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Phylogenomics resolves timing and patterns in the evolution of Australasian Cerambycinae (Coleoptera: Cerambycidae), and reveals new insights into the subfamily-level classification and historical biogeography of longhorn beetles

Mengjie Jin [a,b], Seunggwan Shin [c,d,e], Lauren G. Ashman [a,f], Richard A.B. Leschen [g], Andreas Zwick [a], Roger de Keyzer [h], Duane D. McKenna [c,d,*], Adam Ślipiński [a,*]

[a] Australian National Insect Collection, CSIRO, Canberra, ACT, Australia
[b] State Key Laboratory of Biocontrol, School of Ecology, Sun Yat-sen University, Guangzhou, China
[c] Department of Biological Sciences, University of Memphis, Memphis, TN, USA
[d] Center for Biodiversity Research, University of Memphis, Memphis, TN, USA
[e] School of Biological Sciences, Seoul National University, Seoul 08826, Republic of Korea
[f] Research School of Biology, Australian National University, Canberra 2601, Australia
[g] New Zealand Arthropod Collection, Manaaki Whenua – Landcare Research, Auckland, New Zealand
[h] Research Associate, Entomology, Australian Museum, Sydney, New South Wales, Australia

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ABSTRACT

Cerambycinae is the second-largest subfamily of longhorn beetles in the Southern Hemisphere. The phylogeny of Cerambycinae is poorly known, resulting in a highly artificial tribal-level classification and a largely speculative evolutionary history. We reconstructed the phylogenetic relationships of Cerambycinae at the generic level using anchored hybrid enrichment data from hundreds of nuclear genes, with a primary focus on the extraordinarily diverse faunas of Australia and New Zealand. We also estimated divergence times by incorporating fossil calibrations in our analyses. We identified two main clades within Cerambycinae, which can also be separated morphologically by a distinct type of antennal foramen. We recovered a Late Jurassic origin of crown Cerambycinae. Dorcasominae, which was newly found to have representatives in Australia, was notably derived from within Cerambycinae. We recovered two independent origins of Australian Cerambycinae: one clade originated in the Early Cretaceous and is likely endemic to the Southern Hemisphere, while the other clade appears to have immigrated to Australia, perhaps from the Northern Hemisphere. Within the Australian lineages were multiple independent origins of New Zealand taxa, all of which are relative host-plant generalists. Tribal relationships and assignments are discussed, and based on our results, the following major nomenclatural acts were made: Dorcasominae Lacordaire, 1868 is downgraded to a tribe Dorcasomini of Cerambycinae Latreille, 1804; Neostenini Lacordaire, 1868 **syn. nov.** is treated as a junior synonym of Uracanthini Blanchard, 1851.

1. Introduction

Cerambycidae Latreille, commonly known as the longhorn beetles, is one of the most species-rich beetle families, comprising over 38,000 described species worldwide (Tavakilian and Chevillotte, 2021). These emblematic, predominantly wood-boring beetles, are extremely diverse in morphology and biology and have received considerable recent attention from scientists working on their taxonomy and systematics (reviewed in Švácha and Lawrence, 2014), evolutionary history (e.g., Haddad et al., 2018; Nie et al., 2021), ecology and conservation (e.g., Solano et al., 2013; Jeppsson and Forslund, 2014), genomics (e.g., McKenna et al., 2016; Shin et al., 2021), chemosensory adaptations and behavior (e.g., Millar and Hanks, 2017; Mitchell et al., 2017), and symbiosis and digestive physiology (e.g., Scully et al., 2014). Their classification and relationships have been intensively studied in the past; however, debates regarding the higher-level classification of

* Corresponding authors at: Department of Biological Sciences, University of Memphis, Memphis, TN, USA (D.D. McKenna).
E-mail addresses: dmckenna@memphis.edu (D.D. McKenna), adam.slipinski@csiro.au (A. Ślipiński).

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Cerambycidae continue. Six to eight subfamilies of Cerambycidae are usually recognized: Cerambycinae, Dorcasominae, Lamiinae, Lepturinae, Necydalinae (or as a tribe Necydalini in Lepturinae), Parandrinae (or as an ingroup of Prioninae), Prioninae and Spondylidinae (Švácha and Lawrence, 2014; Haddad and McKenna, 2016; Nie et al., 2021), but further divisions of some subfamilies are preferred by some authors (Tavakilian and Chevillotte, 2021).

The subfamily Cerambycinae, with over 1,800 genera and 12,000 described extant species worldwide (Tavakilian and Chevillotte, 2021), is particularly species rich in the Southern Hemisphere. Nonetheless, a large proportion of Cerambycinae species in the Southern Hemisphere remain undescribed. The monophyly of Cerambycinae has long been contentious. Apparent apomorphic morphological characters have been identified in larvae, including the rounded gouge-like mandibles, and the abruptly constricted clypeus. However, no apomorphic characters have been identified in adults. Unfortunately, the larvae of many taxa are unknown, which has led to misclassification of some species of Cerambycinae; typically, they are erroneously placed in the subfamilies Spondylidinae, Necydalinae or Lepturinae (Švácha and Lawrence, 2014). The division of Cerambycidae into subfamilies has only recently been evaluated via analyses of molecular data. Although they analyzed different numbers and kinds of molecular loci, Zhang et al. (2012, 28S rDNA), Wei et al. (2014, 18S and 28S rDNA), Lee and Lee (2020, 2 mitochondrial genes and 4 nuclear genes), Nie et al. (2021, 13 mitochondrial protein-coding genes), and Haddad et al. (2018, 521 nuclear protein-coding genes; 2021, 469 nuclear protein-coding genes), all recovered a monophyletic Cerambycinae.

Historically, Cerambycinae were often considered related to Lamiinae, but this placement was not confirmed by a thorough study of morphological characters (Napp, 1994; Švácha and Lawrence, 2014). Danilevsky (1979) and Švácha and Lawrence (2014) proposed a close relationship between Cerambycinae and Dorcasominae, and a close relationship between these subfamilies was recovered by Haddad et al. (2018, 2021) in analyses of hundreds of nuclear genes obtained via anchored hybrid enrichment. Dorcasominae contains over 300 species and is quite diverse in Madagascar, which hosts most extant species in the subfamily. Many species of Dorcasominae were previously classified in or near Lepturinae, but they can usually be separated from Lepturinae by the absence of mandibular molar plates or variations on wing venation. Nonetheless, the phylogenetic position of Dorcasominae remains uncertain. Haddad et al. (2018) recovered *Dorcasomus* Audinet-Serville within or as a sister group of Cerambycinae, while Nie et al. (2021) recovered different placements for this taxon in different analyses. The tribal-level classification and phylogenetic relationships among tribes within Cerambycinae remain largely uncertain due to regional bias and reliance on a limited number of adult morphological characters in phylogenetic analyses to date.

The evolutionary history of the mega-diverse Cerambycinae has long interested researchers (e.g., Haddad et al., 2018; Lee and Lee, 2020; Nie et al., 2021). Considering the distribution patterns, plesiomorphic characters and some unpublished phylogenetic results, Švácha and Lawrence (2014) proposed the *ad hoc* scenario that the lineages Cerambycinae/Dorcasominae and Prioninae/Parandrinae originated in the Southern Hemisphere, while the remaining subfamilies (presumed to form a monophyletic group) may be of northern origin. However, these hypotheses cannot be tested since a robust phylogenetic backbone with an appropriate representation of the world taxa does not exist. To provide phylogenetic context for research on Cerambycinae, we used anchored hybrid enrichment (AHE) (Lemmon et al., 2012; Lemmon and Lemmon, 2013; Haddad et al., 2018; Shin et al., 2018) to generate DNA sequence data for a deep sample of Cerambycinae species from Australia and New Zealand. We used the resulting data to reconstruct the phylogeny of Cerambycinae, to investigate tribal-level relationships, and to gain new insights into the macroevolutionary history of the Australasian fauna.

2. Materials and methods

2.1. Taxon sampling and sequencing

Our taxon sample was designed with a focus on the faunas of Australia and New Zealand. In this region, Cerambycinae taxonomy has been systematically revised, but the phylogeny of Cerambycinae remains almost unknown. Ethanol-preserved specimens of Cerambycinae deposited in the Australian National Insect Collection (ANIC) and the New Zealand Arthropod Collection (NZAC) comprised most specimens studied. A total of 109 specimens were sampled, representing 104 cerambycine genera (88 being native to Australia [about 60% of the genera], 11 from New Zealand [36% of the genera], and five from elsewhere; Table S1). Genomic DNA was extracted from thoracic muscle using the DNeasy 96 Blood and Tissue Kit (Qiagen) following its standard protocol for tissue samples, measured by a Qubit fluorometer and a Fragment Analyser (Agilent Technologies), normalized to 100–500 ng of DNA, and sheared to 300–500 bp in size using a QSonica Q800R2 Sonicator (10 secs on, 10 secs off for seven minutes). Individual DNA libraries were built using the NEBNext Ultra II DNA Library Prep Kit (New England Biolabs) and then pooled equimolarly (24 samples per pool at 750 ng total). Hybrid enrichment was performed following the myBaits Hybridization Capture for Targeted NGS protocol (Arbor Biosciences); the AHE probes were designed for Coleoptera by Haddad et al. (2018). Our samples were processed along with an additional 96 samples from another project (DNA extraction, library building and capture). All of the capture pools were then pooled together and sequenced at Novogene (UC Davis, U.S.A.) on a single Illumina Hiseq X Ten lane using a 150 bp PE sequencing kit.

2.2. Bioinformatic workflow

Sequence data were processed following Peters et al. (2017), mainly using the CSIRO computer cluster PEARCEY (Australia) or the High-Performance Computing cluster at the University of Memphis (U.S.A.). Raw reads were trimmed using Trimmomatic v0.39 (Bolger et al., 2014) to remove adapter sequences and low-quality bases, then assembled with SPAdes v3.11.1 (Bankevich et al., 2012). All assemblies were run through Orthograph v0.6.3 (Petersen et al., 2017) to search for the 521 orthologous loci targeted (Haddad et al., 2018; Shin et al., 2018); for this step, data from three reference taxa in OrthoDB v7 (Waterhouse et al., 2013) were used: *Danaus plexippus* (Lepidoptera; Zhan et al., 2011), *Nasonia vitripennis* (Hymenoptera; Werren et al., 2010) and *Tribolium castaneum* (Coleoptera; Richards et al., 2008).

An additional 11 cerambycid species, which were previously sequenced and published by Haddad et al. (2018), were added to our dataset (Table S1). Amino Acid (AA) sequences of all 120 samples were aligned using MAFFT v7.450 (Katoh and Standley, 2013), potential misalignments were detected by Aliscore v2.0 (Misof and Misof, 2009; Kück et al., 2010) and removed, and loci with low phylogenetic information were deleted using MARE v0.1.2-rc (Meyer et al., 2011). The nucleotide (NT) sequences were filtered accordingly using Pal2Nal v14 (Suyama et al., 2006). Single locus alignments of AA and NT data were then checked in AliView (Larsson, 2014), and potential paralogs were identified and removed manually. The Perl script ConcatMatrices v1.2 (https://phylotools.com; Jin et al., 2020) was used to generate the final concatenated dataset. The NT alignment was also used to generate a recoded dataset (Degen1) with the script Degen v1.4 (https://phylotools.com; Zwick et al., 2012), eliminating all synonymous changes by fully degenerating synonymous codons with IUPAC ambiguity codes.

2.3. Phylogenetic analyses

Concatenated gene tree. The three datasets (AA, NT and Degen1) with two different partitioning schemes (by locus and by codon position) were analyzed in parallel for the downstream phylogenetic analyses.

ModelFinder (Chernomor et al., 2016; Kalyaanamoorthy et al., 2017) was used to determine the best-fit substitution models (with + MERGE and –rcluster options); the best-fit model schemes were then used in phylogenetic analyses among all taxa in the program IQTREE v1.6.12 (Nguyen et al., 2015). We performed 200 independent tree searches for each dataset and selected the one with the best likelihood score as the final topology. Statistical values of node support (maximum likelihood bootstrap support or MLBS) were estimated using the slow standard non-parametric bootstrap in IQTREE (−b option; Felsenstein, 1985) with 200 replicates. Phylogenetic relationships from different analyses were compared using the 'comparePhylo' script in R/ape (Paradis and Schliep, 2019).

Species tree estimation. To reduce the confounding effect of incomplete lineage sorting (ILS), we also analyzed the AA, NT and Degen1 datasets in parallel. ML trees were reconstructed for all locus-specific alignments using IQTREE separately, then ASTRAL 5.7.5 (Zhang et al., 2018) was applied to estimate the species tree under the multispecies coalescent model.

2.4. Divergence time estimation

Divergence times were estimated using MCMCtree implemented in paml 4.8 (Yang, 2007, Zhu et al., 2015). NT datasets partitioned by codon position and the optimal ML tree topology was used in this analysis. Four fossil calibration points were used (Table S2): *Cretoprionus liutiaogouensis* was used to constrain the age of the most recent common ancestor (MRCA) of Prioninae and Parandrinae to at least 123 Ma (Wang et al., 2014). The MRCA of Lamiinae was constrained to at least 57 Ma based on the fossils of *Palaeoncoderes* and *Prolamioides* (Piton and Théobald, 1937, Piton, 1940); *Necydalis zangi* (~35 Ma) in Baltic amber was used as the MRCA of Necydalinae (Vitali, 2011); the Baltic amber fossil of *Stenohomalus hoffeinsorum* (~35 Ma) was used to constrain the MRCA of the extant *Stenhomalus* (Vitali, 2014) but set to the branch comprising *Stenohomalus* + *Iphora* + *Longipalpus* considering the tree topology. The root of the phylogeny was constrained to have a maximum age of 180 Ma, following McKenna et al. (2019).

Approximate likelihood calculation in MCMCtree was undertaken to improve the run speed of MCMC, the gamma-Dirichlet prior for the overall substitution rate (rgene gamma) was set to (1, 1), and the prior for the rate-drift parameter (sigma2 gamma) was set to (1, 10). The MCMC chain was run for burnin = 1,000,000 sampfreq = 1,000 and nsample = 10,000. Three independent runs with random seeds were executed to help determine when and if the results converged.

3. Results

3.1. Phylogenetic relationships

The probes were designed to target 521 orthologous nuclear genes shared across Coleopterida. We ultimately retained 351 of these genes for analysis because some did not meet our criteria for inclusion in downstream phylogenetic analyses. Total number of recovered loci for each sample are presented in Table S1, and sequence length of all recovered loci is provided in Tables S3 and S4. All analyses recovered identical relationships for most taxa (Table 1, Figs. 1–2, S1-S5), and the ML tree reconstructed using the Degen1 dataset partitioned by codon was chosen to illustrate the resulting phylogenetic relationships (Fig. 1A). The estimated species tree (Fig. 2A, B) is mostly congruent with the ML tree; several nodes were resolved differently, but these had very low posterior probability support.

The monophyletic Cerambycinae/Dorcasominae branch was divided into two strongly supported clades, indicated as Clades A and B. Clade A includes the subfamily Dorcasominae (labelled as A3), represented by the type genus *Dorcasomus* and three Australian genera formerly placed in Cerambycinae *incertae sedis* (Ślipiński and Escalona, 2016). This topology was recovered by both analytical methods applied to all datasets, although the internal relationships within each of the two clades are not fully resolved. Apart from subclade A3, the main branch of Clade A consists of two maximally supported subclades (indicated as A1 and A2 in Figs. 1–3 to facilitate discussion). Within subclade A1, only two clades were consistently recovered: (1) the New Zealand genera *Votum* Broun and *Zorion* Pascoe were placed at the base of the clade; (2) the Australian taxa classified in Uracanthini and Neostenini (i.e., the clade spanning *Neouracanthus* to *Rhinophthalmus* in the tree) were grouped in the other supported clade. Phylogenetic relationships among the remaining Australian taxa and the Chilean *Zehra coemeterii* (Thomson), which are mostly flower-visiting species, remain unresolved because variable topologies were recovered, typically with very low nodal support.

Within subclade A2, two strongly supported clades were recovered: (1) *Bardistus* Newman and *Tricheops* Newman bear three-lobed eyes, and were revealed as sister taxa, closely related to the ant mimicking genera (*Formicomimus* Aurivillius, *Zoedia* Pascoe, *Pseudocephalus* Newman) and the Chilean wasp mimicking *Callisphyris macropus* Newman (currently misplaced in Lepturinae, Necydalini); (2) Australian Macronini (*Enchoptera* Saunders + *Macrones* Newman) are grouped with Psilomorphini and Rhagiomorphini. The phylogenetic relationships of (*Phalota* Pascoe + (*Diotimana* Hawkins + *Phlyctaenodes* Newman)) are maximally supported, but the position of the unique New Zealand genus *Blosyropus* Redtenbacher, formerly placed in subfamily Lepturinae, remains uncertain within subclade A2.

Phylogenetic relationships within Clade B were recovered with much higher resolution than those in clade A, with the monophyletic tribes Obriini, Cerambycini and Clytini recovered in all analyses and placed near the root of the clade. The sister relationship of *Ipomoria* Pascoe and *Molorchus* Fabricius is maximally supported, but their position in the tree is uncertain. The long-troublesome taxa of Callidiopini and Hesperophanini are widely-spread across subclades B1-B3, rendering most tribes in this group polyphyletic. Besides these two problematic tribes, subclade B1 mainly contains genera from Pytheini, subclade B2 contains restricted Strongylurini, and subclade B3 contains an expanded Phoracanthini.

3.2. Estimation of divergence times

Our results indicate that the MRCA of Cerambycinae appeared in the Late Jurassic (~149 Ma, 95% CI: 186 – 81 Ma, Fig. 3), which is not strongly supported by current fossil evidence but is congruent with other recent molecular analyses (McKenna et al., 2019; Nie et al., 2021). The

Table 1
Percentages of identical nodes recovered by different phylogenetic methods.

	Datasets and partition scheme	1	2	3	4	5	6	7
IQtree	1. Degen1 codon position	\						
	2. Degen1 gene	92%	\					
	3. AA gene	95%	89%					
	4. NT codon position	80%	81%	80%	\			
	5. NT gene	80%	81%	80%	100%	\		
ASTRAL	6. Degen1	78%	78%	76%	76%	76%	\	
	7. AA	76%	72%	76%	72%	72%	78%	\
	8. NT	73%	74%	72%	78%	78%	74%	73%

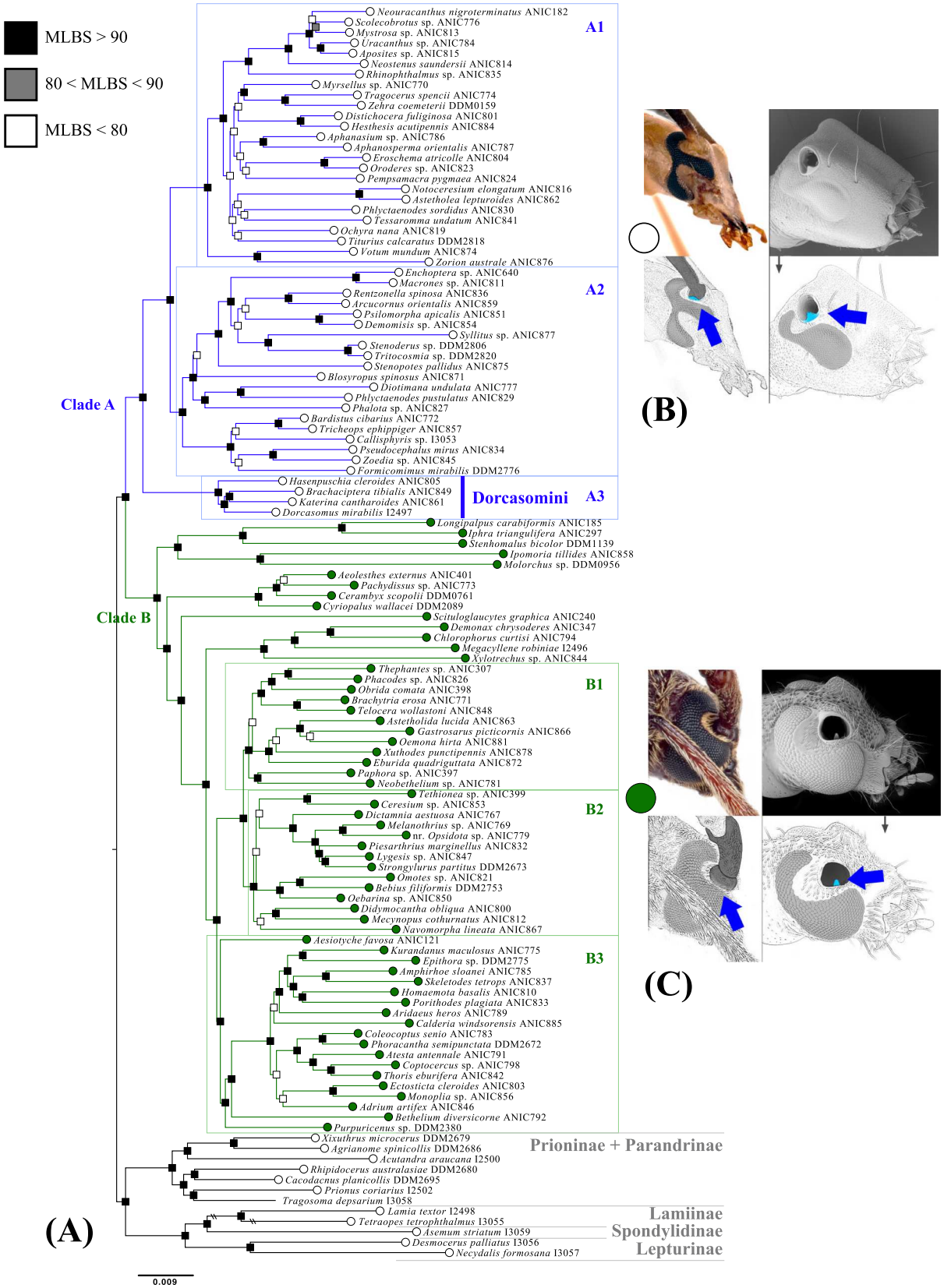

Fig. 1. A) Phylogram of Australasian genera of Cerambycinae resulting from a maximum-likelihood (ML) analysis of fully degenerate nucleotide sequences (Degen1) from 351 nuclear loci, partitioned by codon position. Tip labels provide the taxon name and lab ID, coloured circles indicate the antennal foramen status corresponding to Fig. 1B and 1C. Maximum-likelihood bootstrap values (MLBSs) are shown as squares on each node and are shaded according to the key on the left. **B-C)** morphological images modified from Ślipiński et al. 2021; light blue shade highlights the antennifer while a dark blue arrow indicates the external visibility of the antennifer. B) left: *Tricheops* sp.; right: *Zoedia* sp.; C) left: *Stromatium* sp.; right: *Oebarina* sp. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

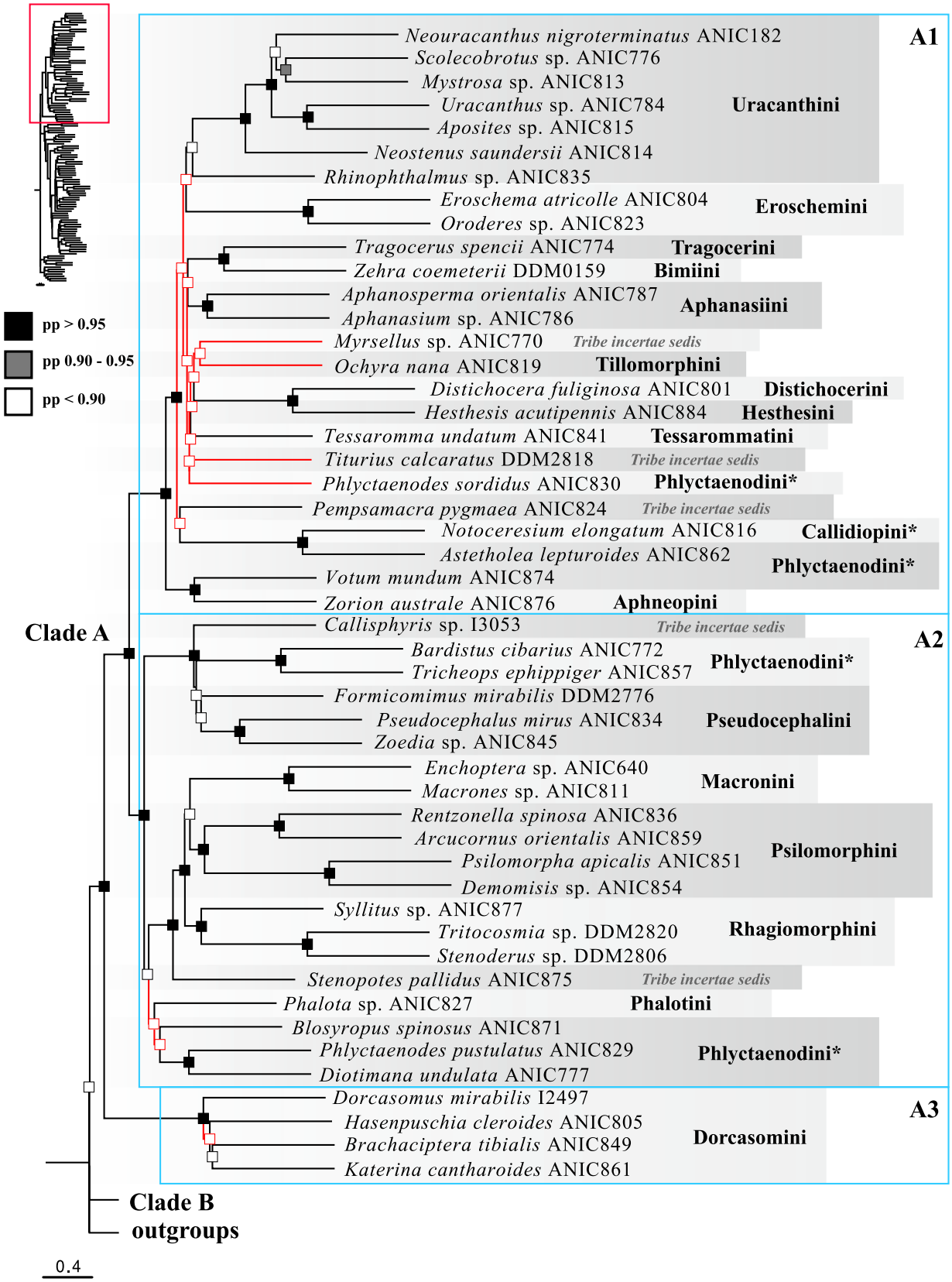

Fig. 2. Phylogram of Australasian genera of Cerambycinae resulting from the ASTRAL-III species tree estimation/analysis of data from fully degenerate nucleotide sequences (Degen1) from 351 nuclear loci. Red branches indicate portions of the topology that are incongruent with the ML tree in Fig. 1A. Tip labels provide the taxon name and lab ID; posterior probabilities (pp) are shown as squares on the nodes, shaded according to the key on the left of the figure. The coloured bars show the tribal classification recognized in this study, with asterisks highlighting the nonmonophyletic tribes recovered in our analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

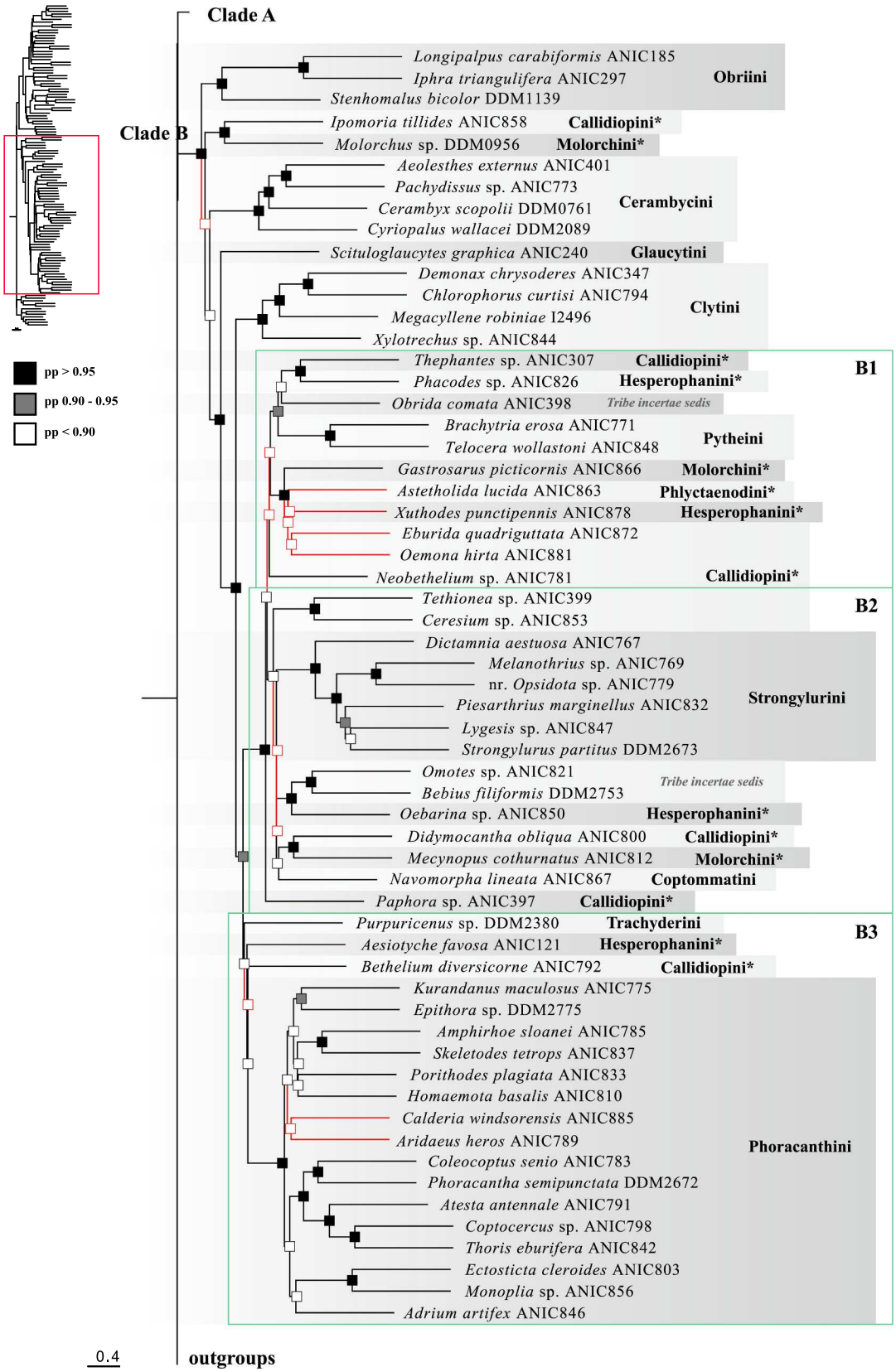

Fig. 2. (*continued*).

two main clades within the subfamily are of Cretaceous origin, both with a similar root age (Clade A, ~131 Ma, 95% CI: 165 – 70 Ma; Clade B, ~135 Ma, 95% CI 169 – 73 Ma). The MRCA of subclade A1 presumably experienced a Late Cretaceous radiation, with a very short root, and most terminal taxa originated between the Late Cretaceous and the Early Paleogene. The MRCA of the core New Zealand group in Clade B

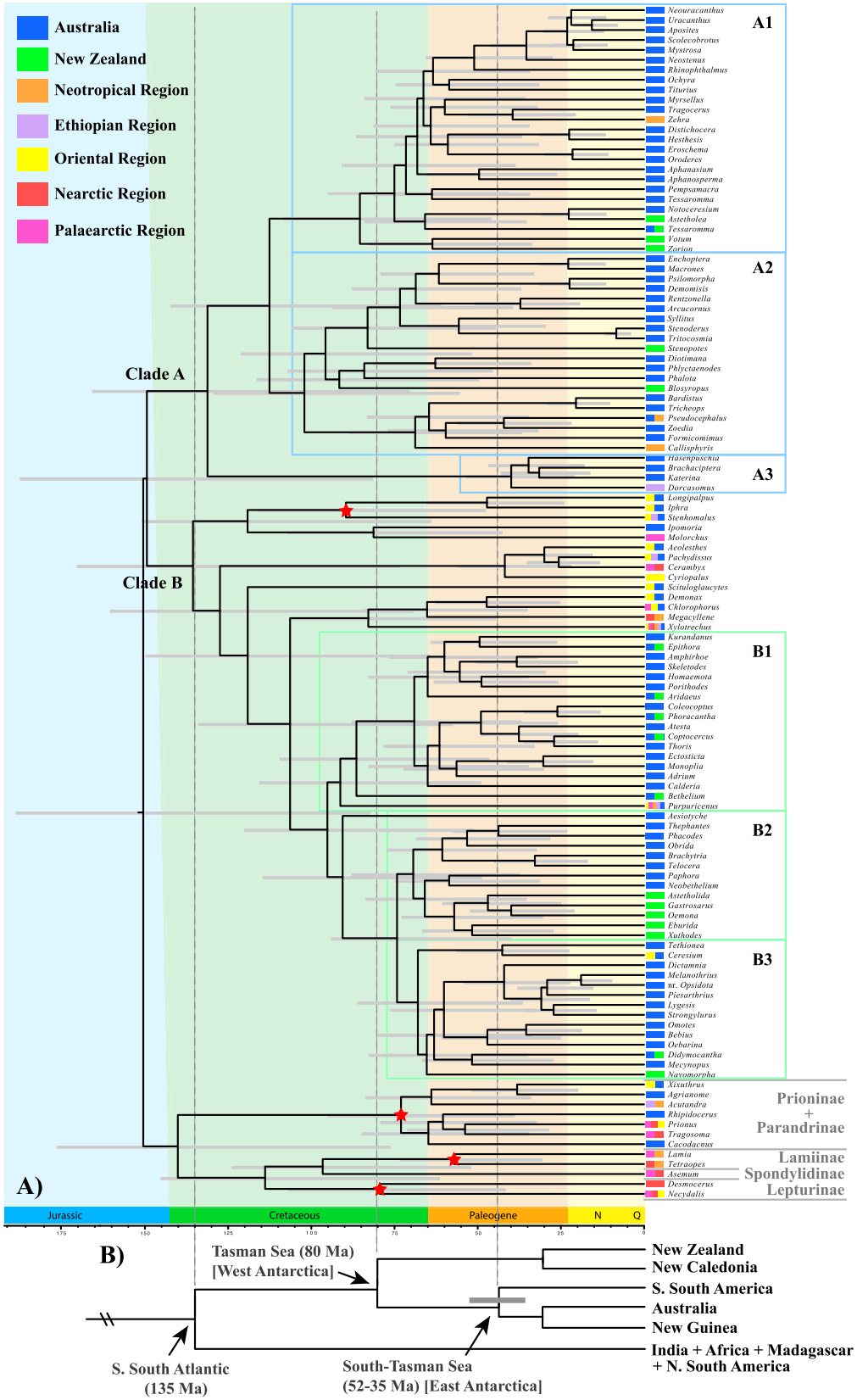

Fig. 3. A) A dated phylogeny of Australasian Cerambycinae genera resulting from MCMCtree analysis of nucleotide sequences (NT) from 351 nuclear loci, partitioned by codon position. 95% CI's of each node are indicated as light grey bars; red stars show the nodes constrained by fossil priors. Tip labels provide the genus name of each taxon, while coloured squares indicate the known geographic distribution of the represented genera. Genera that occur in both Australia and New Zealand are all recorded as introduced from Australia to New Zealand by Sopow et al. (2015, 2017), and treated as native to Australia in our study; **B)** Geological area cladogram representing the relationships among the Southern Hemisphere landmasses based on paleogeographic evidence, modified from Sanmartín and Ronquist (2014). Fig. 3A and B share the same time scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(*Astetholida* Broun to *Xuthodes* Pascoe) was dated to the Late Paleogene (~57 Ma, 95% CI: 72 – 30 Ma). Also, the basal splits of most tribes were inferred to have occurred in the Paleogene.

4. Discussion

4.1. Morphological and biological distinctiveness of Australasian clades

A comprehensive examination of all terminal taxa revealed a distinct character pattern coinciding with the division of Cerambycinae into two clades. These characters involve the morphology of antennal articulation and were first described and illustrated by Ślipiński and Escalona (2016). Specifically, the antennal insertions in taxa belonging to Clade A (Fig. 1B) are located on raised tubercles, the antennal foramen has a thin, usually flat rim, and the antennal articulation (antennifer) is located on the rim and is visible when the antenna is inserted (indicated by the blue arrow in Fig. 1B). All taxa in Clade A show this character, although the articulation in *Blosyropus* is very weak. This type of articulation also occurs in the other subfamilies of Cerambycidae. All taxa in Clade B have a unique type of antennal insertion (Fig. 1C), which was absent in all other groups of Cerambycidae we examined. In these taxa the antennal insertions are flat or concave, the antennal foramen has a thick, often raised rim, the antennal scape is deeply inserted into the foramen and enveloped by the rim, and the antennal articulation point is invisible from outside (indicated by the blue arrow in Fig. 1C). This distinct state may be regarded as an apomorphy for the clade. Interestingly, the genera of Cerambycinae historically misidentified as Spondylidinae are mainly related to taxa in Clade B (P. Švácha, pers. comm.), which suggests this apomorphic character can potentially be used for placement of some difficult taxa in subfamilies lacking dissections or prior knowledge of larvae.

Clade A includes most of the Australasian taxa that have adults adapted to visiting flowers during the daytime (Ślipiński and Escalona, 2016; M.J. and R.D.K. personal observation). The species have finely faceted eyes and usually bright colouration with body features mimicking wasps (Macronini and Hesthesini), ants (Aphneopini), bees (Hesthesini) or lycid beetles (Eroschemini and part of Rhagiomorphini). All known genera that have developed chemical defence glands with outlets located on the head, including *Stenoderus* Dejean and *Syllitus* Pascoe (the stinking longhorn beetles, Moore and Brown, 1971), *Tricheops* and *Bardistus* (species in both genera have three-lobed eyes, Evans and Ślipiński, 2016). However, these genera are recovered on two separate branches within Clade A, suggesting independent origins of these chemical diffusion structures. Clade A also includes *Tragocerus*- the only known Australian genus of longhorn beetles that has adults that can fly without opening their elytra. The taxa of Clade B include some colourful flower-visiting taxa, such as Clytini or Pytheini. Still, the majority of species are somber coloured and crepuscular or nocturnal beetles with large coarsely facetted eyes and often with complex male antennae.

4.2. The phylogenetic position of Dorcasominae

Dorcasomides was first proposed by Lacordaire (1868) for *Dorcasomus* and *Megacoelus* Lacordaire as a group in the subfamily Cerambycinae. Aurivillius (1912) recognised Dorcasomini and lumped six genera into this tribe (*Dorcasomus*, *Neoclosterus* Heller, *Plectogaster* Waterhouse, *Aphelogaster* Kolbe, *Gahania* Distant and *Lycosomus* Aurivillius). However, Quentin and Villiers (1970) redefined the tribe as monotypic for *Dorcasomus* alone. Based on larval characters, Danilevsky (1979) raised the *Apatophysides* of Lacordaire (1868) to the subfamily Apatophyseinae (misspelled as Apatophysinae) containing the genus *Apatophysis* Chevrolat. Švácha and Danilevsky (1987) moved *Dorcasomus* into Apatophyseinae, then Özdikmen (2008) revised the subfamily name as Dorcasominae based on the principle of priority. Danilevsky (2010) retained Apatophyseinae as a separate subfamily from Dorcasominae, which was accepted by Bouchard et al. (2011) but rejected by Švácha and Lawrence (2014). Nie et al. (2021) confirmed that Dorcasomini and Apatophyseini group together using mitochondrial genomes.

The phylogenetic position of Dorcasominae has been debated extensively, and historically most of the taxa were placed within the subfamily Lepturinae. However, Danilevsky (1979) proposed a close relationship of *Apatophysis* and Cerambycinae based on larval characters, consistent with Švácha and Lawrence (2014). Haddad et al. (2018) provided the first solid backbone of Cerambycidae based on analyses of anchored hybrid enrichment data. Still, they recovered incongruent topologies from separate analyses of their NT and AA datasets, with Cerambycinae (represented by two genera) monophyletic and sister to Dorcasominae (represented by *Dorcasomus*) in the AA tree, and Cerambycinae rendered paraphyletic by *Dorcasomus,* with reasonably high nodal support, in the NT tree. While Nie et al. (2021) recovered very unstable placements of Dorcasominae in different analyses using mitochondrial protein coding genes, their data mainly supported Dorcasominae as sister to (Cerambycinae + Prioninae *s.l.*)—Cerambycinae was represented by 19 Palaearctic taxa. In our phylogenetic reconstruction, which has a more comprehensive sampling of Cerambycinae, Dorcasominae is recovered as a basal group in the large Clade A within Cerambycinae. Herein, we propose to include Dorcasomini as a tribe within the subfamily Cerambycinae. Dorcasomini larvae are unique among Cerambycinae in lacking a constricted clypeus and round "gouge-like" mandibles—the characters that have so far been considered as cerambycine synapomorphies (Švácha and Lawrence, 2014). The Australian genera *Katerina*, *Hasenpuschia* and *Brachaciptera* are accordingly moved into Dorcasomini. This placement is also supported by the larval morphology of *Katerina* (de Keyzer et al., in preparation).

4.3. Diversification of Australasian Cerambycinae

Cerambycinae are considered to be the most speciose subfamily of longhorn beetles in Australia (Linsley, 1961; Švácha and Lawrence, 2014; Ślipiński and Escalona, 2016). This raises the interesting question of how Cerambycinae evolved and diversified in Australia. According to our results (Fig. 3), the MRCA of all extant Cerambycinae can be dated back to the Late Jurassic. Shortly thereafter, the two main clades of Cerambycinae were established. The origin of Dorcasomini (~131 Ma, 95% CI: 165 – 70 Ma) in clade A is approximately contemporaneous with the separation of South America and Africa in the Early Cretaceous (~135 Ma, Sanmartín and Ronquist, 2014), though the crown age of Dorcasomini was inferred in the Late Eocene (~39 Ma, 95% CI: 53 – 21 Ma), which may be an underestimate due to our limited taxon sampling. Two major origins were recovered for Australian cerambycine genera (Fig. 3): subclades A1 and A2 are restricted to the Southern Hemisphere, with South American and New Zealand components embedded in Australian genera, which suggests diversification in the supercontinent of Gondwana; while for clade B, most of the Northern Hemisphere taxa are placed near its root, and the endemic Australian taxa (subclades B1-B3) cluster in the crown of the tree with its MRCA dated back to the Late Cretaceous (~95 Ma, 95% CI: 119 – 52 Ma). Considering the estimated age of the entire clade B, which is much younger than the separation of Gondwana from Laurasia, we suspect subclades B1-B3 represent a possible re-entry of Cerambycinae to Australia and experienced further radiations.

Phylogenetic analyses recovered limited resolution within subclade A1, with variable topologies reconstructed using different datasets or methods, and very low nodal support. Weakly supported nodes are often caused by strong incomplete lineage sorting, which can result from rapid speciation. In our analyses, the topology of the estimated species tree for subclade A1 conflicts with the concatenated ML tree. Also, all internal branches are relatively short near the base of subclade A1, both indicating that A1 has possibly undergone rapid radiation, and suggesting that the Late Cretaceous (~75 – 60 Ma, based on our results) was an important period in shaping the species diversity of this clade. Though the driving forces for this process are not clear, a plausible scenario may involve the coevolution of angiospermous plants and herbivorous insects (e.g., Farrell, 1998; McKenna et al., 2009, 2015, described in Haddad and McKenna, 2016). Insect pollination was thought to be a key contributor to the Cretaceous radiation of angiosperms and stimulated

the diversification of insects responding to rapidly diversifying plants. Similar patterns have been illustrated in other groups, e.g., bees (Peters et al., 2017), butterflies (Kawahara et al., 2019), and ladybird beetles (Che et al., 2021), and the coevolution of flowers and insects were inferred as the main driver for rapid speciation. Although there is no direct evidence that all taxa in subclade A1 are pollen or nectar feeders, many genera in subclade A1 are equipped with finely faceted eyes, which is usually linked to diurnal activities (Ji et al., 1991), and have developed various deceptive or chemical defences protecting the adults in exposed environments. These may suggest the long association of these cerambycids and flowers, and indicate the evolutionary history of subclade A1 was strongly influenced by the Late Cretaceous radiation of angiosperms.

In subclades B1-B3, the divergence times of many genera, including Phoracanthini feeding on *Eucalyptus* and related Myrtaceous plants, are estimated at mid or late Paleogene, coinciding with the diversification of these and other plants in Australia following aridification of the continent (Ladiges et al., 2011; Bui et al., 2017). Australia's climate was much warmer and wetter during the Early Eocene (Zachos et al., 2001; Martin, 2006; Crisp and Cook, 2013), and aridification since the Eocene has resulted in spectacular radiations of one or more groups of Australian plants (Renner et al., 2020). Associations between such climate change and species diversification has also been noted in many Australian animal lineages, such as the pygopodoid geckos (Brennan and Oliver, 2017), cicadas (Owen et al., 2017), and cockroaches (Beasley-Hall et al., 2018).

Contained within the Australian lineages are six separate origins of New Zealand genera: the monophyletic *Astetholida* group, whose MRCA is estimated to have a Paleocene origin (~57 Ma, 95% CI: 72 – 30 Ma); *Votum* and *Zorion* are sister taxa and their MRCA was also estimated to have originated in the Early Paleocene (~63 Ma, 95% CI: 82 – 33 Ma); *Astetholea* grouped with the Australian *Notoceresium*, forming a clade whose MRCA was estimated to be from the Early Neogene (~22 Ma, 95% CI: 31 – 11 Ma), which might suggest a more recent dispersal; and the remaining three genera subtend relatively long branches. The somewhat scattered distribution of New Zealand taxa across the tree suggests that there were several separate dispersal events to New Zealand. Alternatively, deeper lineages may have also been shared between Australia, New Zealand, and elsewhere, before New Zealand separated from Gondwana. During the Oligocene, there was a drastic reduction in the coastline of New Zealand (Cooper and Cooper, 1995; Mildenhall et al., 2014). Lineages that survived the marine transgressions and land restructuring that took place at this time were largely saproxylic or edaphic (e.g., Leschen, 2006; Gimmel et al., 2019; Buckley et al., 2020). Thus, the modern species of New Zealand Cerambycinae that survived the Oligocene are relicts of a formerly more diverse fauna.

4.4. Tribal classification of the Australasian Cerambycinae

The current Cerambycinae tribal classification proposed by Lacordaire (1868) relies on the external morphology of adult beetles, and is unquestionably artificial and unsettled (Švácha and Lawrence, 2014; Ślipiński and Escalona, 2016). Before this study, few tribal relationships within Cerambycinae had been studied using phylogenetic methods. Ślipiński and Escalona (2016) revised the genera of Australian Cerambycinae using adult morphology, but were not able to apply the existing tribal classification to their studies of Australian taxa, because they considered it too misleading. Lee and Lee (2020) published the first multigene phylogeny of Palearctic and Oriental Cerambycinae, testing the monophyly of many tribes and demonstrating the importance of larval characters and oviposition-related evidence in the tribal classification. Building on the generic revision of Ślipiński and Escalona (2016), we present here the most comprehensive molecular phylogeny of Australasian Cerambycinae, and endeavor to address the challenges of Cerambycinae tribal classification. In contrast to Lee and Lee's (2020) findings with Palearctic and Oriental genera, where many of the recovered tribes were monophyletic, we have revealed a severely polyphyletic tribal system for the Australasian taxa, with components of several tribes widely distributed across the tree (see Fig. 2 and Table S5). This could be related to the fact that the established tribal system for Australasian taxa is based on Northern Hemisphere taxa. With a predominantly Australasian taxon sampling, we can only make a few changes to the existing classification to avoid introducing unnecessary chaos and uncertainty into the taxonomy of Cerambycinae. Thus, we retain most of the problematic genera as *incertae sedis*, pending further research. Taxonomic changes for para- or polyphyletic tribes are only proposed when a strongly supported monophyletic clade involving its type genus was recovered. Changes to tribal or generic placement are made as follows based on our phylogenetic study, and a detailed list of changes can be found in Table S5:

a) Uracanthini Blanchard, 1851 (=Neostenini Lacordaire, 1868, **syn. nov.**): Lacordaire (1868) established the tribe Neostenini based on the assumptions that the mesocoxal cavity was open to mesepimeron in Neostenini while closed in Uracanthini. The memberships of the groups were later expanded by Aurivillius (1912) and McKeown (1947). Currently, there are three genera classified in Neostenini (*Aposites* Pascoe, 1865, *Mystrosa* Pascoe, 1864, and *Neostenus* Pascoe, 1857), and six in Uracanthini (*Aethiora* Pascoe, 1865, *Emenica* Pascoe, 1875, *Neouracanthus* McKeown, 1938, *Rhinophthalmus* Thomson, 1861, *Scolecobrotus* Hope, 1833, and *Uracanthus* Hope, 1833). Most of these genera were included in our phylogenetic analyses, and they all firmly cluster in a single well supported clade.
b) Aphanasiini Lacordaire, 1868: Includes *Aphanasium* Dejean, 1835, *Aphanosperma* Britton, 1969, but excludes *Myrsellus* McKeown, 1945, which is moved to tribe *incertae sedis*.
c) Aphneopini Lacordaire, 1868: *Zoedia* Pascoe, 1862 is excluded from Aphneopini and moved to tribe Pseudocephalini.
d) Dorcasomini Lacordaire, 1868: subfamily Dorcasominae is downgraded to a tribe in subfamily Cerambycinae, with the addition of *Hasenpuschia* Ślipiński and Escalona, 2016 and *Katerina* Ślipiński and Escalona, 2016; *Brachaciptera* Lea, 1917 is moved from tribe Molorchini to Dorcasomini.
e) Eroschemini Lacordaire, 1868: *Eroschema* Pascoe, 1858, with the addition of *Oroderes* Saunders, 1850 is moved from tribe Macronini to Eroschemini.
f) Macronini Thomson, 1861: Includes *Macrones* Newman, 1841, and *Enchoptera* Saunders, 1850, but excluding *Oroderes* Saunders, 1850.
g) Phoracanthini Newman, 1840: Includes taxa contained in the clade spanning *Kurandanus* Ślipiński and Escalona, 2016 to *Adrium* Pascoe, 1866 in Fig. 2 subclade B3. Within this clade, five genera (*Adrium* Pascoe, 1866, *Ectosticta* Pascoe, 1866, *Homaemota* Pascoe, 1866, *Monoplia* Newman, 1845, *Porithodes* Aurivillius, 1912) are moved from tribe Callidiopini to Phoracanthini. *Aridaeus* Thomson, 1861 is moved from tribe Dichophyiini to Phoracanthini. *Amphirhoe* Newman, 1840 is moved from tribe Rhopalophorini Blanchard, 1845 to Phoracanthini. *Calderia* Ślipiński and Escalona, 2016, and *Kurandanus* Ślipiński and Escalona, 2016 are assigned from tribe *incertae sedis* to Phoracanthini.
h) Pseudocephalini Thomson, 1860: Includes *Pseudocephalus* Newman, 1842, *Formicomimus* Aurivillius, 1897, and *Zoedia* Pascoe, 1862.
i) Pytheini Thomson, 1864: Includes *Brachytria* Saunders, 1840, and *Telocera* White, 1858, but excludes *Titurius* Pascoe, 1875, *Pempsamacra* Newman, 1838 and *Obrida* White, 1846, which are moved from Pytheini to tribe *incertae sedis*.
j) Rhagiomorphini Newman, 1841: Includes *Syllitus* Pascoe, 1859, *Tritocosmia* Newman, 1850, and *Stenoderus* Dejean, 1821, but excludes *Stenopotes* Pascoe, 1875, which is moved from Rhagiomorphini to tribe *incertae sedis*.
k) Strongylurini Lacordaire, 1868: Includes members of the clade spanning *Dictamnia* Pascoe, 1869 to *Strongylurus* Hope, 1834 in Fig. 2

subclade B2. The genera *Bebius* Pascoe, 1864 and *Omotes* Newman, 1842 are moved from Strongylurini to tribe *incertae sedis*.

With our taxon sampling we were unable to resolve relationships in the tribes Callidiopini, Hesperophanini, Phlyctaenodini and Tessarommatini stat. rev. Australasian genera classified in these tribes should remain as placed in their tribes until denser taxon sampling is undertaken, specifically including Pacific and Chilean taxa.

5. Conclusion

The Australasian Cerambycinae comprise two clades which can be separated by a distinct character involving antennal articulation. We propose that these clades diverged in the early Cretaceous. Clade A diversified in the Southern Hemisphere, while a possible re-entry into the Southern Hemisphere is posited for Clade B. Rapid speciation during the Late Cretaceous is apparent in the southern endemic Clade A. Adult beetles in this clade are mainly diurnal, visit flowers, and are often involved in various mimicry complexes with ants, bees, wasps or distasteful beetles (e.g., Lycidae), or they produce noxious defensive substances. The divergence times of most Australian genera in Clade B are estimated to the mid or late Paleogene, which coincides with the diversification of their modern host plant genera—including *Acacia, Eucalyptus,* and related Myrtaceous plants—following aridification of the Australian continent.

The previously recognized subfamily Dorcasominae is recovered as part of Clade A and thus is treated as a tribe of Cerambycinae. Our results reveal that the tribal classification of Australasian Cerambycinae is artificial, and the boundaries of some tribes are revised here based on phylogenetic and morphological evidence. Several additional tribes (mostly larger ones) are not resolved and require additional study.

CRediT authorship contribution statement

Mengjie Jin: Conceptualization, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Seunggwan Shin:** Methodology, Software, Formal analysis. **Lauren G. Ashman:** Validation, Writing – review & editing. **Richard A.B. Leschen:** Resources, Writing – original draft, Funding acquisition. **Andreas Zwick:** Methodology, Formal analysis. **Roger de Keyzer:** Resources, Writing – original draft. **Duane D. McKenna:** Conceptualization, Writing – original draft, Writing – review & editing, Funding acquisition. **Adam Ślipiński:** Conceptualization, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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