Systematics and evolution of the whirligig beetle tribe Dineutini (Coleoptera: Gyrinidae: Gyrininae)

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The phylogeny and evolutionary history of the whirligig beetle tribe Dineutini are inferred from the analysis of 56 morphological characters and DNA sequence data from the mitochondrial gene fragments *COI*, *COII* and *12S*, and the nuclear gene fragments *H3* and *arginine kinase*. Bayesian and maximum likelihood analyses were performed. A Bayesian tip-dating 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, nonmonotypic subgenera. The resulting trees strongly support the monophyly of the Dineutini and the genera *Dineutus* Macleay, 1825, *Macrogyrus* Régimbart, 1882, *Porrorhynchus* Laporte, 1835 and *Enhydrus* Laporte, 1835. The results do not support the distinction of *Andogyrus* Ochs, 1924 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. nov.** is relegated to a subgenus of *Macrogyrus*; the following subgenera are synonymized with *Macrogyrus s.s.* **sensu nov.**: *Australogyrus* Ochs, 1949 **syn. nov.**, *Ballogyrus* Ochs, 1949 **syn. nov.**, *Clarkogyrus* Ochs, 1949 **syn. nov.**, *Megalogyrus* Ochs, 1949 **syn. nov.**, *Orectomimus* Ochs, 1930 **syn. nov.** and *Tribologyrus* Ochs, 1949 **syn nov.**; the subgenus *Stephanogyrus* Ochs, 1955 **syn. nov.** is synonymized with the subgenus *Cyclomimus* Ochs, 1929; the genus *Dineutus* now includes two subgenera: *Cyclous* Dejean, 1833 **sensu nov.** and the *Dineutus s.s.* subgenus **sensu nov.;** the following subgenera are synonymized with the subgenus *Cyclous*: *Callistodineutus* Ochs, 1926 **syn. nov.**, *Paracyclous* Ochs, 1926 **syn. nov.**, *Protodineutus* Ochs, 1926 **syn. nov.** and *Spinosodineutes* Hatch, 1926 **syn. nov.**; and the following subgenera are synonymized with the *Dineutus s.s.* subgenus: *Rhombodineutus* Ochs, 1926 **syn. nov.** and *Merodineutus* Ochs, 1955 **syn nov.** The subgenus *Rhomborhynchus* Ochs, 1926 **incert. sed.** is tentatively moved to the genus *Dineutus*, without phylogenetic placement. The analysis confirms *Mesodineutes*† Ponomarenko, 1977 is a member of the Dineutini. Each genus and subgenus is reviewed in detail with (1) a morphological diagnosis, (2) its taxonomic circumscription, including the placement of species not included in the analysis, (3) known distribution and (4) 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. The historical biogeography of the Dineutini was found to be dominated primarily by dispersal, and we report a new transpacific disjunct distribution for members of the genus *Dineutus*.

ADDITIONAL KEYWORDS: aquatic beetle – anatomy – biogeography – classification – geography – morphology – Phylogenetics.

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 (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

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USA (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 (1882a) 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, 1882a, *Porrorhynchus* Laporte, 1835, *Enhydrus* Laporte, 1835 and *Dineutus* Macleay, 1825. The genus *Dineutus* was first to be split into subgenera by Hatch (1926), 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, 1926; Ochs, 1949). Furthermore, classic gyrinid taxonomists have debated whether *Macrogyrus* is descended from a South American (Hatch, 1926) 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 and (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 (1) assess the monophyly of the currently proposed genera and numerous subgenera, to improve and stabilize classification; (2) construct a time-calibrated phylogenetic tree to understand the relationships of dineutine species and the timing of their evolution; and (3) 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.

MATERIAL AND METHODS

DATA

Taxon sampling and data collection

Our main data set included 73 species of Gyrinidae for the Bayesian phylogenetic analysis (Table S1). Ten outgroup species were selected: *Heterogyrus milloti* Legros, 1953 for Heterogyrinae, four species from the tribe Gyrinini, four from Orectochilini and *Gyretes giganteus*† (Piton, 1940) 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*) *ritsemae* Régimbart, 1882c (only known from the type series from Sulawesi); *Macrogyrus* (*Ballogyrus*) *leopoldi* Ball, 1932 (only known from the holotype specimen from New Guinea) and *Macrogyrus* (*Stephanogyrus*) *caledonicus* (Fauvel, 1867) (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, and no molecular grade specimens were available for analysis. The fossil *Mesodineutes amurensis*† Ponomarenko, 1977 was utilized as the fossil ingroup member.

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.

Fifty-six morphological characters were coded from both external and internal morphology, for use in the Bayesian concatenated analysis. External characters were coded from specimens examined using a SteReo Disovery.V8 (Zeiss) microscope. Scanning electron microscopic (SEM) images were also utilized to examine and code characters. SEM images were taken at the KU Microscopy and Analytical Imaging Laboratory, University of Kansas, Lawrence, KS, USA. 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 colour.

Internal characters came from the female reproductive tract (RT), male genitalia and sperm morphology. Female RTs were prepared following the methods outlined in Miller & Bergsten (2012). The genitalia were illustrated in water using a Camera Lucida attached to a SteReo Disovery.V8 (Zeiss) microscope. Illustrations were then scanned and traced using Adobe Illustrator CS5. Other morphology illustrated was drawn under the camera lucida, and scanned and traced using the same methods.

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 samples 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.

Full description of morphological characters (Appendix) and coding of morphological characters from (Table S2) are available. 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. Morphological characters were mapped on to the preferred phylogenetic tree for Dineutini (Fig. S9) using the 'fast' optimization (ACCTRAN) in WinClada (Nixon, 1999–2002) for visualization of potential synapomorphies, following phylogenetic analysis.

DNA was extracted using a Qiagen DNEasy kit (Valencia, CA, 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 for the phylogenetic analyses, 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 Wild & Maddison (2008) and Miller & Bergsten (2012). Primers and their sources, used for amplification and sequencing, used are listed in Table S3. Gene coverage for each taxon analysed is given 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 of the molecular data and clean up were done using Mesquite 3.01 (Maddison & Maddison, 2015).

Partitioning

The final concatenated data set broadly overlaps that used by Miller & Bergsten (2012), and for this reason the same partitioning scheme, with codon-position specific nuclear and mitochondrial partitions, was used for the final analyses. This partitioning scheme was previously tested and found preferred by a Bayes Factor test over gene-specific partitions (Miller, Bergsten & Whiting, 2009; Miller & Bergsten, 2012). A de novo partitioning scheme analysis was also performed using PartitionFinder 1.1.1 (Lanfear *et al.*, 2012) under the 'greedy' search algorithm, with unlinked branch-lengths, and Akaike information criterion corrected (AICc) model selection. The PartitionFinder analysis confirmed a codon-position-specific partitioning scheme as the best fit. Because the proposed scheme differed slightly in composition of a single partition than the Miller & Bergsten (2012) scheme, a Bayesian tip-dating analysis using the PartitionFinder partition scheme was run, resulting in a nearly identical tree (Fig. S6) to our final preferred Bayesian tree (Fig. S3).

PHYLOGENETIC ANALYSES

Bayesian

Bayesian analysis was implemented using the MPI version of MrBayes 3.2.6 (Ronquist *et al.*, 2012b; Zhang *et al.*, 2015). No substitution model was selected a priori; instead, the reversible-jump Markov chain Monte Carlo (MCMC) method with gamma rate variation across sites was used to test the probability of different models a posteriori during analysis (Huelsenbeck, Larget & Alfaro, 2004; Miller & Bergsten, 2012; Ronquist *et al.*, 2012b). A tip-dating approach was taken for time-calibration (Ronquist *et al.*, 2012a). This technique simultaneously constructs a phylogenetic tree, providing

placement of fossil taxa within the tree and divergence time estimates for the tree (Ronquist *et al.*, 2012a).

To infer the substitution rate for the tip-dating approach, the methods outlined by Ronquist *et al.* (2012a) were followed with the mean age of the fossil *Angarogyrus minimus* Ponomarenko, 1977 (178 Ma) used to calculate the median rate and the mean age of *Mesogyrus antiquus* Ponomarenko, 1973 (161 Ma) for the standard deviation. The fossilized birth-death (FBD) macroevolutionary model (Heath, Huelsenbeck & Stadler, 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 *H. 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 independent gamma rate, 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, Suchard & Drummon, 2013). A value of ESS ≥ 200 was acknowledged as a good indicator of convergence.

Tip-dating has previously been found to give exceptionally old age estimates (Arcila *et al.*, 2015) and result in 'ghost lineages' – lineages lacking exemplars in the fossil record supporting their age (Ronquist *et al.*, 2012a). Despite improvements implemented in MrBayes 3.2.6 mitigating these effects (Zhang *et al.*, 2015), we performed a node-calibrated analysis (Fig. S7) to compare ages with those obtained using the tip-dating method. For the node-calibrated analysis, we used the same settings and methods outlined above, except the fossilization prior was fixed at 0 [necessary for node calibration (Zhang, 2016)], and the following calibration points established with offset exponential priors: the root of the tree, given the ages 174 and 200 (representing the oldest known gyrinid fossils); the orectochiline taxa with 55 and 58, representing the oldest orectochiline fossil, *G. giganteus* and the dineutine taxa at 61–66 representing the oldest definite dineutine fossil, *M. amurensis*. The fossil taxa were deleted from the analysis, as per node-calibration methods in MrBayes 3.2.6 (Zhang, 2016).

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 and S2). As topology stability was the main concern of these analyses, they utilized a subset of taxa, excluding those available only for morphology and *H. milloti* (Figs S1 and S2). Certain problematic species were also removed from analyses to test effects on phylogenetic reconstruction (Figs S4 and S5).

Maximum likelihood

A maximum likelihood (ML) analysis was also performed (Fig. S8) and 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 analysed individually. The genes were then combined to construct a multilocus species tree using ASTRAL-II (Mirarab *et al.*, 2014; Mirarab & Warnow, 2015). One hundred replicates of multilocus bootstrap support (Seo, 2008) were then performed in ASTRAL-II. Morphology was not included in the ML analysis.

All phylogenetic analyses were run on the super computer cluster 'Ulam' at the Center for Advanced Research Computing, University of New Mexico.

BIOGEOGRAPHIC ANALYSIS

The time-calibrated consensus tree (Fig. S3) from the Bayesian tip-dating analysis was used for the biogeographic analysis, with outgroup- and fossil taxa pruned, as well as AyTs832 [*Macrogyrus albertisi* (Régimbart, 1882b)] to remove a polytomy. The analysis was performed using the program R and the package BioGeoBEARS (Matzke, 2013a, b) 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; W, Wallacea; O, Oriental; P, Palearctic; E, Ethiopean region; N, Nearctic; C, Central America; I, West Indies (Fig. 3). The geographic region assigned to each species is available in Table S1. The maximum number of geographic regions a species was allowed to occupy 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 and 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 palaeogeographic 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, Gahagan & Dalziel, 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 New Guinea (Baldwin, Fitzgerald & Webb, 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 are allowed. The dispersal rate coding (Table S4) followed that of Toussaint *et al.* (2016), based on the above palaeogeographic evidence reference for each time slice.

RESULTS

PHYLOGENETIC ANALYSES

The Bayesian tip-dating analysis (Figs 1, 2, S3, S4) 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†* and 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 nov.**) is strongly supported as monophyletic (pp = 1.00) with Palaeocene 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 s.s. Macrogyrus striolatus* (Guérin-Méneville, 1838) is recovered as sister to the remaining species of the *Macrogyrus s.s.,* but with weak support (pp = 0.50). The Australian species *Macrogyrus oblongus* (Boisduval, 1835), *Macrogyrus rivularis* (Clark, 1866) and *Macrogyrus reichei* (Aubé, 1838) 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* (Clark, 1866) 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* (Brullé, 1835) 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 comprises the majority of *Dineutus* species and has strong support for monophyly (*pp* = 0.99); this is the newly defined subgenus *Cyclous* **sensu nov.** 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 placed within the late Eocene (between 44 and 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
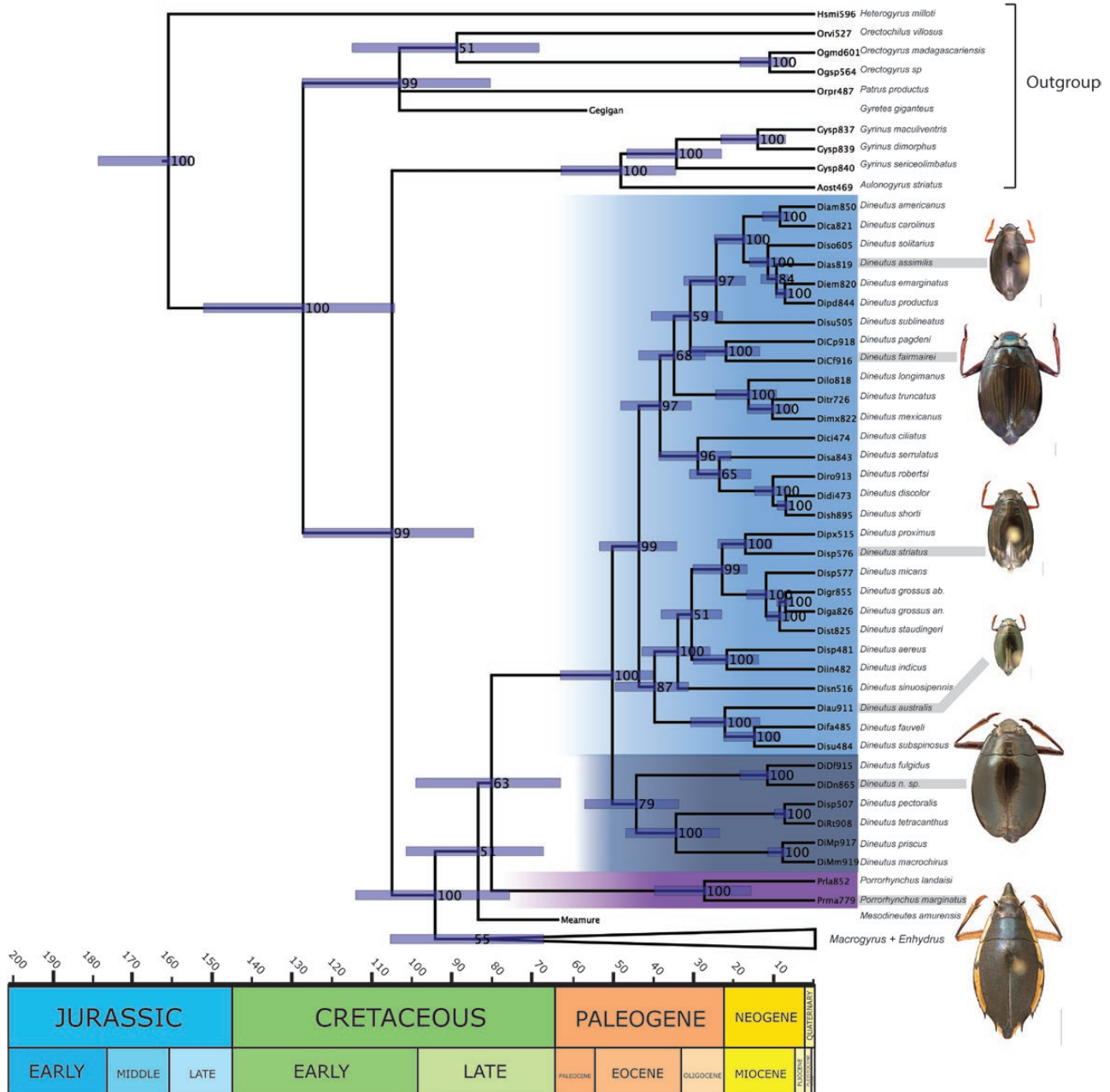
Figure 1. Phylogeny of the Dineutini based on Bayesian tip-dating analysis Part 1. Labels at node denote posterior probability, blue bars indicate 95% hpd for age. The blue clades indicate members of *Dineutus*, with lighter blue showing the subgenus *Cyclous* **sensu nov.** and the dark blue the *Dineutus s.s.* subgenus. Purple indicates the genus *Porrorhynchus*. Species are approximately to relative scale.

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* (Forsberg, 1821), *D. discolor* Aubé, 1838) (Gustafson & Miller, 2015). Interestingly despite exceptionally similar morphology, *D. ciliatus* and *D. robertsi* Leng, 1911 are not recovered as sister species.

Instead *D. ciliatus* is strongly supported (*pp* = 0.96) as sister to a clade comprising *D. serrulatus analis* Régimbart, 1882a (*D. discolor* + *D. shorti* Gustafson & Sites, 2016). The newly described *D. shorti* 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* Sharp,
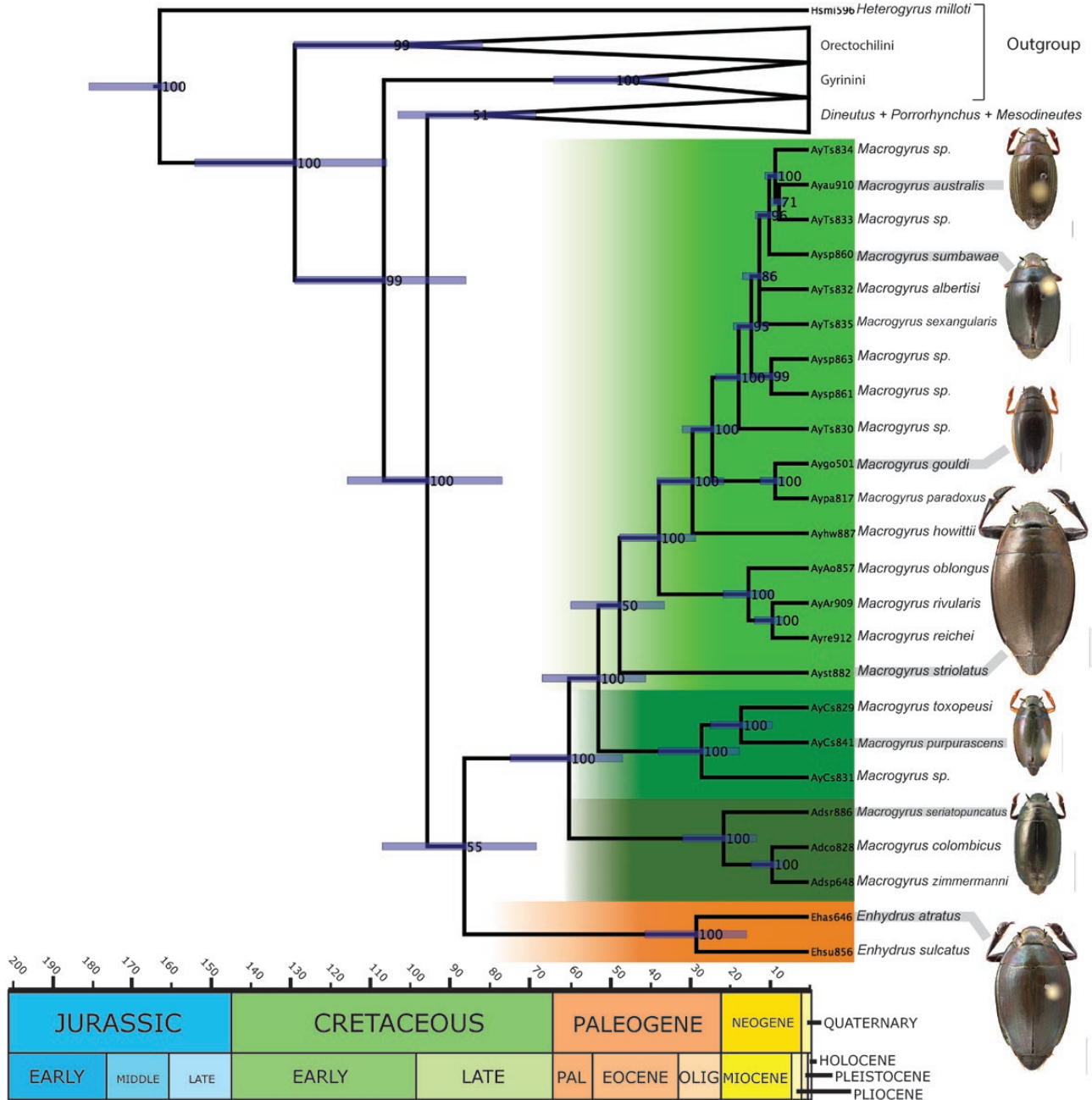
Figure 2. Phylogeny of the Dineutini based on Bayesian tip-dating analysis Part 2. Labels at node denote posterior probability, blue bars indicate 95% hpd for age. The green clades indicate members of *Macrogyrus*, with the lightest green showing the *Macrogyrus s.s.* subgenus, the next darkest members of the subgenus *Cyclomimus*, and the darkest green showing the subgenus *Andogyrus* **stat. nov.** Orange indicates the genus *Enhydrus*. Species are approximately to relative scale.

1873 and *D. mexicanus* Ochs, 1925 which are strongly supported as sisters (*pp* = 1.00) with the Caribbean *D. longimanus* (Olivier, 1795) 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* Ochs, 1937 and *D. fairmairei*

Régimbart, 1882a, 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* (Chevrolat, 1834) is recovered as sister to the remaining members of this clade (*pp* = 0.97). Interestingly another Central American species, *D.*

solitarius Aubé, 1838 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* (Fabricius, 1775) the type species of the subgenus *Cyclous* is strongly supported (*pp* = 1.00) as sister to the African species *D. fauveli* Régimbart, 1884 and *D. subspinosus* (Klug, 1834), both members of *Spinosodineutes*. Interestingly the other member of *Spinosodineutes* included in the analysis, *D. striatus* (Zimmermann, 1916) is strongly supported (*pp* = 1.00) as sister to the large widespread Malagasy species, *D. proximus* Aubé, 1838.

The clade containing the members of the former subgenus *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* this group (*pp* = 1.00). The other Malagasy species *D. proximus* is distantly related, nested well within a clade or primarily mainland Africa species.

The node-calibrated analysis confirmed the ages estimated by the tip-dating analysis were not unrealistically old (Fig. S7). The estimated 95% hpd for node age overlapped for the two dating analyses at their extremes, with the oldest estimates in the node-calibrated analysis (Fig. S7) overlapping the youngest estimates of the tip-dating analysis (Fig. S3).

The ML analysis (Fig. S8) generally supported the broader conclusions of the analysis. There is 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* = 100) and *Cyclomimus* (*bt* = 91.3). *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 may be 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 ANALYSIS

For the ancestral state estimation, the DEC models fit the data significantly better than both DIVALIKE models (Table 1). 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 1). Despite the difference in log-likelihood the DEC and DIVALIKE models recovered nearly identical ancestral state reconstructions (Figs S10–S17). 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 S10–S17). The models either suggest slightly higher 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 S10–S17). 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 S14–S17).

The ancestor of both *Enhydrus* and *Macrogyrus* is recovered as being distributed in South America (Fig. 3, N2). The ancestral state reconstruction supports an origin for *Macrogyrus* in the Paleocene of South America (Fig. 3, N3) with subsequent dispersal to Australia around the early Eocene, coinciding with the Early Eocene Climatic Optimum (Fig. 3, N4). 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, CII, CIII). Dispersal to the Lesser Sunda Islands in Wallacea happened most recently around the mid-Miocene (Fig. 3, CIII).

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, N5). The common ancestor of *Dineutus* (Fig. 3, N6) likely originated similarly in the Oriental region in the early Eocene, around the Early Eocene Climatic Optimum. In the *Dineutus s.s.* subgenus, the common ancestor likely arose in the Oriental region (Fig. 3, N7), with subsequent dispersal to Papua New Guinea

Table 1. Results of BioGeoBEARS statistical comparison of DEC, DEC +*j*, DIVALIKE and DIVALIKE +*j* model fit

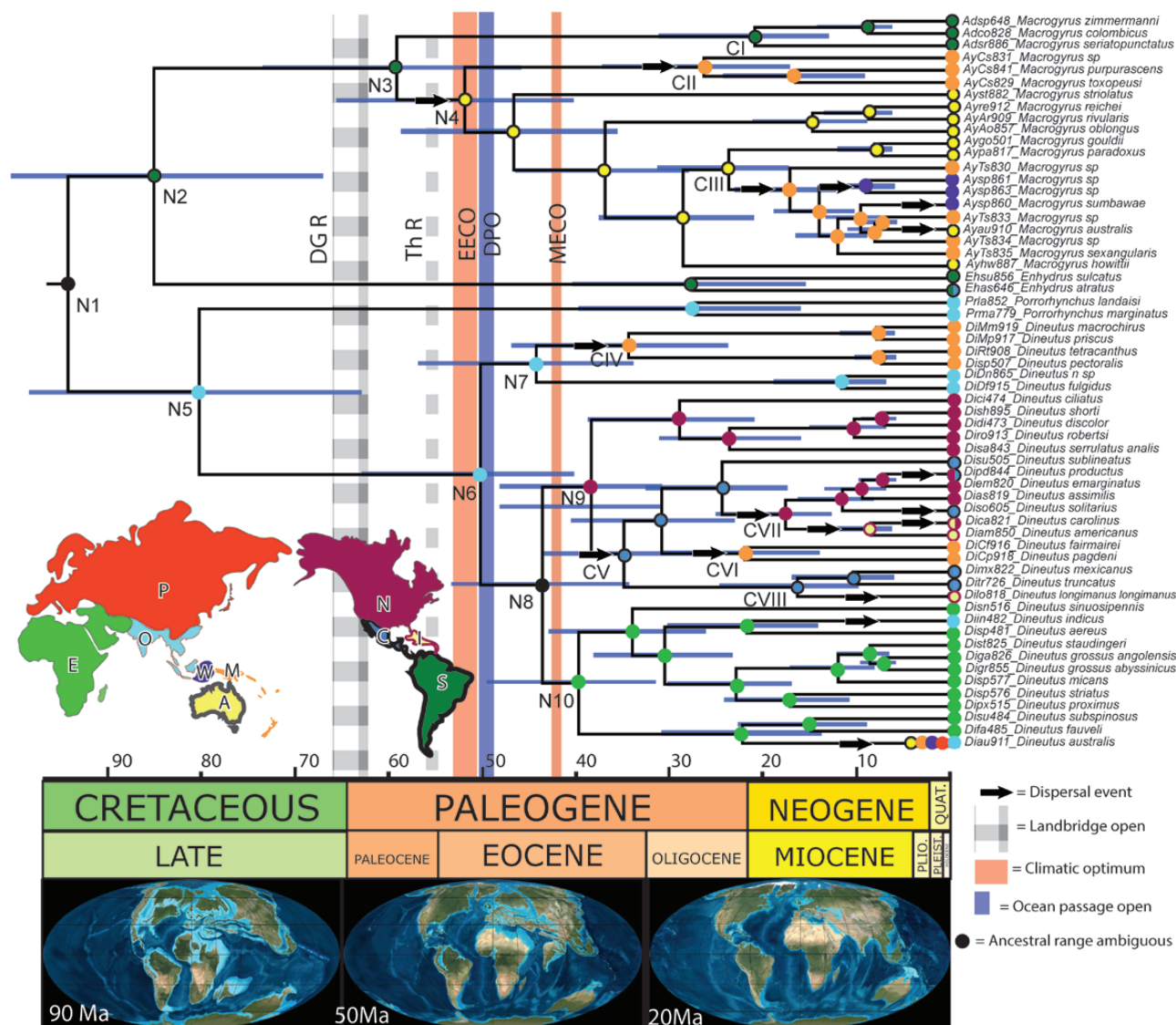|	Ln *L*	Params	*d*	*e*	*j*	AICc	Akaike weights
DEC	−116.4	2	0.0067	1.00E−12	0	236.9	0.072
DEC+*j*	−112.7	3	0.005	1.00E−12	0.061	231.8	0.93
DIVALIKE	−143.4	2	0.005	0.0011	0.17	293.3	4.30E−14
DIVALIKE+*j*	−143.5	3	0.0055	0.001	0.14	293.5	3.90E−14

Figure 3. Historical biogeography of the dineutine whirligig beetles. The Bayesian tip-dated tree 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 S12, S13). 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 colour key for the ancestral state reconstructed. The palaeogeographic maps at bottom, © Colorado Plateau Geosystems used with permission, show continental positions in the major time slices (Blakey, 2008).

around the late Eocene (Fig. 3, CIV). There is considerable ambiguity related to the ancestral range of the common ancestor of the *Dineutus* subgenus *Cyclous* (Figs S10–S17; 3, N8) preventing any conclusions about its location. The primarily North American clade within *Cyclous* is estimated to have had a Nearctic ancestor (Fig. 3, N9) and the primarily African clade an Ethiopian ancestor (Fig. 3, N10). 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, CV). Several dispersal events out of Central America are then inferred around the early Miocene and late Miocene (Fig. 3, CVI, CVII, CVIII).

DISCUSSION

HISTORICAL BIOGEOGRAPHY OF *MACROGYRUS*

Our ancestral range reconstruction supports a South American origin for *Macrogyrus* with dispersal to

Australia in the common ancestor of the subgenera *Cyclomimus* and *Macrogyrus s.s.* (Fig. 3, N4) occurring around the early Eocene, a pattern very similar to that found in percichthyid fish (Chen *et al.*, 2014). While we do not recover a Gondwanan vicariance, the isolation of the subgenus *Andogyrus* likely resulted from the final break up of Gondwana when Drake's Passage opened (Fig. 3, DPO) fully separating South America from western Antarctica around 50 Ma (Lawver & Gahagan, 2003; Livermore *et al.*, 2005), and the opening of the Tasmanian Gateway cut Antarctic ties with Australia (Bijl *et al.*, 2013).

Macrogyrus exhibits a very similar distribution to that of the southern beech, *Nothofagu*s, which has Antarctica fossils (Kvaček & Vodrážka, 2016) and is thought to have originated in the high altitudes of the Southern Hemisphere, such as southern South America (Li & Zhou, 2007). While there are no known *Macrogyrus* fossils from Antarctica, given the earliest diverging *Andogyrus* species, *M. (A.) seriatopunctatus* is Patagonian (Brinck, 1977), it is possible that *Macrogyrus* species were also once found on Antarctica. Similar to the ungulates known from southern South America of the Palaeogene (Reguero *et al.*, 2014), *Macrogyrus* could also have utilized the Wedellian Isthmus (Reguero *et al.*, 2014) [proposed to have served as a land bridge allowing faunal exchange between Patagonia and west Antarctica until around 57 Ma (Reguero *et al.*, 2014)], to disperse to Antarctica, where the cool-temperate climate (Pross *et al.*, 2012) would have allowed the common ancestor of *Cyclomimus* and *Macrogyrus s.s.* passage to Australia until the opening of the Tasmanian Gateway, around 50 Ma (Bijl *et al.*, 2013).

Similar to findings in other aquatic beetles (e.g. *Exocelina*) (Toussaint *et al.*, 2015), Australia served as the source for colonization of New Guinea (Fig. 3, CIII). We also support Toussaint *et al.* (2015) findings that the aquatic beetle fauna of New Guinea is composed of unrelated lineages having repeatedly colonized the region (Fig. 3, CII, CIII, CIV, CVI). This is the case not only in *Macrogyrus*, but also *Dineutus*. Some of the most derived members of *Macrogyrus* (Fig. 3, CIII) were found to occupy the Sunda Islands, similar to platynectine diving beetles (Toussaint *et al.*, 2016). Interestingly, one of the most derived species, *M. australis* (Fig. 3, CIII), is found to have only recently dispersed to Australia from a Melanesian ancestor, where it is now one of the most common and widespread species (Watts & Hamon, 2010).

HISTORICAL BIOGEOGRAPHY OF *DINEUTUS*

The common ancestor of *Dineutus* is reconstructed as arising within the Oriental region during the early Eocene (Fig. 3, N6) with dispersal into the Nearctic and the Ethiopian regions likely occurring during the Mid-Eocene Climatic Optimum (Fig. 3, MECO, N9, N10). This period of time is far too recent for dispersal to the western hemisphere to have occurred over the transatlantic De Geer or Thulean Routes (Fig. 3, DG R, Th R) (Brikiatis, 2014). Thus, the most likely route to the Nearctic would be through Beringia, which during the Eocene was a lush swamp forest occupied by such thermophilic species as primates, tapirs and alligators (Eberle & Greenwood, 2011). This route has also been proposed for dibamid lizards, which have a current Neartic/Oriental disjunct distribution (Townsend, Leavitt & Reeder, 2011). Following the Eocene, during the cooling of the Oligocene, dispersal to Central America occurred (Fig. 3, CV). From here subsequent dispersals to the Caribbean occurred either directly from Central America (Fig. 3, CVIII) or through the Nearctic during the Miocene (Fig. 3, CVII); scenarios similar to that proposed for the origins of volant and freshwater West Indies vertebrate species (Hedges, 1996). All together, these data suggest the *Dineutus* species of the western hemisphere likely dispersed to North America via Beringia, and *Dineutus'* absence in South America is a result of no known species having spread further south than Panama. If a *Dineutus* species were present in South America, it would likely be found in one of the north-western countries, such as Colombia, Ecuador, or Peru, under this scenario.

Interestingly, the species located in the Solomon Islands and Fiji are reconstructed as having diverged from Central American ancestors around the Oligocene (Fig. 3). This transpacific disjunct distribution is similar to that of Fijian iguanas, whose closest relatives are also found in the New World tropics (Gibbons, 1981; Keogh *et al.*, 2008). Whether this represents a long distance ocean dispersal, or a secondary dispersal back across Beringia, will require additional taxon sampling. A critical taxon for answering this question will likely be *D. ritsemae*, a species known only from Sulawesi. *Dineutus ritsemae* appears to be closely related to *D. pagdeni* and *D. fairmairei*, sharing a relatively rare morphological feature, the profemoral subapicoventral tooth being located only on the anterior margin of the profemur's ventral face.

CONCLUSIONS

We found strong support for the monophyly of the Dineutini and the genera *Dineutus, Enhydrus, Macrogyrus* and *Porrorhynchus*. We recovered a historical biogeography of the Dineutini dominated by dispersal and added the dineutine genera *Macrogyrus* and *Dineutus* to the growing number of animal taxa with transpacific distributions. We did not recover

Gondwanan vicariance between the *Macrogyrus* subgenus *Andogyrus* and the remaining species, instead we recovered a dispersal event out of South America to the Austral region, similar to the pattern found in zalmoxid harvestmen (Sharma & Giribet, 2012) and most similar to freshwater percichthyid fish (Chen *et al.*, 2014). Our results support a South America origin of *Macrogyrus*, and the absence of *Dineutus* in South America a result of the genus having yet to disperse there.

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* (Walker, 1858) 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, 1882a; 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, 1926) in the form of a more-or-less equilateral triangle (Fig. 6) (Régimbart, 1882a), (4) lobiform metanepisternum, (5) transverse metacoxae (Fig. 6), (6) female RT with greatly expanded, sac-like spermatheca without a well-differentiated fertilization duct (Figs 11, 12) (Miller & Bergsten, 2012) and (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 regard to the female RT, 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 (1882a). Régimbart (1882a) provided 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 1882a for the Dineutini, with only minor revision. The valid constituent species of the tribe Dineutini have not changed considerably since Régimbart's (1882a) 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, Hosken & Birkhead, 2009), the sperm of the dineutine genera were sampled. The study revealed that *Enhydrus* (Fig. 13A–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, 1882a.

Diagnosis: The genus *Dineutus* can be diagnosed within the Dineutini by the following combination of
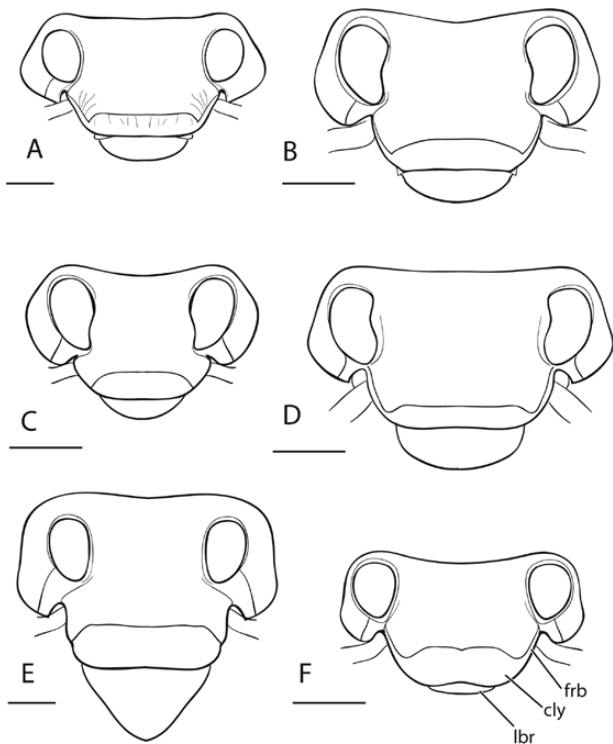

Figure 4. Head capsules of dineutine species, anterior view. Scale bars = 1 mm. Abbreviations: lbr, labrum: cly, clypeus: frb, frontolateral bead. (A) *Enhydrus sulcatus*; (B) *Macrogyrus* (*Macrogyrus*) *australis*; (C) *Dineutus* (*Cyclous*) *australis*; (D) *M.* (*Andogyrus*) *seriatopunctatus*; (E)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

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 and (9) female RT with vaginal shield (Fig. 11B–D) (Brinck, 1980, 1983, 1984). The genus *Dineutus* lacks a single distinct autapomorphy among gyrinid genera. A character that comes close is sexually dimorphic mesotarsal claws, but this character is a synapomorphy shared with *Porrorhynchus* (and potentially *Mesodineutes* Fig. S9); 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, 1882a, 1886, 1892, 1907). Hatch (1926) 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, 1976; Satô, 1962; Mazzoldi, 1995; Watts & Hamon, 2010; Hájek & Reiter, 2014; Gustafson & Miller, 2015; Lee & Ahn, 2015). Currently, the highest diversity is in the Austral region, primarily in New Guinea, but this likely reflects 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.
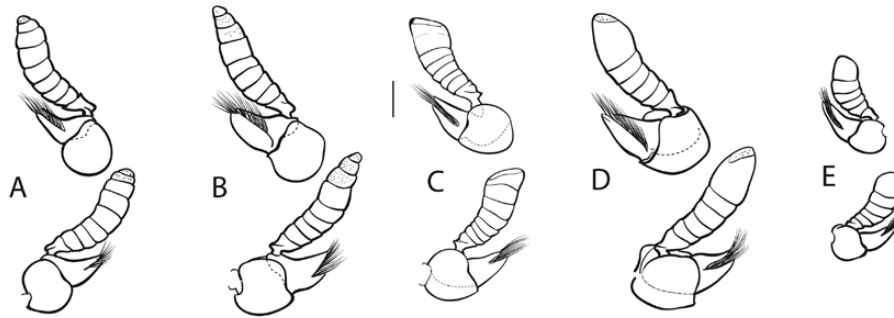
Figure 5. Antennae of dineutine species: above, anterior view; below, posterior. Scale bar = 0.5 mm. (A) *Macrogyrus* (*Macrogyrus*) *australis*; (B) *M.* (*Andogyrus*) *zimmermanni*; (C) *Porrorhynchus landaisi*; (D) *Enhydrus tibialis*; (E) *Dineutus* (*Cyclous*) *australis*.
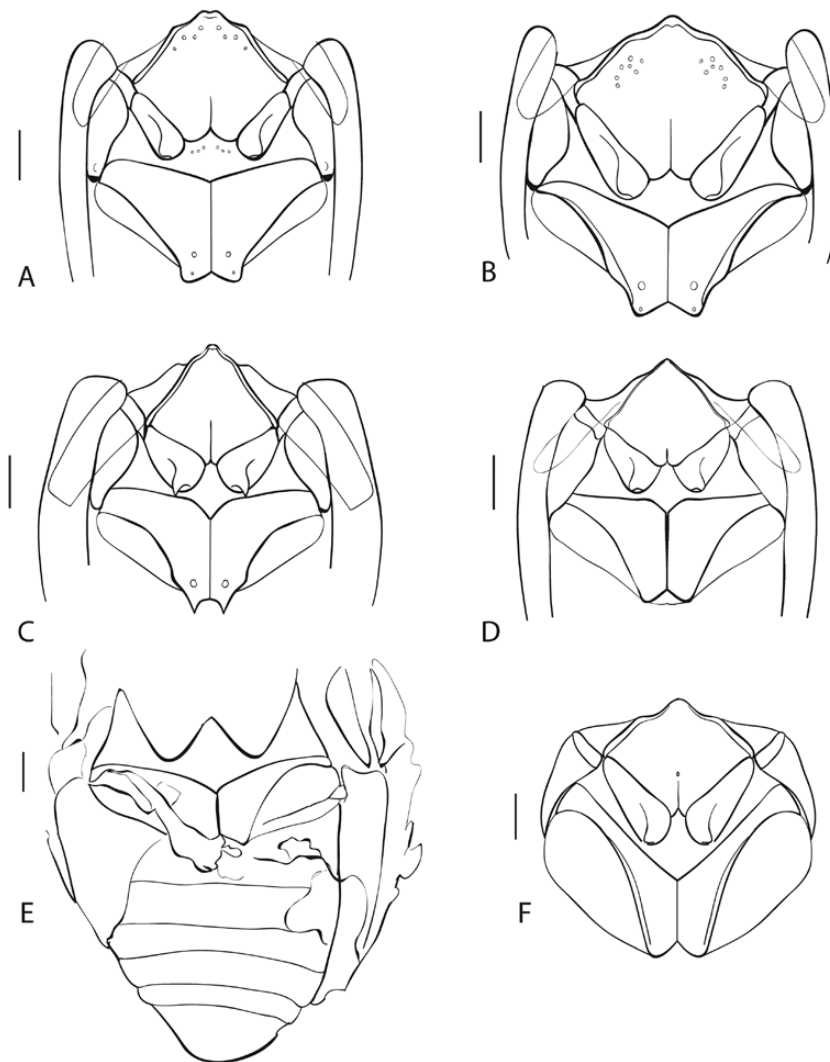

Figure 6. Meso- and meta-ventrites of dineutine species and a gyrinine species, ventral view, scale bars = 1 mm, except (F). (A) *Enhydrus sulcatus*; (B) *Macrogyrus* (*Andogyrus*) *colombicus*; (C) *Porrorhynchus marginatus*; (D) *Dineutus* (*Cyclous*) *carolinus*; (E) *Mesodineutes amurensis*†; (F)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

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

SUBGENUS *DINEUTUS* **SENSU NOV.**
(FIGS 1, 7C, 9E, 11B)

Type species: Dineutus politus Macleay, 1825.

Synonyms: Rhombodineutus Ochs, 1926 **syn. nov.**, *Merodineutus* Ochs, 1955 **syn. nov.**

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 and (5) mesotarsal claws distinctly sexually dimorphic. The *Dineutus s.s.* 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
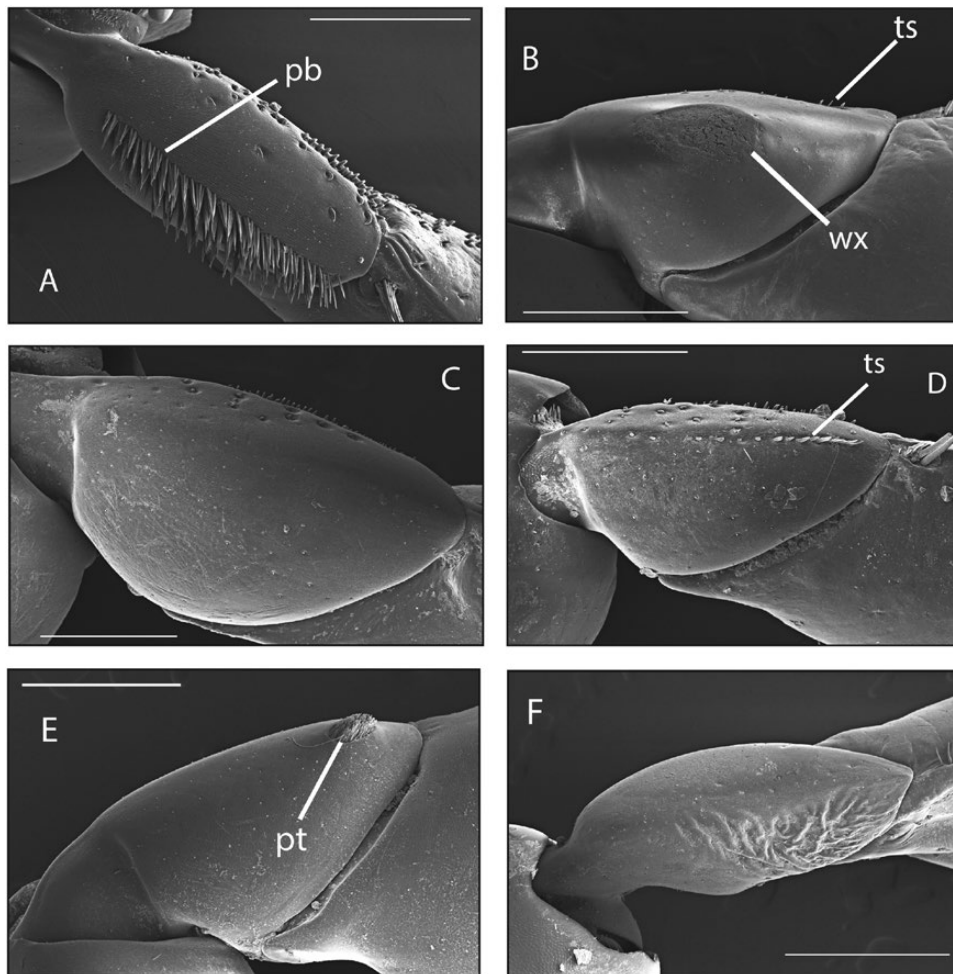

Figure 7. Protrochanters of male dineutine species, ventral view. Abbreviations: ts, protrochanteric setae; wx, waxy spot; pt, protrochanteric setose patch. (A) *Dineutus* (*Cyclous*) *australis*, scale bar = 200 µm. pb, protrochanteric brush; (B) *Dineutus* (*Cyclous*) *proximus*, scale bar = 500 µm; (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*) *albertisi*, scale bar = 500 µm.
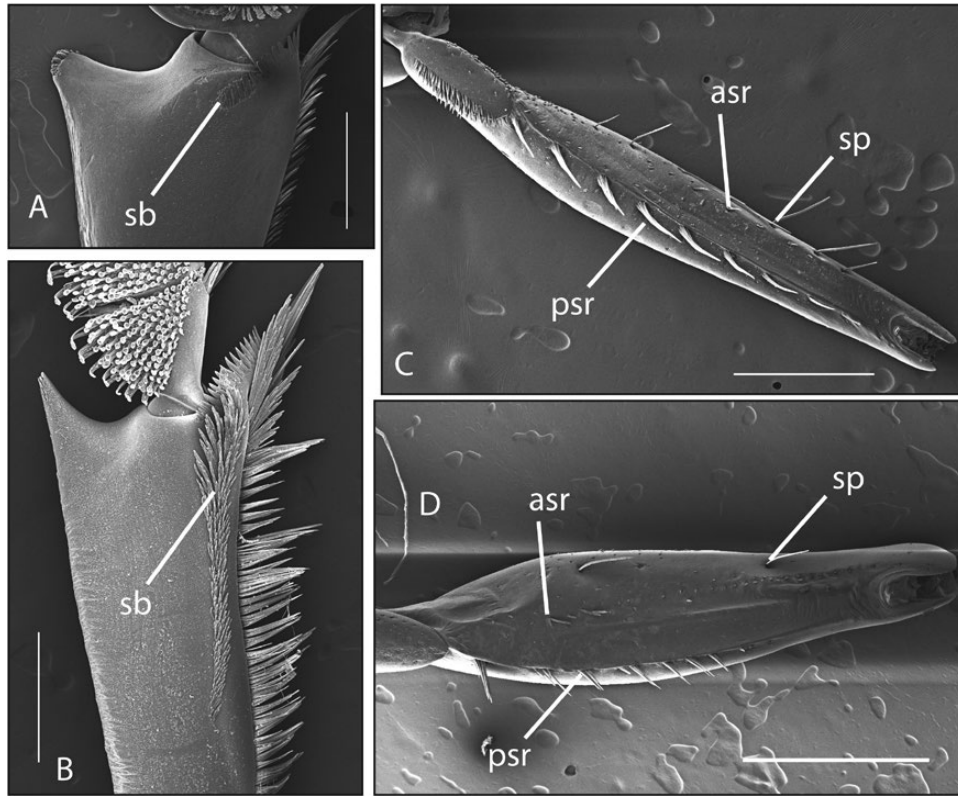
Figure 8. Prolegs of male dineutine species. Abbreviations: sb, setose brush; asr, anterior row of profemoral setae; psr, posterior row of profemoral setae; sp, setigerous puncture. (A) *Macrogyrus* (*Andogyrus*) *zimmermanni* protibial apex, posterior view, scale bar = 400 µm; (B) *Porrorhynchus marginatus* 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.

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. mellyi* Régimbart, 1882a, 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 s.s.* 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 s.s.* 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 NOV.** (FIGS 1, 4C, 5E, 6D, 7A, B, 7D, 8C, 9G, 11C, 13D)

Type species: Dineutus australis (Fabricius, 1775).

Synonyms: Callistodineutus Ochs, 1926 **syn. nov.**, *Cyclinus* Kirby, 1837 **syn. nov.**, *Gyrinodineutus* Ochs, 1926, *Paracyclous* Ochs, 1926 **syn. nov.**, *Protodineutus* Ochs, 1926 **syn. nov.**, *Spinosodineutes* Hatch, 1926 **syn. nov.**
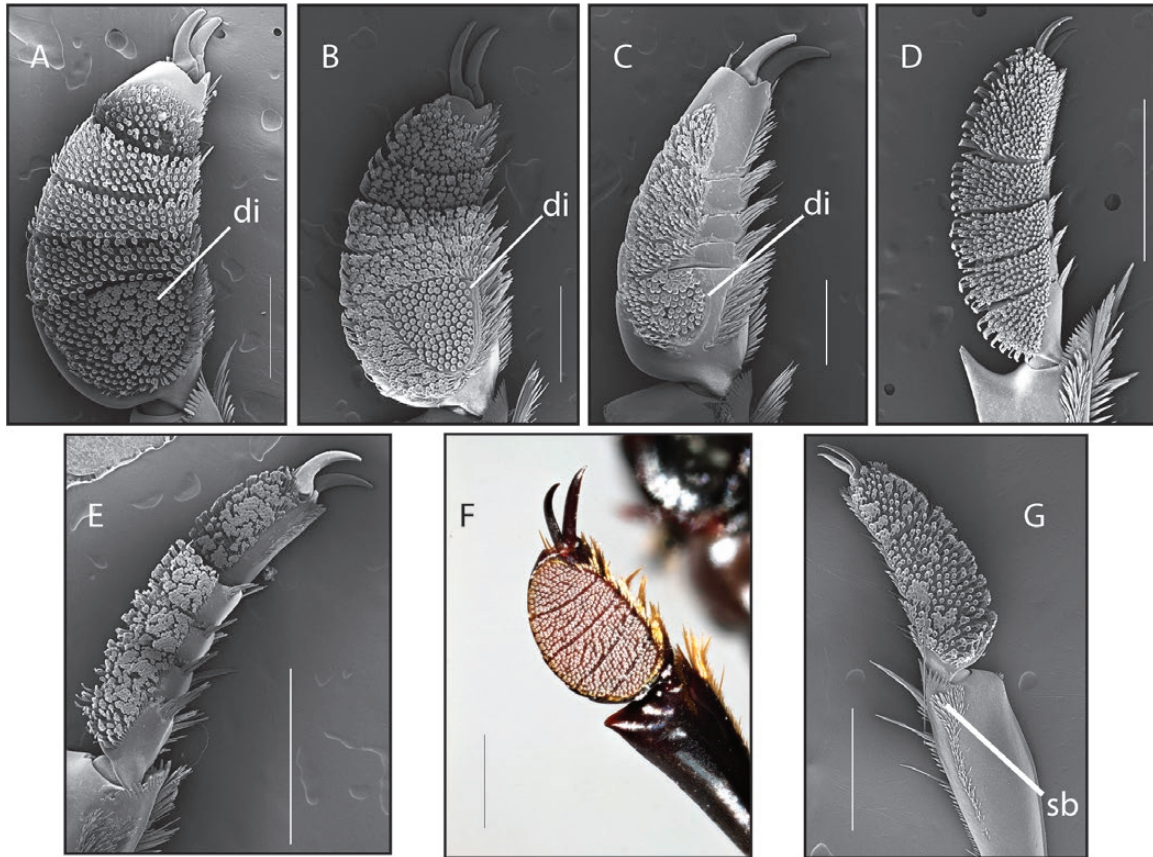
Figure 9. Protarsus of male dineutine species. Abbreviations: di, protarsal discus; sb, setose brush. (A) *Macrogyrus* (*Andogyrus*) *zimmermanni*, scale bar = 500 µm; (B) *M.* (*Macrogyrus*) sp., scale bar = 500 µm; (C) *M.* (*M.*) *albertisi*, scale bar = 500 µm; (D) *Porrorhynchus marginatus*, scale bar = 1 mm; (E) *Dineutus* (*Dineutus*) 'n. sp.', scale bar = 1 mm; (F) *Enhydrus atratus*, scale bar = 2 mm; (G) *D.* (*Cyclous*) *australis*, scale bar = 500 µm.

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 and (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, 1926; Ochs, 1926, 1955; Guignot, 1950; Brinck, 1955b). The first division of *Dineutus* into subgenera was proposed by Hatch (1926), but the majority of subgenera were erected by Ochs (1926) during his precladistic 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
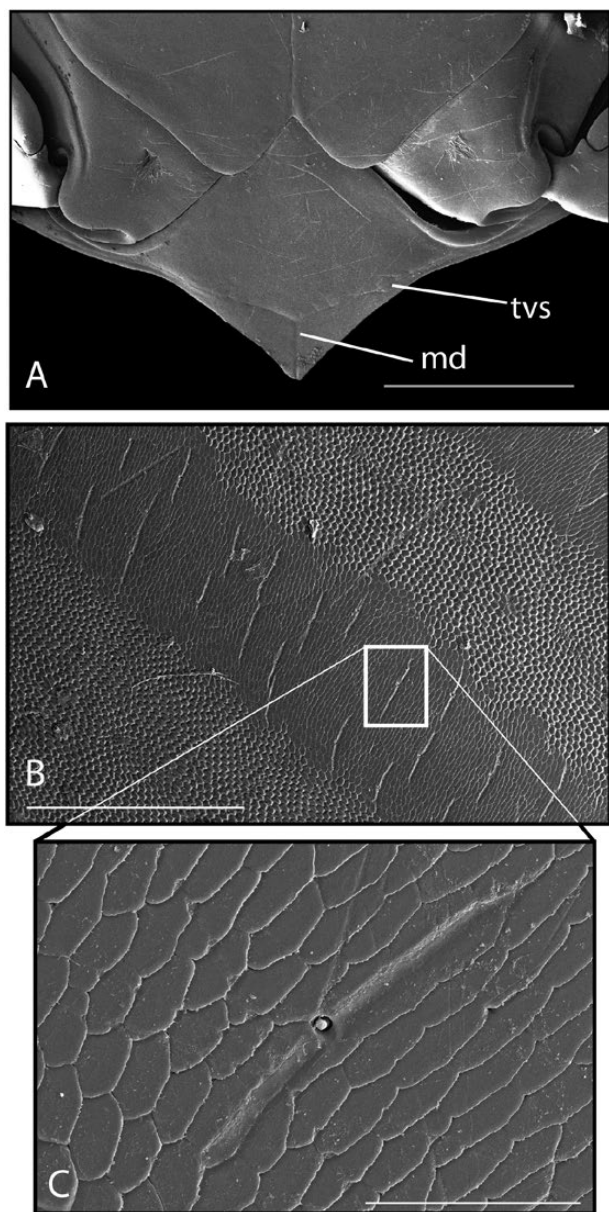
Figure 10. Sculpture of *Macrogyrus* (*Macrogyrus*) *albertisi*. (A) metaventrite. Abbreviations: md, metaventral discrimen; tvs, transverse sulcus, scale bar = 1 mm; (B) elytra with canliculate microsculpture, scale bar = 300 μm; (C) canaliculate microsculpture, scale bar = 40 μm.

Brink (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 Brink (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. ritsemae* was not included in the phylogenetic study, the taxon was studied for morphology. *Dineutus ritsemae* has well-developed sexually dimorphic mesotarsal claws and resembles closely members of the former subgenus *Callistodineutus* having a single profemoral subapicoventral 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 **INCERT. SED.**
(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
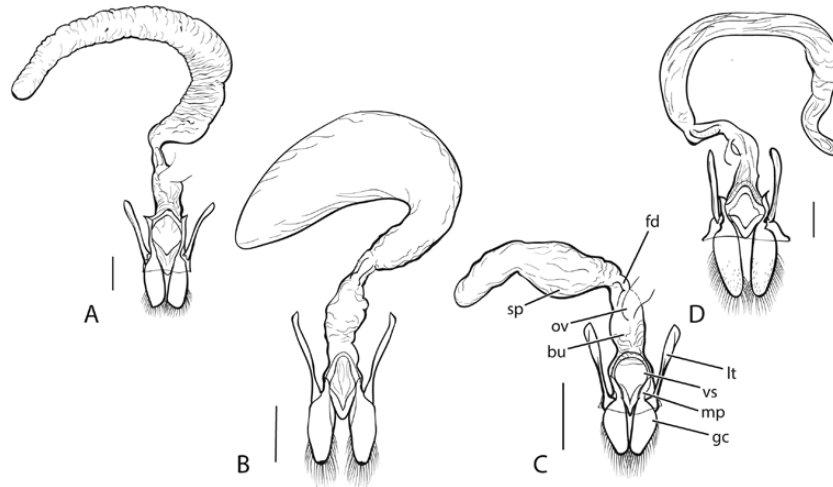
Figure 11. Female reproductive tracts, ventral view. Abbreviations: sp, spermatheca; fd, fertilization duct; ov, common oviduct; bu, bursa; lt, laterotergite; vs, vaginal shield; mp, medial apodeme of gonocoxa; gc, gonocoxa; scale bars = 1 mm. (A) *Porrorhynchus landaisi*; (B) *Dineutus* (*Dineutus*) *tetracanthus*; (C) *D.* (*Cyclous*) *discolor*; (D) *D.* (*Rhomborhynchus*) *depressus*.
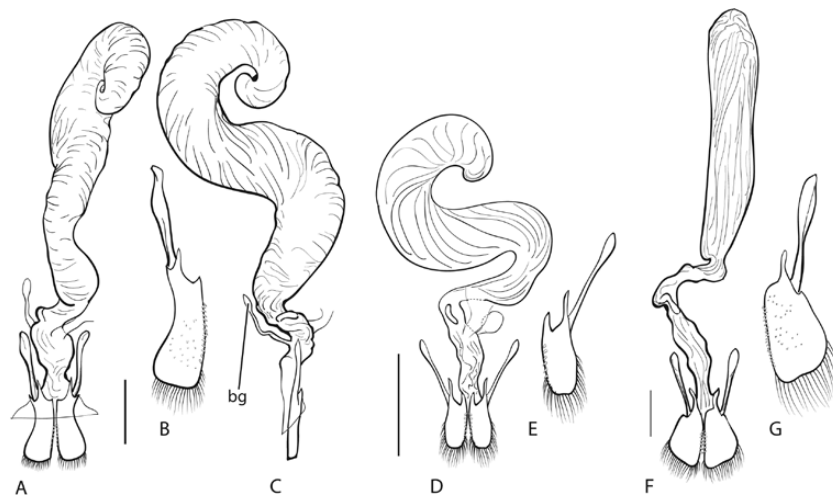

Figure 12. Female reproductive tracts. Abbreviations: bg, bursal gland; scale bars = 1 mm. (A) *Macrogyrus* (*Andogyrus*) *seriatopunctatus*, ventral view; (B) gonocoxa of the same; (C) lateral view of the same; (D) *M.* (*Macrogyrus*) *gouldii*, ventral view; (E) gonocoxa of the same; (F) *Enhydrus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

distolateral corner of the protibia, (5) ventral face of protrochanter apically with series of stout setae, (6) mesotarsal claws weakly sexually dimorphic and (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: One species, *D. depressus*.

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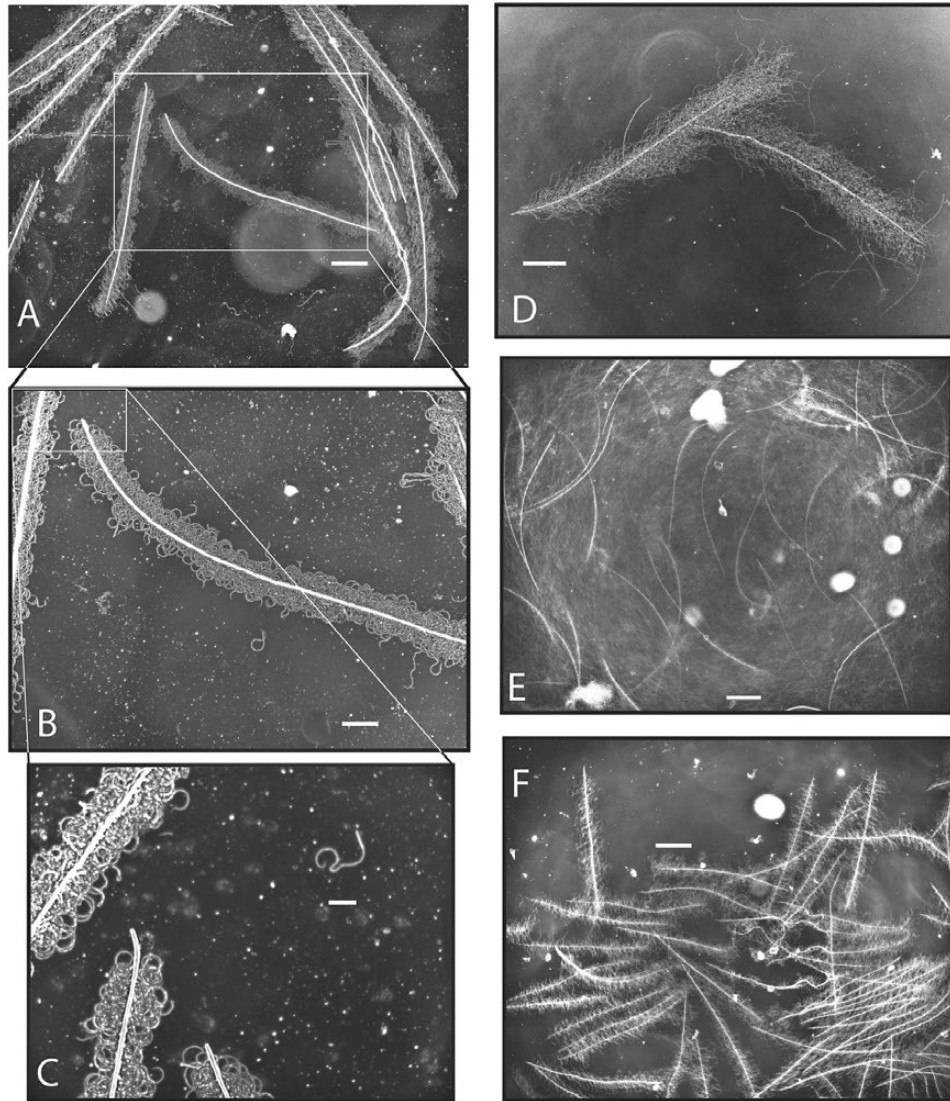
Figure 13. Sperm of dineutine species, exhibiting primary conjugation via spermatostyles. (A) *Enhydrus atratus*, scale bar = 300 µm; (B) the same, scale bar = 50 µm; (C) the same with single sperm, scale bar = 20 µm; (D) *Dineutus emarginatus*, scale bar = 50 µm; (E) *Macrogyrus* (*Macrogyrus*) *rivularis,*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

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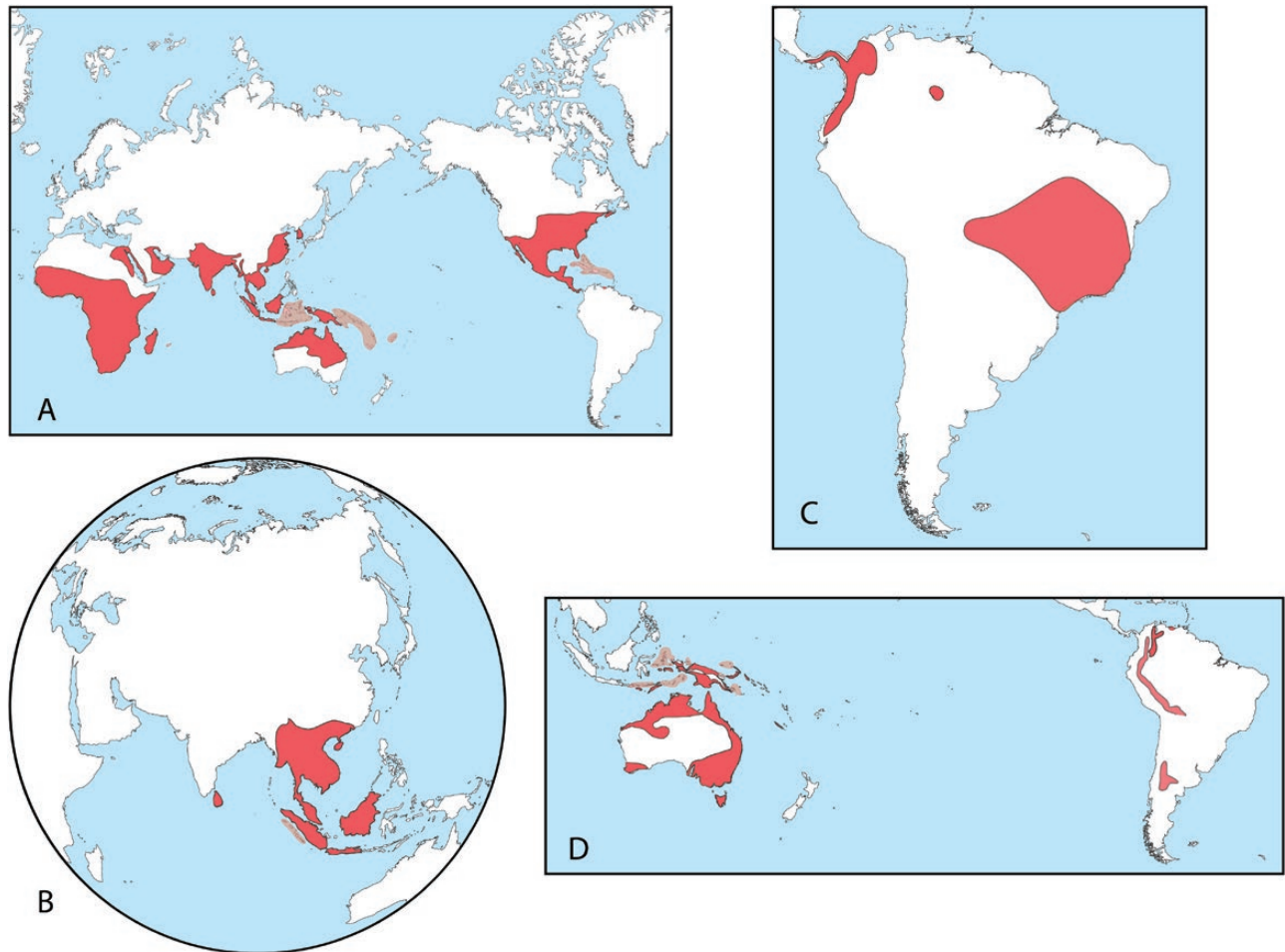
Figure 14. General distribution maps of dineutine genera. (A) *Dineutus*; (B) *Porrorhynchus*); (C) *Enhydrus*; (D) *Macrogyrus*.

features like the elongate labrum and the tubiform spermatheca (Fig. S9, characters 5, 52).

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 and (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 south-eastern 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.g. *E. tibialis*). 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, D, E), (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 below) (Fig. 9A–C), (7) metacoxal process bordered posterolaterally (Fig. 6B) and (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 a distinct 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. 9A–C, di). This character was first described by Régimbart (1882a: 433) and dubbed the discus. This feature is a synapomorphy uniting all the *Macrogyrus* species (Fig. S9).

SUBGENUS *ANDOGYRUS* OCHS, 1924 **STAT. NOV.**
(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) and (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* suggests 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 (1926) proved 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 s.s.* deserve separation into distinct genera, using similar phylogenetic logic.

SUBGENUS *CYCLOMIMUS* OCHS, 1949 **SENSU NOV.**
(FIGS 2, 4F)

Type species: Macrogyrus purpurascens Régimbart, 1882a.

Synonyms: Stephanogyrus Ochs, 1955 **syn. nov.**

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 and (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 (1955) based only on modifications to the elytral apices and reticulation patterning. 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 NOV.**
(FIGS 2, 4B, 5A, 7F, 9B–C, 10, 12D–E, 13F)

Type species: Macrogyrus howittii (Clark, 1866).

Synonyms: Australogyrus Ochs, 1949 **syn. nov.**, *Ballogyrus* Ochs, 1949 **syn. nov.**, *Clarkogyrus* Ochs, 1949 **syn. nov.**, *Megalogyrus* Ochs, 1949 **syn. nov.**, *Orectomimus* Ochs, 1930 **syn. nov.**, *Tribologyrus* Ochs, 1949 **syn. nov.**, *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) and (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, nondiscrete 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 (Figs 10B–C; S9, character 41), which in this analysis is *M. striolatus*. However, the placement of *M. striolatus* is weakly supported (Figs 2, 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 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 it is currently retained as a valid subgenus separate from the *sensu*

stricto, but the composition of *Macrogyrus s.s.* may be subjected 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 and (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. 6C–E), while *Enhydrus* and *Macrogyrus* have a more pentagonal shape (Fig. 6A–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), (5) pronotal transverse impressed line absent, (6) scutellar shield invisible with elytra closed, (7) male protrochanter with setose patch (Fig. 7E), (8) male protarsi narrow (Fig. 9D), (9) protibia expanded distolaterally (Fig. 8B), (10) ventral face of profemur with two rows of setae arranged into large clusters, progressively becoming denser apically, (11) mesotarsal claws weakly sexually dimorphic, (12) metaventrite medially triangular in shape (Fig. 6C) and narrow and (13) female RT with vaginal shield (Fig. 11A). Diagnostic characters (7) and (10) 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 south-eastern 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 the 1980s 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 not visible with elytra closed; mesotarsal claws sexually dimorphic (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) 3
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 clusters becoming denser apically; protrochanter of male without setose patch, variously modified or not; mesotarsal claws sexually dimorphic, often strongly so . . . . *Dineutus*

3. 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. 9A–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 s.s.*
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 s.s.*
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*

ACKNOWLEDGEMENTS

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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, B, D, F). 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, 1926).

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 & 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 medial 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 subapicoventral 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. ritsemae* 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. 8C, 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 these two species. A convergent condition is exhibited in *Macrogyrus albertisi*.

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. 9D–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. 6A–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 and mesonotum

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*.

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 & 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 microsculpture. (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 & 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 & Roughley, 1988; Beutel, 1990; Miller & 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, 1926) 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, C–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 posteromedially 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 coloured; (1) lightly coloured. The venter of many species is darkly coloured, 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 & 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 & 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 & 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 parameres 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).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

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. Preferred Bayesian tip-dating calibration analysis tree including Mesodineutes amurensis. Settings for analysis described in methods, using the Miller & Bergsten, 2012 partitioning scheme. Number at nodes indicate median 95% hpd age.
Figure S4. Bayesian tip-dating calibration analysis results excluding Mesodineutes amurensis, run under same settings as tree in Fig. S3. Number at nodes indicate posterior probability.
Figure S5. Bayesian tip-dating calibration analysis results including P. (Rhomborhynchus) depressus, highlighted in red, run under same settings as tree in Fig. S3. Numbers at nodes indicate posterior probability.
Figure S6. Bayesian tip-dating calibration analysis results including Mesodineutes amurensis. Settings for analysis described in methods, using the PartitionFinder partitioning scheme. Number at nodes indicate median 95% hpd age.
Figure S7. Bayesian node-calibration analysis. Settings for analysis described in methods, using the Miller & Bergsten, 2012 partitioning scheme. Number at nodes indicate median 95% hpd age.
Figure S8. Maximum likelihood tree. Analysis settings outlined in methods section. Numbers at nodes indicate boot strap support.
Figure S9. Morphological characters mapped on phylogenetic tree for Dineutini. Characters mapped using "fast" optimization in WinClada (ACCTRAN). Black hash marks indicate unambiguous changes, white hash marks indicate homoplasious changes or reversals. Numbers above hash marks are character numbers, those below hash marks are state numbers for the derived condition at that branch.
Figure S10. Ancestral state reconstruction results using DEC model. Label at node indicates probable state.
Figure S11. Ancestral state reconstruction results using DEC model. Pie chart at node indicates probable state.
Figure S12. Ancestral state reconstruction results using DEC +j model. Label at node indicates probable state.
Figure S13. Ancestral state reconstruction results using DEC +j model. Pie chart at node shows probable ancestral states.
Figure S14. Ancestral state reconstruction results using DIVALIKE model. Label at node indicates probable state.
Figure S15. Ancestral state reconstruction results using DIVALIKE model. Pie chart at node shows probable ancestral states.
Figure S16. Ancestral state reconstruction results using DIVALIKE +j model. Label at node indicates probable state.
Figure S17. Ancestral state reconstruction results using DIVALIKE +j model. Pie chart at node shows probable ancestral states.
Table S1. Taxa included in the phylogenetic and biogeographic analyses of the Dineutini. Original subgenera proposed for species provided to show sampling coverage. Gene coverage for molecular character dataset is indicated for each taxon as is geographical coding used for the biogeographic analysis. GenBank voucher numbers given for new sequences generated by the study.
Table S2. Character coding for morphological dataset.
Table S3. Primers used for amplification and sequencing.
Table S4. Dispersal rate multiplier coding used for BioGeoBears ancestral state reconstruction analysis. Time strata from top to bottom are TS4, TS3, TS2, TS1.