

1 **The calling songs of some katydids (Orthoptera: Tettigonioidea) from the tropical forests of**
2 **Southeast Asia**

3
4 **Running title:** Calling songs of Southeast Asian katydids

5
6 Ming Kai Tan ^{1*}, Jacob Duncan ^{2†}, Rodzay bin Haji Abdul Wahab ³, Chow-Yang Lee ⁴, Razy Japir ⁵,
7 Arthur Y.C. Chung ⁵, Jessica B. Baroga-Barbecho ⁶, Sheryl A. Yap ^{7,8}, Fernando Montealegre-Z ^{2*}

8
9 ¹ Department of Biological Sciences, National University of Singapore, 16 Science Drive 4,
10 Singapore 117558, Republic of Singapore.

11 ² School of Life Sciences, Joseph Banks Laboratories, University of Lincoln, Green Lane, Lincoln,
12 LN6 7DL, UK

13 ³ Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam, Jalan
14 Universiti, BE1410, Brunei Darussalam

15 ⁴ Department of Entomology, University of California, 900 University Avenue, Riverside, CA
16 92521, USA.

17 ⁵ Forest Research Centre (Sepilok), Sabah Forestry Department, PO Box 1407, 90715 Sandakan,
18 Sabah, Malaysia

19 ⁶ Office of the Vice Chancellor for Research and Extension, University of the Philippines Los
20 Baños, College, Laguna, 4031 Philippines

21 ⁷ Institute of Weed Science, Entomology, and Plant Pathology, College of Agriculture and Food
22 Science, University of the Philippines Los Baños, College, Laguna, 4031 Philippines

23 ⁸ Museum of Natural History, University of the Philippines Los Baños, College, Laguna, 4031
24 Philippines

25 * corresponding authors: orthoptera.mingkai@gmail.com (Ming Kai Tan);

26 fmontealegrez@lincoln.ac.uk (Fernando Montealegre-Z)

27 † joint first author

28
29
30 **Abstract**

31
32 Katydids produce sound by stridulation of the tegmina for signaling and communication. Most
33 katydids are known to sing at ultrasonic frequencies, as compared to crickets. This has drawn
34 interest to investigate the biophysics of ultrasonic sound production and detection, evolution and
35 ecology (including predator–prey interactions) of these katydids. However, most of these studies are
36 based on species from the neotropics, whereas nearly nothing is known about the relatives from
37 another hyper-diverse region, i.e., Southeast Asia. To address this, a concerted effort to document,
38 record, and describe the calling songs of Southeast Asian katydids, especially species which calls at
39 ultrasonic frequencies, were conducted. A study spanning over two years (2018 to 2020) in the
40 Malay Peninsula (Singapore and Malaysia), Borneo (Brunei Darussalam and Sabah), and the
41 Philippines revealed previously unknown calls of 24 katydid species from four subfamilies. The
42 calling songs of Southeast Asian katydid species are highly diversified in both the time and
43 frequency domains. Call structure can range from isolated syllables (e.g., *Holochlora*), continuous
44 trills (e.g., *Axylus philippinus*) to short pulse-trains (e.g., *Euanisous teuthroides*) and complex
45 echemes (e.g., *Conocephalus* spp.). 87.5 % of species have ultrasonic peak frequencies and 12.5 %
46 can be considered extreme ultrasonic callers (peak frequency >40 kHz). The call spectrum ranges
47 from tonal (e.g., spectral entropy is 6.8 in *Casigneta* sp. 2) to resonant (entropy is 8.8 in
48 *Conocephalus cognatus*). Of the 24 species whose calls are described here, we also imaged and
49 described the sound-producing structures of 18 species. This study provides a preliminary overview
50 of the acoustic diversity of katydids in Southeast Asia, and the authors hope to inspire further
51 investigation into the bioacoustics of little-known katydids from Southeast Asia. Amassing a
52 database of calling songs and sound-producing organs from different species can be important to

address the taxonomy impediment while advancing our knowledge about the bioacoustics of Southeast Asian katydids.

Key words: acoustics, calls, frequency, sound-producing organs, stridulation, Tettigoniidae, ultrasound

Introduction

Katydid are a highly speciose group of insects (Mugleston et al. 2018), known for using acoustic signals for communication. Different species can produce very different calling songs in terms of the temporal (e.g., duration, period, call structure) and frequency (e.g., peak frequency, tonality) domains. Females can use such calling songs to discriminate conspecific from heterospecific males (Morris et al. 1994; Heller 1995; Morris 1999; Heller and Hemp 2020). For example, some katydids produce songs at frequency as low as 0.6 kHz (in *Tympanophyllum arcuifolium* (Haan, 1843), see Heller 1995), whereas other species can call at as high as 150 kHz (in *Supersonus aequoreus* Sarria-S. et al., 2014, see Sarria-S et al. 2014). Compared to crickets which generally produce low frequencies (with few exceptions such as lebinthines, see Robillard et al. 2007; Tan et al. 2021), such vast variation in the frequencies makes katydids an ideal subject for studying acoustic communication and its evolution.

Katydid generate sounds by stridulation (Morris and Pipher 1967; Bailey 1970; Ewing 1989; Chivers et al. 2014). Typically, the sound is generated when the scraper on the right tegmen makes contact with the teeth on the stridulatory file on the left tegmen within a cycle of wing movement (Walker and Dew 1972; Morris 1999; Bennet-Clark 2003). In some katydids, the velocity at which the scraper passes through the teeth and the density of the teeth dictate the peak frequency of species calling song, although the mirror area on the right tegmen can also play a role in dictating the peak frequency (Bailey 1969; Montealegre-Z 2012; Chivers et al. 2014). For species which produce extreme ultrasound (>40 kHz), however, it is not mechanically possible for the katydids to move their tegmina at such high velocity. Instead, the scraper is loaded with resilin and may be deformable, allowing elastic energy to be stored and released. This mechanism generates much higher frequency calls than the wing movement velocity would allow (Morris et al. 1994; Montealegre-Z et al. 2006).

Many katydids emit ultrasonic frequency in their calling songs (e.g., Morris and Pipher, 1967; Bailey 1967, 1970). More than 70% of katydids measured so far sing at ultrasonic frequencies (>20 kHz), with some species reaching extreme ultrasonic frequencies (>40 kHz) (Mason et al. 1991; Montealegre-Z et al. 2017). The generation of ultrasonic songs by katydids has its advantages and disadvantages compared to low-frequency calls typically produced by crickets (Morris et al. 1994; Montealegre-Z et al. 2006). Ultrasound has enhanced directionality and radiation efficiency, allowing the males to find mates and be located by females more readily while avoiding detection by predators (Mason and Bailey 1998). For pure-tone callers, another advantage is the ability to avoid eavesdropping by predators, particularly the bats (Belwood and Morris 1987). On the other hand, the decay of energy in ultrasound is more rapid, thus reducing broadcasting distance (Römer and Lewald 1992). Therefore, the ecological and evolutionary consequences of generating ultrasonic songs make these katydids interesting study subjects.

The study of the ecology and evolution of ultrasonic-singing katydids—including the documentation and description of calls (e.g., Montealegre-Z and Morris 1999; ter Hofstede et al. 2020); the systematics (e.g., Siarra et al. 2014, 2016; Chamorro-Rengifo et al. 2014; Chamorro-Rengifo and Braun 2016); biomechanics of sound production (e.g., Morris et al. 1994; Montealegre-Z and Mason 2005; Montealegre-Z et al. 2006, 2017); predator–prey interaction between bats and

katydids (e.g., Libersat and Hoy 1991; ter Hofstede et al. 2010); and sexual selection (e.g., Bailey and Gwynne 1988; Mason and Bailey 1998)—has traditionally been focused on species from the neotropics. Acoustic communication of Southeast Asian orthopterans is less well studied (but see e.g., Heller 1995; Ingrisch 1995, 1998; Riede 1996, 1997; Tan 2011; Heller et al. 2017, 2021; Tan et al. 2019, 2020a). Despite Southeast Asia containing one of the noisiest places, many species are still unknown and need taxonomic description and revision (Tan et al. 2017). Barely anything is known about the biology of many described species beyond their original descriptions.

While taxonomy is crucial for accurately identification and cataloging of bioacoustics data for other studies on ecology, behavior and evolution; the use of bioacoustics can also help overcome the taxonomic impediment. Recent studies have demonstrated that the calling songs of Southeast Asian katydids can be used to resolve taxonomic problems related to species-complex. Heller et al. (2017) used the calling songs to discover cryptic species within the *Ducetia japonica*-species group. Previously thought to be a widely distributed species, it turns out different regions harbor different cryptic species. Tan et al. (2021a) and Heller et al. (2021b) combined calling songs and stridulatory anatomy to address species delineation in *Lipotactes alienus-cum-virescens* and *Mecopoda elongata*-species complexes. In the case of *Lipotactes* Brunner von Wattenwyl, 1898, Tan et al. (2021a) provided a foundation for further taxonomic progress of these little-known katydids from Southeast Asia (Ingrisch 2021; Gorochoy 2021). These demonstrate the importance of combining bioacoustics and the traditional taxonomy of katydids from Southeast Asia.

This study aims to initiate a database containing acoustic and morphological data of Southeast Asian katydids. To document the previously-unknown calling songs of Southeast Asian katydids, we opportunistically collected 24 species from Singapore and other parts of Southeast Asia, recorded their calling songs under ex-situ conditions, and subsequently accurately identified and systematically voucher the specimens. Given the importance of the morphology on the sound-producing organs in dictating key acoustic parameters (e.g., peak frequency, resonance) (Morris and Pipher 1967; Bailey 1970; Montealegre-Z 2009; Montealegre-Z and Postles 2010), we also made images of the sound-producing organs to complement the calling song description. These data can eventually be incorporated into traditional taxonomy and/or for meta-analysis in the future to address the taxonomy impediment while advancing our knowledge about the acoustic communication of these katydids.

Materials and Methods

Collection and husbandry of katydids

Katydids were opportunistically collected by sight (mostly at night but occasionally in the day) from six sites in the Malay Peninsula, Borneo and the Philippines: (1) Singapore from August 2018 to December 2019 and from June to August 2020; (2) Pulau Tioman, Johor, Peninsular Malaysia from 7 to 9 August 2018; (3) Belait and Temburong, Brunei Darussalam from 6 to 18 July 2019; (4) Sandakan, Sabah, East Malaysia from 7 to 12 January 2019 and from 30 September to 4 October 2019; (5) Laguna, Luzon, the Philippines from 11 to 13 May and from 6 to 8 September 2019. Whenever possible, in-situ images were taken using a Canon EOS 500D digital SLR camera with a compact-macro lens EF 100 mm f/2.8 Macro USM, and Canon Macro Twin Lite MT-24EX was used for lighting and flash.

The katydids were kept in insect cages. To avoid dehydration, wet cotton balls were provided, cages were covered with a wet cloth and/or regular spraying was done. The katydids were subjected to light: dark hours corresponding to the locations. They were generally fed with Pedigree Adult Chicken and Vegetables (18% protein, 10% fat, 5% fiber, no salt), or SmartHeart Puppy Beef and Milk Flavor (26% protein, 10% fat, 4% fiber, 10% moisture with salt) dog food (sometimes

crushed). Fruits were also provided occasionally. Meconematinae were fed with living *Drosophila* fruit flies.

Acoustic recordings and analysis

Acoustic recording and analysis generally followed that in Tan et al. (2019, 2020a). All recordings were obtained in laboratory conditions or biological stations in the dark. Calling song of an isolated male placed inside a standardized insect cage (25 cm in diameter and 33 cm tall) with nylon cover was done using a sampling frequency of 256 kHz-samples/s Echo Meter Touch or Echo Meter Touch Pro 2 (based on Knowles FG sensor). The recorder was placed horizontally and at about 2–5 m away from the cage (depending on the loudness of the call to avoid clipping of the recording). It should however be noted that with this type of microphone, a recording distances of less than 2 m is preferred to minimize distortion of the temporal structure of the signal. The triggered recording was used with the Trigger Minimum Frequency set at 20 kHz. However, this is only a trigger and will not affect lower frequencies being recorded. The recorded signals were saved in 12-bit and 16-bit WAV format, respectively. Ambient temperature was logged using a HOBO 8K Pendant® Temperature logger (model: UA-001-08, Onset, Bourne, MA), or a temperature-humidity meter (Smartsensor AR867, Arco Science and Technology Limited, Dongguan, PRC).

The basic katydid song terminology follows Baker and Chesmore (2020):

Calling song = spontaneous song produced by an isolated male to attract a female;

Chirp = a type of echeme consisting of a few definite syllables;

Echeme = a first-order assemblage of syllables;

Echeme-sequence = a first-order assemblage of echemes;

Interval = silent interval between calls and/or pulses, or downtime;

Peak frequency = frequency with the highest energy from the mean spectrum;

Period = interval between the start of successive units (e.g., syllable, echeme);

Pulse = a single unbroken wave train, isolated in time, produced by each tooth impact;

Pulse-train = a series of pulses, isolated in time;

Syllable = single complete stridulatory movement (i.e., opening and closing of wings). Since wing movement was not examined here, the term syllable is used here as an assemblage of pulses isolated in time, and likely to correspond to a single complete stridulatory movement;

Trill = a type of echeme consisting of many syllables;

Verse = a complete sequence of syllables which is separated from other verses by a distinct and prolonged pause.

Additionally, we also used spectral entropy to estimate signal heterogeneity, in which a low value indicates highly tonal signals and a high value indicates broad-band signals (Chivers et al. 2017a).

Parameters of the temporal domain (e.g., call duration/ period and interval) were measured manually using Raven Lite 2.0.0. For frequency domain parameters, custom-written scripts in MATLAB (R2019a; The MathWorks Inc., Natick, MA, United States) were used. This involved determining 2048 Fast Fourier Transformation (FFT) lines, Q_{-3} , and Q_{-10} entropy, spread and flatness.

Specimen curation and identification

The specimens were preserved in absolute analytical-grade ethanol, and later pinned and dry-preserved. For future molecular work, a single hind leg from each specimen was also preserved in absolute analytical-grade ethanol. The katydids were identified using taxonomic papers, including Willemse (1959), Jin (1992), Ingrisch (1995, 1998, 2015), Gorochoy (1998, 2008, 2011, 2013), Tan and Ingrisch (2014), Tan (2014, 2017), Tan et al. (2015, 2018, 2019), Tan and Artchawakom (2017), Jin et al. (2020); and comparing with photographs of type specimens. Taxonomists, specifically Xing-bao Jin, Sigfrid Ingrisch, and Andrei Gorochoy, were also consulted.

209

210 **Sound-producing structure**

211 The left and right tegmina were dissected, whenever possible. Three-dimensional images of the
 212 stridulatory file on the left tegmen, and sound-producing organs on the right tegmen were obtained
 213 with infinite focus microscopy using an Alicona Infinite Focus (model G5) microscope (OPTIMAX
 214 Imaging Inspection and Measurement Limited, Leicestershire, UK).

215

216 **Depositories**

217 The specimens were deposited in:

218 FRC Forest Research Center, Sepilok, Sabah, East Malaysia

219 UBDM Universiti Brunei Darussalam Museum, Brunei Darussalam

220 UPLBMNH University of the Philippines Los Baños, Museum of Natural History, Philippines

221 ZRC Zoological Reference Collection, Lee Kong Chian Natural History Museum,
 222 Singapore

223

224 The sound files were deposited in the Orthoptera Species File (OSF) Online Version 5.0/5.0
 225 (Cigliano et al. 2022).

226

227

228 **Results**

229

230 **Summary**

231 In total, 37 individuals of katydids were collected. Of which, the calling songs of 24 species of
 232 katydids from 20 genera of the subfamilies Conocephalinae (nine species), Lipotactinae (one
 233 species), Meconematinae (seven species), and Phaneropterinae (seven species) were recorded for
 234 the first time (Table 1). The peak frequency of the 24 katydids ranges from as low as 12.6 kHz to as
 235 high as 54.2 kHz in *Paragraecia temasek* Tan & Ingrisch, 2014 and in an unidentified
 236 Meconematini from Sandakan, respectively. Twenty-one species (87.5 %) have peak frequencies at
 237 the ultrasonic range, of which 3 species (12.5 %) can be considered extreme ultrasonic callers (i.e.,
 238 peak frequency >40 kHz) (Table 1). The spectral entropy of the katydids ranges from 6.8 to 8.8 in
 239 *Casigneta* sp. 2 and in *Conocephalus cognatus* (Redtenbacher, 1891), respectively. Of the 24
 240 species whose calls are described here, we also imaged and described the sound-producing
 241 structures of 18 species.

242

243 **Table 1.** Summary of the species recorded in this study.

	Species	Country of origin	Call structure	Spectral entropy	Peak freq. (kHz)
	Subf. Conocephalinae				
1.	<i>Axylus philippinus</i>	Philippines	Continuous trill of disyllabic verse	8.5±0.1	34.7±1.3
2.	<i>Conocephalus cognatus</i>	Singapore	Complex echeme	8.8±0.1	28.7±2.1
3.	<i>Conocephalus exemptus</i>	Singapore	Complex echeme	7.8±0.1	15.5±0.2
4.	<i>Paragraecia temasek</i>	Singapore	Echeme	7.7±0.1	12.6±0.1
5.	<i>Peracca macritchiensis</i>	Singapore	Echeme-sequence	7.4	29.3±1.1
6.	<i>Salomona borneensis</i>	Malaysia	Echeme-sequence	8.4±0.1	13.9±0.4
7.	<i>Salomona maculifrons</i>	Philippines	Sequence of isolated echemes	8.5±0.1	30.5±0.7

8.	<i>Viriacca insularis</i>	Malaysia	Echeme	8.0±0.2	23.1±1.8
9.	<i>Viriacca modesta</i>	Brunei	Echeme-sequence	7.8±0.1	26.0±2.4
	Subf. Lipotactinae				
10.	<i>Lipotactes maculatus</i>	Singapore	Isolated echemes	8.3	33.1±3.1
	Subf. Meconematinae				
11.	<i>Alloteratura lamella</i>	Singapore	Complex echemes or isolated syllables	7.7±0.3	25.5±0.7
12.	<i>Borneopsis cryptosticta</i>	Singapore	Sequence of paired syllables or echemes	8.5±0.3	42.3±2.4
13.	<i>Euanisous teuthroides</i>	Singapore	Echeme	7.4±0.2	30.3±0.7
14.	<i>Kuzicus denticulatus</i>	Singapore	Continuous trill	7.7	39.6±2.4
15.	Meconematini (SDK.19.79)	Malaysia	Continuous trill of paired syllables	7.6	54.2±0.4
16.	<i>Neophisis siamensis</i>	Singapore	Sequences of isolated syllables	7.1	36.7±1.8
17.	<i>Xizicus</i> sp.	Singapore	Continuous trill	7.7	40.9±0.4
	Subf. Phaneropterinae				
18.	<i>Casigneta</i> sp. 1	Singapore	Pulse-train	7.6±0.1	28.7±0.8
19.	<i>Casigneta</i> sp. 2	Singapore	Triplet-syllables	6.8±0.2	28.2±0.2
20.	<i>Holochlora</i> nr. <i>bilobata</i>	Singapore	Isolated syllables	8.1±0.4	33.3±1.0
21.	<i>Phaneroptera brevis</i>	Singapore	Paired-syllables	7.9	21.9±0.8
22.	<i>Phaulula malayica</i>	Singapore	Isolated syllables	7.8	23.6±1.2
23.	<i>Psyrana tigrina</i>	Malaysia	Pulse-train	8.1	35.5±2.1
24.	<i>Scambophyllum sanguinolentum</i>	Singapore	Pulse-train	7.0±0.1	23.7±0.3

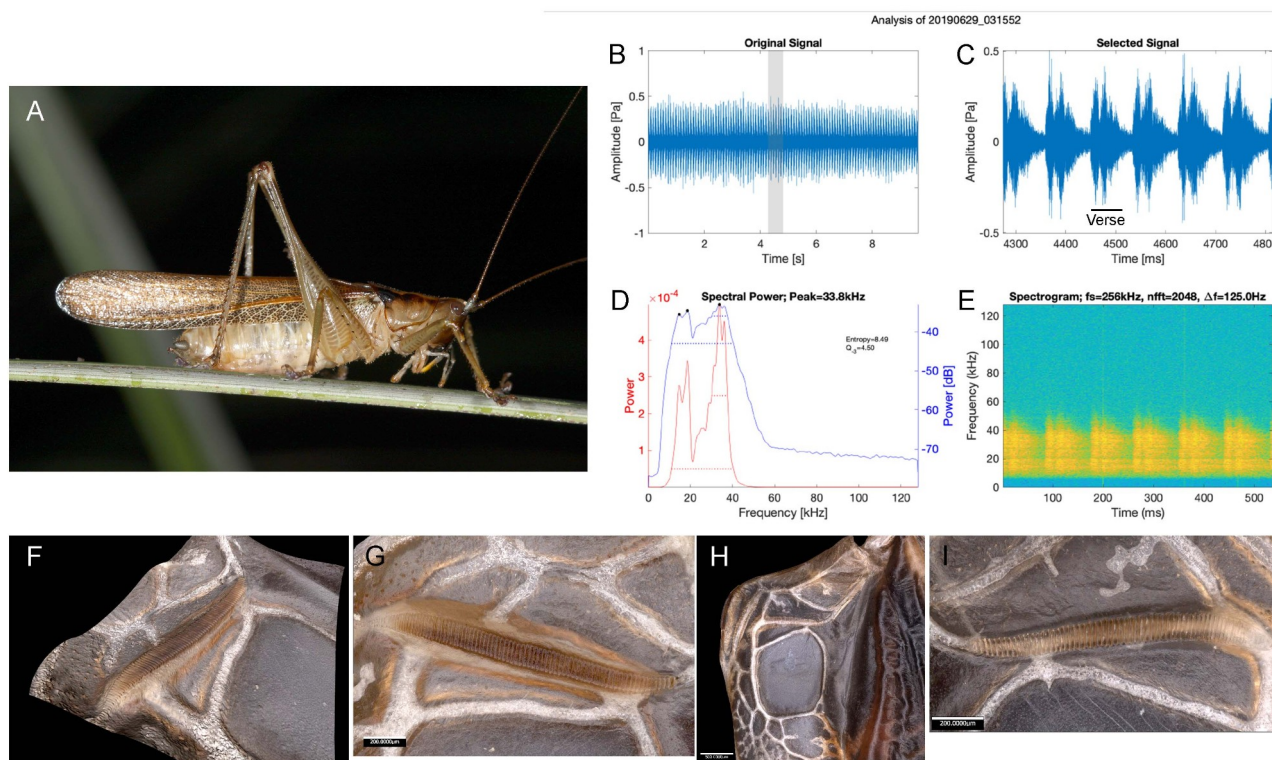
244

245

246 Song and sound-producing structure descriptions

247 *Axylus philippinus* (Hebard, 1922) (n = 1 male, 10 sound files) (Fig. 1).—The calling song is
248 a continuous trill made up of disyllabic verse (each consisting of two amplitude peaks). At 30.0±0.5
249 °C (28.9–30.3 °C), the trill has a verse repetition rate of 11±1 verse s⁻¹ (9–11 verses s⁻¹). The verse
250 period is 92.9±5.5 ms (87.5–104.1 ms). The call spectrum has a peak frequency of 34.7±1.3 kHz
251 (32.5–36.0 kHz), and another peak at 16.4±1.9 kHz (13.5–19.0 kHz) showing energy in the sonic
252 range; and the spectral entropy is 8.5±0.1.

253 Ventrally, the left macropterous tegmen possesses a straight stridulatory file of about 1.556
 254 mm in length with 91 rather broad teeth. The teeth on the stridulatory file of the left tegmen are
 255 fairly uniformly distributed and narrowly spaced apart. The inter-tooth distance is nearly constant
 256 throughout the file. In the mid-part of the stridulatory file, the teeth density is $48.5 \text{ teeth mm}^{-1}$ and
 257 the average tooth width is $105 \mu\text{m}$. The file (Cu2) is slightly elevated on a swollen vein buttress.
 258 The right tegmen has a rectangular mirror that is longer than broad, and a scraper of about 1.203
 259 mm in length with about 59 rather broad teeth and a few indistinct teeth at the anal end of the
 260 scraper.
 261

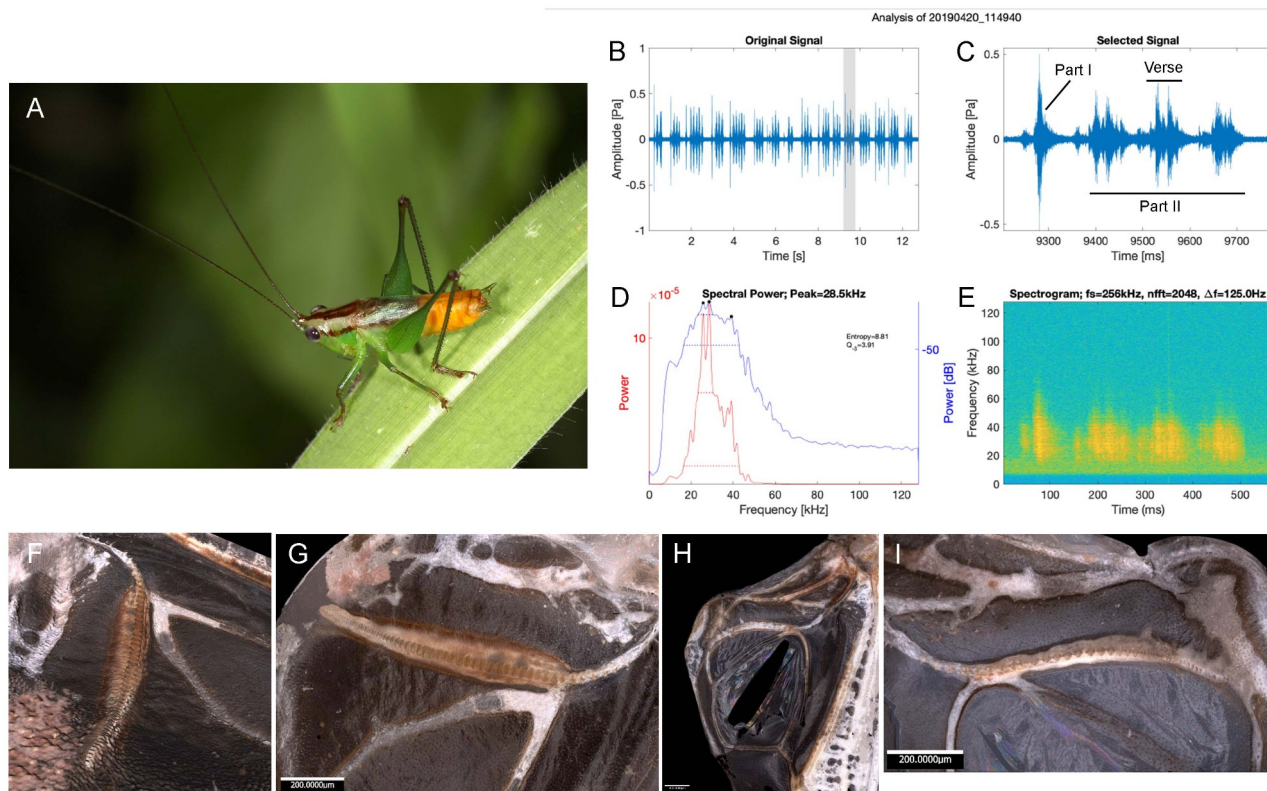


262
 263 **Fig. 1.** *Axylus philippinus* male adult in its natural environment in Laguna, the Philippines (A).
 264 Oscillograms showing a continuous trill (B) and a section of the trill consisting of five complete
 265 verses (C). Power spectrum (D) and spectrogram of the selection (E) of the same five complete
 266 verses. Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same
 267 SF (G), ventral view of the right tegmen sound-producing organs (H), and a ventral view of the
 268 right SF (I).
 269

271 ***Conocephalus cognatus* (Redtenbacher, 1891)** (n = 5 males, 16 sound files) (Fig. 2).—The
 272 calling song is an echeme-sequence made up of complex echemes. Each echeme consists of two
 273 parts. At $29.4 \pm 0.6^\circ\text{C}$ ($27.8\text{--}31.0^\circ\text{C}$), the first part at the start of an echeme consists of a syllable
 274 showing a rapid-decay pulse, with duration of $51.3 \pm 10.7 \text{ ms}$ ($25.0\text{--}67.0 \text{ ms}$) and period of
 275 $88.1 \pm 16.4 \text{ ms}$ ($62.0\text{--}120.0 \text{ ms}$); followed by an interval of $36.9 \pm 16.7 \text{ ms}$ ($6.0\text{--}69.0 \text{ ms}$). The second
 276 part consists of 2–23 verses with a verse repetition rate of $8 \pm 1 \text{ verses s}^{-1}$ ($8\text{--}9 \text{ verses s}^{-1}$). Each verse
 277 shows 2–4 amplitude peaks; verse duration is $80.1 \pm 16.0 \text{ ms}$ ($47.0\text{--}108.0 \text{ ms}$). Often, only the first
 278 part of the calling song is produced. The call spectrum has a peak frequency of $28.7 \pm 2.1 \text{ kHz}$ (25.6--
 279 33.1 kHz), and the spectral entropy is 8.8 ± 0.1 .

280 Ventrally, the left micropterous tegmen possesses a stridulatory file of about 0.988 mm in
 281 length with about 56 teeth. The stridulatory file on the left tegmen is primarily straight and strongly
 282 curving anteriorly at the basal end. The teeth at the anal end are smallest (average tooth width is
 283 $13.4 \mu\text{m}$) and closely packed (average inter-tooth distance is $9.2 \mu\text{m}$); the teeth in the mid-part of
 284 the file are largest (average tooth width is $35.7 \mu\text{m}$) with an average inter-tooth distance of $26.0 \mu\text{m}$;

285 the teeth at the basal end have an average tooth width of 30.5 μm , and are most widely spaced apart
 286 (average inter-tooth distance is 31.8 μm). The file (Cu2) is only slightly elevated on a swollen vein
 287 buttress. The right tegmen has an oblique mirror longer than broad, with the anal margin distinctly
 288 shorter than the basal margin. The scraper on the right tegmen is sinusoidal, about 0.802 mm in
 289 length, with about 37 stout teeth.
 290

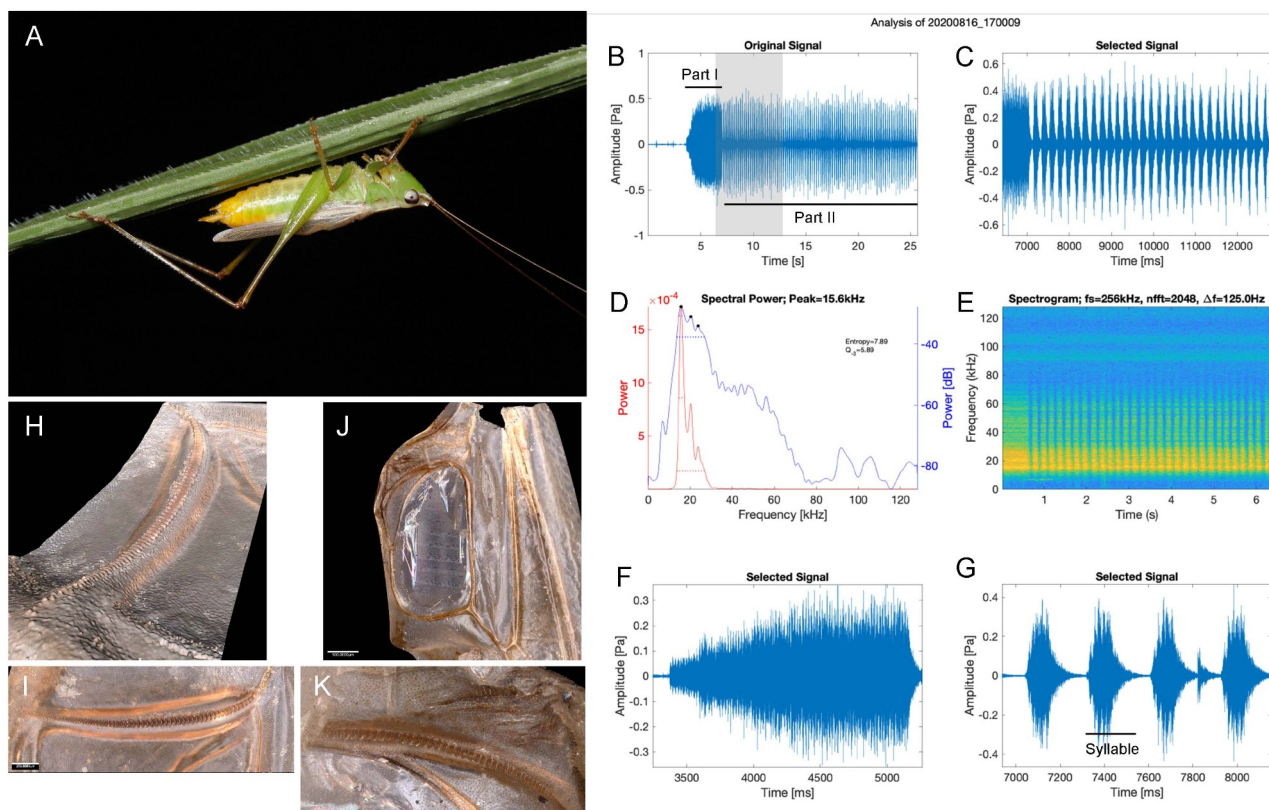


291
 292 **Fig. 2.** *Conocephalus cognatus* male adult in its natural environment in Singapore (A).
 293 Oscillograms showing an echeme-sequence (B) and a complex echeme with two parts (C). Power
 294 spectrum (D) and spectrogram (E) of an echeme made up of two parts. Three-dimensional anal view
 295 of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right
 296 tegmen sound-producing organs (H), and a ventral view of the right SF (I).
 297

298 ***Conocephalus exemptus* (Walker, 1869)** (n = 2 males, 9 sound files) (Fig. 3).—A sound file
 299 was deposited in OSF based on a specimen from Thailand. While the call of the Thailand specimen
 300 consists of an echeme made up of four syllables, the calling song of individuals from Singapore
 301 appears as a complex echeme consisting of two parts. At 29.4 ± 0.1 °C (29.3 – 29.6 °C), the first part,
 302 which is not always present, consists of a verse with duration of 2.6 ± 1.2 s (1.1 – 3.9 s). This verse
 303 shows a series of amplitude peaks with increasing amplitude to a maximum. The second part
 304 consists of a trill made up of a sequence of syllables. Syllable duration is 0.10 ± 0.01 s (0.09 – 0.13 s)
 305 and syllable period is 0.26 ± 0.05 s (0.19 – 0.32 s). The syllables have similar amplitudes as the
 306 maximum amplitude of the first part of the echeme. Each syllable shows 5 ± 1 (4–6) amplitude
 307 peaks. The call spectrum has a peak frequency of 15.5 ± 0.2 kHz (15.2 – 16.0 kHz), and the spectral
 308 entropy is 7.8 ± 0.1 .
 309

310 Ventrally, the left macropterous tegmen possesses a stridulatory file of about 1.761 mm in
 311 length with about 60 stout teeth and a few indistinct ones at the anal end. The stridulatory file on the
 312 left tegmen is faintly curved and strongly curving anteriorly at the basal end. The teeth are smallest
 313 (average tooth width is 38.3 μm) and closely packed (average inter-tooth distance is 18.1 μm) at the
 314 anal end, largest (average tooth width is 59.9 μm) and most widely-spaced (average inter-tooth
 distance is 35.5 μm) in the middle portion. The file (Cu2) is slightly elevated on a swollen vein

315 buttress. The right tegmen has a distinctly elongated mirror. The scraper on the right tegmen is of
 316 about 1.217 mm in length with about 51 stout teeth.
 317



318
 319 **Fig. 3.** *Conocephalus exemptus* male adult in its natural environment in Singapore (A).
 320 Oscillograms showing the start of a complex echeme (B) and a section of the echeme at the end of
 321 the first part and the beginning of the second part (C). Power spectrum (D) and spectrogram (E) of
 322 the echeme at the end of the first part and the beginning of the second part. Oscillograms showing
 323 the first (F) and second (G, showing four syllables) parts of an echeme. Three-dimensional anal
 324 view of the left stridulatory file (SF) (H), ventral view of the same SF (I), ventral view of the right
 325 tegmen sound-producing organs (J), and a ventral view of the right SF (K).
 326

327 ***Paragraecia temasek* Tan and Ingrisch, 2014** (n = 1 male, 20 sound files) (Fig. 4).—The
 328 calling song consists of isolated echemes, but sometimes two to four echemes may aggregate
 329 together. At 28.9 ± 0.1 °C (28.9–29.1 °C), echeme duration is 0.86 ± 0.25 s (0.59–1.54 s). Each
 330 echeme shows a series of syllables with increasing amplitude to a maximum. Each echeme has a
 331 syllable repetition rate of ca. 89 syllables s^{-1} (87–91 syllables s^{-1}). The interval between echemes is
 332 also variable, ranging from 0.13 s to 2.6 s (0.63 ± 0.58 s). Unlike many katydids recorded here, a
 333 harmonic series consisting of three peaks is recorded: fundamental frequency, which is also the
 334 peak frequency of 12.6 ± 0.1 kHz (12.4–12.8 kHz) at the sonic range; followed by peaks of
 335 decreasing energy at 23.9 ± 0.3 kHz (23.0–24.5 kHz) and 36.2 ± 0.4 kHz (35.5–37.0 kHz) at the
 336 ultrasonic range. The call spectrum has a spectral entropy is 7.7 ± 0.1

337 Ventrally, the left macropterous tegmen possesses a very straight stridulatory file of about
 338 1.464 mm in length with more than 250 rather broad teeth. The teeth on the stridulatory file on the
 339 left tegmen are fairly uniformly distributed and very narrowly spaced. In the mid-part of the
 340 stridulatory file, the teeth density is 10.2 teeth mm^{-1} and the average tooth width is 103 μm . The
 341 teeth are most prominent in the middle portion and tooth width tapers gently towards the ends. The
 342 distance between teeth is nearly constant throughout the file. The file (Cu2) is slightly elevated on a
 343 swollen vein buttress. The right tegmen has a rectangular mirror, longer than broad, with curved
 344 anal and basal margins; and a scraper of about 1.129 mm in length, with about 130 rather broad
 345 teeth

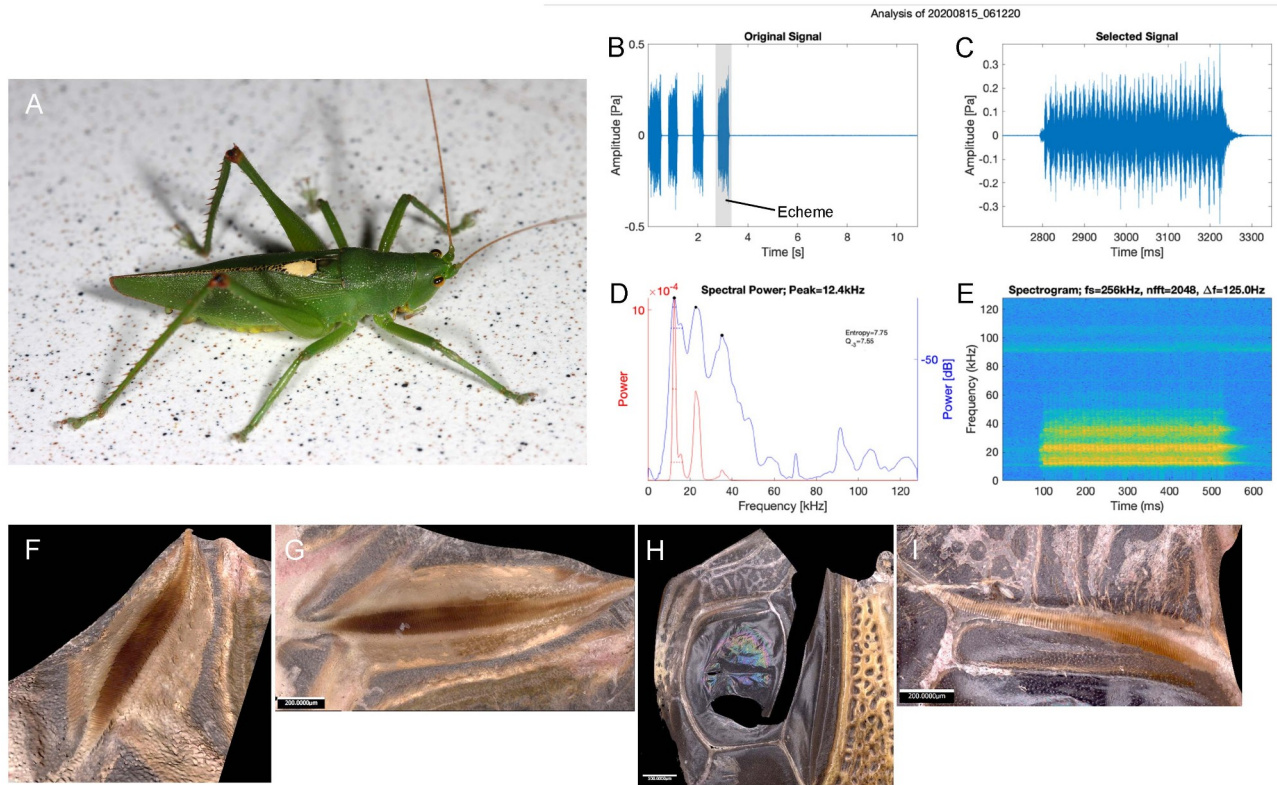


Fig. 4. *Paragraecia temasek* male adult in the lab (A). Oscillograms showing four echemes (B) and a echeme (C). Power spectrum (D) and spectrogram of the same echeme (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right tegmen sound-producing organs (H), and a ventral view of the right SF (I).

Peracca macritchiensis Tan and Ingrisch, 2014 (n = 1 male, 10 sound files) (Fig. 5).—The calling song consists of echeme-sequence made up of echemes of highly variable duration. Sometimes, the echeme sequence lasts for a long duration, appearing as a continuous ‘trill’. At 28.5 ± 1.1 °C (26.9–29.3 °C), the echeme is made up of closely-spaced syllables with a syllable repetition rate of 81 ± 6 syllables s^{-1} (69–91 syllables s^{-1}). Syllable duration is 9.1 ± 1.5 ms (6.2–11.6 ms). The call spectrum has a peak frequency of 29.3 ± 1.1 kHz (27.8–30.8 kHz), and the spectral entropy is 7.4.

Ventrally, the left micropterous tegmen possesses a very straight stridulatory file of about 0.611 mm in length with about 117 rather broad teeth. The teeth on the stridulatory file are fairly uniformly distributed and very narrowly spaced. In the mid-part of the stridulatory file, the teeth density is 20.5 teeth mm^{-1} and the average tooth width is 47.6 μm . The teeth are most prominent in the middle portion and tooth width tapers gently towards the ends. The distance between teeth is nearly constant throughout the file. The file (Cu2) is faintly elevated on a swollen vein buttress. The right tegmen has a pyriform mirror a narrower anterior end.

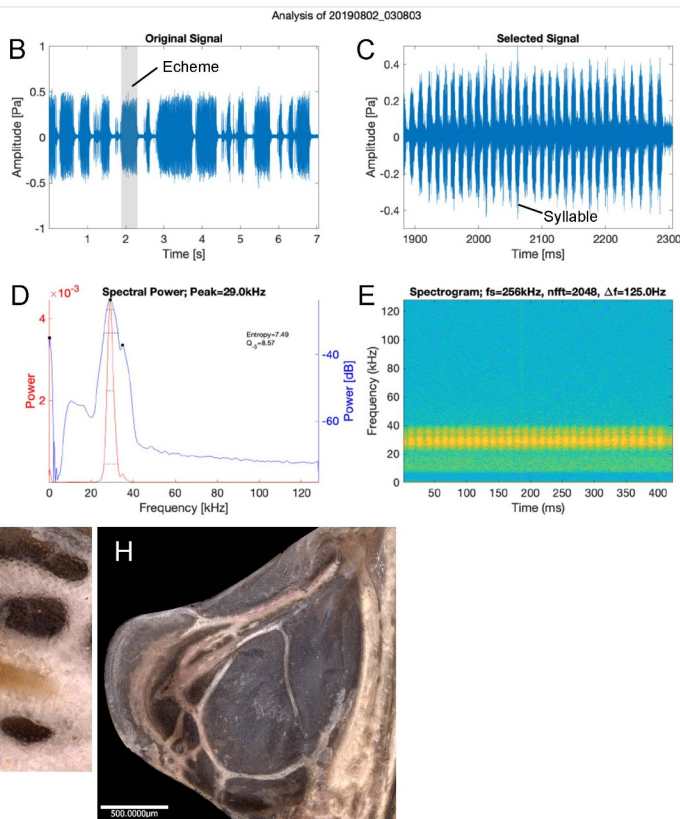


Fig. 5. *Peracca macritchiensis* male adult in its natural environment in Singapore (A). Oscillograms showing an echeme-sequence (B) and a echeme (C). Power spectrum (D) and spectrogram of the same echeme (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), and ventral view of the right tegmen sound-producing organs (H).

Salomona borneensis Willemse, 1959 (n = 1 male, 11 sound files) (Fig. 6).—The calling song is an echeme-sequence made up of fairly isolated echemes. At 28.7 ± 0.2 °C (28.4 – 29.0 °C), the echeme duration is 0.24 ± 0.02 s (0.22 – 0.28 s) and the interval between echemes is 0.33 ± 0.12 s (0.13 – 0.52 s). Each echeme consists of two or three closely-packed syllables, each lasting about 50 ms. The call spectrum has a peak frequency of 13.9 ± 0.4 kHz (13.0 – 14.5 kHz) and another peak at 31.2 ± 1.0 kHz (30.0 – 33.0 kHz) showing energy in the ultrasonic range; and the spectral entropy is 8.4 ± 0.1 .

Ventrally, the left macropterous tegmen possesses a stridulatory file of about 2.872 mm in length with about 79 rather broad teeth. The stridulatory file on the left tegmen is faintly curved and slightly more strongly curving anteriorly at the basal end. The teeth are most prominent in the middle portion and tooth width tapers gently towards the ends. The distance between teeth is fairly similar. The file (Cu2) is slightly elevated on a swollen vein buttress. The right tegmen has a squarish mirror. The scraper on the right tegmen is sinusoidal, with a length of about 2.409 mm in length, and with about 65 rather broad teeth.

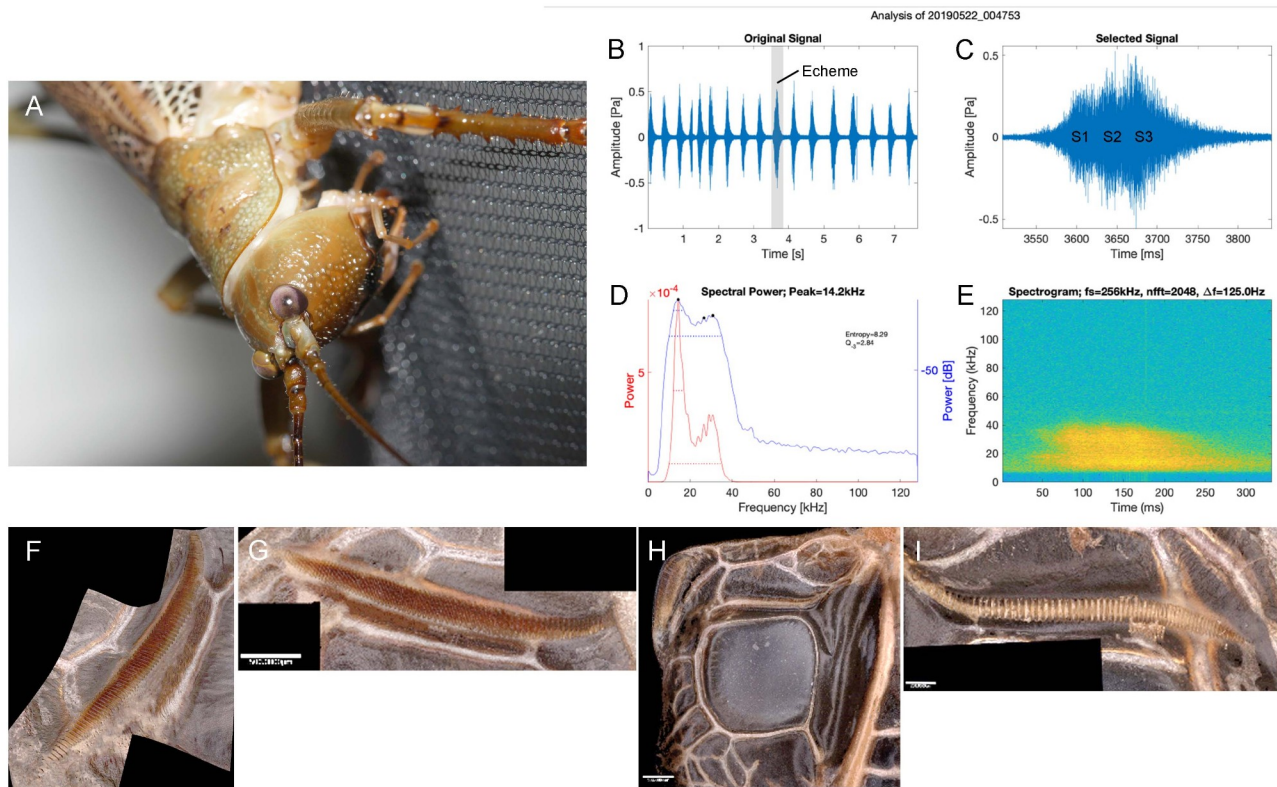


Fig. 6. *Salomona borneensis* male adult in the lab (A). Oscillograms showing an echeme-sequence with 17 echemes (B) and an echeme with three syllables denoted as S1 to S3 (C). Power spectrum (D) and spectrogram of the same echeme (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right tegmen sound-producing organs (H), and a ventral view of the right SF (I).

***Salomona maculifrons* Stål, 1877** (n = 1 male, 15 sound files) (Fig. 7).—The calling song is a sequence of distinctly isolated syllables, occurring either over long duration as a trill or shorter duration as echemes. At 28.2 ± 1.6 °C (26.7–30.5 °C), the syllable has duration of ca. 50 ms, and the interval between syllables is 67 ± 47 ms (17–194 ms). The call spectrum has a peak frequency of 30.5 ± 0.7 kHz (30.5–31.5 kHz) at the ultrasonic range and another peak at 14.2 ± 0.2 kHz (13.9–14.5 kHz) showing energy in the sonic range. The two peaks have relatively similar energy and at times, the non-ultrasonic peak is the dominant frequency. The spectral entropy is 8.5 ± 0.1 .

Ventrally, the left macropterous tegmen possesses a very straight stridulatory file of about 2.274 mm in length with about 87 rather broad teeth. The teeth are largest in the middle portion (average tooth width is 202 μ m) and tooth width tapers gently towards the ends. The teeth are closely packed and the distance between teeth is fairly similar. In the mid-part of the stridulatory file, the teeth density is 40 teeth mm^{-1} . The file (Cu2) is slightly elevated on a swollen vein buttress. The right tegmen has somewhat squarish mirror, but slightly broader than long. The scraper on the right tegmen is of about 1.615 mm in length with about 69 rather broad teeth.

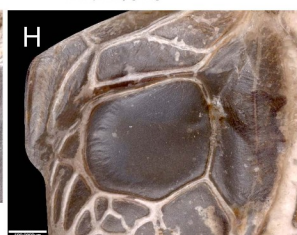
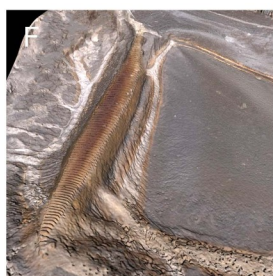
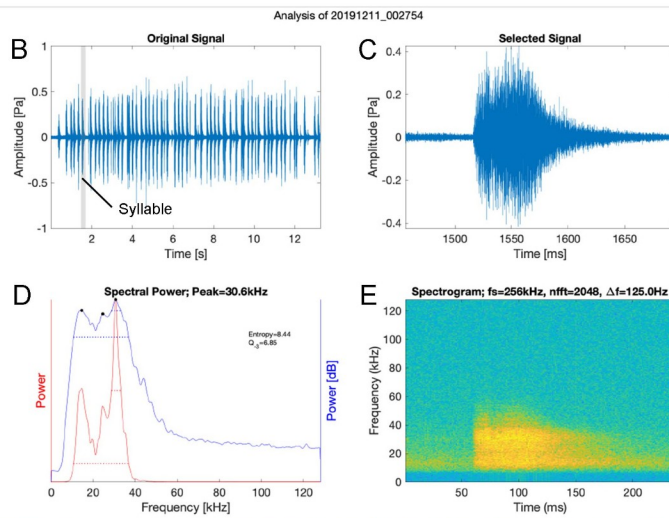


Fig. 7. *Salomona maculifrons* male adult in the lab (A). Oscillograms showing a continuous trill (B) and a syllable (C). Power spectrum (D) and spectrogram of the same syllable (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right tegmen sound-producing organs (H), and a ventral view of the right SF (I).

***Viriacca insularis* Gorochoy, 2011** (n = 1 male, 18 sound files) (Fig. 8).—The calling song is an isolated echeme made up of syllables of increasing amplitude to a maximum. Sometimes, the calling song can occur over long duration as a continuous trill. Each echeme has a syllable repetition rate of 22 ± 1 syllables s^{-1} ($21\text{--}26$ syllables s^{-1}) at 28.5 ± 0.4 °C ($27.7\text{--}29.7$ °C). The call spectrum has a peak frequency of 23.1 ± 1.8 kHz ($21.5\text{--}28.5$ kHz), and the spectral entropy is 8.0 ± 0.2 .

Ventrally, the left micropterous tegmen possesses a stridulatory file of about 1.659 mm in length with more than 100 broad teeth. The stridulatory file is very straight and slightly curving anteriorly at the basal end. The teeth are largest in the middle portion (average tooth width is 103 μm) and tooth width tapers gently towards the ends. The teeth are closely packed and the distance between teeth is fairly similar. In the mid-part of the stridulatory file, the teeth density is 95 teeth mm^{-1} . The file (Cu2) is slightly elevated on a swollen vein buttress. The right tegmen has somewhat triangular mirror with anterior margin rounded and posterior end acute, longer than broad. The scraper on the right tegmen is of about 0.984 mm in length, with about 100 rather broad teeth.

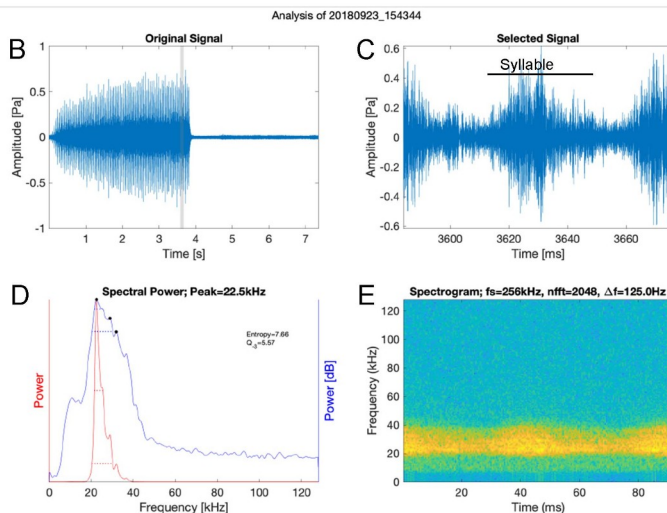


Fig. 8. *Viriaccia insularis* male adult in its natural environment in Pulau Tioman, Malaysia (A). Oscillograms showing an echeme (B) and a syllable (C). Power spectrum (D) and spectrogram of the same syllable (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right tegmen sound-producing organs (H), and a ventral view of the right SF (I).

***Viriaccia modesta* Gorochov, 2013** (n = 2 males, 13 sound files) (Figs. 9).—The calling song is continuous echeme-sequence made up of isolated echemes. Each echeme consists of 1–4 closely-packed syllables. At 25.3 ± 3.0 °C (22.9 – 29.5 °C), the echeme duration is 0.16 ± 0.01 s (0.14 – 0.19 s), the echeme period is 0.23 ± 0.04 s (0.16 – 0.31 s), and the interval between consecutive echemes is 0.07 ± 0.04 s (0.02 – 0.15). Syllable period is 29.3 ± 5.2 ms (21.0 – 38.0 ms). The call spectrum has a peak frequency of 26.0 ± 2.4 kHz (21.8 – 28.6 kHz), and the spectral entropy is 7.8 ± 0.1 .

Ventrally, the left micropterous tegmen possesses a stridulatory file of about 1.451 mm in length with about 159 broad teeth. The file is very straight and faintly curving anteriorly at the basal end. The teeth are largest in the middle portion (average tooth width is 100 μ m), and tooth width tapers gently towards the ends. The teeth are closely packed and the distance between teeth is fairly similar. In the mid-part of the stridulatory file, the teeth density is 10.4 teeth mm^{-1} . The file (Cu2) is slightly elevated on a swollen vein buttress. The right tegmen has rectangular mirror longer than broad, with anterior margin broader and rounded and with posterior margin truncated and narrower. The scraper on the right tegmen is of about 1.072 mm in length, with about 112 rather broad teeth.

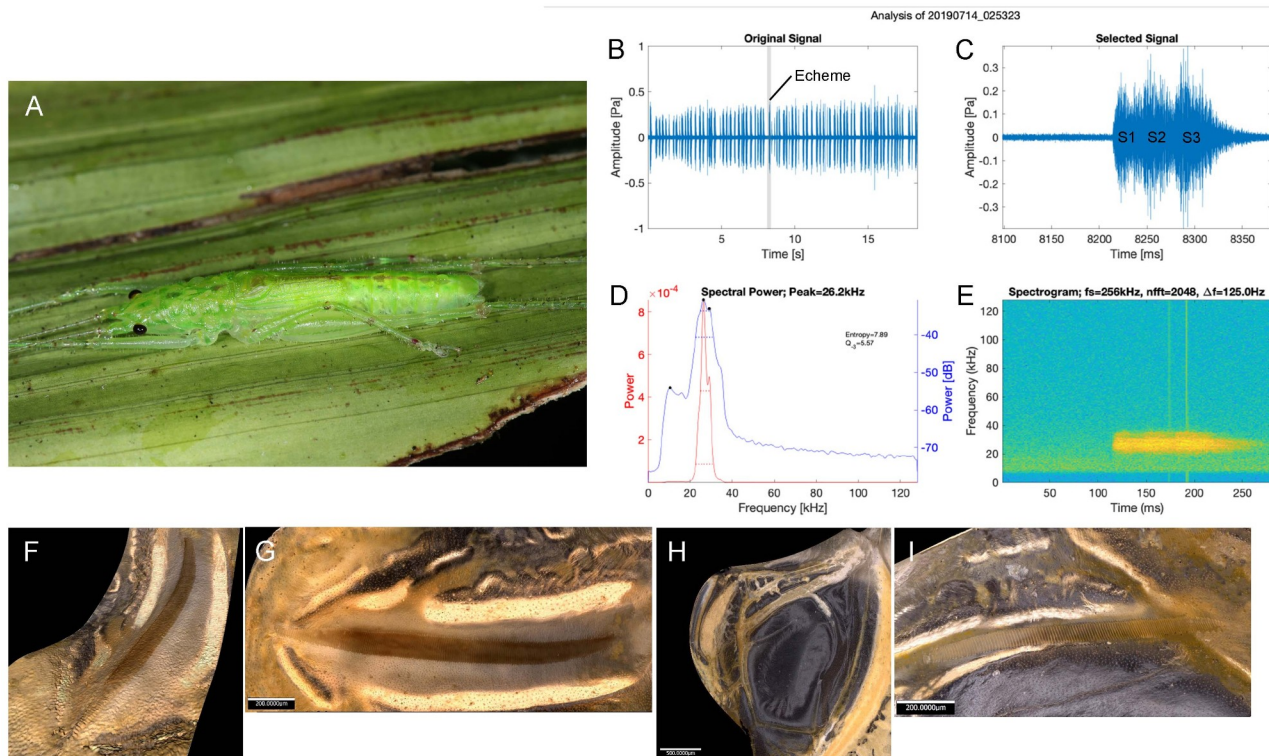


Fig. 9. *Viriaccia modesta* male adult in its natural environment in Belait, Brunei Darussalam (A). Oscillograms showing a continuous echeme-sequence (B) and an echeme with three syllables denoted as S1 to S3 (C). Power spectrum (D) and spectrogram of the same echeme (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right tegmen sound-producing organs (H), and a ventral view of the right SF (I).

***Lipotactes maculatus* Hebard, 1922** (n = 1 male, 16 sound files) (Fig. 10).—The calling song was first described from Bukit Timah (Singapore) by Ingrisch (1995) as a trill or as short echeme of 120–190 ms. We have recorded another individual from Mandai (also Singapore) using ultrasound-sensitive recorder to obtain more precise frequency data. The calling song from Mandai consists of an isolated echeme. The echeme duration is 0.14 ± 0.01 s (0.11–0.16 s), the echeme period is 2.48 ± 0.55 s (1.74–3.51 S), and the interval between echemes is 2.34 ± 0.54 s (1.59–3.35 s) at 28.5 ± 1.1 °C (26.9–29.3 °C). Each echeme consists typically of 4 (3–5) closely-packed syllable. Syllable period is 23.2 ± 1.8 ms (21.0–26.0 ms). The call spectrum has a peak frequency of 33.1 ± 3.1 kHz (25.9–38.2 kHz), and the spectral entropy is 8.3.

Ventrally, the left micropterous tegmen possesses a stridulatory file of about 1.183 mm in length with about 43 stout teeth. The file is slightly curved. The teeth at the anal end are smallest (average tooth width is 13.4 μm) and closely packed (average inter-tooth distance is 16.6 μm); the teeth in the middle of the file are largest (average tooth width is 38.3 μm) and are most widely spaced apart (average inter-tooth distance is 37.3 μm); the teeth at the basal end have an average tooth width is 20.7 μm and an average inter-tooth distance is 27.8 μm. The file (Cu2) is strongly elevated at the anal end on a swollen vein buttress (especially swollen at the anal end). The right tegmen has a triangular mirror. The scraper on the right tegmen is slightly sinusoidal, of about 1.176 mm in length, with about 33 stout teeth and a few indistinct teeth at both ends.

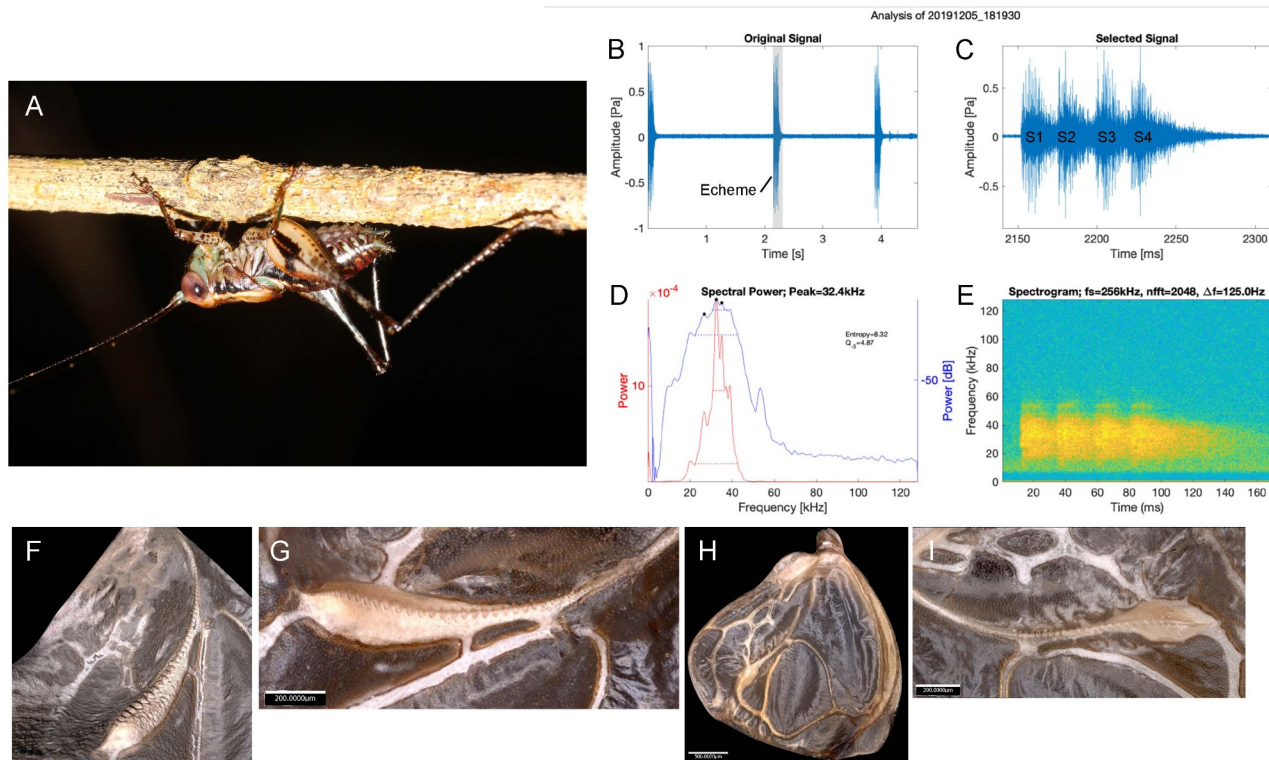


Fig. 10. *Lipotactes maculatus* male adult in its natural environment in Singapore (A). Oscillograms showing three isolated echemes (B) and an echeme with four syllables denoted as S1 to S4 (C). Power spectrum (D) and spectrogram of the same echeme (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right tegmen sound-producing organs (H), and a ventral view of the right SF (I).

Alloteratura lamella Jin, 1995 (n = 2 males, 21 sound files) (Fig. 11).—This species has two song modes. The first song mode consists of a complex echeme made up of two parts: the first part is made up of a few of the isolated syllables and the second part is a verse made up of syllables packed closely together. At 29.2 ± 0.7 °C (28.6–30.5 °C), each syllable of the first part of the calling song has duration of 0.10 ± 0.01 s (0.08–0.11 s), period of 0.33 ± 0.06 s (0.22–0.46 s), and interval between syllables of 0.24 ± 0.06 s (0.12–0.35 s). The verse duration is 1.21 ± 0.40 s (0.39–1.75 s), is made of 29 ± 8 (7–35) closely-spaced syllables, and syllable repetition rate is 20 ± 1 syllables s⁻¹ (18–22 syllables s⁻¹). The second song mode consists of only the isolated syllables. The call spectrum has a peak frequency of 25.5 ± 0.7 kHz (24.6–27.0 kHz), and the spectral entropy is 7.7 ± 0.3 .

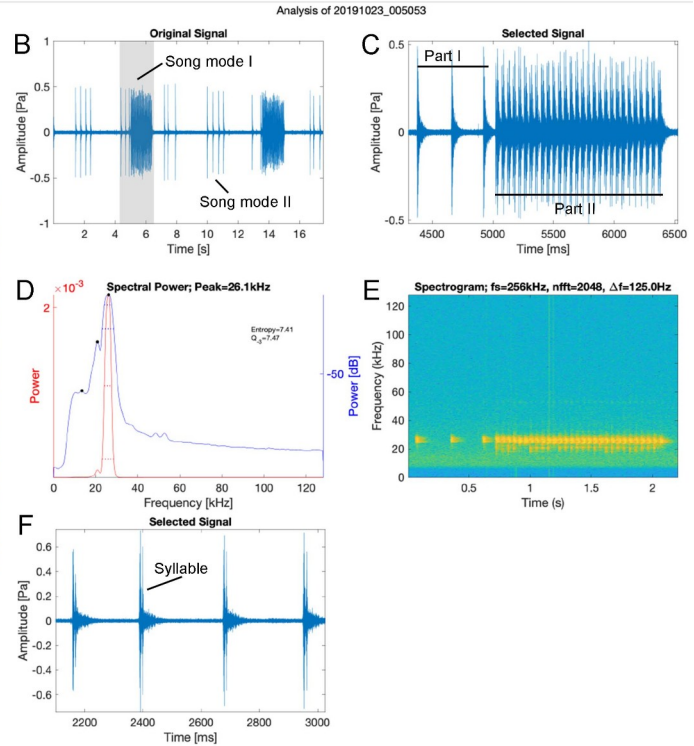


Fig. 11. *Alloteratura lamella* male adult in its natural environment in Singapore (A). Oscillograms showing calling song consisting of both song modes (B) and a complex echeme consisting of three isolated syllables and a verse (C). Power spectrum (D) and spectrogram of the same complex echeme (E). Oscillogram of four isolated syllables representing a second song mode (F).

***Borneopsis cryptosticta* (Hebard, 1922)** (n = 2 males, 17 sound files) (Fig. 12).—Two modes of calling songs were recorded. The first and more commonly recorded one consists of syllables occurring in pairs. At 30.2 ± 0.2 °C (29.9–30.5 °C), each doublet of syllables has duration of 61.2 ± 6.8 ms (50.1–71.1 ms) and period of 0.51 ± 0.14 s (0.35–0.82 s), with the interval between consecutive doublets of 0.45 ± 0.14 s (0.29–0.76 s). The second song mode consists of echeme of at least 6–8 syllables closely spaced together, with the echeme duration of 0.15–0.20 s. For both song modes, the call spectrum has a peak frequency of 42.3 ± 2.4 kHz (38.0–46.5 kHz), and the spectral entropy is 8.5 ± 0.3 .

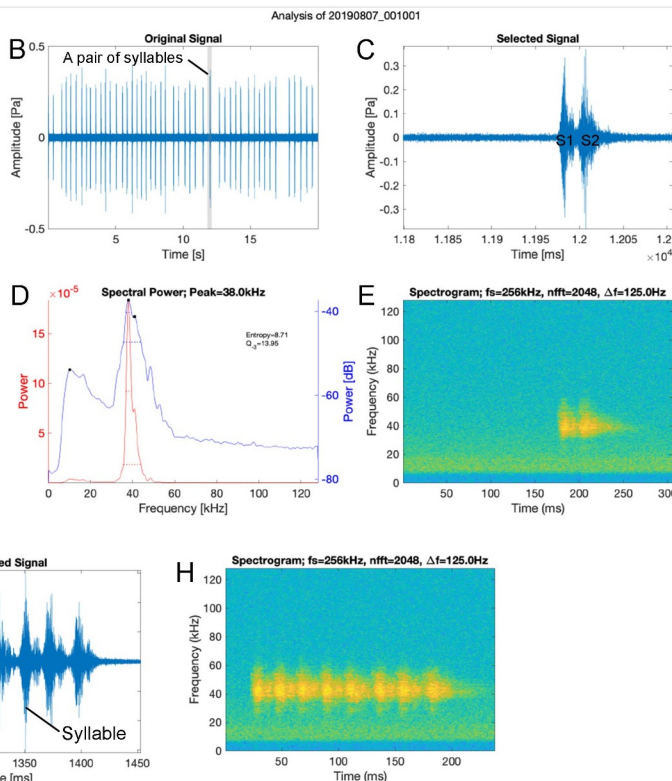


Fig. 12. *Borneopsis cryptosticta* male adult in its natural environment in Singapore (A). Oscillograms showing a doublet of syllables (B) and a doublet of syllables denoted as S1 and S2 (C). Power spectrum (D) and spectrogram of the doublet of syllables (E). Oscillograms showing two echemes (F) and an echeme with eight syllables (G). Power spectrum (H), and spectrogram of the echeme with eight syllables (I).

Euanisous teuthroides (Bolívar, 1905) (n = 1 male, 13 sound files) (Fig. 13).—The calling song consists of echeme which can be highly variable in duration and exhibits frequency modulation. At 29.7 ± 0.3 °C (29.4 – 30.3 °C), syllable period is 5.44 ± 0.35 ms (4.88 – 6.03 ms). At the start of the echeme, the syllable amplitude increases to a maximum, then decreases slightly and plateau. The call spectrum has a peak frequency of 30.3 ± 0.7 kHz (29.5 – 32.0 kHz), and the spectral entropy is 7.4 ± 0.2 .

Ventrally, the left macropterous tegmen possesses a stridulatory file of about 0.671 mm in length, with about 23 stout and squarish teeth. Unlike other species reported here, each tooth exhibits an indentation in the middle. The teeth are similar in size (average tooth width in the middle part of the file is 17.8 μ m) and they are generally widely spaced apart (average inter-tooth distance is 36.1 μ m). The file (Cu2) is strongly elevated on a swollen vein buttress, bent in the middle, with only the basal half possessing the teeth. The right tegmen has a small and rectangular mirror, broader than long, somewhat obsolete. The scraper on the right tegmen is of about 0.550 mm in length, with about 18 stout teeth.

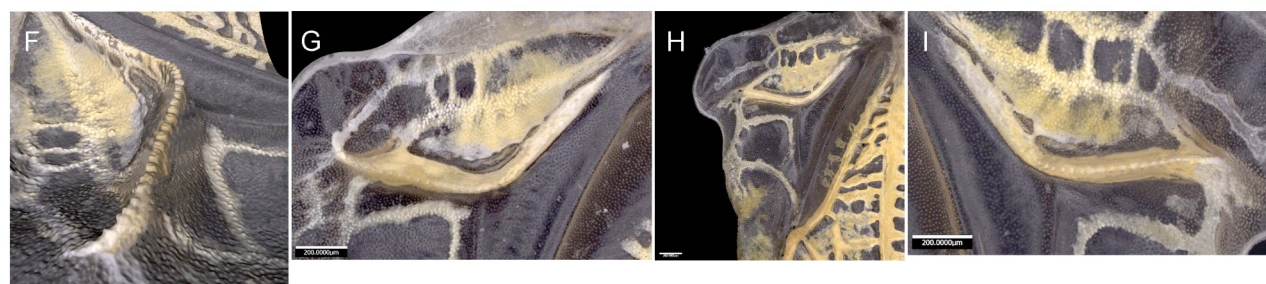
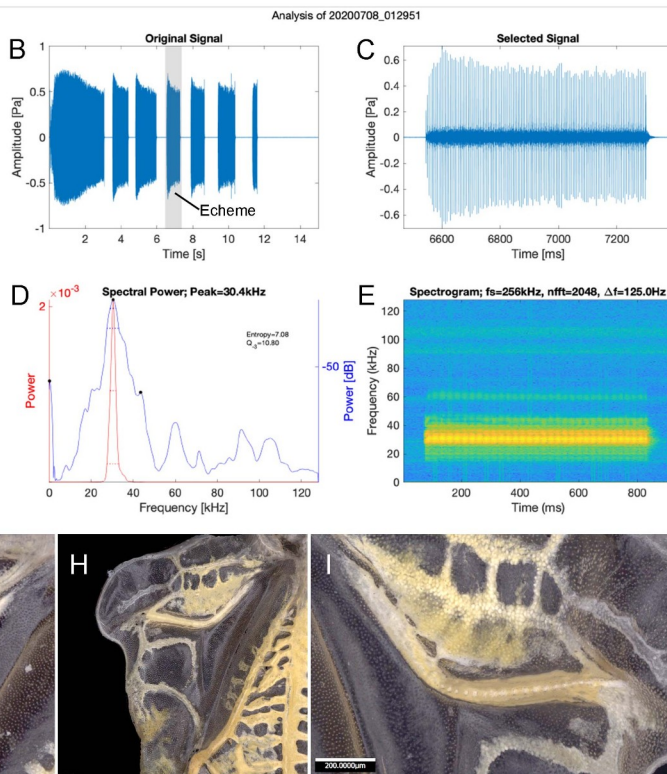


Fig. 13. *Euanisous teuthroides* male adult in its natural environment in Singapore (A). Oscillograms showing seven echemes of varying duration (B) and an echeme (C). Power spectrum (D) and spectrogram of the same echeme (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right tegmen sound-producing organs (H), and a ventral view of the right SF (I).

***Kuzicus denticulatus* (Karny, 1926)** (n = 2 males, 14 sound files) (Fig. 14).—The calling song consists of a continuous trill. At 29.5 ± 0.2 °C (29.2 – 29.9 °C), the trill consists of repetition of syllables with a repetition rate of 187 ± 23 syllables s^{-1} (153 – 249 syllables s^{-1}). Syllable period is 5.44 ± 0.63 ms (4.01 – 6.53 ms). The call spectrum has a peak frequency of 39.6 ± 2.4 kHz (33.4 – 42.2 kHz), and the spectral entropy is 7.7.

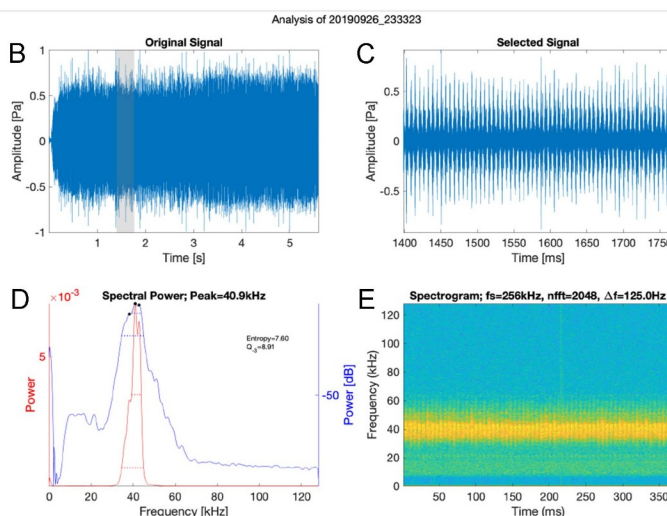
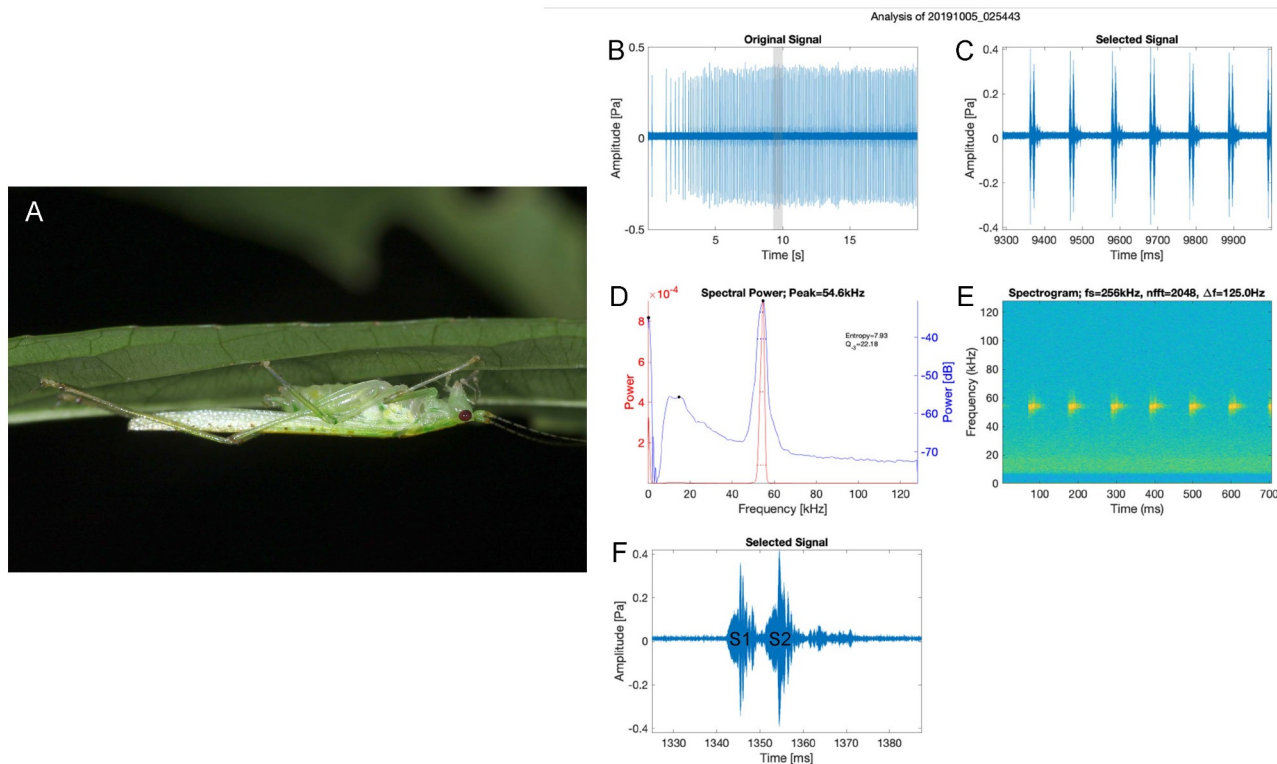


Fig. 14. *Kuzicus denticulatus* male adult in its natural environment in Singapore (A). Oscillograms showing a continuous trill (B) and closer view of the continuous trill (C). Power spectrum (D) and spectrogram of the closer view of the continuous trill (E).

551
552
553
554
555
556
557
558

Meconematini (Sandakan) (n = 1 male, 6 sound files) (Fig. 15).—The calling song consists of a continuous trill made up of syllables occurring in pairs. At 29.3 °C, each doublet has a duration of 33.6 ± 3.6 ms (30.0–41.0 ms), period of 116.3 ± 11.7 ms (95.0–146.0 ms) and an interval between consecutive doublets of 82.7 ± 11.6 ms (63.0–114.0 ms). The first syllable has a duration of 7.3 ± 0.6 ms (7.0–9.0 ms), second syllable has a duration of 8.0 ± 0.7 ms (7.0–10.0 ms). The call spectrum has a peak frequency of 54.2 ± 0.4 kHz (53.5–54.6 kHz), and the spectral entropy is 7.6.



559
560
561
562
563
564
565
566
567
568
569
570

Fig. 15. Meconematini (Sandakan) male adult in its natural environment in Sandakan, Malaysia (A). Oscillograms a continuous trill (B) and a section of the trill with seven doublets of syllables (C). Power spectrum (D) and spectrogram of the seven doublets of syllables (E). Oscillogram showing a doublet of syllables, with the syllables denoted as S1 and S2, in greater details (F).

Neophisis siamensis Jin, 1992 (n = 3 males, 10 sound files) (Fig. 16).—The calling song consists of a sequence of isolated syllables. Each syllable shows two amplitude peaks. At 29.3 ± 0.5 °C (28.5–30.4 °C), syllable duration is 100.6 ± 17.4 ms (57.0–123.0 ms). The interval between syllables is highly variable, ranging from 42.0 to 270.0 ms (107.4 ± 63.6 ms). The call spectrum has a peak frequency of 36.7 ± 1.8 kHz (32.0–38.2 kHz), and the spectral entropy is 7.1.

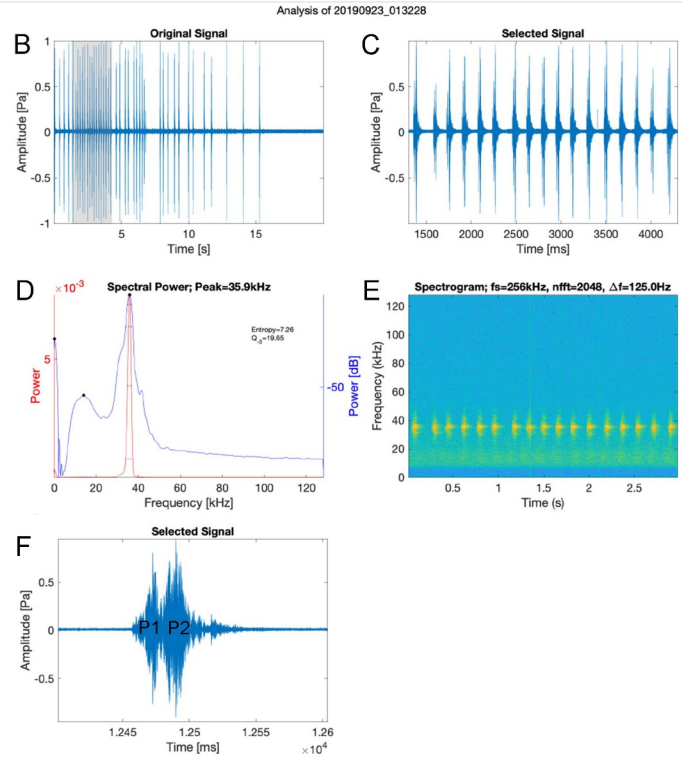


Fig. 16. *Neophisis siamensis* male adult in its natural environment in Singapore (A). Oscillograms showing a sequence of syllables (B) and a section of the sequence with 17 syllables (C). Power spectrum (D) and spectrogram of the 17 syllables (E). Oscillogram showing a single syllable with two amplitude peaks denoted as P1 and P2 (F).

***Xizicus* sp.** (n = 1 male, 7 sound files) (Fig. 17).—The calling song consists of continuous trill made up of isolated syllables of varying amplitudes. Each syllable is made up of two pulses, with the first pulse typically of lower amplitude than the second pulse. At 29.1 ± 0.2 °C (29.0 – 29.6 °C), syllable duration is 56.8 ± 6.3 ms (46.0 – 70.0 ms), period is 75.4 ± 17.1 ms (57.0 – 116.0 ms). The interval between doublets is highly variable, ranging from 3.0 to 62.0 ms (18.6 ± 15.8 ms). The call spectrum has a peak frequency of 40.9 ± 0.4 kHz (40.4 – 41.4 kHz), and the spectral entropy is 7.7 .

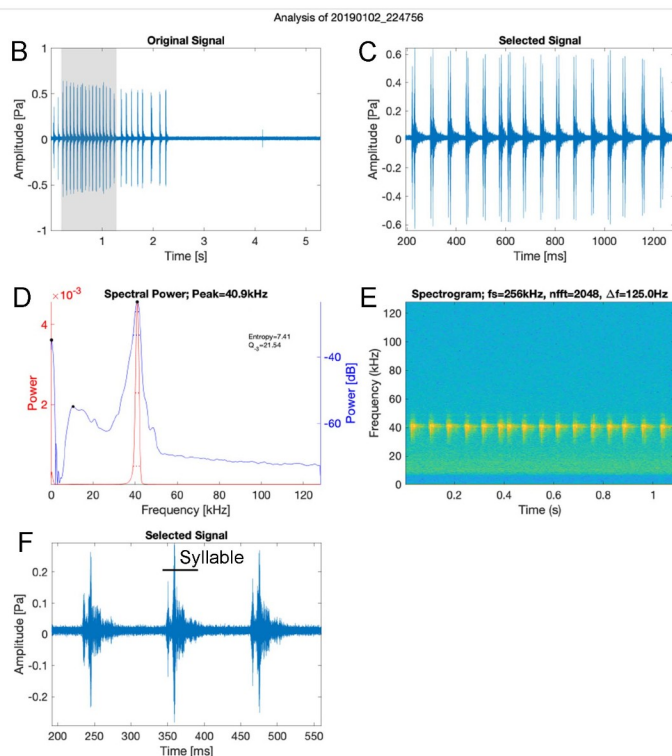


Fig. 17. *Xizicus* sp. 1 male adult in its natural environment in Singapore (A). Oscillograms showing a sequence of syllables (B) and a section of the trill with 16 syllables (C). Power spectrum (D) and spectrogram of the 16 syllables (E). Oscillogram showing three syllables, each with two pulses, in greater details (F).

***Casigneta* sp. 1** (n = 2 males, 15 sound files) (Fig. 18).—The calling song consists of a pulse-train isolated in time. The train may correspond to a long syllable rather than an echeme owing to the presence of frequency modulation. At 29.6 ± 0.6 °C (29.0 – 30.4 °C), each pulse train has duration of 0.36 ± 0.04 s (0.27 – 0.44 s), and is made up of 24 ± 3 (16 – 27) pulses of increasing gradually amplitude over time. The call spectrum has a peak frequency of 28.7 ± 0.8 kHz (27.2 – 30.0 kHz), and the spectral entropy is 7.6 ± 0.1 .

Ventrally, the left macropterous tegmen possesses a stridulatory file of about 1.338 mm in length with about 110 rather broad teeth. The file is substraight, slightly curved at the basal end. The teeth are largest in the middle portion (average tooth width is 125 μ m) and tooth width tapers gently towards the ends. The teeth are most densely packed in the anal end (teeth density is 107 teeth mm^{-1}), then in the middle region of the file (teeth density is 71 teeth mm^{-1}), and least densely packed at the basal end (teeth density is 51 teeth mm^{-1}). The file (Cu2) is barely elevated on a swollen vein buttress. The right tegmen has a trapezoidal mirror. The scraper on the right tegmen is of about 1.323 mm in length with relatively stout teeth.

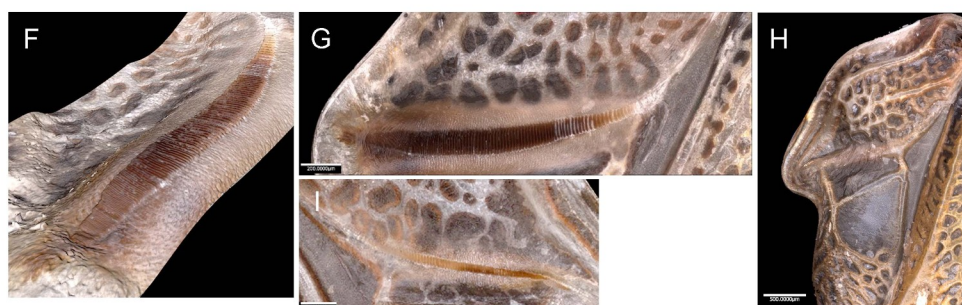
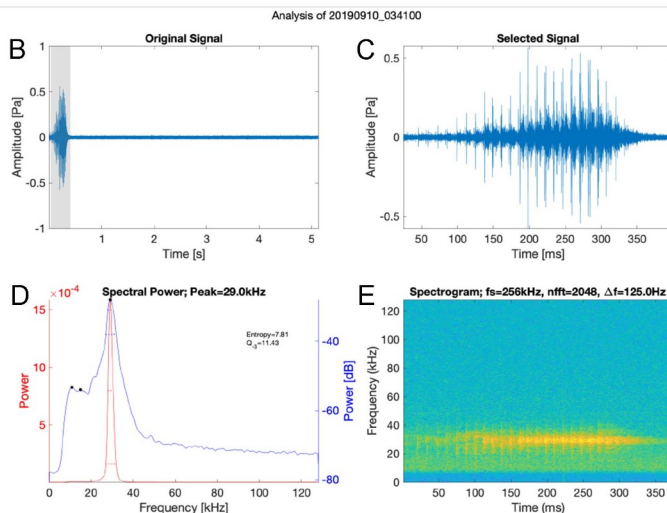


Fig. 18. *Casigneta* sp. 1 male adult in its natural environment in Singapore (A). Oscillograms showing a pulse-train (B) and a closer view of the pulse-train (C). Power spectrum (D) and spectrogram of the same pulse-train (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right tegmen sound-producing organs (H), and a ventral view of the right SF (I).

***Casigneta* sp. 2** (n = 1 male, 19 sound files) (Fig. 19).—The calling song consists probably of isolated syllables, each containing three pulses. At 29.8 ± 0.5 °C (28.7 – 30.1 °C), each triple of pulses has duration of 0.15 ± 0.01 s (0.13 – 0.16 s). The first pulse duration is 12.5 ± 3.5 ms (10.0 – 25.0 ms); the second pulse duration is 12.1 ± 2.2 ms (10.0 – 18.0 ms); the third pulse duration is 12.4 ± 2.6 ms (10.0 – 19.0 ms). The first pulse is more temporally separated from the second and third pulses. The call spectrum has a peak frequency of 28.2 ± 0.2 kHz (27.8 – 28.8 kHz), and the spectral entropy is 6.8 ± 0.2 .

Ventrally, the left macropterous tegmen possesses a stridulatory file of about 1.314 mm in length with about 75 rather broad teeth. The file is substraight, slightly curved at the basal end. The teeth are largest in the middle portion (average tooth width is 95 μ m) and tooth width tapers gently towards the ends. The teeth are closely packed and the distance between teeth is fairly similar. In the mid-part of the stridulatory file, the teeth density is 56 teeth mm^{-1} . The file (Cu2) is barely elevated on a swollen vein buttress. The right tegmen has an elongated rectangular mirror, distinctly longer than broad. The scraper on the right tegmen is of about 0.913 mm in length, with about 52 teeth.

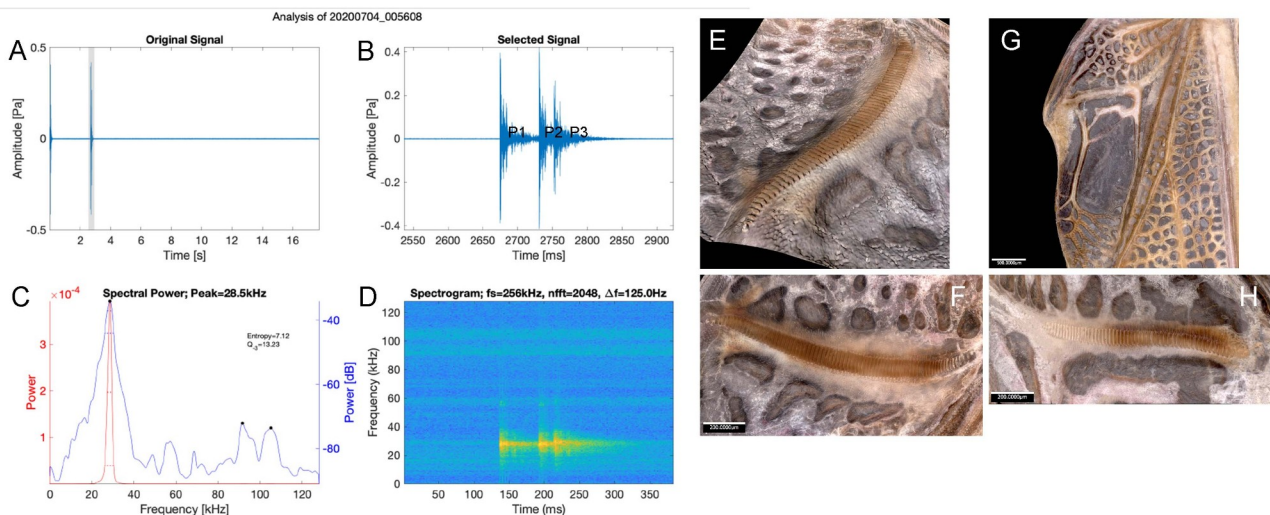


Fig. 19. *Casigneta* sp. 2. Oscillograms showing two triplets of pulses (A) and a triplet of pulses denoted as P1 to P3 (B). Power spectrum (C) and spectrogram of the same triple of pulses (D). Three-dimensional anal view of the left stridulatory file (SF) (E), ventral view of the same SF (F), ventral view of the right tegmen sound-producing organs (G), and a ventral view of the right SF (H).

***Holochlora* nr. *bilobata* (Karny, 1926)** (n = 2 males, 15 sound files) (Fig. 20).—The calling song consists of an isolated syllable. At 29.8 ± 0.4 °C (28.4 – 30.4 °C), syllable duration is 37.2 ± 3.5 ms (29.5 – 45.3 ms). The interval between syllables varies at 4.0 ± 1.7 s (2.3 – 8.6 s). The call spectrum has a peak frequency of 33.3 ± 1.0 kHz (31.5 – 34.9 kHz), and the spectral entropy is 8.1 ± 0.4 .

Ventrally, the left macropterous tegmen possesses a stout stridulatory file of about 1.126 mm in length with about 47 broad teeth. The file is straight. The teeth are largest in the middle portion (average tooth width is 95 μ m) and distinctly smaller at the ends (average tooth width is 38 μ m). The distance between teeth is fairly uniform in the mid-part of the file (teeth density is 44 teeth mm^{-1}), only slightly larger at the ends. The file (Cu2) is strongly elevated in the middle on a swollen vein buttress. The right tegmen has a small triangular mirror, somewhat obsolete. The scraper on the right tegmen is of about 0.633 mm in length with about 32 indistinct teeth.

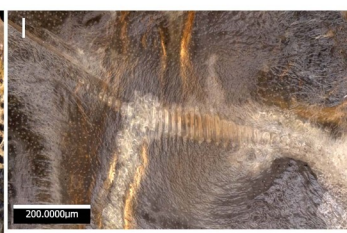
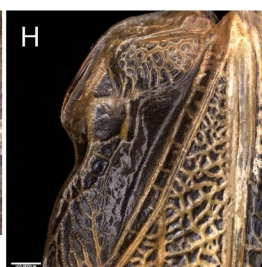
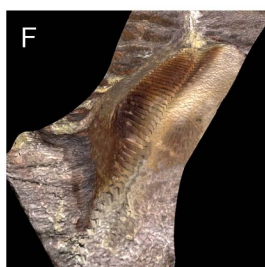
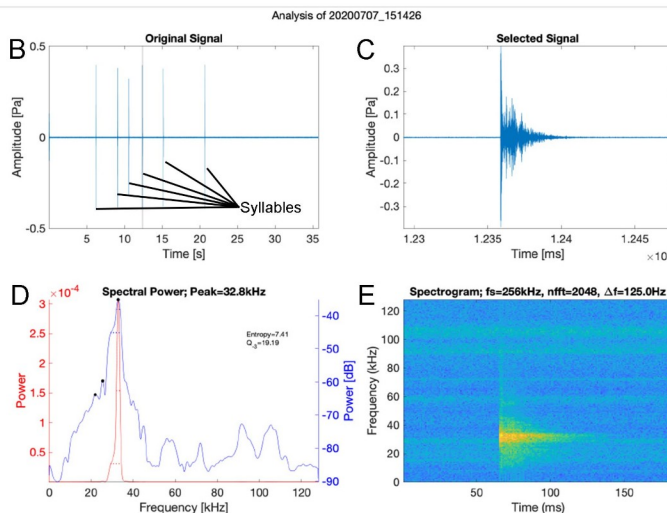


Fig. 20. *Holochlora* nr. *bilobata* male adult in the lab (A). Oscillograms showing six isolated syllables (B) and a closer view of a syllable (C). Power spectrum (D) and spectrogram of the same syllable (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right tegmen sound-producing organs (H), and a ventral view of the right SF (I).

***Phaneroptera brevis* Serville, 1838** (n = 1 male, 11 sound files) (Fig. 21).—The calling song consists of a pair of syllables. At 29.9 ± 0.2 °C (29.6 – 30.2 °C), each pair of syllables has duration of 0.33 ± 0.01 s (0.31 – 0.35 s). The first syllable has a distinctly lower amplitude and shorter duration of 36.3 ± 8.8 ms (22.0 – 50.0 ms) than the second syllable (duration is 53.8 ± 10.9 ms [30.0 – 70.0 ms]). The interval between the two syllables is 0.24 ± 0.02 s (0.21 – 0.27 s). The call spectrum has a peak frequency of 21.9 ± 0.8 kHz (20.3 – 22.8 kHz), and the spectral entropy is 7.9.

Ventrally, the left macropterous tegmen possesses a stridulatory file, somewhat split into two parts connected by a perpendicular ‘bridge’. The entire stridulatory file on the left tegmen is about 1.753 mm in length. The anal part is short and straight of about 0.335 mm in length with about 24 smaller and stout (of uniform size and spacing) teeth. The average tooth width is 34 μ m and the teeth density is 65 teeth mm^{-1} . The main file is straight of about 1.263 mm in length with about 36 larger teeth. The teeth are largest in the middle portion (average tooth width is 86 μ m) and distinctly smaller at the basal end (average tooth width is 52 μ m). The teeth are less densely packed in the middle portion (teeth density is 18 teeth mm^{-1}) compared to the basal end (teeth density is 49 teeth mm^{-1}). The file (Cu2) is faintly elevated in the middle on a swollen vein buttress. The right tegmen has an oblong mirror, distinctly longer than broad.

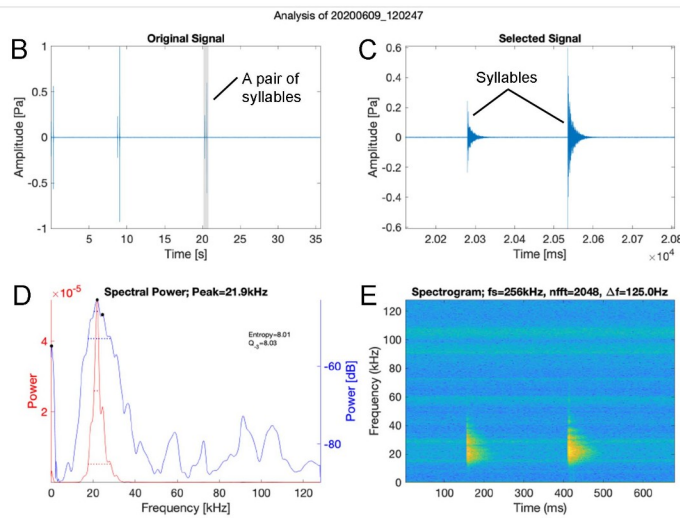


Fig. 21. *Phaneroptera brevis* male adult in its natural environment in Singapore (A). Oscillograms showing three pairs of syllables (B) and a closer view of a pair of syllables (C). Power spectrum (D) and spectrogram of the pair of syllables (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), and ventral view of the right tegmen sound-producing organs (H).

***Phaulula malayica* (Karny, 1926)** ($n = 1$ male, 6 sound files) (Fig. 22).—The calling song consists of isolated syllables appearing as rapid-decay pulses. At 29.3 ± 0.4 °C (29.1 – 30.1 °C), syllable duration is 53.4 ± 7.5 ms (41.0 – 65.0 ms). The interval between syllables varies at 1.6 ± 0.4 s (1.2 – 2.7 s). The call spectrum has a peak frequency of 23.6 ± 1.2 kHz (22.5 – 25.2 kHz). In some instances, however, a second peak in the spectrum of 33.5 – 33.8 kHz can be the dominant frequency. The spectral entropy is 7.8.

Ventrally, the left macropterous tegmen possesses a stridulatory file of about 1.364 mm in length with about 45 broad teeth. The file is straight. The teeth are largest in the middle portion (average tooth width is 112 μ m) and tooth width tapers towards the ends. The teeth are uniformly packed in the mid-part of the stridulatory file (teeth density is 23 teeth mm^{-1}), less densely packed at the anal end (teeth density is 31 teeth mm^{-1}) and more densely packed at the basal end (teeth density is 50 teeth mm^{-1}). The stridulatory file (Cu2) is slightly elevated in the middle on a swollen vein buttress. The right tegmen has a very large mirror, longer than broad.

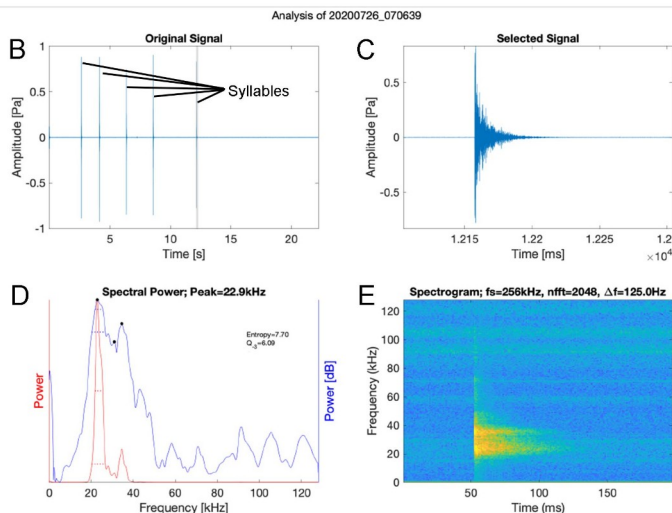


Fig. 22. *Phaulula malayica* male adult in the lab (A). Oscillograms showing five isolated syllables (B) and a closer view of a syllable (C). Power spectrum (D) and spectrogram of the syllable (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), and ventral view of the right tegmen sound-producing organs (H).

***Psyrana tigrina* (Brunner von Wattenwyl, 1878)** (n = 1 male, 14 sound files) (Fig. 23).— The calling song consists of pulse-train isolated in time. At 30.2 ± 0.1 °C (30.0–30.4 °C), each pulse-train has duration of 0.26 ± 0.01 s (0.24–0.28 s) and is made up of numerous pulses of varying amplitudes and duration. The pulses steadily increase in amplitude to a maximum in the initial 0.17 ± 0.01 s (0.16–0.19 s) of the pulse-train, before decreasing rather abruptly in amplitude in the final 0.09 ± 0.01 s (0.06–0.12 s) of the pulse-train. The call spectrum has a peak frequency of 35.5 ± 2.1 kHz (31.8–38.0 kHz), and the spectral entropy is 8.1.

Ventrally, the left macropterous tegmen possesses a stridulatory file of about 2.236 mm in length with about 83 broad teeth. The file is straight. The teeth are largest in the middle portion (average tooth width is 244 μ m) and tooth width tapers at the ends. The teeth are narrowly and uniformly packed in the mid-part of the stridulatory file (teeth density is 34 teeth mm^{-1}). The file (Cu2) is faintly elevated in the middle on a swollen vein buttress. The right tegmen has an elongated rectangular mirror. The scraper on the right tegmen is of about 1.851 mm in length; with about 38 teeth at the anal half and numerous indistinct teeth at the basal half.

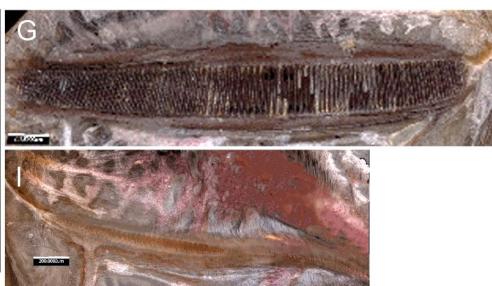
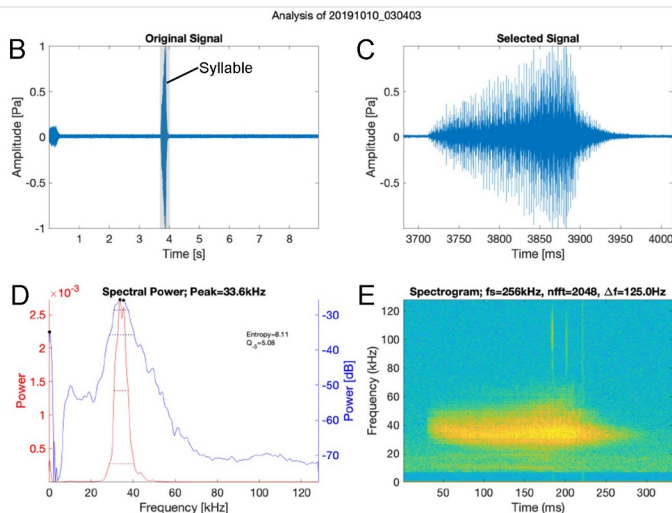


Fig. 23. *Psyrana tigrina* male adult in its natural environment in Sandakan, Malaysia (A). Oscillograms showing an isolated pulse-train (B) and a closer view of the pulse-train (C). Power spectrum (D) and spectrogram of the pulse-train (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right tegmen sound-producing organs (H), and a ventral view of the right SF (I).

***Scambophyllum sanguinolentum* (Westwood, 1848)** (n = 1 male, 8 sound files) (Fig. 24).— The calling song consists of a pulse-train isolated in time very likely a long syllable produced during a single but slow closing wing stroke. Similar syllable patterns have been observed in the genus *Isophya*, e.g. *Isophya costata* (Heller 1988). The syllable, here recognized as pulse trains, can occur in isolation or in doublets or triplets. At 29.7 ± 0.0 °C (29.7 – 29.8 °C), train duration is 0.32 ± 0.01 s (0.30 – 0.35 s). When occurring in doublets or triplets, train period is 0.97 ± 0.18 s (0.78 – 1.38 s) and intervals between trains is 0.64 ± 0.18 s (0.43 – 1.04 s). Each train is made up of 43 ± 2 (39 – 47) pulses, with pulses increasing in amplitude at the start and remain consistent. The call spectrum has a peak frequency of 23.7 ± 0.3 kHz (23.2 – 24.1 kHz) and spectral entropy is 7.0 ± 0.1 .

Ventrally, the left macropterous tegmen possesses a stridulatory file of about 1.509 mm in length with about 53 broad teeth. The file is straight, and strongly bent at the basal third. The average tooth width in the middle region is 46 μ m. Tooth width tapers at the ends. The file (Cu2) is faintly elevated in the middle on a swollen vein buttress. The right tegmen has a squarish mirror. The scraper on the right tegmen is of about 1.208 mm in length with numerous indistinct teeth.

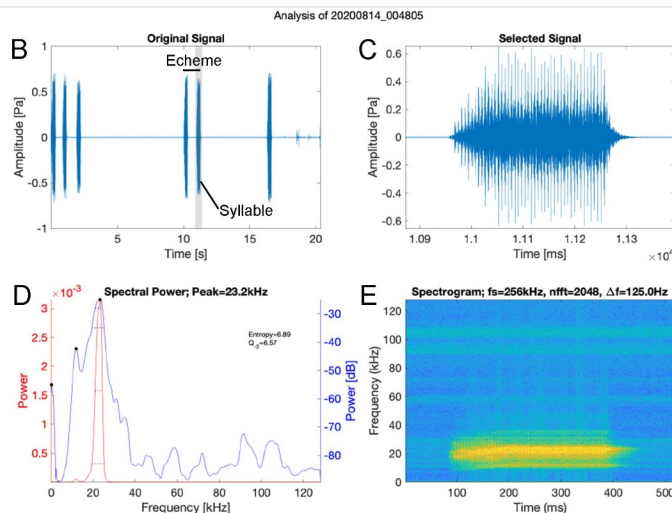


Fig. 24. *Scambophyllum sanguinolentum* male adult in the lab (A). Oscillograms showing two echemes (first one with three syllables and second one with two syllables) followed by an isolated echeme (B) and an echeme (C). Power spectrum (D) and spectrogram of an echeme (E). Three-dimensional anal view of the left stridulatory file (SF) (F), ventral view of the same SF (G), ventral view of the right tegmen sound-producing organs (H) and a ventral view of the right SF (I).

Discussion

Calling songs

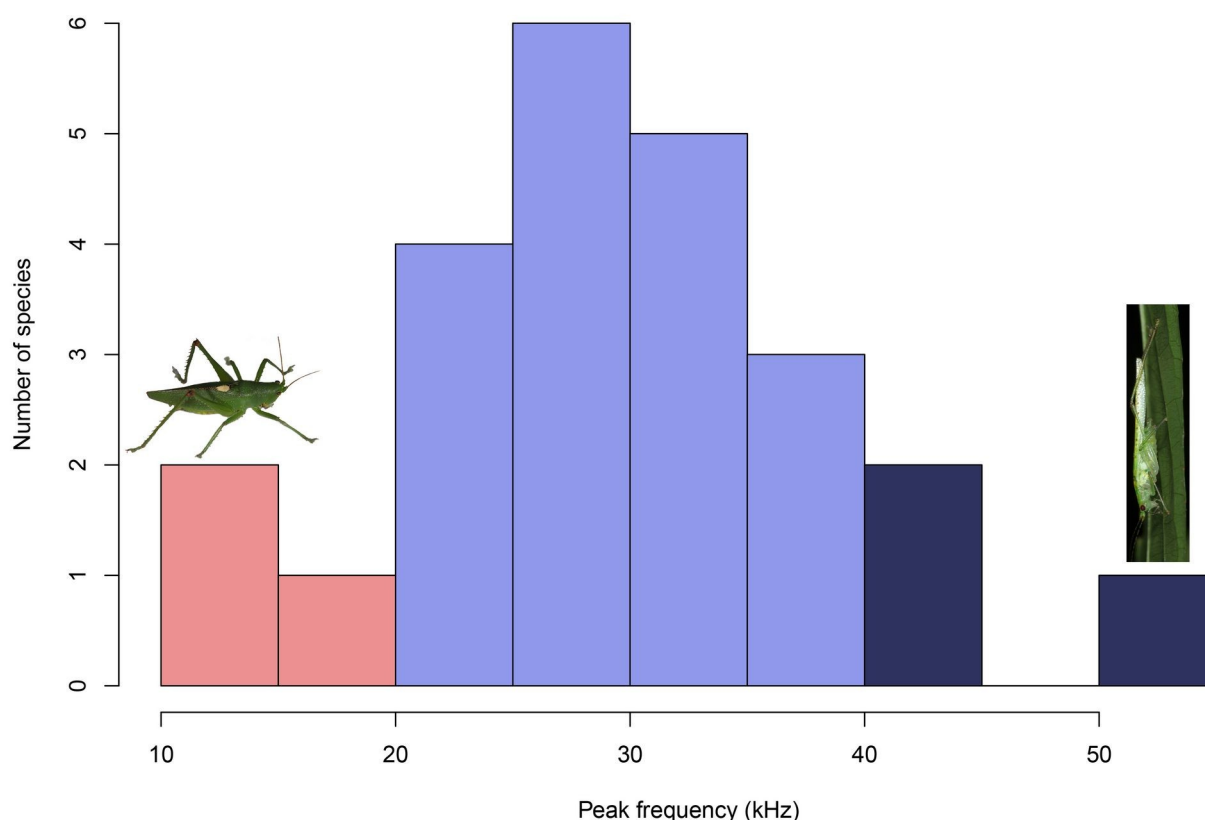
Based on the 24 katydid species recorded in this study (Table 1), we observed that the calling songs of Southeast Asian katydid species are highly diversified in both the time and frequency domains. While some species produce transient calling songs such as relatively simple and isolated pulses in *Holochlora*, species of *Conocephalus* produce complex echemes with two distinct structures within each echeme. Other species produce continuous trills (e.g., in *Axylus* and *Kuzicus*) and a short sequence of trains (e.g., in *Euanisous* and *Psyrana*). Some species, such as the *Alloteratura lamella* and *Borneopsis cryptosticta*, also had two modes of calling song recorded in the laboratory. The *Conocephalus exemptus* represents a curious case, in which the calling songs from Thailand and Singapore differ drastically. Owing that the taxonomy of *Conocephalus* is complicated, it could be that the individuals from Thailand and Singapore represent two different cryptic species, or that this widely-distributed species exhibits population differences in calling songs. Combining the bioacoustic data and further examining the morphology of the ‘species’ from different parts of its distribution can shed light into its bioacoustics and taxonomy.

The call analysis also provides some inputs on the quality of the signal, and we use the quality factor Q (Q_{-3dB}) to investigate this variable. Although Q assumes the spectrum is symmetrical (Bennet-Clark 1999), spectral symmetry is rarely the case in the calls of most katydids, especially for broadband singers. For this reason we present an alternative form to measure the tendency of some signal to random noise. Entropy has been used by different authors to measure this tendency

765 from various perspectives. For example, Sueur et al. (2012) used a normalized form for the
 766 calculated value which will tend towards 0 for a single pure tone, increases with the number of
 767 frequency bands and amplitude modulations, and tends towards 1 for a random noise. Chivers et al.
 768 (2017a) report entropy values of ~5–9 in neotropical katydids (without normalization). Using the
 769 same protocols proposed by Chivers et al. (2017a), here we report entropy values of 6.8–8.8, which
 770 suggest that Chivers et al. (2017a) included species with high tonality (common in many
 771 neotropical Pseudophyllinae).

772
 773 The peak frequency of the 24 Southeast Asian katydids ranges from 12.6 to 54.2 kHz, with more
 774 than 80% of species having energy peaks at ultrasonic range (18 species having peak frequency
 775 between 20 and 40 kHz, 3 species having peak frequency > 40kHz) (Fig. 25). This is congruent
 776 with what was previously documented: most katydids produce ultrasonic sound (Montealegre-Z
 777 2009; Montealegre-Z et al. 2017). Likewise, the three extreme ultrasonic callers (peak frequency
 778 >40 kHz) reported here are species from the subfamily Meconematinae, despite the subfamily is a
 779 paraphyletic group (see Mugleston et al. 2018). We can expect to find more species of katydid
 780 species from the region to produce extreme ultrasound when we collect calls of more species. These
 781 may include species of *Glenophysis* Karny, 1926 from the subfamily Hexacentrinae, a small genus
 782 of katydids found in Southeast Asia (Tan 2012). These katydids share superficial morphological
 783 resemblance with neotropical *Arachnoscelis* Karny, 1911 species and *Supersonus* Sarria-S et al.,
 784 2014 species (both from the subfamily Meconematinae) which can produce calls with frequency
 785 peaking at 70 kHz and above 125 kHz, respectively (Chivers et al. 2014; Sarria-S et al. 2014).
 786 Unfortunately, we have yet to encounter these rare katydids for such a study. Likewise, some
 787 Pseudophyllinae from Southeast Asia can produce exceedingly low frequency (e.g., 0.6 kHz in
 788 *Tympanophyllum arcuifolium* (Haan, 1843)) (Heller 1995), and it will not be surprising to find more
 789 species that produce such low frequencies.

790



791

792 **Fig. 25.** A histogram showing the number of species of katydids and the peak frequency of their
 793 calling songs. The red bars represent sonic callers (<20 kHz), light blue bars represent ultrasonic
 794 callers, and the dark blue bars represent extreme ultrasonic callers (>40 kHz).

795

796 In this study, all six species of Meconematini produce songs with an entirely ultrasonic spectrum.
797 This is congruent to previously reported calls of Meconematini from Africa, such as *Amytta* species
798 (Hemp and Heller 2017; Hemp 2021). Among the species here studied, they are also the only group
799 of katydids which produce extreme ultrasound, specifically *Borneopsis cryptosticta*, *Xizicus* sp. and
800 an unidentified Meconematini from Sandakan (although Tan et al. 2019 also reported extreme-
801 ultrasonic singers among Phlugidini from Southeast Asia). Being highly speciose in Southeast Asia
802 —with at least 104 genera currently known (Cigliano et al. 2022), this group of katydid may hold
803 the key to understanding the evolution of extreme ultrasound production in katydids. However,
804 elucidating the phylogeny of Meconematini is crucial, as the relationships between and among
805 many currently-known genera and species are still unknown and many groups are likely to be
806 paraphyletic. The ability of to produce calls with entirely ultrasonic spectrum and extreme
807 ultrasound are likely to have evolved multiple times and dependent on other factors instead of
808 merely phylogenetic relatedness. Secondly, these predatory katydids usually occur in low
809 abundance and most species were described without having their calls recorded (but see Tan et al.
810 2020b). With continued effort to document the bioacoustics of these katydids, we can expect to find
811 more species of extreme-ultrasonic singers from more genera, as well as more variations in their
812 call structure and peak frequencies among different clades.

813

814 We refrain from classifying each species as either nocturnal or diurnal, even if some species'
815 activity appears rather distinct. For example, transient calling songs of *Holochlora* and *Psyrana*
816 corroborate with field observations suggesting they are most active at night. As the katydids were
817 not always recorded over the entire circadian cycle and many species only have a few recordings
818 from one or two individuals, we could not model the calling activity (see Tan and Robillard 2021).
819 In that study, the authors recorded eneopterine crickets under standardized conditions, modeled
820 their calling activity over 24 hours, and consequently found many species to exhibit complex
821 circadian rhythms in their calling activity (i.e., multiple peaks in calling activity in both day and
822 night time). Sporadic recordings may give an over-simplified impression about whether a species is
823 strictly nocturnal or diurnal.

824

825 **Sound-producing organs**

826 The properties of stridulatory file (length, number of teeth, and teeth density or spacing) and mirror
827 (e.g., stiffness, membrane structure) are important in dictating the frequency and resonance of the
828 calling song (Morris and Pipher 1967; Bailey 1970; Montealegre-Z 2009; Montealegre-Z and
829 Postles 2010; Montealegre-Z et al. 2017). Corroborating with previous studies on neotropical
830 katydids (e.g., Montealegre-Z and Morris 1999), we observed a vast diversity in the morphology of
831 the Southeast Asian katydids. While the left tegmina of most of the reported species have typical
832 straight/ faintly curved stridulatory files with broad teeth (often closely packed together), a few
833 species exhibit peculiarity. *Euanisous teuthroides* have squarish teeth on the stridulatory file, with
834 an indentation in the middle of each tooth. This is not observed in other species reported here.
835 *Phaneroptera brevis* have two parts to their stridulatory file, with the shorter anal half (with smaller
836 teeth) and longer basal half (with larger teeth), as it is typical for the genus *Phaneroptera* (Heller et
837 al. 2017). This may contribute to different call parameters in different parts of the calling songs that
838 has been observed in *Sphagniana sphagnum* (Walker, 1869) and an eneopterine cricket
839 *Eneoptera guyanensis* Chopard, 1931 (see Morris and Pipher 1972; Robillard et al 2015).

840

841 It has been well established that the mirror area correlates negatively with peak frequency of the
842 calling songs in katydids (Morris et al. 1994; Montealegre-Z 2009; Montealegre-Z et al. 2017). We
843 also found species with mirrors of different sizes relative to the tegmina size and shapes. Some
844 Phaneropterinae, i.e., *Holochlora* nr. *bilobata* and *Scambophyllum sanguinolentum*, have rather
845 obsolete mirrors. A typical mirror consists of the CuPa β (and sometimes CuPa α 2) and frame
846 surrounding a clear membrane (Chivers et al. 2017b). In *Holochlora* nr. *bilobata*, the mirror

847 membrane is relatively small, whereas in *Scambophyllum sanguinolentum*, the mirror membrane is
848 made up of an interlaced network of veins.

849 **Bioacoustics and integrative taxonomy**

851 New acoustic data allows us to re-test species hypotheses previously delimited using only
852 morphology. For example, we are able to integrate bioacoustics with traditional taxonomy for the
853 genus *Viriacca* by comparing the calling songs for three of the four known species—*Viriacca*
854 *insularis* from Malay Peninsula, *Viriacca modesta* from Borneo, and previously described calls of
855 *Viriacca viridis* Ingrisch, 1998, also from Malay Peninsula (Ingrisch 1998). Although their sound-
856 producing organs share many similarities, the three species exhibit distinct call structure, frequency,
857 syllable duration, and intervals between syllables. These differences are congruent to the genitalia
858 differences used to diagnose these congeners (Gorochoy 2013). This example also highlight that
859 taxonomy is hypothesis-driven in which species can be re-evaluate with new and different dataset.
860 In light of this, we also recommend using the bioacoustics to validate morphologically-similar
861 congeners in other Southeast Asian katydids. These can include the *Peracca subulicerca* species
862 complex consisting of the *Peracca subulicerca* (Karny, 1926) from Java, and *Peracca tiomani*
863 Gorochoy, 2011 and *Peracca macritchiensis* from Malay Peninsula in which their species
864 characters remain debatable.

865 **Conclusions**

867 We want to emphasize the preliminary nature of this study which is limited by too few species with
868 very few specimens. Nevertheless, by amassing data on the calling songs in understudied katydids
869 from Southeast Asia, this study provides a baseline for building a sound database for Southeast
870 Asian orthopterans. Despite their importance in species recognition, calling songs are not always
871 recorded in taxonomic descriptions. Morphology of sound-producing organs of katydids (e.g.,
872 stridulatory file length, number of teeth, and mirror area) is sometimes overlooked in traditional
873 taxonomy. Incorporating the calling songs and/or sound-producing organs with traditional
874 taxonomy can help address the taxonomy impediment while advancing our knowledge about the
875 bioacoustics of Southeast Asian katydids.

876 **Acknowledgments**

880 The project by MKT in Singapore was funded by the Wildlife Reserves Singapore Conservation
881 Fund (WRSCF). Fieldwork and taxonomic collection by MKT in the Philippines, Sandakan and
882 Brunei Darussalam were granted by the Orthoptera Species File Grant 2018 and 2019 and Percy
883 Sladen Memorial Fund (The Linnean Society of London) 2019, respectively. The EchoMeter Touch
884 Pro 2 was provided by the Wildlife Acoustics Scientific Product Grant 2019. FMZ was funded by
885 the UK Natural Environment Research Council (NERC), grant DEB-1937815. The authors are
886 thankful to Huiqing Yeo (in Singapore, Pulau Tioman and Brunei Darussalam), Siew Tin Toh (in
887 Pulau Tioman and Sandakan), Momin Binti, John Lee Yukang and Saudi Bintang (in Sandakan) for
888 field assistance; to Xing-bao Jin, Sigfrid Ingrisch and Andrei Gorochoy for help with species
889 identification; and to the UP Laguna Land Grant management for the security and accommodation
890 during fieldwork (in Laguna, the Philippines). The permissions for collecting material were granted
891 by the Forestry Department, Ministry of Primary Resources and Tourism, Brunei Darussalam
892 (JPH/PDK/01 Pt 2); the Sabah Biodiversity Centre (JKM/MBS.1000-2/3 JLD.3 (99)) (for
893 Sandakan); the National Parks Board (NP/RP18-064), Singapore; and the Research Promotion and
894 Co-Ordination Committee, Economic Planning Unit, Prime Minister's Department (UPE:
895 40/200/19/3395), Malaysia (for Pulau Tioman). The authors thank the Orthopterists' Society and
896 the Journal of Orthoptera Research for their support in publishing this article.

899 References

- 900
- 901 Bailey WJ (1967) Further investigations into function of mirror in Tettigoniioidea (Orthoptera).
 902 Nature 215: 762–763. <https://doi.org/10.1038/215762a0>
- 903 Bailey WJ (1970) The mechanics of stridulation in bush crickets (Tettigoniioidea, Orthoptera) I.
 904 Tegminal Generator. Journal of Experimental Biology 52: 495–505.
 905 <https://doi.org/10.1242/jeb.52.3.495>
- 906 Bailey WJ, Gwynne DT (1988) Mating system, mate choice and ultrasonic calling in a zaprochiline
 907 katydid (Orthoptera: Tettigoniidae). Behavior 105(3–4): 202–223.
- 908 Baker E, Chesmore D (2020) Standardization of bioacoustic terminology for insects. Biodiversity
 909 Data Journal 8: e54222. <https://doi.org/10.3897/BDJ.8.e54222>
- 910 Belwood JJ, Morris GK (1987) Bat predation and its influence on calling behaviour in neotropical
 911 katydids. Science 238(4823): 64–67. <https://doi.org/10.1126/science.238.4823.64>
- 912 Bennet-Clark, HC (1999) Resonators in insect sound production: how insects produce loud pure-
 913 tone songs. Journal of experimental Biology 202(23): 3347–3357.
- 914 Bennet-Clark, HC (2003) Wing resonances in the Australian field cricket *Teleogryllus oceanicus*.
 915 Journal of Experimental Biology 206(9): 1479–1496. <https://doi.org/10.1242/jeb.00281>
- 916 Chamorro-Rengifo J, Braun H (2016) *Phlugis ocraceovittata* and its ultrasonic calling song
 917 (Orthoptera, Tettigoniidae, Phlugidini). Zootaxa 4107(3): 439–443.
 918 <https://doi.org/10.11646/zootaxa.4107.3.12>
- 919 Chamorro-Rengifo J, Olivier RDS (2017). A new genus of Phlugidini (Orthoptera: Tettigoniidae:
 920 Meconematinae) with asymmetrical mandibles. Zootaxa 4286(3): 391–400.
 921 <https://doi.org/10.11646/zootaxa.4286.3.6>
- 922 Chivers BD, Béthoux O, Sarria-S FA, Jonsson T, Mason AC, Montealegre-Z F (2017b) Functional
 923 morphology of tegmina-based stridulation in the relict species *Cyphoderris monstrosa*
 924 (Orthoptera: Ensifera: Prophalangopsidae). Journal of Experimental Biology 220(6): 1112–1121.
 925 <https://doi.org/10.1242/jeb.153106>
- 926 Chivers BD, Jonsson T, Cadena-Castaneda OJ, Montealegre-Z F (2014) Ultrasonic reverse
 927 stridulation in the spider-like katydid *Arachnoscelis* (Orthoptera: Listrosceledinae). Bioacoustics
 928 23: 67–77. <https://doi.org/10.1080/09524622.2013.816639>
- 929 Chivers BD, Jonsson T, Soulsbury CD, Montealegre-Z F (2017a) Structural biomechanics
 930 determine spectral purity of bush-cricket calls. Biology Letters 13(11): 20170573.
 931 <https://doi.org/10.1098/rsbl.2017.0573>
- 932 Cigliano MM, Braun H, Eades DC, Otte D. (2022) Orthoptera Species File Online. Version 5 (5.0)
 933 Retrieved from: <http://orthoptera.speciesfile.org/HomePage/Orthoptera/HomePage.aspx>
 934 (accessed 27 February 2022)
- 935 Ewing AW (1989) Arthropod Bioacoustics: Neurobiology and Behavior. Cornell University Press,
 936 Ithaca.
- 937 Gorochov AV (1998) New and little known Meconematinae of the tribes Meconematini and
 938 Phlugidini (Orthoptera: Tettigoniidae). Zoosystematica Rossica 7(1): 101–131.
- 939 Gorochov AV (2008) New and little known katydids of the tribe Meconematini (Orthoptera:
 940 Tettigoniidae: Meconematinae) from south-east Asia. Proceedings of the Zoological Institute
 941 RAS 312(1–2): 26–42.
- 942 Gorochov AV (2011) Taxonomy of the katydids (Orthoptera: Tettigoniidae) from East Asia and
 943 adjacent islands. Communication 2. Far East Entomologist 227: 1–12.
- 944 Gorochov AV (2013) Taxonomy of the katydids (Orthoptera: Tettigoniidae) from East Asia and
 945 adjacent islands. Communication 6. Far Eastern Entomologist 259: 1–12.
- 946 Gorochov AV (2021) Taxonomy of the katydids (Orthoptera: Tettigoniidae) from East Asia and
 947 adjacent islands. Communication 14. Far Eastern Entomologist (434): 1–25.
- 948 Heller KG (1988) Bioakustik der europäischen Laubheuschrecken. – Ökologie in Forschung und
 949 Anwendung 1, 358 pp.

950 Heller KG (1995) Acoustic signaling in palaeotropical bushcrickets (Orthoptera: Tettigoniioidea:
951 Pseudophyllidae): Does predation pressure by eavesdropping enemies differ in the Palaeo- and
952 Neotropics? *Journal of Zoology* 237: 469–485. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-7998.1995.tb02775.x)
953 [7998.1995.tb02775.x](https://doi.org/10.1111/j.1469-7998.1995.tb02775.x)

954 Heller KG, Hemp C (2020) Hyperdiverse songs, duetting, and the roles of intra- and intersexual
955 selection in the acoustic communication of the genus *Eurycorypha* (Orthoptera: Tettigoniioidea,
956 Phaneropterinae). *Organisms Diversity and Evolution* 20: 597–617.
957 <https://doi.org/10.1007/s13127-020-00452-1>

958 Heller KG, Baker E, Ingrisch S, Korsunovskaya O, Liu CX, Riede K, Warchałowska-Śliwa E
959 (2021) Bioacoustics and systematics of *Mecopoda* (and related forms) from South East Asia and
960 adjacent areas (Orthoptera, Tettigoniioidea, Mecopodinae) including some chromosome data.
961 *Zootaxa* 5005(2): 101–144. <https://doi.org/10.11646/zootaxa.5005.2.1>

962 Heller KG, Heller M, Volleth M, Samietz J, Hemp C (2021) Similar songs, but different mate
963 localization strategies of the three species of *Phaneroptera* occurring in Western Europe
964 (Orthoptera: Phaneropteridae). *European Journal of Entomology* 118: 111–122.
965 <https://doi.org/10.14411/eje.2021.012>.

966 Heller KG, Ingrisch S, Liu CX, Shi FM, Hemp C, Warchałowska-Śliwa E, Rentz DCF (2017)
967 Complex songs and cryptic ethospecies: the case of the *Ducetia japonica* group (Orthoptera:
968 Tettigoniioidea: Phaneropteridae: Phaneropterinae). *Zoological Journal of the Linnean Society*
969 181: 286–307. <https://doi.org/10.1093/zoolinnean/zlw019>

970 Hemp C (2021) A Field Guide to the Bushcrickets, Wetas and Raspy Crickets of Tanzania and
971 Kenya; with contributions from Andreas Hemp and Klaus-Gerhard Heller. Senckenberg
972 Gesellschaft für Naturforschung. 451pp.

973 Hemp C, Heller KG (2017) Revision of the genus *Amytta* (Orthoptera: Tettigoniidae,
974 Meconematinae) and new species from East Africa. *Zootaxa* 4263(2): 295–317.
975 <https://doi.org/10.11646/zootaxa.4263.2.5>

976 Ingrisch S (1995) Revision of the Lipotactinae, a new subfamily of Tettigoniioidea (Ensifera). *Insect*
977 *Systematics and Evolution* 26(3): 273–320.

978 Ingrisch S (1998) Monograph of the Oriental Agraeciini (Insecta: Ensifera: Tettigoniidae):
979 Taxonomic revision, phylogeny, stridulation, and development. Courier Forschungsinstitut
980 Senckenberg 206: 1–391, Figs. 1–123, Maps 1–3.

981 Ingrisch S (2015) A revision of the *Axylus* group of Agraeciini (Orthoptera: Tettigoniidae:
982 Conocephalinae) and of some other species formerly included in *Nicsara* or *Anthraces*
983 Revision of the Indo-Australian Conocephalinae, part 3. *Zootaxa* 4046 (1): 1–300.
984 <https://doi.org/10.11646/zootaxa.4046.1.1>

985 Ingrisch S (2021) New species and records of the genus *Lipotactes* (Orthoptera: Tettigoniidae:
986 Lipotactinae) from Vietnam, Cambodia, and Thailand. *Journal of Orthoptera Research* 30: 51–
987 65. <https://doi.org/10.3897/jor.30.58095>

988 Jin XB (1992) Taxonomic revision and phylogeny of the tribe Phisidini (Insecta: Grylloptera:
989 Meconematidae) In: Jin XB, Kevan DKM (Eds.), *Theses Zoologicae*, 18, pp. i–vii + 1–360.

990 Jin XB, Liu X, Wang H (2020) New taxa of the tribe Meconematini from South-Pacific and Indo-
991 Malayan Regions (Orthoptera, Tettigoniidae, Meconematinae). *Zootaxa* 4772(1): 1–53.
992 <https://doi.org/10.11646/zootaxa.4772.1.1>

993 Libersat F, Hoy RR (1991) Ultrasonic startle behavior in bushcrickets (Orthoptera; Tettigoniidae).
994 *Journal of Comparative Physiology A* 169(4): 507–514. <https://doi.org/10.1007/BF00197663>

995 Mason A, Bailey W (1998) Ultrasound hearing and male–male communication in Australian
996 katydids (Tettigoniidae: Zaprochilinae) with sexually dimorphic ears. *Physiological Entomology*
997 23(2): 139–149. <https://doi.org/10.1046/j.1365-3032.1998.232069.x>

998 Mason AC, Morris GK, Wall P (1991) High ultrasonic hearing and tympanal slit function in
999 rainforest katydids. *Naturwissenschaften* 78(8): 365–367. <https://doi.org/10.1007/BF01131611>

1000 Montealegre-Z F (2012) Reverse stridulatory wing motion produces highly resonant calls in a
 1001 neotropical katydid (Orthoptera: Tettigoniidae: Pseudophyllinae). *Journal of Insect Physiology*
 1002 58(1): 116–124. <https://doi.org/10.1016/j.jinsphys.2011.10.006>
 1003 Montealegre-Z F (2009) Scale effects and constraints for sound production in katydids (Orthoptera:
 1004 Tettigoniidae): correlated evolution between morphology and signal parameters. *Journal of*
 1005 *Evolutionary Biology* 22(2): 355–366. <https://doi.org/10.1111/j.1420-9101.2008.01652.x>
 1006 Montealegre-Z F, Mason AC (2005) The mechanics of sound production in *Panacanthus*
 1007 *pallicornis* (Orthoptera: Tettigoniidae: Conocephalinae): the stridulatory motor patterns. *Journal*
 1008 *of Experimental Biology* 208(7): 1219–1237. <https://doi.org/10.1242/jeb.01526>
 1009 Montealegre-Z F, Morris GK (1999) Songs and systematics of some Tettigoniidae from Colombia
 1010 and Ecuador I. Pseudophyllinae (Orthoptera). *Journal of Orthoptera Research* 8: 163–236.
 1011 Montealegre-Z F, Morris GK, Mason AC (2006) Generation of extreme ultrasonics in rainforest
 1012 katydids. *Journal of Experimental Biology* 209(24): 4923–4937.
 1013 Montealegre-Z F, Ogden J, Jonsson T, Soulsbury CD (2017) Morphological determinants of signal
 1014 peak frequency in katydids (Orthoptera): a comparative analysis using biophysical evidence of
 1015 wing vibration. *Journal of Evolutionary Biology* 30(11): 2068–2078.
 1016 <https://doi.org/10.1111/jeb.13179>
 1017 Montealegre-Z F, Postles M (2010) Resonant sound production in *Copiphora gorgonensis*
 1018 (Tettigoniidae: Copiphorini), an endemic species from parque nacional natural gorgona,
 1019 Colombia. *Journal of Orthoptera Research* 19: 347–355. <https://doi.org/10.1665/034.019.0223>
 1020 Morris, GK (1999) Song in arthropods. In: *Encyclopedia of Reproduction*, Vol. 4 (Davey KG, ed),
 1021 pp. 508–517. Academic Press, San Diego.
 1022 Morris GK, Mason AC, Wall P, Belwood JJ (1994) High ultrasonic and tremulation signals in
 1023 neotropical katydids (Orthoptera: Tettigoniidae). *Journal of Zoology* 233(1): 129–163.
 1024 <https://doi.org/10.1111/j.1469-7998.1994.tb05266.x>
 1025 Morris GK, Pipher RE (1967) Tegminal amplifiers and spectrum consistencies in *Conocephalus*
 1026 *nigropleurum* (Bruner), Tettigoniidae. *Journal of Insect Physiology* 13: 1075–1085.
 1027 [https://doi.org/10.1016/0022-1910\(67\)90109-6](https://doi.org/10.1016/0022-1910(67)90109-6)
 1028 Morris GK, Pipher RE (1972) The relation of song structure to tegminal movement in *Metrioptera*
 1029 *sphagnorum* (Orthoptera: Tettigoniidae). *Canadian Entomologist* 104: 977–085.
 1030 <https://doi.org/10.4039/Ent104977-7>
 1031 Mugleston JD, Naegle M, Song H, Whiting MF (2018) A comprehensive phylogeny of
 1032 Tettigoniidae (Orthoptera: Ensifera) reveals extensive ecomorph convergence and widespread
 1033 taxonomic incongruence. *Insect Systematics and Diversity* 2(4): 5.
 1034 <https://doi.org/10.1093/isd/ixy010>
 1035 R Core Team (2018) R: A language and environment for statistical computing. R Foundation for
 1036 Statistical Computing, Viennan. [program]
 1037 Riede K (1996) Diversity of sound-producing insects in a Bornean lowland rainforest. In: Edwards
 1038 DS, Booth WE, Choy SC (Eds.), *Tropical rainforest research—current issues*. Dordrecht:
 1039 Springer. Pp. 77–84
 1040 Riede K (1997) Bioacoustic diversity and resource partitioning in tropical calling communities. In:
 1041 Ulrich H (Ed.) *Tropical biodiversity and systematics*. Bonn: Zoologisches Forschungsinstitut und
 1042 Museum Alexander Koenig. Pp. 275–280
 1043 Robillard T, Grandcolas P, Desutter-Grandcolas L (2007) A shift toward harmonics for high-
 1044 frequency calling shown with phylogenetic study of frequency spectra in Eneopterinae crickets
 1045 (Orthoptera, Grylloidea, Eneopteridae). *Canadian Journal of Zoology* 85(12): 1264–1275.
 1046 <https://doi.org/10.1139/Z07-106>
 1047 Robillard T, Montealegre-Z F, Desutter-Grandcolas L, Grandcolas P, Robert D (2013) Mechanisms
 1048 of high-frequency song generation in brachypterous crickets and the role of ghost frequencies.
 1049 *Journal of Experimental Biology* 216(11): 2001–2011. <https://doi.org/10.1242/jeb.083964>

1050 Robillard T, ter Hofstede HM, Orivel J, Vicente NM (2015) Bioacoustics of the neotropical
1051 eneopterinae (Orthoptera, Grylloidea, Gryllidae). *Bioacoustics* 24(2): 123–143.
1052 <https://doi.org/10.1080/09524622.2014.996915>

1053 Römer H, Lewald J (1992) High-frequency sound transmission in natural habitats: implications for
1054 the evolution of insect acoustic communication. *Behavioral Ecology and Sociobiology* 29(6):
1055 437–444.

1056 Sarria-S FA, Buxton K, Jonsson T, Montealegre-Z F (2016) Wing mechanics, vibrational and
1057 acoustic communication in a new bush-cricket species of the genus *Copiphora* (Orthoptera:
1058 Tettigoniidae) from Colombia. *Zoologischer Anzeiger—A Journal of Comparative Zoology* 263:
1059 55–65. <https://doi.org/10.1016/j.jcz.2016.04.008>

1060 Sarria-S FA, Morris GK, Windmill JF, Jackson J, Montealegre-Z F (2014) Shrinking wings for
1061 ultrasonic pitch production: hyperintense ultra-short-wavelength calls in a new genus of
1062 neotropical katydids (Orthoptera: Tettigoniidae). *PLoS One* 9(6): e98708.
1063 <https://doi.org/10.1371/journal.pone.0098708>

1064 Sueur J, Gasc A, Grandcolas P, Pavoine S (2012) Global estimation of animal diversity using
1065 automatic acoustic sensors. In: Le Gaillard J-F, Guarini J-M, Gaill F (Eds), *Sensors for Ecology. Towards Integrated Knowledge of Ecosystems*. Paris: CNRS. Pp. 99–117.

1066 Tan MK (2011) The Copiphorini (Orthoptera: Tettigoniidae: Conocephalinae) in Singapore. *Nature*
1067 in Singapore 4: 31–42.

1068 Tan MK (2012) New species of *Glenophysis* (Orthoptera: Tettigoniidae: Hexacentrinae) from
1069 Singapore, with key to species. *Zootaxa* 3185: 64–68. <https://doi.org/10.11646/zootaxa.3185.1.5>

1070 Tan MK (2014) An annotated checklist of the bush katydids (Orthoptera: Phaneropteridae:
1071 Phaneropterinae) from Singapore, including an illustrated key to species. *Zootaxa* 3884(6): 573–
1072 593. <https://doi.org/10.11646/zootaxa.3884.6.6>

1073 Tan MK (2017) Orthoptera in the Bukit Timah and Central Catchment Nature Reserves (Part 2):
1074 Suborder Ensifera. 2nd Edition. Lee Kong Chian Natural History Museum, National University of
1075 Singapore, Singapore. 101 pages. Uploaded 16 June 2017.

1076 Tan MK, Artchawakom T (2017) Taxonomic review of *Alloteratura* katydid (Orthoptera:
1077 Meconematinae) with the description of one new species from Thailand. *Zootaxa* 4226(1): 103–
1078 112. <https://doi.org/10.11646/zootaxa.4226.1.5>

1079 Tan MK, Choi J, Shankar N (2017) Trends in new species discovery of Orthoptera (Insecta) from
1080 Southeast Asia. *Zootaxa* 4238(1): 127–134. <https://doi.org/10.11646/zootaxa.4238.1.10>

1081 Tan MK, Dawwrueng D, Artchawakom T (2015) Taxonomic review of *Kuzicus* Gorochoy, 1993
1082 (Tettigoniidae: Meconematinae), with two new species from Thailand and key to species.
1083 *Zootaxa* 3999(2): 279–290. <https://doi.org/10.11646/zootaxa.3999.2.7>

1084 Tan MK, Ingrisch S (2014) New taxa and notes of some described species of Agraeciini
1085 (Orthoptera: Tettigoniidae: Conocephalinae) from Malay Peninsula. *Zootaxa* 3765(6): 541–556.
1086 <https://doi.org/10.11646/zootaxa.3765.6.3>

1087 Tan MK, Ingrisch S, Robillard T, Baroga-Barbecho JB, Yap SA (2018) New taxa and notes on
1088 spine-headed katydids (Orthoptera: Conocephalinae: Agraeciini) from the Philippines. *Zootaxa*
1089 4462(3): 331–348. <https://doi.org/10.11646/zootaxa.4462.3.2>

1090 Tan MK, Ingrisch S, Wahab RA, Japir R, Chung AYC (2020a) Ultrasonic bioacoustics and
1091 stridulum morphology reveal cryptic species among *Lipotactes* big-eyed katydids (Orthoptera:
1092 Tettigoniidae: Lipotactinae) from Borneo. *Systematics and Biodiversity* 18(5): 510–524.
1093 <https://doi.org/10.1080/14772000.2020.1769223>

1094 Tan MK, Japir R, Chung AYC (2019) Uncovering the Grylloidea and Tettigoniioidea (Orthoptera:
1095 Ensifera) in the Forest Research Centre (Sepilok) Entomological Collection. *Zootaxa* 4701(4):
1096 301–349. <https://doi.org/10.11646/zootaxa.4701.4.1>

1097 Tan MK, Jin XB, Baroga-Barbecho JB, Yap SA (2020b) Taxonomy and bioacoustics of
1098 Meconematinae (Orthoptera: Tettigoniidae) from Laguna (Philippines: Luzon) *Zootaxa* 4732(4):
1099 527–544. <https://doi.org/10.11646/zootaxa.4732.4.2>

1100

1101 Tan MK, Malem J, Legendre F, Dong J, Baroga-Barbecho JB, Yap SA, Wahab RA, Japir R, Chung
 1102 AYC, Robillard T (2021) Phylogeny, systematics and evolution of calling songs of the
 1103 Lebinthini crickets (Orthoptera, Grylloidea, Eneopterinae), with description of two new genera.
 1104 Systematic Entomology 46(4): 1060–1087. <https://doi.org/10.1111/syen.12510>
 1105 Tan MK, Montealegre-Z F, Wahab RA, Lee CY, Belabut DM, Japir R, Chung AYC (2019)
 1106 Ultrasonic songs and stridulum anatomy of *Asiophlugis* crystal predatory katydids
 1107 (Tettigoniodea: Meconematinae: Phlugidini). Bioacoustics 29(6): 619–637.
 1108 <https://doi.org/10.1080/09524622.2019.1637783>
 1109 Tan MK, Robillard T (2021) Highly diversified circadian rhythms in the calling activity of
 1110 eneopterine crickets (Orthoptera: Grylloidea: Gryllidae) from Southeast Asia. Bioacoustics.
 1111 <https://doi.org/10.1080/09524622.2021.1973562>
 1112 ter Hofstede HM, Kalko EK, Fullard JH (2010) Auditory-based defense against gleaning bats in
 1113 neotropical katydids (Orthoptera: Tettigoniidae). Journal of Comparative Physiology A 196(5):
 1114 349–358. <https://doi.org/10.1007/s00359-010-0518-4>
 1115 ter Hofstede HM, Symes LB, Martinson SJ, Robillard T, Faure P, Madhusudhana S, Page RA
 1116 (2020) Calling songs of neotropical katydids (Orthoptera: Tettigoniidae) from Panama. Journal
 1117 of Orthoptera Research 29(2): 137–201. <https://doi.org/10.3897/jor.29.46371>
 1118 Walker TJ, Dew D (1972) Wing movements of calling katydids: fiddling finesse. Science
 1119 178(4057): 174–176. <https://doi.org/10.1126/science.178.4057.174>
 1120 Willemse C (1959) Notes on the genus *Salomona* Blanchard (Orthoptera, Tettigoniodea, subfam.
 1121 Agraecinae) Publicaties van het Natuurhistorisch Genootschap in Limburg 11 [1958–1959]: 1–
 1122 118, pls. 1–43.
 1123
 1124