Extension of the phasmid genus *Presbistus* to Cambodia with a new species and notes on genitalia and captive breeding (Phasmida, Aschiphasmatidae, Aschiphasmatinae)

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Abstract

A new species of *Presbistus* Kirby, 1896, *Presbistus vitivorus* **sp. nov.**, is described from Cambodia based on both sexes, nymphs, and eggs. Male genitalia and vomer are described and figured. Illustrations of adults, nymphs, specimens in situ, host plants, a distribution map and records on biology and breeding in captivity are provided. The host plants of the species belong to the family Vitaceae. The genus *Presbistus* and the family Aschiphasmatidae are recorded from Cambodia for the first time. The species diversity and the distribution of the genus are discussed, and it is shown that the genus is restricted to Sundaland. A nomenclature for the morphology of the dissected vomer is proposed and tries to homologize the previously used terms.

Keywords

Aedeagus, Aschiphasmatini, Phasmatodea, stick insect, Vitaceae, vomer

Introduction

The genus *Presbistus* Kirby, 1896 belongs to the Aschiphasmatini in the subfamily Aschiphasmatinae and currently contains nine species. Phylogenetic studies have shown Aschiphasmatinae to be monophyletic and the sister group to all remaining Euphasmatodea (Simon et al. 2015).

Presbistus is currently recorded from India, Sri Lanka, Peninsular Malaysia, Sumatra, Java, and Borneo (Brock et al. 2022). Within the Aschiphasmatinae, the genus is characterized by triangular or spine-like tegmina, uniform translucent brown anal region of hind wings, and cylindrical or conical cerci in both sexes. The male has a well-developed vomer and has the end of the abdomen distinctively swollen and club-shaped. The eggs are slightly longer than high and lack setae (Bragg 2001, Seow-Choen 2016).

The vomer, a sclerotized derivative of sternum X, was first introduced by Pantel (1890) as "vomer sous-anal". The vomer is used during mating and clasps the posterior margin of sternum VII of the female, which has evolved into a praeopercular organ (Bradler 2003). Pantel (1915) discussed the structure and variability of the vomer in different subgroups of Phasmatodea and detected a vomer in three genera of "Ascepasmini" (= Aschiphasmatini) including *Presbistus*. Bradler (1999, 2009) argued that the vomer was already present in the phasmatodean ground plan and that it represents a plesiomorphic character for all Euphasmatodea. Most authors have only described the external part of the vomer, and a standardized nomenclature for the different parts of this organ is still needed.

During the study of stick insect specimens collected in the framework of the Global Taxonomy Initiative project "A step further in the entomodiversity of Cambodia," a species belonging to the genus *Presbistus* could not be attributed to any known species.

The phasmid fauna of Cambodia remains poorly studied (Bresseel and Constant 2018b), and the present paper describes the new species as *Presbistus vitivorus* sp. nov., provides useful characters for differentiation, and gives information on its biology and distribution. A nomenclature for the morphological characterization of the vomer in stick insects is proposed.

Materials and methods

Due to their nocturnal behavior (as in most Phasmida), the specimens of *P. vitivorus* sp. nov. were collected at night. A lightweight, water-proof Petzl MYO RXP head torch was used during collecting. The females were kept alive in a mesh pop-up cage (exo terra explorarium) for producing eggs. The wild caught specimens were euthanized by injection with ethanol. The specimens were then stored in airtight plastic "zip" bags containing wood chips commonly used in rodent cages and sprinkled with etylacetate (EtOAc) to prevent rotting, mould, and to keep the specimens flexible. The bags were frozen on arrival, and the specimens were mounted at a later date.

A number of pictures of each specimen were taken using a Canon 700D camera (Canon Inc., Ota City, Tokyo, Japan) equipped with a Sigma 50 mm macro lens (Sigma Corporation, Kawasaki, Japan) for adults or with a Leica EZ4W stereomicroscope (Leica Microsystems Ltd., Wetzlar, Germany) with integrated camera for eggs and male genitalia. The images were stacked using CombineZ software (https://combinezp.software.informer.com) and optimized with Adobe Photoshop CS3. The distribution map was produced using SimpleMappr (Shorthouse 2010).

Observations were done with a Leica EZ4W stereomicroscope, and measurements were taken with an electronic calliper. The dissection of the vomer and aedeagus was done on a fresh specimen using a needle blade. The vomer was extracted after cutting the membrane around the connective ring that separates the internal apodemes from the externally visible body; the aedeagus was extracted after spreading the poculum and cutting the inner membrane around the integument that separates the internal basal apodeme from the external remaining parts of the aedeagus. After extraction, the vomer and aedeagus were boiled for a few minutes in 10% KOH solution to remove the remaining soft parts then rinsed and examined in 70% ethanol. The vomer and aedeagus were preserved in glycerine in a polyethylene genitalia tube and stored under the label of the corresponding specimen.

The nomenclature of the morphological characters follows Bragg (2001) and that of the egg morphology follows Clark-Sellick (1997, 1998). The description of the coloration is based on live specimens.

Acronyms used for the collections.—

RBINS Royal Belgian Institute of Natural Sciences, Brussels, Belgium.
RUPP Royal University of Phnom Penh, Cambodian Entomology Initiative, Phnom Penh, Cambodia.
VNMN Vietnam National Museum of Nature, Hanoi, Vietnam

Abbreviations.—

HT holotype
PT paratype

Results

Taxonomy

Family Aschiphasmatidae Brunner von Wattenwyl, 1893
Subfamily Aschiphasmatinae Brunner von Wattenwyl, 1893
Tribe Aschiphasmatini Brunner von Wattenwyl, 1893

Genus *Presbistus* Kirby, 1896

Presbistus Kirby, 1896: 475. – Kirby 1904: 475 [in Aschiphasminae]. — Redtenbacher 1906: 78 [redescribed]. — Ragge 1955: 377 [wing venation]. — Bradley and Galil 1977: 200 [in Aschiphasmatina]. — Brock 1999: 147, 154, 184 [species from Peninsular Malaysia]. — Bragg 2001: 323, 642 [species from Borneo]. — Zompro, 2004: 318 [in superfamily Aschiphasmatoidea]. — Otte and Brock 2005: 280 [Catalogued]. — Seow-Choen 2016: 359 [species recorded and figured from Borneo]. — Seow-Choen 2017: 128 [species recorded and figured from Singapore]. — Seow-Choen 2018: 577 [species recorded and figured from Sumatra].

Type species.—Perlamorpha peleus Gray, 1835 by original designation.

The genus *Presbistus* can be distinguished from other members of the Aschiphasmatinae by the combination of the following set of characters (adapted from Bragg 2001):

1. Body and legs brown with some black markings.
2. Mesonotum unarmed.
3. Profemora incurving at base; all femora with distinct medioventral carina, armed with at least a few minute spines.
4. Tegmina triangular and spine-like; anal region of hind wing translucent brown.
5. Apex of male abdomen distinctly swollen.
6. Apex of female abdomen almost arrowhead shaped in dorsal view. Subgenital plate with anterior portion globose, posterior half medially keeled and tapering.
7. Cerci cylindrical.
8. Eggs longer than high, lacking setae.

***Presbistus vitivorus* sp. nov.**

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Figs 1–12

*Diagnosis and differentiation.—*The new species is morphologically most similar and believed to be closely related to two Bornean species: *Presbistus marshallae* Bragg, 2008 and *P. appendiculatus* Bragg, 2001. All three species have a cleft anal segment in males, with the left anal lobe (*lal*) shorter than the right (*ral*), and the right anal lobe twisted. In *P. vitivorus* sp. nov., *ral* first curves down towards the front and later upwards, projecting between the right cercus and the posterior margin of tergum IX. Sternite VII of females of the new species is not rounded or bilobed and does not notably project over the base of the operculum. Instead, the posterior portion of tergum VII is slightly narrowing with the praeopercular organ present as a posterior depression with indistinct lateral carinae and concave posteriorly. The new species also has relatively shorter hind wings compared to most of the other species of the genus. There is only a single species with two subspecies that have shorter hind wings: *Presbistus asymmetricus viridialatus* Seow-Choen, 2020 and *Presbistus asymmetricus asymmetricus* Giglio-Tos, 1910.

*Etymology.—*The species name is formed from the plant genus name *Vitis*, belonging to the family of the grapevine Vitaceae and the suffix forming adjective *-vorus* (feminine *-vora*, neuter *-vorum*) meaning "eating" or "devouring". It refers to the feeding preference of the species for plants of the family Vitaceae.

*Type material.—***Holotype: CAMBODIA** • ♂; Pursat prov., Phnom Samkos; 12°13'02"N, 102°55'07"E; 15–18 October 2016; GTI project; Leg J. Constant & J. Bresseel; I.G.: 33.345; RBINS. **Paratypes**: **CAMBODIA** • 7♂, 22♀; same collection data as holotype; 4♂, 19♀: RBINS; 2♂, 2♀: RUPP; 1♂, 1♀: VNMN.

*Additional material.—*CAMBODIA • 10♀; Preah Vihear prov., Be Treed Adventures; 16–21 October 2017, 13°29'44"N, 104°42'36"E; GTI Project; Leg. J. Constant & X. Vermeersch; I.G.: 33.551; 8♀: RBINS; 2♀: RUPP • 3♀; Preah Vihear prov., Be Treed adventures; 16–21 October 2017, 13°29'44"N, 104°42'36"E; GTI Project; Leg. J. Constant & X. Vermeersch; I.G.: 33.551; Ex breeding Tim Bollens, 2018; RBINS • 21♀; Preah Vihear prov., Be Treed adventures; 16–21 October 2017; 13°29'44"N, 104°42'36"E; GTI Project; Leg. J. Constant & X. Vermeersch; I.G.: 33.551; Ex breeding Tim Bollens, 2019; RBINS • Six eggs; same data as holotype;RBINS; RUPP.

*Remark.—*Living females from Phnom Samkos have the alae slightly projecting over the posterior margin of tergum V, but not reaching half of tergum VI. In living females from Be Treed, the

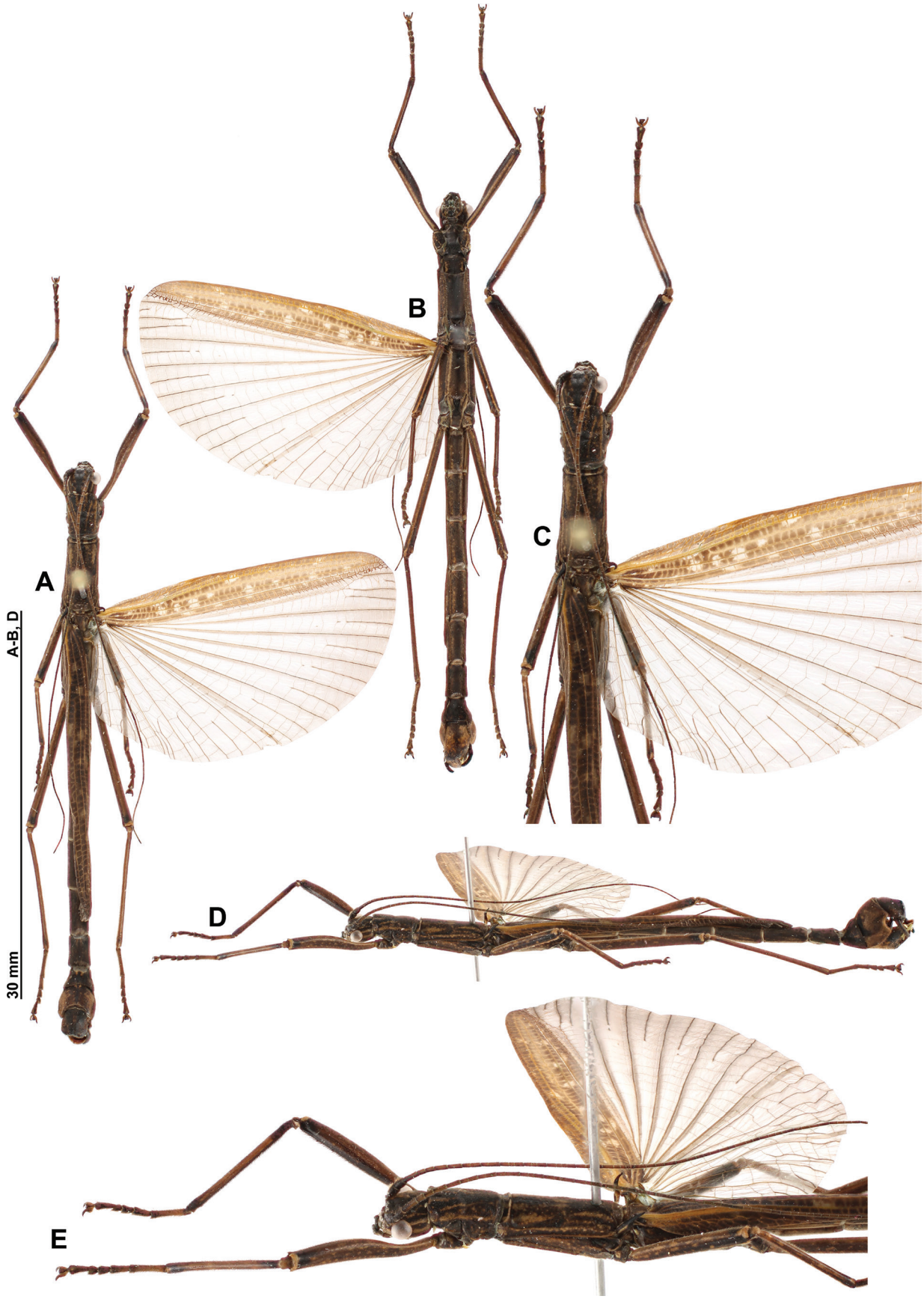

Fig. 1. *Presbistus vitivorus* sp. nov. holotype male (RBINS). **A.** Dorsal view; **B.** Ventral view; **C.** Head and thorax, dorsal view; **D.** Lateral view; **E.** Head and thorax, lateral view; C, E not to scale.

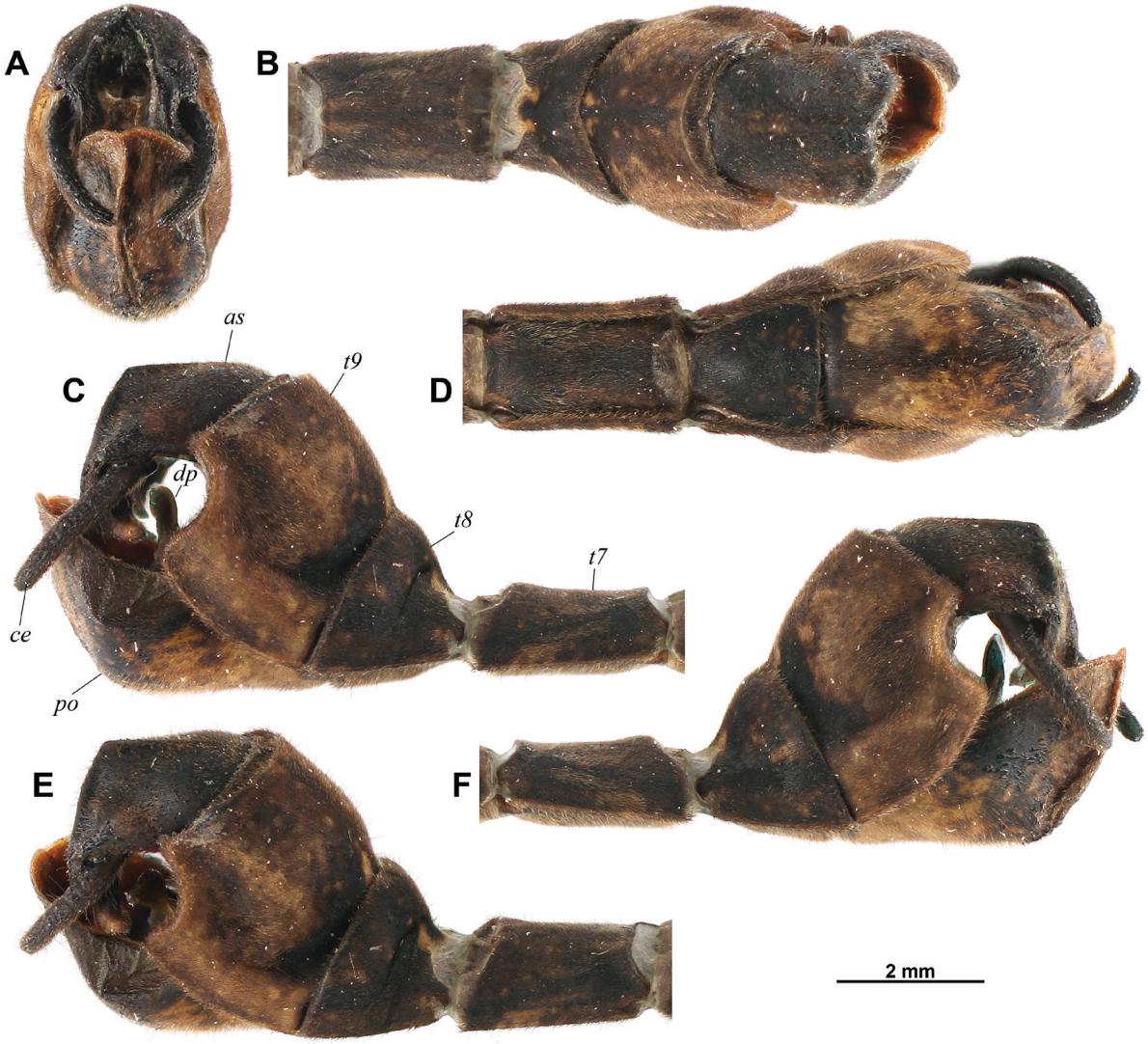

Fig. 2. *Presbistus vitivorus* sp. nov. male terminalia. **A.** Posterior view; **B.** Dorsal view; **C.** Right lateral view; **D.** Ventral view; **E.** Right laterodorsal view; **F.** Left lateral view. Abbreviations: *as,* anal segment. *ce,* cercus. *dp,* dorsal process. *po,* poculum. *t7*, tergum VII. *t8*, tergum VIII. *t9*, tergum IX.

alae are longer and slightly but noticeably projected over half of tergum VI. Breeding efforts have proven that wing length is a stable feature throughout successive generations. Therefore, even if no other differences could be observed, the specimens from Be Treed are not listed as type material.

Description.—**Male.** (Figs 1–5) ***Body***. Setae scattered over complete body, more concentrated in certain areas. Head, pro- and mesonotum brown with distinct black patches. Wings with blackish tegmina; costal area of alae brown with black markings and with basal portion of radius green, anal area infuscate. Femora brownish dorsally with black apex. Tibiae brownish, protibiae with black base and apex; mesotibiae with black apex and metatibiae with indistinct black marking apically.

Head. (Fig. 1C, E) Flattened dorsally, wider than long with a shallow longitudinal impression posteriorly. Eyes strongly protruding. Two minute impressions between the bases of antennae. Antennae reaching about half of abdomen; scapus subcylindrical, roughly as long as pedicellus. Pedicellus cylindrical. First flagellomere longer than pedicellus; flagellomere II shorter than half the length of previous one; following segments varying in length.

Thorax. (Fig. 1C, E) Pronotum longer than wide with posterior margin concave and with a median line in the prozona; prozona slightly higher than metazona from lateral view; lateral margins slightly concave from dorsal view, posterior margin more or less straight. Mesonotum about one third longer than pronotum and parallel-sided; anterior margin slightly concave with raised rim.

Wings. (Fig. 1A, B) Tegmina small, elongate, triangular, and apically acute; pointing straight upwards. Hind wings reaching roughly halfway tergum VI.

Legs. (Fig. 1A, B) Profemora incurved basally. Femora with carinae indistinct, outer ventral carinae with few minute spines. Tibiae with carinae indistinct.

Abdomen and terminalia. (Figs 1A, B, D, 2–5) Terga II–VII of uniform width and terga II–VI only slightly varying in length; tergum VII (*t7*) distinctly shorter; tergum VIII (*t8*) and IX (*t9*) widening towards the posterior; X narrower than IX. Anal segment (*as*) with indistinct mediolongitudinal carina, slightly widening towards the posterior; apex notched. Right anal lobe

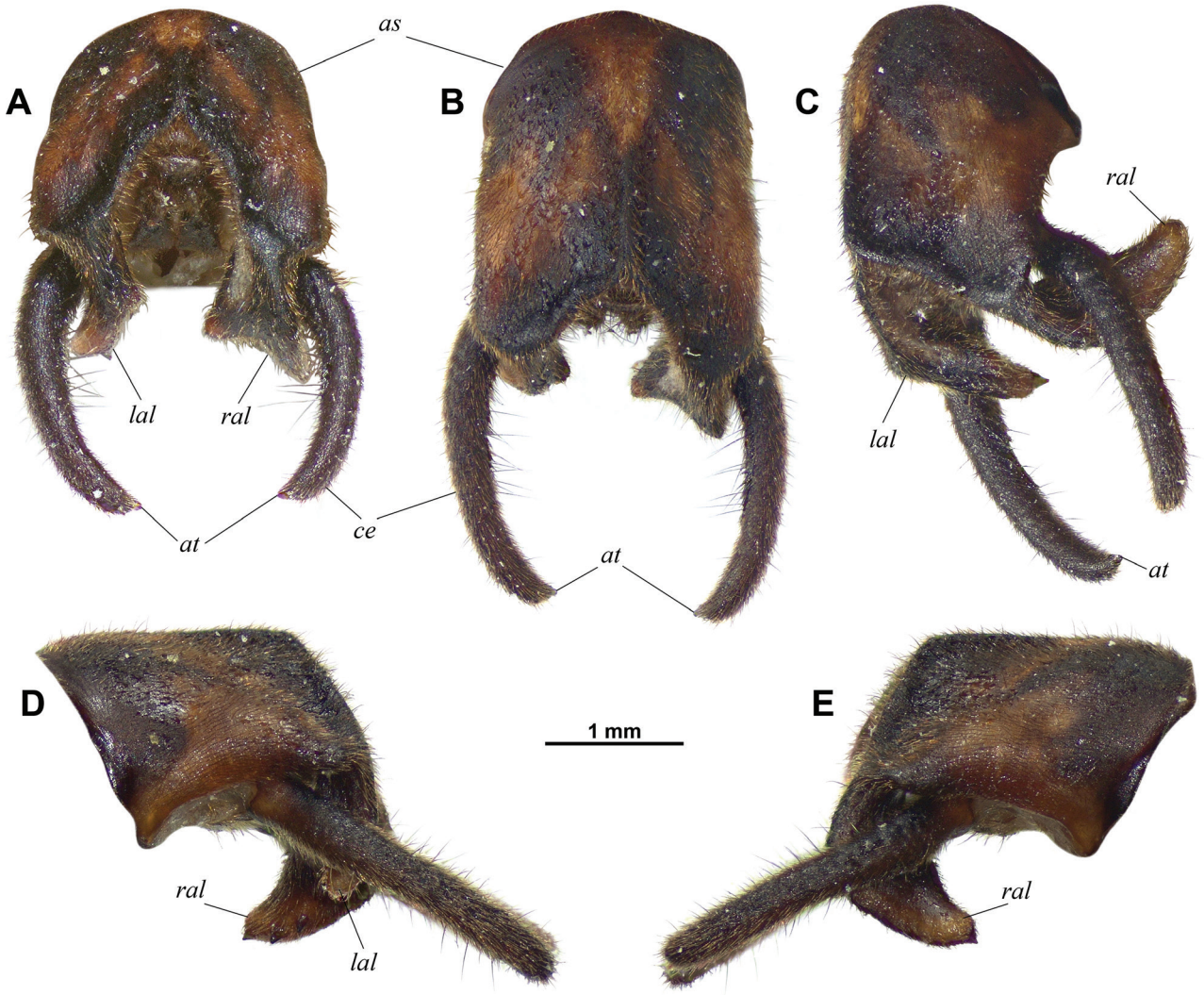

Fig. 3. *Presbistus vitivorus* sp. nov. male anal segment. **A.** Posterior view; **B.** Posterodorsal view; **C.** Right posterolateral view; **D.** Left lateral view; **E.** Right lateral view. Abbreviations: *c*, cercus. *lal*, left anal lobe. *ral*, right anal lobe.

(*ral*) broad at base, distinctly elongated and strongly twisted and curved, projecting between cercus and posterior margin of tergum IX. Left anal lobe (*lal*) distinctly shorter than right one and curved. Cerci (*ce*) black and long, incurved and round in cross section with an apical tooth. Poculum bulgy and angular (110° angle), posterior part with fine mediolongitudinal carina, apex rounded.

Vomer (Fig. 4) well developed. Body (*b*) with narrow base, distinctly elongated, tapering and ending in an apical spine (*as*); ventral part of body distinctly longer than dorsal part. Left and right basal apodemes (*lba, rba*) narrow and elongated, almost as long as the vomer body. External body separated from internal apodemes by sclerotized connective ring (*cr*). Apodemes almost parallel, slightly directed towards each other.

Aedeagus (Fig. 5) with spatulate, elongate, and curved basal apodeme (*ba*) prolongated anterodorsally by a strongly sclerotized plate (dorsal sclerite). Sclerotized plate with elongated club-shaped right basal process (*rbp*), with blunt subtriangular left basal process (*lbp*) and with elongated curved dorsal process (*dp*) bearing minute teeth on anterior surface (Fig. 5F). Caudal portion of aedeagus composed of a series of membranous lobes *(ml*).

Female. (Figs 6, 7)

Body. Setae scattered over complete body, more concentrated in certain areas. Female colored as male except for abdomen. In the female, tergum VII conspicuously paler than the rest of the abdomen.

Head. (Fig. 6C, E) About as long as wide, flattened dorsally. Eyes strongly protruding. Two minute impressions between the bases of the antennae. Antennae reaching about half of abdomen; scapus flattened at base, cylindrical at apex, slightly longer than pedicellus. Pedicellus cylindrical. First flagellomere longer than pedicellus; flagellomere II shorter than half the length of previous segment; following segments vary in length.

Thorax. (Fig. 6C, E) Pronotum longer than wide with anterior margin slightly concave and with a median line in the prozona; prozona slightly higher than metazona from lateral view; impression between pro- and metazona centrally flattened, almost circular, sublaterally with a minute hole; lateral margins slightly concave from dorsal view, posterior margin more or less straight. Mesonotum almost twice as long as pronotum and parallel-sided, with posterior margin slightly concave with a raised rim and anterior margin almost straight.

Wings. (Fig. 6A, B) Tegmina small, elongate, triangular, and apically acute; pointing straight upwards. Hind wings projecting over posterior margin of tergum V but not reaching posterior margin of tergum VI.

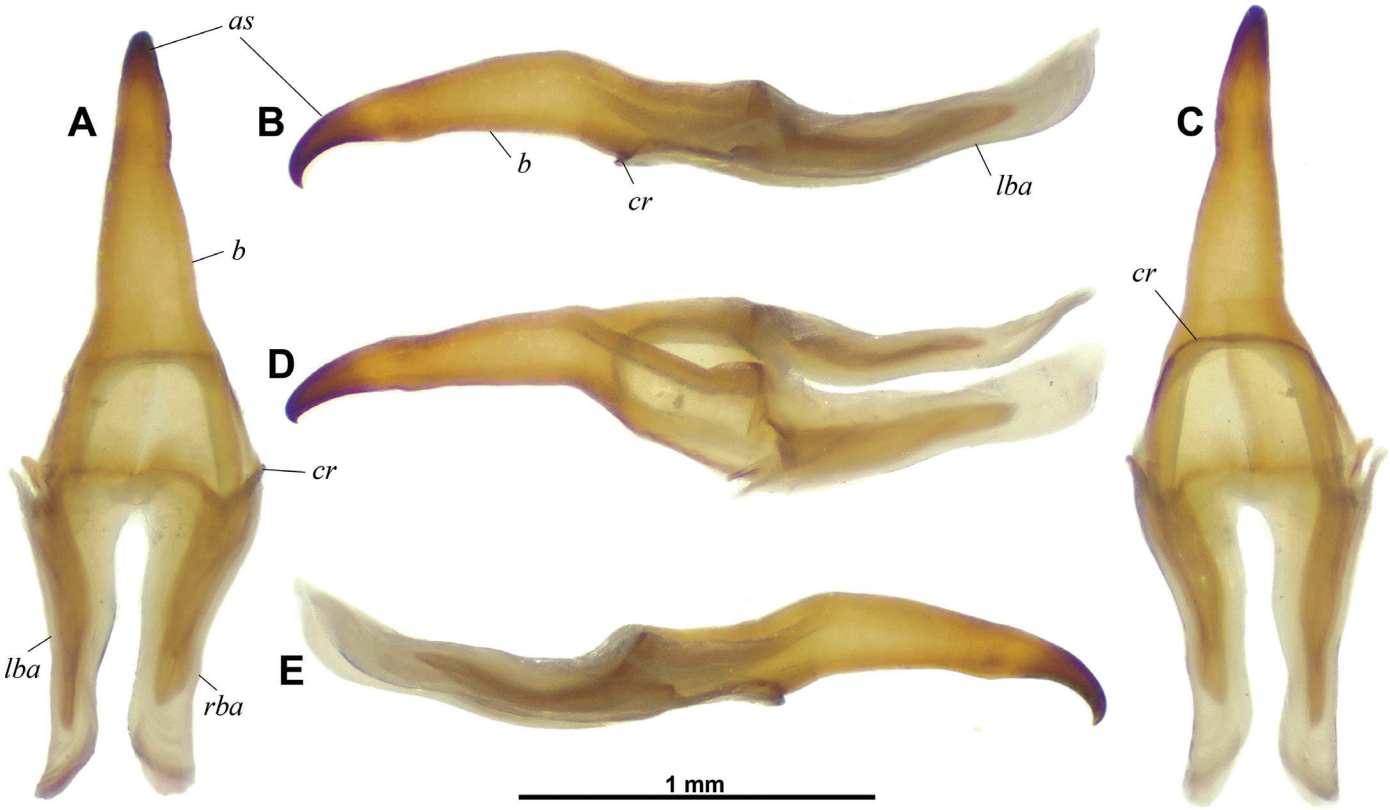

Fig. 4. *Presbistus vitivorus* sp. nov. male vomer. **A.** Ventral view; **B.** Left lateral view; **C.** Dorsal view; **D.** Ventrolateral view; **E.** Right lateral view. Abbreviations: *as*, apical spine. *b*, body. *cr*, connective ring. *lba*, left basal apodeme. *rba*, right basal apodeme.

Legs. (Fig. 6A, B) As in male.

Abdomen. (Figs 6A, B, D, 7) Terga II–V of uniform width, terga VI–VIII slightly widening towards the posterior (this feature usually only visible in living specimens and especially in females with the abdomen swollen with eggs). Terga VII–X getting progressively shorter with VIII–X tectiform. Tergum VIII expanding laterally with lateral margin rounded. Anal segment slightly shorter than tergum IX; apex concave with minute epiproct visible in dorsal view. Cerci narrow, circular in cross section. Sternum VII with praeopercular organ present as a posterior depression with indistinct lateral carinae, indistinctly projecting over base of subgenital plate and concave posteriorly. Subgenital plate with anterior portion globose and with minute impression basally; posterior portion with distinct mediolongitudinal carina, narrowing towards the posterior with apex roundly pointed.

Nymph. (Fig. 8) Newly hatched nymphs have a pinkish body and head. Antennae longer than head and body combined, orange with evenly spaced black markings. Legs slightly setose and completely orange.

Egg. (Fig. 9) Measurements [mm]: length 1.9, width 0.9, height 1.5. Capsule dark reddish brown, surface minutely punctuate without setae; lentil shaped and laterally compressed. Micropylar plate colored like capsule, long and narrow, longitudinally carinate laterally and medially, extending from the operculum across the polar end and back to the operculum. Micropylar cup distinct, displaced towards the polar area; operculum elongate oval, not punctuate, with a raised elongate oval ridge centrally.

Table 1. Measurements [mm] of *Presbistus vitivorus* sp. nov.

Length of	HT ♂	PT ♂♂	PT ♀♀
Body	44.6	42.2–44.1	50.8–57.4
Head	2.6	2.4–2.6	3.1–3.5
Pronotum	3.3	3.1–3.4	3.9–4.4
Mesonotum	5.5	5.5–5.8	6.8–7.6
Tegmina	1.7	1.7–2.0	2.2–2.4
Alae	23.5	21.8–24.6	27.6–30.0
Metanotum	2.1	covered by wings	4.0*
Median segment	3.6	covered by wings	4.9*
Profemora	7.6	7.2–8.2	8.4–9.4
Mesofemora	5.9	5.1–6.2	6.1–6.9
Metafemora	10.4	9.4–10.8	10.9–12.9
Protibiae	6.7	6.3–7.3	6.7–7.9
Mesotibiae	5.9	5.2–6.2	5.9–6.5
Metatibiae	10.4	9.3–11.1	10.0–12.1

* only one specimen measured; others were mounted with wings closed.

Biology.—Wild specimens were found in Phnom Samkos on Vitaceae (identification of the wild Vitaceae by A. Trias-Blasi, pers. com., VII.2019) species belonging to the genus *Tetrastigma* (Miq.) Planch. or *Cayratia* (Baker) Suess. and were fairly numerous on their host plants (Figs 10, 11A–D). Males and females were present in this population, with most males found *in copula* (Fig. 10E). In Be Treed, they were common on Vitaceae of the genus *Ampelocissus* Planch., but only females were found, thus this particular population seems to be parthenogenetic (Fig. 11E–G). From this latter parthenogenetic population, *P. vitivorus* sp. nov. was cultured by T. Bollens (Belgium) on various Vitaceae (*Parthenocissus* spp., *Cissus alata* Jacq., *Vitis vinifera* L.) of which the latter species was the preferred alternative food. The eggs are dropped to the ground, and the young nymphs are bright red in color after hatching but turn green after a few days. They hide mainly underneath leaves and are very fast and hectic when disturbed.

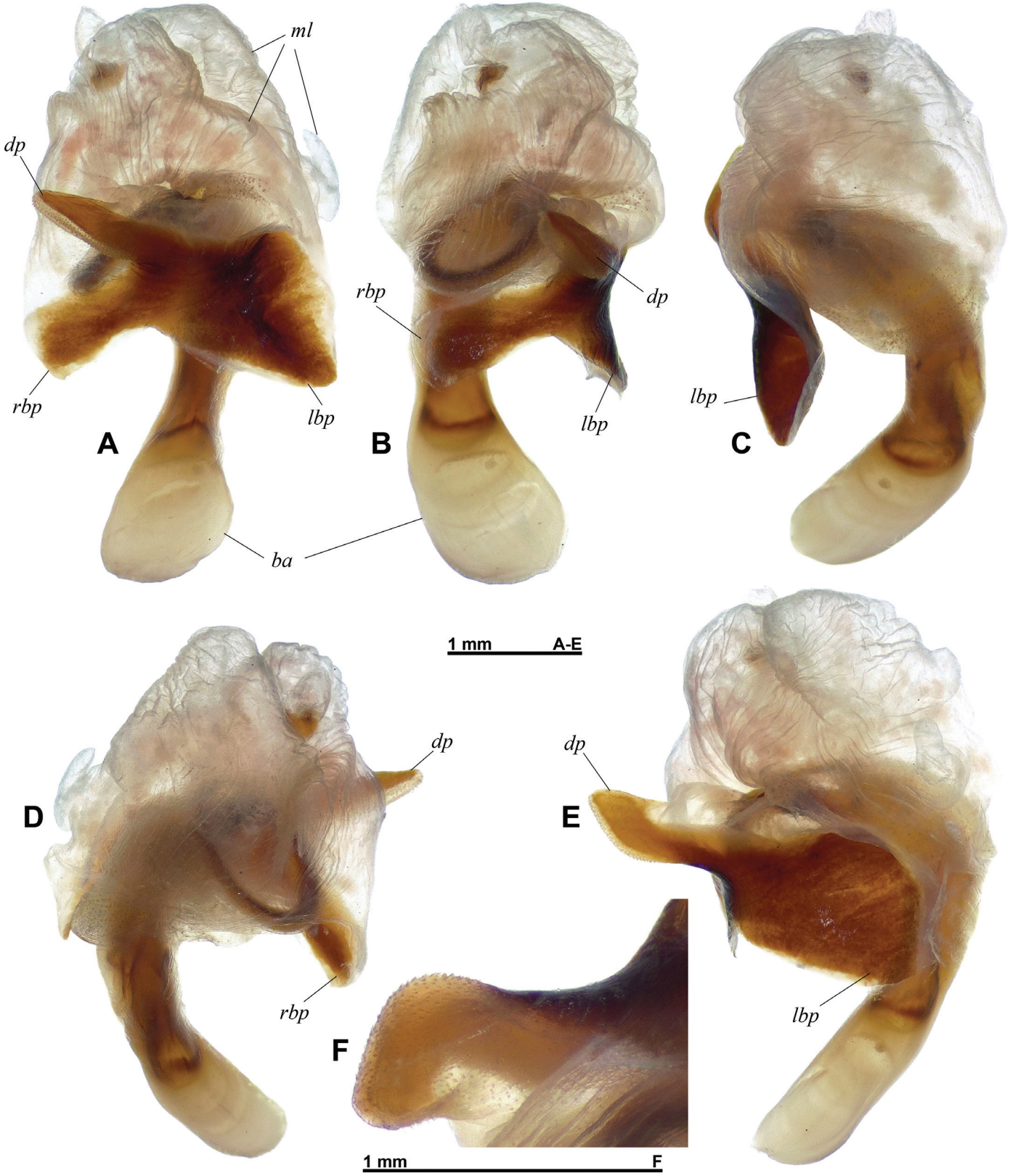

Fig. 5. *Presbistus vitivorus* sp. nov. ♂ aedeagus. **A.** Dorsal view; **B.** Right lateral view; **C.** Left lateral view; **D.** Ventral view; **E.** Laterodorsal view; **F.** Detail of dorsal process. Abbreviations: *ba*, basal apodeme. *dp*, dorsal process. *ml*, membranous lobe. *lbp*, left basal process. *rbp*, right basal process.

Fig. 6. *Presbistus vitivorus* sp. nov. paratype female (RBINS). **A.** Dorsal view; **B.** Ventral view; **C.** Head and thorax, dorsal view; **D.** Lateral view; **E.** Head and thorax, lateral view. C, E not to scale.

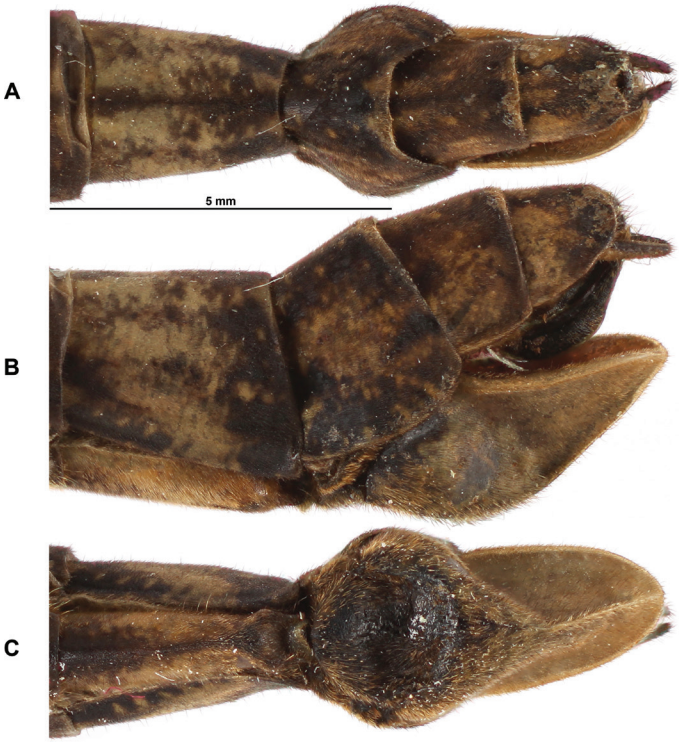

Fig. 7. *Presbistus vitivorus* sp. nov. female, terminalia. **A.** Dorsal view; **B.** Lateral view; **C.** Ventral view.

Fig. 8. *Presbistus vitivorus* sp. nov., newly hatched nymph. Photo credit T. Bollens.

Incubation of eggs was performed without a diapause and lasted 6 months, or with a 5–6 months diapause in the refrigerator and then lasted 4 months after the diapause. Females produce many eggs, with up to 10 eggs dropped per day by each female.

Distribution.—Cambodia: Pursat and Preah Vihear provinces (Fig. 12).

Discussion

Male terminalia.—The morphology of the external terminalia in Aschiphasmatidae was recently studied (Valotto et al. 2016a, b), but the internal male genitalia have remained almost completely

Fig. 9. *Presbistus vitivorus* sp. nov. egg. **A.** Dorsal view; **B.** Lateral view; **C.** Anterolateral view; **D.** Ventral view; **E.** Opercular view; **F.** Polar view; **G.** Posterolateral view.

undocumented. Several studies provide basic information on phasmid genitalia (Chopard 1920, Walker 1922, Snodgrass 1937), but Helm et al. (2011) provided the first detailed study based on the Oriental species *Oxyartes lamellatus* Kirby, 1904 (Lonchodidae, Necrosciinae). Genitalia in Neotropical taxa were recently studied by Heleodoro and Rafael (2019), Chiquetto-Machado and Cancello (2021), and Ghirotto (2021), highlighting the importance of the phallic organ characters for phasmid systematics. At least the large sclerotized and specialized dorsal portion in *Presibistus vitivorus* sp. nov. seems to be homologous to the dorsal sclerite found in all species examined in the previously mentioned studies and coincides with the hypothesis by Helm et al. (2011) that the dorsal sclerite may be present in all or nearly all species of stick insects.

In *Presbistus*, the aedeagus is moderately sclerotized and shows considerable differences when compared to other studied taxa. The aedeagus provides several interesting characters for species differentiation and future phylogenetic considerations, but since our study represents the first documentation of a dissected aedeagus for the subfamily, no conclusions regarding these subjects can be drawn.

The characters of the male vomer are frequently used when describing or differentiating stick insect taxa (Bradler 2009, Bresseel and Constant 2018a, Cumming et al. 2021). The nomenclature proposed here for the dissected vomer can be used in nearly all species, and the structure of the vomer provides useful differential characters when studied from different angles. The suggested nomenclature (Fig. 4) tries to homologize with previously used terms. The vomer of a number of genera has been dissected, such as *Timema* Scudder, 1895 (Timematoidea), *Cryptophyllium* Cumming et al., 2021 (Phyllioidea), *Dajaca* Brunner von Wattenwyl, 1893 (Vallotto et al. 2016a), and *Orthomeria* Kirby, 1904 (Aschiphasmatoidea) (Bradler 1999, Vallotto et al. 2016a, b, Cumming et al. 2021), and these studies show the presence of two basal apodemes (Fig 4: *lba*, *rba*) embedded in the body. The structure and direction of these apodemes can differ considerably between genera.

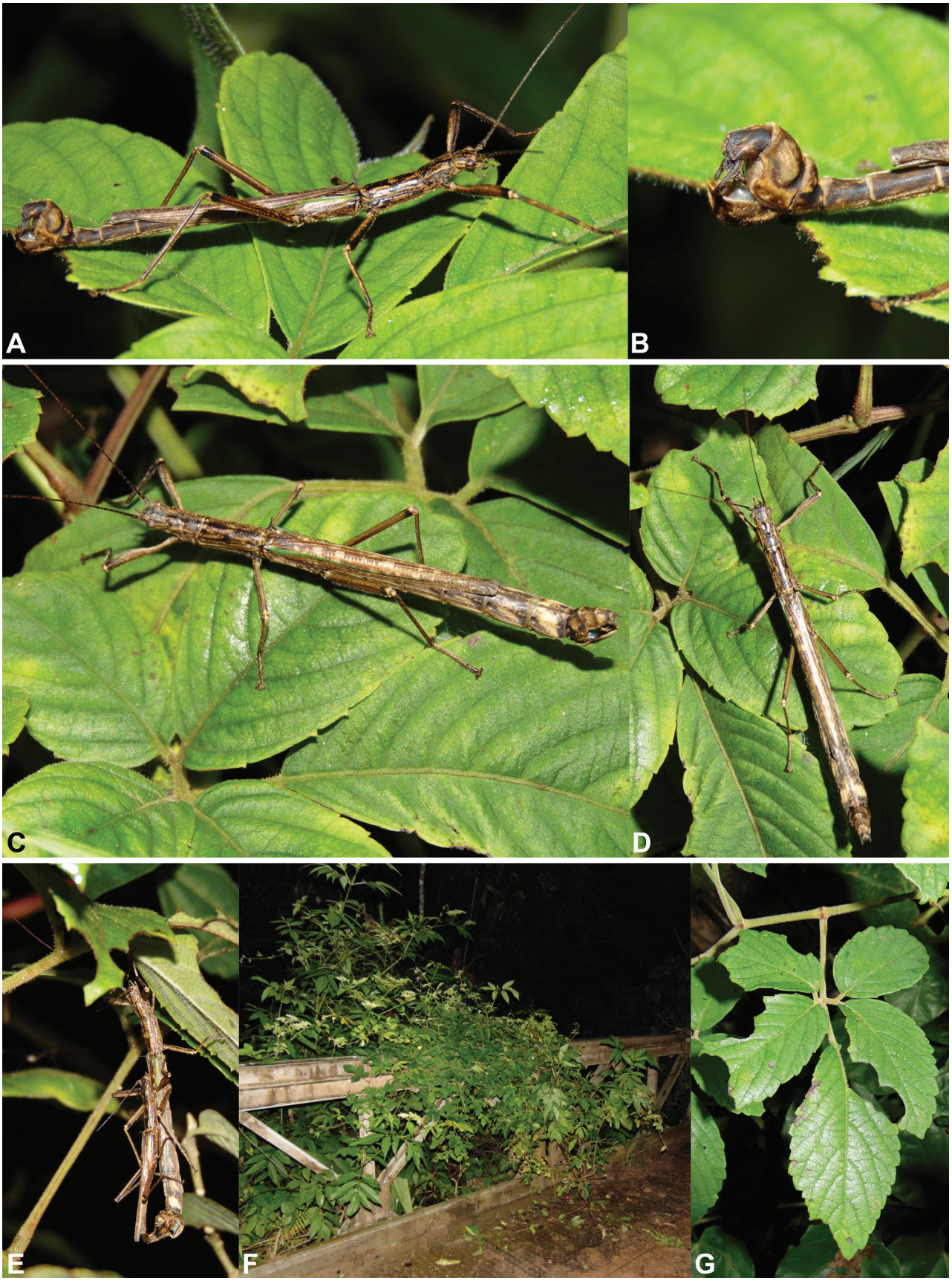

Fig. 10. *Presbistus vitivorus* sp. nov. in nature in Cambodia, Phnom Samkos, 16.X.2016. **A.** Male on Vitaceae sp., laterodorsal view; **B.** Ditto, terminalia, lateral view; **C.** Female on vitaceae sp., laterodorsal view; **D.** Ditto, dorsal view; **E.** Pair in copula, lateral view; **F.** General view of habitat; **G.** Damage on leaves of Vitaceae sp.

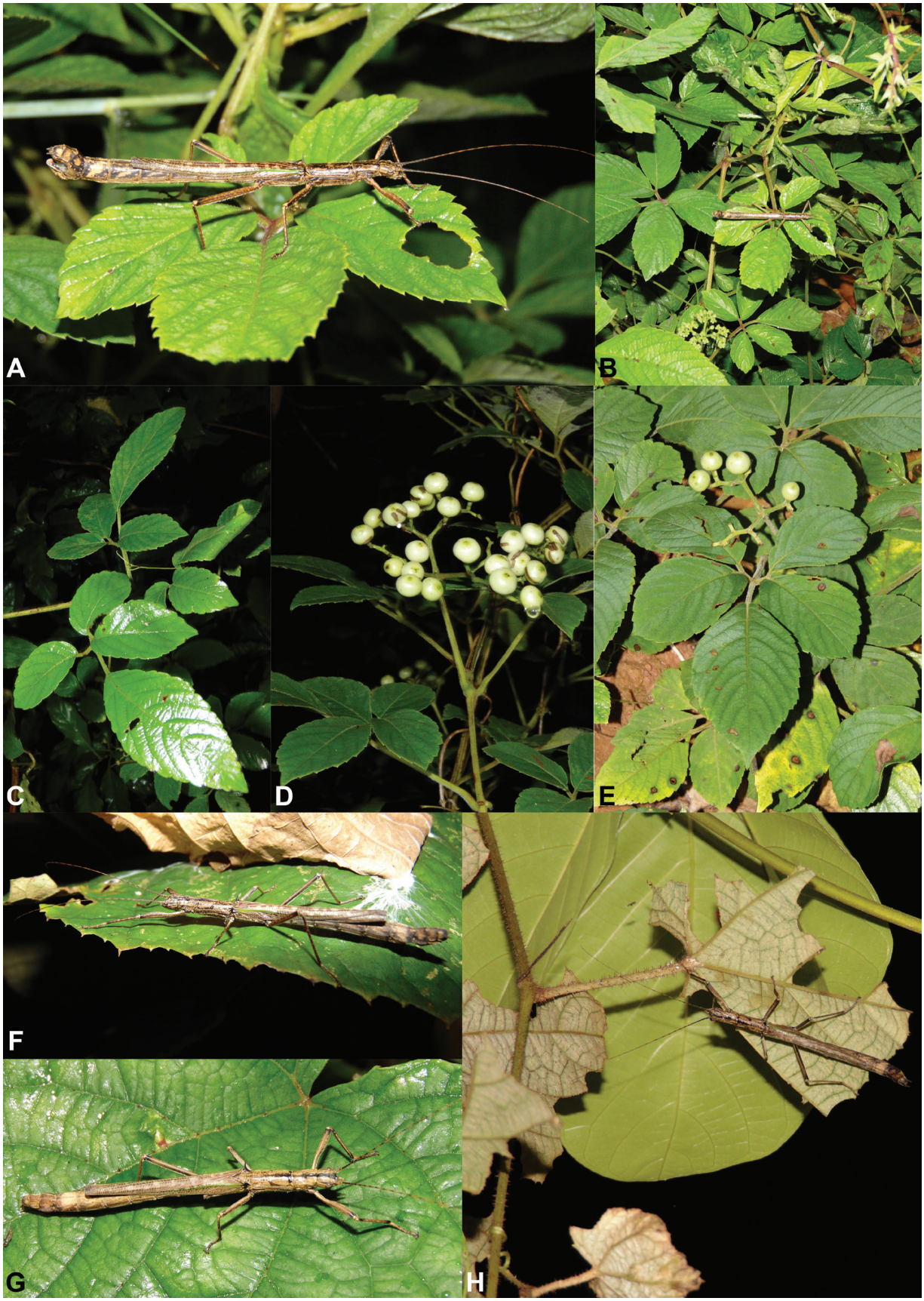

Fig. 11. *Presbistus vitivorus* sp. nov. in nature in Cambodia. **A–E.** Phnom Samkos, 17.X.2016. **A.** Female on Vitaceae sp., lateral view; **B.** Ditto, general view of habitat; **C.** Host plant, Vitaceae sp., leaves; **D.** Host plant, fruit; **E.** Host plant, Vitaceae sp., leaves and fruits; **F, G.** Be Treed, on *Ampelocissus* sp., 16.X.2017; **F.** Female, laterodorsal view; **G.** Female, dorsal view; **H.** Be Treed, female on *Ampelocissus* sp., 19.X.2017.

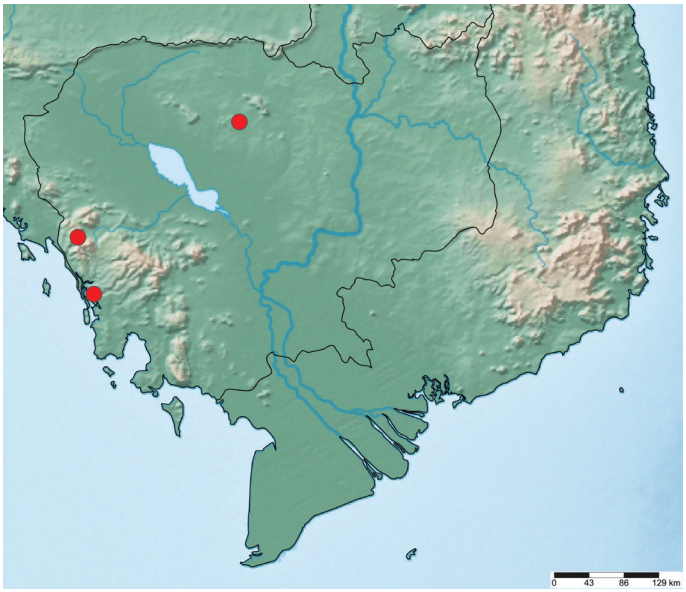

Fig. 12. *Presbistus vitivorus* sp. nov. distribution map.

The body of the vomer (Fig. 4: *b*) refers to the external part of the vomer including the distal ending and is connected to the tegument by the connective ring (Fig. 4: *cr*). The body of the vomer shows considerable variation in shape but most often narrows towards the posterior. This organ can be functionally replaced or can be strongly reduced in genera with a modified tergum X or specialized cerci for clasping the female (Pantel 1915, Bradler 2003, 2009, Hennemann and Conle 2008).

The apical portion of the body of the vomer is often upcurved and armed with one to multiple spines. In many species the vomer ends in a single apical spine (Fig. 4, *as*), referred to as hook(s) or prong(s) by several authors (Bradler 1999, Bradler et al. 2014, Cumming et al. 2021). The apex can sometimes be more complex, bearing two (*Neooxyartes* Ho, 2018, *Cryptophyllium*) or more (*Spinohirasea* Zompro, 2002, *Paramenexenus* Redtenbacher, 1908) sometimes blunt, spines (Hennemann 2007, Bresseel and Constant 2018a, Bradler et al. 2014, Cumming et al. 2021). The body of the vomer can be symmetrical (*Neooxyartes*) to asymmetrical (*Cryptophyllium*) depending on the size and direction of the spine(s) (Bresseel and Constant 2018a, Cumming et al. 2021).

Species diversity and distribution.—With the description of this new taxon there are now ten known *Presbistus* Kirby, 1896 species. The family Aschiphasmatidae is for the first time recorded from Cambodia, with *Presbistus vitivorus* sp. nov being only the fifth species of stick insect described from the country (Brock et al. 2022).

Presbistus peleus (Gray, 1835), the type species, is the most widespread species in the genus and is recorded from India, Peninsular Malaysia, Singapore, Sumatra, and Borneo (Brock et al. 2022). The holotype originates from "Ora Malabariensi" (Gray 1835), considered the Malabar coast (India) by subsequent authors (Brock 1999, Bragg 2001). However, both authors expressed doubts about the accuracy of the original locality, as all subsequent records originate from Sundaland and the genus has never been confirmed in India. Other species described by Gray (1835) bearing the same collecting data and all "ex collection D. Children" have since been recorded from Peninsular Malaysia (Malacca) (Brock 1999, Bragg 2001). Therefore, the Indian record of *P. peleus* is regarded as erroneous. Furthermore, from photographs of the holotype female available from Brock et al. 2022, it appears that *P. crudelis* (Westwood, 1859) from Sri Lanka is not congeneric with the type species of *Presbistus*, *P. peleus* (Gray, 1835), and belongs in a separate, yet undescribed genus that differs from *Presbistus* by the almost straight profemora, the comparatively shorter mesonotum, and the spoon-shaped subgenital plate. Hence, the genus *Presbistus* is removed from the list of stick insects from India and Sri Lanka.

With *P. vitivorus* sp. nov extending the distribution of *Presbistus* to Cambodia, the genus is shown to be distributed over most of Sundaland, comprising Indochina, the Malay Peninsula, Sumatra, Java, and Borneo.

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First record of *Sanaa regalis* (Orthoptera, Tettigoniidae, Pseudophyllinae) from the central Himalayas

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Abstract

A female individual of *Sanaa regalis* (Brunner von Wattenwyl, 1895) was collected in the Tanahun district of Central Nepal in September 2021. This katydid had been reported prior from India in the East Himalayas and Chhattisgarh in Central India. This is the first record of this species from the Central Himalayas, Nepal. The female of this species differs from its congenerics *S. imperialis* (White, 1846) and *S. intermedia* Beier, 1944 in its ovipositor being distinctly black at the base.

Keywords

grasshopper, katydid, Nepal, new distribution, new record, *Sanaa imperialis*, *Sanaa intermedia*

Introduction

Nepal lies in the middle of the Himalayas, with the eastern end in the Eastern Himalayas near Sikkim, the western end in the Western Himalayas near Uttarakhand, and most of the country in the Central Himalayas. The study of the Tettigoniidae fauna of Nepal dates back to Walker (1869) when he described *Incertana concinna* (Walker, 1869), which was presented to him by Maj. Gen. Thomas Hardwicke. Later, Ragge (1961) reported *Ducetia japonica* (Thunberg, 1815) from Pokhara based on a male specimen collected in 1954. Beier (1962) cited *Sanaa imperialis* (White, 1846) from Nepal. Five more species were recorded by Chopard and Dreux (1966): *Conocephalus (Anisoptera) fuscus* (Fabricius, 1793), *Mecopoda elongata* (Linnaeus, 1758), *Himertula kinneari* (Uvarov, 1924), *Letana recticercis* Chopard & Dreux, 1966 and *Dreuxia incerta* Chopard & Dreux, 1966, followed by Bey-Bienko (1968) who added one more species i.e., *Macroteratura (Stenoteratura) janetscheki* (Bey-Bienko, 1968) from East Nepal. Following this, most of the studies have been done by Ingrisch (1987, 1990a, 1990b, 2001, 2002, 2006), Ingrisch and Garai (2001), and Ingrisch and Shishodia (1998). A few other species are listed in Liu and Xia (1992), Kevan and Jin (1993), Joshi and Manandhar (2001), Shishodia et al. (2010), and most recently in Jin et al. (2020), describing *Macroteratura* (*Stenoteratura*) *twinsloba* Liu, 2020 based on a male holotype at Bishop Museum, Honolulu, USA collected in 1966 from Kathmandu. Joshi and Manandhar (2001) reported a genus named *Scuddrina* (possibly a typo for *Scudderia* Stål, 1873) with limited evidence. *Scudderia* is a New World genus, and its occurrence in Nepal is very unlikely. The referred specimen (Orth. 69) may be somewhere in their collection, but there is doubt as to whether it is *Scudderia*. So far, the most recent comprehensive list of Tettigoniidae reported from Nepal is in Ingrisch (2006), with 45 fully identified species plus 6 species identified to genus level only. The Orthoptera Species File lists 40 species of Tettigoniidae recorded from Nepal (Cigliano et al. 2022). This list, however, omits several valid taxa included in Ingrisch (2006): *Conocephalus* (*Chloroxiphidion*) *laetus* (Redtenbacher, 1891), *Conocephalus* (*Anisoptera*) *fuscus* (Fabricius, 1793) (reported as *Conocephalus* (*Xiphidion*) *discolor*), *Conocephalus* (*Anisoptera*) *melaenus* (Haan, 1843), *Euconocephalus pallidus* (Redtenbacher, 1891), *Xiphidiopsis* (*X.*) *lita* Hebard, 1922, and *Holochlora japonica* Brunner von Wattenwyl, 1878. It also omits some taxa reported by Shishodia (2006, 2007) and Shishodia et al. (2010): *Orthelimaea securigera* (Brunner von Wattenwyl, 1878), *Sanaa imperialis* (originally reported by Beier 1962), and *Tegra viridivitta* (Walker, 1870), and two more by Joshi and Manandhar (2001): *Isopsera pedunculata* Brunner von Wattenwyl, 1878 and *Phaneroptera* (*Phaneroptera*) *myllocerca* Ragge, 1956. The last two reported by Joshi and Manandhar (2001) were also omitted by Ingrisch (2006), but Ingrisch (2006) never referenced the aforementioned literature. After examination of the relevant literature, the number of Tettigoniidae recorded from Nepal seems to be around 55. That being said, an updated checklist is required.

Sanaa regalis is a colorful katydid described originally from Sikkim and later reported from Darjeeling, Assam, Nagaland, West Bengal, and Arunanchal Pradesh in the East Himalayas (Ingrisch 2002, Barman 2003, Gogoi et al. 2015) and Raipur, Chhattisgarh in Central India (Gupta and Chandra 2018). It can be recognized by the four large greenish yellow maculae on its brown tegmina. There are several black blemishes on the brown part of the tegmina, and numerous bluish streaks on a black background

on the hindwings. The hindwings are spotted anteriorly. The pronotum is greenish yellow, and the rest of the body is mostly black with tinges of brown in some parts. The subgenital plate of the male is black, while the ovipositor of the female is black at its base (Beier 1962, Barman 2003, Cigliano et al. 2022).

Here, we report the first record of this species from the Central Himalayas in Nepal.

Methods

The individual was seen by the first author as a chance encounter on a rural road in Shuklagandaki Municipality in the Tanahun district of Central Nepal (Fig. 7). In the field, this unique-looking Tettigoniidae could only be identified as a female Pseudophyllinae. The individual was handpicked, stored in a perforated vial, and brought to Pokhara alive for further study. Photographs of the live individual were then taken (Figs 1, 2) using a Canon 7D mark II with 100 mm f/2.8L Macro IS USM lens. For further identification, the individual was euthanized using ethyl acetate, and the specimen was taken to Agriculture and Forestry University (AFU), Chitwan. It was pinned and spread, and photographs of different parts were taken (Figs 3–6) with the same setup as above. The location and altitude of the collection locality were determined using Google Maps, and a map of the study area was created using ArcMap 10.4. The specimen is deposited at Annapurna Natural History Museum, Pokhara.

Identification was done using Beier (1962), Barman (2003), and the Orthoptera Species File (Cigliano et al. 2022). The identification was confirmed by Dr. Sigfrid Ingrisch (Research Museum Alexander Koenig, Germany).

Fig. 1. Female individual of *S. regalis* from Tanahun. Photograph taken in Pokhara on 21 Sept. 2021 on a *Tagetes* L. plant.

Fig. 2. Female individual of *S. regalis* from Tanahun showing the front and ventral sides of the head.

Fig. 3. Habitus (dorsal). Apices of tegmina lost due to improper handling; refer to Fig. 1.

Fig. 4. Habitus (ventral).

Fig. 5. Ovipositor of the female *S. regalis* showing its distinctly black base.

Fig. 6. Habitus (lateral).

Fig. 7. Map of Nepal showing the discovery area.

Results

Taxonomy

Family Tettigoniidae Krauss, 1902
Subfamily Pseudophyllinae Burmeister, 1838
Supertribe Pseudophylliti Burmeister, 1838
Tribe Cymatomerini Brunner von Wattenwyl, 1895

Genus *Sanaa* Walker, 1870

Type species.—*Sanaa regalis* (Brunner von Wattenwyl, 1895)

Comparison with congeners.—There are two other species of *Sanaa*, both reported from the Indomalaya region: *S. intermedia* Beier, 1944, originally reported from Than-Moi, Vietnam, and *S. imperialis* (White, 1846), originally reported from Sylhet, Bangladesh (Orthoptera Species File Version 5.0/5.0). The latter species, however, is also recorded from Nepal (Beier 1962). The female of *S. regalis* differs from that of *S. imperialis* mainly in having its ovipositor black at the base, while the ovipositor of *S. imperialis* is yellow (Barman 2003). Similarly, the ovipositor of *S. intermedia* is yellow-brown at the base (Beier 1962).

Material examined.—NEPAL • 1♀; Mandery, Shuklagandaki, Tanahun, Gandaki Province, 28°02'27"N, 84°01'30"E, 570 m a.s.l.; 20 Sept. 2021; Coll. Sajan K.C.

Previously known distribution.—India: Sikkim, Darjeeling, Assam, Nagaland, Arunanchal Pradesh, West Bengal, Chhattisgarh

Habitat and ecology.—The individual was observed on a rural road near bushes in the mid hills of central Nepal at 15:00 hours (+5.46 GMT) on a clear day. The elevation was 570 m a.sl. Dominant local tree species include *Castanopsis indica* (J. Roxb. ex Lindl.) A. DC. and *Schima wallichii* (DC.) Korth. along with the bushes of *Rubus ellipticus* Sm.

Discussion

Studies of the Orthoptera of Nepal have been scarce in recent years, and it is not surprising to find a species in Nepal that had only ever been reported from neighboring countries. *Sanaa regalis* is probably also found in East Nepal, as well as at higher or lower altitudes, since it has been reported at higher (Sikkim, Darjeeling, Arunanchal Pradesh, Nagaland) and lower (Assam, West Bengal, Chhattisgarh) altitudes in the East Himalayas and Central India.

Further research could significantly extend the knowledge on the Tettigoniidae of Nepal.

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Pylaemenes gulinqingensis sp. nov., a new species of subfamily Dataminae (Phasmida, Heteropterygidae) from Yunnan Province, China

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Abstract

Pylaemenes gulinqingensis **sp. nov.**, from Gulinqing Nature Reserve, Maguan County, Yunnan, China, is described for the first time from two females and six eggs. The types of the new species are deposited in Southwest Forestry University (SWFU), China, as well as in the first author's collection.

Keywords

Dataminae, Datamini, new taxa, stick insects

Introduction

The genus *Pylaemenes* Stål, 1875 belongs to the tribe Datamini in the subfamily Dataminae of the family Heteropterygidae (Bank et al. 2021, Brock et al. 2022). *Pylaemenes* consists of 20 valid taxa and is distributed in the following areas: Vietnam (3 spp.), Indonesia (7 spp.), Malaysia and Singapore (both Peninsular Malaysia and Borneo) (8 spp.), Thailand (1 sp.), and China (1 sp.) (Ho 2013, 2016, 2018, Seow-Chone 2017a, b, 2018, 2020, 2021, Bresseel and Jiaranaisakul 2021, Hennemann 2021, Brock et al. 2022). This genus can be separated from the most related *Orestes* Redtenbacher, 1906 by a combination of the following characteristics: meso- and metanotum flattened or slightly tectiform and with distinctly raised median carina and lateral carinae (the thickened lateral edges of meso- and metanotum) and the conically elevated back of the head (Bresseel and Constant 2018, Bresseel and Jiaranaisakul 2021).

Recent phylogenetic studies have shown the genus *Pylaemenes* to be paraphyletic (Bank et al. 2021). Due to the lack of materials from important areas, the generic attribution of species in this genus remains difficult and needs revision (Bresseel and Jiaranaisakul 2021, Hennemann 2021). In this paper, we describe the second species of *Pylaemenes* from China: *P. gulinqingensis* sp. nov.

Materials and methods

The systematic treatment followed that of Brock et al. (2022) and Bank et al. (2021). The nomenclature of the cephalic armature follows Bresseel and Constant (2020). Egg descriptions follow Clark-Sellick (1997). The specimens were collected directly during night surveys with the help of head torches. Photographs of specimens were taken using a Sony a6300 with LAOWA 60 mm F2.8 Marco. Photos were improved using Adobe Photoshop 2020 and Adobe Lightroom classic. The types of the new species are deposited in Southwest Forestry University (SWFU), China, and the first author's private collection (GHR).

Results

Taxonomy

Pylaemenes Stål, 1875

Type species.—*Phasma coronatum* de Haan, 1842 (= *Pylaemenes coronatus*), by subsequent designation; authority: Kirby (1904).

Distribution.—China (Yunnan); Indonesia; Malaysia; Singapore; Thailand; Vietnam.

Species included from China.—*Pylaemenes pui* Ho, 2013 [China: Pu'er and Xishuangbanna] (Fig. 3D); *Pylaemenes gulinqingensis* sp. nov. [China: Wenshan].

Suggested common name (Chinese).—瘤蝻属

Pylaemenes gulinqingensis sp. nov.

http://zoobank.org/88341FFD-BE99-4BF3-AB26-44D8FAD72EF9
Figs 1–3A, B

Material examined.—**Holotype: CHINA** • ♀; Yunnan Province, Wenshan Zhuang and Miao Autonomous Prefecture, Maguan County; Gulinqing Provincial Nature Reserve; 22.843324°N, 103.984206°E; 25 August 2020; Xiang-Jin Liu leg; SWFU. **Paratype: CHINA** • 1♀; Yunnan Province, Wenshan Zhuang and Miao Autonomous Prefecture, Maguan County; Gulinqing Provincial Nature Reserve; 29 August 2020; Xiang-Jin Liu leg; GHR • 6 eggs (naturally laid by holotype); same information as holotype; SWFU.

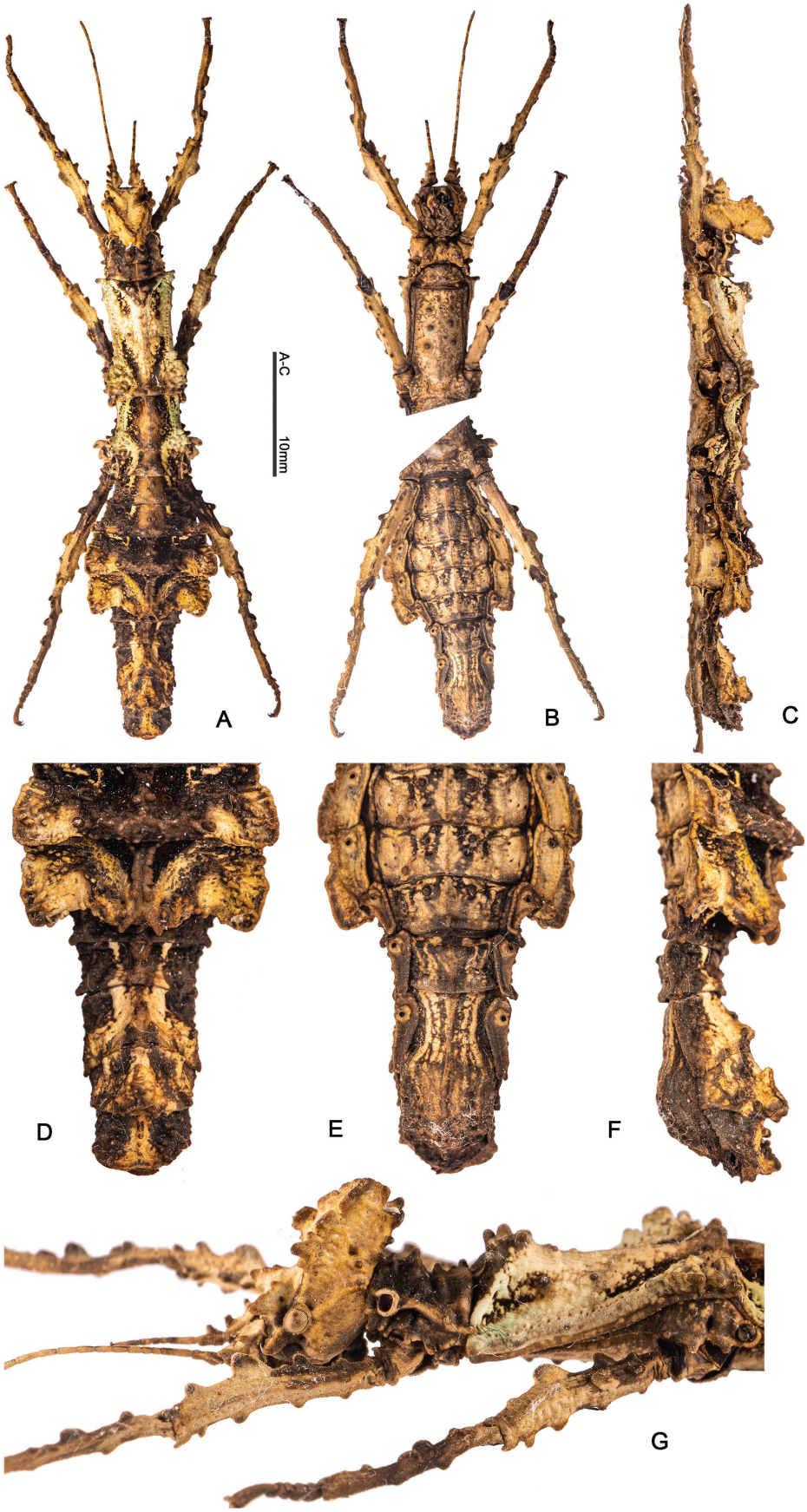

Fig. 1. Female (HT) of *Pylaemenes gulinqingensis* sp. nov. Habitus **A.** Dorsal; **B.** Lateral; **C.** Ventral, end of the abdomen; **D.** Dorsal; **E.** Lateral; **F.** Ventral, head and thorax **G.** Lateral.

Diagnosis.—The females of the new species are very similar to *P. pui*. They share the same elevated structure on the back of the head and strongly widening abdominal terga II–IV, but they can be separated by the lack of x-shaped elevations on terga II–IV and different leg armature (Fig. 1A). In the new species, the lateral margin of the abdominal terga III–IV expansions lateral, like lamellae. The new species is variegated with yellow and green; it resembles a stick covered with moss, while other species of the genus almost all resemble a brown dry stick.

Distribution.—China, Gulinqing Provincial Nature Reserve. Only known from type locality.

Etymology.—The new species is named after the type locality Gulingqing Provincial Nature Reserve.

Description.—**Female**. Small size. Body robust and rough. General color yellow to brown with green variegation.

Head. Occiput strongly projecting posteriorly, cone-like, deep V-shaped in dorsal view, lateral surface punctulate with a shallow notch apically. Occipital spines are triangular humps, posterior supra-occipitals shorter and smaller than anterior supra-occipital spines. Supra-orbital spines strong, laterally compressed and lamellate, directed towards the central coronal spine. Central coronal spine present at the apex of the vertex. Posterior and lateral coronal spines present as conical tubercles (Fig. 1G). Compound eyes round and small with postocular carina behind them. Antennae setose, longer than profemora but shorter than the front legs, with 25 segments. Scapus triangular, with 2 short lobes. Pedicellus shorter than scapus.

Thorax. Pronotum short, trapezoidal, with conspicuous "+" sulcus, four pair tubercles along the longitudinal sulcus, two pairs before the transverse sulcus, two pairs behind; lateral margins with two short tubercles. One cup-like organ on the propleura near the anterior margin. Mesonotum with indistinct carina, the anterior apex of carina with six tubercles irregularly arranged, another two tubercles on the carina; lateral margins widening towards anterior, with several small tubercles elevated apically with the posterior margin elevated. Metanotum median carina distinct, sparsely covered with small granules, lateral margins elevated apically. Metapleura with two crescent-shaped lobes each, widening laterally and almost covering each metacoxa.

Abdomen. Median segment rugose with three granules near posterior margin medially. Terga II–IV gradually widening towards the posterior; terga V slightly narrower than terga IV but wider than terga VI–IX (Fig. 1D). Terga VI to anal segment almost equal in width to each other. Terga III–IV expansions lateral. Terga II–VIII armed with a pair of granules near the posterior margin medially. Terga IX hump. Anal segment shorter than tergum IX, with distinct median carina. Subgenital plate boat shaped, not surpassing the end of the anal segment, with distinct median and lateral carinae. Cerci exposed not obviously, apical round.

Legs. Profemora curved basally; antero-dorsal carina with three lobes and not equal in size; postero-dorsal carina with four lobes, the third one biggest. Protibiae armed with one to two lobes. Mesofemora with antero-dorsal carina with three lobes, increasing in size towards the apex; postero-dorsal carina armed with two lobes. Metafemora with the antero-dorsal carina with four lobes, the third being the biggest; postero-dorsal carina armed with three lobes, the last one ear shaped.

Male. Unknown.

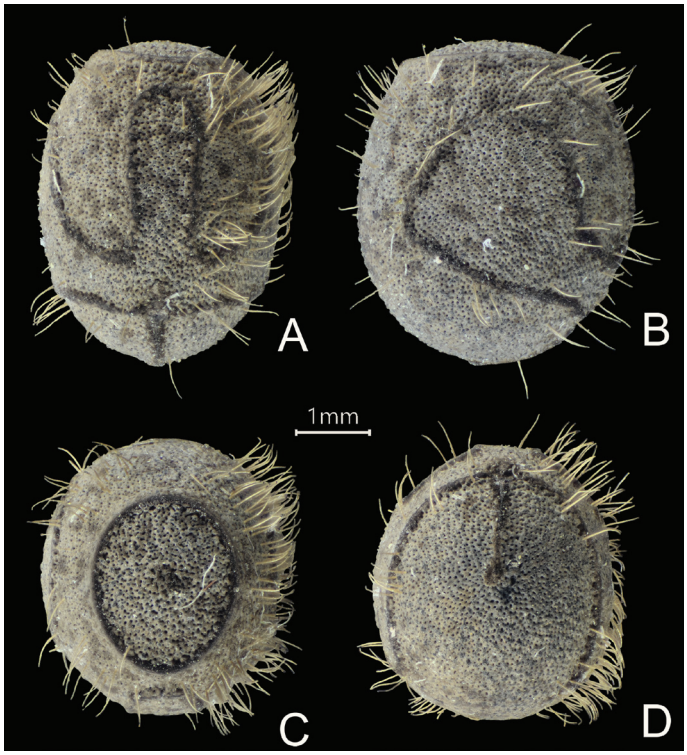

Fig. 2. Egg of *Pylaemenes gulinqingensis* sp. nov. **A.** Dorsal; **B.** Lateral; **C.** Operculum; **D.** Pole.

Egg. Measurements [mm]: Length: 3.6; width: 3.3; height: 4.2. Capsule dark brown with dark spots, oval, posterior pole rounded; surface densely punctulate and sparsely covered with pale setae with a distal black structure. Operculum sub-circular, slightly convex. Micropylar plate tri-lobate with one anterior expansion and two posterior expansions like an inverse Y (Fig. 2A). The margin of micropylar plate darker and indistinctly raised. Median line dark and indistinctly raised.

Measurements (in mm).—♀. Body 39.2–48.5, head 4.5, antennae 15.0, pronotum 3.3–3.8, mesonotum 7.7–10.3, profemora 8.4–9.7, mesofemora 8.2–8.4, metafemora 10.2–10.5, protibiae 8.0–8.8, mesotibiae 6.3–7.0, metatibiae 8.3–9.5.

Discussion

How to differentiate the genera *Pylaemenes* and *Orestes* accurately and deal with the problem of synonymy is the focus of current research on the subfamily Dataminae (Bresseel and Jiaranaisakul 2021, Hennemann 2021). For the species present in China, Ho (2013) described the genus *Hainanphasma* Ho, 2013, with two species—*H. cristatum* Ho, 2013 (Fig. 3C) and *H. diaoluoshanensis* Ho, 2013—both endemic to Hainan, with weak generic distinction. Bresseel and Constant (2018) had already discussed this genus and pointed out examples and problems. Obviously, the genus *Hainanphasma* is doubtful, and a revision of the subfamily Dataminae is needed.

The new species presented here is particular in that it appears variegated like moss. We suggest that this coloration is due to the fact that the new species is from a high-altitude moss forest; unfortunately, no altitude data was recorded in the field collection. Gulinqing Nature Reserve has forests ranging from about 1000 m to over 2000 m. Our type specimens were collected

Fig. 3. Living photos. **A, B.** *Pylaemenes gulinqingensis* sp. nov. (Gulinqing, Yunnan, China); **C.** *Hainanphasma cristata* Ho, 2013 (Mt. jianfengling, Hainan Island, China); **D.** *P. pui* Ho, 2013 (Mengla, Yunnan, China). Photo credit **A–C.** Pei-Lin Liao; **D.** Chao Wu.

in the middle area, and the number of specimens is small. If our hypothesis is true, high-altitude and low-altitude species may show different diversity (both morphologically and molecularly). The Chinese fauna of the subfamily Dataminae currently includes 10 specie, with the description of the new species. However, the species diversity of this subfamily in China is probably higher. Most of the species of this subfamily come from relatively low altitude in southern China. Therefore, in the relatively high-altitude mountains of southern China, there may be interesting species waiting to be discovered. Bank et al. (2021) analyzed the geographical locations of the subfamily Dataminae, including the Wallacea, Borneo, and mainland Asia. Therefore, in places such as Laos, Cambodia, Myanmar, and other places where species are still poorly known, we believe that more species will be discovered.

Acknowledgements

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Three new species of *Amblyrhethus* (Orthoptera, Grylloidea, Gryllidae, Paroecanthini) from Brazil

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Abstract

Amblyrhethus Kirby, 1906 is a genus of arboreal, undergrowth, and shrub crickets comprising, at present, seven species: one from Panama, one from Peru, two from Colombia, two from Brazil, and one with an unprecise locality. These crickets are seldom found in regular active collecting at night, although males produce a rather loud calling song. Unfortunately, their songs have never been recorded, and there is no ecological information for this genus so far. Here, we describe three new species from the Brazilian Atlantic Forest.

Keywords

cricket, Neotropical, new taxa, South America, taxonomy

Introduction

Paroecanthini crickets are far from fully known (Campos and Desutter-Grandcolas 2020, Campos and Souza-Dias 2021). Taxonomic papers from the last ten years demonstrate that these insects are more diverse than expected, and there are probably several species awaiting to be described (Cadena-Castañeda and Noriega 2015, Gorochov 2017, Campos and Desutter-Grandcolas 2020, Campos et al. 2020, Campos and Souza-Dias 2021). These crickets are morphologically diverse, mainly concerning their forewings, with species apterous, brachypterous, or with completely developed forewings (winged), reflecting directly on their communication modalities (Campos and Desutter-Grandcolas 2020). Frequently found on vegetation during the night, from small bushes to tall canopies, they are mainly recognized by the dorsoventrally flattened ovipositor with rather blunt apical valves and the number of hind tibia subapical spurs (five internal and four external, with a few exceptions).

Amblyrhethus Kirby, 1906, initially named *Amblyopus* Saussure, 1878, was proposed as a synonymy since its original name was preoccupied (Kirby 1906). This South American taxon was initially described with three species: *A. brevipes* (Saussure, 1878) (type species from Colombia), *A. capitatus* (Saussure, 1878) (type locality unknown), and *A. depressus* (Saussure, 1878) (Colombia). Two Brazilian species were described a few years later: *A. manni* Rehn, 1917 (northeast Brazil) and *A. natalensis* Rehn, 1917 (northeast Brazil). Hebard (1928) described a species from a single female from Panama, *Amblyrhethus ponderosus* Herbard, 1928. The last described species is *A. nodifer* Chopard, 1956, from Peru.

Although this genus has more than a century since its description, no acoustic, behavioral, ecological, or distributional data are available except the type localities. Here, we describe three new species, more than 60 years after the last publication. All new species are from Brazil: *A. lineatus* sp. nov. (state of Espirito Santo), *A. bahiensis* sp. nov. (state of Bahia), and *A. alagoensis* sp. nov. (state of Alagoas). We also provide a map of the known distribution of *Amblyrhethus* species.

Material and methods

The specimens were individually stored in glass tubes of 80% ethanol. Individuals were analyzed, compared, and described with a Zeiss Stemi DV4 stereomicroscope. External morphology photographs were taken with a Canon SL2 coupled to a 100 mm macro lens. Male phallic complex and female copulatory papilla were immersed in 70% gel alcohol hand sanitizer (Su 2016) and photographed with a Canon SL2 attached to a Zeiss Stemi DV4 stereomicroscope.

Males and females (when available) were dissected to remove the phallic complex and copulatory papilla, respectively. Male genitalia were treated with 10% potassium hydroxide for a few hours to remove muscular tissues and clarify the sclerites. Copulatory papilla was removed, but no chemical treatment was necessary. Male and female genital structures were stored in a 2 µl tube with 80% ethanol and kept with their respective specimens. Forewing's venation nomenclature follows Desutter-Grandcolas et al. (2017), modified by Schubnel et al. (2019). Genital pieces nomenclature follows Desutter (1987), Desutter-Grandcolas (2003), and Campos and Desutter-Grandcolas (2020).

Type localities of *Amblyrhethus* new species were plotted and edited on a map using Quantum-gis 3.16.8 (QGIS Development Team 2022).

Abbreviations.—

General morphology. 1st ter: first abdominal tergite; **met**: metanotum; **I, II, III**: anterior, median, posterior (leg, tarsomere); **F**: femur; **T**: tibia; **iad, iam, iav**: dorsal, median, ventral apical spurs of hind tibia on inner side; **oad, oam, oav**: dorsal, median, and ventral apical spurs of hind tibia on outer side; **TIII**: subapical and apical spurs formula indicated inner/outer respectively, counted from distal spurs upwards.

Forewings. A1: first anal vein; **A2**: second anal vein; **Cua**: anterior branch of cubital vein; **CuP**: posterior branch of cubital vein; **CuPa**: anterior branch of CuP; **CuPb**: posterior branch of CuP; **hv**: harp veins; **M**: medial vein; **M+Cua**: medial vein + anterior branch of cubital vein; **PCu**: postcubital vein (stridulatory vein); **R**: radial vein; **Sc**: subcostal vein.

Male genitalia. LLophi: lateral lophi of pseudepiphallus; **m**: membrane; **PsP**: pseudepiphallic paramere; **EctAp**: ectophallic apodeme; **arc**: ectophallic arc; **End**: endophallic sclerite; **r**: rami.

Institutions.—

ANSP Academy of Natural Sciences of Drexel University, Philadelphia, United States of America;

BOTU Orthoptera Collection, Instituto de Biociências de Botucatu, Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP), Botucatu, Brazil;

MZSP Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

The holotypes, allotypes, and paratypes are will be deposited in BOTU and MZSP. In label transcriptions, slashes (/) separate lines, bars (|) separate labels, parentheses () contain observations, and brackets [] contain interpretations. The described taxa were compared with *Amblyrhethus brevipes* (type material, Orthoptera Species File (OSF) pictures (Cigliano et al. 2022)), *A. manni* (type material, ANSP), and *A. natalensis* (type material, ANSP).

Results

Taxonomy

Order ORTHOPTERA Olivier, 1789
Superfamily GRYLLOIDEA Laicharting, 1781
Family GRYLLIDAE Laicharting, 1781
Subfamily OECANTHINAE Blanchard, 1845
Tribe Paroecanthini Gorochov, 1986
Subtribe Tafaliscina Desutter, 1988

Genus *Amblyrhethus* Kirby, 1906

Type species.—*Amblyrhethus brevipes* (Saussure, 1878).

***Amblyrhethus lineatus* sp. nov.**
https://zoobank.org/2D6DED73-00F2-4E92-B479-3BF06388BDC0
(Figs 1, 2, 7; Table 1)

Material examined.—**Holotype:** BRAZIL • ♂; E[spírito]S[anto], Linhares, Reserva / Vale do Rio Doce. Mata; January 1996; 1 19°09'10"S, 40°03'93"W; F.A.G. Mello & S.S. Nihei leg.; BOTU. **Paratypes:** BRAZIL • 1♂; same information as holotype; MZSP • 1♂; BA[hia], Mucuri, / Fazenda Farol – mata (forest); January 1996; 18°04'01"S, 39°40'23"W; F.A.G. Mello & S.S. Nihei leg.; BOTU.

Type locality.—Brazil, Espírito Santo, Linhares municipality.

Etymology.—From Latin, *linea*, meaning line or band. Allusive to the lateral bands of the species.

Diagnosis.—This species is distinguished from other species of *Amblyrhethus* by the following characters: body with two distinct whitish-to-yellowish bands going laterally from eyes' margin, lateral lobes of pronotum and reaching the margin of forewing, excepting apical field; longitudinally crossed laterally by a whitish-to-yellowish band on both sides, one on each wing field angulations; front, clypeus and gena whitish to yellowish brown, clearly lighter than top of head and remaining medium brown coloration of body; antennomeres whitish with some isolated antennomeres light brown. Basitarsus dorsal spines 3/1. Male forewings: A1 connected to A2; harp crossed by three veins. Male metanotum with two rounded projections, first abdominal tergite with two lamellar projections.

Description.—Head. Fastigium wide, smooth (Fig. 1C). Three ocelli present, aligned in frontal view (Fig. 1C); lateral ocelli rounded, median smaller than lateral ones; frons smooth (Fig. 1C). Antennal scape longer than wide, much narrower than fastigium in frontal view. Maxillary palpi articles 4 and 5 same-sized, article 3 slightly longer; article 5 almost straight (Fig. 1B). Thorax. Dorsal disk wider than long, with bristles on cephalic and caudal margins (Fig. 1A). Dorsal disk cephalic margin slightly concave, caudal margin convex (Fig. 1A). Lateral lobes ventro-cephalic and ventro-caudal angles rounded (Fig. 1B). Forewings longer than abdomen, hindwings as long as forewings (Fig. 1A, B). Legs. TI with tympana on both faces; three apical spurs, two ventral, one dorso-internal. TII with three apical spurs, two ventral, one dorso-internal. TIII subapical spurs 5/4, with one (sometimes two) spine between each spur, six spines above subapical spurs on inner and outer sides. FIII longer than TIII (Fig. 1B). TIII inner apical spurs: iad>iam>iav; outer apical spurs: oam>oav>oad. Basitarsus dorsal spines 3/1; inner apical spur slightly longer than outer apical spur.

Male. Forewings as long as hindwings; anal vein area slightly bulged dorsally (Fig. 1B), A1 connected to A2. Stridulatory vein (PCu vein) present, portion close to CuPa sinuous. Harp crossed by three veins connected to CuPa; first harp vein short, second and third harp veins connected in the proximal region. Mirror as wide as long, divided in the middle by a curved vein. Apical field longer than mirror; lateral field with 14–15 diagonal veins (Fig. 1D). Metanotum with two rounded projections, first abdominal tergite with two lamellar projections (Fig. 1E). Supra-anal plate posterior margin rounded (Fig. 1F); subgenital plate longer than wide, posterior margin convex (Fig. 1G).

Male genitalia: (Fig. 2) Pseudepiphallus: pseudepiphallic sclerite trapezoidal in dorsal and ventral views; almost straight in lateral view; anterior margin somewhat rounded on median region

Table 1. Measurements in mm of *Amblyrhethus lineatus* sp. nov. Abbreviations: **IOD**, inter ocular distance; **HW**, head width; **PL**, pronotum length; **PW**, pronotum width (at midline); **FWL**, forewing length; **LFIII**, length of hind femur; **LTIII**, length of hind tibia.

	IOD	HW	PL	PW	FWL	LFIII	LTIII
Males (n=2)	3	4.9–5	4–4.4	6.5–6.7	18–19	10.1–11	7.7–8.1

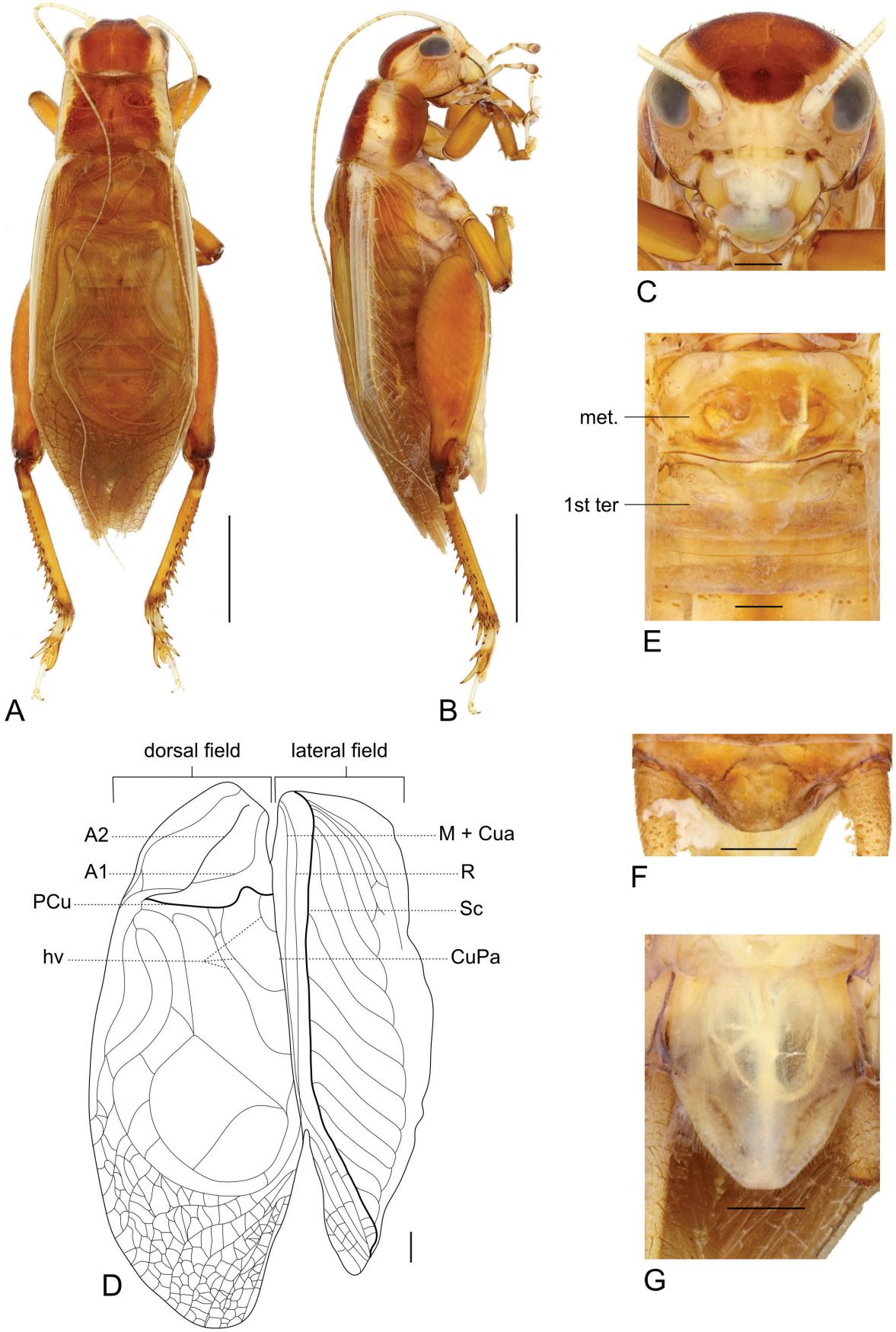

Fig. 1. *Amblyrhethus lineatus* sp. nov., male: **A**. Habitus, dorsal; **B**. Habitus, lateral; **C**. Head, frontal; **D**. Right forewing; **E**. Metanotum and first abdominal tergite; **F**. Supra-anal plate; **G**. Subgenital plate. Scale bars: 5 mm (**A, B**); 1 mm (**C–G**). Abbreviations: see materials and methods.

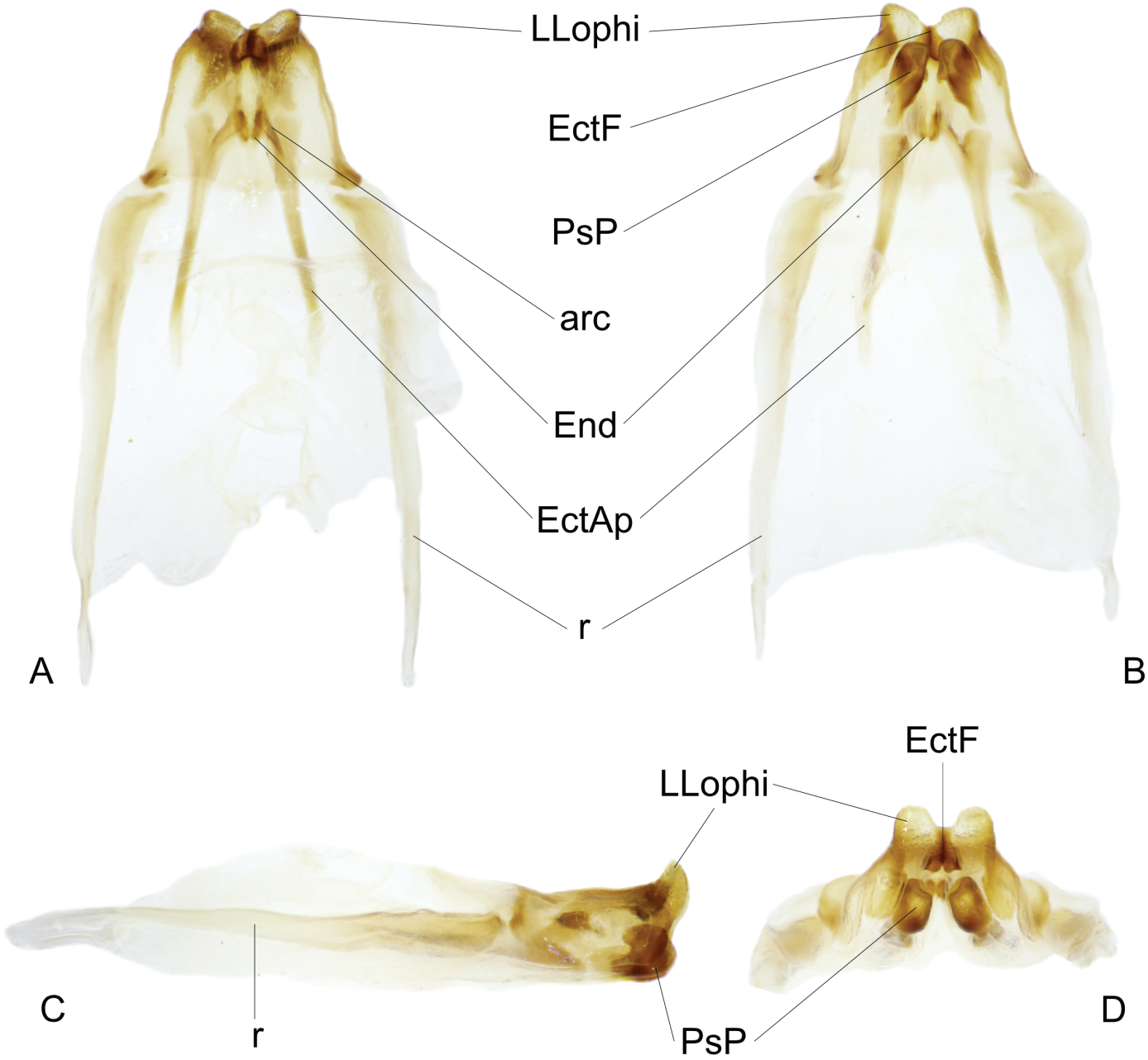

Fig. 2. *Amblyrhethus lineatus* sp. nov., male genitalia: **A**. Dorsal; **B**. Ventral; **C**. Lateral; **D**. Posterior. Scale bar: 1 mm. Abbreviations: see material and methods.

(Fig. 2A). LLophi curved upwards, posterior margin rounded in dorsal and ventral views; ventral face somewhat translucent (Fig. 2A, B). PsP longer than LLophi, inner margin divided into two lobes, not surpassing posterior margin of pseudepiphallic sclerite in dorsal and ventral views (Fig. 2A, B); posterior half wider than anterior half in ventral view (Fig. 2B). Rami straight, two times or more longer than pseudepiphallic sclerite (Fig. 2A–C). Ectophallic invagination: EctF strongly sclerotized, cordiform, on the edge of posterior margin of pseudepiphallic sclerite (Fig. 2A–D). EctAp longer than pseudepiphallic sclerite, slightly curved inwards in dorsal and ventral views (Fig. 2A, B); arc not complete, curved posteriorly; ventral projections of ectophallic invagination as long as arc. Endophallus: End short, u-shaped, in the middle of pseudepiphallic sclerite (Fig. 2B).

Female. Unknown.

Coloration.—Occiput, vertex, and pronotum general coloration reddish brown to dark brown (Fig. 1A, B). Body crossed laterally by a whitish to yellowish band along the fore wings dorsolateral angulation (head, lateral lobes, forewings) (Fig. 1A, B). Occiput reddish brown to dark brown, whitish laterally (Fig. 1A, C); face whitish to yellowish brown (Fig. 1C); antennal scape

whitish; antennomeres whitish with some isolated antenomeres medium brown (Fig. 1B). Forewings slightly translucent, medium brown; region between M+Cua and Sc veins, white. Metanotum and abdominal tergites yellowish-brown (Fig. 1E). Supra-anal plate medium to dark brown, posterior margin darker (Fig. 1F). Abdominal sternites and subgenital plate light brown (Fig. 1G). FI, FII, TI, and TII medium brown to yellowish brown. FIII reddish brown to dark brown, slightly striped, distal margin darker; TIII yellowish brown to medium brown; spurs yellow with apex medium to dark brown; tarsomeres light brown (Fig. 1B).

Amblyrhethus bahiensis sp. nov.

https://zoobank.org/82ED62CF-5218-48DB-BB88-ECBC55168978
(Figs 3, 4, 7; Table 2)

Material examined.—**Holotype:** BRAZIL • ♂; BA[hia], Lençóis / P[ar]q[ue] Nac[ional] da Chapada Diamantina; 12°35'16"S, 41°24'35"W, 600–950 m; 13–19 February 2013; de Mello leg.; CNPq- SISBIOTA | 4453663 | LDC_SIS_001; BOTU.

Type locality.—Brazil, Bahia, Lençóis municipality.

Etymology.—Toponymic, referring to the state of Bahia, Brazil.

Diagnosis.—This species is distinguished from the other species of *Amblyrhethus* by the following characters: male metanotum without projections, first abdominal tergite with two lamellar humps close to anterior margin; supra-anal plate lateral margins finger-shaped. Male genitalia: PsP posterior margin truncated; rami slightly curved inwards; EctAp anterior margin slightly curved outwards in dorsal and ventral views.

Description.—Head. Fastigium wider than long, smooth (Fig. 3C). Three ocelli present, aligned in frontal view (Fig. 3C); lateral ocelli rounded, median ocellus elliptical, smaller than lateral ones; frons smooth (Fig. 3C). Antennal scape longer than wide, thinner than fastigium in frontal view. Maxillary palpi articles 3, 4, and 5 almost same-sized; article 5 sub-straight (Fig. 3B). Thorax. Dorsal disk wider than long, covered by bristles (Fig. 3A). Dorsal disk cephalic margin slightly concave, caudal margin convex (Fig. 3A). Lateral lobes ventro-cephalic and ventro-caudal angles rounded (Fig. 3B). Forewings covering abdomen, hindwings slightly longer than forewings (Fig. 3A, B). Legs. TI with tympana present on inner and outer faces; three apical spurs, two ventral, one dorso-internal. TII with three apical spurs, two ventral, one dorso-internal. TIII subapical spurs 5/4, with one spine between each spur, except proximal spurs with two spines; seven spines above subapical spurs on inner and outer sides. FIII longer than TIII (Fig. 3B). TIII inner apical spurs: iad>iam>iav; outer apical spurs: oam>oav>oad. Basitarsus dorsal spines 3/1; inner apical spur slightly longer than outer apical spur.

Male. Forewings slightly shorter than hindwings; anal area slightly bulged dorsally (Fig. 3B), A1 connected to A2. Stridulatory vein (PCu vein) present, portion close to CuPa strongly sinuous. Harp crossed by four veins connected to CuPa; first and second harp veins shorter than third and fourth; third and fourth harp veins connected in the proximal region. Mirror as wide as long, divided in the middle by a curved vein on its right half. Apical field as long as mirror; lateral field with 12 diagonal veins (Fig. 3D). Metanotum without projections, first abdominal tergite with two lamellar projections close to anterior margin (Fig. 3E). Supra-anal plate posterior margin rounded (Fig. 3F), lateral margins finger-shaped on the middle; subgenital plate as long as wide, posterior margin convex (Fig. 3G).

Male genitalia: (Fig. 4) Pseudepiphallus: pseudepiphallic sclerite trapezoidal in dorsal and ventral views; slightly curved upwards in lateral view; anterior margin somewhat rounded on median region (Fig. 4A). LLophi curved upwards, posterior margin rounded in dorsal and ventral views; ventral face translucent (Fig. 4A, B). PsP longer than LLophi, inner margin not divided, posterior margin truncated, not surpassing posterior margin of pseudepiphallic sclerite in dorsal and ventral views (Fig. 4A, B); posterior half wider than anterior half in ventral view (Fig. 4B). Rami slightly curved inwards in dorsal and ventral views, two or more times longer than pseudepiphallic sclerite (Fig. 4A–C). Ectophallic invagination: EctF strongly sclerotized, triangular, on the edge of posterior margin of pseudepiphallic sclerite (Fig. 4A–D). EctAp longer than pseudepiphallic sclerite, anterior margin slightly curved outwards in dorsal and ventral views (Fig. 4A, B); arc not complete, curved posteriorly; ventral projections of ectophallic invagination shorter than arc. Endophallus: End short, u-shaped in the middle of pseudepiphallic sclerite (Fig. 4B).

Female. Unknown.

Coloration.—Occiput, vertex, and pronotum general coloration reddish brown to medium brown (Fig. 3A, B). Face reddish-brown (Fig. 3C); antennal scape reddish-brown to dark brown; antennomeres yellowish with some isolated antennomeres medium brown (Fig. 3B). Forewings slightly translucent, medium brown. Metanotum whitish brown (Fig. 3E), abdominal tergites medium brown, darker on last segments. Supra-anal plate medium to dark brown, lateral margins darker (Fig. 3F). Abdominal sternites yellowish brown; subgenital plate medium brown (Fig. 3G). FI, FII, TI, and TII medium brown to yellowish brown. FIII yellowish-brown, slightly striped, distal margin darker; TIII yellowish-brown; spurs yellow with apex medium to dark brown; tarsomeres yellowish-brown (Fig. 3B).

Table 2. Measurements in mm of *Amblyrhethus bahiensis* sp. nov. Abbreviations: **IOD**, inter ocular distance; **HW**, head width; **PL**, pronotum length; **PW**, pronotum width (at midline); **FWL**, forewing length; **LFIII**, length of hind femur; **LTIII**, length of hind tibia.

	IOD	HW	PL	PW	FWL	LFIII	LTIII
Male (n=1)	3	4.9–5	4–4.4	6.5–6.7	18–19	10.1–11	7.7–8.1

Amblyrhethus alagoensis sp. nov.

https://zoobank.org/4FDF095B-58E9-42F2-9486-55B7F8708715
(Figs 5, 6, 7; Table 3)

Material examined.—**Holotype:** BRAZIL • ♂; AL[agoas] Quebrangulo / Res[erva] Biol[ógica] Pedra Talhada / Arm[adilha]; Malaise - 1° Bosque; 08–11 September 2002; Refugos; Penteado-Dias & eq[uipe] leg; MZSP. **Allotype:** BRAZIL • ♀; Satuba, Alagoas, Brasil / Área de Proteção Ambiental do Catolé; 25 July 2012; Dias, P.G.B.S, Costa, C.S., Alcântra, D.M.C.; Nihei S.S. leg.; LDC_014; MZSP.

Type locality.—Brazil, Alagoas, Quebrângulo and Satuba municipalities.

Etymology.—Toponymic, referring to the State of Alagoas, Brazil.

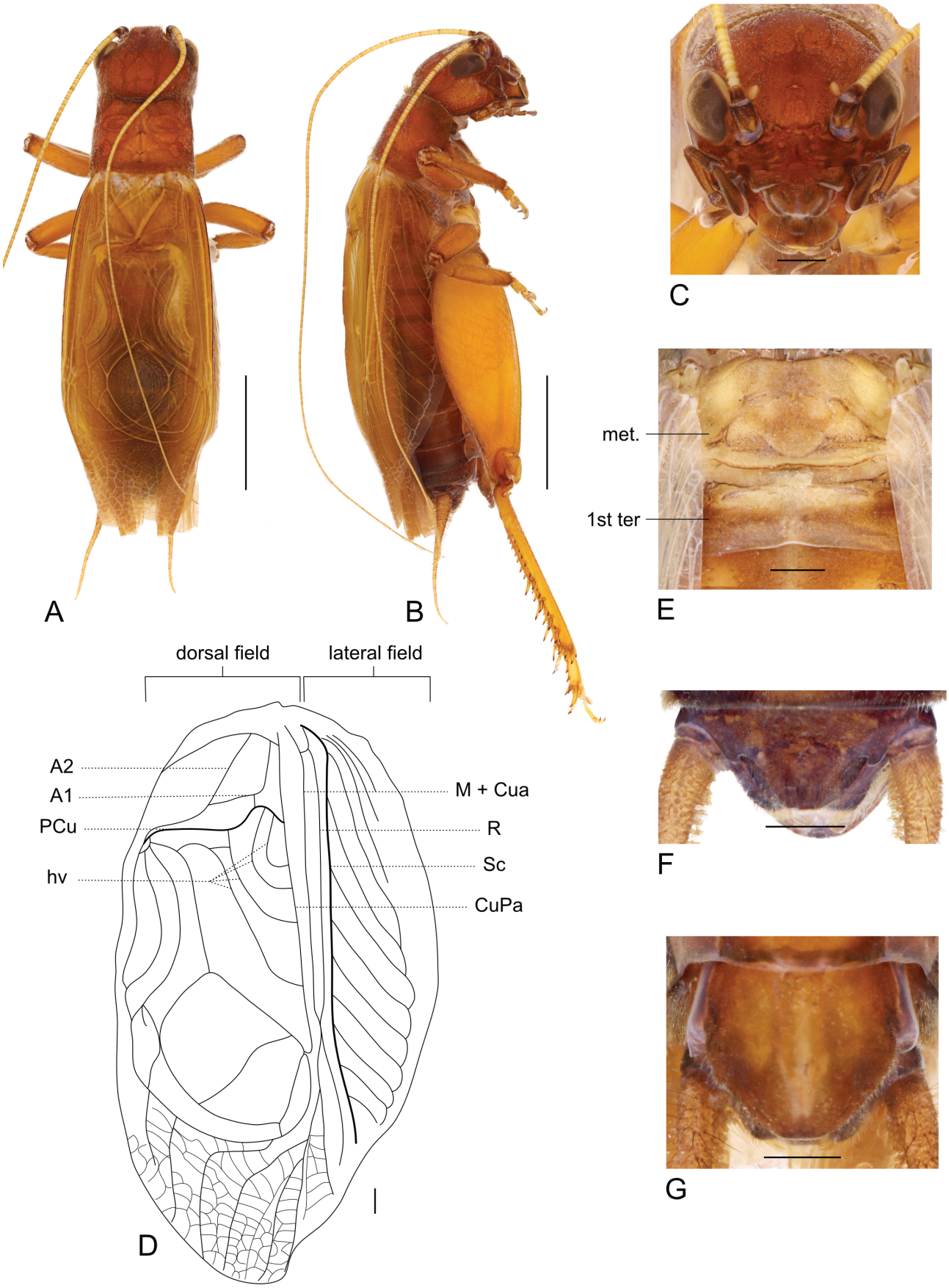

Fig. 3. *Amblyrhethus bahiensis* sp. nov., male: **A**, habitus, dorsal; **B**, habitus, lateral; **C**, head, frontal; **D**, right forewing; **E**, metanotum and first abdominal tergite; **F**, supra-anal plate; **G**, subgenital plate. Scale bars: 5 mm (**A, B**); 1 mm (**C–G**). Abbreviations: see material and methods.

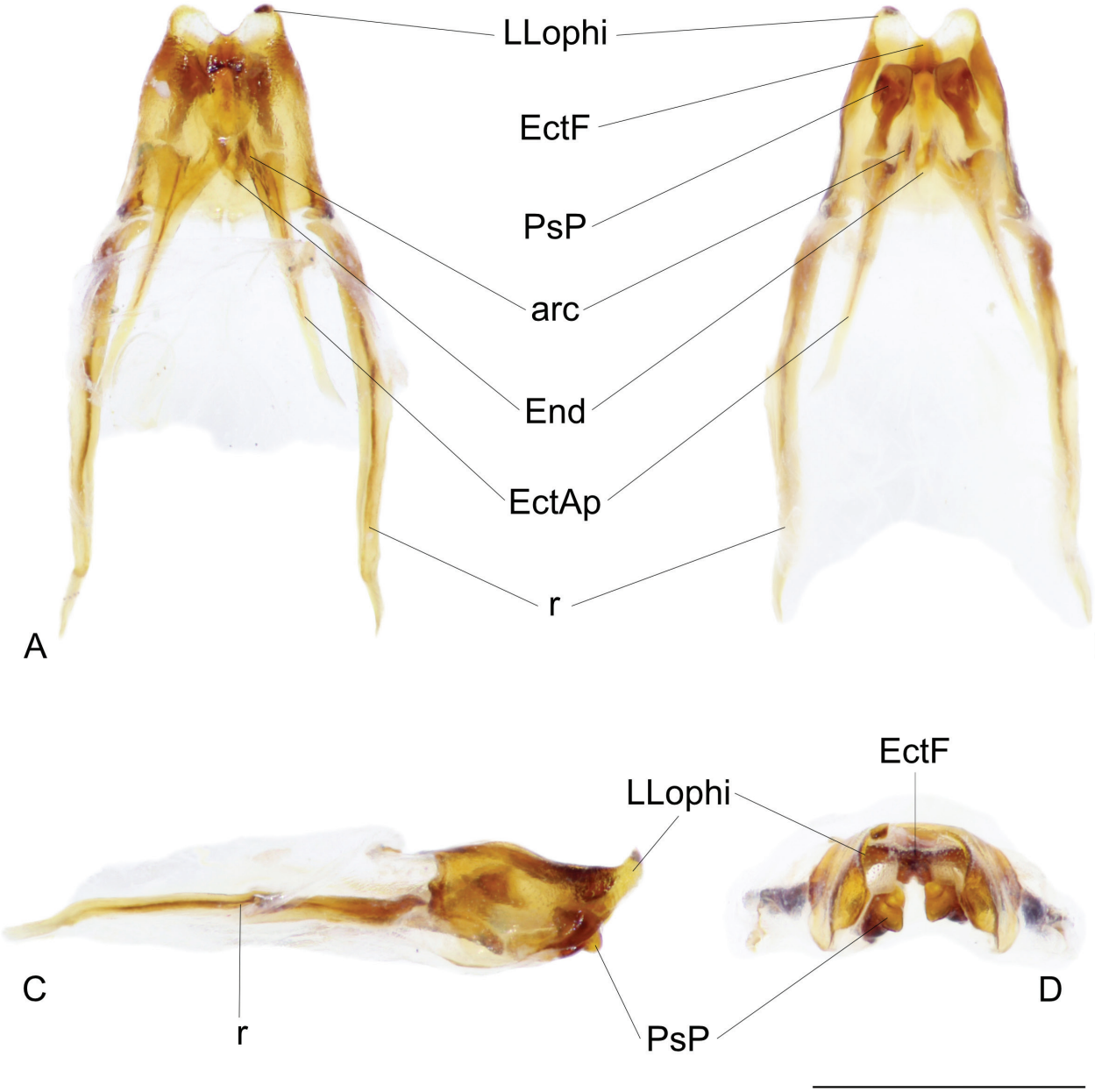

Fig. 4. *Amblyrhethus bahiensis* sp. nov., male genitalia: **A**. dorsal; **B**. ventral; **C**. lateral; **D**. posterior. Scale bar: 1 mm. Abbreviations: Abbreviations: see material and methods.

Diagnosis.—This species is distinguished from other species of *Amblyrhethus* by the following characters: male forewings vein A1 not connected to A2; metanotum with two clusters of bristles on the middle; first abdominal tergite with two rounded projections close to anterior margin. Male genitalia: pseudepiphallic sclerite somewhat enlarged on anterior half, especially at the middle level, rounded in dorsal and ventral views; PsP clavate, EctAp slightly curved inwards in the middle, both in dorsal and ventral views. Copulatory papilla tapered, with two anterior projections.

Description.—Head: Fastigium wide, with bristles laterally (Fig. 5E). Three ocelli present, aligned in frontal view (Fig. 5E); lateral ocelli rounded, median ocellus elliptical, smaller than lateral ones; frons smooth (Fig. 5E). Antennal scape longer than wide, narrower than fastigium in frontal view. Maxillary palpi article 3 the longest, 4 and 5 almost same-sized; article 5 straight (Fig. 5B, D). Thorax: Dorsal disk wider than long, covered by fine pubescence (Fig. 5A, C). Dorsal disk cephalic margin slightly concave, caudal margin convex (Fig. 5A, C). Lateral lobes ventro-cephalic and ventro-caudal angles rounded (Fig. 5B, D). Forewings covering abdomen, hindwings slightly longer than forewings (Fig. 5A–D). Legs: TI with tympana present on inner and outer faces; three apical spurs, two ventral, one dorsal. TII with four apical spurs, two ventral, two dorsal. TIII subapical spurs 5/4, with two spines between each spur, except proximal spurs with three spines; eight spines above subapical spurs on inner and outer sides. FIII longer than TIII (Fig. 5B, D). TIII inner apical spurs: iad>iam>iav; outer apical spurs: oam>oav>oad. Basitarsus dorsal spines 3/1; inner apical spur slightly longer than outer apical spur.

Male. Forewings slightly shorter than hindwings; anal area slightly bulged dorsally (Fig. 5B), A1 not connected to A2. Stridulatory vein (PCu vein) present, portion close to CuPa

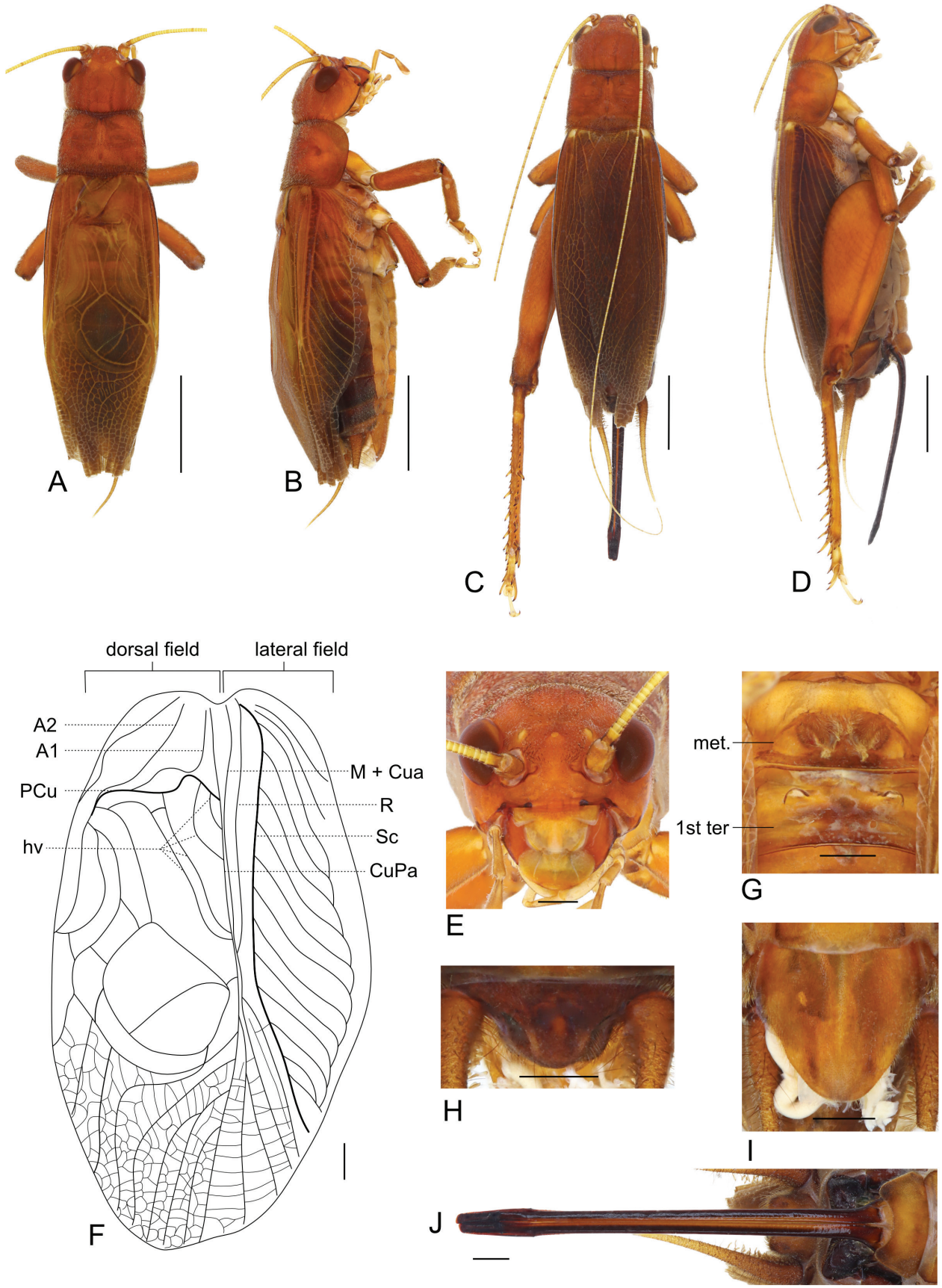

Fig. 5. *Amblyrhethus alagoensis* sp. nov. **A**. Male habitus, dorsal; **B**. Male habitus, lateral; **C**. Female habitus, dorsal; **D**. Female habitus, lateral; **E**. Head, frontal; **F**. Male right forewing; **G**. Male metanotum and first abdominal tergite; **H**. Male supra-anal plate; **I**. Male subgenital plate; **J**. Female subgenital plate and ovipositor. Scale bars 5 mm (**A–D**); 1 mm (**E–J**). Abbreviations: see material and methods.

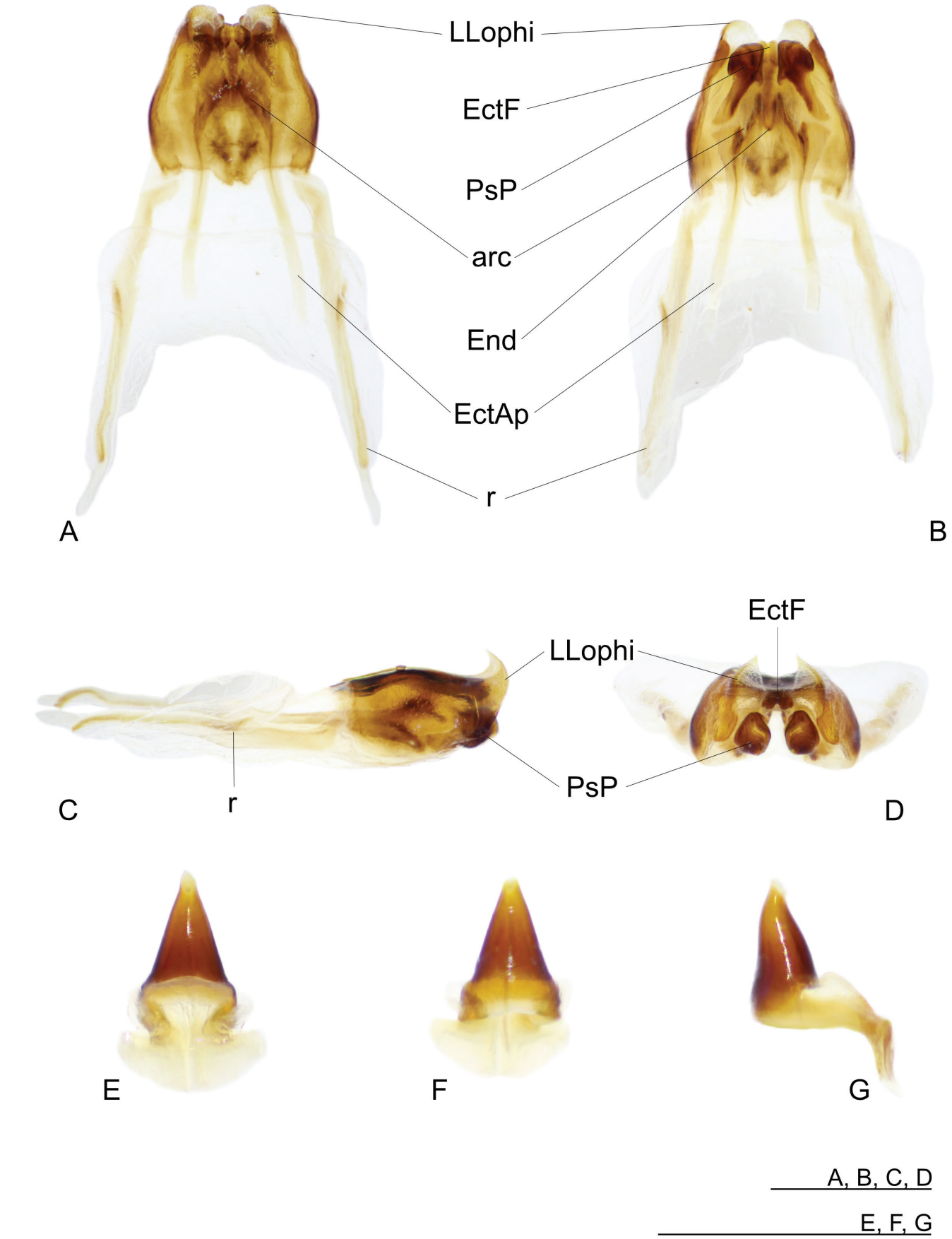

Fig. 6. *Amblyrhethus alagoensis* sp. nov. Male genitalia: **A**. Dorsal; **B**. Ventral; **C**. Lateral; **D**. Posterior. Female copulatory papilla: **E**. Dorsal; **F**. Ventral; **G**. Lateral. Scales 1 mm. Abbreviations: see material and methods.

Fig. 7. Map of the known distribution of *Amblyrhethus* species.

Table 3. Measurements in mm of *Amblyrhethus alagoensis* sp. nov. Abbreviations: **IOD**-inter ocular distance; **HW**-head width; **PL**, pronotum length; **PW**, pronotum width (at midline); **FWL**, forewing length; **LFIII**, length of hind femur; **LTIII**, length of hind tibia; **OL**, ovipositor length.

	IOD	HW	PL	PW	FWL	LFIII	LTIII	OL
Female (n=1)	2.7	5.5	4.1	6	18.1	13.1	11	13
Male (n=1)	2.1	4.2	3.6	4.8	15.1	-	-	-

sinuous. Harp crossed by four veins connected to CuPa; first and second harp veins shorter than third and fourth; third and fourth harp veins connected in the proximal region. Mirror as wide as long, divided in the middle by a curved vein. Apical field longer than mirror; lateral field with 13 diagonal veins (Fig. 5F). Metanotum with two clusters of bristles on the middle, first abdominal tergite with two rounded projections close to anterior margin (Fig. 5G). Supra-anal plate posterior margin rounded (Fig. 5H); subgenital plate longer than wide, posterior margin convex (Fig. 5I).

Male genitalia: (Fig. 6) Pseudepiphallus: pseudepiphallic sclerite trapezoidal in dorsal and ventral views, anterior half inflated; slightly curved upwards in lateral view; anterior margin rounded on median region (Fig. 6A). LLophi curved upwards, posterior margin sub-straight in dorsal and ventral views; ventral face translucent (Fig. 6A, B). PsP clavate, longer than LLophi, not surpassing posterior margin of pseudepiphallic sclerite in dorsal and ventral views, inner margin with anterior projection finger-shaped (Fig. 6A, B). Rami straight in dorsal and ventral views, two times longer than pseudepiphallic sclerite (Fig. 6A–C). Ectophallic invagination: EctF strongly sclerotized, shorter than PsP, trapezoidal on the edge of posterior margin of pseudepiphallic sclerite (Fig. 6A–D). EctAp longer than pseudepiphallic sclerite, slightly curved inwards in the middle in dorsal and ventral views (Fig. 6A, B); arc not complete, curved posteriorly; ventral projections of ectophallic invagination shorter than arc. Endophallus: End short, u-shaped, in the middle of pseudepiphallic sclerite (Fig. 6B).

Female. Larger than male, similar coloration (Fig. 5C, D). Forewings with longitudinal veins crossed by accessory veins. Subgenital plate wider than long, posterior margin concave (Fig. 5J). Ovipositor slightly inclined upwards; apex of ovipositor lateral margins serrulate, posterior margin truncate (Fig. 5C, J). Copulatory papilla bell-shaped, with two posterior thin projections directed ventrally (Fig. 6E–G).

Coloration.—Occiput, vertex, and pronotum general coloration reddish brown (Fig. 5A–D). Face reddish-brown to medium brown (Fig. 5E); antennal scape medium brown; antennomeres yellowish with some isolated antennomeres medium brown (Fig. 5A–D). Forewings slightly translucent, medium brown. Metanotum light brown (Fig. 5G), first three abdominal tergites medium brown, the other tergites dark brown. Supra-anal plate

dark brown (Fig. 5H). Abdominal sternites yellowish brown; subgenital plate medium brown (Fig. 5I). FI, FII, TI, and TII medium brown to reddish brown. FIII reddish brown, slightly striped, distal margin darker; TIII medium brown; spurs yellow with apex dark brown; tarsomeres yellowish-brown (Fig. 5C).

Discussion

Now, with ten valid species, *Amblyrhethus* is the fifth most speciose genus of Paroecanthini. It is right behind *Neometrypus* Desutter, 1988 (13 species), *Angustitrella* Gorochov, 2011 (14 species), *Paroecanthus* Saussure, 1859 (21 species), and *Tafalisca* Walker, 1869 (27 species) (Cigliano et al. 2022). However, knowledge about this genus is very incipient. There are no acoustic, distributional, or ecological data available about this taxon. The difficulty of collecting these crickets could be an important factor contributing to this lack of knowledge (Campos et al. 2020). Such crickets frequently hide on the leaves of bushes and trees, making it difficult to find them. Males are easier to find due to their sound production; however, they are far from being abundant in the field (LDC and FAGM pers. obs.). The difficulty of finding these crickets could also be related to where they hide. There are no records of refuges for *Amblyrhethus* crickets. The relatively short legs related to the body (mainly posterior leg) indicate that the insect could find refuge inside hollow tree branches, a similar type of refuge for other Paroecanthini crickets, such as *Tafalisca* and *Brazitrypa* (Campos et al. 2020).

Four of the seven species of *Amblyrhethus* described before now have an unknown type locality (*A. capitatus*) or an inaccurate type locality, such as *A. brevipes* and *A. depressus* from Colombia, a large country, and *A. ponderosus* from Panama. The low accuracy of the type locality of more than half of *Amblyrhethus* species indicates the need for more data on these crickets, especially field information such as distribution, behavior, and acoustics. These characteristics are crucial to understanding cricket adaptation and diversification. We hope to obtain valuable field data over the next few years on these interesting but poorly known crickets that may have much to tell about evolution, particularly concerning acoustics and habitat adaptation.

Acknowledgments

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New species of awl-head katydids, *Cestrophorus* and *Acanthacara*, from the Andes of Ecuador (Orthoptera, Conocephalinae, Cestrophorini)

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Abstract

The Cestrophorini are small katydids of Ecuador's montane rainforest bearing a prominent awl-shaped fastigium verticis. They are unusual among Conocephalinae in lacking pre-tympanic ear chambers: their eardrums are exposed on their fore tibiae. There are presently two genera, *Cestrophorus* Redtenbacher, 1891 and *Acanthacara* Scudder, 1869. Awl-head habitat includes both climax forest and anthropogenically disturbed areas (e.g., pastures, roadsides) on lower slopes in the drainage of the volcanoes Aliso, Chiles and Tungurahua. At night, males perch on low vegetation and stridulate to attract females. To three extant species, we add a further seven, two in *Cestrophorus* and five in *Acanthacara*. Male calling songs were recorded and analyzed for all three *Cestrophorus* species and for three of the *Acanthacara* spp. We describe and discuss the waveforms of their sinusoid and transient sound pulses in time and frequency domains.

Keywords

bioacoustics, ear, fastigium, montane, sinusoid, song, spectrum, stridulation, transient

Introduction

Dita Klimas and Glenn Morris made several trips to the Ecuadorean Andes (Fig. 1) between 1983 and 2003 in search of tettigoniid sound signals. Near Baños on pasture slopes of Volcán Tungurahua (Fig. 2) and in remnant wet forests southwest of Baeza[1] (Fig. 1), they found species of small conocephaline katydids (Fig. 3). These insects are characterized by a glistening black frons, a prominent, distally attenuated tip-deflected fastigium of the vertex recalling a cobbler's awl (Fig. 4) and, peculiar among conocephalines, superficial tibial tympana, i.e., eardrums not recessed within slitted chambers (Fig. 5). At present, these Andean 'awl-head' insects comprise just two genera: *Cestrophorus* Redtenbacher, 1891 and *Acanthacara* Scudder, 1869 in the tribe Cestrophorini Gorochov, 2015.

The holotype female of *Acanthacara acuta* Scudder, 1869 was collected in 1867 by the naturalist James Orton. As he recounts in *The Andes and the Amazon*, *Or Across the Continent of South America* (Orton 1870), his party journeyed eastward by horse from Quito, over the mountains on a rugged trail via Papallacta to Baeza and Cosanga, then across the Rio Cosanga and on downvalley toward Napo (Archidona, Tena). The Orton expedition's Orthoptera specimens were subsequently identified and named by Samuel H. Scudder (1869); on one of these specimens, a female, Scudder established a monotypic new taxon, *Acanthacara acuta* . This holotype, deposited in the Harvard Museum, lacks forelegs, making it evident why Scudder makes no mention of naked tympana.

In his 1891 monograph on Conocephalidae, Josef Redtenbacher names a conocephalid with superficial tympana: *Cestrophorus paradoxus* Redtenbacher, 1891. "*Ausgezeichnet durch das offene Trommelfell an den Vorderschienen*" [Distinguished by the open tympanum on the fore tibiae.] This species is based upon a lone male specimen labeled as from Madagascar. Label information is "Coll. B. v. Watt. Central Madagascar Dr. H. Dohrn". A very effective colored drawing of the specimen given in Karny's Genera Insectorum (1912, plate 8, item 16) is reproduced here (Fig. 6). On February 10 and 19, 1988, we (Dita Klimas and GKM) collected amongst a large calling deme of this species, males stridulating at dusk in understory vegetation along a trail beside the loud cascade of the Rio Aliso, near where it joins the Rio Cosanga—a locale very far from Madagascar. The two white maculae on the pronotal metazona of the males helped in detection and capture. One supposes Redtenbacher's choice of the name *paradoxus* may have something to do with his finding Madagascar an odd locality or perhaps he reacted to the open eardrums (Since Dohrn only travelled to western Africa, this is likely a case of mislabeling of a specimen coming from his collection in the museum at Stettin).

Recently, Gorochov (2015) described a male specimen of a second *Acanthacara* species, *A. ridiculosa* Gorochov, 2015, taken near the San Rafael Waterfall. This locality is east of the road junction

1 An earthquake in March 1987 damaged the historic townsite of Baeza and led to the creation of a 'displaced Baeza' farther east; our collecting was upslope of the elder Baeza in remnant forest along a path beside a small gurgling stream.

Fig. 1. Part of a map, República del Ecuador, Instituto Geográfico Militar; scale 1:1,000.000. Baños, north of the volcano Tungurahua, is bottom left. Papallacta is top left, just north of Volcan Antisana; Baeza is down-valley to the east. Cosanga the town and Río Cosanga are near map center, a few km beyond Baeza in the direction of Archidona.

at Baeza, farther downvalley in the direction of Coca. Gorochov grouped *Acanthacara* and *Cestrophorus*, making the latter the type genus of a new tribe, Cestrophorini (Gorochov 2015).

We present nine species of Cestrophorini; all but one, *Cestrophorus amplitenuis* sp. nov., are from the drainage of volcanoes Aliso and Tungurahua, including probable males of *Acanthacara acuta*. We have examined a set of photographs of the *A. acuta* type female, kindly provided by Piotr Naskrecki and of higher resolution than those previously available on the Orthoptera Species File Online (Cigliano et al. 2022); our females compare convincingly. The new species *C. amplitenuis* sp. nov. was located in Provincia Carchi, along a road (182) leading from Tofino (nr Tulcan) to the town of Maldonado[2]; a large population of singers were found roadside at night, several kilometers west of the *Espeletia*-dotted paramo of Volcán Chiles and a few kilometers east of Maldonado.

2 Pedro Vicente Maldonado was a famous Ecuadorean scientist, cartographer, etc., of the 18th century. His name appears on two towns in Ecuador: this in Prov. Carchi, but also another in the neighboring Prov. of Esmeraldas.

Fig. 2. Volcán Tungurahua emerges from clouds, 1983.

Fig. 3. A live male of *A. incisa* collected roadside just below the small settlement Pondoa on northern aspect of Volcán Tungurahua, July 1985. Locality in a field name is a bad idea: when what you have christened "Baeza Blackface" is apparently taken later near Baños and you have to reference it as Baños' Baeza Blackface, confusion is likely, especially when these specimens sort into more species later.

Calling song analyses of three of these cestrophorines comprised a poster paper by GKM in 1987 at the VIth International Meeting on Insect Sound and Vibration at Odense, Denmark. At the time, these species were planned to belong to a new genus "*Gymnacoustes*", a reference to their naked tympana. The ISV poster's '*Gymnacoustes isoharmonicus*' (here reproduced as Fig. 17) is the species herein designated *Acanthacara ortoni* sp. nov., and the poster's '*G. unizip*' is *Acanthacara incisa* sp. nov. (Fig. 18). The species epithet *ditachus* resides now in the genus *Cestrophorus*.

A superficially similar undescribed conocephaline from montane areas on the slopes of Volcán Pichincha (near Quito) is readily distinguished from Cestrophorini by its possession of slitted pre-tympanal chambers and a large subnotal resonance chamber formed from the pronotal metazona. This insect is termed "Agraeciine x" by Morris and Mason (1995). This same species is misidentified as *Acanthacara acuta* in a recent paper (Jonsson et al. 2017).

Methods

Dita Klimas and GKM hunted perched katydids by sight at night, scanning by headlamp the vegetation bordering forest paths and taking photographs. The stridulation of tropical tettigoniids is not always useful in revealing a singer's location, but we were also aided by heterodyne devices ('bat detectors'). Specimens were captured by hand-herding into an insect net then transferred individually to small plastic jars. Some field recordings were made using a Sony Walkman tape recorder (WM D6C Stereo Cassette-Corder with an ECM 909 microphone) and are limited to the audio frequency range.

A subset of specimens were individually caged, maintained on pieces of apple, and transported alive via jet aircraft to Toronto, Canada. Here, as they called from a small cylindrical aluminum screen cage, their songs were recorded, with equipment reaching into the ultrasonic (Bruel & Kjaer ¼" microphone 4135 or 1/8"microphone 4138), onto a Racal Store 4 DS Instrumentation Tape Recorder running at 30″/s. The microphone output went initially to a B&K Impulse Precision Sound Level Meter 2204. This in-lab recording system responded to sound frequencies flat to 70 kHz. Room temperature was ~21 °C.

Analysis of analog tape recordings began with digitization. A Krohn-Hite filter (Model 3202) band-passing 125–15000 Hz was employed to anti-alias sound frequencies input to a computer sound card via Cool Edit. The Racal playback was slowed by a factor of 8, so a Cool Edit sample rate of 22050 Hz sufficed to digitize any real-time ultrasonics. Output from the Sony Walkman recorder running in real time was digitized at 48000 samples per second. Fourier transforms were then calculated using the windowing spreadsheet DADiSP (DSP Development Corp.). Figures of time and frequency domain analyses were made using Corel Draw.

Repositories are the Museo de La Plata (MLP) and the Academy of Natural Sciences in Philadelphia (ANSP). Additional pictures, including all holotypes, will be available on Orthoptera Species File Online (Cigliano et al. 2022).

Taxonomy

Cestrophorini Gorochov, 2015

Small agraeciine-like conocephalines with fully exposed tympana. Tegmina in males covering up to the entire abdomen or reduced to about pronotum length; in females, rudimentary or absent. Coloration light yellowish brown to greenish, with whitish, dark brown, or black markings and patterns. Fastigium of vertex

Fig. 4. Scanning electron micrograph (SEM) of male *A. ortoni* fastigium verticis.

Fig. 5. SEM of superficial tympanic membrane on proximal tibia of *A. ortoni*.

acutely pointed, from just projecting beyond antennal scapus to quite long, slightly downcurved or almost straight. Acoustic spiracle tiny, exposed below ventral margin of pronotum. Prosternum unarmed. Ovipositor of females about as long as head and pronotum combined, slightly upcurved (lower margin strongly curved, upper margin little curved or almost straight), moderately broad with acuminate tip. Inhabiting Andean foothills of Ecuador.

Cestrophorus Redtenbacher, 1891

Etymology.—From original description: Greek κέστρο – Latin *subula* [shoemaker's awl] and φέρω – *fero* [bear, carry], surely referring to the notable fastigium: "*fastigium verticis articulo primo antennarum fere duplo longius, subulatum, decurvum*" (Redtenbacher 1891).

Diagnosis.—Small, robust to moderately compact. In males, pronotum posteriorly widened and metazona usually at least slightly elevated; male tegmina covering abdomen completely or leaving only tip exposed, left tegmen uniformly with coarse venation and long cubital vein occupying considerably more than half of total width. Male cerci short, broad, dorsally with obtuse medial lobe, below that terminating in acuminate inward curved spine, and ventrally at the base with another upcurved spine. Male subgenital plate with very short styli, almost looking like latero-terminal tips rather than separately articulated styli, sometimes completely reduced.

Cestrophorus paradoxus Redtenbacher, 1891

Figs 6, 8A, B, 11, 12

Material examined.—ECUADOR • ♂; Río Aliso; 4 Jul. 2003; G.K. Morris leg.; MLP • 6 ♂♂; Río Aliso; 10 Feb. 1988; G.K. Morris leg.; ANSP • 6 ♂♂; Río Aliso; 19 Feb. 1988; G.K. Morris leg.; ANSP • 5 ♂♂; Río Aliso; 4 Jul. 2003; G.K. Morris leg.; ANSP • 1 ♀; Río Aliso; 19 Feb. 1988; G.K. Morris leg.; ANSP • 1♀; Cosanga; 10 Feb. 1988; G.K. Morris leg.; MLP.

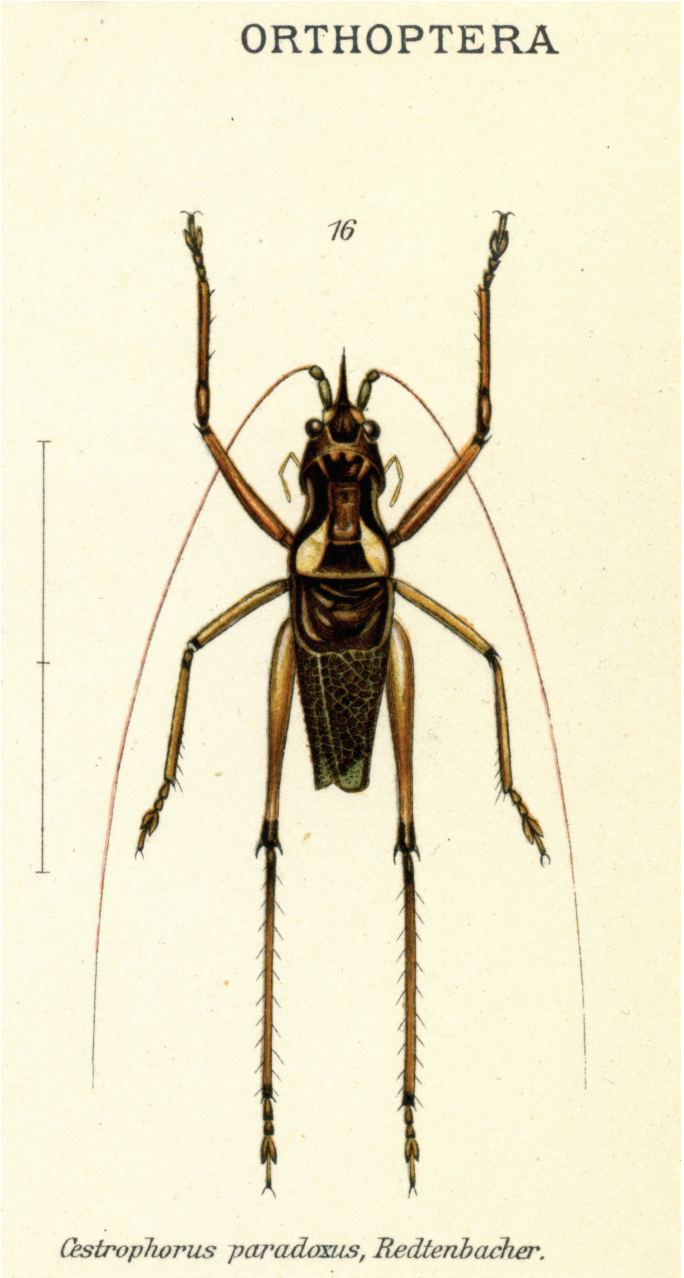

Fig. 6. *C. paradoxus*. Illustration of male adult from Karny H., 1912. Genera Insectorum Orthoptera Fam. Locustidae, Subfam. Agraeciinae (Plate 8, item 16).

Redescription.—Robust with fastigium projecting well beyond scapus. Males with contrasting coloration: fastigium blackish, dorsal surface of pronotum medially dark, in prozona and metazona blackish, in metazona broadly trapezoideal and fringed by a pair of ovoid elongate whitish lateral maculae (Fig. 8A), thin distal portion of hind tibiae blackish. Male tegmina greenish, broadened beyond width of pronotum and covering abdomen completely. Male cerci approximately broadly triangular in dorsal and lateral view, obtuse medial lobes with inconspicuous obtuse and recurved hook, almost touching in the middle, cercus terminating in sharp upcurved spine, and at the base with long and more or less perpendicularly upcurved spine (up to beyond the height of the dorsal hook).

Fig. 7. *C. amplitenuis* pair mating in the field; part of a large deme of singers in shrubby roadside vegetation at the type locality near Ecuador's northern border with Colombia. Female lacks wings.

Measurements.—Male: midline pronotum 4.6 mm, fastigium verticis 1.8 mm, tegmina 9.2 mm; female: midline pronotum 3.8 mm, fastigium verticis 1.7 mm (based on two specimens, no apparent variation in size).

Note.—All specimens—in February 1988 and again in July 2003—were taken from beside a forest path tracing the south bank of the Río Aliso upstream; the site is reached by a (very) secondary road branching west from the main highway just before the town of Cosanga. About 3 km along this sideroad is the lodge Cabañas San Isidro; a few km farther on, a posted sign at an iron bridge identifies the Río Aliso.

Cestrophorus ditachus sp. nov.

https://zoobank.org/39B53563-0D85-42CA-8DF2-80F9C45018AB
Figs 8C, D, 13

('*Gymnacoustes ditachus*' Morris, 1987)

Material examined.—**Holotype:** ECUADOR • ♂; old Baeza; 11 Jul. 1985; G.K. Morris leg.; SN-2, MLP. **Paratypes:** ECUADOR • 1 ♂; old Baeza; 10 Jul. 1985; G.K. Morris leg.; 85-1, Glassy Tegmina, ANSP • 1 ♂; Tungurahua; 25 Feb. 1985; G.K. Morris leg.; GLASSY TEG, SN-3, ANSP • 1 ♀; Cosanga; 19 Feb. 1988; G.K. Morris leg.; MLP • 1 ♀; Cosanga; 19 Feb. 1988; G.K. Morris; ANSP.

Etymology.—Named for its two-part, two-pulse-rate, song structure, readily apparent to the human ear in real time. Greek δι di [two], ταξηοσ tachos [speed]. This insect is also named (inadvertently but deservedly) for Dita Klimas, katydid field photographer extraordinaire.

Diagnosis.—More slender and uniformly colored than *C. paradoxus*, with shorter tegmina. General coloration pale greenish; in males, metazona of pronotum with brown trapezoidal spot fringed by elongate whitish lateral spots. Male tegmina leaving abdomen tip exposed. Females uniformly greenish and apterous. Male cerci with obtusely triangular dorsal lobe (internally with inconspicuous toothlet at the tip) and robust inward-curved acuminate spine, baso-ventral spine with broad base and tapering in perpendicularly upcurved tip; above it on same lobe, another short spine (difficult to see). Styli completely reduced.

Measurements.—Male: midline pronotum 4.3 mm, fastigium verticis 1.7 mm, tegmen 7.5 mm, hind tibiae 8.6 mm; female: mid-

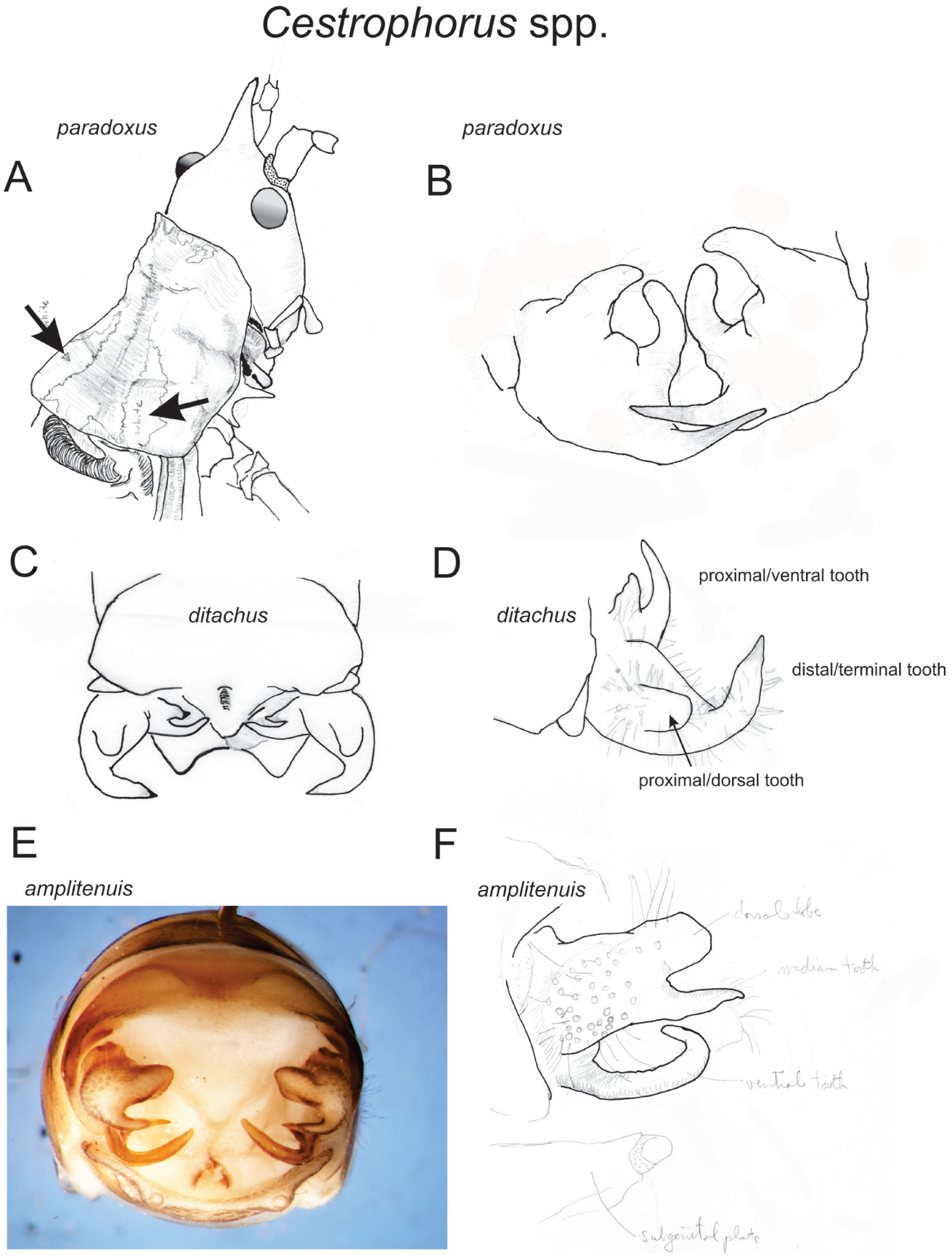

Fig. 8. *Cestrophorus* spp. male genitalia compared. **A.** White pronotal maculae of *C. paradoxus*; **B.** Parameres of *C. paradoxus* 'upside-down dancing anteaters'; **C.** Dorsal aspect *C. ditachus* parameres; **D.** Lateral view of *C. ditachus* paramere; **E.** Photo of terminalia of *C. amplitenuis*; **F.** Lateral aspect of *C. amplitenuis* paramere.

line pronotum 4.1 mm, hind tibiae 9.7 mm, ovipositor 8.7 mm (based on holotype and one paratype).

Field notes.—We hunted in light rain at the [historic pre-earthquake] townsite of Baeza, along a muddy rock-strewn trail fenced by barbed wire, uphill beyond the hospital and cemetery on the night of July 10, 1985. We recorded and captured one male 'agraeciine' of "pearly pale cast", [like *C. paradoxus*] with white maculae prominent laterad on its pronotal metazona, its very pale greenish tegmina shorter than the abdomen, and its eardrums not recessed behind slits [field name 'glassy tegmina']. This specimen is now the holotype male. On July 11, GKM recorded another singer up the eastern branch of the trail above Baeza but failed to capture him.

On July 25, 1985, we drove from Quito and parked part way up Volcán Tungurahua at signed "ecological reserve" hut under construction, below Pondua. Many *C. ditachus* sp. nov. were heard singing from shrubby vegetation scattered about a pasture (never a bovid seen). GKM "recorded a male singing from well above my head in a clump of bamboo and one small hardwood tree. After recording, we bent the bamboo down and searched the foliage with our lights," finding and capturing the presumed singer. "As we left the immediate vicinity of the road and climbed several hundred feet, the incidence of [*C. ditacus sp. nov.*] singers declined to zero. They had ceased calling by 10:30 pm. Chilly and soon one could only hear single quiet lisps recurring at intervals of several seconds, presumably *Acanthacara incisa*."

Cestrophorus amplitenuis sp. nov.

https://zoobank.org/F43EDD15-D715-4F3A-AADD-9426CB04ADFF

Figs 7, 8E, F, 14

Material examined.—**Holotype:** ECUADOR • ♂; Prov. Carchi, hwy 182, e. of Maldonado; 16 Apr. 1990; G.K. Morris leg.; MLP. **Paratypes:** ECUADOR • 1 ♀; Prov. Carchi, hwy 182, e. of Maldonado; 16 Apr. 1990; G.K. Morris leg.; ANSP • 7 ♂♂, 2 ♀♀; Prov. Carchi, hwy 182, e. of Maldonado; 16 Apr. 1990; G.K. Morris leg.; ANSP • 4 ♂♂; Prov. Carchi, nr. road btwn Maldonado and Tulcan, s. of Rio La Plata, 3100 m., primary forest; 26–31 Jul. 1988; Glenn, Pedersen & Wechsler leg.; ANSP on loan to GKM.

Etymology.—Named in reference to the 'dying fall' of each call's amplitude: each song emission begins as intense sinusoids that then diminish (Fig. 14 B,C). Latin *amplio* [made large], *tenuis* [thin].

Diagnosis.—As *C. ditachus,* more slender than *C. paradoxus*. Fastigium short and projecting only a little beyond scapus. General coloration light amber; in males. dorsal surface of pronotum medially dark brown, with whitish lateral fringes, especially in metazona. Male tegmina slender, almost as long as abdomen but leaving tip exposed. Females apterous. Male cerci with obtusely truncated dorsal lobe and acuminate terminal spine; ventro-internal process uniformly thin, fairly long, and slightly twisted.

Measurements.—Male: midline pronotum 4.4 mm, fastigium verticis 1.1 mm, tegmen 7.3 mm, hind tibia 9.1 mm; female: midline pronotum 4.0 mm, fastigium verticis 1.2 mm, hind tibia 9.5 mm, ovipositor 6.7 mm (based on holotype and one paratype).

Field notes.—A road (182) runs west along the Colombian border from Tulcán to Maldonado and beyond. The insects were taken roadside roughly 50 km west of Tulcán. After Tofino, the road climbs the slope of Volcán Chiles into paramo dotted with tall columnar "grey friar" plants. Their flowers are like small sunflowers in clusters. The road was (still is?) a single lane of rough winding dirt that favors switchbacks. We descended into a col of the volcano and passed a strangely colored lake with the strong smell of sulfur in the air. The light was beginning to fade as we crossed a height of land on the west side of the volcano and began to steadily descend. After proceeding downhill for several kilometers, we left the paramo but were not yet into forest. We stopped here to listen, the road bordered by shrubs and sedge, and heard singing.

Acanthacara Scudder, 1869

Etymology.—Not mentioned in the original description; probably derived from Greek ἄκανθα – *ácantha* [thorn] and, as in *Cestrophorus,* certainly referring to the vertex being "prolonged into a sharply pointed, long and curved thorn" (Scudder 1869).

Diagnosis.—Habitus more slender compared to *Cestrophorus*, with more delicately thin and elongate fastigium verticis. Tegmina not much longer than the narrower and more elongate pronotum; in males, the left tegmen with distinctively developed stridulatory area with transparent fields, the vein with the stridulatory file underneath relatively short. Male cerci not conspicuously broad at base and male subgenital plate with distinct styli.

Redescription.—Small and slender, yellowish brown, brachypterous coneheads with strongly oblique face and prominent, almost straight or slightly recurved acuminate fastigium. Body length 17–22 mm; fastigium length almost twice the eye diameter. Pronotum shallow and rounded, dorsal contour flat or almost flat, posteriorly produced and in males diverging overtop bases of short tegmina that are of equal length or little longer than the pronotum, leaving at least half of the abdomen uncovered in live individuals. Stridulatory area of left tegmen subdivided in transparent fields usually free from venation: a speculum lies right behind the short cubital vein, and an adjacent lateral field lies left of this 'mirror'. The cubital vein is fairly bulgy and occupies half or a little more of the total dorsal width of the tegmen. Females are apterous. The tiny acoustic spiracles are directed latero-posteriorly. All genicular lobes except the outer one of the fore tibiae armed. Male cerci at base moderately wide, with more or less prominent distal dorsal process and below that with another inward-directed process that sometimes has a more delicate ventral appendage. Male subgenital plate with short but distinct styli. Coloration ochre or light brown with extensive black markings on face and with darker brown and blackish markings and patterns on pronotum, abdomen and legs. Living in montane woodland.

Notes.—All following diagnoses refer to males. Apart from the development of male tegmina, the species can be distinguished by the shape of male cerci. Measurements of the new species correspond to the holotypes (there is no significant variation among specimens of a particular species and there is little difference in the body size of all species). It is difficult to assign females to corresponding males. Below the species accounts, a key to all seven species is provided.

Acanthacara acuta Scudder, 1869

Figs 9A, 10A

Material examined.—ECUADOR • 1 ♂; Río Aliso, nr San Isidro Resort, 2000 m; 2–6 Jul. 2003; G.K. Morris leg.; MLP • 1 ♂; Baeza; 10 Jul. 1985; ANSP • ♂; Cosanga; 10 Feb. 1988; G.K. Morris leg.; ANSP.

Diagnosis.—Tegmina slightly longer than pronotum; venation at costal margin sometimes greenish. Pronotum sparsely pubescent and with contrasting coloration: lateral lobes dark, dorsal portion light with dark median markings on front and rear margin, sometimes separation of dark lobes and lighter dorsal por-

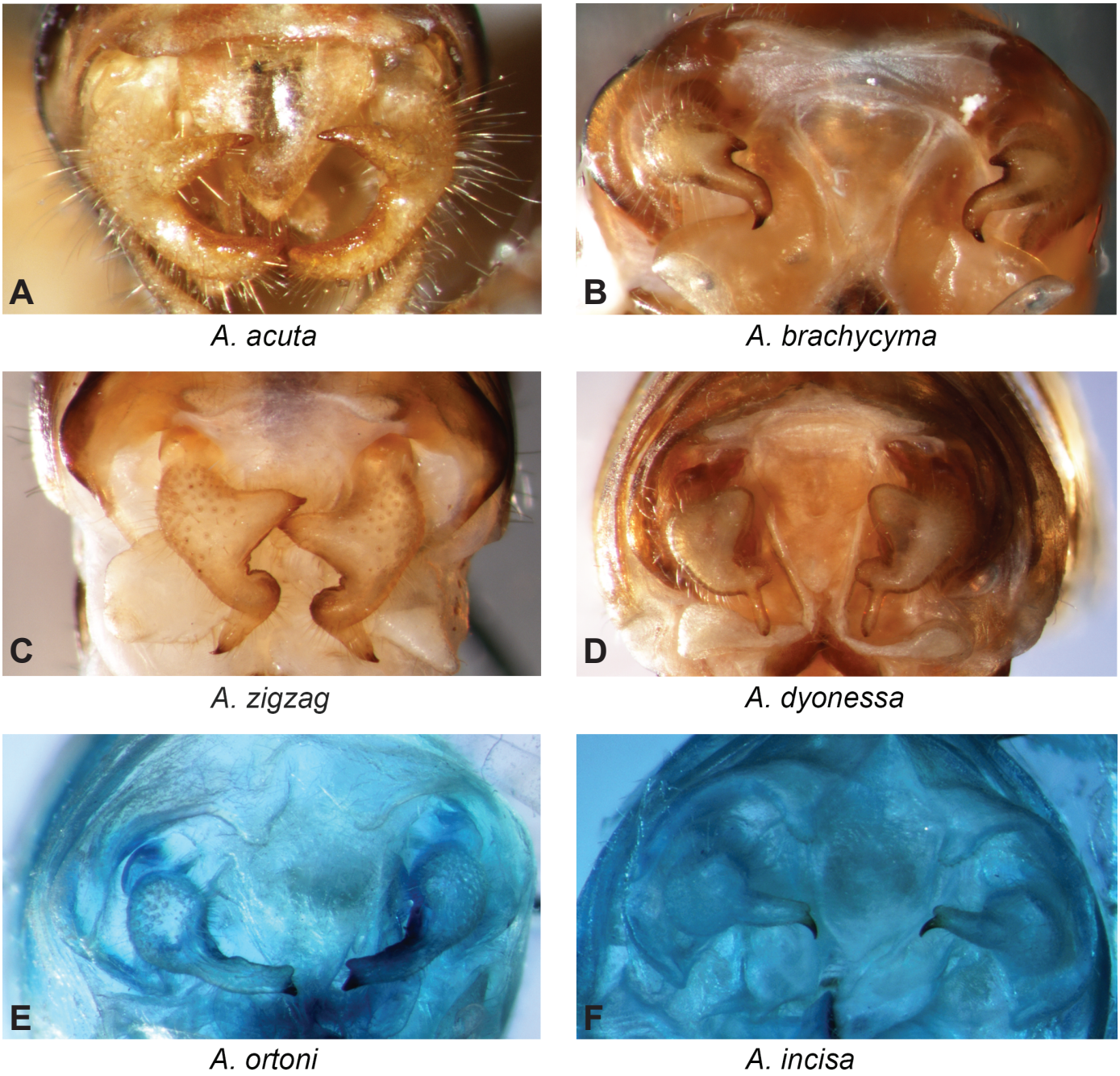

Fig. 9. *Acanthacara* spp. male genitalia compared.

tion developed as light medially restricted lateral stripes on disc. Last tergite shallowly emarginate. Cerci in dorsal portion elongate, inward-curved, and pointed; below that, another, slightly stronger and also inward-directed pointed branch, with dorsally slightly more sclerotized ridge, so the cerci look bifurcate in caudal view. Styli very short but distinctive, 1–2 times as long as wide.

Measurements.—Pronotum 4.2 mm, tegmina 5.1 mm, hind tibiae 9.1 mm.

Notes.—Our three males are so similar to the female holotype of *A. acuta* that we consider them conspecific. Fastigium shape and coloration details of the body match very well (the type is unfortunately lacking all legs except its right middle leg). The female was collected by the naturalist James Orton somewhere between Quito and the Napo region (Scudder 1869). His expedition spent time in Baeza and then camped at a locality about 6 km further south on the banks of the Cosanga River (Orton 1870). This is the very area where our specimens have been found, as well as the ones of the following two new species, which differ in coloration. According to measurements of pronotum and hind femora in the original description, the holotype appears to be adult, not a last-instar nymph as Gurney (1972) suspected.

Acanthacara brachycyma sp. nov.

https://zoobank.org/B40DA89A-98F9-41D6-AE7A-01C907CD5E8A
Figs 9B, 10B, 15

Material examined.—**Holotype:** ECUADOR • ♂; San Isidro, nr Cosanga; 2–6 Jul. 2003; G.K. Morris; MLP. **Paratypes** • 7 ♂♂; San

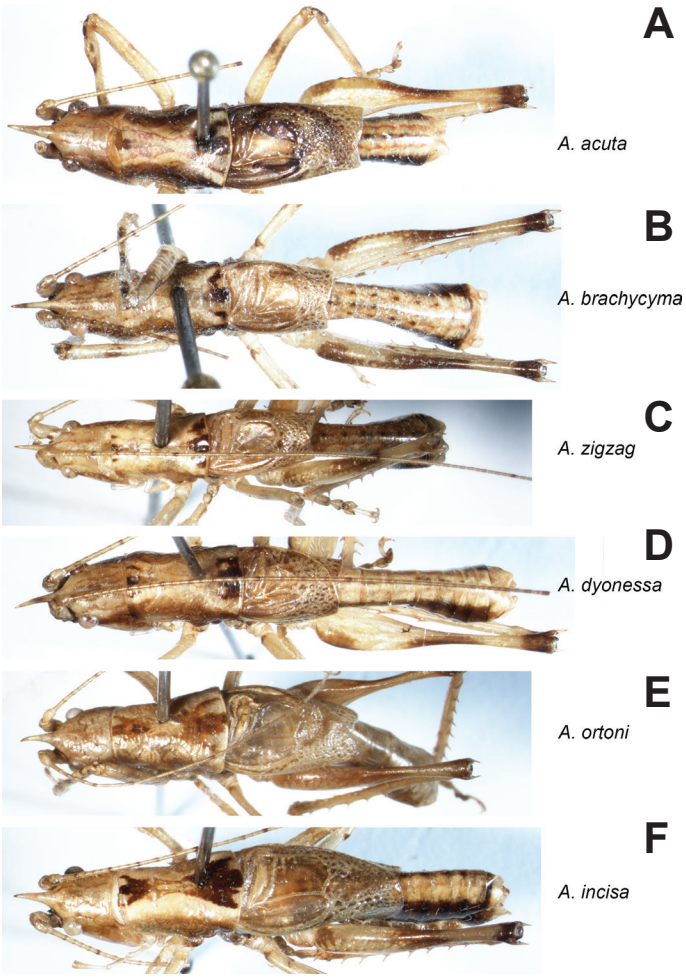

Fig. 10. *Acanthacara* adult males compared in dorsal aspect.

Isidro, nr Cosanga; 2–6 Jul. 2003; G.K. Morris leg.; ANSP • 1 ♂; Cosanga; 10 Feb. 1988; G.K. Morris leg.; ANSP • 1 ♀; San Isidro, nr Cosanga; 2–6 Jul. 2003; G.K. Morris leg.; MLP • 7 ♀♀; San Isidro, nr Cosanga; 2–6 Jul. 2003; G.K. Morris leg.; ANSP.

Etymology.—Greek βραχύς – brachys [short] and κύμα – kyma [wave], a reference to the predominantly ultrasonic spectrum of the song (noun in apposition).

Diagnosis.—Fastigium almost straight, very tip slightly downcurved. Tegmina about as long as pronotum, stridulatory area of left tegmen with translucent fields occupying almost ¾ of total length, the bulgy vein with stridulatory file underneath barely longer than mirror width. Pronotum with small blackish median spot on anterior margin (sometimes surrounded by a pair of smaller spots) and up to five spots on the rear margin, the middle one being the most prominent and the most lateral ones contiguous with the dark coloration of the lateral lobes. Last tergite shallowly bilobate. Cerci with a small dorsal tip and terminating in a ventrally directed process. The dorsal tip is directed medially and obtusely pointed. The ventral process is S-shaped, curving first inward and then downward, with an acute tip.

Notes.—Very similar to *A. ridiculosa* Gorochov, 2015 and distinguished by the following differences: no reticulation on mirror area of left tegmen (dense venation network in *ridiculosa* according to photo in Gorochov 2015, fig. 69, cannot be illumination artifact); rear margin of last tergite shallowly emarginate without distinct lateral tips, rather with very broad lateral lobules (more or less distinctly rounded tips in *ridiculosa*, see ventral view in fig. 71 (Gorochov 2015) for true contour, probably no shrinkage artifact); the secondary (dorsal) tip or process on the cerci is very short when viewed from all possible angles, directed inward, and in approximately same plane as terminal zigzag process (in *ridiculosa*, sticking out in dorsal view, apparently quite long in ventro-lateral view of fig. 72); the zigzag process is distinctly thinner than rest of cercus and fully S-shaped: curved first perpendicularly inward—not quite horizontally but slightly downward—and then halfway-rearward and perpendicularly downward (in *ridiculosa*, not thin over noticeable length, tip close to compact base, the inward-curved part relatively shorter in dorsal view in fig. 70). There are broad, thin and transparent, remotely cup-shaped structures below the cerci into which the latter could be stored, perhaps belonging to the paraproct, without any elongate or pointed processes (in *ridiculosa*, corresponding structure with conspicuous processes visible in fig. 70 and looking acutely pointed in ventral view in fig. 71). Subgenital plate shallowly emarginate, with two lobes between the styli and with very short styli that are hardly twice as long as wide (the subgenital plate of *ridiculosa* has a straight rear margin and the styli considerably longer according to figs 71, 72).

Measurements.—Pronotum 4.3 mm, tegmina 4.0 mm, hind tibiae 9.3 mm.

Acanthacara zigzag sp. nov.

https://zoobank.org/21093D8A-D9B0-486E-A67C-ABA40D71DD7D
Figs 9C, 10C

Material examined.—**Holotype**: ECUADOR • ♂; old Baeza; 10 Jul. 1985; G.K. Morris; MLP. **Paratypes:** ECUADOR • 3 ♂♂; old Baeza; 10 Jul. 1985; G.K. Morris leg.; ANSP • 1 ♂; old Baeza; 23 Apr. 1989; G.K. Morris leg.; ANSP.

Etymology.—Named for the alternating acute-angle direction changes of the male cerci.

Diagnosis.—Very similar to preceding species, with slightly longer cubital vein (longer than width of mirror) and different cerci. Fastigium almost straight. Tegmina of same length as pronotum; pronotum with 1 or 3 small blackish spots on anterior margin and 3 larger spots on rear margin. Last tergite ending in two lobes. Cercus with pointed medial branch, rectangularly inward-directed; below that, another inward-directed process with thinner and downward-directed appendage terminating in acute spinule. The structures below the cerci, mentioned for the previous species (see notes on comparison with *A. ridiculosa* above), here have obtuse posterior tips.

Measurements.—Pronotum 4.0 mm, tegmina 4.3 mm, hind tibiae 7.6 mm.

Acanthacara dyonessa sp. nov.

https://zoobank.org/D5BC4C3E-F9DF-4F7C-99D5-3996BDA5EA9D
Figs 9D, 10D

Material examined.—**Holotype:** ECUADOR • ♂; old Baeza; 8 Apr. 1989; G.K. Morris; SN-2; MLP. **Paratypes:** ECUADOR • 2 ♂♂; Río Huagra Yacu near Baeza; 9 Apr. 1989; G.K. Morris leg.; ANSP • 1 ♂; Baeza; 23 Apr. 1989; G.K. Morris leg.; ANSP • 1 ♂; Baeza; 11 Jul. 1985; G.K. Morris leg.; ANSP.

Etymology.—Greek *dyo* [dive], *nessa* [duck] – referring to shape of male cerci resembling a diving duck.

Diagnosis.—Fastigium slightly longer than in other species. Tegmina as long as pronotum. Pronotum with small blackish spot

on front margin and more or less extensive spot on rear margin. Cerci with bulky and obtuse in- and upward-directed tip, below that with another half as bulky inward-directed process, which has a thin digitiform and pointed ventral appendage. Styli very short and looking like lateral tips of the subgenital plate.

Measurements.—Pronotum 4.5 mm, tegmina 3.9 mm, hind tibiae 9.6 mm.

Acanthacara ortoni sp. nov.

https://zoobank.org/5DFD1F3D-770C-4185-9DEA-AF923FD609A8
Figs 4, 5, 9E, 10E, 16, 17

('*Gymnacoustes isoharmonicus*' – Morris 1987, field name: Baeza Blackface)

Material examined.—**Holotype:** ECUADOR • ♂; Tungurahua, Pondoa; 16 Jul. 1985; G.K. Morris leg.; 85-2; MLP. **Paratypes:** ECUADOR • 1 ♂; Tungurahua, Pondoa; 16 Jul. 1985; G.K. Morris leg.; 85-1; ANSP • 1 ♂; Tungurahua, Pondoa; 16 Jul. 1985; G.K. Morris leg.; 85-3; ANSP • 1 ♂; Tungurahua, Pondoa; 16 Jul. 1985; G.K. Morris leg.; 85-4 [field recorded 1 of 3, 85-1, 85-2, 85-3]; ANSP.

Etymology.—Dedicated to the aforementioned James Orton (1830–1877), Professor of Natural history at Vassar College in New York State, naturalist in South America (Orton 1916, Miller 1982). On his first trip there in 1867 he crossed the continent west to east, starting in Ecuador, securing biological specimens along the way. Among them were 22 new species of orthopterans, including 9 species of katydids (described in Scudder 1869, 3 names of grasshoppers are now considered synonyms). On the way home from his third expedition, after a series of mishaps which affected his health, he unfortunately died during a passage across Lake Titicaca at only 47 years old.

Diagnosis.—Similar to the next species. Tegmina slightly longer than pronotum; dark markings on pronotum indistinct. Last tergite terminally truncate or with broad and shallow emargination (perhaps shrinkage artifact). Cerci with obtuse dorsal tip; below that with curved and tapering inward-directed process, ending with sharp and recurved spine, and above this with small and inconspicuous obtuse tip. Styli about twice as long as wide.

Measurements.—Pronotum 4.7 mm, tegmina 5.2 mm, hind tibiae 8.4 mm.

Acanthacara incisa sp. nov.

https://zoobank.org/5B7E4485-BDD8-4EF1-A73F-86C6939C6954
Figs 3, 9F, 10F, 18, 19

('*Gymnacoustes unizip*' Morris 1987, field name: Baños Blackface)

Material examined.—**Holotype:** ECUADOR • ♂; Tungurahua; 25 Jul. 1985; G.K. Morris leg.; MLP. **Paratypes:** ECUADOR • 1 ♂; Tungurahua; 25 Jul. 1985; G.K. Morris leg.; SN-5, 85-5, Rec.; ANSP • 2 ♂♂; Tungurahua; 26 May 1983; G.K. Morris leg.; ANSP.

Etymology.—Referring to the significant midline emargination of the posterior margin of abdominal tergite IX. In an excess of caution, we are careful to avoid a species name relating to song—e.g., unizip, as given in the ISV poster—for both the preceding *A. ortoni* and *A. incisa*. The two sing in earshot of each other and solitary vs. doubled zips easily distinguish their songs, but some confusion in field naming might have led to misapplication of song to these species.

Diagnosis.—Similar to previous species. Tegmina almost twice as long as pronotum. Pronotum with blackish spot on prozona and posteriorly diverging blackish spot on metazona, both spots connected by more narrow dark coloration in between. Last tergite with deep narrow cleft, wider in distal portion, and the lobes formed by this division with inward-directed tips sporting tiny teeth. Cerci with obtuse dorsal tip as in previous species; below that, with curved inward-directed process; ending also sort of two-tipped, with the lower tip developed as short spinule. Styli almost twice as long as wide.

Measurements.—Pronotum 5.0 mm, tegmina 6.3 mm, hind tibiae 8.4 mm.

Key to species of *Acanthacara* based on males

1 Cerci more or less uniformly bifurcate, with pointed dorsal branch and more prominent pointed ventral branch, both branches directed medially ..... *A. acuta* Scudder, 1869
– Cerci with obtuse or pointed dorsal tip and differently modified ventral portion 2
2 Cerci with more or less pointed dorsal tip and ventral branch ending in a downward projecting and acuminate tip 3
– Cerci with obtuse or little developed dorsal tip, ventral process directed medially; if there are downward-projecting processes, they are clearly set apart from the rest of the ventral branches and much thinner than the latter 5
3 Mirror of left tegmen with venation network ..... *A. ridiculosa* Gorochov, 2015
– Mirror of left tegmen without reticulation 4
4 Cerci with small pointed inward-directed dorsal tip and long ventral process, which is first directed medially and then turns into a downward-projecting acute tip, the horizontal portion being longer than the downward tip ..... *A. brachycyma* sp. nov.
– Cerci with robust pointed inward-directed dorsal tip, the ventral process first directed medially and slightly forward, and then sharply bent perpendicularly downward, ending in an acute tip; the surface of the horizontal portion with microscopic sclerotized toothlets and downward portion longer than horizontal portion in caudal view ..... *A. zigzag* sp. nov.
5 Tegmina as long or shorter than pronotum, cerci with broadly rounded dorsal tip and distinctive ventral branch, consisting of a sturdy and obtuse medially-directed process with a thin downward-projecting appendage, the latter originating slightly before the obtuse tip of the former ..... *A. dyonessa* sp. nov.
– Tegmina longer than pronotum, dorsal tip of cerci indistinct, ventral branch directed medially and tapering into two-tipped end, the ventral tip developed as an acute spine (without downward projecting part) 6
6 Last tergite uniformly light ochreous with caudal margin entire ..... *A. ortoni* sp. nov.
– Last tergite with black anterior third and deep medial emargination ..... *A. incisa* sp. nov.

Cestrophorine signal structure

The mechanical basis of forewing stridulation by katydids is a scraper contacting file teeth to make tegminal speculae oscillate at 'multiplied' frequencies (e.g., *Xiphelimum amplipennis* Morris, Braun & Wirkner, 2016). The diverse sound-pulse patterns thus produced are usefully (for taxonomists) species diagnostic. For each species, time-domain song structure resolves as a relatively stereotyped series of discrete sound pulses, manifesting as distinctive spectra in the frequency domain. Simple sinusoid pulses, sus-

tained in amplitude over several oscillations, will appear spectrally as one to a few peaks of stronger central tendency, i.e., higher Q. More complex transient pulses, grouped in trains, each rapidly decaying from a maximal onset, will appear spectrally as a band of melded peaks tending to a band, i.e., to lower Q. Each transient pulse in a train is surely the acoustic effect of one file-tooth scraper interaction, but a more prolonged sinusoid pulse suggests driven specular oscillators generating at one tooth per wave, coupled or uncoupled (Montealegre-Z et al. 2006).

The call of *C. paradoxus* (Fig. 11) repeats as lisps paired in time (Fig. 11A); each lisp is a train of ~30 very temporally discrete and transient pulses (Fig. 11B). Each pulse is apparently the result of a single tooth-scraper event (pluck or impact?). Close inspection of these complex-wave transients (Fig. 11C) shows them to be remarkably consistent in wave shape, each giving rise (via Fourier analysis) to a low-Q spectral band with a species-characteristic distribution of frequency peaks and subpeaks. (Even tiny spectral subpeaks can be a stable feature of the singer, only shifting as an effect of aspect: see *Conocephalus nigropleurum* Morris & Pipher, 1967.) In *C. paradoxus*, the lisp analyses as a band of sound energy between 8 and 13 kHz, entirely within the audio range (Fig. 11D). This species' calls are readily heard by human ears and devoid of effective ultrasonics (Fig. 11D, 12).

The song of *C. ditachus* (Fig. 13A) is also very audible and, like that of *C. paradoxus*, has a time-domain pattern of stereotypic transients in trains. But it compares to *C. paradoxus* and to the other five cestrophorine species songs as higher in duty cycle and unique in complexity, i.e., there are two rates of transient pulses that present as two different pulse trains to comprise a dual-pattern call. The field-recorded insect of Fig. 13 called steadily from overhead, perched in a sapling. His song pattern repeats every 2 s or so as 5 to 10 high-rate transient pulse trains interspersed with a single longer train of markedly slower rate of pulse repetition (Fig. 13B, C). The two different rates, readily apparent to a human listener, one rate almost 5 times the other, result in only slight differences in high resolution pulse waveforms (Fig. 13D, E) and spectral subpeaks (Fig. 13F, G). A dominant frequency peak for both song parts lies near 7.8 kHz, and there is no sound energy in the high audio 10 –18 kHz. However, ultrasonics are still possible since this record was made with equipment limited to the audio range.

Each call of *C. amplitenuis* is a sinusoidal sustained pulse (Fig. 14A, B), a steady series of identical lisps well-separated by >2 s. The amplitude envelope of this pulse wave-train varies, giving it a ragged appearance (Fig. 14B). In keeping with a strongly simple sinuosity, the spectral energy is concentrated in a relatively narrow high-Q peak at about 11 kHz (Fig. 14D). Ultrasonics in the song are trivial. The big difference between the songs of *C. amplitenuis* and *C. paradoxus* may be understood as the tooth interaction rate: in the former species, there is no down time between tooth contacts, so the speculae are sustained in amplitude as an ongoing sinusoid (Fig. 14C). *C. paradoxus*, by contrast, engages its scraper such that each energy transfer has time to completely dissipate before the next tooth is met. Presumably, the sound-radiating speculum of *C. amplitenuis* makes a prolonged-pulse sinusoid by contacting one tooth for each emitted wave.

The three *Cestrophorus* spp. call loudly in the audio and lack any appreciable ultrasonic spectral component. But songs of the three *Acanthacara* all have significant ultrasonic spectral components. *A. brachycyma* has its most intense output at 30 kHz (Fig. 15D). This species groups short sinusoidal sustained pulses (Fig. 15B, C) into brief 4 or 5-pulse trains (Fig. 15A). Calculation from the sine

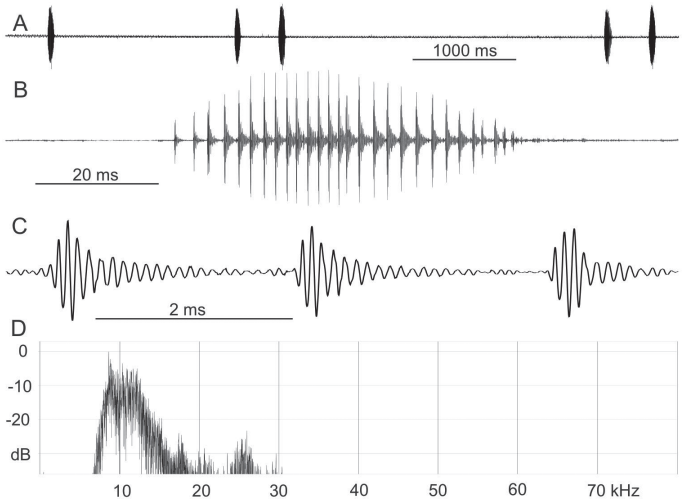

Fig. 11. Song of *C. paradoxus* is an ongoing sequence of lisp pairs. **A.** Sequence at low time resolution showing two complete pairs; **B.** A lisp at higher resolution reveals its composition as a long train of >25 discrete rapid-decay pulses; **C.** Three pulses showing stereotyped waveform detail; **D.** Power spectrum of *C. paradoxus* with frequencies confined to the audio range in a narrow band 8–13 kHz.

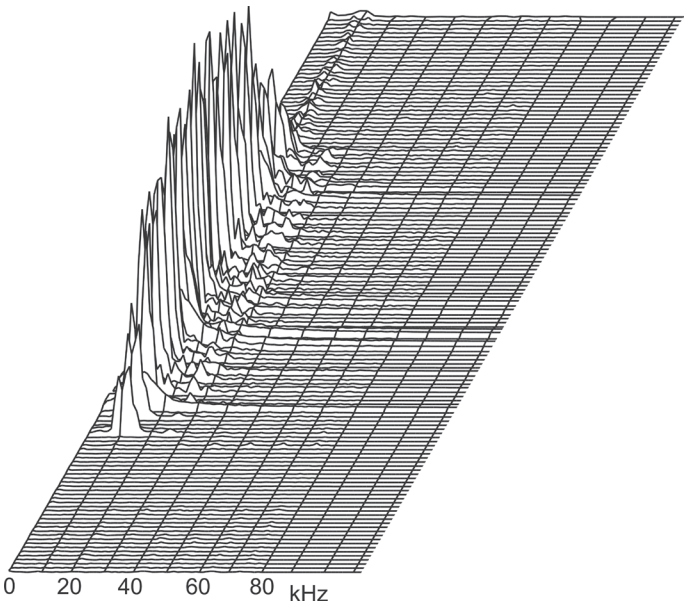

Fig. 12. Waterfall record of one *C. paradoxus* 60-ms pulse train/lisp indicating absence of ultrasonics.

wave yields (of course) a frequency of just about 30,000 Hz. (In 1 millisecond there are 12/.4 waves; in 1 second 1000 X (12/.4) = 30,000 waves). As with *C. amplitenuis*, this might be an instance of contacting one file tooth per each sinusoid wave to create each sustained pulse, i.e., tooth touch rate matches carrier frequency.

The call of *A. ortoni* is heard by a human listener as a sequence of double zips produced at a call rate of 2.2/s at 20.8°C (Fig. 16A). Each double-zip call lasts about 40–50 ms. The first zip begins as a short pulse train of transient pulses (Fig. 16B) fusing into a sustained high-intensity pulse that time-resolves into a characteristic two-cusped sinusoid waveform (Fig. 16C) that is

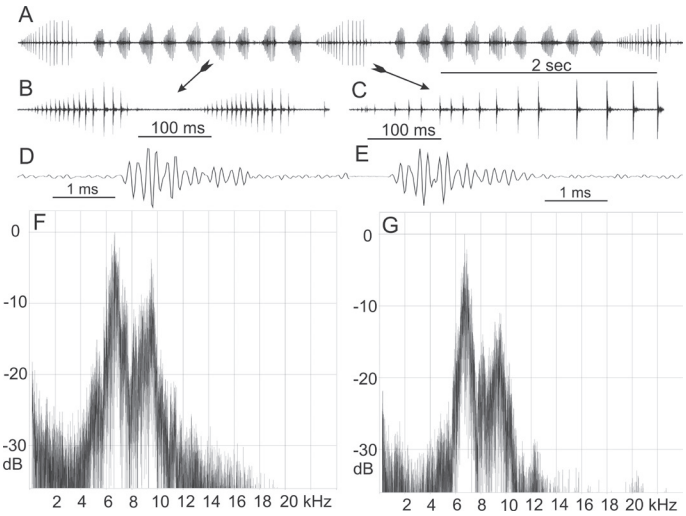

Fig. 13. Field-recorded song (Sony Walkman, audio range only) of *C. ditachus*: trains of pulses characterized by two different pulse rates, slower (SPR) and faster (FPR). **A.** Two complete calls taken from an ongoing sequence. Single SPR train prefaces a 9 FPR-train sequence; **B, D.** FPR trains at higher time resolutions showing waveform of rapid-decay pulses; **C, E.** SPR train at higher time resolution showing waveform of rapid-decay pulses; **F, G.** Audio-limited spectra of FPR and SPR respectively; spectra unaffected by scraper speed, peaking at 6–10 kHz.

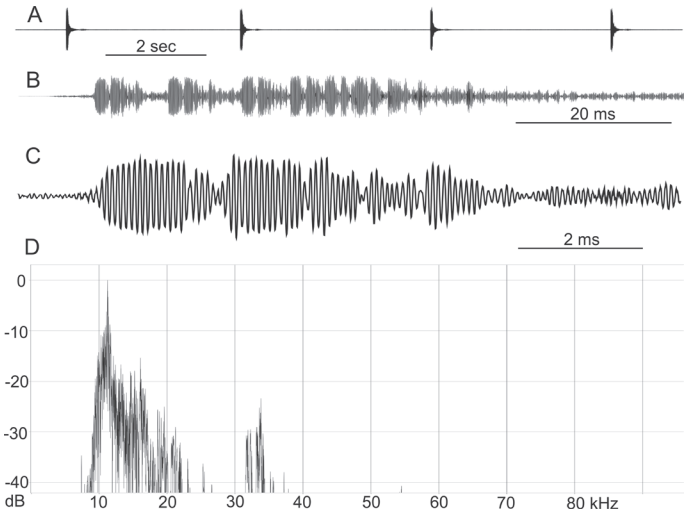

Fig. 14. Song of *C. amplitenuis*. **A.** Regular well-spaced call series; **B. C.** The same call at two levels of time resolution; each emission a prolonged sinusoid wavetrain of quite variable amplitude envelope falling-away; **D.** Audio peak near 11 kHz, spectrum almost without ultrasonics; the sinusoid-tending call is also apparent in the relatively high peakedness, of the spectrum. Lab recording at 21.3 °C.

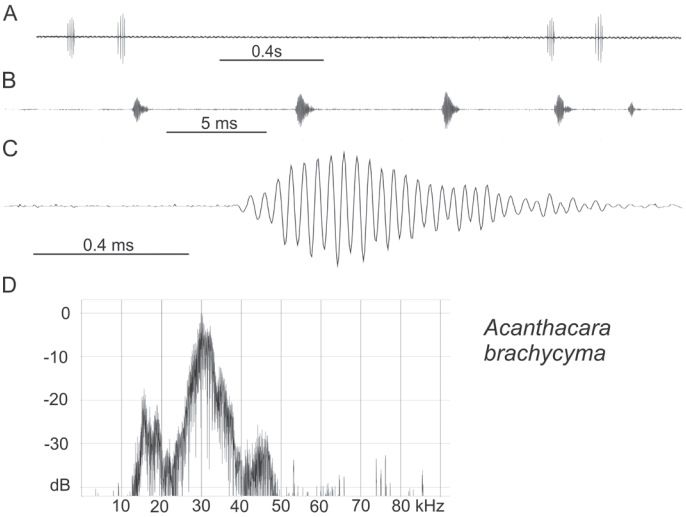

Fig. 15. Song of *A. brachycyma*. **A.** Two calls from an ongoing sequence of paired lisps; each lisp of 5 or so pulses; **B.** One complete lisp at higher time resolution; **C.** High resolution of a single sound pulse shows it to be highly sinusoidal; **D.** Spectrum dominated by ultrasonic peak at 30 kHz.

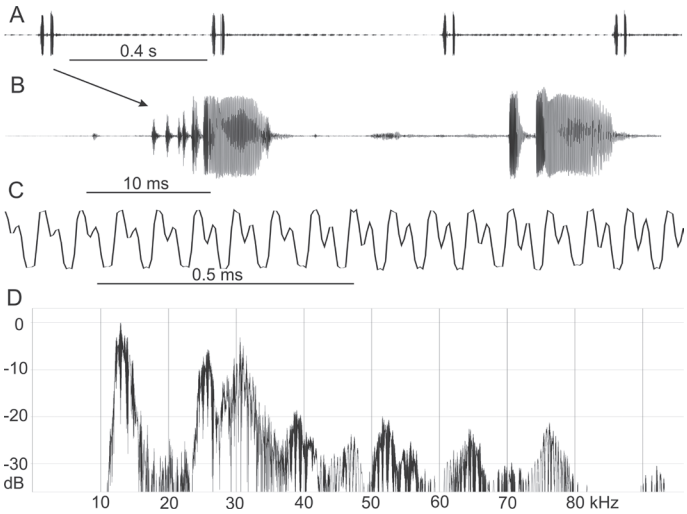

Fig. 16. Song of *A. ortoni*. **A.** Four double-zip emissions; **B.** Higher resolution of first call of record above; **C.** Cusped waveform characteristic of the interplay of two nearly equal harmonics; time sample taken from the prolonged pulse that ends each zip. This wave feature is the basis of the stillborn name *'isoharmonicus'* as used by GKM in his 1987 ISV Poster in Denmark; see Fig. 17 below; **D.** Spectrum shows subequal first (13.5 kHz) and second (27 kHz) harmonic peaks and then lower intensity harmonic peaks that occur well into the ultrasonic. A broad peak around 31 kHz is not part of the harmonic series. The academic editor expressed concern that the *A. ortoni* signal shown here may be slightly overloaded; we think rather that trace C shows the effect of the sampling rate failing to characterize the wave train smoothly at high time resolution. The recording in Fig. 17 is not subject to any possible overload distortion and shows the same harmonic interplay giving a cusped waveform.

dominated by harmonics (Fig. 16D). The second zip of Fig. 16B shows two of these sustained sinusoids, the second of much longer duration. The carrier fundamental at 12.6–13.2 kHz is subequal in intensity to its second harmonic at 25.4–26.0 kHz. The harmonically related frequencies (Fig. 16D) repeat well into the ultrasonic (13 X 2 = 26, X3 = 39, X4 = 52, X5 = 65, X6 = 78 kHz).

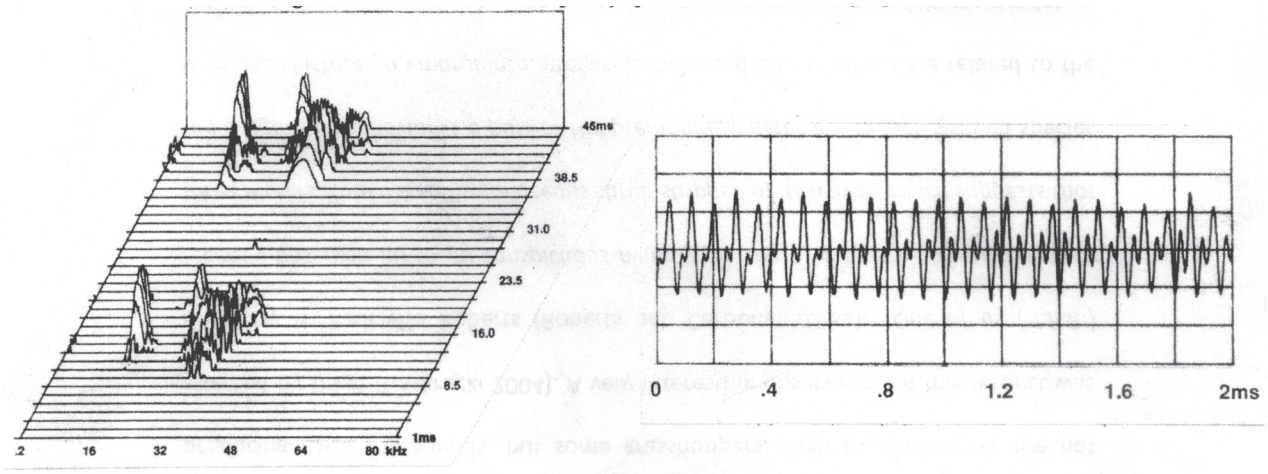

Fig. 17. Figure from 1987 ISV meeting abstract booklet showing a different *A. ortoni* specimen's song analysis; the waveform shown at high resolution is characteristic of subequal harmonics. There remains the possibility that this call is not properly associated with *A. ortoni* but is the call of *A. incisa*; see below.

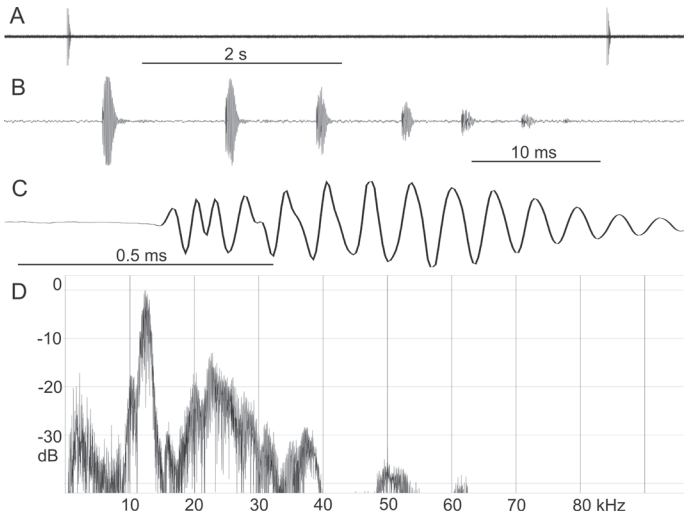

Fig. 18. Song of *A. incisa.* **A.** Two single-lisp calls, seconds apart, taken from a sustained sequence; **B.** At higher time resolution, each call is seen to be a train of 5–6 pulses of fading intensity; **C.** A single pulse at very high resolution reveals its sinusoidal nature; **D.** The power spectrum suggests higher Q generator components with a strongly high-Q peak near 13 kHz and some lesser but significant ultrasonics of 20–28 kHz.

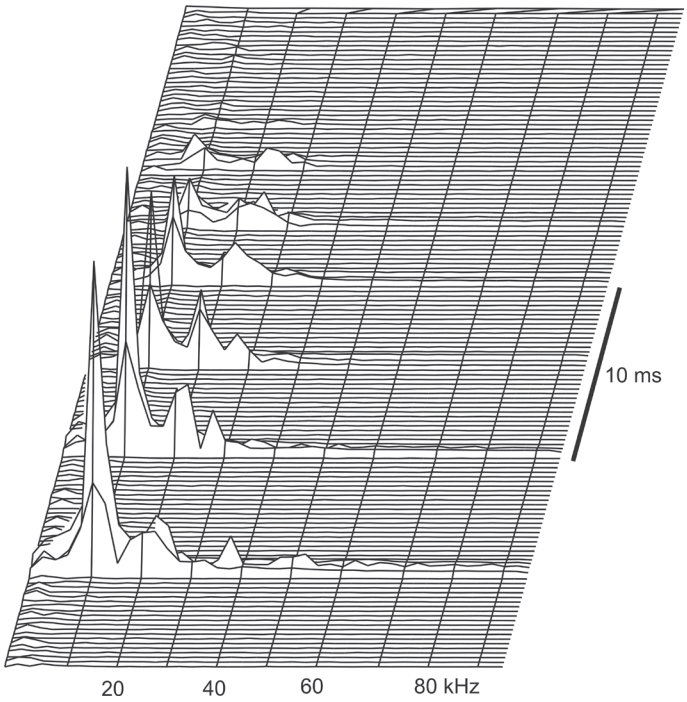

Fig. 19. One call of *A. incisa*; 7 pulses in a waterfall display.

A waterfall display of the double zip of *A. ortoni*, together with its cusped subequal harmonic waveform, is shown for a second specimen of *A. ortoni* (Fig. 17). This latter record formed part of the Insect Sound and Vibration (ISV) poster given in Denmark in 1987. At the ISV meeting, the species was designated as *Gymnacoustes isoharmonicus,* now a *nomen nudum*. The same sort of patterned time domain is characteristic of the Costa Rican katydid *Copiphora rhinoceros* (Morris 1980). The stridulatory basis of these higher harmonics would seem to involve oscillation of tegminal speculae with only the fundamental coinciding with each tooth interaction.

The call of *A. incisa* is a train of a half-dozen short sinusoid pulses successively falling in intensity, given as a single lisp every few seconds (Fig. 18A–C, Fig. 19). A single high-Q (narrow) spectral peak dominates the audio near 13 kHz. Low-frequency and weak ultrasonics, 20 dB down, exist at 20–25 kHz (Figs 18D, 19).

The species-distinctive songs of these cestrophorine species are a typical mix of the familiar frequency domain and time domain physical features that recur in most tettigoniid genera: high-Q, broadband, audio, ultrasound, harmonic, inharmonic, pulses sustained, and pulses transient. But these typical cono-

cephalid songs are listened to with unusual conocephalid ears: foreleg eardrums that are superficial and unoccluded and an acoustic spiracle (stigma) that is very small. Among conocephaloids, a naked ear is apparently unique to Cestrophorini and contrasts with the diverse tympanal coverings—"slits, resonators, pinnae" (Bailey 1990)—of other conocephaloids. So why don't *Acanthacara* and *Cestrophorus* have pretympanal pinnae (sensu lato)?

Beyond mechanical protection, a suggested acoustic function of these pretympanal structures is as ultrasonic wave guides, adding precision to the pressure gradient localization of short-wavelength—ultrasonic—sounds (Bailey 1990, Gwynne 2001). A publication in train (Montealegre-Z, pers. comm.) reports that pinnae of the conocephaloid *Copiphora gorgonensis* are structured to provide enhanced sound detection at high ultrasonic frequencies (>60 kHz), matching the echolocation range of co-occurring insectivorous bats. Perhaps the absence of tympanal coverings of Cestrophorini reflects much reduced bat predation for these small montane species.

It remains puzzling why the unoccluded tympana are combined with such small auditory spiracles. A narrow ear canal reduces sound velocity and, along with its asymmetric bifurcation near the individual tympana, creates different sound paths for each ear, all of which could help to pinpoint the direction of the sound (Veitch et al. 2021). Interestingly, the same rare combination of naked tympana and tiny spiracles is found in two species of Hexacentrinae (genus *Nubimystrix*), known also exclusively from the Andes of Ecuador and living in similar habitat (Braun 2016).

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Hillside lagomorph grazing and its influence on Orthoptera

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Abstract

The effects of lagomorph grazing on the Orthoptera of a small hill in Mistley (southeast England) were studied during the summer of 2020. Transect counts of Orthoptera revealed low sward height with abundant bare earth due to high wild rabbit *Oryctolagus cuniculus* grazing on the high slopes. This intensive grazing led to only field grasshopper *Chorthippus brunneus* (Thunberg, 1815) adults being found in any number on the high slopes, perhaps utilizing the short swards and bare earth as basking and egg-laying habitat. Aspect was also important, with significantly more grasshopper nymphs and *C. brunneus* adults on the south-facing slope than on the northern slope. Soil slippage areas seem like valuable micro-habitats on the south-facing slope, with these 'sun traps' providing excellent basking habitat for nymphs and *C. brunneus*. This study confirms that lagomorph grazing alters hill summit habitats for Orthoptera, benefiting *C. brunneus* and, to a lesser extent, the meadow grasshopper *Pseudochorthippus parallelus* (Zetterstedt, 1821). However, overgrazing of higher hill slopes can exclude tall grass species, such as long-winged conehead *Conocephalus fuscus* (Fabricius, 1793), and reduce assemblage diversity.

Keywords

Acrididae, altitude, bush-crickets, ecology, elevation, hill, rabbit, Tettigoniidae

Introduction

Orthoptera form an important part of grassland ecosystems across Europe (Köhler et al. 1987, Ingrisch and Köhler 1998). Grazing (by both domesticated and wild animals) affects the properties of grasslands that are crucial for orthopteran life-history processes (Gardiner 2018). Intensity of grazing, type of grazer, and rotational or seasonal aspects of the regime have an impact on characteristics of grasslands such as vegetation height, biomass, and plant species (Marini et al. 2008, Fabriciusová et al. 2011, Kurtogullari et al. 2020). In turn, these factors influence the oviposition, dispersal, and feeding behaviors of grasshoppers, thereby affecting the dynamics within Orthoptera assemblages and communities (Gardiner 2018).

Fonderflick et al. (2014) found that the impact of sheep grazing exerted a species-specific influence on a grasshopper assemblage that varied greatly over the season in Mediterranean steppe-like grasslands. They concluded that extensive grazing by sheep tended to homogenize the vegetation structure and led to a temporary reduction in Orthoptera abundance at a pasture scale. Species-specific responses to grazing were also noted in submontane pastures in the Hrubý Jeseník Mountains in the Czech Republic, where the abundance of rufous grasshopper *Gomphocerippus rufus* (Linnaeus, 1758) increased substantially with cattle grazing (Rada et al. 2014). The response of Orthoptera may change from scenarios with introduced domestic livestock to those with wild grazers such as lagomorphs and ungulates. In the Swiss Alps, Spalinger et al. (2012) found no direct effect of wild ungulate grazing (red deer and chamois), although they did observe small-scale alteration of habitats and plant nitrogen (N) content by ungulates that may have affected Orthoptera abundance and diversity.

On sea wall pollinator strips, wild rabbit *Oryctolagus cuniculus* grazing had a significant impact on sward height and adults and nymphs of Roesel's bush-cricket *Roeseliana roeselii* (Hagenbach, 1822) (Gardiner and Fargeaud 2020). The cutting of the pollinator strips allowed rabbits to graze the closed grassland, reducing grass growth and creating patches of exposed soil due to their burrowing activities, which may be favorable for basking nymphs (Gardiner et al. 2002). Grasshoppers of all species have been found in high densities (2.9 adults/m^2) on rabbit-grazed sea walls in Essex when compared with mown flood defenses (0.7 adults/m^2) due to the shorter swards created by lagomorphs (Fargeaud and Gardiner 2018).

Clarke (1948) suggested that excessive grazing by rabbits promoted sparser vegetation comprised of less vigorous grass species, such as sheep's fescue *Festuca ovina*, which was consequently more favorable to grasshoppers. In another study on a heavily rabbit-grazed grassland, the field grasshopper *Chorthippus brunneus* (Thunberg, 1815) was more abundant within an exclosure than on the surrounding grazed grassland (Grayson and Hassall 1985). The authors of that study suggested that the taller vegetation in the exclosure provided better cover from vertebrate predators and

higher-quality food resources for grasshopper nymphs than the shorter grazed vegetation. Intensive grazing by wild rabbit populations in Epping Forest in the UK contributed to the extirpation of the locally scarce common green grasshopper *Omocestus viridulus* (Linnaeus, 1758) from hillside slopes, a species with a preference for tall grassland (Gardiner 2010). The grazing on the slopes created a very homogenously short grassland sward resembling a 'lawn' (Crofts 1999), which may not have provided the necessary shelter or 'cool' microclimate for *O. viridulus*.

Short swards established by lagomorph grazing will have excessively hot temperatures (> 40°C) (Gardiner and Hassall 2009), unlikely to be favorable for grasshoppers in the absence of 'cool' tussocks. In short-grassland habitats, grasshoppers may therefore overheat and have a higher susceptibility to water loss and desiccation than in taller grassland where humidity may be higher and temperatures lower (Haskell 1958). The large body size (and therefore surface area) of grasshoppers such as meadow grasshopper *Pseudochorthippus parallelus* (Zetterstedt, 1821), in which adult females are 16–22 mm long (Marshall and Haes 1988), could make it difficult to cool down quickly in hot environments, meaning behavioral thermoregulation (dispersal to cooler tussocks) is the only option for survival (Gardiner and Hassall 2009). Across Europe, homogenously short swards established by overgrazing are the greatest threat to Orthoptera (affecting 262 species; Hochkirch et al. 2016).

To investigate the overgrazing associated with wild lagomorph grazing, transect counts of Orthoptera on a small hill at Lound Lakes (Suffolk, south-east England) revealed that low sward height due to wild rabbit grazing on the high slopes led to the general absence of tall grass species such as *O. viridulus* and *R. roeselii*. Only nymphs and *C. brunneus* adults were found in any number on the higher slopes, perhaps utilizing the short swards and bare earth as basking habitat (Gardiner 2021). The near exclusion of several orthopteran species from hill summits by rabbit grazing could be an important conservation issue for certain species such as *O. viridulus,* which are scarcer in south-east England (Gardiner 2010). However, the Lound Lakes study was limited due to its relatively small sample size (c. 1500 orthopterans) and lack of replication. A larger dataset with replication is required to further investigate the dynamics of hillside rabbit grazing and, together with the Lound Lakes study, ascertain how it affects Orthoptera abundance in low-altitude landscapes.

The aim of this short paper is to report a detailed study on the orthopteran assemblage of a rabbit-grazed hill in Essex, south-east England. Transect survey results are discussed in relation to grazing by lagomorphs and sward characteristics, and the conservation implications are considered.

Materials and methods

Study site.—The study site at Furze Hills Local Wildlife Site (LoWS) (51°56'9.9528"N, 1°4'41.9412"E) in Mistley, Essex, south-east England, was a small grassy hill composed of grasses such as sweet vernal *Anthoxanthum odoratum* and fescues *Festuca* spp. with a summit of 21 m (69 ft) and 10 m prominence (33 ft) over the surrounding countryside. The hill has free-draining, neutral-acidic sand and gravel soil. Both the southern and northern faces have gentle slopes (maximum gradient 7% and 6%, respectively), while the eastern slope is an agricultural field and the west is rank grassland with ruderal plants and scrub (5% slope). The hillside grassland of the north and south slopes is grazed by lagomorphs: mainly rabbits, but the brown hare *Lepus europaeus* is known in the area. The slopes are composed of *Festuca* spp. and sheep's sorrel *Rumex acetosella* grassland on the upper slopes, along with harebell *Campanula rotundifolia* and the occasional pignut *Conopodium majus*, the latter indicating semi-improved grassland. Semi-improved grassland refers to grassland that has had some agricultural improvement, such as chemical input or reseeding, but still retains floristic interest (Magnificent Meadows 2019). Damp grassland with widespread *H. lanatus*, rush *Juncus* spp., and occasional ragged robin *Silene flos-cuculi* was recorded in wetter locations on the lower slopes and in the basal pastures.

Transect surveys.—Eight 1-m wide × 50-m long transects were established in the lagomorph grazed grassland of the hill (4 transects each for the north and south slopes, Fig. 1), closely following the methodology of Gardiner et al. (2005), Gardiner and Hill (2006), and Gardiner (2021). On both the north and south slopes, two 50-m long transects were located on the low slope (15–17 m AOD) and two on the high slope (18–20 m AOD). All transects were at least 10 m apart to reduce the chances of double-counting individuals during surveys and can be considered independent replicates, similar to bird point counts or line transects (Nur et al. 1999).

Each transect was walked once at a slow, strolling pace (2 km/hr) on 17 occasions from 15 May to 26 August 2020. Nymphs flushed from a 1-m wide band in front of the observer were recorded along transects. As it is difficult (though not impossible, see Thommen 2021) to distinguish between species in the early

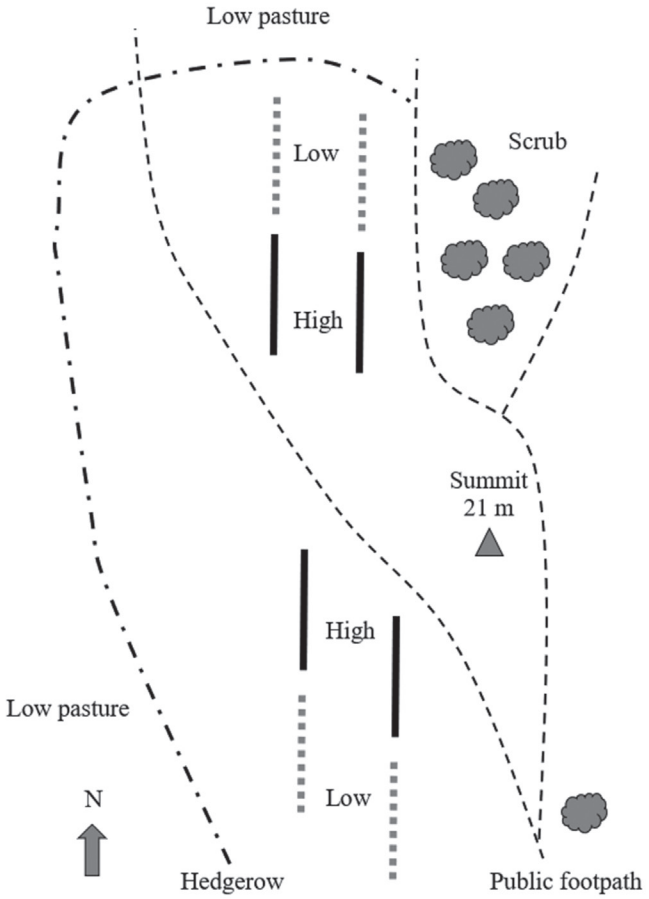

Fig. 1. Layout of the high and low transects on the north and south slopes of Furze Hill. Not to scale.

instars without capture, nymphs of all species were lumped together for recording purposes. With practice, it was relatively easy to ascertain the species of adults without capture (Gardiner and Hill 2006). Adult individuals of all species along transects were recorded to determine assemblage composition and species richness. The weather conditions on survey days were favorable for insect activity, being largely sunny and warm (>17 °C).

Sward height, bare earth, and rabbit grazing evidence.—A total of 80 sward heights were recorded at random positions using a 1-m rule for each of the two transects for both north and south slopes, split evenly between high and low sections in June 2020 (a total of 160 sward heights each for north and south slopes and 160 heights each for high and low slopes). The presence of bare earth in a 1 × 1 m quadrat was also recorded at 10 random locations along each transect. In addition, during the sward height surveys, the number of wild lagomorph (hare and rabbit) droppings (dung balls) were counted for high and low transect sections for both slopes (in 1-m band for length of 50 m transects) to ascertain the level of grazing pressure on each strip (Wood 1988, Gibb and Fitzgerald 1998, Millett and Edmondson 2013). To provide further evidence of wild rabbit grazing, the number of burrow excavations was also recorded on the transects.

Statistical analysis

To correct for non-normality, all data were square-root transformed before analysis (Heath 1995). To determine whether adults (for species where there was enough data for analysis) and nymphs were randomly distributed on the hill slopes, the data for nymphs and adults were pooled for high and low transect sections for the two transects for both the north and south slopes and subjected to a two-way ANOVA (Heath 1995). The independence of transects was assumed, and data for each transect was pooled in a similar way to allow for data analysis in other monitoring studies (Nur et al. 1999). Species richness was also compared for the two transects for both the north and south slopes and subjected to a two-way ANOVA. The frequency of burrow excavations, lagomorph droppings, and sward height were also compared between high and low transect sections on both north and south slopes using a 2-way ANOVA. Significance was accepted as evidence on the following scale in accordance with Muff et al. (in press): *p*-value >0.1 little or no evidence, 0.05–0.1 weak evidence, and <0.05 moderate evidence. There were no instances of strong (p <0.01) or very strong (p <0.001) evidence in this study.

Results

Seven species of Orthoptera were recorded on the south slope of the hill: 6 species on the low transects and 3 species on the high transects (Table 1). In contrast, only 5 species were recorded on the north slope low transects, compared to 3 on the high transects. Species richness was significantly lower on the high transects, although it was unaffected by aspect (Table 2). The most commonly recorded species was *Pseudochorthippus parallelus* (788 adults, 66% of total adults), followed by *Chorthippus brunneus* (385 adults, 32%). Less common species included long-winged conehead *Conocephalus fuscus*, lesser marsh grasshopper *Chorthippus albomarginatus* (De Geer, 1773), and *Roeseliana roeselii*. Dark bush-cricket *Pholidoptera griseoaptera* (De Geer, 1773) and slender groundhopper *Tetrix subulata* (Linnaeus, 1758) were rare species on the south slope, with just one sighting each.

Aspect influenced nymphs, with the south-facing slope having a significantly higher abundance than the northern one, although no elevation effect was noted (Table 2). Numbers of *C. brunneus* adults were significantly influenced by aspect and elevation, with greater abundance on the high transects and the south slope (Table 2). Interestingly, the percentage of nymphs of the total Orthoptera recorded was similar on the low slopes and the north high slope at c. 70% (Table 1). However, on the south high slope, nymphs formed 81% of total Orthoptera.

Lagomorph droppings were significantly more numerous on the high transects compared to the low transects and on the south slope, a pattern reflected by the number of rabbit burrow excavations and sward height (Tables 1, 2).

Table 1. Species richness and number of Orthoptera adults for each species and nymphs on the low and high transects of the south and north slopes of Furze Hill in relation to sward height, bare earth, and lagomorph grazing.

Species/habitat characteristic	South		North		Total
	Low	High	Low	High	
Pseudochorthippus parallelus	348	75	214	151	788
Chorthippus brunneus	93	182	36	74	385
Roeseliana roeselii	7	0	4	0	11
Chorthippus albomarginatus	2	0	1	2	5
Conocephalus fuscus	3	0	1	0	4
Pholidoptera griseoaptera	1	0	0	0	1
Tetrix subulata	0	1	0	0	1
Total adults	454	258	256	227	1195
Total nymphs (all species)	988	1107	622	483	3200
Nymphs (% of total Orthoptera)	69	81	71	68	–
Mean species richness	4.0 ± 0	2.5 ± 0.5	3.5 ± 0.5	3.0 ± 0	–
Mean sward height (mm) ± s.e.	204 ± 0	103 ± 5	251 ± 18	188 ± 47	186 ± 22
Mean bare earth frequency (%)	20 ± 20	95 ± 5	5 ± 5	50 ± 0	30 ± 15
No. lagomorph droppings	138	321	2	73	534
No. rabbit burrow excavations	3	28	2	31	64

Table 2. Results of the 2-way ANOVA analysis (F value displayed) with factor significance (p) and interaction.

Parameters	Elevation		Aspect		Interaction	
	F	p	F	p	F	p
Nymphs (all species)	0.2	0.69	52.4	<0.01	3.8	0.12
Chorthippus brunneus	12.0	0.03	20.5	0.01	0.3	0.62
Pseudochorthippus parallelus	5.2	0.08	0.0	0.97	2.1	0.22
Overall species richness	8.0	0.04	0.0	1.00	2.2	0.21
Sward height	12.4	0.02	7.5	0.05	1.2	0.34
Lagomorph droppings	41.1	<0.01	86.7	<0.01	0.4	0.58
Rabbit burrow excavations	15.8	0.02	0.0	0.93	0.0	0.93

Discussion

The total of seven species recorded on Furze Hill is comparable to other small hills in the east of England, such as Hungry Hill at Lound Lakes (7 species; Gardiner 2021). Species richness of Orthoptera was affected by hill elevation but not by aspect, with fewer species on the high transects. On Furze Hill, *C. brunneus* abundance was significantly affected by elevation and aspect, as the species is more tolerant of short swards (<10 cm) with bare earth on the high slope of the south face than *P. parallelus*. *Pseudochorthippus parallelus* was also affected, although elevation and aspect had a lesser influence on abundance (Table 2). Nymphs (of all species) were significantly more numerous on the south slope compared to

the north, which reiterates the well-studied effect of south-facing slopes being of higher favorability for Orthoptera due to the warm microclimate and high exposure to solar radiation (Voisin 1990, Weiss et al. 2013). Specifically, nymphs formed a high percentage of total Orthoptera on the south-facing high slope, perhaps due to the extremely low sward height and presence of two soil slippage areas with cliffed sand, which may have been oviposition and early instar development sites unsuitable for adults due to the absence of taller vegetation for feeding and shelter.

The habitat preferences of Orthoptera may relate to the choice of oviposition site, food preferences, vegetation height, and grassland management regimes (Clarke 1948, Gardiner 2006, 2009). Waloff (1950) stated that *C. brunneus* and *P. parallelus* lay their egg pods in the superficial layers of the soil. Bare earth is the usual egg-laying site for *P. parallelus*, although this species has been found to oviposit into grass-covered soil (Waloff 1950). Exposed soil may offer other benefits for grasshoppers by providing sites where they can bask (Key 2000), as exposed soil is often much warmer than surrounding vegetation. The high slopes of Furze Hill had a high occurrence of bare earth in the short sward (Fig. 2), where *C. brunneus* may lay its eggs.

Nymphs were evenly distributed between low and high slopes and seemingly more tolerant of shorter swards (<10 cm) with bare earth than adults that required taller vegetation. Early instar grasshopper nymphs of *C. brunneus* and *P. parallelus* are often found in short grassland near oviposition sites, as on Furze Hill's south-facing high slope with soil slippage areas, before moving to taller swards (10–20 cm height) as they mature for feeding and reproduction (Clarke 1948, Richards and Waloff 1954). Adults may then return to bare earth and sparse swards for egg-laying (Richards and Waloff 1954), such as those established by rabbit grazing on the high slopes of Furze Hill. It appeared that *C. brunneus* adults seemed able to utilize the summit's bare earth for basking and oviposition as they did on Hungry Hill at Lound Lakes (Gardiner 2021).

It is important to remember that microclimate may be critical for the development of insect populations (Marshall and Haes 1988). South-facing slopes act as hot 'sun traps' favorable for Orthoptera (Voisin 1990, Gardiner and Dover 2008, Weiss et al. 2013). However, short swards established by lagomorph grazing have excessively hot temperatures (>40°C) similar to hay meadows after cutting (Gardiner and Hassall 2009), which are likely to be favorable for grasshoppers inhabiting warmer vegetation such as *C. brunneus* (Marshall and Haes 1988) but may restrict taller grassland species such as *O. viridulus*, which was generally absent from the heavily rabbit-grazed summit of Hungry Hill at Lound Lakes (Gardiner 2021). Intense lagomorph grazing pressure also largely excluded *R. roeselii*, *C. fuscus*, and *P. griseoaptera* on Hungry Hill, as these species were found on the low slopes and pastures (Gardiner 2021). The latter two tettigonids were absent from heavily rabbit-grazed higher slopes at Furze Hill, which reduced the assemblage species richness. The geology of hills may also influence their micro-topography, the sand and gravel summit of Furze Hill creating ideal acid grassland that is accessible for rabbit grazing and digging. This disturbance leads to patchy, open swards, which are ideal for *C. brunneus* and *P. parallelus*.

On Cleeve Hill in Gloucestershire (UK), several species were found in soil slippage areas that had created a warm microclimate where stripe-winged grasshopper *Stenobothrus lineatus* (Panzer, 1796) was observed in abundance along with *C. brunneus* and *P. parallelus* (Gardiner 2011). Most grasshoppers were found in sheltered hollows or 'amphitheaters' where a warmer, less windy microclimate may be present (Gardiner 2011). On Furze Hill, the two slippage areas on the upper south slope had a prevalence of bare earth and cliff that likely provided a warm soil microclimate and egg-laying opportunities for adults (Fig. 3), particularly *C. brunneus*, which was in significantly higher abundance on the upper slope of the south face. Lagomorph grazing and digging by rabbits probably exacerbates the erosion of vegetation cover and permeates the proliferation of exposed soil.

Other pressure on Furze Hill included trampling by humans around the footpaths that cross the summit. During the 2020 Covid-19 lockdowns, there was noticeably higher trampling pressure (pre-Covid estimate <10 walkers/hour; during this study >20 walkers per hour) on the summit grasslands that formed part of the north and south high slopes in this study. Undoubtedly, this created bare earth in addition to lagomorph grazing and disturbed orthopterans. The significance of this is likely to be minimal compared to the population of rabbits on the hill, and it is unlikely

Fig. 2. South slope zonation from summit acid grassland with sheep's sorrel *Rumex acetosella* (left, red color sward) and abundant field grasshopper *Chorthippus brunneus* into lower, taller grassland (right) at Furze Hill. Photo credit: Tim Gardiner.

Fig. 3. Bare earth and short vegetation in a slope slippage 'amphitheater' utilized by grasshopper nymphs, field grasshopper *Chorthippus brunneus* adults, and slender groundhopper *Tetrix subulata* on a rabbit-grazed hilltop at Furze Hill. Photo credit: Tim Gardiner.

that the presence of enhanced human trampling in response to permitted daily exercise during lockdowns introduced error into the results of this study.

The main source of error in the current survey was the accuracy of the lagomorph dropping counts. Droppings may have been easier to locate in shorter, rabbit-grazed vegetation and would also have dried and been less likely to decay in such situations compared to the taller and moister vegetation present on the lower slopes. Therefore, to provide further evidence of rabbit grazing, the number of burrow excavations was also recorded. This confirmed that rabbit activity was indeed greater on the higher slopes, the digging providing valuable extra bare earth on the upper slope and summit of Furze Hill.

In conclusion, the effects of lagomorph grazing (mostly by rabbits) on a small hill in Essex were quite marked, with the low sward height on the high slopes being favorable for the short sward species *C. brunneus* and, to a lesser extent, *P. parallelus*. Adults of both species were found in abundance on the higher slopes, perhaps utilizing the short swards and bare earth as basking habitat. A meta-analysis of the current study combined with the Lound Lakes data (Gardiner 2021) illustrates the lower species richness on rabbit-grazed hill summits, the absence of species such as *R. roeselii* and *P. griseoaptera*, and the abundance of *C. brunneus* and *P. parallelus* (Table 3). Future studies should focus on determining whether rabbit grazing merely expands favorable habitat for species such as *C. brunneus* or whether bare earth is an attractant for adults moving away from nymphal habitats.

The high slopes also support priority butterfly species such as small heath *Coenonympha pamphilus* (Linnaeus, 1758), which is included within the 24 species of butterfly recorded on Furze Hill (41% of the UK's 59 species). The diversity of butterflies is another example of where a mosaic of bare earth, tall grass, and scrub/wood edge habitat provides the greatest conservation benefit, particularly in a localized area such as Furze Hill. The mosaic of rabbit-grazed semi-improved grassland on a hill, wet basal pastures along a stream, and mature hedgerows means that the full range of successional stages is present in an undulating landscape of value to invertebrates. Where overgrazing from rabbits is a particular problem, it may be necessary to install fencing to prevent them from accessing more species-rich grassland at the base of hills.

Table 3. Meta-analysis matrix with Orthoptera species present in relation to aspect and elevation on rabbit-grazed hillsides from the current study combined with Gardiner (2021). Species in bold are abundant in that scenario.

Elevation	Aspect	
	North-facing	South-facing
High	Ca **Cb** Cf Ov **Pp**	Ca **Cb** Cf Ov **Pp** Ts
Low	Ca **Cb Cf Ov Pp** Rr	Ca **Cb Cf Ov** Pg **Pp** Rr

Species key:
Ca *Chorthippus albomarginatus*; Cb *Chorthippus brunneus*; Cf *Conocephalus fuscus*
Ov *Omocestus viridulus*; Pg *Pholidoptera griseoaptera*; Pp *Pseudochorthippus parallelus*
Rr *Roeseliana roeselii*; Ts *Tetrix subulata*

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Orthoptera in the early stages of post-arable rewilding in south-east England

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Abstract

The ideal aim of rewilding is to restore natural processes to create 'self-willed' ecosystems involving the creation of large areas of habitat subject to stochastic disturbance, connected by favorable corridors for species to disperse along. Reversion of arable farmland to grassland and scrub habitats on Black Bourn Valley nature reserve in Suffolk (south-east England) through non-intervention allowed succession to occur largely unmanaged. Fields in the early stages of rewilding (4–14 years) are found at Black Bourn Valley, while pond creation has been extensive since 2010, creating water edge habitat and heterogeneity to the re-establishing grassland. Monitoring of Orthoptera revealed statistical evidence that species diversity/richness and field grasshopper *Chorthippus brunneus* (Thunberg, 1815), meadow grasshopper *Pseudochorthippus parallelus* (Zetterstedt, 1821), common groundhopper *Tetrix undulata* (Sowerby, 1806) and slender groundhopper *Tetrix subulata* (Linnaeus, 1758) were in higher abundance in fields ≥8 years since arable cropping ceased compared to those 4 years post reversion. Fields ≥8 years old were probably favorable due to the presence of microhabitats for basking and egg-laying orthopterans that included ant hills, sparsely vegetated pond edge and open swards with an abundance of fine-leaved grasses (*Agrostis* and *Festuca* spp.) and a low abundance of leaf litter. Lagomorph grazing by wild brown hare *Lepus europaeus* and rabbit *Oryctoloagus cuniculus* was critical in maintaining exposed soil for Orthoptera in the older fields, while deer paths appeared to create microhabitats that may be utilized by Orthoptera. We postulate that rewilding schemes on arable farmland should use a Rewilding Max approach and avoid the frequent usage of domestic livestock, relying on wild lagomorph and ungulate grazers to maintain an open mosaic habitat structure with only intermittent cattle, horse, or sheep grazing.

Keywords

Acrididae, biodiversity, bush-cricket, conservation, deer, grasshopper, Tettigoniidae, ungulate, wilding

Introduction

Orthoptera form an important part of grassland ecosystems across Europe (Köhler et al. 1987, Ingrisch and Köhler 1998, Humbert et al. 2009). Orders such as Orthoptera (grasshoppers, bush-crickets, and crickets) are an important component of invertebrate assemblages in agricultural ecosystems, particularly as prey for bird and spider species (Joern 1986, Belovsky and Slade 1993, Oedekoven and Joern 1998). Gardiner et al. (2002) suggest that intensively managed farmland habitats such as arable fields, heavily grazed improved pastures, and hay meadows have a low abundance of orthopteran species such as meadow grasshopper *Pseudochorthippus parallelus* (Zetterstedt, 1821) and field grasshopper *Chorthippus brunneus* (Thunberg, 1815). To reverse the decline of insects such as grasshoppers and bush crickets, rewilding of arable farmland may be highly beneficial.

The term rewilding was first used in North America in the 1980s (Noss 1985). Soulé and Noss (1998) proposed three key components of rewilding: large core protected areas, ecological connectivity, and keystone species that translated to the 3Cs of cores, corridors, and carnivores. Over time, Soulé and Noss's original concept has shifted into local interpretations but still incorporates self-regulatory ecosystems with minimal or no anthropogenic influence where wild grazers have a critical role (Dempsey 2021).

The role of wild herbivore grazers, such as lagomorphs (e.g., rabbit *Oryctoloagus cuniculus*) and ungulates (e.g., deer), in managing rewilded grasslands has not been studied in any depth with the aim of rewilding to recreate 'natural' ecosystems (Gordon et al. 2021b). Deer laydown areas and paths represent variation in sward height and could therefore be an influence on sward structure important for Orthoptera. Mixed approaches (e.g., relying on natural processes and introducing domestic grazers) with only minimal conservation intervention can be successful and may be necessary in some situations where non-intervention is not suitable (e.g., urban edge).

In recent times, the aim of rewilding in the UK has focused on restoring natural processes by creating large areas of habitat subject to stochastic disturbance connected by favorable corridors for species to disperse along (Carver and Convery 2021, Gordon et al. 2021a, b). Such ecological restoration on agricultural land that allows habitats to regenerate with a lack of active farmland (e.g., fertiliser application) or conservation management such as controlled livestock grazing is known as Rewilding Max (Gordon et al.

2021a,b). Domestic livestock (cattle, sheep, and ponies) are often used to graze rewilded farmland sites (e.g., Knepp Wildland in West Sussex, UK (Dempsey (2021)) after the initial establishment phase and grassland re-establishment (Casey et al. 2020). This form of conservation intervention without sole reliance on natural grazers is known as Rewilding Lite (Gordon et al. 2021b). However, introduced livestock can have detrimental impacts on Orthoptera where stocking density is too high and resultant sward height too short (Gardiner and Haines 2008). Across Europe, homogenously short swards established by overgrazing is the greatest threat to Orthoptera (affecting 262 species; Hochkirch et al. 2016). The consequences of livestock grazing are largely influenced by the intensity of grazing, type of grazer, and rotational or seasonal aspects of the regime, which in turn have an impact on characteristics of grasslands, such as leaf litter development, plant species presence, sward height, and vegetation biomass (Marini et al. 2008, Fabriciusová et al. 2011, Fonderflick et al. 2014, Rada et al. 2014, Kurtogullari et al. 2020).

The abundance of Orthoptera, particularly grasshoppers, is strongly influenced by sward height, biomass, and the composition and the availability of bare earth (Clarke 1948, Gardiner et al. 2002). Increased herbage biomass and sward height through abandonment of grassland management on rewilded sites could lead to a concomitant decrease in sward temperatures and extinction of light near the soil surface, particularly where leaf litter is allowed to develop (Gardiner et al. 2005). This is an important factor in Orthoptera distribution, as Van Wingerden et al. (1992) suggest that the number of grasshopper species is reduced in such 'cold' grasslands due to slow egg development and delayed hatching, particularly where there is a dense leaf litter layer (Gardiner et al. 2005). In these tall and dense grasslands, the availability of bare earth for the basking and oviposition needs of Orthoptera is often provided by ant hills where eggs are laid and nymphs are found in spring (Richards and Waloff 1954). In European grasslands on abandoned arable land, some authors (e.g., King 2006, 2020, 2021) consider the yellow-meadow ant *Lasius flavus* to be a keystone species due to the bare earth habitat provided by its large mounds of earth.

Orthoptera are ideal for monitoring the effects of rewilding at sites due to established, easily repeated monitoring methods, speed of response to habitat change, and range of species with differing habitat requirements (e.g., bare earth, short grass, tall grass, and scrub species) (Gardiner et al. 2005). Using a simple acoustic and visual transect methodology accompanied by habitat measurements (e.g., sward height and bare earth), we would expect there to be a strong species-specific response to rewilding features (e.g., ant hills) and wild grazing. For example, *C. brunneus* may require the bare earth of ant hills for basking and oviposition, while common green grasshopper *Omocestus viridulus* (Linnaeus, 1758) is a species of tall grassland that may benefit from an absence of lagomorph grazing (Marshall and Haes 1988).

The aim of this paper is to report on a study of the orthopteran assemblage of rewilded grassland on former arable farmland in Black Bourn Valley in Suffolk, UK. Results are discussed in relation to natural grazing pressure (brown hare, rabbit, and deer), grassland age since reversion commenced, and other factors such as sward height and bare earth habitat provided by ant hills and pond banks.

Materials and methods

Study site.—Black Bourn Valley has been owned and managed by Suffolk Wildlife Trust (SWT) since 1995 (it was formerly known as Grove Farm) in Suffolk, UK (52°15'0.4644"N, 0°51'1.422"E). The reserve is 119 ha in area and was previously intensively cropped for agriculture with nitrogen (N) fertilizer applied to a range of annual crops, including winter wheat. The Black Bourn River runs along the eastern edge of the reserve and is adjoined by riverside meadows (outside the scope of this study). The soil is a lime-rich loam and clay with slightly impeded drainage and moderate fertility. The farm had 11 farm ponds extant when SWT acquired the site in 1995. Nine new ponds have been created since 2010 as part of the Freshwater Habitats Trust's (FHT) Million Ponds Project. These ponds have several notably scarce and rare plants (e.g., tassel stonewort *Tolypella intricata*) for which the reserve has been designated a Flagship Pond Site by the FHT.

A total of eight fields were selected for this study due to their differing ages since reversion. Five fields were last plowed and cropped in 2017, two fields were last cropped in 2013, and one was cropped in 2007 (Fig. 1, Table 1). Once cropping ceased, all fields were allowed to naturally revert to grassland and scrub through succession with minimal intervention apart from mowing of footpaths and occasional light grazing (not on an annual basis). Throughout the duration of the 2021 summer study period, there was no active conservation management of any of the fields. A green lane ran through the site, and most fields were surrounded by scrubs or dense hedgerows. There were 10 ponds in the fields last cropped in 2013 or earlier (combined pond area 953 m^2) and six in the fields last cropped in 2017 (combined pond area 562 m^2). Most of the ponds had gently shelving banks (25–50° angle) and were sparsely vegetated.

Transect surveys.—A 1-m wide × 400-m long transect was established in all eight fields. Transects were arranged in a W shape (each arm 100 m) to ensure even coverage of each field and avoid any edge habitat effects. The transect method closely followed the methodology of Gardiner et al. (2005), Gardiner and Hill (2006), and Gardiner (2021). Each transect was walked at a slow, strolling pace (2 km/hr) on 3 occasions from May–August 2021. Adult individuals of all Orthoptera species along all transects were recorded acoustically and visually to determine assemblage composition and species diversity and richness.

Nymphs flushed from a 1-m wide band in front of the observer were recorded along all transects. As it is difficult to distinguish between species in the early instars (though not impossible, see Thommen 2021), numbers for nymphs of all species were lumped together for recording purposes. The surveys were undertaken in vegetation sufficiently short (<50 cm) to minimize the possibility of overlooking nymphs in tall grass or non-stridulating species such as groundhoppers (Tetrigidae) (Gardiner et al. 2005). With practice, it was relatively easy to ascertain the species of adults without capture (Gardiner and Hill 2006), although some species, such as long-winged conehead *Conocephalus fuscus* (Fabricius, 1793) and Roesel's bush-cricket *Roeseliana roeselii* (Hagenbach, 1822), are significantly under-recorded using visual transects (Gardiner and Hill 2006). A dual visual and acoustic monitoring method has been used by Weiss et al. (2013) to ensure complete coverage of the orthopteran fauna of sites. In the current study, a stridulation monitoring technique was used to record adult males of species that stridulated along the transects at the same time as visual monitoring by flushing. Stridulation monitoring has been used to record cryptic species in Essex and has been found to be effective compared to visual sighting transects and pitfall traps (Harvey and Gardiner 2006, Gardiner et al. 2010). Bat detectors were not required in the current study as the first author (TG) was able to reliably detect stridulating males up to 20 m away either side of the transect. The weather conditions on survey days were favorable for insect activity, being largely sunny and warm (>17°C).

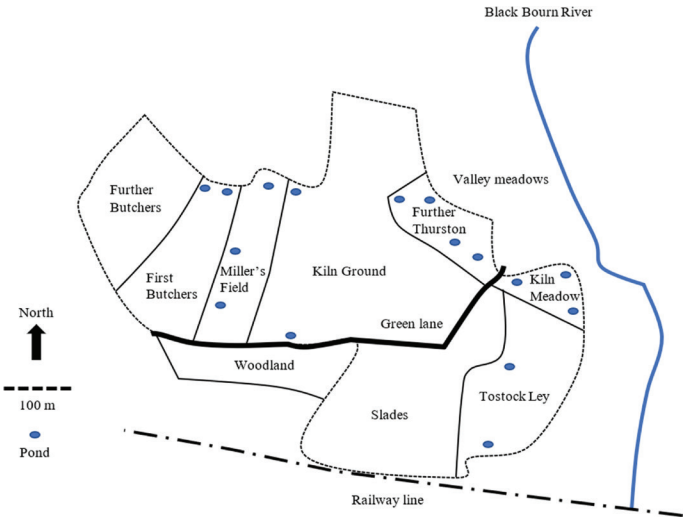

Fig. 1. Layout of the eight experimental fields at Black Bourn Valley with ponds and corridor habitats highlighted.

Table 1. Characteristics of the eight fields that had been taken out of arable cropping.

Field name	Area (ha)	Year since cropping ceased	Habitat on field perimeter	No. ponds	Pond areas (m^2)
Miller's Field	2.0	2007	H, GL	3	50, 80, 260
Further Thurston	2.1	2013	H, GL, M, W	4	80, 72, 98, 138
Kiln Meadow	1.6	2013	H, GL, W	3	32, 50, 140
Tostock Ley	4.4	2017	H	2	85, 90
Kiln Ground	14.7	2017	H, GL, M	2	35, 50
First Butchers	3.0	2017	H, GL	2	125, 130
Further Butchers	5.4	2017	H	0	-
Slades	5.7	2017	H, GL, R	0	-

Key: H = hedge, GL = green lane, M = marsh, R = railway bank, W = woodland

Natural grazing pressure and habitat characteristics surveys.—A total of 40 sward heights were recorded at random positions along the Orthoptera transects using a 1-m rule for each of the eight fields in early September 2021. In each field, ant hills were counted along the 400 m long Orthoptera transects in a 1-m wide band; additionally, the number of individual wild lagomorph (differences between brown hare and rabbit were not determined, so droppings pooled for both species) droppings (dung balls) were recorded in the same 1-m band to ascertain the level of grazing pressure in the fields (Wood 1988, Gibb and Fitzgerald 1998, Millett and Edmondson 2013).

Four of the six British ungulate species have been recorded at Black Bourn Valley: fallow deer *Dama dama*, muntjac *Muntiacus reevesi*, red deer *Cervus elaphus*, and roe deer *Capreolus capreolus*. Due to the known presence of ungulates on site, individual deer pellets (not classified to species) were counted along a 5-m wide × 200-m long transect in each field in October 2021 when the vegetation had died back, allowing easy sighting of fecal matter. The counting of deer droppings (droppings of all species lumped together for analysis) followed the methods of Marques et al. (2001). In addition to the dropping counts, deer laydown areas (flattened areas of grass at least 2 × 2-m in area) and deer paths (parted grass through vegetation) were recorded where they were observed within the 5 × 200-m transect in each field.

In the fields where arable cropping ceased in 2017 and in 2013 or 2007, 2 × 2-m quadrats were randomly surveyed (11 and 7 quadrats, respectively) to collect vegetation data. The number of quadrats surveyed in both field types was approximately proportionate to the number of fields studied in each (i.e., 5/8 fields for 2013 or 2007 = 63%, 11/18 quadrats = 61%). Each plant species recorded in a quadrat, along with bare earth and leaf litter (dead and decaying vegetative material, typically grass in this study), was given a DOMIN value in accordance with National Vegetation Classification survey methods (Rodwell 2006). The DOMIN scale assigns percentage cover of species or habitat features to a numeric grade using the following scale: 1, <4% few individuals; 2, <4% several individuals; 3, <4% many individuals; 4, 4–10%; 5, 11–25%; 6, 26–33%; 7, 34–50%; 8, 51–75%; 9, 76–90%; 10, 91–100% (Rodwell 2006).

Statistical analysis

Orthoptera.—For data analysis, two age classes for the fields were used: 1) fields where arable cropping ceased in 2017 (5 fields) or 2) in 2013 or 2007 (3 fields). This represented either 4-year-old reversion or ≥8 years, since arable cropping terminated. All detections of Orthoptera (visual or acoustic) were summed for each field for the survey period (3 surveys) to determine the relative abundance of adults of each species and nymphs in accordance with previous studies (notably, Weiss et al. 2013). Independence of transects was assumed, and data was pooled for each one in a similar way to data analysis in other monitoring studies (Nur et al. 1999).

Species richness was calculated for each field. Assemblage diversity estimates were also calculated using Version 4.1.2. Species Diversity and Richness software (Pisces Conservation Ltd, IRC House, The Square, Pennington, Lymington, Hampshire) from data collated from each of the two methods. The Shannon-Wiener Diversity Index (H′, Kent and Coker 1992) was calculated using the total number of adult individuals recorded for each Orthoptera species in each field. All data were square-root transformed to correct for non-normality before analysis (Heath 1995).

To determine whether species richness and diversity and the abundance of adults (of all species) and nymphs differed between fields 4 years and 8 or more years since arable reversion began, a Student's t-test was used for all comparisons. The mean abundance of the most abundant species/field was also compared between the two field types. Corrections were made for unequal variance where necessary using Satterthwaite's approximate t-test, which is a method in the Behrens-Welch family (Armitage and Berry 1994, Heath 1995). Significance was accepted as evidence based on the following scale in accordance with Muff et al. in press: p-value >0.1, little or no evidence; 0.05–0.1, weak evidence; <0.05, moderate evidence; <0.01, strong evidence; or <0.001, very strong evidence.

Natural grazing pressure and habitat characteristics surveys.—The counts of ant hills, lagomorph droppings (brown hare and rabbit pooled), deer droppings (all species combined), laydown areas, and paths were individually summed for each field, and along with DOMIN values for bare earth, leaf litter, the five most abundant plant species, bryophytes and plant species richness, data were square-root transformed to correct for non-normality (Heath 1995). To determine whether all of these variables differed between fields 4 years old and those 8 or more years post-arable reversion, a Student's t-test was used in each case with corrections made for unequal variance where necessary using Satterthwaite's approximate t-test (Armitage and Berry 1994, Heath 1995).

Results

Nine species of Orthoptera were recorded on the Black Bourn Valley reserve, including three species uncommon in this area of Suffolk (Table 2). The most commonly recorded species were *P. parallelus* (21% of adult detections) and *R. roeselii* (20%), followed by *C. fuscus* (19%) and *C. brunneus* (12%). Less common species included *O. viridulus* and slender groundhopper *Tetrix subulata* (Linnaeus, 1758) (10% each). The common groundhopper *Tetrix undulata* (Sowerby, 1806) and lesser marsh grasshopper *Chorthippus albomarginatus* (De Geer, 1773) were found in much lower abundance (3%), while the dark bush cricket *Pholidoptera griseoaptera* (De Geer, 1773) was a rarity (1%).

The abundance of 6 of the 9 species (*C. albomarginatus*, *C. brunneus*, *O. viridulus*, *P. parallelus*, *T. subulata*, and *T. undulata*) was highest in one field (Kiln Meadow, cropping ceased 2013; Figs 1, 7) where 30% of the total detections of adult Orthoptera were recorded. For *O. viridulus*, *T. subulata*, and *T. undulata*, a very high percentage of the total recorded adults for each species were from Kiln Meadow and Further Thurston combined (82%, 89%, and 73%, respectively). For *P. griseoaptera*, 83% of adults were recorded from Miller's Field (cropping ceased in 2007).

There was very strong evidence ($p < 0.001$) that species richness and diversity and the abundance of *T. undulata* were significantly higher in fields ≥8 years since cropping cessation compared to those only 4 years since cropping ceased (Table 2). There was moderate evidence ($p < 0.05$) that *C. brunneus* and *P. parallelus* were significantly more abundant in fields ≥8 years old and only weak evidence ($p < 0.10$) for *T. subulata* (Table 2). Very strong evidence ($p < 0.001$) indicated that the most abundant species (% of total number) in each field was significantly higher in the younger fields (c. 43%) compared to the older fields (c. 22%). In 4 out of the 5 fields 4 years post-cropping, *C. fuscus* was the most abundant orthopteran, comprising c. 43% of the total number of Orthoptera overall across the 5 younger fields. In 2 out of the 3 older fields (≥8 years post-cropping), *P. parallelus* was the most abundant species, forming 20.6% of overall sightings. In these older fields, *C. fuscus* comprised only 11.3% of adults.

Table 2. Mean number of Orthoptera nymphs and adults of each species and species diversity and richness in fields 4 and ≥8 years since cropping cessation, significance evidence shown (Student's t-test).

Species	4 years		≥8 years		t value	p	Evidence
Pseudochorthippus parallelus	12.8	± 1.9	36.0	± 11.0	-3.32	0.02	Moderate
Chorthippus brunneus	8.2	± 1.8	23.3	± 3.9	-3.59	0.01	Moderate
Roeseliana roeselii	11.2	± 1.9	28.0	± 11.0	-1.28	0.33	None
Chorthippus albomarginatus	1.6	± 0.5	4.7	± 3.2	-1.23	0.26	None
Conocephalus fuscus	28.4	± 5.6	19.7	± 4.1	1.07	0.33	None
Pholidoptera griseoaptera	0.2	± 0.2	3.7	± 3.2	-1.24	0.34	None
Omocestus viridulus	2.0	± 0.6	26.0	± 11.0	-2.74	0.11	None
Tetrix subulata	0.8	± 0.6	26.0	± 11.6	-3.05	0.09	Weak
Tetrix undulata	0.0	± 0.0	7.3	± 0.9	-15.12	<0.001	Very strong
Nymphs (all species)	38.6	± 16.3	61.0	± 20.4	-0.94	0.38	None
Most abundant species (%)	42.9	± 3.8	22.2	± 1.8	4.40	<0.001	Very strong
Species richness	6.2	± 0.4	8.7	± 0.3	-4.44	<0.001	Very strong
Species diversity	1.5	± 0.1	1.9	± 0.0	-6.32	<0.001	Very strong

There was moderate evidence ($p < 0.05$) that ant hill density, lagomorph droppings, and the number of ponds were significantly higher in fields ≥8 years since cropping cessation (Table 3). Contrastingly, there was very strong evidence ($p < 0.001$) that leaf litter was significantly less abundant in fields ≥8 years since cropping cessation. Only weak evidence was obtained that there was a higher number of deer paths in the older fields ($p < 0.10$).

Of the five most abundant plant species, two were significantly more numerous in fields ≥8 years since cropping cessation: creeping bent *Agrostis stolonifera* (moderate evidence) and red fescue *Festuca rubra* (very strong evidence; Table 4). Overall plant species richness was also significantly higher (very strong evidence) in the older fields (Table 4). In contrast, soft brome *Bromus hordeaceus* was more abundant in fields 4 years post-cropping (strong evidence). Two species, Yorkshire fog *Holcus lanatus* and bristly oxtongue *Helminthotheca echioides*, had similar abundance in both types of field, as did bryophytes (Table 4).

Discussion

Species richness and abundance in a regional context

The total of 9 species recorded at Black Bourn Valley is supplemented by species not observed on the transects, which include the oak bush-cricket *Meconema thalassinum* (De Geer, 1773) and speckled bush-cricket *Leptophyes punctatissima* (Bosc, 1792). *Omocestus viridulus* was relatively abundant, but is a scarce species in central Suffolk (Ling 2000), while the two *Tetrix* groundhoppers are local to the county. On intensively managed arable farmland in south-east England, *O. viridulus* is almost never found (Gardiner 2010b), while groundhoppers such as *T. subulata* are occasionally observed in low numbers along field edge footpaths (Gardiner 2007). The presence of *O. viridulus* in fields 4 and ≥8 years since cessation of arable cropping suggests that this species was quick to establish populations despite an allegedly slow colonization rate of new grasslands and apparent restriction to unimproved grassland (Gardiner 2010b).

The overall density of grasshoppers (234 adults/ha) compares favourably with intensively managed farmland (<100 adults/ha; Gardiner et al. 2002), indicating that rewilding arable land can successfully promote large insect populations in the early stages of reversion to grassland and scrub.

Factors influencing the colonization of rewilded fields

Pond edge.—Pond edge habitat with bryophytes (moss cover) and bare earth established by digging and grazing lagomorphs may be important for *T. undulata* and to a lesser extent *T. subulata* in fields ≥8 years since cropping cessation where there were small farm ponds, particularly those created since 2010, or restored old waterbodies (Fig. 2). Both *Tetrix* groundhoppers were found to occur around the ponds in this study, although this may cause issues with reproductive interference (Hochkirch et al. 2008). Both groundhoppers can be abundant in river valleys such as the Bourn, where they require both sparsely vegetated ground and tall vegetation in close proximity to prevent individuals being washed away during floods (Musiolek and Kočárek 2017). Groundhoppers typically utilize micro-habitats in close proximity and can match their color morph to the substrate for camouflage (Forsman 2000, Ahnesjö and Forsman 2006, Forsman et al. 2011). In this way, melanic forms can be abundant on burned ground or where soil is darker around silty river valley ponds.

Fig. 2. Pond edge habitat with exposed soil in rewilded fields at Black Bourn Valley, valuable for groundhoppers (*Tetrix* spp.) and field grasshopper *Chorthippus brunneus*. Photo credit: Tim Gardiner.

The importance of restoring old ponds by vegetation clearance and creating new ones should be recognized in proposals for rewilding at new sites to benefit orthopterans that require bare earth edges clear of vegetation by lagomorph grazing (Fig. 2).

Ant hills.—To determine why arable reversion to grassland affects Orthoptera, the habitat preferences of species should be examined. Habitat preferences of Orthoptera may relate to the choice of oviposition site, food preferences, vegetation height, and grassland management regimes (Clarke 1948, Gardiner 2006, 2009). Waloff (1950) stated that *C. brunneus* and *P. parallelus* lay their egg pods in the superficial layers of the soil. Bare earth, often on ant hills, is the usual egg-laying site for *P. parallelus*, although this species and *O. viridulus* have been found to oviposit into grass-covered soil (Waloff 1950). Exposed soil on ant hills may offer other benefits for grasshoppers by providing sites where they can bask (Key 2000), as it is often much warmer than surrounding vegetation (Fig. 3). Although bare earth overall did not vary between field types, there were greater numbers of ant hills in fields ≥8 years since cropping cessation, which indicates that micro-heterogeneity in unvegetated habitats may be important for egg-laying and basking *P. parallelus* and *C. brunneus*, which were in higher abundance in the older fields (Table 2). Nymphs were evenly distributed between field types, perhaps reflecting the need for a diversity of resources including bare earth, but also heterogeneity in sward structure, which was similar in both. Early instar grasshopper nymphs of *C. brunneus* and *P. parallelus* are often found in short grassland near oviposition sites before moving to taller swards (10–20 cm height) as they mature (Gardiner et al. 2002). Adults may then return to bare earth and sparse sward patches, such as those established by ant hills or rabbit grazing.

Ant hills in the older fields may have acted as hot 'sun traps' favorable for Orthoptera (Gardiner and Dover 2008, Voisin 1990), particularly species such as *C. brunneus* and *P. Parallelus*, which were in high abundance in those field types where overall species diversity and richness were also high (Table 2).

As succession progresses on rewilded sites, the prevalence of ant hills should be monitored to ensure that this valuable resource for invertebrates persists. If there is a loss of bare earth on ant hills over time, then site managers could consider periodic rotovation of strips through fields for early successional, disturbance-dependent species (e.g., *C. brunneus* and groundhoppers), similar to the management of nearby Breckland heaths (Gardiner 2020). Any rotovation should be irregularly undertaken to avoid too much intervention in natural processes, akin to Rewilding Max. However, a brownfield-type open mosaic habitat with patchy bare earth may only be possible on poor or moderately fertile soils.

Fig. 3. Ant hill (*Lasius* spp.) in rewilded grassland at Black Bourn Valley, probably used for egg-laying and basking by grasshoppers. Photo credit: Tim Gardiner.

Lagomorph grazing.—The aim of Rewilding Max to reinstate natural processes ideally means an absence of introduced livestock, such as cattle, horses, or sheep, relying on wild grazing animals where possible to manage succession. However, at several rewilded sites, livestock has been introduced to control natural processes (Rewilding Lite), while wild grazers, such as lagomorphs and ungulates, have a reduced influence. There is little information on how successful wild grazing animals are in maintaining grasslands in the absence of domestic livestock on rewilded sites.

Wild grazing animals play a significant part in reducing vegetation height and cover (Gardiner 2018, Fargeaud and Gardiner 2018). On sea wall pollinator strips, wild rabbit grazing had a significant impact on sward height and the density of *R. roeselii* adults and orthopteran nymphs (Gardiner and Fargeaud 2020). Rabbits grazed the closed grassland, reducing grass growth and creating patches of exposed soil though their burrowing activities that were favorable for basking nymphs (Gardiner et al. 2002).

Clarke (1948) suggested that excessive grazing by rabbits promotes sparser vegetation comprised of less vigorous grass species (such as sheep's fescue *Festuca ovina*) which is consequently more favorable to grasshoppers, perhaps because of the open sward structure and warmer microclimate (Gardiner and Hassall 2009). It is important to remember that microclimate may be crucial in providing warm temperatures for the development of large Orthoptera populations (Marshall and Haes 1988), particularly in rewilded fields where leaf litter is reduced ≥8 years since cropping cessation allowing greater penetration of solar radiation to the soil surface.

Ant hills and pond edges may assume greater importance in a sward managed only by wild grazers (e.g., brown hares and rabbits). The lagomorph grazing at Black Bourn Valley is mainly assumed to be by brown hares, although some rabbit droppings were located around the ponds where there were bare earth patches (Fig. 2).

Short sward patches established by lagomorph grazing, particularly when allied to sloping pond banks and ant hills, will have excessively hot temperatures (>40°C), similar to hay meadows after cutting (Gardiner and Hassall 2009), which are unlikely to be favored by grasshoppers in the absence of 'cool' tussocks in close proximity. Both field types had mean sward heights >30 cm, which could provide grasshoppers with numerous sheltered 'cool' areas of tall vegetation away from ant hills and pond edges where temperatures may be excessively hot during summer. This behavioral thermoregulation may account for the persistence of species such as *C. brunneus*, *P. parallelus,* and *T. undulata* in fields ≥8 years since cropping cessation where ant hills and sparsely vegetated pond edges (basking and egg-laying sites) were frequently in close proximity to cooler tall vegetation for shade-seeking orthopterans (Fig. 2).

Intensive grazing by unmanaged wild rabbit populations in Epping Forest in the UK led to the extirpation of *O. viridulus*, a grasshopper with a preference for tall grassland (Gardiner 2010b). Rabbits also reduce the abundance of *O. viridulus* through the creation of uniformly short swards with little cover from avian predation and excessively hot microclimates (Gardiner 2021). Therefore, uncontrolled rabbit grazing could pose a threat to *O. viridulus* on heavily grazed areas of rewilded sites. The extent to which rabbits influence the favorability of rewilded grasslands for insect orders such as Orthoptera should be a focus of further research on arable reversion sites.

Table 3. Natural grazing and habitat variables for fields 4 and ≥8 years since cropping cessation; Student's t values and significance evidence shown for differences between means in each row.

Variable	4 years		≥8 years		t value	p	Evidence
Ant hills/field	7.2	± 2.7	40.3	± 18.8	-2.53	0.04	Moderate
Bare earth (mean DOMIN)/quadrat	4.5	± 0.8	3.4	± 0.8	0.74	0.47	None
Deer droppings/field	4.4	± 2.2	3.7	± 2.3	0.20	0.85	None
Deer laydown areas/field	16.2	± 6.3	8.7	± 3.9	0.95	0.38	None
Deer paths/field	33.2	± 3.5	45.3	± 3.8	-2.29	0.06	Weak
Lagomorph droppings/m^2	0.5	± 0.4	3.5	± 0.9	-3.60	0.01	Moderate
Leaf litter (mean DOMIN)/quadrat	4.3	± 0.8	1.0	± 0.8	5.29	0.001	Very strong
No. ponds/field	1.2	± 0.5	3.3	± 0.3	-2.69	0.04	Moderate
Sward height (cm) range/field	83.6	± 9.6	85.0	± 3.2	-0.24	0.82	None
Sward height (cm)/field	44.1	± 5.6	31.4	± 3.5	1.64	0.15	None

The main source of error in this study may be the accuracy of the lagomorph dropping counts. Droppings may have been easier to locate in shorter, lagomorph-grazed vegetation and would have dried and been less likely to decay in such situations compared to the taller and moister vegetation present in some fields. Therefore, the lagomorph dropping counts must be viewed with some caution, and further studies should be undertaken.

Plant species changes and sward height.—Changes in plant species composition may have been a key influence on the abundance of *C. brunneus* and *P. parallelus* in fields ≥8 years since cropping cessation where fine-leaved grasses, *A. stolonifera* and *F. rubra*, were in higher abundance (Table 4, Fig. 4). The development of open sward structure with *Festuca* and *Agrostis* grasses in the older field types benefits these two grasshopper species that require a shorter sward composed of fine-leaved grass species (Gardiner et al. 2002). While neither field type offered the optimal mean sward height for *C. brunneus* and *P. parallelus* of 10–20 cm, the presence of diversity in sward structure in fields 4 and ≥8 years since cropping cessation indicates that patchy habitat was present with shorter swards for grasshoppers (Fig. 4). It also suggests that microhabitats, such as ant hills and pond edges, may assume greater importance in a sward managed only by wild grazers (e.g., brown hares and rabbits). The lagomorph grazing at Black Bourn Valley is mainly assumed to be by brown hares, although some rabbit droppings were located around the ponds where there were bare earth patches (Fig. 2).

Short 'hot' sward patches established by lagomorph grazing are unlikely to be favorable for grasshoppers in the absence of 'cool' tussocks in close proximity. Both field types had a mean sward height >30 cm, which will have provided grasshoppers with numerous sheltered 'cool' areas of tall vegetation away from ant hills and pond edges where temperatures may be excessively hot.

Ungulate grazing.—Wild ungulates are browsers that consume grasses, sedges, shrubs, and trees (Uresk and Dietz 2018). However, the influence of deer grazing on swards was assumed to be minimal at Black Bourn Valley (Table 3), despite the positive (Adler and Proud 2021) and negative (Gardiner 2011) influence it can have elsewhere.

In subalpine pastures in the Swiss Alps, Spalinger et al. (2012) found no direct effect of wild ungulate grazing (red deer and chamois). However, they did observe the small-scale alteration of habitats and plant N content by ungulates, which in turn affected Orthoptera abundance and diversity. Gardiner (2011) noted a reduced species richness of Orthoptera in red deer-grazed enclosures near Broadway Tower in the Cotswolds, UK, where sward height was mainly 5–10 cm with only occasional ungrazed taller vegetation (Gardiner 2011).

Table 4. Mean DOMIN abundance data/field for five most abundant plant species, bryophytes (mosses, liverworts and hornworts) and species richness for fields 4 and ≥8 years since cropping cessation, significance evidence shown (Student's t-test).

Species/family	4 years		≥8 years		t value	p	Evidence
Helminthotheca echioides	4.9	± 1.0	2.3	± 0.5	1.43	0.17	None
Agrostis stolonifera	1.0	± 0.8	3.4	± 0.5	-2.77	0.02	Moderate
Bromus hordeaceus	3.8	± 0.7	0.6	± 0.3	3.65	0.002	Strong
Holcus lanatus	2.9	± 0.9	1.9	± 0.4	-0.02	0.98	None
Festuca rubra	0.6	± 0.5	3.9	± 0.4	-7.05	<0.001	Very strong
Bryophytes	4.8	± 0.4	4.0	± 0.8	1.16	0.29	None
Species richness	13.7	± 1.0	28.3	± 1.1	-4.93	<0.001	Very strong

Fig. 4. Rewilded grassland at 4 years (right) and ≥8 years (left) since cropping cessation. Note the greener vegetation of the soft brome *Bromus hordeaceus*-dominated field (right) compared to the red and brown hues of the creeping bent *Agrostis stolonifera* and red fescue *Festuca rubra* of the older fields. Photo credit: Tim Gardiner.

Deer droppings and laydown areas were not significantly different between field types in the current study, indicating that ungulate grazing was evenly distributed across Black Bourn Valley (Fig. 5). There was weak evidence of greater deer path frequency in older fields (Fig. 6), indicating that ungulate passage may have had localized benefits for grasshoppers that need heterogeneity in sward structure. However, the shorter grass of deer paths was not numerous enough to make a difference to either mean sward height or structural range (Table 4), despite the micro-habitat mosaic and structural diversity that has been observed in other studies (Adler and Proud 2021). Deer may control the regrowth of scrub in the long term to maintain the mosaic of sparse grassland and woody vegetation, while ants and lagomorphs create the necessary bare earth for disturbance-dependent invertebrates. Seed dispersal can also occur due to ingested seeds being deposited across fields in fecal matter from grazing deer and lagomorphs, which may lead to the establishment of *A. stolonifera* swards (Eycott et al. 2007). It is possible that *A. stolonifera* swards favorable for *C. brunneus* and *P. parallelus* have developed along this successional trajectory at Black Bourn Valley.

Unstudied factors influencing colonization

Corridor linkage.—The presence of an ancient green lane corridor with hedgerows and grass margins may have allowed *O. viridulus* to spread quickly into the rewilded fields (Fig. 7). The main population of *O. viridulus* appeared to be centered in two of the older fields where cropping ceased in 2013, from which individuals probably colonized the fields taken out of cropping in 2017. Both fields with high concentrations of *O. viridulus* are located next to a species-rich unimproved meadow and the Black Bourn River Valley, which may have been sources of colonizing grasshoppers and likely explains the fast colonization into rewilded fields (it was present in 7 out of the 8 fields). In the field nearest to Black Bourn River (Kiln Meadow; 100 m), 5 out of 8 of the remaining species were in highest abundance, further highlighting the benefits of connectivity between rewilded fields and corridors to aid quick colonization.

Fig. 5. Deer laydown areas with shorter vegetation (and droppings), creating localized variation in sward structure in both field types. Photo credit: Tim Gardiner.

Range-expanding species such as *C. albomarginatus*, *C. fuscus*, and *R. roeselii*, which are spreading rapidly due to climate change (Gardiner et al. 2002, Gardiner 2009), were early colonizers of fields, being in similar abundance in fields 4 and ≥8 years since cropping cessation (Table 2). These pioneer species benefit from unmanaged grasslands and can build up large populations in such habitats on farmland in the UK (Gardiner et al. 2002, Gardiner 2009). *Conocephalus fuscus* formed just over 40% of the orthopterans counted in fields 4 years since cropping cessation, falling to c. 11% in those ≥8 years since cropping cessation, where *P. parallelus* was the most abundant species.

Scrub development.—In the oldest field (Miller's Field, 2007), which had well-developed scrub patches, *P. griseoaptera* was in its highest abundance, reflecting a well-documented preference for woody habitats (Marshall and Haes 1988). It should also be remembered that patches of scrub are desirable for red-list declining birds such as turtle dove *Streptopelia turtur* and common nightingale *Luscinia megarhynchos*, both of which were recorded in the two rewilded fields where cropping ceased in 2013 (Further Thurston and Kiln Meadow) at Black Bourn Valley. Therefore, light scrub encroachment is desirable from a conservation viewpoint, particularly as it also supports orthopterans such as *L. punctatissima* and *M. thalassinum*, both of which can spread from green lanes into adjacent habitats (Gardiner 2010a). A beating survey of the hedgerows and woodland would reveal the distribution of arboreal bush crickets across the rewilded area.

Fig. 6. Deer paths through tall grassland, creating localized variation in sward structure in older fields. Photo credit: Tim Gardiner.

Soil fertility.—On soils with high fertility (e.g., clay) farmed intensively for years, a low diversity, tussocky sward less favorable to Orthoptera may develop (Gardiner 2006, 2009). Natural regeneration on highly fertile arable soils often produces grassy swards of low diversity with minimal benefits to Orthoptera due to unfavorable tall sward height and lack of structural diversity (Gardiner 2009) or to butterflies that are restricted because of the dearth of nectar sources (Field et al. 2005, 2006, 2007). Therefore, farmland suitable for the maximal rewilding benefits must be carefully chosen. Farmers could remove fields from arable production and rewild them on the infertile or difficult-to-crop parts of their farms, perhaps rewilding 10–15% of total crop area. Rewilding Max may be the preferred option in these circumstances for Orthoptera, in that active conservation grazing is probably unnecessary where wild grazers such as lagomorphs can have a significant beneficial impact for invertebrates.

Conclusion: Can rewilding aid Orthoptera conservation on farmland?

Intensive agriculture has significantly reduced the diversity and abundance of Orthoptera on UK farmland (Gardiner et al. 2002, Cherrill 2010, 2015). Taking less agriculturally productive land out of arable cropping and allowing it to naturally regenerate (Rewilding Max) with minimal domestic livestock grazing and only wild grazing by lagomorphs and ungulates can produce swards that are quickly colonized (c. 4–8 years) by Orthoptera species not usually found on farmland, such as *O. viridulus* or *T. undulata*. Rewilded fields should incorporate features such as old and restored ponds to provide bare earth bank habitat for groundhoppers (e.g., *T. subulata*), while ant hills develop as the grassland matures, providing exposed soil and shorter swards for basking and ovipositing grasshoppers (e.g., *C. brunneus*). Lagomorph grazing in and around ponds and ant hills enhances the value of these bare earth features by maintaining them at an early successional stage. Of course, the response is species specific, and here the heterogeneity of micro-habitat is important to cater for short (e.g., *T. undulata*) and tall grassland (e.g., *O. viridulus*) species. A patchwork of different swards may also help to promote the highest diversity of insects (Kruess and Tscharntke 2002).

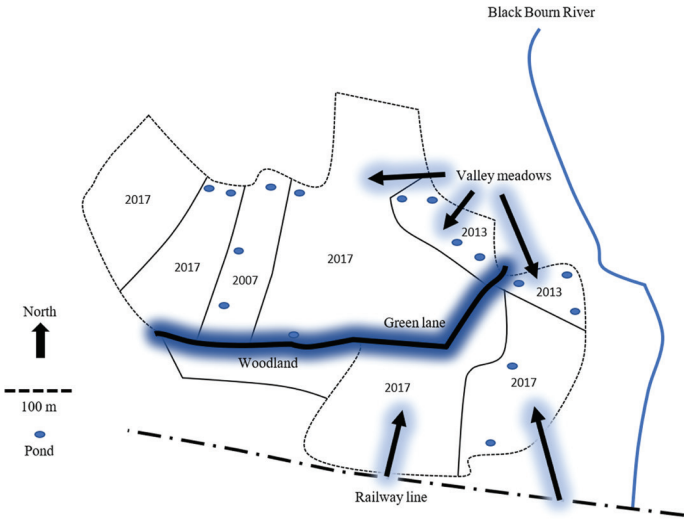

Fig. 7. Layout of the eight experimental fields at Black Bourn Valley (year since cropping cessation shown) showing the likely dispersal corridors onto rewilded farmland and the main green lane corridor, which may have acted as a green highway to fields at greater distance from the river valley corridor.

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Estimation of katydid calling activity from soundscape recordings

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Abstract

Insects are an integral part of terrestrial ecosystems, but while they are ubiquitous, they can be difficult to census. Passive acoustic recording can provide detailed information on the spatial and temporal distribution of sound-producing insects. We placed recording devices in the forest canopy on Barro Colorado Island in Panamá and identified katydid calls in recordings to assess what species were present, in which seasons they were signaling, and how often they called. Soundscape recordings were collected at a height of 24 m in two replicate sites, sampled at three time-windows per night across five months, spanning both wet and dry seasons. Katydid calls were commonly detected in recordings, but the call repetition rates of many species were quite low, consistent with data from focal recordings of individual insects where calls were also repeated rarely. The soundscape recordings contained 6,789 calls with visible pulse structure. Of these calls, we identified 4,371 to species with the remainder representing calls that could not be identified to species. The identified calls corresponded to 24 species, with 15 of these species detected at both replicate sites. Katydid calls were detected throughout the night. Most species were detected at all three time points in the night, although some species called more just after dusk and just before dawn. The annotated dataset provided here serves as an archival sample of the species diversity and number of calls present in the forest canopy of Barro Colorado Island, Panama. These hand-annotated data will also be key for evaluating automated approaches to detecting and classifying insect calls. In changing forests and with declining insect populations, consistent approaches to insect sampling will be key for generating interpretable and actionable data.

Keywords

bush cricket, community ecology, passive acoustic monitoring (PAM), seasonality, Tettigoniidae

Introduction

Insects are integral to terrestrial ecosystems but are often difficult to monitor. Recent research suggests that some, perhaps most, insect species are experiencing steep population declines likely in response to human activities (Dirzo 2014, Thomas 2016, Wagner 2020). It is possible that a quarter to half of the world's insect abundance has disappeared nearly unnoticed, with largely unquantified impacts on higher trophic levels, herbivory, nutrient cycling, and other core ecological processes (Hallmann et al. 2017, Wagner 2019). The uncertainty about these potential losses highlights how little is known about most insect species, from their natural history to their ecology, behavior, and population trends (Simmons et al. 2019, Thomas et al. 2019). To begin to grapple with questions about population changes and trends, we need to understand ecological fundamentals such as what species are present and how communities change across space and time (Montgomery et al. 2020).

In dense forests, many insects are elusive, but not all are silent. Orthopterans (e.g., crickets and katydids), Homopterans (e.g., cicadas), and many other insect species produce sounds (Cigliano et al. 2019) that can reveal their presence. Many of the loudest and most repetitive sounds are mating signals, which are often species-specific, at least within a given habitat (Greenfield 1997, Gerhardt and Huber 2002, Symes 2014). Documenting these sounds can provide a detailed window into the biology and population dynamics of insect species that are central to many food webs (Riede 1998, 2018, Hugel 2012, Penone et al. 2013).

Tropical forests are particularly species rich (Kricher 1999, Hillebrand 2004, Basset et al. 2012), and audio recordings from these environments contain many sounds that can provide clues to the presence, distribution, behavior, and abundance of insects (Riede 1993, Schmidt et al. 2013, Jain et al. 2014). Currently, natural history knowledge of tropical Orthopterans is extremely limited. For most species, little is known about where they occur in the forest, what time of year they mate, and how dramatically populations fluctuate from year to year. Long-term passive acoustic recordings can help address some of these questions. In recent decades, passive acoustic methods have been widely used for monitoring research (Sugai et al. 2019). However, the advertisement calls of many tropical Orthopterans have never been recorded or described. The lack of call descriptions has made it difficult to extract detailed information from long-term audio recordings.

In a small but growing number of locations, careful descriptions of insect acoustic signals have created a way of accessing the rich information contained within acoustic recordings (Danielsen et al. 2009, Cigliano et al. 2019, ter Hofstede et al. 2020).

For this study, we collected acoustic recordings from tropical lowland rainforest in Panamá and used recently published call descriptions (ter Hofstede et al. 2020) to manually identify katydid calls from the recordings, providing information about the spatial and temporal distribution of these katydid species. First, we assessed what species were detected acoustically in the forest canopy, how commonly these species appeared on recordings, and how many signals were detected per unit of time when the species was present. Second, we compared two different recording sites in similar habitats to assess local variations in species composition and call rate. Finally, we assessed how detections varied over short and long timescales, comparing three time-windows within a night, as well as comparing recordings during the wet and dry seasons.

Methods

Our study was conducted in 2019 on Barro Colorado Island (BCI), a protected lowland rainforest in Gatun Lake in the Panama Canal. The vegetation of BCI is predominantly old secondary growth forest with remnant primary forest, particularly in ravines and on steep hillsides (Ricklefs 1975). This forest receives approximately 2600 mm of rain per year, with a dry season that typically begins in December or January and ends in late April or early May (Leigh 1999). To represent rainfall dynamics immediately preceding and during the sampling period, we obtained monthly rainfall data from Nov 2018 to Aug 2019 (Paton 2021). This was compared against the average monthly rainfall from 1979–2019 (Fig. 1).

Recording site selection.—We selected two recording locations, both in large canopy trees [Site 1: 9.16074°N, 79.84073°W, Site 2: 9.16367°N, 79.84038°W]. For each tree, we used a basal area prism to calculate the basal area of the surrounding forest and a spherical densiometer to estimate percent open canopy (Lemmon 1956, Thompson et al. 2006). Forestry measurements were available from sampling that occurred in 2016, three years prior to recording. Measurements were collected by tree climbing during the dry season at 24, 16, and 8 m. One site was comparatively open, while the other was more densely vegetated (Table 1), providing an opportunity to capture more of the potential variation in species composition.

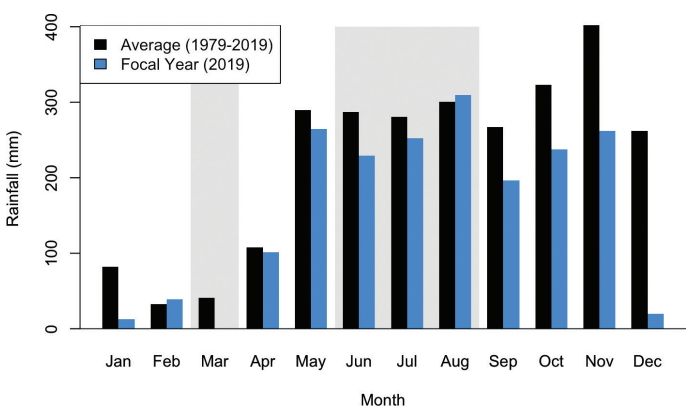

Fig. 1. Monthly rainfall totals showing a 40-year average and during the study period. Gray highlighting indicates months with analyzed acoustic recordings. Rainfall data are adapted from Paton (2021).

Table 1. Site characteristics of recording locations.

	Percent Canopy Cover		Basal Area (ft²/ha)	
Height (m)	Site 1	Site 2	Site 1	Site 2
24	90.6	6.4	80	10
16	97.9	59.4	90	30
8	99.0	81.3	80	40

Acoustic data.—We collected acoustic recordings of the BCI soundscape using Rugged Swift autonomous recording units (K. Lisa Yang Center for Conservation Bioacoustics, Cornell University). The units were suspended at a height of 24 m (corresponding to the canopy layer) and were configured to record for ten minutes at the beginning of each hour from dusk until dawn. The Swifts recorded continuously (mono, WAV format) throughout the deployment using a sampling rate of 96 kHz (16-bit resolution). The sampling rate excluded two of the species described in the ter Hofstede 2020 paper—*Eppia truncatipennis* Stål, 1875 (peak frequency 50 kHz) and *Ischnomela gracilis* Stål, 1873 (peak frequency 74 kHz) (ter Hofstede et al. 2020). The frequency response of the Rugged Swift microphone is relatively flat from 10–25 kHz, but sensitivity decreases linearly by 17 dB between 25 and 45 kHz (Suppl. material 1: Fig. S1). However, *Agraecia festae* (peak frequency ~40 kHz) was commonly detected on the recordings, indicating that ultrasonic species were readily detectable. The microphone sensitivity of the Swift was -44 dBV/Pa (+/-3 dB) based on 0 dB = 1 V/pa at 1 kHz, and the clipping level of the analog-to-digital (ADC) converter was +/- 0.9 V. The units were set with a gain of +35 dB.

We analyzed recordings from five dates corresponding to new moon nights, the darkest time of the month and a time when katydids are known to be most active (Lang et al. 2006, Romer et al. 2010). The selected dates included a day in the extreme dry season (5th March) and four dates during the longer wet season (5th June, 2nd July, 1st and 30th August) (Fig. 1). The dry season sampling only included recordings from Site 2 due to equipment malfunction. To capture the variation in species composition and activity, we analyzed recordings from three time windows on each date: shortly after nightfall (1900 h), at midnight, and just before dawn (0500 h) local time. Times were selected throughout the night to try to capture sounds from any species with limited windows of activity. This sampling strategy resulted in a total of 270 minutes of analyzed recordings. Soundscape recordings and annotation data are publicly available in Dryad (Symes et al. 2021).

Species identification protocol.—We visually reviewed spectrograms using Raven Pro 1.6 (Bioacoustics 2019) with an FFT size of 409 samples (4.26 ms duration with 3 dB filter bandwidth of 338 Hz), 50% frame overlap, and default settings for brightness and contrast. We advanced through the ten-minute recording in increments of approximately three seconds, with frequency presets that displayed 9.5–48 kHz. After locating a call, the window parameters were adjusted as needed to optimize visualization for a specific call. The katydid species with the lowest documented frequency on BCI had a peak frequency of 9.7 kHz (ter Hofstede et al. 2020). Therefore, we annotated calls with a visible pulse structure above 9.5 kHz. We used the dominant frequency of the call to identify potential species matches, and then the duration, interpulse interval, and other unique call characteristics described in ter Hofstede et al. (2020) to verify the species identification. Recordings were initially annotated by a single observer (KBH or DPS) and were subsequently reviewed by two additional observers (LBS and SM).

Nearly all katydid species recorded on BCI have acoustically unique calls. One pair of species, *Anaulacomera* sp. "wallace" and *Hetaira* sp., had exceptionally similar calls, with overlapping ranges of all acoustic parameters (ter Hofstede et al. 2020). These species are differentiated morphologically and genetically (T Robillard, personal communication), and the call similarity is almost certainly convergent. Within the forest, these species may be differentiated by microhabitat preference or diel patterns, but from acoustics alone, it is not possible to differentiate the species. Consequently, calls that fit the acoustic parameters of these species were annotated as [*Anaulacomera* sp. "wallace"/*Hetaira* sp.] to reflect the dual possibilities.

For soundscape recordings, we assessed the total number of calls detected per recording and the number of species present. For each species, we report the median number of calls present in a 10-minute recording that contained the species, as well as the maximum number of calls that we ever detected in a 10-minute soundscape recording.

We compared the soundscape call rate data against call rate data for individual captive insects to begin to assess how many individuals of a given katydid species are detected on a recording. To measure the calling activity of focal insects, we followed the methods of Symes et al. (2020). In brief, individual males were placed singly in mesh cages in a greenhouse and recorded for 24 hours with a Tascam DR-40 recorder at a sampling rate of 96 kHz. Calls were extracted using a custom script and R software (R Core Team 2018), and detections were validated by hand. For the species *Agraecia festae*, sounds were extracted using the template detector in the Raven Pro 2.0 software, with manual review to ensure detection. *A. festae* produces calls that consist of highly variable numbers of pulses, and to capture the variation in the calling activity of this species, we counted the individual two-pulse units that comprise the repetitive component of the call rather than the variable duration calls (for details of call structure, see ter Hofstede et al. (2020)).

In canopy recordings, animals are only known to be present when they are calling, whereas in our captive recordings, we knew that a single focal animal was present at all times. To generate comparable metrics between canopy and captive recordings, we divided 24-hour captive recordings into 10-minute recordings and determined how many of the 10-minute recordings contained calls. Using captive recordings that contained calls, we calculated the median number of calls per recording and the maximum number of calls in any recording for each individual. For each species, we then found the average number of captive recordings containing calls and the average number of calls in captive recordings that contained calls. Finally, we calculated the maximum number of calls observed in any 10-minute recording for any individual.

In addition to identifying calls, we also marked calls that could not be identified to species, referred to here as unmatched calls. The unmatched call class encompasses calls with measurable pulse structure that did not align with any of the katydid calls described in ter Hofstede et al. (2020). Bat echolocation calls could be identified by spectral and temporal patterns, particularly the increasing and then decreasing amplitudes as the bat flew past the microphone, and these calls were excluded from analyses. Although it is possible that some of these unmatched calls were produced by animals other than katydids, it is more likely that they are katydid signals because few other animals are known to produce pulsed signals like these at high frequencies. Including the unmatched class of signals allowed us to evaluate the total number of calls detected by time, date, and location.

By aggregating the data from the individual recordings, we were able to calculate the number of calls and the proportion of recordings that contained each species by site, date, and time of night.

Results

We detected 6,789 total calls, with calls present in all ten-minute recordings. Of these calls, 4,371 were identified to species (Table 2, see supplemental materials for recordings and annotation tables). The remaining 2,418 were unmatched signals that had clear acoustic structures and differed from the described calls of 50 katydid species in ter Hofstede et al. (2020) (Fig. 2). In total, the identified calls represented 23 species, plus a combined class for the acoustically indistinguishable calls of *Anaualcomera* sp. "wallace" and *Hetaira* sp. The number of species detected per recording ranged from one to seven. Some species were detected more often than others, with four of the species being detected only in a single recording. *Anaulacomera spatulata* and *Anaulacomera furcata* were both present in more than 40% of the recordings. These species produced a two-pulse call with stereotyped frequency and interpulse interval, leading to high confidence in these call identifications. These species are the most abundant and second-most abundant species, respectively, among species captured at lights, giving a high congruence between acoustic and light trap sampling (unpublished data).

The calls of *Philophyllia ingens* and *Anaulacomera* sp. "goat" were described in ter Hofstede et al. (2020) and were not identified in these recordings because the calls could not be distinguished reliably from the sounds produced by female phaneropterine katydids during the mating duet. Male *Philophyllia ingens* produce a single short pulse at 10.8 kHz, and *Anaulacomera* sp. "goat" males produce a single short pulse at 27 kHz. In the phaneropterine subfamily, many species engage in mating duets, with females producing a single tick or short series of pulses at a species-specific interval after the male call. Although the signals of female phaneropterine katydids at this site are not described, the soundscape recordings include a variety of short pulses across a range of frequencies that are consistent with the signals of female phaneropterines (Spooner 1995, Heller et al. 2015). We were not confident in our ability to differentiate the calls of

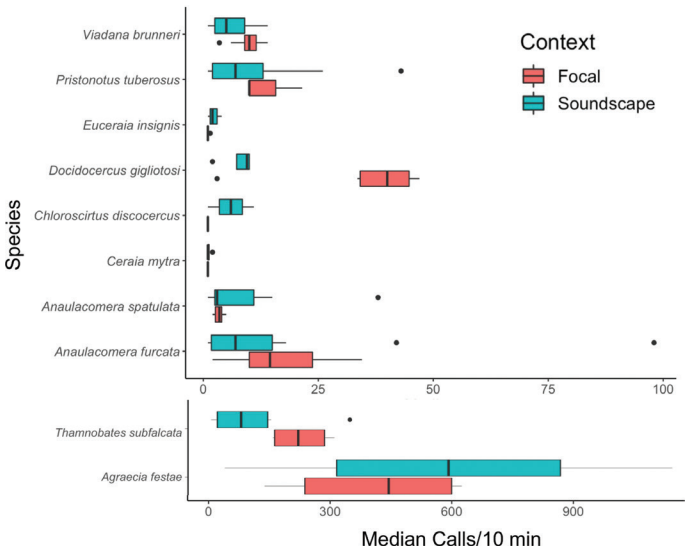

Fig. 2. Comparison of signaling rates between focal and soundscape recordings.

Table 2. A comparison of the number of calls detected in soundscape recordings and in recordings of captive focal individuals. For the soundscape data, total calls represents the number of calls detected across all recordings. Focal data for *Anaulacomera furcata, Anaulacomera spatulata, Ceraia mytra,* and *Euceraia insignis* are from Symes et al. (2021). Data for *Chloroscirtus discocercus* and *Viadana brunneri* are from Symes et al. (2020). Median recordings with calls represents the median number of 10-minute recordings in 24 hours that contained calls.

Species	Soundscape				Focal			
	Total Calls	Prop. files present	Calls/10 min when present		N ind	Median recordings with calls	Calls/10 min when present	
			Median	Max			Median	Max
Unmatched signals	2418	0.96	53.5	376				
Acantheremus major **(Naskrecki, 1997)**	10	0.04	10.0	10				
Acanthodis curvidens **(Stål, 1875)**	1	0.04	1.0	1				
Agraecia festae **(Griffini, 1896)**	1155	0.07	577.5	1118	5	61.0	433.0	1853
Anapolisia colossea **(Brunner von Wattenwyl, 1878)**	3	0.07	1.5	2				
Anaulacomera furcata **(Brunner von Wattenwyl, 1878)**	207	0.44	7.0	98	7	60.0	14.5	318
Anaulacomera sp. "ricotta"	1	0.04	1.0	1				
Anaulacomera spatulata **(Hebard, 1927)**	93	0.41	3.0	38	5	46.0	3.5	20
Anaualacomera sp. "wallace"/*Hetaira* sp.	52	0.22	3.0	36				
Ceraia mytra **(Grant, 1964)**	5	0.15	6.0	2	6	11.0	1.0	2
Chloroscritus discocercus **(Rehn, 1918)**	12	0.07	1.0	11	8	22.0	1.0	4
Docidocercus gigliotosi **(Griffini, 1896))**	31	0.15	9.5	10	6	44.5	40.0	59
Dolichocercus latipennis **(Brunner von Wattenwyl, 1891)**	9	0.15	2.5	3				
Ectemna dumicola **(Saussure & Pictet, 1897)**	47	0.19	3.0	27				
Euceraia atryx **(Grant, 1964)**	5	0.11	1.0	3				
Euceraia insignis **(Hebard, 1927)**	7	0.11	2.0	4	5	8.0	1.0	7
Erioloides longinoi **(Naskrecki & Cohn, 2000)**	34	0.26	3.0	11				
Hyperphrona irregularis **(Brunner von Wattenwyl, 1891)**	19	0.15	4.0	10				
Ischnomela pulchripennis **(Rehn, 1906)**	1622	0.11	711.0	910				
Microcentrum championi **(Saussure & Pictet, 1898)**	3	0.04	3.0	3				
Montezumina bradleyi **(Hebard, 1927)**	157	0.15	41.5	73				
Phylloptera quinquemaculata **(Bruner, 1915)**	2	0.04	2.0	2				
Pristonotus tuberosus **(Stål, 1875)**	182	0.63	7.0	43	3	64.0	10.0	35
Thamnobates subfalcata **(Saussure & Pictet, 1898)**	677	0.26	37.0	350	4	33.0	214.5	481
Viadana brunneri **(Cadena-Castañeda, 2015)**	37	0.22	5.0	14	9	21.0	10.0	129

Philophyllia ingens and *Anaulacomera* sp. "goat" males from the calls of females of the many phaneropterine species that occur in these forests and excluded these species. Among the approximately 80 katydid species we captured at lights, *Philophyllia ingens* ranked 25th and *Anaulacomera* sp. "goat" ranked 22nd in abundance (unpublished data). By excluding these two species, these species are not represented in the total number of calls detected or the number of species per recording, meaning that the overall call count and species diversity may be slightly underrepresented.

Calling rate in cages and soundscapes.—The number of calls produced by a focal individual in a cage fell within the range of the number of calls produced per 10 minutes when a species was present (Table 2, Fig. 2).

Approximately 32% of the clearly visible calls did not correspond to any of the 50 species described in ter Hofstede et al. (2020). We did not attempt to separate these events into sonotypes but present exemplars of some of these sounds (Fig. 3).

Spatial variation.—At Site 1, we detected 17 species, including two species that were detected only at this site (Table 3). At Site 2, we detected 22 species, including seven species that were detected only at this site. Fifteen species were detected in both locations. The proportion of the recordings in which a species was detected was relatively consistent across both sampling locations (Table 3).

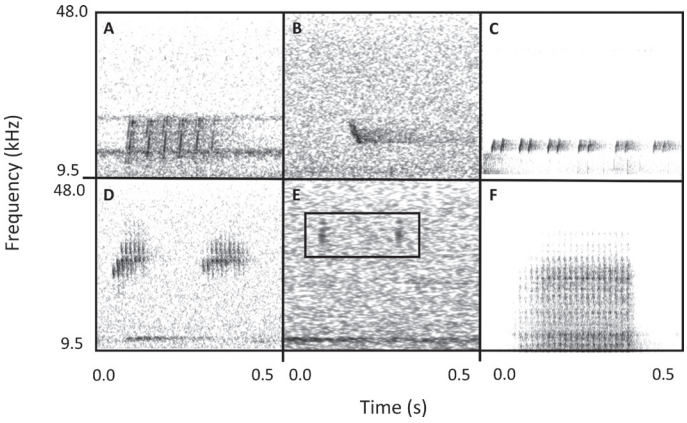

Fig. 3. Examples of calls with visible pulse structures that did not match the acoustic characteristics of the katydid calls described in ter Hofstede et al. (2020). **A.** Clip_009 1:00; **B.** Clip_022 6:19; **C.** Clip_009 7:39; **D.** Clip_013 4:33; **E.** Clip_014 4:33; **F.** Clip_025 0:54.

Time of night.—For species that were detected in the recordings, 63% of species were detected at least once at 1900 h, 63% of species were detected at least once at midnight, and 71% of species were detected at least once at 0500 h (Table 4).

Table 3. The proportion of the recordings in which a species was detected for both sampling sites and the difference in proportion between sites.

Species	Site 1	Site 2	Difference
Unmatched signals	0.92	1.00	-0.08
Acantheremus major	0.08	0.00	0.08
Acanthodis curvidens	0.00	0.07	-0.07
Agraecia festae	0.08	0.07	0.02
Anapolisia colossea	0.00	0.13	-0.13
Anaulacomera furcata	0.42	0.47	-0.05
Anaulacomera sp. "ricotta"	0.08	0.00	0.08
Anaulacomera spatulata	0.33	0.47	-0.13
Anaulacomera sp. "wallace"/ *Hetaira* sp.	0.25	0.20	0.05
Ceraia mytra	0.08	0.20	-0.12
Chloroscirtus discocercus	0.00	0.13	-0.13
Docidocercus gigliotosi	0.17	0.13	0.03
Dolichocercus latipennis	0.08	0.20	-0.12
Ectemna dumicola	0.33	0.07	0.27
Euceraia atryx	0.00	0.20	-0.20
Euceraia insignis	0.08	0.13	-0.05
Erioloides longinoi	0.00	0.47	-0.47
Hyperphrona irregularis	0.25	0.07	0.18
Ischnomela pulchripennis	0.17	0.07	0.10
Microcentrum championi	0.00	0.07	-0.07
Montezumina bradleyi	0.08	0.20	-0.12
Phylloptera quinquemaculata	0.00	0.07	-0.07
Pristonotus tuberosus	0.50	0.73	-0.23
Thamnobates subfalcata	0.17	0.33	-0.17
Viadana brunneri	0.17	0.27	-0.10

Seasonal variation.—Katydid calling occurred during both wet and dry months (Table 5). The number of species detected per 10-minute recording was slightly lower at the end of the dry season in March than in the other recordings.

Table 4. The proportion of ten-minute recordings that contained a given species, and the number of calls detected per ten-minute recording when a species was detected as a function of sampling time.

	Prop. of Recordings with Species			Calls/10 Minutes when Present		
	1900	0000	0500	1900	0000	0500
Unmatched signals	1.00	0.89	1.00	73.0	44.0	31.0
Acantheremus major	0.11	0.00	0.00	10.0		
Acanthodis curvidens	0.11	0.00	0.00	1.0		
Agraecia festae	0.00	0.11	0.11		37.0	1118.0
Anapolisia colossea	0.00	0.00	0.22			1.5
Anaulacomera furcata	0.67	0.44	0.22	15.5	2.0	1.5
Anaulacomera "ricotta"	0.00	0.00	0.11			1.0
Anaulacomera spatulata	0.33	0.11	0.78	14.0	3.0	3.0
Anauaacomera sp. *"wallace"*/ *Hetaira* sp.	0.22	0.00	0.44	3.0		4.5
Chloroscirtus discocercus	0.11	0.11	0.00	11.0	1.0	
Ceraia mytra	0.00	0.33	0.11		1.0	1.0
Docidocercus gigliotosi	0.22	0.22	0.00	9.5	6.0	
Dolichocercus latipennis	0.33	0.00	0.11	3.0		1.0
Ectemna dumicola	0.22	0.22	0.11	21.0	1.0	3.0
Euceraia atryx	0.00	0.22	0.11		2.0	1.0
Euceraia insignis	0.00	0.00	0.33			2.0
Erioloides longinoi	0.33	0.22	0.22	1.0	7.0	4.5
Hyperphrona irregularis	0.22	0.00	0.22	8.5		1.0
Ischnomela pulchripennis	0.11	0.22	0.00	1.0	810.5	
Microcentrum championi	0.00	0.11	0.00		3.0	
Montezumina bradleyi	0.22	0.11	0.11	44.0	1.0	68.0
Phylloptera quinquemaculata	0.00	0.00	0.11			2.0
Pristonotus tuberosus	0.44	0.89	0.56	6.0	12.0	2.0
Thamnobates subfalcata	0.22	0.56	0.00	78.5	37.0	
Viadana brunneri	0.33	0.22	0.11	10.0	4.0	4.0

Discussion

The acoustic environment of Barro Colorado Island is diverse and rich with the sounds of many species of katydids. Every recording contained katydid calls, but even the most ubiquitous species (*Pristonotus tuberosus*) was detected in only 63% of recordings, with most species occurring much less often. Based on the katydids that are captured at lights, the katydid community of BCI is diverse and relatively even (unpublished data), a trend that is reflected in acoustic sampling as well.

For acoustic monitoring, a critical question is how many sites in a forest have to be sampled in order to thoroughly census acoustic insects. In homogeneous tropical forests, at least some insect communities have high alpha diversity and low beta diversity (Novotny et al. 2007). Using multisite sampling and species area models, Basset et al. (2012) predicted that sampling one ha of rainforest would yield approximately 60% of the insect species found by sampling 6000 ha. In this study, we analyzed two sites within the same forest separated by approximately half a kilometer. Sixteen katydid species were detected at both sites, with most species occurring at a similar frequency in both sites. Nine species were detected at only one of the sites. These nine species were generally detected in a small number of recordings, suggesting that these species might be rare overall rather than preferentially associated with one site. Despite differences in canopy cover and forest density between the two sites, our data provide preliminary evidence that acoustic sampling of a relatively small number of locations may provide a reasonably thorough list of species found in that microenvironment, although additional research is required to understand the spatial scale at which communities vary. It is important to note that both recorders used in this study were placed 24 m from the ground. While recordings made at 24 meters might resemble other recordings made at 24 m, this does not mean that these recordings capture the presence of understory katydid species, and for censusing diversity, sampling at multiple heights may well be more important than sampling at many locations.

Katydid calls were commonly detected throughout the night and across seasons. While some species were more commonly detected early or late in the evening, nearly all of the commonly detected species produced calls that were detected at multiple times of night, mirroring the temporal calling patterns observed in recordings of captive focal katydids (Symes et al. 2020). Seasonally, katydids were well represented in all recordings, including during the wet season and at the end of an unusually dry season (Fig. 1). Katydids are caught at lights and in the forest throughout the year, with higher abundance Feb-April (Ricklefs 1975). These species may mate throughout the year, but since many species live for many months and potentially years, they may be present at times when they are not mating. However, the presence of katydid calls in all recordings suggests that at least some katydid species are mating throughout the year.

Table 5. Proportion of ten-minute recordings that contain each species and the number of calls detected per ten minutes when a species is present. Note that the earliest date (Mar 05) is only represented by Site 2.

	Proportion of Recordings with Species					Calls/10 Minutes when Present				
	5-Mar-19	5-Jun-19	2-Jul-19	1-Aug-19	30-Aug-19	5-Mar-19	5-Jun-19	2-Jul-19	1-Aug-19	30-Aug-19
Unmatched signals	1.00	1.00	0.83	1.00	1.00	92.0	40.0	73.0	32.0	42.5
Acantheremus major	0.00	0.00	0.00	0.00	0.17					10.0
Acanthodis curvidens	0.00	0.00	0.00	0.17	0.00				1.0	
Agraecia festae	0.00	0.17	0.00	0.00	0.17		37.0			1118.0
Anapolisia colossea	0.33	0.17	0.00	0.00	0.00	2.0	1.0			
Anaulacomera furcata	0.33	0.67	0.17	0.50	0.50	1.0	13.5	18.0	7.0	1.0
Anaulacomera sp. "ricotta"	0.00	0.00	0.00	0.17	0.00				1.0	
Anaulacomera spatulata	0.33	0.67	0.33	0.33	0.33	3.0	3.5	20.0	1.5	14.5
Anaulacomera sp. " wallace"/*Hetaira* sp.	0.00	0.33	0.33	0.17	0.17		2.5	19.5	1.0	7.0
Chloroscirtus discocercus	0.00	0.00	0.17	0.00	0.17			11.0		1.0
Ceraia mytra	0.00	0.17	0.00	0.17	0.33		1.0		1.0	1.5
Docidocercus gigliotosi	0.00	0.17	0.00	0.17	0.33		10.0		2.0	9.5
Dolichocercus latipennis	0.00	0.17	0.00	0.33	0.17		3.0		2.0	2.0
Ectemna dumicola	0.00	0.17	0.00	0.33	0.33		1.0		14.0	9.0
Euceraia atryx	0.00	0.17	0.00	0.33	0.00		1.0		2.0	
Euceraia insignis	0.00	0.17	0.17	0.17	0.00		2.0	4.0	1.0	
Erioloides longinoi	0.33	0.50	0.17	0.33	0.00	1.0	9.0	3.0	1.0	
Hyperphrona irregularis	0.00	0.17	0.17	0.33	0.00		1.0	7.0	5.5	
Ischnomela pulchripennis	0.33	0.00	0.17	0.00	0.17	711.0		910.0		1.0
Microcentrum championi	0.00	0.00	0.00	0.00	0.17					3.0
Montezumina bradleyi	0.00	0.50	0.00	0.17	0.00		68.0		15.0	
Phylloptera quinquemaculata	0.00	0.00	0.17	0.00	0.00			2.0		
Pristonotus tuberosus	0.33	0.67	0.67	1.00	0.33	1.0	12.0	15.5	4.5	8.0
Thamnobates subfalcata	0.33	0.00	0.33	0.17	0.50	350.0		93.0	4.0	13.0
Viadana brunneri	0.00	0.33	0.33	0.17	0.17		1.5	8.0	14.0	4.0
Number of species detected	8	17	13	18	16					
Average species/10 min	3.3	6.2	4.0	6.0	5.0					

There were a surprising number of high-quality calls that did not match any species in the ter Hofstede et al. (2020) paper, which presents the calls of 50 katydid species from BCI and includes most of the species that are commonly caught at light traps. The katydids of Barro Colorado Island are comparatively well studied and recorded. The authors have caught nearly 8,000 katydids at this site and have documented ~80 species, with 1–2 additional species observed each year. The canopy soundscape recordings contained >10 repeatably recognizable calls between 15 and 40 kHz that did not match commonly recorded katydid species. It is possible that these sounds are produced by some of the 30+ katydid species that are not included in the ter Hofstede et al. (2020) paper. The species that were not included in this publication were rarely observed in light catches or did not produce sound in focal recordings (*e.g.*, *Caulopsis* spp.). Some of these calls could also represent non-katydid insects. However, in recording 55 cricket species from Barro Colorado Island, Heiner Römer and colleagues recorded only two species with calls above 10 kHz (12.1 and 13.8 kHz) (H. Römer and A. Schmidt, personal communication). In a separate study, the cricket species *Ponca hebardi* was recorded at 17.6 kHz, suggesting that high frequency crickets are uncommon but not absent in the BCI soundscape (Benavides-Lopez 2020).

A likely possibility is that these unmatched sounds represent canopy specialist katydid species, some or many of which may not be documented, described, or captured in light catches. In a study of Peruvian katydid species (Nickle 2006), extensive terrestrial surveys generated a thorough list of local katydid species. However, canopy fogging resulted in the novel discovery of additional species of katydids that had never been observed on the ground. Acoustic recording provides evidence to suggest that there may be katydid species on BCI that have never been captured in exhaustive light trap surveys. The prevalence of unmatched calls in these recordings suggests that the number of katydid species in this habitat could be substantially higher than the currently estimated 80 species. Unmatched calls represent a particular challenge for data archiving, particularly because some of these calls may match to species that have been described in other well-studied locations or will be in the future. The acoustic monitoring of habitats will be advanced by developing approaches for comparing unknown sounds against existing sound archives.

Numerous species were documented in ter Hofstede et al. (2020) that did not appear in the recordings made at 24 m height in the forest, even though they are common in light catch data. The absence of many species from canopy recordings may reflect habitat partitioning, with some of these species not occurring or calling in the canopy. In particular, species in the *Arota* and *Phylloptera* genera are conspicuously rare/absent in recordings, despite being common in light catch data and active callers in focal recordings.

The mean number of calls detected per ten-minute recording was generally quite similar between soundscape and focal individual recordings, providing two lines of evidence both supporting low call rates in Neotropical forest katydids. In addition, there was often remarkably good alignment between the call rates in caged focal recordings and the call rates in soundscape recordings. An exception to this is *Anaulacomera spatulata*, where the mean num-

ber of calls detected on the soundscape recording was approximately twice as high as the number detected in a focal recording of a single individual. The abundance of calls on the soundscape recording is consistent with the presence of multiple individuals within range of the microphone and is supported by the fact that *Anaulacomera spatulata* is the most common species in light catches. Another notable exception is *Docidocercus gigliotosi*, where forest recordings contained a mean of 8 calls per recording where it was detected, and focal recordings had a mean of 48 calls in ten minutes. In previous work, *D. gigliotisi* performed documented vertical migrations, calling actively at the ground level and then entering the canopy, where calling rates may be reduced during foraging (Lang and Römer 2008).

Annotation of insect calls can provide detailed insight into the spatial and temporal dynamics of calling insect communities (Riede 2018). While annotation can be time consuming, the annotation of some species is much more challenging than others. In general, distinctive multi-pulse calls with fixed pulse spacing were comparatively easy to identify to species, compared to single pulse calls, which were especially difficult to identify with confidence. In single pulse calls, the lack of repetition made it challenging to confirm species identity and to separate single pulse calls from other sounds in the rainforest, particularly the short replies used by duetting females. Ultimately, we excluded two species that produced single pulse calls (*Philophyllia ingens* and *Anaulacomera* sp. "goat") because we had low confidence in the identification of these single pulse calls. Future projects relying on manual or automated identification may consider the trade-offs between the missing information from excluding these species and the benefit of faster and more confident species identifications.

Detailed understanding of insect communities provides valuable information for conservation and management (Fischer et al. 1997, Thomas 2005). The active debate around the nature and magnitude of insect population declines highlights how little we know about insects, including information about what times of year a given species is present and whether it is active in the canopy and understory (Forister et al. 2019, Janzen and Hallwachs 2019). The absence of basic natural history information obscures trends such as declines in understory insects, or in species that breed in response to specific rainfall regimes. Although call identification is currently a time-consuming process, advances in automated processing, particularly machine learning approaches, are poised to make identification much faster and more accessible. When acoustic sampling occurs across years and sites in a standardized manner, recordings can provide metrics of relative abundance over time and between species and, when combined with information on insect call amplitude and sound attenuation, can be used to calculate absolute density. Detailed information on species composition and relative and absolute abundance will provide greater insight into a central layer of the food web, providing valuable information on the population dynamics of insects, facilitating habitat management and data-driven decision making for conservation.

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Supplementary material 1

Author: Hannah ter Hofstede

Data type: image

Explanation note: Figure S1: Relative microphone sensitivity at frequencies recorded by the Rugged Swift with a sampling rate of 96 samples/s. Points are average values for 5 relative amplitude measurements (one direct recording and four recordings with the speaker 45o off-axis from the microphone with the recorder pointing left, right, up, and down). Grey shading shows ± SD. Grey line is the smoothed moving average of 3 data points.

Link: https://doi.org/10.3897/jor.31.73373.suppl1

A new species of tree cricket (Orthoptera, Gryllidae, Oecanthinae) from Chihuahuan Desert gypsum dunes in the United States and a key to the *nigricornis* species group

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Abstract

A new species of tree crickets, *Oecanthus beameri* **sp. nov.,** is described from the gypsum dunes of White Sands National Park in New Mexico, United States. The new species is currently known only from the type locality, where it appears to be specific to the gypsophile plant hoary rosemary mint (*Poliomintha incana)*. This new species has the narrowed tegmina and calling song that are found in the *nigricornis* species group. Although it has morphological similarities to *O. quadripunctatus* and *O. celerinictus*, there are differences in the subgenital plates, tegminal measurements, coloring, tibial markings, song frequency, and song pulse rate. This new species has been given the common name White Sands tree cricket. We provide a key to all species in the *nigricornis* group. Video and song recordings are available online as Suppl. materials 1–8.

Keywords

bioacoustic, biodiversity, gypsophile, *Oecanthus*, *Poliomintha incana*, White Sands National Park

Introduction

Two genera of Oecanthinae occur in the United States—*Oecanthus* Serville, 1831 and *Neoxabea* Kirby, 1906 (Cigliano et al. 2021; Singing Insects of North America (SINA) website (2021a)). Twenty-two 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 2021b). These groups can be distinguished by characteristics including song type (chirping vs trilling and continuous vs intermittent); 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 (Fulton 1915, Walker 1962, 1963, Walker and Collins 2010). All nine species in the *nigricornis* species group occur in North America: *O. argentinus* Saussure, 1874; *O. celerinictus* Walker, 1963; *O. forbesi* Titus, 1903; *O. laricis* Walker, 1963; *O. nigricornis* Walker, 1869; *O. pini* Beutenmüller, 1894; *O. quadripunctatus* Beutenmüller, 1894; *O. salvii* Collins, 2020; and *O. walkeri* Collins & Symes, 2012.

In 2019, two specimens examined in the collection at the Academy of Natural Sciences of Drexel University (ANSDU) led to this investigation of a new species of *Oecanthus*. Two male specimens (Fig. 1), collected by Raymond H. Beamer (University of Kansas) in 1932 (Suppl. material 1: Beamer 1932 expedition), were found in the drawer containing *O. quadripunctatus*, but were visibly smaller and paler than all other males in the drawer. Fig. 1A, B show these differences when side by side with a male *O. quadripunctatus* in the collection box. Upon closer inspection, one of the specimens could be seen to have markings similar to *O. quadripunctatus*, with the upper outer round mark on the scape very faint, but the vertical line appeared to have a slight interruption midway (Fig. 1C). *O. quadripunctatus* has a total of four (rarely two) marks on the first two antennal segments (Fulton 1915, Walker 1963). Of additional interest was the fact that both of the smaller male specimens were collected in White Sands of New Mexico. White Sands National Park (WSNP) lies within the Chihuahuan desert and is comprised of dunes of bright white gypsum crystals that support gypsophilic plants. Our investigation sought to determine whether these were *O. quadripunctatus*, but smaller and paler because of their habitat, versus a distinct and undescribed species. We conducted a special research and collecting trip to WSNP in September of 2021, with the cooperation of the National Park Service (White Sands National Park, Scientific Research and Collecting Permit# WHSA-2021-SCI-0010), to collect specimens, record songs, and evaluate the habitat characteristics of the potentially new *Oecanthus*. This article describes the new species of *Oecanthus* from White Sands National Park.

Materials and methods

Specimens.—Seven adult males and one adult female of *Oecanthus* were collected on dunes (Fig. 2) adjacent to the Interdune Boardwalk at the WSNP in New Mexico between 21h and 22h from three locations separated by less than 1300 meters. Sunset was 19h15, and the males started calling around 20h, peaking around 21h. All seven males were approximately 1 m above the ground surface, and the female was on the white sand (gypsum) surface at an oatmeal bait trail.

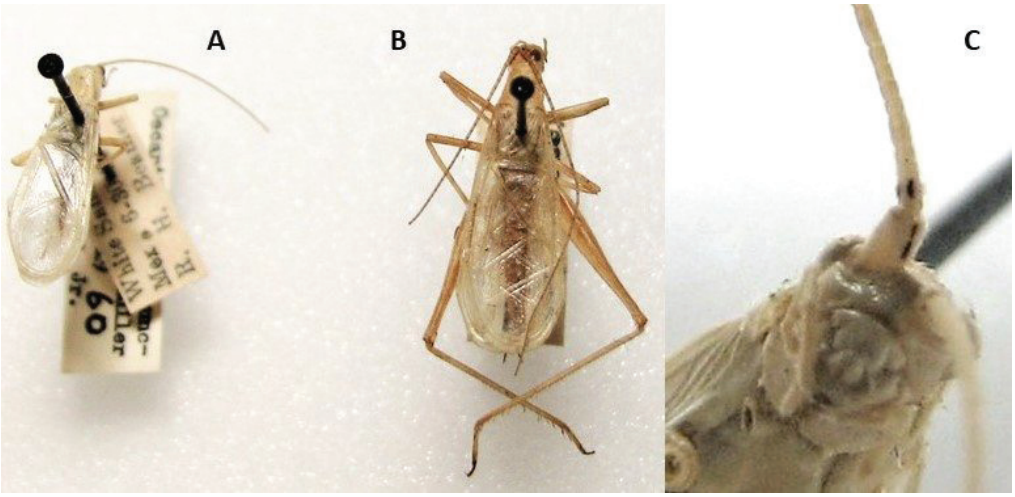

Fig. 1. *Oecanthus* specimens found in a box of *O. quadripunctatus* specimens in the ANSDU collection. **A.** Dorsal view of *O. beameri* sp. nov.; **B.** Dorsal view of *O. quadripunctatus*; **C.** Markings on pedicel and scape of specimen of *O. beameri* sp. nov.

Specimens were located by the calling song of the males and collected manually within two hours of dusk. One female was collected from an oatmeal trail laid on the sand surface at dusk among shrubs of *Poliomintha incana* Gray, 1870, with singing males. No other *Oecanthus* species were heard singing in the area. Four of the eight tree crickets were brought indoors, kept alive, and separated to be recorded, and then preserved in 91% ethyl alcohol for morphological studies. Photographs were made with Canon S5 IS and Canon SX70 cameras. Measurements of the alcohol-preserved specimens were made with a Fischer spindle ruler.

Pinned specimens were dried in a moisture-extracting refrigerator to preserve their delicate greenish-white color. Measurements of the dried specimens, including the holotype, were made with an American Optical binocular dissecting scope and ocular micrometer, with magnification ranging from 10X to 50X. Measurements of alcohol preserved (n=3) and dry pinned specimens (n=3) are presented here as ranges and individually in Suppl. material 2 due to the contraction of dry membranous and some sclerotized tissues of dry pinned specimens.

Genus determination was made with keys from Walker (1967) and SINA (2021a) and review of taxa of *Oecanthus* in the Orthoptera Species File (Cigliano et al. 2021). Along with coloration, body length, antennal markings, cerci length and shape, subgenital plate details, and the female ovipositor, the male characters considered for description included tegmina length and width, stridulatory file length and number of teeth, metanotal gland features, and internal genitalia (focused on copulatory blades).

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), tegminal length (from the thorax joining point to distal end of tegmina along midline), tegminal width (measured at the widest section of the tegmina at rest or the maximum width of the dorsal surface of each tegmen excluding the lateral folds), hind femur length, and cerci length. The male stridulatory file length was measured along the ventral surface of the left tegmen A1 vein (Desutter-Grandcolas et al. 2017), from the first tooth at the A1 vein file lobe, toward the lateral margin of the A1 vein, to the last lateral tooth of the file on the A1 vein. The female ovipositor was measured from the base (originating from the abdomen) to the distal tip.

Online photographic material.—Additional materials examined were photographs posted on iNaturalist: figs 3C, F by James Bailey (https://www.inaturalist.org/observations/102287655); fig. 3D by Jared Shorma (https://www.inaturalist.org/observations/98434363).

Climate and habitat.—White Sands National Park daytime temperatures average from 35°C June through August to 16°C December through February. Night temperatures range from 10–18°C June through August and average -5°C December through February (National Park Service 2021).

The dominant shrub in the area of collection was hoary rosemary mint, *Poliomintha incana*, which is a gypsophile with whitish-green leaves and stems and a very pronounced and unique aromatic fragrance from plant defense chemicals. Many singing males were heard in the area but were not collected, and all were exclusively singing from *P. incana*.

Calling song recording and analyses.—The thermometer was held at the location on the plants where the males were calling immediately after capture on site, and within 10 cm from the indoor containers.

Temperatures of the perch sites of the males singing from the shrubs on site were measured using a hand-held Taylor mercury thermometer. An Accu-rite digital thermometer and an Accu-rite mercury thermometer were used to measure the temperature of the captive singing males.

The male acoustic signals that were recorded in the field at the collection site were recorded using an I-phone 11 held approximately 0.5 m from each calling male. Captive males were recorded with a Canon SX20S that was tested for calibration by recording a reference time audio file with reference tones and comparing the results to the original file. The camera was kept at a distance of less than 10 cm from the individual. Three male tree crickets were kept in large glass vases with mesh tops for observation and recordings. Video recording of a singing male can be viewed in Suppl. material 3. Analyses of audio waveforms and spectrograms were made with the Raven Lite 2.0 program (Cornell Lab 2021b). Additional recordings (Suppl. material 4) from the Macaulay Library of Cornell Lab (2021a) and data from the Singing Insects of North America website (SINA 2021c) were used for the preparation of two graphs

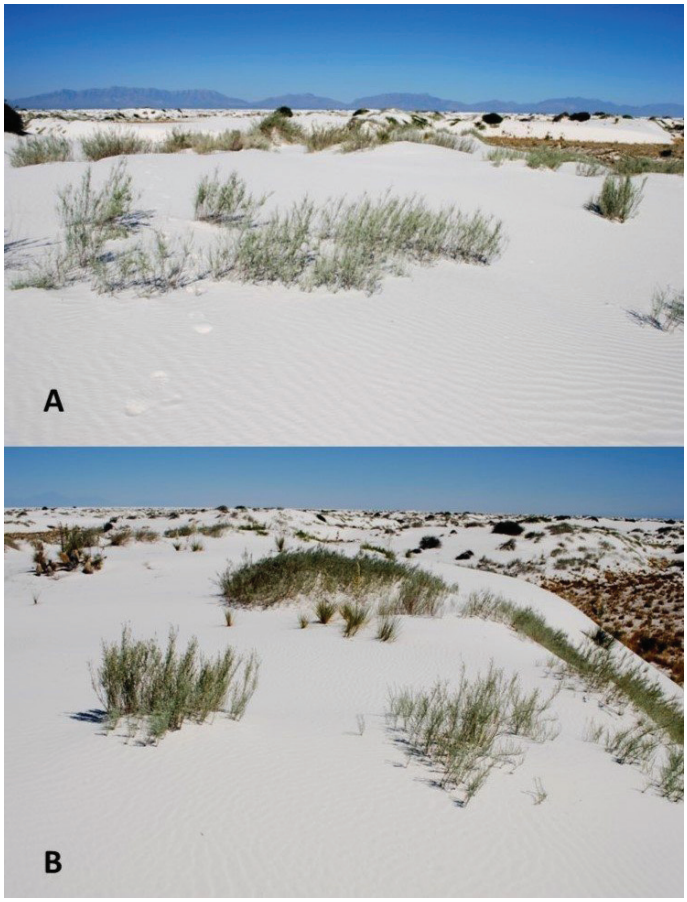

Fig. 2. Habitat photos. **A.** Collection site near Interdune Boardwalk; **B.** White gypsum crystals dune with hoary rosemary mint shrubs (*Poliomintha incana*).

to compare song pulses per second vs temperature and carrier frequency vs temperature with species in the *nigricornis* group.

Depositories.— **MSBA** Museum of Southwestern Biology, Division of Arthropods, University of New Mexico, Albuquerque, USA; **ANSDU** The Academy of Natural Sciences of Drexel University, Philadelphia, USA; **FSCA** Florida State Collection of Arthropods, Gainesville, USA; **CAS** California Academy of Sciences, San Francisco, USA; **TAMU** Texas A & M University, Houston, USA.

Results

Taxonomy

Family Gryllidae Laicharting, 1781
Subfamily Oecanthinae Blanchard, 1845
Tribe Oecanthini Blanchard, 1845
Genus *Oecanthus* Serville, 1831

***Oecanthus beameri* sp. nov.**
https://zoobank.org/95CA19BE-72DB-41C7-915F-CE6AA5D5C9C1
Figs 3A–F, 4A–D, 5A, C, 6A–F

Diagnosis.—The antennal markings of *O. beameri* sp. nov. can total two, three, or four, with the medial mark on the scape usually broken into two pieces (Figs 3C, 4), while *O. quadripunctatus* has either two or four marks with the medial mark on the scape being a solid post, and *O. celerinictus* always has a solid medial mark on the scape and never lacks the upper outer mark on the scape and is never round. The two antennal marks on the pedicel of *O. walkeri* (Collins and Symes 2012) touch, and those of *O. argentinus* touch or nearly touch, while the marks on *O. beameri* sp. nov. do not.

The male and female subgenital plates of *O. beameri* sp. nov. (female: wide shallow notch as in Fig. 5A; male: rounded end as in Fig. 5C) can be distinguished from *O. quadripunctatus* (female: deep narrow notch as in Fig. 5B; male: tapered to a rounded tip as in Fig. 5D). When next to each other, a male *O. beameri* sp. nov. has a lighter coloring and smaller proportion of tegmen width to abdomen width than a male *O. quadripunctatus* (Suppl. material 5). *Oecanthus beameri* sp. nov. lacks the dark black lines across the proximal portion of the hind tibiae that are very common on *O. celerinictus*, but faint lines can be present (Fig. 3F). The deep black setae on the hind femora of *O. salvii* (Collins and Schneider 2020) are not present in *O. beameri* sp. nov. See below for more detailed diagnostic information.

Description.—Face, pronotum, abdomen, and wings pale greenish-white (Fig. 3A–D), color number 97 (Köhler 2012). Eye color pale green. Palpi pale whitish green. Tympanal membrane on fore tibiae whitish green. Tarsi, tibiae, and femora translucent pale mint green. Tibiae without black setae or lateral black lines. Cerci straight and translucent pale green. Scape and pedicel translucent whitish, and remainder of antennomeres translucent whitish. Ventral face of pedicel and scape each with black marks on pale whitish field (Fig. 3C). See examples of antennal marking variations in Fig. 4.

Materials examined.—**Holotype**: USA • ♂; New Mexico, Otero County, White Sands National Park; 32.793055, -106.233611; 10 September 2021; D. Lightfoot leg.; on *Poliomintha incana*; MSBA 74580. Paratypes: Same information as holotype: USA • 1♂; MSBA 74579 • 1♀ (dry pinned), 1♂ (in alcohol); MSBA • 1 ♂ (dry pinned); ANSDU • 1♂ (dry pinned); CAS • 1♂ (in alcohol); FSCA • 1♂ (in alcohol for DNA research); TAMU

Etymology.—Specific epithet in recognition of Raymond Beamer who collected the specimens in 1932 that were discovered in the ANSDU collection in 2019. The common name, White Sands tree cricket, is for the location where this species was discovered with high potential for endemism.

Holotype measurements (mm).—Body length 11.7; tegminal length 9.0, tegminal width 20.0; pronotal length 2.3, distal pronotal width 2.0; hind femur length 9.0; cercus length 2.8; stridulatory file length 2.3; stridulatory teeth number 48.

Male paratypes.—(n=6) Body length (mm) 10.8–13.3; tegminal length 8.5–9.8; tegminal width 3.3–3.9; pronotal length 2.2–2.4; distal pronotal width 1.8–2.2; hind femur length 8.5–9.8; cerci length 2.7–3.1; stridulatory file length (n=5) 1.2–1.5. Right tegminal stridulatory teeth (as in Fig. 6A) number (n=5) 45–49. Tegmina with veins as in Fig. 3A. Subgenital plate with a rounded end (Fig. 5C). Copulatory blades thin with a deep notch separating them fairly equal to the width of one blade (Fig. 6B, C), and a slight indentation at the medial side of the distal end of each blade (6D). The metanotal gland with a rounded triangular

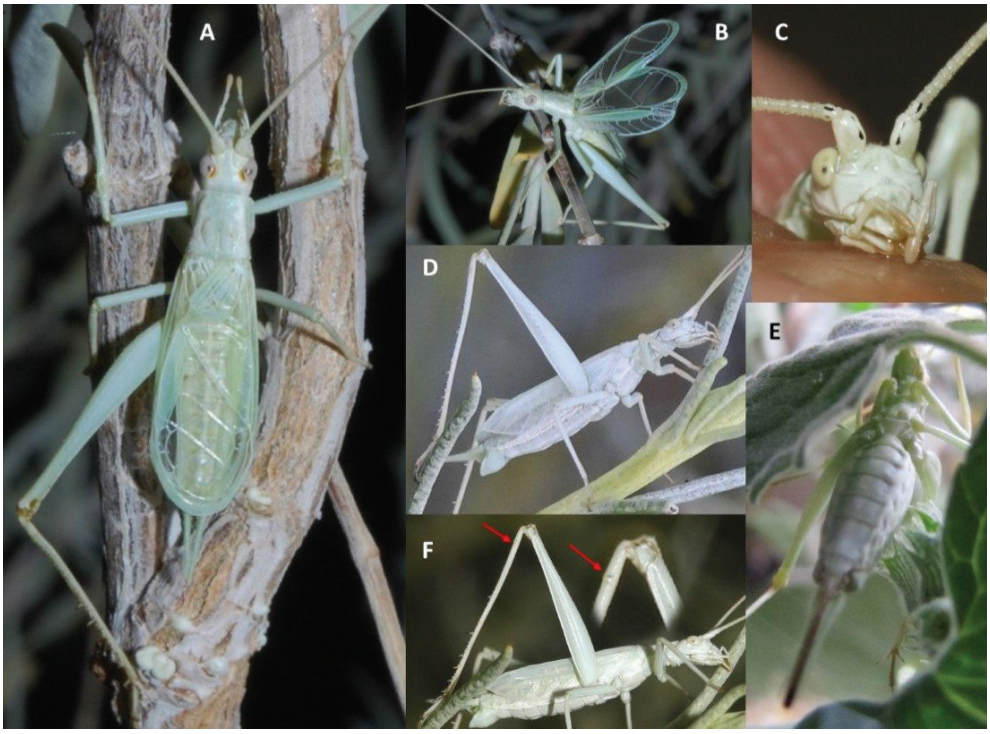

Fig. 3. *Oecanthus beameri* sp. nov. **A.** Male habitus, dorsal view; **B.** Front view of a singing male; **C.** Antennal markings. Photo credit James Bailey, iNaturalist; **D.** Ventral abdomen color of adult male. Photo credit Jared Shorma, iNaturalist; **E.** Ventral abdomen color of adult female; **F.** Faint horizontal lines on proximal portion of hind femora. Photo credit James Bailey, iNaturalist.

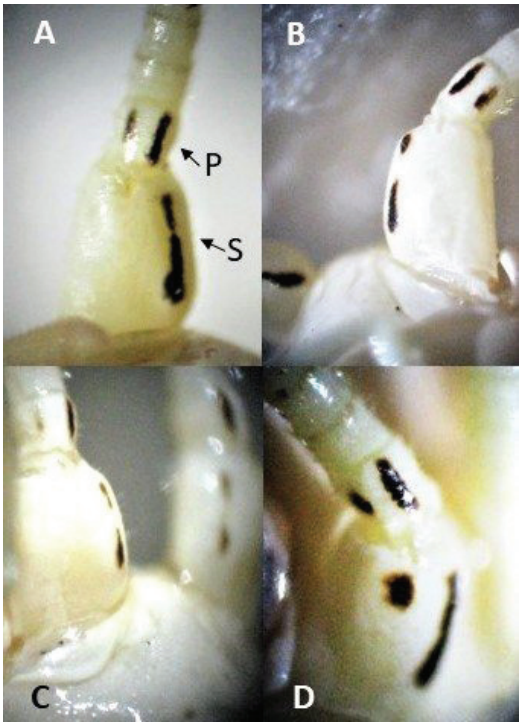

Fig. 4. Variable configurations of black markings on pedicel (P) and scape (S) of *Oecanthus beameri* sp. nov. **A.** Medial mark on scape nearly separated into two sections, with no lateral mark on scape; **B.** Two marks on pedicel, no lateral mark on scape, and medial mark on scape has clear separation into two sections; **C.** Faint lateral mark on pedicel, no lateral mark on scape, and medial mark on scape has clear separation into two sections; **D.** Lateral mark on scape round, and medial mark solidly one line.

depression, bristles running horizontally across the upper edge of the cavity, and no posterior medial lobe (Fig. 6E). These key out and match the diagram in Walker and Gurney (1967) for a member of the *nigricornis* species group. As pointed out by Walker and Gurney (1967), species within a group are difficult to separate based on the metanotal gland.

Female paratype description.—(n=1) Latticed vein pattern on translucent greenish-white wings. Abdomen pale white (Fig. 3E). 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 tip of the ovipositor flared (Fig. 6F) and extending just beyond the tips of the cerci. Distal end of subgenital plate with a wide, shallow notch (Fig. 5A). The only female collected (Fig. 3E) was missing the distal ends of the wings, thus dorsal photos not included.

Oviposition.—The female mated while in captivity and oviposited approximately 24 times into stems of an undetermined species of sage in both nodal and internodal areas (Fig. 7A, B). Species in the *varicornis* and *nigricornis* groups of *Oecanthus* generally oviposit within the stem internodal areas, while species in the *niveus* group prefer to oviposit in the nodal areas (Fulton 1915). Photographs of some *nigricornis* species group members' oviposition marks can be viewed on the Orthoptera Species File website (Cigliano 2021), including *O. quadripunctatus*. It is unknown whether being in captivity affected the locations of oviposition by this *O. beameri* sp. nov. female.

Climate and habitat.—On the day the tree crickets were collected, daytime temperatures reached 32–37°C, and cooled off to 26–31°C in the evening. Males were calling exclusively on hoary rosemary mint, *P. incana*, and were generally restricted to the tops of the gypsum dunes.

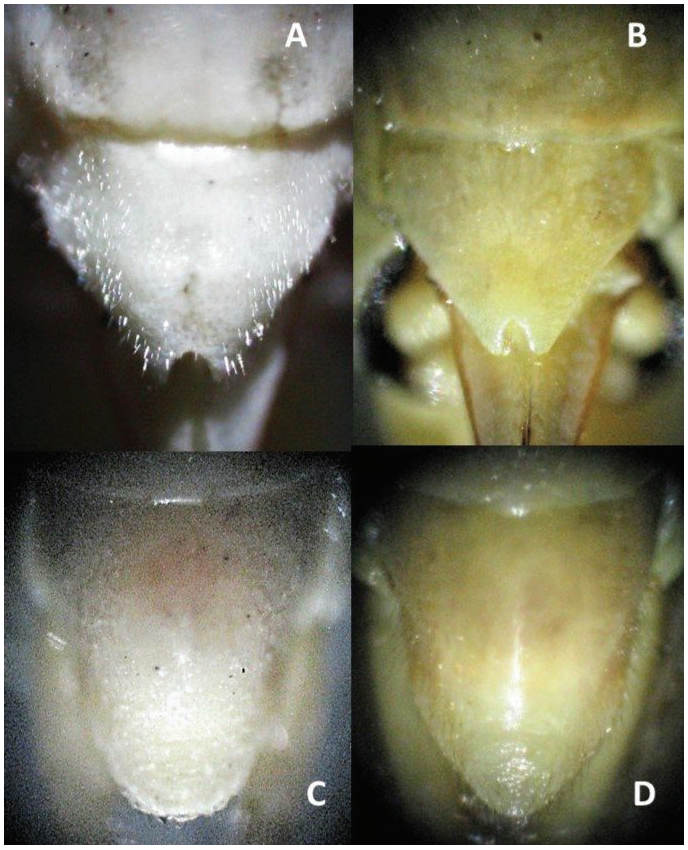

Fig. 5. Adult *Oecanthus* female and male subgenital plates. **A.** Female of *O. beameri* sp. nov.; **B.** Female of *O. quadripunctatus*; **C.** Male of *O. beameri* sp. nov.; **D.** Male of *O. quadripunctatus*

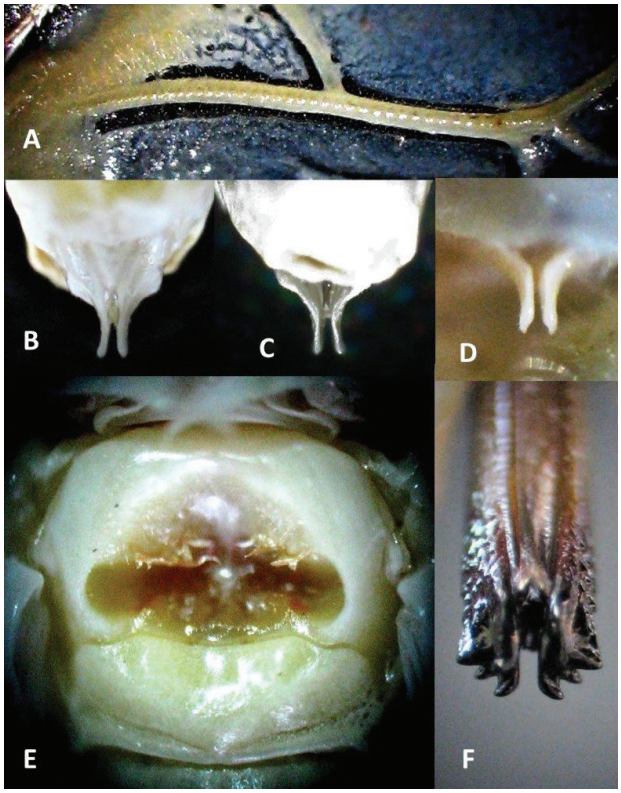

Fig. 6. Structures of adult male and female *Oecanthus beameri* sp. nov. **A.** Male stridulatory file and teeth; **B.** Dorsal view of male internal genitalia; **C.** Ventral view of male internal genitalia; **D.** Ventral view of in situ copulatory blades; **E.** Male metanotal gland; **F.** Female ovipositor.

Character comparisons among species of the nigricornis species group

Colors, patterns and morphology—The antennal markings of *O. beameri* sp. nov. can total two, three, or four, with the medial mark on the scape usually broken into two pieces (Figs 3C, 4A–C), while *O. quadripunctatus* has either two or four marks with the medial mark on the scape being a solid post (SINA 2021c). The male and female subgenital plates of *O. beameri* sp. nov. (male: rounded end as in Fig. 5C; female: wide shallow notch as in Fig. 5A) can be distinguished from *O. quadripunctatus* (male: tapered to a rounded tip as in Fig. 5D; female: deep narrow notch as in Fig. 5B). When next to each other, a male *O. beameri* sp. nov. has a lighter coloring and smaller proportion of tegmen width to abdomen width than a male *O. quadripunctatus* (Suppl. material 5). *O. celerinictus* always has a solid medial mark on the scape and never lacks the upper outer mark on the scape, which is never round. *O. beameri* sp. nov. lacks the dark black lines across the proximal portion of the hind tibiae that are very common on *O. celerinictus*, but faint lines can be present (Fig. 3F). The deep black setae on the hind femora of *O. salvii* (Collins and Schneider 2020) are not present in *O. beameri* sp. nov. The two antennal marks on the pedicel of *O. walkeri* (Collins and Symes 2012) touch, while the marks on *O. beameri* sp. nov. do not.

Song pulse patterns.—The *O. beameri* sp. nov. male calling song is a continuous trill, often lasting 5–9 seconds with pauses of similar lengths, which increases in rate as the ambient temperature rises (Figs 8, 9). Captive males often trilled for up to 30 seconds. Recordings of *O. beameri* sp. nov. were made in the field and in captivity. An onsite recording can be heard in Suppl. material 6, and a captive song sample at a similar temperature can be heard in Suppl. material 7. Recording of side-by-side captive *O. beameri* sp. nov. and *O. quadripunctatus* males at 23.8 °C can be heard in Suppl. material 8. Pulse rate and frequency graphs provide comparisons to other species with similarities in the *nigricornis* group (Figs 9, 10). Four species were not included due to never being totally pale mint green and having black, dark brown, rust, or mahogany color on the ventral surfaces of the abdominal tergites: *O. forbesi*, *O. laricis*, *O. nigricornis*, and *O. pini*.

Dichotomous key for the nigricornis species group—Since *O. beameri* sp. nov., *O. celerinictus*, and *O. quadripunctatus* are members of the *nigricornis* species group, it is not unexpected that no profound differences were evident in the following characters: number of stridulatory teeth number, tegmen configuration, and metanotal gland. The similarities of metanotal glands among species in the *nigricornis* species group can be viewed in Collins and Schneider (2020). The antennal markings of *O. beameri* sp. nov. can match (Fig. 4D) those of *O. quadripunctatus* but are variable in number and configuration (Figs 3C, 4A–C). The distal tip of the subgenital plate of the male *O. beameri* sp. nov. is rounded, while the tip of *O. quadripunctatus* is pointed. The notch in the subgenital plate of the female *O. beameri* sp. nov. is wide and shallow, while the notch in the plate of the female *O. quadripunctatus* is narrow and deeper. Tegminal length and width as well as stridulatory teeth number are similar to *O. celerinictus*, but *O. celerinictus* consistently has a solid medial line on the scape. The antennal markings on the

Fig. 7. Oviposition marks of *O. beameri* sp. nov. female on sage plants provided in captivity. (Red arrows indicate some of the oviposition sites; yellow arrows indicate nodes.) **A.** Internodal placement of eggs; **B.** Nodal placement of eggs.

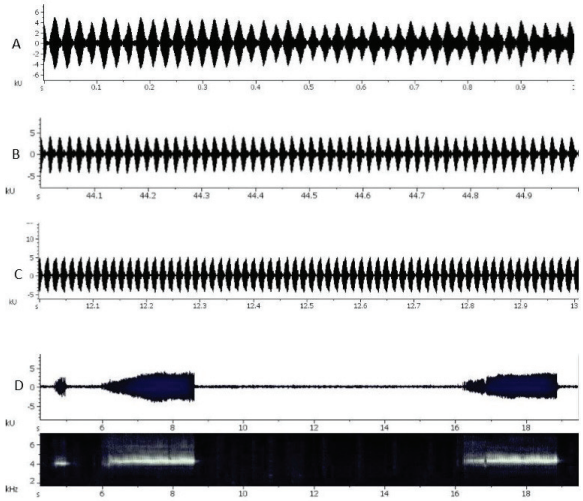

Fig. 8. Waveforms of the calling song of *Oecanthus beameri* sp. nov.; **A.** 43 pulses per second, 20.0 °C; **B.** 56 pulses per second, 23.9 °C; **C.** 64 pulses per second, 26.1 °C; **D.** 15 seconds of trilling at 23.9 °C, carrier frequency 4.4 kHz.

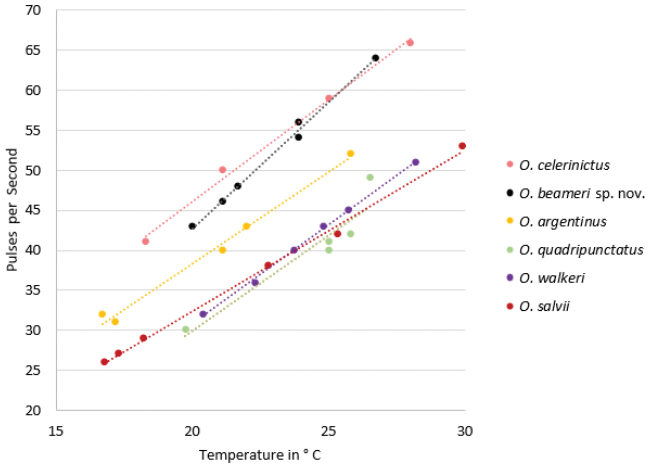

Fig. 9. Song pulses per second by temperature of *Oecanthus beameri* sp. nov., *O. argentinus*, *O. celerinictus*, *O. quadripunctatus*, *O. salvii*, and *O. walkeri*. Data for recordings in Suppl. material 3.

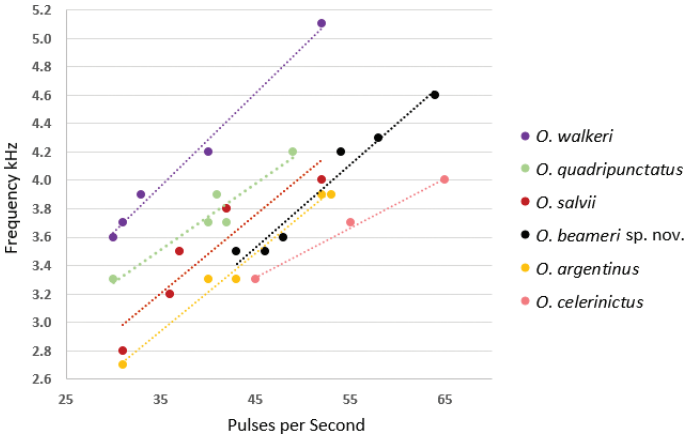

Fig. 10. Change in carrier frequency with pulses per second of *Oecanthus beameri* sp. nov., *O. argentinus*, *O. celerinictus*, *O. quadripunctatus*, *O. salvii*, and *O. walkeri*. Data for recordings in Suppl. material 3.

pedicel of *O. walkeri* touch (Collins and Symes 2012), while those of *O. beameri* sp. nov. do not. A key to species in the *nigricornis* species group is presented below.

Key to the *nigricornis* species group of *Oecanthus*

1 Sternites with dark black, brown, rust, or burgundy 2
– Sternites white/cream/pale green or with very pale reddish brown blocks 5
2 Pronotum mostly brown/rust 3
– Pronotum green, mostly black, or greenish with prominent dark strip/s 4
3 Antennae, head, pronotum, and sternites dark brown color; hosts tamarack and hemlock; length of tegmina < 12 mm ..... *O. laricis*
– Antennae, head, pronotum, and sternites rust color; hosts are most conifers; length of tegmina > 12 mm ..... *O. pini*
4 Song pulse rate > 70 pulses per second at 77 °F/25 °C; frequency > 4.1 kHz at 55 pulses per second; buzzy trilling song; usually with one or two lateral lines on hind tibiae; may be all green, but sternite still black or burgundy; generally in or west of Ohio ..... *O. forbesi*
– Song pulse rate < 65 pulses per second at 77 °F/25 °C; frequency < 4.0 kHz at 55 pulses per second; usually with one or two lateral lines on hind tibiae; may be all green, but sternites still black or burgundy; generally in or east of Ohio ..... *O. nigricornis*
5 Overall light or medium green color, but not pale greenish-white .. 6
– Overall pale greenish-white color 9
6 Lateral mark on scape round or with a slight outward point (may be absent); frequency > 4.2 kHz at 55 pulses per second; male tegminal length > 10 mm; male subgenital plate tapers to a wide point; female subgenital plate with a deep narrow notch; no dark lateral lines on hind tibiae; flute-like trilling song ..... *O. quadripunctatus*
– Lateral mark on scape elongated with outward point 7
7 Black marks on pedicel of equal lengths and widths and touch each other 8
– Black marks on pedicel of different lengths and widths and do not touch each other 9

8 Marks on pedicel touch at bottom to form a V; black rings on antennal segments beyond pedicel; eyes yellow; lateral borders of pronotum always white; prefer narrow-leafed trees and shrubs (e.g., willow, tepejuage)..... *O. walkeri*

– Marks on pedicel touch in center; all four antennal markings thick and dark black; antennal segments beyond pedicel with or without black rings; eye color varies; generally not found in trees..... ..... *O. argentinus*

9 Antennal segments beyond pedicel with black or dark grey rings beyond pedicel; male tegminal length > 10 mm; hind femora with numerous dark black setae .....*O. salvii*

– Antennal segments beyond pedicel without rings or with light brown, pale green or greenish-white rings beyond pedicel; male tegminal length < 10 mm; no dark black setae on hind femora 10

10 Medial mark on scape a solid vertical line; always has lateral antennal markings on both pedicel and scape; one or two lateral lines on tibiae (two hind tibiae most common, but can be four or all six); pale green..... *O. celerinictus*

– Medial mark on scape usually an interrupted vertical line; outer marks on pedicel and scape usually absent or very faint (some individuals match four antennal markings of *O. quadripunctatus)*; lateral tibial lines usually not present or barely visible; pale greenish-white .....*O. beameri* sp. nov.

The known members of the *niveus*, *rileyi*, and *varicornis* species groups can be ruled out with non-matching song types, tegminal widths, antennal markings, or head and antennal coloring. Other western hemisphere species of *Oecanthus* (not found in the United States) can be ruled out for non-matching characters as in Table 1.

Table 1. Non-matching characters of western hemisphere *Oecanthus* species not placed in a group.

Oecanthus species	Characters not matching *O. beameri* sp. nov.	Sources
O. pictipes	L-shaped mark on pedicel	Rehn 1917
O. comma	Comma-shaped mark on pedicel	Walker 1967
O. prolatus	Black teardrop on pedicel	Walker 1967
O. tenuis	Slightly bowed fine line on pedicel	Walker 1967
O. valensis	Thin black line on bright white field	Milach et al. 2016
O. minutus	Dark line on white field	Walker 1967
O. immaculatus	No antennal markings	Walker 1967
O. mhatreae	Long chirps	Collins et al. 2019
O. allardi	Slow chirp rate	Walker and Gurney 1960
O. pallidus	Bursts of trilling	Zefa et al. 2012
O. pictus	Black rings up antennae	Milach et al. 2015
O. jamaicensis	Line behind eye	Walker 1969
O. belti	Red on head	Collins et al. 2014
O. symesi	Yellow color	Collins et al. 2014
O. bakeri	Wide tegmina	Collins et al. 2014
O. nanus	>50 stridulatory teeth	Walker 1967
O. peruvianus	Tegminal length > 10 mm	Walker 1967
O. lineloatus	South of Amazon basin	Walker 1967

Discussion

We describe a new species of *Oecanthus* that belongs to the *nigricornis* species group. This small *Oecanthus* species has a very pale greenish-white color that helps it blend in well with the similar pale whitish-green pastel color of the stem and leaf foliage of hoary rosemary mint, *P. incana*, shrubs growing on the white gypsum dunes. Although morphologically similar to *O. quadripunctatus* in some respects, several characters were distinctly different: the subgenital plates of both males and females, the song pulse rate and frequency, and male tegmen width and length. A potential dwarf species of *O. quadripunctatus*, found in coastal central California on tarweed, was studied by Walker and Rentz (1967) and found to have the same song characters as full-sized *O. quadripunctatus*. Since the only difference found was its size, we ruled it out as being *O. beameri* sp. nov. The lack of dark lateral lines on the tibiae, and the commonly interrupted medial line on the scape rule out *O. celerinictus*.

We were able to separate *O. beameri* sp. nov. from other species in the *nigricornis* group by the following characters: the lack of black setae that are found on *O. salvii*; the antennal markings of *O. argentinus* and *O. walkeri*; and the lack of black, dark brown, rust, or mahogany color on the sternites of *O. forbesi*, *O. laricis*, *O. nigricornis*, *and O. pini*.

O. beameri sp. nov. may be endemic to the gypsum dunes of White Sands, New Mexico (White Sands National Park, and likely also the gypsum dunes of White Sands Missile Range). *O. beameri* sp. nov. also appears to be specialized to live on hoary rosemary mint, based on occurrence and color matching. While *O. beameri* sp. nov. was common at White Sands on hoary rosemary mint, no individuals were heard singing from any of the other plants present. *O. quadripunctatus* is known to occur throughout New Mexico (SCAN 2021; search for *O. quadripunctatus* from the collections of the Museum of Southwestern Biology, University of New Mexico, and from the Insect Collection, New Mexico State University). Additionally, field collecting at White Sands revealed that *O. quadripunctatus* was not found there, and *O. beameri* sp. nov. was not found in locations adjacent to White Sands.

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Supplementary material 1

Author: University of Kansas
Data type: images
Explanation note: Raymond H. Beamer explored the White Sands area in 1932, and collected specimens of Oecanthus. Two specimens were donated to the Academy of Natural Sciences Philadelphia.

Link: https://doi.org/10.3897/jor.31.79036.suppl1

Supplementary material 2

Author: Nancy Collins, David Lightfoot
Data type: Excel spreadsheet
Explanation note: Table showing measurements provided in description of six male paratypes - 3 pinned and 3 from alcohol.

Link: https://doi.org/10.3897/jor.31.79036.suppl2

Supplementary material 3

Author: Nancy Collins
Data type: Video
Explanation note: Captive male *O. beameri* sp. nov. singing.

Link: https://doi.org/10.3897/jor.31.79036.suppl3

Supplementary material 4

Author: Nancy Collins
Data type: Excel workbook
Explanation note: Source recordings data for creation of graphs showing male song rates and frequency.

Link: https://doi.org/10.3897/jor.31.79036.suppl4

Supplementary material 5

Author: Nancy Collins
Data type: Image
Explanation note: Photograph showing an adult male *O. beameri* sp. nov. next to an adult male *O. quadripunctatus*.

Link: https://doi.org/10.3897/jor.31.79036.suppl5

Supplementary material 6

Author: David Lightfoot
Data type: Audio recording
Explanation note: Singing male recorded September 2021 at White Sands National Park - temperature 81-82 F.

Link: https://doi.org/10.3897/jor.31.79036.suppl6

Supplementary material 7

Author: Nancy Collins
Data type: Audio
Explanation note: Captive male *O. beameri* sp. nov. singing - temperature 80 F.

Link: https://doi.org/10.3897/jor.31.79036.suppl7

Supplementary material 8

Author: Nancy Collins
Data type: Audio
Explanation note: Adult males of *O. beameri* sp. nov. and *O. quadripunctatus* are recorded singing to compare the difference in tone.

Link: https://doi.org/10.3897/jor.31.79036.suppl8

Allometric effect of body size and tegmen mirror area on sound generator characters in *Euconocephalus pallidus* (Orthoptera, Tettigoniidae, Copiphorini) from Singapore

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Abstract

Acoustic communication, including allometry of secondary sexual traits and body size, can differ among katydid species from different parts of the world. However, Neotropical species tend to be better studied than their Southeast Asian relatives. This is true for the tribe Copiphorini (Orthoptera, Tettigoniidae). To allow for future comparative studies of Neotropical and Palaeotropical Copiphorini, the allometric relationships between sound generator characters and body size of *Euconocephalus pallidus* from Singapore were examined. Five sound generator characters–tegmen length, stridulatory file length, tooth width, teeth density, and mirror area–were correlated with pronotum length as the proxy for body size. Stridulatory file length, tooth width, and teeth density were also correlated with the mirror area. The relationships were subsequently tested for difference between scaling slope and isometry based on 29 male adults from a single population. All sound generator characters except teeth density exhibited significant positive correlations with pronotum length, whereas teeth density exhibited significant negative correlation with pronotum length. Among them, only tooth width and teeth density scaled hyperallometrically, while the other characters scaled isometrically. As males produce a continuous buzzing call over long durations, larger teeth (i.e., larger tooth width and lower teeth density to accommodate larger teeth) are probably more resistant to age-related abrasion. This may imply that males with larger teeth can produce calls recognized and/or favored by the females over a longer part of the males' adult lifespan. File length and mirror area exhibited isometric scaling. This suggests a stabilizing selection driven by their function in dictating carrier frequency, which females tend to rely on to recognize conspecific males.

Keywords

acoustic communication, cone-headed katydid, mirror, Southeast Asia, stridulatory structure, tegmen morphology

Introduction

Studying the allometric relationships between morphological traits and body size is important to understand the evolutionary patterns of within-species variations in morphology (Shingleton et al. 2007, 2008). Many morphological characters are phenotypically plastic and correlate with body size, often owing to the influence of environmental conditions (Shingleton et al. 2009). Some of the morphological characters under the influence of selection can become disproportionately larger or smaller with increasing body size (i.e., hyperallometry) (Shingleton et al. 2007, 2008, Rodríguez and Eberhard 2019). For example, sexual selection tends to favor the hyperallometry of secondary sexual traits (Bonduriansky and Day 2003; Bonduriansky 2007). Studying the allometric relationships between these traits and body size can offer insights into patterns of sexual selection.

For animals that communicate using sound to find and attract mates, the acoustic signals produced by males can sometimes reveal information about the male condition and/or quality to the female (Bennet-Clark 1998, Bentsen et al. 2006, Brown et al. 2006). The sound generator characters responsible for producing the acoustic signals can thus be subjected to female preference, male–male competition, and sexual selection, and consequently exhibit hyperallometry (Anichini et al. 2017, Rebrina et al. 2020). In some instances, larger sound generator characters are an indication of better body condition, because developing and maintaining these structures can be energetically costly (Del Castillo and Gwynne 2007). Hence, females can exhibit a preference for acoustic signals produced by larger sound generator characters. Furthermore, larger sound generator characters can also be more resistant to wear and tear, conferring males with larger sound generator characters to be more competitive in producing sound to locate and attract mates than males with smaller ones (Ritchie et al. 1995, Anichini et al. 2017).

In many species of katydids (Tettigonioidea Krauss, 1902), males also produce sound to attract females, and the sound generator characters are found on their asymmetrical tegmina (Montealegre-Z 2009, Montealegre-Z et al. 2017). These include the stridulatory file, a specialized serrated vein on the left tegmen that produces sound when the teeth hit against the scraper on the right tegmen, as well as the mirror, a specialized cell membrane on the right tegmen that helps amplify the sound and dictate resonance and frequency (e.g., Morris and Pipher 1967, Bailey 1970, Montealegre-Z and Postles 2010). The biophysical mechanics of sound production, allometry of sound generator characters in katydids, and how they play a role in attracting mates and avoiding predators have been well studied (e.g., Bailey 1967, 1970, Sales and Pye 1974, Heller 1995, Ritchie et al. 1995, Bennet-Clark 1998, Morris

1999). These enabled more recent works that examined allometry of sound generator characters in a broad range of species while accounting for phylogenetic relatedness (e.g., Montealegre-Z 2009) and that focused on targeted species to build on studies of sexual selection in katydids (e.g., Anichini et al. 2017, Rebrina et al. 2020). The comparative study by Montealegre-Z (2009) also demonstrated that many sound generator characters exhibited hyperallometry with body size, but Anichini et al. (2017) and Rebrina et al. (2020) showed that this is not necessarily the case in *Poecilimon* Fischer, 1853 (subfamily Phaneropterinae).

While Anichini et al. (2017) and Rebrina et al. (2020) based their investigation on temperate model species, Montealegre-Z (2009) provided a comparative study of 58 tropical species–most of which are from the Neotropics. Heller (1995) previously demonstrated that the acoustic signaling in Neotropical and Palaeotropical Pseudophyllinae is highly variable owing to different predation pressures in different parts of the world. Likewise, it is also plausible that allometric relationships between sound generator characters and body size can differ among taxonomically related but geographically distant species. Therefore, expanding the investigation of allometry in sound generator characters to lesser-known species may reveal new insights and, consequently, provide a more comprehensive understanding of the evolutionary patterns related to these sound generator characters.

Here, the allometric relationships between sound generator characters and body size of a Palaeotropical katydid species from the tribe Copiphorini Karny, 1912 is examined, specifically from the genus *Euconocephalus* Karny, 1907. Very little is known, apart from a few anecdotal observations, about the katydids from this region (e.g., Tan 2011, 2020, Tiwari and Diwakar 2019). In comparison, Neotropical Copiphorini have been used extensively as study subjects in various studies on acoustic communication (e.g., Montealegre-Z and Mason 2005, Montealegre-Z and Postles 2010, Sarria-S et al. 2016, Celiker et al. 2020). These also include *Neoconocephalus* Karny, 1907, a genus very similar morphologically to *Euconocephalus* (e.g., Counter Jr 1977, Schul and Patterson 2003, Deily and Schul 2004). Building up information about acoustic communication in *Euconocephalus*, including examining their allometry, may eventually allow for comparative inference between species from the Neotropics and Palaeotropics.

For this study, *Euconocephalus pallidus* (Redtenbacher, 1891) was collected, as the species is a relatively large katydid with well-developed sound generator characters suitable for studying allometry with body size. Being the most abundant and widely distributed *Euconocephalus* from Singapore and highly adaptable to both urban and peri-urban habitats (Tan 2011, 2020), *E. pallidus* has the potential to be an important model species to examine acoustic communication of katydids in the context of urbanization. The following questions were investigated: (1) What is the relationship between body size and sound generator characters (both stridulatory structures and mirror)? (2) What is the relationship between the different sound generator characters on different tegmina (e.g., stridulatory file length on the left tegmen *vs.* mirror area on the right tegmen)? And if, as predicted, these relationships are significant, (3) can their isometric or hyperallometric relationships allow for inference about the selection pressures acting on these sound generator organs? By using a similar methodology and addressing similar questions as previous species-targeted studies (see Anichini et al. 2017, Rebrina et al. 2020), the aim was to also examine how generalizable the patterns observed in *Poecilimon* are in the taxonomically more distant *E. pallidus*.

Materials and methods

Study subject.—*Euconocephalus pallidus* inhabits open grassland and is among the largest orthopterans and best fliers from this habitat (Tan 2011, 2020, Tiwari and Diwakar 2019). At night, males produce a distinct loud buzz for a substantially long duration. The dominant frequency of the calls is around 12 kHz (Tan 2020). Multiple males have been observed to call concurrently (Tan 2011).

Sampling.—Between 6 February and 2 April 2019, 29 adult males were collected from an open grassland in Singapore (1.34279N, 103.87751E) known formerly as Bidadari Cemetery. The site has since been cleared for residential development. The katydids were identified using a key in Tan (2011). The katydids were euthanized by freezing, dried and pinned, and subsequently deposited in the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, Singapore. Collections were carried out from this single site within a short period of time, which minimizes potential confounding effects of population, generational, and temporal differences.

Measurement of body size and sound generator characters.—All measurements were done using ImageJ 1.51j8 (Wayne Rasband, Research Services Branch, National Institute of Mental Health, Bethesda, MD, USA) following the approach in Tan et al. (2020).

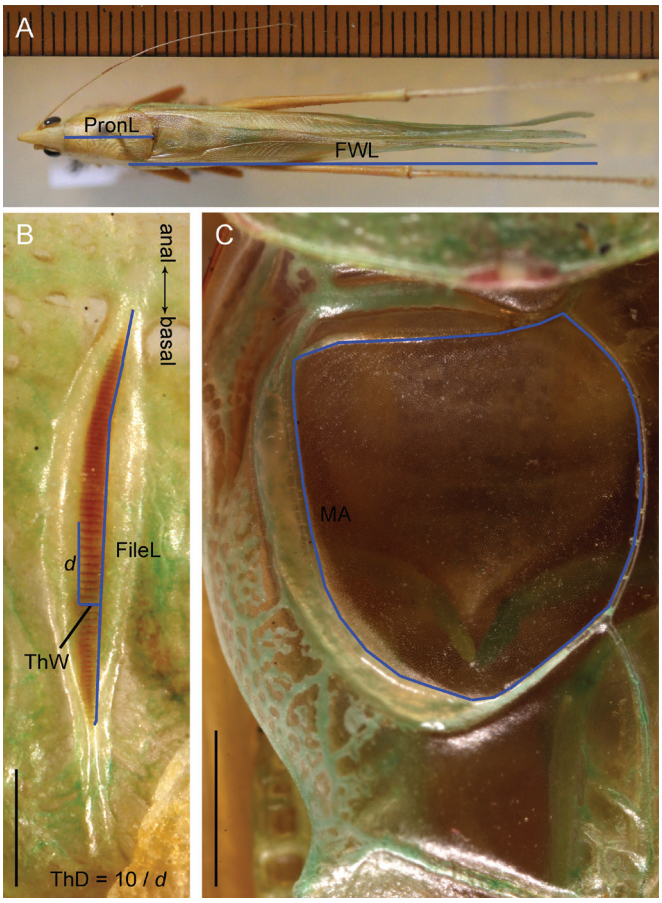

Fig. 1. Measurements of body size and sound generator characters. **A.** Male habitus in dorsal view; **B.** Stridulatory file on the left tegmen in ventral view, scale bar = 0.5 mm; **C.** Mirror area on the right tegmen in dorsal view, scale bar = 1.0 mm. PronL = pronotum length, TL = tegmen length, FileL = file length, ThD = teeth density, ThW = tooth width, *d* = length of 10 teeth in the middle region of the file.

Pronotum length (PronL), measured between the middle of the anterior margin and that of the posterior margin (Fig. 1A), was used as a proxy for body size (Montealegre-Z 2009). To measure the PronL and tegmen length (TL), the dried-pinned specimens were photographed using a Canon EOS 700D digital SLR camera with a Canon EF 100 mm f/2.8 Macro USM lens (Fig. 1A).

Five sound generator characters were examined: TL; stridulatory file length (FileL), tooth width (ThW), and teeth density (ThD) on the left tegmen; and mirror area (MA) on the right tegmen. Measurements of these traits follow those of Rebrina et al. (2020). To measure the sound generator characters, the tegmina were dissected and the stridulatory areas on both left and right tegmen were photographed using the dSLR camera with a Canon MP-E 65 mm f/2.8 USM (1–5×) lens. The FileL was measured as the total length of the stridulatory file on the ventral side of the left tegmen (Fig. 1B). This was done by connecting the posterior ends of the cusp of each tooth of all the visible teeth using the 'segmented line' function in ImageJ. The ThW was determined by obtaining the average tooth width of the teeth in the middle region of the file. The middle region of the file was defined as the central tooth on the file plus five teeth to the basal end and four to the anal end (Fig. 1B). Tooth width was measured between the posterior ends of the cusp of the tooth. The ThD was calculated as the ratio of the 10 teeth previously chosen to the length of the middle region of the file (measured along the edge of the tooth) (Fig. 1B). The MA on the right tegmen was measured using the 'polygon selection' function in ImageJ to connect the inner margin of the vein surrounding the membrane making up the mirror (Fig. 1C).

Analysis

All statistical analyses were done using R software version 4.1.0 (R Core Team 2019). Prior to modeling, all traits were $\log_{10}$-transformed to normalize the distribution and reduce heteroscedasticity (Packard et al. 2011). To examine the allometric scaling of sound generator characters with body size, the approach used by Anichini et al. (2017) and Rebrina et al. (2020) was adopted: a standardized major axis (SMA) regression was fitted for each sound generator character using the 'smatr' R package (Warton et al. 2012), with the PronL as a fixed effect. SMA regression is preferred over ordinary least square (OLS) regressions owing to the lower expected error of the former (Warton et al. 2006, Smith 2009). Moreover, SMA is preferred because both the sound generator characters and body size have similar levels of error as a result of the measurements being collected using the same method and having similar magnitudes (Warton et al. 2006, Smith 009).

The coefficient of determination, R^2, was reported as a measure of the strength of regressions (Kasuya 2019). Effect sizes were interpreted as high ($R^2 > 0.25$), medium ($R^2 > 0.09$), or low ($R^2 > 0.01$) (Cohen 1992). To test for significant difference between the scaling slope and isometry for each sound generator character, the 'slope.test' function of the 'smatr' package was used. 'Slope = 1' was used when a one-dimensional character (e.g., TL, FileL, ThW, and ThD) was scaled with body size (PronL, also one-dimensional). For MA, 'slope = 2' was used since the (two-dimensional) surface area of the mirror increases as a square of body length. This is to account for the assumption that a body grows equally in all three dimensions, i.e., that structure surface area should grow as a square of body length (Hirst et al. 2017, Rebrina et al. 2020).

Results

The average and range (minimum to maximum) of each sound generator character of the 29 males were as follows: PronL = 7.8 mm (7.0–8.7 mm); TL = 40.3 mm (35.4–44.5 mm); FileL = 1.8 mm (1.6–2.0 mm); ThW = 0.12 mm (0.07–0.14 mm); ThD = 39.4 mm^{-1} (29.7–49.0 mm^{-1}); MA = 4.4 mm^2 (3.7–5.0 mm^2).

All sound generator characters exhibited significant correlations with PronL (Fig. 2), with strong effect sizes (i.e., R^2 of the SMA models ranging from 0.3 to 0.5, except for ThD) (Table 1). With the exception of ThD, the remaining sound generator

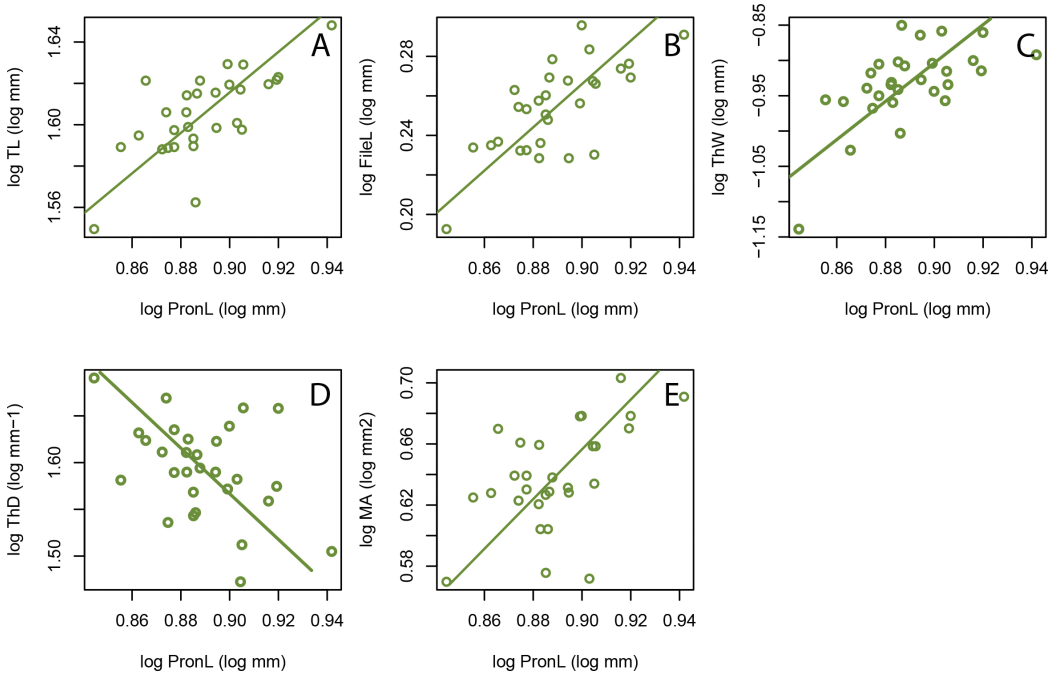

Fig. 2. Relationships between the five sound generator characters with pronotum length (PronL) as body size based on SMA **A.** Tegmen length; **B.** Stridulatory file length; **C.** Tooth width; **D.** Teeth density; **E.** Mirror area. All traits were $\log_{10}$-transformed. The thicker lines indicate hyperallometric relationships, and the thinner lines indicate isometric relationships.

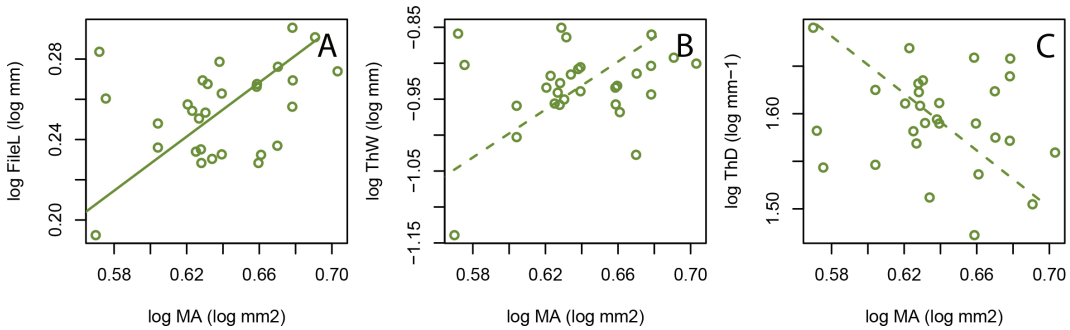

Fig. 3. Relationships between the sound generator characters on the left tegmen with mirror area (MA) on the right tegmen based on SMA **A.** Stridulatory file length; **B.** Tooth width; **C.** Teeth density. All traits were log_{10}-transformed. The dotted lines indicate non-significant relationships, and the thinner lines indicate isometric relationships.

Table 1. Summary of the allometric analysis using SMA of the sound generator characters with pronotum length (PronL) as a proxy for body size and of the sound generator characters on the left tegmen with mirror area (MA). All traits were log_{10}-transformed. Slope $_{SMA}$ refers to the estimate of the SMA model. CI = confidence interval of the slope; R^2 = coefficient of determination of the model. P refers to the p-value of the correlation; P $_{SMA}$ refers to the p-value from the slope test. Asterisks represent significant effects: *P < 0.05; **P < 0.01; ***P < 0.001.

log_{10}-Trait	Slope $_{SMA}$	95% CI	R^2	P	Slope test	P_{SMA}
PronL as a proxy for body size						
TL	0.98	[0.74, 1.29]	0.50	<0.001 ***	1	0.878
FileL	1.10	[0.83, 1.44]	0.50	<0.001 ***	1	0.509
ThW	2.71	[2.00, 3.68]	0.39	<0.001 ***	1	<0.001 ***
ThD	−2.44	[−3.47, −1.72]	0.18	0.022 *	−1	<0.001 ***
MA	1.63	[1.18, 2.26]	0.29	0.002 **	2	0.211
Mirror area (MA)						
FileL	0.67	[0.47, 0.96]	0.15	0.036 *	½	0.101
ThW	1.67	[1.15, 2.42]	0.07	0.17		
ThD	−1.50	[−2.19, −1.03]	0.04	0.31		

characters correlated positively with PronL. Furthermore, there was strong evidence of ThW and ThD scaling hyperallometrically with PronL: ThW increased hyperallometrically about 2.7 times faster than PronL, whereas ThD decreased hyperallometrically about 2.4 times faster than PronL (Table 1). There was very little evidence of TL and FileL scaling more than slope = 1 with PronL, indicating that these characters scale isometrically (Table 1). Likewise, there was also very little evidence of MA scaling more than slope = 2 with PronL, indicating that MA also scales isometrically (Table 1).

FileL exhibited significant correlation with MA (Fig. 3), with moderate effect size (i.e., R^2 of the SMA models = 0.15) (Table 1). However, there was very little evidence of FileL scaling more than slope = ½ with MA. ThW and ThD did not correlate significantly with MA (Fig. 3, Table 1).

Discussion

In the investigated paleotropical katydid, there was significant hyperallometric scaling of tooth width and teeth density with pronotum length. Mainly, larger males of *E. pallidus* bear disproportionately broader teeth and have disproportionately less densely arranged teeth. The rest of the sound-producing characters scaled isometrically with body size. Specifically, larger *E. pallidus* males were found to bear significantly longer tegmina and stridulatory file and larger mirror than smaller males. These results corroborate previous studies showing the influence of male body size on sound generator characters in other katydids, including a comparative study of 38 species by Montealegre-Z (2009) and species-based studies of *Poecilimon* (Anichini et al. 2017, Rebrina et al. 2020).

ThW and ThD exhibited hyperallometric scaling with body size, which has also been reported in *Poecilimon* (Anichini et al. 2017, Rebrina et al. 2020). One possible explanation is that these traits are subjected to positive sexual selection (Bonduriansky 2007) and may be crucial for aggressive male–male competition or as an exhibition of male quality (Eberhard et al. 2018, Rodríguez and Eberhard 2019). The striking of teeth against the scrape can cause wear and tear to the teeth (damage or loss) (Hartley and Stephen 1989). A possible hypothesis is that, since larger teeth are probably more resistant to age-related abrasion, males with larger teeth (i.e., larger ThW and lower ThD to accommodate larger teeth) are more likely to produce calls with signal properties that are recognized and/or preferred by the females over a longer period of their adult life span (Ritchie et al. 1995, Anichini et al. 2017). This could be true for *Euconocephalus* because males produce a continuous buzzing call over long durations. The continuous striking of teeth in such call types can lead to the teeth being more susceptible to wear and tear than katydids that produce shorter echemes.

The sound generator characters FileL and MA exhibited isometric scaling. This is perhaps indicative of stabilizing selection driven by their functions (Bennet-Clark 1998, Anichini et al. 2017). Specifically, FileL and MA are important morphological determinants of the carrier frequency that females tend to rely on for recognizing conspecific males, in which longer FileL and larger MA tend to scale negatively with carrier frequency in katydids (Morris et al. 1994, Montealegre-Z 2009, Montealegre-Z et al. 2017, Rodríguez and Eberhard 2019). This also implies that the variations in FileL and MA within a species should correlate with the normal distribution of wing resonance and carrier frequency to ensure conspecific recognition. Therefore, FileL and MA are probably less likely to be subjected to positive sexual selection.

However, in *Poecilimon*, MA scaled hyperallometrically with body size and was postulated to be under positive sexual selection facilitated by female preference for louder signals (Rebrina et al. 2020), the mirror structure also being important for the amplification of sound (Morris and Pipher 1967, Bailey 1970, Chivers et al. 2017). The same cannot be said for *E. pallidus,* because whether the mirror structure is under sexual selection would be out of the scope of this paper when data on the acoustics and female prefer-

ence of *E. pallidus* were not available. Nonetheless, this illustrates how the scaling of sound generator characters with body size is not always generalizable.

Lastly, TL scaled isometrically with body size in the macropterous *E. pallidus* because the wings of this species are likely to be more important for flight. This species was observed in Singapore to call on tree canopies along streets, suggesting that they can fly and disperse over long distances along green corridors (Tan 2011). A plausible explanation for the positive coupling of TL and body size may be associated with the correlated growth of TL and body size during development, and consequently, the TL becoming fixed in the adult after the final molt (Rebrina et al. 2020). A larger male, therefore, probably has longer wings to facilitate effective flight.

Unfortunately, the examination of the relationships between the sound generator characters, body size, and acoustic signal properties (see Montealegre-Z 2009, Montealegre-Z et al. 2017) was not possible in this study, as acoustic data were unavailable. As a result, inferences about female preference in *E. pallidus* are only speculative and require further testing. Nonetheless, this study provides the basis for further studies into acoustic communication in *E. pallidus* and Southeast Asia Copiphorini. Future studies examining the allometric relationships between sound generator characters and body size among different populations of *E. pallidus*–from urban and peri-urban habitats–can provide insights into the microevolution of these characters. It may also be worth looking into comparative studies by including syntopic congeners [e.g., *E. mucro* (Haan, 1843)] and/or relatives (e.g., *Xestophrys horvathi* Bolívar, 1905) (see Tan 2011).

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First record of *Myrmecophilus* (*Myrmecophilus*) *quadrispinus* for Peru and South America (Orthoptera, Myrmecophilidae)

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Abstract

The first record of the ant cricket *Myrmecophilus* (*Myrmecophilus*) *quadrispinus* Perkins, 1899 for Peru and South America is presented. This species was discovered in the city of Lima in the nests of the ant species *Brachymyrmex cordemoyi* Forel, 1895, and *Pheidole* sp. Westwood, 1939 under a square brick and a stone in two urban gardens.

Keywords

ants, faunistics, first record, myrmecophiles, neotropics, South America

Introduction

Ant crickets of the genus *Myrmecophilus* Berthold, 1827 are small orthopterans known to live as guests in ant nests. Their main distinctive morphological features are their minute size, wingless and ovoid body, slightly long antennae, and oversized hind femora. Their specific body color and the number of spurs on the hind leg are diagnostic characteristics along with the male genitalia and female ovipositor's shape variability (Desutter–Grandcolas 1997, Hebard 1920, Stalling and Birrer 2013, Hsu et al. 2020). Ant crickets are myrmecophiles that live among ants in their nests, probably developing mimicry without inducing aggressive behavior (Hölldobler 1947). *Myrmecophilus* species can be associated with dozens of ant species (Hölldobler 1947, Masloski and Greenwood 2013). Some *Myrmecophilus* species are host-specific, whereas other species are host-generalists and use a wide range of host ant species (Komatsu et al. 2009). Living in the ant nests, they enjoy stable environmental conditions, easy access to food, and a place to hide (Hölldobler and Wilson 1990, Iorgu et al. 2021). Past studies have shown that they primarily feed on the secretions resulting from strigilating their legs with their body and participating in trophallaxis with the ants by imitating their grooming behavior (Wheeler 1900, Wetterer and Hugel 2008).

To date, the genus *Myrmecophilus* includes 63 valid species from three subgenera that have been described worldwide (Hsu et al. 2020, Cigliano et al. 2022). From South America, only *Myrmecophilus* (*Myrmophilina*) *americanus* Saussure, 1877 was reported in Brazil and Colombia (Saussure 1877, Wasmann 1905, Wetterer and Hugel 2008). The genus was also found in Peru by Mónica Narrea Cango (unpublished data), but these findings were never published and the species remained unidentified.

Methods

Ant nests were checked for ant crickets in Lima (Peru) in 2020 and 2021, by the first author. The ant nests were found by turning square bricks and stones from gardens in a 450-m radius around the first author's house. The specimens were caught, frozen, and then preserved in 96% ethanol. Two specimens were preserved in the collection of the first author, which were identified to the family level using the dichotomous keys in Borror and Delong's Introduction to the Study of Insects 7th ed. (Triplehorn and Johnson 2005). *Myrmecophilus* identification was performed using the criteria of Desutter–Grandcolas (1997), Hsu et al. (2020) and by direct comparison with specimens of *Myrmecophilus* (*Myrmecophilus*) *quadrispinus* Perkins, 1899 from France (oversea department Réunion), Japan, and Taiwan and with specimens of *Myrmecophilus* (*Myrmophilina*) *americanus* from Taiwan, Malaysia and Israel, which are deposited in the collection of Thomas Stalling. The ants associated with the *Myrmecophilus* specimens were also collected. The identification was performed following Bolton (1994) and Ortiz (2012) and with the kind support extended by Claudia M. Ortiz Sepúlveda for the identification of *Brachymyrmex cordemoyi* Forel, 1895. The *Pheidole* species has not been further identified. Around one hundred *Pheidole* species are known from Peru, some of which are difficult to identify. The cockroaches associated with the *Brachymyrmex* ant species found were identified following Anisyutkin (2018) and Roth (1998).

Results and discussion

Family Myrmecophilidae Saussure, 1874
Subfamily Myrmecophilinae Saussure, 1874
Tribe Myrmecophilini Saussure, 1874

***Myrmecophilus* (*Myrmecophilus*) *quadrispinus* Perkins, 1899**

Material examined.— PERU • 1 adult ♀; Lima province, Lima; 12°06'19.2"S, 76°58'13.3"W, 170 m a.s.l.; July 2020; in the nest of *Brachymyrmex cordemoyi* Forel, 1895, leg. Nicolás Yuan Naveda • 1 adult ♀; Lima province, Lima; 12°6'25.319"S, 76°58'21.238"W, 169 a.s.l., November 2020; in the nest of *Pheidole* sp., leg. Nicolás Yuan Naveda • 1 adult ♂, Lima province, Lima, 12°6'25.319"S, 76°58'21.238"W, 169 a.s.l., November 2021, leg. Nicolás Yuan Naveda.

A first adult female of *M.* (*M.*) *quadrispinus* was found in July 2020 and a second adult female in November 2020. Both specimens were found and collected from an ant nest under a square brick and a stone, respectively. An adult male specimen was found and collected in November 2021, in an ant nest under a stone. The habitat associated with the gardens was an urban area with several houses, buildings, tracks, sidewalks, and parks (Fig. 1).

The three adult specimens were identified as *M.* (*M.*) *quadrispinus* on the basis of their unique combination of characters: uniform dark brown coloration of the head and body, yellowish cerci (Fig. 2), three dorsal spines positioned in the proximal, medial and distal portions of the metatarsus and outer ovipositor valvae of female (viewed laterally) double pointed (Fig. 3). All other *Myrmecophilus* species show either a different coloration of the body or cerci, a different shape of the ovipositor, or a different number or position of the spines on the tarsus. The *Myrmecophilus* species of North America are distinguished by body color (pale ochreous in *M.* (*Myrmecophilus*) *manni* Schimmer, 1911 and *M.* (*Myrmecophilus*) *nebrascensis* Lugger, 1898) and by the color of the cerci (dark brown in *M.* (*Myrmecophilus*) *pergandei* Bruner, 1884 and *M.* (*Myrmecophilus*) *oregonensis* Bruner, 1884), among other characteristics.

Additionally, the ants found associated with the female specimens were identified as *Brachymyrmex cordemoyi* Forel, 1895, and *Pheidole* sp. Westwood, 1939. The first species coexisted with the cockroach *Pycnoscelus surinamensis* (Linnaeus, 1758). This finding agrees with those of Moretti et al. (2011) indicating that *B. cordemoyi* may be associated with *P. surinamensis* and hence exhibiting domiciliation trend. No ants were detected associated with the male specimen, but the site was only three meters from where the second female was found.

Ant cricket nymphs were also found, but they fled away. Both nymphs and adults were mixed in ant colonies. *B. cordemoyi* and *Pheidole* sp. host ants are smaller than *M.* (*M.*) *quadrispinus* adults.

The finding of *M.* (*M.*) *quadrispinus* represents the first record for Peru and all South America. *M.* (*M.*) *quadrispinus* was previously known from the tropics and subtropics of southeast Asia and the Indian Ocean (Hsu et al. 2020). The ant crickets are difficult to find because of their cryptic mode of living in the ant nests. Therefore, we can assume that *M.* (*M.*) *quadrispinus* or other *Myrmecophilus* species can be found in other regions of Peru and South America in the future.

Fig. 1. Habitat of *Myrmecophilus* (*Myrmecophilus*) *quadrispinus*; Peru, Lima, November 2020. Photo: NYN.

Fig. 2. *Myrmecophilus* (*Myrmecophilus*) *quadrispinus*, female; Peru, Lima, July 2020. Habitus, showing the typical shape and uniform brown body color of the species. Photo: NYN.

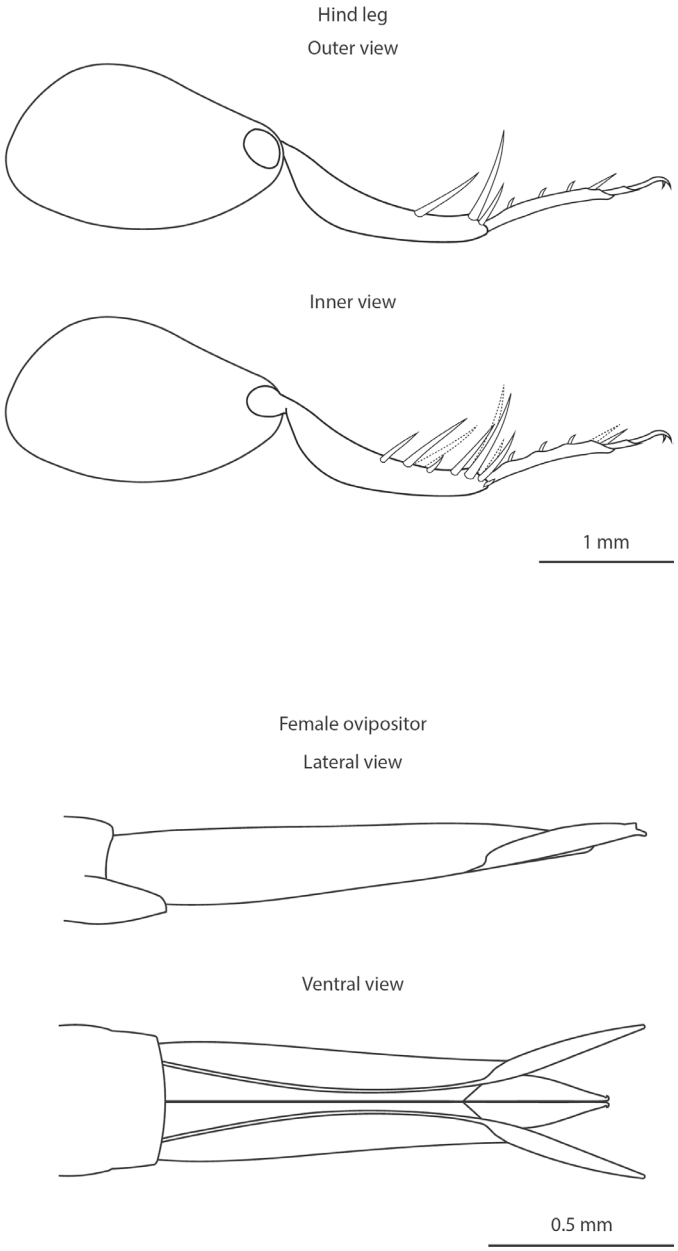

Fig. 3. *Myrmecophilus* (*Myrmecophilus*) *quadrispinus*, female; Peru, Lima, July 2020. Details of the hind leg and the ovipositor of a female. Illustration: NYN.

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