# The first phylogeny of Australasian Lamiinae longhorn beetles (Coleoptera: Cerambycidae) reveals poor tribal classification and a complex biogeographic history

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**Abstract.** We used phylogenomic data and information from the beetle fossil record to reconstruct the phylogeny and historical biogeography of Australasian longhorn beetles (Cerambycidae) in the subfamily Lamiinae. We further focused our study on the distribution of proposed diagnostic morphological characters in Lamiinae, and on the phylogeny of *Rhytiphora* Audinet-Serville, Australia's most species-rich genus of longhorn beetles. Lamiinae was monophyletic, but the majority of tribes were poly- or paraphyletic. Within Lamiinae, we recovered four main clades, including one clade mostly comprised of Australian endemic genera of probable Gondwanan origin. This clade also contained taxa that dispersed from Australia to New Zealand and experienced multiple independent instances of wing loss. Another of the four clades contained Australian genera that colonized the region from Asia, including *Rhytiphora*. The defining feature of *Rhytiphora*, the setose 'sex patches' on the male abdomen, was shared with many other Asian lamiine genera recovered in the same clade. Our results shed new light on the geographic and temporal origins of Australian Lamiinae, revealing an unexpected mixture of both ancient Gondwanan and recent Asian origins. Moreover, we confirmed rampant nonmonophyly at the tribal level among the Australasian genera of Lamiinae. Based on our results, we move 17 genera into Lamiinae *incertae sedis* and six genera into the tribe Ancitini Aurivillius. We also reinstate the tribe Niphonini Pascoe for part of the Asian-Australian Pteropliini Thomson and synonymize *Achriotypa* Pascoe with *Rhytiphora*.

## Introduction

Cerambycidae (a.k.a. longhorn beetles) is one of the most diverse beetle families, with over 36 000 described extant species worldwide (Wang, 2017). While the larvae of Cerambycidae mainly feed inside stressed or dead woody plants (thus playing a significant role in woodland nutrient recycling), some species attack healthy trees and are pests of global economic importance (Ślipiński & Escalona, 2013; McKenna *et al.*, 2016). Adult Cerambycidae exhibit a wide range of external morphologies, including wasp mimics and cryptic camouflaged species with highly sculptured exoskeletons (Linsley, 1959).

Phylogenetic relationships among the subfamilies of Cerambycidae, and the placement of Cerambycidae within superfamily Chrysomeloidea, have long been debated. The problematic taxonomy of Cerambycidae is primarily a consequence of the conflicting classification systems developed concurrently by early researchers and the general unreliability of adult morphological characters (Švácha & Lawrence, 2014). A recent

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molecular phylogeny of Chrysomeloidea supported the recognition of six to eight subfamilies within Cerambycidae, with Oxypeltidae, Disteniidae and Vesperidae as distinct families (Haddad *et al.*, 2018). Haddad *et al.* (2021) expanded this dataset to include the enigmatic taxon *Vesperoctenus* Bates (Vesperidae: Vesperoctenini Vives) and recovered a similar result. The molecular datasets used in these studies, comprised of anchored hybrid enrichment (AHE) data (Lemmon *et al.*, 2012) from over 500 nuclear loci, are substantially larger than all previous studies and include a more comprehensive sample of higher taxa.

The tribal classification of Cerambycidae is inadequate and mostly arbitrary. It is based mainly on local groups or single adult characters (Švácha & Lawrence, 2014; Haddad & McKenna, 2016), particularly within the two largest subfamilies: Lamiinae and Cerambycinae. Among others, the typological and often inaccurate publications of S. Breuning (1934–1987) have greatly confused matters at the generic and species levels in Lamiinae (Ślipiński & Escalona, 2013). Souza *et al.* (2020) is the only study that has assessed the lamiine tribes within a molecular phylogenetic framework. They recovered 11 tribes as monophyletic and 15 tribes as paraphyletic, and accordingly proposed several taxonomic changes. However, their study focused on the type genera of tribes and included very few Australasian species.

Australia is the only continent where Lamiinae is not the most speciose cerambycid subfamily (Fig. 1): there are currently over 1200 species of Australian Cerambycinae, in 142 genera, while the lamiines number fewer than 600 species, in 74 genera (Ślipiński & Escalona, 2016). Several genera of Cerambycinae are distributed in South America and Australia (e.g., *Syllitus* Pascoe). Assuming these genera are monophyletic, it seems likely that the Australian Cerambycinae have a Gondwanan origin. However, lamiines may have only reached Australia via Asia in the Miocene (Gressitt, 1956; Hall, 2013). Nevertheless, the number of endemic Australian lamiine genera is roughly equal to the number of genera shared with Asia (26 and 25, respectively), with another five genera found in both Australia and New Zealand (Ślipiński & Escalona, 2013); this renders the biogeographic origins of the Australian Lamiinae uncertain.

The New Zealand Lamiinae are poorly characterized, with many endemic genera and species in need of taxonomic revision (Kuschel & Emberson, 2008). Breuning (1950, 1962a) listed six genera in Parmenini Mulsant and 12 genera in Acanthocinini Blanchard, and a total of 130 species. Subsequently, six of these genera were dropped, and five others were reinstated (Kuschel, 1990; Leschen *et al.*, 2003). The majority of the New Zealand taxa are wingless, which is interesting given they probably originated from Melanesia (Gressitt, 1956; Schnitzler & Wang, 2005). Several Australian lamiine species are also wingless (across eight genera, four of which are endemic), though none of the Australian Cerambycinae have lost their wings (Ślipiński & Escalona, 2013, 2016).

The most speciose Australian cerambycid genus, *Rhytiphora* Audinet-Serville, comprises more than one-third of all Australian Lamiinae with approximately 200 described extant species (Ślipiński & Escalona, 2013). The genus is currently defined by the presence of two setose patches on the male abdominal ventrite 2 (with some exceptions; Ślipiński & Escalona, 2013). Nearly 40 Australian genera with this trait have been synonymized into *Rhytiphora* accordingly. However, at least 50 more *Rhytiphora* species are found in Southeast Asia, and many Asian genera in the same tribe (Pteropliini Thomson) may also belong to this broad morphological grouping.

In this study, we used the Neuropteroidea-specific AHE probes developed by Haddad *et al.* (2018) to generate DNA sequence data for 139 taxa, most of which were Australian Lamiinae. We then used these data to reconstruct the phylogeny and historical biogeography of the Australasian Lamiinae and study their morphology. Outgroups from other subfamilies of Cerambycidae were selected to facilitate the inclusion of fossil calibrations for dating analyses. Type genera for half of the tribes containing Australian Lamiinae are described from distant continents (Europe or the Americas; Tavakilian & Chevillotte, 2021). Consequently, we predicted that most of these poorly defined tribes would not be monophyletic. We also predicted that the Australian Lamiinae would be relatively recently derived from Asian taxa. Based on previous molecular work (D. McKenna, unpublished data), we expected that *Rhytiphora* would be monophyletic and closely related to *Pterolophia* Newman (Pteropliini) and *Mesosa* Latreille (Mesosini Mulsant).

## Methods

### Sample selection and sequencing

Following the taxonomy of Australian lamiine genera in Ślipiński & Escalona (2013), we chose 96 samples representing 27 Australian genera, eight New Zealand genera and eight Northern Hemisphere genera (collected from China, Thailand, Poland and the USA). Nearly half of the samples were drawn from the genus *Rhytiphora*. Ethanol-preserved specimens were used whenever possible to ensure better quality sequences (Table S1). Genomic DNA was extracted from beetle thoracic muscle, larval tissue or the whole body using the DNeasy 96 Blood and Tissue Kit protocol (Qiagen). Additional DNA extracts were provided by the McKenna Lab (University of Memphis, USA). Each sample's DNA quality was assessed using a Qubit fluorometer (Thermo Fisher) and a Fragment Analyser (Agilent). The samples were then normalized to 100–500 ng of DNA and sheared to a fragment size of 300–500 bp using a Q800R2 Sonicator (QSonica; 10 s on, 10 s off for seven mins total).

Libraries were prepared following the NEBNext Ultra II DNA Library Prep Kit protocol for Illumina (New England Biolabs). Adaptors were diluted 10-fold for the 11 lowest-concentration DNA samples, and SPRIselect beads (Beckman Coulter) were used at the ratios recommended for 300–400 bp size selection (except for the four lowest-concentration DNA samples, which were cleaned without size selection). Samples were dual indexed with one set of NEBNext indices to create 96 unique combinations and then pooled equimolarly (24 samples per pool at
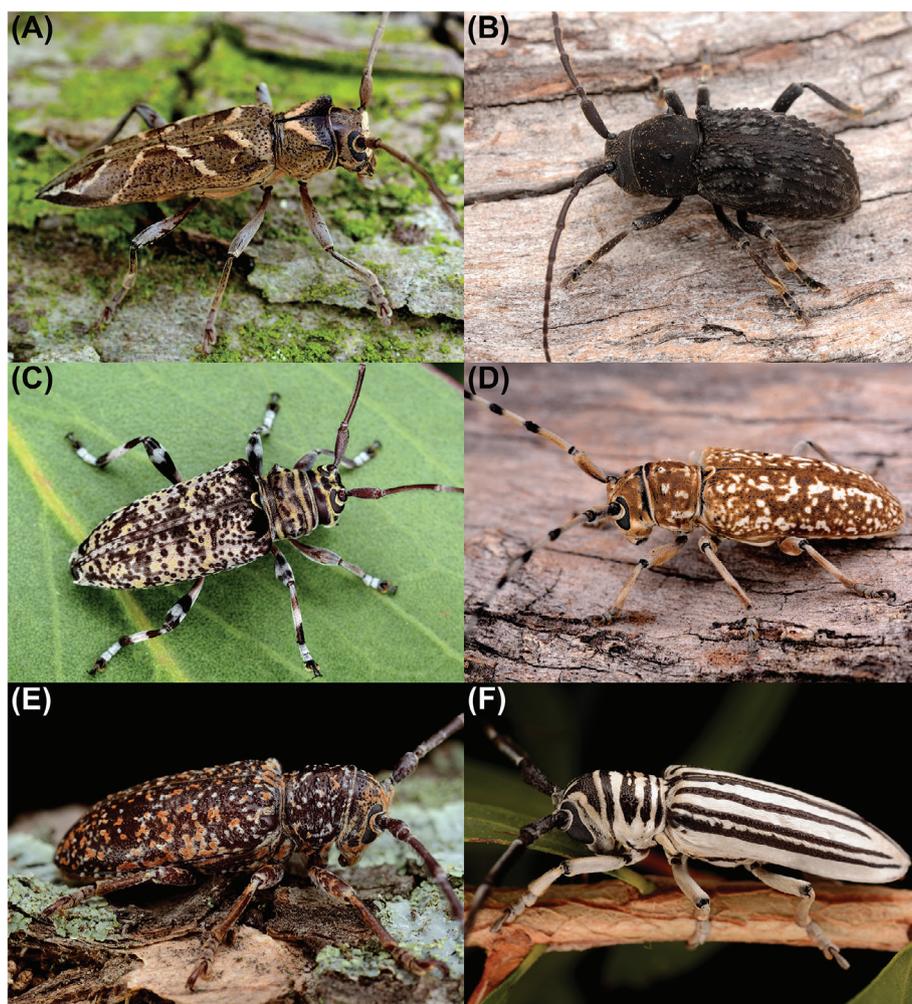
**Fig. 1.** Australian Lamiinae in their natural habitats. (A) *Temnosternus* sp. (B) *Athemistus* sp. (C) *Disterna* sp. (D) *Acalolepta ovina* (Pascoe). (E) *Rhytiphora rubeta* Pascoe. (F) *Rhytiphora dallasii* Pascoe. Photos by R. de Keyzer.

750 ng total). The sample pools were dried in a Savant Speed Vac Concentrator and dissolved in 7 μL of HPLC water.

Hybrid enrichment was performed following the myBaits Hybridization Capture for Targeted NGS protocol (Arbor Biosciences). Specifically, probes and libraries were allowed to hybridize for ~24 h at 65°C, bound to streptavidin-coated beads and washed (also at 65°C), then amplified using KAPA HiFi Hotstart polymerase (Roche) with an annealing temperature of 68°C and an extension time of 30 s (for <500 bp libraries). We used the AHE probes designed for Coleoptera (Haddad *et al.*, 2018). The four capture pools were pooled equimolarly (to 116 ng total) and sent to Novogene at UC Davis (USA) for 150 bp paired-end (PE) sequencing on a single Illumina HiSeq X Ten lane.

Many Asian genera that are potentially close relatives of the focal genus *Rhytiphora* were not available in ethanol; therefore, an additional 24 dried museum specimens were sampled (across Pteropliini and Mesosini; Table S1) for whole-genome shotgun (WGS) sequencing. DNA was extracted from whole bodies with the same Qiagen protocol as before, using individual Zymo-Spin IIC columns. Several samples had high molecular weight DNA and were sheared to approximately 200 bp using a Diagenode Biorupter (30 s on, 30 s off for 20 cycles). Libraries were prepared in half-reactions (25 μL input DNA) using the same NEBNext kit as before, but with no adaptor dilution and a right-side size selection performed after PCR amplification (using Beckman Coulter AMPure XP beads at 0.6× then 0.35×). Samples were single-indexed with two complementary 12-index NEBNext kits, pooled equimolarly, and sequenced on an Illumina NovaSeq6000 S1 flowcell (150 bp PE) at the Biomolecular Resource Facility, Australian National University (AUS).

*Bioinformatic workflow*

The procedure described by Peters *et al.* (2017) was generally followed for processing the sequence data. All analyses were performed on the University of Memphis High-Performance

Computing cluster (USA) or the CSIRO PEARCEY cluster (AUS). The 96 AHE samples were cleaned using Trimmomatic v0.39 (Bolger *et al.*, 2014) to remove adapter sequences and low-quality base calls, then assembled with SOAPdenovo2 v2.04-r241 (63-kmer; Luo *et al.*, 2012). The 24 dried WGS samples were cleaned in the same way but assembled using SPAdes v3.11.1 (Bankevich *et al.*, 2012) and checked for contamination by extracting the 28S sequences and blasting them against the NCBI database (BLAST+ v2.7.1; Camacho *et al.*, 2009). All of the assemblies were searched for the 522 orthologous loci used for AHE (Haddad *et al.*, 2018; Shin *et al.*, 2018) using Orthograph v0.6.3 (Petersen *et al.*, 2017) with three official gene sets from OrthoDB v7 (Waterhouse *et al.*, 2012): *Danaus plexippus* (Linnaeus) (Lepidoptera; Zhan *et al.*, 2011), *Nasonia vitripennis* (Walker) (Hymenoptera; Werren *et al.*, 2010) and *Tribolium castaneum* (Herbst) (Coleoptera; Richards *et al.*, 2008).

At this stage, another 21 samples previously sequenced by the McKenna Lab were added to the dataset (extra Australian Lamiinae and various outgroups; Table S1). All 141 samples (starting with the amino acid sequences) were aligned using MAFFT v7.450 (Katoh & Standley, 2013), and potentially misaligned sections were detected using Aliscore v2.0 (Misof & Misof, 2009; Kück *et al.*, 2010) and removed by AliCUT v2.31 (Kück, 2009). The nucleotide sequences were filtered in the same way and then aligned using Pal2Nal v14 (Suyama *et al.*, 2006), with the amino acid alignment as a guide. The amino acid (aa) and nucleotide (nt) sequences were concatenated into two separate datasets using ConcatMatrices v1.2 (http://phylotools.com; Jin *et al.*, 2020). The programme MARE v0.1.2-rc (Misof *et al.*, 2013) was used on the aa dataset to identify loci with low phylogenetic information (keeping all taxa). The aa and nt datasets were then concatenated again with only the 195 informative loci (out of the total 522 loci), resulting in the final datasets of 34 961 aa and 104 883 bp, respectively. These datasets were examined manually in AliView v1.26 (Larsson, 2014), and potential paralogs (identified as sequences overly divergent from congeners, which could mislead phylogenetic analyses) were removed. We also checked for cross-contamination by blasting the individual loci against themselves and the contigs of other samples from the same sequencing run. Three of the dried WGS samples had very high paralogous content and were subsequently removed from the datasets (Table S1). The nt dataset was also degeneracy-recoded with Degen v1.4 (http://phylotools.com; Zwick *et al.*, 2012), which replaces synonymous codons with IUPAC ambiguity codes.

*Phylogenetic analyses*

The three datasets (nt, degen and aa) were partitioned by locus and analysed with ModelFinder (Chernomor *et al.*, 2016; Kalyaanamoorthy *et al.*, 2017) to determine the best-fitting partitioning scheme and substitution models (using the -*rcluster* option to only consider the top 10% of merging schemes; Lanfear *et al.*, 2014). These partitioning schemes were then used to estimate phylogenetic relationships via maximum likelihood inference in the programme IQ-TREE v1.6.12 (Nguyen *et al.*, 2015). We ran 200 independent tree searches and 200 standard nonparametric bootstrap replicates for each dataset. We then mapped the bootstrap support values onto the maximum likelihood tree (−*sup* option). We also ran another analysis on the aa dataset after removing the five taxa with the highest percentage of missing data (Table S1) to determine whether these taxa affected the topology. The trees were visualized using FigTree v1.4.4 (Rambaut, 2018).

*Molecular dating analyses*

Five fossils were used as calibration points, conservatively set to one taxonomic level above their rank (i.e., fossils of reliable genera were assigned to subfamily root nodes). The oldest known cerambycid, *Cretoprionus liutiaogouensis* (Wang *et al.*, 2014), was used to constrain the most recent common ancestor (MRCA) of Cerambycidae to at least 112 Ma (dates from Ji *et al.*, 2004; as per Shin *et al.*, 2018). Four Baltic amber fossils (of extant genera sampled in our phylogeny) were used to constrain the MRCA of Cerambycinae, Lepturinae, Lamiinae and Spondylidinae: *Stenhomalus hoffeinsorum* (Vitali, 2014), *Necydalis zangi* (Vitali, 2011), *Pogonocherus jaekeli* (Zang, 1905) and *Nothorhina granulicollis* (Vitali, 2009). Given the ongoing debate about the age of Baltic amber (Eocene or Oligocene; Vitali & Daamgard, 2016), we set the minimum age calibrations to a compromise of 34 Ma (the Oligocene–Eocene boundary). The fossil calibrations were applied as soft minimum ages with truncated Cauchy distributions (default settings: offset 0.1, scale parameter 1, left tail probability 0.025). The root of the phylogeny (=Chrysomeloidea MRCA; McKenna, 2014) was constrained to have a hard maximum age of 223 Ma (option RootAge <2.23), following Shin *et al.* (2018).

To test the sensitivity of the dating analyses to prior choice and fossil placements, we also ran three additional analyses. First, a uniform prior distribution was applied to the same fossil calibrations: minimum 34 Ma (1% uncertainty) and maximum 100 Ma (20% uncertainty) for the Baltic amber fossils; minimum 112 Ma (1% uncertainty) and maximum 150 Ma (20% uncertainty) for *Cretoprionus*. We then ran two analyses with these prior settings (Cauchy or uniform) with an alternate fossil arrangement: *Cretoprionus* on the root of Prioninae and *Pogonocherus jaekeli* on the root of Pogonocherini Mulsant.

We created a new nucleotide dataset with the third codon positions removed entirely due to the uncertainty regarding how phylogenetic programmes parse ambiguity codes. We also removed any synonymous first codon positions coding for Leucine or Arginine, as determined by noLR v1.3 (http://phylotools.com; Regier *et al.*, 2008). The noLR dataset was analysed as a single block with ModelFinder to find the best-fitting substitution model out of the six available in both IQ-TREE and PAML v4.8 (Yang, 2007): JC69, K80, F81, HKY85, TN93 and GTR +/− gamma. We then ran 200 independent tree searches in IQ-TREE under the best model (GTR + F + I + G4).

We estimated divergence times with MCMCTree in the PAML package, using the noLR tree with the best likelihood score as the reference topology. The BASEML programme (PAML) was used to calculate ML estimates of the branch lengths under the GTR + gamma model (uncorrelated independent rates clock, single data partition). From the mean tree depth in the BASEML output, we set the gamma-Dirichlet prior for the overall substitution rate (rgene gamma) to G (2, 15) and the prior for the rate-drift parameter (sigma2 gamma) to G (1, 10). The MCMC chain was run for 100 000 generations as burn-in and then sampled every 100 generations until it reached 120 000 samples. Two MCMC runs with random seeds were compared using Tracer v1.7.1 (Rambaut *et al.*, 2018) to determine their convergence and effective sample sizes (>200); the posterior means of the node ages for both runs were also plotted against each other (Fig. S1) in R v3.6.1 (R Core Team, 2019).

### Biogeographical and morphological analyses

The dated phylogeny was trimmed to one tip per genus (for biogeography) or the Pteropliini and Mesosini clade (for morphology) using the *drop.tip* function in the R package APE v5.3 in RStudio v1.2.5019 (Paradis & Schliep, 2018; RStudio Team, 2019). We categorized the sampled taxa into the following geographic areas: Australia (including New Guinea), New Zealand (including off-shore Australian territories such as Lord Howe and Norfolk Islands), Asia (from China and India to Indonesia), Europe and the Americas (Table S2). Many genera occupy more than one area. Geographical distribution data were gathered from Ślipiński & Escalona (2013), the Titan database (Tavakilian & Chevillotte, 2021), Lamiines of the World (Roguet, 2020) and the Catalogue of Life (Roskov *et al.*, 2020).

The ancestral states were estimated using BioGeoBEARS v1.1.2 (Matzke, 2013) under six standard biogeographic models: DEC (Ree & Smith, 2008), DIVALIKE and BAYAREALIKE (likelihood interpretations of DIVA and BayArea; Ronquist, 1997; Landis *et al.*, 2013), with and without the free parameter *j* to model founder events (Matzke, 2014). The models were implemented using maximum likelihood, and the fit was compared with Akaike information criterion weights (Burnham & Anderson, 2002).

We also obtained morphological data for the lamiine genera. Each genus was scored as winged, wings polymorphic (a mixture of winged and wingless species) or wingless (all species wingless or brachypterous; Ślipiński & Escalona, 2013). For each species in the Pteropliini and Mesosini clade, the male abdominal ventrites were examined for the presence of setose sex patches (five species did not have male specimens available). The ancestral states for this clade were estimated using the *ace* function in APE for discrete characters (marginal maximum likelihood reconstruction, equal-rates model). The estimated node and tip states were then mapped onto the matching phylogeny with the *plotTree* function in Phytools v0.6-99 (Revell, 2012).

## Results

### Phylogenetic relationships

The three datasets (nt, degen and aa; Figs S2, S3, S4) produced very similar trees, albeit with poor support for some of the Lamiinae nodes (Fig. 2). Each cerambycid subfamily is monophyletic. Lamiinae is sister to the rest and divided into four main groups: clade A (Pogonocherini), clade B (Australian and New Zealand taxa), clade C (Saperdini Mulsant and Lamiini Latreille) and clade D (Pteropliini and Mesosini), with *Acanthocinus* Dejean and *Sybra* Pascoe sister to ((A + B) (C + D)).

Two genera (*Microlamia* Bates and *Zorilispe* Pascoe) are rogue taxa, occupying different positions within clade B in each analysis, always with low support (Figs S2, S3, S4). The dried WGS samples have relatively stable relationships within clade D, despite having high amounts of missing data (Table S1). When the aa dataset was analysed without the five highest-missing-data taxa, the topology was unchanged (Fig. S5).

A total of 14 lamiine tribes were sampled, with ten tribes represented by more than one genus (Fig. 2; Table S1). Of these 10 tribes, 6 are polyphyletic: Acanthocinini, Apomecynini Thomson and Parmenini are scattered widely across the tree, while Desmiphorini Thomson, Lamiini and Pteropliini are less dispersed but not monophyletic. Several genera are also not monophyletic: *Athemistus* Pascoe, *Somatidia* Thomson and *Stenellipsis* Bates (clade B).

### Dating, biogeography and morphology

We estimated a Jurassic origin of Chrysomeloidea (171 Ma, 95% CI: 223–126 Ma), with the MRCA of Cerambycidae occurring in the late Jurassic to early Cretaceous (129 Ma, 95% CI: 173–104 Ma; Fig. 3). The four main lamiine clades have similar root ages, from the Late Cretaceous to the Palaeocene (mean ages A–D: 64 Ma, 76 Ma, 71 Ma, 73 Ma). The MRCA of the core group of New Zealand taxa (*Ptinosoma* Breuning to *Stenellipsis*) was dated to the Palaeocene–Eocene (53 Ma, 95% CI: 74–39 Ma), and the root age of *Rhytiphora* was dated to the Eocene–Oligocene (38 Ma, 95% CI: 53–29 Ma). The analysis with uniform priors produced very similar results (Fig. S6). The analyses with an alternate fossil arrangement produced older date estimates (e.g., MRCA of Cerambycidae ~188 Ma) but the relative branch lengths within Lamiinae are unchanged (Figs S7, S8).

In the biogeography analysis, the DEC + J model is the best supported (Table S3). The ancestral distributions of the deeper nodes (Cerambycidae and its subfamilies) are mostly ambiguous, although Lamiinae is probably Asian (Fig. 4). The four lamiine clades have the following estimated ancestral ranges: clade A is most likely Asian, clade B is Australian (with several incursions into Asia and New Zealand), clade C and clade D are Asian (although with two American taxa amongst the Mesosini). The wingless lamiine genera are all in clade B, mostly clustered in one group (*Stenellipsis* to *Zorilispe*; Fig. 4).
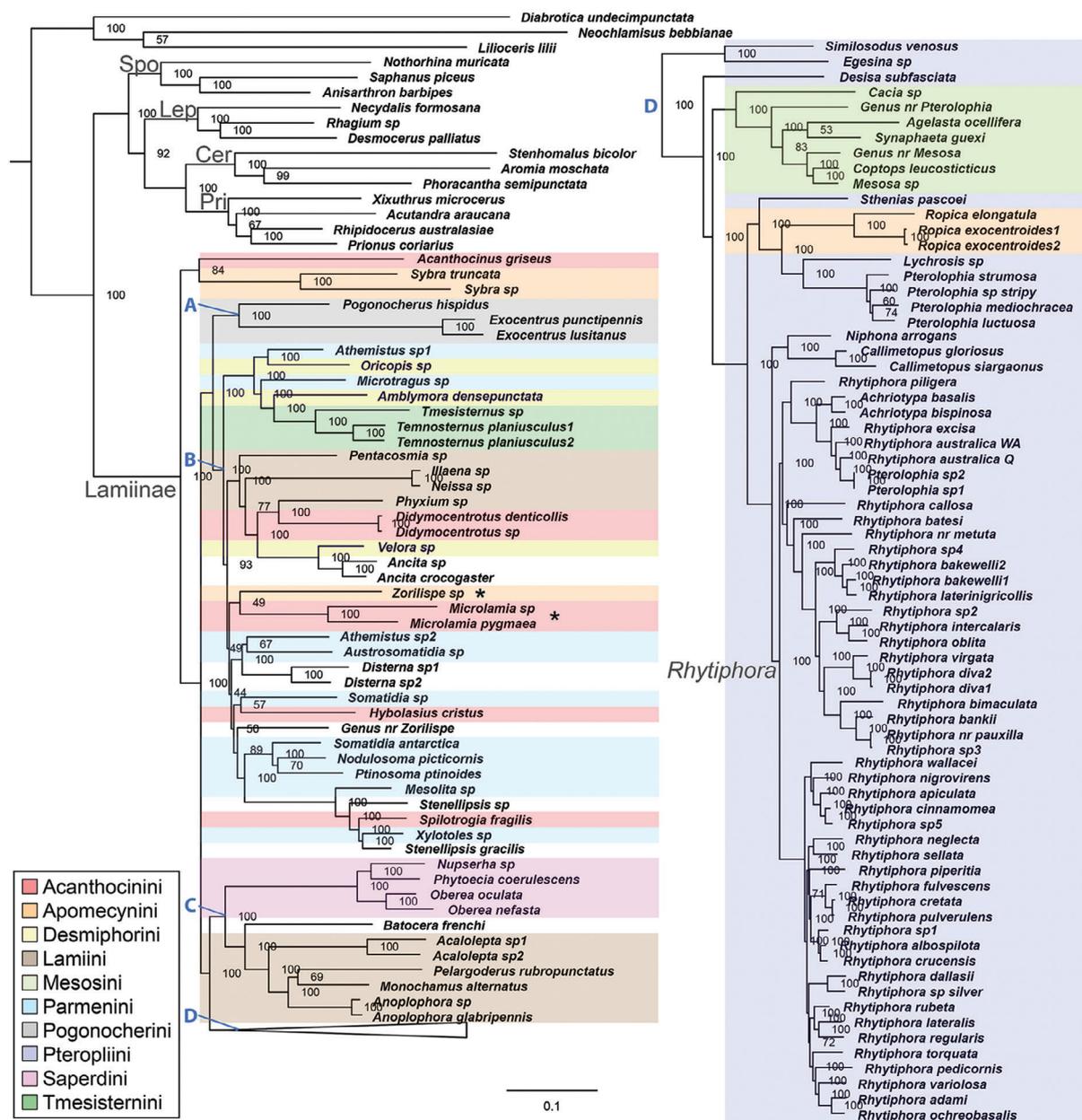
**Fig. 2.** Maximum likelihood phylogeny of Cerambycidae: partitioned IQ-TREE analysis of the nucleotide dataset. Branch supports are bootstrap values (good support: >80%). Subfamilies are labelled (Spo = Spondylidinae, Lep = Lepturinae, Cer = Cerambycinae, Pri = Prioninae), as is the genus *Rhytiphora*. Lamiinae is divided into four main clades (A–D), with clade D expanded on the right. Branches are coloured by tribe, as per the key (only tribes with more than one genus are shown). Rogue taxa (tips with unstable positions in the tree) are labelled with an asterisk (*).

The vast majority of the taxa in clade D have setose sex patches on the male abdominal ventrites (Table 1); clade D's ancestor is estimated to have had sex patches (Fig. 5). The Pteropliini (including *Ropica* Pascoe) mostly have smaller patches, hidden beneath the thickened fringe of ventrite 1, except for *Desisa* Pascoe, *Sthenias* Dejean and approximately half of the *Rhytiphora* species (which have larger, more easily visible patches). The Mesosini have three sets of visible patches on the outer edges of ventrites 2–4 or no patches at all.

## Discussion

### Lamiinae tribal classification

Our results support the hypothesis that the tribes present in Australia but with type genus localities in Europe or the Americas are not monophyletic. Five out of the eight Europe/America-centric tribes sampled are polyphyletic in our tree (Fig. 2): Acanthocinini, Desmiphorini, Lamiini,
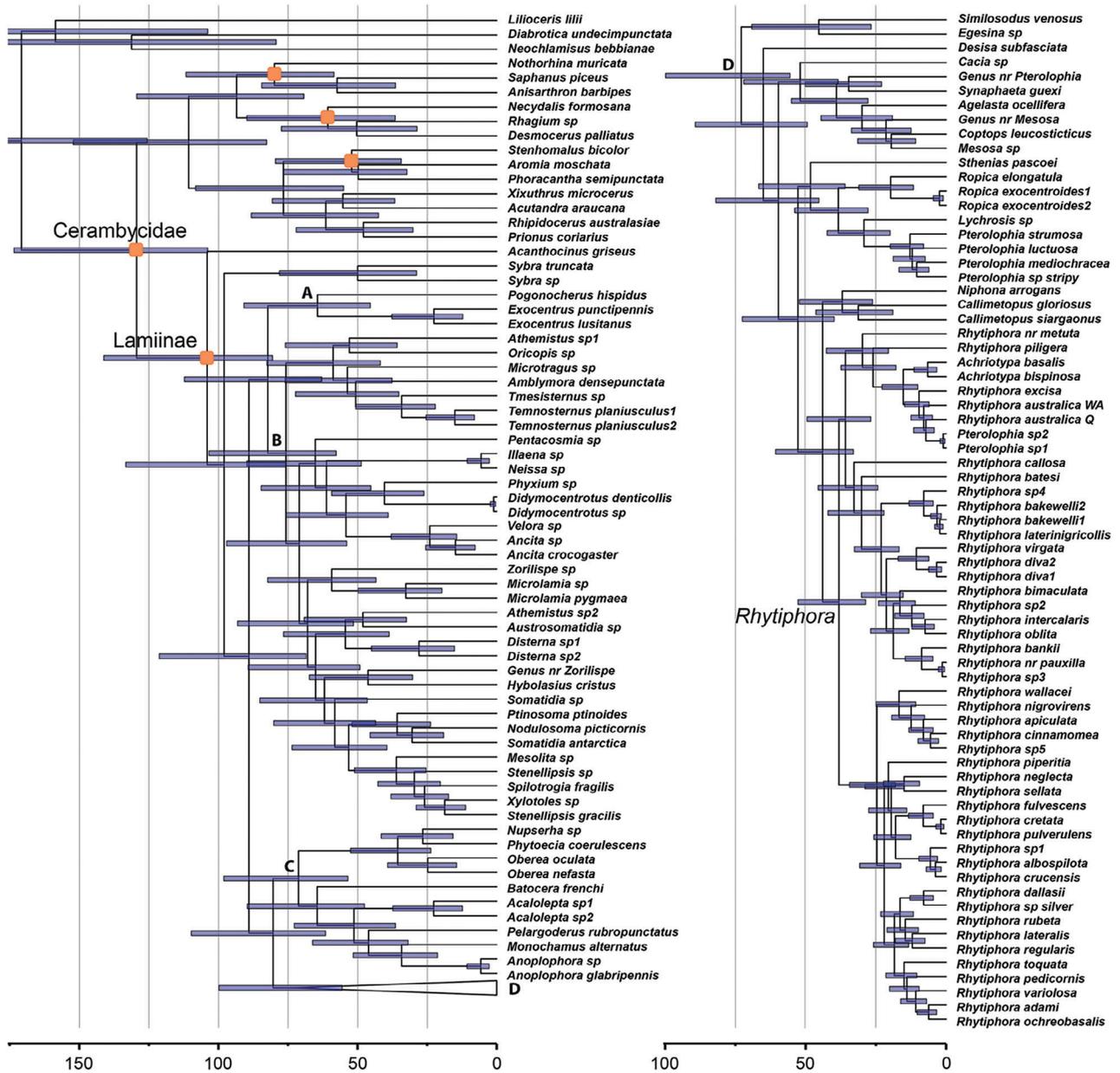
**Fig. 3.** Fossil-calibrated chronogram of Cerambycidae: MCMCTree estimates of lineage divergence times based on the ML analysis of the 'noLR' nucleotide dataset. Blue bars show 95% confidence intervals of node ages and the scale bar is in millions of years (Ma). Cerambycidae, Lamiinae, *Rhytiphora* and the four main lamiine clades (A–D) are labelled, with clade D expanded on the right. Fossil calibration points (with Cauchy priors) are indicated with orange squares.

Parmenini and Pteropliini. The other two tribes (Saperdini and Pogonocherini) are monophyletic. However, this problem is not restricted to the Europe/America-centric tribes: the Asia-centric tribe Apomecynini is also polyphyletic. For the Australia-centric tribes, we sampled only one genus each (Ancitini Aurivillius: *Ancita* Thomson, Enicodini Thomson: *Stenellipsis* and Zygocerini Thomson: *Disterna* Thomson), so we cannot draw conclusions about their monophyly except for Ancitini, which contains only the genus *Ancita* (Tavakilian

& Chevillotte, 2021). Interestingly, the three most speciose Australian lamiine genera (*Athemistus*, *Sybra* and *Rhytiphora*; Ślipiński & Escalona, 2013) are only distantly related to one another.

Our Lamiinae phylogeny is remarkably similar to that of Souza *et al.* (2020), despite having only ~15% overlap in taxon sampling and many more loci (Fig. 6; Table 2). In terms of taxa, both phylogenies recovered *Pogonocherus* Dejean as a near relative of *Exocentrus* Dejean (our clade A, their clade I), *Phytoecia*
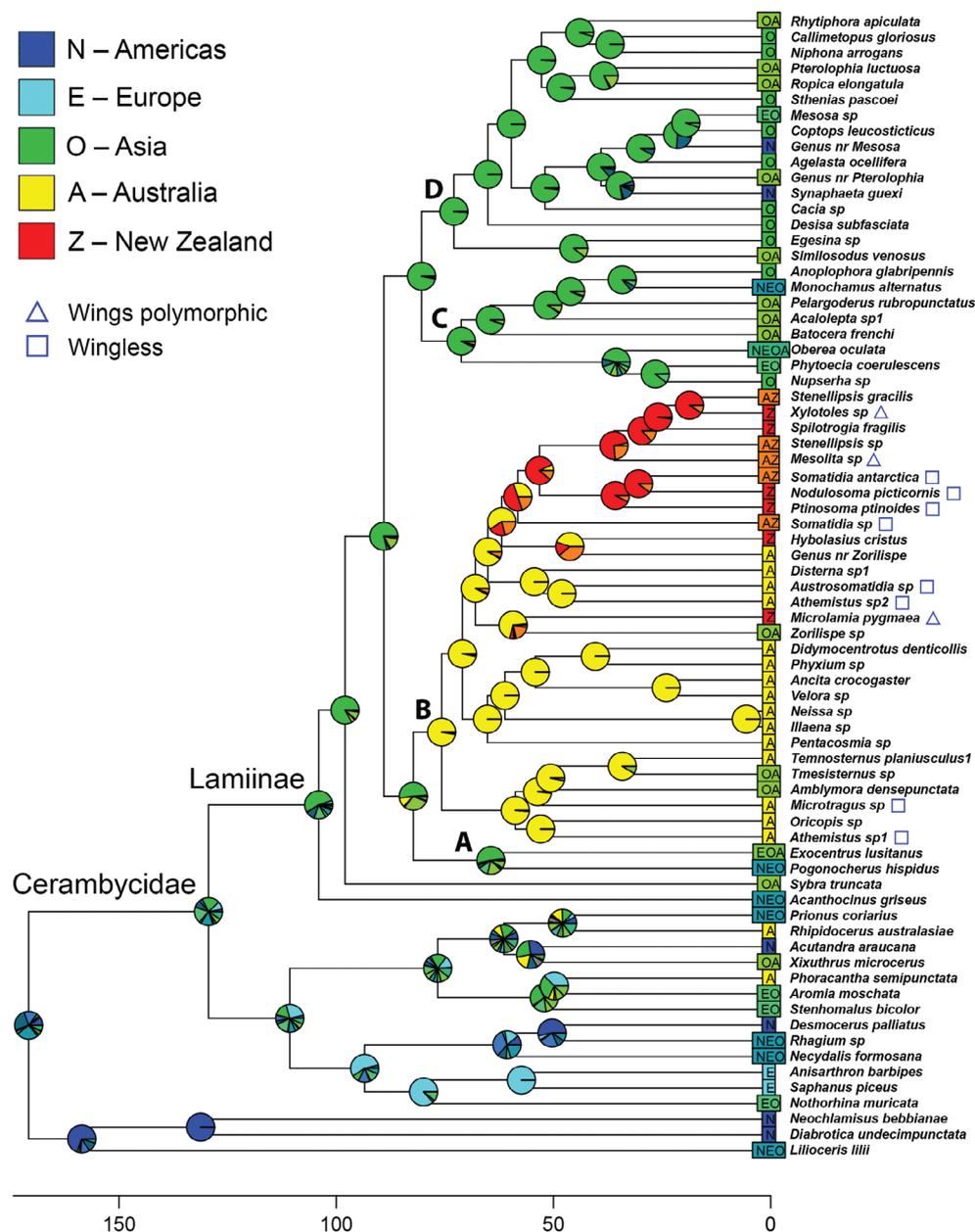
**Fig. 4.** Ancestral geographic range estimation and present-day winglessness of Cerambycidae: ancestral states reconstructed using BioGeoBEARS under the DEC + J model on the dated MCMCTree phylogeny (Fig. 3). A key to the geographic range colours and winglessness symbols is shown at the top left. Pie charts show the probability of the ancestral states at each node. Scale bar is in millions of years (Ma). Cerambycidae, Lamiinae and the four main lamiine clades (A–D) are labelled.

Dejean as a close relative of *Oberea* Dejean (our clade C, their clade O) and *Batocera* Dejean as a near relative of the sampled genera of Lamiini (their clades J–L). In addition, Pteropliini was rendered paraphyletic by *Ropica* and *Mesosa* (our clade D, their clade M). Their clade E (Enicodini) is likely equivalent to our much larger clade B, which mainly consists of Australasian genera, including *Stenellipsis*. Our results are also congruent with the latest phylogeny of Cerambycidae and select other families of Chrysomeloidea, based on mitochondrial

genomes: Nie *et al.* (2021) recovered a clade containing, among other taxa, the genera in our clade C (*Oberea*, *Batocera*, *Anoplophora* Hope and *Monochamus* Dejean) and also a close relationship between *Mesosa* and *Niphona* Mulsant (our clade D).

Although Pogonocherini is monophyletic in our analyses, the more diverse sampling in Souza *et al.* (2020) revealed this tribe to be paraphyletic. Whether *Stenellipsis* belongs in Enicodini is more challenging to address: Souza *et al.* (2020)

**Table 1.** Presence and type of male abdominal sex patches in sampled species of Lamiinae, clade D.

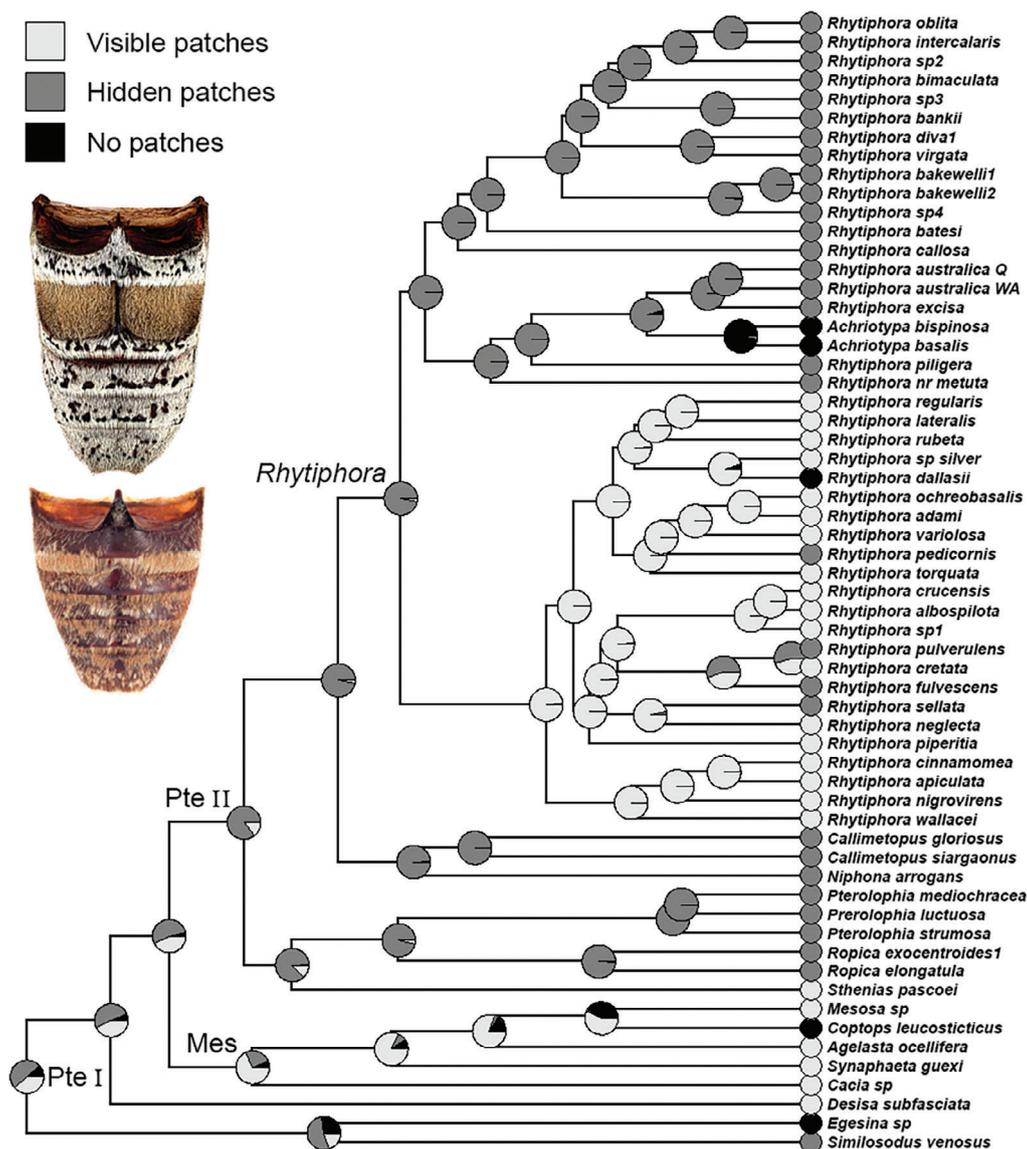| Tribe | Genus | Species | Patch type | Ventrites | Notes |
|-------|-------|---------|------------|-----------|-------|
| Apomecynini | *Ropica* | *elongatula* | Hidden | 2 | |
| Apomecynini | *Ropica* | *exocentroides* | Hidden | 2 | |
| Mesosini | *Agelasta* | *ocellifera* | Visible | 2–4 | Outer edge |
| Mesosini | *Cacia* | *sp* | Visible | 2–4 | Outer edge |
| Mesosini | *Coptops* | *leucosticticus* | Absent | NA | |
| Mesosini | '*Genus near Mesosa*' | *sp* | | | No male available |
| Mesosini | '*Genus near Pterolophia*' | *sp* | | | No male available |
| Mesosini | *Mesosa* | *sp* | Visible | 2–4 | Outer edge |
| Mesosini | *Synaphaeta* | *guexi* | Visible | 2–4 | Outer edge |
| Pteropliini | *Achriotypa* | *basalis* | Absent | NA | |
| Pteropliini | *Achriotypa* | *bispinosa* | Absent | NA | |
| Pteropliini | *Callimetopus* | *gloriosus* | Hidden | 2 | |
| Pteropliini | *Callimetopus* | *siargaonus* | Hidden | 2 | |
| Pteropliini | *Desisa* | *subfasciata* | Visible | 2 | Central; ventrite 2 enlarged |
| Pteropliini | *Egesina* | *sp* | Absent | NA | |
| Pteropliini | *Lychrosis* | *sp* | | | No male available |
| Pteropliini | *Niphona* | *arrogans* | Hidden | 2 | |
| Pteropliini | *Pterolophia* | *luctuosa* | Hidden | 2 | |
| Pteropliini | *Pterolophia* | *mediochracea* | Hidden | 2 | |
| Pteropliini | *Pterolophia* | '*stripy sp*' | | | No male available |
| Pteropliini | *Pterolophia* | '*sp1/sp2*' | | | No male available |
| Pteropliini | *Pterolophia* | *strumosa* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *adami* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *albospilota* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *apiculata* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *australica (QLD)* | Hidden | 2 | Ventrite 1 thin fringe |
| Pteropliini | *Rhytiphora* | *australica (WA)* | Hidden | 2 | Ventrite 1 thin fringe |
| Pteropliini | *Rhytiphora* | *bakewelli/laterinigricollis* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *bankii* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *batesi* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *bimaculata* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *callosa* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *cinnamomea* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *cretata* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *crucensis* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *dallasi* | Absent | NA | |
| Pteropliini | *Rhytiphora* | *diva* | Hidden | 2 | Ventrite 1 thin fringe |
| Pteropliini | *Rhytiphora* | *excisa* | Hidden | 2 | Ventrite 1 thin fringe |
| Pteropliini | *Rhytiphora* | *fulvescens* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *intercalaris* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *lateralis* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *neglecta* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *nigrovirens* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | '*sp near metuta*' | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *oblita* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *ochreobasalis* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *pedicornis* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *piligera* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *piperitia* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *pulverulens* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | *regularis* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *rubeta* | Visible | 2 | Patch covers entire ventrite 2 (enlarged) |
| Pteropliini | *Rhytiphora* | *sellata* | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | '*silver sp*' | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | '*sp1*' | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | '*sp2*' | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | '*sp3/near pauxilla*' | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | '*sp4*' | Hidden | 2 | |
| Pteropliini | *Rhytiphora* | '*sp5*' | | | No male available |
| Pteropliini | *Rhytiphora* | *torquata* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *variolosa* | Visible | 2 | Central |
| Pteropliini | *Rhytiphora* | *virgata* | Hidden | 2 | Ventrite 1 thin fringe |
| Pteropliini | *Rhytiphora* | *wallacei* | Visible | 2 | Central |
| Pteropliini | *Similosodus* | *venosus* | Hidden | 2 | |
| Pteropliini | *Sthenias* | *pascoei* | Visible | 2–4 | Central; ventrites 3–4 hairs but no pit |

**Fig. 5.** Presence of male abdominal sex patches in Lamiinae, clade D: ancestral states reconstructed with APE using the dated MCMCTree phylogeny (Fig. 3). A key to the sex patch types is shown at the top left. Below the key are two images of *Rhytiphora* spp. (abdomen, ventral side) demonstrating visible (top) and hidden (bottom) sex patches. Pie charts show the probability of the ancestral states at each node. Major tribes (Pte = Pteropliini, Mes = Mesosini) and the genus *Rhytiphora* are labelled.

sampled *Stenellipsis* from New Caledonia and found it was most closely related to their other New Caledonian taxa (mostly Enicodini). Our dataset does not include any New Caledonian taxa. However, our two *Stenellipsis* samples are grouped with New Zealand taxa from Acanthocinini and Parmenini (whose morphology is quite different from Enicodini). More extensive sampling of taxa from across Oceania is needed to establish these taxonomic boundaries better.

In this section, we focus on the systematics of clade B, which has the largest number of sampled genera. We discuss clade D separately below. Our results demonstrate the inadequacy of the current tribal classification of Australasian lamiine genera: 81%

of the genera in clade B were placed in nonmonophyletic tribes (Fig. 2). The best solution would be to move these genera out of their widespread tribes and into Australasia-centric tribes such as Ancitini or Zygocerini. New tribes will be necessary as well, but difficult to determine until more of the Australasian genera have been sequenced; this paper only samples about half of the Australian genera listed in Ślipiński & Escalona (2013), and half of the New Zealand genera in Leschen *et al.* (2003). The unsampled Australasian genera will be left in their current tribes, although these are almost certainly incorrect.

None of the Australasian Acanthocinini genera are closely related to the type genus *Acanthocinus*. In Nie *et al.* (2021),
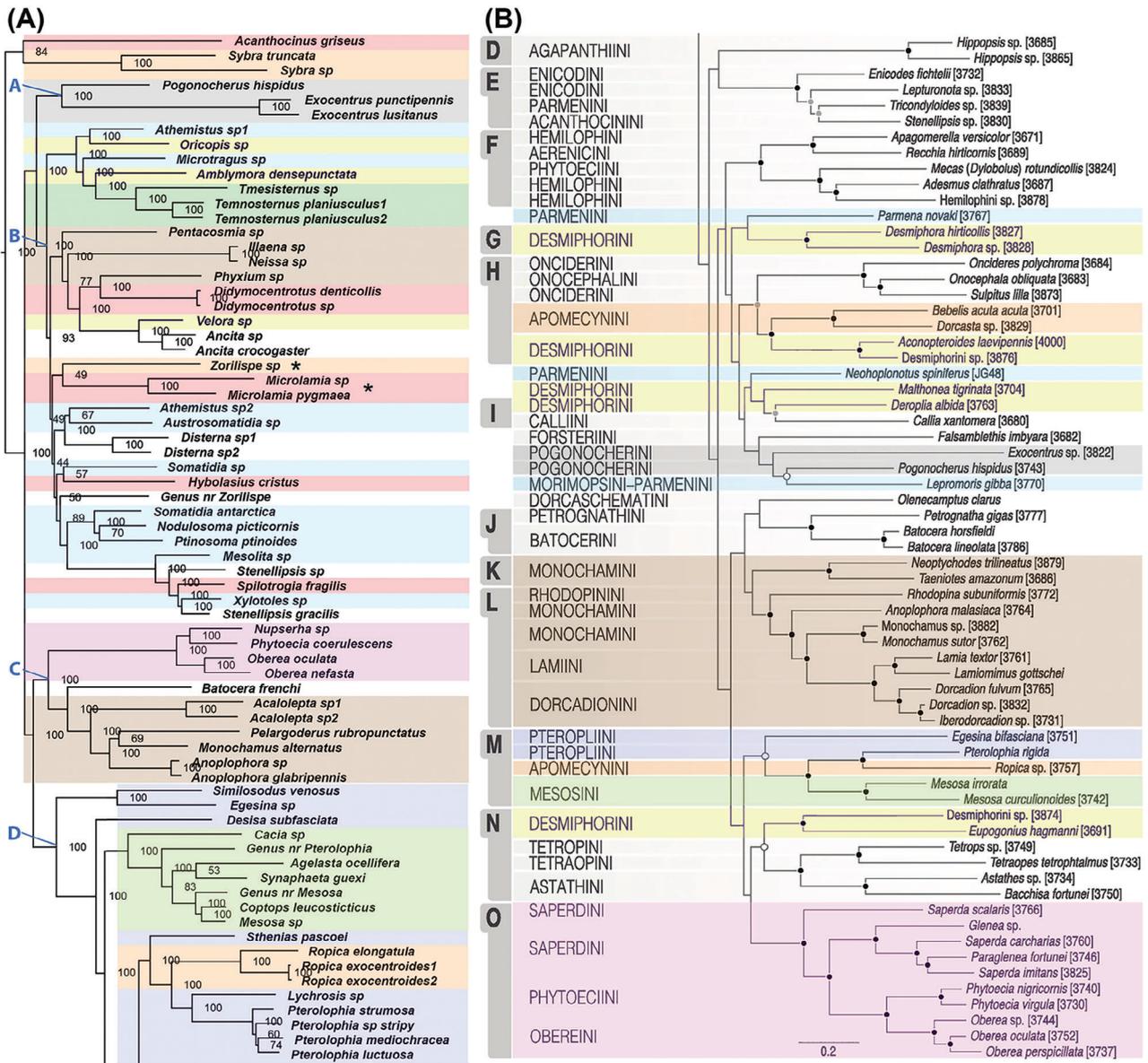
**Fig. 6.** Comparison of two Lamiinae molecular phylogenies. (A) Section of our Fig. 2. (B) Section of Fig. 2A from Souza *et al.* (2020), edited to match our figure's tribal colouring.

*Apomecyna* Dejean was recovered as sister to the rest of Lamiinae with *Acanthocinus* (and others), which suggests that *Sybra* is in the correct tribe; however, the other two Apomecynini (*Zorilispe* and *Ropica*) need to be moved out. Both *Desmiphora* Audinet-Serville and *Parmena* Dejean were sequenced by Souza *et al.* (2020): they are part of a sizeable American-European clade, which includes *Pogonocherus*, so we are assuming none of our Australasian taxa belong to the 'true' Desmiphorini or Parmenini. Similarly, Souza *et al.* (2020) found that *Rhodopina* Gressitt is closely related to *Monochamus* and *Lamia* Fabricius, so the four Australasian genera in clade B that were formerly

assigned to Rhodopinini Gressitt (now Lamiini) do not belong to this tribe; indeed, an alternate classification for these four genera (*Illaena* Erichson, *Neissa* Pascoe, *Pentacosmia* Newman and *Phyxium* Pascoe) places them in Desmiphorini (Tavakilian & Chevillotte, 2021).

The genera *Athemistus*, *Oricopis* Pascoe, *Microtragus* White and *Amblymora* Pascoe form a well-supported paraphyletic group closely related to Tmesisternini Blanchard. Several highly derived morphological traits define Tmesisternini (e.g., prognathous head; Gressitt, 1984), which are not found in these other four genera; therefore, we move these genera to Lamiinae

**Table 2.** Comparison of biogeographic sampling, by genus, in this study, versus Souza *et al.* (2020).

| Study | Number of lamiine genera sampled [estimated total extant genera] | | | |
|---|---|---|---|---|
| | Australasia [300] | Asia [1100] | Europe & Africa [800] | Americas [800] |
| Ashman *et al.* | 39 (26 endemic, 13 shared with Asia) | 12 | 5 | 2 |
| Souza *et al.* | 11 (4 endemic) | 14 | 29 | 43 |
| Genera sampled in both studies | 5 (1 endemic) | 4 | 5 | 0 |

The total number of genera is estimated from Roguet (2020).

*incertae sedis*, pending further investigation. We propose that the next well-supported group (*Pentacosmia* to *Ancita*) be transferred into Ancitini, since *Pentacosmia*, *Phyxium* and especially *Velora* Thomson, are morphologically quite similar to the type genus *Ancita* (generally small and oval-bodied with clavate femurs, long scape and/or tufted antennae). The samples identified as *Illaena* and *Neissa* are more closely related than most congeneric species in the phylogeny (e.g., the two *Ancita* species). The two genera are also very similar morphologically. They should perhaps be synonymized, but this is beyond the scope of this paper, particularly since we have not sequenced the type species of either genus.

The two rogue taxa, *Zorilispe* and *Microlamia*, are unresolved, and therefore, placed in Lamiinae *incertae sedis*. The taxon identified as *Athemistus* 'sp2' probably belongs to an undescribed genus: its general morphology (e.g., spinose pronotum) aligns it with *Athemistus*, but its small body size (6 mm) is more akin to its sister genus *Austrosomatidia* McKeown. Both of these genera look very different than their sister genus *Disterna* (Zygocerini), so they are also moved to Lamiinae *incertae sedis*. The final group in clade B consists of nearly all the genera shared with or endemic to New Zealand. Since the deeper nodes are poorly resolved, and our sampling is incomplete, we place all of these genera (*Somatidia*, *Hybolasius* Bates, *Nodulosoma* Breuning, *Ptinosoma*, *Mesolita* Pascoe, *Spilotrogia* Bates, *Xylotoles* Newman) in Lamiinae *incertae sedis*.

The genus *Somatidia* is not monophyletic. The type species *Somatidia antarctica* (White) is in a well-supported clade with other New Zealand genera (the core New Zealand group), while our Australian sample is recovered with *Hybolasius* and an undescribed Australian genus in a closely related clade. This suggests the Australian species of *Somatidia* should be placed in their own genus, such as Breuning's subgenus *Villososomatidia* (Breuning, 1956), but this will require more detailed sampling. As noted by Ślipiński & Escalona (2013), *Stenellipsis* is part of a complex with *Mesolita* and *Xylotoles* (and, in our tree, *Spilotrogia*). It seems likely that the New Zealand species of *Stenellipsis* belong to *Xylotoles* (assuming the type species *S. bimaculatus* (White) is closely related to *S. gracilis* (White)), while the Australian species (*S. sp* in our tree) belong to a separate genus: *Brachyrhabdus*, described from Queensland by Aurivillius (1917) and synonymized with *Stenellipsis* by Ślipiński & Escalona (2013). But again, such genus-level reclassification is beyond the scope of this paper.

*Biogeography and winglessness*

Our dating analyses place the root of Chrysomeloidea in the Jurassic (Fig. 3; original fossil placement), which agrees with previous estimates (e.g., Wang *et al.*, 2014; Zhang *et al.*, 2018; McKenna *et al.*, 2019; Nie *et al.*, 2021). The Cerambycidae began to diversify in the Cretaceous, coincident with the rise of angiosperms (their main host plants) to ecological dominance (Magallón & Castillo, 2009; Wang, 2017) and consistent with patterns observed in other groups of phytophagous beetles (e.g., McKenna *et al.*, 2009). The estimated crown age of Lamiinae is markedly older than the other subfamilies; however, this is probably an artefact of the relatively much deeper taxon sampling in Lamiinae. We will, therefore, focus our discussion on the two more deeply sampled lamiine clades, B and D.

The MRCA of clade B was dated to approximately the late Cretaceous in Australia (Figs 3, 4). This is inconsistent with our hypothesis of a recent Asian origin of the Australian Lamiinae since the Asian plate did not fully connect with the Australian plate until the early Miocene (Hall, 2013). Instead, our results suggest that the Australian endemic genera have a Gondwanan origin, making their placement in largely Laurasian tribes problematic (Fig. 2). Future studies should include lamiines from South America to further explore the possibility of a Gondwanan origin for the Australian endemic lamiines. Several other genera in clade B might have expanded westward from Australia into Southeast Asia (e.g., *Amblymora* and *Tmesisternus* Latreille), as seen in fig wasps and Jezebel butterflies (Cruaud *et al.*, 2011; Müller *et al.*, 2013).

Clade B also contains all of the New Zealand samples, with the core group (*Ptinosoma* to *Stenellipsis*) root age in the Palaeocene–Eocene (Figs 3, 4). Given that Zealandia separated from Gondwana in the Late Cretaceous (Kamp, 1986), and the New Zealand Lamiinae are less diverse than the Australian taxa, New Zealand was likely colonized via post-Gondwanan dispersal from other areas (Yeates & Cassis, 2017). This is a typical pattern in New Zealand taxa (Wallis & Trewick, 2009; but see Buckley *et al.*, 2020). Evidence of long-distance dispersal from Australia to New Zealand in scale insects and diving beetles (Hardy *et al.*, 2008; Toussaint *et al.*, 2015b) is consistent with this observation. Further sampling will be needed to determine whether the New Zealand taxa arrived from Australia (to the west) or Melanesia (to the north; Gressitt, 1956). Since the position of *Microlamia* is unresolved, it is also unclear how many dispersal events occurred.

The majority of the New Zealand taxa are wingless to some degree (64%; Fig. 4), which seems contradictory to a migrant origin. They may have developed secondary winglessness after arrival (Wagner & Liebherr, 1992), although there are examples of flightless phytophagous beetles dispersing over ocean barriers (Baird *et al.* 2021), perhaps via floating vegetation (Toussaint *et al.*, 2015a; Tänzler *et al.*, 2016). Often winglessness is connected to an increased diversification rate in beetles (Ikeda *et al.*, 2012; Möst *et al.*, 2020), but this does not seem to be the case in the relatively depauperate New Zealand Lamiinae (Leschen *et al.*, 2003). Winglessness is not confined to New Zealand taxa, either: three Australian endemic genera are fully wingless (*Austrosomatidia*, *Athemistus* and *Microtragus*). Wing loss has evolved multiple times in the tribe Parmenini (partly defined by winglessness; Breuning, 1950) and also in other genera. Thus, Parmenini is (unsurprisingly) polyphyletic.

Clade D has a late Cretaceous root age, like clade B, but is estimated to be of Asian origin (Figs 3, 4). Four genera seem to have dispersed into Australasia independently: *Similosodus* McKeown, *Ropica*, *Pterolophia* and *Rhytiphora*. Clade C also contains several genera that probably spread from Asia into Australasia, such as *Acalolepta* Pascoe. Our Australian and Chinese *Acalolepta* samples (Table S1) diverged approximately 23 Ma, when the Sula spur of the Australian plate collided with Sulawesi (Hall, 2013). Several plants and animals have moved between Australasia and Asia following this collision (Crayn *et al.*, 2015; Oliver & Hugall, 2017), including insects (Leys *et al.*, 2002; Kodandaramaiah & Wahlberg, 2007; Balke *et al.*, 2009; Tänzler *et al.*, 2016).

However, the early divergences within the genus *Rhytiphora* predate the Miocene Sula spur collision (root age dated to the Eocene–Oligocene; Fig. 3). The genus could have begun diversifying before it reached Australasia, but it is also possible that *Rhytiphora* colonized the Australian plate before the Miocene. There were island arcs present in the Oligocene, which would have facilitated dispersal between Asia and Australasia (de Boer & Duffels, 1996; Jønsson *et al.*, 2011; Zahirovic *et al.*, 2016). Furthermore, there is evidence of similar Eocene–Oligocene divergences in several taxa of lizards and birds (Skinner *et al.*, 2011; Oliver *et al.*, 2018, 2020). The six New Guinean *Rhytiphora* samples (e.g., *R. diva2* (Thomson), *R. wallacei* (Pascoe); Table S1) are intermingled with the Australian ones, suggesting much more recent taxa exchange via the Pliocene–Pleistocene land bridge (Voris, 2000).

### *Rhytiphora and relatives (clade D)*

As predicted, our dataset places *Rhytiphora* in a clade with Mesosini and the other Pteropliini genera, along with *Ropica* (Fig. 2). Interestingly, its closest relatives are not Australian but the Asian genera *Niphona* and *Callimetopus* Blanchard, both sampled from the Philippines (Fig. 4; Table S1). *Rhytiphora* itself is monophyletic with the inclusion of *Achriotypa* Pascoe and an unknown *Pterolophia* species, closely related to *R. excisa* (Breuning) and *R. australica* (Breuning) (both originally described in Pterolophia; Ślipiński & Escalona, 2013). Given

that we sequenced all of the extant *Achriotypa* species, we can confidently synonymize this genus with *Rhytiphora*.

The presence of setose sex patches on the male abdomen, currently the defining trait of *Rhytiphora*, is not restricted to this genus: 80% of the genera in clade D have sex patches (Fig. 5; Table 1). The Pteropliini taxa have a single set of sex patches on ventrite 2, of varying size, while the Mesosini have three sets of visible patches on ventrites 2–4. The Pteropliini genus *Sthenias* is an exception to this rule: it has three sets of patches, like the Mesosini, but the patches on ventrites 3–4 are less developed than those on ventrite 2. Both tribes have at least one loss of sex patches, even within *Rhytiphora* (*R. dallasii* Pascoe). All of the *Rhytiphora* species with more extensive, visible patches are in the same clade; however, this clade does include species with hidden or absent patches.

Clade D's overall structure (i.e., a paraphyletic Pteropliini) is reflected in Breuning's key to Asian tribes (Breuning, 1962b), which divides Pteropliini into three parts. Breuning distinguishes Mesosini by an oblique carina at the apex of the antennal scape; this character is present in all of our sampled Mesosini that were available for post-sequencing morphological examination. It should be noted that a carinate scape is also found in unrelated Lamiinae, such as *Acalolepta* (clade C) and *Ancita* (clade B).

Unfortunately, the type genus of Pteropliini, *Pteroplius* Lacordaire, has not been sequenced. However, considering its morphology (similar to Lamiini) and its location (Brazil; Tavakilian & Chevillotte, 2021), it is unlikely to be closely related to our Asian-Australian Pteropliini. As discussed above, *Ropica* most likely does not belong to the 'true' Apomecynini. Therefore, we are reinstating the tribe Niphonini Pascoe (as used by McKeown, 1947) to include the following genera: *Sthenias*, *Ropica*, *Pterolophia*, *Niphona*, *Callimetopus* and *Rhytiphora* (inclusive of *Achriotypa*). The other three Pteropliini genera at the base of clade D (*Similosodus*, *Egesina* Pascoe and *Desisa*) are placed in Lamiinae *incertae sedis*. The genus *Pterolophia*, with over 400 species distributed across several continents (Tavakilian & Chevillotte, 2021), requires further study. There is substantial sequence divergence between the four Australasian species of *Pterolophia* and the one Chinese species of *Lychrosis* Pascoe (currently a subgenus of *Pterolophia*), which may reflect a genus-level boundary.

### *Concluding remarks*

This study reports the first molecular phylogeny of the Australian Lamiinae and provides new insights into the evolution of diversity in the species-rich beetle family Cerambycidae. As predicted, most lamiine tribes we sampled are not monophyletic. The Australian endemic genera, in particular, are quite poorly classified: further evidence that the tribes of Lamiinae need to be redefined without resorting to the use of convergent traits like winglessness. Contrary to our hypothesis, the Australian Lamiinae are a mixture of Gondwanan (clade B) and Asian-derived taxa (clades C and D). The New Zealand Lamiinae seem to have originated from post-Gondwanan dispersal, though the exact

pathway is unclear. The Australian genus *Rhytiphora* is part of a clade of Asian origin that also contains other Pteropliini and Mesosini (clade D), as predicted. Most of the taxa in clade D have male abdominal sex patches, so this trait alone cannot be used to characterize *Rhytiphora* (which also contains the two patchless *Achriotypa* species).

Our results support a series of taxonomic changes. The following genera are placed in Lamiinae *incertae sedis*: *Amblymora*, *Athemistus*, *Austrosomatidia*, *Desisa*, *Egesina*, *Hybolasius*, *Mesolita*, *Microlamia*, *Microtragus*, *Nodulosoma*, *Oricopis*, *Ptinosoma*, *Similosodus*, *Somatidia*, *Spilotrogia*, *Xylotoles* and *Zorilispe*. We expand the definition of Ancitini to include *Didymocentrotus* McKeown, *Illaena*, *Neissa*, *Pentacosmia*, *Phyxium* and *Velora*. The genus *Achriotypa* is synonymized with *Rhytiphora*. The tribe Niphonini is reinstated with the following genera: *Callimetopus*, *Niphona*, *Pterolophia*, *Rhytiphora*, *Ropica* and *Sthenias*.

## Supporting Information

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

**Figure S1.** Convergence plots for the four MCMCTree dating analyses, showing the relationship between posterior means of node age estimates among MCMC runs. (A) Analysis with original fossil placement and Cauchy priors. (B) Analysis with original fossil placement and uniform priors. (C) Analysis with alternate fossil placement and Cauchy priors. (D) Analysis with alternate fossil placement and uniform priors.

**Figure S2.** Maximum likelihood phylogeny of Cerambycidae: partitioned IQ-TREE analysis of the nucleotide dataset. Branch supports are bootstrap values and the scale bar is nucleotide sequence change per Ma. Branches that differ between the datasets are coloured red.

**Figure S3.** Maximum likelihood phylogeny of Cerambycidae: partitioned IQ-TREE analysis of the degeneracy-recoded nucleotide dataset. Branch supports are bootstrap values and the scale bar is nucleotide sequence change per Ma. Branches that differ between the datasets are coloured red.

**Figure S4.** Maximum likelihood phylogeny of Cerambycidae: partitioned IQ-TREE analysis of the amino acid dataset. Branch supports are bootstrap values and the scale bar is sequence change per Ma. Branches that differ between the datasets are coloured red.

**Figure S5.** Maximum likelihood phylogeny of Cerambycidae: partitioned IQ-TREE analysis of the amino acid dataset with five taxa removed. Branch supports are bootstrap values and the scale bar is sequence change per Ma. Branches that differ from the full-taxa amino acid dataset are coloured red.

**Figure S6.** Fossil-calibrated chronogram of Cerambycidae: MCMCTree estimates of lineage divergence times based on the ML analysis of the 'noLR' nucleotide dataset (original fossil placement, uniform priors). Blue bars show 95% confidence intervals of node ages, and the scale bar is in millions of years (Ma). Fossil calibration points are indicated with orange squares.

**Figure S7.** Fossil-calibrated chronogram of Cerambycidae: MCMCTree estimates of lineage divergence times based on the ML analysis of the 'noLR' nucleotide dataset (alternate fossil placement, Cauchy priors). Blue bars show 95% confidence intervals of node ages, and the scale bar is in millions of years (Ma). Fossil calibration points are indicated with orange squares.

**Figure S8.** Fossil-calibrated chronogram of Cerambycidae: MCMCTree estimates of lineage divergence times based on the ML analysis of the 'noLR' nucleotide dataset (alternate fossil placement, uniform priors). Blue bars show 95% confidence intervals of node ages, and the scale bar is in millions of years (Ma). Fossil calibration points are indicated with orange squares.

**Table S1.** List of 141 Cerambycidae (and Chrysomelidae) specimens sampled for phylogenetic analyses. Specimens were identified by L. Ashman (ethanol/pinned) or Haddad *et al.* (2018; previous data). Accession number abbreviations: Australian National Insect Collection (A); Duane D. McKenna collection, University of Memphis (DDM and I: see Haddad *et al.*, 2018); New Zealand Arthropod Collection (NZ). Locality abbreviations: New Zealand (NZ); Papua New Guinea (PNG); United States of America (USA).

**Table S2.** Biogeography coding, by genus, for ancestral geographic range reconstruction analyses.

**Table S3.** Results of the BioGeoBEARS geographic range analyses on the dated phylogeny.

## Acknowledgements

## Author contributions

LGA, AZ, AS and DDM designed the project. LGA and SS collected the molecular data; LGA, SS and AZ performed the bioinformatic, phylogenetic and dating analyses; LGA collected and analysed the biogeography and morphology datasets. LGA wrote the initial draft and all authors contributed to revising the manuscript.

## Data availability statement

Raw sequence data has been uploaded to the Sequence Read Archive on Genbank (BioProject number: PRJNA749613). AHE probes are available from Dryad (accession number doi: 10.5061/dryad.v0b7v), as are the final sequence alignments and tree files (doi: 10.5061/dryad.n8pk0p2wc). Data on genetic material contained in this paper are published for non-commercial use only. Use by third parties for purposes other than non-commercial scientific research may infringe the conditions under which the genetic resources were accessed and should not be undertaken without consent from the corresponding author of the paper and/or permission from the original provider of the genetic material.

[Correction added on 09 Nov 2021, after the first online publication: Data availability statement has been updated]

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