The calling songs of some katydids (Orthoptera, Tettigonioidea) from the tropical forests of Southeast Asia

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Abstract

Katydids produce sound for signaling and communication by stridulation of the tegmina. Unlike crickets, most katydids are known to sing at ultrasonic frequencies. This has drawn interest in the investigation of the biophysics of ultrasonic sound production, detection, evolution, and ecology (including predator–prey interactions) of these katydids. However, most of these studies are based on species from the Neotropics, while little is known about katydid species from the hyperdiverse region of Southeast Asia. To address this, a concerted effort to document, record, and describe the calling songs of Southeast Asian katydids, especially species that call at ultrasonic frequencies, was made. A study spanning two years (2018–2020) in the Malay Peninsula (Singapore and Malaysia), Borneo (Brunei Darussalam and Sabah), and the Philippines revealed previously unknown calls of 24 katydid species from four subfamilies. The calling songs of Southeast Asian katydid species are highly diversified in terms of time and frequency. Call structure can range from isolated syllables (e.g., *Holochlora*), continuous trills (e.g., *Axylus philippinus*), to short pulse-trains (e.g., *Euanisous teuthroides*) and complex echemes (e.g., *Conocephalus* spp.), with 87.5% of species having ultrasonic peak frequencies and 12.5% being considered extreme ultrasonic callers (peak frequency >40 kHz). The call spectrum ranges from tonal (e.g., spectral entropy is 6.8 in *Casigneta* sp. 2) to resonant (entropy is 8.8 in *Conocephalus cognatus*). Of the 24 species whose calls are described here, we imaged and described the sound-producing structures of 18. This study provides a preliminary overview of the acoustic diversity of katydids in Southeast Asia, and the authors hope to inspire further investigation into the bioacoustics of little-known katydids from these areas. Amassing a database of calling songs and sound-producing organ illustrations from different species is important to address taxonomic impediments while advancing our knowledge about the bioacoustics of Southeast Asian katydids.

Keywords

acoustics, calls, frequency, sound-producing organs, stridulation, Tettigoniidae, ultrasound

Introduction

Katydids 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 between conspecific and heterospecific males (Morris et al. 1994, Heller 1995, Morris 1999, Heller and Hemp 2020). For example, some katydids produce songs at frequencies as low as 0.6 kHz (e.g., *Tympanophyllum arcufolium* (Haan, 1843); see Heller 1995), whereas other species can call at as high as 150 kHz (e.g., *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 and Tan et al. 2021), such vast frequency variation makes katydids an ideal subject for studying acoustic communication and its evolution.

Katydids generate sounds through 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 of the left tegmen within a cycle of wing movement (Walker and Dew 1972,

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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 the species calling song, although the mirror area on the right tegmen can also play a role in dictating peak frequency (Bailey 1967, Montealegre-Z 2012, Chivers et al. 2014). However, it is not mechanically possible for katydids to move their tegmina at the velocity needed to produce extreme ultrasound (>40 kHz). Instead, to generate much higher frequency calls than wing movement velocity would allow, the scraper of some katydid species is loaded with resilin and deformable, allowing elastic energy to be stored and released (Morris et al. 1994, Montealegre-Z et al. 2006).

Many katydids emit ultrasonic frequency in their calling songs (e.g., Bailey 1967, 1970, Morris and Pipher 1967), with currently more than 70% documented as singing at ultrasonic frequencies (>20 kHz), with some species reaching extreme ultrasonic frequencies (>40 kHz) (Mason et al. 1991, Montealegre-Z et al. 2017). When compared to low-frequency calls typically produced by crickets, the generation of ultrasonic songs by katydids has clear advantages and disadvantages (Morris et al. 1994, Montealegre-Z et al. 2006). Ultrasound has enhanced directionality and radiation efficiency, allowing 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 bats (Belwood and Morris 1987). On the other hand, the decay of energy in ultrasound is more rapid, thus reducing the 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-S et al. 2014, 2016, Chamorro-Rengifo et al. 2014, Chamorro-Rengifo and Braun 2016, Chamorro-Rengifo and Olivier 2017); the 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, with the acoustic communication of Southeast Asian orthopterans being less well studied (but see e.g., Heller 1995, Ingrisch 1995, 1998, Riede 1996, 1997, Tan 2011, Heller et al. 2017, 2021a; Tan et al. 2019b, 2020a). Despite Southeast Asia being one of the noisiest places due to the high diversity of calling insects, many species are still unknown and require taxonomic description and revision (Tan et al. 2017). Beyond their original descriptions, little is known about the biology of many katydid species in Southeast Asia.

While taxonomy is crucial for accurate identification and cataloging of bioacoustics data for studies on ecology, behavior, and evolution, the use of bioacoustics can also help overcome taxonomic impediment. Recent studies have demonstrated that the calling songs of Southeast Asian katydids can be used to resolve taxonomic problems related to species complexes. Heller et al. (2017) used calling songs to classify cryptic species within the *Ducetia japonica* species group. Previously thought to be a widely distributed species, it has been determined that different regions harbor different cryptic species. Tan et al. (2020a) and Heller et al. (2021a) 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. (2020a) provided a foundation for the further taxonomic progress of these little-known katydids from Southeast Asia (Ingrisch 2021, Gorochov 2021). These examples demonstrate the importance of combining bioacoustics and traditional taxonomy to identify species of katydids from Southeast Asia.

This study aimed 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 accurately identified and systematically vouchered the specimens. Given the importance of the morphology of sound-producing organs in dictating key acoustic parameters (e.g., peak frequency and 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 be incorporated into traditional taxonomy and/or used for meta-analysis to overcome taxonomic impediments 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 30 September to 4 October 2019; and (5) Laguna, Luzon, the Philippines from 11 to 13 May and 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 a 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 where they were caught. 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 occasionally provided. Meconematinae were fed with living *Drosophila* fruit flies.

Acoustic recordings and analysis.—Acoustic recording and analysis generally followed that of Tan et al. (2019b, 2020a). All recordings were obtained in laboratory conditions or biological stations in the dark. The calling song of an isolated male placed inside a standardized insect cage (25 cm in diameter and 33 cm tall) with a nylon cover was sampled at a frequency of 256 kHz-samples/s using a Echo Meter Touch or Echo Meter Touch Pro 2 sensor (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 the recording). It should, however, be noted that with this type of microphone, a recording distance 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 to 20 kHz. However, this was only a trigger and did not affect the quality of the recording at lower frequencies (i.e., <20 kHz). The recorded signals were saved in 12-bit and 16-bit WAV formats for Echo Meter Touch or Echo Meter Touch Pro 2 sensor, 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 the impact of each tooth;
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, 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.

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; 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), Gorochov (1998, 2008, 2011, 2013), Tan and Ingrisch (2014), Tan (2014, 2017), Tan et al. (2015, 2018, 2019a), Tan and Artchawakom (2017), Jin et al. (2020), and by comparing them with photographs of type specimens. Taxonomists, specifically Xing-bao Jin, Sigfrid Ingrisch, and Andrei Gorochov, were also consulted.

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).

Depositories.—

FRC	Forest Research Center, Sepilok, Sabah, East Malaysia
UBDM	Universiti Brunei Darussalam Museum, Brunei Darussalam
UPLBMNH	University of the Philippines Los Baños, Museum of Natural History, Philippines
ZRC	Zoological Reference Collection, Lee Kong Chian Natural History Museum, Singapore

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

Results

Summary.—In total, 37 individual katydids were collected. Of these, the calling songs of 24 species from 20 genera of the subfamilies Conocephalinae (nine species), Lipotactinae (one species), Meconematinae (seven species), and Phaneropterinae (seven species) were recorded for the first time (Table 1). The peak frequency of each of the 24 katydids species was found to range from as low as 12.6 kHz in *Paragraecia temasek* Tan & Ingrisch, 2014 to as high as 54.2 kHz in an unidentified Meconematini from Sandakan. Twenty-one species (87.5%) were found to have peak frequencies in the ultrasonic range, of which three species (12.5%) can be considered extreme ultrasonic callers (i.e., peak frequency >40 kHz; Table 1). The spectral entropy of the katydids ranges from 6.8 in *Casigneta* sp. 2 to 8.8 in *Conocephalus cognatus* (Redtenbacher, 1891). Of the 24 species whose calls are described here, we imaged and described the sound-producing structures of 18.

Song and sound-producing structure descriptions

Axylus philippinus **(Hebard, 1922)** (n = 1 male, 10 sound files) (Fig. 1): The calling song is a continuous trill made up of disyllabic echemes (each consisting of two amplitude peaks). At 30.0±0.5°C (28.9–30.3°C), the trill has a echeme repetition rate of 11±1 echeme s^{-1} (9–11 echemes s^{-1}). The echeme 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 (32.5–36.0 kHz) and another peak at 16.4±1.9 kHz (13.5–19.0 kHz) showing energy in the sonic range; the spectral entropy is 8.5±0.1.

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

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

	Species	Country of origin	Call structure	Spectral entropy	Peak freq. (kHz)
	Subf. Conocephalinae				
1.	*Axylus philippinus*	Philippines	Continuous trill of disyllabic echeme	8.5±0.1	34.7±1.3
2.	*Conocephalus cognatus*	Singapore	Complex echeme	8.8±0.1	28.7±2.1
3.	*Conocephalus exemptus*	Singapore	Complex echeme	7.8±0.1	15.5±0.2
4.	*Paragraecia temasek*	Singapore	Echeme	7.7±0.1	12.6±0.1
5.	*Peracca macritchiensis*	Singapore	Echeme sequence	7.4	29.3±1.1
6.	*Salomona borneensis*	Malaysia	Echeme sequence	8.4±0.1	13.9±0.4
7.	*Salomona maculifrons*	Philippines	Sequence of isolated echemes	8.5±0.1	30.5±0.7
8.	*Viriacca insularis*	Malaysia	Echeme	8.0±0.2	23.1±1.8
9.	*Viriacca modesta*	Brunei	Echeme sequence	7.8±0.1	26.0±2.4
	Subf. Lipotactinae				
10.	*Lipotactes maculatus*	Singapore	Isolated echemes	8.3	33.1±3.1
	Subf. Meconematinae				
11.	*Alloteratura lamella*	Singapore	Complex echemes or isolated syllables	7.7±0.3	25.5±0.7
12.	*Borneopsis cryptosticta*	Singapore	Sequence of paired syllables or echemes	8.5±0.3	42.3±2.4
13.	*Euanisous teuthroides*	Singapore	Echeme	7.4±0.2	30.3±0.7
14.	*Kuzicus denticulatus*	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.	*Neophisis siamensis*	Singapore	Sequences of isolated syllables	7.1	36.7±1.8
17.	*Xiphidiopsis* (*Xiphidiopsis*) *dicera*	Singapore	Continuous trill	7.7	40.9±0.4
	Subf. Phaneropterinae				
18.	*Casigneta* sp. 1	Singapore	Pulse train	7.6±0.1	28.7±0.8
19.	*Casigneta* sp. 2	Singapore	Triplet syllables	6.8±0.2	28.2±0.2
20.	*Holochlora* nr. *bilobata*	Singapore	Isolated syllables	8.1±0.4	33.3±1.0
21.	*Phaneroptera brevis*	Singapore	Paired syllables	7.9	21.9±0.8
22.	*Phaulula malayica*	Singapore	Isolated syllables	7.8	23.6±1.2
23.	*Psyrana tigrina*	Malaysia	Pulse train	8.1	35.5±2.1
24.	*Scambophyllum sanguinolentum*	Singapore	Pulse train	7.0±0.1	23.7±0.3

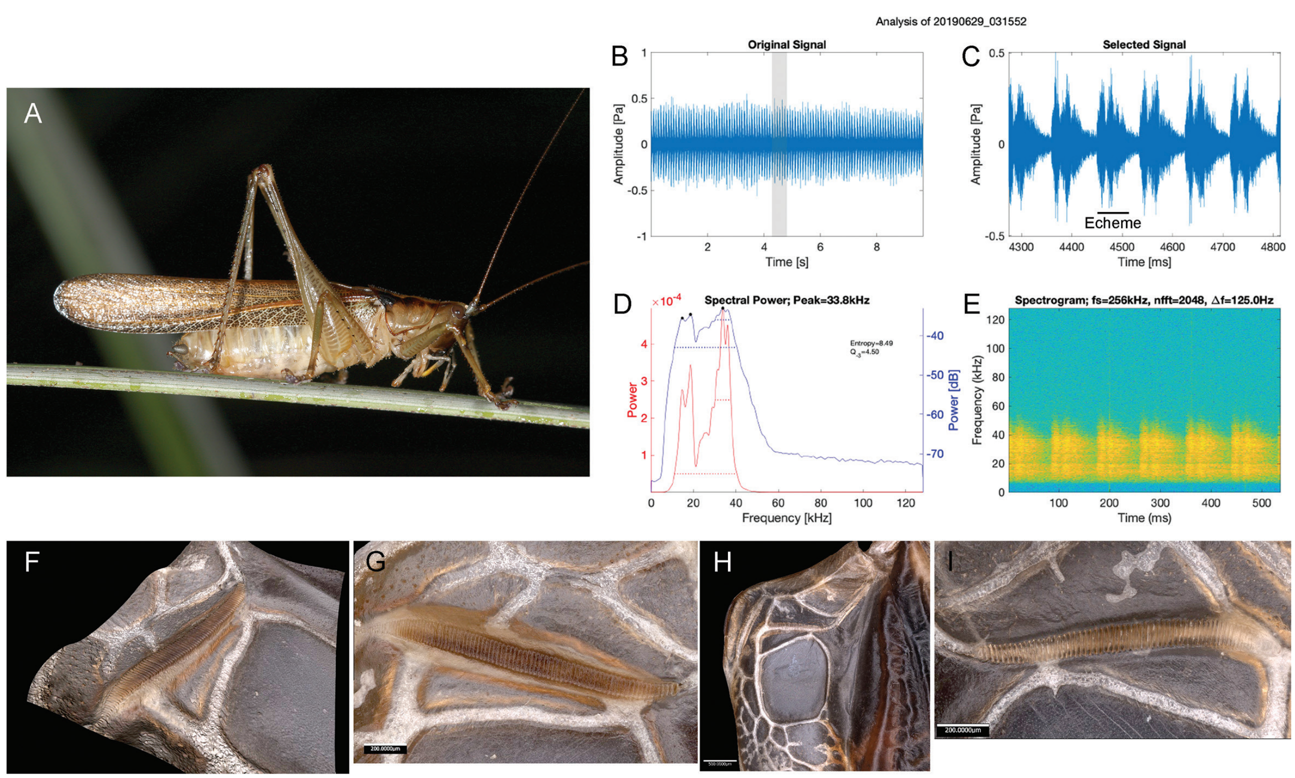

Fig. 1. *Axylus philippinus* male adult in its natural environment in Laguna, the Philippines (**A**). Oscillograms showing a continuous trill (**B**) and a section of the trill consisting of five complete echemes (**C**). Power spectrum (**D**) and spectrogram of the selection (**E**) of the same five complete echemes. 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 ventral view of the right SF (**I**).

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

Ventrally, the left micropterous tegmen possesses a stridulatory file of about 0.988 mm in length with about 56 teeth. The stridulatory file on the left tegmen is primarily straight and strongly curving anteriorly at the basal end. The teeth at the anal end are the smallest (average tooth width is 13.4 µm) and closely packed (average inter-tooth distance is 9.2 µm); the teeth in the mid-part of the file are the largest (average tooth width is 35.7 µm) with an average inter-tooth distance of 26.0 µm. The teeth at the basal end have an average tooth width of 30.5 µm and are most widely spaced apart (average inter-tooth distance is 31.8 µm). The file (Cu2) is only slightly elevated on a swollen vein buttress. The right tegmen has an oblique mirror longer than broad, with the anal margin distinctly shorter than the basal margin. The stridulatory file on the right tegmen is sinusoidal, about 0.802 mm in length, and with about 37 stout teeth.

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

Ventrally, the left macropterous tegmen possesses a stridulatory file of about 1.761 mm in length with about 60 stout teeth and a few indistinct ones at the anal end. The stridulatory file on the left tegmen is faintly curved and strongly curving anteriorly at the basal end. The teeth are smallest (average tooth width is 38.3 µm) and closely packed (average inter-tooth distance is 18.1 µm) at the anal end and 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 buttress. The right tegmen has a distinctly elongated mirror. The stridulatory file on the right tegmen is about 1.217 mm in length with approximately 51 stout teeth.

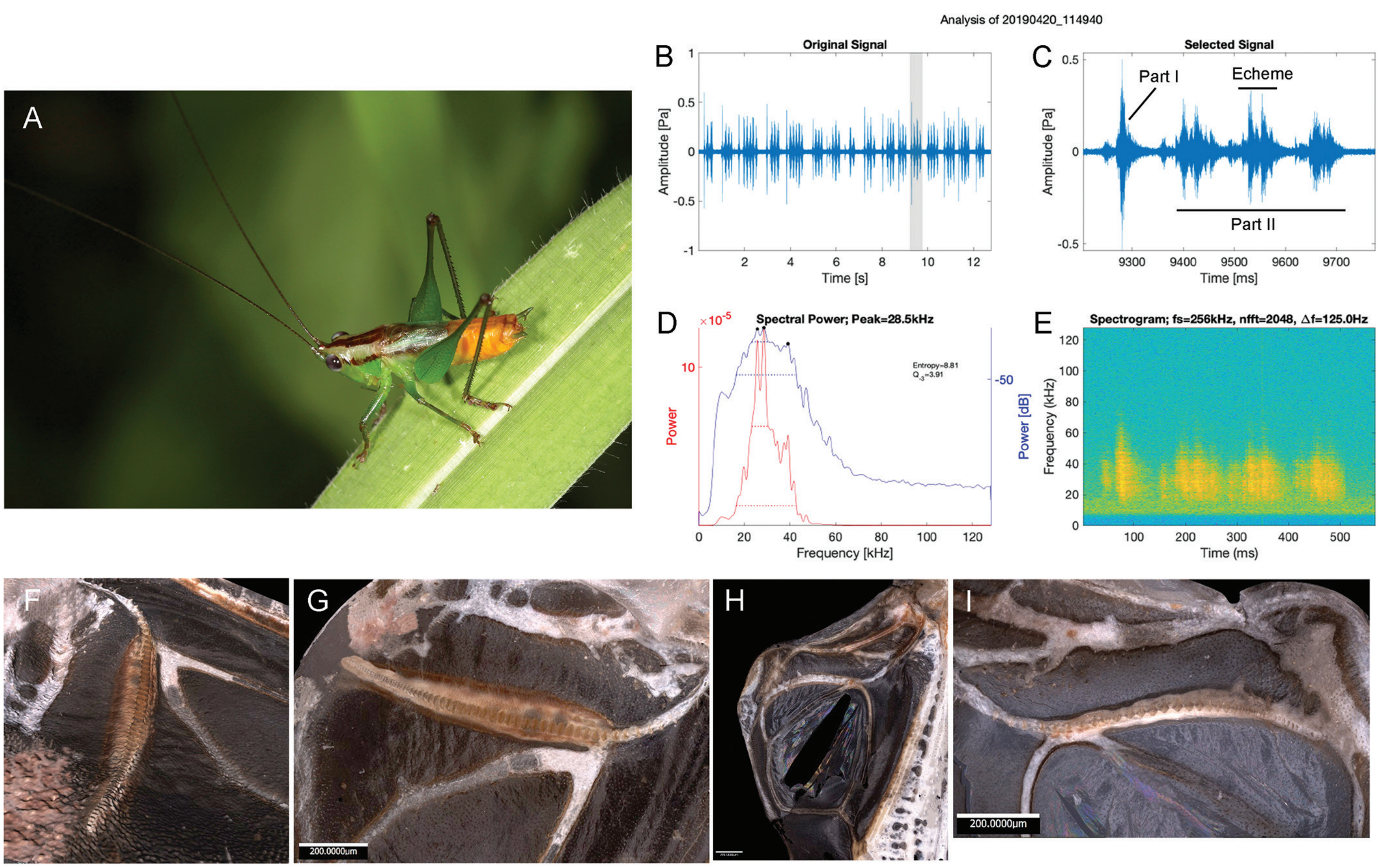

Fig. 2. *Conocephalus cognatus* male adult in its natural environment in Singapore (**A**). Oscillograms showing an echeme sequence (**B**) and a complex echeme with two parts (**C**). Power spectrum (**D**) and spectrogram (**E**) of an echeme made up of two parts. Three-dimensional anal view of the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

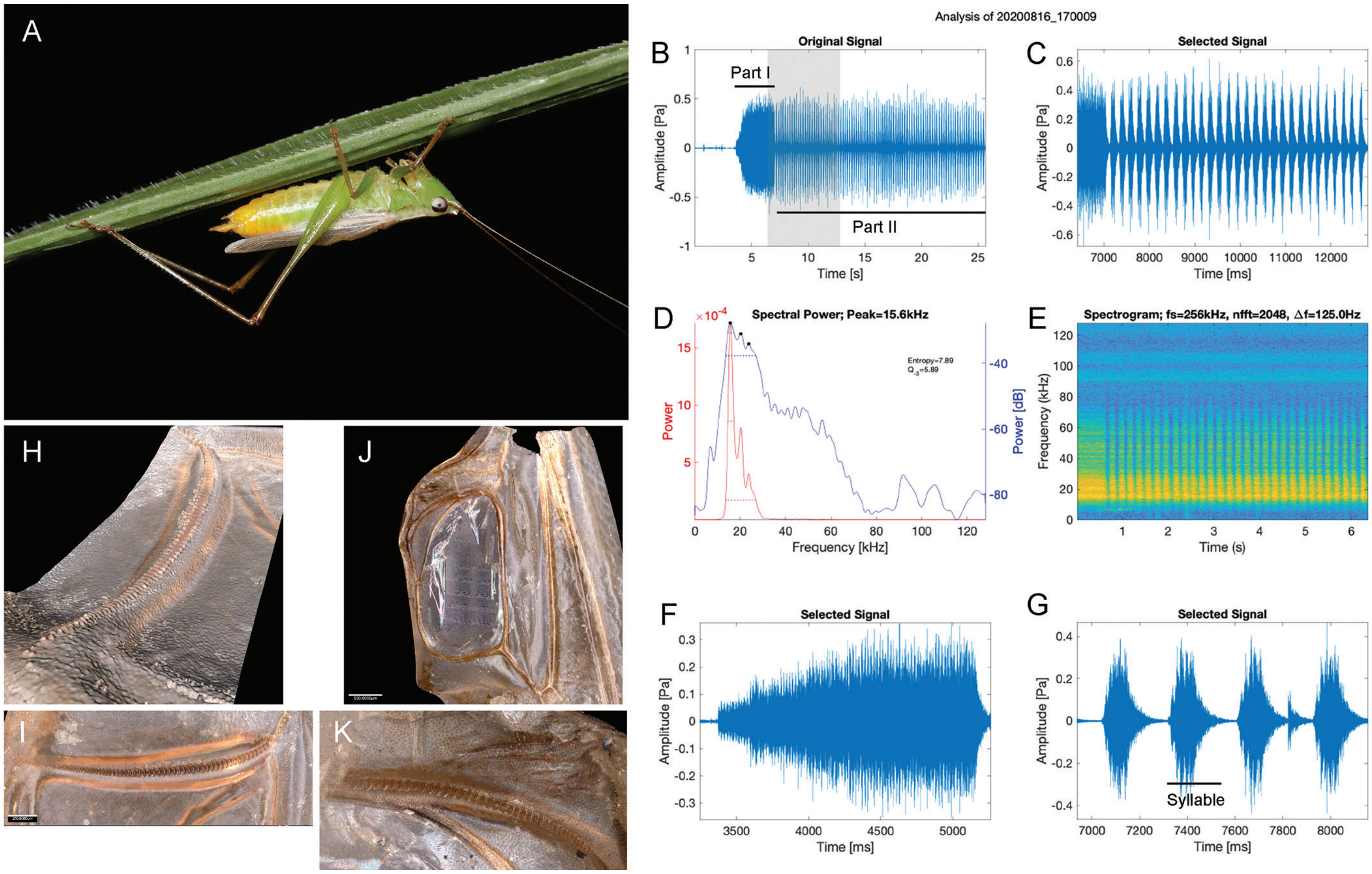

Fig. 3. *Conocephalus exemptus* male adult in its natural environment in Singapore (**A**). Oscillograms showing the start of a complex echeme (**B**) and a section of the echeme at the end of the first part and the beginning of the second part (**C**). Power spectrum (**D**) and spectrogram (**E**)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

Paragraecia temasek **Tan & Ingrisch, 2014** (n = 1 male, 20 sound files) (Fig. 4): The calling song consists of isolated echemes, but sometimes two to four echemes may aggregate 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 echeme shows a series of syllables with increasing amplitude to a maximum. Each echeme has a syllable repetition rate of ca. 89 syllables s^{-1} (87–91 syllables s^{-1}). The interval between echemes is also variable, ranging from 0.13 s to 2.6 s (0.63±0.58 s). Unlike many of the other katydids discussed here, a harmonic series consisting of three peaks was recorded: fundamental frequency, which is also the peak frequency of 12.6±0.1 kHz (12.4–12.8 kHz) at the sonic range, followed by peaks of 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 ultrasonic range. The call spectrum has a spectral entropy of 7.7±0.1.

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

Peracca macritchiensis **Tan & Ingrisch, 2014** (n = 1 male, 10 sound files) (Fig. 5): The calling song consists of an 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 and 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 toward 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 with a narrower anterior end.

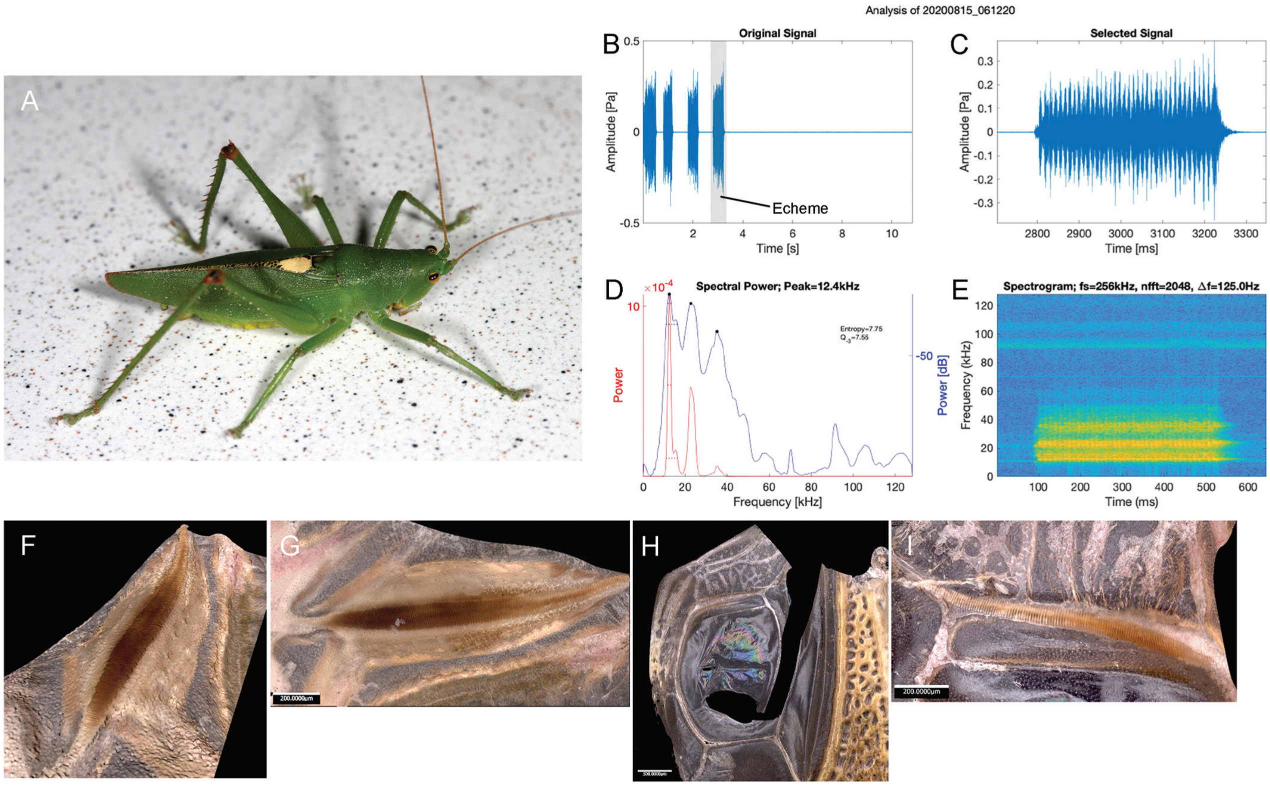

Fig. 4. *Paragraecia temasek* male adult in the lab (**A**). Oscillograms showing four echemes (**B**) and a single echeme (**C**). Power spectrum (**D**) and spectrogram of the same echeme (**E**). Three-dimensional anal view of the left stridulatory file (SF) (**F**), ventral view of the same SF (**G**),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

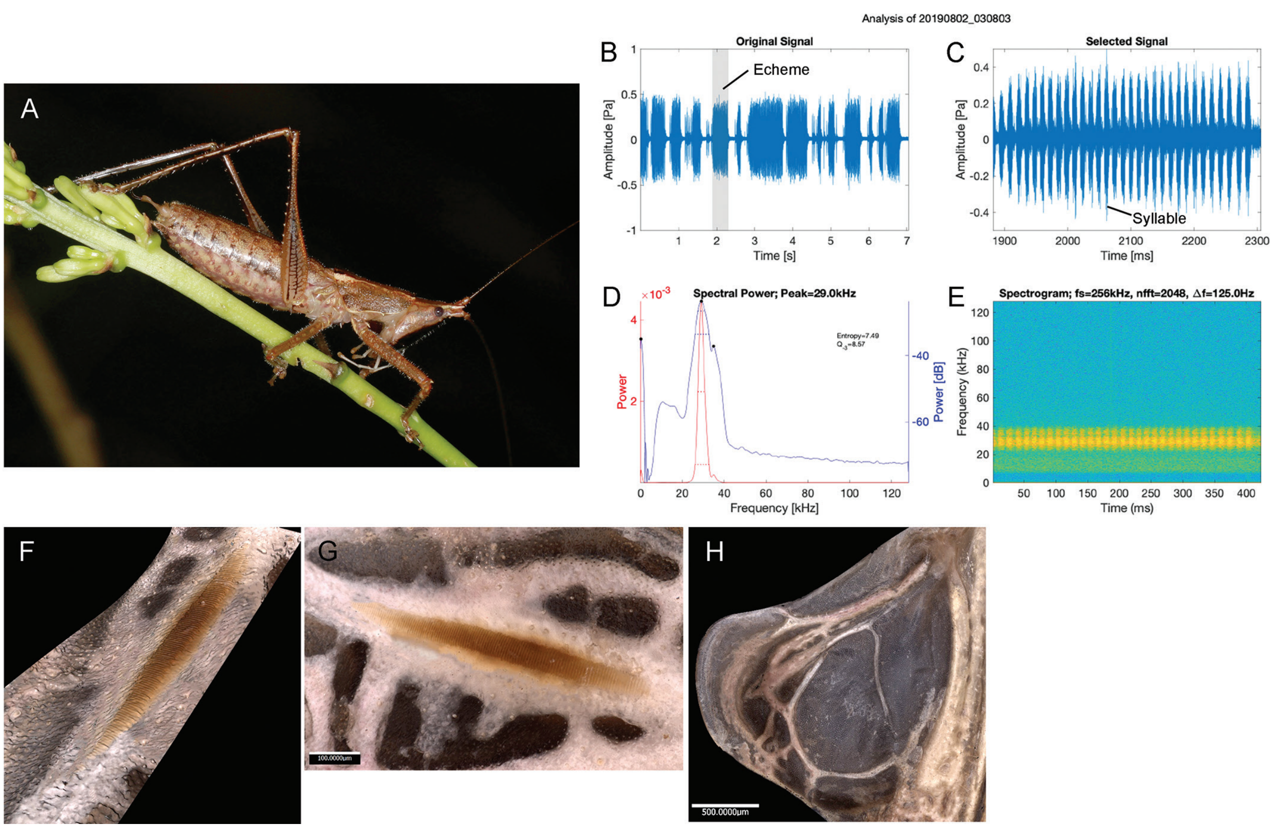

Fig. 5. *Peracca macritchiensis* male adult in its natural environment in Singapore (**A**). Oscillograms showing an echeme sequence (**B**) and a single echeme (**C**). Power spectrum (**D**) and spectrogram of the same echeme (**E**). Three-dimensional anal view of the left stridulatory file (SF) (**F**), 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; 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 toward the ends. The distance between teeth is fairly uniform. The file (Cu2) is slightly elevated on a faintly swollen vein buttress. The right tegmen has a squarish mirror. The stridulatory file on the right tegmen is sinusoidal, with a length of about 2.409 mm and with about 65 rather broad teeth.

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 a long duration as a trill or a shorter duration as echemes. At 28.2±1.6°C (26.7–30.5°C), the syllable has a 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 μm), and tooth width tapers gently toward 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 slightly swollen vein buttress. The right tegmen has a somewhat squarish mirror but slightly broader than long. The stridulatory file on the right tegmen is about 1.615 mm in length with about 69 rather broad teeth.

Viriacca insularis **Gorochov, 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 a long duration as a continuous trill. Each echeme has a syllable repetition rate of 22±1 syllables s^{-1} (21–26 syllables s^{-1}) at 28.5±0.4°C (27.7–29.7°C). The call spectrum has a peak frequency of 23.1±1.8 kHz (21.5–28.5 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 toward

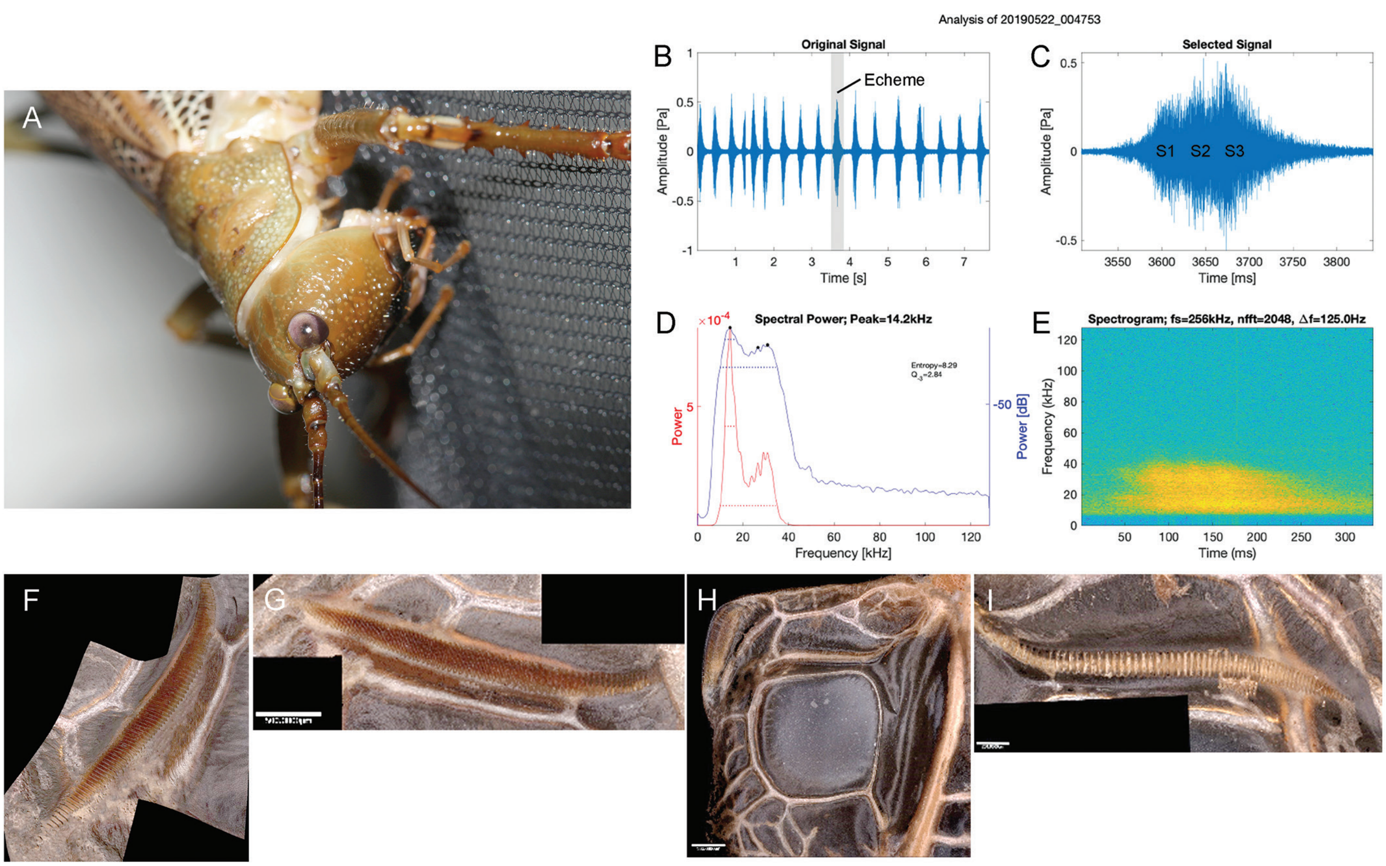

Fig. 6. *Salomona borneensis* male adult in the lab (**A**). Oscillograms showing an echeme sequence with 17 echemes (**B**) and an echeme with three syllables denoted as S1 to S3 (**C**). Power spectrum (**D**) and spectrogram of the same echeme (**E**). Three-dimensional anal view of the left stridulatory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

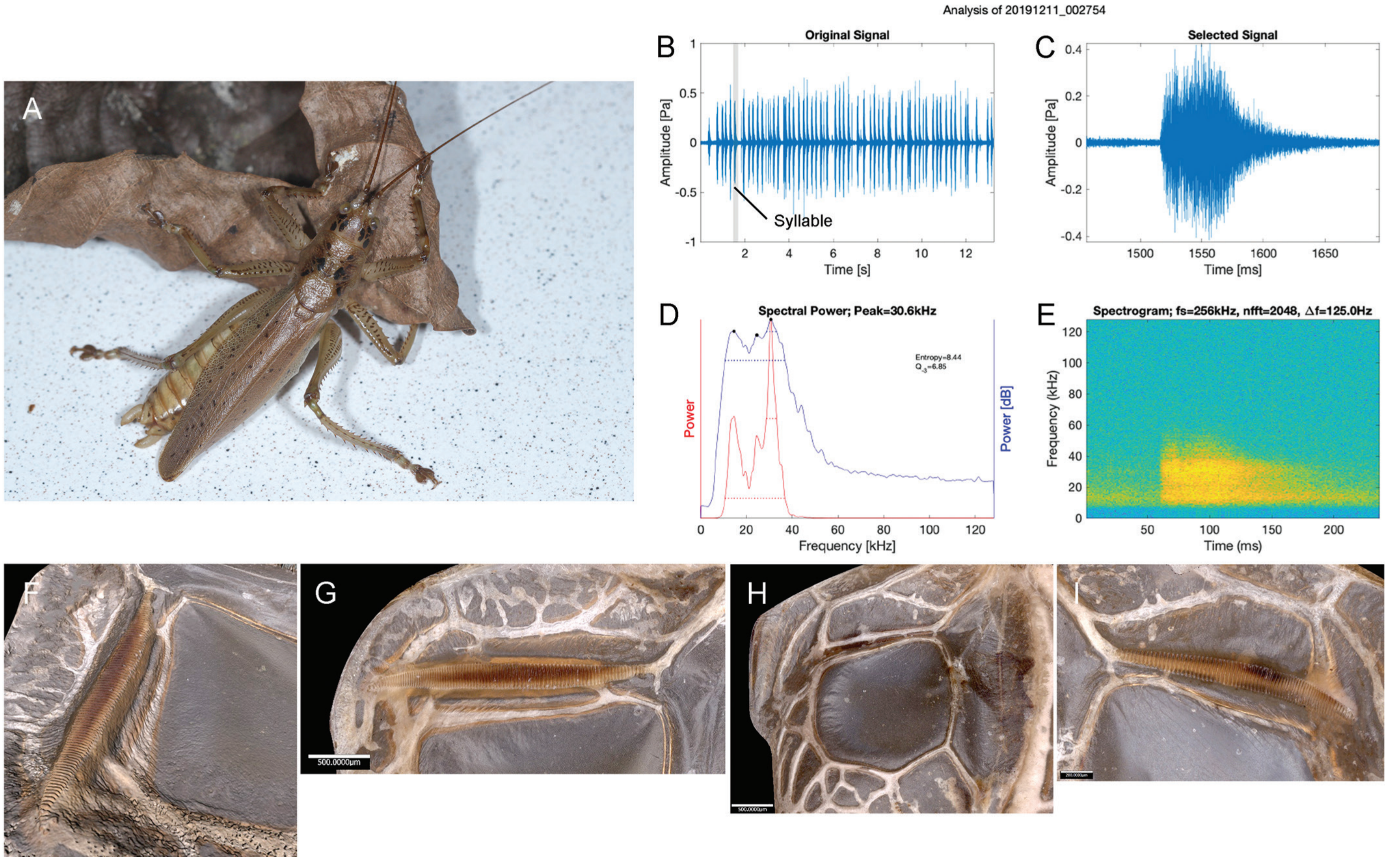

Fig. 7. *Salomona maculifrons* male adult in the lab (**A**). Oscillograms showing a continuous trill (**B**) and a syllable (**C**). Power spectrum (**D**) and spectrogram of the same syllable (**E**). Three-dimensional anal view of the left stridulatory file (SF) (**F**), ventral view of the same SF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

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 a somewhat triangular mirror with anterior margin rounded and posterior end acute, longer than broad. The stridulatory file on the right tegmen is about 0.984 mm in length with about 100 rather broad teeth.

Viriacca modesta **Gorochov, 2013** (n = 2 males, 13 sound files) (Fig. 9): The calling song is a 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 (016–0.31 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 µm), and tooth width tapers gently toward the ends. The teeth are closely packed, and the distance between teeth is fairly uniform. 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 a rectangular mirror longer than broad, with anterior margin broader and rounded and with posterior margin truncated and narrower. The stridulatory file on the right tegmen is about 1.072 mm in length, with about 112 rather broad teeth.

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 echemes of 120–190 ms. We recorded another individual from Mandai (also Singapore) using an 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 typically consists of 4 (3–5) closely packed syllables. 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 of 20.7 µm and an average inter-tooth distance is 27.8 µm. The file (Cu2) is strongly elevated at the anal end and on a very swollen vein buttress (especially swollen at the anal end). The right tegmen has a triangular mirror. The stridulatory file on the right tegmen is slightly sinusoidal, about 1.176 mm in length, with about 33 stout teeth and a few indistinct teeth at both ends.

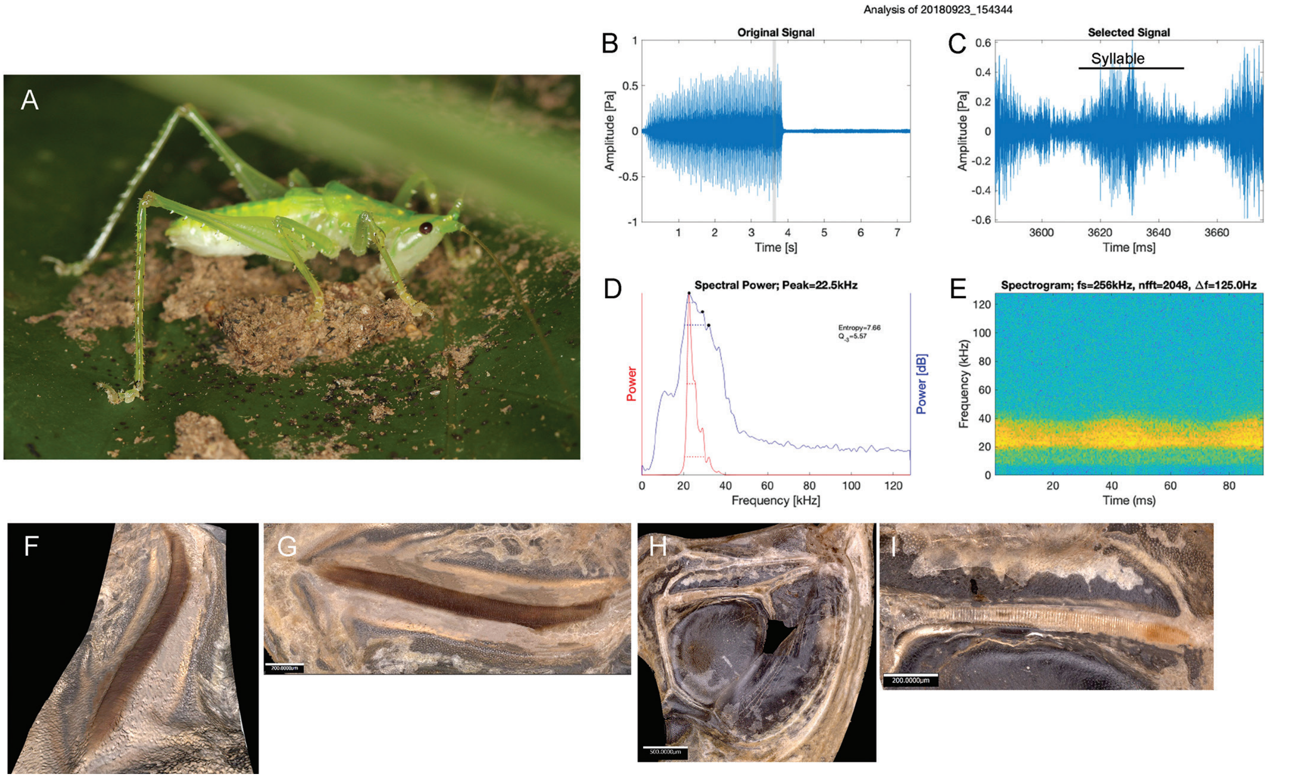

Fig. 8. *Viriacca insularis* male adult in its natural environment in Pulau Tioman, Malaysia (**A**). Oscillograms showing an echeme (**B**) and a syllable (**C**). Power spectrum (**D**) and spectrogram of the same syllable (**E**). Three-dimensional anal view of the left stridulatory file (SF) (**F**),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

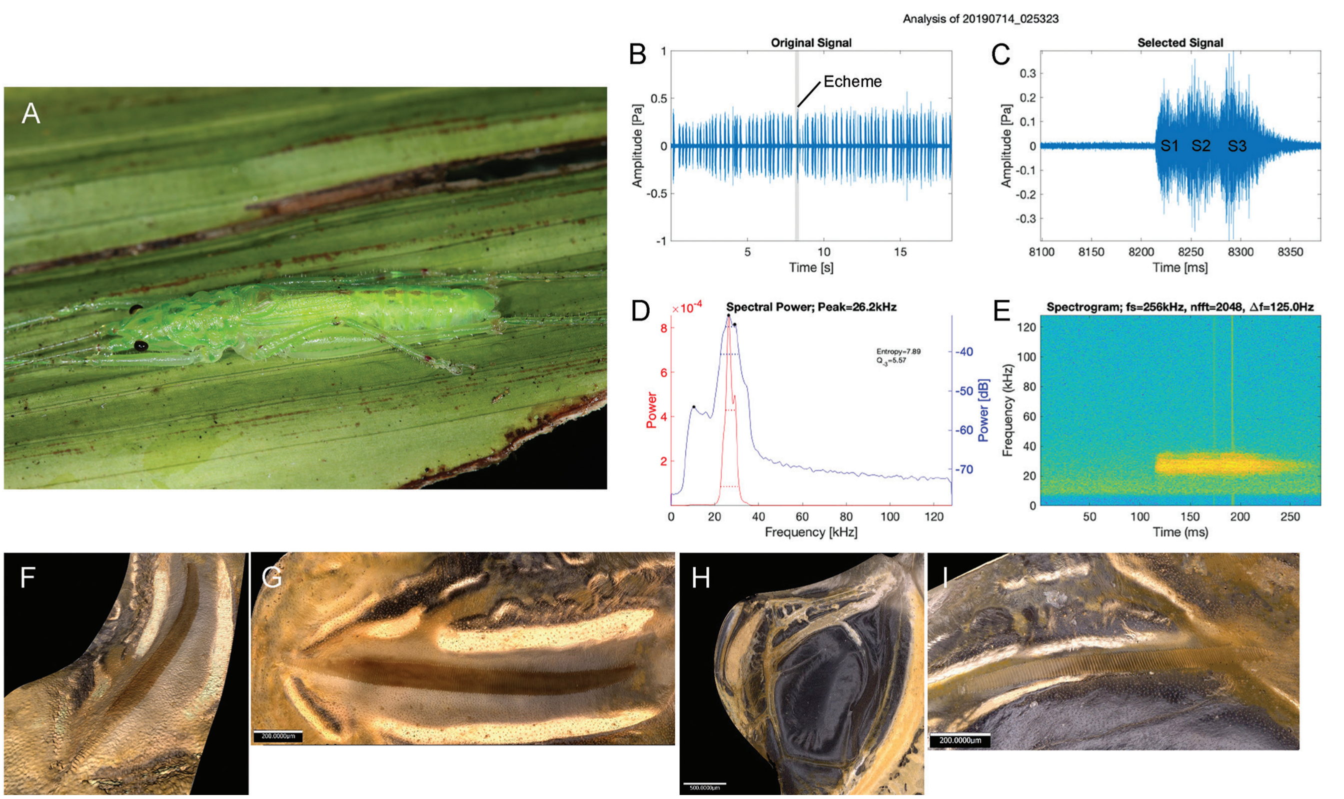

Fig. 9. *Viriacca modesta* male adult in its natural environment in Belait, Brunei Darussalam (**A**). Oscillograms showing a continuous echeme sequence (**B**) and an echeme with three syllables denoted as S1 to S3 (**C**). Power spectrum (**D**) and spectrogram of the same echeme (**E**). Three-dimensional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

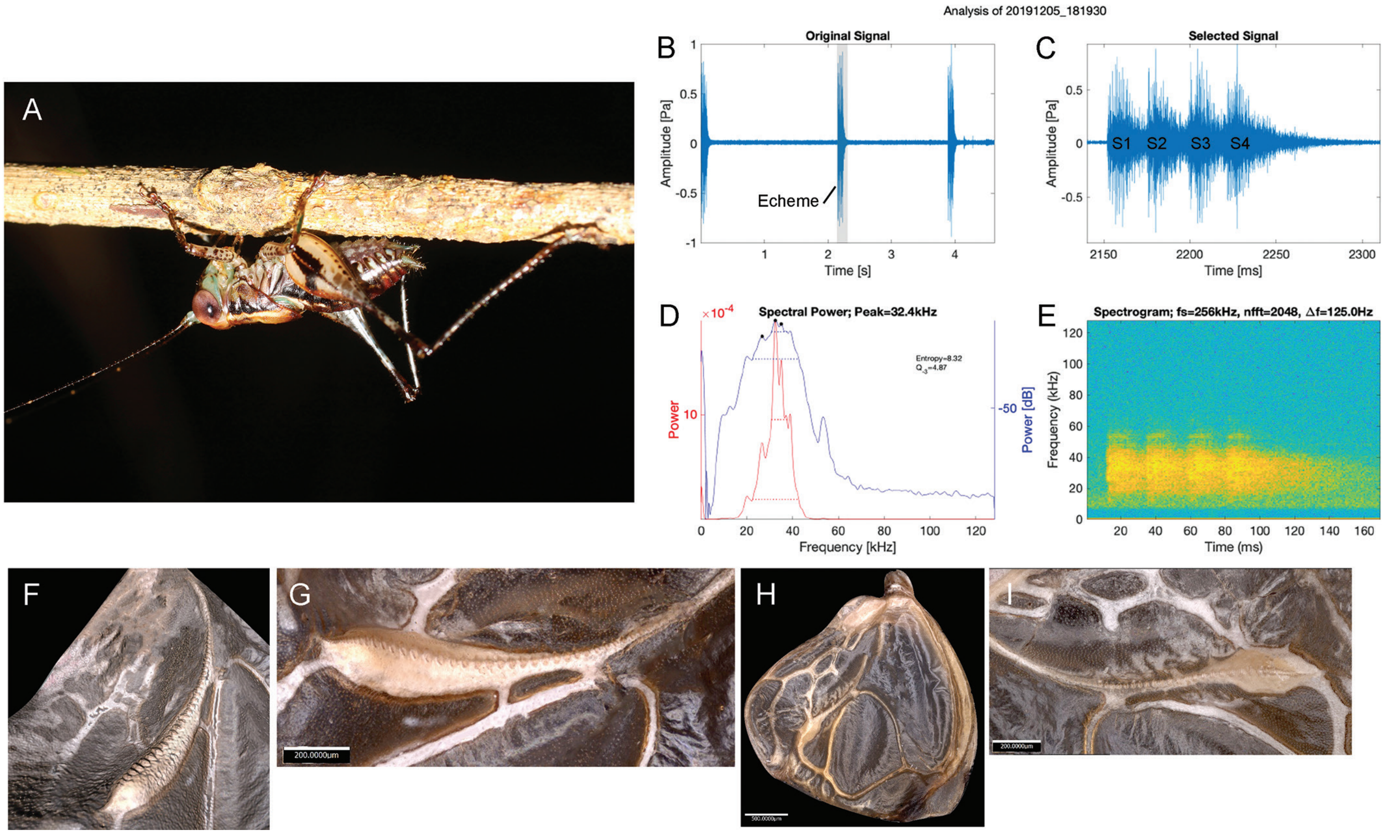

Fig. 10. *Lipotactes maculatus* male adult in its natural environment in Singapore (**A**). Oscillograms showing three isolated echemes (**B**) and an echeme with four syllables denoted as S1 to S4 (**C**). Power spectrum (**D**) and spectrogram of the same echeme (**E**). Three-dimensional anal view 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 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 comprised of a few isolated syllables, and the second part is a echeme 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 a 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 echeme duration is 1.21±0.40 s (0.39–1.75 s), is made of 29±8 (7–35) closely spaced syllables, and the syllable repetition rate is 20±1 syllables s^{-1} (18–22 syllables s^{-1}). The second song mode consists of only 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.

***Borneopsis cryptosticta* (Hebard, 1922)** (n = 2 males, 17 sound files) (Fig. 12): Two modes of calling songs were recorded. The first and most 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 a duration of 61.2±6.8 ms (50.1–71.1 ms) and a 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 echemes of at least 6–8 syllables closely spaced together, with an 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.

***Euanisous teuthroides* (Bolívar, 1905)** (n = 1 male, 13 sound files) (Fig. 13): The calling song consists of echemes that can be highly variable in duration and exhibit frequency modulation. At 29.7±0.3°C (29.4–30.3°C), the 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 plateaus. 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 the 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 m), and they are generally widely spaced (average inter-tooth distance is 36.1 μm). The file (Cu2) is elevated on a slightly 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 stridulatory file on the right tegmen is about 0.550 mm in length, with about 18 stout teeth.

***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 a repetition of syllables at a 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.

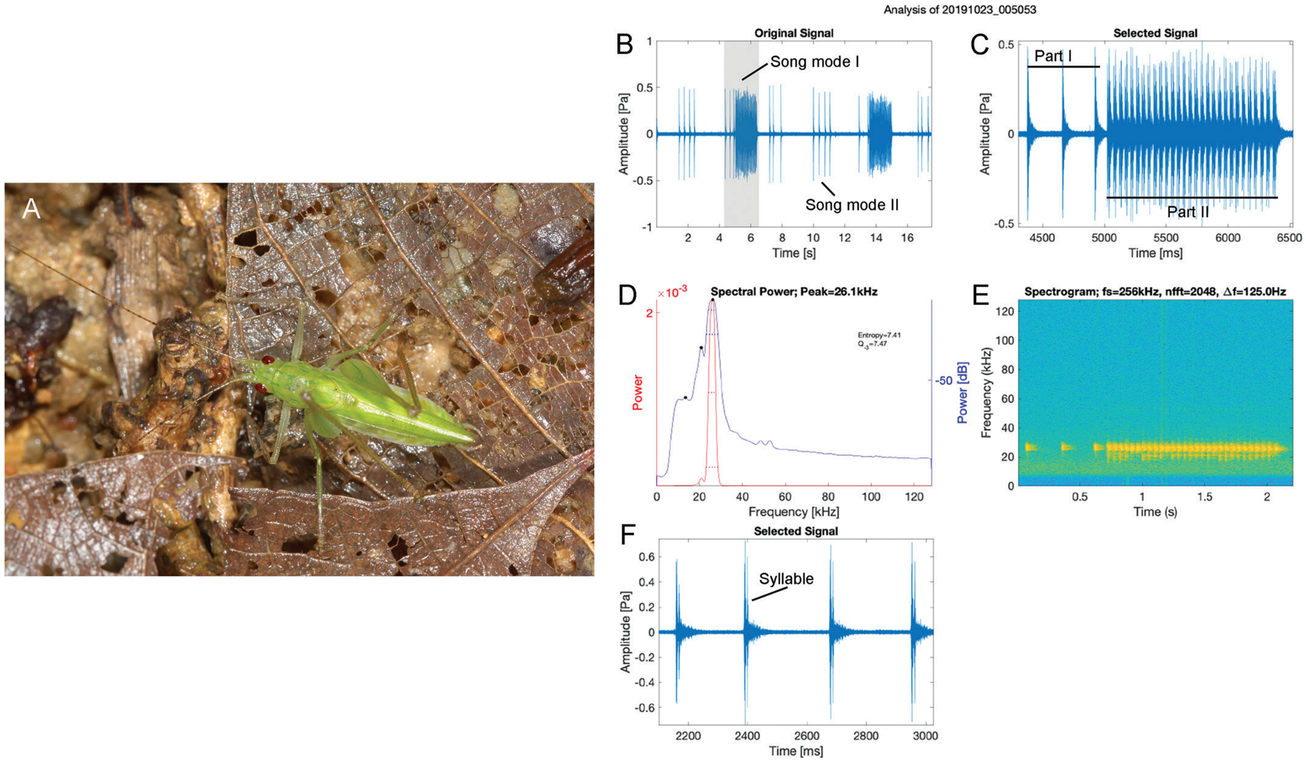

Fig. 11. *Alloteratura lamella* male adult in its natural environment in Singapore (**A**). Oscillograms showing a calling song consisting of both song modes (**B**) and a complex echeme consisting of three isolated syllables and a echeme (**C**). Power spectrum (**D**) and spectrogram of the same complex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

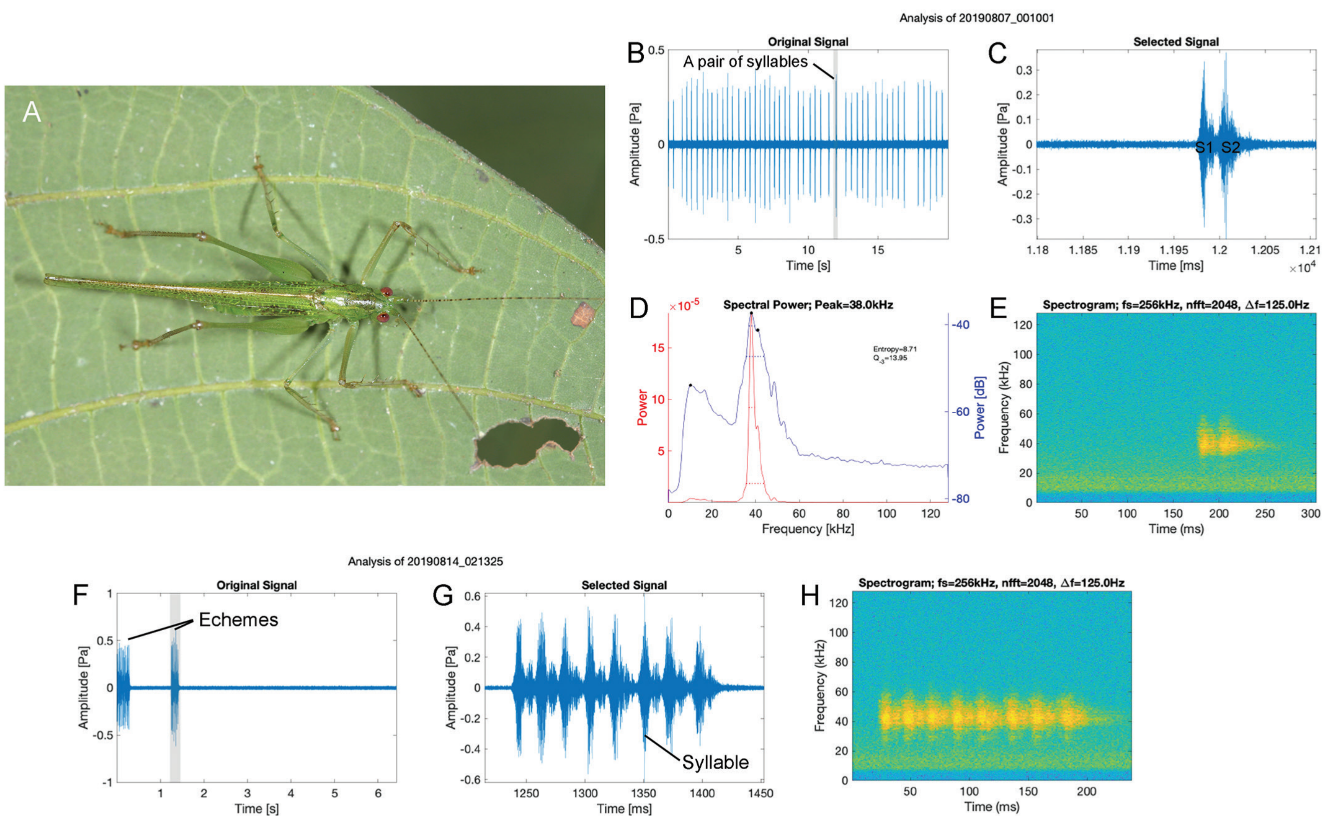

Fig. 12. *Borneopsis cryptosticta* male adult in its natural environment in Singapore (**A**). Oscillograms showing a doublet of syllables (**B**) and a doublet of syllables with the syllables denoted as S1 and S2 (**C**). Power spectrum (**D**) and spectrogram of the doublet of syllables (**E**). Oscillograms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

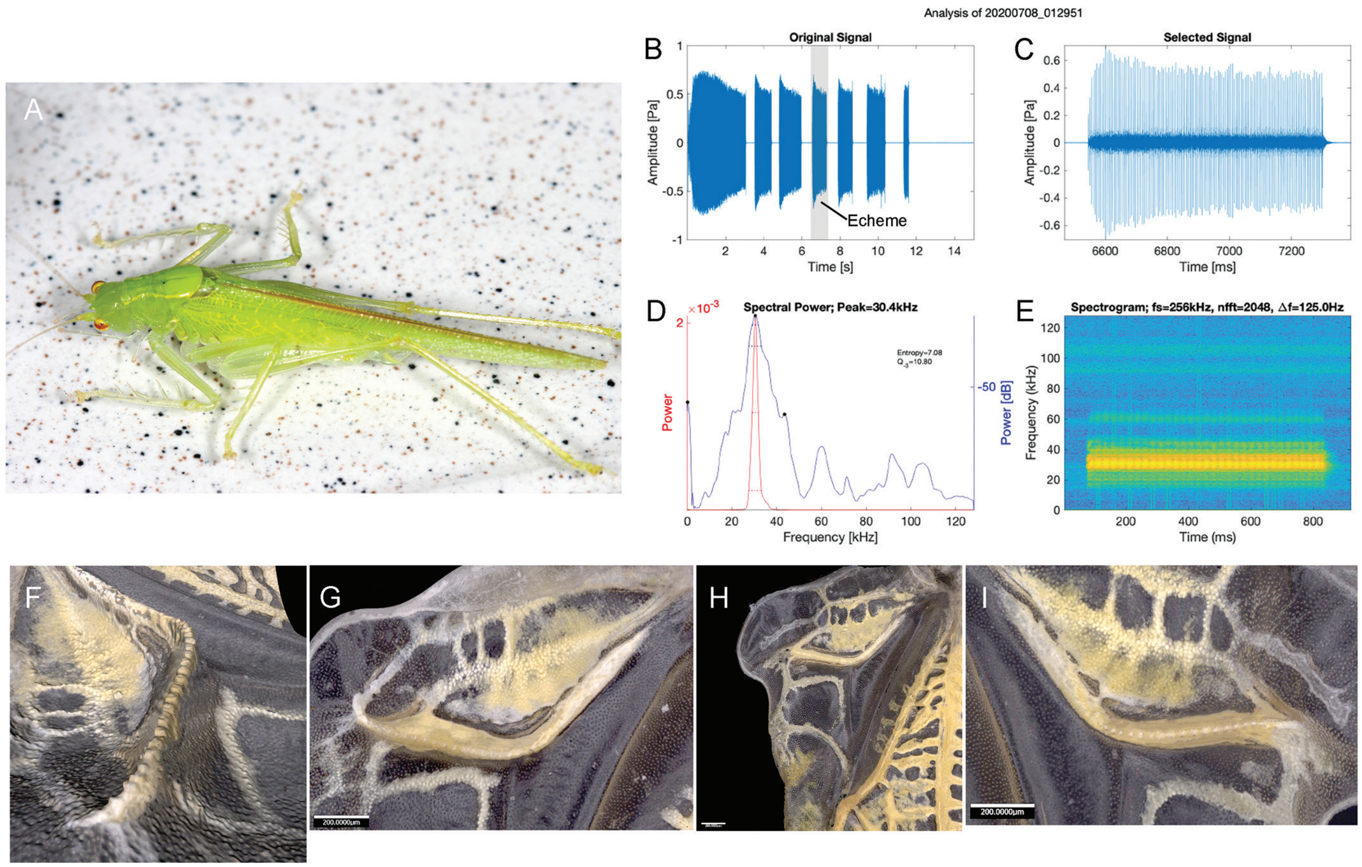

Fig. 13. *Euanisous teuthroides* male adult in the lab (**A**). Oscillograms showing seven echemes of varying duration (**B**) and a single echeme (**C**). Power spectrum (**D**) and spectrogram of the same echeme (**E**). Three-dimensional anal view of the left stridulatory file (SF) (**F**), ventral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

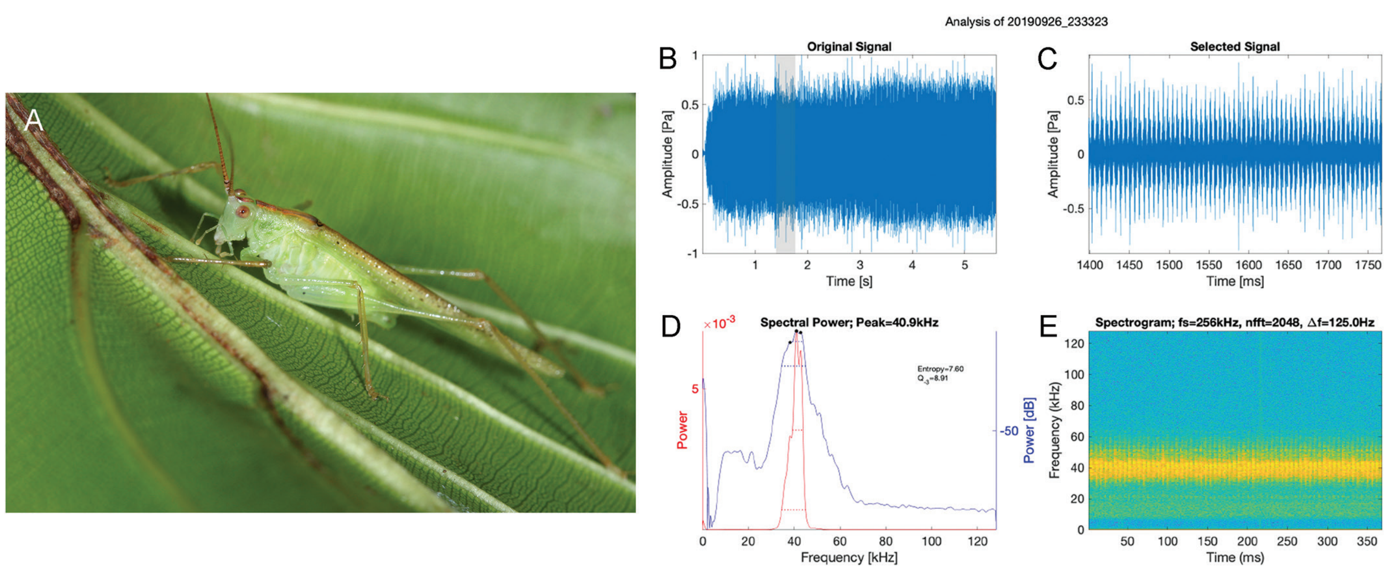

Fig. 14. *Kuzicus denticulatus* male adult in its natural environment in Singapore (**A**). Oscillograms showing a continuous trill (**B**) and closer view of the continuous trill (**C**). Power spectrum (**D**) and spectrogram of the closer view of the continuous trill (**E**).

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), and the 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.

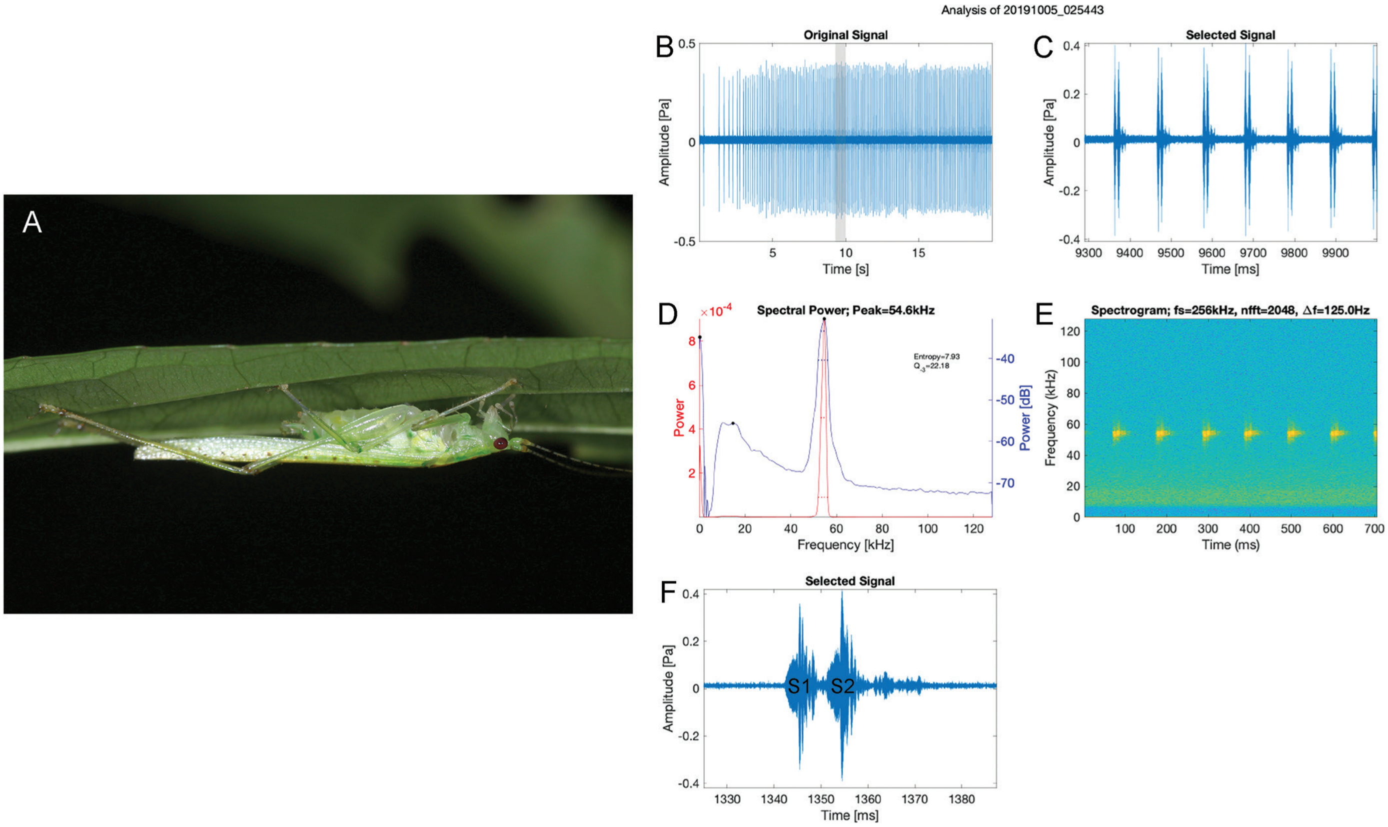

Fig. 15. Meconematini (Sandakan) male adult in its natural environment in Sandakan, Malaysia (**A**). Oscillograms showing a continuous trill (**B**) and a section of the trill with six complete doublets of syllables (**C**). Power spectrum (**D**) and spectrogram of the same six complete doublets of 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.

Xiphidiopsis **(*Xiphidiopsis*)** ***dicera*** **Hebard, 1922** (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) and 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.

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 a duration of 0.36±0.04 s (0.27–0.44 s) and is made up of 24±3 (16–27) pulses of gradually increasing 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 µm), and tooth width tapers gently toward 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 stridulatory file on the right tegmen is about 1.323 mm in length with relatively stout teeth.

Casigneta **sp. 2** (n = 1 male, 19 sound files) (Fig. 19): The calling song appears to consist of isolated syllables, each containing three pulses. At 29.8±0.5°C (28.7–30.1°C), each triple of pulses has a 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), and 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 µm), and tooth width tapers gently toward the ends. The teeth are closely packed, and the distance between teeth is fairly uniform. 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 stridulatory file on the right tegmen is about 0.913 mm in length, with about 52 teeth.

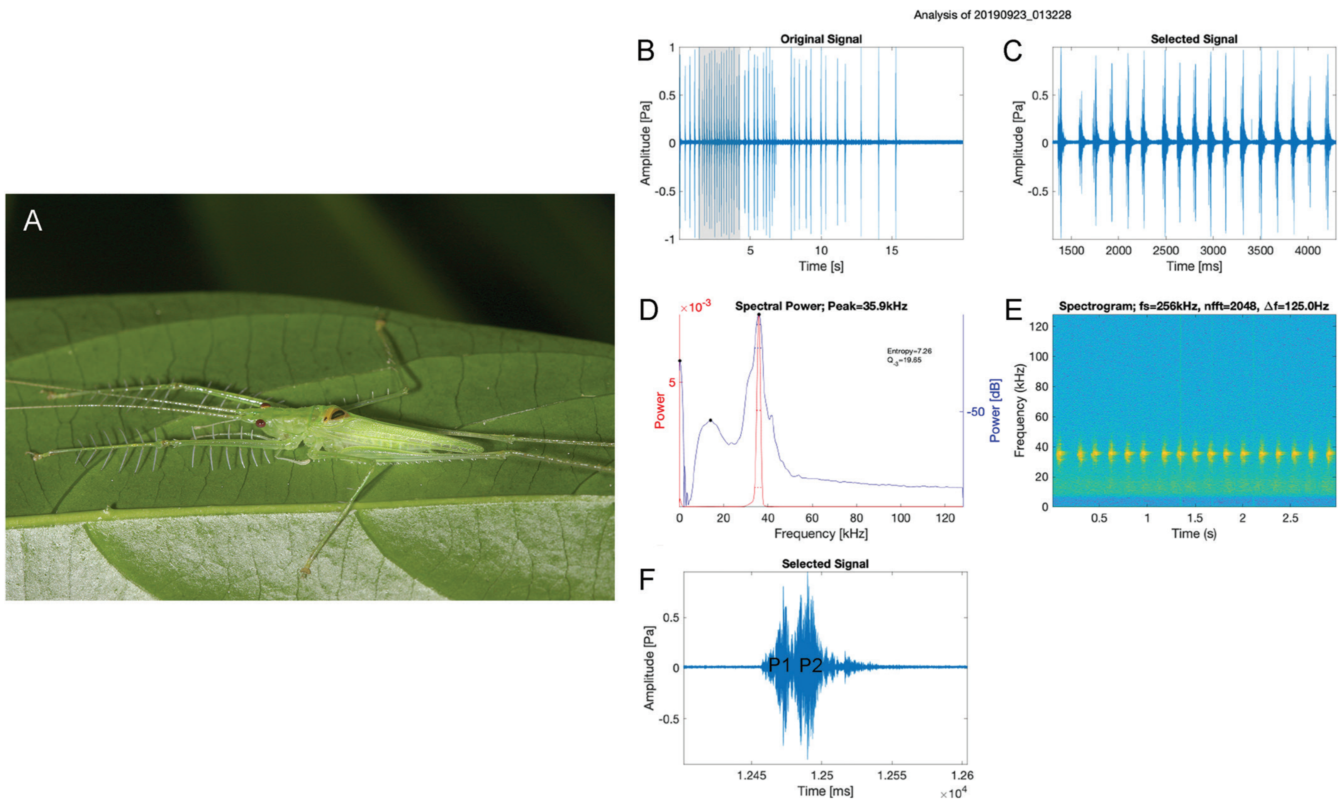

Fig. 16. *Neophisis siamensis* male adult in its natural environment in Singapore (**A**). Oscillograms showing a sequence of syllables (**B**) and a section of the sequence with 17 syllables (**C**). Power spectrum (**D**) and spectrogram of the 17 syllables (**E**). Oscillogram showing a single syllable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

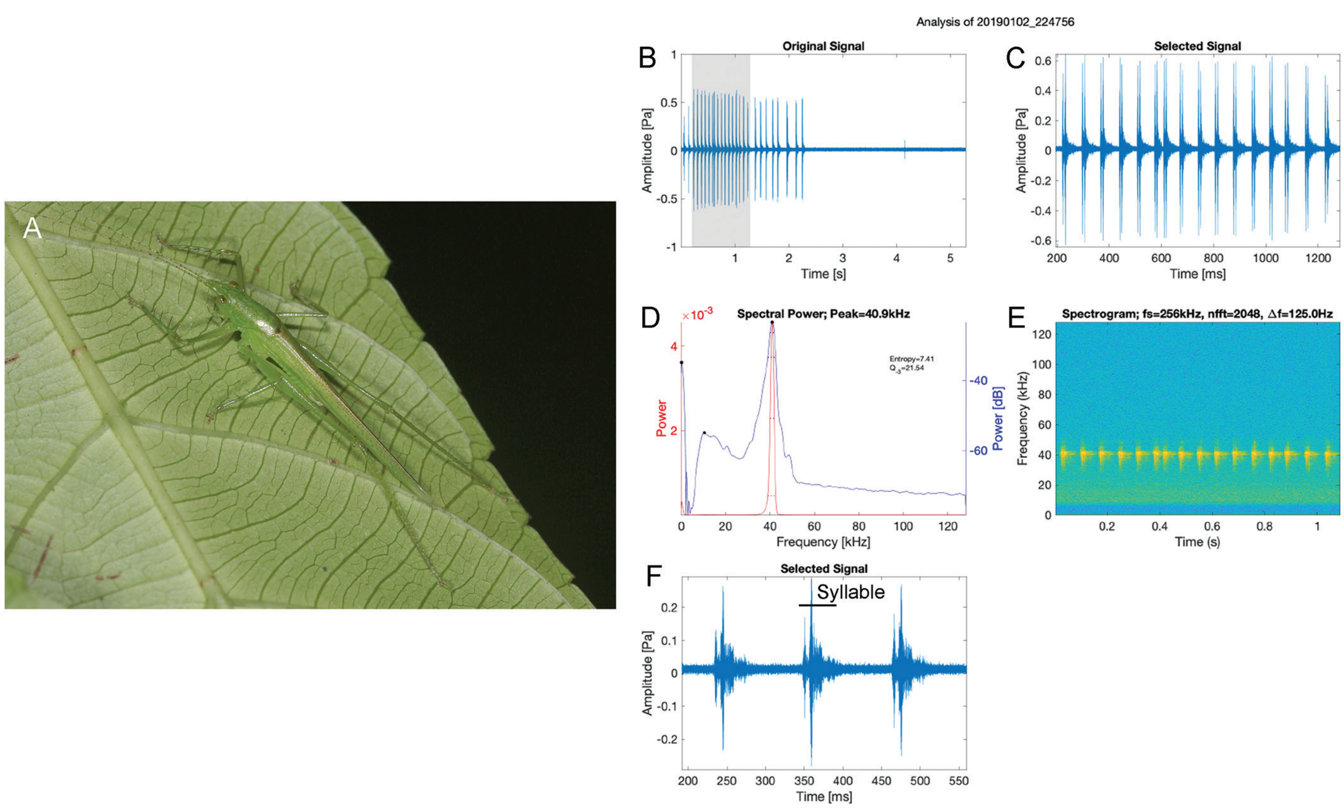

Fig. 17. *Xiphidiopsis* (*Xiphidiopsis*) *dicera* male adult in its natural environment in Singapore (**A**). Oscillograms showing a sequence of syllables (**B**) and a section of the trill with 16 syllables (**C**). Power spectrum (**D**) and spectrogram of the 16 syllables (**E**). Oscillogram showing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

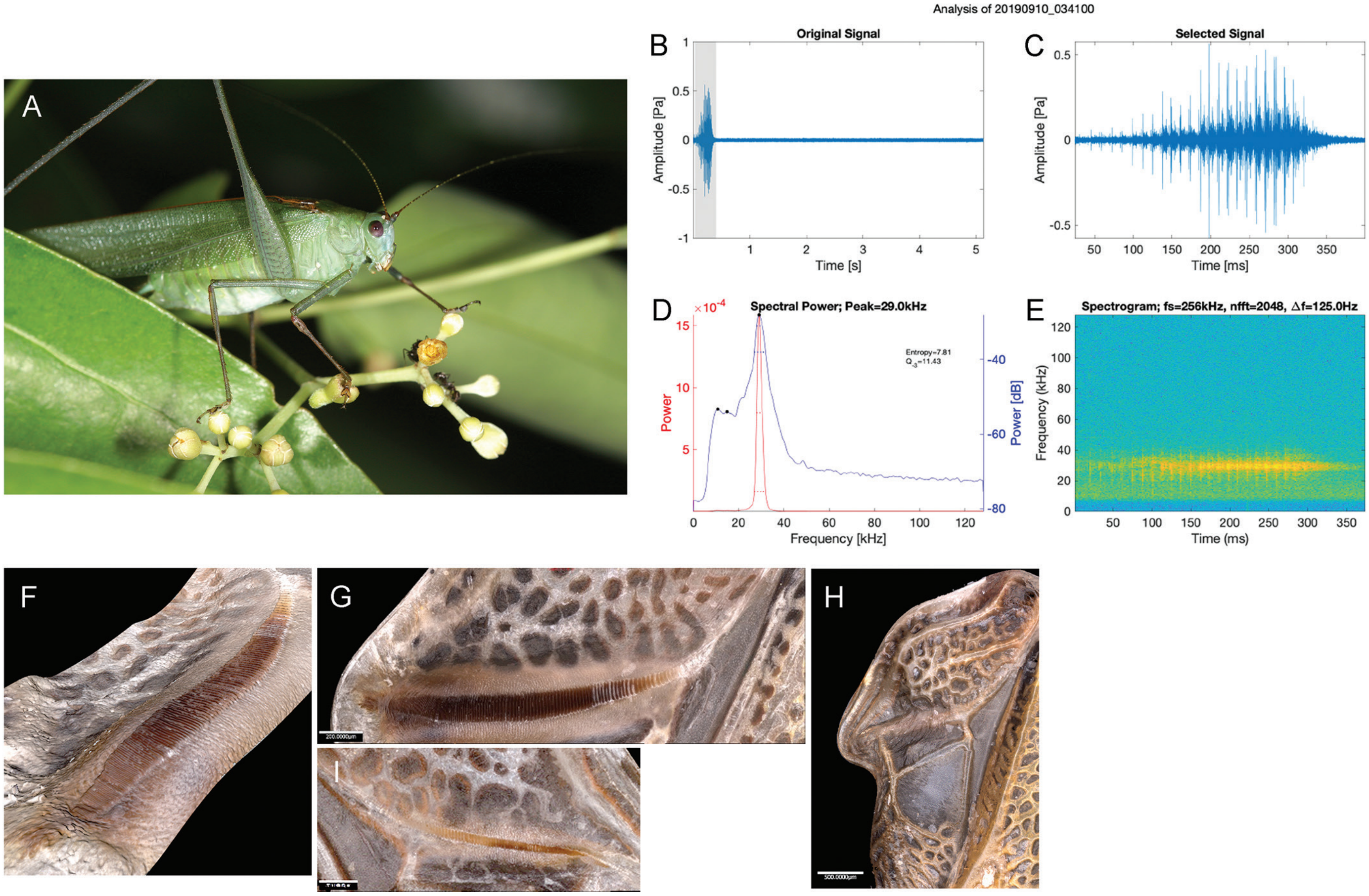

Fig. 18. *Casigneta* sp. 1 male adult in its natural environment in Singapore (**A**). Oscillograms showing a pulse train (**B**) and a closer view of the pulse train (**C**). Power spectrum (**D**) and spectrogram of the same pulse train (**E**). Three-dimensional anal view of the left stridulatory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

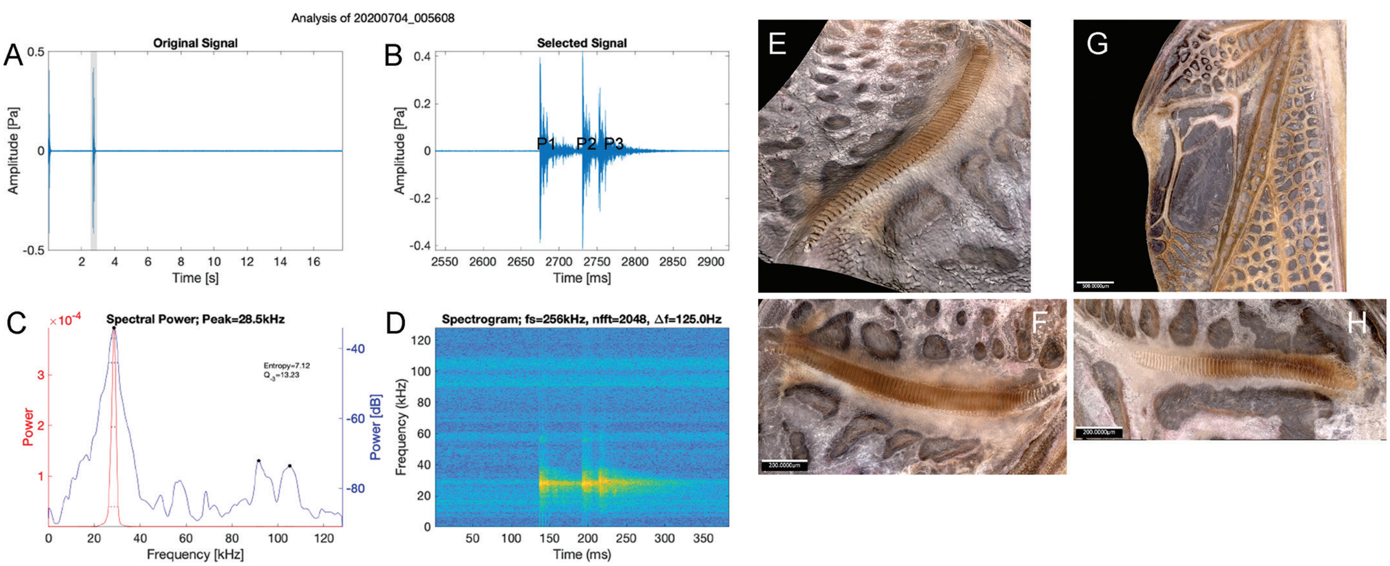

Fig. 19. *Casigneta* sp. 2. Oscillograms showing two triplets of pulses (**A**) and a triplet of pulses denoted as P1 to P3 (**B**). Power spectrum (**C**) and spectrogram of the same triplet of pulses (**D**). Three-dimensional anal view of the left stridulatory file (SF) (**E**), ventral view of the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

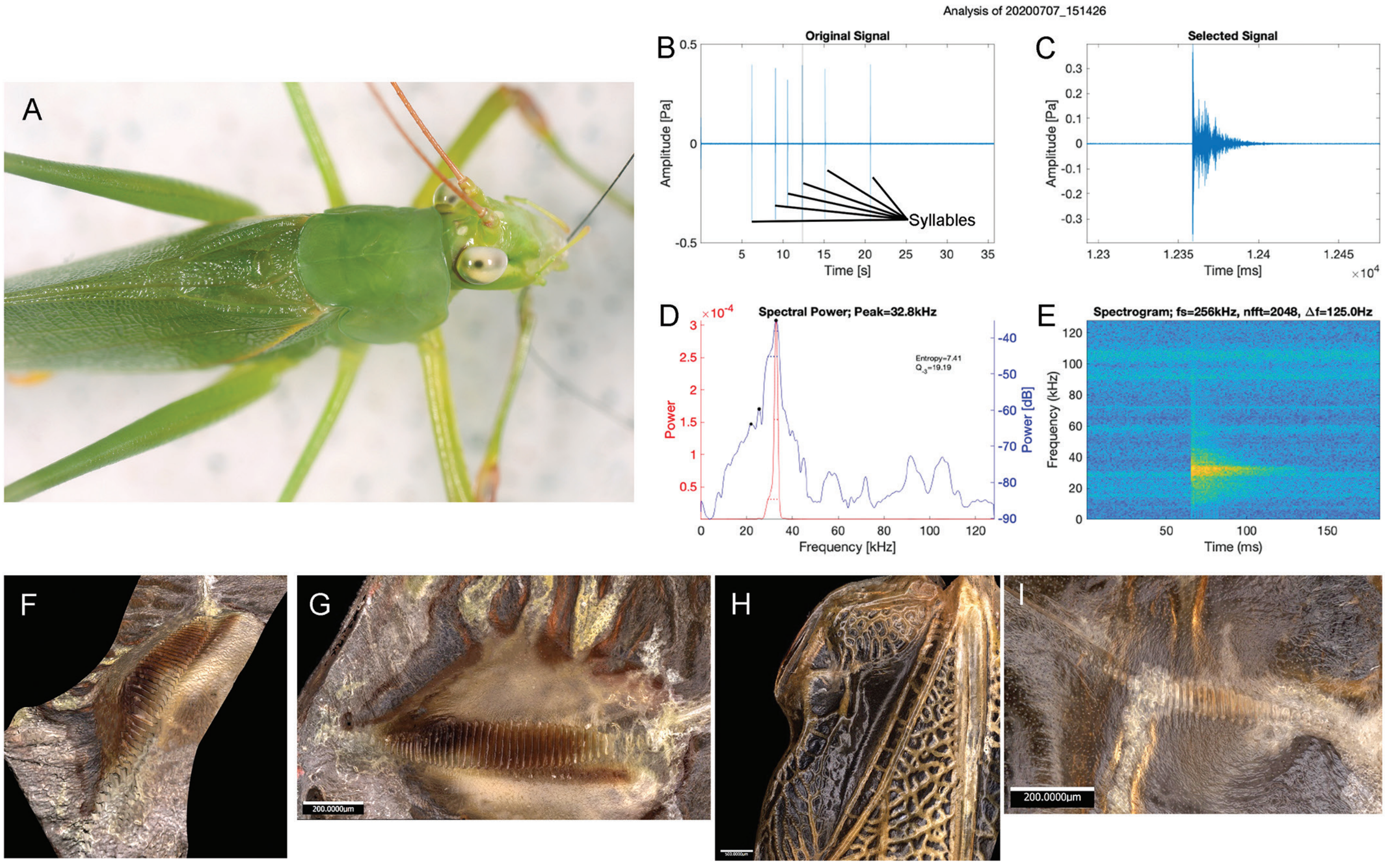

Fig. 20. *Holochlora* nr. *bilobata* male adult in the lab (**A**). Oscillograms showing six isolated syllables (**B**) and a closer view of a syllable (**C**). Power spectrum (**D**) and spectrogram of the same syllable (**E**). Three-dimensional anal view of the left stridulatory file (SF) (**F**),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

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 µm) and distinctly smaller at the ends (average tooth width is 38 µm). 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 elevated in the middle on a very swollen vein buttress. The right tegmen has a small rectangular mirror, somewhat obsolete. The stridulatory file on the right tegmen is about 0.633 mm in length with about 32 indistinct teeth.

***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, about 0.335 mm in length with about 24 smaller and stout (of uniform size and spacing) teeth. The average tooth width is 34 µm, and the teeth density is 65 teeth mm^{-1}. The main file is straight, about 1.263 mm in length with about 36 larger teeth. The teeth are largest in the middle portion (average tooth width is 86 µm) and distinctly smaller at the basal end (average tooth width is 52 µm). 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 slightly swollen vein buttress. The right tegmen has a large oblong mirror, distinctly longer than broad.

***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 two peaks in energy, typically with 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 µm), 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 faintly elevated in the middle on a swollen vein buttress. The right tegmen has a large mirror, longer than broad.

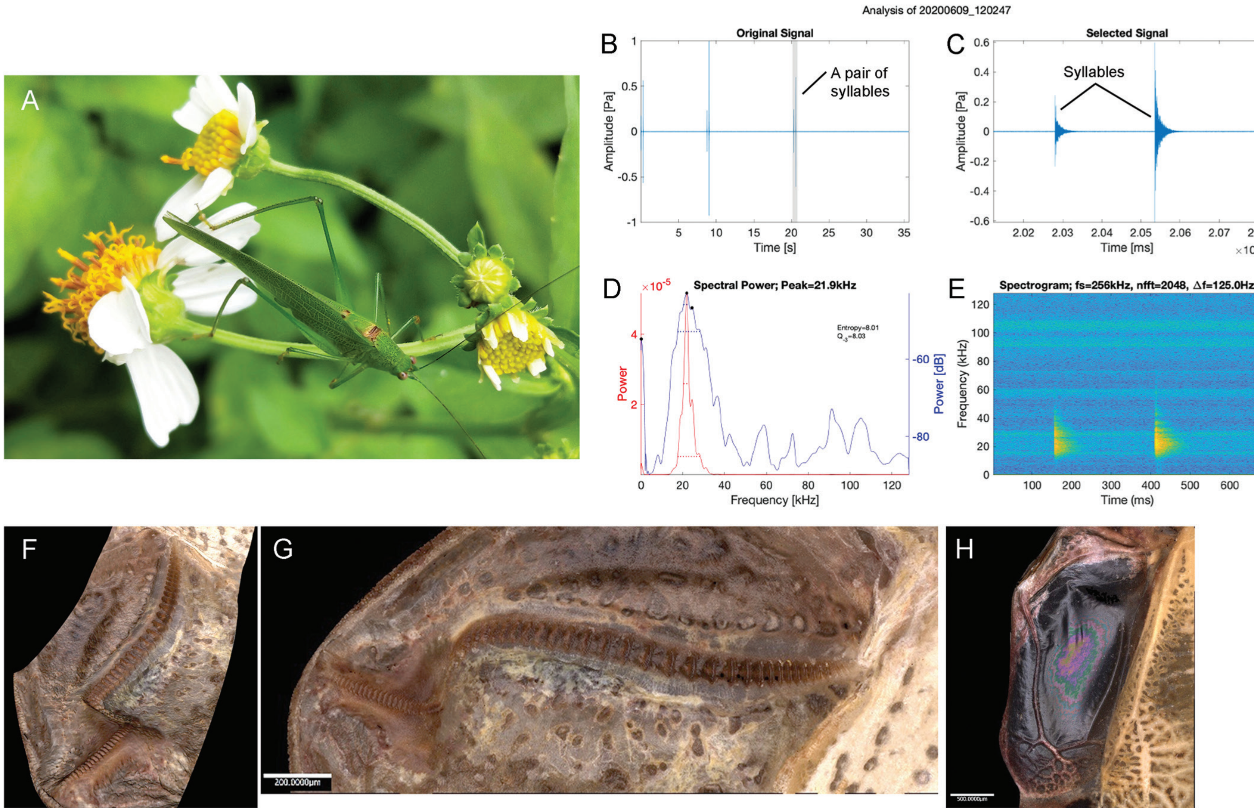

Fig. 21. *Phaneroptera brevis* male adult in its natural environment in Singapore (**A**). Oscillograms showing two complete pairs of syllables (**B**) and a closer view of a pair of syllables (**C**). Power spectrum (**D**) and spectrogram of the pair of syllables (**E**). Three-dimensional anal view 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**).

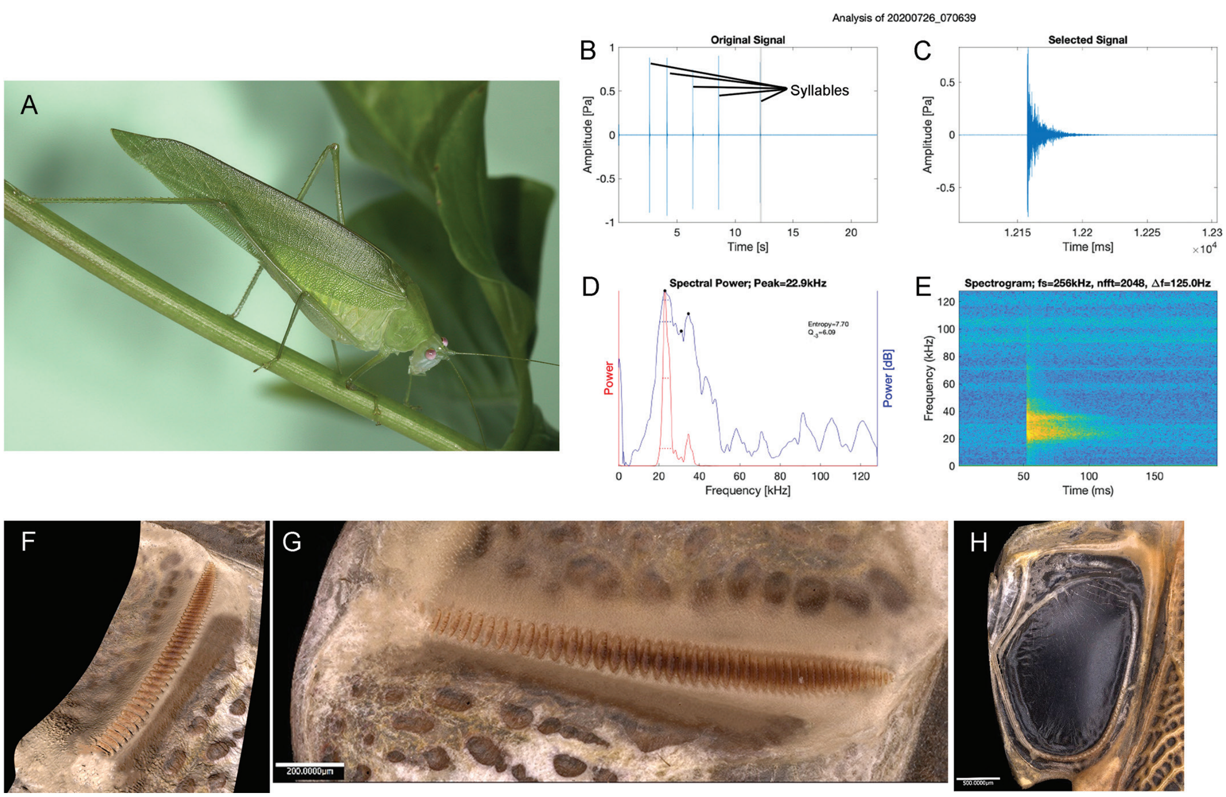

Fig. 22. *Phaulula malayica* male adult in the lab (**A**). Oscillograms showing five isolated syllables (**B**) and a closer view of a syllable (**C**). Power spectrum (**D**) and spectrogram of the syllable (**E**). Three-dimensional anal view of the left stridulatory file (SF) (**F**), ventral view 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 µm), 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 slightly swollen vein buttress. The right tegmen has an elongated rectangular mirror. The stridulatory file on the right tegmen is about 1.851 mm in length with about 38 teeth at the anal half and numerous indistinct teeth at the basal half.

***Scambophyllum sanguinolentum* (Westwood, 1848)** (n = 1 male, 8 sound files) (Fig. 24): The calling song consists of a pulse train isolated in time and 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 are 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 remaining relatively 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 µm. Tooth width tapers at the ends. The file (Cu2) is slightly elevated in the middle on a very swollen vein buttress. The right tegmen has a squarish mirror. The stridulatory file on the right tegmen is about 1.208 mm in length with numerous indistinct teeth.

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 terms of both time and frequency. 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 *Alloteratura*

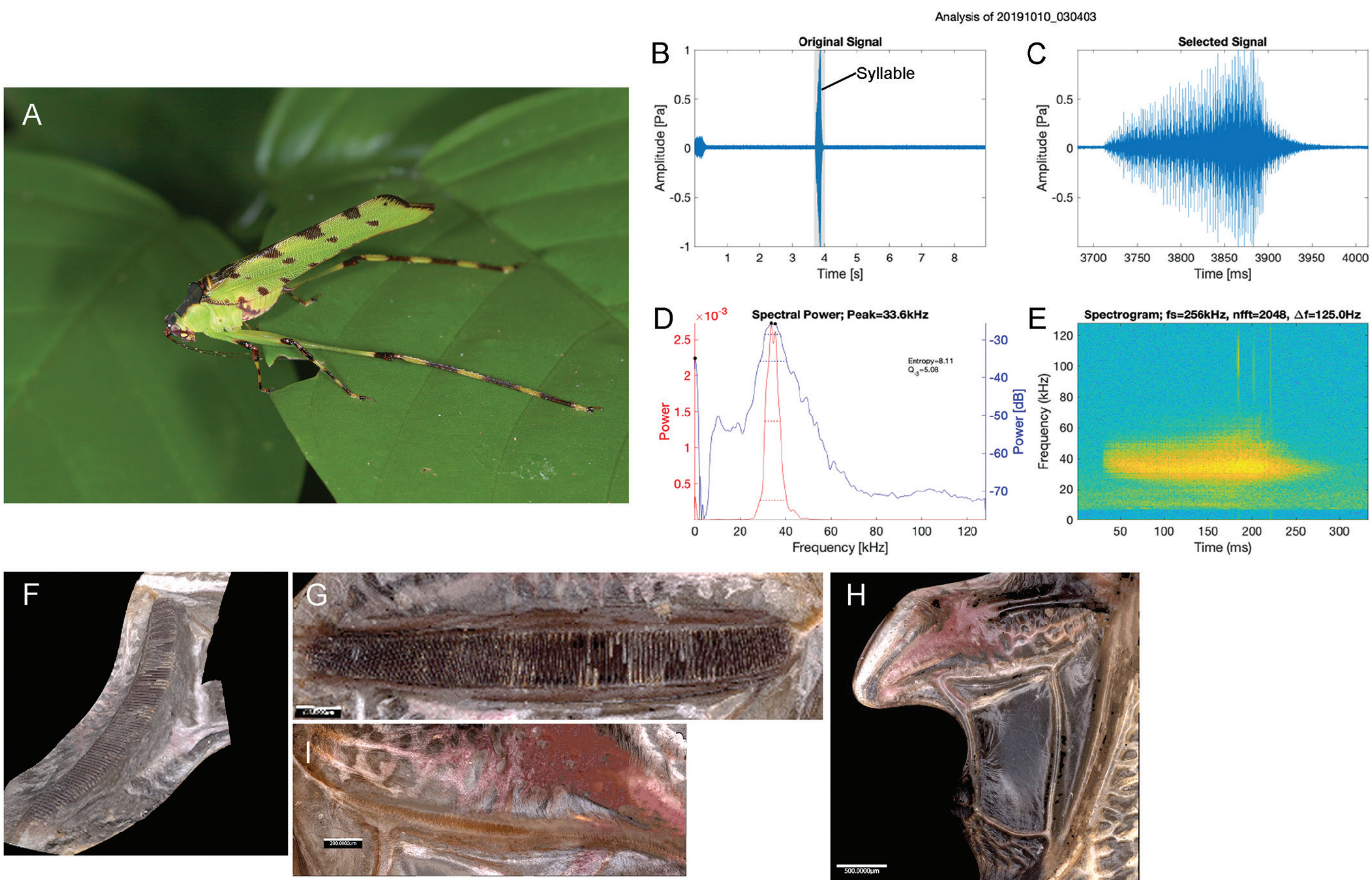

Fig. 23. *Psyrana tigrina* male adult in its natural environment in Sandakan, Malaysia (**A**). Oscillograms showing an isolated pulse train (**B**) and a closer view of the pulse-train (**C**). Power spectrum (**D**) and spectrogram of the pulse train (**E**). Three-dimensional anal view of the left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

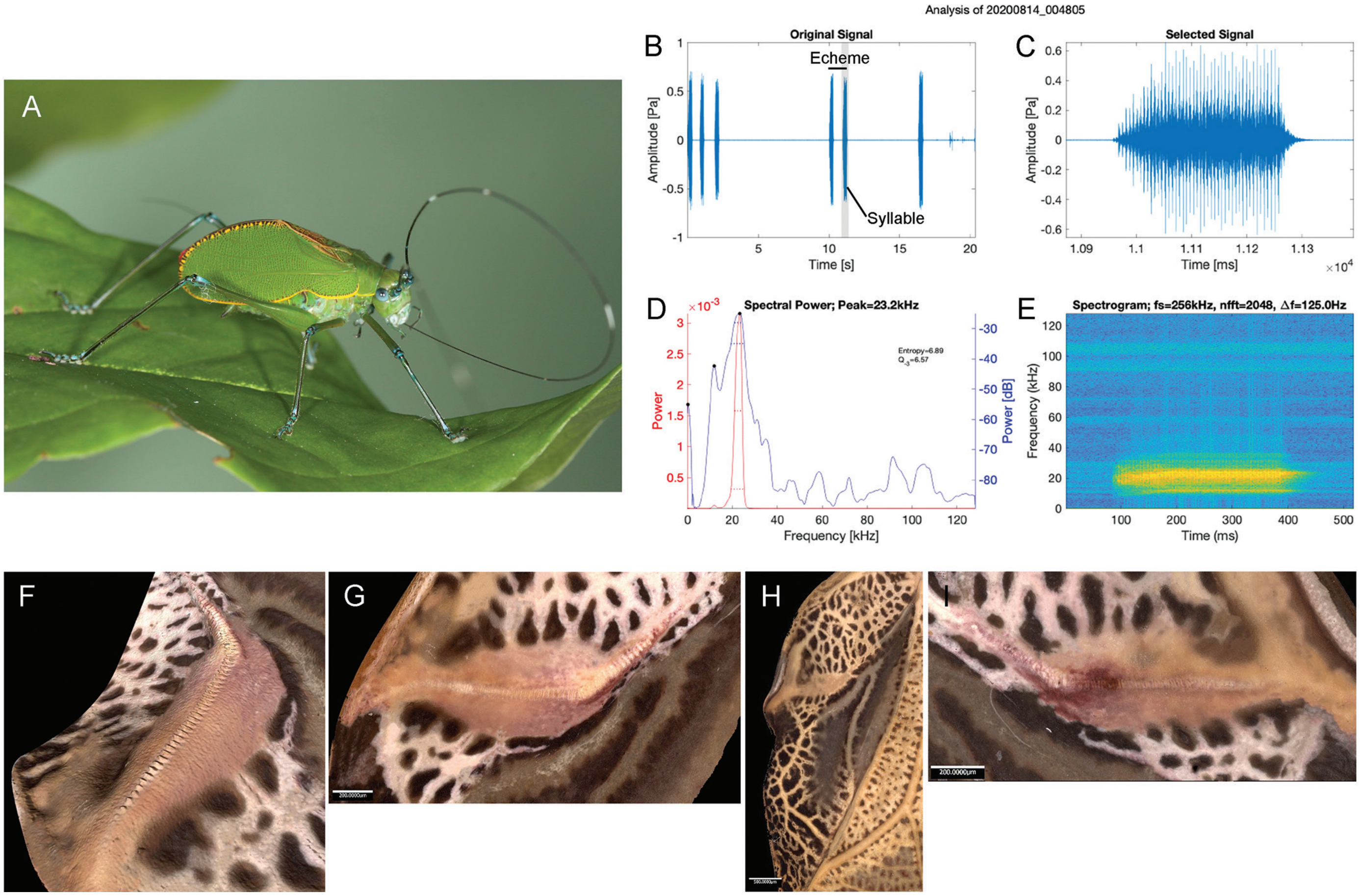

Fig. 24. *Scambophyllum sanguinolentum* male adult in the lab (**A**). Oscillograms showing two echemes (first one with three syllables and second one with two syllables) followed by an isolated syllable (**B**) and a single syllable (**C**). Power spectrum (**D**) and spectrogram of a syllable (**E**). 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 ventral view of the right SF (**I**).

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. Given 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 areas of its distribution can shed light on its bioacoustics and taxonomy.

The call analysis also provides input on the quality of the signal, and we used the quality factor Q (Q_{-3dB}) to investigate this variable. Although Q assumes that 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 means of measuring the tendency of a signal to be a random noise rather than the actual signal from the source (i.e., the katydid call). Entropy has been used by various authors to measure this tendency from various perspectives. For example, Sueur et al. (2012) used a normalized form for the calculated value that tends toward 0 for a single pure tone, increases with the number of frequency bands and amplitude modulations, and tends toward 1 for random noise. Chivers et al. (2017a) report entropy values of ~5–9 in neotropical katydids (without normalization). Using the same protocols proposed by Chivers et al. (2017a), here we report entropy values of 6.8–8.8, which suggests that Chivers et al. (2017a) included species with high tonality (common in many neotropical Pseudophyllinae).

The peak frequency of the 24 Southeast Asian katydids ranges from 12.6 to 54.2 kHz, with more than 80% of species having energy peaks in the ultrasonic range (18 species having a peak frequency between 20 and 40 kHz, and 3 species having a peak frequency > 40 kHz) (Fig. 25). This is congruent with what was previously documented: most katydids produce ultrasonic sounds (Montealegre-Z 2009, Montealegre-Z et al. 2017). The three extreme ultrasonic callers (peak frequency >40 kHz) reported here are species from the subfamily Meconematinae. We can expect to find more species of katydid from the region to produce extreme ultrasound as they are collected. These may include species of *Glenophisis* Karny, 1926 from the subfamily Hexacentrinae, a small genus of katydids found in Southeast Asia (Tan 2012). These katydids share superficial morphological resemblance with neotropical *Arachnoscelis* Karny, 1911 species and *Supersonus* Sarria-S et al., 2014 species (both from the subfamily Meconematinae), which can produce calls with frequency peaking at 70 kHz and above 125 kHz, respectively (Chivers et al. 2014, Sarria-S et al. 2014). Unfortunately, we have yet to encounter these rare katydids for such a study. Likewise, some Pseu-

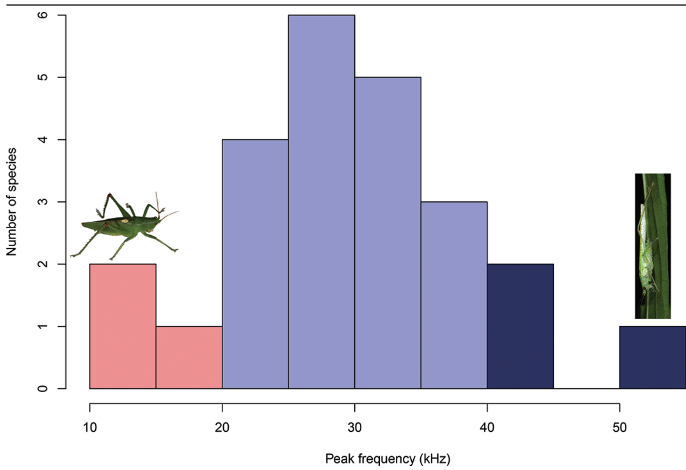

Fig. 25. A histogram showing the number of katydid species and the peak frequency of their calling songs. The red bars represent sonic callers (<20 kHz), light blue bars represent ultrasonic callers, and the dark blue bars represent extreme ultrasonic callers (>40 kHz).

dophyllinae from Southeast Asia can produce exceedingly low frequencies (e.g., 0.6 kHz in *Tympanophyllum arcufolium*) (Heller 1995), and it would not be surprising to find more species that produce such low frequencies.

In this study, all six species of Meconematini were found to produce songs with an entirely ultrasonic spectrum. This is congruent with previous reports of calls of Meconematini from Africa, such as those of *Amytta* Karsch, 1888 species (Hemp and Heller 2017, Hemp 2021). Among the species studied here are also the only group of katydids that produce extreme ultrasound, specifically *Borneopsis cryptosticta*, *Xiphidiopsis* (*Xiphidiopsis*) *dicera* and an unidentified Meconematini from Sandakan (although Tan et al. 2019b also reported extreme-ultrasonic singers among Phlugidini from Southeast Asia). Being highly speciose in Southeast Asia—with at least 104 genera currently known (Cigliano et al. 2022)—this group may hold the key to understanding the evolution of extreme ultrasound production in katydids. However, elucidating the phylogeny of Meconematini is crucial, as the relationships between and among many currently known genera and species are still unknown, and many groups are proabably paraphyletic. The ability to produce calls with entirely ultrasonic spectrum and extreme ultrasound are likely to have evolved multiple times and dependent on other factors instead of merely phylogenetic relatedness. Second, these predatory katydids usually occur in low abundance, and most species were described without having their calls recorded (but see Tan et al. 2020b). With continued effort to document the bioacoustics of these katydids, we can expect to find more species of extreme-ultrasonic singers from more genera, as well as more variations in their call structure and peak frequencies among different clades.

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

Sound-producing organs.—The properties of stridulatory file (length, number of teeth, and teeth density or spacing) and mirror (e.g., stiffness, membrane structure) are important in determining the frequency and resonance of a calling song (Morris and Pipher 1967, Bailey 1970, Montealegre-Z 2009, Montealegre-Z and Postles 2010, Montealegre-Z et al. 2017). Corroborating with previous studies on neotropical katydids (e.g., Montealegre-Z and Morris 1999), we observed vast diversity in the morphology of the Southeast Asian katydids. While the left tegmina of most of the reported species have straight/faintly curved stridulatory files with broad teeth (often closely packed together), a few species exhibit peculiarity. *Euanisous teuthroides* have squarish teeth on the stridulatory file, with an indentation in the middle of each tooth. *Phaneroptera brevis* have two parts to their stridulatory file, with a shorter anal half (with smaller teeth) and longer basal half (with larger teeth), as is typical for the genus *Phaneroptera* (Heller et al. 2017, 2021b). This may contribute to the different call parameters in various parts of the calling songs that have been observed in *Sphagniana sphagnorum* (Walker, 1869) and an eneopterine cricket *Eneoptera guyanensis* Chopard, 1931 (see Morris and Pipher 1972, Robillard et al. 2015).

It has been well established that the mirror area correlates negatively with peak frequency of the calling songs in katydids (Morris et al. 1994, Montealegre-Z 2009, Montealegre-Z et al. 2017). We also found species with mirrors of different sizes relative to tegmina size and shape. Some Phaneropterinae, i.e., *Holochlora* nr. *bilobata* and *Scambophyllum sanguinolentum*, have rather obsolete mirrors. A typical mirror consists of the CuPaβ (and sometimes CuPaα2) and frame surrounding a clear membrane (Chivers et al. 2017b). In *Holochlora* nr. *bilobata*, the mirror membrane is relatively small, whereas in *Scambophyllum sanguinolentum*, the mirror membrane is made up of an interlaced network of veins.

Bioacoustics and integrative taxonomy.—New acoustic data allow us to re-test species hypotheses previously delimited using only morphology. For example, we are able to integrate bioacoustics with traditional taxonomy for the genus *Viriacca* by comparing the calling songs for three of the four known species—*Viriacca insularis* from the Malay Peninsula, *Viriacca modesta* from Borneo, and previously described calls of *Viriacca viridis* Ingrisch, 1998, also from the Malay Peninsula (Ingrisch 1998). Although their sound-producing organs share many similarities, the three species exhibit distinct call structures, frequencies, syllable durations, and intervals between syllables. These differences are congruent with the genitalia differences used to diagnose these congeners (Gorochov 2013). This example also highlights that taxonomy is hypothesis-driven, in which species can be re-evaluated with new and different datasets. In light of this, we also recommend using bioacoustics to validate morphologically similar congeners in other Southeast Asian katydids. These can include the *Peracca subulicerca* species complex consisting of *Peracca subulicerca* (Karny, 1926) from Java, and *Peracca tiomani* Gorochov, 2011 and *Peracca macritchiensis* from Malay Peninsula, in which the species characters remain debatable.

Conclusions

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

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