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Minute moss beetles in the Southern Hemisphere: Molecular phylogeny, historical biogeography and habitat shifts (Coleoptera: Hydraenidae)

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Abstract

Minute moss beetles (Hydraenidae) are one of the most speciose and widespread families of aquatic Coleoptera, with an estimated 4000 extant species, found in the majority of aquatic habitats from coastal rock pools to mountain streams and from the Arctic Circle to the Antarctic islands. Molecular phylogenetic works have improved our understanding of the evolutionary history of the megadiverse *Hydraena*, *Limnebius* and *Ochthebius* in recent years, but most genera in the family have not yet been included in any phylogenetic analyses, particularly most of those which are restricted to the Southern Hemisphere. Using a multimarker molecular matrix, sampling over 40% of described species richness and 75% of currently recognized genera, we infer a comprehensive molecular phylogeny of these predominantly Gondwanan Hydraenidae. Whilst the genera we focus on are morphologically diverse, and currently classified across all four hydraenid subfamilies, our phylogenetic analyses suggest that these Gondwanan genera may instead constitute a single clade. As a result of our findings, the African genus *Oomtelecopon* Perkins **syn.n.** is shown to nest within *Coelometopon* Janssens, the New Zealand *Homalaena* Ordish **syn.n.** and *Podaena* Ordish **syn.n.** are synonymised with *Orchymontia* Broun, and the South African *Pterosthetops* Perkins **syn.n.** is synonymised with *Prosthetops* Waterhouse, resulting in Pterosthetopini Perkins **syn.n.** being synonymised with Prosthetopini Perkins. *Mesoceratops* Bilton & Jäch **gen.n.** is erected to accommodate six former members of *Mesoceration* Janssens, which is shown to be polyphyletic. We propose the replacement name *Orchymontia ordishi* Jäch & Bilton **nom. n.** for *Homalaena dilatata* Ordish, 1984 (now a junior homonym); altogether 39 new combinations are proposed. Our Bayesian divergence times infer an origin for this 'Gondwana group' of genera in Africa plus Madagascar in the mid-Cretaceous and suggest that both vicariant and dispersal processes, together with extinctions, have shaped the biogeographic history of these beetles in the Southern Hemisphere during the Cretaceous, resulting in geographically conserved extant lineages. Finally, we reconstruct ancestral

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†Deceased.

habitat shifts across our phylogeny, revealing numerous changes in habitat occupancy in these genera, including multiple origins of fully terrestrial, humicolous taxa in different regions.

KEYWORDS
beetle evolution, Coleoptera phylogenetics, dispersal, Gondwanan biogeography, vicariance

INTRODUCTION

Beetles have colonized water multiple times, with many of these habitat shifts resulting in widespread and speciose radiations (Bilton et al., 2019; Jäch & Balke, 2008; Short, 2018). With an estimated 4000 extant species (ca. 2000 of which are described), the minute moss beetles or Hydraenidae, may be second only to the diving beetles (Dytiscidae) in terms of global water beetle diversity. Hydraenids are found in all biogeographical regions, from the Arctic to the Antarctic islands and include a high proportion of narrowly endemic taxa, particularly in areas with tropical and subtropical/Mediterranean climates (e.g., Perkins, 2011, 2017; Perkins & Balfour-Browne, 1994; Trizzino et al., 2013). Most hydraenids are small, as their most commonly used English name suggests, modal body size in the family being around 2 mm. Given this small size, the majority of species are associated with relatively shallow water, particularly under stones in streams and rivers or around the margins of small waterbodies, both lentic and lotic, although a number of shifts to different habitats, including the evolution of fully terrestrial lifestyles, are known within the family (e.g., Perkins, 2017; Villastrigo et al., 2019).

In terms of global species diversity, two genera, *Hydraena* Kugelann and *Ochthebius* Leach contain the majority of known hydraenids (Trizzino et al., 2012; Villastrigo et al., 2019), together comprising over 1500 species. Both of these genera, as currently defined, are globally distributed, with representatives in both the Northern and Southern hemispheres. The third relatively speciose hydraenid genus is *Limnebius* Leach, with about 160 described members (Rudoy et al., 2016), most from the Holarctic, but with species on all continents except South America and Antarctica. In addition to these three, 38 other hydraenid genera are currently recognized, the majority of which are restricted to the Southern Hemisphere (Hansen, 1998; Jäch et al., 2016). Phylogenies centring on all three of the large genera have been generated recently and have, in each case, included representatives of closely related, smaller genera. Trizzino et al. (2012) explored the evolution of the cosmopolitan, hyperdiverse genus *Hydraena*, including its sister genus *Adelphydraena* Perkins in their analyses. Rudoy et al. (2016) used a molecular phylogeny to investigate the evolution of male genital morphology in *Limnebius* and included *Laeliaena* Sahlberg, recovered as sister to *Limnebius*. More recently, Villastrigo et al. (2019) investigated the phylogeny of the Ochthebiini, including, as well as most species groups/subgenera of *Ochthebius*, two smaller Southern Hemisphere ochthebiine genera (*Meropathus* Enderlein and *Tympanogaster* Janssens).

However, the majority of hydraenid genera have not been included in any molecular phylogenetic analyses to date. Three of these, *Protochthebius* Perkins, *Prototympanogaster* Perkins and *Typallopatrum* Perkins, clearly belong to the Ochthebiini and were considered by Villastrigo et al. (2019), although not included in their molecular sampling. The remaining ones are found mostly in the Southern Hemisphere, and occupy the entire range of habitats utilized by extant Hydraenidae (with the exception of saline waters), from mountain streams, wetlands, rock pools and wet rock faces, to forest litter (see Bilton, 2014a, 2014b, 2015a, 2015b, 2015c, 2017, 2018; Perkins, 2005a, 2008, 2009, 2017; Perkins & Balfour-Browne, 1994). These genera, here termed the ‘Gondwana group’, are morphologically and ecologically diverse (Figure 1) and classified across all four currently recognized hydraenid subfamilies (see Table 1; Hansen, 1998). We acknowledge that other hydraenid genera, such as *Tympanogaster*, are also restricted to parts of former Gondwana, and that widespread genera (e.g., *Hydraena*) are highly speciose on former Gondwanan terranes, but use this terminology here to link genera considered explicitly in our analyses. Prosthetopinae Perkins were originally erected for seven genera restricted to Africa including the Malagasy Region (Perkins & Balfour-Browne, 1994), to which Jäch (1998a) added *Sebasthetops* Jäch from South Africa. The prosthetopine genera have been divided amongst six tribes, most of which include a single genus (Table 1; Perkins & Balfour-Browne, 1994; Hansen, 1998). Orchymontiinae Perkins were proposed to accommodate three genera of lotic New Zealand hydraenids (*Homalaena* Ordish, *Orchymontia* Broun and *Podaena* Ordish), which Beutel et al. (2003) considered basal within the family, based on an analysis of head morphology. Within Hydraeninae, Perkins (1997) proposed three new tribes: Hydraenidini (South America), Parhydraenini (sub-Saharan Africa and the Malagasy Region) and Madagastrini (Malagasy Region and India) (see Bilton, 2021; Perkins, 1980, 1997, 2009, 2017). Perkins (2017) moved the Madagastrini from the Hydraeninae to the Prosthetopinae, on the basis of antennal segmentation. In the Ochthebiinae, Perkins (1997) proposed the tribe Ochtheosini, to accommodate the morphologically rather isolated *Ochtheosus* Perkins from Chile (see Jäch, 1998b). Finally, Jäch and Díaz (2003, 2004) described two monotypic genera from China: *Edaphobates* Jäch & Díaz and *Ginkgoscia* Jäch & Díaz, which have apparent morphological similarities with Ochtheosini and Madagastrini. Many of the higher taxa of Perkins (1997) are based largely on the structure of the antennal pocket, hypomeron and ventral vestiture. The evolution and character polarity of these features remain unclear, however and, given their critical role in gas exchange (Perkins, 1997), such character systems may be subject to convergence due to strong selection associated with habitat shifts (see Jäch & Díaz, 1998).

Here we present a comprehensively sampled phylogeny of the ‘Gondwana group’ of Hydraenidae, based on a combination of

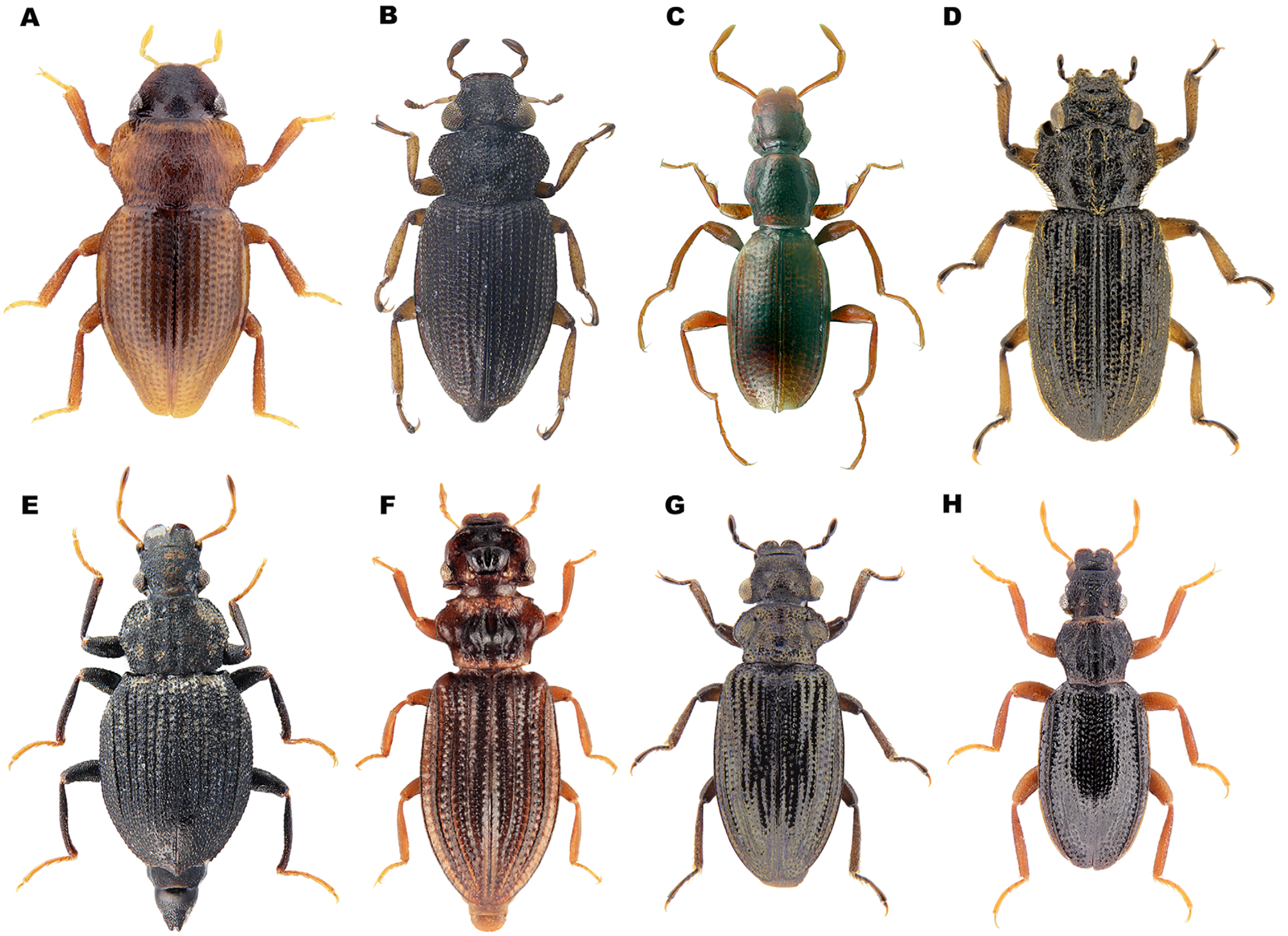

FIGURE 1 Morphological diversity of Gondwanan genera of Hydraenidae (not to scale). (a) *Parhydraena cataracta* Bilton—1.75 mm, humicolous; (b) *Parhydraenida unicornis* Jäch & Delgado—1.60 mm, madicolous; (c) *Podaena aotea* Delgado & Palma—1.85 mm, lotic; (d) *Coelometopon glenavoni* Bilton—2.45 mm, madicolous; (e) *Sebasthetops omaliniformis* Jäch—2.30 mm, lotic; (f) *Nucleotops nimbaceps* Perkins & Balfour-Browne—1.92 mm, humicolous; (g) *Pterosthetops pulcherrimus* Bilton—2.20 mm, madicolous; (h) *Mesoceration piketbergense* Bilton & Mlambo—1.90 mm, lotic.

mitochondrial and nuclear DNA sequence data. We go on to reconstruct the historical biogeography of these beetles, using a dated phylogeny and investigate habitat shifts during their evolution. We also propose a number of taxonomic changes to accommodate our results, including the description of one new genus.

MATERIALS AND METHODS

Taxon sampling

Our analyses included 112 of the 275 described species of the 'Gondwana group' (Table S1; Appendix S1). This included 23 of the 31 previously recognized genera and representatives from almost all regions where these beetles are found (see Table 1).

As outgroups we used 49 species; 42 hydraenids, representing all other major lineages and most genera (*Adelphydraena*, *Hydraena*, *Laeliaena*, *Limnebius*, *Meropathus*, *Ochthebius* and *Tympanogaster*). In the case of megadiverse genera (*Hydraena*, *Limnebius* and *Ochthebius*) we included members of a number of subgenera or species groups. In addition, we added five Ptiliidae, the most likely hydraenid sister group (Lawrence et al., 2011; McKenna et al., 2019; Zhang et al., 2018) and members of two other staphylinoid families: *Derolathus* Sharp sp. (Jacobsoniidae) and *Nicrophorus humator* (Gleditsch) (Silphidae).

DNA extraction and sequencing

Specimens were killed and preserved in absolute ethanol in the field. DNA was extracted with a standard phenol–chloroform extraction, or using commercial extraction kits (typically Qiagen DNeasy Tissue Kit, Hildesheim, Germany) following manufacturers' instructions. DNA samples and voucher specimens are retained in the collections of the Museo Nacional de Ciencias Naturales (MNCN, Madrid, Spain) and Naturhistorisches Museum Wien (NMW, Vienna, Austria). We sequenced fragments of six genes in five sequencing reactions, three mitochondrial [(i) 5′ end of the

TABLE 1 Synopsis of current classification of the 'Gondwana group' of Hydraenidae, with total number of species, number of species included in analyses and antennal configurations (see Appendix S1 for a complete updated checklist)

Genus	Current subfamily	Current tribe	No. spp.	DNA spp.	Antennal segments total (stem + club)
Nucleotops Perkins & Balfour-Browne, 1994	Prosthetopinae	Nucleotopini	4	2	11 (6 + 5)
Protosthetops Perkins, 1994	Prosthetopinae	Protosthetopini	1	0	10 (6 + 4)
Prosthetops Waterhouse, 1879	Prosthetopinae	Prosthetopini	7	7	8 (6 + 2)
Pterosthetops Perkins, 1994	Prosthetopinae	Pterosthetopini	14	9	8 (6 + 2)
Sicilicula Balfour-Browne, 1958	Prosthetopinae	Parasthetopini	9	2	11 (6 + 5)
Parasthetops Perkins & Balfour-Browne, 1994	Prosthetopinae	Parasthetopini	22	6	7–11 (6 + 1–5)
Sebasthetops Jäch, 1998	Prosthetopinae	Parasthetopini	2	2	9 (6 + 3)
Mesoceration Janssens, 1967	Prosthetopinae	Parasthetopini	56	27	7–11 (6 + 1–5)
Davidraena Jäch, 1994	Prosthetopinae	Madagastrini	3	0	11 (6 + 5)
Gondraena Jäch, 1994	Prosthetopinae	Madagastrini	2	0	11 (6 + 5)
Madagaster Perkins, 1997	Prosthetopinae	Madagastrini	8	2	11 (6 + 5)
Menomadraena Perkins, 2017	Prosthetopinae	Madagastrini	6	0	11 (6 + 5)
Trinomadraena Perkins, 2017	Prosthetopinae	Madagastrini	1	0	11 (6 + 5)
Coelometopon Janssens, 1972	Prosthetopinae	Coelometoponini	23	7	11 (6 + 5)
Oomtelecompon Perkins, 2005	Prosthetopinae	Coelometoponini	4	3	11 (6 + 5)
Orchymontia Broun, 1919	Orchymontiinae		14	3	9 (6 + 3)
Podaena Ordish, 1984	Orchymontiinae		11	4	11 (8–9 + 2–3)
Homalaena Ordish, 1984	Orchymontiinae		7	3	10 (8 + 2)
Hydraenida Germain, 1901	Hydraeninae	Hydraenidini	5	3	11 (6 + 5)
Parhydraenida Balfour-Browne, 1975	Hydraeninae	Hydraenidini	12	4	11 (6 + 5)
Haptaenida Perkins, 1997	Hydraeninae	Hydraenidini	1	0	11 (6 + 5)
Pneuminion Perkins, 1997	Hydraeninae	Parhydraenini	10	3	11 (6 + 5)
Parhydraena Orchymont, 1937	Hydraeninae	Parhydraenini	21	10	10 (5 + 5)
Protozantaena Perkins, 1997	Hydraeninae	Parhydraenini	6	1	10 (5 + 5)
Discozantaena Perkins & Balfour-Browne, 1994	Hydraeninae	Parhydraenini	12	4	10 (5 + 5)
Riberazantaena Bilton, 2021	Hydraeninae	Parhydraenini	2	2	10 (5 + 5)
Decarthrocerus Orchymont, 1948	Hydraeninae	Parhydraenini	4	1	10 (5 + 5)
Parhydraenopsis Perkins, 2009	Hydraeninae	Parhydraenini	3	3	10 (5 + 5)
Ochtheosus Perkins, 1997	Ochthebiinae	Ochtheosini	2	2	11 (6 + 5)
Edaphobates Jäch, 2003	Ochthebiinae	Ochtheosini	1	0	9 (4 + 5)
Ginkgoscia Jäch, 2004	Ochthebiinae	Ochtheosini	1	0	11 (6 + 5)

cytochrome c oxidase subunit I (the standard barcode, Herbert et al., 2003) (COI-5′); (ii) 3′ end of cytochrome c oxidase subunit I (COI-3′); (iii) 5′ end of 16S RNA (16S) plus the leucine tRNA transfer (tRNA-Leu) plus 5′ end of NADH dehydrogenase subunit I (NAD1)]; and two nuclear [(iv) an internal fragment of the large ribosomal unit, 28S RNA (28S) and (v) an internal fragment of the small ribosomal unit, 18S RNA (18S)] (see Table S3 in Appendix S1 for details on primers used and typical PCR conditions). Sequences were assembled and edited with Geneious R11 (Biomatters, USA; Kearse et al., 2012); new sequences were deposited in GenBank with accession numbers ON937331–ON937424, ON937426–ON937531, ON938211–ON938311, ON949952-ON950044 and ON968874 (see Table S1).

Phylogenetic inference

All cleaned consensus sequences were imported into Geneious R11 and aligned at the nucleotide level using MUSCLE (Edgar, 2004) for the protein-coding locus CO1 and MAFFT (Katoh & Standley, 2013) for ribosomal loci (18S, 28S) and var_mtDNA. The resulting alignments for each locus were then concatenated in Geneious to perform phylogenetic inference analyses. The final matrix comprised 161 taxa for a total of 3542 aligned nucleotides.

We used IQ-TREE 2.1.2 COVID-edition (Minh et al., 2020) to conduct 100 maximum likelihood tree searches with the concatenated dataset. The optimal partitioning scheme and models of nucleotide substitution were selected using ModelFinder (Kalyaanamoorthy et al., 2017) as implemented in IQ-TREE and using the Akaike Information Criterion corrected (AICc). We relied on six initial partitions, one for each codon position for the CO1 locus, and one partition for each remaining locus (18S, 28S and var_mtDNA). Branch support was investigated using 1000 ultrafast bootstraps (UFBoot; Hoang et al., 2018) and 1000 SH-aLRT tests (Guindon et al., 2010).

Divergence time estimation and historical biogeography

We used BEAST 1.10.4 (Suchard et al., 2018) to infer divergence times with the best scoring IQ-TREE ML tree (out of 100 tree searches) as a fixed input. The best partitioning scheme and models of nucleotide substitution were searched using PartitionFinder2 (Lanfear et al., 2017) with the *greedy* algorithm and the AICc based on the same six initial partitions as in ModelFinder (see above). The resulting scheme had the same number of partitions (six in total). Since there are no reliable fossil calibrations for the 'Gondwana group', we chose to use secondary calibrations from higher-level taxonomic studies of Coleoptera. The recent development of robust dated trees for Coleoptera (e.g., Baca et al., 2021; McKenna et al., 2019; Toussaint, Bloom, & Short, 2017; Zhang et al., 2018) allows the ages of more derived lineages to be constrained with a higher degree of confidence than previously. Here, we relied on estimates from the phylogenomic tree of McKenna et al. (2019) based on a comprehensive RNAseq dataset including most families of beetles and a carefully chosen fossil set. We used three secondary calibrations implemented as normal prior distributions based on the 95% credibility intervals for the corresponding nodes in McKenna et al. (2019): stem Hydraenidae (mean = 149.4, SD = 14.85), stem Jacobsoniidae (mean = 181.5, SD = 14.0) and stem Silphidae (mean = 198.75, 13.34). We used different tree (Yule versus birth-death) and clock priors (one clock for all partitions versus one clock for each partition) to test for potential differences in resulting time estimates. Marginal likelihood estimates (MLE) were calculated for each run using stepping-stone sampling (Baele et al., 2012), with default settings in BEAUti 1.10.4 (Suchard et al., 2018). We generated the Maximum Clade Credibility (MCC) trees of each run with median divergence age estimates in TreeAnnotator 1.10.4 (Suchard et al., 2018).

We used the R-package BioGeoBEARS 1.1.2 (Matzke, 2013) to estimate ancestral ranges in the 'Gondwana group' based on the BEAST MCC tree of the preferred analysis (see Section 3) without outgroups. Analyses were performed under the Dispersal Extinction Cladogenesis (DEC) model (Ree & Smith, 2008) and a likelihood implementation of the Dispersal-vicariance analysis (DIVA) model (Ronquist, 1997) (i.e., DIVALIKE in BioGeoBEARS). The geographical distribution of the 'Gondwana group' was extrapolated from the literature and our own unpublished records. The following areas were used in BioGeoBEARS analyses: Madagascar/Reunion, Mainland Africa, South America and New Zealand. We used a simple approach not relying on time stratification or manually set dispersal rate scalers, considering the reduced number of areas and the evolutionary timeline of the group.

Habitat preference evolution

We reconstructed ancestral habitat preference across the phylogeny of the 'Gondwana group' using the function *make.simmap* (SYM model and 1000 simulations) in the R package phytools 0.7–80 (Revell, 2012). All outgroups were pruned from the best scoring BEAST MCC tree (see Section 3). Habitat preferences were inferred from the literature and personal unpublished data (Bilton & Jäch). All habitat preference observations are summarized in Table S2, with the following categories: madicolous (wet rock faces, M), humicolous (damp forest/plant litter, H), lotic (Lo), lentic (Le) and rock pools (RP).

RESULTS

Molecular phylogeny

Our IQ-TREE ML tree (Figure 2) provides moderate support for the monophyly of the 'Gondwana group' with respect to other major lineages of the family (SH-aLRT = 99; UFBoot = 89). The first split within this clade separates *Madagaster* Perkins from all other genera (SH-aLRT = 77; UFBoot = 50). The remaining genera of the group are mostly recovered as monophyletic in our analyses and are divided into two major clades, albeit with low support (SH-aLRT = 61; UFBoot = 33), corresponding to ([Hydraenidini + *Ochtheosus*] + Parhydraenini) and ([Coelometoponini + Orchymontiinae] + Prosthetopinae), respectively. The Neotropical Hydraenidini, are apparently paraphyletic, since the Chilean *Ochtheosus* (currently included in the Ochthebiinae) is recovered within them, as sister to *Hydraenida* albeit with moderate support (SH-aLRT = 83; UFBoot = 83). The Afrotropical Parhydraenini are recovered as monophyletic with strong support (SH-aLRT = 95; UFBoot = 96), with all genera themselves being monophyletic, with strong support levels (SH-aLRT >80 and UFBoot >95). The Afrotropical Coelometoponini are recovered as sister to the New Zealand Orchymontiinae, albeit with moderate support (SH-aLRT = 89; UFBoot = 76). The two genera currently placed in Coelometoponini are not reciprocally monophyletic, however; *Oomtelecopon* Perkins nesting within *Coelometopon* with strong support (SH-aLRT = 100; UFBoot = 100). Within Orchymontiinae, whilst included species of *Homalaena* and *Orchymontia* are recovered as monophyletic, *Podaena* is paraphyletic with respect to them, this arrangement receiving strong support (SH-aLRT = 100; UFBoot = 100). With the exception of *Madagaster* (see above) genera currently assigned to Prosthetopinae are recovered in a single clade, with strong support (SH-aLRT = 100; UFBoot = 100). Within this, all currently recognized genera are recovered as monophyletic, with the exception of *Prosthetops* Waterhouse/*Pterosthetops* Perkins, which are intermixed with strong support (SH-aLRT = 100; UFBoot = 100) and *Mesoceration*, which is polyphyletic; some members of the *M. rivulare* Perkins &

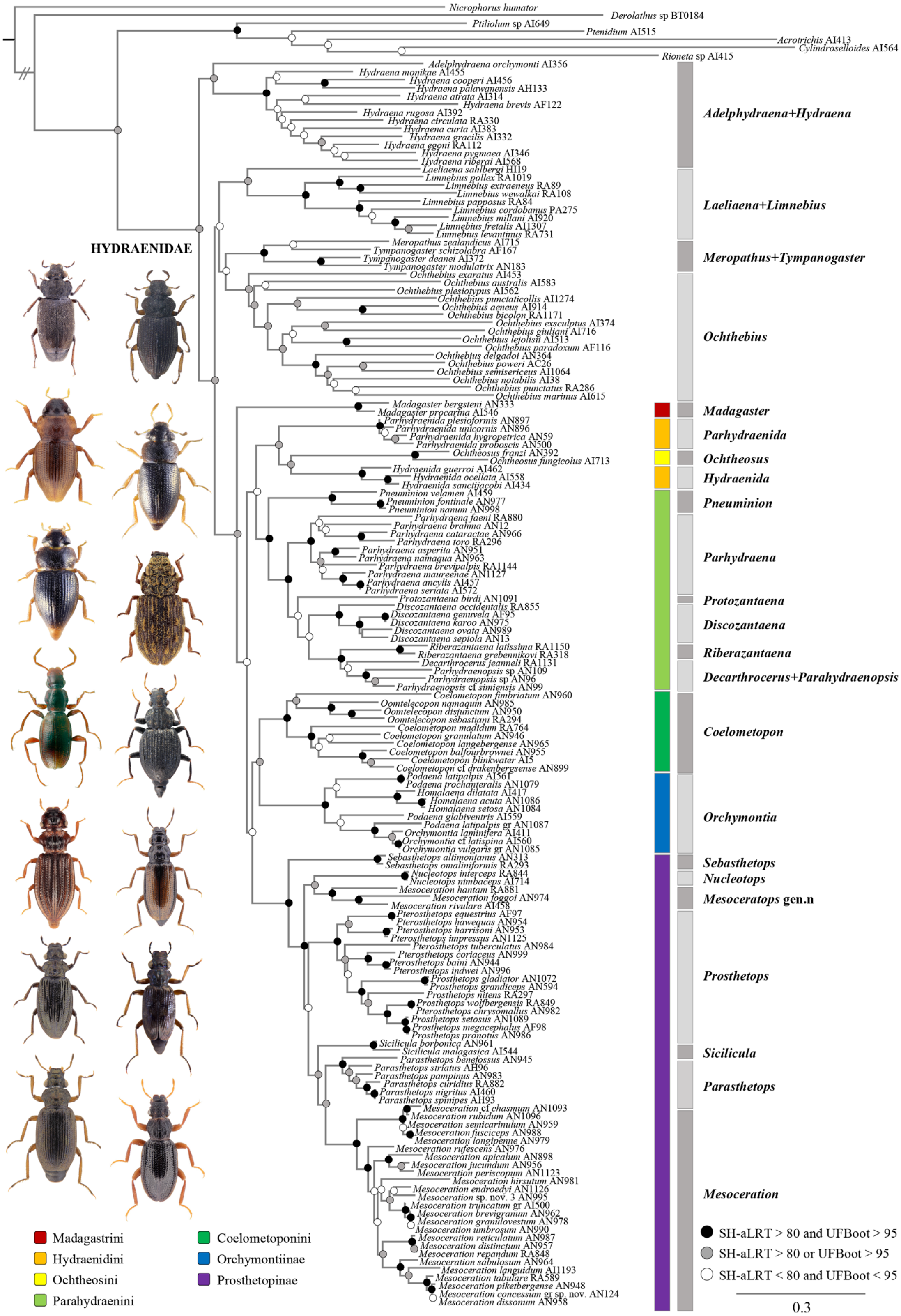

FIGURE 2 Maximum likelihood tree obtained with IQ-TREE (see text), showing branch support, current tribal/subfamily assignment and revised generic placements. Habitus photographs, top left to bottom right as follows: *Madagaster bergsteni* Perkins, *Parhydraenida unicornis* Jäch & Delgado, *Parhydraena cataracta* Bilton, *Protozantaena* cf. *labrata* Perkins, *Riberazantaena grebennikovi* (Perkins), *Oomtelecopon disjunctum* Bilton, *Podaena aotea* Delgado & Palma, *Sebasthetops omaliniformis* Jäch, *Nucleotops nimbaceps* Perkins & Balfour-Browne, *Mesoceration foggoi* Bilton, *Pterosthetops pulcherrimus* Bilton, *Prosthetops wolfbergensis* Bilton, *Parasthetops porcellus* Bilton & *Mesoceration piketbergense* Bilton & Mlambo.

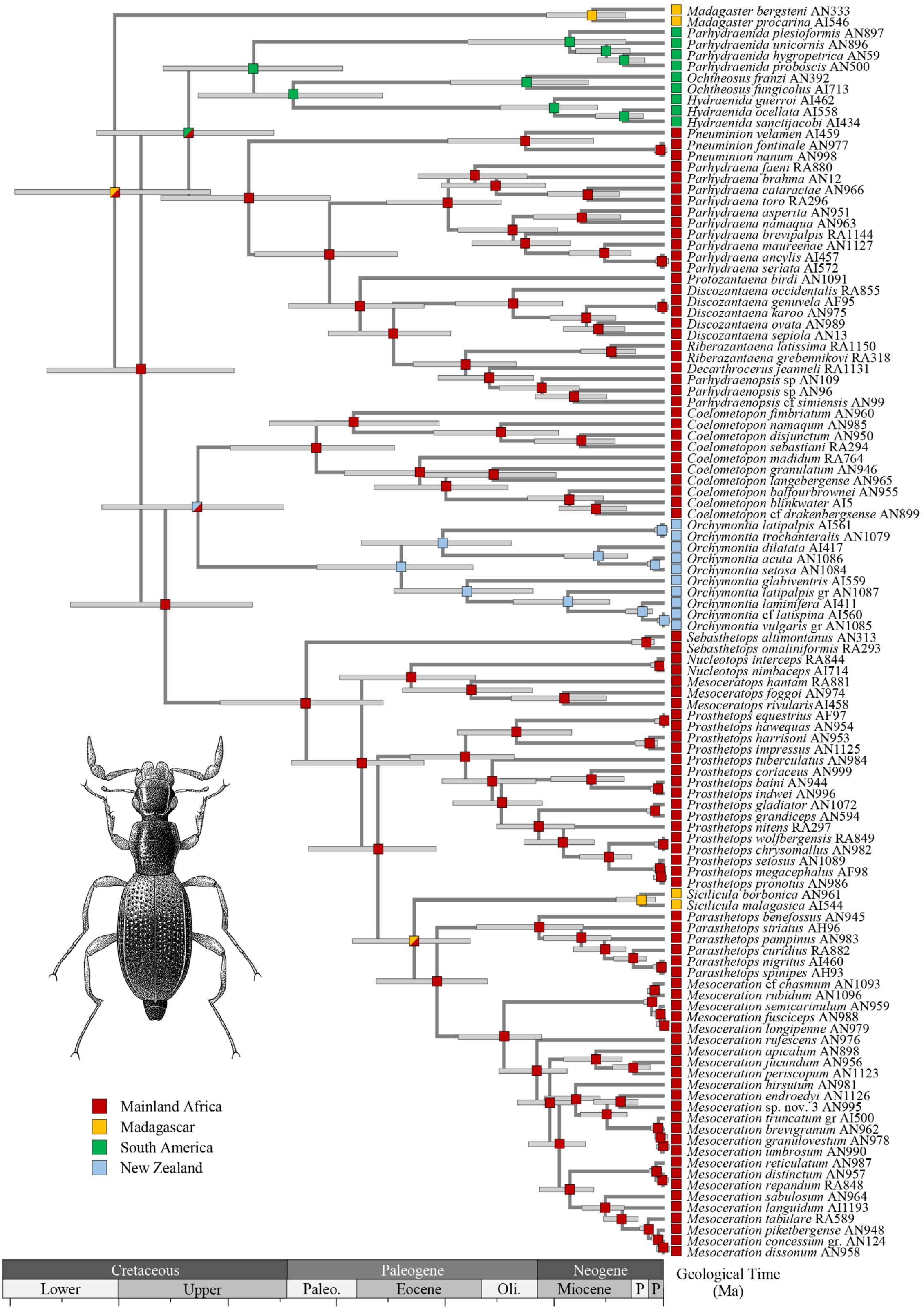

FIGURE 3 Historical biogeography the 'Gondwana group' of Hydraenidae. Chronogram derived from the BEAST analysis using median age estimates with 95% credibility intervals show as horizontal grey bars. Image: *Orchymontia latipalpis* (Ordish) **comb.n.**, Desmond W. Helmore, Wikimedia Commons.

Balfour-Browne species group clustering with *Nucleotops* Perkins & Balfour-Browne rather than other *Mesoceration*.

Divergence time estimation and historical biogeography

Based on MLE comparison, the BEAST analysis using three clocks and a birth-death model was a better fit than the rest (stepping-stone sampling MLE = −75,927.891). Our results derived from this analysis suggest that the 'Gondwana group' originated in the mid-Cretaceous, about 101.2 MYA (CI 83.2–119.8 MYA) (Figure 3). Optimal dates for splits between major lineages are also mostly in the Cretaceous. For instance, the split between *Madagaster* and the rest of the group is dated at about 96.4 MYA (CI 79.2–113.7 MYA), while the two subsequent lineages ([Hydraenidini + *Ochtheosus*] + Parhydraenini) and ([Coelometoponini + Orchymontiinae] + Prosthetopinae), respectively, originated at about 87.6 MYA (CI 71.5–104.4 MYA) and about 91.9 MYA (CI 75.6–109.4 MYA). Radiations within those major lineages mostly begin in the Palaeogene, including South African *Prosthetops*/*Pterosthetops* at about 52.8 MYA (42.1–65.5 MYA) and *Mesoceration*, although clearly some extant species are much younger, having diverged in many cases during the Pleistocene (see Figure 3).

BioGeoBEARS analyses performed under the DEC model (see Figure S1) inferred an origin of the 'Gondwana group' in Africa/Madagascar/South America, whilst analyses performed under the DIVALIKE model (see Figure S2) inferred an origin in Africa/Madagascar. The DIVALIKE model received a significantly better likelihood score (DIVALIKE LnL = 23.88; DEC LnL = 28.81) and the pattern derived from this analysis is therefore the one discussed hereafter. A vicariant pattern was inferred at the origin of the group, with a cladogenetic event resulting in an African ancestor for the clade sister to *Madagaster*, whilst the latter was immediately restricted to Madagascar. We infer two range expansions from Africa to Africa/South America and from Africa to Africa/New Zealand in the Cretaceous about 90 MYA, both followed by vicariance events, with geographic shifts happening immediately after the splits.

Habitat preference evolution

Ancestral state reconstruction analysis revealed that the common ancestor of the 'Gondwana group' was aquatic and lotic, which is still the most common habitat occupied by members of the clade, with a number of shifts to other habitats in most major lineages (Figures 4 and S3). In particular, there have been six apparent shifts to madicoly, four being in the ancestors of *Madagaster*, *Parhydraenida* Balfour-Browne, *Coelometopon* and *Sicilicula* Balfour-Browne. In *Prosthetops/Pterosthetops* there was a shift from a lotic to madicolous lifestyle in the common ancestor of the group, followed by a single shift to occupying lentic mountain rock pools in one lineage. Within this rock pool clade, there has been a further shift back to madicoly in *Pterosthetops chrysomallus* Bilton. Shifts to humicolous terrestrial habitats have occurred four times, in the ancestors of *Ochtheosus*, *Nucleotops* and the *Parhydraena toro* Perkins species group, as well as in the common ancestor of *Discozantaena* Perkins, *Riberazantaena* Bilton, *Decarthrocerus* Orchymont and *Parhydraenopsis* Perkins.

Taxonomy

We describe one new genus and formally synonymise four others and one tribe, in light of our phylogenetic analyses. These taxonomic changes are presented below.

Genus *Mesoceratops* Bilton & Jäch gen.n.

Type species: *Mesoceration rivulare* Perkins & Balfour-Browne, 1994: 87, herein designated.

Diagnosis: With the following combination of characters: 10–11 antennomeres (6 + 4–5 in club); maxillary palpi and legs elongate; labrum with deep, narrow apicomedian emargination; pronotal reliefs strongly shining, without microreticulation, finely and sparsely punctate; 8th elytral interval strongly carinate; elytra without granules; 1st and 2nd elytral series confluent posteriorly; elytral disc with six series of punctures between suture and carina, 5th and 6th series confluent basally; abdomen with ventral plastron vestiture on sterna 1–4 and basal part of 5; distal lobe of aedeagus distinct, bearing gonopore, curved and elongate, attached subapically to right side of main piece in ventral view (see Figure 5).

Etymology: From *Mesoceration* and *Nucleotops*, reflecting the apparent relationships and taxonomic history of this clade.

Distribution: Endemic to South Africa, most species found in the Fynbos Biome of the Western Cape, but extending to the Drakensberg.

This new genus is phylogenetically distant from *Mesoceration* in our molecular analyses, appearing sister to *Nucleotops*. It includes most former members of the *Mesoceration rivulare* group sensu Perkins and Balfour-Browne (1994) and Perkins (2008). The exceptions are *Mesoceration jucundum* Perkins & Balfour Browne and *Mesoceration periscopum* Perkins, which clearly group with other *Mesoceration* species in our analyses. *Mesoceratops* **gen.n.** thus incorporates six species: *Mesoceratops foggoi* (Bilton, 2015) **comb.n.**, *Mesoceratops hantam* (Bilton, 2014a) **comb.n.**, *Mesoceratops maluti* (Perkins, 2008) **comb.n.**, *Mesoceratops rapidensis* (Perkins, 2008) **comb.n.**, *Mesoceratops rivularis* (Perkins & Balfour-Browne, 1994) **comb.n.**, and *Mesoceratops splendorum* (Perkins & Balfour-Browne, 1994) **comb.n.** Of these, *M. maluti*, *M. rapidensis* and *M. splendorum* are assigned to *Mesoceratops* **gen.n.** tentatively, in the absence of molecular data. *Mesoceratops* **gen.n.** can be distinguished from most *Mesoceration* on the above combination of characters, the form of the aedeagus (Figure 5) allowing its members to be distinguished from *M. jucundum* and *M. periscopum*, which instead have the gonopore situated on a small projection at the apex of the main piece.

Genus *Orchymontia* Broun, 1919

Homalaena Ordish, 1984 **syn.n.**

Podaena Ordish, 1984 **syn.n.**

Type species: *Orchymontia spinipennis* Broun, 1919: 108, by monotypy.

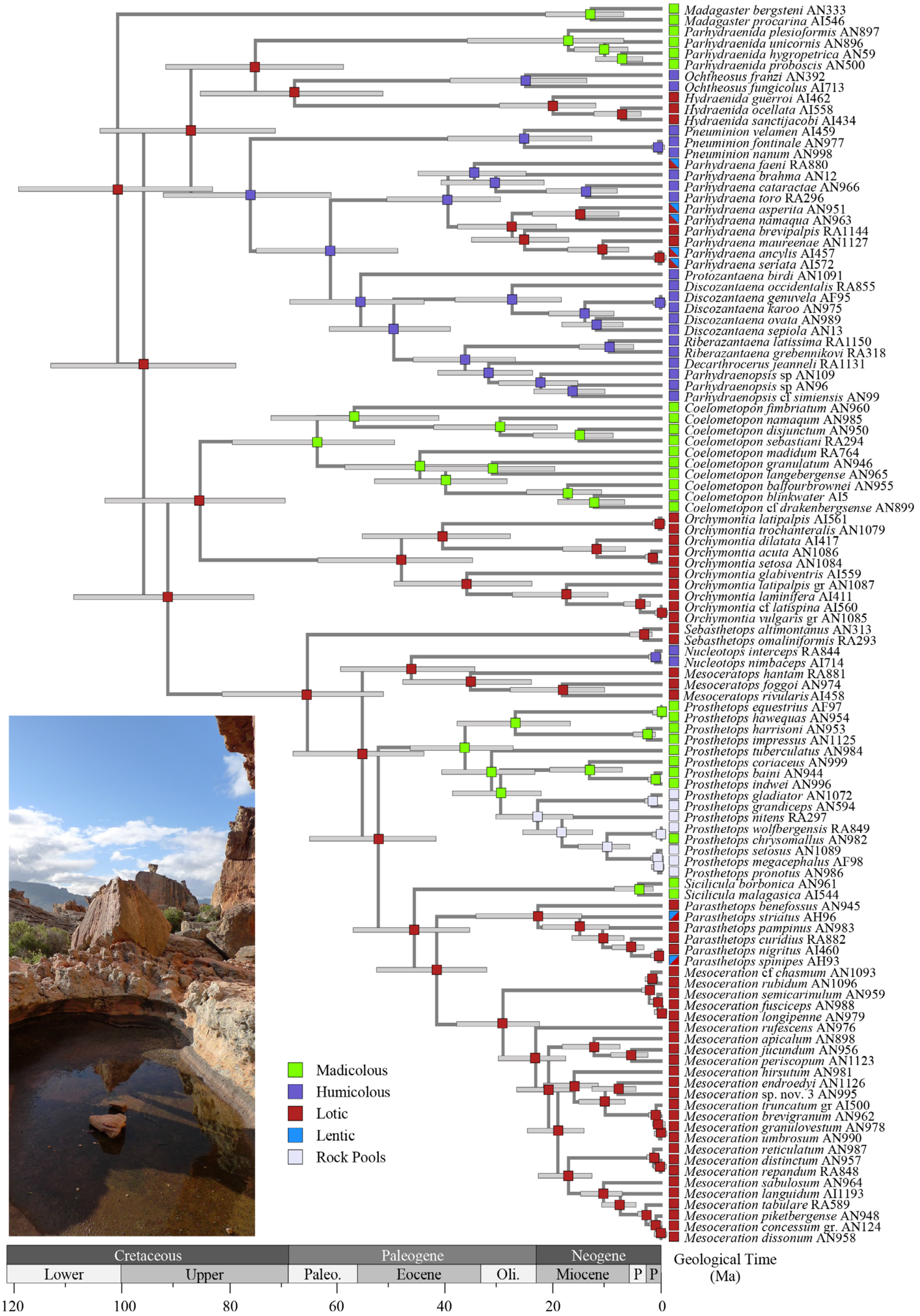

FIGURE 4 Habitat preference evolution in the 'Gondwana group' of Hydraenidae reconstructed in phytools. Photo shows rock pool habitat at Stadsaal Cave, Cederberg, Western Cape Province, South Africa, occupied by *Prosthetops wolfbergensis* Bilton.

Diagnosis: With the following combination of characters: 9–11 antennomeres (6–9 + 2–3 in club); antennal club loosely defined and non-pubescent; legs and maxillary palpi moderately elongate; hypomeral antennal pocket absent, area clothed with hydrofuge pubescence; antennae held in genal antennal pocket at rest; metaventral plaques absent; ventral plastron vestiture dense, short and scale-like.

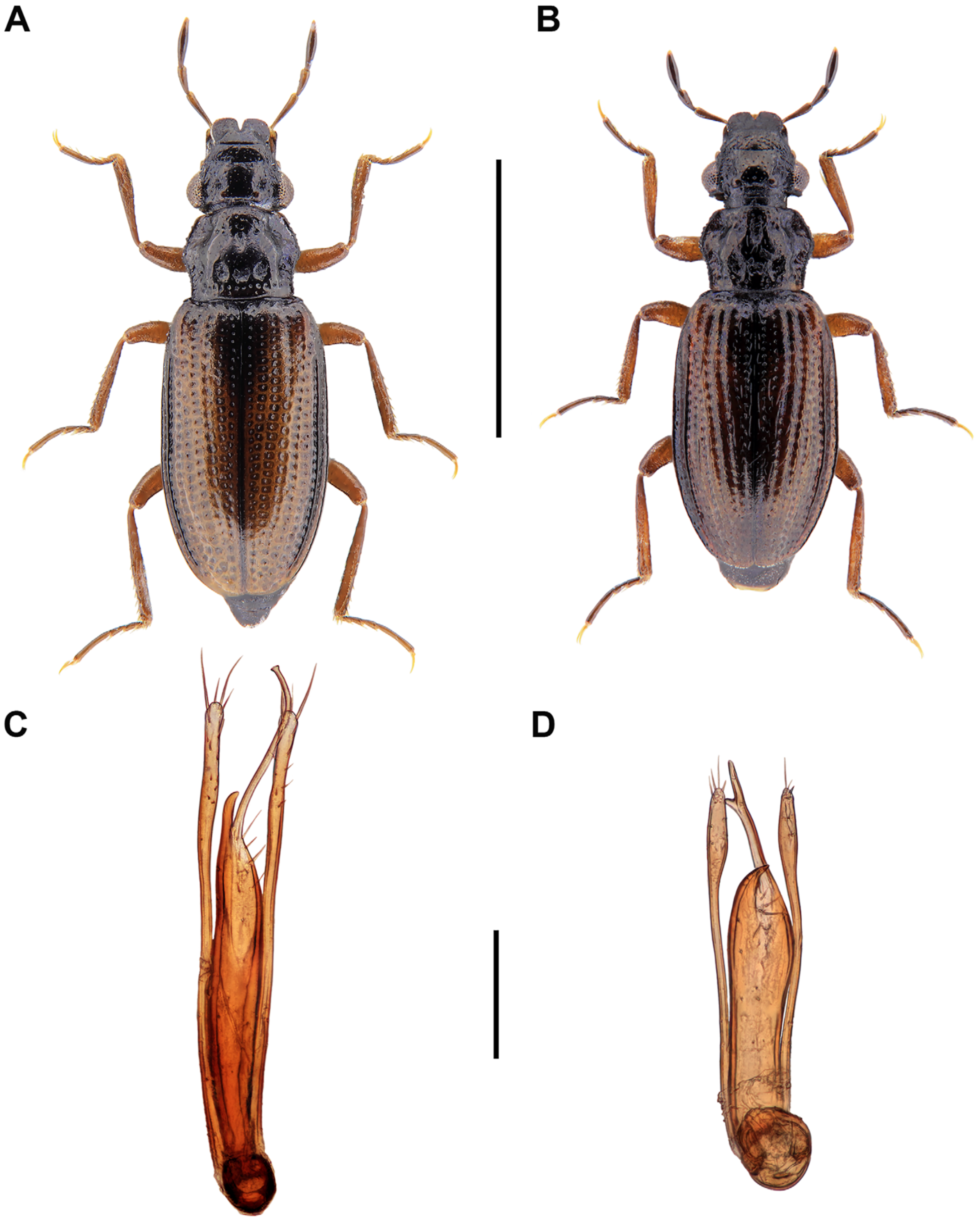

FIGURE 5 *Mesoceratops* **gen. n.**, habitus (a,b) and aedeagi (c,d). (a,c) *Mesoceratops hantam* (Bilton); (b,d) *Mesoceratops foggoi* (Bilton). Scale bars (a,b) = 1 mm; (c,d) = 0.1 mm.

Whilst included members of *Orchymontia* and *Homalaena* appear monophyletic in our molecular analyses, *Podaena* is clearly polyphyletic with respect to them, and our preferred approach is to synonymise the three genera here. This results in the following new combinations: *Orchymontia acuta* (Ordish, 1984) **comb.n.**, *Orchymontia aotea* (Delgado & Palma, 2010) **comb.n.**, *Orchymontia carinata* (Ordish, 1984) **comb.n.**, *Orchymontia dentipalpis* (Ordish, 1984) **comb. n.**, *Orchymontia dispersa* (Ordish, 1984) **comb.n.**, *Orchymontia glabriventris* (Ordish, 1984) **comb.n.**, *Orchymontia hauturu* (Delgado & Palma, 2010) **comb.n.**, *Orchymontia kuscheli* (Ordish, 1984) **comb.n.**, *Orchymontia latipalpis* (Ordish, 1984) **comb.n.**, *Orchymontia mariae* (Delgado & Palma, 2010) **comb.n.**, *Orchymontia moanaiti* (Delgado & Palma, 2010) **comb.n.**, *Orchymontia nelsonensis* (Ordish, 1984) **comb. n.**, *Orchymontia obscura* (Ordish, 1984) **comb.n.**, *Orchymontia setosa* (Ordish, 1984) **comb.n.**, *Orchymontia spatulata* (Ordish, 1984) **comb.n.**, *Orchymontia trochanteralis* (Ordish, 1984). *Homalaena dilatata* Ordish, 1984 becomes a junior homonym of *Orchymontia dilatata* Ordish, 1984, for which we propose the new name *Orchymontia ordishi* Jäch & Bilton **nom.n.**

Genus *Coelometopon* Janssens, 1972

Oomtelecopon Perkins, 2005 **syn.n.**

Type species: *Coelometopon leleupi* Janssens, 1972: 387, by original designation.

Diagnosis: With the following combination of characters: 11 antennomeres (6 + 5 in club); basal antennal segments elongate; legs and maxillary palpi relatively short; head highly modified, with very large, markedly raised compound eyes; dorsal surface rough, granulate, elytra with costae and granulate callosities; granules bearing setae which are simple, bifurcate or trifurcate; hypomeron strongly produced anteriorly; hypomeral antennal pocket deep, narrowly opened ventrally, dorsally opened at well-developed postocular emarginations; abdominal ventrites strongly sclerotized, with deep grooves between segments; plastron vestiture (absent in some species) composed of scale-like setae.

Our molecular analyses show that *Oomtelecopon* nests within *Coelometopon*, hence its synonymization herein, resulting in the following new combinations: *Coelometopon disjunctum* (Bilton, 2015) **comb.n.**, *Coelometopon namaqum* (Bilton, 2016) **comb.n.**, *Coelometopon sebastiani* (Perkins, 2005) **comb.n.**, *Coelometopon setosum* (Perkins, 2005) **comb.n.**

Genus *Prosthetops* Waterhouse, 1879

Pterosthetops Perkins, 1994 **syn.n.**

Type species: *Prosthetops capensis* Waterhouse, 1879: 533 (= *Ochthebius megacephalus* Boheman, 1851: 587), designated by Orchymont, 1913: 319.

Diagnosis: With the following combination of characters: 8 antennomeres (6 + 2 in club); legs moderately to strongly elongate; maxillary palpi short and robust, length equal to or less than width of anterior margin of clypeus; elytra with 9–10 serial puncture rows; posterior margins of abdominal ventrites 1–4 with linear row of elongate, flattened setae; metacoxae without ventral vestiture, at least medially.

As redefined here, *Prosthetops* includes 21 species, all of which are endemic to South Africa. The synonymy of *Pterosthetops* results in the following new combinations: *Prosthetops baini* (Bilton, 2014a) **comb.n.**, *Prosthetops brincki* (Perkins & Balfour-Browne, 1994) **comb. n.**, *Prosthetops chrysomallus* (Bilton, 2017) **comb.n.**, *Prosthetops coriaceus* (Bilton, 2014a) **comb.n.**, *Prosthetops equestrius* (Perkins & Balfour-Browne, 1994) **comb.n.**, *Prosthetops harrisoni* (Perkins & Balfour-Browne, 1994) **comb.n.**, *Prosthetops hawequas* (Perkins, 2008) **comb.n.**, *Prosthetops impressus* (Perkins & Balfour-Browne, 1994) **comb.n.**, *Prosthetops indwei* (Bilton, 2014a) **comb.n.**, *Prosthetops nitidus* (Bilton, 2016) **comb.n.**, *Prosthetops pulcherrimus* (Bilton, 2014a) **comb.n.**, *Prosthetops swartbergensis* (Bilton, 2014a) **comb.n.**, *Prosthetops tuberculatus* (Bilton, 2014a) **comb.n.**, *Prosthetops uitkyki* (Bilton, 2014a) **comb.n.** The synonymy of *Pterosthetops* also results in Pterosthetopini Perkins, 1994 **syn.n.** becoming a junior synonym of Prosthetopini Perkins, 1994, which we formally propose here.

DISCUSSION

Our molecular phylogenetic analyses suggest the monophyly of a morphologically disparate group of hydraenid genera, primarily distributed across landmasses which were formerly part of the supercontinent of Gondwana. Support values for some deeper nodes within this radiation are often rather weak, a finding consistent with a relatively rapid radiation which is difficult to resolve using a limited set of loci (e.g., Robertson et al., 2018; Bank et al., 2021). As detailed above, the genera we focus on here are currently classified across all hydraenid subfamilies, and split into numerous tribes. The beetles included in this 'Gonwana group' are morphologically diverse (see Figure 1), ranging in body size from about 1.3–4.2 mm, making them the largest known hydraenids, if not quite the smallest (Jäch et al., 2016). The range of external morphological variation is in sharp contrast to the relative morphological uniformity seen within the three most diverse hydraenid genera: *Hydraena*, *Ochthebius* and *Limnebius*. This likely relates to the wide range of habitats colonized by the 'Gondwana group', particularly conspicuous shifts to madicoly and terrestrial lifestyles, but may also reflect greater intrinsic morphological lability in these hydraenids. Given this wide ecological and morphological diversity, it is very difficult to identify clear morphological synapomorphies for the clade, and we refrain from formal changes to higher level classification here. One of the best morphological candidates, however, is the configuration of the antennae, most members of the 'Gondwana group' having 11 antennomeres, typically comprising three long basal meres, three shorter intermediate meres and five club meres (see Table 1). This basic pattern has been modified in some genera, through fusion of meres, particularly in the club, and indeed some genera, such as *Mesoceration* and *Parasthetops*, include species with different numbers of club meres as a result of an apparent process of mere fusion (Perkins & Balfour-Browne, 1994). Perkins (1997: 200) notes that this process may be particularly associated with the colonization of benthic microhabitats, where an increasing reliance on plastron respiration reduces functional constraints on the antennae for renewal of the air reservoir. As stated by Perkins (2017) '*it appears that* [antennal segmentation] … *is enigmatically one of the best key characters for the diagnosis*' of this clade morphologically.

A review of the 'Gondwana group' of genera

Genera which we consider members of the 'Gondwana group' (see Table 1) are discussed below, in order of their current subfamilial and tribal placements within the Hydraenidae.

Hydraeninae (Hydraenidini)

Genus *Haptaenida* Perkins, 1997

Type species: *Haptaenida huggerti* Perkins, 1997: 169, by original designation.

Monotypic and lentic; known only from the type locality, a shallow lakeshore at 4100 m in the Ecuadorian Andes. Morphologically close to *Parhydraenida*, as discussed by Perkins (1997); placed here tentatively in the absence of molecular data.

Genus *Hydraenida* Germain, 1901

Type species: *Hydraenida ocellata* Germain, 1901, by monotypy.

Five lotic Neotropical species, all restricted to Chile (Hansen, 1998; Jäch, 1998c; Perkins, 1980; Ribera, 2000). Apparently sister to *Ochtheosus* in our phylogeny, perhaps reflecting the geographical proximity of these two genera.

Genus *Parhydraenida* Balfour-Browne, 1975

Type species: *Parhydraenida reichardti* Balfour-Browne, 1975: 42, by original designation.

Twelve madicolous Neotropical species, eleven restricted to SE Brazil and one in Ecuador, described by Balfour-Browne (1975), Perkins (1980) and Jäch and Delgado (2018). Our phylogenetic analyses suggest *Parhydraenida* as sister to a clade comprised of two other Neotropical genera, *Hydraenida* + *Ochtheosus*.

Hydraeninae (Parhydraenini)

Genus *Decarthrocerus* Orchymont, 1948

Type species: *Decarthrocerus jeanneli* Orchymont, 1948: 35, by original designation.

Four humicolous species, from forest litter in central and eastern Africa.

Genus *Discozantaena* Perkins & Balfour-Browne, 1994

Type species: *Discozantaena genuvela* Perkins & Balfour-Browne, 1994: 124, by original designation.

Twelve humicolous species, all of which are restricted to South Africa, mostly in the Fynbos biome (Bilton & Perkins, 2012; Perkins, 2005a; Perkins & Balfour-Browne, 1994). *Discozantaena* species can be found both by sifting litter and shore washing, many species being associated with the margins of small streams and seeps (Bilton, *pers. obs*.).

Genus *Parhydraena* Orchymont, 1937

Type species: *Hydraena brevipalpis* Régimbart, 1906: 276, by original designation.

A total of 21 species, most of which are aquatic, but with a shift to humicoly in the *P. toro* species group, which currently comprises five species (Bilton, 2018; Perkins, 2009), two of which are represented in our molecular phylogeny. Nineteen of the 21 species known are restricted to South Africa, the other two occurring in Kenya and South Sudan respectively (Perkins, 2009). The terrestrial species of the *P. toro* group included in our analyses nest within the wider South African radiation.

Genus *Parhydraenopsis* Perkins, 2009

Type species: *Parhydraena cooperi* Orchymont, 1948: 721, by original designation.

Three known species, all restricted to mountain streams and seepages in the Ethiopian Highlands (see Perkins, 2009). Several new species are awaiting description.

Genus *Pneuminion* Perkins, 1997

Type species: *Pneuminion velamen* Perkins, 1997: 172, by original designation.

Ten humicolous species, all endemic to South Africa (Bilton & Perkins, 2012; Perkins, 1997, 2004a). Perkins (2009) noted, from a morphological perspective, the rather isolated position of *Pneuminion* amongst similar African genera, something which is reflected by its sister grou position wrt. this group of genera in our molecular analyses. *Pneuminion* retains the 11-segmented antennal configuration which we consider may be an ancestral feature of the 'Gondwana group', whilst all other former Parhydraenini have 10 antennomeres, something which has arisen through a reduction in the number of stem segments, probably via fusion of two of the shorter intermediate meres.

Genus *Protozantaena* Perkins, 1997

Type species: *Protozantaena labrata* Perkins, 1997: 175, by original designation.

Seven species, five in Madagascar, one (*P. labrata*) from Namibia and one (*P. birdi* Bilton) recently described from South Africa (Bilton, 2022; Perkins, 1997, 2009, 2017). Collecting data suggest a mix of aquatic and humicolous habits. The species included in our analyses, *P. birdi* from South Africa is morphologically very close to *P. labrata* and was found in small mountain streams, both in the water and on wet margins.

Genus *Riberazantaena* Bilton, 2021

Type species: *Protozantaena grebennikovi* Perkins, 2009: 47, by original designation.

Contains two humicolous species from the Eastern Arc Mountain forests of Tanzania, one of which was previously described as a *Protozantaena*. Distinguished from the latter on a number of morphological characters. Our molecular analyses demonstrate that these beetles are more closely related to *Decarthrocerus* and *Parhydraenopsis*, which, like *Riberazantaena*, are also found in eastern and central Africa.

Ochthebiinae (Ochtheosini)

Genus *Edaphobates* Jäch & Díaz, 2003

Type species: *Edaphobates puetzi* Jäch & Díaz, 2003: 304, by original designation.

Monotypic and terrestrial, described from a single female sampled from leaf litter in a *Rhododendron* forest in the mountains of Sichuan, China. Originally assigned to the Ochthebiinae, without tribal placement by Jäch and Díaz (2003), who listed a number of morphological synapomorphies with *Ochtheosus*, including the shape of the mentum, the denticulation of the lateral pronotal margin, ridges and a median impression on the metaventrite, a broad median longitudinal groove on tergite VIII and ventrite VI with a transverse ridge separating the smooth anterior half from the pubescent posterior half. Considered under Ochtheosini by Villastrigo et al. (2019). Tentatively placed here in the absence of molecular data; apparently an isolated, presumably relictual taxon.

Genus *Ginkgoscia* Jäch & Díaz, 2004

Type species: *Ginkgoscia relicta* Jäch & Díaz, 2004: 284, by original designation.

Monotypic and lotic; known from four females, collected in a stream flowing through a bamboo forest in Zhejiang, China. Originally classified in the Ochthebiinae, without tribal placement, by Jäch and Díaz (2004), who discuss the morphology of *Ginkgoscia*, including a number of characters shared with *Ochtheosus* on the one hand (shape of mentum, crenulated lateral pronotal margin, structure of metaventrite, tergite VIII with broad median longitudinal groove and ventrite VI with a transverse ridge separating the smooth anterior half from the pubescent posterior half) and *Davidraena* and *Gondraena* (structre of maxillary palpi and antennae) on the other (Jäch & Díaz, 2004). Considered under Ochtheosini by Villastrigo et al. (2019). It is placed here tentatively, in the absence of molecular data.

Genus *Ochtheosus* Perkins, 1997

Type species: *Ochtheosus fungicolus* Perkins, 1997: 125, by original designation.

Two humicolous Chilean species, described by Perkins (1997) and Jäch (1998b). Originally placed in its own tribe (Ochtheosini) within the Ochthebiinae, our molecular analyses suggest that *Ochtheosus* is instead related to the Neotropical *Hydraenida* and *Parhydraenida*. In the original description, Perkins (1997) notes a number of ways in which the morphology of *Ochtheosus* deviates from all other Ochthebiinae, including the presence of 11 antennomeres and the structure of the tentorium, which, amongst taxa examined, shared some features with the New Zealand *Orchymontia* and some South African *Prosthetops* species. Jäch (1998b) also discussed the morphologically isolated nature of *Ochtheosus* wrt. Other Ochthebiinae. The original subfamily placement was apparently made on the basis of structures of the hypomeron which, as discussed above, may be subject to convergence. Whilst the exact position of *Ochtheosus* within the 'Gondwana group' may change with additional molecular data, it seems very unlikely indeed that this taxon is an ochthebiine.

Orchymontiinae

Genus *Orchymontia* Broun, 1919

Although usually considered a basal hydraenid subfamily (Orchymontiinae—Beutel et al., 2003; Delgado & Palma, 2000, 2010), our analyses suggest that this genus is instead nested within the 'Gondwana group' of genera. As redefined here, the genus contains 32 species, all lotic and all found exclusively in New Zealand, where they are the only diverse genus of the family (Ordish, 1984). *Orchymontia*, *Homalaena* and *Podaena* were distinguished from each other on relatively small characters, particularly the number of antennal segments, which are known to vary within other genera of Hydraenidae, particularly through the fusion of articles (see Beutel et al., 2003; Perkins & Balfour-Browne, 1994), as seems to have occurred here, with included *Homalaena* (10-segmented antennae) and *Orchymontia* (9-segmented antennae) apparently related to different lineages of *Podaena* (11-segmented antennae; apparently the ancestral condition in the 'Gondwana group'). The relationship between this New Zealand clade and the African *Coelometopon*, suggested by our molecular phylogenies, may appear rather unexpected on the basis of morphology, but the highly derived habitus of *Coelometopon*, associated with a switch to obligate madicoly, makes the interpretation of morphological characters difficult. In the absence of formal analyses, however, similarities in the fine structure of ventral vestiture (see Perkins, 1997, figures 67–70 and Perkins, 2005b, figures 64–65) and aedeagal anatomy (see Delgado & Palma, 2000, 2010; Ordish, 1984; Perkins, 2005b) tentatively appear to offer morphological support for this relationship, as does abdominal anatomy, the last sternum being concealed beneath the penultimate in female *Orchymontia* and in both sexes of *Coelometopon*. Larval morphology (Delgado & Palma, 2004) suggested a relationship between *Orchymontia* and Hydraeninae, on the basis of seven apparent synapomorphies. It is rather difficult to interpret many of these larval characters, however, particularly in the absence of larval descriptions for other genera of the 'Gondwana group', but the suggested relationships apparently do not reflect the phylogenetic position of *Orchymontia*. A number of new species of this lineage are awaiting description.

Prosthetopinae (Coelometoponini)

Genus *Coelometopon* Janssens, 1972

As redefined, now containing a total of 27 madicolous species, most of which are restricted to South Africa, with a handful of species known north through the Eastern Arc Mountains to Mount Kilimanjaro (Bilton, 2015a, 2016; Perkins, 2005b). Some *Coelometopon* are amongst the largest described hydraenids (Perkins, 2005b). Originally placed in the Madagastrini by Perkins (1997) on the basis of hypomeral features which may represent convergent adaptations to madicoly and more recently (Perkins, 2005b) transferred to its own tribe in the Prosthetopinae. Here we infer that these highly derived hydraenids are sister to the New Zealand *Orchymontia* (see discussion under that genus). Former *Oomtelecopon* species are apparently sister to *C. fimbriatum* Perkins, 2005, itself a rather aberrant species, but not sufficiently differentiated from remaining *Coelometopon* to justify placement in a separate genus. The somewhat derived morphology of the *Oomtelecopon* lineage (see Perkins, 2005b), including the reduction of ventral vestiture, may partly result from the fact that these beetles are more terrestrial than other *Coelometopon*, usually being found beside seeps rather than within them (Bilton, *pers. obs.*). Eastern Arc *Coelometopon* are also somewhat divergent morphologically from most South African species (see Perkins, 2005b), but our molecular phylogeny shows that they (represented by *C. madidum* Janssens, 1972) are nested within the South African radiation, and appear to represent a relatively recent (Eocene–Oligocene) northward expansion of this clade.

Prosthetopinae (Madagastrini)

Genus *Davidraena* Jäch, 1994

Type species: *Davidraena boukali* Jäch, 1994: 95, by original designation.

Described by Jäch (1994) for two madicolous species from southern India (Kerala and Tamil Nadu), to which Perkins (1997) added *D. bacata* Perkins, 1997 from Kerala. We were unable to obtain material of this genus for molecular analyses, but it is morphologically close to *Madagaster*, and was included in the Madagastrini by Perkins (1997).

Genus *Gondraena* Jäch, 1994

Type species: *Gondraena indica* Jäch, 1994: 87, by original designation.

Two madicolous species described by Jäch (1994) from southern India (Kerala and Tamil Nadu). We were unable to obtain material of this genus for molecular analyses, but it is morphologically close to *Madagaster*, and was included in the Madagastrini by Perkins (1997).

Genus *Madagaster* Perkins, 1997

Type species: *Madagaster steineri* Perkins, 1997: 179, by original designation.

Endemic to Madagascar, with eight currently recognized madicolous species (Perkins, 2017). Our results place *Madagaster* at the base of the 'Gondwana group'.

Genus *Menomadraena* Perkins, 2017

Type species: *Menomadraena nitedula* Perkins, 2017: 171, by original designation.

Contains six humicolous Madagascan species, all described in Perkins (2017). Again, we were unable to obtain material of this genus for molecular analyses, but it is morphologically close to *Madagaster*, and was included in the Madagastrini by Perkins (2017).

Genus *Trinomadraena* Perkins, 2017

Type species: *Trinomadraena clusa* Perkins, 2017: 199, by original designation.

Monotypic, madicolous and possibly belonging to *Madagaster* as it is separated from this genus on relatively superficial characters. In the absence of molecular data, however, we retain *Trinomadraena* as a separate genus here.

Prosthetopinae (Nucleotopini)

Genus *Nucleotops* Perkins & Balfour-Browne, 1994

Type species: *Nucleotops nimbaceps* Perkins & Balfour-Browne, 1994: 13, by original designation.

Four humicolous species (Jäch, 1999; Perkins, 2004b), all restricted to South Africa. Sometimes apparently collected far from water, but usually close to it, including in the mist zone around waterfalls and rapids, on damp (but not wet) microalgal covered rocks, in leaf litter etc.

Prosthetopinae (Parasthetopini)

Genus *Mesoceration* Janssens, 1967

Type species: *Mesoceration capense* Janssens, 1967, by monotypy.

The largest genus in the 'Gondwana group', with 50 described species, all of which are lotic and endemic to South Africa, mostly in mountain streams of the Fynbos Biome (Bilton, 2015c; Perkins, 2008). *Mesoceration* species also vary in the number of antennal club meres, this ranging from six to one through an apparent fusion process (Perkins & Balfour-Browne, 1994).

Genus *Mesoceratops* Bilton & Jäch, gen.n.

Six lotic species, associated with fast flowing water and occasionally seeps.

Genus *Parasthetops* Perkins & Balfour-Browne, 1994

Type species: *Parasthetops nigritus* Perkins & Balfour-Browne, 1994: 39, by original designation.

Includes 22 fully aquatic species, mostly lotic, but with some also occupying lentic microhabitats. Again, most species are restricted to South Africa, although the genus is also represented in Namibia and Zimbabwe (Bilton, 2017; Perkins, 2008). *Parasthetops* species vary in the number of antennal club meres, this ranging from six to one through an apparent fusion process (Perkins & Balfour-Browne, 1994).

Genus *Sebasthetops* Jäch, 1998

Type species: *Sebasthetops omaliniformis* Jäch, 1998c: 23, by original designation.

Two lotic species, restricted to fast flowing riffles in cold, high altitude (>1000 m) mountain streams of the Western Cape of South Africa (Bilton, 2013a, 2015b; Jäch, 1998b). Morphologically aberrant, with a distinctive broad, flattened habitus and marked sexual dimorphism, including asymmetrical elytra in the females of *S. altimontanus* Bilton, 2015, unique within the Hydraenidae (Bilton, 2015). Sister g to a large clade of South African genera, apparently diverging in the late Cretaceous-Paleogene, with known extant species originating much more recently in the Neogene. An additional undescribed species is known only from females from the Langeberg in the Western Cape Province (Bilton, 2013a).

Genus *Sicilicula* Balfour-Browne, 1958

Type species: *Sicilicula teres* Balfour-Browne, 1958: 136, by original designation.

Nine species, collected from a variety of aquatic habitats, but mostly madicolous (Perkins, 2017). Eight of these are restricted to Madagascar; one (*S. borbonica* Balfour-Browne, 1958) is endemic to Réunion (Mascarene Islands). Several new species await description.

Prosthetopinae (Prosthetopini)

Genus *Prosthetops* Waterhouse, 1879

As now redefined, members of the genus occur in two very different habitat types, each of which appear to be associated with a particular suite of morphological characters, that has led to these beetles being placed in separate genera (and indeed tribes) in the past (Perkins & Balfour-Browne, 1994). Our phylogenetic analyses suggest that *Prosthetops* evolved as a primarily madicolous lineage, with relatively small body size and short appendages, which corresponds to most members of the former *Pterosthetops*. A single shift to occupying montane rock pools was associated with the evolution of larger body size, large head, long appendages and more strongly marked sexual dimorphism, characteristic of *Prosthetops* as previously defined. *Prosthetops* include the largest hydraenids known to date (Bilton, 2013b). Within this clade there has been at least one recent (Pleistocene) shift back to madicoly and a *Pterosthetops* facies, giving rise to the species described as *Pterosthetops chrysomallus* Bilton, 2017.

Prosthetopinae (Protosthetopini)

Genus *Protosthetops* Perkins, 1994

Type species: *Prosthetops kenyensis* Orchymont, 1948: 56, designated by Perkins (*in* Perkins & Balfour-Browne, 1994: 7).

A single species from Kenya, not collected since its description. Perkins and Balfour-Browne (1994) separate *Protosthetops* from related genera on the basis of shorter maxillary palpi, limited leg setation and the lack of a well-developed ventral plastron vestiture. All of these characters may be associated with the species occupying a riparian or terrestrial habitat. Although Arambourg et al. (1935) provide a map and some notes on the sampling site ('Camp II') on the eastern slope of Mt. Elgon, there is no precise information on the habitat of the hydraenid specimens. Sampling was carried out in forest, springs, streams, bogs, and techniques included washing of wet moss, and sifting plant litter at the margin of a torrent. In the absence of molecular data, the precise relationships of *P. kenyensis* remain unclear.

Historical biogeography of the 'Gondwana group'

All genera of the 'Gondwana group' included in our analyses are distributed on land masses which were formerly part of the supercontinent of Gondwana, across which individual clades are strikingly geographically consistent (Figure 3). Optimal dates from the BEAST analysis suggest that the separations between lineages primarily occurred in the Cretaceous, with credibility intervals extending many of these back to the Lower Cretaceous, at a time when the Gondwanan landmass was actively breaking up (McIntyre et al., 2017).

Our preferred BioGeoBEARS analysis under the DIVALIKE model infers an origin of the 'Gondwana group' in Africa/Madagascar about 101.2 MYA (CI 83.2–119.8 MYA). Even taking the oldest dates from the credibility interval into account (see Figure 3), this was at a time when Africa and Madagascar had already separated as parts of West and East Gondwana, respectively (Schettino & Scotese, 2005; Blackey, 2008; Seton et al., 2012; Müller et al., 2016, 2019; McIntyre et al., 2017; Young et al., 2019), and we consider an African origin for these beetles, followed by overwater dispersal to Madagascar + India the most likely scenario for the origin of these lineages. Madagascar began to separate from the Tanzanian coast in the Kimmeridgian (157 Ma), and has remained at approximately the same distance from Africa since the Aptian (120 MYA; Davis et al., 2016; Reeves et al., 2016; Thompson et al., 2019). Whilst a number of relatively short-lived land bridges may have existed between Africa and Madagascar subsequently, the first of these is not thought to have developed until the Late Cretaceous–Early Palaeocene (66–60 MYA; Masters et al., 2021), suggesting that these hydraenids crossed the Mozambique Channel by other means. Two additional genera, *Davidraena* and *Gondraena*, are known from southern India. Both genera are considered closely related to *Madagaster* (Perkins, 1997, 2017) based on morphology, and whilst it was not possible to obtain fresh material for the present study, their future inclusion in molecular phylogenies would clearly prove illuminating.

The ancestor of the Neotropical *Hydraenida*, *Ochtheosus* and *Parhydraenida* apparently split from related African taxa (Parhydraenini) about 87.6 MYA (CI 71.5–104.4 MYA). By this time, Africa and South America were completely separated (Blakey, 2008), which would imply overwater dispersal, albeit across a narrower South Atlantic. Given the credibility interval from BEAST, however, we cannot rule out a vicariant split between these African and Neotropical lineages, which may represent another example of West Gondwanan vicariance to add to those discussed by Toussaint, Seidel, et al. (2017). Within South America, the inter-relationships between genera appear to match their biogeography; the more northerly distributed *Parhydraenida* being sister to the temperate Chilean *Hydraenida* and *Ochtheosus*. Within the Parhydraenini, the South African *Pneuminion* Perkins diverged from the ancestor of the remaining genera about 76.5 MYA (CI 61.4–92.6 MYA) in the Upper Cretaceous. Whilst most of the diversity of this lineage is found in southern Africa, *Decarthrocerus*, *Parhydraenopsis* and *Riberazantaena* are East African, *Parhydraena* has East African species, and *Protozantaena* has at some point colonized Madagascar, although the absence of Malagasy species in our dataset makes it impossible to date this event. In all cases, however, these appear to represent colonisations from within a southern African clade. A similar pattern, where species from tropical African mountains are nested within Cape clades has been shown to be widespread in a number of plant groups including Proteaceae (Galley & Linder, 2006; Valente et al., 2010).

The New Zealand *Orchymontia* and Afrotropical *Coelometopon* apparently diverged about 85.9 MYA (CI 70.1–103.5 MYA). The common ancestor of these two genera is inferred to be African in BioGeoBEARS, and we suggest that the ancestor of *Orchymontia* colonized East Gondwana from Africa by overwater dispersal, perhaps facilitated by the Crozet and Kerguelen Plateaus, which were subaerial at least three times 100–20 MYA (Bénard et al., 2010; Frey et al., 2020). Analagous events, albeit involving movements into Africa, have been hypothesized from phylogenetic studies of Iridaceae (Goldblatt et al., 2008). Such a scenario implies that members of the *Coelometopon*/*Orchymontia* lineage were formerly widespread on East Gondwana, and have subsequently become extinct, except in New Zealand. Extirpation from Antarctica was inevitable with the onset of almost complete glaciation, although suitable habitats likely persisted here until at least the middle Miocene (Anderson et al., 2011; Francis et al., 2008; Lewis et al., 2008; Prebble et al., 2006; Rees-Owen et al., 2018). It is slightly more difficult to account for the fact that no members of this group occur in Australia. Ancestors of *Orchymontia* likely colonized Zealandia before, or recently after, this landmass separated from East Gondwana, about 85–60 MYA (Allentoft & Rawlence, 2012; McIntyre et al., 2017; Neall & Trewick, 2008; Schellart et al., 2006); Antarctica and Australia split more recently, about 46 MYA (McIntyre et al., 2017; Morra et al., 2013; Upchurch, 2008). Whilst it is not impossible that some members of the 'Gondwana group' persist in southern temperate Australia/Tasmania, this seems unlikely in light of recent work on the hydraenid fauna of these areas (e.g., Perkins, 2006), and it appears increasingly probable that this lineage is genuinely absent, perhaps being lost due to increased aridity during the Neogene (Toussaint et al., 2016). New Zealand is well-known to support a number of phylogenetically isolated, relictual taxa, including some with no close extant relatives elsewhere, such as the iconic tuatara (Gemmell et al., 2020). Insect examples include the world's only extant sooty mould beetles (Cyclaxyridae; Gimmel et al., 2019) and *Lenax mirandus* Sharp (Monotomidae), the only known surviving member of the Lenacini Crowson (Liu et al., 2020). In *Coelometopon*, *C. madidum* and related species in the Eastern Arc Mountains appear to represent Palaeogene colonists from Southern Africa, *C. madidum* diverging from the closest South African species in our phylogeny about 45.1 MYA (CI 32.5–58.9 MYA).

Remaining included genera of the 'Gondwana group' belong to the subfamily Prosthetopinae, and began diversifying in Africa about 65.9 MYA (CI 51.8–81.6 MYA), in the Upper Cretaceous/Palaeogene. Almost all members of this lineage are southern African, with diversity at both genus and species level centred in the Fynbos Biome in the South African Cape, where we assume much of this diversification has occurred. This region is renowned for its exceptional floristic diversity, around 20% of the plant species known from Sub-Saharan Africa being found here, in <1% of the continent's land area (Linder, 2003; Schnitzler et al., 2011). Whilst pollen from many characteristic Fynbos plant groups is present in deposits of Late Cretaceous/Paleogene age from Namaqualand (Scholtze, 1985), these taxa were apparently living under a tropical climate. Tropical and subtropical, mesic forests are usually thought to have dominated the region until the onset of summer drought about 8–10 MYA (Siesser, 1980), although the extent to which these were mixed with open habitats remains uncertain. He et al. (2016) showed that fire-adapted traits had evolved by the Late Cretaceous in Haemodoraceae and Restionaceae. Similarly, Bytebier et al. (2011) used an orchid phylogeny to estimate that fire adaptations appeared in the Miocene, again predating the onset of a fully Mediterranean climate in the region. The radiation of most of the Cape genera also predates the onset of a Mediterranean climate; whilst some closely related species in *Mesoceration*, *Nucleotops*, *Parasthetops* and *Prosthetops*, have speciated in the Plio-Pleistocene, our phylogeny suggests a gradual accumulation of diversity in most groups since the mid-Paleogene. Similar findings have emerged from phylogenetic studies of a number of Cape plant lineages (Linder, 2003; Sauquet et al., 2009; Valente et al., 2011; Valente & Vargas, 2013). The majority of Prosthetopinae are found in relatively open, Fynbos-dominated, fire-prone environments; remnant patches of Afrotemperate forest by contrast supporting a relatively depauperate fauna, with few microendemics. Indeed, nutrient release from fire appears to be important in shaping prosthetopine assemblage composition in stream and rock seepage habitats in the South African Cape (D. T. Bilton, *pers. obs.*).

Within the Cape taxa there has been at least one excursion northeast, leading to the colonization of Madagascar and Réunion by *Sicilicula*. Links between Cape and Malagasy lineages are also seen in Hyphydrini Sharp (Dytiscidae), where the Madagascan *Hovahydrus* Biström is sister to a Cape clade of five genera (Ribera & Balke, 2007). The only member of the Prosthetopinae known from East Africa is *Protosthetops kenyensis* (Orchymont) in Kenya. Although not sampled in our phylogeny, the species' morphology strongly suggests a position nested within this group, implying an origin via northward dispersal from the Cape, as seen in Parhydraenini and *Coelometopon* (see above) and a number of plant taxa (Galley & Linder, 2006; Valente et al., 2010).

Most of the hydraenid genera missing from our analyses overlap biogeographically with included taxa, and are clearly related to sampled genera on the basis of morphology. Amongst excluded genera, the two most interesting, from a biogeographical point of view, are *Edaphobates* and *Gingkoscia*, both of which are known only from their type localities in China (Jäch & Díaz, 2003, 2004). Assuming these genera are members of the 'Gondwana group', their presence outside former Gondwanan terranes could be explained by dispersal out of India, after the subcontinent collided with Eurasia, 55–20 MYA (Loria & Prendini, 2020). Alternative scenarios would be dispersal to the southern margin of Laurasia from a separate East Gondwanan terrane such as the West Burma Block in the Paleogene (Poinar, 2019), or much earlier, perhaps Mid-Cretaceous dispersal from West Gondwana via Europe, as has been postulated for Onychophorans (Oliveira et al., 2016). Clearly, analysis of divergence times for these genera is essential to test between such hypotheses. China is well-known to harbour many relictual lineages in both plants and animals (e.g., Hawlitschek et al., 2012; López-Pujol & Ren, 2009a, 2009b), including a number of other elements which appear to be isolated lineages of Gondwanan ancestry, such as *Acanthochlamys bracteata* P.C. Kao (Velloziaceae) (Sun et al., 2017; Wanga et al., 2021).

Habitat evolution in the 'Gondwana group'

The vast majority of species of the 'Gondwana group' are truly aquatic as adults, with shifts to terrestriality being relatively rare. Within the Hydraeninae, adults of all described *Limnebius* are fully aquatic and most *Hydraena* are aquatic and lotic in the adult stage. A limited, but likely under-estimated number of *Hydraena* species are terrestrial, living in damp tropical forest litter (e.g., Hernando & Ribera, 2017; Perkins, 2017). Within the Ochthebiinae, a number of transitions to terrestriality have occurred in adults, but with the exception of the Australian/Antarctic *Meropathus*, the species concerned usually occupy wet margins rather than areas far away from water. Compared with these two subfamilies, transitions to adult terrestriality have been relatively frequent within the 'Gondwana group' of genera, clearly occurring four times in the taxa included in our phylogeny. Within *Protozantaena*, whilst most species appear to be lotic, some unsampled species, including *P. malagasica* Perkins, have been recorded from sifted forest litter (Perkins, 2009). *Edaphobates* may represent a sixth transition to humicolous terrestrial habitats in the group (Jäch & Díaz, 2003). The other non-stream habitat frequently colonized by members of the 'Gondwana group' are madicolous faces, where (semi)permanent trickles of water flow over exposed rock (Vaillant, 1956). Such habitats have been colonized extensively by these hydraenids, in Africa, Madagascar, India and South America, and these beetles form a key component of the specialized aquatic fauna (e.g., Ribera et al., 2002; Ribera & Bilton, 2007; Spangler & Steiner, 2005) of wet rock faces in these regions. Although a formal analysis of morphological traits in the 'Gondwana group' is beyond the scope of the current work, we strongly suspect that some of the features of the antennal club, antennal pocket, hypomeron and ventral vestiture used in hydraenid classification by Perkins (1997), reflect adaptations to aquatic or humicolous and/or madicolous lifestyles. As such, whilst these characters can identify lineages, they may not always provide a reliable guide to relationships, illustrated by the differences between our phylogeny and existing higher-level classifications.

In *Prosthetops*, multiple habitat transitions appear to have happened within the same lineage. From a madicolous ancestor, a shift to rock pools was associated with the evolution of a distinct habitus, with larger body size, relatively large head, long appendages and stronger sexual dimorphism, corresponding to *Prosthetops* as previously defined. Within this rock pool clade, a further shift back to madicoly has occurred in *Prosthetops chrysomallus* (originally described as a *Pterosthetops*), whose sister species is *Prosthetops wolfbergensis* Bilton, the two being broadly sympatric on the Bokkeveld Plateau at the northern end of the Fynbos Biome, South Africa.

CONCLUSIONS

Our molecular work covers most hydraenid genera unsampled to date, and results in a number of taxonomic changes. Our phylogenetic analyses suggest a different picture of hydraenid inter-relationships than the currently accepted higher classification in this diverse family of true water beetles. Future work should aim to confirm the monophyly of our 'Gondwana group' and investigate the phylogenetic placement of genera we were unable to sample, including *Davidraena* and *Gondraena* in India, but particularly the Chinese *Edaphobates* and *Ginkgoscia*, the only non-Gondwanan members of this putative lineage. Denser taxon sampling in the future would also allow us to test whether specific habitat preferences are associated with higher or lower diversification dynamics. This is especially important considering the existing theoretical framework suggesting that the more ephemeral habitats are, the less genetically structured their inhabitants are likely to be (Ribera, 2008). Despite the lack of a formal macroevolutionary framework in this study, due to incomplete species-level taxon sampling, it is clear that some clades associated with geologically stable lotic habitats (e.g., *Mesoceration*) appear to have diversified more in the Neogene than others. Such a pattern would repay detailed scrutiny, with more comprehensively sampled phylogenies.

AUTHOR CONTRIBUTIONS

David Thomas Bilton: Conceptualization (equal); data curation (equal); formal analysis (supporting); investigation (equal); methodology (equal); project administration (equal); writing – original draft (lead); writing – review and editing (lead). **Manfred Jaech:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Ignacio Ribera:** Conceptualization (equal); data curation (lead); formal analysis (supporting); investigation (equal); methodology (equal); project administration (equal); resources (lead); validation (lead). **Emmanuel Toussaint:** Formal analysis (lead); investigation (supporting); writing – original draft (supporting); writing – review and editing (supporting).

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DATA AVAILABILITY STATEMENT

New sequences from this study are deposited in GenBank, with accession numbers ON937331-ON937424, ON937426-ON937531, ON938211-ON938311, ON949952-ON950044 and ON968874.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. List of new material used in the molecular phylogeny, including voucher numbers, sequence accession numbers and locality information.

Table S2. Geographical occurrence and habitat occupancy.

Table S3. (A) primers used for DNA amplification and sequencing reactions; (B) Typical conditions for polymerase chain reactions.

Figure S1. Results of BIOGeoBEARS analysis using DEC model.

Figure S2. Results of BIOGeoBEARS analysis using DIVALIKE model.

Figure S3. Results of phytools analysis on habitat usage. States as follows: madicolous (D), humicolous (H), lotic (Lo), lentic (Le) and rock pools (RP).

Appendix S1. Checklist of the 'Gondwana group' of genera.

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