*	*giganteus*	55 - 58	Menat, Pay-deDome, France	MNHN
In-	*Miodineutes*	*insignis*	11.0 - 12.0	Öhningen, Switzerland	ESSI

PIN: Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia
MNHN: Muséum National d'Histoire Naturelle, Paris France
NIG: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China
ESSI: Erdwissenschaftliche Sammlung, Swiss Federal Institute of Technology, Zurich, Switzerland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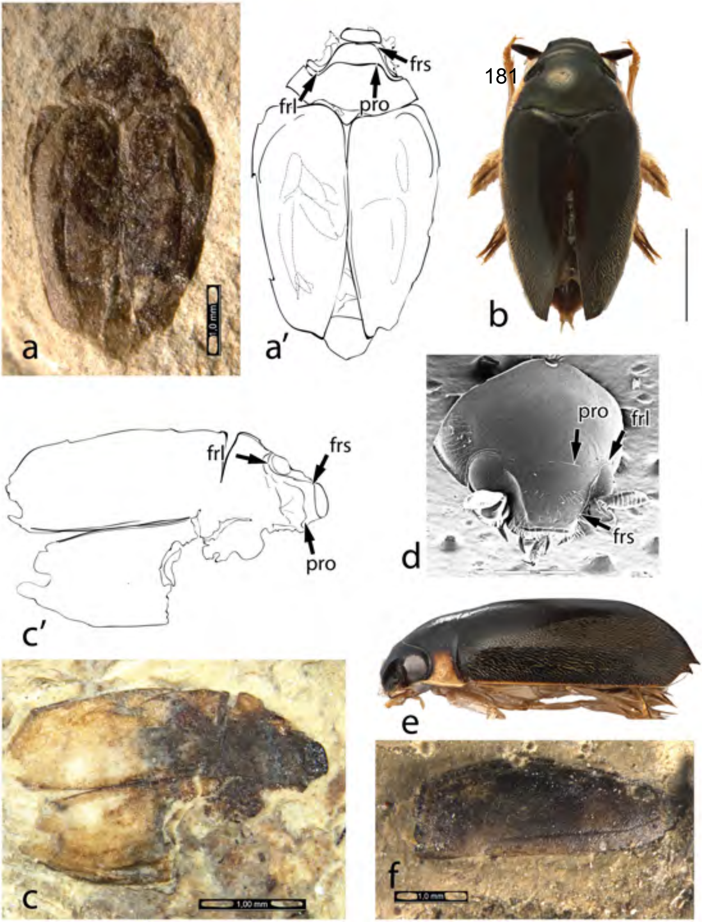
261.36
185.31
130.25
244.35
170.71
134.45
109.33
228.09
196.23
92.62
164.03
108.01
129.14
117.66
149.71
92.54
83.19
127.03
107.75
Spanglerogyrinae
Heterogyrinae
Gyrinini
Dineutini
Orectochilini
Gyrininae
270
250
230
210
190
170
150
130
110
90
70
50
30
10
PERMIAN
TRIASSIC
JURASSIC
CRETACEOUS
PALEOGENE
NEOGENE
QUATERNARY
220 Ma
170 Ma
120 Ma
50 Ma

Subfamily	genus	species	authority	age (Ma)	epoch	fossil deposit locality
Gyrininae	***Protogyrininus***	***sculpturatus***	(Mjöberg, 1905)	**0.126 – 0.012**	**Pleistocene**	nösand, Sweden
	Miodineutes	***insignis***	(Heer, 1862)	**11.62 – 7.26**	**Miocene**	Öhningen, Switzerland
	Miodineutes	***heeri***	Hatch, 1927	**11.62 – 7.26**	**Miocene**	Öhningen, Switzerland
	Miodineutes	***oeningenensis***	Hatch, 1927	**11.62 – 7.26**	**Miocene**	Öhningen, Switzerland
	Dineutus	***longiventris***	Heer, 1862	**11.62 – 7.26**	**Miocene**	Öhningen, Switzerland
	Gyrinus	***aquisextanea***	Nel, 1989	**11.62 – 7.26**	**Miocene**	Gypsum level of Aix, Aix-en-Provence, Bouches-du-Rhone, France
	Gyretes	***giganteus***	(Piton, 1940)	**33.9 – 23.0**	**Oligocene**	Menat, Pay-de-Dome, France
	Orectochilus	**sp**	Nel, 1989	**33.9 – 23.0**	**Oligocen**	Menat, Pay-de-Dome, France
	Gyrinoides	**limbatus**	Motschulsky, 1856	**37.2 – 33.9**	**Oligocene**	Baltic Amber, Europe
	Mesodineutes	***amurensis***	Ponomarenko, 1977	**66.0 – 61.7**	**Paleocene**	Arkhara site, Darmakan Formation, Russian Feeration
	Cretotortor	***archarensis***	Ponomarenko, 1977	**66.0 – 61.7**	**Paleocene**	Arkhara site, Darmakan Formation, Russian Feeration
	Cretotortor	***zherichini***	Ponomarenko, 1973	**93.9 – 89.8**	**Upper Cretaceous**	Kzyl-Zhar deposits, Northeastern Karatau Range, Kazakhstan
Spanglerogyrinae	***Angarogyrus***	***mongolicus***	Ponomarenko, 1986	**125.0 – 113.0**	**Lower Cretaceous**	Gurvan-Eren Formation, Govi-Altai, Mongolia
Heterogyrinae	***Mesogyrus***	***striatus***	Ponomarenko, 1973	**125.0 – 113.0**	**Lower Cretaceous**	Turga Formation, Undurga River, Russian Federation
	Baissogyrus	***savilovi***	Ponomarenko, 1973	**125.0 – 113.0**	**Lower Cretaceous**	Zaza Formation, Buryatia, Russian Federation
	Mesogyrus	***anglicus***	Ponomarenko et al., 2005	**145.0 – 140.2**	**Lower Cretaceous**	Durlston Formation, Swanage, Dorset England, United Kingdom
	Mesogyrus	***elongatus***	Ponomarenko, 2014	**152.1 – 145.0**	**Upper Jurassic**	Sharteg Formation, Altai Province, Mongolia
	Mesogyrus	***antiquus***	Ponomarenko, 1973	**166.1 – 157.3**	**Upper Jurassic**	Karabastau Formation, Karatau-Mikhailovka, Kazakhstan
	Cretotortor	**sp**	Nel, 1989	**182.7 – 174.1**	**Lower Jurassic**	Liège deposit N°IB 974, Bascharage, Luxemborg
Spanglerogyrinae	***Angarogyrus***	***minimus***	Ponomarenko, 1977	**182.7 – 174.1**	**Lower Jurassic**	Cheremkhovskaya Formation, Irkutsk, Russian Federation
	Mesogyrus	***sibiricus***	Ponomarenko, 1985	**189.6 – 182.7**	**Lower Jurassic**	Abasheva Formation, Lyagush'ye, Russian Federation


a
1,0 mm
a′
frs
frl
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b
c′
frl
frs
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d
pro
frl
frs
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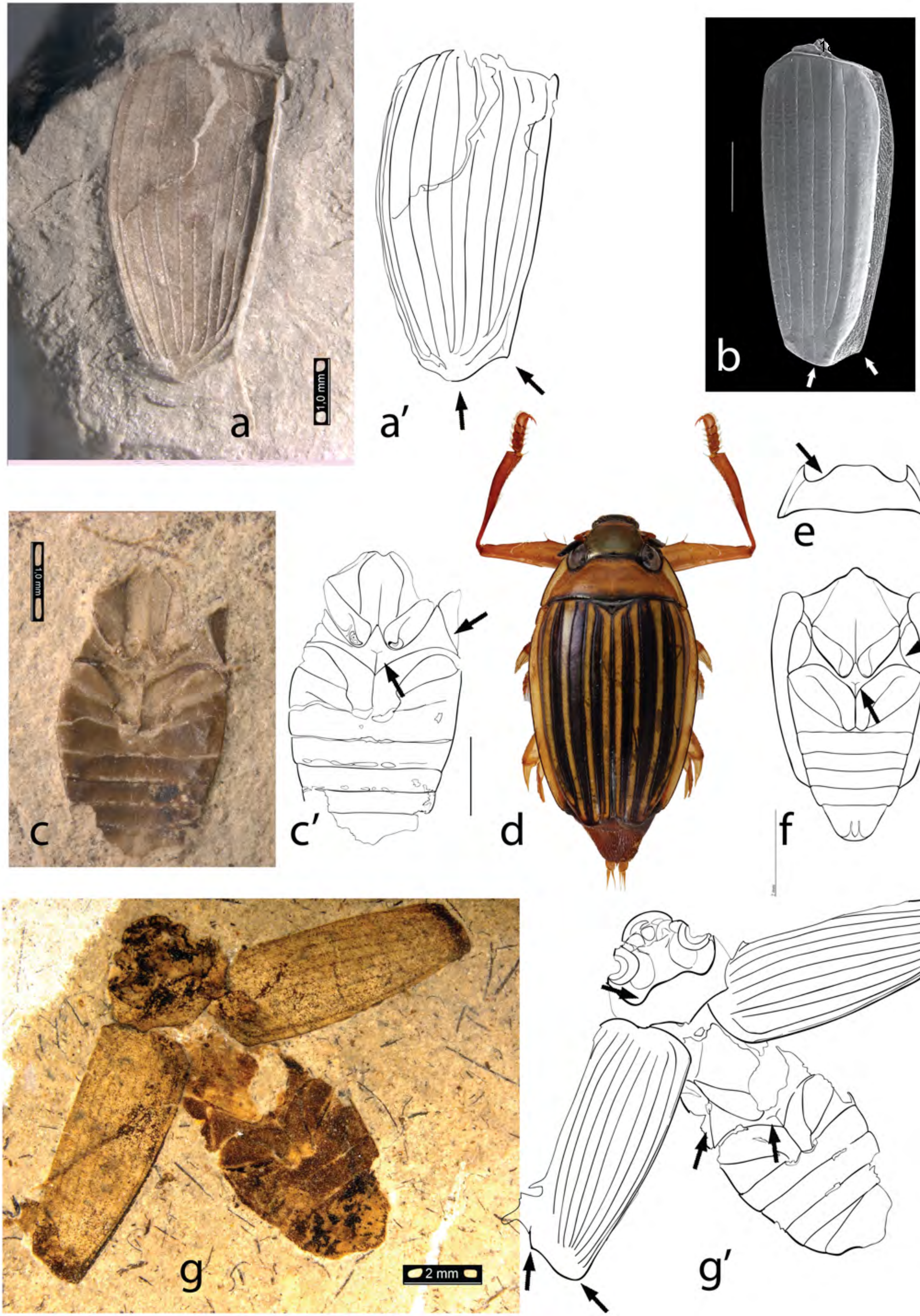
c
1,00 mm
f
1,0 mm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a
a′
b
1,0 mm
c
c′
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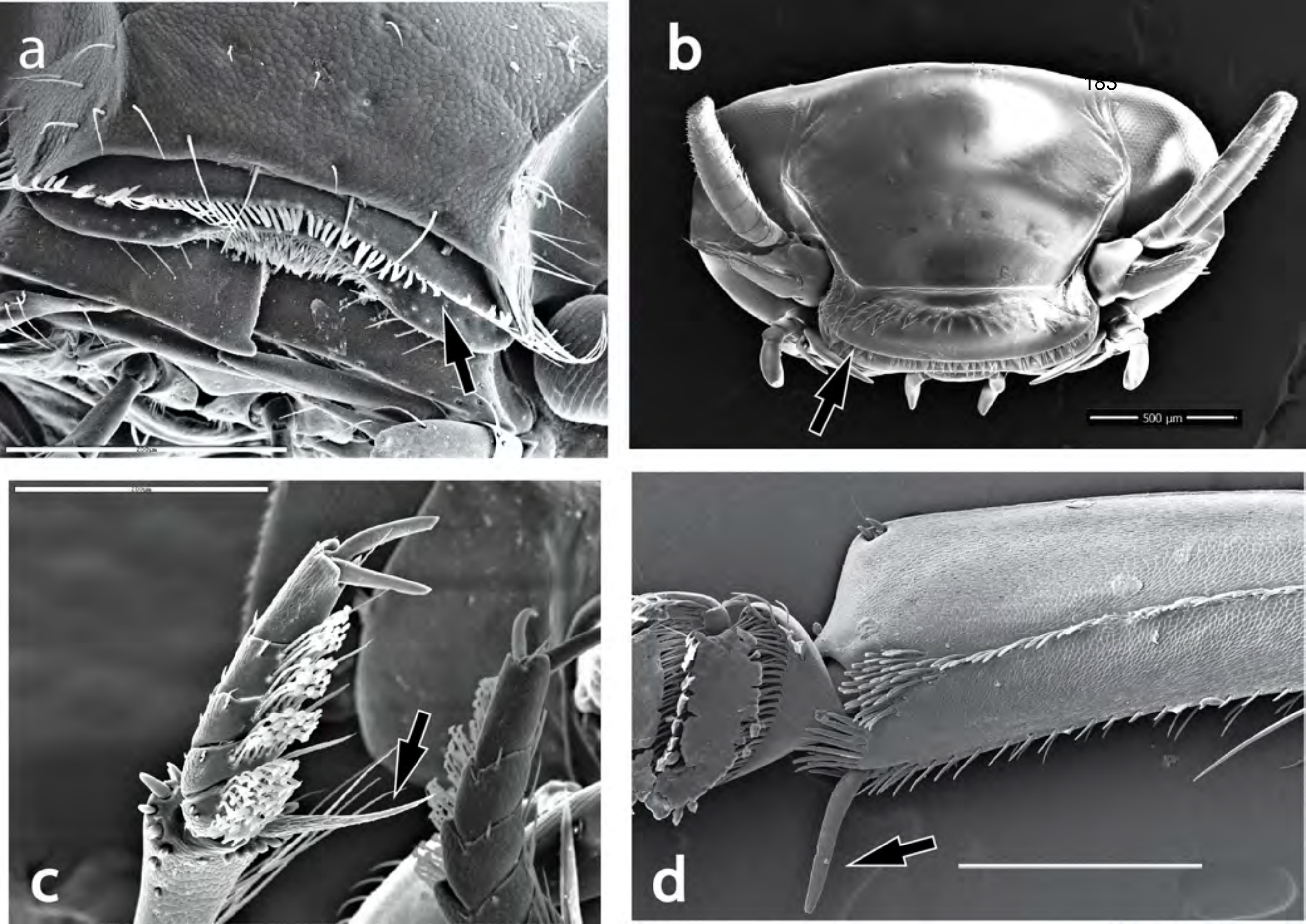
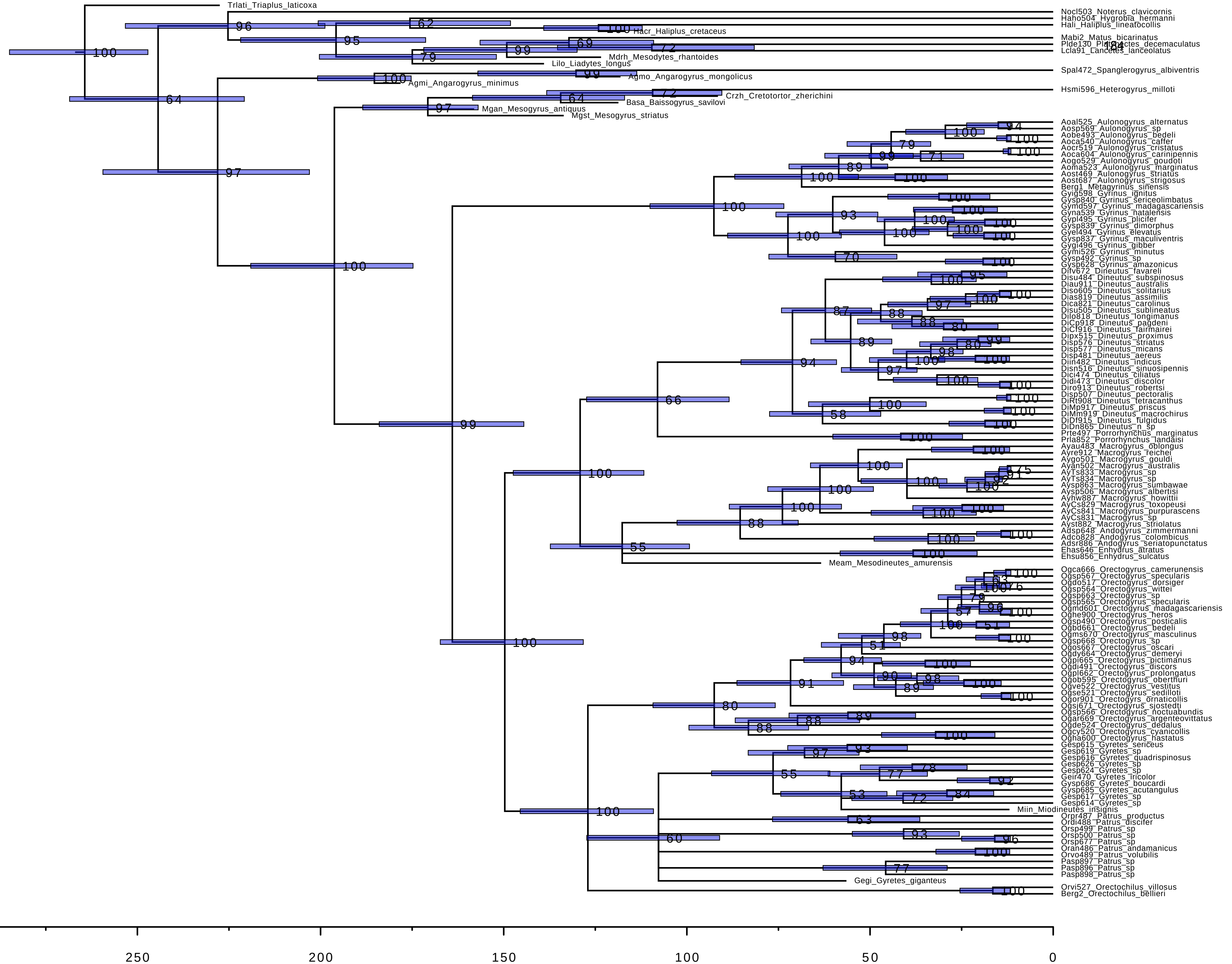
f
2 mm
g
g′


a
b
500 µm
c
d


Trlati_Triaplus_laticoxa
Nocl503_Noterus_clavicornis
Haho504_Hygrobia_hermanni
Hali_Haliplus_lineatocollis
Hacr_Haliplus_cretaceus
Mabi2_Matus_bicarinatus
Plde130_Platynectes_decemaculatus
184
Lcla91_Lancetes_lanceolatus
Mdrh_Mesodytes_rhantoides
Lilo_Liadytes_longus
Spal472_Spanglerogyrus_albiventris
Agmo_Angarogyrus_mongolicus
Agmi_Angarogyrus_minimus
Hsmi596_Heterogyrus_milloti
Crzh_Cretotortor_zherichini
Basa_Baissogyrus_savilovi
Mgan_Mesogyrus_antiquus
Mgst_Mesogyrus_striatus
Aoal525_Aulonogyrus_alternatus
Aosp569_Aulonogyrus_sp
Aobe493_Aulonogyrus_bedeli
Aoca540_Aulonogyrus_caffer
Aocr519_Aulonogyrus_cristatus
Aoca604_Aulonogyrus_carinipennis
Aogo529_Aulonogyrus_goudoti
Aoma523_Aulonogyrus_marginatus
Aost469_Aulonogyrus_striatus
Aost687_Aulonogyrus_strigosus
Berg1_Metagyrinus_sinensis
Gyig598_Gyrinus_ignitus
Gysp840_Gyrinus_sericeolimbatus
Gymd597_Gyrinus_madagascariensis
Gyna539_Gyrinus_natalensis
Gypl495_Gyrinus_plicifer
Gysp839_Gyrinus_dimorphus
Gyel494_Gyrinus_elevatus
Gysp837_Gyrinus_maculiventris
Gygi496_Gyrinus_gibber
Gymi526_Gyrinus_minutus
Gysp492_Gyrinus_sp
Gysp628_Gyrinus_amazonicus
Difv672_Dineutus_favareli
Disu484_Dineutus_subspinosus
Diau911_Dineutus_australis
Diso605_Dineutus_solitarius
Dias819_Dineutus_assimilis
Dica821_Dineutus_carolinus
Disu505_Dineutus_sublineatus
Dilo818_Dineutus_longimanus
DiCp918_Dineutus_pagdeni
DiCf916_Dineutus_fairmairei
Dipx515_Dineutus_proximus
Disp576_Dineutus_striatus
Disp577_Dineutus_micans
Disp481_Dineutus_aereus
Diin482_Dineutus_indicus
Disn516_Dineutus_sinuosipennis
Dici474_Dineutus_ciliatus
Didi473_Dineutus_discolor
Diro913_Dineutus_robertsi
Disp507_Dineutus_pectoralis
DiRt908_Dineutus_tetracanthus
DiMp917_Dineutus_priscus
DiMm919_Dineutus_macrochirus
DiDf915_Dineutus_fulgidus
DiDn865_Dineutus_n_sp
Prte497_Porrorhynchus_marginatus
Prla852_Porrorhynchus_landaisi
Ayau483_Macrogyrus_oblongus
Ayre912_Macrogyrus_reichei
Aygo501_Macrogyrus_gouldi
Ayan502_Macrogyrus_australis
AyTs833_Macrogyrus_sp
AyTs834_Macrogyrus_sp
Aysp863_Macrogyrus_sumbawae
Aysp506_Macrogyrus_albertisi
Ayhw887_Macrogyrus_howittii
AyCs829_Macrogyrus_toxopeusi
AyCs841_Macrogyrus_purpurascens
AyCs831_Macrogyrus_sp
Ayst882_Macrogyrus_striolatus
Adsp648_Andogyrus_zimmermanni
Adco828_Andogyrus_colombicus
Adsr886_Andogyrus_seriatopunctatus
Ehas646_Enhydrus_atratus
Ehsu856_Enhydrus_sulcatus
Meam_Mesodineutes_amurensis
Ogca666_Orectogyrus_camerunensis
Ogsp567_Orectogyrus_specularis
Ogdo517_Orectogyrus_dorsiger
Ogsp564_Orectogyrus_wittei
Ogsp663_Orectogyrus_sp
Ogsp565_Orectogyrus_specularis
Ogmd601_Orectogyrus_madagascariensis
Oghe900_Orectogyrus_heros
Ogsp490_Orectogyrus_posticalis
Ogbd661_Orectogyrus_bedeli
Ogms670_Orectogyrus_masculinus
Ogsp668_Orectogyrus_sp
Ogos667_Orectogyrus_oscari
Ogdy664_Orectogyrus_demeryi
Ogpi665_Orectogyrus_pictimanus
Ogdi491_Orectogyrus_discors
Ogpl662_Orectogyrus_prolongatus
Ogob595_Orectogyrus_oberthuri
Ogve522_Orectogyrus_vestitus
Ogse521_Orectogyrus_sedilloti
Ogor901_Orectogyrs_ornaticollis
Ogsj671_Orectogyrus_sjostedti
Ogsp566_Orectogyrus_noctuabundis
Ogar669_Orectogyrus_argenteovittatus
Ogde524_Orectogyrus_dedalus
Ogcy520_Orectogyrus_cyanicollis
Ogha600_Orectogyrus_hastatus
Gesp615_Gyretes_sericeus
Gesp619_Gyretes_sp
Gesp616_Gyretes_quadrispinosus
Gesp626_Gyretes_sp
Gesp624_Gyretes_sp
Geir470_Gyretes_iricolor
Gysp686_Gyretes_boucardi
Gysp685_Gyretes_acutangulus
Gesp617_Gyretes_sp
Gesp614_Gyretes_sp
Miin_Miodineutes_insignis
Orpr487_Patrus_productus
Ordi488_Patrus_discifer
Orsp499_Patrus_sp
Orsp500_Patrus_sp
Orsp677_Patrus_sp
Oran486_Patrus_andamanicus
Orvo489_Patrus_volubilis
Pasp897_Patrus_sp
Pasp896_Patrus_sp
Pasp898_Patrus_sp
Gegi_Gyretes_giganteus
Orvi527_Orectochilus_villosus
Berg2_Orectochilus_bellieri
250
200
150
100
50
0