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Review of the genus *Pteranabropsis* (Anostostomatidae: Anabropsinae) with description of six new species

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Abstract

The genus *Pteranabropsis* is reviewed. Diagnostic characters for the superficially similar species of the genus are discussed. An extended key to the species is provided. Six new species are described: *P. angusta* **sp. nov.**, *P. cuspis* **sp. nov.**, *P. bavi* **sp. nov.**, *P. copia* **sp. nov.**, and *P. pusilla* **sp. nov.** from northern Vietnam, and *P. guadun* **sp. nov.** from the Wuyishan Mountains in China. Types and all other specimens from Vietnam are stored in ISNB Brussels; those from Wuyishan in ZFMK Bonn.

Keywords

China, diagnostic characters, dichotomous key, distribution, Orthoptera, Vietnam

Introduction

The genus *Pteranabropsis* was established by Gorochov (1988) for *Anabropsis carli* Griffini, 1911 from Vietnam. For eighty years, *Anabropsis carli* was the only named full-winged Anabropsinae from Asia. A more detailed treatment of the genus was given by Gorochov (1998) including a redescription of *P. carli*, description of a new species, *P. carnarius* Gorochov, 1998, and a differential diagnosis between adults and nymphs of both species and tools to differentiate between their juvenile stages and adults of the apterous genus *Apteranabropsis* Gorochov, 1988. Subsequently, Wang et al. (2015) described five new species from China, and Song et al. (2016) described two new species, also from China. Another similar, but micropterous, new species was described by Shi and Bian (2016) in a new but closely related genus *Brevipenna* Shi & Bian, 2016, which is intermediate between *Pteranabropsis* and *Apteranabropsis*.

A collection of Orthoptera obtained from studies of the entomological diversity of Vietnam (Constant and Grootaert 2018) contained a rich number of *Pteranabropsis* specimens from various localities in the northern area of Vietnam, including *P. carli* and *P. carnarius* from the type locality of the latter species (Tam Dao). Several other individuals of the genus collected in the course of that project differed significantly from both species and also from the species of the genus described from China. They are described here as new species. As the species of the genus show a great overall similarity, the differential characters had to be re-evaluated, resulting in an extended key to the species.

Additionally, historical specimens from Guadun (China), formerly identified as *P. carli* and found in the collection of ZFMK, are included in this study and it is proved to be a new species.

Materials and methods

The current study is based on specimens from the research project of "A step further in the Entomodiversity of Vietnam" managed by J. Constant (Constant and Grootaert 2018), housed in the Institut royal des Sciences naturelles de Belgique in Bruxelles.

During the study, I also re-examined two specimens of the genus from the old Klapperich collection held in ZFMK that were collected near Kuatun [current spelling Guadun] in the Wuyishan Mountains, China, in 1938.

A select number of the museum specimens were re-set to allow the studying of wing shapes and venation. Naming of tegminal veins follows Ingrisch (2018). That paper also contains a comparison with former schemes.

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

Abbreviations for depositories.—**MHNG** – Muséum d'histoire naturelle Genève, Switzerland; **ISNB** – Institut royal des Sciences naturelles de Belgique in Bruxelles, Belgium; **ZFMK** – Zoological Research Museum Alexander Koenig Bonn, Germany.

Results

Characters.—Body size, wing length, and wing surface or length to width ratio varies among species, although there is also variation among individuals, especially in the more widespread species. When the wings are spread, they are of some use for identification, especially in brachypterous species, since the wings were reduced to a varying degree, resulting in differences in length to width ratio. Coloration or intensity of coloration of hind wings are occasionally helpful, too. Venation of tegmen follows a common pattern in all species, but in species with shortened wings, especially when the tegmen width becomes narrow due to reduction, the number of media or cubitus branches is reduced.

All three thoracic sternites possess a pair of elongate ventral projections. The metasternal projections differ rather strikingly among groups of species. They provide a useful character for identification and have been used in previous keys.

The male subgenital plate is basically similar in shape, but differs in details among species. Previous authors have used the presence or absence of an incision of the apical margin and the way it is incised as a key character.

The male phallus is fully membranous and lacks sclerites. Although it is structured and the structure is probably species specific, its shape is of restricted use for identification since in many museum specimens it is not preserved in a good enough condition for certain identification. Currently, only Gorochov (1998) has used it to differentiate between *P. carli* and *P. carnarius*. In the present paper it is illustrated for all species studied but not included in the key.

The most significant character for separating the species proved to be the apical area of the long paraproctal outgrowths in males when studied at sufficient magnification. One might speculate that these tools might be used to open the female subgenital plate during pairing, although that has not been observed so far.

The female subgenital plate has as its basic shape a triangular, somewhat vaulted basal area and a narrow prolonged apical area with acute tip. It differs between species by the relation of the length of the anterior to that of the posterior area and by presence or absence of minute modifications at the transient zone.

The presence or absence of spines on the ventral margins of the mid femur has been used in the keys of Wang et al. (2015) and Song et al. (2016). I avoided that character because of individual variation within species.

The tibial tympana are rather large and open on both sides in the basal area of the fore tibia. There is little variation among species. In *P. carnarius*, the open tympana are slightly but markedly smaller than in the equally large *P. carli*. The individuals of the genus are obviously able to hear although the prothoracic spiracle is not open and wide as in Tettigoniidae but covered by three valves and a little larger than the meso- and metathoracic spiracles that are covered by only two valves (Fig. 6C–D, M, R, V). Whether species in the genus can produce sound is unknown. No morphological modifications that could be interpreted as tools for sound production were found, but tremulation and drumming are known in US and New Zealand Anostostomatidae (Vandergast et al. 2017) and might also occur in *Pteranabropsis*. An interesting modification, as compared to the situation in Tettigoniidae, was found in the second plate of the mesopleuron, which is obtuse-angularly prolonged over its whole width, covers the intersegmental membrane, and overlaps at the tip with the metapleuron (Fig. 6C). A similar modification also exists in Gryllacrididae, but is shaped differently. The surface of the metapleuron is covered by transverse parallel riblets; also the anterior surface of the metapleuron and the surface of the mesopleuron are covered by fine and, on the mesopleuron, very weak transverse riblets.

Distribution of the genus in Vietnam.—An examination of all Orthoptera specimens collected at 21 localities during the project "A step further in the Entomodiversity of Vietnam" showed that *Pteranabropsis* specimens had been collected in seven localities, all of them in the northern area of Vietnam (Fig. 8). The collections from central and southern areas of Vietnam investigated during that project did not contain any proof of the occurrence of the genus in those areas. The northern area is, however, somewhat better researched than the remainder of the country: there were twelve localities in northern, five in central, and four in southern Vietnam.

The number of voucher specimens of *Pteranabropsis* per locality varied between one and 14 specimens. The northern area of Vietnam appears to be a center of diversity for this Asian genus, as two additional species described from China, *P. karnyi* Wang et al. 2015 and *P. crenatis* Song et al. 2016, were found close to the border with Vietnam.

Four of the seven localities in which *Pteranabropsis* was found hosted two species of the genus, two localities had only one species, and one locality had three species.

Four of the seven species from Vietnam reported in this paper were found at a single locality, two species in two localities, and only one species, *P. carli*, in five localities. The latter species was also reported from nearby localities in southern China (Song et al. 2016).

Gorochov (1998) reported that at Tam Dao, *P. carli* and *P. carnarius* were found in the same vegetation on leaves and twigs in the undergrowth of forests. He assumed that they live a similar mode of life as "waiting predators". On the other hand, one might assume that species with a similar way of life living together in the same habitat have at least some degree of specialization for using their environment. From the striking difference in the length of the tibial spines between these two species (compare Fig. 6A–B vs. J–K), one might assume that they could be adapted to prey of different size.

Taxonomy

Key to species of *Pteranabropsis* Gorochov, 1988

Remark: The Chinese species are included according to the descriptions and images in Wang et al. (2015) and Song et al. (2016).

1 Third thoracic sternite (metasternum) consisting of a pair of triangular plates with pointed apex. Hind margin of male subgenital plate truncate. Paraproctal outgrowths tapering apically, slightly exceeding hind margin of subgenital plate, with apex acute and strongly diverging. Tibet .... *P. tibetensis* Wang, Liu & Li, 2015

– Either third thoracic sternite terminating into a pair of long cones (Fig. 2H–M) or, if consisting of a pair of triangular plates (Fig. 2N–P), then male subgenital plate with incision from apical margin (Fig. 2E–G).. 2

2 Third thoracic sternite terminating in a pair of roughly triangular plates without or with only short apical cones (Fig. 2N–P). Male subgenital plate with incision from apical margin (Fig. 2E–G). Paraproctal outgrowths in subapical area not or only moderately widened or more strongly swollen and then gradually narrowing into tip; tip pointing slightly dorso-apicad (not strongly upcurved) with a minute sclerotised peg, pad, or rim at tip (Fig. 4E–K) 3

– Third thoracic sternite terminating in a pair of widened elongate plates with long roughly cylindrical apical area or more strongly widened at base and step-like narrowed into narrow apical area (Fig. 2H–M). Male subgenital plate with apical margin truncate or slightly concave, without incision (Fig. 2A–D). Paraproctal outgrowths at end strongly upcurved forming a projection narrowing toward tip, terminating into a minute stiffened tooth, pad or rim at tip (Figs 3A–N, 4A–D).......... 11

3 Hind wings for the most part dark brown (Fig. 1J). Paraproctal outgrowths in subapical area with a distinct subapical ventral widening that acute-angularly narrows towards tip; at tip with a minute, compressed, sclerotised pad (Fig. 4E–G). Ventral spines of fore tibia very long, distinctly longer than in most other species of the genus; longest spines 3.1–3.3 × longer than the width of the tibia (Fig. 6J–K)..*P. carnarius* Gorochov, 1998

– Ventral spines of fore tibia less prolonged, less than three times the width of the tibia; longest spines 2.2–2.8 × longer than the width of the tibia in Vietnamese species. Hind wings often greyish or brownish, subtransparent (Fig. 1H–I). Paraproctal outgrowths of different shape, in subapical area only slightly or not at all widening............ 4

4 Male subgenital plate with apical incision U-shaped (Fig. 2E–F) or rimiform.. 5

– Male subgenital plate with apical incision V-shaped (Fig. 2G) 7

5 Paraproctal outgrowths in middle narrowed, in subapical area faintly widened and lateral surface slightly swollen, narrowing as an elongate oval object towards rounded tip that carries a minute sclerotised pad (Fig. 4H–I). Posterior area of subgenital plate faintly widening apically, with U-shaped incision from apical margin (Fig. 2F). Female subgenital plate with narrow apical area very short, less than half the length of the triangular anterior area (Fig. 5H). Medium sized species (body male 25 mm, tegmen male 40 mm, tegmen female 34 mm). North Vietnam................................ *P. pusilla* **sp. nov.**

– Paraproctal outgrowths without subapical widening, only faintly curved dorsad. Chinese species.. 6

6 Tip of metasternal lobes with a very short cone. Posterior margin of male subgenital plate with a very narrow incision (rimiform). Paraproctal outgrowths in apical area faintly sinuate but of sub-equal width as preceding area; tip membranous, triangular with a stiffened apical rim (after fig. 2E in Song et al. 2016). Female subgenital plate with narrow apical area shorter than triangular anterior area (about half as long). Large species (body male 33–35 mm, tegmen male 44–47 mm, tegmen female 49 mm after Song et al. 2016). China (Hubei, Guangxi, Chongqing, Guizhou)........................*P. crenatis* Song, Bian & Shi, 2016

– Posterior margin of male subgenital plate with a U-shaped incision. Posterior area of subgenital plate rather strongly widening apically. Paraproctal outgrowths largely surpassing tip of subgenital plate, from ventral side with obtuse tips (after drawing 9 in Wang et al. 2015, the exact shape was not described). Large species (body male 33 mm, tegmen 41 mm after Wang et al. 2015). China, Yunnan...*P. tenchongensis* Wang, Liu & Li, 2015

7 Male subgenital plate with apical margin oblique but straight on both sides, in middle with a V-shaped incision with convex margins and obtuse bottom (Fig. 2G). Paraproctal outgrowths in subapical area not widened, only slightly curved dorsad; tip rounded, has a minute sclerotised lamella (Fig. 4J–K). Narrow apical process of female subgenital plate slightly shorter than triangular basal area and with subparallel margins; only in apical third narrowed to acute tip .. *P. guadun* **sp. nov.**

– Different combination of characters 8

8 Metasternal lobes acute triangular. Posterior margin of subgenital plate with V-shaped incision (after fig. 11 in Wang et al. 2015; in text described as "U-shaped"). Posterior area of subgenital plate not or at most faintly widening apically. Paraproctal outgrowths in subapical area straight with acute out-curved tips (after fig. 11 in Wang et al. 2015) ....*P. karnyi* Wang, Liu & Li, 2015

– Different combination of characters 9

9 Lateral margins of male subgenital plate not parallel in apical half. Paraproctal outgrowths in subapical area slightly sinuate but only faintly widened, at tip with a minute thorn or lamella (after fig. 6D in Song et al. 2016)..........................*P. infuscata* Wang, Liu & Li, 2015

– Lateral margins of subgenital plate parallel in apical half 10

10 Incision of posterior margin of subgenital plate shallow, only reaching one sixth of subgenital plate length; occiput with three longitudinal brown stripes (after figs 1D, 7C, F in Song et al. 2016). Paraproctal outgrowths in subapical area straight with obtuse tip (after fig. 17 in Wang et al. 2015) or faintly upcurved but not widened with acute tip pointing dorso-posteriorly (after fig. 7E–F in Song et al. 2016) ....*P. parallela* Wang, Liu & Li, 2015

– Incision of posterior margin of subgenital plate deep, about a quarter of subgenital plate length; occiput with five irregular longitudinal brown stripes (after figs 1B, 3D, F in Song et al. 2016). Paraproctal outgrowths in subapical area rather strongly upcurved but not widened, terminating in a conical tip (after fig. 3E, G in Song et al. 2016) ....*P. incisa* Song, Bian & Shi, 2016

11 Long-winged species; wings distinctly surpassing hind knees of stretched hind legs; tegmen wide (Fig. 1A). Hind wings when spread about 1.8 × wider than long. Male paraproctal outgrowths with dorsally expanded apical area oblique triangular with curved margins and with blunt tip that carries a narrow stiffened lamella at dorso-apical margin (Fig. 3A–D). Female subgenital plate with triangular basal area (1.25–1.45 × longer than wide at base) rather gradually changing into the narrow apical area (Fig. 5A–C) ....*P. carli* (Griffini, 1911)

– Brachypterous; wings reaching or only slightly surpassing hind knees of stretched hind legs; often not reaching tip of ovipositor (Fig. 1B–G). Male paraproctal outgrowths of different shape 12

12 Metasternal lobes with wide basal area more distinctly separated from cylindrical apical area (Fig. 2H, M). Tegmen wider, about 2.2–2.4 × longer than wide (Fig. 1C–E). When spread, hind wings appear semi-circular with straight fore margin (about 1.4 × wider than long). Dorsally expanded apical area of male paraproctal outgrowths elongate with proximal and distal margins less strongly converging, at tip truncate and provided with a narrow sclerotised lamella; distal margin substraight to faintly concave (Fig. 4A–D). Female subgenital plate moderately wide at base, the elongate-triangular basal area longer than the narrow apical area; at the transition zone between both areas with a pair of narrow, elongate lateral depressions separated by a narrow ridge in between (Fig. 5D–F) .... *P. copia* **sp. nov.**

– Metasternal lobes gradually narrowing from the wide basal to the cylindrical apical area (Fig. 2I–L). Tegmen narrower, 2.6–2.9 × longer than wide. The spread hind wings appear semi-oval with straight fore margin (about 1.7–1.8 × wider than long).................................... 13

13 Metasternal lobes with the cylindrical apical area very stout, not distinctly separated from wider basal area, external margin convex or straight (Fig. 2L). Male paraproctal outgrowths in apical area only slightly widening dorsad and at dorsal angle provided with a small, dorso-ventrally compressed projection pointing apicad and carrying at tip a stiffened pad; ventral margin of outgrowth with apical angle widely rounded in lateral view; hind margin of outgrowth in apical view truncate and somewhat widened (Fig. 3J–N) *P. angusta* **sp. nov.**

– Metasternal lobes with the cylindrical apical area less stout, external margin in the transient zone between wide basal and narrow apical area concave (Fig. 2I, K) 14

14 Rather robust species with narrow fore wings (2.9 × longer than wide), hind wings more strongly reduced (Fig. 1B). Male paraproctal outgrowths in apical area with a large, acute-triangular dorsal projection that terminates into a minute stiffened pad; hind margin of outgrowth in lateral view slightly concave, at ventral angle narrowly rounded (Fig. 3E–I) .... *P. cuspis* **sp. nov.**

– Fore wings wider (2.6–2.7 × longer than wide), hind wings less reduced, when spread more cycloid (Fig. 1G). Female subgenital plate moderately wide at base, the elongate-triangular basal area longer than the narrow apical area; at the transition zone between both areas the lateral margins are suddenly constricted such that the narrow apical area has nearly subparallel margins and only at end narrows to acute tip (Fig. 5G) .... *P. bavi* **sp. nov.**

Description of taxa

Pteranabropsis Gorochov, 1988

Type species.—Type species: *Anabropsis carli* Griffini, 1911.

Description.—Large to medium sized species (Fig. 1). General color dark brown to black with irregular light pattern. Head large, ovoid; forehead subsmooth with very fine transverse striation. Fastigium verticis swollen and elevated, surface smooth, with faint depression along midline; lateral ocelli on lateral surfaces of elevation. Face with fastigium frontis separated by a transverse furrow from fastigium verticis. Pronotum with well-defined rim; without lateral angles separating disc from paranota; with indication of a transverse furrow separating a slightly swollen, dorsally flattened, posterior area from funnel-shaped anterior area; anterior and posterior margins substraight in middle, ventral margins convex; hind margin of paranota with humeral angle simply rounded. Prosternal lobes near base compressed triangular, afterwards long spiniform, thin; mesosternal lobes in basal area wide, afterwards elongate, conical to nearly cylindrical with obtuse tip; metasternal lobes varying between species, forming either a simple, roughly triangular plate or with a long sub-cylindrical apical extension (Fig. 2H). Abdomen without stridulatory teeth. Wing length varying among species from slightly longer than covering abdomen to largely surpassing knees of stretched hind legs. Venation of tegmen in fully winged species with two radius and two media branches, cubitus anterior with three branches, cubitus posterior undivided, with 5–6 anal veins. In species with shortened wings the number of media and cubitus branches can be reduced. Fore coxa with a strong spine at swollen anterior surface; also mid-coxa with a smaller spine at anterior surface. Fore tibiae with large uncovered tympana on both sides (Fig. 6). Prothoracic spiracle with three covering valves (Fig. 6D, M, R, V), slightly larger than meso- and metathoracic spiracles that have only two covering valves (Fig. 6C). Number of spines on ventral margins of femora and hind tibiae somewhat variable between species. Fore and middle tibiae with 4 pairs of long spines and one pair of apical spurs on ventral margins (Fig. 6); anterior tibia with one long spine on dorsal inner and an apical spur on both margins, the inner (anterior) distinctly longer than the outer spine; mid tibia with two spines and one spur on dorsal outer and 2–3 spines and one spur on dorsal inner margins.

Male. Ninth abdominal tergite very short; with two short obtuse expansions on hind margin widely separated from each other. Tenth abdominal tergite also very short, with a pair of upcurved hooks inserted just laterally of the expansions of ninth tergite. Paraprocts with a long roughly cylindrical process, its shape, especially the apical area, varies between species (paraproctal outgrowth, Fig. 3–4). Epiproct triangular with shallowly grooved or furrowed surface; tip subobtuse. Subgenital plate in widened basal area with upcurved lateral margins; central disc projecting with parallel or slightly diverging and straight or concave lateral margins; styli present (Fig. 2A–G). Phallus membranous (Fig. 7).

Female. Seventh abdominal sternite unmodified, longer than sixth sternite. Subgenital plate triangular with extended apical projection; shape somewhat variable between species (Fig. 5). Ovipositor elongate, moderately curved throughout; ventral valves shorter than dorsal valves; tip of dorsal valves obtuse, tip of ventral valves acute but hidden under dorsal valves; medial valves narrow, slightly shorter than ventral valves (Fig. 4L–O).

Etymology.—The genus name *Pteranabropsis* Gorochov, 1988 is derived from the name *Anabropsis* Rehn, 1901. The gender of *Anabropsis* is feminine, this should also apply to *Pteranabropsis*. However there are three species names with the masculine ending *-us*: *P. carnarius*, *P. parallelus*, and *P. infuscatus*. The Latin word *carnarius* means "meat eater" and can thus be regarded as noun in apposition. In contrast, the Latin word *parallelus* is an adjective and *infuscatus* a participle. Both names should be emended to the feminine forms *P. parallela* Wang, Liu & Li, 2015 and *P. infuscata* Wang, Liu & Li, 2015 (ICZN 1999, Agreement in gender, Art. 31.2 and 34.2).

Pteranabropsis carli (Griffini, 1911)

Figs 1A, 2A, 2J, 3A–D, 5A–C, 6A–E, 7A–F;
photos of holotype in OSF (Cigliano et al. 2018)
urn:lsid:Orthoptera.speciesfile.org:TaxonName:20152

Holotype (male, not seen).—Vietnam: "Tonkin" (northern area of Vietnam) (Genève, MHNG).

Material examined.—Vietnam: Hoang Lien NP, 22°21'N, 103°46'20"E, 1–5.vii.2013, leg. J. Constant & J. Bresseel (I.G. 32.454), 2 females (Brussels, ISNB); Hoa Binh Prov., Cuc Phuong National Park, 20°19'N, 105°36'30"E, 11–18.viii.2010, leg. J. Constant & P. Limbourg (I.G. 31.668), 1 male (Brussels, ISNB); Ngo Luong Nat. Res., 20°26'16"N, 105°20'15"E, 25–30.vii.2016, leg. J. Constant & J. Bresseel (I.G.: 33.282 GTI project), 1 male (Brussels, ISNB); Nguyen Binh, Cao Bang, Phia Den (Phia Đén), 22°34'N, 105°53'0"E, 8.viii.2010, leg. J. Constant & P. Limbourg (I.G. 31.668), 1 female (Brussels, ISNB); Prov. Vinhfu, Tam Dao N.P., 21°31'N, 105°33'E, 25–28.viii.2010, leg. J. Constant & P. Limbourg (I.G. 31.668), 2 females (Brussels, ISNB); same locality, 25–30.vii.2011, leg. J. Constant & J. Bresseel (I.G. 31.933), 4 females, 2 males (Brussels, ISNB). Identification based on the description in Gorochov (1998).

Diagnosis.—*P. carli* is characterized by the long and moderately wide fore wings; the longest ventral spines of the fore tibia are more than twice as long as the diameter of the tibia. The genicular area of all legs is usually whitish, rarely slightly infumate. The paraproctal outgrowths have the apical area suddenly upcurved, are roughly triangular with the obtuse tip faintly curved posteriorly, and carrying along dorsal margin a fine, compressed, stiffened lamella. The female subgenital plate has the elongate triangular basal area with substraight to slightly concave lateral margins.

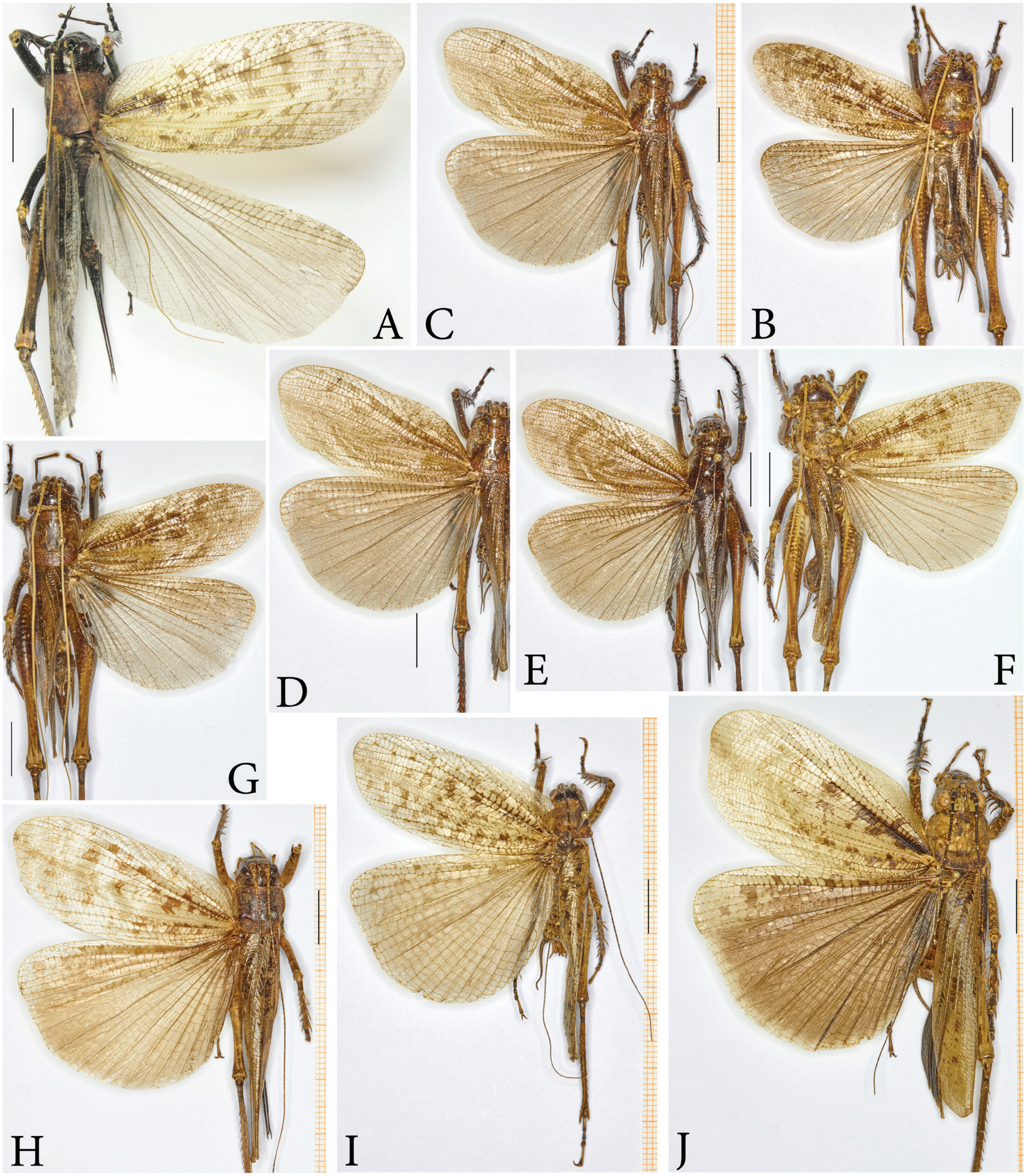

Fig. 1. Habitus dorsal view of *Pteranabropsis* species. **A.** *P. carli* (Griffini, 1911) female; **B.** *P. cuspis* **sp. nov.** male; **C–E.** *P. copia* **sp. nov.** male (**C**), female from Copia (**D**), and female from Hoang Lien (**E**); **F.** *P. angusta* **sp. nov.** male; **G.** *P. bavi* **sp. nov.** female; **H.** *P. guadun* **sp. nov.** female; **I.** *P. pusilla* **sp. nov.** male; **J.** *P. carnarius* Gorochov, 1998 male. Scales 10 mm.

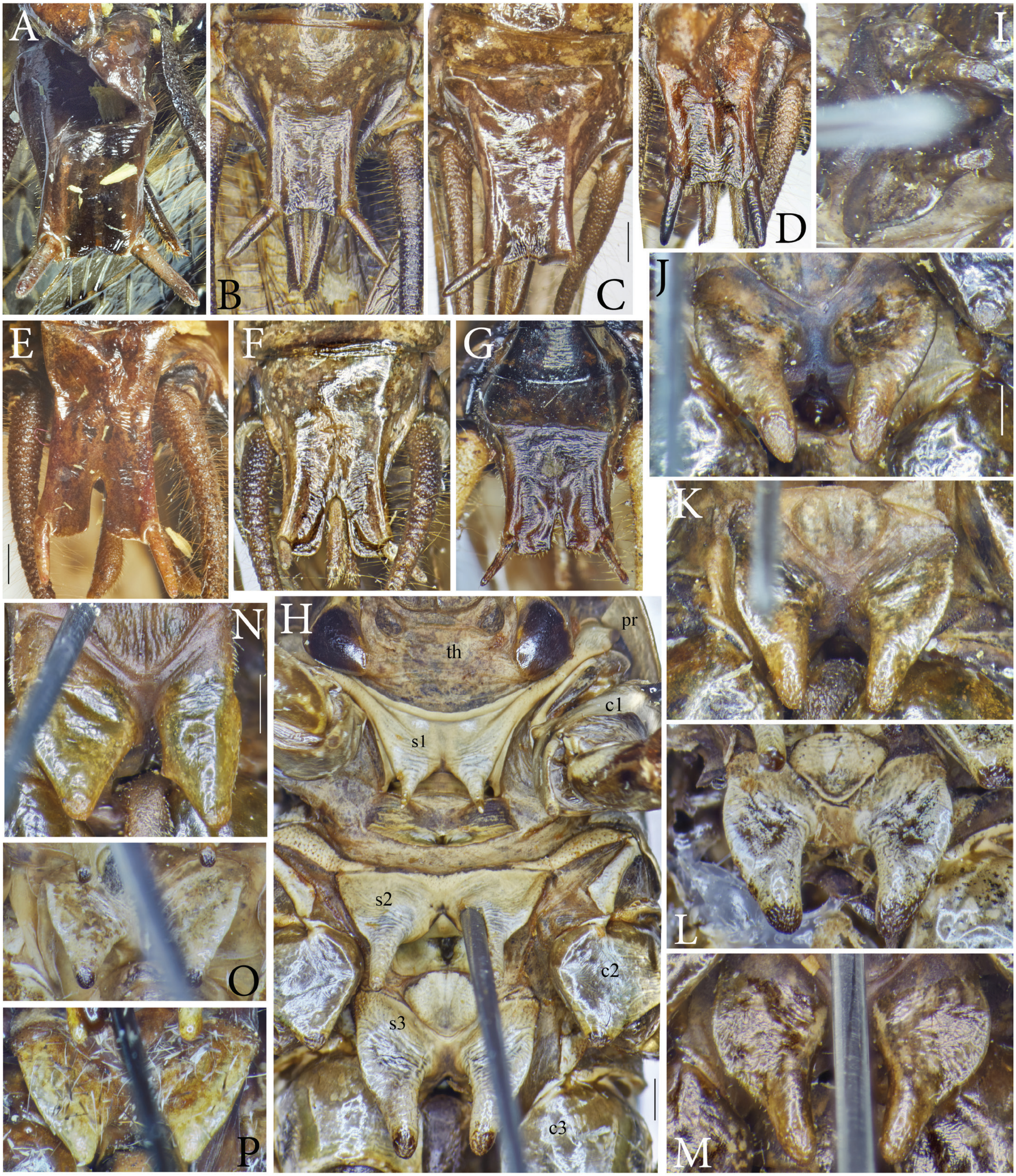

Fig. 2. A–G. Male subgenital plate; **H.** Thoracic sternites; **I–P.** Metasternum of *Pteranabropsis* species: *P. carli* (Griffini, 1911) (**A, J**); *P. cuspis* **sp. nov.** (**B, H**); *P. copia* from type locality (**C, M**); *P. angusta* **sp. nov.** (**D, L**); *P. carnarius* Gorochov, 1998 (**E, N**); *P. pusilla* **sp. nov.** (**F, O**); *P. guadun* **sp. nov.** (**G, P**); *P. copia* from Hoang Lien (**I**); *P. bavi* **sp. nov.** (**K**). Abbreviations: c1 – fore coxa, c2 – mid coxa, c3 – hind coxa, s1 – prosternum, s2 – mesosternum, s3 – metasternum, th – throat with lateral hemispherical sclerites and pair of papillae, pr – underside of pronotum. Scales 1 mm.

The narrow apical area is only slightly shorter than the basal area, about three quarters of the basal area.

Description.—Large species; habitus as genus. Prosternal lobes compressed triangular, at beginning of narrow conical apical area slightly constricted, tip subacute to subobtuse; mesosternal lobes in basal area wide, afterwards elongate conical to nearly cylindrical with subtruncate tip; metasternal lobes compressed, with concave internal and strongly convex external margins; gradually passing over into conical (nearly sub-cylindrical) apical area with obtuse tip (Fig. 2J).

Wings distinctly surpassing hind knees (Fig. 1A). Fore wings 2.3–2.8 × longer than wide. Venation: radius with radius sector arising in about mid-length of tegmen; media free, two-branched, branching behind basal third; cubitus anterior three-branched (CuA + CuPaα + CuPaβ after Béthoux 2012), branching in basal third and before mid-length; cubitus posterior (CuPb) undivided; with five anal veins, the last one incomplete. Hind wings cycloid, about 1.8–2.2 × wider than long.

Legs. Fore coxa with a strong spine at swollen anterior surface; and mid-coxa with a smaller spine at external (= anterior) margin. Fore femur with 3–5 small spines at anterior-ventral margin; mid femur with 3–5 spines at anterior-ventral and 6 smaller spines at posterior-ventral margin. Hind femora with 5–7 external and 4–5 internal small spines on ventral margins; hind tibiae with dorsal spines on inner margin larger than on outer margin, ventral margins with few minute spinules; on both sides with 4 apical spurs, the dorsal two pairs very large, the following pair medium, the ventral-most pair small; internal spurs larger than external counterparts; ventral margin with 2–4 external and 0–1 internal spinules.

Male. Paraproctal outgrowths long, roughly cylindrical with rugose and setose surface, apex obtuse with beaked extension with subobtuse tip that carries a fine, stiff lamella on top (Fig. 3A–D). Subgenital plate with lateral margins upcurved in basal area; ventral surface behind basal third with obtuse lateral carinae, nearly parallel in about apical third and little projecting behind apical margin; apical margin concave, on both sides with a substraight stylus (Fig. 2A). Phallus membranous (Fig. 7A–F).

Female. Subgenital plate acute-angled triangular in more than basal half, terminating into a long apical spine with regularly converging margins to acute tip; at transition between basal and apical areas sometimes slightly sloped (Fig. 5A–C).

Coloration.—Largely black or dark brown with fine and irregular light spots; pronotum reddish-brown or marbled with dark and light flecks; legs largely black with light, often white genicular areas, dorsal surface of fore and mid tibiae of lighter color; posterior half of hind femora and hind tibiae ochre. Face dark brown to black, marbled with numerous small lighter spots, in some specimens also with larger medium to dark brown areas; extension of light and dark areas variable. Tegmen semi-transparent, brown or blackish-brown with larger dark spots between subcosta and cubitus and smaller dark spots in anal area; in anterior area of lighter color. Hind wings semi-transparent with a trace of grey, in anterior area often brownish.

Measurements.—(5 males, 3 females). In mm. Body w/wings: male 65–72, female 65–66; body w/o wings: male 32–37, female 38–39; pronotum: male 8.5–9.5, female 9.5–10.2; tegmen: male 49.5–58.0, female 52.0–57.7; tegmen width: male 18.5–25.0, female 20.0–22.9; hind femur: male 31–34, female 34–36; antenna: male 90–100; ovipositor: female 26.

***Pteranabropsis angusta* sp. nov.**

Figs 1F, 2D, 2L, 3J–N, 6H–I, 7K–N

http://zoobank.org/D81AB88B-A1BE-4BB8-8248-5FA57BABA0D5

urn:lsid:Orthoptera.speciesfile.org:TaxonName:505862

Holotype (male).—Vietnam: Hoa Binh Prov., Cuc Phuong National Park, 20°19'N, 105°36'30"E, 11–18.viii.2010, leg. J. Constant & P. Limbourg (I.G. 31.668) – (Brussels, ISNB).

Other specimens examined.—same data as holotype – 1 male (paratype) (Brussels, ISNB).

Diagnosis.—The new species is similar to *P. carli* but has shorter wings that reach, but do not surpass, the hind knees; the tegmina are narrower and the hind wings smaller. The genicular area of the hind legs is pale but not whitish as in *P. carli*. The main diagnostic character to differentiate this species from *P. carli* and other species of the genus is the shape of the apical area of the male paraproctal outgrowths that have the apical area upcurved as in *P. carli* but longer, near the end are dorso-ventrally compressed instead of laterally compressed, and carry at the tip a stiffened pad pointing apically instead of a dorsal stiffened margin. The curvature of the external margin of the metasternal lobes is stronger than that of the internal margin but markedly less strong than in other species of the genus with conically extended metasternal lobes. Further differences to other species are outlined in the key.

Description.—Medium sized species; habitus as genus. Prosternal lobes compressed triangular, subacute; mesosternal lobes in basal area moderately wide, afterwards elongate conical to nearly cylindrical with obtuse to subtruncate tip; metasternal lobes compressed, with concave internal and convex external margins; gradually passing over into conical, nearly sub-cylindrical, apical area with obtuse tip (Fig. 2L).

Wings just reaching hind knees (Fig. 1F). Fore wings 2.6–2.7 × longer than wide. Venation: radius with radius sector arising between middle and apical third of tegmen; media anterior fused or sub-fused in basal area with radius, separating near end of basal third. In one male the media then divides before mid-length into two branches and the cubitus anterior also simply divides before mid-length into two branches; in the other male on right tegmen only, media anterior, after separation from radius, fuses with a first branch of cubitus anterior and shortly after divides into two branches, while on this tegmen, cubitus anterior divides twice and the first anterior branch fuses with media and shortly after cubitus anterior divides again into two simple branches; cubitus posterior free and undivided, with 5 anal veins, the last one incomplete. Hind wings cycloid, distinctly wider than long (1.70–1.76 ×).

Legs. Fore coxa with a strong spine at swollen anterior surface and mid-coxa with a smaller spine at anterior margin. Fore and middle femora with 2–3 small spines at anterior-ventral margins. Hind femora with 7 external and 6 internal small spines on ventral margins; hind tibiae with dorsal spines on inner margin larger than on outer margin, ventral margins with few minute spinules; both sides with 4 apical spurs, the dorsal two pairs very large, the following pair medium, the ventral-most pair small; internal spurs larger than external counterparts; ventral margin with 2 external and 1 internal spinules.

Male. Paraproctal outgrowths long, roughly cylindrical, widening in apical area with dorsal margin upcurved, later straight

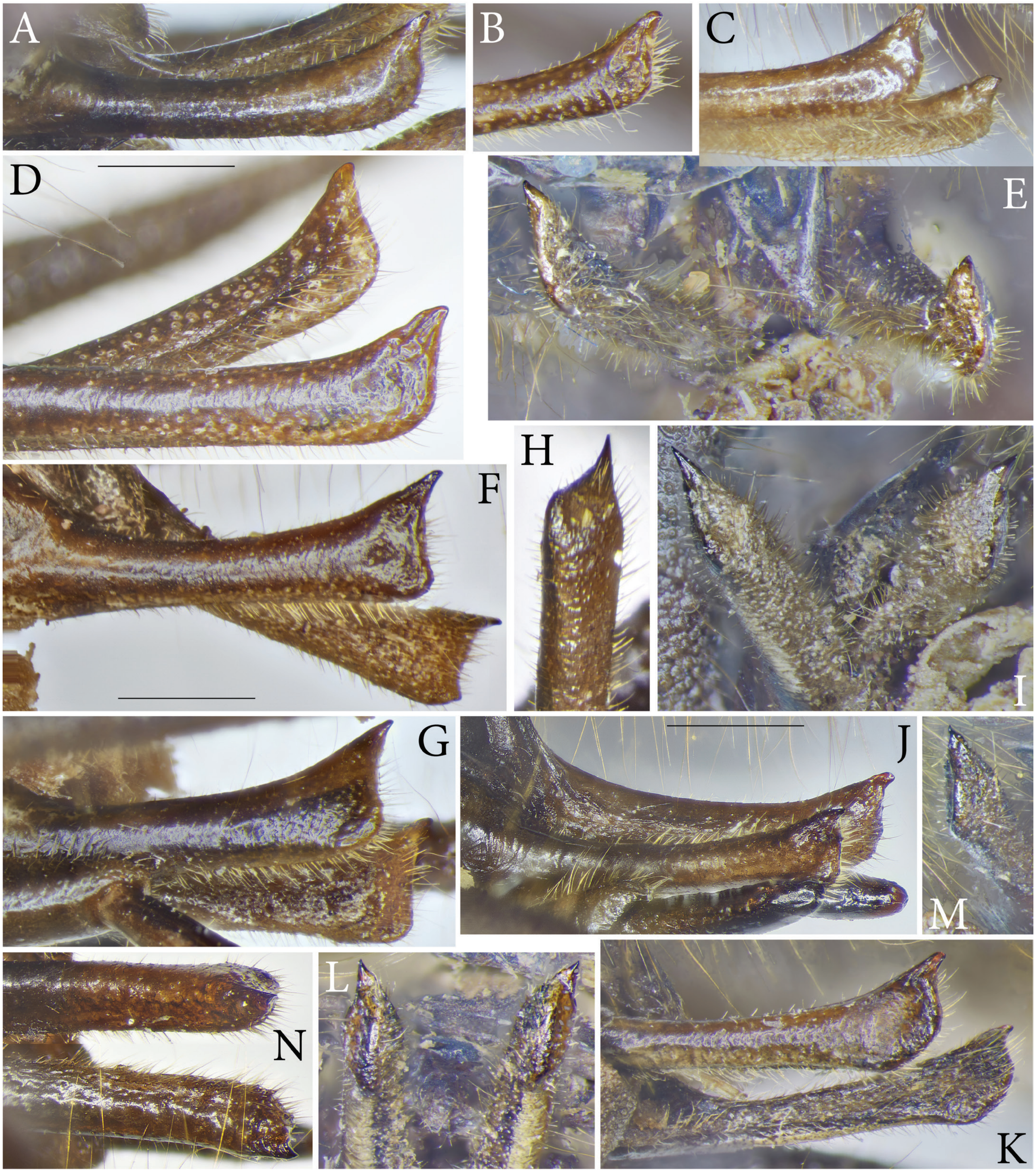

Fig. 3. Male paraproctal outgrowths in full or only apical area in lateral (**A–D, F–G, J–K**), apical (**E, I, L, M**), ventro-apical (**H**), and dorsal view (**N**). **A–D.** *P. carli* (Griffini, 1911) four males from Tam Dao (**A–B**), Cuc Phuong (**C**), and Ngo Luong (**D**); **E–I.** *P. cuspis* **sp. nov.** two males from Ngo Luong; **J–N.** *P. angusta* **sp. nov.** two males from Cuc Phuong. Scales 1 mm.

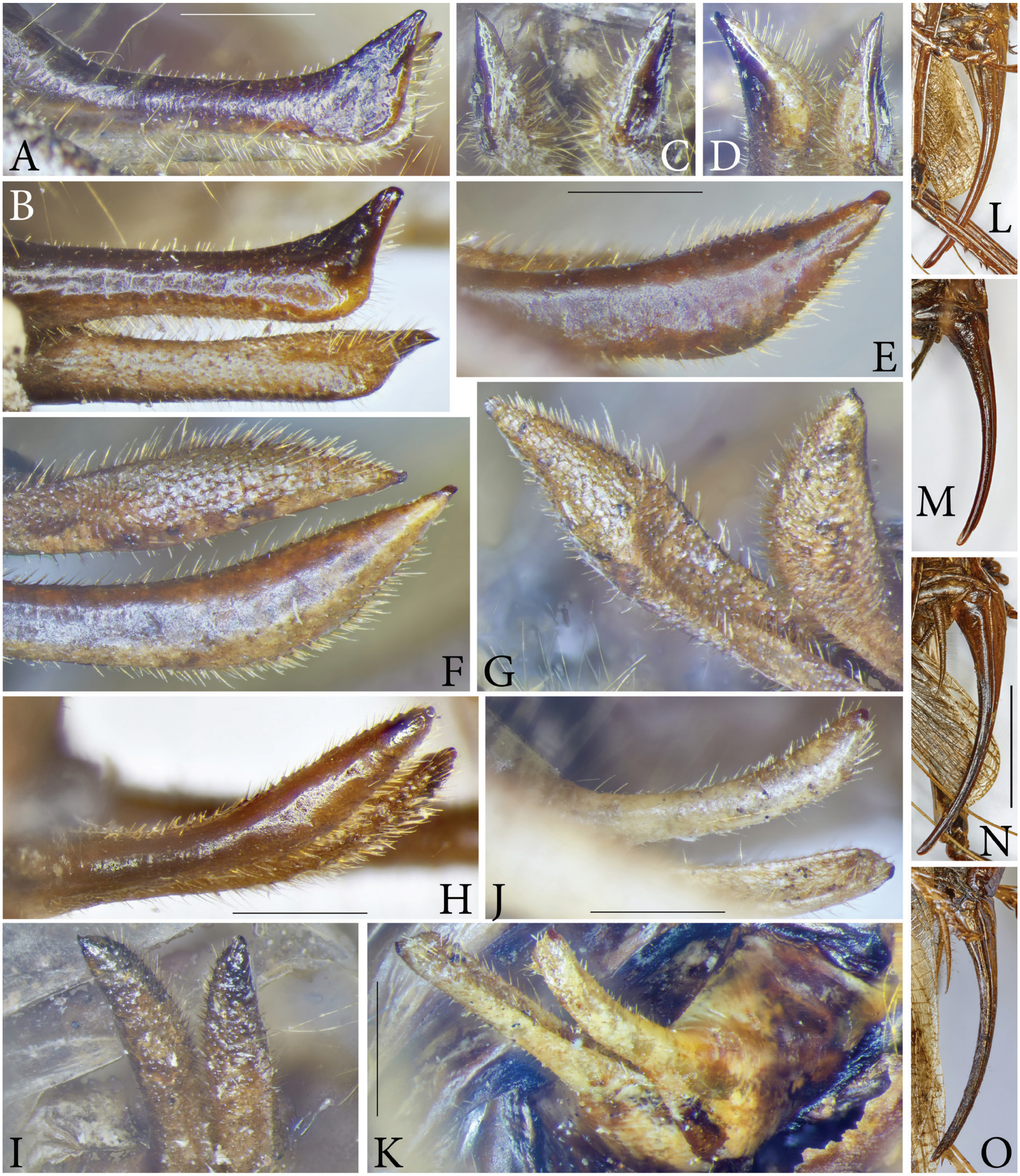

Fig. 4. A–K. Male paraproctal outgrowths in full or only apical area in lateral (**A–B, E–F, H, J**), apical (**C–D, G**), ventro-apical (**I**), and oblique apical view (**K**); **L–O.** Female abdominal apex with ovipositor in lateral view. **A–D.** *P. copia* (2 males); **E–G.** *P. carnarius* Gorochov, 1998 (two males from Tam Dao, in F the hindmost outgrowth is twisted upside down); **H–I.** *P. pusilla* **sp. nov.**; **J–K.** *P. guadun* **sp. nov.**; **L–M.** *P. copia* **sp. nov.** from Copia (L) and Hoang Lien (M); **N.** *P. bavi* **sp. nov.**; **O.** *P. guadun* **sp. nov.** Scales 1 mm, scale for ovipositor 10 mm.

and terminating into a compressed vertical lamella in dorsal area of apical margin, ventral margin broadly rounded (Fig. 3J–N). Epiproct elongate-triangular with slightly sinuate, stiffened and slightly elevated lateral margins. Subgenital plate with lateral margins upcurved and narrowing posteriorly; ventral surface behind basal third with obtuse lateral carinae, nearly parallel in about apical third; in apical area also with a faint median carina; apical margin concave, on both sides with a substraight stylus (Fig. 2D). Phallus membranous (Fig. 7K–N).

Female unknown.

Coloration.—Brown with light and dark spots. Face blackish-brown mixed with yellowish, pale to almost white spots; ocelli distinct. Tegmen semi-transparent, suffused with yellowish-brown except in anterior area, and provided with dark brown spots. Hind wings semi-transparent, slightly smoky.

Measurements.—(2 males). In mm. Body w/wings: 48; body w/o wings: 33–40; pronotum: 9.0–9.2; tegmen: 33.5–34.0; tegmen width: 12.5–13.0; hind femur: 31–32; antenna: 80.

Etymology.—The new species is named for its comparatively narrow wings; from Latin *angustus, angusta* narrow, slim.

Pteranabropsis cuspis sp. nov.

Figs 1B, 2B, 2H, 3E–I, 6F–G, 7I–J

http://zoobank.org/79D26B42-B6EE-4CF1-BC2B-5581B9C8F2D8

urn:lsid:Orthoptera.speciesfile.org:TaxonName:505863

Holotype (male).—Vietnam: Hoa Binh Prov., Ngo Luong Nat. Res., 20°26'16"N, 105°20'15"E, 25–30.vii.2016, leg. J. Constant & J. Bresseel (I.G.: 33.282 GTI project) – (Brussels, ISNB).

Other specimens examined.—Same data as holotype, 2 males (paratypes) (Brussels, ISNB).

Diagnosis.—The new species is similar to *P. angusta* **sp. nov.** but of more robust habitus. Tegmina and hind wings are of similarly shortened shape but slightly more reduced in *P. cuspis* **sp. nov.** Diagnostic for the new species is the shape of the paraproctal outgrowths, which resemble those of *P. carli* (Griffini, 1911) but have the upcurved apical area longer and narrower than in *P. carli* or in *P. angusta* and carry at nearly acute tip a very small, stiffened pad not a stiffened dorsal rim as in *P. carli* and not pointing apicad as in *P. angusta*.

Description.—Medium to large sized species; habitus as genus. Prosternal lobes near base compressed, afterwards long spiniform, thin; mesosternal lobes in basal area moderately wide, afterwards elongate conical to nearly cylindrical with obtuse tip; metasternal lobes compressed, with concave internal and convex external margins; gradually passing over into conical, nearly sub-cylindrical, apical area with obtuse tip (Fig. 2H).

Wings not reaching hind knees (Fig. 1B). Fore wings 2.9 × longer than wide. Venation: radius releases radius sector between middle and apical third of tegmen; media and cubitus anterior both with two branches each that fork from their undivided bases behind basal third of tegmen; cubitus posterior undivided; with four complete anal veins. Hind wings cycloid, distinctly wider than long (1.75 ×).

Legs. Fore coxa with a strong spine at swollen anterior surface; mid coxa with a smaller spine at anterior margin. Fore femur with 1–3 small spines and mid femur with 0–1 spine at anterior-ventral margins. Hind femora with 3–6 external and 3–6 internal small spines on ventral margins; hind tibiae with dorsal spines on inner margin larger than on outer margin, ventral margins with few minute spinules; on both sides with 4 apical spurs, the dorsal two pairs very large, the following pair medium, the ventral-most pair small; internal spurs larger than corresponding external counterparts; ventral margin with 2 external and 0–1 internal spinules.

Male. Subgenital plate with lateral margins slightly concave and narrowing posteriorly; apical margin subtruncate, both sides with a long substraight stylus (Fig. 2B). Paraproctal outgrowths with a rather long oblique-triangular projection from dorso-apical margin that carry at nearly acute tip a very small, stiffened pad; apical margin of outgrowth concave, ventro-apical angle rounded (Fig. 3E–I). Phallus membranous, shaped as in Fig. 7I–J.

Female unknown.

Coloration.—Different shades of brown, faintly spotted; head dark brown mixed with light and with black spots; pronotum and hind femora reddish-brown; hind knees dorsally very light brown; hind tibiae yellowish-brown. Face in different shades of brown, mixed with pale and black spots; pronotum and hind femora reddish-brown; hind knees dorsally ivory yellowish; hind tibiae yellowish-brown. Tegmen semi-transparent with black spots. Hind wings greyish, semi-transparent.

Measurements.—(3 males). In mm. Body w/wings: 45–47; body w/o wings: 35; pronotum: 9.7; tegmen: 33–38; tegmen width: 13; hind femur: 34; antenna: 80–90.

Etymology.—The new species is named for its narrow acute tip of the paraproctal outgrowths; from Latin *cuspis* spine, thorn; noun in apposition.

Pteranabropsis bavi sp. nov.

Figs 1G, 2K, 4N, 5G

http://zoobank.org/DE4A28EC-B640-4932-8DFD-1A750F3D63AE

urn:lsid:Orthoptera.speciesfile.org:TaxonName:505864

Holotype (female).—Vietnam: Hanoi prov., BaVi N.P., 21°4'4"N, 105°21'30"E, 25–29.vi.2015, leg. J. Constant & J. Bresseel (I.G.: 33.092) – (Brussels, ISNB).

Other specimens examined.—Same data as holotype, 1 female (paratype) (Brussels, ISNB).

Diagnosis.—A brachypterous species with wings reaching or slightly surpassing hind knees. The new species differs from all other species of the genus described so far by the shape of the female subgenital plate that has a distinct constriction of both lateral margins at the transition from the wider basal to the narrow apical area while in other species there is either a smooth transition or a faint slope of the surface or there are minute lateral grooves as in *P. copia* **sp. nov.** or *P. carnarius*. In general, habitus and wing shapes of *P. bavi* **sp. nov.** resemble *P. cuspis* **sp. nov.** and *P. angusta* **sp. nov.**, both only known from males, while *P. bavi* **sp. nov.** is only known from females. From *P. angusta* it differs by the longer and thinner cylindrical apical area of the metasternal lobes, and from *P. cuspis* **sp. nov.** by wider tegmina and less reduced hind wings. Both other

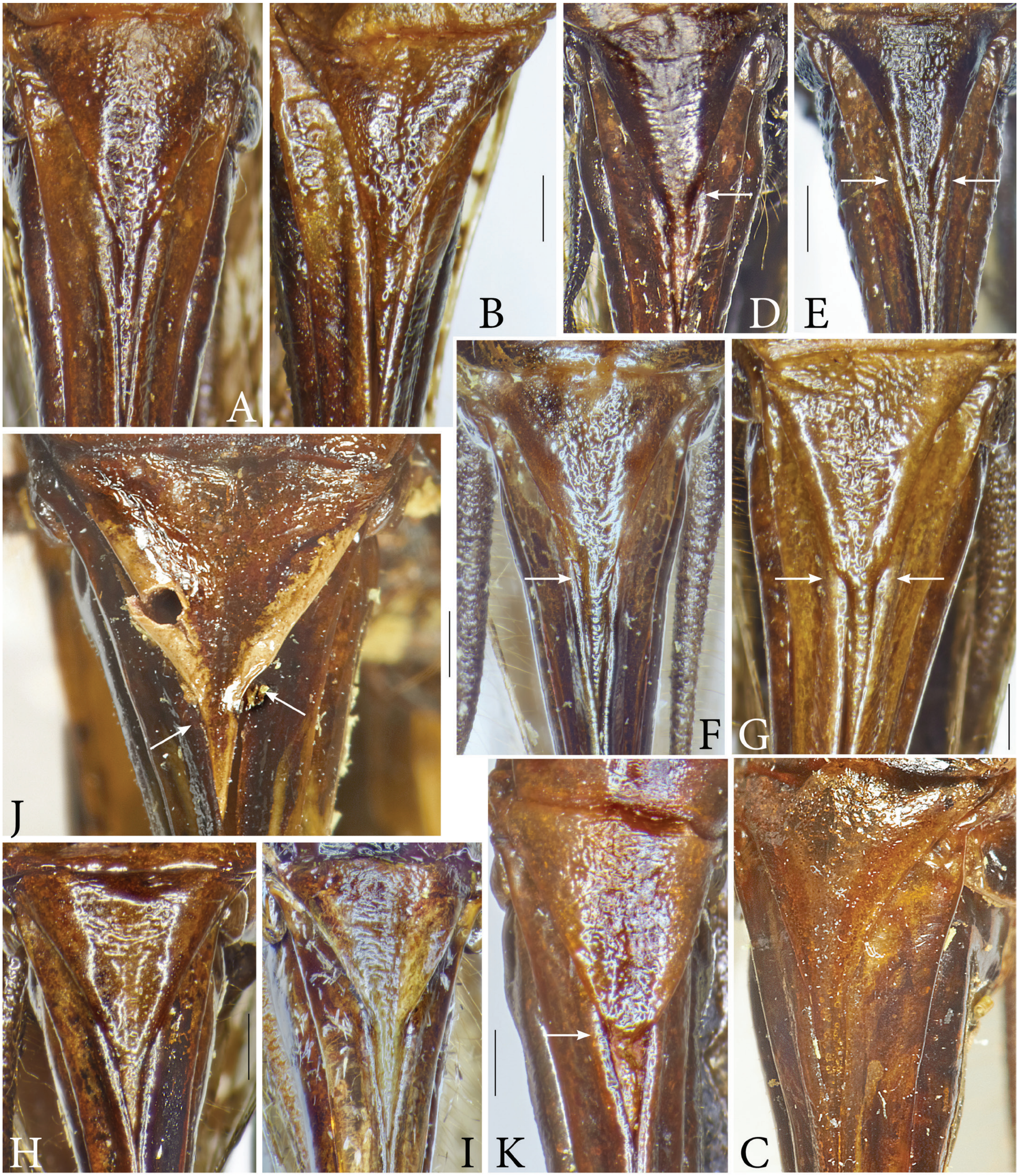

Fig. 5. Female subgenital plate of **A–C.** *P. carli* (Griffini, 1911) from Hoang Lien (**A–B**) and Tam Dao (**C,** in oblique view); **D–F.** *P. copia* **sp. nov.** from Hoang Lien (**D–E**) and Copia (**F**); **G.** *P. bavi* **sp. nov.**; **H.** *P. pusilla* **sp. nov.**; **I.** *P. guadun* **sp. nov.**; **J–K.** *P. carnarius* Gorochov, 1998 from Tam Dao (**J**) and from BaVi (**K,** abdomen laterally compressed). The white arrows point at the small lateral grooves, constrictions or faint steps of the subgenital plates. Scales 1 mm.

species occur in areas close to each other but remote from the locality of *P. bavi*.

Description.—Medium to large sized species; habitus as genus. Prosternal lobes near base compressed, afterwards long spiniform, thin; mesosternal lobes in basal area moderately wide, afterwards elongate conical to nearly cylindrical with obtuse to subtruncate tip; metasternal lobes compressed, with concave internal and convex external margins; gradually passing over into conical, nearly sub-cylindrical, apical area with obtuse tip (Fig. 2K).

Wings not or just reaching hind knees (Fig. 1G). Fore wings 2.6 × longer than wide. Venation: radius with radius sector arising between middle and apical third of tegmen; media two-branched, branching before mid-length; cubitus anterior three-branched, branching before and behind mid-length (on left, folded tegmen, all three veins branching from a single point before mid-length); cubitus posterior undivided; with 5 anal veins, the last one incomplete. Hind wings cycloid, about 1.7 × wider than long.

Legs. Fore coxa with a strong spine at swollen anterior surface; and mid coxa with a smaller spine at anterior margin. Fore femur with 1–3 small spines and mid femur with 3 spines at anterior-ventral margins. Hind femora with 1–5 external and 2–4 internal small spines on ventral margins; hind tibiae with dorsal spines on inner margin larger than on outer margin, ventral margins with few minute spinules; on both sides with 4 apical spurs, the dorsal two pairs very large, the following pair medium, the ventral-most pair small; internal spurs larger than corresponding external counterparts; ventral margin with 2 external and 1 internal spinules.

Male unknown.

Female. Subgenital plate acute-angled triangular in more than basal half, followed by a long spiniform posterior area; lateral margins distinctly constricted at transition between basal and apical areas (Fig. 5G).

Coloration.—Brown with lighter spots, fore and mid femora nearly black, all femora with ivory colored knees; hind femur to a variable extent with dorsal surface light ochre. Head: face blackish-brown with whitish-brown dots and flecks; clypeus, labrum and inner area of mandibles light brown with dark flecks to almost fully black; area around medial and lateral ocelli white, ocelli themselves brown; also anterior dorsal part of fastigium verticis white but midline black; antennae yellowish, only scapus and clypeus black. Tegmen semi-transparent brown with dark spots, in anterior area lighter; hind wings semi-transparent grey, in anterior area brownish.

Measurements.—(2 females). In mm. Body w/wings: 48–50; body w/o wings: 33–37; pronotum: 10.5–11.5; tegmen: 35–37; tegmen width: 13.5; hind femur: 35; antenna: 80; ovipositor: 21.5.

Etymology.—The name of the new species refers to the type locality; noun in apposition.

Pteranabropsis copia sp. nov.

Figs 1C–E, 2C, 2I, 2M, 4A–D, 4L–M, 5D–F, 6S–V, 7G–H

http://zoobank.org/B29BE0BA-E3E2-4341-8E4F-38204C1640A5

urn:lsid:Orthoptera.speciesfile.org:TaxonName:505865

Holotype (male).—Vietnam: Son La prov., Copia Nat. Res., 21°22'12"N, 103°30'42"E, 20–23.vii.2016, leg. J. Constant & J. Bresseel (GTI project, I.G.: 33.282) – (Brussels, ISNB).

Other specimens examined.—Vietnam: same data as holotype – 4 females, 2 males (paratypes) (Brussels, ISNB); Hoang Lien NP, 22°21'N, 103°46'20"E, 1–5.vii.2013, leg. J. Constant & J. Bresseel (I.G. 32.454) – 8 females (Brussels, ISNB).

Diagnosis.—A brachypterous species with wings that only slightly surpass the hind knees. In contrast to other brachypterous species of the genus, the fore wings of *P. copia* **sp. nov.** are rather wide (2.2–2.4 × longer than wide) and the spread hind wings are longer such that they look more like elongated semi-circles, while in most of the other species mentioned they are more ovoid. Moreover, *P. copia* **sp. nov.** differs from other similar species of the genus by the very narrow conical apical area of the metasternal lobes that arises in an almost step-like constriction from the wide basal area. The male paraproctal outgrowths of the new species resemble those of *P. cuspis* **sp. nov.**, but the long dorsal process ends in a rather wide obtuse tip that carries a narrow stiffened rim, while in *P. cuspis* it ends in a subacute tip with minute stiffened pad. The female subgenital plate of *P. copia* is similar to that of *P. carli* but provided in the transient zone between the wide basal and the narrow apical area with small elongate lateral grooves such that the ventral surface of the plate in that area is narrower than the distance between the dorsal lateral margins.

Description.—Medium sized to moderately large species; general habitus as genus. Prosternal lobes near base compressed, afterwards long spiniform, thin; mesosternal lobes in basal area moderately wide, afterwards elongate conical to nearly cylindrical with obtuse tip; metasternal lobes compressed, with concave internal and strongly convex external margins; rather suddenly narrowed into nearly sub-cylindrical apical area with obtuse tip (Fig. 2I, M).

Wings slightly surpassing hind knees (Fig. 1C–E). Fore wings 2.2–2.4 × longer than wide. Venation: radius with radius sector arising between middle and apical third of tegmen; media two-branched, branching before mid-length; cubitus anterior either three-branched, branching in basal third and behind mid-length, or two-branched, branching only in basal third; cubitus posterior free and undivided; with 5 anal veins, the last one incomplete. Hind wings nearly semicircular, about 1.4–1.55 × wider than long.

Legs. Fore coxa with a strong spine at swollen anterior surface; mid coxa with a smaller spine at anterior margin. Fore femur with 1–4 small spines and mid femur with 0–3 spines at anterior-ventral margins; in one male, also with one spine at posterior margin of one mid femur only. Hind femur with 1–6 external and 1–6 small internal spines on ventral margins; hind tibia with dorsal spines on inner margin slightly larger than on outer margin, ventral margins with few minute spinules; on both sides with 4 apical spurs, the dorsal two pairs very large, the following pair medium, the ventral-most pair small; internal spurs larger than external counterparts; ventral margin with 2–3 external and 1 internal spinules.

Male. Paraproctal outgrowths elongate, narrowest in middle, at end with rounded ventral angle, substraight but slightly oblique apical margin and elongate-triangular dorsal process, slightly tilting posteriorly and with truncate tip that carries on top a narrow stiffened lamella (Fig. 4A–D). Subgenital plate in widened basal area only slightly swollen; apical area with subparallel lateral margins that very faintly diverge posteriorly; apical margin substraight but concave in middle; elongate styli inserted at apico-lateral angles (Fig. 2C). Phallus membranous (Fig. 7G–H).

Female. Subgenital plate acute-angled triangular in more than basal half, terminating into a long apical spine with regularly con-

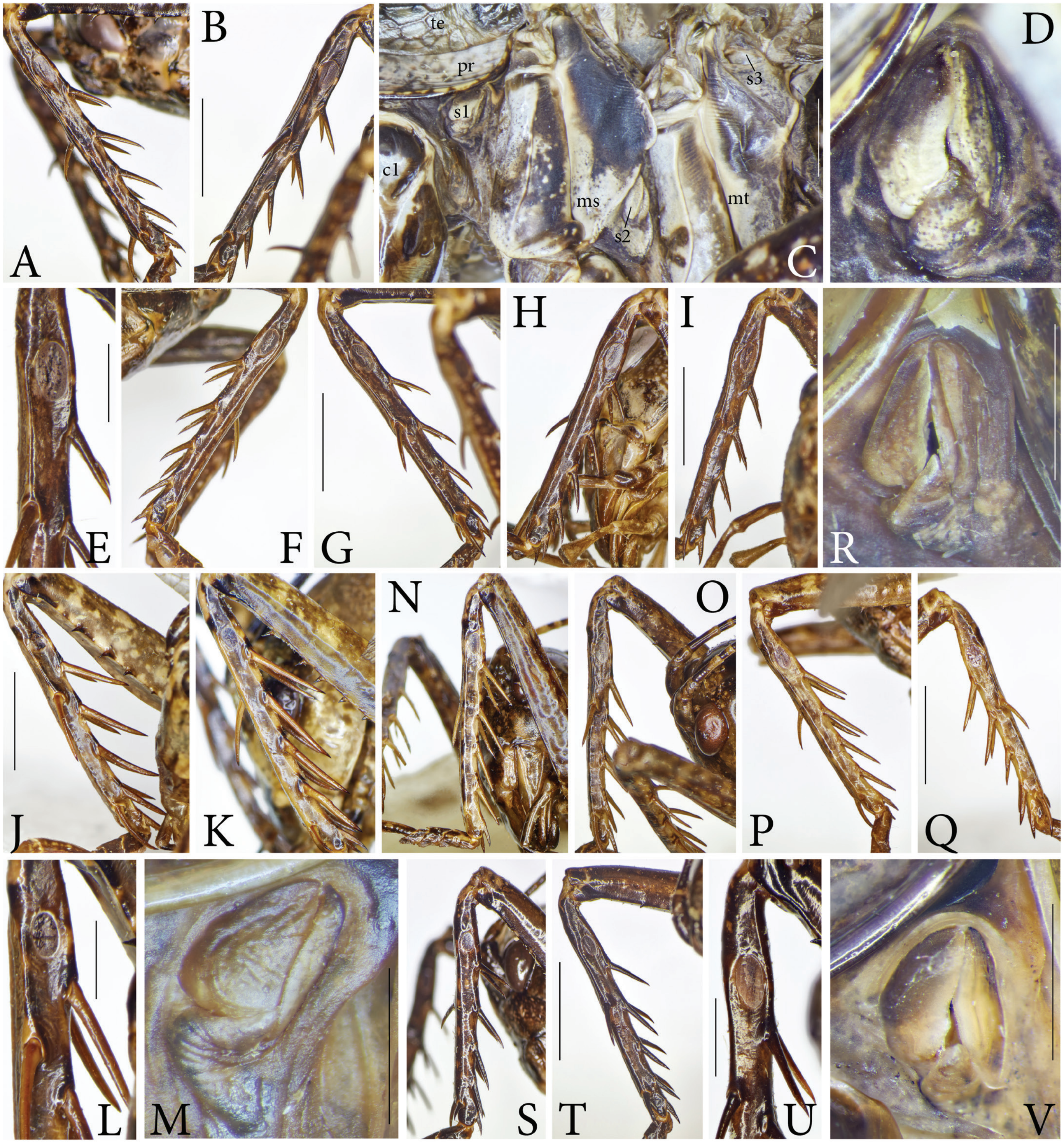

Fig. 6. A–E. *P. carli* (Griffini, 1911) male from Ngo Luong (**A–D**) and Tam Dao (**E**); **F–G.** *P. cuspis* **sp. nov.** male; **H–I.** *P. angusta* **sp. nov.** male; **J–M.** *P. carnarius* Gorochov, 1998 male (**J**) and female from Tam Tao (**K–L**) and from BaVi (**M**); **N–O.** *P. pusilla* **sp. nov.** female; **P–R.** *P. guadun* **sp. nov.** female; **S–V.** *P. copia* **sp. nov.** female (**S–T**) and male (**U–V**) from Copia. – Fore tibia external side (**A, F, H, K, N, P, S**) and internal side (**B, E, G, I–J, L, O, Q, T**); thorax in lateral view (**C**), prothoracic spiracle (**D, M, R, V**). Abbreviations: c1 – anterior coxa, ms – mesothoracic pleurites, mt – metathoracic pleurites, s1-s3 – first, second and third thoracic spiracles. Scales for legs and body, 5 mm; for tympana and spiracles, 1 mm.

verging margins to acute tip; at transition between basal and apical areas with a small elongate groove on both sides (Fig. 5D–F).

Coloration.—Different shades of brown with light and dark brown mottling; head dark brown with light spots; pronotum and hind femora of similar color; hind femora towards apical area indistinctly lighter. Head: face blackish-brown with numerous small and few larger whitish-brown dots, also on scapus; clypeus, labrum and inner area of mandibles more uniformly medium or dark brown. Tegmen semi-transparent brown with indistinct dark spots, along anterior margin lighter; hind wings semi-transparent grey-brown, in anterior area clear, subtransparent.

Measurements.—(3 males, 4 females from Copia). In mm. Body w/ wings: male 48–50, female 46–50; body w/o wings: male 27–31, female 28–35; pronotum: male 6.8–8.0, female 7.5–8.5; tegmen: male 36–38, female 32–37; tegmen width: male 15.5–16.5, female 14.0–15.5; hind femur: male 28.5–29.0, female 27–30; ovipositor: female 19.5–23.0. Index tegmen length : width male 2.24–2.45, female 2.21–2.40.

Measurements.—(8 females from Hoang Lien). In mm. Body w/ wings: female 39–45; body w/o wings: female 28–32; pronotum: female 7.8–8.2; tegmen: female 30–33; tegmen width: female 14; hind femur: female 26–28; ovipositor: female 18–20.

Etymology.—The name of the new species refers to the type locality; noun in apposition.

Pteranabropsis carnarius **Gorochov, 1998**

Figs 1J, 2E, 2N, 4E–G, 5J–K, 6J–M, 7O–P

urn:lsid:Orthoptera.speciesfile.org:TaxonName:20139

Specimens examined.—Vietnam: Hanoi prov., BaVi N.P., 21°4'4"N, 105°21'30"E, 25–29.vi.2015, leg. J. Constant & J. Bresseel (I.G.: 33.092) – 2 females (Brussels, ISNB); Prov. Vinhfu, Tam Dao N.P., 21°31'N, 105°33'E, 25–30.vii.2011, leg. J. Constant & J. Bresseel (I.G. 31.933) – 1 female, 2 males (Brussels, ISNB).

Diagnosis.—In general characters, *P. carnarius* differs from all other species of the genus that I have studied by the wide fore wings, the dark colored hind wings, and by the very long and distinctly curved ventral spines of the fore tibia; the longest of these spines are more than three times (3.3 ×) longer than the width of the tibia while in the other species the longest spines are more than two times longer than the tibia width but shorter than three times (2.2–2.8 ×) and are only slightly curved or substraight. In sex-specific characters, males differ from other species by the paraproctal outgrowths that have the pre-apical area bulging ventrally and then are gradually narrowed to the tip that carries a small stiffened obtuse pad. Females have the subgenital plate wide at base with rather strongly narrowing, substraight lateral margins, and the narrow apical area short, about half the length of the wide anterior area.

Description.—Large species; habitus as genus. Prosternal lobes near base compressed, afterwards long spiniform, thin; mesosternal lobes in basal area moderately wide, about between basal half and basal two thirds compressed, afterwards tubular with obtuse or subtruncate tip; metasternal lobes compressed triangular with faintly concave internal and strongly convex external margins, towards tip swollen conical with obtuse tip; without narrow cylindrical apical area (Fig. 2N).

Wings distinctly surpassing hind knees (Fig. 1J). Fore wings 2.0–2.23 × longer than wide. Venation: radius with radius sector arising behind mid-length of tegmen; media two-branched, branching behind basal third; cubitus anterior three-branched, branching in basal third and behind mid-length; cubitus posterior undivided, at base running very close to first analis; with 5–6 anal veins, the last one incomplete; the first and second anal veins with a short common base; the second vein branching again into 2 veins in subbasal area (thus 6–7 anal veins). Hind wings nearly semicircular, only slightly wider than long (about 1.3 ×).

Legs. Fore coxa with a strong spine at swollen anterior surface; mid coxa with a smaller spine at anterior margin. Fore femur with 5–6 small spines and mid femur with 3–5 spines at anterior-ventral margins, mid femur also with 3–6 posterior-ventral spines. Hind femur with 4–7 external and 2–3 internal small spines on ventral margins; hind tibia with dorsal spines on inner margin slightly larger than on outer margin, ventral margins with few minute spinules; on both sides with 4 apical spurs, the dorsal two pairs very large, the following pair medium, the ventral-most pair small; internal spurs larger than corresponding external counterparts; ventral margin with 3 external and 1 internal spinules.

Male. Paraproctal outgrowths elongate, in subapical area slightly but distinctly widening, somewhat curved dorsad and with converging margins towards subacute tip; at tip provided with a tiny, compressed, obtuse pad (Fig. 4E–G). Subgenital plate in about basal half slightly swollen with convex and approaching lateral margins [in Fig. 2E, barely expressed from freshly molted specimen with still soft cuticula when captured]; in apical half with subparallel or faintly diverging lateral margins which towards tip form rounded lateral carinae, at tip with insertion of stylus; otherwise apical area compressed with apical margin subtruncate, interrupted by a deep incision with rounded bottom. Phallus membranous (Fig. 7O–P).

Female. Subgenital plate wide at base, triangularly narrowing posteriorly and terminating into a short spiniform apical area; basal area nearly twice as long as apical area, faintly sloping in transition zone between both areas (Fig. 5J). In a female from BaVi the baso-lateral areas are curved dorsad, giving the impression of a narrower plate, and the transition zone more strongly expressed (Fig. 5K).

Coloration.—General color light brown, mixed with dark pattern; pronotum light brown to ochre, with or without some darker elements; legs spotted with light and darker flecks. Head: face yellowish-brown with dark spots; clypeus and labrum brown, mouthparts of same color; below median ocellus and at clypeo-frontal suture with black spots, in some individuals also clypeus darkened; antennae in basal area black with white annulation, behind about basal quarter gradually getting lighter towards tip. Tegmen light, semi-transparent with dark brown or nearly black spots; hind wings bright medium to dark brown, along margin transparent, in anterior area semi-transparent with some dark spots along margin; in anterior area of the dark field with few scattered whitish, transparent spots.

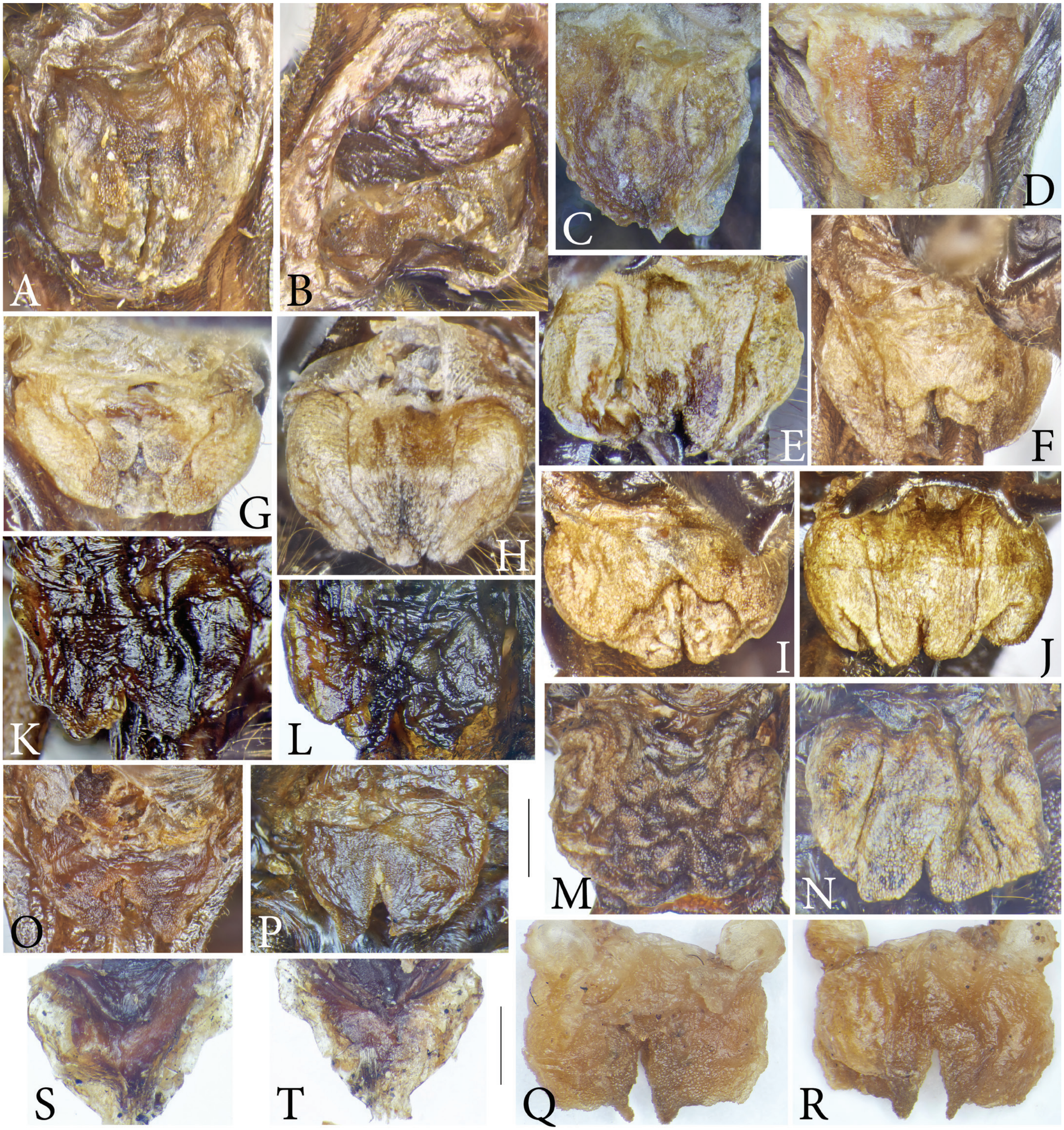

Fig. 7. Male phallic complex of **A–F.** *P. carli* (Griffini, 1911) from Tam Dao (**A–B**), Cuc Phuong (**C–D**) and Ngo Luong (**E–F**); **G–H.** *P. copia* **sp. nov.**; **I–J.** *P. cuspis* **sp. nov.**; **K–N.** *P. angusta* **sp. nov.**; **O–P.** *P. carnarius* from Tam Tao; **Q–R.** *P. pusilla* **sp. nov.**; **S–T.** *P. guadun* **sp. nov.** in dorsal (**A, C, F, G, I, L, M, O, Q, S**) and in ventral (**D, E, H, J, K, N, O, R, T**) view, or in dorsal view with only dorsal lobes flipped proximad, ventral lobe distad (**B**). Scales 1 mm (all images).

Measurements.—(2 males, 3 females). In mm. Body w/wings: male 60–63, female 58–62; body w/o wings: male 36–37, female 38–40; pronotum: male 9.5–10.3, female 10.0–10.5; tegmen: male 45–46, female 44–49; tegmen width: male 21–23, female 20–22; hind femur: male 27–30, female 29–32; antenna: male 90, female 100; ovipositor: female 29–31.

Pteranabropsis pusilla sp. nov.

Figs 1I, 2F, 2O, 4H–I, 5H, 6N–O, 7Q–R

http://zoobank.org/5C6B62DA-413C-49EB-B19C-95190CED3C38

urn:lsid:Orthoptera.speciesfile.org:TaxonName:505866

Holotype (male).—Vietnam: Hoang Lien NP, 22°21'N, 103°46'20"E, 1–5.vii.2013, leg. J. Constant & J. Bresseel (I.G. 32.454) – (Brussels, ISNB).

Other specimens examined.—Same data as holotype, 1 female (paratype) (Brussels, ISNB).

Diagnosis.—In contrast to the other brachypterous species described in this paper, *P. pusilla* **sp. nov.** is related to *P. carnarius* Gorochov, 1998 with regard to the male paraproctal outgrowths, the shape of the phallus, and the shape of the female subgenital plate. It differs by smaller size, the grey semitransparent instead of dark brown hind wings, the tibial spines that are less curved and distinctly shorter, the longest tibial spines is only more than twice as long as the width of the diameter of the fore tibia instead of more than three times that width, and the metasternal lobes being narrower at tip. The paraproctal outgrowths of *P. pusilla* are much less widened in subapical area than in *P. carnarius*, have the tip obtuse instead of subacute, and carry only a minute stiffened pad at tip. The female subgenital plate of the new species is similar to that of *P. carnarius* but the narrow apical area is even shorter than in the latter species: less than half the length of the anterior area instead of about half or slightly more than half of that length.

Description.—Medium to large sized species; habitus as genus. Prosternal lobes near base compressed, afterwards long spiniform, thin; mesosternal lobes in basal area wide, afterwards thin tubular with obtuse tip; metasternal lobes rather short, compressed triangular with faintly concave internal and moderately convex external margin, towards tip short-conical with obtuse tip (Fig. 2O).

Wings in male distinct, in female slightly surpassing hind knees. Fore wings 2.4–2.6 × longer than wide (Fig. 1I). Venation: radius with radius sector arising at beginning of apical third of tegmen; media free, two-branched, branching before mid-length; cubitus anterior three-branched, branching before mid-length and before apical third; cubitus posterior undivided; with 5 anal veins, the last one incomplete. Hind wings nearly semicircular, only slightly wider than long (about 1.35 ×).

Legs. Fore coxa with a strong spine at swollen anterior surface and a blunt tooth at ventro-posterior margin; mid coxa with a smaller spine at anterior margin. Fore femur with 1–4 and mid femur with 2–3 spines at anterior-ventral margins; in one female also with 1–2 spinules on posterior-ventral margin. Hind femur with 5–6 external and 3 internal small spines on ventral margins; hind tibia with dorsal spines on inner margin larger than on outer margin, ventral margins with few minute spinules; on both sides with 4 apical spurs, the dorsal two pairs very large, the following pair medium, the ventral-most pair small; internal spurs larger than corresponding external counterparts; ventral margin with 1 external and 3 internal spinules.

Male. Paraproctal outgrowths long, roughly cylindrical with setose and warty internal surface, in about mid-length faintly constricted, in subapical area only faintly widening and slightly curved dorsad, apex obtuse but with a tiny compressed pad at tip (Fig. 4H–I). Subgenital plate in basal two thirds with convex surface and approaching lateral margins; disc in apical half with rounded lateral carinae, first approaching, afterwards diverging, at tip with insertion of stylus; apical margin transverse substraight, interrupted by a deep incision with rounded bottom (Fig. 2F). Phallus membranous (Fig. 7Q–R).

Female. Subgenital plate wide at base, triangularly narrowing posteriorly and terminating into a short spiniform apical area; basal area nearly twice as long as apical area, slightly sloping in transition zone between both areas (Fig. 5H).

Coloration.—General color light yellowish-brown with dark mottling. Head: face yellowish-brown to light ochre, with or without black flecks; along clypeo-frontal suture with 4 black spots; clypeus brown; below antennal scrobae and on genae with dark spots; vertex mostly black; ocelli white; antennal flagellum in more basal area black with white annulation, farther behind paler. Pronotum brown; anterior margin black, toward sides with white annulation (male) or with alternating black and yellow spots (female). Tegmen light semi-transparent with dark brown spots; hind wings semi-transparent grey, in anterior area light with brown spots.

Measurements.—(1 male, 1 female). In mm. Body w/wings: male 47, female 43; body w/o wings: male 25, female 27; pronotum: male 8.1, female 7.8; tegmen: male 40, female 34; tegmen width: male 16.5, female 13; hind femur: male 24.5, female 25.0; ovipositor: female 23.5.

Etymology.—The name of the new species refers to its smaller size compared to the related species *P. carnarius*; from Latin *pusillus, pusilla* of small size.

Pteranabropsis guadun sp. nov.

Figs 1H, 2G, 2P, 4J–K, 4O, 5I, 6P–R, 7S–T

http://zoobank.org/CA794A7E-4AC5-4746-93E0-0E4383BEF373

urn:lsid:Orthoptera.speciesfile.org:TaxonName:505867

Holotype (male).—China: Fujian, Wuyishan, Kuatun [Guadun], elev. 2300 m, 27°40'N, 117°40'E, 4.ix.1938, leg. J. Klapperich – (Bonn, ZFMK).

Other specimens examined.—Same locality as holotype, 31.vii.1938, leg. J. Klapperich, 1 female (paratype) (Bonn, ZFMK).

Diagnosis.—The male subgenital plate and paraproctal outgrowths of the new species are similar to those of *Pteranabropsis infuscatus* Wang et al., 2015; it differs by larger size, longer wings and longer ovipositor, by the metasternal plates that are roughly triangular without short conical tip instead of with conical tip in *P. infuscatus*. The female subgenital plate is similar in both species but in *P. guadun* **sp. nov.** has the narrow apical area for the greatest basal part rather wide and stout with parallel lateral margins and suddenly distinctly narrowed before tip instead of apical area regularly narrowed to tip.

Description.—Medium to large sized species; habitus as genus. Prosternal lobes near base compressed, afterwards long spiniform, thin; mesosternal lobes in basal area wide, afterwards thin tubular with obtuse tip; metasternal lobes compressed triangular with faintly concave internal and convex external margins, towards tip swollen conical with obtuse tip; without narrow, roughly cylindrical area (Fig. 2P).

Wings distinctly surpassing hind knees (Fig. 1H). Fore wings 2.21–2.23 × longer than wide. Venation: radius with radius sector

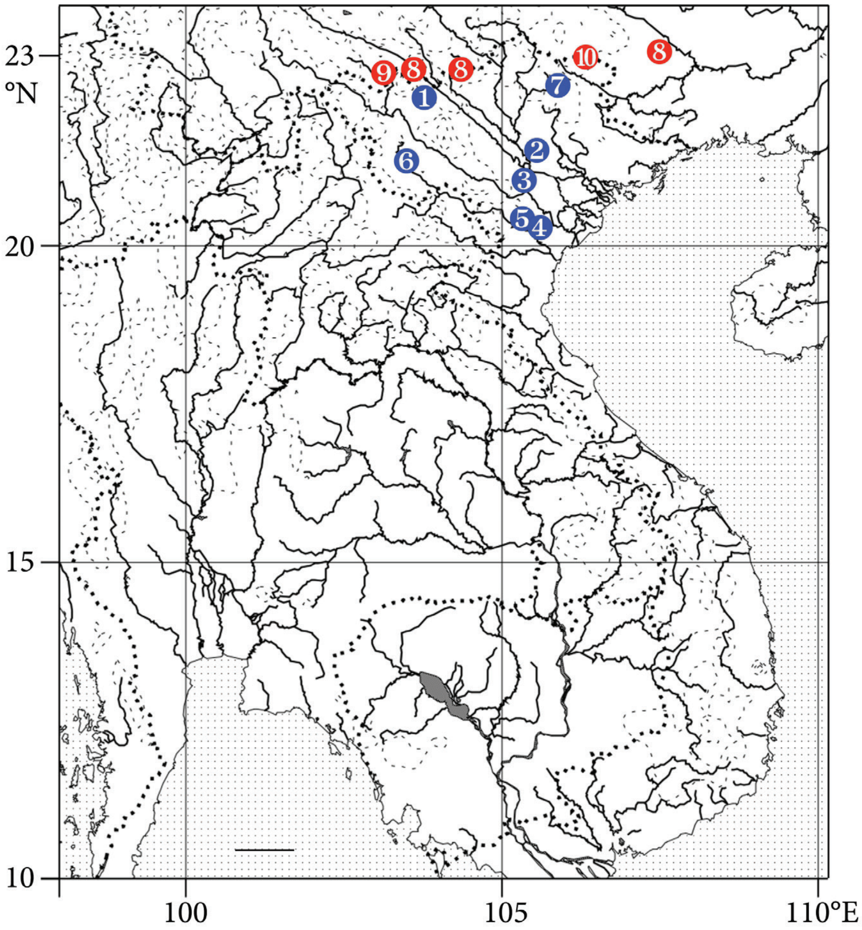

Fig. 8. Distribution of the genus *Pteranabropsis* in Vietnam (blue points **1–7**) and some localities in southern China (red points **8–10**, after Song et al. 2016): **1.** Hoang Lien N.P. (*P. carli* (Grif.), *P. copia* **sp. nov.**, *P. pusilla* **sp. nov.**); **2.** Tam Dao N.P. (*P. carli, P. carnarius* Gor.); **3.** BaVi N.P. (*P. bavi* **sp. nov.**, *P. carnarius*); **4.** Cuc Phuong N.P. (*P. carli, P. angusta* **sp. nov.**); **5.** Ngo Luong Nat. Res. (*P. carli, P. cuspis* **sp. nov.**); **6.** Copia Nat. Res. (*P. copia*); **7.** Phia Den (*P. carli*); **8.** Localities of *P. carli*; **9.** Locality of *P. crenatis* Song et al.; **10.** Locality of *P. karnyi* Wang et al. Scale 100 km.

arising between middle and apical third of tegmen; media two-branched, branching between basal third and mid-length; cubitus anterior three-branched, branching before end of basal third and just before (male) or behind (female) mid-length; cubitus posterior free and undivided; with 5(-6) anal veins, the last one or two incomplete. Hind wings nearly semicircular, only slightly wider than long (about 1.3 ×).

Legs. Fore coxa with a strong spine at swollen anterior surface; mid coxa with a smaller spine at external margin. Fore femur with 4 (female) or 1 (male) small spines and mid femur with 3–4 (female) or 1 (male) spines at anterior-ventral margins, in the female only also with 0–1 spinules at posterior-ventral margin of mid femur. Hind femur with 2–5 external and 2–3 internal small spines on ventral margins; hind tibia with dorsal spines on inner margin slightly larger than on outer margin, ventral margins with few minute spinules; on both sides with 4 apical spurs, the dorsal two pairs very large, the following pair medium, the ventral-most pair small; internal spurs larger than corresponding external counterparts; ventral margin with 3 external and 1 internal spinules.

Male. Paraproctal outgrowths forming a long roughly cylindrical process with setose surface, slightly curved dorsad in subapical area, apex obtuse but with a small compressed pad at tip (Fig. 4J–K). Subgenital plate in about little more than basal half with convex surface and approaching lateral margins; in somewhat less than apical half with faintly diverging lateral margins that, towards tip, form rounded lateral carinae that are slightly diverging posteriorly, at tip with insertion of stylus; otherwise apical area compressed with apical margin subtruncate and slightly oblique on both sides, interrupted by a V-shaped incision (Fig. 2G). Phallus membranous, not well preserved in holotype (Fig. 7S–T).

Female. Subgenital plate wide at base, triangularly narrowing posteriorly and terminating into a spiniform apical area that is distinctly longer than in *P. carnarius*, almost as long as the wide basal area and with sub-parallel lateral margins except for apical third with converging margins to acute tip (Fig. 5I).

Coloration.—General color medium brown, mixed with dark pattern; pronotum dark brown; legs marbled with light and darker flecks. Head: face light yellowish-brown with larger, indistinctly darker flecks and with smaller dark spots. Pronotum uniformly medium brown with light yellowish-brown rim. Tegmen light semi-transparent with dark brown spots; hind wings light semi-transparent with dark brown spots.

Measurements.—(1 male, 1 female). In mm. Body w/wings: male 53, female 55; body w/o wings: male 29, female 30; pronotum:

male 8.3, female 8.3; tegmen: male 41, female 42.5; hind femur: male 26, female 27; tegmen width: male 18.5, female 19; antenna: male 85, female 65; ovipositor: female 23.

Etymology.—The name of the new species refers to the type locality; noun in apposition.

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Short Communication Journal of Orthoptera Research 2019, 28(2): 125-128

The tide is high, but it's holding on: response of the grey bush-cricket, *Platycleis albopunctata*, to a storm surge

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Abstract

Coastal insects may be highly susceptible to population loss due to catastrophic inundation events. At two locations on the east coast of the UK (nature reserve and naturists' beach), the response of the Nationally Scarce grey bush-cricket, *Platycleis albopunctata*, to the December 2013 storm surge was determined from long-term transect monitoring of stridulating males. In the post-surge seasons, males were more frequent on the back dunes, which would have been largely unsubmerged during the tidal event. Lower numbers of *P. albopunctata* were recorded on the fore dunes after 2013, probably due to submergence during the surge tide and extensive shingle deposition on its marram-grass, *Ammophila arenaria*, and open ground habitats smothering overwintering eggs. The heterogeneity of the dune habitat with slacks and ridges may render this species resilient to storm surges.

Keywords

climate, coast, conservation, Orthoptera, sand dune, shingle, Tettigoniidae

Introduction

In December 2013 the UK was hit by the largest storm surge in 60 years, with the severe storm 'Hercules' causing further damage to coastal areas in January 2014 (Spencer et al. 2015). The storm (Xavier) which hit the UK on the 5th and 6th December 2013 resulted in the most serious tidal surge since the disastrous floods of 1953 (Environment Agency 2014). Record sea levels were observed in several locations due to the combination of low pressure interacting with the high tide (Spencer et al. 2015). Fortunately, in eastern England, a largely offshore, westerly wind meant that aggressive wave action on flood defenses was avoided. Where the storm surge of 1953 left 307 dead and 25000 properties flooded on the east coast of England, no flood-related deaths occurred during the 2013 surge, and 1400 properties were inundated (Environment Agency 2014). The improvements to sea wall flood defenses since the 1950s and improved flood warnings (none were issued in 1953) went a long way to ensure that there was no repeat of the devastating 1953 surge.

What is not documented is how coastal invertebrates may be affected by storm surges. The response of the scaly cricket *Pseudomogoplistes vicentae* (IUCN Red Data List - Vulnerable) in the UK to storm surges in 2013/2014 has been studied by Professor Karim Vahed and reported in Sutton et al. (2017). The shingle habitat had been removed at several sites containing this cricket, which may have led to a contraction in populations. Interestingly, *P. vicentae* lays its eggs in driftwood so may be able to recolonize sites after storm damage (Sutton et al. 2017). In Essex, south-east England, there were lower numbers of the mottled grasshopper *Myrmeleotettix maculatus* (included in the Essex Red Data List) after the 2013 storm surge at a reintroduction site on sand dunes (Gardiner and Seago 2015, Gardiner et al. 2017).

The grey bush-cricket, *Platycleis albopunctata*, is a Nationally Scarce coastal species in the UK (Sutton et al. 2017). The insect is a thermophile (Ingrisch and Köhler 1998) with an annual life cycle (Ingrisch 1986). Adults feed on bugs and flies as well as grass-seeds and herbaceous plants (Hein 2004). In many situations in Europe, the preferred locations have plenty of sparse, open ground in dry grassland due to egg-laying in the soil or in dry plant stems (Hein 2004). Its thermophilic nature also dictates its habitat, sparse grassland with bare ground being warmer than taller vegetation (Hein 2004). On the east coast of the UK, *P. albopunctata* is localized and inhabits sand dune and shingle habitats to the north of the Thames Estuary (Gardiner and Seago 2015). These isolated populations at the north of its UK range contain an abundance of exposed soil in sparse grassland susceptible to tidal inundation during storm surges.

Its northern most sites on the east coast of the UK are in the county of Suffolk: on vegetated shingle at Orford Ness and Shingle Street (Ling 2000), saline lagoon edges (Telfer 2013), and in grassland abutting sea walls at Iken (Abrehart 2015) and Havergate Island. Unfortunately, the 2013 storm surge led to widespread flooding of *P. albopunctata* habitat on Havergate Island in particular, which may have proved deleterious to the species. In Essex, ca. 35 km to the south of Shingle Street, *P. albopunctata* is reliably found at only two sites: Colne Point and St. Osyth naturists' beach. This short communication details the response of *P. albopunctata* to the December 2013 surge impact at its only locations on the Essex coast.

Methods

Transect survey.—*Platycleis albopunctata* (Orthoptera: Tettigoniidae) was rediscovered in pitfall traps at Colne Point (Essex, UK) in 2004, after an absence of records for over 50 years (Harvey et al. 2006, Harvey and Gardiner 2006). Previous searches for *P. albopunctata* at Colne Point may have been unsuccessful due to the extremely localized distribution of the species at the site (Harvey and Gardiner 2006) and the tendency of population size to fluctuate largely between years (Gottschalk et al. 2003), which may have led to this species being overlooked by *ad hoc* visual surveys in years with small populations. The ineffectiveness of visual searching may also be compounded by the greyish brown color of *P. albopunctata* adults, which provides effective camouflage in tall and dense stands of marram-grass, *Ammophila arenaria*, where the proportion of green vegetation is low. Recent research suggests that pitfall traps can be very effective at sampling the Orthoptera of sand dunes (Schirmel et al. 2009). However, pitfall traps did not appear to be especially effective for sampling *P. albopunctata* in sand dunes (no significant difference between numbers in pitfall traps and transect counts), despite their efficacy for monitoring ground-active orthopterans such as *M. maculatus* (Schirmel et al. 2009).

A fixed route transect (4.8 km long) was established in 2010 at Colne Point to monitor the only reliable sites for the species in the county (Gardiner et al. 2010). The transect was walked at a slow strolling pace (2 km/h) and all stridulating adult male *P. albopunctata* (Samways 1976), located using a bat detector (Magenta III) set at 28 kHz, were recorded. The transect was subdivided into different sections (a map of the transect sections is kept by all authors and Essex Wildlife Trust (EWT)), two of these being on the fore dunes of Colne Point nature reserve and St. Osyth naturists' beach (<10 m from strandline, 3.5–4 m Above Ordnance Datum (AOD) defined as height relative to the average sea level at Newlyn, Cornwall, UK) and two on the back dunes of the same two sites (>10 m from strandline to approximately 10 m from salt marsh edge, 4–4.6 m AOD).

The December 2013 surge was observed to have affected the spit at its eastern end (on the naturists' beach fore dunes in particular but also on the Colne Point nature reserve) where shingle had been moved and deposited on the fore dunes smothering large areas of *A. arenaria* (Fig. 1), a potentially important habitat for *P. albopunctata*. There was also some deposition on the back dunes (Fig. 2).

The transect encompassed the main sand dunes on the Colne Point nature reserve running from 51°46'18.5"N, 1°02'23.0"E to 51°46'13.0"N, 1°03'42.6"E (south of the creek) and also the dunes on the naturists' beach from 51°46'13.0"N, 1°03'42.6"E to 51°46'16.4"N, 1°04'17.0"E. Because the transect route involved walking the same length of fore (1600 m Colne Point, 800 m for naturists' beach) and back dune (1600 m for Colne Point, 800 m for naturists' beach), the numbers detected in these two areas were directly comparable and represented areas potentially affected by the surge tide.

Post-surge shingle analysis.—The percentage ground cover of *A. arenaria* and shingle substrate were estimated in 10 randomly positioned 50 × 50 cm frame quadrats (0.25 m^2) on the fore dunes and in another 10 quadrats on the back dunes of both Colne Point nature reserve and the naturists' beach. In total 40 quadrats were surveyed, 20 for each site, in September 2015.

Statistical analysis.—For ease of analysis, the annual bat detector counts of *P. albopunctata* in August on the fore and back dunes of both the naturists' beach and Colne Point nature reserve can be totalled into pre-surge (2011–13; three annual surveys) and post-surge (2014–16; three annual surveys) years. All data were square root transformed before analysis to correct for non-normality (Heath 1995). To determine whether *P. albopunctata* differed between the two sites, a Student's t-test was used to compare the mean number of bush-crickets per transect section (2 per site) pre-surge and post-surge.

To ascertain whether there was a preference for the back or fore dunes, the mean stridulation count per site for the back and fore dunes was compared using a Student's t-test for both the pre-surge and post-surge periods. The mean percentage cover per quadrat of shingle and *A. arenaria* for the back and fore dunes were compared using a Student's t-test (Heath 1995).

Fig. 1. Shingle deposition on the fore dunes. Photo credit Tim Gardiner.

Fig. 2. Shingle deposition on the back dunes. Photo credit Tim Gardiner.

Results

Stridulation counts did not differ significantly between the Colne Point nature reserve and naturists' beach either pre-surge (t = -1.78) or post-surge (t = -0.63) (Fig. 3). There was also no significant difference between the stridulation counts on fore and

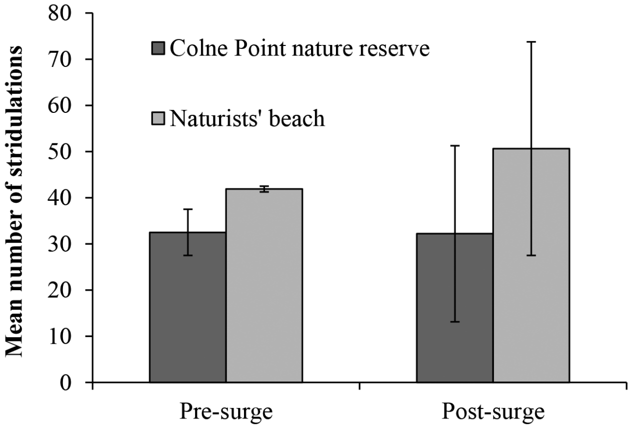

Fig. 3. The mean number of stridulating males recorded on the Colne Point nature reserve and St. Osyth naturists' beach pre- and post-surge.

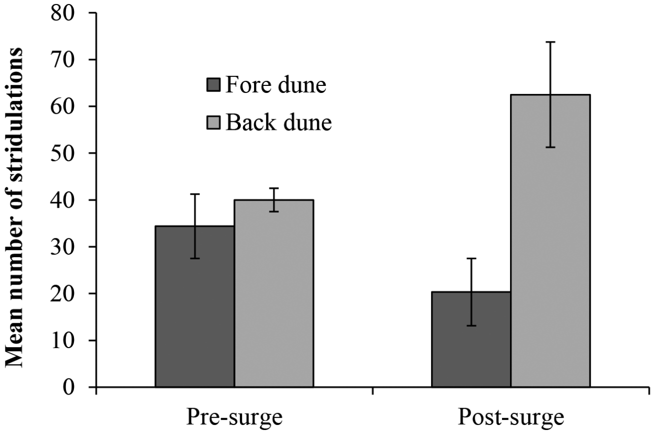

Fig. 4. The mean number of stridulating males recorded on the fore and back dunes pre- and post-surge.

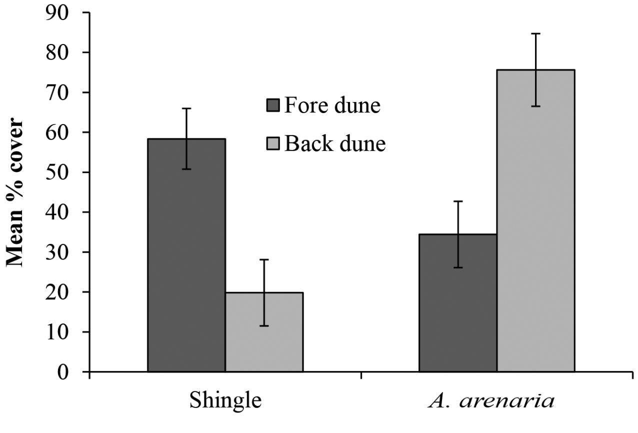

Fig. 5. Mean ground cover of shingle and *Ammophila arenaria* on the fore and back dunes post-surge.

back dunes pre-surge ($t = 0.79$). However, post-surge, stridulating males were much more frequent on the back than the fore dunes ($t = 3.19$, $p = 0.04$) (Fig. 4).

The mean cover of *A. arenaria* on the fore dunes was significantly lower ($t = -2.62$, df, $p = 0.01$) than on the back dunes in total contrast to the cover of shingle which was higher ($t = 4.23$, $p<0.0001$) on the fore dunes post-surge (Fig. 5).

Discussion

Given the requirement for 30000 adults for a bush-cricket population to be viable in heterogeneous environments without optimal surrounding habitat (Griebeler and Gottschalk 2000), highly isolated populations of *P. albopunctata* such as at Colne Point (nearest site at Shingle Street >35 km to north) may be extremely susceptible to extirpation due to catastrophic storm surge events. Once lost from Colne Point and the naturists' beach, its sole populations in the county of Essex, recolonization is extremely unlikely due to the surrounding sub-optimal habitats for this species (arable land and salt marsh).

The December 2013 storm surge levels (AOD) for the nearby Strood (mean 3.88 m, min/max 3.72–3.95 m) (Spencer et al. 2015) suggest that the back dunes will have been above the high water level (>4 m AOD) but not the fore dunes (<4 m AOD). The submergence of the fore dunes may have caused the mortality of *P. albopunctata* eggs laid in the grass, whereas those in the back dunes were probably unharmed, although wave splash may have led to localized inundation. Population abundance of *P. albopunctata* can vary by a factor of 10 between years (Gottschalk et al. 2003), so depending on the severity of the event, it's possible that the species may be dramatically reduced at its outlying coastal sites north of the Thames. On the fore dunes, abundance was reduced by 41% post-surge, while a 57.5% increase was noted on the back dunes (Fig. 4). This indicates that the storm surge did not have the directly devastating impact on the species we envisaged from submergence of its egg habitat. Of greater consequence appeared to be the alteration of dune habitat.

The generally poor growth of *A. arenaria* on the fore dunes of the naturists' beach in particular and significant shingle cover post-surge suggests a poorer environment for *P. albopunctata* due to the sparseness of grass cover and fringe habitat for stridulating males (Hein 2004). It appears that the species may have been affected by the smothering and die-back of its preferred *A. arenaria* tussock and bare sand habitat on the fore dunes and may have dispersed to the relatively unaffected back dunes which maintained fairly dense (>50% cover) *A. arenaria* growth post-surge, while still maintaining the required open ground for basking and oviposition.

The recovery of populations post-surge will have been influenced by the movements of individuals which hatched from eggs that survived the event. The dispersal of *P. albopunctata* (individuals can move 50–350 m) may be determined not only by suitable breeding habitat but by food resources and habitat-specific mortality risk (Hein et al. 2003). Therefore, the matrix of fore and back dunes should allow species to survive the worst effects of a storm surge, providing there is habitat which is not affected by movement of shingle or inundation. Given the speed with which *P. albopunctata* recolonized a fire site at Colne Point (individuals seen on burned ground just 10 months after the fire; Seago and Gardiner 2017), recolonization of the fore dunes may be fairly rapid. Studies on the resilience of other coastal Orthoptera (e.g., *P. vicentae*, Sutton et al. 2017) suggests adaptations to this changing and unstable environment.

Fortunately, *P. albopunctata* appears to be spreading at Colne Point, which may increase its resilience to further storm surges. New sightings of the insect since 2013 on the western spit, seaward slope of the sea wall embankment, and Jetty Ridge, suggest an expanding population. Colonization of the sea wall followed Environment Agency cutting of the seaward face over winter 2013/14 after a single male was heard in 2011 (Gardiner et al. 2015). It is believed that the cutting back of scrub and rank grass on the infrequently mown seaward slope created the patchy sward with exposed soil and tall fringe vegetation which the bush-cricket seems to require (Hein 2004). Breeding populations on the sea wall slopes will shelter the bush-cricket from the worst effects of future storm surges and allow it to spread along the flood defense corridor towards Jaywick to the east and Point Clear to the north.

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A new species and morphometric analysis of *Cladonotella* (Tetrigidae: Cladonotinae)

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Abstract

The genus *Cladonotella* (Tetrigidae: Cladonotinae) consists of four species of pygmy grasshoppers from Java and New Guinea. A new species of *Cladonotella* is described from Siargao Island, Philippines: *Cladonotella spinulosa* **sp. nov.** This represents the first record of *Cladonotella* in the Philippines. To quantify differences between species of *Cladonotella*, we used morphological characters to construct a neighbor-joining tree, and recovered our new species as distinct from congeners. To address the lack of natural history information on *Cladonotella*, we described habitat and other ecological observations made in Siargao Island on our new species.

Keywords

Orthoptera, Philippines, pygmy grasshoppers, Southeast Asia, taxonomy

Introduction

Tetrigidae, commonly known as the pygmy grasshoppers, is a speciose group of orthopterans typically characterized by a pronotum that extends to cover part or all of the abdomen (Hancock 1907a, Günther 1935, Blackith 1992). The tetrigids are distributed globally and previously studied species are known to have a specialized ecology (Tan et al. 2017a). However, classification and taxonomy of many groups of this family are still problematic, despite recent major revisionary works (e.g. Tumbrinck 2014, 2018, Storozhenko 2016, Muhammad et al. 2018). This can be attributed to the lack of clear-cut diagnoses.

Tumbrinck (2014) provided a comprehensive revision of the taxonomy of the subfamily Cladonotinae in Southeast Asia and its adjacent islands, and in New Guinea and Australia. The subfamily is comprised of 75 genera globally. There are 29 genera from Southeast Asia, many of which are still poorly known. One such genus is *Cladonotella* Hancock, 1909, characterized as robust and wingless with a high, elevated, and swollen pronotum between the shoulders, genicular and antegenicular teeth large, and legs covered with humps and lappets. Since the genus is currently known only from the islands of Java and New Guinea (Tumbrinck 2014) (Fig. 1), we can expect species to occur on islands between and/or near these two large islands.

Recent orthopteran surveys in Siargao Island in the Philippines revealed numerous species new to science and new locality records for other orthopterans (Tan et al. 2019a), including Agraeciini katydids and Mogoplistinae, Eneopterinae and Landrevinae crickets (see Tan et al. 2018, 2019b–d, Baroga-Barbecho et al. 2019). In this paper, we describe a new species of *Cladonotella* from the Philippines: *Cladonotella spinulosa* **sp. nov.** This also represents the first record of *Cladonotella* outside Java and New Guinea. This study aims to (1) clarify the taxonomy of *Cladonotella* with the use of morphometrics, (2) to describe new species of *Cladonotella* from Siargao Island, and (3) to perform minor cladistic analysis of the genus, specifically by constructing a neighbor-joining (NJ) tree.

Materials and methods

Collection of new species and species description.—Day and night surveys involving opportunistic collections were conducted by M.K. Tan, J.B. Baroga-Barbecho, and S.A. Yap in the forest-over limestone of Siargao Island (10–100 m.a.s.l.) in Mindanao from 14 to 18 October 2018. A single female was collected and preserved in absolute analytical-grade ethanol and later pinned and dry-preserved. One hind leg was kept in absolute analytic-grade ethanol for future molecular work. The holotype was deposited in the University of the Philippines Los Baños, Museum of Natural History (UPLBMNH), Philippines.

The specimen was photographed using a Canon EOS 500D digital SLR camera with a macro photo lens MP-E 65mm f/2.8 USM (1–5×). Canon Macro Ring Lite MR-14EX was used for lighting and flash. Image editing (including stacking images to produce a final image with high depth of field) was accomplished using Adobe Photoshop CC 2014. Measurements of dried-pinned

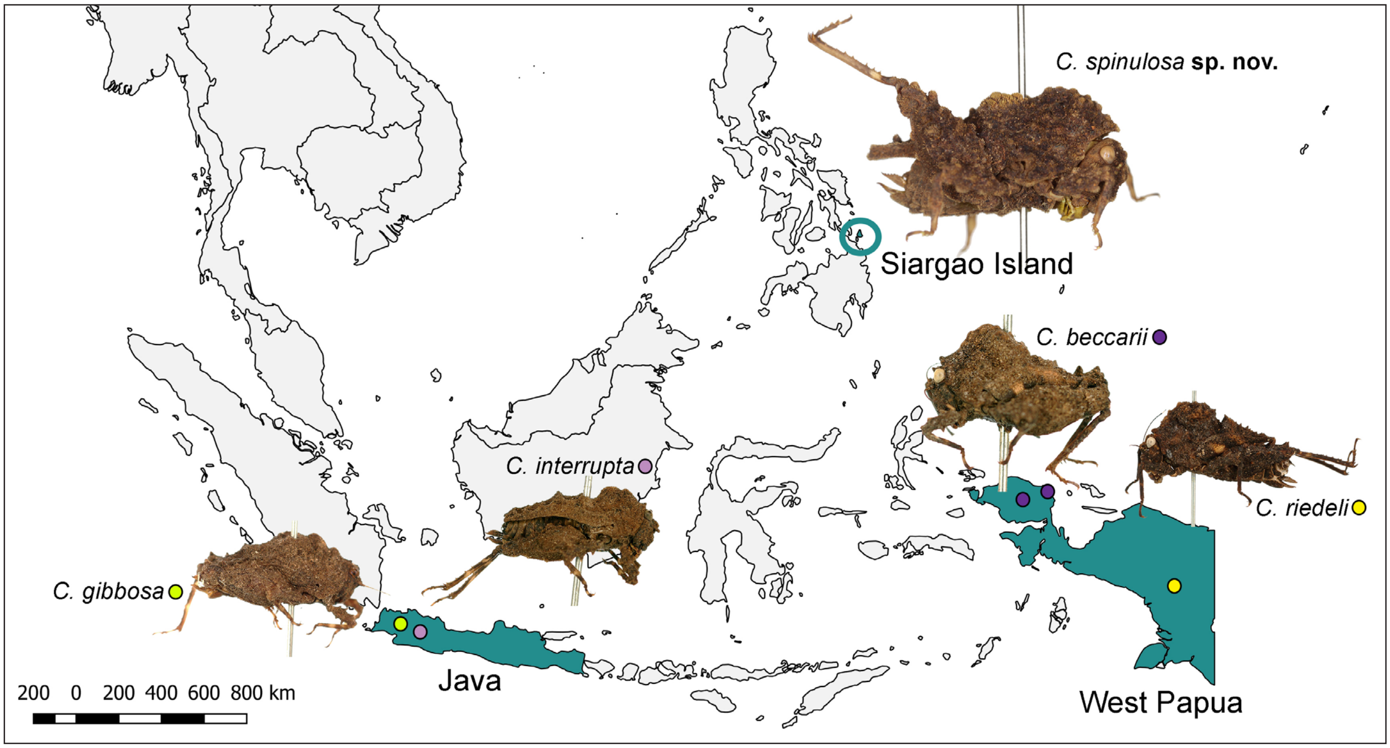

Fig. 1. Map of Southeast Asia. Colored regions indicate the current known distribution of *Cladonotella*. Images by J. Tumbrinck (except for *Cladonotella spinulosa* **sp. nov.**).

specimens were made using ImageJ, with calibration done using a vernier caliper. In the measurements, the following abbreviations are used (sensu Tumbrinck 2014, Tan and Artchawakom 2015):

BL	body length (pronotum + head)
VW	vertex width
EW	eye width
SW	scutellum width
posAG	distance between lower margin of eyes to center of antennal groove
PL	pronotum length
PLW	pronotum lobe width
PAW	width of anterior margin of pronotal disc
PPW	width of posterior margin of pronotal disc
PH	pronotum height (from lateral lobe)
AFL	forefemur length
AFW	forefemur width (maximum)
MFL	mesofemur length
MFW	mesofemur width (maximum)
PFL	posterior femur length
PFW	posterior femur width (maximum, not including lobes)
PTL	posterior tibia length
bPTL	posterior tarsal basal segment length
aPTL	posterior tarsal apical segment length
ODL	ovipositor dorsal valve length
OVL	ovipositor ventral valve length

Comparative material examined.—Cladonotella beccarii (Bolívar, 1898): INDONESIA • Holotype, ♀, West Papua, Ramoi [northwest Doberai Peninsula, Lowland], Feb. 1875, leg. O. Beccari, Museo Civico di Storia Naturale [MSNG] "Giacomo Doria", Genova, Italy; 1 ♀, West Papua, Manokwari, Gunung Meja, ca. 300 m, 23–24 Sep. 1990, leg. A. Riedel,Zoologische Staatssammlung, Munich [ZSM], Germany.

INDONESIA • 1 ♀, holotype of *Cladonotella gibbosa* (Haan, 1842): Java, Gunung Pantjar, 500 m, 11–14 December 1913, leg. M. A. Lieftinck, Staatliches Museum für Tierkunde, Dresden, Germany.

Cladonotella interrupta (Bolívar, 1898): INDONESIA • Holotype, ♀, Giava [Java], Tcibodas, Oct. 1874, leg. O. Beccari, MSNG.

Cladonotella riedeli Tumbrinck, 2014: INDONESIA • Holotype, ♀, West Papua, Jayawijaya Province, Samboka, upper Kolff River, ca. 200 m, 10–14 Oct. 1996, leg. A. Riedel, ZSM.

Morphometric analysis.—To quantify morphometric and morphological differences among congeners of *Cladonotella*, we performed a multivariate analysis of six specimens from five species (including the new species) using seven measurements (see Tumbrinck 2014) and four categorical characters (Table 1). The six specimens (also listed in the section Comparative material examined) include all the female specimens available in the literature (see Tumbrinck 2014, Cigliano et al. 2018). Since there were fewer specimens (owing to the rarity of materials) than characters, we performed a distance-based cluster analysis and built a neighbor-joining (NJ) tree for visualization of the morphometric differences. Since the characters are categorical and continuous with interval levels, Gower distance was used to obtain a pair-wise distance matrix between different individuals using the 'daisy' function in R package 'cluster' (Maechler et al. 2012). Equal weights were provided for the data matrix. The branch length provides an indication of the distance between two particular taxa: the longer the branch length, the greater the distance. The NJ tree was constructed using the 'bionj' function in R package 'ape' (Paradis et al. 2004). To check whether the tree is a good representation of

Table 1. Seven measurements (in mm, data from Tumbrinck 2014) and four categorical characters used for the construction of the neighbor-joining tree. See Materials and methods for the abbreviations for measurements. The remaining abbreviations used here: EP = pronotum elevation in frontal view (B = broadened dorsad, NB = not broadened dorsad); FH = frontal horn of pronotum (P = present, A = absent); PFD = posterior femur dorsal lobe (R = rounded, A = acute); PP = pronotal process (H = humped, B = banded).

Taxa	PL	PLW	PH	PFL	PFW	VW	EW	EP	FH	PFD	PP
C. beccarii	8.71	5.59	4.68	5.72	2.73	1.30	0.48	NB	P	R	H
C. beccarii	9.52	5.92	4.90	5.76	2.72	1.40	0.49	NB	P	R	H
C. gibbosa	9.39	5.44	3.95	5.60	2.40	1.15	0.45	NB	P	A	B
C. interrupta	7.67	4.68	2.86	4.81	1.95	0.90	0.44	NB	A	A	B
C. riedeli	10.67	7.12	6.24	6.64	2.80	1.54	0.61	B	P	A	H
C. spinulosa **sp. nov.**	10.19	4.87	3.84	5.29	2.56	1.72	0.37	NB	P	R	H

the distance matrix, we obtained the correlation between original pairwise distances against pairwise distances on the tree. To evaluate the nodal support on NJ trees, 10,000 standard bootstrap replications were performed using the 'boot.phylo' function in R package 'ape' (Paradis et al. 2004).

Results and discussion

Part I: Morphometric analysis

The NJ tree shows that *Cladonotella spinulosa* **sp. nov.** is distinct from other congeners (with 100% bootstrap nodal support) (Fig. 2). The NJ tree also recovered other species of the genus, supporting traditional taxonomy (Fig. 2). The clade separating *Cladonotella riedeli* Tumbrinck, 2014 of West Papua from *Cladonotella gibbosa* (Haan, 1842) of Java and *Cladonotella interrupta* (Bolívar, 1898) of Java, has nodal support <90%, probably indicating that these are the closest species. The correlation of original pairwise distances with pairwise distances on the tree had a $R^2 = 0.98$, indicating that the tree was a good representation of the distance matrix.

The NJ tree here is limited to only six specimens from five known species. Intra-specific variation could not be assessed here, since we only have one specimen for each species with the exception of *Cladonotella beccarii* (Bolívar, 1898). While our NJ tree demonstrates that the intra-specific variation of *C. beccarii* is distinctly smaller than inter-specific variations among *Cladonotella* species, more specimens should be included in the future. Based on our observations in Siargao Island and previous work on the genus, species of *Cladonotella* appear to be low in abundance in their natural habitats or, most probably, very cryptic to collectors. Currently, our NJ tree represents the only multivariate analysis for

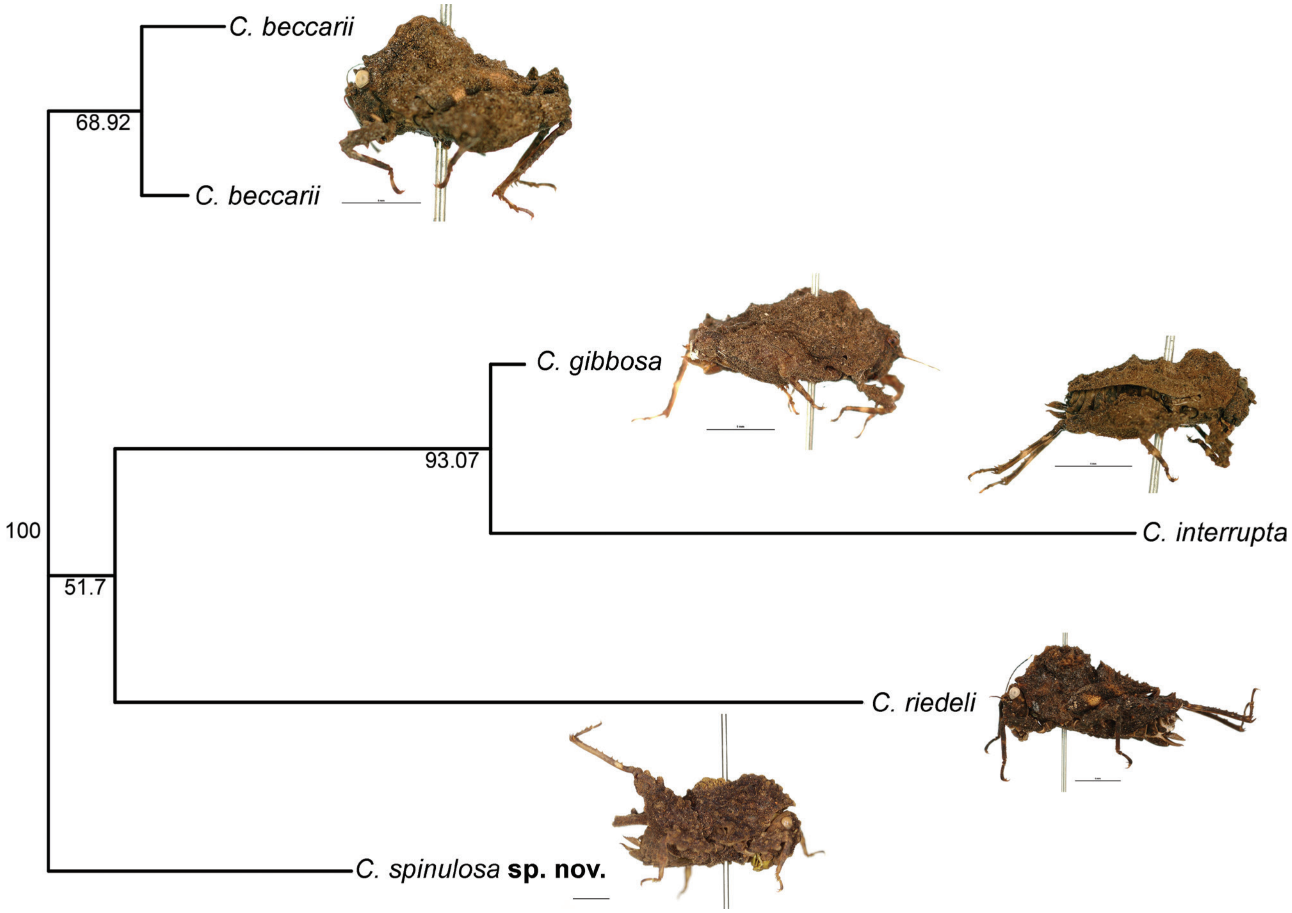

Fig. 2. A neighbor-joining tree of *Cladonotella* based on seven measurements (see Tumbrinck 2014) and four categorical characters. The value indicates nodal support based on 10,000 standard bootstrap replications. Images by J. Tumbrinck (except for *Cladonotella spinulosa* **sp. nov.**).

the genus. We have measured all known specimens, yet the limited data highlight that work on the taxonomy of *Cladonotella* and related genera is far from complete.

Furthermore, the NJ tree does not illustrate evolutionary relationships between the taxa. We have refrained from creating a morphological phylogeny until we can be more confident of the homologous morphological characters. Alternatively, a molecular phylogeny, which has not been performed yet, can also be useful to understand the evolution of *Cladonotella* and other genera of Cladonotinae. However, as many species are represented with only historic museum specimens, there is a need to collect new material from Southeast Asia so that DNA can be more easily extracted and molecular data can be obtained to reconstruct phylogenetic trees.

Although we only collected one female specimen (see Part II: New species description) and we could not examine intra-specific variation, this species is very different from all congeners based on discrete morphological evidence (see Comparison with congeners section) and the NJ tree topology. As such, we are confident that the female specimen represents a novel species.

Part II: New species description

Genus *Cladonotella* Hancock, 1909

Type species.—*Cladonotella gibbosa* (Haan, 1842) [original combination: *Acridium* (*Tetrix*) *gibbosum*]

Remarks.—This genus comprises four species from the islands of Java and Papua (Fig. 1). It is most similar to species from *Gestroana* Berg, 1900 (see Tumbrinck 2014) but also shows similarities with some species of *Potua* Bolívar, 1887 (see Tumbrinck 2018) and *Austrohancockia* Günther, 1938 (see Skejo and Bertner 2017). Tumbrinck (2014) provided a comprehensive description and diagnosis of this genus, as well as comparisons with similar genera and a key to species. The detailed comparison of the *Austrohancockia* group of genera is also given in Skejo and Bertner (2017).

Cladonotella spinulosa Tan et al., sp. nov.

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Figs 3, 4

Material examined.—PHILIPPINES • 1 ♀, holotype of *C. spinulosa*; Surigao del Norte, Siargao Island, Municipality of Del Carmen, Mahayahay, N9.86494, E126.03358, 82.9±7.9 m, 17 Oct. 2018, 1019 hours, on rocky path, leg. M. K. Tan and J. B. Baroga-Barbecho, UPLBMNH.

Diagnosis.—The new species differs from all known species of *Cladonotella* by the combination of the following characters: body very nodular and lobular, with dense spinules on these nodules and lobes; vertex very wide; broader scutellum width; anterior and posterior elevations, hump-shaped (in lateral view), rugose and nodulose; anterior margin of pronotum protruding anteriorly in the middle and extending beyond anterior margin of eyes; pronotum longer and extending beyond ovipositor.

Comparison with congeners.—Apart from the unique characters of this species (in the diagnosis), the new species also differs from *Cladonotella beccarii* (Bolívar, 1898) of Papua by a pronotum with two elevations (instead of one), posterior end of pronotum broader but with a narrower notch in the middle, and legs more lobular and nodular; from *Cladonotella gibbosa* (Haan, 1842) of Java by two distinct and clear-cut elevations on pronotum (instead of a few irregularly shaped elevations), stouter femora; from *Cladonotella interrupta* (Bolívar, 1898) of Java by posterior elevation of pronotum humped-shaped (instead of acute peaks, in lateral view); from *Cladonotella riedeli* Tumbrinck, 2014 of West Papua by lobes and nodules on body not spine-like, sulcation between anterior and posterior elevation of pronotum less deep and truncated, lateral lobe of pronotum not acute at apex.

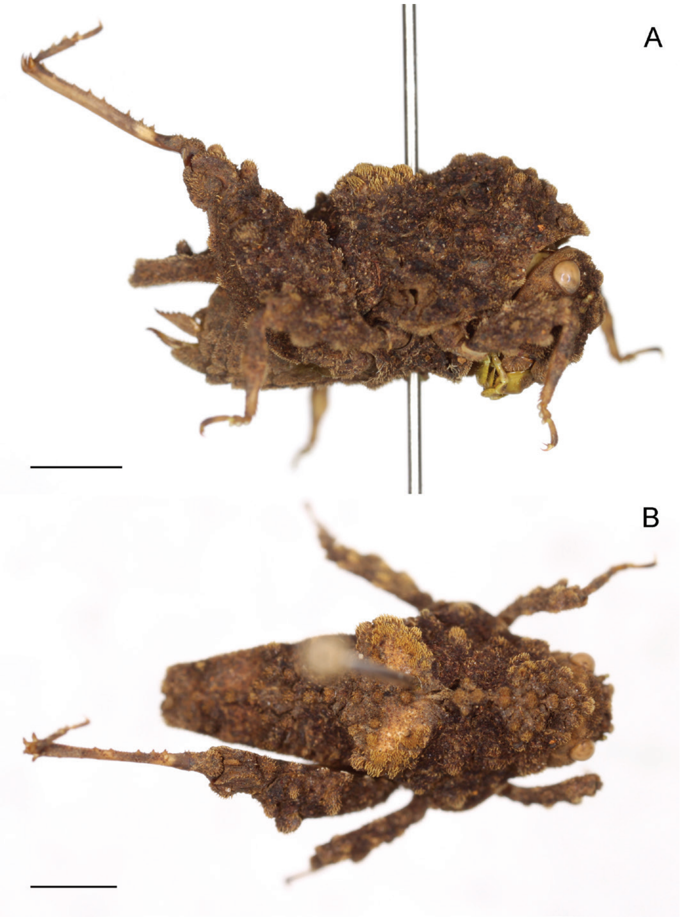

Fig. 3. Habitus of *Cladonotella spinulosa* **sp. nov.** holotype in **A.** Lateral and **B.** Dorsal views. Scale bars: 2 mm.

Holotype description.—Relatively small for the genus. Habitus as shown in Fig. 3. Brown, well camouflaged against forest floor.

Head: In frontal view: Antennal groove inserted 0.2 mm below lower margin of eyes (Fig. 4A). Fastigium convex in frontal view; curved on anterior border (Fig. 4A). Face very rugose and with fractures (Fig. 4A). Frontal costa stout. Bifurcation of the frontal costa in line with middle of eye (Fig. 4A). Facial carinae with spinules, curved in frontal view (Fig. 4A). Scutellum 1 mm wide (Fig. 4A). Compound eyes hemispheric, not exerted above vertex, pale colored, 0.5 times wider than tall. Lateral ocelli just above facial carinae and slightly above antennal groove (Fig. 4A). Margins of clypeal triangle with spinules (Fig. 4A). In dorsal view: apex of fastigium surpasses frontal margin of eyes, emarginated in the middle (Fig. 4B). Vertex very wide (Fig. 4B), 4.6 times wider than eye width. Lateral carinae of fastigium not distinct; median carina like a rounded horn (Fig. 4B). Lateral ocellus between apex of fastigium and antennal groove (Fig. 4B), located posterior of fas-

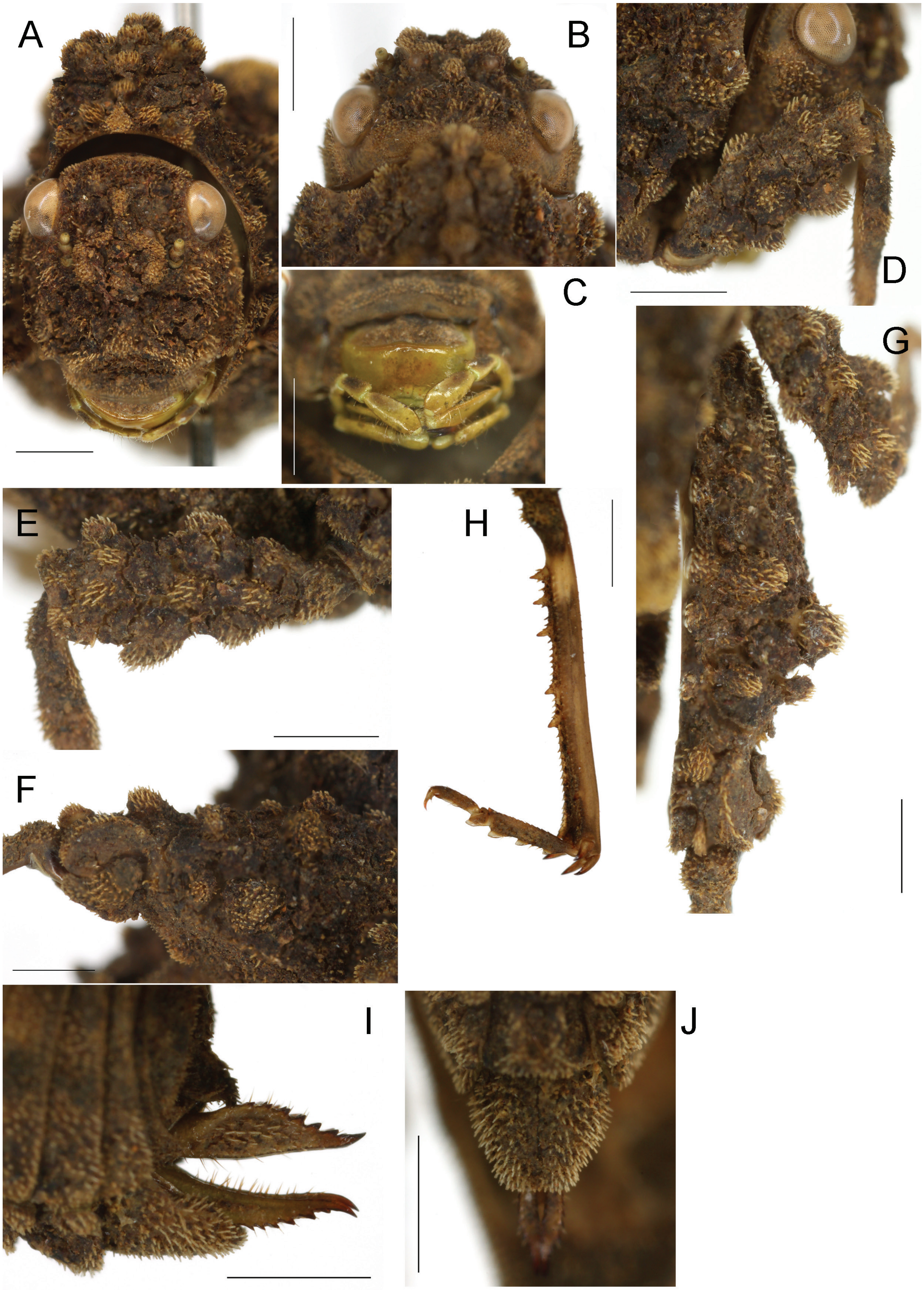

Fig. 4. *Cladonotella spinulosa* **sp. nov.** holotype: **A.** Face and anterior part of pronotum in frontal view; **B.** Head in dorsal view; **C.** Mouthparts in ventro-frontal view; **D.** Anterior and **E.** Middle femora in lateral views. Posterior femur in **F.** Lateral (posterior part) and **G.** Dorsal views; **H.** Posterior tibia and tarsus in lateral view; **I.** Abdominal apex in lateral view; **J.** Subgenital plate in ventral view. Scale bars: 1 mm.

cial carina. In lateral view: frontal costa arched and protruding in front of eyes. Gena with spinules. Mouthparts yellowish. Maxillary palps elongated, with apical (fifth) segment longest, following by third segment; subapical (fourth) segment shorter than both apical and third segments (Fig. 4C).

Pronotum: Pronotum, surpassing ovipositor, 2.1 times longer than wide (pronotal lateral lobe width). In lateral view: With anterior and posterior elevations, hump-shaped, rugose and nodulose (Fig. 3A); nodules covered with yellow spinules; sulcation between elevations wide but shallow (Fig. 3A). Anterior elevation 3.8 mm tall (measured from pronotal lateral lobe width to peak); with lateral margins straight (not tapering or broadening) dorsally in frontal view. Anterior margin of pronotal disc protruding anteriorly in the middle, surpassing anterior margin of eyes as a frontal horn (Fig. 3A). Infrascapular area broad (Fig. 3A). In dorsal view: median carina distinct throughout length of pronotum, with large nodules along the carina, nodules with yellow spinules (Fig. 3B). Second elevation of pronotal disc yellow around the peak. Lateral carinae with large nodules with yellow spinules. Interhumeral carina not distinct. Lateral lobe of pronotum with apex rounded (Fig. 3B). Apical end of pronotal disc truncated, narrowly and shallowly notched in the middle (Fig. 3B).

Legs: Coxae, trochanters, and femora with lobes and nodules, all with yellow spinules. Anterior and middle legs: anterior and middle femora stout (Fig. 4D, E). Anterior femur with three and two lobes along dorsal and ventral margins, three nodules in the external area (Fig. 4D); middle femur with three and two lobes along dorsal and ventral margins, four nodules in the external area (Fig. 4E). Anterior and middle tibiae with stout spinules. Posterior legs: posterior femur about 2.1 times longer than wide, about 1.2 times longer than posterior tibia; with five lobes along dorsal margin, apical one large; with two nodules on dorsal of external area, anterior one larger than posterior one; one large nodule in the middle of the external area; with two lobes along ventral margin, less protruding than dorsal ones (Fig. 4F, G). Knee of posterior femur with yellow spinules along margin (Fig. 4F); both genicular tooth and antegenicular tooth rounded with yellow spinules (Fig. 4F). Posterior tibia dark near the knee, following by a pale ring (Fig. 4H); with large dorsal spines, five on each lateral margin; with many yellow spinules between these dorsal large spines. Basal article of posterior tarsus 1.6 times longer than apical article; middle article very short (Fig. 4H).

Abdomen: Tergites and sternites typically with many spinules. Epiproct with spinules. Ovipositor with yellow spinules along lateral area, especially on dorsal valve; dorsal and ventral valves with hairs along dorsal and ventral margin, denser along dorsal margin (Fig. 4I). Dorsal valve with six dorsal spines, apex acute; ventral valve with five ventral spines, apex also acute but more hooked than dorsal apex; spines on valves increasing larger and robust apically (Fig. 4I). Apices of ovipositor valves red brown (Fig. 4I). Subgenital plate with many yellow spinules, denser laterally; about as long as wide, taper slightly after basal third, apex truncated (Fig. 4J).

Measurements.—(In mm). BL = 10.3, VW = 1.7, EW = 0.4, SW = 1.0, posAG = 0.2, PL = 10.2, PLW = 4.9, PAW = 1.8, PPW = 1.4, PH = 3.8, AFL = 2.1, AFW = 0.9, MFL = 2.5, MFW = 1.0, PFL = 5.3, PFW = 2.6, PTL = 4.4, bHTL = 0.9, aHTL = 0.6, ODL = 1.5, OVL = 1.4.

Fig. 5. Over-limestone forest in Siargao Island, the habitat of *Cladonotella spinulosa* **sp. nov.** The blue arrow indicates the location where the specimen was collected.

Habitats.—The holotype was found on a rocky path within hilly areas of over-limestone forest not too far from the coast (Fig. 5). The rocks on the path were probably limestone and were covered with wet leaf litter and dead branches. Limestone on the surface was also covered with wet mosses. This suggests that the pygmy grasshoppers probably prefer wet microhabitats, as is the case for other Southeast Asian tetrigids (Tan et al. 2017a). The forest on the hill (background of Fig. 5) is bordered by banana and coconut trees.

Etymology.—This species name refers to the many spinules all around the body and is Latin female gender adjective in nominative.

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Research Article Journal of Orthoptera Research 2019, 28(2): 137-143

Oecanthus mhatreae sp. nov. (Gryllidae: Oecanthinae): A new species of tree cricket from Mexico, with an irregular song pattern and unique chirp-like trill configuration

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Abstract

A new species of *Oecanthus* is described from Mexico. *Oecanthus mhatreae* **sp. nov.** occurs in central Mexico in the understory of tropical deciduous forest. *Oecanthus mhatreae* **sp. nov.** is currently known only from the Corregidora area of the Mexican state of Querétaro. The widened tegmina and chirp-like brief trills song are consistent with some members of the *rileyi* species group; however, this new species of tree cricket is different in several aspects. The chirp-like brief trills are generally irregularly spaced, it does not have the expected grouping of the chirp pulses, and the colors of buff, light olive green, or light brown are vastly different than the four known pale green species in the *rileyi* species group of the Western Hemisphere. Morphology, habitat, and song details of this new species, with the common name of Otomi tree cricket, are provided in this paper. Video can be viewed at www.oecanthinae.com.

Keywords

Cimatario, Corregidora, Natasha Mhatre, new species, Otomí, Querétaro, tropical deciduous forest

Introduction

According to the current listing on the Orthoptera Species File online (Cigliano et al. 2019), there are eight genera of Oecanthinae worldwide, but only two occur in Mexico – *Oecanthus* and *Neoxabea*. The genus *Oecanthus* is comprised of 72 species, with ten of them occurring in Mexico (Walker 1967, Cigliano et al. 2019). Of the 23 species of *Oecanthus* in North America, Central America, and the Carribbean, 19 are divided into four main groups: *nigricornis*, *niveus*, *rileyi*, and *varicornis* (Walker 1967, Walker and Collins 2010, Walker 2019a). These groups can be distinguished by characteristics including: calling song character (chirping vs. trilling and continuous vs. intermittent); pulse or chirp rate at given temperatures; regular vs. irregular pattern of pulses or chirps; coloration of the antennae, head, pronotum, and abdomen; antennal markings on the pedicel and scape; and tegminal width.

Oecanthines in the *varicornis* and *nigricornis* species groups have prolonged trilling songs (Walker 1963, 1967), while the *niveus* species group males sing in intermittent bursts of trilling (Walker 1962). In the Western Hemisphere, only the *rileyi* species group tree crickets have highly regular chirping songs (Walker and Collins 2010).

Four chirping species in the *rileyi* species group of *Oecanthus* are currently known to occur in North America, Central America, and the West Indies: *O. alexanderi* Walker, 2010; *O. allardi* Walker & Gurney, 1967; *O. fultoni* Walker, 1962; and *O. rileyi* Baker, 1905. These four species have a chirping song with a grouping of pulses within each chirp, a pale green color with a white abdomen, and a round or oval mark on the pedicel and scape (Walker and Collins 2010).

In 1965, RD Alexander recorded songs of eight unknown chirping oecanthines in Mexico. TJ Walker analyzed the recordings (Walker and Collins 2010) and shared with NC that three songs had no pulse groupings in each chirp, questioning whether they might possibly be a new species group or clade. The chirp-like brief trills of this new tree cricket's song will be referred to as a chirping song for this paper.

A 2019 photograph (Fig. 1) accompanied by a sound recording posted on iNaturalist.org (2019) by IMCG and BVAG from the central Mexican state of Querétaro, led to the investigation of this new species. NC recognized the calling song as a long-trained chirping pattern, but the light brown color with a milky buff pronotum and light brown head was markedly different than other chirping species in North America.

Materials and methods

Habitat.—Specimens were found on private property of IMCG and BVAG in Fraccionamiento Vista Real, Corregidora, Querétaro, Mexico. The property is located adjacent to the Parque Nacional El Cimatario. The property sits on the southern slope of Cerro de Cimatario, an inactive volcano. The primary vegetation of this reserve has been characterized as deciduous tropical forest, cactus shrub, reforestation, and pasture (García-García et al. 2008). After construction activities on the private property, the disturbed lands were recolonized by some ruderal species while other parts were planted with herbs and ornamentals.

BVAG monitored light intensity when the tree crickets were first heard singing over a five-day period. Light intensity measurements were used from online data in the Querétaro area (NWC 2019).

Collection methods.—Areas inhabited by tree crickets were determined both by manual searching and by locating actively singing males. Inhabited vegetation was then searched for adults of both sexes and nymphs. Specimens were collected in hand-held plastic containers. Photographs by BVAG, and sound recordings and specimen photographs by IMCG, were taken January-March 2019.

Measurements were made after the specimens were euthanized by freezing. Specimens were preserved in 70% alcohol until delivery to permanent depositories. Photographs were taken using a Samsung tablet and a Nikon D90 camera with a +4 Macro Close Up Neewer lens. Photographs, video, and sound recordings will be made available for viewing at Cigliano et al. (2019), iNaturalist (2019), and http://www.oecanthinae.com. The key from Walker (1967) was used for verifying the genus. Specimens were examined for the presence/absence of spines on the hind tibiae.

Acoustics.—Calling songs were recorded using recording app Grabadora Amazing MP3 with a Samsung tablet, with the tablet held as close to the singing tree cricket as possible. AVS4YOU Video Converter Software version 11.0 was used to convert MP4 to AVI. DoReMiSoft AVI to WAV Converter software was used to convert AVI files to WAV format. AVS4YOU Audio Editor Software version 6.1.2.375 and Raven Lite 2.0 were used to analyze the WAV sound tracks to make images of their waveforms and sound spectrums to measure the song frequency. Temperatures of the spots where tree crickets were singing were measured using a Taylor Sybron 5460 hand-held Mercury maximum minimum thermometer.

Morphological measurements.—The total body length refers to the midline length from the fastigium to the apex of the subgenital plate, not including antennae, tegmina, limbs, or cerci. The tegminal width was measured at the widest section, while resting atop the abdomen of the male. Pronotal length was measured along the medial line of the pronotum. The female's ovipositor was measured from its base at the distal abdomen to the tip. Photographs and measurements of the ovipositor, cerci, and metanotal gland, as well as counts of the stridulatory teeth, were made with the aid of a Jiusion Digital Microscope Model USB, magnification 40× to 1000×.

Results

Oecanthus mhatreae Collins & Coronado, sp. nov.

http://zoobank.org/A2D3D82F-C1A6-43BD-B795-FFFB2FA652E2

Etymology.—Specific epithet in honor of Natasha Mhatre, who has worked extensively with Oecanthinae and has published many articles focusing on acoustic communication. The pronunciation of mhatreae is MAT-ray-ee [MAT] [rā] [-ee]. The common name, Otomi tree cricket, is after the Otomí, an indigenous people of Mexico inhabiting the central Mexican Plateau region.

Type verification.—The genus *Oecanthus* was determined by the presence of spines on the hind tibiae.

Type material.—MEXICO, holotype ♂, alcohol vial, Querétaro, Corregidora, Fraccionamiento Vista Real, 20°52'20"N, 100°38'80"W; elevation ca 2130 m, understory of tropical deciduous forest, I. Coronado leg., 24 Jan 2019, deposited at Universidad Nacional Autónoma de Mexico (UNAM), Mexico City.

Paratypes: 1 ♀ and 1 ♂, 23–24 January 2019, and 1 ♀ and 1 ♂ 13 February 2019, same location as holotype, deposited at UNAM.

Male holotype description and measurements.—(in mm). Light olive green wings with dark staining along some veins. Pronotum milky buff color. Grayish tan head with four lighter streaks running to pronotum, and light pink patch near scapes. Pedicel and scape pale green. Antennae pale greenish white. Eye color purplish. Palpi translucent tan. Oval black mark on each pedicel and scape. Abdomen light olive green with scattered darker blotches. Femurs translucent olive green; tibiae and tarsi light olive green. Body length 13.5; tegminal length 13.7; tegminal width 6.8; pronotal length 2.2; distal pronotal width 2.4; hind femur length 10; cerci 4.9. The stridulatory file length is 1.5 mm, and the stridulatory teeth count is 36.

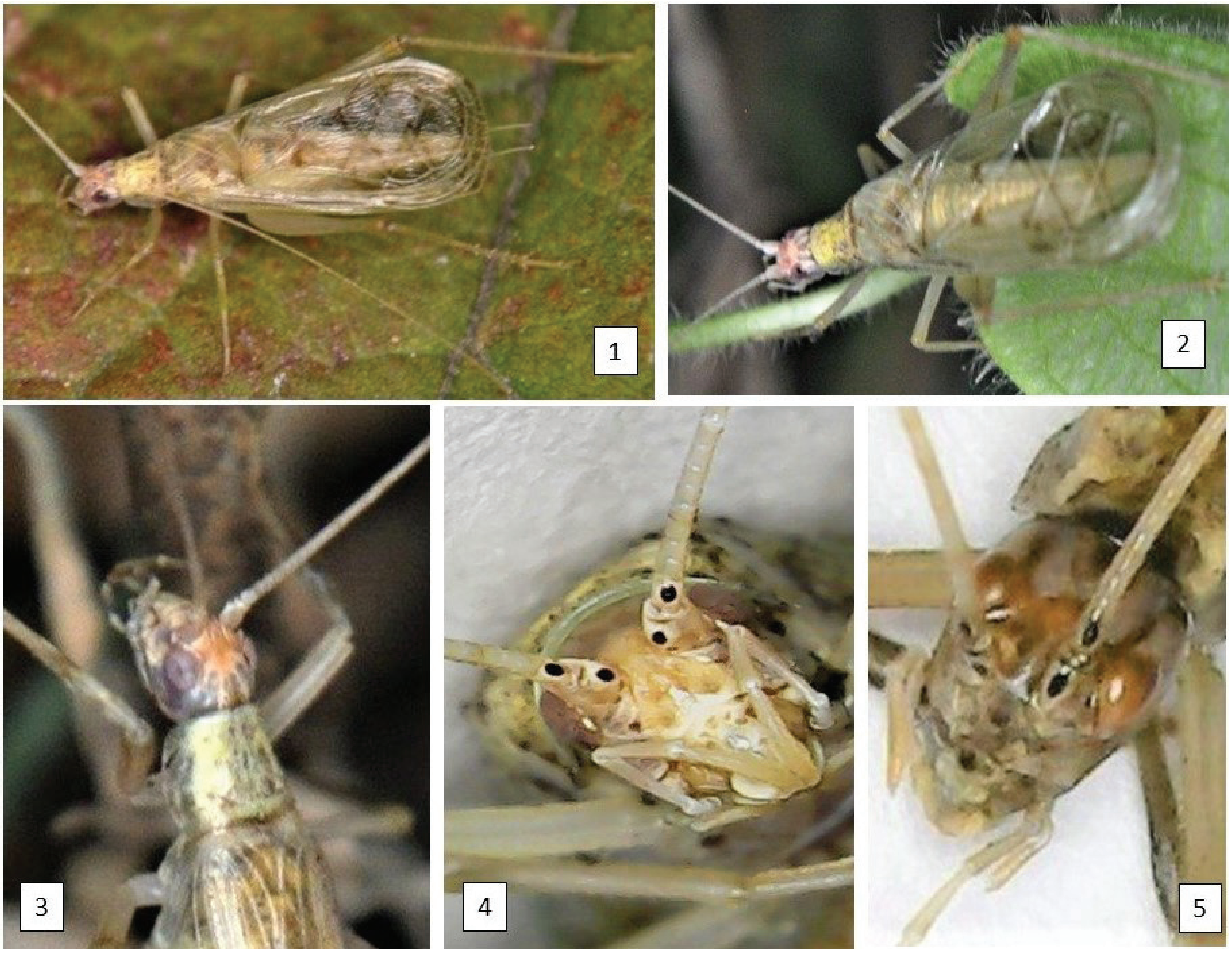
Characters.—Overall color of both sexes can range from light brown (Fig. 1) to light olive green (Fig. 2). Tegmina with dark staining along veins. Head grayish or brownish with small patch ranging from pink to peach. All individuals have four lighter colored vertical streaks on the distal portion of the top of the head extending to under the pronotal shield (Fig. 3). The light brown individuals are not believed to be a true brown form of this species as the pronotum is equally buff colored to the pronotum on the olive green individuals. The patch of color on the head is located even with and just behind the scape. Pedicel and scape colors vary from whitish to greenish to brownish. Ventral surface of pedicel and scape each with one oval black mark (Figs 4, 5). The black mark is situated on a whitish field; however, dead specimens darken and the white may not be readily visible.

Antennae filaments translucent greyish white or tan. Eye color purple to brown. Palpi translucent tan. Pronotum has a milky or creamy buff or light olive color (Figs 1–3, 6). Tympanal membrane on fore tibiae whitish. Ventral abdomen with scattered, slightly darker blotches and speckles; color varies from light olive, buff or tan (Fig. 7). Tarsi light olive or light brown, tibiae olive or tan, femora translucent light olive green or tan. Some individuals with whitish area at ventral femoral-tibial joints. Cerci straight and pale, extending beyond the distal edge of the tegmina. Hind wings do not extend beyond distal edge of tegmina. The metanotal gland photo (Fig. 8) was taken of a dead specimen, and this species darkens from freezing euthanasia. Right tegmen stridulatory file as in Fig. 9 with 32–36 teeth; file length 1.4–1.7 mm.

Paratype males measurements: Body length 12.4–13.0; wing length 11.0–12.0; wing width 5.8–6.9; pronotal length 1.5–2.8; distal pronotal width 2.0; hind femur length 7.0–8.2; cerci length 4.3–5.0.

Paratype female measurements: Female with matching antennal markings and coloring as males. Body length 12.5–12.8; wing length 11.5–12.0; wing width 3.0–3.1; pronotal length 1.9–2.5; distal pronotal width 1.8–2.0; hind femur length 7.5–8.8; cerci length 6.5–6.6; ovipositor length 6.25–6.5. Ovipositor extends slightly beyond the tips of the cerci (Fig. 10).

Nymphs as in photos of 3rd–5th instars (Figs 11–13).



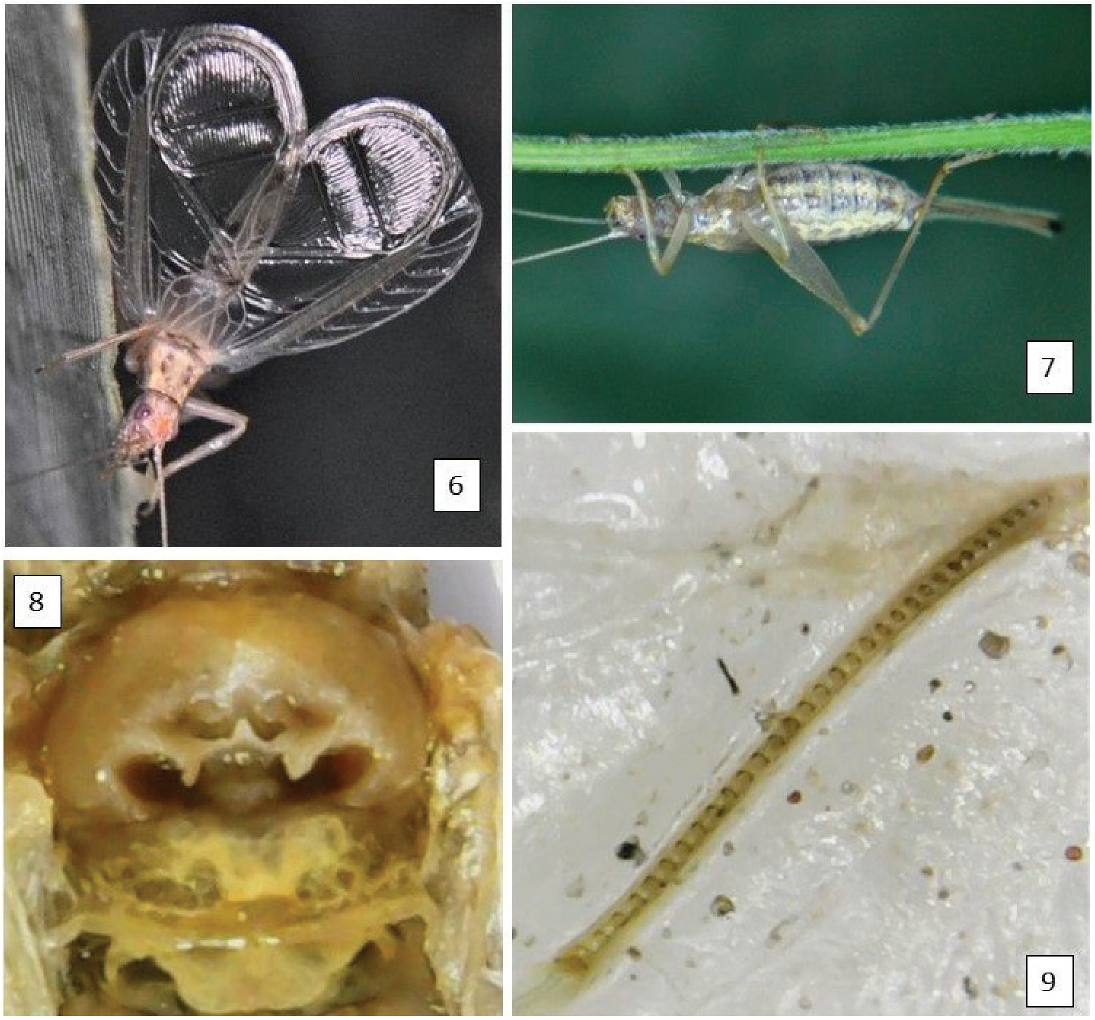
Figs 1–5. *Oecanthus mhatreae* **sp. nov.**: **1.** Light brown male. **2.** Light olive tone male. **3.** Adult female head and pronotum. **4.** Antennal markings on holotype male. **5.** Antennal markings on paratype female.

Habitat.—Tree crickets were found on ten plant species: *Anisacanthus pumilis* (F. Dietr.) Nees; *Cnidoscolus multilobus* (Pax) I. M. Johnston; *Colubrina triflora* Brogn. Ex Sweet; *Croton ciliatoglandulifer* Ortega; *Dasilyrion parryanum* Trel; *Iresine cassiniliformis* S. Schauer; *Justicia candicans* Nees L D Benson; *Ruta graveolens* L; *Senecio salignus* DC.; and *Thunbergia alata* Bojer ex Sims (Martínez and Sandoval 2017). Of these plants, *R. graveolens*, *C. multilobus*, and *T. alata* are introduced species. The only plants Otomi tree crickets were witnessed as actively feeding upon were *C. ciliatoglandulifer*, a native plant, and on *C. multilobus* and *T. alata*, which, unlike the native vegetation, are evergreen plants (Calderón de Rzedowski and Rzedowski 2001).

Climate.—According to records on the National Water Commission website, rainfall totals for Querétaro were (listed in mm from January 2018 through March 2019): 9.2, 10.0, 2.8, 24.1, 39.5, 161.8, 31.4, 71.7, 110.2, 58.6, 31.1, 3.8, 7.5, 2.3, and 4.6. The lowest temperatures occurred in January 2018 (5.3 °C in 2018 and 8.5 °C in 2019). The warmest temperatures from January-March 2019 were 24.7 °C, 28.1 °C, and 29.6 °C.

Behavior.—Light intensity readings ranged from less than 5 W/m^2 to 12 W/m^2 at the time males began singing. Song monitoring in January and February revealed Otomi tree crickets began singing from one minute before to eleven minutes after sunset and were singing within 10 minutes of sunset in temperatures of 17–18 °C and past midnight in temperatures less than 12 °C. The holotype male and one paratype female were video recorded mating while in captivity. A video clip can be viewed at www.oecanthinae.com.

Calling song.—The song pattern and chirp configuration of Otomi tree cricket were instrumental in diagnosing this new Mexican oecanthine. Waveform analysis showed that each chirp was comprised of a long string of pulses with no groupings (Figs 14–16). The recordings taken in the field and in captivity by IMCG were at temperatures of 14 °C–19 °C. The carrier frequency of the calling song at 17 °C was slightly above 2.6 kHz (Fig. 17). One recording revealed the intermittent long chirp song of interest with a faster chirping species in the background (Fig. 18). The faster chirping was 3–4 times faster than the long chirping of this new species, affirming the slow rate of the target species while the highly regu-



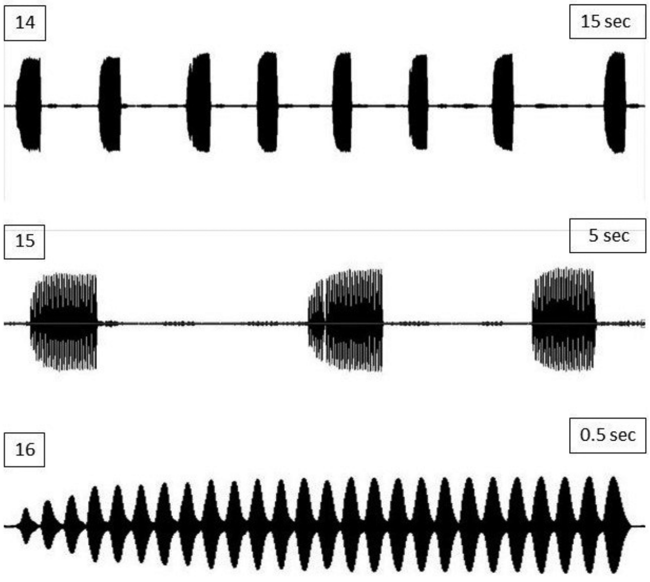
Figs 6–9. *Oecanthus mhatreae* **sp. nov.**: **6.** Singing male showing buffy pronotum (on native plant *Dasilyrion parryanum* Trel.). **7.** Adult female showing blotching on ventral abdomen. **8.** Metanotal gland. **9.** Stridulatory file and teeth.

Fig. 10. Adult female coloring and ovipositor length (on non-native *Ruta graveolens* L.).

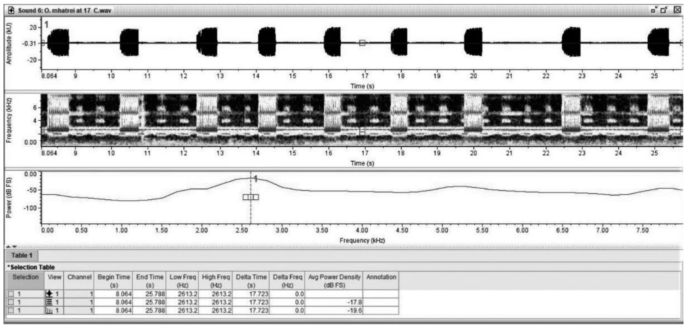
Figs 11–13. *Oecanthus mhatreae* **sp. nov.**: **11.** Abdomen pattern of 3rd instar nymph. **12.** Female 4th or 5th instar nymph. **13.** Male 4th or 5th instar nymph.

lar spacing of the background singer affirmed the irregular pattern of Otomi tree cricket. The irregular chirping pattern and the ungrouped chirp configuration of this new species were compared to the patterns and configurations of four other chirping species, two intermittent trilling species, and one continuous trilling species (Fig. 19). The four chirping species in the *rileyi* species group display grouping of their pulses.

Oecanthus varicornis, from the *varicornis* species group, has continuous trilling with runs of pulses over several seconds, while *O. mhatreae* **sp. nov.** chirps never exceed 0.7 second. Of the three



Figs 14–16. Waveforms of the calling song of *O. mhatreae* **sp. nov.** at 17 °C: **14.** Chirping for 15 seconds. **15.** Three chirps. **16.** A single chirp (0.5 sec duration) with 26 ungrouped pulses.



*Selection Table

Selection	View	Channel	Begin Time (s)	End Time (s)	Low Freq (Hz)	High Freq (Hz)	Delta Time (s)	Delta Freq (Hz)	Avg Power Density (dB FS)	Annotation
1	1	1	8.064	25.788	2613.2	2613.2	17.723	0.0		
1	1	1	8.064	25.788	2613.2	2613.2	17.723	0.0	-17.8	
1	1	1	8.064	25.788	2613.2	2613.2	17.723	0.0	-19.6	

Fig. 17. Audio recording of the calling song of *O. mhatreae* **sp. nov.** at 17 °C showing a carrier frequency of slightly above 2.6 kHz.

intermittent bursts of trilling species, *O. niveus* has a J-shaped mark on the scape (Walker 1962). The second species, *O. exclamationis*, has markings on the pedicel and scape that resemble an inverted exclamation mark (Fulton 1915). The third intermittent bursts of trilling species, *O. leptogrammus*, does have an irregular pattern similar to *O. mhatreae* **sp. nov.**; however, the coloring and antennal markings are markedly different for these two species. *Oecanthus leptogrammus* is very pale green (Collins et al. 2014) and has a thin black line on each pedicel and scape (Walker 1962).

At all temperatures, the chirping pattern of Otomi tree cricket was irregular. This sporadic rate and pattern were unlike any of the other known chirping species in North America. Fig. 20 shows the irregular rate at a variety of temperatures and includes a sample of the early evening warm up song heard most evenings. Since Otomi tree cricket has an irregular chirping pattern, a trend line graph cannot reliably be used for comparison with chirpers with regular patterns. The chirp rate at recorded temperatures was plotted for comparison to the other known songs (Walker 2019b, Cornell Lab 2019) of North American chirping species (Fig. 21, Table 1). The graph displays the general niche that each of these five species occupy.

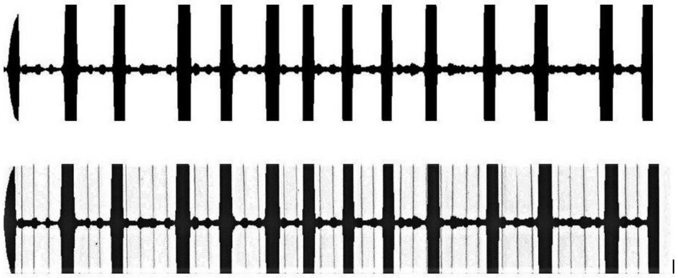


Fig. 18. Calling song recording of *O. mhatreae* **sp. nov.** at 17 °C. The clip was amplified to highlight the background song. This 30-sec clip shows the irregularly spaced *O. mhatreae* **sp. nov.** chirps at a rate of 28 pulses per minute with a yet to be determined chirping species in the background with a highly regular pattern at a rate of 100 chirps per minute.

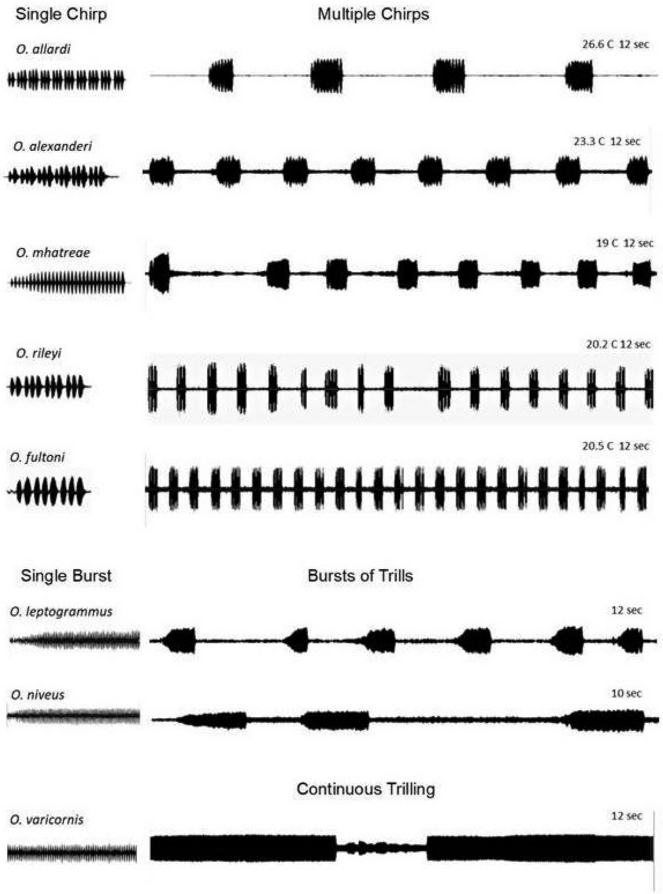


Fig. 19. Comparisons of song patterns, single chirps and single bursts of trilling. *O. mhatreae* **sp. nov.** recorded in Querétaro. All remaining recordings in library of NC. *Oecanthus leptogrammus* and *O. allardi* recorded in Nicaragua; remaining species recorded in the United States.

Diagnosis.—Characters that separate *O. mhatreae* **sp. nov.** from other chirping species of tree crickets in the *rileyi* species group include: 1) an overall darker coloring than the usual very pale green; 2) dark speckles and blotches on the abdomen; 3) dark staining along veins of the tegmina; 4) milky buff or olive color of the pro-

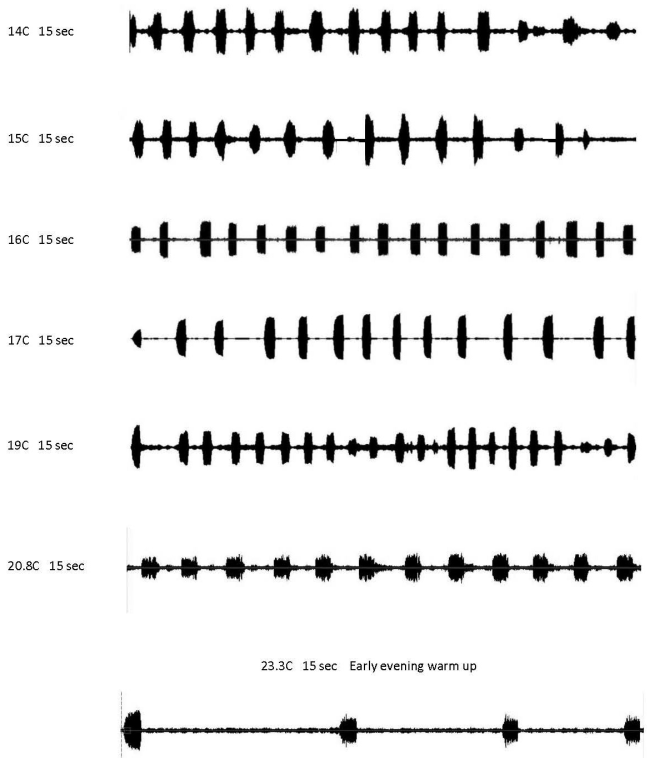


Fig. 20. *Oecanthus mhatreae* **sp. nov.** males chirping in various temperatures.

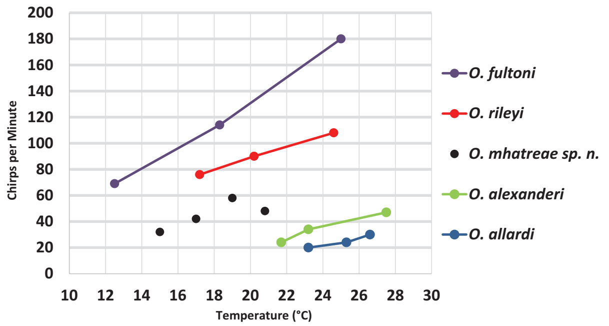


Fig. 21. Graph comparing chirps per minute at given temperatures.

Table 1. Data and sources of chirps per minute at recorded temperatures of *O. mhatreae* **sp. nov.** and other chirping species of *Oecanthus* in North America. Source recordings: SINA – Singing Insects of North America; ML – Macaulay Library; recordings in library of NC; and new recordings for this paper from Querétaro.

Species	Temp C	Ch/min	Source
O. fultoni	12.5	69	SINA 585slo
	18.3	114	SINA 585slj
	25	180	ML 124884
O. rileyi	17.2	76	ML 124705
	20.2	90	ML 124791
	24.6	108	SINA 588sl
O. mhatreae **sp. nov.**	15	32	IC and BG Querétaro
	17	42	
	19	58	
	20.8	48	
O. alexanderi	21.7	24	NC Texas USA
	23.2	34	
	27.5	47	
O. allardi	23.2	20	ML 114499
	25.3	24	ML 125543
	26.6	30	NC Nicaragua

notum; 5) no grouping of the pulses in individual chirps; and 6) an irregular chirping pattern.

Fourteen species of *Oecanthus* found in the Western Hemisphere are not associated with an established species group and not all have recordings of songs available online. Otomi tree cricket's stridulatory teeth count, antennal markings, and song type were compared to those fourteen species, but no matches were found (Table 2).

Discussion

We describe this new species of *Oecanthus* but cannot place it in one of the species groups for Western Hemisphere tree crickets. Although by ear this new species sounds similar to *O. alexanderi* and *O. allardi*, it can be distinguished by the irregular chirping pattern and by the analysis of the configuration of each chirp due to the absence of grouping of pulses. Both *O. alexanderi* and *O. allardi* group the pulses within a single chirp into a 2, 3, 3, 3…pattern (Walker and Collins 2010). *Oecanthus mhatreae* **sp. nov.**, however, has 17–30 pulses in a chirp with no grouping of the pulses.

Table 2. Comparison of characters for 14 other species of *Oecanthus* found south of the United States that are not currently placed in a species group. Gray fields indicate the characters that do not match those of Otomi tree cricket.

Oecanthus Species	Stridulatory Teeth Total	Pedicel Mark	Scape Mark	Song Type	Source Providing Details
mhatreae **sp. nov.**	**32–36**	**Oval**	**Oval**	**Irregular pattern; long chirps**	
comma	44	Comma	Teardrop		Walker 1967
immaculatus	24	No marking	No marking		Bruner 1906; Walker 1967
jamaicensis	27–29	Post	Post	Continuous trilling	Walker 1969
lineolatus	48	Line	Line	Regular trilling chirps	Saussure et al. 1897; Walker 1967
major	34	No marking	Line		Walker 1967
minutus	37–45	No marking	Line or no marking		Walker 1967
nanus	51–54	No marking	No marking		Walker 1967
pallidus	32	Line	Line	Long regular chirps	Zefa et al. 2012
peruvianus	35	No marking	No marking		Walker 1967
pictipes	50–53	L-shape and dot	Line and dot		Rehn 1917; Walker 1967
pictus	47	L-shape	Thick vertical mark	Continuous trilling	Milach et al. 2015
prolatus	28	Oval	Thin post		Walker 1967
tenuis	44	Bowed line	Line		Walker 1967
valensis	38–46	Line	Line		Milach et al. 2016

Since the songs of *O. mhatreae* **sp. nov.** and *O. leptogrammus* are similar in chirp-like trill durations and both species occur in Mexico, care should be taken when trying to identify these species by sound. Although there are limited recordings of *O. leptogrammus*, it has a raspy sound, whereas *O. mhatreae* **sp. nov.** has a flute-like sound. It would be interesting to compare the song of *O. mhatreae* **sp. nov.** with that of *O. comma*. The song of *O. comma* is currently unknown. Of the remaining 14 species of *Oecanthus* not associated with a species group, *O. comma* seems the most likely to have the potential of being grouped with *O. mhatreae* **sp. nov.**, as the antennal markings of *O. comma* are not linear, and it was described as occurring in Mexico.

While Otomi tree cricket is currently known only from Querétaro, Mexico, more investigation is needed to understand its full geographic range, elevations of occurrence, and types of habitat. More exploration is needed throughout Mexico for other undescribed species heard by RD Alexander over 50 years ago.

We encourage others to post submissions of observations to iNaturalist, as we believe there are other new species waiting to be discovered by specialists reviewing photographs and/or sound recordings on this worldwide public website. There are many non-entomologists and citizen scientists eager to provide data for investigations of insects in their locations.

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We thank the California Academy of Sciences for maintaining the website iNaturalist.org, which allows scientists and the general public from around the world to post photographs and sound recordings of insects. We are grateful to Edison Zefa and Klaus-Gerhard Heller for valuable input to the manuscript. We are appreciative of the wealth of knowledge generously shared by Thomas J. Walker. Dr Walker has long been a proponent of open access of articles, which was of immense assistance in our investigation of this new species. NC appreciates the support Thomas J. Walker and Natasha Mhatre give to citizen scientists. We extend thanks to members of the Tree Cricket Appreciation Group and The Orthopterists' Society Group on Facebook, for offering suggestions on verbiage, colors and song tones. The Orthopterists' Society supported the cost of publishing this work.

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Morphology, development, and reproduction of *Eyprepocnemis plorans ibandana* (Orthoptera: Acrididae) in South Cameroon rainforests

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Abstract

Eyprepocnemis plorans ibandana is a very common grasshopper species in open environments and agricultural systems of tropical Africa. It is a pest that significantly benefits from forest degradation in southern Cameroon, hence the need to study the bioecology of this subspecies. We studied the reproduction as well as the morphological characteristics and development times of the post-embryonic instars of *E. p. ibandana*. Sixty-one adult pairs were obtained from sixth instar nymphs caught in grassy vegetation in the Nkolbisson area (Yaoundé) and bred in the laboratory. After hatching, the first instar nymphs were individually placed in cages and fed every two days using fresh leaves of *Manihot esculenta*. The postembryonic development of *E. p. ibandana* took six instars in the male and six to seven instars in the female. Mean nymphal development took 79.16 ± 0.51 days in males, 89.93 ± 0.58 days in 6 instar females and 94.96 ± 1.22 days in 7 instar females. The survival rate of the first instar was low (53%). However, from the second instar on the survival rate was very high (> 87%). Sexual dimorphism is distinct in adults, fifth and sixth nymphal instars. Adults of *E. p. ibandana* took on average 32.57 ± 3.88 days to start mating, and mating lasted 2.12 h on average (1–3 h). Oviposition took place on average 52.03 ± 5 days after first mating; each female deposited one to eleven oothecae with an average of 34.93 ± 2.37 eggs per ootheca. Our study provides important information for the control of this subspecies in southern Cameroon.

Keywords

Cameroon, ecology, grasshopper pests, nymphal development

Introduction

Knowledge of an organism's life cycle is a prerequisite for any management, control, or conservation action (see Peveling 2001, Zeug et al. 2012). This is particularly the case for locusts and grasshoppers, some of which are endangered species (Samways et al. 1995, Samways 1997, Samways and Lockwood 1998), while other species are important pests (FAO 2010, 2018, Zhang et al. 2019). For the most important pest species, their life cycle is well known (see Lecoq 1978, Duranton et al. 1982, Gangwere et al. 1997), but some remain largely unstudied despite their economic importance. This is the case for *Eyprepocnemis plorans* (Charpentier, 1825), which has been the subject of only rare studies (Jago 1963, Lecoq 1980, Hernández and Presa 1984, Olmo-Vidal 1990, Schmidt et al. 1996).

Eyprepocnemis plorans — also called Clover or Berseem grasshopper — is widely distributed in Africa, southern Europe, and southwestern Asia, and consists of four geographic subspecies (Jago 1963, Dirsh 1965, Hernández and Presa 1984, Olmo-Vidal 1990, Schmidt et al. 1996, Cigliano et al. 2018). These include *E. p. plorans* (Charpentier, 1825), which occurs in the Mediterranean and western Asia, *E. p. ornatipes* (Walker, 1870), which is found in the Sahelian zone to northern Kenya and southern Arabia, *E. p. meridionalis* (Uvarov, 1921), which is distributed in east and southeastern Africa and *E. p. ibandana* Giglio-Tos, 1907, which occurs in west and central Africa (Dirsh 1965). The latter subspecies is found in forest and pre-forest areas and has been reported from Benin, Côte d'Ivoire, Ghana, Guinea, Liberia, Mali, Nigeria, Togo, South Sudan, Congo, Angola, Uganda, and Cameroon (Mestre and Chiffaud 2006). *E. plorans* is usually regarded as a minor pest, but damage can occasionally be significant, and this species is regarded as an important polyphagous agricultural pest in some countries. This is the case in Egypt, especially in oases and along the Nile (Nakhla 1957, 1976, COPR 1982). In eastern Algeria, this species consumes potatoes, beans, beets, radishes, and spinach (Harrat and Moussi 2007). It is also present on farmland of southern Cameroon (Mestre and Chiffaud 2006), where it damages crops such as cassava, potato, and beans.

Descamps (1953) studied some aspects of the biology of the species in the Sahelian zone of Cameroon, where the subspecies *E. p. ornatipes* is present (Dirsh 1958). Lecoq (1980) studied the life cycle of *E. p. ornatipes* in the Sudanese zone of West Africa and identified two generations per year and a period of quiescence at the imaginal stage during the dry season. In forest regions where *E. p. ibandana* occurs, the life cycle of the species has not yet been investigated. This is unfortunate not only because of the species' increasing ravaging activities facilitated by forest degradation in southern Cameroon, but also because of data on the life cycles of different subspecies across various eco-geographical regions in the world (Jago 1963, Lecoq 1980, Hernández and Presa 1984, Olmo-Vidal 1990, Schmidt et al. 1996).

In the Sahelian zone, this species is found throughout the year as both nymphs and adults (Lecoq 1988). In Spain, there is only one generation per year, from July to March (Hernández and Presa 1984). Schmidt et al. (1996) bred up to four generations per year in the laboratory of *E. p. plorans* from Sardinia. They observed six post-embryonic nymphal instars in the male and seven instars in the female (mean development time 25 ± 9 days) without any diapause. In *E. p. meridionalis* from Tanzania, Jago (1963) found seven instars in the male and seven to eight in the female. However, data on the life cycle, reproductive biology, and nymphal development of *E. p. ibandana* are lacking. This study aimed to collect these data; specifically, we aimed (1) to determine the number and duration of nymphal instars of *E. p. ibandana*, (2) to morphologically describe each instar, (3) to study the survival rates of these different instars, and (4) to study the reproductive behavior of *E. p. ibandana* in southern Cameroon.

Methods

Study area.—The individuals raised in the laboratory were caught between August 2014 and March 2017 at Nkolbisson, Yaoundé. Yaoundé is located in a semi-deciduous forest area, but the natural vegetation is highly degraded because of anthropic activity. The region is characterized by alternating hills and swamps (Bachelier 1959). The climate is of Guinean equatorial type with four seasons: a short rainy season (mid-March to June), a short dry season (July and August), a long rainy season (September to mid-November), and a short dry season (from mid-November to mid-March). The rainfall is about 1,600 mm per year and temperature varies from 19° to 33°C (Suchel 1987).

Sampling.—Adults of *E. p. ibandana* (n = 61 adult pairs) used in this study were obtained from sixth instar nymphs collected on grass vegetation at Nkolbisson using a sweep net. Nymphs were transported to the laboratory in cylindrical polypropylene plastic boxes (type 1 cages: 9 cm high and 13 cm in diameter) closed with a wire mesh lid. In the laboratory, these nymphs were reared individually in the same type 1 cages on a shelf.

Meteorological data collection in the laboratory.—Temperature and relative humidity (RH) in the laboratory were recorded daily during the experiment (morning, afternoon, and evening) with a Gottingen Thermohygrograph. The temperature and RH during the breeding period are provided in Fig. 1.

Reproduction.—After the final molt of the specimens collected in the field, the adults were paired in 15 wire cages (type 2 cages: 11 cm high and 10 cm in diameter) closed by a mesh cover. Each cage was one third filled with heat-sterilized wet sand, serving as an oviposition medium. Observations were conducted every two days to record pre-mating, mating, oviposition, and hatching dates.

Post-embryonic development.—First instar nymphs obtained from each adult pair were counted and placed individually in type 1 cages, then kept on shelves for development monitoring. A dry stem of *Chromolaena odorata* (14 cm long) was placed in each cage to support molting of the nymphs. Each cage was labeled with hatching date, number, stage, and sex. Each nymph was fed every two days with a cassava leaf (*Manihot esculenta*). The presence of exuviae was recorded daily and the state (dead or alive) of the nymphs was noted. The cages were also cleaned and the leaves used as food were renewed.

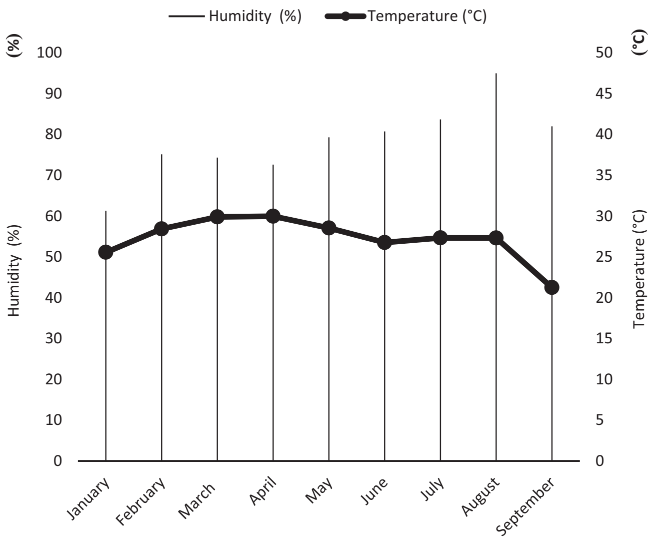

Fig. 1. Variation in temperature and relative humidity from January to September 2017. Laboratory of Zoology Faculty of Science University of Yaoundé 1.

Morphology and morphometrics.—The morphology and morphometry of *E. p. ibandana* were recorded from freshly dead individuals during rearing. The morphological characteristics were observed using a Heerbrugg binocular lens. For each developmental instar, measurements were made and, for paired structures, the right structure was measured and their shape and color were described. The following parameters were measured as described by De Grégorio (1987) and Default (2012): Total body length (Lt): from the tip of the fastigium to the tip of the abdomen, measured in lateral view; length of cephalic capsule (Lcc): length of head from the tip of the fastigium to the most posterior part of the head, measured in dorsal view; width of cephalic capsule (lcc): head width including compound eyes, measured in dorsal view; length of thorax (Lth): from the anterior to posterior margin of pronotum; length of abdomen (Labd): from posterior margin of pronotum to tip of abdomen, measured in lateral view; length of pronotum (Lpr): along midline, measured in dorsal view; length of antenna (La): from the scape to the apex of the last segment of flagellum; number of antennal articles (Na) in the flagellum; length of tegmina (Lel): from the insertion point to the apex of tegmen, measured in dorsal view; length of hind wing (Lai): from the insertion point to the apex of wing, measured in dorsal view; length of hind femur (Lcu1): maximum length of hind femur; length of median femur (Lcu2): maximum length of median femur; length of anterior femur (Lcu3): maximum length of anterior femur; length of hind tibia (Lti1): maximum length of hind tibia; length of mid tibia (Lti2): maximum length of mid tibia; length of anterior tibia (Lti3): maximum length of anterior tibia; number of external spines on hind tibia (Nse).

Drawings were made with the same magnifying glass in a light chamber and at 25–50X magnification.

Data analysis.—Data were analyzed using Excel (version 2016) and PAST (version 2.5) softwares. Excel was used to draw the different curves; PAST was used to calculate averages of development times and morphometric parameters. The averages were compared with the Kruskal-Wallis and Mann Whitney tests at the 5% significance level.

Results

Number of instars and duration of postembryonic development.—In the laboratory, nymphal development of *E. p. ibandana* went through six instars in males and six (75% of females) to seven (25% of females) instars in females (Table 1). The average total development time differed significantly ($p < 0.0001$) between the sexes: 79.16 ± 0.51 (54 to 124 days) in the males, 89.93 ± 0.58 (67 to 131 days) in six-instar females, and 94.96 ± 1.22 (67 to 161 days) in seven-instar females (Table 1). From the fifth nymphal instar onwards, average development times differed significantly ($p<0.0001$) from one instar to another (Table 1).

Nymphal survival rate.—We obtained 2,603 hatchlings, 793 (30.46%) of which reached the adult stage. The transition from the first instar (L1) to the second (L2) was marked by a very high mortality rate (47%), but from the L2 instar on the survival rate was high, with values between 87% and 92% (Fig. 2), resulting in a linear decreasing number of individuals from L2 to the adult stage (Fig. 2).

Reproduction: courtship, mating, and oviposition.—Courtship began 32.47 ± 3.88 days (8 to 59 days) after the final molt, by contact of the palps and antennae between both sexes. The male clung to her pronotum; when the latter was not receptive, the male remained on her back (this could last more than 2 hours). In some cases, the female used her hind legs to prevent the male from clinging to her. When the female was receptive, the male clung to her pronotum with his prothoracic and mesothoracic legs, the metathoracic legs being free and folded. In this position, the male bent his abdomen about 180° to the left or right below that of the female in order to bring the two genital regions into contact. He then introduced his phallus between the genital valves of the female to the vaginal opening. The coupling ($n = 61$) lasted for 2.12 h on average (between 1 and 3 hours) if uninterrupted.

After pairing, the first ootheca was deposited 9 to 70 days later (average 52.03 ± 5 days). Females laid between 1 to 11 egg pods (average 3 ± 1.4) and the number of eggs per ootheca ranged from 14 to 50 (34.93 ± 2.37 on average). On average, the females took 52.02 ± 5.1 days for laying of the first pod, 73.23 ± 6.84 days for the second pod, and 101.3 ± 10.31 days for the third pod.

Morphology of the different developmental stages.—

Egg: The eggs of *E. p. ibandana* are 3 to 5.5 mm long (average 4.37 ± 0.44 mm) and 1 to 1.5 mm in diameter (average 1.00 ± 0.05 mm). The eggs have a yellowish color, an elongated shape, are slightly curved and with rounded ends.

Adults: The general body color is of a variable brown, sometimes light beige, or brown-gray. The eyes are streaked with a small black band highlighting the sub-ocular suture. The pronotal disc is flat, with weakly pronounced lateral carina that are blurred in the metazona; the posterior border is slightly angular. The pronotal disc has two light bands running along the lateral carina and surrounding a dark brown zone; the dark zone narrows towards the anterior and posterior margins; the prosternal process is cylindrical. The elytra and wings are fully developed, slightly shorter, reaching or extending beyond the posterior apex of the abdomen and bearing a beige longitudinal stripe in the median field. The lower outer half of the posterior femora is usually yellow or light beige, lighter than the upper half. The basal half of the posterior tibiae is blue, the apical half reddish with whitish spines and black apices. The posterior tarsi are red.

Males are 21 to 27 mm long (average 24.33 ± 1.60 mm). The head is between 5 and 7 mm (average 6.30 ± 0.67 mm) long; the

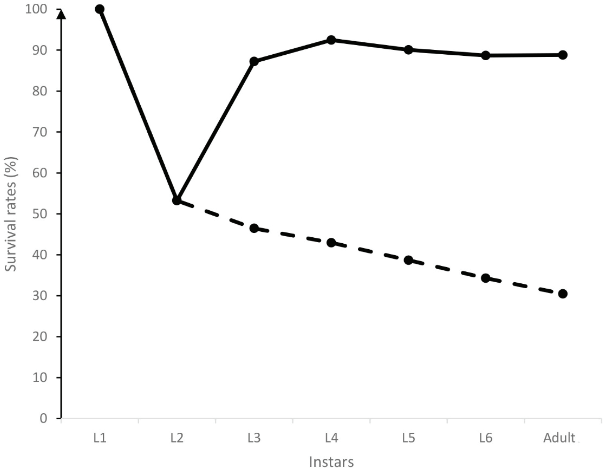

Fig. 2. Survival rate of the nymphal instars of *E. p. ibandana* in the laboratory. Solid line: % survival of each instar; broken line: % of all nymphs still surviving. L1–L6 = nymphal instars 1–6.

Table 1. *Eyprepocnemis plorans ibandana*, male and female nymphal instars average development time (mean ± standard error in days), under laboratory conditions. Number of specimens: 388 males, 325 six instar females, 143 seven instar females.

Sexes	Instars							Kruskal Wallis Test		Total duration
	L1 Nymph	L2 Nymph	L3 Nymph	L4 Nymph	L5 Nymph	L6 Nymph	L7 Nymph	H Value	P Value	
Males										
Duration	12.22 ± 0.13^{aA}	11.32 ± 0.17^{bAB}	11.53 ± 0.17^{bAB}	12.64 ± 0.19^{aA}	13.5 ± 0.20^{cA}	18 ± 0.28^{dA}	–	517	<0.0001	79.16 ± 0.51^{A}
Range	(4–28)	(4–24)	(2–33)	(6–38)	(6–46)	(6–38)				(54–124)
Females of six instars										
Duration	12.78 ± 0.17^{aB}	11.70 ± 0.19^{bA}	12.10 ± 0.22^{bA}	13.72 ± 0.25^{cB}	14.92 ± 0.31^{dB}	24.72 ± 0.48^{eB}	–	249.4	<0.0001	89.93 ± 0.58^{B}
Range	(6–26)	(4–28)	(4–27)	(4–33)	(2–48)	(9–51)				(67–131)
Females of seven instars										
Duration	12 ± 0.27^{aAB}	10.81 ± 0.24^{bB}	11.19 ± 0.30^{bB}	12.74 ± 0.40^{aA}	13 ± 0.34^{aC}	14.27 ± 0.42^{cC}	20.52 ± 0.63^{d}	260.9	<0.0001	94.96 ± 1.22^{C}
Range	(6–26)	(2–21)	(2–27)	(4–33)	(5–32)	(4–37)	(5–56)			(67–161)

Notes: Values in table indicate: mean ± standard error (Min–Max). Legend: Uppercase letters compare values vertically; lowercase letters compare values horizontally.

Fig. 3. *Eyprepocnemis plorans ibandana*, male from Ongot, Cameroon.

Fig. 4. *Eyprepocnemis plorans ibandana*, female, from Ongot, Cameroon.

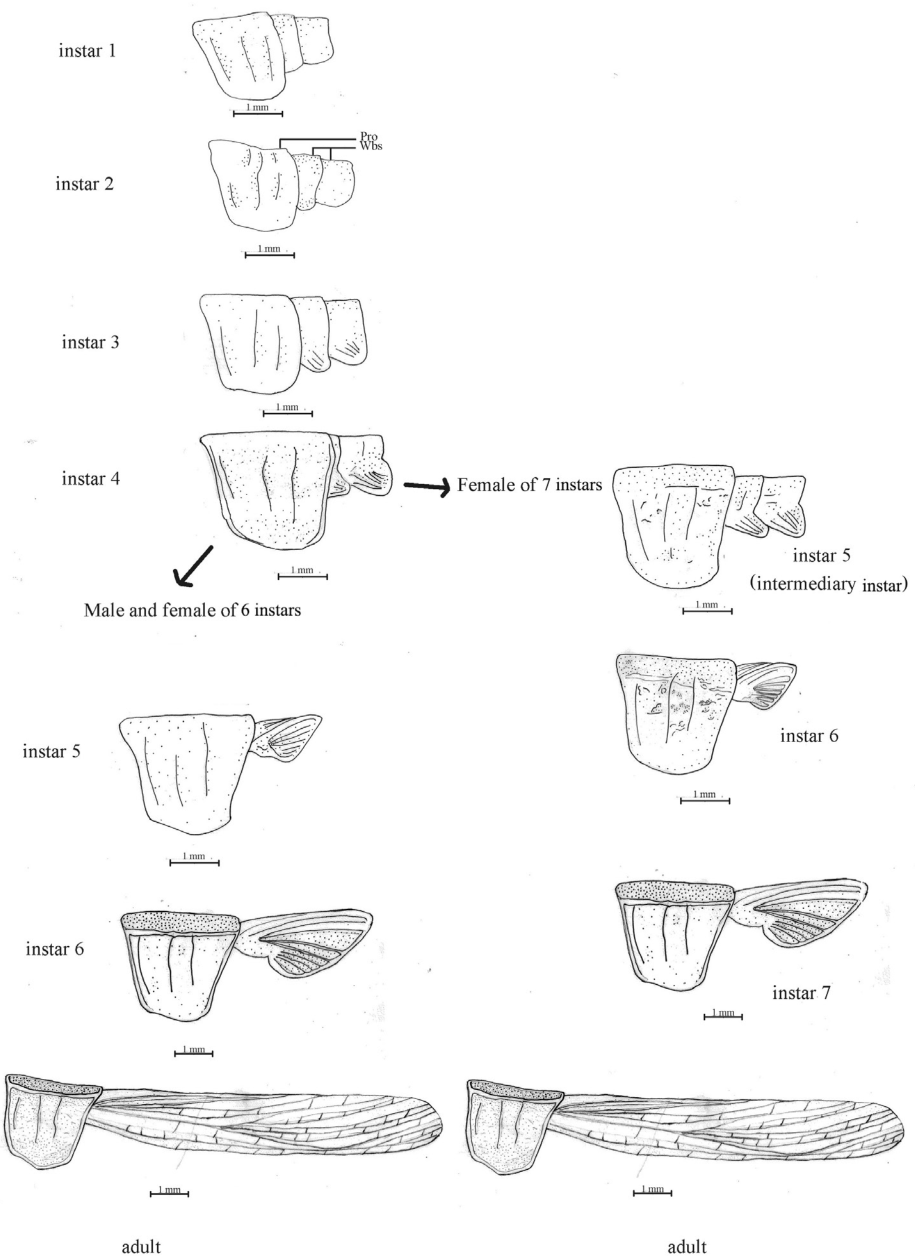

Fig. 5. *Eyprepocnemis plorans ibandana*, postembryonic development of pronotum and wings (lateral view). Pro: pronotum; Wbs: Wing buds.

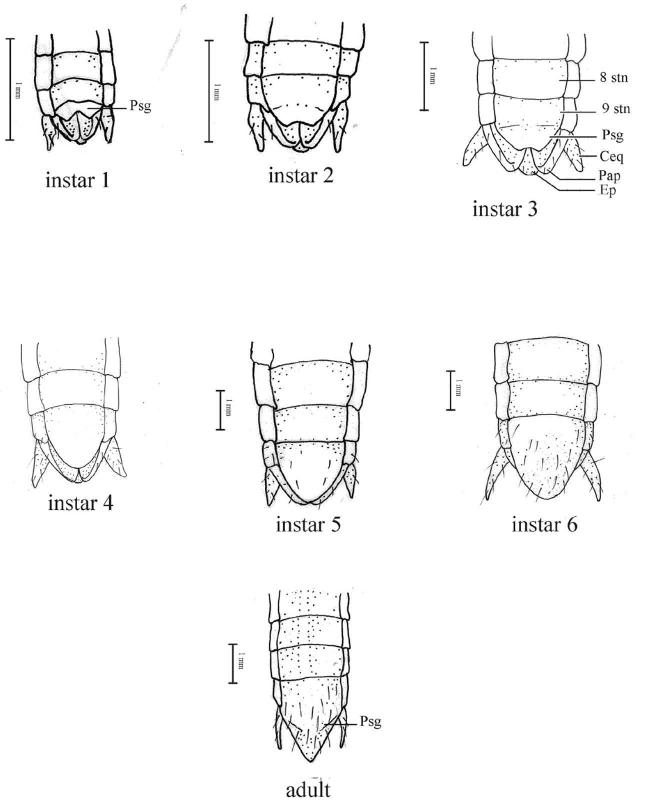

Fig. 6. *Eyprepocnemis plorans ibandana*, postembryonic development of males' external genitalia (ventral view). Ceq: cerci, Ep: epiproct, Pap: paraproct, Psg: subgenital plate, 8 stn: sternite 8, 9 stn: sternite 9.

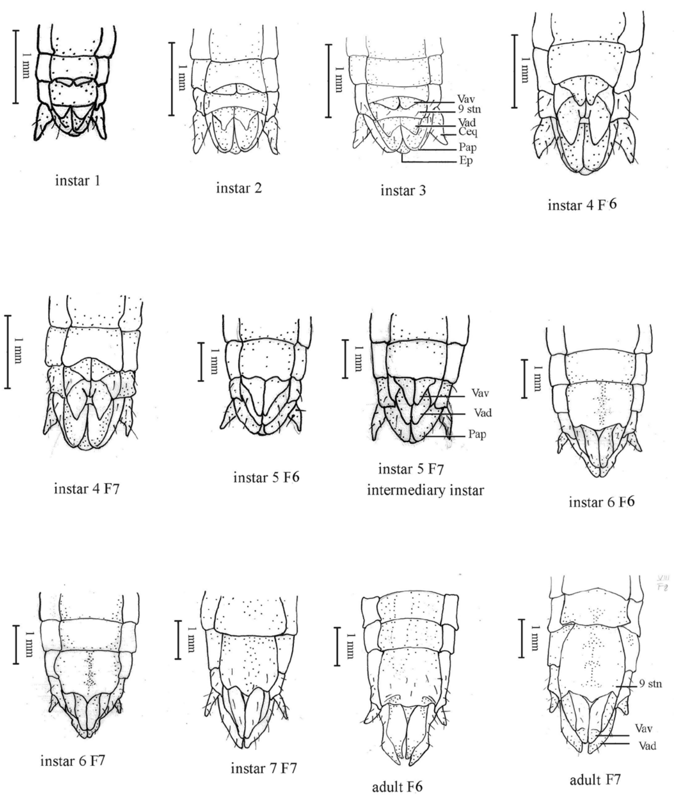

Fig. 7. *Eyprepocnemis plorans ibandana*, postembryonic development of females' external genitalia (ventral view). Ceq: cerci, Ep: epiproct, Pap: paraproct, Vad: dorsal valve, Vav: ventral valve, 9 stn: sternite 9, F6: female of six instars, F7: female of seven instars.

eyes bear six longitudinal eye stripes; the antenna carries 24 articles, measures 9.90 to 10 mm (average 9.99 ± 0.03 mm) and reaches dorsally almost the posterior margin of the pronotum. The thorax measures 6 to 9 mm (average 7.72 ± 0.98 mm); the pronotal disc measures between 4 and 5 mm (average 4.81 ± 0.37 mm). The abdomen is 11 to 14 mm long (average 12.74 ± 0.84 mm); the sub-genital plate is conical with acute apex (Figs 3, 5, 6 and Table 2).

Females that passed through six nymphal instars have a body of 29.80 to 41.70 mm (average 35.86 ± 2.94 mm) long. The head measures 7.10 to 10 mm (average 8.45 ± 0.65 mm); the antenna carries 24 to 25 articles, measures between 9.30 and 12 mm (average 10.74 ± 0.73 mm), and reaches dorsally almost the posterior margin of the pronotum. The eyes bear six clearly visible longitudinal eye stripes. The thorax measures between 9 and 12 mm (average 10.44 ± 0.77 mm). The pronotal disc is between 5.50 and 7 mm (average 6.35 ± 0.49 mm) long. The abdomen measures between 17 and 27.50 mm (average 21.79 ± 2.7 mm). The genital valves are very robust and slightly curved towards the rear. The posterior margin of sternite 8 is undulating without a median process (Figs 4, 5, 7 and Table 2).

Females that passed through seven nymphal instars are not significantly different in size than females that have passed through six instars (Table 2), but they are distinctive in having an eye with seven clearly visible longitudinal eye stripes; the pronotal disc has in its middle part a clearly visible median dark band, surrounded by two clearly visible pale beige lateral carinae and the posterior margin of sternite 8 carries a small median process (Figs 5, 7, and Table 2).

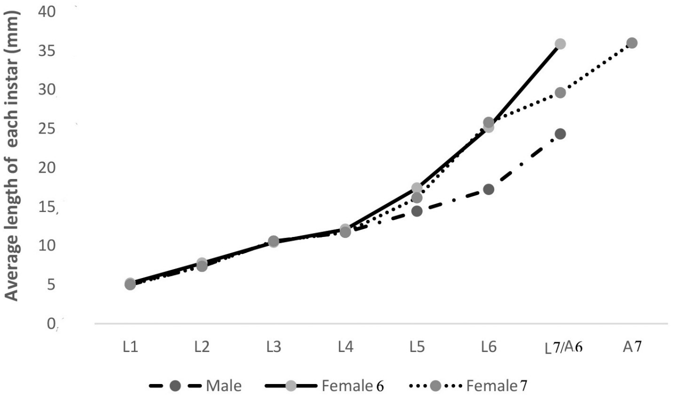

Fig. 8. *Eyprepocnemis plorans ibandana*, increase in body size under laboratory conditions. L= nymph; A= adult.

Common characteristics of the nymphal instars.—The body is usually dark brown in color with spots and light beige bands. The head is weakly conical, dark brown in color with a beige band behind each compound eye, extending onto the anterior border of the pronotum. The fastigium is trapezoid in shape with a slight mid and concave longitudinal depression; it is brown, with a midlength pale beige band extending over the pronotum to the posterior end of the abdomen. The face is light beige with brown spots; the frontal ridge is concave with two more or less parallel longitudinal carinae reaching the base of the mouthparts. The pronotum is cylindrical in shape, weakly roof-like, bearing three brown sutures

Table 2. *Eyprepocnemis plorans ibandana*, male and female measurements of morphological characters.

Instars	Sex/type	Lt	Lcc	lcc	Lth	Labd	Lpr	La	Na
L1	Male	5.01±0.63 (3.20–6.00) (32) A	2.01±0.14 (1.30–2.20) (32) A	1.26±0.12 (1.00–1.50) (32) A	1.83±0.26 (1.20–2.50) (32) A	2.12±0.29 (1.40–2.60) (32) A	0.98±0.06 (0.80–1.10) (32) A	1.70±0.23 (1.10–2.10) (32) A	11±00 (11–11) (32) A
	Female	5.19±0.78 (3.80–6.90) (30) A	2.10±0.17 (2.00–2.90) (30) A	1.29±0.16 (1.00–1.50 (30) A	1.73±0.34 (1.00–2.10) (30) A	2.49±0.60 (1.70–3.90) (30) A	0.98±0.04 (0.90–1.00) (30) A	1.77±0.16 (1.40–2.10) (30) AB	10.63±0.49 (10–11) (30) A
L2	Male	7.35±0.83 (5.90–8.80) (30) B	2.31±0.18 (2.10–2.90) (30) AB	1.83±0.13 (1.50–2.00) (30) B	2.29±0.28 (1.90–3.00) (30) B	3.96±0.56 (2.50–5.00) (30) B	1.29±0.12 (1.10–1.70) (30) B	2.16±0.13 (1.90–2.50) (30) B	15±00 (15–15) (30) B
	Female	7.76±0.73 (6.50–9.30) (30) B	2.48±0.28 (1.30–2.80) (30) B	1.94±0.08 (1.80–2.00) (30) B	2.45±0.25 (2.00–3.00) (30) B	4.05±0.47 (3.00–5.00) (30) B	1.39±0.12 (1.20–1.60) (30) B	2.28±0.18 (2.00–2.60) (30) B	15±00 (15–15) (30) B
L3	Male	10.58±0.76 (9.00–12.00) (30) C	3.18±0.15 (2.90–3.50) (30) C	2.17±0.09 (2.00–2.30) (30) BC	3.29±0.26 (2.80–4.00) (30) C	5.76±0.52 (5.00–7.00) (30) C	1.94±0.08 (1.80–2.00) (30) C	3.07±0.09 (2.90–3.30) (30) C	16.87±0.34 (16–17) (30) C
	Female	10.46±0.72 (9.00–11.50) (28) C	3.21±0.16 (3.00–3.50) (28) C	2.19±0.07 (2.10–2.30) (28) C	3.34±0.28 (2.80–3.80) (28) C	5.69±0.52 (4.60–6.40) (28) C	1.97±0.05 (1.80–2.00) (28) C	3.05±0.12 (2.80–3.30) (28) C	16.71±0.46 (16–17) (28) C
L4	Male	11.71±1.76 (10.1–14.00) (30) C	3.77±0.29 (3.30–4.60) (30) D	2.79±0.34 (2.40–3.90) (30) D	3.60±0.39 (3.00–4.50) (30) C	6.30±0.88 (5.20–8.00) (30) C	2.35±0.24 (2.00–3.10) (30) D	3.78±0.30 (3.20–4.50) (30) D	19.06±0.36 (18–20) (30) D
	Female	12.10±1.38 (9.40–15.00) (31) C	3.85±0.37 (3.00–4.90) (31) D	2.75±0.28 (2.00–3.20) (31) D	3.73±0.46 (2.80–4.70) (31) CD	6.47±0.74 (5.00–8.10) (31) C	2.41±0.34 (1.90–3.00) (31) D	3.84±0.47 (2.90–5.00) (31) D	19.03±0.18 (19–20) (30) D
L5	Male	14.40±1.56 (12.1–18.00) (33) D	4.40±0.27 (4.00–5.00) (33) E	3.09±0.11 (3.00–3.30) (33) E	4.09±0.41 (3.50–5.00) (33) DE	8.04±1.34 (6.10–11.00) (33) D	3.16±0.09 (3.00–3.30) (33) E	4.91±0.27 (4.20–5.30) (33) E	21.09±0.68 (20–22) (33) E
	Female 6	17.3±0.95 (16.00–18.3) (23) E	5.50±0.41 (4.90–6.00) (23) F	3.87±0.21 (3.50–4.00) (23) F	4.93±0.26 (4.30–5.10) (23) F	9.81±0.60 (9.20–10.60) (23) E	4.04±0.16 (3.70–4.20) (23) F	6.09±0.65 (5.00–7.40) (23) F	21.00±00 (21– 21) (23) E
	Female 7	16.05±1.65 (14.5–18.00) (20) E	4.58±0.45 (4.10–5.10) (20) E	3.30±0.26 (3.00–3.60) (20) E	4.26±0.84 (3.30–5.10) (20) E	9.44±1.07 (8.40–10.70) (20) E	3.12±0.15 (3.00–3.30) (20) E	4.64±0.30 (4.30–5.00) (20) E	21.00±00 (21– 21) (20) E
L6	Male	17.20±1.36 (15.0–19.2) (36) E	5.01±0.16 (4.80–5.50) (36) G	3.62±0.28 (3.20–4.00) (36) G	5.27±0.39 (4.80–6.00) (36) F	9.44±1.19 (7.50–11.00) (36) E	3.96±0.23 (3.50–4.30) (36) F	6.23±0.42 (5.50–7.00) (36) F	23.00±00 (23–23) (36) F
	Female 6	25.17±2.00 (21.0–27.0) (30) F	7.18±0.53 (6.50–8.00) (30) H	5.04±0.46 (4.20–5.50) (30) H	7.09±0.57 (6.00–7.70) (30) G	13.88±1.94 (11.0–16.0) (30) F	5.74±0.40 (5.10–6.10) (30) G	8.76±0.95 (7.30–10.00) (30) GH	23.00±00 (23–23) (30) F
	Female 7	25.80±0.54 (25.2–26.7) (32) F	6.93±0.26 (6.50–7.30) (32) H	5.52±0.52 (5.00–6.10) (32) I	7.10±0.25 (6.70–7.50) (32) G	15.15±0.39 (14.8–16.00) (32) G	5.98±0.16 (5.70–6.20) (32) H	8.44±0.88 (7.00–10.00) (32) G	23.00±00 (23–23) (32) F
L7	Female 7	25.61±2.13 (21.0–27.0) (38) F	6.93±0.23 (6.50–7.20) (38) H	4.94±0.31 (4.30–5.30) (38) H	7.15±0.49 (6.10–7.50) (38) G	15.31±1.52 (12.0–16.3) (38) G	5.97±0.22 (5.50–6.20) (38) GH	9.02±0.88 (7.30–10.00) (38) H	24.00±00 (24–24) (38) G
Adult	Male	24.33±1.60 (21.0–27.0) (25) F	6.30±0.67 (5.00–7.00) (25) I	3.99±0.33 (3.90–4.00) (25) F	7.72±0.98 (6.00–9.00) (25) H	12.74±0.84 (11.0–14.0) (25) F	4.81±0.37 (4.00–5.00) (25) I	9.99±0.03 (9.90–10.00) (25) I	24.00±00 (24–24) (25) G
	Female 6	35.86±2.94 (29.8–41.7) (36) G	8.45±0.65 (7.10–10.0) (36) J	5.42±0.36 (5.00–6.00) (36) I	10.44±0.77 (9.00–12.00) (36) I	21.79±2.79 (17.0–27.5) (36) H	6.35±0.49 (5.5–7.0) (36) J	10.74±0.73 (9.30–12.00) (36) J	24.05±0.23 (24–25) (36) G
	Female 7	35.78±4.40 (30.0–44.0) (26) G	8.36±0.42 (8.0–9.20) (26) J	5.43±0.37 (5.00–6.00) (26) I	10.69±1.01 (9.00–13.00) (26) B	23.17±3.94 (17.0–29.00) (26) I	6.36±0.47 (5.7–7.0) (26) J	10.52±0.63 (9.0–11.0) (26) J	24.23±0.43 (24–25) (26) G

Notes: Each value of the table represents: mean and standard error (min- max) (sample size). Within columns, means with same letters are not significantly different. Legend: Lt: length of body. Lcc: length of cephalic capsule. lcc: width of cephalic capsule. Lth: length of thorax. Labd: length of abdomen. Lpr: length of pronotum. La: length of antenna. Na: Number of antennal articles. Lel: length of elytra. Lai: length of the hind wing. Lcu1, Lcu2 and Lcu3: length of femur 1, length of femur 2, length of femur 3. Lti1, Lti2, Lti3: length of tibia 1, length of tibia 2, length of tibia 3. Nse: Number of external spines on hind tibia. L= nymphal instars.

Table 2. Continued. *Eyprepocnemis plorans ibandana*, male and female measurements of morphological characters.

Instars	Sex/type	Lel	Lail	Lcu1	Lcu2	Lcu3	Lti1	Lti2	Lti3	Nse
L1	Male	–	–	0.98±0.04 (0.9–1.00) (32) A	1.06±0.06 (0.90–1.10) (32) A	3.05±0.09 (2.70–3.20) (32) A	0.99±0.03 (0.90–1.00) (32) A	1.09±0.17 (1.00–2.00) (32) A	2.96±0.13 (2.40–3.10) (32) A	1.00±0.00 (1.00–1.00) (32) A
	Female	–	–	0.99±0.04 (0.90–1.10) (30) A	1.08±0.06 (0.90–1.20) (30) A	3.07±0.11 (2.90–3.30) (30) A	0.98±0.04 (0.90–1.00) (30) A	1.06±0.06 (0.90–1.20) (30) A	2.94±0.10 (2.70–3.00) (30) A	1.00±0.00 (1.00–1.00) (30) A
L2	Male	–	–	1.12±0.06 (1.00–1.30) (30) A	1.26±0.09 (1.10–1.50) (30) AB	4.04±0.18 (3.60–4.30) (30) B	1.13±0.06 (1.00–1.30) (30) AB	1.30±0.10 (1.10–1.50) (30) B	3.75±0.19 (3.10–3.90) (30) B	2.00±0.00 (2.00–2.00) (30) B
	Female	–	–	1.17±0.09 (1.00–1.40) (30) A	1.36±0.16 (1.10–1.70) (30) B	4.31±0.25 (3.60–4.80) (30) B	1.15±0.08 (1.00–1.30) (30) B	1.35±0.12 (1.20–1.60) (30) B	3.92±0.22 (3.40–4.30) (30) B	2.00±0.00 (2.00–2.00) (30) B
L3	Male	–	–	1.69±0.08 (1.60–1.90) (30) B	1.85±0.16 (1.20–2.00) (30) C	5.64±0.32 (5.10–6.10) (30) C	1.63±0.14 (1.40–1.90) (30) C	1.85±0.13 (1.50–2.00) (30) C	4.70±0.30 (4.10–5.80) (30) C	3.00±0.00 (3.00–3.00) (30) C
	Female	–	–	1.70±0.11 (1.50–2.00) (28) B	1.91±0.09 (1.70–2.00) (28) C	5.71±0.22 (5.40–6.20) (28) C	1.61±0.11 (1.40–1.90) (28) C	1.90±0.10 (1.70–2.00) (28) C	4.77±0.17 (4.30–5.20) (28) C	3.00±0.00 (3.00–3.00) (28) C
L4	Male	–	–	2.02±0.15 (1.80–2.50) (30) C	2.17±0.26 (1.90–3.00) (30) CD	7.24±0.66 (6.20–9.00) (30) E	2.01±0.21 (1.80–2.50) (30) D	2.27±0.24 (2.00–2.90) (30) D	5.87±0.44 (5.10–7.10) (30) D	4.00±0.00 (4.00–4.00) (30) D
	Female	–	–	2.04±0.19 (1.70–2.70) (31) C	2.16±0.28 (1.60–3.10) (31) D	7.33±0.86 (5.40–9.20) (31) E	1.96±0.18 (1.60–2.30) (31) D	2.35±0.29 (2.00–3.00) (31) D	6.07±0.57 (4.70–7.50) (31) D	4.00±0.00 (4.00–4.00) (31) D
L5	Male	2.11±0.13 (1.90–2.30) (33) A	2.32±0.22 (2.10–2.70) (33) A	2.52±0.36 (1.90–3.00) (33) D	2.85±0.18 (2.50–3.00) (33) E	9.31±0.75 (8.30–11.10) (33) F	2.49±0.24 (2.20–2.90) (33) E	3.13±0.29 (3.00–4.00) (33) E	7.49±0.40 (6.70–8.00) (33) E	5.00±0.00 (5.00–5.00) (33) E
	Female 6	2.82±0.27 (2.30–3.00) (23) A	3.04±0.22 (2.50–3.20) (23) A	3.08±0.17 (2.80–3.30) (23) E	3.51±0.32 (3.00–3.90) (23) F	12.14±0.77 (10.90–12.9) (23) G	3.03±0.23 (2.70–3.50) (23) F	3.97±0.23 (3.40–4.20) (23) F	9.58±0.58 (8.80–10.10) (23) F	5.00±0.00 (5.00–5.00) (23) E
	Female 7	1.25±0.19 (1.20–1.30) (20) A	1.19±0.10 (1.10–1.30) (20) B	2.61±0.26 (2.20–2.90) (20) D	2.86±0.24 (2.60–3.10) (20) E	9.50±0.64 (8.50–10.20) (20) F	2.51±0.24 (2.00–2.70) (20) E	3.05±0.27 (2.50–3.30) (20) E	7.61±0.58 (7.00–8.30) (20) E	5.00±0.00 (5.00–5.00) (20) E
L6	Male	5.55±0.68 (4.00–7.00) (36) B	4.90±0.48 (4.10–6.00) (36) C	3.13±0.19 (3.00–3.70) (36) E	3.67±0.31 (3.10–4.00) (36) F	11.58±0.76 (10.3–13.1) (36) G	3.10±0.24 (2.90–4.00) (36) F	3.88±0.20 (3.50–4.20) (36) F	8.93±0.59 (8.00–10.00) (36) G	6.00±0.00 (6.00–6.00) (36) F
	Female 6	8.01±1.64 (5.20–9.50) (30) C	9.44±1.07 (8.40–10.70) (30) D	4.23±0.60 (3.20–4.80) (30) F	4.69±0.46 (4.00–5.10) (30) G	16.63±0.99 (15.0–18.0) (30) H	4.12±0.10 (4.00–4.10) (30) GH	5.15±0.08 (5.00–5.20) (30) GH	13.14±0.88 (11.5–14.00) (30) H	6.00±0.00 (6.00–6.00) (30) F
	Female 7	8.10±0.18 (7.90–8.40) (32) C	7.09±0.58 (6.10–8.00) (32) D	4.57±0.14 (4.30–4.70) (32) F	5.16±0.19 (5.00–5.50) (32) H	16.87±0.90 (15.2–18.00) (32) H	4.18±0.14 (4.00–4.40) (32) G	5.23±0.20 (5.00–5.50) (32) G	13.19±0.81 (12.0–14.0) (32) I	6.00±0.00 (6.00–6.00) (32) F
L7	Female 7	8.10±0.77 (7.00–10.80) (38) C	7.15±0.51 (6.20–8.00) (38) D	4.44±0.34 (4.00–5.00) (38) F	4.90±0.40 (4.00–5.20) (38) GH	16.83±1.06 (15.0–18.0) (38) H	4.12±0.08 (4.00–4.20) (38) GH	5.15±0.11 (5.00–5.30) (38) GH	12.36±0.45 (11.6–13.20) (38) J	7.00±0.00 (7.00–7.00) (38) G
Adult	Male	20.22±1.57 (17.0–23.0) (25) D	18.29±1.62 (15.3–21.0) (25) E	4.92±0.39 (4.00–5.70) (25) G	5.59±0.39 (5.00–6.00) (25) I	14.66±0.91 (13.0–16.0) (25) I	3.98±0.28 (3.00–4.90) (25) H	4.98±0.22 (4.50–5.90) (25) H	12.31±0.61 (11.0–13.0) (25) J	6.00±0.00 (6.00–6.00) (25) F
	Female 6	28.35±2.05 (23.5–32.00) (36) E	26.07±2.23 (21.5–30.0) (36) F	5.45±0.41 (5.00–6.00) (36) H	6.34±0.44 (5.50–7.00) (36) I	20.83±0.39 (17.0–26.5) (36) J	5.01±0.18 (4.60–5.50) (36) I	6.75±0.45 (6.00–7.30) (36) I	16.39±0.89 (15.0–18.1) (36) K	6.00±0.00 (6.00–6.00) (36) F
	Female 7	28.06±2.63 (24.0–32.0) (26) E	25.61±2.74 (21.5–30.0) (26) F	5.48±0.37 (5.00–6.00) (26) H	6.36±0.44 (6.00–7.10) (26)	20.88±1.82 (17.0–23.2) (26) J	5.23±0.33 (4.90–6.00) (26) J	6.56±0.33 (4.90–6.00) (26) I	16.75±1.11 (14.9–18.6) (26) K	7.00±7.00 (7.00–7.00) (36) S

Notes: Each value of the table represents: mean and standard error (min- max) (sample size). Within columns, means with same letters are not significantly different. Legend: Lt: length of body. Lcc: length of cephalic capsule. lcc: width of cephalic capsule. Lth: length of thorax. Labd: length of abdomen. Lpr: length of pronotum. La: length of antenna. Na: Number of antennal articles. Lel: length of elytra. Lai: length of the hind wing. Lcu1, Lcu2 and Lcu3: length of femur 1, length of femur 2, length of femur 3. Lti1, Lti2, Lti3: length of tibia 1, length of tibia 2, length of tibia 3. Nse: Number of external spines on hind tibia. L= nymphal instars.

dotted with beige spots forming the median carina. The mesosternal space is open, much wider than long, with rounded lobes. The elytra are absent. The abdomen has ten segments visible dorsally and nine visible ventrally. The cerci are conical with an acute apex slightly exceeding the epiproct. The epiproct is triangular, bifurcated and with a rounded apex dorsally beyond the paraprocts (Figs 5–7 and Table 2).

Identification key for post-embryonic instars.—Refer to the key of Jago (1963) on *Eyprepocnemis plorans meridionalis*.

Sexual dimorphism.—We observed a clear sexual dimorphism from 5th nymphal instar to adults. At these instars, the length of body, head, thorax, abdomen, pronotum, antennae, elytra, wings, femora, and metathoracic tibiae are larger in females than in males.

Growth rate.—The growth rate was similar for both sexes from the first nymphal instar to the fourth. Starting from 5th instar, the growth of males became slower than that of the two types of females (six and seven instar females). At the sixth nymphal instar, six instars females increased faster in size than seven instar females, but as the latter passed through an additional instar, there was no significant difference between the sizes of the two types of adult females (Fig. 8).

Discussion

Postembryonic development of E. p. ibandana.—Our study showed that the number of instars varies between the two sexes in *E. p. ibandana*: six in the male and six or seven in the female, confirming the results obtained by Jago (1963) for *E. p. meridionalis*, Hernández and Presa (1984) in Spain for *E. p. plorans*, and Schmidt et al. (1996) in Sardinia. In southern Cameroon, the nymphal development of three pyrgromorphid grasshoppers (*Zonocerus variegatus*, *Pyrgomorpha vignaudii*, *Taphronota ferruginae*) has been studied previously (Kekeunou 2007, Kekeunou et al. 2015, Kekeunou et al. 2018), all of which had a fixed number of six instars in both sexes. On the other hand, a variable number of instars is well known for many Orthoptera species (Uvarov 1966).

The tropical grasshopper *Cornops aquaticum* may have five to seven nymphal instars depending on the host plant, humidity, and its distribution range from Mexico to Argentina (Adis and Wolfgang 2003, Adis et al. 2004). This could be explained by the genetic and environmental indices that are known to be factors affecting growth rates and number of nymphal instars in Orthoptera (Hochkirch and Gröning 2008). This means that females can maximize their fitness by reaching a larger adult body size, which allows them to produce more eggs, while males can maximize their lifetime reproductive success through multiple mating for a relatively short period of time (Sai-Keung 1973, Shine 1989, Hochkirch and Gröning 2008). This is due to the differences in activity patterns of the molting glands, corpora allata, and corpora cardiaca between the sexes. Indeed, molt and metamorphosis in hexapods depend on the circulating peak of ecdysone and juvenile hormone in both sexes (Joly 1968).

From our results, the nymphal development of *E. p. ibandana* was longer than in Jago's (1963) study on *E. p. meridionalis*, which obtained for the male and the female 55.3 and 59.45 days, respectively. These differences may be explained by the different rearing conditions of both studies. Jago (1963) reared his material in the laboratory (approximately 25 °C) in UK, while our study was done in Cameroon in semi-outdoor rearing conditions subject to natural variations in temperature. Differences in temperature are an important reason for the differences observed: our work better reflected field conditions and our results may be closer to what happens in nature than in the laboratory study of Jago (1963). The duration of development is strongly influenced by temperature in all insects (Ratte 1984) as well as by the host plants, e.g., Halouane (1997) and Ould El Hadj et al. (2004) found, respectively, 41 and 43.58 days for nymph development of *S. gregaria* on cabbage, while Ghidaoui (1990) and Ouchene (1995) found, respectively, 61.22 and 29.6 days on lemon and cabbage plus grass. An additional factor influencing development is the size of the cages. Kaufmann (1965) has shown that the life cycle of *Z. variegatus* is shorter in large cages than in smaller cages.

Nymphal survival rate.—The survival rate of the first nymphal instar was quite low in our study compared to the later instars. This lower survival of first instars in the laboratory and in nature is common in other grasshoppers and locusts, e.g., desert locust, Australian plague locust (Dhouib 1994, Seddik 1994, Symmons and Cressman 2001, Ould El Hadj et al. 2004). This reflects a high sensitivity of first nymphal instar that is related to variations in environmental conditions and possibly the monospecific diet they were subjected to in the laboratory. Indeed, *E. p. ibandana* is a species of mesophilic environments with a polyphagous diet in the field (Blanchet 2009). According to Kekeunou et al. (2018), the high mortality of young nymphs could be explained by problems such as inadequate watering, molting, and nutrition. In our study the nymphs were fed with leaves of a single food plant; the nature of this monospecific diet may have affected nymphal development.

Reproduction of E. p. ibandana.—The mating of *E. p. ibandana* is similar to that observed in most other short-horned grasshoppers (Duranton and Lecoq 1990, Symmons and Cressman 2001, Dushimirimana et al. 2012), including also some species from Cameroon such as *T. ferruginea* (Kekeunou et al. 2018), *P. vignaudii* (Kekeunou et al. 2015), and *Z. variegatus* (Kekeunou 2007). Mating started on average 32.47 days after the final molt. This result differs from those obtained by Kekeunou et al. (2018) on *T. ferruginea* and Kekeunou et al. (2015) on *P. vignaudii*, who assessed the time between fledging and first mating at 42.47 days and 12.7 days, respectively. These differences could be explained not only by the time required for each species to reach sexual maturity, but also by the time needed to find favorable ecological conditions, adequate temperature and humidity, and availability of food (Duranton and Lecoq 1990).

We found that a female of *E. p. ibandana* lays between one and eleven oothecae during her adult life-span. The number of eggs per egg pod ranged from 14 to 50. In the laboratory, *S. gregaria* females produce a mean of 22 pods, each containing 47.6 eggs (Wang and Sehnal 2002), which suggests that they produce a total of 1,050 eggs during their entire reproductive life (Dushimirimana et al. 2012). For the same species, Norris (1952) reports 5–9 pods (each pod contained 10 to 140 eggs), while Popov (1958) found no more than 2 or 3 egg-pods for each female. In nature, Chapman et al. (1986) observed 17–77 eggs per ootheca in *Z. variegatus*, but only 6.5 eggs on average by *Miramella alpina* feeding on *Vaccinium myrtillus* and *V. uliginosum* (Asshoff and Hättenschwiler 2005). These differences could be explained by the fact that the number of eggs per ootheca depends on the environmental conditions in which the insects live (Joly 1968), as well as the number of ovarioles of each ovary (Chiffaud and Mestre 1990). Whitman (2008) and Ackman and Whitman (2008) have also shown that a number of other factors, such as the length of the pre-oviposition period and the number of females participating in reproduction, also influence the reproductive capacity of a population.

Sexual dimorphism in E. p. ibandana.—Sexual dimorphism is marked in adults, as well as in 5th and 6th nymphal instar of *E. p. ibandana*. These results corroborate those of Hochkirch and Gröning (2008) who state that in 99% of Caelifera, adult females are larger than males. The larger size of the females probably reflects the need for egg production (Duranton and Lecoq 1990).

Two major hypotheses have been proposed to explain the ultimate causes of dimensional dimorphism: the intersexual competition hypothesis and the differential equilibrium hypothesis (Hochkirch and Gröning 2008). The first suggests that sexual dimorphism is a mechanism to reduce intra-specific competition, allowing the sexes to specialize in different foods. The differential equilibrium hypothesis proposes that different body sizes represent fitness optima of specific sexual shapes, which are caused by their specific life history strategies. Females can maximize their reproductive success by increasing the number (or size) of eggs (selection of fecundity), while males can maximize their reproduction by being more mobile and fertilizing many females in a short time (Hochkirch and Gröning 2008).

Conclusion

Under laboratory conditions, nymphal development of *E. p. ibandana* fed on cassava went through six instars in males and six (75%) or seven (25%) instars in females. The average development time in days was 79.16 in males and 89.93 to 94.96 in females. Fifth and sixth nymphal instars showed slightly longer development times. The survival rate of the first nymphal instar was low in our study compared to the later instars. Data on instar recognition and development times are useful for treatment programs by providing information on what stage the grasshoppers are at and how much time is left for treatment before the more damaging adult stage. It also gives an idea of how quickly treatments need to be performed to reduce nymphal populations in the field and reduce damage.

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Assemblages of orthopteroid insects along environmental gradients in central and southern Madagascar

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Abstract

Madagascar is one of the world hotspots for endemics, and its rapidly changing habitats accelerate the need for their study and conservation. Orthopterans, mantids, phasmids, and cockroaches were sampled in five main habitats (savanna and shrubland, semiarid spiny forest, rainforest, mountain grass- and shrubland, and cultivated habitats) in central and southern Madagascar (41 sites, 0–2250 m a.s.l.) with the aim of getting the first data on their diversity and distribution along environmental gradients shortly after the rainy period. Samples were collected primarily by sweeping herb and shrub vegetation along transects 100 m long and 1–2 m wide (5–8 transects/site) and supplemented using other techniques. Altogether 117 species of orthopteroid insects were found (94 Orthoptera, 7 Mantodea, 4 Phasmida, and 12 Blattodea), among them two katydid species which had been recently described as new to science (*Mimoscudderia longicaudata* Heller & Krištín, 2019, *Parapyrrhicia leuca* Hemp & Heller, 2019). High species diversity was documented: altogether 63 species (53.8%) were present at only one site, 14 (12%) at two sites, and 5 species (4.2%) at three sites. Nonmetric multidimensional scaling analysis on species composition did not clearly separate the assemblages of the sampled sites. Species assemblages from four habitats overlapped due to their similarity. Only assemblages from the rainforest sites were partially separated from the other sites. Cultivated habitats were characterized by the most frequent (F > 50%) and abundant grasshopper species, such as *Acorypha decisa*, *Aiolopus thalassinus rodericensis*, *Oedaleus virgula*, *Gelastorrhinus edax*, *Gymnobothrus* spp,. and *Acrotylus* spp. We found a significant association between habitat management and species rareness, where the number of rare species was higher in natural/unmanaged habitats. However, we found no association between habitat management and the number of endemic species. For several species we provide the first detailed data on their localities and habitat.

Keywords

altitude, biogeography, diversity, ecology, endemism, habitat

Introduction

Madagascar represents one of the most important hotspots of endemism on Earth (Myers et al. 2000, Ganzhorn et al. 2001, Goodman and Benstead 2005, Vences et al. 2009). The contact of tropical dry and rainforests, semi-arid savannas, thorny bushes, as well as a mosaic of cultural steppes offer an excellent opportunity to study animal and plant assemblages along different environmental gradients. Rapidly changing environments are accelerating the need to study them, as well as for the identification of conservation priorities for global biodiversity stability (Goodman and Benstead 2003, Irwin et al. 2010).

Orthopteroid insects are among the most important bio-indicators of the status of integrity of natural habitats, especially habitats with small plot sizes (Gerlach et al. 2013). They are also excellent study systems, e.g., for the coevolution of native and introduced species on some of the Mascarene Islands (Boyer and Rivault 2003). Therefore, assemblages of orthopterous insects, especially brachypterous species, provide valuable information on habitat conditions and the status of sites (Marini et al. 2009). Orthopterans in Madagascar include a large percentage (ca 80–90%) of endemic species (Descamps and Wintrebert 1965, Dirsh and Descamps 1968, Descamps 1971, Wintrebert 1972, Devriese 1991, 1995, Braud et al. 2014, etc.); a similar situation is also known in the phasmids (Bradler and Buckley 2018) and mantids (Ehrmann 2002). Non-endemics show similarities with African or Indomalayan orthopteroid fauna (e.g., Hemp 2009, 2013, Braud et al. 2014, Heller et al. 2018). There are several, though mostly older, studies describing orthopteroid insects in Madagascar. The best known seem to be those on the grasshoppers Acridoidea and Pyrgomorphoidea (Rehn 1953, Dirsh 1962, 1963a, b, 1966, Descamps and Wintrebert 1966, 1967, Dirsh and Descamps 1968) and monkey hoppers (Eumastacoidea; Descamps and Wintrebert 1965, Descamps 1971), with the first identification keys, maps and notes on their biology and habitats. Groundhoppers (Tetrigidae) are also quite well-known (e.g., Günther 1974, Devriese 1991, 1995). The ensiferans are a less-known orthopteran group in Madagascar, e.g., Phaneropterinae, Pseudophyllinae, Conocephalinae (Carl 1914, Ragge 1964, Gorochov and Llorente 2004, Ünal and Beccaloni 2008, 2017, Gorochov 2009, Heller et al. 2018), Meconematinae (Hugel 2012), Gryllidae, Mogoplistidae (Gorochov 2004, 2006, 2014), and there are still species new to science (e.g., Massa 2017a, b, c, d, Heller et al. 2019). Based on recent studies (Hemp 2009, 2013, Hemp et al. 2015, 2017), some tettigoniids (the Agraeciini/Euconchophorini-complex) are related to the studied Agraeciini from Africa, India, and Australia, but within Conocephalinae. A member of this Agraeciini/Euconchophorini-complex seems to have arrived in Madagascar relatively long ago. Hence, a comparison with East African taxa is necessary to know the evolutionary patterns of Malagasy tettigoniids.

The Malagasy mantids were described, e.g., by Mériguet (2005, 2013) and the phasmids, e.g., by Cliquennois (2003, 2008). A comprehensive study on Malagasy cockroaches is still lacking (cf. Princis 1965, 1966, 1969, Vinson 1968).

Today, only 10-15% of Madagascar's natural areas remain relatively well-preserved, while some areas and regions are managed and cultivated with high intensity and some are abandoned or seminatural (Vences et al. 2009, Irwin et al. 2010, Vieilledent et al. 2018). Forest habitats, in particular, are critically endangered by massive deforestation. In 1953, 27% of the island was under forest cover, and by 2000 only 17% was forested. Despite increased environmental awareness in recent decades, deforestation has continued (Irwin et al. 2010). This has had a serious impact, mainly on the many arboricolous and sylvicolous endemic Malagasy Orthoptera species (Braud et al. 2014, Heller et al. 2018). Such changing conditions create a challenge for studying the impact of different intensities of human management in biodiversity. Furthermore, there is a rather steep altitudinal gradient of particular regions from sea level up to nearly 2900 m a.s.l. with different habitats characterized by different moisture, geomorphology, and climate (Goodman and Benstead 2003, Vences et al. 2009).

It is known that the number of orthopterous species and their abundance changes with altitude (Claridge and Singhrao 1978, Grytnes and Vetaas 2002, Hemp 2009), but there is almost no data from Madagascar. Also, information on assemblages along different environmental gradients (e.g., Descamps and Wintrebert 1966) is almost completely lacking. For many endemic Malagasy species, even now the only information on 'Madagascar' exists without any further details on locality or ecology. This is true, for example, for distinctly more than half of all endemic species of phaneropterines (e.g., Heller et al. 2018). Based on these facts, we focused on 1) the diversity and distribution of orthopteroids along environmental gradients (habitat, altitude, management type) at 41 sites in central and southern Madagascar (after the rainy season, in March 2015) and 2) assemblage structure of orthopteroid insects in five different habitats and altitudes (0–2 250 m a.s.l.).

Material and methods

Study area.—Orthopteroid insects were sampled (41 sites) in five main habitats in central and southern Madagascar (Fig. 1). These habitats (> 90% of the site) cover: 1) savanna and shrubland (17 sites); 2) semiarid spiny forests, characterized by dense tangles of octopus trees interspersed with baobabs (6 sites); 3) rainforests with giant forest trees festooned with vines, ferns and orchids (4 sites); 4) mountain grasslands and shrubs (6 sites); and 5) cultivated, human made habitats, such as fields, orchards, parks and gardens (8 sites) (Suppl. material 1, Fig. 2). Considering the natural/cultivated character (management status) of each site, we divided

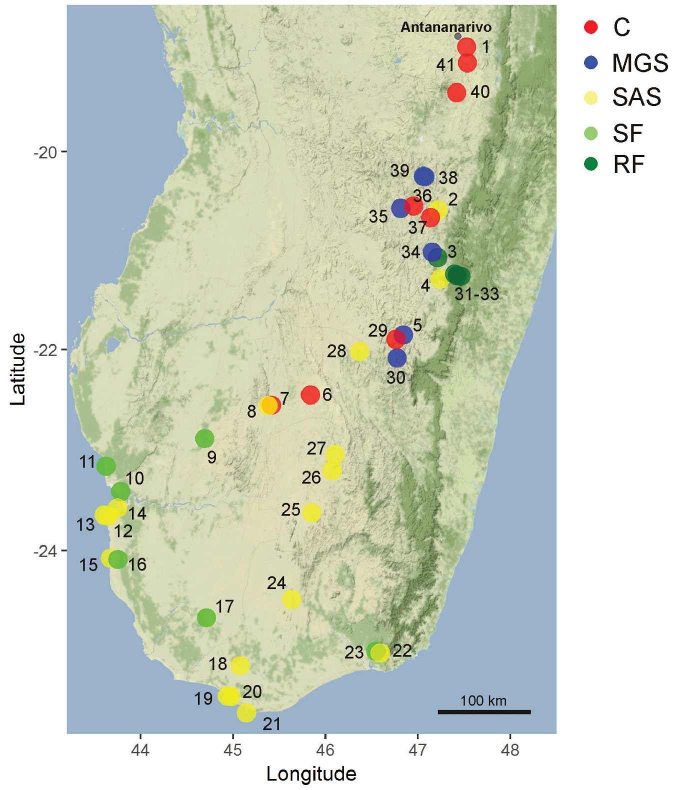

Fig. 1. Study sites (41) of orthopteroid insects in five habitats of central and southern Madagascar (C = cultivated habitats, MGS = mountain grass- and shrubland, RF = rainforest, SAS = savanna and shrubland, SF = semiarid spiny forest.

Fig. 2. Five main habitats studied in Madagascar: **A.** Savanna and shrubland; **B.** Semiarid spiny forests; **C.** Rainforests; **D.** Mountain grasslands and shrubs; **E.** Cultivated, human made habitats, such as fields, orchards, parks and gardens. Photos by A. Krištín.

them into three categories: 1) natural sites – not managed for > 60 years, mostly National Parks or Natural Reserves (17 sites); 2) cultivated (human-made habitats, such as fields, orchards, parks, and gardens, 8 sites); and 3) mixed character of site: natural/cultivated i.e., abandoned, formerly managed pastures and fields with a savanna, and spiny bush character (16 sites). The vertical and horizontal structure of characteristic vegetation with the main plant taxa were described for each study site. Altitudes, GPS coordinates, and all necessary environmental data were recorded (Brower et al. 1990) and the main habitat types were categorized (Moat and Smith 2007).

Study sites.—For each site we list: **management type**: C = managed cultivated habitats, as fields, gardens, orchards, N = nature near, unmanaged habitats, NC = abandoned site, formerly cultivated, with mostly natural vegetation; **GPS coordinates** and **altitude** of the site center.

1. **Antananarivo**, **ZOO Tsimbazaza** (C; 18.92924S, 47.52587E, 1277 m a.s.l.**)**: managed grassland and bush in ZOO park, with riparian vegetation along the lakes, within the city.
2. **Ambositra South** (NC; 20.590497S, 47.215015E, 1325 m a.s.l.): pastures and abandoned fields with scattered bush, in herbal layer with naturalized plants, e.g., *Gladiolus dalenii*, *Lilium* cf. *formosanum*, *Lantana camara*.
3. **Lalatsara Lemur forest** (N; 21.07206S, 47.21173E, 1412 m a.s.l.): rainforest with diverse tree and bushy hygrophilous vegetation, such as bamboo, ferns, palms, endemic orchids (e.g., *Cynorkis lilacina*, *Gastrorchis francoisii*), several introduced plants like ginger (e.g., *Hedychium coronarium*) and *Pereskia* at the forest edges.
4. **Fiarantsoa**, **31 km N** (NC; 21.286989S, 47.240574E, 1275 m a.s.l.): old abandoned fields, bush and pine forest edges with introduced *Lantana camara*.
5. **Anja Community Reserve** (NC; 21.850766S, 46.841926E, 980 m a.s.l.): well-preserved xeric and rocky habitats with succulent flora and evergreen forest (e.g., *Ravenala madagascariensis*). Several of them are endemics (e.g., *Aloe deltoideodonta*, *A. divaricata*, *Euphorbia alluaudii*, *E. bongolavensis*, *E. duranii*, *E. enterophora*, *Kalanchoe beharensis*, *Pachypodium densiflorum*, *Sobennikoffia humbertiana*, *Xerophyta dasylirioides*). On the foot of the Reserve are ruderalized fields with grasslands, lake, and bushy vegetation.
6. **Ihosy (Horombe plateau)** (C; 22.453546S, 45.838313E, 1050 m a.s.l.): grassland and pastures on plateau, covered mostly by grasses *Heteropogon* sp., on rocky fields spiny bush.
7. **Ranohira (park**, **hotel)** (C; 22.556500S, 45.415430E, 840 m a.s.l.): grasslands and park within the village with ruderalized vegetation.
8. **Isalo National Park** (N; 22.559474S, 45.379970E, 920–950 m a.s.l.): well-preserved xeric rocky formations and bushy grasslands with endemic succulents *Aloe isaloensis*, *A. imalotensis*, *Cynanchum*, *Euphorbia*, *Kalanchoe*, *Pachypodium rosulatum*, *Xerophyta dasylirioides*, and bush along the creeks with *Pandanus pulcher*.
9. **Zombitse-Vohibasia National Park** (N; 22.886195S, 44.691791E, 810 m a.s.l.): dry forests and their edges with bushy and grassland vegetation. Within endemic plants are represented families Euphorbiaceae, Acanthaceae (*Crossandra stenandrium*), Apocynaceae, Didieraceae, orchids (just flowering e.g., *Aeranthes* sp., *Habenaria tianae*, *Polystachya* cf. *aurantiaca*), in tree layer are, characteristically, the baobabs *Adansonia za*, *A. grandidieri*, *A rubrostipa*. Naturalized plant species are e.g., genera *Acacia*, *Aloe*, *Ficus*, *Pandanus*.
10. **Toliara east** (NC; 23.412236S, 43.782506E, 85 m a.s.l.): xeric spiny bush and tree habitat with succulent endemics (*Euphorbia fiherenensis*, *Mimosa* sp.).
11. **Réniala Reserve**, **Ifaty** (N; 23.163993S, 43.624652E, 20 m a.s.l.): dry spiny bush and forest with > 2000 plant species, with very old baobas (*Adansonia rubrostipa*) and several species of *Didiereaceae*. Among endemics are succulent species (e.g., *Adenia olaboensis*, *Commiphora mahafaliensis*, *Delonix decaryi*, *Didierea madagascariensis*, *Euphorbia pervilleana*, *Givotia madagascariensis*, *Pachypodium geayi*, *Zanthoxylum decaryi*).
12. **Soalara northeast** (NC; 23.578168S, 43.750159E, 5–40 m a.s.l.): dry spiny bush on steep rocky slopes and sandy habitats in coastal area with many endemic plants (e.g., *Aloe viguieri*, *Commiphora* sp., *Euphorbia leucodendron*, *E. capuronii*).
13. **Anakao** (NC; 23.655606S, 43.651012E, 5–10 m a.s.l.): sandy dunes and coastal habitats with *Euphorbia stenoclada* in tree layer, with some endemic *Aloe* (*A. divaricata*, *A. vaombe*), *Psiadia altissima*, introduced *Euphorbia pulcherrima*, *Agave sisalana*, *Sansevieria*.
14. **Nosy Ve** (N; 23.649328S, 43.605091E, 0–5 m a.s.l.): sandy dunes and coastal habitats on small island near Anakao with breeding population of *Phaeton rubricauda* with *Euphorbia stenoclada* and *Didierea madagascariensis* in tree layer, scattered bush (e.g., *Psiadia altissima*, *Scaevola plumieri*, *Commiphora* sp.), and herbal layer with *Ipomoea pes-caprae*.
15. **Ambola** (N; 24.076576S, 43.674658E, 5–10 m a.s.l.): dry sandy dunes and coastal habitats in the vicinity of Vaombe hotel with *Aloe vaombe*, *E. stenoclada*, *Commiphora* sp., *Uncarina* sp., *Acacia* sp., *Psiadia altissima* in bush and tree layer.
16. **Tsimanampetsosa National Park** (N; 24.086643S, 43.754726E, 5–50 m a.s.l.): limestone plateau with xeric bush and tree vegetation, mostly endemic (e.g., *Acacia bellula*, *Aloe divaricata*, *A. vaombe*, *Alluaudia comosa*, *Alluaudiopsis fiherenensis*, *Commiphora lamii*, *Delonix floribunda*, *E. leucodendron*, *E. mainty*, *E. plagiantha*, *Givotia madagascariensis*, *Operculicarya hyphaenoides*, *Uncarina stellulifera*), with old trees (*Adansonia rubrostipa*, *Pachypodium geayi*) and riparian vegetation along the Tsimanampetsotsa Lake.
17. **Ampanihy**, **6 km northwest** (NC; 24.661890S, 44.710957E, 250 m a.s.l.): spiny dry bush and forest with endemic *Alluaudia dumosa*, *A. humbertii*, *Commiphora* sp., *Dombeya* sp., and *Euphorbia arahaka* and introduced plants, e.g., *Euphorbia tirucalli*, *Opuntia dillenii*.
18. **Beloha**, **16 km N** (NC; 25.131933S, 45.075445E, 300 m a.s.l.): spiny dry bush with endemic *Acacia sakalava*, *Alluaudia dumosa*, *A. humbertii*, *Baudouinia rouxevillei*, *Barleria alluaudii*, and *Operculicarya decaryi*, with small wetland and abandoned pastures and fields.
19. **Lavanono coastal area** (NC; 25.429579S, 44.939260E, 5–10 m a.s.l.): sandy dunes with dry spiny bush and scattered xeric grassland with endemic *Aloe divaricata* and introduced *Agave sisalana*, *A. americana*, *E. stenoclada*, *Opuntia dillenii*, and *O. linguiformis*.
20. **Lavanono N (rocky area)** (N; 25.433282S, 44.978812E, 150 m a.s.l.): dry xeric bushy habitats with endemic *Alluaudia comosa*, *Megistostegium microphylla*, *Operculicarya decaryi*, in shaded sites *Kalanchoe linearifolia*, *Aloe antandroi*, at open plots are typical *Aloe vaotsanda* and introduced *Opuntia dillenii*.
21. **Cape Sainte Marie Reserve** (N; 25.593645S, 45.141987E, 0–165 m a.s.l.): low (< 120 cm) dry spiny bush covers 90% of this windy site, located on the southernmost point of

Madagascar. The most common plants are endemic species of genera *Commiphora*, *Salvadora*, *Megistostegium*, *Operculicarya*, *Alluaudia*, *Aloe* and *Euphorbia*, *Catharantus roseus*, *Tephrosia vohimenaensis*, and introduced *Opuntia* spp.

22. **Andohahela National Park – Mangatsiaka** (N; 24.988649S, 46.545776E, 50–70 m a.s.l.): dry spiny forest and bush on limestones with many old and big endemic plants (e.g., *Alluaudia ascendens*, *A. procera*, *Cedrelopsis grevei*, *Commiphora humbertii*, *C. brevicalyx*, *C. simplicifolia*, *Decarya madagascariensis*, *Euphorbia cylindrifolia*, *E. plagiantha*, *Grewia androyensis*, *Kosteletzkya reflexiflora*, *Pachypodium geayi*, *P. lamerei*, *Senecio cedrorum*, and *Uncarina grandidieri* (for more detailed info see Andriaharimalala et al. 2012).
23. **Andohahela – Tsimelahy River** (NC; 25.005266S, 46.590382E , 70 m a.s.l.): riparian vegetation and ruderalized bushy grassland along the river with some introduced (*Agave sisalana*, *Arundo donax*, *Opuntia monacantha*, *Salvadora angustifolia*) and endemic plants (*Abrahamia grandidieri*, *Alluaudia ascendens*, *A. procera*).
24. **Betroka 174 km S_Ampanaha** (NC; 24.484383S, 45.633321E, 455 m a.s.l.): old abandoned fields with wetland and bush containing endemic plants (*Aloe divaricata*, *Mimosa* sp.) and ruderalized pastures with invasive *Opuntia monacantha*.
25. **Betroka 51 km S_Hasofotsy S** (NC; 23.626795S, 45.850270E, 760 m a.s.l.): ruderalized grasslands, introduced plants (e.g., *Leonotis nepetaefolia*) and pastures with bush.
26. **Betroka 10 km N** (NC; 23.206678S, 46.071662E, 850 m a.s.l.): grassland and bush along the dry riverbed with endemic *Aloe macroclada* and several introduced plants (*Agave sisalana*, *Opuntia linguiformis*, *O. monacantha*).
27. **Betroka 30 km N – Befangitra Horombe plateau** (N; 23.047154S, 46.098617E, 1000 m a.s.l.): isolated well-preserved granite plateau with xeric vegetation and rare endemics, e.g., *Pachypodium horombense*, *Euphorbia horombensis*, *Aloe acutissima*, *Kalanchoe integrifolia*, *K. orgyalis*, *K. synsepala*, *Xerophyta dasylirioides*, surrounded by grasslands.
28. **Ambalavao W 80 km_Zazafotsy N 20 km** (NC; 22.017146S, 46.372121E, 900 m a.s.l.): granite cliffs with xeric succulent flora (e.g., *Aloe acutissima*, *A. deltoideodonta*, *Euphorbia enterophora*, *Kalanchoe hildebrandtii*, *K. synsepala*, *Pachypodium densiflorum*), surrounded by rocky grasslands.
29. **Ambalavao W 25 km_Besoa NW** (C; 21.896802S, 46.760451E, 1100 m a.s.l.): pastures and old fields with scattered *Eucalyptus* trees and endemic plants of *Aloe macroclada*.
30. **Andringitra_Catta camp S** (N; 22.084026S, 46.772666E, 950 1050 m a.s.l.): rocky alpine grasslands and pastures with endemic plants (e.g., *Adenia* sp., *Aloe acutissima*, *A. macroclada*, *Cynanchum* sp., *Dombeya* sp., *Kalanchoe beharensis*, *Pachypodium densiflorum*, *Uapaca bojeri*, *Xerophyta andringitrensis*) and introduced *Pandanus* and pine trees.
31. **Ranomafana Manja** (N; 21.261799S, 47.460840E, 680 m a.s.l.): wet grasslands, bush on the ecotone of village and rainforest with some endemic trees (e.g., *Ravenala madagascariensis*) and cultivated and introduced plants, e.g., *Zingiber* sp., *Hedychium coronarium*, *Musa* sp.
32. **Ranomafana Soarana/Varibolomena trail** (N; 21.256813S, 47.422720E, 920 m a.s.l.): high tropical rainforest with lemurs with few open sites, with many palm species, several orchid species (e.g., endemic *Aerangis citrata*), ferns such as *Asplenium nidus*, and tree form *Cyathea* sp.
33. **Ranomafana Vohiparara trail** (N; 21.238889S, 47.393682E, 1120–1200 m a.s.l.): mountain rainforest in ridge position of the National Park with many orchids (e.g., genera *Bulbophyllum*, *Polystachya*, *Microcoelia*), palms (e.g., *Dypsis*) and some introduced species (*Pandanus*, *Peperomia*, *Tristemma mauritianum*).
34. **Ambositra 70 km S Vohiposa S** (NC; 21.019383S, 47.151838E, 1430 m a.s.l.): diverse rocky grasslands and bush within old, narrow, and managed fields (peanut *Arachis hypogea*, maize) on slopes and terraces, with scattered pine plantations.
35. **Ambatofinandrahana Itremo Mts** (NC; 20.575811S, 46.811050E, 1360 m a.s.l.): xeric rocky grasslands on limestone near marmore quarry Ambatofinandrahana. There are several characteristic endemic succulents (*Aloe capitata*, *A. calcairophila*, *Euphorbia alluaudii*, *Kalanchoe tomentosa*, *Pachypodium densiflorum*, *Xerophyta dasylirioides*), orchids (*Habenaria ambositrana*) surrounded by tapia (*Uapaca bojeri*) and introduced pine stands.
36. **Ambositra W 50 km** (C; 20.553153S, 46.951285E, 1370 m a.s.l.): ruderalized grassland and bush along the river surrounded by rice and maize fields.
37. **Ambositra W 30 km Tsarafandry W** (C; 20.669935S, 47.135434E , 1550 m a.s.l.): rocky habitat (with endemic succulents *Aloe conifera*, *Dombeya macrantha*, *Helichrysum benthamii*, *Kalanchoe tomentosa*, and orchids *Benthamia flavida*, *Cyanotis speciosa*) with pine plantations and fields in surroundings.
38. **Ibity, alpine grasslands** (N; 20.254053S, 47.071768E, 1700 m a.s.l.): alpine rocky grasslands with scattered bush and pine, palm (*Dypsis decipiens*) and tapia trees (*Uapaca bojeri*). On rocky sites there are characteristic endemic succulents *Pachypodium brevicaule*.
39. **Ibity Mts. Ridge** (N; 20.248007S, 47.056952E, 1950–2250 m a.s.l.): alpine scattered bush with *Uapaca bojeri*, *Xerochlamys bojeriana*, in rocky sites with succulent, frequently endemic plants (e.g., *Aloe capitata* var. *quarziticola*, *A. trachyticola*, *Kalanchoe integrifolia*, *Pachypodium brevicaule*, *Tetradenia goudotii*), stapelia (*Cynanchum compactum*), and orchids (*Angraecum*, *Benthamia*, *Bulbophyllum*, *Cynorkis sacculata*, *Habenaria monadenioides*).
40. **Ambatolampy S 77 km S of Tana** (C; 19.401214S, 47.420855E, 1500 m a.s.l.): pastures and managed fields surrounded by scattered bush, eucalyptus, and pine trees.
41. **Tsiafahy S Tana 37 km S** (C; 19.093084N, 47.532912E, 1350 m a.s.l.): edges of ruderalized rice and maize fields, bushy landscape, near pine and eucalyptus plantations with *Mimosa* sp., *Albisia* sp.

Data collection.—Concerning the assemblage structure, orthopteroid species (Orthoptera, Mantodea, Phasmida, and Blattodea) were surveyed shortly after the rainy period, in March (6–30) 2015, almost always during sunny weather. The material was sampled mostly by sweeping (net diameter 40 cm, depth 60 cm) herb and shrub vegetation along transects 100 m long and 1–2 m wide (5–8/site, ca 2000 sweeps per site) (Gardiner et al. 2005). This method was supplemented with acoustical localization, beating of the lower part of trees (when present) and individual collection of specimens. We spent at least three hours of collection at each site. No special sampling techniques were used for ground dwelling species, tetrigids, cockroaches, mantids, and phasmids that could influence the lower species number and their abundance found. Species abundance was estimated on the basis of individuals sampled at the studied sites and expressed using the following semi-quantitative classification scale: 1 – very rare (fewer than 3 adult specimens), 2 – rare (3–10 specimens), 3 – abundant (11–100 specimens), 4 – very abundant (more than 100 specimens). These values for abundance, listed in the results, represent the highest recorded values of adults corresponding to one site (Suppl. material 1).

All the sampled taxa were measured; morphological data were analyzed and documented by photos using a dissecting microscope (OLYMPUS SZ Binocular Stereo Zoom Microscope) and digital cameras (SONY Cyber-shot DSC-P120 and Nikon Coolpix P520) for further identification and comparison and then archived. The insects that were difficult to identify were collected and preserved in 75% alcohol or ethyl acetate for further identification (maximum of 2-3 specimens per species). Phenotypic data were compared with the literature, and the specimens were identified using keys, e.g., in Descamps and Wintrebert (1965), Dirsh and Descamps (1968), Descamps (1971), Wintrebert (1972), Ünal and Beccaloni (2017), Heller et al. (2018), and particular group species files. Some specimens could not be identified to species level (females of cryptic species, crickets, and cockroaches). For assemblage analysis, we numbered them or identified them to genus or higher taxon level (Suppl. material 1).

Systematic nomenclature and endemism status were listed according to the Orthoptera Species File (Cigliano et al. 2019) and the mantid (Otte et al. 2019), phasmid (Brock et al. 2019), and cockroach species files (Beccaloni 2019). The full names of taxa with the author(s) names and their endemism status are given in Appendix 1.

Collection of specimens was done with a permit from the Malagasy government, No. 042/15/MEEF/SG/DGF/DCB.SAP/SCB from 13 February, 2015. The collections are located at the Institute of Forest Ecology SAS and in the collection of K.-G. Heller.

Data analysis.—Ordination analysis was performed using CANOCO 5.0 (Šmilauer and Lepš 2014) to assess the association between species composition and environmental factors. We analyzed 117 species sampled at 41 sites. The environmental variables considered were altitude, latitude (to assess effect of spatial autocorrelation), and habitat type. Nonmetric multidimensional scaling (NMDS) analysis was used to classify the sampled sites based on the species composition. Variation in species composition was assessed using Detrended Correspondence Analysis (DCA) (the length of the gradient was 3.5 SD units); the environmental variables were passively projected onto the ordination to interpret the pattern. As species abundance was assessed using a log-like ordinal scale, no transformation was used for response data; rare species were downweighted, and detrending by segments was performed. To partition variation in species composition by the three environmental factors, Detrended Canonical Correspondence Analysis (DCCA) with an unrestricted Monte Carlo permutation test was used. Again, no transformation was used for the response data; rare species were downweighted, and detrending by segments was performed, with 999 permutations used for testing the significance of the pure and joint effect of the explanatory variables. Association between type of landscape management category (C, C/N, N; see above) and species rareness (% frequency) and endemism, respectively, was assessed using the χ^2 test.

Results

Diversity and distribution of orthopteroid insects.—Altogether 117 species of orthopteroid insects were found (94 Orthoptera, 7 Mantodea, 4 Phasmida, and 12 Blattodea). High species diversity was documented. Altogether 63 species were found only at one site (53.8%), 13 at two sites (11%), and 6 species (5%) at three sites, several of them only as single specimen (Suppl. material 1).

Orthoptera: Altogether we found 94 species (Ensifera 26, Caelifera 68) from 8 families (Ensifera 4, Caelifera 4) and 22 subfamilies (Ensifera 5, Caelifera 17). Within 19 precisely identified Ensifera species, 13 are endemics (68.5%), while four show relations to African fauna and the other two are widespread. A higher endemism rate is shown by Caelifera, in which 58 of the 68 identified species are endemic to Madagascar (85.3%), two species are related to African fauna, two species to Indomalaya, and six are widely distributed, e.g., migratory species *Cyrtacanthacris tatarica*, *Acrotylus patruelis*, *Locusta migratoria*, and *Gastrimargus africanus* (Suppl. material 1). In some caeliferan families, we found only endemic species (e.g., Tetrigidae 6, Pyrgomorphidae 16).

Considering the 50% frequency limit (occurrence > 20 sites), the grasshoppers *Acorypha decisa* (frequency = 76%), *Aiolopus thalassinus rodericensis*, and *Oedaleus virgula* (68%), *Gymnobothrus malagassus* (66%), *Acrotylus patruelis* (59%), *A. aberrans*, *Duronia chloronota*, *Gastrimargus africanus*, and *Gymnobothrus variabilis* (54%) are habitat generalists and widespread species. The frequency and abundance of katydids were lower, with the most frequent species being *Ruspolia differens* (37%) and species of the genera *Tylopsis* (26.8%) and *Conocephalus* (22%). All of these species were found in both natural and cultivated (human made) habitats.

Habitat specialists seem to be species found only in nature and near well-preserved habitats, and most of them were found only at one site, sometimes as only one specimen (Suppl. material 1). Among them found only in the rainforests were: e.g., *Plangia segonoides*, *Ruspolia abrupta*, *Arexion suavis*, *Oxytettix lathraeospanius*, *O. arius*, *Chlorophlaeobella tananarive*, *Schulthessia biplagiata*, three mantid, and two phasmid species; in dry spiny forests: *Mimoscudderia longicaudata*, *Trigonocorypha maxima*, *Amblylakis* sp., *Colossopus grandidieri*, and *Pamphagella stenoptera*; in dry spiny bush *Eurycorypha prasinata*, *Parapyrrhicia leuca*, *Geloius nasutus*, *Gymnohippus marmoratus*, and the mantid *Chopardempusa neglecta*; in savannas and shrubland the grasshoppers *Caprorhinus ranohirae*, *C. zolotarevskyi*, and the phasmid *Achrioptera impennis;* and in open coastal sandy habitats with savanna and shrubland, the grasshopper *Conipoda calcarata* (Suppl. material 1).

The mean species number per site was 14.4, ranging between 6 species (two sites: cultivated and degraded ruderal grassland near Ambositra and a dry spiny bush site in isolated island Nosy Vé) and 26 (mosaic of preserved xeric rocky habitats and edges of evergreen forest and grasslands with bush in the Anja reserve), or 25 species (dry spiny bush in Cape Saint Marie).

Mantodea and Phasmida: We found altogether seven mantid species (six of them endemic to Madagascar) belonging to four families and five subfamilies, and four phasmid species (three of them endemic to Madagascar) from three families and three subfamilies (Suppl. material 1, Appendix 1). All mantid and phasmid species were found mostly as single individuals. The species *Popa spurca crassa* was known till now only from eastern and southern Africa (Patel and Singh 2016). Six of seven mantid species and three of four phasmids were found in natural or well-preserved habitats with low impact of human management, confirming their significance for site conservation. Three species of the genus *Tarachomantis* could be not identified to the species level because the identification key is still being prepared (Meriguet B., in litt.)

Blattodea: Altogether we found 12 cockroach species from three families and five subfamilies. Ten species belong to the family Blaberidae and five blaberid species from the subfamily Oxyhaloinae. We found at least two species endemic to Madagascar (*Aeluropoda insignis*, *Gromphadorhina portentosa*), one species (*Blatella lobiventris*) has an Afro-Malagasy range, and the other species/specimens were identified only to the genus or higher taxon level (Vidlička L., in litt). All the species were found at single sites and in low abundance, mostly as single individuals.

Assemblages of orthopteroid insect in different habitats and altitudes.—NMDS analysis on species composition did not clearly separate the assemblages of the sampled sites (Fig. 3). Assemblages from four habitats overlapped due to their similarity in species composition and their relative abundance. Only assemblages from rainforest sites were partially separated from the other sites, despite the rainforest sites being geographically nearby (Fig. 1).

Rainforest sites had a higher abundance of the species *Phaneroptera sparsa*, *Tylopsis bilineolata* (Ensifera), *Oxytettix arius*, *Duronia chloronota*, and *Finotina radana* and a very high abundance of *Oxya hyla* (Caelifera) (Fig. 4). However, these mostly openland species have colonized forest clearings from adjacent open habitats. Ten of 94 orthopteran species (e.g., three tetrigid species, and *Chlorophlaeobella tananarive*, *Schulthessia biplagiata*), two of four phasmid, and three of seven mantid species were found only in rainforest sites (Suppl. material 1). The cultivated habitats and mountain grass- and shrubland sites and their assemblages were clustered mostly at higher altitudes in the central part of Madagascar. The cultivated habitats were characterized by widespread and abundant grasshoppers, such as *Acrida subtilis*, *Acorypha decisa*, *Gelastorrhinus edax*, *Gymnobothrus madagassus*, and *Oedaleus virgula*, and the katydid *Ruspolia differens*; in savanna and shrubland sites, strong-flying grasshoppers e.g., *Acrotylus aberrans*, *A. patruelis*, *Aiolopus thalassinus rodericensis*, and *Nomadacris septempunctata* were dominant; in the mountain grass- and shrubland habitats the species *Pycnocrania grandidieri*, *Heteracris zolotarevskyi*, *Gelastorhinus edax*, and *Dyscolorhinus squalinus* were characteristic, and we found e.g., *Parahysiella betsileana*, *Heteracris antennata*, *Eyprepocnemis brachyptera*, *Ambositracris ornata*, and *Pyrgomorphella madegassa* only in high mountains. We found the katydids *Mimoscudderia longicaudata*,

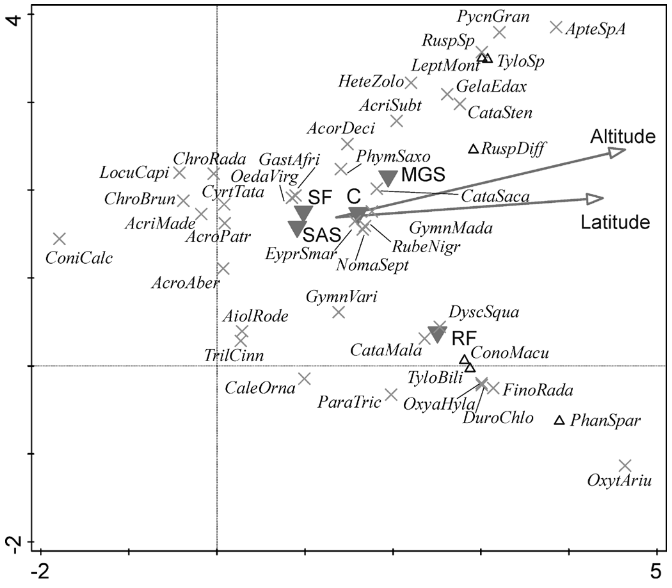

Fig. 4. DCA ordination plot summarizing the differences in orthopteran assemblages along altitudinal and latitudinal gradients in five habitats in central and southern Madagascar. Displayed are 41 species with a weight of more than 2% (6 Ensifera: triangle, 35 Caelifera: x-mark) and no Mantodea, Phasmida, and Blattodea). Abbreviations for the taxa are composed of the first four letters of their genus and species names when taxa were identified to the species level; otherwise the first four letters of the higher taxonomic unit is used. For the full species names, see Appendix 1. Environmental variables are only passively projected into the ordination. C = cultivated habitats, MGS = mountain grassland and shrubland, RF = rainforest, SAS = savanna and shrubland, SF = semiarid spiny forest.

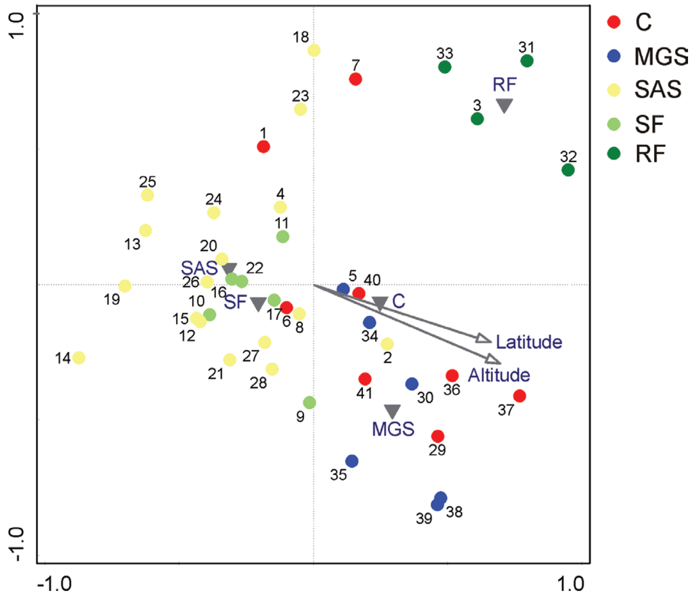

Fig. 3. Classification of 41 sites (central and southern Madagascar, 0–2250 m a.s.l.) based on orthopteroid insect species composition by nonmetric multidimensional scaling (NMDS). C = cultivated habitats, MGS = mountain grass- and shrubland, RF = rainforest, SAS = savanna and shrubland, SF = semiarid spiny forest.

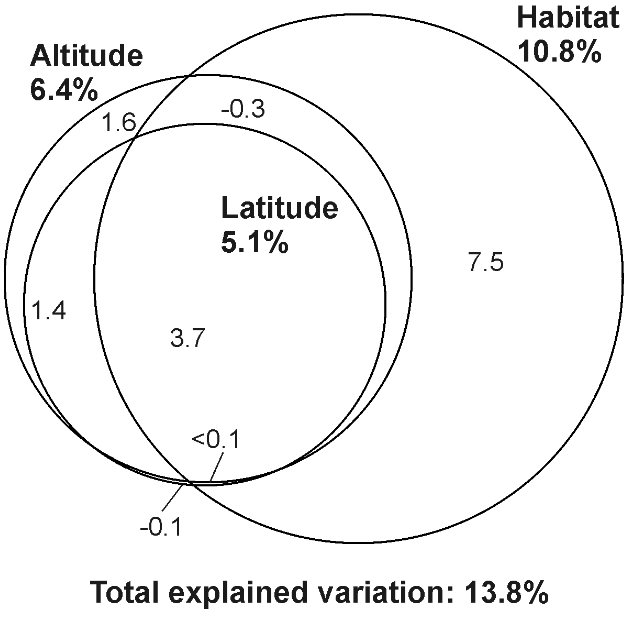

Fig. 5. Variation partitioning (%) in orthopteroid insect assemblages was explained by three variables—habitat, altitude and latitude—using CCA. A unique effect of habitat type and altitude were statistically significant (P < 0.01).

Trigonocorypha maxima, *Amblylakis* sp., and *Colossopus grandidieri* only in spiny forests (Suppl. material 1, Fig. 4).

Eigenvalues for the first and second DCA axes were 0.33 and 0.26, respectively, and the first two axes of the ordination explained 20.7% of the variation in the species data. Altitude and latitude strongly correlated to each other and with the first axis (Fig. 4). The DCA biplot (Fig. 3) indicated that altitude (latitude) was positively correlated with species e.g., *Apteropeoedes* sp., *Oxytettix arius*, *Tylopsis* sp., *Pycnocrania grandidieri*, and *Leptacris monteiroi*, when e.g., *Conipoda calcarata* was found only in lowland sites under 100 m a.s.l. (six sites) and the grasshoppers *Chromacrida brunneriana*, *Pamphagella stenoptera*, *Gelious* and *Gymnohippus* species, as well as the mantid *Chopardempusa neglecta*, only under 150 m a.s.l.

Variation partitioning indicated that a large part of the variation in the composition of the orthopteroid insect assemblages explained by habitat type (10.8%) was shared with altitude and latitude (3.7%). Due to the uneven distribution of habitats along an altitudinal and/or latitudinal gradient (Fig. 1), the unique contribution of habitat was larger than the contribution of the other two variables (Fig. 5).

Landscape management, endemics and species frequency.—When we divided the studied sites into three management categories, we found significantly higher numbers of the most frequent species (25%), 24 vs. 45% (n = 37 vs. 89 species) and significantly lower numbers of species with the lowest frequency (2%), 25 vs. 54% in managed habitats than in natural habitats (χ^2 = 17.81, *P* = 0.007, Fig. 6A). However, we found no statistically significant differences in the number of endemic species among the management levels (χ^2 = 2.53, *P* = 0.28, Fig. 6B), although there was a lower number of endemic species in the managed habitats than in the natural habitats (64 vs 78 %). It is known that species' reactions to anthropogenic disturbance in Madagascar are generally negative, but they still remain poorly known (Irwin et al. 2010, Vieilledent et al. 2018). Our results have confirmed the negative effect of the management practice of deforestation and burning.

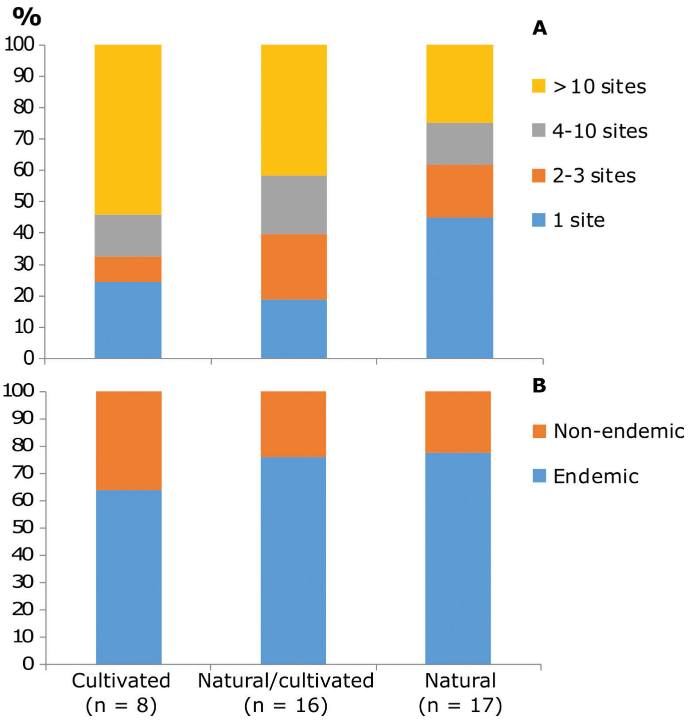

Fig. 6. A. Species frequency and **B.** Endemics in three categories of management (n = number of sites in each category).

Discussion

Diversity of orthopteroid insects in Madagascar.—In Madagascar, the fourth largest island in the world, there are a total of 15 Orthoptera families with 713 species (Cigliano et al. 2019), 21 mantid species from three families (Otte et al. 2019), 77 phasmid species from six families (Brock et al. 2019), and 121 cockroach species from five families (Beccaloni, 2019). These show a high rate of endemism, some having an Afro-Malagasy range. Nonetheless, several Malagasy insect groups are taxonomically more similar to Africa than Asia or Australia (e.g., Goodman and Benstead 2003). This suggests that geographical proximity and trans-oceanic dispersal may be an important determinant of the Malagasy insect fauna. In our study, performed shortly after the rainy period, we found altogether 94 orthopteran species (13.2% of those known in Madagascar) from eight families. They show a high endemism rate within the identified species (83.5%) and a bit more relation to African (7% of species) than to Indomalayan orthopterofauna (4.7% of species) (cf. Cigliano et al. 2019, l.c.) (Appendix 1). Hence, this endemism rate is similar to other insect groups (Goodman and Benstead 2003, Vences et al. 2009).

Two katydid species (*Mimoscudderia longicaudata*, *Parapyrrhicia leuca*) were recently described as new to science, and the latter shows a relation to African fauna (Heller et al. 2019), while two other species (*Plangia segonoides*, *Trigonocorypha maxima*) were found for the first time after their description more than 100 years ago (Carl 1914, Heller et al. 2019). Altogether the 94 orthopteran species found certainly do not represent the final species number in the 41 studied sites, and one could expect a higher number of species during a long-term study in different seasons there. In March, after the rainy season, a relatively high proportion of unidentifiable nymphs (e.g., in Ensifera, Eumastacoidea) and females (*Ruspolia*, *Conocephalus*) was also found. Furthermore, several species groups (mainly crickets Gryllidae, monkey hoppers Eumastacoidea, and katydids of genera *Conocephalus*, *Ruspolia*, and *Tylopsis*) could not be identified to the species level, because the adequate keys for females are still missing and we have no sound recordings of males.

The mantid fauna in Madagascar is insufficiently known, and new species for science are frequently described (e.g., Mériguet 2005, 2013, in prep.). All seven species we found are still not included in the current Mantodea species file (Otte et al. 2019) On the other hand, all four phasmid species we found were already known in Madagascar (Brock et al. 2019).

The relatively low number of cockroach, phasmid, and mantid species we found can be explained by the methods used, with no special sampling techniques (use of light traps, night sampling) applied.

Assemblages of orthopteroid insect in different habitats and altitudes.—Here we present the first information on orthopteroid assemblages in five characteristic habitats and at different altitudes of Madagascar (e.g., Dirsh and Descamps 1968, Braud et al. 2014, Heller et al. 2018). We found habitat to be the most important variable explaining the variation among the particular species assemblages (7.5%, Fig. 5). When we look at the species diversity of these habitats, the highest number of species (51%) was found in savanna and shrubland sites and the lowest (29%) in cultivated sites/habitats. As savanna and shrubland are the most widely distributed habitat types in Madagascar (Moat and Smith 2007), and we sampled 17 such sites (41% of 41 sites), this percentage corresponds to 60 species, including the newly described *Parapyrrhicia leuca* Hemp & Heller, 2019 (Heller et al. 2019). We also found a high number of species (52) also at six high mountain sites (mountain grass- and shrubland), supporting their importance for conservation. Thanks to higher altitude (> 1000 m a.s.l.), this habitat is still less influenced than the lowland sites and habitats, similar to other countries where agriculture dominates (e.g., Grytnes and Vetaas 2002, Hodkinson 2005).

Rainforests are highly endangered habitats (Moat and Smith 2007, Vences et al. 2009, Irwin et al. 2010), and we were only able to sample orthopteroids at four sites. However, we found a relatively high number of species there (38; mainly in protected Ranomafana National Park). Most of these species are habitat specialists (tetrigids, katydids, *Chlorophlaeobella tananarive*, and mantids).

We found the same number of species (38) in semiarid spiny forests, another very characteristic and highly endangered habitat, occurring mostly in SW Madagascar (six sites surveyed), as in rainforests. However, this was the only site at which we found the katydid *Mimoscudderia longicaudata* Heller & Krištín, 2019 (Heller et al. 2019).

As expected, we found the lowest number of species (34) at the eight cultivated habitats sites (fields, orchards, and gardens). Within the most characteristic species, we found the grasshopper species *Aiolopus thalassinus rodericensis*, *Gastrimargus africanus*, *Oedaleus virgula*, *Acrida subtilis*, and *Acrotylus* spp. to be widespread. In more humid sites and rice field ecotones the species *Oxya hyla*, *Paracinema tricolor*, and *Duronia chloronota* were abundant, thus confirming the findings of Descamps and Wintrebert (1966). These habitats are the most changed and disturbed habitats of Madagascar, and most species live in ecotones with shrubland, pastures, and savannas. But the species number found there is still relatively high in comparison to other relatively undisturbed habitats. In this regard, it is important to mention that "disturbed habitats" have evolved differently in different Malagasy regions due to abiotic differences, but also differences in human pressure and land use, invasive and anthropogenic species, and the biotic contrasts between natural and anthropogenic habitat. For example, in southern areas the species might face gentler environmental contrasts between open spiny thicket and grazing lands used by livestock, whereas on the eastern part of the island species might face sharper contrasts between closed rainforest and open rice fields (cf. Irwin et al. 2010).

Altitudinal distribution.—The number of heterometabolous insect species and their abundance changes with altitude. The number of species mostly increases steeply with altitude up to a certain level, giving the maximum species richness at mid-altitudes. Within these mid-altitudes (e.g., some hundreds of metres a.s.l.), only a small change in the number of species is observed, but later, above a critical altitude (specific for each area), a decrease in species richness is evident (e.g., Claridge and Singhrao 1978, Grytnes and Vetaas 2002, Hodkinson 2005, Bidau 2014). In Orthoptera, for example, in East Africa, at the altitudinal gradient of Mt Kilimanjaro, Hemp (2009) found altogether 139 Caelifera species, while the majority of species (76) had their main occurrence in the lower altitudes, in the colline zone (700–1100 m a.s.l.) around the mountain, and 23 species were adapted to mountainous habitats, inhabiting sub-montane and lower montane zones. Only eight of these 23 species showed a clear preference for montane habitats (Hemp 2009). In our study, we could not find the altitudinal preferences of species, because several species were found only in small number of individuals and the material was sampled only during one month. But when we divided our 41 sites into three altitudinal zones, altogether 49 species were found at lower altitudes (< 455 m a.s.l., 15 sites), 73 species at middle altitudes (680–1050 m a.s.l., 13 sites) and 63 species at higher altitudes (1120–2250 m a.s.l.,13 sites). The relatively low number of species at lower altitudes can be explained by human disturbance at these sites, when more habitat changes occurred in frequently managed agricultural areas at lower altitudes and thus more species can survive at higher altitudes that are still less affected by human impact.

In Ensifera, we found more species only at lower altitudes (< 300 m a.s.l.), e.g., *Eurycorypha prasinata*, *Parapyrrhicia leuca*, *Trigonocorypha maxima*, *Colossopus grandidieri*, and *Amblylakis* sp., while at higher altitudes (> 1500 m a.s.l.) we found only species of the genera *Tylopsis* sp., *Conocephalus* sp., and *Ruspolia differens*. In Caelifera, we found more species at higher altitudes (> 1350 m a.s.l.), e.g., *Pycnocrania grandidieri*, and the following species were found only at high altitudes: *Parahysiella betsileana*, *Eyprepocnemis brachyptera*, *Hetaracris antennata*, *Spathosternum malagassum*, *Pyrgomorphella madecassa*, and *Ambositracris* spp. At lower sites (< 300 m a.s.l.), we found only e.g., *Conipoda calcarata* (6 sites, mostly up to 50 m a.s.l.), *Chromacrida brunneriana* (4 sites up to 50 m a.s.l.), *Pamphagella stenoptera*, *Geloius* sp., *Gymnohippus* sp., and *Lavanonia* sp., which supports a few present findings (Dirsh 1963a, b, Descamps and Wintrebert 1965, 1966, Dirsh and Descamps 1968). Comparing our data on altitudinal distribution of Caelifera species with the literature, most of the species have a wide altitudinal distribution from sea level up to 1500 m a.s.l. (Braud et al. 2014). However, we could confirm the occurrence at higher altitudes of several species, e.g., *Eyprepocnemis brachyptera* (Wintrebert 1972, Braud et al. 2014), *Ambositracris* spp., *P. betsileana* (Wintrebert 1972), and *P. madecassa* (Dirsh 1963b, Descamps and Wintrebert 1966), but some species were also found at higher altitudes than previously described (e.g., *H. zolotarevskyi*, *P. grandidieri* now up to 2250 m a.s.l., formerly only up to 300 m and 1200 m a.s.l., respectively).

Notes on distribution and ecology of some species.—Pamphagella stenoptera: We found this cryptic colored and endemic species in the gravel bank of a dry river bed in a dry spiny forest of Andohahela Mangatsiaka National Park (20 March 2015, 2 adult females and a subadult female); this species had been found previously only at four sites of southern and south-western Madagascar (Descamps and Wintrebert 1966, Dirsh and Descamps 1968).

Heteracris antennata: Only limited and outdated data are available on the distribution of this endemic species (Dirsh 1962, Dirsh and Descamps 1968). We found one male in Ibity Mts. (1950 m a.s.l., 29 March 2015) within the mountain grass- and shrubland assemblage together with the mountainous species *E. brachyptera*, *Parahysiella betsileana*, *Pyrgomorphella madegassa*, and *Dyscolorrhinus vittatus* (cf. Dirsh and Descamps 1968).

Rubellia nigrosignata: This normally brachypterous and endemic species was the most frequent (27% of sites) and abundant pyrgomorphid species in our material, occurring from the sea level up to 1550 m a.s.l. Moreover, we regularly found two color forms (mostly yellow-black, less green) and three macropterous individuals (one male and two females) in the coastal shrubland of the south and southwest (Ambola and Cape Saint Marie). Macroptery is rather rare, but known in this species (e.g., Descamps and Wintrebert 1966).

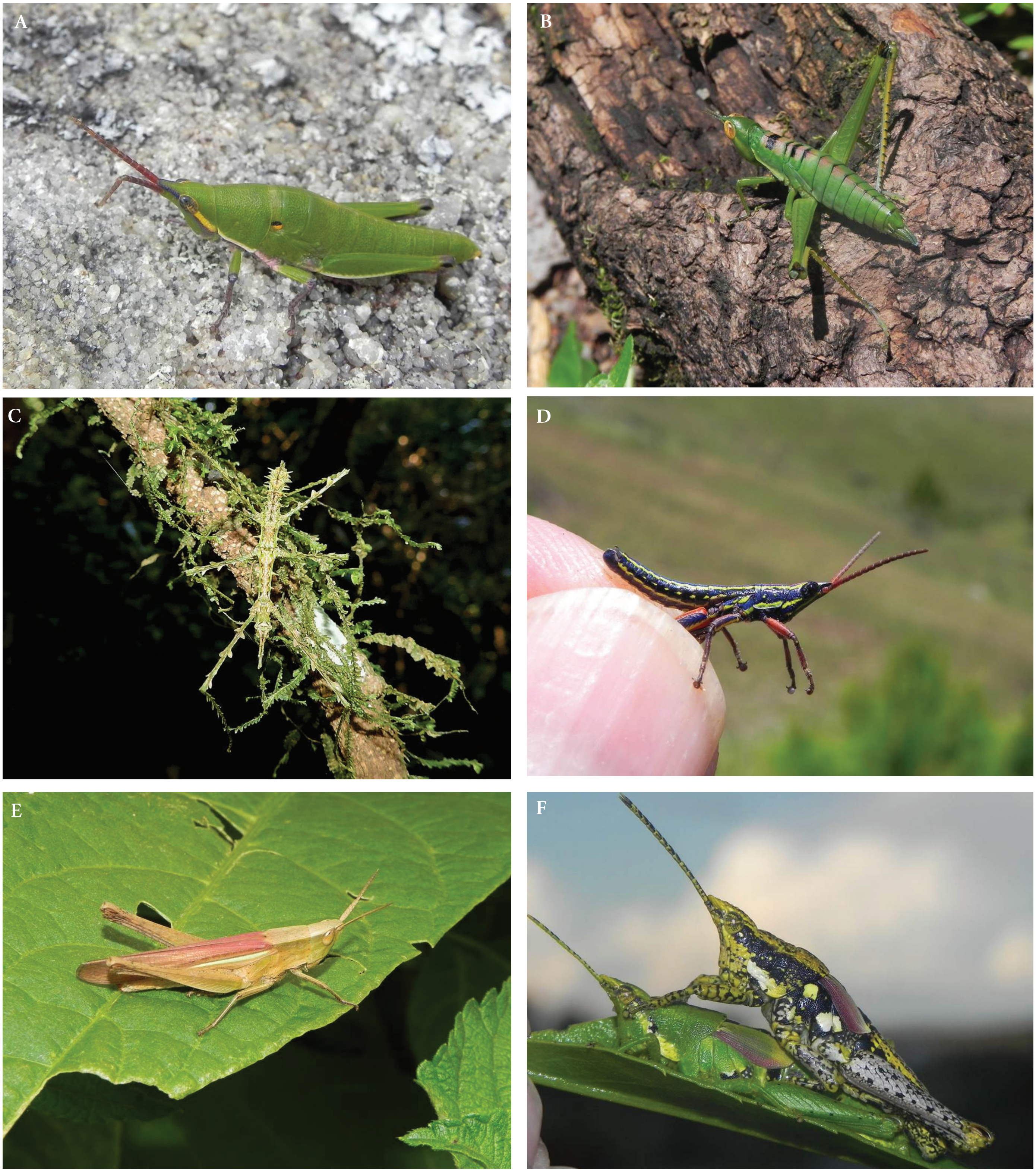

Fig. 7. A. Endemic species *Caprorhinus ranohirae* in savanna and shrubland of Isalo National Park; **B.** Monkey hopper *Apteropeoedes nigroplagiatus* female in semiarid spiny forest of Zombitse National Park; **C.** Cryptic and endemic mantid *Antongilia laciniata* in Ranomafana rainforest; **D.** Endemic *Ambositracris ornata* male in mountain grasslands and shrubs of Ibity Mts.; **E.** Afro-Malagasy species *Duronia chloronota* (yellow pink form) in cultivated habitats near Ambositra, and; **F.** eurytopic and color dimorphic endemic *Rubellia nigrosignata* in copula (shrubland in Anakao). Photos by A. Krištín.

The genus *Caprorhinus* is endemic to Madagascar and adjacent islands, and, in species number, it is the richest grasshopper genus (28 species). We found a few specimens of three species, *C. ranohirae* (savanna and shrubland in Isalo National Park), *C. zolotarevskyi* (shrubland near Fianarantsoa), and *C. kevani* (cultural steppe with bush near Ambatolahy), expanding the present knowledge on their distribution (Wintrebert 1972).

A few specimens of the endemic genera *Gymnohippus and Geloius* were found only in coastal shrubland (March 18, 2015) in south western Madagascar, similarly to Descamps and Wintrebert (1966).

Conspicuous aposematic species of the genus *Phymateus* were found in March only in the nymph stage at six sites, when clusters of nymphs were found in the second instar (one site with 81 individuals), the fourth instar (3 sites with 25–60 individuals), and the sixth instar (two sites with 20–22 individuals). All the nymph clusters were found on toxic host plants from the family Apocynaceae (*Pervillaea venenata*, *Leptadenia madagascariensis*, *Gomphocarpus fruticosus*), similarly to that mentioned by Descamps and Wintrebert (1966) and Braud et al. (2014).

Chlorophlaeobella tananarive: This small endemic species (syn. *Paralobopoma*) was previously found only in eight forested sites of C and E Madagascar (Dirsh and Descamps 1968). We found it in the rainforest of Ranomafana National Park (1150 m a.s.l.).

The most conspicuous eumastacid species, *Apteropeoedes nigroplagiatus*, was found at two sites (forest edge in Andringitra National Park and in a dry spiny forest of Zombitse National Park), which has expanded our knowledge on species distribution (Descamps and Wintrebert 1965). This species and some characteristic orthopteroid species found in particular in five habitats are shown in Fig. 7.

Remarks on data sampling.—Short-term (lasting one month) research has both advantages and disadvantages. The advantage is that in the same phenological aspect we can sample and compare species assemblages from different sites and habitats, but the disadvantage is that there are many species or life stages (e.g., adult males) that could not be found over such a short time or in a specific season. Hence, further research is needed to improve identification keys in some orthopteroid groups and the use of different sampling techniques. We could expect many more species, perhaps several new to science, to be found during systematic surveys over several seasons at the studied sites. In spite of all these methodological problems, we believe that these results can be used in the identification of conservation priorities at the studied sites and in Madagascar's endangered habitats.

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Appendix 1

List of all orthopteroid insect taxa with abbrevations used in the analyses and figures); * species endemic to Madagascar, **Afro-Malagasy distribution, *** Indomalaya- Malagasy distribution, **** widespread species.

Eurycorypha prasinata Stål, 1874* – EuryPras; *Mimoscudderia longicaudata* Heller & Krištín, 2019* –MimoLongi; *Parapyrrhicia leuca* Hemp & Heller, 2019* – ParaLeuc; *Phaneroptera sparsa* Stål, 1857****– PhanSpar; *Xenodoxus* sp.* – XenoSp; *Plangia segonoides* (Butler, 1878)* – PlanSego; *Trigonocorypha maxima* Carl, 1914* – TrigMaxi; *Tylopsis bilineolata* Karsch, 1893** – TyloBili; *Tylopsis* sp. – TyloSp; *Amblylakis* sp.* – AmblSp; *Colossopus grandidieri* Saussure, 1899* – ColoGran; *Conocephalus* (*Anisoptera*) *iris* (Serville, 1838)** – ConoIris; *Conocephalus* (*Anisoptera*) cf. *maculatus* (Le Guillou, 1841)**** – ConoMacu; *Conocephalus* (*Megalotheca*) cf. *marcelloi* Gorochov & Llorente, 2004* – ConoMarc; *Conocephalus* (*Megalotheca*) cf. *xiphidioides* (Karny, 1907)* – ConoXiph; *Conocephalus* sp1. – ConoSpA; *Conocephalus* sp2. – ConoSpB; *Ruspolia differens* (Serville, 1838)** – RuspDiff; *Ruspolia* cf. *abrupta* (Walker, 1869)* – RuspAbru; *Ruspolia* cf. *madagassa* (Redtenbacher, 1891)* – RuspMada; *Ruspolia* sp. – RuspSp; *Gryllotalpa madecassa* (Chopard, 1920)* – GryllMade; Gryllidae g.sp.1 – GryllSp; Podoscirtinae g.sp1. – PodoSpA; Podoscirtinae g.sp2. – PodoSpB; *Oecanthus* cf. *brevicauda* Saussure, 1878** – OecaBrev; *Arexion suavis* Rehn, 1929* – ArexSuav; *Cryptotettix* sp.* – CrypSp; *Oxytettix arius* (Rehn, 1929)* – OxytAriu; *Oxytettix lathraeospanius* (Günther, 1939)* – OxytLath; *Paratettix cinereus* Bolívar, 1887* – ParaCine; *Pseudosystolederus sikorai* Günther, 1939* – PseuSiko; *Acrida madecassa* (Brancsik, 1892)* – AcriMade; *Acrida subtilis* Burr, 1902* – AcriSubt; *Calephorus ornatus* (Walker, 1870) – CaleOrna; *Chlorophlaeobella tananarive* (Dirsh, 1963)* – ChloTana; *Chromacrida radamae* (Saussure, 1899)* – ChroRada; *Chromacrida brunneriana* (Bolívar, 1893)* – ChroBrun; *Duronia chloronota* (Stål, 1876)** – DuroChlo; *Gymnobothrus variabilis* Bruner, 1910* – GymnVari; *Gymnobothrus madacassus* Bruner, 1910* – GymnMada; *Leptacris monteiroi hova* (Karsch, 1896)* – LeptMont; *Acorypha decisa* (Walker, 1870)***– AcorDeci; *Catantops stenocrobyloides* Karny, 1907* – CataSten; *Catantopsis malagassus* (Karny, 1907)* – CataMala; *Catantopsis sacalava* (Brancsik, 1892)*** – CataSaca; *Parahysiella betsileana* Wintrebert, 1972* – ParaBets; *Pamphagella stenoptera* Descamps & Wintrebert, 1966* – PampSten; *Cyrtacanthacris tatarica* (Linnaeus, 1758)****– CyrtTata; *Finotina radama* (Brancsik, 1892)* – FinoRada; *Nomadacris septemfasciata* (Serville, 1838)** – NomaSept; *Rhadinacris schistocercoides* (Brancsik, 1892)* – RhadSchi; *Eyprepocnemis smaragdipes* Bruner, 1910* – EyprSmar; *Eyprepocnemis brachyptera* Bruner, 1910* – EyprBrac; *Heteracris antennata* (Bolívar, 1914)* – HeteAnte; *Heteracris finoti* (Bolívar, 1914)* – HeteFino; *Heteracris nigricornis* (Saussure, 1899)* – HeteNigr; *Heteracris zolotarevskyi* (Dirsh, 1962)* – HeteZolo; *Gelastorrhinus edax* Saussure, 1899* – GelaEdax; *Acrotylus patruelis* (Herrich–Schäffer, 1838)**** – AcroPatr; *Acrotylus aberrans* Bruner, 1910* – AcroAber; *Aiolopus thalassinus rodericensis* (Butler, 1876)* – AiolRode; *Conipoda calcarata* Saussure, 1884* – ConiCalc; *Gastrimargus africanus* (Saussure, 1888)**** – GastAfri; *Locusta migratoria capito* (Saussure, 1884)**** – LocuCapi; *Oedaleus virgula* (Snellen van Vollenhoven, 1869)* – OedaVirg; *Paracinema tricolor* (Thunberg, 1815)**** – ParaTric; *Pycnocrania grandidieri* (Saussure, 1888)* – PycnGran; *Trilophidia cinnabarina* Brancsik, 1892* – TrilCinn; *Oxya hyla* Serville, 1831**** – OxyaHyla; *Spathosternum malagassum* Dirsh, 1962* – SpatMala; *Geloius nasutus* Saussure, 1899* – GeloNasu; *Geloius* sp.* – GeloSp; *Gymnohippus marmoratus* Bruner, 1910* – GymnMarm; *Gymnohippus* sp.* – GymnSp; *Phymateus saxosus* Coquerel, 1861* – PhymSaxo; *Phymateus* sp. – PhymSp; *Pyrgomorphella madecassa* Bolívar, 1904* – PyrgMade; *Rubellia nigrosignata* Stål, 1875* – RubeNigr; *Schulthessia biplagiata* Bolívar, 1905* – SchuBipl; *Ambositracris ornata* Dirsh, 1963* – AmboOrna; *Ambositracris* cf. *morati* Kevan, Akbar & Chang, 1971* – AmboMora; *Caprorhinus ranohirae* Kevan, 1963* – CaprRano; *Caprorhinus zolotarevskyi* Uvarov, 1929* – CaprZolo; *Caprorhinus kevani* Descamps & Wintrebert, 1966* – CaprKeva; *Dyscolorhinus squalinus* Saussure, 1899* – DyscSqua; *Dyscolorhinus vittatus* Kevan, Akbar & Singh, 1964* – DyscVitt; *Acanthomastax bifida* Descamps, 1964* – AcanBifi; *Apteropeoedes nigroplagiatus* Bolívar, 1903* – ApteNigr; *Apteropeoedes* sp1.* – ApteSpA; *Apteropeoedes* sp2. * – ApteSpB; *Apteropeoedes* sp3.* – ApteSpC; *Lavanonia* sp.* – LavaSp; *Wintrebertia* sp. – WintSp; *Tarachomantis* cf. *caldweli* Bates, 1863* – TaraCald; *Tarachomantis* sp1.* – TaraSpA; *Tarachomantis* sp2.* – TaraSpB; *Liturgusella malagassa* Saussure & Zehntner, 1895* – LituMala; *Polyspilota* sp.* – PolySp; *Chopardempusa neglecta* (Paulian, 1958)* – ChopNegl; *Popa spurca crassa* Giglio–Tos, 1917**** – PopaSpur; *Sipyloidea sipylus* (Westwood, 1859)**** – SipySipy; *Antongilia laciniata* Redtenbacher, 1906* – AntoLaci; *Paracirsia* cf. *distincta* (Brunner von Wattenwyl, 1907)* – ParaDist; *Achrioptera impennis* Redtenbacher, 1908* – AchrImpe; *Aeluropoda insignis* Butler, 1882* – AeluInsi; *Gromphadorhina portentosa* (Schaum, 1853)* – GromPort; Oxyhaloinae g.sp1. – OxyhSpA; Oxyhaloinae g.sp2. – OxyhSpB; Oxyhaloinae g.sp3. – OxyhSpC; *Rhabdoblatta* sp. – RhabEpil; Epilamprinae g.sp. – EpilSp; Pycnoscelinae g.sp. – PycnSp; Blaberidae g.sp1. – BlabSpA; Blaberidae g.sp2. – BlabSpB; *Periplaneta* sp. – PeriSp; *Blattella lobiventris* (Saussure, 1895)** – BlattLobi.

Supplementary material 1

Author: Anton Krištín, Klaus-Gerhard Heller, Milan Zemko, Jacques Rakotondranary, Benjamín Jarčuška

Data type: Microsoft Excel file

Explanation note: Orthopteroid insects at 41 sites (5 habitats) of central and southern Madagascar in altitudes between 0 and 2250 m a.s.l. (March 6–30, 2015). (Abundance: 1: less than 3 adult specimens, 2: 3–10 specimens, 3: 11–100 specimens, 4: more than 100 specimens. Landscape type: N = natural, C = cultivated. Habitat: C = cultivated, MGS = mountain grassland & shrub, RF = rainforest, SAS = savanna and shrubland, SF = semiarid spiny forest). For full species names see App. 1

Link: https://doi.org/10.3897/jor.28.34055.suppl1

Taxonomic and biogeographic revision of the genus *Lamellitettigodes* (Orthoptera: Tetrigidae) with description of two new species and additional notes on *Lamellitettix*, *Probolotettix*, and *Scelimena*

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Abstract

The genus *Lamellitettigodes* Günther, 1939 from Southeast Asia is reviewed. The genus currently includes seven species and is transferred to Tetriginae Rambur, 1838. Two new species are described: *Lamellitettigodes novaeguineae* **sp. nov.** from New Guinea and *Lamellitettigodes karwinkeli* **sp. nov.** from Yunnan, People's Republic of China. *Lamellitettigodes palawanicus* Günther, 1939 **stat. nov.** is no longer regarded as a subspecies of *L. contractus*, but a separate species. Two species are transferred from *Euparatettix* Hancock, 1904 to *Lamellitettigodes*: *Lamellitettigodes sagittatus* (Bolívar, 1887) **comb. nov.** and *Lamellitettigodes cultratus* (Bolívar, 1898) **comb. nov.** One species is transferred from *Tetrix* Latreille, 1802 to *Lamellitettigodes* - *Lamellitettigodes signatus* (Bolívar, 1887) **comb. nov**. *Xistra tricristata sumatrana* Bolívar, 1898 **syn. nov.**, *Xistra tricristata* Bolívar, 1898 **syn. nov.**, and *Probolotettix corticolus* Blackith & Blackith, 1987 **syn. nov.** are synonymized with *Lamellitettigodes contractus* (Bolívar, 1887). *Probolotettix kevani* Blackith & Blackith, 1987 **syn. nov.** is synonymized with *Euparatettix personatus* (Bolívar, 1887). Additionally, in the genus *Lamellitettix* Hancock, 1904, *Lamellitettix acutus* Hancock, 1904 **stat. rev.** is retransferred from a subspecies of *Lamellitettix gallinaceus* (Stål, 1877) to a separate species status.

Keywords

China, fauna, Metrodorinae, New Guinea, Southeast Asia, synonymy

Introduction

At the end of August 2019, there were 2031 known Tetrigidae species worldwide (Cigliano et al. 2019). They occur on all the continents and inhabit almost all climatic zones from taiga to rainforests (Tumbrinck and Skejo 2017). Tetrigidae can easily be identified by their pronotum, which typically extends far over the body. This feature is clearly unique and proves the allocation of the species without doubt. Since 2014, the Tetrigidae of New Guinea has been revised in several papers (Tumbrinck 2014a, b, 2015, 2018, Tumbrinck and Skejo 2017). At the beginning of the revision, 67 species were known from New Guinea and the adjacent islands Aru, Biak, Waigeo, and Yapen. With the genus *Lamellitettigodes*, another genus is comprehensively revised within the context of the ongoing revision of the Tetrigidae of New Guinea. The genus was established by Günther (1939) and comprised two species with three subspecies. After 1939, for the first time the genus is fundamentally revised. With the addition of a new species described in this paper, there are currently 145 species known for New Guinea and the adjacent islands.

Material and methods

All specimens originate from the collections of several museums. Various cameras using various lenses were used to take photos, all in macro mode by using a stacking system with an integrated scale bar or with a macro lens and millimeter paper. No post-processing of photographs was done. Millimeter paper was placed close to the photographed specimen and subsequently used to construct a scale bar, included in the photograph, after which the millimeter paper was deleted. The morphological terminology and measurement methods follow Tumbrinck (2014a) and good taxonomic practice suggested in Lehmann et al. (2017). For many localities, the geographical coordinates were identified as accurately as possible by localization of the place found on the labels with different gazetteers and extracted using the Google Earth program. These localities are presented in square brackets.

Depository abbreviations

ANIC	Australian National Insect Collection, CSIRO, Canberra City, Australian Capital Territory, Australia
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
BMEC	Bohart Museum Entomology Collection, Davis, California, USA
BMNH	The Natural History Museum, formerly British Museum (Natural History), London, UK
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA
CDS	Collection Silva, Viçosa, Brasil
CJT	Collection Tumbrinck, Wassenberg, Germany
CMKT	Collection Tan, Singapore

IRSNB	Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium
LEMQ	Lyman Entomological Museum and Research Laboratory, Quebec, Canada
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland
MLU	Martin-Luther-Universität, Zoologisches Institut, Halle, Germany
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNSL	Naturkundemuseum, Leipzig, Germany
MSNG	Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy
MZB	Museum Zoologicum Bogoriense, Bogor, Java, Indonesia
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden
NMEG	Naturkundemuseum Erfurt, Germany
NMI	National Museum of Ireland, Dublin, Ireland
NMW	Naturhistorisches Museum Wien, Austria
OSF	Orthoptera Species File Database (http://orthoptera.speciesfile.org)
RMNH	Naturalis Biodiversity Center, Leiden, The Netherlands
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
SMTD	Staatliches Museum für Tierkunde, Leipzig, Germany
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany
ZMHU	Zoologisches Museum der Humboldt Universität, currently Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany
ZMUC	Universitets København, Zoologisk Museum, København, Denmark

Type specimens abbreviations

Holotype (HT); lectotype (LT); paralectotype (PLT); paratype (PT); syntype (ST).

Results

Taxonomy

Genus *Lamellitettigodes* Günther, 1939

Lamellitettigodes Günther, 1939: 123; Yin et al. 1996: 878; Otte 1997: 46.

Type species.—*Paratettix contractus* (Bolívar, 1887), by original designation.

Taxonomic placement and justification.—Günther (1939) assigned the genus *Lamellitettigodes* to the subfamily of Metrodorinae because of the lateral lobes: they are almost, but not completely, attached as in *Paratettix* Bolívar, 1887. This was the main character used when the subfamily was established by Bolívar (1887), and Günther also adopted it. Today, typically Metrodorinae are mainly characterized by having the median ocellus and the antenna placed below the eyes, a relatively small divergence of the rami of the frontal costa not forming wide scutellum, and a similar length of the first and third segments of the hind tarsus (Pavón-Gonzalo et al. 2012). Many species of Metrodorinae also exhibit the posterior angles of the lateral lobes of the pronotum produced outwards, often becoming acutely spinose. These characters taken together separate the subfamily from the other eight subfamilies of Tetrigidae, although no single character is enough to characterize Metrodorinae by itself (Tumbrinck and Skejo 2017).

In contrast to Metrodorinae, in *Lamellitettigodes* the antenna is inserted at the lower margin of the eyes, and the first segment of the hind tarsus is longer than the third segment. The similarity of *Lamellitettigodes* species with *Paratettix* and *Euparatettix* is clear when comparing all morphological characters from most of the *Paratettix* and *Euparatettix* species of Southeast Asia. *Lamellitettigodes* species have typical characters of Tetriginae: rounded lateral lobes of pronotum close to pronotum (directed downwards, slightly sidewards; this character is somewhat similar to Metrodorinae), presence of posthumeral spots on the pronotum, L-shaped carinae of the vertex, pulvilli of the hind tarsus with apical teeth (absent in some *Lamellitettigodes* species), and hind wings exceeding the tip of the pronotum. Therefore, *Lamellitettigodes* is very close to Tetriginae and did not belong to Metrodorinae: I transfer this genus to the subfamily of Tetriginae.

Description.—Günther (1939) gave a detailed description of the genus, which is no longer applicable in some of its parts and must be amended. An improved redescription based on his description is presented here.

Body of moderate size, slender. Head and pronotum smooth. Head and eye in lateral view not at all or slightly elevated above the pronotal discus. Antenna more than 1.5 times longer than fore femur, dorsal margin of antennal groove a little bit above the ventral margin of eye, between the eyes. Eyes small and in lateral view blunt and indistinctly conoidal. Antenna filiform, 14-segmented in male (including scapus and pedicel), 15-segmented in female. Fastigium of vertex in dorsal view as broad as or a little wider than the eye, fastigium in frontal view between the eyes slightly depressed. Fastigium in dorsal view with well-developed medial, lateral carinae, and fossula. Lateral carina clearly elevated, in lateral view weakly visible above the eyes and short, in dorsal view not converging towards the front, almost parallel, bending over at right angles to the medial carina (L-shaped). Transverse carina of the vertex in dorsal view slightly convex or straight. Frontal costa and facial carina in lateral view visible in front of eye (except in *L. novaeguineae*). Tip of fastigium and its frontal costa in lateral view protuberant. Facial carinae in lateral view concave in front of eye and slightly convex in front of antenna. Last segments of maxillary palps not foliaceous. Anterior margin of pronotum truncated. Pronotum slightly between shoulders. Prozonal carina and median carina clear, slightly elevated (lamellate in *L. cultratus* and *L. novaeguineae*), interhumeral carina absent, internal lateral carinae not clearly visible. Pronotum behind shoulders weakly depressed on both sides of median carina and here very often provided with black spots (posthumeral spots) on each side. Lateral lobes broadly rounded, not as close to body as in *Paratettix*. Tegmen almost as long as the fore femur, rather broad and at the end broadly rounded. Macropterous and macropronotal. Alae clearly exceed the pronotum apex. Hind femora with very small antegenicular and especially genicular teeth, with some sharply tuberculate raised slants of their middle outer surface. Posterior tibia distally not or slightly widened, with a few small spines on upper edges. First segment of the hind tarsus not longer than the third, pulvilli acute, in three species with apical teeth (*L. sagittatus*, *L. signatus*, *L. karwinkeli*). The coloration is highly variable and not a useful feature for either generic or specific diagnosis (as reported for Tetriginae in Lehmann et al. 2017).

Diagnosis.—The genus *Lamellitettigodes* is characterized by a protuberant tip of fastigium and frontal costa (in lateral view); facial carinae in lateral view visible and clearly concave in front of eye and slightly convex in front of antenna. Only in *L. novaeguineae* is tip of pronotum not visible in lateral view, but present. Additional characters for the genus are: 1) lateral carina of the vertex in frontal view clearly elevated as small fastigial horns, but in lateral view weakly visible above the eyes (Plate 5Q, R, V, W); 2) median carina continuous to the tip of the pronotum; 3) clearly keeled or lamellate median carina; and 4) keeled and more or less converging prozonal carinae.

The genus is close to *Euparatettix* and *Paratettix* (see above). In the typical representatives of mentioned genera, the tip of the fastigium is not protruding, but more or less rounded. Also, frontal horns are absent. In *Paratettix* the median carina is absent in the frontal margin of pronotum. A similarity exists also with *Lamellitettix* Hancock, 1904. The type species of the genus is *Lamellitettix acutus* Hancock, 1904 **stat. nov.** Blackith (1988) synonymized *L. acutus* and *L. pluricarinatus* Hancock, 1909 with *Lamellitettix insularis* (Bolívar, 1887), and *L. insularis* and *L. fletcheri* Hancock, 1915 with *Lamellitettix gallinaceus* (Stål, 1877) without giving evidence for the synonymy (Blackith 1992). Types of *L. gallinaceus* were examined by the author in NHRS and those of *L. pluricarinatus* in UMO. *L. acutus* and *L. pluricarinatus* are rather different from *L. gallinaceus* by the form of the pronotum, but it remains uncertain whether *L. acutus* and *L. pluricarinatus* are separate species. Further studies of the type of *L. acutus* and more specimens are needed. *Lamellitettix*, with its genotype *L. acutus*, is different from *Lamellitettigodes* by the tip of the fastigium which is, in lateral view, not protuberant, by the lateral carinae that are curved in dorsal view forward towards the medial carina and are not parallel, and by the lateral lobes that are acutely pointed sidewards. A similarity exists also to *Xistra* Bolívar, 1887 and *Xistrella* Bolívar, 1909. In the typical representatives of *Xistra* and *Xistrella*, the antenna is inserted in a considerable distance below the ventral margin of the eye. In *Lamellitettigodes*, the antenna is inserted as high as the ventral margin of the eye (Plate 5Q–X).

Composition and distribution.—Altogether seven species are now assigned to the genus *Lamellitettigodes*: one hitherto described species (widely distributed *L. contractus* from peninsular Malaysia, Singapore, Sumatra, Java, Borneo, Sulawesi, and Solomon Isl.) supplemented with a subspecies (*L. c. palawanicus* inhabiting Palawan archipelago of the Philippines) here elevated to the species level, two new combinations (widely distributed *L. sagittatus* from Vietnam, Thailand, peninsular Malaysia, Sumatra, Java, Borneo, Philippines, Moluccas Isl., Sulawesi, New Guinea, and Timor, and *L. signatus* from the Philippines) and two species described here as new to science (*L. novaeguineae* inhabiting SE New Guinea, and *L. karwinkeli* inhabiting Yunnan, PR China). One hitherto described species (*L. sumatrana*) and a subspecies (*L. contractus tricristatus*) are synonymized with *L. contractus*.

Key to species of Lamellitettigodes

1 Median carina in frontal part of pronotum compressed and elevated (Plate 1D) .... *L. cultratus* (Bolívar, 1898) **comb. nov.**
– Median carina in frontal part of pronotum not compressed and elevated (Plates 1A–C, 2E, H) 2
2 Distance between upper margin of paired ocelli and frontal margin of fastigium in frontal view less than a diameter of an ocellus (Fig. 1A); bifurcation of the frontal costa into facial carinae near frontal margin of fastigium 3
– Distance between upper margin of paired ocelli and frontal margin of fastigium in frontal view significantly larger than a diameter of an ocellus (Fig. 1B); bifurcation of the frontal costa into facial carinae in frontal view near ocelli or in the middle between ocelli and frontal margin of fastigium 6
3 Pronotum, in lateral view, more or less flattened (Plate 1B, C) 4
– Pronotum, in lateral view, undulated (Plate 2F–H) 5
4 Median carina in lateral view continuously bent to tip of pronotum (Plate 1C) .... *L. signatus* (Bolívar, 1887) **comb. nov.**
– Median carina, in lateral view, not continuously bent to tip of pronotum; in prozona rising again (Plates 1B, 2H) .... *L. sagittatus* (Bolívar, 1887) **comb. nov.**
5 Median carina in lateral view slightly undulated but without depression above beginning of tegmen (Plate 1B) .... *L. novaeguineae* **sp. nov.**
– Median carina in lateral view with depression above beginning of tegmen (Plate 2H) .... *L. karwinkeli* **sp. nov.**
6 Fastigial horns in frontal and lateral view not or slightly visible above eyes (Fig. 2A) .... *L. contractus* (Bolívar, 1887)
– Fastigial horns in frontal and lateral view clearly visible above eyes (Fig. 2B) .... *L. palawanicus* Günther, 1939, **stat. nov.**

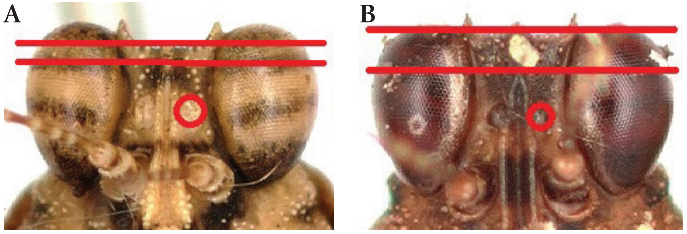

Fig. 1. Comparision of frontal costa between **A.** *L. novaeguineae* ♀ HT and **B.** *L. palawanicus* ♀ NT.

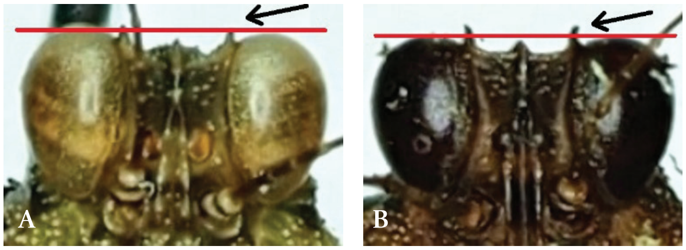

Fig. 2. Comparision of fastigial horns between **A.** *L. contractus* ♀ NT from Sumatra and **B.** *L. palawanicus* ♀ NT.

Lamellitettigodes contractus (Bolívar, 1887)

Plates 1A, 3I, 5Q

Paratettix contractus Bolívar, 1887: 188, 272, 281; Hancock 1907a: 56; Kirby 1910: 33; Bruner 1915: 54; Günther 1935: 262–263; Günther 1937: 136; Günther 1939: 124.
Tetrix contractus: Hancock 1907b: 236, 239; Hancock 1909: 412; Hancock 1913: 52; Günther 1939: 124.
Lamellitettigodes contractus: Günther 1939: 124–125; Steinmann 1970a: 228; Blackith 1992: 100; Paris 1994: 235; Yin et al. 1996: 878; Otte 1997: 46.

Type material.—LT *Lamellitettigodes contractus* (here designated): ♀, [Indonesia, Borneo], MNCN (Cat. Tipos No 243), original label

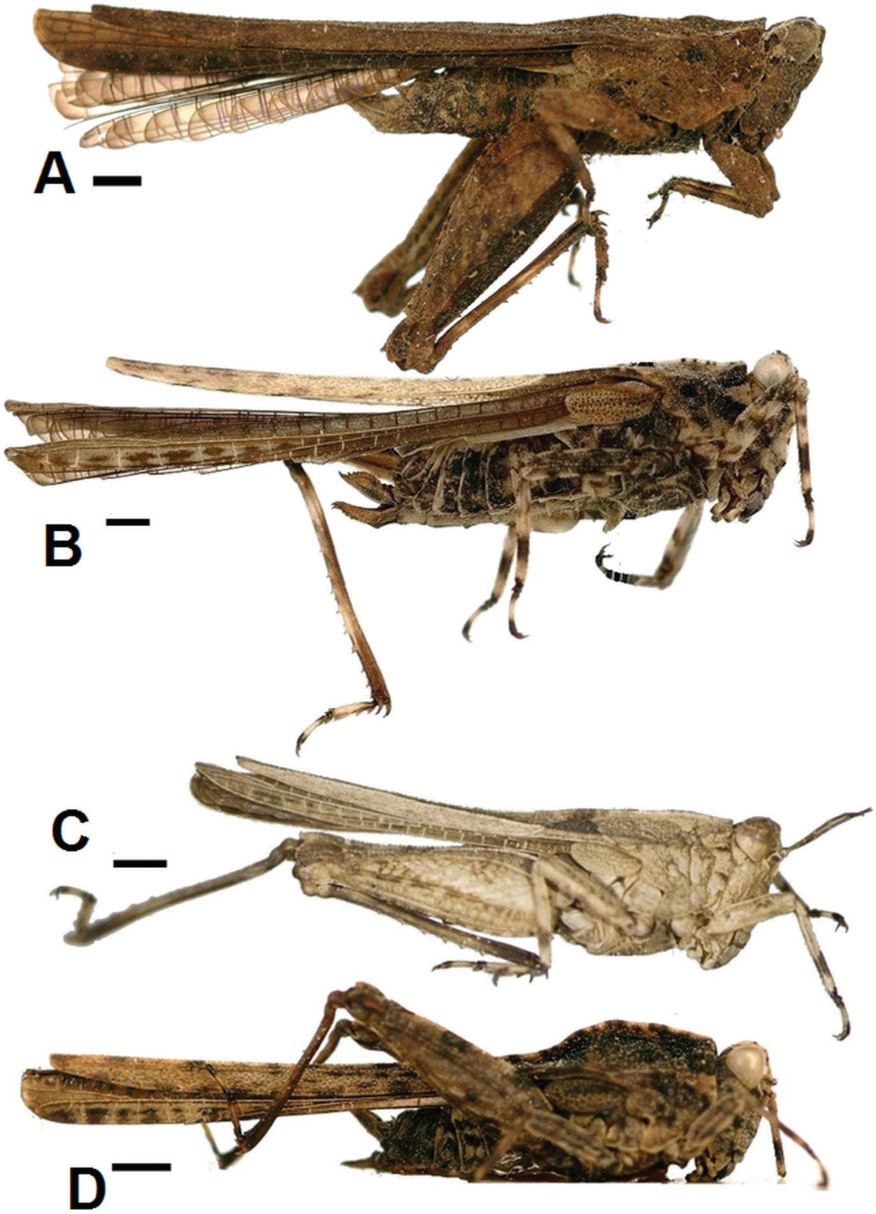

Plate 1. A–D (lateral view). **A.** *Lamellitettigodes contractus*, ♀ HT; **B.** *Lamellitettigodes sagittatus*, ♀ HT; **C.** *Lamellitettigodes signatus*, ♀ HT; **D.** *Lamellitettigodes cultratus*, ♀ HT. Scale bars: 1 mm.

from Bolívar "*Paratettix contractus* Bol." and label "Sintipo ?" from Mercedes Paris.

PLT *Lamellitettigodes contractus* (here designated): ♀, Philippines, NHRS (NRW-ORTH 0013201).

Lamellitettigodes tricristatus (Bolívar, 1898), syn. nov.

Xistra tricristata Bolívar, 1898: 75–76; Hancock 1907a: 46; Kirby 1910: 27; Willemse 1930: 30; Willemse 1931: 44; Günther 1939: 125.
Paratettix tricristatus: Günther 1935: 263.
Lamellitettigodes contractus tricristatus: Günther 1939: 125; Steinmann 1970a: 228; Paris 1994: 251.
Lamellitettigodes tricristatus: Otte 1997: 46.
Tetrix cuspidata Hancock, 1907 (Synonym)
Tetrix cuspidatus Hancock 1907b: 239–240; Hancock 1909: 413; Günther 1935: 263; Günther 1939: 125; Blackith 1992: 100.
Acrydium cuspidata: Kirby 1910: 579.

Type material.—LT *Lamellitettigodes tricristatus* (here designated): ♂, [Indonesia], Java, 1893, leg. H. Fruhstorfer, MNCN (Cat. Tipos No 39)

PLTs *Lamellitettigodes tricristatus* (here designated): 2♂♂+3♀♀, [Indonesia], Java, 1893, leg. H. Fruhstorfer, MNCN (Cat. Tipos No 40–44); ♂, [Indonesia], Java, Sakabumi, 1893, leg. H. Fruhstorfer, IRSNB.

Notes.—Bolívar (1898) described the species under the section Metrodorae as belonging to *Xistra*, while earlier he described *L. contractus* within the section Tettigiae, assigned to the genus *Paratettix*. The two sections were distinguished by morphology of the lateral lobes—projected sidewards in Metrodorae, directed downwards in Tettigiae. When comparing types, I did not see differences in this feature.

Günther (1939) regarded *L. contractus tricristatus* as a subspecies of *L. contractus*, distinguished from the nominal by smaller size, sharper keeled prozonal carinae and, in lateral view, clearly visible fastigial horns (above the eyes). *L. c. tricristatus* should be slightly smaller and should have wavy margins of the fore legs (Günther 1935). All these features are, however, in the range of variation of the species and are not of diagnostic value. Moreover, I did not find reported differences when comparing the types. Otte (1997) gave the specific status to the subspecies only with the reason of occurrence on different islands.

All these data prove that *L. tricristatus* (Bolívar, 1898) is conspecific with *L. contractus*.

Synonym *Tetrix cuspidata* Hancock, 1907

Notes.—Günther (1935) also synonymized *Tetrix cuspidata* Hancock, 1907 with *L. contractus*, but without giving detailed information. I have seen the STs and agree with his decision.

Type material.—LT *Tetrix cuspidata* (here designated): ♀, [Indonesia], Java, Pengalangan, 4000 ft, 1893, leg. Fruhstorfer (Type 727 1/3).

PLTs *Tetrix cuspidata* (here designated): 2♂♂, [Indonesia], Java, Pengalangan, 4000 ft, 1893, leg. Fruhstorfer (Type 727 2/3+3/3).

Hancock refers to four specimens from the same locality but in UMO only three specimens are present.

Lamellitettigodes sumatrana (Bolívar, 1898), syn. nov.

Xistra tricristata var. *sumatrana* Bolívar, 1898: 76; Willemse 1928: 4; Willemse 1930: 30–31; Günther 1935: 262–263; Günther 1939: 124; Paris 1994: 250–251.
Xistra tricristata sumatrana: Hancock 1907a: 46.
Xistra sumatrana: Steinmann 1970a: 230.
Xistra tricristata sumatrensis: Blackith 1992: 100.
Lamellitettigodes sumatrana: Otte 1997: 46.

Type material.—LT *Lamellitettigodes sumatrana* (here designated): ♀, Indonesia, Sumatra, Si-Rambé, XII.1890–III.1891, leg. E. Modigliani, MNCN (Cat. Tipos No 68), original label from Bolívar "*Xistra var. sumatrana* Bol." and label "Sintipo" from Mercedes Paris.

PLTs *Lamellitettigodes sumatrana* (here designated): ♂, ♀, [Indonesia], Sumatra, Si-Rambé, XII.1890–III.1891, leg. E. Modigliani, MNCN (Cat. Tipos No 69–70); 2♂♂, [Indonesia], Mentawei, Si Oban, IV-VIII.1894, leg. E. Modigliani, MNCN (Cat. Tipos No 71, 73); ♂, [Indonesia], Mentawei, Sipora, Sereinu, IV–VIII.1894, leg. E. Modigliani, MNCN (Cat. Tipos No 74); ♀, [Indonesia], Eng[g]ano, Bua-Bua, V–VI.1891, leg. E. Modigliani, MNCN (Cat. Tipos No 72); 7 specimens, [Indonesia], Sumatra, Si-Rambé, XII.1890–III.1891, leg. E. Modigliani, MSNG [not seen]; 5 specimens, [Indonesia], Mentawei, IV–VIII.1894, leg. E. Modigliani, MSNG [not seen]; 2 specimens, [Indonesia], Eng[g]ano, Bua-Bua, V–VI.1891, leg. E. Modigliani, MSNG [not seen]; 1 specimen, [Indonesia], Nias, leg. E. Modigliani, MSNG [not seen]; 2♂♂, 2♀♀, [Indonesia], Sumatra, Si-Rambé, XII.1890-III.1891, leg. E. Modigliani, IRSNB [not seen]; ♀, [Indonesia], Mentawei, Sipora, Sereinu, V–VI.1894, leg. E. Modigliani, RMNH; ♂, [Indonesia], Mentawei, Si Oban, IV-VIII.1894, leg. E. Modigliani; ♀, [Indonesia], Sumatra, Si-Rambé, XII.1890–III.1891, leg. E. Modigliani, NHRS (NRM-ORTH 0013047 + 0013046).

Notes.—Bolívar (1898) described the taxon as a variety of *Xistra tricristata*. In contrast to *L. tricristatus*, the prozonal carinae are not curved to the middle and not keeled. The margins of the fore legs are slightly undulated. Günther (1935) synonymized *Xistra tricristata* var. *sumatrana* with *Paratettix contractus* without giving details. According to Günther (1939), the specimens of *L. sumatrana* have in lateral view only slightly visible elevated lateral carinae above the eyes and wavy median carina in front of and behind the shoulders. In the specimens of *L. contractus* from Borneo, these undulations are weaker. Otte (1997) gave the subspecies a specific status based on occurrence on different islands (as in *L. tricristatus* mentioned above). All these features are within the range of variation of the species and do not represent diagnostic traits. I did not find differences when comparing the types and, therefore, *L. sumatrana* (Bolívar, 1898) (original combination *Xistra tricristata sumatrana*) is regarded as conspecific with *L. contractus*.

Probolotettix corticolus Blackith & Blackith, 1987, syn. nov.

Probolotettix corticolus: Blackith and Blackith 1987: 5–8; Blackith 1990: 89–90; Blackith 1992: 146; Yin et al. 1996: 902 (error: *carticolus*); Otte 1997: 57.

Type material.—HT *Probolotettix corticolus*: ♀, Indonesia, Sulawesi, Minehassa Prov., Dumoga-Bone National Park, 13.III.1985, leg. Blackith, RMNH (not seen, probably lost).

PTs *Probolotettix corticolus*: ♂, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, I.–III.1985, leg. R. & R. Blackith, BMNH; ♀, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, I.–III.1985, leg. R. & R. Blackith, LEMQ; ♂+♀, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, I.–III.1985, leg. R. & R. Blackith, NMI (not seen), MZB (not seen).

Notes.—After the description and the drawing of the HT in Blackith and Blackith (1987), this species is a typical *L. contractus*. I have seen the PT in BMNH and LEMQ and there is no doubt that they are *L. contractus*.

Additional material examined.—Philippines: 3♂♂, Siargao, 9°52'33"N, 126°00'35"E, on leaf, 28 m, 7.IV.2018, leg. M. K. Tan, Yeo, H., Yap, S. A. & Baroga, J. B., CMTK. Indonesia: ♀, Sumatra, Lac de Toba, 1.V.1929, leg. Prince Leopold, RMNH; ♀, Sumatra, Soekaranda, leg. Dohrn, SMTD; ♀, W. Sumatra, Padang Panjang, 28.VIII.1991, leg. W. Guidetti, CJT; ♀, Sumatra, Sibolangit, 550 m, 11.X.1921, leg. J. B. Corporaal, RMNH; ♂, ♀, Sumatra, Fort de Kock, 920 m, 1926, leg. E. Jacobson, RMNH; ♂, Sumatra, Lubuksikaping (Sumatra's Westkust), 450 m, 1926, leg. E. Jacobson, RMNH; 2♂♂, 7♀♀, Sumatra, S. W. Lampong distr., Mt. Tanggamoes, Gisting ult., 500 m, XII.1939, leg. M. A. Lieftinck, RMNH; 2♂♂, Mentawai, Siberoet, 24.+28.IX.1924, leg. H. H. Karny, RMNH; ♂, Mentawai, Sipora, 11.X.1924, leg. H. H. Karny, RMNH; ♀, Nias, Sisobahili I., Tankec, ca. 14 km v. Gunung Sitoli, IX.1991, leg. W. Guidetti, CJT; ♂, ♀, Westjava, Mt. Guntur, Garoet, 1350 m, leg. Overbeck; ♂, ♀, Java, G. Tjikorai, 900 m, X.1934, leg. E. Jacobson, RMNH; ♂, Java, Tjikadjang, Bandjarwangi, W. Java, 800–900 m, 7.–10.IV.1939, leg. M. A. Lieftinck, RMNH; ♂, Java, Penandjoeng Bay, Kalinnoetjang, 300 m, VII.1936, leg. M. A. Lieftinck, RMNH; 3♂♂, 4♀♀, Borneo, Midden O. Borneo, 19.VIII.1925, RMNH, leg. H. C. Siebers; ♀, Borneo, Tabang, Bengen River, East Borneo, 125 m, 10.IX.1956, leg. A. M. R. Wegner, RMNH; ♀, Borneo, O. Borneo, Tandjong Redeb, leg. Mjöberg, NHRS; ♀, Borneo, Sarawak Distr., leg. Mjöberg, NHRS; 3♂♂, 2♀♀, Borneo, Long Navang, leg. Mjöberg, NHRS; 2♂♂, 3♀♀, Borneo, Kajan River, leg. Mjöberg, NHRS; ♀, Borneo, East-Sabah, Sepilok RDC, 5°87'57.57"N, 117°94'75.76"E, leg. T. Kirschey, CJT. Solomon Islands: 2♂♂, Malaita, Auki, 2–20 m, 22.IX.1957, leg. J. L. Gressitt, BPBM.

Differential diagnosis.—*L. contractus* has more or less parallel prozonal carinae, slightly bent backwards. The distance between the upper margin of the superior ocelli and frontal margin of the fastigium is significantly larger than a diameter of an ocellus in frontal view. The species is similar to *L. palawanicus*. This species can be easily separated by the tip of fastigium and frontal costa, which are distinctly protuberant in front of the eyes, and the fastigial horns, which are clearly visible above the eyes.

Measurements.—(in mm) *L. c. contractus* (LT/PLT): Pronotum length 12.61/11.63; pronotum lobe width 3.25/2.92; pronotum height 2.53/1.58; vertex width 0.54/0.45; eye width 0.45/0.45; tegmen length 1.60/1.50; hind wing length 11.18/10.88; postfemur length LT 5.46; postfemur width LT 1.70.

L. c. tricristatus **syn. nov**. LT: Pronotum length 8.71; pronotum lobe width 2.57; pronotum height 1.95; vertex width 0.43; eye width 0.39; tegmen length 1.07; hind wing length 7.28; postfemur length 3.95; postfemur width 1.25.

L. c. sumatrana **syn. nov.** (LT/PLT): Pronotum length 10.40/10.01; pronotum lobe width 2.99/2.73; pronotum height 2.74/2.21; vertex width 0.50/0.49; eye width 0.41/0.39; tegmen length 1.56/1.43; hind wing length 10.27/9.23; postfemur length 5.07/4.55; postfemur width 1.69/1.43.

T. cuspidata (LT/PLT2/3/PLT3/3): Pronotum length 10.79/10.92/8.71; pronotum lobe width 3.25/2.80/2.65; pronotum height 1.65/1.50/1.35; vertex width 0.50/0.47/0.45; eye width 0.47/0.47/0.41; tegmen length 1.55/1.45/1.30; hind wing length 8.97/10.53/8.58; postfemur length 5.20/4.40/4.24; postfemur width 1.65/1.45/1.35.

Additional measurements: (in mm) ♀ Sumatra, Lac de Toba: Pronotum length 9.75; pronotum lobe width 2.95; pronotum height 2.29; vertex width 0.54; eye width 0.41; tegmen length 1.30; hind wing length 9.23; postfemur length 4.88; postfemur width 1.45. ♀, Borneo, Sepilok RDC: Pronotum length 10.79; pronotum lobe width 3.00; pronotum height 1.45; vertex width 0.47; eye width 0.45; tegmen length 1.55; hind wing length 10.27; postfemur length 4.81; postfemur width 1.60. ♂, Solomon Is., Malaita: pronotum length 9.88; pronotum lobe width 2.60; pronotum height 1.45; vertex width 0.47; eye width 0.43; tegmen length 1.35; hind wing length 8.97; postfemur length 4.42; postfemur width 1.40.

Distribution.—The species inhabits the Southeast Asian mainland (Günther 1939), Singapore (Hancock 1909), islands of Southeast Asia - Sumatra (and adjacent Nias, Mentawai, and Enggano), Java, Borneo, Sulawesi (Günther 1939), and finally the Solomon Islands. The species has not been found hitherto in New Guinea. Hancock (1907a), however, refers to New Guinea under *Xistra tricristata*, and Günther (1935) wrote " (...) also known to me from SE New Guinea". I have not been able to detect this species in New Guinea and the Bismarck Archipelago, although it is found to inhabit the Solomon Islands. Hancock's (1907a) and Günther's (1935) records could belong to *L. novaeguineae* **sp. nov.**

Lamellitettigodes sagittatus (Bolívar, 1887), comb. nov.

Plates 1B, 3J, 5R

Paratettix sagittatus Bolívar, 1887: 188, 280–281.
Xistra sagittata: Bolívar 1898: 76; Hancock 1907a: 46; Kirby 1910: 27; Willemse 1930: 31, 207; Günther 1939: 160; Blackith 1992: 197; Paris 1994: 248; Yin et al. 1996: 930 (error: *sagittaria*); Otte 1997: 67
Euparatettix sagittatus: Günther 1937: 138–139; Günther 1938: 2–3, 41; Günther 1941: 155–156; Günther 1942: 345; Steinmann 1970a: 232; Yin et al. 1996: 870; Zheng et al. 2011: 385; Deng 2016: 302.

Type material.—LT *Lamellitettigodes sagittatus* (designated by Paris 1994): ♀, Philippines, Daraga, MNCN (Cat. Tipos No 126), original label from Bolívar "*Xistra sagittata* Bol." and label "Lectotipo" from Mercedes Paris.

ST (= PLT) *Lamellitettigodes sagittatus*: ♀, Philippines, NHRS [referred by Bolívar 1887 but not found in NHRS].

Synonym *Euparatettix pulvillus* Hancock, 1910: 360; Günther, 1937: 131, 138.

HT *Euparatettix pulvillus*: Malaysia, Selangor, Riverside Estate Kwala, IX.1907, leg. H. C. Pratt, UMO.

Note: Günther (1937) synonymized *E. pulvillus* Hancock, 1910 with *L. sagittatus* after the description of Hancock. I have seen the HT and agree with his decision.

Synonym *Tetrix polypictus* Hancock, 1913: 52–53; Günther, 1937: 131, 138; Otte, 1979: 41

Acrydium polypictum: Hancock, 1915: 135.

HT *Tetrix polypictus*: ♀, Malaysia, Borneo, Kuching, ANSP (not seen).

Note: Günther (1937) synonymized *T. polypictus* Hancock, 1913 with *L. sagittatus* after the description of Hancock.

Additional material examined.—Vietnam: 3 ♂♂, 5♀♀, Bac Giang Prov., Tay Yen Tu Nat. Res. Thanh So'n, 18.–21.V.2015, leg. A. Skale, CJT, NMEG; 1 ♀, Thai Nguyen Province, vic. Ngoc Thanh, vic. Me Linh (IEBR station), 21°23'03"N, 105°42'44"E, 2.V.2012, leg. A. Weigel, CJT.

Thailand: ♀, Khao Soi Dao, 15.X.1985, leg. S. Ingrisch, CJT; ♀, Chanthaburi Khao Soi Dao, 12.VI.1988, leg. S. Ingrisch, CJT.

Malaysia: ♀, Selangor, Riverside Estate Kwala, IX.1907, leg. H. C. Pratt, UMO; ♂, 2♀♀, Pahang, Bukit Chitimani along overgrown path at base of limestone crop, 3°26'48"N, 102°0'47"E, 12.III.2016, leg. L. Willemse, RMNH, CJT; ♂, Pahang, Bukit Chitimani along overgrown path at base of limestone crop, 3°26'48"N, 101°55'59"E, 11.III.2016, leg. L. Willemse, RMNH.

Malaysia: Borneo: ♂, Banguey [Pulau Banggi], 1935, SMTD; 6♂♂, 5♀♀, East-Sabah, Sepilok RDC, 16.XI.2016, leg. T. Kirschey, CJT; ♂, ♀, Sabah, Kinabalu National Park, 5.–7.VIII.1984, leg. S. Ingrisch, CJT; ♂, ♀, Sabah, Kinabalu National Park, 8.VIII.1984, leg. S. Ingrisch, ZFMK; ♀, Sarawak, Ng. Jagau, Sg. Ngemah, 3 Div., ex hill padi, single hill sample JF-2-18, 22.XI.1974, leg. D. Munroe, LEMQ.

Indonesia: Sumatra: ♂, Padang, MLU; ♀, Soeruil, IV.1878, ♀, Eng[g]ano, Bua-Bua, V.1891-VI.1891, leg. E. Modigliani, MSNG; RMNH; ♂, 4♀♀, Pangherang-Pisang, X.1890-III.1891, leg. E. Modigliani, MSNG; ♀, Fort de Kock, 920 m, 1925, leg. E. Jacobson, RMNH; 4♂♂, ♀, Anai Kloof (Sumatra's Westkust), 500 m, 1925+1926, leg. E. Jacobson, SMTD, RMNH; ♂, ♀, Medan, Gedong Djohore, 7.II.1928, leg. M. Mohr, RMNH; ♀, S. W. Lampong distr., Mt. Tanggamoes, Gisting ult., 500 m, XII.1939, leg. M. A. Lieftinck, RMNH; ♀, Palembang Office, Dinas Kehutanan, [2°56'42.245"S, 104°43'44.663"E], 17 m, leg. T.Kirschey, CJT;

Mentawai: ♀, Siberoet, 18.IX.1924, leg. H. H. Karny, RMNH;

Sulawesi: ♂, Nr. Morowali, Ranu River area, 27.I.–20.IV.1980, leg. M. J. D. Brendel, BMNH; ♂, street Kotamobagu-Motoling (North Sulawesi), 15.–16.I.2001, leg. M. Hoffmann, MNSL; 2♀♀, Prov. Gorontalo, Taman Nasional Nani Bogani Wartabone, 7.VIII.2016, leg. T. Kirschey, CJT;

Java: ♀, Salatiga, [7°19'S, 110°33'E], leg. W. Roepke, RMNH; ♀, Tjimandala [Cimandala], XII.1923, SMTD; 2♀♀, G. Tjikorai, X.1934, leg. E. Jacobson, RMNH; ♀, Buitanzorg [Bogor], 17.IX.1941, leg. P. A. Blijdorp, RMNH; ♂, Bogor, Botanical Garden, 21.III.1993, leg. S. Ingrisch, CJT; 4♂♂, 8♀♀, Bogor, Botanical Garden, 6°35'51"S, 106°47'58"E, 21.II.+31.VII.2016, leg. T. Kirschey, CJT; ♀, Surabaya 43 km SW, Mt. Pennggungan, hotel PPLH, 370 m, 7°36'29"S, 112°09'40"E, 18.–19.VIII.2017, leg. D. Telnov, NMEG;

Borneo: ♂, Tandjong Redeb, leg. Mjöberg, NHRS;

Moluccas: ♀, Buru, Nal Beti, 10.V.1921, leg. L. J. Toxopeus, RMNH; ♀, Isl. Batjan, Salawaku river, 50–100m, 17.VI.1963, RMNH;

Aru: ♀, Aru, Wokan, 1873, leg. O. Beccari, MSNG;

Waigeo: 3♂♂, 4♀♀, 3 km W Waisai, 40–50 m, 0°26'04"S, 130°47'41"E, 18.II.2012, leg. D. Telnov, CJT, NMEG;

West Papua: ♂, ♀, Cyclops Mts., Sabron, Camp 2 [2°30'S, 140°25'E], 2000 ft, VI.1936, leg. L. E. Cheesman, BMNH; ♀, Cyclops Mts., Sabron, Camp 1 [2°30'S, 140°25'E], 1200 ft, 13.V.1936, leg. L. E. Cheesman, BMNH; ♀, Cyclops Mts., Sabron, Camp 1 [2°30'S, 140°25'E], 9300 ft, VI.1936, leg. L. E. Cheesman, BMNH; ♀, Cyclops Mts., Jayapura, Sentani, [2°36'S, 140°37'E], 100 m, 15.VI.1959, leg. J. L. Gressitt, BPBM; 3♀♀, Waris, S. of Hollandia [Jayapura], [3°11'S, 140°53'E], 450–500 m, 8.–15.VIII.1959, leg. T. C. Maa, CJT; 2♂♂, Doberai Peninsula, Arfak mts., Anggi Gigi Lake S env., Uper vill., 2200 m, 1°18'05"S, 133°54'24"E, 10.–11.IX.2015, leg. D. Telnov, CJT;

Papua New Guinea: ♂, Standlager bei Malu, [4°13'S, 142°49'E], leg. S. G. Bürgers, III.–IV.1912, ZMHU; ♂, Kokoda, 1200 ft, VIII.1933, leg. L. E. Cheesman, SMTD; ♂, Kokoda, 1200 ft, VII.1933, leg. L. E. Cheesman, BMNH; ♂, Orrori, 3500 ft, VII.1933, leg. L. E. Cheesman, BMNH; ♂, Upper Jimmy Valley, Wum, [5°34'S, 144°35'E], 840 m, 18.VII.1955, leg. J. L. Gressitt, BPBM; 2♂♂,2♀♀, Lae, Gurukor, under Coffee, 1800 ft, 7.VII.1957, leg. J. H. Ardley, ANIC; 2♀♀, Gurukor, Wampi Valley, under Coffee, [6°49'S, 146°37'E], 3000 ft, 7.VII.1957, leg. J. H. Ardley, ANIC; 2♀♀, Maprik [3°39'S, 143°03'E], 18.X.1957, leg. J. Smart, BMNH; ♀, Bokondini, 40 km N of Baliem Val., 1300 m, 5.–11.XI.1961, leg. S. & L. Quate, BPBM; 2♀♀, Bulolo, 800–900 m, 14.XI.1961, leg. J. & M. Sedlacek, BPBM; 4♂♂, 4♀♀, Lae, [6°44'S, 144°00'E], 10 m, 18.I.–24.I.1962, BPBM; ♂, Keria, Amazon Bay area, 1650 ft, 29.VI.–22.VII.1962, leg. W. W. Brandt, ANIC; ♀, Sum-Sum, 64 km N. of Wau, 15.II.1963, leg. H. W. Clissold, BPBM; 2♀♀, Wau, [7°20'S, 146°43'E], 1200 m, 15.IV.1963, leg. J. Sedlacek, BPBM; ♂, 7.V.1963, Ambunti, Sepik River, 200 m, leg. R. Straatman, BPBM; ♀, Northern district, Managalese area, VIII.1964, leg. R. Pullen, ANIC; ♂, Popondetta, [8°46'S, 148°14'E], 25 m, VI.1966, leg. Shanahan & Lippert, BPBM; ♀, Markham R. to Gabensis Village near Lae, 30.V.1967, leg. R. E. & R. M. Blackith, ANIC; 2♂♂, 3♀♀, Mt. Missim, [7°13'S, 146°49'E], 1800 m, 20.VII.1969, leg. J. L. Gressitt & Y. Hirashima, BPBM; ♂, 2♀♀, Morobe Prov., Wau, W.E.I., 22.V + 25.V.1982, leg. P. Grootaert, IRSNB; ♂, ♀, Brahman Miss. (St. 017), 5.+6.V.1988, leg. J. van Stalle, IRSNB; ♂, Madang Prov., Bundi [5°43'S, 145°13'E], 8.V.–10.V.1988, leg. J. van Stalle, IRSNB.

Differential diagnosis.—*L. sagittatus* has, together with *L. signatus and L. karwinkeli,* pulvilli of the hind tarsi bearing apical teeth. Bifurcation of the frontal costa into facial carinae is close to the transverse carinae of the vertex. In *L. signatus*, the median carina is bent to the tip of the pronotum while in *L. sagittatus* and *L. karwinkeli* the median carina rises again in the prozona. In contrast to *L. karwinkeli*, the median carina of *L. sagittatus* is flat or weakly wavy. In frontal view, there is a right angle between lateral and transverse carina in *L. karwinkeli,* while in *L. sagittatus* the angle is rounded.

Notes.—Günther (1937) retransferred this species to *Euparatettix*, with the note "although certainly related to *Lamellitettigodes*". Günther wrote in 1939 (translation): "I tend to think that the real affinity [of *Lamellitettigodes*] at least to *Euparatettix sagittatus* Bol. exists; but this species represents a true *Paratettix* or *Euparatettix*, and is to be left in these genera." *L. sagittatus* corresponds much better to the genus characteristics of *Lamellitettigodes* than those of *Euparatettix* or *Paratettix*. The carinae are clearly keeled. The prozonal carinae are the same as in *L. contractus*, and the tip of the fastigium is clearly protuberant in lateral view. I have examined the HT of *Euparatettix pulvillus* and agree with the synonymization by Günther (1937). I have not examined the type of *Tetrix polypictus* and was not able to check the synonymization by Günther (1937).

Specimens of *L. sagittatus* have variable size and coloration. Specimens from New Guinea have in frontal view less flattened fastigium than specimens from other regions. However, they belong to *L. sagittatus* because all other characteristics are the same.

Measurements.—(in mm) HT: Pronotum length 11.05; pronotum lobe width 3.00; pronotum height 2.07; vertex width 0.43; eye width 0.50; tegmen length 1.50; hind wing length 11.18; postfemur length 5.20; postfemur width 1.65.

E. pulvillus HT: Pronotum length 12.22; pronotum lobe width 3.19; pronotum height 3.37; vertex width 0.56; eye width 0.56; tegmen length 1.59; hind wing length 12.35; postfemur length 5.60; postfemur width 1.80.

Distribution.—The species inhabits Vietnam, Thailand, peninsular Malaysia, Sumatra and adjacent islands (Enggano, Mentawai), Java, Borneo, the Philippines, Moluccas Isl. (= whole Southeast Asia after Günther 1938), New Guinea (with adjacent islands Aru, Waigeo), and Timor (Günther 1937).

***Lamellitettigodes signatus* (Bolívar, 1887), comb. nov.**

Plates 1C, 3K, 5S

Tettix signatus Bolívar, 1887: 268.
Acrydium signatum: Kirby 1910: 45.
Tetrix signatus: Bruner 1915: 54; Blackith 1992: 185; Paris 1994: 249; Otte, 1997: 131.
Tetrix signata: Steinmann 1970a: 233; Yin et al. 1996: 920.

Type material.—HT (designated as LT by Mercedes Paris 1994) *Lamellitettigodes signatus*: ♀, Philippines, [Prov. Eastern Samar], Dolores, MNCN (Cat. Tipos No 123), original label from Bolívar "*T. signatus* Bol." and label "Lectotipo" from Mercedes Paris.

Additional material examined.—Indonesia: ♀, Indonesia, Ins. Buru, leg. H. Kühne, NMW.

Differential diagnosis.—*L. signatus* is unique in having median carina extended in a small flattened arch to the frontal margin of pronotum. Other characters are the shorter pronotum and hind wings, but possibly in other species there are specimens with shortened pronotum and hind wings that have not been found yet.

Measurements.—(in mm) HT: Pronotum length 10.89; pronotum lobe width 3.00; pronotum height 2.54; vertex width 0.66; eye

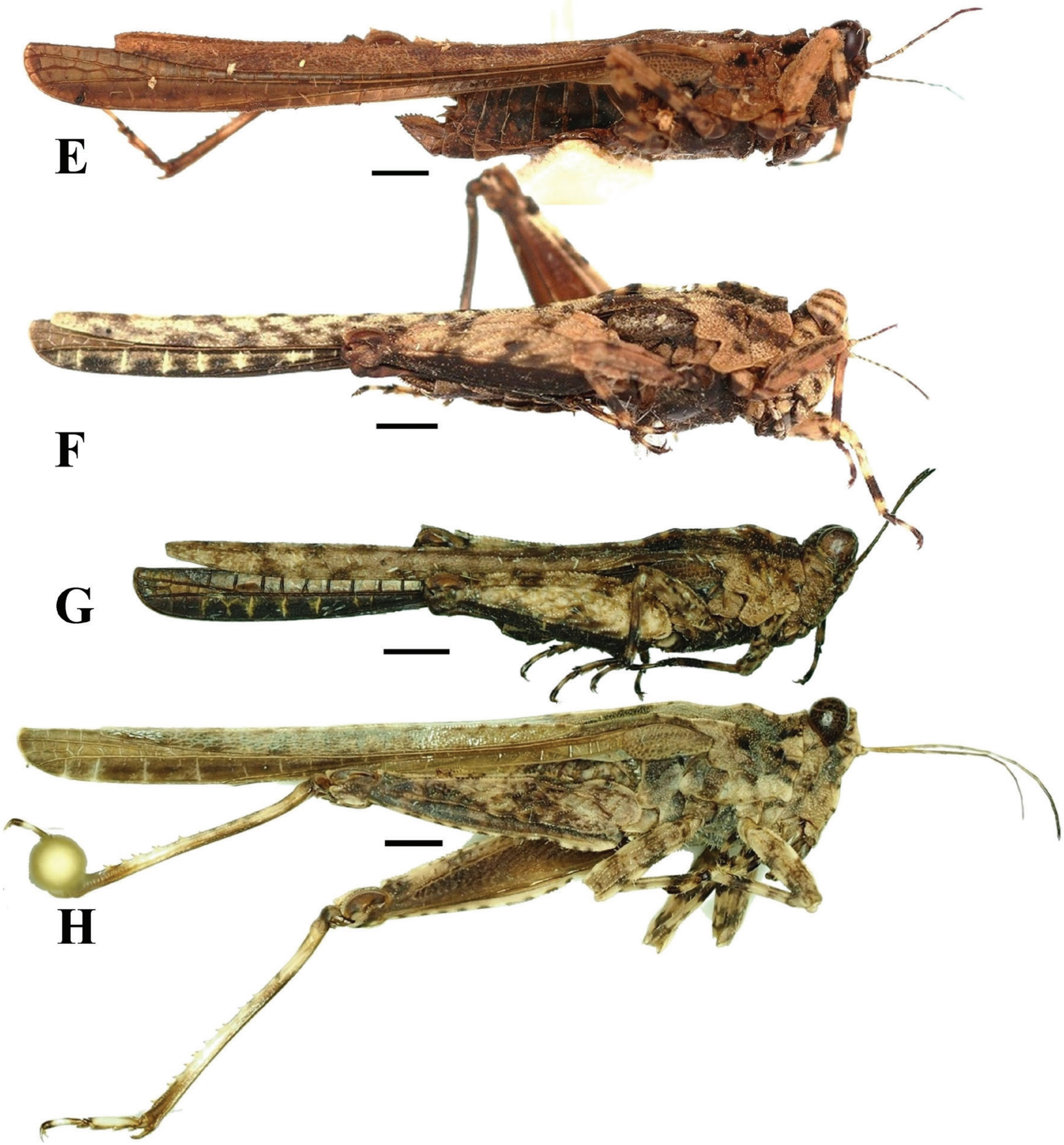

Plate 2. E–H (lateral view). **E.** *Lamellitettigodes palawanicus* (SMTD), ♀; **F.** *Lamellitettigodes novaeguineae*, ♀ HT; **G.** *Lamellitettigodes novaeguineae*, ♂ PT 9/12; **H.** *Lamellitettigodes karwinkeli*, ♀ HT. Scale bars: 1 mm.

width 0.55; tegmen length 1.54; hind wing length 9.94; postfemur length 6.69; postfemur width 1.95.

Distribution.—Known from the locus typicus (Dolores, Philippines) and from Buru (Maluka, Indonesia).

I identified one ♀ from Thailand (Khon Kaen, Nam Nao National Park, 24.V.1988, leg. S. Ingrisch, CJT) as *Lamellitettigodes* cf. *signatus*, but further investigations are needed to confirm this identification.

Lamellitettigodes cultratus (Bolívar, 1898), comb. nov.

Plates 1D, 3L, 5T

Paratettix cultratus Bolívar, 1898: 188, 77–78; Hancock 1907: 56; Kirby 1910: 33; Günther 1936: 349; Günther 1938: 3, 41; Steinmann 1970b: 162; Paris 1994: 236; Yin et al. 1996: 895.
Euparatettix cultratus: Blackith 1992: 63.

Type material.—HT *Lamellitettigodes cultratus*: ♀, [Indonesia, West-Papua], Andai [0°55'S, 134°01'E], VIII.1872, leg. L. M. D'Albertis, MSNG.

Additional material examined.—Indonesia: West Papua, Biak NE, 10 km N Bosnik, prim. Urwald, 10.II.1998, leg. A. Weigel, NMEG; ♀, Biak, Kampong, Landbouw, 40 m, 25.–28.V.1958, leg. J. L. Gressitt & T. C. Maa, ZFMK; ♀, Biak, Mangrowawa, 50–100 m, 29.V.1959, leg. T. C. Maa, CJT; ♂, ♀, West Papua, Star Range, Sibil (op licht), [4°45'S, 140°40'E], 1260 m, 16.V.1959, Neth. New Guinea Exp. 1959, RMNH; ♀, West Papua, Nabire, S. Geelvink Bay, [3°22'S, 135°28'E], 0–30 m, 2.–9.VII.1962, leg. J. L. Gressitt, CJT; 2♂♂, ♀, West Papua, Nabire, S. Geelvink Bay, [3°22'S, 135°28'E], 10–40 m, 10.X.1962, light trap, leg. N. Wilson, CJT; ♂, ♀, West Papua, Nabire, jungle along stream, 5–50 m, 25.VIII.–2.IX.1962, leg. H. Holtmann, BPBM; ♀, West Papua, Bodem, [1°58'S, 138°44'E], 10.–17.VII.1959, leg. T. C. Maa, BPBM; ♀, West Papua, Bodem, 11

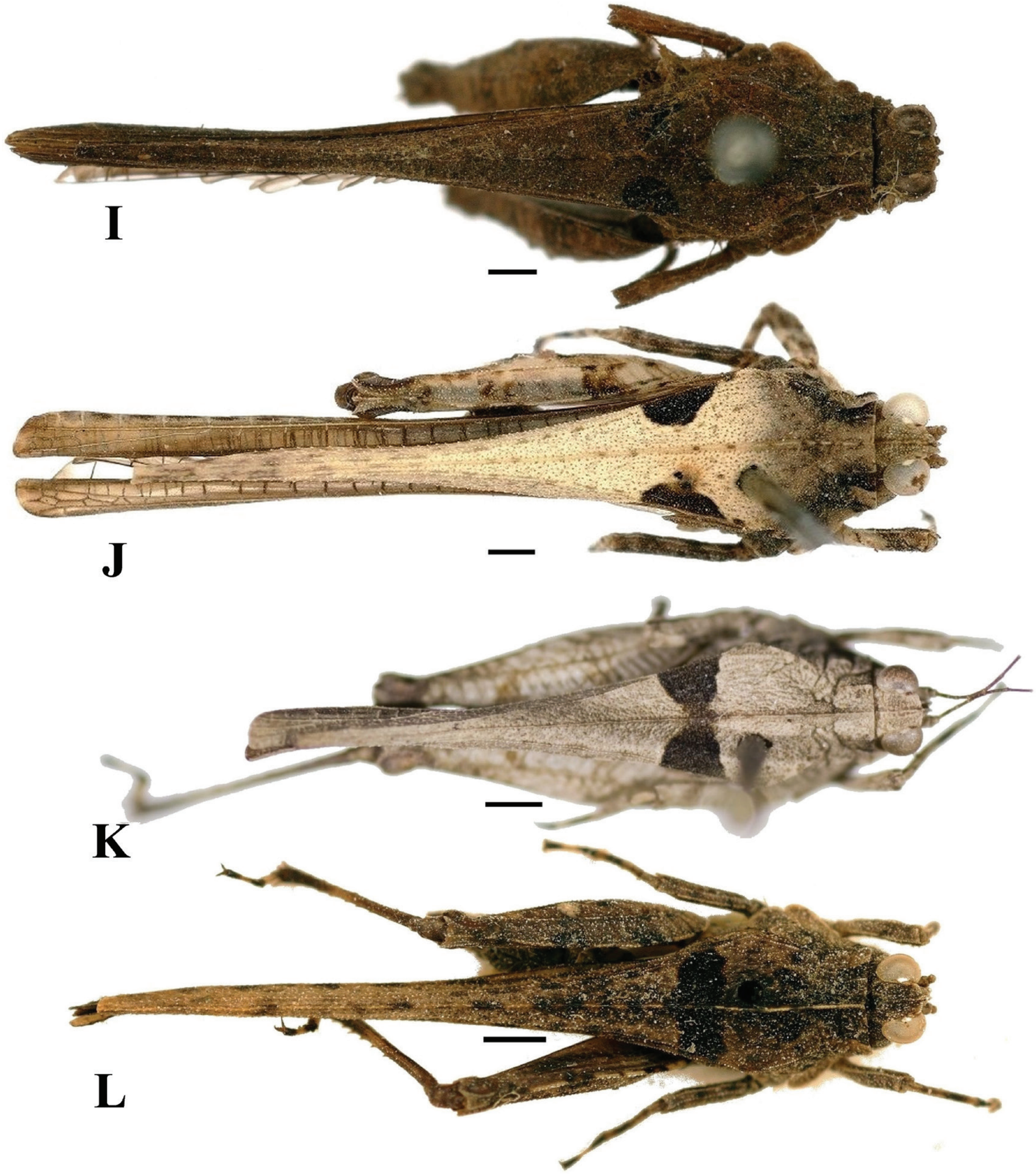

Plate 3. I–L (dorsal view). **I.** *Lamellitettigodes contractus*, ♀ HT; **J.** *Lamellitettigodes sagittatus*, ♀ HT; **K.** *Lamellitettigodes signatus*, ♀ HT; **L.** *Lamellitettigodes cultratus*, ♀ HT. Scale bars: 1 mm.

km SE of Oerberfaren, [1°58'S, 138°44'E], 100 m, 7.–17.VII.1959, M. V. light trap, leg. T. C. Maa, CJT; ♂, West Papua, Vogelkop, Manokwari, [0°52'S, 134°05'E], 75 m, 11.VIII.1957, leg. H. D. Elmo, CJT; ♂, West Papua, River Tor (mouth), 4 km E of Hol Maffen, [1°59'S, 138°58'E], 19.VII.1959, leg. T. C. Maa, CDS; ♂, West Papua, Cyclops Mountains, Jayapura, Sentani, [2°36'S, 140°37'E], 100 m, 15.VI.1959, leg. J. L. Gressitt, BPBM; ♀, West Papua, Waris, S of Hollandia, [3°11'S, 140°53'E], 400–450 m, 1.–7.VIII.1959, leg. T. C. Maa, CJT. Papua New Guinea: ♀, Gulf Prov., Lakekamu Basin, Ivimka Res. Station, 120 m, 7°44'S, 146°30'E, 18.IV.2000, leg. T. A. Sears, CJT; 2♀♀, [Central Prov.], Kokoda, [8°39'S, 147°15'E], 1200 ft, VIII.1933, leg. L.E. Cheesman, BMNH & SMTD; 2♀♀, [Central Prov.], Kokoda, [8°39'S, 147°15'E], 1200 ft, VIII.1933, leg. L.E. Cheesman, BMNH; ♂, Orrori, 3500 ft, VII.1933, leg. L. E. Cheesman, BMNH; ♂larve, ♀larve, [Northern Prov.], Kokoda-Pitoki, 400 m, [8°55'S, 147°44'E], 23.III.1956, leg. J. L. Gressitt, BPBM; ♀ larve, [Northern Prov.], Kokoda-Pitoki, 450 m, [8°55'S, 147°44'E], 24.III.1956, leg. J. L. Gressitt, CJT; ♀, [Morobe Prov.], Garaina, [7°53'S, 147°08'E], 830 m, 13.–15.I.1968, leg. J. & M. Sedlacek, BPBM; ♀, [Morobe Prov.], Garaina, [7°53'S, 147°08'E], 550–750 m, 16.I.1968, leg. J. & M. Sedlacek, BPBM; ♀, [Western Prov.], Fly River, Olsobip, [5°23'S, 141°32'E], 700–1150 m, leg. J. & M. Sedlacek, CJT; 2♀♀, [Western Highlands Prov.], Upper Jimmi Valley, Wum, [5°34'S, 144°35'E], 840 m, 18.VII.1955, leg. J. L. Gressitt, MNSL & BPBM; ♂, [Chimbu Prov.], Karimui, South of Goroka, [6°30'S, 144°51'E], 1000 m, 2.VI.1961, leg. J. L. & M. Gressitt, ZFMK;

♀ larve, New Britain, Karavat (+ 20 km), sous de vieilles souches, 300 m, 18.VII.1979, leg. J. D. Bourne, MHNG; ♂, New Britain, Gazelle Pen., Upper Warangoi, 350–600 m, 28.–29.XI.1962, leg. J. Sedlacek, CJT; ♀ larve, New Ireland, Danu, Kalili Bay, 30.IV.1962, leg. Noona Dan Expedition 61–62, ZMUC.

Differential diagnosis.—*L. cultratus* is unique in having highly lamellate and arcuate median carina above the shoulders. This character is already visible in nymphal stages. Additional unique characters are the short and strongly converging prozonal carinae and short antennae (1.3 times longer than fore femur).

Measurements.—(in mm) Pronotum length HT 12.09; pronotum lobe width 2.90; pronotum height HT 2.15; vertex width HT 0.54; eye width HT 0.47; tegmen length HT 1.50; hind wing length HT 11.18; postfemur length HT 4.70; postfemur width HT 1.45.

Distribution.—The species inhabits New Guinea, Biak, and the Bismarck Archipelago – New Britain and New Ireland.

Lamellitettigodes palawanicus Günther, 1939, stat. nov.

Plates 2E, 4M, 5U

Lamellitettigodes contractus palawanicus Günther, 1939: 79–80.

Type material.—LT *Lamellitettigodes palawanicus* (here designated): ♀, Philippines, N. Palawan, Binaluan, XI-XII.1913, leg. G. Boettcher, SDEI.

PLTs *Lamellitettigodes palawanicus* (here designated): 11♂♂, 7♀♀, Philippines, N. Palawan, Binaluan, XI-XII.1913, leg. G. Boettcher, SDEI.

Note: Günther refers to 4♂♂, 15♀♀ as STs.

Additional material examined.—2♀♀, Philippines, N. Palawan, Binaluan, XI-XII.1913, leg. G. Boettcher, SMTD.

Differential diagnosis.—*L. palawanicus* has almost parallel prozonal carinae that are slightly bent backwards. The distance between upper margin of superior ocelli and frontal margin of the fastigium, in frontal view, is significantly larger than the diameter of ocellus. The species is similar to *L. contractus*. *L. palawanicus* can be separated from the similar species by the tip of fastigium and frontal costa that are distinctly protuberant in front of the eyes and by fastigial horns that are clearly visible above the eyes.

Measurements.—(in mm) ♀, Philippines, Binaluan (SMTD): Pronotum length 11.96; pronotum lobe width 3.4; pronotum height 1.90; vertex width 0.50; eye width 0.45; tegmen length 1.60; hind wing length 12.74; postfemur length 6.50; postfemur width 1.95.

Distribution.—The species is hitherto known only from Palawan (Binaluan), the Philippines.

Lamellitettigodes novaeguineae sp. nov.

http://zoobank.org/DF0F6588-4DC4-477B-9E4E-F7DC8DD56A76

Plates 2F, G, 4N, O, 5V, W

Material examined.—HT *Lamellitettigodes novaeguineae*: ♀, Papua New Guinea, Gulf Prov., Lakekamu Basin, Ivimka Res. Station (Malaise Trap), 7°44'S, 146°30'E, 120 m, 4.–6.III.2000, leg. T. A. Sears, BMEC.

Type material.—PTs *Lamellitettigodes novaeguineae*: ♂, ♀ (1/12+2/12), Papua New Guinea, Gulf [Prov.], Lakekamu Basin, Ivimka Res. Station, (M[alaise]T[rap]), 7°44'S, 146°30'E, 120 m, 4.–6.III.2000, leg. T. A. Sears, BMEC (deposited in ZFMK); 3♀♀ (3/12–5/12), Papua New Guinea, Gulf [Prov.], Lakekamu Basin, Ivimka Res. Station, 7°44'S, 146°30'E, 120 m, 5.III.2000, leg. T. A. Sears, BMEC; ♀ (6/12), Papua New Guinea, Gulf [Prov.], Lakekamu Basin, Ivimka Res. Station, (M[alaise]T[rap]), 7°44'S, 146°30'E, 120 m, 19.–23.IV.2000, leg. T. A. Sears, BMEC (deposited in BMNH); ♀ (7/12), Papua New Guinea, Gulf [Prov.], Lakekamu Basin, Ivimka Res. Station, 7°44'S, 146°30'E, 120 m, 15.–20.IV.2000, leg. T. A. Sears, BMEC (deposited in ZMHU); ♀ (8/12), Papua New Guinea, Gulf [Prov.], Lakekamu Basin, Ivimka Res. Station, (M[alaise]T[rap]), 7°44'S, 146°30'E, 120 m, 18.IV.2000, leg. T. A. Sears, BMEC (deposited in RMNH); ♂ (9/12), Papua New Guinea, Gulf [Prov.], Lakekamu Basin, Ivimka Res. Station, 7°44'S, 146°30'E, 120 m, 18.IV.2000, leg. T. A. Sears & binatung brigade, BMEC (deposited in RMNH); ♂ (10/12), Papua New Guinea, Gulf [Prov.], Lakekamu Basin, Ivimka Res. Station, (M[alaise]T[rap]), 7°44'S, 146°30'E, 120 m, 26.III.2000, leg. T. A. Sears & binatung brigade, BMEC; 2♀♀ (11/12+12/12), Papua New Guinea, Fly River, Kiunga, 35 m, VIII.1969, leg. J. & M. Sedlacek, BPBM.

Diagnosis.—The species is easily recognizable by the raised median carina with broad depression between the shoulders. This depression clearly distinguishes it from *L. cultratus*. It is also slightly raised in Chinese *L. karwinkeli* but does not reach the same height and is not lamellated. As a further feature, the fastigium tip is only slightly visible in front of the eyes.

Description.—Body of moderate size and slender. Head and pronotum smooth. Head and eye in lateral view weakly elevated above the pronotal discus. Dorsal margin of antennal groove slightly above the ventral margin of eye. Eyes small and in lateral view blunt and indistinctly conoidal. Antenna filiform, 14-segmented in male (including scapus and pedicel), while 15-segmented in female, 1.5–2.0 times longer than fore femur. Fastigium of vertex in dorsal view slightly wider than one eye. Fastigium in frontal view between the eyes slightly depressed. Fastigium in dorsal view with well-developed medial and lateral carinae and fossulae. Lateral carina clearly elevated, but in lateral view as high as the dorsal margin of eyes, short, not converging towards the front, bending over at nearly right angles to the medial carina. Transverse carina in dorsal view straight. Frontal costa and facial carina in lateral view minimally visible in front of eye. Tip of fastigium and frontal costa in lateral view slightly, but still clearly, protuberant. Bifurcation of frontal costa into facial carinae between dorsal margin of lateral ocelli and transverse carina, close to transverse carina by less than one diameter of ocellus. Facial carinae in lateral view clearly concave in front of eye and slightly convex in front of antenna. Last segments of maxillary palp not widened. Anterior margin of the pronotum truncated. Pronotum slightly widened between shoulders. Clearly keeled prozonal carinae converging backwards. Median carina distinctly lamellate from anterior margin of the pronotum to the end of tegmen, with a broad depression between shoulders. Interhumeral carinae absent. Internal lateral carinae weak. Pronotum behind shoulders weakly depressed on both sides of median carina, with large black spots like a broad black band (posthumeral). Lateral lobes broadly rounded, more or less close to body. Tegmen almost as long as the fore femur, rather broad, at the end broadly rounded. Macropterous and macropronotal. Alae clearly exceed the pronotum apex. Fore and middle femora short and widened, with wavy margins. Hind femora with very small antegenicular and especially genicular teeth and with some sharply tuberculated raised lobes on the middle outer surface. Posterior tibia distally not or weakly widened, with a few small spines on upper edges. First segment of the hind tarsus not longer than third segment. Pulvilli acute.

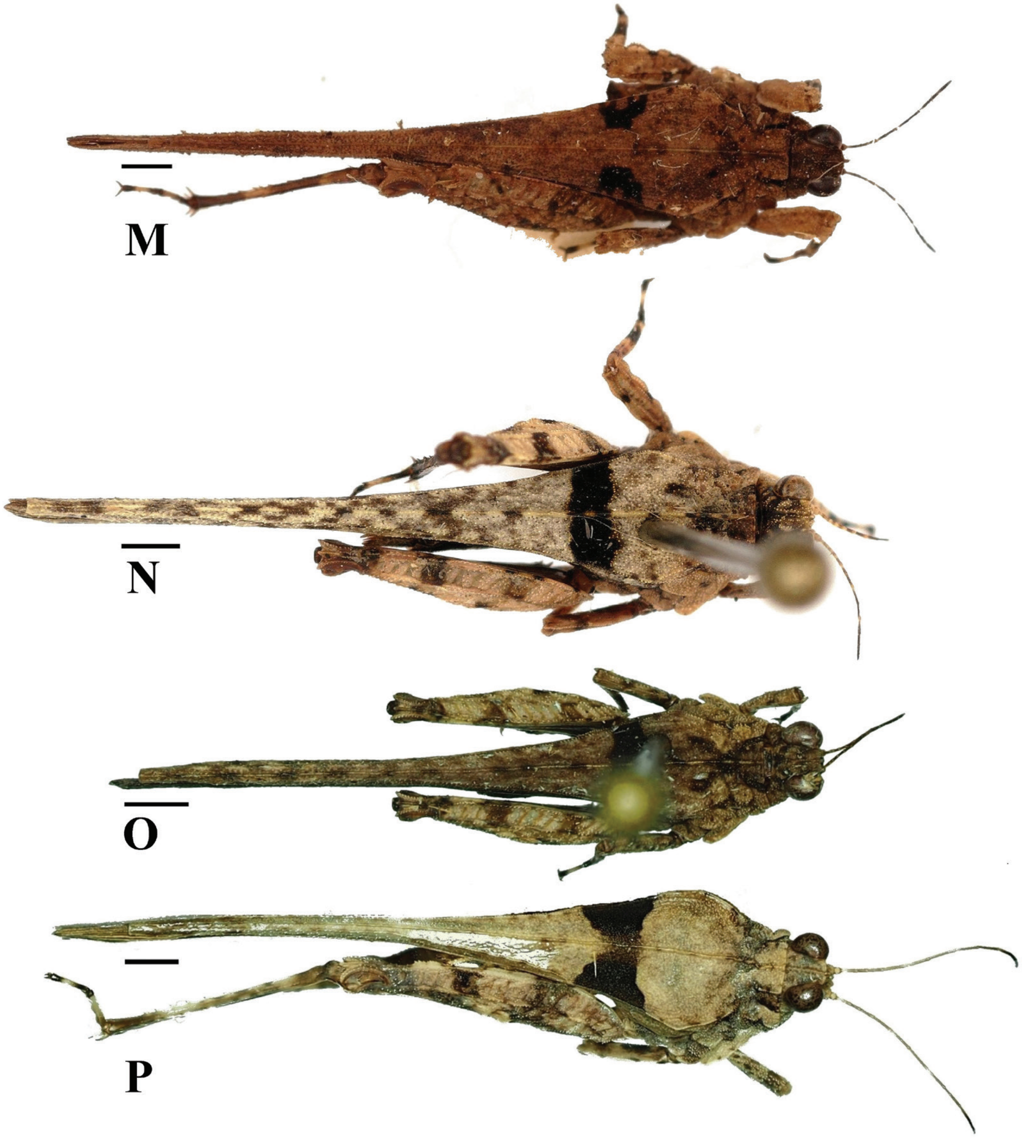

Plate 4. M–P (dorsal view). **M.** *Lamellitettigodes palawanicus* (SMTD), ♀; **N.** *Lamellitettigodes novaeguineae*, ♀ HT; **O.** *Lamellitettigodes novaeguineae*, ♂ PT 9/12; **P.** *Lamellitettigodes karwinkeli*, ♀ HT. Scale bars: 1 mm.

Measurements.—(in mm) HT: Pronotum length 12.87; pronotum lobe width 3.10; pronotum height 1.85; vertex width 0.52; eye width 0.45; tegmen length 1.50; hind wing length 10.79; postfemur length 4.68; postfemur width 1.45.

3 PT♂♂: Pronotum length 9.88–10.40, average 10.18; pronotum lobe width 2.35–2.45, average 2.40; pronotum height 1.3–1.55, average 1.42; vertex width 0.43–0.43, average 0.43; eye width 0.39–0.43, average 0.41; tegmen length 1.20–1.25, average 1.23; hind wing length 8.97–9.75, average 9.45; postfemur length 4.00–4.10, average 4.05; postfemur width 1.15–1.20, average 1.16.

9 PT♀♀+HT: Pronotum length 10.27–12.74, average 11.62; pronotum lobe width 2.75–3.10, average 2.96; pronotum height 1.65–1.90, average 1.82; vertex width 0.43–0.52, average 0.49; eye width 0.41–0.45, average 0.43; tegmen length 1.30–1.65, average 1.51; hind wing length 9.36–11.96, average 10.88; postfemur length 4.30–4.75, average 4.55; postfemur width 1.30–1.50, average 1.38.

Pictures of HT and PT are available in higher resolution in OSF (Cigliano et al. 2019).

Distribution.—The species is only known from lowlands in the South of New Guinea (surroundings of Fly River and Lakekamu River).

Etymology.—The species is named after the island of New Guinea (*Nova Guinea*) where it is an endemic species of the genus *Lamellitettigodes*. The specific epitheton is made of two words, adjective and noun of the first (A) Latin declension, both in Genitive case (*Novae Guineae* = *novaeguineae*).

Lamellitettigodes karwinkeli sp. nov.

http://zoobank.org/85026102-A4E2-412C-9310-A8432766EED2

Plates 2H, 4P, 5X

Material examined.—HT *Lamellitettigodes karwinkeli*: ♀, China, S-Yunnan, Xishuangbanna, 23 km NW Jinghong, vic. NA Ban Village (NNNR), 22°10'N, 100°39'E, 700–1000 m, V.–VII.2009 (diverse traps), leg. L. Meng, NMNG.

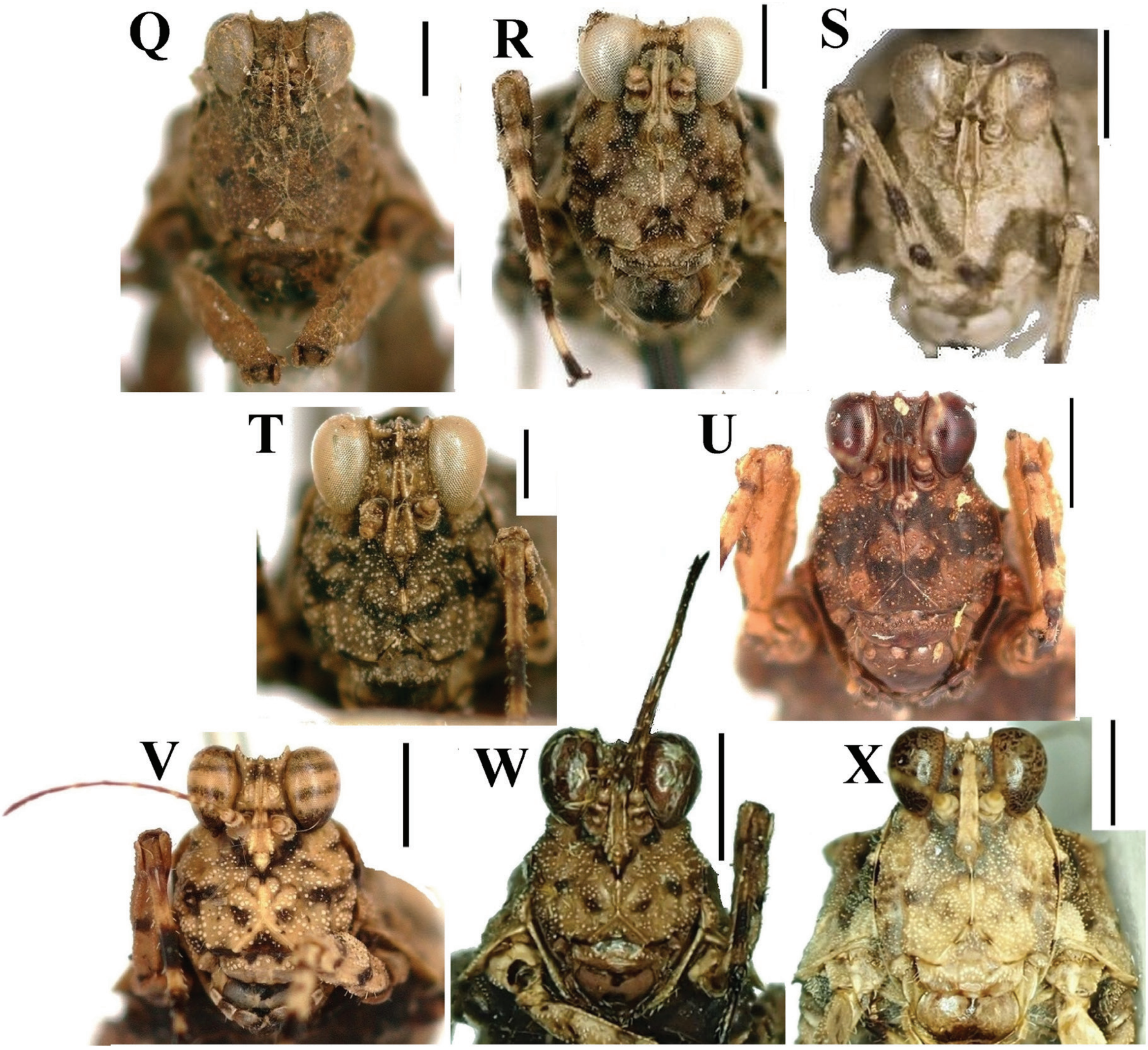

Plate 5. Q–X (frontal view). **Q.** *Lamellitettigodes contractus*, ♀ HT; **R.** *Lamellitettigodes sagittatus*, ♀ HT; **S.** *Lamellitettigodes signatus*, ♀ HT; **T.** *Lamellitettigodes cultratus*, ♀ HT; **U.** *Lamellitettigodes palawanicus* (SMTD), ♀; **V.** *Lamellitettigodes novaeguineae*, ♀ HT; **W.** *Lamellitettigodes novaeguineae*, ♂ PT 9/12; **X.** *Lamellitettigodes karwinkeli*, ♀ HT. Scale bars: 1 mm.

Diagnosis.—*L. karwinkeli*, together with *L. sagittatus* and *L. signatus* species, has pulvilli with apical teeth. Together with *L. sagittatus* it is a species with long and slender antennae (more than 2 times longer than fore femur. It differs from *L. sagittatus* by the higher pronotum with a broad depression between the shoulders and morphology of fastigium; in frontal view the ventral margin of transverse carina form a right angle with the lateral carina in *L. karwinkeli,* while it is rounded in *L. sagittatus*.

Description.—Body long and slender. Head and pronotum smooth. Head and eye in lateral view clearly elevated above pronotal discus. Dorsal margin of antennal groove between eyes, slightly above ventral margin of eye. Eyes small and in lateral view blunt and indistinctly conoidal. Antenna (4.5 mm) filiform with long and slender segments, 15-segmented in female (including scapus and pedicel), 2.4 times longer than fore femur. Fastigium of vertex in dorsal view smaller than width of one eye. Fastigium in frontal view between the eyes depressed. Ventral margin of transverse carina forming with lateral carina square (right angle). Fastigium in dorsal view with well-developed medial and lateral carinae and fossulae. Lateral carina clearly elevated, but in lateral view as high as the dorsal margin of eye, short and not converging towards front, bending over at right angles to the medial carina. Transverse carina in dorsal view slightly convex. Frontal costa and facial carina in lateral view clearly visible in front of eye. Tip of fastigium and frontal costa in lateral view distinctly protuberant. Bifurcation of frontal costa into facial carinae close to transverse carina. Facial carinae in lateral view clearly concave in front of eye and slightly convex in front of antenna. Last segments of maxillary palp not widened. Anterior margin of pronotum truncated. Pronotum expanded between shoulders. Clearly keeled prozonal carinae slightly converging backwards. Median carina from the anterior margin of the pronotum to the level of the end of tegmen distinctly keeled, with two flattened elevations before and behind shoulders. Interhumeral carinae absent. Internal lateral carinae weak. Pronotum behind shoulders weakly depressed on both sides of median carina with black spots (posthumeral spots) forming broad black band. Lateral lobes broadly rounded, more or less close to body. Tegmen slightly shorter than fore femora, slender, at the end broadly rounded. Macropterous and macropronotal. Alae clearly exceed the pronotum apex. Fore and middle femora slender, with slightly undulated margins. Hind femora with very small antegenicular and especially genicular teeth, with some sharply tuberculate raised lobes on the middle outer surface. Posterior tibia distally not or weakly widened, with a few small spines on upper edges. First segment of the hind tarsus not longer than the third segment of tarsus. Pulvilli distinctly acute with apical teeth.

Measurements.—(in mm) HT: Pronotum length 15.05; pronotum lobe width 3.50; pronotum height 2.15; vertex width 0.47; eye width 0.56; tegmen length 1.65; hind wing length 12.61; postfemur length 6.11; postfemur width 1.43.

Pictures of HT are available in higher resolution in OSF (Cigliano et al. 2019).

Distribution.—The species is only known from the type locality near Xishuangbanna (Yunnan, PR China).

Note: I cannot find any other species of *Lamellitettigodes* from PR China. There are likely to be further species from PR China that should be assigned to *Lamellitettigodes*, but since there are only drawings and only a few photographs, such work remains for future revisions.

Etymology.—This species is dedicated to Fabian Karwinkel, a great ornithologist and a committed young conservationist from Northrhine-Westphalia. The specific epitheton is second (US) declension Genitive case of the Fabian's Latinized version of the surname (*Karwinkelus = karwinkeli*).

Probolotettix Günther, 1939

Probolotettix kevani Blackith & Blackith, 1987, **syn. nov.**
Probolotettix kevani: Blackith and Blackith 1987: 5–8; Blackith 1990: 89–90; Blackith 1992: 146; Yin et al. 1996: 902; Otte 1997: 57.

Type material.—HT *Probolotettix kevani*: ♂, Indonesia, Sulawesi Tengah, Ramu Camp, Kolonodale area, 5.II.1980, leg. P. G. Kevan, LEMQ.

PTs *Probolotettix kevani*: ♂, Indonesia, Sulawesi, Minehassa Prov., Dumoga-Bone National Park, I.–III.1985, leg. R. & R. Blackith, BMNH, NHMUK10924442; 3♂♂, 2♀♀, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, leg. Blackith, NMI, MZB, MNHNP (not seen); ♀, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, VII.1985, leg. Butlin, NHMUK10924441; ♀, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, 17.V.–16. VII.1985, leg. Butlin, LEMQ; ♂, ♀, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, 17.V.–16.VII.1985, leg. Butlin, BMNH, NMI (not seen); ♀, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, at light, 19.VII.1985, leg. Butlin, RNMH (not seen, probably lost); ♀, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, 6.VII.1985, leg. Kirk-Spriggs, BMNH.

The HT is a typical *E. personatus* (elevated head, short prozona, hind tibia with a bright light ring). Therefore, I synonymize *Probolotettix kevani* with *E. personatus*. The description and the drawing of the PT in Blackith and Blackith (1987) refer to a typical Lamellitettigodes sagittatus and I was able to examine three PTs in BMNH and one paratype in LEMQ: there is no doubt that they are *L. sagittatus* and do not belong to a new species or to *Euparatettix personatus*.

Scelimena Serville, 1838

Scelimena novaeguineae (Bolívar, 1898)

Notes.—I published a wrong specimen as LT (Tumbrinck 2018). The male from IRSNB is a PLT. The correct LT is the following specimen: ♂, Indonesia, New Guinea, Haveri [9°22'S, 147°32'E], leg. Loria, vii-xi.1893. It is one specimen of a series of 43 specimens from Haveri. The other 42 are PLT.

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Discovery of an acoustically locating parasitoid with a potential role in divergence of song types among sympatric populations of the bush cricket *Mecopoda elongata*

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Abstract

The bush cricket *Mecopoda elongata* provides a striking example of sympatric intraspecific divergence in mating signals. Five completely distinct song types are found in various parapatric and sympatric locations in South India. While there is convincing evidence that population divergence in *M. elongata* is being maintained as a result of divergence in acoustic signals, cuticular chemical profiles, and genital characters, the causes of the evolution of such divergence in the first place are unknown. We describe the discovery of a tachinid parasitoid with an orthopteroid hearing mechanism affecting *M. elongata*. This parasitoid may have a role in driving the extraordinary divergence that had occurred among *M. elongata* song types. Over two years we sampled individuals of three sympatric song types in the wild and retained individuals in captivity to reveal rates of parasitization. We found that all three song types were infected with the parasitoid but that there were significant differences among song types in their probability of being infected. The probability of tachinid parasitization also differed between the two sampling periods. Therefore, it is possible that parasitoid infection plays a role in song type divergence among sympatric bush cricket populations.

Keywords

cryptic species, katydid, speciation, Tachinidae

Introduction

In host-parasite coevolution, hosts evolve mechanisms to avoid parasite attack and parasites evolve counter-mechanisms to detect and infect hosts efficiently. Instances of insect parasitoids, whose larvae parasitize their host for nutrition and development, eventually causing the death of the host, are abundant in nature (Godfray and Shimada 1999, Santos and Quicke 2011). They mostly belong to the order Hymenoptera (78%) or to the family Tachinidae, order Diptera (20%) (Feener and Brown 1997, Godfray and Shimada 1999). Each host species is typically parasitized by 2–8 parasitoid species and hosts for each parasitoid tend to be closely related species (Santos and Quicke 2011). Parasitoids can be grouped into idiobionts or koinobionts depending on the host's ability to live after being parasitized (Santos and Quicke 2011). Typically, unlike idiobionts, most koinobionts are endoparasites that affect young hosts, have longer developmental stages, and a shorter adult life. They are normally pro-ovigenic and have a smaller host range compared to ectoparasitic idiobionts (Santos and Quicke 2011). Widely distributed tachinids are parasitoids on a variety of insect orders including Lepidoptera, Orthoptera, Coleoptera, Hymenoptera, Heteroptera, and many others (Feener and Brown 1997, Stireman et al. 2005, Cerretti et al. 2014) due to the ability of their larvae to avoid host immune responses (Feener and Brown 1997). Such a koinobiont tachinid parasitoid that exploits its orthopteran hosts' acoustic communication is the subject of this study.

Tachinid parasitoids (especially of tribe Ormiini) have evolved to take advantage of intraspecific acoustic communication particularly in orthopteran and hemipteran species (Lehmann 2003, Lakes-Harlan and Lehmann 2014). Early studies to identify this phenomenon of acoustic exploitation found that females of the tachinid fly *Euphasiopteryx ochracea* (now, *Ormia ochracea*) showed phonotaxis to song playback of the field cricket *Gryllus integer* (Cade 1975). *O. ochracea* females were also found to be more attracted to host male choruses than to single host callers (Cade 2010). *O. ochracea* females bear orthopteroid hearing organs (featuring a prominent pressure sensitive tympanum exposed to the air but receiving sound from both sides), which are most sensitive in the 4 to 6 kHz range, corresponding to the dominant frequency range of the calls of one of their hosts, *Gryllus rubens* (Robert et al. 1992). Parasitoid infection affects the male host's calling ability, which gradually declines until his death (Cade 1984).

Calling and chorusing behavior in orthopterans is thought to have evolved under selection to avoid exploitative parasites or predators (Greenfield 1983, Cade and Wyatt 1984, Henry 1994). Currently, the two most studied dipteran parasitoid groups are tachinids belonging to tribe Ormiini and sarcophagids belonging to tribe Emblemasomatini, parasitizing crickets and bush crickets (Orthoptera) and cicadas (Hemiptera), respectively, with the help of independently evolved hearing mechanisms (Hedwig and Robert 2013, Lakes-Harlan and Lehmann 2014). The sarcophagid genus *Emblemasoma* has been found to target cicada males calling during the day (Farris et al. 2008).

In contrast, 68 species belonging to the Ormiini tribe of the Tachinidae family are predominantly parasitoids that can acoustically locate bush cricket hosts that call at night (Lehmann 2003). For example, *Therobia leonidei* (a tachinid parasitoid) locates its tettigoniid (*Poecilimon* sp.) host males by eavesdropping on their calls (Lakes-Harlan and Heller 1992). Other similar host-dipteran parasitoid systems include the bush cricket *Neoconocephalus robustus* and tachinid *Ormia brevicornis*, the bush cricket *Scapteriscus vicinus* and tachinid *Ormia depleta*, the bush cricket *Orocharis luteolira* and tachinid *Ormia dominicana*, the bush cricket *Sciarasaga quadrata* and tachinid *Homotrixa alleni*, the cicada *Okanaga rimosa* and sarcophagid *Colcondamyia auditrix* (Cade 1984), and many others (reviewed in Feener and Brown 1997, Zuk and Kolluru 1998, and Lehmann 2003). Here we describe our observation of a tachinid parasitoid infecting an orthopteran host, *Mecopoda elongata*. This system is of particular interest because the mate-attracting auditory signals exploited by the parasitoid also form the basis of an intra-specific reproductive isolating mechanism that has been implicated in incipient speciation in this group (Dutta et al. 2017).

The bush cricket species *Mecopoda elongata* can be divided into five song types that are morphologically very similar (Nityananda and Balakrishnan 2006). These song types show subtle differences in genital morphology and cuticular lipid profiles (Dutta et al. 2018) and females of one of the song types, Chirper, show a strong preference for their own call type (Dutta et al. 2017). There appear to be only a few records of known tachinid parasitoids parasitizing lepidopterans in India (Sathe 2012, Shendage and Sathe 2012), but there has been no published evidence of tachinid parasitoids affecting *M. elongata* males or any calling orthopteran species from India that we are aware of (Crosskey 1976). India has many tachinids (>140 species), as well as 1033 described orthopteran species/subspecies within 398 genera and 21 families consisting of mostly acoustically communicating crickets and bush crickets (Gryllidae and Tettigoniidae) (O'Hara et al. 2009, Chandra and Gupta 2013). In this study, we describe a hitherto unknown relationship between a tachinid fly and three distinct song types of *M. elongata*. These three song types differ considerably in their temporal features (Fig. 1). However, the spectral features (for example, dominant frequency) of their songs appear similar (Nityananda and Balakrishnan 2006). Since the evolutionary origins of these song types are unknown, the potential for acoustically orienting parasitoids to have played a role in their divergence is an obvious point of interest.

The objectives of our study were 1) to describe the tachinid parasitoids affecting *M. elongata* populations and 2) to determine whether there were any differences in the prevalence of parasitoid infection among *M. elongata* song types.

Methods

Field sampling was carried out in Kervashe, Hurabi, and Heringe locality around Kadari field station (13°13'N, 75°05'E), Karnataka, India. Adult *M. elongata* males were collected opportunistically from the three sites between January and March each year for a period of two years (2013–2014). The sampling took place between 7:30 pm and 9:30 pm at night on at least two dates for a given location each year. *M. elongata* males were identified as Double Chirper, Two Part, and Helicopter by listening to their calls and recording them when possible. While Double Chirper calls consist of only chirps and Helicopter calls consist only of trill, Two Part consists of both chirp and trill components (Fig. 1). *M. elongata* males that were captured were housed individually in plastic boxes (15 cm × 7 cm × 5 cm) and fed *ad libitum* on oat flakes (Quaker Oats, Morten Seeds & Grains Pty. Ltd.), fish food (Taiyo Grow, Taiyo Petproducts [P] Ltd.) and water. These males were observed over subsequent days for parasitoid infection. An *M. elongata* male was considered infected if it was found dead inside the plastic box along with presence of an ovoid tachinid pupa.

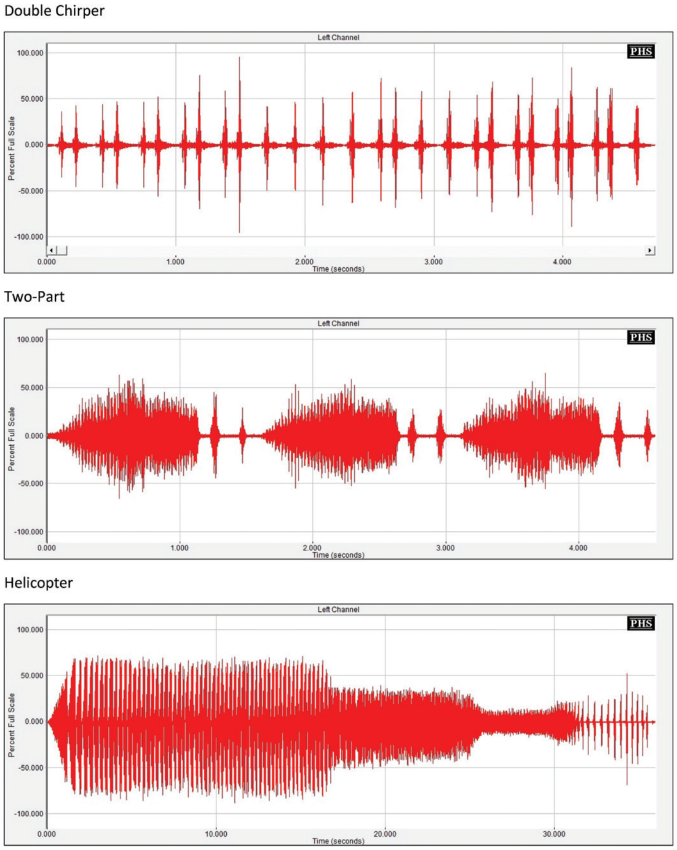

Fig. 1. Oscillograms showing distinct temporal features of the three *M. elongata* song types: Double Chirper, Two Part, and Helicopter.

There is general agreement over the classification of the family Tachinidae (Stireman et al. 2005) into either four (Wood 1987) or five subfamilies (Crosskey 1976). Between these two alternative classificatory schemes, the subfamily Tachininae appears consistently as a taxonomic group in both but forms a diverse group in many respects and is probably not monophyletic (Cerretti et al. 2014). The classifications of groups within the Tachininae is incomplete and awaits further refinement, which will benefit from better information about their reproductive behavior (oviposition methods, host location, and selection) and ecology (host utilization and life history). We used a Leica M165C microscope to identify the fly as tachinid and took photographs of important characters presented in this study using a Leica DFC290 digital camera fitted to this microscope. Diagnostic features of the Tachinidae (Crosskey 1976) that appear on the newly discovered fly are as follows:

1. Adults have subscutellum and meral bristles.
2. First instar larvae do not have mandibles or they are vestigial.
3. Anterior cephalophryngeal skeleton appears as a hook or axe-like beak.

We used a generalized linear modelling (GLM) framework to analyze categorical predictors (song type, location, year, and their interactions) with potential associations with tachinid infection. This approach allowed us to examine potential interactions between song type and predictors as well as their potential independent effects on parasitization probability. Tachinid infection was modelled as a binary variable using logit as a canonical link function with infected song type individuals assigned 1 and uninfected individuals assigned 0. Model 1 included song type, location, and year as linear predictors while model 2 also included the two-way interactions between song type, location, and year. By comparing the two models (model 1 AIC = 132.81, model 2 AIC = 140.7), we found that model 1 had the best fit (the difference in AIC values was more than 7 and the difference between null deviance and residual deviance was 81.67 with a loss of only 5 degrees of freedom), indicating that interactions between song type and other predictors were not important in explaining variation in parasitization probability.

Results

Morphology of the tachinid fly.—The tachinid fly found parasitizing *M. elongata* appears to belong to a single typical muscoid dipteran fly species of around 10 mm long (Fig. 2). It has a pair of red compound eyes and two distinct halteres (Fig. 2). The prothoracic auditory spiracles (AS) are enlarged and it has a typical furry peritreme (the integument that surrounds the spiracles) and clearly visible hairs on the anterior side (Fig. 3). It is a hearing tachinid (most likely belonging to the tribe Ormiini) featuring a hearing organ (a modified inflated prosternum) between its head and thorax on the ventral side (Fig. 4), with morphology and position similar to that of the well-studied ear of *Therobia leonidei* and *Ormia ochracea* (Lakes-Harlan and Heller 1992, Hedwig and Robert 2013). The prosternal tympanal membrane (PTM) is separated by a ridge from the coxa that is also large. The larva that comes out of an infected animal is 20 mm long and forms an ovoid pupa 10 mm long. The species-level identity of the tachinid fly could not be ascertained due to the unavailability of a dipteran/tachinid taxonomist in India and the stringent regulation of the export of biological material that prevented us from seeking an identification outside of India. However, our aim here was not primarily taxonomic; rather, it was to establish that all instances we found were of the same species and to examine its potential significance for the evolution of its *M. elongata* host.

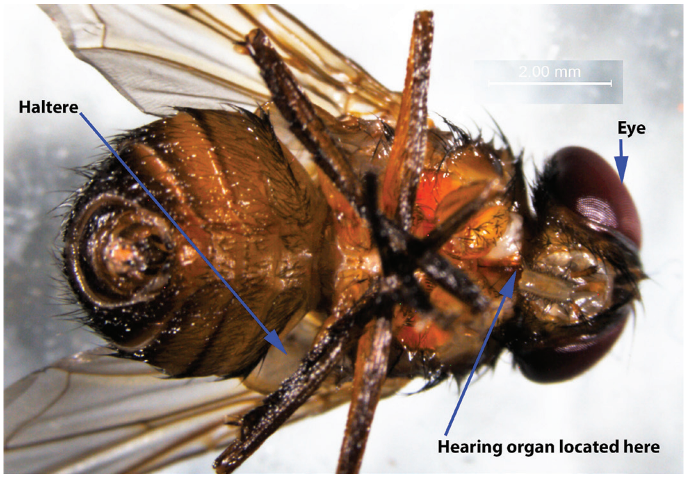

Fig. 2. External morphology of tachinid parasitoid affecting *M. elongata* song types.

Our 2014 collection of *M. elongata* males included 11 infected individuals. The mean larval emergence time was 6.9 days (standard deviation = 1.64, range 5–10 days), which is typical for tachinid flies (Stireman et al. 2005). Larval emergence led to the death of *M. elongata* males, which often lived for some hours after larval emergence but died within the same day. In 9 out of 11 cases, a single larva emerged and in the remainder, 2 larvae emerged, suggesting a slightly lower rate of hosting multiple parasites than is found in *Ormia ochracea* infections of *Teleogryllus oceanicus* and some *Gryllus* species. Although the latter species typically harbor 1 to 2 larvae, they may support up to 8 larvae in extreme cases in *T. oceanicus* (Adamo et al. 1995, Kolluru and Zuk 2001). Of the 13

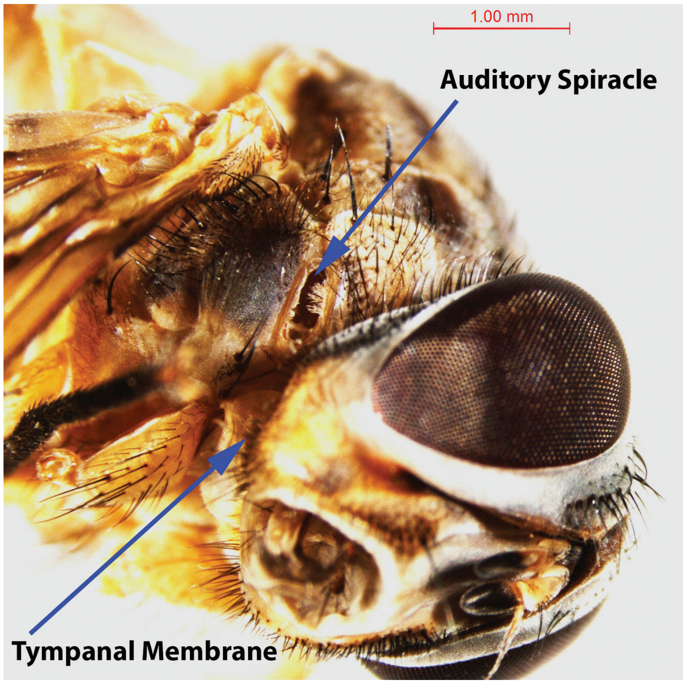

Fig. 3. Auditory spiracle encircled by peritreme and tympanal membrane of tachinid parasitoid affecting *M. elongata* song types.

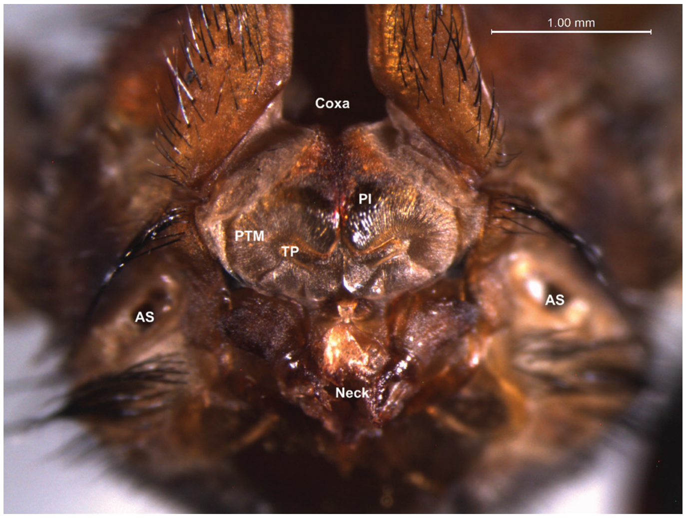

Fig. 4. Modified inflated prosternum acting as a hearing organ in tachinid fly affecting *M. elongata* song types. AS: auditory spiracle, PTM: prosternal tympanal membrane, TP: tympanal pit, and PI: prosternal inflation (Lakes-Harlan and Heller 1992, Hedwig and Robert 2013).

pupae observed in 2014, 8 emerged as adult flies after a mean of 11 days (standard deviation = 1.3, range 9–13 days). It was clear that all the parasites emerging in the lab were of the same species of tachinid, as described above.

Tachinid infection of different song types.—Over the two years of study (2013 and 2014), tachinid infections were found in all three *M. elongata* song types (Double Chirper, Two Part, and Helicopter) found at our collection sites (Fig. 5). Details of the *M. elongata* male samplings and recorded infection in percentages and sample size (n) are given in Table 1.

Analysis of deviance by F test on model 1 showed that song type (F = 5.37, p = 0.00467) and year (F = 70.0, p < 0.0001) both had significant effects on tachinid infection rate. However, sampling locations did not have any effect on the tachinid parasitization of *M. elongata* males, suggesting that instances of tachinid infection were similar in the three locations we sampled. GLM analysis also supported our finding that there was significantly higher parasitoid infection of all three *M. elongata* song types in the year 2013 (27 infected out of 47 = 57%) compared to 2014 (11 infected out of 173 = 6%). In the GLM analysis, we assigned Helicopter song type as the reference class for comparing tachinid infection probability with the other two *M. elongata* song types. We found that when a sampled *M. elongata* individual was of the song type Two Part rather than Helicopter, there was an increasing probability of tachinid infection that was statistically significant (Wald z-statistic (z) = 2.002, p = 0.0453). However, when a sampled individual was Double Chirper rather than Helicopter, the probability of tachinid infection was not significantly different (Wald z-statistic (z) = 0.867, p = 0.386); i.e., Double Chirper and Helicopter did not differ in their probability of contracting tachinid infection. We, therefore, had evidence that song types differ in their probability of being parasitized with an indication that the Two Part song type was more likely to be parasitized than either Helicopter or Double Chirper song types at the locations we sampled.

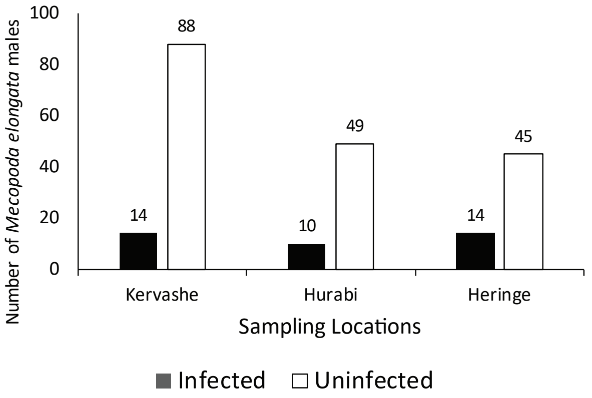

Fig. 5. The number of infected and uninfected *M. elongata* individuals sampled at the three different sampling sites within the two-year sampling period (2013–14).

Table 1. Sampling details of calling *Mecopoda elongata* males belonging to three song types that were collected from three different localities across two years leading to the discovery of tachinid parasitism.

Song type	Location	Year	Infected (%)	Uninfected (%)
Double Chirper	Kervashe	2013	47 (n=7)	53 (n=8)
	Heringe	2013	100 (n=3)	0 (n=0)
	Kervashe	2014	0 (n=0)	100 (n=56)
	Heringe	2014	0 (n=0)	100 (n=20)
	Hurabi	2014	13 (n=5)	87 (n=34)
Helicopter	Kervashe	2013	38 (n=5)	62 (n=8)
	Heringe	2013	73 (n=11)	27 (n=4)
	Kervashe	2014	0 (n=0)	100 (n=4)
	Heringe	2014	0 (n=0)	100 (n=17)
	Hurabi	2014	0 (n=0) *	0 (n=0) *
Two Part	Kervashe	2013	100 (n=1)	0 (n=0)
	Heringe	2013	0 (n=0) *	0 (n=0) *
	Kervashe	2014	8 (n=1)	92 (n=12)
	Heringe	2014	0 (n=0)	100 (n=4)
	Hurabi	2014	25 (n=5)	75 (n=15)

* represents cases where no *Mecopoda* males of the particular song type could be found

Discussion

Tachinid flies (Stireman et al. 2005, Cerretti et al. 2014) have not been extensively studied and little is known about their evolution, ecology, and behavior (Stireman et al. 2005). The diversification of host use appears to have evolved after the acquisition of parasitoid life history since all known tachinids are parasitoids (Feener and Brown 1997, Lehmann 2003). This study is the first record of a paleotropical parasitoid affecting *M. elongata* males or any calling orthopteran species from India. This confirmation follows a recent anecdotal account of Malaysian *M. elongata* infected by larvae of a parasitoid fly belonging to family Tachinidae (Hartbauer et al. 2011). Although the distribution and abundance of *M. elongata* has not been systematically studied, preliminary opportunistic sampling in known *M. elongata* habitats indicates that there is possibility of a high proportion of the *M. elongata* population being infected by tachinid parasitoids. Our generalized linear model suggested that the probability of the parasitoid infection in *M. elongata* varied significantly between years and was dependent upon the song type of potential hosts. The sampling locations and the various interactions among predictors did not contribute to the parasitization likelihood.

Fifty seven percent (27 out of 47) of *M. elongata* sampled during 2013 were infected by the tachinid fly. This high rate of infection is also seen in the *Therobia leonidei-Poecilimon* parasitoid-host system (Heller and von Helversen 1993). At such high infection rates, there is inevitably strong selection on *M. elongata* from tachinid parasitoids with the potential for this to drive changes in acoustic signals that reduce detection probability (Hedwig and Robert 2013). The proportion of parasitoid-infected *M. elongata* individuals, however, drastically declined for the year 2014 (11/173 = 6%) suggesting a possible density dependent host-parasite interaction (although further study is needed to confirm this).

We found that all three song types (varying predominantly in their temporal characteristics) included some infected individuals, indicating that if the presence of parasitoids has influenced the evolution of song types, it has not allowed any of the song types that we studied to avoid parasitization completely. Parasitoids are known to exploit the spectral features of host songs that are generally conserved among closely related species (Lehmann 2003). Tachinids may be able to locate the different *Mecopoda* male songs by exploiting the dominant frequency of their call rather than the temporal features such as call structure and call rate. The different *M. elongata* song types do not differ strongly in dominant frequency (Nityananda and Balakrishnan 2006), a situation also observed among song types in *Therobia leonidei* (Lakes-Harlan and Heller 1992, Robert et al. 1992) that is parasitized by the tachinid *Homotrixa alleni*, which also fails to show any preference among the different hosts it parasitizes (Lehmann 2003).

However, the fact that there were differences among sympatric song types in their rate of parasitization suggests that there could still be a coevolutionary relationship between the tachinid flies and their host. In this study, we found evidence that Two Part has a higher probability of parasitization than the other two song types. It is interesting to note that the mating calls of Two Part has both chirp and trill component while Double Chirper and Helicopter calls consist of only chirp or trill components, respectively. In another study of two closely related bush cricket species of the genus *Poecilimon* that have calls differing in the number of syllables in chirps, it was found that the parasitoid *T. leonidei* parasitized the *Poecilimon* species with polysyllables three to four times more often than the monosyllabic species (Lehmann and Heller 1998). A study by Wagner (1996) indicates that tachinid parasitoids find it easier to locate hosts with more call components. If parasitization is indeed a strong selection pressure on *M. elongata* Two Part populations, it is possible that the Two Part population split into Double Chirper and Helicopter song types with each retaining only one of the two components of Two Part call and both having a lower rate of parasitization.

Since 2010, field collections of *M. elongata* have been done at various times post monsoon (starting from September when mating season is about to start) from sites around Kadari field station. At our collection sites, the *M. elongata* breeding season begins at the end of September or the start of October. However, most tachinid infection, when it was discovered and studied in 2013 and 2014, appeared to occur at the end of the *M. elongata* mating season in February and March. *M. elongata* individuals collected before February were unaffected by parasitization. This suggests that the tachinid parasitoid life cycle lags that of the *M. elongata* reproductive cycle in Kervashe, Hurabi, and Heringe by four months. This trend was also seen in *Ormia ochracea* (Paur and Gray 2011); presumably the parasitoids are able to survive the *M. elongata* nonbreeding season either through diapause or through exploiting an alternative host, although which of these life-history strategies it employs remains to be determined.

Parasites have long been acknowledged to be a potentially important factor for both sympatric and allopatric divergence of host species leading to host speciation. However, there is limited direct evidence of parasitism leading to host diversification (Buckling and Rainey 2002). *M. elongata* song types are a promising system that could throw light on the role of parasites in speciation.

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Response of orthopterans to macroclimate changes: A 15-year case study in Central European humid grasslands

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Abstract

Orthoptera is a good indicator taxon of macroclimate changes. In our case study, we analyzed data of orthopterans, vegetation, and macroclimate collected yearly from 2002 through 2017 in Central European humid grasslands. During the study period, the annual mean temperature increased, while the relative abundance of moderately hygrophilic orthopteran species decreased significantly. On the other hand, the species richness and diversity of the assemblages increased due, mostly, to an increase of graminicole/thermophilic species. According to our results, the conservation of the hygrophilic orthopteran assemblages of Central European humid grasslands under global warming can only be ensured by adequate land management, which can at least mitigate the effects of climate change resulting in the warming and drying of humid habitats.

Keywords

climate change, Hungary, indicator, landscape management, monitoring, species richness

Introduction

Global climate change has a significant impact on insect populations and assemblages, both directly (in terms of temperature, precipitation, and seasonal changes) and indirectly (changes in vegetation productivity and quality characteristics, presence and spread of predators and pathogenic organisms) (Ryrholm 2001, Lightfoot 2006, Menéndez 2007). Orthopterans seem to be a good indicator for the monitoring of macroclimate changes, as their distribution, density, and assemblage structure are mostly determined by climatic conditions (Dreux 1962, Wingerden et al. 1992, Rácz et al. 1994, Guido and Chemini 2000, Squitier and Capinera 2002, Gardiner and Hassall 2009, Buri et al. 2013, Kenyeres et al. 2018). The mild effects of global climate change include variations in the phenological characteristics of the orthopteran species. According to the laboratory test results of Fielding and Defoliart (2010), in the cases of *Melanoplus borealis* (Fieber) and *Melanoplus sanguinipes* (Fabricius) a temperature increase of 2, 3, and 4°C results in earlier hatching by 3, 5, and 7 days, respectively. This phenomenon was also observed in Hungary between 1958 and 2009: the hatching of early species such as *Isophya costata*, *Isophya stysi*, *Isophya kraussii*, and *Isophya camptoxypha*, shifted earlier and earlier at a rate of 2–3 days/decade, due to the increasing spring mean temperature (Szabó et al. 2014).

Another important phenomenon resulting from global warming is the change in the area boundary of the Orthoptera species according to their cold tolerance (Uvarov 1931, Burton 2001). European species were observed to be expanding to the north due to global warming including, among others, *Phaneroptera falcata* and *Phaneroptera nana* (Kočárek et al. 2008), *Ruspolia nitidula*, *Mecostethus parapleurus* (Holuša et al. 2007) and *Roeseliana roeselii* (Gardiner 2009, Wissmann et al. 2009). The results of the impact of climate change on density of orthopterans are contradictory; there are some localities where an increase has been found while in others a decrease in density was observed (Bale et al. 2002, O'Neill et al. 2008, Laws and Belovsky 2010). This may be due to the locality-specific reaction of insects to climate change influenced by several circumstances of the habitat (e.g., altitude), nutrition (e.g., polyphagous vs. monophagous) and climatic requirements of the dominant species (Bale et al. 2002). Flightless, habitat-specialist species with a restricted area are particularly vulnerable to the effects of climate change. Their yearly population size, in many cases, responds very sensitively to some climate parameters (Kenyeres et al. 2018).

In the case of European species, climate change, although to a negligible extent when compared to the above, also influences the composition of the orthopteran assemblages through the increase in the chances of survival of the species that overwinter in an imago state (Kiritani 2006).

According to our earlier experiences gained in various regions of Central Europe, the impact of climate change on the orthopteran assemblages is really pronounced in humid grassland habitats (Kenyeres and Cservenka 2014). In this case study, we analyzed the data of orthopterans, vegetation, and macroclimate collected yearly between 2002 and 2017 under the monitoring program of the Fertő-Hanság National Park Directorate. Our main questions included: 1) What changes can be seen in the relative abundance of different life forms and eco-types over the 15-year period? 2) Can changes be detected in the relative abundance of species? 3) Is it possible to show relationships between the diversity parameters of orthopteran assemblages and parameters of the macroclimate? We hypothesized that changes in macroclimate (increasing temperature and decreasing precipitation) may result in an increase of thermophilic species and in a decrease of hygrophilic species.

Material and methods

Study area.—The study area (240 ha) (Fig. 1) belongs to the Hanság mesoregion of the Kisalföld macroregion. It is located at an altitude of ~114 m a.s.l. and is characterized by large flatlands.

The potential vegetation of Hanság, having previously had hydrological connections with Lake Fertő, which is 30 km away, is moorlands, fens, and marshlands. The drainage of the Hanság area started with the Romans, but the recent hydrological conditions are the result of interventions carried out in the last 100 years. At present, the natural vegetation of the region is restricted to some patches covered by large, mesic grasslands, mosaiced and surrounded by forests, scrubs, and tree plantations. The study area is dominated by intrazonal bog and fen soils. The level of the groundwater is permanently around 1 m. Turf resulting from loosening organic material is about half a meter. The average total duration of annual insolation in the region is 1,900 hours. Mean annual temperature is around 10.1 °C. The average annual precipitation is 630 mm (Dövényi 2010).

Experimental design.—The study area included two habitat-mosaics: a large area of contacting parcels dominated by humid grasslands and a smaller one on a comb of the local microrelief with humid and semi-dry grasslands impacted by forest areas (Fig. 1). Seven sampling sites were established as 50×50 m sized quadrats. Data collection was carried out from 2002 to 2017. All quadrats were consistently used: 1–2 were extensively grazed and 3–7 were mowed once a year in early June.

Environmental parameters.—Measurements of the main vegetation parameter (average height of the vegetation) were carried out on 3 plots in each sampling site during each orthopteran sampling. The height of the vegetation was measured in cm with the use of a 30 cm wide and 100 cm high white card. The total cover of the vegetation showed only small differences between 90 and 100% cover, so this parameter was not included in the experiment.

Regarding the 2002–2005 interval, we used public macroclimate data (annual mean temperature and precipitation) from the Hungarian Meteorological Service (www.met.hu), but from 2006 we used detailed daily macroclimate data from the Fertő-Hanság National Park Directorate (coordinates of data collection: 47°42'13.55"N, 17°10'40.43"E). We used the following derived parameters as potential background variables: seasonal (winter: December-February, spring: March-May, summer: June-August) annual and mean precipitation; seasonal and annual values of mean, minimum and maximum temperature; seasonal and annual values of mean, minimum and maximum humidity; mean of the monthly active and effective thermic amount (10 °C).

Orthoptera.—During the study period (2002–2017), sampling of the Orthoptera took place every June, July, August, and September.

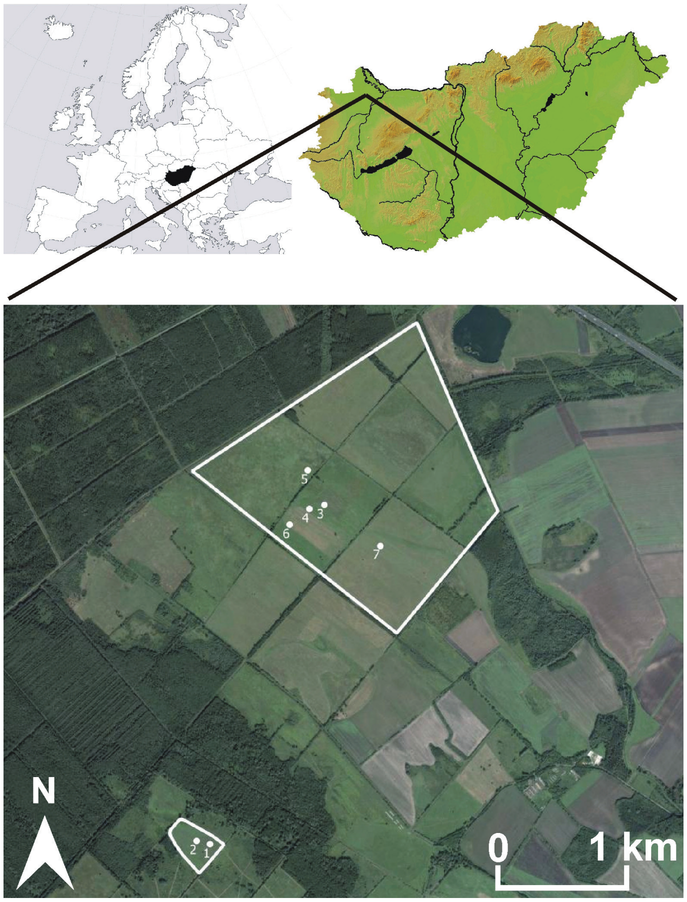

Fig. 1. Location map of the study area in Hungary.

Samplings were carried out by sweep-netting within the 50×50 m sampling sites (altogether 448 samples). Species abundances were recorded by 300 sweeps per sampling site. Sweep-netted samples were identified to species level following Harz (1969, 1975). Scientific nomenclature follows Cigliano et al. (2017).

The categories defined by Uvarov (1977) and Ingrisch and Köhler (1998) were used for classification of life forms (arbusticole: species found in habitats dominated by shrub-sized items; pratinicole: species found in grasslands of tall grass; graminicole: species found in grasslands of short grass; geophilic: species found in grasslands characterized by a high percentage of bare soil; pseudo-psammophilic: species found in different types of grasslands but usually having a high density in sandy grasslands).

The characterization of the climatic requirements of the species as thermophilic, moderately-thermophilic, mesophilic, moderately-hygrophilic, and hygrophilic were assigned based on Varga (1997), Rácz (1998), and Ingrisch and Köhler (1998).

Statistical analysis.—Samples collected in the same sampling sites in the same year were pooled (the number of pooled samples was 112). The pooled samples were used for calculating assemblage variables and statistical analyses. Shannon diversity, species number, relative abundances of detected species, of life forms, and of species-groups with different climatic requirements were calculated and used as Orthoptera variables in the statistical analyses. The mean values of Orthoptera response variables were calculated for comparison.

The Mann-Kendall trend test was used to evaluate temporal trends for both the Orthoptera variables and the macroclimate data. Generalized linear models (response variables: parameters of Orthoptera showed statistically significant decreasing or increasing trends; predictor variables: macroclimate data) were performed. Canonical correspondence analysis based on Orthoptera species data and environmental parameters were also compiled. All statistical analyses were performed using the Past 3.14. software package (Hammer et al. 2001).

Results

Orthoptera species.—Thirty-four Orthoptera species comprising 11,191 individuals were recorded at the sampling sites. The most prevalent species was *Bicolorana bicolor* with 1,779 individuals (16%), followed by *Chorthippus brunneus* with 1,530 individuals (14%), *Roeseliana roeselii* with 1,317 individuals (12%), *Pseudochorthippus parallelus* with 1,261 individuals (11%), *Conocephalus fuscus* with 1,084 individuals (10%), *Chorthippus mollis* with 1,042 individuals (9%), *Chorthippus biguttulus* with 742 individuals (7%), *Euchorthippus declivus* with 392 individuals (4%), *Stenobothrus lineatus* with 368 individuals (3%), *Euthystira brachyptera* with 330 individuals (3%), *Chrysochraon dispar* with 312 individuals (3%), and *Mecostethus parapleurus* with 194 individuals (2%) (see Appendix 1).

Trends in Orthoptera parameters.—During the study a significant decreasing trend in the relative abundance of moderately-hygrophilic species (Fig. 2A), a non-significant increasing in the relative abundance of thermophilic species (Fig. 2B), and a significant increasing trend in the relative abundance of graminicole species (Fig. 2C) were detected. Species richness also showed a significant increase (Fig. 2D). Of the species recorded, the relative abundance of mesophilic *Chrysochraon dispar* and thermophilic *Euchorthippus declivus* increased significantly (Fig. 3A, C), while the moderately-hygrophilic *Roeseliana roeselii* showed a significant decrease (Fig. 3B).

Trends in macroclimate parameters.—A significant increasing trend was seen in the data of annual mean temperature (Fig. 4A); while annual precipitation showed no clear trend (Fig. 4B), mean monthly precipitation showed a non-significant decrease from 2006 to 2017 (Fig. 4C).

Effects of macroclimate parameters.—Based on the results of the generalized linear models, annual mean temperature and annual minimum temperature were found to be significant predictors of the relative abundance of graminicole, pratinicole, and thermophilic species, of the species number, and of the diversity of the assemblages. The increase of annual mean temperature and annual minimum temperature were found to be significant predictors of a higher relative abundance of graminicole thermophilic species, a lower relative abundance of pratinicole species, and higher orthopteran species diversity and species richness (Table 1). Also, the relative abundance of graminicole species and the diversity of the assemblages were positively related to mean temperature in summer. Besides, orthopteran diversity and the relative abundance of moderately thermophilic and thermophilic species were positively related to the means of the monthly active and effective thermic amount (10 °C).

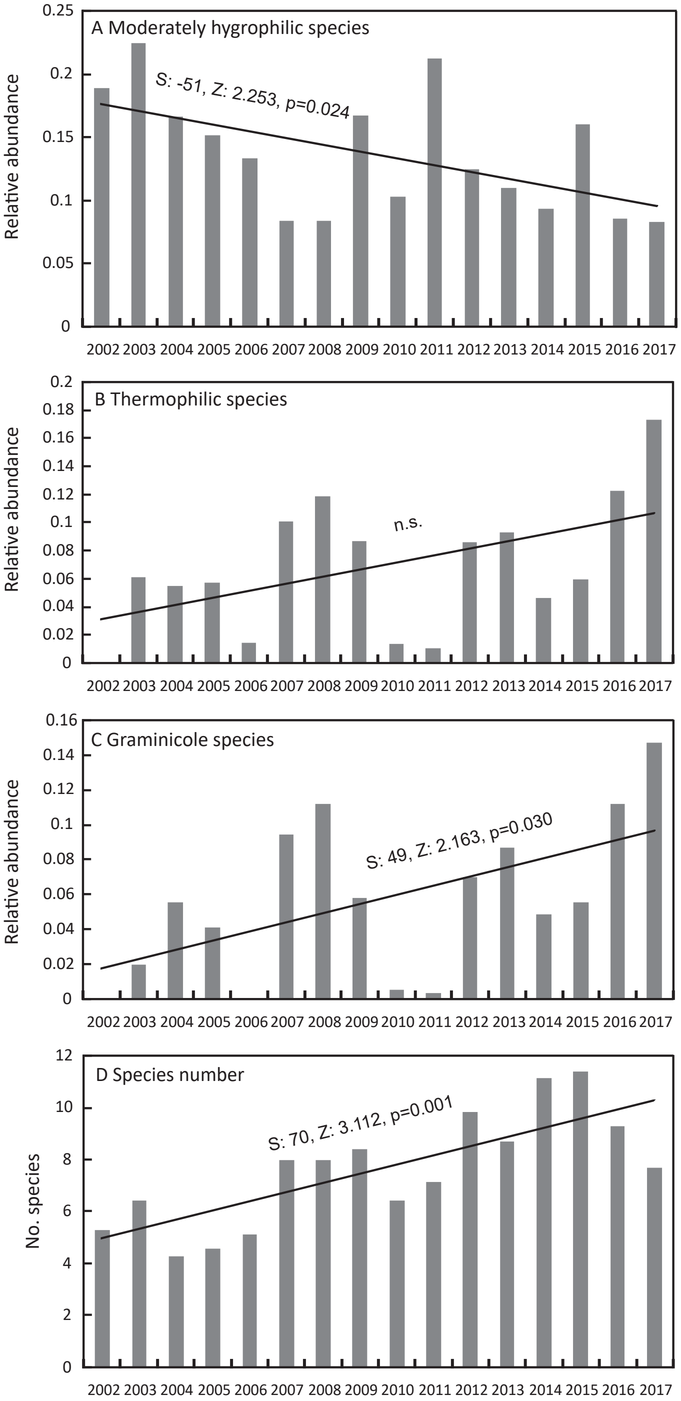

Fig. 2. Decreasing and increasing trends in the relative abundance of some orthopteran parameters (2002–2017). Temporal trends were evaluated by the Mann-Kendall trend test.

Based on canonical correspondence analysis (CCA) ordination, the relative abundance of graminicole species, thermophilic species, and *Euchorthippus declivus* were positively correlated with mean temperature in summer (Fig. 5). The relative abundance of *Roeseliana roeselii* was negatively correlated with the latter parameter. The relative abundance of pratinicole species and *Conocephalus fuscus* were positively correlated to high precipitation in spring (Fig. 5). Species richness was affected by annual mean and minimum temperature and also by monthly active and effective thermic amount (10 °C) (Fig. 5).

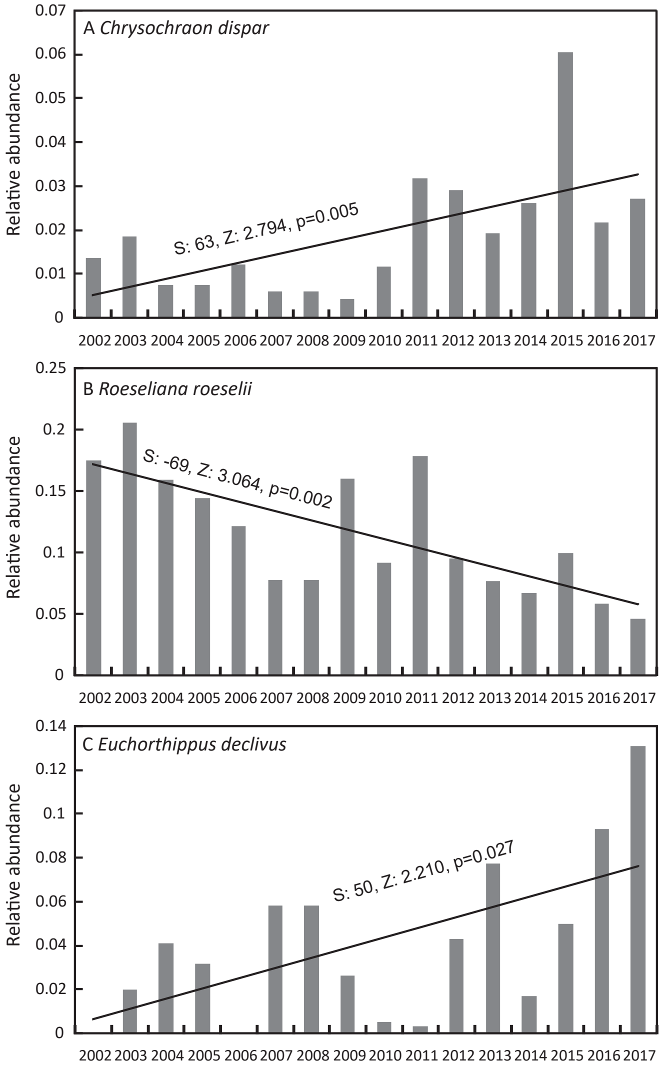

Fig. 3. Significant decreasing and increasing trends in the relative abundance of some characteristic Orthoptera species in the studied grasslands (2002–2017). Temporal trends were evaluated by the Mann-Kendall trend test.

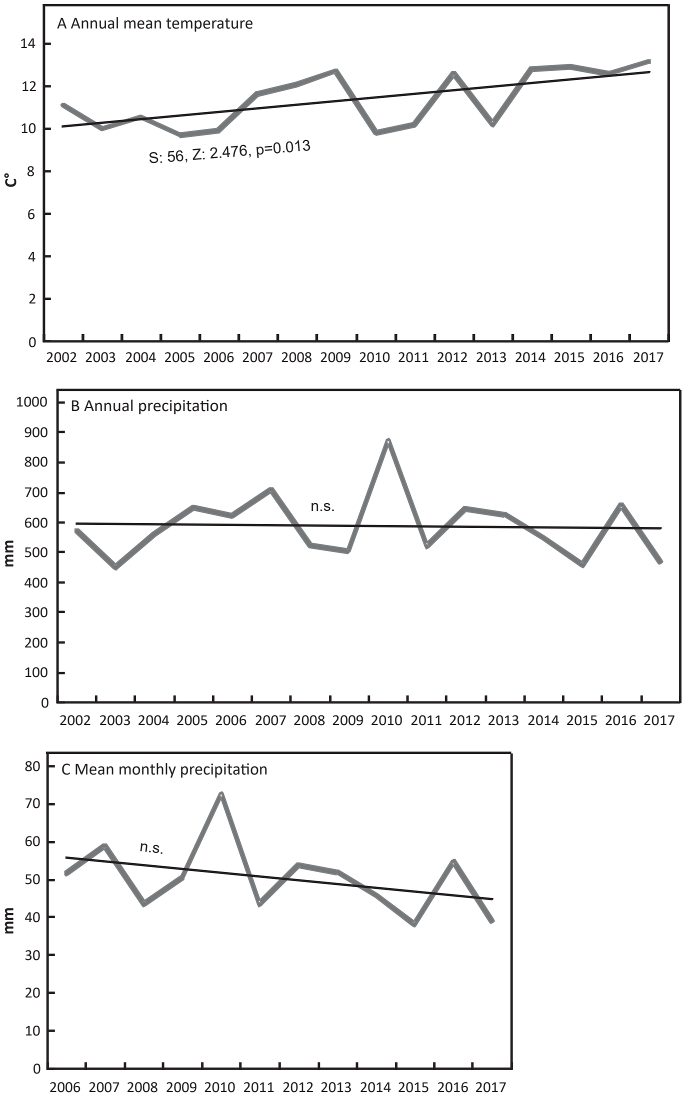

Fig. 4. Trends in macroclimate parameters on the studied area (2002–2017). Temporal trends were evaluated by the Mann-Kendall trend test.

Discussion

Global warming (Bale et al. 2002), which has a complex effect on insect communities, is an existing phenomenon in Central Europe (Anders et al. 2014). It is well known that species-specific ecological requirements make the orthopterans particularly sensitive to climate change (Wessely et al. 2017). Between 2002 and 2017, the annual average temperature increased significantly in the humid grasslands of the Carpathian Basin that we studied. No trend was identified in annual rainfall. In the grasslands investigated, the relative abundance of moderately hygrophilic orthopteran species decreased significantly, while the relative abundance of thermophilic species increased.

These results suggest that species adapted to cooler climates are more sensitive to climate change (Butterfeld and Coulson 1997). It should be noted that the fluctuation in macroclimate data more than the gradual increase in mean temperature (Fig. 4A) may have a stronger negative impact on certain species in the long run (Easterling et al. 2000). During the study period, the relative abundance of graminicole species also increased which might be related not only to the macroclimate changes, but also to the eutrophication of the grasslands (Lind et al. 2017).

In our study, the effect of macroclimate change was also detectable at species level. The vertical and horizontal area expansion of thermophilic species as a result of global warming which has been described in several areas (Kočárek et al. 2008, Breitenmoser 2015, Kettermann and Fartmann 2018) was also observed in this study. Over the course of the study, some species were found in the sample areas which were not present in the early years, possibly due to their dry-hot climatic requirements (e.g., *Calliptamus italicus*, *Euchorthippus declivus*, *Omocestus petraeus*, and *Platycleis affinis*). Of the results related to the change in the local relative abundance of the species, a significant decrease in the relative abundance of the moderately-hygrophilic *Roeseliana roeselii* is remarkable, although the species is represented in the whole dataset with a large number of specimens. In recent decades, the northward expansion of *Roeseliana roeselii* and

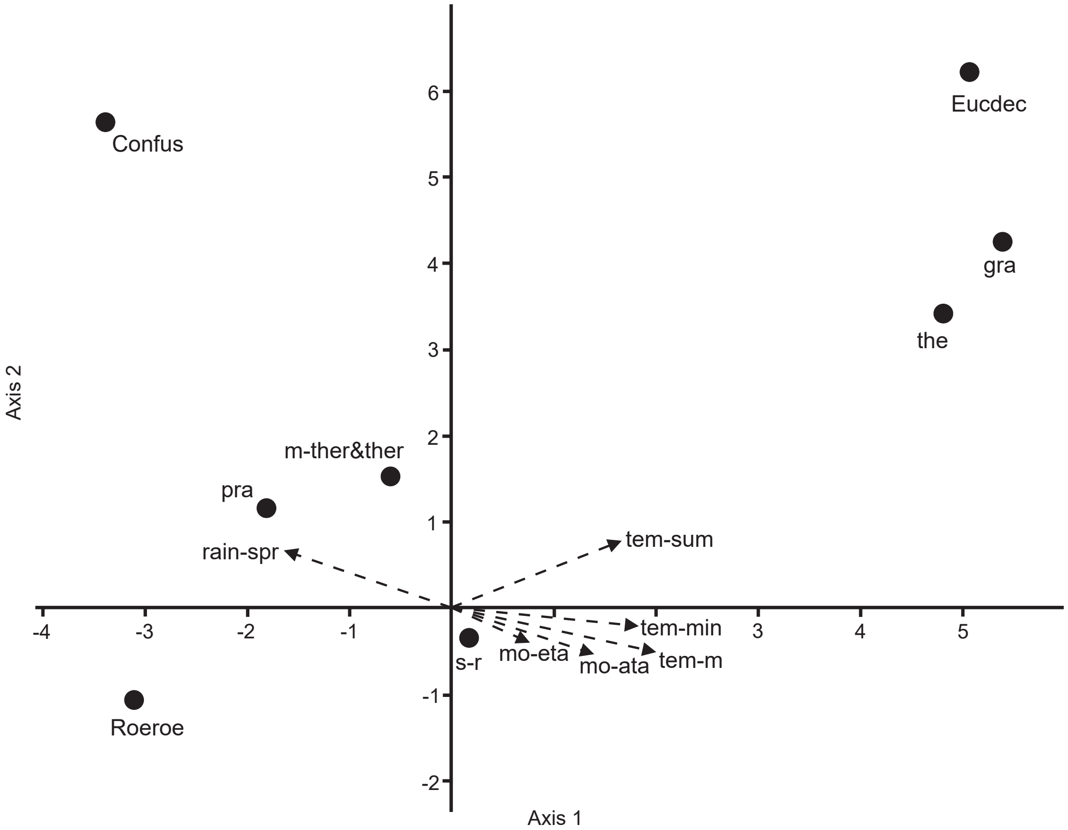

Fig. 5. CCA ordination based on Orthoptera parameters and environmental parameters (Confus: *Conocephalus fuscus*; Eucdec: *Euchorthippus declivus*; gra: graminicole species; mo-ata: mean of the monthly active thermic amount (10°C); mo-eta: mean of the monthly effective thermic amount (10°C); m-ther&ther: moderately-thermophilic and thermophilic species; pra: pratinicole species; rain-spr: rainfall in spring; Roeroe: *Roeseliana roeselii*; s-r: species richness; tem-m: annual mean temperature; tem-min: annual minimum temperature; tem-sum: mean temperature in summer; the: thermophilic species).

Table 1. Significant results of GLM testing of macroclimate effects on Orthoptera assemblages (* P<0.05; ** P<0.01; *** P<0.001; data for the mean of the monthly active and effective thermic amount and precipitation were log transformed).

Response variable	Predictor variable	Estimate	St.err.	p
Roeseliana roeselii	Mean temp. in summer	-16.634	6.146	**
Euchorthippus declivus	Mean temp. in summer	16.701	6.061	**
Graminicole species	Mean temp. in summer	14.194	5.102	**
	Annual mean temp.	14.467	6.715	**
	Annual min. temp.	24.513	8.943	**
Pratinicole species	Annual mean temp.	-18.041	7.436	*
	Annual min. temp.	-28.779	8.940	**
Diversity	Annual mean temp.	16.789	5.733	**
	Annual min. temp.	19.768	8.605	*
	Mean of the monthly active thermic amount (10°C)	0.698	0.253	**
	Mean of the monthly effective thermic amount (10°C)	0.932	0.344	**
	Mean temp. in summer	12.109	4.757	*
	Precipitation in spring	-1.844	0.867	*
Species number	Precipitation in spring	-0.052	0.025	*
	Annual mean temp.	0.508	0.158	**
Thermophilic species	Annual mean temp.	16.551	6.299	**
	Annual min. temp.	22.859	8.486	**
Moderately thermophilic and thermophilic species	Mean of the monthly active thermic amount (10°C)	0.302	0.108	**
	Mean of the monthly effective thermic amount (10°C)	0.411	0.145	**

Conocephalus fuscus, also occurring in the humid grasslands of Central Europe, was recorded in northern and northwestern Europe (Kleukers et al. 1996, Fartmann 2004, Wissmann et al. 2009). On the one hand, this latter phenomenon confirms the fact that the impact of global warming is more intense in areas closer to the poles (Bale et al. 2002). It is not only recent experiences, but also the results explored in the case of climate changes in earlier geologic epochs (Coope 1970), which indicate that insects do not adapt to the changed conditions in the case of climate change, but follow it by changing their areas.

In conclusion, in the Central European humid grasslands studied, the increase in the annual mean temperature most intensively affected negatively the relative abundance of moderately hygrophilic orthopteran species. The expansion of thermophilic species could also be observed within the study area (they occupied habitats that were not previously suitable for them). The number of species and diversity of the local orthopteran assemblages was higher as the annual average temperature increased. From a conservation point of view, this is not necessarily a positive fact. The orthopteran assemblages of humid grasslands in Central Europe are normally characterized by low diversity, due to the dominance of some hygrophilic and moderately hygrophilic species. According to our results, the conservation of the main characteristics of the Central European humid grasslands, under global warming, can only be ensured by adequate land management.

Suggestions for adequate land management

Due to the causes of global warming, the following suggestions for adequate local land management of humid grasslands in Central Europe are suggested: (1) Spatial mosaic grassland management by changing the patches abandoned throughout the season every year. (2) Exclusion of grazing or, at the most, only in an extensive manner during autumn. (3) Abandonment of mowing in extremely dry years with a warm spring (except for patches affected by invasive plant species). The above options can result in a mitigating effect of the denser vegetation (Cox and Moore 1980, Schoonhoven et al. 1998), which regulates the microclimate of the humid grasslands.

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Appendix 1

Species composition and abundance of the samples pooled per year (LF: life form; EF: ecotype form; arbu: arbusticole; geo: geophilic; gra: graminicole; pra: pratinicole; psps: pseudo-psammophilic; hyg: hygrophilic; mes: mesophilic; m-hyg: moderately-hygrophilic; m-ther: moderately-thermophilic; ther: thermophilic).

Taxon	LF	EF	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
Bicolorana bicolor (Philippi, 1830)	pra	m-ther	34	159	138	112	157	94	94	71	138	192	128	31	24	158	147	102
Chorthippus brunneus (Thunberg, 1815)	pra	m-ther	21	130	24	45	50	100	91	96	336	72	206	47	112	104	62	34
Roeseliana roeselii (Hagenbach, 1822)	pra	m-hyg	46	176	37	44	60	69	70	126	96	174	82	67	64	102	70	34
Pseudochorthippus parallelus (Zetterstedt, 1821)	pra	mes	45	8	18	17	104	58	58	51	144	106	116	120	122	114	152	28
Conocephalus fuscus (Fabricius, 1793)	pra	hyg	21	60	26	29	24	50	51	52	152	134	28	89	134	130	58	46
Chorthippus mollis (Charpentier, 1825)	pra	mes	6	56	0	0	72	50	64	102	236	31	108	75	72	66	64	40
Chorthippus biguttulus (Linnaeus, 1758)	pra	m-ther	4	61	0	0	22	59	60	58	47	64	96	91	78	49	20	33
Euchorthippus declivus (Brisout de Barneville, 1848)	gra	ther	0	20	18	14	0	28	28	20	6	4	42	52	14	36	64	46
Stenobothrus lineatus (Panzer, 1796)	pra	m-ther	2	22	27	26	0	21	22	6	12	47	24	38	60	15	40	6
Euthystira brachyptera (Ocskay, 1826)	pra	mes	11	42	0	0	25	20	19	52	0	50	22	20	30	34	5	0
Chrysochraon dispar (Germar, 1834)	pra	m-hyg	5	24	3	2	9	6	5	4	13	46	27	18	36	68	26	20
Mecostethus parapleurus (Hagenbach, 1822)	pra	hyg	7	0	0	0	0	0	0	0	0	0	5	0	16	47	64	55
Chorthippus dorsatus (Zetterstedt, 1821)	pra	mes	12	8	0	8	0	0	0	14	0	0	8	13	28	25	8	12
Decticus verrucivorus (Linnaeus, 1785)	pra	mes	6	0	0	0	2	3	2	9	8	13	8	19	2	8	9	10
Tettigonia viridissima Linnaeus, 1758	arbu	mes	0	0	8	12	14	12	11	6	2	7	0	0	8	5	4	0
Calliptamus italicus (Linnaeus, 1758)	gra	ther	0	0	0	0	0	15	14	9	0	0	2	6	17	4	0	11
Conocephalus dorsalis (Latreille, 1804)	pra	hyg	0	0	6	2	0	0	0	0	12	11	4	15	16	2	1	0
Omocestus petraeus (Brisout de Barneville, 1856)	gra	ther	0	0	7	3	0	0	6	13	0	0	21	0	0	0	11	0
Phaneroptera falcata (Poda, 1761)	arbu	ther	0	6	0	0	4	3	1	21	10	0	11	0	0	0	0	0
Omocestus haemorrhoidalis (Charpentier, 1825)	pra	ther	0	21	0	6	0	0	0	0	0	9	5	3	0	2	7	3
Pseudochorthippus montanus (Charpentier, 1825)	pra	hyg	13	21	0	0	0	0	0	0	0	0	0	0	0	0	0	8
Tetrix subulata (Linnaeus, 1758)	geo	hyg	0	0	0	0	0	0	0	0	31	0	3	0	0	0	0	0
Ruspolia nitidula (Scopoli, 1786)	pra	m-hyg	0	0	0	0	0	0	0	3	0	2	0	11	0	0	3	5
Chorthippus oschei Helversen, 1986	pra	mes	10	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Omocestus rufipes (Zetterstedt, 1821)	pra	mes	0	0	0	0	0	5	0	0	0	0	5	0	0	0	6	0
Chorthippus dichrous (Eversman, 1859)	pra	mes	0	0	0	0	0	0	0	0	0	0	0	0	6	0	4	2
Tetrix tenuicornis (Schalberg, 1893)	pra	ther	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oecanthus pellucens (Scopoli, 1763)	pra	m-ther	0	0	3	5	0	0	0	0	0	0	0	0	0	0	0	0
Leptophyes albovittata (Kollar, 1833)	arbu	ther	0	0	0	0	3	0	0	0	0	0	0	0	1	2	0	0
Stethophyma grossum (Linnaeus, 1758)	pra	hyg	3	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aiolopus thalassinus (Fabricius, 1781)	gra	m-ther	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
Stenobothrus nigromaculatus (Herrich-Schäffer, 1840)	gra	ther	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Platycleis grisea (Fabricius, 1781)	pra	ther	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	0
Platycleis affinis Fieber, 1853	psps	ther	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	1

Effects of water extracts of frass from three locust species and various plants on oviposition and embryonic development in the desert locust, *Schistocerca gregaria*

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Abstract

The water extract of desert locust, *Schistocerca gregaria*, frass collected in the wild had an oviposition inhibitory (OI) effect when mixed with sand and presented to adults. Likewise, the leaves of six plant species, as well as frass produced by desert locusts fed with these plants, exerted OI effects when compared with the control sand wetted with water alone. In general, frass extracts had a greater OI effect than the extracts of leaves. The OI effect was also observed when adult desert locusts were exposed to extracts of frass produced by two other locusts, the Bombay locust, *Nomadacris succincta*, and the migratory locust, *Locusta migratoria*, fed with rescue grass, *Bromus catharticus*. Among the three species of locust, desert locust and migratory locust frass exerted a greater OI effect than Bombay locust frass. Frass samples extracted with hot and cool water produced similarly high OI effects, indicating that bacterial involvement during extraction is unlikely. Hatching rates of desert locusts were significantly reduced by extracts of all of the above mentioned frass when the extracts were mixed with sand and used to incubate the eggs. In contrast, the lethal effects of leaf extracts on the hatching rates varied depending on the plant species. The embryos became deformed within four days when three-day-old eggs were incubated in sand containing frass extracts from desert locusts fed with rescue grass, whereas no apparent morphological changes were observed when seven-day-old eggs were similarly tested, although their hatching rate was significantly reduced.

Keywords

behavior, choice test, egg hatching, oviposition inhibitory effect, plague locust

Introduction

The desert locust, *Schistocerca gregaria*, is potentially the most destructive insect pest in the world. During the last major desert locust outbreak in 2003–2004, eight million people in the Sahel were affected, and crop losses caused by the locust infestation amounted to 80–100% of the expected yields (Brader et al. 2006). At low population densities, the nymphs of this species tend to avoid one another and seldom cause damage to agricultural crops. Desert locusts are relatively sedentary, and adults live solitary lives except during the mating period. However, during outbreaks, desert locusts move in bands or swarms and eat host plants voraciously, causing serious damage to agricultural crops (Uvarov 1966, 1977, Pener 1991, Pener and Simpson 2009). One of the characteristics that enables desert locust populations to grow so quickly is a high reproductive potential, and female adults frequently produce egg pods, each containing 65–75 eggs (Uvarov 1966).

The oviposition behavior and activity of acridid species are greatly influenced by soil properties such as water content (Norris 1968, Ji et al. 2007), pH (Ji et al. 2007), and chemical composition (Woodrow 1965a, b, Norris 1968, Newland and Yates 2008, Woodman 2017). Recently, Tanaka and Sugahara (2017) observed that adult female desert locusts kept in their rearing cages for several days avoided laying egg pods in old sand and demonstrated that locust frass and rescue grass, *Bromus catharticus*, leaves fed as feed contained one or more factors inhibiting oviposition. These oviposition inhibitory (OI) factors are water-soluble and heat-stable. Water extracts of frass also inhibited embryonic development of this locust when mixed with sand and used to incubate eggs. It is not known whether the factors inhibiting oviposition and embryonic development are the same or not, because chemical identification of the factors has not been performed. It is also not clear whether the OI effect and lethal effect on embryos are present in frass produced by locusts in the wild, or only by locusts in the laboratory. In this study, we addressed the following questions: 1) Does frass produced by locusts in the wild exert OI effects? 2) Does frass produced by other locust species exert OI effects on desert locusts? 3) Does frass produced by desert locusts after feeding on other plants exert an OI effect on desert locusts? 4) Is there bacterial involvement in the production of OI effects? 5) How do these frass and plant extracts affect embryonic development in desert locusts? This paper reports results obtained in relation to these questions and discusses their significance.

Materials and methods

Insects and plants.—The desert locust colony used in this study was originally collected in Niger in 2004 by Prof. H. J. Ferenz, and nymphs and adults were maintained in groups as previously described (Tanaka and Sugahara 2017). The migratory locust, *Locusta migratoria*, and the Bombay locust, *Nomadacris succincta* (also known as *Patanga succincta*), were collected in 2016 on Minami-Daito Island, Okinawa, Japan. Desert locusts were fed leaves of rescue grass (*Bromus catharticus*, BC), orchard grass (*Dactylis glomerata*, DG), sorghum (*Sorghum bicolor*, SB), Japanese mustard spinach (*Brassica rapa* var. *perviridis*, BR), romaine lettuce (*Lactuca sativa* var. *longifolia*, LS), and cabbage (*Brassica oleracea* var. *capitata*, BO), depending on the season. Migratory locusts were supplied with leaves of rescue grass, orchard grass, sorghum, or silver grass (*Miscanthus sinensis*, MS). Wheat bran was also constantly supplied. Adult Bombay locusts were reared on leaves of rescue grass.

The plants supplied as feed were grown at research plots of the National Institute of Agro-biological Sciences at Ohwashi (NIASO) and the National Agriculture and Food Research Organization (NARO), with the exception of the silver grass, which was collected in the field, and the romaine lettuce and cabbage, which were purchased from supermarkets.

Sample preparation and assay method.—The frass and cut leaves (1–2 cm^2) used in the experiments were dried at a relative humidity of 10–40% for three days in the rearing room of NIASO. The frass used in the experiments were collected in the Tsukuba laboratory, except for the frass obtained from desert locusts reared on romaine lettuce at the High Agronomic Institute of Chott Mariem in Tunisia in 2016, and the frass collected under umbrella thorn trees, *Acacia tortilis*, at Boulenoir (21°14'23"N, 16°34'26"W) and Soueissiya (21°16'35"N, 16°44'55"W) in Nouadhibou, Mauritania, in 2016 and 2017, respectively.

Each frass or leaf sample (30 g in dry weight) was soaked in water (300 ml) overnight at room temperature, and the solution was filtered according to previously described methods (Tanaka and Sugahara 2017). In brief, 55 ml of the extract solution was mixed with 270 g of sterilized sand in a plastic cup, which was presented to sexually mature locusts in a wooden-framed cage (42 × 22 × 42 cm) covered with nylon screens. A cup containing sand wetted with water alone was used as a control.

The number of ovipositing females in cages varied from 20 to > 50, depending on age, and thus the number of egg pods laid varied from one experiment to another. The holes made by adult females and egg pods laid were counted daily, and the egg pods laid in the sand were removed. After removing the egg pods, the sand surface of each cup was cleaned and flattened. This procedure was repeated until a total of at least 20 egg pods were collected except for treatments in which sexually mature locusts dug many holes but laid only a few eggs into any sand cup at least for 4 days. Because ovipositing holes are easily filled when the sand is dry, the sand surface was sprayed with water every day. In this study, daily numbers of egg pods laid and ovipositing holes observed were compared between treatments. To obtain frass from locusts fed with various plants, the locusts were fed each plant for at least two days before collecting test frass for experiments.

To determine whether the OI factor was a result of bacterial activity during extraction, frass samples (30 g in dry weight) from desert locusts fed with *B. catharticus* were soaked in boiling water (300 ml) in a water bath for 3 min, and the solution was filtered as described above. After cooling for 7 min, the filtrated solution (hot water extract) was mixed with sterilized sand as described above. For comparison, another set of frass samples was soaked in water (300 ml) at room temperature for 10 min, and the solution was filtered and mixed with sand (cool water extract). Three sand cups containing hot water extract, cool water extract, and water were presented to locusts in the same cage and the numbers of egg pods laid and holes were recorded daily.

Effects of frass and leaf extracts on egg hatching rates.—Egg pods were first incubated in clean sand in vinyl cups (diameter, 3 cm; height, 4 cm) with a lid, and egg pods were usually incubated in five groups of 20 eggs. Egg pods were buried as a mass in the test sand or clean sand on days one, three, or seven. Egg pods were incubated at 30°C under constant illumination and checked for hatching every day until no more hatching was observed.

Measurements of egg widths and embryonic antennal lengths.—Maximum egg widths were measured for eggs incubated at 30°C using an ocular micrometer installed in a binocular microscope. Embryonic antennal lengths were similarly measured after 6–11 eggs were fixed in water at 90–100°C for 10 min and were subsequently dissected.

Data analyses.—The numbers of egg pods and oviposition holes were analyzed with a t-test or Tukey's multiple range test after analysis of variance (ANOVA) using a statistics service available at http://www.gen-info.osaka-u.ac.jp/MEPHAS/kaiseki.html. The hatching percentages were analyzed with the generalized linear mixed model (GLMM), which was calculated by the function "lmer" of the program package lme4 using the software R version 3.4.2 (R Development Core Team 2018).

Results

OI effects of water extracts of desert locust frass collected under umbrella thorn trees in Mauritania.—Extracts of the two desert locust frass samples collected underneath umbrella thorn trees in Mauritania in 2016 and 2017 had similar effects on oviposition. Few or no egg pods were laid on average in the sand treated with frass extracts, whereas more than 5 pods were laid on average into the control sand kept in the same cages, and these differences were statistically significant (Fig. 1A, B; $t = -5.01$, df = 13, $p = 0.001$ and $t = -6.21$, df = 10, $p = 0.001$ for samples 1 and 2). In contrast, no significant difference was observed in the mean number of holes dug in each pair of cups (Fig. 1C, D; t-test, $p = 0.08$ and 0.14 for samples 1 and 2).

OI effects of water extracts of frass produced by locusts fed with romaine lettuce.—High OI activity was observed in extracts of frass produced by desert locusts fed with romaine lettuce in Tunisia. No egg pod was laid in the cups containing the extracts, whereas a daily average of 6.3 egg pods (94 pods in total) were laid in the control cups ($t = -8.12$, df = 14, $p < 0.001$; Fig. 2A). The number of holes observed was similar between the treated and control cups (t-test, $p = 0.27$, df = 14; Fig. 2B).

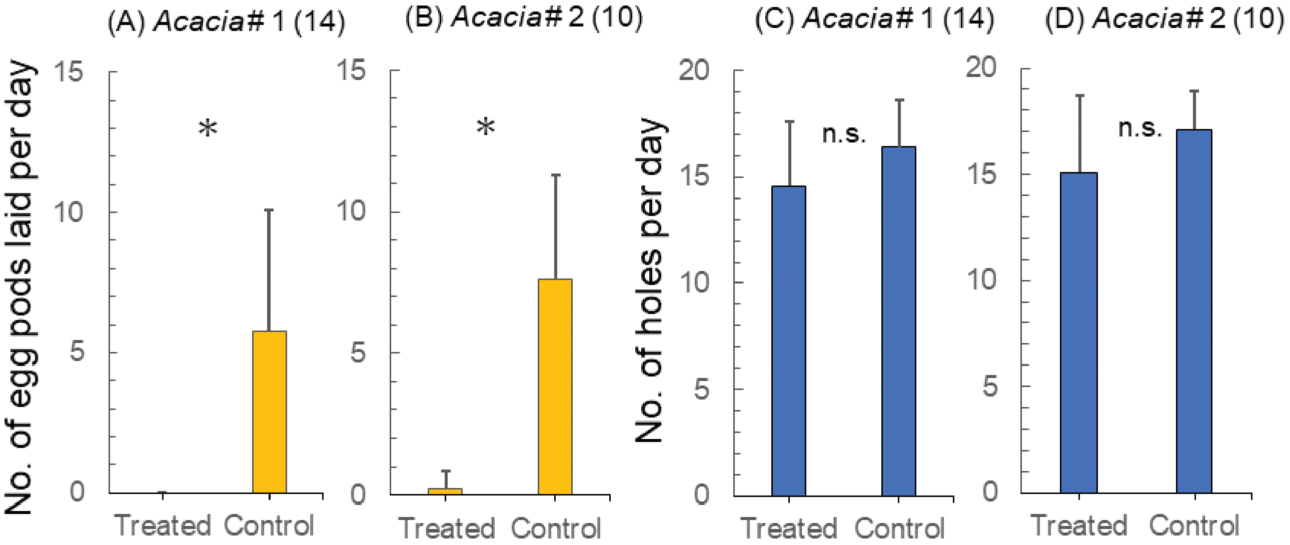

Fig. 1. Effects of water extracts of desert locust frass collected under umbrella thorn trees in the Mauritanian desert on the number of **A.**, **B.** Egg pods laid, and **C.**, **D.** Holes dug by adult female desert locusts presented with extracts mixed with sand. Frass were collected at sites #1 and #2 in 2016 and 2017, respectively. Two cups containing frass extracts (treated) and water (control) were simultaneously presented to locusts in each of two locust cages for seven or five days, and the data were combined. Numbers in parentheses indicate the total numbers of days observed. Bars on histograms indicate one standard deviation. Asterisks indicate a significant difference at the 5% level with a t-test. n.s. indicates no significant difference.

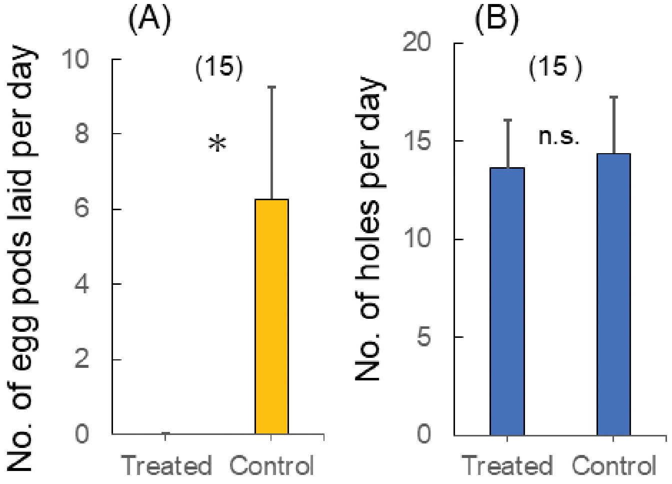

Fig. 2. Effects of water extracts of frass obtained from lab-reared desert locust fed with romaine lettuce in Tunisia on the number of **A.** Egg pods laid and **B.** Holes dug by adult female desert locusts presented with sand mixed with frass extracts. Two cups containing frass extracts (treated) and water (control) were simultaneously presented to locusts in each of two locust cages for seven or eight days, and the data were combined. Numbers in parentheses indicate the total numbers of days observed. Asterisks indicate a significant difference at the 5% level with a t-test. n.s. indicates no significant difference.

OI effect of water extracts of frass produced by desert locusts fed with various plants.—Fig. 3 illustrates the effects of extracts of leaves and frass produced by desert locusts that were fed with six different plants on oviposition. When three cups containing leaf extract, frass extract, and water were presented under choice, desert locusts laid egg pods mainly into the control cups, and only a few or no egg pods were deposited into the cups containing extracts of frass and leaves irrespective of the plant species used. A comparison of oviposition activity between cups containing water (control) and frass extract (Suppl. material 1: Fig. S1) or leaf extract (Suppl. material 2: Fig. S2) was also performed. The results indicated that locusts laid few egg pods into the cups containing frass or leaf extracts, and laid egg pods almost exclusively into the control cups irrespective of the plant species used. These results indicate that all plants and frass tested exerted OI effects.

The OI effects were compared between the extracts of frass and leaves. In this experiment, no water cup was included because, as shown in Fig. 3, locusts given a choice laid almost exclusively into the water sand cup. Significant differences were observed in the number of egg pods between the two treatments for orchard grass, romaine lettuce, and silver grass (Fig. 4A, D, F), whereas no significant differences were observed for cabbage, sorghum, and Japanese mustard spinach (Fig. 4B, C, E). In these experiments, desert locusts laid only small numbers of egg pods overall, but they dug 50–123 holes during the test periods, indicating that digging activity was high, but oviposition was strongly repressed. In general, the OI effect was stronger for the frass extracts than for the leaf extracts.

OI effects of frass produced by other acridid species.—Frass obtained from rescue grass-fed Bombay locusts and migratory locusts exerted OI effects when the water extracts were mixed with sand and presented to adult desert locusts together with control sand wetted with water alone. In both experiments, when desert locusts were exposed to extracts of frass from the two locusts (Bombay and migratory locusts), few or no egg pods were laid in the treated sand, whereas approximately five egg pods were laid daily in the control sand (Fig. 5A, C). In contrast, no significant difference was observed in the mean number of holes between the treated and control sand cups in both experiments (t = –1.09, df = 28, p = 0.28 for Bombay locusts and t = 1.73, df = 18, p = 0.64 for migratory locusts, Fig. 5B, D). These results indicate that frass from both

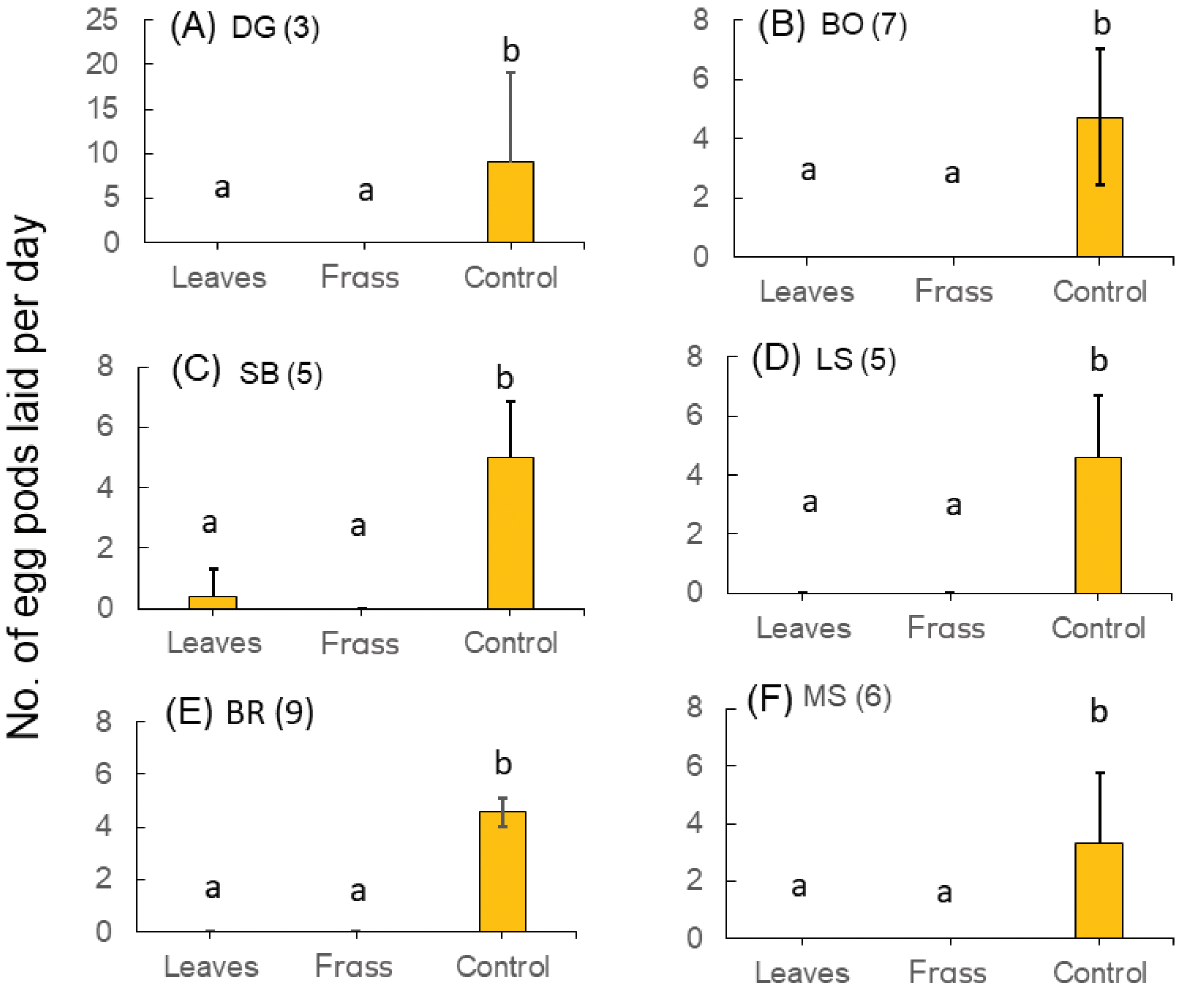

Fig. 3. Effects of water extracts of leaves of various plants and desert locust frass collected after locusts fed on these plants on the numbers of egg pods laid by adult female desert locusts presented with sand mixed with extracts. Sand wetted with water was also presented as a control. Three cups containing leaf, frass extract, and water (control) were simultaneously presented to locusts in one (**A, C, D**) or two locust cages (**B, E, F**) for three to five days, and the data were combined in (**B**), (**E**), and (**F**). Numbers in parentheses indicate the total numbers of days observed. Bars on histograms indicate one standard deviation. Different letters in each panel indicate significant differences at the 5% level with Tukey's multiple comparison test. DG, *Dactylis glomerata* (orchard grass); BO, *Brassica oleracea* var. *capitata* (cabbage); SB, *Sorghum bicolor* (sorghum); LS, *Lactuca sativa* var. *longifolia* (romaine lettuce); BR, *Brassica rapa* var. *perviridis* (Japanese mustard spinach); MS, *Miscanthus sinensis* (silver grass).

Bombay locusts and migratory locusts exerted OI effects on desert locusts but did not affect digging activity.

When water extracts of frass produced by the three locust species (desert, Bombay, and migratory locusts) were mixed with sand and presented to adult desert locusts simultaneously, the number of egg pods laid per day was significantly lower in treatments using the frass extracts from desert locusts and migratory locusts than in treatments using frass extracts from Bombay locusts (Fig. 6A; Tukey's multiple test, df = 18, $p < 0.05$ in both experiments), whereas no significant differences were observed in the numbers of holes dug by desert locusts exposed to frass extracts from the three locust species (Fig. 6B; ANOVA, $F = 2.16$, df = 2, 18, p = 0.14 and $F = 0.88$, df = 2, 18, p = 0.92 for light and dark histograms).

OI effects of hot and cool water extracts of frass of desert locusts fed with rescue grass.—Desert locusts laid no egg pod into sand cups containing hot and cool water extracts during the 4-day observation period and laid a daily average of 6 egg pods into a sand cup containing water (Fig. 7A), indicating that the OI factor was extracted with both hot and cool water. In contrast, no significant difference was observed in the number of holes made per day among the three cups (Fig. 7B, ANOVA, $F = 0.19$, p= 0.83, df = 2, 9).

Effects of water extracts of frass and plants on desert locust egg hatching rates.—Water extracts of frass collected under umbrella thorn trees had a different effect on desert locust egg hatching rates than the control treatment did. The desert locust eggs treated with extracts of the frass sample collected in 2016 had a significantly lower hatching rate than the control eggs (Table 1A, GLMM, $p < 0.05$), whereas those treated with extracts of the frass sample collected in 2017 had a similar hatching rate to that of the control eggs (Table 1A, GLMM, $p > 0.05$). Exposing desert locust eggs to extracts of frass collected from locusts fed with different test plants including romaine lettuce, orchard grass, sorghum, silver grass,

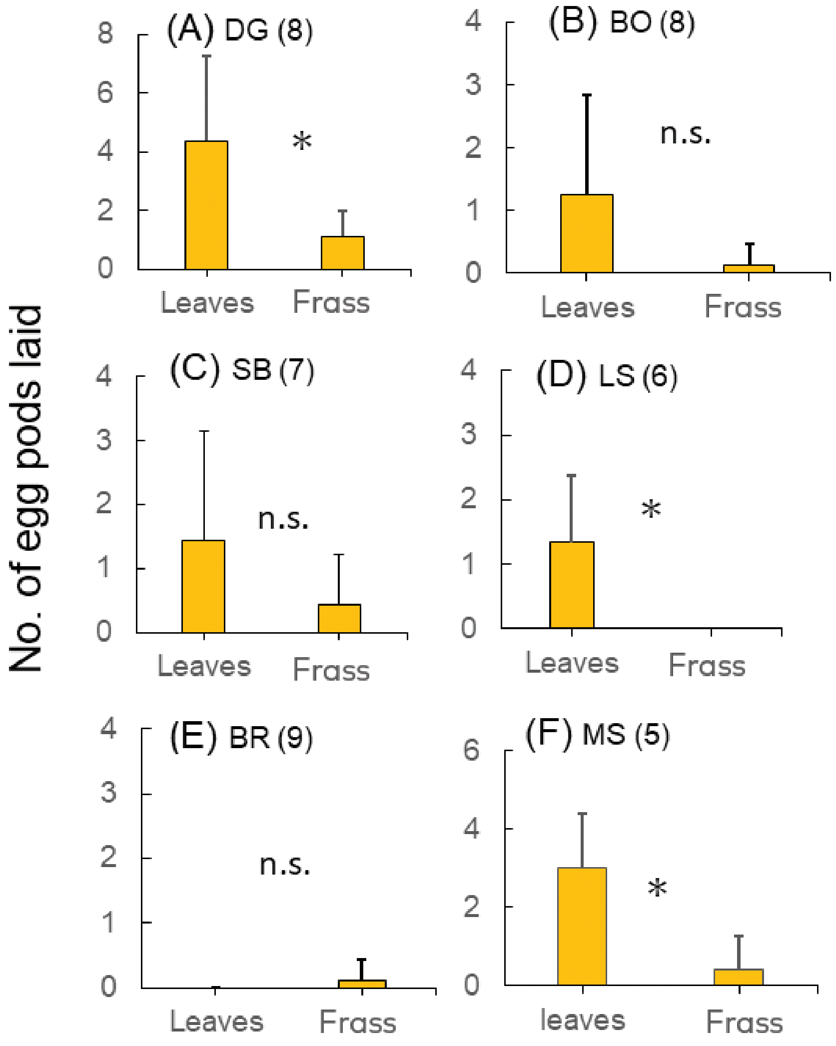

Fig. 4. Effects of water extracts of leaves of various plants and desert locust frass after locusts fed on these plants on the numbers of egg pods laid when extracts were mixed with sand and presented to adult female desert locusts. Two cups containing leaf and frass extracts were simultaneously presented to locusts in each of two locust cages for three to five days, and the data were combined. Numbers in parentheses indicate the total numbers of days observed. Bars on histograms indicate one standard deviation. Asterisks indicate significant differences at the 5% level with a t-test. n.s. indicates no significant difference. DG, *Dactylis glomerata* (orchard grass); BO, *Brassica oleracea* var. *capitata* (cabbage); SB, *Sorghum bicolor* (sorghum); LS, *Lactuca sativa* var. *longifolia* (romaine lettuce); BR, *Brassica rapa* var. *perviridis* (Japanese mustard spinach); MS, *Miscanthus sinensis* (silver grass).

Japanese mustard spinach, and cabbage resulted in significantly lower hatching rates than exposing eggs to the control treatment (Table 1B–G, GLMM, $p < 0.05$). Water extracts of different plants had different effects on desert locust egg hatching rates, depending on the species. Extracts of leaves of orchard grass, sorghum, and silver grass did not significantly affect egg hatching rates compared to the control eggs (Table 1I–K, GLMM, $p > 0.05$), whereas extracts of leaves of romaine lettuce, Japanese mustard spinach, and cabbage significantly reduced egg hatching rates (Table 1H, L, M, GLMM, $p < 0.05$).

Effects of water extracts of frass produced by Bombay locusts and migratory locusts on desert locust egg hatching rates.—Incubating eggs in sand wetted with frass extracts from Bombay locusts and migratory locusts significantly reduced the hatching rate of desert locust eggs compared to the control treatment, i.e., eggs incubated in the sand wetted with water (Fig. 8A, B, GLMM, $p < 0.001$ each). The hatching rate was significantly lower for the eggs treated with the frass extracts from migratory locusts than for those treated with the frass extracts from Bombay locusts (GLMM, $p < 0.001$), whereas no significant difference was observed between the two controls (GLMM, $p = 0.96$).

Effect of water extract of rescue grass-fed desert locust frass on embryonic development.—For the desert locust control eggs, the maximum egg widths on days one to three were similar (Fig. 9A; ANOVA, $F = 1.67$, df = 2, 27, $p = 0.21$), and maximum egg widths increased significantly on day four compared with day three ($t = -10.49$, df = 18, $p < 0.001$). The maximum egg width leveled off from day eight onward. In contrast, the maximum width of eggs incubated in the sand treated with the frass extract on day three increased slightly on day four (Tukey's multiple comparison, $p < 0.05$) but showed no further increase (Tukey's multiple comparison, $p > 0.05$).

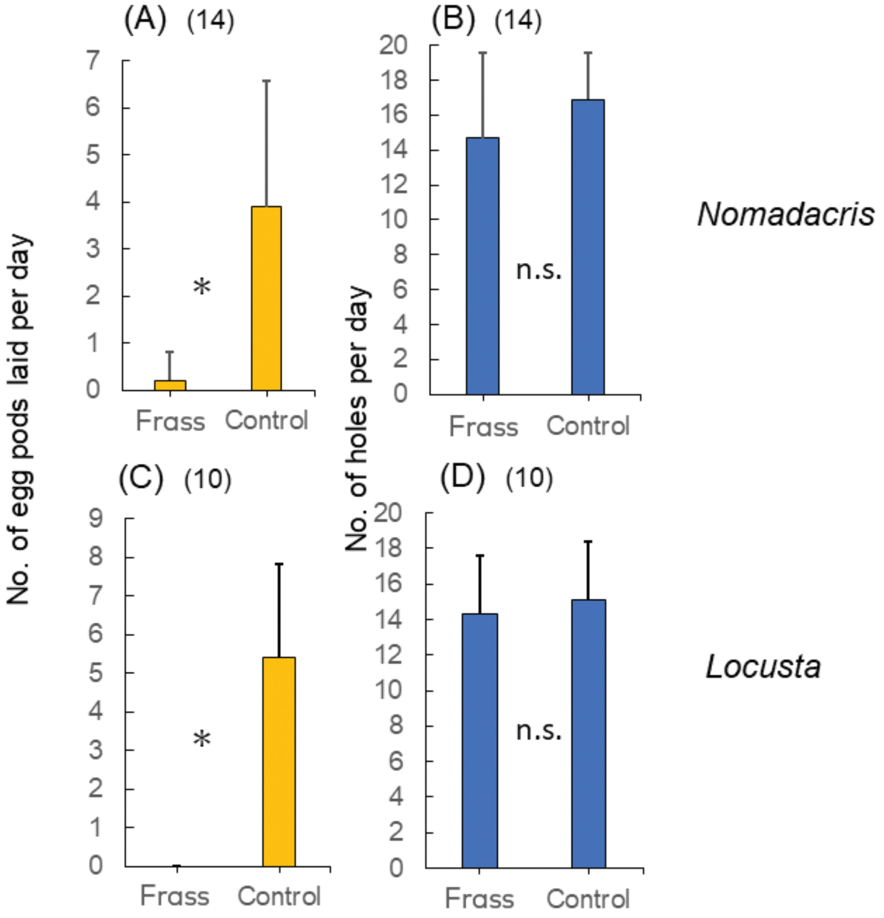

Fig. 5. Effects of water extracts of frass produced by **A**, **B.** Bombay locusts and **C**, **D.** Migratory locusts fed with rescue grass leaves on the numbers of egg pods laid (**A**, **C**) and holes dug (**B**, **D**) by adult female desert locusts presented with extracts mixed with sand. Two cups containing frass extract (treated) and water (control) were simultaneously presented to locusts in each of two locust cages, and the data were combined. Numbers in parentheses indicate the total numbers of days observed. Bars on histograms indicate one standard deviation. Asterisks indicate significant differences at the 5% level with a t-test. n.s. indicates no significant difference.

Table 1. Effects of water extracts of desert locust frass fed with various plants (A–G) and water extracts of those plants (H–M) on egg hatching rates. Five or three groups of 20 eggs were buried in sand wetted with each extract and water alone (control) within three days after oviposition and were observed for hatching at 30°C. Comparisons with controls were made with GLMM. Frass collected under two umbrella thorn trees in 2016 and 2017 were designated as AT #1 and AT #2. LS, *Lactuca sativa* var. *longifolia* (romaine lettuce); DG, *Dactylis glomerata* (orchard grass); SB, *Sorghum bicolor* (sorghum); MS, *Miscanthus sinensis* (silver grass); BR, *Brassica rapa* var. *perviridis* (Japanese mustard spinach); BO, *Brassica oleracea* var. *capitata* (cabbage).

ID	Treatments	No. of eggs	Total no. of hatched eggs	Total no. of dead eggs	P value	ID	Treatments	No. of eggs	Total no. of hatched eggs	Total no. of dead eggs	P value
	Frass						**Leaves**				
A	AT #1	20 × 5	22	78	0.007		AT #1	ND			
	AT #2	20 × 5	55	45	0.563		AT #2	ND			
	Control	20 × 5	61	39			Control	ND			
B	LS	20 × 5	5	95	<0.001	H	LS	20 × 5	52	48	0.037
	Control	20 × 5	86	14			Control	20 × 5	86	14	
C	DG	20 × 5	33	67	0.008	I	DG	20 × 3	83	17	0.945
	Control	20 × 5	80	20			Control	20 × 3	85	15	
D	SB	20 × 5	10	90	<0.001	J	SB	20 × 5	85	15	0.516
	Control	20 × 5	83	17			Control	20 × 5	91	9	
E	MS	20 × 5	1	99	<0.001	K	MS	20 × 5	85	15	0.202
	Control	20 × 5	94	6			Control	20 × 5	79	21	
F	BR	20 × 5	0	100	<0.001	L	BR	20 × 5	21	79	<0.001
	Control	20 × 5	85	15			Control	20 × 5	73	27	
G	BO	20 × 5	67	36	<0.001	M	BO	20 × 5	64	36	0.002
	Control	20 × 5	33	64			Control	20 × 5	91	9	

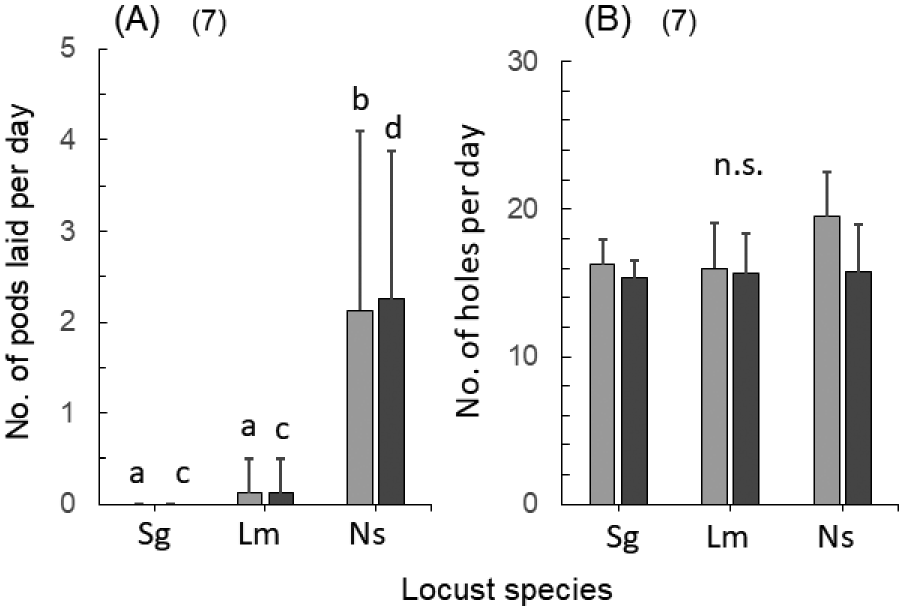

Fig. 6. Effects of water extracts of frass produced by desert locusts (Sg), migratory locusts (Lm), and Bombay locusts (Ns) fed with rescue grass leaves on the number of **A.** Egg pods and **B.** Holes dug by adult desert locusts presented with extracts mixed with sand. Three cups containing frass extracts of the three locust species were simultaneously presented to locusts in each of two locust cages (light and dark histograms) for seven days. Numbers in parentheses indicate the total numbers of days observed. Bars on histograms indicate one standard deviation. Different letters in each comparison (light or dark histograms) in (**A**) indicate significant differences at the 5% level with Tukey's multiple comparison test. n.s. indicates no significant differences in each comparison with ANOVA (light or dark histograms).

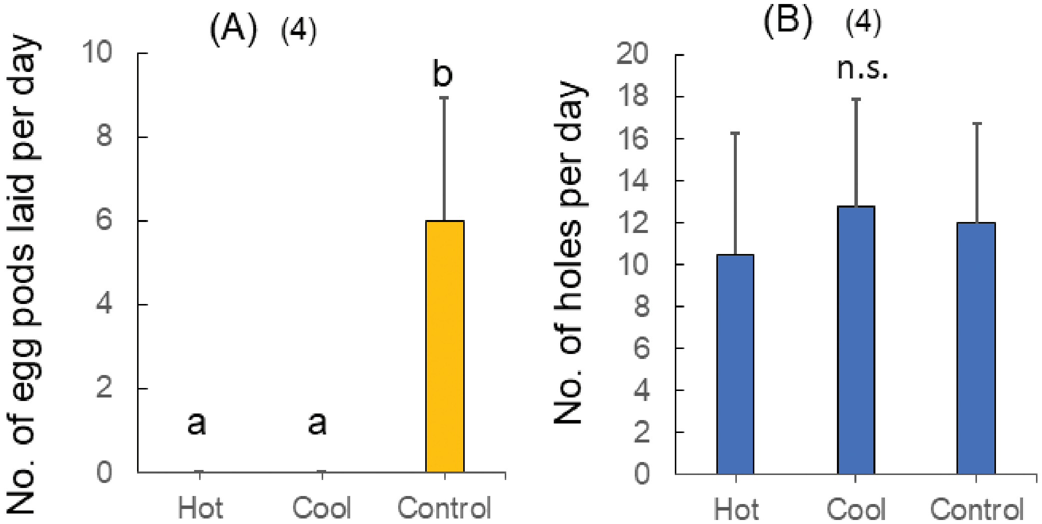

Fig. 7. Effects of hot and cool water extracts of rescue grass-fed desert locust frass on the number of **A.** Egg pods laid and **B.** Holes dug by adult female desert locusts. Frass were extracted with boiling and cool water and the extracts were mixed with sand. Sand cups containing these extracts and water as a control were presented to locusts in the same cage for 4 days. Numbers in parentheses indicate the total numbers of days observed. Bars on histograms indicate one standard deviation. Different letters in (**A**) indicate significant differences at the 5% level with Tukey's multiple comparison test. n.s. in (**B**) indicates no significant difference with ANOVA at the 5% level.

The mean antennal length (± SD) for the control embryos on day three was 0.16 ± 0.04 mm (n = 10), increased to 2.48 ± 0.27 mm by day 13, and subsequently leveled off.

In contrast, the embryos treated with the frass extract slightly increased their antennal length by day five, but no further elongation was observed through day 11 when the eggs darkened and some contained only amorphous embryos (Fig. 9B; ANOVA, *F* = 7.65, df = 4, 33, p = 0.07). The difference in the mean values of the two groups became significant from day seven onward (t-test, p < 0.001 each). Examples showing embryos on days five and nine are shown in Fig. 9C–F. The embryos treated with the frass extract reached stage VI–VII, according to the embryonic stages described for desert locusts by Shulov and Pener (1963) and were deformed (Fig. 9F).

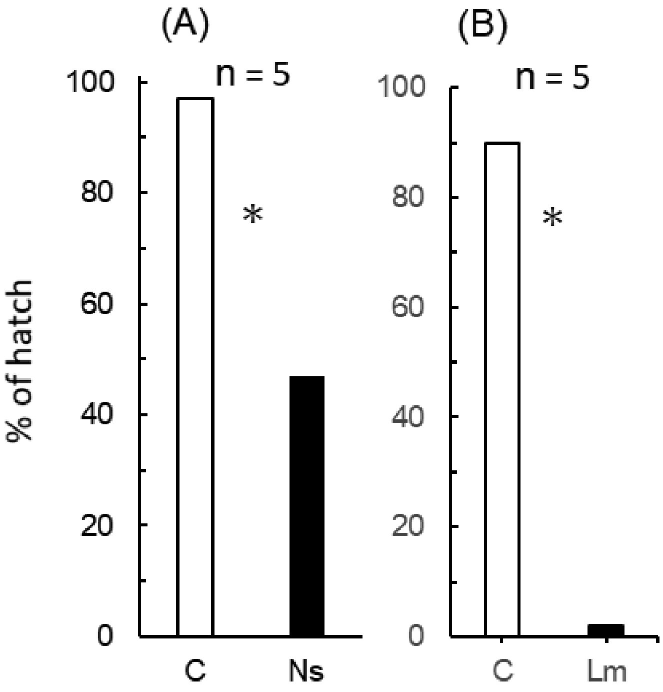

Fig. 8. Effects of water extracts of rescue grass-fed Bombay locust (Ns) and migratory locust (Lm) frass on desert locust egg hatching rates. Five groups of 20 eggs were buried in sand wetted with each extract and water alone (control, C) within three days after oviposition and were observed for hatching at 30°C. Asterisks indicate significant differences at the 5% level with GLMM.

The incubation of eggs in the sand treated with frass extract and water alone, respectively, on day seven onward showed no significant difference on day 13 (the day before hatching) for either egg widths (t = 1.56, df = 18, p = 0.14; data not shown) or antennal lengths (t = 0.823, df = 10, p = 0.43; Suppl. material 3: Fig. S3). However, the hatching rate was significantly lower in the eggs treated with the frass extract (41.7%, n = 60) than in the controls (90.0%, n = 60, GLMM, p < 0.001), indicating that mortality occurred after embryogenesis was completed.

Discussion

Locusts ready to lay eggs must find a suitable site for oviposition. The ovipositing behavior consists of digging and laying eggs (Uvarov 1977). Locusts search and probe for a suitable site by using olfactory and visual signals in the environment. Norris (1968) reported that adult female desert locusts avoided laying eggs close to plants when placed in a cage 152 cm long with fresh grass at one end of the cage and without grass at the other end. Dry grass and alcohol extracts of grass also had a significant oviposition repellent effect. However, it is unknown whether this repellent effect of grass is exerted on the digging behavior, egg laying behavior, or both, because the number of digs was not described. Norris (1968) also demonstrated that more eggs were laid close to straw-colored raffia than to green raffia, indicating the involvement of a visual factor in oviposition behavior. In the present study, cups with visually similar sand surfaces were presented to locusts. As such, the differences observed in oviposition activity were unlikely to be visually influenced.

Locusts may dig holes in the soil but do not necessarily lay eggs (Norris 1963). One female desert locust was observed dig-

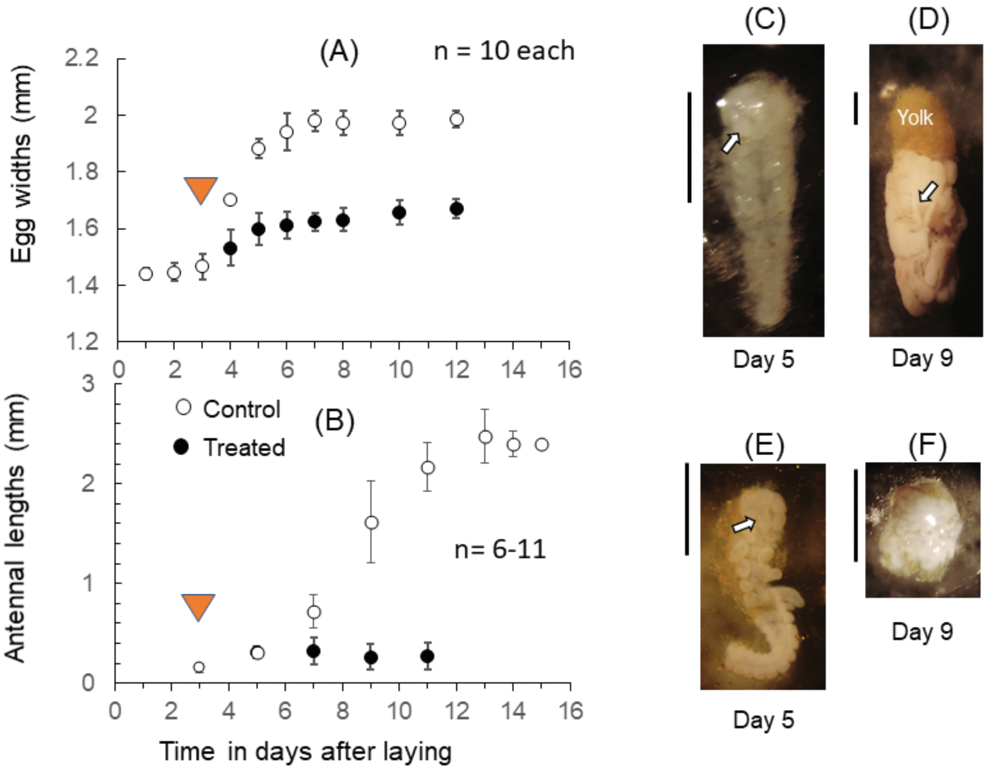

Fig. 9. Effects of water extracts of rescue grass-fed desert locust frass on **A.** Egg widths (mean ± SD; n = 10) and **B.** Antennal lengths of embryos (mean ± SD; n = 6–11). Eggs were incubated in sand wetted with the frass extract (treated) or water (control) on day three after oviposition at 30°C. **C–F.** Photographs show embryos observed on days 5 and 9. Triangles in (**A**) and (**B**) indicate the time when the treatment started. Vertical bars in **C–F** indicate 1 mm. White arrows indicate an embryonic antenna in **C–E**.

ging up to 32 holes before laying an egg pod (Norris 1968). In our laboratory, one female desert locust was observed to dig as many as 18 holes in a sand cup for 24 h without laying any eggs (Tanaka, S. unpublished observation). Therefore, the number of holes observed in the present study may only indicate that at least some female adults were actively engaged in oviposition behavior.

It has been reported that frass of desert locusts fed with rescue grass contain a water-soluble factor that inhibits oviposition (Tanaka and Sugahara 2017). Rescue grass has its origin in South America and was introduced to a wide range of temperate, subtropical, and tropical countries (Verloove 2012). Therefore, it remains unknown whether similar OI effects are also present in locust frass produced in the wild. The present study demonstrates that frass of wild desert locusts, collected under umbrella thorn trees in the Mauritanian desert, also exerted an OI effect. In Tunisia, romaine lettuce is a crop grown outdoors where desert locusts can feed on it. Frass collected from locusts fed with this plant in the laboratory in Tunisia were also observed to exert an OI effect. This observation was confirmed with adult desert locusts fed the same plant grown in Japan (Fig. 3D; Suppl. materials 1,2: Figs S1D and S2D).

In the present study, five other plants (i.e., in addition to rescue grass) were separately fed to adult desert locusts, and the produced frass and leaves of each plant were tested for the OI effect by simultaneously presenting three sand cups containing extracts of the frass, extracts of the leaves, and only water (as a control) to locusts. The results were similar in all the plant species tested; few or no egg pods were laid in the sand cups containing frass and leaf extracts, and most or all egg pods were laid in the control cups. Similar results were observed when these extracts were separately presented to locusts with a control sand cup (Suppl. materials 1,2: Figs S1 and S2). When sand cups containing leaf and frass extracts were simultaneously presented to locusts with no control sand cup, oviposition activity was generally low, although a high rate of digging activity was observed. In general, more egg pods were laid in sand cups containing leaf extracts than those containing frass extracts, indicating that the OI effect of the frass extracts was greater than that of the leaf extracts.

The OI effect was also observed in extracts of frass obtained from two other locust species, i.e., Bombay locusts and migratory locusts, when tested on desert locusts. Water extracts of frass produced by both locust species fed with rescue grass almost completely inhibited oviposition by desert locusts. Among the water extracts made with frass obtained from the three locust species, those from desert locusts had the greatest OI effect, followed by those from migratory locusts and Bombay locusts when tested against adult desert locusts, although the difference between the first two was not statistically significant. In contrast, the number of holes dug was similar among the three extracts, indicating that the frass extracts did not differentially affect digging behavior in desert locusts.

Tanaka and Sugahara (2017) reported that the OI factor contained in frass was heat-stable. Although they heated the filtrated solution immediately after extraction with water, there is the possibility that bacterial activity was involved in the production of the active compound(s) during extraction. The present study tested this possibility by extracting frass with boiling water and mixing the filtrated solution with sterilized sand. The results showed that OI effects of hot water extracts were as strong as those of cool water extracts, indicating that the OI factor was not produced by bacteria during the extraction process.

As observed for the frass produced by desert locusts fed with rescue grass in a previous study (Tanaka and Sugahara 2017), the frass extracts obtained from desert locusts that were fed with five other plant species in the laboratory significantly reduced egg hatching rates when mixed with sand and used to incubate eggs. One of the frass samples collected under umbrella thorn trees also had a similar effect, but the other sample did not. This difference might have been related to the stability of the active compounds, as it is not known how long the frass had remained on the sand surface in the desert before collection. The difference in the lethal effects on eggs between the two frass samples might indicate that the active compounds affecting egg hatching rates and those affecting oviposition activity are different. This hypothesis should be tested in the future.

The water extracts of rescue grass leaves do not affect egg hatching rates (Tanaka and Sugahara 2017). Similar results were obtained for orchard grass, silver grass, and sorghum in the present study. However, significant effects on egg hatching rates were observed for leaves of romaine lettuce and the two cruciferous species, Japanese mustard spinach and cabbage. The differences in the lethal effects on eggs among different plants are not easy to interpret. However, these results suggest that the active compounds are present only in some specific plants. Alternatively, the results might represent differences in the amounts of active compounds contained in the plants or different elution efficiencies of the active compounds from leaves of different plants. Identification of the active compounds present in these plant species and frass produced by locusts will help address this problem.

The frass extracts of rescue grass-fed desert locusts suppressed embryonic development when the eggs were incubated with sand mixed with the extracts three days after oviposition. All treated embryos remained in the anatrepsis stage, which is the stage before the embryo rotates inside the eggshell (Shulov and Pener 1963). Water absorption that occurred during days three to seven in the control eggs was also inhibited by the frass extract, which was likely to be related to the suppressed embryonic development. The lethal effect was observed even when the eggs were treated with frass extracts during the second half of embryonic development (Tanaka and Sugahara 2017). This was confirmed in the present study, as seven-day-old embryos had reduced hatching rates, but there were no apparent morphological abnormalities after incubation in the sand containing frass extracts. Therefore, the frass extracts apparently exerted effects on locust embryos at different stages in different ways.

The ecological significance of the behavioral and developmental responses of *S. gregaria* to frass and leaf extracts observed in the present study is not clear. Although this phenomenon should be confirmed using wild locusts or a recently established laboratory colony, we observed similar OI effects of frass extracts in another laboratory strain derived from Ethiopia and in another locust, *L. migratoria* (Tanaka, S. unpublished observation). Therefore, the present results were not specific to the laboratory strain used. Stower et al. (1958) observed that desert locusts laid eggs at some distance from plants in the field. It is not clear whether this pattern was a result of the effects of plants on the probing, egg laying, or both behaviors of locusts. However, an area close to host plants may have a high probability of being covered with frass or leaves and the habit of avoiding laying eggs close to plants might have evolved due to their inhibitory effects on locust embryos. Some host plants of desert locusts in the desert contain toxic compounds such as alkaloids (Simões et al. 2016). It would be interesting to examine how such plants or frass produced by locusts fed these plants affect oviposition and egg survival because information obtained from such observations might provide insights into the development of a new control measure against this notorious pest insect.

In conclusion, inhibitory effects on oviposition and embryonic development in desert locusts were observed not only for the frass produced by laboratory-reared locusts, but also for the frass produced by locusts in the wild. The locust frass and leaves of seven plants tested so far, including rescue grass (Tanaka and Sugahara 2017), consistently exerted great OI effects. In general, the extracts of the frass had higher inhibitory effects on embryonic development than extracts of the leaves of the plants. The OI effects were also detected in the frass produced by migratory locusts and Bombay locusts when tested on desert locusts, suggesting the possibility that some common biologically active compounds are contained in their frass.

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Supplementary material 1

Author: Seiji Tanaka, Toyomi Kotaki, Yudai Nishide, Amel Ben-Hamouda, Khemais Abdellaoui, Mohamed Abdallahi Bahah Ebbe, Sidi Ould Ely

Data type: multimedia

Explanation note: **Fig. S1.** Effects of water extracts of desert locust frass after feeding on various plants on the numbers of egg pods laid when adult female desert locusts were presented with extracts mixed with sand.

Link: https://doi.org/10.3897/jor.26.34665.suppl1

Supplementary material 2

Author: Seiji Tanaka, Toyomi Kotaki, Yudai Nishide, Amel Ben-Hamouda, Khemais Abdellaoui, Mohamed Abdallahi Bahah Ebbe, Sidi Ould Ely

Data type: multimedia

Explanation note: **Fig. S2.** Effects of water extracts of leaves of various plants on the numbers of egg pods laid when presented to adult female desert locusts mixed with sand.

Link: https://doi.org/10.3897/jor.26.34665.suppl2

Supplementary material 3

Author: Seiji Tanaka, Toyomi Kotaki, Yudai Nishide, Amel Ben-Hamouda, Khemais Abdellaoui, Mohamed Abdallahi Bahah Ebbe, Sidi Ould Ely

Data type: multimedia

Explanation note: **Fig. S3.** Effects of water extracts of rescue grass-fed desert locust frass on antennal lengths of embryos (A, mean ± SD; n = 6–10).

Link: https://doi.org/10.3897/jor.26.34665.suppl3

Review Article Journal of Orthoptera Research 2019, 28(2): 205-219

What determines the number of auditory sensilla in the tympanal hearing organs of Tettigoniidae? Perspectives from comparative neuroanatomy and evolutionary forces

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Abstract

Insects have evolved complex receptor organs for the major sensory modalities. For the sense of hearing, the tympanal organ of Tettigoniidae (bush crickets or katydids) shows remarkable convergence to vertebrate hearing by impedance conversion and tonotopic frequency analysis. The main auditory receptors are scolopidial sensilla in the *crista acustica*. Morphological studies established that the numbers of auditory sensilla are species-specific. However, the factors determining the specific number of auditory sensilla are not well understood. This review provides an overview of the functional organization of the auditory organ in Tettigoniidae, including the diversification of the *crista acustica* sensilla, a list of species with the numbers of auditory sensilla, and a discussion of evolutionary forces affecting the number of sensilla in the *crista acustica* and their sensitivity. While all species of Tettigoniidae studied so far have a *crista acustica*, the number of sensilla varies on average from 15–116. While the relative differences or divergence in sensillum numbers may be explained by adaptive or regressive changes, it is more difficult to explain a specific number of sensilla in the *crista acustica* of a specific species (like for the model species *Ancistrura nigrovittata*, *Copiphora gorgonensis*, *Gampsocleis gratiosa*, *Mecopoda elongata*, *Requena verticalis*, or *Tettigonia viridissima*): sexual and natural selection as well as allometric relationships have been identified as key factors influencing the number of sensilla. Sexual selection affects the number of auditory sensilla in the *crista acustica* by the communication system and call patterns. Further, positive allometric relationships indicate positive selection for certain traits. Loss of selection leads to evolutionary regression of the auditory system and reduced number of auditory sensilla. This diversity in the auditory sensilla can be best addressed by comparative studies reconstructing adaptive or regressive changes in the *crista acustica*.

Keywords

acoustic communication, behavior, *crista acustica*, katydid, sexual selection

Acoustic communication and behavior of Tettigoniidae

The study of insect hearing is an interdisciplinary field of research that has highlighted the great diversity of tympanal organs in different taxa (Fullard and Yack 1993, Hoy and Robert 1996, Yager 1999, Stumpner and von Helversen 2001, Yack 2004, Yack and Dawson 2007, Römer 2018). The tympanal organs in insects usually consist of one or two tympanal membranes, a tracheal sack, and a scolopidial organ containing sensory neurons (Hoy 1998, Yager 1999, Yack 2004, Römer 2018). Tympanal hearing organs occur on almost all locations of the insect body and with a great variation in the number of sensory neurons (scolopidial sensilla) associated with the tympanal membranes. The sensilla numbers can vary between only one in notodontid moth and hawkmoth up to 2000 in cicadas and (atympanate) bladder grasshoppers (Yager 1999, Yack 2004, Strauß and Stumpner 2015). For several tympanal ears, sensillum numbers range between 20–100 auditory sensilla (Yager 1999), and within Orthoptera, locusts and crickets usually have 50–70 auditory sensilla. Differences in the set of sensilla have been discussed for adaptive modifications relating to specific hearing functions (e.g., Strauß and Stumpner 2015). In Tettigoniidae, the tympanal organs are located in the proximal tibia of the forelegs, with tympanal membranes at the anterior and posterior side (Fig. 1A). These hearing organs with auditory sensilla in the *crista acustica* (CA) are generally broadly tuned and cover frequency ranges from low sound into ultrasonic frequencies (e.g., Kalmring et al. 1990, Rössler and Kalmring 1994, Rössler et al. 1994, Schul and Patterson 2003).

With more than 6500 species (Ingrisch and Rentz 2009, Mugleston et al. 2013), Tettigoniidae are an ideal taxon to study proximate and ultimate aspects of acoustic signalling and the design and diversification of ears. Hearing in Ensifera in general and in tettigoniids in particular likely evolved for detection and localization of potential mates (Bailey 1991, Stumpner and von Helversen 2001, Robinson and Hall 2002, Greenfield 2016) by calls that are species-specific in temporal pattern (Gwynne 2001, Robinson and Hall 2002). Male tettigoniids usually produce acoustic signals by tegminal stridulation, and females perform phonotaxis towards the males (unidirectional communication system). However, this signalling system was expanded into duets with females producing a reply call in few tettigoniid taxa (bidirectional communication system) (Nickle and Carlysle 1975, Bailey 2003, Heller et al. 2015), and males or both sexes move towards the other signaller. Selection requires the sensitivity for conspecific call frequencies and the recognition of the temporal pattern in the conspecific signals over other species' signals. While highest auditory sensitivity can match with the carrier frequency of the calls, there are also cases of mismatches between their call spectra and the frequency tuning of the ears known (e.g., Bailey and Römer 1991, Römer and Bailey 1998, see also Mason 1991 for a mismatch in the prophalangopsid *Cyphoderris monstrosa*). The transmission of sound signals is highly influenced by the environment, as vegetation filters particularly higher frequency components depending on the distance (Römer and Lewald 1992, Robinson and Hall 2002).

Hearing further allows predator detection and evasion, male aggressive behavior, and male spacing (Bailey 1985, 1991, Gwynne 2001, Robinson and Hall 2002). In particular, echolocating bats are important predators of tettigoniids (Belwood 1990, Kalka et al. 2008, Jones et al. 2014, ter Hofstede et al. 2017). Since bats evolved after the appearance of stridulatory structures in Tettigoniidae, the evolutionary sequence of hearing is likely to first involve intraspecific communication and then have expanded to higher ultrasonic ranges to include bat detection (Bailey 1991, Hoy 1992, Stumpner and von Helversen 2001, Greenfield 2016), while early insectivorous mammals likely also preyed upon stridulating insect (Hoy 1992). Tettigoniidae can hear bat echolocation calls and developed behavioral responses (Pollack 2015): certain species stop calling as it exposes the signaller (Faure and Hoy 2000, ter Hofstede et al. 2010), or animals in flight evade the sound source by dropping (Libersat and Hoy 1991) or changing flight orientation (Schulze and Schul 2001, Kilmer et al. 2010). In the tonotopically ordered CA (see below), the frequency contents of intraspecific calls or bat echolocation calls are processed by the adequately tuned sensilla. This tonotopic organization also allows intensity (distance) analysis (Hennig et al. 2004, Stumpner and Nowotny 2014, Römer 2016): further populations of sensilla will get recruited if the stimulus amplitudes increase to levels that also excite sensory neurons tuned to different best frequencies (Höbel and Schul 2007). The recruitment of sensilla for intensity discrimination is well documented for *Requena verticalis* with 22 auditory sensilla (Römer et al. 1998, Römer 2016). With the species-specific number of auditory sensilla and length of the auditory organ, the differences in thresholds extend the dynamic range of the hearing organ, and the number of sensilla can not only influence the accuracy of representing frequency resolution but also of amplitude differences (Römer 2016).

Selection and evolutionary adaptations of the tettigoniid hearing organ

Selection acts in a complex setting of acoustic signalling that includes the communication system, signal transmission, signalling distance (active space), and background noise. By the functions of hearing in mate detection and predator evasion, both sexual and natural selection affect the hearing organs in Tettigoniidae. Adaptations are notable in particular in the size differences of spiracles, which can be related to specific acoustic behaviors and selection pressures between sexes (e.g., Bailey and Römer 1991, Heller et al. 1997a, Mason and Bailey 1998, Strauß et al. 2017). In some circumstances, evolutionary forces may be difficult to identify by studying only the phenotypes, as selection pressures may overlap or even act in different directions (see Strauß and Stumpner 2015). After the loss of sexual selection, especially regressive evolution—in general, the decrease or reduction of a specific structure in some dimension like size, length, or number of elements—has been noted for spiracles and tympana, and this can also be analyzed for effects on the CA (the reduction of sensillum numbers) in a comparative approach. Drawing on the literature for several tettigoniid groups, here the neuroanatomical and physiological evidence for adaptations in the number of auditory sensilla in the CA is summarized and discussed.

Anatomical and neuronal structures of the tettigoniid tympanal hearing organ

The auditory organ in tettigoniids follows a ground plan of neuronal and anatomical elements, which can vary considerably in their morphology across different species (Bailey 1990, 1993, Lakes and Schikorski 1990, Rössler et al. 2006). These hearing organs show a remarkable evolutionary convergence to the vertebrate hearing organs for impedance conversion and frequency representation (Montealegre-Z et al. 2012, Palghat Udayashankar et al. 2012, Hildebrandt 2014).

The tympanal membranes are areas of thinned cuticle. The membranes can be openly exposed, but in other species can also be located behind tympanal covers or tympanal flaps (Bailey 1993). In the latter cases, sound enters to the tympana through thin tympanal slits (Fig. 1B, C). These flaps are supposed to contribute to the directionality of hearing (Bailey and Stephen 1978, Mason et al. 1991, Bailey 1993). In some species, so-called pinnae form around the tympana which leave a broader slit over the tympana (Bailey 1993). In some species like the Australian *Beiericolya tardipes* (Meconematinae), the Peruvian *Bufotettix auchenacophoroides* (Pseudophyllinae), and the Asian *Lacipoda immunda* (Pseudophyllinae), the proximal tibia is swollen so that it forms cups around the tympana and orients the opening dorsally on the tibia (Bailey 1990, Rentz 2001, Nickle 2006). The cup formation is described as most elaborated in *Phisis* and *Decolya* (Meconematinae) (Bailey 1990).

The neuronal responses to sound entering via the tympanal membranes are stronger for relatively lower frequencies (Hummel et al. 2011, Stumpner and Nowotny 2014), and low frequency sound travels relatively poor in the acoustic trachea (Jonsson et al. 2016). Rather than sound acting on the outer surface of the tympanal membranes, the major input to the hearing organ is via the acoustic spiracle in the prothorax, especially for higher sound frequencies (Lewis 1974, Nocke 1975, Michelsen et al. 1994, Bailey 1998, Hummel et al. 2011, Stumpner and Nowotny 2014, Jonsson et al. 2016). This enlarged acoustic spiracle is usually permanently open (for one exception see Römer and Bailey 1998), and continues into the acoustic bulla in the prothorax and the acoustic trachea that runs through the thorax into the foreleg and passively amplifies the sound input (Bailey 1993, Heinrich et al. 1993). The sizes of the spiracle and bulla differ between species (Mason et al. 1991, Stumpner and Heller 1992, Bailey 1993, Heinrich et al. 1993) and even between sexes of the same species (Bailey and Römer 1991, Heller et al. 1997a, Mason and Bailey 1998, Strauß et al. 2014). In addition, extensive differences in the sizes of bulla and spiracles occur between larger taxonomic groups, e.g., Phaneropterinae, Pseudophyllinae, and Tettigoniinae (Bailey 1990, 1993, Mason et al. 1991). In the proximal tibia, the acoustic trachea splits into an anterior and posterior branch at the level of the tympana (Fig. 1B; Schwabe 1906, Schumacher 1975a, Lin et al. 1994, Sickmann et al. 1997), forming a "bicompartmental receptor region" (Heinrich et al. 1993). The split into the two tracheal branches occurs only distally of the proximal sensilla of the CA (Rössler et al. 1994, Sickmann et al. 1997). The tracheal branches align laterally behind the anterior and posterior tympanum (Fig. 1B).

The principal sensory organ processing acoustic stimuli is the *crista acustica* (CA) located within the foreleg tibia between the

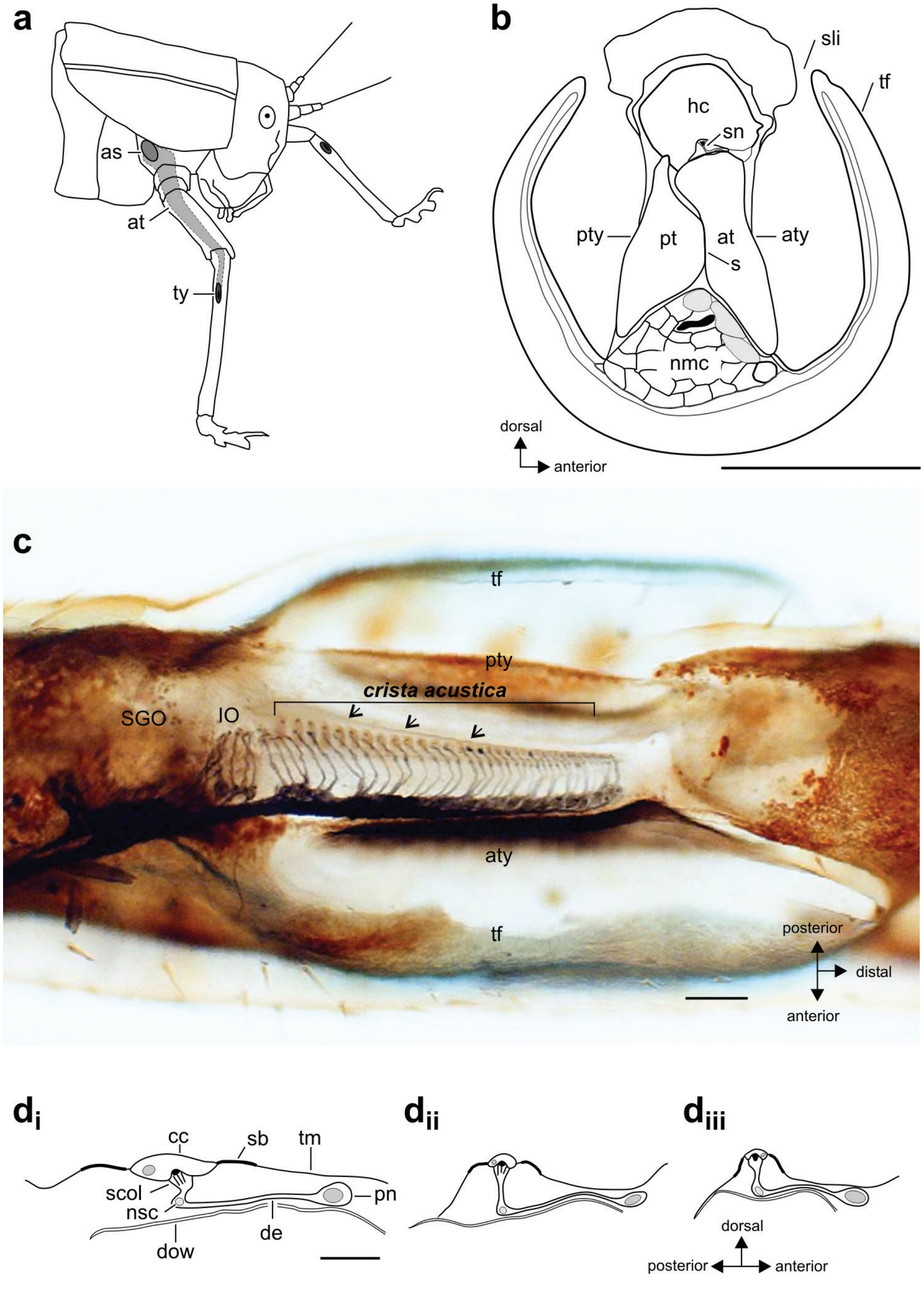

Fig. 1. The auditory system of bushcrickets. **A.** Schematic of the acoustic trachea (at) from the acoustic spiracle (as) in the thorax into the foreleg with tympanal membranes (ty) in the proximal tibia; **B.** Transverse section of the tibia at the level of the tympana and *crista acustica* in *Gampsocleis gratiosa*; in Gampsocleis gratiosa; **C.** The sensory organs in the proximal tibia of the male *Tettigonia viridissima*. The dorsal cuticle has been removed after axonal tracing of the tympanal nerve with cobalt solution to stain sensory neurons of the subgenual organ (SGO), intermediate organ (IO) and *crista acustica*. The *crista acustica* is placed between the anterior tympanum (aty) and posterior tympanum (pty). The tympanal flaps (tf) cover the tympanal membranes. Arrows indicate the tectorial membrane; **D.** Morphological differences of sensory neurons along the *crista acustica* from *G. gratiosa*, showing the (d_i) third-most proximal, (d_{ii}) middle, and (d_{iii}) third-most distal sensillum. Abbreviations: at, anterior trachea; aty, anterior tympanum; cc, cap cell; de, dendrite; dow, dorsal tracheal wall; hc, haemolymph channel; IO, intermediate organ; nmc, nerve muscle channel; nsc, nucleus of scolopale cell; pn, perikarya of sensory neurons; pt, posterior trachea; pty, posterior tympanum; s, septum; sb, supporting band; scol, scolopale cap and rods; SGO, subgenual organ; sli, slit; sn, sensory neuron; tf, tympanal flap; tm, tectorial membrane. Scales: 500 µm (**B**), 100 µm (**C**), 50 µm (**D**). Figure **A.** reprinted from Strauß et al. 2014, with permission from John Wiley and Sons. **B.**, **D.** redrawn from Lin et al. 1994, with permission from John Wiley and Sons.

tympana (Fig. 1C). The sensory neurons are scolopidial sensilla located over the tracheal branches arranged in the proximo-distal axis of the tibia (Fig. 1B–D), covered by the tectorial membrane, which is triangular in shape with a curvilinear surface. The CA is part of the complex tibial organ together with other scolopidial organs: the subgenual organ, the intermediate organ and the accessory organ (Fig. 1C; Lakes and Schikorski 1990, Rössler et al. 2006, Strauß et al. 2016). The CA sensilla are attached to the tectorial membrane and the dorsal wall of the acoustic trachea but are not in direct contact with the tympana (Fig. 1B, D; Lakes and Schikorski 1990). The sensilla are placed dorsally of the acoustic trachea (the dorsal wall) and are mainly arranged linearly. Their dendrites run over the anterior tracheal branch from the anterior to the posterior tibia (Fig. 1B, C) and terminate in cap cells linked to the tectorial membrane (Fig. 1D). The sensilla are overall morphologically similar throughout the CA (Lin et al. 1994, Kalmring et al. 1995b) but decrease from proximal to distal in the size of cap cells, along with the width of the tectorial membrane and the width of the dorsal tracheal wall (Fig. 1D) (Rössler 1992a, Lin et al. 1994, Rössler and Kalmring 1994, Kalmring et al. 1995a, Sickmann et al. 1997, Hummel et al. 2017). This correlates to the physiological changes in sensory tuning of individual sensilla, with their best frequency increasing from lower to higher frequencies from the proximal to the distal end of the CA (Zhantiev and Korsunovskaya 1978, Oldfield 1982, Stölting and Stumpner 1998, Hummel et al. 2017), and forms a tonotopically arranged filter bank that allows frequency analysis (Stölting and Stumpner 1998, Hennig et al. 2004, Stumpner and Nowotny 2014, Montealegre-Z and Robert 2015). Anatomical variation between species is also expressed in the number of auditory sensilla in the CA.

Scolopidial sensilla are primary sensory neurons that send their axon into the corresponding segmental ganglion of the central nervous system to form synapses with first order interneurons. The tonotopic representation is maintained in the central projection of auditory afferents (Römer 1983, Stumpner 1996, Stölting and Stumpner 1998, Baden and Hedwig 2010). For the tonotopical organization, different physiological adaptations have been proposed (Hennig et al. 2004). Morphological changes in the organ size, organ height, dendrite length, and cap cell size correlate with the shift in frequency tuning (Hummel et al. 2017, Scherberich et al. 2017). The tonotopic frequency representation is formed by sound-induced travelling waves at the attachment/cap cells and in certain species also at the acoustic vesicle, a modified part of the haemolymph channel in the dorsal tibia (Montealegre-Z et al. 2012, Palghat Udayashankar et al. 2012, Stumpner and Nowotny 2014, Montealegre-Z and Robert 2015, Sarria-S et al. 2017). In such cases, the integrity of the acoustic vesicles and the lipidic fluid it contains are necessary for expressing travelling waves (Montealegre-Z et al. 2012).

The CA also occurs in the atympanate mid- and hind-legs with a gradual decrease in the number of sensilla (Friedrich 1927, 1928, Knetsch 1939, Schumacher 1975b, 1979), but lacks the auditory specializations such as tympanal membranes, an enlarged trachea and tectorial membrane, elaborate supporting bands, or smaller size of scolopale caps (e.g., Lin et al. 1994). The physiology of these atympanate organs remains unresolved (Rössler et al. 2006), but they lack the high sensitivity to airborne sound found in the forelegs (Rössler 1992b, Kalmring et al. 1994). Notably, some atympanate taxa of Ensifera have a sensory organ present in all leg pairs, the *crista acustica* homologue, that is homologous to the tettigoniid auditory sensilla, with a number of sensilla similar to the forelegs of tympanate bush crickets (Strauß and Lakes-Harlan 2008, 2010).

Physiological responses to airborne sound were noted also from the the subgenual organ (SGO) and the intermediate organ (IO), usually responding to relatively low frequency at high stimulus intensities (Kalmring et al. 1994, Stumpner 1996, Höbel and Schul 2007), though higher frequency responses were found in the distal IO (Stölting and Stumpner 1998). Both organs also respond with high sensitivity to substrate vibrations (Kalmring et al. 1994). Here, the focus is on the CA as the sensory organ mainly adapted to airborne sound detection.

Comparative neuroanatomy of the *crista acustica*

The CA has been investigated in several species of Tettigoniidae, and these comparative neuroanatomical studies showed that the number of auditory sensilla is species-specific (Knetsch 1939, Schumacher 1979, Lakes and Schikorski 1990). The sensillum numbers in closely related species are usually similar but not identical (Lakes and Schikorski 1990). Sensillum numbers for tettigoniid species are presented in Table 1, with numbers between a minimum of 12–14 sensilla (*Supersonus* and *Phlugis* spp., Meconematinae; F. Montealegre-Z, personal communication) and a maximum of 116 sensilla (male *Ancylecha fenestrata*, Phaneropterinae; Scherberich et al. 2017). In most species, the CA contains 25–35 sensilla. It could be assumed that well-developed hearing organs also tend to increase the number of sensory neurons if possible, e.g., for better signal detection against noise (Stumpner and Nowotny 2014). The number of auditory sensilla is thus an important indicator of the elaboration or regression of the hearing organ when compared within a specific taxon. Within Orthoptera, a higher number of auditory sensilla is found in both crickets and locusts in comparison to Tettigoniidae (crickets: Eibl 1978, Klose 1996; locusts: Michel and Petersen 1982).

Within a genus, tettigoniid species usually have highly similar sensillum numbers, though larger differences occasionally occur (*Poecilimon*; Strauß et al. 2014). The variation in sensillum numbers between individuals from one species is usually very low (Lakes and Schikorski 1990, Rössler 1992b). Slight differences between individuals caused different averages as reported, for example, in *T. viridissima* (Schumacher 1973, Kalmring et al. 1995a, b, Strauß et al. 2012). Such ranges of differences have been reported for few species, e.g., in *Ancistrura nigrovittata* the mean number is 37, with rare extremes of 32, 33, and 40 CA sensilla found (Ostrowski and Stumpner 2010). Commonly, the sexes show no differences in the number of CA sensilla. A notable case of dimorphism exists in *Ancylecha fenestrata* where males have a significantly higher number of auditory sensilla and a longer CA than females (Scherberich et al. 2016, 2017; see below). In another case, males of *Ancistrura nigrovittata* have on average two sensilla more in the CA than females (Ostrowski and Stumpner 2010).

Notably, the number of auditory sensilla is not directly related to the CA length (Schumacher 1979, Lakes and Schikorski 1990, Strauß et al. 2017), and between species, fewer sensilla can be found in a longer CA (e.g., Rössler et al. 1994). The scolopidial sensilla can occur highly concentrated in the distal CA (Rössler et al. 1994, Kalmring et al. 1995a), leading to pairs or even triplets of somata at the same proximo-distal level (Sickmann et al. 1997, Strauß et al. 2012, Hummel et al. 2017). These findings raise the question of how differences in the number of auditory sensilla relate to the tonotopic frequency analysis, and what factors affect these changes in numbers.

For Tettigoniidae, a relatively high number of species have been investigated for the neuroanatomy of the hearing organs.

Table 1. Number of auditory sensilla in the *crista acustica* of Tettigoniidae. If one species is covered by several references, usually the number which includes mean and standard deviation is cited. Relatively large differences in sensillum numbers reported between studies based on different techniques or sample sizes are also referenced for a few species.

Species	CA sensilla	Tympana	Reference
Bradyporinae			
Deracantha onos	23	covered	O. S. Korsunovskaya, personal communication
Zichya baranovi	15	covered	Zhantiev et al. 1995
Conocephalinae: Conocephalini			
Conocephalus fuscus	26	covered	Knetsch 1939, Schumacher 1979
Conocephalus dorsalis	25	covered	Schumacher 1979
Conocephalus nigropleurum	28	covered	Fullard et al. 1989
Conocephalinae: Copiphorini			
Copiphora gorgonensis	28	covered	Montealegre-Z et al. 2012
Neoconocephalus robustus	35±1	covered	Strauß et al. 2017
Neoconocephalus bivocatus	Males: 34±1 Females: 34±2	covered	Strauß et al. 2017
Neoconocephalus exiliscanorus	35±1	covered	Strauß et al. 2017
Neoconocephalus nebrascensis	Males: 32±1 Females: 33±1	covered	Strauß et al. 2017
Neoconocephalus ensiger	32±1	covered	Strauß et al. 2017
Neoconocephalus triops	34±1	covered	Strauß et al. 2017
Neoconocephalus retusus	33	covered	Strauß et al. 2017
Neoconocephalus palustris	Males: 33±1 Females: 32	covered	Strauß et al. 2017
Neoconocephalus affinis	32±1	covered	Strauß et al. 2017
Mygalopsis marki	20	covered	Oldfield 1984
	24±1		Kalmring et al. 1995b
Ruspolia nitidula (syn. *Homorocoryphus nitidulus*)	31	covered	Knetsch 1939
	35		Schumacher 1979
Ephippigerinae			
Ephippiger ephippiger	28±1	covered	Rössler 1992b
Ephippiger perforatus	27	covered	Lakes and Schikorski 1990
Uromenus rugosicollis	30	covered	Lakes and Schikorski 1990
Hetrodinae			
Acanthoplus longipes	27±2	open	Kowalski and Lakes-Harlan 2013
Acanthoplus discoidalis	27±1	open	Kowalski and Lakes-Harlan 2013
Acanthoproctus diadematus	33±2	covered	Kowalski and Lakes-Harlan 2013
Enyaliopsis sp.	28±2	open	Kowalski and Lakes-Harlan 2013
Spalacomimus liberiana	26	covered	Kowalski and Lakes-Harlan 2013
Listroscelidinae: Requenini			
Requena verticalis	22	covered	Römer et al. 1998
Meconematinae			
Supersonus spp.	12–14	covered, tympanal slits asymmetrical	Sarria-S et al. 2014, F. Montealegre-Z, personal communication
Phlugis spp.	12–14	open tympana	F. Montealegre-Z, personal communication
Meconema thalassinum	21	open	Knetsch 1939
	16		Schumacher 1973
Meconema meridionale	15	open	Schumacher 1979
Mecopodinae			
Mecopoda elongata	48±2	open	Strauß et al. 2012
	45		Hummel et al. 2017
Phaneropterinae: Ephippithytae			
Caedicia simplex	35	open	Oldfield 1982
Polichne sp.	32	open	Oldfield 1984
Phaneropterinae: Barbitistini			
Ancistrura nigrovittata	37	open	Ostrowski and Stumpner 2010
Leptophyes punctatissima	28±1	open	Rössler et al. 1994
	24		Knetsch 1939
	22		Schumacher 1973
Leoptophyes albovittata	22	open	Knetsch 1939
Isophya pyrenaea	27	open	Knetsch 1939
Isophya modestior	34±2	open	Strauß et al. 2014

Table 1. (Continued).

Species	CA sensilla	Tympana	Reference
Poecilimon ornatus	38±1	open	Strauß et al. 2014
Poecilimon gracilis	34±1	open	Strauß et al. 2014
Poecilimon elegans	32±1	open	Strauß et al. 2014
Poecilimon chopardi	30±1	open	Strauß et al. 2014
Poecilimon intermedius	17±1	open	Lehmann et al. 2007
Poecilimon ampliatus	21±1	open	Lehmann et al. 2007
Polysarcus denticauda	49±2	open	Sickmann et al. 1997
Phaneropterinae: Holochlorini			
Ancylecha fenestrata	Males: 116 (md) Females: 86 (md)	anterior covered, posterior open	Scherberich et al. 2017 Kowalski 2010
Phaneropterinae: Phaneropterini			
Phaneroptera falcata	39	open	Schumacher 1973
Phaneropterinae: Steirodontini			
Stilpnochlora couloniana	45–55	open	Lakes-Harlan and Scherberich 2015
Phasmodinae			
Phasmodes ranatriformis	16–18	no tympanum	Lakes-Harlan et al. 1991
Pseudophyllinae			
Nastonotus foreli	22	covered	F. Montealegre-Z, personal communication
Tettigoniinae: Decticini			
Decticus verrucivorus	33±1	covered	Rössler and Kalmring 1994
Decticus albifrons	34±1	covered	Rössler and Kalmring 1994
Tettigoniinae: Gampsocleidini			
Gampsocleis gratiosa	33±1	covered	Lin et al. 1994
Tettigoniinae: Tettigoniini			
Tettigonia viridissima	37 36±1	covered	Schumacher 1973 Kalmring et al. 1995a
Tettigonia cantans	35±1	covered	Kalmring et al. 1995a
Tettigoniinae: Platycleidini			
Bicolorana bicolor	23	covered	Schumacher 1973
Metrioptera roeselii	26		Kowalski 2010
Metrioptera brachyptera	24	covered	Knetsch 1939, Schumacher 1979
Platycleis albopunctata (syn. *denticulata*)	23	covered	Schumacher 1973
Psorodonotus illyricus	31±1	covered	Kalmring et al. 1995b
Tettigoniinae: Pholidopterini			
Pholidoptera griseoaptera	24±1	covered	Rössler et al. 1994
Zaprochilinae			
Kawanaphila nartee	18±1	open	Bailey and Römer 1991, Rentz 1993

This becomes apparent in comparison to the crickets, the other ensiferan group studied in detail for the neurobiological substrate for hearing (Pollack and Hedwig 2017), where the tympanal organ anatomy has been analysed mainly for a few selected model species (summary: Ball et al. 1989): *Gryllus bimaculatus*, *Gryllus campestris* (Michel 1974, Eibl 1978), *Achaeta domesticus* (Schwabe 1906), *Teleogryllus commodus* (Klose 1996), several Eneopterinae species (Schneider et al. 2017), and the mogoplistine *Cycloptiloides canariensis* with a unique hearing organ (Michel 1979). The research on diverse tettigoniid lineages not only addressed the neurophysiology of sound processing, but also led to the study of the effects of species divergence, the differences in the communication system, and the evolutionary regression of the hearing organs on the structure of the CA.

Functional and evolutionary factors influencing the sensillum numbers in the *crista acustica*

The sense of hearing provides important adaptations for mate recognition and localization as well as predator (bat) detection. Such positive selection for hearing will result in well-developed hearing organs with auditory receptors detecting frequency ranges of both intraspecific calls and ultrasonic frequencies of bats. However, additional factors could affect the structure of the hearing organs, like genetic drift, allometry, and phylogenetic constraints (structures preserving the ancestral state) as well as physical constraints (see Strauß and Stumpner 2015 for tympanal organs in general). From the comparative data, it can be concluded that CA under sexual and natural selection usually contain 22–50 sensilla, with most species having 25–40 auditory sensilla. These numbers thus appear to be adequate and adaptive to allow sound detection, frequency resolution, intensity discrimination, and input to the CNS for directional and temporal analysis, though smaller numbers do not necessarily exclude these physiological functions. For example, *Meconema thalassinum* does not use tegminal stridulation and has a low number of 16 auditory sensilla (Schumacher 1973, 1979), and in the tympanal hearing organ of this species, travelling waves were recorded over the CA that indicate frequency analysis (F. Montealegre-Z, personal communication). As both higher and lower numbers from the most common numbers are found, the evolutionary events behind the extreme values can be analyzed based on this comparative background. In addition, functional and physiological data are required to characterize the changes in the sensory organs further. Below, the different evolutionary forces are discussed for the CA, with expected outcomes of the effect of selection. Neutral evolution (drift) is difficult to support directly by comparing anatomical traits or physiological features, as it is supported by the lack of evidence for explanations based on adaptions or constraints if detailed information on the genetic polymorphisms that encode a trait is not available (Schul et al. 2014). It likely contributes to the regression of auditory systems if a selection pressure ceases (e.g., Lakes-Harlan et al. 1991, Lehmann et al. 2007, Strauß and Stumpner 2015).

Evolutionary regression in the hearing organ.—Strong evidence for the role of selection pressures on the tympanal organs can be obtained from species where either natural or sexual selection have ceased. In these cases, often a regression is noted that can reduce the size of spiracles of the acoustic trachea, and potentially also the number of auditory sensilla. Such regression could be due to neutral evolution (drift) after selection ceases to maintain a certain structure, or auditory sensilla could be selected against, as they require energy to develop and maintain (see e.g., Laughlin et al. 1998). Case studies under which conditions and to what extent such regressions occur are discussed below.

Sexual dimorphism: Australian *Kawanaphila* show a notable sexual dimorphism in the auditory system, with a smaller auditory spiracle in males than in females and also smaller acoustic bulla in the prothorax (Bailey and Römer 1991, Mason and Bailey 1998). Three species in the genus have been studied, revealing a gradient in the reduction of the acoustic spiracle. While in *Kawanaphila yarraga* the auditory spiracle in males is significantly smaller than in females, in males of *K. nartee* and *K. mirla* no external auditory spiracle is developed, and males thus show decreased auditory sensitivity compared to females (Bailey and Römer 1991, Mason and Bailey 1998). Blocking the auditory spiracle in *K. nartee* females resulted in a reduced sensitivity similar to conspecific males (Bailey and Römer 1991). The number of CA sensilla in *K. nartee* males and females is not different between sexes, with 18 ± 1 sensory neurons (Bailey and Römer 1991). The CA of the other *Kawanaphila* species has not been studied for the number of sensilla, and such data might complement the evidence for gradual regression in these species. The auditory behavior of males also differs, with decreased male competition in *K. mirla* that is acoustically mediated between callers as indicated by lower distances between males (Mason and Bailey 1998) to the absence of any auditory behavior in male *K. nartee* (Bailey and Simmons 1991). This gradual decrease in the auditory function of males from different species and intraspecific dimorphism indicate that the male hearing organ is the result of an evolutionary regression from a well-developed auditory system. Since in *K. mirla* the regression is already anatomically and physiologically detectable, while auditory behavior of male-male competition still occurs, the decline in hearing function seems not to have triggered the regression (Mason and Bailey 1998).

Mimesis: A further reduction is found in the Australian stick katydid, *Phasmodes ranatriformis*. These mimetic animals remarkably resemble stick insects, and do not produce acoustic signals (Rentz 1993), resulting in a weakened selection pressure for hearing. Spiracles are small and tympana are only weakly expressed in males and females as depressions with thinner leg cuticle (Lakes-Harlan et al. 1991, Rentz 1993). The CA is present in the legs of females and males with 16–18 sensilla in the foreleg (Lakes-Harlan et al. 1991), also indicating a low elaboration of the auditory sense.

Parthenogenesis: In tettigoniids, parthenogenesis (loss of males) is rare but presents an interesting evolutionary scenario, since selection for intraspecific signal detection ceases without males producing acoustic signals. In *Poecilimon intermedius*, an obligate parthenogenetic species, only females occur (Lehmann et al. 2011) and the number of auditory sensilla is very low at 17 ± 1, even lower than in the sister species *P. ampliatus* (21 ± 1). This indicates an evolutionary regression of the hearing organ, while selection pressure from predators may have maintained some hearing function (Lehmann et al. 2007).

Change of signalling behavior: In two *Meconema* species, acoustic signals are not produced by tegminal stridulation as males of *M. thalassinum* and *M. meridionale* produce sound and likely vibration signals by tapping or drumming with the hind leg on the substrate (Sismondo 1980, Vahed 1996, Ingrisch and Rentz 2009). In these species with open tympana, the number of auditory sensilla is very low at 15 (*M. meridionale*) and 16 (*M. thalassinum*) sensilla (Schumacher 1979). However, the CA in *M. thalassinum* expresses travelling waves, indicating functional hearing (F. Montealegre-Z, personal communication). Female bush crickets of certain species can also use vibrational signals produced during wing stridulation for orientation toward males over shorter distances (*Ephippiger ephippiger*: Stiedl and Kalmring 1989). Since the most sensitive vibration receptor in the tibia is the subgenual organ (Fig. 1C), the tapping may also affect the signal detection by both auditory and vibratory sensilla, initiating a regressive process of the CA. However, since neuroanatomical data from related species with tegminal stridulation species are not available, the degree of regression is unclear in this case. Notably, even lower numbers of CA sensilla are also found in meconematine species with ultrasonic calls by tegminal stridulation (12–14 sensilla, Table 1; F. Montealegre-Z, personal communication).

Influence of the communication system on the auditory system.—Depending on the communication system, different selective requirements can also differentially affect the auditory organs between the sexes. In Phaneropterinae, acoustic duets are most common (Heller et al. 2015), and the auditory behaviour has been studied in detail in the genus *Poecilimon* (Heller and von Helversen 1986, 1993, Heller 1990). The communication system in most species is bidirectional with male calls, and softer and short female replies (Heller and von Helversen 1986, Heller et al. 1997b, von Helversen et al. 2015). For the detection of the female replies, males should be selected for higher auditory sensitivity, morphologically reflected in larger spiracles to amplify the sound. In addition, males could benefit from summation of more sensilla to detect the soft and short female responses. In *Poecilimon*, the bidirectional communication system is also the evolutionary ancestral state for the group (see Heller 1990). However, in three distinct lineages the female reply was abolished (in the *P. ampliatus* group, the *P. propinquus* group, and in *P. jablanicensis* of the *P. ornatus* group), resulting in a secondary unidirectional communication system in which males should no longer be selected for higher auditory sensitivity. Testing for the possible correlation between the auditory system and the communication system showed the expected correlation of spiracle sizes with the communication system, with consistently larger spiracles in bidirectional signalling species. In addition, spiracles in males of these species are larger than in conspecific females, supporting the influence of sexual selection for higher male hearing sensitivity. Spiracle sizes in unidirectionally signalling species are smaller but show no sex-specific differences in spiracle size. The expected higher number of auditory sensilla was found in species with a bidirectional communication system (32–38 sensilla), with a strong relationship to body size (allometry, see also below). Notably, the sensillum numbers in *P. chopardi* (*P. propinquus* group) are only slightly lower (at 29 sensilla), while in species of the *P. ampliatus* group, they are ~30% lower than the correlation to body size would indicate (decreased to 17–21 sensilla) and with similar smaller spiracle sizes in both groups (Strauß et al. 2014). Thus, representatives in the groups with a secondary unidirectional signalling show evidence for an evolutionary regression in the auditory structures. These differences in *Poecilimon* auditory sensilla are the greatest variation between tettigoniid species from the same genus known so far, highlighting the evolutionary changes in the *Poecilimon* auditory system and the importance of sexual selection. It is uncertain why the degree of sensilla regression differs between members of the *P. ampliatus* and *propinquus* group. Further, it is difficult to identify the evolutionary starting point for the regression—if this started with the loss of the female reply reducing the selection for high sensitivity (larger spiracles) or if a reduced spiracle size led to a lower auditory sensitivity and the loss of female responses (Strauß et al. 2014). The evolutionary shift from bidirectional to unidirectional communication may depend on the mating success of females in relatively high population densities (*P. ampliatus*: von Helversen et al. 2012), the active distance between the mates, and the effective range of the acoustic signalling system (von Helversen et al. 2015). Here, the complexity of the acoustic environment is important as well, including the role of background noise (Römer and Bailey 1998), signal transmission (Römer 2016), and natural selection by predators that may maintain the hearing organs (Lehmann et al. 2007).

Does a correlation exist between carrier frequency of the communication signal and CA design?.—Tettigoniid tympanal organs are broadly tuned (Kalmring et al. 1990, Rössler and Kalmring 1994, Rössler et al. 1994). So far, a general correlation between spectral characteristics of the intraspecific signals and the number of auditory sensilla has been difficult to identify (Rössler et al. 2006): while the sensitivity of the auditory organ results from the summed activity of the CA sensilla and structures like the spiracles and bullae, similar tuning of receptors from different species or the absolute auditory sensitivity are not dependent on the overall number of CA sensilla (Rössler and Kalmring 1994, Scherberich et al. 2017). A change in carrier frequency of calls might affect the tuning of sensilla in the hearing organ, rather than the overall number of auditory sensilla. However, to detect extremely short female replies in duets, an increased number of auditory sensilla activated simultaneously could benefit the signal detection (see below for the auditory fovea).

Auditory sensilla with highly similar frequency tuning were found despite significant differences in the CA length and number of CA sensilla, both in related species (Kalmring et al. 1992) and also in more distantly related species (Kalmring et al. 1995b). Physiological data from some other species, however, showed specific hearing tuning for individual sensilla that adapt the frequency range to intraspecific call frequencies by broadening (*Neoconocephalus bivocatus*: Höbel and Schul 2007) or narrowing (*Ancylecha fenestrata*: Scherberich et al. 2016) the frequency response. The tonotopic organization of sensilla also contributes to intensity coding as stimuli at higher amplitudes activate both the sensilla tuned to the specific stimulus frequency together with sensilla tuned to other best frequencies that are also activated at increased amplitudes due to their broad tuning ranges (Römer et al. 1998, Hennig et al. 2004, Höbel and Schul 2007, Stumpner and Nowotny 2014). Whether such recruitment at higher amplitudes could affect the hearing organ to extend the set of auditory sensilla significantly is so far unclear.

Currently, the frequency representation over the CA is characterized only for a few species. The relative proportions of low vs. high frequency receptors differ along the CA, however, and are often adapted to the main frequency of calls by a relatively higher proportion of sensilla tuned to conspecific call frequencies (Kalmring et al. 1990, 1993, Rössler et al. 2006). This was shown by Current Source Density (CSD) analysis using a multiunit electrode system to record neuronal ensemble activities of sensory afferents in the auditory neuropile by their field potentials in relation to stimuli of different frequencies (Breckow et al. 1982, Rössler et al. 1990). However, this correlation so far provides no direct explanation for why a specific number of CA sensilla evolved in a given species. In *Neoconocephalus*, the number of CA sensilla from nine species was statistically negatively correlated to the species' call frequency (Strauß et al. 2017). Since this correlation was also found for the CA length and body size, it was assumed to indicate an allometric relationship (see below), because larger animals have larger stridulatory structures that produce calls in lower frequencies, and body size also influences the number of CA sensilla and CA length.

Frequency representation in an auditory fovea: The auditory fovea is an adaptation of frequency representation by highly similar tuning of multiple adjacent CA sensilla. In this case, frequency tuning is not linearly graded over the CA length. For the duetting phaneropterine *Ancylecha fenestrata*, a remarkable sexual dimorphism was shown where the ears of males contain 35% more auditory sensilla (median: 116) compared to females (86), and also a longer CA (Scherberich et al. 2016, 2017). Irrespective of the difference between sexes, this is the highest number of CA sensilla reported so far (Table 1). Physiologically, their CA shows an interrupted gradient in frequency tuning with a central region of 55 sensilla, where the change in characteristic frequency is less steep than at the proximal and distal CA ends. These sensilla in males are tuned to the dominant frequency of the female acoustic reply to male calls at about 10 kHz, and thus mediate the male phonotaxis. Females respond to male calls with a single, short sound of 42 ms duration (median; Scherberich et al. 2016). The auditory fovea can contribute to directional hearing of the very short and rare female response signals, as population coding from increased numbers of afferents improves the processing of temporal and intensity interaural differences at interneuron level to locate a sound source more reliably (Scherberich et al. 2017). The tuning of the auditory fovea also concurs in morphology with a CA region of similar organ height that does not follow the curvature of the CA surface (Scherberich et al. 2017). This organization is a sex-specific (male) adaptation relating to the specific duetting communication and indicates a strong sexual selection for detecting the signals of potential mates and shows most clearly an adaptive increase in auditory sensilla. Similar functional organizations with adjacent sensilla tuned to the same characteristic frequency are also found in CAs with less sensilla (< 30; Oldfield 1985, Montealegre-Z et al. 2012), but by far not as strong as in the case of *A. fenestrata*—this is the only case of a tettigoniid hearing organ with over 100 auditory sensilla known so far.

Adaptive significance for CA changes as a result of temporal call pattern.—The recognition of call patterns is carried out by the central nervous system, while the auditory sensilla code the temporal/syllable pattern (Schul and Rössler 1993, Pollack 1998). Hence, differences in call patterns are not expected to be a major influence on CA sensilla. One possible exception is the signal duration, which in cases of short acoustic signals would benefit from more sensilla that provide stronger input to the CNS (see the above discussion on the auditory fovea).

The North American genus *Neoconocephalus* is a study model for the evolutionary diversification of call patterns and their recognition mechanisms (Schul et al. 2014). Among tettigoniids, the male *Neoconocephalus* calls have notably narrow frequency bands with center frequencies mainly at 10–15 kHz (Schul and Patterson 2003). The ancestral call pattern in *Neoconocephalus* is characterized by continuous calls with single pulses at fast repetition rates (Schul et al. 2014). During the evolutionary radiation of the group, the call patterns diversified repeatedly into discontinuous calls, slow repetition rates, and/or double pulses (Schul et al. 2014). The evolutionary diversification is highlighted e.g., by the repeated evolution of double-pulsed calls (Schul et al. 2014, Frederick and Schul 2016). Studying the CA anatomy of nine species representing different taxonomic groups, life histories, call patterns, and call center frequencies, similar averages from 32–35 sensilla between the species were documented (Strauß et al. 2017). A similar number of 35 sensilla is found in the most closely related *Ruspolia* (*R. nitidula*, Schumacher 1979), suggesting that the ancestral *Neoconocephalus* already had a number of auditory sensilla in these ranges. The variation between *Neoconocephalus* species was influenced by the species specificity as well as body size (allometry), but not by phylogenetic relationships.

Statistical analysis for standardized effects of the call pattern also revealed correlations with CA sensillum numbers and CA length (Fig. 2). Male calls with slow pulse rates correlated with significantly more CA sensilla and longer CA (Fig. 2A), continuous calls with the increased number of CA sensilla (Fig. 2B), and double pulses with a longer CA (Fig. 2C). In the latter case, double pulsed calls also correlate with a higher number of sensilla, though the increase was not statistically significant. These correlations indicate a clear influence of sexual selection on the CA.

The findings are notable since the analysis of temporal call patterns is not carried out by the sensilla but in the central nervous system. The increased number of sensilla in species with slow-calling rates may be most easy to explain, as they could be an adaptation to shorter signals by providing a relatively stronger input to the CNS by additional sensilla. In addition, indirect effects of acoustic signalling on the CA are likely (Strauß et al. 2017). The correlation of discontinuous calls with lower sensillum numbers may depend on the behavioral ecology of signallers since discontinuously calling species have higher population densities (Greenfield 1990), which in turn may relax the selection on the auditory system. A continuously calling species (*N. affinis*) occurring in relatively high population densities (Greenfield 1983) also had relatively low CA sensilla (Strauß et al. 2017). Notably, not all evolutionary-derived call patterns in *Neoconocephalus* correlate to the increased number of CA sensilla (Fig. 2). While the differences in CA sensilla between *Neoconocephalus* species are small compared to those found in *Poecilimon*, the evolution of call patterns and call recognition mechanisms triggered the recent radiation of the group (Schul et al. 2014) and the hearing organs might diverge further in response.

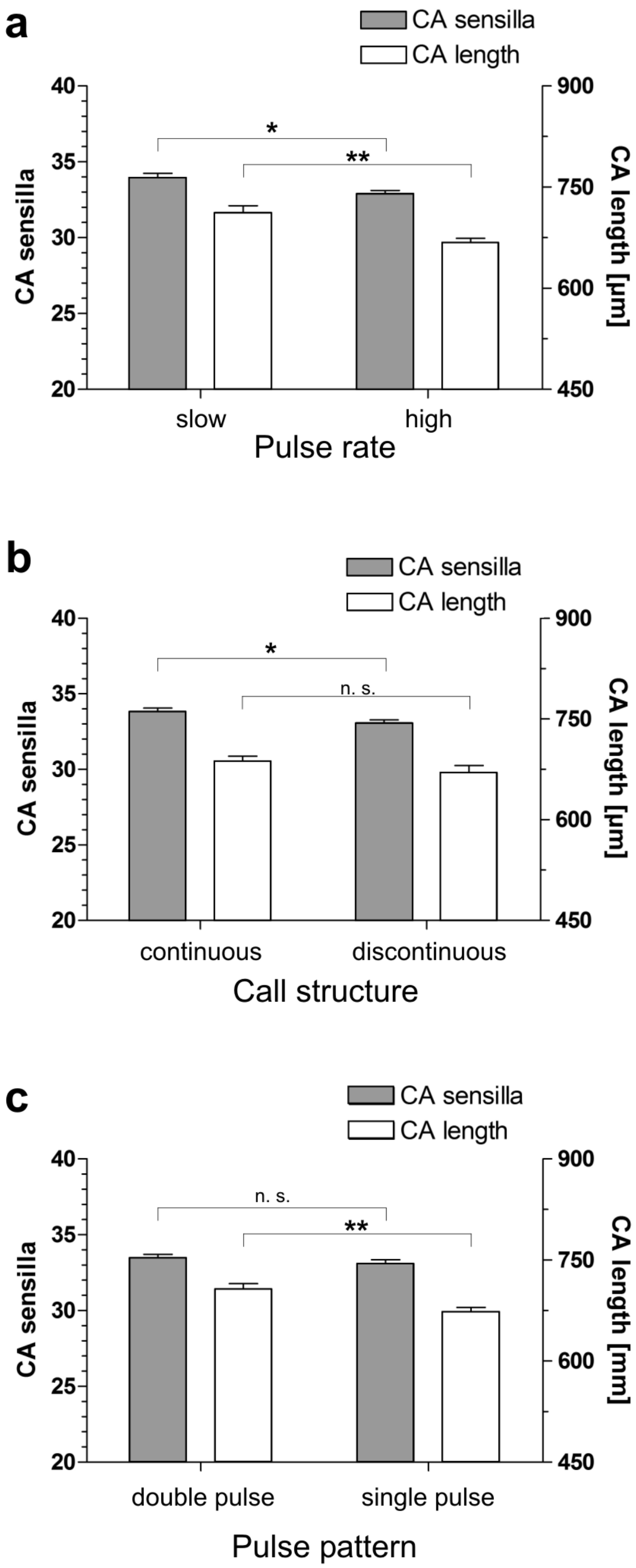

Fig. 2. Standardized effects of call patterns in *Neoconocephalus* on the number of CA sensilla and CA length for **A**. Pulse rate; **B**. Structure of continuous or discontinuous calls; and **C**. Pulse pattern. The evolutionary derived call characters are a slow pulse rate, discontinuous calls, and double pulses. Significance levels: * 0.05 > p > 0.01; ** 0.01 > p > 0.001. Adapted from Strauß et al. 2017, with permission from John Wiley and Sons.

Allometry.—Allometry refers to the relation of a structure to body size. It can highlight the influence of selection between body size and a morphological character under investigation, inferred from positive allometry and low morphological variation in the character (see also Bailey and Kamien 2001 for sound transmitting structures and Anichini et al. 2017 for stridulatory structures). Hence, a larger body size would predict a longer CA and/or a higher number of auditory sensilla. Different features in the tettigoniid auditory system, like the spiracle and tracheal bulla size, were shown to be determined by allometry (Bailey 1998, Bailey and Kamien 2001). If larger individuals have larger spiracles they are more sensitive, that sensitivity can be determined by allometric relationships (*Requena verticalis*: Bailey 1998, but see also Römer et al. 2008 with a broader species sampling). The correlation of auditory sensillum numbers to body size was first suggested by Knetsch (1939), albeit with limited data from nine species and diverse genera. Closely related species were analyzed for *Poecilimon* (Strauß et al. 2014) and *Neoconocephalus* (Strauß et al. 2017) with a substantial influence of body size found on the CA for both groups, but evolutionary changes were also detected that affected the sensillum numbers more strongly: the reduction of acoustic signalling as well as adaptations to temporal call features such as the pulse rate, pulse pattern, and call structure can override the allometric relationship (see above). Allometry is thus one among several factors influencing the CA.

Different traits have been used as a measure for body size, such as the body length (Knetsch 1939), pronotum length (Bailey 1998, Bailey and Kamien 2001), hind femur length (Lehmann 1998, Bailey and Kamien 2001, Schul and Patterson 2003, Strauß et al. 2014, Anichini et al. 2017), or foreleg tibia length (Knetsch 1939). As shown for *R. verticalis*, hind femur and pronotum length are not isometrically related (Bailey and Kamien 2001), and the choice of anatomical parameter(s) to measure allometry is important.

Phylogenetic ancestral states.—Phylogenetic constraints result in a retained character state in successively evolving species. Constraints would set limits on the evolutionary changes in a character and counter the influence of selection pressures, retaining an ancestral situation. For the CA, the studies including outgroups found both cases were specific adaptations (*Neoconocephalus*: Strauß et al. 2017) and regressive changes (*Poecilimon*: Strauß et al. 2014) indicate the importance of sexual selection for elaborate CAs and argue against a phylogenetic constraint on sensillum numbers in these taxa. Certainly, further comparative studies including multiple species and outgroup species will give more insights on the adaptive significance of sensillum numbers.

A neuroanatomical feature that was discussed as a possible ancestral state are the distally concentrated sensilla in the CA of *Polysarcus denticauda*, leading to pairs or triplets of somata (Sickmann et al. 1997) and a loss of frequency resolution for frequencies above 20 kHz in these sensilla (Kalmring et al. 1996). Such a crowded organization of somata and dendrites was also found in several species of Phaneropterinae with thin tympana and a variable number of sensilla (Strauß et al. 2012), which makes an ancestral situation in *P. denticauda* less likely.

Relation to tympanum structure.—It has been noted that species with open tympana often have higher numbers of auditory sensilla (Lakes and Schikorski 1990). For example, *Mecopoda elongata* and *Polysarcus denticauda* have close to 50 CA sensilla and open tympana. *P. denticauda* is also exceptional as it has very thick tympana (Sickmann et al. 1997). *Supersonus* spp. have narrow asymmetric slits (Sarria-S et al. 2014) and exceptionally few CA sensilla with 12–14 (F. Montealegre-Z, personal communication). However, notable exceptions for this relationship between CA sensilla and tympanum morphology exist, as one of the species with the lowest known sensillum numbers has open tympana (*Phlugis* spp.) and the species with the highest known sensillum number (*Ancylecha fenestrata*) has a cover at the anterior tympanum. Specific evolutionary scenarios for increasing or decreasing sensillum numbers obviously override a possible relation with the tympanum morphology in these cases.

Diversity of tettigoniid auditory organs and evolutionary causes

With respect to the number of CA sensilla, only a small fraction of the tettigoniid species has been studied so far. Neuroanatomical and physiological studies have revealed a diversity in the number of auditory sensilla among tettigoniid species that is species-specific. To characterize the auditory system of any species, the number of CA sensilla is an important parameter, together with tympanal and tracheal dimensions and the hearing threshold curve. So far, the tonotopic organization of the CA has been studied in even fewer species, and it remains to be analyzed how the changes in neuron numbers affect frequency representation and the accuracy of frequency discrimination (Rössler and Kalmring 1994). Obviously, the auditory system consists of successive levels of signal analysis in the central nervous system, and further processing in the auditory pathway may increase or decrease the relevance of specific cues for the receiver (e.g., Stumpner and Nowotny 2014).

While comparative studies indicate divergences in the number of CA sensilla between species, it is so far easier to explain such divergence in adding or reducing sensilla than to explain the functional requirements which determine a certain number of sensilla in a specific species. Such cases of divergence indicate the importance of multiple determinants. The elaborate auditory system of Tettigoniidae is formed by several selective forces: natural and sexual selection as well as allometry (Stumpner and von Helversen 2001, Robinson and Hall 2002, Strauß and Stumpner 2015), which makes it more difficult to analyze the contribution of specific influences. For a tympanal organ that is shaped by sexual and natural selection, it is somewhat difficult to determine the lower end of sensillum numbers since some species which show no regressive elements have numbers such as 24 sensilla (*Mygalopsis*, *Pholidoptera*) or 22 sensilla (*Requena verticalis*, *Nastonotus foreli*). *Poecilimon ampliatus* with 21 sensilla, compared to related species from the genus, shows evidence for regression both for the spiracles and the CA sensilla. This highlights the importance of a comparative approach covering several species. However, the strong influence of sexual selection even at the level of the CA sensilla can be detected for several model groups (Lehmann et al. 2007, Strauß et al. 2017).

Based on the currently available knowledge, some groups of tettigoniids are promising candidates for further studies of neuroanatomy and the functional morphology of the CA: For the large group of Pseudophyllinae with over 1000 species, important physiological experiments have shown ultrasonic call frequencies and directional hearing mediated by tympanal slits rather than sound input via the small spiracles (Mason et al. 1991), but the CA is so far only rarely studied (see *Nastonotus foreli*, Table 1).

A detailed analysis of the CA for such species with ultrasonic carrier frequencies of calls (Morris et al. 1994, Montealegre-Z et al. 2006) will be important to study the CA frequency representation. For the Australian *K. nartee*, which produces narrow ultrasonic calls, the number of sensilla is rather low at 18 CA sensilla (Gwynne and Bailey 1988, Bailey and Römer 1991). Remarkably, species calling at ultrasonic frequency ranges can have an even lower number of CA sensilla (*Supersonus*: 12–14 sensilla; F. Montealegre-Z, personal communication), inviting further investigations and functional comparisons.

Biomechanical analysis in *Onomarchus uninotatus* (Pseudophyllinae) showed fascinating adaptations for the two tympanal membranes with differential tympanal tuning (acoustic partitioning) of the anterior tympanum as a low-pass filter and the posterior tympanum as a high-pass filter (Rajaraman et al. 2013). The structure and mechanics of the CA and associated elements would be interesting for their organization in this case.

Further work on already researched groups will extend the understanding of evolutionary changes in the CA. For example, in the genus *Poecilimon*, the CA anatomy of relatively few species is known. Additional data are relevant from those species already studied with respect to auditory physiology (*P. laevissimus*, *P. thessalicus*: Stumpner and Heller 1992), hearing organ embryology (*P. affinis*: Meier and Reichert 1990), or the acoustic communication system (unidirectional signalling in the *P. propinquus* group, and further bidirectional species of the *P. ornatus* group and the unidicrectional *P. jablanicensis*: Chobanov and Heller 2010) to better understand auditory adaptations and diversification in the CA.

Finally, allometry in the CA is worth exploring in more detail, both within and between species. For tettigoniids, the influence of allometry on CA sensilla is not studied in detail for intraspecific variation, which would be interesting to address for different communication systems and the influence of selection. For studies on the auditory system of additional tettigoniid species, the question of what determines the number of auditory sensilla can guide the analysis of the hearing organ and can also be expected to give insights relevant to sensory evolution.

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