

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 Palaeocene (*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

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most species-rich families on Earth (Grebennikov & 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). *Arachnobas* 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 Ithyporini (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. Cimberididae (two species), Nemomychidae (two species), Anthribidae (seven species), Attelabidae (six species), Belidae (seven species), Caridae (one species), and Brentidae (16 species) and important subfamilies of Curculionidae, e.g. Bagoinae (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 (EF1 α) 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 FASCONCAT 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 MODELFINDER as implemented in IQ-TREE v.1.6.10 (Nguyen *et al.*, 2015; Chernomor *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 ($-\text{pers}$ 0.2). All analyses were run with edge-proportional partition models ($-\text{spp}$). 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

($-\text{nm}$ 10 000). Additionally, we also performed 1000 replicates of the Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-aLRT, 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 (Lemey *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 (Lemey *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 Cryptorhynchinae, 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

Table 1. Results of BEAST model tests

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	C05 ^a	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	C13 ^a	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

^aRuns not converged. PS, path sampling; BF, Bayes factor; SS, stepping-stone sampling; BD, birth-death model.

Table 2. Fossils used for calibration

No.	Node	Fossil taxon	Formation/strata	Minimum age (Ma)	Reference documenting fossil
1	Curculionoidea (crown)	<i>Archaeorrhynchus and Eobelus</i>	Kazakhstan, Karabastau Formation	151.0	Arnoldi (1977)
2	Curculionidae (stem)	<i>Arariperhinus monnei</i>	Brazil, Crato Formation	113.0	Santos <i>et al.</i> (2011)
3	Brentidae (crown)	<i>Orapaeus cretaceus</i>	Botswana, Orapa Kimberlite	87.4	Kuschel (1994)
4	Entiminae (stem)	<i>Polydrusus</i>	Europe, Baltic amber	37.8	Yunakov & Kirejtshuk (2011)
4a	Entiminae (stem)	<i>Dorotheus guidensis</i>	Chile, Dorothea Formation	66.0	Kuschel (1959)

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 †*Leehermania 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

Table 3. Results of the BIOGEOBEARS analyses

Model	Ln L	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.

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) Palearctic, (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 (Ezcurra & 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

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 lack 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; Shin *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 Urodontidae 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 Oxycoryninae (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, Bagoinae (*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, Scolytinae, Curculioninae, Conoderinae and Cryptorhynchinae s.l. (C06, BI: PP = 0.22). In the ML analyses, it is recovered adelphic to *Lyterius* (Baridinae), 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 *Hypera* (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 *Chalcodermus* (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

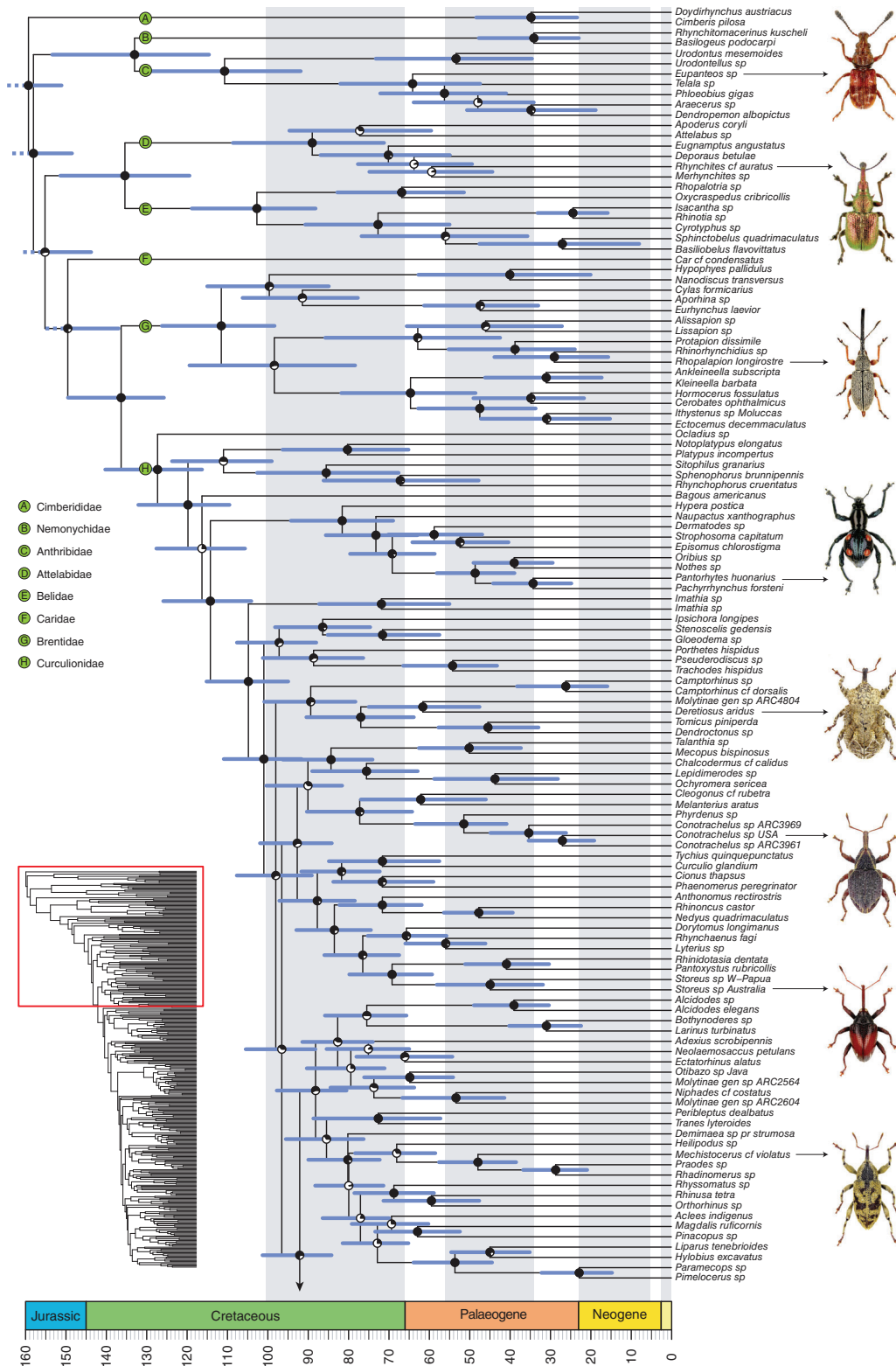


Fig. 1. Phylogeny of Curculionoidea, focused on Cryptorhynchinae s.s. Results of the best Bayesian inference analysis (C06) in BEAST, implementing uniform calibration priors, unlinked clock models and a birth-death (BD) tree model. Pie charts represent the relative node support, as measured by the posterior probability (PP). Red branches indicate members of the polyphyletic tribe Psepholacini. [Colour figure can be viewed at wileyonlinelibrary.com].

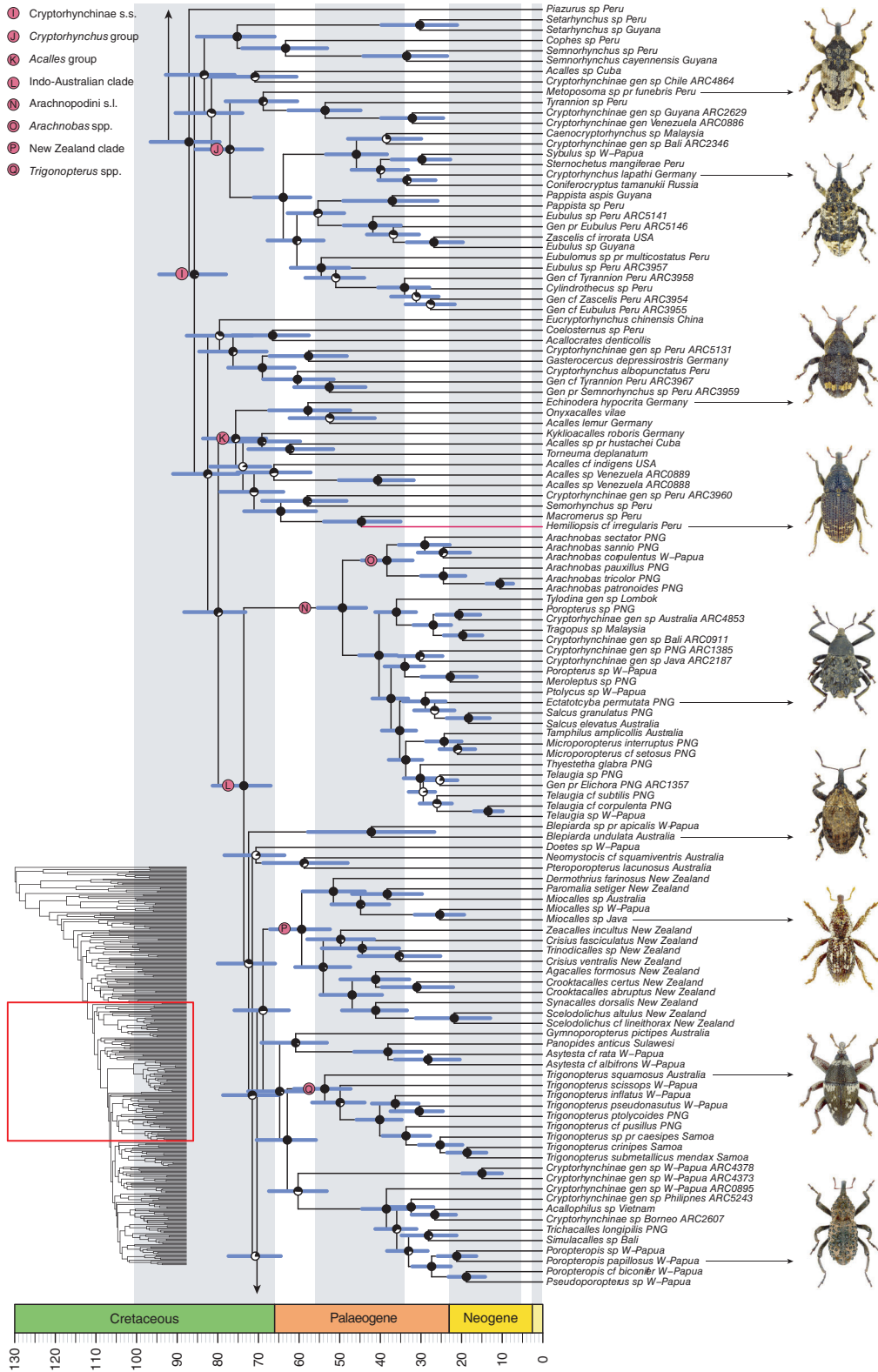


Fig. 1. Continued. [Colour figure can be viewed at wileyonlinelibrary.com].

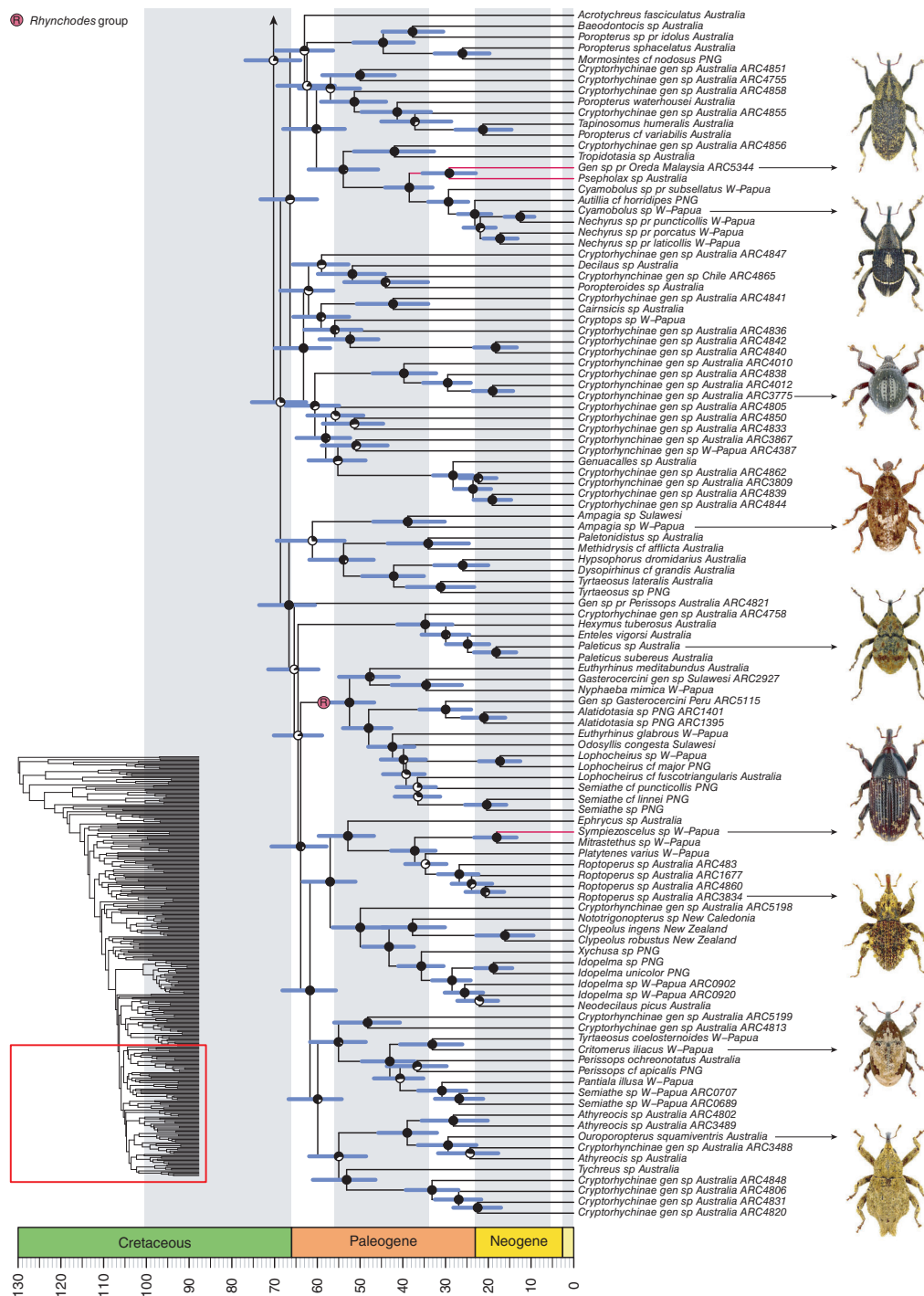


Fig. 1. Continued. [Colour figure can be viewed at wileyonlinelibrary.com].

among the different ML and BI analyses, and nodal support for their relationships is generally low. The ‘*Acalles* group’ was moderately supported (ML: SH-aLRT = 69.3, UFBoot = 36), whereas the ‘*Cryptorhynchus* group’ was recovered with maximum nodal support (ML: SH-aLRT = 100, UFBoot = 100). The ‘Indo-Australian clade’ (ML: SH-aLRT = 100, UFBoot = 99)

was nested within lineages of American and Palearctic distribution. Within this group, a monophyletic Arachnopodini s.l. (ML: SH-aLRT = 100, UFBoot = 100), including the genus *Arachnobas* (Arachnopodini s.s., ML: SH-aLRT = 99.2, UFBoot = 100), the ‘*Rhynchodes* group’ (ML: SH-aLRT = 100, UFBoot = 100), as well as the ‘New Zealand clade’ (ML:

SH-aLRT = 99.3, UFBoot = 95) and the nine species of *Trigonopterus* included (ML: SH-aLRT = 99, UFBoot = 90), all had significant nodal support. The tribe Psepholacini in its current concept was recovered as polyphyletic. The Indo-Australian genera *Psepholax* and *Oreda* were related to a clade comprising *Cyamobolus*, *Autilia* and *Nechyrus*; *Sympiezoscetus* was found sister to *Mitrastethus*, and the clade of both is related to *Platytenes* and *Roptoperus*. The Neotropical *Hemiliopsis* was related to other South American genera. The polyphyly of Psepholacini is not entirely surprising as their main characters (cylindrical body shape, tibiae with suprauncal projection; Lyal, 1993) are presumably adaptations to their habit of tunnelling, respectively, in dead wood or bark (Jordal *et al.*, 2011). Interestingly, *Mitrastethus* and *Sympiezoscetus* dwell in the decomposing bark of fallen *Araucaria* hoop pines and both genera are related to *Platytenes*, having a similar habitat in dead *Areca* palms. *Psepholax*, *Oreda*, *Cyamobolus*, *Autilia* and *Nechyrus* are usually found on dry wood of angiosperm trees. There was only one Neotropical genus included, i.e. *Hemiliopsis*, which is related to other South American genera.

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 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. Arachnopedini 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 *Arachnobas* 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 ‘*Rhynchodes* group’ at *c.* 52.3 Ma (95% HPD: 45.43–58.54). The emergence of Curculionoida 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. Atelabidae 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

Table 4. Results of BEAST divergence time estimations

No.	Code	Cryptorhynchinae s.s.	<i>Cryptorhynchus</i> group	Indo-Australian clade	Arachnopedini s.l.	<i>Arachnobas</i> spp.	<i>Trigonopterus</i> spp.	New Zealand clade	<i>Rhynchodes</i> group
1	C01	87.77 (77.91–98.41)	78.63 (68.55–88.82)	76.55 (67.62–85.84)	52.43 (54.96–72.50)	42.85 (34.06–51.08)	63.02 (53.08–72.75)	63.11 (53.06–72.82)	54.79 (46.59–62.58)
2	C02	86.72 (76.26–97.80)	78.21 (67.31–89.00)	75.77 (66.38–85.83)	54.66 (45.38–64.44)	43.45 (34.45–53.10)	53.28 (45.10–61.51)	59.14 (49.77–68.37)	54.75 (46.85–63.39)
3	C05 ^a	84.50 (75.66–93.14)	76.50 (67.11–84.86)	72.99 (65.10–80.59)	49.23 (42.78–55.24)	38.23 (31.35–43.52)	52.94 (45.71–59.92)	57.81 (50.60–64.75)	52.28 (45.43–58.54)
4	C06	85.66 (77.83–94.32)	76.90 (68.93–85.34)	73.48 (66.85–81.17)	49.18 (43.34–55.30)	38.25 (31.90–44.46)	53.55 (47.17–61.14)	59.23 (52.26–67.03)	52.46 (46.66–58.19)
5	C11	85.06 (77.45–94.74)	76.47 (68.97–85.51)	73.75 (67.15–82.02)	46.66 (40.91–52.57)	36.49 (30.55–42.62)	59.93 (52.38–68.50)	60.70 (53.41–69.28)	54.79 (46.27–57.84)
6	C13 ^a	86.36 (79.36–93.69)	75.82 (68.58–83.15)	73.77 (67.02–78.95)	46.30 (53.80–65.20)	36.37 (30.77–42.56)	52.17 (45.63–58.76)	56.55 (50.85–62.84)	56.79 (51.29–62.85)
7	C21	88.22 (80.16–97.47)	77.67 (69.80–86.84)	74.29 (67.34–82.35)	49.30 (42.91–55.72)	37.76 (31.55–44.11)	52.47 (45.99–59.74)	58.20 (51.61–65.26)	53.27 (47.30–60.07)
8	C23	83.45 (76.67–90.49)	74.91 (68.38–82.13)	71.93 (66.20–78.38)	46.26 (40.12–52.74)	36.37 (30.13–42.84)	52.40 (46.66–58.55)	57.13 (50.55–63.51)	55.64 (49.68–61.65)

^aRuns not converged.

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 Palaearctic 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 concordant 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 *Macrogyrus* whirligig beetles in the Palaeocene. A similar pattern was suggested for *Platynectes* diving beetles in the Eocene (Toussaint *et al.*, 2017b), and for Hydrobiusini and *Oocyclus* 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 drifting 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 Arachnopedini 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. Unmack *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 netwing beetles endemic to New Guinea (Bocek & Bocak, 2019) recovers a similar age (51 Ma). The origin of corvid birds from New Guinea is dated from the Eocene *c.* 45 Ma (Jönsson *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

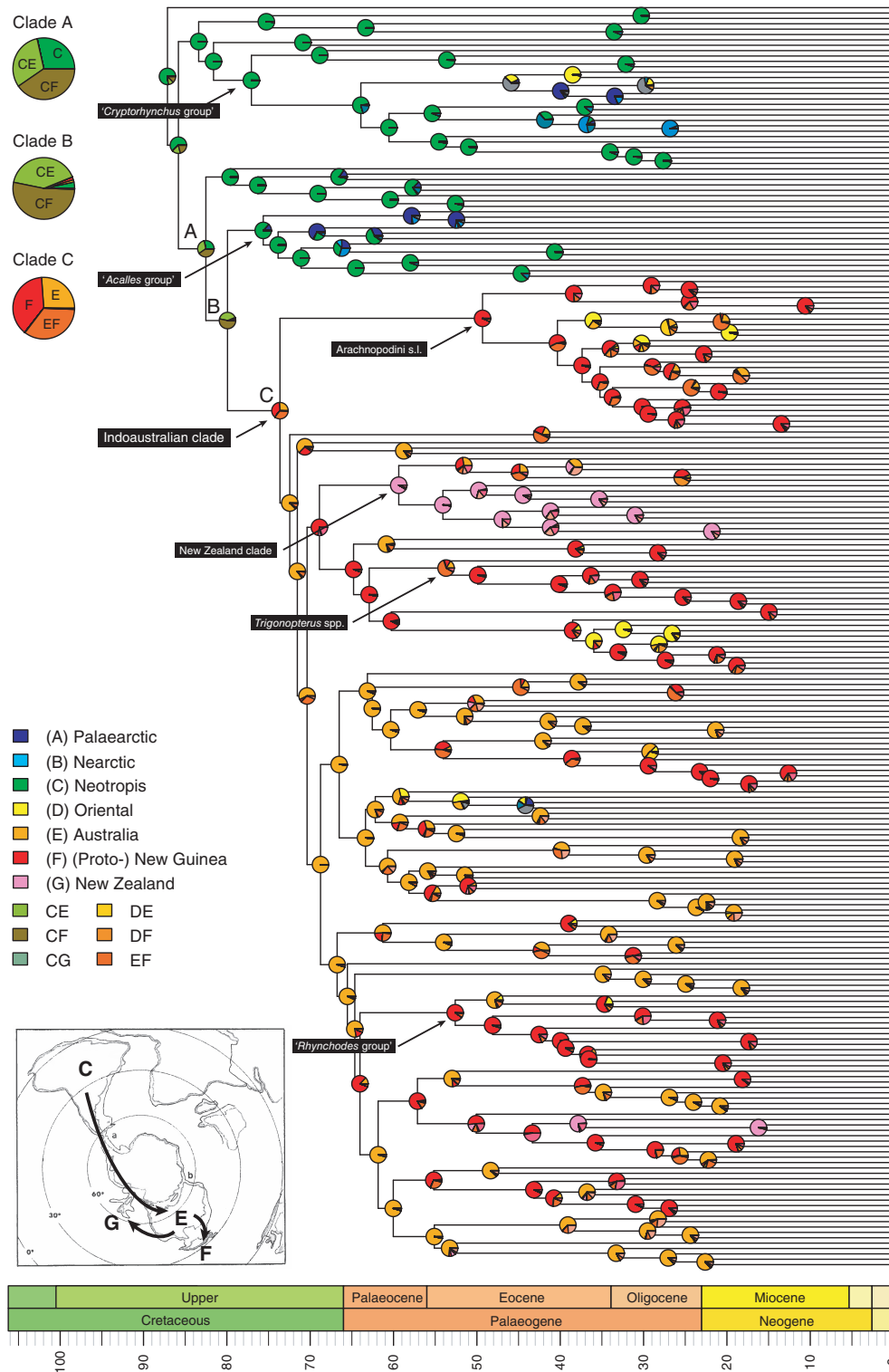


Fig. 2. Estimation of the historical biogeography for Cryptorhynchinae s.s. using a dispersal–extinction–cladogenesis model in BIOGEOBEARS. The coloured boxes represent the seven areas implemented in the palaeogeographical model, as well as the six most important ranges discussed in the text. Pie charts 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. [Colour figure can be viewed at wileyonlinelibrary.com].

some 25–23 Ma (Waters & Craw, 2006), which is in line with the multitaxon analysis of Wallis & Jorge (2018).

Conclusion

We reconstructed the biogeographical history of Cryptorhynchinae, 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. Cryptorhynchinae 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 (Whitfield & 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 Cryptorhynchinae 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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