Phylogeny and systematics of the longhorn beetle genus *Rhytiphora* (Coleoptera: Cerambycidae)

Rhytiphora fumata from Rainbow, Victoria (credit: Roger de Keyzer)

Lauren Ashman

March 2021

A thesis submitted for the degree of Doctor of Philosophy of
The Australian National University

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of the author's knowledge, it contains no material previously published or written by another person, except where due reference is made in the text.

Lauren Ashman
March 2021

Acknowledgements

They say it takes a village to raise a child, and that is certainly true of producing a PhD thesis as well. First of all, huge thanks to my supervisors: Adam Ślipiński and Andreas Zwick from CSIRO, Dave Rowell and Craig Moritz from ANU. I am so grateful for your steadfast encouragement and guidance over the last four years. You always took the time to help me through the rough patches (like bioinformatics), make sure I wasn't cutting corners, and celebrate the final result (that glorious phylogeny).

I would like to thank everyone at ANIC for supporting me along the way. The Beetle Crew came on field trips with me: Mengjie Jin also accompanied me on visits to interstate and overseas museums, and patiently shared her coding with me; Lingzi Zhou and Zhenhua Liu put up with me yelling at my computer in our office (sorry!), and provided advice and light conversation; Hermes Escalona helped out with phylogenetic analyses; Kim Pullen and Tom Weir shared their decades of entomological knowledge and also helped me interpret the scribbles on old specimen labels. Di Hartley, James Nicholls and Vidushi Patel helped me in the molecular lab, Luisa Teasdale and Alex Gofton helped with bioinformatics. Thanks to Federica Turco, Robyn Meier, Debbie Jennings and all the curatorial team for keeping the collection running (and keeping me supplied with cake!). Thanks to my fellow ANIC-Rowell Lab PhD students for sharing my journey: Xuankun Li, James Lumbers, Yun Hsiao and Mahin Chavoshi Jolfaei. And thanks to Bronte Sinclair and Isabella Robinson, who arrived just in time to help me through the worst of the pandemic by sharing my love of all things geeky.

I also need to thank the members of the McKenna Lab at the University of Memphis, particularly Duane McKenna, Seunggwan Shin and Cristian Beza-Beza: without you, my first chapter would not exist and I would not have survived my first trip to the US. Thanks to all the citizen scientists who sent me their field observations of *Rhytiphora*, particularly Roger de Keyzer and Stuart Harris, whose specimens and photographs were instrumental to my project.

Thanks to the whole E&E family at ANU: you always made me feel welcome and included, even though I spent most of my time across the road at CSIRO and only occasionally ventured into Robertson for free food and conversation. Thanks to all the other invertebrate taxonomy PhD students across Australia, for making the Australian Entomological Society conferences more enjoyable and welcoming me into the community of young creepy-crawly enthusiasts.

Thanks to my other friends, scientists and non-scientists alike: you helped keep me sane through this long journey. And finally, thanks to my family. My parents kept me fed and watered, even though this whole PhD thing seemed to be taking longer than first promised; my sister whisked me away into fantastical worlds and made sure I kept up my creative writing; my brother and his wife produced two adorable children (which beats my single thesis) and kept me supplied with movies and funky socks.

This research is supported by an Australian Government Research Training Program (AGRTP) Scholarship and an Australian National University Dean's Merit HDR Supplementary Scholarship in Science.

Preface

The thesis chapters are presented as self-contained manuscripts in preparation to be submitted. Each chapter, therefore, has its own Introduction, References and Supplementary Information; the References section at the end of the thesis only includes the citations used in the main Introduction and Conclusion sections (see Table of Contents). As the chapters have not yet been submitted to their respective journals, I have used one journal citation style throughout the thesis to ensure consistency. Chapter 1 is a broad-scale phylogenetic analysis of the Australian and New Zealand Lamiinae (Coleoptera: Cerambycidae). Chapter 2 is a more in-depth analysis of the morphology, biogeography and genetic relationships of the Australian *Rhytiphora* species. Chapter 3 updates the taxonomy of the Australian *Rhytiphora* species. All taxonomy presented in this thesis is only officially recognised upon publication.

Abstract

The classification and phylogenetic relationships of longhorn beetles, a diverse and ecologically important group, have been debated for decades, with neither morphological nor molecular data achieving a satisfactory resolution. *Rhytiphora*, the largest Australian genus of the subfamily Lamiinae, is no exception. The current concept of the genus encompasses around 200 species (from nearly 40 former genera), united by a putative apomorphy: setose ‘sex patches’ on the male abdomen, probably involved in dispersing pheromones. However, these sex patches are not unique to *Rhytiphora*. In this thesis, multiple nuclear loci were sequenced from museum specimens to produce the first molecular phylogeny of the Australasian Lamiinae, using fossil calibration data to estimate the branch lengths in real time. This phylogeny indicates that the tribal classification of the Australasian Lamiinae is largely incorrect, and the Australian genera form two clades: an older clade containing the Australian endemics and all the New Zealand taxa; and a younger clade with close ties to Asia, including the focal genus *Rhytiphora*. Many of the genera in this younger clade have male sex patches. The tribal classification of the sampled genera was revised, moving many Australian endemics to Lamiinae *incertae sedis* and reinstating the tribe Niphonini for *Rhytiphora* and five other Asian-Australian genera. Mitochondrial sequences were then used to reconstruct the phylogeny of *Rhytiphora* and examine patterns of morphological evolution and biome distributions. The Australian *Rhytiphora* species form two distinct clades. Nine morphological traits are correlated with these clades, including sex patches, body size and eye emargination. Clade 1 has mostly tropical species, while clade 2 has more mesic and arid zone species; both clades show evidence of multiple biome shifts between species groups. On the basis of these results, the morphological definition of the genus was revised, providing diagnostic features to distinguish *Rhytiphora* from related genera. Both molecular results and examination of type material were used to revise the *collaris* group, describe a new species, and construct an updated checklist of 162 Australian species (involving many new synonymies). These results shed light on an important part of Australia’s insect fauna, improving the tribal classification of Lamiinae and providing insight into the previously unknown biogeographic history of the Australian longhorn beetles. They also improve our understanding of the phylogeny, morphology, biogeography and species-level taxonomy of the diverse genus *Rhytiphora*.

Table of Contents

List of Figures

List of Tables

Introduction

LONGHORN BEETLES

The longhorn beetles (Cerambycidae) are a large, diverse family of phytophagous beetles that mostly feed on woody plants. Of the six subfamilies (Table 1), Lamiinae is the largest with about 21,000 described species (over half of all cerambycid species; Švácha & Lawrence 2014). Lamiinae is especially diverse in the tropics, but only 536 species are described from Australia, whereas the subfamily Cerambycinae has over 1200 Australian species (across more varied habitats; Ślipiński & Escalona 2016). It seems likely that Lamiinae reached Australia relatively recently, from Asia, while Cerambycinae has Gondwanan origins (Gressitt 1956).

Subfamily	**Distribution**	**No. species (worldwide)**	**No. species (Australia)**
Lamiinae	Worldwide (mostly tropical)	21,000+	536
Spondylidinae	Northern Hemisphere	160	2 (introduced)
Lepturinae (incl. Necydalini)	Northern Hemisphere	1,570	0
Cerambycinae	Worldwide (mostly southern)	11,000+	1250
Dorcasominae*	Eurasia, Africa	340	2? (unconfirmed)
Prioninae (incl. Parandrini)	Worldwide (mostly tropical)	1,270	100

Table 1. List of Cerambycidae subfamilies: data from Wang (2017), Ślipiński & Escalona (2016), Jin *et al.* (2020). *Dorcasominae may be paraphyletic with Cerambycinae (see Haddad *et al.* 2018; Nie *et al.* 2021).

As the name suggests, longhorn beetles have long antennae, with the insertions almost always anchored in raised tubercules; Lamiinae are characterised by brush-like antennal cleaners on the first two pairs of legs, a strongly deflexed head (except some Tmesisternini) and legless larvae (Ślipiński & Escalona 2013). Although some genera contain brightly coloured species or wingless ant mimics, the majority of Australian Lamiinae have camouflaging colouration and often sculptured exoskeletons (Linsley 1959). Most species have a stridulatory device in the prothorax, presumably for defence, since they mainly produce sounds when disturbed (Švácha & Lawrence 2014).

Male Lamiinae do not have pectinate antennae, as some other cerambycids do; instead, their antennae are filiform and so less suitable for detecting pheromones over long distances (Schneider 1964). However, the male antennae are usually longer than the female antennae; in some species of *Acalolepta*, the antennae can be three times as long as the male's body, which may facilitate mate location by touch rather than olfaction (Ślipiński & Escalona 2013). All cerambycids locate suitable host plants using chemical cues, including volatiles produced by the plant itself and pheromones from conspecifics (usually short-range) and other phytophagous beetles (Allison *et al.* 2004). Host specificity varies among species, from specialists to broad-range generalists that feed on both angiosperms and gymnosperms (Duffy 1963; Linsley 1959).

Lamiinae adults must feed on leaves or fresh bark before mating, a unique characteristic in cerambycids (adults of other subfamilies feed on flowers, sap or not at all; Švácha & Lawrence 2014). Females usually search for suitable host plants, while males search and compete for females. The larvae cannot disperse from the host plant where eggs are deposited, so the quality of the chosen plant will determine the fitness of the young (Allison *et al.* 2004). Lamiinae females chew 'egg scars' into the bark or stem and lay a single egg into each incision (Ślipiński & Escalona 2013). Some lamiine *Rhytiphora* females also girdle living branches near the oviposition site, creating weakened host material for their young to feed on (Froggatt 1923).

Early instar larvae typically feed in the phloem and then burrow into the harder xylem before pupation; the larvae possess various enzymes (e.g. cellulases, chitinases) and yeast-like symbionts to aid digestion (Švácha & Lawrence 2014). Cerambycid larvae play a major role in recycling dead wood, physically breaking down the tissues and creating access routes for fungi and other invertebrates (Ślipiński & Escalona 2013). However, most Lamiinae feed on living tissue of both woody and herbaceous plants.

Several species of the lamiine genus *Anoplophora* are pests of worldwide economic importance. The Asian Longhorn beetle *Anoplophora glabripennis* is devastating hardwood trees in Europe and the US and is a serious quarantine concern in Australia (Lingafelter & Hoebeke 2002; Ślipiński & Escalona 2013). The adults of the lamiine Pine Sawyer beetle, *Monochamus alternatus*, are vectors of the nematode that causes pine wilt disease in Europe, Asia and the US (Akbulut & Stamps 2012). In Australia, the Fig Longicorn *Acalolepta mixta* is a serious pest of grapevines in the Hunter Valley (Goodwin *et al.* 1994). On the other hand, many lamiine species are used across the world as biological control agents; for example, *Lagocheirus funestus* was imported from Mexico in 1935 to control the prickly pear in Queensland, albeit with little success (Haseler 1966).

SYSTEMATICS OF CERAMBYCIDAE AND LAMIINAE

The phylogenetic relationships of Cerambycidae, both among other families in the superfamily Chrysomeloidea and among its subfamilies, have been long debated. The problematic systematics of Cerambycidae can be attributed to multiple, conflicting classifications developed at the same time by early researchers (Švácha & Lawrence 2014). Three former subfamilies have been elevated to family status based on larval morphology (Oxypeltidae, Disteniidae and Vesperidae; Švácha & Danilevsky 1987), and the remaining subfamilies have also changed over time (e.g. Dorcasominae was only recognised as a separate subfamily within the last 40 years and is missing from most phylogenetic studies). Lamiinae, however, has been recognised as a subdivision of Cerambycidae since the 19th century; it is a monophyletic group well defined by larval morphology (legless with elongate heads; Švácha & Lawrence 2014). While the six currently recognised subfamilies are mostly monophyletic, their relationships are still unclear (Haddad & McKenna 2016).

Within Lamiinae, the tribal classification is inadequate and mostly arbitrary, based on local groups or single adult characters; the prolific and often inaccurate publications of S. Breuning (1894–1983) have greatly confused matters at the generic and species levels (Ślipiński & Escalona 2013). There have been many molecular and morphological studies addressing Chrysomeloidea classification (see below), but there is only one published molecular study that focuses on the lower classification of Lamiinae (Souza *et al.* 2020).

One of the few studies focusing on Cerambycidae classification suffered from poor taxon representation, which resulted in inaccurate coding and ancestral state estimation of the morphological characters (i.e. potential parellelisms overlooked: Napp 1994; Švácha & Lawrence 2014). The use of molecular data is particularly valuable in the systematics of cerambycids, where adult characters are often unreliable and the more useful larval characters are unknown for many species (Haddad *et al.* 2018).

Recent Chrysomeloidea studies, often using a few genes (mitochondrial or ribosomal) in conjunction with a morphological character matrix, have concentrated their taxon sampling within Chrysomelidae, the other large family in Chrysomeloidea (Farrell & Sequeira 2004; Gómez-Zurita *et al.* 2008; Marvaldi *et al.* 2009; Raje *et al.* 2016; Reid 1995). As a result, the relationships between the Cerambycidae subfamilies are conflicting and poorly supported, with Cerambycidae *sensu stricto* rendered paraphyletic when the three related families were included in the sampling (Haddad & McKenna 2016). Traditionally, the morphologically conserved Prioninae has been placed at the 'base' of the tree and Lamiinae in a more 'derived' position, but current molecular data support the opposite arrangement (Haddad *et al.* 2018; Raje *et al.* 2016; Švácha & Lawrence 2014).

A recent Chrysomeloidea phylogeny used a dataset of 522 nuclear loci and 35 taxa, including multiple samples of all six Cerambycidae subfamilies and representatives of all seven currently recognised families of Chrysomeloidea (Haddad *et al.* 2018). Despite some uncertainty in the topology, Lamiinae (and Spondylidinae) is consistently sister to the rest of Cerambycidae *sensu stricto*, with Prioninae sister to (Cerambycinae + Dorcasominae). Interestingly, Lamiinae is sister to Spondylidinae, a small Northern Hemisphere subfamily with no obvious apomorphies (i.e. generic adult and larval morphology, in contrast to the highly diversified Lamiinae; Švácha & Lawrence 2014).

Haddad *et al.* (2018) used next-generation sequencing (NGS) and anchored hybrid enrichment (AHE), which uses short DNA probes to target hundreds of conserved 'anchor' sequences flanked by more variable regions (Lemmon *et al.* 2012). AHE is cost-effective and capable of resolving phylogenetic relationships across a large group, using probes designed from a small number of species with sequenced genomes, which makes AHE ideal for non-model organisms and museum specimens (i.e. no RNA required: Bi *et al.* 2013; Haddad *et al.* 2018; Lemmon & Lemmon 2013). However, as mitochondrial data is historically easier to obtain, the majority of publicly available Cerambycidae sequence data is from mitochondrial or ribosomal genes rather than nuclear loci (Haddad & McKenna 2016).

In another study, Nie *et al.* (2021) used mitochondrial genomes to estimate the Chrysomeloidea phylogeny, increasing the sample size to 151 taxa (but potentially introducing the problem of saturation; Timmermans *et al.* 2016). Their dataset recovered a polyphyletic Cerambycidae, with ((Cerambycinae + Prioninae) + Dorcasominae) sister to the smaller Chrysomeloidea families, while Lepturinae is sister to (Lamiinae + Spondylidinae). A previous mitochondrial phylogeny showed similar results (Wang *et al.* 2019). Clearly, more work is required to resolve these discrepancies between different Chrysomeloidea molecular datasets.

Souza *et al.* (2020) used five loci and 130 taxa to examine the tribal-level relationships within Lamiinae (see Chapter 1 Discussion). They found that the lamiine genera form five main clades, and at least 15 tribes of the 46 sampled are not monophyletic. This study is a crucial first step towards creating an accurate tribal classification of Lamiinae, but their taxon sampling is not comprehensive. Since the focus of the study was to sample the available type genera of the tribes, their dataset included no taxa from Australia and only a few taxa from Indonesia and New Caledonia.

STUDY GENUS: *RHYTIPHORA*

The lamiine genus *Rhytiphora* comprises about 200 Australian species, more than a third of all Australian lamiine species, with about 50 more in SE Asia (e.g. historically *Prosoplus* species in New Guinea; Ślipiński & Escalona 2013). It is likely that the genus originated in Asia, but this thesis will focus on the more speciose Australian radiation. *Rhytiphora* is quite morphologically diverse: 6–39 mm long with different body shapes corresponding to formerly recognised genera e.g. *Symphyletes* and *Penthea* (Fig. 1). Eye size ranges from medium to large and the elytra are smooth to tuberculate, plainly coloured to elaborately patterned with bright or cryptic colouration, indicating both diurnal and nocturnal habits. There is little sexual dimorphism apart from the male sex patches (see below); males tend to have slightly larger eyes and longer (unmodified) antennae, and in most species have a spine at the base of the front legs.

Rhytiphora is found across Australia, with the majority of species diversity found along the north and east coasts and at least one species in Tasmania, which has few lamiines otherwise. While most species have been collected from *Acacia* or Myrtaceae, other species have been recorded on grass trees (*Xanthorrhoea*), Casuarinaceae and a range of native and introduced herbaceous plants (Duffy 1963; Hawkeswood 1985; Webb 1987). *Rhytiphora diva* (formerly *Zygrita*) is a minor pest of alfalfa and soybean crops in Queensland, as larval feeding damages and occasionally kills the plants (Jarvis & Smith 1946).

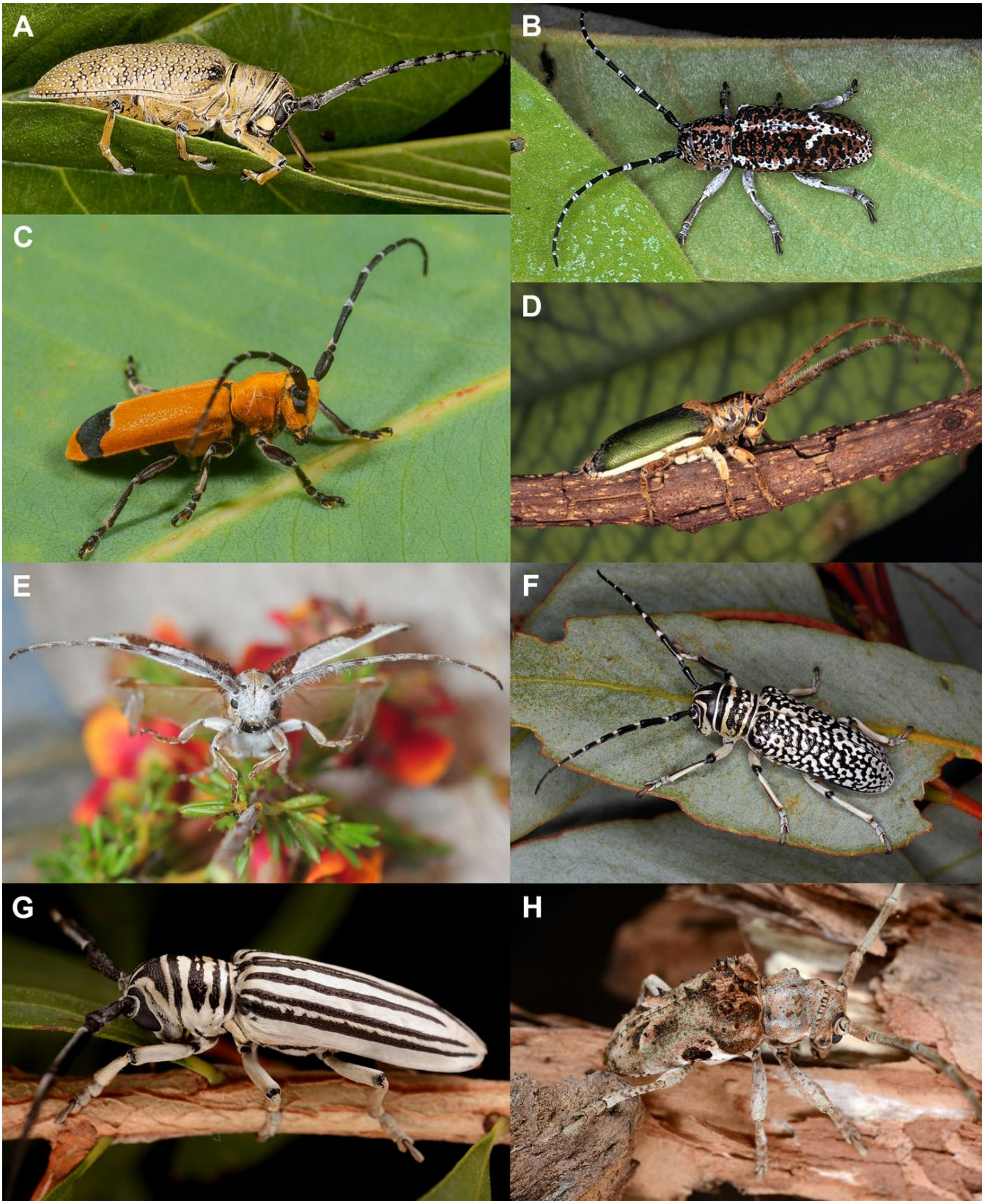

Figure 1. *Rhytiphora* species in their natural habitats. **A:** *Rhytiphora albospilota*, © P. Zborowski. **B:** *Rhytiphora pardalina*, © P. Zborowski. **C:** *Rhytiphora diva*, © J. Lochman. **D:** *Rhytiphora nigrovirens*, © P. Zborowski. **E:** *Rhytiphora lateralis*, © S. Harris. **F:** *Rhytiphora saundersii*, © A. Sundholm. **G:** *Rhytiphora dallasii*, © R. de Keyzer. **H:** *Rhytiphora obliqua*, © R. de Keyzer.

Rhytiphora is characterised by paired setose patches on male abdominal ventrite 2 (and rarely 3), comb-like antennal cleaner on mesotibia, 5-segmented tarsi and rounded antennal scape without apical carina (Ślipiński & Escalona 2013). The 38 formerly recognised genera encompassed by this description did not have stable morphological definitions and are now united based on the presence of variously sized male 'sex patches' (which might be involved in pheromone dispersal and therefore reproduction). However, the apomorphic status of the male sex patches has not been examined thoroughly; at least two *Rhytiphora* species appear to have lost these sex patches (McKeown 1938), and the genus *Pterolophia* has similar structures located on the membrane beneath ventrite 1 (not externally visible). Preliminary molecular work supports a monophyletic *Rhytiphora* (including former genera *Prosoplus*, *Symphyletes* and *Penthea*), sister to *Pterolophia* (D. McKenna, unpublished data), however, the species relationships remain unclear.

RESEARCH OBJECTIVES

To date, there has been only one molecular study that focuses on the tribal classification of Lamiinae (Souza *et al.* 2020), but this does not include any Australian taxa. Similarly, there are no published molecular phylogenies of the newly expanded *Rhytiphora* genus; while less important than other lamiine genera from an agricultural perspective, this genus makes up a significant proportion of Australia's longhorn beetle biodiversity. This thesis aims to increase our understanding of the *Rhytiphora* genus by investigating its relationship to other Australian and Asian lamiine genera (Chapter 1), examining its internal relationships and morphological traits (Chapter 2), and updating its taxonomy at the species level (Chapter 3).

Chapter 1 is a broad-scale phylogenetic analysis of the Australian and New Zealand Lamiinae. Following Haddad *et al.* (2018), I used AHE nuclear data to reconstruct the first molecular phylogeny of the Australasian Lamiinae, placing *Rhytiphora* in a broader context and revealing the complex biogeographic history of the Australasian longhorn beetles.

Chapter 2 is a more in-depth analysis of the morphology, biogeography and genetic relationships of the Australian *Rhytiphora* species. I used mitochondrial data for this project, because in order to maximise the number of species sampled I needed to use pinned museum specimens, which have degraded, low concentration DNA less suitable for AHE.

Chapter 3 updates the taxonomy of the Australian *Rhytiphora* species. I used the genetic insights from the previous two chapters, as well as conducting a thorough examination of holotypes and other museum specimens. I provide a new morphological definition and species checklist for the genus, including the description of one new species.

Chapter 1: The first phylogeny of Australasian Lamiinae longhorn beetles (Coleoptera: Cerambycidae) reveals poor tribal classification and a complex biogeographic history

Authors: Lauren G. Ashman[1,2], Seunggwan Shin[3,4], Andreas Zwick[2], Adam Ślipiński[2], Duane D. McKenna[3]

[1] Research School of Biology, Australian National University, Canberra, Australia

[2] Australian National Insect Collection, CSIRO, Canberra, Australia

[3] Department of Biological Sciences, University of Memphis, Memphis, TN, U.S.A.

[4] School of Biological Sciences, Seoul National University, Seoul, Republic of Korea

ABSTRACT

One of the most diverse beetle families in the world is the longhorns (Cerambycidae), with about 36,000 species and hundreds of poorly defined tribes. Lamiinae is the largest subfamily, dominating the longhorn fauna on all continents except Australia. We used anchored hybrid enrichment and fossil calibrations to reconstruct the first phylogeny of the Australasian Lamiinae (Cerambycidae; mainly Australia and New Zealand taxa), and examined their biogeographic history. We recovered a monophyletic Lamiinae with four main clades, within which the majority of tribes are non-monophyletic. One clade is mostly comprised of Australian endemic genera, probably of Gondwanan origin (based on ancestral reconstruction analyses) with subsequent dispersal to New Zealand and multiple instances of wing loss. Another clade contains Australian genera that dispersed from Asia, including Australia's most diverse longhorn genus, *Rhytiphora* Audinet-Serville. We discovered that the defining feature of this genus, the setose 'sex patches' on the male abdomen, is actually shared with many other Asian genera in the same clade. Our results shed light on the previously understudied Australian Lamiinae, revealing a mixture of ancient Gondwanan and recent Asian origins, and a clear need to revise the tribal classification of the Australasian genera. 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 synonymise *Achriotypa* Pascoe with *Rhytiphora*.

INTRODUCTION

Cerambycidae (longhorn beetles) is one of the largest beetle families, with over 36,000 species described worldwide (Wang 2017). The larvae mostly feed inside stressed or dead woody plants, playing a major role in woodland nutrient recycling, while other species attack healthy trees and are pests of global economic importance (Ślipiński & Escalona 2013). The adults show a great range of morphologies, from wasp mimics to camouflaged species with highly sculptured exoskeletons (Linsley 1959).

The phylogenetic relationships among its subfamilies, and the placement of Cerambycidae within the superfamily Chrysomeloidea, have been long debated. The problematic taxonomy of Cerambycidae can be attributed to the conflicting classification systems developed concurrently by early researchers, and the general unreliability of adult morphological characters (Švácha & Lawrence 2014). A recent molecular phylogeny of Chrysomeloidea supported six to eight subfamilies within Cerambycidae, with Oxypeltidae, Disteniidae and Vesperidae as distinct families (Haddad *et al.* 2018). The dataset used in that study was substantially larger than in previous studies, using anchored hybrid enrichment (AHE) to target over 500 loci across Chrysomeloidea (Lemmon *et al.* 2012).

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

Australia is the only continent where Lamiinae is not the most speciose cerambycid subfamily: 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). Given that several genera are distributed in South America and Australia (e.g. *Syllitus* Pascoe), it seems likely the cerambycines are of Gondwanan origin, while the 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 characterised, 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, with a total of 130 species. Subsequently, six of these genera were dropped, and five others 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). A number of Australian lamiine species are also wingless (across eight genera, four of which are endemic), though none of the Australian cerambycines have lost their wings (Ślipiński & Escalona 2013, 2016).

The largest Australian cerambycid genus, *Rhytiphora* Audinet-Serville, comprises more than a third of all Australian Lamiinae with ~200 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). Nearly 40 Australian genera with this trait have been synonymised into *Rhytiphora* accordingly (Slipinski & Escalona 2013; but see Weigel & Skale 2014). However, there are at least 50 more *Rhytiphora* species found in Southeast Asia, as well as many Asian genera in the same tribe (Pteropliini Thomson) that may also fall within this broad morphological grouping.

In this study, we used the Chrysomeloidea-specific AHE probes developed by Haddad *et al.* (2018) to generate sequence data for 139 taxa, mostly Australian Lamiinae, and estimate their phylogenetic relationships. Outgroups from other subfamilies were selected in order to include fossil calibrations for dating analyses; we also examined patterns of biogeography and morphology. As the type genera for half of the tribes currently employed for the Australian Lamiinae are described from distant continents (Europe or the Americas; Tavakilian & Chevillotte 2020), we predict that most of these poorly defined tribes will not be monophyletic. We also predict that the Australian Lamiinae will be relatively recently derived from Asian taxa. Based on previous molecular work (D. McKenna, unpublished data), we predict that *Rhytiphora* will be a monophyletic group, 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 USA). Nearly half of the samples were drawn from the related genera *Rhytiphora* and *Pterolophia*. Ethanol-preserved specimens were used whenever possible to ensure better quality sequences (Table S1). Genomic DNA was extracted from 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). The DNA quality for each sample was assessed using a Qubit fluorometer (Thermo Fisher) and a Fragment Analyser (Agilent). The samples were then normalised to 100–500 ng of DNA and sheared to a fragment size of 300–500 bp using a Q800R2 Sonicator (QSonica; 10 secs on, 10 secs 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 750 ng total). The sample pools were dried in a Savant Speed Vac Concentrator and dissolved in 7 uL of HPLC water.

Hybrid enrichment was performed following the myBaits Hybridisation Capture for Targeted NGS protocol (Arbor Biosciences); probes and libraries were allowed to hybridise for ~24 hours 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 secs (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 secs on, 30 secs off for 20 cycles). Libraries were prepared in half reactions (25 uL 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 0.6x then 0.35x). 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

For processing the sequence data, the procedure described by Peters *et al.* (2017) was generally followed. 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 (Kück *et al.* 2010; Misof & Misof 2009) and removed. 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) datasets were concatenated using ConcatMatrices v1.2 (http://phylotools.com; Jin *et al.* 2020). The program 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 informative 195 out of the total 522 loci, resulting in the final datasets of 34,961 aa and 104,883 bp. These datasets were examined manually in AliView v1.26 (Larsson 2014), and potential paralogs were deleted. We also checked for cross-contamination by blasting the individual loci against themselves, and against 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 removes all synonymous changes by replacing 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 the phylogenetic relationships using the maximum likelihood program IQ-TREE v1.6.12 (Nguyen *et al.* 2015). We ran 200 independent tree searches and 200 standard nonparametric bootstrap replicates for each dataset. The bootstrap support values were then mapped onto the best likelihood tree (*–sup* option). We also ran another analysis on the aa dataset, having removed the five taxa with the highest percentage of missing data (Table S1), to determine whether these taxa affected the topology. The trees were visualised using FigTree v1.4.4 (Rambaut 2018).

Molecular dating analyses

Five fossils were used as calibration points, 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., was used to constrain the most recent common ancestor (MRCA) of Cerambycidae to at least 112 Mya (Shin *et al.* 2018; Wang *et al.* 2014). 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 (Vitali 2014), *Necydalis zangi* Vitali (Vitali 2011), *Pogonocherus jaekeli* Zang and *Nothorhina granulicollis* Zang (Vitali 2009; Zang 1905). Given the debate around the age of Baltic amber (Eocene or Oligocene; Vitali & Daamgard 2016), we set the minimum age calibrations to 34 Mya (the Oligocene–Eocene boundary). The root of the phylogeny (=Chrysomeloidea MRCA) was constrained to have a maximum age of 223 Mya, following Shin *et al.* (2018).

Due to the uncertainty regarding how phylogenetic programs parse ambiguity codes, we created a new nucleotide dataset with the third codon positions removed entirely. 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, 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 program (PAML) was used to calculate the ML estimates of the branch lengths under the GTR+gamma model (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).

Biogeographical and morphological analyses

We separated the geographic distributions of the sampled taxa into seven categories, reflecting the Australasia-centric focus of our sampling: Australia (including New Guinea), Australia (mainland) and New Zealand, New Zealand (including off-shore Australian territories such as Lord Howe and Norfolk Islands), Asia (from China and India to Indonesia), Australia and Asia, Europe, and the Americas. For those genera with Palaearctic or Holarctic distributions, which were mostly non-lamiines, we chose the continent that the sequenced specimen or species had come from (Table S2). Geographical distribution data was gathered from Ślipiński & Escalona (2013), the Titan database (Tavakilian & Chevillotte 2020), Lamiines of the World (Roguet 2020) and the Catalogue of Life (Roskov *et al.* 2020).

We also obtained morphological data for the lamiine genera: each genus was scored as fully winged, partially wingless (a mixture of winged and wingless species) or fully 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 dated phylogeny was trimmed to one tip per genus (for biogeography) or to 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; R Core Team 2019; RStudio Team 2019). The ancestral states for both datasets were estimated using the *ace* function 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. S1–S3) produced very similar ML trees, albeit with poor support for some of the Lamiinae nodes (Fig. 1). Each cerambycid subfamily is monophyletic. Lamiinae is sister to the rest and divided into four main groups: clade A (Pogonocherini Mulsant), 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. S1–S3). The dried WGS samples have quite 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. S4).

A total of 14 lamiine tribes were sampled, with 10 tribes represented by more than one genus (Fig. 1; Table S1). Of these 10 tribes, six are polyphyletic: Acanthocinini, Apomecynini Thomson and Parmenini are scattered widely across the tree, while Desmiphorini Thomson, Lamiini and Pteropliini are less dispersed but definitely 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 Mya, 95% CI: 223–126 Mya), with the MRCA of Cerambycidae occurring in the late Jurassic to early Cretaceous (129 Mya, 95% CI: 173–104 Mya; Fig. 2). The four main lamiine clades have similar root ages, from the late Cretaceous to the Paleocene (mean ages A–D: 64 Mya, 76 Mya, 71 Mya, 73 Mya). The MRCA of the core group of New Zealand taxa (*Ptinosoma* Breuning to *Stenellipsis*) is dated to the Paleocene–Eocene (53 Mya, 95% CI: 74–39 Mya), and the root age of *Rhytiphora* is dated to the Eocene–Oligocene (38 Mya, 95% CI: 53–29 Mya).

The ancestral distributions of the deeper nodes (Cerambycidae and its subfamilies) are estimated as European (Fig. 3). The four lamiine clades have different estimated ancestral ranges: clade A is European, clade B is Australian (with several incursions into Asia and New Zealand), clade C is ambiguous but probably Eurasian, while clade D is probably 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. 3).

The vast majority of the taxa in clade D have setose sex patches on the male abdominal ventrites (Table 1); the ancestor of clade D is estimated to have had sex patches (Fig. 4). The Pteropliini (including *Ropica* Pascoe) mostly have smaller patches, hidden beneath the thickened fringe of ventrite 1, except for *Desisa* Pascoe*, Sthenias* Dejean and about 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.

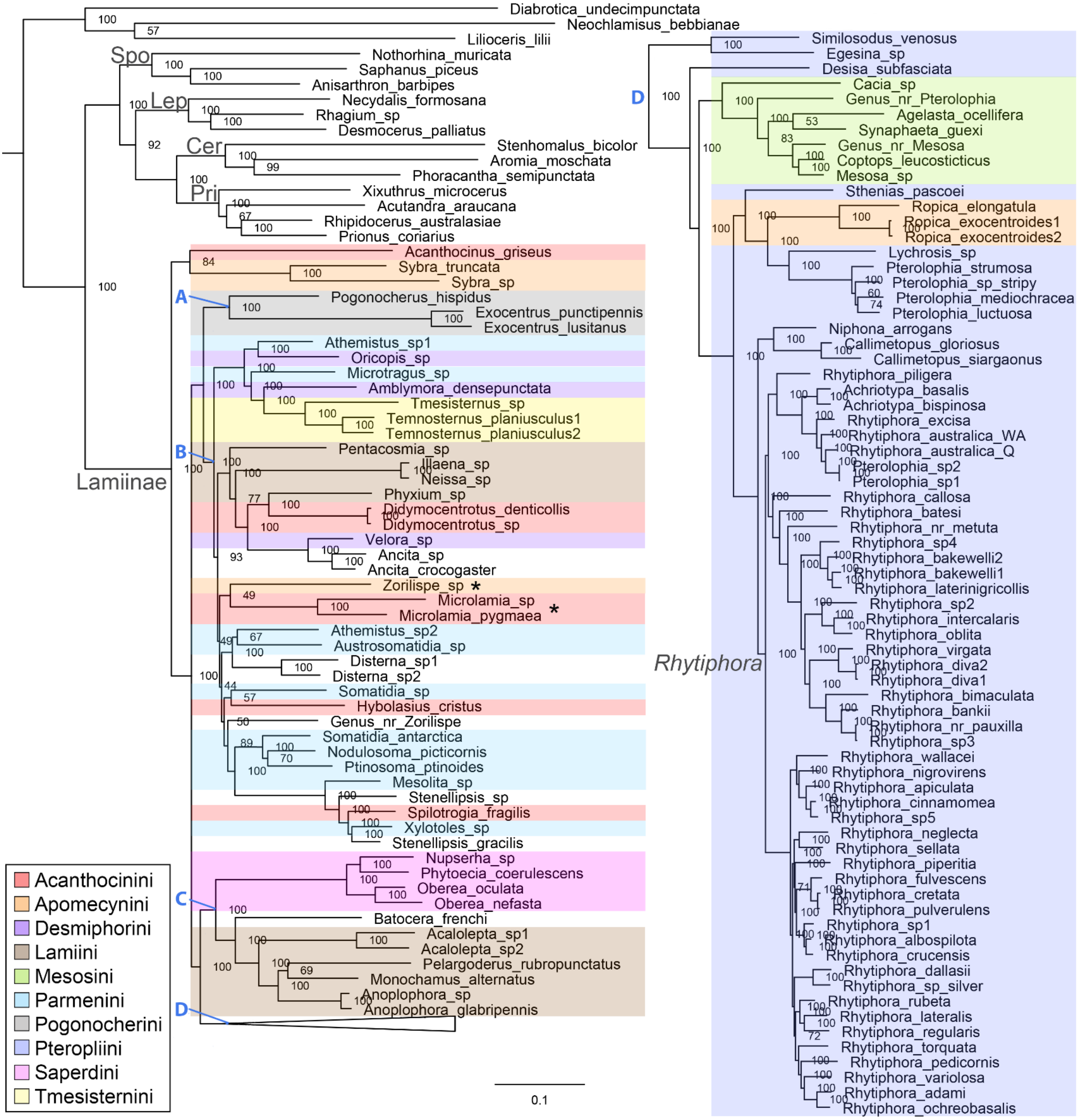

Figure 1. Maximum likelihood phylogeny of Cerambycidae: partitioned IQ-TREE analysis of the nucleotide dataset. Branch supports are bootstrap values (good support: >80%) and the scale bar is nucleotide sequence change per Mya. Subfamilies are labelled (Spo=Spondylidinae, Lep=Lepturinae, Cer=Cerambycinae, 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 are labelled with an asterisk (*).

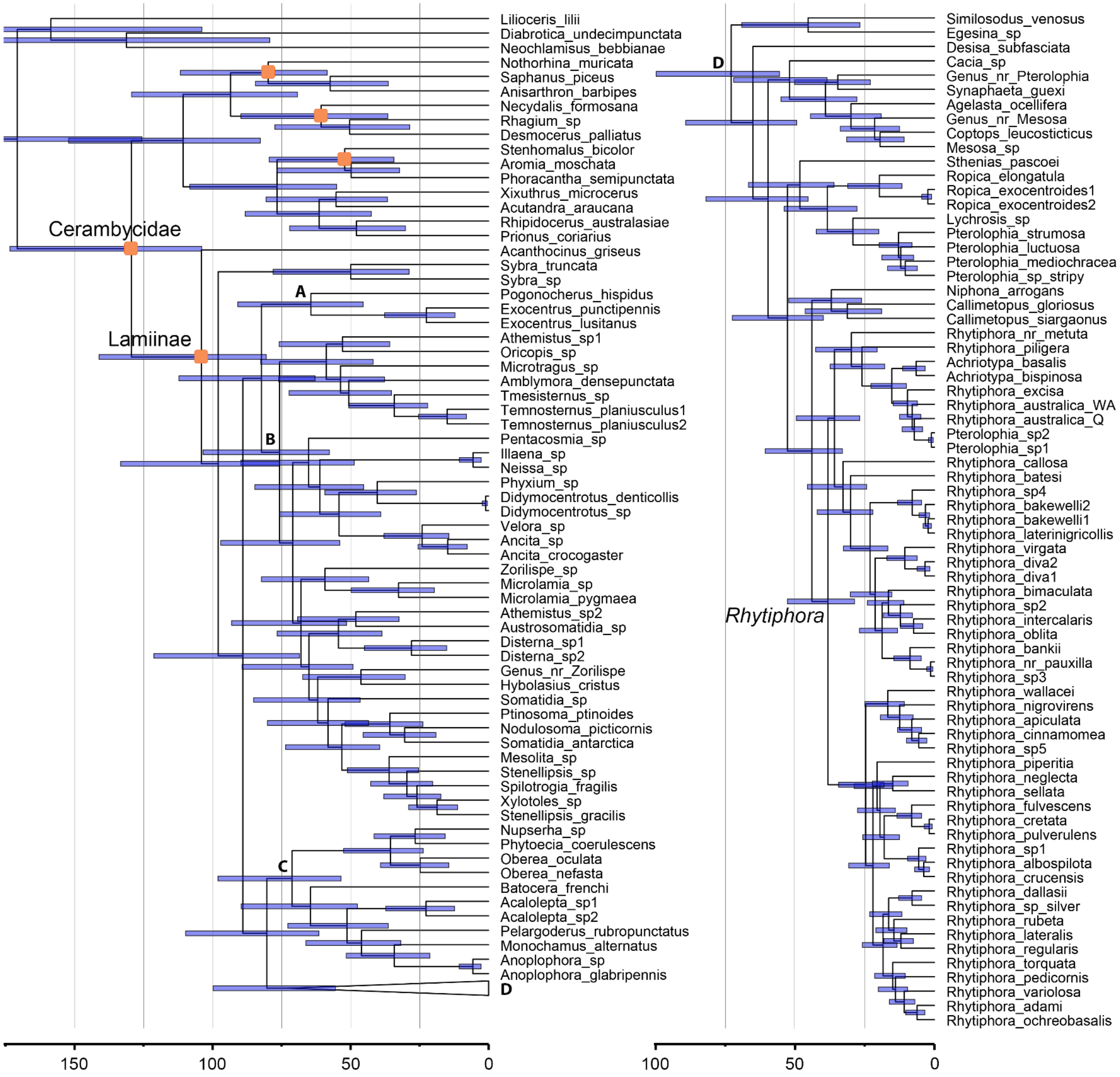

Figure 2. Fossil-calibrated chronogram of Cerambycidae: MCMCTree estimates of lineage divergence times based on the ML analysis of the 'noLR' nucleotide dataset. Blue bars show 95% confidence intervals of node ages, and the scale bar is in millions of years ago (Mya). Cerambycidae, Lamiinae, *Rhytiphora* and the four main lamiine clades (A–D) are labelled, with clade D expanded on the right. Fossil calibration points are indicated with orange squares.

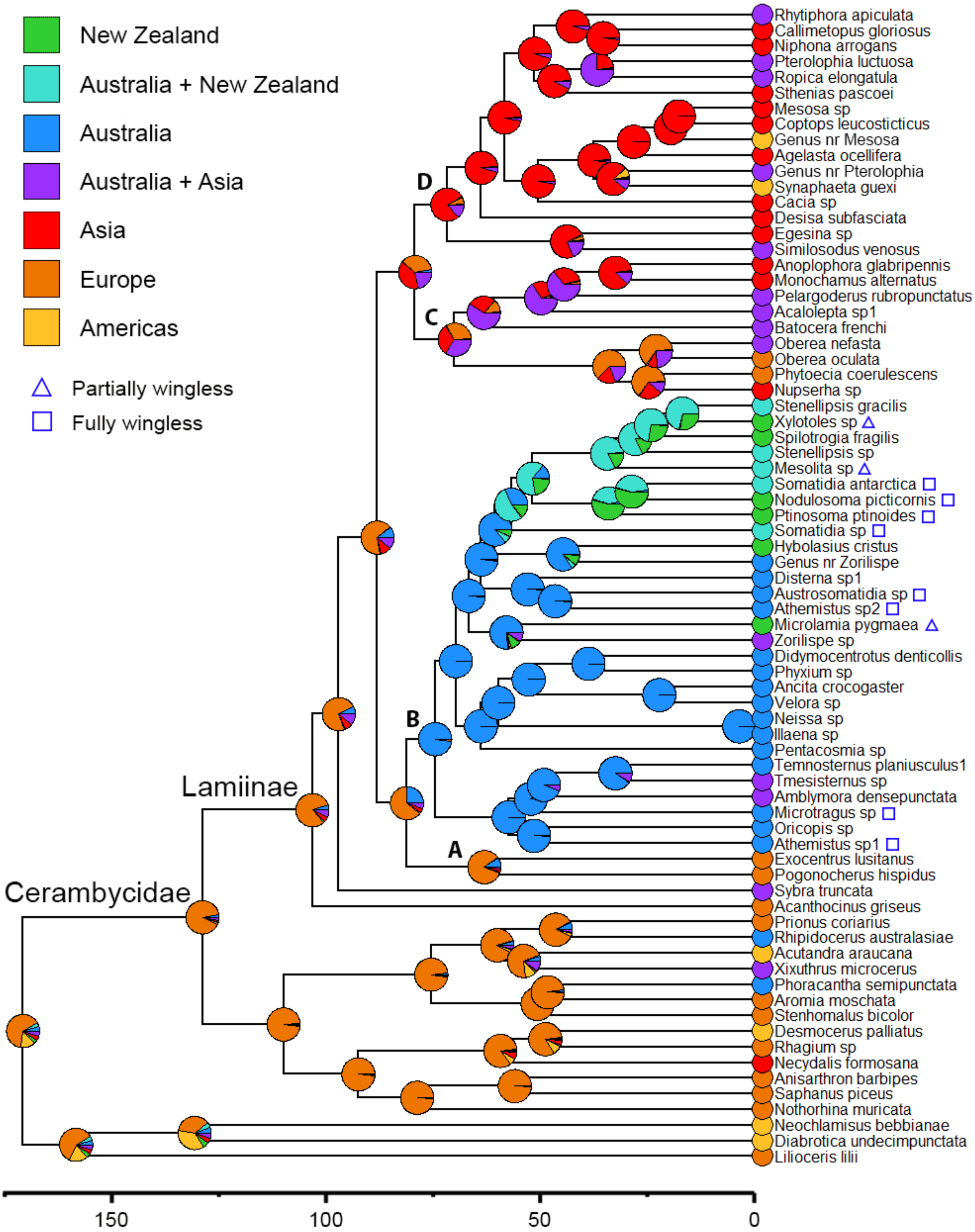

Figure 3. Ancestral geographic range estimation and present-day winglessness of Cerambycidae: ancestral states reconstructed with APE using the dated MCMCTree phylogeny (Fig. 2). A key to the geographic range colours and winglessness symbols is shown at the top left. Pie charts show the probability of the ancestral states at each node. Scale bar is in millions of years ago (Mya). Cerambycidae, Lamiinae and the four main lamiine clades (A–D) are labelled.

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; vent 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	Vent 1 thin fringe
Pteropliini	Rhytiphora	australica (WA)	Hidden	2	Vent 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	Vent 1 thin fringe
Pteropliini	Rhytiphora	excisa	Hidden	2	Vent 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 vent 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	Vent 1 thin fringe
Pteropliini	Rhytiphora	wallacei	Visible	2	Central
Pteropliini	Similosodus	venosus	Hidden	2	
Pteropliini	Sthenias	pascoei	Visible	2-4	Central; vent 3-4 hairs but no pit

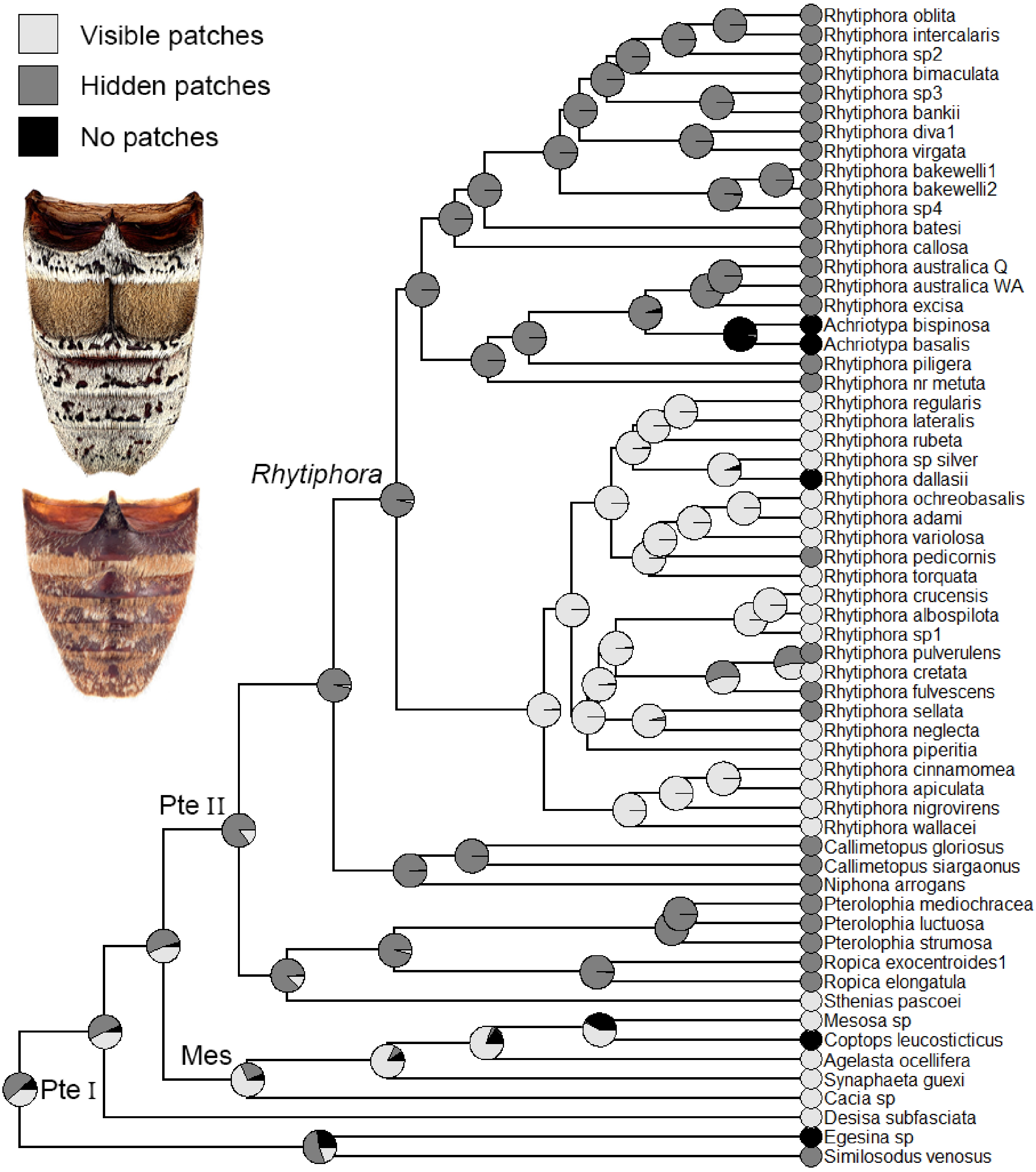

Figure 4. Presence of male abdominal sex patches in Lamiinae, clade D: ancestral states reconstructed with APE using the dated MCMCTree phylogeny (Fig. 2). A key to the sex patch types is shown at the top left. Below the key are two images of *Rhytiphora* spp. (abdomen, ventral side) demonstrating visible (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.

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 unlikely to be monophyletic. Five out of the eight Europe/America-centric tribes sampled are polyphyletic in our tree (Fig. 1): Acanthocinini, Desmiphorini, Lamiini, 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, though Ancitini could be considered monophyletic since *Ancita* is its only member (Tavakilian & Chevillotte 2020). Interestingly, the three most speciose Australian lamiine genera (*Athemistus*, *Sybra* and *Rhytiphora*; Ślipiński & Escalona 2013) are only distantly related to each other.

Our Lamiinae phylogeny is remarkably similar to that of Souza *et al.* (2020), despite having only ~15% overlap in taxon sampling and very different loci (Fig. 5; Table 2). Both phylogenies have *Pogonocherus* Dejean related to *Exocentrus* Dejean (our clade A, their clade I), *Phytoecia* Dejean related to *Oberea* Dejean (our clade C, their clade O), *Batocera* Dejean related to Lamiini genera (their clades J–L), and Pteropliini rendered paraphyletic by *Ropica* and *Mesosa* (our clade D, their clade M). It is likely that their clade E (Enicodini) is equivalent to our much larger clade B, which mostly consists of Australasian genera including *Stenellipsis*. Our results are also congruent with the latest Chrysomeloidea phylogeny (Nie *et al.* 2021), which recovered a clade containing, among others, 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. The question of whether *Stenellipsis* belongs in Enicodini is more difficult to address: Souza *et al.* (2020) 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, but our two *Stenellipsis* samples are grouped together with New Zealand taxa from Acanthocinini and Parmenini (which are quite morphologically different to *Enicodes* Gray, which is winged with a strongly elongate body and expanded head capsule). Further work, with more extensive sampling across Oceania, will be needed to fully establish these taxonomic boundaries.

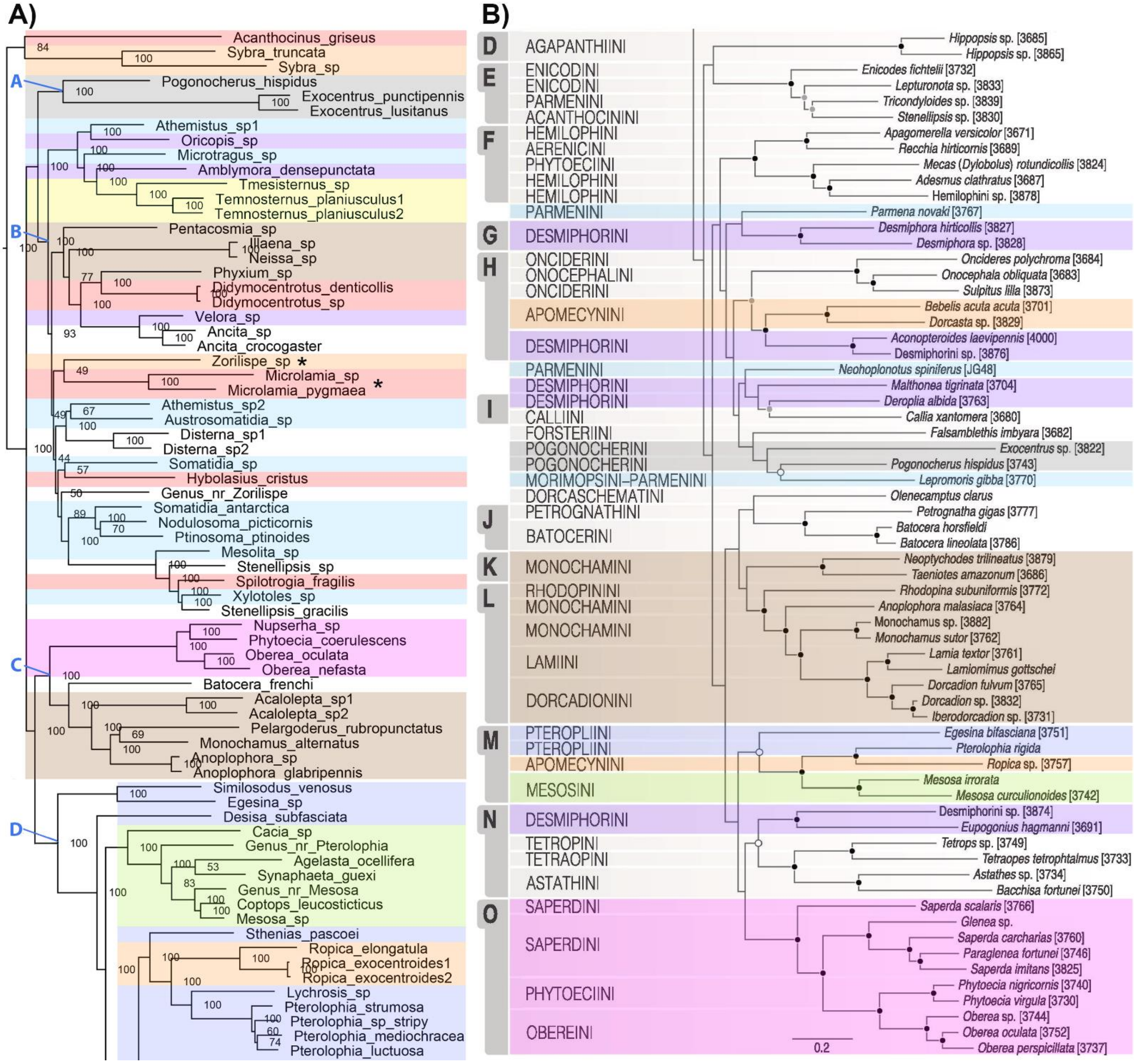

Figure 5. Comparison of two Lamiinae molecular phylogenies. **A:** Section of our Figure 1. **B:** Section of Figure 2A from Souza *et al.* (2020), edited to match our figure's tribal colouring.

Table 2. Comparison of biogeographic sampling, by genus, in this study (Ashman *et al.*) vs. Souza *et al.* (2020). The total number of genera is estimated from Roguet (2020).

Study	**Number of lamiine genera sampled [estimated total]**			
	Australasia [300]	**Asia [1100]**	**Europe & Africa [800]**	**Americas [800]**
Ashman *et al.*	39	12	5	2
Souza *et al.*	5	20	29	43

In this section we will focus on the systematics of clade B, which has the greatest number of sampled genera, and discuss clade D separately below. Our results clearly demonstrate the inadequacy of the current tribal classification of Australasian lamiine genera: 81% of the genera in clade B are placed in non-monophyletic tribes (Fig. 1). 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), *Apomecyna* Dejean is sister to the rest of Lamiinae with *Acanthocinus* (and others), which suggests that *Sybra* is in the correct tribe but 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 large American-European clade with *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.

The genera *Athemistus*, *Oricopis* Pascoe, *Microtragus* White and *Amblymora* Pascoe form a well-supported paraphyletic group closely related to Tmesisternini Blanchard. This tribe is defined by several highly derived morphological traits (e.g. prognathous head; Gressitt 1984) which are not found in these four genera; therefore, we move these genera to Lamiinae *incertae sedis* pending further investigation. We propose that the next well-supported group (*Pentacosmia* Newman to *Ancita*) all be moved into Ancitini, as *Pentacosmia*, *Phyxium* Pascoe 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* Erichson and *Neissa* Pascoe are more closely related than most of the congeneric species in the phylogeny (e.g. the two *Ancita* species). The two genera are also very similar morphologically and should perhaps be synonymised, but that is out of the scope of this paper 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 to 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; as 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 falls just outside with *Hybolasius* and an undescribed Australian genus. This suggests the Australian species of *Somatidia* should be placed in their own genus, such as Breuning's subgenus *Villososomatidia* (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* (including the type species *S. bimaculatus* White) belong to *Xylotoles*, while the Australian species (*S. sp* in our tree) belong to a separate genus: *Brachyrhabdus*, described from Queensland by Aurivillius (1917) and synonymised with *Stenellipsis* by Ślipiński & Escalona (2013). But again, such genus-level reclassification is beyond the limited sampling of this paper.

Biogeography and winglessness

Our dating analyses place the root of Chrysomeloidea in the Jurassic (Fig. 2), which agrees with previous estimates (McKenna *et al.* 2019; Nie *et al.* 2021; Zhang *et al.* 2018). The Cerambycidae began to diversify in the Cretaceous, coinciding with the proliferation of their main current host plants, the angiosperms (Magallón & Castillo 2009; Wang 2017). The estimated root 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. Similarly, the estimated ancestral geographic areas of the other subfamilies are heavily influenced by our sampling bias (mostly European; Fig. 3), and the geographic range of 'basal' groups does not necessarily reflect the ancestral area anyway (Heads 2014). We will therefore focus our discussion on the two more deeply sampled lamiine clades, B and D.

The MRCA of clade B is dated to approximately the late Cretaceous in Australia (Figs. 2–3). This does not support 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 are in fact Gondwanan, which explains why their placement in largely Laurasian tribes is so problematic (Fig. 1). Unfortunately, we did not sample any lamiines from South America, which could provide further evidence for a Gondwanan origin. Several other genera in clade B might have expanded westwards 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 Paleocene–Eocene (Figs. 2–3). Given that Zealandia separated from Gondwana in the late Cretaceous (Kamp 1986), and the New Zealand Lamiinae are less diverse than the Australian taxa, it is likely that New Zealand was colonised via post-Gondwanan dispersal from other areas (Yeates & Cassis 2017). This is a common pattern in New Zealand taxa (Wallis & Trewick 2009), and there is evidence of long-distance dispersal from Australia to New Zealand in scale insects and diving beetles (Hardy *et al.* 2008; Toussaint *et al.* 2015a). 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); it is also unclear how many dispersal events occurred, as the position of *Microlamia* is unresolved.

The majority of the New Zealand taxa are wingless to some degree (64%; Fig. 3), 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, perhaps via floating vegetation (Tänzler *et al.* 2016; Toussaint *et al.* 2015b). 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*). Clearly wing loss has evolved multiple times, so it is unsurprising that the tribe Parmenini (partly defined by winglessness; Breuning 1950) is polyphyletic.

Clade D has a late Cretaceous root age, like clade B, but is estimated to be of Asian origin (Figs. 2–3). 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 Mya, which is when the Sula spur of the Australian plate collided with Sulawesi (Hall 2013). A number of plants and animals have moved between Australasia and Asia following this collision (Crayn *et al.* 2015; Oliver & Hugall 2017), including insects (Balke *et al.* 2009; Kodandaramaiah & Wahlberg 2007; Leys *et al.* 2002; Tänzler *et al.* 2016).

The early divergences within the genus *Rhytiphora*, however, predate the Miocene Sula spur collision (root age dated to the Eocene–Oligocene; Fig. 2). The genus could have begun diversifying before it reached Australasia, but it is also possible that *Rhytiphora* colonised 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), and there is evidence of similar Eocene–Oligocene divergences in several lizard and bird taxa (Oliver *et al.* 2018, 2020; Skinner *et al.* 2011). 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 data places *Rhytiphora* in a clade with Mesosini and the other Pteropliini genera, along with *Ropica* (Fig. 1). Interestingly, its closest relatives are not Australian but the Asian genera *Niphona* and *Callimetopus* Blanchard, both sampled from the Philippines (Table S1, Fig. 3). *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 existing *Achriotypa* species, we can confidently synonymise this genus with *Rhytiphora* (see Chapter 3).

The presence of setose sex patches on the male abdomen, currently the defining trait of *Rhytiphora*, is not restricted to this genus alone: 80% of the genera in clade D have sex patches (Table 1, Fig. 4). 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* itself (*R. dallasii* Pascoe). All of the *Rhytiphora* species with larger, visible patches are in the same clade; however, this clade does include species with hidden or absent patches as well.

The overall structure of clade D (i.e. a paraphyletic Pteropliini) is reflected in Breuning's key to Asian tribes (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 (Brasil; Tavakilian & Chevillotte 2020), it is unlikely to be closely related to our Asian-Australian Pteropliini. 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*, which has over 400 species across several continents (Tavakilian & Chevillotte 2020), requires further study; there is substantial sequence divergence between our four Australasian species and one Chinese *Lychrosis* Pascoe (currently a subgenus of *Pterolophia*), which could reflect a genus-level boundary.

Concluding remarks

This study reports the first molecular phylogeny of the Australian Lamiinae, providing valuable insights into the evolution of the species-rich beetle family Cerambycidae. The majority of lamiine tribes we sampled are not monophyletic, as predicted. The Australian endemic genera in particular are quite poorly classified. This provides 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), which is also the case for New Zealand zopherid beetles (Buckley *et al.* 2020). 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 characterise *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 synonymised with *Rhytiphora*. The tribe Niphonini is reinstated with the following genera: *Callimetopus*, *Niphona*, *Pterolophia*, *Rhytiphora*, *Ropica* and *Sthenias*.

ACKNOWLEDGEMENTS

We thank Richard Leschen, Petr Švácha, Roger de Keyzer, Paul Hutchinson, David Rentz, Jack Hasenpusch and Jacek Kurzawa for donating specimens sequenced. We thank Diana Hartley and Mengjie Jin for helping with DNA extraction. Nick Matzke provided advice on the biogeographic analyses. Petr Švácha, Craig Moritz and Dave Rowell provided comments on the manuscript. This project was funded by grants from the Australian Government Department of Agriculture and Water Resources, the Australian Biological Resources Study and the Centre for Biodiversity Analysis in Canberra (to AS and LGA), and US National Science Foundation grant DEB:1355169 (to DDM). LGA was funded by the Australian National University and an Australian Government Research Training Program domestic scholarship. The authors declare no conflicts of interest.

REFERENCES

Aurivillius, C. (1917) Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia 1910–1913, Part 12, Cerambycidae. *Arkiv för Zoologi* 10, 1–50.

Balke, M., Ribera, I., Hendrich, L., Miller, M.A., Sagata, K., Posman, A., Vogler, A.P. & Meier, R. (2009) New Guinea highland origin of a widespread arthropod supertramp. *Proceedings of the Royal Society B: Biological Sciences* 276, 2359–2367. https://doi.org/10.1098/rspb.2009.0015

Bankevich, A., Nurk, S., Antipov, D., Gurevich, A.A., Dvorkin, M., Kulikov, A.S., Lesin, V.M., Nikolenko, S.I., Pham, S., Prjibelski, A.D., Pyshkin, A. V., Sirotkin, A. V., Vyahhi, N., Tesler, G., Alekseyev, M.A. & Pevzner, P.A. (2012) SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology* 19, 455–477. https://doi.org/10.1089/cmb.2012.0021

de Boer, A.J. & Duffels, J.P. (1996) Historical biogeography of the cicadas of Wallacea, New Guinea and the West Pacific: a geotectonic explanation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 124, 153–177. https://doi.org/https://doi.org/10.1016/0031-0182(96)00007-7

Bolger, A.M., Lohse, M. & Usadel, B. (2014) Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* 30, 2114–2120. https://doi.org/10.1093/bioinformatics/btu170

Breuning, S. (1950) Revision des Parmenini. *Longicornia* 1, 29–159.

Breuning, S. (1956) Notes sur les Lamiaires. *Longicornia* 3, 703–722.

Breuning, S. (1962a) A contribution to the knowledge of the Lamiinae (Coleoptera, Cerambycidae) of New Zealand. *Transactions of the Royal Society of New Zealand* 2, 73–108.

Breuning, S. (1962b) Bestimmungstabelle der Lamiiden-Triben nebst Revision der Pteropliini der asiatischen Region (Col. Cerambycidae) I. Teil. *Entomologische Arbeiten aus dem Museum G. Frey* 13, 371–493.

Buckley, T.R., Lord, N.P., Ramón-Laca, A., Allwood, J.S. & Leschen, R.A.B. (2020) Multiple lineages of hyper-diverse Zopheridae beetles survived the New Zealand Oligocene Drowning. *Journal of Biogeography* 47, 927–940. https://doi.org/10.1111/jbi.13776

Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K. & Madden, T.L. (2009) BLAST+: architecture and applications. *BMC Bioinformatics* 10, 421.

https://doi.org/10.1186/1471-2105-10-421

Chernomor, O., von Haeseler, A. & Minh, B.Q. (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* 65, 997–1008. https://doi.org/10.1093/sysbio/syw037

Crayn, D.M., Costion, C. & Harrington, M.G. (2015) The Sahul–Sunda floristic exchange: dated molecular phylogenies document Cenozoic intercontinental dispersal dynamics. *Journal of Biogeography* 42, 11–24. https://doi.org/10.1111/jbi.12405

Cruaud, A., Jabbour-Zahab, R., Genson, G., Couloux, A., Yan-Qiong, P., Da Rong, Y., Ubaidillah, R., Pereira, R.A.S., Kjellberg, F., van Noort, S., Kerdelhué, C. & Rasplus, J.-Y. (2011) Out of Australia and back again: the world-wide historical biogeography of non-pollinating fig wasps (Hymenoptera: Sycophaginae). *Journal of Biogeography* 38, 209–225. https://doi.org/10.1111/j.1365-2699.2010.02429.x

Gressitt, J.L. (1956) Some distribution patterns of Pacific Island faunae. *Systematic Zoology* 5, 11–47. https://doi.org/10.2307/2411649

Gressitt, J.L. (1984) Systematics and biogeography of the longicorn beetle tribe Tmesisternini. *Pacific Insects Monograph* 41, 1–263.

Haddad, S., Shin, S., Lemmon, A., Lemmon, E., Svacha, P., Farrell, B., Ślipiński, A., Windsor, D. & McKenna, D. (2018) Anchored hybrid enrichment provides new insights into the phylogeny and evolution of longhorned beetles (Cerambycidae). *Systematic Entomology* 43, 68–89. https://doi.org/10.1111/syen.12257

Hall, R. (2013) The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *Journal of Limnology* 72, 1–17. https://doi.org/10.4081/jlimnol.2013.s2.e1

Hardy, N.B., Gullan, P.J., Henderson, R.C. & Cook, L.G. (2008) Relationships among felt scale insects (Hemiptera: Coccoidea: Eriococcidae) of southern beech, *Nothofagus* (Nothofagaceae), with the first descriptions of Australian species of the *Nothofagus*-feeding genus *Madarococcus* Hoy. *Invertebrate Systematics* 22, 365–405. https://doi.org/10.1071/IS07032

Heads, M. (2014) *Biogeography of Australasia: A Molecular Analysis*. Cambridge University Press, New York.

Ikeda, H., Nishikawa, M. & Sota, T. (2012) Loss of flight promotes beetle diversification. *Nature Communications* 3, 648. https://doi.org/10.1038/ncomms1659

Jin, M., Zwick, A., Ślipiński, A., Marris, J.W.M., Thomas, M.C. & Pang, H. (2020) A comprehensive phylogeny of flat bark beetles (Coleoptera: Cucujidae) with a revised classification and a new South American genus. *Systematic Entomology* 45, 248–268. https://doi.org/10.1111/syen.12392

Jønsson, K.A., Fabre, P.-H., Ricklefs, R.E. & Fjeldså, J. (2011) Major global radiation of corvoid birds originated in the proto-Papuan archipelago. *Proceedings of the National Academy of Sciences* 108, 2328–2333. https://doi.org/10.1073/pnas.1018956108

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A. & Jermiin, L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14, 587–589. https://doi.org/10.1038/nmeth.4285

Kamp, P.J.J. (1986) Late Cretaceous-Cenozoic tectonic development of the southwest pacific region. *Tectonophysics* 121, 225–251. https://doi.org/https://doi.org/10.1016/0040-1951(86)90045-4

Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30, 772–780. https://doi.org/10.1093/molbev/mst010

Kodandaramaiah, U. & Wahlberg, N. (2007) Out-of-Africa origin and dispersal-mediated diversification of the butterfly genus *Junonia* (Nymphalidae: Nymphalinae). *Journal of Evolutionary Biology* 20, 2181–2191. https://doi.org/10.1111/j.1420-9101.2007.01425.x

Kück, P., Meusemann, K., Dambach, J., Thormann, B., von Reumont, B.M., Wägele, J.W. & Misof, B. (2010) Parametric and non-parametric masking of randomness in sequence alignments can be improved and leads to better resolved trees. *Frontiers in Zoology* 7, 10. https://doi.org/10.1186/1742-9994-7-10

Kuschel, G. (1990) Beetles in a suburban environment: a New Zealand case study. The identity and status of Coleoptera in the natural and modified habitats of Lynfield, Auckland (1974-1989). *DSIR Plant Protection Report* 3, 1–118.

Kuschel, G. & Emberson, R.M. (2008) Notes on *Hybolasius trigonellaris* Hutton from the Chatham Islands (Coleoptera: Cerambycidae: Lamiinae). *New Zealand Entomologist* 31, 89–92. https://doi.org/10.1080/00779962.2008.9722170

Lanfear, R., Calcott, B., Kainer, D., Mayer, C. & Stamatakis, A. (2014) Selecting optimal partitioning schemes for phylogenomic datasets. *BMC Evolutionary Biology* 14, 82. https://doi.org/10.1186/1471-2148-14-82

Larsson, A. (2014) AliView: a fast and lightweight alignment viewer and editor for large datasets. *Bioinformatics* 30, 3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Lemmon, A.R., Emme, S.A. & Lemmon, E.M. (2012) Anchored hybrid enrichment for massively high-throughput phylogenomics. *Systematic Biology* 61, 727–744. https://doi.org/10.1093/sysbio/sys049

Leschen, R.A.B., Lawrence, J.F., Kuschel, G., Thorpe, S. & Wang, Q. (2003) Coleoptera genera of New Zealand. *New Zealand Entomologist* 26, 15–28. https://doi.org/10.1080/00779962.2003.9722105

Leys, R., Cooper, S.J.B. & Schwarz, M.P. (2002) Molecular phylogeny and historical biogeography of the large carpenter bees, genus *Xylocopa* (Hymenoptera: Apidae). *Biological Journal of the Linnean Society* 77, 249–266. https://doi.org/10.1046/j.1095-8312.2002.00108.x

Linsley, E.G. (1959) Ecology of Cerambycidae. *Annual Review of Entomology* 4, 99–138.

Luo, R., Liu, B., Xie, Y., Li, Z., Huang, W., Yuan, J., He, G., Chen, Y., Pan, Q., Liu, Y., Tang, J., Wu, G., Zhang, H., Shi, Y., Liu, Y., Yu, C., Wang, B., Lu, Y., Han, C., Cheung, D.W., Yiu, S.-M., Peng, S., Xiaoqian, Z., Liu, G., Liao, X., Li, Y., Yang, H., Wang, J., Lam, T.-W. & Wang, J. (2012) SOAPdenovo2: an empirically improved memory-efficient short-read de novo assembler. *GigaScience* 1, 2047-217X-1–18. https://doi.org/10.1186/2047-217X-1-18

Magallón, S. & Castillo, A. (2009) Angiosperm diversification through time. *American Journal of Botany* 96, 349–365. https://doi.org/10.3732/ajb.0800060

McKenna, D.D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D.J., Donath, A., Escalona, H.E., Friedrich, F., Letsch, H., Liu, S., Maddison, D., Mayer, C., Misof, B., Murin, P.J., Niehuis, O., Peters, R.S., Podsiadlowski, L., Pohl, H., Scully, E.D., Yan, E. V., Zhou, X., Ślipiński, A. & Beutel, R.G. (2019) The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences of the United States of America* 116, 24729–24737. https://doi.org/10.1073/pnas.1909655116

McKeown, K.C. (1947) Catalogue of the Cerambycidae (Coleoptera) of Australia. *Australian Museum Memoir* 10, 1–190. https://doi.org/10.3853/j.0067-1967.10.1947.477

Misof, B., Meyer, B., von Reumont, B.M., Kück, P., Misof, K. & Meusemann, K. (2013) Selecting informative subsets of sparse supermatrices increases the chance to find correct trees. *BMC Bioinformatics* 14, 348. https://doi.org/10.1186/1471-2105-14-348

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

Biology 58, 21–34. https://doi.org/10.1093/sysbio/syp006

Möst, M.H., Donabauer, M., Arthofer, W., Schlick-Steiner, B.C. & Steiner, F.M. (2020) Towards an evolutionary history of European-Alpine *Trechus* ground beetles: species groups and wing reduction. *Molecular Phylogenetics and Evolution* 149, 106822. https://doi.org/10.1016/j.ympev.2020.106822

Müller, C.J., Matos-Maraví, P.F. & Beheregaray, L.B. (2013) Delving into *Delias* Hübner (Lepidoptera: Pieridae): fine-scale biogeography, phylogenetics and systematics of the world's largest butterfly genus. *Journal of Biogeography* 40, 881–893. https://doi.org/10.1111/jbi.12040

Nguyen, L.-T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32, 268–274. https://doi.org/10.1093/molbev/msu300

Nie, R., Vogler, A.P., Yang, X.-K. & Lin, M. (2021) Higher-level phylogeny of longhorn beetles (Coleoptera: Chrysomeloidea) inferred from mitochondrial genomes. *Systematic Entomology* 46, 56–70. https://doi.org/10.1111/syen.12447

Oliver, P.M., Brown, R.M., Kraus, F., Rittmeyer, E., Travers, S.L. & Siler, C.D. (2018) Lizards of the lost arcs: mid-Cenozoic diversification, persistence and ecological marginalization in the west pacific. *Proceedings of the Royal Society B: Biological Sciences* 285, 20171760. https://doi.org/10.1098/rspb.2017.1760

Oliver, P.M., Heiniger, H., Hugall, A.F., Joseph, L. & Mitchell, K.J. (2020) Oligocene divergence of frogmouth birds (Podargidae) across Wallace's Line. *Biology Letters* 16, 20200040. https://doi.org/10.1098/rsbl.2020.0040

Oliver, P.M. & Hugall, A.F. (2017) Phylogenetic evidence for mid-Cenozoic turnover of a diverse continental biota. *Nature Ecology & Evolution* 1, 1896–1902. https://doi.org/10.1038/s41559-017-0355-8

Paradis, E. & Schliep, K. (2018) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, 526–528. https://doi.org/10.1093/bioinformatics/bty633

Peters, R.S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., Kozlov, A., Podsiadlowski, L., Petersen, M., Lanfear, R., Diez, P.A., Heraty, J., Kjer, K.M., Klopfstein, S., Meier, R., Polidori, C., Schmitt, T., Liu, S., Zhou, X., Wappler, T., Rust, J., Misof, B. & Niehuis, O. (2017) Evolutionary history of the Hymenoptera. *Current Biology* 27, 1013–

1018. https://doi.org/10.1016/j.cub.2017.01.027

Petersen, M., Meusemann, K., Donath, A., Dowling, D., Liu, S., Peters, R.S., Podsiadlowski, L, Vasilikopoulos, A., Zhou, X., Misof, B. & Niehuis, O. (2017) Orthograph: a versatile tool for mapping coding nucleotide sequences to clusters of orthologous genes. *BMC Bioinformatics* 18, 111. https://doi.org/10.1186/s12859-017-1529-8

R Core Team (2019) R: a language and environment for statistical computing.

Rambaut, A. (2018) FigTree, version 1.4.4.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67, 901–904. https://doi.org/10.1093/sysbio/syy032

Regier, J.C., Shultz, J.W., Ganley, A.R.D., Hussey, A., Shi, D., Ball, B., Zwick, A., Stajich, J.E., Cummings, M.P., Martin, J.W. & Cunningham, C.W. (2008) Resolving arthropod phylogeny: exploring phylogenetic signal within 41 kb of protein-coding nuclear gene sequence. *Systematic Biology* 57, 920–938. https://doi.org/10.1080/10635150802570791

Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Richards, S., Gibbs, R.A., Weinstock, G.M. & Consortium, T.T.G.S. (2008) The genome of the model beetle and pest *Tribolium castaneum*. *Nature* 452, 949–955.

Roguet, J.-P. (2020) Lamiaires du Monde. Available from: https://lamiinae.org (April 17, 2020)

Roskov, Y., Ower, G., Orrell, T., Nicolson, D., Bailly, N., Kirk, P.M., Bourgoin, T., DeWalt, R.E., Decock, W., van Nieukerken, E. & Penev, L. eds. (2020) *Species 2000 & ITIS Catalogue of Life, 2020-04-16 Beta*. Species 2000, Leiden, the Netherlands. Available from: https://www.catalogueoflife.org/col (May 15, 2020)

RStudio Team (2019) RStudio: integrated development for R.

Schnitzler, F.R. & Wang, Q. (2005) Revision of *Zorion* Pascoe (Coleoptera: Cerambycidae), an endemic genus of New Zealand. *Zootaxa*, 1–42. https://doi.org/10.11646/zootaxa.1066.1.1

Shin, S., Clarke, D.J., Lemmon, A.R., Moriarty Lemmon, E., Aitken, A.L., Haddad, S., Farrell, B.D., Marvaldi, A.E., Oberprieler, R.G. & McKenna, D.D. (2018) Phylogenomic data yield new and robust insights into the phylogeny and evolution of weevils. *Molecular Biology and*

Evolution 35, 823–836. https://doi.org/10.1093/molbev/msx324

Skinner, A., Hugall, A.F. & Hutchinson, M.N. (2011) Lygosomine phylogeny and the origins of Australian scincid lizards. *Journal of Biogeography* 38, 1044–1058. https://doi.org/10.1111/j.1365-2699.2010.02471.x

Ślipiński, A. & Escalona, H.E. (2013) *Australian Longhorn Beetles (Coleoptera: Cerambycidae) Volume 1: Introduction and Subfamily Lamiinae*. CSIRO Publishing, Melbourne, 503 pp.

Ślipiński, A. & Escalona, H.E. (2016) *Australian Longhorn Beetles (Coleoptera: Cerambycidae) Volume 2: Subfamily Cerambycinae*. CSIRO Publishing, Melbourne, 613 pp.

Souza, D. de S., Marinoni, L., Laura Monné, M. & Gómez-Zurita, J. (2020) Molecular phylogenetic assessment of the tribal classification of Lamiinae (Coleoptera: Cerambycidae). *Molecular Phylogenetics and Evolution* 145, 106736. https://doi.org/10.1016/j.ympev.2020.106736

Suyama, M., Torrents, D. & Bork, P. (2006) PAL2NAL: robust conversion of protein sequence alignments into the corresponding codon alignments. *Nucleic Acids Research* 34, W609–W612. https://doi.org/10.1093/nar/gkl315

Švácha, P. & Lawrence, J.F. (2014) Cerambycidae Latreille, 1802. In: R. A. B. Leschen and R. G. Beutel (Eds), *Handbook of Zoology, Arthropoda: Insecta, Coleoptera, Beetles, Volume 3: Morphology and Systematics (Phytophaga)*. Walter de Gruyter GmbH, Berlin, pp. 77–177.

Tänzler, R., Van Dam, M.H., Toussaint, E.F.A., Suhardjono, Y.R., Balke, M. & Riedel, A. (2016) Macroevolution of hyperdiverse flightless beetles reflects the complex geological history of the Sunda Arc. *Scientific Reports* 6, 18793. https://doi.org/10.1038/srep18793

Tavakilian, G. & Chevillotte, H. (2020) Base de données Titan sur les Cerambycidés ou Longicornes. Available from: http://titan.gbif.fr/ (February 13, 2020)

Toussaint, E.F.A., Condamine, F.L., Hawlitschek, O., Watts, C.H., Porch, N., Hendrich, L. & Balke, M. (2015a) Unveiling the diversification dynamics of Australasian predaceous diving beetles in the Cenozoic. *Systematic Biology* 64, 3–24. https://doi.org/10.1093/sysbio/syu067

Toussaint, E.F.A., Tänzler, R., Rahmadi, C., Balke, M. & Riedel, A. (2015b) Biogeography of Australasian flightless weevils (Curculionidae, Celeuthetini) suggests permeability of Lydekker's and Wallace's Lines. *Zoologica Scripta* 44, 632–644. https://doi.org/10.1111/zsc.12127

Vitali, F. (2009) The cerambycids included in Baltic amber: current knowledge status with the description of new taxa (Coleoptera, Cerambycidae). *Denisia* 26, 231–242.

Vitali, F. (2011) Six new fossil Cerambycids included in Baltic and Saxon amber. *Entomapeiron (P. S.)* 4, 1–36.

Vitali, F. (2014) New fossil cerambycids (Coleoptera: Cerambycidae) from Baltic amber belonging to the collection Hoffeins. *Baltic Journal of Coleopterology* 14, 103–112.

Vitali, F. & Daamgard, A.L. (2016) *Dicentrus mehli* sp. n. (Coleoptera: Cerambycidae) implies close trophic association between Opsimini and *Calocedrus*, dating the Baltic amber back to the early Oligocene. *Baltic Journal of Coleopterology* 16, 37–43.

Voris, H.K. (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* 27, 1153–1167. https://doi.org/10.1046/j.1365-2699.2000.00489.x

Wagner, D.L. & Liebherr, J.K. (1992) Flightlessness in insects. *Trends in Ecology & Evolution* 7, 216–220. https://doi.org/https://doi.org/10.1016/0169-5347(92)90047-F

Wallis, G.P. & Trewick, S.A. (2009) New Zealand phylogeography: evolution on a small continent. *Molecular Ecology* 18, 3548–3580. https://doi.org/10.1111/j.1365-294X.2009.04294.x

Wang, B., Ma, J., McKenna, D.D., Yan, E. V., Zhang, H. & Jarzembowski, E.A. (2014) The earliest known longhorn beetle (Cerambycidae: Prioninae) and implications for the early evolution of Chrysomeloidea. *Journal of Systematic Palaeontology* 12, 565–574. https://doi.org/10.1080/14772019.2013.806602

Wang, Q. ed. (2017) *Cerambycidae of the World: Biology and Pest Management*. Taylor & Francis Group, Boca Raton.

Waterhouse, R.M., Tegenfeldt, F., Li, J., Zdobnov, E.M. & Kriventseva, E. V (2012) OrthoDB: a hierarchical catalog of animal, fungal and bacterial orthologs. *Nucleic Acids Research* 41, D358–D365. https://doi.org/10.1093/nar/gks1116

Weigel, A. & Skale, A. (2014) On the taxonomy, synonymy and faunistics of the Apomecynini of the Asian-Australian Region (Insecta: Coleoptera: Cerambycidae: Lamiinae). Part 5: Nomenclatural corrections. *Vernate* 33, 221–223.

Werren, J.H., Richards, S., Desjardins, C.A., Niehuis, O., Gadau, J., Colbourne, J.K. & The Nasonia Genome Working Group (2010) Functional and evolutionary insights from the genomes of three parasitoid *Nasonia* species. *Science* 327, 343–348.

Yang, Z. (2007) PAML 4: Phylogenetic Analysis by Maximum Likelihood. *Molecular Biology and*

Evolution 24, 1586–1591. https://doi.org/10.1093/molbev/msm088

Yeates, D.K. & Cassis, G. (2017) Australian Insect Biogeography: Beyond Faunal Provinces and Elements towards Processes. In: M. C. Ebach (Ed), *Handbook of Australasian Biogeography*. CRC Press, Boca Raton, pp. 215–240.

Zahirovic, S., Matthews, K.J., Flament, N., Müller, R.D., Hill, K.C., Seton, M. & Gurnis, M. (2016) Tectonic evolution and deep mantle structure of the eastern Tethys since the latest Jurassic. *Earth-Science Reviews* 162, 293–337. https://doi.org/https://doi.org/10.1016/j.earscirev.2016.09.005

Zang, R. (1905) Coleoptera Longicornia aus der Berendtschen Bernsteinsammlung. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 1905, 232–245.

Zhan, S., Merlin, C., Boore, J.L. & Reppert, S.M. (2011) The monarch butterfly genome yields insights into long-distance migration. *Cell* 147, 1171–1185.

Zhang, S.-Q., Che, L.-H., Li, Y., Dan, L., Pang, H., Ślipiński, A. & Zhang, P. (2018) Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications* 9, 205. https://doi.org/10.1038/s41467-017-02644-4

Zwick, A., Regier, J.C. & Zwickl, D.J. (2012) Resolving discrepancy between nucleotides and amino acids in deep-level arthropod phylogenomics: differentiating serine codons in 21-amino-acid models S. R. Gadagkar (Ed). *PLOS ONE* 7, e47450. https://doi.org/10.1371/journal.pone.0047450

SUPPLEMENTARY INFORMATION (FIGURES S1–4, TABLES S1–2)

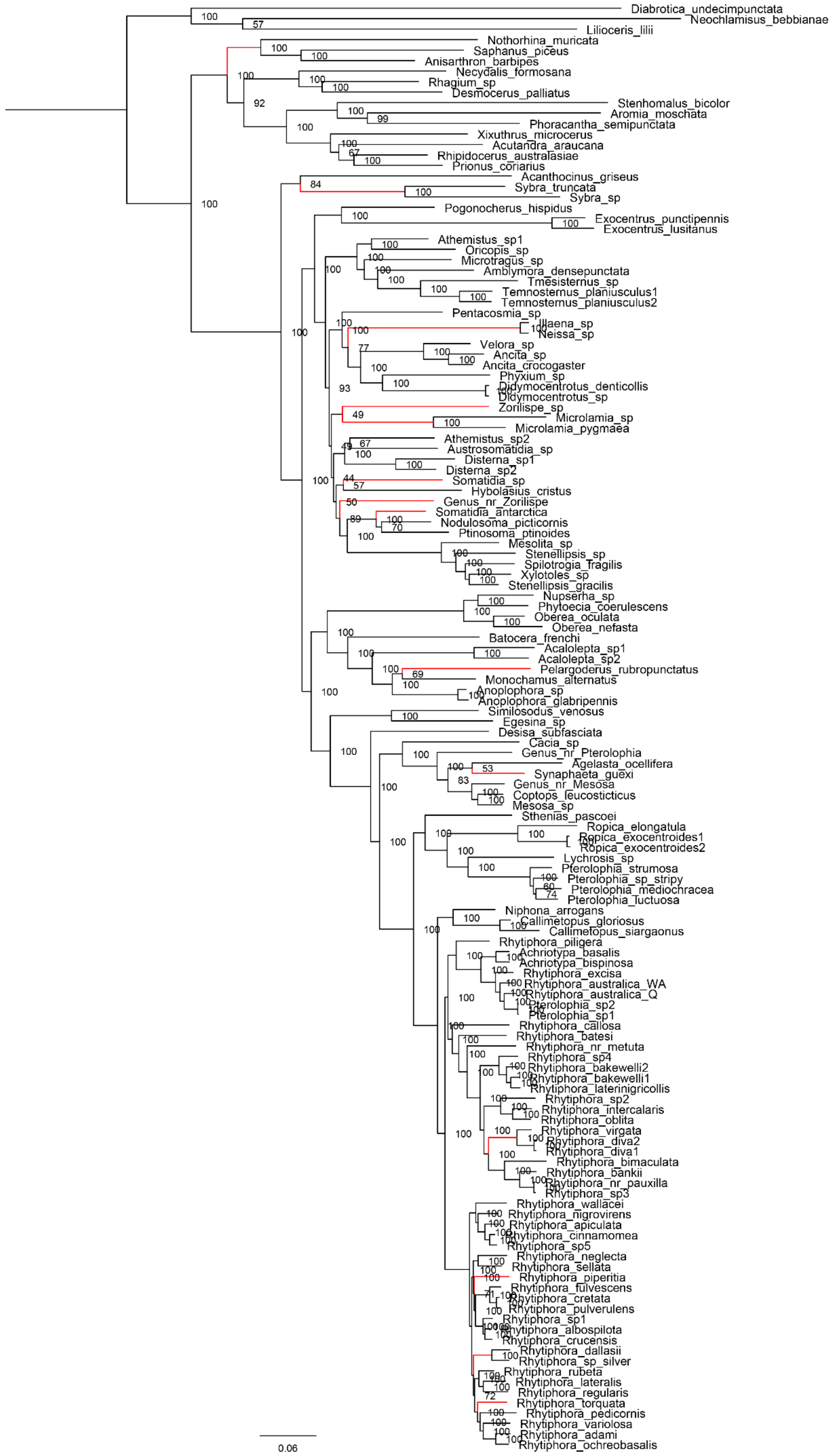

Figure S1. Maximum likelihood phylogeny of Cerambycidae: partitioned IQ-TREE analysis of the nucleotide dataset. Branch supports are bootstrap values and the scale bar is nucleotide sequence change per Mya. Branches that differ between the datasets are coloured red.

Figure S2. 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 Mya. Branches that differ between the datasets are coloured red.

Chapter 1: Supplementary Information (Figures S1–4, Tables S1–2)

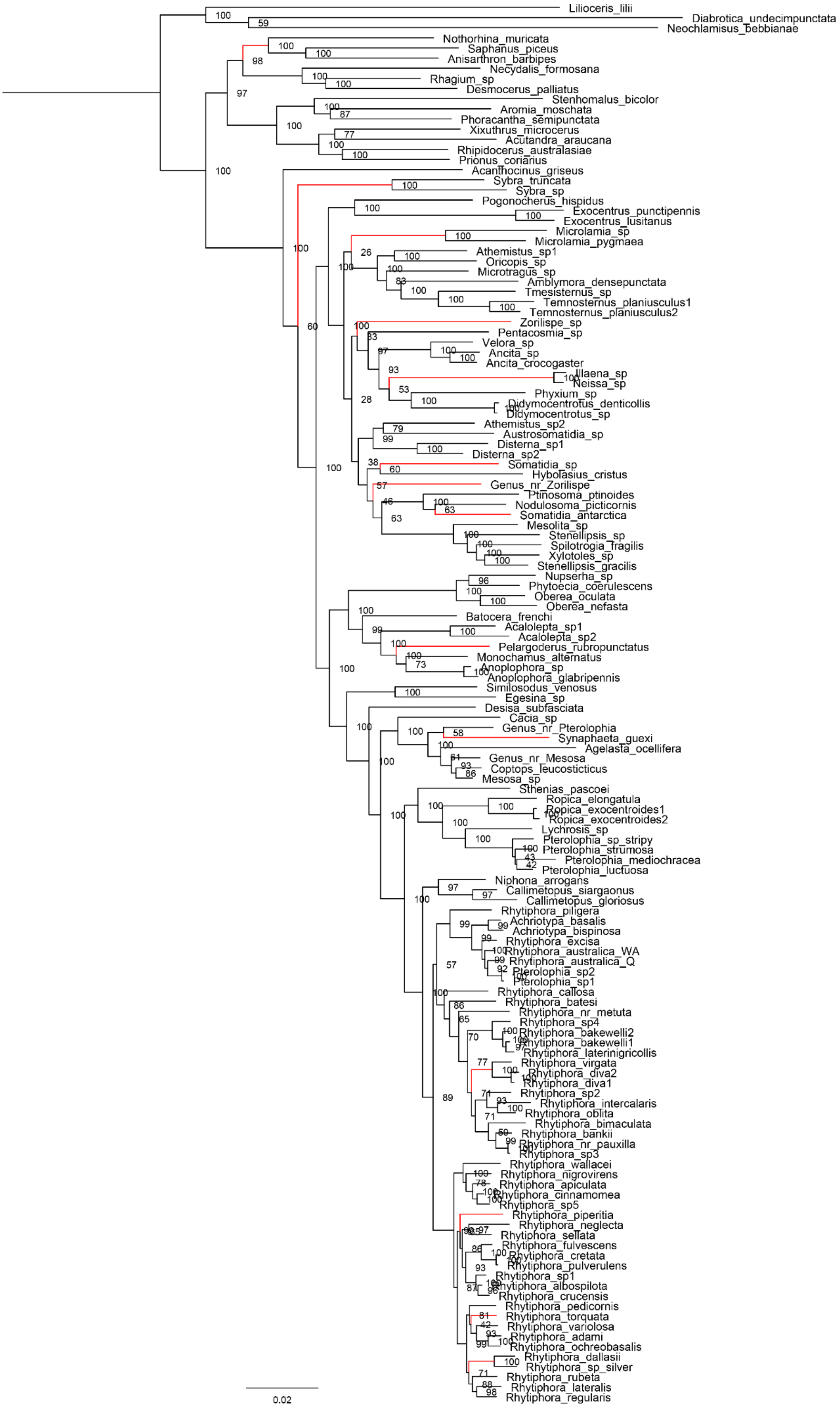

Figure S3. Maximum likelihood phylogeny of Cerambycidae: partitioned IQ-TREE analysis of the amino acid dataset. Branch supports are bootstrap values and the scale bar is sequence change per Mya. Branches that differ between the datasets are coloured red.

Figure S4. Maximum likelihood phylogeny of Cerambycidae: partitioned IQ-TREE analysis of the amino acid dataset with five taxa removed. Branch supports are bootstrap values and the scale bar is sequence change per Mya. Branches that differ from the full-taxa AA dataset are coloured red.

Chapter 1: Supplementary Information (Figures S1–4, Tables S1–2)

Table S1. List of 141 Cerambycidae (and Chrysomelidae) specimens sampled for phylogenetic analyses. 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).

Accession no.	**Subfamily**	**Tribe**	**Genus**	**Species**	**Locality**	**Specimen condition**	**Missing data (%)**
A066410	Lamiinae	Pteropliini	*Rhytiphora*	*apiculata*	Australia	Ethanol	14.06
A066429	Lamiinae	Pteropliini	*Rhytiphora*	*bankii*	Australia	Ethanol	34.78
A066504	Lamiinae	Pteropliini	*Rhytiphora*	*diva (1)*	Australia	Ethanol	26.28
A066513	Lamiinae	Pteropliini	*Pterolophia*	*luctuosa*	Australia	Ethanol	24.46
A066539	Lamiinae	Pteropliini	*Rhytiphora*	*"sp near pauxilla"*	Australia	Ethanol	27.20
A066543	Lamiinae	Pteropliini	*Rhytiphora*	*pedicornis*	Australia	Ethanol	28.31
A066547	Lamiinae	Pteropliini	*Rhytiphora*	*adami*	Australia	Ethanol	23.18
A066548	Lamiinae	Pteropliini	*Rhytiphora*	*bakewelli (2)*	Australia	Ethanol	28.82
A066550	Lamiinae	Pteropliini	*Rhytiphora*	*ochreobasalis*	Australia	Ethanol	36.40
A066569	Lamiinae	Apomecynini	*Ropica*	*exocentroides (1)*	Australia	Ethanol	28.07
A066648	Lamiinae	Pteropliini	*Rhytiphora*	*virgata*	Australia	Ethanol	33.41
A066758	Lamiinae	Pteropliini	*Rhytiphora*	*fulvescens*	Australia	Ethanol	37.61
A068441	Lamiinae	Pteropliini	*Rhytiphora*	*batesi*	PNG	Pinned	64.93
A068442	Lamiinae	Pteropliini	*Rhytiphora*	*intercalaris*	PNG	Pinned	53.43
A068445	Lamiinae	Pteropliini	*Rhytiphora*	*bankii*	Philippines	Pinned	**99.78**
A068446	Lamiinae	Pteropliini	*Rhytiphora*	*diva (2)*	PNG	Pinned	21.12
A068448	Lamiinae	Pteropliini	*Rhytiphora*	*wallacei*	PNG	Pinned	36.31
A068452	Lamiinae	Pteropliini	*Rhytiphora*	*bimaculata*	PNG	Pinned	95.02
A068453	Lamiinae	Pteropliini	*Pterolophia*	*mediochracea*	PNG	Pinned	76.14
A068455	Lamiinae	Pteropliini	*Pterolophia*	*"stripy sp"*	PNG	Pinned	19.58
A068456	Lamiinae	Pteropliini	*Sthenias*	*pascoei*	Thailand	Pinned	60.21
A068457	Lamiinae	Pteropliini	*Xiphotheata*	*moellendorfii*	PNG	Pinned	**99.45**
A068459	Lamiinae	Pteropliini	*Rhytiphora*	*"sp near metuta"*	PNG	Pinned	93.96
A068460	Lamiinae	Mesosini	*Coptops*	*leucosticticus*	Malaysia	Pinned	28.06
A068462	Lamiinae	Mesosini	*Synaphaeta*	*guexi*	USA	Pinned	94.84
A068463	Lamiinae	Pteropliini	*Similosodus*	*venosus*	Australia	Ethanol	18.96
A068464	Lamiinae	Pteropliini	*Achriotypa*	*basalis*	Australia	Pinned	31.23
A068466	Lamiinae	Pteropliini	*Achriotypa*	*bispinosa*	Australia	Pinned	28.70
A068467	Lamiinae	Pteropliini	*Callimetopus*	*siargaonus*	Philippines	Pinned	98.39
A068468	Lamiinae	Pteropliini	*Callimetopus*	*gloriosus*	Philippines	Pinned	27.96
A068469	Lamiinae	Pteropliini	*Niphona*	*arrogans*	Philippines	Pinned	37.48
A068472	Lamiinae	Pteropliini	*Egesina*	*sp*	Thailand	Pinned	66.66
A068473	Lamiinae	Pteropliini	*Desisa*	*subfasciata*	Thailand	Pinned	56.15
A068474	Lamiinae	Mesosini	*Mesosa*	*sp*	Thailand	Pinned	**99.83**
A068476	Lamiinae	Mesosini	*Agelasta*	*ocellifera*	Philippines	Pinned	92.92
A068477	Lamiinae	Mesosini	*Cacia*	*sp*	Philippines	Pinned	44.14
A073366	Lamiinae	Lamiini	*Anoplophora*	*sp*	China	Ethanol	30.83
A073783	Lamiinae	Pteropliini	*Rhytiphora*	*albospilota*	Australia	Ethanol	31.89
A073784	Lamiinae	Pteropliini	*Rhytiphora*	*australica (WA)*	Australia	Ethanol	25.07
A073785	Lamiinae	Pteropliini	*Rhytiphora*	*australica (QLD)*	Australia	Ethanol	32.65

A073787	Lamiinae	Pteropliini	*Rhytiphora*	*bakewelli (1)*	Australia	Ethanol	33.39
A073789	Lamiinae	Pteropliini	*Rhytiphora*	*callosa*	Australia	Ethanol	29.81
A073792	Lamiinae	Pteropliini	*Rhytiphora*	*cinnamomea*	Australia	Ethanol	23.68
A073794	Lamiinae	Pteropliini	*Rhytiphora*	*cretata*	Australia	Ethanol	33.44
A073795	Lamiinae	Pteropliini	*Rhytiphora*	*crucensis*	Australia	Ethanol	24.89
A073796	Lamiinae	Pteropliini	*Rhytiphora*	*dallasii*	Australia	Ethanol	29.27
A073802	Lamiinae	Pteropliini	*Rhytiphora*	*lateralis*	Australia	Ethanol	35.65
A073804	Lamiinae	Pteropliini	*Rhytiphora*	*neglecta*	Australia	Ethanol	32.26
A073807	Lamiinae	Pteropliini	*Rhytiphora*	*nigrovirens*	Australia	Ethanol	32.59
A073808	Lamiinae	Pteropliini	*Rhytiphora*	*oblita*	Australia	Ethanol	33.11
A073809	Lamiinae	Pteropliini	*Rhytiphora*	*piperitia*	Australia	Ethanol	25.68
A073811	Lamiinae	Pteropliini	*Rhytiphora*	*pulverulens*	Australia	Ethanol	35.35
A073813	Lamiinae	Pteropliini	*Rhytiphora*	*regularis*	Australia	Ethanol	25.65
A073815	Lamiinae	Pteropliini	*Rhytiphora*	*rubeta*	Australia	Ethanol	22.70
A073818	Lamiinae	Pteropliini	*Rhytiphora*	*"silver sp"*	Australia	Ethanol	30.67
A073819	Lamiinae	Pteropliini	*Rhytiphora*	*"sp5"*	Australia	Ethanol	21.04
A073820	Lamiinae	Pteropliini	*Rhytiphora*	*"sp1"*	Australia	Ethanol	18.28
A073821	Lamiinae	Pteropliini	*Rhytiphora*	*"sp2"*	Australia	Ethanol	23.65
A073823	Lamiinae	Pteropliini	*Rhytiphora*	*"sp3"*	Australia	Ethanol	26.02
A073824	Lamiinae	Pteropliini	*Rhytiphora*	*"sp4"*	Australia	Ethanol	13.95
A073825	Lamiinae	Pteropliini	*Rhytiphora*	*torquata*	Australia	Ethanol	20.67
A073826	Lamiinae	Pteropliini	*Rhytiphora*	*variolosa*	Australia	Ethanol	31.19
A073835	Lamiinae	Pteropliini	*Pterolophia*	*strumosa*	Australia	Ethanol	23.89
A073836	Lamiinae	Pteropliini	*Pterolophia*	*"sp2"*	Australia	Ethanol	21.28
A073840	Lamiinae	Lamiini	*Acalolepta*	*"sp1"*	Australia	Ethanol	20.95
A073841	Lamiinae	Desmiphorini	*Amblymora*	*densepunctata*	Australia	Ethanol	24.58
A073843	Lamiinae	Ancitini	*Ancita*	*sp*	Australia	Ethanol	39.24
A073845	Lamiinae	Ancitini	*Ancita*	*crocogaster*	Australia	Ethanol	27.78
A073847	Lamiinae	Parmenini	*Athemistus*	*"sp1"*	Australia	Ethanol	33.96
A073848	Lamiinae	Parmenini	*Athemistus*	*"sp2"*	Australia	Ethanol	33.72
A073849	Lamiinae	Parmenini	*Austrosomatidia*	*sp*	Australia	Ethanol	33.20
A073850	Lamiinae	Acanthocinini	*Didymocentrotus*	*denticollis*	Australia	Ethanol	34.92
A073852	Lamiinae	Zygocerini	*Disterna*	*"sp1"*	Australia	Ethanol	35.20
A073854	Lamiinae	Zygocerini	*Disterna*	*"sp2"*	Australia	Ethanol	29.69
A073855	Lamiinae	Lamiini	*Illaena*	*sp*	Australia	Ethanol	39.67
A073858	Lamiinae	Parmenini	*Mesolita*	*sp*	Australia	Ethanol	25.10
A073861	Lamiinae	Acanthocinini	*Microlamia*	*sp*	Norfolk Is.	Ethanol	37.99
A073862	Lamiinae	Lamiini	*Pelargoderus*	*rubropunctatus*	Australia	Ethanol	17.57
A073865	Lamiinae	Lamiini	*Pentacosmia*	*sp*	Australia	Ethanol	42.68
A073866	Lamiinae	Lamiini	*Phyxium*	*sp*	Australia	Ethanol	38.45
A073868	Lamiinae	Apomecynini	*Ropica*	*elongatula*	Australia	Ethanol	31.10
A073869	Lamiinae	Apomecynini	*Ropica*	*exocentroides (2)*	Australia	Ethanol	36.16
A073871	Lamiinae	Enicodini	*Stenellipsis*	*sp*	Australia	Ethanol	34.73
A073874	Lamiinae	Apomecynini	*Sybra*	*truncata*	Australia	Ethanol	29.94
A073875	Lamiinae	Apomecynini	*Sybra*	*sp*	Australia	Ethanol	26.19
A073876	Lamiinae	Tmesisternini	*Temnosternus*	*planiusculus (1)*	Australia	Ethanol	32.58
A073877	Lamiinae	Tmesisternini	*Temnosternus*	*planiusculus (2)*	Australia	Ethanol	35.99
A073879	Lamiinae	Acanthocinini	*Didymocentrotus*	*sp*	Australia	Ethanol	36.14
A073881	Lamiinae	Desmiphorini	*Velora*	*sp*	Australia	Ethanol	34.73

A073883	Lamiinae	NA	*"Genus near Zorilispe"*	*sp*	Australia	Ethanol	28.69
A073885	Lamiinae	Lamiini	*Acalolepta*	*"sp2"*	China	Ethanol	33.99
A073888	Lamiinae	Lamiini	*Monochamus*	*alternatus*	China	Ethanol	25.01
A073890	Lamiinae	Saperdini	*Nupserha*	*sp*	China	Ethanol	26.57
A073893	Lamiinae	Pteropliini	*Lychrosis*	*sp*	China	Ethanol	28.49
A073894	Lamiinae	Pogonocherini	*Exocentrus*	*punctipennis*	Poland	Ethanol	28.36
A073895	Lamiinae	Pogonocherini	*Exocentrus*	*lusitanus*	Poland	Ethanol	22.91
A073896	Lamiinae	Saperdini	*Oberea*	*oculata*	Poland	Ethanol	28.07
A073923	Lamiinae	Lamiini	*Anoplophora*	*glabripennis*	USA	Ethanol	24.49
DDM0441	Lamiinae	Mesosini	*"Genus near Mesosa"*	*sp*	Costa Rica	Ethanol	37.83
DDM0681	Lamiinae	Mesosini	*Mesosa*	*sp*	Thailand	Ethanol	31.79
DDM0748	Spondylidinae	Saphanini	*Saphanus*	*piceus*	Czech Republic	Previous data	45.33
DDM0753	Lamiinae	Saperdini	*Phytoecia*	*coerulescens*	Slovakia	Previous data	47.77
DDM1093	Lamiinae	Pogonocherini	*Pogonocherus*	*hispidus*	Czech Republic	Previous data	32.99
DDM1111	Spondylidinae	Anisarthrini	*Anisarthron*	*barbipes*	Slovakia	Previous data	38.67
DDM1114	Spondylidinae	Asemini	*Nothorhina*	*muricata*	Czech Republic	Previous data	42.17
DDM1122	Lamiinae	Acanthocinini	*Acanthocinus*	*griseus*	Czech Republic	Previous data	48.59
DDM1139	Cerambycinae	Obriini	*Stenhomalus*	*bicolor*	Slovakia	Previous data	41.68
DDM2479	Lamiinae	Parmenini	*Microtragus*	*sp*	Australia	Ethanol	34.26
DDM2480	Lamiinae	Saperdini	*Oberea*	*nefasta*	Australia	Ethanol	31.55
DDM2485	Lamiinae	Pteropliini	*Rhytiphora*	*piligera*	Australia	Ethanol	31.79
DDM2487	Lamiinae	Tmesisternini	*Tmesisternus*	*sp*	Australia	Previous data	42.66
DDM2489	Cerambycinae	Callichromatini	*Aromia*	*moschata*	Eastern Europe	Previous data	46.69
DDM2492	Lepturinae	Rhagiini	*Rhagium*	*sp*	Eastern Europe	Previous data	35.70
DDM2672	Cerambycinae	Phoracanthini	*Phoracantha*	*semipunctata*	Australia	Previous data	49.66
DDM2679	Prioninae	Macrotomini	*Xixuthrus*	*microcerus*	Australia	Previous data	60.94
DDM2680	Prioninae	Meroscelisini	*Rhipidocerus*	*australasiae*	Australia	Previous data	42.55
DDM2682	Lamiinae	Batocerini	*Batocera*	*frenchi*	Australia	Previous data	70.81
DDM2688	Lamiinae	Pteropliini	*Rhytiphora*	*sellata*	Australia	Ethanol	40.32
DDM2717	Lamiinae	Lamiini	*Neissa*	*sp*	Australia	Ethanol	37.87
DDM2718	Lamiinae	Desmiphorini	*Oricopis*	*sp*	Australia	Ethanol	26.65
DDM2723	Lamiinae	Pteropliini	*Rhytiphora*	*laterinigricollis*	Australia	Ethanol	37.61
DDM2725	Lamiinae	Pteropliini	*Pterolophia*	*"sp1"*	Australia	Ethanol	18.49

DDM2726	Lamiinae	Mesosini	*"Genus near Pterolophia"*	*sp*	Australia	Ethanol	30.04
DDM2727	Lamiinae	Pteropliini	*Rhytiphora*	*excisa*	Australia	Ethanol	35.02
DDM2730	Lamiinae	Parmenini	*Somatidia*	*sp*	Australia	Ethanol	32.42
DDM2744	Lamiinae	Apomecynini	*Zorilispe*	*sp*	Australia	Ethanol	35.67
I2500	Prioninae	Parandrini	*Acutandra*	*araucana*	Argentina	Previous data	30.95
I2502	Prioninae	Prionini	*Prionus*	*coriarius*	Czech Republic	Previous data	22.33
I2530	Galerucinae [Chrysomelidae]	Luperini	*Diabrotica*	*undecimpunctata*	USA	Previous data	30.01
I3056	Lepturinae	Desmocerini	*Desmocerus*	*palliatus*	USA	Previous data	38.37
I3057	Lepturinae	Necydalini	*Necydalis*	*formosana*	Japan	Previous data	23.25
I3061	Cryptocephalinae [Chrysomelidae]	Fulcidacini	*Neochlamisus*	*bebbianae*	USA	Previous data	45.37
I3062	Criocerinae [Chrysomelidae]	Criocerini	*Lilioceris*	*lilii*	USA	Previous data	45.86
NZ21579	Lamiinae	Parmenini	*Nodulosoma*	*picticornis*	NZ	Ethanol	27.12
NZ22188	Lamiinae	Parmenini	*Ptinosoma*	*ptinoides*	NZ	Ethanol	28.98
NZ22913	Lamiinae	Acanthocinini	*Hybolasius*	*cristus*	NZ	Ethanol	31.04
NZ23076	Lamiinae	Parmenini	*Xylotoles*	*sp*	NZ	Ethanol	29.56
NZ25544	Lamiinae	Enicodini	*Stenellipsis*	*gracilis*	NZ	Ethanol	30.85
NZ25623	Lamiinae	Acanthocinini	*Microlamia*	*pygmaea*	NZ	Ethanol	30.94
NZ25918	Lamiinae	Acanthocinini	*Spilotrogia*	*fragilis*	NZ	Ethanol	18.17
NZ34100	Lamiinae	Parmenini	*Somatidia*	*antarctica*	NZ	Ethanol	32.37

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

Genus	**Species representative**	**Region**	**Notes**
Acalolepta	*"sp1"*	Australia + Asia	Sampled from Australia
Acanthocinus	*griseus*	Europe	Genus in Americas, Europe, Asia; sampled from Czech Republic
Acutandra	*araucana*	Americas	Genus in Americas, Africa; sampled from Argentina
Agelasta	*ocellifera*	Asia	One species in Melanesia; sampled from Philippines
Amblymora	*densepunctata*	Australia + Asia	Sampled from Australia
Ancita	*crocogaster*	Australia	Genus also in Papua New Guinea; sampled from Australia
Anisarthron	*barbipes*	Europe	Genus in Europe, Middle East; sampled from Slovakia
Anoplophora	*glabripennis*	Asia	Sampled from USA (introduced)
Aromia	*moschata*	Europe	Genus in Europe, Asia; sampled from eastern Europe
Athemistus	*"sp1"*	Australia	Sampled from Australia (endemic)
Athemistus	*"sp2"*	Australia	Sampled from Australia (endemic)
Austrosomatidia	*sp*	Australia	Sampled from Australia (endemic)
Batocera	*frenchi*	Australia + Asia	Sampled from Australia
Cacia	*sp*	Asia	Few species in Melanesia; sampled from Philippines
Callimetopus	*gloriosus*	Asia	Sampled from Philippines
Coptops	*leucostictícus*	Asia	Few species in Africa, Middle East, Melanesia; sampled from Malaysia
Desisa	*subfasciata*	Asia	Sampled from Thailand
Desmocerus	*palliatus*	Americas	Sampled from USA
Diabrotica	*undecimpunctata*	Americas	Sampled from USA
Didymocentrotus	*denticollis*	Australia	Sampled from Australia (endemic)
Disterna	*"sp1"*	Australia	Genus also in Papua New Guinea; sampled from Australia
Egesina	*sp*	Asia	Sampled from Thailand
Exocentrus	*lusitanus*	Europe	Genus in Africa, Europe, Asia, Australia; sampled from Poland
"Genus near Mesosa"	*sp*	Americas	Sampled from Costa Rica
"Genus near Pterolophia"	*sp*	Australia + Asia	Sampled from Australia
"Genus near Zorilispe"	*sp*	Australia	Undescribed genus, probably endemic
Hybolasius	*cristus*	New Zealand	One species in Chatham Islands
Illaena	*sp*	Australia	Sampled from Australia (endemic)
Lilioceris	*lilii*	Europe	Genus in Europe, Asia; sampled from USA (introduced)
Mesolita	*sp*	Australia + New Zealand	Most species Australian; sampled from Australia
Mesosa	*sp*	Asia	Few species in Africa, Europe; sampled from Thailand
Microlamia	*pygmaea*	New Zealand	Sampled from Norfolk Island
Microtragus	*sp*	Australia	Sampled from Australia (endemic)
Monochamus	*alternatus*	Asia	Genus in Americas, Europe, Africa, Asia; sampled from China
Necydalis	*formosana*	Asia	Genus in Americas, Europe, Asia; sampled from Japan
Neissa	*sp*	Australia	Sampled from Australia (endemic)
Neochlamisus	*bebbianae*	Americas	Sampled from USA
Niphona	*arrogans*	Asia	Few species in Africa; sampled from Philippines

Nodulosoma	*picticornis*	New Zealand	
Nothorhina	*muricata*	Europe	Genus in Europe, Middle East, India; sampled from Czech Republic
Nupserha	*sp*	Asia	Genus in Africa, Asia; sampled from China
Oberea	*nefasta*	Australia + Asia	Genus in Americas, Europe, Africa, Asia, Australia; sampled from Australia
Oberea	*oculata*	Europe	Genus in Americas, Europe, Africa, Asia, Australia; sampled from Poland
Oricopis	*sp*	Australia	Sampled from Australia (endemic)
Pelargoderus	*rubropunctatus*	Australia + Asia	Most species Asian; sampled from Australia
Pentacosmia	*sp*	Australia	Sampled from Australia (endemic)
Phoracantha	*semipunctata*	Australia	Genus also in Papua New Guinea; sampled from Australia
Phytoecia	*coerulescens*	Europe	Genus in Africa, Europe, Asia; sampled from Slovakia
Phyxium	*sp*	Australia	Most species Papua New Guinea; sampled from Australia
Pogonocherus	*hispidus*	Europe	Genus in Americas, Europe, Africa, Asia; sampled from Czech Republic
Prionus	*coriarius*	Europe	Genus in Americas, Europe, Asia; sampled from Czech Republic
Pterolophia	*luctuosa*	Australia + Asia	Few species in Africa; sampled from Australia
Ptinosoma	*ptinoides*	New Zealand	One species in Chatham Islands
Rhagium	*sp*	Europe	Genus in Americas, Europe, Asia; sampled from eastern Europe
Rhipidocerus	*australasiae*	Australia	Sampled from Australia (endemic)
Rhytiphora	*apiculata*	Australia + Asia	Sampled from Australia
Ropica	*elongatula*	Australia + Asia	Sampled from Australia
Saphanus	*piceus*	Europe	Genus in Europe, Middle East; sampled from Czech Republic
Similosodus	*venosus*	Australia + Asia	Most species Asian; sampled from Australia
Somatidia	*antarctica*	Australia + New Zealand	Genus also in New Caledonia; sampled from New Zealand
Somatidia	*sp*	Australia + New Zealand	Genus also in New Caledonia; sampled from Australia
Spilotrogia	*fragilis*	New Zealand	
Stenellipsis	*gracilis*	Australia + New Zealand	Genus also in New Caledonia; sampled from New Zealand
Stenellipsis	*sp*	Australia + New Zealand	Genus also in New Caledonia; sampled from Australia
Stenhomalus	*bicolor*	Europe	Genus in Africa, Europe, Asia, Melanesia; sampled from Slovakia
Sthenias	*pascoei*	Asia	Few species in Africa; sampled from Thailand
Sybra	*truncata*	Australia + Asia	Few species in Africa; sampled from Australia
Synaphaeta	*guexi*	Americas	Sampled from USA
Temnosternus	*planiusculus (1)*	Australia	Sampled from Australia (endemic)
Tmesisternus	*sp*	Australia + Asia	Most species Papua New Guinea; sampled from Australia
Velora	*sp*	Australia	Genus also in Papua New Guinea; sampled from Australia
Xixuthrus	*microcerus*	Australia + Asia	Sampled from Australia
Xylotoles	*sp*	New Zealand	Few species in Chatham, Lord Howe, Norfolk Islands
Zorilispe	*sp*	Australia + Asia	One species in Africa; sampled from Australia

Chapter 2: Redefining *Rhytiphora*: a phylogenetic and morphological study of Australia's largest longhorn beetle genus (Coleoptera: Cerambycidae)

Authors: Lauren G. Ashman[1,2], Diana Hartley[2], Mengjie Jin[2,3], David M. Rowell[1], Luisa Teasdale[2], Andreas Zwick[2], Adam Ślipiński[2]

[1] Research School of Biology, Australian National University, Canberra, Australia

[2] Australian National Insect Collection, CSIRO, Canberra, Australia

[3] State Key Laboratory of Biocontrol, School of Life Sciences/School of Ecology, Sun Yat-Sen University, Guangzhou, China

ABSTRACT

Rhytiphora Audinet-Serville is the most speciose longhorn beetle (Cerambycidae) genus in Australia, with about 200 species (from nearly 40 former genera) distributed across the entire continent. We used whole genome shotgun sequencing and COI barcoding of museum specimens to reconstruct the phylogeny of *Rhytiphora,* and analyse its morphological diversity and biogeographic history. We recovered a monophyletic *Rhytiphora* containing two distinct clades, within which all of the former genera (except *Achriotypa*) are paraphyletic. Nine morphological traits (including body size and the male setose 'sex patches') show strong phylogenetic signal and can be used to differentiate between the two clades. One clade is mainly restricted to Australia's tropical north, while the other, larger clade has many species along the mesic east coast. Both clades have experienced multiple biome shifts, displaying a remarkable flexibility in habitat occupancy.

INTRODUCTION

Approximately a quarter of the world's animal species are beetles, and one of the largest families is the Cerambycidae or longhorn beetles, with at least 35,000 species worldwide (Švácha & Lawrence 2014). Longhorn larvae typically feed inside woody or herbaceous plants, and many species cause economic losses in the agricultural and forestry industries (Wang 2017). The largest of the eight subfamilies is Lamiinae, with over 21,000 species in nearly 3,000 genera; there are almost 80 tribes, which are universally recognised as inaccurate and in need of revision (Ślipiński & Escalona 2013; Souza *et al.* 2020).

One of the largest lamiine tribes is Pteropliini Thomson, with historically about 200 genera distributed across the world, including: 16 genera in the Americas (including the type genus *Pteroplius* Lacordaire), 37 in Africa and Europe, 121 in Asia, and 25 in Australia and the Pacific Islands (Roguet 2020). Breuning (1962, 1963) defined Pteropliini as follows: antennal scape without carina, never very long and thin; mesotibia without dorsal groove or tubercule; claws simple and divergent. A recent molecular analysis (Chapter 1) found that several Pteropliini genera are paraphyletic; *Pterolophia* Newman is sister to *Ropica* Pascoe (Apomecynini Thomson), and *Achriotypa* Pascoe falls within a monophyletic *Rhytiphora* Audinet-Serville (despite its lack of sex patches; see below). Consequently, these four genera were moved into the reinstated tribe Niphonini Pascoe, along with three Asian Pteropliini genera.

Rhytiphora encompasses more than a third of the Australian lamiines, with about 200 described species in Australia and at least 50 more in New Guinea and Southeast Asia (Ślipiński & Escalona 2013). Currently *Rhytiphora* is defined by paired setose 'sex patches' on the male abdominal ventrite 2, mesotibial antennal cleaner without groove and rounded antennal scape without carina. This unites 38 former Australian genera (most of which were poorly defined by variable characters), including: *Eczemotes* Pascoe*, Hathliodes* Pascoe, *Penthea* Dejean, *Platyomopsis* Thomson, *Prosoplus* Blanchard and *Symphyletes* Newman.

Rhytiphora species range in size from 6 to 39 mm long, with an oval to elongate body. Eyes vary in size and are deeply emarginate or completely divided by the antennal tubercules. Antennae can be shorter or longer than the elytra (generally longer in males), with a sparse or dense ventral fringe, and slender to clavate scapes. Elytra are smooth to tuberculate, with short setae frequently creating a bright or cryptic colour pattern. Males often have a spine on the procoxae, and rarely a ventral tubercule on the protibiae. Sex patches vary in size, from being hidden beneath the thickened fringe of ventrite 1 through to covering the entire surface of ventrite 2.

Rhytiphora is found across all of Australia's major biomes (wet tropics, mesic zone, monsoonal tropics and arid zone) with the majority of described species found in the mesic biome. The wet tropics is regarded as the oldest biome in Australia: these rainforests were once widespread in the Cretaceous, and are now restricted to a few patches along the northeast coast with high levels of endemism (Byrne *et al.* 2011; Crisp & Cook 2013). The temperate mesic zone stretches down the east coast, as well as the isolated southwest corner of Australia, and harbours a large proportion of Australia's biodiversity (Byrne *et al.* 2011). The monsoonal tropics of northern Australia formed in the late Eocene and contains a mix of widespread and narrow-range taxa (Bowman *et al.* 2010). The arid zone is the youngest biome (only fully forming 4–1 Mya), yet its mesic-derived taxa are quite diverse (Byrne *et al.* 2008).

We used dried museum specimens for our molecular analyses, as the CSIRO pinned collection has a much higher species diversity than the ethanol collection. Since these specimens have degraded DNA, we focused on high copy number genes that are relatively easy to sequence and assemble: the mitochondrial protein-coding genes. We generated sequence data for 71 species: mainly Australian *Rhytiphora*, as well as a few New Guinean species and representatives from *Pterolophia* and *Ropica* (the two Australian genera most closely related to *Rhytiphora*; Chapter 1). We reconstructed the phylogeny and examined various morphological traits to see which taxonomic characters, if any, correlate with the genetic relationships. Species distributions across the Australian biomes were also studied in the context of the phylogeny.

METHODS

Sample selection and sequencing

We used two different sequencing approaches in this paper: whole genome shotgun (WGS) and DNA barcoding. We chose 24 pinned specimens from the Australian National Insect Collection (ANIC): 22 common *Rhytiphora* species covering a range of former genera, a sample from the closely related genus *Pterolophia* and an outgroup (Table S1). Genomic DNA was extracted from hind legs using the DNeasy 96 Blood and Tissue Kit protocol (Qiagen), and then examined on a Fragment Analyzer (Agilent Technologies). The less degraded samples were sheared to 200-500bp with a Diagenode Bioruptor Pico in preparation for WGS sequencing on an Illumina platform.

Libraries were prepared using the NEBNext Ultra II DNA Library Prep Kit (New England BioLabs), substituting ethanol with isopropanol in the adaptor ligation cleanup (step 1.3) with the Agencourt RNAClean XP Kit (Beckman Coulter) to retain more of the short DNA fragments. Samples were dual indexed with NEBNext Multiplex Oligos and amplified for 10–17 PCR cycles. The final libraries (along with 72 samples from other projects) were pooled by size into four groups at equimolar concentrations (20 nM of DNA in 30 µL). The pool with the weakest samples was concentrated using a Genevac miVac duo concentrator (Scitek). The samples were sequenced as 125 bp paired-end reads on four lanes of an Illumina HiSeq 2500 at the Kinghorn Centre for Clinical Genomics, Garvan Institute of Medical Research (Sydney, Australia).

We also sequenced the cytochrome c oxidase I (COI) barcode region from 56 ethanol-preserved specimens. DNA was extracted from thorax muscle using the ChargeSwitch Forensic DNA Purification Kit (Invitrogen), with the following alterations to the manufacturer's protocol: half quantities of buffer, incubation for three hours, and 50 µL final elution. The COI region was amplified using two smaller overlapping fragments, based on the primer pairs Ill_LCO1490 x Ill_C_R and Ill_B_F x Ill_HCO2198 (CR and BF; Shokralla *et al.* 2015) but redesigned to be fully degenerate and with a M13 tail (Regier & Shi 2005). The two fragments were amplified in separate PCR reactions with a hot start touchdown protocol to avoid non-specific amplification: 25 cycles with an annealing temperature of 55°C, then 13 cycles annealing at 45°C.

Dual indexing primers (8 bp barcodes based on Hamming codes; Bystrykh 2012) were added to the M13 reverse complements to re-amplify the PCR amplicons (10 cycles annealing at 50°C); the two amplicons from each sample were tagged with the same dual index combination. The amplicons were pooled, cleaned with 1.2x AMPure XP beads (Beckman Coulter) and measured with a Qubit 2.0 fluorometer. Dual-indexed libraries were built using the same NEBNext kits as above, ligating single-indexed adapters to the already dual-indexed amplicons to achieve cost-effective triple indexing. Libraries were quantified with the NEBNext Library Quant Kit (New England Biolabs), pooled at 2 nM and sequenced on an Illumina MiSeq flowcell (300 bp PE reads) at the Biomolecular Resource Facility, Australian National University.

Bioinformatic workflow

The raw WGS reads were cleaned using FastUniq v1.1 (Xu *et al.* 2012) to remove PCR duplicates and Trimmomatic v0.36 (Bolger *et al.* 2014) to remove adaptors and low-quality base calls. The cleaned read quality was assessed using FastQC v0.11.5 (Andrews 2010). The cleaned reads were assembled using SPAdes v3.11.1 (*de novo*; Bankevich *et al.* 2012) or NOVOPlasty v2.6.7 (seeded with NCBI Genbank COI sequence AB439179.1, *Anoplophora chinensis* Forster; Dierckxsens *et al.* 2016). The assemblies were then blasted against a reference mitochondrial genome (Genbank sequence KT726932.1: *A. chinensis*) to pull out contigs matching mitochondrial genes (BLAST+ v2.7.1; Camacho *et al.* 2009). The contigs were checked for external contamination (blasting against the NCBI database) and internal cross-contamination (custom pipeline to blast samples against themselves).

The contigs were imported into Geneious v10.2.2 (Biomatters) and 10 samples were mapped to the *A. chinensis* reference to obtain the full 15k bp mitochondrial genome (14 samples already had the full mt-genome assembled *de novo*; 92% of samples had coverage of 20 or greater). The final mt-genome contigs were annotated using the MITOS website (Bernt *et al.* 2013) and rearranged to the same starting point (*trnI*) before being aligned with MUSCLE v3.8.425 (Edgar 2004). The 13 protein-coding (PC) genes were extracted from the alignment, visually checked, and exported to AliView v1.21 (Larsson 2014) to be realigned (with MUSCLE) as translated amino acids. The resulting nucleotide (nt) and amino acid (aa) alignments were then imported back into Geneious for concatenation.

We separately ran six additional pinned samples from Chapter 1 through the same process, and aligned these with the original 24 WGS samples to create the 'core' dataset of 13 PC genes (30 taxa, 10,827 bp; Table S1). The assembled contigs of another eight *Rhytiphora* species from the same project, enriched for nuclear loci, were blasted against the reference mt-genome to pull out any mitochondrial bycatch; these contigs were processed in the same way as the WGS samples, resulting in patchy coverage of 4–9 PC genes. These eight enrichment samples were aligned with the 30 WGS samples, and 56 *Rhytiphora* COI barcodes (see below), to create the 'expanded' dataset (94 taxa; Table S1).

For the COI barcodes, a Perl pipeline was created to analyse the reads and produce one COI sequence for each sample. The reads were demultiplexed and primers removed by the custom Perl script, and PE reads merged using PEAR v0.9.6 (Zhang *et al.* 2014). The CR and

BF fragments were pooled separately, and operational taxonomic units (OTUs) were generated using Mothur (Schloss *et al.* 2009) with a 99% minimum identity for clustering. The CR-OTUs were merged with their matching BF-OTUs by comparing the identical overlap regions. We then used a decision-maker algorithm (Fig. S1) to produce the final concatenated COI sequence from the best (highest coverage) candidate OTUs.

Phylogenetic analyses

Both the core and the expanded datasets had three types of data: amino acids, nucleotides, and degeneracy-recoded nucleotides as produced by Degen v1.4 (synonymous codons replaced with IUPAC ambiguity codes; Zwick *et al.* 2012). All six datasets were partitioned by gene (aa) or gene and codon position (nt and degen), and then analysed with ModelFinder (Chernomor *et al.* 2016) to determine the best-fitting substitution models and partitioning scheme. These were then applied using IQ-TREE v1.6.12 (Nguyen *et al.* 2015) on the CSIRO PEARCEY computing cluster to estimate the phylogenetic relationships.

For the core datasets, we ran 200 standard nonparametric bootstrap replicates and 100 independent tree searches, then mapped the bootstrap support values onto the best likelihood tree (*–sup* option). The expanded datasets had more unstable topologies, due to the limited data available for the 56 COI taxa (maximum of 657 bp, in contrast to the 10,827 bp of the 30 WGS core taxa). We ran 200 tree searches for aa and degen datasets and 760 tree searches for the nt dataset (with 200 bootstrap replicates). An additional analysis was performed on the expanded nt dataset with eight rogue taxa removed (200 bootstrap replicates, 500 tree searches).

We then pruned 25 species from the expanded nt dataset (duplicate COI taxa and the two outgroups) and ran Bayesian analyses using BEAST v2.6.3 (Bouckaert *et al.* 2019) on the CIPRES Science Gateway v3.3 (Miller *et al.* 2010). The *Rhytiphora* root age was set to 53–29 Mya, based on a fossil calibrated Lamiinae phylogeny (see Chapter 1), using a Normal prior (mean = 38, standard deviation = 6). The pruned dataset was partitioned into first plus second and third codon position and analysed with bModeltest (Bouckaert & Drummond 2017) to determine the best substitution models for the unlinked sites; the clock (relaxed log normal; Drummond *et al.* 2006) and tree (birth-death) models were linked across the partitions. Default priors were used except for the mean clock rate (Uniform distribution 0–1, initial value = 0.1). We performed two independent runs for 40 million generations, sampling every 4000, which were then examined in Tracer v1.7.1 (Rambaut *et al.* 2018) for convergence. Effective sample sizes (ESS) were >200, and the two runs were combined using LogCombiner v2.6.2 (Bouckaert *et al.* 2019) with a 10% burn-in. We used TreeAnnotator v2.6.2 (Bouckaert *et al.* 2019) to produce the maximum clade credibility tree with mean node heights. All trees were visualised using FigTree v1.4.4 (Rambaut 2018).

Morphological and biogeographic analyses

We created a matrix of 67 morphological traits using Open DELTA v1.02 (Atlas of Living Australia 2017) and scored the original 24 WGS samples. We mapped the traits onto the phylogeny using Mesquite v3.6 (Maddison & Maddison 2018; data not shown) and chose a subset of 11 traits with strong phylogenetic patterns: body size, various eye and antennae traits, pronotum and mesoventrite shape, protibial tubercules and sex patches (total 14 measurements; some traits were treated as both discrete and continuous). These traits were then scored for all of the sequenced Niphonini species (Table S2) and analysed using the dated BEAST tree in in RStudio v1.2.5019 (R Core Team 2019; RStudio Team 2019).

The traits were visualised using the *contMap* or *plotTree* functions in Phytools v0.6-99 (Revell 2012), with the ancestral states of discrete traits estimated using the *ace* function in APE v5.3 (Paradis & Schliep 2018). Some traits' phylogenetic patterns had weakened with the addition of extra taxa, so we calculated phylogenetic signal using Blomberg's *K* for the continuous traits (Blomberg *et al.* 2003) in Phytools and the *D* statistic for the discrete traits (converted to binary where possible; Fritz & Purvis 2010) in Caper v1.0.1 (Orme *et al.* 2018). We used phylogenetic generalised least squares (PGLS) in NLME v3.1-149 (Pinheiro *et al.* 2020) to test for correlations between mean body size and the other morphological traits, and between body size and biome (see below).

We gathered locality information from all the specimens at ANIC and assigned each species to a biome category (Table S2): wet tropics (north Queensland and/or New Guinea), monsoonal tropics, mesic zone (temperate east coast or southwest Australia) and arid zone. For the few species found across more than one biome, we used the biome of the majority and/or sequenced specimens. Ancestral states were estimated for the BEAST tree using BioGeoBEARS v1.1.2 (Matzke 2013) under six standard biogeographic models: DEC (Ree & Smith 2008), DIVALIKE and BAYAREALIKE (likelihood interpretations of BayArea and DIVA; Landis *et al.* 2013; Ronquist 1997), 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 AICc weights (Burnham & Anderson 2002). The BEAST tree was then edited in Mesquite to reflect the alternate topology (see Results), and the ancestral states were estimated again on the edited tree.

RESULTS

Phylogenetic relationships

The core dataset produced stable topologies, with only three differences between the data types (with roughly equal support; Fig. 1). The core nt dataset places *Rhytiphora neglecta* Pascoe sister to the *deserti–pulverulens* clade, the degen dataset has *R. nigrovirens* Donovan sister to *R. solandri* Fabricius, and the aa dataset places *R. piligera* Macleay sister to (*R. australica* Breuning + *Achriotypa*). The expanded dataset is more variable: both the degen and aa datasets have multiple polytomies even in the best supported topologies (Figs. S2–3).

The expanded nt dataset produced several topologies with equal likelihoods (Fig. 2). The alternate topologies (A–E) are: *R. pustulosa* Pascoe in a polytomy with the *'sp3'–bimaculata* and *'sp4'–bakewelli* clades, *R. pedicornis* Fabricius sister to the *cinnamomea–wallacei* clade, the *fulvescens–pulverulens* clade sister to the *amicula–'nr ochbas'* clade, the *lateralis–rubeta* clade sister to the entire *cinerascens–neglecta* clade, and the *'sp1 Cairns'–regularis* clade sister to (the *'sp silver'–saundersii* clade + the rest of clade 2) (Figs. S4–5).

The core and expanded datasets recovered the same two *Rhytiphora* clades, with congruent internal relationships except for the placement of *R. armatula* White and *R. lateralis* Pascoe. The deeper nodes within the two clades are poorly supported, especially in the expanded dataset; removing the main rogue taxa (A, B and D in Fig. 2) generally improved support, but not significantly (only two more nodes reached >80% bootstrap support; Fig. S6).

The dated BEAST tree is very similar to the expanded nt topology (with *R. pustulosa* in the alternate position), with two minor shifts: *R. batesi* Tavakilian & Nearns is sister to *R. callosa* Ślipiński & Escalona, and *R. 'nr ochbas'* is sister to the *fulvescens–pulverulens* clade (Fig. 3). There are still several poorly supported nodes, particularly in clade 2. The root age of *Rhytiphora* is about 35 Mya (47–22 Mya), with clade 1 diversifying earlier than clade 2.

Morphology and biogeography

Four morphological traits effectively distinguish the two *Rhytiphora* clades: body size, eye emargination, antennal fringe and sex patch size (Figs. 4–5). Most of the other traits are also consistent with the clades (Figs. S7–11). Clade 1 species are mostly small-bodied with divided eyes, medium-length upper lobes, broadly separated antennae, slender to medium scape (2.2–3.4x length by width), sparse antennal fringe, angulate or sloped mesoventrite, no protibial tubercules and small sex patches. Clade 2 species are mostly medium- to large-bodied with emarginate eyes, small- to medium-length upper lobes, narrow to medium antennal separation, medium to robust scape (1.6–2.8x length by width), dense antennal fringe, sloped mesoventrite, protibial tubercules present or absent and large sex patches.

All of the morphological traits have significant phylogenetic signal, though eye upper lobe length and pronotum shape have less signal than the rest (Table S3). Body size is significantly correlated with eye emargination and upper lobe length (Table 1); larger-bodied species tend to have emarginate eyes with small upper lobes. When *Ropica* and *Pterolophia* are removed from the dataset, eye upper lobe becomes more significant ($F = 4.91$, $p = 0.030$), while the other traits are unchanged. There is no relationship between body size and biome (Table 1).

Table 1. Results of PGLS analyses on mean body size of *Rhytiphora* and related genera. Significance is indicated with an asterisk (p = 0.05–0.01*, p = 0.01–0.001**).

Correlating trait	***F* statistic**	***p* value**
Eye emargination (class)	6.92	0.002**
Number of joining eye rows	1.06	0.308
Eye upper lobe length (ratio)	4.00	0.050*
Antennal separation (ratio)	0.53	0.471
Scape shape (ratio)	1.04	0.310
Antennal fringe (class)	1.26	0.265
Pronotum type (class)	1.72	0.194
Pronotum shape (ratio)	0.35	0.555
Pronotum vs. elytra width (class)	0.03	0.855
Mesoventrite angle (class)	1.02	0.316
Protibial tubercules (class)	0.004	0.948
Sex patch size (class)	1.90	0.157
Biome (class)	0.70	0.556

For the biogeography analysis, the DIVALIKE+J model is the best supported (Table S4). The ancestral biome of *Rhytiphora* is ambiguous (Fig. 6). The ancestral biome of clade 1 is most likely the wet tropics, while clade 2 probably has a mesic ancestor. Both clades have a widespread ‘basal’ group with species from all four biomes, and a larger ‘inner group’ with mostly tropical (clade 1) or mesic (clade 2) species. The analysis on the alternate topology infers an ambiguous clade 2 ancestor, with a mesic ancestor for the inner group (Fig. S12).

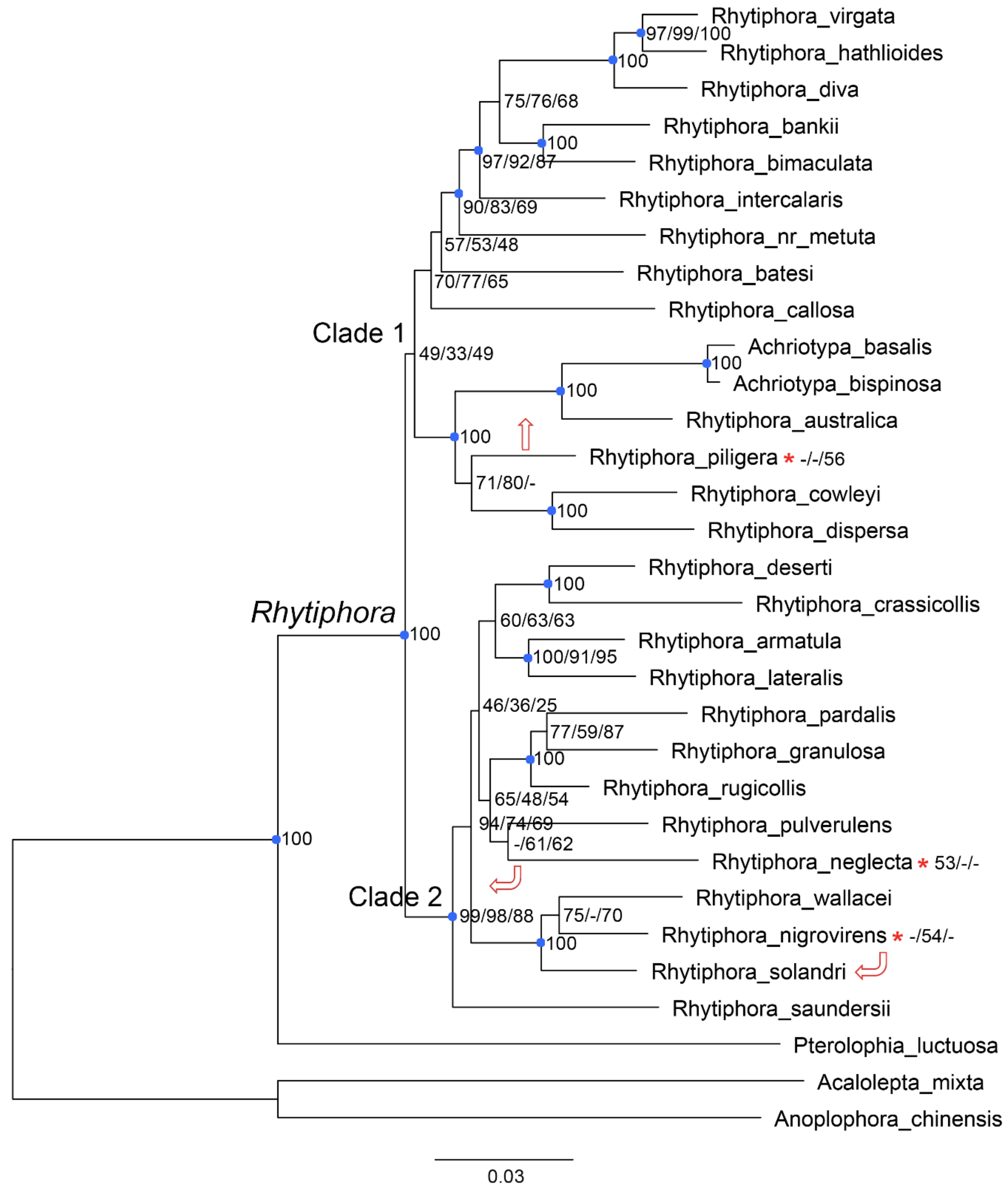

Figure 1. Maximum likelihood phylogeny of *Rhytiphora*: partitioned IQ-TREE analysis of the core dataset. Branch supports are bootstrap values (nt/degen/aa datasets; nodes with >80% support for at least two datasets are marked with blue) and the scale bar is nucleotide sequence change per Mya. Rogue taxa are indicated with an asterisk (*) and alternate placements indicated with arrows. *Rhytiphora* and the two clades are labelled.

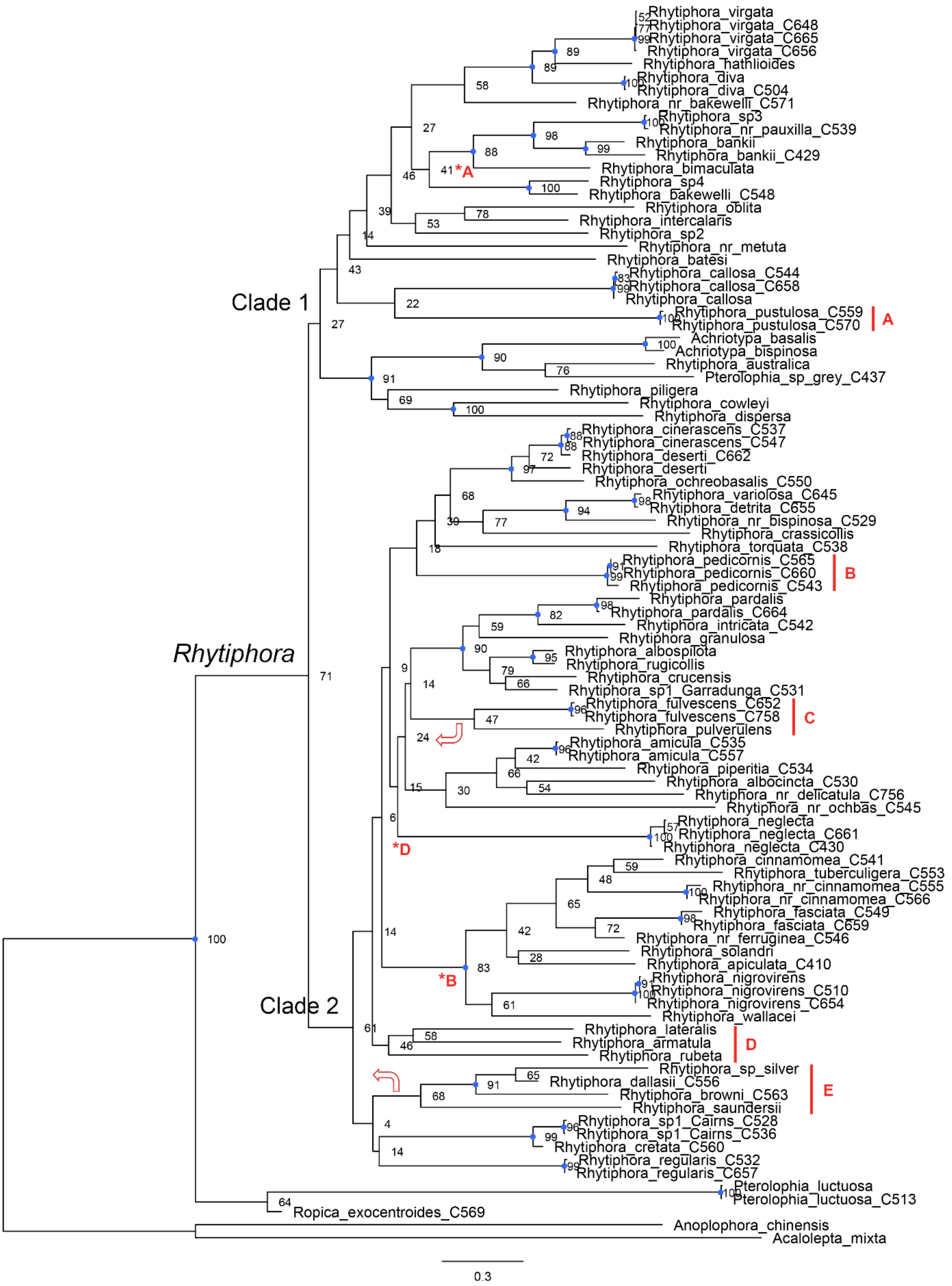

Figure 2. Maximum likelihood phylogeny of *Rhytiphora*: partitioned IQ-TREE analysis of the expanded nucleotide dataset. Branch supports are bootstrap values (>80% support marked with blue) and the scale bar is nucleotide sequence change per Mya. Rogue taxa are labelled A–E and alternate placements indicated with an asterisk (*) or an arrow. *Rhytiphora* and the two clades are labelled.

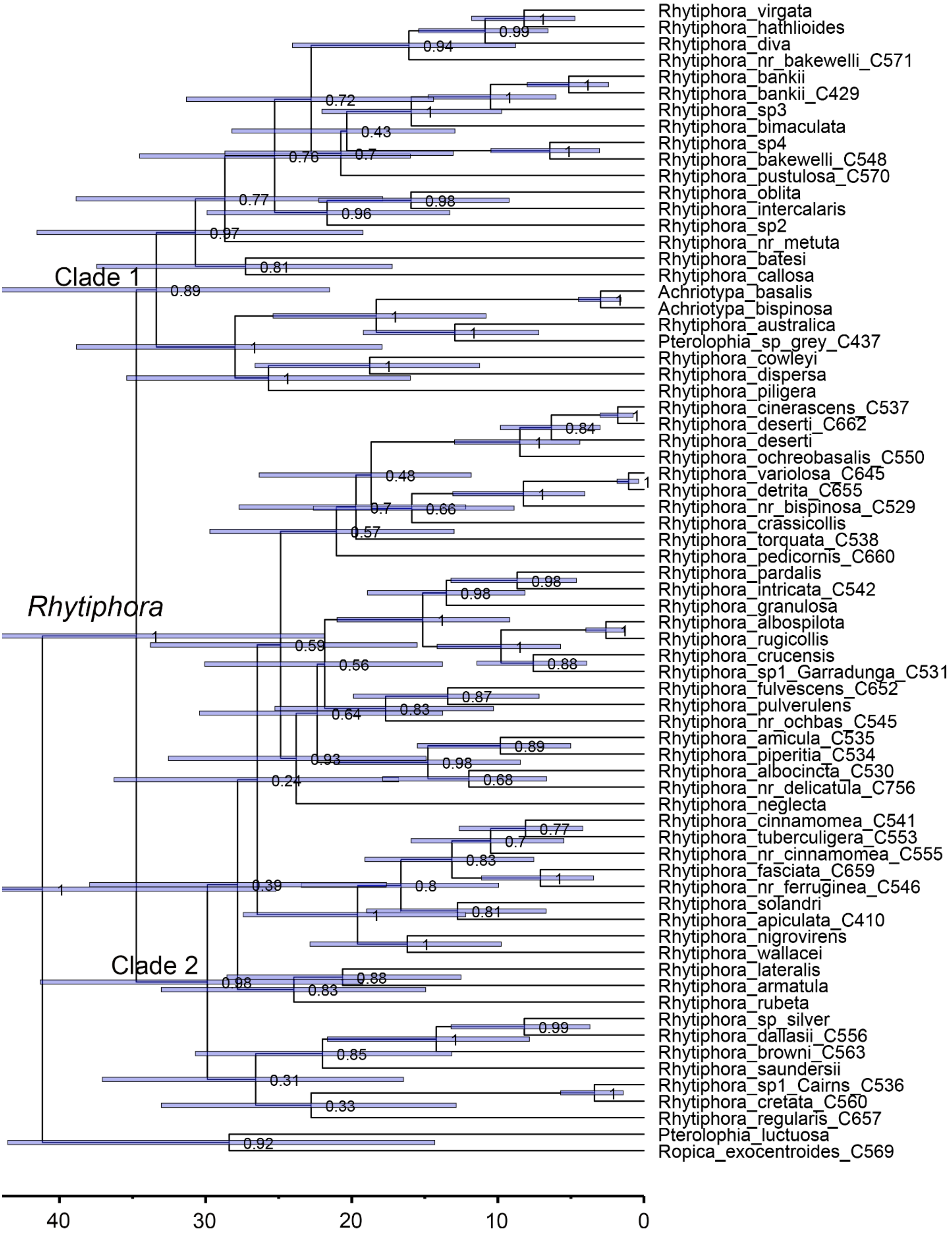

Figure 3. Bayesian phylogeny of *Rhytiphora*: partitioned and dated BEAST analysis of the pruned nucleotide dataset. Branch supports are posterior probabilities and the scale bar is in millions of years ago (Mya). The blue bars show the 95% highest posterior density of node ages. *Rhytiphora* and the two clades are labelled.

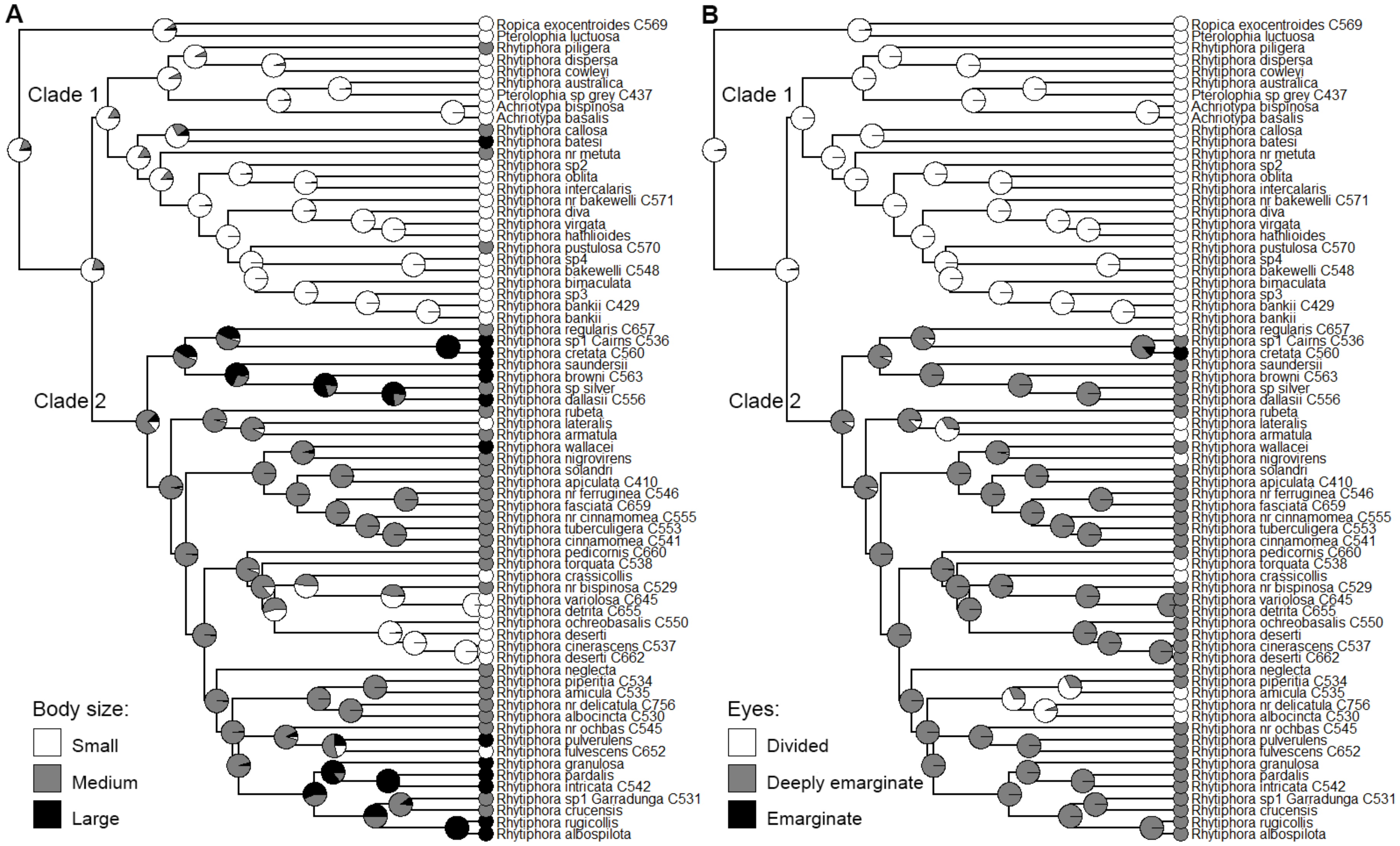

Figure 4. Ancestral morphological trait estimation of *Rhytiphora*: ancestral states reconstructed using APE on the dated BEAST phylogeny (Fig. 3). The two *Rhytiphora* clades are labelled. **A:** Analysis of body size, coded as small (5–15 mm), medium (15–22 mm) or large (22+ mm). **B:** Analysis of eye shape, coded as divided (no joining ommatidia rows), deeply emarginate (1–2 rows) or emarginate (3+ rows).

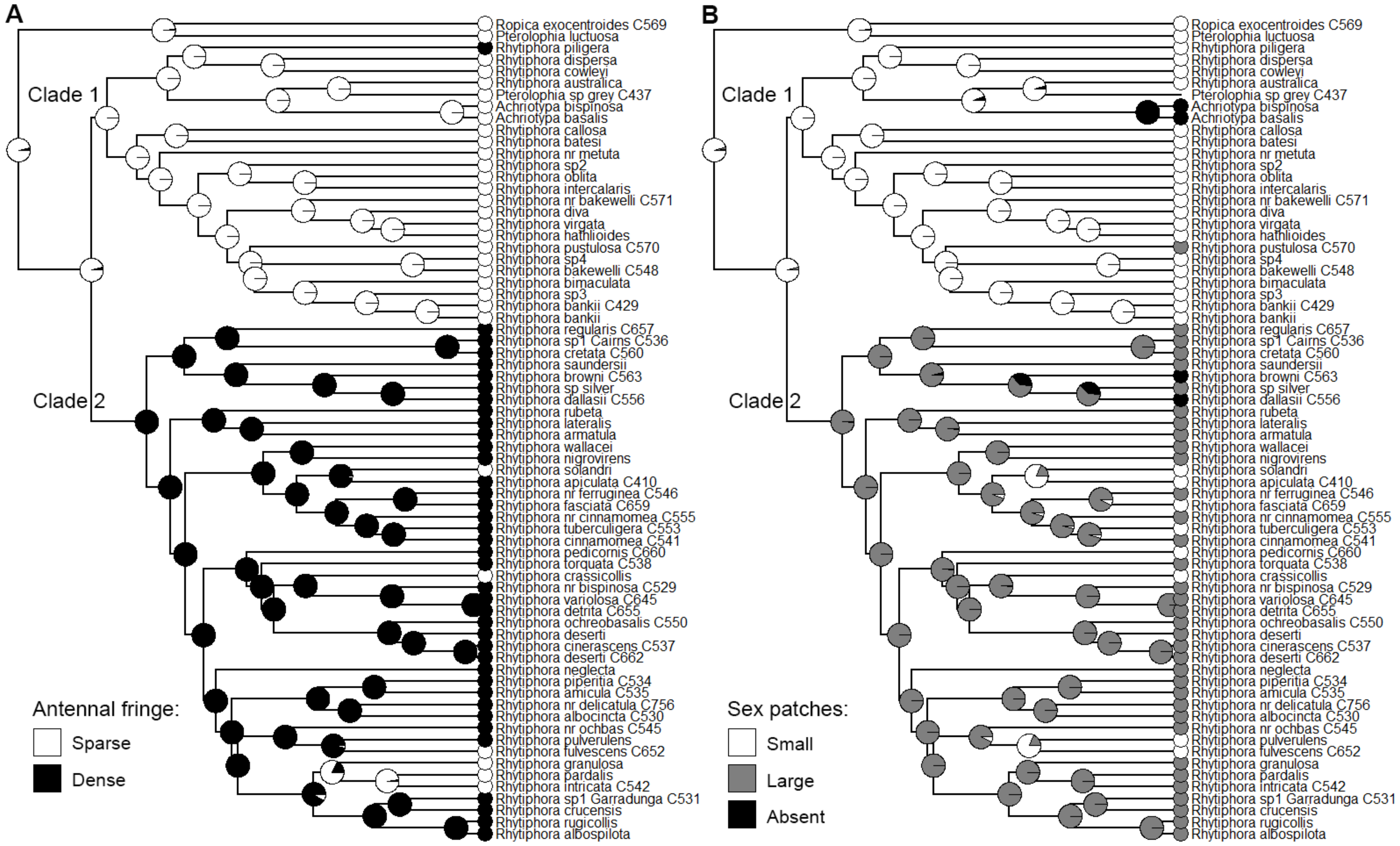

Figure 5. Ancestral morphological trait estimation of *Rhytiphora*: ancestral states reconstructed using APE on the dated BEAST phylogeny (Fig. 3). The two *Rhytiphora* clades are labelled. **A:** Analysis of antennal fringe, coded as sparse or dense. **B:** Analysis of sex patch size, coded as small (<½ ventrite 2), large (>½ ventrite 2) or absent.

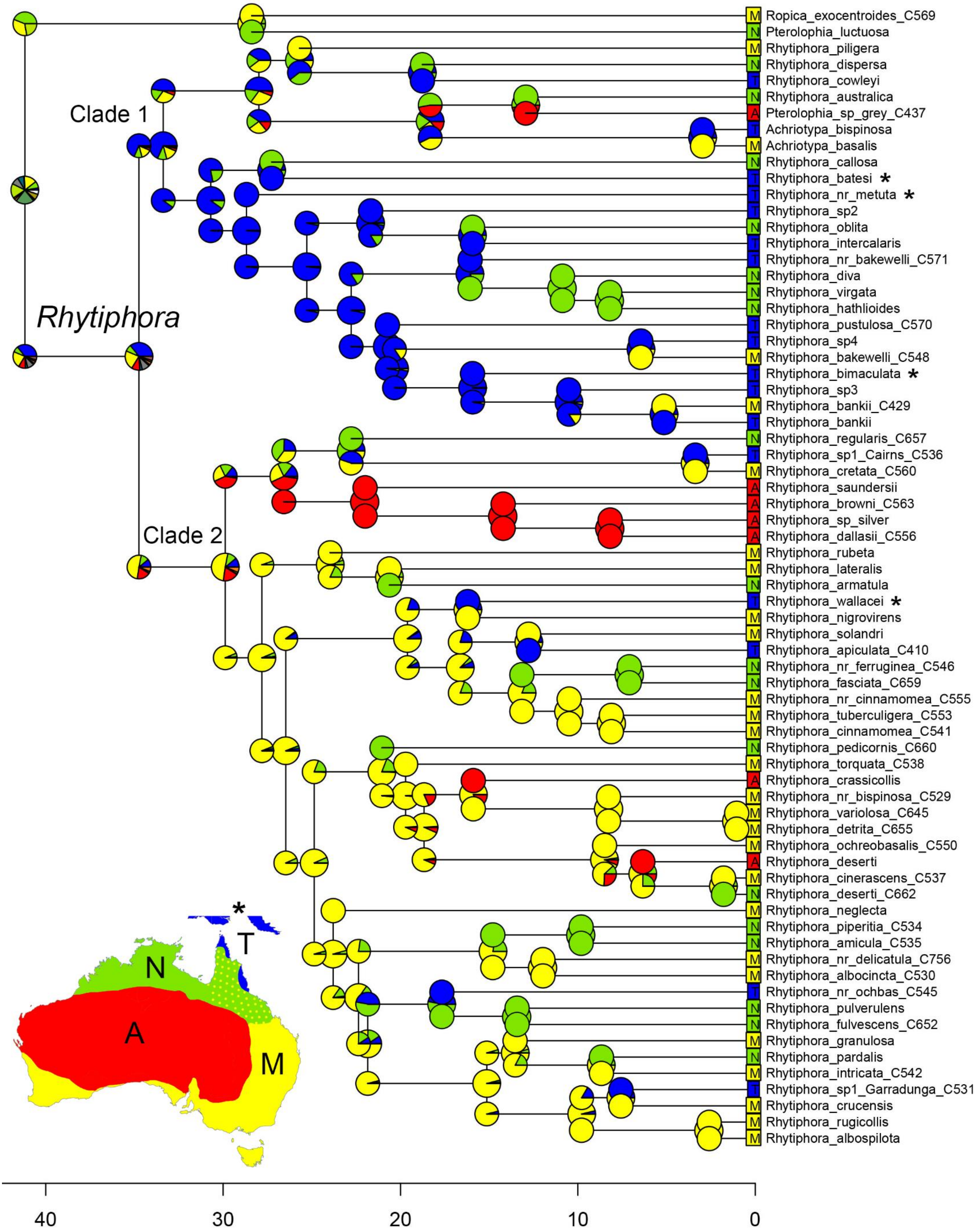
Clade 1
Rhytiphora
Clade 2
M Ropica_exocentroides_C569
N Pterolophia_luctuosa
M Rhytiphora_piligera
N Rhytiphora_dispersa
T Rhytiphora_cowleyi
N Rhytiphora_australica
A Pterolophia_sp_grey_C437
T Achriotypa_bispinosa
M Achriotypa_basalis
N Rhytiphora_callosa
T Rhytiphora_batesi *
T Rhytiphora_nr_metuta *
T Rhytiphora_sp2
N Rhytiphora_oblita
T Rhytiphora_intercalaris
T Rhytiphora_nr_bakewelli_C571
N Rhytiphora_diva
N Rhytiphora_virgata
N Rhytiphora_hathlioides
T Rhytiphora_pustulosa_C570
T Rhytiphora_sp4
M Rhytiphora_bakewelli_C548
T Rhytiphora_bimaculata *
T Rhytiphora_sp3
M Rhytiphora_bankii_C429
T Rhytiphora_bankii
N Rhytiphora_regularis_C657
T Rhytiphora_sp1_Cairns_C536
M Rhytiphora_cretata_C560
A Rhytiphora_saundersii
A Rhytiphora_browni_C563
A Rhytiphora_sp_silver
A Rhytiphora_dallasii_C556
M Rhytiphora_rubeta
M Rhytiphora_lateralis
N Rhytiphora_armatula
T Rhytiphora_wallacei *
M Rhytiphora_nigrovirens
M Rhytiphora_solandri
T Rhytiphora_apiculata_C410
N Rhytiphora_nr_ferruginea_C546
N Rhytiphora_fasciata_C659
M Rhytiphora_nr_cinnamomea_C555
M Rhytiphora_tuberculigera_C553
M Rhytiphora_cinnamomea_C541
N Rhytiphora_pedicornis_C660
M Rhytiphora_torquata_C538
A Rhytiphora_crassicollis
M Rhytiphora_nr_bispinosa_C529
M Rhytiphora_variolosa_C645
M Rhytiphora_detrita_C655
M Rhytiphora_ochreobasalis_C550
A Rhytiphora_deserti
M Rhytiphora_cinerascens_C537
N Rhytiphora_deserti_C662
M Rhytiphora_neglecta
N Rhytiphora_piperitia_C534
N Rhytiphora_amicula_C535
M Rhytiphora_nr_delicatula_C756
M Rhytiphora_albocincta_C530
T Rhytiphora_nr_ochbas_C545
N Rhytiphora_pulverulens
N Rhytiphora_fulvescens_C652
M Rhytiphora_granulosa
N Rhytiphora_pardalis
M Rhytiphora_intricata_C542
T Rhytiphora_sp1_Garradunga_C531
M Rhytiphora_crucensis
M Rhytiphora_rugicollis
M Rhytiphora_albospilota
*
T
N
A
M
40
30
20
10
0

Figure 6. Ancestral geographic range estimation of *Rhytiphora*: ancestral states reconstructed using BioGeoBEARS under the DIVALIKE+J model on the dated BEAST phylogeny (Fig. 3). Scale bar is in millions of years ago (Mya). Biomes are labelled as follows: wet tropics (T) is blue, with New Guinean species indicated by an asterisk (*); monsoonal tropics (N) is green; mesic (M) is yellow; arid zone (A) is red. The biome map is adapted from Peel *et al.* (2007). *Rhytiphora* and the two clades are labelled.

DISCUSSION

Phylogeny

We recovered *Rhytiphora* as monophyletic (inclusive of *Achriotypa*) in each of the datasets, with *Pterolophia* and *Ropica* forming a sister clade (Figs. 1–3). The genus is split into two distinct clades (approximately 1:2 species ratio), which have fairly stable internal relationships despite generally low support values; the rogue taxa never switch clades between the different datasets. Clade 2 is more internally unstable than clade 1, as it has a higher percentage of COI taxa (which have less phylogenetic information than the WGS taxa). Our topologies are broadly congruent with those in Chapter 1: clade 1 is nearly identical, apart from the position of (*R. 'sp4'* + *R. bakewelli* Pascoe), while clade 2 has the same species groups but in a different arrangement, with *R. cretata* Pascoe and *R. regularis* Gahan separated. The estimated divergence times are also similar, with an Eocene–Oligocene *Rhytiphora* root age and the more speciose clade 2 diversifying later than clade 1.

None of the former genera now encompassed by *Rhytiphora* (with more than one species sampled) are monophyletic, except for *Achriotypa* (Fig. S4). The species previously assigned to *Prosoplus* (e.g. *R. bankii* Fabricius and *R. oblita* Pascoe) are closely related within clade 1, but are rendered paraphyletic by at least *R. virgata* Breuning, *R. hathlioides* Breuning and *R. diva* Thomson (formerly in *Hathliodes*, *Xiphotheopsis* Breuning and *Zygrita* Thomson; Table S1). In Chapter 1, we likewise found *Prosoplus* to be paraphyletic. Clade 1 also contains several former *Pterolophia* species (including *Achriotypa*), two former *Symphyletes* species (*R. pustulosa* and *R. piligera*) and single representatives of other former genera e.g. *Cairnsia* Blackburn, *Eczemotes* and *Menyllus* Pascoe. Clade 2 contains the majority of the former *Symphyletes* species, all the former *Platyomopsis* and *Penthea* species, and the original *Rhytiphora* species (including the type species *R. rugicollis* Dalman). Potentially, these two *Rhytiphora* clades could be recognised as two separate genera; however, producing a good morphological definition of clade 1, in particular, would be difficult (and unwise without first sequencing the rest of the Australian *Rhytiphora* species).

Morphology

In combination, the 11 morphological traits can assign nearly all of the sampled species to the correct clade (Figs. 4–5, S7–11). Three species have misleading morphology (i.e. traits that are consistent with the other, incorrect clade; *R. piligera*, *R. crassicollis* Pascoe and *R. fulvescens* Pascoe) and one species is ambiguous (*R. pustulosa*). The only former genus with species found across both clades, *Symphyletes* has the greatest morphological diversity (as well as the largest number of sampled species; Fig. S4, Table S1). Its 16 species range from 12 to 24 mm long, spanning the three body size categories (Fig. 4A; Table S2); the former *Prosoplus* species (clade 1) are all small-bodied, while the original *Rhytiphora* species (clade 2) are medium- to large-bodied.

Both eye emargination (Fig. 4B) and sex patch size (Fig. 5B) match the phylogenetic clades more consistently than the former genus groupings. Species from *Symphyletes*, *Penthea* and the original *Rhytiphora* can have divided or emarginate eyes, a fact largely overlooked in the previous key to Australian Pteropliini (Breuning 1963). This key did, however, recognise the divided eyes of the two clade 1 species *R. piligera* and *R. pustulosa*, and accordingly placed them into separate genera from the rest of the former *Symphyletes*. Eye emargination is correlated with body size (Table 1), which suggests there is a scaling effect where smaller-bodied species tend to have divided eyes, although there are exceptions to this trend (e.g. *R. batesi* and *R. deserti* Blackburn).

Sex patches are also uninformative for delineating the former genera. *Symphyletes*, *Penthea* and the original *Rhytiphora* species can have either small or large sex patches, and there is at least one independent loss of sex patches in both clades: the *Achriotypa* species (clade 1), *R. browni* McKeown and *R. dallasii* Pascoe (clade 2). To our knowledge the only other *Rhytiphora* species without sex patches is *R. macleayi* Lea, which is very similar to *R. dallasii*. Previously, the genus *Achriotypa* was considered to be distinct from *Pterolophia* and *Rhytiphora* because it lacked sex patches (Ślipiński & Escalona 2013); here, and in Chapter 1, we find both *Achriotypa* species fall within *Rhytiphora* clade 1.

About 86% of the 44 species in clade 2 have a dense antennal fringe (Fig. 5A), while all but one of the 24 species in clade 1 have a sparse fringe. This is consistent with Breuning's key

(1963), which defined *Rhytiphora* (inclusive of many former *Symphyletes* and *Platyomopsis* species) as having very densely fringed antennae, and moved the few exceptions (e.g. *R. fulvescens* and *R. granulosa* Guérin-Méneville) to separate genera (*Mesiphiastus* Breuning and *Depsages* Pascoe). Our dataset, however, firmly places these species within clade 2 along with the densely fringed species. Breuning's key defined *Penthea* as having a broad body and sparse antennal fringe, which is consistent with three of the four former *Penthea* species sampled here; the fourth species, *R. saundersii* Pascoe, has a dense fringe and is quite distantly related to the others.

All of the former *Prosoplus* species in clade 1 have a sharply angulate mesoventrite (and prosternal process; Fig. S10B); three other species, closely related to the *Prosoplus* group, also have an angulate mesoventrite (*R. callosa*, *R. batesi* and *R. 'nr metuta'*). This is reflected in Breuning's key, which listed several genera including *Prosoplus*, *Menyllus* and *Eczemotes* as having a truncate mesoventrite. The three species which always render *Prosoplus* paraphyletic (*R. virgata*, *R. hathlioides* and *R. diva*) have a rounded mesoventrite, but they do have an angulate prosternal process. Therefore, the *callosa–virgata* clade (Figs. 1–2) could be defined by its angulate prosternal process and/or mesoventrite, and only *R. pustulosa* would not conform. Interestingly, the two closest genera to *Rhytiphora* (*Niphona* Mulsant and *Callimetopus* Blanchard; Chapter 1) have a sharply angulate prosternal process and mesoventrite, while the genera in the next clade (*Sthenias* Dejean*, Ropica* and *Pterolophia*) all have rounded surfaces.

There are only four species of *Rhytiphora* that do not have projecting humeral angles (i.e. near-equal pronotum and elytra width; Fig. S10A): the *Achriotypa* species, *R. virgata* and *R. hathlioides* (all in clade 1). The latter two species are vertically striped and have been observed feeding on grasses (pers. comm.), so a streamlined body shape may be adaptive for clinging to (and being camouflaged on) slender plant stalks, rather than an indicator of phylogenetic relatedness. Pascoe (1866) stated that the humeral angles vary considerably within and among *Hathliodes* species, and several species described in *Hathlia* Hope have since been moved to *Sybra* Pascoe (Ślipiński & Escalona 2013). Another rare trait that seems to have evolved multiple times in *Rhytiphora* is the male protibial tubercules, found in eight clade 2 species (Fig. S11A) and probably used to cling to the female's back during copulation.

Biogeography

We did not find a significant relationship between biome and mean body size (Table 1). This contradicts the expectation that small insects (with a high surface area to volume ratio, and therefore greater rate of evaporative water loss) should evolve to become bigger in arid environments (Bujan *et al.* 2016). Our dataset samples roughly half of the total species diversity of the Australian *Rhytiphora*, and the arid zone is underrepresented compared to the other biomes (about 30% of arid species sampled, versus 45–60% of species from other biomes). However, large-bodied species are found in every biome (Figs. 4, 6) and only 33% of all the arid zone species (of known size and locality) are large-bodied. Thus, desiccation may not be a major selective force in this group, or perhaps these species have alternative adaptations to a drier habitat. It is worth noting that nearly all of the sampled arid zone species have large lower eye lobes, a trait which is correlated with nocturnality in beetles (Lawrence & Ślipiński 2013).

About 64% of the species in clade 2 are distributed in the arid and mesic zones, while 79% of the clade 1 species are in the wet or monsoonal tropics (Fig. 6). It appears that clade 1 has mostly stayed in the wetter, tropical parts of Australia, i.e. those most similar to its ancestral environment in Asia (see Chapter 1), with only a few species venturing south along the east coast. The more speciose clade 2, however, has spread right across central and southern Australia, reaching both the southeast and southwest corners as well as the central deserts (Table S2). Many arthropod groups have adapted to, and diversified in, Australia's drier biomes: coastal diving beetles spread inland and colonised the arid zone groundwater ecosystems (Toussaint *et al.* 2015), eucalypt-feeding sawflies radiated into the mesic zone alongside their host plants (Schmidt & Walter 2014), and mygalomorph spiders colonised the Pilbara and central arid zone from the monsoonal tropics several times (Huey *et al.* 2019).

The Australian *Rhytiphora* species are labile in their habitat preferences, with multiple biome shifts apparent in both clades (Fig. 6). The New Guinean species are dispersed across the phylogeny, with the tropical *R. wallacei* Pascoe sister to the mesic *R. nigrovirens*. There are only a few places on the tree where 3–4 sister species share the same biome (e.g. the *virgata–diva* and *'sp silver'–saundersii* clades), as expected under niche conservatism theory (Wiens & Graham 2005). Thus, *Rhytiphora* is one of the many groups of Australian taxa, including plants (Cardillo *et al.* 2017), spiders (Huey *et al.* 2019), mammals (Roycroft *et al.* 2020) and reptiles (Brennan & Keogh 2018), that readily transition between biomes.

Concluding remarks

This study presents a detailed morphological and phylogenetic analysis of Australia's largest longhorn beetle genus, elucidating its previously unknown morphological evolution and biogeographic history. The genus *Rhytiphora* is monophyletic, with two distinct clades that diverged in the Eocene–Oligocene. All but one of the former genera now encompassed by *Rhytiphora* are paraphyletic, including *Prosoplus*, which falls within a group of species that nearly all have an angulate prosternal process and/or mesoventrite. We discovered that a number of morphological traits can distinguish the two *Rhytiphora* clades, particularly body size, eye emargination, antennal fringe and sex patch size. Clade 1 has mostly tropical species, while clade 2 diversified into the mesic and arid zones. The Australian *Rhytiphora* radiation has shifted between biomes many times, adding to a growing body of evidence that Australian taxa are highly adapted to environmental changes.

ACKNOWLEDGEMENTS

We thank Roger de Keyzer, David Rentz, Paul Hutchinson and Jack Hasenpusch for donating specimens we sequenced. Craig Moritz provided advice on the biogeographic analyses and comments on the manuscript. This project was funded by grants from the Australian Government Department of Agriculture and Water Resources, the Australian Biological Resources Study and the Centre for Biodiversity Analysis (to AS and LGA). LGA was funded by the Australian National University and an Australian Government Research Training Program domestic scholarship. The authors declare no conflicts of interest.

REFERENCES

Andrews, S. (2010) FastQC: a quality control tool for high throughput sequence data.

Atlas of Living Australia (2017) Open DELTA: a Java implementation of the DELTA suite of programs.

Bankevich, A., Nurk, S., Antipov, D., Gurevich, A.A., Dvorkin, M., Kulikov, A.S., Lesin, V.M., Nikolenko, S.I., Pham, S., Prjibelski, A.D., Pyshkin, A. V., Sirotkin, A. V., Vyahhi, N., Tesler, G., Alekseyev, M.A. & Pevzner, P.A. (2012) SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology* 19, 455–477. https://doi.org/10.1089/cmb.2012.0021

Bernt, M., Donath, A., Jühling, F., Externbrink, F., Florentz, C., Fritzsch, G., Pütz, J., Middendorf, M. & Stadler, P.F. (2013) MITOS: improved de novo metazoan mitochondrial genome annotation. *Molecular Phylogenetics and Evolution* 69, 313–319. https://doi.org/10.1016/J.YMPEV.2012.08.023

Blomberg, S.P., Garland JR., T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioural traits are more labile. *Evolution* 57, 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Bolger, A.M., Lohse, M. & Usadel, B. (2014) Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* 30, 2114–2120. https://doi.org/10.1093/bioinformatics/btu170

Bouckaert, R., Vaughan, T.G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F.K., Müller, N.F., Ogilvie, H.A., du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., Suchard, M.A., Wu, C.-H., Xie, D., Zhang, C., Stadler, T. & Drummond, A.J. (2019) BEAST 2.5: an advanced software platform for Bayesian evolutionary analysis. *PLOS Computational Biology* 15, e1006650. https://doi.org/10.1371/journal.pcbi.1006650

Bouckaert, R.R. & Drummond, A.J. (2017) bModelTest: Bayesian phylogenetic site model averaging and model comparison. *BMC Evolutionary Biology* 17, 42. https://doi.org/10.1186/s12862-017-0890-6

Bowman, D.M.J.S., Brown, G.K., Braby, M.F., Brown, J.R., Cook, L.G., Crisp, M.D., Ford, F., Haberle, S., Hughes, J., Isagi, Y., Joseph, L., McBride, J., Nelson, G. & Ladiges, P.Y. (2010) Biogeography of the Australian monsoon tropics. *Journal of Biogeography* 37, 201–216. https://doi.org/10.1111/j.1365-2699.2009.02210.x

Brennan, I.G. & Keogh, J.S. (2018) Miocene biome turnover drove conservative body size evolution across Australian vertebrates. *Proceedings of the Royal Society B: Biological Sciences* 285, 20181474. https://doi.org/10.1098/rspb.2018.1474

Breuning, S. (1962) Bestimmungstabelle der Lamiiden-Triben nebst Revision der Pteropliini der asiatischen Region (Col. Cerambycidae) I. Teil. *Entomologische Arbeiten aus dem Museum G. Frey* 13, 371–493.

Breuning, S. (1963) Revision der Pteropliini der australischen Region (Coleoptera, Cerambycidae). *Entomologische Abhandlungen aus dem Staatliches Museum fur Tierkunde in Dresden* 29, 1–274.

Bujan, J., Yanoviak, S.P. & Kaspari, M. (2016) Desiccation resistance in tropical insects: causes and mechanisms underlying variability in a Panama ant community. *Ecology and Evolution* 6, 6282–6291. https://doi.org/10.1002/ece3.2355

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.

Byrne, M., Steane, D.A., Joseph, L., Yeates, D.K., Jordan, G.J., Crayn, D., Aplin, K., Cantrill, D.J., Cook, L.G., Crisp, M.D., Keogh, J.S., Melville, J., Moritz, C., Porch, N., Sniderman, J.M.K., Sunnucks, P. & Weston, P.H. (2011) Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *Journal of Biogeography* 38, 1635–1656. https://doi.org/10.1111/j.1365-2699.2011.02535.x

Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A.J., Cooper, S., Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porch, N. & Wyrwoll, K.H. (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology* 17, 4398–4417. https://doi.org/10.1111/j.1365-294X.2008.03899.x

Bystrykh, L. V (2012) Generalized DNA barcode design based on Hamming codes. *PLOS ONE* 7, e36852. https://doi.org/10.1371/journal.pone.0036852

Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K. & Madden, T.L. (2009) BLAST+: architecture and applications. *BMC Bioinformatics* 10, 421. https://doi.org/10.1186/1471-2105-10-421

Cardillo, M., Weston, P.H., Reynolds, Z.K.M., Olde, P.M., Mast, A.R., Lemmon, E.M., Lemmon, A.R. & Bromham, L. (2017) The phylogeny and biogeography of *Hakea* (Proteaceae) reveals the role of biome shifts in a continental plant radiation. *Evolution* 71, 1928–1943.

https://doi.org/https://doi.org/10.1111/evo.13276

Chernomor, O., von Haeseler, A. & Minh, B.Q. (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* 65, 997–1008. https://doi.org/10.1093/sysbio/syw037

Crisp, M.D. & Cook, L.G. (2013) How was the Australian flora assembled over the last 65 million years? A molecular phylogenetic perspective. *Annual Review of Ecology and Systematics* 44, 303–324. https://doi.org/10.1146/annurev-ecolsys-110512-135910

Dierckxsens, N., Mardulyn, P. & Smits, G. (2016) NOVOPlasty: de novo assembly of organelle genomes from whole genome data. *Nucleic Acids Research* 45, e18. https://doi.org/10.1093/nar/gkw955

Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. (2006) Relaxed phylogenetics and dating with confidence. *PLOS Biology* 4, e88. https://doi.org/10.1371/journal.pbio.0040088

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32, 1792–1797. https://doi.org/10.1093/nar/gkh340

Fritz, S.A. & Purvis, A. (2010) Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conservation Biology* 24, 1042–1051. https://doi.org/10.1111/j.1523-1739.2010.01455.x

Huey, J.A., Hillyer, M.J. & Harvey, M.S. (2019) Phylogenetic relationships and biogeographic history of the Australian trapdoor spider genus *Conothele* (Araneae: Mygalomorphae: Halonoproctidae): diversification into arid habitats in an otherwise tropical radiation. *Invertebrate Systematics* 33, 628–643.

Landis, M.J., Matzke, N.J., Moore, B.R. & Huelsenbeck, J.P. (2013) Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology* 62, 789–804. https://doi.org/10.1093/sysbio/syt040

Larsson, A. (2014) AliView: a fast and lightweight alignment viewer and editor for large datasets. *Bioinformatics* 30, 3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Lawrence, J.F. & Ślipiński, A. (2013) *Australian Beetles Volume 1 : Morphology, Classification and Keys*. CSIRO Publishing, Melbourne.

Maddison, W.P. & Maddison, D.R. (2018) Mesquite: a modular system for evolutionary analysis.

Matzke, N.J. (2013) BioGeoBEARS: BioGeography with Bayesian (and Likelihood) Evolutionary

Analysis in R Scripts.

Matzke, N.J. (2014) Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology* 63, 951–970. https://doi.org/10.1093/sysbio/syu056

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*. , pp. 1–8.

Nguyen, L.-T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32, 268–274. https://doi.org/10.1093/molbev/msu300

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N. & Pearse, W. (2018) CAPER: Comparative Analyses of Phylogenetics and Evolution in R.

Paradis, E. & Schliep, K. (2018) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pascoe, F.P. (1866) On the Longicornia of Australia, with a list of all the described species. *Journal of the Linnean Society, Zoology* 9, 80–112.

Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* 11, 1633–1644.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2020) nlme: linear and nonlinear mixed effects models.

R Core Team (2019) R: a language and environment for statistical computing.

Rambaut, A. (2018) FigTree, version 1.4.4.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67, 901–904. https://doi.org/10.1093/sysbio/syy032

Ree, R.H. & Smith, S.A. (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* 57, 4–14. https://doi.org/10.1080/10635150701883881

Regier, J.C. & Shi, D. (2005) Increased yield of PCR product from degenerate primers with nondegenerate, nonhomologous 5′ tails. *BioTechniques* 38, 34–38. https://doi.org/10.2144/05381BM02

Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Roguet, J.-P. (2020) Lamiaires du Monde. Available from: https://lamiinae.org (April 17, 2020)

Ronquist, F. (1997) Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology* 46, 195–203. https://doi.org/10.1093/sysbio/46.1.195

Roycroft, E.J., Nations, J.A. & Rowe, K.C. (2020) Environment predicts repeated body size shifts in a recent radiation of Australian mammals. *Evolution* 74, 671–680. https://doi.org/10.1111/evo.13859

RStudio Team (2019) RStudio: integrated development for R.

Schloss, P.D., Westcott, S.L., Ryabin, T., Hall, J.R., Hartmann, M., Hollister, E.B., Lesniewski, R.A., Oakley, B.B., Parks, D.H., Robinson, C.J., Sahl, J.W., Stres, B., Thallinger, G.G., Van Horn, D.J. & Weber, C.F. (2009) Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Applied and Environmental Microbiology* 75, 7537–7541. https://doi.org/10.1128/AEM.01541-09

Schmidt, S. & Walter, G.H. (2014) Young clades in an old family: major evolutionary transitions and diversification of the eucalypt-feeding pergid sawflies in Australia (Insecta, Hymenoptera, Pergidae). *Molecular Phylogenetics and Evolution* 74, 111–121. https://doi.org/https://doi.org/10.1016/j.ympev.2014.02.002

Shokralla, S., Porter, T.M., Gibson, J.F., Dobosz, R., Janzen, D.H., Hallwachs, W., Golding, G.B. & Hajibabaei, M. (2015) Massively parallel multiplex DNA sequencing for specimen identification using an Illumina MiSeq platform. *Scientific Reports* 5, 9687. https://doi.org/10.1038/srep09687

Ślipiński, A. & Escalona, H.E. (2013) *Australian Longhorn Beetles (Coleoptera: Cerambycidae) Volume 1: Introduction and Subfamily Lamiinae*. CSIRO Publishing, Melbourne, 503 pp.

Souza, D. de S., Marinoni, L., Laura Monné, M. & Gómez-Zurita, J. (2020) Molecular phylogenetic assessment of the tribal classification of Lamiinae (Coleoptera: Cerambycidae). *Molecular Phylogenetics and Evolution* 145, 106736. https://doi.org/10.1016/j.ympev.2020.106736

Švácha, P. & Lawrence, J.F. (2014) Cerambycidae Latreille, 1802. In: R. A. B. Leschen and R. G.

Beutel (Eds), *Handbook of Zoology, Arthropoda: Insecta, Coleoptera, Beetles, Volume 3: Morphology and Systematics (Phytophaga)*. Walter de Gruyter GmbH, Berlin, pp. 77–177.

Toussaint, E.F.A., Condamine, F.L., Hawlitschek, O., Watts, C.H., Porch, N., Hendrich, L. & Balke, M. (2015) Unveiling the diversification dynamics of Australasian predaceous diving beetles in the Cenozoic. *Systematic Biology* 64, 3–24. https://doi.org/10.1093/sysbio/syu067

Wang, Q. ed. (2017) *Cerambycidae of the World: Biology and Pest Management*. Taylor & Francis Group, Boca Raton.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* 36, 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

Xu, H., Luo, X., Qian, J., Pang, X., Song, J., Qian, G., Chen, J. & Chen, S. (2012) FastUniq: a fast de novo duplicates removal tool for paired short reads. *PLOS ONE* 7, e52249. https://doi.org/10.1371/journal.pone.0052249

Zhang, J., Kobert, K., Flouri, T. & Stamatakis, A. (2014) PEAR: a fast and accurate Illumina Paired-End reAd mergeR. *Bioinformatics* 30, 614–620. https://doi.org/10.1093/bioinformatics/btt593

Zwick, A., Regier, J.C. & Zwickl, D.J. (2012) Resolving discrepancy between nucleotides and amino acids in deep-level arthropod phylogenomics: differentiating serine codons in 21-amino-acid models S. R. Gadagkar (Ed). *PLOS ONE* 7, e47450. https://doi.org/10.1371/journal.pone.0047450

SUPPLEMENTARY INFORMATION (FIGURES S1–12, TABLES S1–4)

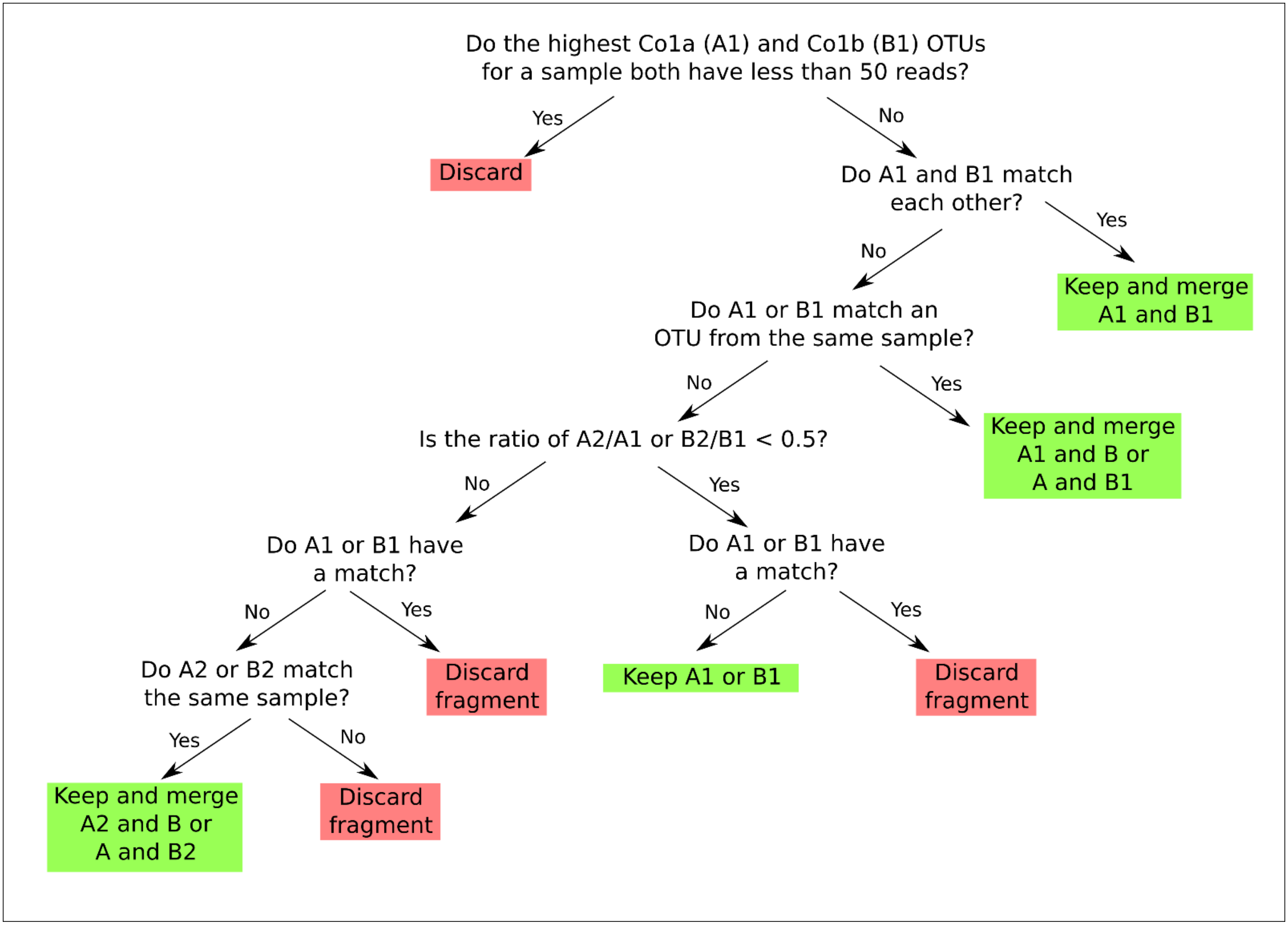

Figure S1. Flowchart of the decision-maker algorithm used to generate the final COI sequences. A1 and B1 refer to the CR and BF fragments of the COI gene that were amplified and analysed separately.

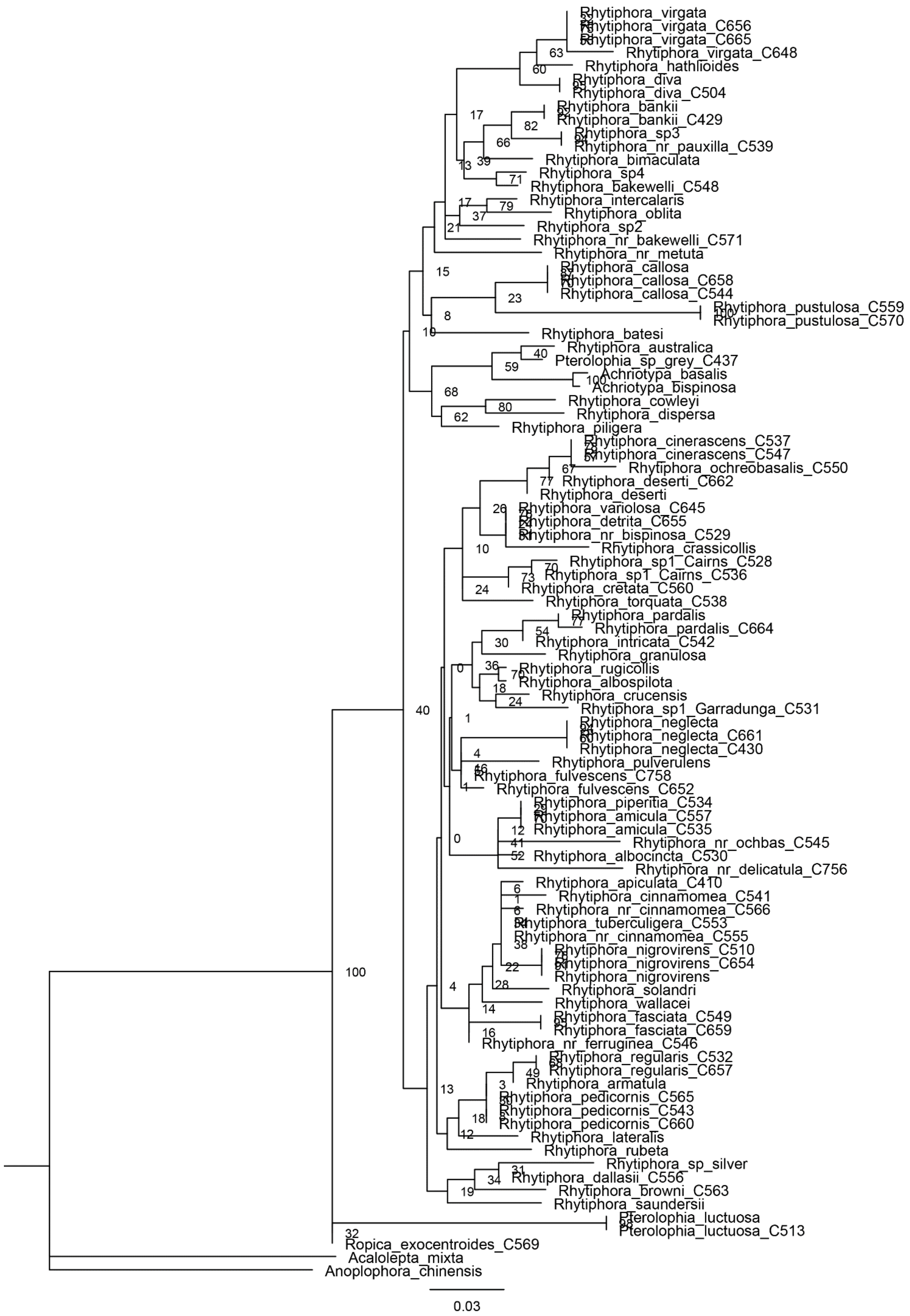

Figure S2. Maximum likelihood phylogeny of *Rhytiphora*: partitioned IQ-TREE analysis of the expanded degeneracy-recoded nucleotide dataset. Branch supports are bootstrap values and the scale bar is nucleotide sequence change per Mya.

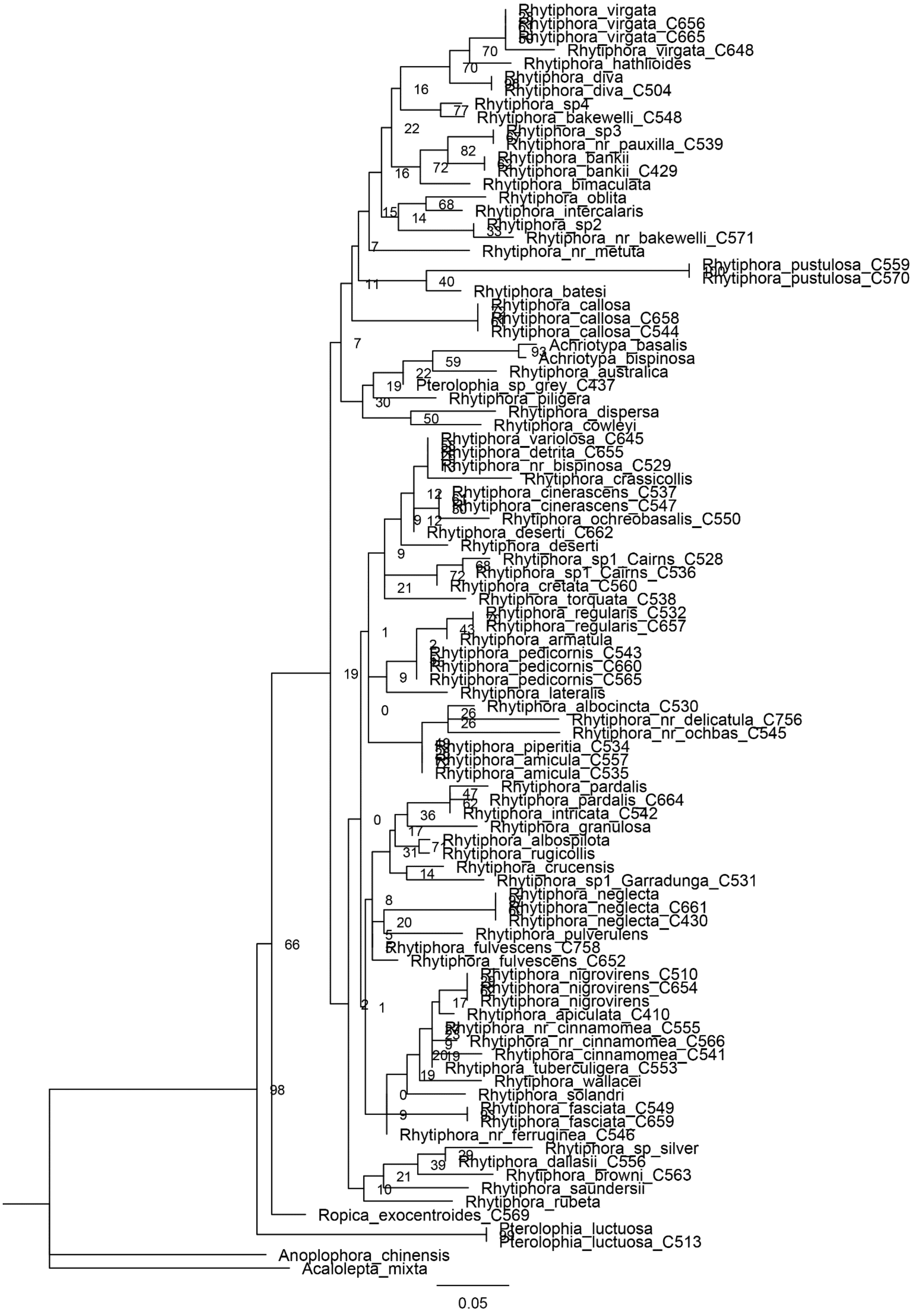

Figure S3. Maximum likelihood phylogeny of *Rhytiphora*: partitioned IQ-TREE analysis of the expanded amino acid dataset. Branch supports are bootstrap values and the scale bar is sequence change per Mya.

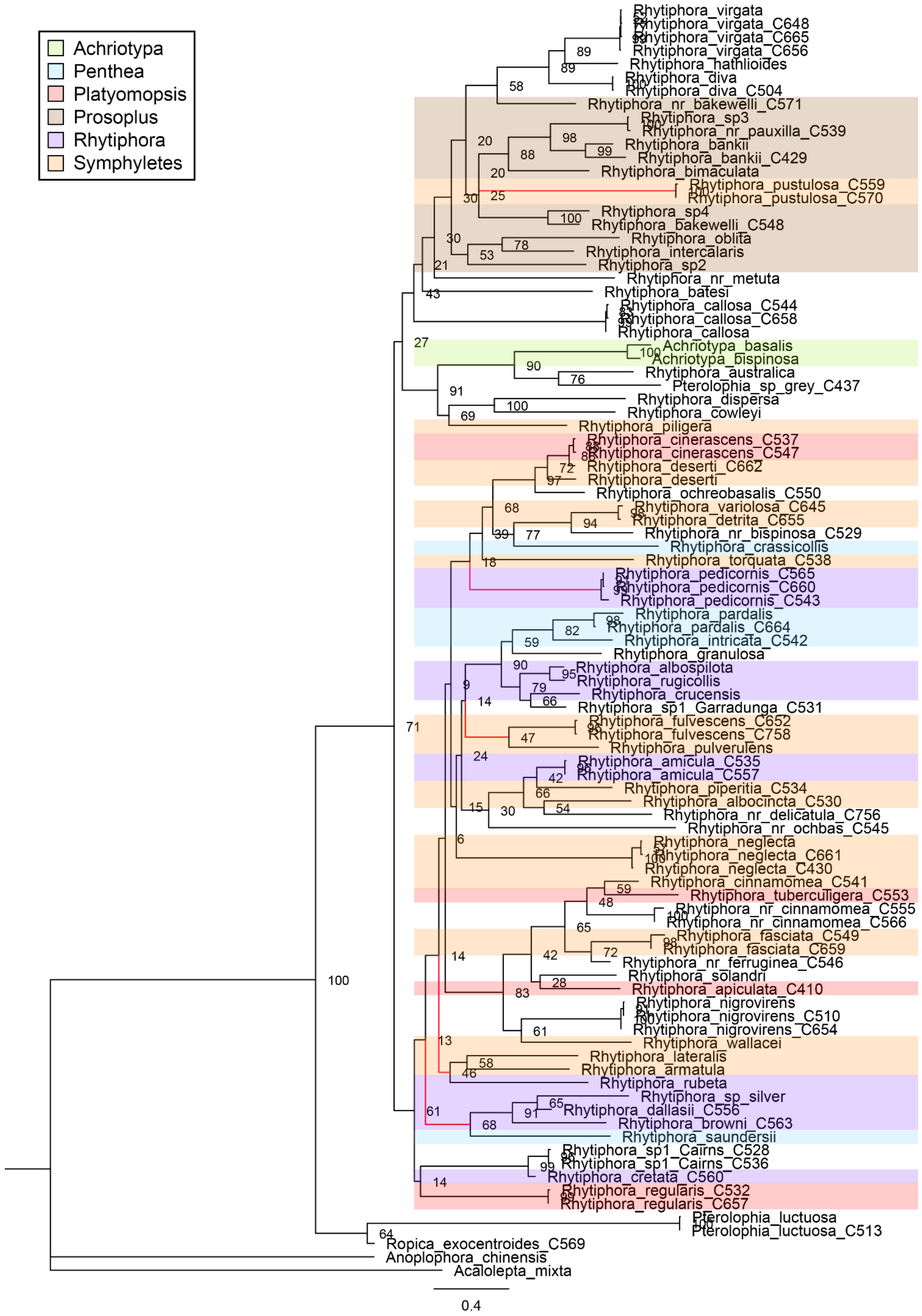

Figure S4. Maximum likelihood phylogeny of *Rhytiphora*: partitioned IQ-TREE analysis of the expanded nucleotide dataset (tree search #149). Branch supports are bootstrap values and the scale bar is nucleotide sequence change per Mya. Rogue taxa are coloured red, and major former genera are coloured as per the key.

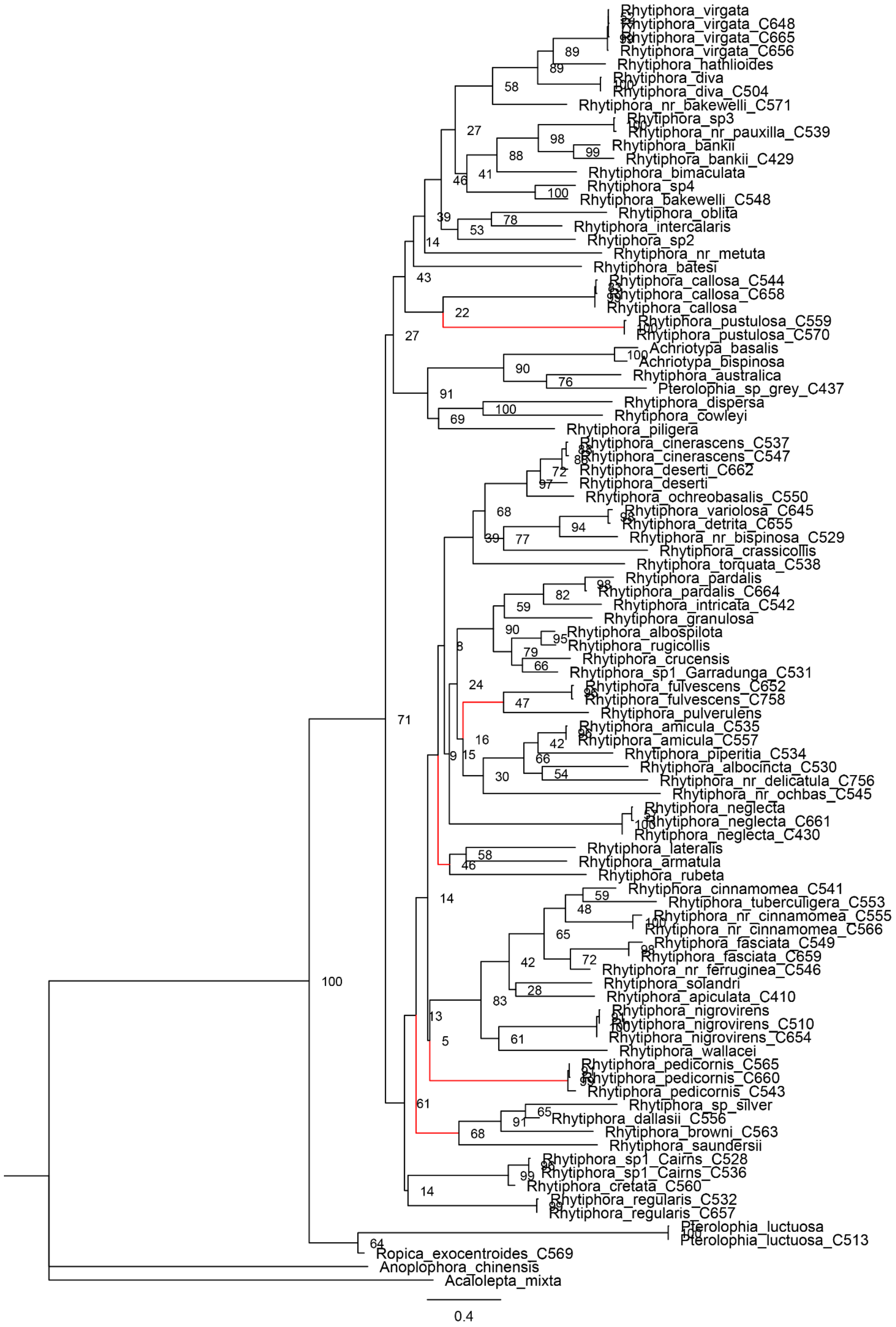

Figure S5. Maximum likelihood phylogeny of *Rhytiphora*: partitioned IQ-TREE analysis of the expanded nucleotide dataset (tree search #201). Branch supports are bootstrap values and the scale bar is nucleotide sequence change per Mya. Rogue taxa are coloured red.

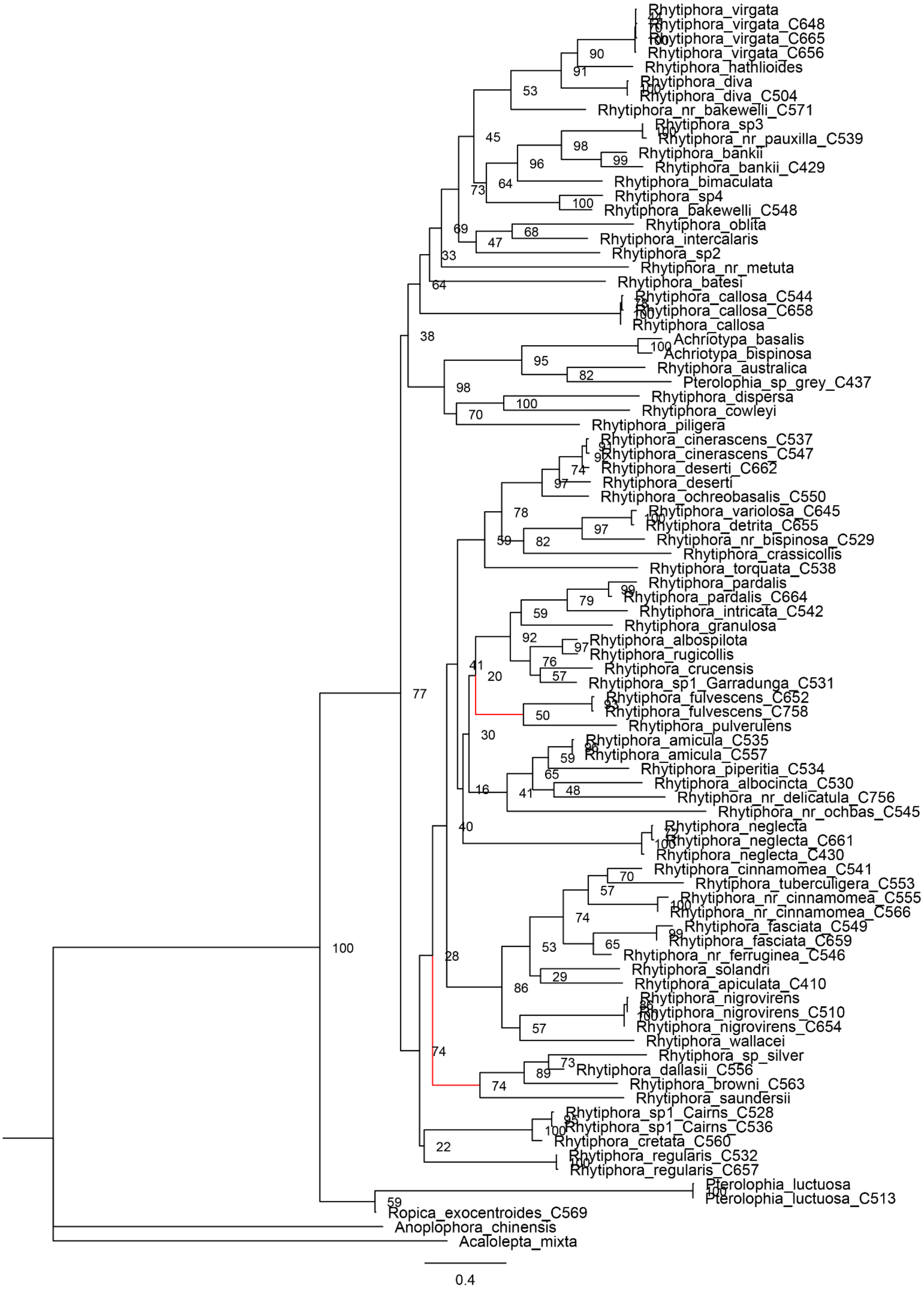

Figure S6. Maximum likelihood phylogeny of *Rhytiphora*: partitioned IQ-TREE analysis of the expanded nucleotide dataset with eight rogue taxa removed. Branch supports are bootstrap values and the scale bar is nucleotide sequence change per Mya. Rogue taxa are coloured red.

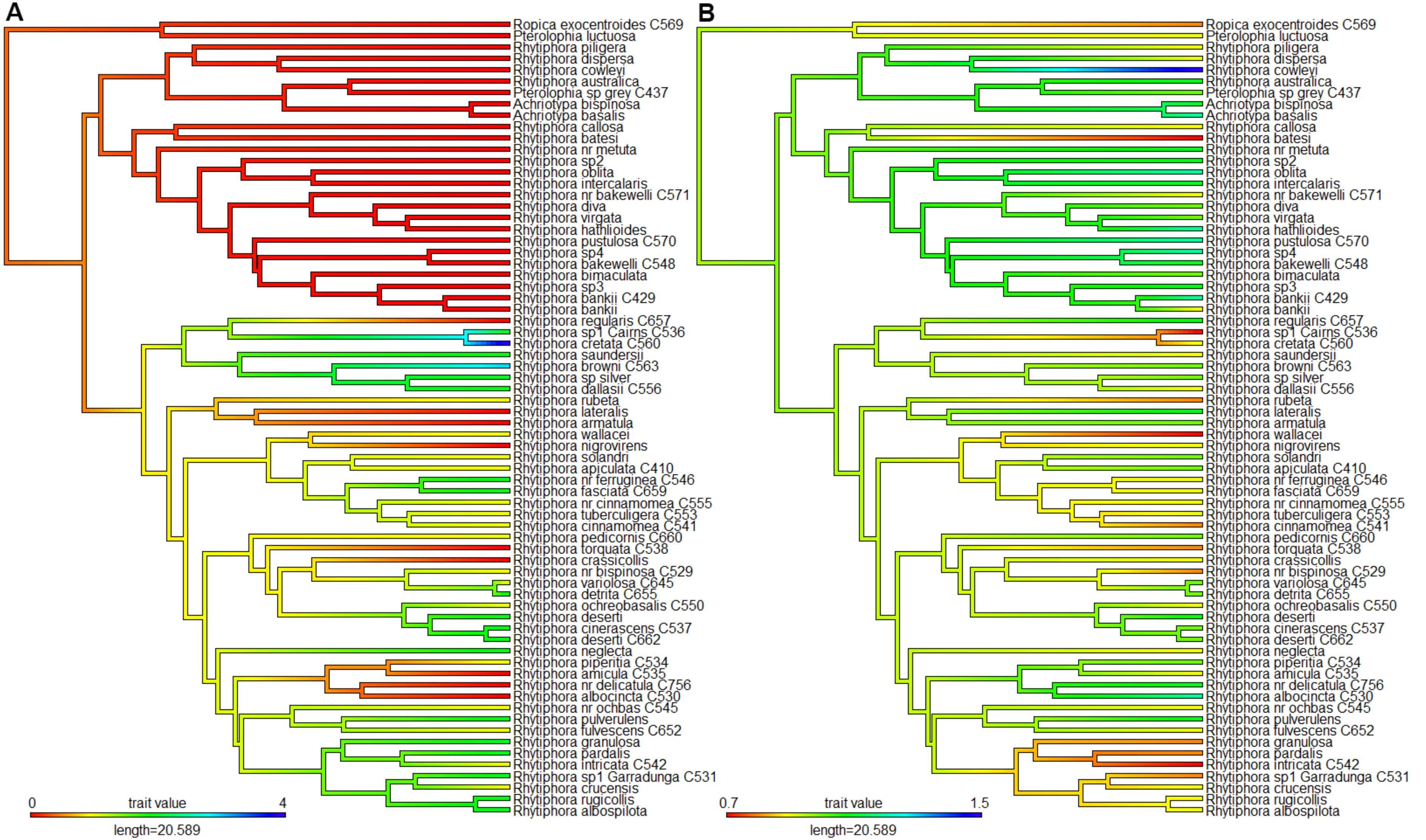

Figure S7. Ancestral morphological trait estimation of *Rhytiphora*: ancestral states reconstructed using APE on the dated BEAST phylogeny. **A:** Analysis of eye row number (ommatidia joining two lobes). **B:** Analysis of eye upper lobe length (maximum length, vertex to frons, divided by antennal socket length).

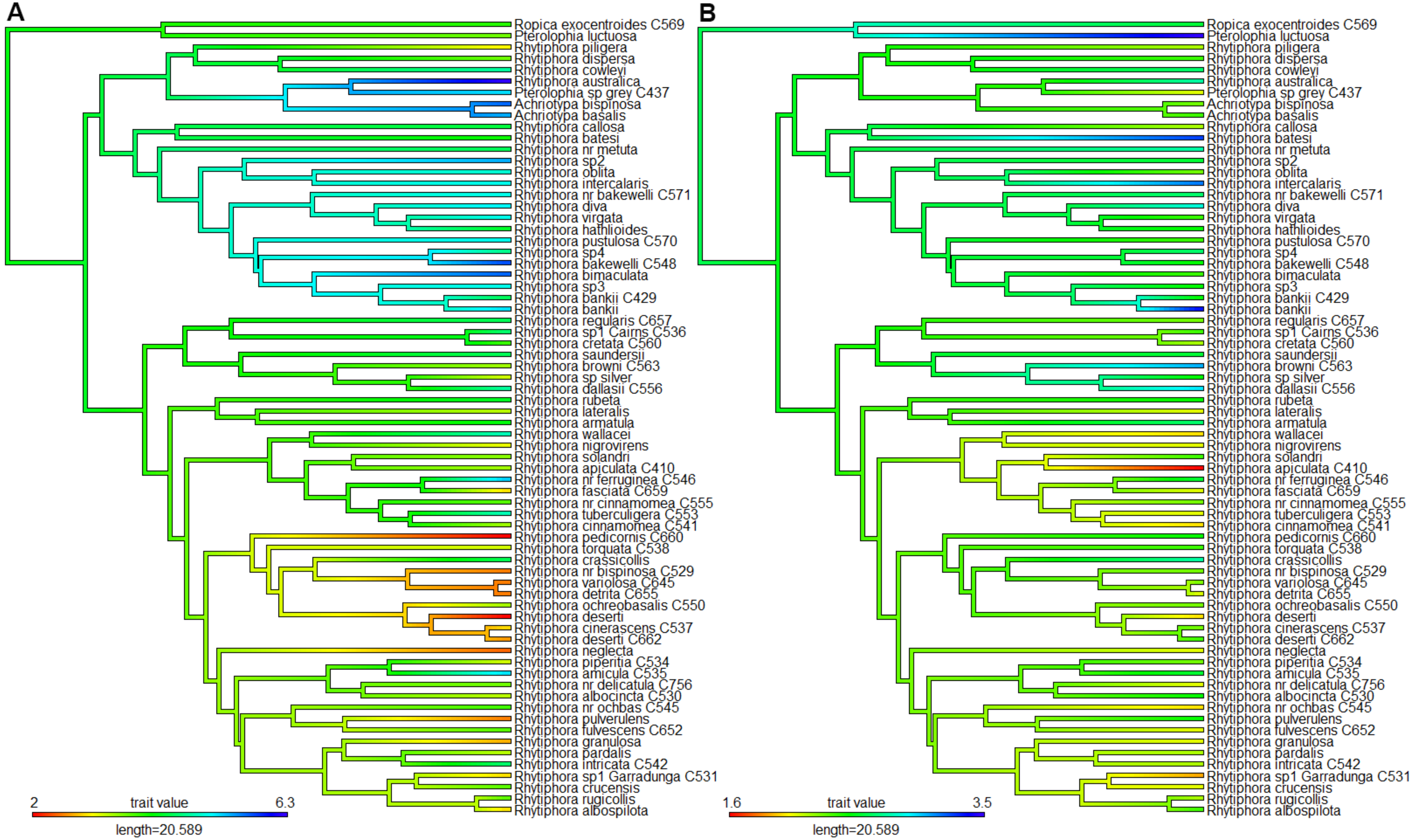

Figure S8. Ancestral morphological trait estimation of *Rhytiphora*: ancestral states reconstructed using APE on the dated BEAST phylogeny. **A:** Analysis of antennal separation (distance between antennal socket inner rims divided by socket width). **B:** Analysis of scape shape (length divided by width).

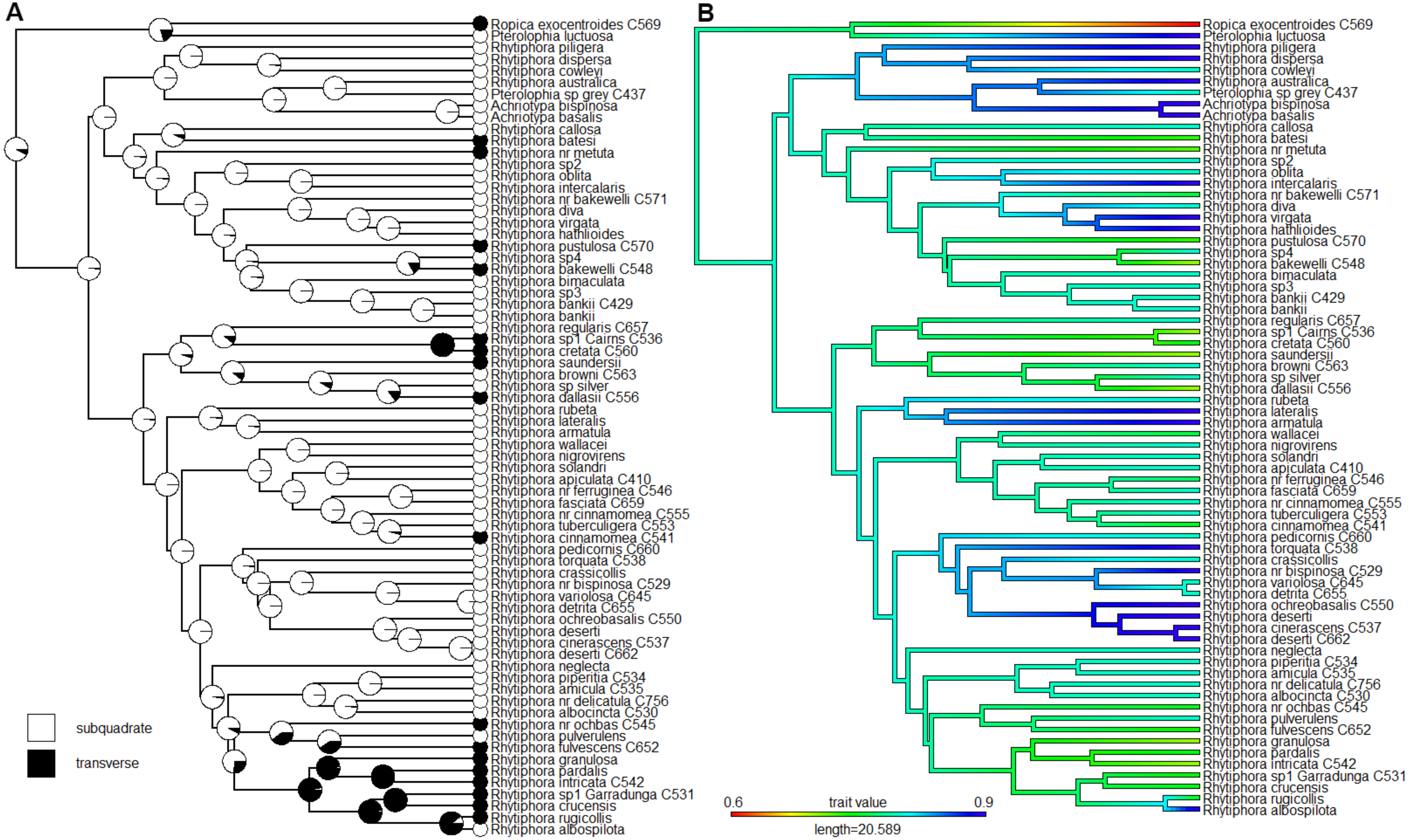

Figure S9. Ancestral morphological trait estimation of *Rhytiphora*: ancestral states reconstructed using APE on the dated BEAST phylogeny. **A:** Analysis of pronotum type, coded as subquadrate (≥0.76 length:width) or transverse (≤0.75 length:width). **B:** Analysis of pronotum shape (length divided by width).

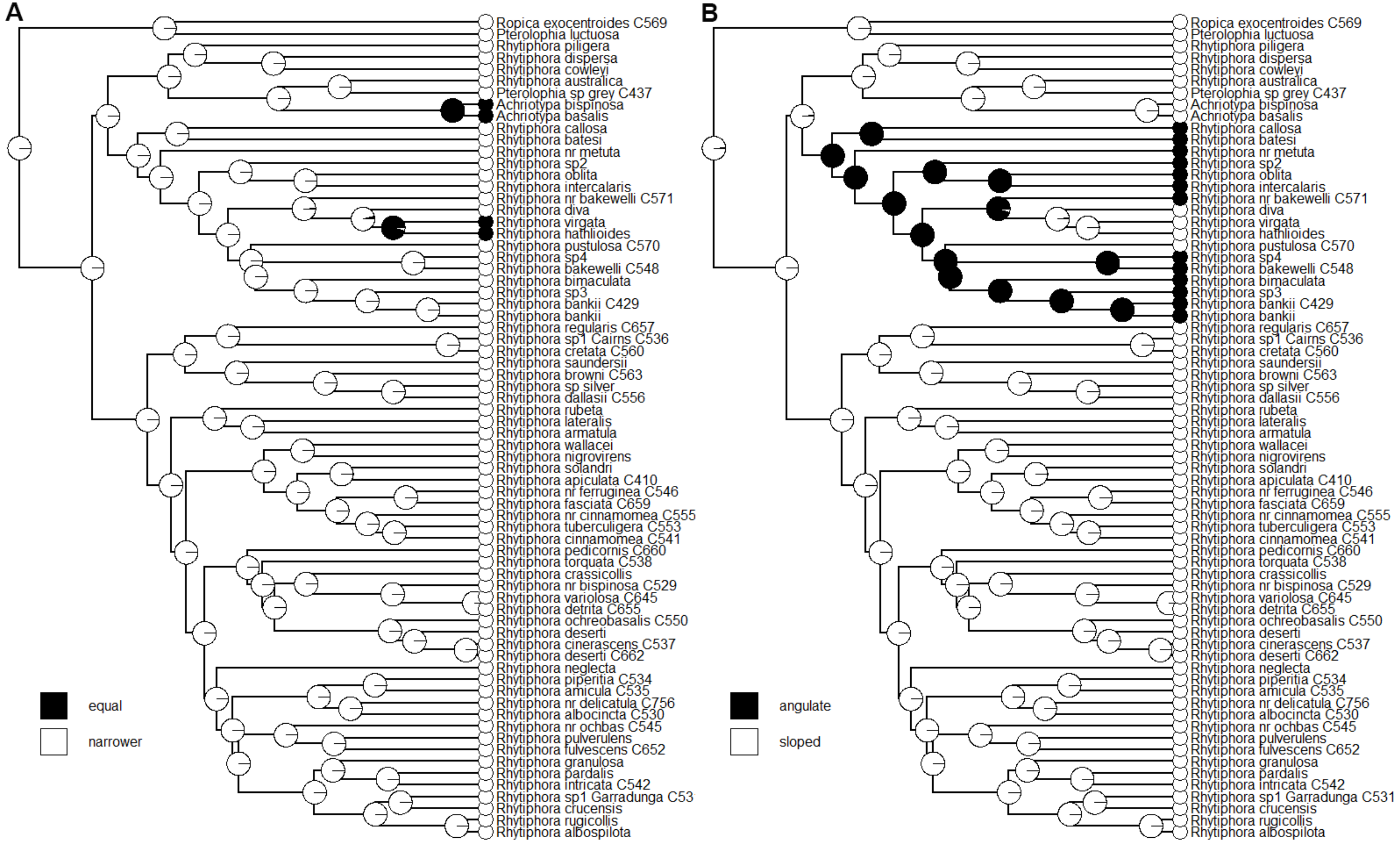

Figure S10. Ancestral morphological trait estimation of *Rhytiphora*: ancestral states reconstructed using APE on the dated BEAST phylogeny. **A:** Analysis of pronotum vs. elytra width, coded as equal or narrower (i.e. projecting humeral angles). **B:** Analysis of mesoventrite, coded as angulate (*Prosoplus*) or sloped.

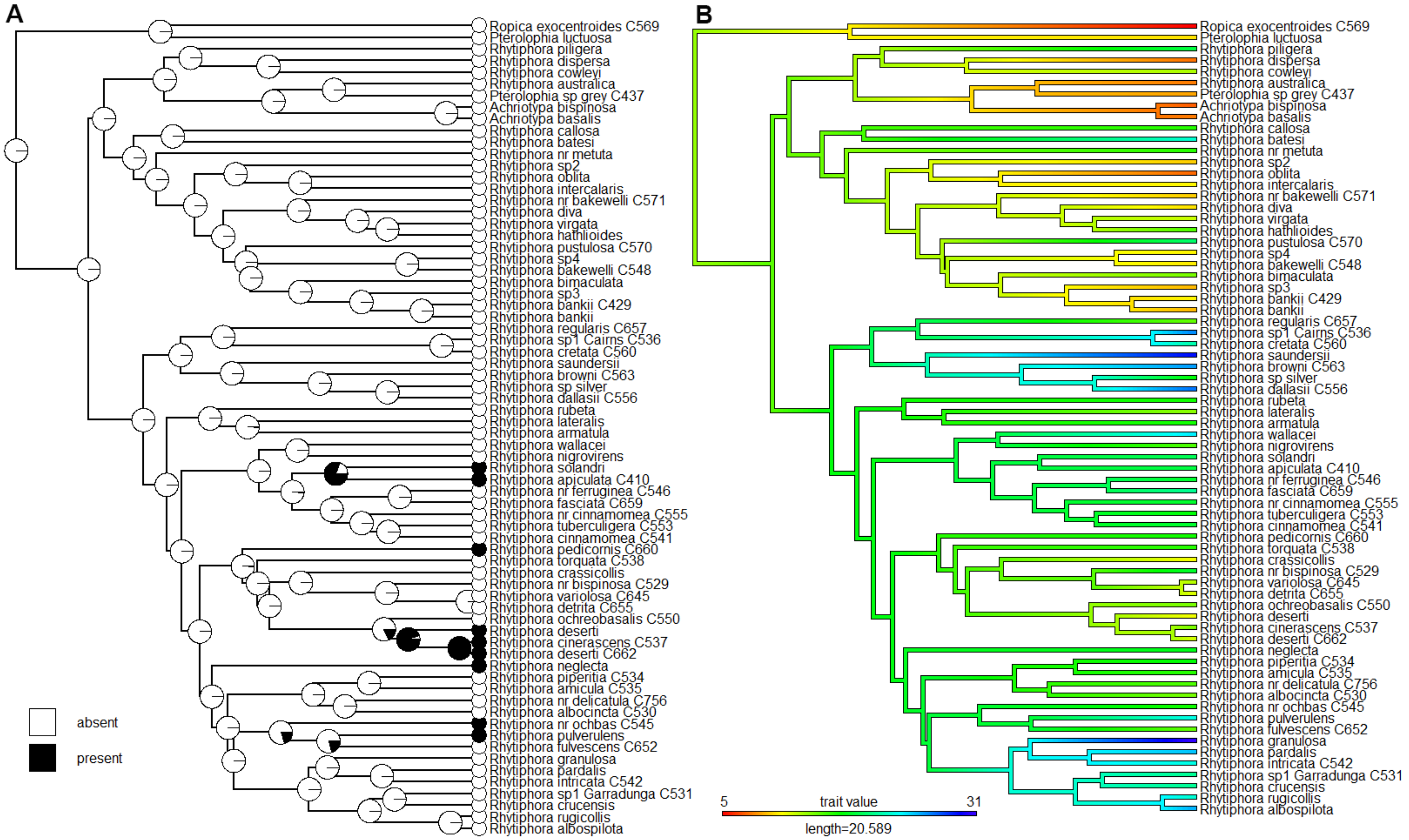

Figure S11. Ancestral morphological trait estimation of *Rhytiphora*: ancestral states reconstructed using APE on the dated BEAST phylogeny. **A:** Analysis of male protibial tubercules, coded as present or absent. **B:** Analysis of mean body size (average of minimum and maximum recorded body size, in mm).

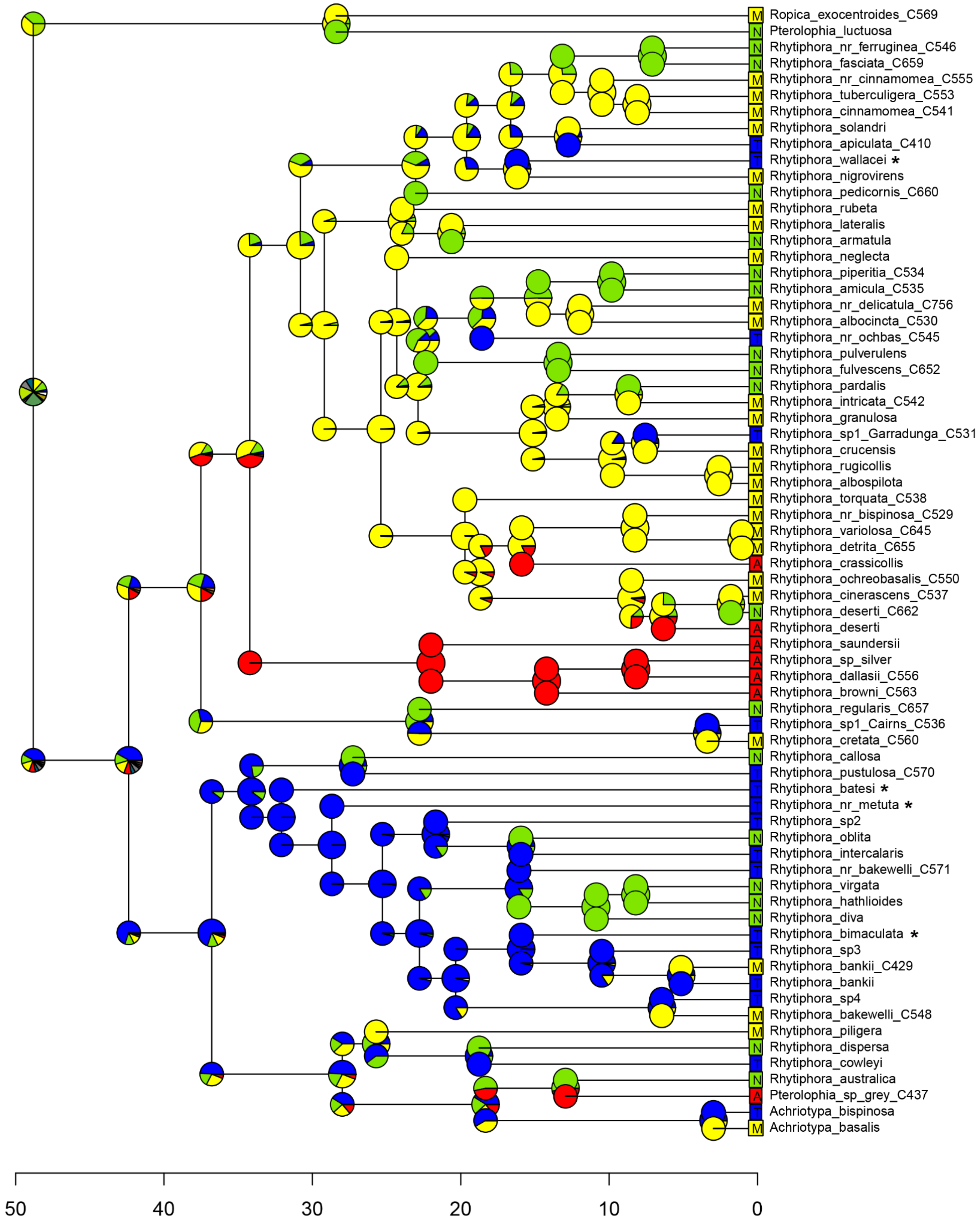

Figure S12. Ancestral geographic range estimation of *Rhytiphora*: ancestral states reconstructed using BioGeoBEARS under the DIVALIKE+J model on the alternate topology. Scale bar is in millions of years ago (Mya). Biomes are labelled as follows: wet tropics (T) is blue, with New Guinean species indicated by an asterisk (*); monsoonal tropics (N) is green; mesic (M) is yellow; arid zone (A) is red.

Chapter 2: Supplementary Information (Figures S1–12, Tables S1–4)

Table S1. List of 94 Lamiinae specimens sequenced for phylogenetic analyses. All specimens are lodged at the Australian National Insect Collection. Locality abbreviations: New South Wales (NSW), Northern Territory (NT), Queensland (QLD), South Australia (SA), Victoria (VIC), Western Australia (WA); Papua New Guinea (PNG).

Accession no.	Genus	Species	Locality	Specimen condition	Dataset	No. genes	Original genus
66410	*Rhytiphora*	*apiculata*	QLD	Ethanol	Expanded	1	*Platyomopsis*
66429	*Rhytiphora*	*bankii*	QLD	Ethanol	Expanded	1	*Lamia/Niphona/Prosoplus*
66430	*Rhytiphora*	*neglecta*	QLD	Ethanol	Expanded	1	*Symphyletes*
66437	*Pterolophia*	*"grey sp"*	QLD	Ethanol	Expanded	1	NA
66504	*Rhytiphora*	*diva*	WA	Ethanol	Expanded	1	*Zygrita*
66510	*Rhytiphora*	*nigrovirens*	no label	Ethanol	Expanded	1	*Saperda*
66513	*Pterolophia*	*luctuosa*	QLD	Ethanol	Expanded	1	*Lychrosis/Mycerinus*
66528	*Rhytiphora*	*"sp1 from Cairns"*	QLD	Ethanol	Expanded	1	NA
66529	*Rhytiphora*	*"sp near bispinosa"*	QLD	Ethanol	Expanded	1	NA
66530	*Rhytiphora*	*albocincta*	QLD	Ethanol	Expanded	1	*Rhytiphora/Saperda/Symphyletes*
66531	*Rhytiphora*	*"sp1 from Garradunga"*	QLD	Ethanol	Expanded	1	NA
66532	*Rhytiphora*	*regularis*	WA	Ethanol	Expanded	1	*Platyomopsis*
66534	*Rhytiphora*	*piperitia*	WA	Ethanol	Expanded	1	*Rhytiphora/Symphyletes*
66535	*Rhytiphora*	*amicula*	WA	Ethanol	Expanded	1	*Rhytiphora*
66536	*Rhytiphora*	*"sp1 from Cairns"*	QLD	Ethanol	Expanded	1	NA
66537	*Rhytiphora*	*cinerascens*	QLD	Ethanol	Expanded	1	*Platyomopsis*
66538	*Rhytiphora*	*torquata*	QLD	Ethanol	Expanded	1	*Symphyletes*
66539	*Rhytiphora*	*"sp near pauxilla"*	QLD	Ethanol	Expanded	1	NA
66541	*Rhytiphora*	*cinnamomea*	QLD	Ethanol	Expanded	1	*Symphyletes*
66542	*Rhytiphora*	*intricata*	WA	Ethanol	Expanded	1	*Penthea*
66543	*Rhytiphora*	*pedicornis*	QLD	Ethanol	Expanded	1	*Lamia/Rhytiphora*
66544	*Rhytiphora*	*callosa*	QLD	Ethanol	Expanded	1	*Menyllus/Sysspilotus*
66545	*Rhytiphora*	*"sp near ochreobasalis"*	QLD	Ethanol	Expanded	1	NA
66546	*Rhytiphora*	*"sp near ferruginea"*	QLD	Ethanol	Expanded	1	NA
66547	*Rhytiphora*	*cinerascens*	QLD	Ethanol	Expanded	1	*Platyomopsis*
66548	*Rhytiphora*	*bakewelli*	QLD	Ethanol	Expanded	1	*Niphona* (moved to *Prosoplus*)
66549	*Rhytiphora*	*fasciata*	QLD	Ethanol	Expanded	1	*Symphyletes*
66550	*Rhytiphora*	*ochreobasalis*	QLD	Ethanol	Expanded	1	*Saperdopsis*
66553	*Rhytiphora*	*tuberculigera*	QLD	Ethanol	Expanded	1	*Platyomopsis*
66555	*Rhytiphora*	*"sp near cinnamomea"*	WA	Ethanol	Expanded	1	NA
66556	*Rhytiphora*	*dallasii*	WA	Ethanol	Expanded	1	*Rhytiphora*
66557	*Rhytiphora*	*amicula*	WA	Ethanol	Expanded	1	*Rhytiphora*
66559	*Rhytiphora*	*pustulosa*	QLD	Ethanol	Expanded	1	*Rhytiphora/Symphyletes*
66560	*Rhytiphora*	*cretata*	no label	Ethanol	Expanded	1	*Rhytiphora*

66563	*Rhytiphora*	*browni*	WA	Ethanol	Expanded	1	*Rhytiphora*
66565	*Rhytiphora*	*pedicornis*	NT	Ethanol	Expanded	1	*Lamia/Rhytiphora*
66566	*Rhytiphora*	*"sp near cinnamomea"*	WA	Ethanol	Expanded	1	NA
66569	*Ropica*	*exocentroides*	QLD	Ethanol	Expanded	1	*Ropica*
66570	*Rhytiphora*	*pustulosa*	QLD	Ethanol	Expanded	1	*Rhytiphora/Symphyletes*
66571	*Rhytiphora*	*"sp near bakewelli"*	QLD	Ethanol	Expanded	1	NA
66645	*Rhytiphora*	*variolosa*	QLD	Ethanol	Expanded	1	*Symphyletes*
66648	*Rhytiphora*	*virgata*	QLD	Ethanol	Expanded	1	*Hathliodes*
66652	*Rhytiphora*	*fulvescens*	QLD	Ethanol	Expanded	1	*Symphyletes*
66654	*Rhytiphora*	*nigrovirens*	QLD	Ethanol	Expanded	1	*Saperda*
66655	*Rhytiphora*	*detrita*	WA	Ethanol	Expanded	1	*Rhytiphora/Symphyletes*
66656	*Rhytiphora*	*virgata*	QLD	Ethanol	Expanded	1	*Hathliodes*
66657	*Rhytiphora*	*regularis*	NT	Ethanol	Expanded	1	*Platyomopsis*
66658	*Rhytiphora*	*callosa*	QLD	Ethanol	Expanded	1	*Menyllus/Sysspilotus*
66659	*Rhytiphora*	*fasciata*	QLD	Ethanol	Expanded	1	*Symphyletes*
66660	*Rhytiphora*	*pedicornis*	WA	Ethanol	Expanded	1	*Lamia/Rhytiphora*
66661	*Rhytiphora*	*neglecta*	QLD	Ethanol	Expanded	1	*Symphyletes*
66662	*Rhytiphora*	*deserti*	NT	Ethanol	Expanded	1	*Symphyletes*
66664	*Rhytiphora*	*pardalis*	QLD	Ethanol	Expanded	1	*Lamia/Penthea*
66665	*Rhytiphora*	*virgata*	QLD	Ethanol	Expanded	1	*Hathliodes*
66756	*Rhytiphora*	*"sp near delicatula"*	QLD	Ethanol	Expanded	1	NA
66758	*Rhytiphora*	*fulvescens*	QLD	Ethanol	Expanded	1	*Symphyletes*
67037	*Acalolepta*	*mixta*	NT	Pinned	Core	13	*Monohammus*
67039	*Pterolophia*	*luctuosa*	QLD	Pinned	Core	13	*Lychrosis/Mycerinus*
67040	*Rhytiphora*	*bankii*	Christmas Is.	Pinned	Core	13	*Lamia/Niphona/Prosoplus*
67041	*Rhytiphora*	*intercalaris*	QLD	Pinned	Core	13	*Atyporis* (moved to *Prosoplus*)
67042	*Rhytiphora*	*cowleyi*	QLD	Pinned	Core	13	*Cairnsia*
67043	*Rhytiphora*	*hathlioides*	NT	Pinned	Core	13	*Xiphotheopsis*
67044	*Rhytiphora*	*virgata*	QLD	Pinned	Core	13	*Hathliodes*
67046	*Rhytiphora*	*dispersa*	NT	Pinned	Core	9	*Notolophia*
67047	*Rhytiphora*	*diva*	QLD	Pinned	Core	13	*Zygrita*
67048	*Rhytiphora*	*crassicollis*	NSW	Pinned	Core	13	*Penthea*
67051	*Rhytiphora*	*callosa*	QLD	Pinned	Core	13	*Menyllus/Sysspilotus*
67052	*Rhytiphora*	*armatula*	QLD	Pinned	Core	13	*Symphyletes*
67053	*Rhytiphora*	*lateralis*	VIC	Pinned	Core	13	*Symphyletes*
67054	*Rhytiphora*	*deserti*	NT	Pinned	Core	13	*Symphyletes*
67055	*Rhytiphora*	*piligera*	QLD	Pinned	Core	13	*Acanthocinus/Symphyletes*
67057	*Rhytiphora*	*pulverulens*	NT	Pinned	Core	13	*Lamia/Symphyletes*
67058	*Rhytiphora*	*neglecta*	QLD	Pinned	Core	13	*Symphyletes*
67059	*Rhytiphora*	*solandri*	QLD	Pinned	Core	13	*Lamia*
67060	*Rhytiphora*	*nigrovirens*	QLD	Pinned	Core	13	*Saperda*
67061	*Rhytiphora*	*pardalis*	QLD	Pinned	Core	13	*Lamia/Penthea*
67063	*Rhytiphora*	*saundersii*	WA	Pinned	Core	13	*Penthea/Rhytiphora*
67065	*Rhytiphora*	*granulosa*	QLD	Pinned	Core	13	*Lamia*
67068	*Rhytiphora*	*rugicollis*	NSW	Pinned	Core	13	*Lamia/Rhytiphora*
67098	*Rhytiphora*	*australica*	NT	Pinned	Core	13	*Pterolophia*

68441	*Rhytiphora*	*batesi*	PNG	Pinned	Core	12	*Eczemotes*
68448	*Rhytiphora*	*wallacei*	PNG	Pinned	Core	13	*Symphyletes*
68452	*Rhytiphora*	*bimaculata*	PNG	Pinned	Core	13	*Prosoplus*
68459	*Rhytiphora*	*"sp near metuta"*	PNG	Pinned	Core	13	NA
68464	*Achriotypa*	*basalis*	NSW	Pinned	Core	9	*Achriotypa*
68466	*Achriotypa*	*bispinosa*	QLD	Pinned	Core	12	*Pterolophia*
73783	*Rhytiphora*	*albospilota*	QLD	Ethanol	Expanded	9	*Rhytiphora*
73795	*Rhytiphora*	*crucensis*	SA	Ethanol	Expanded	6	*Rhytiphora*
73808	*Rhytiphora*	*oblita*	QLD	Ethanol	Expanded	9	*Niphona* (moved to *Prosoplus*)
73815	*Rhytiphora*	*rubeta*	NSW	Ethanol	Expanded	9	*Rhytiphora*
73818	*Rhytiphora*	*"silver sp"*	WA	Ethanol	Expanded	8	NA
73821	*Rhytiphora*	*"sp2"*	QLD	Ethanol	Expanded	4	NA
73823	*Rhytiphora*	*"sp3"*	QLD	Ethanol	Expanded	4	NA
73824	*Rhytiphora*	*"sp4"*	QLD	Ethanol	Expanded	6	NA

Table S2. Summary of morphological traits and geographic distribution of the Niphonini species. Male specimens were used as much as possible; see captions of Figs. 4–5, S7–11 for explanation of measurements. Biome abbreviations: arid zone (AZ), mesic zone (ME), monsoonal tropics (MT), wet tropics (T). Secondary biome, if applicable, is in brackets. Species from New Guinea are indicated with one asterisk (*), and species from southwest (not east) Australia are indicated with two asterisks (**).

Species	**Body size (class)**	**Body size (mean)**	**Eye shape**	**Eye rows**	**Eye upper length**	**Ant. separation**	**Scape shape**	**Ant. fringe**	**Pronotum (class)**	**Pron. shape**	**Pron. vs elytra**	**Mesov. angle**	**Protib. tubercules**	**Sex patch**	**Biome**
Achriotypa basalis	small	8	divided	0	1.2	5.4	2.4	sparse	subquadrate	0.9	equal	sloped	absent	absent	ME
Achriotypa bispinosa	small	7.25	divided	0	1.1	5.7	2.3	sparse	subquadrate	0.9	equal	sloped	absent	absent	T
Pterolophia luctuosa	small	10.5	divided	0	0.9	3.6	3.5	sparse	subquadrate	0.9	narrower	sloped	absent	small	MT
Pterolophia sp grey C437	small	9	divided	0	1	5.2	2.1	sparse	subquadrate	0.8	narrower	sloped	absent	NA	AZ
Rhytiphora albocincta C530	medium	14.5	divided	0	1.2	3.3	2.5	dense	subquadrate	0.8	narrower	sloped	absent	large	ME
Rhytiphora albospilota	large	25.5	deep-emarg	2	0.9	2.9	2.4	dense	subquadrate	0.9	narrower	sloped	absent	large	ME
Rhytiphora amicula C535	medium	16.5	divided	0	0.9	5.2	2.6	dense	subquadrate	0.8	narrower	sloped	absent	large	MT
Rhytiphora apiculata C410	medium	19	deep-emarg	1	1	3.4	1.6	dense	subquadrate	0.8	narrower	sloped	present	small	T
Rhytiphora armatula	medium	17	divided	0	1	4.1	2.7	dense	subquadrate	0.9	narrower	sloped	absent	large	MT
Rhytiphora australica	small	8	divided	0	1.1	6.3	2.8	sparse	subquadrate	0.9	narrower	sloped	absent	small	MT
Rhytiphora bakewelli C548	small	10.75	divided	0	1.1	5.8	2.5	sparse	transverse	0.7	narrower	angulate	absent	small	ME

Rhytiphora bankii	small	9.5	divided	0	0.9	5.2	3.4	sparse	subquadrate	0.8	narrower	angulate	absent	small	T
Rhytiphora bankii C429	small	11	divided	0	1.2	4.4	2.5	sparse	subquadrate	0.8	narrower	angulate	absent	small	ME (MT)
Rhytiphora batesi	large	22.5	divided	0	0.7	4	3.3	sparse	transverse	0.73	narrower	angulate	absent	small	T*
Rhytiphora bimaculata	small	14.5	divided	0	1	5.7	2.4	sparse	subquadrate	0.8	narrower	angulate	absent	small	T*
Rhytiphora browni C563	large	26	deep-emarg	3	1	3.4	3.1	dense	subquadrate	0.8	narrower	sloped	absent	absent	AZ
Rhytiphora callosa	medium	16.5	divided	0	0.9	4.3	2.2	sparse	subquadrate	0.8	narrower	angulate	absent	small	MT
Rhytiphora cinerascens C537	small	14.5	deep-emarg	2	1	2.9	2.3	dense	subquadrate	0.9	narrower	sloped	present	large	ME
Rhytiphora cinnamomea C541	medium	18.5	deep-emarg	1	0.8	3.4	2	dense	transverse	0.75	narrower	sloped	absent	large	ME
Rhytiphora cowleyi	small	13.25	divided	0	1.5	4.7	2.7	sparse	subquadrate	0.8	narrower	sloped	absent	small	T
Rhytiphora crassicollis	small	11.5	divided	0	0.9	4.4	2.8	sparse	subquadrate	0.8	narrower	sloped	absent	small	AZ
Rhytiphora cretata C560	large	21.5	emarg	4	0.9	3.8	2.2	dense	transverse	0.75	narrower	sloped	absent	large	ME
Rhytiphora crucensis	medium	21	deep-emarg	1	0.9	3.7	2.1	dense	transverse	0.75	narrower	sloped	absent	large	ME**
Rhytiphora dallasii C556	large	27	deep-emarg	2	0.9	4.7	3	dense	transverse	0.7	narrower	sloped	absent	absent	AZ
Rhytiphora deserti	small	11.5	deep-emarg	2	1.1	2	2	dense	subquadrate	0.9	narrower	sloped	present	large	AZ
Rhytiphora deserti C662	small	12.25	deep-emarg	2	1	2.6	2.4	dense	subquadrate	0.9	narrower	sloped	present	large	MT
Rhytiphora detrita C655	small	12	deep-emarg	2	1	2.5	2.1	dense	subquadrate	0.8	narrower	sloped	absent	large	ME**

Rhytiphora dispersa	small	7.75	divided	0	0.9	3.6	2.4	sparse	subquadrate	0.9	narrower	sloped	absent	small	MT
Rhytiphora diva	small	10.5	divided	0	1	5.1	2.9	sparse	subquadrate	0.8	narrower	sloped	absent	small	MT (AZ, ME)
Rhytiphora fasciata C659	medium	21	deep-emarg	2	0.9	2.9	2.1	dense	subquadrate	0.8	narrower	sloped	absent	small	MT
Rhytiphora fulvescens C652	small	15	deep-emarg	1	0.9	3.7	2.1	sparse	transverse	0.74	narrower	sloped	absent	small	MT
Rhytiphora granulosa	large	31	deep-emarg	2	0.8	2.7	2.1	sparse	transverse	0.7	narrower	sloped	absent	large	ME
Rhytiphora hathlioides	small	15.5	divided	0	1.2	4.2	2.5	sparse	subquadrate	0.9	equal	sloped	absent	small	MT
Rhytiphora intercalaris	small	11	divided	0	1.1	5	3.2	sparse	subquadrate	0.9	narrower	angulate	absent	small	T
Rhytiphora intricata C542	large	23	deep-emarg	1	0.7	4.5	2.2	sparse	transverse	0.7	narrower	sloped	absent	large	ME**
Rhytiphora lateralis	small	14	divided	0	1.1	3.3	2.1	dense	subquadrate	0.9	narrower	sloped	absent	large	ME
Rhytiphora neglecta	medium	18	deep-emarg	2	0.9	2.4	2.1	dense	subquadrate	0.8	narrower	sloped	present	large	ME
Rhytiphora nigrovirens	medium	15.5	divided	0	0.9	3.1	2.1	dense	subquadrate	0.8	narrower	sloped	absent	large	ME
Rhytiphora nr bakewelli C571	small	10	divided	0	0.9	5	2.7	sparse	subquadrate	0.76	narrower	angulate	absent	small	T
Rhytiphora nr bispinosa C529	medium	18.5	deep-emarg	1	0.8	2.5	2.3	dense	subquadrate	0.9	narrower	sloped	absent	large	ME
Rhytiphora nr cinnamomea C555	medium	18.5	deep-emarg	1	0.9	3.7	2.3	dense	subquadrate	0.8	narrower	sloped	absent	large	ME**
Rhytiphora nr delicatula C756	medium	15.5	divided	0	1.1	3.6	2.1	dense	subquadrate	0.8	narrower	sloped	absent	large	ME

Rhytiphora nr ferruginea C546	medium	18.5	deep-emarg	2	0.9	5.3	2.6	dense	subquadrate	0.77	narrower	sloped	absent	large	MT (ME)
Rhytiphora nr metuta	medium	16.5	divided	0	1.1	4.4	2.8	sparse	transverse	0.72	narrower	angulate	absent	small	T*
Rhytiphora nr ochbas C545	medium	17	deep-emarg	1	0.9	3.8	2	dense	transverse	0.75	narrower	sloped	present	large	T
Rhytiphora oblita	small	7.5	divided	0	1.2	4.9	2.3	sparse	subquadrate	0.8	narrower	angulate	absent	small	MT (ME)
Rhytiphora ochreobasalis C550	small	14.5	deep-emarg	1	0.9	3.4	2.3	dense	subquadrate	0.9	narrower	sloped	absent	large	ME
Rhytiphora pardalis	large	25	deep-emarg	2	0.8	3.3	2.2	sparse	transverse	0.75	narrower	sloped	absent	large	MT (AZ, ME)
Rhytiphora pedicornis C660	medium	17	deep-emarg	1	1	2	2.5	dense	subquadrate	0.8	narrower	sloped	present	small	MT
Rhytiphora piligera	medium	19	divided	0	0.9	3	2.2	dense	subquadrate	0.9	narrower	sloped	absent	small	ME
Rhytiphora piperitia C534	medium	17.5	deep-emarg	1	1	3.2	2.3	dense	subquadrate	0.8	narrower	sloped	absent	large	MT
Rhytiphora pulverulens	large	23	deep-emarg	2	1.1	2.5	2.5	dense	subquadrate	0.8	narrower	sloped	present	small	MT (ME)
Rhytiphora pustulosa C570	medium	20	divided	0	1.2	5	2.4	sparse	transverse	0.73	narrower	sloped	absent	large	T
Rhytiphora regularis C657	medium	15	divided	0	1.1	4.4	2.3	dense	subquadrate	0.8	narrower	sloped	absent	large	MT
Rhytiphora rubeta	medium	17	deep-emarg	1	0.8	4.2	2.5	dense	subquadrate	0.8	narrower	sloped	absent	large	ME
Rhytiphora rugicollis	large	22.5	deep-emarg	2	0.9	3.7	2.2	dense	transverse	0.75	narrower	sloped	absent	large	ME
Rhytiphora saundersii	large	29.5	deep-emarg	2	0.9	4.4	2.6	dense	transverse	0.7	narrower	sloped	absent	large	AZ

Rhytiphora solandri	medium	19.5	deep-emarg	1	1	3.5	2.4	sparse	subquadrate	0.8	narrower	sloped	present	small	ME
Rhytiphora sp silver	medium	17.5	deep-emarg	2	1	3.2	2.5	dense	subquadrate	0.8	narrower	sloped	absent	large	AZ
Rhytiphora sp1 Cairns C536	large	26.5	deep-emarg	2	0.7	4.5	2.4	dense	transverse	0.7	narrower	sloped	absent	large	T
Rhytiphora sp1 Garrad. C531	medium	21	deep-emarg	2	0.8	2.9	1.9	dense	transverse	0.74	narrower	sloped	absent	large	T
Rhytiphora sp2	small	10	divided	0	1.1	5.4	2.6	sparse	subquadrate	0.8	narrower	angulate	absent	small	T
Rhytiphora sp3	small	9.5	divided	0	1.1	5	2.5	sparse	subquadrate	0.8	narrower	angulate	absent	small	T
Rhytiphora sp4	small	11	divided	0	1.2	4.6	2.7	sparse	subquadrate	0.8	narrower	angulate	absent	small	T
Rhytiphora torquata C538	medium	16.5	divided	0	0.8	3.2	2.4	dense	subquadrate	0.9	narrower	sloped	absent	large	ME
Rhytiphora tuberculigera C553	medium	17.5	deep-emarg	1	0.9	4.8	2.1	dense	subquadrate	0.8	narrower	sloped	absent	small	ME
Rhytiphora variolosa C645	small	13	deep-emarg	1	1	2.5	2.3	dense	subquadrate	0.8	narrower	sloped	absent	large	ME
Rhytiphora virgata	small	12.5	divided	0	1	5	2.4	sparse	subquadrate	0.9	equal	sloped	absent	small	MT
Rhytiphora wallacei	large	24	deep-emarg	1	0.7	4.8	2	dense	subquadrate	0.76	narrower	sloped	absent	large	T*
Ropica exocentroides C569	small	5	divided	0	0.8	3.9	2.6	sparse	transverse	0.6	narrower	sloped	absent	small	ME

Table S3. Results of phylogenetic signal tests on morphological traits of the Niphonini species. Signal is measured by Blomberg's *K* (continuous traits; 0 = no signal) and the *D* statistic (binary traits; 1 = no signal). Significance is indicated with an asterisk (p = 0.01–0.001**, p <0.001***).

Morphological trait	**Statistic**	***p* value**
Body size (mean)	$K = 1.35$	0.001**
Eye emargination (class)	$D = -1.25$	<0.001***
Number of joining eye rows	$K = 0.94$	0.001**
Eye upper lobe length (ratio)	$K = 0.66$	0.001**
Antennal separation (ratio)	$K = 0.80$	0.001**
Scape shape (ratio)	$K = 0.85$	0.001**
Antennal fringe (class)	$D = -1.30$	<0.001***
Pronotum type (class)	$D = 0.09$	0.006**
Pronotum shape (ratio)	$K = 0.63$	0.001**
Pronotum vs. elytra width (class)	$D = -1.77$	<0.001***
Mesoventrite angle (class)	$D = -2.01$	<0.001***
Protibial tubercules (class)	$D = -0.90$	<0.001***
Sex patch size (class)	$D = -1.13$	<0.001***

Table S4. Results of BioGeoBEARS geographic range analyses on the dated BEAST phylogeny.

Model	**Log likelihood**	**No. parameters**	***d***	***e***	***j***	**AICc**	**AICc weight**
DEC	-144.6	2	8.70E-03	1.10E-02	0	293.3	4.40E-25
DEC+J	-88.37	3	1.00E-12	1.00E-12	0.15	183.1	0.37
DIVALIKE	-130.2	2	8.70E-03	3.00E-03	0	264.6	7.60E-19
DIVALIKE+J	-88.07	3	1.00E-12	1.00E-12	0.14	182.5	0.5
BAYAREALIKE	-162.5	2	4.50E-03	4.60E-02	0	329.3	6.70E-33
BAYAREALIKE+J	-89.4	3	1.00E-12	1.00E-12	0.14	185.2	0.13

Chapter 2: Supplementary Information (Figures S1–12, Tables S1–4)

Chapter 3: A review of the Australian *Rhytiphora* species (Coleoptera: Cerambycidae)

Authors: Lauren G. Ashman[1,2], Adam Ślipiński[2]

[1] Research School of Biology, Australian National University, Canberra, Australia

[2] Australian National Insect Collection, CSIRO, Canberra, Australia

ABSTRACT

We present a review of the Australian species of *Rhytiphora* Audinet-Serville, 1835, the largest longhorn beetle (Cerambycidae) genus in Australia. The morphological definition of the genus is updated, including key characteristics of its two subclades and useful features to distinguish *Rhytiphora* from closely related genera. The *collaris* group of *Rhytiphora* is revised and *Rhytiphora garnetensis* **sp. nov.** is described from Queensland. Lectotypes are designated for *R. amicula* White, 1859, *Symphyletes vestigialis* Pascoe, 1864, *Symphyletes compos* Blackburn, 1902, *R. maculosella* Blackburn, 1902, *R. uniformis* Blackburn, 1901, *R. piperitia* Hope, 1842 and *Symphyletes humeralis* White, 1858. We provide a new checklist of the Australian *Rhytiphora* species which, incorporating synonymies and other changes, reduces the total number of species from 206 to 162. The following species have been synonymised (junior synonym listed first): *Coptops abdominalis* White, 1858 synonymised with *Lamia bankii* Fabricius, 1775; *Penthea adamsae* McKeown, 1938 synonymised with *Penthea macularia* Pascoe, 1867; *R. affinis* Breuning, 1970 synonymised with *Symphyletes farinosus* Pascoe, 1863; *Prosoplus albidus* Aurivillius, 1917 and *Prosoplus minimus* Breuning, 1938 synonymised with *Corrhenes pauxilla* Blackburn, 1901; *Prosoplus albostriatus* Breuning, 1938 and *Prosoplus demarzi* Breuning, 1963 synonymised with *Niphona oblita* Pascoe, 1863; *Saperda albocincta* Guérin-Méneville, 1831, *Symphyletes compos* Blackburn, 1902, *R. donovani* Newman, 1851, *R. intertincta* Pascoe, 1867, *R. maculosella* Blackburn, 1902, *R. parafarinosa* Breuning, 1970, *R. vermiculosa* Breuning, 1970 and *Symphyletes vestigialis* Pascoe, 1864 synonymised with *Saperda collaris* Donovan, 1805; *R. albolateraloides* Breuning, 1970 synonymised with *Platyomopsis cinerascens* Aurivillius, 1917; *Symphyletes anaglyptus* Pascoe, 1867, *Saperdopsis* *armata* Thomson, 1864, *Symphyletes moratus* Pascoe, 1863 and *Symphyletes vetustus* Pascoe, 1862 synonymised with *Lamia pulverulens* Boisduval, 1835; *Symphyletes arctos* Pascoe, 1865 synonymised with *Symphyletes fumatus* Pascoe, 1864; *Pterolophia australica* Breuning, 1938 synonymised with *Apomecyna nigrita* Pascoe, 1859; *R. barnardi* Breuning, 1982 synonymised with *Symphyletes capreolus* Pascoe, 1867; *Platyomopsis basalis* Aurivillius, 1917 synonymised with *Saperdopsis ochreobasalis* Breuning, 1938; *R. corrhenoides* Breuning, 1970 synonymised with *Corrhenes cruciata* Pascoe, 1875; *R. dawsoni* Breuning, 1970 synonymised with *Symphyletes fasciatus* Blackburn, 1901; *Symphyletes defloratus* Pascoe, 1869 synonymised with *Symphyletes gallus* Pascoe, 1864; *Trichoprosoplus demarzi* Breuning, 1961 and *Paradaxata spinosa* Breuning, 1938 synonymised with *Paradaxata villosa* Breuning, 1938; *Prosoplus elongatus* Breuning, 1938 synonymised with *Prosoplus metallescens* Breuning, 1938; *Corrhenes flavovittata* Breuning, 1938, *Saperda funesta* Pascoe, 1859, *Anaesthetis lepida* Germar, 1848 and *Cobria rufa* Breuning, 1961 synonymised with *Saperda paulla* Germar, 1848; *Corrhenes guttulata* Pascoe, 1865, *Corrhenes macmillani* Gilmour, 1950 and *Saperda mystica* Pascoe, 1863 synonymised with *Saperda stigmatica* Pascoe, 1863; *Xiphotheopsis hathlioides* Breuning, 1961 synonymised with *Xiphohathlia lobata* Breuning, 1961; *Symphyletes iliacus* Pascoe, 1866 synonymised with *Symphyletes deserti* Blackburn, 1896; *Saperdopsis laterialba* Breuning, 1938 synonymised with *Symphyletes satelles* Pascoe, 1865; *Etaxalus laterialbus* Breuning, 1968 synonymised with *Achriotypa basalis* Pascoe, 1875; *Prosoplus laterinigricollis* Breuning, 1961 and *Prosoplus mediofasciatus* Breuning, 1938 synonymised with *Niphona bakewelli* Pascoe, 1859; *R. leucolateralis* Breuning, 1970 synonymised with *R. subargentata* Breuning, 1970; *Penthea lichenosa* McKeown, 1942 and *Penthea obscura* Breuning, 1961 synonymised with *Penthea scenica* Pascoe, 1863; *Sysspilotus macleayi* Pascoe, 1865 and *Menyllus maculicornis* Pascoe, 1864 synonymised with *Menyllus rotundipennis* Breuning, 1968; *R. multituberculata* Breuning, 1966 synonymised with *Saperdopsis sellata* Breuning, 1938; *Symphyletes nodosus* Newman, 1842 synonymised with *Acanthocinus piliger* Macleay, 1826; *R. parantennalis* Breuning, 1970 synonymised with *R. obsoleta* Breuning, 1938; *Hathliodes pseudomurinus* Breuning, 1938 synonymised with *Hathliodes virgatus* Breuning, 1938; *Penthea sectator* Pascoe, 1865 synonymised with *Penthea crassicollis* Pascoe, 1864; *R. simsoni* Blackburn, 1901 synonymised with *R. mista* Newman, 1842; *Penthea solida* Pascoe, 1863 synonymised with *Lamia vermicularia* Donovan, 1805; *Platyomopsis spinosa* Thomson, 1864 synonymised with *Lamia obliqua* Donovan, 1805;

R. truncata Breuning, 1940 synonymised with *R. piperitia* Hope, 1842; *R. uniformis* Blackburn, 1901 synonymised with *Platyomopsis delicatula* McKeown, 1948; *Mimiphiastus vivesi* Breuning, 1978 synonymised with *Symphyletes variolosa* Pascoe, 1862. *Pterolophia bispinosa* Breuning, 1938 is renamed to *R. subovata* (junior homonym of *Saperdopsis bispinosa* Breuning, 1938), *R. browni* McKeown, 1938 is reinstated as its own species, and *Corrhenes flavovittata demarzi* Breuning, 1963 is elevated to species status and renamed *R. rentzi* (junior homonym of *Trichoprosoplus demarzi*). A number of species complexes that require genetic confirmation before being synonymised (or separated) are discussed.

INTRODUCTION

The longhorn beetles (Cerambycidae) are a large, diverse family of phytophagous beetles that mostly feed on woody plants. Of its eight subfamilies, Lamiinae is the largest with about 21,000 described species (over half of all cerambycid species; Švácha & Lawrence 2014). About a third of the Australian lamiines are endemic (26 genera), with a similar number also distributed in New Guinea (13 genera) and north into Asia (12 genera); five genera co-occur in New Zealand, while ten genera are widespread across the Old World (Roguet 2020; Ślipiński & Escalona 2013).

The lamiine genus *Rhytiphora* Audinet-Serville comprises about 200 Australian species (more than a third of all Australian Lamiinae), with at least 50 more in New Guinea and Southeast Asia, where it likely originated (Ślipiński & Escalona 2013). *Rhytiphora* is morphologically diverse (Fig. 1), with a body size ranging from 6–39 mm long and different body shapes corresponding to the formerly recognised Pteropliini Thomson genera, e.g., *Prosoplus* Blanchard, *Symphyletes* Newman and *Penthea* Dejean. Eye size ranges from medium to large, and the elytra are smooth to tuberculate, plainly coloured to elaborately patterned with bright or cryptic colouration, indicating both diurnal and nocturnal habits. There is little sexual dimorphism apart from the male sex patches (see below); males tend to have slightly larger eyes and longer (unmodified) antennae, and in most species have a spine on the coxa of the front legs.

According to Ślipiński & Escalona (2013), *Rhytiphora* is characterised by paired setose patches on male abdominal ventrite 2 (and rarely 3), comb-like antennal cleaner on mesotibia, 5-segmented tarsi and rounded antennal scape without apical carina. The 38 formerly recognised genera encompassed by this description did not have stable morphological definitions, and are now united on the basis of the variously sized male setose ‘sex patches’, structures that may be involved in pheromone dispersal, and therefore reproduction. Recent molecular studies support *Rhytiphora* as a distinct clade, monophyletic with the inclusion of the two *Achriotypa* Pascoe species (Chapters 1 & 2). The nearest Australian genera are *Ropica* Pascoe and *Pterolophia* Newman, which both have similar male sex patches hidden on the membrane beneath ventrite 1. Updated morphological definitions of *Rhytiphora* and its two subclades, as determined by our molecular data, are presented here.

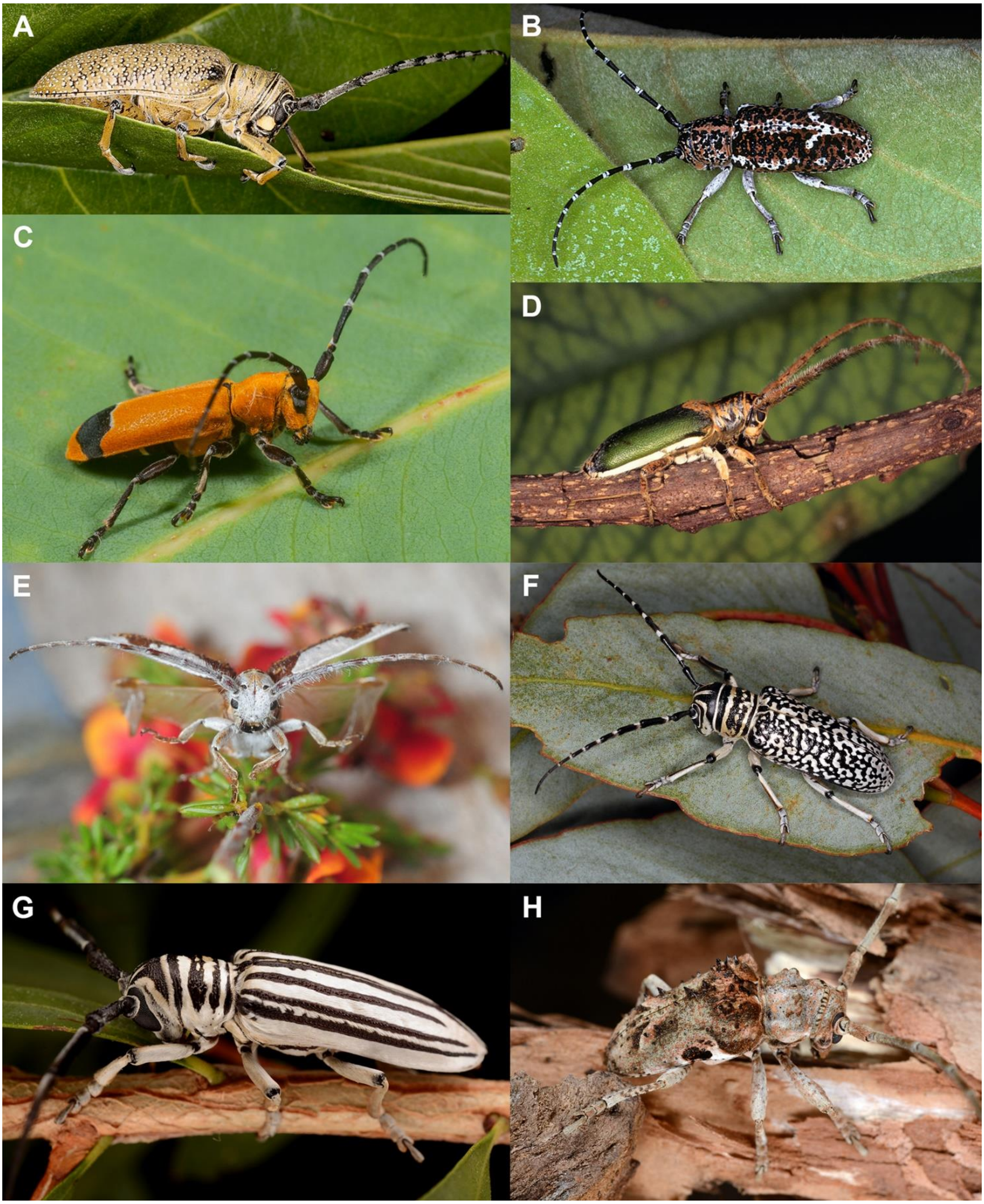

Figure 1. *Rhytiphora* species in their natural habitats. **A:** *Rhytiphora albospilota* Aurivillius, © P. Zborowski. **B:** *Rhytiphora pardalina* (Breuning), © P. Zborowski. **C:** *Rhytiphora diva* (Thomson), © J. Lochman. **D:** *Rhytiphora nigrovirens* (Donovan), © P. Zborowski. **E:** *Rhytiphora lateralis* (Pascoe), © S. Harris. **F:** *Rhytiphora saundersii* (Pascoe), © A. Sundholm. **G:** *Rhytiphora dallasii* Pascoe, © R. de Keyzer. **H:** *Rhytiphora obliqua* (Donovan), © R. de Keyzer.

The first modern treatment of *Rhytiphora*, by Ślipiński & Escalona (2013), focused mainly on genus level synonymies and only encompassed the Australian species (largely following Breuning's 11-volume Catalogue of the Lamiines of the World; Breuning 1969). Tavakilian & Nearns (2014a; b) examined the New Guinean and Southeast Asian species affected by the expansion of *Rhytiphora*, and renamed 28 homonyms. In Chapter 1, we synonymised *Achriotypa* with *Rhytiphora* based on molecular data. In this paper, we again focus on the more speciose Australian radiation, with the aim of identifying and establishing synonymies amongst the available type specimens; several types could not be found. We provide a list of species incorporating 41 taxonomic changes, discuss 20 potential synonymies, and also revise the *collaris* group (including the description of one new Australian species).

METHODS

Specimens were examined using a Leica M80 dissecting microscope with an eyepiece graticule. A range of morphological traits were recorded in Open DELTA v1.02 (Atlas of Living Australia 2017) for holotype comparisons, including: body shape, eye size, antennal insertions, setae colour patterns, exoskeleton sculpturing, elytral apices and male sex patches. New digital photographs were taken using a BK Plus Lab System (Dun Inc.) or Canon EOS 7D, or provided by museum staff.

Species distributions were determined from specimen labels, type localities and McKeown's 1947 catalogue of Australian Cerambycidae. Host plant records were collected from specimen labels, published literature (Duffy 1963; Hall 1980; Webb 1987; Sirait *et al.* 2020), the Titan database (Tavakilian & Chevillotte 2020) and citizen scientists' field observations (see Acknowledgements).

Australian state and territory abbreviations/acronyms are as follows: Australian Capital Territory (ACT), New South Wales (NSW), Northern Territory (NT), Queensland (QLD), South Australia (SA), Tasmania (TAS), Victoria (VIC), Western Australia (WA). Acronyms for institutions storing *Rhytiphora* specimens are listed below.

AM: Australian Museum, Sydney, Australia

ANIC: Australian National Insect Collection, CSIRO, Canberra, Australia

BMNH: British Museum of Natural History, London, UK

DAFWA: Department of Agriculture and Food of Western Australia, Perth, Australia

DMAG: Doncaster Museum and Art Gallery, UK

EMHU: Entomological Museum Hokkaido University, Japan

EVC: Eduard Vives Collection, Barcelona, Spain

HSC: Herbert Schmid Collection, Vienna, Austria

MHNL: Musée d'Histoire Naturelle de Lyon, France

MM: Macleay Museum, University of Sydney, Australia

MNHN: Muséum National d'Histoire Naturelle, Paris, France

MV: Museum Victoria, Melbourne, Australia

MZL: Musée de Zoologie de Lausanne, Switzerland

NHMB: Naturhistorisches Museum Basel, Switzerland

NMP: National Museum Prague, Czech Republic

NRM: Naturhistoriska Riksmuseet, Stockholm, Sweden

OUMNH: Oxford University Museum of Natural History, UK

PHIC: Paul Hutchinson Insect Collection, Perth, Australia

QM: Queensland Museum, Brisbane, Australia

RBI: Royal Belgian Institute of Natural Sciences, Brussels, Belgium

RNH: Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands

USNM: United States National Museum, Washington DC, USA

WAM: Western Australian Museum, Perth, Australia

ZMB: Museum für Naturkunde Berlin, Germany

ZMH: Zoologishes Museum Hamburg, Germany

DEFINITION OF *RHYTIPHORA* AND ITS SUBCLADES

Rhytiphora Audinet-Serville. Type species by monotypy *Lamia rugicollis* Dalman (Fig. S1K). Both the genus and species name (Greek and Latin, respectively) refer to the rugose pronotum.

Diagnosis

Body size small to large (6–39 mm), oval to elongate body shape (2.5–4x as long as broad). Frontoclypeus square to rectangular (Fig. 4D–E). Eyes medium to large, finely or coarsely faceted, lobes fully divided or joined by 1–3 ommatidia rows (Fig. 2A, C); upper lobes and antennal insertions usually broadly separated. Antennal scape smooth (no carina or punctures), glabrous or finely setose, straight, slender to clavate, not obviously ventrally flattened, distinctly shorter than antennomere 3, not extending far beyond anterior margin of pronotum. Antennomere 3 usually longer than antennomere 4; antennae shorter to slightly longer than elytra (longer in males), ventrally fringed.

Prothorax subquadrate to transverse, pronotal disc smooth to slightly tuberculate, lateral margin with or without small anterior tubercule. Prosternal process very narrow, rounded or angulate (Fig. 2B); procoxal cavity closed posteriorly, with lateral extension and exposed protrochantin; male procoxae usually with small to large spine (Fig. 2D). Elytra smooth to tuberculate, usually covered with short dense setae. Legs short, femurs slightly swollen, protibia usually straight, mesotibial antennal cleaner without sulcus (Fig. 2E), tarsi 5-segmented. Claws simple, narrowly divergent. Mesoventrite elevated anteriorly, with or without angulate projection; mesocoxae narrowly separated, cavities open to mesepimeron. Male abdominal ventrite 2 with small to large paired sex patches (rarely absent).

Clade 1: usually small-bodied (<15 mm; can be larger). Eyes divided (Fig. 2A), upper lobes medium sized (~1.1x as long as antennal socket). Antennae broadly separated (insertions separated by 4–6x socket width), scape slender to moderately swollen (2.5–3.5x as long as broad), ventral fringe sparse. Prosternal process and mesoventrite angulate (Fig. 2B) or sloped, male protibial tubercules absent. Sex patches small (Fig. 2F). This clade includes species formerly assigned to *Prosoplus* and *Pterolophia*.

Clade 2: usually medium- to large-bodied (>15 mm; can be smaller). Eyes usually emarginate (Fig. 2C), upper lobes small to medium sized (0.7–1.1x antennal socket). Antennae moderately separated (insertions 2–4x apart), scape moderately to significantly swollen (1.5–3x as long as broad), ventral fringe usually dense. Prosternal process and mesoventrite sloped, male protibial tubercules present or absent. Sex patches usually large (Fig. 2G). This clade includes the original *Rhytiphora* species, as well as former *Platyomopsis* Thomson and *Penthea* species.

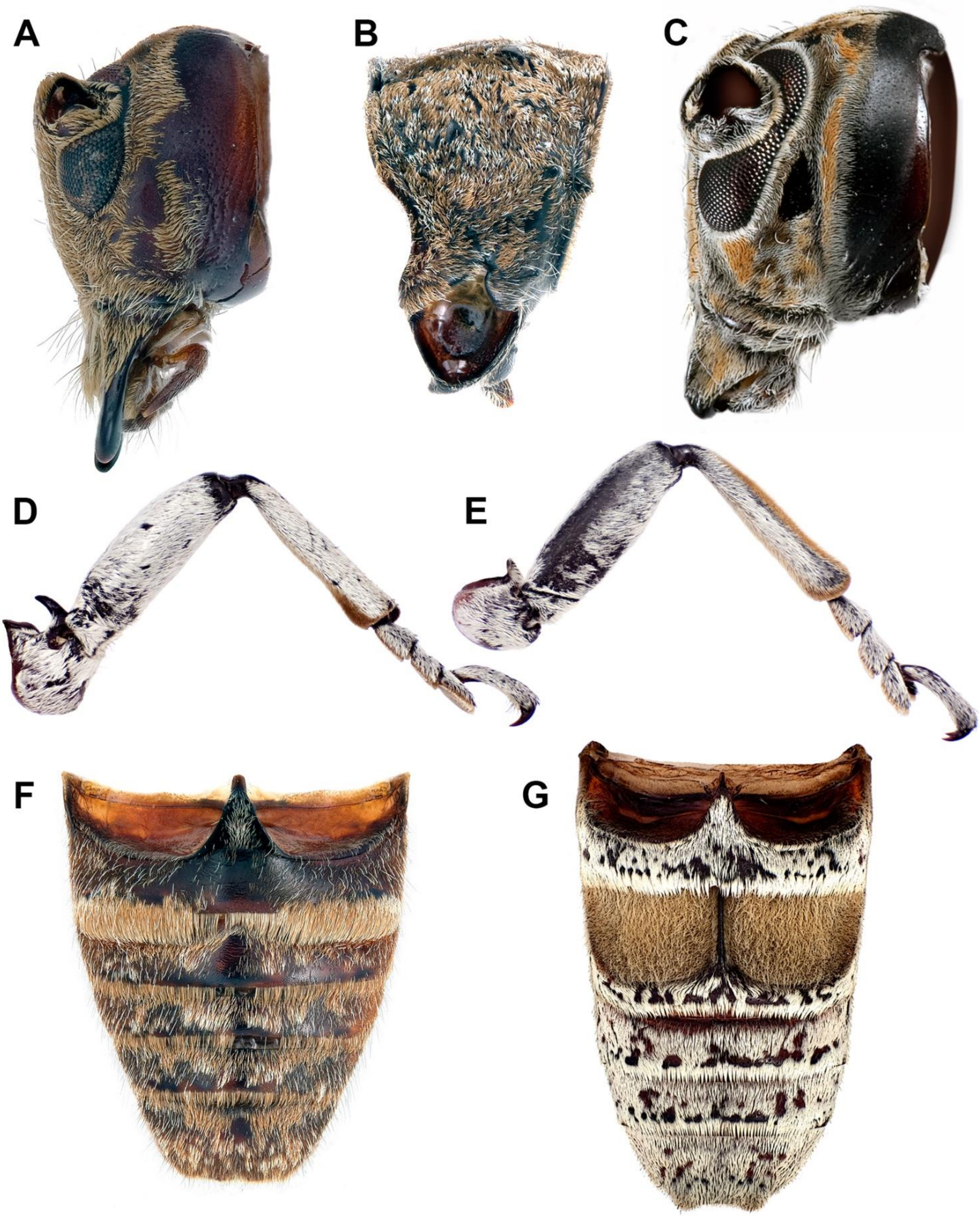

Figure 2. Representative *Rhytiphora* species, dissections. **A:** Clade 1 head, lateral. **B:** Clade 1 prothorax, lateral. **C:** Clade 2 head, lateral. **D:** foreleg. **E:** mid leg. **F:** Clade 1 male abdomen, ventral. **G:** Clade 2 male abdomen, ventral.

Remarks

The Australian *Rhytiphora* species fall into two phylogenetic clades (see Chapter 1); characteristic morphological traits are listed above. Four species contradict their clades' typical morphology (see Chapter 2): *Rhytiphora piligera* Macleay and *R. pustulosa* Pascoe in clade 1; *R. crassicollis* Pascoe and *R. fulvescens* Pascoe in clade 2. Both clades have at least one New Guinean endemic species. Clade 2 also contains a species group with punctate antennal scapes (all other *Rhytiphora* species have smooth scapes): *R. argentata* Breuning, *R. browni* McKeown, *R. dallasii* Pascoe, and *R. macleayi* Lea.

Rhytiphora is currently placed in Niphonini Pascoe, along with five other former Pteropliini genera from Australia and Southeast Asia (see Chapter 1). The other two Australian genera can be distinguished from *Rhytiphora* as follows: *Ropica* species are very small-bodied (4–7 mm) with 4-segmented tarsi and emarginate mesotibia; *Pterolophia* species are usually small-bodied with a ventrally flattened antennal scape (Ślipiński & Escalona 2013). *Niphona* Mulsant also has a ventrally flattened scape, with a male mesotibial tubercule in some species; *Callimetopus* Blanchard has a punctate and rugose scape, with a metallic cuticle in the Philippine species. *Sthenias* Dejean (at least *Sthenias pascoei* Ritsema) has an inwardly curved scape, emarginate mesotibia, and three sets of male sex patches on ventrites 2–4.

Another three former Pteropliini genera (now *incertae sedis*) are fairly closely related to Niphonini: *Desisa* Pascoe, *Egesina* Pascoe and *Similosodus* McKeown (see Chapter 1). All three can be distinguished from *Rhytiphora* by their longer scape (as long as antennomere 3); *Desisa* and *Similosodus* have a ventrally flattened scape (punctate in *Similosodus*), while *Egesina* and *Similosodus* have antennae scattered with long, sparse setae (not just the ventral side). *Egesina* also has clavate femurs and no male sex patches.

REVISION OF THE *RHYTIPHORA COLLARIS* GROUP

The species *R. collaris* Donovan belongs to a distinct group of five species with broadly separated antennae, small eyes and a curved white lateral stripe on the elytral shoulders. The group consists of: *R. garnetensis* **sp. nov.**, *R. amicula* White, *R. collaris*, *R. delicatula* McKeown and *R. piperitia* Hope. We have mitochondrial data for all of these species except *R. delicatula*, that confirm they are closely related but distinct genetic lineages (see Chapter 2). Here we redescribe the species of the *collaris* group, as well as the morphologically similar (but genetically distant) *R. argentata*.

Key to species of the collaris group

1. Clypeus short (in line with mandibular articulation), with membranous anteclypeus visible beneath; elytra with lateral white stripe usually extending from base to apex (Fig. 5E); metanepisternum usually white . . . . ***R. collaris***

– Clypeus extended beyond mandibular articulation, sometimes covering membranous anteclypeus; elytra lateral white stripe never extending beyond basal third of elytron (Fig. 5A–C); metanepisternum not white . . . . .2.

2. Prothorax with distinct transverse grooves on pronotal disc and anterior tubercule at lateral margin . . . . 3.

– Prothorax without distinct transverse grooves on pronotal disc or anterior tubercule at lateral margin . . . . 4.

3. Eyes deeply emarginate; antennal tubercules ~3.2 widths apart; antennomeres 3–7 with banded setae (Fig. 5F); elytra usually heavily mottled with dorsal dark patches (Fig. 4B; may be faded); male genitalia with parameres apically tapered, penis pointed (Fig. 6E) . . . . ***R. piperitia***

– Eyes fully divided; antennal tubercules ~3.9 widths apart; antennomeres 3–7 with plain setae (Fig. 5C); elytra lightly mottled without dorsal dark patches (Fig. 3F); male genitalia with parameres apically blunt, penis rounded (Fig. 6B) . . . . ***R. amicula***

4. Eyes fully divided, lower lobes ~3.4 widths apart; clypeus flat; antennal tubercules ~3.2 widths apart; elytral base tuberculate, heavily mottled with ochre setae (Fig. 3A); metaventrite with ochre patches above metacoxae (Fig. 3B); male genitalia with parameres apically tapered (Fig. 6A) . . . . ***R. garnetensis* sp. nov.**

– Eyes deeply emarginate, lower lobes ~4.3 widths apart; clypeus arcuate; antennal tubercules ~3.8 widths apart; elytral base granulate, lightly mottled with ochre setae (Fig. 3E); metaventrite without ochre patches; male genitalia with parameres apically blunt (Fig. 6D) . . . . ***R. delicatula***

***Rhytiphora garnetensis* sp. nov. (Figs. 3A–C, 4E, 5A, 6A)**

Description. Body small to medium-sized, elongate: body length 13.2–17.0 mm (holotype 15.0 mm), width 4.5–6.0 mm (holotype 5.1 mm). Winged. Dark brown with grey setae, ochre mottling and brown patches on elytra (Figs. 3A–C, 5A).

Head deflexed, frontoclypeus rectangular (Fig. 4E). Eyes moderately faceted, ringed with white setae (ochre on outer rim), lobes fully divided. Lower lobes separated by 3.3–3.5 times eye width, approximately same length as gena. Upper lobes separated by 2.2 times width of antennal socket, same length as antennal socket. Antennal tubercules fairly prominent, separated by 3.2 times width of antennal socket. Clypeus flat, slightly extended beyond mandibular articulation, sometimes covering membranous anteclypeus; mandibles apically pointed, maxillary and labial palps fusiform (Fig. 4E). Frontoclypeus grey with ochre mottling, gena white below eye, occipital suture with ochre outline. Antennae 11-segmented, extending slightly beyond elytral apices in male, with ventral fringe of long, dense setae on antennomeres 2–11. Scape smooth, expanding apically, 2.1 times as long as wide, 4 times longer than antennomere 2, shorter than antennomere 3, posteriorly extending a little beyond anterior margin of pronotum. Antennomere 3 longer than 4. Antennomeres covered with fine grey setae.

Prothorax subquadrate, 0.8 times as long as wide, base distinctly narrower than elytral shoulders. Lateral margins with slight anterior ridge; pronotal disc finely punctate with very shallow transverse grooves, setae grey with ochre mottling. Prosternal process narrow, arcuate. Procoxae without spiniform projection in males.

Elytra finely punctate, granulate in basal third with two distinct projections (short row of tubercules). Elytral base dark brown and heavily mottled with ochre, except for thin grey line at suture; thin, curved white line on lateral margin, not extending beyond basal third. Rest of elytra grey, lightly mottled with ochre, with brown circular patch at beginning of apical third. Elytral apices distinctly truncate.

Legs covered with fine grey setae, hind legs mottled with ochre; male protibial tubercule absent. Mesoventrite arcuate without anterior projection. Metaventrite twice as long as mesoventrite, setae mostly grey with central white and posterior ochre patches.

Abdominal ventrite 2 slightly longer than 1 in male, with broad yellow sex patches covering almost entire surface; fringe of ventrite 1 slightly thicker in male than other ventrite fringes. Ventrite 5 slightly longer than 4 in female, with sharp apical divot and endocarina.

Male genitalia: parameres narrowly separated at base, broadly separated at apices, thick, apically tapered and setose; penis tip rounded (Fig. 6A).

Types. Holotype male (Figs. 3A–B, 5A): QLD: 17.84°Sx144.95°E 25km W of Mt Garnet, 13–14 Feb 2010, J. Hasenpusch, 19663 (ANIC 25-074497). Paratypes (6 specimens): N. QLD: 38km W. Mt. Garnet, J. Hasenpusch, 3 Feb 2016 (1 female, ANIC 25-066756); Australia N Qld. 30km W Mt Garnet, 6-11-10, P. Hasenpusch (1 female in ethanol, ANIC); 11.45S 142.35E Heathlands, QLD 15–26 Jan. 1992 T. A. Weir, I. D. Naumann at light (2 males, ANIC; male genitalia dissection, Fig. 6A); 11.57S 142.38E/11.41S 142.28E QLD 22km SbyE/15km NWbyW Heathlands 27/28 Jan. 1992, A. Ewart *Melaleuca* swamp/*Eucalyptus tetradonta* forest, at light (2 males, ANIC; Figs. 3C, 4E).

Other material examined. Rockhampton, Queensland E. Sutton (1 specimen, ANIC). This specimen is damaged and so has not been made a paratype.

Distribution and host plants. Northern to central Queensland coast. Localities include: Heathlands, Mount Garnet, Rockhampton. Specific host plants are unknown, but specimens have been collected from light traps set in predominately Myrtaceae habitats.

Etymology. This species is named after its type locality: to the west of Mount Garnet (in the Tablelands Region of Queensland, Australia).

Remarks. *R. garnetensis* **sp. nov.** is most similar morphologically to *R. delicatula* and *R. pulcherrima* Breuning from Western Australia (Fig. 3D–E), but can be distinguished using the following traits: *R. delicatula* is slightly more elongate (body 3.3 times as long as wide) with smaller eyes (lower lobes 4.3 widths apart, just longer than gena, not fully divided from upper lobe), extended but arcuate clypeus, antennal tubercules slightly further apart (3.8 widths apart), no tubercules and far fewer ochre setae at the elytra base, no ochre on the metaventrite, and slightly different male genitalia (parameres apically blunt; Fig. 6D); *R.*

pulcherrima has smaller eyes (lower lobes 3.9 widths apart) joined by 1 row of ommatidia, bigger male sex patches (covering whole of enlarged ventrite 2) and different colouring: ochre occiput, central brown patch on the pronotum, elytra with lateral silver-white patch in the central third, edged with brown, and ochre patches in the apical third.

One paratype from Mt Garnet has been sequenced (ANIC 25-066756, *R. 'nr delicatula'*; Chapter 2): *R. garnetensis* **sp. nov.** is closely related to *R. collaris* (ANIC 25-066530), *R. piperitia* (ANIC 25-066534) and *R. amicula* (ANIC 25-066535, 25-066557) (Figs. 3–5). All three of these species have distinct transverse grooves on the pronotum, no ochre patch on the metaventrite and no tubercules at the elytra base; *R. piperitia* and *R. amicula* also have a tubercule at the pronotum lateral margin. *R. collaris* has a short clypeus (in line with mandibular articulation), mottled or banded antennae, striped pronotum, white metanepisternum, heavily mottled elytra with no dorsal dark patches and the lateral white stripe usually extending beyond the basal third. *R. piperitia* has banded antennae, mottled or striped pronotum, heavily mottled elytra with smaller, not ochreous dark patches at the base and diagonal white and brown patches in the apical third. *R. amicula* has smaller sex patches (covering half of male ventrite 2) and no dorsal dark patches or heavy ochre mottling on the elytra.

***Rhytiphora amicula* White (Figs. 3F, 5C, 6B)**

Rhytiphora amicula White, 1859: 122. TL: Victoria River, Northern Territory (type in BMNH, examined here)

Moved to *Rhytiphora (Setomopsis) amicula*: Breuning, 1961a: 273

Description. Body small to medium-sized, elongate: body length 14.5–28.0 mm, width 4.8–6.0 mm. Winged. Dark brown with grey setae and fine ochre mottling (Figs. 3F, 5C).

Head deflexed, frontoclypeus rectangular. Eyes moderately faceted, ringed with yellow-white setae, lobes fully divided. Lower lobes separated by 3.3–4.3 times eye width, approximately same length as gena. Upper lobes separated by 2.3 times width of antennal socket, 0.9 times as long as antennal socket. Antennal tubercules fairly prominent, separated by 3.9 times width of antennal socket. Clypeus arcuate, slightly extended beyond mandibular articulation, sometimes covering membranous anteclypeus; mandibles apically pointed, maxillary and labial palps fusiform. Frontoclypeus grey mottled with ochre, gena yellow-white below eye, occipital suture with ochre outline. Antennae 11-segmented, extending slightly beyond elytral apices in male, with ventral fringe of long, dense setae on antennomeres 2–11. Scape smooth, expanding apically, 2.3 times as long as wide, 4 times longer than antennomere 2, shorter than antennomere 3, posteriorly extending to anterior margin of pronotum. Antennomere 3 longer than 4. Antennomeres covered with fine grey setae.

Prothorax subquadrate, 0.8 times as long as wide, base distinctly narrower than elytral shoulders. Lateral margins with small anterior tubercule; pronotal disc finely punctate with transverse grooves, setae grey with fine ochre mottling. Prosternal process narrow, arcuate. Procoxae without spiniform projection in males.

Elytra finely punctate, granulate in basal third, without distinct basal projections. Elytra setae grey with fine, even ochre mottling; thin, curved white line on lateral margin with dark grey above, not extending beyond basal third. Elytral apices truncate.

Legs covered with fine grey setae; male protibial tubercule absent. Mesoventrite arcuate without anterior projection. Metaventrite twice as long as mesoventrite, setae grey with ochre mottling and central white strip.

Abdominal ventrite 2 with broad yellow-grey sex patches in male, covering half of ventrite length and mostly overlaid by thick fringe of ventrite 1. Ventrite 5 slightly longer than 4 in female, with slight apical divot and endocarina.

Male genitalia: parameres narrowly separated, thick, apically blunt and setose; penis tip rounded (Fig. 6B).

Types examined. Lectotype male, here designated: Victoria R. Depot // North Australia (BMNH).

Other material examined: 128.2555°E 15.7144°S, WA, Wyndham, The Grotto, 70m a.s.l., 3 APR 2014, MV-lamp, Cocking, Su & Zwick leg (1 specimen, ANIC 25-066535; Figs. 3F, 5C); Kununurra, WA 9 Apr. 1962, I. F. B. Common (1 specimen, ANIC; male genitalia dissection, Fig. 6B); 128.7122°E 15.6543°S, WA, Kununurra, Research Stn, 40m a.s.l., 31 MAR 2014, MV-lamp, Cocking, Su & Zwick leg (1 specimen, ANIC 25-066557); 6.4km S-SW of Victoria River Downs, NT (above Wickham River) 19 June, 1973, L. P. Kelsey (2 specimens, ANIC); 9 mi. SSE of Gordon Downs H. S./25 mi. ESE of Broome, WA 13/16 iv. 1963, L. J. Chinnick (6 specimens, ANIC).

Distribution and host plants. Western to central north coast (Western Australia and Northern Territory), potentially extending east to Queensland border. Localities include: Broome, Gordon Downs, Kununurra, Victoria River, (Musselbrook Mining Camp). Host plants unknown.

Remarks. Two specimens from WA have been sequenced (ANIC 25-066535, 25-066557; Chapter 2): *R. amicula* is closely related to *R. garnetensis* **sp. nov.** (see above), *R. piperitia* and *R. collaris*, and is also morphologically similar to *R. delicatula* (Figs. 3–5). *R. piperitia* and *R. collaris* have mottled or banded antennae (with tubercules slightly closer together: 3.2–3.3 widths apart); *R. piperitia* and *R. delicatula* have deeply emarginate eyes (not fully divided); *R. collaris* and *R. delicatula* are slightly more elongate (body 3.3–3.4 times as long as wide). *R. piperitia* usually has heavily mottled elytra with dorsal dark patches, but when specimens are faded it can be difficult to distinguish this species from *R. amicula*; in these cases, the male genitalia may be helpful (*R. piperitia* has apically tapered parameres and a pointed penis; Fig. 6E). *R. collaris* has a short clypeus (in line with mandibular articulation), striped pronotum, white metanepisternum, dark elytra with heavy ochre mottling and the lateral white stripe usually extending beyond the basal third, and larger sex patches (covering almost whole ventrite). *R. delicatula* has no distinct grooves on the pronotum and brown-mottled elytra with dorsal dark patches.

Rhytiphora collaris (Donovan) (Figs. 4A, 5E, 6C)

Saperda collaris Donovan, 1805: plate 5. TL: "New South Wales" (type not found)

Symphyletes vestigialis Pascoe, 1864a: 226. TL: South Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Platyomopsis) vestigialis*: Breuning, 1961a: 275

Saperda albocincta Guérin-Méneville, 1831: 137. TL: Port Jackson, New South Wales (type not found). **New synonym**

Rhytiphora donovani Newman, 1851: 129. TL: "New Holland" (type not found). **New synonym**

Symphyletes compos Blackburn, 1902: 319. TL: Hughenden, Queensland (type in BMNH, examined here). **New synonym**

Rhytiphora maculosella Blackburn, 1902: 320. TL: Queensland (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora (Platyomopsis) albocincta*: Breuning, 1961a: 275

Rhytiphora intertincta Pascoe, 1867: 302. TL: Gawler, South Australia (type in BMNH, examined by Ślipiński & Escalona 2013). **New synonym**

Moved to *Rhytiphora (Rhytiphora) intertincta*: Breuning, 1961a: 272

Rhytiphora (Saperdopsis) parafarinosa Breuning, 1970a: 375. TL: Dawson District, Queensland (type in MNHN, examined here). **New synonym**

Rhytiphora (Setomopsis) vermiculosa Breuning, 1970b: 471. TL: Queensland (type in MNHN, examined here). **New synonym**

Description. Body small to medium-sized, elongate: body length 10.0–19.0 mm, width 3.0–6.0 mm. Winged. Dark brown-black with ochre setae (striped pronotum, mottled elytra) and lateral white stripe on elytra (Figs. 4A, 5E).

Head deflexed, frontoclypeus rectangular. Eyes moderately faceted, ringed with ochre setae, lobes fully divided. Lower lobes separated by 3.7–4.7 times eye width, approximately same length as gena. Upper lobes separated by 2.2 times width of antennal socket, 1.2 times as long as antennal socket. Antennal tubercules fairly prominent, separated by 3.3 times width of antennal socket. Clypeus flat, short (in line with mandibular articulation), with membranous anteclypeus visible beneath; mandibles apically slightly pointed, maxillary and labial palps fusiform. Frontoclypeus ochre, occipital suture with ochre outline. Antennae 11-segmented, extending slightly beyond elytral apices in male, with ventral fringe of long, dense setae on antennomeres 2–11. Scape smooth, gradually expanding apically, 2.5 times as long as wide, 4 times longer than antennomere 2, shorter than antennomere 3, posteriorly extending a little beyond anterior margin of pronotum. Antennomere 3 longer than 4. Antennomeres usually mottled with grey-white setae (sometimes forming distinct bands).

Prothorax subquadrate, 0.8 times as long as wide, base distinctly narrower than elytral shoulders. Lateral margins with distinct anterior ridge; pronotal disc finely punctate with transverse grooves, setae ochre and usually forming distinct transverse stripes. Prosternal process narrow, arcuate. Procoxae sometimes with small spiniform projection in males.

Elytra finely punctate, granulate in basal and central thirds, without distinct basal projections. Elytra dark, heavily mottled with yellow-ochre setae; thin, curved white line on lateral margin, usually extending beyond basal third (either as complete, unbroken line to apices or interrupted by ochre mottling). Elytral apices slightly truncate.

Legs mottled with ochre setae; male protibial tubercule absent. Mesoventrite arcuate without anterior projection. Metaventrite twice as long as mesoventrite, metanepisternum and adjacent metaventrite usually white, rest of metaventrite mottled ochre.

Abdominal ventrite 2 with broad yellow-brown sex patches in male, covering almost entire surface; fringe of ventrite 1 slightly thicker in male than other ventrite fringes. Ventrite 5 slightly longer than 4 in female, with slight apical divot and endocarina.

Male genitalia: parameres narrowly separated at base, touching at apices, thick, apically blunt and setose; penis tip with slight projection (Fig. 6C).

Types examined. Lectotype male, here designated (*Symphyletes vestigialis*): South Australia J. Odewahn (BMNH). Lectotype male, here designated (*Symphyletes compos*): Hughenden, N. Queensland C. French (BMNH). Lectotype female, here designated (*Rhytiphora maculosella*): Queensland (BMNH). Holotype female (*Rhytiphora parafarinosa*): Dawson distr. (Barnard coll.) (MNHN). Holotype female (*Rhytiphora vermiculosa*): Queensland (MNHN).

Other material examined: 35.30S 150.24E Bawley Point, NSW 8.1.94, D. C. F. Rentz, K. McCarron (1 specimen, ANIC 25-067050; Figs. 4A, 5E); Waterfall NSW 8/82 S. Watkins // S. G. Watkins Collection Donated 2001 (1 specimen, ANIC; male genitalia dissection, Fig. 6C); 3.9km Nth. Harrington E Taree NSW 29.XII.93 Acacia // S. G. Watkins Collection Donated 2001 (1 specimen, ANIC); 18-1-15 Cairns N. Q., J. Hasenpusch (1 specimen, ANIC 25-066530).

Distribution and host plants. Mesic east coast from Queensland down to South Australia. Localities include: Cairns, Hughenden, Rockhampton, Brisbane, Taree, Sydney, Canberra, Wyperfeld, Gawler. This species has been collected from *Acacia*, *Allocasuarina*, *Angophora* and *Casuarina* trees, as well as *Dodonaea*, *Rosa* and *Viminaria* shrubs.

Remarks. One specimen from Cairns has been sequenced (ANIC 25-066530, *R. albocincta*; Chapter 2): *R. collaris* is closely related to *R. garnetensis* **sp. nov.** (see above), *R. piperitia* and *R. amicula*, and is also morphologically similar to *R. delicatula* (Figs. 3–5). The latter three species have a clypeus extended beyond the mandibular articulation, grey mottled metanepisternum and elytra with the lateral white stripe never extending beyond the basal third. *R. piperitia* and *R. amicula* are also slightly less elongate (body 3.0–3.1 times as long as wide); *R. piperitia* and *R. delicatula* have deeply emarginate eyes (not fully divided); *R. amicula* and *R. delicatula* have plain grey antennae (with tubercules slightly further apart: 3.8–3.9 widths apart) and no transverse stripes on the pronotum. *R. piperitia* has banded antennae and dorsal dark patches on the elytra. *R. amicula* has grey elytra with fine ochre mottling, and smaller sex patches (covering only half of ventrite 2). *R. delicatula* has no distinct grooves on the pronotum and pale grey elytra with dorsal dark patches.

***Rhytiphora delicatula* (McKeown) (Figs. 3E, 5B, 6D)**

Rhytiphora uniformis Blackburn, 1901: 40. TL: "N. W. Australia" (type in BMNH, examined here). Junior secondary homonym of *Aegomomus uniformis* (Pascoe, 1864)

Rhytiphora blackburni Tavakilian & Nearns, 2014a: 106. Replacement name for *R. uniformis* (Blackburn, 1901)

Platyomopsis delicatula McKeown, 1948: 60. TL: Carnarvon, Western Australia (type in AM, examined by Ślipiński & Escalona 2013). **New synonym**

Moved to *Rhytiphora (Setomopsis) delicatula*: Breuning, 1961a: 273

Description. Body small to medium-sized, elongate: body length 15.0–17.0 mm, width 4.4–5.1 mm. Winged. Dark brown with pale grey setae, slight ochre mottling and distinct brown patches on elytra (Figs. 3E, 5B).

Head deflexed, frontoclypeus rectangular. Eyes moderately faceted, ringed with white setae, deeply emarginate, lobes connected by 1 row ommatidia. Lower lobes separated by 4.3–4.4 times eye width, slightly longer than gena (gena 0.8–0.9 times as long as lower lobe). Upper lobes separated by 2.3 times width of antennal socket, 0.9 times as long as antennal socket. Antennal tubercules fairly prominent, separated by 3.8 times width of antennal socket. Clypeus arcuate, slightly extended beyond mandibular articulation, sometimes covering membranous anteclypeus; mandibles apically pointed, maxillary and labial palps fusiform. Frontoclypeus grey-white, sometimes mottled with ochre. Antennae 11-segmented, extending slightly beyond elytral apices in male, with ventral fringe of long, dense setae on antennomeres 2–11. Scape smooth, expanding apically, 2.3 times as long as wide, 4 times longer than antennomere 2, shorter than antennomere 3, posteriorly extending to anterior margin of pronotum. Antennomere 3 longer than 4. Antennomeres covered with fine grey setae.

Prothorax subquadrate, 0.8 times as long as wide, base distinctly narrower than elytral shoulders. Lateral margins with distinct anterior ridge; pronotal disc finely punctate with no distinct grooves or granules, setae pale grey with slight ochre mottling. Prosternal process narrow, arcuate. Procoxae without spiniform projection in males.

Elytra finely punctate, granulate in basal third, without distinct basal projections. Elytral shoulders each with large brown patch; thin, curved white line on lateral margin, not extending beyond basal third. Rest of elytra pale grey, lightly mottled with ochre and brown, with small brown patch at beginning of apical third. Elytral apices truncate.

Legs covered with fine grey setae; male protibial tubercule absent. Mesoventrite arcuate without anterior projection. Metaventrite twice as long as mesoventrite, setae pale grey with central white strip.

Abdominal ventrite 2 with broad yellow-brown sex patches in male, covering majority of ventrite length; fringe of ventrite 1 slightly thicker in male than other ventrite fringes. Ventrite 5 slightly longer than 4 in female, with slight apical divot and endocarina.

Male genitalia: parameres narrowly separated at base, thick, apically blunt and setose; penis tip rounded (Fig. 6D).

Types examined. Lectotype female, here designated (*Rhytiphora uniformis*): N. W. Australia (BMNH). Holotype male (*Platyomopsis delicatula*): Carnarvon, N. W. Australia H. W. Brown (AM).

Other material examined: Marloo Stn. Wurarga, WA 1931–1941, A. Goerling (2 specimens, ANIC 25-061931; Figs. 3E, 5B, 6D).

Distribution and host plants. Western Australia. Localities include: Carnarvon, Wurarga. Host plants for this species are unknown.

Remarks. This species has not been sequenced, but it is morphologically similar to *R. garnetensis* **sp. nov.** (see above), *R. piperitia*, *R. amicula* and *R. collaris* (Figs. 3–5). The latter three species have distinct transverse grooves on the pronotum; *R. piperitia* and *R. collaris* also have mottled or banded antennae (with tubercules slightly closer together: 3.2–3.3 widths apart), and *R. amicula* and *R. collaris* have fully divided eyes. *R. piperitia* has larger eyes (lower lobes 3.5–3.7 widths apart) and different colouring (heavily mottled ochre and brown, with diagonal white and brown patches in the apical third of the elytra). *R. amicula* is slightly less elongate (body 3.0 times as long as wide) with no dorsal dark patches or brown mottling on the elytra. *R. collaris* has a short clypeus (in line with mandibular articulation), striped pronotum, white metanepisternum, heavily mottled elytra with no dorsal dark patches and the lateral white stripe usually extending beyond the basal third.

***Rhytiphora piperitia* Hope (Figs. 4B, 5F, 6E)**

Rhytiphora piperitia Hope, 1842: 429. TL: Port Essington, Northern Territory (type in OUMNH, examined here)

Symphyletes humeralis White, 1858: 269. TL: Port Essington, Northern Territory (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Setomopsis) piperitia*: Breuning, 1961a: 272

Rhytiphora truncata Breuning, 1940: 424. TL: Duringo, Queensland (type in USNM, examined by Lingafelter *et al.* 2014). Junior secondary homonym of *Aegomomus truncatus* (Pascoe, 1864). **New synonym**

Rhytiphora truncatoides Tavakilian & Nearns, 2014a: 106. Replacement name for *R. truncata* (Breuning, 1940)

Description. Body small to medium-sized, elongate: body length 12.0–23.0 mm, width 3.9–7.4 mm. Winged. Dark brown with grey setae, heavily mottled ochre and brown, elytra with brown dorsal patches (Figs. 4B, 5F).

Head deflexed, frontoclypeus rectangular. Eyes moderately faceted, ringed with yellow-white setae, lobes connected by 1 row ommatidia. Lower lobes separated by 3.5–3.7 times eye width, approximately same length as gena. Upper lobes separated by 2.3 times width of antennal socket, 1.0 times as long as antennal socket. Antennal tubercules fairly prominent, separated by 3.2 times width of antennal socket. Clypeus flat or arcuate, extended beyond mandibular articulation, usually covering membranous anteclypeus; mandibles apically slightly pointed, maxillary and labial palps fusiform. Frontoclypeus yellow, occipital suture with yellow outline. Antennae 11-segmented, extending slightly beyond elytral apices in male, with ventral fringe of long, dense setae on antennomeres 2–11. Scape smooth, expanding apically, 2.3 times as long as wide, 4 times longer than antennomere 2, shorter than antennomere 3, posteriorly extending to anterior margin of pronotum. Antennomere 3 longer than 4. Antennomeres 3–7 distinctly banded with grey-white setae (apical quarter of antennomeres glabrous).

Prothorax subquadrate, 0.8 times as long as wide, base distinctly narrower than elytral shoulders. Lateral margins with small anterior tubercule; pronotal disc finely punctate with transverse grooves, setae grey with ochre and brown mottling. Prosternal process narrow, arcuate. Procoxae without spiniform projection in males.

Elytra finely punctate, granulate in basal and central thirds, without distinct basal projections. Elytral shoulders each with large brown patch; thin, curved white line on lateral margin, not extending beyond basal third. Rest of elytra grey, heavily mottled ochre and brown, usually with diagonal white and brown patch at beginning of apical third. Elytral apices distinctly truncate.

Legs grey, mottled with ochre and brown; male protibial tubercule absent. Mesoventrite arcuate without anterior projection. Metaventrite twice as long as mesoventrite, setae grey with ochre mottling and central white strip.

Abdominal ventrite 2 with broad yellow sex patches in male, covering majority of ventrite length; fringe of ventrite 1 slightly thicker in male than other ventrite fringes. Ventrite 5 slightly longer than 4 in female, with slight apical divot and endocarina.

Male genitalia: parameres narrowly separated at base, thick, apically tapered and setose; penis tip with slight projection (Fig. 6E).

Types examined. Lectotype female, here designated (*Rhytiphora piperitia*): Port Essington (OUMNH; Fig. S1F). Lectotype, here designated (*Symphyletes humeralis*): Port Essington (BMNH).

Other material examined: 11.50S, 142.30E Bertie Creek, 12km SW of Heathlands, Qld, 13 Mar. 1992, D. C. F. Rentz, Stop 6 (1 specimen, ANIC 25-058414; Figs. 4B, 5F); CSIRO Entomology NT. Tony Ahern's 12°40'42.1"s 131°21'43.8"e 13 Nov. 1998 M. Hoskins // Adelaide River Floodplains ex. *Mimosa pigra* pupa 23 Nov.- em 14 Dec. 1998 (1 specimen, ANIC; male genitalia dissection, Fig. 6E); Lee Point, Darwin, NT 8 Mar 1967, M. S. Upton (1 specimen, ANIC); 12°11'S; 131°0'E (GPS) NT: Gunn Point Rd, nr Howard Springs Nat. Res., 7 March 1999, D. C. F. Rentz, Stop 36 (1 specimen, ANIC); 128.0232°E 16.0135°S WA, El Questro, Zebedee Springs carpark, 150m a.s.l., 5 APR 2014, MV-lamp. Cocking, Su & Zwick leg (1 specimen, ANIC 25-066534).

Distribution and host plants. North coast (Western Australia, Northern Territory and Queensland). Localities include: Kununurra, Cobourg Peninsula, Borroloola, Cape York, Cairns, Rockhampton. This species has been collected from *Acacia*, *Bauhinia*, *Casuarina* and *Peltophorum* trees, as well as the weed *Mimosa pigra*.

Remarks. One specimen from the Kimberley has been sequenced (ANIC 25-066534; Chapter 2): *R. piperitia* is closely related to *R. garnetensis* **sp. nov.** (see above), *R. collaris* and *R. amicula*, and is also morphologically similar to *R. delicatula* (Figs. 3–5). *R. collaris* and *R. amicula* have fully divided eyes; *R. amicula* and *R. delicatula* have plain grey antennae (with tubercules slightly further apart: 3.8–3.9 widths apart). *R. collaris* has a short clypeus (in line with mandibular articulation), usually mottled antennae, white metanepisternum, elytra with no dorsal dark patches and the lateral white stripe usually extending beyond the basal third. *R. amicula* has grey elytra with fine ochre mottling and no dorsal dark patches, but when *R. piperitia* specimens are faded (i.e. no distinct markings on elytra) it can be difficult to tell these species apart; in these cases, the male genitalia may be helpful (*R. amicula* has apically blunt parameres and a rounded penis; Fig. 6B). *R. delicatula* has smaller eyes (lower lobes 4.3–4.4 widths apart), no distinct grooves on the pronotum, and pale grey, lightly mottled elytra with small circular brown patches in the apical third.

Rhytiphora argentata **Breuning (Figs. 4C–D, 5D, 6F)**

Rhytiphora (Rhytiphora) argentata Breuning, 1938a: 95. TL: Wurarga, Western Australia (neotype in ANIC, examined here)

Description. Body small to medium-sized, elongate: body length 12.0–21.2 mm (neotype 14.5 mm), width 3.8–6.4 mm (neotype 4.2 mm). Winged. Dark brown with silver-white setae, forming longitudinal stripes and stippling on elytra (Figs. 4C, 5D).

Head deflexed, frontoclypeus square, eyes slanted (Fig. 4D). Eyes moderately faceted, ringed with white setae, deeply emarginate, lobes connected by 2 rows ommatidia. Lower lobes separated by 2.6–3.4 times eye width, slightly longer than gena (gena 0.8–0.9 times as long as lower lobe). Upper lobes separated by 1.6 times width of antennal socket, same length as antennal socket. Antennal tubercules fairly prominent, separated by 3.2 times width of antennal socket. Clypeus arcuate with membranous anteclypeus visible beneath, mandibles apically obtuse, maxillary and labial palps blunt (Fig. 4D). Frontoclypeus yellow-white (setae often rubbed off), gena white, occipital suture with faint white outline. Antennae 11-segmented, extending slightly beyond elytral apices in male, with ventral fringe of long, dense setae on antennomeres 2–11. Scape coarsely punctate, gradually expanding apically, 2.5 times as long as wide, 4 times longer than antennomere 2, shorter than antennomere 3, posteriorly extending a little beyond anterior margin of pronotum. Antennomere 3 longer than 4. Antennomeres 3–11 covered with fine setae, white (3–5) darkening to tan (6–11).

Prothorax subquadrate, 0.8 times as long as wide, base distinctly narrower than elytral shoulders. Lateral margins without tubercules; pronotal disc finely punctate with shallow transverse grooves and two small median granules, mottled with fine silver-white setae. Prosternal process narrow, arcuate. Procoxae without spiniform projection in males.

Elytra finely punctate, granulate in basal and central thirds, without distinct basal projections. Silver-white setae forming thin and thick longitudinal stripes along elytral suture and lateral margins respectively, interrupted by granules; dark brown surface exposed between longitudinal stripes, mottled with silver-white spots usually forming longitudinal rows. In some specimens the dorsal setae on pronotum and elytra are faded to yellow. Elytral apices slightly truncate.

Legs covered with fine white setae; male protibial tubercule absent. Mesoventrite arcuate without anterior projection. Metaventrite twice as long as mesoventrite with central strip of dense silver-white setae.

Abdominal ventrite 2 with broad yellow sex patches in male, covering majority of ventrite length; fringe of ventrite 1 slightly thicker in male than other ventrite fringes. Ventrite 5 slightly longer than 4 in female, with slight apical divot and endocarina.

Male genitalia: parameres thick, apically blunt and setose; penis tip with slight projection (Fig. 6F).

Types. Neotype male (Figs. 4C–D, 5D): Marloo Stn. Wurarga, WA 1931–1941, A. Goerling (here designated; ANIC 25-061934).

Other material examined: Marloo Stn. Wurarga, WA 1931–1941, A. Goerling (6 specimens, ANIC; male genitalia dissection, Fig. 6F); WA: 25km N. Kumarina 10 Mar 2015 MV Light P. M. Hutchinson (2 specimens in ethanol, ANIC 25-073818); 20.22S, 134.14E 30km N. of Wauchope, NT 132.x.72, M. S. Upton (2 specimens, ANIC); 63km N. of Wubin, WA 26. Jan. 1999, P. Hutchinson // *Rhytiphora* on *Acacia* stem (1 specimen, PHIC); Die Hardy Ra. West. Aust. 2. Feb. 2000 P. Hutchinson // *Rhytiphora* to light (1 specimen, PHIC); L. Monger West. Aust. 8. Jan. 2002 P. Hutchinson // to light (1 specimen, PHIC); 45km E. of Yalgoo W. Aust. 4. Mar. 2008, P. Hutchinson // *Platyomopsis* on *Acacia* (1 specimen, PHIC); Australia: N. WA Newman, Dec 24, 1975, E. Exley & R. Storey on *Eucal.* // ex UQIC Collection (1 specimen, QM); Cue/ Southern Cross/Carnavon/Dedari/Geraldton WA H. W. Brown (12 specimens, AM); WA: 25km E of Sandstone 17 Jan. 1989, M. S. & B. J. Moulds (17 specimens, AM); W. Australien Marloo Station Wurarga XI–XII 1934/II 1935, Gebr./A Goerling S. G. (2 specimens, RBI). The specimens from Wauchope, Newman and Sandstone are of a different colour to the rest (dorsal setae yellow-orange).

Distribution and host plants. Southwest to central Western Australia, potentially extending into southern Northern Territory. Localities include: Perth, Southern Cross, Wubin, Die Hardy Range, Geraldton, Wurarga, Cue, Kumarina, Newman, (Wauchope). This species has been collected from *Acacia* and *Eucalyptus* trees.

Remarks. The original type of *R. argentata* was unable to be found in Prague (NMP) and has presumably been lost. Breuning's description (1938a, 1963b with corrected measurements) matches the above specimens in all characters except for antennal length (described as much shorter than the body in the female holotype, while all female specimens we examined had antennae the same length as the body). However, given that the *R. argentata* description mentions the punctate scape (rare in *Rhytiphora*) and the distinctive elytral colour pattern, we have used the above specimens to redescribe *R. argentata* rather than create a new species.

One specimen from Kumarina has been sequenced (ANIC 25-073818, *R. 'sp silver'*; Chapters 1 & 2), and is closely related to the *dallasii* group (*R. dallasii, R. browni* and *R. macleayi*). *R. argentata* can be easily distinguished from these species by its smaller body size and different colour pattern: the *R. dallasii* group all have broad black and silver stripes and banded antennae (Figs. 1G, S1C). Morphologically, *R. argentata* is more similar to the *collaris* group, particularly *R. piperitia* (Figs. 4B, 5F); it can be distinguished from these species by its larger eyes, punctate scape and thick silver-white lateral stripe on the elytra (present even in the yellower, faded specimens).

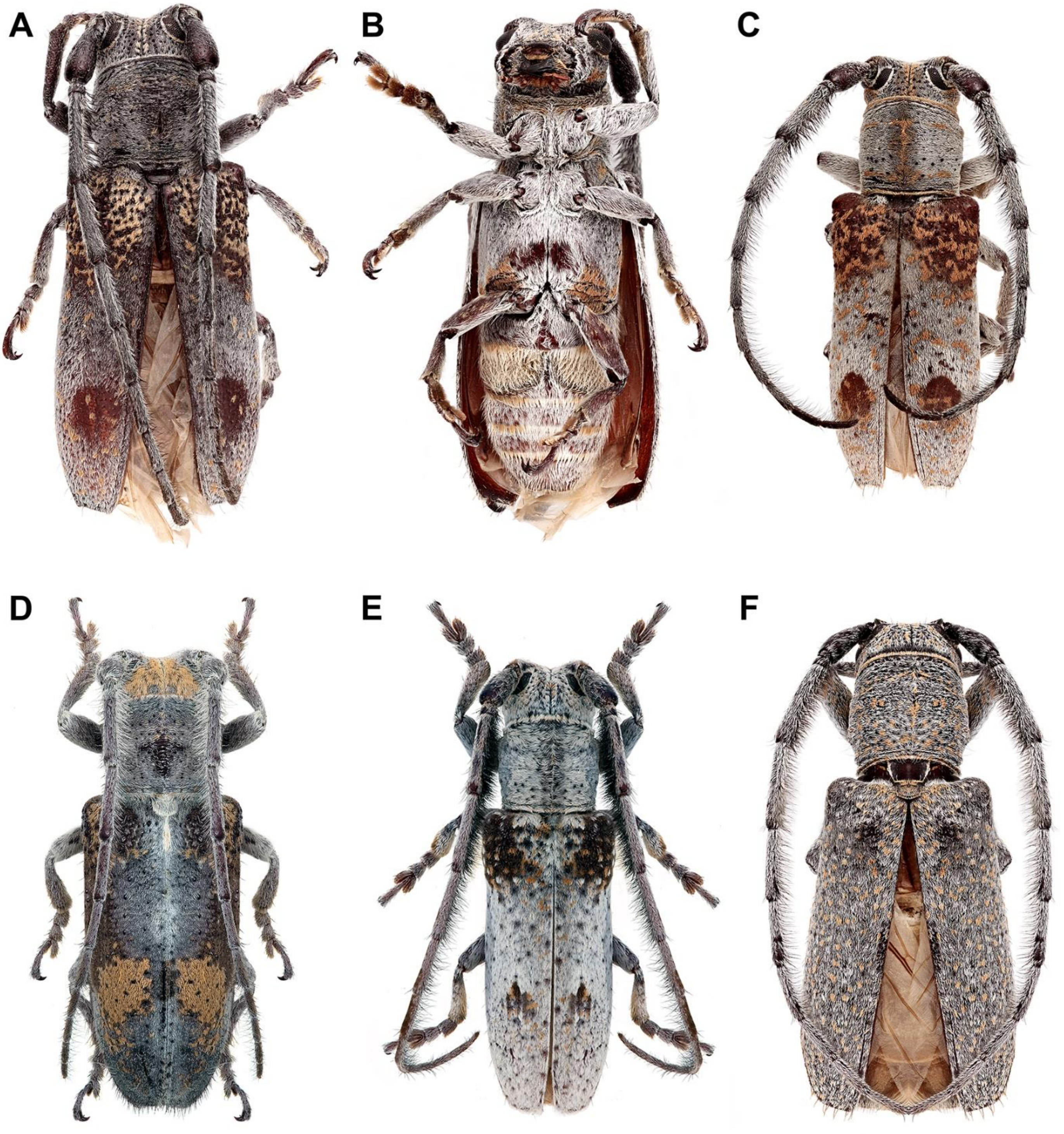

Figure 3. *Rhytiphora* species, dorsal and ventral. **A–B:** *Rhytiphora garnetensis* **sp. nov.** holotype (ANIC 25-074497). **C:** *Rhytiphora garnetensis* **sp. nov.** paratype. **D:** *Rhytiphora pulcherrima*. **E:** *Rhytiphora delicatula* (ANIC 25-061931). **F:** *Rhytiphora amicula* (ANIC 25-066535).

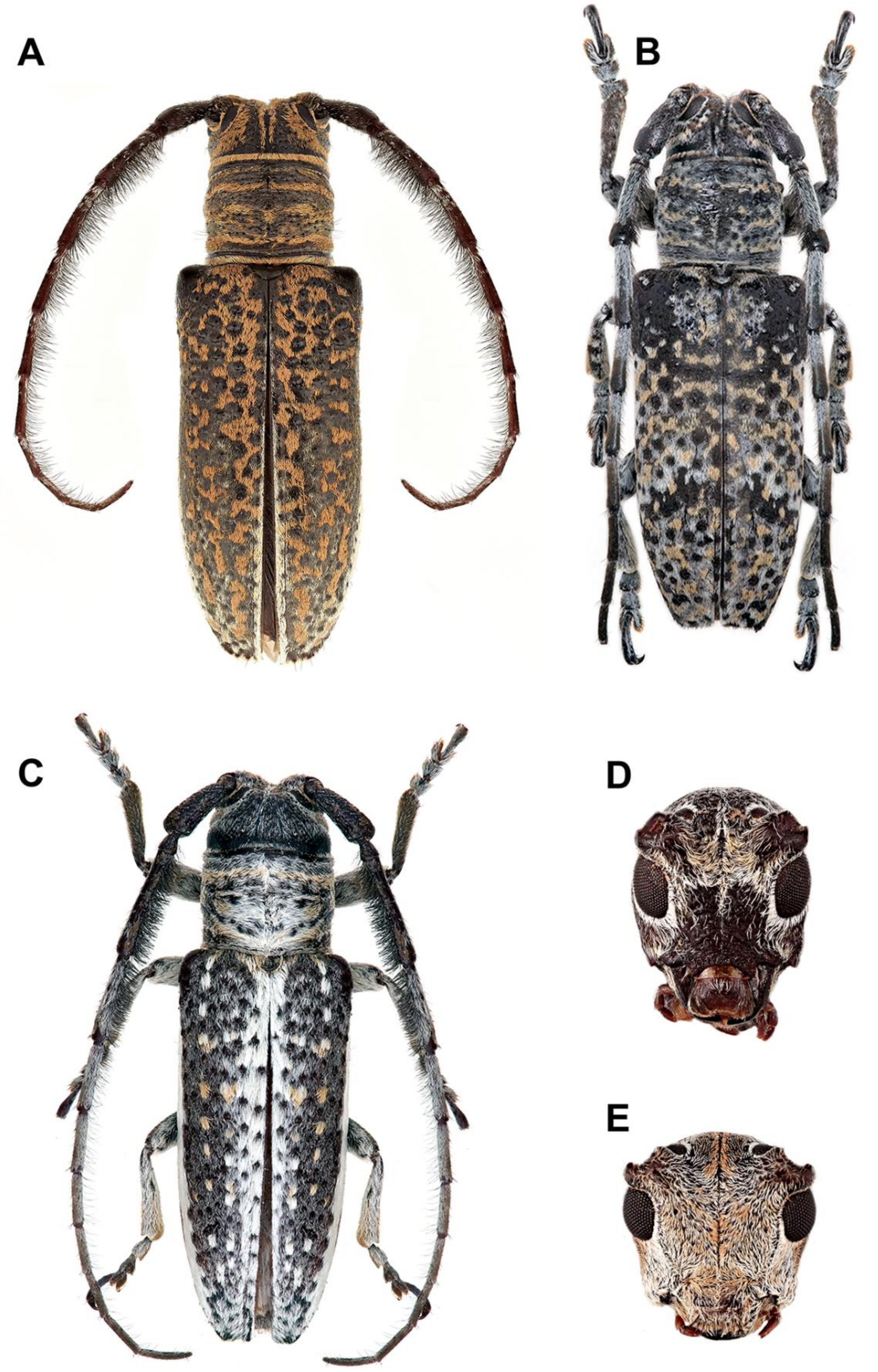

Figure 4. *Rhytiphora* species, dorsal and frontal (head only). **A:** *Rhytiphora collaris* (ANIC 25-067050). **B:** *Rhytiphora piperitia* (ANIC 25-058414). **C–D:** *Rhytiphora argentata* neotype (ANIC25-061934). **E:** *Rhytiphora garnetensis* **sp. nov.** paratype.

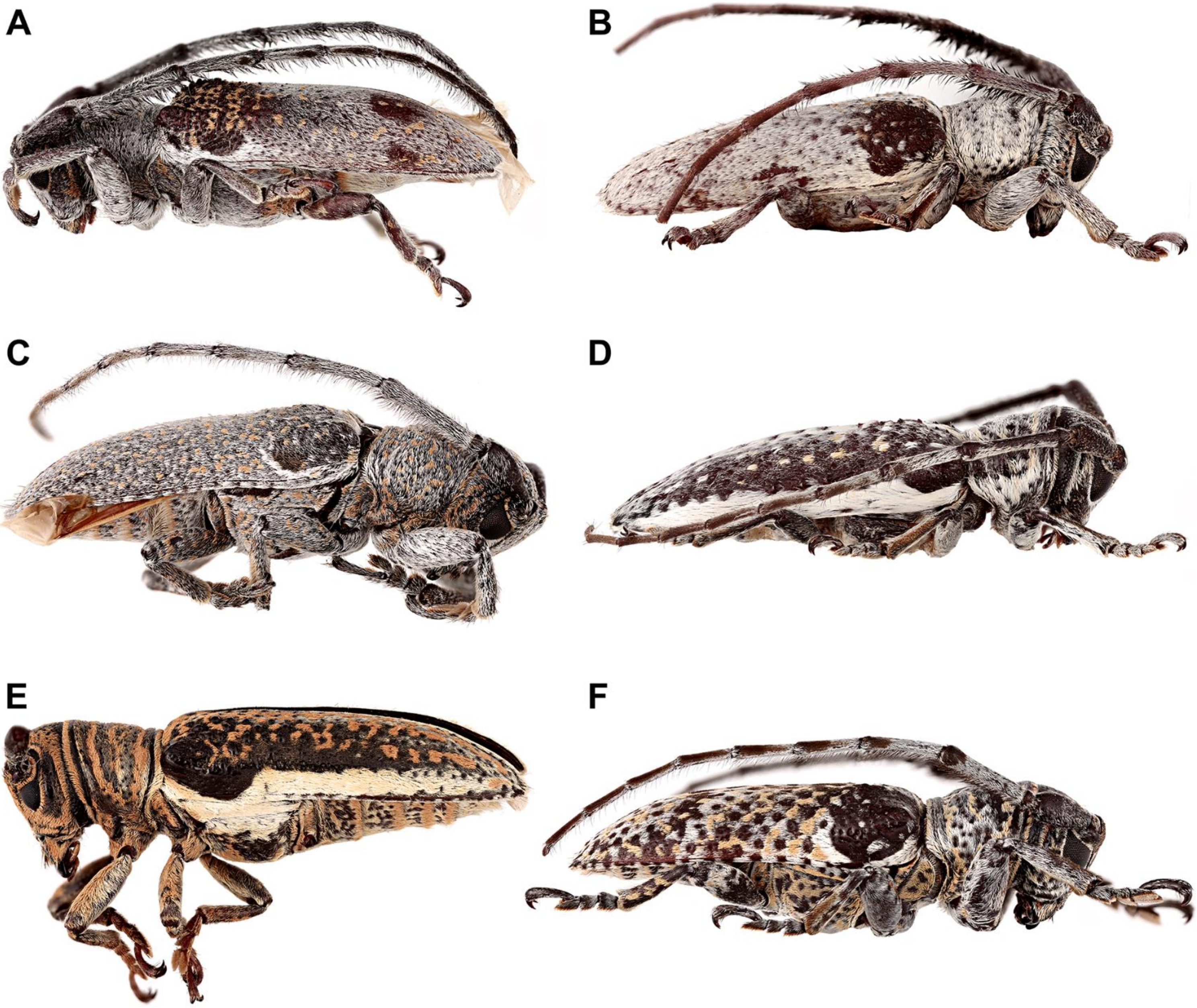

Figure 5. *Rhytiphora* species, lateral. **A:** *Rhytiphora garnetensis* **sp. nov.** holotype (ANIC 25-074497). **B:** *Rhytiphora delicatula* (ANIC 25-061931). **C:** *Rhytiphora amicula* (ANIC 25-066535). **D:** *Rhytiphora argentata* neotype (ANIC25-061934). **E:** *Rhytiphora collaris* (ANIC 25-067050). **F:** *Rhytiphora piperitia* (ANIC 25-058414).

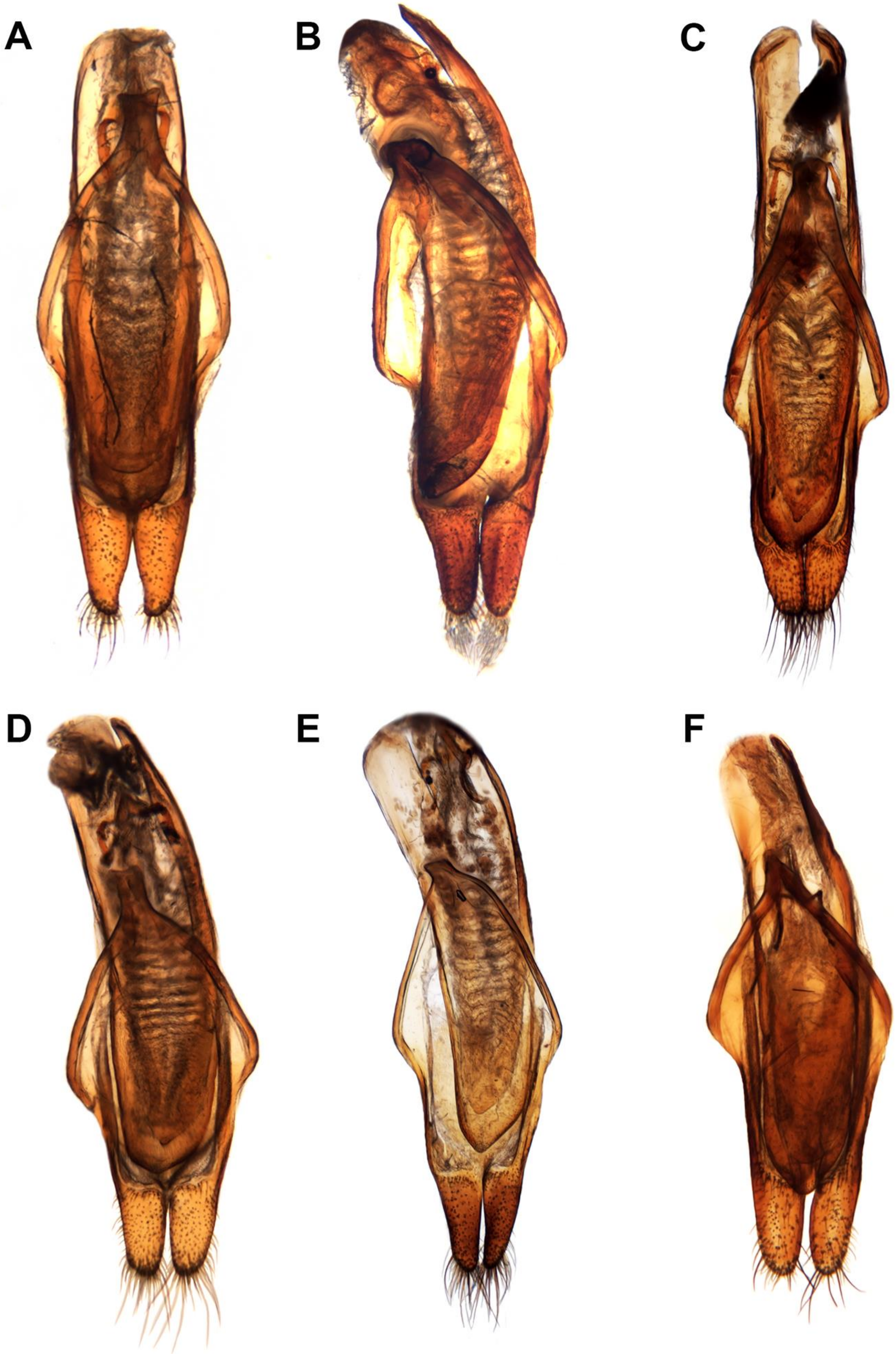

Figure 6. *Rhytiphora* species, male genitalia (penis and tegmen). **A:** *Rhytiphora garnetensis* **sp. nov.** paratype. **B:** *Rhytiphora amicula*. **C:** *Rhytiphora collaris*. **D:** *Rhytiphora delicatula* (ANIC 25-061931). **E:** *Rhytiphora piperitia*. **F:** *Rhytiphora argentata*.

LIST OF AUSTRALIAN *RHYTIPHORA*

Species marked with an asterisk (*) require DNA confirmation: see Discussion.

albicollis (Breuning)

Saperdopsis albicollis Breuning, 1938c: 362. TL: Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) albicollis*: Breuning, 1961a: 273

Distribution: WA

Host plants: unknown

albolateralis (Breuning)

Saperdopsis albolateralis Breuning, 1938c: 363. TL: Cooktown, Queensland (type not found)

Moved to *Rhytiphora (Saperdopsis) albolateralis*: Breuning, 1961a: 274

Distribution: QLD

Host plants: unknown

albospilota Aurivillius

Rhytiphora albospilota Aurivillius, 1893: 168. TL: Queensland (type in NRM, examined by Ślipiński & Escalona 2013)

Rhytiphora leucospila Gahan, 1893: 195. TL: Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Rhytiphora) albospilota*: Breuning, 1961a: 272

Distribution (uncertain): QLD, NSW, (VIC)

Host plants: *Eucalyptus coolabah, E. pilularis*

amicula White

Rhytiphora amicula White, 1859: 122. TL: Victoria River, Northern Territory (type in BMNH, examined here)

Moved to *Rhytiphora (Setomopsis) amicula*: Breuning, 1961a: 273

Distribution: WA, NT

Host plants: unknown

antennalis Breuning

Rhytiphora antennalis Breuning, 1938c: 366. TL: Mulgrave River, Queensland (type in ZMH, not examined)

Moved to *Rhytiphora (Rhytiphora) antennalis*: Breuning, 1961a: 272

Distribution: QLD

Host plants: unknown

apiculata (Aurivillius)

Platyomopsis apiculata Aurivillius, 1916: 353. TL: “Australia” (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora apiculata*: Ślipiński & Escalona, 2013: 200

Distribution: QLD

Host plants: unknown

argentata Breuning

Rhytiphora (Rhytiphora) argentata Breuning, 1938a: 95. TL: Wurarga, Western Australia (neotype in ANIC, examined here)

Distribution (uncertain): WA, (NT)

Host plants: *Acacia* sp.; *Eucalyptus* sp.

argenteolateralis McKeown

Rhytiphora argenteolateralis McKeown, 1948: 61. TL: Southern Cross, Western Australia (type in AM, examined here)

Moved to *Rhytiphora (Rhytiphora) argenteolateralis*: Breuning, 1961a: 272

Distribution: WA

Host plants: unknown

argus Pascoe*

Rhytiphora argus Pascoe, 1867: 302. TL: Rockhampton, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) argus*: Breuning, 1961a: 274

Distribution: QLD

Host plants: *Eucalyptus* sp.

armatula (White)*

Symphyletes armatulus White, 1859: 122. TL: “Northern Australia” (type in BMNH, examined here)

Moved to *Rhyitphora (Platyomopsis) armatula*: Breuning, 1961a: 275

Distribution: QLD, NT, WA

Host plants: *Melaleuca dealbata, M. viridiflora*

bakewelli (Pascoe)

Niphona bakewelli Pascoe, 1859: 38. TL: Moreton Bay, Queensland (type in BMNH, examined here)

Moved to *Rhytiphora bakewelli*: Ślipiński & Escalona, 2013: 201

Prosoplus mediofasciatus Breuning, 1938c: 358. TL: New South Wales (type in NRM, examined by Ślipiński & Escalona 2013). **New synonym**

Moved to *Rhytiphora mediofasciata*: Ślipiński & Escalona, 2013: 206

Prosoplus (Prosoplus) laterinigricollis Breuning, 1961d: 14. TL: “Australia” (type in MHNL, not examined). **New synonym**

Moved to *Rhytiphora laterinigricollis*: Ślipiński & Escalona, 2013: 205

Distribution: NT, QLD, NSW, VIC

Host plants: *Acacia* sp.; *Acradenia euodiiformis*; *Cytisus scoparius*; *Ficus macrophylla*; *Pararchidendron* sp.; *Xanthium occidentale*

bankii (Fabricius)*

Lamia bankii Fabricius, 1775: 176. TL: “Cap. B. S.” [=Cape of Good Hope, South Africa] (type not found)

Acanthocinus hollandicus Boisduval, 1835: 491. TL: “New Holland” (type not found)

Nyphona insularis Pascoe, 1859: 39. TL: “Aru”, Indonesia (type in BMNH, examined by Ślipiński & Escalona 2013)

Niphona irata Pascoe, 1862b: 464. TL: Lizard Island, Queensland (type in BMNH, examined here)

Niphona miscella Pascoe, 1863: 529. TL: Port Denison, Queensland (type in BMNH, examined here)

Niphona torosa Pascoe, 1864a: 223. TL: South Australia (type in BMNH, examined here)

Aegomomus musivus Pascoe, 1864b: 65. TL: “Kaioa”, Indonesia (type in BMNH, examined by Ślipiński & Escalona 2013)

Micracantha nutans Sharp, 1878: 209. TL: Honolulu, Hawaii (type in BMNH, examined by Ślipiński & Escalona 2013)

Zaeera (Zaeeralia) vaulogeri Pic, 1925: 28. TL: “Tonkin”, Vietnam (type in MNHN, not examined)

Prosoplus uchiyamai Matsushita, 1935: 120. TL: Caroline Islands, Palau (type in EMHU, not examined)

Moved to *Rhytiphora bankii*: Ślipiński & Escalona, 2013: 201

Coptops abdominalis White, 1858: 273. TL: Port Essington, Northern Territory (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora abdominalis*: Ślipiński & Escalona, 2013: 199

Distribution (uncertain): Australia: WA, NT, QLD, (NSW, SA); Papua New Guinea; Indonesia; Christmas Island; (Malaysia; Thailand; Vietnam; China; Philippines; Japan; Micronesia (Palau); Polynesia (Hawaii))

Host plants: *Acacia crassicarpa*; *Agave sisalana*; *Caesalpinia [Libidibia] ferrea*; *Cajanus indicus*; *Calotropis procera*; *Capparis* sp.; *Citrus* sp.; *Chenopodium auricomum*; *Crotalaria* sp.; *Erythrina* sp.; *Euphorbia* sp.; *Gossypium tomentosum*; *Hibiscus* sp.; *Leucaena glauca*; *Mimosa pigra*; *Prosopis* sp.; *Saccharum officinarum*; *Stylosanthes scabra*; *Xanthium occidentale*

basalis (Pascoe) **comb. nov.**

Achriotypa basalis Pascoe, 1875: 72. TL: Rope’s Creek, New South Wales (type in BMNH, examined by Ślipiński & Escalona 2013)

Etaxalus laterialbus Breuning, 1968: 225. TL: Queensland (type in MNHN, examined by Tavakilian & Nearns 2014a). Junior secondary homonym of *Saperdopsis laterialba* (Breuning, 1938). **New synonym**

Rhytiphora hermesi Tavakilian & Nearns, 2014a: 105. Replacement name for *R. laterialba* (Breuning, 1968)

Distribution: QLD, NSW

Host plants: *Acacia decurrens, A. parramattensis*

basicristata (Breuning)

Saperdopsis basicristata Breuning, 1938c: 366. TL: Queensland (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) basicristata*: Breuning, 1961a: 273

Distribution: QLD, NT, WA

Host plants: unknown

batesi Tavakilian & Nearns

Eczemotes guttulata Bates, 1877: 158. TL: Duke of York Island, Papua New Guinea (type in MNHN, not examined). Junior secondary homonym of *Corrhenes guttulata* (Pascoe, 1865)

Rhytiphora batesi Tavakilian & Nearns, 2014a: 104. Replacement name for *R. guttulata* (Bates, 1877)

Distribution (uncertain): (Australia: QLD); Papua New Guinea

Host plants: unknown

bispinosa (Breuning)

Saperdopsis bispinosa Breuning, 1938c: 364. TL: Queensland (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) bispinosa*: Breuning, 1961a: 273

Distribution: Australia: QLD; Papua New Guinea

Host plants: unknown

browni McKeown **st. rev.**

Rhytiphora browni McKeown, 1938: 212. TL: Cue, Western Australia (type in AM, examined here)

Here removed from synonymy with *Rhytiphora (Rhytiphora) macleayi* (Breuning, 1961a: 272)

Distribution: WA

Host plants: *Acacia grasbyi*

cairnsi Tavakilian & Nearns

Saperdopsis marmorata Breuning, 1938c: 362. TL: Cairns, Queensland (type in BMNH, examined here). Junior secondary homonym of *Prosoplus marmoratus* (Breuning, 1938)

Rhytiphora cairnsi Tavakilian & Nearns, 2014a: 105. Replacement name for *R. marmorata* (Breuning, 1938)

Distribution: QLD

Host plants: unknown

cana (McKeown)*

Platyomopsis canus McKeown, 1948: 60. TL: Mount Jackson, Cue, Western Australia (type in AM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Platyomopsis) cana*: Breuning, 1961a: 275

Distribution: WA

Host plants: unknown

capeyorkensis Tavakilian & Nearns

Corrhenodes marmoratus Breuning, 1973a: 42. TL: Queensland (type not found). Junior secondary homonym of *Prosoplus marmoratus* (Breuning, 1938)

Rhytiphora capeyorkensis Tavakilian & Nearns, 2014a: 105. Replacement name for *R. marmorata* (Breuning, 1973)

Distribution: QLD

Host plants: unknown

capreola (Pascoe)

Symphyletes capreolus Pascoe, 1867: 304. TL: Rockhampton, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) capreolus*: Breuning, 1961a: 274

Rhytiphora (Saperdopsis) barnardi Breuning, 1982: 16. TL: Dawson District, Queensland (type in MNHN, examined here). **New synonym**

Distribution: QLD

Host plants: unknown

cinerascens (Aurivillius)*

Platyomopsis cinerascens Aurivillius, 1917: 40. TL: Queensland (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) cinerascens*: Breuning, 1961a: 274

Rhytiphora (Saperdopsis) albolateraloides Breuning, 1970b: 470. TL: Dawson district, Queensland (type in MNHN, examined here). **New synonym**

Distribution: QLD

Host plants: unknown

cinnamomea (Pascoe)*

Symphyletes cinnamomeus Pascoe, 1859: 59. TL: Moreton Bay, Queensland (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) cinnamomea*: Breuning, 1961a: 274

Distribution: QLD

Host plants: unknown

collaris (Donovan)

Saperda collaris Donovan, 1805: plate 5. TL: "New South Wales" (type not found) (white lateral stripe assumed complete; see Discussion)

Symphyletes vestigialis Pascoe, 1864a: 226. TL: South Australia (type in BMNH, examined here) (white lateral stripe complete)

Moved to *Rhytiphora (Platyomopsis) vestigialis:* Breuning, 1961a: 275

Saperda albocincta Guérin-Méneville, 1831: 137. TL: Port Jackson, New South Wales (type not found) (white lateral stripe assumed complete). **New synonym**

Rhytiphora donovani Newman, 1851: 129. TL: "New Holland" (type not found) (white lateral stripe assumed complete). **New synonym**

Symphyletes compos Blackburn, 1902: 319. TL: Hughenden, Queensland (type in BMNH, examined here) (white lateral stripe incomplete). **New synonym**

Rhytiphora maculosella Blackburn, 1902: 320. TL: Queensland (type in BMNH, examined here) (white lateral stripe incomplete). **New synonym**

Moved to *Rhytiphora (Platyomopsis) albocincta*: Breuning, 1961a: 275

Rhytiphora intertincta Pascoe, 1867: 302. TL: Gawler, South Australia (type in BMNH, examined by Ślipiński & Escalona 2013) (white lateral stripe incomplete). **New synonym**

Moved to *Rhytiphora (Rhytiphora) intertincta*: Breuning, 1961a: 272

Rhytiphora (Saperdopsis) parafarinosa Breuning, 1970a: 375. TL: Dawson District, Queensland (type in MNHN, examined here) (white lateral stripe incomplete). **New synonym**

Rhytiphora (Setomopsis) vermiculosa Breuning, 1970b: 471. TL: Queensland (type in MNHN, examined here) (white lateral stripe incomplete). **New synonym**

Distribution: QLD, NSW, ACT, VIC, SA

Host plants: *Acacia dealbata*, *A. decurrens*, *A. longifolia*, *A. mollissima*; *Allocasuarina distyla*; *Angophora* sp.; *Casuarina* sp.; *Dodonaea* sp.? ("hoy bush"); *Rosa* sp.; *Viminaria juncea*

costata (Pascoe)*

Penthea costata Pascoe, 1863: 539. TL: Sydney, New South Wales (type in BMNH, examined here)

Penthea pullina Pascoe, 1863: 539. TL: Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora costata*: Ślipiński & Escalona, 2013: 202

Distribution: WA, NT, QLD, NSW

Host plants: unknown

costulata (Pascoe)

Hathliodes costulatus Pascoe, 1867: 305. TL: Champion Bay, Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora costulata*: Ślipiński & Escalona, 2013: 202

Distribution: WA

Host plants: unknown

cowleyi (Blackburn)

Cairnsia cowleyi Blackburn, 1895: 225. TL: North Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora cowleyi*: Ślipiński & Escalona, 2013: 202

Distribution: QLD

Host plants: unknown

crassicollis (Pascoe)*

Penthea crassicollis Pascoe, 1864a: 227. TL: "Interior of Australia" (type in BMNH, examined here)

Penthea picta Pascoe, 1864a: 227. TL: South Australia (type in BMNH, examined here)

Moved to *Rhytiphora crassicollis*: Ślipiński & Escalona, 2013: 202

Penthea sectator Pascoe, 1865: 358. TL: South Australia (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora sectator*: Ślipiński & Escalona, 2013: 211

Distribution: WA, SA, NT, QLD, NSW, VIC

Host plants: *Atriplex lindleyi, A. pseudocampanulata, A. vesicaria*; *Chenopodium* sp.; *Eucalyptus camaldulensis*; *Salsola* sp.? ("roly poly")

cretata Pascoe*

Rhytiphora cretata Pascoe, 1859: 60. TL: Moreton Bay, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Rhytiphora) cretata*: Breuning, 1961a: 272

Distribution: QLD, NSW

Host plants: *Alphitonia excelsa*; *Casuarina cristata*

crucensis McKeown

Rhytiphora crucensis McKeown, 1948: 61. TL: Southern Cross, Western Australia (type in AM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Rhytiphora) crucensis*: Breuning, 1961a: 272

Distribution (uncertain): WA, (SA)

Host plants: *Casuarina* sp.

cruciata (Pascoe)

Corrhenes cruciata Pascoe, 1875: 71. TL: Gayndah, Queensland (type in BMNH, examined here)

Moved to *Rhytiphora (Rhytiphora) cruciata*: Breuning, 1961a: 272

Rhytiphora (Saperdopsis) corrhenoides Breuning, 1970a: 374. TL: Dawson District, Queensland (type in MNHN, examined here). **New synonym**

Distribution: QLD

Host plants: *Dodonaea* sp.? ("fernleaf shrub")

cylindrica (Breuning)

Corrhenispia cylindrica Breuning, 1938c: 379. TL: Nicol Bay, Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora cylindrica*: Ślipiński & Escalona, 2013: 202

Distribution: WA

Host plants: unknown

dallasii Pascoe

Rhytiphora dallasii Pascoe, 1869: 207. TL: Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Rhytiphora) dallasii*: Breuning, 1961a: 272

Distribution: WA, NT, QLD

Host plants: *Acacia* sp.

decipiens (Pascoe)

Symphyletes decipiens Pascoe, 1863: 532. TL: Adelaide, South Australia (type in BMNH, examined here)

Symphyletes derasus Pascoe, 1863: 532. TL: New South Wales (type in BMNH, examined here)

Symphyletes bathursti Pascoe, 1866: 85. TL: Gawler, South Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Platyomopsis) decipiens*: Breuning, 1961a: 275

Distribution: QLD, NSW, ACT, VIC, SA

Host plants: *Acacia dealbata, A. longifolia*; *Allocasuarina* sp.

delicatula (McKeown)*

Rhytiphora uniformis Blackburn, 1901: 40. TL: “N. W. Australia” (type in BMNH, examined here). Junior secondary homonym of *Aegomomus uniformis* (Pascoe, 1864)

Rhytiphora blackburni Tavakilian & Nearns, 2014a: 106. Replacement name for *R. uniformis* (Blackburn, 1901)

Platyomopsis delicatula McKeown, 1948: 60. TL: Carnarvon, Western Australia (type in AM, examined by Ślipiński & Escalona 2013). **New synonym**

Moved to *Rhytiphora (Setomopsis) delicatula*: Breuning, 1961a: 273

Distribution: WA

Host plants: unknown

denisoniana Ślipiński & Escalona

Hathliodes moratus Pascoe, 1866: 89. TL: Port Denison, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013). Junior secondary homonym of *Symphyletes moratus* (Pascoe, 1863)

Rhytiphora denisoniana Ślipiński & Escalona, 2013: 202. Replacement name for *R. morata* (Pascoe, 1866)

Distribution: QLD, NT, WA

Host plants: unknown

dentipes (Blackburn)

Symphyletes dentipes Blackburn, 1894a: 202. TL: Queensland (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) dentipes*: Breuning, 1961a: 273

Distribution (uncertain): QLD, (NSW, VIC)

Host plants: *Acacia harpophylla*

deserti (Blackburn)*

Symphyletes iliacus Pascoe, 1866: 84. TL: Champion Bay, Western Australia (type in BMNH, examined here). Junior secondary homonym of *Etaxalus iliacus* (Pascoe, 1865)

Rhytiphora adami Tavakilian & Nearns, 2014a: 105. Replacement name for *R. iliaca* (Pascoe, 1866)

Symphyletes deserti Blackburn, 1896: 301. TL: Alice Springs, Northern Territory (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora (Saperdopsis) deserti*: Breuning, 1961a: 274

Distribution (uncertain): WA, NT, SA, (QLD)

Host plants: unknown

detrita Hope*

Rhytiphora detrita Hope, 1842: 429. TL: Port Essington, Northern Territory (type in OUMNH, examined here)

Symphyletes subminiatus Pascoe, 1866: 84. TL: Perth, Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) detrita*: Breuning, 1961a: 274

Distribution: WA, NT

Host plants: *Acacia* sp.

devota (Pascoe)

Symphyletes devotus Pascoe, 1866: 83. TL: Perth, Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) devota*: Breuning, 1961a: 273

Distribution: WA, NT, QLD

Host plants: *Acacia* sp.; *Callistris* sp.; *Casuarina* sp.; *Citrus* sp.; *Crotalaria* sp.

dispar (Blackburn)*

Iphiastus dispar Blackburn, 1894a: 204. TL: Cape York, Queensland (type in MV, not examined)

Rhytiphora fasciata Blackburn, 1894b: 106. TL: North Queensland (type not found)

Moved to *Rhytiphora dispar*: Ślipiński & Escalona, 2013: 203

Distribution (uncertain): QLD, (WA)

Host plants: *Melaleuca* sp.

dispersa (Pascoe)

Notolophia dispersa Pascoe, 1859: 47. TL: "Northern Australia" (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora dispersa*: Ślipiński & Escalona, 2013: 203

Distribution (uncertain): NT, (WA)

Host plants: *Vachellia farnesiana*

diva (Thomson)

Zygrita diva Thomson, 1860: 69. TL: "New Holland" (type in MNHN, examined here; elytra with one pair black spots)

Zygrita nigrozonata Thomson, 1860: 70. TL: "New Holland" (type in MNHN, examined here; elytra with three pairs black spots)

Zygrita diva apicalis Aurivillius, 1917: 42. TL: Kimberley, Western Australia (type in NRM, not examined; elytra with one pair large black spots)

Zygrita diva nigripennis Breuning, 1948: 2. TL: Port Moresby, Papua New Guinea (type in BMNH, not examined; elytra entirely black)

Zygrita diva papuana Breuning, 1955: 70. TL: "Moroko", Papua New Guinea (type in MNHN, examined here; elytra half black)

Zygrita diva uniformis Breuning, 1963b: 13. TL: "Australia" (type in BMNH, not examined; elytra with no black spots)

Moved to *Rhytiphora diva*: Ślipiński & Escalona, 2013: 203

Distribution: Australia: WA, NT, QLD, NSW; Papua New Guinea

Host plants: *Cenchrus* sp.; *Cirsium vulgare*? ("black thistle"); *Crotalaria* sp.; *Glycine max*; *Leptospermum* sp.; *Medicago sativa*; *Mimosa pigra*; *Senna obtusifolia*; *Sesbania* sp.

dunni Breuning

Rhytiphora (Saperdopsis) dunni Breuning, 1972: 31. TL: Cairns, Queensland (type in MZL, not examined)

Distribution: QLD

Host plants: unknown

elongata (Breuning)

Corrhenes elongata Breuning, 1938c: 378. TL: "Australia" (type in BMNH, examined here)

Moved to *Rhytiphora elongata*: Ślipiński & Escalona, 2013: 203

Distribution: Australia

Host plants: unknown

escalonai Tavakilian & Nearns

Saperdopsis albofasciata Breuning, 1938c: 365. TL: Western Australia (type in BMNH, examined here). Junior secondary homonym of *Prosoplus albofasciatus* (Breuning, 1938)

Rhytiphora escalonai Tavakilian & Nearns, 2014a: 104. Replacement name for *R. albofasciata* (Breuning, 1938)

Distribution: WA

Host plants: unknown

excisa (Breuning)

Pterolophia excisa Breuning, 1938c: 312. TL: Wyndham, Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora excisa*: Ślipiński & Escalona, 2013: 203

Distribution: WA, NT

Host plants: unknown

farinosa (Pascoe)

Symphyletes farinosus Pascoe, 1863: 533. TL: Sydney, NSW (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) farinosa*: Breuning, 1961a: 274

Rhytiphora (Rhytiphora) affinis Breuning, 1970b: 470. TL: "Australia" (type in MNHN, examined here). Junior secondary homonym of *Prosoplus affinis* (Breuning, 1938). **New synonym**

Rhytiphora slipinskii Tavakilian & Nearns, 2014a: 104. Replacement name for *R. affinis* (Breuning, 1970)

Distribution: QLD, NSW

Host plants: *Eucalyptus* sp.; *Melaleuca quinquenervia*

fasciata (Blackburn)

Symphyletes fasciatus Blackburn, 1901: 39. TL: Port Mackay, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) fasciata*: Breuning, 1961a: 274

Rhytiphora (Saperdopsis) dawsoni Breuning, 1970a: 374. TL: Dawson District, Queensland (type in MNHN, examined here). **New synonym**

Distribution: QLD, NT, WA

Host plants: unknown

ferruginea (Aurivillius)*

Platyomopsis ferruginea Aurivillius, 1917: 39. TL: Noonkanbah, Kimberley, Western Australia (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) ferruginea*: Breuning, 1961a: 274

Distribution (uncertain): WA, (NT)

Host plants: unknown

flavescens (Breuning)

Prosoplus flavescens Breuning, 1938c: 359. TL: "Australia" (type in NHMB, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora flavescens*: Ślipiński & Escalona, 2013: 203

Distribution: Australia

Host plants: unknown

fraserensis (Blackburn)

Symphyletes fraserensis Blackburn, 1893: 198. TL: Fraser Range, Western Australia (type in AM, examined here)

Moved to *Rhytiphora (Platyomopsis) fraserensis*: Breuning, 1961a: 275

Distribution (uncertain): WA, (SA, VIC)

Host plants: *Xanthorrhoea* sp.

frenchi (Blackburn)*

Platyomopsis frenchi Blackburn, 1890: 132. TL: Yilgarn, Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Platyomopsis) frenchi*: Breuning, 1961a: 275

Distribution: WA

Host plants: unknown

frenchiana Breuning

Rhytiphora frenchi Blackburn, 1895: 225. TL: "N. W. Australia" (type in MV, not examined). Junior secondary homonym of *Platyomopsis frenchi* (Blackburn, 1890)

Rhytiphora frenchiana Breuning, 1961a: 272. Replacement name for *R. frenchi* (Blackburn, 1895)

Distribution (uncertain): WA, (NSW)

Host plants: unknown

freyi (Breuning)*

Notocorrhenes freyi Breuning, 1961c: 150. TL: Beswick, Northern Territory (type in NHMB, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora freyi*: Ślipiński & Escalona, 2013: 204

Distribution: NT

Host plants: unknown

fulva (Pascoe)

Corrhenes fulva Pascoe, 1875: 70. TL: Rockhampton, Queensland (type in BMNH, examined here)

Moved to *Rhytiphora fulva*: Ślipiński & Escalona, 2013: 204

Distribution: QLD

Host plants: *Solanum nemophilum*?; *Xanthium occidentale*

fulvescens (Pascoe)*

Symphyletes fulvescens Pascoe, 1863: 531. TL: Port Denison, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Mesiphiastus (Mesiphiastus) fulvescens unicolor Breuning, 1963b: 168. TL: Somerset, Queensland (type not found)

Moved to *Rhytiphora fulvescens*: Ślipiński & Escalona, 2013: 204

Distribution: WA, NT, QLD

Host plants: *Sida cornifolia*? ("flannel weed")

fumata (Pascoe)*

Symphyletes fumatus Pascoe, 1864a: 224. TL: South Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) fumata*: Breuning, 1961a: 273

Symphyletes arctos Pascoe, 1865: 356. TL: Western Australia (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora (Saperdopsis) arctos*: Breuning, 1961a: 273

Distribution (uncertain): WA, SA, NT, (QLD, VIC)

Host plants: unknown

gallus (Pascoe)*

Symphyletes gallus Pascoe, 1864a: 226. TL: "Interior of Australia" (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) gallus*: Breuning, 1961a: 274

Symphyletes defloratus Pascoe, 1869: 207. TL: Champion Bay, Western Australia (type in BMNH, examined here). **New synonym**

Here removed from synonymy with *Rhytiphora (Saperdopsis) cinnamomea* (Breuning, 1961a: 274)

Distribution (uncertain): WA, NT, (SA, QLD, NSW)

Host plants: unknown

garnetensis Ashman & Ślipiński **sp. nov.**

Rhytiphora garnetensis. TL: Mount Garnet, Queensland (type in ANIC, examined here)

Distribution: QLD

Host plants: unknown

glauerti (McKeown)*

Corrhenes glauerti McKeown, 1948: 62. TL: Bulong, Western Australia (type in WAM, examined here)

Moved to *Rhytiphora glauerti*: Ślipiński & Escalona, 2013: 204

Distribution: WA

Host plants: unknown

godeffroyi (Breuning)

Zaeeropsis godeffroyi Breuning, 1943: 30. TL: Gayndah, Queensland (type in ZMH, not examined)

Moved to *Rhytiphora godeffroyi*: Ślipiński & Escalona, 2013: 204

Distribution: QLD

Host plants: unknown

gracilis (Breuning)

Corrhenodes gracilis Breuning, 1942: 131. TL: “Australia” (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora gracilis*: Ślipiński & Escalona, 2013: 204

Distribution: Australia

Host plants: unknown

grammica (Pascoe)

Hathlia grammica Pascoe, 1859: 49. TL: “Northern Australia” (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora grammica*: Ślipiński & Escalona, 2013: 204

Distribution: NT

Host plants: unknown

granulosa (Guérin-Méneville)

Lamia granulosa Guérin-Méneville, 1831: 133. TL: “New Holland” (type not found)

Moved to *Rhytiphora granulosa*: Ślipiński & Escalona, 2013: 204

Distribution: QLD, NSW

Host plants: *Eucalyptus* sp.

grisella (Pascoe)

Corrhenes grisella Pascoe, 1875: 70. TL: Nicol Bay, Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora grisella*: Ślipiński & Escalona, 2013: 205

Distribution: WA, NT

Host plants: unknown

heros (Pascoe)*

Symphyletes heros Pascoe, 1863: 530. TL: “Interior of Northern Australia” (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) heros*: Breuning, 1961a: 274

Distribution (uncertain): NT, (SA, QLD)

Host plants: unknown

imitans (Breuning)

Prosoplus (Prosoplus) imitans Breuning, 1961d: 17. TL: Christmas Island (type in BMNH, not examined)

Moved to *Rhytiphora imitans*: Ślipiński & Escalona, 2013: 205

Distribution: Christmas Island (south of Java, Indonesia)

Host plants: unknown

intercalaris (Pascoe)

Atyporis intercalaris Pascoe, 1867: 301. TL: Cape York, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora intercalaris*: Ślipiński & Escalona, 2013: 205

Distribution: Australia: QLD; Papua New Guinea

Host plants: *Xanthium occidentale*

intricata (Pascoe)*

Penthea intricata Pascoe, 1864a: 227. TL: South Australia (type in BMNH, examined here)

Moved to *Rhytiphora intricata*: Ślipiński & Escalona, 2013: 205

Distribution (uncertain): SA, (WA, VIC)

Host plants: *Acacia fimbriata*; *Eucalyptus crebra*

lanosa (Pascoe)

Symphyletes lanosus Pascoe, 1869: 208. TL: Champion Bay, Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) lanosa*: Breuning, 1961a: 273

Distribution: WA

Host plants: unknown

lateralis (Pascoe)

Symphyletes lateralis Pascoe, 1858: 250. TL: Swan River, Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Trichomopsis) lateralis*: Breuning, 1961a: 275

Distribution: WA, SA, QLD, NSW, ACT, VIC

Host plants: *Acacia dealbata*; *Callytrix tetragona*; *Cassinia* sp.; *Dillwynia* sp.; *Leptospermum* sp.

laterivitta (Breuning)

Saperdopsis laterivitta Breuning, 1938b: 59. TL: Swan River, Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) laterivitta*: Breuning, 1961a: 274

Distribution: WA

Host plants: unknown

lenta (Blackburn)

Symphyletes lentus Blackburn, 1901: 38. TL: "N. W. Australia" (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora lenta*: Ślipiński & Escalona, 2013: 205

Distribution: WA

Host plants: unknown

lobata (Breuning)

Xiphohathlia lobata Breuning, 1961c: 147. TL: Humpty Doo, Northern Territory (type in NHMB, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora lobata*: Ślipiński & Escalona, 2013: 206

Xiphotheopsis hathlioides Breuning, 1961d: 6. TL: Queensland (type in RBI, examined here). **New synonym**

Moved to *Rhytiphora hathlioides*: Ślipiński & Escalona, 2013: 205

Distribution: WA, NT, QLD, NSW

Host plants: *Eleocharis* sp.; *Mimosa pigra*

macleayi Lea

Rhytiphora macleayi Lea, 1912: 34. TL: Kookynie, Western Australia (type in MV, examined here)

Moved to *Rhytiphora (Rhytiphora) macleayi*: Breuning, 1961a: 272

Distribution: WA

Host plants: unknown

macularia (Pascoe)*

Penthea macularia Pascoe, 1867: 303. TL: "North Australia" (type in BMNH, examined here)

Moved to *Rhytiphora macularia*: Ślipiński & Escalona, 2013: 206

Penthea adamsae McKeown, 1938: 213. TL: Rockhampton, Queensland (type in AM, examined here). **New synonym**

Here removed from synonymy with *Penthea (Melanopenthea) melanosticta* (Breuning, 1961a: 276)

Distribution (uncertain): QLD, (NT, WA)

Host plants: unknown

maculicornis (Pascoe)*

Symphyletes maculicornis Pascoe, 1858: 250. TL: Swan River, Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Rhytiphora semivestita Pascoe, 1866: 86. TL: Perth, Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) maculicornis*: Breuning, 1963b: 207

Distribution: WA

Host plants: *Paraserianthes lophantha*

marmoreoides Tavakilian & Nearns*

Rhytiphora marmorea Breuning, 1942: 129. TL: Western Australia (type in USNM, examined by Lingafelter *et al.* 2014). Junior secondary homonym of *Prosoplus marmoreus* (Breuning, 1938)

Rhytiphora marmoreoides Tavakilian & Nearns, 2014a: 105. Replacement name for *R. marmorea* (Breuning, 1942)

Distribution: WA

Host plants: unknown

mastersi (Blackburn)*

Penthea mastersi Blackburn, 1897b: 97. TL: North West Australia (type in BMNH, examined here)

Moved to *Rhytiphora mastersi*: Ślipiński & Escalona, 2013: 206

Distribution: WA

Host plants: unknown

melanosticta (Pascoe)*

Penthea melanosticta Pascoe, 1875: 72. TL: Nicol Bay, Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora melanosticta*: Ślipiński & Escalona, 2013: 206

Distribution: WA, NT

Host plants: unknown

metallescens (Breuning)

Prosoplus elongatus Breuning, 1938c: 348. TL: Wyndham, Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013). Junior secondary homonym of *Corrhenes elongata* (Breuning, 1938)

Rhytiphora elongatissima Ślipiński & Escalona, 2013: 203. Replacement name for *R. elongata* (Breuning, 1938)

Prosoplus metallescens Breuning, 1938c: 352. TL: Rockhampton, Queensland (type in ZMH, not examined). **New synonym**

Moved to *Rhytiphora metallescens*: Ślipiński & Escalona, 2013: 206

Distribution: WA, NT, QLD

Host plants: unknown

metuta (Pascoe)

Symphyletes metutus Pascoe, 1859: 40. TL: Aru Islands, Indonesia (type in BMNH, examined by Ślipiński & Escalona 2013)

Eczemotes agnata Pascoe, 1864b: 81. TL: Saylee, New Guinea [=West Papua, Indonesia] (type not found)

Moved to *Rhytiphora metuta*: Ślipiński & Escalona, 2013: 206

Distribution: Australia: QLD; Papua New Guinea; Indonesia

Host plants: unknown

mista Newman

Rhytiphora mista Newman, 1842b: 362. TL: Port Phillip, Victoria (type in BMNH, examined here)

Rhytiphora caprina Newman, 1842b: 362. TL: Port Phillip, Victoria (type in BMNH, examined here)

Moved to *Rhytiphora (Rhytiphora) mista*: Breuning, 1961a: 272

Rhytiphora simsoni Blackburn, 1901: 41. TL: Tasmania (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora (Rhytiphora) simsoni*: Breuning, 1961a: 272

Distribution: TAS, VIC, NSW

Host plants: *Acacia* sp.; *Allocasuarina* sp.; *Casuarina littoralis*; *Exocarpos* sp.

mjoebergi (Aurivillius)

Platyomopsis mjoebergi Aurivillius, 1917: 41. TL: Mount Tamborine, Queensland (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Platyomopsis) mjoebergi*: Breuning, 1961a: 275

Distribution: QLD, NSW

Host plants: *Argyrodendron actinophyllum*

modesta (Blackburn)

Symphyletes modestus Blackburn, 1890: 131. TL: Port Lincoln District, South Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) modesta*: Breuning, 1961a: 274

Distribution (uncertain): SA, VIC, NSW, QLD, (WA)

Host plants: *Acacia oxycedrus*

molitorius (Aurivillius)

Hathliodes molitorius Aurivillius, 1917: 33. TL: Kimberley District, Western Australia (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora molitorius*: Ślipiński & Escalona, 2013: 207

Distribution: WA

Host plants: unknown

multiguttata (Breuning)

Prosoplus multiguttatus Breuning, 1938c: 349. TL: Mount Bellenden Ker, Queensland (type not found)

Moved to *Rhytiphora multiguttata*: Ślipiński & Escalona, 2013: 207

Distribution: QLD

Host plants: unknown

multispinis (Breuning)*

Platyomopsis multispinis Breuning, 1938c: 361. TL: Hermannsburg, Northern Territory (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Platyomopsis) multispinis*: Breuning, 1961a: 275

Distribution: NT, SA

Host plants: unknown

murina (Pascoe)

Hathlia murina Pascoe, 1859: 50. TL: "Northern Australia" (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora murina*: Ślipiński & Escalona, 2013: 207

Distribution (uncertain): WA, NT, (QLD)

Host plants: unknown

neglecta (Pascoe)

Symphyletes neglectus Pascoe, 1863: 534. TL: Sydney, New South Wales (type in BMNH, examined by Ślipiński & Escalona 2013)

Symphyletes solutus Pascoe, 1863: 535. TL: Port Denison, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Symphyletes egenus Pascoe, 1864a: 225. TL: "North Australia" (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) neglecta*: Breuning, 1961a: 273

Distribution: QLD, NSW, ACT, VIC

Host plants: *Acacia longifolia, A. mearnsii, A. melanoxylon, A. pendula*; *Camellia* sp.?; *Cedrela australis*; *Citrus* sp.; *Diospyros fasciculosa*; *Euroschinus falcata*; *Morus* sp.; *Pentaceras australe*; *Robinia* sp.; *Wisteria* sp.

nigrita (Pascoe)

Apomecyna nigrita Pascoe, 1859: 49. TL: "Northern Australia" (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora nigrita*: Ślipiński & Escalona, 2013: 207

Pterolophia australica Breuning, 1938c: 326. TL: Mulgrave River, Queensland (type in NHMB, examined by Ślipiński & Escalona 2013). **New synonym**

Moved to *Rhytiphora australica*: Ślipiński & Escalona, 2013: 200

Distribution (uncertain): QLD, NT, (WA)

Host plants: unknown

nigropunctata (Breuning)*

Pararhytiphora nigropunctata Breuning, 1938b: 59. TL: Cairns, Queensland (type in BMNH, examined here)

Moved to *Rhytiphora nigropunctata*: Ślipiński & Escalona, 2013: 207

Distribution: QLD

Host plants: unknown

nigrosparsa (Breuning)*

Pararhytiphora nigrosparsa Breuning, 1938c: 367. TL: Cairns, Queensland (type in BMNH, examined here)

Moved to *Rhytiphora nigrosparsa*: Ślipiński & Escalona, 2013: 207

Distribution: QLD

Host plants: unknown

nigrothorax (McKeown)*

Corrhenes nigrothorax McKeown, 1942: 104. TL: North West Australia (type in AM, examined here)

Moved to *Rhytiphora nigrothorax*: Ślipiński & Escalona, 2013: 207

Distribution: WA

Host plants: unknown

nigrovirens (Donovan)

Saperda nigrovirens Donovan, 1805: plate 5. TL: "New South Wales" (type not found)

Moved to *Rhytiphora (Platyomopsis) nigrovirens*: Breuning, 1961a: 275

Distribution (uncertain): QLD, NSW, VIC, (TAS)

Host plants: *Acacia decurrens, A. juniperina, A. longifolia, A. mearnsii*; *Allocasuarina distyla*; *Alphitonia excelsa*; *Drypetes deplanchei*; *Ozothamnus diosmifolius*; *Persoonia* sp.; *Pittosporum revolutum, P. undulatum*; *Syzygium* sp.

obenbergeri Breuning

Rhytiphora (Platyomopsis) obenbergeri Breuning, 1938a: 95. TL: Gawler, South Australia (type not found)

Distribution: SA

Host plants: unknown

obliqua (Donovan)*

Lamia obliqua Donovan, 1805: plate 6. TL: "New South Wales" (type not found)

Moved to *Rhytiphora (Platyomopsis) obliqua*: Breuning, 1961a: 275

Platyomopsis spinosa Thomson, 1864: 52. TL: "Morton Bay", Queensland? (type in MNHN, examined here). **New synonym**

Moved to *Rhytiphora (Platyomopsis) spinosa*: Breuning, 1961a: 275

Distribution: QLD, NSW, SA

Host plants: *Angophora* sp.; *Eucalyptus* sp.; *Kunzea* sp.

oblita (Pascoe)*

Niphona oblita Pascoe, 1863: 530. TL: New South Wales (type in BMNH, examined here)

Moved to *Rhytiphora oblita*: Ślipiński & Escalona, 2013: 208

Prosoplus albostriatus Breuning, 1938c: 358. TL: "Australia" (type in NRM, examined by Ślipiński & Escalona 2013). **New synonym**

Moved to *Rhytiphora albostriata*: Ślipiński & Escalona, 2013: 199

Prosoplus (Prosoplus) demarzi Breuning, 1963a: 447. TL: Mount Molloy, Queensland (type in NHMB, examined by Ślipiński & Escalona 2013). Junior secondary homonym of *Trichoprosoplus demarzi* (Breuning, 1961). **New synonym**

Rhytiphora molloiensis Ślipiński & Escalona, 2013: 207. Replacement name for *R. demarzi* (Breuning, 1963)

Distribution: NT, QLD, NSW

Host plants: *Acacia holosericea; Jacksonia purpurescens*; *Mimosa pigra*

obscura (Breuning)*

Saperdopsis obscura Breuning, 1938c: 363. TL: "Australia" (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) obscura*: Breuning, 1961a: 273

Distribution: Australia

Host plants: unknown

obsoleta Breuning*

Rhytiphora (Saperdopsis) obsoleta Breuning, 1938a: 95. TL: "New Holland" (type not found)

Rhytiphora (Rhytiphora) parantennalis Breuning, 1970a: 373. TL: Dawson District, Queensland (type in MNHN, examined here). **New synonym**

Distribution: QLD

Host plants: unknown

ocellata (Breuning)

Saperdopsis ocellata Breuning, 1938c: 362. TL: Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) ocellata*: Breuning, 1961a: 273

Distribution: WA

Host plants: unknown

ochreobasalis (Breuning)

Platyomopsis basalis Aurivillius, 1917: 37. TL: Kimberley, Western Australia (type in NRM, examined by Ślipiński & Escalona 2013). Junior secondary homonym of *Achriotypa basalis* (Pascoe, 1875)

Saperdopsis ochreobasalis Breuning, 1938c: 363. TL: Cooktown, Queensland (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora (Saperdopsis) ochreobasalis*: Breuning, 1961a: 274

Distribution (uncertain): WA, SA, NT, QLD, (NSW)

Host plants: unknown

ochreomarmorata Breuning*

Rhytiphora ochreomarmorata Breuning, 1939a: 69. TL: Somerset, Queensland (type not found)

Moved to *Rhytiphora (Rhytiphora) ochreomarmorata*: Breuning, 1961a: 272

Distribution: QLD

Host plants: unknown

ochreopicta (Breuning)*

Prosoplus ochreopictus Breuning, 1940: 423. TL: Queensland (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora ochreopicta*: Ślipiński & Escalona, 2013: 208

Distribution: QLD

Host plants: unknown

ochrescens Breuning

Rhytiphora (Setomopsis) ochrescens Breuning, 1970c: 10. TL: “Australia” (type in HSC, not examined)

Distribution: Australia

Host plants: unknown

odewahnii Pascoe

Rhytiphora odewahnii Pascoe, 1866: 86. TL: Gawler, South Australia (type not found)

Moved to *Rhytiphora (Rhytiphora) odewahnii*: Breuning, 1961a: 272

Distribution: SA

Host plants: unknown

onychina Ślipiński & Escalona

Etaxalus marmoratus Breuning, 1950: 267. TL: "Australia" (type not found). Junior secondary homonym of *Prosoplus marmoratus* (Breuning, 1938)

Rhytiphora onychina Ślipiński & Escalona, 2013: 208. Replacement name for *R. marmorata* (Breuning, 1950)

Distribution: Australia

Host plants: unknown

pallida (Aurivillius)

Platyomopsis pallida Aurivillius, 1917: 38. TL: Nookanbah, Kimberley, Western Australia (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora pallida*: Ślipiński & Escalona, 2013: 208

Distribution: WA

Host plants: unknown

pardalina (Breuning)

Penthea pardalina Breuning, 1942: 130. TL: Bloomfield River, Queensland (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora pardalina*: Ślipiński & Escalona, 2013: 208

Distribution: QLD

Host plants: *Jacksonia thesioides*

pardalis (Newman)

Lamia pardalis Newman, 1842a: 414. TL: Sydney, New South Wales (type in BMNH, examined by Ślipiński & Escalona 2013)

Penthea pardalis occidentalis Aurivillius, 1917: 42. TL: Kimberley, Western Australia (type not found)

Moved to *Rhytiphora pardalis*: Ślipiński & Escalona, 2013: 208

Distribution: WA, NT, SA, QLD, NSW

Host plants: *Acacia aulacocarpa, A. cunninghamii, A. holosericea, A. leptostachya*; *Casuarina* sp.; *Eucalyptus* sp.

paulla (Germar)*

Saperda paulla Germar, 1848: 230. TL: Adelaide, South Australia (type not found)

Moved to *Corrhenes (Corrhenes) paulla*: Breuning, 1961a: 276

Corrhenes (Corrhenes) paulla grisea Breuning, 1963b: 239. TL: Moreton Bay, Queensland (type in BMNH, examined here)

Corrhenes (Corrhenes) paulla fuscosignata Breuning, 1970a: 375. TL: Dawson District, Queensland (type in MNHN, examined here)

Moved to *Rhytiphora paulla*: Ślipiński & Escalona, 2013: 209

Anaesthetis lepida Germar, 1848: 228. TL: Adelaide, South Australia (type not found). **New synonym**

Moved to *Rhytiphora lepida*: Ślipiński & Escalona, 2013: 205

Saperda funesta Pascoe, 1859: 53. TL: Adelaide, South Australia (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora funesta*: Ślipiński & Escalona, 2013: 204

Corrhenes flavovittata Breuning, 1938c: 378. TL: "Australia" (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora flavovittata*: Ślipiński & Escalona, 2013: 204

Cobria rufa Breuning, 1961b: 316. TL: "New Holland" (type in ZMB, examined by Ślipiński & Escalona 2013). **New synonym**

Moved to *Rhytiphora rufa*: Ślipiński & Escalona, 2013: 210

Distribution: SA, NT, QLD, NSW

Host plants: *Chrysanthemum* sp.; *Helichrysum* sp.; *Jacksonia purpurescens*; *Melaleuca* sp.; *Sclerolaena muricata* (as *Bassia quinquecuspis*); *Senecio quadridentatus*; *Xanthium occidentale, X. spinosa*

pauxilla (Blackburn)

Corrhenes pauxilla Blackburn, 1901: 43. TL: North West Australia (type in BMNH, examined here)

Corrhenes cordata McKeown, 1942: 103. TL: Endeavour River, Queensland (type in AM, examined here)

Moved to *Rhytiphora pauxilla*: Ślipiński & Escalona, 2013: 209

Prosoplus albidus Aurivillius, 1917: 33. TL: Broome, Western Australia (type in NRM, examined by Ślipiński & Escalona 2013). **New synonym**

Moved to *Rhytiphora albida*: Ślipiński & Escalona, 2013: 199

Prosoplus minimus Breuning, 1938c: 350. TL: Port Darwin, Northern Territory (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora minima*: Ślipiński & Escalona, 2013: 206

Distribution: WA, NT, QLD

Host plants: *Calotropis procera*; *Ficus opposita*; *Mimosa pigra*

pedicornis (Fabricius)

Lamia pedicornis Fabricius, 1775: 170. TL: "New Holland" (type not found)

Rhytiphora tuberculata Hope, 1842: 429. TL: Port Essington, Northern Territory (type in OUMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) pedicornis*: Breuning, 1961a: 273

Distribution: Australia: WA, NT, QLD; Papua New Guinea

Host plants: *Alstonia* sp.? ("quinine bush"); *Casuarina equisetifolia*; *Cathormion umbellatum*; *Crotalaria* sp.? ("rattle pods"); *Eucalyptus polycarpa*; *Mimosa pigra*; *Stylosanthes scabra*; *Xanthorrhoea* sp.

persimilis (Breuning)

Hathliodes persimilis Breuning, 1938c: 343. TL: Kimberley, Western Australia (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora persimilis*: Ślipiński & Escalona, 2013: 209

Distribution: WA

Host plants: unknown

petrorhiza (Boisduval) *incertae sedis*

Lamia petrorhiza Boisduval, 1835: 502. TL: "New Holland" (type not found)

Moved to *Rhytiphora petrorhiza*: Gemminger & von Harold, 1873: 3089

Distribution: Australia

Host plants: unknown

piligera (Macleay)

Acanthocinus piliger Macleay, 1826: 452. TL: "Australia" (type in ANIC, examined here)

Moved to *Rhytiphora (Saperdopsis) piligera*: Breuning, 1961a: 273

Symphyletes nodosa Newman, 1842b: 362. TL: Port Phillip, Victoria (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora nodosa*: Ślipiński & Escalona, 2013: 208

Distribution: QLD, NSW, ACT, VIC

Host plants: *Acacia decurrens, A. mearnsii*; *Eucalyptus* sp.; *Exocarpos* sp.; *Leptospermum* sp.? ("tea-scrub"); *Xanthorrhoea* sp.

piperitia Hope

Rhytiphora piperitia Hope, 1842: 429. TL: Port Essington, Northern Territory (type in OUMNH, examined here)

Symphyletes humeralis White, 1858: 269. TL: Port Essington, Northern Territory (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Setomopsis) piperitia*: Breuning, 1961a: 272

Rhytiphora truncata Breuning, 1940: 424. TL: Duringo, Queensland (type in USNM, examined by Lingafelter *et al.* 2014). Junior secondary homonym of *Aegomomus truncatus* (Pascoe, 1864). **New synonym**

Rhytiphora truncatoides Tavakilian & Nearns, 2014a: 106. Replacement name for *R. truncata* (Breuning, 1940)

Distribution: QLD, NT, WA

Host plants: *Acacia auriculiformis*; *Bauhinia* sp.; *Casuarina equisetifolia*; *Mimosa pigra*; *Peltophorum pterocarpum*

polymita Pascoe

Rhytiphora polymita Pascoe, 1859: 60. TL: Moreton Bay, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Rhytiphora) polymita*: Breuning, 1961a: 272

Distribution: QLD, NSW, VIC, SA

Host plants: *Acacia pendula*

posthumeralis Breuning

Rhytiphora (Trichomopsis) posthumeralis Breuning, 1964: 726. TL: Norseman, Western Australia (type in NHMB, examined by Ślipiński & Escalona 2013)

Distribution: WA

Host plants: unknown

pubiventris (Pascoe)

Symphyletes pubiventris Pascoe, 1862a: 339. TL: Kangaroo Island, South Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Symphyletes angasii Pascoe, 1864a: 225. TL: South Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora pubiventris*: Ślipiński & Escalona, 2013: 209

Distribution: WA, SA, VIC, NSW, QLD

Host plants: *Avicennia marina*; *Citrus limonia*; *Melaleuca uncinata*

pulcherrima Breuning

Rhytiphora (Trichomopsis) pulcherrima Breuning, 1965: 86. TL: Marloo Station, Wurarga, Western Australia (type not found)

Distribution: WA

Host plants: unknown

pulverulens (Boisduval)*

Lamia pulverulens Boisduval, 1835: 501. TL: "New Holland" (type not found)

Symphyletes sodalis Pascoe, 1859: 41. TL: Moreton Bay, Queensland (type in BMNH, examined here)

Symphyletes munitus Pascoe, 1863: 536. TL: Clarence River, New South Wales (type in BMNH, examined here)

Symphyletes ingestus Pascoe, 1863: 537. TL: Sydney, New South Wales (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) pulverulea*: Breuning, 1961a: 273

Symphyletes vetustus Pascoe, 1862b: 464. TL: Lizard Island, Queensland (type in BMNH, examined here). **New synonym**

Saperdopsis armata Thomson, 1864: 53. TL: "New Holland" (type in MNHN, examined here). **New synonym**

Here removed from synonymy with *Rhytiphora (Saperdopsis) piligera* (Breuning, 1961a: 273)

Symphyletes moratus Pascoe, 1863: 536. TL: Port Denison, Queensland (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora (Saperdopsis) morata*: Breuning, 1963b: 194

Symphyletes anaglyptus Pascoe, 1867: 303. TL: Rockhampton, Queensland (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora (Saperdopsis) anaglypta*: Breuning, 1961a: 273

Distribution: Australia: NT, QLD, NSW, VIC; Papua New Guinea

Host plants: *Acacia bidwillii, A. longifolia, A. penninervis*; *Apophyllum anomalum*; *Avicennia marina*; *Cajanus indicus*; *Citrus* sp.; *Codonocarpus cotinifolius*; *Commersonia bartramia*; *Eugenia* sp.; *Ficus* sp.; *Mimosa pigra*; *Tamarix aphylla*; *Wisteria* sp.

pustulosa (Pascoe)

Symphyletes pustulosus Pascoe, 1864b: 78. TL: Aru Islands, Indonesia (type in BMNH, examined by Ślipiński & Escalona 2013)

Rhytiphora latifasciata Pascoe, 1875: 72. TL: Cape York, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Platyomopsis pustulosum trobriandensis Breuning, 1970b: 470. TL: "Kiriwini", Trobriand Islands, Papua New Guinea (type in MNHN, examined here)

Moved to *Rhytiphora pustulosa*: Ślipiński & Escalona, 2013: 210

Distribution: Australia: QLD; Papua New Guinea; Indonesia

Host plants: *Ficus opposita*; *Homalanthus populifolius*

queenslandensis Tavakilian & Nearns

Mesiphiastus (Pubiphiastus) laterialbus Breuning, 1970a: 375. TL: Dawson District, Queensland (type in MNHN, examined here). Junior secondary homonym of *Saperdopsis laterialba* (Breuning, 1938)

Rhytiphora queenslandensis Tavakilian & Nearns, 2014a: 105. Replacement name for *R. laterialba* (Breuning, 1970)

Distribution: QLD

Host plants: unknown

regularis (Gahan)*

Platyomopsis regularis Gahan, 1893: 193. TL: Roebuck Bay, Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Platyomopsis) regularis*: Breuning, 1961a: 275

Distribution (uncertain): WA, NT, (QLD, NSW)

Host plants: *Corymbia* sp.? ("bloodwood"); *Eucalyptus* sp.

rentzi Ashman & Ślipiński* **new name**

Corrhenes (Corrhenes) flavovittata demarzi Breuning, 1963b: 447. TL: Mount Molloy, Queensland (type in NHMB, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora flavovittata*: Ślipiński & Escalona, 2013: 204; here elevated to species status. Junior secondary homonym of *Trichoprosoplus demarzi* (Breuning, 1961)

Distribution (uncertain): QLD, NSW, (NT, WA)

Host plants: *Tagetes minuta*

Etymology: named after Dr David Rentz, an avid and generous collector of longhorns from Kuranda, Queensland

rosei Olliff*

Rhytiphora rosei Olliff, 1890: 10. TL: Coonamble, New South Wales (type in AM, examined here)

Moved to *Rhytiphora (Rhytiphora) rosei*: Breuning, 1961a: 272

Distribution: QLD, NSW

Host plants: *Acacia harpophylla, A. pendula*

rotundipennis (Breuning)

Menyllus maculicornis Pascoe, 1864b: 87. TL: Aru Islands, Indonesia (type in BMNH, examined by Ślipiński & Escalona 2013). Junior secondary homonym of *Symphyletes maculicornis* (Pascoe, 1858)

Sysspilotus macleayi Pascoe, 1865: 360. TL: New South Wales (type in BMNH, examined by Ślipiński & Escalona 2013)

Rhytiphora callosa Ślipiński & Escalona, 2013: 201. Replacement name for *R. maculicornis* (Pascoe, 1864)

Menyllus rotundipennis Breuning, 1968: 230. TL: Rockhampton, Queensland (type in MNHN, examined here). **New synonym**

Moved to *Rhytiphora rotundipennis*: Tavakilian & Nearns, 2014a: 105

Distribution (uncertain): Australia: WA, NT, QLD, (NSW, VIC); Papua New Guinea; Indonesia

Host plants: *Dodonaea* sp.? ("wild hop bush")

rubeta Pascoe

Rhytiphora rubeta Pascoe, 1863: 538. TL: Sydney, New South Wales (type in BMNH, examined here)

Moved to *Rhytiphora (Rhytiphora) rubeta*: Breuning, 1961a: 272

Distribution: QLD, NSW, VIC, SA

Host plants: *Acacia linifolia, A. longifolia, A. parramattensis*

rubriventris (Breuning)

Saperdopsis rubriventris Breuning, 1938c: 362. TL: Kuranda, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) rubriventris*: Breuning, 1961a: 274

Distribution: QLD

Host plants: unknown

rugicollis (Dalman)

Lamia rugicollis Dalman, 1817: 169. TL: “New Holland” (type not found)

Lamia porphyrea Boisduval, 1835: 501. TL: “New Holland” (type not found)

Moved to *Rhytiphora rugicollis*: Audinet-Serville, 1835: 38

Distribution: QLD, NSW, ACT, VIC

Host plants: *Acacia longifolia*; *Eucalyptus saligna*

saga Pascoe

Rhytiphora saga Pascoe, 1865: 358. TL: Perth, Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013)

Distribution: WA

Host plants: unknown

sannio (Newman)*

Lamia sannio Newman, 1838: 498. TL: “New Holland” (type in BMNH, examined here)

Moved to *Rhytiphora (Rhytiphora) sannio*: Breuning, 1961a: 272

Distribution (uncertain): QLD, NSW, (VIC)

Host plants: *Eucalyptus coolibah, E. microcarpa*

satelles (Pascoe)*

Symphyletes satelles Pascoe, 1865: 357. TL: Western Australia (type in BMNH, examined here)

Symphyletes simius Pascoe, 1866: 85. TL: Champion Bay, Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) satelles*: Breuning, 1961a: 274

Saperdopsis laterialba Breuning, 1938c: 363. TL: Wyndham, Western Australia (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora (Saperdopsis) laterialba*: Breuning, 1961a: 274

Distribution: WA

Host plants: unknown

saundersii (Pascoe)*

Penthea saundersii Pascoe, 1857: 103. TL: Swan River, Western Australia (type in BMNH, examined here)

Rhytiphora spenceri Blackburn, 1897a: 38. TL: Central Australia (type in BMNH, examined here)

Rhytiphora blackburni Aurivillius, 1922: 163. TL: “Roma near Warramboo”, Western Australia (type in RNH, not examined)

Moved to *Rhytiphora (Rhytiphora) saundersii*: Breuning, 1961a: 272

Distribution (uncertain): WA, NT, SA, (NSW)

Host plants: *Acacia* sp.; *Hakea* sp.

scenica (Pascoe)*

Penthea scenica Pascoe, 1863: 540. TL: Port Denison, Queensland (type in BMNH, examined here)

Penthea miliaris Pascoe, 1863: 540. TL: Port Denison, Queensland (type in BMNH, examined here)

Moved to *Rhytiphora scenica*: Ślipiński & Escalona, 2013: 211

Penthea lichenosus McKeown, 1942: 103. TL: Coen River, Queensland (type in AM, examined here). **New synonym**

Moved to *Rhytiphora lichenosa*: Ślipiński & Escalona, 2013: 205

Penthea (Melanopenthea) obscura Breuning, 1961d: 17. TL: Cooktown, Queensland (type in RBI, examined here). Junior secondary homonym of *Saperdopsis obscura* (Breuning, 1938). **New synonym**

Rhytiphora pascoei Ślipiński & Escalona, 2013: 209. Replacement name for *R. obscura* (Breuning, 1961)

Distribution: QLD

Host plants: *Tephrosia astragaloides*

sellata (Breuning)

Saperdopsis sellata Breuning, 1938c: 364. TL: Rockhampton, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) sellata*: Breuning, 1961a: 273

Rhytiphora (Platyomopsis) multituberculata Breuning, 1966: 248. TL: Queensland (type in ZMB, examined by Ślipiński & Escalona 2013). **New synonym**

Distribution: QLD

Host plants: *Acacia harpophylla*

sherlockensis Tavakilian & Nearns

Saperdopsis albescens Breuning, 1938c: 365. TL: Sherlock River, Western Australia (type in BMNH, examined by Ślipiński & Escalona 2013). Junior secondary homonym of *Prosoplus albescens* (Breuning, 1938)

Rhytiphora sherbockensis Tavakilian & Nearns 2014b: 157. Replacement name for *R. albescens* (Breuning, 1938); corrected here to *R. sherlockensis* as per ICZN Article 33.2

Distribution: WA

Host plants: unknown

solandri (Fabricius)

Lamia solandri Fabricius, 1775: 177. TL: "New Holland" (type not found)

Saperda leprosa Boisduval, 1835: 517. TL: "New Holland" (type not found)

Moved to *Rhytiphora (Saperdopsis) solandri*: Breuning, 1961a: 274

Distribution (uncertain): QLD, NSW, ACT, (VIC, SA)

Host plants: *Xanthorrhoea australis, X. resinosa*

sospitalis Pascoe*

Rhytiphora sospitalis Pascoe, 1865: 358. TL: Western Australia (type in BMNH, examined here)

Symphyletes duboulayi Pascoe, 1866: 83. TL: Perth, Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) sospitalis*: Breuning, 1961a: 274

Distribution: WA

Host plants: *Acacia saligna*; *Hakea linearis*

stigmatica (Pascoe)*

Saperda stigmatica Pascoe, 1863: 544. TL: Port Denison, Queensland (type in BMNH, examined here)

Moved to *Rhytiphora stigmatica*: Ślipiński & Escalona, 2013: 211

Saperda mystica Pascoe, 1863: 545. TL: New South Wales (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora mystica*: Ślipiński & Escalona, 2013: 207

Corrhenes guttulata Pascoe, 1865: 355. TL: New South Wales (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora guttulata*: Ślipiński & Escalona, 2013: 205

Corrhenes macmillani Gilmour, 1950: 542. TL: Townsville, Queensland (type in DMAG, not examined). **New synonym**

Moved to *Rhytiphora macmillani*: Ślipiński & Escalona, 2013: 206

Distribution (uncertain): QLD, NSW, (NT, SA, WA)

Host plants: *Medicago sativa*

subargentata Breuning

Rhytiphora (Rhytiphora) subargentata Breuning, 1970a: 373. TL: Dawson District, Queensland (type in MNHN, examined here)

Rhytiphora (Rhytiphora) leucolateralis Breuning, 1970a: 470. TL: “Geraldton, Queensland” [Geraldton is in WA] (type in MNHN, examined here). **New synonym**

Distribution (uncertain): QLD, (WA)

Host plants: unknown

subovata Ashman & Ślipiński **new name**

Pterolophia bispinosa Breuning, 1939b: 195. TL: Queensland (type in BMNH, examined by Ślipiński & Escalona 2013). Junior secondary homonym of *Saperdopsis bispinosa* (Breuning 1938)

Moved to *Achriotypa bispinosa*: Ślipiński & Escalona, 2013: 87

Distribution: QLD

Host plants: unknown

Etymology: named for its slightly oval body shape (distinct from its sister *R. basalis*)

subregularis Breuning*

Rhytiphora (Platyomopsis) subregularis Breuning, 1973b: 14. TL: Queensland (type not found)

Distribution: QLD

Host plants: unknown

subtuberculata (White)*

Symphyletes subtuberculatus White, 1858: 269. TL: “Australia” (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora subtuberculata*: Ślipiński & Escalona, 2013: 211

Distribution: Australia

Host plants: unknown

tigrina (Blackburn)*

Penthea tigrina Blackburn, 1901: 37. TL: Coolgardie, Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora tigrina*: Ślipiński & Escalona, 2013: 211

Distribution: WA

Host plants: unknown

torquata (Pascoe)

Symphyletes torquatus Pascoe, 1875: 71. TL: Gayndah, Queensland (type in RBI, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Platyomopsis) torquata*: Breuning, 1961a: 275

Distribution: QLD

Host plants: *Pleiogynium timoriense*

transversesulcata Breuning

Rhytiphora transversesulcata Breuning, 1938c: 367. TL: Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Rhytiphora) transversesulcata*: Breuning, 1961a: 272

Distribution: QLD

Host plants: unknown

transversevittata (Breuning)

Cobria transversevittata Breuning, 1979: 14. TL: Gawler, South Australia (type not found)

Moved to *Rhytiphora transversevittata*: Ślipiński & Escalona, 2013: 212

Distribution: SA

Host plants: unknown

tuberculigera (Breuning)

Platyomopsis tuberculigera Breuning, 1938b: 42. TL: Queensland (type in RBI, examined here)

Moved to *Rhytiphora (Platyomopsis) tuberculigera*: Breuning, 1961a: 275

Distribution: QLD

Host plants: unknown

undata (Montrouzier)

Penthea undata Montrouzier, 1855: 65. TL: Woodlark Island, Papua New Guinea (type not found)

Penthea conferta Pascoe, 1859: 40. TL: Aru Islands, Indonesia (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora undata*: Ślipiński & Escalona, 2013: 212

Distribution: Australia: QLD; Papua New Guinea; Indonesia

Host plants: unknown

undulata (Breuning)

Corrhenes undulata Breuning, 1938c: 379. TL: Cairns, Queensland (type in BMNH, examined here)

Moved to *Rhytiphora undulata*: Ślipiński & Escalona, 2013: 212

Distribution: QLD

Host plants: unknown

variolosa (Pascoe)*

Symphyletes variolosus Pascoe, 1862a: 340. TL: Moreton Bay, Queensland (type in BMNH, examined here)

Symphyletes vicarius Pascoe, 1865: 356. TL: New South Wales (type in BMNH, examined here)

Moved to *Rhytiphora (Saperdopsis) variolosa*: Breuning, 1961a: 274

Mimiphiastus vivesi Breuning, 1978: 134. TL: Queensland (type in EVC, examined by Ślipiński & Escalona 2013). **New synonym**

Moved to *Rhytiphora vivesi*: Ślipiński & Escalona, 2013: 212

Distribution (uncertain): QLD, NSW, (VIC, NT)

Host plants: *Acacia decurrens, A. longifolia*

vermicularia (Donovan)*

Lamia vermicularia Donovan, 1805: plate 6. TL: “New South Wales” (type not found)

Moved to *Rhytiphora vermicularia*: Ślipiński & Escalona, 2013: 212

Penthea solida Pascoe, 1863: 538. TL: Clarence River, New South Wales (type in BMNH, examined here). **New synonym**

Moved to *Rhytiphora solida*: Ślipiński & Escalona, 2013: 211

Distribution: QLD, NSW, VIC

Host plants: *Acacia decurrens, A. linifolia*

villosa (Breuning)*

Paradaxata villosa Breuning, 1938c: 344. TL: Wyndham, Western Australia (type in BMNH, examined here)

Moved to *Rhytiphora villosa*: Ślipiński & Escalona, 2013: 212

Paradaxata spinosa Breuning, 1938c: 345. TL: Queensland (type in NHMB, examined by Ślipiński & Escalona 2013). Junior secondary homonym of *Platyomopsis spinosa* (Thomson, 1864). **New synonym**

Rhytiphora confusa Ślipiński & Escalona, 2013: 201. Replacement name for *R. spinosa* (Breuning, 1938)

Trichoprosoplus demarzi Breuning, 1961c: 151. TL: Beswick, Northern Territory (type in NHMB, examined by Ślipiński & Escalona 2013). **New synonym**

Moved to *Rhytiphora demarzi*: Ślipiński & Escalona, 2013: 202

Distribution: WA, NT, QLD

Host plants: unknown

virgata (Breuning)

Hathliodes virgatus Breuning, 1938c: 343. TL: Port Denison, Queensland (type in BMNH, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora virgata*: Ślipiński & Escalona, 2013: 212

Hathliodes pseudomurinus Breuning, 1938c: 343. TL: Kimberley, Western Australia (type in NRM, examined by Ślipiński & Escalona 2013). **New synonym**

Moved to *Rhytiphora pseudomurina*: Ślipiński & Escalona, 2013: 209

Distribution: WA, NT, QLD

Host plants: unknown

viridescens (Breuning)

Platyomopsis viridescens Breuning, 1938c: 361. TL: Moreton Bay, Queensland (type in BMNH, examined here)

Moved to *Rhytiphora (Platyomopsis) viridescens*: Breuning, 1961a: 275

Distribution: QLD, NSW

Host plants: unknown

viridis (Breuning)

Saperdopsis viridis Breuning, 1938c: 365. TL: Queensland (type in NRM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora (Saperdopsis) viridis*: Breuning, 1961a: 274

Distribution: QLD, NSW

Host plants: unknown

waterhousei Pascoe*

Rhytiphora waterhousei Pascoe, 1864a: 228. TL: South Australia (type in BMNH, examined here)

Moved to *Rhytiphora (Rhytiphora) waterhousei*: Breuning, 1961a: 272

Distribution: SA, VIC

Host plants: unknown

woodlarkiana (Montrouzier)

Penthea woodlarkianus Montrouzier, 1855: 65. TL: Woodlark Island, Papua New Guinea (types in MNHN & RBI, examined here)

Moved to *Rhytiphora woodlarkiana*: Ślipiński & Escalona, 2013: 213

Distribution (uncertain): (Australia: QLD); Papua New Guinea

Host plants: unknown

ziczac (McKeown)

Sodus? zic-zac McKeown, 1942: 104. TL: Bowen, Queensland (type in AM, examined by Ślipiński & Escalona 2013)

Moved to *Rhytiphora ziczac*: Ślipiński & Escalona, 2013: 213

Distribution: QLD

Host plants: unknown

DISCUSSION

We have acquired 10 new type photographs during the course of this study (Fig. S1). We have also collated several type photographs taken by Ślipiński & Escalona (2013) but not included in the final publication (Fig. S2). Species complexes requiring further investigation (marked with an asterisk in the species list) are discussed below, listed alphabetically.

Rhytiphora species complexes

R. argus, *R. dispar*, *R. nigropunctata* and *R. nigrosparsa* are all described from QLD and are fairly similar morphologically (large-bodied and large-eyed with black spots on the elytra). These four species need to be sequenced to confirm whether they are distinct genetic lineages, or one species with variable setal colouring (yellow/orange to grey).

The species *R. bankii* is extremely widespread, with records from Australia through Southeast Asia to China, Japan and even Hawaii (although this may be a human introduction; McKeown 1947). Indeed, the type locality in the original publication is listed as South Africa (Cape of Good Hope; Fabricius 1775), though this may be incorrect; Gahan (1893) does not discuss his reasoning for synonymising *Lamia bankii* with *Acanthocinus hollandicus* and other Australasian species. Given that no other *Rhytiphora* species has such an extensive distribution, *R. bankii* specimens from across the Pacific region should be sequenced to determine whether there are cryptic species; we already have mitochondrial data which show that two specimens from Queensland and Christmas Island (south of Java, Indonesia) have genetic divergence equivalent to that of other *Rhytiphora* species (see Chapter 2).

R. cana, *R. cinerascens*, *R. deserti* and *R. satelles* are very similar morphologically and need sequencing to confirm the species boundaries. There is at least one specimen (ANIC 25-66662) from northern NT which is morphologically closest to *R. deserti* (central Australia) but genetically closer to *R. cinerascens* (QLD; Chapter 2).

R. cinnamomea (QLD), *R. gallus* (central Australia) and *R. ferruginea* (WA) have very similar colouration but different eye sizes (*R. cinnamomea* lower lobes separated by 3.2x eye width; *R. gallus* 2.4x; *R. ferruginea* unknown). Phylogenetically they form a clade with *R. fasciata* and *R. tuberculigera* (see Chapter 2), which are both described from QLD and morphologically distinct. The *R. cinnamomea* specimen (ANIC 25-66541) is more closely related to a specimen from WA with similarly small eyes (ANIC 25-66555) than it is to another QLD specimen with larger eyes (ANIC 25-66546). More extensive sampling, combined with an examination of the *R. ferruginea* holotype, is needed to determine how many lineages there are and which described species, if any, they correspond to.

We synonymised several morphologically similar species under *R. collaris* (Figs. 4A, 5E): *Saperda albocincta*, *R. intertincta*, *R. parafarinosa*, *R. vermiculosa* and *Symphyletes vestigialis*. We used the oldest available name for this species, although the holotype of *Saperda collaris* is missing and the species is depicted as having entirely black elytra (Donovan 1805). In his description of *Saperda albocincta*, Guérin-Méneville (1831) notes that the holotype of *S. collaris* is very similar to his new species and may have simply lost the yellow setae that form the distinctive elytral patterning seen in *S. albocincta*. In the absence of any specimens with black elytra matching *S. collaris*, and on the basis of Guérin-Méneville's comment, we have synonymised these species. We also synonymised the subspecies of *S. albocincta* as they did not make geographic sense (grouping NSW with SA rather than QLD); the corresponding morphological trait (full or patchy white lateral stripe on elytra) is noted beside each type.

R. costata (Australia-wide), *R. intricata* (SA), *R. tigrina* (WA) and *R. vermicularia* (east coast) have different colour patterns but very similar body size, shape and sculpturing (large-bodied, oval, transverse rugose pronotum, longitudinally ridged elytra). Sequencing is needed to confirm species distributions and boundaries (i.e. *R. tigrina* may be a yellow western morphotype of *R. vermicularia*); it is likely these species form a clade with the distinctive *R. pardalis* which, like *R. costata*, is widely distributed across Australia.

The holotypes of *R. cretata* (QLD) and *R. heros* (NT) have similar elytral patterns but different antennae and pronotum colouring (plain vs. striped). There are also intermediate specimens from QLD with plain antennae and striped pronotum (e.g. Fig. 134D in Ślipiński & Escalona 2013). It is possible that *R. heros* is the same species as *R. cretata*, and the holotype has simply lost the setae on its antennae and pronotum; sequencing specimens across the geographic and morphological gradients will provide further insight.

R. detrita (north and west coast; Fig. S1A) and *R. variolosa* (east coast) are quite similar morphologically but do have different elytral patterns (ochre lateral stripe and dorsal mottling vs. just ochre spots). However, in Chapter 2 we found very little genetic divergence between these two species; more extensive sampling is needed to determine whether *R. detrita* and *R. variolosa* are separate species or one widespread species.

We examined the holotypes of *Corrhenes flavovittata* and *C. flavovittata demarzi* and found several morphological differences (e.g. antennae and elytral setae patterns; Fig. S3). We therefore elevated *C. flavovittata demarzi* to species status (here renamed *R. rentzi*), pending genetic confirmation: *R. rentzi* is quite similar to *R. stigmatica*. We have synonymised *C. flavovittata* with *R. paulla*, along with several other species with similar white markings on the antennae, pronotum and elytra: *Saperda funesta, Anaesthetis lepida* and *Cobria rufa*. We have used the name *R. paulla* as that holotype is presumably better preserved than *A. lepida*, which from its description (in the same publication as *R. paulla*) seems to have lost most of its setae. It would be worthwhile using sequence data to determine how many lineages exist in this large species complex of *R. paulla*.

R. frenchi and *R. frenchiana* have similar names but are very different species. Most of the specimens we have seen labelled as *R. frenchi* in Australian collections match the description of Blackburn's (1895) *Rhytiphora frenchi*, now renamed *R. frenchiana* Breuning (Fig. S1L): large-bodied (18 lines = ~38 mm) with a mottled black and white pattern similar to that of *R. saundersii* (Fig. 1F; also see below). The senior homonym, *R. frenchi* (originally *Platyomopsis*; Blackburn 1890), is a smaller grey-haired species resembling *R. armatula* and *R. obliqua* (Fig. 1H) but without such pronounced elytral spines. These three species, as well as *R. multispinis*, *R. regularis* and *R. subregularis* (Fig. S4), are often confused and would benefit from sequencing to confirm the species boundaries (especially for *R. regularis* and *R.*

subregularis, which may be red western/brown eastern morphotypes of the same widespread species).

R. freyi (Fig. S2D) has similar elytra to *R. villosa* (colour pattern and basal tufts of long setae) but a different pronotum (colour pattern more similar to *R. oblita*). Sequencing is needed to determine how many lineages exist.

R. fulvescens and *R. subtuberculata* have similar body shape and white markings on the elytra, but are predominately different colours. White's (1858) description of *Symphyletes subtuberculatus* mentions an ochreous variant of the grey holotype, which may refer to what Pascoe (1863) described as *Symphyletes fulvescens*. Sequencing of both colour varieties is needed to confirm whether there are one or two species.

R. fumata and *R. obscura* are quite similar morphologically, but *R. obscura* has much fainter elytral patterning. Closer examination of the *R. obscura* holotype, and genetic sequencing of similar specimens (if not the original holotypes themselves), will determine whether these two species should be synonymised.

The colour pattern of *R. glauerti* appears to be intermediate between that of *R. crassicollis* (banded pronotum) and *R. macularia* (finely mottled elytra; Fig. S2I). Only *R. crassicollis* has been sequenced (see Chapter 2); more extensive sampling, across all three species' geographic ranges, is needed to confirm the species boundaries.

R. maculicornis and *R. sospitalis* (both WA) are very similar morphologically except for a white diagonal marking in the apical third of the elytra (present in *R. maculicornis*, absent in *R. sospitalis*). There are also two species from QLD with similar body size, shape and colouring: *R. obsoleta* and *R. ochreomarmorata*. Sequencing of all four species will determine how many lineages there are.

R. marmoreoides (WA), *R. rosei* (east coast) and *R. saundersii* (western to central Australia) share a distinctive black and white elytral pattern (Fig. 1F); *R. marmoreoides* and *R. rosei* are more finely mottled than *R. saundersii*, yet do not overlap geographically. Sequencing specimens from across Australia is needed to confirm the species boundaries. *R. frenchiana* also has black and white elytral patterning, but can be distinguished from the above three species by the white lateral stripe on the elytra (Fig. S1L).

R. mastersi (WA), *R. melanosticta* (WA and NT) and *R. scenica* (QLD) have similar morphology (banded antennae, orange/white elytra with black spots; Fig. S5). There are several specimens with colouration partway between *R. mastersi* and *R. melanosticta*;

sequencing is required to determine the species' genetic, morphological and geographic boundaries. *R. pardalina* (Fig. 1B) has a similar colour scheme to the above three species, but lacks a lateral pronotum spine and has a unique elytral pattern consistent across many specimens.

R. ochreopicta is similar to *R. oblita* except for the white diagonal marking in the apical third of the elytra (absent in *R. ochreopicta*, present in *R. oblita*). Sequencing is needed to establish whether or not this morphological difference corresponds to distinct lineages.

There is a complicated history of *R. piligera* and *R. pulverulens*, with some incorrect synonymies due to mislabelling of specimens (McKeown 1947). Here we have restricted *R. piligera* to the original type, housed in ANIC (Fig. S1E), and the newly synonymised *Symphyletes nodosus* (which are both brown with basal elytral tubercules and clavate antennal scape). We united all the large, grey, diagonally striped species under *R. pulverulens*: *Saperdopsis armata, Symphyletes anaglyptus, S. ingestus, S. moratus, S. munitus, S. sodalis* and *S. vetustus* (but not *R. devota* from WA). Defined thus, this species is distributed widely across the eastern half of Australia, as well as New Guinea; sequencing specimens across this range would allow us to determine whether *R. pulverulens* is one widespread or multiple convergent species. *R. sundaensis* (Fig. S1I) from the Maluku province of Indonesia is very similar morphologically to the Australian *R. pulverulens*, but has been left separate pending genetic confirmation.

The holotypes of *R. sannio* (east coast) and *R. waterhousei* (south coast) have very similar body size and shape, but different elytral colouration (red with diagonal markings vs. yellow without markings). However, there are specimens from NSW with intermediate colouration. It is possible that *R. waterhousei* is a southern variant of *R. sannio*; sequencing across the geographic and morphological gradient is needed to determine whether distinct lineages exist.

Other remarks

The checklist includes several species which may not belong in *Rhytiphora*. The species originally described as *Lamia petrorhiza* is listed here as *Rhytiphora incertae sedis* (or '*gen. dub.*' in Gemminger & von Harold 1873), but until the holotype can be located and examined it is difficult to tell what genus this species belongs to. The holotype of *R. nigrothorax* is only 4 mm long (2 mm shorter than the smallest confirmed *Rhytiphora*) and has unusually moniliform antennomeres 6–11. Closer examination of the holotype, as well as sequencing of morphologically similar specimens, will confirm whether this species belongs in *Rhytiphora*.

It is interesting to note that at least two groups of species, in different subclades of *Rhytiphora*, appear to have lost the characteristic male sex patches: *R. basalis* and *R. subovata* (originally described in *Achriotypa* and *Pterolophia*; Ślipiński & Escalona 2013); *R. dallasii, R. browni* and *R. macleayi* (originally described in *Rhytiphora*; McKeown 1938). The latter three species are very similar morphologically (distinctive longitudinal stripes; Figs. 1G, S1C) and are also unusual in having a punctate antennal scape, a trait shared only with the closely related *R. argentata* (Figs. 4C, 5D; Chapter 2).

The host plant records presented in the checklist are also collated in the Supplementary Information (Table S1). *Rhytiphora* is found on both woody and herbaceous plants; some species are polyphagous, with many different host records (e.g. *R. bankii*, *R. nigrovirens*, *R. pulverulens*), while others are apparent specialists (e.g. *R. solandri*, only found on grass trees). The most common host plant genus is *Acacia*. Both Clade 1 and 2 have Fabaceae as the most common host plant family (~65% of sequenced species with host records), followed by Myrtaceae for clade 2 (50% of species) or grasses and daisies for clade 1 (Poales and Asteraceae; 50% of species).

The following are updated species identifications for *Rhytiphora* appearing in Ślipiński & Escalona (2013): Figs. 125C, 125F, 126C, 137A are *R. lateralis*; Fig. 126B is *R. collaris*; Fig. 127B–C is probably *R. fumata*; Fig. 127E is *R. crucensis*; Fig. 127F is *R. mista*; Fig. 128A is *R. scenica*; Fig. 128E is *R. rosei*; Figs. 129D, 133B are *R. paulla*; Fig. 130B is *R. obliqua*; Fig. 130E is *R. piperitia*; Fig. 130F is *R. rotundipennis*; Fig. 131B is *R. argentata*; Fig. 131C is *R. farinosa*; Fig. 131D is *R. fulvescens*; Figs. 132D, 137B are probably *R. subregularis*; Figs. 133C, 135B are *R. pedicornis*; Figs. 133F, 137D are *R. queenslandensis*; Fig. 134E is *R. undata*; Fig. 136C is *R. frenchiana*; Fig. 137E is *R. solandri*; Fig. 200G is the *Rhytiphora (Saperdopsis) corrhenoides* holotype.

Concluding remarks

This study presents a thorough review of Australia's largest longhorn genus: *Rhytiphora*. We updated the morphological definition of the genus to include the two genetically identified subclades and diagnostic features to separate *Rhytiphora* from related Asian-Australian genera. The *collaris* group was revised, and a new species described. Following extensive examination of type specimens, we created a new checklist of the Australian *Rhytiphora* species with many species synonymised; however, more sequencing is required to fully resolve the taxonomic questions within this widespread radiation of longhorn beetles.

ACKNOWLEDGEMENTS

We would like to thank all the museum staff who supported our visits and provided critical specimen loans and/or type photographs: Chris Reid, Derek Smith (AM); Beulah Garner (BMNH); Cameron Brumley, Andras Szito (DAFWA); Jude Philp (MM); Azadeh Taghavian (MNHN); Lucinda Gibson (MV); Katherine Child, Amoret Spooner (OUMNH); Karin Koch, Susan Wright (QM); Alain Drumont (RBI); Ben Parslow (SAM); Nikolai Tatarnic (WAM). Mengjie Jin accompanied LGA on many of these museum visits and took photographs of useful specimens. We are also indebted to the following Australian beetle collectors for providing new host plant and geographic range records: Paul Hutchinson, Stuart Harris, Roger de Keyzer, Garry Webb, Jack Hasenpusch, Andreas Urban, Len van der Waag, Ken Walker, Simon Ong. Andreas Zwick and David Rowell provided comments on the manuscript. LGA was funded by the Australian National University (including a Vice-Chancellor's Travel Grant) and an Australian Government Research Training Program domestic scholarship. The authors declare no conflicts of interest.

REFERENCES

Atlas of Living Australia (2017) Open DELTA: a Java implementation of the DELTA suite of programs.

Audinet-Serville, J.G. (1835) Nouvelle classification de la famille des longicornes (suite). *Annales de la Société Entomologique de France* 4, 5–100, 197–228.

Aurivillius, C. (1893) Verzeichniss der von den Herren C. Lumholtz und C. Fristedt im nördlichen Queensland gesammelten Cerambyciden. *Entomologisk Tidskrift* 1893, 153–169.

Aurivillius, C. (1916) Neue oder wenig bekannte Coleoptera Longicornia. 16. *Arkiv för Zoologi* 10, 335–359.

Aurivillius, C. (1917) Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia 1910–1913, Part 12, Cerambycidae. *Arkiv för Zoologi* 10, 1–50.

Aurivillius, C. (1922) *Coleopterorum Catalogus, pars 73. Cerambycidae: Lamiinae I*. W. Junk, Berlin, 1–322 pp.

Bates, H.W. (1877) On the Coleoptera collected by the Rev. G. Brown, C.M.Z.S., on Duke-of-York Island, New Ireland, and New Britain. *Proceedings of the Scientific Meetings of the Zoological Society of London* 1877, 156–159.

Blackburn, T. (1890) Further notes on Australian Coleoptera with descriptions of new genera and species. Part VIII. *Transactions of the Royal Society of South Australia* 13, 121–160.

Blackburn, T. (1893) Scientific results of the Elder Exploring Expedition: Coleoptera (continued). *Transactions of the Royal Society of South Australia* 16, 177–202.

Blackburn, T. (1894a) Notes on Australian Coleoptera with descriptions of new genera and species. Part XIII. *Proceedings of the Linnean Society of New South Wales* (2)8, 185–208.

Blackburn, T. (1894b) Notes on Australian Coleoptera with descriptions of new genera and species. Part XV. *Proceedings of the Linnean Society of New South Wales* (2)9, 85–108.

Blackburn, T. (1895) Further notes on Australian Coleoptera with descriptions of new genera and species. Part XVIII. *Transactions of the Royal Society of South Australia* 19, 201–258.

Blackburn, T. (1896) Coleoptera (exclusive of the Carabidae). In: B. Spencer (Ed), *Report on the work of the Horn Scientific Expedition to Central Australia. Part II. Zoology*. Dulau, London, pp. 254–308.

Blackburn, T. (1897a) Further notes on Australian Coleoptera with descriptions of new genera and species. Part XXI. *Transactions of the Royal Society of South Australia* 21, 28–39.

Blackburn, T. (1897b) Further notes on Australian Coleoptera with descriptions of new genera and species. Part XXII. *Transactions of the Royal Society of South Australia* 21, 88–98.

Blackburn, T. (1901) Further notes on Australian Coleoptera with descriptions of new genera and species. Part XXVIII. *Transactions of the Royal Society of South Australia* 25, 15–44.

Blackburn, T. (1902) Further notes on Australian Coleoptera, with descriptions of new genera and species. Part XXXI. *Transactions of the Royal Society of South Australia* 26, 288–321.

Boisduval, J.B.A. (1835) *Voyage de Découvertes de l'Astrolabe exécuté par ordre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M.J. Dumont d'Urville. Faune entomologique de l'Océan Pacifique, avec l'illustration des insectes nouveaux recueillis pendant le voyage. Deuxième partie. Coléoptères et autres orders*. J. Tastu, Paris, vii + 716 p.

Breuning, S. (1938a) Einige neue Cerambyciden aus den Sammlungen des Nationalmuseums Prag. (Col.). *Acta Entomologica Musei Nationalis Pragae Cechoslovakensis* 16, 93–96.

Breuning, S. (1938b) Nouveaux Cerambycidae (Col.). *Novitates Entomologicae* 8, 30–63.

Breuning, S. (1938c) Novae species Cerambycidarum VI. *Festschrift zum 60, Geburtstage von Professor Dr. Embrik Strand* 4, 180–392.

Breuning, S. (1939a) Neue Lamiinae (Cerambycidae, Coleoptera) aus dem Museo Civico di Storia Naturale in Genua. *Memorie della Società Entomologica Italiana* 18, 53–79.

Breuning, S. (1939b) Novae species Cerambycidarum VII. *Festschrift zum 60, Geburtstage von Professor Dr. Embrik Strand* 5, 144–290.

Breuning, S. (1940) Novae species Cerambycidarum X. *Folia Zoologica et Hydrobiologica* 10, 407–437.

Breuning, S. (1942) Novae species Cerambycidarum XI. *Folia Zoologica et Hydrobiologica* 11, 113–175.

Breuning, S. (1943) Novae species Cerambycidarum XII. *Folia Zoologica et Hydrobiologica* 12, 12–66.

Breuning, S. (1948) Nouvelles formes de Lamiaires (deuxième partie). *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 24, 1–47.

Breuning, S. (1950) Quelques nouveaux Lamiaires (Coleoptera, Cerambycidae) du Riksmuseum. *Arkiv för Zoologi* 1, 265–274.

Breuning, S. (1955) Nouveaux Lamiaires du Muséum national d'Histoire Naturelle (2e Note) [Col. Cerambycidae] (suite). *Bulletin de la Société Entomologique de France* 60, 70–77.

Breuning, S. (1961a) *Catalogue des Lamiaires du Monde (Col. Ceramb.)*. Museums G. Frey, 4.

Tutzing bei München, 183–284 pp.

Breuning, S. (1961b) Neue Cerambyciden aus den sammlungen des Zoologischen Museums der Humboldt-Universität zu Berlin (Coleoptera, Cerambycidae). *Mitteilungen aus dem Zoologischen Museum in Berlin* 37, 297–328.

Breuning, S. (1961c) Neue oder schlecht bekannte Cerambyciden (Col.). *Entomologische Arbeiten aus dem Museum G. Frey* 12, 140–160.

Breuning, S. (1961d) Nouvellles formes de Lamiaires (Treizième Partie). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 37, 1–44.

Breuning, S. (1963a) Neue Lamiinae aus dem Museum G. Frey. *Entomologische Arbeiten aus dem Museum G. Frey* 14, 446–455.

Breuning, S. (1963b) Revision der Pteropliini der australischen Region (Coleoptera, Cerambycidae). *Entomologische Abhandlungen aus dem Staatliches Museum fur Tierkunde in Dresden* 29, 1–274.

Breuning, S. (1964) Neue Lamiinae (Col. Cerambycidae) aus den Beständen des Museums G. Frey. *Entomologische Arbeiten aus dem Museum G. Frey* 15, 725–730.

Breuning, S. (1965) Neue Cerambyciden aus den Sammlungen des Zoologischen Museums der Humboldt–Universität zu Berlin (Coleoptera, Cerambycidae) (vierter teil). *Mitteilungen aus dem Zoologischen Museum in Berlin* 41, 81–93.

Breuning, S. (1966) Neue Cerambyciden aus den Sammlungen des Zoologischen Museums der Humboldt-Universitat zu Berlin (Coleoptera, Cerambycidae). *Mitteilungen aus dem Zoologischen Museum in Berlin* 42, 229–258.

Breuning, S. (1968) Nouveaux Cerambycidae Lamiinae des collections du Muséum de Paris. *Bulletin de la Société Entomologique de France* 73, 225–232.

Breuning, S. (1969) *Catalogue des Lamiaires du Monde (Col. Ceramb.)*. Museums G. Frey, 11. Tutzing bei München, 865–1069 pp.

Breuning, S. (1970a) Nouveaux Coléoptères Cerambycidae Lamiinae des collections du Muséum de Paris. *Bulletin du Muséum National d'Histoire Naturelle* (2)42, 363–377.

Breuning, S. (1970b) Nouveaux Coléoptères Cerambycidae Lamiinae des collections du Muséum de Paris. *Bulletin du Muséum National d'Histoire Naturelle* (2)42, 460–488.

Breuning, S. (1970c) Révision des Nyctimenini, Hyborhabdini et Zygocerini (Coleoptera, Cerambycidae, Lamiinae). *Bulletin et Annales de la Société Entomologique de Belgique* 106, 77–117.

Breuning, S. (1972) Descriptions de cinq nouvelles espèces de Lamiinae de la coll. Chassot (Col. Cerambycidae). *Bulletin de la Société Entomologique de Mulhouse* 1972, 29–31.

Breuning, S. (1973a) Neue Formen von Lamiinae (Coleoptera). *Mitteilungen aus dem Zoologischen Museum in Berlin* 49, 41–45.

Breuning, S. (1973b) Neue Lamiinen (Coleoptera, Cerambycidae) aus der Sammlung des Ungarischen Naturwissenschaftlichen Museums. *Folia Entomologica Hungarica (n.s.)* 26, 9–17.

Breuning, S. (1978) Nouvelles espèces de Lamiinae (Cerambycidae) de la coll. Vives. *Miscellania Zoologica* 4, 131–136.

Breuning, S. (1979) Descriptions de nouveaux genres et espèces de Lamiinae (Col. Cerambycidae). *Bulletin de la Société Entomologique de Mulhouse* 1979, 13–15.

Breuning, S. (1982) Diagnoses préliminaires de nouveaux Lamiinae du Muséum National d'Histoire Naturelle de Paris [Coleoptera, Cerambycidae]. *Annales de la Société Entomologique de France (n.s.)* 18, 9–29.

Dalman, J.W. (1817) *Sistens descriptiones novarum pecierum Schönherr C.J.: Appendix ad C.J. Schönherr Synonymian Insectorum*. Lewerentziana, Scari, Vol. 1(3), 144 p.

Donovan, E. (1805) *An Epitome of the Natural History of the Insects of New Holland, New Zealand, New Guinea, Otaheite, and other Islands in the Indian, Southern, and Pacific Oceans: including the figures and descriptions of one hundred and fifty-three species*. E. Donovan, F.C. & J. Rivington, London, iv unnumbered pls 41 p.

Duffy, E.A.J. (1963) *A Monograph of the Immature Stages of Australasian Timber Beetles (Cerambycidae)*. British Museum (Natural History), London.

Fabricius, J.C. (1775) *Systema Entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*. Libraria Kortii, Flensburgi & Lipsiae, xxvii + 832 p.

Gahan, C.J. (1893) Notes on the longicornia of Australia and Tasmania. Part I., with a list of the species collected by Mr. J.J. Walker, R.N., F.L.S., and descriptions of new forms. *Transactions of the Entomological Society of London* 1893, 165–197.

Gemminger, M. & von Harold, E. (1873) Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus. *Munich* 10, 2989–3232.

Germar, E.F. (1848) Beiträge zur Insektenfauna von Adelaide. *Linnaea Entomologica* 3, 153–247.

Gilmour, E.F. (1950) New and rare Lamiinae. *Longicornia* 1, 537–556.

Guérin- Méneville, F.É. (1831) *Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de Sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825, sous le ministère et conformément aux instructions de S. E. M. Le Marquis de Clermont-Tonnerre, ministre de la marine; et publié sous les auspices de son Excellence Mgr. Le Cte De Chabrol, Ministre de la Marine et des Colonies, par M.L.I. Duperrey. Zoologie, par M. Lesson*. Arthus Bertrand, pl. 5, Tome second. — 2e partie. Paris.

Hall, T.J. (1980) Attack on the legume *Stylosanthes scabra* (Vog.) by *Platyomopsis pedicornis* (F.) (Coleoptera: Cerambycidae). *Journal of the Australian Entomological Society* 19, 277–279.

Hope, F.W. (1842) Observations on the Coleoptera of Port Essington, in Australia with descriptions of the following new species. *Annals and Magazine of Natural History* (1)9, 423–430.

Lea, A.M. (1912) On a new *Rhytiphora* in the National Museum Melbourne. *Memoires of the National Museum* 4, 33–35.

Lingafelter, S.W., Nearns, E.H., Tavakilian, G.L., Monné, M.A. & Biondi, M. (2014) *Longhorned Woodboring Beetles (Coleoptera: Cerambycidae and Disteniidae) Primary Types of the Smithsonian Institution*. Smithsonian Institution Scholarly Press, Washington, D.C., v–xviii + 1–390 pp.

Macleay, W.S. (1826) Appendix B. Annulosa. Catalogue of insects, collected by Captain King R.N. In: P. P. King (Ed), *Narrative of a survey of the intertropical and western coasts of Australia*. John Murray, London, pp. 438–469.

Matsushita, M. (1935) Beitrag zur cerambycidenfauna von Mikronesien. *Transactions of the Sapporo Natural History Society* 14, 115–122.

McKeown, K.C. (1938) Notes on Australian Cerambycidae IV. *Records of the Australian Museum* 20, 200–216.

McKeown, K.C. (1942) Australian Cerambycidae VI. Descriptions of new species mostly from Queensland. *Records of the Australian Museum* 21, 81–105.

McKeown, K.C. (1947) Catalogue of the Cerambycidae (Coleoptera) of Australia. *Australian Museum Memoir* 10, 1–190. https://doi.org/10.3853/j.0067-1967.10.1947.477

McKeown, K.C. (1948) Australian Cerambycidae VIII. Notes on a collection from the Western Australian Museum, with descriptions of new species. *Records of the Australian Museum*

22, 49–63.

Montrouzier, P. (1855) Faune de l'île de Woodlark ou Moiou. *Annales de la Société d'Agriculture de Lyon* 2, 1–114.

Newman, E. (1838) Entomological notes. *The Entomological Magazine* 5, 483–500.

Newman, E. (1842a) Entomological notes, CXII (continued). *The Entomologist* 1, 413–415.

Newman, E. (1842b) List of insects collected at Port Philip, South Australia, by Edmund Thomas Higgins, Esq. *The Entomologist* 1, 361–369.

Newman, E. (1851) Descriptions of new insects from New Holland. *The Zoologist* 9, appendix cxxviii–cxxxii.

Olliff, A.S. (1890) Contributions towards a knowledge of the Coleoptera of Australia. VI. New Lamellicornia and Longicornia. *Proceedings of the Linnean Society of New South Wales* (2)5, 1–11.

Pascoe, F.P. (1857) On new genera and species of Longicorn Coleoptera, part II. *Transactions of the Entomological Society of London (n.s.)* 4, 97–112.

Pascoe, F.P. (1858) On new genera and species of Longicorn Coleoptera, part III. *Transactions of the Entomological Society of London (n.s.)* 2, 236–266.

Pascoe, F.P. (1859) On new genera and species of Longicorn Coleoptera, part IV. *Transactions of the Entomological Society of London (n.s.)* 1–2, 12–61.

Pascoe, F.P. (1862a) Notices of new or little-known genera and species of Coleoptera, part III. *Journal of Entomology* 1, 319–370.

Pascoe, F.P. (1862b) On some new Coleoptera from Lizard Island, north-eastern Australia. *Annals and Magazine of Natural History* 3, 461–467.

Pascoe, F.P. (1863) Notes on the Australian longicornia, with descriptions of sixty new species. *Transactions of the Entomological Society of London* (3)1, 526–570.

Pascoe, F.P. (1864a) Descriptions of some new Australian Longicornia. *Journal of Entomology* 2, 223–245.

Pascoe, F.P. (1864b) Longicornia Malayana; or, a descriptive catalogue of the species of the three longicorn families Lamiidae, Cerambycidae and Prionidae collected by Mr. A. R. Wallace in the Malay Archipelago. *Transactions of the Entomological Society of London* (3)3, 1–96.

Pascoe, F.P. (1865) A second series of descriptions of new Australian longicornia. *Journal of Entomology* 2, 352–374.

Pascoe, F.P. (1866) On the Longicornia of Australia, with a list of all the described species. *Journal of the Linnean Society, Zoology* 9, 80–112.

Pascoe, F.P. (1867) Supplement to the list of Australian longicornia. *Journal of the Linnean Society, Zoology* 9, 300–308.

Pascoe, F.P. (1869) Descriptions of some new species of Lamiidae. *Annals and Magazine of Natural History* (4)3, 203–211.

Pascoe, F.P. (1875) Notes on Coleoptera, with descriptions of new genera and species, part III. *Annals and Magazine of Natural History* (4)15, 59–73.

Pic, M. (1925) Nouveautés diverses. *Mélanges Exotico-Entomologiques* 44, 1–32.

Roguet, J.-P. (2020) Lamiaires du Monde. Available from: https://lamiinae.org (April 17, 2020)

Sharp, D. (1878) On some Longicorn Coleoptera from the Hawaiian Islands. *Transactions of the Entomological Society of London* 1878, 201–210.

Sirait, B.A., Sinulingga, N.G.H.B., Samosir, M.N., Tavares, W. de S., Kkadan, S.K., Tarigan, M. & Duran, A. (2020) First Report of *Myllocerus scapularis* Roelofs (Coleoptera: Curculionidae) and *Rhytiphora bankii* (Fabricius) (Coleoptera: Cerambycidae) on Commercial Plantings of *Acacia crassicarpa* (Fabaceae) in Indonesia. *The Coleopterists Bulletin* 74, 404–407. https://doi.org/10.1649/0010-065X-74.2.404

Ślipiński, A. & Escalona, H.E. (2013) *Australian Longhorn Beetles (Coleoptera: Cerambycidae) Volume 1: Introduction and Subfamily Lamiinae*. CSIRO Publishing, Melbourne, 503 pp.

Švácha, P. & Lawrence, J.F. (2014) Cerambycidae Latreille, 1802. In: R. A. B. Leschen and R. G. Beutel (Eds), *Handbook of Zoology, Arthropoda: Insecta, Coleoptera, Beetles, Volume 3: Morphology and Systematics (Phytophaga)*. Walter de Gruyter GmbH, Berlin, pp. 77–177.

Tavakilian, G. & Chevillotte, H. (2020) Base de données Titan sur les Cerambycidés ou Longicornes. Available from: http://titan.gbif.fr/ (February 13, 2020)

Tavakilian, G. & Nearns, E.H. (2014a) New nomenclatural changes for 2014: I. The genus *Rhytiphora* Audinet-Serville, 1835 (Coleoptera, Cerambycidae, Lamiinae). *Les Cahiers Magellanes (NS)* 15, 99–108.

Tavakilian, G. & Nearns, E.H. (2014b) New nomenclatural changes for 2014: II. Corrigendum & Addenda (Coleoptera, Cerambycidae). *Les Cahiers Magellanes (NS)* 16, 157–158

Thomson, J. (1860) *Essai d'une classification de la famille des cérambycides et matériaux pour servir à une monographie de cette famille*. Paris, xvi + 128 p.

Thomson, J. (1864) Systema Cerambycidarum ou exposé de tous les genres compris dans la famille des Cérambycides et familles limitrophes. *Mémoires de la Société Royale des Sciences de Liège* 19, 1–540.

Webb, G.A. (1987) Larval host plants of Cerambycidae (Coleoptera) held in some Australian insect collections. *Technical Paper, Forestry Commission of New South Wales* 38, 1–19.

White, A. (1858) Descriptions of some apparently unrecorded species of longicorn beetles, belonging to the genera *Phrissoma*, *Nyphona*, &c. *Annals and Magazine of Natural History* (3)2, 264–276.

White, A. (1859) Descriptions of unrecorded species of Australian Coleoptera of the families Carabidae, Buprestidae, Lamellicornia, Longicornia, etc. *Proceedings of the Zoological Society of London* 1859, 117–123.

SUPPLEMENTARY INFORMATION (FIGURES S1–5, TABLE S1)

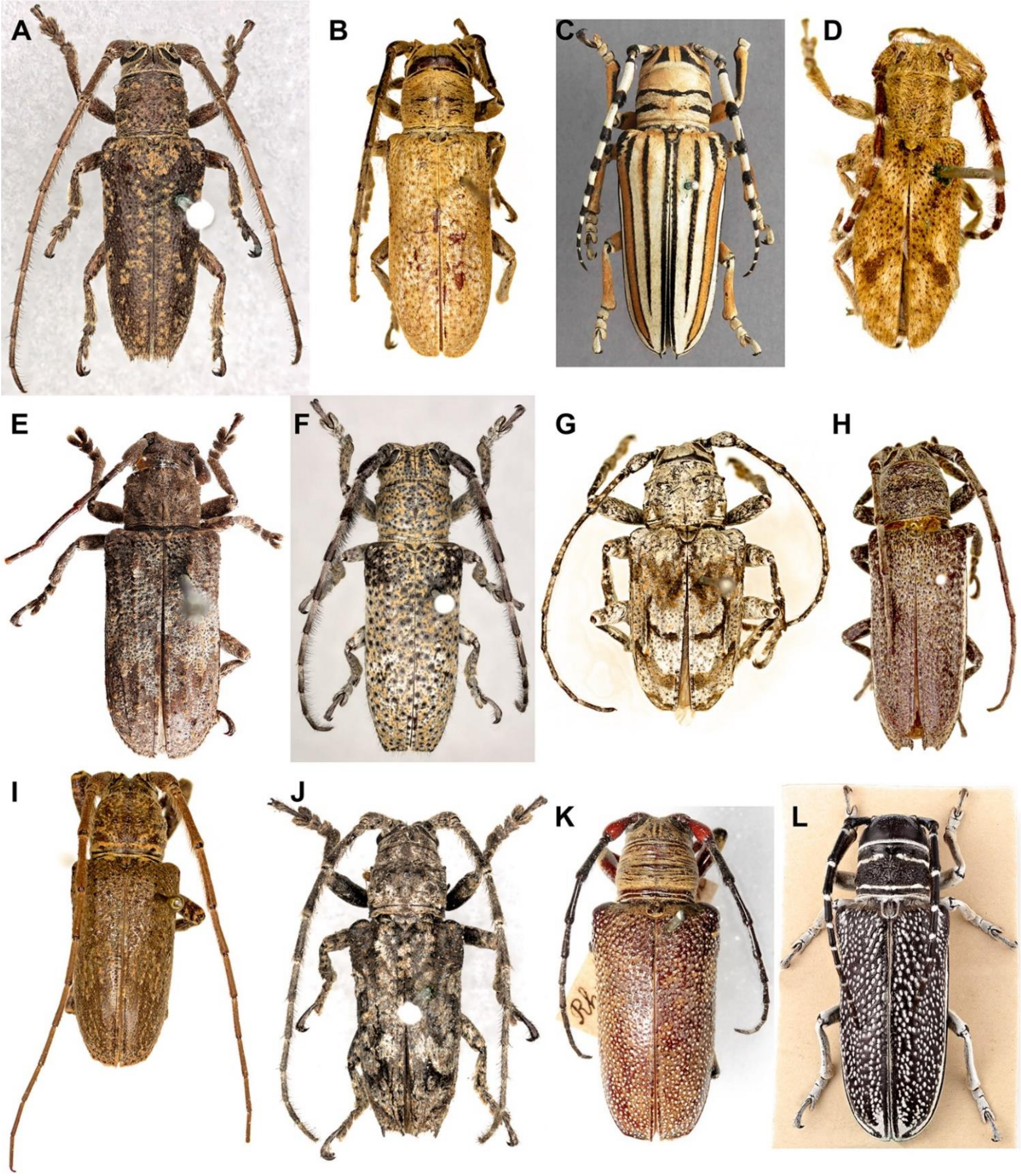

Figure S1. *Rhytiphora* species, holotypes (A–J) and reference photos (K–L). **A:** *Rhytiphora detrita* Hope. **B:** *Mesiphiastus (Pubiphiastus) laterialbus* Breuning. **C:** *Rhytiphora macleayi* Lea. **D:** *Corrhenes (Corrhenes) paulla fuscosignata* Breuning. **E:** *Acanthocinus piliger* Macleay. **F:** *Rhytiphora piperitia* Hope. **G:** *Menyllus rotundipennis* Breuning. **H:** *Rhytiphora (Rhytiphora) subargentata* Breuning. **I:** *Rhytiphora (Saperdopsis) tenimberensis* Breuning [*R. sundaensis*]. **J:** *Rhytiphora tuberculata* Hope. **K:** *Rhytiphora rugicollis* (Dalman). **L:** *Rhytiphora frenchiana* Breuning.

Figure S2. *Rhytiphora* species, holotypes. **A:** *Prosoplus (Prosoplus) demarzi* Breuning. **B:** *Prosoplus elongatus* Breuning. **C:** *Platyomopsis frenchi* Blackburn. **D:** *Notocorrhenes freyi* Breuning. **E:** *Hathlia grammica* Pascoe. **F:** *Rhytiphora leucospila* Gahan. **G:** *Penthea lichenosus* McKeown. **H:** *Xiphohathlia lobata* Breuning. **I:** *Penthea macularia* Pascoe. **J:** *Sysspilotus macleayi* Pascoe. **K:** *Menyllus maculicornis* Pascoe.

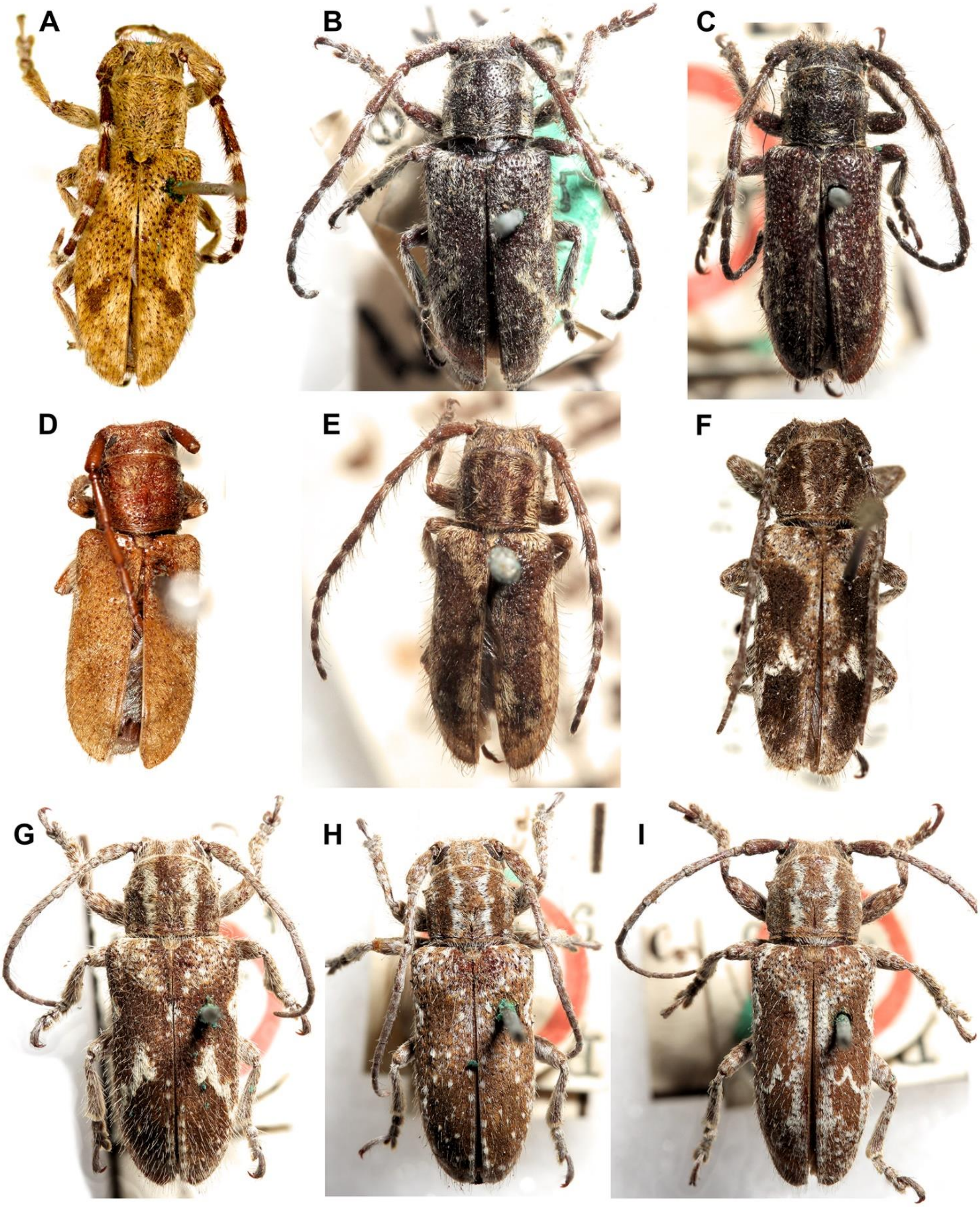

Figure S3. *Rhytiphora paulla* and similar species, holotypes. **A:** *Corrhenes (Corrhenes) paulla fuscosignata* Breuning. **B:** *Corrhenes (Corrhenes) paulla grisea* Breuning. **C:** *Saperda funesta* Pascoe. **D:** *Cobria rufa* Breuning. **E:** *Corrhenes flavovittata* Breuning. **F:** *Corrhenes (Corrhenes) flavovittata demarzi* Breuning [*R. rentzi*]. **G:** *Saperda stigmatica* Pascoe. **H:** *Corrhenes guttulata* Pascoe. **I:** *Saperda mystica* Pascoe.

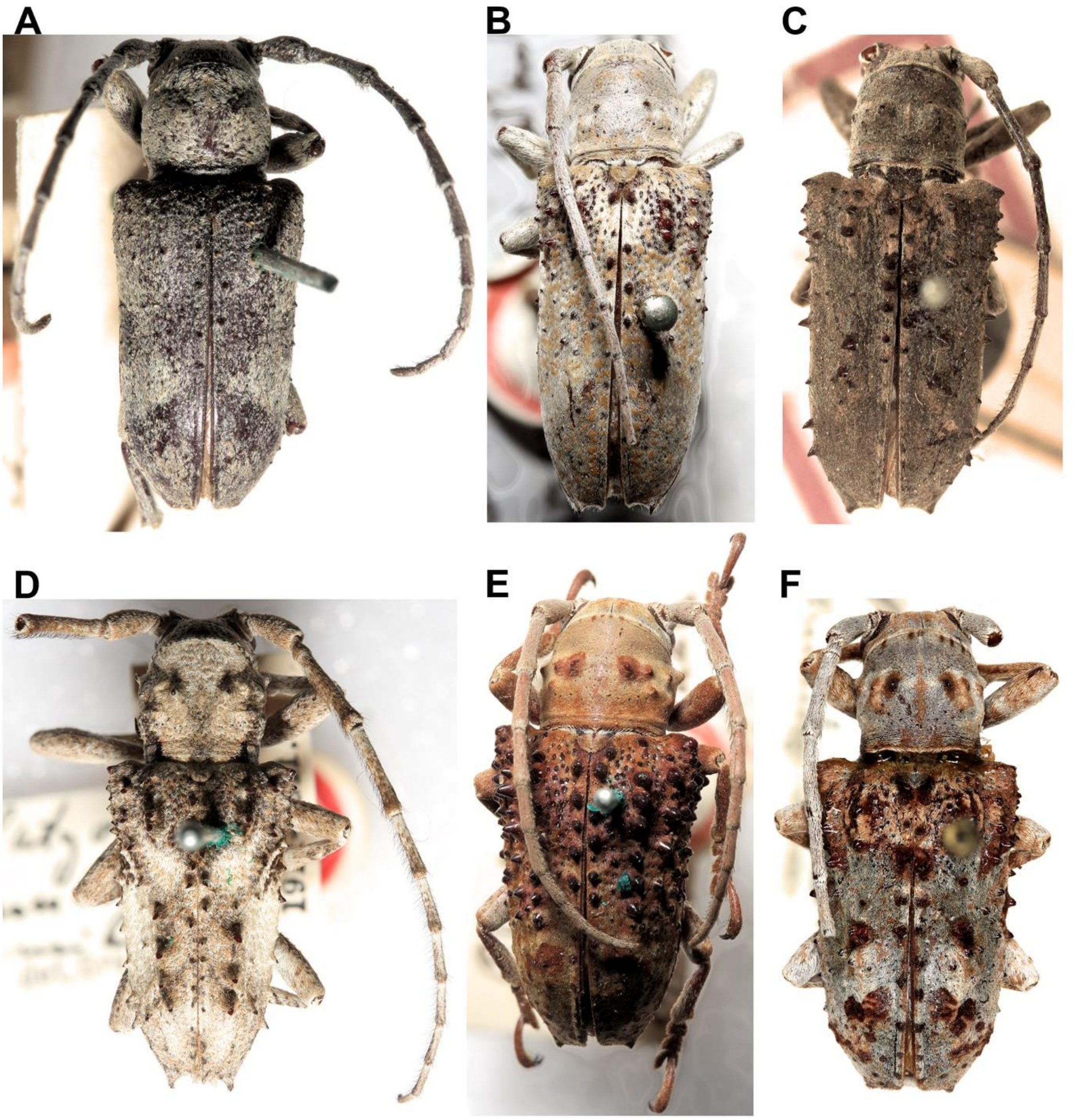

Figure S4. *Rhytiphora frenchi* and similar species, holotypes (A–E) and reference photo (F). **A:** *Platyomopsis frenchi* Blackburn. **B:** *Symphyletes armatulus* White. **C:** *Platyomopsis spinosa* Thomson. **D:** *Platyomopsis multispinis* Breuning. **E:** *Platyomopsis regularis* Gahan. **F:** *Rhytiphora (Platyomopsis) subregularis* Breuning.

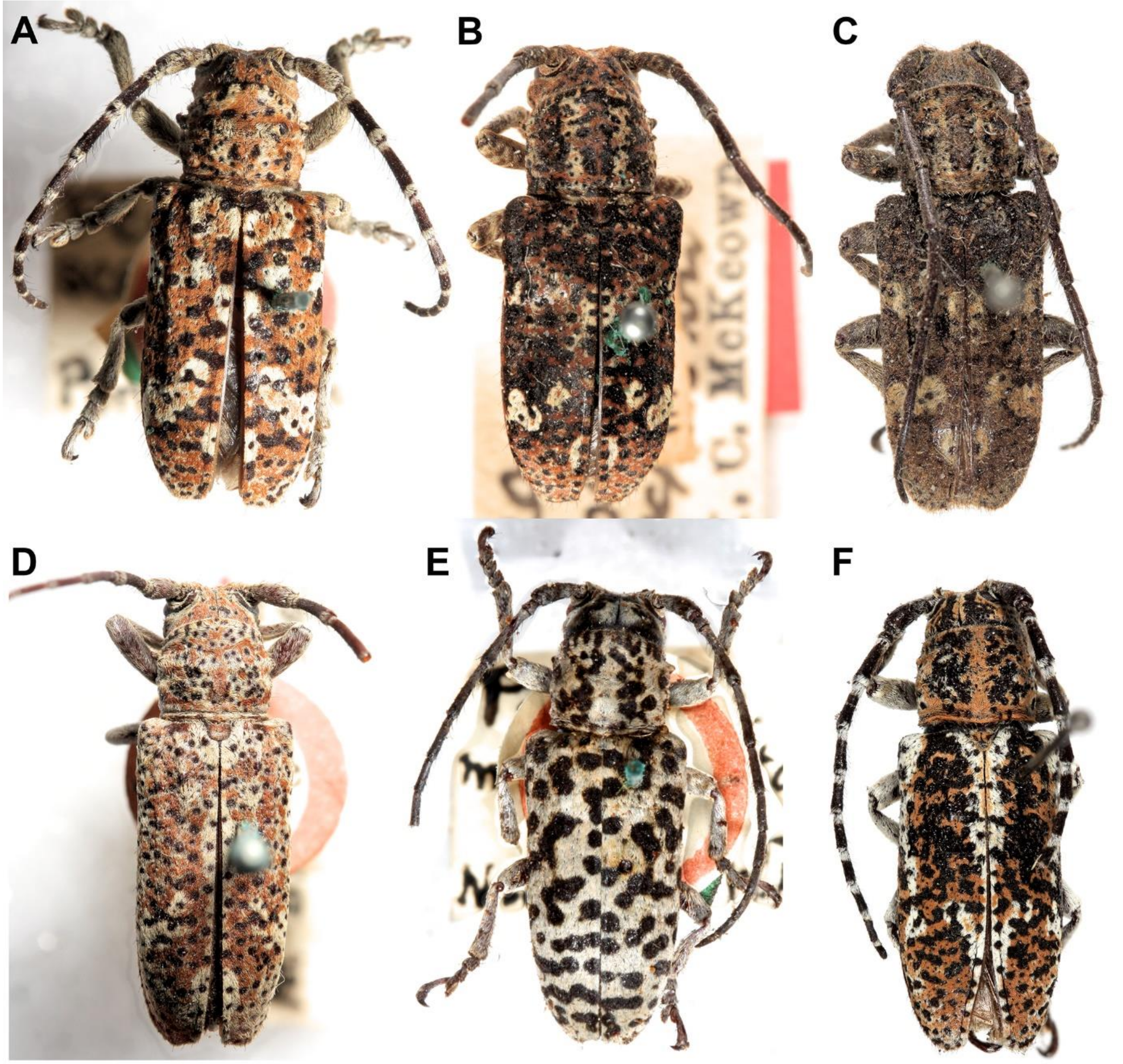

Figure S5. *Rhytiphora scenica* and similar species, holotypes. **A:** *Penthea scenica* Pascoe. **B:** *Penthea lichenosus* McKeown. **C:** *Penthea (Melanopenthea) obscura* Breuning. **D:** *Penthea mastersi* Blackburn. **E:** *Penthea melanosticta* Pascoe. **F:** *Penthea pardalina* Breuning.

Chapter 3: Supplementary Information (Figures S1–5, Table S1)

Table S1. Host plant records for *Rhytiphora* species.

Species	**Clade (if known)**	**Host plant (genus and species)**	**Host plant (family and order)**
albospilota	2	*Eucalyptus coolabah, E. pilularis*	Myrtaceae, Myrtales
argentata	2	*Acacia* sp.; *Eucalyptus* sp.	Fabaceae, Fabales; Myrtaceae, Myrtales
argus		*Eucalyptus* sp.	Myrtaceae, Myrtales
armatula	2	*Melaleuca dealbata, M. viridiflora*	Myrtaceae, Myrtales
bakewelli	1	*Acacia* sp.; *Acradenia euodiiformis*; *Cytisus scoparius*; *Ficus macrophylla*; *Pararchidendron* sp.; *Xanthium occidentale*	Asteraceae, Asterales; Fabaceae, Fabales; Moraceae, Rosales; Rutaceae, Sapindales
bankii	1	*Acacia crassicarpa*; *Agave sisalana*; *Caesalpinia [Libidibia] ferrea*; *Cajanus indicus*; *Calotropis procera*; *Capparis* sp.; *Citrus* sp.; *Chenopodium auricomum*; *Crotalaria* sp.; *Erythrina* sp.; *Euphorbia* sp.; *Gossypium tomentosum*; *Hibiscus* sp.; *Leucaena glauca*; *Mimosa pigra*; *Prosopis* sp.; *Saccharum officinarum*; *Stylosanthes scabra*; *Xanthium occidentale*	Apocynaceae, Gentianales; Asparagaceae, Asparagales; Asteraceae, Asterales; Capparaceae, Brassicales; Chenopodaceae, Caryophyllales; Euphorbiaceae, Malpighiales; Fabaceae, Fabales; Malvaceae, Malvales; Poaceae, Poales; Rutaceae, Sapindales
basalis	1	*Acacia decurrens, A. parramattensis*	Fabaceae, Fabales
browni	2	*Acacia grasbyi*	Fabaceae, Fabales
collaris	2	*Acacia dealbata*, *A. decurrens*, *A. longifolia*, *A. mollissima*; *Allocasuarina distyla*; *Angophora* sp.; *Casuarina* sp.; *Dodonaea* sp.? ("hoy bush"); *Rosa* sp.; *Viminaria juncea*	Casuarinaceae, Fagales; Fabaceae, Fabales; Myrtaceae, Myrtales; Rosaceae, Rosales; Sapindaceae, Sapindales
crassicollis	2	*Atriplex lindleyi, A. pseudocampanulata, A. vesicaria*; *Chenopodium* sp.; *Eucalyptus camaldulensis*; *Salsola* sp.? ("roly poly")	Chenopodaceae, Caryophyllales; Myrtaceae, Myrtales
cretata	2	*Alphitonia excelsa*; *Casuarina cristata*	Casuarinaceae, Fagales; Rhamnaceae, Rosales
crucensis	2	*Casuarina* sp.	Casuarinaceae, Fagales
cruciata		*Dodonaea* sp.? ("fernleaf shrub")	Sapindaceae, Sapindales
dallasii	2	*Acacia* sp.	Fabaceae, Fabales
decipiens		*Acacia dealbata, A. longifolia*; *Allocasuarina* sp.	Casuarinaceae, Fagales; Fabaceae, Fabales
dentipes		*Acacia harpophylla*	Fabaceae, Fabales
detrita	2	*Acacia* sp.	Fabaceae, Fabales
devota		*Acacia* sp.; *Callistris* sp.; *Casuarina* sp.; *Citrus* sp.; *Crotalaria* sp.	Casuarinaceae, Fagales; Cupressaceae, Pinales; Fabaceae, Fabales; Rutaceae, Anacardiaceae
dispar		*Melaleuca* sp.	Myrtaceae, Myrtales
dispersa	1	*Vachellia farnesiana*	Fabaceae, Fabales

diva	1	*Cenchrus* sp.; *Cirsium vulgare*? ("black thistle"); *Crotalaria* sp.; *Glycine max*; *Leptospermum* sp.; *Medicago sativa*; *Mimosa pigra*; *Senna obtusifolia*; *Sesbania* sp.	Asteraceae, Asterales; Fabaceae, Fabales; Myrtaceae, Myrtales; Poaceae, Poales
farinosa		*Eucalyptus* sp.; *Melaleuca quinquenervia*	Myrtaceae, Myrtales
fraserensis		*Xanthorrhoea* sp.	Xanthorrhoeaceae, Asparagales
fulva		*Solanum nemophilum*?; *Xanthium occidentale*	Asteraceae, Asterales; Solanaceae, Solanales
fulvescens	2	*Sida cornifolia*? ("flannel weed")	Malvaceae, Malvales
granulosa	2	*Eucalyptus* sp.	Myrtaceae, Myrtales
intercalaris	1	*Xanthium occidentale*	Asteraceae, Asterales
intricata	2	*Acacia fimbriata*; *Eucalyptus crebra*	Fabaceae, Fabales; Myrtaceae, Myrtales
lateralis	2	*Acacia dealbata*; *Callytrix tetragona*; *Cassinia* sp.; *Dillwynia* sp.; *Leptospermum* sp.	Asteraceae, Asterales; Fabaceae, Fabales; Myrtaceae, Myrtales
lobata	1	*Eleocharis* sp.; *Mimosa pigra*	Cyperaceae, Poales; Fabaceae, Fabales
maculicornis		*Paraserianthes lophantha*	Fabaceae, Fabales
mista		*Acacia* sp.; *Allocasuarina* sp.; *Casuarina littoralis*; *Exocarpos* sp.	Casuarinaceae, Fagales; Fabaceae, Fabales; Santalaceae, Santalales
mjoebergi		*Argyrodendron actinophyllum*	Malvaceae, Malvales
modesta		*Acacia oxycedrus*	Fabaceae, Fabales
neglecta	2	*Acacia longifolia, A. mearnsii, A. melanoxylon, A. pendula*; *Camellia* sp.?; *Cedrela australis*; *Citrus* sp.; *Diospyros fasciculosa*; *Euroschinus falcata*; *Morus* sp.; *Pentaceras australe*; *Robinia* sp.; *Wisteria* sp.	Anacardiaceae, Meliaceae and Rutaceae, Sapindales; Ebenaceae and Theaceae, Ericales; Fabaceae, Fabales; Moraceae, Rosales
nigrovirens	2	*Acacia decurrens, A. juniperina, A. longifolia, A. mearnsii*; *Allocasuarina distyla*; *Alphitonia excelsa*; *Drypetes deplanchei*; *Ozothamnus diosmifolius*; *Persoonia* sp.; *Pittosporum revolutum, P. undulatum*; *Syzygium* sp.	Asteraceae, Asterales; Casuarinacea, Fagales; Fabaceae, Fabales; Myrtaceae, Myrtales; Pittosporaceae, Apiales; Proteaceae, Proteales; Putranjivaceae, Malpighiales; Rhamnaceae, Rosales
obliqua		*Angophora* sp.; *Eucalyptus* sp.; *Kunzea* sp.	Myrtaceae, Myrtales
oblita	1	*Acacia holosericea; Jacksonia purpurescens*; *Mimosa pigra*	Fabaceae, Fabales
pardalina		*Jacksonia thesioides*	Fabaceae, Fabales
pardalis	2	*Acacia aulacocarpa, A. cunninghamii, A. holosericea, A. leptostachya*; *Casuarina* sp.; *Eucalyptus* sp.	Casuarinaceae, Fagales; Fabaceae, Fabales; Myrtaceae, Myrtales
paulla		*Chrysanthemum* sp.; *Helichrysum* sp.; *Jacksonia purpurescens*; *Melaleuca* sp.; *Sclerolaena muricata* (as *Bassia quinquecuspis*); *Senecio quadridentatus*; *Xanthium occidentale, X. spinosa*	Asteraceae, Asterales; Chenopodaceae, Caryophyllales; Fabaceae, Fabales; Myrtaceae, Myrtales

pauxilla		*Calotropis procera*; *Ficus opposita*; *Mimosa pigra*	Apocynaceae, Gentianales; Fabaceae, Fabales; Moraceae, Rosales
pedicornis	2	*Alstonia* sp.? ("quinine bush"); *Casuarina equisetifolia*; *Cathormion umbellatum*; *Crotalaria* sp.? ("rattle pods"); *Eucalyptus polycarpa*; *Mimosa pigra*; *Stylosanthes scabra*; *Xanthorrhoea* sp.	Apocynaceae, Gentianales; Casuarinaceae, Fagales; Fabaceae, Fabales; Myrtaceae, Myrtales; Xanthorrhoeaceae, Asparagales
piligera	1	*Acacia decurrens, A. mearnsii*; *Eucalyptus* sp.; *Exocarpos* sp.; *Leptospermum* sp.? ("tea-scrub"); *Xanthorrhoea* sp.	Fabaceae, Fabales; Myrtaceae, Myrtales; Santalaceae, Santalales; Xanthorrhoeaceae, Asparagales
piperitia	2	*Acacia auriculiformis*; *Bauhinia* sp.; *Casuarina equisetifolia*; *Mimosa pigra*; *Peltophorum pterocarpum*	Casuarinaceae, Fagales; Fabaceae, Fabales
polymita		*Acacia pendula*	Fabaceae, Fabales
pubiventris		*Avicennia marina*; *Citrus limonia*; *Melaleuca uncinata*	Acanthaceae, Lamiales; Myrtaceae, Myrtales; Rutaceae, Sapindales
pulverulens	2	*Acacia bidwillii, A. longifolia, A. penninervis*; *Apophyllum anomalum*; *Avicennia marina*; *Cajanus indicus*; *Citrus* sp.; *Codonocarpus cotinifolius*; *Commersonia bartramia*; *Eugenia* sp.; *Ficus* sp.; *Mimosa pigra*; *Tamarix aphylla*; *Wisteria* sp.	Acanthaceae, Lamiales; Capparaceae and Gyrostemonaceae, Brassicales; Fabaceae, Fabales; Malvaceae, Malvales; Moraceae, Rosales; Myrtaceae, Myrtales; Rutaceae, Sapindales; Tamaricaceae, Caryophyllales
pustulosa	1	*Ficus opposita*; *Homalanthus populifolius*	Euphorbiaceae, Malpighiales; Moraceae, Rosales
regularis	2	*Corymbia* sp.? ("bloodwood"); *Eucalyptus* sp.	Myrtaceae, Myrtales
rentzi		*Tagetes minuta*	Asteraceae, Asterales
rosei		*Acacia harpophylla, A. pendula*	Fabaceae, Fabales
rotundipennis	1	*Dodonaea* sp.? ("wild hop bush")	Sapindaceae, Sapindales
rubeta	2	*Acacia linifolia, A. longifolia, A. parramattensis*	Fabaceae, Fabales
rugicollis	2	*Acacia longifolia*; *Eucalyptus saligna*	Fabaceae, Fabales; Myrtaceae, Myrtales
sannio		*Eucalyptus coolibah, E. microcarpa*	Myrtaceae, Myrtales
saundersii	2	*Acacia* sp.; *Hakea* sp.	Fabaceae, Fabales; Proteaceae, Proteales
scenica		*Tephrosia astragaloides*	Fabaceae, Fabales
sellata	2	*Acacia harpophylla*	Fabaceae, Fabales
solandri	2	*Xanthorrhoea australis, X. resinosa*	Xanthorrhoeaceae, Asparagales
sospitalis		*Acacia saligna*; *Hakea linearis*	Fabaceae, Fabales; Proteaceae, Proteales
stigmatica		*Medicago sativa*	Fabaceae, Fabales
torquata	2	*Pleiogynium timoriense*	Anacardiaceae, Sapindales
variolosa	2	*Acacia decurrens, A. longifolia*	Fabaceae, Fabales
vermicularia		*Acacia decurrens, A. linifolia*	Fabaceae, Fabales

Conclusion

THESIS SUMMARY

The phylogenetic relationships within the superfamily Chrysomeloidea, and the internal structure of the diverse family Cerambycidae, have been long debated. The single published molecular study on the tribal classification of the subfamily Lamiinae (Souza *et al.* 2020) does not include any Australian taxa, so their placement in widespread Northern Hemisphere tribes has not been properly assessed. I used genomic-level sequencing to reconstruct the phylogeny of *Rhytiphora* and other Australasian lamiine genera, placing them in a worldwide context by including other taxa sequenced by the McKenna lab (partly published in Haddad *et al.* 2018). I performed fossil-calibrated dating analyses and examined the biogeographic history of the Australasian Lamiinae. I discovered that the Australian lamiine genera have multiple origins, with one clade of old endemic taxa (including all the New Zealand lamiines) and another clade of Asian-derived taxa (including *Rhytiphora* and many related Asian genera that also have male sex patches). Consequently, I updated the tribal classification of the sampled Australasian genera, moving *Rhytiphora* into the reinstated tribe Niphonini. This is the first time the Australasian Lamiinae have been examined in a phylogenetic context, and my research illuminates the evolutionary history of this important insect group.

Rhytiphora is Australia's largest cerambycid genus, yet very little is known about its internal species relationships, morphological evolution or biogeographic history. I reconstructed the species-level phylogeny of the Australian *Rhytiphora* from mitochondrial sequence data, and then mapped the species' biome distributions and morphological traits. I found that the Australian *Rhytiphora* species form two distinct clades, corresponding to nine morphological traits (such as body size and sex patch type). One of these genetic clades is mostly restricted to the northern parts of Australia, while the other clade has spread south across the continent. These results provide valuable insight into the unparalleled radiation of *Rhytiphora* in Australia.

The taxonomy of the Australian *Rhytiphora* species has not been reviewed since Ślipiński & Escalona (2013) synonymised 38 former genera with similar morphological traits: in particular, setose sex patches on the male abdomen. I produced a new morphological definition of *Rhytiphora* within the context of the Asian-Australian tribe Niphonini, including key traits of its two genetic clades (as established in the previous chapters). Following careful examination of Australian insect collections and available type specimens (mostly in European institutions), I updated the number of Australian species from 206 to 162, revised the *collaris* group, and described a new species from Queensland. This review establishes a much clearer picture of the Australian species diversity of *Rhytiphora*, and provides a framework for future research into this charismatic genus.

FUTURE STUDIES

My research provides our first glimpse into the phylogenetic relationships of the Australasian Lamiinae; however, much work remains to be done before these genera can be properly sorted into tribes. The remaining half of the Australian and New Zealand genera, and ideally all of the type genera of the lamiine tribes, will need to be sequenced and added to the existing phylogeny. There are also many Asian Pteropliini genera that have not been sampled, which may belong in Niphonini (with *Rhytiphora*) or a different tribe. Paraphyletic trans-Tasman genera, such as *Somatidia* and *Stenellipsis*, need to be examined in more detail. Sampling more taxa from Melanesia and South America will help clarify the biogeographic history of the Australasian region (i.e. the potential Gondwanan origin). Other types of molecular data, such as transcriptomes, could also prove useful in resolving the position of rogue taxa and other poorly supported nodes (Misof *et al.* 2014).

The mitochondrial phylogeny, while unprecedented, only covers about 50% of the Australian *Rhytiphora* species: we have only seen half of the picture. Denser taxon sampling, especially for the rarely collected arid zone species, is required. More *Rhytiphora* species from New Guinea should be included as well, especially for biogeographic analyses; so far, only six specimens from New Guinea have been sequenced. And of course, we should not focus exclusively on lab work and forget the need to collect more specimens in the field. A lot of *Rhytiphora* species are only recorded from light traps, with no knowledge of their host plants, life histories or population numbers.

The updated checklist of Australian *Rhytiphora* species incorporates 41 taxonomic changes, mostly synonymies, resulting in a new total of 162 species. There are, however, many outstanding taxonomic issues that will require detailed population-level sequencing to resolve, such as the *R. bankii*, *R. paulla* and *R. pulverulens* species complexes. Mitochondrial

DNA is the easiest to obtain from historical museum specimens, but can be unreliable where introgression has occurred between closely related lineages (Toews & Brelsford 2012); methods that sequence restriction enzyme fragments of the genome could be a suitable alternative (e.g. hyRAD; Suchan *et al.* 2016). A full taxonomic revision of the Australian *Rhytiphora* would address these species complexes, and would also involve designating neotypes for those species where the original holotype is considered to have been lost. Finally, a similar review should be conducted on the non-Australian *Rhytiphora* species, i.e. those from Asia and Melanesia. It is likely that New Guinea is almost as species-rich as Australia, but the fauna has not been well studied.

References

Akbulut, S. & Stamps, W.T. (2012) Insect vectors of the pinewood nematode: a review of the biology and ecology of *Monochamus* species. *Forest Pathology* 42, 89–99. https://doi.org/10.1111/j.1439-0329.2011.00733.x

Allison, J.D., Borden, J.H. & Seybold, S.J. (2004) A review of the chemical ecology of the Cerambycidae (Coleoptera). *Chemoecology* 14, 123–150. https://doi.org/10.1007/s00049-004-0277-1

Bi, K., Linderoth, T., Vanderpool, D., Good, J.M., Nielsen, R. & Moritz, C. (2013) Unlocking the vault: next-generation museum population genomics. *Molecular Ecology* 22, 6018–6032. https://doi.org/10.1111/mec.12516

Duffy, E.A.J. (1963) *A Monograph of the Immature Stages of Australasian Timber Beetles (Cerambycidae)*. British Museum (Natural History), London.

Farrell, B.D. & Sequeira, A.S. (2004) Evolutionary rates in the adaptive radiation of beetles on plants. *Evolution* 58, 1984–2001. https://doi.org/10.1554/03-453

Froggatt, W.W. (1923) *Forest Insects of Australia*. Government Printer, Sydney, 171 pp.

Gómez-Zurita, J., Hunt, T. & Vogler, A.P. (2008) Multilocus ribosomal RNA phylogeny of the leaf beetles (Chrysomelidae). *Cladistics* 24, 34–50. https://doi.org/10.1111/j.1096-0031.2007.00167.x

Goodwin, S., Pettit, M.A. & Spohr, L.J. (1994) *Acalolepta vastator* (Newman) (Coleoptera: Cerambycidae) infesting grapevines in the Hunter Valley, New South Wales 1. Distribution and dispersion. *Australian Journal of Entomology* 33, 385–390. https://doi.org/10.1111/j.1440-6055.1994.tb01257.x

Gressitt, J.L. (1956) Some distribution patterns of Pacific Island faunae. *Systematic Zoology* 5, 11–47. https://doi.org/10.2307/2411649

Haddad, S. & McKenna, D.D. (2016) Phylogeny and evolution of the superfamily Chrysomeloidea (Coleoptera: Cucujiformia). *Systematic Entomology* 41, 697–716. https://doi.org/10.1111/syen.12179

Haddad, S., Shin, S., Lemmon, A., Lemmon, E., Svacha, P., Farrell, B., Ślipiński, A., Windsor, D. & McKenna, D. (2018) Anchored hybrid enrichment provides new insights into the phylogeny and evolution of longhorned beetles (Cerambycidae). *Systematic Entomology*

43, 68–89. https://doi.org/10.1111/syen.12257

Haseler, W.H. (1966) The status of insects introduced for the biological control of weeds in Queensland. *Australian Journal of Entomology* 5, 1–4. https://doi.org/10.1111/j.1440-6055.1966.tb00668.x

Hawkeswood, T.J. (1985) New larval host plants for ten Australian longicorns (Coleoptera, Cerambycidae). *Giornale Italiano di Entomologia* 2, 393–398.

Jarvis, H. & Smith, J.H. (1946) Lucerne Pests. *Queensland Agricultural Journal* 62, 79–89.

Jin, M., Zwick, A., Ślipiński, A., Marris, J.W.M., Thomas, M.C. & Pang, H. (2020) A comprehensive phylogeny of flat bark beetles (Coleoptera: Cucujidae) with a revised classification and a new South American genus. *Systematic Entomology* 45, 248–268. https://doi.org/10.1111/syen.12392

Lemmon, A.R., Emme, S.A. & Lemmon, E.M. (2012) Anchored hybrid enrichment for massively high-throughput phylogenomics. *Systematic Biology* 61, 727–744. https://doi.org/10.1093/sysbio/sys049

Lemmon, E.M. & Lemmon, A.R. (2013) High-throughput genomic data in systematics and phylogenetics. *Annual Review of Ecology, Evolution, and Systematics* 44, 99–121. https://doi.org/10.1146/annurev-ecolsys-110512-135822

Lingafelter, S.W. & Hoebeke, E.R. (2002) *Revision of the genus Anoplophora (Coleoptera: Cerambycidae).* Entomological Society of Washington, Washington, D.C., 236 pp.

Linsley, E.G. (1959) Ecology of Cerambycidae. *Annual Review of Entomology* 4, 99–138.

Marvaldi, A.E., Duckett, C.N., Kjer, K.M. & Gillespie, J.J. (2009) Structural alignment of 18S and 28S rDNA sequences provides insights into phylogeny of Phytophaga (Coleoptera: Curculionoidea and Chrysomeloidea). *Zoologica Scripta* 38, 63–77. https://doi.org/10.1111/j.1463-6409.2008.00360.x

McKeown, K.C. (1938) Notes on Australian Cerambycidae IV. *Records of the Australian Museum* 20, 200–216.

Misof, B., Liu, S., Meusemann, K., Peters, R.S., Donath, A., Mayer, C., Frandsen, P.B., Ware, J., Flouri, T., Beutel, R.G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler, T., Rust, J., Aberer, A.J., Aspöck, U., Aspöck, H., Bartel, D., Blanke, A., Berger, S., Böhm, A., Buckley, T.R., Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M., Greve, C., Grobe, P., Gu, S., Huang, Y., Jermiin, L.S., Kawahara, A.Y., Krogmann, L., Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li, Z., Li, J., Lu, H., Machida, R., Mashimo, Y., Kapli, P., McKenna, D.D., Meng, G., Nakagaki, Y., Navarrete-Heredia, J.L., Ott, M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., von Reumont, B.M., Schütte, K., Sekiya, K., Shimizu, S., Slipinski, A., Stamatakis, A., Song, W., Su, X., Szucsich, N.U., Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein, M., Tong, X., Uchifune, T., Walzl, M.G., Wiegmann, B.M., Wilbrandt, J., Wipfler, B., Wong, T.K.F., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D.K., Yoshizawa, K., Zhang, Q., Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou, L., Ziesmann, T., Zou, S., Li, Y., Xu, X., Zhang, Y., Yang, H., Wang, J., Wang, J., Kjer, K.M. & Zhou, X. (2014) Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346, 763–767. https://doi.org/10.1126/science.1257570

Napp, D.S. (1994) Phylogenetic relationships among the subfamilies of Cerambycidae (Coleoptera-Chrysomeloidea). *Revista Brasileira de Entomologia* 38, 265–419.

Nie, R., Vogler, A.P., Yang, X.-K. & Lin, M. (2021) Higher-level phylogeny of longhorn beetles (Coleoptera: Chrysomeloidea) inferred from mitochondrial genomes. *Systematic Entomology* 46, 56–70. https://doi.org/10.1111/syen.12447

Raje, K.R., Ferris, V.R. & Holland, J.D. (2016) Phylogenetic signal and potential for invasiveness. *Agricultural and Forest Entomology* 18, 260–269. https://doi.org/10.1111/afe.12158

Reid, C.A.M. (1995) A cladistic analysis of subfamilial relationships in the Chrysomelidae *sensu lato* (Chrysomeloidea). In: J. Pakaluk and A. Ślipiński (Eds), *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson. Vol. 2.* , pp. 559–631.

Schneider, D. (1964) Insect antennae. *Annual Review of Entomology* 9, 103–122.

Ślipiński, A. & Escalona, H.E. (2013) *Australian Longhorn Beetles (Coleoptera: Cerambycidae) Volume 1: Introduction and Subfamily Lamiinae*. CSIRO Publishing, Melbourne, 503 pp.

Ślipiński, A. & Escalona, H.E. (2016) *Australian Longhorn Beetles (Coleoptera: Cerambycidae) Volume 2: Subfamily Cerambycinae*. CSIRO Publishing, Melbourne, 613 pp.

Souza, D. de S., Marinoni, L., Laura Monné, M. & Gómez-Zurita, J. (2020) Molecular phylogenetic assessment of the tribal classification of Lamiinae (Coleoptera: Cerambycidae). *Molecular Phylogenetics and Evolution* 145, 106736. https://doi.org/10.1016/j.ympev.2020.106736

Suchan, T., Pitteloud, C., Gerasimova, N.S., Kostikova, A., Schmid, S., Arrigo, N., Pajkovic, M., Ronikier, M. & Alvarez, N. (2016) Hybridization capture using RAD probes (hyRAD), a new tool for performing genomic analyses on collection specimens. *PLOS ONE* 11, e0151651.

Švácha, P. & Danilevsky, M.L. (1987) Cerambycoid larvae of Europe and Soviet Union (Coleoptera, Cerambycoidea). Part 1. *Acta Universitatis Carolinae, Biologica* 30 [1986], 1–176.

Švácha, P. & Lawrence, J.F. (2014) Cerambycidae Latreille, 1802. In: R. A. B. Leschen and R. G. Beutel (Eds), *Handbook of Zoology, Arthropoda: Insecta, Coleoptera, Beetles, Volume 3: Morphology and Systematics (Phytophaga)*. Walter de Gruyter GmbH, Berlin, pp. 77–177.

Timmermans, M.J.T.N., Barton, C., Haran, J., Ahrens, D., Culverwell, C.L., Ollikainen, A., Dodsworth, S., Foster, P.G., Bocak, L. & Vogler, A.P. (2016) Family-level sampling of mitochondrial genomes in Coleoptera: compositional heterogeneity and phylogenetics. *Genome Biology and Evolution* 8, 161–175. https://doi.org/10.1093/gbe/evv241

Toews, D.P.L. & Brelsford, A. (2012) The biogeography of mitochondrial and nuclear discordance in animals. *Molecular Ecology* 21, 3907–3930. https://doi.org/https://doi.org/10.1111/j.1365-294X.2012.05664.x

Wang, J., Dai, X.-Y., Xu, X.-D., Zhang, Z.-Y., Yu, D.-N., Storey, K.B. & Zhang, J.-Y. (2019) The complete mitochondrial genomes of five longicorn beetles (Coleoptera: Cerambycidae) and phylogenetic relationships within Cerambycidae. *PeerJ* 7, e7633. https://doi.org/10.7717/peerj.7633

Wang, Q. ed. (2017) *Cerambycidae of the World: Biology and Pest Management*. Taylor & Francis Group, Boca Raton.

Webb, G.A. (1987) Larval host plants of Cerambycidae (Coleoptera) held in some Australian insect collections. *Technical Paper, Forestry Commission of New South Wales* 38, 1–19.