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Revisiting the calling songs of katydids (Orthoptera: Tettigonioidea) from the tropical forests of Southeast Asia

Lewis B. **Holmes**[1], Ming Kai **Tan**[2*], Razy **Japir**[3], Arthur Y. C. **Chung**[3], Jewel Anne G. **Salvador**[4], Olga Macas **Nuñeza**[4], Amira Aqilah **Muhammad**[5], Nurul Ashikin **Abdullah**[5], Trung Thanh **Vu**[6,7], Thai Hong **Pham**[7] & Fernando **Montealegre-Z**[1*]

Abstract. Based on field collection and recording of katydids from Borneo (specifically Sabah in East Malaysia), the Philippines (specifically Mindanao), the Malay Peninsula (Singapore and Peninsular Malaysia) and Indochina (specifically Vietnam) between 2021 and 2024 (approximately three years), we describe the calling songs of 25 katydid species from four subfamilies (i.e., Conocephalinae, Meconematinae, Phaneropterinae, and Pseudophyllinae). The new acoustics data validates numerous widely-known observations and hypotheses about katydid calling songs. Firstly, most katydids produce ultrasonic sounds. Notably, an unknown and probably undescribed species of Meconematini (Philippines) produces calling songs with a peak frequency of 88.0 kHz, the highest known for Southeast Asian taxa. Our study also confirms that the subfamily Meconematinae is a major katydid group in which taxa produce songs with an entirely ultrasonic spectrum and extreme ultrasonic songs, whereas the subfamily Pseudophyllinae can produce exceedingly low frequencies (<10 kHz). This study also substantiates that katydid songs are very diverse in the call structure, ranging from isolated simple syllables in some Phaneropterinae to echemes or echeme-sequences and complex songs in *Conocephalus*. This diversity in calling songs corresponds to the diverse morphology of their sound-producing organs. Based on three allopatric species of *Scytocera* and three *Phaulula* species, we show that the calling song parameters and previously unknown morphology of the sound-producing organs corroborate with the traditional morphological characters (e.g., abdominal appendages and titillators) used to diagnose katydid congeners. This also further confirms that bioacoustics and the sound-producing organs can be useful to better understand species boundaries for taxa from this region.

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

INTRODUCTION

Tettigoniidae (Insecta: Orthoptera), commonly known as katydids or bush crickets, is a diverse and widespread family consisted of more than 8,000 known species globally (Cigliano et al., 2024). Like most other groups of orthopterans, they produce sound through stridulation for communication (Morris & Pipher, 1967; Bailey, 1970; Ewing, 1989; Chivers et al., 2014). However, unlike crickets, katydids generally produce calling songs with higher frequency and relatively broad-banded spectra, and many species produce calling songs with energy often peaking at the ultrasonic frequency range (Mason et al., 1991; Montealegre-Z et al., 2017). Some extreme ultrasonic singers include *Supersonus* (Meconematinae: Phisidini) from the Neotropics that produce calling songs peaking at 150 kHz (Sarria-S et al., 2014). Since these calling songs are crucial for conspecific recognition, different katydid species tend to produce species-specific calling songs which are different in terms of temporal (e.g., duration, period, call structure) and frequency (e.g., peak frequency, tonality) domains (Heller, 1995; Ingrisch, 1995, 1998; Riede, 1996, 1997; Tan, 2011; Heller et al., 2017, 2021; Tan et al., 2019a, 2020a).

Wallacea, Sundaland, and the Philippines are biodiversity hotspots (Myers et al., 2000), and at least 1,900 katydid species are known to occur in Indochina, Malesia, and New Guinea (Cigliano et al., 2024). Unfortunately, the calling songs of most katydids remain unknown. There are generally very few experts in studying both the morphology and bioacoustics of katydids from this region. Moreover, not

Accepted by: *Wendy Y. L. Wang*

[1]School of Life Sciences, Joseph Banks Laboratories, University of Lincoln, Green Lane, Lincoln, LN6 7DL, UK; Email: fmontealegrez@lincoln.ac.uk (*corresponding author)

[2]Lee Kong Chian Natural History Museum, Faculty of Science, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Republic of Singapore; Email: orthoptera.mingkai@gmail.com (*corresponding author)

[3]Forest Research Centre (Sepilok), Sabah Forestry Department, PO Box 1407, 90715 Sandakan, Sabah, Malaysia

[4]Department of Biological Sciences, College of Science and Mathematics, Mindanao State University-Iligan Institute of Technology, Tibanga, Iligan City 9200, Philippines

[5]Institute of Biological Sciences, Faculty of Science, Universiti Malaya, Kuala Lumpur 50603, Malaysia

[6]Graduate School of Science and Technology, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Hanoi, Vietnam

[7]Mientrung Institute for Scientific Research, Vietnam National Museum of Nature, VAST, 321 Huynh Thuc Khang, Hue, Vietnam

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all species sing vigorously, and considerable effort and time are needed to record the calling songs, whether in the field or under laboratory conditions. Consequently, the calling songs of many common species remain unknown, and many more new species have been described without their calling songs ever documented.

There have been substantial attempts to document the calling songs of katydids around the world. These include taxa from the Neotropics (e.g., Morris et al., 1989; Montealegre-Z & Morris, 1999; Naskrecki, 2000; Braun, 2002; ter Hofstede et al., 2020; Heller & Helb, 2024) and the Afrotropics (e.g., Naskrecki, 2000; Hemp et al., 2023). Montealegre-Z et al. (2006, 2017) and Chivers et al. (2014, 2017) are also some recent works that advanced our understanding of the mechanism of sound production in katydids, especially those that produce ultrasonic songs. In Southeast Asia, while some studies focused on examining ecological and behavioural aspects of katydid singing (Heller, 1995; Riede, 1996, 1997), others focused on using katydid songs to help delineate cryptic species (Heller et al., 2017, 2021; Tan et al., 2020a; Salvador et al., 2024). Similar to Ingrisch (1995, 1998), Tan et al. (2023) also attempted to describe the calling songs of katydids from Southeast Asia. Nevertheless, such documentations cover only a tiny proportion of the total katydid diversity in Southeast Asia.

Here, based on more recent fieldwork, we document and describe the calling songs of another 25 species from different parts of Southeast Asia, most of which are previously unknown. Following the methods in Tan et al. (2023), the calling songs of male katydids were recorded under ex-situ conditions, then identified and systematically vouchered in natural history depositories. Additionally, the sound-producing organs of both the left and right tegmina were described using images from infinite focus microscopy.

MATERIAL AND METHODS

Collection and husbandry of katydids. Between 2021 and 2024, katydids were opportunistically collected by sight (mostly at night but occasionally in the day) from different parts of the Malay Peninsula, Borneo, the Philippines and Indochina: (1) Singapore; (2) Panti Forest Reserve in Johor, Peninsular Malaysia; (3) Sandakan, Mount Trus Madi, Tenompok, and Bukit Hampuan in Sabah, East Malaysia; (4) Claveria and Mount Malindang in Mindanao, Philippines; (5) Bạch Mã National Park in Vietnam (Fig. 1). 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. Husbandry of katydids follows that in Tan et al. (2023).

Acoustic recordings and analysis. Acoustic recording and analysis generally followed that in Tan et al. (2019a, 2020a, 2023). All recordings were obtained in laboratory conditions or biological stations at night in the dark. Recording of the calling song of an isolated male placed inside a standardised insect cage (25 cm in diameter and 33 cm tall) with nylon cover was done one at a time, using a sampling frequency of 256 kHz-samples/s Echo Meter Touch Pro 2 (based on Knowles FG sensor) or Wildlife Acoustics Song Meter (SM) Mini acoustic recorder. The recorder was placed horizontally and at most 1–2 m away from the cage. For the Echo Meter Touch, the triggered recording was used with the Trigger Minimum Frequency set at 20 kHz. 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).

The basic katydid song terminology follows Baker & Chesmore (2020) and Tan et al. (2023):
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.

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_{-3dB}, and Q_{-10dB} entropy, spread and flatness. We used spectral entropy to estimate signal heterogeneity, in which a low value indicates the call approaches a pure-tone signal, and a high value indicates that the signal approached a broadband (Chivers et al., 2017; Tan et al., 2023). We also use the quality factor Q (Q_{-3dB}) to estimate the purity of the signal. Q was calculated from the spectral band following one of the methods proposed by Bennet-Clark (1999), however this assumes that the spectrum is symmetrical around the dominant peak. Therefore, Q values are only reported for species showing symmetrical frequency spectrum, and not those with broad-band spectra.

It should be noted that the response functions of both Echo Meter Touch Pro 2 (based on Knowles FG sensor) and Wildlife Acoustics Song Meter (SM) Mini acoustic recorder

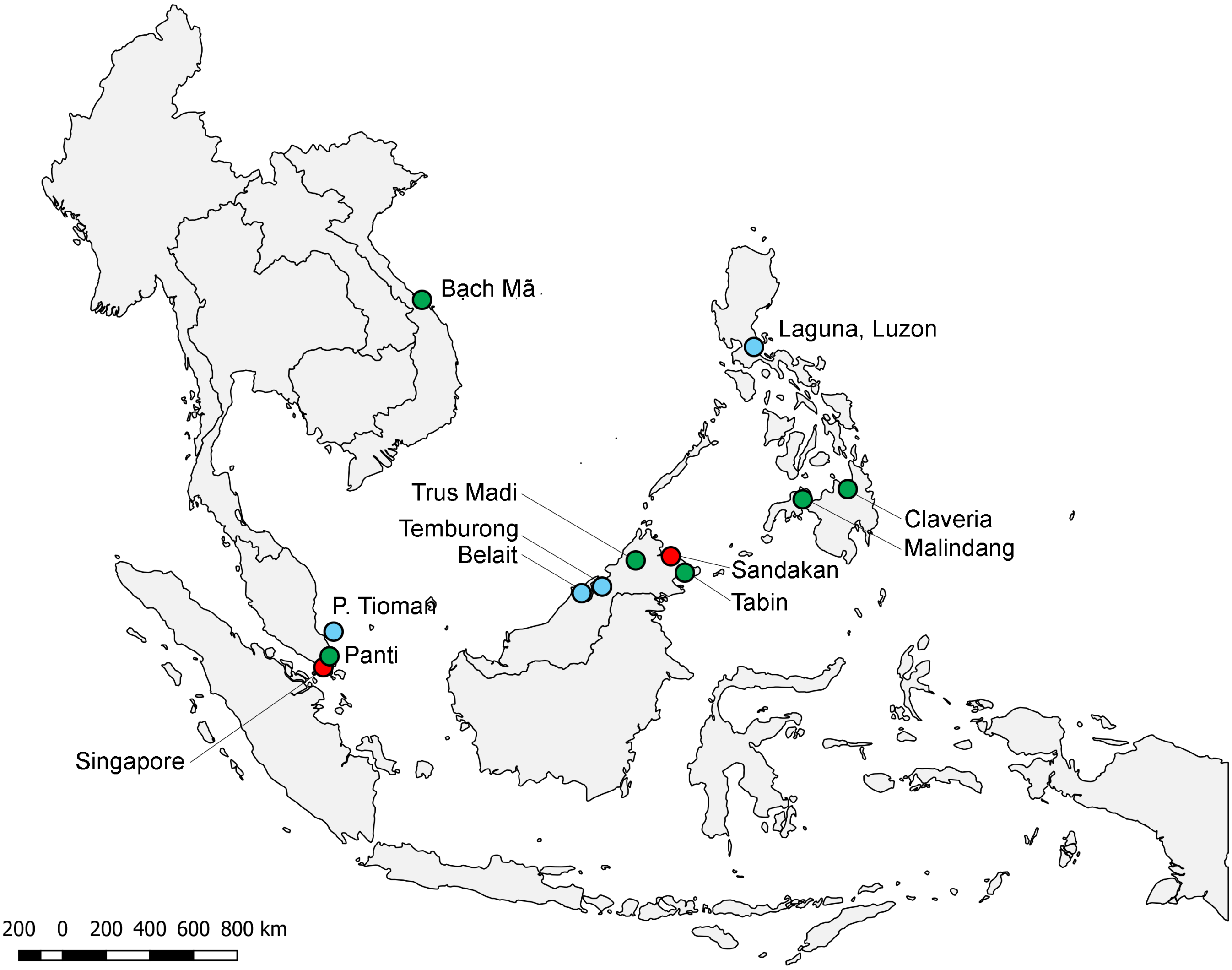

Fig. 1. Map of Southeast Asia with the sampling sites indicated and labeled for both Tan et al. (2023) and this study. The green circle represents new sampling sites from this study, the blue circle represents sampling sites from Tan et al. (2023), and the red circle represents sampling sites from both studies.

are different, and that each response function for each recorder is not flat and not calibrated during recording. Manufacturer's information for the Echo Meter Touch Pro 2 suggests that the response is relatively flat between 1–50 kHz, oscillating around ±10 dB (85–90 dB). Between 50 and 120 kHz, the response gradually decreases, nearly linearly, from 80 to 60 dB. Most of the calls described here are below 50 kHz, except the calling songs of *Delorita pulchra* and Meconematini sp., for which the spectral shape presented merely provides a good representation of reality. Manufacturer's information for the SM Mini suggests that the response is relatively flat between 1–10 kHz, oscillating around ±10 dB (105–115 dB). Between 10 and 20 kHz, the response gradually decreases linearly from 115 to 90 dB. Response curve for frequencies above 20 kHz was not available.

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 based on original descriptions in literature and published identification keys, including Ragge (1956); Ingrisch (1998, 2011, 2015); Gorochov (1998, 2004, 2008a, 2008b, 2009, 2013, 2016a, 2016b); Gorochov & Voltshenkova (2009); Tan (2014, 2017); Tan & Artchawakom (2017); Tan & Wahab (2017); Tan et al. (2019b, 2019c, 2020b); Jin et al. (2020) and comparisons with photographs of type specimens available on the Orthoptera Species File (Cigliano et al., 2024).

Sound-producing structure. The left and right tegmina were dissected, whenever possible. Three-dimensional images of the stridulatory file on the left tegmen, and sound-producing organs on the right tegmen were obtained with infinite focus microscopy using an Alicona Infinite Focus (model G5) microscope (OPTIMAX Imaging Inspection and Measurement Limited, Leicestershire, UK). The inter-tooth distance (mm) was measured from the edge of the cusp of one tooth to the cusp of the next one (Montealegre-Z & Mason, 2005), from the anal end to the last tooth at the basal end of the left tegminal stridulatory file. The tooth length (mm) as an indication of tooth size was also measured from the anterior to the posterior ends of the cusp of each tooth [equivalent to tooth width used in Tan et al. (2023)]. Tooth density was calculated as the total number of teeth divided by the file length (in mm).

Table 1. Summary of the species recorded in this study. The mean and standard deviation (±s.d.) were reported for peak frequency. Abbreviations for recording device: EMT = Echo Meter Touch Pro 2; SM Mini = Wildlife Acoustics Song Meter (SM) Mini.

	Species	Country of Origin	Call structure	Spectral entropy	Peak freq. (kHz)	Recording device
	Subf. Conocephalinae					
1.	*Anthracites pyramidalis*	Philippines	Echemes	7.48	22.0±1.0	EMT
2.	*Anthracites zebra*	Philippines	Tri-syllabic echeme trill	8.50	23.1±0.6	EMT
3.	*Bispinolakis longicauda*	East Malaysia	Trill	6.21	20.8±0.5	EMT
4.	*Conocephalus* sp.	East Malaysia	Complex call	8.30	23.2±0.8	EMT
5.	*Eumacroxiphus* (*Eumacroxiphus*) *diffundatus*	East Malaysia	Isolated syllables	9.43	19.4±1.4	SM Mini
6.	*Palaeoagraecia philippina*	East Malaysia	Echemes with paired syllables	8.48	19.5±2.1	EMT
7.	*Sacculiphallus dyaka*	East Malaysia	Echemes with paired syllables	7.61	23.4±0.3	EMT
8.	*Scytocera borneensis sandakani*	East Malaysia	Isolated syllables	8.05	34.6±1.8	EMT
9.	*Scytocera* cf. *kemneri*	Singapore	Echemes	8.52	23.9±0.9	SM Mini
10.	*Scytocera* cf. *longicornis*	Philippines	Echemes	7.03	24.0±0.3	EMT
	Subf. Meconematinae					
11.	*Alloteratura* (*Meconemopsis*) *longa*	East Malaysia	Irregular echemes	5.91	23.4±0.4	EMT
12.	*Grigoriora* sp.	Vietnam	Isolated syllables	8.56	45.8±0.7	EMT
13.	*Odonturisca epiproctalis*	East Malaysia	Isolated syllables	6.47	21.5±0.2	EMT
14.	Meconematini sp.	Philippines	Isolated syllables	8.54	88.0±2.1	EMT
	Subf. Phaneropterinae					
15.	*Arnobia pilipes tropica*	Peninsular Malaysia, Singapore	Pulse-trains	7.98	26.4±1.3	SM Mini
16.	*Deflorita pulchra*	East Malaysia	Echemes	9.13	61.8±1.8	EMT
17.	*Elimaea* (*Bornelimaea*) *sympatrica*	East Malaysia	Syllable group	8.62	16.7±1.8	SM Mini
18.	*Elimaea* (*Rhaebelimaea*) *signata*	Singapore	Isolated syllables	8.81	14.3±1.5	SM Mini
19.	*Leptoderes ornatipennis*	East Malaysia	Isolated syllables	7.01	8.4	SM Mini
20.	*Phaneroptera neglecta*	Philippines	Syllable group	9.48	29.9±1.3	SM Mini
21.	*Phaulula* cf. *ensigera*	Philippines	Syllable group	9.12	30.0±1.1	SM Mini
22.	*Phaulula* cf. *galeata*	Philippines	Syllable group	8.35	21.3±0.5	SM Mini
23.	*Phygela marginata*	East Malaysia	Paired syllables	7.36	11.7±0.4	SM Mini
24.	*Stictophaula* sp.	Singapore	Isolated syllables	8.97	25.1±2.8	SM Mini
	Subf. Pseudophyllinae					
25.	*Phyllomimus* (*Phyllomimus*) cf. *detersus*	Philippines	Echemes with paired syllables	6.46	7.0±0.1	SM Mini

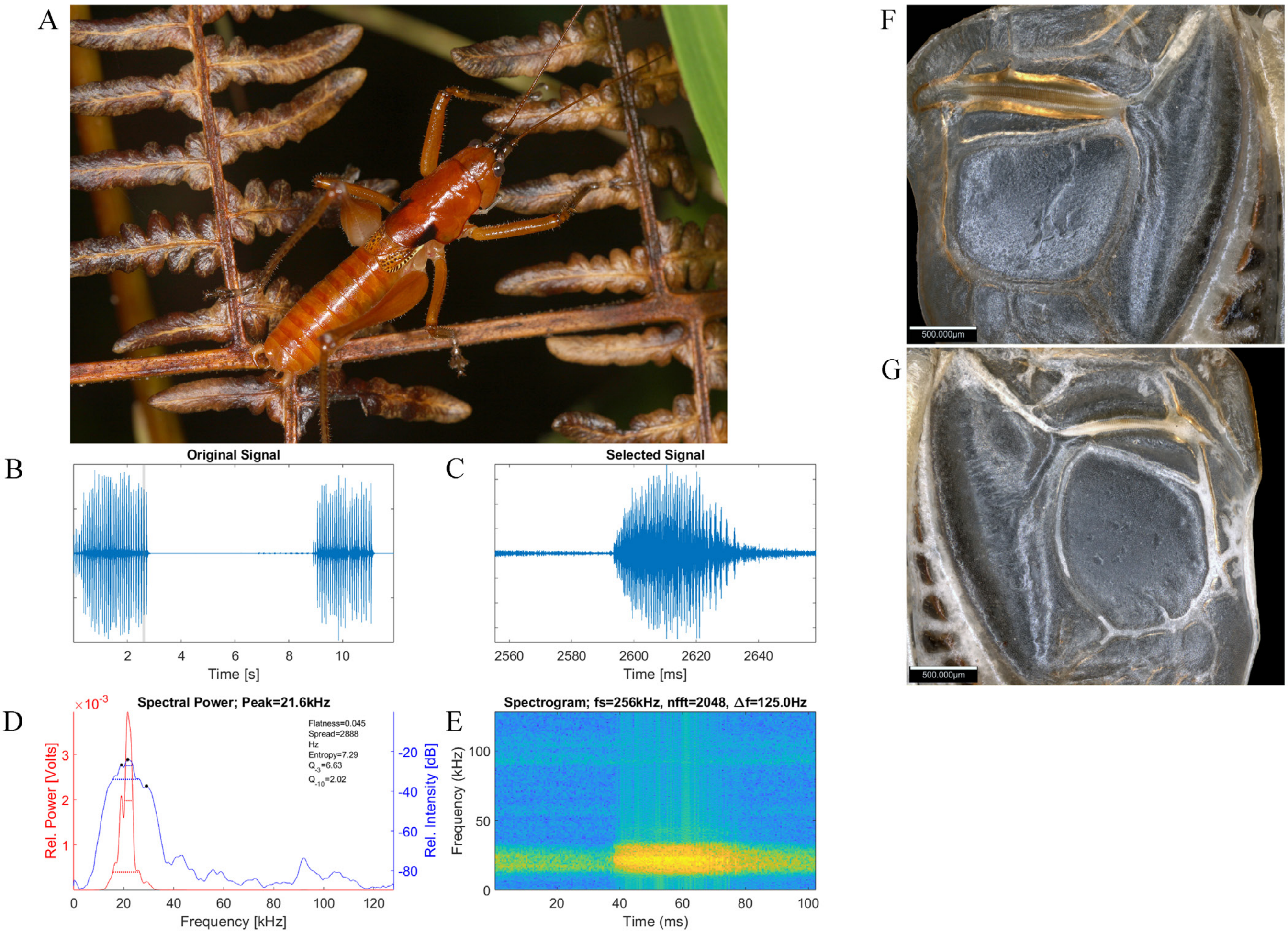

Fig. 2. *Anthracites pyramidalis* male adult in the field at Mindanao, Philippines (A). Oscillograms showing two echemes (B) and a syllable (C). Power spectrum (D) and spectrogram (E) of a syllable. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

Depositories. Specimens will be deposited in the Zoological Reference Collection (ZRC), housed at the Lee Kong Chian Natural History Museum, Singapore. Sound files will be deposited in the Xeno-Canto sound database (www.xeno-canto.org).

RESULTS

In total, we recorded the calling songs of 25 species from 20 genera of the subfamilies Conocephalinae (10 species and seven genera), Meconematinae (four species and four genera), Phaneropterinae (10 species and eight genera) and Pseudophyllinae (one species and one genus) (Table 1). 12 recorded species originated from Borneo (specifically Sabah in East Malaysia), eight species from the Philippines (specifically Mindanao), four species from the Malay Peninsula (four species from Singapore and one species from Peninsular Malaysia), and one species from Indochina (specifically Vietnam). *Phyllomimus* (*Phyllomimus*) cf. *detersus* has the lowest peak frequency of 7.0±0.1 kHz reported here, whereas Meconematini sp. (Philippines) has the highest peak frequency of 88.0±2.1 kHz. The calling song of *Alloteratura* (*Meconemopsis*) *longa* has the most tonal frequency spectrum with its spectral entropy of 5.91, whereas that of *Phaneroptera neglecta* has the most broad-band frequency spectrum with its spectral entropy of 9.48.

SONG AND SOUND-PRODUCING STRUCTURE DESCRIPTIONS

Subfamily Conocephalinae

Anthracites pyramidalis Ingrisch, 2015

(n = 2 males, 17 calling songs)
(Fig. 2)

At 19.3°C, calling song made up of echemes, each containing ca. 29±4 (23–39) closely-spaced syllables. Average echeme duration 2.40±0.35 s (1.92–3.17 s). Within each echeme, average syllable duration 40.6±3.8 ms (34.9–48.3 ms), average syllable period 81.8±4.7 ms (72.9–90.2 ms) and average silent interval between consecutive syllables 41.2±4.1 ms (34.7–50.2 ms). Call spectrum with peak frequency 22.0±1.0 kHz (18.8–23.3 kHz). Spectral entropy 7.3–7.5 and Q_{-3dB} 6.7–10.2.

Micropterous species. Ventrally, left tegmen with stridulatory file faintly sinuous, ca. 1.47 mm in length, lined with 108

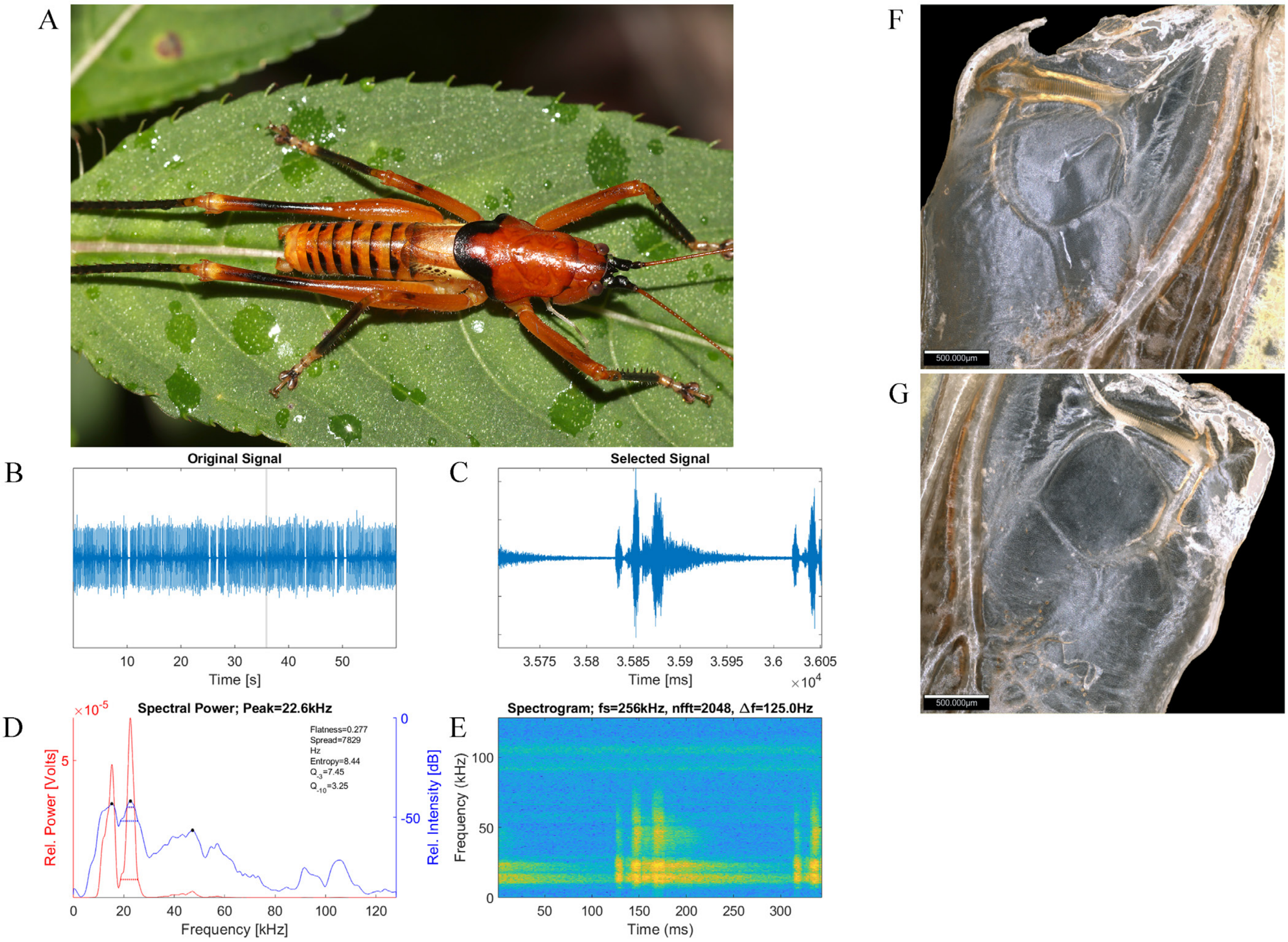

Fig. 3. *Anthracites zebra* male adult in the field at Mindanao, Philippines (A). Oscillograms showing sequence of tri-syllabic trill (B) and two tri-syllables (second incomplete) (C). Power spectrum (D) and spectrogram (E) of the syllable. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

long and slender teeth, a few indistinct teeth at basal end. Average tooth density 73 teeth per mm. Teeth on stridulatory file of left tegmen relatively equally sized (except towards both ends), fairly uniformly-distributed and narrowly spaced apart; inter-tooth distance nearly constant throughout file. Mid-part of stridulatory file with average tooth length 64 µm, average inter-tooth distance 16 µm. Left file (Cu2) elevated on slightly widened and swollen vein buttress. Right tegmen with mirror broadly ovular, membrane smooth and transparent, stridulatory file ca. 1.18 mm in length with ca. 79 teeth.

Anthracites zebra Hebard, 1922

(n = 2 males, 28 calling songs)
(Fig. 3)

At 27.8°C, calling song consists of continuous trill made up of tri-syllabic echemes (echeme trill). Average duration of three triplets 52.7±2.5 ms (48.7–63.2 ms) and average durations of first, second and third syllables 7.0±1.3 ms (3.7–8.8 ms), 9.4±1.4 ms (7.1–12.7 ms), and 14.6±2.2 ms (10.5–18.2 ms), respectively. First syllable has lowest amplitude, followed by second and third syllables. Call spectrum peaks at 23.1±0.6 kHz (22.3–24.3 kHz, ultrasonic range), and another peak at 15.5±0.3 kHz (15.3–15.8 kHz, sonic range). Peaks have similar energy. Spectral entropy of ultrasonic peak 8.5–8.5 and Q_{-3dB} 6.2–7.5.

Micropterous species. Ventrally, left tegmen with stridulatory file fairly straight, ca. 1.09 mm in length, lined with 73 long and slender teeth and three small teeth at anal end; file slightly curved at both ends. Average tooth density 67 teeth per mm. Teeth on stridulatory file of left tegmen of relatively equally sized (except towards both ends), fairly uniformly distributed and narrowly spaced apart. Mid-part of stridulatory file with average tooth length 109 µm and average inter-tooth distance 20 µm. Left file (Cu2) elevated on slightly widened and swollen vein buttress. Right tegmen with mirror squarish, longer than broad, membrane smooth and transparent, stridulatory file ca. 0.88 mm in length with ca. 74 teeth.

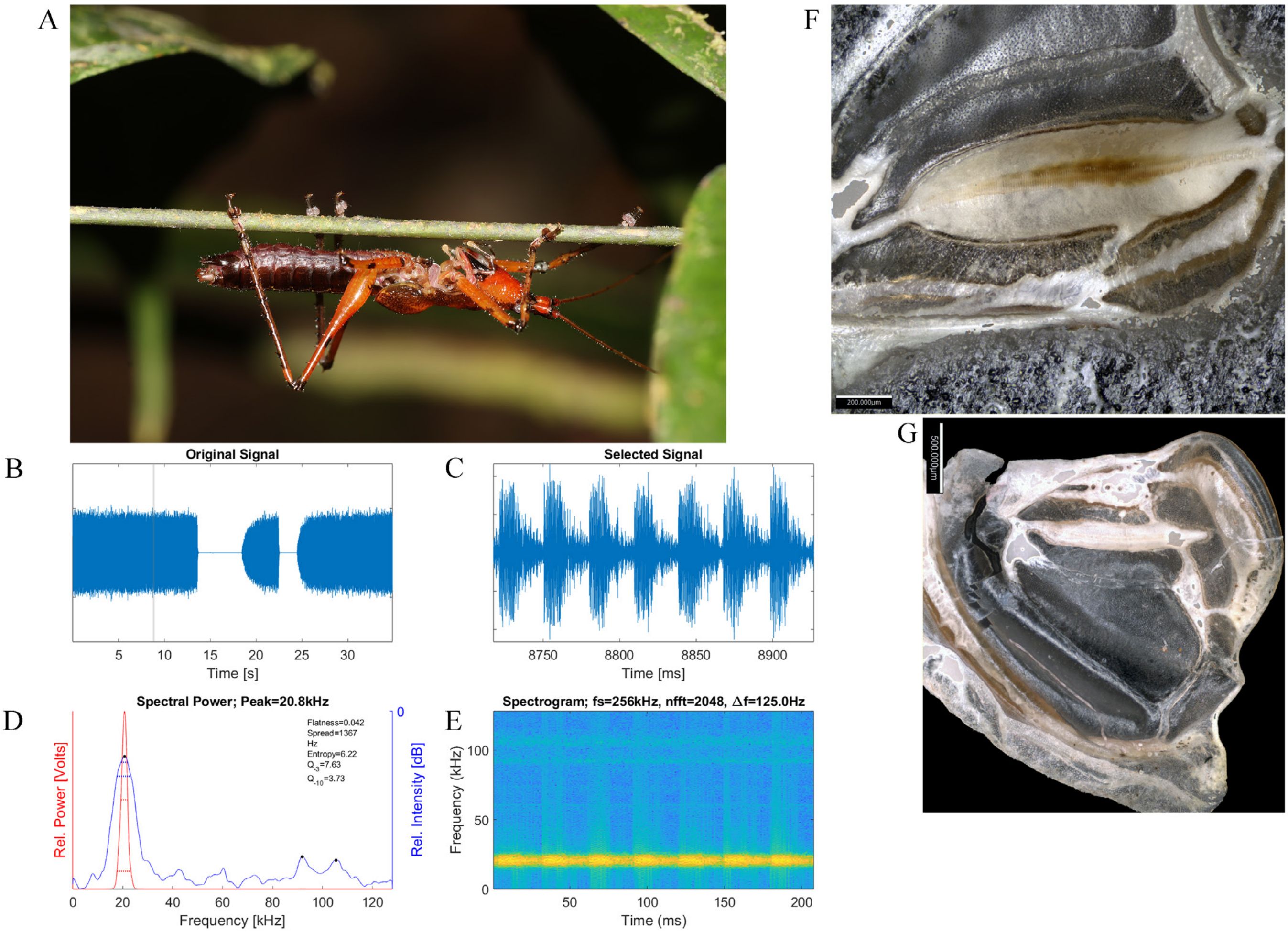

Fig. 4. *Bispinolakis longicauda* male adult in the field at Sabah, East Malaysia (A). Oscillograms showing continuous trill with two interruptions (B) and seven syllables (C). Power spectrum (D) and spectrogram (E) of the echemes. Ventral view of the left tegminal stridulatory file (F), and ventral view of the right tegmen sound-producing organs (G).

Bispinolakis longicauda Ingrisch, 1998
(n = 1 male, 12 calling songs)
(Fig. 4)

At 24.6°C, calling song consists of continuous trill, i.e., repetition of closely-spaced syllables. Average syllable duration 16.5±1.5 ms (14.4–18.6 ms), average syllable period 31.1±1.7 ms (29.3–33.7 ms) and average silent interval between consecutive syllables 14.6±0.8 ms (12.8–15.7 ms). Call spectrum with peak frequency 20.8±0.5 kHz (19.8–21.3 kHz). Spectral entropy ca. 6.2 and Q_{-3dB} 7.6–8.6.

Micropterous species. Ventrally, left tegmen with stridulatory file straight, ca. 1.31 mm in length, lined with 160 long and very slender teeth. Average tooth density 122 teeth per mm. Teeth on stridulatory file of left tegmen relatively equally sized (except towards ends), very narrowly spaced apart and fairly uniformly distributed throughout file (except anal- and basal-most teeth). Mid-part of stridulatory file with average inter-tooth distance 8 µm, and average tooth length 69 µm. Left file (Cu2) elevated on very swollen and broadly widened vein buttress. Right tegmen with mirror narrow triangular with distal end being narrower end, membrane smooth and transparent, stridulatory file slender, ca. 1.12 mm in length.

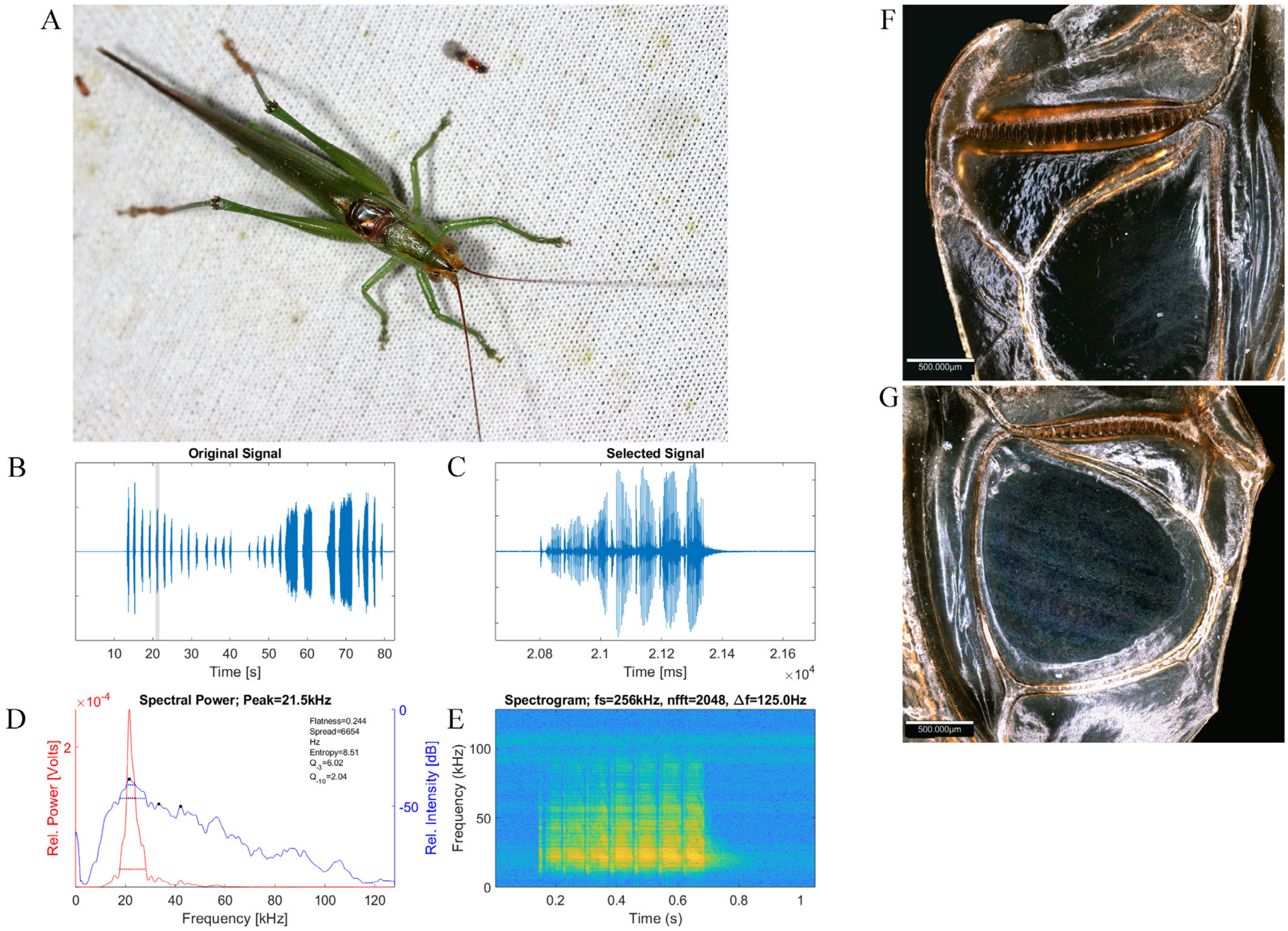

Fig. 5. *Conocephalus* sp. male adult in the field at Sabah, East Malaysia (A). Oscillograms showing the two call types highlighting the first call type (B) and one echeme with seven syllables (C). Power spectrum (D) and spectrogram (E) of the echeme. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

Conocephalus sp.
(n = 1 male, 11 calling songs)
(Fig. 5)

At 24.6°C, two types of calling song recorded. First type consists of echeme made up of 7±1 (5–7) discrete syllables and average duration 0.49±0.06 s (0.36–0.54 s). Amplitude increases with each syllable within echeme. Average duration for first syllable slightly shorter, i.e., 65.9±3.6 ms (60.9–70.4 ms). Average syllable duration 69.4±3.1 ms (64.2–74.5 ms), average syllable period 78.6±1.8 ms (76.0–81.5 ms) and average silent interval between consecutive syllables 9.3±2.5 ms (5.5–12.5 ms).

Second song type consists of trill. Trill duration ranges from 2.4–3.5 s. Average syllable duration also longer, i.e., 75.8±2.0 ms (73.7–77.6 ms), average syllable period 85.0±0.2 ms (84.8–85.1 ms) and average silent interval between consecutive syllables 8.1±0.8 ms (7.5–8.6 ms).

Call spectrum peaks at 23.2±0.8 kHz (21.8–24.3 kHz, ultrasonic range). Spectral entropy 8.0–8.6 and Q_{-3dB} value 5.4–6.0.

Macropterous species. Ventrally, left tegmen with stridulatory file straight, ca. 1.98 mm in length, lined with 32 long but fairly broad teeth; file at basal end slightly curved. Average tooth density 16 teeth per mm. Teeth on stridulatory file of left tegmen relatively equally sized (except towards ends), relatively broadly spaced apart and fairly uniformly distributed throughout file. Mid-part of stridulatory file with average inter-tooth distance 86 µm and average tooth length 146 µm. Left file (Cu2) only slightly elevated on slightly swollen and widened vein buttress. Right tegmen with mirror broadly ovular, membrane smooth and transparent, and stridulatory file sinuous, ca. 1.41 mm in length with ca. 26 teeth slightly shorter (stouter) than those on left tegmen.

This species differs clearly in morphology from the congeners recorded in Borneo: *Conocephalus borneensis* (Redtenbacher, 1891), *Conocephalus cognatus* (Redtenbacher, 1891), *Conocephalus maculatus* (Le Guillou, 1841) and *Conocephalus melaenus* (Haan, 1843) (Cigliano et al., 2024). It may indicate that this is an undescribed species, but the taxonomy of Southeast Asian *Conocephalus* requires re-examination. However, this is out of the scope of this paper.

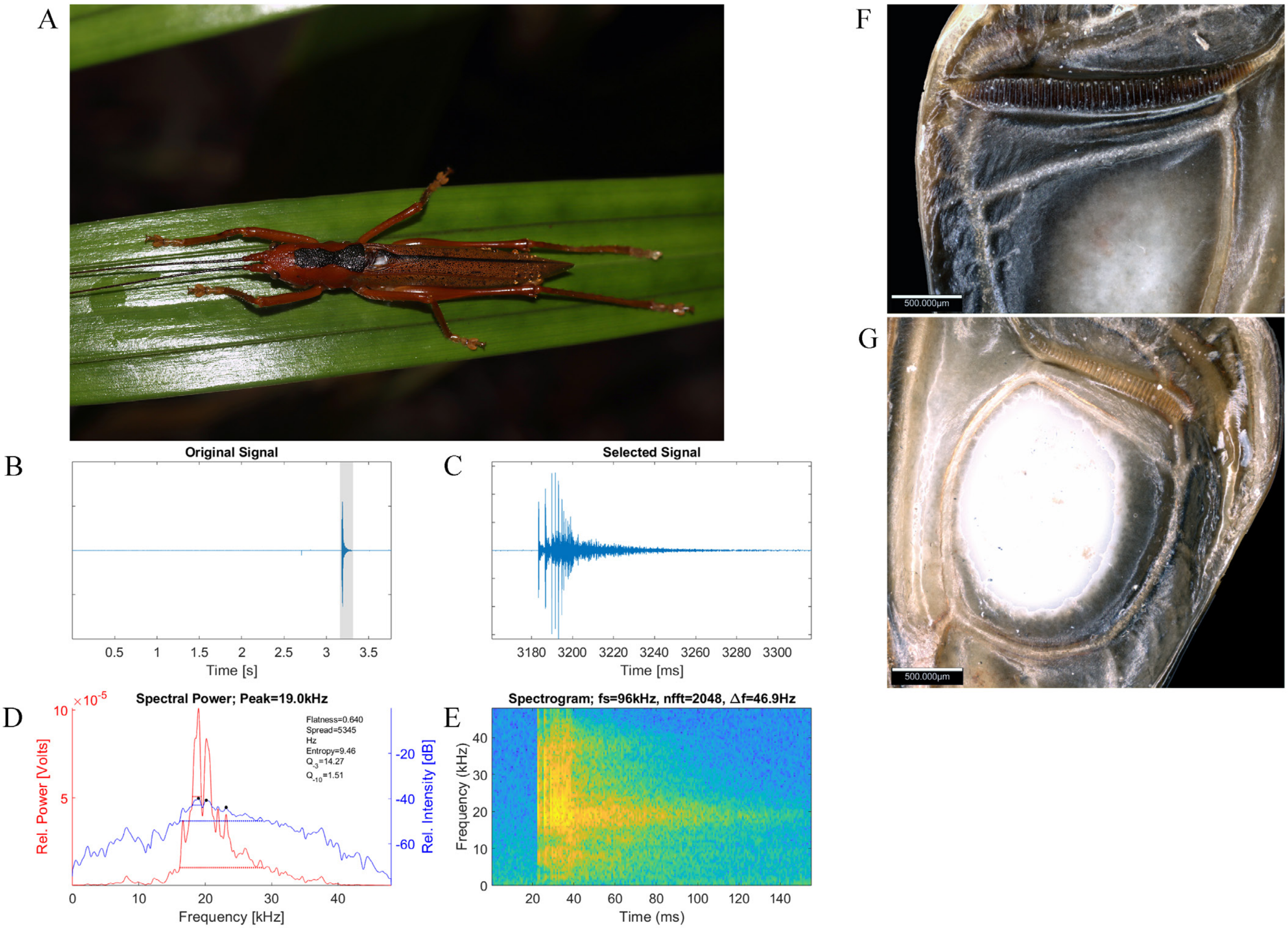

Fig. 6. *Eumacroxiphus* (*Eumacroxiphus*) *diffundatus* male adult in the field at Sabah, East Malaysia (A). Oscillograms showing an isolated syllable (B, C). Power spectrum (D) and spectrogram (E) of the isolated syllable. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

Eumacroxiphus (_Eumacroxiphus_) _diffundatus_ Ingrisch, 1998
(n = 1 male, 16 calling songs)
(Fig. 6)

At 30.0°C, calling song consists of isolated syllables. Average duration of syllable 16.7±2.3 ms (12.5–21.2 ms) made up of numerous pulses of varying amplitudes. First few pulses lower amplitudes, before steadily increasing to maximum. Average pulse duration 0.3±0.1 ms (0.2–0.5 ms), average pulse period 1.8±0.2 ms (1.5–2.3 ms) and average silent interval between consecutive pulses 1.5±0.2 ms (1.2–2.0 ms). Call spectrum with peak frequency 19.4±1.4 kHz (16.8–22.0 kHz), and spectral entropy 9.4–9.5. Frequency spectrum broad-band, energy ranging between ~15 kHz and nearly 30 kHz and not symmetrical; therefore Q_{-3dB} value not meaningful for this species and not reported here.

Macropterous species. Ventrally, left tegmen with stridulatory file straight, ca. 2.33 mm in length, lined with 58 long and slightly broad teeth; file slightly curved at basal end. Average tooth density 25 teeth per mm. Teeth on stridulatory file of left tegmen relatively equally sized (except at ends), relatively broadly spaced apart and fairly uniformly distributed throughout file. Mid-part of stridulatory file with average inter-tooth distance 50 µm and average tooth length 200 µm. Left file (Cu2) only slightly elevated on barely swollen and barely widened vein buttress. Right tegmen with mirror oblong, longer than broad, membrane smooth and transparent, and stridulatory file ca. 1.40 mm in length with ca. 37 teeth slightly shorter than those on left tegmen and at basal end having a few indistinct teeth.

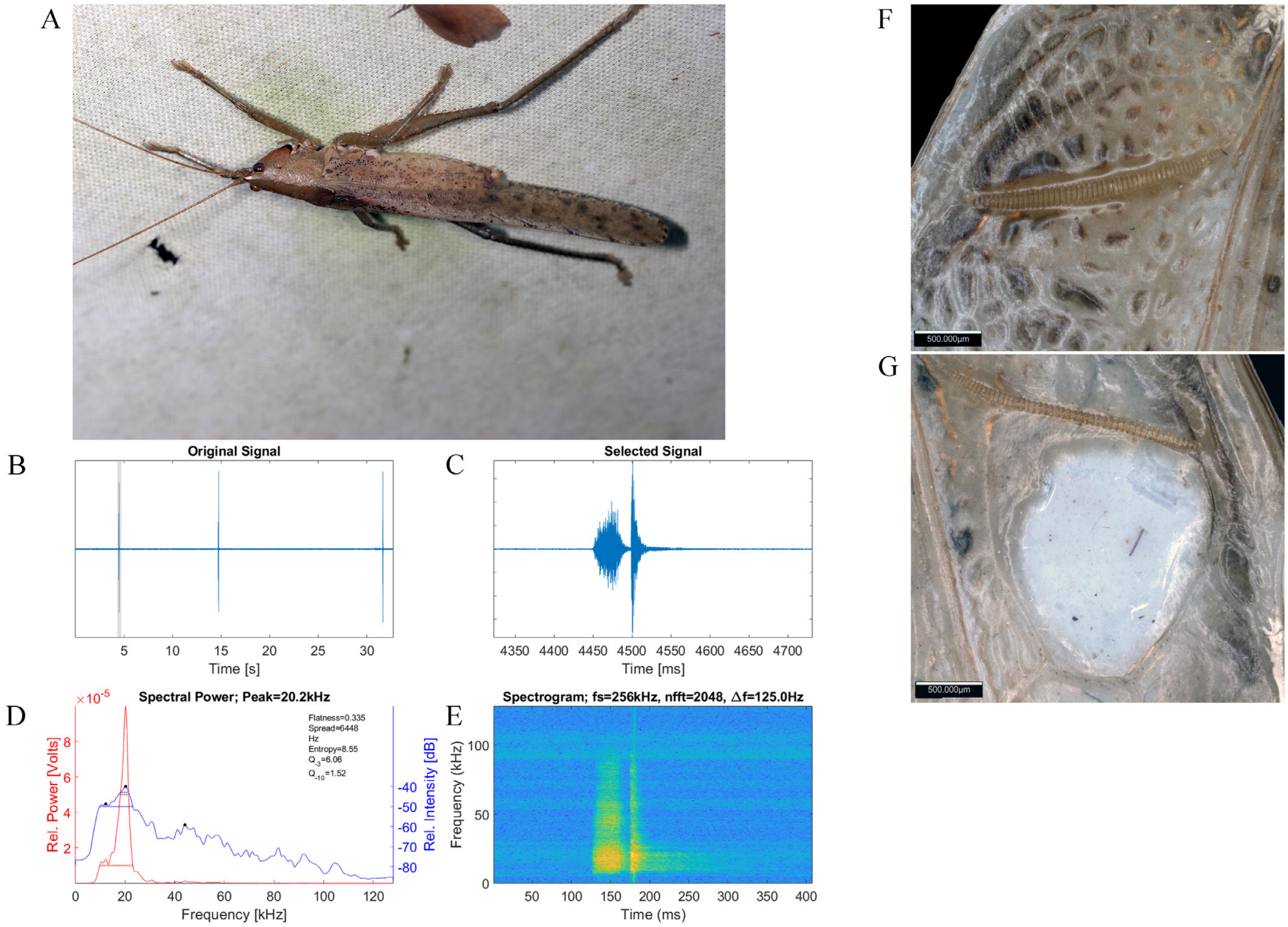

Fig. 7. *Palaeoagraecia philippina* male adult in the field at Sabah, East Malaysia (A). Oscillograms showing three echemes (B) and one echeme with paired syllables (C). Power spectrum (D) and spectrogram (E) of the echeme. Ventral view of the left tegminal stridulatory file (F), and ventral view of the right tegmen sound-producing organs (G).

Palaeoagraecia philippina **(Karny, 1926)**
(n = 1 male, 11 calling songs)
(Fig. 7)

At 24.7°C, calling song an isolated echeme made up of a pair of discrete syllables. Average echeme duration 62.7±3.1 ms (57.1–68.0 ms) and average silent interval between consecutive echemes 19.0±10.2 s (10.2–39.7 s). Within each echeme, first syllable with average duration 37.6±1.9 ms (33.2–39.8 ms) and lower amplitude than second syllable; second syllable with distinctly shorter duration, i.e., 14.8±2.9 ms (8.4–18.9 ms); average syllable period 25.7±2.3 ms (22.2–29.1 ms) and average silent interval between two syllables 10.9±2.1 ms (8.8–15.4 ms). Call spectrum with peak frequency 19.5±2.1 kHz (14.3–21.3 kHz) and spectral entropy 8.5–8.6. Frequency spectrum broad-band, energy ranging between ~10 kHz and 23 kHz and not symmetrical.

Macropterous species. Ventrally, left tegmen with stridulatory file straight, ca. 2.06 mm in length, with 53 relatively long and slender teeth. Average tooth density 26 teeth per mm. Teeth on stridulatory file of left tegmen relatively equally sized (except at both ends), relatively broadly spaced apart and fairly uniformly distributed throughout file. Mid-part of stridulatory file with average inter-tooth distance 46 µm and average tooth length 132 µm. Left file (Cu2) only slightly elevated on barely enlarged and faintly swollen vein buttress. Right tegmen with mirror ovular, longer than broad, membrane smooth and transparent, and stridulatory file very straight, ca. 2.10 mm in length with ca. 51 teeth slightly shorter than those on left tegmen and at basal end having a few indistinct teeth.

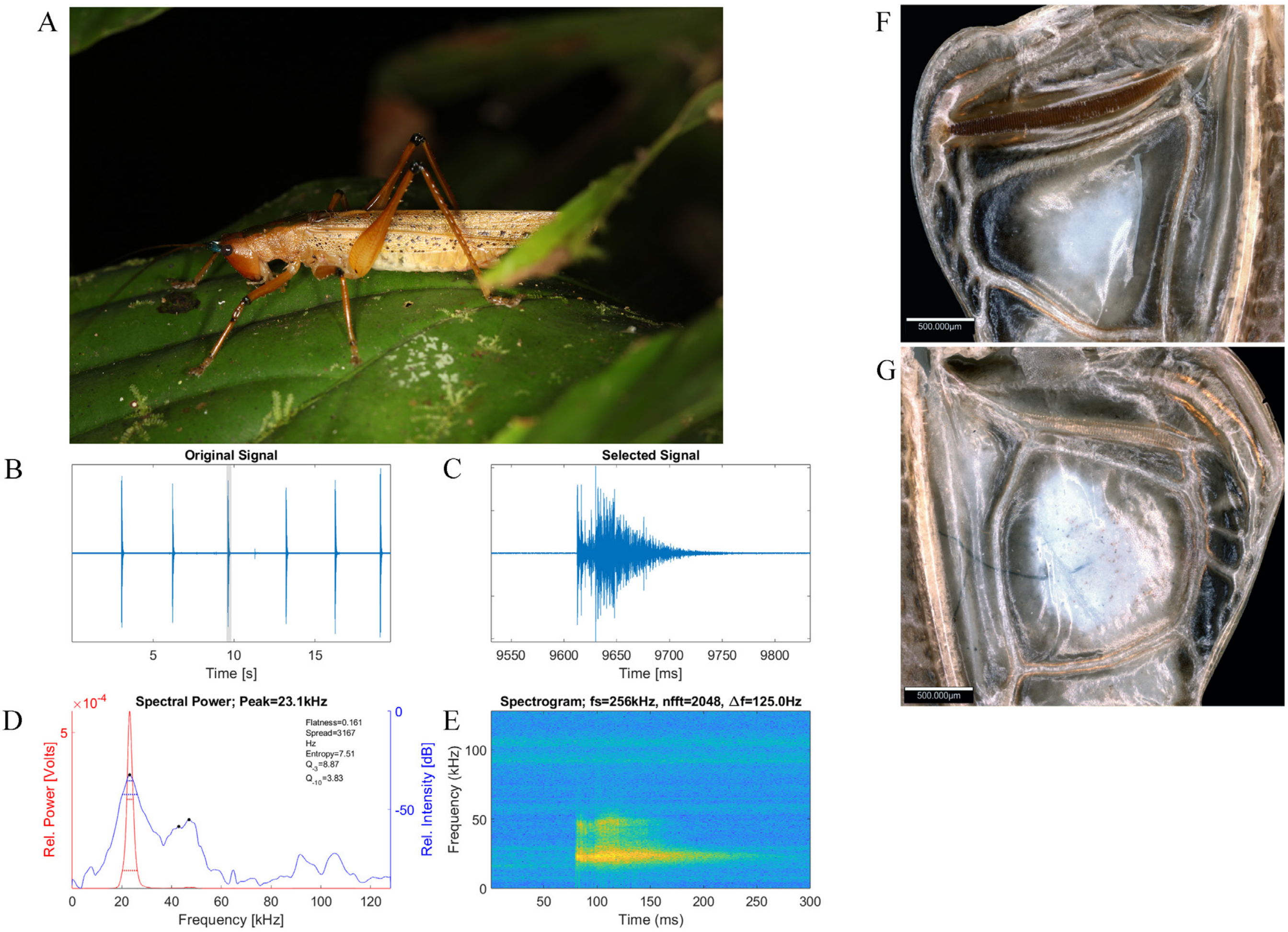

Fig. 8. *Sacculiphallus dyaka* male adult in the field at Sabah, East Malaysia (A). Oscillograms showing six echemes (B) and one echeme with paired syllables (C). Power spectrum (D) and spectrogram (E) of the echeme. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

***Sacculiphallus dyaka* (Hebard, 1922)**
(n = 1 male, 20 calling songs)
(Fig. 8)

At 26.8°C, calling song seems to be composed of either (1) isolated echeme made up of a pair of discrete syllables or (2) major syllable with two hemisyllables produced during opening (default scratching sound in many species) and closing of tegmina. Average echeme duration 42.3±2.4 ms (36.9–46.7 ms) and average silent interval between consecutive echemes 3.92±1.89 s (2.21–9.36 s). Within each echeme, first syllable with shorter duration 8.4±2.0 ms (5.4–12.3 ms) and typically made up of 3±1 (2–4) pulses. Average duration of second syllable 23.7±2.0 ms (19.4–28.8 ms); average syllable period 18.5±1.2 ms (16.6–21.3 ms) and average silent interval between two syllables 10.1±1.1 ms (7.8–11.8 ms). Call spectrum with peak frequency 23.4±0.3 kHz (22.8–23.8 kHz, ultrasonic range), spectral entropy 7.5–7.6 and Q_{-3dB} 8.6–8.9.

Macropterous species. Ventrally, left tegmen with stridulatory file straight, ca. 1.87 mm in length, lined with 91 relatively long and slender teeth. Average tooth density 49 teeth per mm. Teeth on stridulatory file of left tegmen relatively equally sized (except at both ends), relatively narrowly spaced apart and fairly uniformly distributed throughout file. Mid-part of stridulatory file with average inter-tooth distance 22 µm and average tooth length 135 µm. Left file (Cu2) only slightly elevated on slightly enlarged and slightly swollen vein buttress. Right tegmen with mirror squarish with basal margin slightly longer than anal margin, membrane smooth and transparent, and stridulatory file very straight, ca. 1.23 mm in length, with ca. 60 teeth slightly shorter than those on left tegmen and at basal end having a few indistinct teeth.

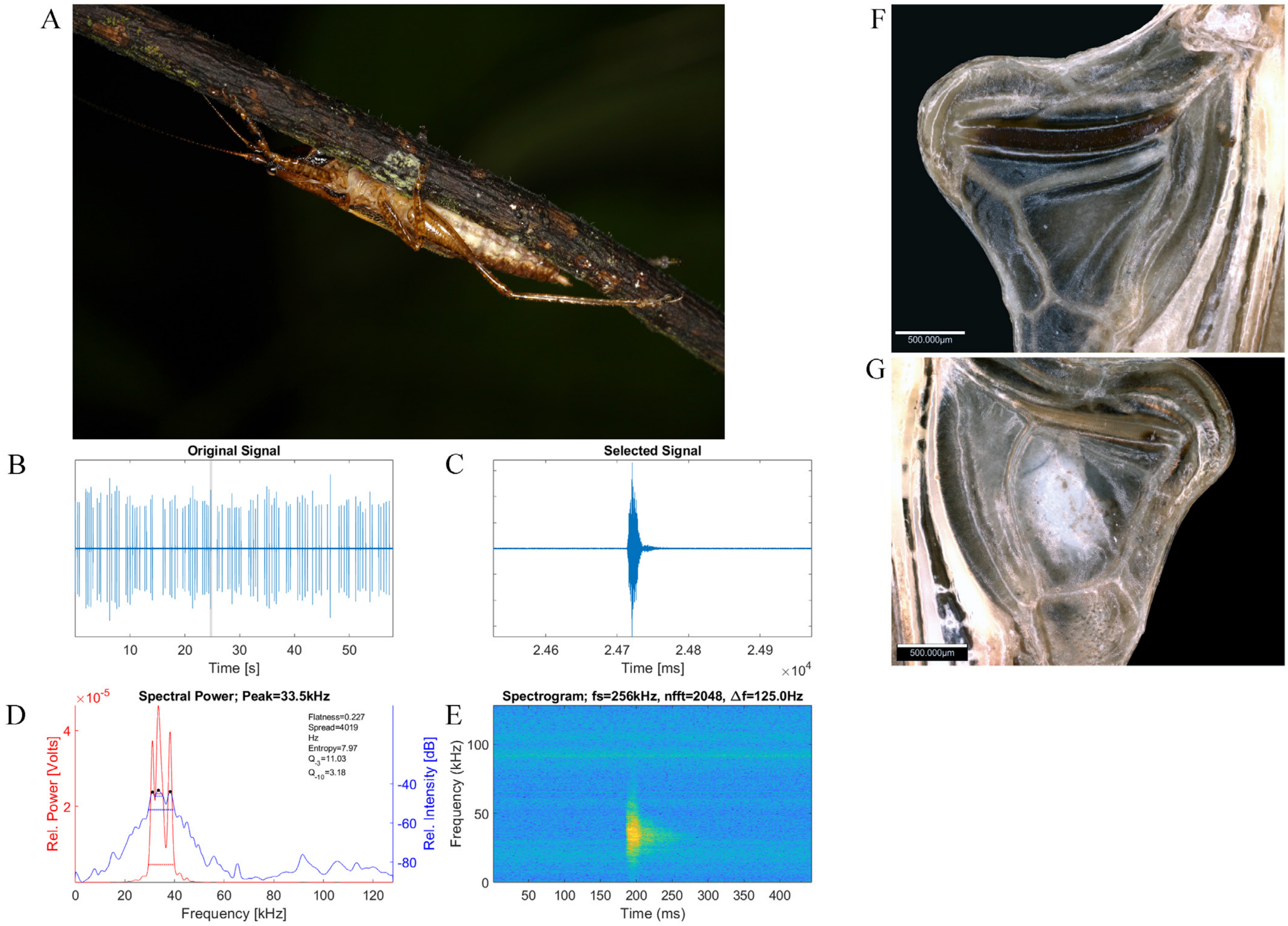

Fig. 9. *Scytocera borneensis sandakani* male adult in the field at Sabah, East Malaysia (A). Oscillograms showing series of isolated syllables (B) and an isolated syllable (C). Power spectrum (D) and spectrogram (E) of the isolated syllable. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

Scytocera borneensis sandakani Gorochov, 2016
(n = 1 male, 20 calling songs)
(Fig. 9)

At 31.4°C, calling song a series of isolated syllables. Average syllable duration 22.2±1.8 ms (18.3–24.8 ms), average syllable period can be variable, i.e., 0.88±0.45 s (0.34–1.76 s) and likewise, average silent interval between consecutive syllables also variable, i.e., 0.86±0.45 s (0.32–1.74 s). Call spectrum with peak frequency 34.6±1.8 kHz (31.3–38.8 kHz, ultrasonic range), and spectral entropy 8.0–8.1. Frequency spectrum broad-band, energy ranging between 30–40 kHz and not symmetrical.

Semi-micropterous species. Ventrally, left tegmen with stridulatory file slightly curved, ca. 1.73 mm in length, with 140 relatively long and very slender teeth. Average tooth density 81 teeth per mm. Teeth on stridulatory file of left tegmen relatively equally sized (except at ends), narrowly spaced apart and fairly uniformly distributed throughout file. Mid-part of stridulatory file with average inter-tooth distance 14 µm and average tooth length 144 µm. Left file (Cu2) only slightly elevated on slightly enlarged and slightly swollen vein buttress. Right tegmen with mirror pentagonal, with basal margin longer than anal margin, and anterior margin longer than posterior margin, membrane smooth and transparent, and stridulatory file very straight, ca. 1.16 mm in length with ca. 90 teeth slightly shorter than those on left tegmen.

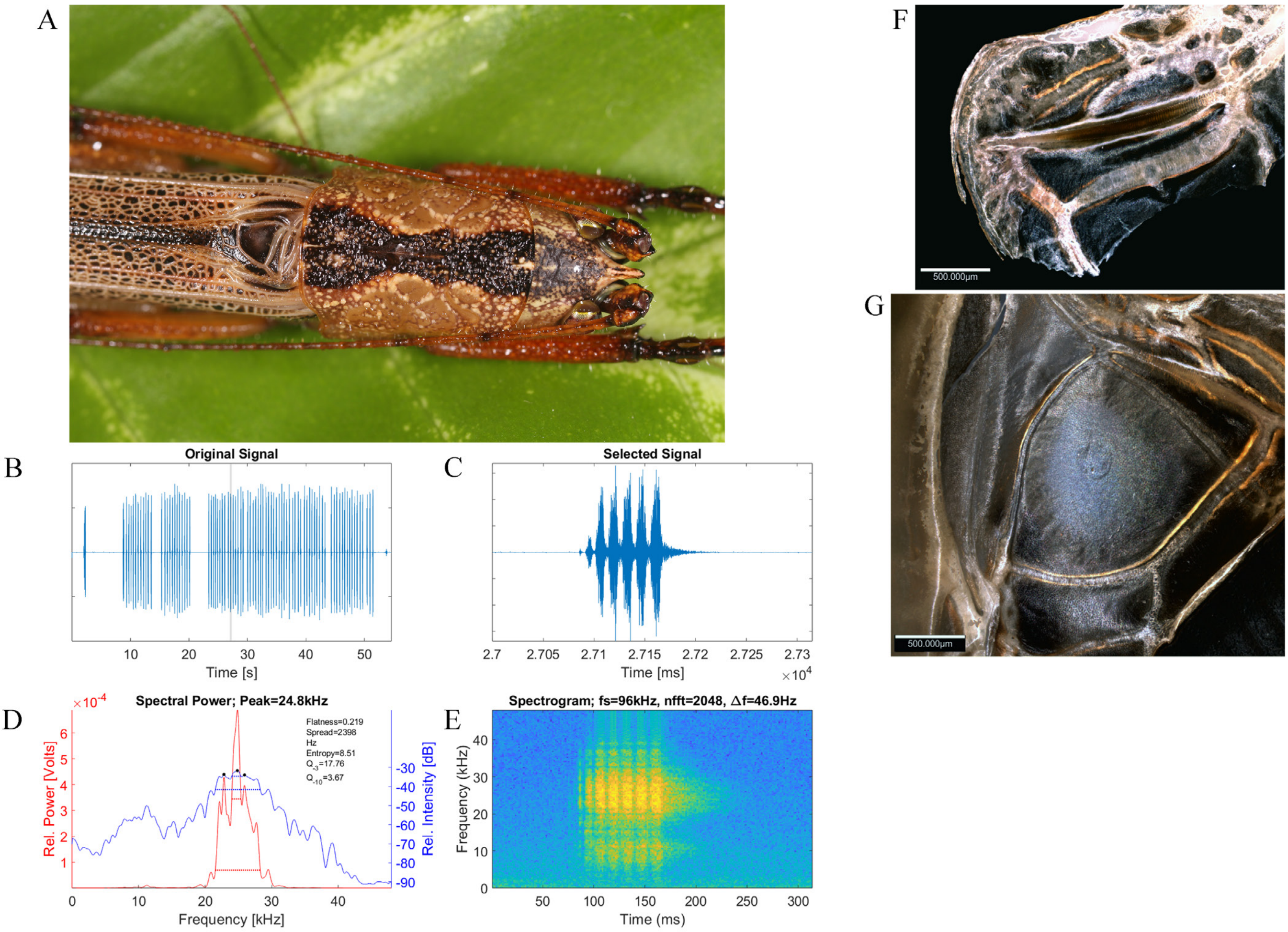

Fig. 10. *Scytocera* cf. *kemneri* male adult in the field in Singapore (A). Oscillograms showing a series of isolated echemes (B) and one echeme with six syllables (C). Power spectrum (D) and spectrogram (E) of the isolated syllable. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

Scytocera cf. _kemneri_ Karny, 1926
(n = 1 male, 14 calling songs)
(Fig. 10)

At 29.6°C, calling song consists of series of echemes fairly closely-spaced from each other. Each echeme consists of 7±1 (6–9) syllables and average echeme duration 84.8±8.5 ms (79.7–112.4 ms). Average syllable duration 9.2±1.1 ms (7.7–11.4 ms), average syllable period 14.5±3.5 ms (12.1–23.7 ms) and average silent interval between consecutive syllables 5.3±2.8 ms (2.8–12.3 ms). First or first-two syllables tend to be distinctly lower amplitudes than the other syllables in the echeme. Within each syllable, pulses steadily increase in amplitude to maximum before decreasing. Call spectrum with peak frequency 23.9±0.9 kHz (23.0–25.0 kHz) and spectral entropy ca. 8.5. Frequency spectrum broad-band, energy ranging between ~20 kHz and ~30 kHz and not symmetrical.

Semi-micropterous species. Ventrally, left tegmen with stridulatory file faintly curved, ca. 1.66 mm in length, with 110 relatively long and slender teeth. Average tooth density 66 teeth per mm. Teeth on stridulatory file of left tegmen relatively equally sized (except at the ends), narrowly spaced apart and fairly uniformly distributed throughout file. Mid-part of stridulatory file with average inter-tooth distance 17 µm and average tooth length 98 µm. Left file (Cu2) slightly elevated on slightly enlarged and slightly swollen vein buttress. Right tegmen with mirror shield-shaped, with anterior margin straight, membrane smooth and transparent, and stridulatory file faintly curved, ca. 1.12 mm in length, with ca. 78 teeth slightly shorter than those on left tegmen.

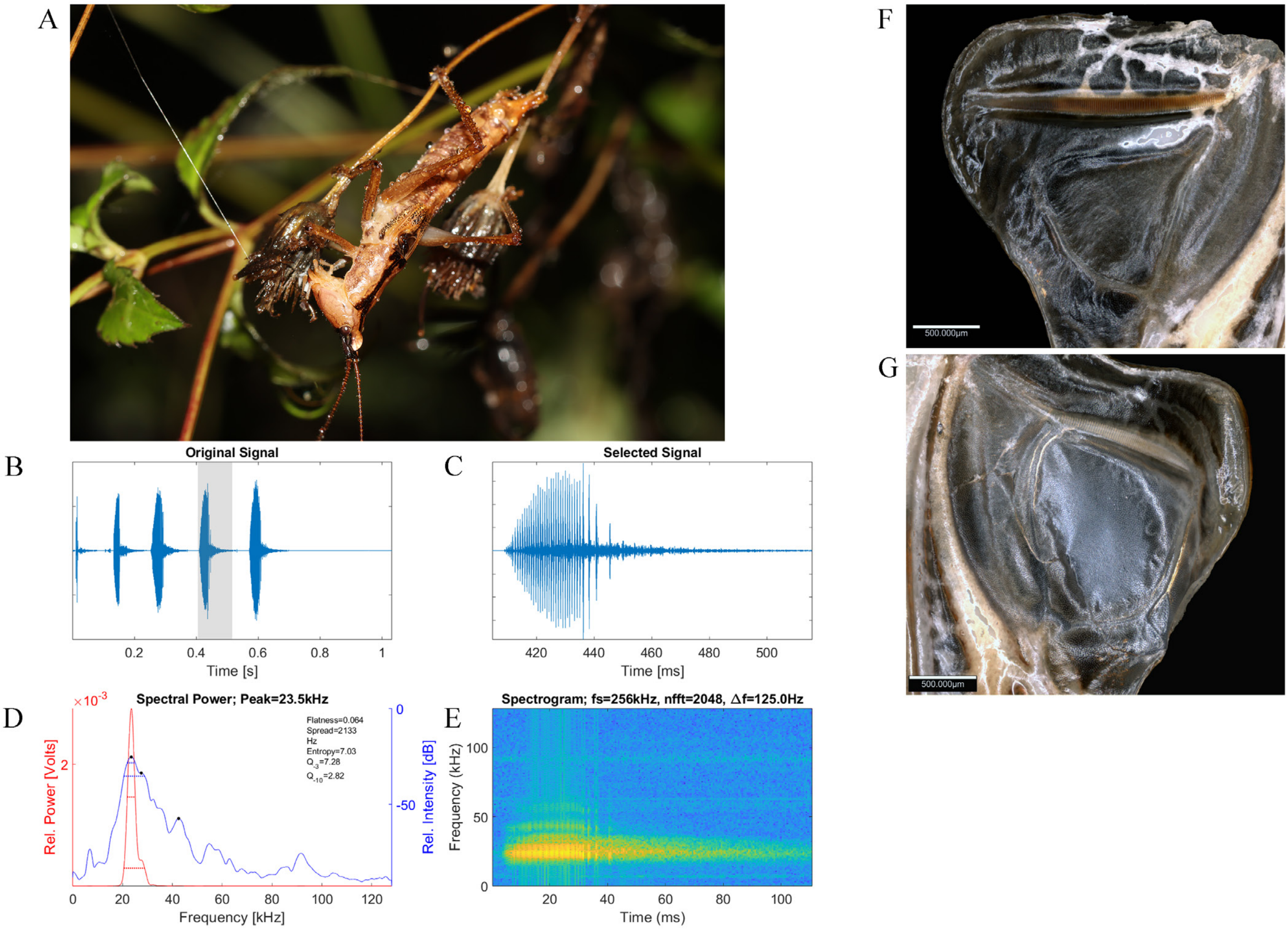

Fig. 11. *Scytocera* cf. *longicornis* male adult in the field at Mindanao, Philippines (A). Oscillograms showing an echeme made up of five pulse-trains (B) and one pulse-train (C). Power spectrum (D) and spectrogram (E) of the pulse-train. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

***Scytocera* cf. *longicornis* Redtenbacher, 1891**

(n = 1 male, 1 calling song)
(Fig. 11)

At 25.9°C, calling song consists of echeme made up of five syllables appearing as pulse-trains. Echeme duration 0.60 s. First syllable with shorter duration. Average pulse-train duration 33.6±9.2 ms (19.9–39.7 ms) and each pulse-train made up of varied number of discrete pulses ranging from 19–47. Average silent interval between consecutive pulse-trains 0.11±0.01 s (0.10–0.13 s). Pulses steadily increase in amplitude to maximum before decreasing. Call spectrum with peak frequency 24.0±0.3 kHz (23.8–24.2 kHz), spectral entropy ca. 7.0 and Q_{-3dB} ca. 7.3.

Micropterous species. Ventrally, left tegmen with stridulatory file straight, ca. 1.96 mm in length, lined with 134 relatively long and slender teeth. Average tooth density 68 teeth per mm. Teeth on stridulatory file of left tegmen narrowly spaced apart, but more so at basal half than anal half. At basal half of stridulatory file, average inter-tooth distance 19 µm and average tooth length 129 µm; at anal half of stridulatory file, average inter-tooth distance 12 µm and average tooth length 103 µm. Left file (Cu2) slightly elevated on slightly enlarged and slightly swollen vein buttress. Right tegmen with mirror ovular, with anterior margin somewhat straight, membrane smooth and transparent, and stridulatory file very straight, ca. 1.03 mm in length, with ca. 75 teeth slightly shorter than those on left tegmen and at basal end having a few indistinct teeth.

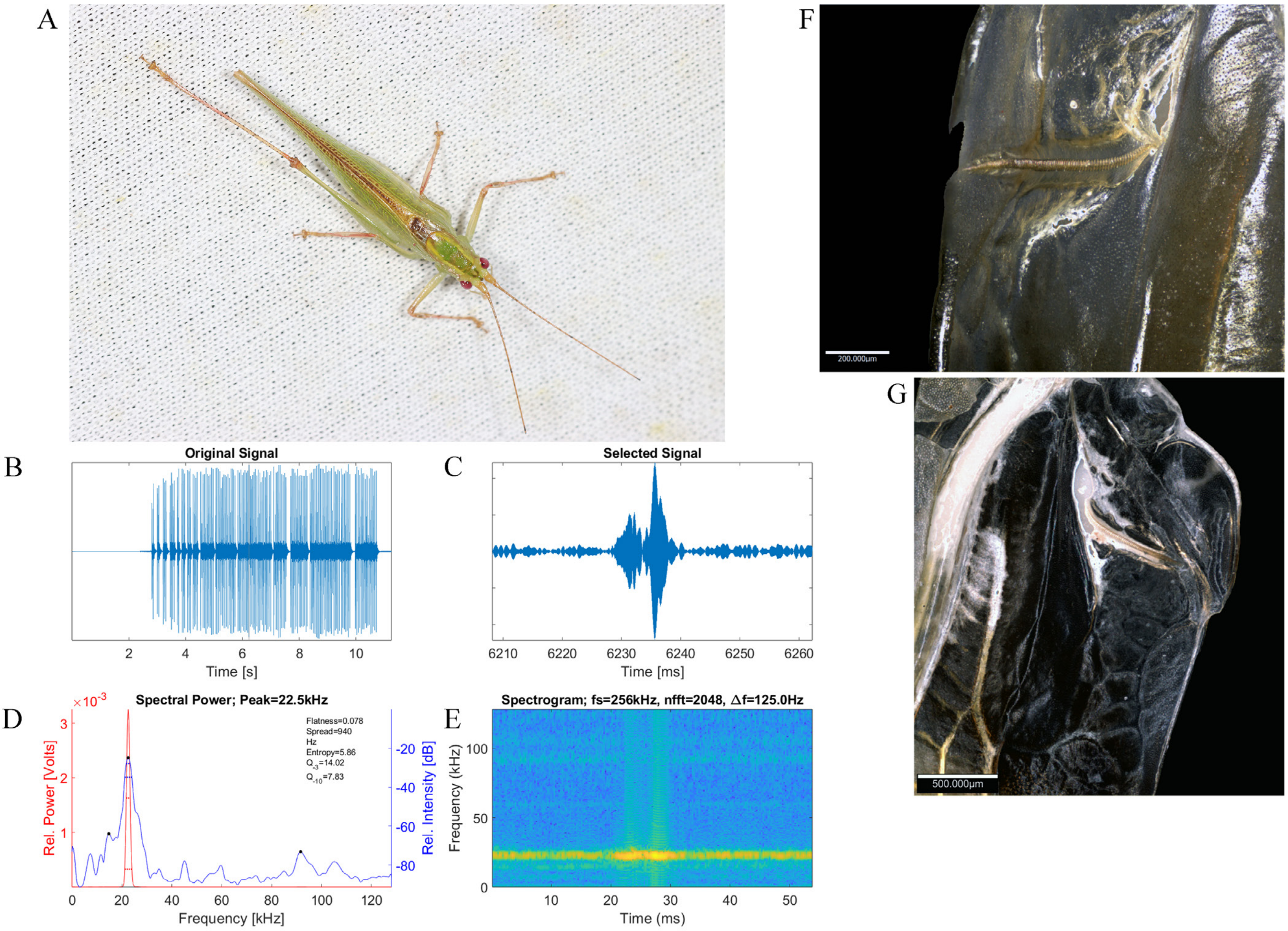

Fig. 12. *Alloteratura* (*Meconemopsis*) *longa* male adult in the field at Sabah, East Malaysia (A). Oscillograms showing a sequence of irregular echeme (B) and one isolated syllable (C). Power spectrum (D) and spectrogram (E) of the isolated syllables. Ventral view of the left tegminal stridulatory file (F), and ventral view of the right tegmen sound-producing organs (G).

Subfamily Meconematinae

***Alloteratura* (*Meconemopsis*) *longa* Gorochov, 2008**
(n = 1 male, 20 calling songs)
(Fig. 12)

At 29.4°C, calling song consists of sequence of irregular echeme or 'broken' trill. Each echeme varying duration made up of irregular groups of syllables. Each echeme consists of two to more than 17 isolated syllables. Average echeme duration 0.31±0.23 s (0.06–0.79 s). Average syllable duration 9.8±1.6 ms (7.3–14.4 ms), average syllable period 47.6±2.3 ms (43.8–53.5 ms) and average silent interval between consecutive syllables 37.9±2.5 ms (33.1–44.1 ms). Call spectrum with peak frequency 23.4±0.4 kHz (22.8–23.8 kHz, ultrasonic range). Spectral entropy ca. 5.9 and Q_{-3dB} 13.5–14.0.

Macropterous species. Ventrally, left tegmen with stridulatory file faintly sinuous, 0.67 mm in length, lined with ca. 105 short and slender teeth; file slightly curved at both ends. Average tooth density 157 teeth per mm. Teeth on stridulatory file of left tegmen relatively equally sized (except at ends) and at mid-part of file, average tooth length 41 µm. Teeth narrowly spaced apart, but distinctly more narrowly spaced at anal half than basal half. Left file (Cu2) not elevated on widened vein buttress. Right tegmen with mirror very broad and short, distinctly broader than long, membrane smooth and transparent, and stridulatory file ca. 0.76 mm in length, with ca. 99 rather small teeth slightly shorter than those on left tegmen and a few indistinct teeth at anal end.

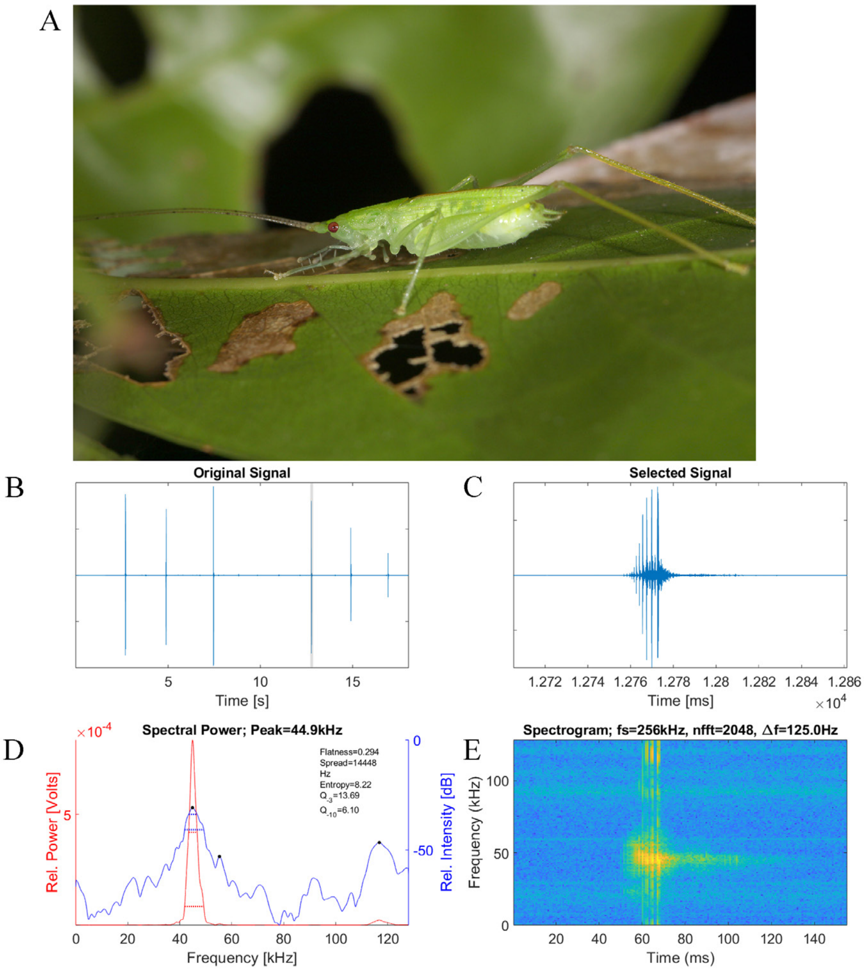

Fig. 13. *Grigoriora* sp. male adult in the field at Bạch Mã, Vietnam (A). Oscillograms showing six isolated syllables (B) and one isolated syllable (C). Power spectrum (D) and spectrogram (E) of the pulse-train.

***Grigoriora* sp.**
(n = 2 males, 34 calling songs)
(Fig. 13)

At 21.4°C, calling song consists of isolated syllables delivered as pulse-trains. Average syllable duration 16.1±2.1 ms (12.2–20.7 ms) and made up of 7±1 (5–8) pulses of varying amplitudes. Average syllable period 2.84±1.05 s (1.77–5.92 s) and average silent interval between consecutive syllables 2.83±1.05 s (1.75–5.90 s). Within each syllable, average pulse duration 0.6±0.1 ms (0.4–0.8 ms), average pulse period 2.8±0.7 ms (1.7–3.9 ms) and average silent interval between consecutive pulses 2.2±0.7 ms (1.2–3.2 ms). Call spectrum with peak frequency 45.8±0.7 kHz (44.3–47.3 kHz). Discrete pulses in the syllable delivered with negative frequency modulated effect between ~50 and 40 kHz. Spectral entropy 8.2–8.6 and Q_{-3dB} 13.7–18.0.

This is potentially a new species, but more work is still needed to confirm, and this would be out of the scope of this paper.

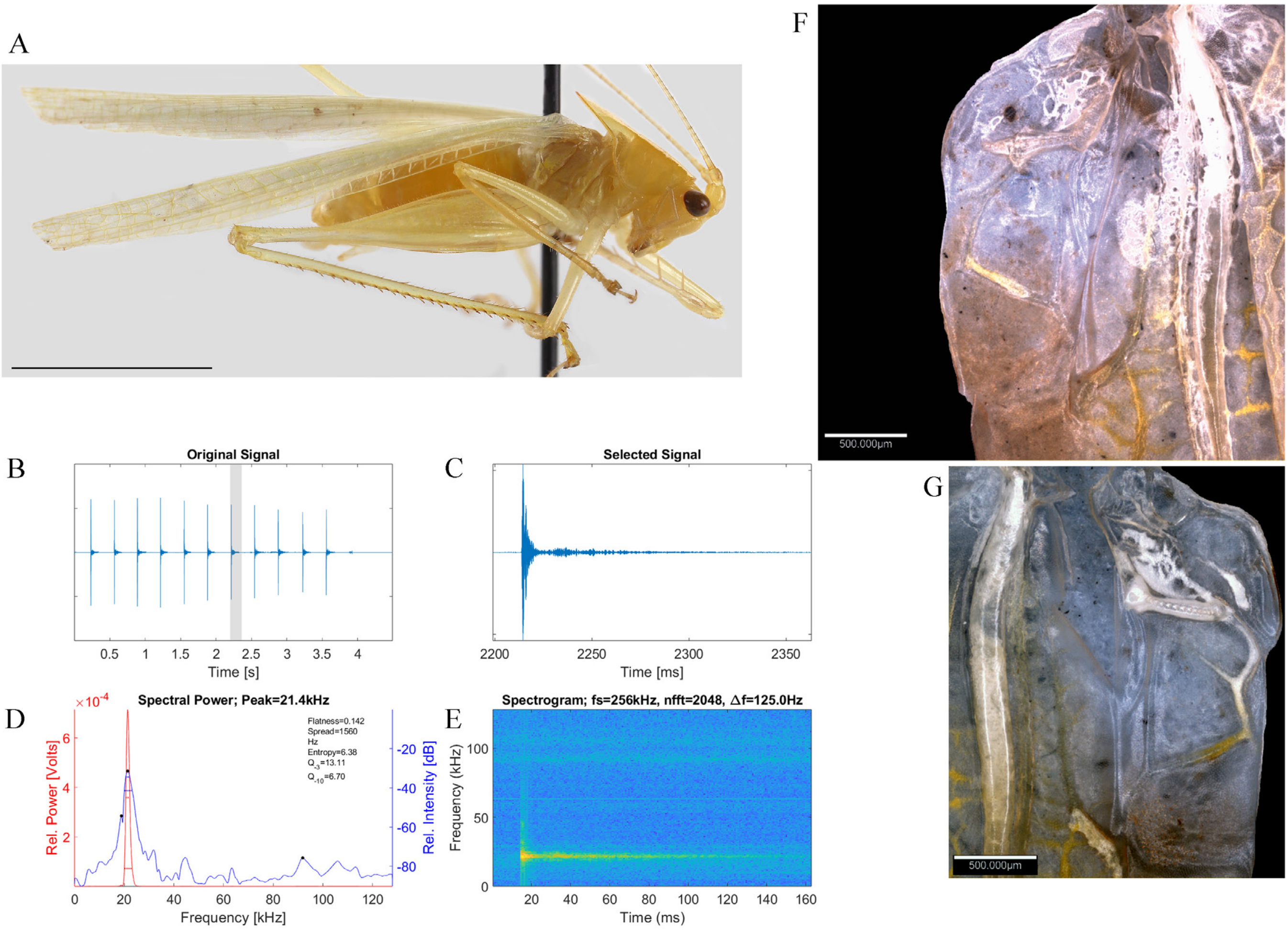

Fig. 14. *Odonturisca epiproctalis* male adult dry-pinned, from Sabah, East Malaysia (A). Oscillograms showing a series of 11 isolated syllables (B) and one syllable (C). Power spectrum (D) and spectrogram (E) of the isolated syllables. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

Odonturisca epiproctalis Gorochov, 2008
(n = 1 male, 31 calling songs)
(Fig. 14)

At 27.4°C, calling song is sequence of isolated syllables. Syllable duration 2.9±0.4 ms (1.9–3.5 ms) and average syllable period 0.31±0.02 s (0.29–0.34 s). Call spectrum with peak frequency 21.5±0.2 kHz (21.3–21.8 kHz). Spectral entropy 6.4–6.5 and Q_{-3dB} 12.8–13.1.

Macropterous species. Ventrally, left tegmen with stridulatory file generally straight, ca. 0.64 mm in length, lined with ca. 18 very stout and broad (roundish) teeth; file bent at basal end. Average tooth density 28 teeth per mm. Teeth on stridulatory file of left tegmen relatively equally sized (except at the ends), fairly uniformly distributed and very broadly spaced apart. Mid-part of stridulatory file with average inter-tooth distance 43 µm and average tooth length 29 µm. Left file (Cu2) slightly elevated on barely swollen and widened vein buttress. Right tegmen with mirror very large, parallelogram, membrane smooth and transparent, and stridulatory file ca. 0.49 mm in length and slightly curved at basal end, with ca. 15 teeth of subequal length as those in left tegminal stridulatory file.

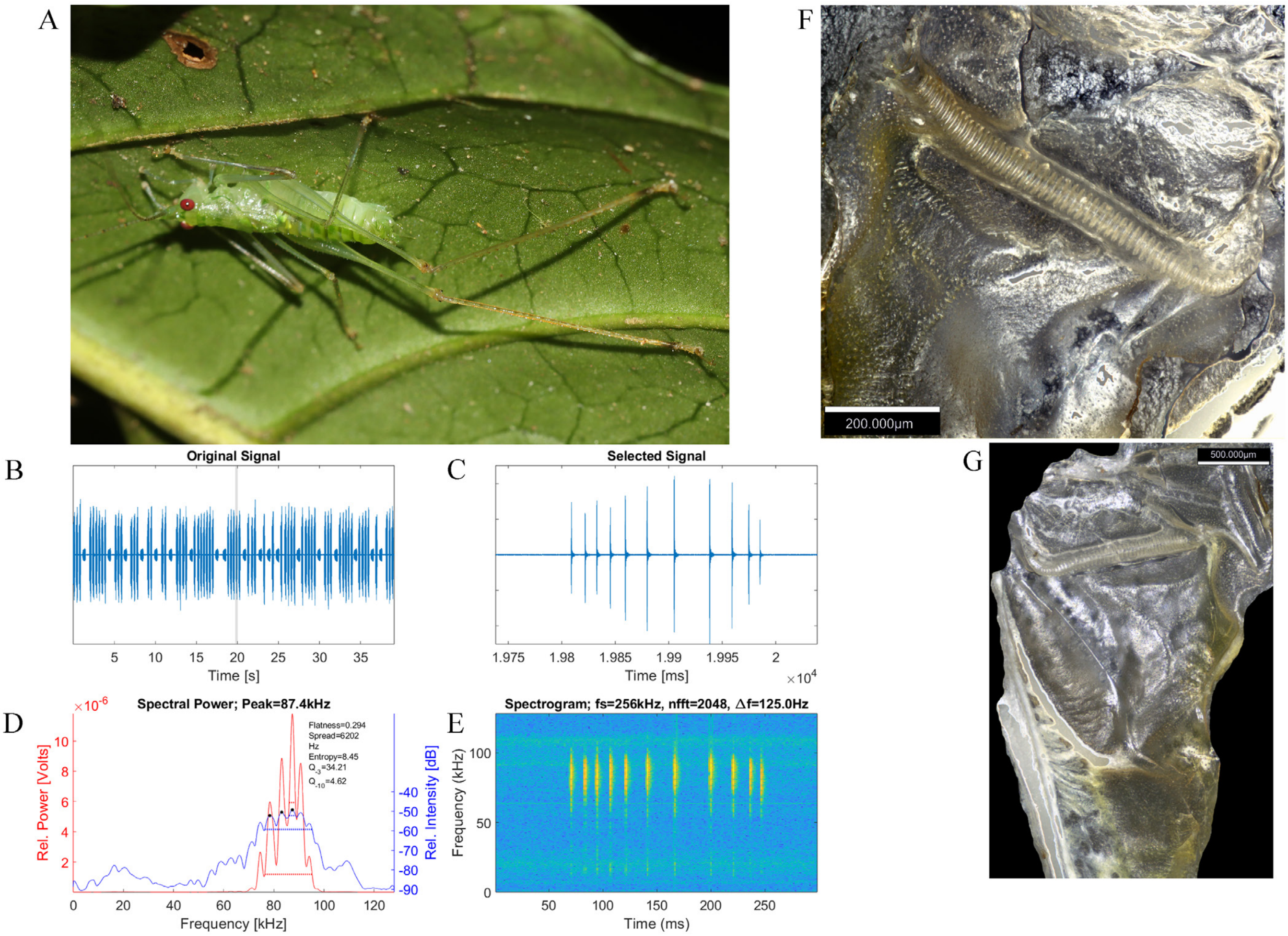

Fig. 15. Meconematini sp. male adult in the field at Mindanao, Philippines (A). Oscillograms showing series of syllables irregularly packed in groups (B) and a syllable (C). Power spectrum (D) and spectrogram (E) of the group. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

Meconematini sp. [Philippines]
(n = 1 male, 20 calling songs)
(Fig. 15)

At 26.1°C, calling song is a series of syllables, each made up of 10±1 (9–12) pulses. Each group preceded by small amplitude sound produced perhaps by reversed friction during open stroke. Average syllable duration 0.21±0.02 s (0.18–0.25 s), average silent interval between consecutive syllables 0.20±0.07 s (0.12–0.34 s) and average syllable period 0.40±0.06 s (0.33–0.53 s). Within each syllable, average pulse duration 0.43±0.05 s (0.40–0.50 s). Silent interval between consecutive pulses greater in middle than at start, i.e., 38.2±7.5 ms (24.6–50.1 ms) compared to 12.8±1.2 ms (10.9–15.7 ms), respectively. Consequently, period between consecutive pulses also greater in middle than at start, i.e., 38.6±7.5 ms (25.1–50.5 ms) compared to 13.3±1.2 ms (11.3–16. ms), respectively. Call spectrum with peak frequency 88.0±2.1 kHz (85.0–91.9 kHz, ultrasonic range). Spectral entropy ca. 8.5. Frequency spectrum broadband, energy ranging between ~75 kHz and ~95 kHz and not symmetrical.

Micropterous species. Ventrally, left tegmen with stridulatory file substraight, ca. 0.77 mm in length, lined, with ca. 55 relatively long and slightly broad teeth; file bent at ca. 90° at basal end and slightly curved just before anal end. Average tooth density 71 teeth per mm. Teeth on stridulatory file of left tegmen relatively equally sized (except at ends), fairly uniformly distributed and fairly broadly spaced apart. Mid-part of stridulatory file with average inter-tooth distance 16 µm and average tooth length 52 µm. Left file (Cu2) slightly elevated on a barely swollen and widened vein buttress. Right tegmen with mirror very broad harp-shaped, with fold near basal margin, membrane smooth and transparent, and stridulatory file ca. 0.63 mm in length and bent at basal end, with ca. 49 teeth of subequal length as those in left tegminal stridulatory file.

This is potentially a new species and/or genus. The shortened wings and unique abdominal apex and genitalia make this species clearly different from other Meconematini reported in the Philippines (Tan et al., 2025). More material is also needed for determining the genus and species and this would be out of the scope of this paper.

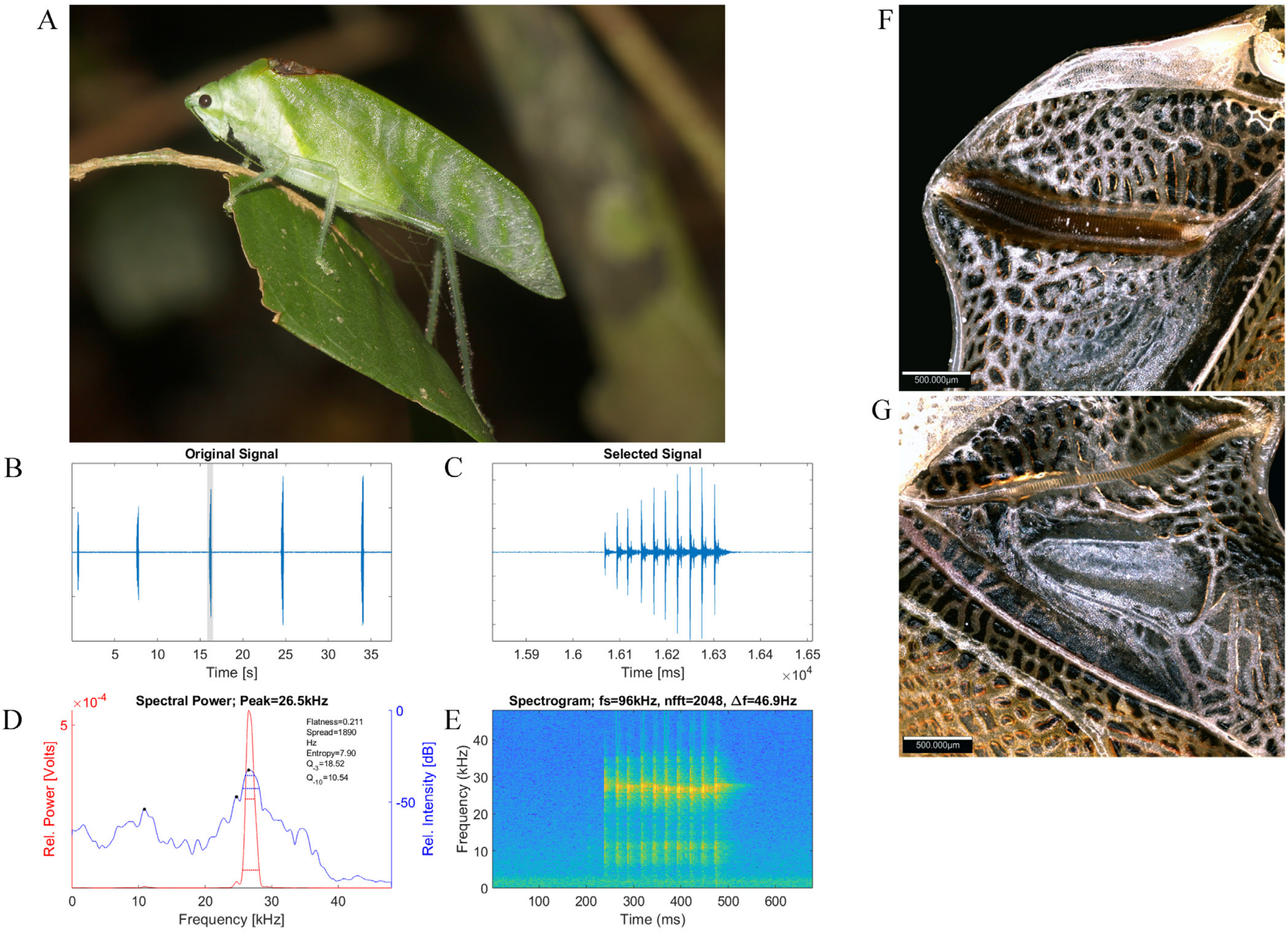

Fig. 16. *Arnobia pilipes tropica* male adult in the field at Panti, Peninsular Malaysia (A). Oscillograms showing five pulse-trains (B) and one pulse-train with 10 pulses (C). Power spectrum (D) and spectrogram (E) of the pulse-train. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

Subfamily Phaneropterinae

Arnobia pilipes tropica **Gorochov, 1998**
(n = 3 males, 27 calling songs)
(Fig. 16)

Two calling songs recorded. At 29.9°C, the first song type, more common, consists of isolated syllables appearing as pulse-trains. Average syllable duration 0.28±0.02 s (0.25–0.33 s). Each syllable made up of 12±1 (10–13) discrete pulses. Pulses steadily increase in amplitude to maximum before decreasing. Average pulse duration 3.6±1.5 ms (2.0–8.0 ms), average syllable period 26.8±2.0 ms (23.0–29.3 ms) and average silent interval between consecutive pulses 23.2±1.9 ms (19.6–25.7 ms).

At 30.6°C, the second song type, only observed in males collected from Panti Forest Reserve, also consists of isolated syllables. However, it differs by distinctly longer average syllable duration, i.e., 0.46±0.07 s (0.34–0.58 s) with distinctly fewer number of discrete pulses, i.e., 4±1, 3–5. Consequently, average syllable period 124.3±22.7 ms (96.0–169.0 ms) and average silent interval between consecutive pulses 120.8±22.6 ms (92.9–164.0 ms) was much longer in this song type. Average pulse duration however not different from first song type, i.e., 3.5±1.0 ms (2.1–5.0 ms).

Call spectrum with peak frequency 26.4±1.3 kHz (24.3–28.4 kHz), discrete pulses delivered in unusual sequential frequency-modulated pattern, across syllable, starting at ~30 kHz, dropping to ~26 kHz and going up again to ~30 kHz. (Fig. 16C). Spectral entropy 7.9–8.0 and Q_{-3dB} 18.5–23.0.

Macropterous species. Ventrally, left tegmen with stridulatory file faintly bent, ca. 1.83 mm in length, lined with ca. 82 long and slender teeth; file slightly curved at both ends. Teeth on stridulatory file of left tegmen relatively equally sized (except at ends), fairly uniformly distributed and narrowly spaced apart. Average tooth density 45 teeth per mm. Inter-tooth distance nearly constant throughout file. Mid-part of stridulatory file with average tooth length 156 µm and average inter-tooth distance 26 µm. Left file (Cu2) slightly elevated on swollen and slightly widened vein buttress. Right tegmen with mirror small, obliquely positioned and narrow triangular, with its basal end being the narrower end, membrane smooth and transparent surrounded by network of interlaced crossveins, and stridulatory file slender, ca. 2.08 mm in length with ca. 88 teeth distinctly shorter than those on left tegmen.

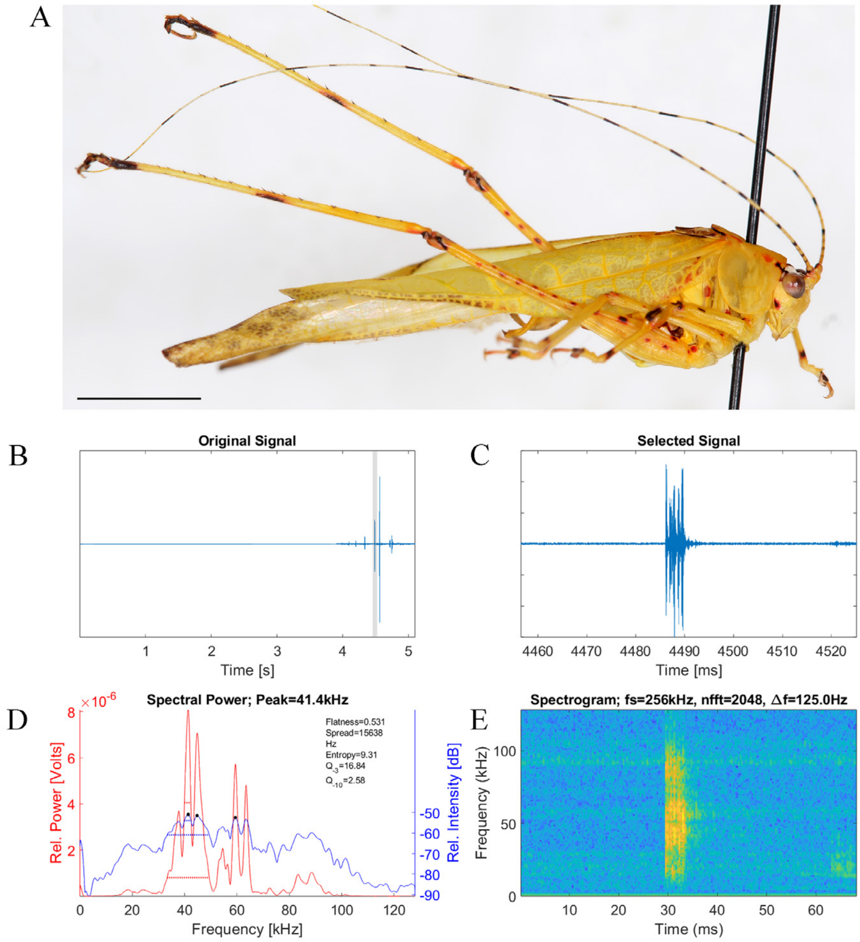

Fig. 17. *Deflorita pulchra* male adult dry-pinned, from Sabah, East Malaysia (A). Oscillograms showing an echeme with eight syllables (B) and a syllable (C). Power spectrum (D) and spectrogram (E) of the syllable.

Deflorita pulchra **Gorochov, 2008**
(n = 1 male, 6 calling songs)
(Fig. 17)

At 24.8°C, calling song an echeme made up of 6–7 isolated syllables of increasing amplitudes. Average echeme duration 0.72±0.7 s (0.67–0.8 s). Syllable duration 4.3±0.6 ms (3.7–5.1 ms) and average syllable period 0.12±0.04 s (0.7–0.15 s). Call spectrum with peak frequency of either 61.8±1.8 kHz (60.3–83.8 kHz) or 43.9±1.9 kHz (41.8–45.3 kHz) and spectral entropy 9.1–9.3. Frequency spectrum broadband, energy ranging from ~30 kHz and ~65 kHz and not symmetrical.

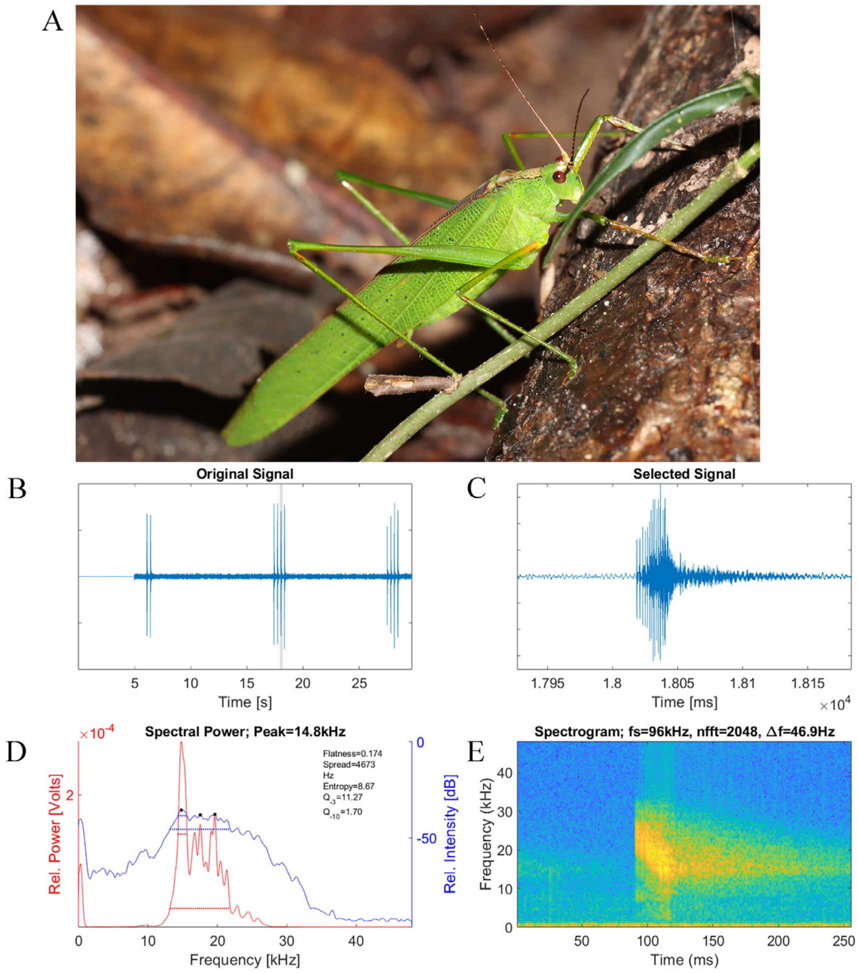

Fig. 18. *Elimaea* (*Bornelimaea*) *sympatrica* male adult in the field at Sabah, East Malaysia (A). Oscillograms showing a three series of syllables, first one with two syllables, followed by subsequent ones with four syllables (B) and one syllable (C). Power spectrum (D) and spectrogram (E) of the syllable.

Elimaea (Bornelimaea) sympatrica Gorochov, 2009
(n = 1 male, 15 calling songs)
(Fig. 18)

At 25.1°C, calling song consists of sequence of average of 3±1 (1–5) syllables, with two and four syllables most commonly recorded. Each syllable with average duration 28.3±6.0 ms (17.1–38.3 s) and made up of 15±3 (10–20) syllables of varying amplitudes. Average syllable period 0.32±0.01 s (0.31–0.33 s) and average silent interval between consecutive syllables 0.29±0.01 s (0.20–0.27 s). Call spectrum with peak frequency 16.7±1.8 kHz (14.7–20.2 kHz), and spectral entropy 8.6–8.7. Spectrogram analysis shows clear frequency modulation of syllables between ~25 and 11 kHz, with energy centres around 15 kHz. Such frequency modulation causes a broad-band spectrum.

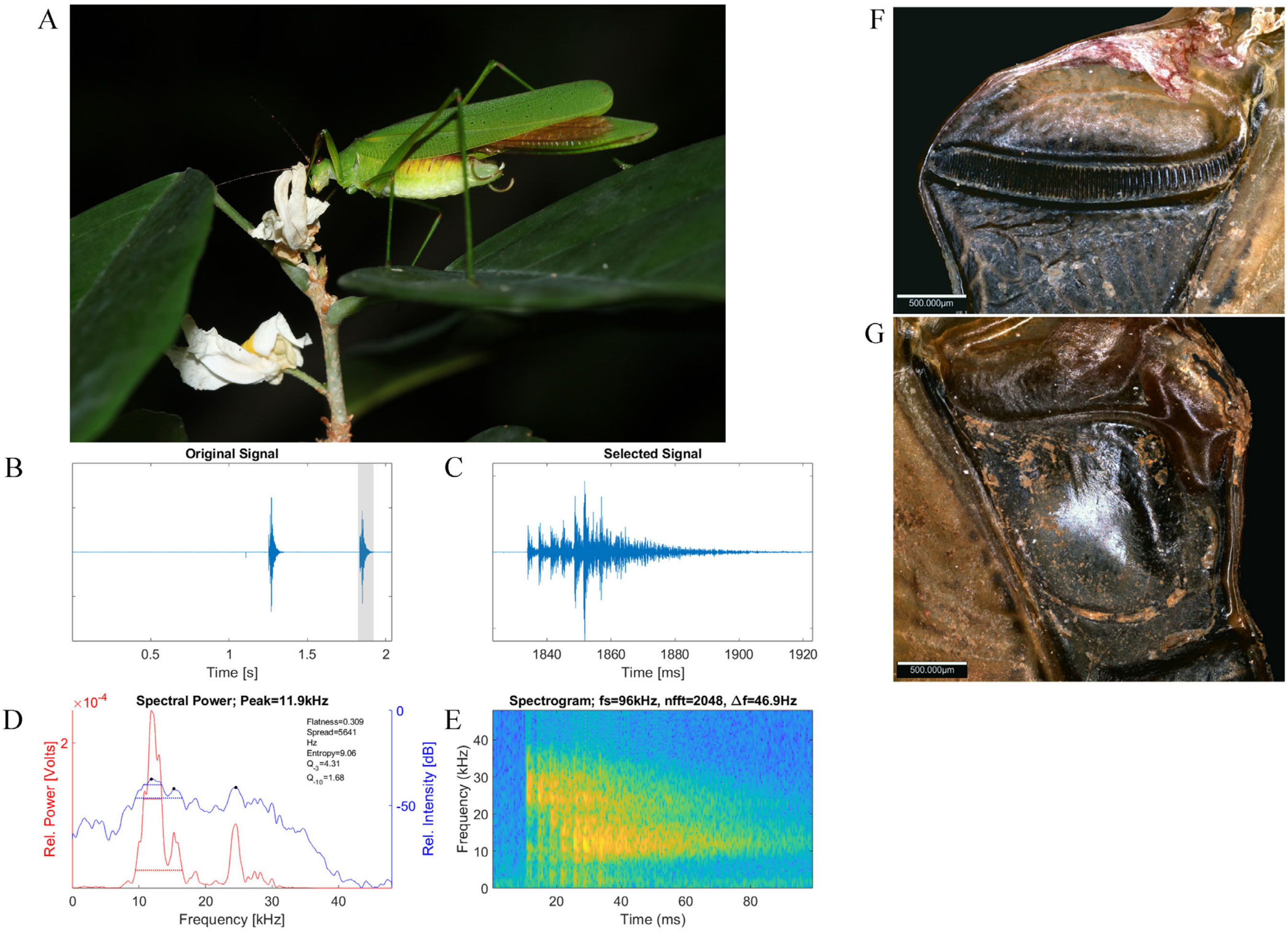

Fig. 19. *Elimaea* (*Rhaebelimaea*) *signata* male adult in the field in Singapore (A). Oscillograms showing two isolated syllables (B) and a syllable (C). Power spectrum (D) and spectrogram (E) of the syllable. Ventral view of the left tegminal stridulatory file (F), and ventral view of the right tegmen sound-producing organs (G).

Elimaea (*Rhaebelimaea*) *signata* Brunner von Wattenwyl, 1878

(n = 2 males, 19 calling songs)
(Fig. 19)

At 28.5°C, calling song consists of isolated syllables made up of discrete pulses. Average duration of syllable 38.1±6.4 ms (25.8–51.7 ms) and made up of 5–9 discrete pulses of varying amplitudes. Typically, three pulses at middle of syllables having distinctly higher amplitude. Call spectrum with peak frequency 14.3±1.5 kHz (11.0–15.0 kHz). Interestingly, syllable frequency modulated between 30 and 10 kHz, but this modulation not as smooth as in *E. sympatrica*. Such 'broad modulation' could result from individual discrete pulses being modulated as scraper progresses on stridulatory file, and perhaps damped nature of the wings. Spectral entropy 8.8–9.1.

Macropterous species. Ventrally, left tegmen with stridulatory file faintly curved, ca. 2.31 mm in length, lined with 66 long and fairly broad teeth; file more curved at basal end. Average tooth density 29 teeth per mm. Teeth at basal half distinctly stouter and more broadly spaced apart than teeth at anal half. At basal part of stridulatory file, average inter-tooth distance 60 µm and average tooth length 193 µm. At anal part, average inter-tooth distance 34 µm and average tooth length 225 µm. Left file (Cu2) only slightly elevated on barely swollen vein buttress. Right tegmen with mirror oblong, slightly longer than wide, membrane smooth and transparent.

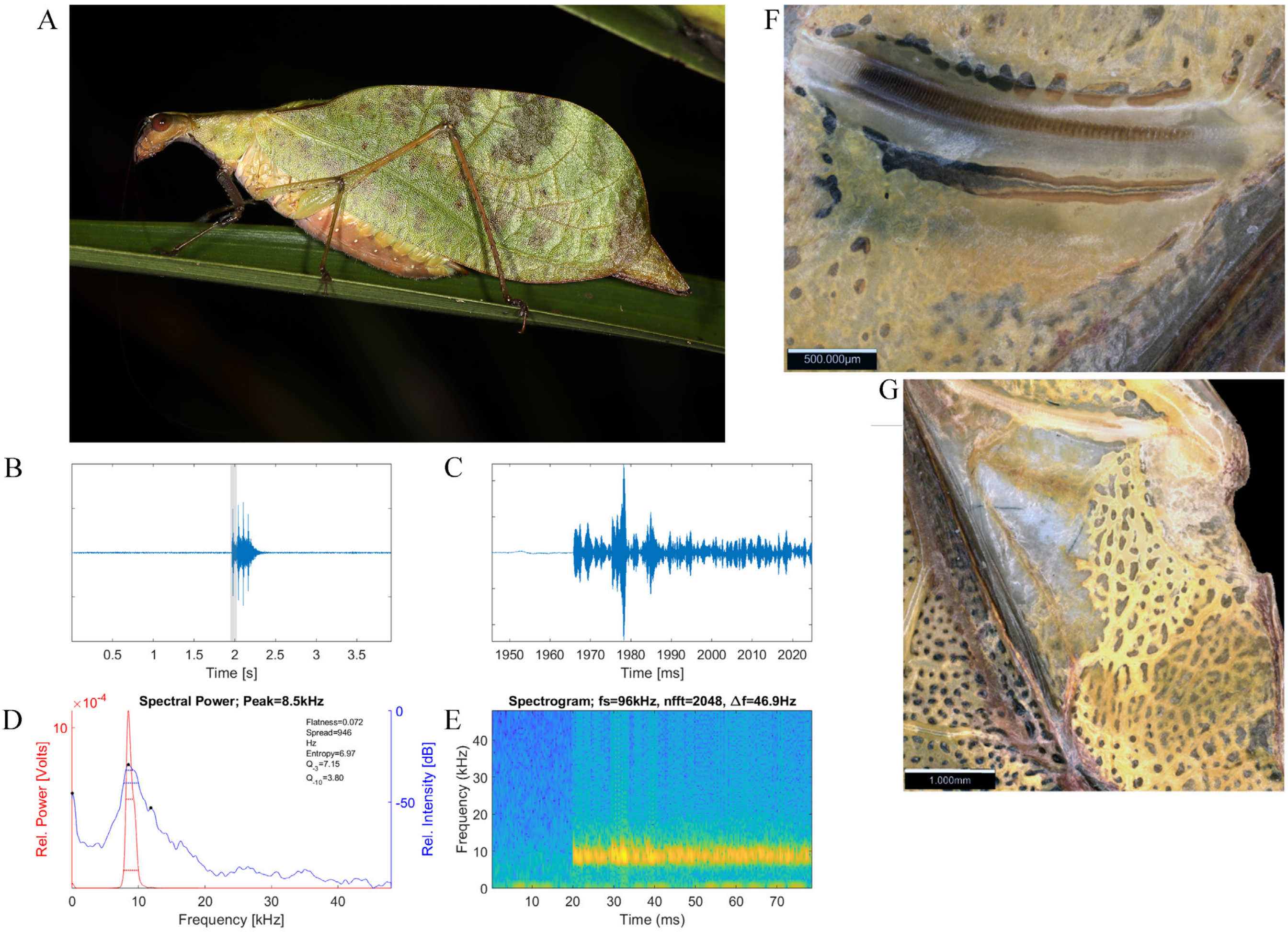

Fig. 20. *Leptoderes ornatipennis* male adult in the field at Sabah, East Malaysia (A). Oscillograms showing an isolated syllable (B, C). Power spectrum (D) and spectrogram (E) of the first part of the syllable. Ventral view of the left tegminal stridulatory file (F), and ventral view of the right tegmen sound-producing organs (G).

Leptoderes ornatipennis **Serville, 1838**
(n = 1 male, 1 calling song)
(Fig. 20)

At 28.5°C, calling song appears to be made up of long syllable produced by gradual and slow wing closure, which produces a few discrete pulses, well isolated in time. Syllable duration 0.24 s. Pulses with similar amplitude, duration range from 23–29 ms. Call spectrum with peak frequency 8.4 kHz, spectral entropy ca. 7.0 and Q_{-3dB} 4.5–7.2.

Macropterous species. Ventrally, left tegmen with stridulatory file slightly curved, ca. 2.61 mm in length, lined with ca. 91 teeth and a few indistinct ones at basal end. Average tooth density 35 teeth per mm. At anal end of stridulatory file, first ten teeth stouter, more broadly spaced apart with average inter-tooth distance of 36 µm. Next ca. 30 teeth distinctly slenderer and longest (average tooth length 129.7 µm) and narrowly spaced apart with average inter-tooth distance 19 µm. Basal third of file with average tooth length 87 µm and average inter-tooth distance 38 µm; longer but less stout than first ten anal teeth. Left file (Cu2) slightly elevated on widened and swollen vein buttress. Right tegmen with mirror obliquely positioned and narrow triangular, longer than broad and with anal half having network of accessory cross-veins, and stridulatory file slender, ca. 2.14 mm in length, with ca. 46 teeth distinctly shorter than those on left tegmen.

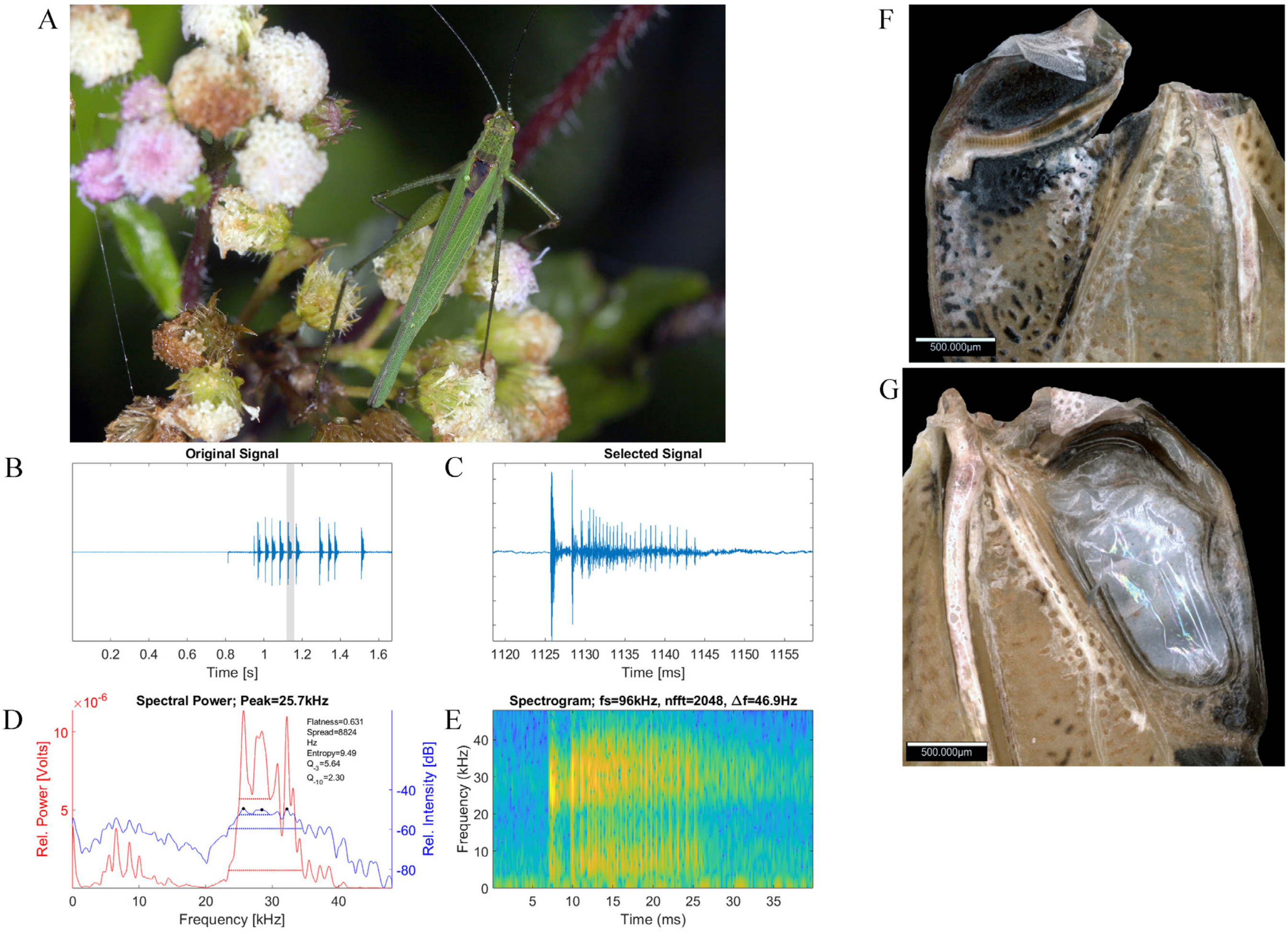

Fig. 21. *Phaneroptera neglecta* male adult in the field at Mindanao, Philippines (A). Oscillograms showing three syllable groups with six, three, one syllables, respectively (B) and a syllable (C). Power spectrum (D) and spectrogram (E) of the syllable. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

***Phaneroptera neglecta* (Karny, 1926)**
(n = 1 male, 16 calling songs)
(Fig. 21)

At 29.7°C, calling song made up of groups of syllables. Average duration of each group 0.18±0.10 s (0.06–0.39 s and made up of variable number of three to eight syllables. Average syllable duration 16.4±2.5 ms (10.8–19.5 ms), average syllable period 42.1±3.9 ms (33.3–50.6 ms) and average silent interval between consecutive syllables 25.8±4.4 ms (18.4–35.0 ms). Call with very broad band spectrum showing energy in two areas, broad peak below 10 kHz, and another at around 29.9±1.3 kHz (26.9–32.5 kHz, at ultrasonic range). Both areas broadband. Spectral entropy ca. 9.5.

Macropterous species. Ventrally, left tegmen with stridulatory file faintly sinuous, ca. 1.11 mm in length, lined with ca. 56 fairly slender teeth; file slightly curved before anal end. Teeth on stridulatory file of left tegmen relatively equally sized (except at tends), fairly uniformly distributed and narrowly spaced apart. Average tooth density 50 teeth per mm. Inter-tooth distance nearly constant throughout file. Mid-part of stridulatory file with average tooth length 68 µm and average inter-tooth distance 23 µm. Left file (Cu2) slightly elevated on barely widened and swollen vein buttress. Right tegmen with mirror oblong, much longer than broad, membrane smooth and transparent.

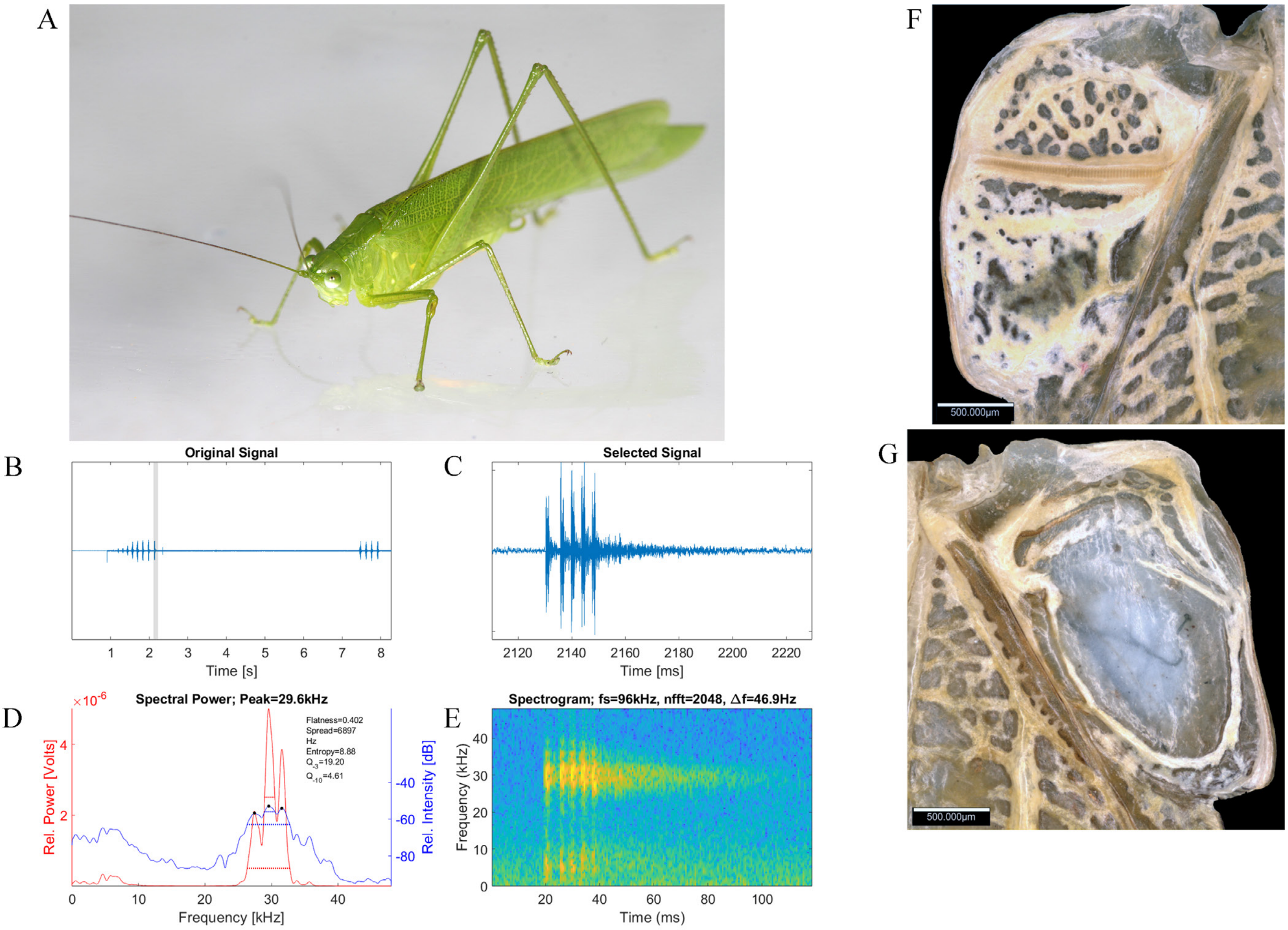

Fig. 22. *Phaulula* cf. *ensigera* male adult in captivity at Mindanao, Philippines (A). Oscillograms showing two syllable groups, each with eight and four syllables, respectively (B) and a syllable with five pulses (C). Power spectrum (D) and spectrogram (E) of the syllable. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

Phaulula cf. _ensigera_ (Karny, 1926)
(n = 1 male, 9 calling songs)
(Fig. 22)

At 20.4°C, calling song made up of 6±2 (4–8) syllable groups with average duration 0.75±0.19 s (0.49–0.99 s). Average syllable duration 27.0±4.2 ms (19.6–35.9 ms), average syllable period 0.15±0.01 s (0.13–0.16 s) and average silent interval between consecutive syllables 0.13±0.01 s (0.11–0.14 ms). Within each syllable, first few pulses with much lower amplitude, then subsequent pulses steadily increase in amplitude to maximum before decreasing. Call spectrum with peak frequency 30.0±1.1 kHz (28.4–32.0 kHz) and spectral entropy 8.9–9.1. Frequency spectrum broad-band, energy ranging between ~25 kHz and ~35 kHz and not symmetrical.

Macropterous species. Ventrally, left tegmen with stridulatory file mostly straight, ca. 1.32 mm in length, with ca. 66 relatively short and relatively slender teeth; file slightly curved at basal end. Teeth on stridulatory file of left tegmen almost equally sized (except at ends), fairly uniformly distributed and narrowly spaced apart. Average tooth density 50 teeth per mm. Inter-tooth distance nearly constant throughout file. Mid-part of stridulatory file with average tooth length 60 µm and average inter-tooth distance 23 µm. Left file (Cu2) slightly elevated on swollen and slightly widened vein buttress. Right tegmen with mirror large oval, longer than broad, membrane smooth and transparent, and stridulatory file slender, ca. 0.98 mm in length, with teeth distinctly shorter than those on left tegmen.

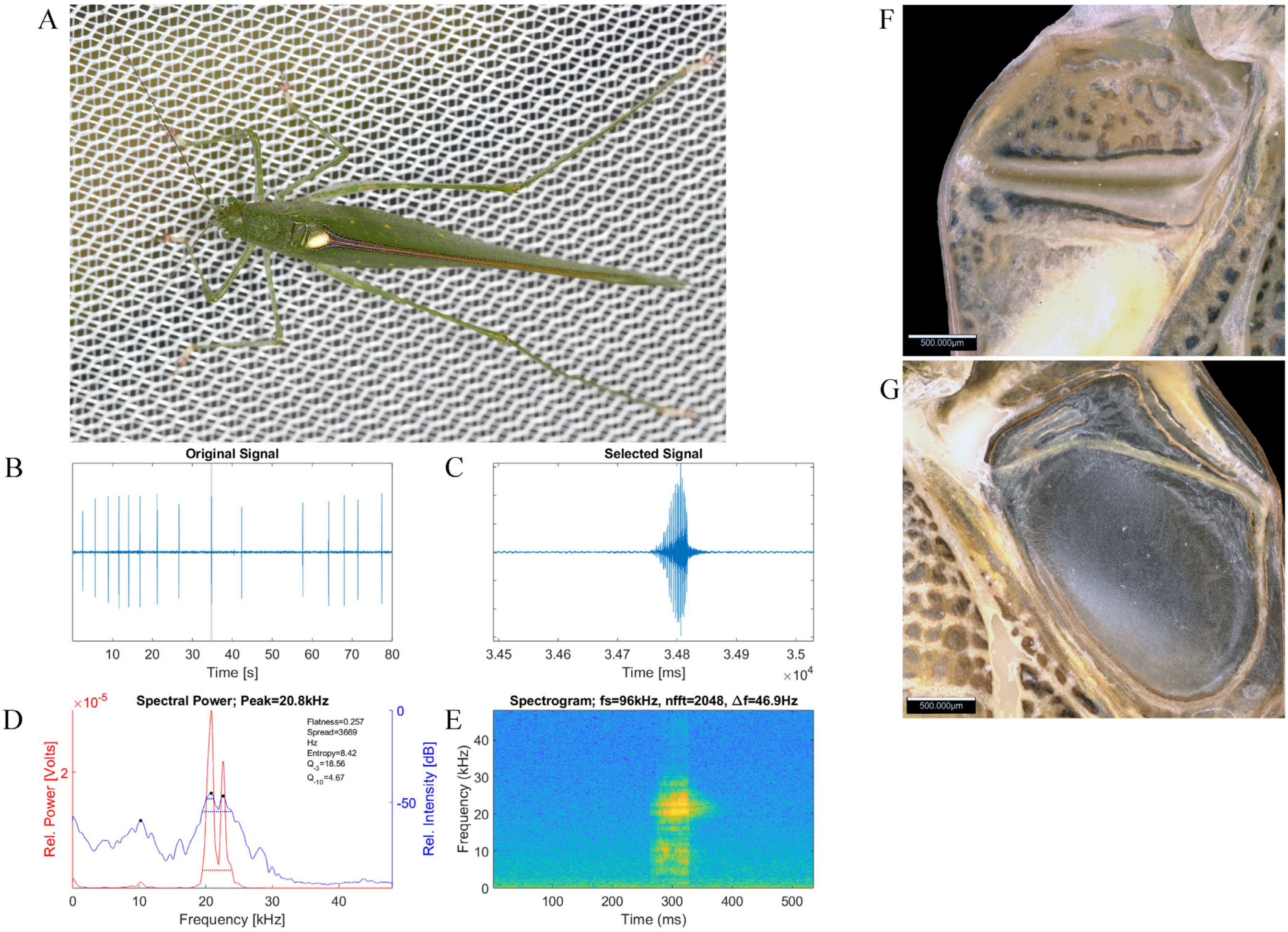

Fig. 23. *Phaulula* cf. *galeata* male adult in captivity at Mindanao, Philippines (A). Oscillograms showing a series of syllables (B) and a syllable (C). Power spectrum (D) and spectrogram (E) of the syllable. Ventral view of the left tegminal stridulatory file (F), and ventral view of the right tegmen sound-producing organs (G).

Phaulula cf. _galeata_ (Hebard, 1922)
(n = 2 males, 18 calling songs)
(Fig. 23)

At 28.5°C, calling song consists of groups of five or six syllables of discrete pulse-trains. Average pulse-train duration 51.5±5.1 ms (36.9–58.4 ms). Average silent interval between consecutive pulse-trains 5.71±3.55 s (1.90–18.09 s). Within each pulse-train, pulses steadily increase in amplitude to maximum before decreasing slightly at last few pulses. Average syllable duration 2.0±0.3 ms (1.3–2.6 ms), average syllable period 3.5±0.3 ms (2.9–4.0 ms) and average silent interval between consecutive syllables 1.6±0.4 ms (1.1–2.6 ms). Call spectrum with peak frequency 21.3±0.5 kHz (20.1–21.8 kHz), spectral entropy 8.3–8.4 and Q_{-3dB} 14.8–18.6.

Macropterous species. Ventrally, left tegmen with stridulatory file mostly straight, ca. 1.70 mm in length, with ca. 110 relatively short and slender teeth; file slightly curved at basal end. Teeth on stridulatory file of left tegmen almost equally sized (except at ends), fairly uniformly distributed and narrowly spaced apart. Average tooth density 65 teeth per mm. Inter-tooth distance nearly constant throughout the file. Mid-part of stridulatory file with average tooth length 80 μm and average inter-tooth distance 20 μm. Left file (Cu2) slightly elevated on swollen and slightly widened vein buttress; buttress distinctly widened at basal end compared to anal end. Right tegmen with mirror large oval, membrane smooth and transparent, and stridulatory file slender with teeth distinctly shorter than those on left tegmen.

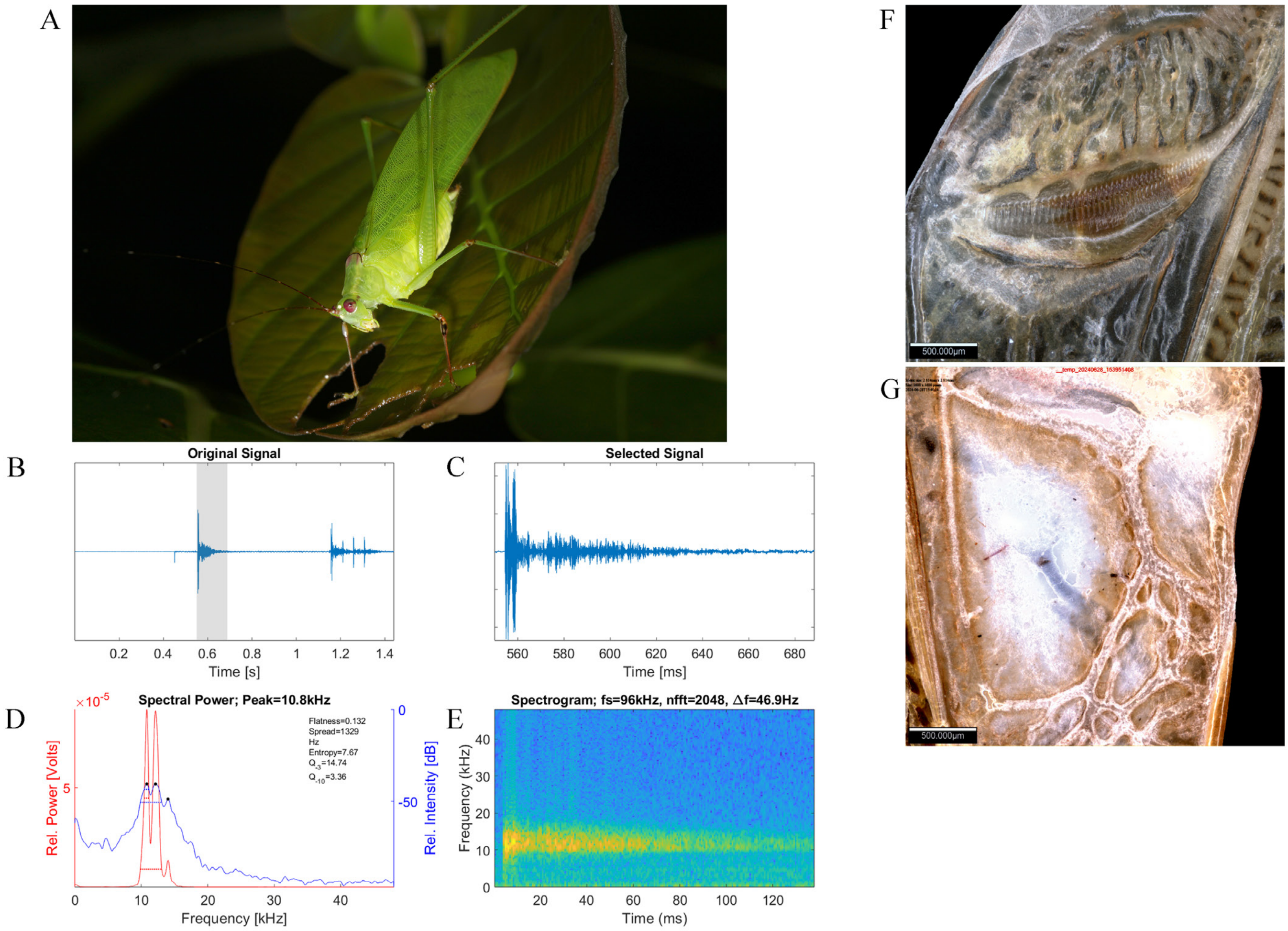

Fig. 24. *Phygela marginata* male adult in the field at Sabah, East Malaysia (A). Oscillograms showing two isolated echemes (B) and an isolated bi-syllabic echeme (C). Power spectrum (D) and spectrogram (E) of the first echeme. Ventral view of the left tegminal stridulatory file (F), and ventral view of the right tegmen sound-producing organs (G).

Phygela marginata Brunner von Wattenwyl, 1878
(n = 1 male, 10 calling songs)
(Fig. 24)

At 27.8°C, calling song consists of a pair of isolated syllables. Average duration of each pair 0.75±0.02 s (0.73–0.77 s). First syllable with average duration 51.3±16.7 ms (32.1–61.3 ms). Second syllable with average duration 150.2±3.8 ms (146.6–154.2 ms) and ends with two or three clicks. Average silent interval between two syllables 0.55±0.02 s (0.52–0.57 s). Call spectrum with peak frequency 11.7±0.4 kHz (11.0–12.1 kHz), spectral entropy 7.4–7.7 and Q_{-3dB} 12.3–14.7.

Macropterous species. Ventrally, left tegmen with stridulatory file mostly straight, ca. 2.10 mm in length, with ca. 46 very long and relatively robust teeth and a few indistinct teeth at basal end; file faintly curved at basal end. Teeth on stridulatory file of left tegmen largest at mid-part of stridulatory file, fairly uniformly distributed and narrowly spaced apart. Average tooth density 22 teeth per mm. Inter-tooth distance nearly constant throughout file, slightly more spaced apart towards anal end. Mid-part of stridulatory file with average tooth length 213 µm and average inter-tooth distance 44 µm. At end part of stridulatory teeth, average inter-tooth distance 57 µm. Left file (Cu2) elevated on swollen and widened vein buttress. Right tegmen with mirror large, shaped like elongated pentagon, membrane smooth and transparent.

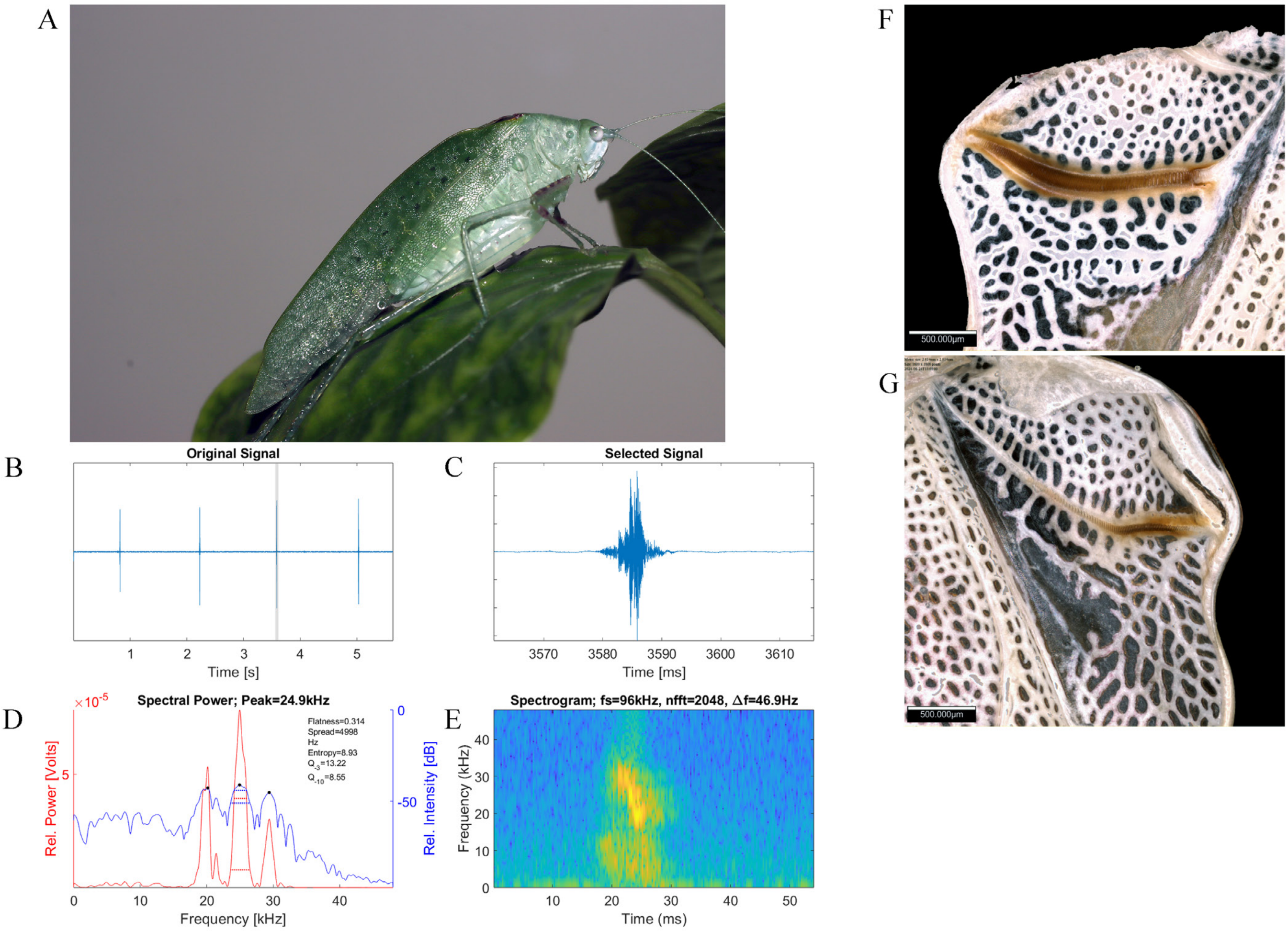

Fig. 25. *Stictophaula* sp. male adult in captivity from Singapore (A). Oscillograms showing four isolated syllables (B) and an isolated syllable (C). Power spectrum (D) and spectrogram (E) of the isolated syllable. Ventral view of the left tegmen sound-producing organs (F), and ventral view of the right tegmen sound-producing organs (G).

***Stictophaula* sp.**
(n = 1 male, 13 calling songs)
(Fig. 25)

At 29.3°C, calling song made up of isolated syllables. Average syllable duration 5.0±0.1 ms (3.8–5.8 ms) and average syllable period 1.52±0.09 s (1.36–1.64 s). Call can have broad-band spectrum, energy peaks at around 22.3 kHz; or showing remarkable negative frequency modulation between ~30 and 16 kHz, which reflects in spectral energy as three energy peaks at ca. 19.3 kHz, 24.7 kHz and 27.0 kHz. Spectral entropy of strongest peak (at 24.7 kHz) 8.9–9.0 and Q_{-3dB} 13.2–16.3.

Macropterous species. Ventrally, left tegmen with stridulatory file distinctly curved, ca. 1.90 mm in length, lined with ca. 105 teeth; file curved anal of mid-part of stridulatory file. Average tooth density 55 teeth per mm. Teeth on basal part of stridulatory file more robust (broader) and more broadly-spaced apart; average tooth length 84.2 µm and average inter-tooth distance 32 µm. Anal end of mid-part of stridulatory file, average tooth length largest at 127 µm and average inter-tooth distance 14 µm. Left file (Cu2) barely elevated on barely swollen and slightly widened vein buttress. Right tegmen with mirror obliquely positioned and narrow triangular, area interlaced with network of veins, and stridulatory file slender and sinuated, ca. 1.49 mm in length with ca. 87 teeth distinctly shorter than those on left tegmen.

This is potentially a new species, but more work is still needed to confirm and this would be out of the scope of this paper.

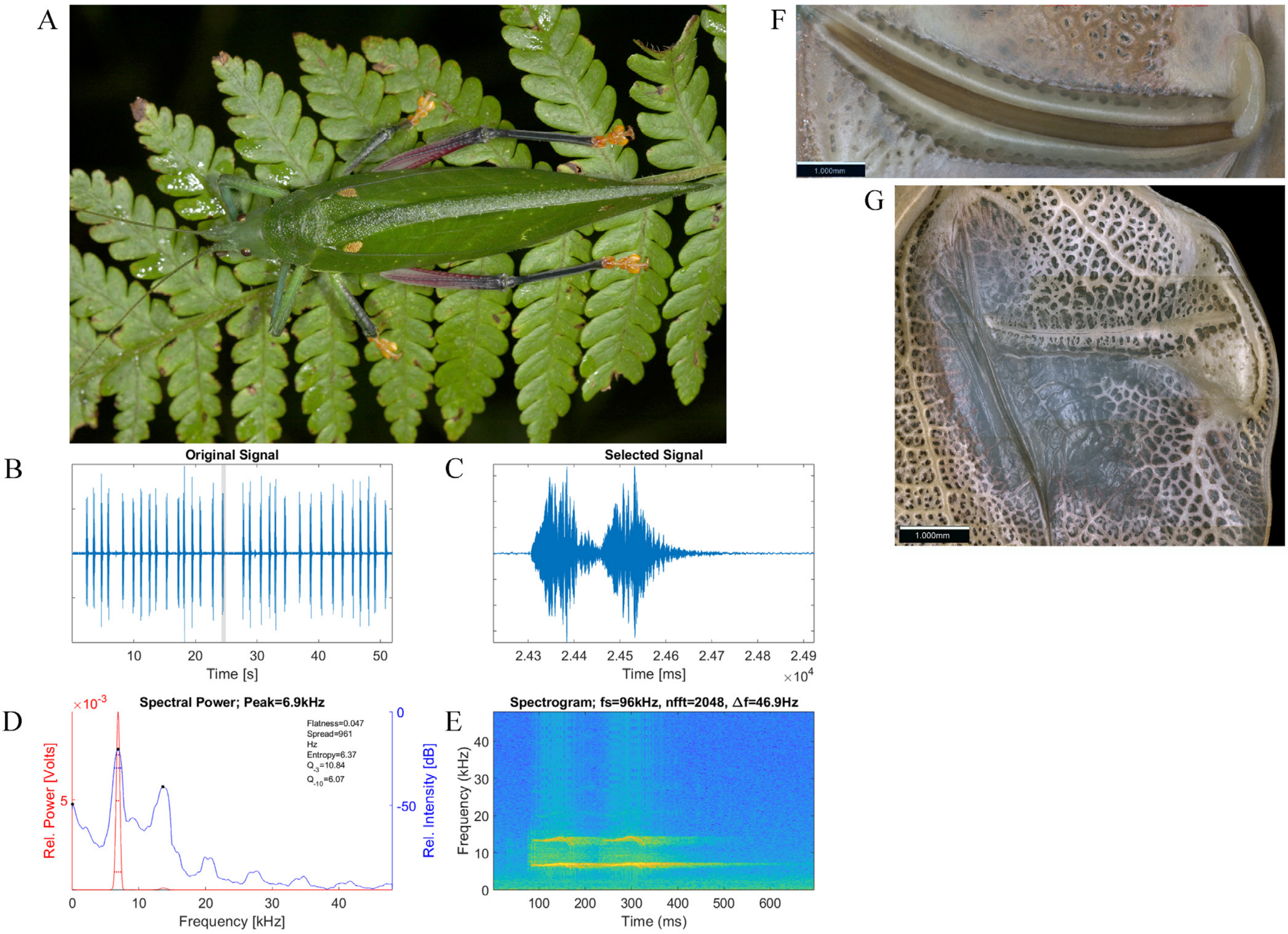

Fig. 26. *Phyllomimus* (*Phyllomimus*) cf. *detersus* male adult in the field at Mindanao, Philippines (A). Oscillograms showing a series of echemes (B) and an echeme with two syllables (C). Power spectrum (D) and spectrogram (E) of the echeme. Ventral view of the left tegminal stridulatory file (F), and ventral view of the right tegmen sound-producing organs (G).

Subfamily Pseudophyllinae

***Phyllomimus* (*Phyllomimus*) cf. *detersus* (Walker, 1869)**
(n = 1 male, 20 calling songs)
(Fig. 26)

At 25.8°C, calling song consists of echeme sequence made up of a pair of closely-spaced syllables. Average echeme duration 0.32±0.01 s (0.29–0.34 s) and average silent interval between consecutive echemes 1.01±0.33 s (0.60–1.90 s). Within each echeme, average durations of first and second syllables 0.14±0.01 s (0.12–0.15 s) and 0.16±0.01 s (0.14–0.18 s), respectively. Average syllable period 0.16±0.01 s (0.14–0.17 s) and average silent interval between two syllables 0.02±0.01 s (0.01–0.03 s). Frequency spectrum consists of harmonic series with fundamental frequency, also peak frequency, 7.0±0.1 kHz (6.8–7.4 kHz). Spectral entropy 6.4–6.5 and Q_{-3dB} 10.7–10.8.

Li et al. (2019) reported that *Phyllomimus* (*Phyllomimus*) *detersus* produced broadband calls with peak frequency of 14 kHz, based on data obtained from BioAcoustica database (Baker et al., 2015). The difference may be due to different environmental conditions in China and Philippines where the recordings were taken. Alternatively, the taxonomy of this species has not been studied since numerous taxa were synonymised under this species (Cigliano et al., 2024), including *Pseudophyllus sinensis* Walker, 1869 described from China. Therefore, calling songs recorded from China and Philippines may belong to different species. Nevertheless, we did not find data on BioAcoustica database associated with this species, consequently we could not compare the calling songs or specimens.

Macropterous species. Ventrally, left tegmen with stridulatory file curved, ca. 8.18 mm in length, with many long and very slender teeth; file bends at nearly 90° at basal end, forming lobe perpendicular to length of stridulatory file. Teeth on stridulatory file of left tegmen almost equally sized (except at ends), fairly uniformly distributed and very narrowly spaced apart. Tooth density at anal end of stridulatory file 0.05 teeth per µm; at mid-part of stridulatory file 0.05 teeth per µm; at basal part of the length of stridulatory file 0.09 teeth per µm; at lobular part at basal end of stridulatory file 0.06 teeth per µm. Left file (Cu2) strongly elevated on very swollen and widened vein buttress. Right tegmen with mirror rectangular, with area interlaced with networks of veins.

DISCUSSION

After combining the data obtained using similar methodology and analyses from Tan et al. (2023), we have acoustic data for a total of 49 katydid species from 36 genera and five subfamilies. New data from the additional 25 species here confirms what was previously known about the highly diversified calling songs and sound-producing organs among katydids.

Firstly, it has been reported that globally, most katydids produce ultrasonic sounds (Montealegre-Z, 2009, Montealegre-Z et al., 2017; Heller et al., 2017, 2021; ter Hofstede et al., 2020). Tan et al. (2023) reported that 80% of 24 species documented have energy peaks in the ultrasonic range (18 species having peak frequencies between 20 and 40 kHz, and three species having peak frequencies > 40 kHz). Here, the new data further corroborates these observations, with 72% of the species having energy peaks in the ultrasonic range (15 species having peak frequencies between 20 and 40 kHz, and three species having peak frequencies > 40 kHz). Both datasets combined indicate that 39 out of the 49 species from Southeast Asia (80%) produce songs with spectral energy peaking at above 20 kHz, further attesting that most katydids produce songs with peak frequency in the ultrasonic range.

Southeast Asian species of the subfamily Meconematinae (n = 11) generally produce songs with an average peak frequency of 40.7 kHz (21.5–88.0 kHz), as seen in the species discussed in the current study and those described in Tan et al. (2023). This finding further corroborates previous work on other Meconematinae: *Asiophlugis* from Southeast Asia producing calls with energy peaking at 40–60 kHz (Tan et al., 2019a); the Neotropical species *Arachnoscelis arachnoides* (at ca. 80 kHz), *Speculophlugis*, and *Phlugis* (at ca. 50 kHz) (Montealegre-Z et al., 2006, 2017; Chivers et al., 2014, Woodrow et al., 2019), and *Supersonus* (ca. 125–150 kHz) (Sarria-S et al., 2014); as well as 16 African representatives of the genera *Afrophisis*, *Amytta*, and *Phlugidia* (ca. 35–50 kHz) (Hemp, 2021). Here, we also document the calling song of an unknown species of Meconematini from the Philippines with a peak frequency of 88 kHz — the highest frequency among known calling songs of Southeast Asian taxa. The call structure of this unknown species is also similar to those of the Neotropical genera *Phlugis*, *Arachnoscelis*, and *Supersonus*.

At the other end of the frequency spectrum, Pseudophyllinae from Southeast Asia have been documented to produce very low-frequency calls (Heller, 1995). Here, we describe the calling song of *Phyllomimus* (*Phyllomimus*) cf. *detersus* from the Philippines with peak frequency at 6.5 kHz, the lowest among the katydids described here. It is also lower than eight of the nine Southeast Asian Pseudophyllinae reported in Heller (1995). The lowest recorded calling song of a katydid probably belongs to a species of *Tympanophyllum* recorded in Borneo, in which the peak frequency is less than 1 kHz and resembles frog calls (Heller, 1995; Riede, 1996).

Frequency domains of katydid calling songs can vary greatly among taxa. In this study, the spectral entropies of katydid calling songs varied widely (5.91–9.48), with an average of 7.9. Many species produce broad-band calls, which is also observed in Neotropical species (see ter Hofstede et al., 2020). However, there are some species that produce highly tonal calls, including *Alloteratura* (*Meconemopsis*) *longa* and *Bispinolakis longicauda*. This has also been reported in Neotropical taxa such as *Copiphora* (see Montealgre-Z & Postles, 2010). Some species also produce songs with a harmonic frequency series, including *Phyllomimus* (*Phyllomimus*) cf. *detersus* and *Paragraecia temasek*. Heller (1995) further documented three other Pseudophyllinae (i.e., *Tympanophyllum arcufolium* (Haan, 1843), *Promeca sumatrana* Beier, 1954, and *Promeca perakana* Beier, 1954) producing harmonic frequency series with energy peaking at the fundamental frequency. *Triencentrus atrosignatus* (Brunner von Wattenwyl, 1895) from the Neotropics also produces a harmonic series, but the call spectrum peaks at the second harmonic, rather than the first (Montealegre-Z & Morris, 1999). Between *Phyllomimus* (*Phyllomimus*) cf. *detersus* and *Paragraecia temasek*, the entropy of each harmonic frequency is higher in the latter species, further demonstrating the highly varied frequency domains among katydid calling songs.

Our study illustrates that a broad diversity of call structure in katydid songs exists. We found a few species that produced simple songs made up of isolated simple syllables, notably from representatives of the subfamily Phaneropterinae. Some other species, again mostly from the subfamily Phaneropterinae, also produced isolated pulse-trains. Most other species either produced echemes or echeme-sequences, as well as continuous trills. Interestingly, based on three species recorded here and Tan et al. (2023), we found that *Conocephalus* generally produce complex songs, where the echeme-sequences have different echemes with differing structures in the time domain.

The diverse calling songs of katydids may reflect their variable sound-producing organs. Stridulatory files on the left tegmina of katydids tend to be highly variable in length, from 0.6 mm in *Peracca macritchiensis* to 8.2 mm in *Phyllomimus* cf. *detersus* documented in Tan et al. (2023) and this study respectively. Similarly, the number of teeth on the stridulatory file can range from 18 very stout, broad, and roundish teeth in *Odonturisca epiproctalis* to more than 400 slender and closely packed teeth in *Phyllomimus* (*Phyllomimus*) cf. *detersus*; and the average tooth length ranges from 17.8 µm in *Euanisous teuthroides* to 244 µm in *Psyrana tigrina* (both species reported in Tan et al., 2023). With respect to stridulatory file shape, that of *Phaneroptera brevis* has a stridulatory file separated into two parts—the basal part which is a typical file with large teeth and the anal end with a separate row of distinctly smaller teeth (Tan et al., 2023). This is distinct from a typical katydid stridulatory file, which consists of a single row of teeth and is typically relatively straight to slightly curved.

We observed that in general, congeners have clear-cut differences in calling songs especially in terms of time and frequency domains, as well as morphology of sound-producing organs. In this study, the three allopatric species of *Scytocera* from Borneo, the Philippines, and the Malay Peninsula have different call structures, though the peak frequencies may be similar, e.g., between *Scytocera* cf. *longicornis* from the Philippines and *Scytocera* cf. *kemneri* from Singapore. Sound-producing organs of the latter two congeners are also very different in morphology. In another example, three *Phaulula* species, *Phaulula* cf. *ensigera* and *Phaulula* cf. *galeata* from the Philippines and *Phaulula malayica* (Karny, 1926) from Singapore (see Tan et al., 2023), also produce calling songs with different call structures and peak frequencies. In fact, the two Philippine species, i.e., *Phaulula* cf. *ensigera* and *Phaulula* cf. *galeata* occur in sympatry in Mindanao. These demonstrate that differences in calling song parameters generally corroborate traditional morphological characters (e.g., abdominal appendages and titillators) used to delimit species.

Our attempt to describe the calling songs of katydids is the first step to further understanding of bioacoustics of katydids in Southeast Asia and utilising these data for other fields of research. As more sound data becomes available, calling songs can be used as additional data to support integrative taxonomic research on Southeast Asian taxa (e.g., Tan et al., 2019a, 2020a). Beyond using these data for species delimitation and taxonomy, it is also potentially interesting to examine how these songs and stridulatory morphology may have evolved through ancestral state reconstruction. However, this is presently a challenge, given that the phylogeny of katydids remains unstable, and many subfamilies are not necessarily monophyletic (Mugleston et al., 2013, 2018). Most Southeast Asian katydid species are also not represented in recent studies examining phylogenetic relationships in Tettigoniidae (see Mugleston et al., 2013, 2018).

Accumulation of sound data for Southeast Asian katydids can also contribute to ecoacoustic studies. Soundscape recordings are now well-established monitoring tools in ecoacoustics and contributed by even citizen scientists with the availability of relatively cheap ultrasound recorders. Bioacoustic monitoring has already been proposed to be a potentially useful tool in biodiversity assessment and conservation (Riede, 1998). However, a major challenge to making these data meaningful is the lack of knowledge of the species producing the different calls. It is necessary to (1) record and build calling song libraries; (2) characterise the song elements unique to different species so that they can be used for their diagnoses in bioacoustics monitoring; and (3) ensure physical specimens of the katydids are available for cross-referencing and re-examination.

The documentation of the calling songs of katydids (and other orthopterans) can be time-consuming, laborious and remains far from completion. However, it also offers opportunities to better understand and appreciate overlooked aspects of the natural soundscape contributed by these insects, especially in Southeast Asia where not much is known in this field.

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