Historical biogeography of the hyperdiverse hidden snout weevils (Coleoptera, Curculionidae, Cryptorhynchinae)

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Abstract. The first dated phylogeny of the weevil subfamily Cryptorhynchinae is presented within a framework of Curculionoidea. The inferred pattern and timing of weevil family relationships are generally congruent with previous studies, but our data are the first to suggest a highly supported sister-group relationship between Attelabidae and Belidae. Our biogeographical inferences suggest that Cryptorhynchinae s.s. originated in the Late Cretaceous (c. 86 Ma) in South America. Within the ‘Acalles group’ and the ‘Cryptorhynchus group’, several independent dispersal events to the Western Palaearctic via the Nearctic occurred in the Late Cretaceous and Early Paleogene. A second southern route via Antarctica may have facilitated the colonization of Australia in the Late Cretaceous (c. 82 Ma), where a diverse Indo-Australian clade probably emerged c. 73 Ma. In the Early Eocene (c. 50–55 Ma), several clades independently dispersed from Australia to proto-New Guinea, i.e. the tribe Arachnopodini s.l., the ‘Rhynchodes group’ and the genus Trigonopterus. New Zealand was first colonized in the Late Paleocene (c. 60 Ma). Divergence time estimations and biogeographical reconstructions indicate that the colonization of New Guinea is older than expected from current geological reconstructions of the region.

Introduction

With c. 400,000 described species, beetles are the most species-rich group of known animals. Understanding the mechanisms that govern the assembly of such an astonishing diversity is therefore of great significance. Yet the evolution of many major beetle groups remains little explored due to a lack of fossil-based dated phylogenies. For the economically important and evolutionarily interesting weevils (Curculionoidea), only few studies have attempted to provide sound temporal estimations of divergence times at higher taxonomic ranks (e.g. McKenna et al., 2009; Gunter et al., 2016; Shin et al., 2018). Delimitation of many larger weevil subfamilies and tribes is often ambiguous, and current classifications are mainly based on ad hoc decisions rather than phylogenetic reconstructions (Oberprieler et al., 2007, 2014). This often hampers the compilation of reliable datasets to estimate divergence times and, consequently, comprehensive phylogenetic reconstructions and divergence dating are restricted to few well-defined weevil subfamilies, such as Platypodinae (Jordal et al., 2011; Jordal, 2015), Apioninae (Winter et al., 2017), and Ceutorhynchinae (Letsch et al., 2018). Another challenge for weevil dating is the choice of reliable fossil calibrations. Weevil fossils are legion, but many of these cannot be assigned to extant weevil families or subfamilies without contention. Legalov (2012) compiled an overview of weevil fossils from the Mesozoic, with several recent updates (Legalov, 2014a, 2014b). However, the assignment of many of these fossils to extant families is still questionable and under debate (e.g. Oberprieler et al., 2014; Gunter et al., 2016), leaving only a handful of suitable fossils to use in divergence time dating analyses.

Cryptorhynchinae (hidden snout weevils) are one of the most diverse groups of Curculionidae, themselves one of the two
most species-rich families on Earth (Grebenikov & Newton, 2009). They share a unique morphological feature that distinguishes them from most other weevil groups. As a defensive pose, they retract their rostrum into a canal formed by pro- and mesosternal structures while their legs are usually folded in a ventral position. Thus, feigning death, they often simulate natural objects, such as seeds, small stones or twigs (Lyal, 1993; van de Kamp et al., 2014).

The most comprehensive approach to address the phylogenetic relationships of Cryptorhynchinae included 105 ingroup genera representing all geographic regions (Riedel et al., 2016). This study tested the monophyly of Cryptorhynchinae and revealed a monophyletic Cryptorhynchinae s.s., excluding the tribes Aedemonini and Camptorhinini. The taxonomic status and classification of Cryptorhynchinae are under discussion because their main character of morphological identification, i.e. a rostral furrow combined with a mesosternal receptacle, is prone to convergence (Lyal, 2014; Riedel et al., 2016). The choice of uniting them within the polyphyletic subfamily ‘Molytinae’ (Oberprieler et al., 2007; Lyal, 2014) hardly improved the situation.

Taxonomic diversity of Cryptorhynchinae peaks in the Australian and Neotropical regions, followed by the Pacific Islands, and then the Oriental and the Holarctic regions. Cryptorhynchinae (s.s.) appear largely absent from the Afrotropics, where they seem to be replaced by the tribe Aedemonini (Molytinae). Even small isolated islands may host substantial radiations (Paulay, 1985). Based on the high percentage of new species added by recent taxonomic revisions, a total of > 15 000 Cryptorhynchinae species can be anticipated (e.g. Eberle et al., 2012; Setliff, 2012; Tänzler et al., 2012; Riedel et al., 2013, 2014; Luna-Cozar et al., 2014; Riedel & Narakusumo, 2019). Recent studies on the Western Palaearctic Cryptorhynchinae of the Acalles group (Astrin & Stüben, 2008; Astrin et al., 2012) and the Indo-Australian genus Trigonopterus Fauvel (Tänzler et al., 2014, 2016; Toussaint et al., 2017b) provided insights into their evolution, but the systematics and evolution of the highly diverse South American and Indo-Australian faunas remain largely unexplored. Many species and genera of the litter fauna are still undescribed, while the relationships and composition of major groups are in equal need of study.

The current classification of Cryptorhynchinae s.s. is more than problematic: as most of the established tribes and subtribes, such as Gasterocercini, Tylodina and Mecistostylina, appear to be polyphyletic, Riedel et al. (2016) advocated for the use of Cryptorhynchinae s.s. without any subcategories. Some biogeographically defined groups appeared highly supported, i.e. a large Indo-Australian clade or a smaller clade comprising the majority of the New Zealand fauna, but these cannot be named formally unless a larger portion of the existing genera can be assigned and/or characters are identified that allow their morphological diagnosis.

Estimates of reliable divergence times of major groups of Cryptorhynchinae are still missing. However, methods inferring the potentially differential diversification among clades, i.e. speciation and extinction over space and time, or the impact of specific traits (e.g. lifestyle features, morphological characters or geographical distributions) as driving forces on diversification, rely on the analyses of dated phylogenetic trees sufficiently representing the species richness of focal clades (e.g. Morlon, 2014; Ng & Smith, 2014; Maddison & FitzJohn, 2015; Rabosky & Goldberg, 2015). Studies such as the ones focusing on the evolutionary history of the extremely diverse Trigonopterus, possibly with >1000 species in New Guinea alone, also depend on sound estimates of their evolutionary age. Thus, the retrieval of a robust maximum age for Trigonopterus is one goal of the present study. As the sister group of Trigonopterus remains unknown but is presumably found among the wingless genera of Cryptorhynchini, i.e. ‘Tylodina’, we tried to include as many lineages of them as possible. A large portion of these edaphic species is still undescribed, even at genus level, which leads to an unusually high number of unidentified taxa contained in the dataset. In some cases, taxonomic problems preclude a robust identification (Riedel, 2017). Arachnomas Boisduval is a peculiar genus recently recognized as belonging to the Indo-Australian clade of Cryptorhynchinae (Riedel et al., 2016). It is endemic to the Papuan region and absent from Australia, and thus a likely candidate of a radiation confined to New Guinea or a Proto-New Guinea insular setting. As such, it may have a similar history of diversification as Trigonopterus and, in combination, both taxa may provide insights into the biogeographic history of this area.

The goals of the present study are to present a robust phylogeny of Cryptorhynchinae with comprehensive taxon sampling of Cryptorhynchinae s.s. from all major geographic regions (this forms the basis for a revised classification) and to generate reliable divergence time estimates and historical biogeography of major clades within the group.

Materials and methods

Taxon sampling

The dataset of Riedel et al. (2016) is used here in part: some species representing Aedemonini, Camptorhinini, Cleogonini and Ihyporini (Cryptorhynchinae s.l.) have been deleted as relationships among ‘Molytinae’ are outside the scope of this study. A considerable number of additional Cryptorhynchinae s.s. (112 species) and outgroups representing other weevil families (41 species) have been added. We included representatives of all weevil families, i.e. Cerambycidae (two species), Nemonychidae (two species), Anthribidae (seven species), Attelabidae (six species), Belidae (seven species), Caridae (one species), and Brentidae (16 species) and important subfamilies of Curculionidae, i.e. Bagoineae (one species), Hyperinae (one species), Platypodinae (two species) and Scolytinae (two species). Sequences were retrieved from either GenBank, or the Barcode Of Life Database (BOLD; Ratnasingham & Hebert, 2007).

Genomic DNA of 123 additional specimens were extracted nondestructively (Riedel et al., 2010) using the DNeasy (Qiagen, Hilden, Germany) and NucleoSpin 96 Tissue kits (Macherey-Nagel, Düren, Germany). Primers and PCR conditions principally follow Toussaint et al. (2017b). In total, the dataset consisted of the mitochondrial 16S and the
nuclear 18S and 28S ribosomal RNA genes, as well as the protein-coding genes cytochrome c oxidase subunit 1 (COI), arginine kinase (ArgK), carbamoyl-phosphate synthetase 2 (CAD), elongation-factor 1 alpha (EF1α) and enolase (EN). For an overview of samples, markers, and accession numbers, see Appendix S1.

**Phylogenetic analyses**

Alignment procedures for all protein-coding and ribosomal RNA genes were separately conducted with the online version of the program **MAFFT** v.7.409 (Katoh & Standley, 2013; Katoh et al., 2017), applying the automatic method search (protein-coding genes, FFT-NS-1 method; rRNA genes, L-INS-i method). Alignments of ribosomal RNA genes are challenging, as positional homology of variable regions is hard to obtain. We therefore excluded ambiguous positions in all ribosomal RNA alignments with the software **ALISCORE** v.2.0 (Misof & Misof, 2009). The alignments of all genes were subsequently assembled using the software **FASCNCONCAT** v.1.0 (Kück & Meusemann, 2010). Codon positions of each protein-coding gene, as well as each ribosomal RNA gene were defined as distinct partitions a priori. This resulted in a dataset comprising 5690 nucleotides and 18 partitions.

We used **MODELSELECT** as implemented in **IQ-TREE** v.1.6.10 (Nguyen et al., 2015; Chennomwar et al., 2016; Kalyaanamoorthy et al., 2017) to find the best-fitting partitioning and model scheme. Due to small partitions, we deliberately refrained from using the free-rate model approach in IQ-TREE (B. Q. Minh, personal communication), and also restricted the model search solely to those models supported by the Bayesian inference (BI) software package **BEAST** (Drummond et al., 2012) for both maximum likelihood (ML) and BI analyses. For ML tree reconstruction analyses, we used **IQ-TREE** v.1.6.10. Based on the detected partition-model scheme, we performed 100 independent tree searches with a random start tree and decreased perturbation strength (–pers 0.2). All analyses were run with edge-proportional partition models (–spp). Nodal support was assessed using 1000 ultrafast bootstrap replicates (UFBoot; Minh et al., 2013), with the ‘bnni’ option to reduce the risk of overestimating branch support (Hoang et al., 2018), and an increased maximum number of iterations to stop (–nm 10 000). Additionally, we also performed 1000 replicates of the Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-A-LRT, Guindon et al., 2010).

**Divergence time estimation**

Divergence times were estimated in a Bayesian Markov chain Monte Carlo (MCMC) framework, using the software **BEAST** v.1.10.2 (Lemeau et al., 2018). For all **BEAST** analyses we used the topology from the best ML tree obtained by **IQ-TREE** as starting tree and constrained the monophyly of all families, except Anthribidae, which was polyphyletic in the ML analyses. Instead we constrained the monophyly of Urodontinae and Anthribinae. Each analysis was run for 125 million generations (sampling every 10 000 generations). The number of generations discarded as burn-in was based on the examination of posterior distributions in **TRACER** v.1.7.1 (Rambaut et al., 2014). Post burn-in samples were combined across runs to summarize parameter estimates and used to generate a maximum clade credibility (MCC) tree with median node heights using **TREEANNOTATOR** v.1.10.2 (Lemeau et al., 2018).

To test the impact of different tree priors, clock model partitioning, fossil calibration schemes, and fossil calibration prior densities on the age estimations of Cryptorrhynchinae, we conducted eight independent MCMC analyses (Table 1). In a first setup (C0), we compared different tree models, i.e. diversification process priors, using either a Yule (pure-birth) tree prior (C01, C05) or a birth-death model (BD) prior (C02, C06). The partitioning scheme and models of nucleotide substitution were the same as for the ML analyses. For the clock model priors, we used the uncorrelated lognormal relaxed-clock (UCLN) model (Drummond et al., 2006). In the different analyses, the clock models were either linked (C01, C02) or unlinked (C05, C06) among the partitions. To test the fit of different parameter settings, we used Bayes factors (BFs), obtained by marginal likelihood estimations (MLEs) of all four analyses, using the path sampling (PS) and stepping-stone sampling (SS) methods in **BEAST** with default parameter settings (Baele et al., 2012). Using the resulting best model scheme, we ran additional analyses with the fossil calibration schemes described in the following.

To calibrate the relaxed clocks in **BEAST**, we followed the calibration schemes used in Shin et al. (2018). As our ML

| No. | Code | Clock | Tree | Fossils | Prior | PS          | BF          | SS          | BF          |
|-----|------|-------|------|--------|-------|-------------|-------------|-------------|-------------|
| 1   | C01  | UCLN1 | Yule | 2      | uni   | –335 444.44 | 2125.09     | –335 461.85 | 2069.93     |
| 2   | C02  | UCLN1 | BD   | 2      | uni   | –335 442.33 | 2120.88     | –335 455.94 | 2058.12     |
| 3   | C05a | UCLN13| Yule | 2      | uni   | –334 389.32 | 14.85       | –334 426.88 | –           |
| 4   | C06  | UCLN13| BD   | 2      | uni   | –334 381.89 | –           | –334 428.95 | 4.13        |
| 5   | C11  | UCLN13| BD   | 3a     | uni   | –334 429.98 | 96.17       | –334 459.70 | 65.62       |
| 6   | C15a | UCLN13| BD   | 3a     | exp   | –334 443.97 | 124.14      | –334 494.74 | 135.72      |
| 7   | C21  | UCLN13| BD   | 3b     | uni   | –334 468.74 | 173.69      | –334 506.36 | 158.95      |
| 8   | C23  | UCLN13| BD   | 3b     | exp   | –334 485.30 | 206.80      | –334 523.76 | 193.74      |

*Runs not converged. PS, path sampling; BF, Bayes factor; SS, stepping-stone sampling; BD, birth-death model.*
tree reconstruction results differ slightly from those of Shin et al. (2018), we only applied compatible fossil calibrations (Table 2). Similar to Shin et al. (2018), we tested the effect of two alternative fossils for Entiminae, using three different fossil-calibrating schemes: C0, no Entiminae fossil; C1, including the supposed oldest Entiminae fossil of the genus Dorotheus (Kuschel, 1959); C2, including a younger Entiminae fossil of the genus Polydrusus (Yunakov & Kirejtshuk, 2011). To consider a potential impact of the fossil calibration prior densities on the divergence dating analyses, we independently applied exponential and uniform calibration priors (Ho & Phillips, 2009). Uniform prior estimates were applied with a hard lower bound provided by the minimum age of particular fossil layer intervals (Table 2). The hard upper bound for the maximum age of Curculionoidea was provided by the age of oldest polyphagan beetle †Lechermania prorova (223 Ma; Chatzimanolis et al., 2012). For the maximum age of Curculionidae + Brentidae, Brentidae and Entiminae, the upper bound was provided by the proposed maximum age of Curculionidae (151 Ma; Oberprieler et al., 2014). Exponential prior estimates were applied with identical hard lower bounds defined by fossil layer intervals and an adapted soft upper bound, so that 95% of the distribution lay between the fossil age and 223 Ma.

### Biogeographical analyses

Biogeographical analyses were conducted using BIogeobears v.1.1.2 (Matzke, 2013) as implemented in the r v.3.5.3 statistical software (R Development Core Team, 2019). BIogeobears estimates ancestral ranges under different models; it uses the dispersal extinction cladogenesis (DEC) model (Ree & Smith, 2008), as well as likelihood interpretations of the dispersal-vicariance analysis (DIVA) model (Ronquist, 1997) and the BAYAREA model (Landis et al., 2013). It further implements a parameter describing founder-event speciation (+J), which allows cladogenetic events where one daughter lineage colonizes a new range via founder-event speciation, while the other retains the ancestral range. While this parameter has been shown to result in higher likelihood compared with models ignoring this parameter (Matzke, 2012, 2014), its use has recently been criticized (Ree & Sanmartín, 2018). Models incorporating +J have the tendency to underestimate anagenetic dispersal events at ancestral nodes in favour of ‘jump dispersal’, which can potentially distort the ancestral range reconstruction of ancient groups with a proposed widespread distribution, such as Cryptorhynchinae s.s., which are almost cosmopolitan. As the statistical comparison to models excluding founder-event speciation has also been suggested to be inaccurate, we refrained from implementing models including founder-event speciation in the present study. The Akaike information criterion corrected for small sample size was used to compare the fit of all models with the given data (Table 3). Ancestral range reconstructions were estimated using the MCC tree from the best BEAST analysis (see later). Prior to the analysis, all outgroups except Piazurus were removed to avoid an impact of more distant outgroups on the area reconstruction. The number of maximum areas per ancestral range was constrained to three. Studies focusing on ancestral area reconstruction methodology have shown that a larger maximum number of areas led to an overestimation of ancestral area sizes, neglecting the often limited vagility of the studied groups (Kodandaramaiah, 2009, 2010). Therefore, we selected the following seven regions for the BIogeobears analyses: (A) Palaearctic, (B) Nearctic, (C) Neotropical, (D) Oriental, (E) Australia, (F) (Proto-) New Guinea including Samoa, and (G) New Zealand and New Caledonia. We also generated three time slices to reflect tectonics throughout the Cenozoic following recent palaeogeographic works (Ezcura & Agnolín, 2012; Seton et al., 2012). Appendix S3 provides details on dispersal probabilities and area connections over time.

### Results and Discussion

#### Phylogenetic analyses

Results of the MLE runs of the eight different BI analyses are shown in Table 1. Based on BF comparisons between the analyses with two fossil calibrations (C01, C02, C05 and C06), unlinked clock models represented a better fit (C05 and C06). Among the latter, the MLE comparisons were equivocal, as PS

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**Table 2.** Fossils used for calibration

| No. | Node Fossil taxon | Formation/stria | Minimum age (Ma) | Reference documenting fossil |
|-----|-------------------|-----------------|------------------|-----------------------------|
| 1   | Curculionoidea (crown) | Archaeorhynchus and Eobulus | Kazakhstan, Karabastau Formation | 151.0 | Arnoldi (1977) |
| 2   | Curculionidae (stem) | Araripenerthus monnei | Brazil, Crato Formation | 113.0 | Santos et al. (2011) |
| 3   | Brentidae (crown) | Orapaecus cretaceus | Botswana, Orapa Kimberlite | 87.4 | Kuschel (1994) |
| 4   | Entiminae (stem) | Polydrusus | Europe, Baltic amber | 37.8 | Yunakov & Kirejtshuk (2011) |
| 4a  | Entiminae (stem) | Dorotheus guidensis | Chile, Dorotea Formation | 66.0 | Kuschel (1959) |

**Table 3.** Results of the BIogeobears analyses

| Model | LnL | No. | d | e | j | AICc | AICw |
|-------|-----|-----|---|---|---|------|------|
| DEC   | -434.3 | 2   | 0.01 | 0.01 | 0 | 872.7 | 1.00 |
| DIVALIKE | -443.8 | 2   | 0.01 | 0.01 | 0 | 891.7 | 0.00 |
| BAYAREALIKE | -457.5 | 2   | 0.01 | 0.01 | 0 | 919.1 | 0.00 |

AICc, bias corrected Akaike’s information criterion; AICw, Akaike weight; DEC, Dispersal-Extinction-Cladogenesis; d, rate of dispersal; e, rate of extinction; j, relative probability of founder-event speciation at cladogenesis.
and SS sampling methods indicate different best model schemes. SS suggested the analysis with a Yule tree model (C05) as the best (BF = 4.13), whereas PS favoured a BD tree model (C06; BF = 14.85). However, as the effective sample size of log likelihood and other parameters of the C05 analysis did not converge after 125 million generations, we relied on BD tree models in all further analyses with additional fossil calibration points (C11, C13, C21 and C21). However, the analysis with two fossils (C06; shown in Fig. 1) generally shows a better marginal likelihood value than the models with additional calibration points. In the following, we discuss the results of all eight BI runs, as well as the best ML tree reconstruction results.

Nodal supports from UFBoot and SH-aLRT of the best ML analysis, as well as posterior probability (PP) values of the best BI analysis (C06) are provided in the text for the discussed relationships. All tree reconstruction analyses results are provided in Appendix S2.

Both BI and ML tree reconstructions show some differences in higher-level weevil relationships, mainly due to the inconsistent position of Car (Caridae) and Urodontinae, whose relationship generally lacks strong nodal support. In the ML analyses, as well as the BI analyses based on linked clock models (C01, C02) and one BI analysis based on unlinked clock models (C23), Anthribidae appeared polyphyletic as Anthribinae are recovered sister to Nemonychidae (ML: SH-aLRT = 94.4, UFBoot = 50), and Urodontinae are recovered sister to a clade comprising the remaining families (ML: SH-aLRT = 96.7, UFBoot = 43), except for Car as the single representative of the family Caridae, which appeared as the first branch in the tree (ML: SH-aLRT = 8.7, UFBoot = 61). By contrast, most analyses based on unlinked clock and BD tree models (C05, C06, C11, C13, C21) recovered Anthribidae (Anthribinae + Urodontinae) as monophyletic (C06, BI: PP = 0.99) and Caridae as sister to the clade Brentidae + Curculionidae (C06, BI: PP = 0.76). The position of Caridae as sister group to the clade Brentidae + Curculionidae in the BI analyses with unlinked clock models, supports its recognition as a distinct family and is consistent with phylogenetic studies based on adult and larval characters (Morrone & Marvaldi, 2000; Marvaldi et al., 2002), as well as recent large-scale molecular analyses (McKenna et al., 2009; Haran et al., 2018). The inconsistent position of Urodontinae among the analyses generally reflects the uncertainty of their phylogenetic placement. The placement of Urodontinae as sister to Anthribinae in most BI analyses corroborates their inclusion into Anthribidae, as proposed by Kuschel (1995) and further recovered by the phylogenomic study of Shin et al. (2018), as well as by a molecular analysis of Australian weevils (Gunter et al., 2016). By contrast, the isolated position of Urodontinae in the ML analyses and their relationship to Attelabidae, or Attelabidae + Belidae in the remaining BI analyses, corroborate Crowson (1984) and Thompson (1992), which placed Urodontinae as a family separate from Anthribidae.

A sister-group relationship of Attelabidae and Belidae was recovered in the ML and in all BI analyses based on unlinked clock models and usually had significant support (ML: SH-aLRT = 95.7, UFBoot = 70; C06, BI: PP = 0.97). However, this relationship generally contrasts with most previous morphological and molecular studies to date and was only recovered in one of several analyses by Shin et al. (2018). However, this study only included the subfamily Oxyocoryrinae (Belidae), and the support for Attelabidae and Belidae was low. The sister-group relationship of Brentidae and Curculionidae, recovered in all analyses, is consistent with recent large-scale molecular studies (McKenna et al., 2009; Haran et al., 2013; Gillett et al., 2014; Gunter et al., 2016; Shin et al., 2018) and studies based on morphological data (Morrone & Marvaldi, 2000; Marvaldi et al., 2002). Within the true weevils (Curculionidae), the patterns among the early diverging clades are also generally consistent with most previous molecular studies, showing Brachycerinae (represented by Ocladius) as sister to the remaining weevils (ML: SH-aLRT = 94.9, UFBoot = 78; C06, BI: PP = 0.96), and a close relationship of the subfamilies Dryophthorinae, Bagoineae (Bagous) and Platypodinae; thus supporting an early monocot association of the true weevils (see Marvaldi et al., 2002; Oberprieler et al., 2007). The position of Bagous is generally ambiguous; it is inferred either as sister to Platypodinae (C01, C05, C11), to Platypodinae + Dryophthorinae (C02, C13, C21, C23) or as sister to higher Curculionidae, i.e. Entiminae, Hyperinae, Molytinae, Scoylotrinae, Curculioninae, Conoderinae and Cryptorhynchinae s.l. (C06, BI: PP = 0.22). In the ML analyses, it is recovered adelphic to Lyterius (Belidae), but with low nodal support (ML: SH-aLRT = 48.9, UFBoot = 37). This variable position of Bagous further reflects the inconsistent status of this genus as a member of Brachycerinae (Oberprieler et al., 2007; Gunter et al., 2016), as isolated sister group to ‘higher’ Curculionidae (Gillett et al., 2014; Shin et al., 2018), or nested within a clade of Dryophthorinae and Platypodinae (McKenna et al., 2009).

A well-supported sister-group relationship between Entiminae and Hyperinae (single representative of Hyperinae) is further recovered (ML: SH-aLRT = 99.5, UFBoot = 100; C06, BI: PP = 1.00) as sister to the remaining assemblage of Curculioninae, Molytinae, Conoderinae and Cryptorhynchinae s.l. (ML: SH-aLRT = 99.8, UFBoot = 100; C06, BI: PP = 0.95), thus supporting the ‘CEGH-clade’ (Cyclominae, Entiminae, Gonipterini, and Hyperini), as defined by Gunter et al. (2016). The genus Alcidodes, found nested within Cryptorhynchinae in the BI analysis of Riedel et al. (2016) is now placed in Curculioninae + Molytinae. The ML analysis shows Alcidodes as sister to Chalcoderus (ML: SH-aLRT = 78, UFBoot = 81), whereas the BI analyses suggest a weakly supported sister-group relationship with Cleoninae (C06, BI: PP = 0.49).

Cryptorhynchinae s.s. were recovered as monophyletic in all ML and BI analyses but only with moderate support (ML: SH-aLRT = 84.7, UFBoot = 82). By contrast, the Conoderinae s.s. appeared polyphyletic with the genus Piazurus as sister of all Cryptorhynchinae s.s. (ML: SH-aLRT = 96.1, UFBoot = 61). The sister-group relationship of Cryptorhynchinae s.s. and Piazurus, as the only representative of the diverse and Neotropical Piazurini, is an interesting finding and should be tested in future analyses by including additional species of Neotropical Conoderinae. Within Cryptorhynchinae s.s., the major clades retrieved are largely consistent with the analyses of Riedel et al. (2016). However, the positions of these clades are not consistent.
**Fig. 1.** Phylogeny of Curculionoidea, focused on Cryptorrhynchinae s.s. Results of the best Bayesian inference analysis (C06) in BEAST, implementing uniform calibration priors, unlinked clock models and a birth-death (BD) tree model. Pie charts represent the relative node support, as measured by the posterior probability (PP). Red branches indicate members of the polyphyletic tribe Psepholacini.

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Fig. 1. Continued.
among the different ML and BI analyses, and nodal support for their relationships is generally low. The ‘Acalles’ group was moderately supported (ML: SH-αLRT = 69.3, UFBoot = 36), whereas the ‘Cryptorhynchus’ group was recovered with maximum nodal support (ML: SH-αLRT = 100, UFBoot = 100). The ‘Indo-Australian clade’ (ML: SH-αLRT = 100, UFBoot = 99) was nested within lineages of American and Palaearctic distribution. Within this group, a monophyletic Arachnopodini s.l. (ML: SH-αLRT = 100, UFBoot = 100), including the genus Arachnophas (Arachnopodini s.s., ML: SH-αLRT = 99.2, UFBoot = 100), the ‘Rhynchodes group’ (ML: SH-αLRT = 100, UFBoot = 100), as well as the ‘New Zealand clade’ (ML:
Divergence times and historical biogeography of Cryptorhynchinae

Differences in the divergence time estimates between the eight analyses were only marginal, with largely overlapping credibility intervals (Table 4). According to the analysis with the best marginal likelihood (C06), the origin of Cryptorhynchinae s.s. was in the late Cretaceous c. 85.7 Ma [95% highest posterior density (HPD): 79.41–96.45]. The Cryptorhynchus group, which is mainly distributed in the Neotropics, also appeared in the late Cretaceous c. 76.5 (95% HPD: 67.11–84.86), as well as the Indo-Australian clade c. 72.2 Ma (95% HPD: 65.10–80.59). The New Zealand clade appeared in the Palaeocene c. 57.8 Ma (95% HPD: 50.60–64.75). Other relevant groups emerged in the Early Eocene. Arachnopodini s.l., whose distribution is mostly in the Indo-Australian region, has an origin c. 49.2 Ma (95% HPD: 43.34–55.30), and the exclusively New Guinean genus Arachnopus appeared c. 38.2 Ma (95% HPD: 31.35–43.52). The genus Trigonopterus appeared at c. 53 Ma (95% HPD: 45.71–59.92) and the ‘Rhyynchodes group’ at c. 52.3 Ma (95% HPD: 45.43–58.54). The emergence of Curculioidea in the Late Jurassic c. 159 Ma (95% HPD: 151.0–172.17) is consistent with earlier studies on beetle or weevil divergence time estimations (Hunt et al., 2007; McKenna et al., 2009; Gunter et al., 2016; Zhang et al., 2018). However, this age is considerably younger than in the phylogenomic study of Shin et al. (2018) and also younger than in Toussaint et al. (2017b), which focused on higher-level relationships within beetles. Attelabidae and Belidae c. 135 Ma (95% HPD: 119.32–151.34), as well as Brentidae and Curculionidae c. 136 Ma (95% HPD: 125.65–149.42), all emerged in the Early Cretaceous. The appearance of these groups is congruent to most other studies (McKenna et al., 2009; Gunter et al., 2016; Zhang et al., 2018), but Shin et al. (2018) show an earlier emergence of Belidae.
and Attelabidae. The inferred pattern further supports the contemporary radiation of flowering plants, which probably diversified in the Jurassic and Early Cretaceous (e.g. Magallón et al., 2015; Sauquet et al., 2017), and major weevil groups. The evolutionary success of weevils in relation to the radiation of angiosperms has frequently been proposed (Farrell et al., 1998; Marvaldi et al., 2002; McKenna et al., 2009), but is still under debate. To test the impact of different factors that may have shaped the diversification of weevils, such as insect–plant associations, the focus of shallower phylogenetic levels (e.g. subfamilies) has been proposed (Franz & Engel, 2010). There is an ongoing process of establishing such a ‘mid-level classification’ (Gunter et al., 2016) in weevil phylogenetics (e.g. Winter et al., 2017; Letsch et al., 2018), and our present study provides a first dataset for the inference of evolutionary scenarios in Cryptorhynchinae.

Among the different analyses performed in BIOGEOBEARS, the DEC model was significantly preferred over the DIVALIKE and BAYAREA models (Akaike weight = 1; shown in Fig. 2). The ancestral range estimated by the DEC model for Cryptorhynchinae s.s. was South America (C = 0.62, CE = 0.16, CF = 0.21). The initial radiation within Cryptorhynchinae s.s. was characterized by a further diversification of the ‘Cryptorhynchus group’ and its relatives in South America (C = 0.99). Within the ‘Cryptorhynchus group’ several species independently colonized North America, Eurasia and the Australian region in the Eocene. A similar pattern was recovered for members of the originally Neotropical ‘Acalles group’ and its relatives (C = 0.86), which also colonized the Western Holarctic even earlier in the Late Cretaceous. A colonization of the Palaeartic from South America was also found, for instance, by Toussaint et al. (2017a) for Hydrophilus water scavenger beetles and can be explained by either long-distance dispersal or range expansion via the Nearctic followed by regional extinction. The occurrence of North American representatives in both groups supports the latter scenario. For the subsequent radiation of Cryptorhynchinae s.s., a range expansion to Australia and Proto-New Guinea was estimated (clade A: C = 0.28, CE = 0.31, CF = 0.40; clade B: CE = 0.41, CF = 0.53) between 73 and 91 Ma, and the origin of the Indo-Australian clade was recovered in Australia and/or Proto-New Guinea (clade C: E = 0.26, F = 0.38, EF = 0.35) at c. 73 Ma, indicating a continental range expansion via dispersal from South America possibly through Antarctica in the Late Cretaceous. This scenario is consistent with a proposed connection between South America and Australia via a land bridge through Antarctica until c. 60 Ma (Scotese, 2004; Seton et al., 2012). This pattern has recently been suggested for several beetle clades using a combination of Bayesian relaxed-clock dating and parametric historical biogeography. For instance, Kim & Farrell (2015) proposed a hypothesis in which Chiasognathini stag beetles expanded their range towards Antarctica in the Cretaceous. Gustafson & Miller (2017) suggested the colonization of Antarctica by Macrogryrus whirliigig beetles in the Palaeocene. A similar pattern was suggested for Platynectes diving beetles in the Eocene (Toussaint et al., 2017b), and for Hydrobiusini and Ooecylus water scavenger beetles in the Cretaceous (Toussaint & Short, 2017, 2018). This pattern therefore seems to be much more common than previously thought and is supported by recent palaeoclimatic evidence. Antarctica had a much warmer climate during most the Cenozoic due to its connection with other components of the Gondwana supercontinent. As a result, Cenozoic favourable landscapes existed in Antarctica with dense forests (subtropical at times) that could have hosted a diverse fauna before the setup of a polar climate on this land mass (Poole & Cantrill, 2006; Francis et al., 2008). Glaciations only initiated after Australia started rifting away in the Oligocene and triggered ecosystem turnover in Antarctica (Galeotti et al., 2016; McKay et al., 2016). With Australia’s position between Antarctica and Proto-New Guinea, a colonization of Australia prior to Proto-New Guinea is plausible. The subsequent early radiation of the Indo-Australian clade in Australia corroborates this hypothesis. However, the occurrence of one Chilean species deeply nested in the ‘Indo-Australian clade’ indicates that this clade may in fact have evolved in a more widespread Gondwanan range, including South America, possibly in the southern temperate environment of Nothofagus forests. An equally plausible explanation could be a recolonization of southern South America: the case of Strongylopterus distributed in both New Zealand and Chile underlines the potential of dispersal of wood-inhabiting weevils in the subantarctic region, possibly by sea currents. A denser taxon sampling in southern Australia, New Zealand and Chile should be attempted in the future.

Within the ‘Indo-Australian clade’, subsequent dispersal events to Proto-New Guinea took place three times independently at around the same time, i.e. c. 50–55 Ma, by Arachnophodini s.l., the crown group of Trigonopterus (excluding the T. squamosus group), and the ‘Rhynchodes group’. This timing is much earlier than expected and contrasts with geological reconstructions that anticipate the first major land areas not to have emerged before 35 Ma (‘peninsular orogeny’; Ufford & Cloos, 2005) or 20 Ma (formation of the northern arc of New Guinea; Hall, 2009), although the first volcanic arcs in the area appeared as early as 60 Ma (Hall, 2009) and the Papuan Ultramafic Belt ophiolite has an age of c. 58 Ma (Baldwin et al., 2012). These latter dates are in line with our current reconstruction and indicate that New Guinea may have acted as a museum of diversity in addition to being a cradle as suggested by recent evolutionary studies focusing on the island fauna (e.g. Umack et al., 2013; Georges et al., 2014; Toussaint et al., 2014; Janda et al., 2016; Oliver et al., 2017; Lam et al., 2018; Tallowin et al., 2018). Our study brings more evidence to the potential role of New Guinea as an older land mass that may have hosted the early stages of several island clades. For instance, a time-calibrated phylogeny of netting beetles endemic to New Guinea (Bocek & Bocak, 2019) recovers a similar age (51 Ma). The origin of corvoid birds from New Guinea is dated from the Eocene c. 45 Ma (Jønsson et al., 2011; Aggerbeck et al., 2014). New Guinean endemic mayflies also possibly have originated as early as the Eocene on the island (Cozzarolo et al., 2019). These results suggest that substantial areas may have been subaerial in Proto-New Guinea much earlier than hitherto expected. The age of the Palaeocene ‘New Zealand clade’ conflicts with the hypothesis of Oligocene marine transgression of New Zealand.
Fig. 2. Estimation of the historical biogeography for Cryptorhynchinae s.s. using a dispersal–extinction–cladogenesis model in Biogeobears. The coloured boxes represent the seven areas implemented in the palaeogeographical model, as well as the six most important ranges discussed in the text. Pie charts at the nodes of the tree represent the relative probabilities of the ancestral areas. The map represents the historical southern dispersal route from South America to Australia, New Guinea and New Zealand.
some 25–23 Ma (Waters & Craw, 2006), which is in line with the multiltaxon analysis of Wallis & Jorge (2018).

Conclusion

We reconstructed the biogeographical history of Cryptorrhynchinae, with an origin in the Neotropical region during the Cretaceous. Two distinct colonization routes are proposed: a northern route, which led to at least two independent dispersals to both North America and Eurasia, and a southern route, which possibly facilitated the colonization of Australia, New Guinea and New Zealand via Antarctica in the Late Cretaceous. Within the Indo-Australian clade, the reconstructed lengths and divergence times of the early branches are conspicuously short, and many nodes are only moderately supported, leading to incongruent relationship hypotheses between the distinct analyses. This pattern further indicates a rapid radiation of the ‘Indo-Australian clade’ after its arrival in Australia. Cryptorrhynchinae constitute c. 30% of the Australian weevil fauna (Pullen et al., 2014) and further comprise the majority of Australian weevils using dead wood as a food resource. This may indicate that the stage was set for their rapid radiation once they reached the Australian continent. However, ‘ancient rapid radiations’ phenomena have been proposed to substantially impede phylogenetic reconstructions (Whittfield & Lockhart, 2007; Whitfield & Kjer, 2008). Together with the still highly incomplete taxon sampling of the Indo-Australian fauna (Riedel et al., 2013; Pullen et al., 2014; Riedel & Tänzler, 2016), scenarios about the evolution of ecological and/or morphological traits, which might have facilitated their radiation, remain uncertain (Franz & Engel, 2010; Gunter et al., 2016). We therefore propose to focus on lower taxonomical levels that allow a denser taxon sampling and thus more precise inferences of diversification pattern. Previous studies on the evolution of the Indo-Australian genus Trigonopterus could already reconstruct several radiations of these weevils in the geologically complex Indo-Australian archipelago. They generally place the colonization of New Guinea, Indonesia and New Caledonia in the Late Miocene (Tänzler et al., 2016, 2016; Toussaint et al., 2017c. However, these studies did not infer the divergence times of Trigonopterus in a taxonomically larger context and could not therefore implement calibration fossils. The proposed age of Trigonopterus (c. 54 Ma) recovered in the present study, however, indicates a much older diversification of this genus. With this age estimation at hand, and in combination with the ongoing taxonomic research (Riedel et al., 2013, 2014; Riedel & Narakusumo, 2019), future studies on the evolution of the genus Trigonopterus could help to elucidate the Cenozoic history of Cryptorrhynchinae weevil diversification in the Indo-Australian regions.

Supporting Information

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

Appendix S1. List of specimens, markers, and GenBank accession numbers.

Appendix S2. Details on the dispersal rate scaler and adjacency matrices applied in BIogeobears.

Appendix S3. Results of the eight Bayesian Inference (BI) runs in BEAST, as well as the best tree of 100 IQ-TREE analyses.

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References

Aggerbeck, M., Fjeldså, J., Christidis, L., Fabre, P.-H. & Jønsson, K.A. (2014) Resolving deep lineage divergences in core corvoid passerine birds supports a proto-Papuan Island origin. Molecular Phylogenetics and Evolution, 70, 272–285.
Arnold, L.V. (1977) Rhynchophora and family Eobelidae [pp. 142–175]. Mezozoyskie Zhestkokrylye. Trudy Paleonticheskogo Instituta Akademii Nauk SSSR, 161, 1–204.
Astrin, J.J. & Stüben, P.E. (2008) Phylogeny in cryptic weevils: molecules, morphology and new genera of western Palaearctic Cryptorrhynchinae (Coleoptera: Curculionidae). Invertebrate Systematics, 22, 503–522.
Astrin, J.J., Stüben, P.E., Misof, B., Wägele, J.W., Gimmich, F., Rau-pach, M.J. & Ahrens, D. (2012) Exploring diversity in cryptorrhynchine weevils (Coleoptera) using distance-, character- and tree-based species delineation. Molecular Phylogenetics and Evolution, 63, 1–14.
Baele, G., Li, W.L.S., Drummond, A.J., Suchard, M.A. & Lemey, P. (2012) Accurate model selection of relaxed molecular clocks in Bayesian phylogenetics. Molecular Biology and Evolution, 30, 239–243.
Gillett, C.P., Crampton-Platt, A., Timmermans, M.J., Jordal, B., Emer-
Crowson, R.A. (1984) On the systematic position of
etal.
Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Bordyj,
& Gascuel, O. (2010) New algorithms and methods to esti-
mate maximum-likelihood phylogenies: assessing the performance of
PhyML 3.0. Systematic Biology, 59, 307–321.

Baldwin, S.L., FitzGerald, P.G. & Webb, L.E. (2012) Tectonics of the
New Guinea region. Annual Review of Earth and Planetary Sciences, 40, 495–520.

Bocek, M. & Bocak, L. (2019) The origins and dispersal history of the
trichaline net-winged beetles in Southeast Asia, Wallacea, New
Guinea and Australia. Zoological Journal of the Linnean Society, 185,
1079–1094.

Chatzimanolis, S., Grimaldi, D.A., Engel, M.S. & Fraser, N.C. (2012)
Chernomor, O., von Haeseler, A. & Minh, B.Q. (2016) Terrace aware
Cozzarolo, C.-S., Balke, M., Buerki, S.
Franz, N.M. & Engel, M.S. (2010) Can higher-level phylogenies
Explain from pooled total DNA elucidates the phylogeny of weevils
(Coleoptera: Curculionoidea) and establish the monophyly of larval ecophagy. Molecularphylogenetics and Evolution, 67, 156–166.

Ho, S.Y.W. & Phillips, M.J. (2009) Accounting for calibration uncertain-
ty in phylogenetic estimation of evolutionary divergence times. Systematic Biology, 58, 367–380.

Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2018) UFBoot2: improving the ultrafast bootstrap approximation. Molecular Biology and Evolution, 35, 518–522.

Hunt, T., Bergsten, J., Levkanicova, Z. et al. (2007) A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. Science, 318, 1913–1916.

Janda, M., Matos-Maraví, P., Borovanska, M., Jan, Z., Youngerman, E. & Pierce, N.E. (2016) Phylogeny and population genetic structure of the ant genus Acrotylus (Hymenoptera : Formicidae) in Papua New Guinea. Invertebrate Systematics, 30, 28–40.

Jønsson, K.A., Fabre, P.-H., Ricklefs, R.E. & Fjeldså, J. (2011) Major global radiation of corvid birds originated in the proto-Papuan archipelago. Proceedings of the National Academy of Sciences, 108, 2328–2333.

Jordal, B.H. (2015) Molecular phylogeny and biogeography of the weevil subfamily Platyptinae reveals evolutionarily conserved range patterns. Molecular Phylogenetics and Evolution, 92, 294–307.

Jordal, B.H., Sequeira, A.S. & Cognato, A.I. (2011) The age and phylogeny of wood boring weevils and the origin of subsociality. Molecular Phylogenetics and Evolution, 59, 708–724.

Kalyaanamoorthi, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A. & Jerumiin, L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods, 14, 587–589.

van de Kamp, T., dos Santos Rolo, T., Vagović, P., Baumbach, T. & Riedel, A. (2014) Three-dimensional reconstructions come to life – interactive 3D pdf animations in functional morphology. PLOS ONE, 9, e102355.

Katoh, K., Udagawa, J. & Yamada, K.D. (2017) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics, 20, 1160–1166.

Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence align-
ment software version 7: improvements in performance and usability. Molecular Biology and Evolution, 30, 772–780.

Kim, S.I. & Farrell, B.D. (2015) Phylogeny of world stag beetles (Coleoptera: Lucanidae) reveals a Gondwanan origin of Darwin’s stag beetle. Molecular Phylogenetics and Evolution, 86, 35–48.

Kodandaramaiah, U. (2009) Vagility: the neglected component in historical biogeography. Evolutionary Biology, 36, 327–335.

Kodandaramaiah, U. (2010) Use of dispersal–vicariance analysis in biogeography – a critique. Journal of Biogeography, 37, 3–11.

Kück, P. & Meusemann, K. (2010) FASconCAT: convenient han-
dling of data matrices. Molecular Phylogenetics and Evolution, 56, 1115–1118.

Kuschel, G. (1959) Un Curculionido del cretácio superior, primer insecto fósil de Chile. Investigaciones Zoológicas Chilenas, 5, 49–54.

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Kuschel, G. (1994) Nemonychidae of Australia, New Guinea and New Caledonia. Zimmerman EC Australian weevils (Coleoptera: Curculionoidea), 1, 563–637.

Kuschel, G. (1995) A phylogenetic classification of Curculionoidea to families and subfamilies. Memoirs of the Entomological Society of Washington, 14, 5–33.

Lam, A., Toussaint, E.F.A., Kindler, C., Dam, M.H.V., Panjaitan, R., Roderick, G.K. & Balke, M. (2018) Stream flow alone does not predict population structure of diving beetles across complex tropical landscapes. Molecular Ecology, 27, 3541–3554.

Landis, M.J., Matzke, N.J., Moore, B.R. & Huaelsenbeck, J.P. (2013) Bayesian analysis of biogeography when the number of areas is large. Systematic Biology, 62, 789–804.

Legalov, A.A. (2012) Fossil history of Mesozoic weevils (Coleoptera: Curculionoidea). Insect Science, 19, 683–698.

Legalov, A.A. (2014a) The oldest Brentidae and Curculionidae (Coleoptera: Curculionoidea) from the Turonian of Kzyl-Dzhar (Kazakhstan). Historical Biology, 26, 6–15.

Legalov, A.A. (2014b) New Nemonychidae, Brentidae and Curculionidae (Coleoptera: Curculionoidea) from the Aptian of Bon-Tsagau. Historical Biology, 26, 6–15.

Lyal, C.H.C. (1993) Coleoptera: Cryptorhynchinae. Fauna of New Zealand, 29, 1–308.

Lyal, C.H.C. (2014) 3.7. 7 Molytinae Schoenherr, 1823. Coleoptera: Cryptorhynchinae. Tylodina) of Chiapas, Mexico. Zootaxa, 3788, 1–63.

Magallón, S., Gómez-Acevedo, S., Sánchez-Reyes, L.L. & Hernández-Hernández, T. (2015) A taxonomically monograph of the genus Tylodinus Champion (Coleoptera: Curculionidae: Cryptorhynchinae: Tylodina) of Chiapas, Mexico. Zootaxa, 3788, 1–63.

Marvaldi, A.E., Sequeira, A.S., O’Brien, C.W. & Farrell, B.D. (2002) Molecular and morphological phylogenetics of weevils (Coleoptera, Curculionoida): do niche shifts accompany diversification? Systematic Biology, 51, 761–785.

Matzke, N.J. (2012) Founder-event speciation in BioGeoBEARS package dramatically improves likelihoods and alters parameter inference in Dispersal-Extinction-Cladogenesis (DEC) analyses. Frontiers of Biogeography, 4(suppl 1), 210.

Matzke, N.J. (2013) Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. Frontiers of Biogeography, 5, 4.

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

McKenna, D.D., Sequeira, A.S., Marvaldi, A.E. & Farrell, B.D. (2009) Temporal lags and overlap in the diversification of weevils and flowering plants. Proceedings of the National Academy of Sciences, 106, 7083–7088.

Minh, B.Q., Nguyen, M.A.T. & Haeseler, v.a. (2013) Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution, 30, 1188–1195.

Misof, B. & Misof, K. (2009) A Monte Carlo approach successfully identifies randomness in multiple sequence alignments: a more objective means of data exclusion. Systematic Biology, 58, 21–34.

Morlon, H. (2014) Phylogenetic approaches for studying diversification. Ecology Letters, 17, 508–525.

Ng, J. & Smith, S.D. (2014) How traits shape trees: new approaches for detecting character state-dependent lineage diversification. Journal of Evolutionary Biology, 27, 2035–2045.

Poole, I. & Cantrill, D. (2006) Cretaceous and Cenozoic vegetation of Antarctica integrating the fossil wood record. Geological Society, London, Special Publications, 258, 63–81.

Pullen, K.R., Jennings, D. & Oberprieler, R.G. (2014) Annotated catalogue of Australian weevils (Coleoptera: Curculionoidea). Zootaxa, 3896, 1–481.

Paulay, G. (1985) Adaptive radiation on an isolated oceanic Island: the Cryptorhynchinae (Curculionidae) of Rapa revisited. Biological Journal of the Linnean Society, 26, 95–187.

Riedel, A. & Narakusumo, R.P. (2019) One hundred and three new records: ANDRILL and beyond. Geological Society, London, Special Publications, 457, 285–300.

Riedel, A., Daawia, D. & Balke, M. (2010) Deep cox1 divergence and temporal lags and overlap in the diversification of weevils (Coleoptera, Curculionoidea): a reappraisal based on larval and adult morphology. Insect Systematics & Evolution, 31, 43–58.

Riedel, A. (2017) The weevil genera Nyphaeba Pascoe and Pantia Pascoe and the problems of an unstable nomenclature in orphaned taxa. Zootaxa, 4244, 377–389.

Riedel, A., Daawia, D. & Balke, M. (2010) Deep cox1 divergence and hyperdiversity of Trigonopterus weevils in a New Guinea mountain range (Coleoptera, Curculionidae). Zoologica Scripta, 39, 63–74.

Riedel, A. & Narakusumo, R.P. (2019) One hundred and three new species of Trigonopterus weevils from Sulawesi. ZooKeys, 828, 1–153. https://doi.org/10.3897/zookeys.828.32200.

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