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**Phylogenetic relationships in the cricket tribe
Xenogryllini (Orthoptera, Gryllidae, Eneopterinae) and
description of the Indian genus *Indigryllus* gen. nov.**

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1 **Phylogenetic relationships in the cricket tribe Xenogryllini (Orthoptera, Gryllidae,**
2 **Eneopterinae) and description of the Indian genus *Indigryllus* gen. nov.**

3

4 **Page headlines: Phylogeny of Xenogryllini**

5

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20 **Abstract**

21 Subfamily Eneopterinae is known greatly for its diversified acoustic modalities and disjunct
22 distribution. Within Eneopterinae, tribe Lebinthini is the most studied group, due to its highest species
23 diversity (*ca.* 150 species in 12 genera), endemic distribution on the islands of Southeast Asia and of
24 the South West Pacific, males' ability to produce high-frequency calling songs and evolution of
25 females' vibrational response. To investigate the distribution pattern and diversification of acoustic
26 and behavioural attributes in a larger frame, clear understanding of phylogenetic relationships within
27 other tribes of Eneopterinae is vital. In this study, we focus on the tribe Xenogryllini, sister group of
28 Lebinthini. Xenogryllini, as opposed to Lebinthini, is known by fewer species (11 species in 2 genera),
29 distributed widely in continental Asia and Africa, and for producing low-frequency calling songs. We
30 describe a new genus *Indigryllus* with a new species of the tribe Xenogryllini, discovered from the
31 Southwest of India. We used eight genetic markers to reconstruct the phylogenetic relationships. The
32 resultant phylogenetic tree is used to compare and discuss distribution patterns and acoustic modalities
33 between Lebinthini and Xenogryllini.

34

35 **Keywords:** Western Ghats, *Xenogryllus*, *Pseudolebinthus*, Lebinthini, Biogeography, Systematics

36

37 1. INTRODUCTION

38 The crickets of the subfamily Eneopterinae have been studied for the diversity of their communication
39 signals and related structures (e.g., Robillard & Desutter-Grandcolas 2004a, b; Robillard et al., 2013;
40 ter Hofstede et al., 2015; Schneider et al., 2017), and for their biogeographical patterns (Nattier et al.,
41 2011; Vicente et al., 2017; Dong et al., 2018). Most of these recent works have focused on the tribe
42 Lebinthini, that shows the highest species diversity (*ca.* 150 species in 12 genera; Cigliano et al.,
43 2019) and endemic distribution in the islands of Southeast Asia and South West Pacific. The
44 Lebinthini have also developed an original system of communication involving female vibrational
45 responses to male high-frequency calling songs and loss of phonotaxis (ter Hofstede et al., 2015). To
46 investigate how this diversity emerged and how the original traits evolved, it is necessary to
47 investigate the context in which it happened. Being the sister group of Lebinthini, the tribe
48 Xenogryllini therefore is the best “control lineage” to better understand the evolution of unique
49 features in Lebinthini. A taxonomic and phylogenetic focus on the Xenogryllini is thus particularly
50 needed.

51 Tribe Xenogryllini is a group of crickets with contrasting features under subfamily Eneopterinae.
52 It is currently known only by two genera, *Xenogryllus* Bolívar, 1890 (eight species) and
53 *Pseudolebinthus* Robillard, 2006 (three species) according to recent revision works (Jaiswara et al.,
54 2018 & 2019). Unlike Lebinthini, members of Xenogryllini are distributed widely in continental
55 regions, from Asia to Africa. Calling songs have recently been documented for five species of the
56 genus *Xenogryllus* and is unknown for *Pseudolebinthus* (Jaiswara et al., 2018). As opposed to
57 Lebinthini, Xenogryllini members produce calling songs with longer syllables and lower dominant
58 frequencies. In the present study, we describe a new genus and a new species of Xenogryllini from
59 South India, *Indigryllus kudremu* Robillard & Jaiswara gen. nov. et sp. nov. and provide an emended
60 key to Xenogryllini genera. Considering the recent advances in information with respect to species
61 diversity, distribution and acoustic signals for Xenogryllini, this study focuses on establishing
62 phylogenetic relationships among species of all three genera of the tribe. According to the resultant
63 phylogenetic relationships we contrast Xenogryllini and Lebinthini in terms of species diversity,

64 patterns of distribution and signals of communication. In the light of comparable taxonomic treatment,
65 we assess whether Xenogryllini are truly less diversified than Lebinthini, as suggested earlier
66 (Robillard & Desutter-Grandcolas, 2004b). We then discuss how different are the distributions and
67 calling songs of both tribes with respect to their parallel biogeographical history and evolution of an
68 original system of communication in Lebinthini.

69

70 **2. MATERIAL AND METHODS**

71

72 **2.1. Taxonomy**

73 Specimens of *Indigryllus kudrmu* gen. nov. et sp. nov. come from a field work expedition in India
74 (2007) and are deposited in the collections of Zoological Survey of India, Kolkata (ZSI) and Muséum
75 national d'Histoire naturelle, Paris (MNHN). The descriptions of the new genus and species follow
76 terminologies as proposed by Robillard et al. (2014). Observations of external morphological
77 characters and dissection of male and female genitalia were performed using Leica stereomicroscopes
78 MZ16. Terminologies for male forewing (FW) venation follow Ragge (1995) and Robillard &
79 Desutter-Grandcolas (2004b). Male and female genitalia were dissected from dry preserved specimens
80 by making a small slit between paraproct and subgenital plate. Female copulatory papilla was
81 dissected out by cutting the membrane between ovipositor and subgenital plate. Dissected genitalia
82 were cleared in 10% cold KOH solution and preserved in glass vials containing glycerine.
83 Terminologies for genitalia follow Desutter (1987), modified in Desutter-Grandcolas (2003) and
84 Robillard & Desutter-Grandcolas (2004a). Imaging of male and female genitalia were made using an
85 AmScope MU1000 digital camera (www.Amscope.com) or with a Canon EOS 40D Digital SLR
86 camera. To highlight the structural components of male and female genitalia, water solution
87 containing a drop of JBL Punktol was used. To fix orientations and stabilization of genitalia for
88 photography, a clear and viscous Power Plast Hand Sanitizer was used following Su (2016).

89

90 **Abbreviations**

91 General morphology: FI, FII, FIII, fore, median, hind femur; FW, forewing; TI, TII, TIII, fore, median,
92 hind tibia; Tarsomere I/II/III-1: basal segment of fore, median and hind leg tarsomere.

93 Tegminal venation: 1A-4A, first to fourth anal veins; CuA, anterior cubitus; CuA1, CuA2, ...
94 first, second, ... branches of CuA; CuP, posterior cubitus; M, median vein; R, radial vein; Sc, subcostal
95 vein and its branches; c1-3, first to third cells of C alignment; d1 cell (mirror), first cell(s) of D
96 alignment; d2, second cell of D alignment; e1, first cell of E alignment.

97

98 **2.2. Taxon sampling**

99 The tribe Xenogryllini is composed of three genera and 12 valid species: *Xenogryllus* Bolívar (8
100 species), *Pseudolebinthus* Robillard (3 species) and *Indigryllus kudremu* Robillard & Jaiswara gen.
101 nov. et sp. nov. (1 species). To reconstruct the phylogeny of the tribe Xenogryllini, a total of 20
102 individuals representing 8 species belonging to the three genera were sampled: *Xenogryllus* is
103 represented by 6 species sampled for 1-4 populations per species (the species *X. lamottei* Robillard and
104 *X. maniema* Robillard & Jaiswara are represented by only old specimens which could not be
105 sequenced); *Pseudolebinthus* is represented by one individual of *P. gorochovi* Robillard; *Indigryllus*
106 by one individual of the species *I. kudremu* sp. nov.

107 For outgroup selection, we referred to a previous study (Anso et al., 2016) and selected 8
108 species representing all five tribes of the Eneopterinae subfamily, as well as two more distant species
109 belonging to the subfamily Gryllinae. Whenever possible, we obtained DNA sequence data from the
110 same previous voucher specimens. See Table 1 for detailed information about taxon and genetic
111 markers.

112

113 2.3. DNA markers, PCR amplification and sequence alignment

114 We used DNA markers from eight genes, five from the mitochondrial and three from the nuclear
115 genome based on previous studies (Robillard & Desutter-Grandcolas, 2006; Nattier et al., 2011, 2012
116 & 2013; Chintaun-Marquier et al., 2016). The mitochondrial markers were partial sequences of the
117 *12S rRNA* gene (*12S*, amplicon ~ 400 bp), the *16S rRNA* gene (*16S*, ~ 500 bp), of the *cytochrome b*
118 gene (*Cytb*, ~ 400 bp), and of the *cytochrome c oxidase subunit 1* (*CO1*, ~ 750 bp) and *subunit 2* (*CO2*,
119 ~ 400 bp). Nuclear markers were partial sequences of protein coding *histone H3* gene (*H3*, ~ 330 bp),
120 and partial sequences of two non-protein-coding genes corresponding to nuclear ribosomal subunits
121 *18S rRNA* (*18S*, ~ 650 bp) and *28S rRNA* (*28S*, ~ 400 bp).

122 DNA extraction, PCR amplification and sequencing for all studied taxa, except for three Indian
123 *X. transversus* samples, were carried out at Service de Systématique Moléculaire of the MNHN,
124 following the protocols as described in Nattier et al. (2012). For the Indian *X. transversus* specimens
125 (lab codes: Xtr_715, 765, 766; see details in Table 1), DNA was extracted using QIAGEN DNeasy
126 Blood & Tissue Kits at IISER Mohali, and sequencing was outsourced to 1st BASE DNA Sequencing
127 Services (Base Asia).

128 Primers and annealing temperatures for each DNA marker are given in Table 2. Sequences were
129 cleaned and checked for sequencing errors in Sequencher v.4.9 (Gene Codes Co.) and BioEdit
130 v.7.0.5.3 (Hall, 1999), then blasted with NCBI blast tools, and submitted to GenBank (Table 1). The
131 *CO1* sequences of *X. marmoratus* specimens were discarded because of the suspicion of pseudogenes.
132 The sequences were aligned with MAFFT version 7 online (Kuraku et al., 2013; Katoh et al., 2017).
133 The complete combined dataset consists of 3,684 aligned base pairs (bp) for a total of 35 terminals
134 available as supplementary material S1: 416 bp for *12S*, 521 bp for *16S*, 707 bp for *CO1*, 335 bp for
135 *CO2*, 346 bp for *Cytb*, 328 bp for *H3*, 652 bp for *18S* and 379 bp for *28S*.

136

137 2.4. Phylogenetic analyses

138 Preliminary phylogenetic analyses were carried out for each DNA marker to check for possible
139 contaminations and artifacts, using the IQ-TREE web server (<http://iqtree.cibiv.univie.ac.at/>;
140 Trifinopoulos et al., 2016). The aligned sequences of all eight markers were further concatenated in
141 Geneious R9.0.2 (Biomatter Ltd., New Zealand, www.geneious.com, Kearse et al., 2012).

142 The concatenated dataset was analyzed using Bayesian inference (BI) and maximum likelihood
143 (ML). For both BI and ML, PartitionFinder V2.1.1 (Lanfear et al., 2017) was used to determine the
144 best-fit partitioning schemes and the associated substitution models. One partition was specified for
145 each of the non-protein-coding genes (*12S*, *16S*, *18S* and *28S*) and one partition per codon for the
146 protein-coding genes (*CO1*, *CO2*, *Cytb* and *H3*). PartitionFinder analyses were carried out using the
147 default ‘greedy’ algorithm option and either the ‘*mrBayes*’ or ‘*raxml*’ set of models (for BI and ML
148 analyses, respectively). The Bayesian information criterion (BIC) was preferentially used to compare
149 partitioning schemes and substitution models following Ripplinger and Sullivan (2008).

150 Bayesian inference analyses were performed using MrBayes 3.2.6 (Ronquist et al., 2012) and
151 ML analyses using IQ-TREE 1.6.2 (Nguyen et al., 2015). All corresponding analyses were performed
152 on the CIPRES Science Gateway 3.3 (Miller et al., 2015) web portal.

153 For ML analyses, best-scoring trees were obtained using heuristic searches relying on 100
154 random-addition replicates. Clade support was assessed using non-parametric bootstrap; for each
155 analysis 1,000 bootstrap replicates were conducted. Nodes supported by bootstrap support values (BS)
156 $\geq 70\%$ were considered strongly supported following Hillis and Bull (1993).

157 For BI analyses we conducted two independent runs with eight Markov chain Monte Carlo
158 (MCMC): one cold and seven incrementally heated that ran for 50 million generations with trees
159 sampled every 1,000 generations. We used a conservative burn-in of 12.5 million generations per run
160 after checking for stability on the log-likelihood curves and the split-frequencies of the runs in Tracer
161 v.1.7 (Rambaut et al., 2014). Support of nodes for MrBayes analyses was provided by clade posterior

162 probabilities (PP) as directly estimated from the majority-rule consensus topology. A clade with a PP
163 value higher than 0.95 was considered as well supported following Erixon et al. (2003).

164

165 3. RESULTS

166 3.1. Phylogenetic results

167 The complete DNA sequence matrix comprises 3,684 base pairs sampled for 35 terminals (Table 1 and
168 Supporting information S1). The separate ML analyses of each DNA marker show no major conflict in
169 topology (see Supporting information S2).

170 The best-fit partition schemes and substitution models used in BI and ML analyses of the
171 combined datasets are showed in Supporting information (S3). Both BI and ML phylogenetic analyses
172 yielded robust and largely congruent topologies (Fig. 7, see also Supporting information S4 for
173 original outputs of both BI and ML analyses).

174 In both analyses, the subfamily Eneopterinae and the tribe Xenogryllini are recovered as
175 monophyletic with high support values (PP of 1.0 and BS of 100% for Eneopterinae, and PP of 1.0 and
176 BS of 99% for Xenogryllini). The sister relationship between tribes Lebinthini and Xenogryllini is
177 strongly supported by the ML analysis (BS of 93%), but not by the BI analysis, where the tribe
178 Lebinthini is paraphyletic, with the Xenogryllini being sister of the main clade of the Lebinthini with
179 low PP value (0.68).

180 Within the tribe Xenogryllini, all species are recovered as monophyletic. In both analyses,
181 *Xenogryllus* is recovered as sister of *Indigryllus* (BS of 100% and PP of 1.0), and this clade is sister to
182 *Pseudolebinthus* (BS of 99% and PP of 1.0). Within *Xenogryllus*, the species *X. mozambicus* and *X.*
183 *eneopteroides* from Africa form a well-supported clade in both BI and ML analyses (PP of 1.0 and BS
184 of 100%); they form the sister group of a clade including the remaining species distributed in Asia. In
185 the latter clade, except for well-defined position of *X. marmoratus* (BS of 80% and PP of 1.0) as sister
186 to the other species, the positions of *X. transversus*, *X. maichauensis* and *X. ululiu* are not well-
187 supported: In BI analysis, *X. transversus* is found as the sister species of the clade (*X. ululiu* – *X.*

188 *maichauensis*), while the ML analysis finds *X. maichauensis* as the sister species of (*X. transversus* –
189 *X. uluii*).

190
191 **3.2. Systematics**

192
193 **3.2.1. Key to Xenogryllini genera modified from Robillard (2006)**

194 1. TII with two inner apical spurs. FWs and hind wings of similar dimensions in male and female
195 (Fig.1). Male. Forewing venation (Fig. 3A-B): left and right forewings similar in sclerotization and
196 colouration; harp oblique veins not swollen, with an incomplete oblique between diagonal and first
197 complete oblique; harp distal angle concave; FWs cells with thin longitudinal wrinkles on surface.

198 *Male genitalia*: pseudepiphallic sclerite longer than rami (Fig. 4); basis of pseudepiphallus sclerotized
199 (Fig. 4A); ectophallic arc not sclerotized; ectophallic fold entirely sclerotized; lateral arms of
200 endophallic sclerite very long (Fig. 4B); endophallic crest absent. Female. FWs and hind wings as long
201 as in male. Ovipositor apex well differentiated, rounded (Fig. 6A-
202 B)..... 2.

203 – TII with one inner apical spur. Male with longer FWs than female, hind wings absent in both sexes.
204 Male. Forewing venation: left FW less sclerotized than right FW; harp with swollen oblique veins,
205 without an incomplete vein between diagonal and first harp vein; harp distal angle flat; FW cells
206 without longitudinal wrinkles. *Male genitalia* (Fig. 5D): pseudepiphallic sclerite shorter than rami,
207 basis of pseudepiphallus membranous; ectophallic arc slightly sclerotized; ectophallic fold partly
208 sclerotized; lateral arms of endophallic sclerite short; endophallic crest absent. Female. FWs very
209 short, not reaching second abdominal tergite; hind wings vestigial. Ovipositor apex little
210 differentiated, pointed..... *Pseudolebinthus*

211 Robillard, 2006

212

213 2. Eyes small and located on face (Fig. 2D-F). FIII narrow along its whole length. FWs as long or
214 slightly longer than abdomen in both sexes. Hind wings longer than FWs, forming a tail posterior to
215 FWs. Male. *Male genitalia*: Pseudepiphallic parameres with one strong rectangular ventral lobe
216 covered with scale-like sculptures (Fig. 5B-C). Female. Apex of ovipositor spatula-shaped (Fig.
217 6B)..... *Xenogryllus* Bolívar,
218 1890

219 – Eyes larger and lateral (Fig. 2A-C). FIII wide basally, muscular. FWs reaching abdomen mid-length,
220 hind wings vestigial. Male. *Male genitalia*: Pseudepiphallic parameres with two short claw-shaped
221 sclerotized lobes ventrally (Fig. 4D). Female. Apex of ovipositor triangular (Fig.
222 6A).....*Indigryllus* Robillard & Jaiswara gen. nov.

223

224 3.2.2. *Indigryllus* Robillard & Jaiswara gen. nov.

225

226 **Type species.**

227 *Indigryllus kudremu* Robillard & Jaiswara sp. nov.

228

229 **Etymology**

230 The genus name is derived from India and the suffix *-gryllus* in reference to the name *Xenogryllus*.

231

232 **Diagnosis**

233 *Indigryllus* presents all the characteristics of *Xenogryllini*, but majorly shares a combination of
234 morphological features of *Xenogryllus* and *Pseudolebinthus* (Fig. 1A-D). The new genus resembles
235 *Pseudolebinthus* by shape of head and eyes, brachypterous wings barely reaching abdomen mid-length
236 in males, shorter in females (but longer in *Indigryllus* than in females of *Pseudolebinthus*), muscular
237 FIII (thinner in *Xenogryllus*), and long, rather slender abdomen. *Indigryllus* is however more similar to

238 *Xenogryllus* in terms of size, homogeneous light brown colouration, male FWs symmetry, without
239 swellings of harp veins as in *Pseudolebinthus*, and male genitalia with long sclerotized
240 pseudepiphallid lophi (Fig. 5A).

241

242 **Description**

243 Size average for the tribe. Head shape (Fig. 2A-C) close to that of *Pseudolebinthus* and tribe
244 Lebinthini, with eyes larger and more protruding than in *Xenogryllus*. In dorsal view (Fig. 2A), eyes
245 combined width represents ca. 45% of head width, as for example in *Macrobenthus* Robillard & Dong,
246 2016. Head slightly higher than wide in facial view (Fig. 2B); face with a whitish mask with black
247 spots as in *Xenogryllus*, underlined laterally with a dark line prolonged on eyes; flat in lateral view
248 (Fig. 2C). Fastigium twice as wide as scape, almost square, slightly divergent apically, not
249 discontinuous from vertex nor furrowed longitudinally; fastigium twice as wide as scape, with many
250 setae up to median ocellus. Ocelli flat, arranged in a wide triangle; lateral ocelli almost circular,
251 located at basis of fastigium; median ocellus ellipsoidal, subapical in location. Scape small. Antennae
252 thin. Maxillary palpi long, their 5th joint as long as 3rd and slightly widened apically. Pronotum dorsal
253 disc slightly wider than long, posterior margin straight; lateral margins not carinated. TI with two
254 tympana; inner tympanum covered by a sclerotized expansion, its membrane visible along a small
255 longitudinal slit only; outer tympanum oval in shape, its surface smooth. TI with two inner and two
256 outer apical spurs. TII with two inner spurs of equal lengths, and two outer spurs, the dorsal the
257 longest. FIII apex filiform, their bases muscular, wider than in *Xenogryllus*. TIII serrulated over their
258 whole length, slightly furrowed dorsally, with four pairs of subapical spurs and three pairs of apical
259 spurs; inner and outer spurs (both subapical and apical) of almost similar size, straight and slightly
260 curved apically. Abdomen long and slender, conical.

261 *Male*. Metanotal glandular structures well developed, similar to that of *Xenogryllus*, with a large
262 median process on scutum, scutellum raised medially and carrying a bunch of setae oriented
263 anteriorly. Posterior part of mesonotum setose and extended posteriorly, covering metanotal scutum.
264 Hind wings shorter than the FWs. FWs short (Fig. 3A-B), reaching two thirds of abdomen length,

265 symmetrical, not widened as in *Xenogryllus*. FW cells with longitudinal wrinkles as in *Xenogryllus*.
266 FWs light brown, translucent, with the following pattern of black spots on dorsal field: wide black
267 transverse band anterior to transverse part of 1A, black marking in cell c1 and in anterior and external
268 corners or mirror. Harp wide, oblique veins as in *Xenogryllus*, with two complete bisinuate veins and
269 one incomplete vein posteriorly. Mirror large and rounded, as in *Xenogryllus*, crossed at mid-length by
270 a complete accessory vein. Cell d2 widened. Apical field short, including four narrow cell alignments.
271 Lateral field crossed by numerous projections of Sc along its whole length, as in *Xenogryllus*.
272 Subgenital plate clog-shaped, its apex slightly indented.

273 *Male genitalia* (Fig. 4A-D). Close to *Xenogryllus*, with long sclerotized pseudepiphallic lophi (Fig.
274 5A), their apex with a short inner hook-shaped dorsal expansion. Membrane at anterior basis of
275 pseudepiphallus slightly sclerotized, as in *Xenogryllus*; anterior margin of pseudepiphallus
276 strengthened by a ventral sclerotization. Rami rather short and strong, their apex slightly convergent.
277 Pseudepiphallic parameres strong, with a strong dorsal lobe and two ventral lobes clearly
278 individualised (Fig. 4D); surface of parameres thinly denticulate. Ectophallic fold homogeneously
279 sclerotized. Ectophallic arc not sclerotized, as in *Xenogryllus*; ectophallic apodemes long, lamellate
280 apically; their basis with strong ventral arms. Endophallic sclerite forming a wide flat plate rounded
281 anteriorly, with long thin lateral arms oriented posteriorly and a long medio-posterior expansion fused
282 with ectophallic fold. Endophallic apodeme with a thin dorsal median crest and narrow lateral
283 lamellas.

284 *Female*. FWs shorter than in males (Fig. 3C), not reaching abdomen mid-length; colouration pale
285 brown; dorsal field with six strong longitudinal veins; lateral field triangular; M vein faint; R/Sc area
286 wide, brown with faint transverse veins; Sc with two projections. Subgenital plate slightly indented
287 apically (Fig. 6C). Apex of ovipositor rounded and smooth, more pointed than in *Xenogryllus* (Fig.
288 6A).

289 *Female genitalia*. Copulatory papilla (Fig. 6E-G) more elaborate than in *Xenogryllus*, with a wide
290 cylindrical basal part sclerotized ventrally, and a narrowed cylindrical apical membranous part, thinly
291 plicate and slightly folded ventrally.

292

293 **3.2.3. *Indigryllus kudremu* Robillard & Jaiswara sp. nov.**

294 (Figs 1A-D; 2A-C; 3B-C; 4A-D; 5A; 6A, C, E-G; 7)
295

296 *Xenogryllus* n. sp. – Robillard & Desutter-Grandcolas, 2004a: 579; 2004b: 275 (morphological
297 phylogeny); 2006: 644.

298 *Xenogryllus* sp. – Nattier et al., 2011: 2201 (molecular phylogeny); Vicente et al., 2017: 2203
299 (historical biogeography).

300

301 **Type material**

302 *Holotype*, ♂, **India**: Kudremukh, 29.V.2007 KWC-93-00.229, identified *Xenogryllus marmoratus* S.

303 Rawat & R. Balakrishnan (ZSI). *Allotype*, ♀, **India**: Same locality, date and collector as HT, KCW-

304 92-00.228, identified *Xenogryllus* sp. by R. Balakrishnan, lab code for molecular sample X3Xsp2

305 (ZSI). *Paratype* (1 ♂), **India**: same locality, date and collector as HT, NCW-0230, identified

306 *Xenogryllus carmichaeli*? by R. Balakrishnan, identified *Xenogryllus* sp. by T. Robillard, MEB cerque

307 g., lab code for molecular sample Xsp (MNHN-EO-ENSIF2738).

308

309 **Type locality**

310 India, Karnataka, Chikkamagaluru district, Kudremukh.

311

312 **Etymology**

313 The species is named after the type locality.

314

315 **Diagnosis**

316 *Indigryllus kudremu* sp. nov. is recognized by its light colouration, brachypterous wings in both sexes,
317 long abdomen, and male genitalia with pseudepiphallic lophi forming two blades partly fused basally
318 (Fig. 5A), close to that of *X. marmoratus*, converging basally, their apex diverging, with a short hook-
319 shaped dorsal expansion.

320

321 **Description**

322 In addition to the characters of the genus, colouration mostly ochre (Fig. 1A-D); vertex with four faint
323 longitudinal brown bands and two triangular lines posterior to eyes (Fig. 2A). Scapes with dark brown
324 patterns; antennae uniformly yellow brown, except first article dark brown. Pronotum dorsal disc light
325 brown, mottled with orange brown; pronotum lateral lobes almost homogeneously golden brown with
326 black dots, dorsal margin underlined with dark brown; anterior ventral corner with a yellow spot;
327 posterior margin mottled with yellow and dark brown. FI-II yellow brown mottled with dark brown;
328 TI-II and Ta-I-II yellow dark brown apically. FIII almost homogeneously orange brown. Abdomen
329 light brown mottled with black, whitish ventrally. Cerci long, their inner face dark, rest light brown.

330 *Male*. FWs mostly light brown (Fig. 3B), veins light brown or yellow; anterior dark brown colouration
331 on dorsal field including whole width of 1A. Apical field with yellow brown longitudinal veins and
332 strong dark brown transverse veins. Lateral field with 12-14 (n = 2) projections of Sc and 3-6 more
333 ventral veins.

334 *Male genitalia* (Fig. 4A-D). Pseudepiphallic lophi long (Fig. 5A), setose, curved dorsally in lateral
335 view, forming two blades partly fused basally, converging at mid-length then diverging apically; apex
336 of lophi with short inner hook-shaped dorsal expansions.

337 *Female*. Ovipositor short, about half of FIII length.

338 *Calling song*. Unknown.

339 *Measurements*. See Table 3.

340

341 **Distribution and natural history**

342 The type locality is in the west of the Western Ghats, one of the evergreen forests in India. Since the
343 species was never found again in the same or close-by areas therefore, we hypothesize that the type
344 locality does not correspond to the natural habitat of the species.

345 The type specimens were found in a backyard garden that had diverse plantation, but was
346 dominated by areca nuts. The garden was least managed and had pineapple, hibiscus, paper mulberry
347 and other shrubs. The specimens were collected during the monsoon season when the average
348 temperature ranges between 25 to 37°C and average humidity is *ca.* 77%.

349

350 **4. DISCUSSION**

351

352 **4.1. Diversity and distribution of the Xenogryllini**

353 The taxonomic revision of the Xenogryllini achieved in Jaiswara et al. (2018, 2019) and completed
354 here by the description of the new genus *Indigryllus*, was based on the thorough study of specimens
355 from natural history collections belonging to 17 institutions and on field work in Mozambique, China
356 and India. These studies reveal that the Xenogryllini tribe is relatively less diversified compared to the
357 other tribes of the subfamily Eneopterinae, and more specifically to its sister tribe, the Lebinthini. The
358 taxonomic revisions clarified the status of all previously described species and subspecies and added
359 five new species to the Xenogryllini: three to *Xenogryllus* (Jaiswara et al., 2019), one to
360 *Pseudolebinthus* (Jaiswara et al., 2018), and the new genus *Indigryllus* with one new species from
361 Southern India. The combination of these three studies allows drawing a map of distribution for all the
362 species of the Xenogryllini (Figure 8).

363 The discovery of *Indigryllus* is particularly relevant to improve the knowledge of eneopterines.
364 First, it is the first record of Eneopterinae in the southern half of India. Until now, eneopterines were
365 represented in the region only by some populations of *X. transversus* distributed in Northern and
366 Eastern India and in Pakistan (Bhowmik, 1976, 1985; Saeed et al., 1990). Second, *Indigryllus* shows

367 original combination of characters from the other two genera of the tribe: it is brachypterous with long
368 abdomen and large eyes as *Pseudolebinthus*, while its male genitalia and FW venation are clearly
369 more similar to that of *Xenogryllus*. As mentioned in the taxonomic part, *I. kudremu* sp. nov. is
370 documented by three specimens only, collected once, and the type locality belongs to the west of the
371 Western Ghats, one of the evergreen forests in India. Since the species was never found again in the
372 same area, we hypothesize that its type locality may not correspond to the natural habitat of the
373 species. The Western Ghats is one of the biodiversity centres in India; therefore, it has been a focus
374 region for numerous recent faunal discoveries in diverse groups such as frogs, birds, shield tail snakes
375 and lizards (e.g., Kuramoto & Joshy, 2003; Giri et al., 2004; Biju & Bossuyt, 2005, 2009; Biju et al.,
376 2009; Robin et al., 2017; Jins et al., 2018; Sadasivan et al., 2018; Raj et al., 2018; Agarwal *et al.*,
377 2018). In the last two decades, only a handful of new cricket species belonging to Gryllidae,
378 Phalangopsidae and Pteroplistinae have been described (Gorochoy, 2002, 2003, 2009, 2018; Desutter-
379 Grandcolas & Jaiswara, 2012; Jaiswara & Desutter-Grandcolas, 2014). Present discovery of
380 *Indigryllus* suggests that the region of the Western Ghats may still keep some undescribed lineages of
381 crickets.

382

383 **4.2. Phylogenetic relationships and biogeographical patterns**

384 The molecular phylogenetic analysis confirms the monophyly of the tribe Xenogryllini with a high
385 support, and its sister relationship with the Lebinthini tribe. These results are consistent with the
386 previous phylogenetic analyses based on a lower Xenogryllini sampling with morphological
387 (Robillard & Desutter-Grandcolas, 2004a; Robillard, 2006) and DNA sequence data (Nattier et al.,
388 2011; Vicente et al., 2017). The paraphyly of the Lebinthini found in the BI analysis is probably due to
389 low taxonomic sampling of this tribe in our study, since the Lebinthini are clearly monophyletic and
390 distinct from the Xenogryllini in all previous phylogenetic studies, as recovered by our ML analysis.

391 Within Xenogryllini, the new Indian genus *Indigryllus* is the sister group of *Xenogryllus*, which
392 is distributed in Asia and Africa. The clade that they form together is sister to *Pseudolebinthus*, which
393 is endemic to Southeast Africa. This pattern suggests a complex biogeographical history, which was

394 partly addressed, but shortly discussed, in the study of Vicente et al. (2017). The study included
395 representatives from the three Xenogryllini genera (*Indigryllus kudremu* was identified as
396 “*Xenogryllus* sp.” and *Peudolebinthus gorochovi* as “*Pseudolebinthus* sp.”). The study also dated the
397 stem group of the Xenogryllini, revealing the split between Xenogryllini and Lebinthini *ca.* 59.64 Ma,
398 and the Xenogryllini crown group *ca.* 52.35 Ma. The results of the ancestral area reconstructions
399 suggested an origin of Xenogryllini both in Asia and India (DEC results), suggesting that Africa was
400 colonized twice independently by the Xenogryllini after 50 Ma: once by *Pseudolebinthus* and once by
401 *Xenogryllus eneopteroides*, which was the only species of the genus distributed in Africa at the time of
402 this study. The new lineages of Xenogryllini recently described, including three new species of
403 *Xenogryllus* from Africa and the additional information concerning the geographical distribution of the
404 tribe, question these conclusions. In particular, among the new species of *Xenogryllus*, *X. lamottei*
405 Robillard, 2018, more resembles morphologically the species distributed in Asia (no lateral carinae
406 on pronotum, shape of pseudepiphallic lophi of male genitalia). It suggests an alternative
407 biogeographic scenario, involving an early colonization of Africa by the Xenogryllini and a later
408 independent recolonization event of India and of continental Southeast Asia by *Indigryllus* and by a
409 clade of *Xenogryllus*. Since several new species including *X. lamottei* could not be included in our
410 phylogenetic study, the biogeographic hypothesis could not be tested. The biogeographic history of the
411 Xenogryllini will have to be revisited by considering these new data into account in order to address
412 specifically the routes and timing of colonization between Asia and Africa.

413

414 **4.3. Comparison between tribes Xenogryllini and Lebinthini**

415 The recent systematic revision of the Xenogryllini (Jaiswara et al., 2018 & 2019) highlights several
416 interesting contrasts between the Xenogryllini and its sister tribe, the Lebinthini, in terms of species
417 diversity, distribution patterns and signals of communication.

418 As hypothesised by Robillard & Desutter-Grandcolas (2004a), there is a taxonomic imbalance
419 between the two tribes. The species ratio Lebinthini / Xenogryllini was 34/7 in 2004, but the recent
420 taxonomic discoveries in both clades changed drastically this ratio: with a similar taxonomic

421 treatment, the Xenogryllini now includes a total of 12 species under 3 genera, whereas the Lebinthini
422 include *ca.* 150 species under 12 genera (*e.g.*, Robillard et al., 2014; Vicente et al., 2015; Anso et al.,
423 2016; Robillard et al., 2016; Robillard & Su, 2018), and many Lebinthini taxa yet remain undescribed
424 (T. Robillard, pers. obs.). This contrast is corroborating the hypothesis that the Lebinthini were likely
425 subject to a taxonomic radiation, possibly in relation with their innovations in terms of communication
426 system (Robillard et al., 2007).

427 Xenogryllini and Lebinthini are also contrasted in terms of distribution patterns. The
428 Xenogryllini are mostly distributed in continental regions, except for *X. marmoratus* which is found
429 both in continental Asia (China, South Korea) and in islands of Japan, China (Taiwan, Hainan) and Sri
430 Lanka (Fig. 8). In contrast, the Lebinthini fully express their species diversity when they are
431 distributed in islands (*e.g.*, Desutter-Grandcolas & Robillard, 2006; Nattier et al., 2012; Dong et al.,
432 2018). As a consequence, the two tribes only barely overlap in their marginal distributions in coastal
433 regions of China and Japan, where a few Lebinthini occur in sympatry with *X. marmoratus*. In
434 association with this difference of tribe distribution, the species of the tribes differ by their range sizes:
435 the Xenogryllini species, and in particular that of *Xenogryllus*, show relatively large distribution areas.
436 This feature may be due to their continental distribution and the fact that they live in open habitats. In
437 contrast, very high rates of speciation have been demonstrated in crickets distributed on islands
438 (Mendelson & Shaw, 2005). The Lebinthini species living on islands are most often found in forested
439 areas; they also usually have more restricted distributions, which could in turn promote higher rates of
440 speciation (Dong et al., 2018). These differences could partly explain the imbalance of diversity
441 observed between the two tribes. However, exceptions exist, as for example the Lebinthini species
442 *Cardiodactylus novaeguineae* (Haan, 1842), which lives in open coastal areas and shows a very large
443 distribution across the Western Pacific (Robillard & Ichikawa, 2009).

444 The last factor distinguishing Xenogryllini and Lebinthini are their modalities of
445 communication, which are understudied in the Xenogryllini. The calling songs of five *Xenogryllus*
446 species were recently formally described (Jaiswara et al., 2019), but that of *Indigryllus* and
447 *Pseudolebinthus* species remain unknown. It would thus be erroneous to pretend that the Xenogryllini

448 are characterized by calling songs made of long syllables with relatively low frequencies, since these
449 features are probably linked with the peculiar morphology of the males of *Xenogryllus*, which present
450 widened FWs and long stridulatory files carrying a high number of teeth, two characteristics favoring
451 the production of long syllables and low frequencies. The two other *Xenogryllini* genera,
452 *Pseudolebinthus* and *Indigryllus*, were never acoustically recorded, and although very particular in
453 their own ways, they do not share these morphological features of *Xenogryllus*. It is thus impossible
454 yet to predict the features of their calling songs, except that they are probably different from that of
455 *Xenogryllus*. Comparatively, the songs of the Lebinthini are generally characterised by shorter
456 syllables and high dominant frequencies. These acoustic features participate to a new system of
457 communication which was recently described, involving absence of female phonotaxis and female
458 vibratory response to male calls (ter Hofstede et al., 2015). These differences, and in particular the
459 innovations allowing the Lebinthini to use new communication resources as key innovations in a
460 context of adaptive radiation, has been proposed as a possible explanation for the imbalance of
461 diversity observed between the two tribes (Robillard & Desutter-Grandcolas, 2004a). Now that both
462 tribes were subject to comparable taxonomic revisions, the hypothesis of adaptive radiation will have
463 to be formally tested in future studies by estimating rates of speciation, extinction and adaptive
464 phenotypic evolution using comparative phylogenetic methods (*e.g.*, Herrera, 2017).

465

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495

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726 **Tables**

727 **Table 1.** Taxon and gene sampling. List of all Eneopterinae crickets and outgroups used in this study with current geographical distribution and GenBank
 728 accession numbers. NA means missing data. Abbreviation of museums: IISERM- Indian Institute of Science Education and Research Mohali, Punjab, India;
 729 MNHN-Muséum national d'Histoire naturelle, Paris, France; ZFMK- Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany; ZIN-
 730 Zoological Institute, Russian Academy of Sciences, S. Petersburg, Russia and ZSI- Zoological Survey of India, Kolkata, India.

Species	Voucher / Lab code (type status)	16S	12S	COI	COII	Cytb	18S	28S	H3
<i>Acheta domesticus</i> (Linnaeus, 1758)	MNHN-EO-ENSIF3523 / Adom	AF248698	ADZ97611	JX897403	JX897439	AF248682	AD18SITS1	JX897465	KR903150
<i>Agnotecous meridionalis</i> Desutter-Grandcolas, 2006	MNHN-ENSIF-2772 / AmelP	JX897349	JX897401	JX897420	NA	JX897311	JX897579	JX897488	JX897553
<i>Agnotecous meridionalis</i> Desutter-Grandcolas, 2006	MNHN-EO-ENSIF-2771 / AmePB	JX897350	JX897402	JX897410	JX897442	JX897313	JX897597	JX897489	JX897550
<i>Cardiodactylus novaeguineae</i> (Haan, 1844)	MNHN-ENSIF2038 / C3CnoNC	JF972520	JF972504	MH662977	MH662880	JF972488	JF972535	MH663420	NA
<i>Cardiodactylus novaeguineae</i> (Haan, 1844)	MNHN-EO-ENSIF2030 / C2CnoPe	JF972521	JF972506	KU705563	KU705551	JF972490	JF972537	KR903500	KR903151
<i>Eneoptera guyanensis</i> Chopard, 1931	MNHN-EO-ENSIF2741 / Egu	AY905301	AY905272	JX897404	KU705553	AY905355	AY905331	KU705581	JX897547
Eurepini sp.	MNHN-EO-ENSIF3155 / Eursp	KR903674	KR903834	KU705565	KU705554	KR903331	KR904028	KR903503	KR903153
<i>Gryllus bimaculatus</i> De Geer, 1773	MNHN-EO-ENSIF3524/3404 / Gbi	AF248685	AY905292	NA	KU705555	AF248659	AF514509	KR903002	KR903154
<i>Indigryllus kudremu</i> sp.nov.	ZSI / X3Xsp2 (AT)	KY595509	KY595483	KY646248	MK761340	AY905377	AY905345	KY605247	KY646293
<i>Lebinthus bitaeniatus</i> Stål, 1877	MNHN-EO-ENSIF4393 / L18LbiP1	MK761250	MK761274	MK761331	MK761341	MK761353	MK761293	MK761313	MK761370
<i>Lebinthus bitaeniatus</i> Stål, 1877	MNHN-EO-ENSIF4394 / L28LbiP2	MK761252	MK761275	MK761332	NA	MK761354	MK761294	MK761314	MK761371
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN-EO-ENSIF2740 / L8LbiS1 (PT)	JF972524	KR904017	KU705567	KU705557	JF972493	KR904199	KR903665	KR903321
<i>Lebinthus luae</i> Robillard & Tan, 2013	MNHN / L10LbiS3	MK761253	MK761276	MK761333	MK761342	MK761355	MK761295	MK761315	MK761372
<i>Microbinthus santoensis</i> Robillard, 2009	MNHN-EO-ENSIF2484 / L7LsaPe	KU705528	KU708011	KU705569	NA	KU705535	KU705543	KU705585	KU705601
<i>Microbinthus santoensis</i> Robillard, 2009	MNHN-EO-ENSIF2437 / LsaV (PT)	JF972527	JF972511	JX897405	JX897441	JF972495	JF972542	JX897467	JX897548
<i>Nisitrus vittatus</i> (Haan, 1842)	MNHN-EO-ENSIF2742 / NviS	MH575026	MH575158	KU705572	NA	MH662741	AY905340	KR903667	JX897546
<i>Pseudolebinthus gorochovi</i> Robillard, 2018	ZIN / X17PsMal1 (HT)	KY595508	KY595472	KY646231	NA	NA	KY595511	KY605231	MK761373
<i>Xenogryllus eneopteroides</i> Bolívar, 1890	MNHN-EO-ENSIF3159 / XenAC	KR903829	KR904023	KY646249	NA	KR903490	KR904205	KR903670	KR903328
<i>Xenogryllus eneopteroides</i> Bolívar, 1890	MNHN-EO-ENSIF3442 / XenCI	MK761256	MK761279	NA	NA	NA	MK761298	NA	MK761375
<i>Xenogryllus eneopteroides</i> Bolívar, 1890	MNHN-EO-ENSIF3442 / XenGA	MK761257	MK761280	NA	NA	NA	MK761299	MK761318	MK761376
<i>Xenogryllus maichauensis</i> Gorochov, 1992	ZFMK / XtrTh	MK761258	NA	NA	NA	MK761357	NA	NA	MK761377
<i>Xenogryllus marmoratus</i> (Haan, 1844)	MNHN-EO-ENSIF3161 / Xma2	KR903830	KR904024	NA	MK761343	KR903491	KR904206	NA	KR903329
<i>Xenogryllus marmoratus</i> (Haan, 1844)	MNHN-EO-ENSIF1599 / XmaCh1	KY595510	KY595484	NA	MK761344	KY646274	KY595518	KY605248	KY646292
<i>Xenogryllus marmoratus</i> (Haan, 1844)	MNHN-EO-ENSIF1594 / XmaCh2	MK761261	MK761283	NA	MK761345	MK761360	MK761302	MK761320	MK761379
<i>Xenogryllus marmoratus</i> (Haan, 1844)	MNHN-EO-ENSIF3562 / XmaCh3	MK761262	MK761284	NA	MK761346	MK761361	MK761303	MK761321	MK761380
<i>Xenogryllus mozambicus</i> Robillard, 2019	MNHN-EO-ENSIF1515 / XenMoz (PT)	MK761263	MK761285	MK761336	NA	MK761362	MK761304	NA	MK761381
<i>Xenogryllus transversus</i> (Walker, 1869)	IISERM / Xtr715	MK761264	MK761286	NA	NA	MK761363	MK761305	MK761322	MK761382

<i>Xenogryllus transversus</i> (Walker, 1869)	IISERM / Xtr765	MK761265	NA	MK761337	NA	MK761364	MK761306	MK761323	MK761383
<i>Xenogryllus transversus</i> (Walker, 1869)	IISERM / Xtr766	MK761266	NA	NA	NA	MK761365	NA	MK761324	MK761384
<i>Xenogryllus transversus</i> (Walker, 1869)	MNHN-EO-ENSIF87 / XtrIn	JF972530	NA	KY646247	MK761347	JF972499	KY595519	KY605246	KY646294
<i>Xenogryllus ululiu</i> Gorochov, 1990	ZIN / X18XulV2	MK761268	MK761287	NA	MK761348	NA	MK761308	MK761326	MK761386
<i>Xenogryllus ululiu</i> Gorochov, 1990	ZIN / X19XulSi	MK761269	MK761288	NA	MK761349	MK761367	MK761309	MK761327	MK761387
<i>Xenogryllus ululiu</i> Gorochov, 1990	MNHN-EO-ENSIF4385 / X20XulCam1	MK761270	MK761289	NA	MK761350	NA	MK761310	MK761328	MK761388
<i>Xenogryllus ululiu</i> Gorochov, 1990	ZIN / X21XulCam2	MK761271	MK761290	NA	MK761351	NA	MK761311	MK761329	MK761389
<i>Xenogryllus ululiu</i> Gorochov, 1990	ZFMK / Xulth	MK761272	MK761291	MK761339	NA	MK761368	NA	NA	NA

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735 **Table 2.** Characteristics of the eight DNA markers and primers used in this study and in the
736 phylogenetic analyses.
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	Gene	Primer name	Sequencing primers (5' - 3')	Reference	Annealing temperature	Amplicon size
Mitochondrial	CO1	L2	GCAACGATGATTATTTTCCACT	Nattier et al. (2012), modified from Folmer et al. (1994)	48-50°C	~750 bp
		H2	CCTGGTAAAATTAGAATGTAAACTTCTG			
	CO2	co2a	GGTCAAACAATTGAGTCTATTTGAAC	Shapiro et al. (2006)	55°C	~400 bp
		co2e	CCACAAATTTCTGAACATTGACCA			
		RNa	TACWMAYCGWTTYCTTYTTGAAGGWC	Nattier et al. (2012), modified from Contreras & Chapco (2006)	47°C	
	Cytb	Rne	CGACCTGGAGTTGCATCAG			
		427F	YTWGTWCAATGARTMTGAGG	Robillard & Desutter- Grandcolas (2006)	48°C	~400 bp
800R	CCYARTTTATTAGGAATTGATCG					
12S	F	TACTATGTTACGACTTAT	Kambhampati (1995)	48°C	~400 bp	
	R	AAACTAGGATTAGATACCC				
16S	AG	CGCCTGTTTATCAAAAACATGT	Robillard & Desutter- Grandcolas (2006)	55°C	~500 bp	
	BG	AGATCACGTAAGAATTTAATGGTC				
Nuclear	H3	HexAF	ATGGCTCGTACCAAGCAGACGGC	Maroja et al. (2009)	58°C	~330 bp
		HexAR	ATATCCTTGGGCATGATGGTGAC			
	28SA	C1'	ACCCGCTGAATTTAAGCAT	Jamieson et al. (2002)	55°C	~400 bp
		D2b	GTTAGACTCCTTGGTCCGT			
	18S	A2	ATGGTTGCAAAGCTGAAAC	Giribet et al. (1999)	52°C	~650 bp
9R		GATCCTTCCGCAGGTTACCTA	Giribet et al. (1996)			

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Table 3. Measurements of *Indigryllus kudremu* sp. nov.

	BL	PronL	PronW	FWL	FWW	FIII	FIIIW		
Holotype male	21.2	3.1	4.9	10.3	5.0	18.4	4.5		
Male paratype	22.3	2.9	4.8	10.7	5.0	18.6	4.9		
(Male mean)	(21.8)	(3)	(4.9)	(10.5)	(5.0)	(18.5)	(4.7)		
Female allotype	18.8	3.5	4.8	4.2	3.4	18.3	5.0		
	TIII	TIIIs				TaIIIs			OL
		Ias	Ibs	Oas	Obs	Ids	Ods	Ols	
Holotype male	17.9	9	11	12	10	0	3	3	-
Male paratype	18.5	10	7	18	10	0	4	3	-
(Male mean)	(18.2)	(10)	(9)	(15)	(10)	(0)	(4)	(3)	-
Female allotype	18.7	8	12	15	13	1	6	3	10.5

742 **Figure legends**

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744 **Figure 1.** *Indigryllus kudremu* sp. nov.: male in dorsal (A) and lateral (B) views, female in dorsal (C)
745 and lateral (D) views. Scale bar: 5 mm.

746 **Figure 2.** Head view: *Indigryllus kudremu* sp. nov. in dorsal (A), facial (B) and lateral views (C);
747 *Xenogryllus eneopteroides* in dorsal (D), facial (E) and lateral views (F). Scale bar: 1 mm.

748 **Figure 3.** *Indigryllus kudremu* sp. nov.: male forewing venation (A-B) and terminologies used in the
749 systematic part, female forewing venation (C). Scale bars: 1 mm.

750 **Figure 4.** *Indigryllus kudremu* sp. nov.: male genitalia in dorsal (A), ventral (B) and lateral (C) views,
751 detail of pseudepiphallic parameres in ventral view (D). Scale bar: 1 mm.

752 **Figure 5.** Right pseudepiphallic lophi of male genitalia in dorsal view: (A) *Indigryllus kudremu* sp.
753 nov.; (B) *Xenogryllus eneopteroides*; (C) *Xenogryllus transversus* and (D) *Pseudolebinthus*
754 *africanus*. Symbols: Preapical hook-like expansion figured in gray or with a black arrow;
755 dotted parts represent membranous areas; thin lines represent folds and reliefs in sclerites.
756 Scale bar: 1 mm.

757 **Figure 6.** Apex of female ovipositor: (A) *Indigryllus kudremu* sp. nov. and (B) *Xenogryllus*
758 *eneopteroides*. Apex of female subgenital plate and base of ovipositor in ventral view: (C)
759 *Indigryllus kudremu* sp. nov. and (D) *Xenogryllus eneopteroides*. Female copulatory papilla:
760 (E-G) *Indigryllus kudremu* sp. nov. and (H-I) *Xenogryllus eneopteroides*.

761 **Figure 7.** Bayesian Inference tree of Xenogryllini tribe based on the concatenated dataset of eight
762 genetic markers. ML bootstrap (BS) and Bayesian posterior probability (PP) support values
763 are indicated for each node on the right; clades not recovered by the BI analysis are indicated
764 by a symbol *. Clades corresponding to species are shaded with a colour scale. Represented
765 species (from top to bottom): *Agotecous sarramea*, *Lebinthus bitaeniatus*, *Xenogryllus*
766 *transversus*.

767 **Figure 8.** Distribution map of the species belonging to the Xenogryllini tribe. Each colour point
768 represents a collecting locality based on recent revision studies of *Xenogryllus* (Jaiswara et al.,
769 2019) and *Pseudolebinthus* (Jaiswara et al., 2018). Map designed using the software QGIS
770 (QGIS Development Team (2018).

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773 **List and legend of supporting information**

774

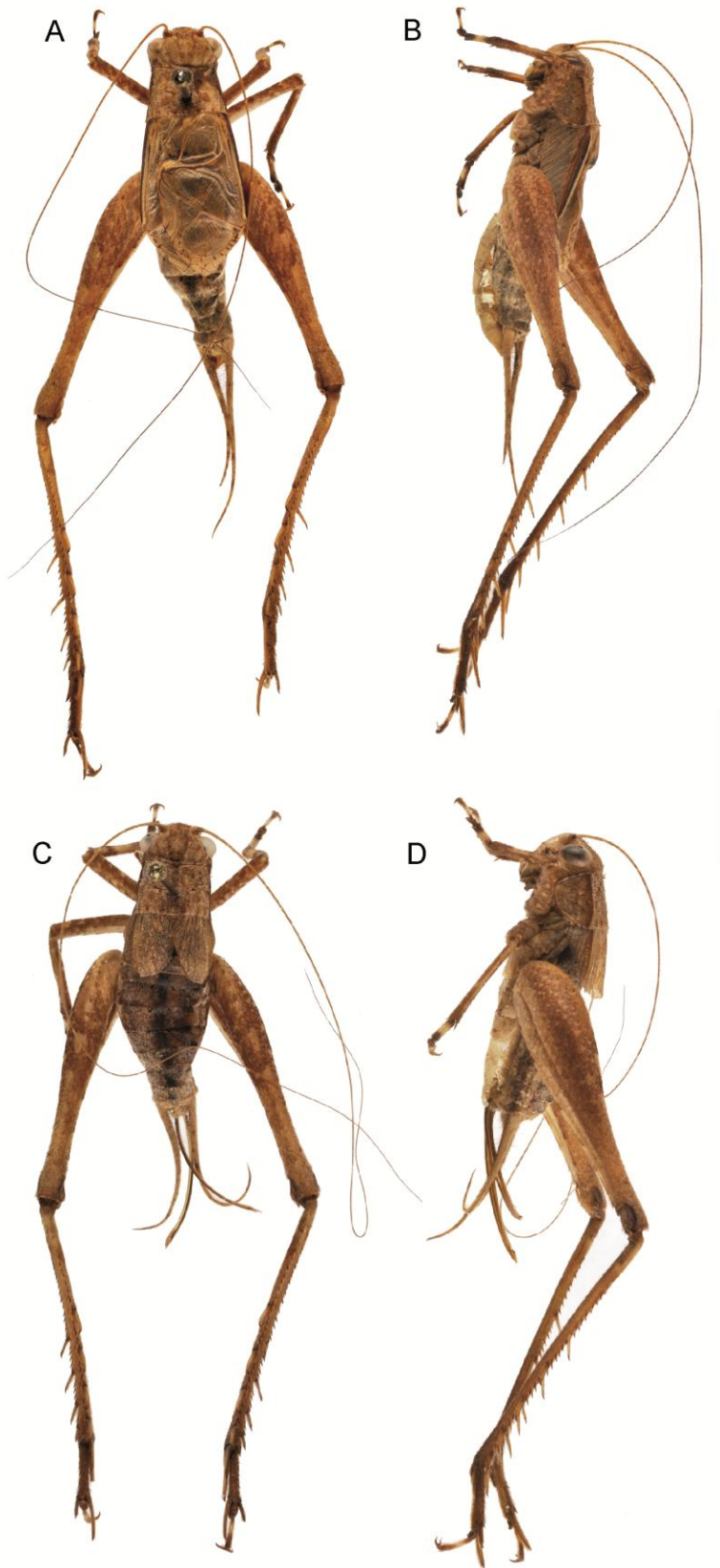
775 **S1.** Sequence alignment of the concatenated molecular genetic markers generated by Geneious.

776 **S2.** Results of preliminary maximum likelihood (ML) analyses for each genetic marker.**S3.** Best-fit
777 models of sequence evolution and partitioning schemes selected with PartitionFinder.

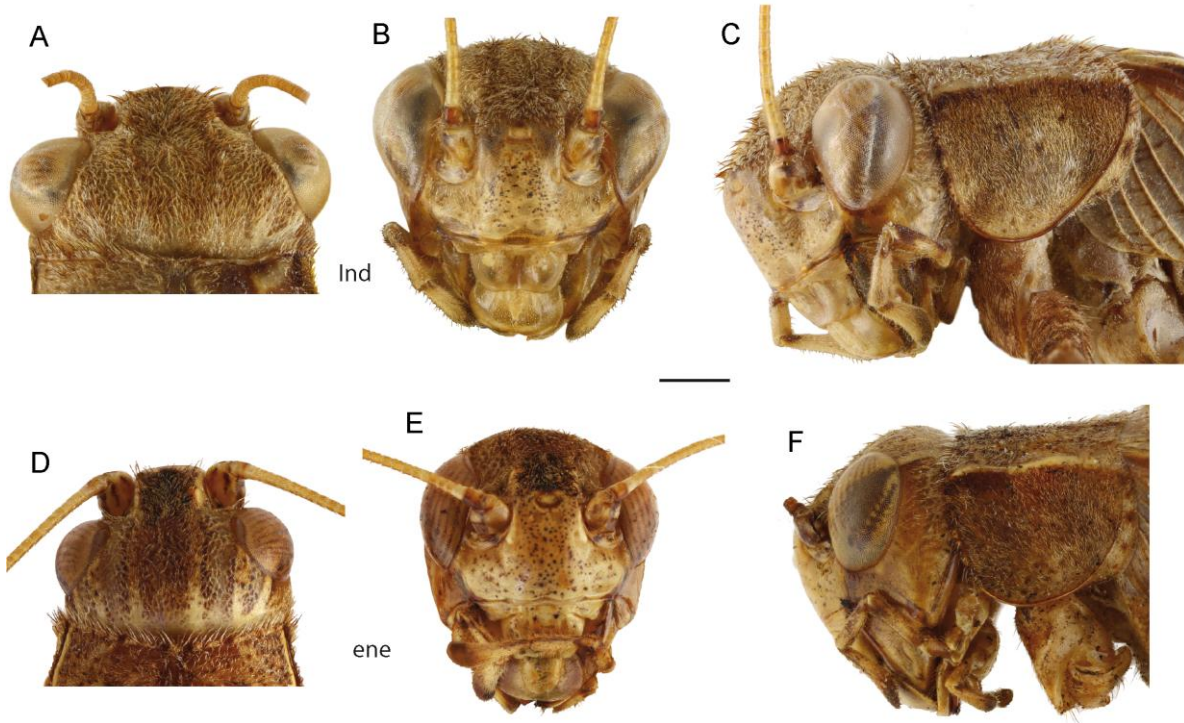
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779 **S4.** Original output results of Bayesian inference (BI) and Maximum likelihood (ML) analyses for
780 concatenated dataset.

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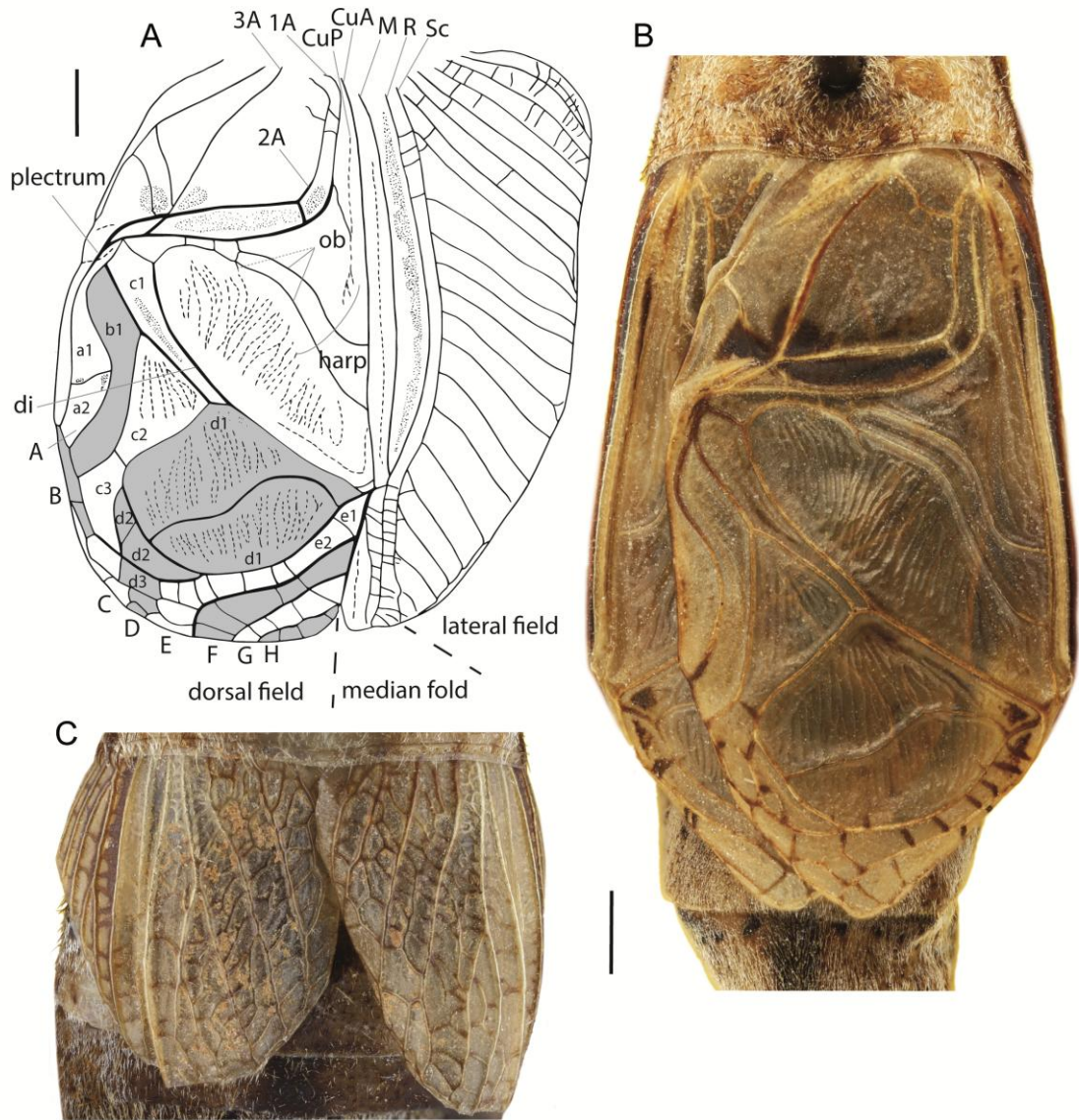


784 Fig.2



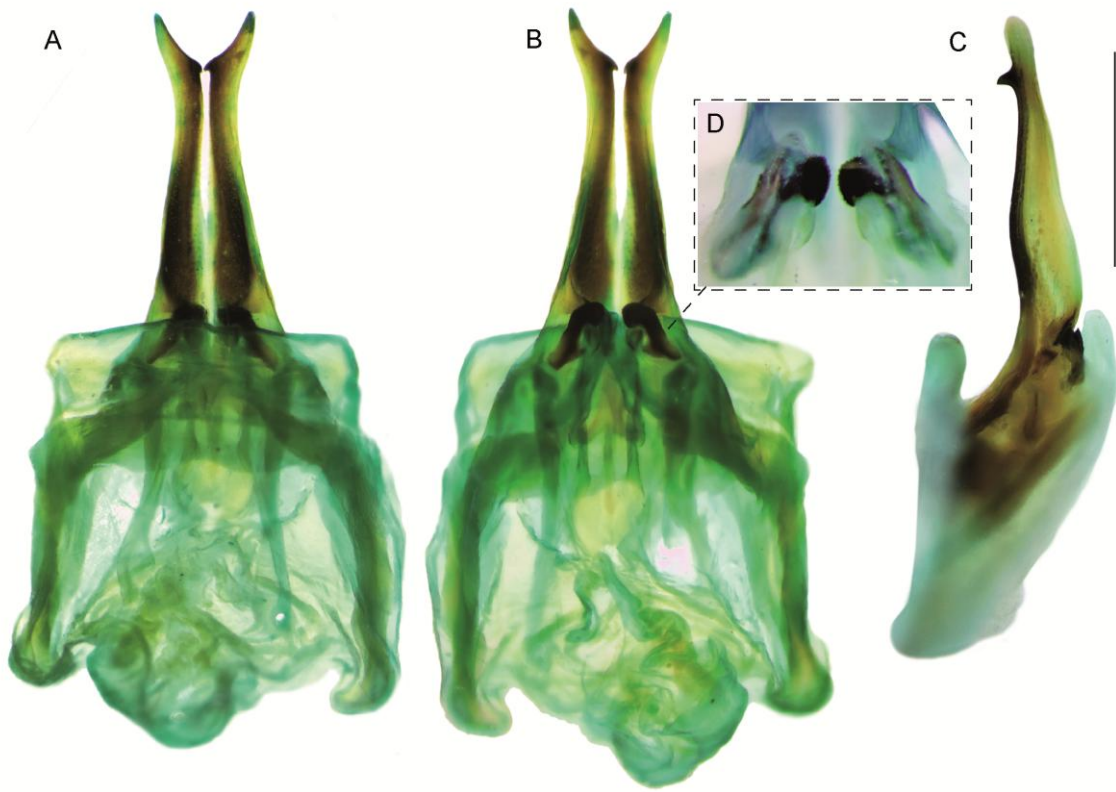
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788 Fig.3



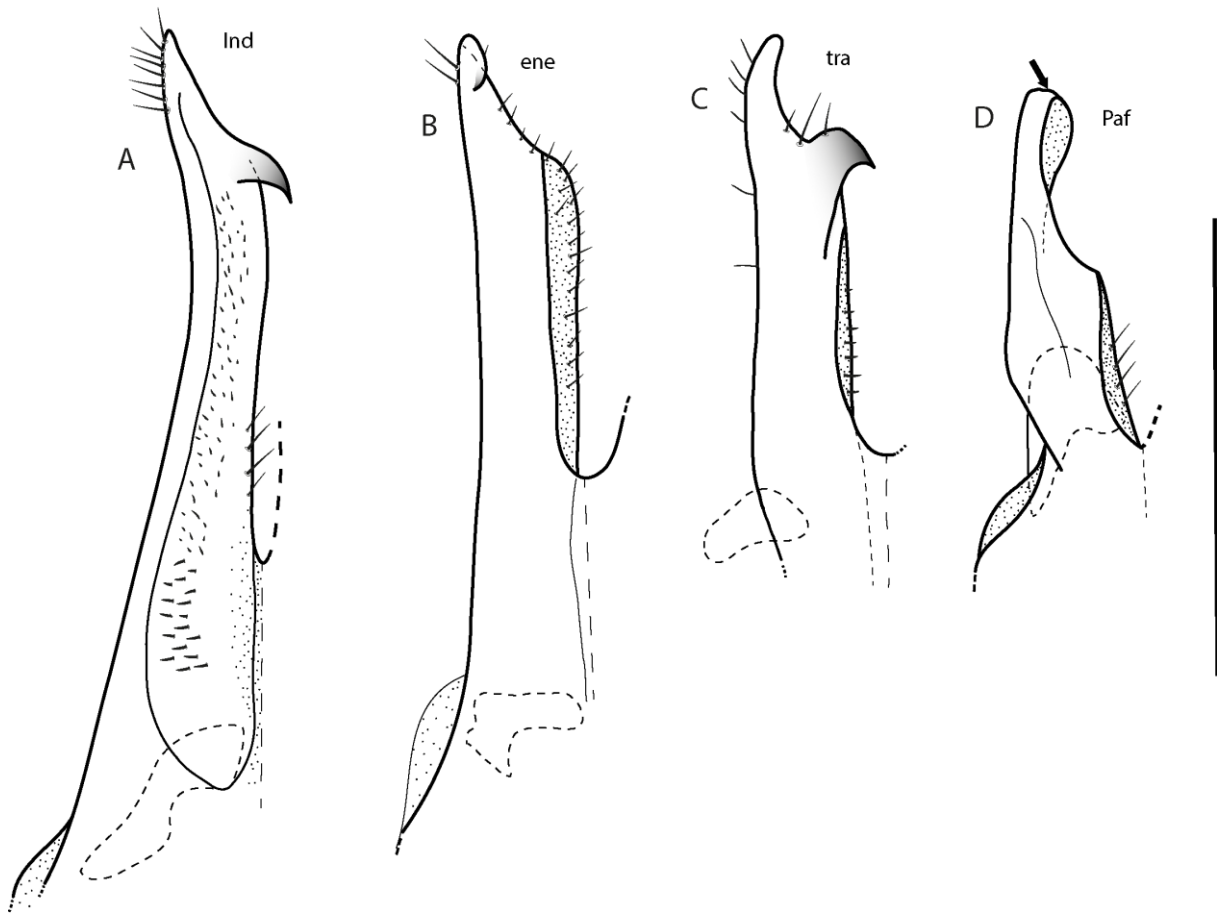
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792 Fig.4



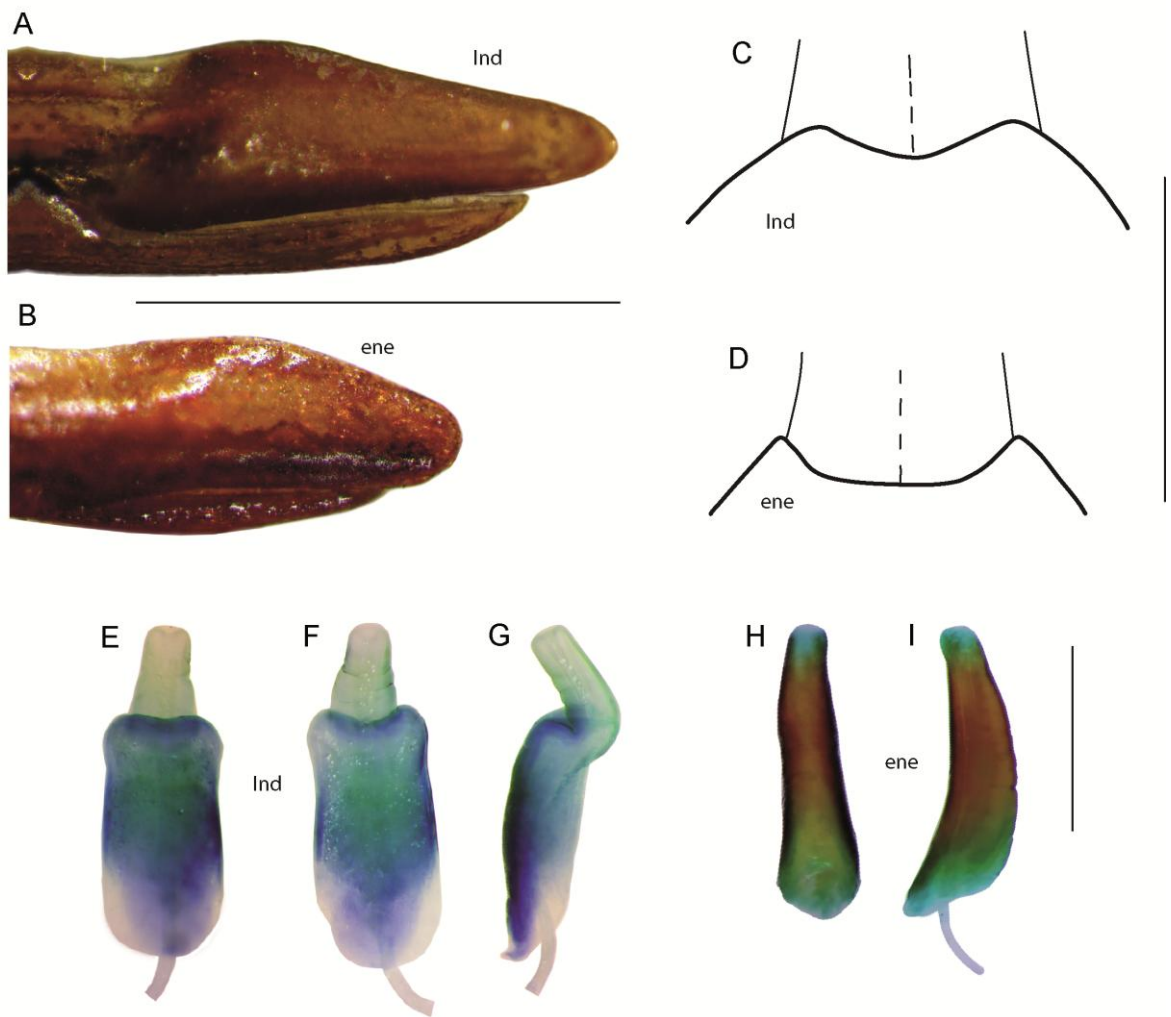
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795 Fig.5



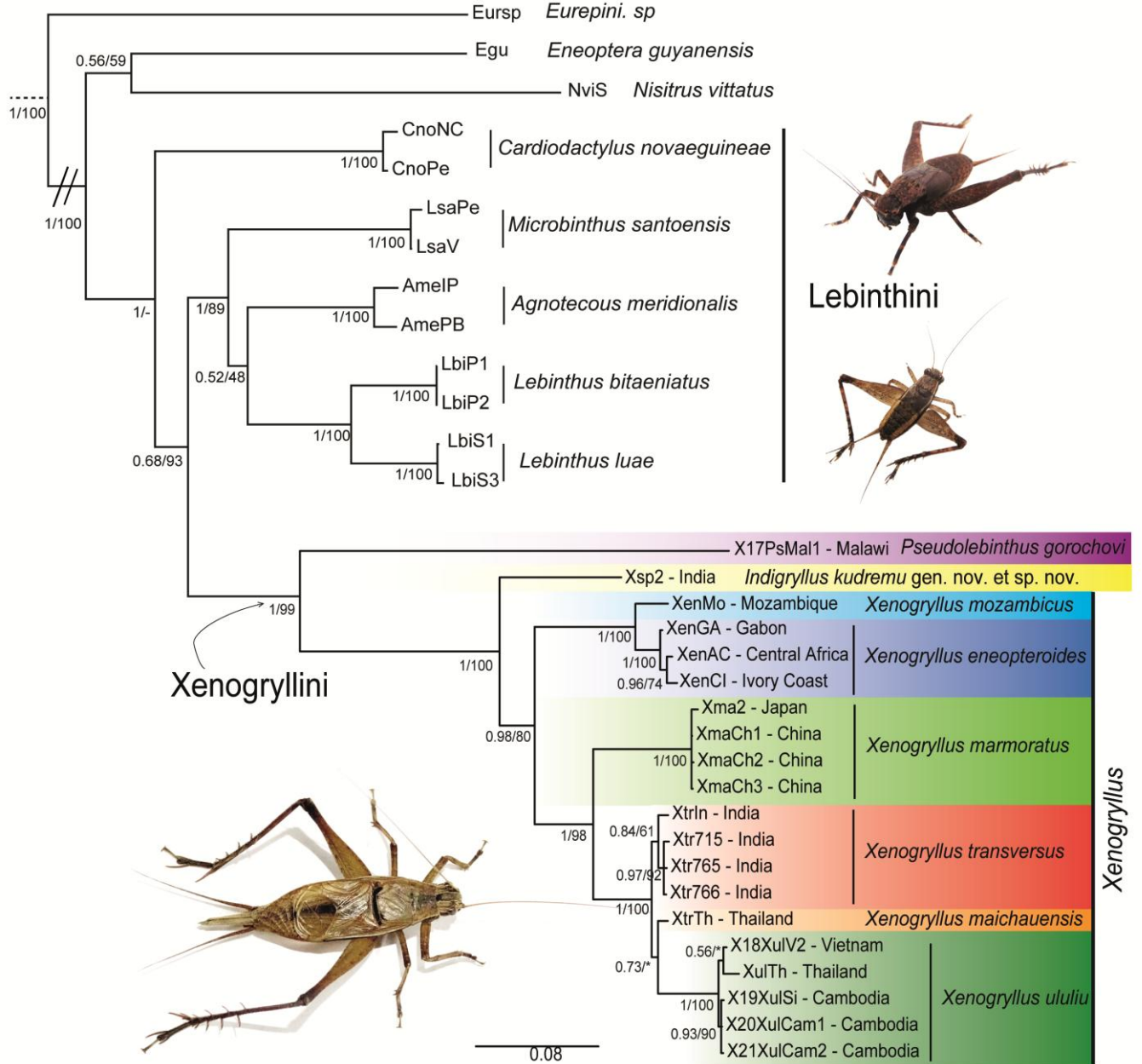
796
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798 Fig.6
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804 Fig.7



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