A new species of *Physocrobylus* (Caelifera: Acridoidea: Acrididae: Coptacrinae), with notes on the phenology and habitat of the genus

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Abstract

A new species of *Physocrobylus*, *P. venetus* **sp. nov.**, is described from the Nguru Mountains of Tanzania. It is the third species in the genus restricted to Tanzanian localities. While *P. venetus* **sp. nov.** and *P. tessa* Hochkirch prefer moister forest communities from lowland to submontane forest in the East Usambara and Nguru Mountains, *P. burtti* Dirsh is an inhabitant of Miombo woodlands.

Keywords

East Africa, grasshopper, lowland forest, submontane forest, Tanzania, taxonomy

Introduction

The genus *Physocrobylus* was erected by Dirsh (1951) on a single female collected in the Kiboriani Hills, Mpwapwa District of Tanzania. Dirsh placed it in Catantopinae. Jago (1978) assigned *Physocrobylus* to Euryphyminae and described the male of *P. burtti*. When Hochkirch (1996) detected a second species of the genus, *P. tessa*, in the East Usambara Mountains, the genus *Physocrobylus* was transferred to Coptacrinae because it shared a furcula and the transverse fold on the subgenital plate with this subfamily.

Up to now, few specimens of the two members of the genus *Physocrobylus* have been collected. In the entomological collection of London (NHML), besides the female holotype of *P. burtti*, there are a couple of specimens that were collected by Jago from a locality 44 miles north of Dodoma (East Chenene Forest Reserve). Hochkirch collected specimens of *P. tessa* in the East Usambara Mountains at Amani at an elevation of about 800–1000 m in protected patches of submontane to montane forest. The East Usambara Mountains were intensively surveyed by our team. Survey sites included several lowland wet forest reserves such as Magoroto Forest Estate, the Nilo Forest Reserve, and the Mtai Forest Reserve, as well as the Amani Nature Reserve, the Kwamkoro Forest Reserve, and other patches on the Amani plateau. Thus, more data on the distribution and the habitat requirements of *P. tessa* became available and are presented in this paper. A third species of the genus was discovered in the submontane forests of the Nguru Mountains. *Physocrobylus venetus* **sp. nov.**, a common inhabitant in the Nguru Mountains, is here described.

Material and methods

Measurements.—The total body length refers to the body length of the insect from head to the tip of the abdomen.

Depositories.—CCH: Collection of Claudia Hemp. NHML: Natural History Museum, London, UK.

Results

Physocrobylus venetus sp. nov.

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Type material.—**Holotype** male. Tanzania, Nguru Mountains, submontane forest, 1100–1200 m, 6.05336°S, 37.56076°E – 6.06702°S, 37.57339°E. June 2017. Depository: CCH.

Paratypes. 11 males, 13 females, 3 female nymphs, same data as holotype and February 2017, March 2017, November 2017, January 2018, March 2019, and March 2020. Depository: CCH.

1 male (NHML 013454600), 1 female (NHML 013454558), same data as holotype. Depository: NHML.

Description.—**Male.** General coloration: Dorsally broad brown fascia running over head, pronotum, and abdomen; this brown fascia medially with three fine white lines, interrupted at each segment; end of abdomen light brown and white lines obsolete. Eyes reddish. Legs green, hind knees dark, tibiae bright blue (Fig. 1A–C).

Head and antennae. Antenna about body length or slightly shorter; antennal segments much longer than wide. Eyes globular, strongly protruding. Fastigium verticis very narrow between eyes, appears only as a callous ridge; in front of eyes widening to rhomboid structure (Fig. 2A). Frontal ridge typical for genus, strongly projecting in front of eyes; shallow concave and punctured; carinae below the ocellus flat and almost obsolete.

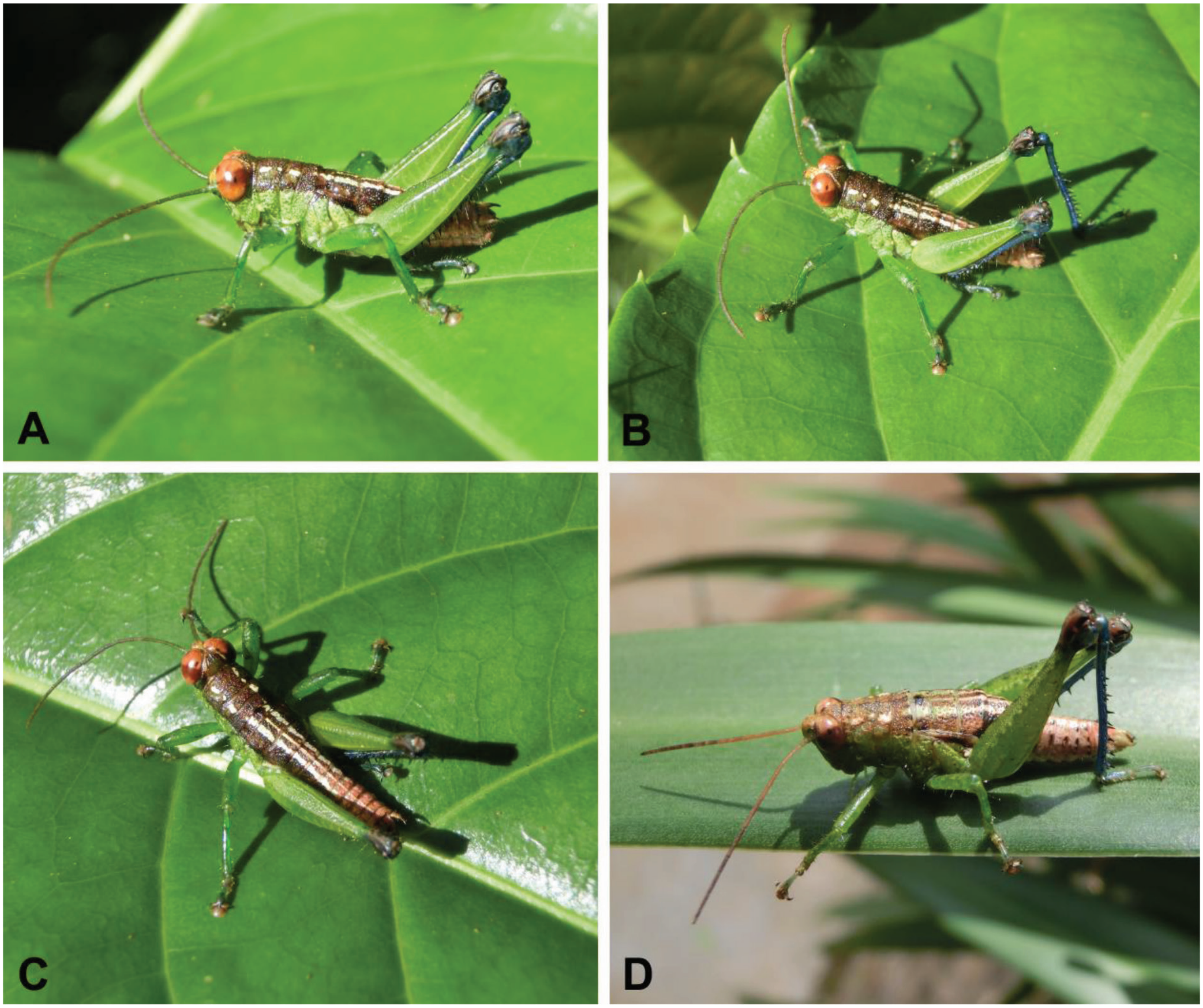

Fig. 1. *Physocrobylus venetus* **sp. nov. A–C.** Male; and **D.** Female.

Thorax. Thorax strongly wrinkled and impressed with dots, deeply crossed by two sulci; lateral carinae absent. Anterior margin evenly rounded; posterior margin medially incurved (Fig. 2A). Prosternal tubercle conical, laterally compressed. Tegmina strongly reduced, elongate lobes with narrow anterior part, slightly widening posteriorly, broadly rounded and with reduced venation (Fig. 3C). Alae absent.

Legs. Fore and mid femora round, with largest diameter in the middle; unarmed. Hind femora stout; unarmed. Fore and mid tibiae also roundish, unarmed except for black spurs; fore tibiae with three outer and two inner spurs, mid tibiae each with an outer and an inner pair of spurs. Hind tibiae with double row of dorsal long spines, white at the base, with black tips; on inner side, two large and laterally flattened spurs, on outer side, a pair of smaller but also enlarged stout spurs. Tarsi of light color; mid tarsal segment very short, the other two segments about 3 times as long as the middle one.

Abdomen. Supra-anal plate typical for Coptacrinae, elongate, tongue-like with elevated lateral margins and a rounded tip (Fig. 4C). Furcula of 10th abdominal tergite well developed. Cerci slightly longer than supra-anal plate; inwardly curved and laterally slightly compressed. Subgenital plate with well-developed transverse fold. Epiphallus as in Fig. 5. Bridge divided (Fig. 5A), lophi curved, almost tri-angular with acute apices (Fig. 5C, D), posterior processes narrow and elongated with rounded apices, anterior processes rounded (Fig. 5A). Ancorae well developed (Fig. 5A).

Female. Coloration similar to male but duller and also with bright blue hind tibiae. Larger and stouter but with same spination of the legs (Figs 1D, 2C). Supra-anal plate elongate, anterior part sculptured (Fig. 6A). Subgenital plate broad with acute tip at posterior margin (Fig. 6B).

Measurements.—(mm) Males (n = 6). Body length: 14.7–16.7; Median length of pronotum: 2.5–3.4; length of tegmina: 3.1–3.7; length of hind femur: 10.1–11.2.

Females (n = 6). Body length: 20.1–22.0; Median length of pronotum: 3.7–4.2; length of tegmina: 3.5–4.3; length of hind femur: 14.0–14.5.

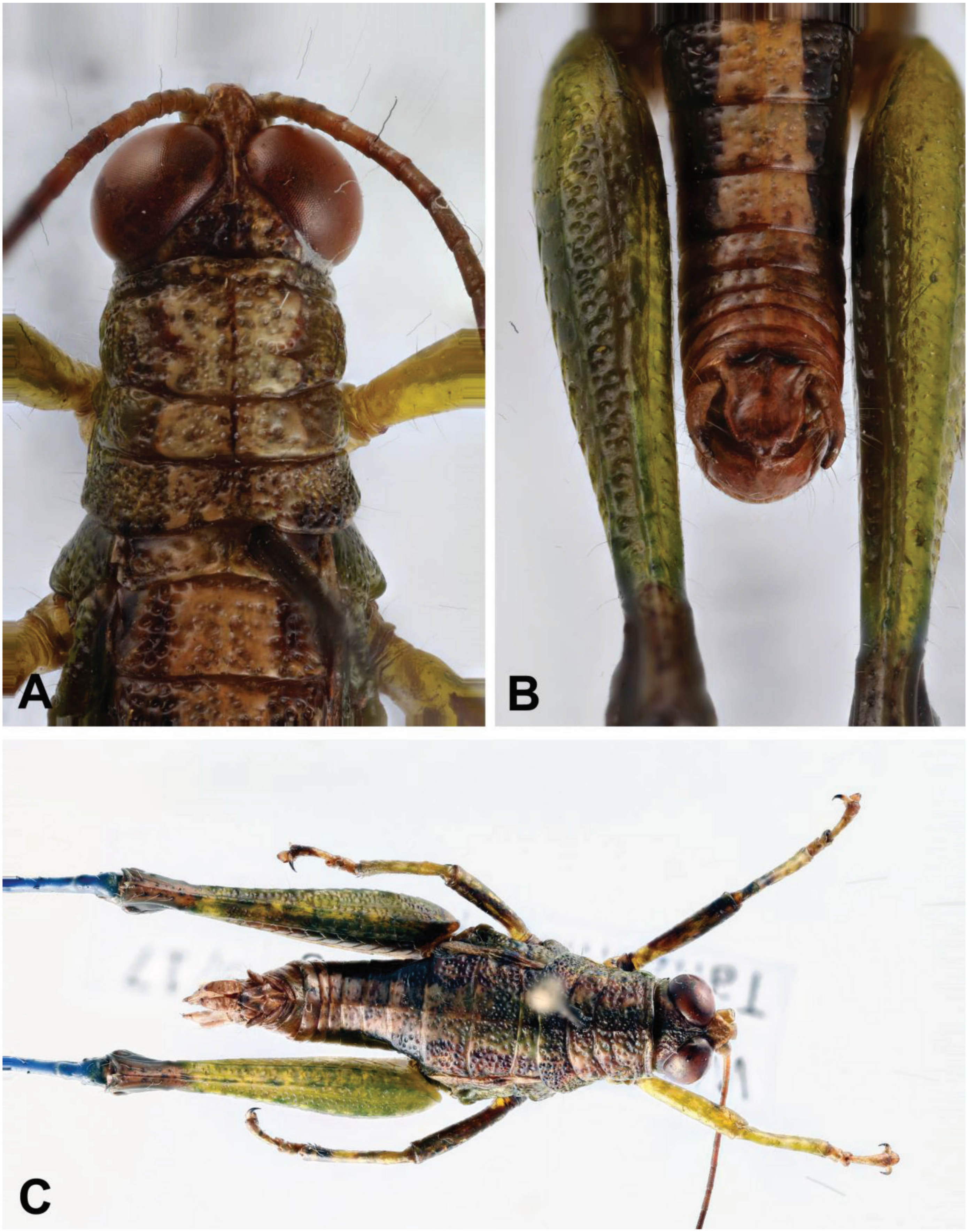

Fig. 2. Details of *Physocrobylus venetus* **sp. nov. A.** Male, head, dorsal view; **B.** Abdomen, dorsal view; and **C.** Female, dorsal habitus.

Fig. 3. Right tegmen of male *Physocrobylus* species. **A.** *P. burtti*; **B.** *P. tessa*; and **C.** *P. venetus* **sp. nov.**

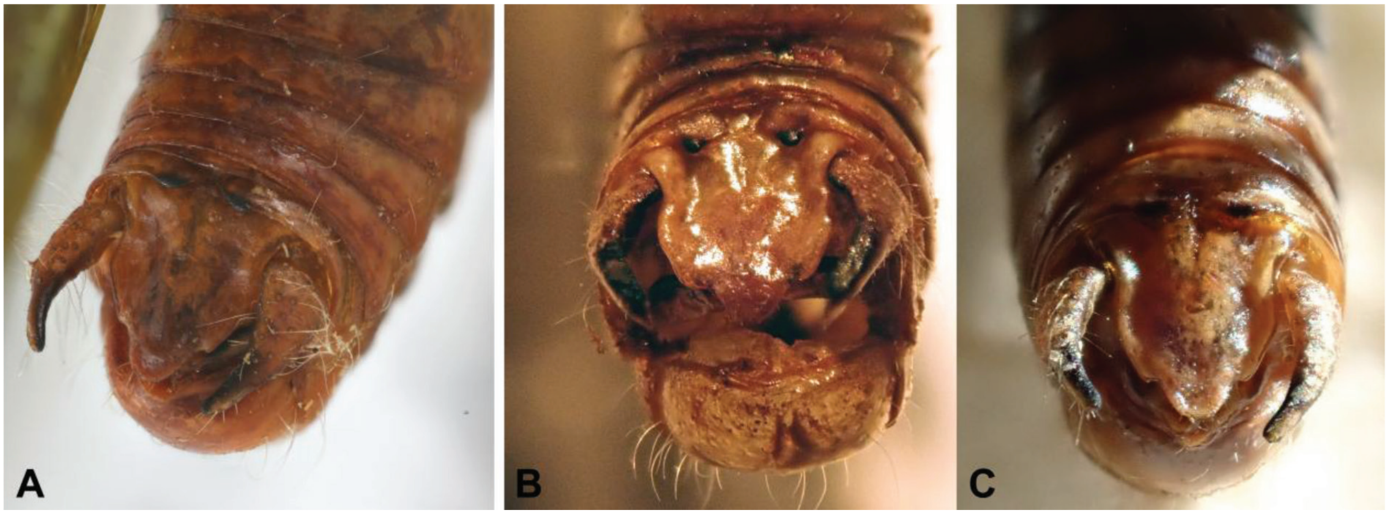

Fig. 4. Abdominal apices of male *Physocrobylus* species. **A.** *P. burtti*; **B.** *P. tessa*; and **C.** *P. venetus* **sp. nov.**

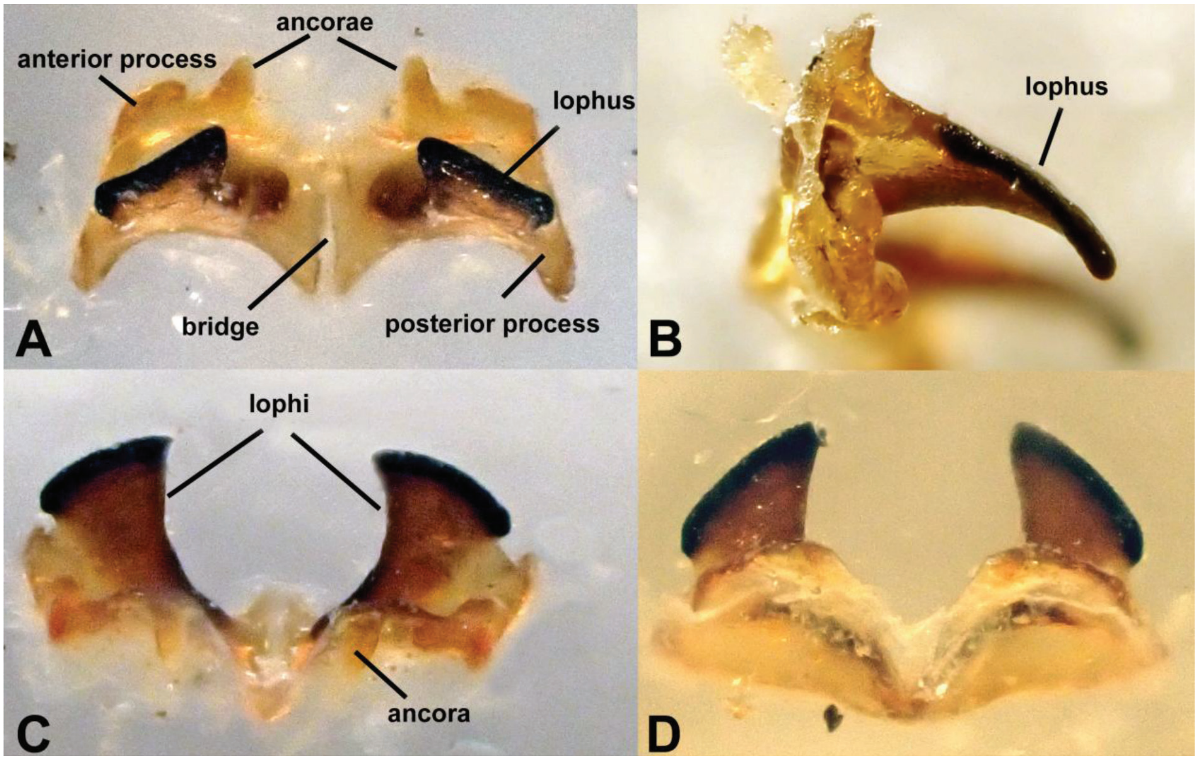

Fig. 5. Epiphallus of male *Physocrobylus venetus* **sp. nov. A.** Dorsal view; **B.** Lateral view; **C.** Anterior axial view as epiphallus is situated when looking at opened apex of animal; and **D.** Posterior axial view.

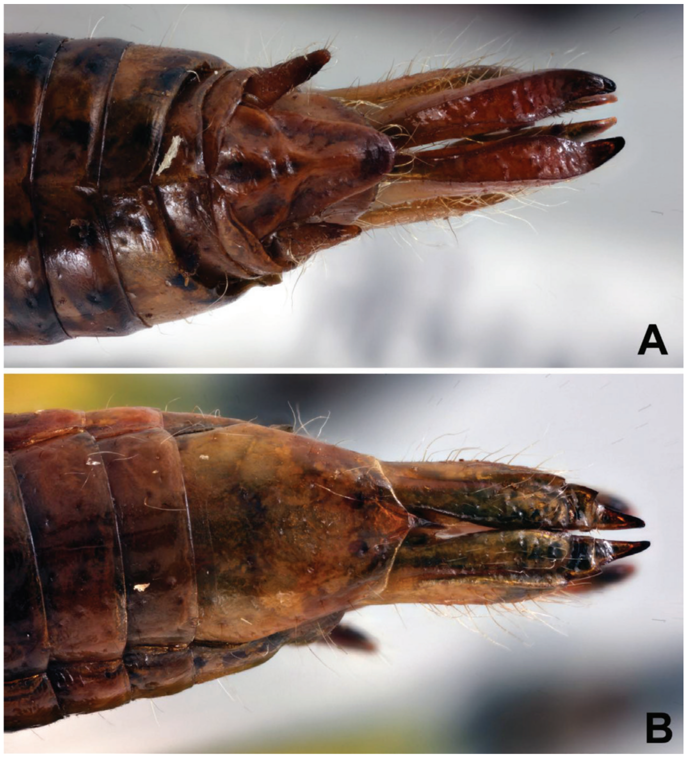

Fig. 6. Abdominal apex of female *Physocrobylus venetus* **sp. nov.** **A.** Dorsal view; and **B.** Ventral view.

Diagnosis.—In habitus and size, *P. venetus* **sp. nov.** is similar to *P. tessa* from the East Usambara Mountains but is less stout, while *P. burtti* is smaller and very stout (Fig. 7). Pronotum posteriorly not as wide as in *P. tessa*. Also, the coloration of *P. venetus* **sp. nov.** differs from both other *Physocrobylus* species. The femora are bright green in *P. venetus* **sp. nov.** while they are brown or speckled brown in the other two species, although specimens of *P. tessa* from the Nilo Forest Reserve population can also have partly dark green legs or speckled green legs (Fig. 7). Easily distinguished also by the bright blue tibiae in both sexes of *P. venetus* **sp. nov.**, while *P. tessa* has brown to green hind tibiae and *P. burtti* has brown tibiae in both sexes. The tegmina in males of the three species are of similar shape, all reduced to elongate lobes with reduced venation (Fig. 3). However, *P. tessa* has slightly broader tegmina compared to the other two species. Differences are also found in the outer genitalic morphology of the males (Fig. 4). The male cerci of *P. burtti* are thick and rugose in the basal half with tips round and marked darker brown to black. The cerci of both *P. tessa* and *P. venetus* **sp. nov.** are laterally compressed, especially in the apical half, and darker to black at their tips. All three species have differently shaped epiphalli (see fig. 1d, e in Hochkirch (1996), figs 5–7 in Jago (1978) and fig. 5). Similar to *P. tessa*, the ectophallus has two sclerotized ridges.

Etymology.—From latin: *-venetus* = green, blue–green, because of the blue tibiae and partly green body and legs.

Distribution.—Tanzania, Nguru Mountains.

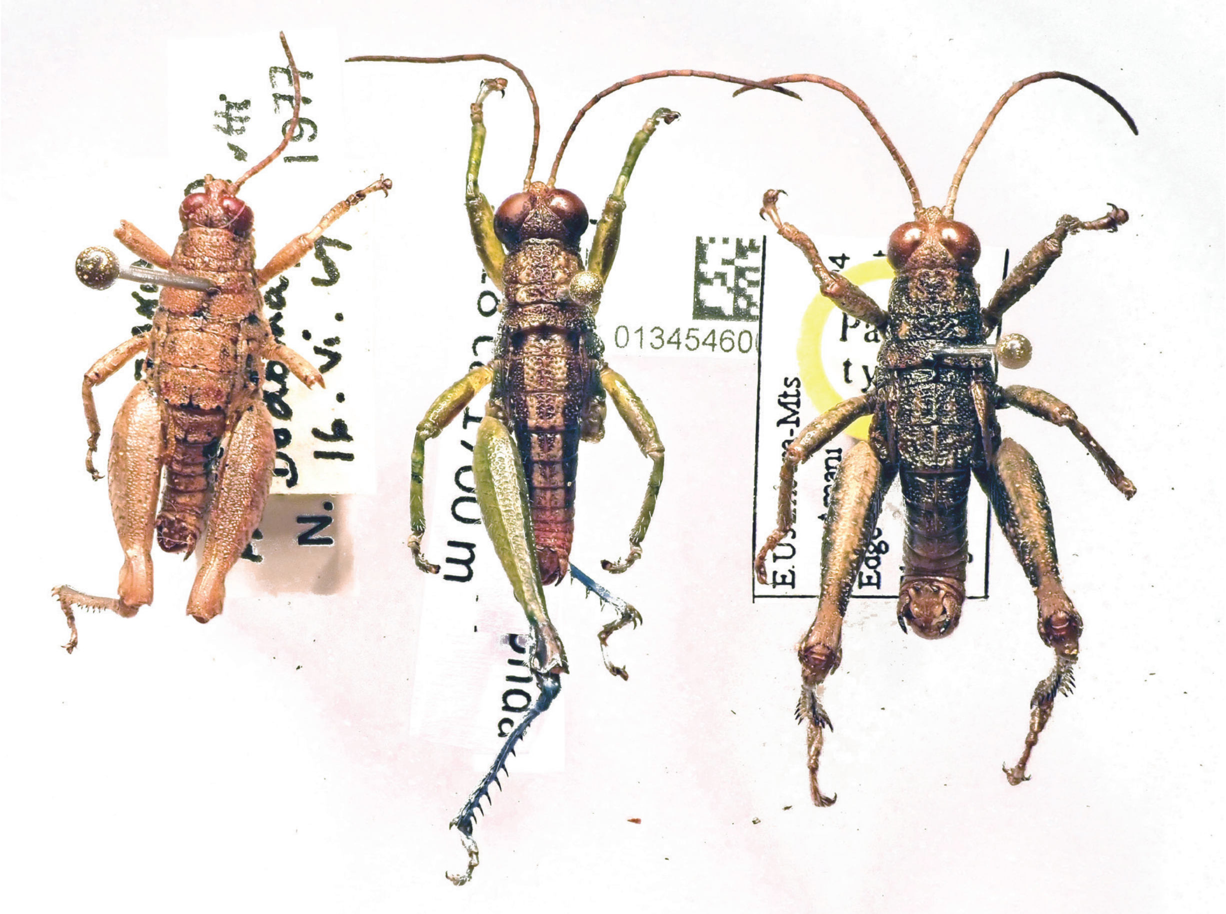

Fig. 7. Dorsal habitus of male *Physocrobylus* species. From left to right: *P. burtti*, *P. venetus* **sp. nov.**, and *P. tessa*.

Notes on the habitat of Physocrobylus *species.*—Both *P. venetus* **sp. nov.** and *P. tessa* occur in submontane forests in the litter layer and on low herbs; they are, however, restricted to different mountain areas. *P. tessa* is a rather rare species in submontane and montane elevations in the East Usambara Mountains. Most adults are found from November until about April. In the East Usambara Mountains, several forest reserves offer protection for some of the last lowland wet forests in eastern Africa. Numerous individuals were collected in Magoroto Forest Estate at elevations between 670 to 880 m a.s.l., indicating that lowland wet forests harbor higher numbers of this forest dwelling species, and in the Nilo Forest Reserve. In the latter, single individuals were even collected in July, indicating that the species may be present year-round. Very few individuals of *P. tessa* have been found so far at Kwamkoro Forest Reserve on the plateau of the East Usambara Mountains near Amani at elevations of around 900 m, although the area was surveyed for *P. tessa* many times and at different times of the year. The Nguru Mountains have been deforested below about 700 m, thus only submontane and montane forests still exist in this area. Specimens of *P. venetus* **sp. nov.** are more common during the warm time of the year, from about November to April, but individuals were also collected in June and July. Thus, the phenology is similar to *P. tessa* in the East Usambara Mountains.

Little information is available for the third species, *P. burtti*. Although the area where *P. burtti* occurs was visited several times (Hemp and Heller 2019), this species was not collected by our team. The holotype was collected in the Mpwapwa area of Tanzania, but detailed information of the habitat is lacking. The type locality at the Kiboriani Hills where the District city of Mpwapwa is located has transformed almost completely to maize fields (see also Hemp and Heller 2019) but formerly was covered by Miombo woodlands. *P. burtti* was also collected 44 miles north of Dodoma, in the East Chenene Forest Reserve, which is also the type locality for other species (e.g., *Odonturoides insolitus* Ragge, 1980). This forest reserve, today heavily impacted by illegal charcoaling, consists of typical Miombo woodlands at elevations between 1200 and 1550 m a.s.l. Thus, *P. burtti* probably is a dweller of the ground layer in this forest type and, thus, occupies a completely different ecological niche than the other two *Physocrobylus* species, which prefer moister habitats.

Acknowledgements

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Research Article Journal of Orthoptera Research 2021, 30(1): 7–16

Oecanthus rohiniae sp. nov. (Gryllidae: Oecanthinae): A new chirping tree cricket of the *rileyi* species group from Mexico

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Abstract

A new species of *Oecanthus* is described from Mexico. *Oecanthus rohiniae* **sp. nov.** occurs in central Mexico in the understory of tropical deciduous forest and is currently known only from Mexico. This new species has the coloring, antennal markings, slightly widened tegmina, and calling song that are found in the *rileyi* species group. Although morphologically very similar to *Oecanthus fultoni*, the shapes of the distal hooks on the male copulatory blades differ between the two species. There are also differences in the song pulse patterns and chirp rate response to temperature. This new species has been given the common name Cri-Cri tree cricket. Video and song recordings are available online.

Keywords

bioacoustic, biodiversity, Querétaro, tropical deciduous forest

Introduction

According to the Orthoptera Species File (Cigliano et al. 2020), the subfamily Oecanthinae Blanchard, 1845, is represented by nine genera: *Oecanthodes* Toms & Otte, 1988; *Oecanthus* Serville, 1831; *Viphyus* Otte, 1988; *Leptogryllus* Perkins, 1899; *Prognathogryllus* Brunner von Wattenwyl, 1895; *Thaumatogryllus* Perkins, 1899; *Neoxabea* Kirby, 1906; *Xabea* Walker, 1869; and *Paraphasius* Chopard, 1927. Two of these genera occur in Mexico—*Oecanthus* and *Neoxabea*. Twenty of the species of *Oecanthus* in North America, Central America, and the Caribbean are divided into four main species groups: *nigricornis*, *niveus*, *varicornis*, and *rileyi* (Walker 1962, 1963, Walker and Collins 2010, Singing Insects of North America 2020b). These groups can be distinguished by characteristics including song type (chirping vs trilling and continuous vs intermittent); song pulse or chirp rate at given temperatures; regular vs irregular pattern of pulses or chirps; coloration of the antennae, head, pronotum, and abdomen; antennal markings on the pedicel and scape; and tegminal width (Walker 1962, 1963, Walker and Collins 2010). Four species in the *rileyi* species group are currently known to occur in North America, Central America and the Caribbean (Walker 1967, Collins et al. 2014): *O. alexanderi* Walker, 2010 (Walker and Collins 2010); *O. allardi* Walker & Gurney, 1960; *O. fultoni* Walker, 1962; and *O. rileyi* Baker, 1905.

In 1960, Walker and Gurney published the description of *O. allardi* and included details of ten specimens of snowy tree cricket from Tamaulipas and Michoacán, Mexico. In 1965, Richard D. Alexander traveled throughout Mexico and recorded Orthoptera and other singing animals. Notes from his recordings include six tapes that mention '*fultoni*' with adjectives such as slow, fast, and grouped or not grouped (Suppl. material 1: historical recordings). No further investigations of chirping tree crickets are known to have occurred in Mexico until the description of *O. mhatreae* Collins & Coronado, 2019 (Collins et al. 2019).

In 2019, a photograph accompanied by a sound recording (iNaturalist 2020) posted on iNaturalist.org from the central Mexican state of Querétaro led to the investigation of a new species of *Oecanthus* tree cricket. The chirping song pattern, widened tegmina, and orange area on the head are characters found in the *rileyi* species group. Although other photos from Mexico of tree crickets resembling the *rileyi* species group have been posted on iNaturalist, none had previously been accompanied by recordings of their songs. After reviewing all material, it was discovered that the samples did not correspond to any of the described taxa. This paper describes a new species of *Oecanthus* collected in Querétaro.

Material and methods

Specimens.—Adults and nymphs of *Oecanthus* were collected from a private property and immediate surrounding areas of Fraccionamiento Vista Real, Corregidora, State of Querétaro, Mexico. This locality is near Parque Nacional El Cimatario, on the southern slope of Cerro de Cimatario. Specimens were initially located by the song of the males and collected manually. Females and nymphs were found in the same area. Tree crickets were brought indoors in plastic containers (15 × 15 × 20 cm) with holes on the side for ventilation. The males and females were kept alive and separated to be recorded and then preserved in 70% ethyl alcohol for morphological studies. Photographs and measurements of diagnostic characters were made with a Jiusion Digital Microscope Model USB, magnification 40× to 1000× (ovipositor, cerci, and metanotal gland), MOTIC-SWZ168739 stereo-microscope at 40× and equipped with a 10 mp digital camera (internal genitalia). Characters considered for description are as follows: body length, head colors, antennal colors and markings, pronotum in dorsal view, tegmina length and width, stridulatory file, metanotal gland, cerci, subgenital plate, and internal genitalia (copulatory blades). Additional characters for females included the ovipositor, subgenital plate and cerci. The following measurements were made: body length—from the tip of the labrum to the apex of the subgenital plate; pronotum length (from anterior to posterior margin along midline); pronotum width (at the widest distal portion in dorsal view); tegmina length (from the thorax joining point to distal end of tegmina along midline); tegminal width (measured at the widest section of tegmina at rest); hind femur length; and cerci length. The females' ovipositors were measured from the base (closest portion to the abdomen) to the distal tip. Copulatory blades (Fulton 1915) project from the male genitalia complex and are situated just above the subgenital plate. These genitalia structures have also been referred to as pseudepiphallus (Chopard 1961, 1969), lophi medians [middle lobes] (Desutter 1987), or main lobe of pseudepiphallus (Zefa et al. 2012). The genitalia of Mexican specimens were treated with an aqueous solution of 10% potassium hydroxide (Rocha-Sánchez et al. 2018, Barrientos-Lozano and Rocha-Sanchez 2013). No chemicals were used on the *O. fultoni* specimen from the USA. Genus determination was made with keys from Walker (1967) and SINA (2020a) and review of taxa of *Oecanthus* in the Orthoptera Species File (Cigliano et al. 2020).

Calling song recording and analyses.—The male acoustic signal was recorded in the field and indoors using a Samsung Galaxy Tab S4 tablet model SM-T830, the app Grabadora Amazing, and a Mix-Mart 8 GB, PCM, 1536 kbps digital voice recorder. Audio devices were tested for calibration by recording a reference time audio file with reference tones and comparing the results to the original file. The recording devices were kept at a distance of approximately 10 cm from the individual. Analyses of song recordings were made with the Raven Pro 1.6 program (Cornell Lab 2020). Audio waveforms were created using the programs Raven Lite 2.0 or Raven Pro 1.6 (Cornell Lab 2020). Grouped pulse patterns were determined by counting individual pulses within each chirp. A chirp consists of varying numbers of pulses, and each pulse corresponds to a single closure of the tegmina (Walker and Collins 2010). Ten randomly chosen chirp periods were measured for each recording to determine the chirps per minute rate for that sample. Additional recordings (Suppl. material 2: source recordings) from the Macaulay Library of Cornell Lab (2020) were used for the preparation of two graphs to compare chirps per minute vs temperature and carrier frequency vs temperature, with additional species in the *rileyi* group. Regression lines for the sampled *O. rohiniae* **sp. nov.** population were calculated in Microsoft Excel for Mac, Version 16.16.22 (200509) (2016). The slopes of the regression lines for *O. rohiniae* **sp. nov.** and *O. fultoni* were compared using the t-test procedure for paired samples from Wonnacott and Wonnacott (1977).

Climate.—Temperatures were measured using an ELMECO DTM2 digital thermocouple thermometer with a range of -50°C to 1000°C, with an accuracy of 0.1°C. Ambient temperature and rainfall ranges [climatologia/temperaturas-y-lluvias/resumenes-mensuales-de-temperaturas-y-lluvias] for 2018 and 2019 were taken from the National Water Commission weather website (NWC 2020). The light intensity was determined using a HIOKI model 3422 digital luxmeter with a range of 0 to 2000 Lx (1Lx accuracy) and using data from the NWC website.

Results

Oecanthus rohiniae Collins & Coronado-González, sp. nov.

http://zoobank.org/EE607E6F-B950-4FDF-BCA0-742177F85FD4

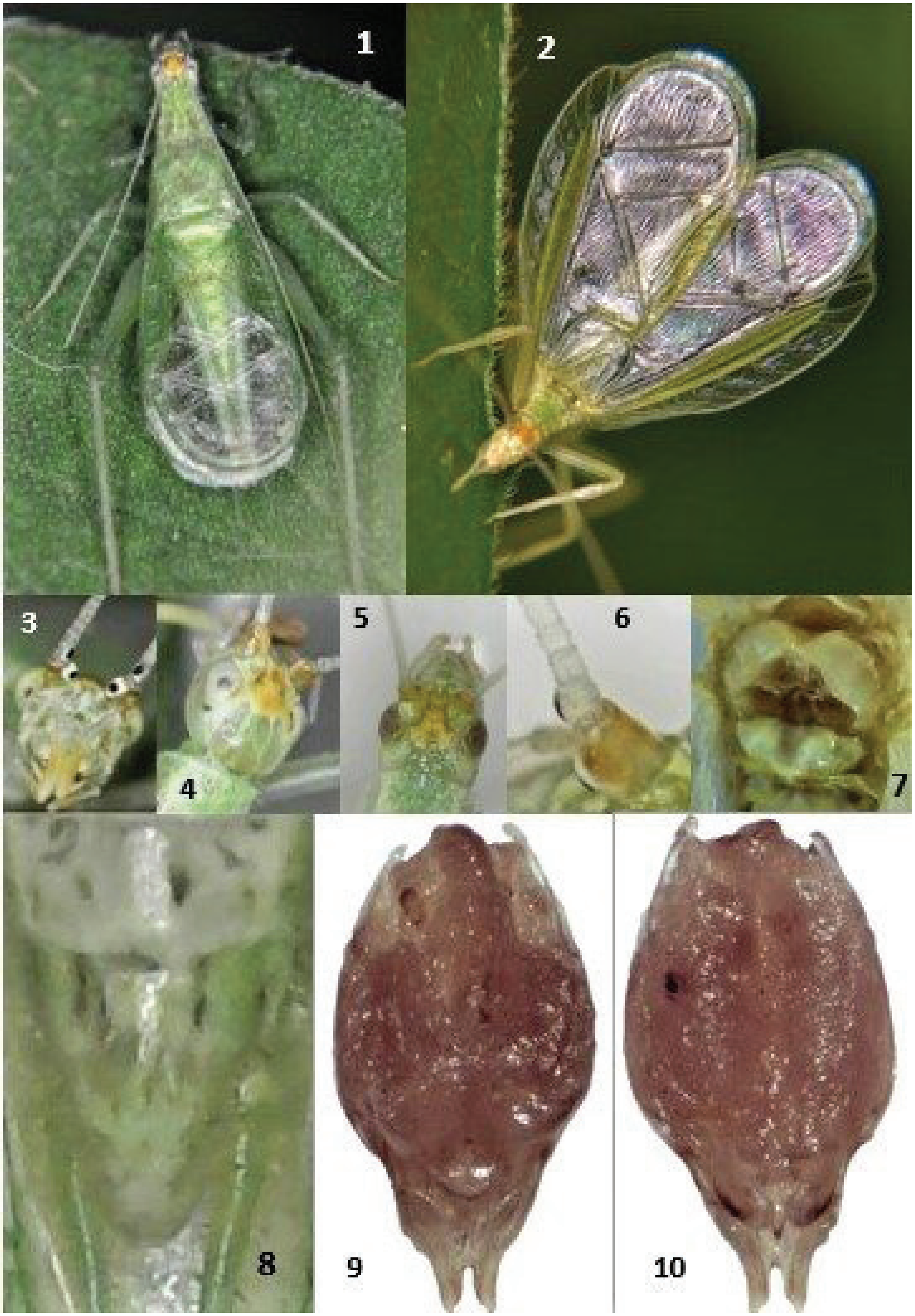
Material examined.—**Holotype:** MEXICO • ♂; Querétaro, Corregidora; 2130 MASL; 30.xi.2019; 20°52'20"N, 100°38'80"W; I. Coronado leg.; deposited Universidad Nacional Autónoma de México (IB-UNAM). **Paratypes:** MEXICO • 2 ♂, 3 ♀; same locality as holotype; 2 ♂, 2 ♀ deposited Tecnológico Nacional de México-Instituto Tecnológico de Ciudad Victoria (TecNM-ITCV); 1♀deposited IB-UNAM.

Etymology.—Specific epithet in recognition of Rohini Balakrishnan whose research involves bioacoustics, animal behavior, ecology, and systematics. Her list of publications includes several that focus on or include tree crickets. The common name, Cri-Cri tree cricket, is named for Cri-Cri: El Grillito Cantor (Cri-Cri: The Little Singing Cricket), which was a character created by Francisco Gabilondo Soler, a Mexican composer and performer of children's songs. Additionally, the sound this tree cricket makes is written as "cri, cri…" in Spanish.

Holotype measurements.—Body length 13.0 mm; tegminal length 13.0, tegminal width 6.0; pronotal length 2.0, distal pronotal width 2.0; hind femur length 7.0; cerci 5.0; stridulatory file length 1.8. Right tegminal stridulatory teeth total 46.

Description.—Face pale; head with area of pale orange (Figs 4, 5). Scape translucent orange, pedicel translucent whitish (Fig. 6), and remainder of antennomeres translucent whitish. Ventral face of pedicel and scape each with one ovoid or rounded black mark on white field (Figs 3, 19). Eye color pale cream to violet. Palpi pale golden orange with whitish tips. Pronotum light green. Tympanal membrane on fore tibiae whitish. Wing color greenish. Ventral abdomen whitish with blotches of light green (Fig. 8). Tarsi, tibiae, and femora translucent pale green; some individuals with blackish thin line down inner femora. Cerci straight and translucent pale green.

Males.—Hind wings and cerci extend beyond distal edge of tegmina (Fig. 1). Tegmina with veins as in Fig. 2. Body length 13.0–13.5 mm; tegminal length 13.0–13.5, tegminal width 5.8–6.0; pronotal length 2.0, distal pronotal width 2.0–2.2; hind femur length 7.0–7.6; cerci 5.0; stridulatory file length 1.8–2.0. Right tegminal stridulatory teeth total 46–48. Metanotal gland with triangular opening, and bristles running horizontally across the top of the opening (Fig. 7). Subgenital plate tapers to a rounded tip (Fig. 8). Copulatory blades with rounded medial sides and a notch separating them slightly narrower than width of a blade. Each blade with a small hook at distal tip (Figs 9, 10).



Figs 1–10. *Oecanthus rohiniae* **sp. nov.**, male. **1.** Habitus; **2.** Singing male showing the tegmina in raised position; **3.** Head in frontal view showing the antennal marks; **4.** Rounded patch of color on head; **5.** Notched patch of color on head; **6.** Antennal base, lateral view; **7.** Metanotal gland; **8.** Subgenital plate in ventral view; **9.** Internal genitalia in ventral view; **10.** Internal genitalia in dorsal view.

Figs 11–13. *Oecanthus rohiniae* **sp. nov.**, female; **11.** Habitus, female eating on *Croton cilatoglandulifer* Ort; **12.** Cerci; **13.** Ovipositor.

Morphological diagnosis.—Oecanthus rohiniae **sp. nov.** can be distinguished from O. *rileyi* by differences in antennal markings and from *O. fultoni* by differences in the distal hooks of the copulatory blades of the male genitalia. The antennal markings of *O. rohiniae* **sp. nov.** are centered and fairly equal in size (Figs 3, 20). The antennal marking on the pedicel of *O. rileyi* is positioned at the top of the segment, and is approximately one-half the size of the marking on the scape (Fig. 22). A drawing in Walker and Gurney (1960) of male genitalia shows that the distal ends of the copulatory blades of *O. fultoni* appear rounded with sharply pointed medially opposing hooks (Fig. 27). The distal ends of the copulatory blades of *O. rohiniae* **sp. nov.** are more blunted, and the tips of the hooks are less pointed (Fig. 23). A second drawing in Walker and Gurney (1960) shows an undetermined *rileyi* species group tree cricket from Tamaulipas, Mexico (Fig. 24) with hook position similar in appearance to *O. rohiniae* **sp. nov.** Photos of the lateral view of the blades of *O. rohiniae* **sp. nov.** (Fig. 25) and *O. fultoni* (Fig. 28) highlight the hook tip differences.

Female description.—(Figs 11–13) Latticed vein pattern on translucent greenish wings. Body length 11.5 mm; pronotal length 2.0, distal pronotal width 2.0; hind femur length 7.0; cerci 4.5; ovipositor length 3.5. The length of the hindwings is variable. The tip of the ovipositor does not extend beyond the tips of the cerci.

Figs 14, 15. Characters of *O. rohiniae* **sp. nov.** nymphs: Even rows of white rounded markings on the abdomen, black speckles on the hind femora, and black rings on the antennal filaments.

Nymphs.—(Figs 14, 15) Straight rows of white rounded marks on the abdomen, black speckles on the hind femora, and evenly spaced black rings on the antennal filaments. Nymphs of various instar stages, as well as adults, were encountered year round.

Distribution and habitat.—Cri-Cri tree crickets have only been collected in the type locality in the biogeographic province of the Trans-Mexican Volcanic Belt, in the State of Querétaro, located in the Central-South part of Mexico. The vegetation was categorized by dry shrubland with cacti (crassifolia), grassland (mattoral), reinvading natural vegetation on disturbed land (ruderal), and introduced plants. A total of 33 plant species were able to be identified in the type locality (Calderón de Rzedowski and Rzedowski 2001, Martínez-Sandoval 2017). Adults and nymphs of this new species of tree cricket were observed on 14 of these plant species and were witnessed feeding on eight plant species (native plants: *Asclepias curassavica* L., *Croton cilatoglandulifer* Ort., *Justicia candicans* (Nees) L.D., *Lantana camara* L., *Lantana hirta* Graham, *Colubrina triflora* Brogn Ex Sweet (also oviposition) and introduced plants: *Calendula officinalis* L., *Cnidoscolus multilobus* (Pax) I. M. Johnst, *Ruta graveolens* L., and *Thunbergia alata* Bojer Ex Sims). An ovipositing female as well as nymphs were found on *Colubrina triflora* Brogn. Ex Sweet, a native plant. Nymphs were found on three native plants: *Lantana hirta* Graham, *L. camara L, and C. cilatoglandulifer* Ort.

Climate and light intensity.—National Weather Commission (NWC 2020) data for 2009–2019 showed the coldest months as December and January (lowest 4.0 °C) and the warmest months as April and May (highest 33.2 °C). The driest months tend to be November through March (lowest 0.0 mm) and the wettest months tend to be June through September (highest 207.0 mm). Males sing just before or after sunset with light measurements of 5 W/m^2 and temperatures as low as 11.0 °C.

Acoustics, chirp rates, frequencies, and slopes.—Recordings were made in the field and in captivity for *O. rohiniae* **sp. nov.** A sample recording can be heard in Suppl. material 3: WAV, and a stridulating male can be viewed in Suppl. material 4: MPG. After plotting the data of temperature vs chirps per minute and carrier frequency vs temperature, linear regression lines were calculated for *O. rohiniae* **sp. nov.**, *O. fultoni, and O. rileyi*. The linear regression for temperature vs chirps per minute of *O. rohiniae* **sp. nov.** was calculated to be y=7.0418× – 5.3551, and at 25.0°C the chirps per minute rate was 171 (Fig. 17). The linear regression for carrier frequency (kHz) vs temperature (degrees celsius) of *O. rohiniae* **sp. nov.** was calculated to be y=0.0685× + 0.09002, and at 25.0°C the carrier frequency was 2.61 kHz (Fig. 18). The chirps per minute rate vs temperature response of *O. rohiniae* **sp. nov.** is distinctly different from *O. rileyi*. The slopes of both *O. rohiniae* **sp. nov.** and *O. fultoni* were further examined using a t-test analysis. This analysis resulted in a t-value of $t(47)=3.08$ with a probability value of $p=0.0035$, clearly indicating that the slopes of the chirps per minute vs temperature response for both species are significantly different at the 99% level.

Chirp pulse pattern comparisons and diagnosis.—Visual inspection of song oscillograms revealed that *O. rohiniae* **sp. nov.** has chirps with grouped pulses. The chirp pulse grouping patterns of *O. rohiniae* **sp. nov.** are 2-2, 2-3, 2-3-2 or 2-3-3 (Fig. 19). Of the 601 individual chirps examined, 76.9% were 2-3 or 2-3-2 patterns. The predominant patterns for *O. fultoni* were 2-3 or 2-3-3. We found

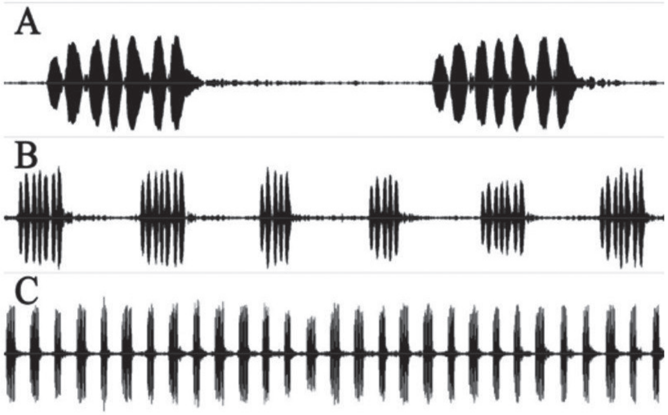


Fig. 16. Oscillograms of the calling song of *O. rohiniae* **sp. nov.** at 17.0°C. **A.** Two chirps; **B.** Three seconds of chirping; **C.** 15 seconds of chirping.

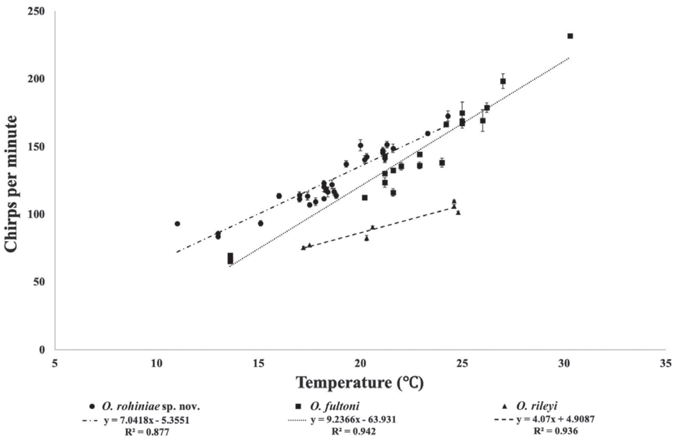


Fig. 17. Change in chirps per minute with temperature of *O. rohiniae* **sp. nov.**, *O. fultoni*, and *O. rileyi*. Data for *O. fultoni* and *O. rileyi* recordings in Suppl. material 2: source recordings.

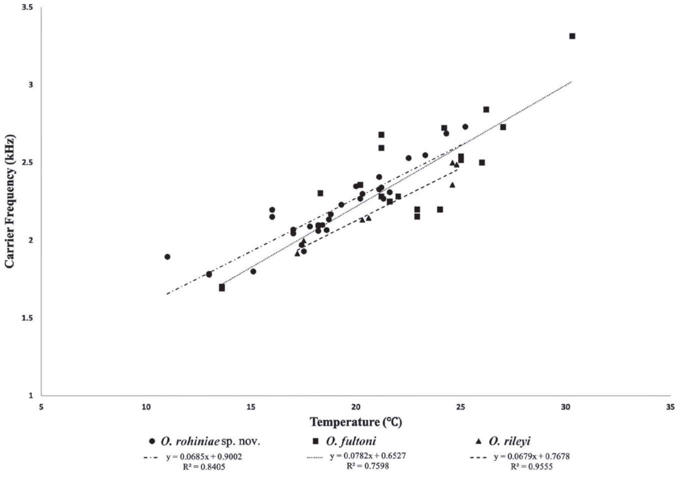


Fig. 18. Change in carrier frequency with temperature of *O. rohiniae* **sp. nov.**, *O. fultoni*, and *O. rileyi*. Data for *O. fultoni* and *O. rileyi* recordings in Suppl. material 2: source recordings.

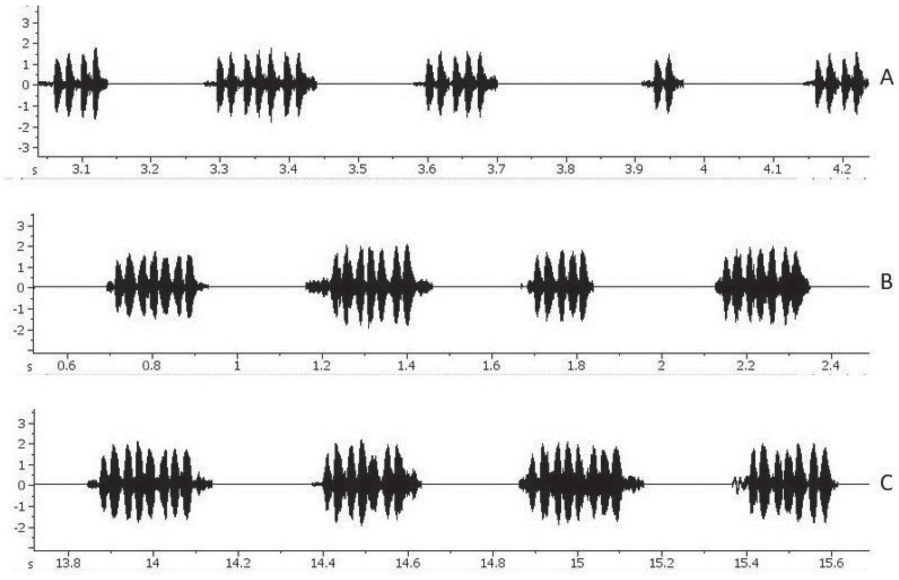


Fig. 19. Pulses per chirp patterns of *O. rohiniae* **sp. nov.** **A**. 2-3 or 2-2 pulses pattern; **B**. 2-3-2 or 2-3 pattern; **C**. 2-3-3 pattern.

two instances of apparent aborted chirps with a single 2-pulse grouping, but we found no recordings of a singing *O. fultoni* with a 2-3-2 pattern. Table 1 shows the percentage of occurrence for chirp pulse patterns for *O. rohiniae* **sp. nov.**, *O. fultoni*, and *O. rileyi*. Since *O. rohiniae* **sp. nov.** has a total of 11 or less pulses per chirp, both *O. alexanderi* and *O. allardi* can be ruled out as their chirps consist of 17–23 or 29–35 pulses, respectively (Walker and Collins 2010). *Oecanthus mhatreae* does not have grouping of pulses in each chirp (Collins et al. 2019).

Other species comparisons.—The known members of the *nigricornis*, *niveus*, and *varicornis* species groups can be ruled out with non-matching song types, tegminal widths, antennal markings, or antennal coloring. Other western hemisphere species of *Oecanthus* can be ruled out for non-matching characters as in Table 2.

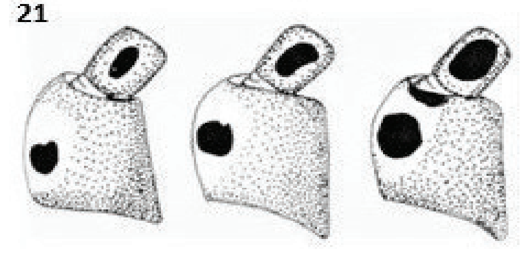
Morphological comparisons.—Since both *O. rohiniae* **sp. nov.** and *O. fultoni* are members of the *rileyi* species group, it is not unexpected that no profound differences were evident in the following characters: coloring, antennal markings, metanotal gland, number of stridulatory teeth, tegmen venation, and subgenital plates. The pedicel of *O. rohiniae* **sp. nov.** has a centered black mark more than one half the size of that on the scape (Fig. 20), which is also found on *O. fultoni* (Fig. 21) but not on *O. rileyi* (Fig. 22). These markings can be either round or ovoid. The copulatory blades of *O. rohiniae* **sp. nov.** have distal hooks that appear somewhat blunted and are positioned at a slight angle (Fig. 23), while those of *O. fultoni* have hooks that are more sharply pointed with tips that reach further midline (Fig. 26). These differences can be compared to drawings in Walker and Gurney (1960) comparing male genitalia of a *rileyi* species group tree cricket from Tamaulipas, Mexico (Fig. 24) with a snowy tree cricket from Ohio (Fig. 27). While we cannot proclaim that the drawing of the Tamaulipas tree cricket in Fig. 24 is *O. rohiniae* **sp. nov.**, the differences in the two drawings do affirm that more than one species of the *rileyi* group exists in Mexico. The difference in the appearance of the hooks on fresh specimens can be seen from a lateral view of the blades, as in Figs 25, 28.

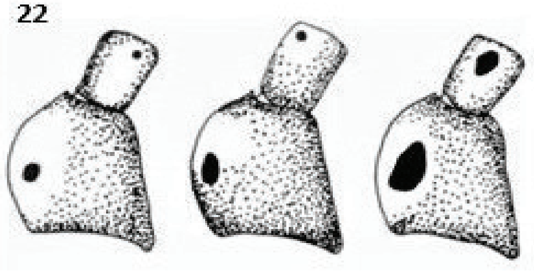
Table 1. Occurrence percentages of grouped pulses per chirp patterns of *O. rileyi*, *O. fultoni*, and *O. rohiniae* **sp. nov.** (n = number of individual chirps sampled).

Pulse pattern usage percentage		
Species	**Pattern**	**Percent**
O. rileyi	2-3-3-3	49.5
(n=198)	2-3-3	40.4
	2-3-3-3-3	6.1
O. fultoni	2-3-3	78.4
(n=679)	2-3	16.2
	2-3-3-3	1
	2	0.7
	3-3	0.15
O. rohiniae **sp. nov.**	2-3	41.9
(n=601)	2-3-2	35
	2-3-3	16.1
	2-2	3.9

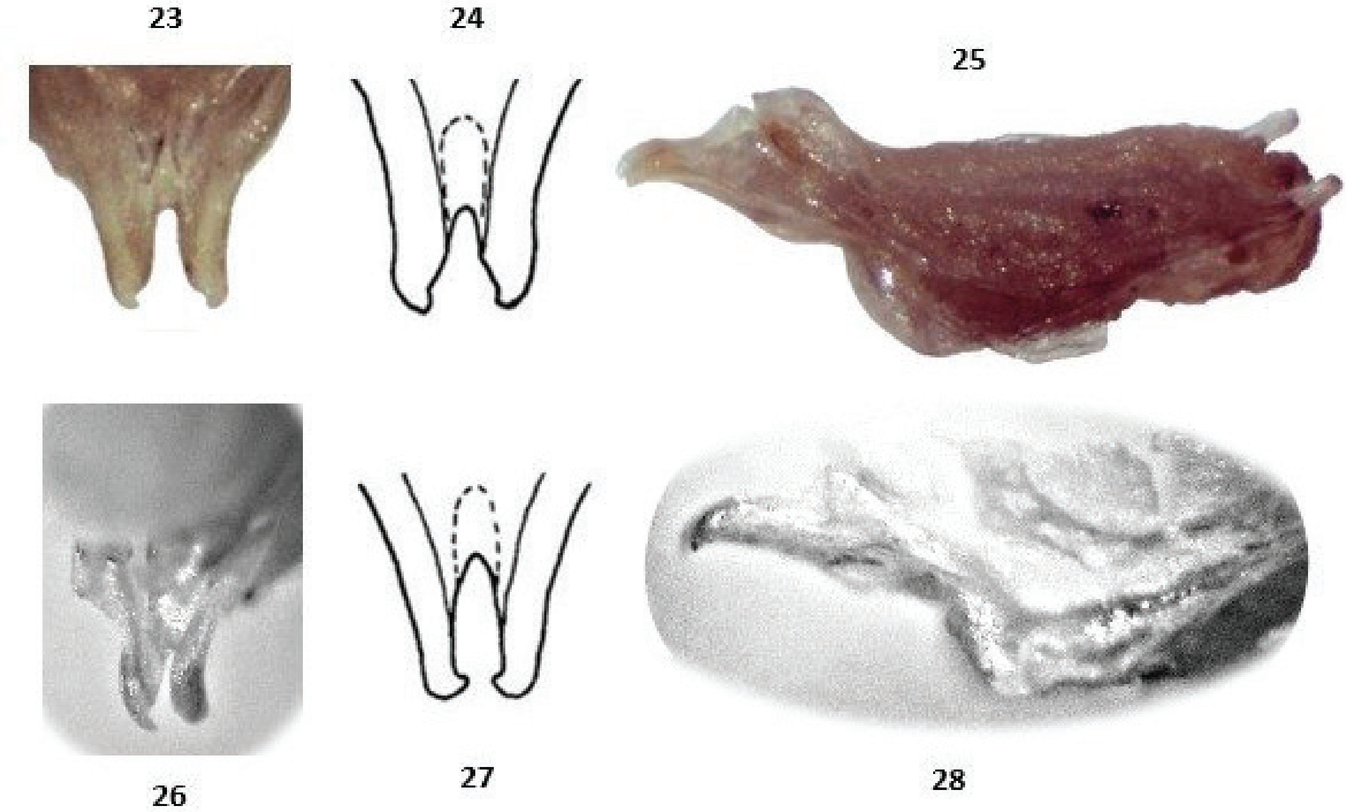
Table 2. Non-matching characters of western hemisphere *Oecanthus* species outside the species groups of *nigricornis*, *niveus*, *rileyi*, and *varicornis*.

Oecanthus **species**	**Nonmatching characters**	**Sources**
major	Proximal antennal flagellum dark	T. Walker 1967
comma	Comma-shaped mark on pedicel	T. Walker 1967
prolatus	Linear mark on scape	T. Walker 1967
lineolatus	Linear antennal markings	T. Walker 1967
tenuis	Linear antennal markings	T. Walker 1967
valensis	Linear antennal markings	Milach et al. 2016
minutus	No or linear antennal markings	T. Walker 1967
immaculatus	No antennal markings	T. Walker 1967
nanus	No antennal markings	T. Walker 1967
peruvianus	No antennal markings	T. Walker 1967
pictipes	Post-ocular lines	T. Walker 1967
pallidus	Bursts of trilling	Zefa et al. 2012
pictus	Trilling song	Milach et al. 2015
belti	Trilling song	Collins et al. 2014
symesi	Trilling song	Collins et al. 2014
jamaicensis	Trilling song	T. Walker 1969
bakeri	Trilling song	Collins et al. 2014





Figs 20–22. Shapes and locations of black markings on pedicel and scape. **20.** *O. rohiniae* **sp. nov.**; **21.** *O. fultoni* (SINA 2020b); **22.** *O. rileyi* (SINA 2020c).



Figs 23–28. Copulatory blades of male genitalia. **23.** Close up ventral view of *O. rohiniae* **sp. nov.**; **24.** Drawing of an undetermined *rileyi* species group tree cricket from Tamaulipas, Mexico (Walker and Gurney 1960); **25.** Lateral view of *O. rohiniae* **sp. nov.**; **26.** Close up ventral view of *O. fultoni* from Texas, USA; **27.** Drawing of *O. fultoni* from Ohio USA (Walker and Gurney 1960); **28.** Lateral view of *O. fultoni* from Wisconsin, USA.

Discussion

We described a new species of *Oecanthus* that falls into the *rileyi* species group. We were able to rule out other chirping species by the following characters: Size and position of the black mark on the pedicel rules out *O. rileyi*; short chirps (less than nine pulses per chirp) rule out *O. alexanderi* and *O. allardi*; and the grouping of pulses in each chirp rules out *O. mhatreae.*

Oecanthus fultoni is morphologically quite similar to *O. rohiniae* **sp. nov.**, however the distal hooks on the male copulatory blades of *O. rohiniae* **sp. nov.** have a slightly blunted point, while the hooks of *O. fultoni* are more sharply pointed. Recorded chirps of *O. fultoni* do not include the 2-3-2 pulse pattern as in chirps of *O. rohiniae* **sp. nov.** T-test analysis of the regression lines for chirps/min rate as it varies with temperature for *O. rohiniae* **sp. nov.** and *O. fultoni* indicated a significant difference between the two species.

A list of recordings by Alexander, which includes notations of '*fultoni*' tree crickets, can be viewed in Suppl. material 1: historical recordings. In 1966, Thomas J. Walker analyzed several of Alexander's recordings. With his permission, we provide a table of these analyses in Suppl. material 5: analyses of historical recordings. These recordings shed light on the need for further investigation of chirping tree crickets in Mexico. Although the Cri-Cri tree cricket is currently only described from Querétaro, there have been other photos from Mexico of similar looking tree crickets submitted to iNaturalist.

Acknowledgements

We thank the California Academy of Sciences for maintaining the website iNaturalist.org, which allows scientists and the general public from around the world to post photographs and sound recordings of insects. We are grateful to Thomas J. Walker, Professor Emeritus, University of Florida, for the wealth of knowledge he generously shares. We thank Thomas Moore, Professor Emeritus, University of Michigan, Museum of Zoology, for his diligent search for Alexander's tapes. We also thank Ludivina Barrientos-Lozano, Professor and Researcher of Tecnológio Nacional de México-Instituto Tecnológico de Ciudad Victoria, and Alejandro Zaldivar Riverón, Professor and Researcher, Instituto de Biología, Universidad Nacional Autónoma de México, who offered lab facilities and assistance. Finally, we appreciate valuable suggestions by Tony Robillard , Edison Zefa, Klaus-Gerhard Heller, and an anonymous reviewer for improving this paper. The Orthopterists' Society provided funding for publishing this paper.

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Supplementary material 1

Author: Thomas Moore

Data type: Notes of recordings

Explanation note: Notes for recordings made by Richard D. Alexander throughout Mexico in 1965 – with notations for 'fultoni' like tree crickets.

Link: https://doi.org/10.3897/jor.30.50039.suppl1

Supplementary material 2

Author: Wil Hershberger

Data type: Song data

Explanation note: Excel spreadsheet showing source recordings and data from Macaulay Lab for *O. fultoni* and *O. rileyi*.

Link: https://doi.org/10.3897/jor.30.50039.suppl2

Supplementary material 3

Author: Bruno Govaerts

Data type: WAV file

Explanation note: WAV file with a recording of *O. rohiniae* sp. nov. made in Querétaro, Mexico. Outdoors – Temperature 16.0°C.

Link: https://doi.org/10.3897/jor.30.50039.suppl3

Supplementary material 4

Author: Bruno Govaerts
Data type: Video
Explanation note: MPG file with a video of a singing male *O. rohiniae* sp. nov. taken outdoors in Querétaro, Mexico. A singing *O. mhatreae* is in the background.

Link: https://doi.org/10.3897/jor.30.50039.suppl4

Supplementary material 5

Author: Thomas J. Walker
Data type: Song Analyses
Explanation note: Song analyses by Thomas J Walker in 1966 of Richard D Alexander's 1965 recordings from Mexico, which included '*fultoni*' tree crickets.

Link: https://doi.org/10.3897/jor.30.50039.suppl5

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Life history of the false flower mantid (*Harpagomantis tricolor* Linnaeus, 1758) (Mantodea: Galinthiadidae) and its distribution in southern Africa

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Abstract

The false flower mantid is the common name for the Mantodea species *Harpagomantis tricolor* (Linnaeus, 1758). This species uses camouflage as a defense mechanism. Limited information (Kaltenbach 1996, 1998) exists on its distribution in southern Africa or about its life history. This species, and Mantodea to an extent, are not usually included in biodiversity studies from this region. The aim of this study was to determine the distribution of this species in southern Africa based on museum collection records and to study the biology of *Harpagomantis tricolor* under captive breeding conditions. The distribution of *Harpagomantis* and its morphological variety, i.e., *discolor*, were determined utilising the historical insect collection records of seven national museums throughout South Africa. Field collected *H. tricolor* males and females were mated and reared under laboratory conditions to record their life history parameters of nymphal duration, oothecae structure, size and incubation duration, adult longevity, and sex ratio. The results of this study indicate that the mean duration of the lifecycle of *H. tricolor* is 191.33 ± 37.96 days. All but three *H. tricolor* individuals had five nymphal instars, and the mean duration of the nymphal stage was 140.20 ± 31.03 days. The mean duration of copulation was six hours, while the average incubation period of oothecae was 144.71 ± 9.33 days. These results indicate that oothecae of *H. tricolor* probably overwinter under field conditions and that males of this species have evolved various mechanisms to increase the likelihood of ensuring their own genetic offspring. This study bridges the gap in rudimental research in which Mantodea, in general, has been overlooked and establishes a basis on which ecological interactions, habitat preferences, and imminent threats to *H. tricolor* can be established.

Keywords

camouflage, copulation, longevity, praying mantis

Introduction

Harpagomantis Kirby is one of four genera in the newly rearranged family of Galinthiadidae (Roy and Stiewe 2014, Svenson et al. 2015, Schwarz and Roy 2019). Within the *Harpagomantis* genus, there were two known species: *Harpagomantis tricolor* (Linnaeus, 1758) and *Harpagomantis discolor* (Stål, 1877). However, *H. discolor* was found to be a morphological variety of *H. tricolor*, and thus the only species within this genus is *H. tricolor*. *Harpagomantis*, *Galinthias*, *Congoharpax*, and *Pseudoharpax* were previously classified as Hymenopodidae. However, due to molecular evidence and the phylogenetic results reported by Svenson and Whiting (2009) and Svenson et al. (2015), these genera were found to be outside of Hymenopodidae and were moved to the new family Galinthiadidae (Roy and Stiewe 2014). Svenson et al. (2015) reported that the high level of homoplasy in the external morphology of these mantids contributed to the discrepancies in species identification based on molecular and morphological characteristics, as these did not align. Thus, these genera were originally classified within the Hymenopodidae family. However, morphological characteristics were also used to aid the rearrangement of these families in an article in which the Mantodea order and its families were revised and rearranged (Schwarz and Roy 2019).

Harpagomantis have been described as "false flower" mantids and are pink with green bands and sometimes yellow eyes (Fig. 1). *Harpagomantis* are reported to live on flowers where they camouflage and wait motionlessly for prey (O'Toole 2003). Camouflage in mantid species has been reported as the primary defense mechanism of these insects (Edmunds 1971), and *H. tricolor* is no exception. It has been recorded during biodiversity survey studies in South Africa, largely in the western Cape region (Grobbelaar et al. 1999, Brand and Samways 2009, Magoba and Samways 2010) and the Highveld grassland biome (Botha et al. 2018, Greyvenstein et al. 2020b). However, the distribution of this species is based solely on studies by Kaltenbach (1996, 1998). The latter study found this genus widespread in southern Africa and included eight of the nine South African provinces and records from Botswana, Lesotho, Namibia, Zambia, and Zimbabwe.

Cardoso et al. (2020) recently reported being concerned about the worldwide decline in insect populations and that only 20% of the total insect diversity has been named. Research is required to bridge this gap in knowledge and correct the bias in insect studies that have largely focused on specific taxa such as butterflies and pollinators (Cardoso et al. 2020). Samways et al. (2020) indicated that mapping the distribution of specific species could contribute to determining their range expansion, threat identification, and habitat favorability. This will aid in bridging the gap in knowledge regarding the distribution, biology, and ecology of the majority of insect species. Similarly, Svenson et al. (2015) reported that the ecology of most Mantodea species remains unknown. Although various studies have been done on Mantodea ecology, very few have been conducted in South Africa and with species of this region. The information available about species' ecology, observations, and biology in South Africa is based on either citizen science or very old publications that could be outdated.

The aim of this study was to determine the distribution of the genus *Harpagomantis* in southern Africa and to study the biology of *H. tricolor* under captive breeding conditions.

Materials and methods

Species distribution database.—Distribution records of *Harpagomantis* spp. were collected during visits to the following institutions that host curated insect collections in South Africa: Ditsong Museum of Natural History (Pretoria), Agricultural Research Council (Biosystematics Division, Pretoria), National Museum (Bloemfontein), Albany Museum (Grahamstown), Rhodes University (Grahamstown), Durban Natural Science Museum, Iziko South African Museum (Cape Town), and KwaZulu-Natal Museum (Pietermaritzburg). Most specimens in these collections were previously identified by foreign visiting taxonomists, and many were sent for identification to the Vienna Museum in Germany, the University of Drexel in Philadelphia, USA, the Muséum national d'Histoire naturelle (MNHN) in Paris, France, and the research collection of Nicolas Moulin in Montérolier, France.

Harpagomantis specimens and distribution labels were photographed (Canon D1300) and digitized, after which this data was used to compile a distribution database of the species. The database contains the following information for each specimen record: genus and species name (to the available level of identification), collector's details and collection date where available, and the geo-referenced locality. Scientific literature (Ehrmann 2002, Svenson 2015, Schwarz and Roy 2019) was used to determine the current nomenclature within the genus. All locality data were georeferenced using the principles suggested by Wieczorek et al. (2004). Subsequently, all coordinates were converted from degrees, minutes, and seconds (DMS) to decimal degrees (DD) (gps-coordinates.net). Decimal degrees were used for developing distribution maps for *H. tricolor*, the *H. discolor* variety, and the specimens that have not been morphologically distinguished in southern Africa by means of GIS software (ArcMaps, Version 10.6.1). The collection dates recorded for each specimen were used to generate intervals of 11 years (i.e., 1856–1867 and 1868–1879) to compile a graph indicating the number of specimens collected over time and during certain intervals.

Rearing and biology.—Specimens were collected in the Grassland biome in the North West and Free State provinces of South Africa during the summer of 2016/2017. Adults of these field-collected individuals were mated, and nymphs that emerged from oothecae were used to rear a sufficient number of individuals to observe under captive breeding and rearing conditions. A sub-sample of the field-collected specimens was identified by Nicolas Moulin (honorary associate to MNHN) to confirm the species identification.

For breeding purposes, pairs of males and females were placed in glass containers. Glass containers (40 cm × 20 cm × 20 cm) were used to ensure that ample space was available for the male to avoid sexual cannibalism before, during, or after mating. To further limit the likelihood that females would cannibalize the males, ample food was provided before the male was introduced into the breeding container. The duration of copulation was recorded per breeding pair (Fig. 1c). After copulation concluded, the male was removed from the breeding container. The terrariums (15 cm × 10 cm × 20 cm) in which females were kept after mating were checked daily for the presence of oothecae that were laid overnight. Oothecae were removed and put into small containers (5 cm diameter and 5 cm high) inside a desiccator. A humidity level of 68 ± 5% was maintained in the closed desiccator, following the method described by Solomon (1951). The desiccator was kept in an insect rearing room at a temperature of 27 ± 1 °C with a 14L:10D photoperiod cycle until nymphs emerged from the oothecae.

Rearing of nymphs was done under controlled conditions (Fig. 1d). Each specimen was placed into a terrarium (7 cm diameter and 15 cm high) with three holes (each 2 cm in diameter) covered with gauze to allow air flow. Thin twigs (5 mm × 10 cm) were placed inside each jar for climbing and hanging purposes, especially during moults. Food was provided every second day at the same time as fine water mist was sprayed into each container. Live aphids (*Brevicoryne* spp.) (Hemiptera: Aphididae) were provided as food for first- to third-instar nymphs, after which live crickets (*Acheta* sp., Orthoptera: Gryllidae) of different sizes (nymphal instars, i.e., pinheads) were provided. After moulting to the second-instar, nymphs were removed from the communal terrariums and placed in separate terrariums to prevent cannibalism. Nymphs were reared until adulthood, after which males and females were identified. This was done by counting the number of abdominal segments and the appearance of the wings. *Harpagomantis tricolor* females have shorter wings (barely covering the abdomen) and six abdominal segments, while males have eight segments and wings that are longer than the abdomen (McMonigle 2013, Fatimah et al. 2016, Brannoch et al. 2017) (Fig. 1a, b).

The following life history parameters were recorded during this study: size of oothecae, number of egg chambers inside fertilized and unfertilized oothecae, copulation duration, number of days between moults, and survival rate (based on nymphs reaching the adult phase). The mean number of days between moults and days to adulthood were calculated separately for males and females. The data discussed in this paper were recorded for 45 individuals (14 males and 31 females) that completed their life cycles. The mean duration of male and female life cycles was calculated, and the hatch and survival rates were determined. A distinction was also made between different types of oothecae, i.e., fertilized and unhatched (produced by field-collected females of which the mating status was not known). The length, width, and height of each ootheca were recorded based on descriptions by Brannoch et al. (2017). The ootheca length was measured along the area of emergence, excluding the residual process (Brannoch et al. 2017, Greyvenstein et al. 2020a). To determine the number of eggs per ootheca, oothecae were dorsally dissected along the length and inspected under a microscope, as was done by Greyvenstein et al. (2020a). Measurements of ootheca parameters were done as indicated in Fig. 1e.

Data analysis.—The descriptive statistics (means and standard error) and the statistical analyses of the developmental parameters were done using Statistica Version 13.3 (TIBCO Software Inc., 2017). Shapiro-Wilk normality test was used to determine if the data were normally distributed, and data that were not normally distributed were log-transformed. T-tests were used to determine if differences existed between the length, width, height, and the number of eggs per ootheca between the two types of oothecae (i.e., fertilized and unfertilized). T-tests were also used to determine if differences existed between the mean numbers of days between moults, adult longevity, and mean number of days required by nymphs to reach adulthood.

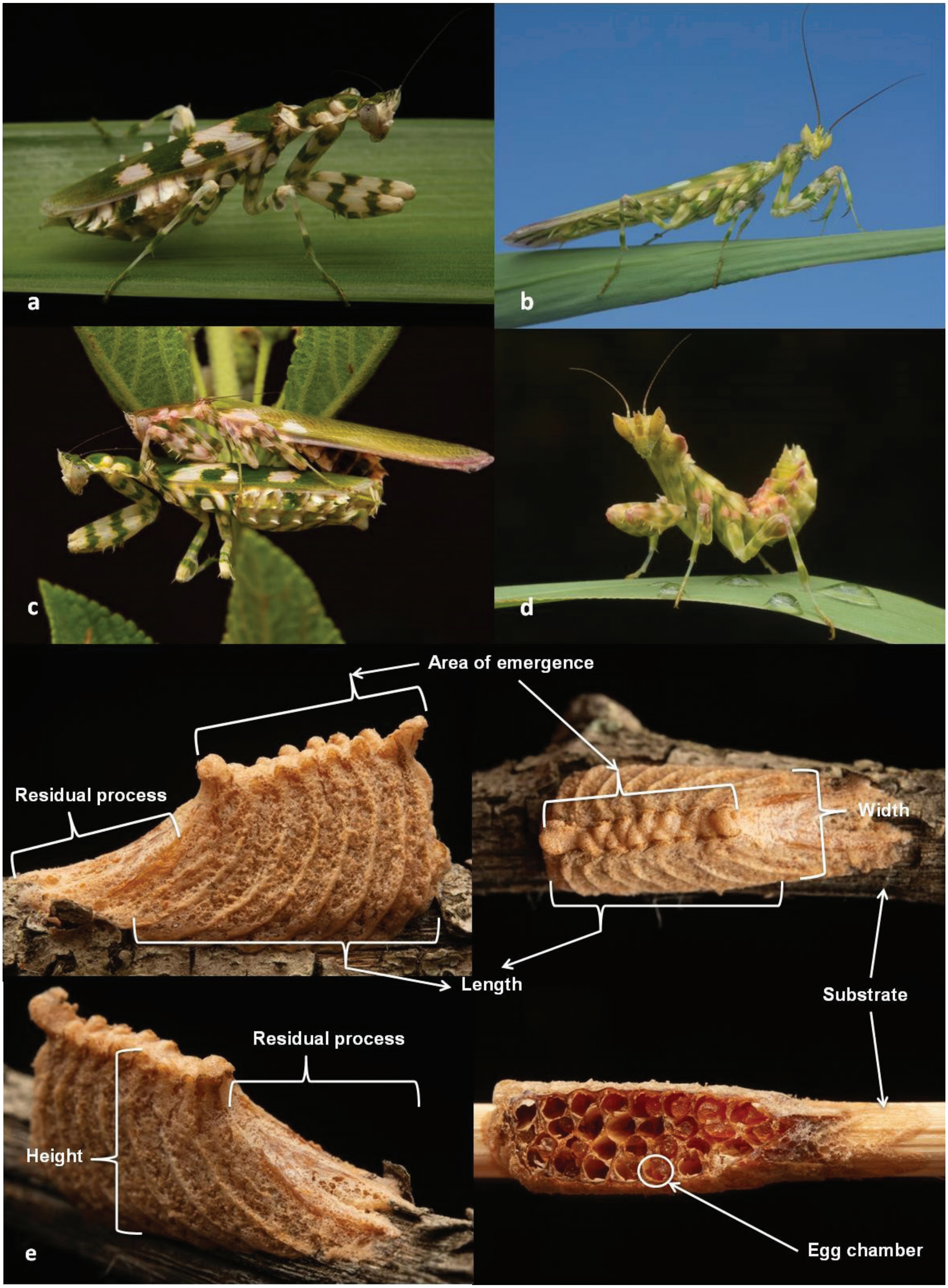


Fig. 1. *Harpagomantis tricolor* female. **a.** Male; **b.** Copulating adults; **c.** Fifth-instar nymph; **d.** General morphology of the oothecae; **e.** Indicating different parameters and areas of interest as suggested by Brannoch et al. (2017). Photographs by Paul Janse van Rensburg.

Results

Distribution.—The distribution records reported in this paper were compiled from records available in the seven South African institutions that host curated arthropod collections. Results should be viewed in this context, since no museum records beyond those residing in South Africa were included. The results of this study and the following previously published studies (Kaltenbach 1996, 1998, Grobbelaar et al. 1999, Brand and Samways 2009, Magoba and Samways 2010, Botha et al. 2018, Greyvenstein et al. 2020b), to our knowledge, are the only studies to include distribution records of this species. The distribution records included records of *Harpagomantis tricolor* as well as the *discolor* morphological species variety from the following southern African counties: Botswana, Eswatini, Lesotho, Mozambique, Namibia, and Zimbabwe (Fig. 2).

A total of 290 specimen records were accounted for, of which 272 were collected within the borders of South Africa (this includes specimens collected in Lesotho and Eswatini). The remaining 18 records of *H. tricolor* were distributed as follows: two specimens collected in Botswana, six in Namibia, four in Mozambique, and six in Zimbabwe (Fig. 2). *H. tricolor* records were collected throughout South Africa and neighboring countries (Fig. 2). The distribution of *H. tricolor* in South Africa seems to be predominantly towards the eastern region of the country, with a few specimen records from the western region, specifically in the Western Cape Province (Fig. 2). The oldest *H. tricolor* specimen record was collected in 1876 in Cape Town. Only four specimens were collected between 1876 and 1887, while the largest number (37) were collected between 1912 and 1923 (Fig. 3). Between 1972 and 2019, the average number of specimens collected during the three 11-year intervals was 31 (Fig. 3). Only 48 specimen records (18%) were collected within protected areas of South Africa, while 224 records (82%) were collected outside these areas. These 48 specimens were collected in 11 different provincial nature reserves (19 records), four private nature reserves (14 records), two national parks (9 records), and one specimen was collected in each of a world heritage site, a protected forest area, and a local nature reserve (Fig. 4).

Biology.—The ootheca of *H. tricolor* is not covered in the usual foamy sheath that is characteristic of a variety of Mantodea, although exceptions do exist (McMonigle 2013). The oothecae are usually small, light brown in color, almost rectangular in shape, and slightly dorsally flattened (Fig. 1e). The residual process is not elongated or extended into any shape or point. In cases where the oothecae of *H. tricolor* were attached to the stem of a flowering plant in the field, they most likely resembled a thorn. Eggs were arranged in adjacent rows of between three and five eggs each (Fig. 1e). The residual process was also investigated but did not contain any egg chambers.

In this study, 19 oothecae were produced by field-collected females mated under captive breeding conditions. Seven of these did not hatch and 12 oothecae did hatch. In total, 63 nymphs emerged from the 12 fertile oothecae under captive breeding conditions. No significant differences were recorded between the length, width, height, or number of eggs of the fertilized or unhatched oothecae. Mean ootheca length was 8.5 ± 4.11 mm, containing 17.26 egg ± 6.66 chambers per ootheca (Table 1). The mean width and height of an ootheca was 4.37 ± 0.76 mm and 6.15 ± 0.83 mm, respectively (Table 1).

Developmental parameters.—Of the 63 neonate nymphs that hatched from the 12 different oothecae throughout this study, 45 completed their lifecycles (14 males and 31 females). The mean duration between mating and the production of an ootheca was

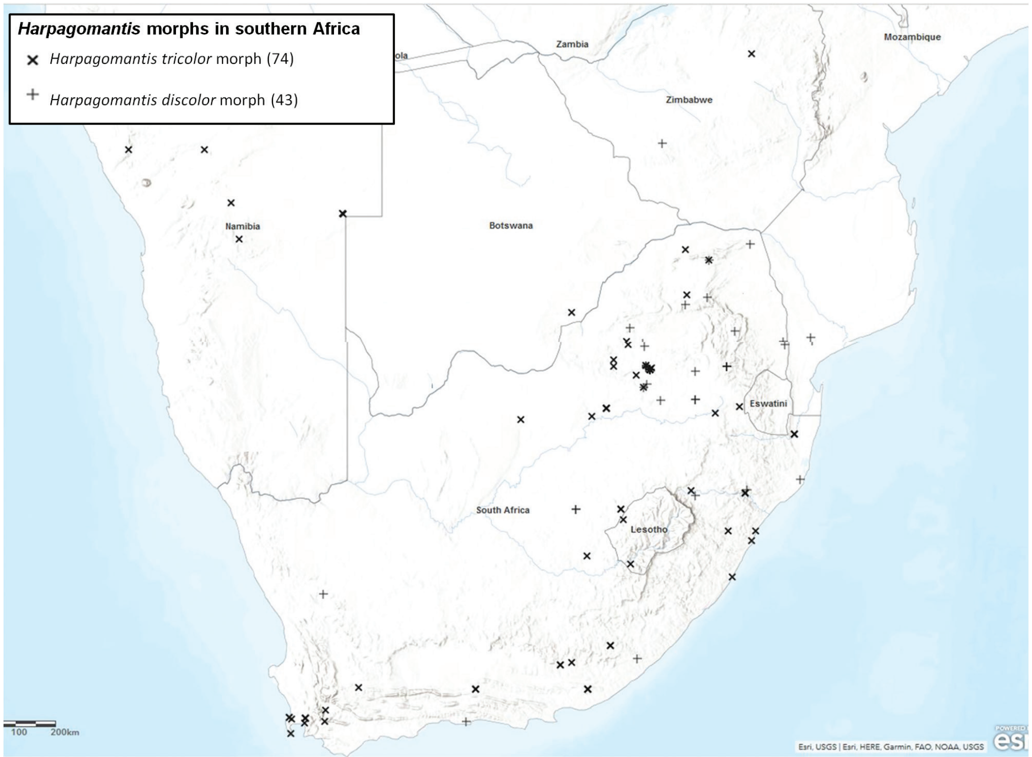


Fig. 2. Distribution records of *Harpagomantis tricolor* and its morph (discolor) that occur in southern Africa. Numbers in brackets indicate the number of individual records per variety.

11.82 ± 9.51 days, and the act of copulation itself continued for approximately six hours (Table 3). The incubation period of an ootheca was approximately 20 weeks (143 days). The mean hatch rate was 31%, while the average survival rate was almost 68% (Table 2). The sex ratio differed between the various oothecae, but the mean sex ratio (M:F) was 1:1.5. Two of the oothecae produced only males, while another two produced only females (Table 2).

No significant differences were recorded between the average duration per instar of females and males. The nymphal period took approximately 20 weeks to complete (Table 3). However, females required a longer nymphal period (145.71 ± 29.88 days) than males (128.00 ± 31.09 days), even though this difference was not significant. The mean duration of the lifecycle of *H. tricolor* individuals in this study was six months (191.33 ± 37.96 days).

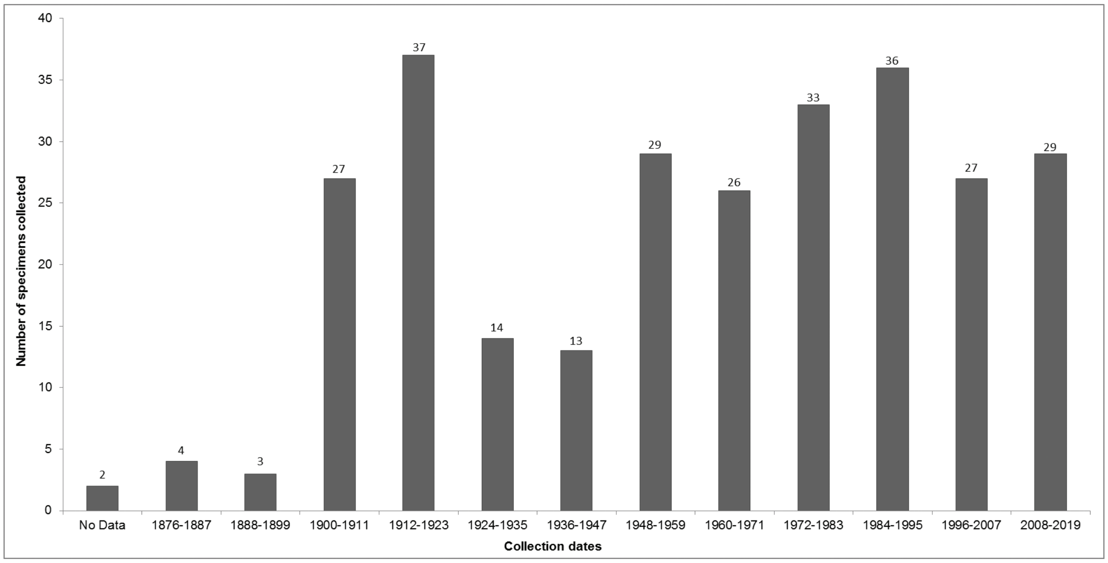
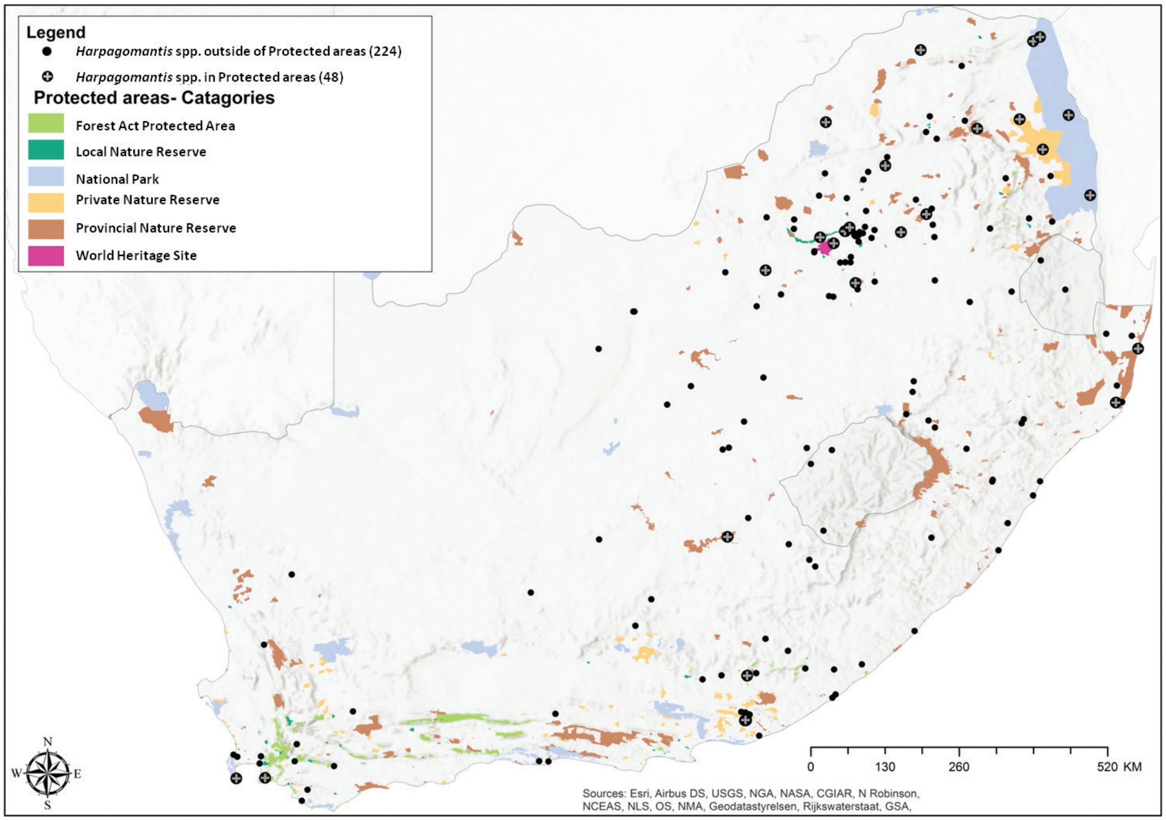


Fig. 3. Number of *Harpagomantis* species records collected in southern Africa during different time periods.



Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA,

Fig. 4. Distribution records of *Harpagomantis* species collected in protected and non-protected areas of South Africa.

Table 1. Mean size and number of egg chambers inside the various types of oothecae of *Harpagomantis tricolor* reared under captive breeding conditions. SD = standard deviation.

Oothecae (19)		Length (mm) ± SD	Width (mm) ± SD	Height (mm) ± SD	Number of eggs/ootheca ± SD
T-test	t-value	0.573	0.986	0.058	0.267
	p-value	0.574	0.338	0.954	0.792
Overall (19)		8.58 ± 4.11	4.37 ± 0.76	6.15 ± 0.83	17.26 ± 6.66
Unhatched (7)		7.86 ± 2.24	4.14 ± 0.69	6.14 ± 1.21	16.71 ± 7.20
Fertilized (12)		9.00 ± 4.63	4.50 ± 0.80	6.17 ± 0.58	17.58 ± 6.63

Table 2. Mean duration (in days) of each of the life stages of *Harpagomantis tricolor* and differences between male and female development under captive breeding and rearing conditions. Three of the females developed to the sixth-instar and were not included in the table below.

Life stage	Mean duration (days ± SD)			t-value	p-value
	Overall	Males	Females		
Ootheca (incubation period)	144.71 ± 9.33	142.51 ± 10.90	145.68 ± 8.55	1.057	0.297
First instar	26.62 ± 11.07	25.36 ± 9.91	27.19 11.67±	0.373	0.710
Second instar	24.67 ± 15.63	28.57 ± 17.51	22.90 ± 14.66	-1.110	0.273
Third instar	27.67 ± 13.06	33.38 ± 18.5	25.42 ± 9.37	-1.784	0.082
Fourth instar	41.55 ± 22.91	49.00 ± 29.63	39.24 ± 20.47	-0.838	0.407
Fifth instar	51.50 ± 13.28	54.00 ± 9.00	51.06 ± 14.06	-0.499	0.624
Copulation to oothecae (days)*	11.82 ± 9.51	12.27 ± 8.67	11.63 ± 9.99	-0.135	0.894
Copulation duration (hours)**	06:10 ± 0.04	06:15 ± 0.04	06:08 ± 0.03±	-0321	0.750
Total nymphal period (days)***	140.20 ± 31.03	128.00 ± 31.09	145.71 ± 29.88	1.776	0.082
Adult longevity (days)****	51.11 ± 39.76	31.57 ± 29.72	59.93 ± 40.97	-0.509	0.613
Period from hatch to death (days)	191.33 ± 37.96	161.71 ± 20.47	204.71 ± 36.58	-0.509	0.613

* duration of period between male and female copulation and production of ootheca; ** duration of male and female copulation; *** from ootheca hatch to final moult (first-instar to fourth/fifth-instar); **** duration of adult phase.

Table 3. The mean hatch rate, survival rate, and gender dynamics that resulted from each of the field-collected *H. tricolor* females (12 individuals) that were kept in the laboratory and each of their associated fertile oothecae (12).

Ootheca number	Oothecae incubation (days)	No. of eggs per ootheca	Hatch rate (%)	Survival (%)	Male (%)	Female (%)	Sex Ratio (♂:♀)
Ootheca 1	123	16	81.25	69.23	33.33	66.67	1:2
Ootheca 2	149	14	28.57	100	0.00	100.00	0:4
Ootheca 3	145	19	31.58	100	83.33	16.67	1:0.2
Ootheca 4	155	18	33.33	50	33.33	66.67	1:2
Ootheca 5	127	16	25.00	100	0.00	100.00	0:4
Ootheca 6	138	18	16.67	100	33.33	66.67	1:2
Ootheca 7	145	15	20	33.33	100.00	100.00	1:1
Ootheca 8	156	9	44.44	50	100.00	0.00	2:0
Ootheca 9	153	36	13.89	60	33.33	66.67	1:2
Ootheca 10	147	12	25.00	66.67	0.00	100.00	0:2
Ootheca 11	143	21	14.29	66.67	50.00	50.00	1:1
Ootheca 12	139	17	35.29	16.67	60.00	40.00	1:0.67
Mean ± (SD)	143.33 ± 10.31	17.58 ± 6.63	30.78 ± 18. 35	67.71 ± 28. 04	43.89 ± 36.15	64.44 ± 33.46	1:1.5

Discussion

Distribution patterns of Harpagomantis tricolor *in southern Africa.*—Although there have been some discrepancies in the past regarding the species within this genus, it is assumed that two morphological varieties exist: *H. tricolor* and *H. discolor*. Specimen records throughout the museum collections in South Africa exist for both morphological varieties (morphs). According to Stål (1877) and Giglio-Tos (1927), *H. discolor* males do not have a brown spot on the hindwings, and the species is generally larger than *H. tricolor*. Rehn (1927) reported that *H. tricolor* was a much smaller species with limited distribution (mostly in the Western Cape region of South Africa), while *H. discolor* occurs throughout South Africa but predominantly in the northern region. The latter species is also believed to be larger and have elongated processes on the eyes (non-visual elongations that do not contain ommatidia).

However, Karny (1908) indicated that *H. discolor* could be a variety of *H. tricolor*. This view was shared by Beier (1955), who stated that *H. discolor* was a "pigment-poor" variety of *H. tricolor*. A similar conclusion was drawn by Kaltenbach (1996), and this species was therefore considered an intra-species variety (in size and color) of *H. tricolor* and, according to Kaltenbach (1996), *H. discolor* is a synonym of *H. tricolor.* Ehrmann (2002) agreed with Beier (1953, 1955) and Kaltenbach (1996) and noted that *H. discolor* was a synonym for *H. tricolor*.

Rehn (1927) indicated the possibility of a clinal North-South differentiation between the two *Harpagomantis* morphs. Similarly, Kaltenbach (1994) noted a clinal variation of the subspecies of *Bisanthe* Stål, 1876, also in southern Africa. Kaltenbach (1994) described *B. menyharthi menyharthi* (Brancsik, 1895) to have a northern distribution (towards Zambia), while *B. menyharthi raggei* was recorded largely in the south towards Zimbabwe and Botswana (South of the Zambezi river). Although Kaltenbach (1994) indicated that temperature could have played a role in the clinal differentiation of the subspecies of *Bisanthe* in southern Africa, other factors could also be responsible for such observed differentiations. For example, Lombardo (1995) noted that the Great Rift Valley tectonic plate could be the dividing line between the clinal differentiations noted in the subspecies of *Popa spurca* Stål, 1856 (*Popa spurca spurca* Stål, 1856 and *Popa spurca crassa* Giglio-Tos, 1917) in Africa. The Great Rift Valley has been shown to be an important natural barrier for various invertebrate species, especially *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) and *Sesamia cretica* Lederer (Lepidoptera: Noctuidae), and is suspected to be the cause of their genetic differentiation into different clades towards the south, east, and west of the Rift Valley (Sezonlin et al. 2006, Assefa et al. 2015, Goftishu et al. 2016). This, as well as temperature (as indicated by Kaltenbach 1994), could be contributing factors to the differentiation reported in some African mantid species as well and should be further investigated. Despite this possible differentiation, the morphological variety, *discolor*, of *H. tricolor* remains a synonym, and thus only one species is known within the *Harpagomantis* genus.

The *discolor* variety of *H. tricolor* was last recorded in 1977 in Harkerville in the western Cape, while *H. tricolor* (except for the specimen collected during this study) was also collected in the western Cape during 2015 at Stellenbosch. It should further be noted that 176 *H. tricolor* specimens were recorded during this study; however, the morphological variety of these specimens could not be identified.

Literature on *H. tricolor* is somewhat scarce, but some studies have reported on the distribution of this genus. For example, in 1999, *H. tricolor* was collected on an indigenous plant species, *Delairea odorata* (Asteraceae) (Cape Ivy), which occurs along the east coast of South Africa (Grobbelaar et al. 1999). This mantid species was also recorded in fynbos and native vegetation that were cleared of alien invasive trees (Magoba and Samways 2010) as well as in the De Hoop Nature Reserve, a World Heritage site in the western Cape (Brand and Samways 2009). *Harpagomantis* specimens were also recorded in the Highveld grassland biome of South Africa (Botha et al. 2018, Greyvenstein et al. 2020b). Beyond these studies, the distribution of this genus is recorded to be throughout South Africa, but predominantly in Western Cape, KwaZulu Natal, and Transvaal (Beier 1955). Patel et al. (2016) listed the distribution of this genus to include Botswana, Namibia, Mozambique, and Zimbabwe, which is similar to the distribution of the genus described by Kaltenbach (1996). As the results of this study indicate (Fig. 2), various regions in South Africa (i.e., the Northern Cape, Free State, and parts of the Eastern Cape) had very few to no distribution records. Thus, these regions should be the priority of future investigations to determine if the extent of the distribution of this mantid species as presented in this study is a true representation with regards to *H. tricolor* in South Africa. This will also shed some light on the fact that these areas might have been underrepresented or under-investigated in previous collection efforts and, thus, few museum specimens from within these regions exist.

Gillon and Roy (1968) reported that a similar species, *Pseudoharpax virescences* Serville, 1839 (Mantodea: Galinthiadidae), occurs from Senegal to Cameroon, while more recently Moulin et al. (2017) and Moulin (2018) reported *Congoharpax aberrans* La Greca, 1954, and various other Galinthiadidae species to be found in the western tropical African countries: the Congo Republic, DR Congo, Cameroon, Ghana, Ivory Coast, and Gabon. These regions should be investigated in the future, as they could be a possible habitat of *H. tricolor* beyond that recorded in this study. Similarly, museum specimen records in European countries should also be incorporated, and citizen science platforms, such as iNaturalist and iSpot, should be used to establish the distribution of this species.

Ecomorphs (morphologically similar characteristics that align with particular habitats, such as certain camouflage capabilities) of mantids such as *Harpagomantis* are suspected to have evolved several times in different geographic regions due to similar habitats and ecological pressures (Svenson and Whiting 2009, Wieland 2013, Svenson et al. 2015). The morphological foundation of Mantodea taxonomy has caused inconsistencies, since the biogeographical distribution of ecomorph species was not previously considered and because a range of species that are morphologically similar occur on other continents. For example, *H. tricolor* in South Africa and species of the genus *Creobroter* Audinet (Mantodea: Hymenopodidae) from India (More and Prashant 2018) are morphologically similar. Thus, future investigations could shed some light on the extent of differentiation between the North and South *H. tricolor* varieties.

Many specimens were collected in Gauteng province, which is the region in South Africa with the highest human population density. This high population density could explain the large numbers of specimens collected in this region (Greyvenstein et al. 2020a). However, as reported by Grytnes and Romdal (2008), this could also be due to ease of access to natural areas where specimens can be collected outside of protected areas. In this study, most specimens were collected in provincial nature reserves. Davis et al. (2005) indicated that the Department of Agriculture, Conservation, Environment and Land Affairs has focused on protecting as much local flora and fauna as possible in provincial and local nature reserves in highly populated areas throughout South Africa.

This study suggests that provincial nature reserves, more so than national parks, may create refuge areas for species in a mosaic of disturbed and highly populated areas. An example of a provincial and/or local area that can be regarded as a refuge for birds in highly developed areas was reported by Wang et al. (2013) in China, where the Hengshui Lake nature reserve, close to the city of Jizhou, was created as a safe place for migratory and endangered bird species. However, more research is needed to determine if protected areas serve as refuges for less mobile species such as mantids. Future investigations should, therefore, be conducted to determine if *Harpagomantis* species are still present within provincial nature reserves, as suggested by the historic specimen records.

Biology.—Since no previous information on the biology of *H. tricolor* could be found, comparisons of its biology are made with species such as *Ephestiasula pictipes* Wood-Mason, 1879 (Mantodea; Hymenopodidae) (Vanitha et al. 2016), which is in the Hymenopodidae family, from where *H. tricolor* was moved based on molecular evidence (Svenson et al. 2015). Due to the lack of literature about the particular biological parameters measured in this study, the investigations reported by Vanitha et al. (2016) will be used for comparison purposes. The study by Gillon and Roy (1968) indicated various biological parameters of the related species *Pseudoharpax virescences* Serville, 1839 (Mantodea: Galinthiadidae) and will thus be also be used as a comparison to *H. tricolor*. The shapes of the oothecae of *H. tricolor* and *P. virescences* are similar, but *H. tricolor* oothecae are longer and wider than those of *P. virescences*.

Larsen (2002) suggested that the structure and morphology of mantid oothecae provide them with the ability to survive harsh environmental conditions. The function of the shell shape of some mantid oothecae, for example that of *Gongylus* Thunberg, 1815 (Mantodea: Empusidae) and *Empusa* Illiger (Mantodea: Empusidae), is to divert heat (Larsen 2002). Another explanation for the unique shape and color of the oothecae of some species is that they aid in crypsis (Thomann 2002). The shape and color of *H. tricolor* oothecae resemble, to an extent, the tubercle or auxiliary buds of plants. This could be an adaptation of this mantid species to blend into its environment, which is suggested to be predominantly on flowering plants, thus allowing the oothecae to be more inconspicuous and limiting unwanted investigation from potential predators. The ootheca of *H. tricolor* is an example of the wide variety of structural diversity and cryptic adaptations that are found throughout the oothecae of Mantodea (Rivera and Svenson 2016). Their small size (length, width, and height) contributes to their inconspicuousness, especially on thorny vegetation. The frequency of *H. tricolor* oothecae attached to various plant species, as well as the placement of the oothecae on the plants themselves, should be investigated in the future to assess the possibility of oothecae structures as cryptic adaptations and their effectivity as such.

The number of eggs within the oothecae of *P. virescences* was reported to be between 12 and 13 hatchlings per oothecae (Gillon and Roy 1968). Unfortunately, no dissections were made by Gillon and Roy (1968); thus, the number of eggs was not reported. Suckling (1984) reported an average of 34 eggs per ootheca for *Orthodera ministralis* (Fabricius, 1775) (Mantodea: Mantidae), which is close to the maximum number of eggs recorded for *H. tricolor* in this study. No differences were observed between any of the size parameters of fertilized and unhatched oothecae in this study. This is in contrast to the significant differences in size of fertilized and unhatched oothecae of *Galepsus lenticularis* (Saussure, 1872) (Mantodea: Tarachodidae) (Greyvenstein et al. 2020a). Similarly, Greyvenstein et al. (2020a) reported differences with regards to the number of eggs inside fertilized and unhatched oothecae. This was not the case for *H. tricolor,* as no differences in this regard were recorded in this study. It was noted that no oothecae were laid by the captively reared adult females, which is also in contrast to results reported by Greyvenstein et al. (2020a) for *G. lenticularis*. The oothecae of *G. lenticularis* have been described as "primitive" and resembling that of the Blattodea (Ene 1964, Greyvenstein et al. 2020a), those of *H. tricolor* could suggest a more advanced species based on their evolutionary history. To this point, different behaviors and biological adaptations could also be a result of their different evolutionary histories. The difference in evolutionary traits/ages of the species, environmental stimuli, food-related resources, or survival strategies could have been the reason that the captively reared *H. tricolor* females did not oviposit unfertilized oothecae (oothecae produced without mating).

Developmental parameters.—The extended incubation period of *H. tricolor* oothecae (145 days) recorded in this study was much longer than that reported by Vanitha et al. (2016) for *E. pictipes*. It is possible that under natural environmental conditions, the oothecae of *H. tricolor* undergoes diapause during winter, but under captive rearing conditions at a constant temperature and humidity, this incubation period was shorter. Overwintering of oothecae has been reported for some Mantodea species, such as *Brunneria borealis* Scudder, 1896 (Mantodea: Coptopterygidae); *Tenodera aridifolia sinensis* Saussure, 1871 (Mantodea: Mantidae); and *Mantis religiosa* Linnaeus, 1758 (Mantodea: Mantidae) (Kaltenbach 1963, Berg et al. 2011, McMonigle 2013, Maxwell 2014, Svenson et al. 2015, Hurd et al. 2019). A high hatch rate and low survival rate were reported by Vanitha et al. (2016) for *E. pictipes,* while the opposite was recorded for *H. tricolor* in this study. Hatch and survival rates can be influenced by frequency of feeding, food resources, genetics, and temperature, depending on the survival strategy of the species (Matthews and Matthews 1978, Hurd and Eisenberg 1984, Suckling 1984, Iwasaki 1996, Vanitha et al. 2016, Christensen and Brown 2018). The average duration of the period between mating and production of an ootheca in this study was 12 days, while E. *pictipes* only required a week to produce the first ootheca after females mated (Vanitha et al. 2016).

The average duration of copulation for *H. tricolor* was six hours. McMonigle (2013) reported that sperm transfer occurs within 30 minutes of the initial copulation action of mantids. The extended copulation period is suggested to be a form of safeguarding of the genetic prodigy of the male since this behavior results in decreased competition with other males (Prokop and Vaclav 2005). Beyond decreasing sperm competition, males in a better condition (fitness) were also reported to copulate longer with females (Prokop and Vaclav 2005, Holwell 2006). Strategic ejaculation and adjustment of developmental duration has also been reported in males of *Pseudomantis albofimbriata* (Stål, 1860) (Mantodea: Mantidae), when these males were reared in a male-dominated environment (Allen et al. 2011). The latter authors reported that male development was slower under conditions where many males were present, while the opposite was observed when many females were present. Allen et al. (2011) indicated that male mantids took longer to mature and suggested that this could indicate more investment in the development of testes. These males also copulated for a significantly longer time and transferred more sperm per copulation event (Allen et al. 2011). Multiple paternity has been documented for *T. aridifolia* by Watanabe et al. (2011) who suggested the existence of competition between males of the same mantis species for copulation or mating opportunities. It should be noted that the artificiality of the mating conditions within this study could have contributed to the mating behavior results; however, the possible stress induced by the artificiality was reduced as much as possible by, for example, ensuring the container in which mating occurred was ample, that individuals collected from the field were only bred with after two days to allow the insects to acclimate to the artificial conditions of the container, and that the container was not moved or disturbed when the breeding pair were introduced to the single container but only observed to record the data.

Sexual dimorphism in size where males are smaller than females has been observed in various mantid species (Wieland 2013). Some examples of mantid species with size sexual dimorphism are *Creobroter* sp. Stål, 1877 (Hymenopodidae), *Polyspilota aeruginosa* (Goeze, 1778) (Mantidae), *Parasphendale* sp. (Miomantidae), and *Theopropus elegans* (Westwood, 1832) (Mantidae) (McMonigle 2013). Differences in size and color between sexes were noted for *H. tricolor* in this study. However, the duration of the adult stages did not differ significantly between males and females of *H. tricolor*. Differences in antennal morphology were also noted between male and female *T. aridifolia* from the sixth instar onwards (Carle et al. 2014). *Pseudomantis albofimbriata* (Stål, 1860*)* and *G. lenticularis* exhibit sexual dimorphism, as the wings of males are fully developed while females are flightless (Holwell et al. 2006, Greyvenstein et al. 2020a). Sexual dimorphism between males and females in wings and size could be due to the males having to find potential reproductive partners. Males of a smaller size could be more cryptic and more difficult to observe by predators. The smaller size of males also has dispersal advantages, as it could increase their ease of flight.

Conclusions

This study is the first attempt at mapping the distribution of *Harpagomantis* in South Africa and recording the biology of *H. tricolor*. The distribution of false flower mantids in South Africa seems to be predominantly towards the northeastern region, in the savanna and grassland biomes. Extended copulation duration of this species could be a by-product of males trying to decrease sperm competition, which could also have led to the short duration of the male nymphs compared to female nymphs of *H. tricolor*. It is suggested that this species goes into diapause in the ootheca phase.

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Description and photographs of cricket parental care in the wild

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Abstract

Although certain forms of parental care are relatively widespread phenomena among insects, within Orthoptera, parental care is rare. Short-tailed burrowing crickets (*Anurogryllus* spp.) are among the few members of this order for which extensive parental care has been documented. However, accounts of parental care in *Anurogryllus* have been largely under laboratory conditions, and observations of this behavior in the wild are rare. Herein we present photographic observations from a mountain slope in Honduras where we discovered an active *Anurogryllus* brood chamber where an adult female was tending her brood. We present these results in the context of parental care in insects and compare our observations with those reported in past literature published on *Anurogryllus* crickets' parental behavior.

Keywords

behavior, eggs, Honduras, nymphs, Orthoptera, short-tailed cricket

Introduction

Parental care, though widespread and important across many vertebrate taxa (Balshine 2012), is broadly rare among invertebrates (Trumbo 2012). In insects, parental care has evolved independently several times (e.g., in Hymenoptera, Coleoptera, Blattodea, Dermaptera) but is thought to be largely absent from other insect orders. In Orthoptera, parental investment takes one of two main forms: pre-mating and post-mating (Gwynne 1983). Pre-mating parental investment is common in Orthoptera (especially Ensifera; Gwynne 1983) whereby males provide their mates with a nutrient-rich spermatophylax, which is an appendage of spermatophores often containing a high proportion of protein. Post-mating parental investment (i.e., parental care), on the other hand, is much less common in Orthoptera and varies from digging burrows to protect nymphs from predators (e.g., Gryllotalpidae, Phaneropterinae: Gwynne 1983) to the protection of eggs (e.g., *Neotridactylus apicialis* (Say, 1825): Gwynne 1983) to maternal care for their young (e.g., *Anurogryllus muticus* (De Geer, 1773): West and Alexander 1963, Lee and Loher 1995; *Hemiandrus* spp.: Gwynne 2004). Despite being uncommon in Orthoptera, post-mating parental care occurs more commonly in a variety of related insect orders as a means to maximize juvenile survival (e.g., Blattodea: Nalepa 1988; Dermaptera: Kölliker 2007). For example, the wood roach *Cryptocercus punctulatus* Scudder, 1862 provides biparental care to nymphs for as long as three years (Nalepa 1988).

Among Orthoptera, crickets in the genus *Anurogryllus* Saussure, 1877 provide exceptional parental care to their young, with care frequently lasting for several weeks (West and Alexander 1963, Weaver and Sommers 1969). As first detailed by West and Alexander (1963) and Weaver and Sommers (1969), *Anurogryllus muticus* females extensively clean their eggs, provision nymphs with forage collected outside the burrow and trophic eggs, and vigorously defend young from males and other intruders to their burrow (West and Alexander 1963). Although parental care in *Anurogryllus* spp. is well described in captivity, few accounts of parental care in this unique orthopteran genus exist from the wild, and no published photographs exist of natural *Anurogryllus* brood chambers where this rare example of orthopteran parental care is known to occur. This is an important gap in the literature as species behaviors in the wild may differ drastically from those observed in captivity (Alvarez and Nicieza 2003, Tenger-Trolander et al. 2019). For the first time herein, we provide photographs of the natural brood chamber of an *Anurogryllus* cricket observed in a mountain rain forest in northern Honduras.

Materials and methods

Our observations were made on 1 February 2017 at Rio Santiago Nature Reserve in San Francisco, Atlántida, Honduras (15.592223°N, -87.062514°E; 150 m) at 20:55 (Fig. 1). This region is heavily forested and dominated by contiguous broadleaf evergreen forest. On the evening when our observations were made, the temperature was approximately 19 °C and the sky was overcast with light rain. Our observation occurred during a reptile/amphibian survey through the nature reserve during which we rolled stones and other objects to document resident wildlife. During this survey, we rolled a small stone with dimensions approximately 7.5 × 13 cm. This stone, which was sitting atop the soil within the forest path, was covering the brood chamber of an *Anurogryllus* cricket (Fig. 1). Female *Anurogryllus* are readily identified by their habitus in general (e.g., wing structure), but especially by their greatly reduced ovipositor, consistent with their common name: the short-tailed cricket (Weaver and Sommers 1969). They are also the only known Gryllids that exhibit parental care of nymphs (West and Alexander 1963, Weaver and Sommers 1969), making brooding females very easy to identify. With that in mind, and because detailed descriptions of *Anurogryllus* species present in Honduras are lacking, we did not attempt to identify the crickets observed at species level. Four photographs were taken to document the observation. The record was also posted to the citizen science platform iNaturalist (https://www.inaturalist.org/observations/5089680).

Results

The main brood chamber was ~57 mm long by ~23 mm wide (Fig. 2) and included a single entrance (~31 mm in length) facing west that allowed travel between the burrow and the soil surface. This brood chamber contained 1) an adult female *Anurogryllus* cricket, 2) three *Anurogryllus* nymphs (first instar), and 3) three *Anurogryllus* eggs. We did not observe *Anurogryllus* nymphs attached to the underside of the rock and thus believe this was the complete brood (three nymphs, three eggs). During our brief encounter with these crickets, including photographing them from several angles, the female was reluctant to expose the nymphs and made no attempt to abandon the brood. After documenting the event, the stone was carefully replaced, and the crickets were not harmed.

Discussion

Parental care is common in some insect orders (e.g., Hymenoptera) but remarkably rare in others (e.g., Orthoptera: Trumbo 2012). Among the best documented cases of extensive orthopteran maternal care are the ground wētā (*Hemiandrus* spp.) and crickets in the genus *Anurogryllus* (West and Alexander 1963, Smith et al. 2013). We believe our observations constitute the first published photographs of an opened, active *Anurogryllus* cricket brood chamber in the wild. Although *Anurogryllus* crickets are known to become highly abundant in some areas (West and Alexander 1963), nearly all published studies of their breeding behavior have been restricted to captive conditions. This is surprising given that the natural history and ecology of *Anurogryllus* crickets has been studied for over a half century and the species is widespread across many states and countries (West and Alexander 1963, Erregger and Schmidt 2018). Although we expect broad reproductive behaviors to remain largely consistent between captivity and the wild, insect behavior can be impacted by captive conditions in profound ways (Tenger-Trolander et al. 2019), underscoring the importance of such natural history observations.

In many regards, the *Anurogryllus* sp. brood chamber observation was similar to those reported in the literature for *A. muticus*. For example, West and Alexander (1963) observed female *A. muticus* to construct a brood chamber several centimeters deep into loose soil, linked to the surface by a single connecting channel, though these observations all occurred within a captive environment where burrowing depth was constrained. In contrast, Weaver and Sommers (1969) created plastic casts of *A. muticus* burrows in the wild and found them to be multi-chambered and as deep

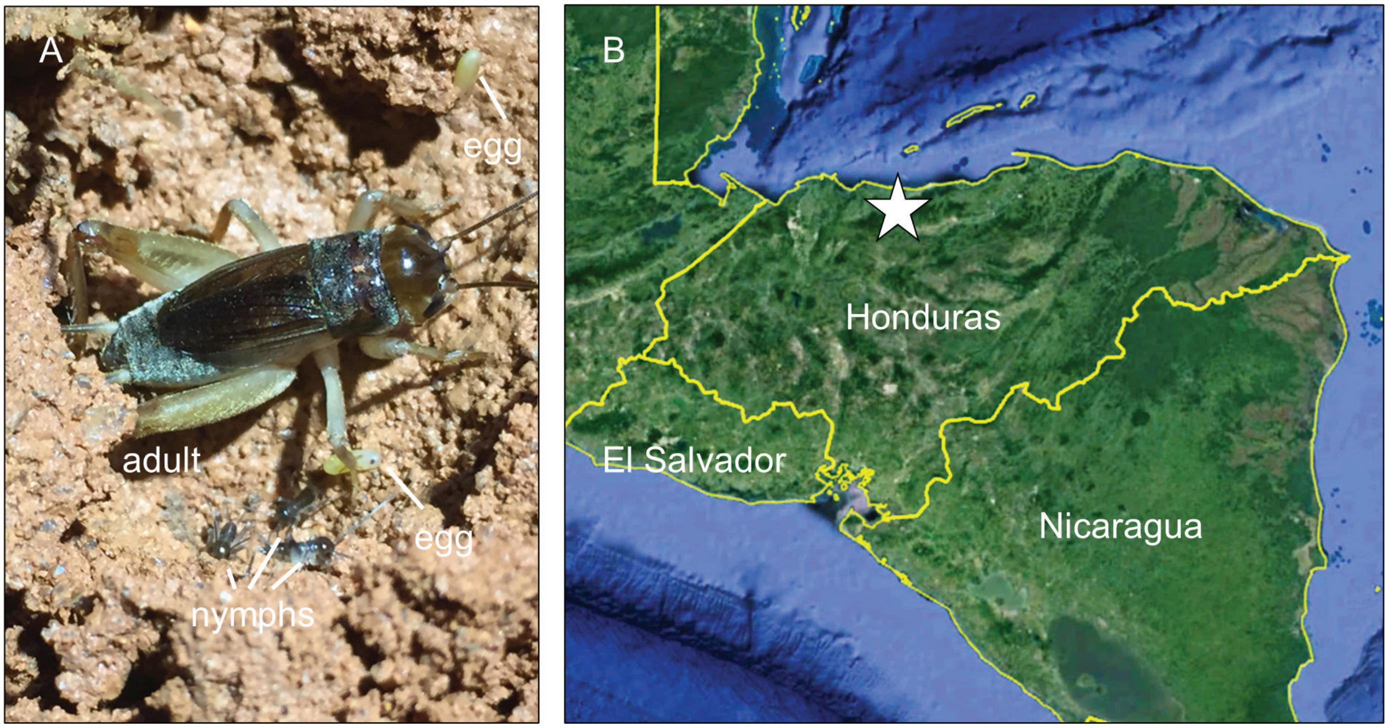

Fig. 1. A. Female *Anurogryllus* cricket with eggs and nymphs observed in northern Honduras; **B.** Map of northern Honduras; star represents observation location.

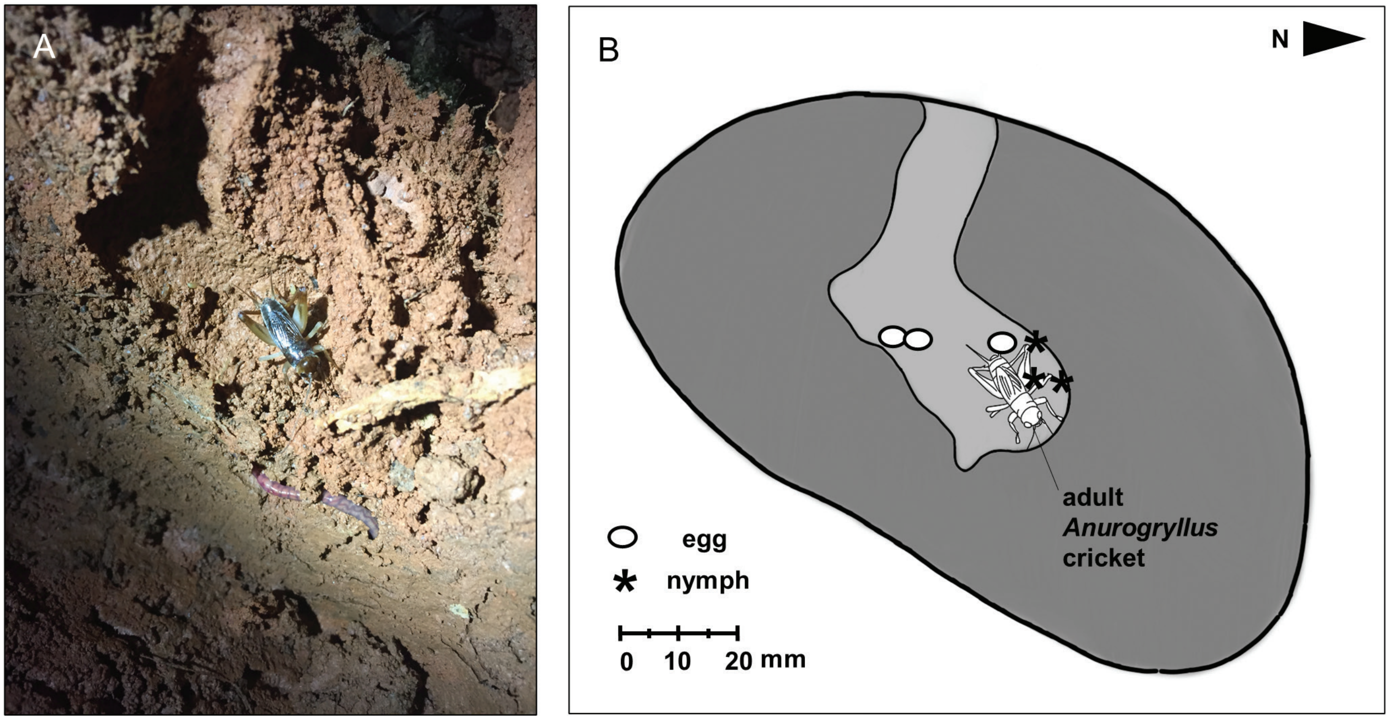

Fig. 2. A. Photo of a female *Anurogryllus* cricket in a brood chamber beneath a stone on a forest path in Honduras; **B.** Drawing simplifying the structure of the brood chamber (scale bar approximated from cricket body size. The brood chamber, shown in light gray, was beneath the footprint of a small stone that was largely in direct contact with the soil (dark gray). The chamber contained an adult female *Anurogryllus* cricket as well as three eggs (open circles) and three first-instar nymphs (asterisks). Map data 2019 (c) Google.

as 50 cm into the soil. In this way, the burrow we observed at Rio Santiago was more similar to those reported by West and Alexander (1963) from the lab than those by Weaver and Sommers (1969) in Louisiana, US. Although we did not measure the burrow's depth at Rio Santiago, we can safely conclude that it was <5 cm deep and contained only an "upper chamber" (*sensu* Weaver and Sommers 1969) with no lower chambers (Fig. 2). Our observation that eggs and nymphs co-occuring is also consistent with past literature suggesting that adults lay eggs successionally (i.e., each individually over the course of several days), sometimes even with nymphs in their burrows (Lee and Loher 1995, Erregger personal observation).

The *Anurogryllus* from Honduras was unique from those previously reported for *Anurogryllus* in several ways: the Rio Santiago brood chamber contained far fewer nymphs (n = 3) and eggs (n = 3; Fig. 2) than those reported by others (up to 129 eggs or 89 nymphs/burrow; Weaver and Sommers 1969). One possible explanation for fewer nymphs and eggs (as compared to previous reports by e.g., Weaver and Sommers 1969) might be the habitat context of the brood chamber. *Anurogryllus* cricket burrows are best known from grassland habitats (Erregger, personal observation), whereas the burrow described here was deep within a closed-canopy forest. Although *Anurogryllus* crickets are foraging generalists, 'typical' food sources (e.g., seeds, flowers, leaves) may have been limited within the forest, thus limiting reproductive output. This observation is potentially supported by our idea of no vegetative provisions within the burrow (Fig. 2). Indeed, *A. muticus* are known to conspicuously provision their young nymphs with vegetation gathered outside the burrow when food is abundant. Vegetational structures are also used to insulate the chamber from intruders during the day and when the female leaves the burrow (Erregger, personal observation from Panama). Thus, other factors, such as predation pressure, also have an impact on their survival rate (Erregger and Schmidt 2018). Furthermore, the geographic location (i.e., elevation level) and the soil characteristics (e.g., for digging) might be restricting factors, reducing survival success. The differences we report here for an *Anurogryllus* brood chamber in the wild as compared to those studied in captivity highlight the importance of wild observation, as natural conditions and ecological context clearly drive at least some variation in life history for short-tailed crickets.

Our observations of an *Anurogryllus* brood chamber provide interesting insights into the parental care behaviors present within Orthoptera. Although some aspects of *Anurogryllus* breeding behavior were confirmed in the wild by our record, others (e.g., brood size, provisioning behavior, etc.) appear to vary among regions, species, and/or study context (e.g., lab vs. field). Given this, several important limitations of our observation should be kept in mind. First, the brood chamber we observed represents a single observation; how typical any components of this observation are in the broader context of the life history of *Anurogryllus* would require a much more thorough examination. Moreover, the species identity of the *Anurogryllus* brood we observed here remains unknown—species-specific life history differences may explain some of the differences we report here as compared to laboratory observations. Still, the different life history pattern we observed in Honduras in contrast to those observed in the lab highlights the need to assess species behavior across multiple contexts, including both in a lab setting and the wild.

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The luring mantid: Protrusible pheromone glands in *Stenophylla lobivertex* (Mantodea: Acanthopidae)

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Abstract

The hitherto unknown pheromone gland of female *Stenophylla lobivertex* Lombardo, 2000, a poorly understood praying mantis distributed in the Neotropics, is described and figured. In contrast to other mantodeans, this species has a protrusible, bifurcated (Y-shaped) gland of 6 mm length. It is protracted by sexually receptive females during nighttime and only when undisturbed. The significance of this morphological and behavioral adaptation is discussed in light of the reproductive strategy of the species and its assumed rarity in the natural habitat.

Keywords

Calling behavior, Neotropics, praying mantis, reproductive strategy

Introduction

Morphologically and phylogenetically unique taxa often exhibit traits not found in related groups (Pavoine et al. 2005, Redding et al. 2008). Such traits might provide crucial information on the evolution of morphological and behavioral characters that cannot be inferred from the study of their relatives alone. Among insects, notable examples are the stenopelmatoid ensiferan *Cooloola* Rentz, 1980 (Rentz 1999), the phasmatodean *Dryococelus* Gurney, 1947 (Buckley et al. 2008), and the mantodean *Metallyticus* Westwood, 1835 (Wieland 2008). This also highlights the importance of including such taxa in phylogenetic analyses.

Mate attraction is facilitated through pheromones in many insect taxa, and praying mantises (Mantodea) are no exception. Behavioral experiments suggesting pheromone emission of praying mantis females were first described by Kelner-Pillault (1957), who observed a caged European mantis female (*Mantis religiosa* Linnaeus, 1758) attracting males from surrounding habitats. Meanwhile, several observations in captivity and in the wild have documented pheromone-emitting behavior in many mantodeans (e.g., Edmunds 1975, Robinson and Robinson 1979; Hurd et al. 2004; Gemeno et al. 2005; Perez 2005, Holwell et al. 2007, Maxwell et al. 2010, Berg et al. 2011, Schwarz 2018). Hurd et al. (2004) were the first to show that a pheromone is indeed produced by sexually active female mantodeans.

During the attracting behavior, usually named “calling”, the apex of the abdomen is bent ventrad in long-winged species (to an extreme in Acanthopinae; Robinson and Robinson 1979), exposing the intersegmental membrane between the sixth and seventh tergite, where the pheromone gland is located. In the groups studied so far, this membrane protrudes, at most, very slightly.

Here, we present a unique sexual attraction mechanism exhibited by the leaf-like mantis *Stenophylla lobivertex* Lombardo, 2000, a member of the exclusively Neotropical family Acanthopidae (Schwarz and Roy 2019).

Materials and methods

We observed and documented the behavior of four females from November 2017 to June 2018 (N = 1) and from October 2019 to March 2020 (N = 3). The first observations were made by the second author in a female from the Panguana research station (9°37'S, 74°56'W, 260 m a.s.l.) in Amazonian Peru. Three additional females were part of a captive bred stock, likewise from Peru, obtained by the first author from a Mantodea breeder in Germany.

Results

As in other species studied so far, the pheromone gland of *Stenophylla lobivertex* is located between the sixth and seventh tergite. It is inflated into a Y-shaped structure during calling and usually sticks out almost vertically from the body (Fig. 1), but each lobe can also be moved in a tentacle-like manner. The fully inflated organ is 6 mm long, about 1 mm thick at both ends and filled with haemolymph, which gives the organ a greenish-blue appearance. Tracheae can be seen shining through the thin membrane.

The captive stock females continued to call after being mated multiple times but produced unfertile oothecae, indicating that the copulations might have been unsuccessful. Our observations so far suggest that calling behavior is reduced in females older than six months.

Fig. 1. Pheromone gland of *Stenophylla lobivertex*. **A.** Lateral view of calling female; **B.** Pheromone gland in anterolateral view; **C.** Pheromone gland in posterolateral view. Photos by C. J. Schwarz.

Calling in *Stenophylla* occurred, like in other mantodeans, over the course of 2–5 hours per night and only in deep darkness and when undisturbed. Temperature during the observational period reached 26 to 29°C by day and 22 to 24°C by night, at 70–90% relative humidity. The protraction of the gland occurred over the course of several minutes, but upon disturbances, such as vibrations or illumination by artificial lights, the pheromone gland was retracted instantly.

Discussion

So far, *Stenophylla lobivertex* is the only species of more than 2,500 known mantodean species whose pheromone gland has evolved into a distinct, inflatable morphological structure. While the pheromone glands can attain the shape of a pair of small bulges in some other taxa (e.g., Acanthopinae, *Tarachodes* Burmeister, 1838: Edmunds 1975, Robinson and Robinson 1979), no other known mantodean inflates its pheromone gland into a Y-shaped structure. However, the two congeners of *S. lobivertex* might possess a similar structure.

The significance of this unique structure remains speculative at this point, but we argue that this type of protrusible gland with its increased surface might be able to distribute pheromones more efficiently than the less elaborate glands of other mantodean species. This structure might, therefore, help to assure efficient mate finding in a species apparently characterized by low population density in combination with a short reproductive period.

Stenophylla are rarely observed in nature, and only a handful of specimens of the three known species are present in museum collections. The rarity of this taxon might be partly due to its reproductive K strategy (MacArthur and Wilson 1967). Preliminary observations on captive specimens revealed that females produce only 3–5 oothecae during their lifetime, which contain at most 30 eggs (Rönisch and Schwarz 2019). Females guard their egg cases until the young hatch; the hatchlings are 13 mm long (as compared to 40–44 mm in adults). The natural phenology of *Stenophylla* is unknown, but during more than 35 years of regular collections at the Panguana field station in Peru, adult specimens (deposited in the Staatliches Museum für Naturkunde, Karlsruhe [SMNK], the Zoologische Staatssammlung München [ZSM], and in the collection of CJS) were only found in the months of August to October (Schwarz et al. 2020). The specimens of the type series were captured in October and November (Lombardo 2000). Finding a sexual partner when population density is low and adults are not found year-round is challenging. This is especially true in a highly complex rainforest ecosystem and thus may explain the need for an elaborate and “safe-proof” sexual attraction mechanism in this mantodean.

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Conservation possibilities of *Isophya costata* (Orthoptera: Tettigoniidae: Phaneropterinae) based on frequency, population size, and habitats

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Abstract

Isophya costata Brunner von Wattenwyl, 1878, commonly called the Keeled Plump Bush-cricket, is an endemic Natura 2000 species in the Carpathian Basin and is included in the IUCN Red List of Threatened species. We used extensive data collection from Hungary retrieved between 2004 and 2019 from 700 sampling sites spread over an area of 12,700 km^2 to examine the occurrence of the species in different regions in grasslands of similar structure but different origin, naturalness, and character. The results confirmed that *I. costata* currently occurs with the highest number of populations and highest density in regularly mowed, mesophilic hayfields rich in dicotyledonous plants (Arrhenatheretalia). The species also appears in smaller numbers in grasslands adjacent to hayfields, such as wetland meadows (*Molinion coeruleae*), marsh meadows (*Deschampsion caespitosae, Alopecurenion pratensis*), and edge habitats dominated by herbaceous plants. However, the results show that the extension of these habitats has a negatively significant correlation with both the occurrence of the species and its density. *Isophya costata* occurs in steppe meadows much less frequently than in mesophilic hayfields. The species is endemic to the Pannonian Steppe, and the key to their conservation is by maintaining stocks of hayfields in the species' area of distribution. According to this study, overseeding of mowed grasslands leads to the decline of the species. To preserve *I. costata*, it is necessary to eliminate trampling in its areas of occurrence (prohibition of grazing) and encourage late-season mowing adapted to the phenology of the species (not as early as mid-July) or, if this is not feasible, mosaic-type treatment leaving unmown patches (e.g., 1/3 of the plot).

Keywords

Carpathian Basin, endemic species, grassland character, hayfields, mowing, overseeding

Introduction

Isophya costata Brunner von Wattenwyl, 1878 is an endemic, postglacial-steppe relict species (Varga 1995) found in the Carpathian Basin. It is a highly protected species of community importance (Natura 2000) in Hungary, and as such, it is included in the IUCN Red List of Threatened species (Chobanov et al. 2016). The species has long been the focus of research because of its habitat loss due to cultivation, abandonment of mowing, etc. (Nagy 1974) that has led to the Hungarian Red Book classifying it as an endangered species (Rakonczay 1989). *I. costata* is mostly found in Hungary (Nagy and Rácz 2014). Based on previous studies, *I. costata* may have been a characteristic species of loess meadows and closed-steppe meadows rich in dicotyledonous plants that later adapted to hayfields rich in dicotyledonous species, similar to their previous habitats but formed under anthropogenic influence. These hayfields have become the primary habitat of *I. costata* (Kenyeres et al. 2004, Bauer and Kenyeres 2006, Kenyeres et al. 2009).

Thanks to recent systematic research new occurrence data have been revealed – not only in Hungary, but also in Slovakia (Nuhlíčková et al. 2017), Serbia (Szövényi and Szekeres 2011, Ivković and Horvat 2020), Austria (Zuna-Kratky et al. 2017), and Romania (Iorgu et al. 2008).

In the present study, the data collection covers about a quarter of the territory of Hungary and took place between 2004 and 2019. We sought to answer the following questions: (1) What regional differences can be detected in the frequency of the occurrence of *I. costata* among the regions within the study area? (2) Are there any differences in terms of the frequency of occurrence of the species among its potential habitats with a similar structure but different species composition, origin, and landscape history? (3) Can the effects of the condition and use of the studied grasslands (regularly mowed, overseeded, shrubbing, humid, semi-dry, dry, etc.) on the occurrence of the species be revealed? (4) Does the density of the species correlate with the local surface cover of the studied habitat types?

Methods

Between 2004 and 2019, we examined the presence/absence, density, and habitat requirements of *I. costata* (Figs 1, 2) at 700 sites (12,700 km^2) in northwestern Hungary. The study area was divided into 12 regions (Fig. 3) according to landscape and biogeography. The CORINE Landcover habitat structure of the regions and the distribution of the studied grasslands among habitat types are shown in Fig. 4 and Table 1.

Fig. 1. Male (left) and female (right) specimens of *Isophya costata*.

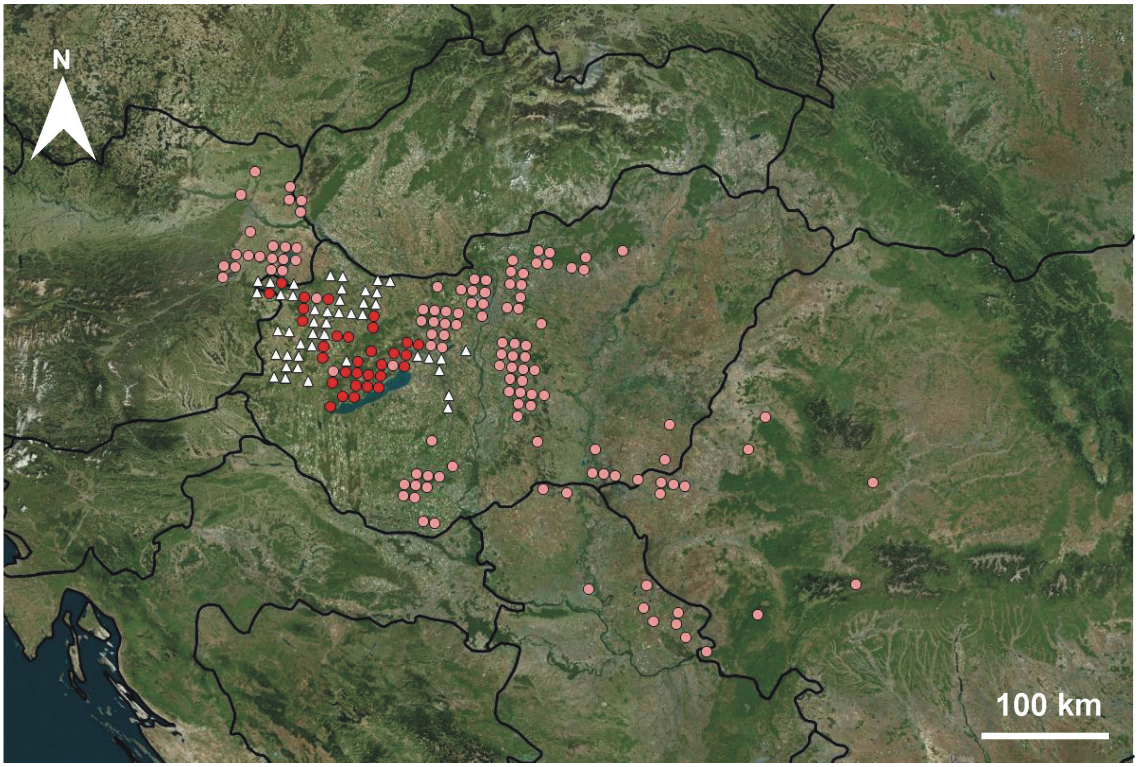

Fig. 2. Known distribution of *Isophya costata* in the Carpathian Basin at the level of ETRS quadrates (circle: presence data of the species; red circle: presence data of this study; triangle: absence data of this study).

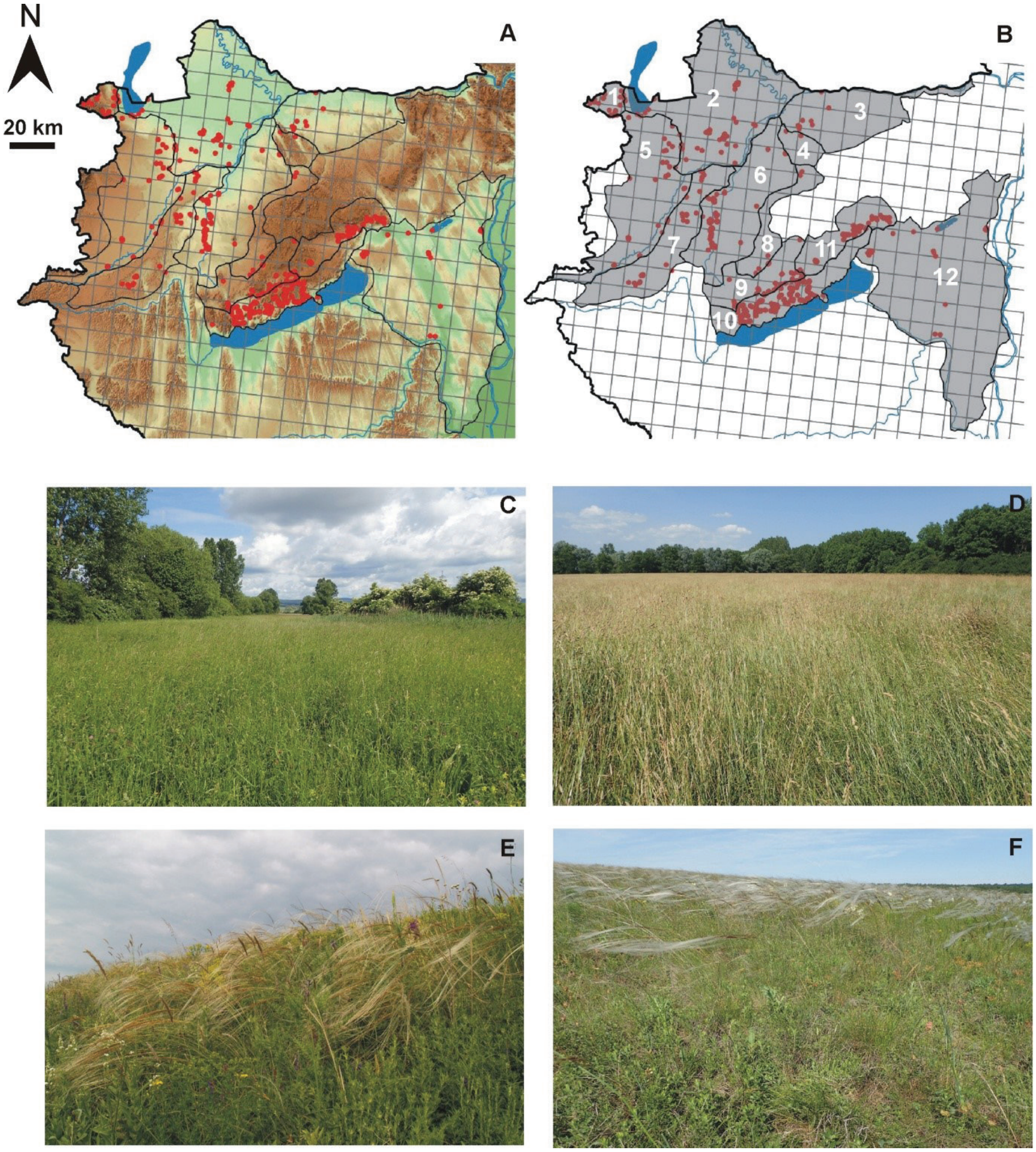

Fig. 3. Sub-areas of the study area (**A**, **B.**) (1: Alpokalja, 2: Győr Basin, 3: Komárom-Esztergom Plain, 4: Pannonhalma Region, 5: Sopron-Vas Plain, 6: Marcal Basin, 7: Kemeneshát, 8: Bakonyalja, 9: Southern Bakony, 10: Balaton Uplands, 11: Eastern Bakony, 12: Mezőföld), sampling sites (red points), and the most typical studied habitat-types: **C.** Typical hayfield rich in dicotyledonous plant species; **D.** Overseeded hayfield poor in dicotyledonous plant species; **E.** Loess steppe; **F.** Slope steppe.

Table 1. Extent (mean±SE) and habitat types of the grasslands containing the study quadrates (N=700).

Habitat type	Range in hectare (mean±SE)	N
Red beds	3.64±0.64	3
Rich fens	14.32±3.52	12
Mesotrophic wet meadows	6.74±0.67	107
Hayfields	6.40±0.97	190
Overseeded hayfields	13.20±3.41	88
Calcareous rocky steppes	4.03±0.45	116
Slope steppes on stony soils	3.59±0.62	39
Closed forest steppe meadows	2.29±0.47	32
Closed steppes on loess	0.68±0.27	12
Uncharacteristic mesic grasslands	2.86±0.42	23
Uncharacteristic dry and semi-dry grasslands	5.20±0.86	78

Sweep-netting, direct observation, and acoustic detection were performed at the studied 10×10 m quadrates for the duration (30 minutes). All detected individuals were recorded. Based on the number of individuals registered in the study quadrates, we determined the presence/absence data and the density of the species per square meter related to the habitat patch concerned. During sampling, we recorded the type of the habitat according to the Hungarian General National Habitat Classification System (Á-NÉR): red bed, rich fen, mesotrophic wet meadow, hayfield/overseeded hayfield, calcareous rocky steppe, slope steppe on stony soils, closed forest steppe meadow, closed steppe on loess, uncharacteristic mesic, and dry and semi-dry grassland. We also recorded the naturalness (natural, pseudo-natural: anthropogenic hayfields with good naturalness, shrubby, disturbed, and overseeded) and microclimatic conditions (humid: directly affected by water and

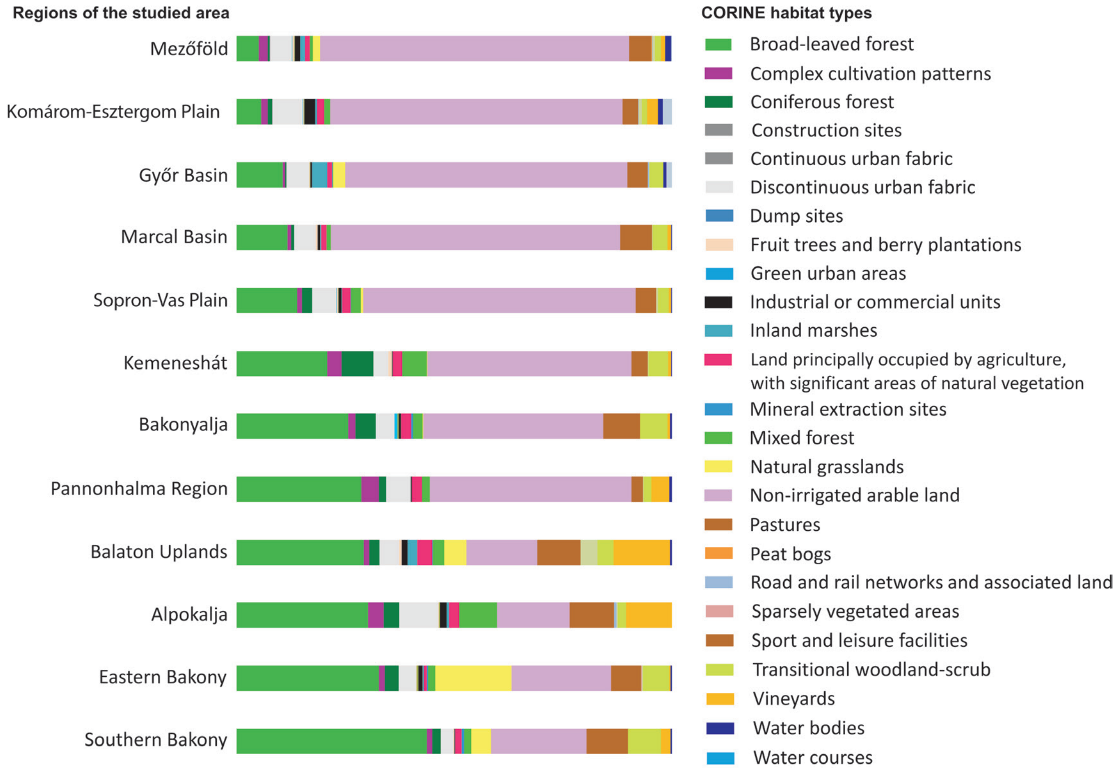

Fig. 4. Relative frequency of CORINE habitat types in the studied sub-areas.

characterized by water supply for at least a part of the year; mesophilic: closed, semi-dry grasslands; dry: xerophilous grasslands with open soil surfaces).

We determined the size of the habitat type corresponding to the quadrates studied based on data collected in the field by handheld computer (Trimble Juno3B) with the use of QGIS 2.16 software (QGIS Development Team 2016).

A basic database containing the records of all sites (N = 700) was used for analyses, but a database containing the relative frequency (rel. freq.) of the recorded variables at the ETRS quadratic level was also generated (N = 78). Furthermore, we determined the sub-areal (12 regions) indicators for the presence/absence of the species (Ns: number of sampling sites with presence/absence of *I. costata*, and Rf: relative frequency of presence of *I. costata*). The relationships between the presence/absence of the species and the presence/absence of the habitat types and habitat characteristics studied were examined by Generalized Linear Models (GLM) with binomial distribution. Division of the habitats with the presence of *I. costata* among habitat characteristics recorded (habitat types, naturalness, structure, and microclimate) were described by bar charts. The paired t-test was used to evaluate statistical differences among the variables. In order to analyse the relationship between the density of *I. costata* and environmental data at the European Terrestrial Reference System (ETRS) quadrate scale (in which the dependent variable was the mean density of *I. costata*; the habitat variables were mean of the patch size; and the relative frequencies (rel. freq.) of the recorded habitat types were categorized according to in the Habitat Classification System (Á-NÉR), to their naturalness and to their microclimatic conditions; see above), single tests of GLM (Poisson distribution) were used. Overdispersion was not detected in the variables. Statistical procedures were performed using PAST 2.16 (Hammer et al. 2001) and CANOCO 4.5 (Braak and Smilauer 2002) software packages.

Results

Regional differences.—Of the 700 study sites, the presence of the species was detected at 280 locations.

The frequency of the species showed significant regional differences (Fig. 5). *I. costata* proved to be particularly frequent (rel. freq. of positive cases: 0.63) in the Balaton Uplands subarea (267 study sites), presumably because of the richness of potential habitats in the region. Among the studied quadrates, the proportion of hayfield habitat type was high (rel. freq.: 0.42), but slope steppes on stony soils (rel. freq.: 0.15), rich fens (rel. freq.: 0.15), and uncharacteristic dry and semi-dry grasslands (rel. freq.: 0.15) habitat types were also significantly present. Of the grasslands studied, the proportion of pseudonatural (rel. freq.: 0.55) and mesophilic (rel. freq.: 0.59) patches was very high.

Roughly a third of the 112 study sites showing the presence of the species were in the Eastern Bakony region (rel. freq.: 0.29). In this region, most of the grasslands studied were calcareous rocky steppes habitat type (rel. freq.: 0.80) with a significant share of uncharacteristic dry and semi-dry grassland habitat types (rel. freq.: 0.15). Most sites included in the study were edaphic dry grasslands (rel. freq.: 0.76) with a dry microclimatic character (rel. freq.: 0.98).

Also, we found the presence of the species in about a third of the 72 study sites in the Marcal Basin region (rel. freq.: 0.32). The majority of the examined patches (rel. freq.: 0.51) belonged to the rich fens habitat type, with a significant number of hayfields and overseeded hayfields (rel. freq.: 0.32 and 0.10). In terms of character, the grasslands studied were pseudo-natural (rel. freq.: 0.81), humid (rel. freq.: 0.58), or semi-dry (rel. freq.: 0.32).

Among the regions with less than 10% of the total sample, *I. costata* was found in about a third of the study sites. This

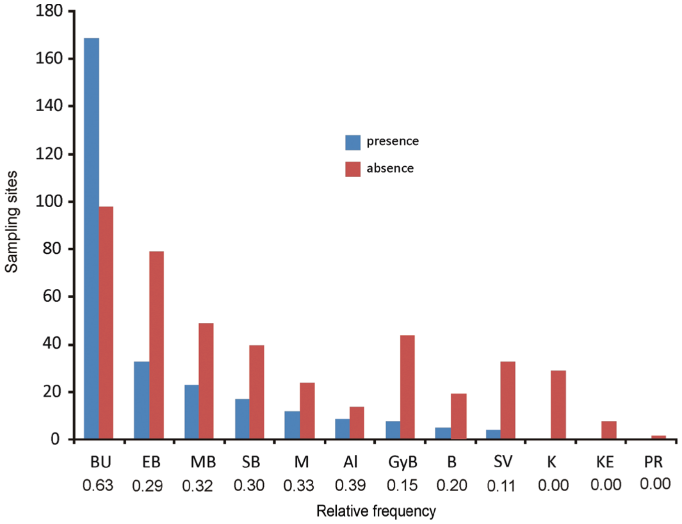

Fig. 5. Presence or absence and relative frequency of presence of *Isophya costata* in the studied regions (BU: Balaton Uplands; EB: Eastern Bakony; MB: Marcal Basin; SB: Southern Bakony; M: Mezőföld; Al: Alpokalja; GyB: Győr Basin; B: Bakonyalja; SV: Sopron-Vas Plain; K: Kemeneshát; KE: Komárom-Esztergom Plain; PR: Pannonhalma Region).

includes Southern Bakony (no. of samples: 57, rel. freq.: 0.30), Mezőföld (no. of samples: 36, rel. freq.: 0.33), and in the Alpokalja region (no. of samples: 23, rel. freq.: 0.39). From a microclimatic point of view, the grasslands under review were dry (rel. freq.: 0.68) and semi-dry (rel. freq.: 0.30) in all three regions. In the sampling quadrates of the Southern Bakony, uncharacteristic dry and semi-dry grasslands (rel. freq.: 0.28), hayfields (rel. freq.: 0.26), rich fens (rel. freq.: 0.28), and slope steppes on stony soil (rel. freq.: 0.26) habitats occurred in a roughly balanced proportion. Among the grasslands examined, pseudo-natural patches (rel. freq.: 0.40) were dominant, but the proportion of disturbed (rel. freq.: 0.30) and shrubby (rel. freq.: 0.25) habitats were also high. Closed forest-steppe meadows (rel. freq.: 0.31) and closed steppes on loess habitat types (rel. freq.: 0.31) were dominant in the studied grasslands of the Mezőföld region, but hayfields (rel. freq.: 0.26) also occurred (rel. freq.: 0.17). Among the grasslands examined, shrubby (rel. freq.: 0.33), pseudo-natural (rel. freq.: 0.22), disturbed (rel. freq.: 0.22), and edaphic patches (rel. freq.: 0.22) were present in a balanced proportion. In the Alpokalja region, in addition to the dominant hayfields (rel. freq.: 0.26), rich fens (rel. freq.: 0.13), and overseeded hayfields (rel. freq.: 0.13) habitat types also occurred. Of the grasslands studied, pseudo-natural patches (rel. freq.: 0.61) were dominant, but the proportion of overseeded (rel. freq.: 0.13) habitats was also high.

In the other sub-areas, either the species was not detected or the frequency of its occurrence was very low. Of these, the Bakonyalja should be highlighted, where most of the grasslands examined belonged to the pseudo-natural, but rather dry, microclimate occurrences of the hayfield (rel. freq.: 0.80) habitat type. However, the number of samples (corresponding to the occurrence of potential *I. costata* habitats) was low in this region. The other sub-areas can be divided into two groups. The examined patches of the Győr Basin (N = 52), Kemeneshát (N = 29) and Sopron-Vas Plain (N = 37) predominantly belonged to overseeded hayfield habitat type (rel. freq.: 0.55–0.68), the character of which was determined by overseeding (rel. freq.: 0.55–0.70) and dry stock climate (rel. freq.: 0.59–0.83). The dominant habitat types in the Komárom-Esztergom Plain (N = 8) and Pannonhalma Hills (N = 2) regions can be classified as diverse: rich fens (rel. freq.: 0.38–0.50), overseeded hayfields (rel. freq.: 0.00–0.38), uncharacteristic dry and semi-dry grasslands (rel. freq.: 0.00–0.25), and closed steppes on loess (rel. freq.: 0.00–0.50). In terms of character, both humid (rel. freq.: 0.38–0.50) and dry (rel. freq.: 0.50–0.63) grasslands were determined to be in high proportion in these regions, and also in terms of naturalness, several types occurred: pseudo-natural (rel. freq.: 0.13–0.50), shrubbing (rel. freq.: 0.00–0.50), disturbed (rel. freq.: 0.00–0.50) and overseeded (rel. freq.: 0.00–0.70).

Habitat requirements.—Based on the data as a whole, more than half (51.1%) of the sampled quadrates with the presence of the species were hayfields rich in dicotyledonous plant species (Fig. 6). Additional occurrences were distributed among nine different habitat types, of which the proportion of marsh meadows (12.9%) and calcareous rocky steppes (12.5%) were significant.

In terms of habitat character (Fig. 6), most occurrences were found in regularly mowed hayfields (64.6%) showing good naturalness or edaphic steppes (14.6%). The proportion of disturbed or shrubby grasslands among positive samples was 12.1% and 7.14%, respectively, and the presence of *I. costata* was rarely observed on overseeded hayfields (1.4%). In terms of microclimate, 66.4% of the grasslands where the species occurred were semi-arid, 27.9% were dry, and only 5.7% were humid.

GLM (Table 2) of the data on all study quadrates showed a significant positive correlation between the presence of *I. costata* and the presence of hayfields rich in dicotyledonous plant species. Significant negative relationships were seen between the occurrence of *I. costata* and the presence of overseeded hayfields, mesotrophic wet meadows, and uncharacteristic dry and semi-dry grasslands.

Density.—The density of *I. costata* in the study quadrates was 0.24 individuals/m^2 (mean ± 0.11). There was no significant correlation between species density and size of the habitat patch ($p=0.609$, $R^2=0.00037$).

GLM showed (a) a significant positive correlation ($p=0.004$, $R^2=0.301$) between the mean density of *I. costata* at the ETRS quadrate level and the frequency of hayfields rich in dicotyledonous plant species (Fig. 7) and (b) a significant negative correlation ($p<0.001$, $R^2=0.462$) between the mean density of *I. costata* at the ETRS quadrate level and the frequency of grasslands characterized by humid microclimate (Fig. 7).

Discussion

Our results show that, although the Keeled Plump Bush-cricket can be found in several areas on steppe meadows, loess grasslands, and other grassland types (weedy humid grasslands, marsh meadows, etc.), their highest density populations live on regularly mowed hayfields rich in dicotyledonous plant species, confirming our earlier statement (Bauer and Kenyeres 2006). According to this study, the species rarely occurs in overseeded hayfields or, if it does, only in very small numbers. This may be related to the fact that overseeding is usually done with grass species, leading to the decline of dicotyledonous plant species cover (Blackmore and Goulson 2014). Also, the soil surface is regularly damaged by overseeding (e.g., harrowing, ploughing) (Cardarelli et al. 2020), which is fatal in terms of the reproduction of *I. costata*, which lays its eggs in the upper-most layers of the soil (Nagy and Rácz 2014). Intensive mowing of the whole plot is also pervasive, which can lead to a further reduction of the cover of dicotyledonous plant

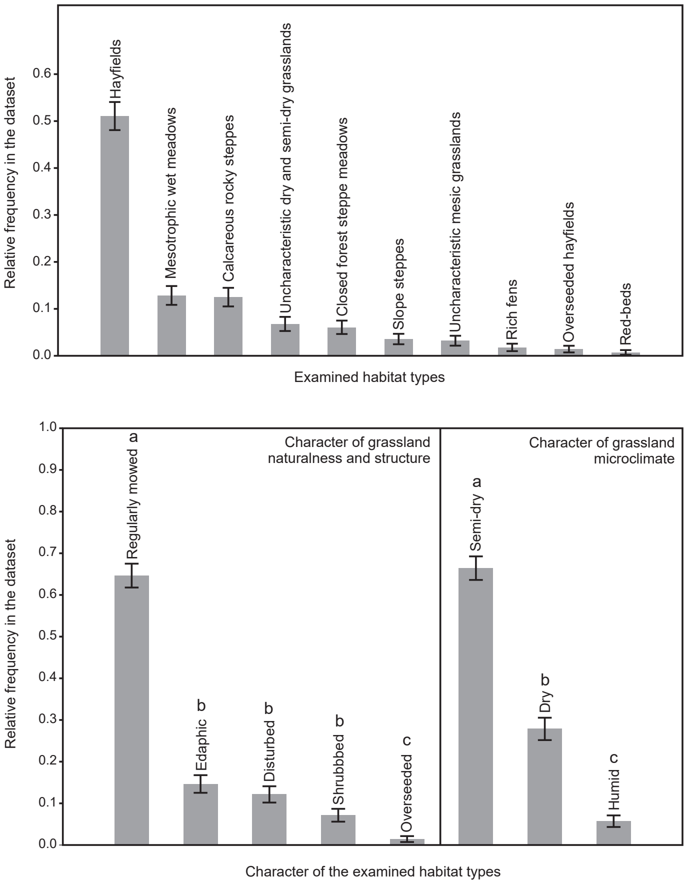

Fig. 6. Bar charts (±SE) of the studied habitat types with a presence of *Isophya costata* and bar charts (±SE) of the studied habitats (characterized by different naturalness, structure, and microclimate) with a presence of *Isophya costata.*

species to a level that is no longer able to meet the dicotyledonous nutritional requirements of *I. costata* (Orci et al. 2007); in this situation, the grasslands become unsuitable for maintaining the species' populations (Kenyeres et al. 2004).

The presence of *I. costata* in hayfields rich in dicotyledonous plant species and the absence of the species in overseeded mowed grasslands was also reflected in the sub-areas of the study. In the Balaton Uplands sub-area, which showed the highest frequency of the species, the prevalence of large hayfields rich in dicotyledonous plant species was substantial. The Balaton Uplands sub-area is also characterized by the occurrence of steppe grasslands, which is a priori favourable for the species (Varga 1995). In addition to the above, the extent of potential habitats for *I. costata* in the Balaton Uplands has increased due to the impact of humans, such as through deforestation and the establishment of grasslands maintained by mowing. Typically, extensive mowing creates large anthropogenic hayfields rich in dicotyledonous plant species with a physiognomy very similar to steppes. However, according to our results, *I. costata* occurs with a much lower frequency in steppe grasslands, and in sub-areas dominated by that habitat type (e.g., Eastern Bakony), than in hayfields. These grasslands have a similar structure to hayfields but are less advantageous to *I. costata* in terms of protection from both predators (Kruess and Tscharntke 2002, Gardiner and Haines 2008) and weather challenges, as these grasslands have a different structure and shorter grass (Kenyeres et al. 2018).

Table 2. Results of GLM with binomial distribution of presence/absence data of *Isophya costata* and the studied habitat types, with indication of p-, R-values and estimates (grassland types examined using more than five quadrates and with a mean larger than 1 hectare were used).

Presence of	*Isophya costata*		
	p	**R**	**est.**
Rich fens	n.s.	-0.053	-57.81
Mesotrophic wet meadows	0.043	-0.471	-251.44
Hayfields	<0.001	2.358	-270.28
Overseeded hayfields	<0.001	-2.775	-184.61
Calcareous rocky steppes	n.s.	-0.464	-241.94
Slope steppes on stony soils	n.s.	-0.623	-97.71
Closed forest steppe meadows	n.s.	0.172	-75.84
Uncharacteristic mesic grasslands	n.s.	-3.319	-75.69
Uncharacteristic dry and semi-dry grasslands	<0.001	-1.331	-170.63

The other sub-areas characterized by typical, but fewer, occurrences of the species (Southern Bakony, Mezőföld, Bakonyalja, Marcal Basin) have a similar landscape to the Balaton Uplands sub-area. *I. costata* can also be considered frequent in the Alpokalja sub-area (Vienna Basin), where loess grasslands and steppe meadows rich in dicotyledonous plant species (assumed to be the original habitat of the species) were present before the landscape was changed by human activities (Bauer and Kenyeres 2006, Kenyeres et al. 2009). Based on this extensive study, *I. costata* is also extremely rare in the intermediate, lowland areas (Győr Basin, Sopron-Vas Plain, Kemeneshát, and Komárom-Esztergom Plain) The potential habitats of *I. costata* in these areas, dominated by arable lands, have drastically changed, and most of the remaining grasslands in these areas are located in depressions and, thus, are dominated not by semi-dry hayfields, but by marsh meadows with a humid microclimate that are less suitable for the ecological requirements of *I. costata*. According to the results of previous (Kenyeres et al. 2017, 2018) and the present study, grasslands with humid climates negatively correlate with the occurrence of the species and its density.

Conservation possibilities.—From the perspective of species protection, it is essential to highlight that trampling, fires, and mowing in spring and early summer are a threat to *I. costata* due to its phenological characteristics and low mobility. The species places its eggs 1–2 cm deep in the soil, making them easily destroyed by passing fires. Among grassland management procedures, interventions involving soil damage seriously endanger a population's survival; ploughing and overseeding are lethal, but harrowing, with only a few centimeters of soil damage, can also significantly endanger the success of the species.

In areas where *I. costata* occurs, the prohibition of grazing and tourism that cause trampling is justified; in hayfields, the application of late mowing (beginning of July at the earliest) or, if this is not feasible, mosaic-type treatment leaving unmown patches (e.g., 1/3 of the plot) is recommended (Kenyeres et al. 2017, 2018). The latter is justified by the fact that from the second half of May, which is the typical mowing period of these meadows, the species is in its adult state when reproduction and egg-laying take place. Also, in the distribution area of *I. costata*, mowed grasslands are often located between intensively used arable lands, and it is important for their conservation to reduce the use of pesticides in this area (Ivković and Horvat 2020).

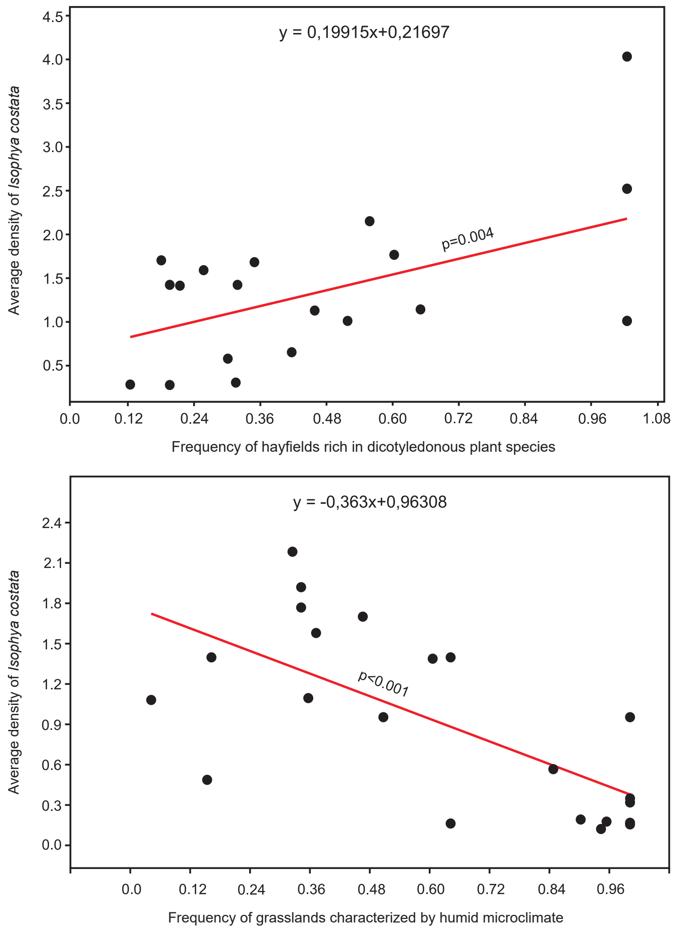

Fig. 7. Results of GLM testing of the effect of the presence of hayfields rich in dicotyledonous plant species and of the presence of grasslands characterized by a humid microclimate on the density of *Isophya costata* (based on data in ETRS quadrat, N=78).

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Substrate-borne vibration in Pacific field cricket courtship displays

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Abstract

While thought to be widely used for animal communication, substrate-borne vibration is relatively unexplored compared to other modes of communication. Substrate-borne vibrations are important for mating decisions in many orthopteran species, yet substrate-borne vibration has not been documented in the Pacific field cricket *Teleogryllus oceanicus.* Male *T. oceanicus* use wing stridulation to produce airborne calling songs to attract females and courtship songs to entice females to mate. A new male morph has been discovered, purring crickets, which produce much quieter airborne calling and courtship songs than typical males. Purring males are largely protected from a deadly acoustically orienting parasitoid fly, and they are still able to attract female crickets for mating though typical calling song is more effective for attracting mates. Here, we document the first record of substrate-borne vibration in both typical and purring male morphs of *T. oceanicus.* We used a paired microphone and accelerometer to simultaneously record airborne and substrate-borne sounds produced during one-on-one courtship trials in the field. Both typical and purring males produced substrate-borne vibrations during courtship that temporally matched the airborne acoustic signal, suggesting that the same mechanism (wing movement) produces both sounds. As previously established, in the airborne channel, purring males produce lower amplitude but higher peak frequency songs than typical males. In the vibrational channel, purring crickets produce songs that are higher in peak frequency than typical males, but there is no difference in amplitude between morphs. Because louder songs (airborne) are preferred by females in this species, the lack of difference in amplitude between morphs in the substrate-borne channel could have implications for mating decisions. This work lays the groundwork for investigating variation in substrate-borne vibrations in *T. oceanicus*, intended and unintended receiver responses to these vibrations, and the evolution of substrate-borne vibrations over time in conjunction with rapid evolutionary shifts in the airborne acoustic signal.

Keywords

communication, purring crickets, *Teleogryllus oceanicus*

Introduction

Natural and sexual selection have created complex and beautiful signals through which organisms communicate. These signals are presented in a broad spectrum of sensory modalities, ranging from visual, such as the colorful dances of male jumping spiders, to chemical, like the sweet scent flowers produce to attract pollinators. One of the oldest, yet least understood, modes of communication is substrate-borne vibration, in which vibrations are sent and carried through a substrate (e.g., the stem of a leaf or dirt) to a receiver (Hill 2009, Cocroft et al. 2014). The ubiquitous presence of vibrosensory systems, including campaniform sensilla, hair sensilla, and chordotonal organs, in nearly all insects supports the ancient origin of mechanosensory communication (Hoy and Robert 1996, Lakes-Harlan and Strouβ 2014). Vibrational communication is part of the auditory mode of communication, but it is a discrete channel because of the difference in media through which, and types of waves by which, vibrations are propagated. Auditory signals are primarily sent through a fluid medium like air as longitudinal pressure waves and typically travel long distances, while vibrational signals are primarily sent through a solid medium, are often characterized by low-frequencies, and generally travel relatively short distances as boundary waves, specifically Rayleigh waves through the ground or boundary waves through plants (Čokl and Virant-Doberlet 2003, Caldwell 2014, Hill et al. 2019). Unlike sounds that travel through air, body size does not constrain pitch for vibrational signals (except for those produced via tremulation), meaning that a small animal can potentially produce a very lowfrequency substrate-borne vibration (Cocroft and Rodríguez 2005, Caldwell 2014).

Due to the human perceptual bias for airborne sound and technological limitations, we learned of the ubiquity of substrate-borne vibrations in animal communication relatively recently (Virant-Doberlet et al. 2019). It is estimated that upwards of 200,000 species of insects use substrate-borne vibrations in both inter- and intra-specific communication (Cocroft and Rodríguez 2005, Hill et al. 2019). Mechanisms by which such communicative vibrations are produced are diverse and include, but are not limited to, percussion, stridulation, and tremulation (Čokl and Virant-Doberlet 2003, Hill 2009). For example, tremulation—moving the whole body without touching the substrate—is common in orthopterans (e.g., in the bush cricket *Onomarchus uninotatus* (Serville, 1838),

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Rajaraman et al. 2015, 2018, and in katydids, Morris et al. 1994; reviewed in Stritih and Čokl 2014) and can be important for mate choice (e.g., in groundhopper *Tetix ceperoi* (Bolívar, 1887), Kočárek 2010; in katydid *Conocephalus nigropleurum* (Bruner, 1891), de Luca and Morris 1998). Adding further complexity, while many insect species rely exclusively on substrate-borne vibrations for communication, many others employ a combination of both substrate-borne vibrations and other signaling modalities, either with each individual component presenting unique information or with both components providing information relative to the other (Hebets and Papaj 2005, Higham and Hebets 2013, Caldwell 2014). Airborne sound is a likely modality to be paired with substrate-borne vibrations, as the production of airborne sound unavoidably excites energy in the substrate-borne vibrational channel, whether via direct coupling of the signaler's body to the substrate or induction of airborne waves to the substrate (e.g., Stölting et al. 2002, Caldwell 2014).

Stridulation, in which two body parts are rubbed together to produce sound, is the primary mechanism of both vibratory and airborne signal production in numerous insect and arachnid species and often functions in intersexual (e.g., Elias et al. 2010), intrasexual (e.g., Hill and Shadley 1997), and interspecific communication such as aposematic warnings (e.g., Masters 1979). Among orthopteran species, stridulation is typically associated with the production of an acoustic signal; however, in several species, stridulation has also been shown to simultaneously produce substrate-borne vibrations that function in signaler localization (in the field cricket *Gryllus bimaculatus* De Geer, 1773, Weidemann and Keuper 1987 and the bush cricket *Tettigonia cantans* (Fuessly, 1775), Latimer and Schatral 1983) and territory establishment among males (in bush crickets *Tettigonia viridissima* (Linnaeus, 1758), Schatral et al. 1985 and *T. cantans*, Keuper and Kühne 1983). Despite the increasing effort to document substrate-borne vibration in Orthoptera, we have just begun, and most species remain unexplored (Cocroft and Rodríguez 2005, Benediktov 2009).

Pacific field crickets, *Teleogryllus oceanicus* (Le Guillou, 1841), signal in multiple modalities, including using stridulation to produce an airborne signal, but substrate-borne vibration has not been documented. Male *T. oceanicus* use an airborne acoustic calling song to attract females from a distance and then produce a different airborne acoustic courtship song in close one-on-one encounters with females. Females use these courtship songs and chemical signals from cuticular hydrocarbons to make mate choice decisions (Balakrishnan and Pollack 1997, Pascoal et al. 2017). In the Hawaiian Islands, the typical airborne acoustic calling song also attracts an acoustically orienting predator, the parasitoid fly *Ormia ochracea* (Bigot, 1889). *O. ochracea* facilitated the evolution of an obligately silent male morph of *T. oceanicus* (Zuk and Kolluru 1998, Zuk et al. 2006) and is likely playing a role in the evolution of a newly discovered male morph, purring crickets (Tinghitella et al. 2018, Tinghitella et al. 2021). Purring crickets are a new acoustic morph in Hawaii in which males use wing stridulation to produce airborne acoustic signals that are lower in amplitude and more broadband than typical male songs. The mean peak frequency is higher for purring males than typical males, and there is more variation in peak frequency among purring males compared to typical males (Tinghitella et al. 2018). Phonotaxis experiments have revealed that female crickets use the purring song to locate mates, and the role of the purr in courtship is still uncertain (Tinghitella et al. 2018). Some female *O. ochracea* can also locate hosts using the purr, but they overwhelmingly prefer typical males in field choice tests (Tinghitella et al. 2021).

The first objective of this study was to investigate the presence of substrate-borne vibrations in purring and typical *T. oceanicus* courtship songs. We hypothesized that *T. oceanicus* males generate substrate-borne vibrations during courtship as a result of the energy generated via stridulation propagating through both the air and substrate. Caldwell (2014) stated that any acoustic signaler that is in contact with a substrate will also produce a substrate-borne signal as a byproduct of the airborne signal. Since purring crickets were just discovered, this investigation is timely because shifts to substrate-borne communication channels have been previously associated with a reduction in airborne signals. In a famous example, it was hypothesized that Panamanian katydids evolved an attenuated song in response to acoustically orienting predators, and that this change in song was coupled with an increase in vibrational signals (Belwood and Morris 1987, Morris et al. 1994). There are also examples of animals shifting signals into vibrational channels in response to abiotic factors like darkness (Partan 2017). In our study system, the purring morph has reduced amplitude in the airborne channel (Tinghitella et al. 2018), likely due, in part, to selective pressure from an acoustically orienting parasitoid (Zuk and Kolluru 1998).

Our second objective was to compare the amplitude and peak frequency of substrate-borne vibrations between purring and typical males. Because airborne acoustic signals (both calling song and courtship song) differ in peak frequency and amplitude between typical and purring male morphs (Tinghitella et al. 2018), we hypothesized that substrate-borne vibrations produced via stridulation would also differ in frequency and amplitude between male morphs. Specifically, typical courtship song has a lower peak frequency (median = 5.0 kHz) than purring courtship song (median = 7.6 kHz) in the airborne channel (Tinghitella et al. 2018). Finally, we hypothesized that the mechanism of substrate-borne sound production was through wing movement during stridulation, as seen in other orthopterans (Keuper and Kühne 1983, Weidemann and Keuper 1987). If substrate-borne vibrations and airborne sounds are produced through the same mechanism (wing movement during stridulation), then the two sounds should have matching temporal patterns.

Material and methods

We traveled to Hawaii to record substrate-borne vibration produced by wild-caught male *Teleogryllus oceanicus* during courtship. After discovering purring crickets on Molokaʻi in 2016 and noting the presence of substrate-borne vibration at that time, we began measuring vibrations in the field in 2017. We refined our methods and began recording both vibrational and airborne acoustic songs simultaneously during field seasons in June 2018, December 2018, and June 2019. We conducted this study alongside a larger survey of courtship behavior across four islands (Hawaii, Oʻahu, Molokaʻi, and Kauai) that included many populations of both typical and purring male morphs (unpublished). For a subset of these courtship trials, we used a simultaneous recording technique to record both air-borne and substrate-borne songs from 13 typical males and 14 purring males.

The collection of animals and courtship trials were conducted identically on all islands and on all occasions. We collected adult males and females from grassy disturbed areas (lawns) and housed them, separated by sex, in 27 × 39 × 17 cm plastic containers. We provided rabbit food, egg cartons for shelter, and moist cotton for water. After at least 48 hours of isolation from the opposite sex, we randomly selected one male and one female for each courtship

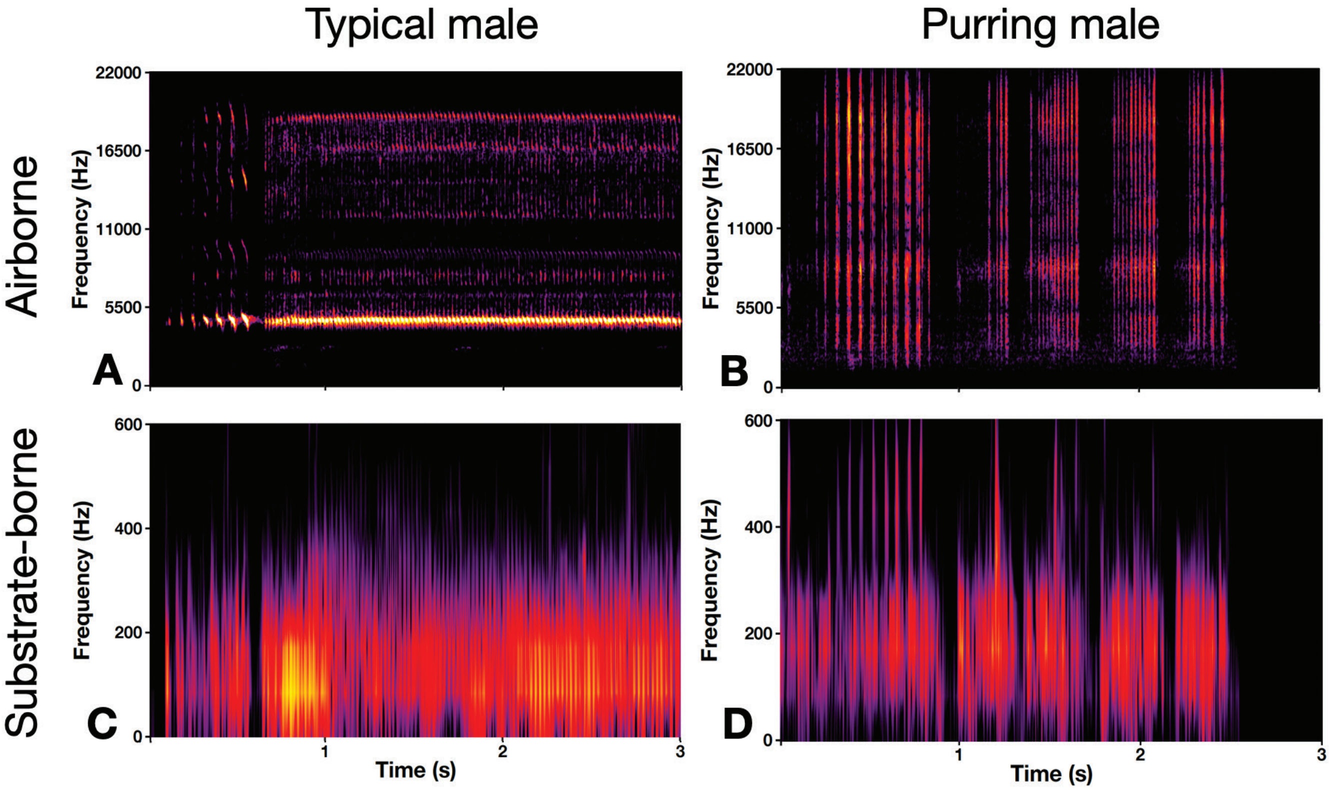

Fig. 1. Representative spectrograms showing the same song in an airborne channel (**A** and **B**) and a substrate-borne vibrational channel (**C** and **D**) for a typical male (**A** and **C**) and a purring male (**B** and **D**). Time is shown on the x-axis (seconds), and the colors (purple < red < orange < yellow) represent the power present at the various frequencies shown on the y-axis.

trial. The male and female paired in each courtship trial were always from the same population and were assayed on the island from which they were collected. We measured the width of the pronotum of each individual using digital calipers, and then placed both animals in a 1.5-L deli cup equipped with recording gear. Since some purring males produce very low-amplitude songs (Tinghitella et al. 2018), we began recording at the first visual observation of stridulation. The wing posture and motor behavior during stridulation is the same in the derived silent morph as it is in ancestral-typical males (Schneider et al. 2018) as well as in the purring morph (unpublished). Recordings lasted 10 minutes after the male began stridulating. If mounting occurred, we disrupted the copulation and returned animals to group housing separated by sex so as not to influence mating in the wild population. Females and males were never used more than once in courtship trials. After completing all trials, we released animals back into their natal grassy fields.

In order to record the substrate-borne vibrational and airborne components of the courtship song, we designed a courtship experimental container (deli cup) that used an accelerometer and a microphone to record both components simultaneously as separate audio tracks. This allowed us to determine whether the auditory signal and vibrational component were coupled and produced through the same mechanism of wing movement. Because these recordings took place in the field across islands, an accelerometer was the most portable and effective option for recording substrate-borne vibrations. To record vibrations, we attached an accelerometer (Knowles Acoustics, BU series 1771-000) to a piece of circular filter paper that fit perfectly in the bottom of the round 1.5-L deli cup (following Dierkes and Barth 1995). The cord from the accelerometer fit through a small hole in the wall of the cup and traveled through a custom converter before entering a dual-input Roland Rubix 22 audio interface. The Roland Rubix audio interface box allows two inputs (in this case, the substrate-borne input and a simultaneously recorded audio track) and was attached to a laptop computer. For the airborne signal, we used a Rode NTG2 Multi-Powered Condenser Shotgun Microphone mounted 10 cm above the filter paper. The gain was set to 80% for both the microphone and accelerometer inputs. We recorded both tracks simultaneously. For a subset of observations, we also video-recorded trials to verify that the visual stridulation matched the audio and vibrational tracks we recorded. Because all trials took place with only red light in a dark room, we used a low-light action video camera (SiOnyx Aurora IR night vision camera).

After collecting recordings in the field, we uploaded WAV files into Audacity for analysis (version 2.3.0, https://www.audacityteam.org). To capture variation within each male's courtship song, we located and analyzed three songs within each male's recording: the first and second complete songs within the first continuous bout of calling and the last complete song within the final continuous bout of calling. For all song analyses, we used the same three songs from each male.

In order to test our hypothesis that males produce substrate-borne vibrations using the same mechanism—wing movement—that they use to produce airborne acoustic signals, we first measured the temporal components of both tracks. In Audacity, we visually identified the chirp and trill portions of the song; these two distinct sections of courtship song were visible in both the acoustic track and the vibrational track in both male typical and purring morphs (Fig. 1). Following Simmons et al. (2010), we measured several features of each song in milliseconds: the total chirp length, the interval of silence between the chirp and the trill, the total trill length, and the trill/chirp interval. We also noted the start time within the recording for each song (three per male) for both the microphone track and the accelerometer track to verify that they matched.

We used Audacity to measure the peak frequency and amplitude of both the purring and typical songs. We analyzed the microphone tracks separately from the accelerometer tracks. One challenge in our data set was the fact that both males and females move nearly continuously for the duration of courtship interactions, producing broadband noise that overlapped the low-end frequencies visible in the accelerometer track. To ensure we did not disrupt normal male and female courtship behavior, we chose not to tether animals or have males court dead females; instead, we removed sections of the audio recordings that contained noise associated with locomotion after confirming that we could unambiguously identify these parts of the recordings using the video-recorded courtship trials. For audio tracks, we analyzed the entire trill portion of the three songs for each male after removing broadband noise associated with locomotion and applying a high-pass filter that removed all frequencies below 1500 Hz. For the accelerometer track, we used the same three songs for each male and selected the longest section of the trill portion of each song that was not interrupted by locomotor noise. For the accelerometer track, we applied a low-pass filter that removed all frequencies above 1000 Hz. We then used the plot spectrum function (settings: Hanning window, size = 2,048, log frequency axis) to extract peak frequency and the contrast function to extract the amplitude (values acquired as root mean squared (RMS) in dB) of each song relative to ambient noise. We used separately recorded background noise in each recording space as a baseline of 0 dB. Decibels run on a logarithmic scale, so we converted dB to a linear scale (amplitude ratio) to accurately compare amplitude among songs. This amplitude measure is called linear amplitude, and it does not have a unit of measure (hereafter referred to as amplitude).

To analyze these data, we modeled the channels (airborne microphone track and substrate-borne accelerometer track) separately with morph (purring or typical) as the main effect in each model. Because we analyzed three songs per male, we included individual ID as a random effect nested within morph (typical or purring) in each two-way ANOVA. We ran repeated measures two-way ANOVAs for the four dependent variables: airborne peak frequency, airborne amplitude, substrate-borne peak frequency, and substrate-borne amplitude. We used the mean and standard deviation of the airborne and substrate-borne frequency and amplitude data sets to calculate effect sizes using Cohen's D (Cohen 1977). Next, to compare temporal patterns between channels (airborne and substrate-borne), we compared the two channels for a given male and a given song using paired t-tests for the three temporal measures: trill length, chirp length, and the interval between the chirp and trill. All analyses were conducted in JMP (JMP Version 14).

Results

As hypothesized, we detected substrate-borne vibrations in the courtship songs of male *T. oceanicus* (Fig. 1). We recorded substrate-borne vibrations in every male that we measured, including both typically singing males and purring males.

When comparing purring and typical males, the airborne acoustic signals differed in the ways previously demonstrated. As

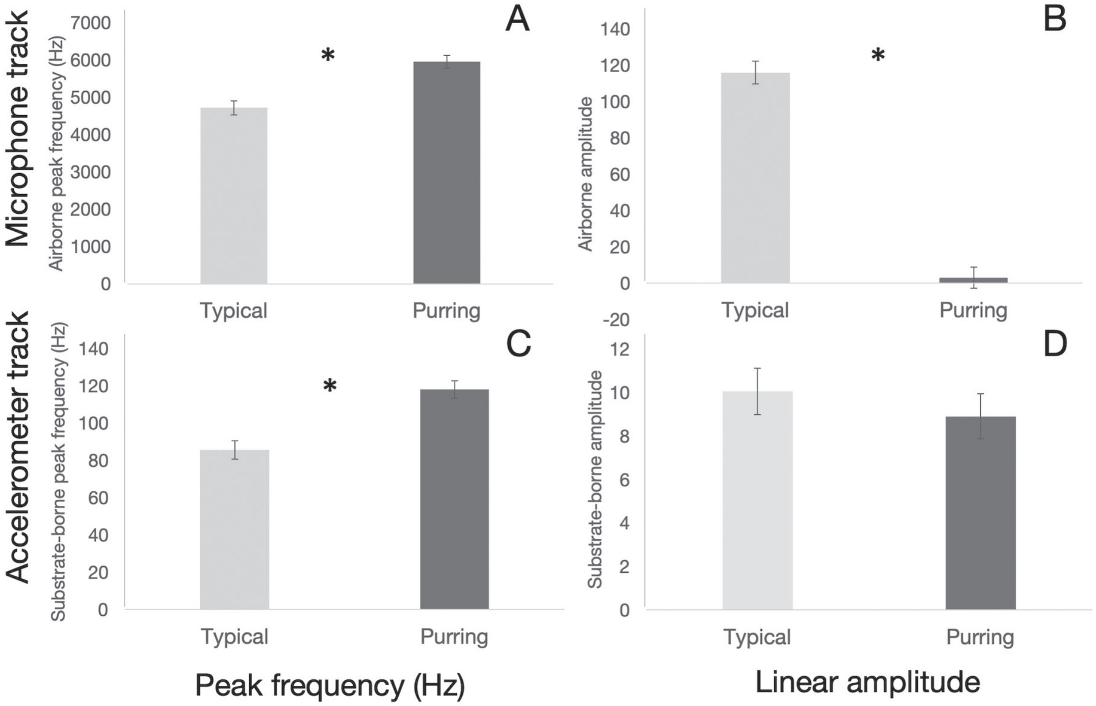

Fig. 2. Bar graphs showing the mean (equal to least squares means) and standard error (error bars) for different measures of song in typical (light gray) and purring (dark gray) male *T. oceanicus.* **A.** Peak frequency of airborne acoustic signals recorded with a microphone; **B**. Linear amplitude of airborne acoustic signals recorded with a microphone. **C.** Peak frequency of substrate-borne vibrations recorded with an accelerometer; **D.** Linear amplitude of substrate-borne vibrations recorded with an accelerometer. The asterisk indicates $p<0.001$. Effect sizes (Cohen's D) are as follows: **A.** 1.83, **B.** 4.46, **C.** 1.05, and **D.** 0.27.

in Tinghitella et al. (2018), the average frequency was higher for purring males (mean ± SE: 5955.8 ± 178.7 Hz) than typical males (4723.3 ± 185.4 Hz, $F_{25} = 22.9$, $p < 0.0001$; Fig. 2A), and the average amplitude was lower for purring males (3.1 ± 6.0) than typical males (115.9 ± 6.2, $F_{25} = 172.32$, $p < 0.0001$; Fig. 2B). When we compared substrate-borne vibrations, we found a similar pattern for frequency, but not for amplitude. Substrate-borne vibrations in purring males were higher in peak frequency (118.0 ± 4.8 Hz) than typical males (85.5 ± 5.0 Hz, $F_{25} = 22.40$, $p < 0.0001$; Fig. 2C). There was no difference in amplitude between morphs in the substrate-borne channel (purring = 8.9 ± 1.0, typical = 10.1 ± 1.1; $F_{25} = 0.601$, $p = 0.45$; Fig. 2D). The size of the effects between purring and typical males were as follows: airborne peak frequency = 1.83, airborne amplitude = 4.46, substrate-borne peak frequency = 1.05, and substrate-borne amplitude = 0.27.

Finally, we predicted that wing movement produced both the airborne signals and substrate-borne vibrations. For all songs analyzed, the start time in milliseconds was a perfect match for the microphone and accelerometer recordings. The temporal pattern also matched when we compared simultaneously recorded airborne signals and substrate-borne vibrations (for example, see Fig. 1). Of the 81 songs analyzed, only two individuals were not an exact match for chirp length (0.001 and 0.002 milliseconds off). Similarly, only six individuals were not an exact match when we compared trill length and seven when we compared the interval between the trill and the chirp. In each case, the difference was less than 0.002 milliseconds. In paired t-tests, there was no difference between the airborne and substrate-borne vibrations in chirp length ($t_{79} = 0.44$, $p = 0.66$), trill length ($t_{79} = -0.80$, $p = 0.42$), and the interval between the trill and the chirp ($t_{79} = 0.76$, $p = 0.45$).

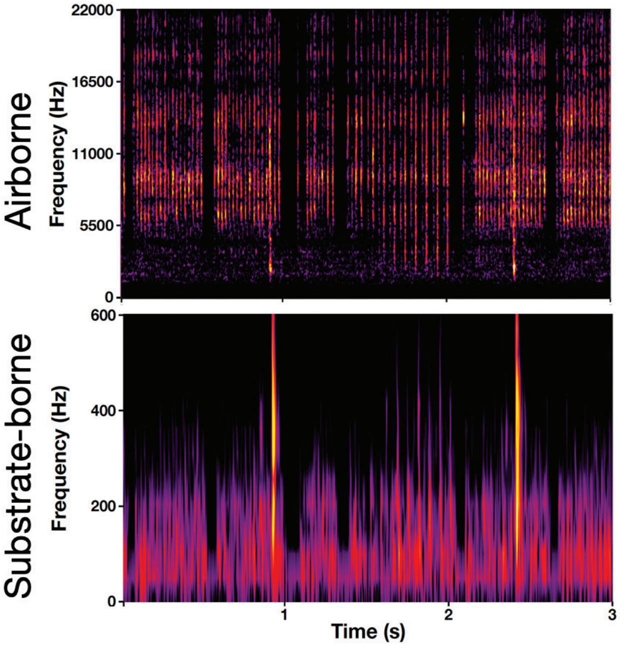

Fig. 3. Representative spectrograms from a microphone recording (airborne: top) and an accelerometer recording (substrate-borne: bottom) for a purring male that illustrates the broadband percussive sound present in many of our recordings. Percussive strikes (presumably with forelegs) appear as white vertical bars just before 1 second and at 2.5 seconds. The time is shown on the x-axis (seconds), and the colors (purple < red < orange < yellow < white) represent the power present at the various frequencies shown on the y-axis.

We also detected vibrations that were not associated with stridulation and were not associated with locomotion. These high-power broadband vibrations were present in 19 of the 27 field-recorded individuals (Fig. 3) and appear percussive. Video footage suggested that the percussive bursts were produced through foreleg drumming: males could be seen striking the substrate with either the right or left foreleg repeatedly, and all males used both legs (Suppl. material 1: video). For example, the male in the Suppl. material 1: video makes several drums with his left leg, followed by one drum with his right leg and then a pause. For the 19 males that exhibited drumming, we randomly selected one drum from the first song that contained drumming, one drum from the second song that contained drumming, and one drum from the last song that contained drumming. Following the methods described above to extract data from the accelerometer track (substrate), we analyzed the peak frequency and amplitude of the three drums per male. We also counted the number of drums during each of the three songs. The drumming sounds had an average peak frequency of 105 ± 19.5 kHz (mean ± standard deviation) and an amplitude of 49 ± 54 (Fig. 3). There was an average of 5.6 ± 2.9 drums per song.

Discussion

This is the first documentation of substrate-borne vibration in *T. oceanicus.* We recorded vibrations in two different male morphs of *T. oceanicus* (typical and purring) that appear to be generated through the movement of the wings, as the pattern in the vibrational channel perfectly matches the airborne signal. When we compared typical and purring males, we found that typical males produced lower peak frequency sounds in both the airborne (Fig. 2a) and the vibrational channel (Fig. 2c). For amplitude, typical males produced sounds that were many times louder than purring males in the airborne channel (Fig. 2b), but there was no difference between morphs in amplitude in the vibrational channel (Fig. 2d).

As expected, purring males differed from typical males in the airborne channel, with a mean peak frequency of 4.7 kHz for typical males and 6.0 kHz for purring males. These values are similar to those of Tinghitella et al. (2018), who reported a median peak frequency of 5.0 kHz for typical males and 7.6 kHz for purring males. Amplitude also matched previous results, with typical males producing significantly louder songs than purring males in the airborne channel. Because we used linear amplitude instead of decibels, which are on a logarithmic scale, we can linearly compare values of amplitude across male morphs. Thus, in the airborne channel, the amplitude of the typical song was 38 times greater than that of the purring song (115 divided by 3).

In the substrate-borne channel, purring males produced vibrations that were higher in frequency than typical males, but the difference was not as dramatic as in the airborne channel; the effect size was 1.05 for substrate-borne compared to 1.83 in the airborne channel. As expected, the peak frequencies were much lower in the substrate-borne channel, ranging from 32 to 176 Hz. Because higher frequencies attenuate more quickly in soil, we would expect substrate-borne vibrations to be lower in frequency (Čokl and Virant-Doberlet 2003, Caldwell 2014), and small-bodied species can produce low-frequency vibrations through stridulation (Cocroft and Rodríguez 2005). The frequency range measured for *T. oceanicus* matches that of other known species of Orthoptera that send airborne and substrate-borne vibrations through wing stridulation: *G. bimaculatus* at 30–500 Hz (Weidemann and Keuper 1987) and *T. cantans* at 0–800 Hz (Keuper and Kühne 1983). We did not detect a difference in amplitude between morphs in the substrate-borne channel. This suggests that the differences in wing morphology between morphs only affect amplitude in the airborne channel and not the substrate-borne channel. Purring males have a reduction in the size of the harp and mirror (resonating structures) compared to typical males (Tinghitella et al. 2018 and unpublished). Thus, resonating structures on the wings (harp and mirror) play a key role in amplifying sound in the airborne channel but do not seem to affect the transfer of the vibration to the substrate.

We found support for our hypothesis that wing movement produces both airborne signals and substrate-borne vibrations. Temporal components of song matched when we compared the microphone track to the accelerometer track, and these included start time, chirp length, trill length, and the interval between the chirp and the trill. These values were almost a perfect match in every category except for a few that differed by 0.001 milliseconds, which can be attributed to human and equipment error. We were unable to distinguish between substrate-borne vibrations produced via coupling of the male to the substrate (through the legs or abdomen) or induction of airborne waves to the substrate. Future work could make this distinction by not allowing the stridulating male to come in contact with the substrate or by adapting methods from Keuper and Kühne (1983) where different substrates were tested. Regardless of the mechanism (direct coupling or induction of waves to the substrate), our results support the claim that the production of an acoustic signal unavoidably excites vibrations in the substrate on which a signaler is resting (Caldwell 2014), and our work adds to the growing literature documenting coupled airborne and substrate-borne sound produced by stridulation in Orthopterans (e.g., *T. cantans*, Latimer and Schatral 1983; *T. viridissima*, Schatral et al. 1985; *G. bimaculatus*, Weidemann and Keuper 1987).

The big question remaining is whether female *T. oceanicus* can sense the substrate-borne vibrations and whether they affect mate choice. First, the ability to detect, receive, and translate vibrations is ancient and ubiquitous, found throughout vertebrates and arthropods (Hoy and Robert 1996, Cocroft and Rodríguez 2005, Hill 2009, Lakes-Harlan and Straub 2014). In *T. oceanicus*, males and females use cerci to detect sounds between 0 and 1000 Hz (Hoy et al. 1982, Pollack et al. 1998). Air flow and air currents produced by wing movements rather than stridulation can produce low-frequency (<70 Hz) air vibrations that are detectable through cerci up to a few centimeters away in *Gryllus bimaculatus* (Kämper and Dambach 1985). Similarly, it has been suggested that air currents produced by stridulating *T. oceanicus* males can be perceived by females, but substrate-borne vibration was not measured in that study (Pollack et al. 1998). The subgenual organ in the tibia is also a likely candidate for the detection of low-frequency vibrations in *T. oceanicus* (Lakes-Harlan and Strauß 2014), as it is used to detect substrate-borne vibrations as low as 50 Hz in related species (e.g., *Gryllus bimaculatus* and *Gryllus campestris*; Dambach 1989), and the substrate-borne vibrations we measured are above that 50 Hz threshold (85.5 Hz for typical and 118.0 Hz for purring).

When discussing the detectability of these substrate-borne vibrations for *T. oceanicus*, we should consider amplitude and the average distance that vibrations travel through soil. While we did not measure female response to substrate-borne vibration in this study, Pollack et al. (1998) used electrodes inserted into abdominal interneurons from the cerci to show that female *T. oceanicus* can "hear" low-frequency sounds produced by male wing movement from 2 cm away. We measured vibrations in a courtship context where females are a few centimeters from a signaling male, well within the range of perception for *T. oceanicus*, and our amplitude measurements were adjusted for background noise (e.g., 9.5 represents a signal that exceeded background noise, 0). In other Orthopterans that produce both airborne and substrate-borne vibrations via stridulation, *G. major* vibrations travel up to a meter through the soil from a signalling male's burrow (Hill and Shadley 1997), *T. cantans* vibrations travel about a meter through plant stems (Keuper and Kühne 1983), and *G. bimaculatus* vibrations are detectable 20 cm away in dry soil (Weidemann and Keuper 1987). Additionally, while the amplitudes we measured (purring = 8.9 ± 1.0, typical = 10.1 ± 1.1) should be detectable over the short distances associated with courtship (1–2 cm), it is possible that the percussive sounds we detected may travel further since the amplitude was much greater (49 ± 54). Following methods described by Hill and Shadley (2001), we plan to measure the distance over which substrate-borne vibrations are detectable in *T. oceanicus* in a future study.

While the first step is to explore the ability of *T. oceanicus* to detect the vibrations that courting males are producing, the next step is to assess the use of vibrations in mate choice. This could be explored using playback experiments with an electrodynamic shaker played alone or in combination with an airborne signal (Cocroft and Rodríguez 2005). There are numerous examples of substrate-borne vibrational signals playing a key role in mate choice in Orthoptera (e.g., de Luca and Morris 1998, Cocroft and Rodríguez 2005, Kočárek et al. 2010). In *T. oceanicus*, it has been suggested that the cerci detection system evolved to detect terrestrial predators like frogs (Hoy et al. 1982). It is possible that this predator detection system has been co-opted for use in mate choice. Other studies have used phylogenetic approaches to demonstrate that vibrational communication evolved from existing responses like locomotion (Scott et al. 2010) and a startle response (ter Hofstede et al. 2015). We might expect the rapid evolution of acoustic song (silent morph, Zuk et al. 2006; purring morph, Tinghitella et al. 2018) and the evolution of relaxed female preferences (Tinghitella and Zuk 2009) in *T. oceanicus* to shape both the substrate-borne vibrations and the sensory capabilities of and preference for those vibrations. Additionally, selection may differ between the airborne and substrate-borne channels; louder airborne songs are preferred by *T. oceanicus* females, but there is no difference in amplitude between morphs in the substrate-borne channel. Thus, investigations of whether substrate-borne vibrations play a role in *T. oceanicus* courtship should compare populations with different morphs, simultaneously measure airborne song, and monitor both detection and preference over time in this rapidly evolving system.

While valuable, this work has limitations. First, we used filter paper as our substrate, which was appropriate for our question since we compared morphs measured on an identical substrate. However, because the composition of any substrate imposes frequency filters on substrate-borne vibrations, we expect the spectral characteristics found in this study to differ from those recorded on natural substrates. Future works should measure and characterize these substrate-borne vibrations on natural and variable substrates (e.g., following Hill 2001). Second, while our interindividual variation was low, suggesting that our sample size adequately captured the patterns between morphs, a larger sample across more populations would give a more holistic view of substrate-born vibration in Hawaiian *T. oceanicus.* More-advanced equipment, such as a high-speed video camera and a laser vibrometer, would also allow us to tease apart the way in which wing movement translates to substrate-borne vibrations (air movement or contact between file and scraper traveling through the legs).

As with most discoveries, this work lays the groundwork for future questions. In addition to exploring how *T. oceanicus* females detect and use substrate-borne vibrations, we must also recognize that communication happens in a network (Virant-Doberlet et al. 2014, 2019). Our network has multiple senders (signaling males), intended receivers (female crickets), and unintended receivers that are conspecifics (satellite males) and heterospecifics (parasitoid flies). The eavesdropping predators, *O. ochracea*, are an important driver of the rapid evolution of airborne signals in *T. oceanicus*, and because they are airborne aerial predators, vibration may be hidden from this natural selection. However, vibrations are likely susceptible to a different set of unintended predatory receivers, such as spiders (Virant-Doberlet et al. 2019). Eavesdropping male crickets may also be able to use vibration to locate singing males for satellite behavior. Finally, future work should also explore other parts of substrate-borne vibrations, such as the broadband percussive taps produced by the forelegs. RMT has conducted courtship trials in the field for the past 15 years and did not observe this behavior until 2017. To date, no literature has been published documenting this behavior in *T. oceanicus*, but drumming (percussive) behavior is a commonly utilized mechanism of vibrational signal production among diverse arthropods (e.g., fiddler crabs, Aicher and Tautz 1990; termites, Röhrig et al. 1999; wetas, Gwynne 2004; mole crickets, Hayashi et al. 2018; reviewed in Hill 2012), and drumming may be important even when there are other mechanisms producing substrate-borne vibrations (in our case, wing stridulation), as seen in a stink bug that uses tremulation, buzzing, abdomen vibration, and drumming (Kavčič et al. 2013). Finally, drumming may function in both the substrate-borne and airborne channels (Hill 2012).

This work is a first look at substrate-borne vibration in *T. oceanicus* and answers calls by many to explore communication in the vibrational channel (e.g., Hill 2001, Cocroft and Rodríguez 2005). This work lays the foundation for future research on variation in substrate-borne vibration in *T. oceanicus*, intended and unintended receiver responses to these vibrations, and the coevolution of substrate-borne vibrations with other courtship signals, such as airborne and chemical signals.

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Supplementary material 1

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New species and records of the genus *Lipotactes* (Orthoptera: Tettigoniidae: Lipotactinae) from Vietnam, Cambodia, and Thailand

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Abstract

Six new species of the genus *Lipotactes* Brunner, 1898 are described: three species from Vietnam – *L. serratus* **sp. nov.**, *L. angulatus* **sp. nov.**, *L. productus* **sp. nov.**; two species from Cambodia – *L. discus* **sp. nov.** and *L. samkos* **sp. nov.**; and one species from Thailand – *L. saengeri* **sp. nov.** The diagnostic characters are illustrated. Additional records are reported for *L. vietnamicus* Gorochov, 1993 and *L. azureus* Gorochov, 1996. The striking azure blue color of the alive male of *L. azureus* that contrasts with the green and white museum specimen is documented. An updated key to the species of *Lipotactes* from Vietnam, Cambodia, and Thailand is provided.

Keywords

Cambodia, diagnostic key, South-East Asia, Taxonomy, Thailand, Vietnam

Introduction

The genus *Lipotactes* comprises small- to medium-sized species that are known to occur in Asia from South China in the northwest to Sulawesi in the southeast. Thus far, 25 species are known, of which seven have been reported from Vietnam, one from Cambodia, and four from Thailand (Cigliano et al. 2020). The species occurrence in Vietnam and Cambodia has been mainly studied by Gorochov (1993, 1996, 1998), with additional data by Ingrisch (1995) and Helfert and Sänger (2009). Species from China have recently been reviewed by Feng et al. (2017), while Wang and Shi (2020) estimated the effect of global warming on the potential distribution based on the present distribution information and climate data.

It has been shown that species related to *L. alienus* Brunner, 1898 and *L. virescens* Ingrisch, 1995 can be differentiated based on stridulation and the shape of the stridulatory area, especially the stridulatory file (Tan et al. 2020). However, such a study requires fresh and living specimens. The strongly reduced male wings are almost completely hidden under the pronotum, such that the file and mirror cannot be studied without cutting the wings off from the body. Also, the differences in stridulation and the stridulatory apparatus correspond to distinct differences in the shape of the male cercus (Ingrisch 1995, Tan et al. 2020).

In the current study, species delimitation is based mainly on the shape and extensions of the male cerci. The variation of these organs allows differentiation between the species, as already shown in Ingrisch (1995) and Gorochov (1996). Species with a similar basic structure of the cerci often replace each other geographically, while species that occur close to each other in the same locality or in nearby localities usually show more pronounced differences in the cerci and their extensions.

The male phallus of *Lipotactes* species is often fully membranous and thus not useful for identification. Phallus sclerites, which may act as titillators, have been reported only in species related to *L. azureus* Gorochov, 1996 thus far (Gorochov 1996).

A recent research project of the Institut Royal des Sciences Naturelles de Belgique in Brussels on the entomological diversity of Vietnam and Cambodia (Constant and Grootaert 2020) provided a reasonably high number of new specimens of the genus from localities distributed throughout Vietnam and Cambodia; this made it necessary for an updated overview of the species and their distribution in the area. During the study, it became necessary to re-examine the specimens reported by Helfert and Sänger (2009) as *L. khmericus* Gorochov, 1998 from Southeast Thailand, as the collection in ISNB contained a new species from Cambodia with a similar basic cercus structure as *L. khmericus*. Thus, it was possible that the specimens from Southeast Thailand may also have similar male cerci that differ in detail.

A marked increase in the number of species in Vietnam and Cambodia added to the necessity for an updated key to the species. The key provided here is restricted to males, as the females of most species do not show enough characters to identify them on morphological characters without knowing the corresponding male. Also, females are only known for 12 of the 18 species considered for the present publication.

The type localities for the *Lipotactes* species described from Vietnam, Cambodia, or Thailand are presented in Fig. 1. *L. virescens* Ingrisch, 1995, described from Trang province in the very south of Thailand, is not presented as its type locality lies south of the area presented on the map.

Materials and methods

The current study is mainly based on specimens from the research project "A step further in the Entomodiversity of Vietnam" managed by J. Constant (see Constant and Grootaert 2020).

A total of 34 specimens from 12 localities were available for the study. Of these, 28 specimens from eight localities could be sorted into seven distinct species according to the male abdominal appendages. From four other localities combined, only six females were available for study. Of these, five specimens from three localities were found to be similar to *L. azureus* Gorochov, 1996, which belongs to a group of five species that mainly differ by details of the male abdominal appendages (Gorochov 1996). In this paper, another species of this group is described. The females of these species are similar and described only for three of the five species, preventing a reliable identification to species level without a corresponding male. Another single female from central Cambodia has a subgenital plate similar to *L. silvestris* Ingrisch, 1990, although there are distinct differences. Its main characters are described below, but naming it is delayed until a corresponding male is found.

A selected number of the museum specimens were re-set to allow the study of the fine details of the male cerci and sclerotized genital structures if present.

Documentation of the specimens studied was done by photography using a Canon D500 mounted to a copy stand for habitus images and a Canon D6 mounted to the photo adapter of a Motic M5 for microscopic images. The images were processed by CaptureOne and stacked with Zerene Stacker.

To prepare the key to species, characters for species that I did not study were adapted from Gorochov (1993, 1996, 1998).

Names of the localities, provinces, etc. for the specimens studied are given as printed on the labels, including the geographical coordinates. Additional information not on labels is mentioned within brackets. The names of the type localities of previously described species are given as in the original publication or in OSF (Cigliano et al. 2020). The spelling of some localities may differ in small details even though they refer to the same place.

Depositories

ISNB	Institut royal des Sciences naturelles de Belgique, Brussels, Belgium
NMW	Naturhistorischen Museum Wien, Vienna, Austria
ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia

Results

Taxonomy

Family Tettigoniidae Krauss, 1902
Subfamily Lipotactinae Ingrisch, 1995

Genus *Lipotactes* Brunner von Wattenwyl, 1898

Type species: Lipotactes alienus Brunner von Wattenwyl, 1898

Species of the genus are characterized by their large head with big eyes compared to a rather small body. Many species are at least partly predators. They are able to follow flying insect with their large eyes and catch them out of the air.

***Lipotactes azureus* Gorochov, 1996**

Figs 1, 2A–C, 3J–L

Lipotactes azureus Gorochov, 1996: 32

Type locality.—Vietnam, Vinfu prov., Tamdao 800–900 m.

Type material.—VIETNAM • 3 males (including holotype), 1 female, 5 female nymphs; ZIN [not examined]

Material examined.—VIETNAM • 2 females, 6 males; Prov. Vinhfu, Tam Dao N.P. [= National Park]; 21°31'N, 105°33'E, 25–30 Jul. 2011; J. Constant and J. Bresseel leg.; I.G. 31.933; ISNB.

Measurements.—(2 males, 1 female; in mm) Body w/o wings: male 10.5–11.7, female 13.2; pronotum: male 3.9–4.0, female 4; tegmen: male 1.6–1.9, female 0; hind femur: male 11.0–11.5, female 13.4; ovipositor: female 8.6.

Discussion.—This species has been described in detail by Gorochov (1996). It was named for the azure coloration of the alive male mixed with a black pattern. That azure color appears ivory white in museum specimens, while the legs are mostly green. I use this opportunity to illustrate the change of coloration between an alive male and a museum specimen (Fig. 2A, B). The females do not show the same striking coloration but display various shades of brown with black marks. A female from Tam Dao has fore- and mid-legs with remnants of green. Thus, one may suppose that at least some females of this species have green legs when alive.

Remark.—The female specimens from the type locality were clued to cardboard. Thus, a female from Ba Vi, Hanoi, Vietnam, was used to document the subgenital plate, although no male from that locality was available to verify the identification.

***Lipotactes vietnamicus* Gorochov, 1993**

Figs 1, 2H–I, 3G–I

Lipotactes vietnamicus Gorochov, 1993: 59

Type locality.—Vietnam, Prov. Hasonbinh, Cuc Phuong Nature Reserve.

Type material.—VIETNAM • 1 male (holotype), 2 females (paratypes); ZIN [not examined]

Material examined.—VIETNAM • 1 female, 1 male; Hoa Binh Prov., Cuc Phuong N.P. [= National Park]; 20°19'N, 105°36'30"E; 19–23 Jul. 2011, J. Constant and J. Bresseel leg.; I.G. 31.933; ISNB.

Measurements.—(1 male, 1 female; in mm) Body w/o wings: male 13.5, female 15; pronotum: male 4.2, female 4.7; tegmen: male 3, female 0; hind femur: male 13, female 14.5; anterior femur: male 4, female 4; ovipositor: female 8.

Discussion.—This species was described in detail by Gorochov (1996) and was also reported from China by Feng et al. (2017). Some images are given for comparison with the new species described below.

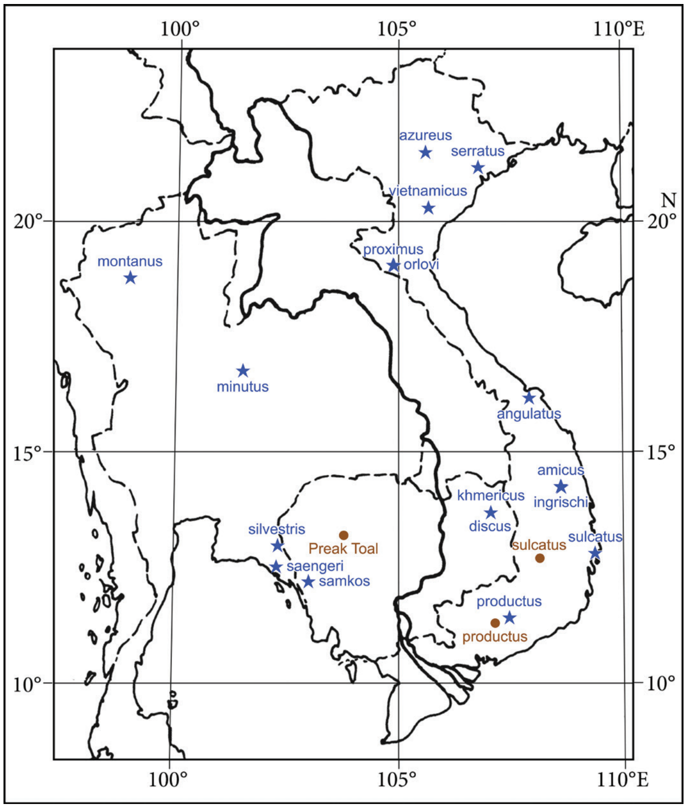

Fig. 1. Type localities of *Lipotactes* species described from Vietnam, Cambodia, and Thailand; blue stars mark localities of holotypes, brown dots mark localities of a female paratype if not identical to locality of corresponding holotype; Preak Toal marks the locality of an unnamed female described in this publication. The species of the pairs *L. amicus* Gorochov, 1993 and *L. ingrischi* Gorochov, 1996; *L. discus* sp. nov. and *L. khmericus* Gorochov, 1998; and *L. orlovi* Gorochov, 1996 and *L. proximus* Gorochov, 1996 have been described from nearby localities. The type locality of *L. virescens* Ingrisch, 1995 lies south of the limits of this map.

Lipotactes serratus sp. nov.

http://zoobank.org/A93B534D-3059-4748-9006-F3BFAFE6D0CA
Figs 1, 2D–G, 3A–F

Material examined.—**Holotype:** VIETNAM • male; Tay Yen Tu Nat. Res. [= Nature Reserve]; 21°11'10"N, 106°43'25"E; 7–11 Jul. 2013; J. Constant and J. Bresseel leg.; I.G. 32.454;ISNB. **Paratypes**: VIETNAM • 6 females, 1 male; same data as for holotype; ISNB.

Diagnosis.—In general appearance and coloration of males, the new species strongly resembles *L. azureus* Gorochov, 1996, although there are differences in details: the male pronotum is slightly prolonged and elevated posteriorly, almost completely covering the tegmen in dorsal view instead of leaving the apical area free, and the black band along the apical margin of the pronotum is broader than in *L. azureus*; in females, the black lateral bands of the pronotum are less distinct and gradually pass over into the brighter surrounding area, and the ovipositor is not as stout and less strongly curved as in *L. azureus*. The male cercus resembles that of *L. proximus* Gorochov, 1996, although the dorsal internal process has the internal margin straight, not concavely incised, and the process in apical view is more strongly upcurved; the ventral internal process has the dorsal surface concave as in *L. azureus* but is distinctly longer and resembles that of *L. orlovi* Gorochov, 1996, *L. proximus*, and *L. vietnamicus* Gorochov, 1993. The narrow apical area of the male cercus resembles, by its more pronounced bend, that of *L. orlovi* or *L. vietnamicus*. From all four mentioned species, it differs by the tip of the narrow apical area of the male cercus that is not acute nor slightly spinose but terminates into a serrate apical cone. The male phallus is provided with a parallel running pair of elongate granular sclerites that are triangularly widening at base; the apical areas of these sclerites are strictly parallel, neither deviating and narrowing as in *L. vietnamicus*, nor widened as in *L. orlovi*, nor curved outwards as in *L. azureus* or setose at tip as in *L. proximus*; the tips of these sclerites are acute rather than obtuse as in the other four species; the unpaired medial sclerite hardly reaches the end of the triangular widening of the elongate sclerites.

Description.—Medium-sized species. Males with white bodies and green legs, both with black ornaments (Fig. 2D); females brown with black ornaments (Fig. 3A).

Male. Pronotum with two transverse furrows, posterior area prolonged and almost fully covering tegmen. Tenth abdominal tergite at hind margin with a rather deep concave incision in middle. Epiproct with deep medial furrow. Cercus with stout basal area wider than long, at external angle prolonged into a narrow and little curved process that terminates into a strong spine that carries along margins acute teeth (Fig. 2F); at the internal apical angle of the wide basal area, prolonged into a dorsal and a ventral process; the dorsal process wide, compressed, and slightly upcurved with subtruncate apical margin and rounded distal but subangular proximal angle. The distal margin of the process is curved ventrad to meet the ventral process at base but narrows towards tip; the ventral process roughly elongate, triangular with rounded tip and concave dorsal surface, also somewhat upcurved (Fig. 2E, G). Phallus with two paired and one unpaired sclerites; paired sclerites triangular at base and prolonged into long, nearly straight, and parallel apical extensions with finely granular surface and only slightly narrowing towards obtuse tip; unpaired sclerite short with obtuse tip, not surpassing the triangular basal area of the lateral sclerites (Fig. 2E). Subgenital plate with roundly approaching lateral margins; apical margin sub-angularly incised; styli long and narrow (Fig. 2G).

Coloration. Face and vertex white with a medium to light brown medial band from end of vertex to clypeus and with a pair of slightly darker, medium brown subocular bands continued on mandibles; clypeus light green with brown rim; vertex with a wide black transverse band between compound eyes. Antennae annulated. Pronotum white with brown rim; in anterior area, with a pair of roughly rectangular black spots with projecting posterior angles and a triangular white spot; along hind margin and including part of paranota, with a wide black band that narrows from middle to lateral areas. Tegmen green. Abdominal tergites white; tergites 2–7 and 10 with black lateral bands. Cerci light brown with dark dots, internal processes getting darker towards tips. Subgenital plate in dorsal view white; styli brown. Legs green with numerous black dots at femora and tibiae; hind femur in widened basal area with a black oblique band followed by a black ring at beginning of narrow apical area; also black around hind knee on femur and tibia.

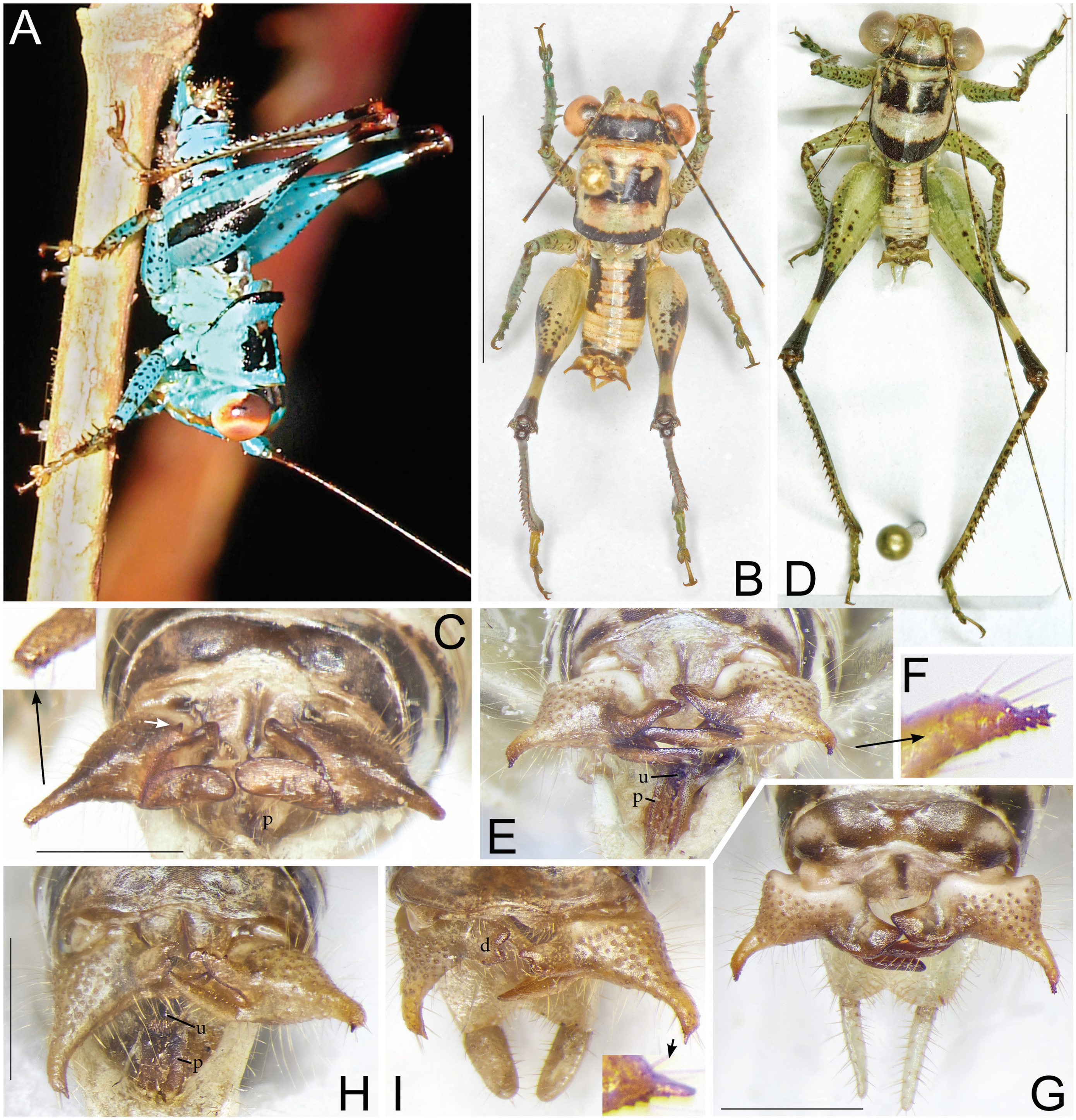

Fig. 2. *Lipotactes* males: **A–C.** *L. azureus* Gorochov, 1996; **D–G.** *L. serratus* sp. nov.; **H–I.** *L. vietnamicus* Gorochov, 1993. **A.** Alive male in habitat (photo credit Jérôme Constant); **B, D.** Male dorsal view; **C, E, H.** Abdominal apex in apical view; **G, I.** In dorsal view; **F.** Tip of cercus greatly enlarged (also insets in **C** and **I**). Abbreviations: d, dorso-medial projection of cercus; p, paired phallus sclerites; u, unpaired phallus sclerite. The white arrow in C indicates the spine at base of the upper process. Scales for habitus: 10 mm; for cerci: 1 mm.

Female. Subgenital plate with strongly convex lateral margins; more or less membranous and slightly projecting at subtruncate apical margin, with faint medial furrow (Fig. 3D). Ovipositor elongate, upcurved, regularly narrowed towards acute tip; ventral margin very finely serrulate before end (Fig. 3E, F).

Coloration. Face light or dark reddish brown, mouthparts of lighter color; vertex with complete or incomplete black transverse band between compound eyes (Fig. 3B, C). Antennae annulated. Pronotum brown with incomplete black lateral bands; transverse furrows very weak, but both furrows with a pair of short but deep impressions.

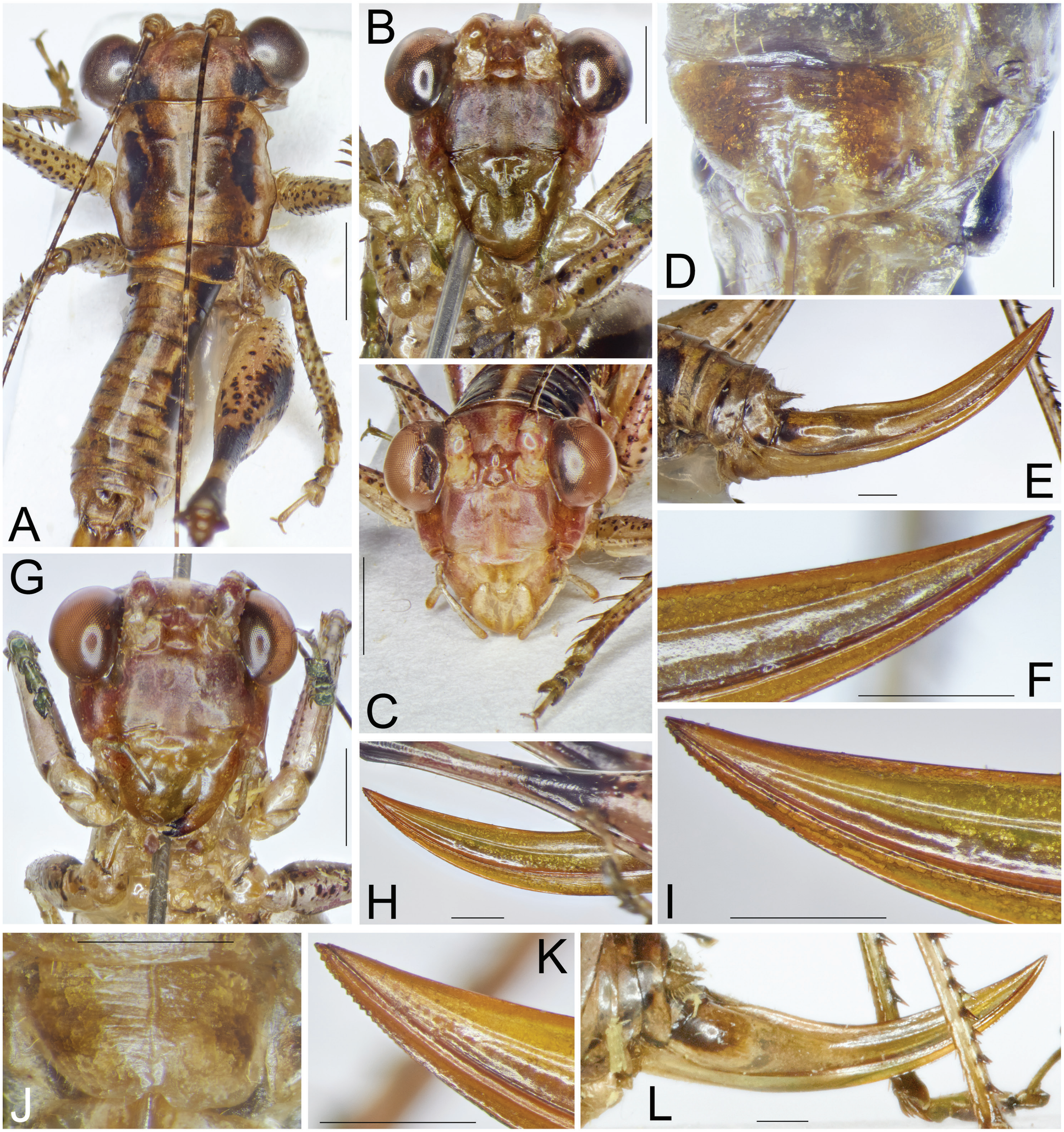

Fig. 3. *Lipotactes* females: **A–F.** *L. serratus* sp. nov.; **G–I.** *L. vietnamicus* Gorochov, 1993 from Cuc Phuong; **J, K.** *L. cf. azureus* Gorochov, 1996 from BaVi; **L.** *L. azureus* Gorochov, 1996 from Tam Dao. **A.** Habitus dorsal view; **B, C, G.** Face; **D, J.** Subgenital plate; **E, H, L.** ovipositor; **F, I, K.** End of ovipositor with serrate ventral margin. Scales for habitus and face: 5 mm; others: 1 mm.

Abdomen brown; segments 1–7 with black lateral bands. Legs as in male but of brown foundational color. Ovipositor medium brown.

Measurements.—(2 males, 6 females; in mm) Body w/o wings: male 10.0–10.5, female 11.5–15.0; pronotum: male 4.0–4.2, female 3.2–4.2; tegmen: male 2, female 0; hind femur: male 11–12, female 12–14; anterior femur: male 3.5–4.0, female 3.7–5.0; antenna: female 70; ovipositor: female 7.0–9.5.

Etymology.—The name of the new species refers to the apical spine of the male cercus that carries acute teeth along margins; from Latin *serrare* meaning “to saw”.

Lipotactes sp.

Material examined. [females only]—VIETNAM • 2 females; Cat Ba N.P. [= National Park]; 20°48′N, 107°0'20"E; 12–16 Jul. 2013; J. Constant and J. Bresseel leg.; I.G. 32.454;ISNB. 1 female; Cham-Chu N. R. [= Nature Reserve]; 22°12′N, 105°6'0"E; 8–12 Jul. 2015, J. Constant and J. Bresseel leg.; I.G.: 33.092; – ISNB. 1 female, 1 nymph male; Hanoi prov., BaVi N.P.; 21°4'4"N, 105°21'30"E; 25–29 Jun. 2015; J. Constant and J. Bresseel leg.; I.G.: 33.092; ISNB.

Discussion.—Five species related to and including *L. azureus* were differentiated by Gorochov (1996), of which one species, *L. sinicus* (Bey-Bienko, 1959), is from China, and four species are from North Vietnam. These species were all based on the characteristic shapes of the male cerci and sclerites found on the male phallus. Both characters follow a common basic structure, which is markedly modified between species. For two of these five species, the females are still unknown. In the current paper, another species of this group from Northern Vietnam is described. Although females of these species can be differentiated as a group from other Vietnamese *Lipotactes* species by the absence of a weak concavity at the end of the dorsal margin of the ovipositor, no characters are reported so far to differentiate between the females of these species.

In the collection of specimens studied for this publication, there were four females and one nymph without corresponding adult males from three localities that are not one of the type localities of the described species. These specimens do not show any conspicuous diagnostic difference from the female of *L. azureus*, although they are missing the green color of the legs. I abstain from arranging these females to any of the named species.

Lipotactes angulatus sp. nov.

http://zoobank.org/A36B713F-8A3D-4AFB-860D-71FAED728B0E

Figs 1, 4A–H

Material examined.—**Holotype:** VIETNAM • male; Central Vietnam, Bach Ma N.P. [= National Park]; 16°12′N, 107°52′E; 15–16 Jul. 2011; J. Constant and J. Bresseel leg.; I.G. 31.933; ISNB. **Paratypes:** VIETNAM • 3 males; same data as for holotype; ISNB.

Diagnosis.—A predominantly green species that does not seem to be close to any other *Lipotactes* species reported so far from Vietnam. It is missing the striking black and pale color pattern and the complex internal process of the cercus found in the species reported from the more northern areas of Vietnam (e.g., *L. azureus* Gorochov, 1996 or *L. vietnamicus* Gorochov, 1993), but it also does not show the dull color pattern of species found in South Vietnam and Cambodia (e.g., *L. ingrischi* Gorochov, 1996), although it shares with both groups of species the possession of a narrow apical area of the male cercus that differs in shape from that of the other species. From coloration, the new species resembles *L. virescens* Ingrisch, 1995. It differs by the shape of the male cercus, which has a strongly widened base, incurved and narrow apical area, and a long and angularly curved internal process instead of a short and narrow internal process with a tubercle at base. Regarding the internal process of the male cercus, the new species resembles *L. hamatus* (Karny, 1931) described from Sulawesi. It differs by the strongly widened cercus base, the curved tip of the cercus, the larger and more strongly bent internal process, by the posteriorly widened and elevated disc of the pronotum, and by the strongly inflated tegmina.

Description.—Medium-sized species of predominantly green coloration with dark pattern (Figs 4A–B).

Male. Pronotum prolonged with diverging lateral margins to behind mid length, inflated in posterior half; anterior margin bend-up and rounded, appearing in dorsal view concave, posterior margin widely rounded; first transverse sulcus distinct and entire; second and third transverse sulcus hardly distinct except second sulcus on paranota. Tegmen strongly inflated (Fig. 4D). Tenth abdominal tergite in dorsal area somewhat prolonged, but apical margin widely concave in middle (Fig. 4F). Epiproct large with a deep medial furrow. Cerci rather short, extremely widened at base and, there, almost as wide as long; internal margin strongly narrowed towards narrow tip of cercus; tip slightly curved mediad; from ventral side of base of cercus with a compressed elongate internal process that is rather narrow and bent before mid-length in an almost 90°-angle mediad and slightly narrowed towards tip (Fig. 4E–G). The processes from both cerci almost touching each other in the middle. Subgenital plate wider than long with concave basal and convex lateral margins; apical margin subtruncate, very faintly concave between bases of styli; ventral surface convexly swollen in basal half, followed by a narrow conical swelling in middle (Fig. 4H).

Coloration. Head green; vertex with a pair of black bands that fuse to a single band at median ocellus and with a pair of short black lines from behind compound eyes to occiput. Frons green with three black vertical bands: two lateral bands from below compound eyes to tip of mandibles and one medial band from median ocellus to tip of labrum (Fig. 4C). Antennae with flagellum black with sparse white spots. Pronotum green with posterior area, anterior and posterior margins reddish brown, which may be partly due to discoloration in the set specimen. Tegmen brownish transparent; margin green. Abdomen discolored. Legs green, consperse with black dots; hind femur with apical area black and with a black stroke in pre-apical area restricted to dorsal margin. Male cerci of general color but internal–ventral surface and internal process black; male subgenital plate of light color; styli darkened.

Female. Unknown.

Measurements.—(4 males; in mm) Body w/o wings: male 14–16; pronotum: male 6.2–6.8; tegmen: male 5.0–5.3; hind femur: male 11.8–12.5; anterior femur: male 4–5; antenna: male 60–65.

Etymology.—The name of the new species refers to the angular internal tooth of the male cercus; from Latin *angularis*: angular.

Lipotactes productus sp. nov.

http://zoobank.org/136F5906-B869-4B88-B7BD-566AA323BFB4

Figs 1, 5A–D, 6F–H

Material examined.—**Holotype:** VIETNAM • male; South Vietnam, Cat Tien NP [= National Park]; 11°26′N, 107°26′E; 6–16 Jul. 2012; J. Constant and J. Bresseel leg.; I.G.: 32.161; ISNB. **Paratypes:** VIETNAM • 1 female, 2 males; South Vietnam, Dong Nai Biosphere Res.; 11°18′N, 107°6′E; 25 Jun.–6 Jul. 2012; J. Constant and J. Bresseel leg.; I.G.: 32.161; ISNB.

Diagnosis.—The new species is very similar to *L. sulcatus* Ingrisch, 1995 and *L. ingrischi* Gorochov, 1996 in general appearance, size, and coloration. It differs from both by the shape of the male cerci that are conical with a vertically oriented, rounded process in basal area and terminating into a rather long styliform apical area that

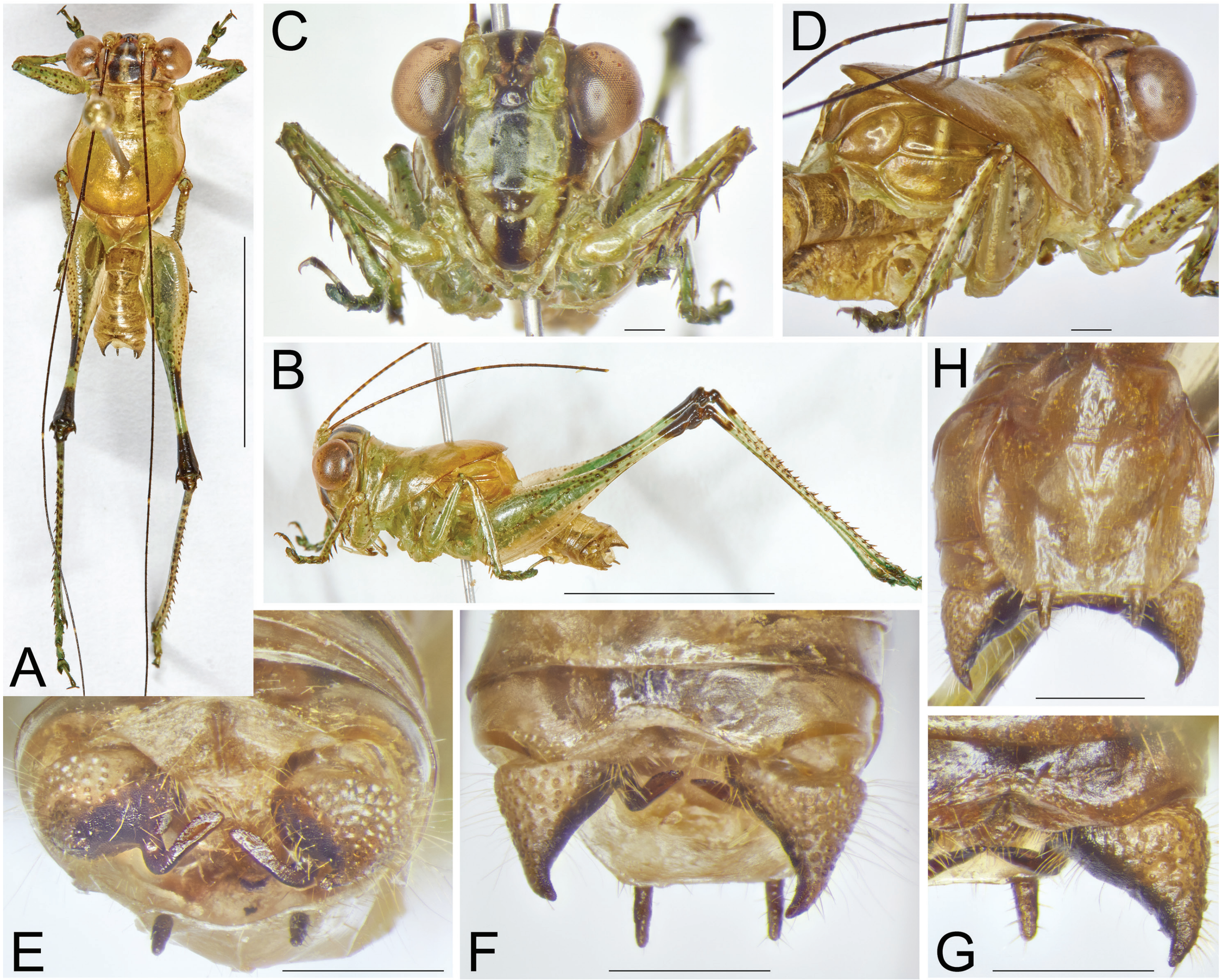

Fig. 4. *Lipotactes angulatus* sp. nov. males. **A.** Habitus dorsal view; **B.** Habitus lateral view; **C.** Frons; **D.** Anterior area of body with oblique apical view on tegmen; **E–G.** Abdominal apex in apical view (**E**) and in dorsal view of different males (**F, G**); **H.** Subgenital plate and cerci in ventral view. Scales for habitus (**A–B**): 5 mm; others (**C–H**): 1 mm.

is pointing straight behind, while in *L. sulcatus*, the cercus is rather narrow at base then widens to a process before mid-length and the styliform apical area appears attached and is pointing apico-lateral. In *L. ingrischi*, the male cercus has a short stout basal area with a horizontally oriented internal process that is distinctly wider at tip than at base, and the styliform apical area is pointing strongly laterad. More closely related to *L. productus* sp. nov. is *L. discus* sp. nov., described below. Both species have a vertically oriented, rounded process in the basal area of the male cercus to which, on the ventral side, a styliform process is appended. They differ in that the rounded internal process is somewhat spherical in *L. productus* with the styliform process flattened and arising from the proximo-ventral angle, while in *L. discus* the process is conical and the styliform process arises from the ventro-distal angle. In addition, the narrow apical area of the cercus is pointing straight behind in *L. productus* while oblique outwards in *L. discus*. Moreover, the tenth abdominal tergite has the apical margin slightly bilobate in the former while slightly concave in the latter species.

Description.—Small sized species of yellowish to grayish brown coloration with dark pattern.

Male. Pronotum convexly raised in posterior area. Tenth abdominal tergite slightly bilobate in middle. Cerci narrow conical with a long and narrow cylindrical apical area (Fig. 6H). In subbasal area of cercus, with a roughly circular internal process with strongly convex posterior surface and delimited from cercus stem by a weak furrow; at ventral side, a short, compressed, obtuse extension arises from the base of the process (Fig. 6F–G). Subgenital plate with strongly convex underside and with convex lateral margins that are at tip prolonged posteriorly into short, compressed, apical lobes that are separated by a wide concavity from each other and carry on the underside rather long styli (Fig. 6G).

Female. Subgenital plate wider than long, slightly curved from one side to the other; apical margin faintly concave (specimen glued on cardboard with subgenital plate only visible from behind). Ovipositor with ventral valves only faintly upcurved in

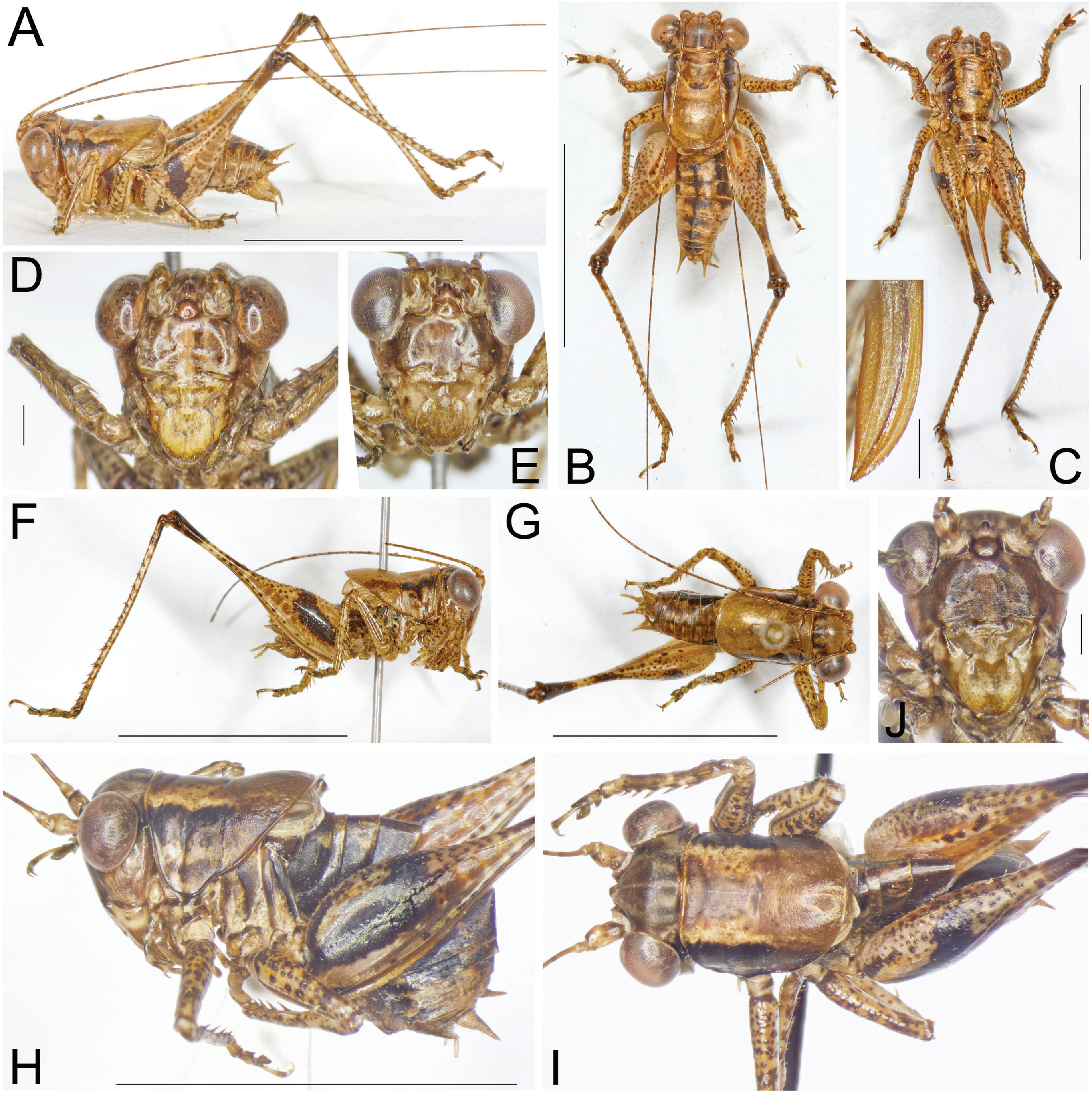

Fig. 5. *Lipotactes* sp. **A, B, D.** *L. productus* sp. nov. male; **C.** Female; **E–G.** *L. discus* sp. nov. male; **H–J.** *L. samkos* sp. nov. male. **A, F, H.** Habitus lateral view; **B, C, G, I.** Habitus dorsal view; **D, E, J.** Face. Inset in **C.** Apical half of ovipositor in lateral view. Scales for habitus: 10 mm; for face and ovipositor: 1 mm.

about apical half, more strongly upcurved towards tip; ventral margin in apical area provided with a few minute teeth: ten teeth in the specimen at hand; dorsal valves at base slightly depressed, then with dorsal margin nearly straight to almost mid-length; in subapical area, distinctly concave, then widened and convex, and in apical area, concave again to tip (Fig. 5C inset).

Coloration (both sexes). Grayish to ochre brown with black marks. Frons yellowish brown or ochre with little irregular, rather narrow, dark vertical bands. Vertex with two narrow black bands along midline and irregular black spots behind eyes. Pronotum with black bands along lateral angles that do not reach the hind margin. Abdominal tergites with transverse black spots along midline to last tergite and with black lateral bands to about mid-length of abdomen. Legs with numerous dark brown to black dots. Hind femur with an upcurved black band from base and with black hind knees, the latter prolonged anteriorly into a medium to dark brown spot and another but rather indistinct dark brown spot at the beginning of the narrow apical area.

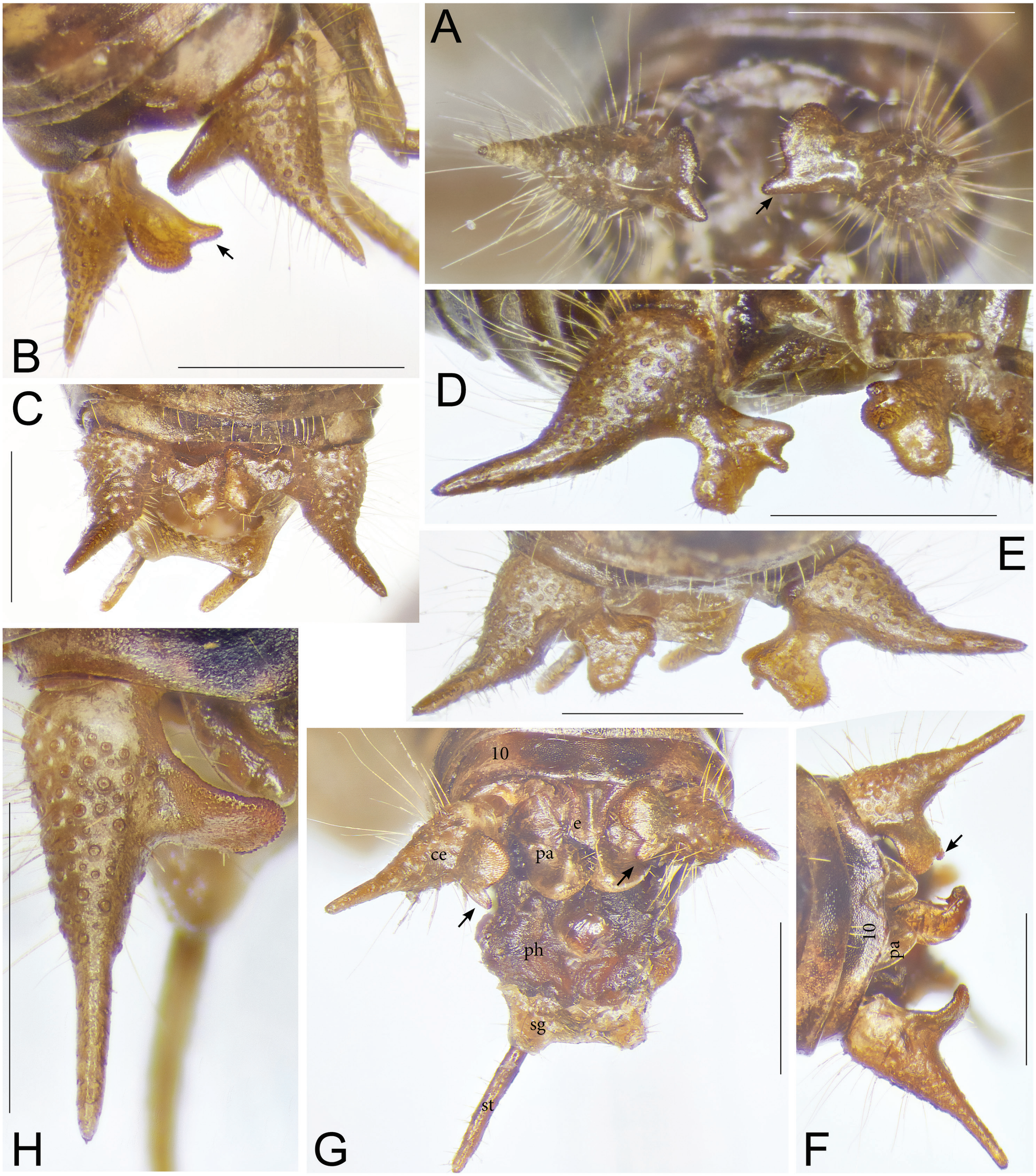

Fig. 6. *Lipotactes* sp. **A, B.** *L. discus* sp. nov.; **C–E.** *L. samkos* sp. nov.; **F–H.** *L. productus* sp. nov. **A, G.** Male abdominal apex with cerci in apical view; **B.** Oblique dorsal view; **C.** Dorsal view in situ; **E, F.** Dorsal view with cerci spread sideward; **D.** Oblique ventral view; **H.** Left cercus in dorsal view. Arrows point at ventral extension of internal process of the male cercus. Abbreviations: 10, tenth abdominal tergite; ce, cercus; e, epiproct; pa, paraproct; ph, phallus; sg, subgenital plate; st, stylus. All scales 1 mm.

Measurements.—(3 males, 1 female; in mm) Body w/o wings: male 11.5–12.0, female 11.0; pronotum: male 4.3–4.7, female 3.5; tegmen: male 2.5–3.3, female 0; hind femur: male 12.0–13.5, female 12.0; antenna: male 60; ovipositor: female 5.5.

Etymology.—The name of the new species refers to the prolonged narrow apical area of the male cercus; from Latin *productus*: prolonged, produced, elongated.

Lipotactes discus sp. nov.

http://zoobank.org/59C27D18-874F-4BA9-A41B-3AED24E6F588

Figs 1, 5E–G, 6A–B

Material examined.—**Holotype:** CAMBODIA • male; Ratanakiri, Yeak Laom Lake env. [= environment]; 13°44′N, 107°1′E; 9–11 Oct. 2017; J. Constant and X. Vermeersch leg.; I.G. 33.551; ISNB.

Diagnosis.—In general appearance and shape of the male cerci, the new species is similar to *L. productus* sp. nov. It differs by the male cercus that has a more strongly conical basal area and the narrow apical area shorter and pointing outwards instead of straight behind, also by the internal process of the cercus that stands vertically to the cercus axis and is roughly disc-shaped in both species but has a conical tooth arising from the ventro-distal angle in *L. discus* sp. nov. while slightly shorter and arising from the proximo-ventral angle of the process in *L. productus* sp. nov. Moreover, the apical margin of the tenth abdominal tergite is slightly bilobate in *L. productus* sp. nov. but simply concave in *L. discus* sp. nov. From *L. khmericus* Gorochov, 1998 that lives in the same larger area, the new species differs strikingly by the shape of the internal process of the male cercus that is vertically inserted in *L. discus* sp. nov. while horizontally inserted and terminating into three short lobes of different shapes in *L. khmericus*. Moreover, in the new species, the narrow apical area of the cercus is relatively shorter (about 0.65 times the length of the basal area) and gradually narrows from the wider and conical basal area, while in *L. khmericus,* it is relatively longer (about 0.85 times) and abruptly narrows from the basal area.

Description.—Small sized species of yellowish to grayish brown coloration with dark pattern.

Male. Pronotum with apical area prolonged and slightly elevated, with three transverse furrows; the first furrow distinct on disc and on paranota, the second furrow restricted to paranota, and the third furrow weak on disc, distinct on paranota (Fig. 5F, G). Cerci conical with little out-curved narrow apical area with subacute tip; cercus trunk in subbasal area with a vertical, compressed circular process that is prolonged in a ventro-distal angle into a cone; margin of process and cone finely granular; disc in upper basal area slightly swollen on distal side (Fig. 6A, B). Subgenital plate with lateral margins convex, in apical area straight; apical margin roundly excised; long styli inserted on underside at lateral tips of subgenital plate.

Coloration. Grayish to ochre brown with black marks. Frons yellowish brown to ochre with indistinctly delimited lighter and darker areas; clypeus and labrum of lighter color, mandibles yellowish white, darkened towards tip, with a rounded black spot in subbasal area. Vertex with six short longitudinal black bands from hind margin. Pronotum with black bands along lateral angles reaching the hind margin. Abdominal tergites brown with black lateral bands. Legs yellowish brown with numerous dark brown to black dots. Hind femur with an upcurved black band from base and with black apical area that is preceded by a pale ring and by a black stroke restricted to dorsal margin.

Female. Unknown.

Measurements.—(1 male; in mm) Body w/o wings: 9; pronotum: 3.5; tegmen: 2.5; hind femur: 10; anterior femur: 2.8.

Etymology.—The name of the new species refers to the basic shape of the internal process of the male cercus, from Latin *discus*, noun in apposition.

Lipotactes samkos sp. nov.

http://zoobank.org/DB59CA99-92AB-4DB4-B003-72EA021418B8

Figs 1, 5H–J, 6C–E, 7C

Material examined.—**Holotype:** CAMBODIA • male; Pursat, Phnom Samkos; 12°13'2"N, 102°55'7"E; 15–18 Oct. 2016; J. Constant and J. Bresseel leg.; I.G.: 33.345 GTI project; ISNB.

Diagnosis.—The basic shape of the internal process of the male cercus of the new species is similar to that in *L. khmericus* Gorochov, 1998, as it is oriented horizontally and has the proximal marginal area down-bent. However, in *L. samkos* sp. nov., the internal margin is slightly wavy, while in *L. khmericus*, it has a distinct rounded incision; as a result, the straight posterior margin of the process appears as such in the new species, while it is part of the internal margin in *L. khmericus*. Additionally, a narrow ventral spine of the internal process arises from the underside of the process while from the ventro-internal margin in *L. khmericus*. The apical area of the cercus stem is slightly conical, distinctly bent outward, and with an obtuse tip in the new species, while that area is suddenly narrowed at base and subcylindrical with an acute spinose tip in *L. khmericus*. From *L. saengeri* sp. nov., the new species differs by the shape of the internal process of the male cercus, the shape and inserting position of a small ventro-medial spine at the internal margin of the process, and by the conical instead of cylindrical and more strongly outwards bent apical area of the cercus. *L. ingrischi* Gorochov, 1996 also has a horizontal internal process of the male cercus, but the new species differs by the shape of the internal process and by the narrow apical part of the cercus that is much less curved laterad instead of strongly curved laterad.

Description.—Small sized species of yellowish to grayish brown coloration with dark pattern.

Male. Pronotum with three faint transverse furrows indistinct or absent on disc; apical area prolonged and slightly elevated (Fig. 5H, I). Tenth abdominal tergite short, apical margin very faintly concave in middle. Epiproct elongate-triangular, apex obtuse and slightly curved posteriorly. Paraproctes spoon-shaped with short stem and large bowl-shaped processes below internal processes of cerci. Cerci conical with slightly out-curved narrow apical area with subacute tip; cercus trunk in subbasal area provided with a horizontal internal process with rather long and flat proximal area that in dorsal view is strongly widening towards both sides into a rounded proximal lobe and a strongly swollen, subtruncate, or little convex distal lobe (Fig. 6E). In dorsal view and when at rest, the sub-straight internal margins of the processes of both cerci touching each other in the middle but deviating distally (Fig. 6C). On ventral side of the process, the anterior margin terminates into a conus; moreover, there is another short, but somewhat compressed conus from below the internal margin of the process (Fig. 6D). Phallus membranous. Subgenital plate slightly wider than long with marked disc and up-bent lateral margins; apical margin wide and shallowly concave; styli inserted on underside at lateral angles of disc of subgenital plate (Fig. 6C).

Coloration. Yellowish to reddish brown with black pattern. Face with mixed flecks of yellowish and blackish brown; clypeus and mouthparts yellowish with brown flecks; vertex with six longitudinal dark brown bands. Pronotum with black band in upper area of paranota followed downwards by whitish, blackish, and again whitish bands; disc yellowish with darker staining in anterior half, red brown in posterior half. Tergites mostly black with few lighter spots, last three abdominal tergites and cerci mostly yellowish brown; subgenital plate medium brown. Legs yellowish brown with numerous rather large black dots; hind femur in about basal third with a wide black band that is bent to dorsal margin at end, narrow apical area with dorsal margin little darkened, followed by a long whitish ring and then shining black to tip; hind tibia rather pale with indistinct darker flecks, only apical area and lateral margin of tarsal segments partly black.

Female. Unknown.

Measurements.—(1 male; in mm) Body w/o wings: 11; pronotum: 4.2; tegmen: 2; hind femur: 11; anterior femur: 3.

Lipotactes saengeri sp. nov.

http://zoobank.org/9F28BFD3-48A0-4CC9-90B4-ADB68BEF4293
Figs 1, 7A, B

Lipotactes khmericus – Helfert & Sänger 2009

Material examined.—**Holotype:** THAILAND • male; Chanthaburi, Khao Sabap; 12°32'58.13"N, 102°11'55.32"E; 9 Sep. 2008; B. Helfert and K. Sänger leg.; NMW. **Paratype:** THAILAND • 1 male; same data as for holotype; NMW. Other material: THAILAND • 1 female; same data as for holotype; not re-examined; NMW.

Diagnosis.—The new species is similar to *L. khmericus* Gorochov, 1998 and *L. samkos* sp. nov. It differs from both by the shape of the internal process of the male cercus that has the anterior area flat and extended anteriorly, not down-bent as in both other species, but the central area of that process is slightly swollen instead of flat. The small ventral thorn of the process has an acute instead of obtuse tip and inserts nearly in the middle of the internal ventral margin instead of closer to the anterior margin in both other species; the internal margin of the process is slightly three-lobular instead of distinctly lobular in *L. khmericus* or sub-straight in *L. samkos*. The narrow apical area of the male cercus is cylindrical and moderately out-curved in *L. saengeri* sp. nov., conical and more strongly out-curved in *L. samkos*, while only faintly out-curved but suddenly narrowed at base and provided with an apical spine in *L. khmericus*.

Description.—Small sized species of yellowish to grayish brown coloration with dark pattern.

Male. Tenth abdominal tergite short, apical margin in central area slightly concave in strict dorsal view. Epiproct triangular with blunt tip and medial furrow. Cercus in more than basal half conical, following apical area slightly out-bent and sub-cylindrical with blunt tip; in basal area with a large, dorso-ventrally compressed, internal process that is behind basal incision widening slightly to three-lobate internal margin: basal lobe rounded, flat, medial lobe with slightly convex dorsal surface and also with rounded tip from which the ventro-internal margin gives rise to an acute, conical spine with granular surface and pointing medio-ventrad; apical lobe of rectangular appearance with rounded angles, separated by only a shallow incision from medial lobe (Fig. 7A, B). Subgenital plate with shallowly concave apical margin; styli inserted at both sides of concavity.

Female. Described and figured in detail by Helfert and Sänger (2009) as *L. khmericus*. Subgenital plate with a simple, roughly oval outline without modification.

Coloration (*both sexes*). Museum specimens formerly conserved in alcohol; grayish pale to light ochre brown with dark blackish brown marks. Frons with indistinctly delimited lighter and darker areas; clypeus and labrum of lighter color, mandibles light gray, darkening towards tip. Pronotum with brownish disc and with black bands along lateral angles reaching the hind margin or the second transverse sulcus. Abdominal tergites light brown with black lateral bands. Legs light brownish with numerous dark brown to black dots. Hind femur on external side in more than basal quarter almost white with a blackish band in middle that is upcurved at end, afterwards with numerous large black dots; hind knees blackish brown. Hind tibiae at base and end also darkened. Photos of alive male and female are figured in Helfert and Sänger (2009).

Measurements.—(2 males; in mm) Body w/o wings: 12.7–13.1; pronotum: 4.5–4.6; tegmen: 2.3–2.4; hind femur: 10.9–11.8.

Etymology.—The new species is named after one of the collectors, Dr. Karl Peter Sänger (1939–2019), well known for his work on the ecology of European Orthoptera who, in his later years, became interested in the tropical fauna (see Waitzbauer 2019).

Lipotactes sp.

Figs 1, 8A–E

Material examined.—CAMBODIA • 1 female; Siem Reap, Preak Toal; 13°14'32"N, 103°39'5"E; 6–14 Aug. 2005; Danny Jump leg.; ISNB.

Discussion.—Including the two new species described in this paper, three *Lipotactes* species are so far known from Cambodia based on marked differences of the male cerci, which is thought to be of isolating value between the species. Unfortunately, none of the females of these species have been collected at the type localities; thus, it is not possible to assign single females collected at other localities of the country to one of these species.

The type localities of both *L. khmericus* Gorochov, 1998 and *L. discus* sp. nov. lie in the Ratanakiri province of Cambodia. Both species were identified based on the male abdominalia. The female from Preak Toal has a subgenital plate with widened base and semi-oval widening of central area resembling the shape in *L. silvestris* Ingrisch, 1990 from Khao Soi Dao in Southeastern Thailand, differing by the circular apical depression of the subgenital plate and the incised hind margin. The female from Preak Toal also differs clearly from the female described in Helfert and Sänger (2009) that has a simple semi-oval shaped subgenital plate with apical margin convex without groove or basal widening. The closest locality from which a male of *Lipotactes* has been reported is that of *L. samkos* sp. nov., which is over 300 km away from Preak Toal. It is uncertain if the female belongs to that species, although it cannot be excluded. Thus, it is best to avoid naming the female until more material from the area becomes available.

Description.—Small sized species of yellowish to grayish brown coloration with dark pattern.

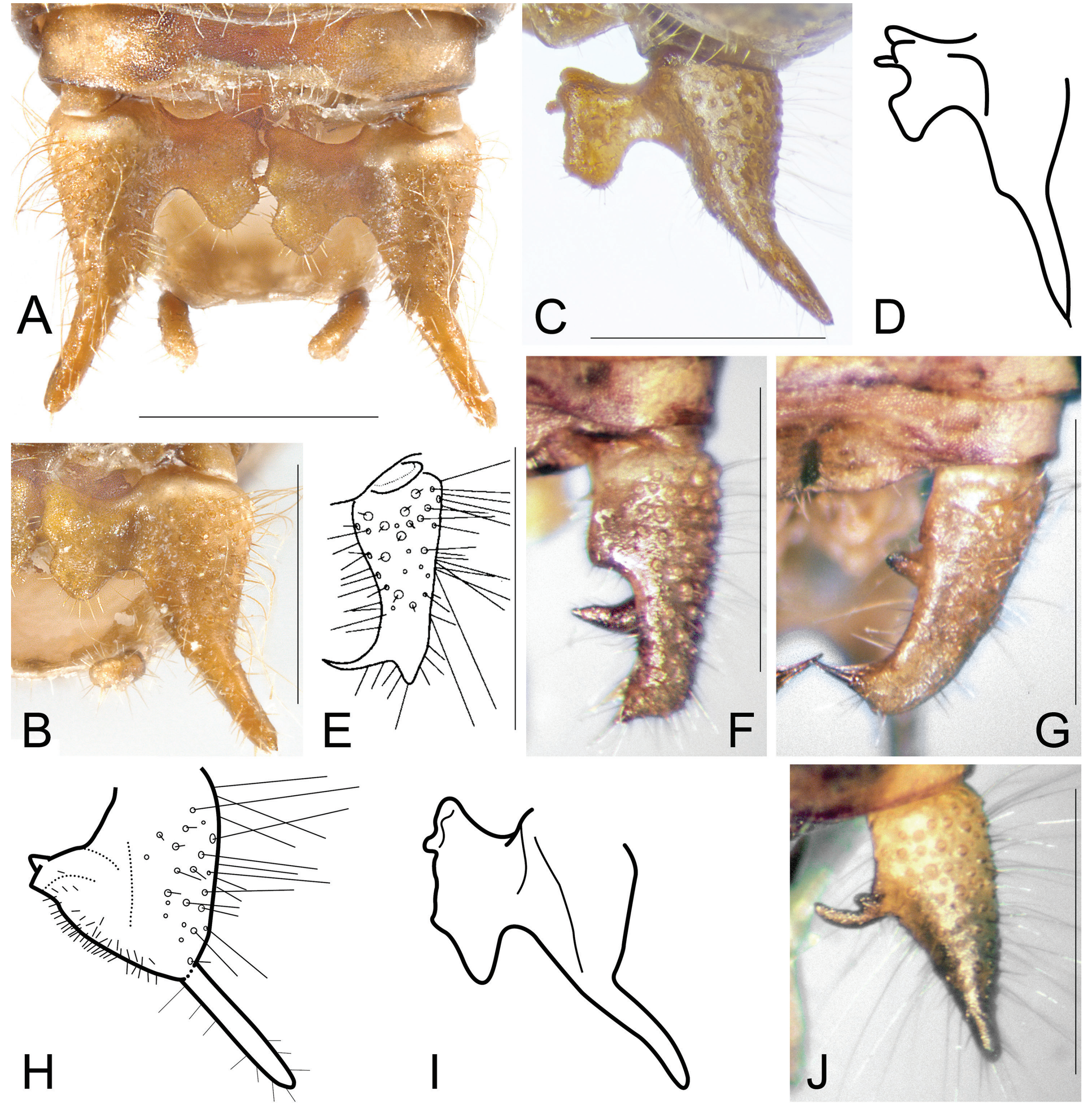

Fig. 7. *Lipotactes* sp. **A–B.** *L. saengeri* sp. nov.; **C.** *L. samkos* sp. nov.; **D.** *L. khmericus* Gorochov, 1998; **E.** *L. minutus* Ingrisch, 1995; **F.** *L. silvestris* Ingrisch, 1990; **G.** *L. montanus* Ingrisch, 1990; **H.** *L. sulcatus* Ingrisch, 1995; **I.** *L. ingrischi* Gorochov, 1996; **J.** *L. virescens* Ingrisch, 1995. **A.** Abdominal apex with cerci in dorsal view; **B.** Cercus in oblique dorsal view from behind; **C–J.** Cercus in dorsal view. Photos A–B from NMW NOaS Image Collection, photo credit H. Bruckner; figures D and I redrawn from Gorochov (1996 and 1998); figures E and H from Ingrisch (1995). All scales 1 mm; line drawings **D** and **H–I** not to scale.

Female. Subgenital plate wider than long; lateral areas very short; central area swollen and roundly projecting behind narrow lateral areas; the projecting part with a deep membranous groove in middle, at apex concave; laterally of the groove, the surface is swollen on both sides (Fig. 8C). Ovipositor slightly curved; dorsal margin in middle concave, then slightly convex and only very faintly concave before acute tip; ventral margin behind substraight basal area concave to acute tip, in apical area provided with about six tiny teeth (Fig. 8D, E).

Coloration. Frons with irregular brownish–yellowish pattern; labrum and mandibles of lighter color; vertex with six slightly expressed dark longitudinal bands from hind margin (Fig. 8B). Pronotum with black bands along lateral angles that almost but not completely reach the hind margin. Abdominal tergites brown with black

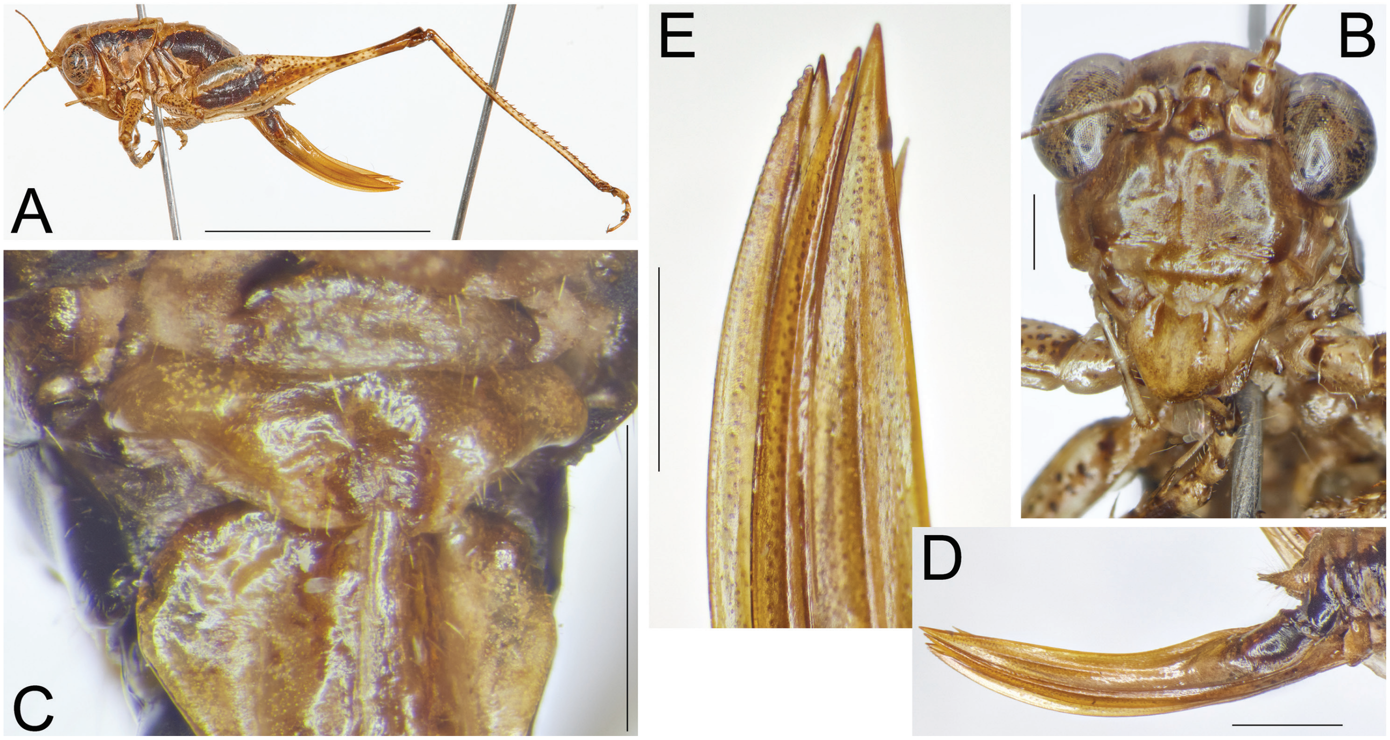

Fig. 8. *Lipotactes* sp. female from Preak Toal, Cambodia: **A.** Habitus, lateral view; **B.** Face; **C.** Subgenital plate and base of ovipositor in ventral view; **D.** Ovipositor in lateral view; **E.** End of ovipositor in greater magnification. Scales 10 mm (**A**), 1 mm (**B–E**).

lateral bands. Legs yellowish brown with numerous dark brown to black dots. Hind femur with a black band from base that has the upcurved part largely reduced; the black apical spot becomes brownish anteriorly and the pre-apical dark spot is only indicated (Fig. 8A).

Measurements.—(1 female; in mm) Body w/o wings: 10.5; pronotum: 4; tegmen: 0; hind femur: 11; anterior femur: 2.8; ovipositor: 7.5.

Key to species of the genus *Lipotactes* from Vietnam, Cambodia, and Thailand

This key works only with males, as females are not known for all species concerned, and the morphology of related species is very similar. Data for species that were not studied or re-examined for the present publication are adapted from Gorochov (1993, 1996, 1998) and Ingrisch (1995).

1 Males of predominantly green general color mixed with light and with black pattern, or of whitish color that appears shiny blue in alive individuals of some species. Females are known to have a light brown or green general color with a black pattern. Male cercus with strongly widened basal area, either short conical or nearly quadrangular, in both cases with a short narrow conical or sub-cylindrical apical area from external-apical angle of wide basal area (Figs 2G–I, 4F, G) or male cercus simply conical with a forked internal tooth with rather short and simple branches behind end of basal third (Fig. 7J).......... 2

– Males of light brown general color with black pattern. Male cercus elongate, either with a subapical internal tooth (if the pronounced tip of cercus appears truncate) or conical with a distinct narrow apical area that is pointing straight behind or bent more or less outward; in basal area with internal process that varies between species (Figs 6A–H, 7A–I).. 8

2 Male cercus with strongly widened basal area, either short conical or nearly quadrangular, in both cases with a short narrow conical or sub-cylindrical apical area from external-apical angle of wide basal area (Figs 2G, I, 4F). North and Central Vietnam 3

– Male cercus simply conical with a forked internal tooth with rather short and simple branches behind end of basal third (Fig. 7J). Trang province of Thailand and Peninsular Malaysia...................................
.... *L. virescens* Ingrisch, 1995

3 Often head with distinct transverse dark cross-belt between posterior halves of eyes, in females often interrupted in middle or completely missing (Figs 2B, 3A). Pronotum in male with dark stripe along posterior margin of disk (Fig. 2A, B, D). Male cerci short, wider than long, from apical external angle with a narrow extension of about same length as wide basal area; wide basal area from internal margin with a huge process consisting of a dorsal and a ventral branch varying in shape between species (Fig. 2C, E, H). Male phallus with a pair of elongate sclerites and a shorter unpaired sclerite (Fig. 2E). Dorsal margin of ovipositor in all species with known females in subapical area without concavity but running straight into tip (Fig. 3E, F, H, I)...................... 4

– Green species with black dots. Pronotum prolonged behind and with widened posterior area (Fig. 4A). Head with a pair of longitudinal black bands along midline of vertex and a pair of narrow black lines behind eyes; face with three black vertical bands (Fig. 4C); hind femora green with hind knees black and a narrow black stroke on dorsal margin in apical area (Fig. 4B). Male cerci conical with wide base and narrow, slightly inwardly curved apical area; at base with a compressed, band-shaped but angularly bent internal process (Fig. 4E–G). Phallus membranous. Female unknown. Central Vietnam ...
.... *L. angulatus* sp. nov.

4 Pronotum with large dark spots occupying the middle part of disk in male. Male cerci with rounded or truncate apex of upper inner process (Fig. 2C, 2G); narrow apical extension of cercus either ob-

tuse with a minute spinule at inner angle or with a distinct, laterally serrate spine at tip (Fig. 2C, F). Male subgenital plate with long and narrow styli 5

– Pronotum with small dark spots in the middle of disk or without spots. Male cerci with bifurcated apex of the upper inner process and more or less narrow lower inner process (Fig. 2H, I); narrow apical extension of cercus either narrowed into acute tip or with a distinct smooth spine at tip (Fig. 2I) 6

5 Male cerci with a small spine at proximal base of concave upper inner process; upper inner process partly upcurved with rounded margin; lower inner process wide; narrow apical extension of cercus with a minute, hardly visible spinule at tip (Fig. 2C). Male genitals with narrow paired sclerites bearing no visible small setae at apex and unpaired sclerite approximately 1.5 times shorter than paired one. Northern Vietnam ....*L. azureus* Gorochov, 1996

– Male cerci with upper inner process sinuate in apical view, in dorsal view nearly flat with truncate inner margin; lower inner process in apical view narrow, in dorsal view triangular; narrow apical extension of cercus with a strong spine at tip that carries along margins acute teeth (Fig. 2F). Male genitals with unpaired medial sclerite reaching only the end of the widened base of the narrow paired sclerites; the paired sclerites slightly narrowing towards tip (Fig. 2E). Northern Vietnam ....*L. serratus* sp. nov.

6 Narrow apical extension of cercus with a distinct acute and smooth spine at tip (Fig. 2H, I). Elytra in male small, protruding in the rear only faintly from beneath the pronotum. Male genitals with narrow, paired sclerites with obtuse tip, approximately two times longer than unpaired sclerite. Male subgenital plate with rather short and wide styli (Fig 2I). Northern Vietnam......... *L. vietnamicus* Gorochov, 1993

– Narrow apical extension of cercus with acute tip or with a minute spinule at tip 7

7 Pronotum in male with short posterior process of disk and narrow dark stripe along posterior margin of disk. Narrow apical extension of male cercus narrowed into acute tip. Male genitals with narrow paired sclerites bearing noticeable small setae at apex and with unpaired sclerite approximately 1.5 times shorter than the paired one. Northern Vietnam ....*L. proximus* Gorochov, 1996

– Pronotum in male with more or less long posterior process of disk and wide dark stripe along posterior margin of disk. Male genitals without noticeable small bristles at apex of paired sclerites. Elytra in male large, protruding approximately 1 mm in the rear from beneath pronotum; male genitals with wide paired sclerites approximately 1.2 times longer than unpaired sclerites. Northern Vietnam .....*L. orlovi* Gorochov, 1996

8 Male cercus in basal third to half with internal margin expanded with straight or little convex internal surface followed behind by a stout conical internal tooth or basal widening slightly expressed and cercus with a curved subapical internal tooth; apex of cercus obliquely truncate, rounded, or forming a short cone.................................. 9

– Male cercus without basal widening but with an internal process of various shapes in basal half; apical area of cercus prolonged into a narrow conical or subcylindrical process pointing straight behind or bent outward...11

9 Cercus conical with weak convex widening of basal area, with a subapical curved internal tooth with acute tip, cercus proper terminating into a short cone (Fig. 7E) ....*L. minutus* Ingrisch, 1995

– Cercus with marked internal widening for basal third or half with straight internal margin that is gradually or abruptly narrowed at end; tip of cercus subtruncate with external angle rounded and internal angle extended into a minute cone or a distinct spine 10

10 Cercus with internal expansion strongly expressed with straight internal margin for almost half of cercus length; at end suddenly narrowed, followed behind by a conical shape and at base faintly curved internal tooth; apex of cercus obliquely truncate with a minute cone at apical internal angle (Fig. 7F). Southeastern Thailand ....*L. silvestris* Ingrisch, 1990

– Cercus with internal expansion less expressed and restricted to basal third; at end gradually narrowed, followed by a conical internal tooth; tip of cercus rounded and slightly curved mediad, with a long acute spine at apical internal angle (Fig. 7G). North and West Thailand .... *L. montanus* Ingrisch, 1990

11 Male tenth abdominal tergite in middle of apical margin with a process that terminates on both sides into a short acute process. Male cercus nearly parallel-sided in basal half, finger-shaped in apical area, internal process arising at or slightly behind middle of cercus, in dorsal view narrow, running nearly parallel to cercus stem and terminating slightly before tip of cercus. Male subgenital plate with a pair of spine-like outgrowths at bases of styli. Southern Vietnam ....*L. amicus* Gorochov, 1993

– Male tenth abdominal tergite in middle of apical margin slightly concave with a faint medial protuberance or apical margin with a pair of short conical processes. Male subgenital plate without spines at bases of styli.. 12

12 Male cercus with basal area rather short, provided over most of the length of the cercus stem with a huge, dorso-ventrally compressed internal process of roughly triangular shape but with margins convex and at tip dividing into a pair of tubercles; styliform apical process rather long, pointing distinctly outwards (Fig. 7H). Southern Vietnam .... *L. sulcatus* Ingrisch, 1995

– Male cercus of different shape 13

13 Male cercus with internal process standing horizontally to the main cercus axis, slightly constricted after it arises from the cercus stem and then strongly widening towards inner margin 14

– Male cercus with internal process standing vertically to the main cercus axis, of disc-shaped outline with ventral process 17

14 Male tenth abdominal tergite faintly projecting in middle. The styliform apical area of the male cerci bent rather strongly sideward; the internal process of the male cerci widening towards inner margin at anterior and posterior sides; the inner margin roughly convex with small protuberances (Fig. 7I). Southern Vietnam .... *L. ingrischi* Gorochov, 1996

– Male tenth abdominal tergite with apical margin simply concave or almost sub-straight in middle. The styliform apical area of the male cerci only moderately curved laterad or almost straight. Internal process of cercus of different shape... 15

15 Cerci with internal process roughly in one level, only in midline little convexly elevated and faintly sloping towards anterior and posterior margin, inner margin slightly trilobate, on underside of central lobe with an acute conical process pointing ventro-mediad; narrow apical area of cercus cylindrical, slightly bent outward, tip obtuse with or without a very minute spinule (Fig. 7A, B)............*L. saengeri* sp. nov.

– Cerci with internal process that has the anterior area of process bent ventrad with ventral margin obtuse or terminating into a cone; another process from ventral inner margin of the process appears to insert in the basal third of the process and ends in an obtuse tip.............16

16 Male cercus suddenly narrowed before styliform apical process that is pointing only slightly outward; cercus stem with a large, horizontally oriented internal process from base to about end of basal third, slightly widening medially, especially towards distal angle, and terminating into two lobes separated by a distinct incision and a conical process from ventral inner margin (Fig. 7D). Cambodia............. ....*L. khmericus* Gorochov, 1998

– Male cercus gradually narrowed into a styliform apical area that is moderately but distinctly curved laterad; cercus stem with a large, horizontally oriented internal process that starts with a parallel-sided, dorso-ventrally compressed area that is widening towards both sides and swollen along inner and hind margins, the processes of both sides touching each other along midline when at rest (Fig. 6C); on the ventral side, the anterior margin of the process is bent ventrad and prolonged into an obtuse cone; next to this cone, there is another short, little compressed process with an obtuse tip (Fig. 6D); in dorsal view, the internal process of the cercus is not divided into lobes but with faintly wavy internal and straight apical margin (Fig. 7C). Cambodia .... *L. samkos* sp. nov.

17 Male tenth abdominal tergite with apical margin slightly bilobate in middle, interrupted by a narrow concavity. Male cercus elongate, with long styliform apical process pointing straight behind, in subbasal area on internal side with a large rounded internal process with convex posterior surface, separated from cercus stem by a shallow furrow and provided at ventro-proximal angle with a short styliform process (Fig. 6F–H). Female ovipositor with a concave subapical widening of the dorsal margin followed by shallow concavity. Southern Vietnam .... *L. productus* sp. nov.

– Male tenth abdominal tergite with apical margin simply concave in middle. Male cercus remarkably conical, in sub-basal area provided with a roughly circular internal process standing vertically to the main cercus axis; it has the proximal surface slightly concave, the distal surface slightly convex and is provided at ventro-distal angle with a conical process; styliform apical process of cercus acute-conical, not very long, pointing moderately outwards (Fig. 6A, B). Cambodia .... *L. discus* sp. nov.

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First observations of the Atlantic beach cricket, *Pseudomogoplistes vicentae* (Grylloidea: Mogoplistidae), in the Basque autonomous community, Spain

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Abstract

The Atlantic beach cricket *Pseudomogoplistes vicentae* Gorochov, 1996 (Orthoptera: Grylloidea: Mogoplistidae) is among the rare Orthoptera species that live exclusively in coastal habitats. It inhabits cobble beaches from North Africa to Great Britain, with populations known in Morocco, Portugal, Spain, France, Channel Islands, Wales and England. *P. vicentae* was found on the Spanish continental coast for the first time in 2018, in Asturias. The discovery of three populations in the Basque autonomous community (Northern Spain) is reported here, and useful information for increasing its detection and monitoring its populations is provided.

Keywords

Europe, Palearctic region, scaly crickets, understudied insects, vulnerable species

Introduction

Beach crickets (*Pseudomogoplistes* spp.) live exclusively in coastal stony habitats, in a narrow band of the shoreline upon the influence of sea movements caused by tides and storms. They are ground dwelling crickets which hide below the shingles or debris of the wrack line. Closely dependents on this rare habitat and thus having small areas of occupancy, *Pseudomogoplistes* species are threatened by habitat alteration and destruction. Heavy storm surges, marine pollution (oil spill) and beach excavation are already known to affect local populations in Great Britain (Sutton 2015) and the coming rise of oceans due to climate change is repeatedly cited as a major threat (Sutton 2015, Vahed 2019). Except in Great Britain and France, little is known on the precise distribution of *Pseudomogoplistes* spp.

Out of the five *Pseudomogoplistes* species previously described (Table 1), two are present on continental Western European coasts: *Pseudomogoplistes squamiger* (Fischer, 1853) on the Mediterranean beaches, and *Pseudomogoplistes vicentae* Gorochov, 1996 on the Atlantic beaches (Fig. 1). *P. vicentae* was described by Gorochov (1996) from specimens collected in Morocco and Portugal and is currently considered a vulnerable species in Europe and Great Britain (Hochkirch et al. 2016, Sutton 2017) and close to extinction in France (Sardet and Defaut 2004). Its presence is reported in four localities in England and Wales—Branscombe (Devon), Marloes sands and Dale beaches (Pembrokeshire) and Chesil beach (Dorset) (Sutton 2017, Vahed 2019)—as well as in the Channel Islands—Sark and Guernsey (Bourgaize 2019); Northern France, including Brittany and Normandy (Bretagne vivante 2017, Stallegher 2019); and Spain, including the Canary Islands and Asturias (Gorochov and Llorente 2001, Kleukers et al. 2018). However, on the continental coasts of Spain, only one population has been discovered very recently, i.e., in Asturias (Kleukers et al. 2018). Observations of the Atlantic beach cricket in three locations of the Basque autonomous community, north of the Iberian Peninsula and roughly 200–250 km away from the population observed in Asturias are reported here. Useful information to improve *Pseudomogoplistes vicentae* detection is also provided.

Methods

After an adult male *Pseudomogoplistes* spp. specimen was found by chance on the 13th of July 2019, trapped in an empty plastic water bottle on the beach of Agiti kala (San-Sebastian/Donostia, 43°18'27.3"N, 2°04'21.3"W, Gipuzkoa, Basque autonomous community, northern Iberian Peninsula), I conducted a survey at this site on the 3rd and 4th of August. I first looked for beach crickets in an accumulation of red drift algae, but the abundance of jumping sand fleas (Crustacea: Amphipoda: Talitridae) and the absence of any cricket led me to abandon the search in this micro-habitat. I then searched for crickets by looking beneath large stones that could be easily moved and digging between cobbles during the afternoon in a non-standardized way. Later, survey was performed at night between 23:00 and 01:00 using a headlamp (Ultra Rush model, Petzl). The beach crickets were searched for using two methods: (1) opportunistic searching on the surface of cobbles and rocks for ten to forty-five minutes scouting sequences, from the high water line to approximately 15 m upward and (2) using heads of cooked shrimps deposited on the top of rocks as alimentary bait. Twenty-two baits, separated by approximately

Table 1. *Pseudomogoplistes* species, their known distribution, and conservation status according to Hochkirch et al. (2016) for Europe, Sutton (2015) for Great Britain, and Sardet and Defaut (2004) for France.

Species	Known distribution	Conservation status
P. squamiger Fischer, 1853	Mediterranean coast of Albania: Karaburun peninsula (Ponel et al. 2013); Algeria: Tamenfoust (Sahnoun et al. 2010); Croatia: Dubrovnik, Lokrum and Šipan islands (Sombke and Schlegel 2007, Puskás et al. 2018, Skejo et al. 2018); France: Frioul, Riou, Planier, and Porquerolle islands, Banyuls, Bormes-les-Mimosa, Giens, Hyères, La Croix-Valmer, Le Pradet, Port-Vendres Ramatuelle, (Maurin 1999, Berville et al. 2012, Dusoulier 2017), Corsica island (Braud et al. 2002); Greece: Kos and Tilos islands (Sotiris 2017); Italy (Fontana et al. 2002, Baroni et al. 2013); Spain: Alicante and Castellón (Gorochov and Llorente 2001, Luccià Pomares 2002); Malta (Gauci et al. 2005); A (dubious?) mention in the Atlantic coast of Spain in Canarias islands (Bland et al. 1996).	LC[1] in Europe. Close to extinction in France
P. byzantius Gorochov, 1995	Black sea coast of Crimea: Cape Martyan reserve, Karadag nature reserve (Gorochov 1984, Gorochov 1995); Mediterranean coast of Greece: Thassos island (Gorochov 1995, Willemse et al. 2018).	EN[1] in Europe
P. turcicus Gorochov, 1995	Turkey: Okurcalar beach (Gorochov 1995).	Unevaluated. Okurcalar beaches are very unnatural today.
P. vicentae Gorochov, 1996	Atlantic coast of Channel islands: Guernesey and Sark (Bourgaize 2019); Morocco: Tanger (Gorochov 1996); Portugal: Algarve (Praia do Castelejo), Lisboa (Cabo Raso) (Gorochov 1996); Spain: Gran Canaria (Maspalomas) (Gorochov and Llorente 2001), Asturias (Kleukers 2018); Great Britain: Devon (Branscombe), Pembrokeshire (Marloes sands and Dale beaches), and Dorset (Chesil Beach) (Sutton 2017, Vahed 2019); Ssp. *P. vicentae septentrionalis* in France: Manche, Côte d'Or (Stallegher 2019); A (dubious ?) mention in the Mediterranean coast of Algeria (Habibas islands) (Gorochov and Llorente 2001).	VU[1] in Europe VU in Great Britain Close to extinction in France
P. madeirae Gorochov & Marshall, 2001	Madeira island (Funchal) (Gorochov and Marshall 2000)	DD[1] in Europe

[1] DD: Data deficient; LC: Least concern; Vu: Vulnerable; EN: Endangered species.

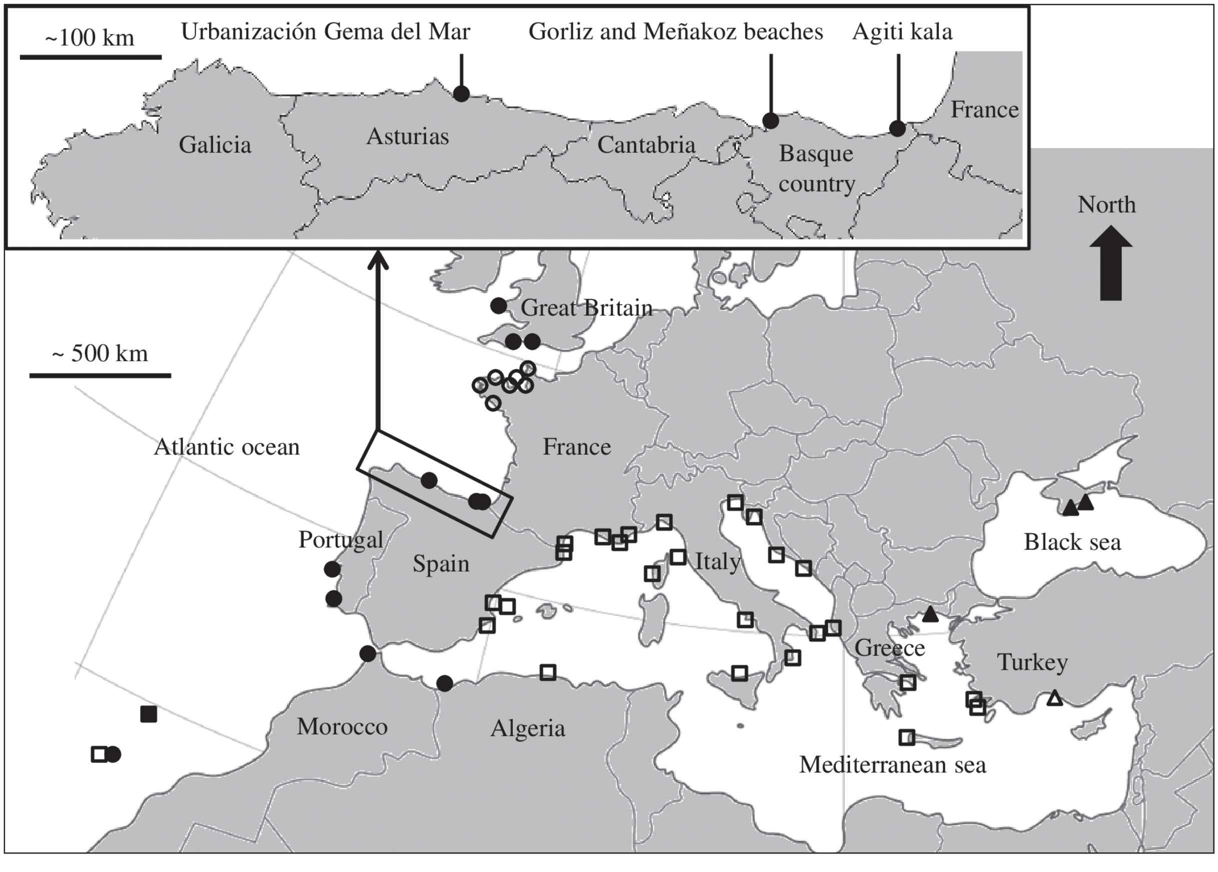

Fig. 1. Distribution of the beach cricket species (*Pseudomogoplistes* spp.). **A**. Distribution of *P. byzantius* (black triangle), *P. madeirae* (black square), *P. squamiger* (white square), *P. turcicus* (white triangle), *P. vicentae* (black circle), *P. vicentae septentrionalis* (white circle); **B**. Focus on the distribution of *P. vicentae* in northern Spain.

2 m, were deposited and checked thirty minutes later. Crickets were photographed with a compact digital camera (Canon PowerShot G9 X Mark II). In respect with local environmental laws, no cricket was captured.

A survey was also performed in two other sites of the Basque autonomous community, at Gorrondatxe Beach (Getxo, 43°22'54.7"N, 3°00'50.3"W) on August 6, 2019, and Meñakoz Beach in Bizkaia Province (Gorliz, 43°23'43.4"N, 2°59'06.6"W) on August 12, 2019. These beaches were identified as putative favorable habitats (i.e., coves or beaches with large (>30 m) cobble deposits) from Google Maps. These searches were done during the day in a non-standardized way, as in Agiti kala.

Results

Because of its brown body covered by numerous scales with an enlarged abdomen tip, the first specimen found in Agiti kala was identified as a male *Pseudomogoplistes* sp. according to the descriptions of *P. vicentae* and *P. squamiger* provided in Sardet et al. (2015). Then, based on the distribution of the different *Pseudomogoplistes* species, *Pseudomogoplistes vicentae* Gorochov (1996) was considered the best candidate species as it is the only beach cricket species largely found on the Atlantic seashores (Fig. 1). This identification was then confirmed through the comparison of pictures of one male anal plate (Fig. 2) to the descriptions provided by Gorochov (1996) and Sardet et al. (2015): Pictures showed a "medial shallow concavity bearing group of hairs" (Gorochov 1996) as expected for *P. vicentae* and did not show any lateral tufts of dense tawny bristles that would have been expected for *P. squamiger*. In the current state of our knowledge of *Pseudomogoplistes* taxonomy, specimens found can thus be regarded as *P. vicentae*.

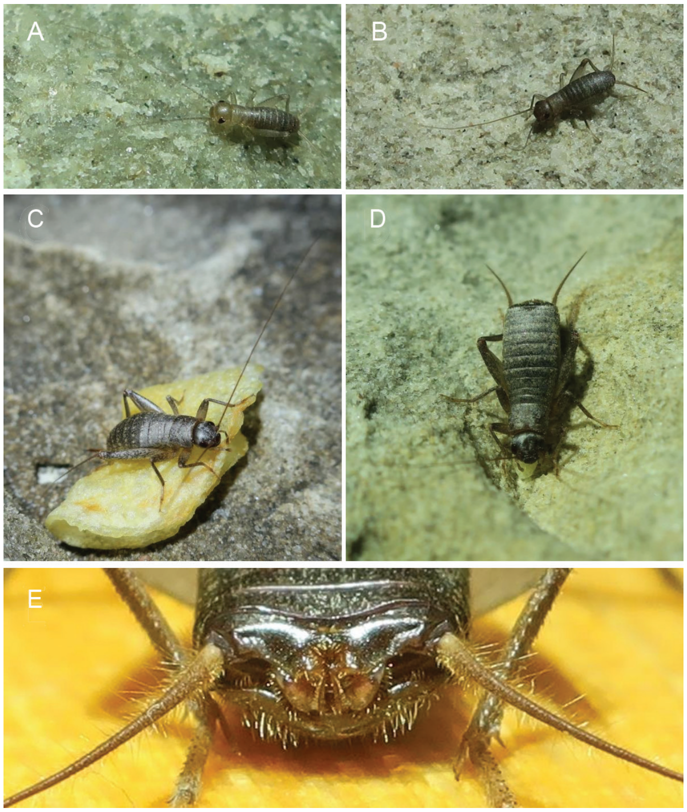

Fig. 2. Night sights of the Atlantic beach cricket *Pseudomogoplistes vicentae* in Agiti kala (San-Sebastian, Gipuzkoa, Basque autonomous community). **A**. Young nymph; **B**. Intermediary nymph; **C**. Adult female feeding on a piece of potato chip; **D**. Adult male observed on the upward face of cobbles; **E**. Posterior view of a male abdomen showing the anal plate with a median shallow concavity.

In total, more than 20 adults and 30 nymphs could be observed, among which six females and five males could be photographed. During diurnal surveys, no crickets could be found beneath large stones, while three nymphs could be found digging into cobbles. At night, opportunistic searches led to observation of both nymphs and adults (Fig. 2) walking on cobble surface at an average rate of 10.2 individuals per hour (Table 2). Both males and females could be observed in similar proportions. Bait observation also proved to be efficient for cricket detection: eight out of 22 baits (36%) attracted between one to three crickets after 30 minutes. During those nights, three individuals were found dead: two were trapped in an empty can of beer and one in a piece of plastic holding a small amount of water.

On Gorrondatxe Beach, three nymphs were discovered. In Meñakoz Beach (Fig. 3), one nymph and one adult male were found.

Table 2. Observations of the Atlantic beach cricket *Pseudomogoplistes vicentae* during nocturnal opportunistic search in Agiti kala, San-Sebastian, Gipuzkoa, Basque autonomous community. Scouting sequence duration: duration of a continuous sequence dedicated to opportunistic scouting for crickets walking over the cobbles. Rate of encounter: total number of crickets observed during a scouting sequence divided by the duration of this scouting sequence and expressed on an hourly base.

Night	Scouting sequence duration (min)	Female	Male	Unknown sex adult	Nymphs	Total	Rate of encounter (indiv./h)
August 3, 2019	45	1	0	0	3	4	5.3
	25	1	2	0	1	4	9.6
	10	0	1	0	0	1	6.0
August 4, 2019	30	0	1	0	5	6	12.0
	30	2	1	1	3	7	14.0
August 15, 2019	30	2	1	1	3	7	14.0

Discussion

Observations of *P. vicentae* in three sites of the Basque autonomous community have increased knowledge of its distribution in Europe and continental Spain. The Gorrondatxe Beach population is roughly 200–250 km away from the population observed in Asturias by Kleukers et al. (2018), while Agiti kala population is 550–600 km from the nearest northern population in France (Herbrecht 2007). The fact that *P. vicentae* could be found quite easily in Agiti kala, Gorrondatxe Beach, and Meñakoz Beach confirms that this species has suffered a lack of study, as suggested by Kleukers et al. (2018). Our results suggest that further observations can be expected in northern Portugal and Spain (Galicia, Cantabria, and Basque autonomous community), and even in southern France, in the region of Pyrénées Atlantiques.

The first specimens of *P. vicentae* found in England and France were initially regarded as accidentally introduced Mediterranean beach cricket, *P. squamiger* (Chopard 1951, Sutton 1999); these were only later identified as *P. vicentae*. Morère and Livory (1999) described the specimens from France (Carolles, Manche region, Normandy) as slightly different from *P. vicentae*, described by

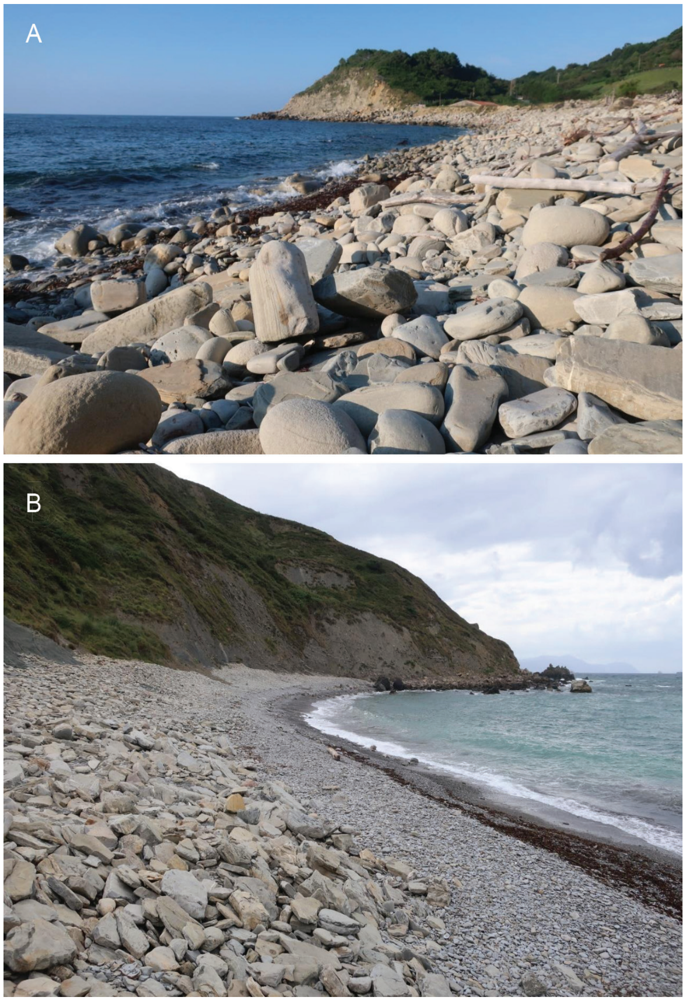

Fig. 3. Habitat of the Atlantic beach cricket *Pseudomogoplistes vicentae* at **A.** Agiti kala, San-Sebastian and **B.** Meñakoz Beach, Gorliz, Basque autonomous community.

Gorochov (1996). Based on slight differences of the male's anal plate and genitalia, Morère and Livory (1999) assigned French specimens to a new taxon, *Pseudomogoplistes vicentae septentrionalis*. Today, the French populations are considered to belong to *P. vicentae septentrionalis*, while the subspecific status of populations from other locations (England, Guernsey Islands, Canary Islands, and Asturias) is not addressed. Whether populations from the Basque autonomous community belong to the nominal subspecies *P. vicentae vicentae* or to the subspecies *P. vicentae septentrionalis* cannot be addressed here, as no specimen was captured and the subspecific status of the closest population in Asturias is unknown. This situation highlights a need for a clarification of the subspecific status of these populations and other populations from Spain and England through a morphological and/or a genetic comparison with French populations.

These observations also provided some behavioral information on *P. vicentae*. While nocturnal observations did not efficiently detect *P. squamiger* (Dusoulier 2017), they were efficient for detecting *P. vicentae*. This may allow the monitoring of *P. vicentae* populations through non-intrusive standardized observations along transects. The crickets were also observed to be attracted to food baits, such as cooked shrimps and other types of food abandoned on the beach (grilled sardine waste and potato chips). This may be lethal when the crickets become trapped in food packaging, such as bottles, cans, or boxes. Such trapping is, however, already used in England to monitor *P. vicentae* populations with pit-fall traps baited with cat biscuits (Gardiner 2009, Vahed 2019). Baited pit-fall traps should be used for a detection campaign of other *P. vicentae* populations in putative favorable shores of the northern Iberian Peninsula and southern France.

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I thank Antonia and Jose-Mari Iribar for hosting me and providing facilities at Agiti kala. This study did not require insect lethal capture and was run with respect to the Spanish and Basque autonomous community environmental laws. The precise location of *P. vicentae* observations were communicated to the entomological section of the local scientific society, Aranzadi.

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Aspects of the life history and ecology of two wingless grasshoppers, *Eremidium armstrongi* and *Eremidium browni* (Lentulidae), at the Doreen Clark Nature Reserve, KwaZulu-Natal, South Africa

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Abstract

Most grasshopper species have simple and similar life cycles and histories; however, different environmental and ecological factors have different effects on their distribution, sexes, and developmental stages, with effects varying among species. If we are to conserve grasshoppers, we need to understand their ecology and life histories. The aim of this study was to investigate aspects of the life histories and ecology of two recently described co-occurring, congeneric species of wingless grasshoppers, *Eremidium armstrongi* (Brown, 2012) and *Eremidium browni* Otte & Armstrong, 2017, at the Doreen Clark Nature Reserve near Pietermaritzburg, South Africa. These two species have limited extents of occurrence, only being known from an endangered forest type in parts of the midland area of KwaZulu-Natal Province, South Africa, and therefore may need conservation action to ensure their long-term survival. No significant differences in the abundances of the two *Eremidium* grasshoppers were found, but their phenologies differed, with the adults of *E. armstrongi* being present before the adults of *E. browni*, with some overlap in presence over time. The *Eremidium* grasshoppers were only found in the forest and were more abundant in the forest margin. The *Eremidium* grasshoppers fed on soft plants from several families. Information on dietary differences between the species is required to determine whether there is potential competition between them. An adult *E. browni* female kept in an *ex situ* terrarium laid eggs in the soil, and nymphs took approximately two months to hatch.

Keywords

adult densities, adult turnover, competition avoidance, microhabitat selection, sympatric congeners

Introduction

The order Orthoptera is an important element of biodiversity, contributing significantly to the species richness on earth (Bekele 2001). Grasshoppers are considered the most important members of Orthoptera for their contribution to biomass, abundance, and diversity (Mahmood et al. 2004). Grasshoppers are epigeic invertebrates that sometimes form compact groups comprised of several individuals, which can be hoppers and/or winged adults, or they can be polyphenic (Capinera et al. 1997, Song 2011). The eggs of a mature female are laid in egg pods or clusters in the soil, in the stems of plants, or in rotten wood (Johnsen 1985). Once the egg hatches, the nymph gradually changes into its mature form. Grasshoppers are phytophagous insects (Johnsen 1985), and they can be the primary plant consumers in grassland ecosystems (Gardiner et al. 2005). The nymph and adult display similar feeding patterns. However, both life stages may respond differently to different landscape types at different scales (Bekele 2001).

Biotic and abiotic factors, such as host vegetation, plant diversity, habitat structure, predators, changes in seasonality, light intensity, precipitation, and elevation, influence grasshopper diversity and population dynamics (Bekele 2001, Mahmood et al. 2004, Sirin et al. 2010, Branson 2011, Ely et al. 2011). Grasshoppers are ectotherms, and their body temperature strongly influences most of their physiological processes; their ability to tolerate ambient environmental temperatures and humidity has the potential to determine their richness, spread, ecology, behavior, and the overall fitness of an individual (Willott and Hassall 1998). Therefore, the diversity and abundance of grasshoppers is relatively low in areas dominated by forest, as these habitats are not suitable for most grasshopper species (Sergeev 2011).

The grasshoppers in the family Lentulidae Dirsh, 1956 are wingless. Certain genera in this family, such as *Eremidum*, have species with small distribution ranges that occur in forests in the province of KwaZulu-Natal and elsewhere in South Africa (e.g., Brown 2012, Otte 2015, Otte and Armstrong 2017). Since various forest types and forests are endangered in KwaZulu-Natal due to clearing, logging, other forest products extraction, fire, and alien plant encroachment (Mucina and Rutherford 2006, Jewitt et al. 2016), these endemic grasshopper species are of conservation concern. However, little is known about the life histories and ecology of these species, potentially hampering conservation efforts.

The present study focuses on aspects of the life history and ecology of two species, *Eremidium armstrongi* (Brown, 2012) and *E. browni* (Otte & Armstrong, 2017) found in Doreen Clark Nature Reserve near Pietermaritzburg, South Africa. These grasshoppers inhabit the Endangered Eastern Mistbelt Forest type (Jewitt 2018) in a restricted area of the midland region of KwaZulu-Natal Province, South Africa. Although these two species may require conservation action for their long-term survival, almost nothing is known about their life history and ecology. The main objectives of this study were to determine the time of year during which adults of each species were present, estimate densities and the number of adult individuals of each species in the sampled habitat area, identify microhabitat features that may explain microhabitat preferences of the species, investigate how far the distribution of *Eremidium* grasshoppers extended into grassland, and, if possible, ascertain how two very similar species can co-occur.

Materials and methods

Study area.—The Doreen Clark Nature Reserve (29°57.85'S, 30°28.92'E; Fig. 1) is in the suburb of Winterskloof, north-west of Pietermaritzburg, in the KwaZulu-Natal province of South Africa. The vegetation in this protected area of approximately five hectares is the Southern Mistbelt Forest and Midlands Mistbelt Grassland (Fig. 1; Mucina and Rutherford 2006). The greater part of the reserve is covered by forest, containing a genus of conifers known as *Podocarpus* as well as many other genera of angiosperms. The forest meets the grassland at the narrow forest-grassland ecotone, where many insect species can be found, including *E. armstrongi* and *E. browni*. Between the forest margin and the grassland lies a hiking trail, which contributes to the human disturbances experienced by the Doreen Clark Nature Reserve. The study site was situated along the hiking trail, extending approximately 15 m on either side (Fig. 2). At the beginning of the hiking trail, grasses in the grassland were tall and green, reducing in height and becoming drier as the trail moved more towards the west. A small stream runs through the forest. The forest is multistory, with a largely herbaceous understory of forest grasses, sedges, ferns, forbs, etc.

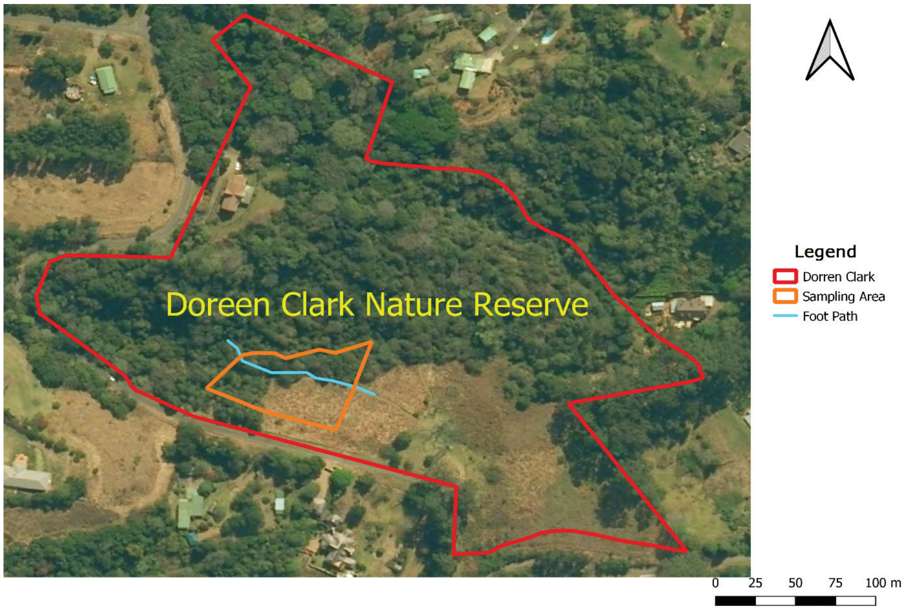

Fig. 1. Study site, Doreen Clark Nature Reserve (including sampling area and section of the foot path).

Fig. 2. Hiking trail, with the grasslands (left) and forest margin (right) of the trail.

Estimation of time of year of presence and number of adults in the sampled area.—A quantitative direct count method using quadrats was used (Richards and Waloff 1954, Gardiner et al. 2005, Samways et al. 2010). Twenty-seven 1-m^2 quadrats (Fig. 3), each made from gardening twine and secured at the corners by 3-in nails, were placed uniformly in the study area on 12 November 2018 and left out in the field for the study period. The quadrats were placed 5 m apart to minimize the probability of double-counting grasshoppers. Twelve quadrats were placed along the forest margin, and the remainder of the quadrats extended into the forest, ending near the stream bank.

Sampling was carried out on 15 days spread out over 3 months (13 November 2018 – 14 January 2019). These months were chosen because previous observations determined that *E. armstrongi* adults were present during October and November, and *E. browni* adults were present in December and January. Sampling days were selected based on weather conditions of temperatures greater than 20 °C to ensure that the grasshoppers were active and could be easily seen. On each sampling day, the sequence in which the quadrats were sampled was reversed from that of the previous occasion to reduce bias caused by variation in sampling time. Sampling was carried out between 9 am and midday, local time.

Species turnover with time of year was determined for adult males only because it was difficult to differentiate between nymphs and females of the two species in the field. These data were obtained from the quadrat counts on the total (15) sampling occasions and plotted over time to show the turnover of the species.

The average density per square meter of *E. armstrongi* and *E. browni* observed over the first five sampling occasions (for *E. armstrongi*) and over the last five sampling occasions (for *E. browni*) was calculated from the data. The sampling occasions are given in Table 1. The dates of each sampling occasion were chosen to avoid overlap in the presence of adults of both species. All adult females recorded on a particular sampling occasion were assumed to be of the same species as the males present. The area of the sampling site was calculated using a geographical information system (GIS; QGIS 3.4.15 Madeira) and geographical coordinates collected by a hand-held global positioning system (GPS; Garmin GPSMAP 64). The average number of individuals of both species at the sampling site was then calculated. Average male to female ratios for *E. armstrongi* and *E. browni* over the five sampling occasions for each were calculated from the raw data.

An independent *t*-test was performed using the statistical package SPSS (IBM Corp. Released 2019. IBM SPSS Statistics Subscription for Windows, Trial Version) to determine if the adult densities of the two species differed significantly within the study area. The assumption of equal variance was tested by performing Levene's Test for equality of variances, and the assumption that the data are normally distributed was tested using the one-sample Kolmogorov-Smirnov test. The assumptions of equality of variances and normal distribution were met ($F = 2.327$, df = 8, $p = 0.166$; $\alpha = 5.3177$). Thereafter, an independent samples *t*-test was used to test the null hypothesis that the abundance for *E. armstrongi* did not differ significantly from that of *E. browni* at a significance level of $p < 0.05$.

Identification of microhabitats.—To identify and describe the microhabitats favored by each species, the Braun-Blanquet method (Mueller-Dombois and Ellenberg 1974) was used. This assessment was done to see how the variation in vegetation in the 27

Table 1. Number of adult males and females recorded during each sampling occasion, mean (± one standard deviation) number of adults per day, estimated mean total number of adults in the sampled area (877 m^2), and estimated adult sex ratio.

E. armstrongi (N = 5)			*E. browni* (N = 5)		
Date	Males	Females	Date	Males	Females
13 Nov 2018	4	7	08 Jan 2019	5	7
20 Nov 2018	5	13	09 Jan 2019	8	8
26 Nov 2018	6	4	10 Jan 2019	6	7
29 Nov 2018	8	10	11 Jan 2019	6	9
01 Dec 2018	6	9	14 Jan 2019	4	7
Total	**29**	**43**	**Total**	**29**	**38**
Mean (± 1 S.D.)	14.20 (± 3.564)		Mean (± 1 S.D.)	13.40 (± 2.302)	
Mean/m^2	0.53		Mean/m^2	0.50	
Mean/877 m^2	468		Mean/877 m^2	435	
Male:Female	1:1.5		Male:Female	1:1.3	

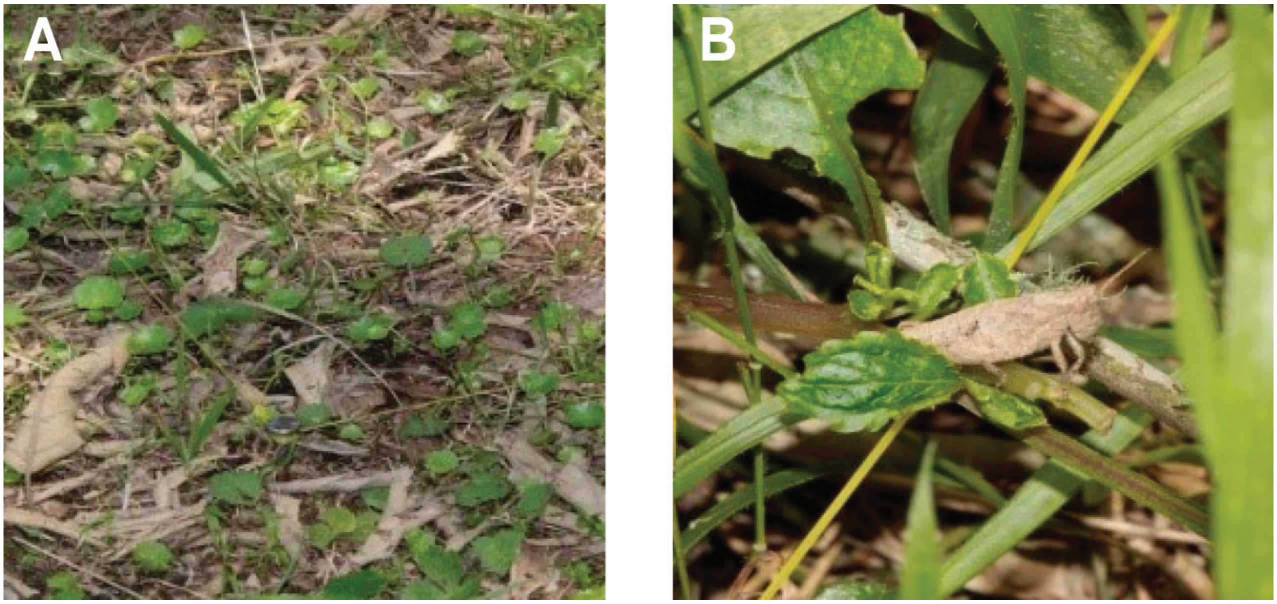

Fig. 3. Sampling quadrat (**A**) and female *Eremidium armstrongi* on the boundary of the quadrat (**B**).

plots relates to the abundance of *E. armstrongi* and *E. browni* in order to determine microhabitat preferences. The Braun-Blanquet scale used is given in Table 2.

The species of all plants found within each quadrat, starting from quadrat 1, was recorded using a labelling system (e.g., P1 = *Plectranthus laxiflorus* Benth.). Thereafter, the vegetation cover of each plant species found within each quadrat was recorded using the Braun-Blanquet scale. To ensure that the feeding and other behavior of the grasshoppers were undisturbed, a specimen of each representative plant species in the sampling quadrats was collected using a hand spade and labelled according to the code assigned to it once sampling was completed. These plants were then pressed and dried and identified to the closet known taxonomic group using two plant field guides (Pooley 1998 and Oudtshoorn 1999) and by comparison with specimens in the Bews Herbarium at the University of KwaZulu-Natal, Pietermaritzburg. The degree of constancy for each plant species was calculated by counting the number of quadrats the plant species occupied.

A simple observation method was undertaken in the field to identify what plant species the grasshoppers fed on. The grasshoppers were observed from a distance. If the plant species was unknown, it was allocated a number and a sample taken for later identification in the laboratory. To determine where eggs were laid and the incubation period, a pair of mature grasshoppers from each species, *E. armstrongi* and *E. browni*, were captured and kept in captivity. A terrarium was created using a fish tank (61 cm × 32 cm × 33 cm) in which soil and plants from the Doreen Clark Nature Reserve were added. Soil was placed at the bottom of the tank to a depth of approximately 5 cm, and the plants were placed in the soil to provide food and shelter. The tank was covered with shade cloth in such a way as air could circulate and placed near a window for sunlight and heat. Water was added to the tank regularly to prevent plants from dying, and fresh food plants were collected as needed from the study site. The grasshoppers were monitored daily.

Distribution of Eremidium *grasshoppers into the grassland.*—The distribution of the two grasshopper species into the grassland was investigated using a transect sampling method. Strip transects were created using a GPS, starting at the hiking trail and extending into the grassland, with each transect approximately 5 m apart. On each transect, three people sampled: one in the middle and two approximately 1 m away on either side. Sampling was carried out over three days, and only the adults of each species were captured and identified along transects. After identification, each grasshopper was released behind the samplers to avoid resampling the same individuals. The coordinates of each grasshopper identified along the transects were uploaded into GIS software and used to map the extent of their distribution into the grassland.

Table 2. Braun-Blanquet scale.

Symbol/Scale	Vegetation cover
r	Some individuals
+	Many individuals but < 1%
1	1–5%
2	6–25%
3	26–50%
4	51–75%
5	>75%

Results

Period of presence of adults.—On the first five sampling occasions (during the period of 13 November to 01 December 2018), only *E. armstrongi* adult males were present, and during the last five sampling occasions (during the period of 08 to 14 January 2019), only *E. browni* adult males were present. On the intervening five sampling occasions (during the period of 12 to 18 December 2018), both *E. armstrongi* and *E. browni* adult males were present (Fig. 4). The data for both the males of both species show an asymmetrical bell-curve distribution, with the peak value for *E. armstrongi* of 8 males on the fourth sampling occasion (29 November 2018) and with the peak value for *E. browni* of 8 males on the twelfth sampling occasion (09 January 2019).

Estimated number of adult individuals.—The total number of *E. armstrongi* adults recorded over the five days of sampling was 72 individuals, with an average of 14 adult individuals per day, and the total number of *E. browni* adults was 67 individuals, averaging 13 individuals per day (Table 1). The calculated area for the sampling area in the forest margin habitat, as indicated in Fig. 1, was 877 m^2. *Eremidium armstrongi* had a higher estimated number of adult individuals in the sampled habitat area than *E. browni*, with a difference of 33 individuals (Table 1). The male to female ratio is biased towards females in both species (Table 1), with *E. armstrongi* having a higher female ratio compared to *E. browni*. There is a greater variation of values in the *E. armstrongi* dataset than that of *E. browni* (Table 1). The mean number for *E. armstrongi* is greater than that of *E. browni* (Table 1), but not significantly so ($t = 0.422$, df = 8, $p = 0.684$).

Microhabitats.—Over the five sampling occasions, a total of 59 *E. armstrongi* (both sexes combined) were recorded in the 12 quadrats at the margin of the forest and 13 *E. armstrongi* in the 15 quadrats in the forest interior; the respective numbers for *E. browni* were 52 and 15 (Table 3). *E. armstrongi* was observed to occur significantly more than expected in the quadrats at the forest margin ($\chi^2_{1, 99} = 13.614$, $p < 0.001$), as was *E. browni* ($\chi^2_{1, 94} = 9.743$, $p < 0.002$). The two quadrats with the highest total mean number for both species were quadrats 5 and 17, and two plant species were recorded with high degrees of constancy (Table 3). Quadrat 5 had no bare ground and had more than 75% cover of Poaceae and 6–25% cover of *Centella asiatica* (L.) Urb. This quadrat was on the

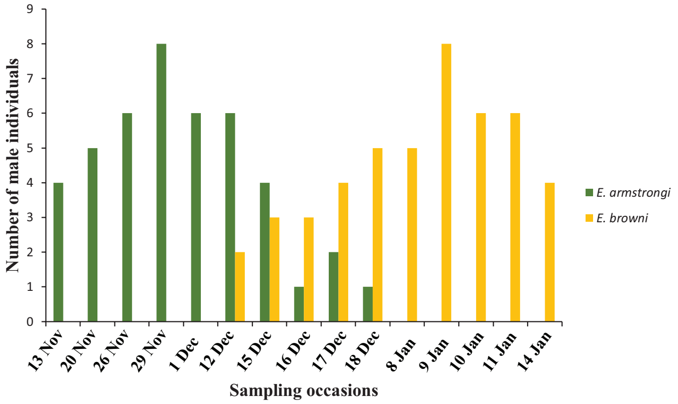

Fig. 4. Variation in number of male *Eremidium armstrongi* and *Eremidium browni* counted in quadrats over time.

Table 3. Mean number (over five sampling occasions) of adult *Eremidium armstrongi* and *Eremidium browni* counted and Braun-Blanquet plant cover-abundance in each quadrat. Forest margin quadrat numbers and data are italicized. Refer to Table 1 for explanation of the symbols.

Quadrat number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	Degree of constancy
Mean no. *E. armstrongi*	0.8	0.6	0.4	0	4	0.2	0.2	0.4	0	0.6	1.2	0	0.2	0.4	0	0	3	0	0.4	0.4	0.6	0	0.2	0	0	0.6	0.2	
Mean no. *E. browni*	0.4	0.8	0.4	0	3.8	0.2	0.2	1	0.2	0.2	0.4	0	0.6	1.6	0	0	2	0.4	0.2	0	0	0	0.2	0	0	0.8	0	
Plant species																												
Plectranthus laxiflorus	+				1						4						3		1		+							6
Monopsis stellarioides	+																+											2
Miscanthus capensis	2																											1
Prosphytochloa prehensis	4																											1
Cheilanthes viridis vars *viridis*	1				+																							2
Impatiens hochstetteri		3	2		+	+	2	+	1			+		1				+	1		1	+	+	+	+	r	+	18
Hypoestes forskaolii		r		+					3		1		+					+	2	+	2		1		1	2	2	13
Asparagus plumosus		+				r																						2
Piper capense		1	r												+	r				+			2	r	+		r	9
Isoglossa cooperi		2	1																									2
Justicia campylostemon			1			1	1								+			+										5
Desmodium repandum			+						+			+			+	r							+	r				7
Dioscorea sylvatica			1	1			+																					3
Tricalysia lanceolata			r	+																								2
Polystichum trankeiense				1	+			+	2																		2	5
Poaceae					5			+																				2
Centella asiatica					2												1		+									3
Sanicula elata						+			+														2					3
Cyperus sphaerospermus						2																						1
Crassula c.f. pellucida								+				r		1					2				r			2		6
Achyranthes aspera								+																				1
Oplismenus hirtellus									1					+					+					1				4
Tradescantia fluminensis										3			3					1	1	5	r	5						7
Diclis reptans														5			1										+	3
Thunbergia alata														1			2											2
Selaginella kraussiana															1							r		+		1	+	5
Bare ground		1	1	5		3	5	5	2	3		5	3		5	5					2		3	5	5		2	17

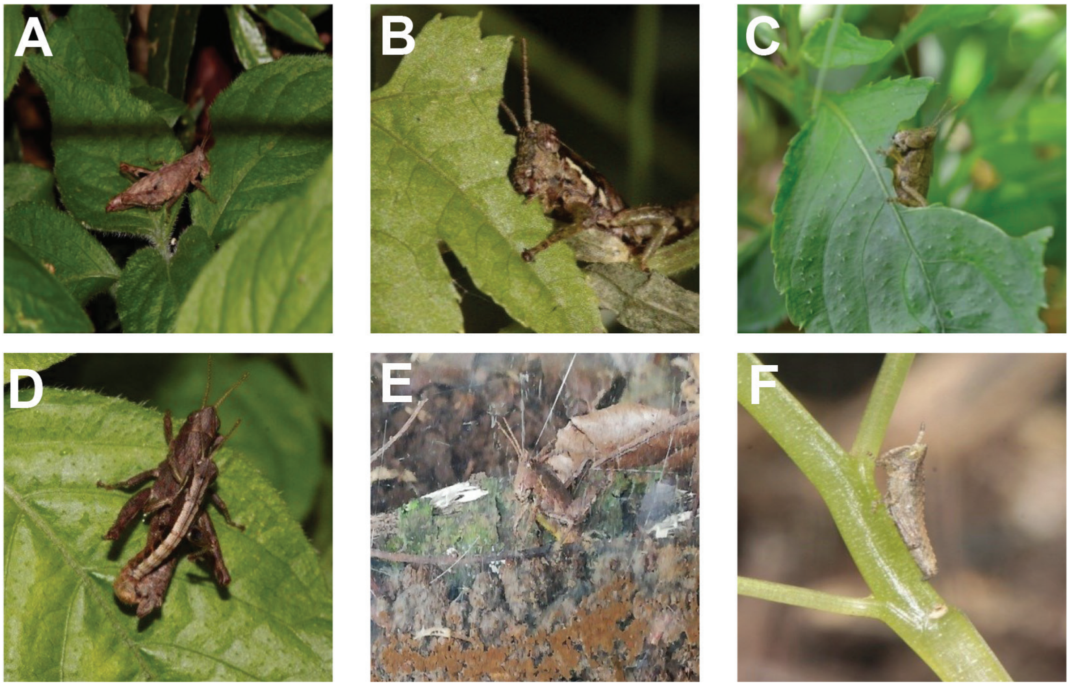

Fig. 5. *Eremidium armstrongi* female feeding on *Hypoestes forskaolii* (**A**), *Eremidium armstrongi* male feeding on *Diplocyclos palmatus* (**B**), *Eremidium* species female feeding on *Impatiens hochstetteri* (**C**), *Eremidium browni* mating (**D**), *Eremidium browni* female laying her eggs in the terrarium (**E**), and *Eremidium browni* nymph hatched in terrarium (**F**).

Fig. 6. Extent of the distribution of *Eremidium* grasshoppers into the grassland.

forest margin and received a fair amount of sunlight. It was noted that quadrat 17 was similar to quadrat 5, which was located on the forest margin and had no bare ground. Between 25–50% of the quadrat was covered by *Plectranthus laxiflorus* Benth. and 6–25% by *Thunbergia alata* Bojer ex Sims (Table 3; Fig. 5), which received a fair amount of sunlight. Most of the remaining quadrats in which either *E. armstrongi* or *E. browni* were observed contained the food plants *Impatiens hochstetteri* Warb. or *Hypoestes forskaolii* (Vahl) R.Br. or both (Table 3), while quadrats 1 and 2 received a fair amount of sunlight. Another recorded food plant species, *Diplocyclos palmatus* (L.) C.Jeffrey, was not found in any of the quadrats. Most of the quadrats where no *Eremidium* species were observed had a relatively high percentage cover of bare ground (Table 3). The female *E. browni* in the terrarium was observed laying eggs in the soil (Fig. 5).

Distribution into the grassland.—Fig. 6 indicates the 12 transects that were sampled and the positions of *Eremidium* grasshoppers that were found along these transects over the three sampling days. The sampling area included both grassland and forest. Only one male individual was observed along each of transects 1 and 4, two along transect 5, three along each of transects 7 and 8, four along transect 12, six along transect 6, and seven along transect 9. No individual was found along transects 3, 10, and 11. Transect 9 was located at the margin of the forest. The *Eremidium* grasshoppers recorded along transect 6 were at the margin of the forest, and those along transect 12 were in the forest. No individual was found in the grassland interior (Fig. 6).

Discussion

Grasshopper diversity and populations in any area are influenced by topography, vegetation, and soil (Lockwood and Lockwood 2008). They respond to a combination of interacting abiotic and biotic factors that vary over time and space (Branson 2008). However, the direct, indirect, and interacting effects of host vegetation, competition, weather conditions, and other factors on grasshopper population dynamics are still poorly understood (Skinner and Child 2000, Branson 2008). There has been much debate between ecologists about the role of intrinsic and extrinsic factors controlling population dynamics (Ritchie 1996). Grasshoppers show variations in their life history, with each species responding differently to these factors (Branson 2004). According to Latchininsky et al. (2011), general grasshopper distribution trends for different regions have been described. However, the processes and factors affecting grasshopper species richness patterns at the different scales are still being elucidated. Local distribution trends have been discussed with regards to grasshopper diversity in relation to vegetative species composition, habitat structure (Latchininsky et al. 2011), and the overall microhabitat of the species (e.g., Joern 1982). Complex interactions between competing necessities influence habitat selection behavior (Ahnesjö and Forsman 2006), and the use of resources, such as food and microhabitats, among grasshopper species is influenced by biotic associations (Joern 1979).

Most grasshopper species have specific microhabitat preferences. These preferences are based on the multiple abiotic and biotic factors that make up the microhabitat. Some of these factors include resource availability (e.g., food or nutrients), microclimate variations (e.g., light intensity, temperature, humidity, and precipitation), structural qualities, suitable hiding places, predation, and competition (Joern 1982, Ahnesjö and Forsman 2006). For grasshoppers, some abiotic factors that influence microhabitat utilization and population size are microclimate, plant structure, plant species richness and abundance, soil characteristics, availability of acceptable oviposition sites and food plants, and suitable hiding places. Hemp and Hemp (2003) used phytosociological relevés, applying the Braun-Blanquet method to ascertain the grasshopper coenoses in the plant communities distinguished in the high-altitude grasslands on Mount Kilimanjaro. They could also determine the microhabitat preferences of species from the data. Only a few studies have shown evidence that biotic factors, such as predation and competition, influence microhabitat selection (Joern 1982).

According to Joern and Klucas (1993), wherever there are herbivorous insects such as grasshoppers, food may become limited, resulting in competitive interactions, something which is of interest yet remains poorly understood. The congeners *E. armstrongi* and *E. browni* are similar in their appearance but also in their microhabitat preferences and densities. Since these two species share the same microhabitat and possibly food source, they may avoid potentially adverse interaction through differences in phenology, as indicated by the adult male numbers over time (Fig. 4). Competition for resources is a possible reason why *E. armstrongi* and *E. browni* illustrate a peak number of adult male individuals (and, by extension, adult females) when only a single species is present, allowing sympatry of two very similar species. The adults of *E. armstrongi* were observed in the field between October and December 2018, while the adults of *E. browni* were observed between December and February 2019. The number of adult individuals of *E. armstrongi* and *E. browni* were similar in the sampled habitat area (Table 1), with a slight difference in the recorded male to female ratio.

General feeding behavior in grasshoppers, such as food plant specificity, number of taxa in the diet, and the type of vegetation they feed on, is varied (Joern 1983), with most grasshopper species feeding selectively on a variety of plant species from different families (Sword and Dopman 1999), but preference is evident (Joern 1979). Such grasshoppers are referred to as polyphagous, and this has been seen at an individual, population, and species level (Sword and Dopman 1999). Work done by Rowell (1978) suggested that this view is true for grasshoppers found in the temperate zone, and further studies show a greater degree of specificity in grasshoppers of the tropic zones. *Eremidium* species are temperate zone grasshoppers that feed on plants from different families (Fig. 5). At Doreen Clark Nature Reserve, they displayed some level of preference by feeding on soft green vegetation while apparently avoiding vegetation with waxy and sticky surfaces. They were observed feeding on *Impatiens hochstetteri* Warb. (family: Balsaminaceae), *Hypoestes forskaolii* (Vahl) R.Br. (family: Acanthaceae), and *Diplocyclos palmatus* (L.) C.Jeffrey (family: Cucurbitaceae). Observations of feeding by *E. armstrongi* and *E. browni* were too few to determine whether they differ in the plant species in their diets, and the method used does not allow extrapolation to a general conclusion.

Eremidium grasshoppers were only found along the forest-grassland edge and into the forest interior, probably as a result of particular microhabitat requirements. The perceived differences in microhabitat between the forest interior, its margin, and grassland include vegetation composition and structure, light intensity, temperature, and soil compactness. The grassland interior consists of, *inter alia*, tall, hairy grasses containing relatively large amounts of silica in the body structure and more compacted soils exposed to direct weather conditions (light intensity, temperature, and precipitation). The forest floor, in contrast, consists of soft green vegetation, moist soft soils, and dappled sunlight. The microhabitat in the sampled area was suitable for *Eremidium* grasshoppers, but more suitable towards the margin of the forest (Table 3), perhaps owing to the greater availability of sunlight. This area may be thermally suitable for egg production, as mating has been observed at the edge on many occasions. Temperature plays an important role in the fitness and survival of grasshoppers; since grasshoppers are ectotherms, their body temperature influences the activities, ecology and, eventually, overall fitness and development of an individual (Kemp 1986, Willott and Hassall 1998, Ahnesjö and Forsman 2006). Therefore, grasshoppers need to select thermally suitable microhabitats (Ahnesjö and Forsman 2006). In the forest, the canopy cover provides shade with patches of sunlight that filters through to the forest floor and that the *Eremidium* grasshoppers can use to regulate their body temperatures.

Grasshoppers select areas that best suit all their requirements because some microhabitats may provide one factor (e.g., shelter from predators) but may lack other important factors (e.g., suitable temperatures, foodplants) needed by the species for survival (Ahnesjö and Forsman 2006). *Eremidium* grasshoppers were found in quadrats that had food plants and bare ground and that received some sunlight for thermoregulation. Depending on the species, grasshopper eggs are laid in the soil where conditions are suitable for growth (Dempster 1963, Lockwood and Lockwood 2008), with a female producing one or more pods containing 3 to 200 eggs each (Lockwood and Lockwood 2008). A female *E. browni* laid eggs in the soil of an *ex situ* terrarium, which were determined from the date of appearance of nymphs in the terrarium (Fig. 5) to take approximately two months to hatch.

Conclusion

Eremidium armstrongi and *E. browni* are two recently described species of grasshoppers; to conserve them for future generations, it is important to understand their life histories and ecology. The two species are very similar, with no significant difference in abundances. Both species occupy the same specific microhabitat with a short period of overlap. Both *E. armstrongi* and *E. browni* are selective for microhabitat and were found to be most abundant along the margin of the forest, but also occurred in the forest interior. Food plants included one species in each of three families in the sampled area, but more observations on feeding are needed to determine whether the two *Eremidium* species differ in diet. Further research needs to be done to improve understanding of the two species, especially in terms of diet and reproductive behavior. Diagnostic features of the adult females of *E. armstrongi* and *E. browni* that can be easily seen in the field should be elucidated to enable researchers to tell them apart more easily.

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Short Communication Journal of Orthoptera Research 2021, 30(1): 81–85

Calling and courtship songs of the rare, robust ground cricket, *Allonemobius walkeri*

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Abstract

In the original description of *Allonemobius walkeri* Howard & Furth, 1986, the authors describe the species' calling songs in a table that included trill length, length of the interval between trills, pulse rate, and carrier frequency for four individuals. Further investigation of the acoustics of this species reveals that the calling songs are composed of syllables organized into echemes composed of a varying number of syllables, and organized into groups of echemes, of variable length. The echemes are separated by intervals of various lengths. The calling song is pleasing to the ear, with ~27 syllables per second and a carrier frequency of ~7.7 kHz at 25°C. The characteristics of the echemes and echeme intervals are significantly different when the cricket is singing in sunlight compared to darkness. In sunlight, echemes are shorter, but echeme intervals are longer. There is no effect on calling bout lengths. Courtship songs are quieter than calling songs, with a random delivery of soft and loud chirps in addition to fainter, rhythmic sounds randomly distributed between the chirps. Courtship songs are interspersed with long bouts of calling songs with displays lasting hours.

Keywords

acoustic communication, Nemobiinae, song characteristics

Introduction

Allonemobius walkeri Howard & Furth, 1986 is a rare species of the cricket family Trigonidiidae, subfamily Nemobiinae, found in grassy areas in open sun or at woodland edges next to open, grassy fields in North America (Howard and Furth 1986). They are often found with *Allonemobius allardi* (Alexander and Thomas 1959), but not in all locations. Because of its rarity, *Allonemobius walkeri's* calling songs were briefly described in 1986 (Howard and Furth 1986), but there was no mention of courtship songs.

Under field conditions, singing males may perch in direct sunlight even when apparently hidden under grassy vegetation. This direct sunlight elevates their body temperature well above the ambient conditions in a phenomenon known as sun effects. Under these conditions, it is nearly impossible to know the exact temperature that a singing male cricket is experiencing. These sun effects can be eliminated by recording singing males indoors out of direct sunlight or by using low-E glass that blocks the transmission of a large percentage of the infrared radiation that would warm the crickets.

For field researchers, knowing the songs of singing orthoptera is of great importance to facilitate collection, population estimation, range delineation, and teaching others about these insects. Recently, there has been a significant increase in the use of automated audio recording units to collect field data regarding species richness, population density, and seasonal timing of appearance of singing orthoptera (Forrest 1988, Newson et al. 2017, Riede 2018). A clear description of the songs of different common species can often be gleaned from the literature, and exemplars can be found in sound libraries. However, it is sometimes difficult to find a description or audio example of rare species that would allow researchers to identify confusing audio specimens from field recordings. In this study, I have extensively recorded five individuals of *Allonemobius walkeri* under two lighting conditions (sunlight and darkness), and I have recorded the courtship songs of two males with a female. I describe in detail the characteristics of the calling and courtship songs.

Materials and methods

I collected one male in 2019 and four males and one female in 2020 from a grassy meadow next to a mixed deciduous woodland at a wildlife preserve in Jefferson County, West Virginia, USA. All specimens were maintained in plastic containers that were modified by removing most of the plastic from the sides and lid. The open areas were then covered with no-see-um netting held in place with hot glue. These singing cages are practically transparent to sound. The crickets were fed with iceberg lettuce, Fluker's High-calcium Cricket Diet (Port Allen, LA), and water *ad libitum*. Audio recordings were made in an anechoic room, with dim or no light or in sunlight coming through a south-facing window. The windows were composed of Low-E glass that filtered out much of the infrared radiation, thereby keeping the temperature of the insects more consistent with the ambient temperature of the room. Temperatures were taken with either a Cooper Atkins DFP450W digital pocket thermometer (Middlefield, CT, USA) or a Digi-Sense ZM-94460-78 receiver and ZM-90205-10 transmitter (Vernon Hills, IL, USA). All recordings of calling and courtship songs were made with a Sound Devices 702, Sound Devices MixPre-6 (Reedsburg, WI, USA), or a Zoom F8n digital recorder (Hauppauge, NY, USA) at a sampling rate of 96 kHz at 24-bit depth. The microphone, a Sennheiser MKH 8020 RF condenser (Solrød Stand, Denmark), was placed within 8 cm of the singing males. Audio recordings were processed with Adobe Audition CC 2020 (San Jose, CA, USA) and examined using Raven Pro v 1.6.1 (Cornell Lab of Ornithology). Data analysis was performed in Microsoft Excel (Redmond, WA, USA) and DataGraph software (Chapel Hill, NC, USA).

Courtship songs were recorded by placing a female in a cage with the male, placing the cage in a dimly lit anechoic room, and allowing the insects to interact overnight. Two different males were used for capturing courtship songs. The same female was used for both sessions.

Acoustic terminology follows Baker and Chesmore (2020): a unit of sound produced by one closing stroke of the cricket tegmina is called a syllable; syllables are grouped into short echemes which are organized into calling bouts. Echemes and calling bouts were selected either manually or using a band limited detector in Raven Pro 1.6.1. The detector settings for selecting echemes were minimum frequency = 5.5 kHz, maximum frequency = 9 kHz, minimum duration = 0.60372 s, maximum duration = 600.00363 s, minimum separation = 0.10449 s, minimum occupancy (%) = 18.0, SNR threshold (dB) = 18.0, block size = 9.99619, hop size = 1.99692, and percentile = 10.0. The detector used selects the echemes very accurately. All selections were inspected to make certain that all echemes were selected and that the selection boundaries were accurate. A pause lasting 30 seconds or longer was used to differentiate one calling bout from the next. Comparisons of means were performed on Log10 transformed data due to significant skewness of the raw data with *t*-tests performed in Microsoft Excel 2016 using the data analysis add-on.

Results

The calling songs of *A. walkeri* are composed of calling bouts that average 17.1 ± 14.5 minutes (range from 1.18–121.10 minutes) (n = 5 individual insects, 395 calling bouts). The calling bouts are broken into echemes that average 7.132 s (CI (confidence interval), 3.221–15.792) (range 0.263–594.442 s) (n = 5, 34,039). The intervals between echemes (the echeme intervals), average 0.881 s (CI, 0.375–2.069) (range 0.104–39.59 s) (n = 5, 33,642) (Fig. 1A). Each echeme begins at a low amplitude, crescendos rapidly, and remains at the maximum amplitude for the remainder of the echeme (Fig. 1B). The power ratio of the first few syllables to those of the main portion of the echeme is ~1:10 (11 dB FS).

Calling song characteristics varied significantly when the cricket was singing in bright sunlight versus darkness, with echeme intervals being longer in sunlight and echemes being longer in darkness. However, calling bouts do not differ between sunlight and darkness (Table 1). Temperature readings in the sunlight coming through the windows were within ±1.5 °C of those taken in the shade in the same room.

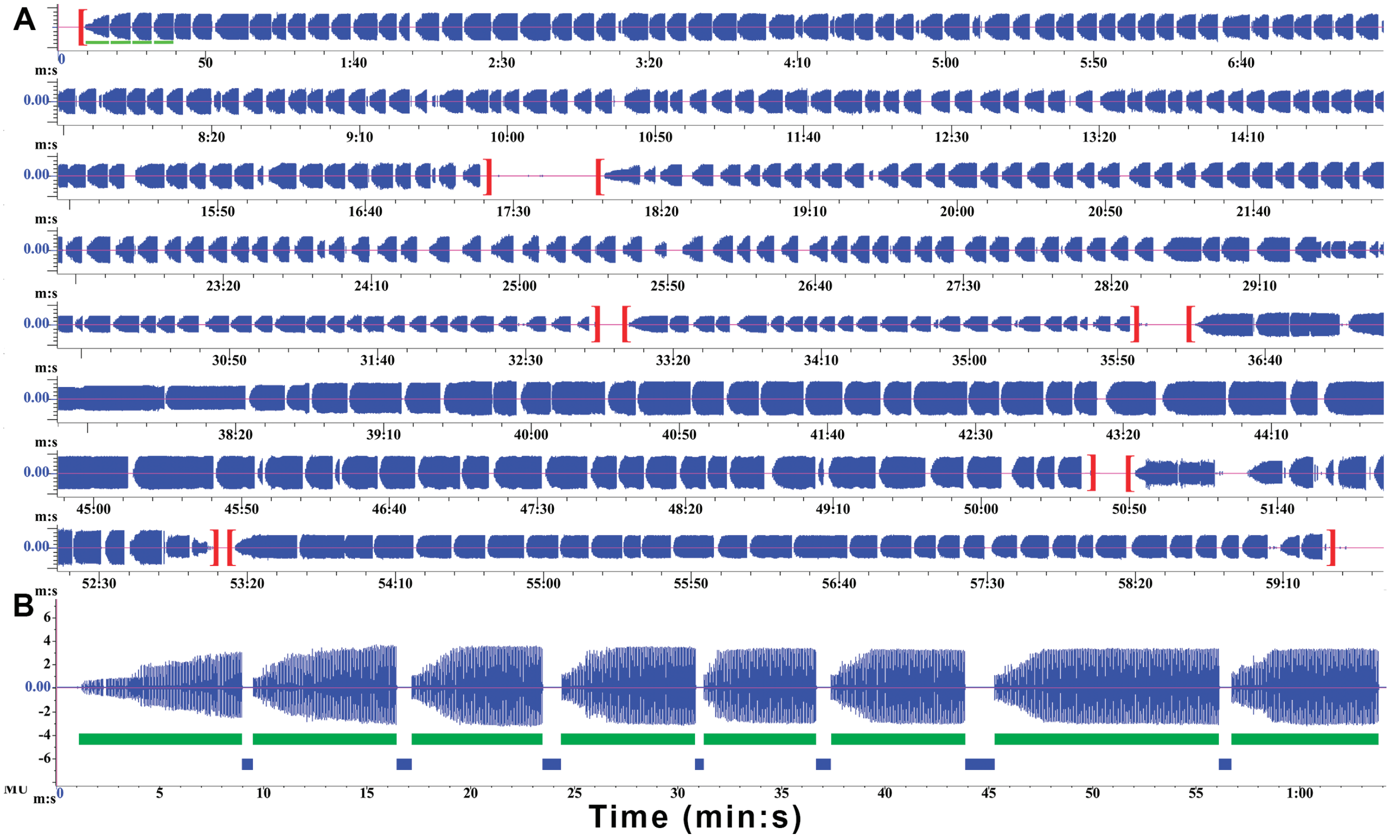

Fig. 1. A. Oscillogram showing the structure of the calling songs of *A. walkeri.* Calling bouts are boxed by red brackets, and echemes are underlined with green bars. The oscillogram shows the varying lengths of the calling bouts, echemes, and echeme intervals. **B.** Time expanded detail of the first minute and five seconds of **A**, showing echemes underlined with green bars and echeme intervals underlined with blue bars. The time scale for both oscillograms is minutes:seconds.

The trilling character of the calling song comes from the individual syllables of the echemes. Syllables are produced on the closing stroke of the male's tegmina, with the opening stroke being mostly silent (Walker and Carlysle 1975) (Fig. 2). The opening stroke does show that the file teeth graze over the scrapper as the tegmina are moved laterad at a varying rate of speed during the opening stroke. The tegmina accelerate from rest to a rapid rate then slow down, pausing briefly before the closing stroke. At 25.0°C, the closing stroke (syllable) is 17.26 ± 1.48 ms, the opening stroke is 20.42 ± 2.21 ms, the carrier frequency is 7.93 ± 0.58 kHz, and the syllables per second are 26.52 ± 0.63 (n = 2, 100). Combining my data with that from Thomas J. Walker's data (SINA. 2020. Singing Insects of North America [https://sina.orthsoc.org/529a.htm]), the trend line for carrier frequency vs syllable per second was calculated to be y = 0.15436× + 3.6269, $R^2 = 0.823$ (n = 15, 51) (Fig. 3).

Table 1. *Allonemobius walkeri* calling song characteristics in sunlight and darkness; *t*-test analysis showed a statistically significant difference, with echeme interval lengths being longer in sunlight and echeme lengths being longer in darkness. Calling bouts lengths did not differ between the treatments (n includes songs from two individuals recorded in both sunlight and darkness; statistics were performed on Log_{10} transformed data).

Treatment	mean	+CI	-CI	n	p
Echeme interval sunlight (s)	0.9630	0.9906	0.9362	2003	<0.00001
Echeme interval dim/dark (s)	0.5418	0.5611	0.5230	1079	
Echeme duration sunlight (s)	6.4040	6.6032	6.2108	2027	<0.00001
Echeme duration dim/dark (s)	13.1947	14.1172	12.3325	1099	
Calling bout sunlight (min)	12.9122	15.4099	10.8193	85	0.6582
Calling bout dim/dark (min)	12.3509	13.5332	11.2720	310	

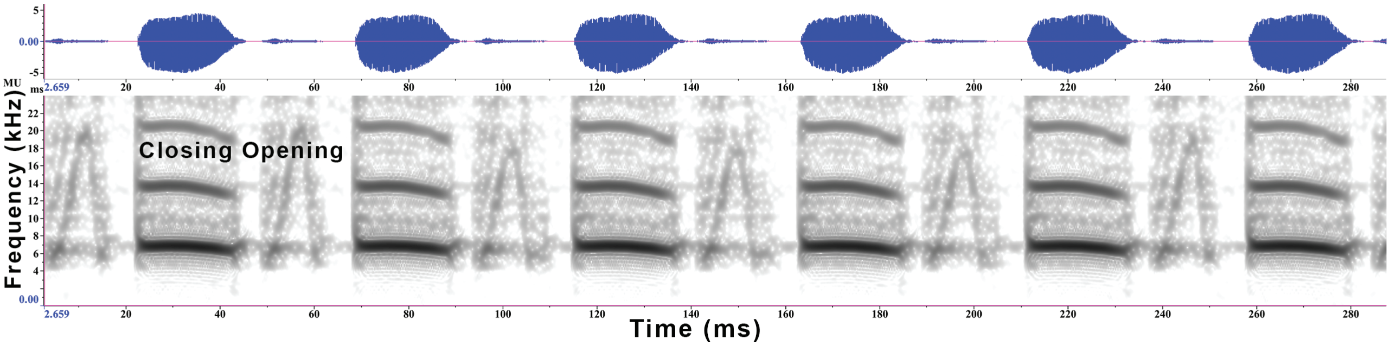

Fig. 2. Oscillogram and audio spectrogram of the calling song of *A. walkeri* showing the closing and opening strokes of the male's tegmina. The closing stroke produces a loud syllable, and the opening stroke is nearly silent but audible when the microphone is close to the singing cricket. Time is in milliseconds.

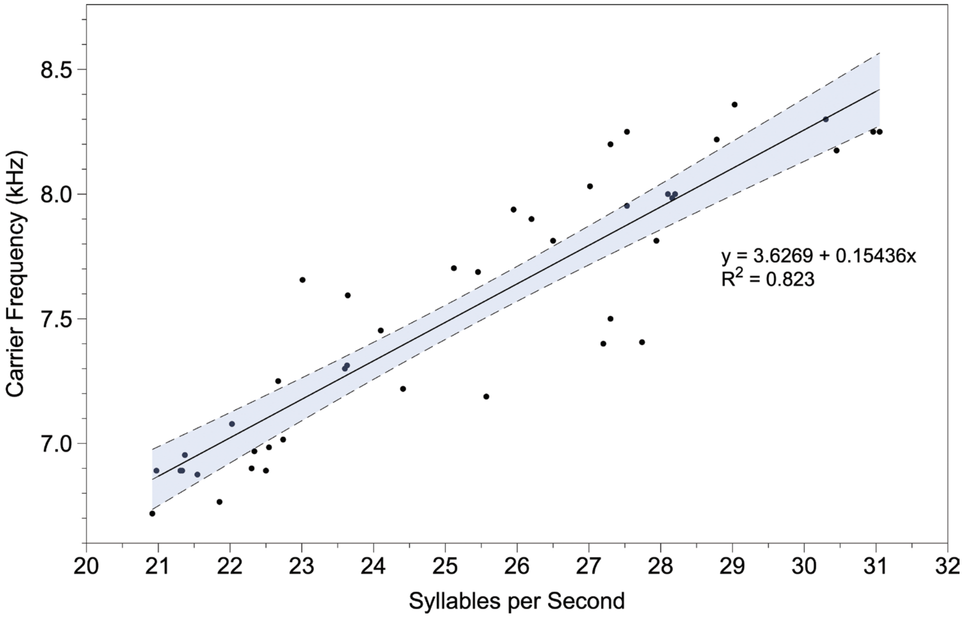

Fig. 3. Graph and regression line with 95% confidence interval of carrier frequency (kHz) versus syllables per second for the calling songs of *Allonemobius walkeri* (n = 15 individual, 51 echemes). Created from combining my data with that of Dr. TJ Walker, SINA 2020.

The courtship song of this species is different from their calling song and is similar to the courtship songs of other *Allonemobius* species, with some similarities to the courtship songs of *Gryllus pennsylvanicus* (Burmeister 1838) and *Gryllus veletis* (Alexander and Bigelow 1960) (Burmeister 1838, Alexander and Bigelow 1960, Alexander 1961). The courtship song of *A. walkeri* is composed of soft, rolling sounds with numerous soft chirps and occasional loud chirps (Alexander and Thomas 1959, Ewing and Hoyle 1965) (Fig. 3). There is no particular pattern to the courtship songs, which can proceed for many minutes within hours-long acoustic sessions (Zuk et al. 2008) and are accompanied by long bouts of calling songs. The shorter, softer chirps of a courtship song average 8.73 ± 3.33 ms at 6.543 ± 0.209 kHz and the longer, louder chirps (which are more like the chirps of calling songs) average 17.48 ± 2.74 ms at 6.660 ± 0.148 kHz (n, 272, at 23.5°C). The syllable rate of the soft and loud chirps varies considerably during delivery. The courtship song's rolling quality appears to be achieved by the male cricket enhancing the sounds made by the tegmina during the opening stroke (the softer, fainter traces in Fig. 4) (Alexander 1961). During an 11.7-hour session, a male sang courtship songs for 2.9 hours interspersed in 6.6 hours of calling songs (Fig. 5). To further demonstrate the difference in the rhythm and character of *A. walkeri's* courtship song in comparison to its calling song, Figure 6 shows both song types at the same time scale.

Discussion

Identification of field recordings of rare cricket species, whether obtained in person or autonomously, can be aided by the existence of reference materials or detailed descriptions of their calling songs (Riede 2018). The only available reference describing the calling songs of *Allonemobius walkeri* is by Howard and Furth in 1986. Having extensively recorded the calling songs of several male *A. walkeri*, I was able to determine the finer details of their songs. I found that the calling songs are composed of echemes of varying lengths that are arranged into calling bouts that also vary in length. Each echeme is separated from the next by an echeme interval of varying length. I also found that there is a significant ef-

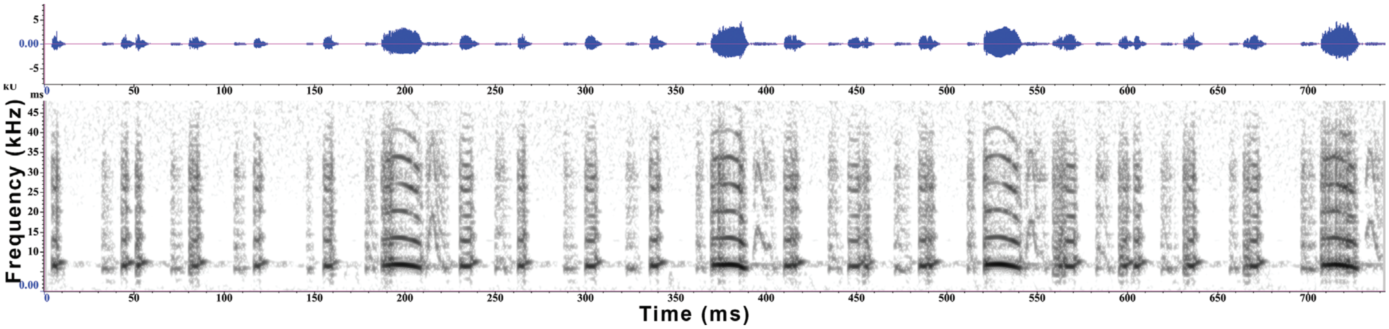

Fig. 4. Detail of courtship song of *A. walkeri*. The spectrogram shows the random nature of the syllables in both length and loudness of the short, softer and long, louder chirps, as well as the fainter, random, opening stroke sounds that create the rolling nature of these songs. Time is in milliseconds.

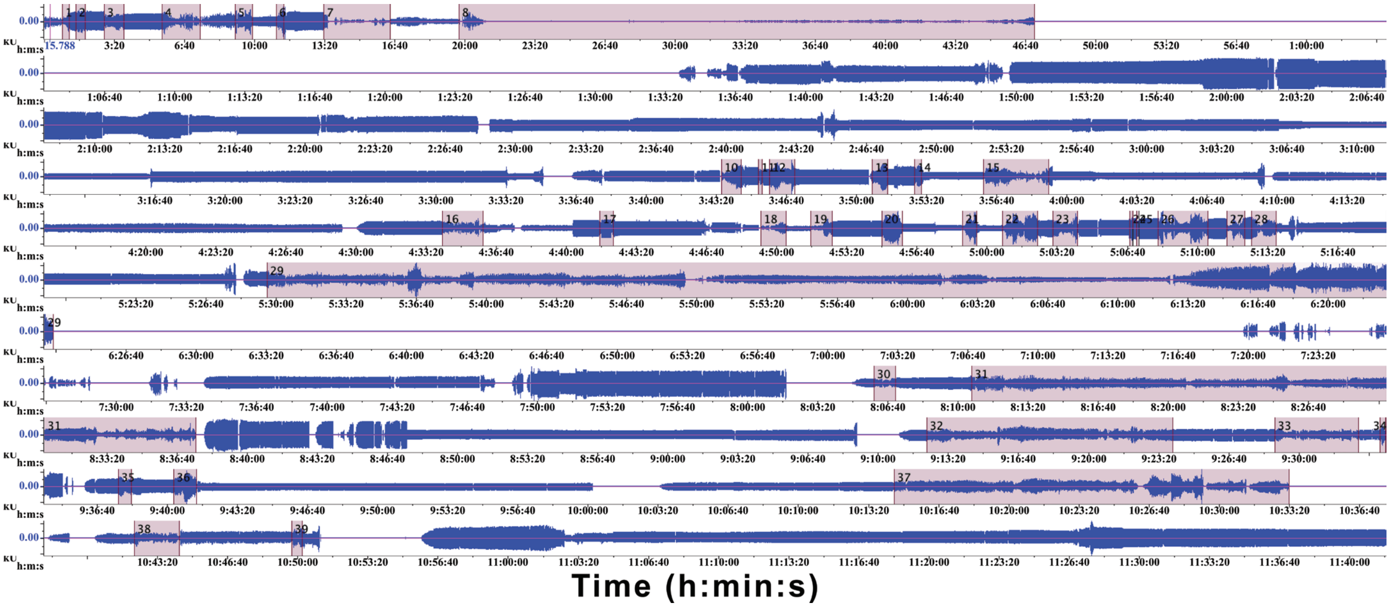

Fig. 5. Oscillogram of the courtship song of *A. walkeri*. The oscillogram shows an entire courtship display with courtship songs (highlighted) interspersed with calling songs and periods of silence. (The amplitude of the songs varies greatly as the cricket moves and changes position relative to the microphone.) Time is hours:minutes:seconds.

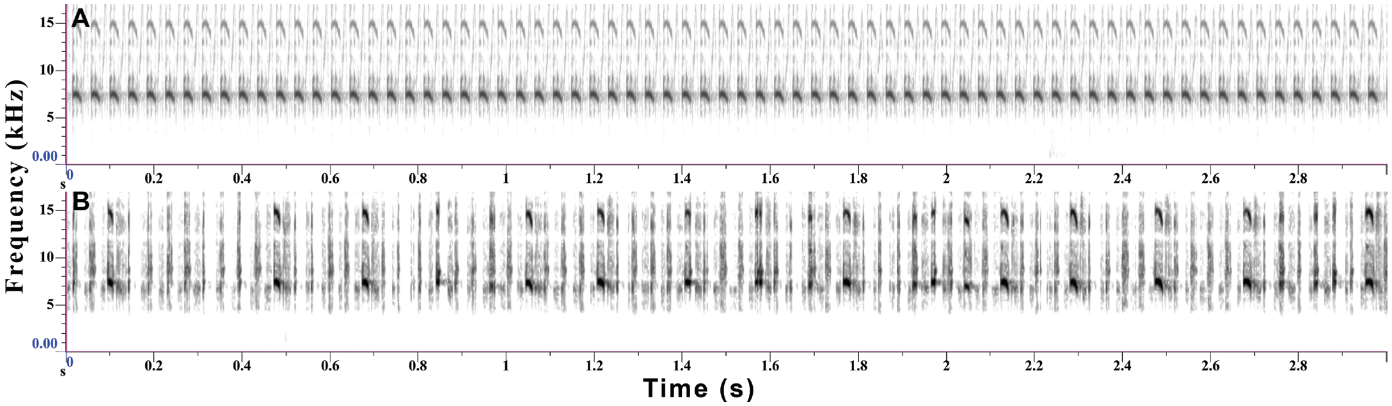

Fig. 6. A. Spectrogram of three seconds of calling song. **B.** Spectrogram of three seconds of courtship song. This comparison shows the distinct difference in the rhythm and character of the two song types of this species.

fect of sunlight on the lengths of the echemes (longer in darkness) and echeme intervals (longer in sunlight) that does not appear to be the result of temperature effects. Further research into the effects of bright light or sunlight (with a minimization of temperature differences) on the singing behavior of ground crickets is needed to determine the underlying reasons for these observed effects on song structure.

I found that the courtship songs of *A. walkeri*, as with the courtship songs of other Nemobiinae, are composed of random brief and long chirps accompanied by rolling, softer sounds. Examination of the audio spectrograms seems to support the conclusion that these softer sounds are the result of the male crickets enhancing the sounds made by the tegmina during the opening stroke. High-speed videography or Doppler-laser vibrometry would be needed to determine exactly how the cricket is creating these sounds.

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I thank the Potomac Valley Audubon Society for granting permission to study this species at their preserve and for the permit to collect specimens. I am grateful to Dr. Thomas J. Walker, Professor Emeritus, University of Florida, for his generous sharing of his knowledge and data. I am also thankful to the Orthoperists' Society for providing funding to publish this paper and to Dr. Klaus-Gerhard Heller and Tony Robillard for invaluable improvements to this manuscript. I would like to thank David H. Funk for numerous conversations about this species and for sharing his data with me.

All audio recordings associated with this project are archived at the Macaulay Library, Cornell Lab of Ornithology, ML numbers 305704–305815.

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Revision of the tusked bush-crickets (Tettigonioidea: Pseudophyllinae: *Dicranostomus*) with description of the hitherto unknown sexes

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Abstract

The genus *Dicranostomus* belongs to the very few Orthoptera with elongated mandibular processes, here called tusks. However, it is also one of the least studied genera from whose two species only one female and two males have been known so far. We present additional material from both species and sexes that confirms that the males have the relatively longest (2–2.8 times pronotal length) tusks of all Orthoptera. Surprisingly, the females of both species differ in this character: females of *D. monoceros* have tusks and those of *D. nitidus* do not. Based on a comparison with other species, we hypothesize that the species use holes that males can defend and use to monopolize the females.

Keywords

Eucocconotini, mandible, Peru, South America, taxonomy, weapon

Introduction

In many species of animals, males possess elaborate structures used mainly in intraspecific fights over access to females (Emlen 2008). Among mammals, well-known examples include antlers in deers, horns in bovids, and tusks in elephants. In many, but not all, of these species, the weapons are also found in a reduced version in females. In insects, impressive examples of such structures are observed, e.g., in Lucanidae (stag beetles; see Emlen 2008 for other species).

Such weapons are relatively rare among Orthoptera. There are some species where the mandibles are enlarged only in males (see review in Field and Deans 2001, Gorochov 2012), but only in very few species are these special structures found to be used (or, with good reasons, assumed to be used) in the context of antagonistic intraspecific contacts. Males with tusks are found in five species of the family Anostostomatidae [see Field and Deans 2001; in the New Zealand tusked wetas, a monophyletic group of three species in two genera (Trewick and Morgan-Richards 2004) and in two South African species, in *Libanasidus vittatus* (Kirby, 1899) and in *Libanasa capicola* (Péringuey, 1916)]. In the superfamily Tettigonioidea, there are two genera with tusks. Three species of the Neotropical genus *Listroscelis* Serville, 1831 (Listroscelidinae) have one asymmetrical tusk on the left mandible only (Fialho et al. 2014), while the two known species of the Neotropical genus *Dicranostomus* Dohrn, 1888 (Pseudophyllinae) have a tusk on both mandibles. *Dicranostomus nitidus* Brunner von Wattenwyl, 1895, so far known only from two males, has the relatively longest tusks of all Orthoptera, ranging from 2 to 2.7 times the pronotal length (Brunner von Wattenwyl 1895, Gurney 1950). The second species was, until recently, known from a single female that, interestingly, also bears tusks, but which are distinctly shorter than that of male *D. nitidus*. Having obtained some more specimens of this fascinating genus, including the missing sexes of both species, we herein revise the genus and provide a review of all available data.

Methods

All specimens were dried, pinned, and photographed using a CANON EOS 1200D. Photos of cerci and mirrors were taken using a dissecting microscope (OLYMPUS SZ Binocular Stereo Zoom Microscope) and a digital camera (SONY Cyber-shot DSC-P120). The inter-tooth distances were measured as the mean between every eleven teeth (ten intervals), starting at the anal end, using ADOBE PHOTOSHOP Elements 6.

The specimens, collected between 2013 and 2018, were obtained from a trader with an export license (http://gerfor.regionloreto.gob.pe/dublincore/biblioteca/descargar/4269/4500000100020_7.PDF).

Depositories.—

CH	Private collection of K.-G. Heller;
C_Helb	Private collection of M. Helb;
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;
MZPW	Polish Academy of Science, Museum of the Institute of Zoology Warszawa, Poland.

Results

Taxonomy

Family Tettigoniidae Krauss, 1902
Subfamily Pseudophyllinae Burmeister, 1838
Tribe Eucocconotini Beier, 1960

Genus *Dicranostomus* Dohrn, 1888

Type species: Dicranostomus monoceros Dohrn, by original monotypy

Redescription.—[based on Dohrn 1888 (in Latin), Beier 1960 (in German)].

Medium sized (body length 2.5–4.0 cm), yellowish-brown animals (habitus; Fig. 1). Head as broad as pronotum or broader. Frons shiny, smooth. Fastigium frontis elongated, curved or straight. Fastigium verticis compressed, narrow, with longitudinal furrow. Antennae very long, scapus unarmed. Male mandible at base with a very long, horizontally directed tusk (Fig. 2). Pronotum smooth or slightly granulated, with delicate anterior and medially deeply incised posterior sulcus; metazona flat, only slightly longer than mesozona, laterally no edges, humeral sinus very weak; side lobes longer than high, ventrally nearly straight and finely edged, caudally weakly ascending, anterior edges even more broadly rounded than the also broadly rounded posterior edges. Openings of the tympanic organ in the fore tibia directing dorsally, slit-like. Auditory prothoracal spiracle quite small, just below the respiratory spiracle. Tegmina just surpassing abdomen, gradually becoming narrow, costal area with wide-meshed veins, Sc (subcosta) and R veins separated. The male mirror on both the left and right wing is translucent (Fig. 3). Teeth in stridulatory file regularly spaced (Fig. 4). Rs (radius sector) arising at the beginning of the apical quarter, media (M) and Sc stalked. Alae roundish, shorter than tegmina. Prosternum with two close spines between prothoracic legs. Mesosternal lobes pointed. Metafurcal pit deep. Middle coxae two-pronged. All femora ventrally armed. Inner genicular lobes of mid and hind femora with spine. Fore tibiae dorsally at the inner edge with a series of small humps. Mid tibiae dorsally with one to three spines internally. Supraanal plate triangular or rounded. Male cerci thick, nearly straight, with subapical spine and apical process (Fig. 5). Male subgenital plate distally narrowed, styli rod-like. Female subgenital plate transverse, slightly incised. Ovipositor short, relatively broad and slightly up-curved, at the upper edge very delicately crenulated (Fig. 6).

Distribution.—South America, Peru (Fig. 7).

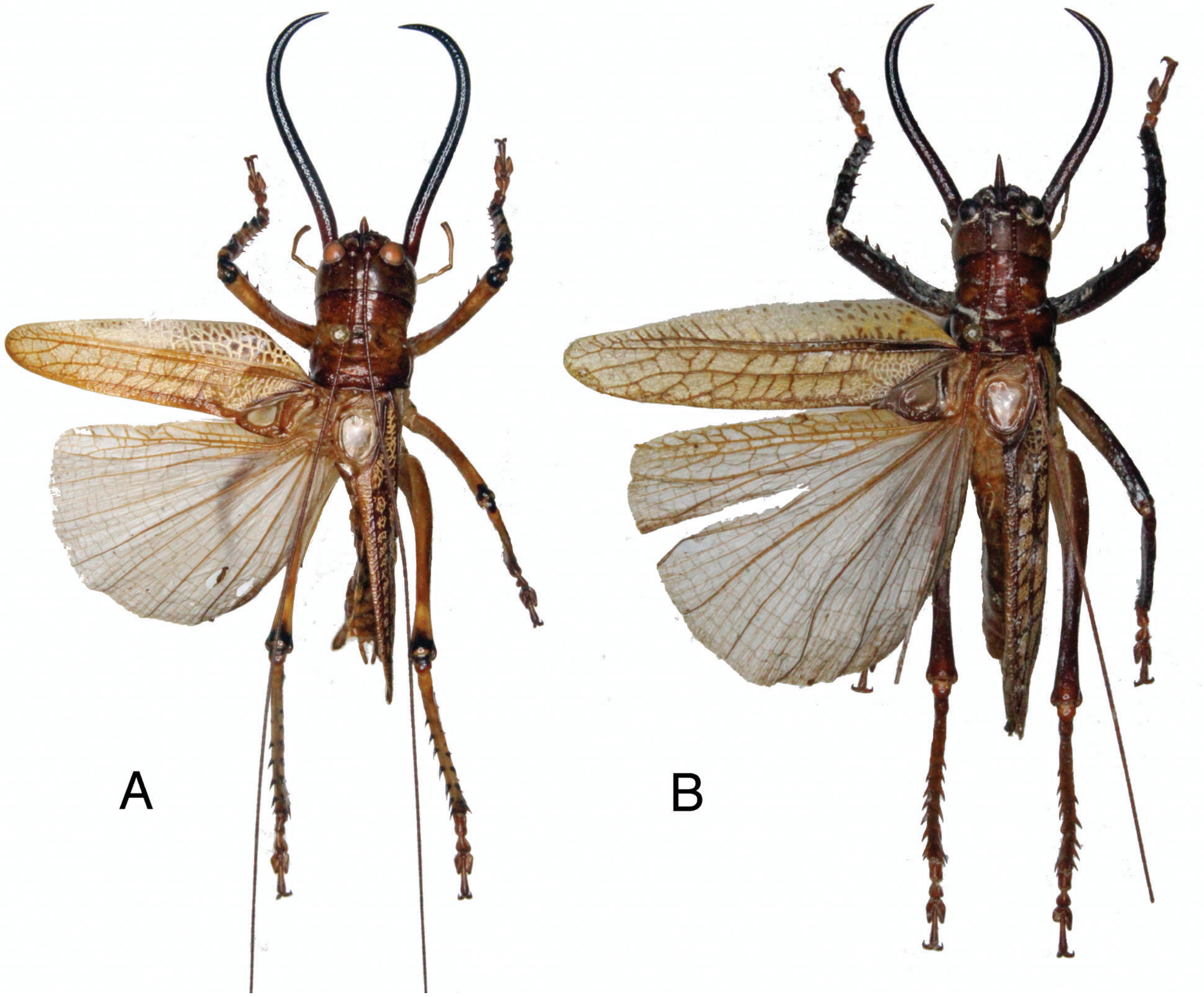

Fig. 1. Male habitus of **A.** *Dicranostomus monoceros* and **B.** *D. nitidus* (same scale for both figures).

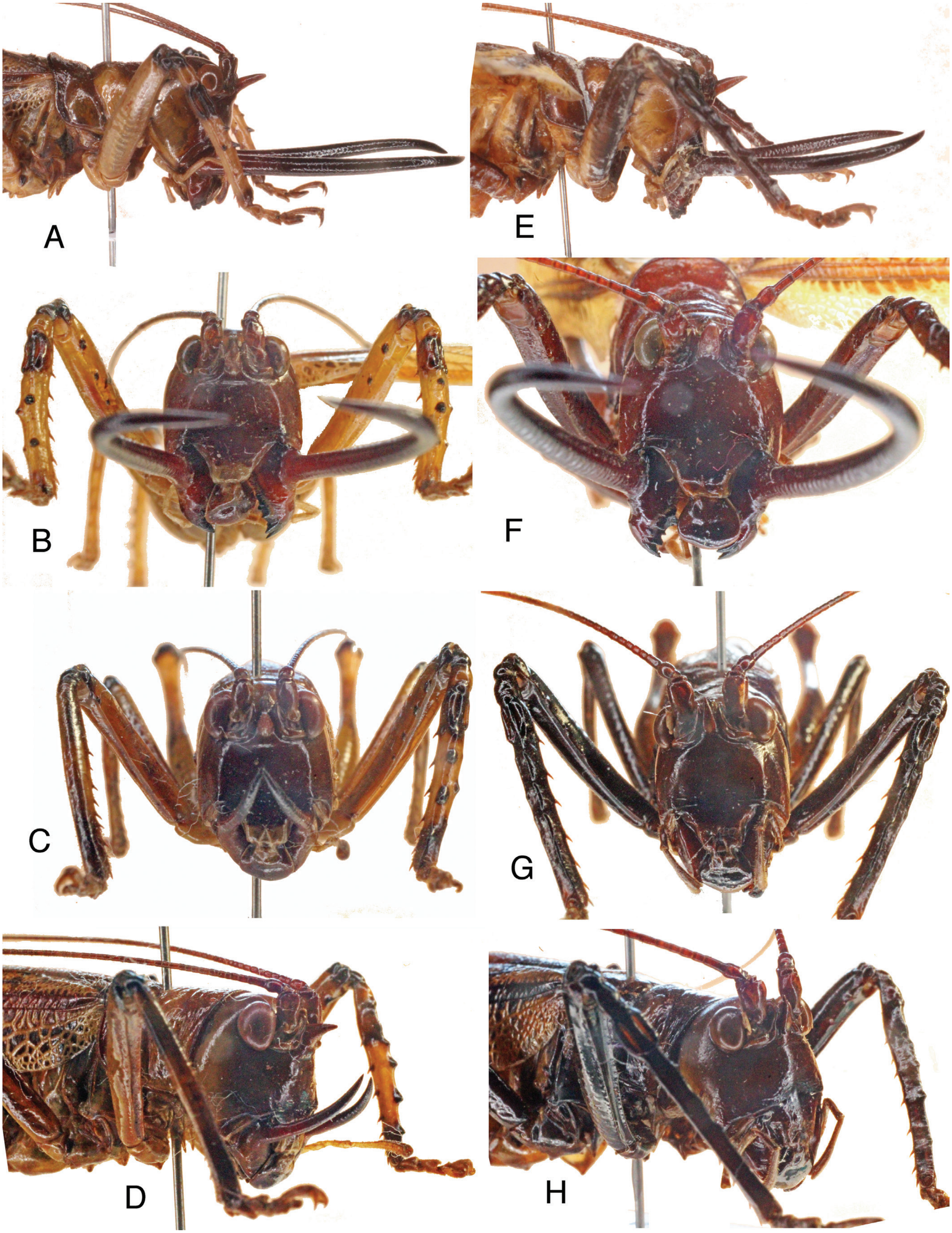

Fig. 2. Morphological details of *Dicranostomus monoceros* (**A–D**) and *D. nitidus* (**E–H**; same scale for corresponding figures). **A, E.** Male head lateral; **B, F.** Male head frontal; **C, G.** Female head frontal; **D, H.** Female head semilateral.

Key to species (after Brunner von Wattenwyl 1895)

1 Pronotum weakly granulated. Knees and spines on legs black .... *D. monoceros*

– Pronotum smooth, glossy. Spines on legs and knees same color as leg .... *D. nitidus*

Dicranostomus monoceros Dohrn, 1888

Figs 1A, 2A–D, 3A, B, 4A, 5A, 6A

Dicranostomus monoceros Dohrn, 1888: 362

Holotype.—PERU • ♀; Cumbasi Peruviae ad Huallagam; [Cumbaza]; MZPW. [photos in Cigliano et al. 2021].

Material examined.—PERU • 2♂; San Martin Region, Prov. Rioja, Nueva Cajamarca; 10 Nov. 2016; local collector; C_Helb8771-C_Helb8772 • 1♀, 1♂; San Martin Region, Prov. Rioja, Nueva Cajamarca; Mar. 2018; local collector; C_Helb8773-C_Helb8774 • 2♂; San Martin Region, Prov. Rioja, confluente Altomayo river/Naranjos; 8 Mar. 2018 & 25 Apr. 2018; local collector; C_Helb8775, ♂ C_Helb8776.

Remarks.—Up to now, the species was known only by the female holotype. In one female (C_Helb8773), the right foreleg is irregularly developed. Its tibia does not have a tympanic organ or dorsal black tubercles (Fig. 2).

Redescription.—General characters as genus.

Male. Fastigium frontis elongated horizontally (Fig. 2), mandibles each with one long (2.1–2.8 times as long as pronotum) process (tusk) (Figs 1, 2; Table 1). Pronotum weakly granulated. Fore and mid femora ventrally with 3 spines, hind femora with 4 spines at anterior edge. Fore tibiae dorsally with 2–3 large, black, blunt spine-like tubercles at the anterior and two small tubercles at the posterior edge, ventrally with ca. 6 spines on both sides, mid tibia dorsally with 1–2 spines on posterior edge, ventrally with ca. 6 spines on both sides, hind tibia with ca. 8 spines on all edges, the dorsal larger than the ventral spines. Mirror cell in left tegmen triangular with broadly rounded distal tip, on right tegmen larger, subquadratical (Fig. 3). Stridulatory file on lower side of left tegmen with ca. 130 regularly spaced teeth (inter-tooth interval 20–23 µm; Fig. 4; n=1 file). Supraanal plate transverse, distally rounded. Subgenital plate elongated, with ca. 1 mm long styli. Cerci with internal subapical spine and blunt apical process directed very slightly inwards.

Female. General characters as genus and male. Mandibles each with one long (0.8–0.9 times as long as pronotum), slightly upcurved process (tusk). Subgenital plate transverse, at the end straightly cut and distally slightly notched in the middle.

Coloration. Head with tusks and pronotum chestnut (tusks becoming darker towards the tips); legs yellowish, but knees, tympanic organ and tubercles in the fore tibia and larger spines in all legs black. Tegmina as in *D. nitidus* (see below). In some animals, the anterior and central lower parts of the paranota are brighter and more yellowish than the other parts.

Measurements.—See Table 1.

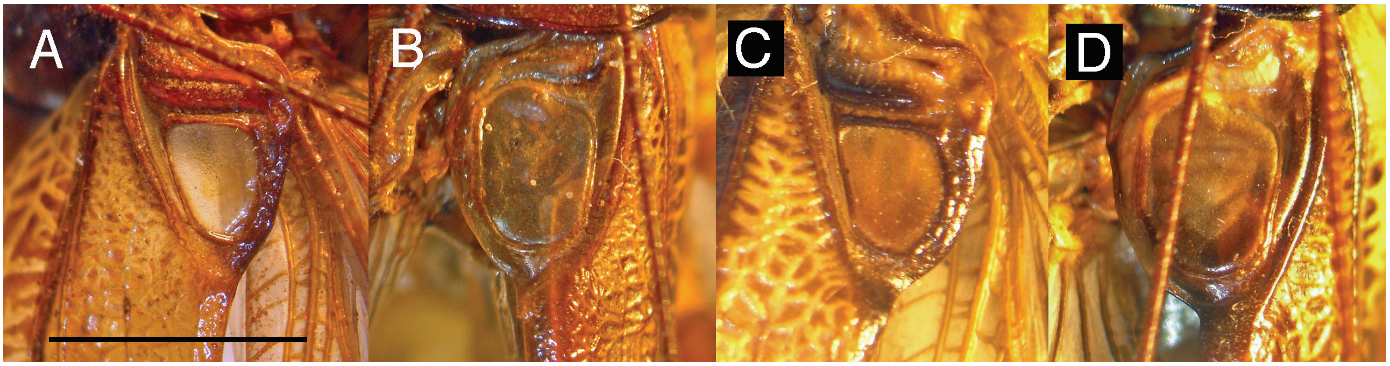

Fig. 3. Mirror cells of *Dicranostomus monoceros* (**A, B**) and *D. nitidus* (**C, D**). **A, C.** Left tegmen; **B, D.** Right tegmen. Scale bar: 5 mm.

Table 1. Measurements of males and females of both species of *Dicranostomus* (*data from Beier 1960).

Species	Specimen	Sex	Measurements (in mm)								
	#		body	body + tusk	pronotum	fore femur	hind femur	tegmen	antenna	tusk	ovipositor
D. monoceros	type*	♀	28		6.5	10.5	19	27	-	6	15
	C_Helb8773	♀	32	35	6.5	10.5	16.5	23	120	5.5	15.5
	C_Helb8771	♂	27	41	6	10	14.5	20	95	16	
	C_Helb8772	♂	32	44	7	11	16	21.5	95	15	
	C_Helb8774	♂	29	44	6	10.5	15.5	22	95	16.5	
	C_Helb8775	♂	27	40	6.5	10.5	16	21	-	16.5	
	C_Helb8776	♂	28.5	40	6.5		15.5	21	80	17	
D. nitidus	type*	♂	30		7	11.5	20	22	-	14	
	Gurney 1950	♂	35	58	7.5	12	19	26	-	20	
	CH4220	♂	38	53	7.5	12	20.5	27	-	18	
	C_Helb8769	♂	36	47	7.5	12	19.5	26	72	13.5	
	C_Helb8770	♀	33	-	7.5	12	20	28.5	100		17.5
	C_Helb8777	♂	36	49	7.5	13	19	27.5	68	17	

Dicranostomus nitidus **Brunner von Wattenwyl, 1895**

Figs 1B, 2E–H, 3C, D, 4B, 5B, 6B

Dicranostomus nitidus Brunner von Wattenwyl, 1895: 180

Holotype.—PERU • no details; ISNB. [photos in Cigliano et al. 2021].

Published record.—PERU • 1♂; Department of Huanuco, Fundo Sinchono, 37 miles east of Tingo Maria on the road to Pucallpa; 1700 m a.s.l.; 5 Aug. 1947; Jose Schunke leg.; (Gurney 1950).

Material examined.—PERU • 1♂; Oxapampa; Feb.–Apr. 1984; Rainer Marx leg.; CH4220 • 1♂, 1♀; Prov. Huanuco, Huanuco Road, between Huanaco and Tingo Maria, Malqui [Macora?] town, fog area [sic]; Aug. 2013; local collector; C_Helb8769-C_Helb8770 • 1♂; San Martin Region, Prov. Rioja, Nueva Cajamarca; Mar. 2018; local collector [assumed exchange of labels—see list for localities of *monoceros*]; C_Helb8777

Remark.—The species was known only by the male holotype and another male, described by Gurney (1950).

Reescription.—General characters as genus.

Male. Fastigium frontis elongated horizontally (Fig. 2), mandibles each with one long (1.8–2.7 times as long as pronotum) process (tusk) (Figs 1, 2, Table 1). Pronotum smooth. Fore and mid femora ventrally with 3–4 spines, hind femora with 4–6 spines at anterior edge. All tibiae ventrally with several spines on both sides; however, hind tibia ventrally only with few spines at tip of poste-

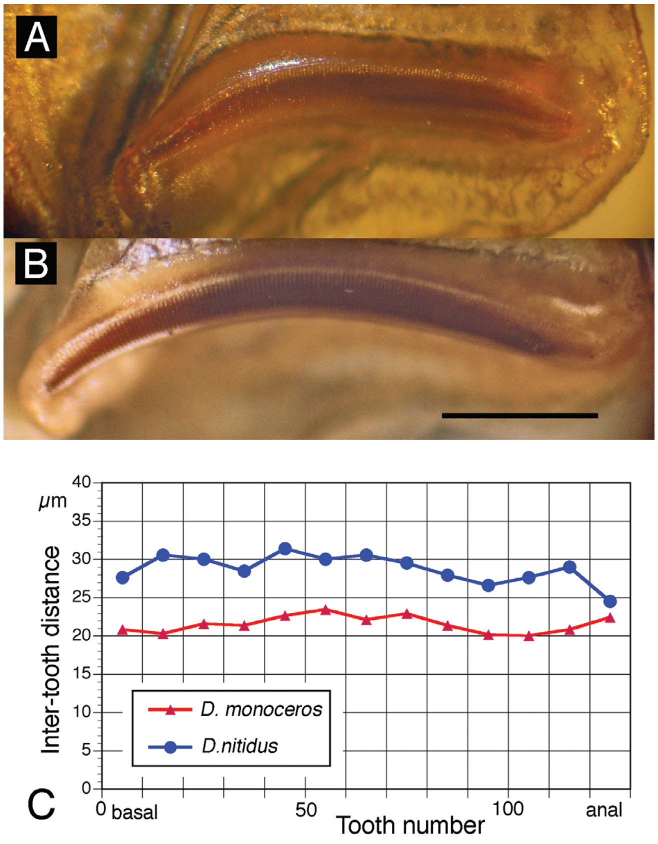

Fig. 4. Stridulatory files in *Dicranostomus*. **A.** *D. monoceros* (C_Helb8775); **B.** *D. nitidus* (CH4225); **C.** Inter-tooth distances (specimens as in **A**, **B**). Scale bars: 1 mm (**A**, **B**).

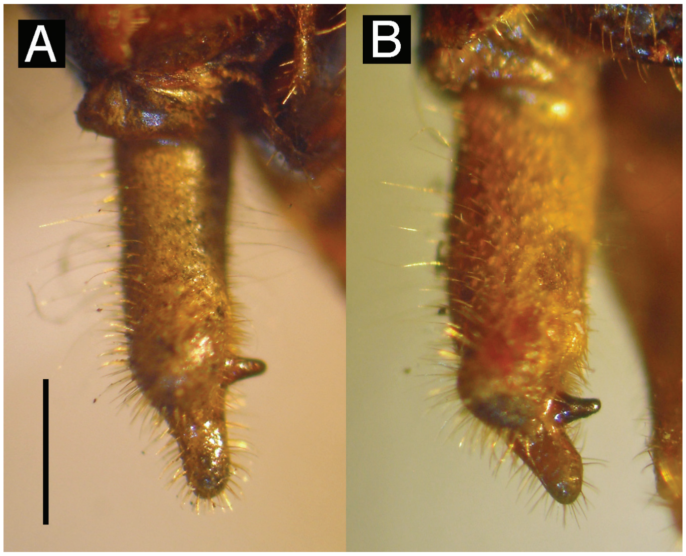

Fig. 5. Male cerci of **A.** *Dicranostomus monoceros* and **B.** *D. nitidus*. Scale 1 mm.

Fig. 6. Ovipositor of **A.** *Dicranostomus monoceros* and **B.** *D. nitidus* (same scale for both figures).

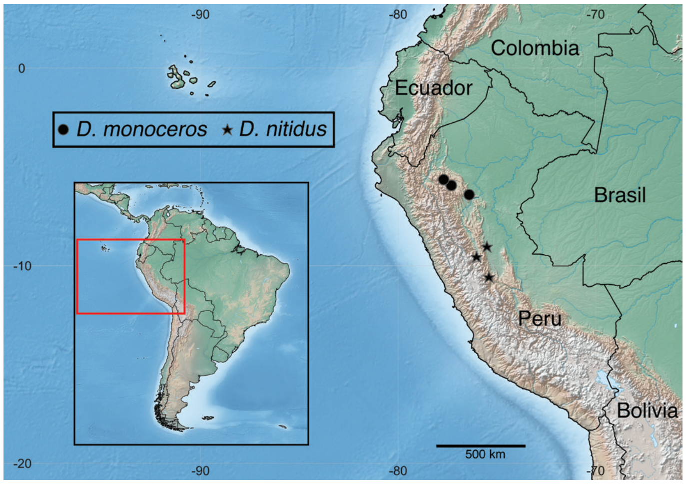

Fig. 7. Distribution map of *Dicranostomus* (all known localities; map based on SimpleMappr (Shorthouse 2010)).

rior edge. Fore tibiae dorsally with 4–5 blunt spine-like tubercles at the anterior edge, ventrally with ca. 6 spines on both sides, midtibia dorsally with 1–2 spines on posterior edge, ventrally with ca. 6 spines on both sides, hind tibia with ca. 8 spines on each edge, the dorsal larger than the ventral spines; however, ventrally only with few spines at tip of posterior edge. Mirror cells in both tegmina subquadratical; in the right larger than in the left (Fig. 3). Stridulatory file on lower side of left tegmen with ca. 130 regularly spaced teeth (inter-tooth interval 24–32 µm = tooth density ca. 30 mm^{-1}; Fig. 4; n=1 file), Supraanal plate transverse, distally rounded, or broadly cut off. Subgenital plate elongated, with ca. 1 mm long styli. Cerci with internal subapical spine and blunt apical process, directed inwards at an angle of about 40 degrees (Fig. 5).

Female. General characters as genus and male. Fastigium frontis elongated vertically (Fig. 2), mandibles without process (tusk). Subgenital plate transverse, at the distal end slightly and triangularly elongated and slightly incised in the middle.

Coloration. "Head, thorax and legs chestnut, the tibiae darker, the mandibular appendages practically black, palpi pale. …. tegmen with veins brown, cellules and membrane yellowish, much brighter toward base in costal area; wing with veins pale brown, membrane slightly fuscous" (Gurney 1950). However, other specimens (C_Helb8769, C_Helb8777) not chestnut, but more olive-brown with pro- and metazona of pronotum darker than mesozona or pronotum uniform.

Measurements.—See Table 1.

Discussion

The genus *Dicranostomus* belongs to the tribe Eucocconotini, which is part of the supertribe Pleminiiti Brunner von Wattenwyl, 1895 (Braun 2015) (or the subfamily Pleminiinae; Gorochov 2012). Within this tribe, the genus is most similar to *Gnathoclita* Haan, 1843 (see Gorochov 2012), with both genera having the "dorsal surface of anterior tibiae granular or with distinctive tubercles" (Cadena-Castañeda and Monzón-Sierra 2014). According to the key provided by these authors, males of the two genera are easily separable by their mouth parts: *Dicranostomus* males have tusks and *Gnathoclita* males have enlarged mandibles. The females, however, differ only in the presence of dorsal spine(s) on the middle tibia in *Dicranostomus*. Only *D. monoceros* females have tusks like their males. Possibly, both genera can also be separated by the presence of an elongated (either horizontally or vertically) fastigium frontis in *Dicranostomus.* Such a structure is not described nor figured for any *Gnathoclita (s.str.; sensu* Gorochov 2018) species [see *G. izerskyi* Gorochov, 2018, *G. peruviana* Carl, 1921 (Gorochov 2014), *G. laevifrons* Beier, 1960, *G. sodalis* Brunner von Wattenwyl, 1895, and *G. vorax* (Stoll, 1813) (Beier 1960)], although data for females are sparse.

Dicranostomus and *Gnathoclita* are also similar in the shape of their mirrors (compare Fig. 4 to figs 20, 21, 27, 28 in Gorochov 2018, and to fig. 7D in Hugel 2019) and—to a limited extent—in their stridulatory files. In tooth number, *Dicranostomus* (130 teeth) is situated between the two known *Gnathoclita* species (*G. vorax* c.101 teeth (Hugel 2019), *G. sodalis* 217 teeth (Montealegre-Z and Morris 1999)). The inter-tooth distances in both species (*G. vorax* 30 µm; *G. sodalis* 10 µm) correlate negatively with the carrier frequencies of their resonant songs (*G. vorax,* 8.8 kHz; *G. sodalis,* 16 kHz). From these data, it can be assumed that *Dicranostomus* males also sing in this audio range (but perhaps with each species at a different peak frequency) and that they can be located with unaided ears.

Unfortunately, no data are available concerning the function of the most distinctive structure of *Dicranostomus*: the tusks. These tusks are the longest found among Orthoptera in comparison to the male body size (measured relative to pronotal length) and are clearly longer than in the well-known tusked wetas (Table 2). In *Dicranostomus,* the tusks do not show any indication of being stridulatory structures, as documented for some wetas (Field 2001). However, although there are no observations of the use of the tusks, there are three lines of evidence that all point in the same direction. In his review about animal weapons, Emlen (2008) writes in the context of resource-defense or female-defense mating systems: "In a surprising diversity of taxa, these critical resources were burrows or tunnels where females lay eggs, and the especially defensible nature of burrows may have played an important role in favoring the evolutionary enlargement of weapons in these cases." In line with these conclusions, the three New Zealand orthopteran species with long tusks (see Table 1) all inhabit burrows in the ground or holes in trees (see Trewick and Morgan-Richards 2014 for a review). The tusked king cricket *Libanasidus vittatus* digs holes every night but may sometimes return to previously used holes (Bateman and Toms 1998). Also supporting these ideas, new behavioral observations in the genus *Gnathoclita,* sister to *Dicranostomus* (e.g., Gorochov 2012), have shown that *G. vorax* also inhabits the hollow dead stems of plants, with the males displaying "a form of mate guarding" (Hugel 2019). Thus, in our opinion, it is a plausible hypothesis that *Dicranostomus* inhabits holes, probably in plant material, and that the males defend these safe places against rivals using their tusks. Holes in plants are also used by other acoustically active species like frogs (e.g., the tree hole frog *Metaphrynella sundana*; Lardner & bin Lakim 2002). In *Disceratus* Scudder, 1869, a related genus, its low acoustically determined population density is used as an argument against male to male combat (Braun 2016). Thus, other reasons for

Table 2. Absolute and relative (compared to pronotum) tusk length in Orthoptera.

Species	Specimen(s)	Sex	Length (in mm) of			Tusk length / pronotum length	Source
			pronotum	hind femur	Tusk (range)		
D. monoceros	mean	♂	6.4	15.5	16.2 (15.17)	2.5	this paper
	mean	♀	6.5	17.8	5.8 (5–6)	0.9	this paper
D. nitidus	mean	♂	7.4	19.6	17.1 (18–27)	2.2	this paper
Motuweta isolata	holotype	♂	15	38.0	26.0	1.7	Johns 1997
	paratype	♂	10	28.0	9.0	0.9	Johns 1997
	mean	♂	12.5	33.0	17.5	1.4	Johns 1997
Motuweta riparia	mean	♂	7.7	24.0	6.4 (3–12)	0.8	Gibbs 2002
Anisoura nicobarica	holotype	♀	4.6	10.6	0.0		Ander 1933
	syn. *monstrosa*	♂			6.0	c. 1.3	Salmon 1950
Libanasidus vittatus	mean	♂	9	21.5	7.5 (7–8)	0.8	Péringuey 1916
Libanasa capicola	holotype	♂		17.0	7.0	0.8	from figure; Péringuey 1916

the tusks should not be excluded. Completely unknown, however, is the function of the female tusks in *D. monoceros*. Females of *D. nitidus* do not possess tusks, but they have a strongly elongated fastigium frontis, as found in both sexes of *D. monoceros* and in *D. nitidus* males. Gwynne (2001) speculated on the probability of female-to-female interactions in *D. monoceros*, and certainly the access, possession, and defense of holes may be important for females as well. Unfortunately, data to confirm or deny this are missing.

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A new subspecies of the mantis *Hierodula patellifera* (Mantodea: Mantidae) from the Daito Islands, the Ryukyus, Japan

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Abstract

A new subspecies of the Asian mantis *Hierodula patellifera* (Audinet-Serville, 1839), *Hierodula patellifera daitoana* **ssp. nov.**, is described based on specimens collected from the Daito Islands, the Ryukyus, Japan. This new subspecies is distinguished from the nominotypical subspecies *H. patellifera patellifera* in adulthood by the relatively larger body size, the larger number of antennal segments, the presence of a white marking along the dorsal-inner surface on the procoxa, and marginal spines of the procoxa comprising two large and several small tooth-like projections.

Keywords

Dictyoptera, Kita-daito-jima Island, Minami-daito-jima Island, nymph, Okinawa, taxonomy

Introduction

The mantis species *Hierodula patellifera* (Audinet-Serville, 1839) (Mantodea: Mantidae) is widely distributed in the Oriental and eastern Palearctic regions, including India, Nepal, China, Taiwan, Korea, Japan, Vietnam, Thailand, Malaysia, Singapore, New Guinea, Java, Sumba, the Philippines, Italy, France, and Hawaii (Fig. 1; Ehrmann 2002, Leong 2009, Ehrmann and Borer 2015, Patel and Singh 2016, Mukherjee et al. 2017, Battiston et al. 2019, Moulin 2020). In Japan, it is distributed in Honshu, Shikoku, Kyushu, and the Ryukyus (Nakamine 2016, Oshima et al. 2020). It is readily distinguished from other members of the genus by the marginal spines of the procoxa, which are two to five in number, white or yellow, well defined, and tear drop shaped (Leong 2009, Zhu et al. 2012, Chatterjee and Srinivasan 2013, Majumder et al. 2015, Shcherbakov and Anisyutkin 2018). In this species, a single subspecies, *H. patellifera manillana* Giglio-Tos, 1912, was formerly recognized as part of the Philippine population by Giglio-Tos (1912) and Beier (1935), although no justification for this designation was provided. However, this subspecies has been considered a synonym of *H. patellifera* by Ehrmann (2002) and subsequent authors (Nakamine 2016, Otte et al. 2020). At present, *H. patellifera* has no infraspecific taxa.

The Daito Islands consist of five oceanic islands located in the Philippine Sea southeast of the main island of Okinawa, Japan. Among these islands, those of Kita-daito-jima and Minami-daito-jima, which are populated by humans, lie approximately 360 km from the nearest neighboring island, Okinawa-jima, and provide a unique isolated ecosystem populated by several endemic species (Shimizu 2003).

During an investigation of the mantis fauna of the Daito Islands between 2015 and 2018, I collected several individuals of an indeterminate *Hierodula* species from both Kita-daito-jima Island and Minami-daito-jima Island. Detailed observations of the male genitalia indicated that these individuals were clearly specimens of *H. patellifera* (Fig. 2); however, other morphological characters, including the relative length of the body, number of antennal segments, coloration of the procoxae, and shape of the marginal spines, were distinctly different from those of other populations of the species. Eventually, I considered the possibility that the Daito Islands population is a distinct subspecies.

In the present paper, I describe this putative subspecies of *H. patellifera* from the Daito Islands, for which the name *Hierodula patellifera daitoana* **ssp. nov.** is proposed.

Materials and methods

Hierodula patellifera daitoana **ssp. nov.** was occasionally collected by K. Oshima between 2015 and 2018. Day and night surveys involving opportunistic collections were conducted on Minami-daito-jima Island from February 17 to 20, 2015 and May 14 to 17, 2016, and on Kita-daito-jima Island from September 24 to 26, 2016 and June 24 to 28, 2018. Individuals that were nymphs at the time of collection were reared to adulthood and then dried for morphological observations. The specimens were examined under a stereoscopic microscope (SZ60; Olympus, Tokyo, Japan), and photographs were taken using a digital camera (EOS8000D; Canon, Tokyo, Japan). Measurements of body length (from the anterior margin of the pronotum to the apex of the wing) were taken using a ruler. Observations and photographs were based on both fresh and dried specimens. The type specimens have been deposited in the Laboratory of Entomology, Tokyo University of Agriculture, Atsugi, Japan (LETUA).

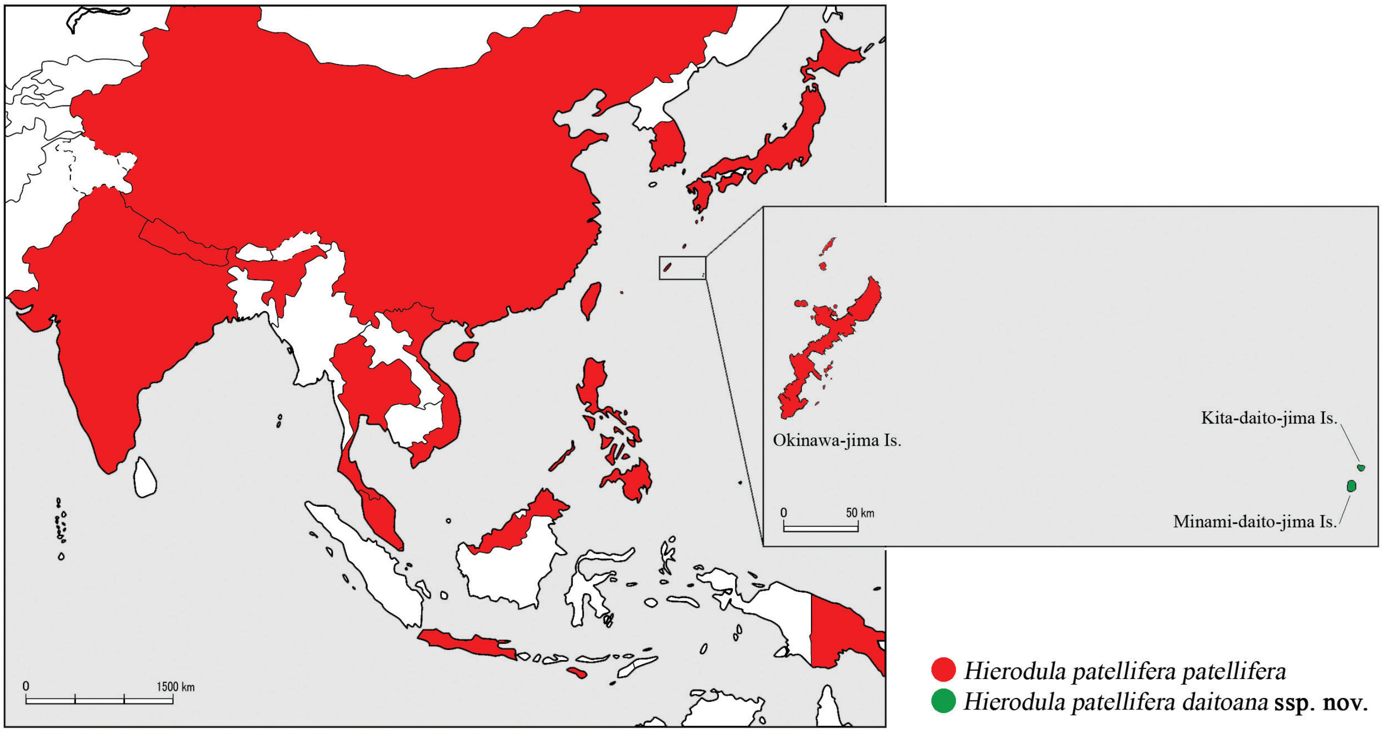

Fig. 1. Total known distribution of *Hierodula patellifera* in Asia.

Results

Taxonomy

Family Mantidae Latreille, 1802
Subfamily Hierodulinae Brunner de Wattenwyl, 1893
Genus *Hierodula* Burmeister, 1838
Nominal species *Hierodula membranacea* (Burmeister, 1838)

Hierodula patellifera daitoana ssp. nov.

http://zoobank.org/19A70420-0A90-493A-9CE5-E8F839CFE2C3
Figs 2–5, 7

Type material.—**Holotype:** JAPAN • ♂; Okinawa, Shimajiri-gun, Kita-daito-jima Is., Kita-daito-son, Minato; 25°57'16"N, 131°17'17"E; 24 Jun. 2018; K. Oshima leg.; LETUA-IC-2021-00001. **Paratypes:** JAPAN • 1♂, 2♀; (collected as nymphs); Okinawa, Shimajiri-gun, Kita-daito-jima Is., Kita-daito-son, Minato; 25°57'19"N, 131°17'16"E; 25–26 Oct. 2016; K. Oshima leg.; LETUA-IC-2021-00002–00004 • 2♂; Okinawa, Shimajiri-gun, Kita-daito-jima Is., Kita-daito-son, Minato; 25°57'16"N, 131°17'17"E; 24–25 Jun. 2018; K. Oshima leg.; LETUA-IC-2021-00005–00006 • 2♂, 2♀ (collected as nymphs); Okinawa, Shimajiri-gun, Kita-daito-jima Is., Kita-daito-son, Minato; 25°57'19"N, 131°17'16"E; 24–26 Jun. 2018; K. Oshima leg.; LETUA-IC-2021-00007–00010 • 1♂ (collected as nymph); Okinawa, Shimajiri-gun, Minami-daito-jima Is., Minami-daito-son, Kita; 25°51'59"N, 131°14'50"E; 17 Feb. 2015; K. Oshima leg.; LETUA-IC-2021-00011 • 1♀ (collected as nymph); Okinawa, Shimajiri-gun, Minami-daito-jima Is., Minami-daito-son, Kita; 25°51'58"N, 131°14'50"E; 16 Apr. 2016; K. Oshima leg.; LETUA-IC-2021-00012 • 1♀ (collected as nymph); Okinawa, Shimajiri-gun, Minami-daito-jima Is., Minami-daito-son, Ikenosawa; 25°49'12"N, 131°13'18"E; 17 Apr. 2016; K. Oshima leg.; LETUA-IC-2021-00013.

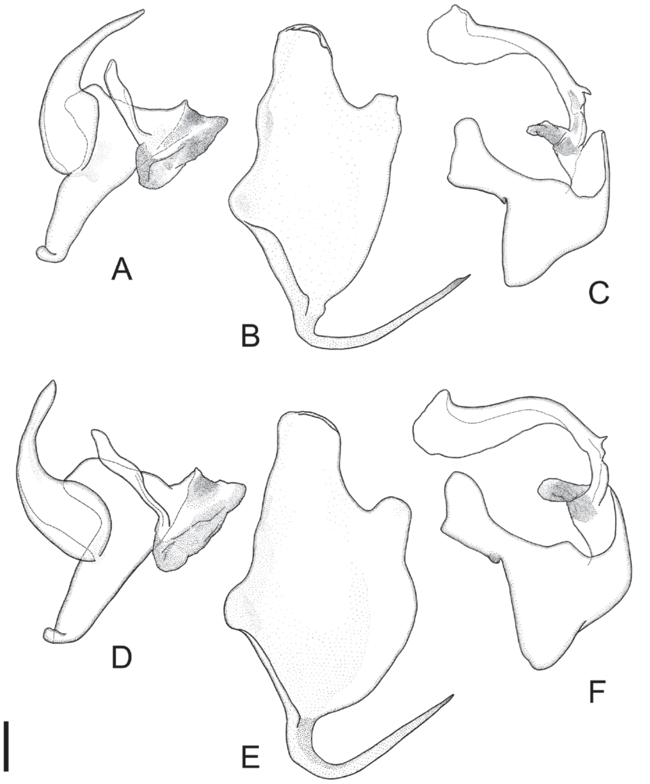

Fig. 2. Disarticulated genital complex (to isolate the individual phallomeres) of *Hierodula patellifera*, male, dorsal view: **A–C.** *Hierodula patellifera patellifera* from Okinawa-jima Is.; **D–F.** *Hierodula patellifera daitoana* **ssp. nov.**, from Kita-daito-jima Is. (holotype); **A, D.** Left phallomere; **B, E.** Ventral phallomere; **C, F.** Right phallomere. Scale bar: 1 mm.

Fig. 3. *Hierodula patellifera daitoana* **ssp. nov.**, male, holotype. Habitus, dorsal view. Scale bar: 10 mm.

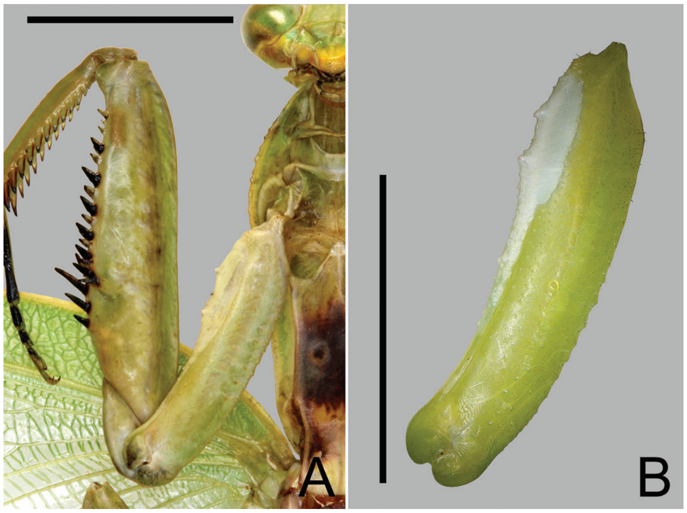

Fig. 4. Procoxa of *Hierodula patellifera daitoana* **ssp. nov.**, lateral view: **A.** Male, holotype; **B.** Female, paratype, before discoloration. Scale bars: 10 mm.

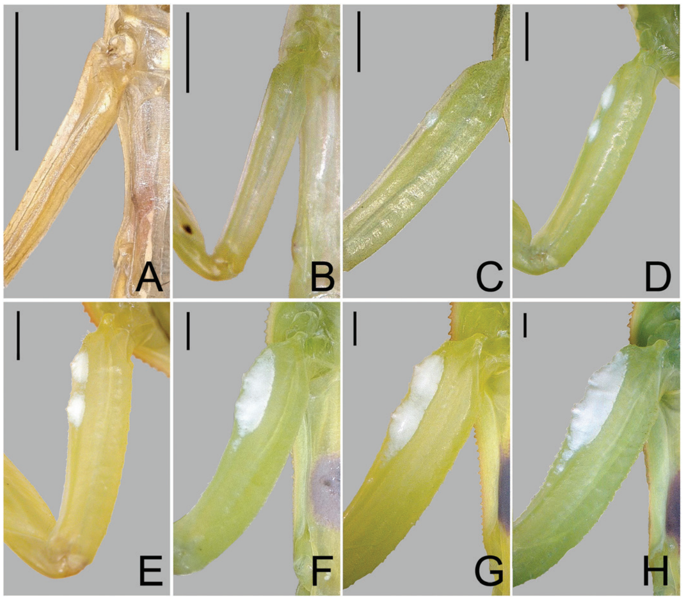

Fig. 5. Procoxa in nymphal stages of *Hierodula patellifera daitoana* **ssp. nov.**, male, lateral view: **A.** 1st instar; **B.** 2nd instar; **C.** 3rd instar; **D.** 4th instar; **E.** 5th instar; **F.** 6th instar; **G.** 7th (penultimate) instar; **H.** 8th (last) instar. Scale bars: 1 mm.

Fig. 6. Habitats of *Hierodula patellifera daitoana* **ssp. nov.** on Kita-daito-jima Island.

Subspecies characters.—Adult: Differs from the nominotypical subspecies *H. patellifera patellifera* by having the following characters: Body length 64–77 mm in males, 69–79 mm in females; antenna at most 115-segmented in both sexes; procoxa (Fig. 4A, B) with a large white marking along dorsal-inner surface (white marking may become unclear in dry specimens), and with 2 large and several small tooth-like marginal spines (not well-defined). Nymph: Procoxa of 1st- and 2nd-instars (Fig. 5A, B) lacking white markings and marginal spines; procoxa of 3rd instar (Fig. 5C) with or without a small white marking, and with slightly developed, tooth-like marginal spines; procoxa of 4th instar (Fig. 5D) with 2 small, white markings and with slightly developed, tooth-like marginal spines; procoxa of 5th instar (Fig. 5E) with 2 medium-sized, irregular, white markings and with 2 large (somewhat developed) and several small tooth-like marginal spines; procoxa of 6th- to last-instars (Fig. 5F–H) with a large-sized and irregular white marking and with 2 large (well developed) and several small tooth-like marginal spines.

Distribution.—Kita-daito-jima Is. and Minami-daito-jima Is., the Ryukyus, Japan.

Etymology.—This subspecific name is named after the Daito Islands, the type locality of the subspecies; an adjective.

Fig. 7. A *Hierodula patellifera daitoana* **ssp. nov.** female and ootheca immediately after oviposition.

Ecology.—During my surveys, adults and nymphs appeared from May to July and in all seasons, respectively. Both adults and nymphs were found in grassland adjacent to a sugarcane field (Fig. 6) and forest edges, particularly on the bushy tree *Acalypha wilkesiana* Müll. Arg. (Euphorbiaceae). Some specimens were also found in a residential area. Oothecae were laid on twigs and trunks as well as on artificial objects (Fig. 7).

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