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Short title for header: systematics and evolution of Lebinthini

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► **To cite this version:**

Ming Kai Tan, Julien Malem, Frédéric Legendre, Jiajia Dong, Jessica Baroga-barbecho, et al.. 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. Systematic Entomology, inPress, 10.1111/syen.12510 . hal-03319446

HAL Id: hal-03319446

<https://hal.science/hal-03319446v1>

Submitted on 12 Aug 2021

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4

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32

33 **Abstract**

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

56

57 Introduction

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

66 There are still large gaps in knowledge about the relative importance of different drivers
67 of acoustic divergence and how acoustic divergence facilitates speciation (Wilkins *et al.*, 2013).
68 While bats, birds, frogs, and crickets are among the best studied animals in the field of
69 bioacoustics for addressing these questions, crickets and their relatives are particularly useful
70 model organisms because of their small size, short generation time, and relatively simple
71 mechanisms of sound production (Horch *et al.*, 2017). On a macroevolutionary scale, Song *et al.*
72 (2020) recently demonstrated how sound production and hearing influenced species
73 diversification in orthopterans. Given its broad scale, this study could not offer insights into how
74 acoustics communication evolved in specific groups, which remain crucial to address because
75 acoustic communication in different taxa can have vastly different evolutionary trajectories.

76 To investigate how acoustic traits evolved and diversified, a clear phylogenetic context
77 is also needed, which necessitates prior taxonomic and biological studies for as many species
78 as possible. This can be a challenge, especially for cricket species from hyper-diverse regions
79 such as Southeast Asia, where rapid species diversification may have occurred (Dong *et al.*,
80 2018), and where many species remain undescribed or very poorly known, with little
81 information beyond their original descriptions.

82 The Lebinthini crickets offer an opportunity to overcome these challenges and address
83 questions on the evolution of acoustics traits. This is a diverse tribe within the subfamily
84 Eneopterinae and is mostly distributed in Southeast Asia, the Western Pacific archipelagos,
85 and northern South America (Vicente *et al.*, 2017). The tribe is characterized by its species
86 richness, as it includes half of the extant described eneopterine genera (15/26 including two
87 new genera described here), and more than half of the described species of the subfamily
88 (Cigliano *et al.*, 2021). It also contains the most speciose eneopterine genus, *Cardiodactylus*
89 Saussure, with more than 80 species (e.g., Otte, 2007; Robillard *et al.*, 2014; Dong & Robillard,
90 2016). The Lebinthini crickets are also highly diverse in terms of wing morphology, ranging
91 from brachypterous to fully winged species, and acoustic signals. These crickets have an
92 alternative communication system to most other crickets (ter Hofstede *et al.*, 2015), involving
93 major changes in every component of the usual cricket system of communication: Males

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

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

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

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

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

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

154

155

156 **Materials and methods**

157

158 ***Taxonomy***

159 The taxonomic analysis in this study resulted from international collaborative works that
160 led to recent descriptions of numerous taxa from the Philippines (e.g., Robillard *et al.*, 2013;
161 Robillard & Yap, 2015; Baroga-Barbecho *et al.*, 2020), Brunei Darussalam (e.g., Tan & Wahab,
162 2018), Malaysia (e.g., Tan *et al.*, 2019a, 2019b), Singapore (e.g., Robillard, 2011b; Robillard
163 & Tan, 2013; Tan & Robillard, 2014), and Indonesia (e.g., Robillard *et al.*, 2014).

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

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

175

176 **Observations and morphological analysis**

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

183 The terminology for male tegminal veins and cells follows Ragge (1955) and Robillard &
184 Desutter-Grandcolas (2004a). Male and female genitalia dissection and imaging follow the
185 methodology described in Salazar *et al.* (2020). Male genitalia terminology follows Desutter
186 (1987), modified in Desutter-Grandcolas (2003) and Robillard & Desutter-Grandcolas (2004).

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

189

190 **Acoustic analyses**

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

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

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

211 For all species but *F. tehtari* **sp. nov.**, the recordings were analyzed with Avisoft-SASLab
212 Pro version 4.40 (Specht, 2008). The recordings of *F. tehtari* **sp. nov.** were measured with
213 Avisoft Lite 2.0.0 and using power spectra generated with Fast Fourier Transformation (FFT),
214 with Hanning window of window length 512, and at 256,000 sampling frequency using the
215 'spec' function from the R package seewave (Sueur *et al.*, 2008) in the R software version
216 3.5.1 (R Development Core Team, 2018).

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

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

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

236

237 ***Phylogenetic analyses***

238 **Taxon Sampling**

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

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

248 Among the Lebinthini, the sampling was most extensive for the subtribe Lebinthina
249 (41/63 Lebinthina; 3/8 Ligypterina, 9/85 Cardiodactylina), in particular for the species of the
250 three focal genera in the taxonomic study (*Lebinthus* and two new genera), for which we
251 considered several individuals per species from distinct localities, whenever material was
252 available. We collected data for 1 to 19 individuals per species (mean = 3.14 ± 4.8).

253

254 **DNA markers, PCR amplification and sequence alignment**

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

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

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

274

275 **Phylogenetic inferences**

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

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

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

283 For ML analyses, data were partitioned by gene marker and the best model for each
284 marker was found using IQ-TREE ModelFinder (Kalyaanamoorthy *et al.*, 2017), as detailed in
285 Table S2. ML analyses were run using the IQ-TREE 1.6. 2 web portal (Nguyen *et al.*, 2015)
286 (<http://iqtree.cibiv.univie.ac.at/>; Trifinopoulos *et al.* 2016) using the option 'Edge-unlinked
287 partitions'. For comparison, an additional ML analysis was performed in IQ-TREE using fixed
288 models as defined by the best-fit partitioning schemes and the associated substitution models
289 used in the BI analysis (see below). Branch support was assessed by conducting 1,000
290 bootstrap replicates (standard bootstrap). Branches with bootstrap support values (BS) $\geq 75\%$
291 were considered strongly supported.

292 For BI analyses, PartitionFinder V2.1.1 (Lanfear *et al.*, 2017) was used to determine the
293 best-fit partitioning schemes and the associated substitution models were implemented in
294 MrBayes (Ronquist *et al.*, 2012) using corrected Akaike Information Criterion (AICc; Akaike,
295 2011). We separated coding genes into partitions by codon position to account for variation of
296 substitution rates. We performed a Bayesian inference (BI) analysis using MrBayes v.3.2.7
297 (Ronquist *et al.*, 2012) by launching two simultaneous runs for a total of eight Markov chains
298 running for 100 million generations and sampling every 10000 generations. We assessed the
299 convergence of samples using Tracer v.1.7.1 (Rambaud *et al.*, 2018) by checking the stability
300 of the log-likelihood curve and the split frequencies of the runs and used a 10% burn-in
301 because of the rapid convergence of the runs. Support for each branch was derived from the
302 posterior probabilities (PP) observed on the majority-rule consensus tree; a PP ≥ 0.95 was
303 considered as well supported following Erixon *et al.* (2003).

304

305 ***Divergence time estimation***

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

315 In the absence of clear a fossil record attributable to Eneopterinae, a previous study used
316 an extended outgroup approach to estimate the divergence times of this clade using multiple
317 unambiguous fossils from several cricket families (Vicente *et al.*, 2017). Except for the
318 Lebinthini, our sampling of the other tribes is similar to that of Vicente *et al.* (2017). Therefore,
319 we used the results from this study to define four secondary calibration points as follows, each
320 point being enforced using normal distributions centered on previously estimated median ages:
321 F(1) the node for the most recent common ancestor (MRCA) of Eneopterinae was assigned a
322 95% interval of 63.28–96.76 Ma (normalPrior mean = “76.29” stdev = “9.0”), (2) the node for
323 the MRCA of the tribe Eurepini was assigned an interval of 46.93–74.24 Ma (normalPrior mean
324 = “58.26” stdev = “7.0”), (3) the node for the MRCA of the tribes Xenogryllini and Lebinthini
325 was assigned an interval of 49.22–76.12 Ma (normalPrior mean = “59.64” stdev = “7.5”), and
326 (4) the node for the MRCA of the genus *Eneoptera* Burmeister was assigned an interval of
327 16.25–30.66 Ma (normalPrior mean = “22.26” stdev = “3.7”).

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

334

335 **Ancestral state reconstructions (ASR) of acoustic traits**

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

340 For the discrete traits (SONG, ECHE, NDF), we fit three different models of trait evolution
341 using the function fitDiscrete from the R package *geiger* (Harmon *et al.* 2008). These models
342 differ in the assumptions about number of transition rates as follows: Equal rates (ER) allows
343 a single transition rate between all states), symmetric (SYM) has identical forward and reverse
344 transitions and all-rates-different (ARD), has unique parameters for each rate. Each model was
345 run over 1000 generations. From the results we selected the model with the lowest value of
346 sample-size corrected AICc. For the selected model, we estimated ancestral states of each
347 trait using Bayesian MCMC using the *make.simmap* function in the R package *phytools* (Revell
348 2012) with 100 simulations. We obtained the trait estimates at the nodes by averaging the
349 values over all generations, excluding a 20% burn-in.

350 For the continuous trait DF, we reconstructed the ancestral states using the function
351 *anc.Bayes* in *phytools* (Revell, 2012), by running a MCMC with 1,000,000 generations, the first
352 200,000 generations being discarded as burn-in.

353

354 ***Phylogenetic signal***

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

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

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

367

368 **Results**

369

370 ***Phylogenetic results***

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

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

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

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

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

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

406

407 **Divergence time estimation**

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

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

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

419 The crown groups of the new subtribes were dated as follows: Ligypterina: 43.41 Ma
420 (95% HPD: 34.17–52.90 Ma), Cardiodactylina: 45.28 Ma (95% HPD: 37.33–53.82), Lebinthina:
421 40.08 Ma (95% HPD: 33.21–47.57 Ma). Based on these results, *Fadinthus* diverged from

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

424

425 **Ancestral state reconstructions**

426 Based on sample-size corrected AICc values, the model selection analyses gave a best
427 fit to the ER model for the discrete traits SONG, ECHE, and NDF (Supporting information Table
428 S4). The estimated ancestral values of each trait using Bayesian MCMC are presented in Fig.
429 3 and detailed below.

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

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

454

455 **Phylogenetic signal**

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

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

462 For the continuous trait DF, the phylogenetic signal was low, based on its estimate with
463 both the parameters λ ($\lambda = 0.74$, $p < 0.001$) and K ($K = 0.485605$, $p: 0.001$). K being lower than
464 1 suggested that dominant frequency values diverged more between closely related species
465 than expected under Brownian motion evolution.

466

467 Discussion

468

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

473

474 *Phylogeny of Eneopterinae*

475 This study provides a new well-resolved phylogenetic framework for Eneopterinae
476 despite the focus on the tribe Lebinthini. The results confirm the monophyly of the five
477 recognized tribes, with strong support as previously found (Robillard & Desutter-Grandcolas,
478 2004a, 2006; Nattier *et al.*, 2011; Vicente *et al.*, 2017; Jaiwara *et al.*, 2019). Our results also
479 confirm the position of the tribe Eurepini as the sister group to the rest of the subfamily and the
480 tribe Lebinthini as the sister group of the tribe Xenogryllini. The relative positions of the tribes
481 Nisitrini and Eneopterini forming a clade placed as the sister group of Xenogryllini + Lebinthini
482 is not as well supported in both the ML and BI analyses. This relationship was suggested in a
483 previous study, also with low support (Jaiswara *et al.*, 2019). In other studies, Eneopterini was
484 found as sister group to a clade grouping Nisitrini, Xenogryllini, and Lebinthini (Robillard *et al.*,
485 2004a, 2006, Nattier *et al.*, 2011, Vicente *et al.*, 2017). Future studies employing Next-
486 Generation Sequencing (NGS) and genomic datasets with a more complete taxonomic
487 sampling for these two tribes will be necessary to resolve the current ambiguity in their
488 relationships. However, we do not expect any significant consequences for the ASR results
489 presented in this study, nor on the general evolutionary conclusions.

490

491 *Phylogeny and classification of Lebinthini*

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

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

499 *Ligypterina*—The subtribe Ligypterina is distinguished from the other subtribes by its
500 Neotropical distribution. It is sister group to the rest of the tribe Lebinthini, which is comprised
501 by the two other subtribes, Cardiodactylina and Lebinthina. Ligypterina includes two species-
502 poor genera, *Ponca* and *Ligypterus*, comprising two and six valid species, respectively. Both
503 genera are similar in terms of general morphology (head shape, FW venation pattern), genitalic
504 anatomy in both males and females (Robillard & Desutter-Grandcolas, 2005), and by the
505 frequency spectrum of the male's calling song, in which the third harmonic peak dominates
506 (Robillard *et al.*, 2015). The dating analysis indicated that these two genera diverged around
507 43 Ma.

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

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

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

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

555

556 *Phylogenetic relationships within Lebinthina*

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

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

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

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

579

580 *Evolution of calling songs in Eneopterinae*

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

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

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

603 Using the updated phylogeny pruned to the 42 eneopterine species with acoustic data,
604 we tested hypotheses related to the evolutionary history of their calling songs, both on the
605 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 Euprepini 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

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

651 The second trait about spectral features of the calls corresponds to the harmonic of the
652 dominant peak within the frequency spectrum. The results complement the results for the DF
653 trait and support the hypothesis that, after reaching the high-frequency range, call frequencies
654 changed a lot within the Lebinthini through harmonic hopping, i.e., by changing the nature of
655 the dominant frequency. Our results showed that the high frequencies in Lebinthini occurred
656 concomitantly with a change of nature of the dominant frequency as suggested by Robillard *et*
657 *al.* (2007). This initial shift corresponded to harmonic hopping from the fundamental frequency
658 (f1) to the harmonic f3. Harmonic f3 then remained dominant in all the members of the
659 subtribes *Cardiodactylina* and *Ligypterina* as hypothesized earlier (Robillard *et al.*, 2014,
660 2015). Interestingly, the Lebinthina then underwent a subsequent diversification in terms of
661 nature of dominant frequency.

662 Increases in frequency values leading to ultrasound values are not always linked with
663 changes in the nature of the dominant frequency: *Gnominthus* reached ultrasonic frequencies
664 by reversing the dominant frequency from f2 to f3, whereas the opposite happened in
665 *Falcerminthus*, which reversed from f2 to f1 while acquiring ultrasonic calls. The most striking
666 cases of ultrasonic calls (DF > 25 kHz) occurred in a f2 dominant-frequency context in
667 *Pixibinthus* and *Microbinthus* independently. The highest frequency values are thus found in
668 the Lebinthina, in clades where the dominant frequency is mainly harmonic f2, whereas the f3-
669 dominant frequency songs remain below the ultrasound threshold. To produce 28 kHz for a
670 cricket with f2-dominant frequency, such as *Pixibinthus sonicus*, a fundamental frequency of
671 14 kHz is required, whereas many species in the *Cardiodactylina* and *Ligypterina* clades are
672 producing frequencies in this intermediate range using the third harmonic (hence with a
673 fundamental frequency three times lower). This suggests that the relationships between
674 stridulatory structures (file tooth number and inter-tooth distance), FW closure speeds and
675 wing resonance capacities are both diverse and complex, resulting in complex changes in the
676 calling song. This diversity likely conceals diverse morpho-functional mechanisms associated
677 with various evolutionary potentialities.

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

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

684

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

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

706

707

708 **Systematic part**

709

710 **Family Gryllidae**

711

712 **Subfamily Eneopterinae Saussure, 1874**

713

714 **Tribe Lebinthini Robillard, 2004**

715

716 **Subtribe Cardiodactylina Robillard & Tan, subtribe n.**

717 Type genus: *Cardiodactylus* Saussure, 1878

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

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

723

724 **Subtribe Ligypterina Robillard & Tan, subtribe n.**

725 Type genus: *Ligypterus* Saussure, 1878

726 Contained genera: *Ligypterus* Saussure, 1878; *Ponca* Hebard, 1928

727 Diagnosis: The members of the subtribe Ligypterina are either brachypterous or macropterous;
728 they are characterized by a functional stridulatory apparatus in males with a modified mirror
729 area, male genitalia with large pseudepiphallic lophi and an indented anterior margin. They are
730 distributed in the Neotropical region (Central America and northern part of South America) (Fig.
731 1B).

732

733 **Subtribe Lebinthina Robillard & Tan, subtribe n.**

734 Type genus: *Lebinthus* Stål, 1877

735 Contained genera: *Agnotecous* Saussure, 1878; *Centurarius* Robillard, 2011; *Fadinthus*
736 Robillard & Tan, **gen. nov.**; *Falcerminthus* Robillard & Tan, **gen. nov.**; *Gnominthus* Robillard
737 & Vicente, 2015; *Julverninthus* Robillard & Su, 2018; *Lebinthus* Stål, 1877; *Macrobinthus*
738 Robillard & Dong, 2016; *Microbinthus* Robillard & Dong, 2016; *Pixibinthus* Robillard & Anso,
739 2016.

740 Diagnosis: The members of the subtribe Lebinthina all have brachypterous FWs and lack HWs;
741 males are characterized by functional stridulatory structures with a vestigial mirror area. As for
742 Cardiodactylina, they are distributed in Southeast Asia and in most archipelagos of the
743 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.

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

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

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

825 **Calling song.** For the species for which calling song is documented (*L. bitaeniatus* and *L.*
826 *luae*), syllables are very indented (amplitude modulation resulting in pauses within the
827 syllable). Song organized in two parts, the initial one consisting of well-spaced syllables, the
828 second part forming a short trill. The spectrum consists of a broad band at high frequency (15–
829 30 kHz).

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

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

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

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

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

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

841 **Remarks.** The genus *Lebinthus* has been used until recently to refer to all the brachypterous
842 species of Lebinthini which were not from New Caledonia (Oshiro, 1996; Desutter-Grandcolas,
843 1997; Robillard, 2009, 2010, 2011; Robillard & Tan, 2013; Robillard *et al.*, 2013). The diversity
844 uncovered recently for this group of species necessitated the definition of several new genera
845 and the redefinition of the genus as restricted to the species close to the type species and
846 easily recognized by their yellow longitudinal bands from which the type species name is
847 derived.

848

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

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

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

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

853

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–

891 120°); stridulatory file with teeth both on transverse and on angle parts of 1A. CuP usually not
892 visible except basally (*F. puyos*, *F. truncatipennis*, and *F. villemantae*). Diagonal vein very faint,
893 usually visible on anterior half, faint posteriorly. Harp wide, occupying most of dorsal field
894 surface, with a strong transverse harp vein, poly-furcated anteriorly and delimiting a well-
895 rounded false mirror, i.e., a distinctive area located on harp posterior corner (not homologous
896 to the mirror of other crickets). CuA anterior part strong, its distal part weak, slightly curved
897 inward near apex. Mirror (d1) not differentiated. Apical field absent, with no bifurcation of CuA
898 posterior to diagonal vein. Lateral field with 5–6 strong longitudinal veins. Subgenital plate
899 elongated, clog-shaped.

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

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

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

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

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

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

- 928 **Included species and distribution (arranged alphabetically, TL: type locality):**
929 *F. dannybaletai* (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 pseudepiphallic lophi little differentiated, either with or without a short median plate between
954 them; pseudepiphallic 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 pseudepiphallic 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)

1001 **Included species.**

1002 *Fadinthus buruensis* (Robillard, 2010), **comb. nov.**—Indonesia: Buru Island (TL)

1003 *Fadinthus miri* Robillard & Tan, **sp. nov.**—Malaysia: Sarawak (TL)

1004 *Fadinthus tehtari* Tan, Wahab & Robillard, **sp. nov.**—Brunei Darussalam: Belait (TL)

1005

1006 ***Fadinthus miri* Robillard & Tan, sp. nov.**

1007 (Figs. 1, 5D, 6A–C, 6J, 6K)

1008 urn:lsid:zoobank.org:act:FA8687B2-F615-438D-9D22-9AEDE4320C87

1009 **Type material.** *Holotype*, ♂, MALAYSIA: East Malaysia, Sarawak, Miri, Lambir Hills National
1010 Park, 100–300 m a.s.l., forest, 29.iii.–1.iv.2012 (A. V. Gorochoy, M. Berezin, E. Tkatsheva, L.
1011 Kamskov) (ZIN). *Allotype*, ♀, MALAYSIA: same information as holotype (ZIN). *Paratypes*:
1012 MALAYSIA, same information as holotype: 2 ♀ (ZIN); 1 ♂, molecular sample L90, 1 ♀ (MNHN-
1013 EO-ENSIF10870–10871).

1014 **Additional material examined.** MALAYSIA: 1 juvenile, same information as holotype, (ZIN).

1015 **Distribution.** Miri (Sarawak, East Malaysia).

1016 **Diagnosis.** Species close to *F. tehtari* **sp. nov.**, from which it differs by lighter coloration,
1017 longer male FWs, with more distinct veins on dorsal field, and differences in male genitalia,
1018 with well separated pseudepiphallic lophi and pseudepiphallic parameres oriented posteriorly.
1019 From *F. buruensis*, both new species differ by male FWs venation with a more distinct oblique
1020 vein, less differentiated mirror, and male genitalia with pseudepiphallic parameres without
1021 ventral lobes, and longer female FWs slightly overlapping (shorter and separated in *F.*
1022 *buruensis*).

1023 **Description.** Size average. Coloration dark brown. Head dorsum with four wide dark brown
1024 longitudinal bands, area posterior to eyes yellow with a dark spot. Fastigium wider than long,
1025 setose, dark brown, with a yellow line apically. Scape light brown with faint darker patterns;
1026 antennae light brown. Face light brown, with variable dark brown patterns on frons and below
1027 antennae. Mouthparts variably mottled with dark brown and yellow; maxillary palpi generally
1028 pale brown, apical segment with apex slightly expanding and darkened apically, subapical
1029 segment shorter than apical and third segments and darkened basally. Lateral part of head
1030 with a dark brown stripe. Pronotum: Dorsal disk slightly trapezoidal, posterior margin sub-
1031 straight; yellow brown mottled with dark brown, lateral edges always whitish, posterior area
1032 mostly dark brown; lateral lobes black dorsally, ventral margin dark brown, with lighter corners
1033 visible only in lightest specimens. Legs: Fore and mid legs light brown, femora with dark brown
1034 spots, tibiae with dark rings. FIII brown, with strong striated dark patterns on outer faces, knees
1035 dark brown; TIII with dark rings. Tarsomeres I/III-1 yellow brown, apices dark brown. Abdomen
1036 orange brown mottled with dark brown dorsally, yellowish brown ventrally. Cerci yellowish
1037 brown, with dark rings.

1038 **Male:** FWs reaching half of abdomen length. FW coloration (Fig. 5D): Cells and veins brown,
1039 not translucent; veins brown except anterior parts of anal veins orange brown and anterior
1040 lateral corner of FW yellowish. FW venation (Fig. 5D): 1A slightly curved. CuP not visible. CuA
1041 faint, straight along its whole length. Diagonal vein very faint. Harp wide, with one very faint
1042 oblique vein bisinuate. Mirror not differentiated from other cells. Longitudinal veins of dorsal
1043 field strong apically, transverse veins weaker. Apical field very short, including one bifurcation
1044 of CuA posterior to diagonal vein. Lateral field dark brown, area between M and R pale orange;
1045 with 6–7 (n = 2) strong longitudinal veins including M, R, Sc; Sc without bifurcating veins.
1046 Supra-anal plate tongue-shaped, its posterior margin truncated.

1047 *Male genitalia* (Figs. 6A–C): Pseudepiphallic sclerite stout and trapezoidal; posterior apex with
1048 a wide indentation between short lateral lophi, forming wide triangles slightly diverging. Anterior
1049 margin of pseudepiphallic sclerite slightly indented. Rami short, half as long as pseudepiphallic
1050 sclerite. Pseudepiphallic parameres elongated posteriorly, with a small dorsal lobe and an
1051 oversized ventral lobe forming a right angle in lateral view; apex of ventral lobe widened,
1052 forming a twisted spatula. Ectophallic arc thick, slightly curved posteriorly, with long ventro-
1053 lateral expansions sclerotized basally and membranous apically. Ectophallic fold mostly
1054 membranous, with a thin Y-shaped ventral sclerotization. Ectophallic apodemes long and
1055 slightly divergent, exceeding anterior margin of pseudepiphallic sclerite. Endophallic sclerite
1056 trifurcated posteriorly, with a short median expansion and two short lateral arms; anterior
1057 region elongate and sinuous, almost reaching anterior margin of pseudepiphallic sclerite;
1058 endophallic apodeme made of a median crest and lateral lamellas.

1059 **Female:** FWs rounded, reaching third tergite, slightly or not overlapping; dorsal field brown
1060 with 6–7 longitudinal veins, including 5–6 strong orange brown vein and 1 thin vein being part
1061 of a narrow yellow lateral band; dorsal field without distinct transverse veins. Lateral field dark
1062 brown, with 3–4 strong dark brown longitudinal veins, without distinct transverse veins.
1063 Ovipositor shorter than FIII; apex lanceolate, slightly denticulate on dorsal edge.

1064 *Female genitalia:* Female copulatory papilla mostly membranous, with a wide rounded base
1065 and a conical apex folded ventrally in lateral view (Fig. 6J, 6K).

1066 **Juvenile:** Coloration light brown, mottled with dark brown; lateral lobe of pronotum black
1067 dorsally, ventral margin yellow with a wide dark brown spot; lateral side of abdomen with a
1068 black spot on second tergite.

1069 **Measurements.** See Table 1.

1070 **Habitat and life history traits.** Unknown.

1071 **Calling song.** Unknown.

1072 **Etymology.** The species is named after the type locality, city of Miri in Sarawak.

1073

1074 ***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. bitaeniatus* 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 pseudepiphallid 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... *Macrobithus* 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. ... *Julvernithus* 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

1237 **Acknowledgments**

1238 We thank the two anonymous reviewers for their comments to improve the manuscript and
1239 Hannah ter Hofstede for looking in detail through the manuscript as a native English speaker.
1240 We also thank Andrej Gorochov (ZIN) for providing samples from the collections of Saint
1241 Petersburg and Camille Desjonquères for her help with ASR analyses. MKT thanks Huiqing
1242 Yeo (in Brunei Darussalam), Siew Tin Toh (in Bukit Larut and Sandakan), Momin Binti, John
1243 Lee Yukang, and Saudi Bintang (in Sandakan) for field assistance. The permissions for
1244 collecting specimens were granted by the Forestry Department, Ministry of Primary
1245 Resources and Tourism, Brunei Darussalam and the Biodiversity Research and Innovation
1246 Centre (BioRIC) (JPH/PDK/01 Pt 2 and BioRIC/HOB/TAD/51-80 respectively) and the Sabah
1247 Biodiversity Centre (JKM/MBS.1000-2/3 JLD.3 (99)) (for Sandakan). The work of MKT at
1248 MNHN was supported by the Fyssen Foundation Postdoctoral Fellowship; and fieldwork was
1249 supported by the Orthoptera Species File Grant 2019 under the taxonomic research project
1250 titled "Contribution to the species diversity and acoustic data on Orthoptera from Sandakan
1251 (Borneo, East Malaysia, Sabah)" and Percy Sladen Memorial Fund (The Linnean Society of
1252 London) under the project titled "Advancing biodiversity informatics of Orthoptera from Brunei

1253 Darussalam". Molecular work was undertaken at the 'Service de Systématique Moléculaire'
1254 (UMS 2700-2AD CNRS-MNHN). We are grateful to Delphine Gey and Céline Bonillo (MNHN)
1255 for their help in the acquisition of the molecular data.

1256

1257

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- 1511

1512 **Figure captions**

1513 **Fig. 1.** BI tree showing the phylogeny of Lebinthini (A). Support values for both BI and ML
1514 analyses are given at nodes (BI pp/ML bootstrap); posterior probabilities below 0.90 and
1515 bootstrap values below 70% are considered as low support and are represented as -/-. Nodes
1516 not present in the ML tree are indicated as * instead of a bootstrap value. Map representing
1517 the known distribution of tribes and subtribes of Eneopterinae (B).

1518
1519 **Fig. 2.** Simplified dated phylogeny resulting from BEAST analyses of the species-level dataset,
1520 using a Yule Process tree prior. Median age estimates are given above each node; horizontal
1521 bars on nodes represent the 95% highest posterior density interval of age estimates; posterior
1522 probabilities are indicated below nodes, with values below 0.90 considered as weak support
1523 and represented as -.

1524
1525 **Fig. 3.** Reconstruction of the ancestral states for four acoustic calling song traits: structure of
1526 call (A), echeme structure (B), dominant frequency (C), and nature of dominant frequency (D).

1527
1528
1529 **Fig. 4.** Face in anterior views (A, C, E) and head and pronotum in lateral views (B, D, F) of
1530 *Lebinthus luae* (A, B), *Falcerminthus sanchezi* **gen. nov.** (C, D), and *Fadinthus tehtari* **gen. et**
1531 **sp. nov.** (E, F). Scale bar: 1 mm.

1532
1533 **Fig. 5.** Male FWs in dorsal views of *Lebinthus luae* (A), *Falcerminthus estrellae* **gen. nov.** (B),
1534 *Fadinthus tehtari* **gen. et sp. nov.** (C), and *Fadinthus miri* **gen. et sp. nov.**. Scale bar: 1 mm.

1535
1536 **Fig. 6.** Male and female genitalia of *Fadinthus miri* **gen. et sp. nov.** (A–C, J, K), and *Fadinthus*
1537 *tehtari* **gen. et sp. nov.** (D–F, L, M), and other representative species from Lebinthina (G–I).
1538 Male genitalia photographed in dorsal (A, D, G–I), ventral (B, E) and lateral (C, F) views; female
1539 copulatory papilla in dorsal (J, L) and lateral (K, M) views. Scale bar: 0.5 mm.

1540
1541 **Fig. 7.** *Fadinthus tehtari* **gen. et sp. nov.** male (A) and female (B) adults, and nymphs (C, D)
1542 when alive. The natural habitat of the species in Belait District, Brunei Darussalam (E).

1543
1544 **Fig. 8.** Male calling song of *Fadinthus tehtari* **gen. et sp. nov.**: oscillograms showing four
1545 calling songs (A), one calling song (B); spectrogram of calling song (C); oscillogram showing
1546 the second part of the call (D); power spectrum of one syllable in the first part of the call (E).

1547
1548 **Table captions**

1549 **Table 1.** Measurements of *Fadinthus miri* **sp. nov.** and *Fadinthus tehtari* **sp. nov.**
1550 Abbreviations: BL, body length; PronL, pronotum length; PronW, pronotum width; FWL,
1551 forewing length; FWW, forewing width; FIIIL, length of hind femur; FIIIW, width of hind femur;
1552 TIIIL, length of hind tibia; TallIs, number of hind tarsomere spines; las, number of inner spines
1553 on hind tibia dorsal side above the spurs; lbs, number of inner spines on hind tibia dorsal side
1554 between the spurs; Oas, number of outer spines on hind tibia dorsal side above the spurs;
1555 Obs, number of outer spines on hind tibia dorsal side between the spurs; TallIOs, number of
1556 outer spines on dorsal side of third hind tarsomere; OL, ovipositor length.

1557

1558 **Supporting information**

1559 **Fig. S1.** IQtree ML gene trees inferred for each separate marker 12S (a), 16S (b), COI (c),
1560 COII (d), Cytb (e), 18S (f), 28S (g), H3 (h). Bootstrap support values above 70 % are
1561 represented by a grey circle proportional to the support (see scale on the left left side of the
1562 tree)

1563

1564 **Fig. S2.** IQ-TREE ML analyses of the concatenated dataset. (a) results of the analysis using 8
1565 gene partitions with models determined using IQ-TREE Model Finder. (b) results of the
1566 analysis using five fixed models defined by the best-fit partitioning schemes and the associated
1567 substitution models used in the BI analysis (see below). Bootstrap support values above 75%
1568 are represented by a grey circle proportional to the support (see scale on the left side of the
1569 tree)

1570 **Fig. S3.** Dated phylogeny resulting from BEAST analyses of the species-level dataset, using
1571 birth-death tree speciation priors. Median age estimates are presented on nodes; horizontal
1572 bars on nodes are also used to provide the 95% highest posterior density interval of age
1573 estimates.

1574

1575 **Table S1.** List of specimens and the gene sequences sampled for the phylogenetic tree and
1576 ASR. Lab codes marked by * were used in the dating analysis as representative of the
1577 species when more than one individual have been sequenced.

1578

1579 **Table S2.** Models used in the phylogenetic analyses: models inferred with IQ-TREE
1580 ModelFinder (ML analysis) and best Best-fit models of sequence evolution and partitioning
1581 schemes selected with PartitionFinder ('unlinked branch lengths' option) for Bayesian
1582 Inference (MrBayes/BEAST), with codon position is denoted by pos1, pos2 and pos3.
1583 Subsets are denoted by P1 to Pn.

1584

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.

1590

1591

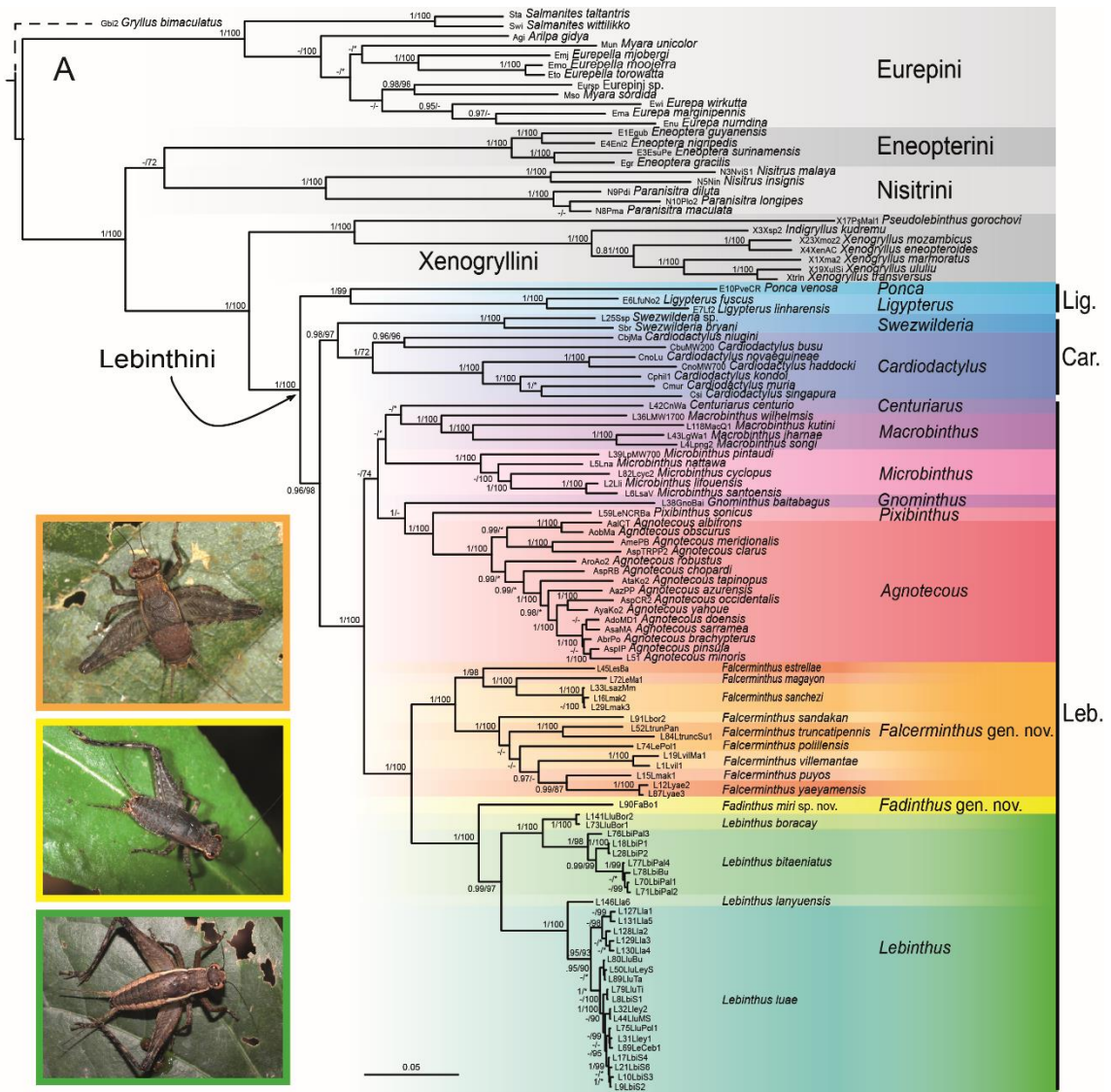
1592 **Table 1.** Measurements of *Fadinthus miri* **sp. nov.** and *Fadinthus tehtari* **sp. nov.**
 1593 Abbreviations: BL, body length; PronL, pronotum length; PronW, pronotum width; FWL,
 1594 forewing length; FWW, forewing width; FIILL, length of hind femur; FIIIW, width of hind femur;
 1595 TIILL, length of hind tibia; TallIs, number of hind tarsomere spines; las, number of inner spines
 1596 on hind tibia dorsal side above the spurs; lbs, number of inner spines on hind tibia dorsal side
 1597 between the spurs; Oas, number of outer spines on hind tibia dorsal side above the spurs;
 1598 Obs, number of outer spines on hind tibia dorsal side between the spurs; TallIOs, number of
 1599 outer spines on dorsal side of third hind tarsomere; OL, ovipositor length.

1600

	BL	PronL	PronW	FWL	FWW	FIILL	FIIIW	TIILL	TIIIs				TallIOs	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)

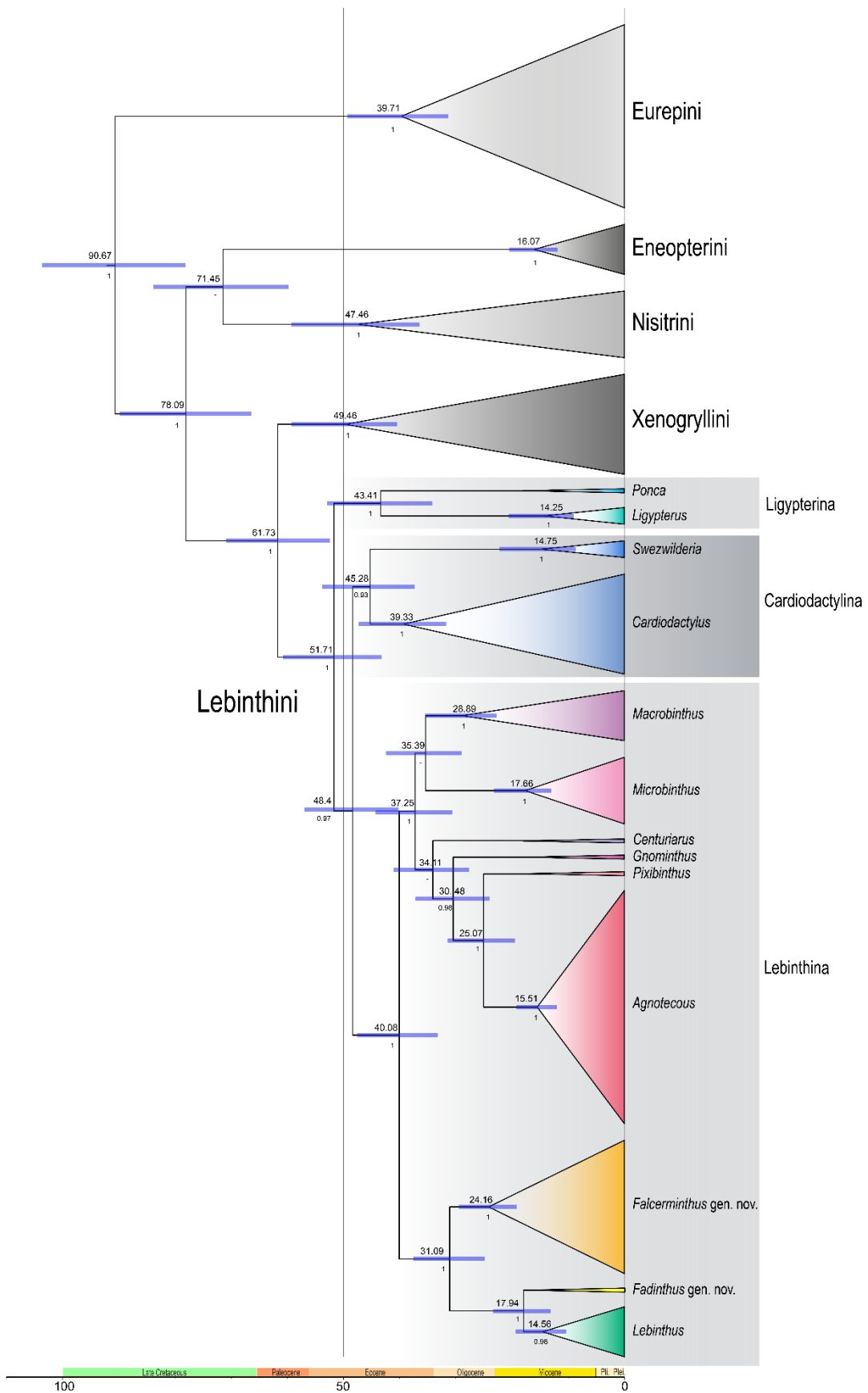
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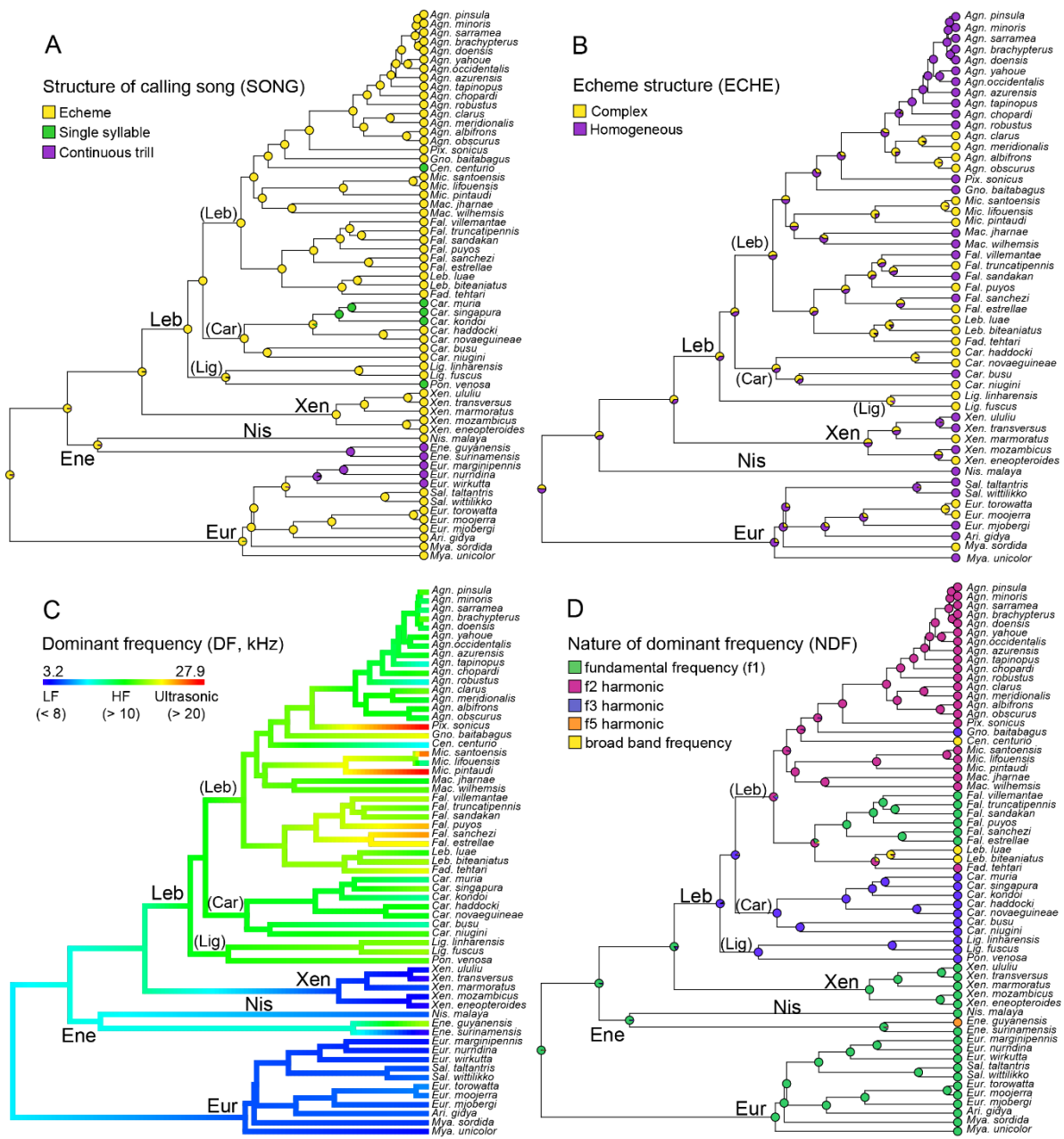
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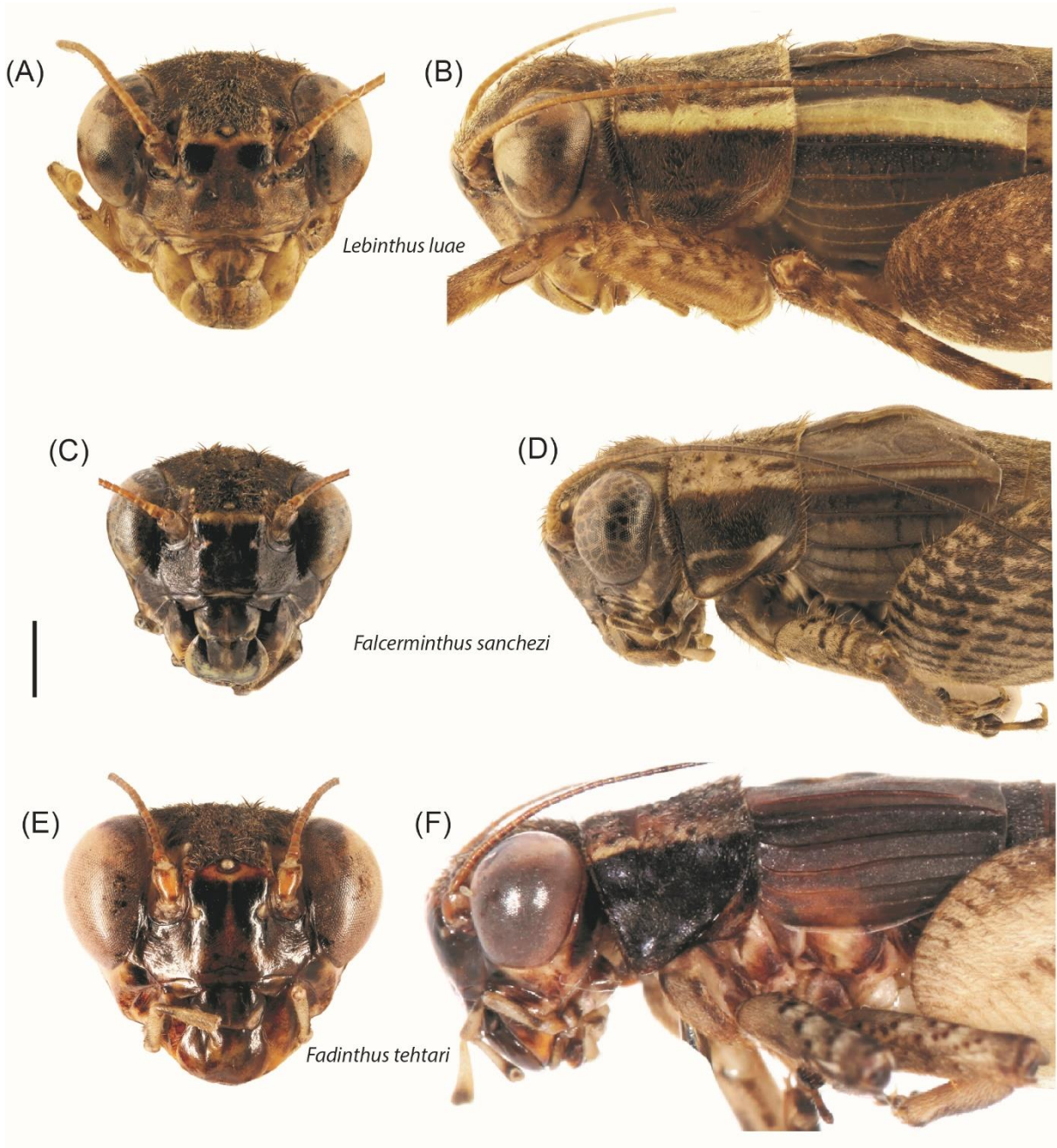
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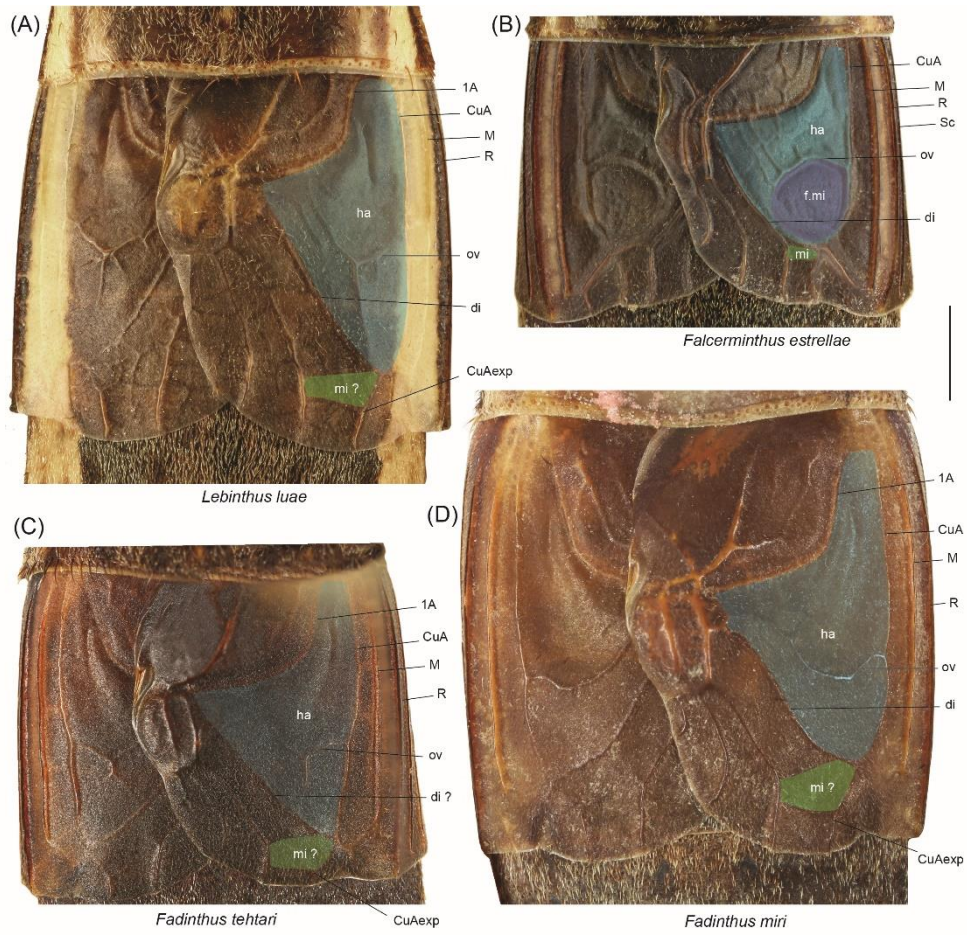
1611 Fig.4



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1614 Fig.5



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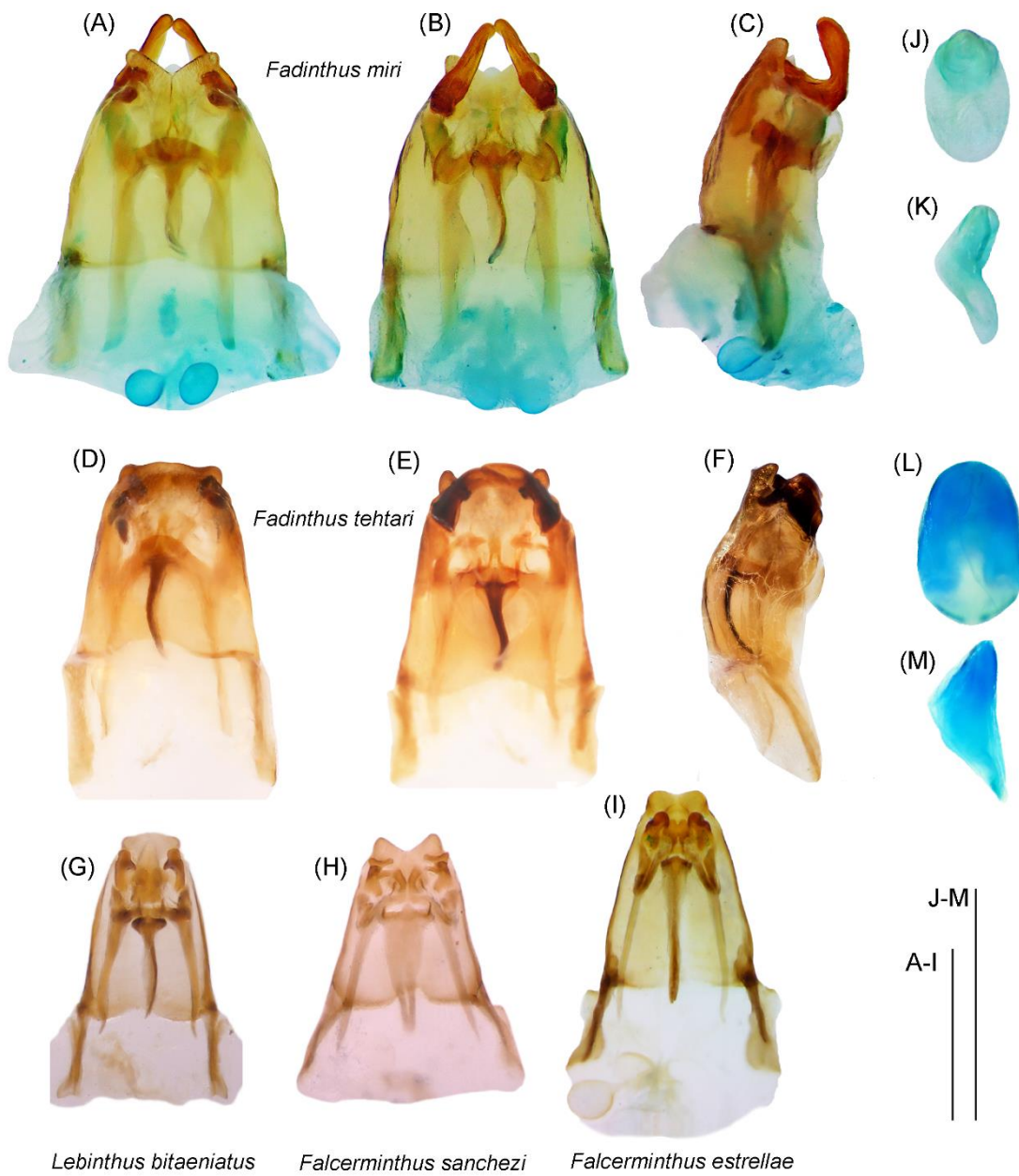
1617 Fig.6



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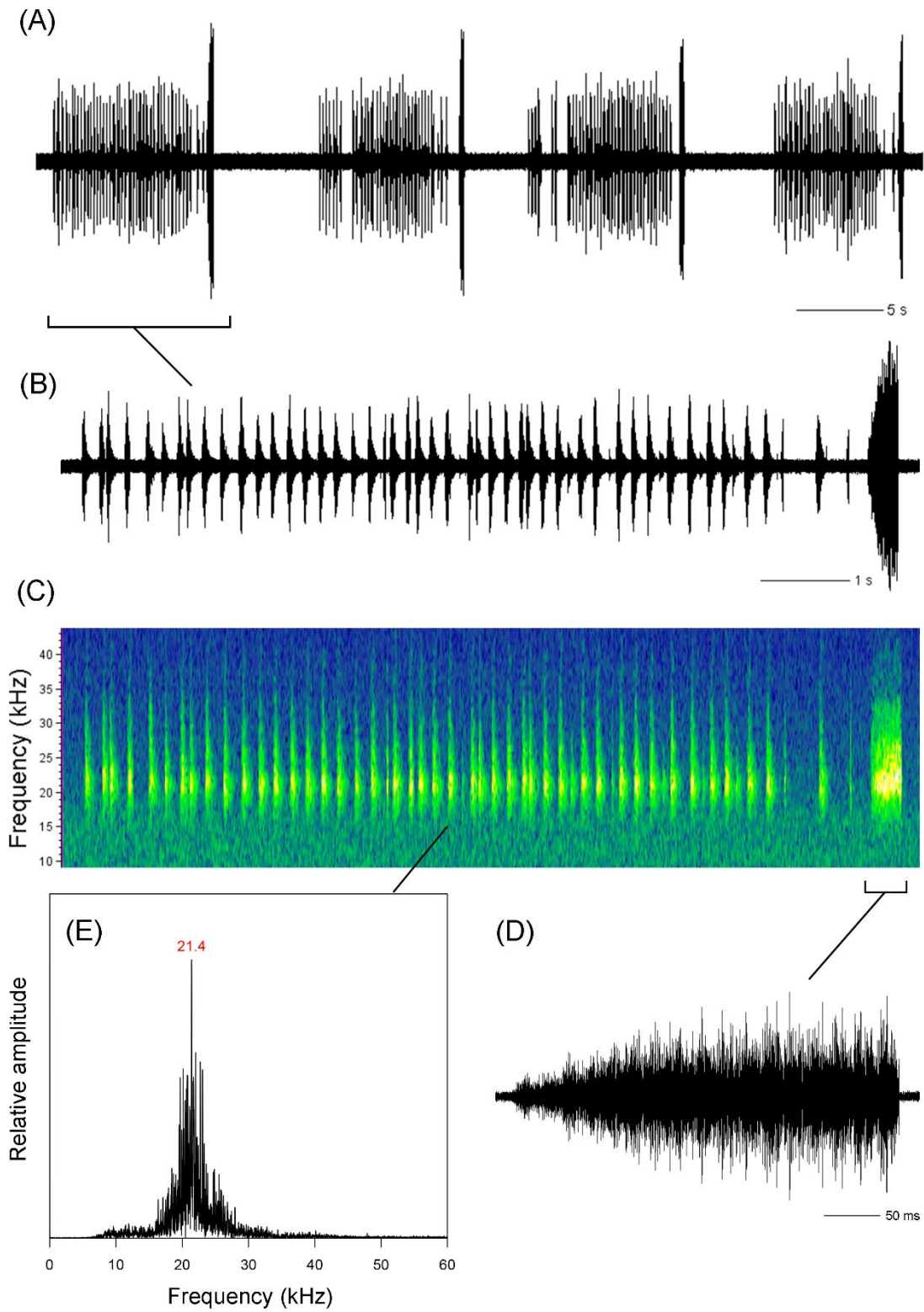
1619

1620 Fig.7



1623

1624 Fig.8



1625

1626

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	*AaICT	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 wikutta</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)	MK76127 5	MK76125 2	MK761354	MK76129 4	MK76133 2	-	MK76131 4	MK76137 1
<i>Lebinthus bitaeniatus</i> Stål, 1877	ZIN	L77LbiPal4	Philippines (Palawan)	MZ50183 0	MZ49725 9	-	-	MZ50686 1	-	MZ50556 6	MZ47606 3
<i>Lebinthus bitaeniatus</i> Stål, 1877	ZIN	L78LbiBu	Philippines (Palawan)	MZ50182 8	MZ50880 3	MZ475917	-	MZ50688 6	MZ47601 6	MZ50885 9	MZ54097 5
<i>Lebinthus bitaeniatus</i> Stål, 1877	MNHN-EO-ENSIF4393	L70LbiPal1	Philippines (Palawan)	MZ50183 2	MZ50879 7	-	MZ49738 8	-	-	MZ50884 7	-
<i>Lebinthus bitaeniatus</i> Stål, 1877	MNHN-EO-ENSIF4394	L71LbiPal2	Philippines (Palawan)	MZ50182 9	MZ50879 2	MZ475918	MZ50882 7	MZ50688 9	-	MZ50886 1	MZ47606 4
<i>Lebinthus boracay</i> Baroga, Yap & Robillard, n. sp.	BVZ_JBB030	*L141LluBor2	Philippines (Boracay)	MZ50870 0	-	-	-	-	-	-	MZ47606 5
<i>Lebinthus boracay</i> Baroga, Yap & Robillard, n. sp.	MNHN-EO-ENSIF11257	L73LluBor1	Philippines (Boracay)	MZ50869 9	-	-	-	-	-	-	MZ47606 6
<i>Lebinthus lanyuensis</i>	MNHN-EO-ENSIF1746	*L146Lla6	China (Taiwan)	MZ50870 2	-	-	-	-	-	-	-
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-EO-ENSIF2740	*L8Lbis1	Singapore	KR90401 7	JF97252 4	JF972493	KR90419 9	KU70556 7	KU70555 7	KR90366 5	KR90332 1
<i>Lebinthus luae</i> Robillard & Tan, 2013	UPLB-MNH-PNM13493	L127Lla1	Philippines (Batanes)	MZ50870 3	-	-	-	-	-	-	-
<i>Lebinthus luae</i> Robillard & Tan, 2013	UPLB-MNH-PNM13480	L128Lla2	Philippines (Batanes)	MZ50877 3	-	-	-	-	-	-	-
<i>Lebinthus luae</i> Robillard & Tan, 2013	UPLB-MNH-PNM13478	L129Lla3	Philippines (Batanes)	MZ50876 7	-	-	-	-	-	-	-
<i>Lebinthus luae</i> Robillard & Tan, 2013	UPLB-MNH-PNM13485	L130Lla4	Philippines (Batanes)	MZ50876 9	-	-	-	-	-	-	-
<i>Lebinthus luae</i> Robillard & Tan, 2013	UPLB-MNH-PNM13502	L131Lla5	Philippines (Batanes)	MZ50877 0	-	-	-	-	-	-	MZ47606 7
<i>Lebinthus luae</i> Robillard & Tan, 2013	ZIN	L80LluBu	Philippines (Sulawesi)	MZ50876 3	MZ49726 3	-	MZ49741 7	MZ50689 5	-	MZ50561 6	MZ47606 8

<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	L75LluPo1	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>Macrobithus kutini</i> Robillard & Su, 2018)	ANIC_14_005048	*L118MacQ1	Australia	MZ50877 7	MZ50881 0	-	MZ50884 4	MZ50916 2	MZ47602 9	-	MZ47608 1
<i>Macrobithus 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>Macrobithus 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>Microbithus 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>Microbithus 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>Microbithus cyclopus</i> (Robillard, 2010)	ZIN	*L82Lcyc2	Indonesia (New Guinea)	MZ50877 8	-	MZ475932	MZ50884 5	MZ50916 4	-	MZ50884 6	MZ47608 4
<i>Microbithus 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>Microbithus 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>Pixibithus 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> Gorochof, 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 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

1630 **Table S2.** Models used in the phylogenetic analyses: models inferred with IQ-TREE ModelFinder (ML
 1631 analysis) and best-fit models of sequence evolution and partitioning schemes selected with
 1632 PartitionFinder ('unlinked branch lengths' option) for Bayesian Inference (MrBayes/BEAST), with
 1633 codon position is denoted by pos1, pos2 and pos3. Subsets are denoted by P1 to Pn.

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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

1636

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

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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>Centuriarus 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 luae</i> Robillard & Tan, 2013	*L8Lbis1	E	C	B	16.7	Robillard & Tan 2013
<i>Ligypterus linharensis</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>Macrobenthus jhamae</i> (Bhowmik, 1981)	*L43LgWa1	E	H	F2	15.7	Robillard <i>et al.</i> , 2016
<i>Macrobenthus wilhelmsis</i> Robillard & Dong, 2016	*L36LMW17 00	E	H	F2	18.1	Robillard <i>et al.</i> , 2016
<i>Microbenthus lifouensis</i> (Desutter-Grandcolas, 1997)	*L2Lli	E	C	F2	11.6	Robillard & Desutter-Grandcolas, 2011
<i>Microbenthus pintaui</i> Robillard & Dong, 2016	*L39LpMW7 00	E	C	F2	27.9	Robillard <i>et al.</i> , 2016
<i>Microbenthus 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>Pixibenthus sonicus</i> Anso & Robillard, 2016	*L59LeNCR Ba	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> Gorochov, 1990	*19XulSi	E	H	F1	4.8	Jaiswara <i>et al.</i> , 2019

1640 **Table S4.** AICc (sample-size corrected AIC) for ASR analyses of three discrete traits. Best-fit models
1641 are mentioned in bold.

1642

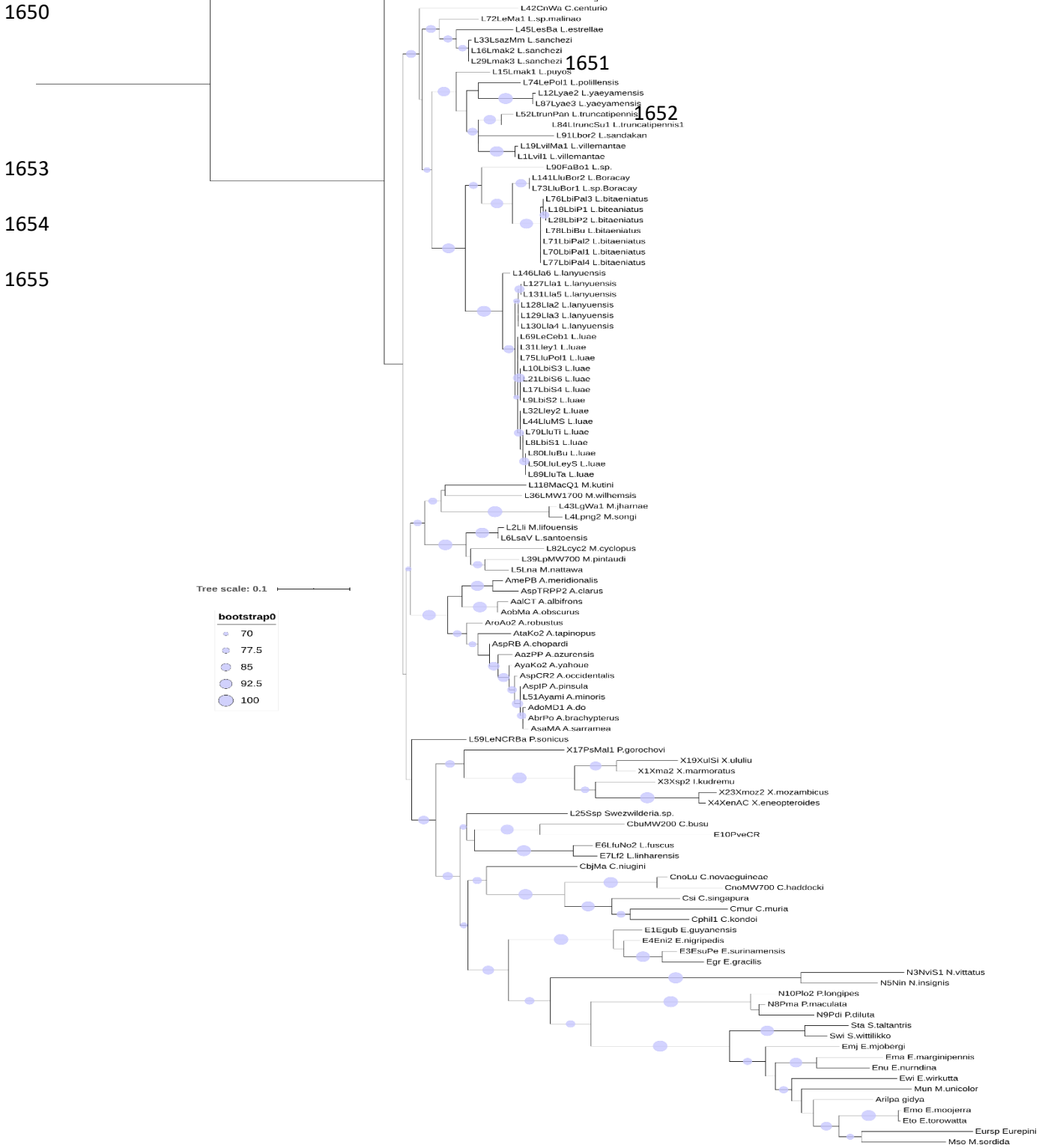
Traits	Models		
	ER	SYM	ARD
SONG	45.065	48.619	55.465
ECHE	60.069	60.069	62.221
NDF	73.663	87.422	114.481

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1644

1645 **S-Figure 1.** IQtree ML gene trees inferred for each separate marker. 12S (a), 16S
 1646 (b), COI (c), COII (d), Cytb (e), 18S (f), 28S (g), H3 (hi). Bootstrap support values
 1647 above 75% are represented by a grey circle proportional to the support (see scale on
 1648 the left side of the tree)

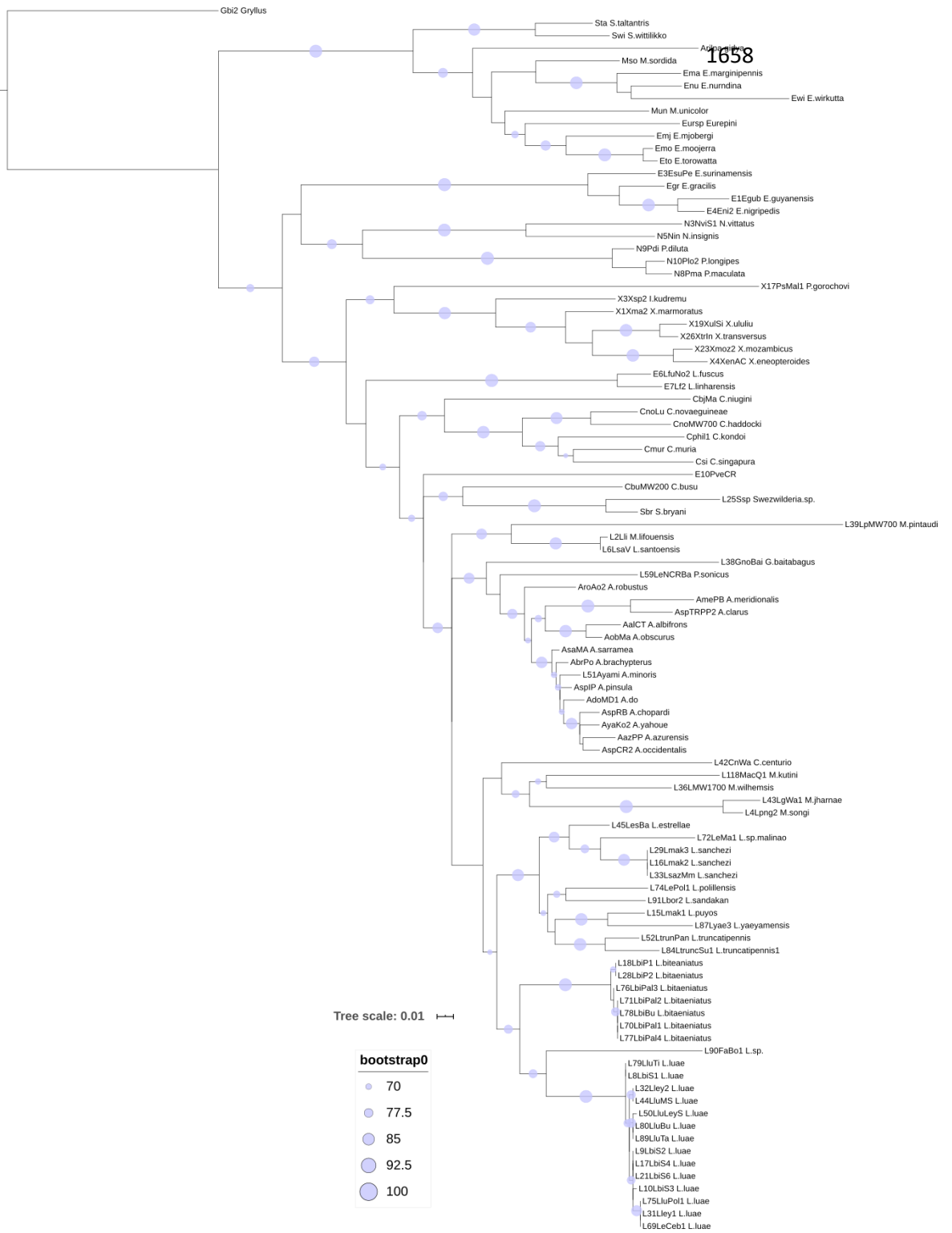
1649 **(a) 12S**



1656 (b) 16S

1657

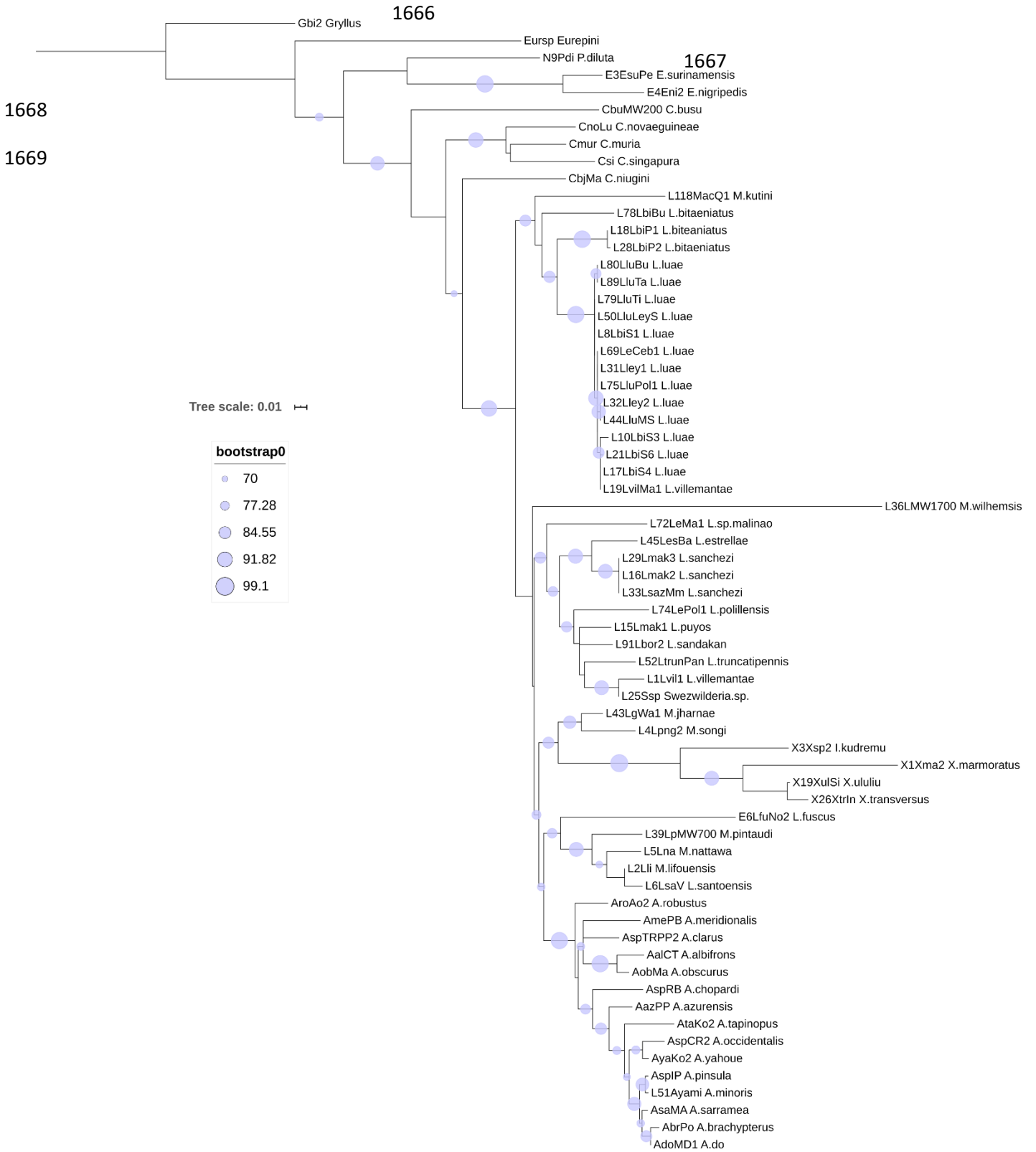
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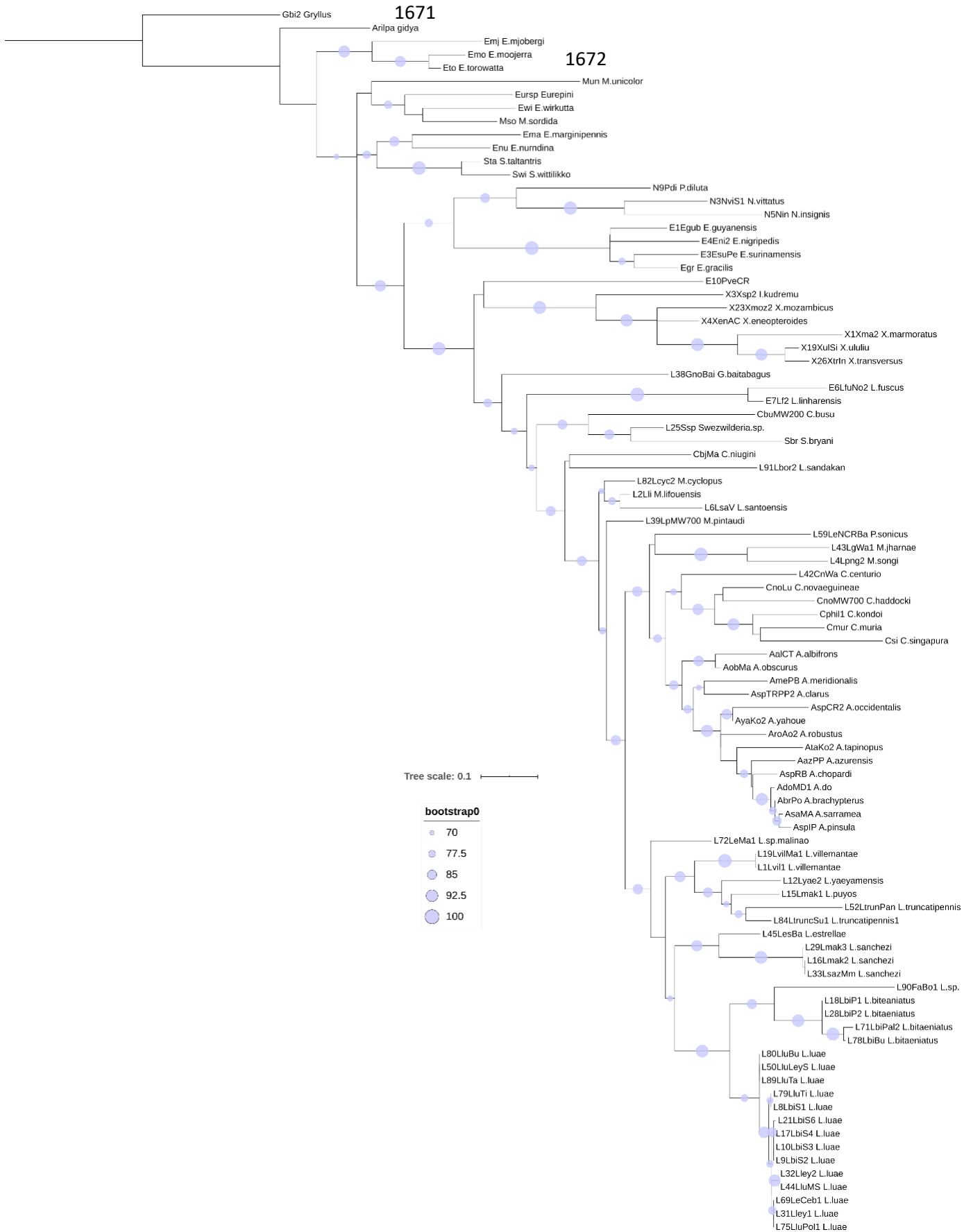
1660 (c) COI



1665 (d) COII

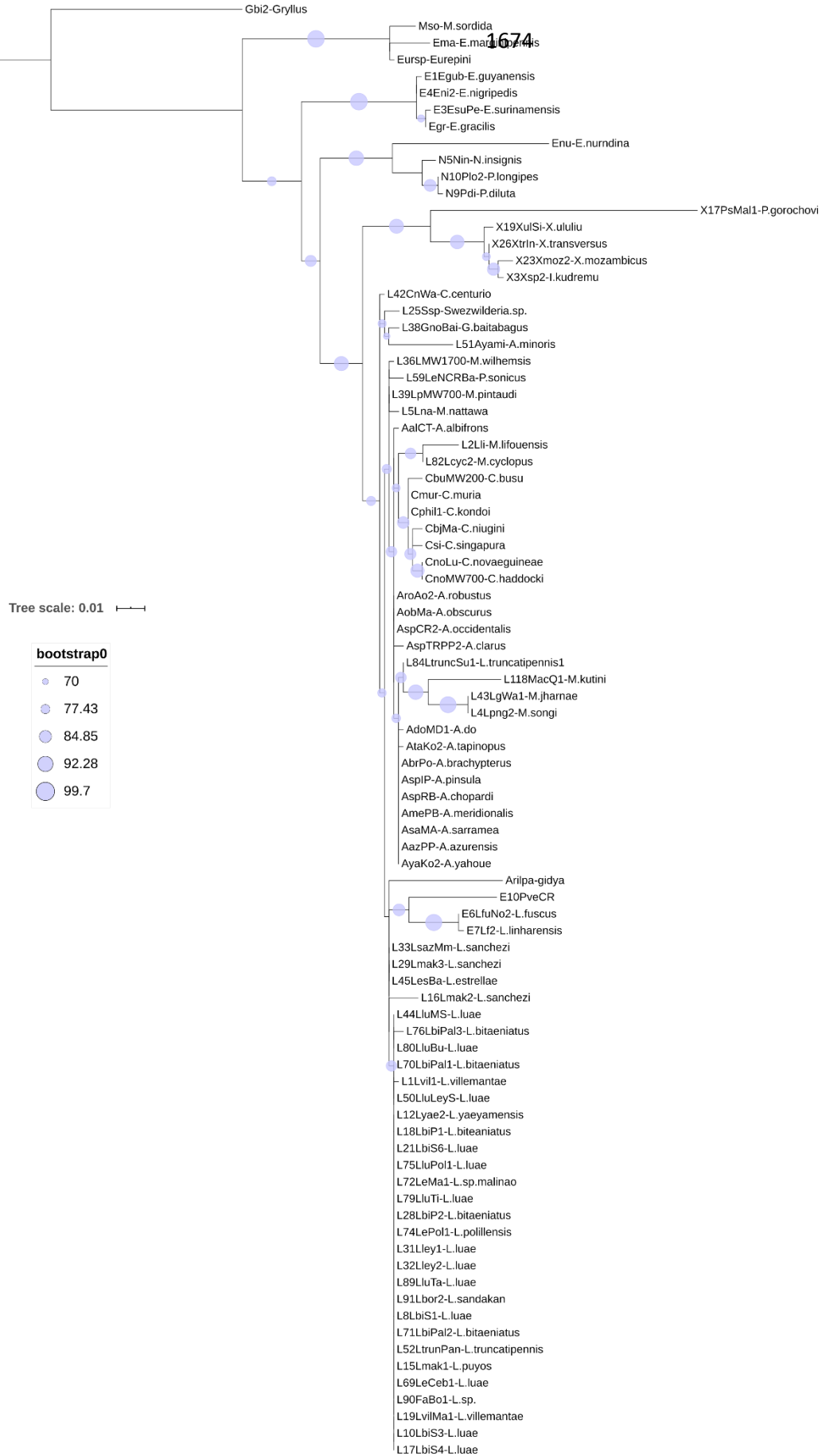


1670 (e) Cytb



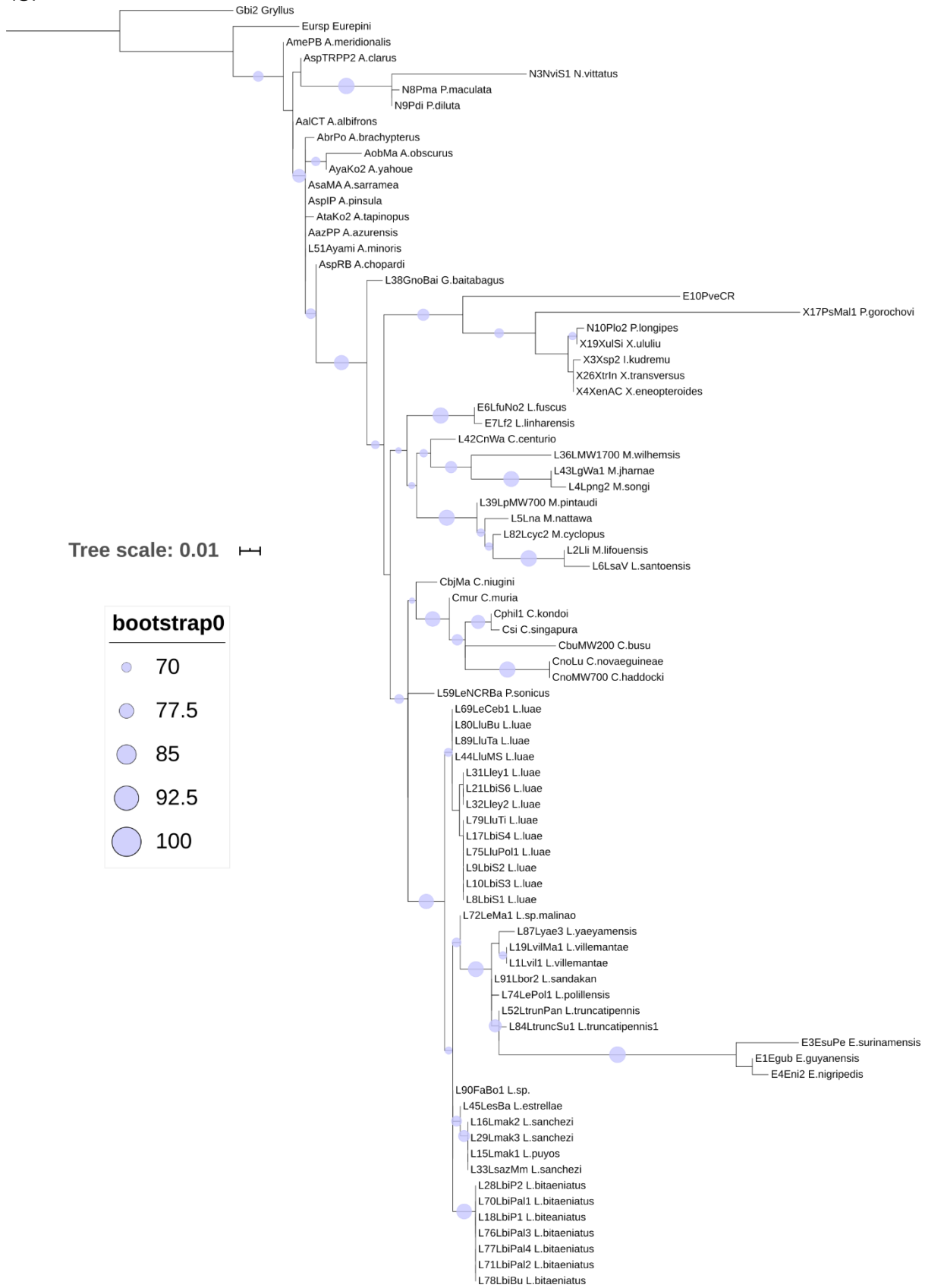
1673 (f) 18S

1675
1676
1677
1678



1679

1680 (g) 28S



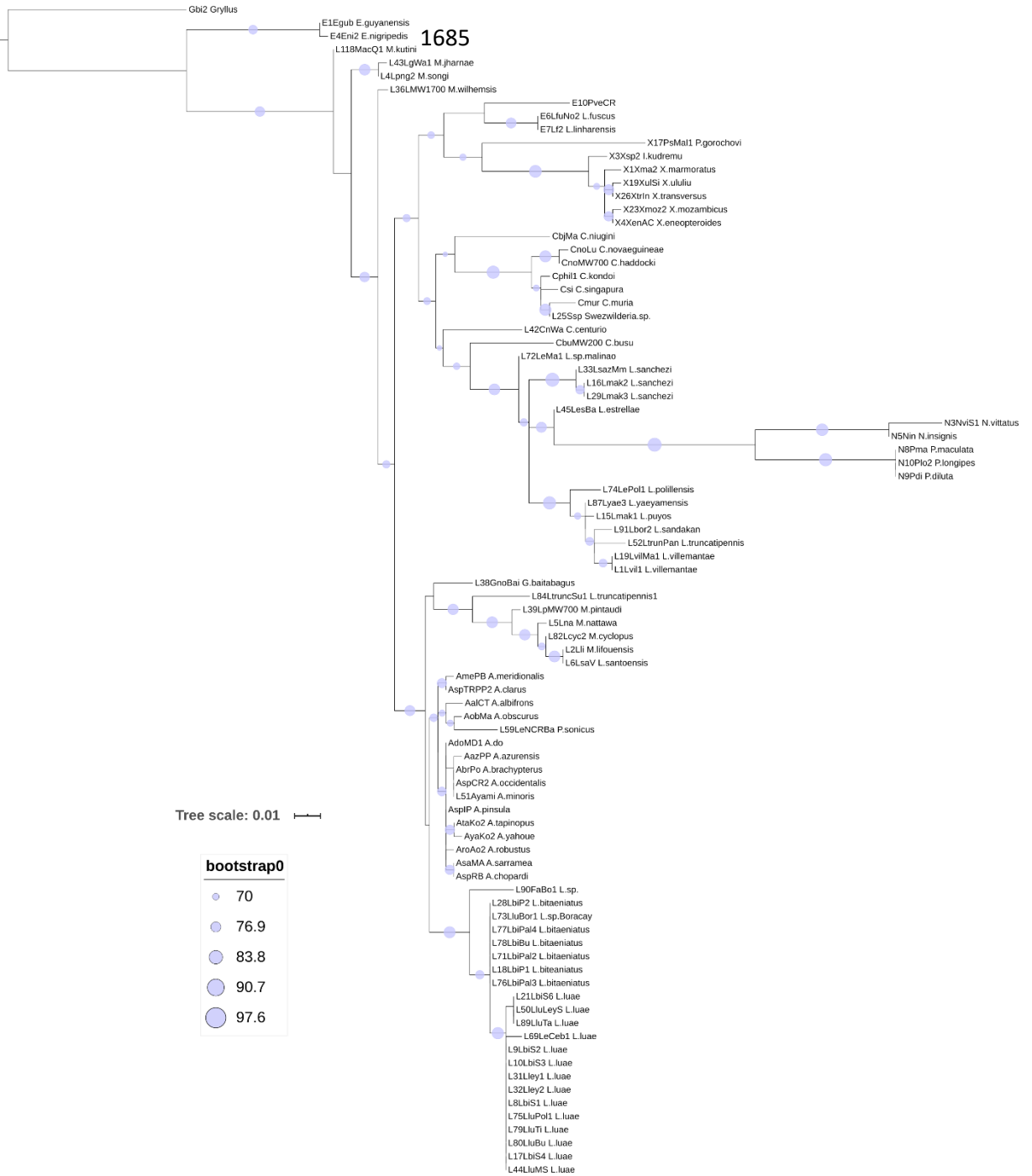
1681

1682 (h) H3

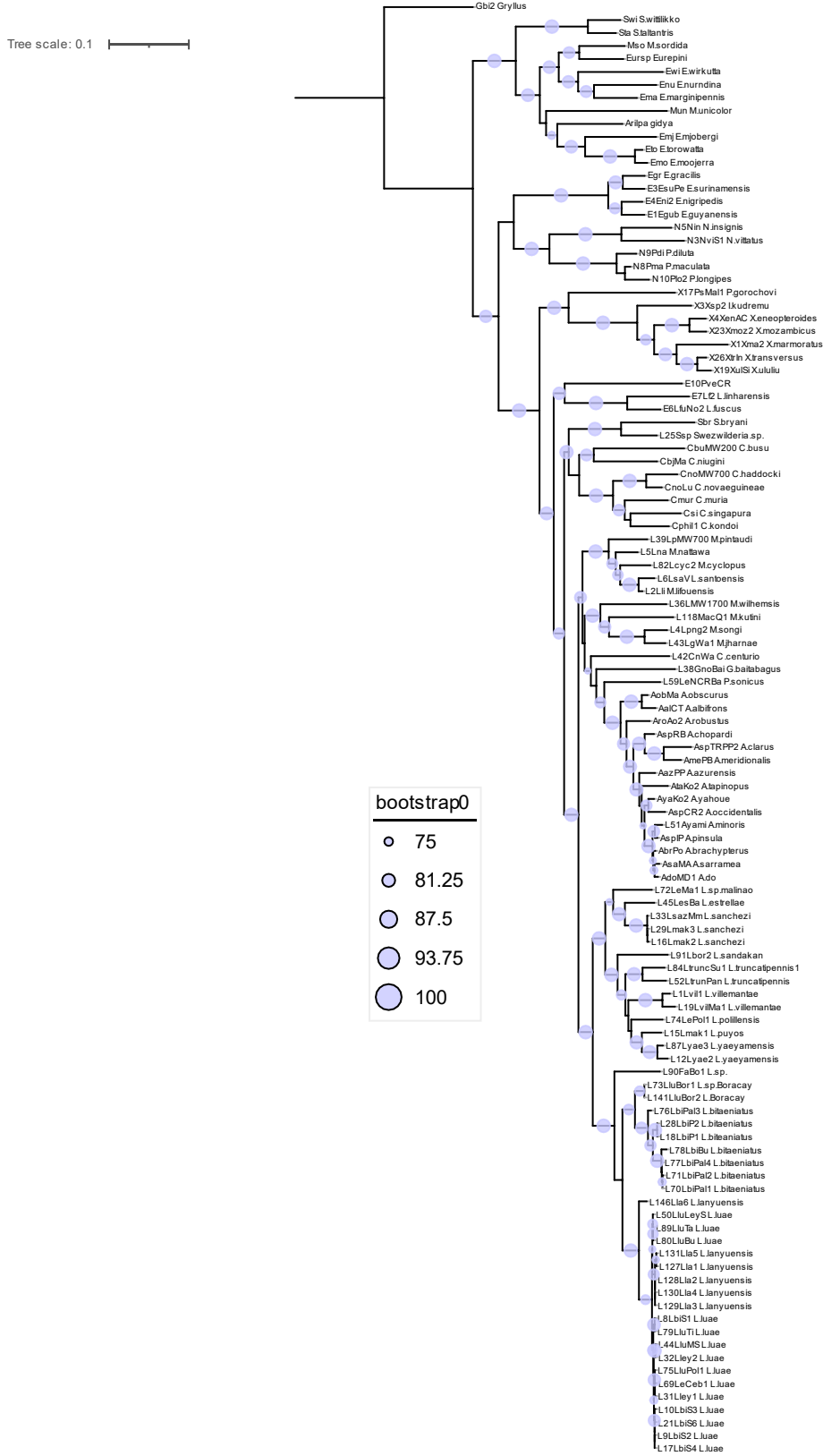
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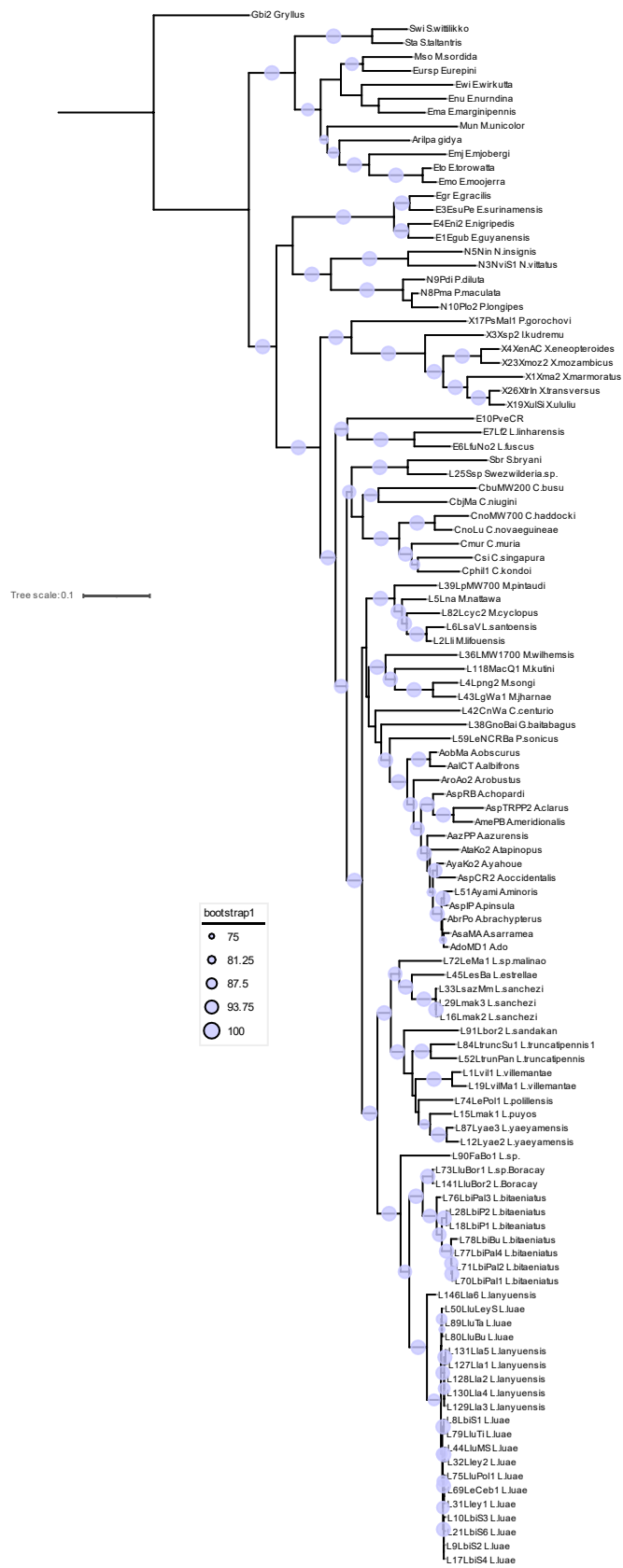
1687 **S-Figure 2.** IQ-TREE ML analyses of the concatenated dataset. (a) results of the analysis
1688 using 8 gene partitions with models determined using IQ-TREE ModelFinder. (b) results of
1689 the analysis using five fixed models defined by the best-fit partitioning schemes and the
1690 associated 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

(b)

1696



1697

1698

1699 S-Fig3. Original outputs for dating analyses from BEAST

