Ligypterus najtae n. sp. from Mounts Tumuc-Humac in French Guiana (Orthoptera, Grylloidea, Gryllidae, Eneopterinae)

Natállia VICENTE
Universidade Federal de Viçosa, Departamento de Biologia Animal,
Avenida Peter Henry Rolfs s/n. Viçosa, Minas Gerais, CEP 36570-900 (Brazil)
natalliavicentte@gmail.com

Tony ROBILLARD
Institut de Systématique, Évolution et Biodiversité, ISYEB –
UMR 7205 CNRS, MNHN, UPMC, EPHE,
Muséum national d'Histoire naturelle, Sorbonne Universités,
case postale 50, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
tony.robillard@mnhn.fr

Published on 31st March 2017

urn:lsid:zoobank.org:pub:8F2A88F4-6067-4AD8-A0BC-2EBB7BD082C7

Vicente N. & Robillard T. 2017. — *Ligypterus najtae* n. sp. from Mounts Tumuc-Humac in French Guiana (Orthoptera, Grylloidea, Gryllidae, Eneopterinae). *Zoosystema* 39 (1): 125-136. https://doi.org/10.5252/z2017n1a14

KEY WORDS
Lebinthini,
French Guiana,
crickets,
high frequencies,
new species.

ABSTRACT
Ligypterus najtae n. sp., a new species of Neotropical Eneopterinae Saussure, 1874 cricket, is described from Mounts Tumuc-Humac in French Guiana. Description focusses on general morphology, male and female genitalia, and forewing venation. Bioacoustical analyses of the calling song reveal that this species uses high-frequency signals.

MOTS CLÉS
Lebinthini,
Guyane française,
grillons,
hautes fréquences,
espèce nouvelle.

RÉSUMÉ
Ligypterus najtae *n. sp., des Monts Tumuc-Humac, Guyane française (Orthoptera, Grylloidea, Gryllidae, Eneopterinae).*
Ligypterus najtae n. sp., une nouvelle espèce de grillon Eneopterinae Saussure, 1874 néotropicale, est décrite des monts Tumuc-Humac en Guyane française. La description porte sur la morphologie générale, les genitalia mâles et femelles et la nervation. L'analyse du chant d'appel révèle l'utilisation de signaux à hautes fréquences chez cette espèce.

INTRODUCTION

The cricket subfamily Eneopterinae Saussure, 1874 (sensu Robillard & Desutter-Grandcolas 2008) is little diversified in the Neotropical region compared to other cricket clades (e.g., Desutter-Grandcolas 1991, 1992a, b) and to what is known about this clade in other tropical regions (e.g., Otte & Alexander 1983; Nattier *et al.* 2011; Robillard *et al.* 2014, 2016). In the Neotropics, Eneopterinae are represented by only twelve species belonging to three genera (*Eneoptera* Burmeister, 1838: five species, *Ligypterus* Saussure, 1878: five species and *Ponca* Hebard, 1928: two species) (Robillard & Desutter-Grandcolas 2005, 2013). Despite this lack of numerical diversity, the Neotropical eneopterines prove very interesting in terms of acoustic innovations. Recent studies have addressed the complex call pattern and calling behavior of *Eneoptera guyanensis* Chopard, 1931 (Desutter-Grandcolas 1998; Robillard & Desutter-Grandcolas 2011), and have suggested that all eneopterine genera from the Neotropics use high frequencies to communicate, based on the rich harmonic content of their songs (Robillard *et al.* 2015). The species addressed in this study highlighted, however, differences in the use of these high frequencies, confirming with acoustic clues that *Eneoptera* and *Ponca-Ligypterus* are separate lineages belonging to different tribes, as suggested by molecular phylogenies (Nattier *et al.* 2011; Vicente *et al.* in press).

As part of the ongoing bioacoustical studies on eneopterines (e.g., Robillard *et al.* 2007, 2013), we describe here *Ligypterus najtae* n. sp., a new species from Mounts Tumuc-Humac in French Guiana. The description focusses on general morphology, coloration, genitalia and forewing venation in both sexes. We also describe the calling song and habitat of the species.

MATERIAL AND METHODS

Material examined

The material examined here belongs to the collections of the Muséum national d'Histoire naturelle, Paris (MNHN online type data base: https://science.mnhn.fr/institution/mnhn/collection/eo/item/search/form). Specimens were collected by F. Legendre and S. Hugel during the 'Our Planet Reviewed' Initiative, Guyane 2014-2015 Expedition', organized by the Muséum national d'Histoire naturelle de Paris and Pro-Natura International.

Male tegminal venation

Terminologies for male tegminal veins and cells follow that of Desutter-Grandcolas (2003) for Ensifera, and Robillard & Desutter-Grandcolas (2004a) and Robillard *et al.* (2014) for the subfamily Eneopterinae more specifically.

Male and female genitalia

Male and female genitalia have been dissected in softened specimens by cutting the membranes between the paraprocts and the subgenital plate, or between the ovipositor and the subgenital plate respectively; they have been cleaned with cold KOH and have been observed using a binocular microscope Leica MZ16 at magnifications up to 115, and then kept in glycerine in vials pinned under specimens. Male genitalia terminology follows that by Desutter (1987), modified in Desutter-Grandcolas (2003) and Robillard & Desutter-Grandcolas (2004a). Photographs of male genitalia were obtained using an AmScope MU1000 digital camera (www.Amscope.com). Genitalia were stained with a drop of Punktol (JLB, Germany).

Acoustic data

The basic cricket song terminology follows Ragge & Reynolds (1998): one song unit is called a syllable and corresponds to one opening-closure cycle of the male forewings. Two males of *L. najtae* n. sp. have been recorded in the laboratory. Automatic recordings were made with a modified Condenser Microphone Capsule CM16 (Avisoft Bioacoustics, Berlin), with a flat frequency response from three to 150 kHz (R. Specht pers. comm.), and using the program Avisoft Triggering Harddisk Recorder version 2.97 and a 8-Pre MOTU sound card at a sampling frequency of 96 kilo-samples per second (16 bit). Song features were measured using the automatic commands under Avisoft-SASLab Pro version 4.40 (Specht 2008). Voucher recordings are deposited in the Sound Library of the MNHN.

Abbreviations

General morphology

FI, FII, FIII	fore medianhind femur;
FW	forewing;
HW	hind wing;
TI TII TIII	foremedian hind tibia;
Tarsomere III-1, III-3	first and third segments of hind leg tarsomere.

Tegminal venation

1A-4A	first to fourth anal veins;
CuA	anterior cubitus;
CuA1, CuA2…	first, second… bifurcations of CuA;
CuP	posterior cubitus;
M	media vein;
R	radial vein;
Sc	subcostal vein;
c1-3	first to third cells of C alignment;
d1 cell (mirror)	first cell(s) of D alignment.

Male genitalia

ect ap	ectophallic apodeme;
ect arc	ectophallic arc;
ect fo	ectophallic fold;
end sc	endophallic sclerite;
pse pa	pseudepiphallic paramere;
r	rami.

Measurements

FIIIL	length of hind femora;
FIIIW	width of hind femora;
FWL	forewing length;
FWW	forewing width (at the level of maximal width);
Ias	inner spines on TIII dorsal side above the spurs;
Ibs	inner spines on TIII dorsal side between the spurs;
Oas	outer spines on TIII dorsal side above the spurs;

Obs	outer spines on TIII dorsal side between the spurs;
OL	ovipositor length;
PronL	pronotum length;
PronW	pronotum width;
TaIII-1 spines	number of spines on external edge of first tarsomere of hind legs spines on external face of tarsomere indicated in parentheses;
TIIIL	length of hind tibiae.

Institution

MNHN	Muséum national d'Histoire naturelle, Paris.

SYSTEMATICS

Subfamily Eneopterinae Saussure, 1874
Tribe Lebinthini Robillard, 2004

Genus *Ligypterus* Saussure, 1878

Type species. — *Enoptera heydeni* Saussure, 1874.

Diagnosis. — Among Eneopterinae genera *Ligypterus* is similar to *Ponca*, except for brachypterous wings and genitalia, and resembles *Lebinthus* in general appearance, with a small size, stocky shape and brachypterous wings reaching two thirds of abdomen length. Genus characterized by shape of head with large, very protruding eyes, pattern of coloration, FW venation and male genitalia with very indented basal margin of pseudepiphallus and rather long and thin membranous pseudephiphallic lophi.

Ligypterus najtae n. sp.
(Figs 1-8)

Type material. — **Holotype**. ♂. Guyane. Monts Tumuc-Humac, Massif du Mitaraka, 2.235494N, 54.44768O (C100), 350 m / 2.233664N, 54.4419O (C1000), 415 m, Planète revisitée Guyane 2015, 23.II-10.III.2015, nuit, sur plante, mort en élevage, enregistrement appel-F0-male2, F. Legendre & S. Hugel (MNHN-EO-ENSIF4165).
Allotype.♀. Same informations as holotype (MNHN-EO-ENSIF4166).
Paratypes. 7 ♂, 1 ♀. Guyane. Monts Tumuc-Humac, Massif du Mitaraka, 2.235494N, 54.44768O (C100), 350 m / 2.233664N, 54.4419O (C1000), 415 m, Planète revisitée Guyane 2015, 23.II-10.III.2015, nuit, sur plante, F. Legendre & S. Hugel: 1 ♂ (FL193), échantillon moléculaire E46, (MNHN-EO-ENSIF4169); 3 ♂, 1 ♀ (FL208, FL211, FL290, FL210) (MNHN-EO-ENSIF4170-ENSIF4173); 1 ♂, mort en élevage, enregistrement appel-FO-male1 (MNHN-EO-ENSIF4167); 1 ♂ (SH190), h = 50 cm, échantillons moléculaires LDG525/559 (MNHN-EO-ENSIF1706).

Additional material examined. — Guyane. Same informations as paratypes, two juveniles (FL 207, FL291) (MNHN).

Type locality. — French Guiana, Mounts Tumuc-Humac, 2.233664N, 54.4419W, 415 m.

Etymology. — The species is dedicated to Judith Najt, who kindly welcomed TR in her research team when she was at the head of the ESA8043 CNRS (former name of current ISYEB-UMR7205). As team leader, Judith was always able to provide support, advice and coffee to students knocking at her door. Since TR's master project was dealing with Neotropical eneopterines (Robillard & Desutter-Grandcolas 2005), it was natural to dedicate this new *Ligypterus* species to Judith.

Diagnosis. — Species close to *L. fuscus* Chopard, 1920, from which it differs by male genitalia: pseudepiphallus wider, lophi widened laterally and more separate from each other, pseudepiphallic parameres separated by their width (almost touching each other in *L. fuscus*); and by shape of female copulatory papilla: rounded apex folded ventrally (straight and not rounded in *L. fuscus*).

Description

Size rather large for the genus, typical stocky shape. Coloration contrasted yellow to orange brown, mottled with dark brown (Fig. 1). Head dorsum yellow with six dark brown longitudinal bands (Fig. 2B), the two widest behind antennae forming one anterior punctuation, the two median bands punctuated along their whole length (Fig. 2B). Fastigium dark brown, yellow apically, with a black area posterior to median ocellus. Ocelli yellow. Eyes dark brown, with a wide longitudinal light band in dorso-lateral region. Scapes yellow with brown stains. Face mostly yellow with variable dark brown patterns (Fig. 2A), including area below the antennae extended dorsally below median ocellus, two dark stains on clypeus forming a circular pattern and central area of labrum; lateral part of head yellow or whitish with dark spots (Fig. 2C). Mandibles yellow with dark patterns; maxillary palpi mostly dark brown with yellow areas, their fifth article dark brown with a yellowish ring. Pronotum (Fig. 1): dorsal disk rectangular, wider than long, densely setose with two marks near anterior margin; coloration orange brown mottled with dark and light spots, lateral margins yellow; posterior margin straight, mostly light colored, with variable dark stains; lateral lobe with a black band underlying dorso-lateral margin, progressively lighter ventrally; ventral margin concave in median region. Legs: FI-II yellow with black spots, TI-II yellow with dark rings. Trochanter yellow. FIII yellow mottled with whitish and black spots, with strong striated dark brown patterns on outer faces; knees dark brown; TIII dark brown with faint yellowish spots. Abdomen dark brown. Cerci mostly yellow brown with dark spots.

Male

FW (Fig. 3A) reaching beyond abdomen mid-length, mostly translucent brown with dark brown area anterior to 1A, and pale areas including CuA vein and anal node area, other veins dark brown. FW venation typical of genus: 1A slightly bisinuated near angle, with 116 stridulatory teeth, nine on basal angle and 107 on transverse part of file. Harp longer than wide, with one strong V-shaped oblique vein. Mirror (d1) wider than long, crossed by an accessory vein in posterior quarter and extended posteriorly by widened d2, d1+d2 forming a wide ellipsoid area. Cell c1 narrow. Lateral field mostly brown, area between M and R vein dark brown to black; Sc with seven (n = 4) bisinuated branches and three more ventral veins.

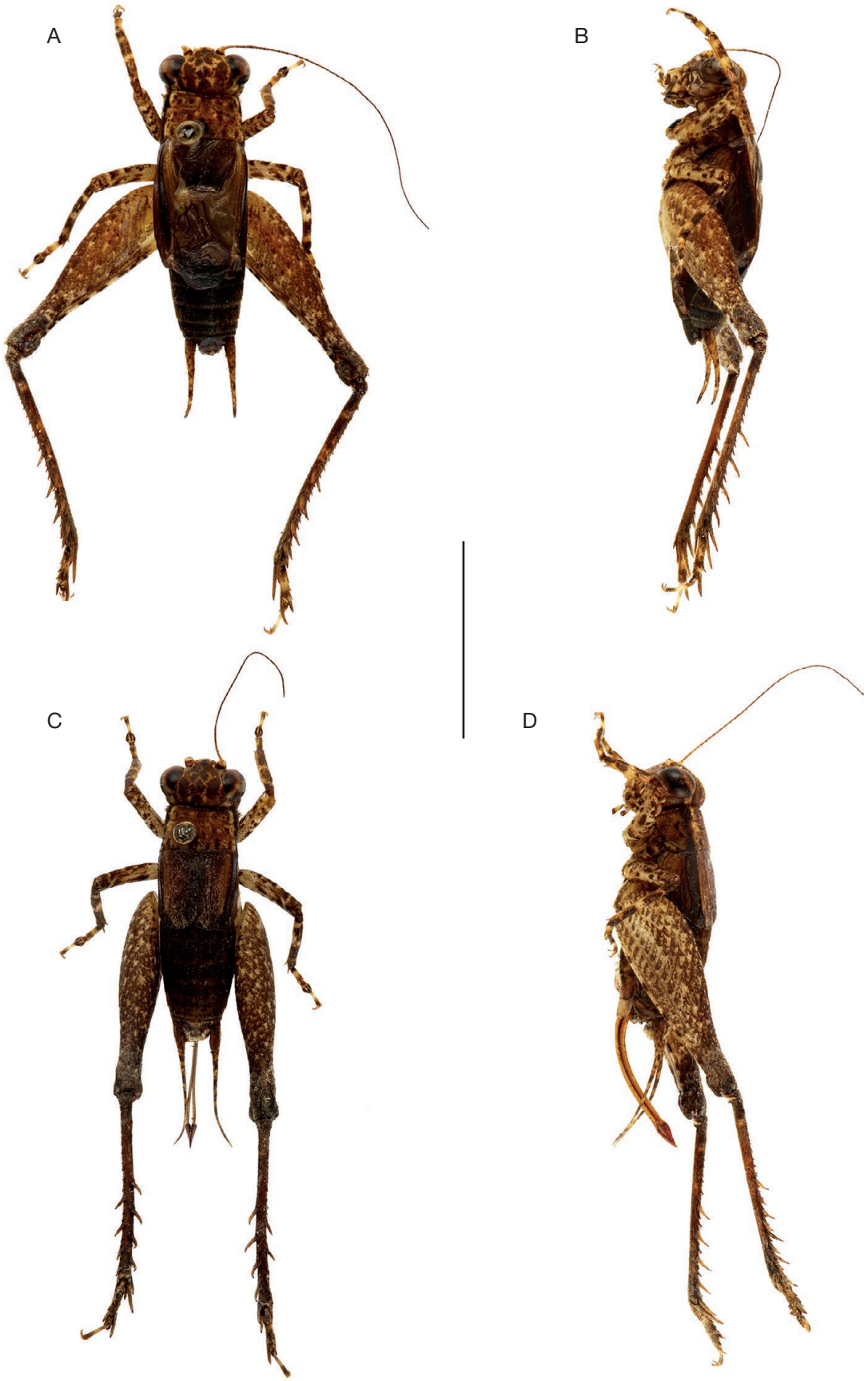

FIG. 1. — *Ligypterus najtae* n. sp.: **A**, **B**, male holotype in dorsal (**A**) and lateral (**B**) views; **C**, **D**, female allotype in dorsal (**C**) and lateral (**D**) views. Scale bar: 1 cm.

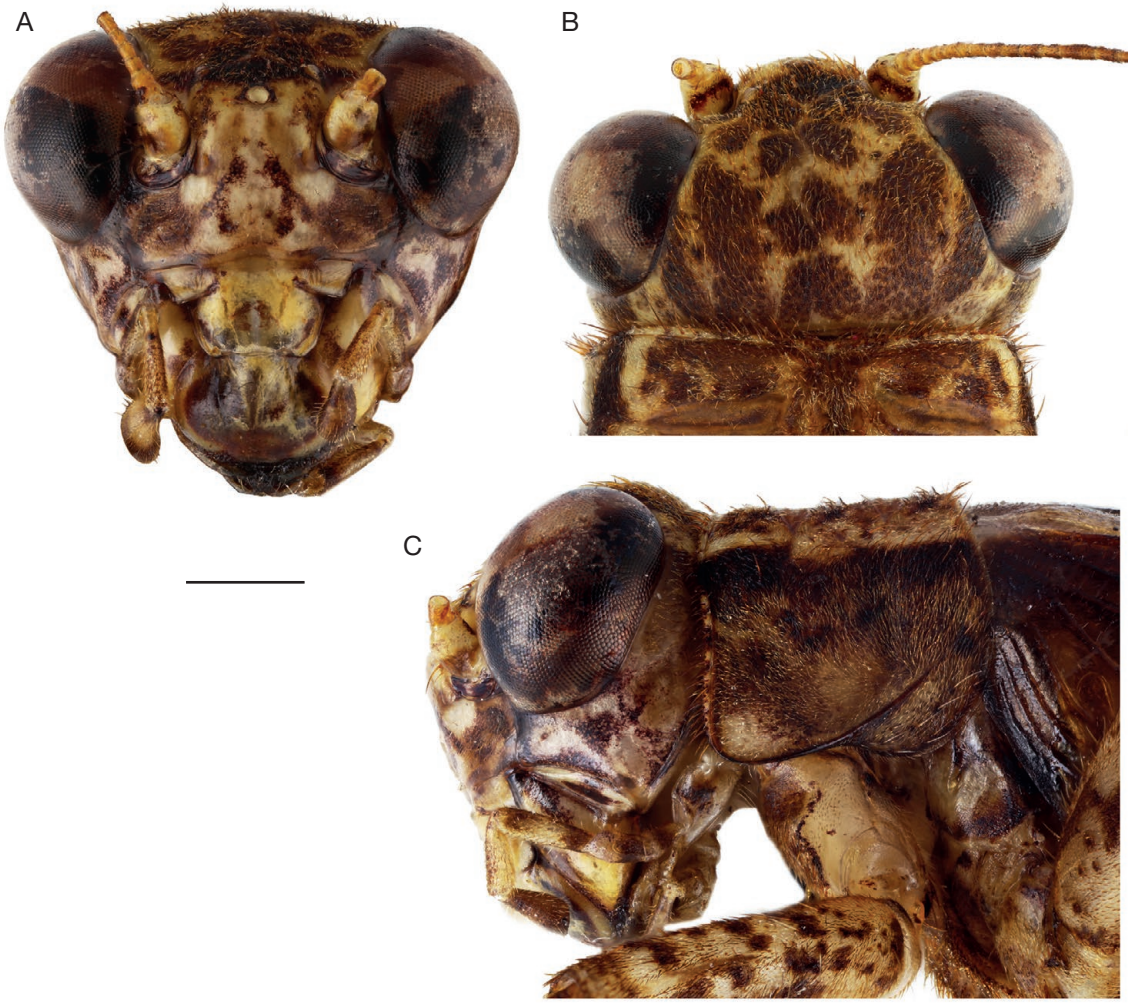

Fig. 2. — *Ligypterus najtae* n. sp.: head in facial (**A**), dorsal (**B**) and lateral (**C**) views. Scale bar: 1 mm.

Male genitalia
Pseudepiphallus triangular (Fig. 4), less widened laterally than in *L. fuscus*, with shorter triangular posterior lophi, widened basally and more separated than in *L. fuscus*; in lateral view (Fig. 5), lophi clearly sclerotized dorsally, membranous ventrally with a wide basal membranous lobe. Rami straight, shorter than rest of pseudepiphallus. Pseudepiphallic parameres widely separated, very sclerotized, with one lobe oriented dorsally and two ventral lobes finely denticulate; posterior lobe elongate, anterior one rounded with membranous basis. Ectophallic fold with two J-shaped lateral sclerites. Endophallic sclerite large, with two strong postero-lateral arms and a median triangular expansion; endophallic apodeme made of a median crest shorter than in *L. fuscus*.

Female
FWs shorter than in males (Figs 1; 3B; 7A, B), slightly overlapping, dark brown with orange veins; venation with five main longitudinal veins and strong transverse ones barely distinguishable the ones from the others, forming a dense network of veins. Lateral field with area between M and R dark as in males.

Female genitalia
Copulatory papilla close to that of *L. heydeni*; circular basal ring with a short posterior expansion; apex rounded, smaller than in *L. heydeni*, folded ventrally.

Juvenile
First instars dark brown with whitish spot on head (Fig. 7C); later instars more similar to adults in coloration.

Measurements
See Table 1.

Habitat and life history traits
Ligypterus najtae n. sp. was found on low vegetation in/near the leaf litter in forested areas, from where males sing during night time (Fig. 7A, B).

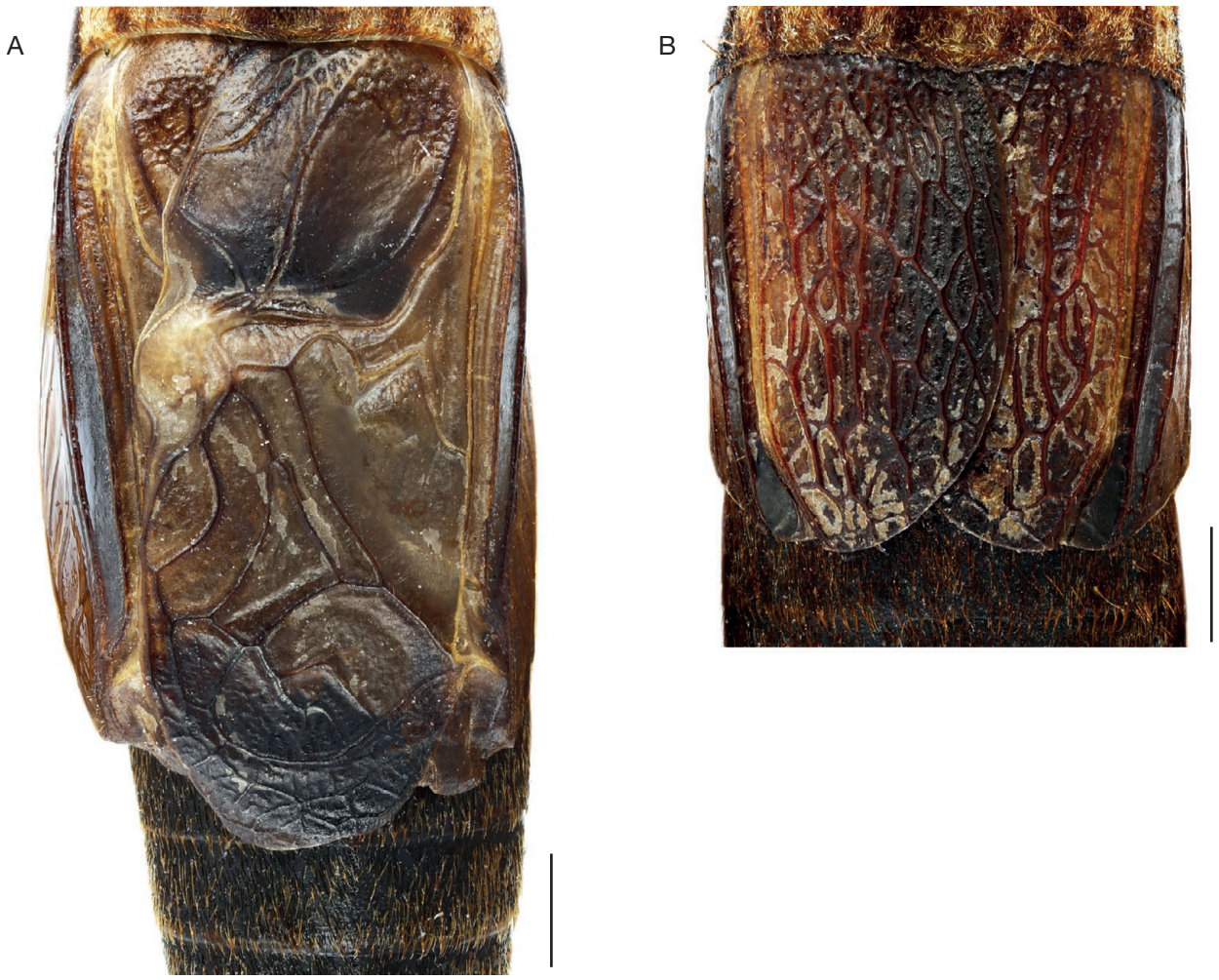

Fig. 3. — *Ligypterus najtae* n. sp.: **A**, male forewing venation; **B**, female forewing venation. Scale bars: 1 mm.

Calling song

The calling song of *L. najtae* n. sp. (Fig. 8) was recorded in the laboratory (Table 2). At 25°C (FO-male2), the song echeme is made of 20-25 syllables (m = 22.3 ± 1.4) and lasts for 300 ± 25 ms, for an echeme period of 2.44 ± 0.34 s (duty cycle = 12.2%). Most echemes show an irregular beginning comprising 2-3 syllables (m = 2.1 ± 0.3, n = 12), separated by a pause of 54 ± 10 ms from a more regular trill comprising 18-23 syllables (trill duration = 215 ± 31 ms). Syllables are short (duration = 8.8 ± 0.1 ms; period = 11.5 ± 3.4 ms) and show a slightly indented amplitude profile. The spectrum shows a clear dominant peak at 18.54 ± 0.29 kHz corresponding to the third harmonic of a lower fundamental frequency (*c.* 6.2 kHz).

Compared to that of *L. fuscus* (Robillard *et al.* 2015; table 2), the song of *L. najtae* n. sp. has a similar echeme structure, but shows a longer irregular beginning and a slightly lower dominant frequency (19.73 kHz in *L. fuscus*). Syllables have a similar duration in both species, with a shorter syllable period in *L. najtae* n. sp. Song files of two recorded specimens (MNHN-EO-ENSIF4165 and MNHN-EO-ENSIF4167) have been deposited in the MNHN Sound Library with the following inventory numbers, MNHN-SO-2017-32 and MNHN-SO-2017-33 respectively.

DISCUSSION

The new species described here is the second species of *Ligypterus* documented from French Guiana. Robillard & Desutter-Grandcolas (2005) estimated a diversity of five *Ligypterus* species, which seemed similar in their habits and association with forests. The real species diversity of this genus is however hard to evaluate. The remarkable similarity between the species and, at the same time, subtle morphological variability within species along their distributions, contribute to the evidence that we may be dealing with one or several species' complexes, which is suggested by preliminary molecular analyses.

The described species present a disjunct distribution in South America, with records restricted on the two rainforest blocks, Amazonia and the Atlantic Forest. This characteristic makes them a suitable model for studies concerning likely routes of former forest connections and the directionality of dispersal between Amazonia and the Atlantic Forest. Such studies will however first necessitate a dense and comprehensive sampling in these regions, coupling specimens, molecular data and acoustic recordings to assess species diversity using integrative taxonomy.

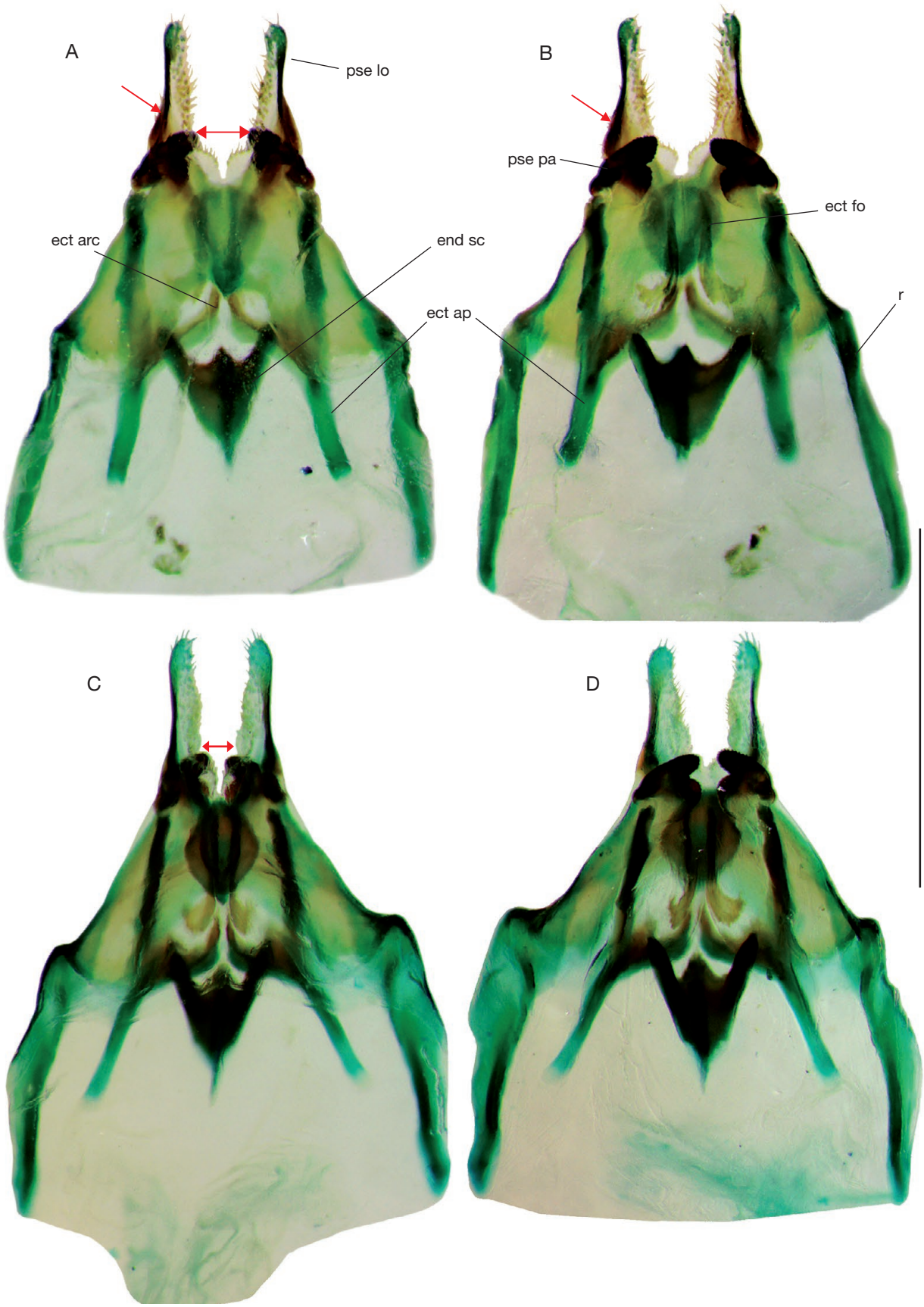

FIG. 4. — **A**, **B**, *Ligypterus najtae* n. sp.: male genitalia in dorsal (**A**) and ventral (**B**) views; **C**, **D**, *Ligypterus fuscus* Chopard, 1920: male genitalia in dorsal (**C**) and ventral (**D**) views. The red arrows indicate the windened part of pseudepiphallic lophi. Scale bar: 1 mm.

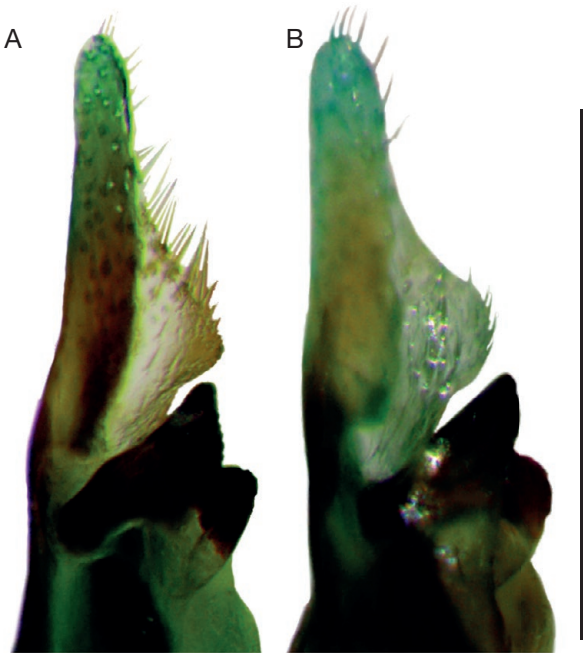

FIG. 5. — **A**, *Ligypterus najtae* n. sp., apex of male genitalia in lateral view; **B**, *Ligypterus fuscus* Chopard, 1920, apex of male genitalia in lateral view. Scale bar: 0.5 mm.

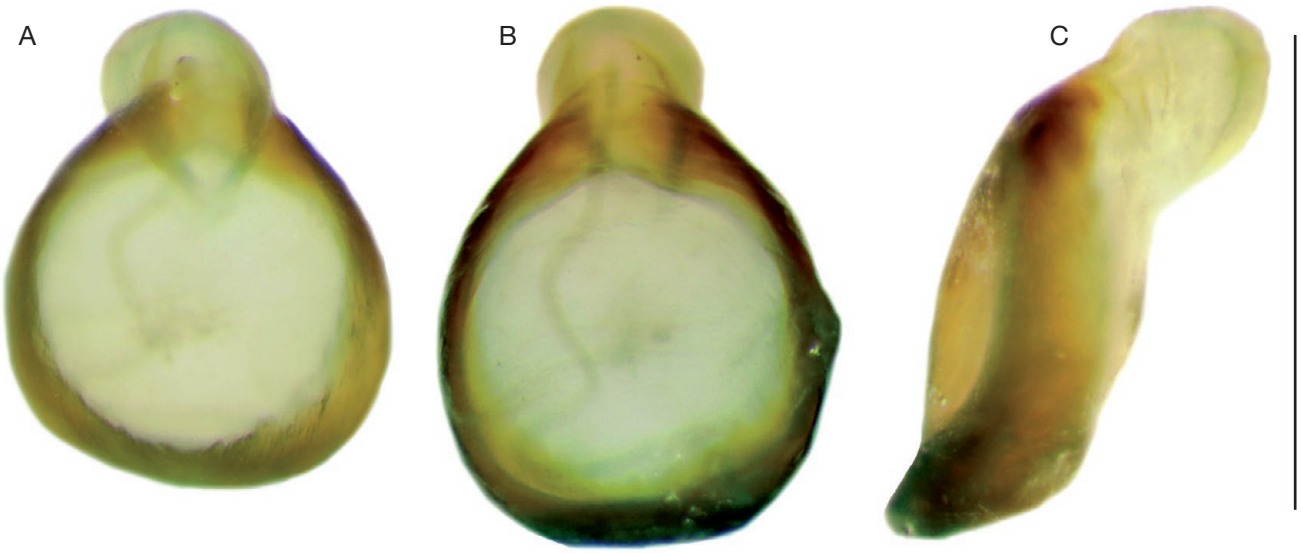

FIG. 6. — *Ligypterus najtae* n. sp., female copulatory papilla in ventral (**A**), dorsal (**B**), and lateral views (**C**). Scale bar: 0.5 mm.

In terms of acoustic communication, the discovery of this new species with high-frequency calling songs close to the ultrasounds is consistent with the reanalysis of the song of *L. fuscus* (Robillard *et al.* 2015). It suggests that all the species of this genus might have adopted this type of signals, also shared by all the lineages belonging to the tribe Lebinthini (Robillard & Desutter-Grandcolas 2004b). A new system of communication was recently discovered in Lebinthini, involving male-female high-frequency sound and vibrational duets (ter Hofstede *et al.* 2015). Although it is likely that the Neotropical Lebinthini may have adopted this system of communication, given that they share the spectral innovations of the Southeast Asian and Western Pacific lineages of Lebinthini, confirmation will have to be brought through field observations and lab experiments.

Fig. 7. — *Ligypterus najtae* n. sp.: **A**, female on low vegetation; **B**, male in leaf litter; **C**, juvenile (second instar). Photographs: S. Hugel (A); T. Robillard (B, C).

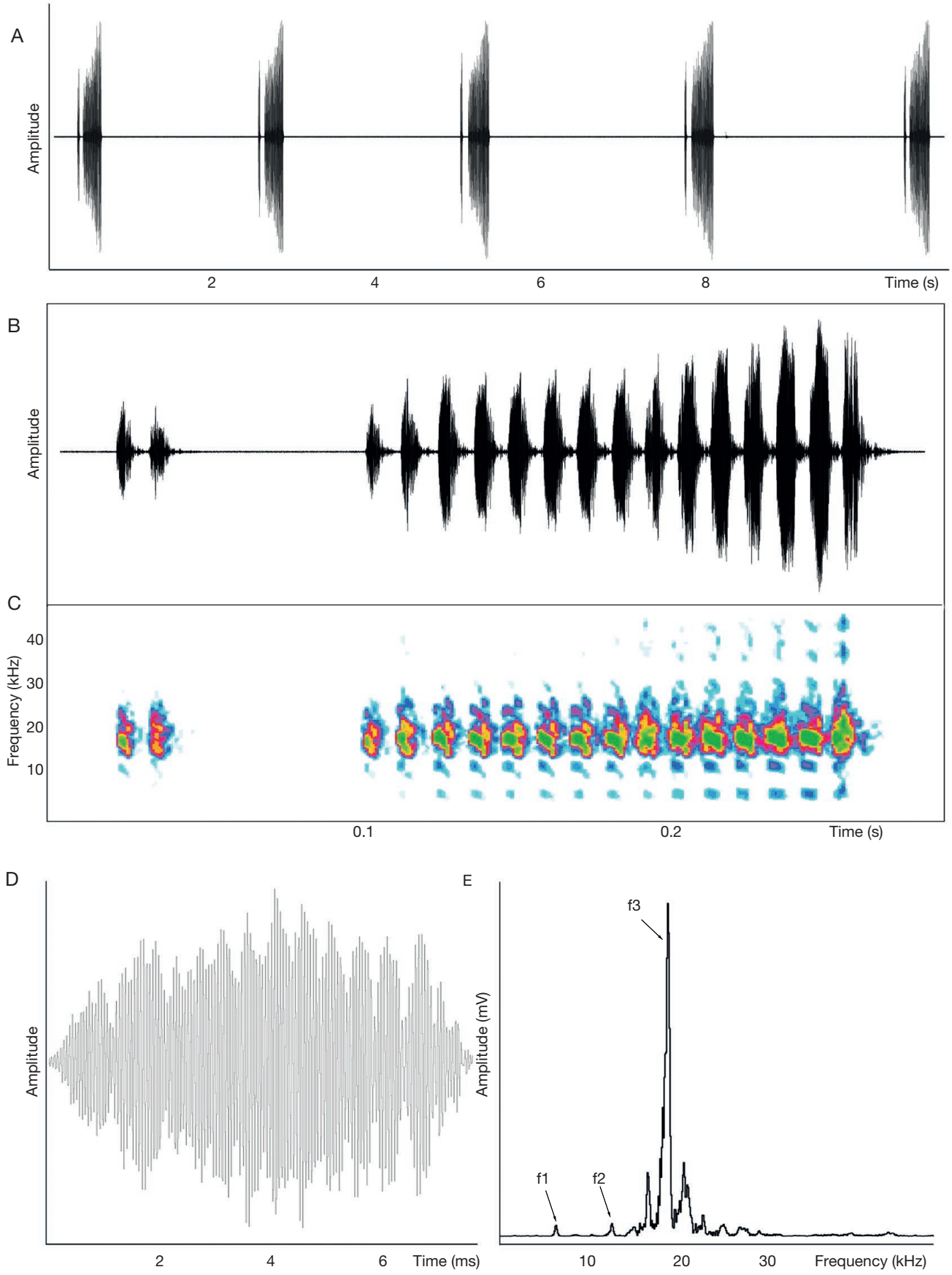

FIG. 8. — Calling song of *Ligypterus najtae* n. sp.: **A**, oscillogram of five echemes; **B**, **C**, oscillogram (**B**) and sonogram (**C**) of one echeme; **D**, **E**, detailed oscillogram (**D**) and frequency spectrum (**E**) of one syllable. Arrows on spectrum indicate the harmonic series (f1, f2, f3) derived from fundamental frequency f1.

TABLE 1. — Measurements (in mm, except for spine numbers) of *Ligypterus najtae* n. sp.

								TIII spine numbers					
	PronL	PronW	FWL	FWW	FIIIL	FIIIW	TIIIL	Ias	Ibs	Oas	Obs	TaIII-1 spines	OL
Male holotype	2.3	4.1	7.9	3.8	11.7	3.6	10.4	7	6	9	7	3(1)	–
Males (n=5)	2.3-2.5	3.8-4.3	7.4-7.9	3.6-3.8	10.9-13.7	3.2-4	9.8-12	6-8	6-7	8-11	6-10	2-3 (1)	–
(male mean)	(2.4)	(4.1)	(7.6)	(3.7)	(12.3)	(3.7)	(11)	(7)	(7)	(9)	(7)	(2(1))	–
Female allotype	2.5	3.9	4.3	2.6	12.4	3.9	10.4	6	6	8	5	2(1)	8.1
Females (n=2)	2.2-2.5	3.9-4.4	4.3-5	2.6-2.7	12.4-13.8	3.9-4.4	10.4-10.8	6	5-6	8-10	5	2(1)	8.1-8.6
(female mean)	(2.4)	(4.2)	(4.2)	(2.7)	(13.1)	(4.2)	(10.6)	(6)	(6)	(9)	(5)	(2(1))	(8.4)

TABLE 2. — Comparison of calling song between *Ligypterus najtae* n. sp. and *L. fuscus* Chopard, 1920 (values from Robillard & Desutter-Grandcolas 2005 and Robillard *et al.* 2015).

	***L. najtae* n. sp. EO-ENSIF4167**	***L. najtae* n. sp. EO-ENSIF4165**	***L. najtae* n. sp. mean values**	***L. fuscus* n. sp. mean values**
Temperatures	23.2°C	25°C	–	28°C
Echeme duration (ms)	379 ± 32	300 ± 25	340 ± 29	517 ± 35
Echeme period (ms)	1301 ± 242	2447 ± 340	1874 ± 291	1547 ± 179
Syllables per echeme	21.7 ± 2.0	22.3 ± 1.4	22 ± 1.7	30 ± 2
Syllable duration	8.0 ± 1.4	8.8 ± 0.1	8.4 ± 0.7	8 ± 1
Syllable period (ms)	14.4 ± 5.8	11.5 ± 3.4	13.0 ± 4.6	19 ± 8
Dominant frequency (kHz)	19.26 ± 0.73	18.54 ± 0.29	18.9 ± 0.51	19.73

Acknowledgements

We thank Frédéric Legendre and Sylvain Hugel for collecting the specimens during the 'Our Planet Reviewed' Initiative, Guyane 2014-2015 Expedition', organized by the Muséum national d'Histoire naturelle de Paris and Pro-Natura International. We also thank Simon Poulain (CNRS) for his help in taking pictures of the specimens, and Laure Desutter and Ming Kai Tan for helpful suggestions on the manuscript.

REFERENCES

DESUTTER L. 1987. — Structure et évolution du complexe phallique des Gryllidea (Orthoptera) et classification des genres néotropicaux de Grylloidea.1re partie. *Annales de la Société entomologique de France* (N. S.) 23: 213-239.

DESUTTER-GRANDCOLAS L. 2003. — Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta* 32: 525-561. https://doi.org/10.1046/j.1463-6409.2003.00142.x

DESUTTER-GRANDCOLAS L. 1991. — Les Phalangopsidae néotropicaux (Orthoptera: Gryllidae). I. Les Strogulomorphini. *Annales de la Société entomologique de France* (N. S.). 27: 465-481.

DESUTTER-GRANDCOLAS L. 1992a. — Les Phalangopsidae de Guyane française (Orthoptères, Grylloidea): systématique, éléments de phylogénie et de biologie. *Bulletin du Muséum national d'Histoire naturelle*, Paris 14: 93-177.

DESUTTER-GRANDCOLAS L. 1992b. — Les Phalangopsidae néotropicaux (Orthoptera: Grylloidea). II. Le groupe des Aclodae. *Annales de la Société entomologique de France* (N. S.) 28: 171-199.

DESUTTER-GRANDCOLAS L. 1998. — Broad-frequency modulation in cricket (Orthoptera, Grylloidea) calling songs: two convergent cases and a functional hypothesis. *The Canadian Journal of Zoology* 76: 2148-2163. https://doi.org/10.1139/z98-152

NATTIER R., ROBILLARD T., DESUTTER-GRANDCOLAS L., COULOUX A. & GRANDCOLAS P. 2011. — Older than New Caledonia emergence? A molecular phylogenetic study of the Eneopterine crickets (Orthoptera: Grylloidea). *Journal of Biogeography* 38: 2195-2209. https://doi.org/10.1111/j.1365-2699.2011.02563.x

OTTE D. & ALEXANDER R. D. 1983. — The Australian crickets. *Monographs of the Academy of Natural Sciences of Philadelphia* 22: 1-477.

RAGGE D. R. & REYNOLDS W. J. 1998 — The songs of the grasshoppers and crickets of Western Europe. Colchester: Harley Books. 591 s., 593 p.

ROBILLARD T. & DESUTTER-GRANDCOLAS L. 2004a. — Phylogeny and the modalities of acoustic diversification in extant Eneopterinae (Insecta, Orthoptera, Grylloidea, Eneopteridae). *Cladistics* 20: 271-293. https://doi.org/10.1111/j.1096-0031.2004.00025.x

ROBILLARD T. & DESUTTER-GRANDCOLAS L. 2004b. — High-frequency calling in Eneopterinae crickets (Orthoptera, Grylloidea, Eneopteridae): An adaptive radiation revealed by phylogenetic analysis. *Biological Journal of the Linnean Society* 83: 577-584. https://doi.org/10.1111/j.1095-8312.2004.00417.x

ROBILLARD T. & DESUTTER-GRANDCOLAS L. 2005. — A revision of the Neotropical Eneopterinae crickets (Orthoptera, Grylloidea, Eneopteridae) with a phylogenetic discussion. *Insect Systematics and Evolution* 35: 411-435. https://doi.org/10.1163/187631204788912427

ROBILLARD T. & DESUTTER-GRANDCOLAS L. 2008. — Clarification of the taxonomy of extant crickets of the subfamily Eneopterinae (Orthoptera: Grylloidea; Gryllidae). *Zootaxa* 1789: 66-68.

ROBILLARD T. & DESUTTER-GRANDCOLAS L. 2011. — The complex stridulatory behavior of the cricket *Eneoptera guyanensis* Chopard (Orthoptera: Grylloidea: Eneopterinae). *Journal of Insect Physiology* 57 (6): 694-703. https://doi.org/10.1016/j.jinsphys.2011.02.005

ROBILLARD T. & DESUTTER-GRANDCOLAS L. 2013. — Eneopterinae crickets from Costa Rica: an emended list (Orthoptera, Grylloidea). *Zoosystema* 35 (4): 489-494. https://doi.org/10.5252/z2013n4a3

ROBILLARD T., DONG J., LEGENDRE F. & AGAUVOA S. 2016. — The brachypterous Lebinthini crickets from Papua New Guinea, with description of two new genera and four new species (Orthoptera: Gryllidae: Eneopterinae) *in* ROBILLARD T., LEGENDRE F., VILLEMANT C. & LEPONCE M. (eds), *Insects of Mount Wilhelm, Papua New Guinea*. Muséum national d'Histoire naturelle, Paris: 149-202 (Mémoires du Muséum national d'Histoire naturelle; 209).

Robillard T., Gorochov A. V., Poulain S. & Suhardjono Y. R. 2014. — Revision of the cricket genus *Cardiodactylus* (Orthoptera, Eneopterinae, Lebinthini): the species from both sides of the Wallace line, with description of 25 new species. *Zootaxa* 3854: 104 p. https://doi.org/10.11646/zootaxa.3854.1.1

Robillard T., Grandcolas P. & Desutter-Grandcolas L. 2007. — A shift toward harmonics for high-frequency calling shown with phylogenetic study of frequency spectra in Eneopterinae crickets (Orthoptera, Grylloidea, Eneopteridae). *Canadian Journal of Zoology* 85: 1264-1275. https://doi.org/10.1139/Z07-106

Robillard T., Montealegre-Z. F., Desutter-Grandcolas L., Grandcolas P. & Robert D. 2013a. — Mechanisms of high frequency song generation in brachypterous crickets and the role of ghost frequencies. *Journal of Experimental Biology* 216: 2001-2011. https://doi.org/10.1242/jeb.083964

Robillard T., ter Hofstede H. M., Orivel J. & Vicente N. M. 2015. — Bioacoustics of the Neotropical Eneopterinae (Orthoptera, Grylloidea, Gryllidae). *Bioacoustics* 24(2): 123-143. https://doi.org/10.1080/09524622.2014.996915

Specht R. 2008. — *Avisoft-SASLab Pro: Sound Analysis and Synthesis Laboratory*. Avisoft Bioacoustics, Berlin.

ter Hofstede H., Schöneich S., Robillard T. & Hedwig B. 2015. — Evolution of a communication system by sensory exploitation of startle behavior. *Current Biology* 25: 1-8. https://doi.org/10.1016/j.cub.2015.10.064

Vicente N., Kergoat G.J., Dong J., Yotoko K., Legendre F., Nattier R. & Robillard T. 2017. — In and out of the Neotropics: historical biogeography of Eneopterinae crickets. *Journal of Biogeography* in press.

Submitted on 19 October 2016;
accepted on 16 December 2016;
published on 31st March 2017.