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1 **Ultrasonic bioacoustics and stridulum morphology reveal cryptic species among**
2 ***Lipotactes* big-eyed katydids (Orthoptera: Tettigoniidae: Lipotactinae) from Borneo**

3

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15

16 **Running title:** Ultrasonic bioacoustics and taxonomy of Lipotactinae

17

18 **Abstract**

19

20 Lipotactinae is an elusive monophyletic subfamily of katydids (Orthoptera: Tettigoniidae)
21 unique to Asia and comprising two genera—*Lipotactes* and *Mortoniellus*. Nearly nothing is
22 known beyond their original descriptions. The stridulum morphology is rarely examined and
23 described in taxonomy and their acoustics are only known for six species, none of which is
24 from Borneo. New *Lipotactes* specimens collected from Borneo—Belait and Kuala Belalong
25 in Brunei and Sandakan in Sabah—were initially identified as *Lipotactes alienus* and/or

26 *Lipotactes virescens* based on traditional morphological characters. However, the structures
27 of male calling songs of individuals from Kuala Belalong and Sandakan were profoundly
28 different from each other and from the known songs of *L. virescens* from Thailand and
29 Peninsular Malaysia. This led us to examine the morphology of the Bornean specimens more
30 closely. By integrating call structures, stridulum morphology and traditional morphology, we
31 establish that the specimens from Borneo are different from *L. virescens* and that the
32 populations from Kuala Belalong, Belait and Sandakan represent different ethospecies. Here,
33 we describe the species from Sandakan as *Lipotactes kabili* **n. sp.** We also demonstrate that
34 both stridulum morphology and call structures can be useful in separating Lipotactinae
35 species because inter-specific differences are larger than intra-specific differences.

36

37 **Key words:** Brunei Darussalam, Sabah, Southeast Asia, ethospecies, new species, taxonomy

38

39

40

41 **Introduction**

42

43 Katydid communicate by stridulating with their forewings to produce sound (Montealegre-Z,
44 2009). More than 70% of the species with known songs sing at ultrasonic frequencies (>20
45 kHz) (Montealegre-Z et al., 2006, 2017). The ability to communicate at ultrasonic
46 frequencies has drawn academic interest to study their biomechanics by investigating the
47 stridulatory anatomy of the wings (e.g., Montealegre-Z, 2009, 2012; Montealegre-Z et al.,
48 2017). However, ultrasonic-singing katydids are still poorly known in many aspects. These
49 include whether their songs can be used to differentiate the species by bioacoustic signals
50 because inter-individuals to inter-species variations are rarely examined (partly owing to
51 insufficient specimens). Particularly, knowledge of bioacoustics of katydids from the hyper-
52 diverse Southeast Asia remains remarkably poor—owing to the sheer number of species,
53 difficulty of identifying them and relative lack of regional expertise—until recently (Tan et
54 al., 2019).

55

56 The katydids of the subfamily Lipotactinae Ingrisch, 1995 are examples in which their
57 bioacoustics are understudied. This small monophyletic subfamily is nowadays endemic to
58 Asia (but see Gorochoy, 2010) and comprises two genera, *Lipotactes* Brunner von Wattenwyl,
59 1898 and *Mortoniellus* Griffini, 1909 with 24 species in *Lipotactes* and seven species in
60 *Mortoniellus* (Ingrisch, 1995; Muggleston et al., 2018; Cigliano et al., 2019). These katydids
61 are characterised by disproportionately large heads (and eyes), highly reduced and modified
62 tegmina for singing, and legs armed with predatory spurs. Most species are recognised by
63 their genitalia morphology and colour patterns on the pronotum and hind femur. Ingrisch
64 (1995) erected the subfamily and provided the most thorough treatment on the biology and
65 acoustics of this group to date. Since then, a few additions to this subfamily were published,

66 but Lipotactinae is still poorly known with very few references to them beyond the original
67 descriptions (Gorochov, 1993, 1996, 1998; Chang et al., 2005; Shi & Li, 2009; Feng et al.,
68 2017).

69

70 The bioacoustics of Lipotactinae is known from only five *Lipotactes* and one *Mortoniellus*
71 species from Thailand, West Malaysia, Singapore and Sumatra, all of which were reported by
72 Ingrisch (1995). More recently, Wang & Shi (2020) also report the songs of one *Lipotactes*
73 from China. The calling songs of Lipotactinae typically consist of verses (often crescendoing)
74 or continuous trains, and peak at ultrasonic frequencies (Ingrisch, 1995). However,
75 stridulation was considered to have limited use in separating species (Ingrisch, 1995). The
76 stridulum anatomy is also generally precluded in species descriptions and taxonomic studies
77 (except for *Lipotactes montanus* Ingrisch, 1990 [Ingrisch, 1995]), even though the subfamily
78 comprises only species with highly reduced tegmina modified for singing. This may be
79 because the wings are concealed under the pronotum and are required to be dissected to
80 examine the stridulatory organs

81

82 The tegmina of Lipotactinae are highly modified for singing, which in turn is imperative to
83 communicate and attract conspecific females. Thus, the stridulum morphology, along with
84 the acoustic parameters of the songs, can be useful for differentiating species, especially
85 morphologically cryptic ones, and help resolve problems with delimitation of species. During
86 recent orthopteran samplings in Borneo (i.e., Brunei Darussalam and Sabah), we collected
87 males and females of *Lipotactes* (Fig. 1) that were tentatively identified to either *Lipotactes*
88 *alienus* Brunner von Wattenwyl, 1898 or *L. virescens* Ingrisch, 1995. *L. alienus* is the type
89 species of *Lipotactes* but was originally described from only one female from Borneo, River
90 Baram (Brunner, 1898). Ingrisch (1995) described *L. virescens* from South Thailand/

91 Malaysia but also included specimens from Borneo. When the new specimens from Borneo
92 were compared with the description and images in Ingrisch (1995) using traditional
93 characters (i.e., genitalia and patterns), we were led to believe that these two species are
94 morphologically very similar, and that *L. virescens* specimens from Borneo (as listed in
95 Ingrisch, 1995) may belong to a different species (may or may not be *L. alienus*). The
96 characters also exhibit population variations, suggesting that there may exist a species
97 complex of *L. alienus-cum-virescens* from Borneo.

98

99 To elucidate these morphologically cryptic species, we examined previously unknown
100 characters, specifically the acoustic parameters in the frequency (e.g., peak frequency) and
101 time (e.g., pulse repetition rates) domains and stridulum morphology (i.e., mirror area and
102 harp area, stridulatory file). We evaluated whether these characters can reveal information on
103 the species boundaries of *Lipotactes*. Our prediction is that these new characters can help
104 unravel the *Lipotactes* from Borneo into different putative ethospecies which are different
105 from *L. virescens* from Thai-Malay Peninsula. Here, we also describe previously unknown
106 acoustic signatures and stridulum morphology of the Bornean species.

107

108

109 **Material and methods**

110

111 *Collection and depositories of katydids*

112 Field collections and observations were made in the Belait and Temburong Districts of
113 Brunei Darussalam between 23 February and 3 March 2019 and between 6 and 18 July 2019;
114 as well as in Sandakan, Sabah between 8 and 12 January 2019 and between 30 September
115 and 4 October 2019. Specimens were collected by sight during night and day. Whenever

116 possible, in-situ images were taken using a Canon EOS 500D digital SLR camera with a
117 compact-macro lens EF 100 mm f/2.8 Macro USM and Canon Macro Twin Lite MT-24EX
118 was used for lighting and flash. Specimens collected by Tan & Wahab (2018) from Kuala
119 Belalong Field Studies Centre (Temburong, Brunei Darussalam) and Tan & Kamaruddin
120 (2016) from Bukit Larut (Perak, Peninsular Malaysia) were also examined.

121

122 *Specimen identification and curation*

123 Identification was done using descriptions of all known *Lipotactes* species: Gorochov (1993,
124 1996, 1998); Ingrisich (1995); Chang et al. (2005); Shi & Li (2009). The specimens were
125 preserved in absolute analytical-grade ethanol and later pinned and dry-preserved. For
126 studying and documenting the distribution of teeth at the stridulatory file, the left tegmen was
127 removed from fresh specimens using micro-scissors. For ethanol-preserved specimens, small
128 amount of dilute KOH was added to relax the specimens before dissection. A single hind leg
129 from each specimen was also preserved in absolute analytic-grade ethanol for future
130 molecular work.

131

132 Close-up images of morphological features (including stridulum morphology) were done
133 using a Canon macro photo lens MP-E 65 mm f/2.8 USM (1–5×). Image-editing was
134 accomplished using Adobe Photoshop CC 2014 (Adobe Systems Incorporated, San Jose, CA,
135 USA).

136

137 *Acoustic recordings and analysis*

138 Acoustic recording and analysis generally followed that in Tan et al. (2019). In the biological
139 stations in Brunei Darussalam and Sandakan, the katydids were kept in insect cages with
140 nylon netting. Acoustic recording was done using a sampling frequency of 256 kHz-

141 samples/s Echo Meter Touch (based on Knowles FG sensor) placed horizontally and at about
142 2–5 m away from the cage. The katydid usually (but not always) sings while clinging onto
143 the side of the cage (thus positioning with dorsal surface facing the recording device).
144 Ambient temperature was logged using a HOBO 8K Pendant® Temperature logger (model:
145 UA-001-08, Onset, Bourne, MA). The recorded signals were saved in 12-bit WAV format.
146
147 Acoustic parameters (e.g., peak frequency, mean frequency, repetition rate, song duration)
148 were extracted using the ‘specan’ function in the open source R package WarbleR version
149 1.1.14 (Araya-Salas and Wright, 2017) in the R software version 3.5.1 (R Development Core
150 Team, 2018). Sample size, from which the arithmetic means and standard deviations were
151 calculated from, was denoted by the number of sound files. To filter out low or high
152 background noise before performing measurements, the lower and upper limits of a
153 frequency bandpass filter (in kHz) were set at 15 kHz and 120 kHz respectively so
154 measurements of the frequency domain were obtained only between the frequency range. To
155 generate power spectra using FFT, we used the function ‘spec’ at 256,000 sampling
156 frequency, using Hanning window of window length 512. To compare the acoustic
157 parameters, we fitted linear mixed effects models using the acoustic parameters as the
158 response variables, population at which the katydid was collected as the fixed effect and
159 temperature at the time of recording as random intercept to determine least-square means of
160 each acoustic parameters to account for temperature effect. This was done using the ‘lmer’
161 function from the R package ‘lme4’ (Bates et al., 2014).

162

163 *Measurement of morphological traits*

164 We measured the maximum length and width and area of mirror and harp; inter-tooth
165 distance and tooth length. Measurements were accomplished using ImageJ 1.51j8 (Wayne

166 Rasband, Research Services Branch, National Institute of Mental Health, Bethesda, MD,
167 USA).

168

169 *Terminologies*

170 For the description of songs, terminologies follow that by Ingrisch (1995) and Tan et al.
171 (2019): verse = complete sequence of syllables which is separated from other verse by a
172 distinct and prolonged pause; syllable = one complete cycle of tegminal movement; pulse = a
173 single unbroken wave train isolated in time by significant amplitude; peak frequency =
174 frequency with highest energy from the mean spectrum; mean frequency = weighted average
175 of frequency by amplitude; pulse duration = duration of the pulse; pulse repetition rate =
176 number of discrete pulses per second.

177

178 For the description of stridulum morphology, terminologies follow that by Béthoux (2012)
179 and Chivers et al. (2017): CuPb = posterior branch of posterior cubitus (CuP); h1 = anterior
180 portion of harp area; h2 = median portion of harp area; h3 = posterior part of harp area.

181

182 For the description of stridulatory file, terminologies follow that of Montealegre-Z and
183 Mason (2005) and Tan et al. (2019): inter-tooth distance = distance from the edge of the cusp
184 of one tooth to the cusp of the next one; tooth length = distance from the anterior to the
185 posterior ends of the cusp of each tooth.

186

187 For the measurements, the following abbreviations are used: BL = body length; HL = head
188 length; HW = head width (include eyes); PL = pronotum length; PW = pronotum width (at
189 metazona); TL = tegmen length; HFL = hind femur length; HTL = hind tibia length; OL =
190 ovipositor length.

191

192 ***Depositories***

193 All sound files were uploaded to the Orthoptera Species File Online Version 5.0/5.0

194 (Cigliano et al., 2019).

195

196 The dry-pinned specimens were deposited:

197 FRC Forest Research Centre, Sepilok, Sandakan, East Malaysia

198 UBDM Universiti Brunei Darussalam Museum, Brunei Darussalam

199 ZRC Zoological Reference Collection, Lee Kong Chian Natural History Museum,

200 Singapore

201

202

203 **Results**

204

205 ***Part I: taxonomy***

206 ***Lipotactes alienus* Brunner von Wattenwyl, 1898** (Figs. 1.1, 2.1, 2.5, 3.1, 5.1, 6.1)

207 Material examined. — Brunei Darussalam, Temburong District: 1 female (KB.16.37), Ulu

208 Temburong National Park, canopy walk, primary dipterocarp forest, N4.55196 E115.15990,

209 234.4±5.9 m, 1851h, on foliage of shrub, 25 September 2016, coll. M.K. Tan; 1 female

210 (KB.16.62), Temburong District, Kuala Belalong Field Studies Centre, Ashton Trail, primary

211 dipterocarp forest, N4.54712 E115.15726, 123.7±9.5 m, 2152h, on branch of tree after rain,

212 26 September 2016, coll. M.K. Tan; 1 male (KB.19.11) Ashton Trail, primary dipterocarp

213 forest, N4.54561 E115.15679, 109.3±11.9 m, 1948h, on foliage near ground, 13 July 2019,

214 coll. M.K. Tan & H. Yeo (UBDM and ZRC). Brunei Darussalam, Belait District: 1 male

215 (BR.19.37), Andulau Forest Reserve, N4.62420 E114.51322, 84.6±7.0 m, 1818h, under

216 foliage 28 February 2019, coll. M.K. Tan & H. Yeo (UBDM) (note that any reference to the
217 population/ individuals from Belait in the text does not include this specimen but instead refer
218 to *Lipotactes* ethospecies [Belait] [see below]).

219 Remarks. — The females are sufficiently described in Ingrisch (1995). Females collected
220 from Kuala Belalong resemble *L. alienus* by colour patterns on hind femur (including black
221 hind knee); dark markings on pronotum dorsal disk, metanotum and abdominal tergite; shape
222 of subgenital plate. We inferred that the males collected from the same trail Kuala Belalong
223 are therefore probably the undescribed males of *L. alienus*. However, we recommend that
224 DNA data may be needed to match the females from Kuala Belalong with the holotype (and
225 specimens from Long Pa Sia [see Ingrisch 1995]) to be completely certain.

226 Description of male. — Very similar to *L. virescens*: size, colouration; pronotum with
227 anterior margin and transverse sulcus black and M- or U-shaped black markings on dorsal
228 disk similar to *L. virescens* males (Fig. 2.1, see also Ingrisch 1995: Fig. 65); but differs by:
229 generally lighter colouration. Tenth abdominal tergite prolonged behind in middle,
230 prolongation more broadly rounded (Fig. 3.1). Cercus more slender at apex (instead of
231 uniformly conical in *L. virescens*), basal lobe of internal process distinctly larger, length
232 nearly reaching mid-point of internal process. Subgenital plate with two pronounced lateral
233 lobes at apex (where styli are inserted); apex between base of styli strongly emarginated.
234 Stylus dark, long and slender (Fig. 3.1).

235

236 ***Lipotactes virescens* Ingrisch, 1995** (Figs. 1.2, 2.2, 2.6, 3.2, 5.2, 6.2)

237 Material examined. — 1 male (LAR.15.135), Peninsular Malaysia, Perak, Taiping, near
238 Sungei Larut, young secondary forest and forest edge, N4.85418 E100.76057, 62.7±5.3 m, on
239 branch, 19 June 2015, coll. M.K. Tan & S.T. Toh (ZRC).

240 Remarks. — Specimens from Borneo previously examined and identified as *L. virescens* in
241 Ingrisch (1995) probably belong to either one of our ethospecies collected from Sandakan
242 and Belait or other currently unknown ethospecies. We consider *L. virescens* to occur only in
243 Thai-Malay Peninsula and not in Borneo.

244

245 ***Lipotactes kabili* Tan, Japir and Chung, new species** (Figs. 1.3, 1.4, 2.3, 2.7, 3.3, 4, 5.3, 6.3)

246 Material examined. — Holotype (male, SDK.19.101), East Malaysia, Sabah, Sandakan,

247 Sepilok, Kabili Sepilok Forest Reserve, primary and old secondary dipterocarp forest,

248 N5.87014 E117.93778, 81.8±6.4 m, 2029h, on foliage near ground, 3 October 2019, coll.

249 M.K. Tan & John Lee Yukang (FRC).

250 Paratypes (2 males and 1 female): same locality, 1 female (SDK.19.74), N5.86952

251 E117.93882, 49.3±5.9 m, 2005h, on foliage, 1 October 2019, coll. M.K. Tan, Razy Japir &

252 John Lee Yukang; 1 male (SDK.19.98), N5.86926 E117.93940, 52.7±6.9 m, 1936h, on

253 foliage, 3 October 2019, coll. M.K. Tan & John Lee Yukang; 1 male (SDK.19.102),

254 N5.87039 E117.93772, 82.0±6.2 m, 2042h, on branch, 3 October 2019, coll. M.K. Tan &

255 John Lee Yukang (ZRC).

256 Remarks. — The individuals from Sandakan are remarkably different from other Bornean

257 species in their acoustic signals and in shape of the stridulatory apparatus (especially the

258 stridulatory file). We also compared with *Mortoniellus macrognathus* Ingrisch, 1995 from

259 Poring and Danum Valley in Sabah but differs by shape of cercus (despite the presence of

260 inner process), pronotum and hind femoral colouration and shape of female subgenital plate.

261 We are confident that this population represents a valid species of Lipotactinae.

262 Diagnosis. — This new species differs from all known congeners by the following characters:

263 pronotum with dense black patterns and with metazona brown; male cercus conical, with

264 inner process and with apex styliform; inner process of male cercus elongated and somewhat

265 lamellated, with posterior margin convexly curved but anterior margin straight, with basal
266 lobe large and cylindrical; female subgenital plate distinctly wider than long with apex
267 roundly and narrowly emarginated in middle.

268 Description of male. — Pronotum with metazona prolonged and slightly elevated (Fig. 2.7).

269 Pattern on pronotum dorsal disk similar to that of *L. alienus* and *L. virescens*: anterior margin
270 and transverse sulcus black, a circa M-shaped figure behind sulcus; but differs by: the figure
271 behind sulcus thicker (bolder), and the anterior area of the metazona with a broad U-shaped
272 figure that fades posteriorly into the darkened apex of pronotum (Fig. 2.3). Posterior femur
273 with a reddish stroke that reaches the base and dorsal margin; hind knee darkened, but not as
274 dark as female.

275 Tegmen with dorsal field 3.0 mm long and 2.8–2.9 mm wide; lateral field infumated (Fig.
276 5.3). h1 distinctly less wide than mirror width, h2 narrowly pyriform, with anal end rounded
277 and with frame nearly touching CuPb at the basal end; mirror large and distinctly wider than
278 long (Fig. 5.3). Stridulatory file on CuPb crescent shaped, ca. 2 mm long, with 84 evenly
279 distributed teeth (Fig. 6.3). Apical area of tegmen narrowly truncated (Fig. 5.3).

280 Tenth abdominal tergite and epiproct as in *L. virescens* (Fig. 3.3): tenth abdominal tergite
281 incised in the middle; epiproct triangular, apex obtuse, with a faint medio-longitudinal furrow.

282 Male cercus large and conical, with inner process, apex characteristically styloform; inner
283 process of male cercus elongate and somewhat lamellate, with posterior margin convexly
284 curved but anterior margin straight, apex obtuse; inner process with basal lobe large and
285 cylindrical (Fig. 3.3). Subgenital plate with lateral lobes at apex greatly spaced, posterior
286 margin broadly emarginated. Stylus relatively stout, dark coloured, cylindrical, with apex
287 obtuse (Fig. 3.3). Phallus membranous.

288 Description of female. — Pronotum dorsal disk pattern similar to males, but M-shaped figure
289 even more prominent (Figs. 4.1, 4.2). Wings absent. Posterior femur with a strong black

290 stroke that reaches the base and dorsal margin; hind knee darkened. Abdominal tergite black
291 laterally. Tenth abdominal tergite with posterior margin truncated in the middle; epiproct
292 tongue-shaped with apex obtuse (Fig. 4.3). Subgenital plate concealed at base by preceding
293 sternite, transverse (distinctly wider than long), tapering towards apex; apex roundly and
294 narrowly emarginated in middle (Fig. 4.4). Ovipositor slightly surpassing posterior femur,
295 straight in basal third, then feebly narrowed and curved dorsad, apical third widening feebly
296 before tapering into acute apex; ventral valve finely serrulated at ventro-apical margin (Fig.
297 4.5).

298 Measurements. — See Table 1.

299 Distribution. — This species is so far known only from Sandakan.

300 Etymology. — This species name is named after the type locality, Kabil; noun in apposition.

301

302 ***Lipotactes ethospecies* (Belait)** (Figs. 1.5, 1.6, 2.4, 2.8, 3.4, 5.4, 6.4)

303 Material examined. — Brunei Darussalam, Belait District: 1 female (BR.19.6), Jalan (= Road)

304 Labi near Andulau Forest Reserve, N4.63354 E114.51073, 76.8±7.9 m, 1947h, under foliage,

305 24 February 2019, coll. M.K. Tan & H. Yeo; 1 male (BR.19.51), Jalan Labi at Teraja,

306 N4.28456 E114.41866, 40.0±5.7 m, 2005h, on tree sapling branch, 1 March 2019, coll. M.K.

307 Tan & H. Yeo; 1 male (BR.19.56), Jalan Labi at Teraja, N4.28485 E114.41828, 50.1±5.5 m,

308 2045h, on tree sapling branch, 1 March 2019, coll. M.K. Tan & H. Yeo (UBDM and ZRC).

309 Remarks. — The two populations from Brunei may represent either two subspecies or species.

310 The males can be distinguished by stridulum morphology, shape of cerci and subgenital plate,

311 patterns on pronotum. However, females from Belait are almost indistinguishable from those

312 from Kuala Belalong. Since we did not have acoustic data for this population, we prefer to

313 putatively consider this population as tentative *ethospecies* instead of describing a new

314 species to avoid future synonymy or taxonomic confusion.

315

316 ***Part II: stridulum morphology***

317 Tegmen in *Lipotactes* is highly modified: dorsal field with large and well-defined mirror area
318 (among other well-defined resonators) and few veins, usually transparent (although with
319 some darkened veins in *L. kabili n. sp.* and *L. ethospecies* (Belait) , Figs. 5.3, 5.4); apical area
320 of dorsal field and lateral field more infumated (Fig. 5).

321

322 Harp area differs between different species in size and shape. h1 can be slender (distinctly
323 less wide than mirror width) in *L. kabili n. sp.* (Fig. 5.3) but very broad (nearly as wide as
324 mirror width) in *L. ethospecies* (Belait) (Fig. 5.4). h2 differs between different species in size:
325 smallest in *L. ethospecies* (Belait) (0.08 mm²) (Fig. 5.4) and largest in *L. kabili n. sp.* (0.12–
326 0.15 mm²) (Fig. 5.3) and *L. alienus* (0.12 mm²) (Fig. 5.1). h2 in *L. kabili n. sp.* are
327 exceptionally narrower and more transverse than other species (Fig. 5.3). We did not compare
328 area of h3 because the vein demarcating the area at the anal end is not always clear.

329

330 Mirrors in all species are always wider than long but range from 1.16 times wider than long
331 in *L. alienus* (Fig. 5.1) to 1.46 in *L. kabili n. sp.* (Fig. 5.3); the mirror area also varies in size:
332 ranging from 0.60 mm² in *L. ethospecies* (Belait) (Fig. 5.4) to 1.24–1.27 mm² in *L. kabili n.*
333 ***sp.*** (Fig. 5.3). As expected, venation is typically conserved although variation between
334 species is greater than within (Fig. 5).

335

336 The stridulatory file on the left tegmen differs drastically between different species.
337 Specifically, it differs by number and distribution teeth in both, inter-tooth distance and tooth
338 length, even though the stridulatory files are generally crescent shaped (Figs. 6, 7). Tooth
339 number is lowest in *L. ethospecies* (Belait) (14), followed by *L. alienus* (28) and *L. virescens*

340 (39). *L. kabili* n. sp. have distinctively more teeth (84) but the teeth are more densely and
341 evenly distributed than in the other populations (Fig. 7).

342

343 ***Part III: calling songs***

344 The calling songs of *Lipotactes* from Borneo consist of verses (Fig. 8) in the near-ultrasonic
345 to ultrasonic frequencies, thus being faintly audible to human ear. The songs are non-resonant
346 owing to broad distribution of frequencies; but usually consist of two peaks, one higher than
347 the other (Fig. 9). These characters are somewhat similar to the known songs of other
348 Lipotactinae. We also observed that *Lipotactes* exhibit intra-individual variation in their
349 calling songs, as in the case of *L. alienus*. Two song types were considered as the songs have
350 vastly different time domain.

351

352 **Calling song type I of *L. alienus* from Kuala Belalong (n = 9 songs, 1 male):** At 24.4–29.2
353 °C, the male calling song consists of a verse, average verse duration 790 ± 130 ms (507–997
354 ms), with variable amplitude modulation in the time domain (Fig. 8.1). Each verse consists of
355 an average of 48 ± 12 (27–70) pulses (probably syllables) and its repetition rate is 61.2 ± 13.0 s⁻¹
356 (53.2 – 89.8 s⁻¹). Average pulse duration is 16.9 ± 2.8 ms (11.1–18.8 ms) (Fig. 8.2). Each pulse
357 is made up of a series of closely-spaced impulses (Fig. 8.3). Arithmetic mean frequency is
358 36.9 ± 0.4 kHz, arithmetic mean peak frequency is 35.5 ± 0.9 kHz and arithmetic mean
359 fundamental frequency is 23.8 ± 3.1 kHz (Fig. 9.1).

360

361 **Calling song type II of *L. alienus* from Kuala Belalong (n = 8 series of songs, 1 male):**

362 Another song type was identified from the same individual. At 24.4 °C, the song also consists
363 of a continuous series of verses, albeit each verse duration is shorter at an average of 267 ± 80
364 ms (175–434 ms). Each verse consists of an average of 13 ± 5 (8–24) pulses (probably

365 syllables) and its repetition rate is $49.5 \pm 2.8 \text{ s}^{-1}$ ($45.7\text{--}55.3 \text{ s}^{-1}$). Average pulse duration is
366 $20.3 \pm 1.1 \text{ ms}$ ($18.1\text{--}21.9 \text{ ms}$). Arithmetic mean frequency is $37.4 \pm 0.4 \text{ kHz}$, arithmetic mean
367 peak frequency is $36.6 \pm 1.2 \text{ kHz}$ and arithmetic mean fundamental frequency is $16.8 \pm 1.1 \text{ kHz}$.

368

369 **Calling song of *L. kabili* n. sp. from Sandakan (n = 19 songs, 1 male):** The song is unique
370 among the known songs of Lipotactinae. At $30.1 \text{ }^\circ\text{C}$, each male calling song consists of a
371 verse of 8 ± 4 ($3\text{--}15$) crescendoing syllables closely-spaced together in time, song average
372 duration $1222 \pm 565 \text{ ms}$ ($470\text{--}2350 \text{ ms}$) (Fig. 8.4). Each average syllable duration is 14.3 ± 1.5
373 ms ($12.5\text{--}19.9 \text{ ms}$) (Fig. 8.5). Each syllable consists of 26 ± 6 ($21\text{--}45$) rapid-decaying pulses.
374 Average rapid-decay duration is $5.6 \pm 0.7 \text{ ms}$ ($3.2\text{--}6.6 \text{ ms}$) and pulse repetition rate is
375 $183.5 \pm 33.6 \text{ s}^{-1}$ ($152.5\text{--}310.9 \text{ s}^{-1}$) (Fig. 8.6). Arithmetic mean frequency is $38.1 \pm 0.3 \text{ kHz}$,
376 arithmetic mean peak frequency is $28.7 \pm 0.3 \text{ kHz}$ and arithmetic mean fundamental frequency
377 is $20.5 \pm 1.2 \text{ kHz}$ (Fig. 9).

378

379 When the temperature at the time of recording was accounted for in the models, the mean
380 peak frequency and mean frequency of the songs are still markedly different between *L.*
381 *alienus* from Kuala Belalong and *L. kabili* n. sp. from Sandakan (Figs. 9, 10.1, 10.2). As
382 expected, the frequency domain of the two song types belonging to *L. alienus* are not
383 different (Figs. 9, 10.1, 10.2). For the time domain of the song, verse/ syllable duration is
384 drastically different between the two song types of *L. alienus* from Kuala Belalong and *L.*
385 *kabili* n. sp. from Sandakan (Fig. 10.3). The two song types of *L. alienus* can be
386 differentiated mainly verse/ syllable duration (Fig. 10.3). The pulse duration, and hence pulse
387 repetition rate, is markedly different between *L. alienus* and *L. kabili* n. sp., but not so
388 between the two song types of *L. alienus* (Figs. 10.4, 10.5).

389

390 **Discussion**

391 *Integrative taxonomy of Bornean Lipotactes*

392 Prior to the comparison of call and stridulatory structures between *L. virescens* from South
393 Thailand and Malaysia and the populations from Borneo, we thought that individuals from
394 Borneo are merely variants of *L. virescens* (based on new specimens and Ingrisch [1995]).
395 This is owing to the characteristic male cerci that have a stout lobe at the base of the inner
396 process, seen previously only in *Lipotactes virescens* but also in some *Mortoniellus* species
397 (Ingrisch, 1995). *Lipotactes* specimens from Borneo also exhibit this character with variation
398 in shape and size. We also observed a gradient in colouration and patterns on the pronotum
399 dorsal disk among the different populations: individuals from Belait being most prominent
400 and darkest, followed by those from Sandakan (i.e., *L. kabili* n. sp.), *L. virescens* and
401 individuals from Kuala Belalong being lightest. Although *Lipotactes* congeners display
402 differences in colour intensity and pattern on pronotum, such characters usually call for great
403 caution when used to differentiate species. Other traditional characters such as subgenital
404 plate and styli also show variations among the Bornean populations but it was difficult to
405 ascertain if they represent species differences.

406

407 For the first time, the male calling songs of Lipotactinae were recorded from individuals
408 collected in Kuala Belalong (Brunei) and Sandakan (Sabah)—both in Borneo. The songs are
409 very different from one another and from those in South Thailand and Malaysia. Specifically,
410 both the time and the frequency domains of the songs are clearly distinguishable between
411 songs from Kuala Belalong (Brunei) and Sandakan (Sabah). By comparing the new acoustic
412 data with the literature (i.e., Ingrisch, 1995), it was clear that the time domain of the call
413 structure between the Bornean individuals and *L. virescens* from South Thailand and
414 Peninsular Malaysia, even though we could not precisely compare the frequency domain (see

415 Ingrisch, 1995). Specifically, the reported (sensu Ingrisch, 1995) repetition rate of *L.*
416 *virescens* (ca. 71–101 s⁻¹) is drastically higher than in *L. alienus* but lower than individuals
417 from Sandakan. The peak frequency is at 35–40 kHz, which is comparable to *L. alienus* but
418 higher than individuals from Sandakan.

419

420 That the bioacoustics signals differ profoundly shed new lights into the species boundaries of
421 *L. virescens*. This prompted us to re-evaluate the morphology of the Bornean specimens more
422 closely and eventually helped us cluster the specimens into three groups: (1) population from
423 Belait, (2) population from Kuala Belalong (probably *L. alienus*) and (3) population from
424 Sandakan (here described as *L. kabili* n. sp.). Upon closer examination, the specimens from
425 Borneo consistently differ from *L. virescens* from the Thai-Malay Peninsula by larger inner
426 process and basal lobe, in addition to the call structures. Individuals from Belait also
427 invariably have the inner process more strongly curved than other populations. All
428 individuals from Sandakan have distinctly styliform cerci and the inner process more
429 lamellate than other populations. The styli in individuals from Belait and Kuala Belalong are
430 more slender whereas in Sandakan individuals they are most the stout among all populations.
431

432 ***Stridulation and stridulum morphology in Lipotactes***

433 The stridulum morphology of *L. virescens* and the Bornean groups are found to be different
434 and can be used to differentiate species even though the characters were not formerly used for
435 taxonomy of Lipotactinae. The dissimilarities in the radiating structure, including the harp
436 and mirror, may have implications on the differences in call structure. The properties of the
437 membrane structure and frame structure of the mirror can dictate the spectral energy, and thus
438 the resulting frequencies, of the song in katydids (Bennett-Clark, 2003; Sarria-S et al., 2016;
439 Chivers et al., 2017). In *Lipotactes*, the mirror on the left tegmen is seemingly functional.

440 This illustrates that the asymmetrical tegminal system in which a single radiating structure on
441 the right tegmen facilitates the production of tonal, extreme ultrasonic songs (Montealegre-Z
442 & Postles, 2010; Sarria-S et al., 2016; Chivers et al., 2017), is not necessarily typical in
443 modern katydids. Instead, a symmetrical tegminal system may be typical for short-winged
444 species with tegmina covered by pronotum (e.g., *Afroanthracites* in Hemp et al., 2015). Now
445 that we have established empirical evidence that both the frequency domain of the call
446 structure and the resonator can be different between populations of *Lipotactes*, the functions
447 of the left mirror and harp area warrant further investigation to enhance our knowledge on the
448 biomechanics of sound production in Lipotactinae.

449

450 The morphology of the stridulatory files in Bornean *Lipotactes* is also diverse. Most
451 interestingly, stridulatory files can range from those with a few large and separated teeth (i.e.,
452 *L. alienus* and individuals from Belait) to those with systematically distributed teeth (i.e.,
453 individuals from Sandakan). For *L. alienus* and individuals from Belait, the few teeth may
454 help distort and recoil scraper at high speed to produce ultrasonic songs, typical of katydids
455 that sing at extreme ultrasonic frequencies (Montealegre-Z & Mason, 2005; Montealegre-Z,
456 et al., 2006; Tan et al., 2019). For the individuals from Sandakan, the file morphology is more
457 representative of many ensiferans in which the systematic distribution of teeth helps maintain
458 constant tooth rate strike (e.g., Robillard et al., 2013; Heller et al., 2017; Heller & Hemp,
459 2018). This may explain why the time domain of the song of Sandakan individuals is distinct
460 from that of *L. alienus* even though we did not find both extreme ultrasonic songs and lower
461 frequency songs respectively. We postulate that there may exist more than one type of sound
462 production mechanism among morphologically cryptic *Lipotactes* from Borneo and
463 recommend further investigation into the biomechanics of the stridulatory file. This may

464 include examining the wing movements using high-speed cameras and detecting for resilin in
465 scraper (Montealegre-Z et al., 2006).

466

467 We observed that there is a marked disparity in the call structure and stridulum morphology
468 among different Bornean *Lipotactes* as compared to the cryptic morphology of their male
469 cerci. This may be explained by potentially complicated communication preceding mating.
470 We speculate that the males sing for the females to recognise and locate them (probably with
471 aid of the visual sense during dusk time or day time as known from other Lipotactini [e.g.,
472 some *Mortoniellus* species] [Ingrisch, 1995]) and assess the mate quality as typical in other
473 katydids (Heller et al., 2017). Furthermore, vibrational communication in ensiferans is also
474 more common than previously thought (Morris et al., 1995; ter Hofstede, 2015). It will not be
475 a surprise that some Lipotactinae exhibit such communication given that some of them are
476 leaf-dwellers (and leaf are excellent medium for such communication).

477

478 ***Conclusions***

479 Our findings offered insights into the usefulness of stridulation and stridulum morphology for
480 separating species of *Lipotactes*. We found that inter-population differences in stridulation
481 and stridulum morphology are generally larger than intra-population differences, even though
482 our sample size is somewhat small (attributed to the difficulty of collecting males). This
483 oppose to postulation by Ingrisch (1995) that there is probably a lack of evolutionary pressure
484 in Lipotactinae for the displacement of call structures, especially since the visual sense is
485 seemingly well developed. The morphological, anatomical and acoustic evidence support the
486 assumption that the populations from Belait, Kuala Belalong and Sandakan probably belong
487 to a species-complex that also includes the described species *L. alienus* and *L. virescens*. We

488 are also confident enough to consider the individuals from Sandakan as a unique species: *L.*
489 *kabili* n. sp.

490

491 However, our findings also raised new questions with regard to the Lipotactinae. The shape
492 of male cercus with the long inner process and shorter lobe is typical of some *Mortoniellus*
493 from Borneo and Sulawesi and not unique for the *L. alienus-virescens* species complex. This
494 led to whether the shape of the male cercus is a good character to differentiate between
495 species and whether similarity in the shape of the male cercus is congruent with the
496 phylogeny. If not, we will need to consider whether the arrangement into genera needs to be
497 evaluated anew. The study of more specimens from other parts of Borneo and a wider area of
498 Southeast Asia, along with the incorporation of phylogenetic analyses will further validate
499 the status of Bornean *Lipotactes*.

500

501

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503

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518

519

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614

615

616 **Table 1.** Measurements (all in mm) of *Lipotactes kabili* n. sp.

	BL	HL	HW	PL	PW	TL	HFL	HTL	OL
Male holotype	10.1	1.6	4.9	4.1	3.2	2.4	10.7	9.4	—
Male paratypes (n = 2)	9.6– 10.9	1.5– 2.0	5.0– 5.2	4.2– 4.4	3.3– 3.6	2.4	10.9	9.8	—
Female paratype (n = 1)	9.9	2.0	5.0	2.6	3.2	—	11.5	9.5	7.1

617

618 **Figure captions**

619

620 **Figure 1.** Morphologically similar *Lipotactes* in the natural environment from different parts
621 of Borneo: *L. alienus* female from Kuala Belalong (1), *L. virescens* male from Bukit Larut (2),
622 *L. kabili n. sp.* male (3) and female (4), and *L. ethospecies* (Belait) males (5, 6).

623

624 **Figure 2.** Habitus of dry-pinned male *Lipotactes* in dorsal (1–4) and lateral (5–8) views: *L.*
625 *alienus* (1, 5), *L. virescens* (2, 6), *L. kabili n. sp.* (3, 7), and *L. ethospecies* (Belait) (4, 8).
626 Scale bars: 5 mm.

627

628 **Figure 3.** Abdominal apex of male *Lipotactes*: *L. alienus* (1), *L. virescens* (2), *L. kabili n. sp.*
629 (3), and *L. ethospecies* (Belait) (4). Scale bars: 1 mm.

630

631 **Figure 4.** *Lipotactes kabili n. sp.* female: habitus in dorsal (1) and lateral (2) views;
632 abdominal apex in dorsal (3) and ventral (4) views; ovipositor in lateral view (5). Scale bars:
633 5 mm (1, 2); 2 mm (3–6).

634

635 **Figure 5.** Left tegmen of *Lipotactes* in ventral view: *L. alienus* (1), *L. virescens* (2), *L. kabili*
636 *n. sp.* (3), and *L. ethospecies* (Belait) (4). Scale bars: 1 mm.

637

638 **Figure 6.** Stridulatory file on left tegmen of *Lipotactes* in ventral view: *L. alienus* (1), *L.*
639 *virescens* (2), *L. kabili n. sp.* (3), and *L. ethospecies* (Belait) (4). Scale bars: 0.2 mm.

640

641

642 **Figure 7.** Tooth distribution on the stridulatory file of *Lipotactes* based on inter-tooth
643 distance (1) and tooth length variations (2). Trend lines are generalised additive model fits.
644 The tooth number corresponds to the first tooth from the anal end to the last tooth at the basal
645 end of the left stridulatory file.

646

647 **Figure 8.** Oscillograms of the *Lipotactes* songs: *L. alienus* (1–3) and *L. kabili n. sp.* (4–6).

648

649 **Figure 9.** Power spectra of the *Lipotactes* songs: *L. alienus* (1) and *L. kabili n. sp.* (2). The
650 relative amplitude scale is scaled between 0 and 1.

651

652 **Figure 10.** Mean plots on the comparison of the time and frequency domains of the
653 *Lipotactes* song. The dot represents the least-square means and the horizontal line represents
654 the 95% confidence interval (CI).

655

656