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**Phylogeny, systematics and evolution of calling songs of the Lebinthini crickets
(Orthoptera, Grylloidea, Eneopterinae), with description of two new genera**

Short title for header: systematics and evolution of Lebinthini

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Abstract

The Lebinthini crickets are distributed in Southeast Asia, Western Pacific, and tropical South America. They represent more than half of the described species in the subfamily Eneopterinae. These crickets are morphologically and behaviorally diverse, varying in body size, wing morphology (ranging from brachypterous to fully winged), and acoustic signals. They also have a distinctive communication system: high-frequency calling, vibratory signaling, duetting and lack of phonotaxis in females. To investigate how these traits evolved and diversified, a clear phylogenetic context is needed with taxonomic and biological data for as many species as possible. Since 2010, the numbers of known species and genera in the tribe have grown considerably, but the type genus *Lebinthus* and the tribe classification lacked a general revision based on phylogenetic inferences. In this paper, we study the systematics of the Lebinthini and present new phylogenetic results confirming the monophyly of Lebinthini and the relationships established by previous studies. The phylogeny allows us to define three monophyletic subtribes within the Lebinthini with clear morphological features and distribution areas: Cardiodactylina **subtribe n.**, Lebinthina **subtribe n.** and Ligypterina **subtribe n.** We also redefine *Lebinthus* and described two new genera related to *Lebinthus*, *Falcerminthus* **gen. nov.** and *Fadinthus* **gen. nov.**, each characterized by clear-cut morphological, anatomical, and acoustic features. Using ancestral state reconstructions, we investigate the evolution of the diverse calling songs in Lebinthini. We demonstrated that both trills and monosyllabic calls were acquired multiple times instead of evolving from simple to complex temporal patterns as suggested from previous studies. We also found that temporal traits and the dominant frequency evolve in a very dynamic way, and that the harmonic of the call that is the dominant frequency seems to undergo diversification in the subtribe Lebinthina.

Introduction

A wide variety of animals—such as insects, arachnids, fish, anurans, mammals and birds—use acoustic signals to choose mates and defend resources (Wilkins *et al.*, 2013). For individuals producing sound, the sound signals can pose a risk by also drawing the attention of predators and parasites (Wilkins *et al.*, 2013). The evolutionary consequences are that acoustic traits can exhibit various degrees of within- and between-species variation, driven by different natural or sexual selection pressures (e.g., Gerhardt, 1991; Gerhardt & Huber, 2002; Wilkins *et al.*, 2013). Therefore, how these traits and, in turn, acoustic communication evolve has long fascinated evolutionary biologists (Bradbury & Vehrencamp, 2011).

There are still large gaps in knowledge about the relative importance of different drivers of acoustic divergence and how acoustic divergence facilitates speciation (Wilkins *et al.*, 2013). While bats, birds, frogs, and crickets are among the best studied animals in the field of bioacoustics for addressing these questions, crickets and their relatives are particularly useful model organisms because of their small size, short generation time, and relatively simple mechanisms of sound production (Horch *et al.*, 2017). On a macroevolutionary scale, Song *et al.* (2020) recently demonstrated how sound production and hearing influenced species diversification in orthopterans. Given its broad scale, this study could not offer insights into how acoustics communication evolved in specific groups, which remain crucial to address because acoustic communication in different taxa can have vastly different evolutionary trajectories.

To investigate how acoustic traits evolved and diversified, a clear phylogenetic context is also needed, which necessitates prior taxonomic and biological studies for as many species as possible. This can be a challenge, especially for cricket species from hyper-diverse regions such as Southeast Asia, where rapid species diversification may have occurred (Dong *et al.*, 2018), and where many species remain undescribed or very poorly known, with little information beyond their original descriptions.

The Lebinthini crickets offer an opportunity to overcome these challenges and address questions on the evolution of acoustics traits. This is a diverse tribe within the subfamily Eneopterinae and is mostly distributed in Southeast Asia, the Western Pacific archipelagos, and northern South America (Vicente *et al.*, 2017). The tribe is characterized by its species richness, as it includes half of the extant described eneopterine genera (15/26 including two new genera described here), and more than half of the described species of the subfamily (Cigliano *et al.*, 2021). It also contains the most speciose eneopterine genus, *Cardiodactylus* Saussure, with more than 80 species (e.g., Otte, 2007; Robillard *et al.*, 2014; Dong & Robillard, 2016). The Lebinthini crickets are also highly diverse in terms of wing morphology, ranging from brachypterous to fully winged species, and acoustic signals. These crickets have an alternative communication system to most other crickets (ter Hofstede *et al.*, 2015), involving major changes in every component of the usual cricket system of communication: Males

produce high-frequency calls (10–28 kHz) (Robillard & Desutter-Grandcolas, 2004b), females lack phonotaxis and instead produce vibrational signals in response to male calls, and males locate females via vibrotaxis. This novel communication system was previously described for the Lebinthini from Asia, and a recent study demonstrated that it is also found in a Neotropical species, and is therefore likely shared by the whole tribe (Benavides-Lopez *et al.*, 2020). The same study dated the origin of this behavior to coincide with the origin of echolocation in bats and also documented male duets involving both acoustic and vibratory signals, another unique behavior for crickets (Benavides-Lopez *et al.*, 2020).

According to previous systematic studies, the tribe is a monophyletic group including three main lineages (e.g., Nattier *et al.*, 2011; Vicente *et al.*, 2017). One clade comprising the genera *Ponca* Hebard (long-winged) and *Ligypterus* Saussure (brachypterous) is distributed in the northern Neotropics. A second clade includes only long-winged species, belonging to the monophyletic genus *Cardiodactylus*, distributed in Asia and in the South-west Pacific region (e.g., Dong *et al.*, 2018), as well as a small genus including a few mute species distributed in Fiji and Samoa (*Swezwilderia* Chopard). Lastly, a third clade is composed of only brachypterous species, more diverse morphologically than *Cardiodactylus*, but sharing the same distribution area in Asia and in the South-west Pacific region as this genus.

Since 2010, the number of described brachypterous species and genera has increased considerably. These newly described taxa are thought to be related to the genus *Lebinthus* Stål, which appeared as a paraphyletic assemblage in several phylogenetic studies (Nattier *et al.* 2011; Anso *et al.* 2016). To clarify the taxonomy of this clade, several new genera were recently described from New Guinea [*Centuriarus* Robillard (Robillard, 2011a), *Gnominthus* Robillard & Vicente (Vicente *et al.*, 2015), *Microbinthus* Robillard & Dong, *Macrobinthus* Robillard & Dong (Robillard *et al.*, 2016)], New Caledonia [*Pixibinthus* Robillard & Anso (Anso *et al.*, 2016)], and Australia [*Julverninus* Robillard & Su (Robillard & Su, 2018)]. These descriptions distinguished clear morphological entities and made *Lebinthus* monophyletic in the most recent phylogenetic study (Vicente *et al.*, 2017). However, several new genera, previously considered as “*Lebinthus*”, remain undescribed. As a consequence of these taxonomic studies, the phylogenetic relationships within the Lebinthini need to be clarified and their classification revised.

In this paper, we studied the systematics of the Lebinthini with a focus on the species from Southeast Asia, and subsequently reconstructed their phylogeny. The phylogenetic results allowed us to define three monophyletic subtribes within the Lebinthini with distinct morphological features and distribution areas: *Cardiodactylina* **subtribe n.**, *Lebinthina* **subtribe n.** and *Ligypterina* **subtribe n.** The brachypterous species of Lebinthini distributed in Southeast Asia were split into three genera, which can be characterized morphologically and acoustically. We redefined the genus *Lebinthus* as a homogenous group characterized by

clear-cut morphological, anatomical, and acoustic features. We also described two new genera related to *Lebinthus*, *Falcerminthus* **gen. nov.** and *Fadinthus* **gen. nov.**, both characterized by easily recognized synapomorphies, and the taxonomic study also resulted in the description of two new species in the new genus *Fadinthus*.

We used this updated phylogenetic context to address questions about the evolution of the most characteristic features of the acoustic signals of these crickets. Few authors have analyzed the evolutionary origin of cricket song diversity (Alexander, 1962; Otte, 1992), and even more rarely in a phylogenetic context, due to the absence of detailed phylogenies for most cricket lineages. Only a few studies have been carried out at the genus level on *Gryllus* Linnaeus (Harrison & Bogdanovich, 1995; Huang *et al.* 2000; Desutter-Grandcolas & Robillard, 2003, Robillard *et al.* 2006) and *Laupala* Otte (Shaw, 1999), and at the subfamily level on eneopterine crickets (e.g., Robillard & Desutter-Grandcolas, 2004a, b, 2011). The exceptionally diverse calling songs in this clade make it ideal for this kind of phylogenetic study. We used the phylogenetic tree to reconstruct the ancestral states and estimate the phylogenetic signal of the main acoustic features of the calling songs: their general temporal pattern (i.e., structure of calling song and echeme structure), their frequency (value and nature of the dominant frequency). Specifically, we aimed to test the hypotheses formalized by Robillard & Desutter-Grandcolas (2011): (i) whether the temporal features of the eneopterine songs become more complex across species through evolutionary time; and (ii) whether the spectral features are more stable evolutionarily than temporal features, due to the fact that temporal features mostly depend on behavioral variables while spectral parameters are constrained by sound-producing morphological structures (e.g., Bennet-Clark, 1970, 2003; Nocke, 1971; Michelsen & Nocke, 1974; Elliott & Koch, 1985; Montealegre-Z. *et al.*, 2009).

Materials and methods

Taxonomy

The taxonomic analysis in this study resulted from international collaborative works that led to recent descriptions of numerous taxa from the Philippines (e.g., Robillard *et al.*, 2013; Robillard & Yap, 2015; Baroga-Barbecho *et al.*, 2020), Brunei Darussalam (e.g., Tan & Wahab, 2018), Malaysia (e.g., Tan *et al.*, 2019a, 2019b), Singapore (e.g., Robillard, 2011b; Robillard & Tan, 2013; Tan & Robillard, 2014), and Indonesia (e.g., Robillard *et al.*, 2014).

New field collections and observations were made by MKT and RW in the Belait and Temburong Districts of Brunei Darussalam between 23 February and 3 March 2019 and between 6 and 18 July 2019. Specimens were located visually both day and night to observe the crickets' habitat and different types of activity (e.g., calling, mating, foraging, and feeding).

Newly collected specimens were deposited in the collections of Universiti Brunei Darussalam Museum, Brunei Darussalam (UBDM) and Muséum national d'Histoire naturelle, Paris (MNHN). The other material examined for the taxonomic revisions and descriptions of new taxa belong to the collections of the MNHN and Zoological Institute, Russian Academy of Sciences, S. Petersburg (ZIN). Detailed lists of material presented in previous studies contributed to this synthetic work, but were not extensively recalled here, although relevant references are mentioned in the systematic part of this study.

Observations and morphological analysis

Direct observations and dissections were made using a binocular microscope (Leica model MZ16) at magnifications up to 115. Photographs of habitus and detailed morphology were made with a digital SLR camera (Canon EOS 6D) using a macro photo lens MP-E 65mm f/2.8 USM (1-5×). Image stacking using digital image processing software (Helicon Remote version 9.3.1. W and Helicon Focus 6.8.0) was used to increase the depth of field for photographs.

The terminology for male tegminal veins and cells follows Ragge (1955) and Robillard & Desutter-Grandcolas (2004a). Male and female genitalia dissection and imaging follow the methodology described in Salazar *et al.* (2020). Male genitalia terminology follows Desutter (1987), modified in Desutter-Grandcolas (2003) and Robillard & Desutter-Grandcolas (2004).

Abbreviations for general morphology, tegminal venation, male genitalia, and measurements follow Robillard & Desutter-Grandcolas (2004) and Robillard & Tan (2013).

Acoustic analyses

The basic cricket acoustic terminology follows Ragge & Reynolds (1998): a song unit is named syllable and corresponds to one opening-closure cycle of the male forewings; and group of syllables, named echeme, forms a call unit in the context of acoustic communication.

Species' call traits were obtained from published resources when available, or from newly recorded files (Supporting information Table S3). Acoustic features for the following species' calling songs are reported for the first time in this study: *Agnotecous albifrons* Desutter-Grandcolas, *A. azurensis* Desutter-Grandcolas, *A. chopardi* Desutter-Grandcolas, *A. clarus* Desutter-Grandcolas, *A. doensis* Desutter-Grandcolas, *A. meridionalis* Desutter-Grandcolas, *A. obscurus* (Chopard), *A. minoris* Robillard, *A. occidentalis* Desutter-Grandcolas, *Falcerminthus truncatipennis* (Chopard), and *Fadinthus tehtari* **sp. nov.** These species were recorded either in the field or in the laboratory, during or after field expeditions. We used a modified condenser microphone (Avisoft Bioacoustics, Berlin; model CM16), with a flat frequency response from 3 to 150 kHz (R. Specht pers. comm.); for recordings made in the field, the microphone was connected to a digital field recorder (Fostex FR-2LE; 96 kilo-samples

per second sampling frequency, 16 bit); in the laboratory, automatic recordings were made using the program Avisoft Triggering Harddisk Recorder version 2.97 and a 8-Pre MOTU sound card at a sampling frequency of 96 kilo-samples per second (16 bit). The calling song of *F. tehtari* **sp. nov.** was recorded with an Echo Meter Touch 1 with a Knowles FG sensor placed 50 cm away from the cage (25 cm in diameter and 33 cm tall) in which the male was housed.

For all species but *F. tehtari* **sp. nov.**, the recordings were analyzed with Avisoft-SASLab Pro version 4.40 (Specht, 2008). The recordings of *F. tehtari* **sp. nov.** were measured with Avisoft Lite 2.0.0 and using power spectra generated with Fast Fourier Transformation (FFT), with Hanning window of window length 512, and at 256,000 sampling frequency using the 'spec' function from the R package seewave (Sueur *et al.*, 2008) in the R software version 3.5.1 (R Development Core Team, 2018).

The temporal patterns of the songs were estimated on oscillograms. Two traits were coded to reflect the main types of temporal patterns in the calling songs in the subfamily as defined in Robillard & Desutter-Grandcolas (2011): one trait coded for the general type of temporal pattern (SONG): continuous trill, single-syllable call, or call structured in echemes; the second trait coded for the two main types of echemes found across the species (ECHE): echemes simple, where all syllables have more or less similar duration and period, and a more complex temporal structure, usually involving two parts within echeme, with different syllable duration or period.

The spectral parameters of the songs were estimated on frequency spectra and spectrograms. The dominant frequency of the songs was the frequency value showing the highest amplitude in the species' spectrum; the harmonic peak corresponding to this dominant frequency was noted as the nature of dominant frequency. Two other traits were coded for the frequency of the calling song: the dominant frequency value (DF) was coded as a continuous trait, and one trait was coded to address the nature of this dominant frequency (NDF): fundamental frequency (first harmonic; f1), one of the upper harmonics (f2–5), or without harmonic structure (broad-band frequency).

All vouchers of recording files were deposited in the Sound Library of the MNHN (<https://sonotheque.mnhn.fr/>) under reference numbers MNHN-SO-XXX (details in Supporting information Table S3).

Phylogenetic analyses

Taxon Sampling

The tribe Lebinthini is composed of 15 genera (including the new genera described here), comprising a total of 156 described species (Cigliano *et al.*, 2021), among which 63 correspond to Lebinthina **subtribe n.**, 85 to Cardiodactylina **subtribe n.** and 8 to Ligypterina **subtribe n.**

To reconstruct the phylogeny of Lebinthini, we used 110 terminal taxa representing 80 eneopterine species. All the Lebinthini genera but *Julverninus* were represented, for a total of 53 Lebinthini species. As outgroups, all the genera of the four other eneopterine tribes were also represented by 1–5 species (7 Xenogryllini, 5 Nisitrini, 4 Eneopterini and 12 Eurepini species) and one more distant species belonging to the subfamily Gryllinae (*Gryllus bimaculatus* De Geer, used as the most external outgroup).

Among the Lebinthini, the sampling was most extensive for the subtribe Lebinthina (41/63 Lebinthina; 3/8 Ligypterina, 9/85 Cardiodactylina), in particular for the species of the three focal genera in the taxonomic study (*Lebinthus* and two new genera), for which we considered several individuals per species from distinct localities, whenever material was available. We collected data for 1 to 19 individuals per species (mean = 3.14 ± 4.8).

DNA markers, PCR amplification and sequence alignment

We used DNA markers from eight genes, five from the mitochondrial and three from the nuclear genomes based on previous studies on this cricket clade (Robillard & Desutter-Grandcolas, 2006; Nattier *et al.*, 2011, 2012; Chintauan-Marquier *et al.*, 2016). The mitochondrial markers were partial sequences of the 12S rRNA gene (12S, amplicon ~ 400 bp), the 16S rRNA gene (16S, ~ 500 bp), the *cytochrome b* gene (*Cytb*, ~ 400 bp), and the *cytochrome c oxidase subunit 1* (CO1, ~ 750 bp) and *subunit 2* (CO2, ~ 400 bp). Nuclear markers were partial sequences of protein coding *histone H3* gene (*H3*, ~ 330 bp), and partial sequences of two non-protein-coding genes corresponding to nuclear ribosomal subunits 18S rRNA (18S, ~ 650 bp) and 28S rRNA (28S, ~ 400 bp).

DNA extraction, PCR amplification, and sequencing for all newly generated sequences were carried out at Service de Systématique Moléculaire of the MNHN, following the protocols described in Dong *et al.* (2018), including primers and annealing temperatures for each DNA marker. The sequences generated for this study were deposited in GenBank with accession numbers presented in Supporting information Table S1.

Sequences were cleaned and checked for sequencing errors in Sequencher v.4.9 (Gene Codes Co.) or Geneious R9.0.2 (Biomatter Ltd., New Zealand, www.geneious.com, Kearse *et al.*, 2012), and BioEdit v.7.0.5.3 (Hall, 1999), then blasted with NCBI blast tools. The sequences were aligned with MAFFT version 7 online (Kuraku *et al.*, 2013; Katoh *et al.*, 2017). The complete combined dataset consists of 3726 aligned base pairs (bp) for 110 terminals.

Phylogenetic inferences

To check for possible contamination, sequencing artifacts and pseudogenes, preliminary phylogenetic analyses were carried out for each DNA marker with Maximum likelihood (ML)

using the IQ-TREE web server with the default options (<http://iqtree.cibiv.univie.ac.at/>; Trifinopoulos *et al.*, 2016) (Song *et al.*, 2008).

The aligned sequences of all eight markers were concatenated in SequenceMatrix version 1.7.8 (Vaidya *et al.*, 2011). The concatenated dataset was then analyzed using ML and Bayesian inference (BI).

For ML analyses, data were partitioned by gene marker and the best model for each marker was found using IQ-TREE ModelFinder (Kalyaanamoorthy *et al.*, 2017), as detailed in Table S2. ML analyses were run using the IQ-TREE 1.6.2 web portal (Nguyen *et al.*, 2015) (<http://iqtree.cibiv.univie.ac.at/>; Trifinopoulos *et al.* 2016) using the option 'Edge-unlinked partitions'. For comparison, an additional ML analysis was performed in IQ-TREE using fixed models as defined by the best-fit partitioning schemes and the associated substitution models used in the BI analysis (see below). Branch support was assessed by conducting 1,000 bootstrap replicates (standard bootstrap). Branches with bootstrap support values (BS) $\geq 75\%$ were considered strongly supported.

For BI analyses, PartitionFinder V2.1.1 (Lanfear *et al.*, 2017) was used to determine the best-fit partitioning schemes and the associated substitution models were implemented in MrBayes (Ronquist *et al.*, 2012) using corrected Akaike Information Criterion (AICc; Akaike, 2011). We separated coding genes into partitions by codon position to account for variation of substitution rates. We performed a Bayesian inference (BI) analysis using MrBayes v.3.2.7 (Ronquist *et al.*, 2012) by launching two simultaneous runs for a total of eight Markov chains running for 100 million generations and sampling every 10000 generations. We assessed the convergence of samples using Tracer v.1.7.1 (Rambaud *et al.*, 2018) by checking the stability of the log-likelihood curve and the split frequencies of the runs and used a 10% burn-in because of the rapid convergence of the runs. Support for each branch was derived from the posterior probabilities (PP) observed on the majority-rule consensus tree; a PP ≥ 0.95 was considered as well supported following Erixon *et al.* (2003).

Divergence time estimation

We generated a species-level dataset with one specimen per sampled species to conduct dating and subsequent analyses. Divergence times were estimated using Bayesian relaxed clocks as implemented in BEAST 1.10.4 (Suchard *et al.*, 2018). The partitions and substitution models were selected using PartitionFinder 1.1.1 (Lanfear *et al.*, 2012) with the Bayesian information criterion (Ripplinger & Sullivan, 2008). BEAST analyses were performed on the CIPRES Science Gateway using BEAGLE to improve and speed up the likelihood calculation (Ayres *et al.*, 2012; Miller *et al.*, 2015). For each clock model/partitioning scheme an uncorrelated log-normal relaxed clock was implemented. The Tree Model was set to a Yule Process (Gernhard, 2008).

In the absence of clear a fossil record attributable to Eneopterinae, a previous study used an extended outgroup approach to estimate the divergence times of this clade using multiple unambiguous fossils from several cricket families (Vicente *et al.*, 2017). Except for the Lebinthini, our sampling of the other tribes is similar to that of Vicente *et al.* (2017). Therefore, we used the results from this study to define four secondary calibration points as follows, each point being enforced using normal distributions centered on previously estimated median ages: F(1) the node for the most recent common ancestor (MRCA) of Eneopterinae was assigned a 95% interval of 63.28–96.76 Ma (normalPrior mean = “76.29” stdev = “9.0”), (2) the node for the MRCA of the tribe Eupini was assigned an interval of 46.93–74.24 Ma (normalPrior mean = “58.26” stdev = “7.0”), (3) the node for the MRCA of the tribes Xenogryllini and Lebinthini was assigned an interval of 49.22–76.12 Ma (normalPrior mean = “59.64” stdev = “7.5”), and (4) the node for the MRCA of the genus *Eneoptera* Burmeister was assigned an interval of 16.25–30.66 Ma (normalPrior mean = “22.26” stdev = “3.7”).

BEAST analyses consisted of 50 million generations of MCMC with parameters and trees sampled every 1000 generations. A burn-in of 25% was applied after checking the traces in Tracer. Posterior distributions of trees obtained from distinct analyses were combined using LogCombiner v1.8.4 (<http://beast.bio.ed.ac.uk/>). The maximum credibility tree, median ages and their 95% highest posterior density (HPD) were generated with TreeAnnotator v1.8.4 (<https://github.com/beast-dev/beastmcmc/releases/tag/v1.8.4>).

Ancestral state reconstructions (ASR) of acoustic traits

We used the consensus topology inferred by the BEAST analysis to study the evolution of the main acoustic features of the calling songs of these crickets. Three discrete and one continuous traits were coded based on new acoustic measurements from this study and data from recent taxonomic descriptions (see Supporting information Table S3).

For the discrete traits (SONG, ECHE, NDF), we fit three different models of trait evolution using the function fitDiscrete from the R package *geiger* (Harmon *et al.* 2008). These models differ in the assumptions about number of transition rates as follows: Equal rates (ER) allows a single transition rate between all states), symmetric (SYM) has identical forward and reverse transitions and all-rates-different (ARD), has unique parameters for each rate. Each model was run over 1000 generations. From the results we selected the model with the lowest value of sample-size corrected AICc. For the selected model, we estimated ancestral states of each trait using Bayesian MCMC using the *make.simmap* function in the R package *phytools* (Revell 2012) with 100 simulations. We obtained the trait estimates at the nodes by averaging the values over all generations, excluding a 20% burn-in.

For the continuous trait DF, we reconstructed the ancestral states using the function *anc.Bayes* in *phytools* (Revell, 2012), by running a MCMC with 1,000,000 generations, the first 200,000 generations being discarded as burn-in.

Phylogenetic signal

We estimated the phylogenetic signal for acoustic traits to evaluate whether the distribution of each trait across the phylogeny follows a Brownian motion evolution hypothesis or shows divergent evolutionary trends, suggesting the action of particular selection pressures acting on the trait evolution.

To estimate the phylogenetic signal of the three discrete traits (SONG, ECHE, NDF), we quantified δ -value, where a high positive value indicates higher phylogenetic signal (Borges *et al.*, 2019). Significance of δ -value was determined based on 100 iterations.

To estimate the strength of signal to a Brownian motion model of the evolution of a continuous trait (i.e., DF), we quantified the Blomberg's K (value ranging from 0 to greater than 1) (Blomberg *et al.*, 2003) and Pagel's λ (value ranging from 0 to 1) (Pagel, 1999) using the function *phylosig* from the R package *phytools* (Revell, 2012). $K = 1$ and $\lambda = 1$ indicate a Brownian motion evolution.

Results

Phylogenetic results

The separate ML analyses of each DNA marker showed no major conflict in topology (see Supporting information Figure S1). The best-fit partition scheme and substitution models used in BI analyses of the combined datasets consisted of five partitions (detailed in Supporting information Table S2). Both BI and ML phylogenetic analyses yielded robust and largely congruent topologies (Fig. 1A, see also Supporting information Fig. S2 for results of ML analysis).

In each analysis, the five tribes within the Eneopterinae were recovered as monophyletic with maximum support values (PP of 1.0 and BS of 100% for Eurepini, Eneopterini, Nisitrini, Xenogryllini, and Lebinthini). The sister relationship between the tribes Lebinthini and Xenogryllini was also strongly supported (PP of 1.0 and BS of 100%).

Within the tribe Lebinthini, the new subtribes were recovered as monophyletic with strong support: Ligypterina (PP of 1 and BS of 99%); Cardiodactylina (PP of 0.98 and BS of 99%) and Lebinthina (PP of 1 and BS of 100%). The Ligypterina was found as the sister group of a clade formed by Cardiodactylina and Lebinthina with strong support values (PP of 0.96 and BS of 98%).

Within the Lebinthina, two major clades appeared: (1) a less-supported clade (PP < 0.95 and BS of 74%) including the genera distributed in the eastern part of the subtribe's distribution (New Guinea, Solomon Islands, Vanuatu and New Caledonia: *Macrobinthus*, *Microbinthus*, *Centuriarus*, *Gnominthus*, *Agnotecous* Saussure, and *Pixibinthus*); and (2) its highly-supported sister clade (PP of 1 and BS of 100%), including the Lebinthina genera from South-east Asia (west of New Guinea island): *Falcerminthus*, sister group of *Lebinthus* + *Fadinthus* with high support (PP of 1 and BS of 100%). Within clade 1, generic relationships had variable support due to the unstable positions of *Centuriarus* and *Gnominthus*, whereas the two genera from New Caledonia, *Pixibinthus* and *Agnotecous*, were unambiguously found as sister groups (PP of 1 and BS of 100%).

In all the analyses, all genera and species were recovered as monophyletic when tested. The new genus *Falcerminthus* was recovered as monophyletic with high support values (PP of 1 and BS of 100%), as well as the newly defined *Lebinthus* (PP of 0.99 and BS of 97%).

Within *Falcerminthus*, one clade included three species from the Philippines (*F. magayon* (Baroga-Barbecho & Robillard), *F. estrellae* (Robillard), *F. sanchezi* (Bolívar)) with high support (PP of 1 and BS of 98%), as the sister group of the rest of the genus, also well supported (PP of 1 and BS of 100%). Within *Lebinthus*, both ML and BI analyses recovered *L. boracay* Baroga-Barbecho, Yap & Robillard as the sister of *L. bitaeniatatus* Stål with a high support (PP of 1 and BS of 100%), these two species forming the sister group of a clade formed by *L. lanyuensis* Oshiro and *L. luae* Robillard & Tan (PP of 1 and BS of 100%).

Divergence time estimation

The best-fit partition scheme and substitution models used in BEAST analyses for the species-level dataset consisted of five partitions presented in Supporting information Table S2. The topology recovered by BEAST analysis relying on these partitions/clocks converged quickly, with all parameters showing ESS values ≥ 200 .

The analysis yielded robust results, with a topology congruent with previous BI/ML analyses. Most clades corresponding to tribes, subtribes and genera were recovered (Fig. 2, see also Supporting information Fig. S3); differences only occurred in the relationships within tribe Eurepini and within one subclade of the subtribe Lebinthina.

Age estimates for the subfamily Eneopterinae suggested an origin in the Late Cretaceous ca. 90.67 Ma (95% HPD: 78.09–103.67 Ma), and for the tribe Lebinthini in the early Eocene ca. 51.71 Ma (95% HPD: 43.25–60.75 Ma).

The crown groups of the new subtribes were dated as follows: Ligypterina: 43.41 Ma (95% HPD: 34.17–52.90 Ma), Cardiodactylina: 45.28 Ma (95% HPD: 37.33–53.82), Lebinthina: 40.08 Ma (95% HPD: 33.21–47.57 Ma). Based on these results, *Fadinthus* diverged from

Lebinthus ca. 17.94 Ma (95% HPD: 13.10–23.41 Ma); *Lebinthus* originated ca. 14.56 Ma (95% HPD: 10.33–19.33 Ma) and *Falcerminthus* ca. 24.16 Ma (ca. 19.18–29.51 Ma).

Ancestral state reconstructions

Based on sample-size corrected AICc values, the model selection analyses gave a best fit to the ER model for the discrete traits SONG, ECHE, and NDF (Supporting information Table S4). The estimated ancestral values of each trait using Bayesian MCMC are presented in Fig. 3 and detailed below.

The results suggested that the calling song had an echeme structure for most of the history of the subfamily. Single-syllable calls evolved several times independently and apically in the three Lebinthini subtribes (Fig. 3A): In the genera *Ponca*, *Centuriarus*, and in some *Cardiodactylus* species. Similarly, homogeneous trills evolved twice, in the genera *Eneoptera* and *Eurepa* Walker. Ancestral echeme structure was less clear-cut in the results (Fig. 3B) for most of the deepest nodes of the phylogeny, but clearer results were found at the node corresponding to the ancestor of Lebinthini + Xenogryllini, and in the most basal nodes in the Lebinthini, for which an ancestral complex echeme was supported. From complex, the temporal pattern reversed to simple multiple times within the Lebinthini, but the results also suggested that echeme structure varied within most genera or between closely related ones.

Results for the continuous dominant frequency trait (DF) suggested that eneopterines used low-frequency calls ancestrally (Fig. 3C). Two clear independent shifts occurred toward high frequencies, one within the genus *Eneoptera*, and one at the base of the tribe Lebinthini. Within Lebinthini, ultrasound calls evolved multiple times from high frequencies, in the genera *Fadinthus*, *Falcerminthus*, *Microbinthus*, *Gnominthus*, and *Pixibinthus*. The results regarding the nature of the dominant frequency (NDF) suggested that the dominant frequency was ancestrally the fundamental frequency f1 (Fig. 3D), and remained so in the tribes Eurepini, Eneopterini, Nisitrini and Xenogryllini. The increase of frequency in *Eneoptera* corresponds to an apical shift of the dominant frequency to the harmonic f5. The base of tribe Lebinthini is then characterized by a transition in the dominant frequency from the fundamental frequency f1 to the harmonic f3, in the subtribes Ligypterina and Cardiodactylina. The subtribe Lebinthina shows another shift in dominant frequency, from f3 to f2, followed by multiple subsequent changes, involving reversals toward f1 in *Falcerminthus*, or toward f3 in *Gnominthus*, or a loss of harmonic structure (broad-band spectrum) in *Lebinthus* and *Centuriarus*.

Phylogenetic signal

The phylogenetic signal estimated with δ for the discrete traits was high for the trait SONG ($\delta = 16.8$, $p < 0.001$), suggesting that the main temporal structure of the call showed phylogenetic inertia. Phylogenetic signal was lower for ECHE ($\delta = 2.9$, $p < 0.001$), indicating

that echeme structure was more labile than expected by the phylogeny. Phylogenetic signal was high for the NDF ($\delta = 18.9$, $p < 0.001$), indicating that the nature of dominant frequency tends to be constrained by the phylogeny.

For the continuous trait DF, the phylogenetic signal was low, based on its estimate with both the parameters λ ($\lambda = 0.74$, $p < 0.001$) and K ($K = 0.485605$, $p: 0.001$). K being lower than 1 suggested that dominant frequency values diverged more between closely related species than expected under Brownian motion evolution.

Discussion

The detailed taxonomic study and the robust phylogeny presented here reaffirm the monophyletic status of the Lebinthini genera and provide the most up-to-date understanding of in the phylogenetic relationships in this diverse group of crickets, hence permitting further investigation of their evolutionary history and acoustic traits.

Phylogeny of Eneopterinae

This study provides a new well-resolved phylogenetic framework for Eneopterinae despite the focus on the tribe Lebinthini. The results confirm the monophyly of the five recognized tribes, with strong support as previously found (Robillard & Desutter-Grandcolas, 2004a, 2006; Nattier *et al.*, 2011; Vicente *et al.*, 2017; Jaiwara *et al.*, 2019). Our results also confirm the position of the tribe Eurepini as the sister group to the rest of the subfamily and the tribe Lebinthini as the sister group of the tribe Xenogryllini. The relative positions of the tribes Nisitrini and Eneopterini forming a clade placed as the sister group of Xenogryllini + Lebinthini is not as well supported in both the ML and BI analyses. This relationship was suggested in a previous study, also with low support (Jaiswara *et al.*, 2019). In other studies, Eneopterini was found as sister group to a clade grouping Nisitrini, Xenogryllini, and Lebinthini (Robillard *et al.*, 2004a, 2006, Nattier *et al.*, 2011, Vicente *et al.*, 2017). Future studies employing Next-Generation Sequencing (NGS) and genomic datasets with a more complete taxonomic sampling for these two tribes will be necessary to resolve the current ambiguity in their relationships. However, we do not expect any significant consequences for the ASR results presented in this study, nor on the general evolutionary conclusions.

Phylogeny and classification of Lebinthini

The tribe Lebinthini was found to contain three robust clades that are here raised to subtribes to clarify the systematics of this diverse tribe. Subtribes, and the resulting classification of Lebinthini, are based on distinct morphological traits, acoustic traits and geographical distributions (Fig. 1B), and they are supported by the molecular phylogenetic

results that include most described genera. According to the dating analysis, the tribe diverged ca. 51 Ma (Fig. 2), which is similar to the age found by Vicente *et al.* (2017) based on a less extensive taxonomic sampling.

Ligypterina—The subtribe Ligypterina is distinguished from the other subtribes by its Neotropical distribution. It is sister group to the rest of the tribe Lebinthini, which is comprised by the two other subtribes, Cardiodactylina and Lebinthina. Ligypterina includes two species-poor genera, *Ponca* and *Ligypterus*, comprising two and six valid species, respectively. Both genera are similar in terms of general morphology (head shape, FW venation pattern), genitalic anatomy in both males and females (Robillard & Desutter-Grandcolas, 2005), and by the frequency spectrum of the male's calling song, in which the third harmonic peak dominates (Robillard *et al.*, 2015). The dating analysis indicated that these two genera diverged around 43 Ma.

Cardiodactylina—The main topological difference between our phylogenetic results and the previous study by Vicente *et al.* (2017) is the position of the genus *Swezwilderia*, which there was found, with low support values, as the sister group of the Neotropical clade corresponding to the subtribe Ligypterina. In our study *Swezwilderia* is the sister group of the genus *Cardiodactylus*, together forming the subtribe Cardiodactylina with high support values. This relationship is consistent with conclusions of some previous phylogenetic studies (Robillard & Desutter-Grandcolas, 2006; Dong *et al.*, 2018) that placed *Swezwilderia* as the sister group of *Cardiodactylus* within the Lebinthini. This relationship is also consistent with the hypothesis initially made by Chopard (1929) when he described the genus *Swezwilderia*, noticing that it looked like a “small *Cardiodactylus*”. The relationship with *Cardiodactylus* is indeed consistent with the general morphological features shared by these two genera, such as head shape, macroptery, and female FW venation. However, male FW venation and male genitalia structure are difficult to compare between the two genera because they are both highly modified, making hypotheses of homology difficult.

Interestingly, *Swezwilderia* contains only three valid species (needing revision) and is distributed in the easternmost part of the Western Pacific region (in Samoa and the Fiji islands), whereas its sister group, *Cardiodactylus*, is species-rich (more than 80 described species) and distributed throughout all of Southeast Asia and the Western Pacific region, (e.g., Otte, 2007; Robillard *et al.*, 2014). The dating results suggest that the two genera diverged ca. 45 Ma, which is consistent with previous results about the biogeography of *Cardiodactylus* suggesting an origin of the genus in islands of the Pacific, with multiple colonizations of the Southeast Asian continent (Dong *et al.*, 2018).

Lebinthina—The subtribe Lebinthina within the tribe Lebinthini corresponds to the clade characterized by species having brachypterous wings and being distributed in Southeast Asia and in the Western Pacific. This clade has been recognized as a taxonomic group in previous

studies and has been referred to as “brachypterous Lebinthini” or as the “*Agnotecous-Lebinthus*” clade (Robillard *et al.*, 2007, 2013, 2016). Until 2011, this group only included a few species from the genera *Agnotecous* and *Lebinthus*, but recent taxonomic revisions and field work have revealed an unsuspected diversity resulting in the discovery and description of many new genera and species from Australia (Robillard & Su, 2018), New Guinea (Robillard, 2011; Vicente *et al.*, 2015; Robillard *et al.*, 2016), New Caledonia (Anso *et al.*, 2016), and Southeast Asian archipelagoes (this study). Interestingly, this subtribe is the sister group to Cardiodactylina with which it shares more or less the same distribution (Fig. 1B). The two subtribes however differ in terms of generic diversity (two genera in Cardiodactylina vs. nine in Lebinthina) while being comparable in terms of the number of species. This suggests that species within Lebinthina has a higher rate of morphological diversification compared to those in Cardiodactylina (i.e., *Cardiodactylus*). This may be related with the main morphological difference between the two subtribes, i.e., their wing morphology. It is likely that the long wings of *Cardiodactylus* species provided greater dispersal capabilities (Dong *et al.*, 2018). Lebinthina might speciate at similar rates but experience greater isolation because of lower dispersal capabilities due to loss of flight, resulting in higher diversification through emergence of multiple morphological groups of species. This hypothesis will need to be addressed with a more complete phylogenetic context and comparative phylogenetic methods. However, in the light of the last decade of taxonomic studies, field work, and materials examined in natural history collections, we would predict that, while more species of both subtribes still await discovery and formal description, the current trend will prevail: numerous new species of *Cardiodactylus* and numerous new genera and species within the Lebinthina.

Phylogenetic relationships within Lebinthina

The molecular phylogeny presented here provides strong evidence to support the monophyly of the morphological species groups recognized in *Lebinthus* (sensu Baroga-Barbecho *et al.*, 2020). Previously, brachypterous eneopterines from Southeast Asia were generally classified as *Lebinthus*. New insights from the phylogeny have allowed us to redefine *Lebinthus* and describe two new genera based on morphological, acoustic, and molecular evidence (see Systematic part below).

The phylogenetic relationships within the subtribe Lebinthina can be addressed because of the dense taxonomic sampling for this clade. The results confirm the monophyly of all the tested genera and suggest that the subtribe is subdivided in two main groups of genera, which reflect their distribution: one clade includes the genera distributed mainly in the eastern region (eastern clade), including New Guinea, New Caledonia, Vanuatu, and the Solomon Islands; whereas the second clade includes *Lebinthus* and the new genera *Falcerminthus* and *Fadinthus*, and is strictly distributed west of New Guinea (western clade). These two main

clades were also recovered by Vicente *et al.* (2017) and were supported by both our BI and ML analyses, with relatively weak support for the eastern clade and strong support for the western clade.

The relationships among genera found here confirm some of the relationships proposed previously: In the eastern clade, the sister relationship between *Agnotecous* and *Pixibinthus* was confirmed with high support values (Anso *et al.* 2016), but the relative positions of the other genera remain to be clarified. In the western clade, the sister relationship of *Fadinthus* and *Lebinthus* was well supported, as well as their sister-group relationship with *Falcerminthus*, confirming morphological and bioacoustic similarities.

Evolution of calling songs in Eneopterinae

While a few lineages have become mute (e.g., Salazar *et al.*, 2020), the subfamily Eneopterinae is highly diverse in terms of acoustic signals. A similar pattern is found among Lebinthini, in particular in the subtribe Cardiodactylina where *Swezwilderia* species are mute, while the numerous species of *Cardiodactylus* show a great, yet largely unexplored, diversity of calling songs. This acoustic diversity is seen in both temporal patterns, ranging from single syllable calls to complex echemes, and the f3 dominant frequency, ranging from 12–20 kHz with a few species having broad-band calls without detectable harmonics (e.g., Robillard & Desutter-Grandcolas, 2011; Robillard *et al.*, 2014; Dong & Robillard, 2016).

The subtribe Lebinthina is most remarkable for the high diversity of frequency spectra of the species' calling songs, in addition to the diversity of their temporal patterns. In Lebinthina, the dominant frequency of the song is always high frequency (above 10 kHz), but the dominant frequency's harmonic differs greatly: it is the second harmonic in most genera (*Agnotecous*, *Microbinthus*, *Macrobinthus*, *Pixibinthus*, *Fadinthus* **gen. nov.**), the third harmonic in *Gnominthus* (as in Cardiodactylina and Ligypterina), the fundamental frequency in *Falcerminthus* **gen. nov.**, or the call is a broad-band in frequency in *Lebinthus* and *Centurarius*. Interestingly, the harmonic of the dominant frequency appears more or less consistent at the genus level, perhaps because it is related to the morphology of the FW resonant areas and its venation.

The Lebinthina also includes all the species reaching the highest frequency values among Lebinthini. Their song frequencies range well above the ultrasound limit (20 kHz) in several genera, the highest values seen in *Pixibinthus sonicus* (ca. 28 kHz; Anso *et al.*, 2016) and *Microbinthus* spp. (ca. 26 kHz; Robillard, 2009; Robillard *et al.*, 2016).

Using the updated phylogeny pruned to the 42 eneopterine species with acoustic data, we tested hypotheses related to the evolutionary history of their calling songs, both on the temporal patterns and spectral parameters.

606

607 *Evolution of temporal patterns*—According to previous studies, we expected to see a
608 trend in the evolution of temporal patterns from simple to more complex calling songs (Otte,
609 1992; Robillard & Desutter-Grandcolas, 2011). The ASR results, however, suggest that the
610 ancestral eneopterine calls were mainly echemes and that both continuous trills and
611 monosyllabic calls (i.e., simpler patterns) were acquired secondarily and multiple times.
612 Continuous trills occur in Eurepini and *Eneoptera*, as found in Robillard & Desutter-Grandcolas
613 (2011). The rest of the subfamily mostly shows echeme-type calling songs, including most
614 species of Lebinthini. A few clades within the tribe, however, have simpler, monosyllabic calls
615 (i.e., one FW closure produced one call unit), which evolved independently multiple times.
616 Monosyllabic calls could be seen continuous trills with very long silent gaps between syllables,
617 but they function very differently from continuous trills in terms of communication. Several
618 studies in the distantly related species *Cardiodactylus muria* Robillard (ter Hofstede *et al.*,
619 2015) and *Ponca hebardi* Robillard (Benavides-Lopez *et al.*, 2020) demonstrated that each
620 monosyllabic call provokes one female response and is thus functionally equivalent of the
621 echemes produced by other Lebinthini species. On the contrary, continuous trills likely elicit
622 female phonotaxis. Therefore, temporal patterns of the calls underwent multiple, but
623 functionally different, independent simplifications across the phylogeny. Its high phylogenetic
624 signal, however, suggests that song type evolution is constrained by the phylogeny.

625 Echeme complexity showed ASR results less easy to interpret, with ambiguous ancestral
626 states for most of the deepest nodes and many trait changes leading to either more complex
627 or simpler echemes in sister lineages, both at the tribal and generic levels, and sometimes
628 between sister species. This pattern was supported by the low phylogenetic signal for this trait,
629 which suggest that echeme inner structure evolved dynamically in multiple directions, including
630 in Lebinthini. Therefore, although the general pattern is found across the phylogeny (with
631 exceptions), the fine temporal patterns of the calls appear to be relatively labile and probably
632 under selection from multiple factors acting on communication systems. These also refute the
633 simple hypothesis that call evolution follows a general trend from low to high complexity.

634

635 *Evolution of spectral parameters*—Our results only partly support the hypothesis that the
636 spectral features of the calls are evolutionarily more stable than the temporal patterns (which
637 prove partly stable themselves as discussed above). The first trait concerning the values of
638 dominant frequency across the phylogeny shows that DF has shifted from low to high values
639 only a few times in the history of Eneopterinae: once recently in the genus *Eneoptera* in the
640 particular context of a unique and specialized modification of the morphology and behavior
641 related to stridulation in the species *Eneoptera guyanensis* Chopard (Desutter-Grandcolas,
642 1998, Robillard & Desutter-Grandcolas, 2011; Robillard *et al.*, 2015); and once corresponding

to the origin of the whole Lebinthini tribe, as suggested in an earlier study on the origin of high-frequencies (Robillard & Desutter-Grandcolas, 2004a). From these high-frequency values, calling songs secondarily became ultrasonic (>20 kHz) at least five times independently within the Lebinthini, in the genera *Pixibinthus*, *Gnominthus*, *Microbinthus*, *Falcerminthus*, and *Fadinthus* (Fig. 3C: orange and red branches). In addition, several taxa reversed secondarily to lower-frequency calls, without going lower than 10 kHz (Fig. 3C: turquoise branches). This suggests that, once high frequencies have been acquired, frequency values kept evolving in a very dynamic way, which is well supported by the low phylogenetic signal for this trait.

The second trait about spectral features of the calls corresponds to the harmonic of the dominant peak within the frequency spectrum. The results complement the results for the DF trait and support the hypothesis that, after reaching the high-frequency range, call frequencies changed a lot within the Lebinthini through harmonic hopping, i.e., by changing the nature of the dominant frequency. Our results showed that the high frequencies in Lebinthini occurred concomitantly with a change of nature of the dominant frequency as suggested by Robillard *et al.* (2007). This initial shift corresponded to harmonic hopping from the fundamental frequency (f1) to the harmonic f3. Harmonic f3 then remained dominant in all the members of the subtribes Cardiodactylina and Ligypterina as hypothesized earlier (Robillard *et al.*, 2014, 2015). Interestingly, the Lebinthina then underwent a subsequent diversification in terms of nature of dominant frequency.

Increases in frequency values leading to ultrasound values are not always linked with changes in the nature of the dominant frequency: *Gnominthus* reached ultrasonic frequencies by reversing the dominant frequency from f2 to f3, whereas the opposite happened in *Falcerminthus*, which reversed from f2 to f1 while acquiring ultrasonic calls. The most striking cases of ultrasonic calls (DF > 25 kHz) occurred in a f2 dominant-frequency context in *Pixibinthus* and *Microbinthus* independently. The highest frequency values are thus found in the Lebinthina, in clades where the dominant frequency is mainly harmonic f2, whereas the f3-dominant frequency songs remain below the ultrasound threshold. To produce 28 kHz for a cricket with f2-dominant frequency, such as *Pixibinthus sonicus*, a fundamental frequency of 14 kHz is required, whereas many species in the Cardiodactylina and Ligypterina clades are producing frequencies in this intermediate range using the third harmonic (hence with a fundamental frequency three times lower). This suggests that the relationships between stridulatory structures (file tooth number and inter-tooth distance), FW closure speeds and wing resonance capacities are both diverse and complex, resulting in complex changes in the calling song. This diversity likely conceals diverse morpho-functional mechanisms associated with various evolutionary potentialities.

These results suggest that there is a certain amount of uncoupling between the value of the dominant frequency and the harmonic that generates the dominant frequency, and the

flexible nature of this relationship might have contributed to the diversification of the frequency spectra in Lebinthini. The precise interplay between the mechanisms of sound production systems, frequency values, and harmonic hopping will necessitate additional investigations to understand the mechanisms involved in this rich evolutionary context.

Broader conclusions on the evolution of acoustic communication—Our findings on the evolution of temporal patterns and spectral parameters in Lebinthini crickets also add more evidence for how acoustic communication can evolve. That call architecture is partly stable across lineages, but finer temporal patterns are relatively labile among closely related species, has implications beyond our study system. In birds, Price *et al.* (2007) showed in the New World orioles (*Icterus* Brisson) that complex songs evolved multiple times independently in the phylogeny. The complexity of songs can also evolve differently in different clades. For example, many vocal characters of oropendolas birds were found to be highly conserved (Price & Lanyon, 2002). Evidence of variable evolutionary trajectories further illustrate the importance of studying acoustic communication in different taxa.

Our study on the evolutionary history of acoustic traits in Eneopterinae is likely to be the most comprehensive study for a cricket clade thus far. Additional studies using larger datasets are needed to have a more detailed understanding of the evolutionary history of calling song in these crickets. Nonetheless, our results offer a framework to study the evolution of acoustic traits in other crickets or orthopteran groups. For example, Tettigoniodea species also produce either low-frequency or ultrasonic calls (Montealegre-Z *et al.*, 2006; Montealegre-Z, 2009) and temporal patterns that are either simple or complex (e.g., Heller & Hemp, 2019; ter Hofstede *et al.*, 2020), but phylogenetic studies investigating how spectral features and call complexity evolve in specific groups within this clade are lacking. This can be partly attributed to the enormous effort needed to acquire both taxonomic and biological data for as many species as possible before addressing comparative studies.

Systematic part

Family Gryllidae

Subfamily Eneopterinae Saussure, 1874

Tribe Lebinthini Robillard, 2004

Subtribe Cardiodactylina Robillard & Tan, subtribe n.

Type genus: *Cardiodactylus* Saussure, 1878

Contained genera: *Cardiodactylus* Saussure, 1878; *Swezwilderia* Chopard, 1925

Diagnosis: The members of the subtribe Cardiodactylina are characterized by their long wings (FWs and HWs). They either possess a functional stridulatory apparatus in males with modified mirror area (*Cardiodactylus*) or no stridulatory structures (*Swezwilderia*). They are distributed in Southeast Asia and in most archipelagos of the Western Pacific region (Fig. 1B).

Subtribe Ligyppterina Robillard & Tan, subtribe n.

Type genus: *Ligyppterus* Saussure, 1878

Contained genera: *Ligyppterus* Saussure, 1878; *Ponca* Hebard, 1928

Diagnosis: The members of the subtribe Ligyppterina are either brachypterous or macropterous; they are characterized by a functional stridulatory apparatus in males with a modified mirror area, male genitalia with large pseudepiphallic lophi and an indented anterior margin. They are distributed in the Neotropical region (Central America and northern part of South America) (Fig. 1B).

Subtribe Lebinthina Robillard & Tan, subtribe n.

Type genus: *Lebinthus* Stål, 1877

Contained genera: *Agnotecous* Saussure, 1878; *Centurarius* Robillard, 2011; *Fadinthus* Robillard & Tan, **gen. nov.**; *Falcerminthus* Robillard & Tan, **gen. nov.**; *Gnominthus* Robillard & Vicente, 2015; *Julverninus* Robillard & Su, 2018; *Lebinthus* Stål, 1877; *Macrobinthus* Robillard & Dong, 2016; *Microbinthus* Robillard & Dong, 2016; *Pixibinthus* Robillard & Anso, 2016.

Diagnosis: The members of the subtribe Lebinthina all have brachypterous FWs and lack HWs; males are characterized by functional stridulatory structures with a vestigial mirror area. As for Cardiodactylina, they are distributed in Southeast Asia and in most archipelagos of the Western Pacific region (Fig. 1B).

744

745 **Eneopterinae *insertae sedis***

746 Genus *Antillobinthus* Yong & Desutter-Grandcolas, 2020—This genus described from Cuba
747 and including one species, does not present the key features of the Lebinthini such as inner
748 tympanum covered by a cuticular fold, female ovipositor with denticulate apex, structure of
749 male genitalia (Robillard & Desutter-Grandcolas, 2004a). No phylogenetic data could be
750 included yet to test its relationship with the other eneopterine tribes, or to place this genus in
751 the appropriate subtribe. Conservatively, we propose to maintain it within the subfamily as
752 genus *insertae sedis*.

753

754 ***Lebinthus* Stål, 1877**

755 (Figs. 1, 2, 4A, 4B, 5A, 6G)

756 *Lebinthus* Stål, 1877: 50; Bolívar, 1889: 425; Kirby, 1906: 88; Chopard, 1968: 353; Otte &
757 Alexander, 1983: 307; Desutter-Grandcolas, 1990: 239 (Eneopteridae: Eneopterinae), 1997:
758 171; Otte, 1994: 67; Oshiro, 1995: 45; Yin & Liu, 1995: 210; Oshiro, 1996: 117; Robillard &
759 Desutter-Grandcolas, 2008: 67 (Lebinthini); Robillard, 2010: 26; Robillard *et al.*, 2013: 51;
760 Robillard & Tan, 2013: 712; Baroga-Barbecho *et al.*, 2020: 401; Cigliano *et al.*, 2021
761 (Orthoptera Species File Online).

762 Synonym name: *Paraeneopterus* Saussure, 1878. Synonymized by Robillard & Desutter-
763 Grandcolas, 2008: 67.

764

765 **Type species.** *Lebinthus bitaeniatus* Stål, 1877

766 **Material examined.** See Robillard & Tan, 2013: 712; Baroga-Barbecho *et al.*, 2020.

767 **New diagnosis.** Among Lebinthina genera, *Lebinthus* has an average to short size and is
768 characterized by its brown coloration with two yellow or whitish bands running on the whole
769 body; head as wide as high in facial view; eyes large and prominent; body slender, with a
770 rather long abdomen; FIII long and thin. Male diagnostic characters include CuA vein straight
771 apically; harp with one faint oblique vein almost straight; mirror not differentiated; male genitalia
772 with pseudepiphallic lophi little differentiated, separated by a short median plate; and average-
773 sized pseudepiphallic parameres. Female diagnostic characters include: FWs as long as in
774 male, slightly overlapping, ovipositor longer than FIII. From *Falcerminthus*, *Lebinthus* differs
775 by general body shape more elongate (stockier in *Falcerminthus*), male FWs with CuA straight
776 apically, harp without false mirror, and male genitalia with characteristic shape of
777 pseudepiphallic lophi little differentiated. From *Fadinthus*, *Lebinthus* mostly differs by absence
778 of longitudinal bands along body, head as high as wide in facial view (wider than high in
779 *Fadinthus*), eyes slightly smaller (very large in *Fadinthus*), lateral lobes of pronotum with a
780 lighter ventral margin with a variable dark pattern (lateral lobes almost entirely dark brown in

781 *Fadinthus*), and male genitalia with average-sized pseudepiphallic parameres (oversized in
782 *Fadinthus*).

783 **Redescription.**

784 Genus of average size, body slender, with a rather long abdomen, characterized by brown
785 coloration with two yellow or whitish bands running on the whole body (Fig. 4B). Head forming
786 an equilateral triangle in facial view, as high as wide. Head dorsum yellow brown with six dark
787 brown longitudinal bands more or less distinct. Eyes large and prominent (Fig. 4A). Face yellow
788 brown to darker brown, with a dark facial band or large spots between scapes (Fig. 4A).
789 Pronotum dorsal disk trapezoidal, almost square, wider than long, its posterior margin straight,
790 usually dark brown, its lateral edges yellow. Lateral lobes black dorsally, ventral margin orange
791 brown to yellow with a dark brown pattern, including the ventral corner and a brownish
792 longitudinal line (Fig. 4B). Legs: TI with two tympana; inner tympanum covered by a flat
793 sclerotized expansion, its membrane visible along a small longitudinal slit only; outer
794 tympanum ellipsoidal, its membrane transversally plicate in dorsal half. TI with two inner and
795 one outer apical spurs. TII with two inner and two outer spurs. FIII muscular and long, with a
796 linear region before knee. TIII serrulated on its whole length, slightly furrowed longitudinally
797 and with four pairs of subapical spurs and three pairs of apical spurs; inner spurs long and
798 curved, outer spurs shorter and straight. Legs I and II light brown to yellow brown, femora with
799 brown spots and longitudinal patterns, tibiae with rings. FIII long and thin. TIII with distinct
800 brown rings. Abdomen: Tergites dark brown with two yellow or whitish bands running
801 longitudinally.

802 **Male:** Metanotal glands absent. FWs short, reaching one third of abdomen length; narrow,
803 lateral field almost as long as dorsal field (Fig. 5A). Harp wide, with one harp vein almost
804 straight. Diagonal vein very faint posteriorly. Distal part of CuA straight. Apical field very small,
805 with one bifurcation of CuA posterior to diagonal vein. Mirror not differentiated. Subgenital plate
806 elongate, clog-shaped.

807 *Male genitalia* (Fig. 6G): Pseudepiphallic sclerite trapezoidal, convex dorsally, its apex slightly
808 trilobate, including a short median expansion and two lophi barely individualized, slightly
809 divergent and finely setose. Anterior margin bisinuate, with a median indentation.
810 Pseudepiphallic parameres of average size, with a wide sclerotized basis, trilobate (instead of
811 C-, F- or L-shaped in *Falcerminthus*), including a postero-dorsal lobe and two ventral lobes,
812 the anterior one usually rounded and curved anteriorly. Ectophallic fold with variable ventral
813 sclerotization, its apex membranous; ectophallic apodemes long. Endophallic sclerite
814 elongated and thin anteriorly, with short lateral arms and a small medio-posterior expansion;
815 endophallic apodeme usually formed by small lateral lamellas and of a large dorsal median
816 crest.

Female: FWs as long as in male, always slightly overlapping. Lateral angle of FWs with a narrow yellow longitudinal band including a faint vein. Dorsal field with 5–6 strong parallel longitudinal veins, its apical area either rounded or angular. Lateral field with 3–5 longitudinal veins. Ovipositor longer than FIII, its apex dorsal margin finely denticulate.

Female genitalia: Copulatory papilla conical, with a narrow basal sclerotized area on ventral face; apex rounded.

Habitat and life history. Activity mostly diurnal, documented species live in open forested areas in secondary habitats or in the open near forest.

Calling song. For the species for which calling song is documented (*L. bitaeniatatus* and *L. luae*), syllables are very indented (amplitude modulation resulting in pauses within the syllable). Song organized in two parts, the initial one consisting of well-spaced syllables, the second part forming a short trill. The spectrum consists of a broad band at high frequency (15–30 kHz).

Distribution. Indonesia (Sumatra and West Java), Malaysia (northern Borneo), Palau, Philippines (Luzon, Palawan, Leyte, and Mindanao), Singapore and surrounding islands, Taiwan (Lanyu I.).

Species included and distribution (arranged alphabetically; TL: type locality).

L. bitaeniatatus Stål, 1877—**Philippines:** Luzon (TL), Palawan, Mindoro, Masbate.

L. boracay Baroga-Barbecho, Yap & Robillard, 2020—**Philippines:** Boracay (TL).

L. lanyuensis Oshiro, 1996—**Taiwan:** Taiwan, Lanyu I. (TL).

L. luae Robillard & Tan, 2013—**Singapore:** Singapore (TL) (Pulau Ubin, Pulau Semakau, Sentosa Island, Bukit Timah, Labrador); **Philippines:** Batanes, Luzon, Leyte, Cebu, Palawan, Sulu; **Indonesia:** Sumatra, West Java; Riau Islands, Sulawesi; **Palau;** **Malaysia:** Johor (Mersing) (<https://www.inaturalist.org/observations/20944134>, 20725496); Borneo (Sabah).

Remarks. The genus *Lebinthus* has been used until recently to refer to all the brachypterous species of Lebinthini which were not from New Caledonia (Oshiro, 1996; Desutter-Grandcolas, 1997; Robillard, 2009, 2010, 2011; Robillard & Tan, 2013; Robillard *et al.*, 2013). The diversity uncovered recently for this group of species necessitated the definition of several new genera and the redefinition of the genus as restricted to the species close to the type species and easily recognized by their yellow longitudinal bands from which the type species name is derived.

***Falcerminthus* Robillard & Tan, gen. nov.**

(Figs. 1, 2, 4C, 4D, 5B, 6H, 6I)

urn:lsid:zoobank.org:act:8BB986A6-8482-4B67-9D59-D102C26B5F9E

Type species. *Lebinthus sanchezi* Bolívar, 1889, by subsequent designation

854 **Material examined.** See Robillard, 2010; Robillard *et al.*, 2013: 712; Baroga-Barbecho *et al.*,
855 2020.

856 **Diagnosis.** Among Lebinthina genera, *Falcerminthus* **gen. nov.** has a size ranging from very
857 short to average, coloration contrasted without longitudinal bands along body; head as wide
858 as high in facial view; eyes large and prominent; body stocky, with a rather short abdomen;
859 FIII rather short. Male diagnostic characters include CuA vein curved innerly near apex, harp
860 with one strong oblique vein, poly-furcated anteriorly and delimiting a rounded false mirror, i.e.,
861 a distinctive area located on harp posterior corner (not homologous to the mirror of other
862 crickets); mirror not differentiated; male genitalia with pseudepiphallic lophi short but well
863 differentiated, without a median plate between them; pseudepiphallic parameres average-
864 sized. Female diagnostic characters include: FWs shorter than in male, close together at their
865 bases but usually not overlapping; ovipositor shorter than FIII. From *Lebinthus*, *Falcerminthus*
866 mostly differs by body shape stockier (more elongate in *Lebinthus*), male FWs with a
867 characteristic false mirror; CuA curved apically; male genitalia with short pseudepiphallic lophi,
868 female FWs and ovipositor shorter. From *Fadinthus*, *Falcerminthus* mostly differs by head as
869 high as wide in facial view (wider than high in *Fadinthus*), eyes slightly smaller (very large in
870 *Fadinthus*), lateral lobes of pronotum with a lighter ventral margin with a characteristic dark
871 pattern (lateral lobes almost entirely dark brown in *Fadinthus*), and male genitalia with average-
872 sized pseudepiphallic parameres (oversized in *Fadinthus*).

873 **Description.** Size small to average for the subtribe. Vertex rounded, prolonged by trapezoidal
874 fastigium almost as long as wide. Head dorsum also with longitudinal bands more or less
875 distinct. Eyes large and prominent; in dorsal view eyes combined width represents ca. 49% of
876 head width in *F. sanchezi* and *F. puyos*, 52% in *F. sandakan* and *F. estrellae* and 54% in *F.*
877 *polillensis*. Head triangular in facial view, almost as wide as high. Face coloration variable,
878 from black to yellow with various patterns (Fig. 4C). Ocelli similar to *Lebinthus*. Scapes small.
879 Pronotum dorsal disk trapezoidal typical of subtribe, usually dark brown, its lateral edges
880 yellow. Lateral lobes 1.2–1.3 times longer than high (except in *F. sandakan*, about as long as
881 wide); black dorsally, ventral margin yellow with a variable median dark brown pattern (Fig.
882 4D). Legs: TI with two tympana typical of subtribe. TI and TII with similar number of apical
883 spurs as *Lebinthus*. FIII muscular, rather short, without linear region before knee. TIII typical
884 of subtribe. Legs I and II light brown to yellow brown, femora with brown spots and longitudinal
885 patterns, tibiae with rings. TIII with distinct dark brown rings. TaIII-1 with 2–3 spines on dorsal
886 outer edges and 0–2 on outer face. FWs short in both sexes, not reaching abdomen mid-
887 length; HWs absent. Cerci typical of subtribe. Abdomen: Tergites brown to dark brown, without
888 longitudinal bands.

889 **Male:** Metanotal glands absent. Dorsal field of FWs not longer than lateral field. FWs longer
890 than wide, longer than pronotum. FW venation (Fig. 5B): 1A vein (file) widely curved (>100–

120°); stridulatory file with teeth both on transverse and on angle parts of 1A. CuP usually not visible except basally (*F. puyos*, *F. truncatipennis*, and *F. villemantae*). Diagonal vein very faint, usually visible on anterior half, faint posteriorly. Harp wide, occupying most of dorsal field surface, with a strong transverse harp vein, poly-furcated anteriorly and delimiting a well-rounded false mirror, i.e., a distinctive area located on harp posterior corner (not homologous to the mirror of other crickets). CuA anterior part strong, its distal part weak, slightly curved inward near apex. Mirror (d1) not differentiated. Apical field absent, with no bifurcation of CuA posterior to diagonal vein. Lateral field with 5–6 strong longitudinal veins. Subgenital plate elongated, clog-shaped.

Male genitalia (Figs. 6H, 6I): Pseudepiphallos triangular, usually elongate, its basal margin straight or slightly indented in the middle, posterior apex with short paired lophi. Rami short, parallel to slightly diverging anteriorly. Pseudepiphallic parameres average sized and sclerotized, variable in shape, their basis strong. Ectophallic apodemes parallel and long, reaching beyond anterior margin of pseudepiphallic sclerite. Ectophallic arc well sclerotized. Ectophallic fold with two ventral sclerites of variable shapes, sometimes fused together. Endophallic sclerite Y-shaped, comprising a long anterior region and a short median expansion and lateral arms posteriorly. Endophallic apodeme with well-developed lateral lamellas and a narrow dorsal median crest.

Female: FWs very short, shorter than in male, barely reaching posterior margin of first tergite, close together at their bases but usually not overlapping. Dorsal field usually oblique posteriorly (rounded in *F. estrellae* and *F. sanchezi*); dorsal field and lateral field with more or less distinct longitudinal veins. Ovipositor shorter than FIII, its apex acute, most often slightly denticulate on dorsal edge.

Female genitalia: Female copulatory papilla rounded, almost entirely membranous, sometimes with a basal sclerotized ring; apex rounded, generally folded ventrally.

Calling song. In *F. estrellae*, *F. puyos*, *F. sanchezi*, *F. truncatipennis*, and *F. villemantae*, the calling song consists of a short trill of ca. 58–118 syllables of ca. 1.0–11.6 s each, with a peak frequency near or slightly above 20 kHz. In *F. sandakan*, calling song consists of long trills (more than 500 syllables of ca. 15.4 s each) with a peak frequency slightly below 20 kHz. For all documented species, the high dominant frequency (18–22 kHz) corresponds to the fundamental peak of the call spectrum.

Etymology. The genus is named after *Lebinthus* and the prefix “Falcern” corresponding to the combination of the English word “false” and the Bahasa Indonesian word “cermin” (= mirror), as the genus is characterized by the presence of the false mirror in the male’s harp.

Distribution. East Malaysia (Borneo: Sandakan), Indonesia (Sipura Island, South Sulawesi, Sumatra, West Java), Japan, Philippines (Luzon, Palawan, Mindanao, and Visayas Islands), Taiwan.

928 **Included species and distribution (arranged alphabetically, TL: type locality):**
 929 *F. dannybaletei* (Baroga-Barbecho & Robillard, 2020) **comb. nov.**—**Philippines:** Panay (TL)
 930 *F. estrellae* (Robillard, 2015) **comb. nov.**—**Philippines:** Leyte (TL)
 931 *F. hamus* (Baroga-Barbecho & Robillard, 2020) **comb. nov.**—**Philippines:** Palawan (TL)
 932 *F. magayon* (Baroga-Barbecho & Robillard, 2020) **comb. nov.**—**Philippines:** Luzon (TL)
 933 *F. sanchezi* (Bolívar, 1889) **comb. nov.**—**Philippines:** Luzon (TL)
 934 *F. truncatipennis* (Chopard, 1929) **comb. nov.**—**Indonesia:** Sumatra, West Java, Sipora I.
 935 *F. yaeyamensis* (Oshiro, 1996) **comb. nov.**—**Japan:** Yonaguni I. (TL)
 936 *F. palaceus* (Baroga-Barbecho & Robillard, 2020) **comb. nov.**—**Philippines:** Mindanao (TL)
 937 *F. parvus* (Baroga-Barbecho & Robillard, 2020) **comb. nov.**—**Philippines:** Mindanao (TL)
 938 *F. polillensis* (Baroga, Yap & Robillard, 2016) **comb. nov.**—**Philippines:** Polillo I. (TL), Luzon,
 939 Negros Oriental
 940 *F. puyos* (Robillard, 2013) **comb. nov.**—**Philippines:** Luzon (TL)
 941 *F. sandakan* (Tan, Japir, Chung & Robillard, 2019) **comb. nov.**—**East Malaysia:** Sabah (TL)
 942 *F. villemantae* (Robillard, 2010) **comb. nov.**—**Indonesia:** Sulawesi (TL)

943

944 ***Fadinthus* Robillard & Tan, gen. nov.**

945 (Figs. 1, 2, 4E, 4F, 5C, 5D, 6A–F, 6J–M, 7, 8)

946 urn:lsid:zoobank.org:act:C543BE32-952B-41C3-8346-1A33803E66D3

947 **Type species.** *Fadinthus miri* Robillard & Tan, new species

948 **Diagnosis.** Among Lebinthina genera, *Fadinthus* gen. nov. has a short to average size,
 949 coloration without longitudinal bands along body; head wider than high in facial view; eyes very
 950 large and prominent; body rather elongate, with an average abdomen length; FIII rather long.
 951 Male diagnostic characters include very faint venation of dorsal field in FWs, CuA vein straight
 952 apically, harp with one faint oblique vein, mirror not differentiated; male genitalia with short
 953 pseudepiphallallic lophi little differentiated, either with or without a short median plate between
 954 them; pseudepiphallallic parameres oversized; ectophallic arc with converging ventral
 955 expansions. Female diagnostic characters include: FWs shorter than in male, close together
 956 at their bases but not overlapping; ovipositor shorter than FIII. From *Lebinthus*, *Fadinthus*
 957 mostly differs by body color without longitudinal bands, male FWs with very weak venation,
 958 male genitalia with oversized pseudepiphallallic parameres and ectophallic ventral expansions,
 959 and female FWs and ovipositor shorter. From *Falcerminthus*, *Fadinthus* mostly differs by head
 960 wider than high in facial view (as high as wide in *Falcerminthus*), eyes larger (smaller in
 961 *Falcerminthus* and *Lebinthus*), lateral lobes of pronotum almost entirely dark brown (with a
 962 lighter ventral margin with a characteristic dark pattern in *Falcerminthus* and *Lebinthus*), and
 963 male genitalia with oversized parameres.

964 **Description.** Size small to average for the subtribe. Vertex similar to *Falcerminthus*. Eyes very
965 large, in dorsal view eyes combined width represents ca. 58% of head width (46% in *Lebinthus*
966 *bitaeniatus*). Head triangular in facial view, ca. 1.2 wider than high. Ocelli typical of subtribe,
967 forming a wide triangle. Scapes small. Pronotum dorsal disk trapezoidal and typical of subtribe,
968 almost entirely dark brown or black. T1 with two tympana typical of subtribe. T1 and TII with
969 same number of spurs as other genera of subtribe. FIII muscular and rather long, without a
970 short linear region before knee. TIII typical of subtribe. TaIII-1 with two dorso-apical spines and
971 a row of spines on outer dorsal edge; without lateral outer spine. FWs very short in both sexes,
972 not reaching abdomen mid-length; HWs absent. Abdomen: Tergites brown to dark brown,
973 without longitudinal bands. Cerci similar to *Falcerminthus*.

974 **Male:** Metanotal glands absent. Dorsal field of FWs as long as lateral field. FWs longer than
975 wide, slightly longer than pronotum dorsal disk. FW venation: 1A vein (file) strongly curved.
976 CuP absent. CuA weak, straight apically. Diagonal vein weak. Harp wide, almost flat, with
977 either no oblique vein (*F. buruensis*) or one faint incomplete oblique vein, without a distinctive
978 rounded area. Mirror (d1) undifferentiated. M vein not reaching tip of FWs. Apical field either
979 very short or absent, most often including one faint bifurcation of CuA posterior to diagonal
980 vein. Lateral field with 5 strong longitudinal veins including R, Sc and 3 more ventral veins;
981 latero-dorsal angle made by R; Sc without bifurcating veins.

982 *Male genitalia:* Pseudepiphallic sclerite stout; posterior apex forming small lophi little
983 differentiated, either with or without a short median plate between them. Rami short.
984 Pseudepiphallic parameres elongate and oversized, variable in shape and orientation among
985 species. Ectophallic arc wide, slightly curved posteriorly, with converging ventral expansions
986 more or less sclerotized. Ectophallic fold short and wide, including two thin sclerites fused
987 together apically. Ectophallic apodemes long, more or less parallel. Endophallic sclerite trident
988 shaped, including a long triangular area anteriorly, and posteriorly short lateral arms and a
989 triangular median expansion; endophallic apodeme with a narrow median crest and lateral
990 lamellas.

991 **Female:** FWs short, shorter than in male, barely reaching posterior margin of first tergite, either
992 well separated (*F. buruensis*) or slightly overlapping (*F. tehtari* and *F. miri*), oblique posteriorly;
993 dorsal field and lateral field with strong longitudinal veins. Ovipositor shorter than FIII, its apex
994 acute, slightly denticulate on dorsal edge.

995 *Female genitalia:* Female copulatory papilla rounded, almost entirely membranous, without
996 ventral sclerite nor basal plate; apex rounded, generally folded ventrally.

997 **Etymology.** The genus is named after *Lebinthus* and the prefix “Fad”, corresponding to the
998 abbreviation of Fadet. Fadet is a kind of gnome in the occidental folklore, and “Fad” also relates
999 to the ‘faded’ or barely visible veins in the male’s harp of these species.

1000 **Distribution.** Brunei Darussalam, Indonesia (Buru Island), Malaysia (Sarawak)

Included species.

Fadinthus buruensis (Robillard, 2010), **comb. nov.**—Indonesia: Buru Island (TL)

Fadinthus miri Robillard & Tan, **sp. nov.**—Malaysia: Sarawak (TL)

Fadinthus tehtari Tan, Wahab & Robillard, **sp. nov.**—Brunei Darussalam: Belait (TL)

***Fadinthus miri* Robillard & Tan, sp. nov.**

(Figs. 1, 5D, 6A–C, 6J, 6K)

urn:lsid:zoobank.org:act:FA8687B2-F615-438D-9D22-9AEDE4320C87

Type material. *Holotype*, ♂, MALAYSIA: East Malaysia, Sarawak, Miri, Lambir Hills National Park, 100–300 m a.s.l., forest, 29.iii.–1.iv.2012 (A. V. Gorochoy, M. Berezin, E. Tkatsheva, L. Kamskov) (ZIN). *Allotype*, ♀, MALAYSIA: same information as holotype (ZIN). *Paratypes*: MALAYSIA, same information as holotype: 2 ♀ (ZIN); 1 ♂, molecular sample L90, 1 ♀ (MNHN-EO-ENSIF10870–10871).

Additional material examined. MALAYSIA: 1 juvenile, same information as holotype, (ZIN).

Distribution. Miri (Sarawak, East Malaysia).

Diagnosis. Species close to *F. tehtari* **sp. nov.**, from which it differs by lighter coloration, longer male FWs, with more distinct veins on dorsal field, and differences in male genitalia, with well separated pseudepiphallic lophi and pseudepiphallic parameres oriented posteriorly. From *F. buruensis*, both new species differ by male FWs venation with a more distinct oblique vein, less differentiated mirror, and male genitalia with pseudepiphallic parameres without ventral lobes, and longer female FWs slightly overlapping (shorter and separated in *F. buruensis*).

Description. Size average. Coloration dark brown. Head dorsum with four wide dark brown longitudinal bands, area posterior to eyes yellow with a dark spot. Fastigium wider than long, setose, dark brown, with a yellow line apically. Scape light brown with faint darker patterns; antennae light brown. Face light brown, with variable dark brown patterns on frons and below antennae. Mouthparts variably mottled with dark brown and yellow; maxillary palpi generally pale brown, apical segment with apex slightly expanding and darkened apically, subapical segment shorter than apical and third segments and darkened basally. Lateral part of head with a dark brown stripe. Pronotum: Dorsal disk slightly trapezoidal, posterior margin substraight; yellow brown mottled with dark brown, lateral edges always whitish, posterior area mostly dark brown; lateral lobes black dorsally, ventral margin dark brown, with lighter corners visible only in lightest specimens. Legs: Fore and mid legs light brown, femora with dark brown spots, tibiae with dark rings. FIII brown, with strong striated dark patterns on outer faces, knees dark brown; TIII with dark rings. Tarsomeres I/III-1 yellow brown, apices dark brown. Abdomen orange brown mottled with dark brown dorsally, yellowish brown ventrally. Cerci yellowish brown, with dark rings.

Male: FWs reaching half of abdomen length. FW coloration (Fig. 5D): Cells and veins brown, not translucent; veins brown except anterior parts of anal veins orange brown and anterior lateral corner of FW yellowish. FW venation (Fig. 5D): 1A slightly curved. CuP not visible. CuA faint, straight along its whole length. Diagonal vein very faint. Harp wide, with one very faint oblique vein bisinuate. Mirror not differentiated from other cells. Longitudinal veins of dorsal field strong apically, transverse veins weaker. Apical field very short, including one bifurcation of CuA posterior to diagonal vein. Lateral field dark brown, area between M and R pale orange; with 6–7 ($n = 2$) strong longitudinal veins including M, R, Sc; Sc without bifurcating veins. Supra-anal plate tongue-shaped, its posterior margin truncated.

Male genitalia (Figs. 6A–C): Pseudepiphallic sclerite stout and trapezoidal; posterior apex with a wide indentation between short lateral lophi, forming wide triangles slightly diverging. Anterior margin of pseudepiphallic sclerite slightly indented. Rami short, half as long as pseudepiphallic sclerite. Pseudepiphallic parameres elongated posteriorly, with a small dorsal lobe and an oversized ventral lobe forming a right angle in lateral view; apex of ventral lobe widened, forming a twisted spatula. Ectophallic arc thick, slightly curved posteriorly, with long ventro-lateral expansions sclerotized basally and membranous apically. Ectophallic fold mostly membranous, with a thin Y-shaped ventral sclerotization. Ectophallic apodemes long and slightly divergent, exceeding anterior margin of pseudepiphallic sclerite. Endophallic sclerite trifurcated posteriorly, with a short median expansion and two short lateral arms; anterior region elongate and sinuous, almost reaching anterior margin of pseudepiphallic sclerite; endophallic apodeme made of a median crest and lateral lamellas.

Female: FWs rounded, reaching third tergite, slightly or not overlapping; dorsal field brown with 6–7 longitudinal veins, including 5–6 strong orange brown vein and 1 thin vein being part of a narrow yellow lateral band; dorsal field without distinct transverse veins. Lateral field dark brown, with 3–4 strong dark brown longitudinal veins, without distinct transverse veins. Ovipositor shorter than FIII; apex lanceolate, slightly denticulate on dorsal edge.

Female genitalia: Female copulatory papilla mostly membranous, with a wide rounded base and a conical apex folded ventrally in lateral view (Fig. 6J, 6K).

Juvenile: Coloration light brown, mottled with dark brown; lateral lobe of pronotum black dorsally, ventral margin yellow with a wide dark brown spot; lateral side of abdomen with a black spot on second tergite.

Measurements. See Table 1.

Habitat and life history traits. Unknown.

Calling song. Unknown.

Etymology. The species is named after the type locality, city of Miri in Sarawak.

***Fadinthus tehtari* Tan, Wahab & Robillard, sp. nov.**

1075 (Figs. 1, 2, 4E, 4F, 5C, 6D–F, 6L, 6M, 7, 8)

1076 urn:lsid:zoobank.org:act:7C5BFB10-41F4-4698-9009-10BCDF2CF8BF

1077 **Type material.** *Holotype*, ♂ (BRU.19.75), BRUNEI DARUSSALAM: Belait District, Andulalu
1078 Forest Reserve, N4.62179 E114.51311, 73.7±7.4 m, on foliage near ground, 9.vii.2019 1923
1079 hours (M. K. Tan & H. Yeo) (UBDM). *Allotype*, ♀ (BRU.19.76): collected together with the
1080 holotype (ZRC). *Paratypes*, BRUNEI DARUSSALAM, Belait District, Andulalu Forest Reserve:
1081 1 ♀ (BRU.19.9), N4.62231, E114.51028, 99.3±5.6 m, on forest floor, 24.ii.2019 2038 hours (M.
1082 K. Tan & H. Yeo) (MNHN-EO-ENSIF10867); 1 ♀ (BRU.19.10), N4.62231, E114.51028,
1083 99.3±5.6 m, on forest floor, 24.ii.2019 2038 hours, molecular sample L206 (M. K. Tan & H.
1084 Yeo) (MNHN-EO-ENSIF10868); 1 ♀ (BRU.19.12), N4.62232, E114.51036, 100.5±5.5 m, on
1085 foliage near ground, 24.ii.2019 2043 hours (M. K. Tan & H. Yeo) (MNHN-EO-ENSIF10872); 1
1086 ♀ (BRU.19.21), N4.62473, E114.51240, 64.5±8.0 m, on forest floor, 26.ii.2019 0940 hours (M.
1087 K. Tan & H. Yeo) (MNHN-EO-ENSIF10869); 1 ♀ (BRU.19.27), N4.62515, E114.51218,
1088 78.1±7.8 m, on forest floor, 26.ii.2019 1100 hours (M. K. Tan & H. Yeo) (MNHN-EO-
1089 ENSIF11258); 1 ♀ (BRU.19.65), N4.62501, E114.51672, 122.4±6.9 m, fern foliage near
1090 ground, 6.vii.2019 2040 hours (M. K. Tan & H. Yeo) (MNHN-EO-ENSIF10873); 1 ♀
1091 (BRU.19.67), N4.63363, E114.51276, 30.8±5.7 m, leaf litter near forest edge, 7.vii.2019 0931
1092 hours (M. K. Tan & H. Yeo) (MNHN-EO-ENSIF10874); 1 ♀ (BRU.19.71), N4.63356,
1093 E114.51189, 63.5±6.5 m, on foliage near ground, 8.vii.2019 2000 hours (M. K. Tan & H. Yeo)
1094 (MNHN-EO-ENSIF11062).

1095 **Distribution.** Belait (Brunei Darussalam).

1096 **Diagnosis.** Species close to *F. miri* sp. nov., from which it differs by darker coloration, shorter
1097 male FWs, with very faint venation on dorsal field, and differences in male genitalia, with little-
1098 separated pseudepiphallic lophi, with a median expansion between them, and converging,
1099 claw-shaped pseudepiphallic parameres. From *F. buruensis*, both new species differ by male
1100 FW venation with a more distinct oblique vein, less differentiated mirror, and pseudepiphallic
1101 parameres of male genitalia without ventral lobes, and longer, slightly overlapping female FWs
1102 (shorter and separated in *F. buruensis*).

1103 **Description.** Size small. Coloration dark brown, with slight individual variations. Head dorsum
1104 with four wide but dark brown longitudinal bands, area posterior to eyes dark brown. Eyes dark
1105 brown, with a dark pink dorso-longitudinal band. Fastigium wider than long, dark brown, setose
1106 (with dark brown setae). Scape whitish with faint darker patterns; antennae brown. Face shiny
1107 dark brown, with a light transverse band in the middle ventral of median ocellus (Fig. 4E).
1108 Mouthparts variably mottled with dark brown and yellow brown (Fig. 4E); maxillary palpi
1109 generally pale yellow brown, apical segment with apex slightly expanding and darkened
1110 apically, subapical segment shorter than apical and third segments and darkened at the base,
1111 third segments mostly pale yellow brown. Lateral part of head yellow posterior to eyes, genae

1112 with a black stripe (Fig. 4F). Pronotum: Dorsal disk slightly trapezoidal, anterior margin straight
1113 and lined with black setae, posterior margin substraight; yellow brown mottled with dark brown,
1114 lateral edges always whitish, posterior area mostly dark brown. Lateral lobes black (Fig. 4F).
1115 Legs: Fore and mid legs light brown, femora with dark brown spots, tibiae with dark rings. FIII
1116 brown, with strong striated dark patterns on outer faces, knees dark brown; TIII with dark rings.
1117 Tarsomeres I/III-1 yellow brown, apices dark brown. Abdomen red brown mottled with dark
1118 brown dorsally, with two lateral rows of faint yellow spots along abdomen in some specimens;
1119 yellowish brown ventrally. Cerci yellowish brown, with dark rings.

1120 **Male:** FWs reaching base of 4th abdominal tergite. FW coloration (Fig. 5C): Cells very dark
1121 brown, not translucent; veins dark brown except anterior parts of anal veins orange brown. FW
1122 venation (Fig. 5C): 1A slightly curved, CuP not visible. CuA faint, straight along its whole length.
1123 Diagonal vein very faint. Harp triangular, with one very faint oblique vein barely complete.
1124 Mirror not differentiated from other cells. Longitudinal veins of dorsal field faint apically, as
1125 transverse veins. Apical field very short, including one short bifurcation of CuA posterior to
1126 diagonal vein. Lateral field dark brown, area between M and R red brown; with 6 strong
1127 longitudinal veins including M, R, Sc; Sc without bifurcating veins. Supra-anal plate tongue-
1128 shaped, posterior margin truncated.

1129 *Male genitalia (Figs. 6D–F):* Pseudepiphallic sclerite stout and trapezoidal; posterior apex
1130 truncated, feebly emarginated in the middle; with very short lateral lophi stout (barely
1131 surpassing apex in dorsal view), broad (wider than long) and rounded, and pointing slightly
1132 ventrad; anterior margin slightly indented. Rami relatively short, slightly shorter than
1133 pseudepiphallic sclerite, prolonging its trapezoidal shape. Pseudepiphallic parameres
1134 elongated, their oversized ventral lobe falcate and converging, touching each other. Ectophallic
1135 arc narrowly curved to nearly straight. Ectophallic fold with a ventral sclerotization made of two
1136 thin sclerites converging posteriorly. Ectophallic apodemes long and slightly divergent,
1137 exceeding anterior margin of pseudepiphallus. Endophallic sclerite strongly sclerotized and
1138 sinuous, posterior end with a median crest with two short lateral processes perpendicular to
1139 apodeme, barely exceeding anterior margin of pseudepiphallus; endophallic apodeme made
1140 of weakly sclerotized lateral lamellas.

1141 **Female:** FWs short, rounded, going slightly beyond middle of second tergite, only overlapping
1142 at base; dorsal field dark brown, with a thin lateral yellow band; with four strong orange brown
1143 longitudinal veins, without distinct transverse veins; most lateral longitudinal vein located in
1144 yellow band faint. Lateral field dark brown, with 4-5 strong dark brown longitudinal veins,
1145 without distinct transverse veins. Subgenital plate trapezoidal, apical margin emarginated.
1146 Ovipositor shorter than FIII; apex lanceolate, slightly denticulate on dorsal edge.

1147 *Female genitalia:* Female papilla oblong, mostly membranous, oval in dorsal and ventral views,
1148 posterior and anterior ends with obtuse apices (Figs. 6L, 6M).

1149 **Juvenile:** First instar dark brown dorsally, lighter ventrally; whitish cerci with apical black rings.
1150 Later instars with similar coloration as adults; head dorsum pale, otherwise dark brown mottled
1151 with pale yellow (Figs. 7C, 7D).

1152 **Measurements.** See Table 1.

1153 **Habitat and life history traits.** *Fadinthus tehtari* **sp. nov.** lives in the forest floor, hiding in the
1154 leaf litter but can also be found on foliage near the ground (Fig. 7E). The species appears most
1155 active during the day and males generally sing only in the day.

1156 **Calling song** (Fig. 8): Time domain of the song is similar to that of *L. bitaeniatatus* and *L. luae*.
1157 In the field ($t^{\circ}\text{C} = 25.8\text{--}27^{\circ}\text{C}$), the calling song lasts for 9.97 ± 3.74 s (3.93–16.16 s) and is
1158 made of very indented syllables (amplitude modulation resulting from pauses within the FW
1159 closure). The call is organized in two parts, the initial one consisting of 50 ± 24 (11–82) well-
1160 spaced syllables (syllable duration = 0.06 ± 0.01 s [0.03–0.06 s]; syllable period = 0.18 ± 0.02
1161 s [0.15–0.24 s]), the second part being a short trill (duration = 0.47 ± 0.05 s [0.36–0.57 s])
1162 made of syllables set very close together. Each syllable is made of discrete pulses, produced
1163 by regular plectrum pauses, which in turn are caused by a discontinuous closing phase. Such
1164 a pattern produces a broad-band spectrum between 14.6 and 43.4 kHz, with main energy
1165 centered at nearly 21.5 ± 0.3 kHz, which corresponds to the second harmonic peak of the
1166 spectrum.

1167 **Distribution.** This species is currently known only from Andulau Forest Reserve in Belait
1168 District of Brunei Darussalam. This species is relatively abundant among leaf litter but was not
1169 found in Kuala Belalong (see Tan & Wahab, 2018) and other parts of Belait District.

1170 **Etymology.** The species name refers to *Teh Tarik* (= pulled tea, in Malay with origin from
1171 Hokkien dialect). *Teh Tarik* is a traditional drink in Malaysia and Brunei Darussalam where the
1172 species is found; and is also the national drink of Malaysia. The male genitalia of the new
1173 species resemble an inverted cup of *Teh Tarik*, with the posterior dark sclerotized parts
1174 resembling tea dust, lightly sclerotized pseudophallic sclerites resembling the tea color and
1175 membranous tissues at the anterior end resembling the pale frothy top of the tea.

1176

1177 **Key to Lebinthini subtribes and genera**

1178 1. Distributed in the Neotropical region... *Ligypterina* subtribe n. (3)

1179 -. Distributed in the Southeast Asia and in the Western Pacific region... 2

1180

1181 2. Macropterous, with long wings (FWs and HWs)... *Cardiodactylina* subtribe n. (4)

1182 -. Brachypterous, without HWs... *Lebinthina* subtribe n. (5)

1183

1184 3. Brachypterous, FWs reaching two thirds of abdomen length, HWs short below FWs...

1185 *Ligypterus* Saussure, 1878

1186 -. Macropterous, FWs as long as abdomen, HWs surpassing FWs... *Ponca* Hebard, 1928
1187
1188 4. Males with functional stridulatory apparatus and modified mirror area... *Cardiodactylus*
1189 Saussure, 1878
1190 -. Males without stridulatory structures on fully developed FWs... *Swezwilderia* Chopard, 1925
1191
1192 5. Fastigium narrow, face relatively higher than wide. Legs long, FI distinctly longer than
1193 pronotum width, abdomen short, reaching only middle of FIII. ... *Centuriarus* Robillard, 2011
1194 -. Fastigium wider, face about as high as wide. Legs stouter, FI shorter or as long as pronotum
1195 width, abdomen longer, apex reaching beyond middle of FIII... 6
1196
1197 6. Distributed west of New Guinea (New Caledonia, New Guinea, Solomon Islands,
1198 Vanuatu)... 7
1199 -. Distributed east of New Guinea (Borneo, Japan, Java, Malay Peninsula, Philippines
1200 archipelago, Sulawesi, Sumatra, Taiwan)... 12
1201
1202 7. Distributed in New Caledonia... 8
1203 -. Not distributed in New Caledonia... 9
1204
1205 8. Larger in size, pronotum length >3.0 mm. Lateral field of FWs longer than dorsal field; male
1206 FW with well-developed mirror ... *Agnotecous* Saussure, 1878
1207 -. Size distinctly smaller, pronotum length <2.1 (males), <2.3 mm (females). Lateral and dorsal
1208 fields of FWs of similar lengths ... *Pixibinthus* Robillard & Anso, 2016
1209
1210 9. Larger in size, pronotum length >3.0 mm... 10
1211 -. Smaller in size, pronotum length <3.0 mm... 11
1212
1213 10. Male FWs with harp area distinctly longer than wide; female FWs >4.0 mm, overlapping
1214 with each other, with striking cross veins... *Macrobinthus* Robillard & Dong, 2016
1215 -. Male FWs with harp area forming an equilateral triangle; female FWs very small <2.0 mm,
1216 never overlapping with each other, without striking cross veins. ... *Julverninus* Robillard &
1217 Su, 2018
1218
1219 11. Pronotum length <2.1 (males), <2.3 mm (females). Face mostly black. Male harp with one
1220 oblique vein... *Microbinthus* Robillard & Dong, 2016

1221 -. Pronotum length >2.4 (males), >2.6 mm (females). Face with white, brown and black patterns
 1222 Male harp with a characteristic bisinuated oblique vein delimiting a bump in middle of harp...
 1223 *Gnominthus* Robillard & Vicente, 2015
 1224
 1225 12. Body more elongated, with yellowish/whitish longitudinal bands along the whole body.
 1226 Female FWs and ovipositor relatively long... *Lebinthus* Stål, 1877
 1227 -. Body generally stouter, Body without yellowish/whitish longitudinal bands along the whole
 1228 body. Female FWs and ovipositor relatively short ... 13
 1229
 1230 13. Body stout to average sized. Head wider than high in facial view, eyes larger; lateral lobes
 1231 of pronotum almost entirely dark brown; male FW with mirror undifferentiated; male genitalia
 1232 with over-sized pseudepiphallic parameres ... *Fadinthus* **gen. nov.**
 1233 -. Body stout. Head as high as wide in facial view, eyes smaller; lateral lobes of pronotum with
 1234 a lighter ventral margin; male FW with rounded false mirror; male genitalia with average-sized
 1235 pseudepiphallic parameres... *Falcerminthus* **gen. nov.**
 1236

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References

- Akaike H. (2011) Akaike's Information Criterion. In: Lovric M. (eds) International Encyclopedia of Statistical Science. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-04898-2_110
- Alexander, R.D. (1962) Evolutionary change in cricket acoustical communication. *Evolution*, **16**, 443–467.
- Anso, J., Barrabe, L., Desutter-Grandcolas, L., Jourdan, H., Grandcolas, P., Dong, J. & Robillard, T. (2016) Old Lineage on an old Island: *Pixibinthus*, a new cricket genus endemic to New Caledonia shed light on gryllid diversification in a hotspot of biodiversity. *PLoS One*, **11**, e0150920.
- Ayres, D.L., Darling, A., Zwickl, D.J., Beerli, P., Holder, M.T., Lewis, P.O., Huelsenbeck, J.P., Ronquist, F., Swofford, D.L., Cummings, M.P., Rambaut, A. & Suchart, M.A. (2012) BEAGLE: an application programming interface and high-performance computing library for statistical phylogenetics. *Systematic Biology*, **61**, 170–173.
- Baroga-Barbecho, J.B., Tan, M.K., Yap, S.A. & Robillard, T. (2020). Taxonomic study of *Lebinthus* Stål, 1877 (Orthoptera: Gryllidae: Eneopterinae) with description of six new species in the Philippines. *Zootaxa*, **4816**, 401–438.
- Benavides-Lopez, J.L., ter Hofstede, H. & Robillard, T. (2020) Novel system of communication in crickets originated at the same time as bat echolocation and includes male-male multimodal communication. *The Science of Nature*, **107**, 1–6.
- Bennet-Clark, H.C. (1970) The mechanism and efficiency of sound production in mole crickets. *Journal of Experimental Biology*, **52**, 619–652.
- Blomberg, S.P., Garland Jr, T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.
- Bolívar, I. (1889) Enumeración de Gríllidos de Filipinas. *Anales de la Sociedad Española de Historia Natural*, **18**, 415–431.
- Chintauan-Marquier, I.C., Legendre, F., Hugel, S., Robillard, T., Grandcolas, P., Nel, A., Zuccon, D. & Desutter-Grandcolas, L. (2016) Laying the foundations of evolutionary and systematic studies in crickets (Insecta, Orthoptera): a multilocus phylogenetic analysis. *Cladistics*, **32**, 54–81.

- 1287 Borges, R., Machado, J.P., Gomes, C., Rocha, A.P. & Antunes, A. (2019) Measuring
1288 phylogenetic signal between categorical traits and phylogenies. *Bioinformatics*, **35**, 1862–
1289 1869.
- 1290 Bradbury, J.W. & Vehrencamp, S.L. (2011) Principles of animal communication. 2nd.
1291 Sunderland, Massachusetts: Sinauer.
- 1292 Cigliano, M.M., Braun, H., Eades, D.C. & Otte, D. (2021) Orthoptera Species File. Version
1293 5.0/5.0. (01/01/2021) <http://Orthoptera.SpeciesFile.org>.
- 1294 Chopard, L. (1929) Orthoptera palaeartica critica. VII. Les Polyphagiens de la hune
1295 palearctique. *Eos*. 5. 223–358.
- 1296 Chopard, L. (1968) Family Gryllidae: Subfamilies Mogoplistinae, Myrecophilinae,
1297 Scleropterinae, Cachoplistinae, Pteroplistinae, Pentacentrinae, Phalangopsinae,
1298 Trigonidiinae, Eneopterinae; Family Oecanthidae, Gryllotalpidae. In: Beier, M. (ed.),
1299 Orthopterorum Catalogus. Volume 12. Uitgeverij Dr. W. Junk N. V.'s, Gravenhage. Pp. 215–
1300 500.
- 1301 Desutter, L. (1987) Structure et évolution du complexe phallique des Gryllidea (Orthoptera) et
1302 classification des genres néotropicaux de Grylloidea. 1re partie. *Annales De La Société*
1303 *Entomologique De France (N.S.)*, **23**, 213–239.
- 1304 Desutter-Grandcolas, L. (1990). Etude Phylogénétique, biogéographique et écologique des
1305 grylloidea néotropicaux (Insectes, Orthoptères) PhD thesis. Université Paris XI–Orsay,
1306 Orsay. 347 pp.
- 1307 Desutter-Grandcolas, L. (1998) Broad-frequency modulation in cricket (Orthoptera, Grylloidea)
1308 calling songs: two convergent cases and a functional hypothesis. *Canadian Journal of*
1309 *Zoology*, **76**(12), 2148–2163.
- 1310 Desutter-Grandcolas, L. (2003) Phylogeny and the evolution of acoustic communication in
1311 extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta*, **32**, 525–561.
1312 <https://doi.org/10.1046/j.1463-6409.2003.00142.x>
- 1313 Dong, J., Kergoat, G. J., Vicente, N., Rahmadi, C., Xu, S. & Robillard, T. (2018) Biogeographic
1314 patterns and diversification dynamics of the genus *Cardiodactylus* Saussure (Orthoptera,
1315 Grylloidea, Eneopterinae) in Southeast Asia. *Molecular Phylogenetics and Evolution*, **129**,
1316 1–14.
- 1317 Dong, J.J. & Robillard, T., (2016) The *Cardiodactylus* crickets from Eastern New Guinea, with
1318 description of five new species (Orthoptera: Gryllidae: Eneopterinae) In: Robillard, T.,
1319 Legendre, F., Villemant, C. & Leponce, M. (Eds.), Insects of Mount Wilhelm, Papua New
1320 Guinea, Mémoires du Muséum National d'Histoire Naturelle 209. Muséum national
1321 d'Histoire Naturelle, Paris, pp. 203–258.
- 1322 Elliott, C.J.H. & Koch, U.T. (1985) The clockwork cricket. *Naturwissenschaften*, **72**, 150-153.

1323 Erixon, P., Svennblad, B., Britton, T. & Oxelman, B. (2003) Reliability of Bayesian posterior
 1324 probabilities and bootstrap frequencies in phylogenetics. *Systematic Biology*, **52**, 665–673.

1325 Gernhard, T. (2008) The conditioned reconstructed process. *Journal of Theoretical Biology*,
 1326 **253**, 769–778.

1327 Gerhardt, H.C. (1991) Female mate choice in treefrogs: static and dynamic acoustic criteria.
 1328 *Animal Behavior*, **42**, 615–635.

1329 Gerhardt, H.C. & Huber, F. (2002) Acoustic Communication in Insects and Anurans: Common
 1330 Problems and Diverse Solutions. I.L., U.S.A.: University of Chicago Press. 542 pp.

1331 Harrison, R.G. & Bogdanowicz, S.M. (1995) Mitochondrial DNA phylogeny of North American
 1332 field crickets: perspectives on the evolution of life cycles, songs, and habitat associations.
 1333 *Journal of Evolutionary Biology*, **8**, 209–232.

1334 Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. (2008) GEIGER:
 1335 investigating evolutionary radiations. *Bioinformatics*, **24**, 129–131.

1336 Heller, K.G. & Hemp, C. (2019) Extremely divergent song types in the genus *Aerotegmina*
 1337 Hemp (Orthoptera: Tettigoniidae: Hexacentrinae) and the description of a new species from
 1338 the Eastern Arc Mountains of Tanzania (East Africa). *Bioacoustics*, **28**(3), 269–285.

1339 Horch, H.W., Mito, T., Popadic, A., Ohuchi, H. & Noji, S. (2017) The cricket as a model
 1340 organism. Springer, Tokyo, 376 pp.

1341 Huang, Y., Orti, G., Sutherlin, M., Duhachek, A. & Zera, A. (2000) Phylogenetic relationships
 1342 of North American field crickets inferred from mitochondrial DNA data. *Molecular*
 1343 *Phylogenetics and Evolution*, **17**, 48–57.

1344 Jaiswara, R., Dong, J., Ma, L., Yin, H. & Robillard, T. (2019) Taxonomic revision of the genus
 1345 *Xenogryllus* Bolívar, 1890 (Orthoptera, Gryllidae, Eneopterinae, Xenogryllini). *Zootaxa*,
 1346 **4545**, 301–338.

1347 Kalyanamoorthy, S., Minh, B.Q., Wong, T.F.K., von Haeseler, A. & Jermin, L.S. (2017)
 1348 ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods*,
 1349 **14**, 587–589. <https://doi.org/10.1038/nmeth.4285>

1350 Katoh, K., Rozewicki, J. & Yamada, K.D. (2017) MAFFT online service: multiple sequence
 1351 alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics*, 1–7.

1352 Kirby, W.F. (1906) Orthoptera Saltatoria. Part I. (Achetidae et Phasgonuridae) *A Synonymic*
 1353 *Catalogue of Orthoptera (Orthoptera Saltatoria, Locustidae vel Acridiidae)*, **2**, i–viii, 1–562.

1354 Kuraku, S., Zmasek, C.M., Nishimura, O. & Katoh, K. (2013) aLeaves facilitates on-demand
 1355 exploration of metazoan gene family trees on MAFFT sequence alignment server with
 1356 enhanced interactivity. *Nucleic Acids Research*, **41**, 22–28.
 1357 <https://doi.org/10.1093/nar/gkt389>

1358 Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T., Calcott, B. (2017) PartitionFinder 2: new
1359 methods for selecting partitioned models of evolution for molecular and morphological
1360 phylogenetic analyses. *Molecular Biology and Evolution*, **34**, 772–773.

1361 Michelsen, A. & Nocke, H. (1974) Biophysical aspects of sound communication in insects. In:
1362 Treherne, J.E., Berridge, M.J. & Wigglesworth, V.B. (Eds.) *Advances in insect physiology*
1363 (Vol. 10). Academic Press. Pp. 247–296.

1364 Miller, M.A., Schwartz, T., Pickett, B.E., He, S., Klem, E.B., Scheuermann, R.H., Passarotti,
1365 M., Kaufman, S. & O'Leary, M.A. (2015) A RESTful API for access to phylogenetic tools via
1366 the CIPRES Science Gateway. *Evolutionary Bioinformatics*, **11**, 43–48.

1367 Montealegre-Z, F., Morris, G.K. & Mason, A.C. (2006) Generation of extreme ultrasonics in
1368 rainforest katydids. *Journal of Experimental Biology*, **209**, 4923–4937.

1369 Montealegre-Z, F., Windmill, J.F., Morris, G.K., & Robert, D. (2009) Mechanical phase shifters
1370 for coherent acoustic radiation in the stridulating wings of crickets: the plectrum mechanism.
1371 *Journal of Experimental Biology*, **212**, 257–269.

1372 Nattier, R., Grandcolas, P., Elias, M., Desutter-Grandcolas, L., Jourdan, H., Couloux, A. &
1373 Robillard, T. (2012) Secondary sympatry caused by range expansion informs on the
1374 dynamics of microendemism in a biodiversity hotspot. *PLoS One*, **7**, e48047.

1375 Nattier, R., Robillard, T., Desutter-Grandcolas, L., Couloux, A. & Grandcolas, P. (2011) Older
1376 than New Caledonia emergence? A molecular phylogenetic study of the eneopterine
1377 crickets (Orthoptera: Grylloidea). *Journal of Biogeography*, **38**, 2195–2209.

1378 Nguyen, L.T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q., (2015) IQTREE: A fast and
1379 effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular*
1380 *Biology and Evolution*, **32**, 268–274.

1381 Nocke, H. (1971) Biophysik der Schallerzeugung durch die Vorderflügel der Grillen. *Zeitschrift*
1382 *für vergleichende Physiologie*, **74**, 272–314.

1383 Oshiro, Y. (1996) Description of a new species of the genus *Lebinthus* Stål (Orthoptera,
1384 Gryllidae) from Lan Yu Island, Taiwan. *Japanese Journal of Systematic Entomology*, **2**,
1385 117–121.

1386 Otte, D. (1992) Evolution of cricket songs. *Journal of Orthoptera Research*, **1**, 25–49.

1387 Otte, D. (1994) Orthoptera Species File. 1. Crickets (Grylloidea) Orthopterists's Society and
1388 the ANSP, Philadelphia, PA.

1389 Otte, D. (2007) New species of *Cardiodactylus* from the western Pacific region (Gryllidae:
1390 Eneopterinae). *Proceedings of the Academy of Natural Sciences of Philadelphia*, **156**, 341–
1391 400.

1392 Otte, D. & Alexander, R.D. (1983) The Australian crickets. *Monographs of the Academy of*
1393 *Natural Sciences of Philadelphia*, **22**, 1–477.

1394 Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

1395 Price, J.J., Friedman, N.R. & Omland, K.E. (2007) Song and plumage evolution in the new
 1396 world orioles (*Icterus*) show similar lability and convergence in patterns. *Evolution*, **61**, 850–
 1397 863.

1398 Price, J.J. & Lanyon, S.M. (2002) Reconstructing the evolution of complex bird song in the
 1399 oropendolas. *Evolution*, **56**, 1514–1529.

1400 R Development Core Team (2018) R: A language and environment for statistical computing.
 1401 Vienna (Austria): R Foundation for Statistical Computing.

1402 Ragge, D.R. (1955) The wing venation of the Orthoptera Saltatoria. British Museum (Natural
 1403 History), London, 159 pp.

1404 Ragge, D.R. & Reynolds, W.J. (1998) The songs of the grasshoppers and crickets of Western
 1405 Europe. Colchester (UK): Harley Books.

1406 Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014) Tracer v1.6, Available from
 1407 <http://beast.bio.ed.ac.uk/Tracer>.

1408 Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other
 1409 things) *Methods in Ecology and Evolution*, **3**, 217–223.

1410 Robillard, T. (2010) New species of the genus *Lebinthus* (Orthoptera, Grylloidea,
 1411 Eneopterinae, Lebinthini) from Indonesia and the Solomon Islands. *Zootaxa*, **2386**, 25–48.
 1412 <http://dx.doi.org/10.11646/zootaxa.2386.1.2>

1413 Robillard, T. (2011a) *Centurarius* n. gen., a new genus of Eneopterinae crickets from Papua
 1414 (Insecta, Orthoptera, Grylloidea). *Zoosystema*, **33**, 49–60.

1415 Robillard, T. (2011b) New *Cardiodactylus* species from unsuspected places in Southeast Asia
 1416 (Orthoptera, Grylloidea, Eneopterinae). *Zootaxa*, **2909**, 14–26.

1417 Robillard, T., Gorochoy, A.V., Poulain, S., Suhardjono, Y.R. (2014) Revision of the cricket
 1418 genus *Cardiodactylus* (Orthoptera, Eneopterinae, Lebinthini): the species from both sides
 1419 of the Wallace line, with description of 25 new species. *Zootaxa*, **3854**, 1–104.

1420 Robillard, T. & Desutter-Grandcolas, L. (2004a) Phylogeny and the modalities of acoustic
 1421 diversification in extant Eneopterinae (Insecta, Orthoptera, Grylloidea, Eneopteridae).
 1422 *Cladistics*, **20**, 271–293.

1423 Robillard, T. & Desutter-Grandcolas, L. (2004b) High-frequency calling in Eneopterinae
 1424 crickets (Orthoptera, Grylloidea, Eneopteridae): adaptive radiation revealed by phylogenetic
 1425 analysis. *Biological Journal of the Linnean Society*, **83**, 577–584.

1426 Robillard, T. & Desutter-Grandcolas, L. (2006) Phylogeny of the cricket subfamily
 1427 Eneopterinae (Orthoptera, Grylloidea, Eneoptidae) based on four molecular loci and
 1428 morphology. *Molecular Phylogenetics and Evolution*, **40**, 643–661.

1429 Robillard, T. & Desutter-Grandcolas, L. (2008) Clarification of the taxonomy of extant crickets
 1430 of the subfamily Eneopterinae (Orthoptera: Grylloidea; Gryllidae). *Zootaxa*, **1789**, 66–68.
 1431 <http://dx.doi.org/10.11646/zootaxa.1789.1.3>

- 1432 Robillard, T. & Desutter-Grandcolas, L. (2011) Evolution of calling songs as multicomponent
1433 signals in crickets (Orthoptera: Grylloidea: Eneopterinae). *Behaviour*, **148**, 627-672.
- 1434 Robillard, T., Dong, J., Legendre, F. & Agauvoa, S. (2016) The brachypterous Lebinthini
1435 crickets from Papua New Guinea, with description of two new genera and four new species
1436 (Orthoptera: Gryllidae: Eneopterinae) In Robillard, T., Legendre, F., Villemant, C. &
1437 Leponce, L. (Eds.), Insects of Mount Wilhelm, Papua New Guinea. Mémoires du Muséum
1438 national d'Histoire Naturelle, 209 (pp. 149– 202) Paris, France: Muséum National d'Histoire
1439 Naturelle. ISBN: 978-2-85653-784-8.
- 1440 Robillard, T., Grandcolas, P., & Desutter-Grandcolas, L. (2007) A shift toward harmonics for
1441 high-frequency calling shown with phylogenetic study of frequency spectra in Eneopterinae
1442 crickets (Orthoptera, Grylloidea, Eneopteridae). *Canadian Journal of Zoology*, **85**, 1264–
1443 1275.
- 1444 Robillard, T., Legendre, F., Desutter-Grandcolas, L. & Grandcolas, P. (2006) Phylogenetic
1445 analysis and alignment of behavioral sequences by direct optimization. *Cladistics*, **22**, 602–
1446 –633.
- 1447 Robillard, T. & Su, YN. (2018) New lineages of Lebinthini from Australia (Orthoptera: Gryllidae:
1448 Eneopterinae). *Zootaxa*, **4392**, 241–266. doi: 10.11646/zootaxa.4392.2.2.
- 1449 Robillard, T. & Tan, M.K. (2013) A taxonomic review of common but little known crickets from
1450 Singapore and the Philippines (Insecta: Orthoptera: Eneopterinae). *The Raffles Bulletin of*
1451 *Zoology*, **61**, 705–725.
- 1452 Robillard, T., ter Hofstede, H.M., Orivel, J. & Vicente, N.M. (2015) Bioacoustics of the
1453 neotropical eneopterinae (Orthoptera, Grylloidea, Gryllidae) *Bioacoustics*, **24**(2), 123–143.
- 1454 Robillard, T. & Yap, S. (2015) The Eneopterinae crickets from Leyte Island (Philippines) with
1455 description of two new species [Insecta: Orthoptera: Grylloidea: Gryllidae]. *Raffles Bulletin*
1456 *of Zoology*, **63**, 69–90.
- 1457 Robillard, T., Yap, S. & Yngente, M.V. (2013) Systematics of cryptic species of *Lebinthus*
1458 crickets in Mount Makiling (Grylloidea, Eneopterinae). *Zootaxa*, **3693**, 049–063.
- 1459 Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B.,
1460 Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian
1461 phylogenetic inference and model choice across a large model space. *Systematics Biology*,
1462 **61**, 539–542.
- 1463 Salazar, K., Murphy, R. J., Guillaume, M., Nattier, R. & Robillard, T. (2020) *Pseudolebinthus*
1464 *lunipterus* sp. nov.: a striking deaf and mute new cricket from Malawi (Orthoptera, Gryllidae,
1465 Eneopterinae). *PeerJ*, **8**, e8204.
- 1466 Shaw, K.L. (1999) A Nested Analysis of Song Groups and Species Boundaries in the Hawaiian
1467 Cricket Genus *Laupala*. *Molecular Phylogenetics and Evolution*, **11**, 332–341.

1468 Specht, R. (2011) Avisoft-SASLab version 5.10. copyright 1990–2011, Avisoft Bioacoustics,
 1469 Berlin. Available from: <http://www.avisoft.com> (accessed 22 January 2014)

1470 Stål, C. (1877) Orthoptera nova ex Insulis Philippinis. *Öfversigt af Kongl. Vetenskaps-*
 1471 *akademiens förhandlingar*, **34**, 35–58.

1472 Song, H., Buhay, J.E., Whiting, M.F., & Crandall, K.A. (2008) Many species in one: DNA
 1473 barcoding overestimates the number of species when nuclear mitochondrial pseudogenes
 1474 are coamplified. *Proceedings of the National Academy of Sciences*, **105**, 13486–13491.

1475 Suchard, M.A., Lemey, P., Baele, G., Ayres, D.L., Drummond, A.J. & Rambaut, A. (2018)
 1476 Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus*
 1477 *Evolution*, **4**, vey016.

1478 Sueur, J., Aubin, T., Simonis, C. (2008) Seewave, a free modular tool for sound analysis and
 1479 synthesis. *Bioacoustics*, **18**, 213–226.

1480 Tan, M.K., Japir, R. & Chung, A.Y.C. (2019a) Uncovering the Grylloidea and Tettigoniodea
 1481 (Orthoptera: Ensifera) in the Forest Research Centre (Sepilok) Entomological Collection.
 1482 *Zootaxa*, **4701**, 301–349.

1483 Tan, M. K., Japir, R., Chung, A. Y. C. & Robillard, T. (2019b) Crickets of the subfamily
 1484 Eneopterinae (Orthoptera: Grylloidea) from Sandakan, Sabah: one new species and calling
 1485 songs of a sympatric species. *Zootaxa*, **4619**, 347–363.

1486 Tan, M. K. & Robillard, T. (2014) A new species of *Cardiodactylus* (Orthoptera: Grylloidea:
 1487 Eneopterinae) from Singapore. *Zootaxa*, **3764**, 364–376.

1488 Tan, M. K. & Wahab, R. A. (2018) Preliminary study on the diversity of Orthoptera from Kuala
 1489 Belalong Field Studies Centre, Brunei Darussalam, Borneo. *Journal of Orthoptera*
 1490 *Research*, **27**, 119–142.

1491 ter Hofstede, H.M., Schöneich, S., Robillard, T. & Hedwig, B. (2015) Evolution of a
 1492 communication system by sensory exploitation of startle behavior. *Current Biology*, **25**,
 1493 3245–3252.

1494 ter Hofstede, H.M., Symes, L.B., Martinson, S.J., Robillard, T., Faure, P., Madhusudhana, S.
 1495 & Page, R.A. (2020) Calling songs of Neotropical katydids (Orthoptera: Tettigoniidae) from
 1496 Panama. *Journal of Orthoptera Research*, **29**, 137–201.

1497 Trifinopoulos, J., Nguyen, L.-T., von Haeseler, A. & Minh, B.Q. (2016) W-IQ-TREE: a fast
 1498 online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, **44**: 232–
 1499 235. <https://doi.org/10.1093/nar/gkw256>

1500 Vicente, N.M., Olivero, P., Lafond, A., Dong, J. & Robillard, T. (2015) *Gnominthus* gen. nov.,
 1501 a new genus of crickets endemic to Papua New Guinea with novel acoustic and behavioural
 1502 diversity (Insecta, Orthoptera, Gryllidae, Eneopterinae). *Zoologischer Anzeiger—A Journal*
 1503 *of Comparative Zoology*, **258**, 82–91. <https://doi.org/10.1016/j.jcz.2015.06.005>

1504 Vicente, N., Kergoat, G.J., Dong, J., Yotoko, K., Legendre, F., Nattier, R. & Robillard, T. (2017)
1505 In and out of the Neotropics: historical biogeography of Eneopterinae crickets. *Journal of*
1506 *Biogeography*, **44**, 2199–2210.

1507 Wilkins, M.R., Seddon, N. & Safran, R. J. (2013) Evolutionary divergence in acoustic signals:
1508 causes and consequences. *Trends in Ecology & Evolution*, **28**, 156–166.

1509 Yin, H. & Liu, X.-W. (1995) Descriptions of two new species and a new recorded species of
1510 Grylloidea (Orthoptera) from China. *Sinozoologia*, **12**, 281–284.

1511

Figure captions

Fig. 1. BI tree showing the phylogeny of Lebinthini (A). Support values for both BI and ML analyses are given at nodes (BI pp/ML bootstrap); posterior probabilities below 0.90 and bootstrap values below 70% are considered as low support and are represented as -/-. Nodes not present in the ML tree are indicated as * instead of a bootstrap value. Map representing the known distribution of tribes and subtribes of Eneopterinae (B).

Fig. 2. Simplified dated phylogeny resulting from BEAST analyses of the species-level dataset, using a Yule Process tree prior. Median age estimates are given above each node; horizontal bars on nodes represent the 95% highest posterior density interval of age estimates; posterior probabilities are indicated below nodes, with values below 0.90 considered as weak support and represented as -.

Fig. 3. Reconstruction of the ancestral states for four acoustic calling song traits: structure of call (A), echeme structure (B), dominant frequency (C), and nature of dominant frequency (D).

Fig. 4. Face in anterior views (A, C, E) and head and pronotum in lateral views (B, D, F) of *Lebinthus luae* (A, B), *Falcerminthus sanchezi* **gen. nov.** (C, D), and *Fadinthus tehtari* **gen. et sp. nov.** (E, F). Scale bar: 1 mm.

Fig. 5. Male FWs in dorsal views of *Lebinthus luae* (A), *Falcerminthus estrellae* **gen. nov.** (B), *Fadinthus tehtari* **gen. et sp. nov.** (C), and *Fadinthus miri* **gen. et sp. nov.**. Scale bar: 1 mm.

Fig. 6. Male and female genitalia of *Fadinthus miri* **gen. et sp. nov.** (A–C, J, K), and *Fadinthus tehtari* **gen. et sp. nov.** (D–F, L, M), and other representative species from Lebinthina (G–I). Male genitalia photographed in dorsal (A, D, G–I), ventral (B, E) and lateral (C, F) views; female copulatory papilla in dorsal (J, L) and lateral (K, M) views. Scale bar: 0.5 mm.

Fig. 7. *Fadinthus tehtari* **gen. et sp. nov.** male (A) and female (B) adults, and nymphs (C, D) when alive. The natural habitat of the species in Belait District, Brunei Darussalam (E).

Fig. 8. Male calling song of *Fadinthus tehtari* **gen. et sp. nov.**: oscillograms showing four calling songs (A), one calling song (B); spectrogram of calling song (C); oscillogram showing the second part of the call (D); power spectrum of one syllable in the first part of the call (E).

Table captions

Table 1. Measurements of *Fadinthus miri* **sp. nov.** and *Fadinthus tehtari* **sp. nov.**
Abbreviations: BL, body length; PronL, pronotum length; PronW, pronotum width; FWL, forewing length; FWW, forewing width; FIIIL, length of hind femur; FIIIW, width of hind femur; TIILL, length of hind tibia; Tallls, number of hind tarsomere spines; las, number of inner spines on hind tibia dorsal side above the spurs; lbs, number of inner spines on hind tibia dorsal side between the spurs; Oas, number of outer spines on hind tibia dorsal side above the spurs; Obs, number of outer spines on hind tibia dorsal side between the spurs; TallIOs, number of outer spines on dorsal side of third hind tarsomere; OL, ovipositor length.

Supporting information

Fig. S1. IQtree ML gene trees inferred for each separate marker 12S (a), 16S (b), COI (c), COII (d), Cytb (e), 18S (f), 28S (g), H3 (h). Bootstrap support values above 70 % are represented by a grey circle proportional to the support (see scale on the left side of the tree)

Fig. S2. IQ-TREE ML analyses of the concatenated dataset. (a) results of the analysis using 8 gene partitions with models determined using IQ-TREE Model Finder. (b) results of the analysis using five fixed models defined by the best-fit partitioning schemes and the associated substitution models used in the BI analysis (see below). Bootstrap support values above 75% are represented by a grey circle proportional to the support (see scale on the left side of the tree)

Fig. S3. Dated phylogeny resulting from BEAST analyses of the species-level dataset, using birth-death tree speciation priors. Median age estimates are presented on nodes; horizontal bars on nodes are also used to provide the 95% highest posterior density interval of age estimates.

Table S1. List of specimens and the gene sequences sampled for the phylogenetic tree and ASR. Lab codes marked by * were used in the dating analysis as representative of the species when more than one individual have been sequenced.

Table S2. Models used in the phylogenetic analyses: models inferred with IQ-TREE ModelFinder (ML analysis) and best Best-fit models of sequence evolution and partitioning schemes selected with PartitionFinder ('unlinked branch lengths' option) for Bayesian Inference (MrBayes/BEAST), with codon position is denoted by pos1, pos2 and pos3. Subsets are denoted by P1 to Pn.

1585 **Table S3.** List of species and coding of acoustic traits used for the ancestral state
1586 reconstruction analyses

1587

1588 **Table S4.** AICc (sample-size corrected AIC) for ASR analyses of three discrete traits. Best-fit
1589 models are mentioned in bold.

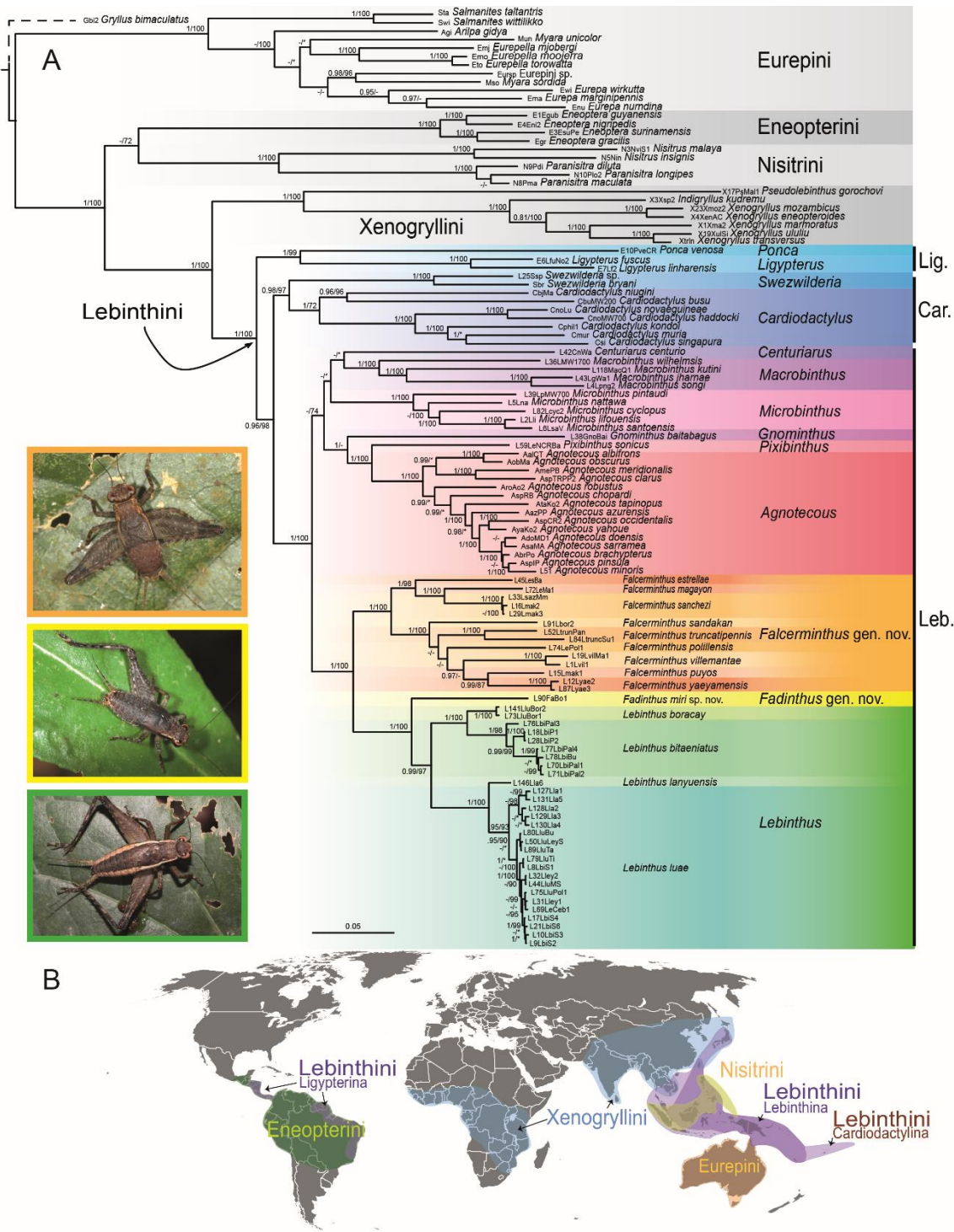
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Table 1. Measurements of *Fadinthus miri* **sp. nov.** and *Fadinthus tehtari* **sp. nov.**
Abbreviations: BL, body length; PronL, pronotum length; PronW, pronotum width; FWL, forewing length; FWW, forewing width; FIIL, length of hind femur; FIIW, width of hind femur; TIIL, length of hind tibia; TIIIs, number of hind tarsomere spines; las, number of inner spines on hind tibia dorsal side above the spurs; lbs, number of inner spines on hind tibia dorsal side between the spurs; Oas, number of outer spines on hind tibia dorsal side above the spurs; Obs, number of outer spines on hind tibia dorsal side between the spurs; TIIIOs, number of outer spines on dorsal side of third hind tarsomere; OL, ovipositor length.

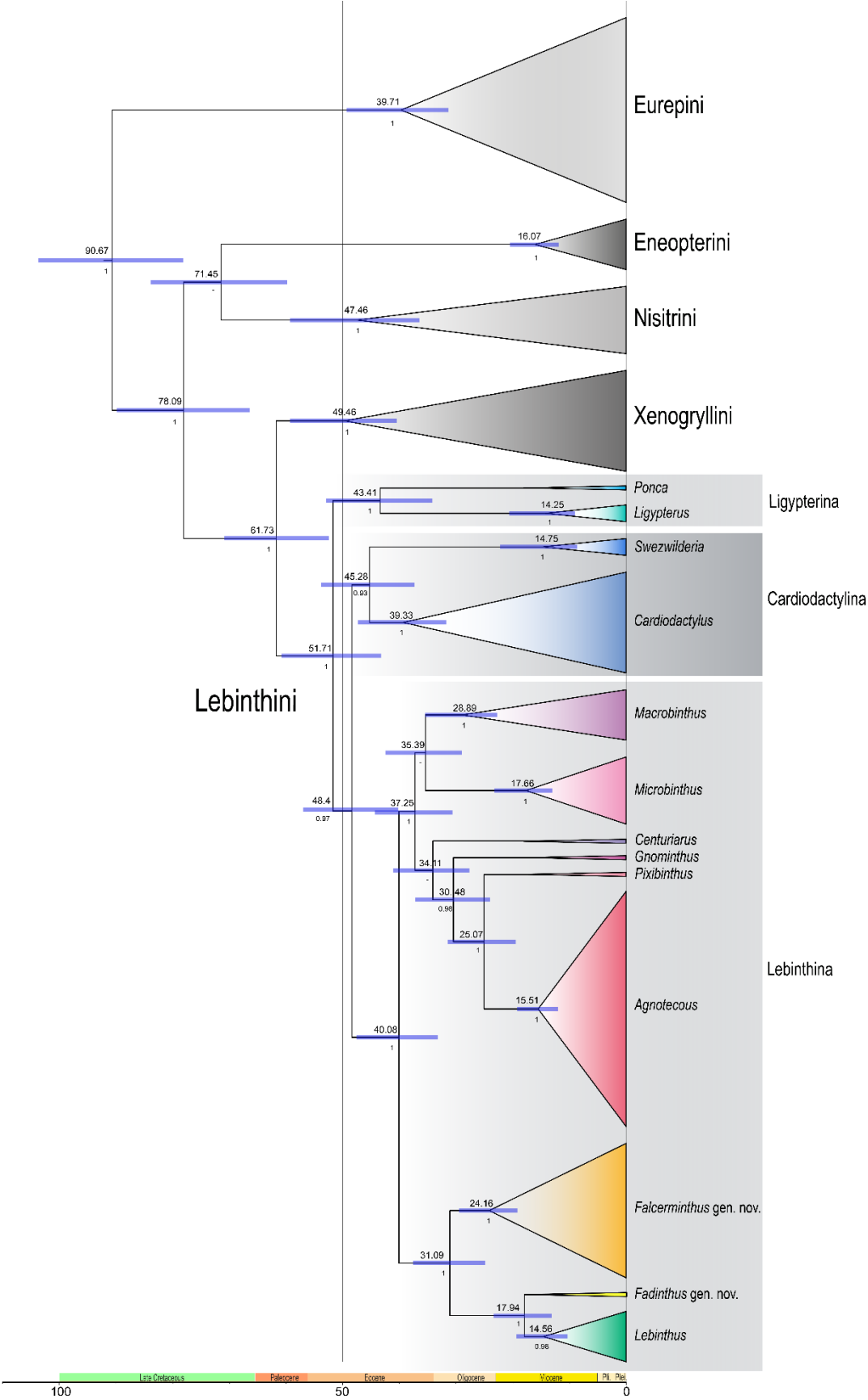
	BL	PronL	PronW	FWL	FWW	FIIL	FIIW	TIIL	TIIIs				TIIIOs	OL
									las	lbs	Oas	Obs		
<i>F. miri</i> sp. n.														
Male holotype	13.7	2.7	3.8	4.4	3	11.2	3.8	9.3	8	7	12	7	3	-
Males paratype	13.8	2.7	3.8	4.3	3	11.5	4.1	9.3	9	5	12	7	3	-
Female allotype	13.7	2.6	3.7	3.1	-	11.3	3.8	11	6	4	11	7	3	10
Females (n=4)	11.6-14.9	2.3-2.7	3.6-4.1	2.5-3.1	-	9.1-11.9	3-4	7.1-11	5-6	4-5	9-11	5-7	2-4	8.9-10
(Female mean)	(13.3)	(2.6)	(3.8)	(2.8)	-	(10.4)	(3.5)	(9.2)	(6)	(5)	(10)	(6)	(3)	(9.4)
<i>F. tehtari</i> sp. n.														
Male holotype	14	2.4	3.5	3.5	3	11.1	3.8	9.3	7	5	11	6	3	-
Female allotype	15.2	2.6	3.8	2.6	-	11.4	3.8	9.2	6	7	14	6	3	10
Females (n=5)	14-15.3	2.6-3	3.6-4	2.6-2.9	-	11.3-12.2	3.8-4.2	9.2-10.1	6-8	4-7	10-14	4-7	3	10-10.6
(Female mean)	(14.5)	(2.7)	(3.8)	(2.7)	-	(11.8)	(3.9)	(9.5)	(7)	(5)	(12)	(6)	(3)	(10.2)

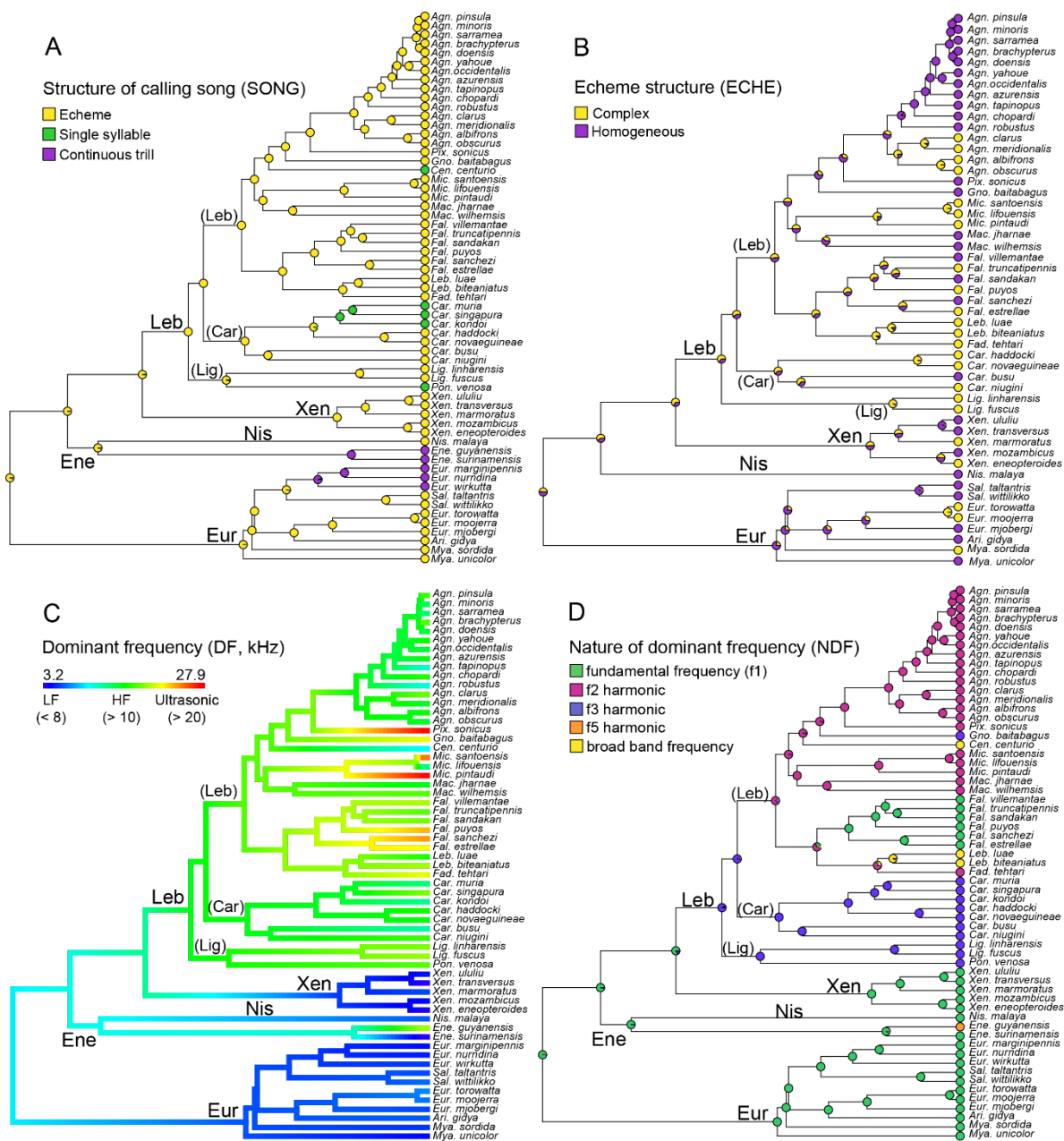
1603 Fig. 1



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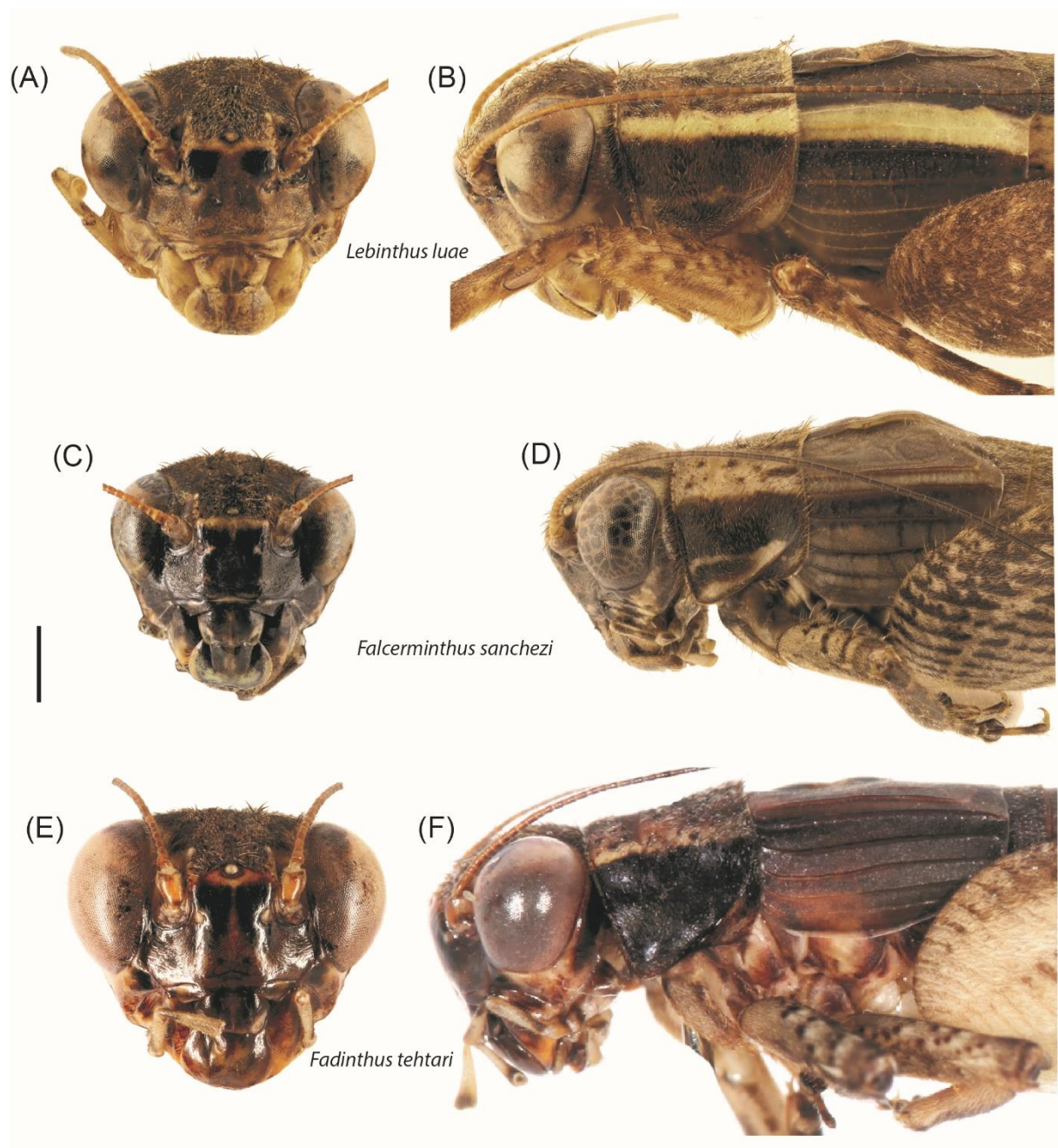
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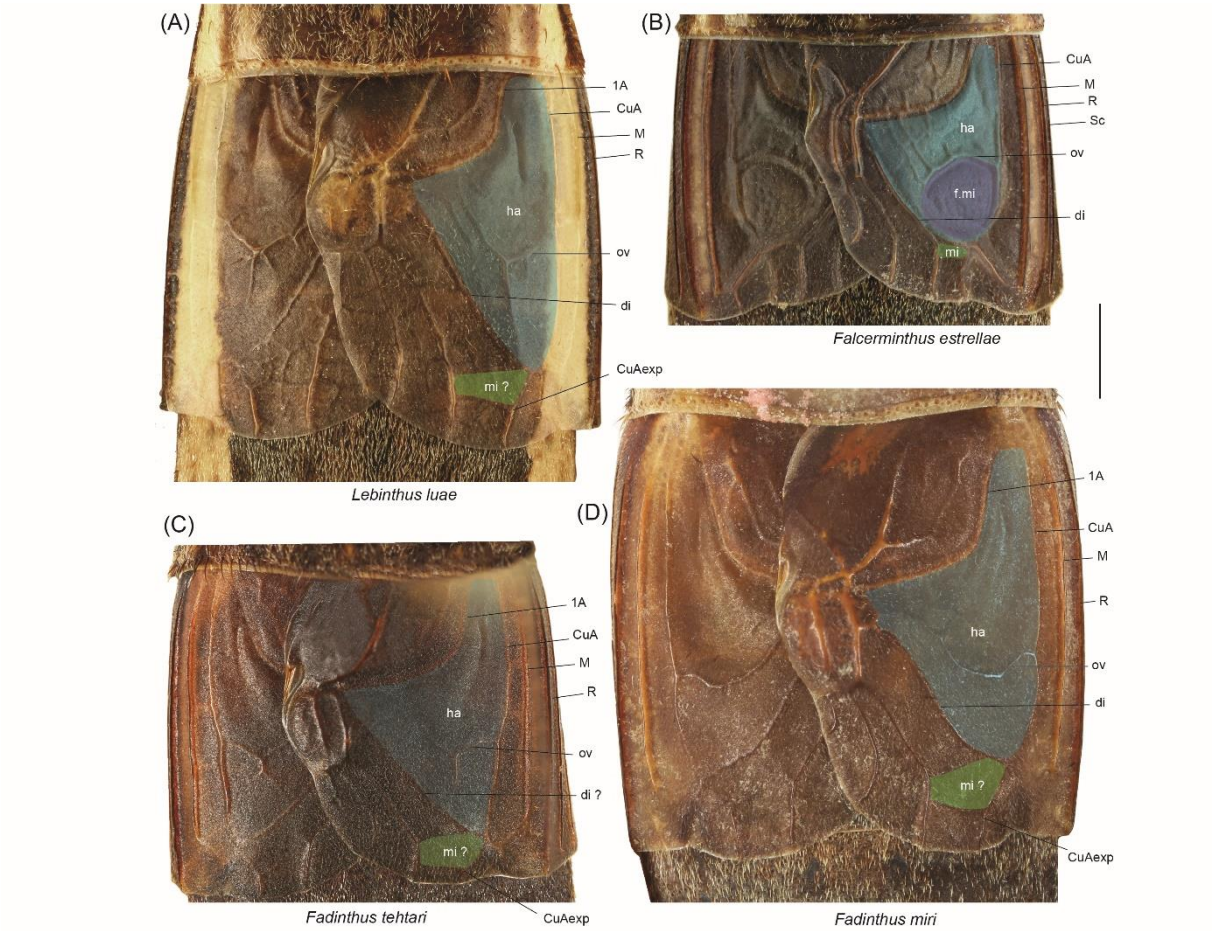
1611 Fig.4



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1614 Fig.5



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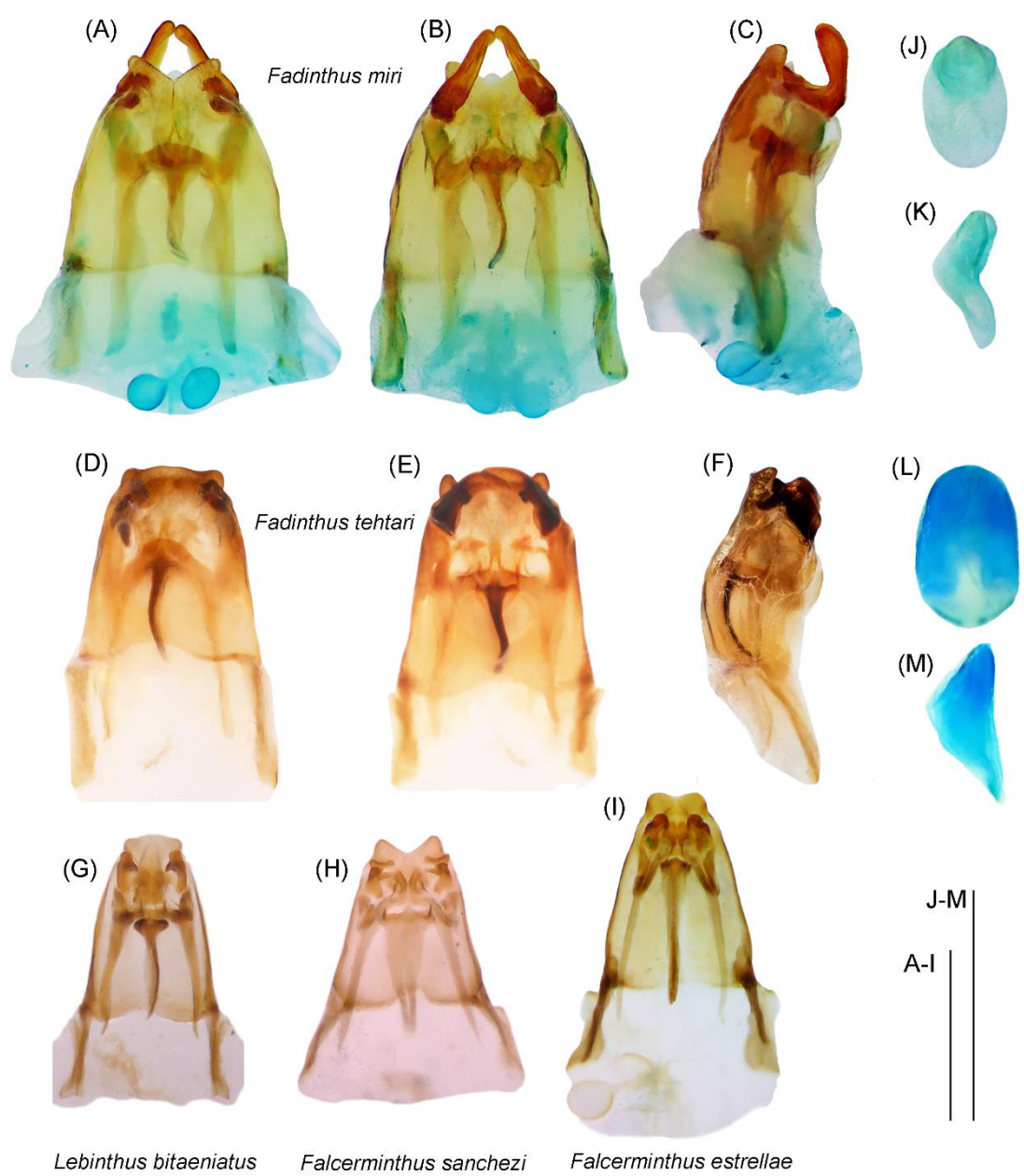
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1617 Fig.6



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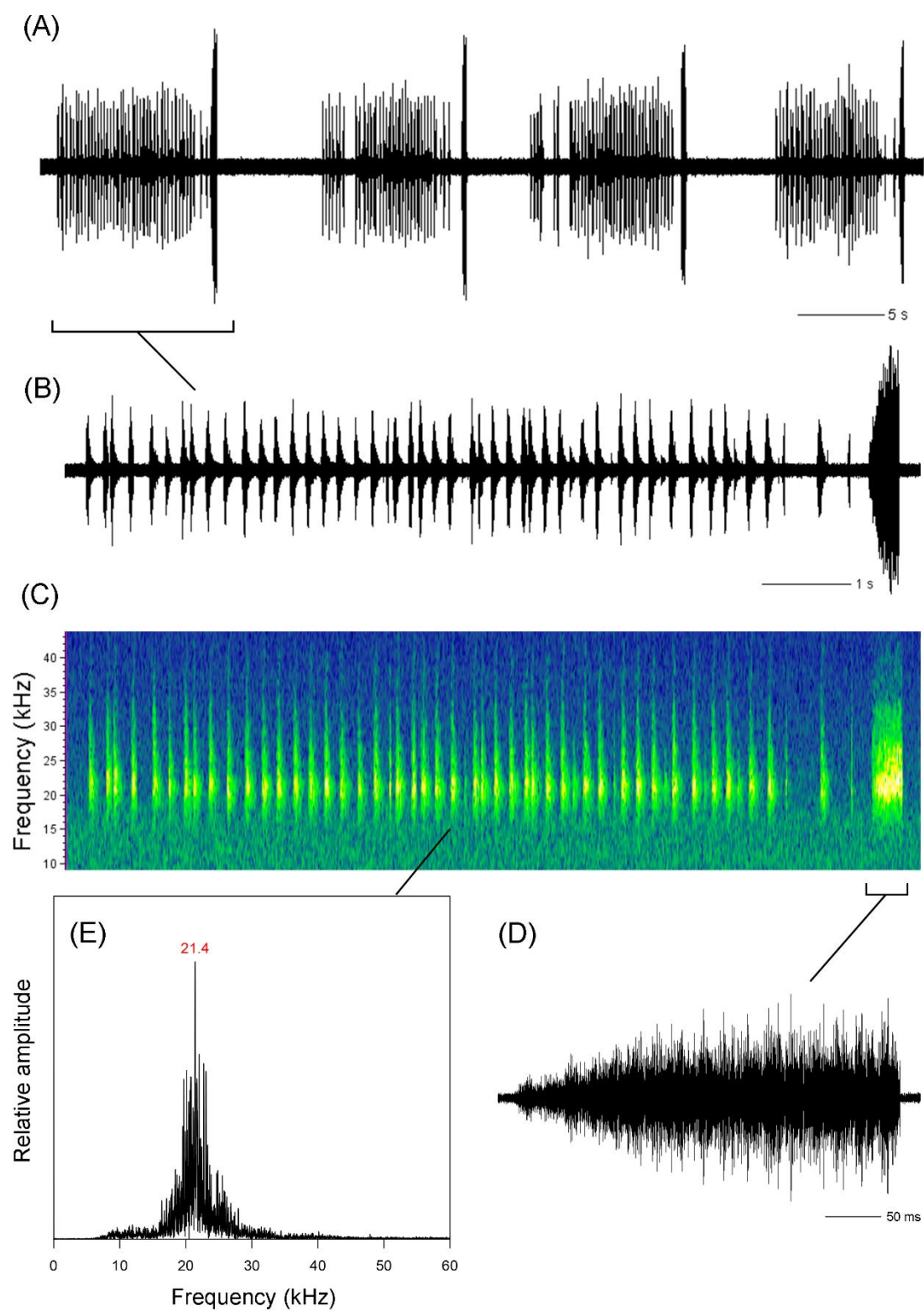
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1620 Fig.7



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1624 Fig.8



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1627 **Table S1.** List of specimens and the gene sequences sampled for the phylogenetic tree and ASR. Lab codes marked by * were used in the
1628 dating analysis as representative of the species when more than one individual have been sequenced.

Species	Collection/Voucher	Lab code	Origin	12S	16S	CytB	18S	COI	COII	28S	H3
<i>Agnotecous albifrons</i> Desutter-Grandcolas, 1997	MNHN-EO-ENSIF2767	*AalCT	New Caledonia	JX89739 4	JX89735 3	JX897314	JX89758 3	JX89741 8	JX89744 6	JX89749 0	JX89757 2
<i>Agnotecous azurensis</i> Desutter-Grandcolas, 2006	MNHN-EO-ENSIF2778	*AazPP	New Caledonia	JX89739 0	JX89736 1	JX897332	JX89759 3	JX89742 7	JX89745 5	JX89747 3	JX89756 8
<i>Agnotecous brachypterus</i> Gorochoy, 1986	MNHN-EO-ENSIF2664	*AbrPo	New Caledonia	JX89738 2	JX89737 0	JX897341	JX89759 6	JX89743 2	JX89745 9	JX89748 5	JX89757 1
<i>Agnotecous chopardi</i> Desutter-Grandcolas, 2006	MNHN-EO-ENSIF2781	*AspRB	New Caledonia	JX89739 1	JX89736 3	JX897335	JX89760 1	JX89741 1	JX89744 0	JX89746 9	JX89755 9
<i>Agnotecous clarus</i> Desutter-Grandcolas, 2006	MNHN-EO-ENSIF2788	*AspTRPP2	New Caledonia	JX89740 0	JX89734 7	JX897324	JX89759 0	JX89740 7	JX89745 1	JX89749 2	JX89755 4
<i>Agnotecous doensis</i> Desutter-Grandcolas, 2006	MNHN-EO-ENSIF2782	*AdoMD1	New Caledonia	JX89738 1	JX89736 8	JX897340	JX89759 2	JX89743 1	JX89746 0	JX89748 0	JX89755 8
<i>Agnotecous meridionalis</i> Desutter-Grandcolas, 2006	MNHN-EO-ENSIF2771	*AmePB	New Caledonia	JX89740 2	JX89735 0	JX897313	JX89759 7	JX89741 0	JX89744 2	JX89748 9	JX89755 0
<i>Agnotecous obscurus</i> (Chopard, 1970)	MNHN-EO-ENSIF2785	*AobMa	New Caledonia	JX89739 3	JX89735 7	JX897320	JX89758 7	JX89741 2	JX89745 0	JX89748 7	JX89757 6
<i>Agnotecous minoris</i> Robillard, 2010	MNHN-EO-ENSIF3351	*L51	New Caledonia	MZ50181 6	MZ49717 0	-	MZ49727 7	MZ50662 0	MZ47600 8	MZ50527 3	MZ47604 9
<i>Agnotecous occidentalis</i> Desutter-Grandcolas, 2006	MNHN-EO-ENSIF2765	*AspCR2	New Caledonia	JX89738 6	JX89736 2	JX897322	JX89758 9	JX89743 4	JX89746 1	-	JX89757 0
<i>Agnotecous pinsula</i> Robillard, 2010	MNHN-EO-ENSIF2624	*AspIP	New Caledonia	JX89738 3	JX89736 9	JX897338	JX89759 9	JX89742 9	JX89745 7	JX89748 4	JX89756 2

<i>Agnotecous robustus</i> (Chopard, 1915)	MNHN-ENSIF-2752	*AroAo2	New Caledonia	JX89737 5	JX89735 9	JX897333	JX89758 8	JX89740 6	JX89744 3	-	JX89755 5
<i>Agnotecous sarramea</i> Desutter-Grandcolas, 1997	MNHN-EO-ENSIF2764	*AsaMA	New Caledonia	JX89738 0	JX89737 2	JX897342	JX89759 8	JX89743 0	JX89745 6	JX89747 1	JX89756 1
<i>Agnotecous tapinopus</i> Saussure, 1878	MNHN-EO-ENSIF2770	*AtaKo2	New Caledonia	JX89737 8	JX89734 4	JX897327	JX89760 5	JX89742 2	JX89745 4	JX89747 0	JX89755 6
<i>Agnotecous yahoue</i> Otte, 1987	MNHN-EO-ENSIF2766	*Ayako2	New Caledonia	JX89738 7	JX89736 6	JX897334	JX89760 2	JX89743 8	JX89746 3	JX89747 8	JX89754 9
<i>Arilpa gidya</i> Otte & Alexander, 1983	ANIC	*Agi	Australia	AY90526 8	AY90529 7	AY905351	AY90532 7	-	-	JX89748 8	-
<i>Cardiodactylus busu</i> Otte, 2007	MNHN-EO-ENSIF109	*C58CbuMW200	Papua New Guinea (New Guinea)	MH57495 3	MH57505 9	MH662838	MH66312 9	MH66303 5	MH66293 5	MH66334 1	MH66314 5
<i>Cardiodactylus haddocki</i> Dong & Robillard, 2016	MNHN-EO-ENSIF3541	*C64CnoMW700	Papua New Guinea (New Guinea)	MH57497 6	MH57508 3	MH663014	MH66291 1	MH66281 7	MH66310 6	MH66335 9	MH66326 5
<i>Cardiodactylus kondoi</i> Otte, 2007	MNHN-EO-ENSIF1555	*C41Cphil1	Philippines (Luzon)	MH57509 7	MH57498 8	MH662803	MH66309 2	MH66300 0	MH66289 9	MH66336 9	MH66321 3
<i>Cardiodactylus muria</i> Robillard, 2014	MNHN-EO-ENSIF3481	*C18Cmur	Indonesia (Java)	MH57511 5	MH57500 5	MH662763	MH66307 6	MH66298 3	MH66288 4	MH66338 7	MH66323 8
<i>Cardiodactylus niugini</i> Dong & Robillard, 2016	MNHN-EO-ENSIF113	*C54CbjMa	Papua New Guinea (New Guinea)	MH57511 6	MH57500 6	MH662759	MH66307 5	MH66298 2	MH66288 3	MH66338 8	MH66318 6
<i>Cardiodactylus novaeguineae</i> (Haan, 1842)	MNHN-EO-ENSIF1925	*C72CnoLu	Western Pacific	MH57512 7	MH57501 8	MH662755	MH66306 5	MH66297 0	MH66287 4	MH66341 5	MH66319 7
<i>Cardiodactylus singapura</i> Robillard, 2011	MNHN-EO-ENSIF2759	*C12Csi2	Singapore	MH57514 7	MH57504 0	MH662769	MH66304 7	MH66295 0	MH66285 4	MH66339 8	MH66322 6
<i>Centurarius centurio</i> (Brunner von Wattenwyl, 1898)	MNHN-EO-ENSIF96	*L42CnWa	Papua New Guinea (New Guinea)	MZ50181 5	MZ49717 1	MZ475907	MZ50881 3	MZ50666 5	-	MZ50883 5	MZ47605 0
<i>Eneoptera gracilis</i> Robillard, 2005	MNHN-EO-ENSIF233	*Egr	Peru	AY90527 1	AY90530 0	AY905354	AY90533 0	-	-	-	-
<i>Eneoptera guyanensis</i> Chopard, 1931	MNHN-EO-ENSIF2741	*E1Egu	French Guiana	AY90527 2	AY90530 1	AY905355	AY90533 1	JX89740 4	-	KR90350 2	JX89754 7

<i>Eneoptera nigripedis</i> Robillard, 2005	MNHN-EO-ENSIF3563	*E4Eni2	Colombia	KY59547 5	KY59550 4	KY646266	KY59551 6	KY64624 1	-	KY60523 8	KY64628 0
<i>Eneoptera surinamensis</i> (De Geer, 1773)	MNHN-EO-ENSIF147	*E3EsuPe	Peru	KY59547 4	KY59550 3	KY646265	KY59551 7	KY64624 0	-	KY60523 7	-
<i>Eurepa marginipennis</i> (White, 1841)	ANIC/ZIN_A7EuCoo	*Ema	Australia	AY90527 4	AY90530 3	AY905357	JF97254 0	-	-	KY60524 9	-
<i>Eurepa nurndina</i> Otte & Alexander, 1983	ANIC	*Enu	Australia	JF97250 9	AY90530 4	AY905358	AY90533 4	-	-	-	-
<i>Eurepa wikturta</i> Otte & Alexander, 1983	ANIC	*Ewi	Australia	AY90527 5	AY90530 5	AY905359	-	-	-	-	-
<i>Eurepella mjobergi</i> (Chopard, 1925)	ANIC	*Emj	Australia	AY90527 6	AY90530 6	AY905360	-	-	-	-	-
<i>Eurepella moojera</i> Otte & Alexander, 1983	ANIC	*Emo	Australia	AY90527 7	AY90530 7	AY905361	-	-	-	-	-
<i>Eurepella torowatta</i> Otte & Alexander, 1983	ANIC	*Eto	Australia	AY90527 8	AY90530 8	AY905362	-	-	-	-	-
<i>Eurepini</i> sp.	MNHN-EO-ENSIF3155	*Eursp	Australia	KR90383 4	KR90367 4	KR903331	KR90402 8	KU70556 5	-	KR90350 3	KR90315 3
<i>Fadinthus miri</i> Robillard & Tan n. sp.	MNHN-EO-ENSIF10870	*L90FaBo1	Malaysia (Borneo)	MZ50849 8	MZ50879 0	MZ475908	MZ50881 6	MZ50915 9	-	MZ50883 3	MZ47605 1
<i>Falcerminthus estrellae</i> (Robillard, 2015)	UPLB-MNH	*L45LesBa	Philippines (Leyte)	KY59549 0	KY59549 3	KY646264	KY59552 7	KY64623 9	-	KY60523 6	KY64628 2
<i>Falcerminthus magayon</i> Baroga & Robillard, 2020	JBB008	*L72LeMa1	Philippines (Luzon)	MZ50852 7	MZ50878 9	MZ475909	MZ50880 8	MZ50915 3	-	MZ50883 7	MZ47605 2
<i>Falcerminthus polillensis</i> (Baroga et al. 2016)	MNHN-EO- ENSIF80	*L74LePol1	Philippines (Polillo)	MZ50870 5	MZ50878 7	-	MZ50880 4	MZ50915 5	MZ47600 9	MZ50883 6	MZ47605 3
<i>Falcerminthus puyos</i> (Robillard 2013)	MNHN-EO-ENSIF3193	*L15Lmak1	Philippines (Luzon)	MZ50870 1	MZ50879 9	MZ475910	MZ50881 8	MZ50912 7	MZ47601 0	MZ50884 2	MZ47605 4
<i>Falcerminthus sanchezi</i> (Bolívar, 1889)	MNHN-EO-ENSIF3227	L29Lmak3	Philippines (Luzon)	KY59548 7	KY59549 5	KY646262	KY59552 5	KY64623 7	-	KY60523 4	KY64628 5

<i>Falcerminthus sanchezi</i> (Bolívar, 1889)	MNHN-EO-ENSIF3684	*L33LsazMm	Philippines (Luzon)	MZ50870 4	MZ50879 3	MZ475911	MZ50881 1	MZ50915 8	MZ47601 1	MZ50883 0	MZ47605 5
<i>Falcerminthus sanchezi</i> (Bolívar, 1889)	UPLB-MNH	L16Lmak2	Philippines (Luzon)	MZ50886 2	MZ50879 1	MZ475912	MZ50881 7	MZ50912 8	MZ47601 2	MZ50883 2	MZ47605 6
<i>Falcerminthus sandakan</i> (Tan, Japir, Chung & Robillard, 2019)	MNHN-EO-ENSIF1499	*L91Lbor2	Malaysia (Borneo)	MZ50885 2	MZ50879 4	MZ475913	MZ50880 9	MZ50915 6	MZ47601 3	MZ50884 8	MZ47605 7
<i>Falcerminthus truncatipennis</i> (Chopard, 1929)	MNHN-EO-ENSIF1733	*L52LtrunPan	Indonesia (Java)	MZ50886 4	MZ50880 1	MZ475914	MZ50880 6	MZ50915 7	MZ47601 4	MZ50884 0	MZ47605 8
<i>Falcerminthus truncatipennis</i> (Chopard, 1929)	ZIN	L84LtruncSu1	Indonesia (Sumatra)	MZ50886 5	MZ50880 5	MZ475915	MZ50881 5	-	-	MZ50883 1	MZ47605 9
<i>Falcerminthus villemantae</i> (Robillard, 2010)	MNHN-EO-ENSIF2739	*L1Lvii	Indonesia (Sulawesi)	JF97251 2	JF97252 6	JF972496	JF97254 3	KU70557 0	KU70555 9	KU70558 6	KU70560 2
<i>Falcerminthus villemantae</i> (Robillard, 2010)	MNHN-EO-ENSIF2583	L19LviiMa1	Indonesia (Sulawesi)	MZ50886 3	-	MZ475916	MZ50881 9	-	MZ47601 5	MZ50883 4	MZ47606 0
<i>Falcerminthus yaeyamensis</i> (Oshiro, 1996)	Ichikawa col.	*L12Lyae2	Japan (Yonaguni I.)	KY59548 6	-	KY646261	KY59552 4	-	-	KY60523 3	-
<i>Falcerminthus yaeyamensis</i> (Oshiro, 1996)	ZIN	L87Lyae3	Japan (Ishigaki I.)	MZ50886 6	MZ50880 0	-	-	-	-	-	MZ47606 1
<i>Gnomithus baitabagus</i> Vicente & Robillard, 2015	MNHN-EO-ENSIF3553	*L38GnoBaii	Papua New Guinea (New Guinea)	KY59548 8	KY59549 2	KY646260	KY59551 2	KY64623 2	-	KY60523 0	KY64627 6
<i>Gryllus bimaculatus</i> De Geer, 1773	MNHN-EO-ENSIF3524/3404	*Gbi/Gbi2	Lab colony	AY90529 2	KR90367 5	KR903332	KR90402 9	KY64623 4	KU70555 5	KR90350 4	KR90315 4
<i>Indigryllus kudremu</i> Robillard & Jaiswara, 2019	MNHN-EO-ENSIF2738(1)/Xsp2	*X3Xsp2	India	KY59548 3	KY59550 9	AY905377(1)	AY90534 5 (1)	KY64624 8	MK76134 0	KY60524 7	KY64629 3
<i>Lebinthus bitaeniatus</i> Stål, 1877	ZIN	L76LbiPal3	Philippines (Palawan)	MZ50183 1	MZ49725 8	-	MZ49738 4	MZ50685 1	-	MZ50885 6	MZ47606 2
<i>Lebinthus bitaeniatus</i> Stål, 1877	MNHN-EO-ENSIF4393	*L18LbiP1	Philippines (Luzon)	MK76127 4	MK76125 0	MK761353	MK76129 3	MK76133 1	MK76134 1	MK76131 3	MK76137 0

<i>Lebinthus bitaeniatus</i> Stål, 1877	MNHN-EO-ENSIF4394	L28LbiP2	Philippines (Luzon)	MK761275	MK761252	MK761354	MK761294	MK761332	-	MK761314	MK761371
<i>Lebinthus bitaeniatus</i> Stål, 1877	ZIN	L77LbiPal4	Philippines (Palawan)	MZ501830	MZ497259	-	-	MZ506861	-	MZ505566	MZ476063
<i>Lebinthus bitaeniatus</i> Stål, 1877	ZIN	L78LbiBu	Philippines (Palawan)	MZ501828	MZ508803	MZ475917	-	MZ506886	MZ476016	MZ508859	MZ540975
<i>Lebinthus bitaeniatus</i> Stål, 1877	MNHN-EO-ENSIF4393	L70LbiPal1	Philippines (Palawan)	MZ501832	MZ508797	-	MZ497388	-	-	MZ508847	-
<i>Lebinthus bitaeniatus</i> Stål, 1877	MNHN-EO-ENSIF4394	L71LbiPal2	Philippines (Palawan)	MZ501829	MZ508792	MZ475918	MZ508827	MZ506889	-	MZ508861	MZ476064
<i>Lebinthus boracay</i> Baroga, Yap & Robillard, n. sp.	BVZ_JBB030	*L141LluBor2	Philippines (Boracay)	MZ508700	-	-	-	-	-	-	MZ476065
<i>Lebinthus boracay</i> Baroga, Yap & Robillard, n. sp.	MNHN-EO-ENSIF11257	L73LluBor1	Philippines (Boracay)	MZ508699	-	-	-	-	-	-	MZ476066
<i>Lebinthus lanyuensis</i>	MNHN-EO-ENSIF1746	*L146Lla6	China (Taiwan)	MZ508702	-	-	-	-	-	-	-
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-EO-ENSIF2740	*L8Lbis1	Singapore	KR904017	JF972524	JF972493	KR904199	KU705567	KU705557	KR903665	KR903321
<i>Lebinthus luae</i> Robillard & Tan, 2013	UPLB-MNH-PNM13493	L127Lla1	Philippines (Batanes)	MZ508703	-	-	-	-	-	-	-
<i>Lebinthus luae</i> Robillard & Tan, 2013	UPLB-MNH-PNM13480	L128Lla2	Philippines (Batanes)	MZ508773	-	-	-	-	-	-	-
<i>Lebinthus luae</i> Robillard & Tan, 2013	UPLB-MNH-PNM13478	L129Lla3	Philippines (Batanes)	MZ508767	-	-	-	-	-	-	-
<i>Lebinthus luae</i> Robillard & Tan, 2013	UPLB-MNH-PNM13485	L130Lla4	Philippines (Batanes)	MZ508769	-	-	-	-	-	-	-
<i>Lebinthus luae</i> Robillard & Tan, 2013	UPLB-MNH-PNM13502	L131Lla5	Philippines (Batanes)	MZ508770	-	-	-	-	-	-	MZ476067
<i>Lebinthus luae</i> Robillard & Tan, 2013	ZIN	L80LluBu	Philippines (Sulawesi)	MZ508763	MZ497263	-	MZ497417	MZ506895	-	MZ505616	MZ476068

<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-ENSIF-EO1578	L50LluLeyS	Philippines (Leyte)	MZ50876 1	MZ49726 2	MZ475919	MZ49751 0	MZ50742 3	MZ47601 7	-	MZ47606 9
<i>Lebinthus luae</i> Robillard & Tan, 2013	ZIN	L89LluTa	Philippines (Sulawesi)	MZ50876 6	MZ50880 2	MZ475920	MZ50882 1	MZ50916 9	MZ47601 8	MZ50561 7	MZ47607 0
<i>Lebinthus luae</i> Robillard & Tan, 2013	ZIN	L79LluTi	Malaysia (Tioman)	MZ50877 4	MZ49726 5	MZ475921	MZ50882 5	MZ50743 0	MZ47601 9	MZ50562 0	MZ47607 1
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-EO-ENSIF1761	L32Lley2	Philippines (Leyte)	MZ50876 0	MZ49726 7	MZ475922	MZ50882 3	MZ50917 0	MZ47602 0	MZ50561 9	MZ47607 2
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-EO-ENSIF1755	L44LluMS	Philippines (Maripipi)	MZ50876 2	MZ50879 5	MZ475923	MZ49751 2	MZ50917 1	MZ47602 1	MZ50562 1	MZ47607 3
<i>Lebinthus luae</i> Robillard & Tan, 2013	UPLB-MNH	L75LluPol1	Philippines (Pollilo)	MZ50877 1	MZ49727 0	MZ475924	MZ50882 8	MZ50755 0	MZ47602 2	MZ50885 5	MZ47607 4
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-EO-ENSIF1716	L31Lley1	Philippines (Leyte)	MZ50877 2	MZ49726 9	MZ475925	MZ50882 9	MZ50755 1	MZ47602 3	MZ50885 3	MZ47607 5
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-EO-ENSIF1543	L69LeCeb1	Philippines (Cebu)	MZ50876 4	MZ49727 2	MZ475926	MZ50882 6	MZ50756 4	MZ47602 4	MZ50563 2	MZ47607 6
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-EO-ENSIF3090	L17LbiS4	Singapore	MZ50876 8	MZ49727 1	MZ475927	MZ50882 4	MZ50916 3	MZ47602 5	MZ50884 9	MZ47607 7
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-EO-ENSIF3205	L21LbiS6	Singapore (Semakau)	MZ50876 5	MZ50879 6	MZ475928	MZ50882 2	MZ50916 6	MZ47602 6	MZ50885 0	MZ47607 8
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-EO-ENSIF	L10LbiS3	Singapore (Sentosa)	MK76127 6	MK76125 3	MK761355	MK76129 5	MK76133 3	MK76134 2	MK76131 5	MK76137 2
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-EO-ENSIF10663	L9LbiS2	Singapore (Pulau Ubin)	MZ50877 5	MZ49727 4	MZ475929	-	MZ50916 1	-	MZ50885 4	MZ47607 9
<i>Ligypterus linharensis</i> Robillard, 2005	MNHN-EO-ENSIF18	*E7Lf2	Brazil	AY90528 1	AY90531 1	AY905366	AY90533 8	KY64624 3	-	KY60523 9	KY64628 3
<i>Ligypterus fuscus</i> Chopard, 1920	MNHN	*E6LfuNo2	French Guiana	KR90401 8	KR90382 5	KR903487	KR90420 0	MZ50757 7	MZ47602 7	KR90366 6	KR90332 2
<i>Macrobinthus jharnae</i> (Bhowmik, 1981)	MNHN-EO-ENSIF76	*L43LgWa1	Papua New Guinea (New Guinea)	MZ50877 6	MZ50879 8	MZ475930	MZ50882 0	MZ50916 7	MZ47602 8	MZ50885 8	MZ47608 0

<i>Macrobinthus kutini</i> Robillard & Su, 2018)	ANIC_14_005048	*L118MacQ1	Australia	MZ50877 7	MZ50881 0	-	MZ50884 4	MZ50916 2	MZ47602 9	-	MZ47608 1
<i>Macrobinthus songi</i> Robillard & Dong, 2016	MNHN-EO-ENSIF157	*L4Lpng2	Papua New Guinea (New Ireland)	MZ50878 0	MZ50881 4	MZ475931	MZ50884 1	MZ50916 8	MZ47603 0	MZ50885 7	MZ47608 2
<i>Macrobinthus wilhelmsis</i> Robillard & Dong, 2016	MNHN-EO-ENSIF100	*L36LMW1700	Papua New Guinea (New Guinea)	MZ50877 9	MZ50881 2	-	MZ50883 8	MZ50916 5	-	MZ50885 1	MZ47608 3
<i>Microbinthus lifouensis</i> (Desutter-Grandcolas, 1997)	MNHN-EO-ENSIF1346	*L2Lli	New Caledonia (Lifou)	AY90527 9	AY90530 9	AY905364	AY90533 6	KU70556 6	KU70555 6	KU70558 3	KU70559 9
<i>Microbinthus nattawa</i> (Robillard, 2009)	MNHN-EO-ENSIF2564	*L5Lna	Vanuatu (Espiritu Santo)	JF97251 0	JF97252 5	JF972494	JF97254 1	KU70556 8	KU705558	KU70558 4	KU70560 0
<i>Microbinthus cyclopus</i> (Robillard, 2010)	ZIN	*L82Lcyc2	Indonesia (New Guinea)	MZ50877 8	-	MZ475932	MZ50884 5	MZ50916 4	-	MZ50884 6	MZ47608 4
<i>Microbinthus pintaui</i> Robillard & Dong, 2016	MNHN-EO-ENSIF4374	*L39LpMW700	Papua New Guinea (New Guinea)	MZ50878 8	MZ50880 7	MZ475933	MZ50884 3	MZ50917 2	MZ47603 1	MZ50886 0	MZ47608 5
<i>Microbinthus santoensis</i> (Robillard, 2009)	MNHN-EO-ENSIF2437	*L6LsaV	Vanuatu (Espiritu Santo)	JF97251 1	JF97252 7	JF972495	JF97254 2	JX89740 5	JX89744 1	JX89746 7	JX89754 8
<i>Myara sordida</i> Walker, 1869	ANIC	*Mso	Australia	AY90528 2	AY90531 2	AY905367	AY90533 9	-	-	-	-
<i>Myara unicolor</i> (Chopard, 1951)	ANIC	*Mun	Australia	AY90528 3	AY90531 3	AY905368	-	-	-	-	-
<i>Nisitrus insignis</i> Saussure, 1878	MNHN-EO-ENSIF4180	*N5Nin	Indonesia (Sumatra)	KY59549 1	KY59549 6	KY646272	MZ50883 9	-	-	-	KY64629 5
<i>Nisitrus malaya</i> (Robillard & Tan, 2020)	MNHN-EO-ENSIF2742	*NviS1	Singapore	KY59547 8	KY59549 9	KY646270	KR90420 1	KU70557 2	-	KR90366 7	JX89754 6
<i>Pixibinthus sonicus</i> Anso & Robillard, 2016	MNHN-ENSIF-EO105	*L59LeNCRBa	New Caledonia	KU70801 2	KU70553 0	KU705538	KU70554 6	KU70557 7	-	KU70559 2	KU70560 8
<i>Paranisitra diluta</i> Gorochoy, 2009	MNHN-EO-ENSIF3680	*N9Pdi	Indonesia (Biak)	KY59548 2	KY59550 0	KY646273	KY59551 3	KY64624 6	MZ47603 2	KY60524 5	KY64628 9
<i>Paranisitra longipes</i> Chopard, 1925	MNHN-EO-ENSIF3157	*N10Plo2	Philippines (Luzon)	KR90402 0	KR90382 7	-	KR90420 2	KU71528 7	-	KR90366 8	KR90332 5

<i>Paranisitra maculata</i> Gorochoy, 2009	MNHN-EO-ENSIF3683	*N8Pma	Philippines (Mindoro)	KY59548 1	KY59550 1	-	-	-	-	KY60524 4	KY64629 0
<i>Ponca venosa</i> Hebard, 1928	MNHN-EO-ENSIF3158	*E10PveCR	Costa Rica	KR90402 1	KR90382 8	KR903489	KR90420 3	KY64624 4	-	KR90366 9	KR90332 6
<i>Pseudolebinthus</i> <i>gorochovi</i> Robillard, 2018	ZIN-X17	*X17PsMal1	Malawi	KY59547 2	KY59550 8	-	KY59551 1	KY64623 1	-	KY60523 1	MK761373
<i>Salmanites taltantris</i> Otte & Alexander, 1983	ANIC	*Sta	Australia	AY90528 7	AY90531 7	JF972497	-	-	-	-	-
<i>Salmanites wittilliko</i> Otte & Alexander, 1983	ANIC	*Swi	Australia	AY90528 8	AY90531 8	AY905373	-	-	-	-	-
<i>Swezildaeria bryani</i> Chopard, 1929	MNHN-EO-ENSIF450	*Sbr	American Samoa (Tutuila)	-	AY90531 9	AY905374	-	-	-	-	-
<i>Swezwilderia</i> sp.	MNHN-EO-ENSIF2737	*L25Ssp	Fiji (Viti Levu)	JF97251 4	JF97252 9	JF972498	JF97254 5	KU70557 9	MZ47603 3	-	KR90332 7
<i>Xenogryllus eneopteroides</i> Bolivar, 1890	MNHN-EO-ENSIF3159	*XenAC	Central African Republic	KR90402 3	KR90382 9	KR903490	KR90420 5	KY64624 9	-	KR90367 0	KR90332 8
<i>Xenogryllus marmoratus</i> (Haan, 1844)	MNHN-EO-ENSIF3161	*Xma2	Japan	KR90402 4	KR90383 0	KR903491	KR90420 6	-	MK76134 3	-	KR90332 9
<i>Xenogryllus transversus</i> (Walker, 1869)	MNHN-EO-ENSIF87	*XtrIn	India	JF97251 5	JF97253 0	JF972499	KY59551 9	KY64624 7	MK761347	KY60524 6	KY64629 4

Table S2. Models used in the phylogenetic analyses: models inferred with IQ-TREE ModelFinder (ML analysis) and best-fit models of sequence evolution and partitioning schemes selected with PartitionFinder ('unlinked branch lengths' option) for Bayesian Inference (MrBayes/BEAST), with codon position is denoted by pos1, pos2 and pos3. Subsets are denoted by P1 to Pn.

Analyses	Partitions	Models
Maximum likelihood analysis (IQ-TREE inferred models)	P1: 12S P2: 16S P3: CO2 P4: CytB P5: H3 P6: 18S P7: 28S P8: CO1	GTR+F+I+G4 GTR+F+I+G4 TIM2+F+I+G4 TIM2+F+I+G4 TN+F+I+G4 TIM2e+I+G4 TIM2+F+I+G4 GTR+F+I+G4
Bayesian inference (BI) analyses	P1: 12S, Cytb_pos2 P2: 16S, COI_pos2 P3: 28SA, CytB_pos3, COI_pos3 CO2_pos1, CO2_pos2, H3_pos1, H3pos2 P4: 18S, CO2_pos3 P5: H3 pos_3, CytB pos_1	GTR + I + G GTR + I + G GTR + I + G SYM + I + G GTR + I + G
Bayesian evolutionary analyses by sampling trees (BEAST)	P1: 12S, CO2_pos1, CO2_pos2, CO2_pos3, Cytb_pos2 P2: 16S P3: CO1_pos3, Cytb_pos1 P4: CO1_pos1, CO1_pos2, Cytb2_pos3, H3_pos2, H3_pos3 P5: 18S, 28SA, H3_pos1	GTR+I+G GTR+I+G GTR+G TrN+I+G GTR+I+G

1637 **Table S3.** List of species and coding of acoustic traits used for ancestral state reconstructions analyses
1638

Species	Lab code	Song type (SONG) T: continuous trill S : single syllable E : echeme	Echeme structure (ECHE) H Homogeneous C: composed of 2 parts	Nature of dominant frequency F1/F2/F3/F4/F5/B(broa d-band)	Dominant frequency (continuous)	Reference (Sound reference number)
<i>Agnotecous albifrons</i> Desutter-Grandcolas, 1997	*AalCT	E	C	F2	16.3	This study (MNHN-SO-2021-251)
<i>Agnotecous azurensis</i> Desutter-Grandcolas, 2006	*AazPP	E	H	F2	15.7	This study (MNHN-SO-2018-101)
<i>Agnotecous brachypterus</i> Gorochov, 1986	*AbrPo	E	H	F2	19.2	Robillard <i>et al.</i> , 2010
<i>Agnotecous chopardi</i> Desutter-Grandcolas, 2006	*AspRB	E	H	F2	16.9	This study (MNHN-SO-2021-252)
<i>Agnotecous clarus</i> Desutter-Grandcolas, 2006	*AspTRPP2	E	C	F2	18.6	This study (MNHN-SO-2018-102)
<i>Agnotecous doensis</i> Desutter-Grandcolas, 2006	*AdoMD1	E	H	F2	13.9	This study (MNHN-SO-2021-254)
<i>Agnotecous meridionalis</i> Desutter-Grandcolas, 2006	*AmePB	E	C	F2	15.2	This study (MNHN-SO-2018-99)
<i>Agnotecous obscurus</i> (Chopard, 1970)	*AobMa	E	C	F2	15.1	This study (MNHN-SO-2021-255)
<i>Agnotecous minoris</i> Robillard, 2010	*L51	E	H	F2	13.5	This study (MNHN-SO-2021-256)
<i>Agnotecous occidentalis</i> Desutter-Grandcolas, 2006	*AspCR2	E	H	F2	14.9	This study (MNHN-SO-2021-257)
<i>Agnotecous pinsula</i> Robillard, 2010	*AspIP	E	H	F2	18.5	Robillard <i>et al.</i> , 2010
<i>Agnotecous robustus</i> (Chopard, 1915)	*AroAo2	E	H	F2	10.9	Robillard <i>et al.</i> , 2013
<i>Agnotecous sarramea</i> Desutter-Grandcolas, 1997	*AsaMA	E	H	F2	13.1	Robillard & Desutter-Grandcolas, 2011
<i>Agnotecous tapinopus</i> Saussure, 1878	*AtaKo2	E	H	F2	11.2	This study (MNHN-SO-2021-258)
<i>Agnotecous yahoue</i> Otte, 1987	*Ayako2	E	H	F2	16.3	Robillard & Desutter-Grandcolas, 2011

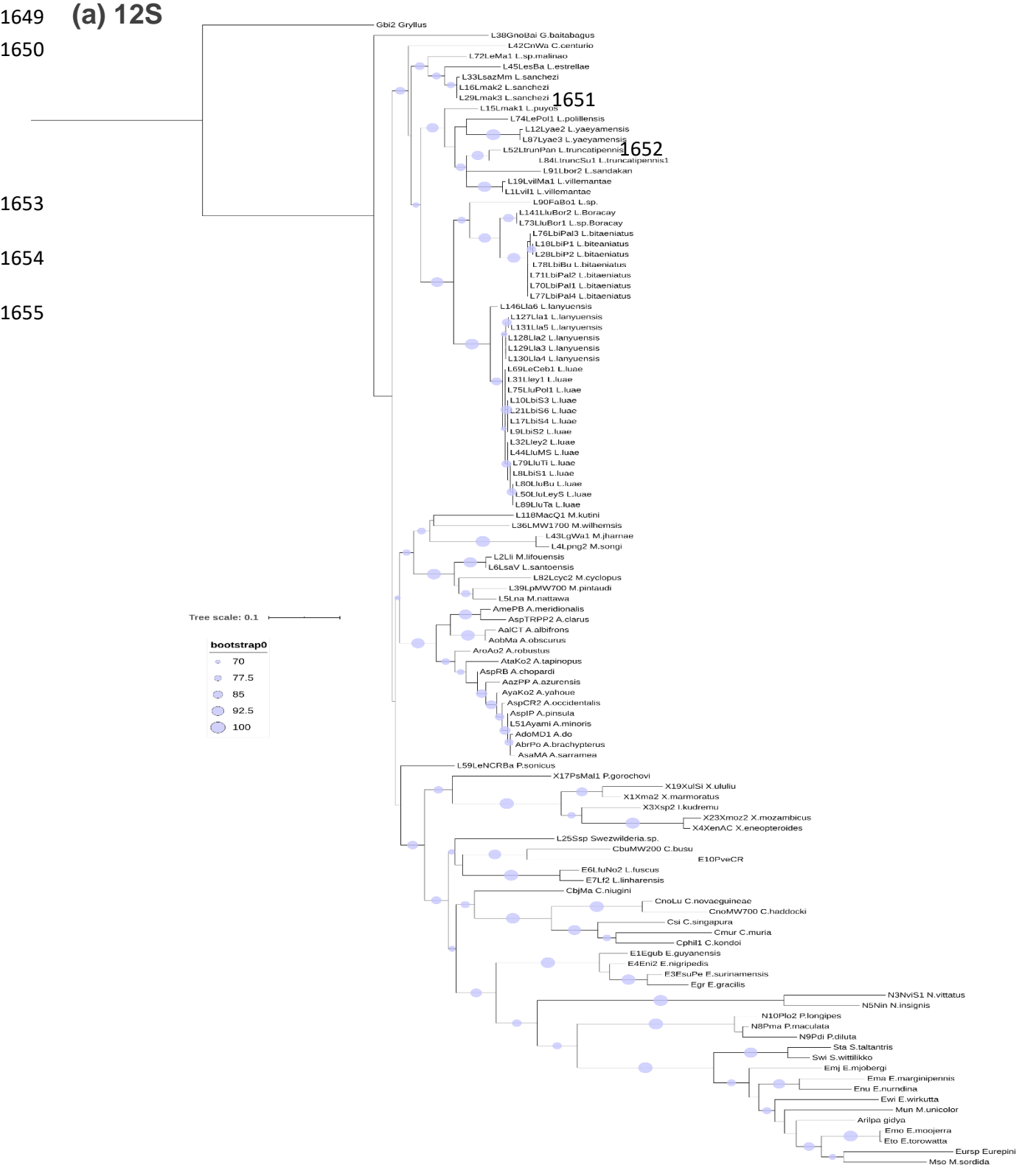
<i>Arilpa gidya</i> Otte & Alexander, 1983	*Agi	E	H	F1	6.4	Robillard & Desutter-Grandcolas, 2011
<i>Cardiodactylus busu</i> Otte, 2007	*C58CbuMW 200	E	H	F3	12.3	Dong & Robillard, 2016
<i>Cardiodactylus haddocki</i> Dong & Robillard, 2016	*C64CnoMW 700	E	C	F3	16.4	Dong & Robillard, 2016
<i>Cardiodactylus kondoi</i> Otte, 2007	*C41Cphil1	S	-	F3	12.8	Robillard <i>et al.</i> , 2014 (MNHN-SO-2015-2)
<i>Cardiodactylus muria</i> Robillard, 2014	*C18Cmur	S	-	F3	13.3	Robillard <i>et al.</i> , 2014
<i>Cardiodactylus niugini</i> Dong & Robillard, 2016	*C54CbjMa	E	C	F3	17.5	Dong & Robillard, 2016
<i>Cardiodactylus novaeguineae</i> (Haan, 1842)	*C72CnoLu	E	C	F3	15.8	Robillard & Ichikawa, 2009 (MNHN-SO-2014-377)
<i>Cardiodactylus singapura</i> Robillard, 2011	*C12Csi2	S	-	F3	19	Robillard, 2011
<i>Centurarius centurio</i> (Brunner von Wattenwyl, 1898)	*L42CnWa	S	-	B	10.2	Robillard <i>et al.</i> , 2016
<i>Eneoptera guyanensis</i> Chopard, 1931	*E1Egu	T	-	F5	20	Robillard <i>et al.</i> , 2015 (MNHN-SO-2014-348)
<i>Eneoptera surinamensis</i> (De Geer, 1773)	*E3EsuPe	T	-	F1	3.2	Robillard & Desutter-Grandcolas, 2011 (MNHN-SO-2014-362)
<i>Eurepa marginipennis</i> (White, 1841)	*Ema	T	-	F1	4.7	Robillard & Desutter-Grandcolas, 2011
<i>Eurepa nurdina</i> Otte & Alexander, 1983	*Enu	T	-	F1	5	Robillard & Desutter-Grandcolas, 2011
<i>Eurepa wikurtta</i> Otte & Alexander, 1983	*Ewi	T	-	F1	5.7	Robillard & Desutter-Grandcolas, 2011
<i>Eurepella mjobergi</i> (Chopard, 1925)	*Emj	E	H	F1	6	Robillard & Desutter-Grandcolas, 2011
<i>Eurepella moojera</i> Otte & Alexander, 1983	*Emo	E	C	F1	7	Robillard & Desutter-Grandcolas, 2011
<i>Eurepella torowatta</i> Otte & Alexander, 1983	*Eto	E	C	F1	7.6	Otte & Alexander, 1983
<i>Fadinthus tehtari</i> n. sp.	*L90FaBo1	E	C	F2	21.5	This study (MNHN-SO-2021-253)
<i>Falcerminthus estrellae</i> (Robillard, 2015)	*L45LesBa	E	C	F1	22	Robillard & Yap, 2015
<i>Falcerminthus puyos</i> (Robillard 2013)	*L15Lmak1	E	C	F1	23.7	Baroga <i>et al.</i> , 2020 (MNHN-SO-2020-1882)
<i>Falcerminthus sanchezi</i> (Bolívar, 1889)	*L33LsazMm	E	H	F1	24.4	Robillard <i>et al.</i> , 2013
<i>Falcerminthus sandakan</i> (Tan, Japir, Chung & Robillard, 2019)	*L91Lbor2	E	H	F1	18.8	Tan <i>et al.</i> , 2019
<i>Falcerminthus truncatipennis</i> (Chopard, 1929)	*L52LtrunPa n	E	C	F1	19.8	This study (MNHN-SO-2021-250)
<i>Falcerminthus villemantae</i> (Robillard, 2010)	*L1Lvil	E	H	F1	20.1	Robillard, 2010
<i>Gnominthus baitabagus</i> Vicente & Robillard, 2015	*L38GnoBai	E	H	F3	21.7	Vicente <i>et al.</i> , 2015 (MNHN-SO-2015-24)

<i>Lebinthus bitaeniatus</i> Stål, 1877	*L18LbiP1	E	C	B	19.9	Robillard & Tan, 2013
<i>Lebinthus luæ</i> Robillard & Tan, 2013	*L8Lbis1	E	C	B	16.7	Robillard & Tan 2013
<i>Ligypterus linhagensis</i> Robillard, 2005	*E7Lf2	E	C	F3	19	Robillard & Desutter-Grandcolas, 2005
<i>Ligypterus fuscus</i> Chopard, 1920	*E6LfuNo2	E	C	F3	19.7	Robillard <i>et al.</i> , 2015
<i>Macrobinthus jharnae</i> (Bhowmik, 1981)	*L43LgWa1	E	H	F2	15.7	Robillard <i>et al.</i> , 2016
<i>Macrobinthus wilhelmsis</i> Robillard & Dong, 2016	*L36LMW1700	E	H	F2	18.1	Robillard <i>et al.</i> , 2016
<i>Microbinthus lifouensis</i> (Desutter-Grandcolas, 1997)	*L2Lli	E	C	F2	11.6	Robillard & Desutter-Grandcolas, 2011
<i>Microbinthus pintaui</i> Robillard & Dong, 2016	*L39LpMW700	E	C	F2	27.9	Robillard <i>et al.</i> , 2016
<i>Microbinthus santoensis</i> (Robillard, 2009)	*L6LsaV	E	C	F2	26.6	Robillard, 2009 (MNHN-SO-2014-383)
<i>Myara sordida</i> Walker, 1869	*Mso	E	C	F1	5.6	Robillard & Desutter-Grandcolas, 2011
<i>Myara unicolor</i> (Chopard, 1951)	*Mun	E	H	F1	4.5	Robillard & Desutter-Grandcolas, 2011
<i>Nisitrus malaya</i> Robillard & Tan, 2021	*NviS1	E	H	F1	6.4	Robillard & Tan, 2013 (MNHN-SO-2020-2854)
<i>Pixibinthus sonicus</i> Anso & Robillard, 2016	*L59LeNCRBa	E	H	F2	27.9	Anso <i>et al.</i> , 2016 (MNHN-SO-2015-14)
<i>Ponca venosa</i> Hebard, 1928	*E10PveCR	S	-	F3	18	Robillard <i>et al.</i> , 2015
<i>Salmanites taltantris</i> Otte & Alexander, 1983	*Sta	E	H	F1	6.8	Robillard & Desutter-Grandcolas, 2011
<i>Salmanites wittilliko</i> Otte & Alexander, 1983	*Swi	E	H	F1	6	Robillard & Desutter-Grandcolas, 2011
<i>Xenogryllus eneopteroides</i> Bolivar, 1890	*XenAC	E	C	F1	3.6	Robillard & Desutter-Grandcolas, 2011
<i>Xenogryllus marmoratus</i> (Haan, 1844)	*Xma2	E	C	F1	6	Jaiswara <i>et al.</i> , 2019 (MNHN-SO-2018-58)
<i>Xenogryllus. mozambicus</i> Robillard, 2019	X23Xmoz2	E	H	F1	3.3	Jaiswara <i>et al.</i> , 2019 (MNHN-SO-2018-140)
<i>Xenogryllus transversus</i> (Walker, 1869)	*XtrlN	E	H	F1	4.5	Jaiswara <i>et al.</i> , 2019
<i>Xenogryllus ululiu</i> Gorochoy, 1990	*19XulSi	E	H	F1	4.8	Jaiswara <i>et al.</i> , 2019

Table S4. AICc (sample-size corrected AIC) for ASR analyses of three discrete traits. Best-fit models are mentioned in bold.

Traits	Models		
	ER	SYM	ARD
SONG	45.065	48.619	55.465
ECHE	60.069	60.069	62.221
NDF	73.663	87.422	114.481

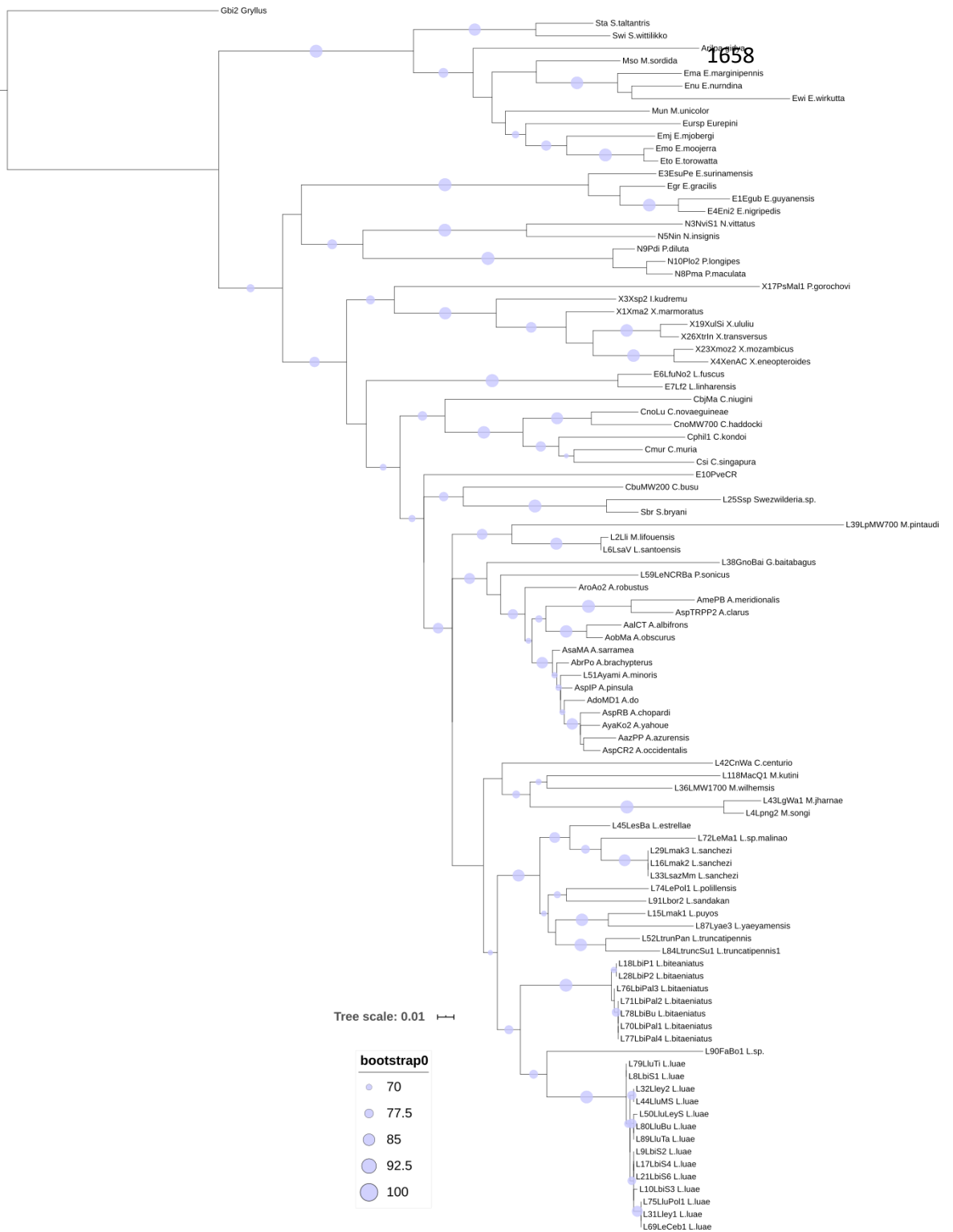
S-Figure 1. IQtree ML gene trees inferred for each separate marker. 12S (a), 16S (b), COI (c), COII (d), Cytb (e), 18S (f), 28S (g), H3 (hi). Bootstrap support values above 75% are represented by a grey circle proportional to the support (see scale on the left side of the tree)



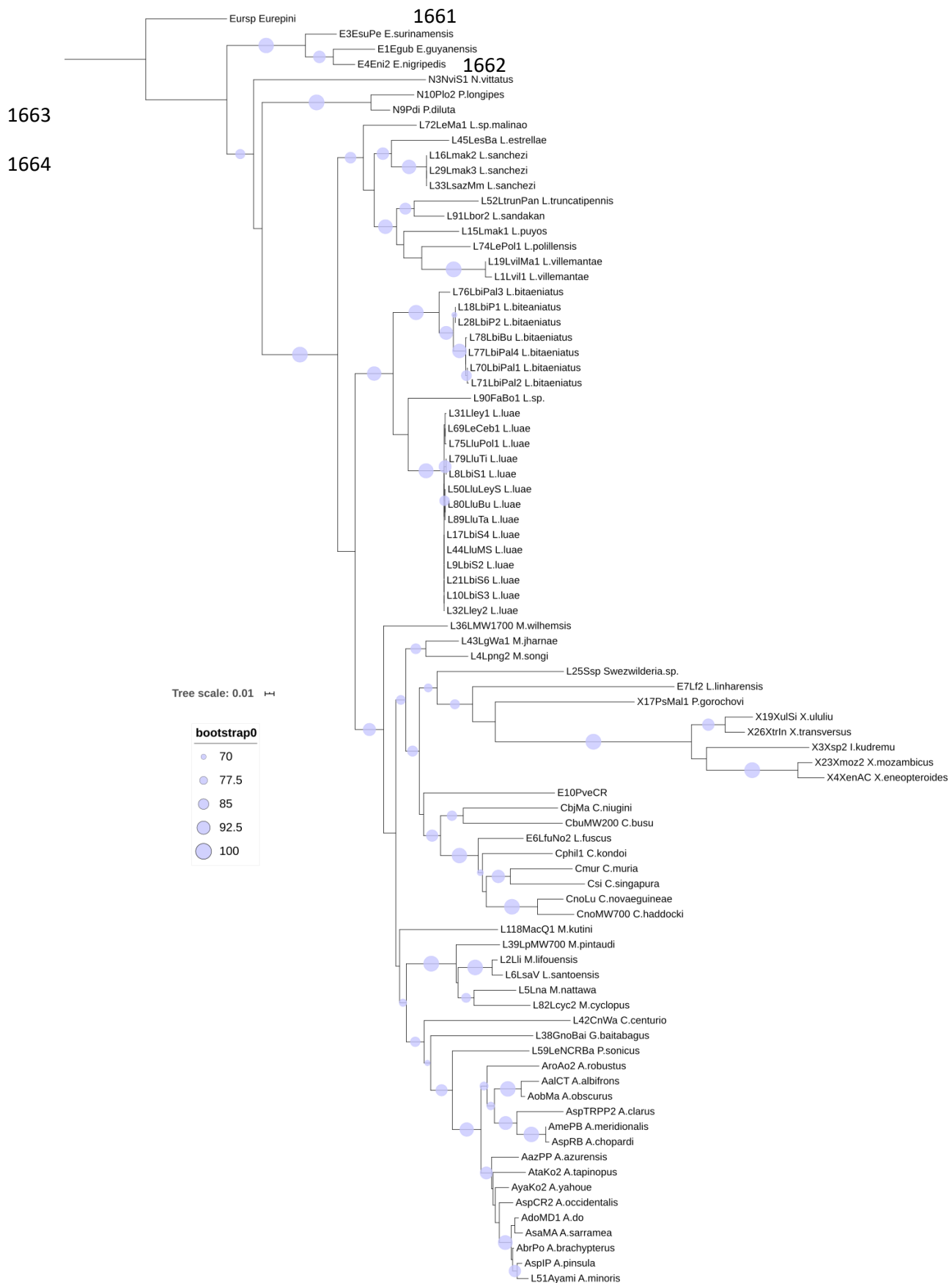
1656 (b) 16S

1657

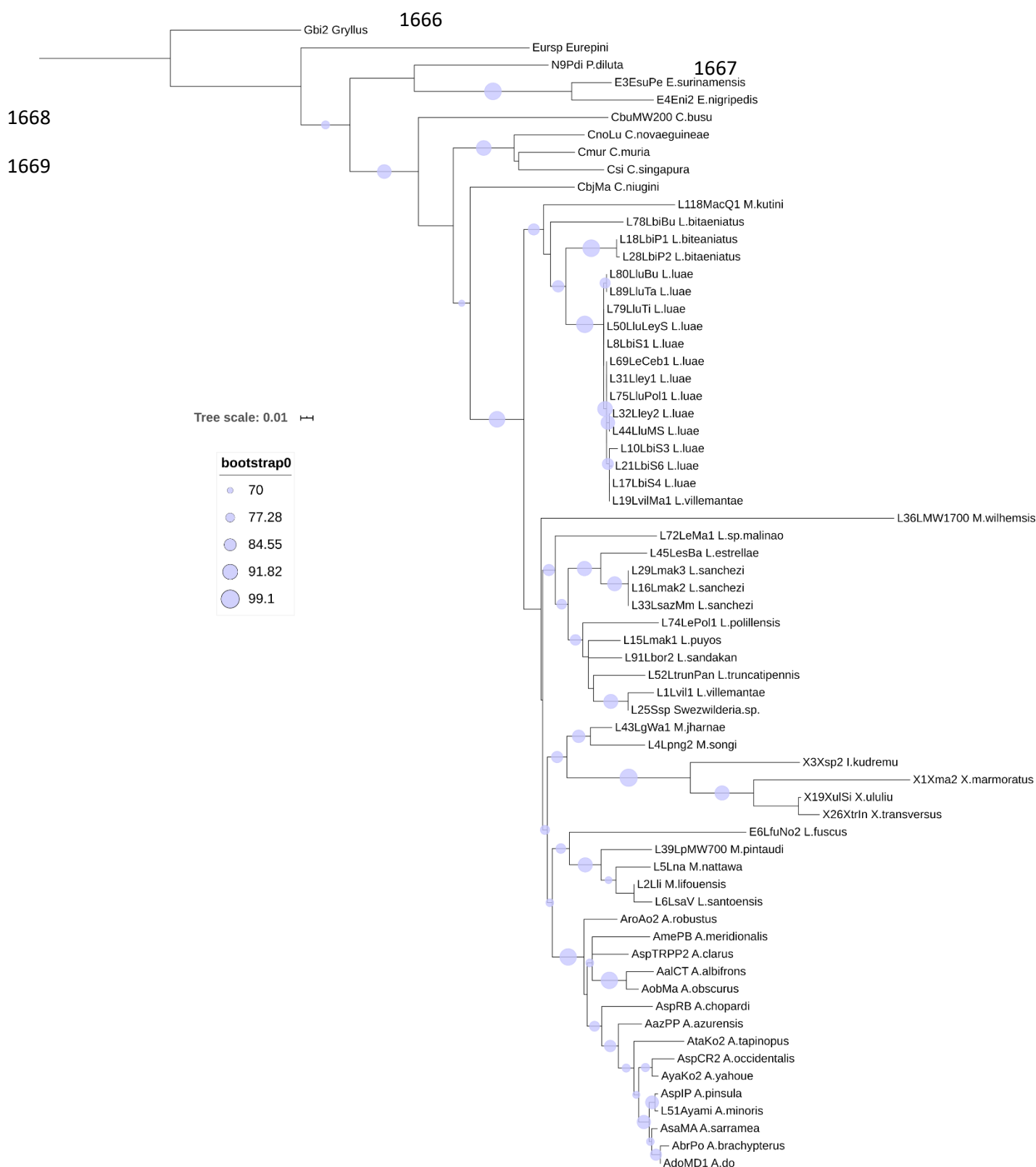
1659



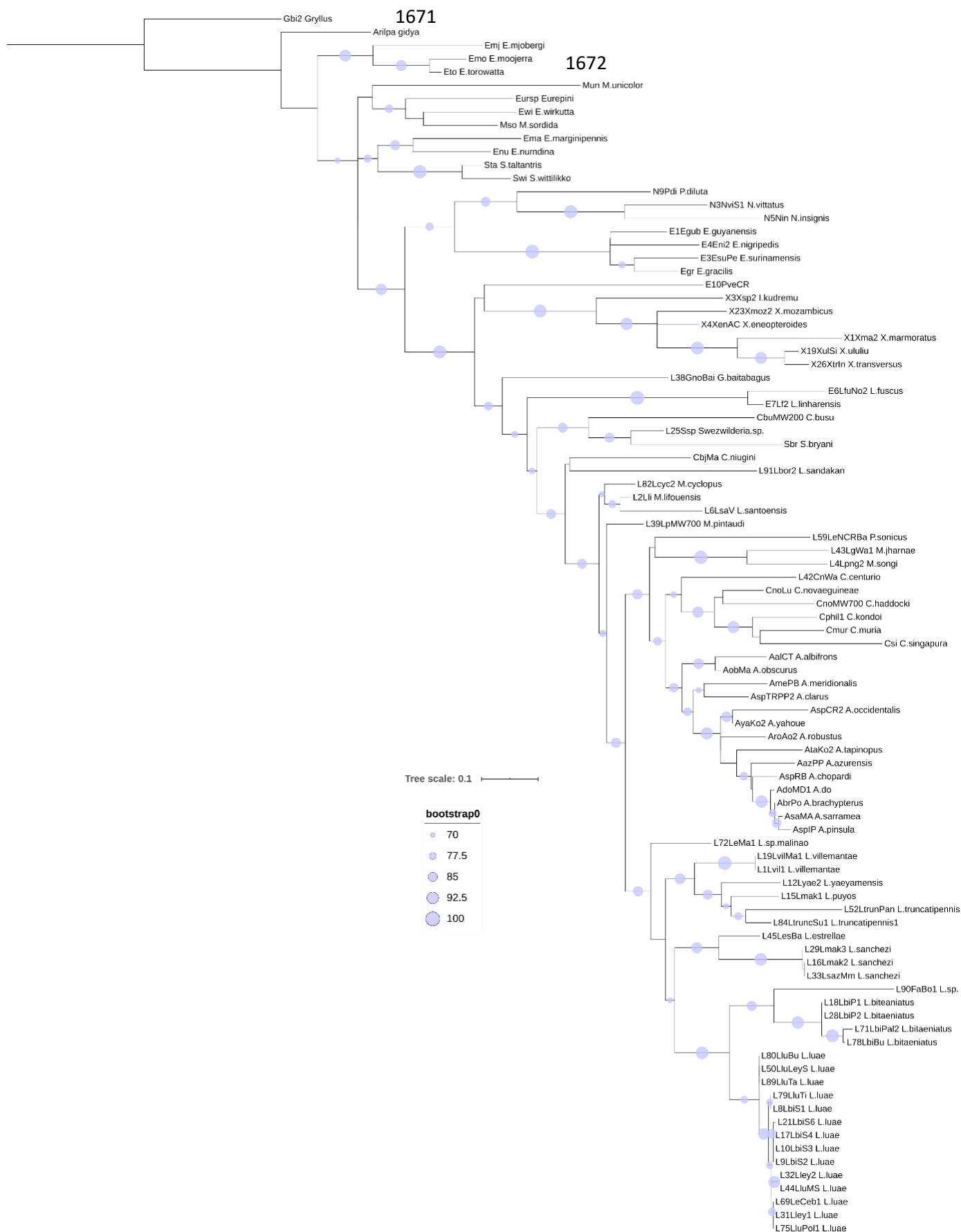
1660 (c) COI



1665 (d) COII



1670 (e) Cytb



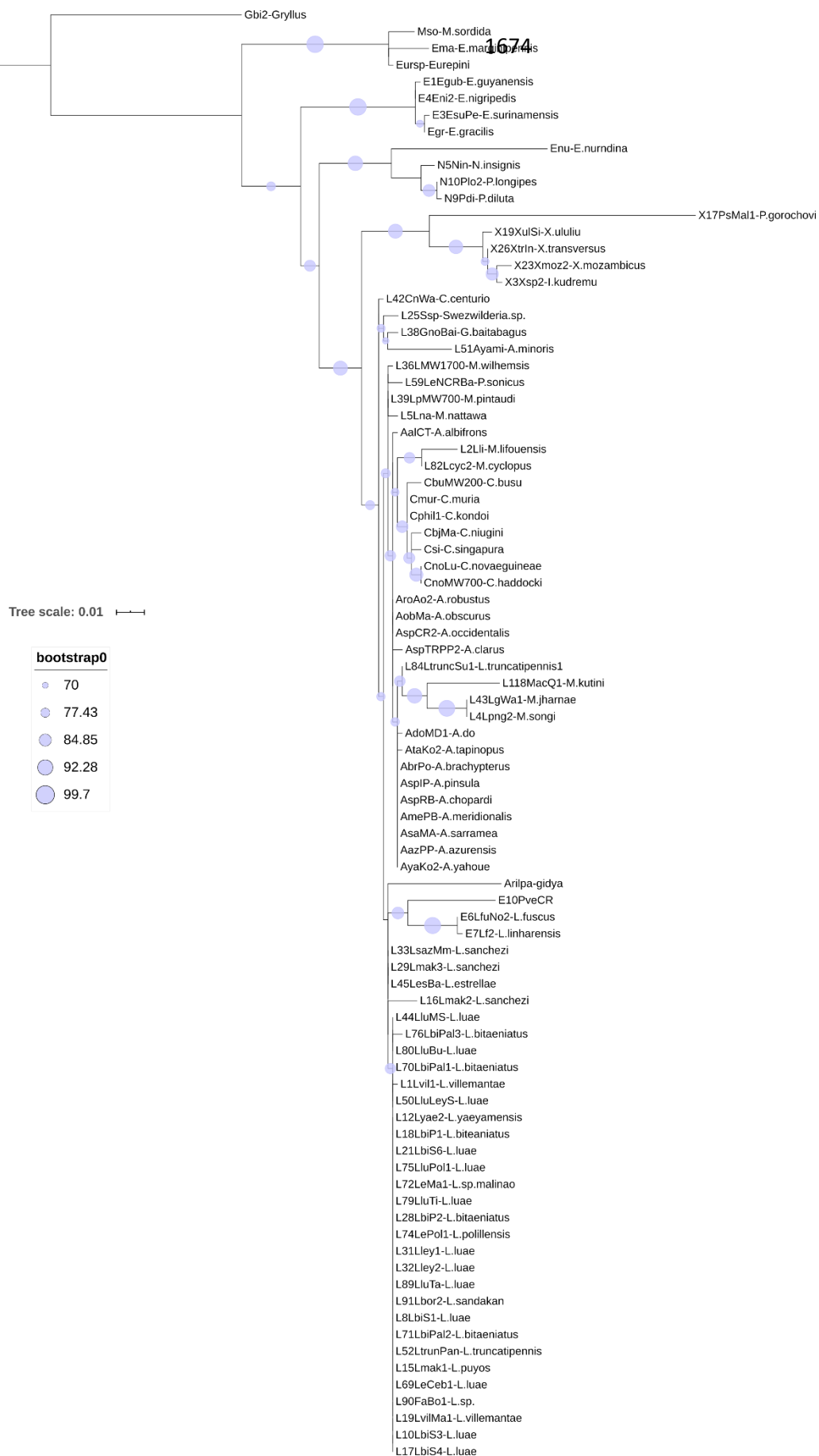
1673 (f) 18S

1675

1676

1677

1678



1680 (g) 28S



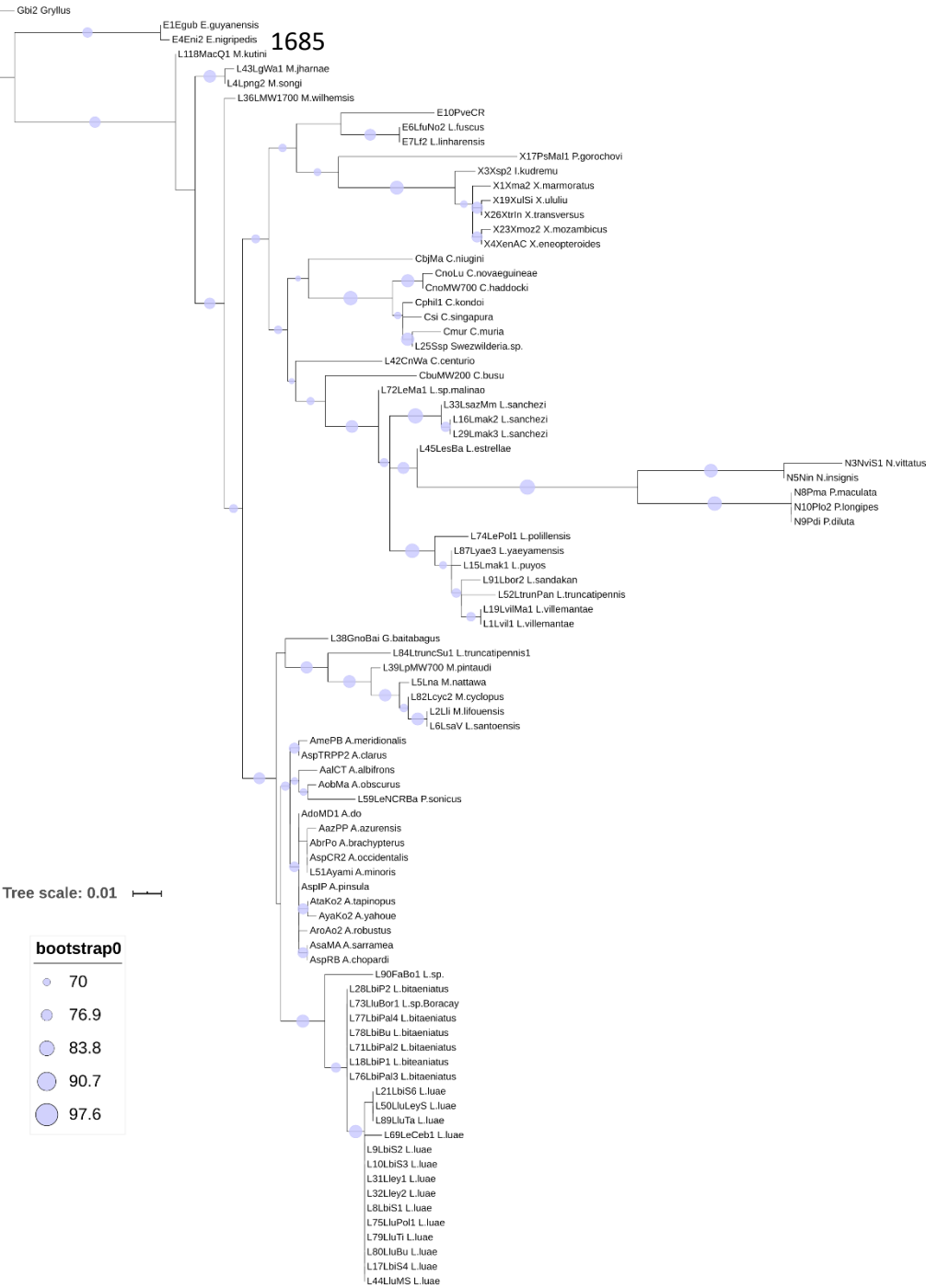
8

1682 (h) H3

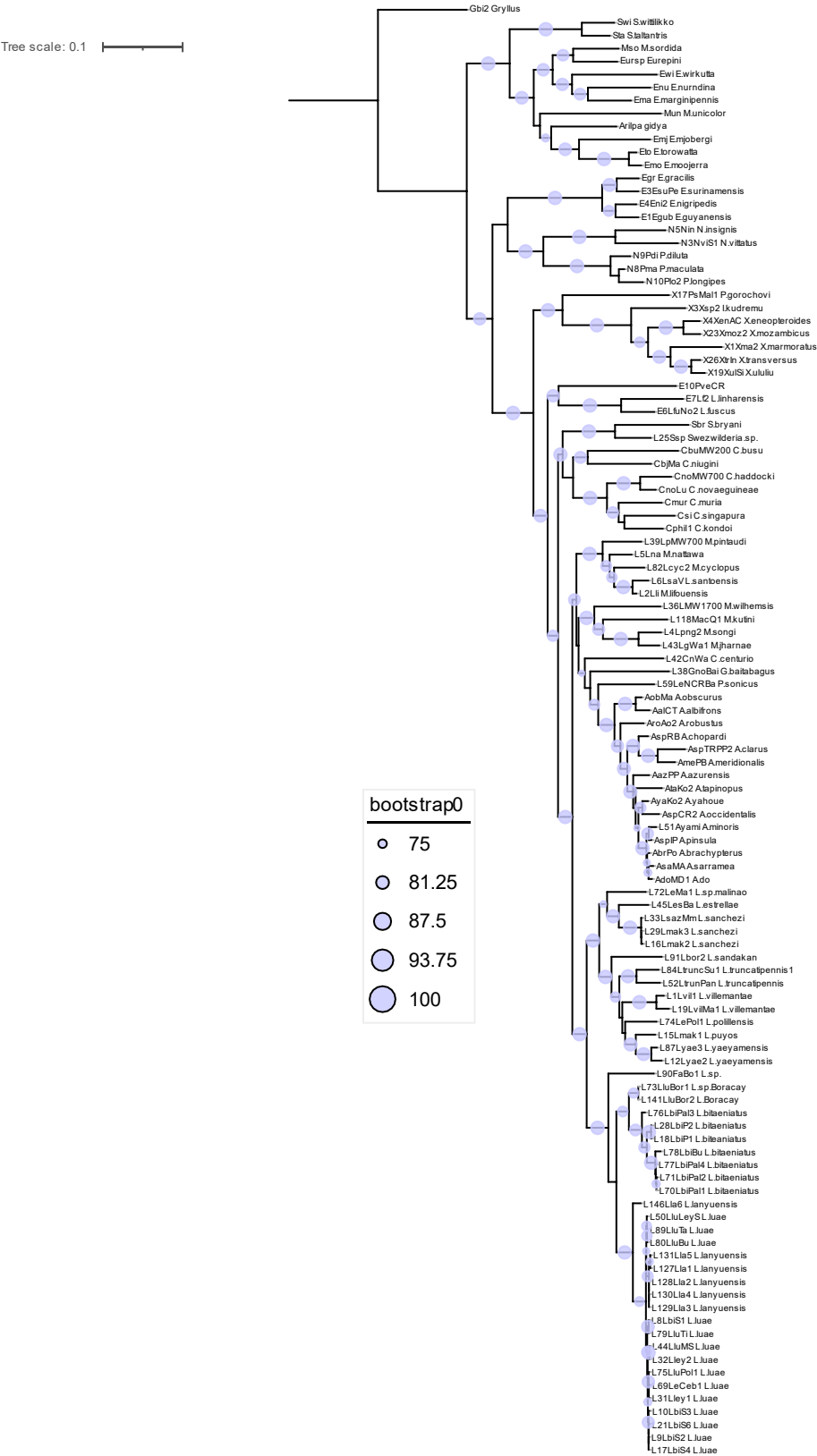
1683

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1686



1687 **S-Figure 2.** IQ-TREE ML analyses of the concatenated dataset. (a) results of the analysis
1688 using 8 gene partitions with models determined using IQ-TREE ModelFinder. (b) results of
1689 the analysis using five fixed models defined by the best-fit partitioning schemes and the
1690 associated substitution models used in the BI analysis (see below). Bootstrap support values
1691 above 75% are represented by a grey circle proportional to the support (see scale on the left
1692 side of the tree)



1695
1696

(b)



1697
1698

