A new species of *Burttia* Dirsh (Caelifera, Acridoidea, Acrididae, Catantopinae) from the Eastern Arc Mountains of Tanzania

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Abstract

A new species of *Burttia* Dirsh, *B. caerulea* sp. nov., is described from the Nguru Mountains of Tanzania. It is the second species in the genus, both being restricted to Tanzanian localities. Both *B. sylvatica*, known only from the Uluguru Mountains, and *B. caerulea* sp. nov. are morphologically very similar in habitus and outer morphology, suggesting a recent speciation.

Keywords

East Africa, grasshopper, taxonomy

Introduction

The genus *Burttia* Dirsh, 1951 was erected by Dirsh (1951). The type species, *B. sylvatica* Dirsch, 1951, is endemic to the Uluguru Mountains in Tanzania. Except for its description, no biological or ecological information is available on this small catantopine genus. The genus is characterized by being flightless without any trace of wings, a rugose integument, and antennae that are longer than the head and the pronotum together and compressed at the base. The head is conical and the fastigium verticis acutely angular, with the apex strongly projecting forwards and with a longitudinal concavity. The occipital carinula is sharp and the frons strongly oblique. The dorsum of the pronotum is almost flat, with a well-developed median carinula. Three narrow sulci cross the dorsum of the pronotum. The prosternal process is conical with a wide base. The subgenital plate is upcurved with an obtuse apex. The valves of the ovipositor in females are long and slender, with slightly curved apices (Dirsh 1965).

In the Nguru Mountains of Tanzania, a second, morphologically very similar species was found and is described in this paper. The biogeography of *Burttia* and of Orthoptera taxa restricted to the Eastern Arc Mountains is discussed.

Materials and methods

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

Genital preparations.—For genital preparations, specimens were relaxed in water, the phallus extracted manually, macerated in 5% KOH, then neutralized in 5% acetic acid and stained with acid fuchsin.

Depositories.—CCH: Collection of Claudia Hemp.

Results

Taxonomy

Family Acrididae
Subfamily Catantopinae

Genus *Burttia* Dirsh, 1951

Type species.—*B. sylvatica* Dirsh, 1951, by original monotypy

Burttia caerulea Hemp, sp. nov.

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Type material.—**Holotype:** TANZANIA • male; Nguru Mountains, montane forest above Ubiri, 1740 m; -6.044233°, 37.562823°; February 2021; CCH.

Paratypes: TANZANIA • 3 males, 4 females; same data as holotype; CCH.

Diagnosis.—*Burttia caerulea* sp. nov. is morphologically very similar to *B. sylvatica* and thus fits exactly the generic description given by Dirsh (1965). Even the coloration is similar, although males of *B. caerulea* n. sp. have brighter blue bases of the antennae (Fig. 1). Overall, *B. caerulea* sp. nov. is larger and stouter than *B. sylvatica* (Fig. 2). Both species have large, paired tubercles on the supra-anal plate, but while those of *B. sylvatica* are vertical and rounded, those of *caerulea* sp. nov. are pointed towards the rear and more acute. The male supra-anal plate of *caerulea* is proportionately shorter than that of *sylvatica*, and it has paired longitudinal depressions basally, unlike the single midline depression of *sylvatica*

Fig. 1. *Burttia* species. **A.** *B. caerulea* sp. nov. from the Nguru Mountains; **B.** *B. sylvatica* from the Uluguru Mountains.

Fig. 2. Male of *Burttia* species. Left: *B. caerulea* sp. nov.; right: *B. sylvatica*. *B. caerulea* sp. nov. is larger and stouter than *B. sylvatica*.

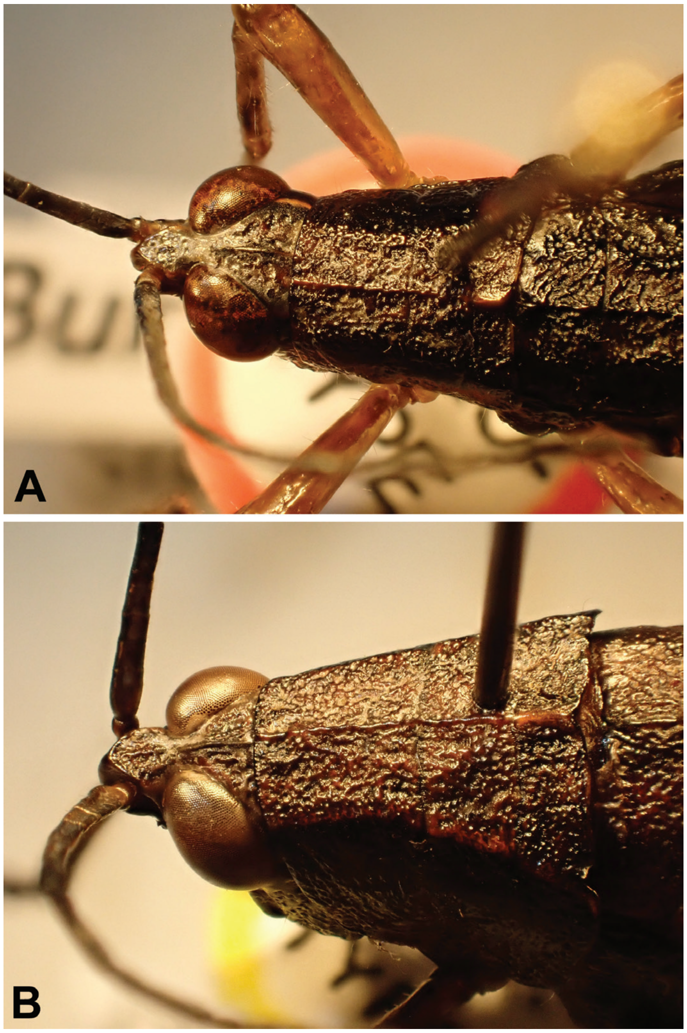

Fig. 3. Lateral view of head and pronotum of male (**A**) and female (**B**) *Burttia caerulea* sp. nov.

(Fig. 6A, B). Other differences are found in the epiphallus (Fig. 5). *B. sylvatica* has a smaller epiphallus compared to *B. caerulea* sp. nov. with smaller lophi. On the shoulder between the lophi and the bridge in *B. sylvatica*, only small humps are present that are roundish and more pronounced in *B. caerulea* sp. nov. (compare Figs 5, 6F, H). *B. sylvatica* is endemic to the Uluguru Mountains while *B. caerulea* sp. nov. is only known from the montane zone in the Nguru Mountains. The linear distance between these mountain ranges is about 100 km.

Etymology.—From Latin: *-caeruleum* = blue, because of the blue bases of the male antennae.

Description.—**Male**. Body, part of face, and outer sides of knees of hind legs dark brown. Legs creamy to white except for black tarsi and greyish blue hind tibiae. With broad white fascia across face. Bases of antennae blue (Fig. 1A). Antenna about 1.5 times longer than head and pronotum, compressed at base (Fig. 2A). Eyes oval, prominent. Fastigium verticis angular, with apex forming a rostrum, as described for the genus. Frons strongly oblique (Fig. 1A), upper part of frontal ridge strongly protruding in front of eyes, sulcate. Dorsum of pronotum with well-developed median carina (Fig. 3A). Integument of whole body strongly wrinkled (Fig. 2). As described for the genus, prosternal process very pointed with a broad base. No trace of wings. Supra-anal plate elongate with two well-developed tubercles near middle of supra-anal plate (Figs 4A, 6B). Subgenital plate upcurved, with obtuse apex (Figs 4A, 6B). Epiphallus divided, with large complex lophi; ancorae small and inwardly directed (Fig. 5B). Paired post-epiphallic sclerites present. Endophallic structures normal, aedeagus partly sheathed in ectophallic membrane (Fig. 6K).

Female. Larger and stouter than male (Fig. 1A), almost uniformly dark brown, without white fascia on face. As in male, with a median carina on the pronotum (Fig. 3B). Supra-anal plate elongate with a median ridge (Fig. 7A). Valves slender with curved apices, cerci short. Subgenital plate with slightly excurved posterior margin (Fig. 7B, C).

Measurements (mm).—Males (N = 4): Body length: 15.6–18.0; Medial length of pronotum: 3.1–3.4; length of hind femur: 10.1–10.3. Females (N = 4): Body length: 22.6–22.8; Medial length of pronotum: 4.3–4.5; length of hind femur: 13.0–14.4.

Habitat.—Along forest edges and in understory vegetation of montane forest, often on the forest floor among litter.

Distribution.—Tanzania, Nguru Mountains.

Discussion

Burttia was a monotypic catantopine genus up to now, with the species *B. sylvatica* described from the Uluguru Mountains. The second species described in this paper is morphologically closely related to *B. sylvatica*, since only minor differences are found in their outer appearance; the colour pattern and the phallic complexes of both species are very similar. Also, the habitat is analogous, both species being litter and herb dwellers of montane forest.

Taxonomic aspects

Dirsh (1951, 1965) placed *Burttia* in the Catantopinae, an ill-defined subfamily that has a history of use as a repository for tropical species that do not fall readily into other, better-defined, Old World subfamilies. Dirsh (1951) noted that *Burttia* "is not closely related to any known Catantopine genus". Our examination of the phallic complex shows that, in comparison with other Catantopine genera, *Burttia* is unusual in the following features:

A) Two small sclerites are found in the epiphallic membrane posterior to the epiphallus, approximately midway to the cingulum (Fig. 6C, D). Such post-epiphallic sclerites are common in some Acrididae (for example, the Neotropical Ommatolampinae) but, to our knowledge, have not been found previously in the Catantopinae.

B) The epiphallus is divided medially into two symmetrical halves. This arrangement is characteristic of some subfamilies (Oxyinae, Coptacrinae, and Euryphyminae) but is very rare in the Catantopinae, where it is known only in *Merehana* Kevan, 1957 and *Anischnansis* Dirsh, 1959, both of which are considered to be exceptional genera.

C) Dirsh (1951) suggested that *Burttia* might be related to the catantopine genus *Gemeneta* Karsch, 1892, another apterous African forest floor dweller, recently revised by Oumarou-Ngoute and Kekeunou (2017). Our examination of the phallic complex of *Burttia* spp. does not support this hypothesis, as the two genera are

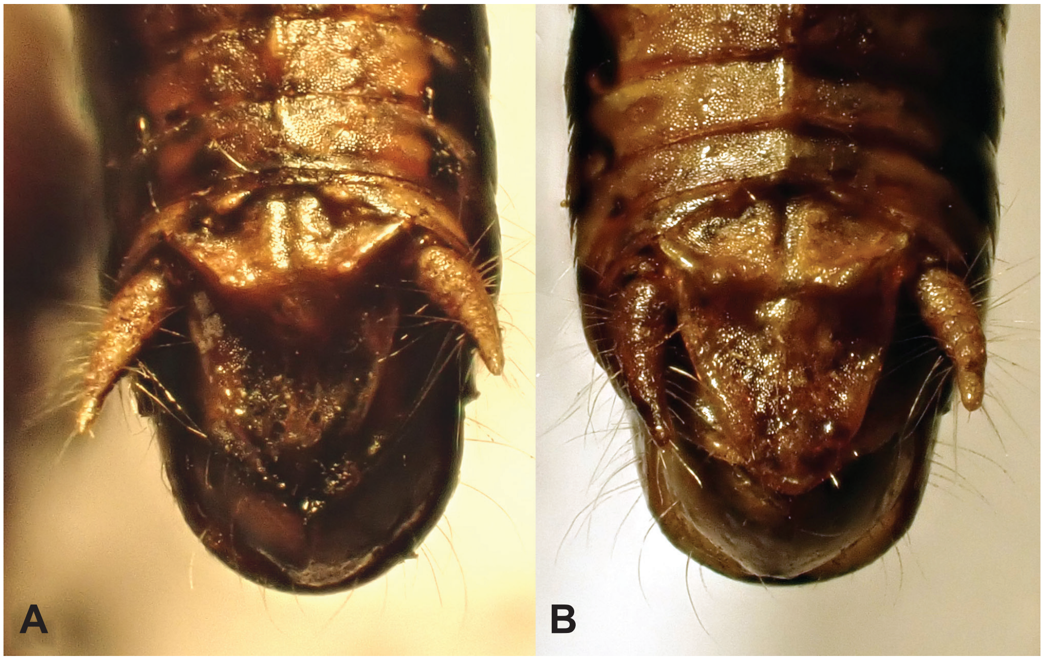

Fig. 4. Abdominal apices, dorsal view, of male *Burttia caerulea* sp. nov. (**A**) and *B. sylvatica* (**B**).

Fig. 5. Anterior axial view as epiphallus as situated when looking at opened apex of abdomen. **A.** *Burttia sylvatica*; **B.** *B. caerulea* sp. nov.

very different in this respect. Their external morphological similarity (aptery, dark coloration) is more likely due to convergent adaptation to identical habitat and lifestyle.

Due to the paucity of available material and a wish to avoid damage to a unique specimen, we did not dissect out the endophallus of *B. caerulea* sp. nov. However, visual inspection showed that it appeared to be identical in all respects with that of *B. sylvatica* (Figs 5, 6). Only the epiphalli show any obvious difference between the two species.

Biogeography

The Nguru Mountains, situated between the Usambara and Pare Mountains in the north of Tanzania and e.g., the Ukaguru, Rubeho, Uluguru, and Udzungwa Mountains further south harbour a mix of species typical for the Eastern Arc Mountains. Thus, the Ngurus share species of the Eastern Arc endemics *Philoscirtus* Karsch, 1896 (Hemp et al. 2015b) and *Physocrobylus* Dirsh, 1951 with the Usambara Mountains (not occurring further south), while the second species of *Burttia*, *B. sylvatica*, is endemic to the Uluguru Mountains in the north. Other flightless genera endemic to the Eastern Arc Mountains (and coastal forests) are the Pseudophyllinae genera *Pseudotomias* Hemp, 2016 (Hemp 2016) and *Dendrobia* Hemp & Ingrisch, 2017 (Hemp et al. 2017), distributed throughout these ancient mountain ranges. In Conocephalinae, *Afroagraecia* Ingrisch & Hemp, 2013 and *Afroanthracites* Hemp & Ingrisch, 2013 occur with at least one species on most of the Eastern Arc Ranges. Molecular phylogenetic analyses and studies on the acoustics have shown that species of the Agraeciini genus *Afroanthracites* are closely related to each other and have speciated during the past 1–2 million years—after the formation of Mt Kilimanjaro, which serves as a time marker (Hemp et al. 2015a, 2016). The same time scales were found in, e.g., the Ccoptacrinae genus *Parepistaurus* Karsch, 1896 or members of the family Lentulidae (*Rhainopomma* Jago, 1981, *Altiusambilla* Jago, 1981) (Hemp et al. 2015c, 2020). Even fully alate and thus more mobile Orthoptera speciated in the Eastern Arc Mountains and in coastal forests such as the Phaneropterinae *Lunidia* Hemp, 2010 (Hemp et al. 2010; Hemp 2017), showing on the one hand that the Eastern Arc Mountains harbor many old taxa on a generic level, isolated many million years ago during the fragmentation of the once continuous forest belt connecting west, central, and east Africa. On the other hand, climatic fluctuations over the past few million years were probably the motor for young radiations in the above-mentioned genera, as shown for the Hexacentrinae genus *Aerotegmina* Hemp, 2001 (Grzywacz et al. 2021) or suggested for the Pseudophyllinae *Pseudotomias* Hemp, 2016 (Hemp 2016). *Pseudotomias*, or *Stenampyx* Hemp, 2020 (Hemp 2020) probably have close relatives in central and west Africa. Further studies, including screening of the montane zones in the Eastern Arc Mountains and including molecular and cytogenetical analyses, should be conducted to illuminate modes and times of speciation of various Orthoptera taxa in East Africa.

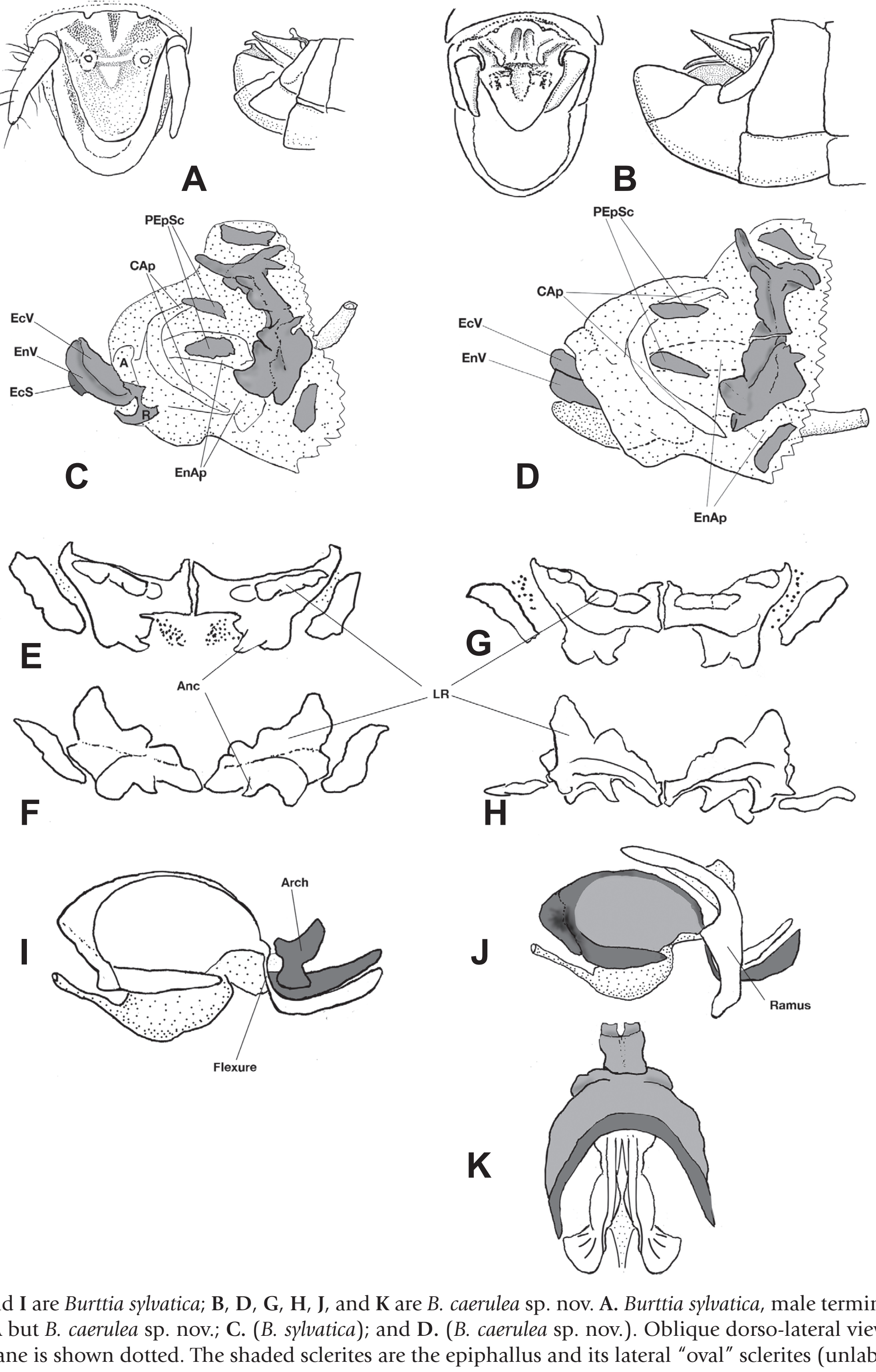

Fig. 6. A, **C**, **E**, **F**, and **I** are *Burttia sylvatica*; **B**, **D**, **G**, **H**, **J**, and **K** are *B. caerulea* sp. nov. **A.** *Burttia sylvatica*, male terminalia in dorsal and lateral views; **B** as **A** but *B. caerulea* sp. nov.; **C.** (*B. sylvatica*); and **D.** (*B. caerulea* sp. nov.). Oblique dorso-lateral view of entire phallic complexes. Membrane is shown dotted. The shaded sclerites are the epiphallus and its lateral "oval" sclerites (unlabelled, at the right-hand edge of each figure), the paired post-epiphallic sclerites (PEpSc), the right-hand side ectophallic ramus (R) in **C** only, and the aedeagal valves (EcV, ectophallic (dorsal) aedeagal valve; EnV, endophallic (ventral) aedeagal valve; EcS, fragment of ectophallic sheath left adhering to ventral valve during dissection). The remaining sclerites are indicated only by outlines, indistinctly visible through the membrane (A, arch; CAp, cingular apodemes; EnAp, endophallic (basal) apodemes). **E, F.** *Burttia sylvatica*, epiphallus; **E.** dorsal view; **F.** axial view. Note trilobed lophal ridge (LR), divided epiphallic bridge, and large irregularly shaped "oval" sclerites and inwardly directed ancorae (Anc). **G** and **H** as **E** and **F** but *B. caerulea* sp. nov. Phallic complex with ectophallic membrane, zygoma, cingulum, and rami removed to expose the arch and the endophallic flexure. Arch and LHS ectophallic valve shaded. **J.** *Burttia caerulea* sp. nov. Phallic complex with ectophallic membrane removed, showing endophallus, cingulum with LHS ramus and LHS ectophallic valve. Endophallus shaded. **K** as **J** but dorsal view. Ectophallic elements shaded.

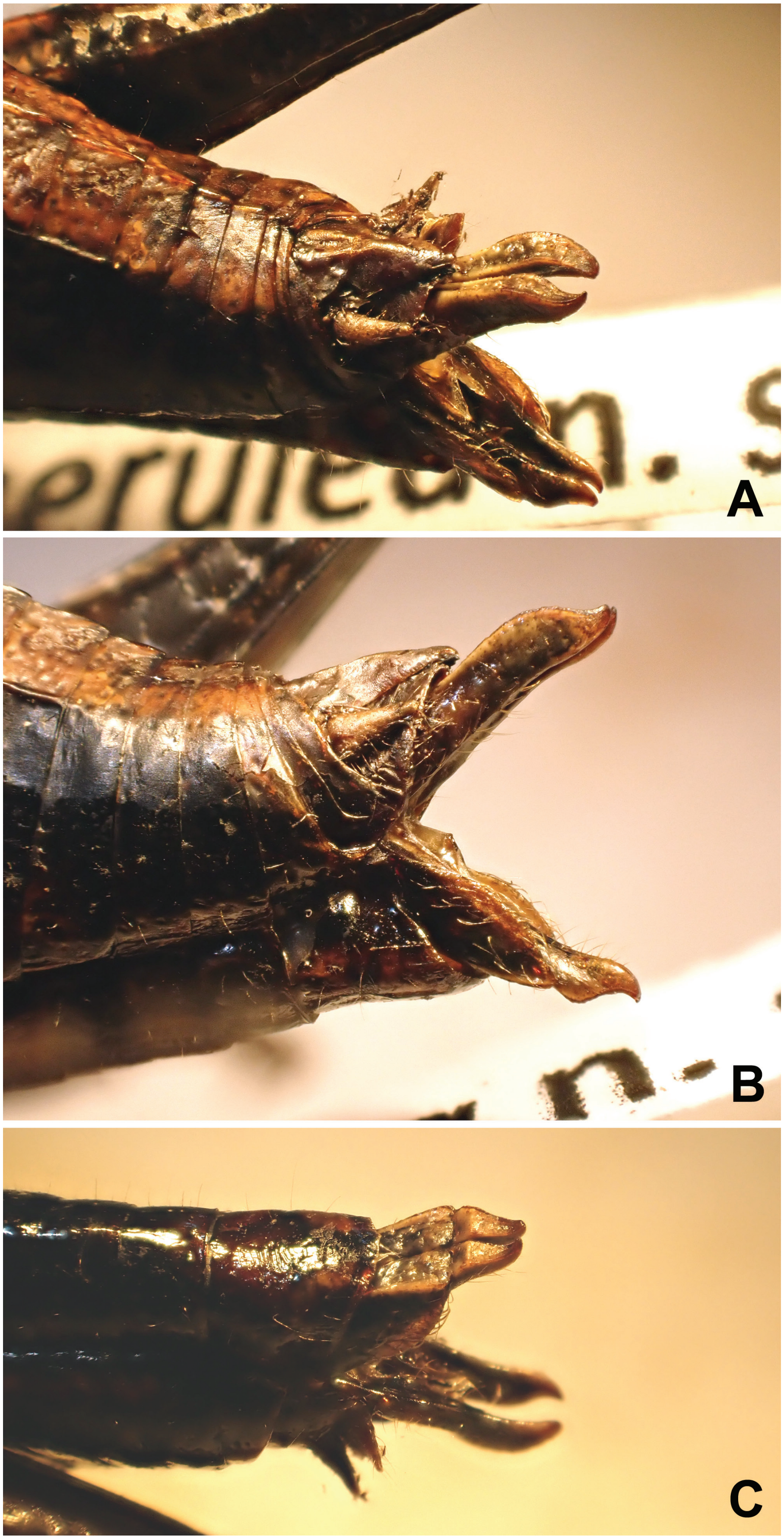

Fig. 7. Abdominal apex of female *Burttia caerulea* sp. nov. **A.** semilateral; **B.** lateral; **C.** semilateral view.

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Rugabinthus, a new genus of Lebinthina (Orthoptera, Gryllidae, Eneopterinae) from New Guinea

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Abstract

Brachypterous crickets from the monophyletic group of Lebinthina were traditionally grouped under the genus *Lebinthus*. However, the morphology and calling song are highly diversified, prompting the erection of numerous genera to reclassify the species. Based on the strong characteristic fold carrying the diagonal vein of the male forewing, a new genus of cricket from the subtribe Lebinthina is described: *Rugabinthus* **gen. nov.** This brachypterous genus is endemic to the island of New Guinea and nearby islands. We redescribe the type species *Rugabinthus leopoldi* (Chopard, 1931) **comb. nov.** and describe 12 new species, *R. manokwari* **sp. nov.**, *R. kencana* **sp. nov.**, *R. maoke* **sp. nov.**, *R. nabire* **sp. nov.**, *R. albatros* **sp. nov.**, *R. karimui* **sp. nov.**, *R. yayukae* **sp. nov.**, *R. biakis* **sp. nov.**, *R. mamberamo* **sp. nov.**, *R. tariku* **sp. nov.**, *R. faowi* **sp. nov.**, and *R. baduri* **sp. nov.** We also transferred *R. newguineae* (Bhowmik, 1981) **comb. nov.** and provide a key to all known species of *Rugabinthus* **gen. nov.**

Keywords

Grylloidea, Lebinthini, new species, Papua, Southeast Asia, taxonomy

Introduction

The tribe Lebinthini Robillard, 2004 is comprised of a highly speciose clade of crickets with diverse morphologies, ranging from the tiny brachypterous *Pixibinthus* Robillard & Anso, 2016 to the large and fully winged species of the genus *Cardiodactylus* Saussure, 1878. Male lebinthines produce high-frequency calls (10–28 kHz), and their call structure can also be highly diverse, ranging from a few chirps to a combination of a series of chirps followed by a trill (e.g., Robillard and Desutter-Grandcolas 2004a, 2004b, 2011, Tan et al. 2021). Lebinthines have been demonstrated to be important species for the study of insect communication systems. A new communication system using vibrational responses (including vibrotaxis) to high-frequency male calls and population-specific microevolution and plasticity in acoustic properties was recently discovered (ter Hofstede et al. 2015, Benavides-Lopez et al. 2020, Tan and Robillard 2021a, b).

Among the Lebinthini, the subtribe Lebinthina is distributed in the hyper-diverse yet poorly studied Southeast Asia and the western Pacific. This clade includes many taxa that are still being discovered. In particular, two genera of Lebinthina were described from Southeast Asia, *Fadinthus* Robillard & Tan, 2021, and *Falcerminthus* Robillard & Tan, 2021 (see Tan et al. 2021), which include numerous new species (Baroga-Barbecho et al. 2016, 2020, Tan et al. 2019).

Continued efforts to sample the region where Lebinthina is distributed and discover new species with diverse morphologies have led to recent insights about how species are related and should be classified. Traditionally, *Lebinthus* included most brachypterous species of Lebinthini. However, as new information about these species became available, their classification has been more accurately revised (Tan et al. 2021) and the subtribe Lebinthina Robillard & Tan, 2021 has been defined. Multiple new genera have also been erected, including *Centuriarus* Robillard, 2011 (Robillard 2011), *Gnominthus* Robillard & Vicente, 2015 (Vicente et al. 2015), *Microbinthus* Robillard & Dong, 2016, and *Macrobinthus* Robillard & Dong, 2016 (Robillard et al. 2016) from New Guinea; *Pixibinthus* Robillard & Anso, 2016 from New Caledonia (Anso et al. 2016); *Falcerminthus* Robillard & Tan, 2021 and *Fadinthus* Robillard & Tan, 2021 from Southeast Asia (Tan et al. 2021); and *Julverninthus* Robillard & Su, 2018 from Australia (Robillard and Su 2018). These studies revealed that most *Lebinthus* species known before 2010 corresponded to distinct genera, and that the island of New Guinea possesses the highest diversity of genera and species of the Lebinthina clade (Tan et al. 2021, Tan and Robillard 2021c).

Pursuing the taxonomic revision of the species described from New Guinea, we found that *Lebinthus leopoldi* Chopard, 1931 (Fig. 1) differs from the Lebinthina genera that are currently recognized. It shows unique morphological features in the male forewing (FW), including a strong fold carrying the diagonal vein (Fig. 2). In addition, study of undetermined material from several natural history museums, mostly collected in the western half of New Guinea, revealed numerous new species that share the characteristics of *L. leopoldi* (Fig. 3). Hence, we propose a new genus name for these species: *Rugabinthus* **gen. nov.** We redescribe the type species *Rugabinthus leopoldi* (Chopard, 1931) **comb. nov.** and describe 12 new species, as well as providing a key to all known species of *Rugabinthus* **gen. nov.** We also transfer *R. newguineae* (Bhowmik, 1981) **comb. nov.** to this new genus.

Materials and methods

Materials.—Specimens in MNHN were studied in addition to materials loaned from BPBM, MZB, NHMUK, RBINS, RMNH, and ZIN (see abbreviations below).

Morphology.—Male tegminal veins and cells follow the terminology of Robillard and Desutter-Grandcolas (2004a). Male and female genitalia were 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 were observed after cleaning with cold KOH and then kept in glycerine. Male genitalia are named according to Desutter (1987), modified in Desutter-Grandcolas (2003) and Robillard and Desutter-Grandcolas (2004a). For abbreviations, see below.

Close-up images of habitus and morphological features were obtained using a Canon EOS 6D digital SLR camera with a macro photo lens MP-E 65 mm f/2.8 USM (1–5×). Imaging stacking was done using Helicon Remote version 9.3.1. W and Helicon Focus 6.8.0. Photographs of male and female genitalia were done with a binocular microscope Leica MZ16 with an AMScope Microscope Eyepiece Camera (MU1000, 10 MP Aptina Colour, CMO50) attached via an AmScope FMA050 fixed microscope adaptor and the software ToupView. Image editing was accomplished using CombineZP version 1.0 and Adobe Photoshop CC2014. To highlight the structural components of genitalia, a water solution containing a drop of JBL Punktol was used. To fix orientations and stabilization of geni talia for photography, a clear and viscous hand sanitizer was used following Su (2016).

Abbreviations.—
Depositories:

BPBM	Bernice Pauahi Bishop Museum, Hawaii, U.S.A.;
MNHN	Muséum national d'Histoire naturelle, Paris, France;
MZB	Museum Zoologicum Bogoriense, Bogor, Java, Indonesia;
NHMUK	Natural History Museum, London, U.K.;
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium;
RMNH	Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands;
ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

General morphology:

I, II, III	front, median, hind, respectively (femora, legs, tibiae);
F	femora;
FW	forewing;
TaIII-1	basal segment of hind leg tarsomere;
T	tibiae.

Tegminal venation:

1A–4A	first to fourth anal veins;
CuA	anterior cubital vein;
CuA1, CuA2, …	first, second, … bifurcations of CuA;
CuP	posterior cubital vein;
M	median vein;
Sc	subcostal vein;
R	radial vein;
c1–3	first to third cells of C alignment;
d1 cell (mirror)	first cell(s) of D alignment;
d2	second cell of D alignment;
e1	first cell of E alignment;
ha	harp area.

Measurements:

FIIIL	length of hind femora;
FIIIW	width of hind femora;
FWL	forewing length;
FWW	forewing width (at the level of maximal width);
OL	ovipositor length;
PronL	pronotum length;
PronW	pronotum width;
TIIIL	length of hind tibiae.

Results

Taxonomy

Family Gryllidae Laicharting, 1781
Subfamily Eneopterinae Saussure, 1874
Tribe Lebinthini Robillard, 2004
Subtribe Lebinthina Robillard & Tan, 2021

Genus *Rugabinthus* Robillard & Tan, gen. nov.

http://zoobank.org/5239CAF1-F14C-4332-8153-2EC75E03CF0D

Type species.—Lebinthus leopoldi Chopard, 1931

Etymology.—Genus named after the Latin word "Ruga" for wrinkle or fold, referring to the characteristic fold on the male FW carrying the diagonal vein.

Distribution.—Island of New Guinea: Indonesia (West Papua) and Papua New Guinea (Fig. 3).

Diagnosis.—Among the Lebinthina genera, *Rugabinthus* species are average to large sized and stocky with a dark brown coloration. General shape close to that of *Macrobinthus*, also from New Guinea, from which it differs by male FWs with a narrow triangular harp (shield shaped in *Macrobinthus*) occupying half of FW width, with a characteristic and strong diagonal fold carrying the diagonal vein and cell c1, and separating FWs in two distinct areas; file vein area also characterized by a strong bean-shaped sclerotization; harp with a strong transverse oblique vein, bi- or poly-furcated anteriorly; venation posterior to diagonal fold usually faint and reticulated, longitudinal veins only strong at apex. Eyes prominent and large as in *Macrobinthus* compared to *Agnotecous* and *Centuriarus*; face as high as wide (higher than wide in *Macrobinthus*), close to that of *Lebinthus*. Microptery in both sexes, FWs not reaching mid-length of abdomen. Mirror not differentiated (slightly differentiated in *Macrobinthus*). CuA almost straight (clearly curved inwards in *Macrobinthus*). Male genitalia with pseudepiphallus usually elongate, its posterior apex highly variable in size and shape, rami short; pseudepiphallic parameres made of two main lobes variable in shape and orientation; endophallic sclerite very long, trifid posteriorly. Female: FWs shorter than in males, very slightly overlapping, generally rounded posteriorly. Ovipositor rather long, its apex slightly denticulate on dorsal edge. Female copulatory papilla usually rounded, with a C-shaped basal sclerite; apex rounded, generally folded ventrally.

Description.—Size variable, medium to large for the subtribe. Dorsum of head rounded, prolonged by trapezoidal fastigium almost as long as wide (Fig. 4). Head dorsum with six wide dark brown longitudinal bands more or less distinct (Fig. 4). Eyes large and prominent. Head triangular in facial view, almost as wide as high (Fig. 5). Face coloration usually red brown to dark brown or black, with various color patterns; most species with four pale brown or yellow dots forming a square on face (two between scapes, and two above epistomal suture) (Fig. 5). Maxillary palpi brown or dark brown (sometimes black in dark species) with lighter brown rings. Ocelli pale, forming a rather wide triangle; median ocellus slightly oval, lateral ocelli small and rounded. Scapes small. Antennae usually dark brown with yellow brown rings. Lateral part of head dark brown with a yellow spot below eye and a yellow band behind eye (Fig. 6). Pronotum dorsal disk trapezoidal, wider than long, its posterior margin straight, usually dark brown with lateral edges yellow (Fig. 4). Lateral lobes of pronotum longer than high, most often uniformly red brown or black dorsally, its ventral margin mostly dark brown, sometimes with a yellow pattern (Fig. 6). Legs: TI with two tympana; inner tympanum covered by a flat sclerotized expansion, its membrane visible along a small longitudinal slit only; outer tympanum ellipsoidal, its membrane transversally plicate in dorsal half. TI with two inner and two outer apical spurs. TII with two inner and two outer spurs. FIII muscular. TIII serrulate on their whole length, slightly furrowed dorsolongitudinally and with four pairs of subapical spurs and three pairs of apical spurs; inner spurs long and curved, outer spurs shorter and straight. Legs I and II light brown to yellow brown, femora with brown spots and longitudinal patterns, tibiae with brown rings. TaIII-1 with 4–5 spines on dorsal outer edge, without spines on dorsal inner edge. TIIIs and tarsomeres brown with spines and spurs with dark apices. FWs short in both sexes, not reaching abdomen mid-length; hind wings absent. Cerci well developed, nearly as long as abdomen. Abdomen: Tergites brown to dark brown, without longitudinal bands.

Male. Metanotal glands absent. Dorsal field of FWs not distinctly longer than lateral field. FWs longer than wide, longer than pronotum dorsal disk. FW venation (Figs 2, 7): 1A vein (file) transverse part straight, variably curved at basal end, bisinuate anteriorly to angle, forming a notch in most species. Genus characterized by a large bean-shaped sclerotization posterior to transverse part of file vein (1A), including base of chords. Diagonal vein straight or faintly sinusoidal, strong basally, fainter posteriorly. Harp triangular, longer than wide, occupying approximately half of dorsal field surface; with a strong characteristic fold along posterior face, carrying diagonal vein and cell c1 and delimiting dorsal field of FW in two distinct parts; harp with a strong transverse oblique vein, bi- or poly-furcated anteriorly; area posterior to diagonal fold with weak reticulated venation, cell alignments almost indistinct except at apex and main longitudinal veins weak except at apex. CuA anterior part strong throughout, straight, slightly curved inward near apex. Mirror (d1) usually not differentiated. Apical field short, including one or two cell alignments. Lateral field with 5–6 strong longitudinal veins; Sc vein without bifurcation. Subgenital plate elongated, clog-shaped, slightly pointed; inner side of subgenital plate with lateral swellings. Epiproct and subgenital plate brown.

Male genitalia: (Figs 8, 11, 15, 20, 24) Pseudepiphallus triangular, variable in length but usually elongate, its basal margin straight or variably indented in the middle, posterior apex usually somewhat truncated, sometimes slightly acute, rarely with paired lophi. Rami very short, usually shorter than half of pseudepiphallus length, parallel to slightly diverging anteriorly. Pseudepiphallic parameres average sized and sclerotized, variable in shape, with posterior apex usually enlarged, their basis strong. Ectophallic apodemes parallel and long, usually reaching beyond anterior margin of pseudepiphallic sclerite. Ectophallic arc well sclerotized, transverse. Ectophallic fold with two ventral sclerites of variable shapes, sometimes fused together. Endophallic sclerite Y-shaped, comprising a long anterior region and a short median expansion and lateral arms posteriorly.

Female. FWs very short, shorter than in male, reaching or slightly surpassing posterior margin of first tergite, close together and usually slightly overlapping at their bases. Dorsal field usually oblique posteriorly (more so in some species than others); dorsal field and lateral field with more or less distinct longitudinal veins (Fig. 9). Dorsal field with cells brown and mottled and veins brown; lateral field with cells brown mottled with gray, and veins brown.

Female genitalia: Ovipositor most often slightly longer than FIII, slightly denticulate on dorsal edge, its apex acute. Female copulatory papilla rounded, almost entirely membranous, sometimes with a basal sclerotized ring; apex rounded, generally folded ventrally (Fig. 10).

Calling song.—Unknown.

Natural history.—The rare information obtained from photographs from iNaturalist suggest that these crickets are found in the leaf litter and in the foliage of low-lying vegetation in forest (Fig. 3).

Included species.—(14 in total; ordered by similarity)

R. leopoldi (Chopard, 1931) **comb. nov.**
R. mamberamo **sp. nov.**
R. yayukae **sp. nov.**
R. faowi **sp. nov.**
R. kencana **sp. nov.**
R. manokwari **sp. nov.**
R. maoke **sp. nov.**
R. biakis **sp. nov.**
R. nabire **sp. nov.**
R. tariku **sp. nov.**
R. albatros **sp. nov.**
R. baduri **sp. nov.**
R. karimui **sp. nov.**
R. newguineae (Bhowmik, 1981) **comb. nov.**

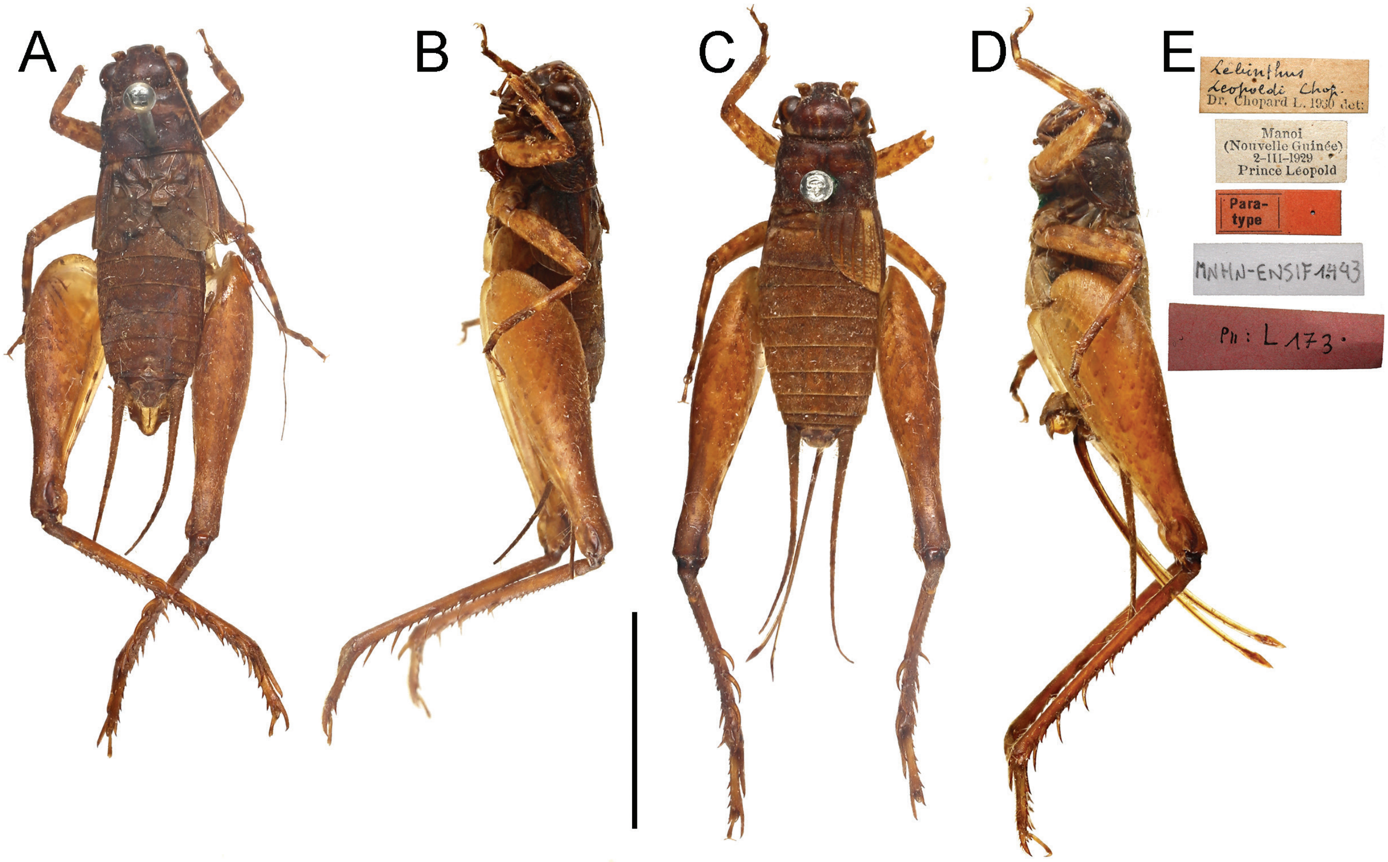

Fig. 1. *R. leopoldi* (Chopard, 1931) **comb. nov.** male (**A, B**) and female (**C, D**) habitus in dorsal (**A, C**) and lateral (**B, D**) views. Paratype labels (**E**). Scale bar: 10 mm.

Rugabinthus leopoldi (Chopard, 1931) comb. nov.

(Figs 1, 3, 4A, 5A, 6A, 7A, 8A, 9A, 10A, 11A, 11B)

Lebinthus leopoldi Chopard, 1931: 7; 1968: 354; Cigliano et al. 2021 (Orthoptera species file online).

Material examined.—**Holotype:** INDONESIA • ♂; West Papua, Manoi [Sorong Manoi]; 2 March 1929; Prince Leopold leg.; RBINS. **Allotype:** INDONESIA • ♀; same information as holotype; RBINS. **Paratypes:** INDONESIA • 3♂, 4♀; same information as holotype; RBINS • 1♂; West Papua, Manoi [Sorong Manoi]; 2 March 1929; Prince Leopold leg.; MNHN-EO-ENSIF1441 • 1♀; same information as holotype; molecular sample L173; MNHN-EO-ENSIF1443 • 1♀; same information as holotype; MNHN-EO-ENSIF1442.

Type locality.—INDONESIA: West Papua: Manoi

Diagnosis.—This species differs from all congeners by male genitalia with pseudepiphallus more rectangular, very elongate, its posterior part curved posteriorly, its apex truncated with small paired apical lophi; lophi triangular with obtuse apex.

Redescription.—Average size among congeners (Fig. 1). Dorsum of head with broad red brown bands barely separated (Fig. 4A). Fastigium red brown (Fig. 4A). Scapes red brown with some dark patches. Fastigium verticis brown with two vertical yellow brown stripes diverging ventrad, frons brown with two yellow brown

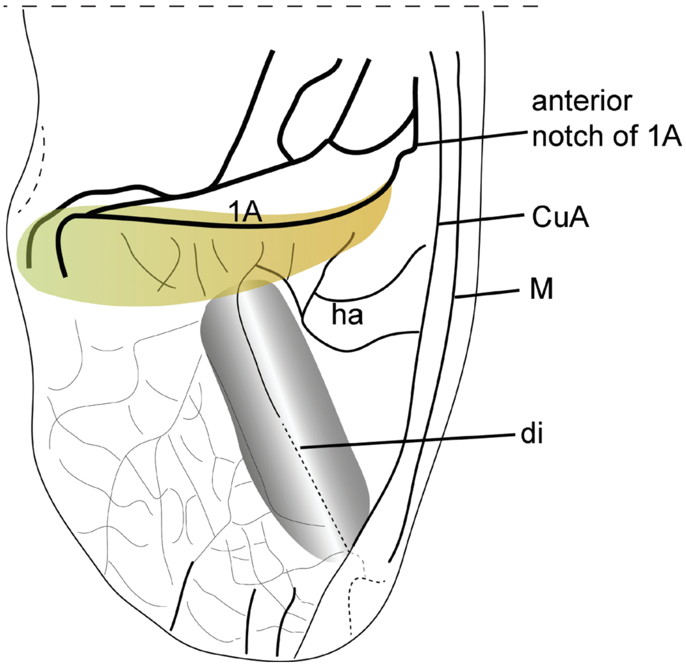

Fig. 2. Schematic venation of male FW of *Rugabinthus*. The gray area represents the diagonal fold carrying the diagonal vein; the yellow area represents the bean-shaped strong sclerotization along 1A vein.

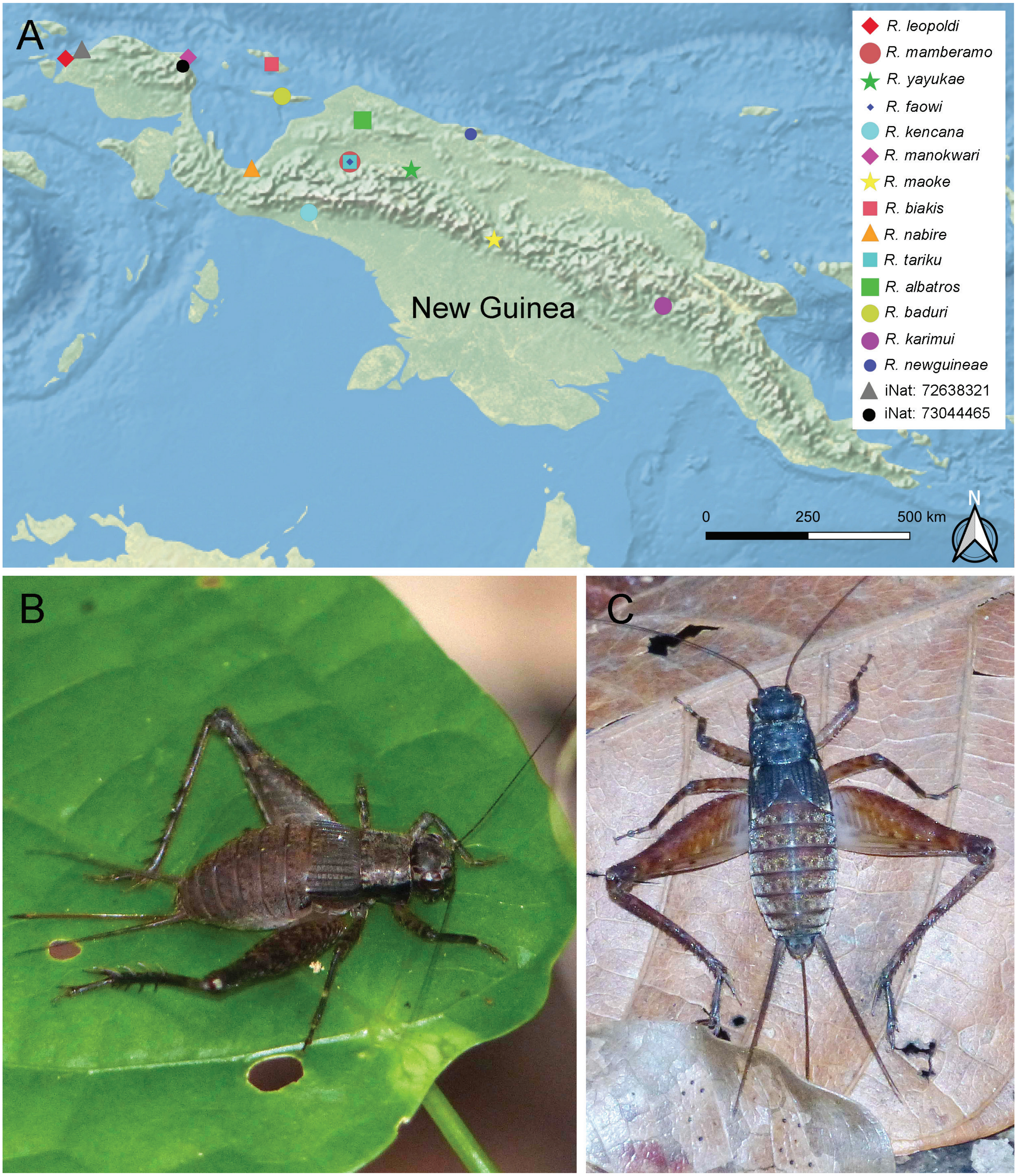

Fig. 3. A. Map of New Guinea island showing the distribution of *Rugabinthus* species; **B.** Female *Rugabinthus* species in their natural habitats in Acemo, South Manokwari (https://www.inaturalist.org/observations/73044465) and **C.** Malagufuk (https://www.inaturalist.org/observations/72638321). Photo credit: Benoît Segerer.

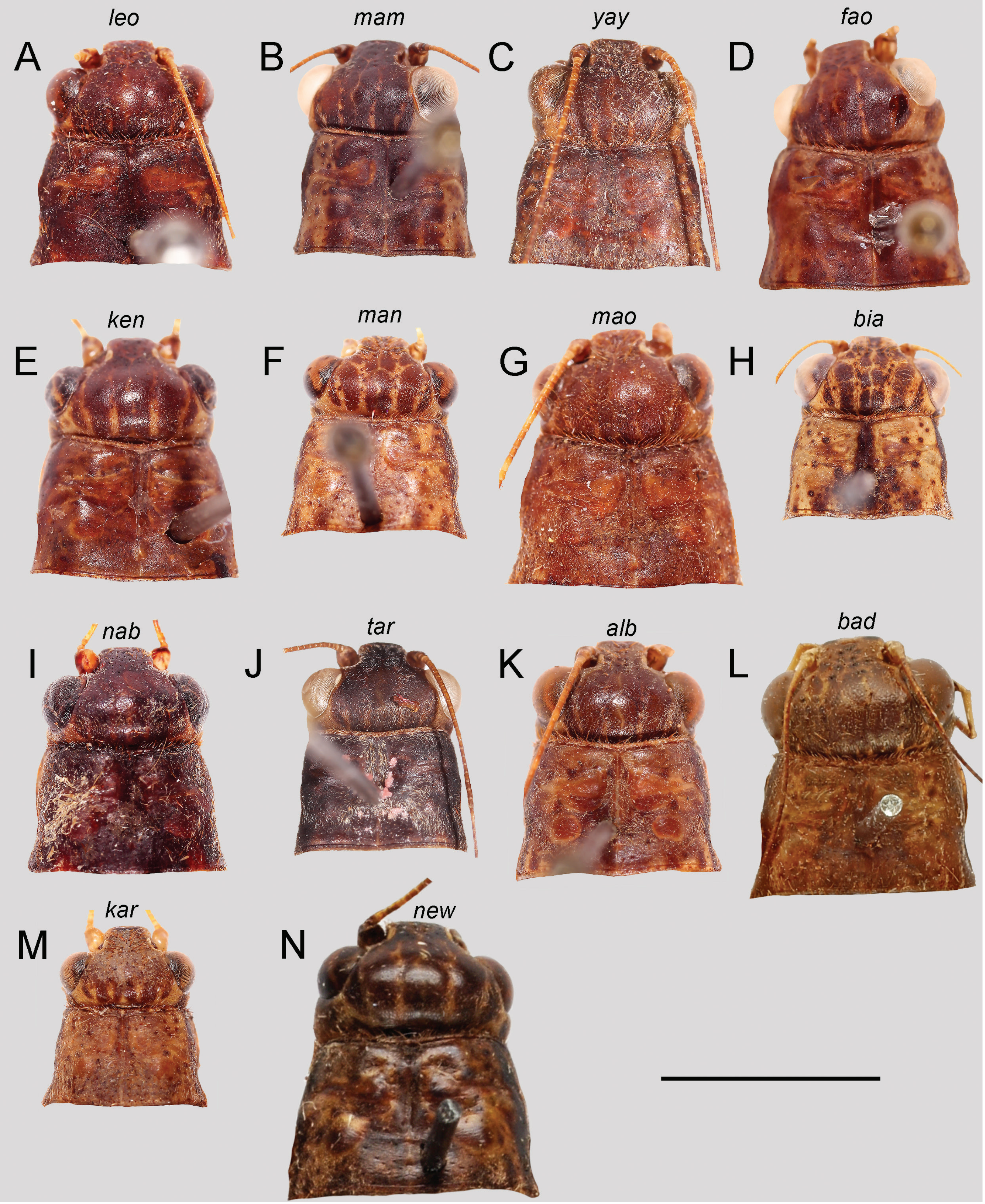

Fig. 4. Head and pronotum in dorsal views: **A.** *R. leopoldi* (Chopard, 1931) **comb. nov.**; **B.** *R. mamberamo* **sp. nov.**; **C.** *R. yayukae* **sp. nov.**; **D.** *R. faowi* **sp. nov.**; **E.** *R. kencana* **sp. nov.**; **F.** *R. manokwari* **sp. nov.**; **G.** *R. maoke* **sp. nov.**; **H.** *R. biakis* **sp. nov.**; **I.** *R. nabire* **sp. nov.**; **J.** *R. tariku* **sp. nov.**; **K.** *R. albatros* **sp. nov.**; **L.** *R. baduri* **sp. nov.**; **M.** *R. karimui* **sp. nov.**; **N.** *R. newguineae* (Bhowmik, 1981) **comb. nov.** Scale bar: 5 mm.

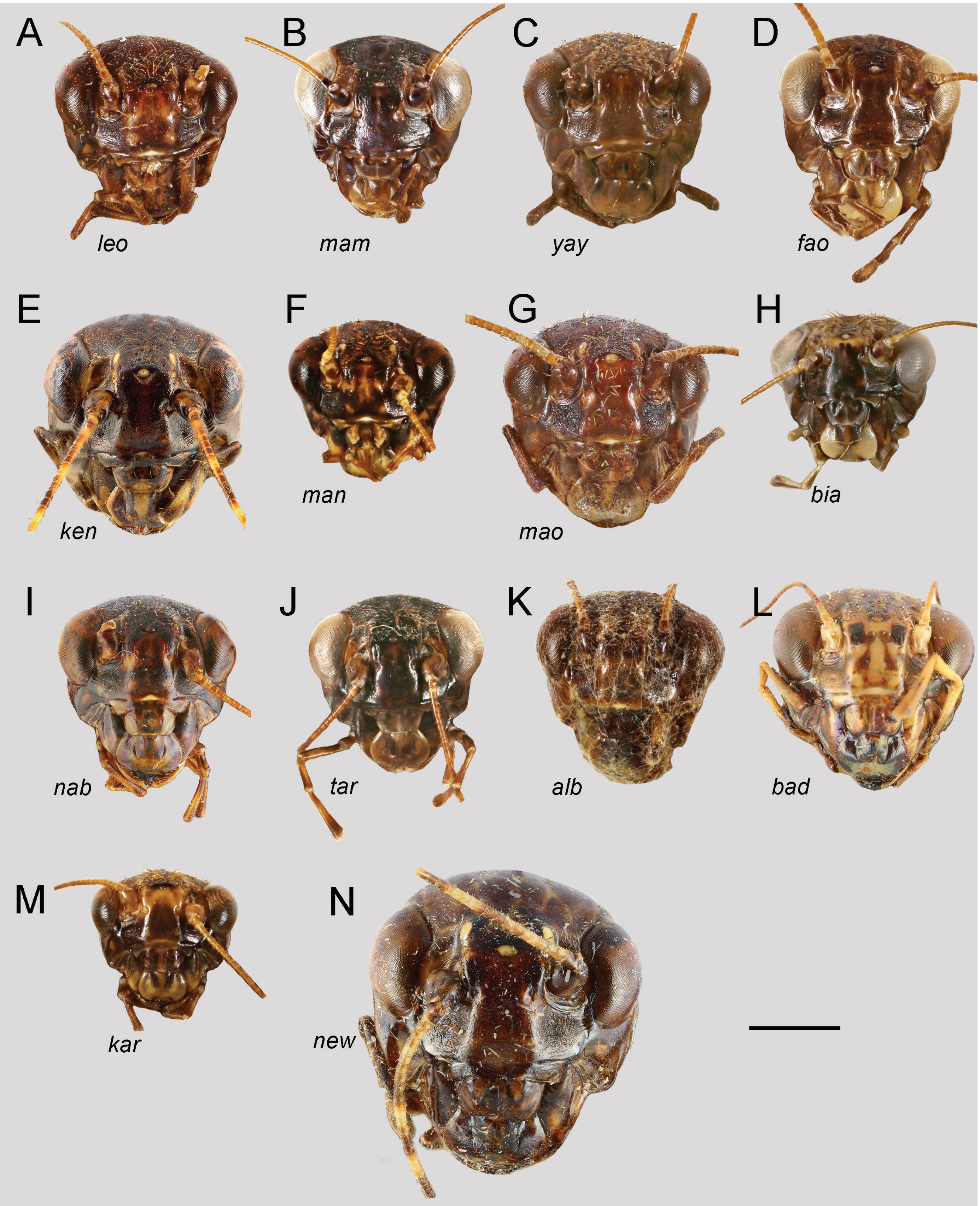

Fig. 5. Face: **A.** *R. leopoldi* (Chopard, 1931) **comb. nov.**; **B.** *R. mamberamo* **sp. nov.**; **C.** *R. yayukae* **sp. nov.**; **D.** *R. faowi* **sp. nov.**; **E.** *R. kencana* **sp. nov.**; **F.** *R. manokwari* **sp. nov.**; **G.** *R. maoke* **sp. nov.**; **H.** *R. biakis* **sp. nov.**; **I.** *R. nabire* **sp. nov.**; **J.** *R. tariku* **sp. nov.**; **K.** *R. albatros* **sp. nov.**; **L.** *R. baduri* **sp. nov.**; **M.** *R. karimui* **sp. nov.**; **N.** *R. newguineae* (Bhowmik, 1981) **comb. nov.** Scale bar: 2 mm.

Fig. 6. Head and pronotum in lateral views: **A.** *R. leopoldi* (Chopard, 1931) **comb. nov.**; **B.** *R. mamberamo* **sp. nov.**; **C.** *R. yayukae* **sp. nov.**; **D.** *R. faowi* **sp. nov.**; **E.** *R. kencana* **sp. nov.**; **F.** *R. manokwari* **sp. nov.**; **G.** *R. maoke* **sp. nov.**; **H.** *R. biakis* **sp. nov.**; **I.** *R. nabire* **sp. nov.**; **J.** *R. tariku* **sp. nov.**; **K.** *R. albatros* **sp. nov.**; **L.** *R. baduri* **sp. nov.**; **M.** *R. karimui* **sp. nov.**; **N.** *R. newguineae* (Bhowmik, 1981) **comb. nov.** Scale bar: 5 mm.

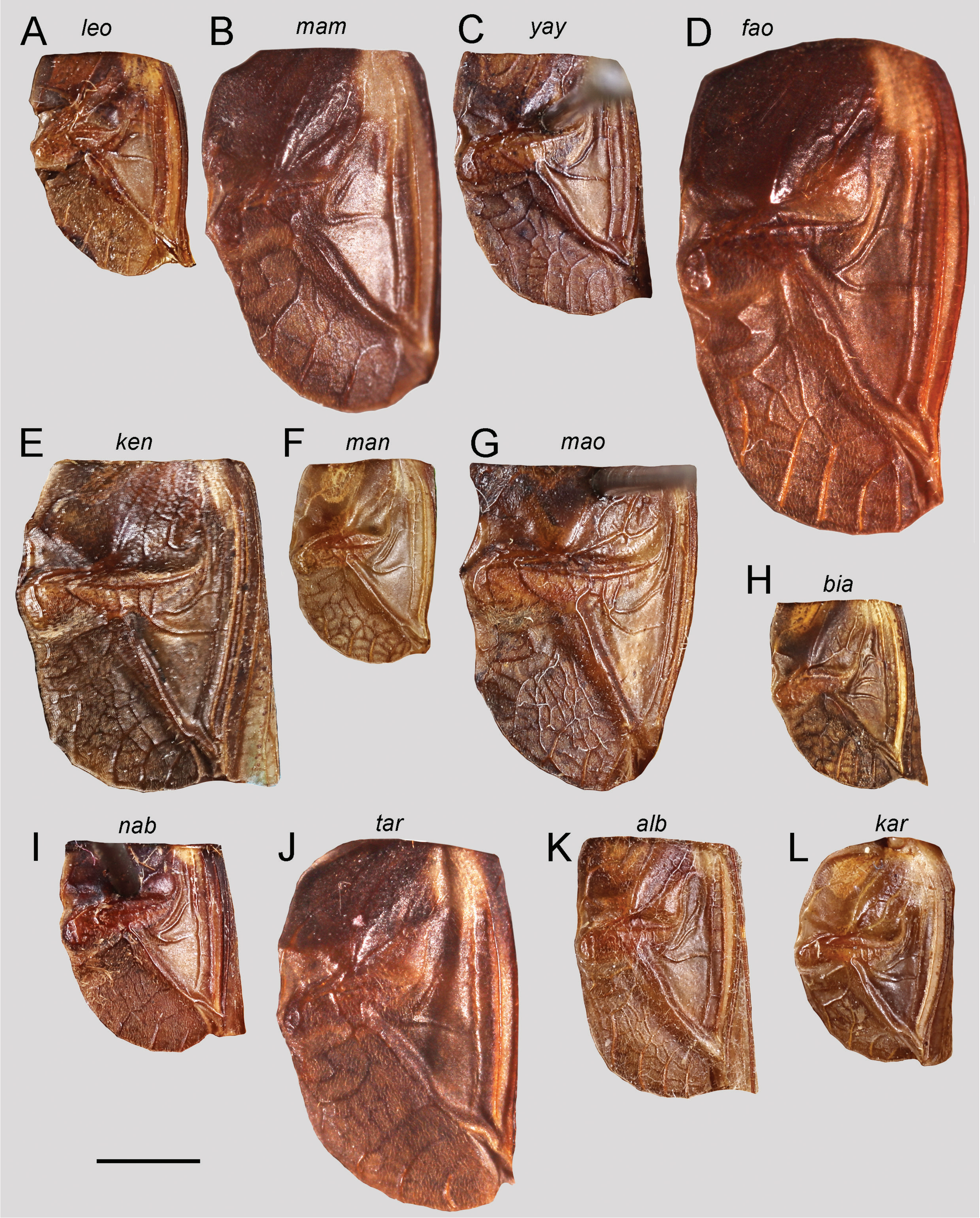

Fig. 7. Male FW in dorsal views: **A.** *R. leopoldi* (Chopard, 1931) **comb. nov.**; **B.** *R. mamberamo* **sp. nov.**; **C.** *R. yayukae* **sp. nov.**; **D.** *R. faowi* **sp. nov.**; **E.** *R. kencana* **sp. nov.**; **F.** *R. manokwari* **sp. nov.**; **G.** *R. maoke* **sp. nov.**; **H.** *R. biakis* **sp. nov.**; **I.** *R. nabire* **sp. nov.**; **J.** *R. tariku* **sp. nov.**; **K.** *R. albatros* **sp. nov.**; **L.** *R. karimui* **sp. nov.** Scale bar: 2 mm.

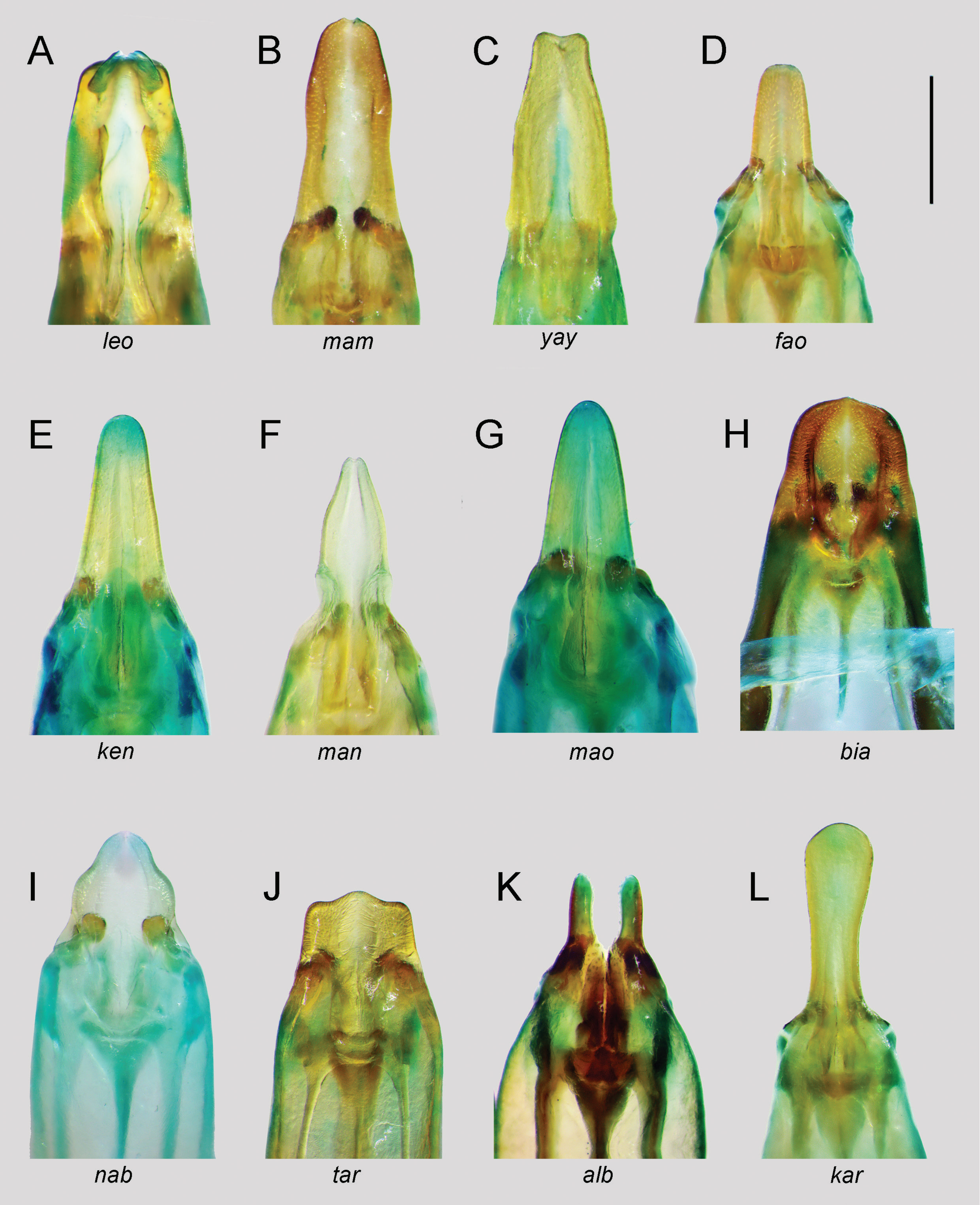

Fig. 8. Male genitalia in dorsal view; posterior apex of pseudepiphallus: **A.** *R. leopoldi* (Chopard, 1931) **comb. nov.**; **B.** *R. mamberamo* **sp. nov.**; **C.** *R. yayukae* **sp. nov.**; **D.** *R. faowi* **sp. nov.**; **E.** *R. kencana* **sp. nov.**; **F.** *R. manokwari* **sp. nov.**; **G.** *R. maoke* **sp. nov.**; **H.** *R. biakis* **sp. nov.**; **I.** *R. nabire* **sp. nov.**; **J.** *R. tariku* **sp. nov.**; **K.** *R. albatros* **sp. nov.**; **L.** *R. karimui* **sp. nov.** Scale bar: 0.5 mm.

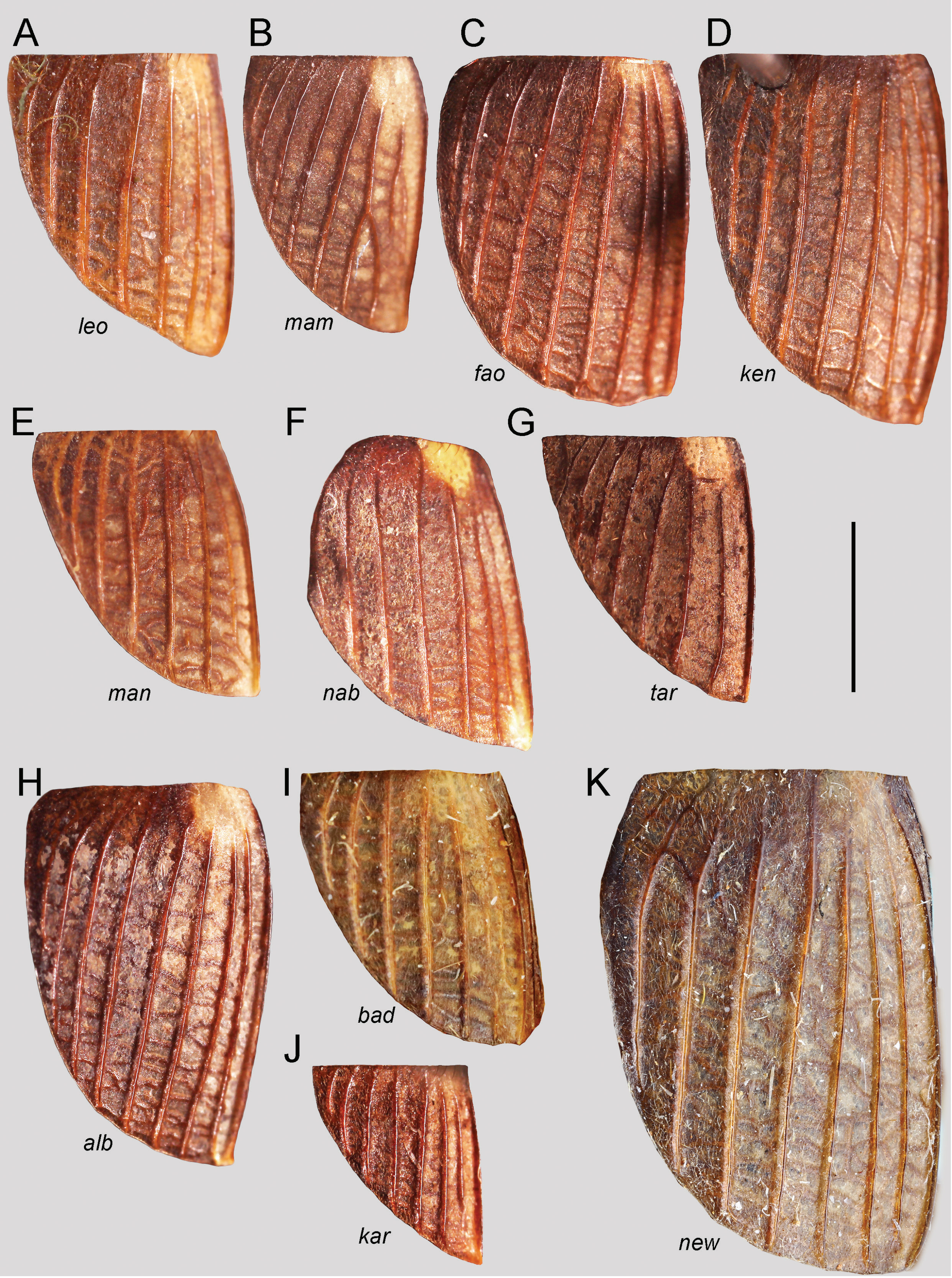

Fig. 9. Female FW in dorsal views: **A.** *R. leopoldi* (Chopard, 1931) **comb. nov.**; **B.** *R. mamberamo* **sp. nov.**; **C.** *R. faowi* **sp. nov.**; **D.** *R. kencana* **sp. nov.**; **E.** *R. manokwari* **sp. nov.**; **F.** *R. nabire* **sp. nov.**; **G.** *R. tariku* **sp. nov.**; **H.** *R. albatros* **sp. nov.**; **I.** *R. baduri* **sp. nov.**; **J.** *R. karimui* **sp. nov.**; **K.** *R. newguineae* (Bhowmik, 1981) **comb. nov.** Scale bar: 2 mm.

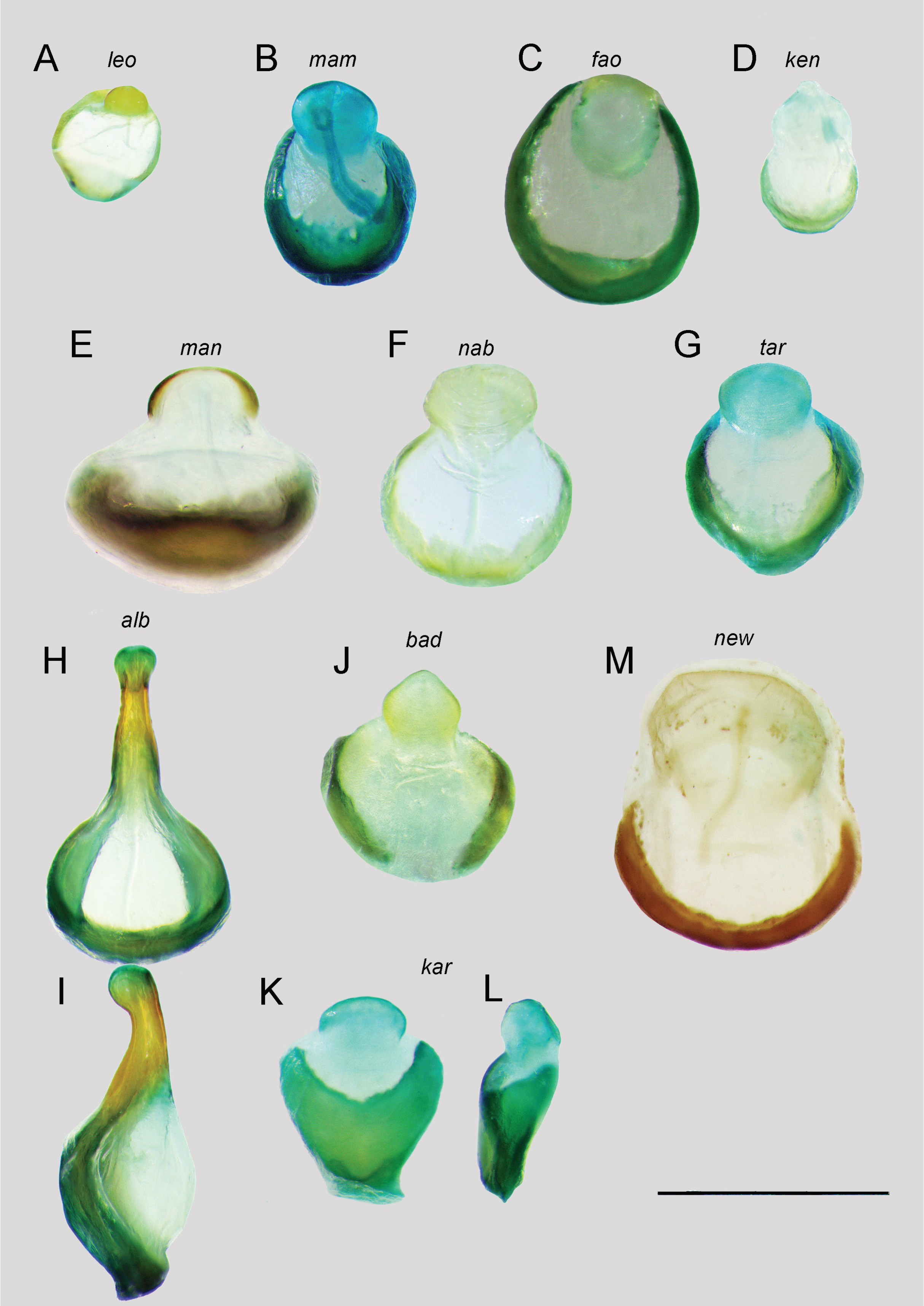

Fig. 10. Female copulatory papilla in ventral (all except **I, K**) and lateral (**I, K**) views. **A.** *R. leopoldi* (Chopard, 1931) **comb. nov.**; **B.** *R. mamberamo* **sp. nov.**; **C.** *R. faowi* **sp. nov.**; **D.** *R. kencana* **sp. nov.**; **E.** *R. manokwari* **sp. nov.**; **F.** *R. nabire* **sp. nov.**; **G.** *R. tariku* **sp. nov.**; **H, I.** *R. albatros* **sp. nov.**; **J.** *R. baduri* **sp. nov.**; **K, L.** *R. karimui* **sp. nov.**; **M.** *R. newguineae* (Bhowmik, 1981) **comb. nov.** Scale bar: 0.5 mm.

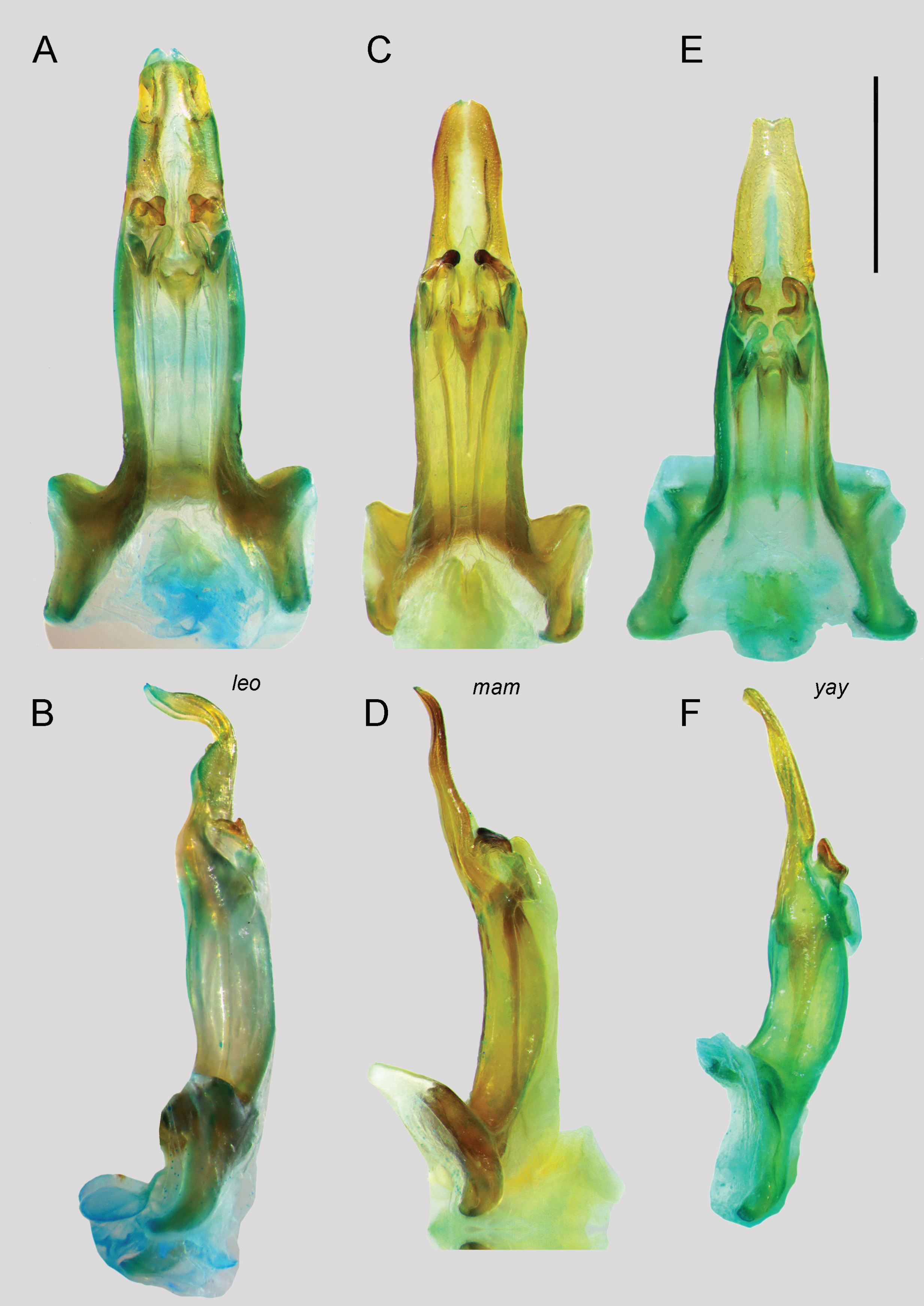

Fig. 11. Male genitalia ventral (**A**, **C**, **E**) and lateral (**B**, **D**, **F**) views: **A**, **B.** *R. leopoldi* (Chopard, 1931) **comb. nov.**; **C**, **D.** *R. mamberamo* **sp. nov.**; **E**, **F.** *R. yayukae* **sp. nov.** Scale bar: 1 mm.

spots ventral of stripes; clypeus sometimes darkened, mouthparts yellow brown to red brown (Fig. 5A). Pronotal disk red brown with lighter lateral ovular spots near anterior half and some faint lighter spots along posterior margin (Fig. 4A). Lateral lobes of pronotum dark brown, with yellow spot at anterior ventral corner (Fig. 6A). FIs and FIIs generally yellow brown with brown spots and rings; TIs and TIIs brown with two yellow brown rings. FIIIs brown, knees slightly darker.

Male. FW reaching apex of third tergite; apex rounded. FW coloration (Fig. 7A): Dorsal field cells and veins mostly brown; area between M and R yellow brown; basal area with a wide cream-colored spot on external corner. Lateral field dark brown. FW venation typical of genus; 1A slightly bisinuate anterior to angle; oblique vein trifurcated, posterior branch straight and transverse.

Male genitalia: (Figs 8A, 11A, 11B) Pseudepiphallus forming a very elongate rectangle, its basal margin slightly indented in the middle, lateral margins widened basally, forming wide shoulders carrying base of rami; posterior part of pseudepiphallus narrow, distinctly curved dorsally posterior to pseudepiphallic parameres, with two short dorsal pre-apical expansions (Fig. 8A); posterior apex truncated, posterior apex with small paired lophi, triangular with obtuse apex. Rami wide, very short, way shorter than half the pseudepiphallus length, diverging anteriorly, with posterior end protruding externally. Pseudepiphallic parameres strongly bent in basal half (~90°), with posterior apex enlarged, bean shaped. Ectophallic apodemes thin, parallel, and long, reaching beyond anterior margin of pseudepiphallic sclerite. Endophallic sclerite with anterior region very short and not reaching anterior margin of pseudepiphallic sclerite, with lateral arms elongated, tongue-shaped, and longer than median expansion.

Female. FW reaching base of third tergite, with basal area with a cream-colored oblong spot without clearly defined margin, forming two indistinct spots near base and apex; lateral field dark brown (Fig. 9A).

Female genitalia: Ovipositor about as long as FIII. Copulatory papilla very small, rounded, apex folded ventrally, short, pointed; dorsal face with a sclerotized area; ventro-anterior end base forming an oval ring (Fig. 10A).

Measurements.—See Table 1.

***Rugabinthus mamberamo* sp. nov.**

http://zoobank.org/31AB9356-DC05-4203-AD3B-F7257C4B611E
(Figs 3, 4B, 5B, 6B, 7B, 8B, 9B, 10B, 11C, 11D, 12)

Material examined.—**Holotype:** INDONESIA • ♂; West Papua, Fawi [Faowi] village in upper part of Tariku River (tributary of Mamberamo River), partly low-lying forest and partly forest on hills; 29 January–17 February 2012; A. Gorochov leg.; molecular sample L94; ZIN. **Paratype:** INDONESIA • 1♀; same information as holotype; MNHN-EO-ENSIF1758.

Type locality.—INDONESIA: West Papua: Faowi

Etymology.—This species is named after Mamberamo River; noun in apposition. The name is derived from the main river rather than the tributary Tariku River because it has more elongated and larger male genitalia compared to the sympatric species *R. tariku* **sp. nov.**

Diagnosis.—This new species differs from all congeners by male genitalia, with pseudepiphallus very slender and very elongate, close to that of *R. leopoldi* from which it differs by posterior apex forming a long flat spoon slightly curved dorsally near apex, looking like a simpler version of *R. leopoldi*, with thinner pre-apical expansions, apex somewhat truncated, without lophi; pseudepiphal-

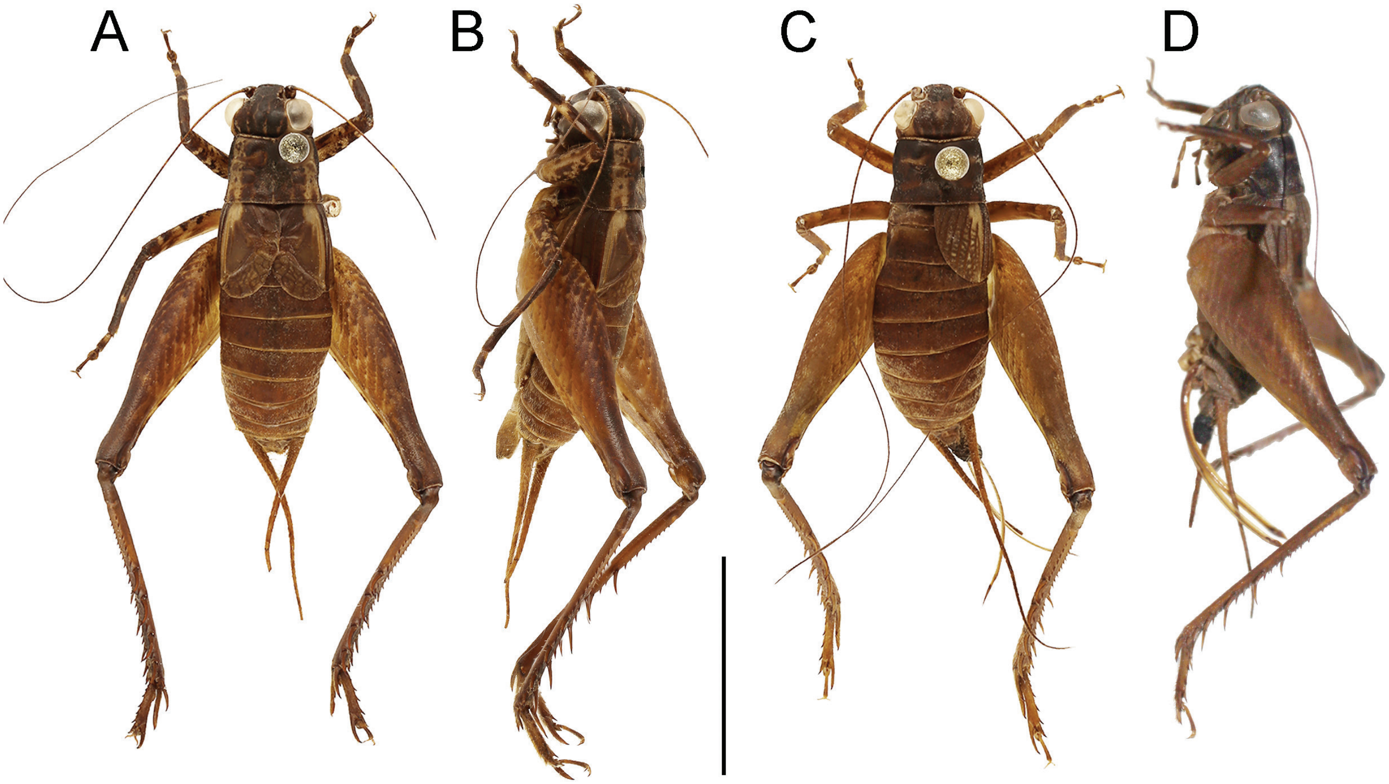

Fig. 12. *R. mamberamo* **sp. nov.** male (**A, B**) and female (**C, D**) habitus in dorsal (**A, C**) and lateral (**B, D**) views. Scale bar: 10 mm.

Table 1. Measurements (in mm).

	PronL	PronW	FWL	FWW	FIIIL	FIIIW	TIIIL	OL
***R. leopoldi* (Chopard, 1931)**								
Male paratype MNHN1441	3.0	4.9	4.5	3.0	13.7	3.9	10.4	-
Female paratype MNHN1443	3.3	4.9	3.8	2.8	14.3	4.5	12.2	14.1
Female paratype MNHN1442	3.2	5.0	4.0	2.6	14.2	4.5	10.9	14.8
***R. mamberamo* sp. nov.**								
Male holotype	3.0	4.4	4.3	2.8	12.4	3.6	11.0	-
Female paratype	3.0	4.4	3.7	2.6	12.3	3.9	10.7	9.1
***R. yayukae* sp. nov.**								
Male holotype	2.8	4.8	5.7	3.8	13.9	4.1	10.1	-
Males (n = 4)	2.6–3.3 (2.9)	4.7–5.0 (4.8)	4.9–6.0 (5.5)	3.8–4.5 (4.0)	13.4–15.6 (14.2)	4.1–4.7 (4.3)	10.1–12.6 (11.7)	-
***R. faowi* sp. nov.**								
Male holotype	2.9	3.6	4.6	2.6	11.9	3.7	10.7	-
Males (n = 4)	2.9–3.3 (3.0)	3.6–5.2 (4.6)	4.6–6.7 (5.8)	2.6–3.5 (3.2)	11.9–15.8 (13.9)	3.7–4.5 (4.1)	10.7–13.1 (11.9)	-
Females (n = 4)	3.4–3.6 (3.5)	5.0–5.3 (5.1)	4.4–4.6 (4.5)	2.8–2.8 (2.6)	16.4–17.0 (16.7)	4.9–5.2 (5.0)	15.0–15.6 (15.4)	19.2–21.0 (20.2)
***R. kencana* sp. nov.**								
Male holotype	3.0	5.0	6.9	5.0	-	-	-	-
Males (n = 2)	3.0–3.4 (3.2)	5.0–5.1 (5.13	6.4–6.9 (6.7)	4.3–5.0 (4.7)	14.9 (14.9)	4.6 (4.6)	13.9 (13.9)	-
Female paratype	3.2	5.1	4.5	2.8	16.2	4.7	14.1	17.9
***R. manokwari* sp. nov.**								
Male holotype	2.9	4.4	4.1	3.2	11.7	3.8	10.4	-
Female paratype	2.9	4.4	3.5	2.5	13.4	3.7	12.1	10.9
***R. maoke* sp. nov.**								
Male holotype	3.4	5.8	6.5	4.7	18.0	5.2	11.0	-
Male paratype	3.6	5.5	6.5	5.0	17.3	4.9	15.8	-
***R. biakis* sp. nov.**								
Male holotype	2.5	3.9	3.9	2.7	10.7	2.7	8.6	-
Males (n = 4)	2.4–2.5 (2.5)	3.9–4.0 (4.0)	3.7–2.4 (3.9)	2.7 (2.7)	10.4–11.3 (10.8)	2.7–3.5 (3.1)	7.9–9.1 (8.5)	-
***R. nabire* sp. nov.**								
Male holotype	3.1	4.5	4.4	3.1	12.8	4.0	11.1	-
Males (n = 3)	2.8–3.1 (3.0)	4.3–4.7 (4.6)	4.1–4.4 (4.3)	3.1–3.4 (3.3)	12.8 (12.8)	3.8–4.0 (3.9)	11.0–11.1 (11.1)	-
Female paratype	3.0	4.6	4.4	2.8	15.2	3.1	11.5	13.6
***R. tariku* sp. nov.**								
Male holotype	2.7	4.0	4.3	2.8	12.1	3.1	9.8	-
Males (n = 4)	2.6–3.0 (2.7)	4.0–4.4 (4.2)	4.2–4.7 (4.4)	2.3–2.8 (2.6)	11.8–12.6 (12.2)	3.1–3.8 (3.6)	9.8–10.7 (10.2)	-
Female (n = 2)	2.8–3.2 (3.0)	4.0–4.7 (4.4)	3.5 (3.5)	2.7(2.7)	12.2–13.2 (12.7)	3.8 (3.8)	10.8–11.9 (11.4)	9.5–10.8 (10.2)
***R. albatros* sp. nov.**								
Male holotype	2.9	4.7	5.8	3.5	15.7	4.6	13.0	-
Males (n = 3)	2.9–3.1 (3.0)	4.5–4.8 (4.7)	5.2–5.8 (5.5)	3.0–3.5 (3.3)	14.8–15.7 (15.4)	4.6–4.7 (4.6)	12.5–13.7 (13.0)	-
Female paratype	3.1	4.8	4.7	2.8	14.2	4.6	12.9	19.0
***R. baduri* sp. nov.**								
Female holotype	3.2	5.2	3.5	2.5	13.0	4.5	10.4	13.4
***R. karimui* sp. nov.**								
Male holotype	2.0	3.6	3.7	3.0	9.5	3.3	8.0	-
Male paratype	2.7	3.9	4.2	2.9	8.8	2.9	8.1	-
Female paratype	2.3	3.2	2.4	2.0	7.7	3.0	7.8	8.0

lic parameres stout, weakly curved, apex strongly sclerotized and rounded. From the sympatric species *R. tariku* **sp. nov.**, the new species differs by larger size and by male and female genitalia.

Description.—Average sized among congeners (Fig. 12). Dorsum of head with broad red brown bands narrowly separated (Fig. 4B). Fastigium red brown (Fig. 4B). Scapes dark brown. Fastigium verticis and frons dark brown, frons without spots; clypeus and mouthparts dark brown, labrum yellow brown (Fig. 5B). Pronotal disk dark red brown, lateral parts yellow brown mottled with red brown patterns (Fig. 4B). Lateral lobes of pronotum dark brown, distinctly darker than disk (Fig. 6B). FIs and FIIs yellow brown with dense dark spots and patterns; TIs and TIIs dark brown with a cream-colored spot or incomplete ring in middle. FIIIs brown, knees dark brown to black. Tergites brown, with posterior margin darker.

Male. FWs reaching middle of third abdominal tergite. FW coloration (Fig. 7B): Dorsal field cells and veins mostly brown; with area between M and R infumate cream-colored; basal area with a medium cream-colored spot on external corner. Lateral field brown in dorsal half, gray brown in ventral half. FW venation typical of genus; 1A angle broken by a flat segment; oblique vein posterior branch almost straight. Apical field very small, with only one straight cell alignment posterior to D alignment. Apex of dorsal field rounded.

Male genitalia: (Figs 8B, 11C, 11D) Pseudepiphallus very slender and elongate, very sclerotized; slightly concave in lateral view, raised dorsally at base and apex; its basal margin almost straight, with a dorsal sclerotized plate; widened laterally, forming wide shoulders carrying bases of rami; lateral margins substraight; posterior part of pseudepiphallus elongate, forming a flat narrow spoon slightly concave, with two thin dorsal pre-apical expansions (Fig. 11C); posterior apex somewhat truncated, without lophi. Rami very short, way shorter than half the pseudepiphallus length. Pseudepiphallic parameres stout, weakly curved, their apex strongly sclerotized and rounded. Endophallic sclerite narrow, Y-shaped, with anterior region short and not reaching anterior margin of pseudepiphallic sclerite, with lateral arms elongated and slender, without median posterior expansion.

Female. FWs slightly surpassing second tergite. Dorsal field with a cream-colored oval spot at base without clearly defined margin (Fig. 9B).

Female genitalia: Ovipositor distinctly shorter than FIII. Copulatory papilla globular, its basal part with an irregular sclerotization forming a basal rim, with a large, rounded apex, mostly membranous and curved ventrally (Fig. 10B).

Measurements.—See Table 1.

Rugabinthus yayukae sp. nov.

http://zoobank.org/F2E2AF2E-A052-4128-A8F2-2E050707A859
(Figs 3, 4C, 5C, 6C, 7C, 8C, 11E, 11F, 13)

Material examined.—**Holotype:** INDONESIA • ♂; Mountain slope above Bernhard Camp, 750 m; 19 March 1939; L. J. Toxopeus leg.; MZB-ORTH10791. **Paratypes:** INDONESIA • 1♂; Mountain slope above Bernhard Camp, 100 m; 8? April 1939; L. J. Toxopeus leg.; molecular sample L178; MZB-ORHT9414 • 1♂; Araucaria Camp 800 m; 3 March 1939; L. J. Toxopeus leg. (MZB-ORHT 9417); molecular sample L212; MNHN-EO-ENSIF1728 • 1♂; N. Guinea, Bor?, ca. 400 m?; 8 April 1911; Dr P. N. Kampen Ned N.W Guinea Exp. leg.; RMNH.

Type locality.—INDONESIA: West Papua, Bernhard Camp.

Etymology.—The species is dedicated to Prof. Yayuk R. Suhardjono from the Zoological Museum, Cibinong Science Centre in Jakarta-Bogor (Indonesia).

Diagnosis.—This new species differs from all congeners by male genitalia, with characteristic shape of pseudepiphallus, its apical part tapering into a subacute apex and pseudepiphallic parameres including a median inner process and a triangular apex. The new species is close to *R. faowi* **sp. nov.** by general shape of male genitalia and shape of endophallic sclerite but differs by apex of pseudepiphallus and pseudepiphallic parameres.

Description.—Average to large sized among congeners (Fig. 13). Dorsum of head with broad red brown bands barely separated (Fig. 4C). Fastigium red brown (Fig. 4C). Scapes dark brown. Antennae yellow brown basally, distally brown with yellow rings. Fastigium verticis red brown with a faint yellow brown T-shaped pattern; frons brown without spots; clypeus and mouthparts brown (Fig. 5C). Pronotal disk red brown with very few irregular yellow brown patterns, with a yellow brown stripe near the latero-posterior margin (Fig. 4C). Lateral lobe of pronotum slightly darker than disk (Fig. 6C). FIs and FIIs brown with few spots; TIs and TIIs dark brown with one yellow brown ring in middle. FIIIs brown, knees dark brown to black. Tergites brown, with posterior margin darker.

Male. FWs reaching middle of fourth abdominal tergite. FW coloration (Fig. 7C): Dorsal field cells and veins mostly brown, with a faint spot on external corner. Lateral field red brown, with ventral margin cream-colored. FW venation typical of genus, 1A slightly bisinuate anterior to angle. Harp longer than wide; posterior branch of oblique vein almost straight and transverse. Mirror (d1) slightly differentiated. Apical field with three parallel cell align-

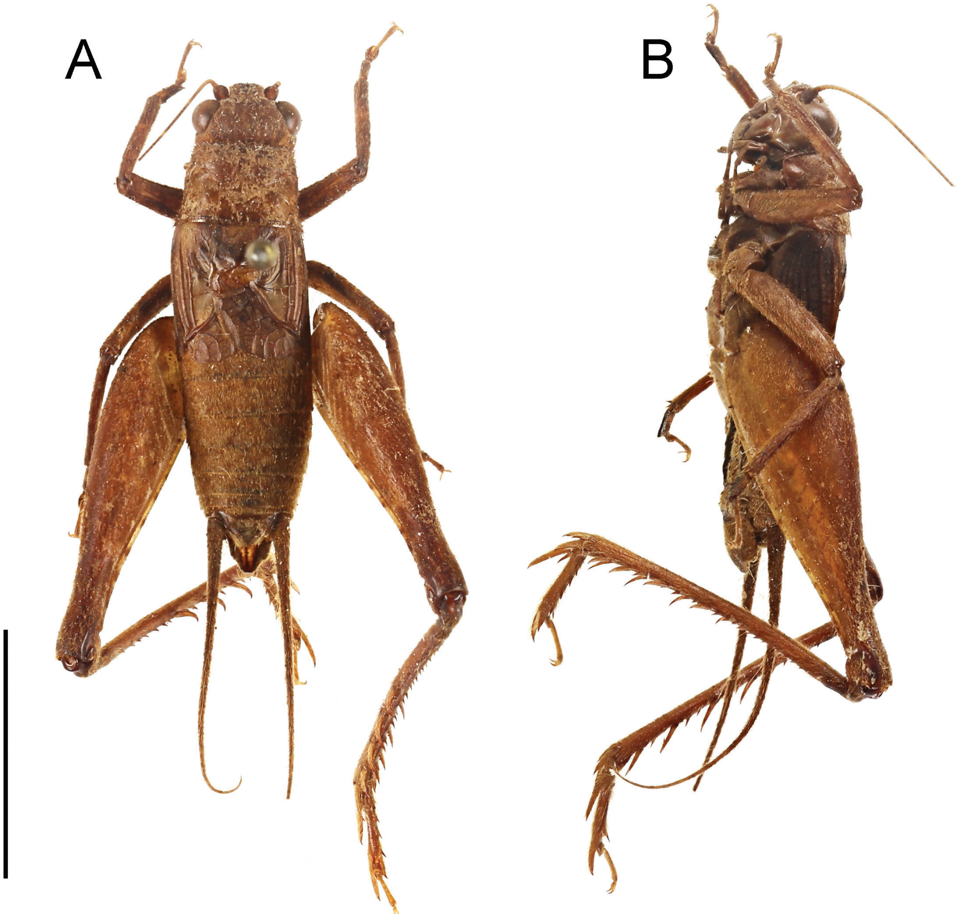

Fig. 13. *R. yayukae* **sp. nov.** male habitus in dorsal (**A**) and lateral (**B**) views. Scale bar: 10 mm.

ments (E–F–G) posterior to mirror. Apex of dorsal field obliquely rounded. Lateral field with projections of Sc slightly sinuous.

Male genitalia: (Figs 8C, 11E, 11F) Pseudepiphallus elongate, not convex dorsally, its basal margin straight, slightly widened laterally at base of rami and raised dorsally; lateral margin at basal half parallel and wider, tapering in middle into apical half; apical half faintly tapering then straightening at apex; posterior apex truncated and faintly indented in the middle. Rami very short, much shorter than half the pseudepiphallus length. Pseudepiphallic parameres C-shaped, with inner lobe in middle with apical half triangular, tapering into a subacute apex; inner lobe straight, perpendicular to paramere. Ectophallic apodemes parallel and long, usually reaching beyond anterior margin of pseudepiphallic sclerite. Endophallic sclerite with anterior region elongate, almost reaching anterior margin of pseudepiphallic sclerite; posterior part with short triangular lateral arms, without median expansion.

Female. Unknown.

Measurements.—See Table 1.

Rugabinthus faowi sp. nov.

http://zoobank.org/40095825-464D-47BA-8171-19AE6950E3D9
(Figs 3, 4D, 5D, 6D, 7D, 8D, 9C, 10C, 14, 15A, 15B)

Material examined.—**Holotype**: INDONESIA • ♂; West Papua, Fawi [Faowi] village in upper part of Tariku River (tributary of Mamberamo River), partly low-lying forest and partly forest on hills; 29 January–17 February 2012; A. Gorochov leg.; molecular sample L92; ZIN. **Paratypes:** INDONESIA • 1♀; same information as holotype; ZIN • 4♂, 6♀; same information as holotype; ZIN • 1♂, 1♀; same information as holotype; MZB • 1♂, 1♀; same information as holotype; MNHN-EO-ENSIF11144–ENSIF11145.

Type locality.—INDONESIA: West Papua: Faowi.

Etymology.—This species is named after the type locality Faowi; noun in apposition. Even though three species of *Rugabinthus* are found in Faowi, this species was the most abundantly collected.

Diagnosis.—This new species is close to *R. manokwari* **sp. nov.**, *R. kencana* **sp. nov.,** and *R. maoke* **sp. nov.** in terms of male FW venation with 1A not indented, and by male genitalia with pseudepiphallus triangular. This new species differs from *R. manokwari* **sp. nov.** by larger size, darker coloration, apex of pseudepiphallus not indented, and slight difference in shape of pseudepiphallic parameres. This new species differs from *R. kencana* **sp. nov.** and *R. maoke* **sp. nov.** by lateral margins of pseudepiphallus more indented in the middle and shape of pseudepiphallic parameres.

Description.—Large sized among congeners (Fig. 14). Dorsum of head with broad red brown bands narrowly separated (Fig. 4D). Fastigium red brown (Fig. 4D). Scapes red brown. Fastigium verticis and frons brown, frons with very faint light spots; clypeus and mouthparts brown, labrum distinctly cream-colored (Fig. 5D). Pronotal disk red brown with some irregular yellow brown patterns laterally and near the anterior margin, with lighter lateral ovular spots near anterior half and with a yellow brown stripe near the latero-posterior margin (Fig. 4D). Lateral lobes not darker

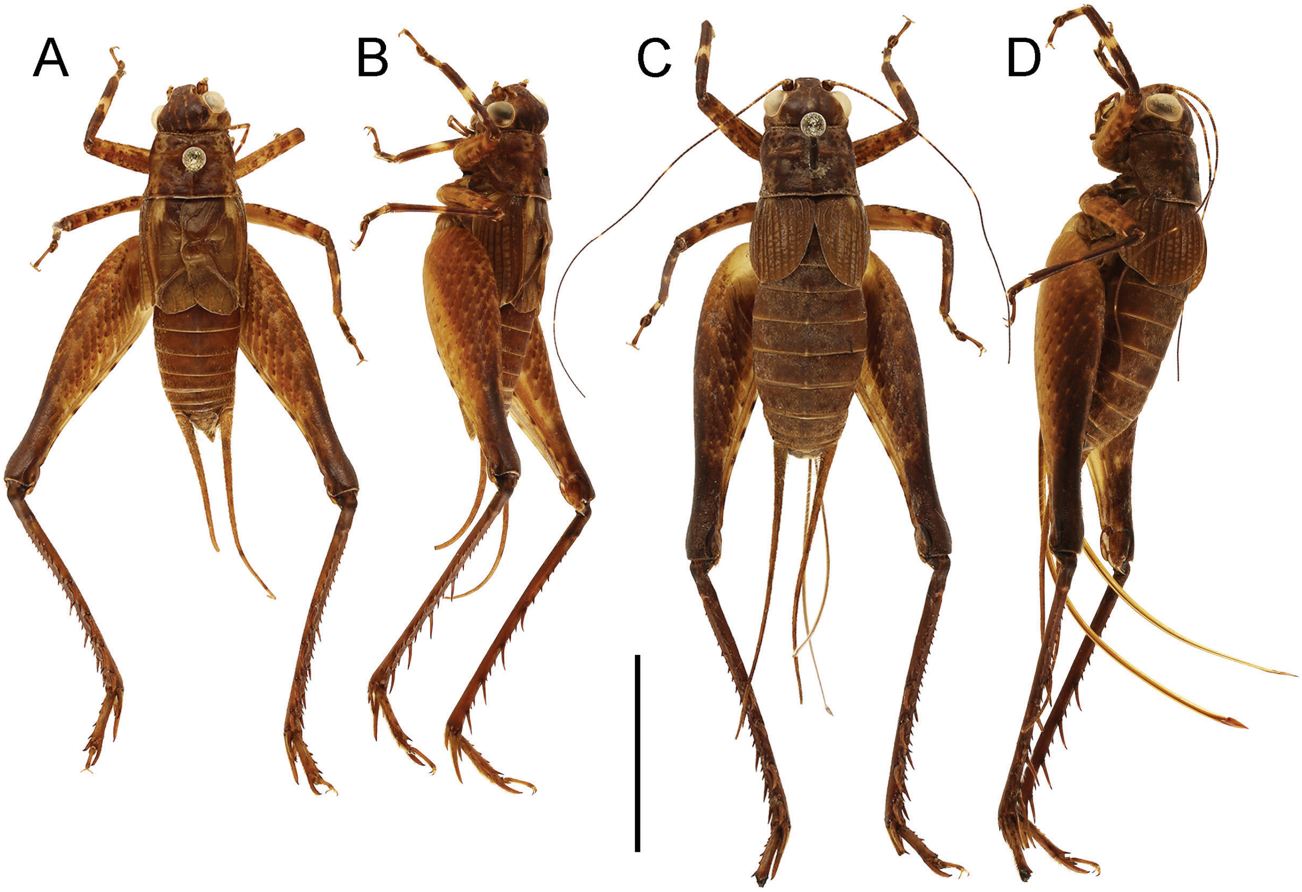

Fig. 14. *R. faowi* **sp. nov.** male (**A**, **B**) and female (**C**, **D**) habitus in dorsal (**A**, **C**) and lateral (**B**, **D**) views. Scale bar: 10 mm.

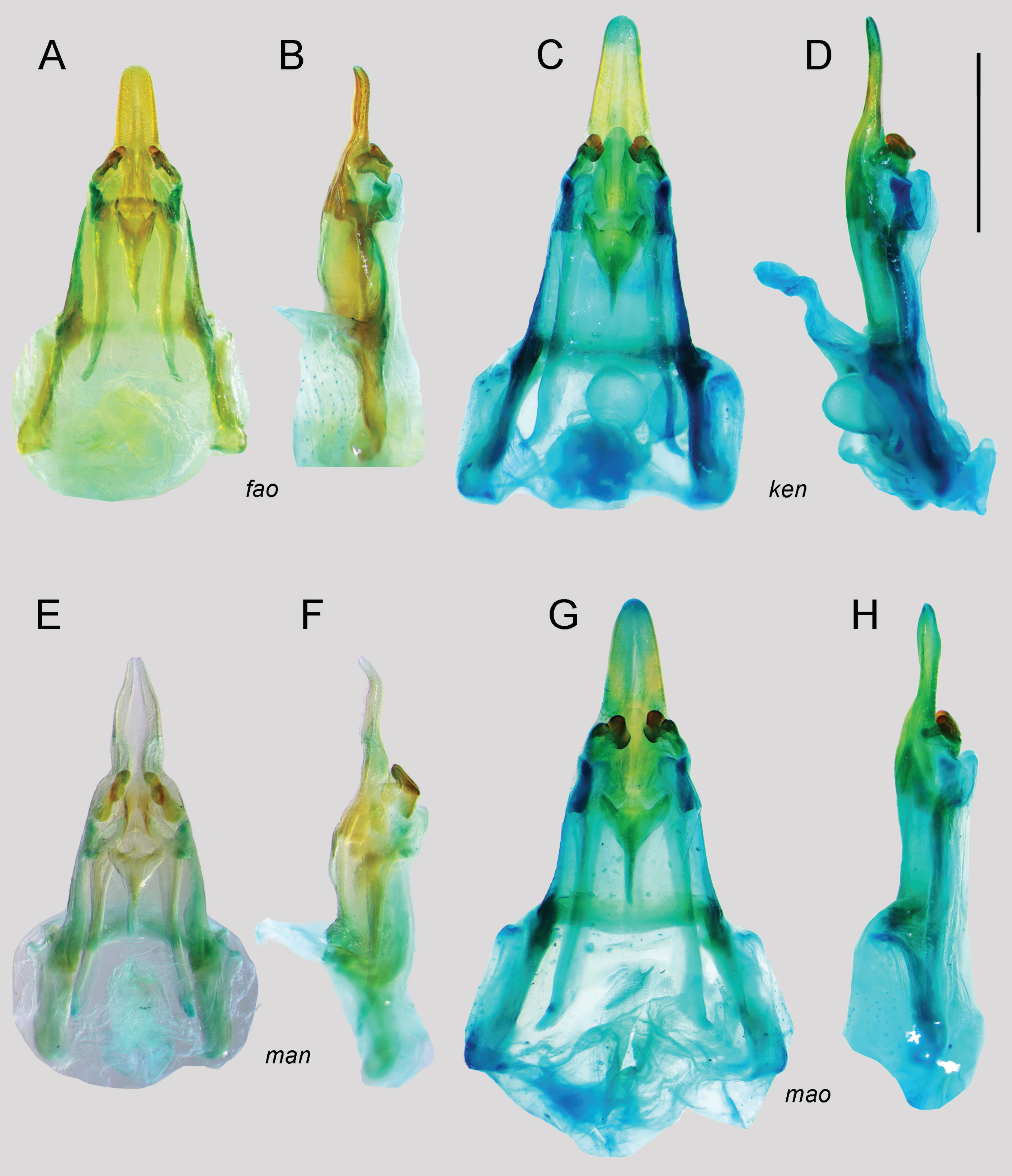

Fig. 15. Male genitalia ventral (**A, C, E, G**) and lateral (**B, D, F, H**) views: **A, B.** *R. faowi* **sp. nov.**; **C, D.** *R. kencana* **sp. nov.**; **E, F.** *R. manokwari* **sp. nov.**; **G, H.** *R. maoke* **sp. nov.** Scale bar: 1 mm.

than disk (Fig. 6D). FIs and FIIs yellow brown with dense dark spots and patterns (less dense in inner surface of FIIs); TIs dark brown with a broad cream-colored ring in middle, TIIs with one or two incomplete rings. FIIIs brown, knees dark brown to black. Tergites brown, with posterior margin darker.

Male. FWs reaching middle of fourth abdominal tergite. FW coloration (Fig. 7D): Dorsal field cells and veins mostly brown; with area between M and R infumate cream-colored; basal area with a cream-colored spot on external corner. Lateral field with brown veins, cells with dorsal part brown, otherwise cream-colored. FW venation typical of genus; 1A forming a right angle, slightly bisinuate anterior to angle; oblique vein posterior branch almost straight, anterior one bifurcated. Apical field with two cell alignment posterior to D alignment. Apex of dorsal field rounded.

Male genitalia: (Figs 8D, 15A, 15B) Pseudepiphallus triangular, slightly convex dorsally in lateral view; its basal margin straight, not indented, slightly widened laterally at base of rami; basal third much wider and lateral margins tapering to a narrower apical third; posterior third forming a thick spoon-like finger, gently tapering into a narrow posterior apex, truncated and without lophi. Rami short, shorter than half of pseudepiphallus length, slightly diverging anteriorly. Pseudepiphallic parameres stout, somewhat straight, and not bent or curved, with small internal lobule in middle, apex not swollen and obtuse. Ectophallic fold triangular, membranous apically, with parallel lateral sclerites. Ectophallic apodemes parallel and long, surpassing beyond anterior margin of pseudepiphallic sclerite with lateral arms elongated triangular. Endophallic sclerite with anterior region triangular, barely reaching anterior margin of pseudepiphallic sclerite; its posterior apex trident-like, with tongue-shaped lateral arms not surpassing large median posterior expansion.

Female. FW slightly surpassing second tergite, with a small cream-colored rounded spot at base and one fainter at apex (Fig. 9C).

Female genitalia: Ovipositor distinctly longer than FIII. Copulatory papilla globular, its base with a semi-complete ring-like sclerotization; apex folded ventrally, short and rounded, slightly sclerotized on apical face (Fig. 10C).

Measurements.—See Table 1.

Rugabinthus kencana sp. nov.

http://zoobank.org/DE3097D6-3C0D-4170-9657-807576C2BC19
(Figs 3, 4E, 5E, 6E, 7E, 8E, 9D, 10D, 15C, 15D, 16)

Material examined.—**Holotype:** INDONESIA • ♂; West Papua, Timika (Irian Jaya Freeport Concession Timika); lowland forest, Kuala Kencana nr. sewage plant; 4°26.21'S, 136°51.84'W, 100 m; 17–24 March 1997; S. Miller, Peggie, Yaku, Ubaidillah leg.; molecular sample L46; MZB-ORHT97020. **Paratypes:** INDONESIA • 1♀; West Papua, Timika (Irian Jaya Freeport Concession Timika); lowland rainforest, Kuala Kencana Light Ind. Park 4°26.21'S 136°52.59'W, 100 m, Malaise trap 1 (site 5); (MZB 97024); MNHN-EO-ENSIF3552 • 1♂; West Papua, Freeport MT2 plot #5; 12–25 March 1997; molecular sample L11LFRE1; (MZ-BORTH97025-5); MNHN-EO-ENSIF1760.

Type locality.—INDONESIA: West Papua: Kuala Kencana.

Etymology.—The species is named after the type locality: Kuala Kencana; noun in apposition.

Diagnosis.—This new species differs from all congeners by its large size, the large triangular shape of male pseudepiphalllus, and stout pseudepiphallic parameres, gently curved but not bent in middle, apex swollen and bilobate. The new species is very similar to *R. maoke* **sp. nov.** but differs by overall smaller size, male FW venation with two cell alignments in apical field (instead of one in *R. maoke* **sp. nov.**), shape of oblique vein, and male genitalia with distinctly smaller pseudepiphallus and endophallic sclerite shorter anteriorly (forming a Y-shape in *R. maoke* **sp. nov.**), with lateral arms pointing more posteriorly. The male genitalia are also similar to *R. manokwari* **sp. nov.** but differ by the absence of indentation at base of the apical third of lateral margin and shape of pseudepiphallic parameres.

Description.—Large sized among congeners (Fig. 16). Dorsum of head with broad red brown bands faintly to narrowly separated (Fig. 4E). Fastigium red brown (Fig. 4E). Scapes dark brown, posterior part yellow with a dark spot. Fastigium verticis and frons black, and black beneath scapes; clypeus and mouthparts pale brown with darker patterns (Fig. 5E). Pronotal disk red brown with some faint and irregular paler brown patterns (Fig. 4E).

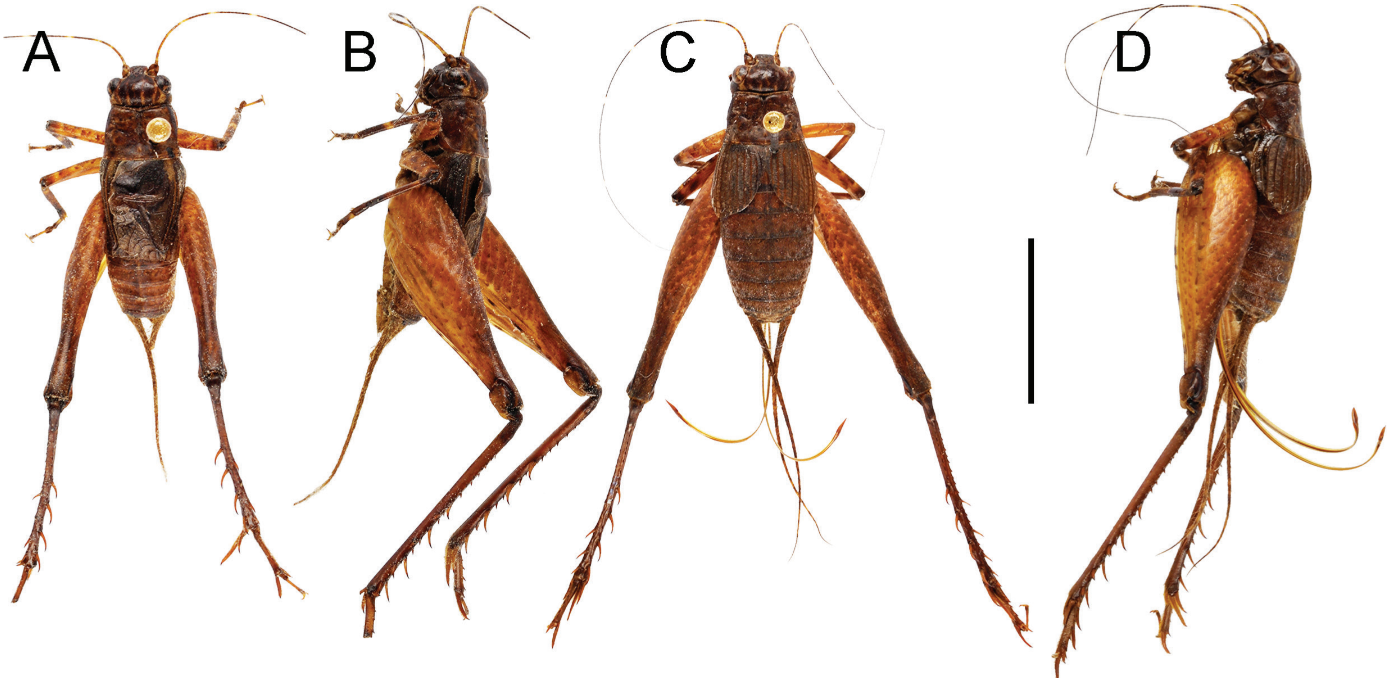

Fig. 16. *R. kencana* **sp. nov.** male (**A, B**) and female (**C, D**) habitus in dorsal (**A, C**) and lateral (**B, D**) views. Scale bar: 10 mm.

Lateral lobes slightly darker than disk, dark brown except a yellow spot on ventral margin (Fig. 6E). FIs and FIIs brown with a few dark spots near knees, TIs and TIIs dark with pale yellow rings. FIIIs brown, knees dark brown. Tergites brown, with posterior margin darker.

Male. FWs reaching apex of fourth abdominal tergite. FW coloration (Fig. 7E): Dorsal field cells and veins mostly brown; with area between M and R dark brown; basal area with a small cream-colored spot on external corner. Lateral field red brown, with ventral region more yellow brown. FW venation typical of genus; 1A forming a right angle, without notch anterior to angle; oblique vein bifurcated, posterior branch almost straight. Cells of D alignment homogeneous. Apex of dorsal field obliquely rounded. Apical field with two cell alignments.

Male genitalia: (Figs 8E, 15C, 15D) Pseudepiphallus triangular, its basal margin straight, not indented; basal third much wider, lateral margin tapering to a narrower apical third; apical third tapering into a narrow posterior apex, not narrowed preapically, apex subacute, without lophi. Rami short, slightly shorter than half of pseudepiphallus length, slightly diverging anteriorly. Pseudepiphallic parameres stout, gently curved but not bent in middle, apex swollen and bilobate. Ectophallic apodemes parallel and long, widened apically, surpassing beyond anterior margin of pseudepiphallic sclerite. Endophallic sclerite with anterior region triangular, barely reaching anterior margin of pseudepiphallic sclerite; its posterior apex trident-like, with short lateral arms not surpassing median posterior expansion.

Female. FW faintly surpassing apex of third tergite, homogeneously brown, without a basal spot (Fig. 9D).

Female genitalia: Ovipositor slightly longer than FIII. Copulatory papilla very small, somewhat rectangular, its basal part with sclerotization forming a basal rim, apex almost as wide as base, ended by a narrow stout and truncated lobule (Fig. 10D).

Measurements.—See Table 1.

Rugabinthus manokwari sp. nov.

http://zoobank.org/AB112D2B-497F-4577-A9EE-42160922A12C
(Figs 3, 4F, 5F, 6F, 7F, 8F, 9E, 10E, 15E, 15F, 17)

Material examined.—**Holotype:** INDONESIA • ♂; West Papua, Manokwari, Vogelkop, 75 m; 24 July 1957; D. Elmo Hardy leg.; BPBM. **Paratype:** INDONESIA • 1♀; West Papua, Manokwari town, primary forest on hills near sea; 4–6 November 2004; A. Gorochov leg.; molecular sample L88; ZIN.

Type locality.—INDONESIA: West Papua: Manokwari

Etymology.—The species is named after the type locality Manokwari; noun in apposition.

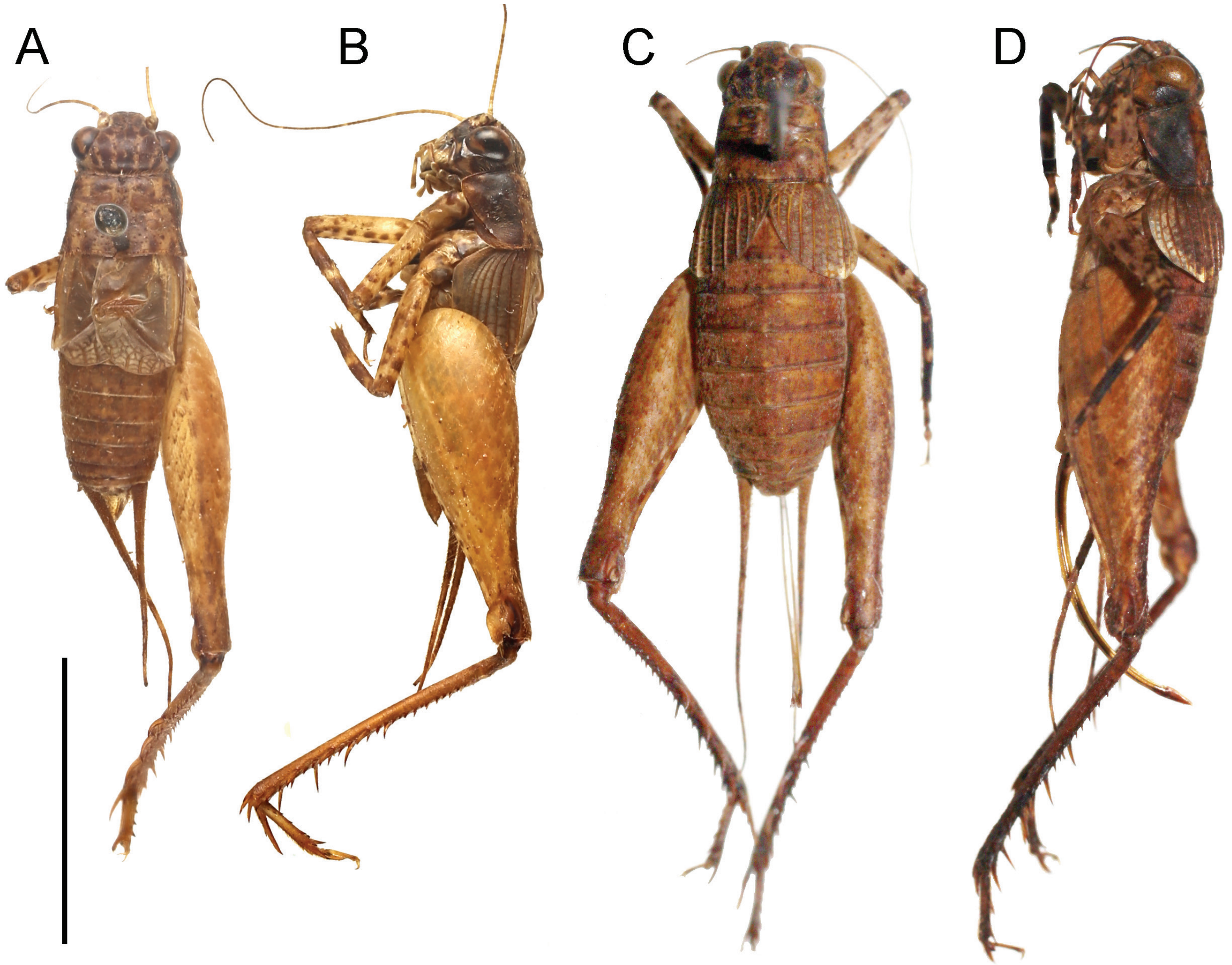

Fig. 17. *R. manokwari* **sp. nov.** male (**A, B**) and female (**C, D**) habitus in dorsal (**A, C**) and lateral (**B, D**) views. Scale bar: 10 mm.

Diagnosis.—This new species differs from all congeners by lighter coloration, including pronotal disk yellow brown with sparse red brown patterns, and shape of male genitalia. Among species group, *R. manokwari* **sp. nov.** differs by male genitalia with pseudepiphallus indented dorsally at base of apical region and tapering to a narrower apex. This species has similar pale coloration as *R. biakis* **sp. nov.** but differs by absence of longitudinal median stripe in the pronotal disk and by shape of male genitalia.

Description.—Size average for the genus (Fig. 17). Dorsum of head yellow brown with five well-separated red brown longitudinal bands, middle one corresponding to incomplete fusion of two bands (Fig. 4F). Fastigium yellow brown with red brown patterns. Scapes yellow brown with dark patterns. Antennae yellow basally, distally brown with pale yellow rings. Fastigium verticis black with a yellow cross-shaped pattern; frons dark brown to black with two lateral yellow spots, black beneath scapes; clypeus and mouthparts black dorsally, pale yellow ventrally (Fig. 5F). Head lateral side red brown, genae slightly lighter with a triangular pale spot. Pronotal disk yellow brown mottled with dark brown (Fig. 4F). Lateral lobes of pronotum distinctly darker than disk, dark red brown, with a paler stripe near ventral margin (Fig. 6F). FIs and FIIs mostly cream-colored with a few well-defined brown spots, knee areas brown; TIs and TIIs dark brown with a cream-colored ring in middle. FIIIs yellow brown, knees brown. Tergites unicolorous brown.

Fig. 18. *R. maoke* **sp. nov.** male habitus in dorsal (**A**) and lateral (**B**) views. Scale bar: 10 mm.

Male. FW reaching base of fourth abdominal tergite. FW coloration (Fig. 7F): Cells and veins of dorsal field mostly brown; area between M and R creamed-colored; basal area with a cream-colored spot on external corner. Lateral field red brown, with ventral region more yellow brown. FW venation typical of genus; 1A slightly bisinuate anterior to angle; oblique vein bifurcated, posterior branch slightly sinuous. Apex of dorsal field rounded; apical parts of its longitudinal veins very strong. Apical field reduced, including few cells of E alignment only.

Male genitalia: (Figs 8F, 15E, 15F). Pseudepiphallus triangular, its basal margin slightly indented in the middle, basal third much wider, lateral margins indented and tapering to a narrower apical third, elongate as characteristic of the species group. Apical third narrowed in dorsal view, slightly concave dorsally, tapering into a narrow posterior apex; slightly truncated and indented apically. Rami short, slightly shorter than half of pseudepiphallus length, slightly diverging anteriorly. Pseudepiphallic parameres stout, not bent in middle, apical half finger-like with subacute apex. Ectophallic apodemes parallel and long, surpassing beyond anterior margin of pseudepiphallic sclerite. Endophallic sclerite with anterior region short and barely reaching anterior margin of pseudepiphallic sclerite, with posterior lateral arms tongue-shaped and slightly longer than median expansion.

Female. FW reaching middle of second tergite, with an apical indistinct cream-colored spot (Fig. 9E).

Female genitalia: Ovipositor shorter than FIII. Copulatory papilla conical, smaller and stout; apex folded ventrally, short, pointed; dorsal face with a sclerotized area; ventro-anterior end forming an oval to pyriform rim (Fig. 10E).

Measurements.—See Table 1.

Rugabinthus maoke sp. nov.

http://zoobank.org/DA4BAC81-EDD1-4F86-921B-4AC602F47257
(Figs 3, 4G, 5G, 6G, 7G, 8G, 15G, 15H, 18)

Material examined.—**Holotype:** INDONESIA • ♂; West Papua, Star Range; 25 m; 10 September 1959; Neth. New Guinea Exped 1959 leg.; RMNH. **Paratype:** INDONESIA • 1♂; West Papua, Star Range; 25 m; 10 September 1959; Neth. New Guinea Exped 1959 leg.; molecular sample L179; MNHN-EO-ENSIF1757.

Type locality.—INDONESIA: West Papua: Star Range

Etymology.—This species is named after the Maoke Mountain Range where Star Range was situated within; noun in apposition.

Diagnosis.—This new species is very similar to *R. kencana* but differs by overall larger size, distinctly larger pseudepiphallus, and endophallic sclerite with lateral arms more elongated and pointing more externally.

Description.—Large sized among congeners (Fig. 18). Dorsum of head with broad red brown bands faintly to narrowly separated (Fig. 4G). Fastigium red brown (Fig. 4G). Scapes dark red brown. Fastigium verticis and frons dark red brown, black beneath scapes; clypeus and mouthparts pale brown with darker patterns (Fig. 5G). Pronotal disk red brown with some faint and irregular paler brown patterns (Fig. 4G). Lateral lobes faintly darker than disk, dark brown except for a yellow spot on ventral margin (Fig. 6G).

FIs and FIIs yellow brown with a few dark spots near knees, TIs dark with a pale yellow ring in middle, TIIs mostly dark. FIIIs brown, knees dark brown. Tergites brown, with posterior margin darker.

Male. FWs reaching base of fourth abdominal tergite. FW coloration (Fig. 7G): Dorsal field cells and veins mostly brown; with area between M and R dark brown; basal area with a small cream-colored spot on external corner. Lateral field red brown, with ventral region more yellow brown. FW venation typical of genus; 1A forming a right angle, without notch anterior to angle; oblique vein bifurcated, posterior part sinuated. Cells of D alignment widened posteriorly. Apex of dorsal field obliquely rounded.

Male genitalia: (Figs 8G, 15G, 15H) Pseudepiphallus very similar to *R. kencana*, triangular with an indented, narrow apical third with subacute apex, but differs by being distinctly larger. Rami, pseudepiphallic parameres and ectophallic apodemes similar. Endophallic sclerite with anterior region triangular, not reaching anterior margin of pseudepiphallic sclerite, with long posterior lateral arms pointing diagonally and surpassing median expansion.

Female. Unknown.

Measurements.—See Table 1.

Rugabinthus biakis sp. nov.

http://zoobank.org/D074F7D3-D6C5-463C-8D3E-4EFD304AD4C9

(Figs 3, 4H, 5H, 6H, 7H, 8H, 19, 20A, 20B)

Material examined.—**Holotype:** INDONESIA • ♂; West Papua, Biak Island (not far from N. coast of W New Guinea), secondary forest on hill near vill. Corem; 14–15 November 2004; A. Gorochov leg.; ZIN. **Paratypes:** INDONESIA • 1♂; same information as holotype; molecular sample L86; MZB • 1♂; Biak Island (not far from N. coast of W New Guinea), secondary forest on hill near vill. Corem; 14–15 November 2004; A. Gorochov leg.; MNHN-EO-ENSIF1745.

Fig. 19. *R. biakis* **sp. nov.** male habitus in dorsal (**A**) and lateral (**B**) views. Scale bar: 10 mm.

Other material.—INDONESIA • 1 juvenile; West Papua, Biak Island, Biak Town, forest on not high hill near airport; 17–20 January 2012; leg. A. Gorochov; molecular sample L85; ZIN.

Type locality.—INDONESIA: West Papua: Biak.

Etymology.—The species is named after the type locality: Biak Island.

Diagnosis.—This new species differs from all congeners by its small size; dorsum of head yellow brown with five well-separated and well-defined dark brown longitudinal bands; pronotal disk yellow brown with a median dark brown longitudinal band and sparse but well defined dark brown spots of different sizes; lateral lobe contrasting dark in coloration. It also differs from all congeners by male genitalia with pseudepiphallus rectangular, stouter than congeners, apex truncated forming a short posterior plate with a small median nodule.

Description.—Small sized among congeners (Fig. 19). Dorsum of head yellow brown with five well-separated and well-defined dark brown longitudinal bands, middle band widest resulting from fusion of two bands, partly split anteriorly (Fig. 4H). Fastigium yellow brown with dark brown patterns. Scapes brown. Antennae yellow brown basally, distally brown with yellow rings. Fastigium verticis and frons black, frons with two faint yellow brown spots, eyes underlined with yellow; clypeus and mouthparts dark brown to black, labrum distinctly cream-colored (Fig. 5H). Maxillary palpi cream-colored with brown patterns. Pronotal disk yellow brown with a median dark brown longitudinal band and sparse but well defined dark brown spots of different size (Fig. 4H). Lateral lobes of pronotum entirely dark brown, distinctly darker than disk (Fig. 6H). Legs pale yellow brown with well-defined brown spots and rings. FIs and FIIs mostly cream-colored with a few well-defined brown spots, knees brown; TIs and TIIs dark brown with a cream-colored ring in middle. FIIIs cream-colored with numerous oblique dark brown bands, knees dark brown. Tergites unicolorous dark brown.

Male. FWs reaching middle of fourth abdominal tergite. FW coloration (Fig. 7H): Dorsal field cells and veins mostly brown; some veins near basal area cream-colored; M vein orange brown; area between M and R infumate cream-colored; basal area with a large cream-colored spot on anterior corner and another one near 1A and 2A. Lateral field dark red brown in dorsal half, gray brown in ventral half. FW venation typical of genus, 1A bisinuate anterior to angle; oblique vein base faded, both its posterior and anterior branches almost straight. Apex of dorsal field obliquely rounded.

Male genitalia: (Figs 8H, 20A, 20B) Pseudepiphallus rectangular, stouter, and shorter than in congeners, very wide laterally at base of rami, its basal anterior margin almost straight, lateral margin generally parallel, apex truncated, forming a short posterior plate, slightly concave dorsally, with a small median nodule. Rami short, but longer than half of pseudepiphallus length. Pseudepiphallic parameres strongly bent 90° in the middle, apex strongly sclerotized and forming two stout lobules. Ectophallic apodemes surpassing anterior margin of pseudepiphallic sclerite. Endophallic sclerite short, barely reaching anterior margin of pseudepiphallus, with thin posterior lateral arms and a very small medio-posterior expansion.

Female. Unknown.

Measurements.—See Table 1.

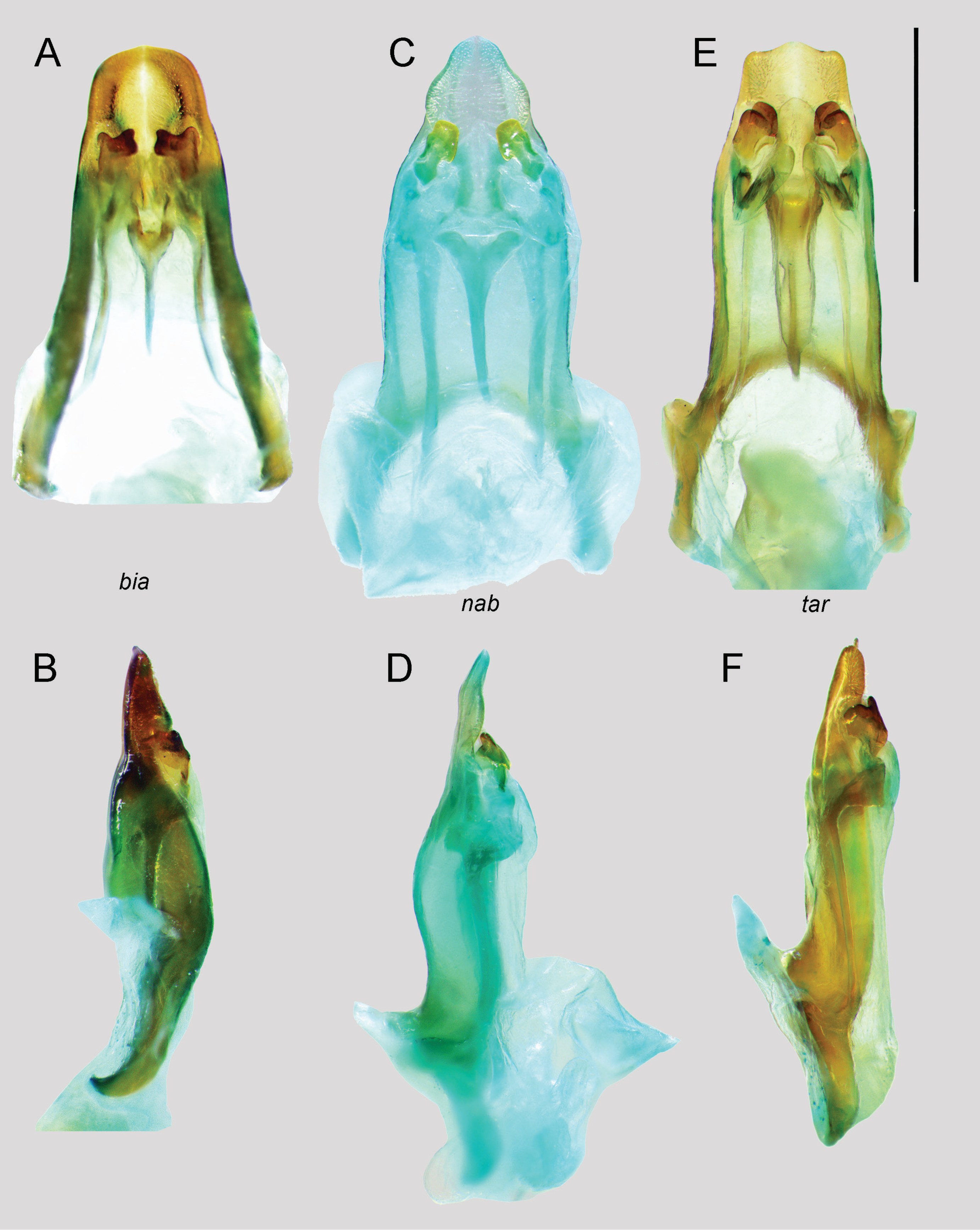

Fig. 20. Male genitalia ventral (**A, C, E**) and lateral (**B, D, F**) views: **A, B.** *R. biakis* **sp. nov.**; **C, D.** *R. nabire* **sp. nov.**; **E, F.** *R. tariku* **sp. nov.** Scale bar: 1 mm.

Rugabinthus nabire sp. nov.

http://zoobank.org/EB99A2A4-2D8A-46A9-89B8-247023253B58
(Figs 3, 4I, 5I, 6I, 7I, 8I, 9F, 10F, 20C, 20D, 21)

Material examined.—**Holotype:** INDONESIA • ♂; West Papua, Nabire, S. Geelvink Bay, 5–50 m; 25 August–2 September 1962; J. Sedlacek leg.; BPBM. **Paratypes:** INDONESIA • 1♀; West Papua, Nabire, S. Geelvink Bay, 0–30 m; 2–9 September 1962; J. L. Gressitt leg.; BPBM • 1♂; West Papua, Nabire, S. Geelvink Bay, 10–40 m; 13 October 1962; N. Wilson leg.; molecular sample L162; BPBM • 1♂; West Papua, Nabire, S. Geelvink Bay; 16 September 1962; Malaise trap, in jungle; H. Holtmann leg.; MNHN-EO-ENSIF11332 • 1♂; West Papua, Nabire, S. Geelvink Bay, 10–40 m; sweeping; 12 October 1962; N. Wilson leg.; BPBM.

Type locality.—INDONESIA: West Papua: Nabire.

Etymology.—The species is named after the type locality, Nabire; noun in apposition.

Diagnosis.—This new species differs from all congeners by male subgenital plate rounded apically (pointed in all congeners) and male genitalia with stout pseudepiphallus, slightly convex dorsally, its posterior part very short, slightly concave dorsally, with apex narrowed forming two small lophi with subacute apices; basal margin of pseudepiphallus strongly indented in the middle; pseudepiphallic parameres stout, posterior half forming an internal lobe, apex truncated. Except for the respective original characters of each species, in particular in the shape of the apical part of the pseudepiphallus, the male genitalia of the new species resemble that of *R. karimui* **sp. nov.** and *R. albatros* **sp. nov.**

Description.—Average sized among congeners (Fig. 21). Dorsum of head with 6 broad dark red brown bands barely separated (Fig. 4I). Fastigium dark red brown (Fig. 4I). Scapes yellow brown with red brown bands. Fastigium verticis dark brown with a faint M-shaped yellow brown pattern, frons dark brown with two faint yellow brown spots; clypeus and mouthparts yellow brown with dark brown patterns (Fig. 5I). Pronotal disk and lateral lobe unicolorous dark red brown, pronotal disk with two faint lateral spots along posterior margin, lateral lobe not darker than disk (Figs 4I, 6I). FIs and FIIs cream-colored with dark spots, TIs and TIIs dark brown with one median pale ring. FIIIs yellow brown in ventral half to red brown in dorsal half, knees dark brown. Tergites brown.

Male. FWs slightly surpassing apex of fourth abdominal tergite. FW coloration (Fig. 7I): Dorsal field cells and veins mostly brown; area between M and R whitish; basal area with a small cream-colored well-defined spot on external corner. Lateral field dark red brown, with ventral margin cream-colored. FW venation typical of genus; 1A bisinuate anteriorly to angle; oblique vein bifurcated, posterior branch almost straight. Apex of dorsal field rounded. Apical field with only few cells in E alignment. Apex of longitudinal veins in dorsal field strong. Subgenital plate short, its apex rounded.

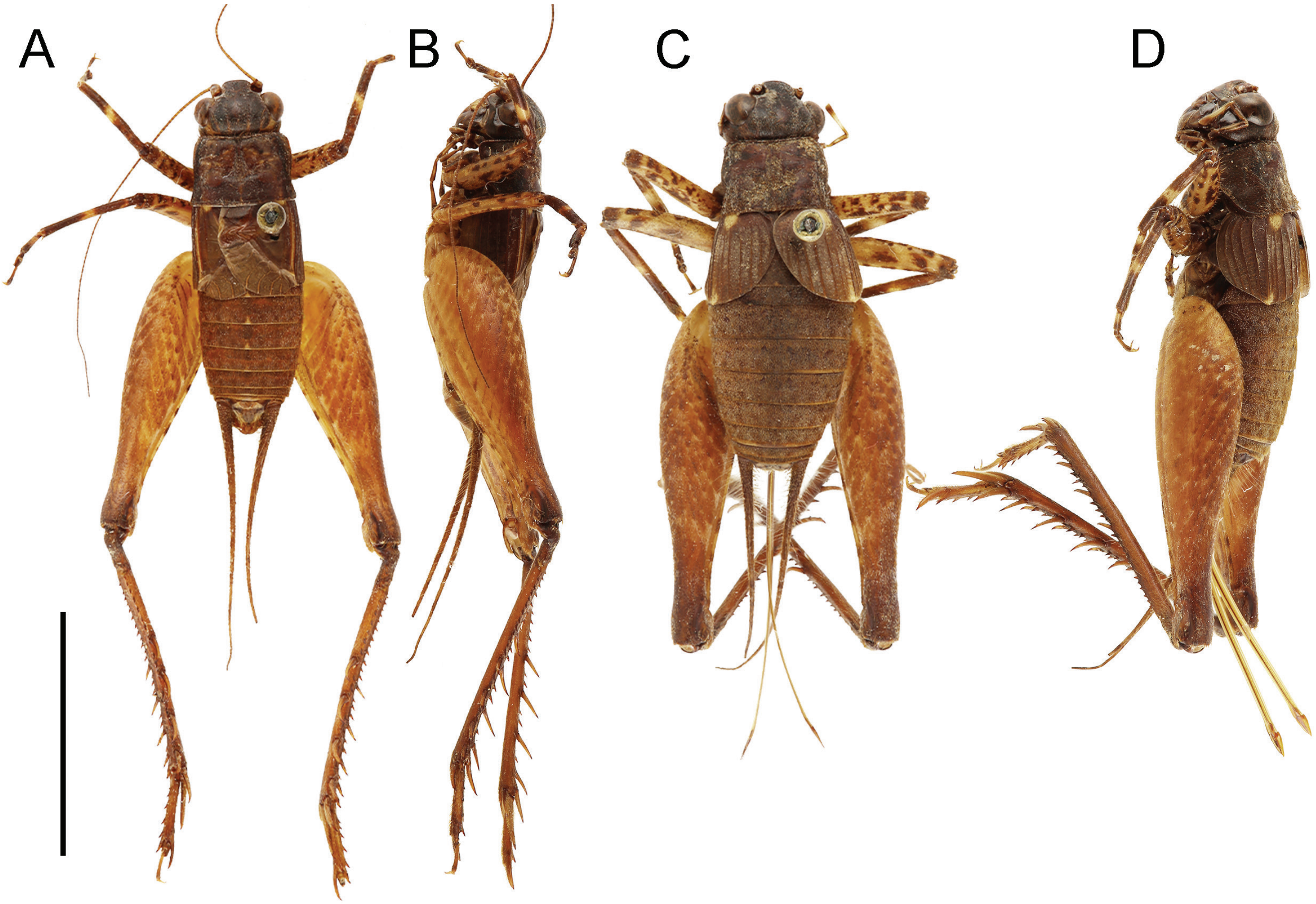

Fig. 21. *R. nabire* **sp. nov.** male (**A**, **B**) and female (**C**, **D**) habitus in dorsal (**A**, **C**) and lateral (**B**, **D**) views. Scale bar: 10 mm.

Male genitalia: (Figs 8I, 20C, 20D) Pseudepiphallus triangular, stouter, convex dorsally, its basal margin straight but strongly indented in the middle and slightly raised dorsally. Lateral margins generally parallel, tapering near apex into a narrow posterior end. Posterior part of pseudepiphallus short, concave dorsally, its apex indented in the middle, forming two small lophi with subacute apices; lophi more developed ventrally, slightly setose. Rami very short, shorter than half of pseudepiphallus length. Pseudepiphallic parameres stout, posterior half forming an internal lobe, apex truncated. Ectophallic apodemes surpassing anterior margin of pseudepiphallic sclerite. Endophallic sclerite with anterior region slightly surpassing anterior margin of pseudepiphallic sclerite; posterior apex of endophallic sclerite with long, rounded and diverging arms, median expansion not distinct.

Female. FW reaching apex of second tergite, brown with two clearly defined triangular, cream-colored spots laterally, at base and apex (Fig. 9F).

Female genitalia: Ovipositor shorter than FIII. Copulatory papilla with a large rounded apical part strongly plicate; ventro-anterior end forming a rounded rim (Fig. 10F).

Measurements.—See Table 1.

Rugabinthus tariku sp. nov.

http://zoobank.org/D6961759-141B-40F6-95ED-524D310B8CE2

(Figs 3, 4J, 5J, 6J, 7J, 8J, 9G, 10G, 20E, 20F, 22)

Material examined.—**Holotype:** INDONESIA • ♂; West Papua, Fawi [Faowi] village in upper part of Tariku River (tributary of Mamberamo River), partly low-lying forest and partly forest on hills; 29 January–17 February 2012; A. Gorochov leg.; molecular sample L93; ZIN. **Paratypes:** INDONESIA • 1♂, 1♀; same information as holotype; ZIN • 1♂, 1♀; same information as holotype; MNHN-EO-ENSIF11142–ENSIF11143 • 1♂, same information as holotype; MZB.

Type locality.—INDONESIA: West Papua: Faowi.

Etymology.—This species is named after the Tariku River; noun in apposition. This species is named after the tributary river rather than the main Mamberamo River, because it has smaller and stouter male genitalia compared to the sympatric species *R. mamberamo.*

Diagnosis.—This new species differs from all congeners by male FW venation with extremely indented 1A vein, with its transverse part restricted to inner half of FW, and by male genitalia with pseudepiphallus rectangular, its basal margin strongly indented in the middle, slightly widened laterally near base of rami. Posterior part of pseudepiphallus short and trilobate, with two short stout lophi linked by a thin sclerotized plate forming a median lobe; pseudepiphallic parameres very stout, strongly bent 90° in the middle. General shape of male genitalia similar to that of *R. biakis*, from which the new species differs by apex of pseudepiphallus, base of rami, and parameres; the two species also differ in body coloration. From the sympatric species *R. mamberamo*, the new species differs by smaller size and by male and female genitalia.

Description.—Small to average sized among congeners (Fig. 22). Dorsum of head with broad red brown bands barely separated (visible only near posterior margin) (Fig. 4J). Fastigium dark red

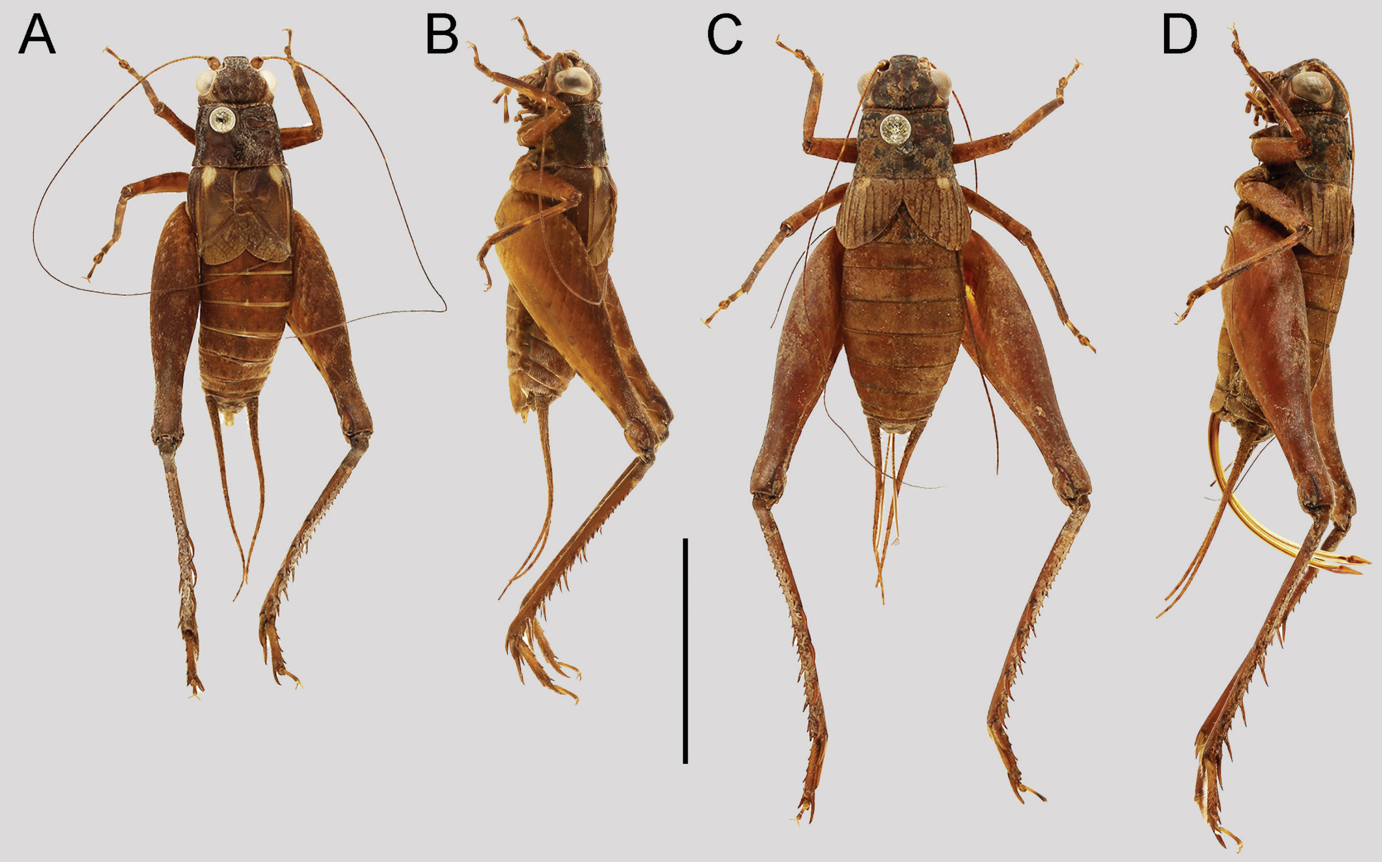

Fig. 22. *R. tariku* **sp. nov.** male (**A, B**) and female (**C, D**) habitus in dorsal (**A, C**) and lateral (**B, D**) views. Scale bar: 10 mm.

brown (Fig. 4J). Scapes red brown. Fastigium verticis and frons dark brown, frons with faint yellow brown spots; clypeus and mouthparts dark brown, labrum yellow brown (Fig. 5J). Pronotal disk dark brown with anterior margin yellow brown and posterior margin with some faint irregular yellow brown spots (Fig. 4J). Lateral lobes not darker than disk (Fig. 6J). Legs pale brown with few dark brown spots and patterns. FIIIs brown, knees dark brown to black. Tergites brown, with posterior margin darker.

Male. FWs reaching middle of third abdominal tergite. FW coloration (Fig. 7J): Dorsal field cells and veins mostly brown; with area between M and R infumate cream-colored; basal area with a cream-colored spot on lateral corner. Lateral field dark brown, more gray–brown near ventral margin. FW venation typical of genus, with 1A vein strongly bisinuate, forming a big notch restricting transverse part of 1A to inner half of FWs. Oblique vein posterior branch almost straight; anterior branch simple. Apex of dorsal field rounded.

Male genitalia: (Figs 8J, 20E, 20F) Pseudepiphallus short and rectangular, its basal margin strongly indented in the middle, slightly raised dorsally, widened laterally at base of rami. Lateral margins parallel; posterior part of pseudepiphallus short, apex truncated, forming three lobules, including two stout lophi linked by a thin sclerotized plate forming the median lobe. Rami short, shorter than half of pseudepiphallus length. Pseudepiphallic parameres very stout, strongly bent 90° in the middle, apex strongly enlarged and sclerotized and forming two stout lobules. Ectophallic fold forming a wide plate apically, with thin parallel sclerites. Ectophallic apodemes surpassing anterior margin of pseudepiphallic sclerite, with lateral arms elongated. Endophallic sclerite very elongated anteriorly, forming a wide triangular plate carrying a narrow crest dorsally; its posterior apex with thin lateral arms but without median expansion.

Female. FW slightly surpassing second tergite, with a distinct cream-colored rounded spot at base (Fig. 9G).

Female genitalia: Ovipositor distinctly shorter than FIII. Copulatory papilla globular, its basal part with an irregular sclerotization forming a basal rim with a short basal plate curved dorsally; apex rounded, folded ventrally and slightly sclerotized (Fig. 10G).

Measurements.—See Table 1.

Rugabinthus albatros sp. nov.

http://zoobank.org/520A61FC-E62E-4AD0-99E3-238E844FAFA7

(Figs 3, 4K, 5K, 6K, 7K, 8K, 9H, 10H, 10I, 23, 24A, 24B)

Material examined.—**Holotype:** INDONESIA • ♂; West Papua, Albatros Bivak V. Mamberamo [Mamberamo River, Albatros Bivouac]; 1926; v. Leeuwen leg.; molecular sample L177; MZB-ORTH1974. **Paratypes:** INDONESIA • 1♂; same information as holotype; MZB-ORTH8968 • 1♂; same information as holotype; (MZB-ORTH8957); molecular sample L211; MNHN-EO-ENSIF11141 • 1♀; West Papua, Kasonaweja Village on Mamberamo River near Van Rees range, forest on not-high hills; 25–27 January 2012; A. Gorochov leg.; molecular sample L95; ZIN.

Other material.—INDONESIA • 1 juvenile; same information as holotype; ZIN.

Type locality.—INDONESIA: West Papua: Mamberamo River, Albatros Bivouac.

Etymology.—The species is named after the type locality: Albatros; noun in apposition.

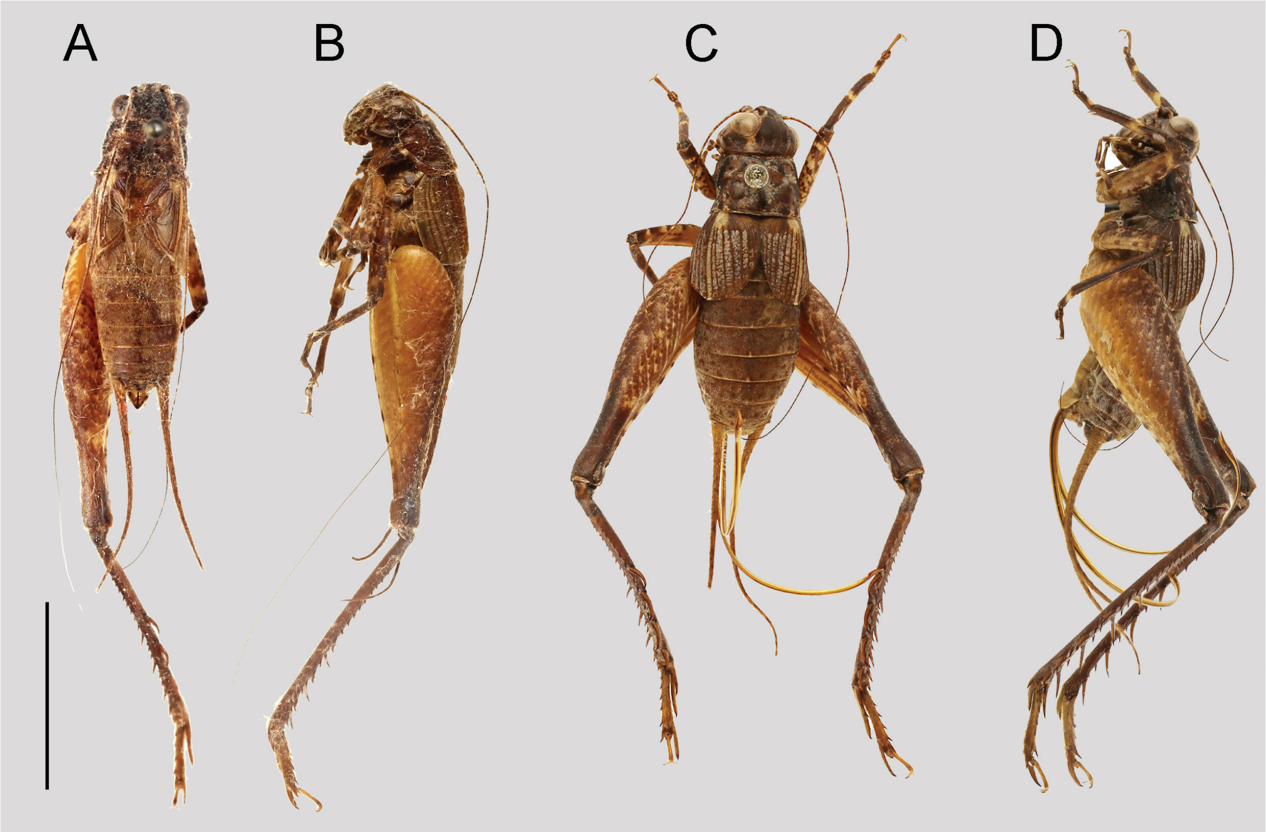

Fig. 23. *R. albatros* **sp. nov.** male (**A, B**) and female (**C, D**) habitus in dorsal (**A, C**) and lateral (**B, D**) views. Scale bar: 10 mm.

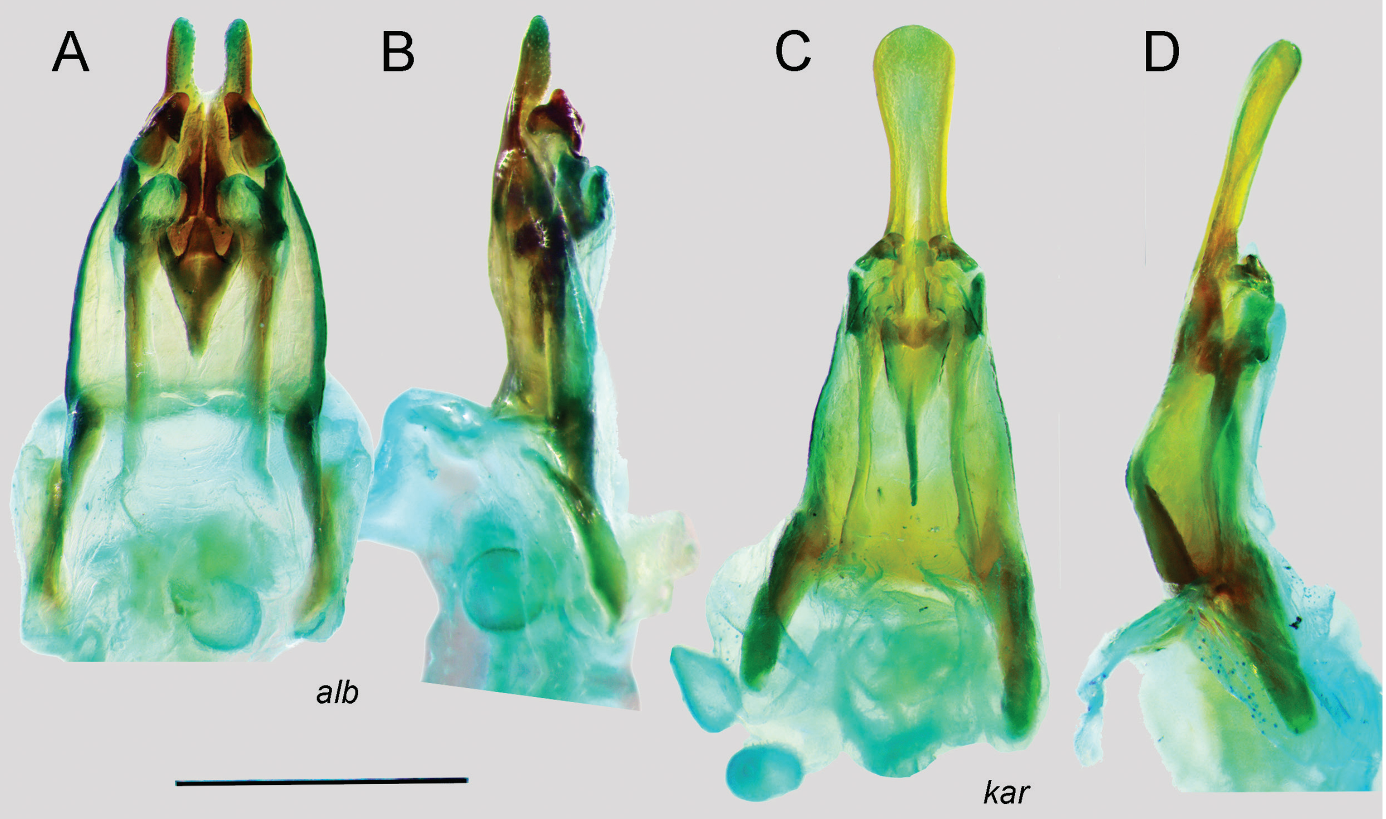

Fig. 24. Male genitalia ventral (**A, C**) and lateral (**B, D**) views: **A, B.** *R. albatros* **sp. nov.**; **C, D.** *R. karimui* **sp. nov.** Scale bar: 1 mm.

Diagnosis.—This new species differs from all congeners by male genitalia with pseudepiphallus forming at the posterior end two long straight lophi with subacute apices and by female copulatory papilla with a very thin elongate apex.

Description.—Average to large sized among congeners (Fig. 23). Dorsum of head with broad red brown bands narrowly separated (Fig. 4K). Fastigium red brown (Fig. 4K). Scapes yellow brown with red brown bands. Fastigium verticis brown with faint yellow vertical stripes, frons light brown without spots in the middle, dark brown ventral of scapes; clypeus and mouthparts red brown (Fig. 5K). Pronotal disk red brown with some irregular yellow brown patterns, lighter lateral ovular spots near anterior half and with a yellow brown stripe near latero-posterior margin (Fig. 4K). Lateral lobe of pronotum unicolorous dark red brown, not distinctly darker than disk (Fig. 6K). FIs, FIIs, TIs, and TIIs dark brown with yellow brown spots and rings. FIIIs brown, knees and posterior third of FIIIs dark brown. Tergites brown with posterior margin darker.

Male. FWs reaching middle of fourth abdominal tergite. FW coloration (Fig. 7K): Dorsal field cells and veins mostly brown with area between M and R infumate cream-colored; basal area with a small cream-colored spot on external corner. Lateral field hyalinous brown. FW venation typical of genus; 1A notch anteriorly to angle strong, making anterior part of harp wider; harp elongate, almost twice as long as wide. Oblique vein bifurcated, posterior branch slightly bisinuate, anterior branch bifurcated near 1A angle. Apical field with one cell alignment posterior to mirror. Apex of dorsal field rounded.

Male genitalia: (Figs 8K, 24A, 24B) Pseudepiphallus triangular, stouter, not convex dorsally in lateral view, its basal margin slightly indented in the middle, lateral margin generally parallel, not widened basally at base of rami, gently tapering into apex; apex forming two long straight lophi with subacute apices. Rami very short, about half the pseudepiphallus length. Pseudepiphallic parameres stout. Endophallic sclerite with a main Y shape; anterior region short and not reaching anterior margin of pseudepiphallic sclerite; posterior apex trilobate, with stick-like lateral arms and with a large median posterior expansion.

Female. FWs slightly surpassing second tergite. Dorsal field with a distinct cream-colored rounded spot at base and a tiny apical spot (Fig. 9H).

Female genitalia: Ovipositor distinctly longer than FIII. Copulatory papilla cupular basally, circled by a narrow sclerite expanded in apical region as parallel sclerotization; apex elongate and folded ventrally, terminated by a rounded area (Figs 10H, 10I).

Measurements.—See Table 1.

Rugabinthus baduri sp. nov.

http://zoobank.org/0FD67CC5-65D2-4831-82BF-81BE5102408E

(Figs 3, 4L, 5L, 6L, 9I, 10J, 25)

Material examined.—**Holotype:** INDONESIA • ♀; West Papua: Yapen Island, Aiam Range, Mount Baduri, Japen Seroei Camp 1, 1000 ft. a.s.l.; September 1938; B.M. 1938-593; molecular sample L172; L. E. Cheesman leg; NHMUK.

Type locality.—INDONESIA: West Papua: Yapen Island, Mount Baduri.

Etymology.—This species is named after the type locality, Mount Baduri; noun in apposition.

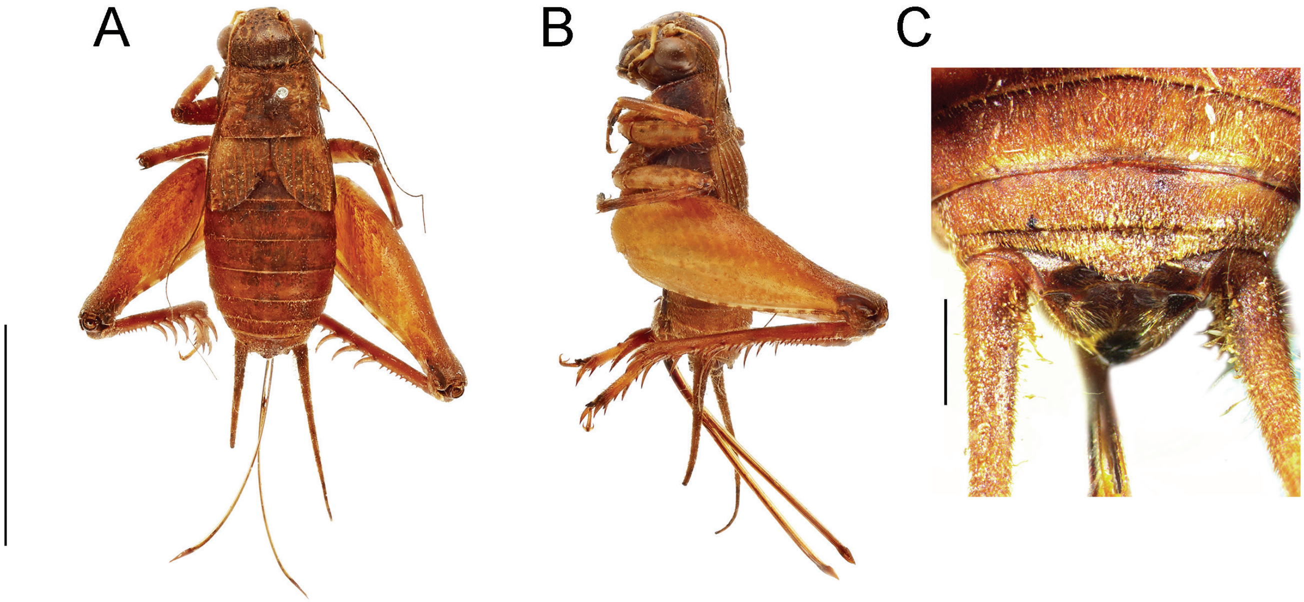

Fig. 25. *R. baduri* **sp. nov.** female habitus in dorsal (**A**) and lateral (**B**) views; and female abdominal apex in dorsal view (**C**). Scale bars: 10 mm (**A, B**), 1 mm (**C**).

Diagnosis.—This new species differs from all congeners by its stocky shape, frons mostly cream-colored with some dark patterns, scapes whitish, and by last abdominal tergite forming a median sinuate expansion above suranal plate.

Description.—Average sized among congeners, but stocky (Fig. 25). Dorsum of head with broad red brown bands narrowly separated (Fig. 4L). Fastigium yellow-brown mottled with brown (Fig. 4L). Scapes whitish with some faint brown patterns. Fastigium verticis cream-colored with two lateral rectangular dark spots beside scapes; two median oval brown spots expanded ventrad to frons as band. Frons yellow brown with brown bands widening and diverging from each other; slightly brownish beneath scapes. Clypeus yellow-brown and brown in middle, mouthparts brown to dark; maxillary palpi mostly yellow (Fig. 5L). Pronotal disk brown with faint light-colored patterns laterally (Fig. 4L). Lateral lobes distinctly darker than pronotal disk, dark brown except red brown near ventral margin (Fig. 6L). FIs and FIIs yellow brown with large dark spots and patterns, knees dark-brown; TIs and TIIs brown with very faint pale bands. FIIIs brown, knees dark brown to black.

Male. Unknown.

Female. Last abdominal tergite forming a median sinuate expansion partly covering suranal plate (Fig. 25C). FW slightly surpassing second tergite, not clearly overlapping. Dorsal field with a very faint cream-colored rounded spot at base (Fig. 9I).

Female genitalia. Ovipositor about as long as FIIIs. Copulatory papilla globular, its base with two hemi-circular ring-like sclerites; apex short, rounded with tip slightly pointed, folded ventrally, and slightly sclerotized dorsally (Fig. 10J).

Measurements.—See Table 1.

Remark.—This new species is known only by the female type specimen, which makes it difficult to place it in a particular genus among the Lebinthina. Its stocky shape first suggested it could belong to *Gnominthus*, but a molecular phylogenetic study in preparation revealed that this species belongs to the clade corresponding to *Rugabinthus* without ambiguity.

Rugabinthus karimui sp. nov.

http://zoobank.org/D299D902-F486-4B1B-8E75-D3E52967B681
(Figs 3, 4M, 5M, 6M, 7L, 8L, 9J, 10K, 10L, 24C, 24D, 26)

Material examined.—**Holotype:** PAPUA NEW GUINEA • ♂; Karimui, 1000 m; 2–3 June 1961; J. L. Gressitt leg.; BPBM. **Paratypes:** PAPUA NEW GUINEA • 1♀; Karimui, South of Goroka, 1000 m; 3 June 1961; G. L. and M. Gressitt leg.; molecular sample L210; BPBM • 1♂; Karimui; 4 June 1961; J. L. Gressitt leg.; malaise trap; molecular sample L49; (BPBM); MNHN-EO-ENSIF11333.

Type locality.—PAPUA NEW GUINEA: Karimui.

Etymology.—The species is named after the type locality: Karimui; noun in apposition.

Diagnosis.—This new species differs from all congeners by smaller size, short male FWs without apical field, and shape of male and female genitalia. Male subgenital plate more elongate than in congeners, with a short apical expansion. Male genitalia very different from all congeners, characterized by elongate apical part of pseudepiphallus forming a long spoon-like finger.

Description.—Small sized among congeners (Fig. 26). Dorsum of head yellow brown with 6 narrow red brown irregular longitudinal bands (Fig. 4M). Fastigium unicolorous red brown (Fig. 4M). Scapes yellow brown. Antennae basally yellow brown, distally dark brown with some light rings. Fastigium verticis brown with a pale yellow-brown n-shaped pattern; frons brown in middle with 2 small yellow spots, black beneath scapes; clypeus and mouthparts dark brown dorsally, labrum and ventral part of mouthparts yellow (Fig. 5M). Pronotal disk yellow brown with some irregular red-brown patterns most prominent near anterior and posterior margins (Fig. 4M). Lateral lobe of pronotum red brown, distinctly darker than disk, with 2 light spots in antero-ventral corner (Fig. 6M). Legs yellow brown with dark brown spots. FIIIs brown, knees dark brown. Tergites brown, with posterior margin darker.

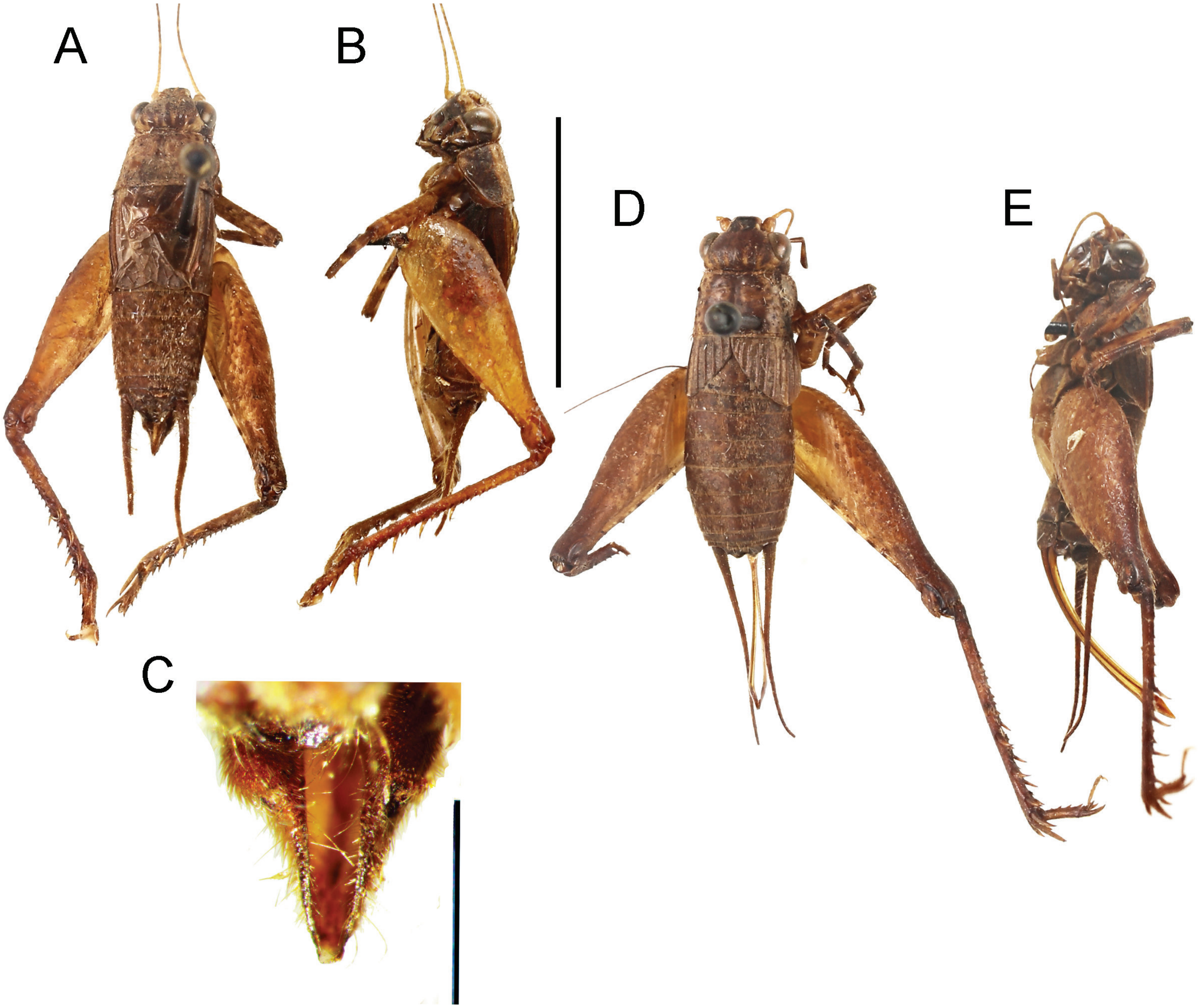

Fig. 26. *R. karimui* **sp. nov.** male (**A, B**) and female (**D, E**) habitus in dorsal (**A, D**) and lateral (**B, E**) views; and male subgenital plate in ventral view (**C**). Scale bars: 10 mm (all except **C**); 1 mm (**C**).

Male. FW very short, reaching apex of third abdominal tergite. FW coloration (Fig. 7L): Dorsal field cells and veins mostly brown; some veins near basal area cream-colored; with area between M and R infumate cream-colored; basal FW area with a large cream-colored spot including base of CuA, 1A and 2A. Lateral field brown, with ventral margin cream-colored. FW venation typical of genus; 1A notch anteriorly to angle strong; oblique vein bifurcated, posterior and anterior branches slightly bisinuate and almost parallel. Apex of dorsal field very short and rounded; D alignment limited to 2 cells; apical field absent. Subgenital plate very elongate, pointed, with a short apical expansion (Fig. 26C).

Male genitalia: (Figs 8L, 24C, 24D) Pseudepiphallus elongate, slightly convex dorsally, its basal margin slightly convex, prolonged anteriorly by a sclerotized plate; lateral margin tapering into apical third, most narrow at apical third; posterior of apical third elongated spoon shaped, its apex rounded. Rami very short, way shorter than half the pseudepiphallus length. Pseudepiphallic parameres small, posterior half broadly bulbous and stout. Ectophallic apodemes parallel and long, usually reaching anterior margin of pseudepiphallic sclerite. Endophallic sclerite elongate, with anterior region long but barely reaching anterior margin of pseudepiphallic sclerite; with lateral arms of sclerite narrowly triangular.

Female. FW reaching middle of second tergite; brown, without basal spot (Fig. 9J).

Female genitalia: Ovipositor slightly longer than FIII. Copulatory papilla conical, smaller and stout; apex folded ventrally, short, pointed; dorsal face with a sclerotized area; ventro-anterior end forming an oval to pyriform rim (Figs 10K, 10L).

Measurements.—See Table 1.

Rugabinthus newguineae (Bhowmik, 1981) comb. nov.

(Figs 3, 4N, 5N, 6N, 9K, 10M, 27)

Larandopsis newguineae Bhowmik, 1981[1979]: 39 - Desutter-Grandcolas and Jaiswara 2012: 31, according to Bhowmik's

descriptions and illustrations belonging to *Lebinthus* [but not moved to *Lebinthus*] - Cigliano et al. 2021 (Orthoptera Species Files Online).
Macrobinthus newguineae - Robillard et al. 2016: 178.

Material examined.—**Holotype:** INDONESIA • ♀; Dutch New Guinea: Cyclops Mts, Sabron Camp 2; 2000 ft; July 1936; identified *Larandopsis newguineae* Bhowmik by H. K. Bhowmik, 1973; L. E. Cheesman leg; BMNH-1936-271.

Other material.—INDONESIA • 1♀; N. New Guinea, "Boven-Jemomaissin" ca. 400 m; 4 April 1911; molecular sample L199; Dr P. N. v. Kampen, Ned. Nw. Guinea Exp leg; RMNH • 1♀; N. New Guinea; 1911; Dr P. N. v. Kampen, Ned. Nw. Guinea Exp leg; RMNH • 1♀; N. New Guinea; April–May 1911; Dr P. N. v. Kampen, Ned. Nw. Guinea Exp leg; RMNH.

Type locality.—INDONESIA: Cyclops Mts.

Emended diagnosis.—Among congeners, *R. newguineae* **comb. nov.** is characterized by its large size, FWs not reaching abdomen mid-length but well developed, coloration homogeneously dark brown, and very long ovipositor.

Description.—See Robillard et al. (2016).

Remark.—This species is known only by female specimens until now, which makes it difficult to place it in a genus among the Lebinthina because several genera share the same general shape, such as *Rugabinthus* and *Macrobinthus*, while being mostly characterized by male characters (FW venation and genitalia). A molecular phylogenetic study in preparation revealed that this species belongs to the clade corresponding to *Rugabinthus*, justifying the new combination proposed here.

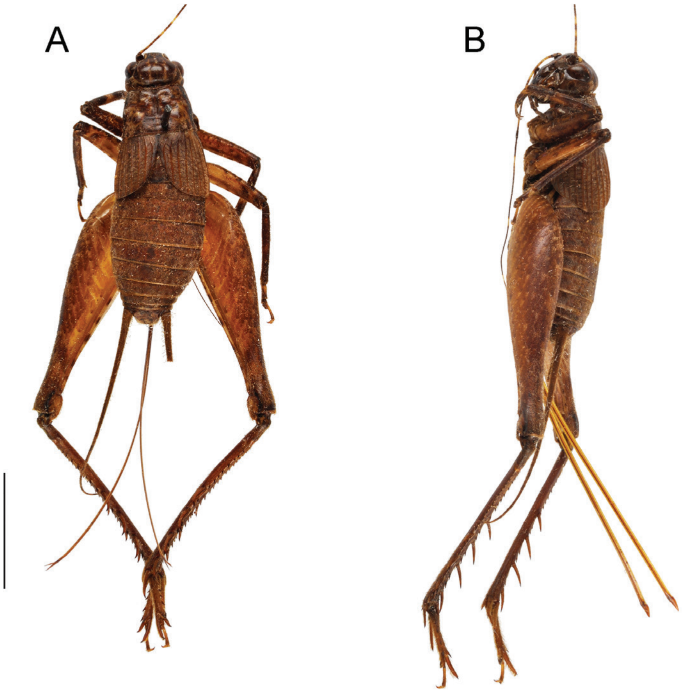

Fig. 27. *R. newguineae* (Bhowmik, 1981) **comb. nov.** female habitus in dorsal (**A**) and lateral (**B**) views. Scale bar: 10 mm. Modified from Robillard et al. (2016)

Key to species of *Rugabinthus*

1 Frons mostly whitish/cream-colored with some dark patterns; scapes whitish..*R. baduri*
– Frons mostly dark colored; scapes dark colored.. 2
2 Distinctly larger, PronL > 4.5 mm ....*R. newguineae*
– Smaller, PronL < 4.0 mm 3
3 Dorsum of head with broad red brown bands narrowly separated. Pronotum dorsal disk generally red brown, sometimes with few lighter patterns.. 4
– Dorsum of head yellow brown with five well-separated red brown longitudinal bands. Pronotum dorsal disk yellow brown with dark patterns.. 12
4 From Faowi 5
– From other parts of New Guinea and not in Faowi 7
5 Pronotum dorsal disk with lateral parts entirely yellow brown or cream-colored, appearing like a lateral bands (even with brown spots within this band).. 6
– Pronotum dorsal disk unicolorous brown or only with sparse yellow brown patterns..*R. tariku*
6 Face black. Labrum yellow brown. Male FWs longer, FWL > 5.5 mm, reaching middle of third abdominal tergite ....*R. mamberamo*
– Face brown. Labrum cream-colored. Male FWs shorter, FWL < 4.5 mm reaching middle of fourth abdominal tergite..*R. faowi*
7 Pseudepiphallus with apex forming two long straight lophi with subacute apices ....*R. albatros*
– Pseudepiphallus with apex truncated or tapering, not producing into two long lophi 8
8 Pseudepiphallus with apex truncated.. 9
– Pseudepiphallus with apex tapered..10
9 Male FWs shorter, < 5.0 mm. Fastigium verticis brown with two vertical yellow brown stripes diverging ventrad. Pseudepiphallic parameres strongly bent in basal half (~90°), with posterior apex enlarged, bean-shaped ....*R. leopoldi* (Chopard, 1931)
– Male FWs longer, > 5.0 mm. Fastigium verticis red brown with a faint yellow brown T-shaped pattern. Pseudepiphallic parameres with inner process in middle with apical half triangular..*R. yayukae*
10 Male FWs longer, > 6.0 mm. Pseudepiphallus elongated, slenderer... 11
– Male FWs shorter, < 5.0 mm. Pseudepiphallus triangular, stouter ....*R. nabire*
11 Smaller in size, male FIIIL < 17.0 mm. Male genitalia distinctly smaller, endophallic apodeme with lateral lamellas pointing posteriorly. Distribution: Kuala Kencana ....*R. kencana*
– Larger in size, male FIIIL > 17.0 mm. Male genitalia distinctly larger, endophallic apodeme with lateral lamellae pointing diagonally more externally. Distribution: Star Range ....*R. maoke*
12 Fastigium verticis and frons black. Labrum cream-colored .... *R. biakis*
– Fastigium verticis black but with some yellow patterns. Labrum darker colored… 13
13 Smaller in size, FIIIL < 10 mm. Fastigium verticis with a pale yellow-brown n-shaped pattern…..*R. karimui*
– Larger in size, FIIIL > 11 mm. Fastigium verticis with a (+) cross-shaped yellow brown pattern…..*R. manokwari*

Discussion

The new genus *Rugabinthus* presented in this study includes 14 species in total, from different parts of the New Guinea Island (mostly in the western part) and from closely related islands (Japen I., Biak I.). Except for two new combinations, most species belonging to the genus are new and are currently known only from a single locality. Given the low numbers of specimens for most of these species, and given that Lebinthini are usually abundant when specifically collected, it would appear that the material studied here originated primarily from anecdotal side collections. Thus, this suggests that a large diversity of crickets from New Guinea remains undocumented; we postulate that the restricted distributions may be due to largely incomplete sampling on the island and that the true distribution of each species is still unknown.

Because close-by localities host very different species, with one locality (Faowi) hosting up to three sympatric species, we hypothesize that the diversity of the genus is underestimated. Evidence also suggests that *Rugabinthus* may show a high level of endemism across New Guinea, similar to or higher than the endemism documented in New Caledonia for *Agnoteccous*, another genus of Lebinthina (Desutter-Grandcolas and Robillard 2005, Nattier et al. 2012). Adding *Rugabinthus* to the already high number of Lebinthini reported from New Guinea, in tandem with their morphological and acoustic diversity (Robillard et al. 2016, Tan et al. 2021, Tan and Robillard 2021c), suggests that this large island may have played a major role in the diversification of these crickets, as found at the scale of the genus *Cardiodactylus* (Dong et al. 2018).

Furthermore, there is little biological data existing for species of *Rugabinthus*. The calls and natural history for this genus are completely unknown, since most of the materials examined here were based on old museum collections. This highlights the importance of continued survey of the vast areas of New Guinea, some parts of which remain unexplored. Emphasis should also be placed on collecting natural history data, including the recording of calls and behaviors, given the importance of Lebinthina species in the study of communication systems.

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A field study on *Saga pedo* (Ensifera, Tettigoniidae, Saginae): Spatial behavior of adult specimens

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Abstract

Despite its large size, the protected predatory bush-cricket *Saga pedo* (Pallas, 1771) is difficult to study in the field. This is mainly due to its strong mimicry, prevalent night activity, and low population density. The aim of this study was to investigate the spatial behavior of some adult individuals through the use of luminescent tags and recording their occurrences at night. The monitored individuals moved considerably during the oviposition period and were found more frequently in small sections of the study area. Two models for count data were implemented to try to explain this behavior. The results indicate that their spatial behavior was predominantly related to the prey availability in the available environment. In addition, predation on the Hymenoptera *Sphex funerarius* Gussakovskij, 1934 is reported for the first time.

Keywords

Count data, Orthoptera, *Sphex funerarius*, UV light, zero-inflated

Introduction

In Europe, *Saga pedo* (Pallas, 1771) is considered the largest insect among Orthoptera (Willemse 1996, Massa et al. 2012, Trizzino et al. 2013). Nevertheless, observing this species in its environment can be difficult, considering its cryptic mimicry and prevailing nocturnal activity (Willemse 1996, Lemonnier-Darcemont et al. 2009, 2016). These traits, combined with the low density that is the result of the species being an obligate predator almost exclusively of other Orthoptera (Kaltenbach 1970, Fontana and Cussigh 1996, Massa et al. 2012, Lemonnier-Darcemont et al. 2016) and the ecology of a parthenogenetic organism (Matthey 1941, 1948, Kaltenbach 1970, Kolics et al. 2012, Lemonnier-Darcemont et al. 2009, 2016), place practical limitations on carrying out field studies. The goal of this study was to investigate the spatial behavior of some adult individuals during the oviposition period by estimating the distances travelled, the relationship between occurrences, and some ecological variables registered in the field.

Marking is commonly used in the field to follow the movements and activities of individual insects and could also be applied to Orthoptera (Gangwere et al. 1964, Hagler and Jackson 2001). Narisu and Schell (1999) described a marking method based on using fluorescent powder that can increase the ease of recapture and reduce the need for manpower and time spent searching. Other authors have successfully experimented with the application of reflective tape on the femur, improving the night re-sighting of specimens (Heller and von Helversen 1990, Hein et al. 2003). A similar marking protocol, but with phosphorescent tags, was also successfully tested on *S. pedo* (Holuša et al. 2013). However, the use of highly visible marks can increase the predation rate. In the present study, I tried to minimize this effect in order to follow the movements of individuals as long as possible during the oviposition period.

S. pedo is included in Appendix II of the Berne Convention and Annex IV of the "Habitats Directive" 92/43/EEC and is classified as LC (Least Concern) in the European IUCN Red List of Threatened Species. However, subpopulations are usually small, and the European population is severely fragmented (Hochkirch et al. 2016).

Methods

Study area.—The study was conducted in NW Italy, in the protected area SCI IT1110030 Oasi xerotermiche della Valle di Susa – Orrido di Chianocco e Foresto. This site hosts vegetation characterized by the presence of Mediterranean and steppic floristic species (Sindaco et al. 2009). Within this site, a survey area of 3745 m^2 was chosen that consisted of a xeric grassland at an altitude of about 625 m above sea level, with southern exposure, a slope of 33%, covered by sparse shrub/tree vegetation and rocks, and surrounded by small wooded areas.

Sampling.—To find the *S. pedo* specimens, the study area was thoroughly inspected on two consecutive sunny days in early August 2019, using a 1.20 m long stick, useful for quickly inspecting the vegetation, as already tested in previous studies on this species (Holuša et al. 2013, Anselmo 2019). Given the aim of the study and the strong cryptic mimicry that characterizes this species, a particular protocol was performed for marking each captured adult specimen. A tag of about 0.8 × 0.8 cm was attached around the right hind femur, consisting of green-yellow adhesive tape fluorescing only under ultraviolet (UV) light and reinforced with a bead of strong glue. A unique identification code has been applied to each tag. The time taken to carry out the marking operations was approximately five minutes per individual, mainly to allow the glue to set. The manipulation and marking protocol were authorized by the Italian Institute for Environmental Protection and Research (ISPRA).

Afterwards, the survey area was covered every four nights from early August to early September (from 10 pm to 1 am), spotting the marked individuals thanks to a powerful blacklight (i.e., Wood's lamp) and the luminescence of the tags, which were visible up to 8 m away. For each recapture, the insect's exact position and behavior were reported.

Ecological covariates.—The variables used for the analysis were measured on 15 August 2019 in sunny and windless conditions. To do this, the aerial imagery of the survey area was divided into a 3 × 3 m grid with QGIS (ver. 2.18.25), and the resulting map was used as a cartographic base in a GPS device. Data from the following covariates were collected in each of the resulting 416 grid cells: an estimate of prey abundance obtained from the sum of the number of Orthoptera and Mantodea trapped within a standard sampling surface of 0.16 m^2 (defined in the field by a plastic cylinder) used three times randomly on the ground; visual estimate of the percentage of bare soil; visual estimate of the average height of the grass; and presence/absence of tree or shrub.

Data analysis.—The movements of each insect were analyzed with QGIS (ver. 2.18.25), measuring the linear distances between the occurrences in each survey recorded with a GPS.

To investigate the relationships between the occurrences of the specimens and the ecological covariates, two generalized linear models (GLM) for count data were produced. GLM are commonly used for count data, with family Poisson or negative binomial (P or NB) depending on the distribution of the response variable (Zuur et al. 2009). If the response variable contains more zeros than expected in the frequency distribution, mixture models such as zero-inflated (ZI) or two-part models such as hurdle (H) are used (Zuur et al. 2009). When zero inflation is present, the frequency distribution of the response variable has a large spike at zero, a common situation for ecological count data (Welsh et al. 1996, Cunningham and Lindenmayer 2005, Martin et al. 2005, Wenger and Freeman 2008, Zuur et al. 2009, Lyashevska et al. 2016). Within the ZI models,d zero-inflated Poisson (ZIP) and zero-inflated negative binomial (ZINB) are distinguished, depending on whether there is overdispersion in the count data (Zuur et al. 2009).

The models were performed for two different count data for each grid cell, referring to the whole study period: the number of individuals and the number of occupancy events. All combinations of ecological variables were used to implement the models after checking for the absence of strong correlations between them. The selection of the models was made based on the Akaike Information Criterion (AIC), a widely used evaluation method to compare models (Zuur et al. 2009). All statistical analyses were performed in R (ver. 3.6.3).

Results

Sampling and behavioral observations.—Seven *Saga pedo* adult specimens were captured, marked, and released on 2 and 3 August, 2019. Most individuals were sampled on the first day of research (n = 5). It was possible to spot the individuals on tufts of grass at a height between 5 and 30 cm from the ground (mean = 13 cm, SD = 8 cm), two of which were seen consuming freshly caught prey: *Mantis religiosa* Linnaeus, 1758 and *Sphex funerarius* Gussakovskij, 1934 (Fig. 1). Three *S. pedo* were at the base of the same bush, with a distance of about 50 cm between them.

The recapture was performed every four nights, from 3 August 2019 until 5 September 2019, consisting of nine surveys. It was possible to spot the specimens up to 8 m on tufts of grass, on bushes, and on bare soil at a height between 0 and 98 cm from the ground (mean = 24 cm, SD = 20 cm). However, some individuals

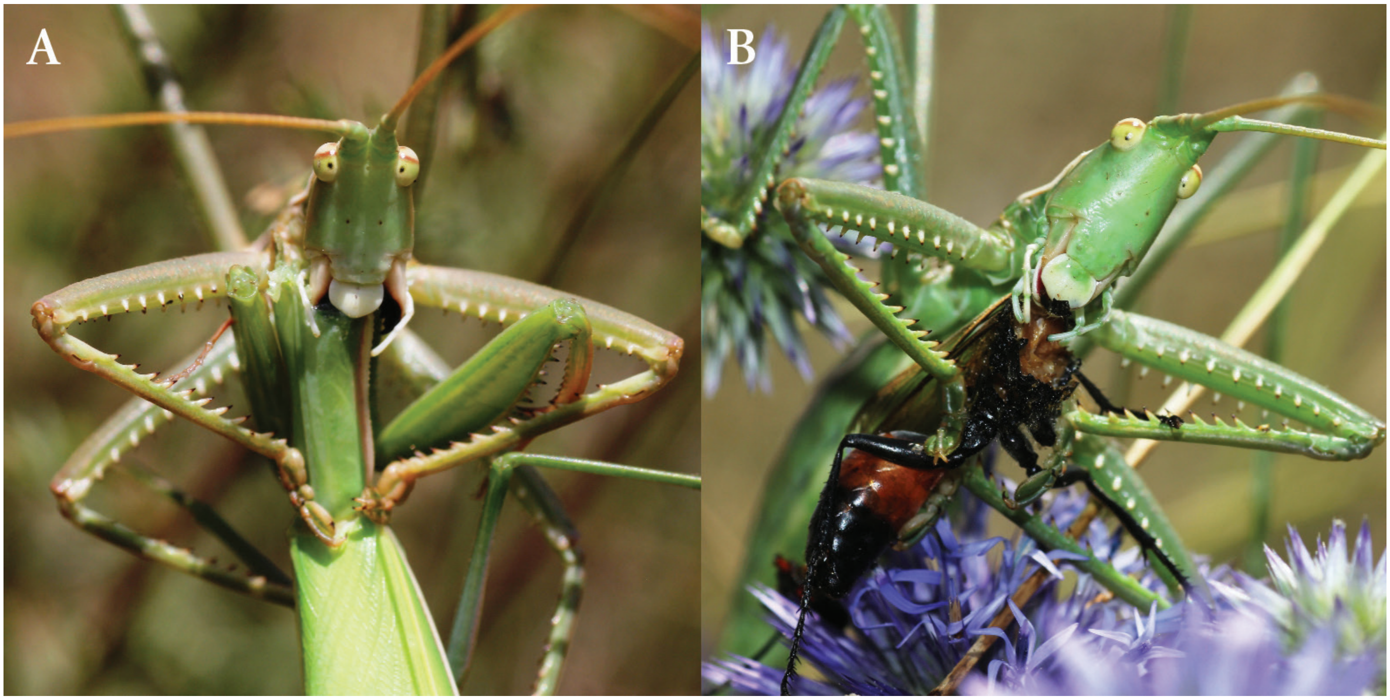

Fig. 1. Behavioral observations. **A.** Predation on *Mantis religiosa*; **B.** Predation on *Sphex funerarius*.

Fig. 2. Behavioral observations. **A.** Oviposition (7 August 2019, 23:05 pm); **B.** Ovipositor cleaning (11 August 2019, 22:30 pm).

were not recaptured in every survey (Table 1). In the recapture surveys, the individuals were apparently motionless, and in 3 cases, it was possible to observe oviposition (Fig. 2A). One individual was observed cleaning the ovipositor, behavior that suggests recent laying of the eggs (Lemonnier-Darcemont et al. 2016) (Fig. 2B). On some occasions, 2–3 individuals were found simultaneously, with less than 100 cm between them.

Table 1. Recapture events of marked individuals during the monitoring period.

ID	Survey date								
	3.VIII	7.VIII	11.VIII	15.VIII	19.VIII	23.VIII	27.VIII	1.IX	5.IX
A01	•		•	•	•	•	•	•	•
A02	•	•	•	•	•	•	•	•	•
A03	•	•		•	•	•		•	
A04	•	•	•	•			•	•	•
A05	•	•		•	•	•		•	
B01	•	•	•	•	•	•		•	
B02	•			•	•	•	•	•	•

Data analysis.—The individual distance travelled during the whole study period has wide variability, between 18 and 201 m (mean = 96 m, SD = 63 m), which is the sum of the linear distances measured between the occurrences for each individual (Fig. 3).

To better understand the use of space made by the species, some models were implemented based on the ecological covariates collected. All the count data show strong positive skewness, with zero-inflation in frequency distribution (Fig. 4A); this was confirmed using the vcdExtra package in R (Friendly and Meyer 2016). Therefore, the ZIP and ZINB models were chosen as implemented in the countreg package in R (Zeileis et al. 2008). The models that best explain the two different types of count data are ZIP models with only the covariate of the abundance of the potential prey (Table 2). The hanging rootograms (Kleiber and Zeileis 2016) in Fig. 4B show the models fitting for the two-count data: departures from expected counts are smaller, and the zero-count bin is always well fitted. However, there were some small deviations from the observed data, particularly in the highest counts.

Discussion

Saga pedo individuals regularly move for hunting, shelter, or laying eggs (Lemmonier-Darcemont et al. 2016). Holuša et al. (2013), in a study done in the Czech Republic, reported daily distances for adults between 0.5 and 2 m, with peaks at 14 and 37.5 m. Richard (2010) found a mean of 2.87 m in a favorable habitat in France. Thus, as confirmed by the results of the present case study, *S. pedo* individuals show a remarkable capacity for movement. To make a comparison, if we divide the mean distance traveled by individuals by the 33 days of the entire study period, we can estimate a mean daily shift of 2.9 m. Moreover, it cannot be ruled out that the tags applied to individuals limited the displacements to some extent. Without marking, individuals might be expected to move more easily and thus cover more distances.

Following the movements of the small sample of monitored *S. pedo*, it can be said that the spatial behavior seems related to specific ecological conditions. As evidenced by the models, the marked individuals mostly frequented the areas particularly rich in Orthoptera and Manotidea prey. The two types of modelled count data express this evidence quite differently: the number of different individuals that occupied the cells shows that some of these are especially attractive, particularly those characterized by high availability of prey. The number of occupancy events indicates a greater likelihood of observing the species in these cells rather than in those with scarce availability of food resources. Furthermore, individuals were sometimes spotted simultaneously on these sites, within a short distance of each other. This suggests that the species constantly moves to hunt and is able to identify the best places to do so. Therefore, in the

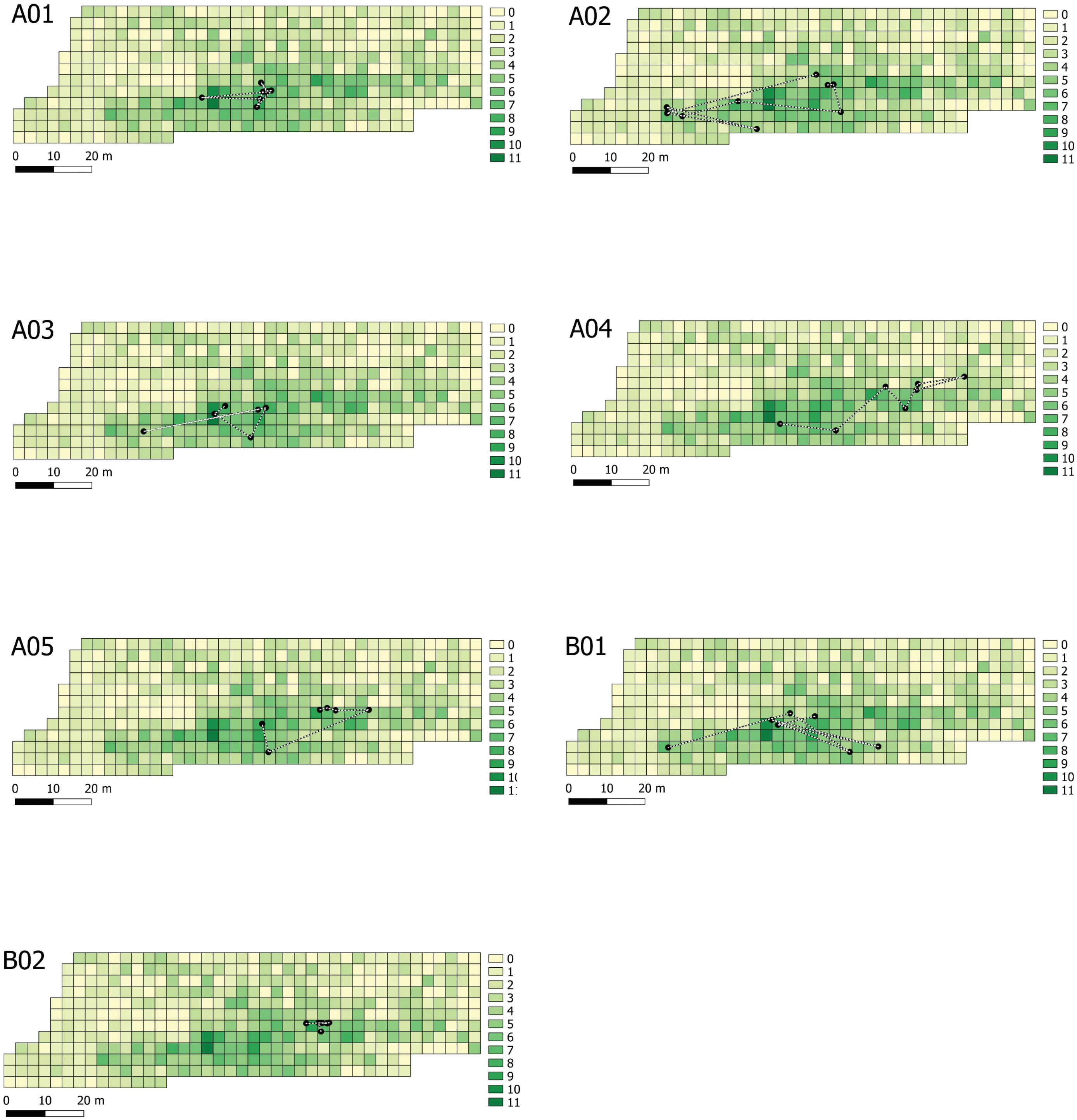

Fig. 3. Displacements of individuals monitored (lines and points) and abundance of prey in the grid cells (green scale).

case of discontinuous prey density, the possibility of observing more than one individual at a short distance becomes possible, and this could at least partially explain other aggregation events reported by Kaltenbach (1970), Fontana and Cussigh (1996), Carrière (2004), and Anselmo (2019).

The marking method was fairly efficient; in most cases, it was possible to spot individuals from a considerable distance. However, not all individuals were recaptured in every survey. This could be due to the difficulty encountered in spotting the tags at ground level, when individuals were among the bottom of the grass, or because they may have moved away from the study area; it is also possible that some individuals died due to predation or a natural decrease in abundance.

Predation on *Sphex funerarius* represents the first such observation made in nature and indicates that *S. pedo* can feed on other orders of insects in addition to Orthoptera and Mantodea, as was believed until recently (Kaltenbach 1970, Fontana and Cussigh 1996, Massa et al. 2012, Lemonnier-Darcemont et al. 2016). Conservation of *S. pedo* should include efforts to maintain high availability and diversity of prey through high biodiversity in grasslands.

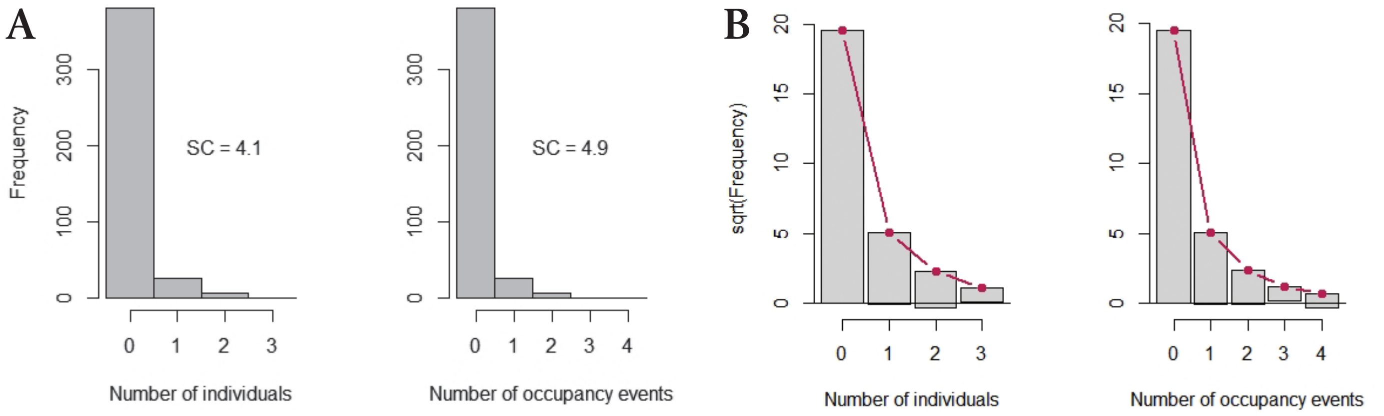

Fig. 4. A. Frequency distribution of count data in the grid cells (SC =skewness coefficient). **B.** Hanging rootograms of best models. Expected counts are shown by the thick line and observed counts are shown as bars. Bar not reaching the zero line indicates that the model over predicts the count; bar exceeding the zero line indicates that the model under predicts the count.

Table 2. Results of the models. The best supported covariate combination for each model is shown with the corresponding AIC score. Letters correspond to the following covariates: A = abundance of potential prey; B = percentage of bare soil; C = average height of the grass; D = presence/absence of tree or shrub.

Model	Number of individuals		Number of occupancy events	
	Covariate	AIC	Covariate	AIC
ZIP	A	171.6	A	176.9
ZINB	A + B + C + D	171.9	A	178.8

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Nemobius sylvestris (Orthoptera, Trigonidiidae, Nemobiinae) in North America

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Abstract

The wood cricket *Nemobius sylvestris* (Bosc, 1792) is herein reported in North America for the first time. The species is currently known to be established in the vicinity of Rochester, New York, and Seattle, Washington, indicating two separate introductions. It is unclear when the species was first introduced to the region, nor what its potential ecological effects may be. The presence of this species in the USA was first noted via photos posted to iNaturalist, highlighting the value of citizen/community science platforms in detecting novel introductions.

Keywords

introduced species, United States

Introduction

Introduced insect species in North America have been of significant public interest in recent years due to the establishment and subsequent spread of major invasive pests such as the emerald ash borer *Agrilus planipennis* Fairmaire, 1888, and spotted lanternfly *Lycorma delicatula* (White, 1845) (Herms and McCullough 2014, Lee et al. 2019). The insect order Orthoptera contains some of the world's most significant pest species, including the desert locust *Schistocerca gregaria* Forsskål, 1775 (Song 2004), yet of the approximately 18 nonnative species of Orthopterans established in North America, only five have reached pest proportions, all crickets. Three species of South American *Neoscapteriscus* Cadena-Castañeda, 2015, mole crickets established for decades in the southern USA are major turfgrass pests but have been controlled in recent years due to the combined efforts of several different biocontrol agents (Frank and Walker 2006). The European mole cricket *Gryllotalpa gryllotalpa* (Linnaeus, 1758), introduced into the northeastern USA, was responsible for root damage in nurseries in New Jersey (Weiss 1915). An unidentified species of *Orocharis* (currently misidentified on SINA as *Xenogryllus unipartitus* (Karny, 1915) (Tony Robillard pers. com.) caused damage to lychee groves in Homestead, FL, during the 1990s (SINA 2021). Introduced members of other orthopteran families, such as Tettigoniidae (katydids), have not affected humans so far and appear to have negligible ecological impact.

Newly introduced organisms may be noticed first by private citizens. Recently, citizen/community platforms such as iNaturalist.org have provided the first detection for numerous introduced species and helped in tracking the expanding ranges of such species (Agarwal 2017, Pelozuelo et al. 2020). In this note, I report on the establishment of a European species of cricket, *Nemobius sylvestris* (Bosc, 1792) (Orthoptera: Trigonidiidae), in the USA that was first detected via iNaturalist. This species is native to much of Europe and northern Africa, where it occurs in the leaf litter of open deciduous woodland edges (Brouwers and Newton 2009). It exhibits a two-year life cycle in the UK in which overwintering eggs hatch in June/July, nymphs develop to 5th instar by fall, overwinter in leaf litter, and mature the following summer (Gabbutt 1959). The species is widespread in its native range but is listed as a species of conservation concern in the UK due to its need for intact woodland habitats (Brouwers and Newton 2009).

Materials and methods

Records.—Photos of an unidentified cricket species were posted to iNaturalist by several different users in late 2020 and early 2021. The author discovered these images while identifying Orthopteran images on the website and recognized that they did not represent any native North American species. Additional records from iNaturalist were found by searching for observations of crickets in the vicinity of the previously located observations, as well as in other states bordering the east and west coasts. The crickets pictured were tentatively determined to be *Nemobius sylvestris* based on comparisons with photos from the Orthoptera Species File online (Cigliano et al. 2021). The author visited the locality of the most recent New York iNaturalist photo on May 24th, 2021 and collected seven nymphs. These individuals were taken into captivity and reared on a diet of carrots, lettuce, and fish flakes. Identification was verified using Vickery and Johnstone (1970) from the adult specimens once these individuals matured. A male and female of *Allonemobius socius* (Scudder, 1877), collected in College Station, Texas, were utilized for comparisons.

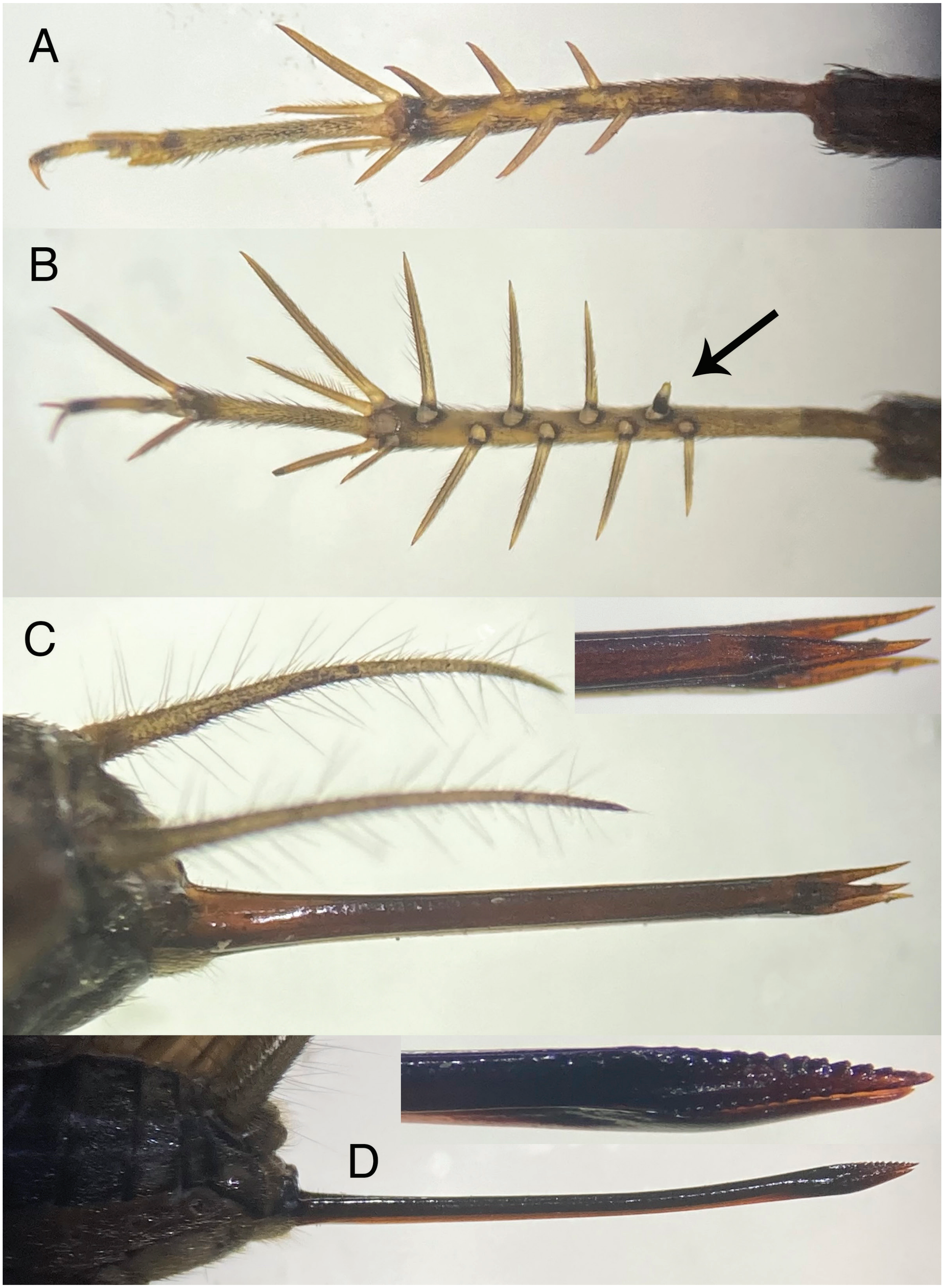

Fig. 1. Morphological characters of *Nemobius sylvestris* compared to *Allonemobius socius*. **A**. *N. sylvestris* male right hind tibia, dorsal view; **B**. *A. socius* male right hind tibia, dorsal view. Arrow points to glandular tibial spine; **C**. *N. sylvestris* ovipositor. Inset shows detail; **D**. *A. socius* ovipositor. Inset shows detail.

Photographs and maps.—Photographs of living specimens were taken using a Canon EOS Rebel T3 with attached Canon 100 mm macro lens and an external flash (Sunpak Auto 383 Super connected with a CowboyStudio 4 Channel Wireless Hot Shoe Flash Trigger and Receiver). Details of the hind tibiae and ovipositor were photographed using an iPhone and a Leica ES2 dissecting scope. All images were processed using Adobe Lightroom CC to crop and adjust white balance. Composite figures were put together with Adobe Photoshop CC. Maps were created with SimpleMappr (Shorthouse 2010). GPS data were acquired using Google Maps.

Specimens.—Specimens are deposited at the Cornell University Insect Collection (CUIC, Ithaca, NY, USA) and the Texas A&M University Insect Collection (TAMUIC, College Station, TX, USA).

Results

Nemobius sylvestris (Bosc, 1792)

Material examined.—USA • 4♂, 3♀; New York, Monroe Co, Channing H. Philbrick Park; 43.127598, -77.482463; 24 May 2021; B. Woo leg;. 1♂, CUIC; 3♂, 3♀, TAMUIC • 1 nymph; same locality; 08 May 2021; https://www.inaturalist.org/observations/78163683 • 1 nymph; same locality; 26 May 2021; https://www.inaturalist.org/observations/80436300 • 1 nymph; same locality; 03 June 2021; https://www.inaturalist.org/observations/82337154 • 1 nymph; same locality; 25 June 2021; https://www.inaturalist.org/observations/84491906 • 1♀; Univ. of Rochester River Campus; 43.131557, -77.631649; 11 September 2020; https://www.inaturalist.org/observations/65836637 • 1♂; MLK Jr. Memorial Park; 43.154131, -77.6023841; 16 July 2021; https://www.inaturalist.org/observations/87327902 • 1 nymph; Washington; King Co.; Renton; 47.4827, -122.225945; 12 May 2021; https://www.inaturalist.org/observations/78524305 • 1 nymph; SeaTac Park; 47.481667, -122.313611; 07 May 2021; https://www.inaturalist.org/observations/82370524 • 1♀; Renton; 07 November 2020; https://www.inaturalist.org/observations/64390177 • 1 nymph; 106th Ave NE; 47.701607, -122.198671; 23 October 2020; https://www.inaturalist.org/observations/63410553 • 1 nymph; Renton; 47.492725, -122.180177; 08 July 2020 https://www.inaturalist.org/observations/52450292 • 1 nymph; Codiga Park; 47.489145, -122.26908; 26 April 2020; https://www.inaturalist.org/observations/43798862 • 1♀; McAuliffe Park; 47.704563, -122.197816; 06 October 2019; https://www.inaturalist.org/observations/34487275 • 1♀; Bothell Landing Park; 47.756939, -122.210152; 07 October 2018; https://www.inaturalist.org/observations/17427199 • 1 nymph; Hitt's Hill Park; 47.55413, -122.285381; 28 April 2018; https://www.inaturalist.org/observations/11708950 • 1 nymph; same locality and date; https://www.inaturalist.org/observations/11708950 • 1 nymph; Lewis Creek Park; 47.550518, -122.124166; 25 May 2017; https://www.inaturalist.org/observations/29595726 • 1♂; White Center; 01 November 2014;https://www.inaturalist.org/observations/1082123 • 1♀; Westcrest Park; 01 November 2014; https://www.inaturalist.org/observations/1054939 • 1 nymph, Pierce Co.; 3rd St. E; 47.257305, -122.180313; 20 June 2020; https://www.inaturalist.org/observations/50369172.

Characters to separate from native North American crickets.—The genus *Nemobius* currently includes six species distributed in the Old World and in the Neotropics, although Barranco et al. (2013) reviewed these six species and concluded that only *N. sylvestris* (the type species of the genus) and their newly described *N. interstitialis* Barranco, Gilgado & Ortuño, 2013, are likely to belong in the genus. *N. interstitialis* can be ruled out since it lacks tympana, possesses differently shaped tegmina, and occurs in a restricted, partially subterranean, rocky habitat (Barranco et al. 2013). Historically, the entire Nemobiine fauna of the USA was included in *Nemobius* (Hebard 1913) before being split into five different genera by Vickery and Johnstone (1970): *Allonemobius*, *Eunemobius*, *Neonemobius*, *Pictonemobius*, and *Hygronemobius*. *Nemobius sylvestris* can be separated from all other members of the subfamily present in North America by several morphological characters, most notably the absence of glandular hind tibial spines in the male (present in males of all North American genera) and female ovipositor shape and tooth dentation (Fig. 1). The ovipositor is straight,about as long as the hind femur, and without teeth. Straight ovipositors are also found in *Allonemobius* and *Pictonemobius*, but these genera possess large teeth on the upper valves (Vickery and Johnstone 1970). The distoventral spurs of the hind tibiae of *Nemobius* are unequal in length, with the inner spur slightly shorter than the outer. In the North American genera, these spurs are either equal in length or the inner spur is much longer than the outer. In the field, both adults and nymphs of *N. sylvestris* may be recognized by their unique color pattern, which is unlike any other North American nemobiine: head black with pale Y-shaped marking, and pronotum very pale with dark speckles (Figs 2, 3).

In Washington (WA), the only other nemobiine species present is *Allonemobius fasciatus* (De Geer, 1773), which has the distoventral spurs more robust, with the inner spur longer than the outer. It also has a toothed ovipositor as described above, as well as longitudinal stripes on the head that are absent in *Nemobius. A. fasciatus* occurs in open grassy meadows as opposed to the woodland leaf litter habitat of *N. sylvestris*.

In New York (NY), there are five species of *Allonemobius*, two of *Neonemobius*, and one of *Eunemobius*. These are all readily distinguishable from *Nemobius* by the hind tibial spur armature, ovipositor shape, and color patterns. All of these species are also univoltine, with only eggs overwintering. Habitat is another useful clue—of the eight native NY species, only three habitually inhabit woodland leaf litter.

Habitat and phenology in New York State.—At Channing H. Philbrick Park, nymphs (Fig. 2) were collected in leaf litter of a small patch of forest surrounded by suburbs. Although the major forest trees were native species, such as *Platanus occidentalis* L., most of the lower vegetation in the area consisted of introduced invasive European plants, including *Chelidonium majus* L., *Vincetoxicum rossicum* (Kleopow) Barbar., *Artemisia vulgaris* Burm.f., *Alliaria petiolata* (M.Bieb.) Cavara & Grande, *Vinca minor* L., and *Hedera helix* L.. Nymphs of *Nemobius sylvestris* were easy to collect as they were far less active than native NY ground crickets (pers. obs.). Individuals cohabitated well and were never seen to cannibalize. In captivity under similar temperature conditions to outdoors, the first male matured on June 20th and the first female on June 28th.

Discussion

This note represents the first documented occurrence of *Nemobius sylvestris* in North America and is also the first Nearctic record of the genus *Nemobius* as currently defined; a thorough taxonomic revision of the genus is needed. As in its native range, the species overwinters as mid-instar nymphs here, with adults living from

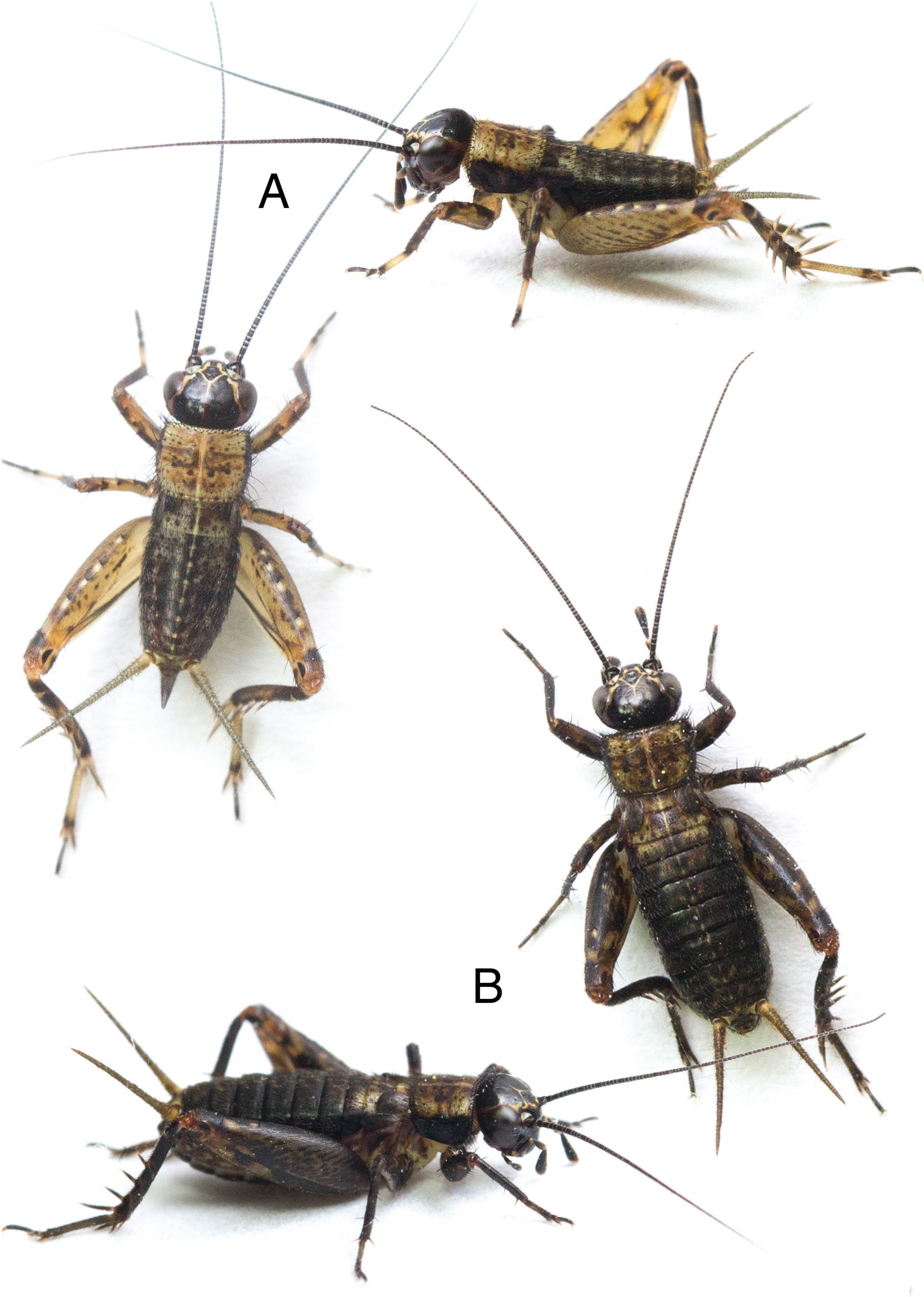

Fig. 2. *Nemobius sylvestris* female (**A**) and male (**B**) nymphs from Channing H. Philbrick Park.

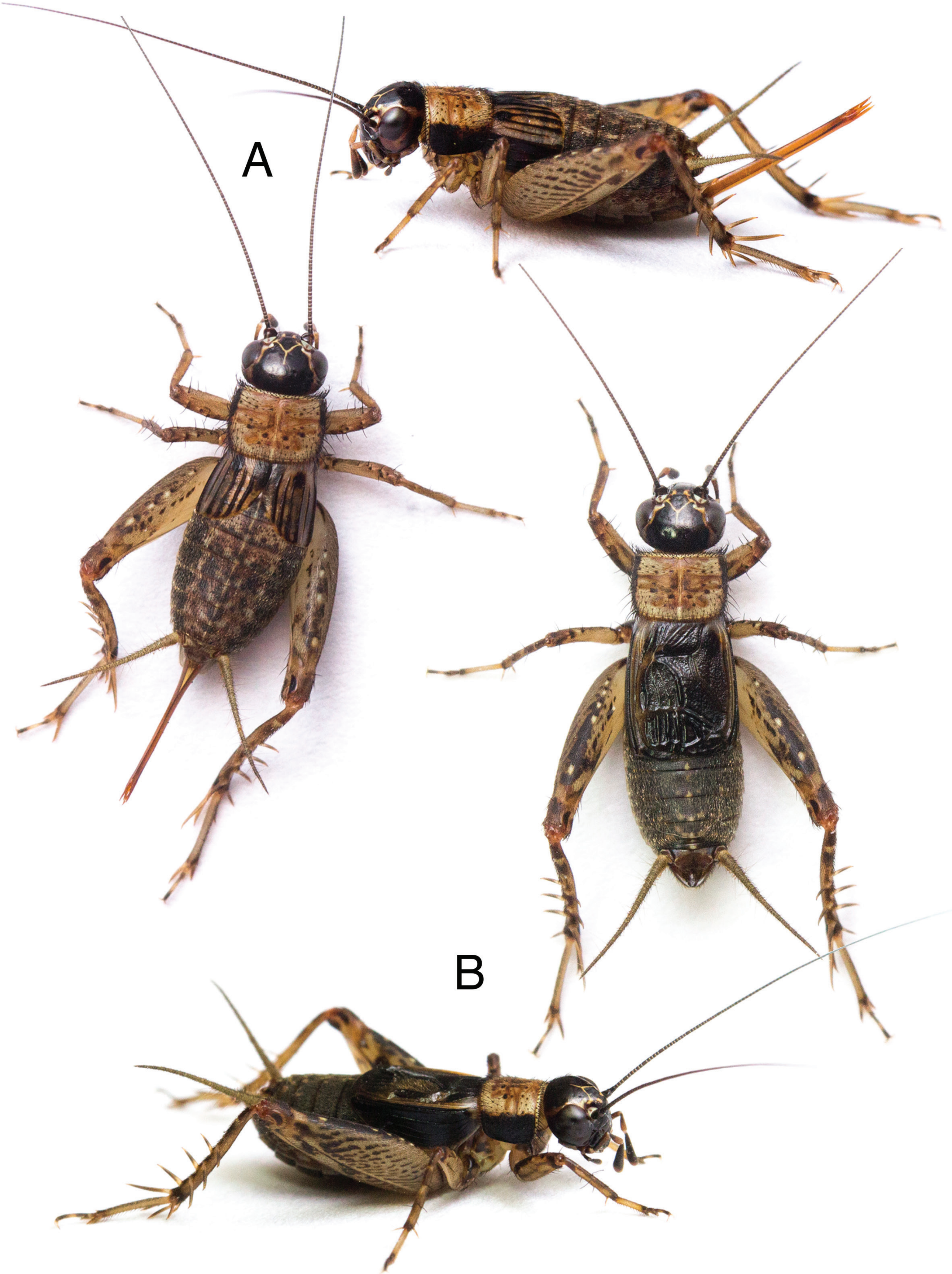

Fig. 3. *Nemobius sylvestris* female (**A**) and male (**B**) adults from Channing H. Philbrick Park.

Fig. 4. Current documented distribution of *Nemobius sylvestris* in the USA.

early summer until fall. Further work would be needed to confirm the presence of the two-year life cycle in North American populations. In searching through cricket images from across the USA, the author was only able to find putative *Nemobius* images from WA and NY. These two widely separated populations (Fig. 4) are around cities with much commerce and international exchange. The WA population has been present since at least 2014 and is so far known only from photos; although the insects in the photos are readily separable from any other cricket species occurring in the area based on color pattern, specimens should be collected from this area to properly document their presence. The NY population has been present since at least 2020. It is unknown how long the species has actually occurred in the USA, since it is inconspicuous and does not occur in homes or damage agricultural crops. *N. sylvestris* is unlikely to become a pest due to its generalist feeding habits and current restriction to habitats containing mainly introduced species. It may, however, eventually spread to more intact native forests, where its effects on native leaf litter fauna cannot be predicted. There is another introduced European Orthopteran in the Rochester NY area, *Leptophyes punctatissima* (Bosc, 1792), that has also apparently escaped notice for quite some time and continues to have a restricted range (SINA 2021). Genetic comparisons of the introduced populations with those in Europe would be warranted to determine their exact origins. The introduced populations of these Orthopteran species should be monitored to detect range expansions or any negative effects on native flora and fauna.

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First records of three exotic giant mantid species on the Croatian coast

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Abstract

Some giant mantid species of the genera *Sphodromantis* Stål, 1871 and *Hierodula* Burmeister, 1838 have been found spreading their distribution through the Palearctic, but none of the species have been recorded from the Adriatic coast of Croatia, where numerous local species already coexist, such as *Mantis religiosa* (Linnaeus, 1758) and *Iris oratoria* (Linnaeus, 1758). In this study, we present the first records of the giant African mantis (*Sphodromantis viridis* (Forskål, 1775)), the Indochina mantis (*Hierodula patellifera* Serville, 1839), and the giant Asian mantis (*Hierodula tenuidentata* Saussure, 1869) from Croatia. A small population of *S. viridis* was observed in the southernmost county of Croatia (Dubrovnik); a single record of *H. patellifera* comes from the westernmost part of the country (Istria), while the first two specimens of *H. tenuidentata* were observed in the central part of the Croatian coast (Šibenik). These alien species represent three new taxa for the mantid fauna of Croatia, which now counts 9 or 10 species (depending on inclusion of *Ameles heldreichi* Brunner von Wattenwyl, 1882). The fast spreading of these species in Europe proves their adaptation to regions where they have arrived; thus, future monitoring of the species must be conducted in order to determine their impact on native fauna.

Keywords

alien, allochtonous, Dubrovnik, Europe, *Hierodula patellifera*, *Hierodula tenuidentata*, Istria, Mantodea, new records, Šibenik, *Sphodromantis viridis*, spreading

Introduction

Mantids are large predatory insects, so people have been observing them from prehistory (Battiston et al. 2010, Kolnegari et al. 2020). More than 2500 species are known (Otte et al. 2021), with the greatest diversity being in the tropical regions (Schwarz and Roy 2019, Otte et al. 2021). Mantid fauna of the Western palearctic consists of about 130 species (Battiston et al. 2010), while, for example, Vietnam is home to almost 70 species (Shcherbakov and Anisyutkin 2018). Few species are shared between tropical and temperate regions; this study shines the spotlight on three.

Until now, small Croatian Mantodea fauna consisted of seven species belonging to five genera (*Ameles* Burmeister, 1838, *Empusa* Illiger, 1798, *Geomantis* Pantel, 1896, *Iris* Saussure, 1891 and *Mantis* Linnaeus, 1758) (Rebrina et al. 2014), but the giant African mantis (*Sphodromantis viridis* (Forskål, 1775)), the Indochina mantis (*Hierodula patellifera* Serville, 1839), and the giant Asian mantis (*Hierodula tenuidentata* Saussure, 1869) are expected to spread into the country soon. *S. viridis* is widespread in the sub-Saharan region and is known to be very adaptable to different kinds of environments, including anthropized ones (Battiston et al. 2020a). In Europe, it was known only from Southern Spain (Bolívar 1876, Gangwere and Morales Agacino 1970) until it was recorded in Mallorca (Canyelles and Alomar 2006) and in Central Spain (Cabanillas 2017) and eventually Portugal (Marabuto et al. 2014, Oliveira and Ferreira 2019), France (Battiston et al. 2020a), Italy (Battiston et al. 2017, 2019, 2020a), and Greece (Battiston et al. 2020a). On the other hand, *H. patellifera* and *H. tenuidentata* are native to Asia. The first European records of the former species date back to 2013 in Southern France (Moulin 2020) and 2015 in Italy (Battiston et al. 2020a); the earliest European record of the latter was from Crimea (Werner 1916), where it was rediscovered 100 years later. It is now widespread along the entire coast of the peninsula, from where it started its expansion northwards in other parts of Ukraine (Pushkar and Kavurka 2016). Soon after, European records of *H. tenuidentata* began to be reported frequently. Today, the species is known to be present in Bulgaria and Greece (Romanowski et al. 2019), Albania (van der Heyden 2018), Italy (Battiston et al. 2018), North Macedonia (Cianferoni et al. 2018), Serbia (Vujić et al. 2021), and Romania (Pintilioaie et al. 2021). This study provides further insight into the spread of these species in Europe.

Materials and methods

Hierodula patellifera *finding.*—A single female was found in Novigrad (Istria) on a palm tree near a road edge. The specimen was photographed and uploaded to Biologer (an open platform for collecting biodiversity data) (Popović et al. 2020).

Hierodula tenuidentata *findings.*—Two adult specimens were observed and photographed in the garden center "Dubrava" in Dubrava near Šibenik.

Sphodromantis viridis *findings.*—In early November 2020, an adult male was attracted to the terrace light of a family home on Lapad peninsula in Dubrovnik. The specimen was collected, dry pinned, and deposited in the Dubrovnik Natural History Museum (DNHM). When preparation of the manuscript began based on this single male, the authors were convinced that the male individual represented the only record until it was decided to search the surrounding area for oothecas. Archival photos revealed sighting of a spherical ootheca from November 2019 observed on *Nerium oleander* L. in a camping area close to where the adult male was collected. The camping area (Fig. 4G) was visited again in March 2021, and another ootheca was found.

Online records.—iNaturalist was searched for specimens that could represent *Sphodromantis* or *Hierodula* specimens, and a single photograph depicting a nymph unidentifiable to species level was found (https://www.inaturalist.org/observations/53351490).

Identification and systematics.—The collected specimens were identified based on the morphological characteristics described in Battiston et al. (2019, 2020b). At first glance, giant mantids of the genera *Sphodromantis* and *Hierodula* can be distinguished from the native, similarly sized *Iris oratoria* (Linnaeus, 1758) or *Mantis religiosa* (Linnaeus, 1758) by the presence of white-colored stigmas on the tegmina (Figs 2A, 3A, 4C). Both species of the genus *Hierodula* spreading through Europe (*H. patellifera* and *H. tenuidentata*) have three dark-colored horizontal lines on the ventral part of the thorax (Fig. 2B), which are absent in *S. viridis* (Fig. 4A). Additionally, differences exist in the shape and length of the pronotum, which is long and thin in *Sphodromantis* (Fig. 4B) but short and ovoidal in *Hierodula* (Fig. 3A). The two *Hierodula* species may be separated by the morphology of the inner margin of the anterior coxa. In *H. patellifera*, it is equipped with yellowish spines with basal plates (Fig. 2B, C), while basal plates are absent in *H. tenuidentata* (Fig. 3B). The higher systematics follow Battiston et al. 2010, while species nomenclature follows the Mantodea species file (Otte et al. 2021). In the literature, *H. tenuidentata* is sometimes reported under its synonym, *T. transcaucasica*. Most probably, *H. tenuidentata*

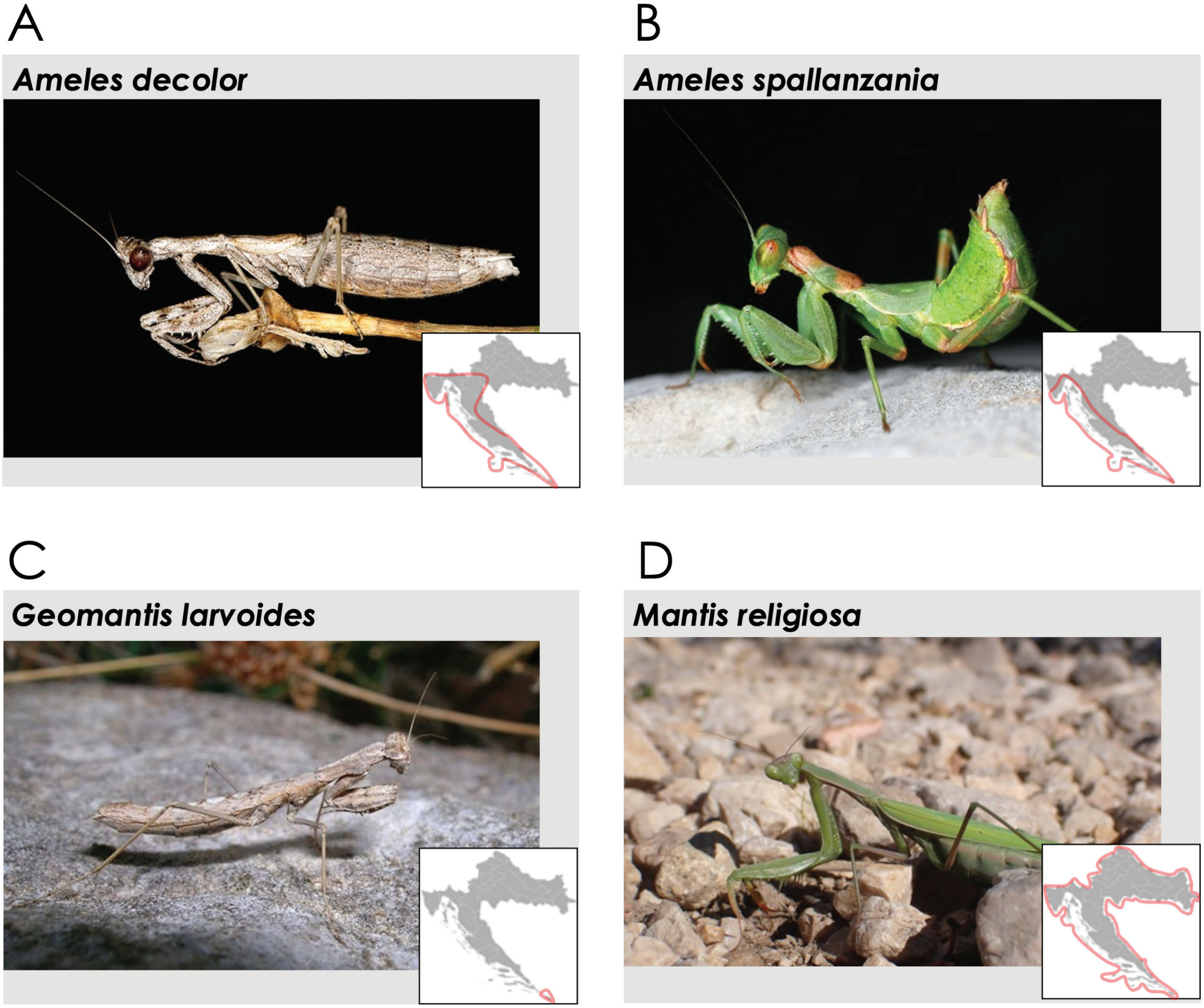

Fig. 1. Native Croatian Amelidae and Mantidae representatives and their distribution areas in Croatia. **A.** *Ameles decolor*; **B.** *Ameles spallanzania*; **C.** *Geomantis larvoides*; **D.** *Mantis religiosa*. (Photo credit **A, B**. Gernot Kunz; **C.** Radomir Jaskula; **D.** Matea Martinović).

represents a single species distributed from India to Europe (Battiston et al. 2018).

Results

Order Mantodea

Family Mantidae Burmeister, 1838

Composition and distribution in Croatia.—Hitherto, at least four species belonging to three genera (*Ameles*, *Mantis*, *Geomantis*) have been reported from the country (Rebrina et al. 2014). In current taxonomy (Schwarz and Roy 2019), *Ameles* belongs to Amelidae; thus, it is no longer included in Mantidae, so the following checklist includes members of both families in the Croatian fauna. Distribution follows data from Rebrina et al. (2014), GBIF (2021), and iNaturalist (2021). This study presents the first records of members of two more genera, *Hierodula* and *Sphodromantis*, found to be present in Croatia.

Checklist of genera and species of Croatian Amelidae and Mantidae with new records of alien taxa

Genus *Ameles* Burmeister, 1838

Species *A. decolor* (Charpentier, 1825) (Fig. 1A), common in the Adriatic and Dinaric regions.

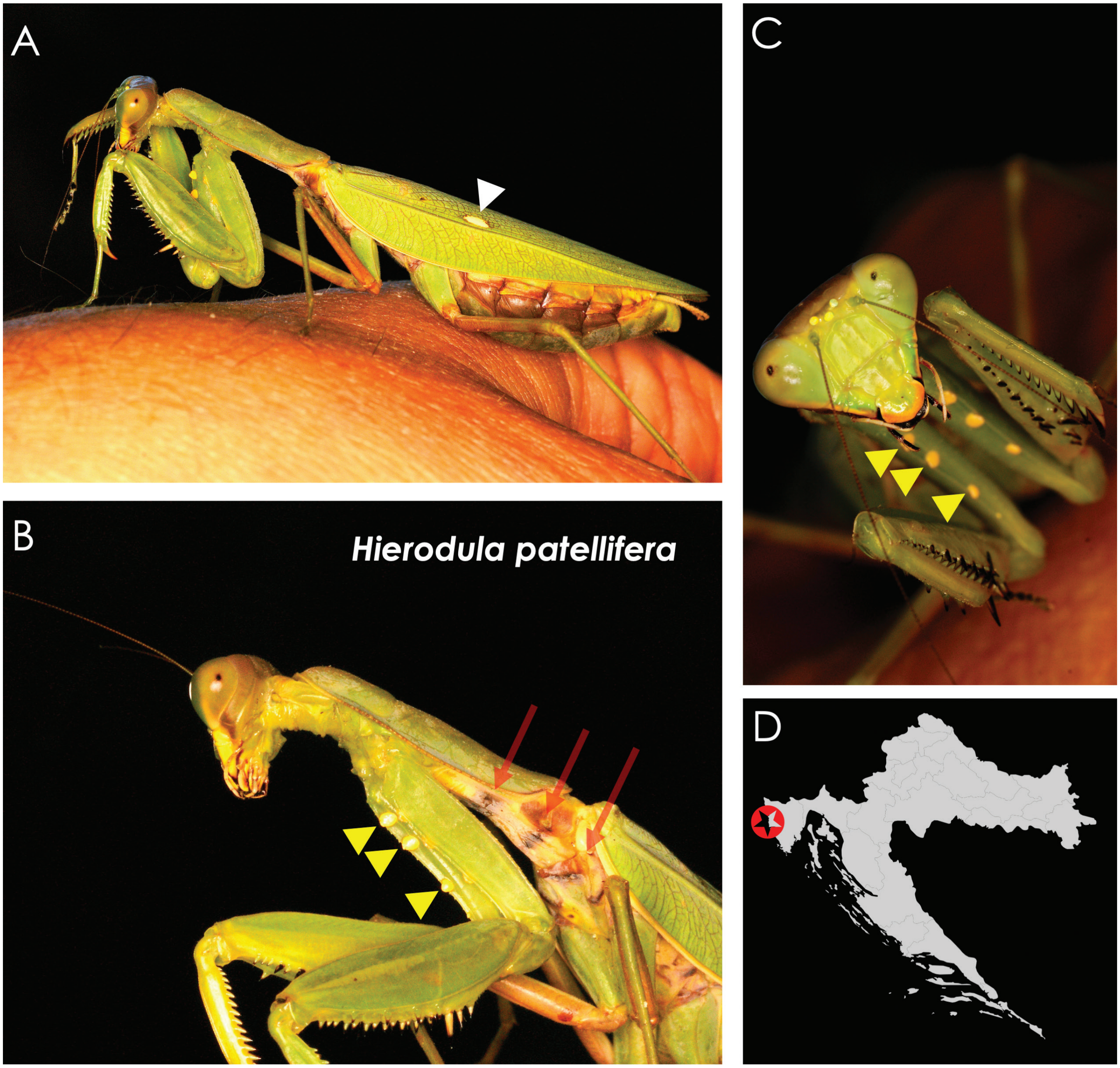

Fig. 2. *Hierodula patellifera* Serville, 1839, female. **A**. Presence of the white-colored stigma on the tegmina; **B**. Lateral view, yellow spines with basal plates on the anterior coxa and dark-colored horizontal lines on the ventral part of the thorax; **C**. Frontal view, yellow spines with basal plates on the anterior coxa; **D**. Map with locality of the first Croatian record, western-most part of the Adriatic coast. Photo credit: Marko Lengar.

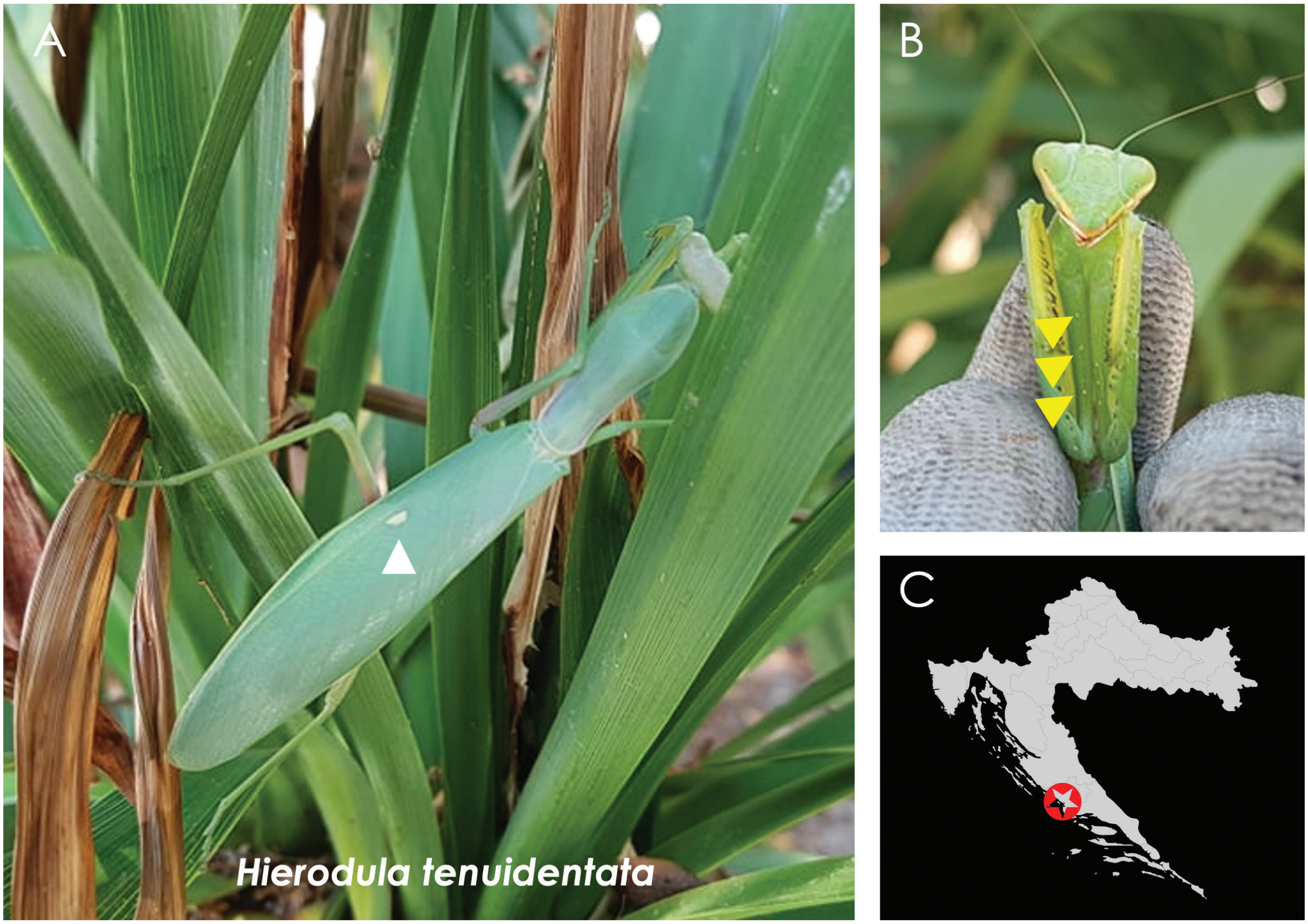

Fig. 3. *Hierodula tenuidentata* Saussure, 1869, female. **A**. Dorsal view, presence of white-colored stigma on the tegmina, pronotum; **B**. Ventral view, yellow spines without basal plates on the anterior coxa; **C**. Map with locality of the first Croatian record, central part of the Adriatic coast. Photo credit: Sebastian Ćato.

** Species *A. heldreichi* Brunner von Wattenwyl, 1882, could be present in the far south. Presence of *A. heldreichi* in the Adriatic coast is doubtful (M. Villani, pers. comm.). Shape of the eyes is unreliable diagnostic trait, so the reports of *A. heldreichi* from Croatia are questionable; all records should be regarded as *A. decolor*.

Species *A. spallanzania* (Rossi, 1792) (Fig. 1B), common in the Adriatic and Dinaric regions.

Genus *Geomantis* Pantel, 1896

Species *G. larvoides* Pantel, 1896 (Fig. 1C), known only from Dubrovnik Area.

Genus *Hierodula* Burmeister, 1838

Species *H. patellifera* Serville, 1839, newly reported for the country (Fig. 2)

First record for Croatia.—1♀; Istria County: Novigrad: Dajla, residental area [45°21′05.7″N, 13°32′42.8″E], 6 m a.s.l., 21.XI.2020, obs. M. Lengar.

Species *H. tenuidentata* Saussure, 1869, newly reported for the country (Fig. 3)

First record for Croatia.—1♀ and 1♂; Šibenik-Knin County: Šibenik: Dubrava kod Šibenika, Garden center "Dubrava" [43°44′08.7″N, 15°56′46.4″E], 84 m a.s.l., 21.VIII.2021, obs. S. Ćato.

Genus *Mantis* Linnaeus, 1758

Species *M. religiosa* (Linnaeus, 1758) (Fig. 1D), widespread in whole country.

Genus *Sphodromantis* Stål, 1871

Species *S. viridis* (Forskål, 1775), newly reported for the country (Fig. 4).

First records for Croatia.—(1/3) ootheca (Fig. 4D), Dubrovnik-Neretva County: Dubrovnik: Lapad peninsula, camping area [42°39′47.7″N, 18°04′11.8″E], 23 m a.s.l., 11.XI.2019, obs. M. Martinović; (2/3) ootheca (Fig. 4E), same place as the first one, 26.III.2021, obs. M. Martinović; (3/3) 1♂ Dubrovnik-Neretva

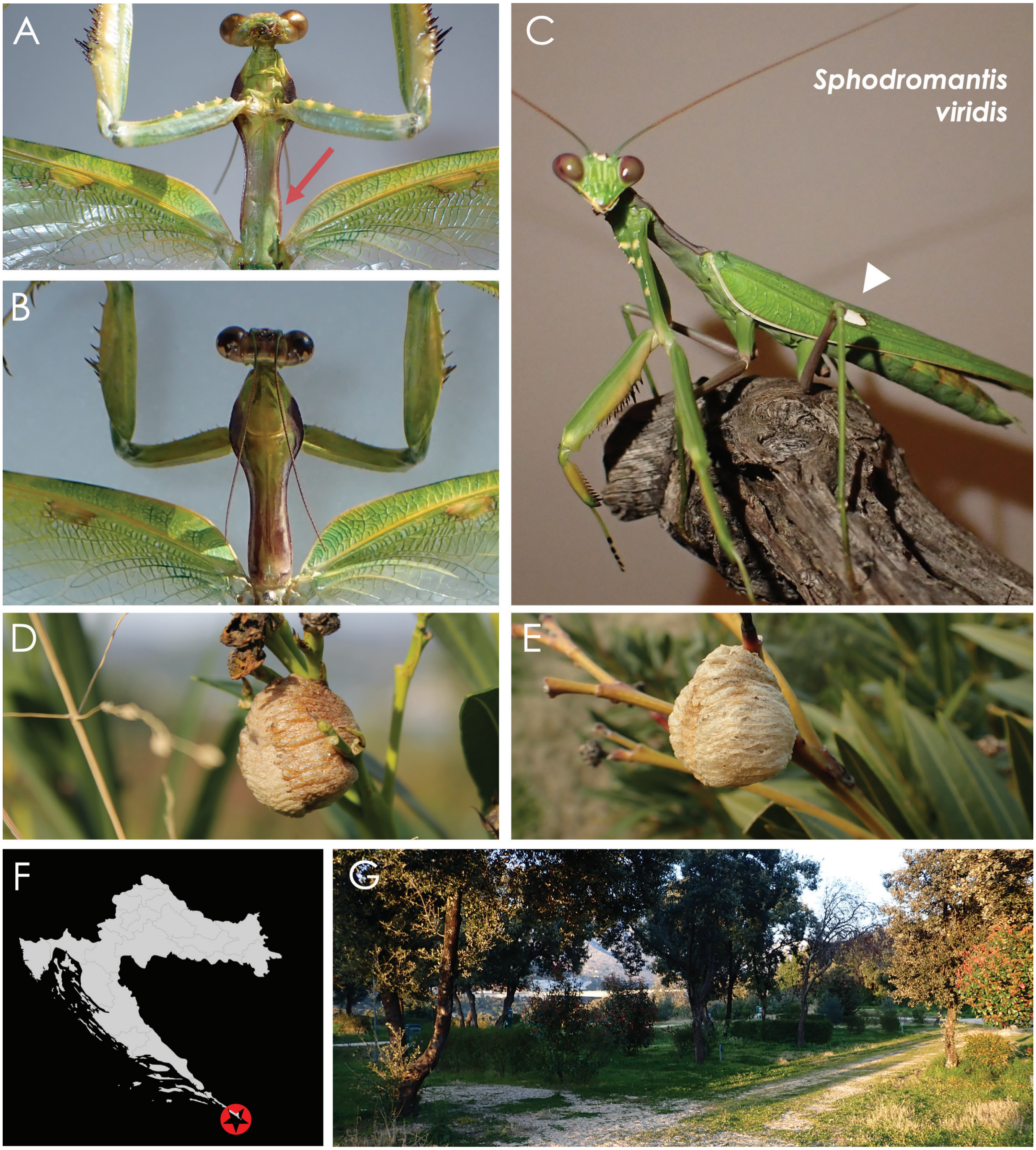

Fig. 4. *Sphodromantis viridis* (Forskål, 1775), male. **A**. Absence of the dark-colored horizontal lines on the ventral part of the thorax; **B**. Pronotum; **C**. Presence of the white-colored stigma on the tegmina; **D**. Ootheca from 2019; **E**. Ootheca from 2021; **F**. Map with locality of the first Croatian record, southernmost part of the Adriatic coast; **G**. Camping area and habitat where small population of *S. viridis* was established. Photo credit: Matea Martinović.

County: Dubrovnik: Lapad, residential area, [42°39′39.5″N, 18°04′42.1″E], 12 m a.s.l., 3.XI.2020, obs. & coll. M. Martinović.

Taxa not identified to species level.—Besides the new records identified to species level, a juvenile specimen was observed on 13th July 2020 by Dennis Aagaard in a small tourist area called Zaton near Zadar; the photo was published on iNaturalist (observation number 53351490). The nymph in the photo has its abdomen bended at an angle of 90°, which is a diagnostic character related to the juvenile stages of both *S. viridis* and *Hierodula* species. Nymphs of

M. religiosa have the abdomen held parallel to the ground from the first to the last moult (Battiston et al. 2019). Although not identifiable to the species level from the photo, this record signals the possibility that *H. tenuidentata* Saussure, 1869 is already widespread in Dalmatia. More records are anticipated soon.

Discussion

Finding a single male of an allochthonous mantid species could be overlooked, but finding two oothecas at the same place two years apart suggests that a small population of *S. viridis* has been established in Southern Croatia (Fig. 4F). Dubrovnik is on the itineraries of many cruise ships, and it is included in both Western and Eastern Mediterranean cruise routes. During their round-trip excursions, some cruise ships visit several port cities in southern Spain, France, Italy, Cyprus, Turkey, and Greece, which are already inhabited by *S. viridis*, before arrival in Dubrovnik. The cruise-ship route probably served as a pathway of introduction for *S. viridis* to Croatia. The locality where the small population of *S. viridis* was recorded is situated on the Lapad peninsula, right at the entrance to the Port of Dubrovnik. The species is likely attracted to the lights of ships staying the night in the Mediterranean ports within the species' distribution area; in this way, they arrive in Dubrovnik as a blind passenger, either from the western Mediterranean (Southern Spain) or from the Middle East (Cyprus, Turkey). This hypothesis is in accordance with insights on the human-assisted speed of expansion of *S. viridis* across the Mediterranean region (Battiston et al. 2020a). However, there are many other plausible causes. For example, oothecae may have come attached to plants or other commercial goods or attached to tourists' cars or personal items. Finding two specimens of *H. tenuidentata* in the garden center "Dubrava" in Dubrava near Šibenik (Fig. 3C) adds credence to the possibility of human-assisted expansion of this species in Europe, as the garden center sells plants imported from various areas in Italy where *H. tenuidentata* is known to be present (Battiston et al. 2018). Unfortunately, a lack of evidence means we can only propose hypotheses to be tested by future dispersals within the region. We will continue to monitor the garden center in order to assess whether the species already has the population established.

As in France and Italy where individuals of *H. patellifera* were observed mainly on trees (Battiston et al. 2020b, Moulin 2020), the female specimen found in late November 2020 on a palm tree is further confirmation of the arboreal habits of this species. The arrival of *H. patellifera* in the westernmost part of the Croatian Adriatic (Fig. 2D) is likely a result of natural dispersal from the neighboring Northern Italy where several fragmented and reproducing sub-populations exist (Battiston et al. 2020b).

There is currently no evidence of invasive behavior from these alien species. However, they have only been present for a short period, and their impact on local fauna should be determined by detailed research conducted over the span of many years. Comparative studies are needed to determine whether *Hierodula* and *Sphodromantis* represent direct competition to *Mantis*, *Iris*, or *Empusa*. *Sphodromantis* is not expected to spread much, as it prefers habitats influenced by the Mediterranean climate. *Hierodula* species are, however, expected to spread more, considering that *H. tenuidentata* is already surviving the cold Pannonian winters in Serbia (Vujić et al. 2021). On the other hand, the native area of distribution of *H. patellifera* includes localities with similar climate, such as that of Northern Italy and Central Europe (Battiston et al. 2020b). Thus, *Hierodula* can be expected to colonize the Mediterranean, Pannonian, and the Dinaric region.

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The pet mantis market: a first overview on the praying mantis international trade (Insecta, Mantodea)

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Abstract

Praying mantises have recently gained popularity as domestic pets. Moreover, they are increasingly being bred and sold in fairs and pet markets or collected in the wild and reared by amateurs or professional marketers for the hobbyist community. This market is not well known, and its implications on the biology and conservation of these insects are complex and difficult to predict. For this study, a comprehensive survey was submitted to various hobbyists within this community to evaluate their knowledge of these insects and to assess their preferences for certain species characteristics (such as shape, color, behaviors, dimensions, ease of breeding, and rarity) over others. The aggregation of this data allowed for the generation of a formula that is herein proposed to predict targets and developments within the market in order to help identify conservation issues for vulnerable species. Both problems and opportunities of the pet mantis market are discussed, such as the absence of specific regulations or the potential for a stronger collaboration between the market community and scientists.

Keywords

animal selling, biodiversity, breeding, conservation, hobby, insects, laws

Introduction

Over the last decade, interest in insects as domestic pets has shown a remarkable increase. From the first butterfly farms launched in the mid-nineteenth century that produced exhibits for museums and public insectariums, the market of these unconventional pets has shifted towards pet shops and domestic rearing. This novel market has yet to be investigated from a scientific perspective, and the few statistical data available are mostly outdated, even though this market is quite financially lucrative. Within the butterfly trade alone, top suppliers generate about 100 million dollars each year worldwide (Parson 1992). In more recent years, pet shops, insect fairs, and markets have introduced other exotic insects and other invertebrates, such as beetles, stick insects, mantises, spiders, scorpions, and snails. These market introductions are typically small in number but may experience unexpected booms. For example, when the price for a single adult stag beetle reached approximately $5,000 in Japan, the country introduced a law to allow more species to be imported each year, with an average total annual increase of about 375% from 1999 to 2003 (Goka et al. 2004).

Before the actual size of this trading industry was determined, the first evidence of an existing black market appeared in press media (e.g., FOX19 (2020), The Sun US (2020), WDRB Media (2020)), suggesting that its value was already significant and increasing. Although data exists concerning the trade of some butterflies and a few beetles (15 genera of Lepidoptera and 2 of Coleoptera are listed in the CITES appendices and discussed in international laws), almost nothing is known about orthopteroid insects such as stick insects and mantises. In particular, after their first appearance in some thematic insect fairs (see Fig. 1) some decades ago, mantises now have a constant presence in many general pet animal fairs/markets in Europe, USA, and Japan—the three world regions known to be principal importers of exotic insect pets. Rearing mantises at home is not easy and requires at least some basic knowledge on the biology of these insects—sometimes even of the particular species—which is something that has yet to be detailed by scientific literature. Despite these problems, the number of social media posts and the proliferation of specific pages on mantis rearing and breeding suggests that the interest in keeping mantises as pets has increased dramatically in recent years.

The conservation of mantises is also an almost unexplored field (Battiston 2014, Battiston et al. 2014), as this group of insects suffers from data deficiency in taxonomy, population trends, threats, and the impact of commerce that hinders their inclusion on red lists and in legislation. For example, law and policy regulations are explicitly invoked, even if on different/unknown scales, as conservation action is needed for three data deficient mantis species in the IUCN Red List of Threatened

Fig. 1. Mantises sold in an exotic animal market fair in Italy. Photo credit R. Battiston.

Species (*Perlamantis alliberti* Guerin-Meneville, 1843, in Battiston 2020; *Empusa pennicornis* Pallas, 1773 in Shcherbakov and Battiston 2020a; and *Iris polystictica* Fischer-Waldheim, 1846 in Shcherbakov and Battiston 2020b). In the recently compiled IUCN red list assessments of the Mantodea of Europe, 12 of the 37 species listed and assessed at a global level are classified as of least concern, 9 as threatened or extinct, and 16 as data deficient (IUCN Red List of Threatened Species – Mantodea). Europe is neither the richest region for mantis diversity nor the most representative for these insects, but it is probably the most entomologically well-known and studied area. Even with this long tradition of scientific research, the knowledge and conservation of these insects is still poor.

Almost no data exist on collecting activities and quantities in the wild and how collecting may impact a species that is abundant in its habitat. The voluntary or accidental release of a reared exotic species into foreign ecosystems is also a problem. *Mantis religiosa* Linnaeus, 1758 and *Tenodera sinensis* Saussure, 1871 were accidentally introduced in the late nineteenth century into the USA. These species were then bred as a biological control agent and spread in large numbers over most of the country, where they now have a stable population, but their impact is still not well understood (Anderson 2018). More significant is the case of *Miomantis* Saussure, 1870, an African mantis frequently bred commercially and privately, that was recently found in the wild with vital populations in Portugal (Marabuto 2014), USA (Anderson 2018), and New Zealand, where it is impacting the local species (Fea et al. 2013). In the last few years, the mantis fauna of Europe have greatly increased; this increase has been hypothesized to be due to the diffusion of exotic species in nature and the resultant competition with native species (Battiston et al. 2018, 2020, Schwarz and Ehrmann 2018, Shcherbakov and Govorov 2020). Their origin, whether from escaped/released pet breedings or from oothecae attached to trading goods, is still under debate, but each species probably has its own history.

Because of the lack of direct data on this market, especially from the supply side, we collected indirect information from consumers through a survey designed to analyze the desires of buyers of insects as domestic pets. These data were then used to estimate the direction of this market by pointing out the possible targeted genera or species from a conservation perspective.

Materials and methods

During 2018, an online anonymous survey was used to collect information from mantis enthusiasts. The survey was translated into different languages (English, Italian, Spanish, and Russian) and spread around the internet primarily though social media and web communities known to deal with general entomology or those specific to mantises. The survey consisted of 24 questions on four main areas of investigation: 1) generalities on the compiler and motivation to buy and rear mantises, 2) relationship between the compiler and the market, 3) knowledge of the compiler on the

Table 1. Principal descriptive characters used to identify the commercial value of a species divided by the main categories (shape, colors, behaviors, dimensions, ease of breeding, and rarity on the market) and the value points (from 1 to 5) given to each.

Value Points	Shape	Color	Behavior	Dimensions (Adult)	Ease Of Breeding	Rarity
1	Generalist	Homogeneous	No particular behaviors	Very small (<3 cm)	Low resistance of the species outside their natural habitat	Available in almost any insect fair/market
2	Slightly lobed	Heterogeneous	Specialized cryptic posture	Small (3–5 cm)	Terrarium that accurately replicates the specie's natural habitat	Uncommon species in fairs/shops
3	Evident expansions	Some particular aposematic/ cryptic colors	Particular aposematic or deimatic posture	Medium (5–7 cm)	Daily control over the main habitat parameters (temp., hum., food)	Rare species, available mostly through direct contact
4	Peculiar	Evident aposematic and/or cryptic colors	Unique static postures	Large (7–9 cm)	Species moderately adaptable to different habitat parameters	Species held only by very few breeders
5	Unique and spectacular	Unique camouflage and/ or aposematic coloration	Complex rituals (mating, hunting, etc.)	Huge (>9 cm)	Species very adaptable and anthropophilic	Species not yet introduced in the market

international animal trade market and its regulations, and 4) perception of the problems and opportunities that arise from buying and rearing mantises.

Based on the answers to the preferred characters considered in the choice of a certain species of mantis (Table 1), a predictive formula is proposed here to estimate the general value of a single species on the market to *a priori* predict how the market may evolve and determine which species may be the targets of trade in the near future.

Each of the identified characters—shape (S), colors (C), behaviors (B), dimensions (D), ease of breeding (E), and rarity on the market (R)—was rated in the survey from 1 (less important) to 5 (most important). Subsequently, each of these characters was weighted considering their relative importance as reported in the survey. These weights (respectively: a, b, c, d, e, f) were calculated from the sum of the relative number of votes obtained in the survey for each character over the total and given in percentages.

The economic value (V) of each mantis species was calculated using the sum of all the characters values proposed as variables (respectively S, C, B, D, E, R) multiplied for their relative weight coefficients obtained from the preferences given in the survey, and two additional coefficients (X, Y) were included to level out the output value according to present market prices as the best fitting model. This last calibration on the current market prices was done using a second survey presented to 10 known sellers from different European countries who specialize in mantises, asking them to give a price for a sub-adult or adult individual from a list of the best-selling mantis species in the present market.

The final formula to calculate and forecast the economic value (V) of a mantis species is as follows:

$$V = \frac{Sa + Cb + Bc + Dd + Ee + Rf}{X} + Y$$

For this study, the mantis market was monitored and studied from 2018 to 2022 using social media and websites. To evaluate the interest in mantises as pets, the Google Trends tool was used to compare the appearance of the general keyword 'mantis' in the Google search engine from January 2004 to January 2022 and all over the world in all categories versus the category "pets and animals". Since the word 'mantis' also refers to well-known comic superheroes, video game characters, or non-insect animals, the following keywords were excluded for in the search: marvel, comics, shrimp, guardians, and game.

Results

A total of 181 surveys from 28 countries were compiled and processed. The participants in this survey ranged in age from 19 to 30 years (53%), and most bought mantises for personal curiosity (39%) or scientific/professional interest (29%). Beautiful looking species (52%) were preferred over rare ones (11%), and the ease of rearing the species was essentially irrelevant (9%). To obtain a beautiful species, the typical breeder/enthusiast expressed being willing to spend over \$30 (27%), while a general price ranging between \$20 and \$30 was considered good for a single mantis individual (46%). For the privilege of rearing exclusive/rare species, spending an amount over the average was considered reasonable by approximately one in every four participants (26%). The preferred choice of insect stage was mostly young nymphs (44%) or oothecae (14%), which are usually less expensive than adults (9%). A low price is sometimes more important than the stage (14%), but many buyers also consider the shipping circumstances, such as the distance and time needed for transport (19%).

More than 80 genera of mantis are currently sold and reared, but 6 are most common and preferred—*Hierodula* Burmeister, 1838 (23%), *Phyllocrania* Burmeister, 1838 (21%), *Creobroter* Westwood, 1889 (14%), *Sphodromantis* Stål, 1871 (12%), *Mantis* Linnaeus, 1758 (12%), and *Hymenopus* Serville, 1831 (11%)—over others (7%).

The relationship of the buyer with the seller is usually transparent (73%), and trade seems to take place mostly on the white market, but approximately one in every four transactions leave the buyer perceiving a lack of transparency from the seller or are done without the appropriate permits. In shipping, the contents of a package carrying a living mantis is often explicit, especially where required (29%), but the insect is usually not declared, mostly in an attempt to bypass customs bureaucracy or avoid problems caused by delayed delivery of delicate, live insects.

The participants frequently reported that a mantis in their possession did not come from the market; rather, it was directly collected in the wild (59%) and, in this case, it was usually reared until natural death (31%) or released near the place of capture (25%). The insect was released several kilometers away from the collecting place in only a few cases. Collecting in the wild was rarely declared by the seller, but it was privately communicated or understood by the buyer in 26% of transactions.

The participants' average knowledge on mantis-trade legislation was mostly low or fragmented, especially at the international level: 77 to 90% of the answers on this subject (ranging from CITES annexes to the Nagoya protocol) were identified as not known or incorrect.

The formula proposed to calculate the current mantis value (V) of a species considering the variable characters obtained from the survey is as follows:

$$V = \frac{2.5S + 1.9C + 1.8B + 1.4D + 1.1E + 1.3R}{20} + 2.7$$

When V values were compared with the respective average prices declared by the sellers (Fig. 2), the average error obtained between these two values for each species was 16%. It should be noted that the declared prices varied from one seller to another, with an average difference (max-min) of 30%; price also varied depending on insect stage, with young neanids being cheaper than adults or subadults. Rarity was also a variable character because it changes over time and evolves with the market; however, rarity is a variable that can be changed according to current market conditions.

We found that the trend of the keyword mantis has decreased in the last 18 years (2004–2022), while its presence in the category 'pets and animals' has increased (Fig. 3).

Discussion

The impact of the mantis trade market both on the general animal trade economy and upon conservation of these insects is still far from being fully understood. The general output obtained from our analysis, however, fits well with a young and still rapidly evolving market. The dynamics and average prices spent for these pets are now comparable to that of many fishes, reptiles, birds, or mammals, considering also that the lifetime of mantises is much

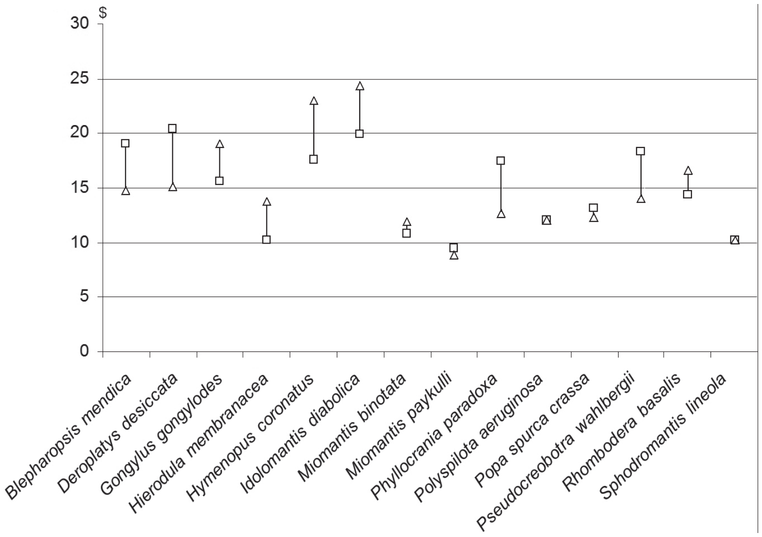

Fig. 2. Average prices (in US dollars, y axis) of the most commonly traded species (x axis) declared by the sellers (triangles) and calculated as the mantis value V (squares).

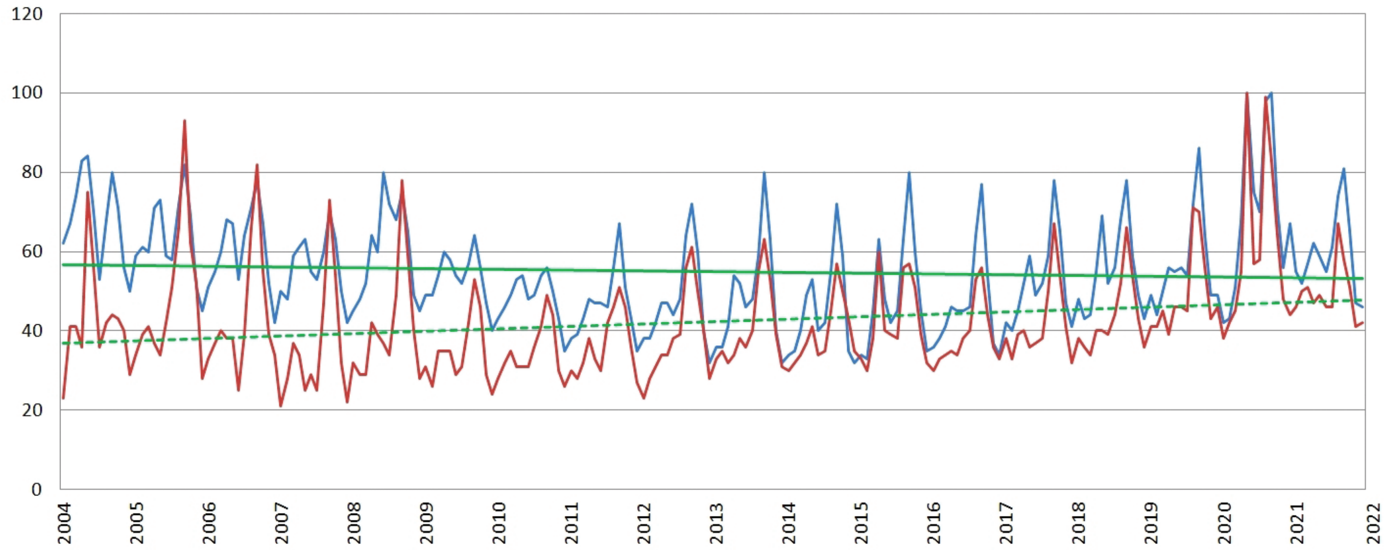

Fig. 3. Google trends of the keyword 'mantis' from 2004 to 2022 (x axis). The appearance (y axis, in a default scale from 0 to 100) of the general term (blue line, continuous green trend-line) is compared to its presence in the category 'pets and animals' (red line, dashed green trend-line).

shorter, on average, than that of vertebrate pets. While this market is probably still a small niche of the global animal trade market, the money that it generates is currently unquantifiable and may hold some surprises.

Buyers are mostly curious enthusiasts with a poor knowledge of the market dynamics and the laws behind it, although they seem to generally care about their pets, collecting information on them and their needs when available. Collecting specimens from the wild instead of rearing them from first instars may be an easier option for many occasional breeders, especially if the breeder resides in a tropical country that host the highest diversity of species as well as the most preferred ones.

The release of exotic species into non-native habitats appears to be limited, and, at this time, the arrival of alien species is more likely to be caused by cargo or accidental transport of oothecae (Battiston et al. 2018, 2020, Shcherbakov and Govorov 2020). However, voluntary pet release should be considered in future studies on the prevention of such spreading, especially related to more generalist and well-adapting species.

It should be noted that spikes in the interest in mantises is rather predictable; most of the internet searches (Fig. 3, positive peaks) identified in this study occurred in September, a month when, in temperate regions, many mantis species reach the adult stage and are more active and visible in nature.

The impact of this market on mantises and their environment remains unquantifiable, but there is evidence that a good number of individuals insects or oothecae are collected in the wild, and this may have a significant impact on the local populations of some species. The high number of oothecae, often collected in nature and in single localities, that are sold through social media sites are a clear sign of this threat, especially when related to uncommon native species (e.g., *Idolomantis diabolica* (Saussure, 1869), one of the rarest, most desirable and highly priced species on the market; Fig. 4). Even more common species already under the pressure of alien competitors, as is the case for *Stagmomantis carolina* (Johansson, 1763) in the United States (Maxwell and Eitan 1998, Anderson 2018), may suffer from intensive field collecting. Also, unpredictable effects may emerge from the commerce of non-native species. Removing oothecae of the Asian *Tenodera angustipennis* Saussure, 1869 from a North American field may be good for the local ecosystem, but these oothecae can spread to other localities, increasing the potential threat on other vulnerable ecosystems; moreover, they are not easily distinguished from the oothecae of *Stagmomantis carolina* (Fig. 4), whose removal can be counterproductive, as explained above.

For future interventions, assigning a price that takes the insect's habitat into consideration may promote the value of nature and biodiversity in specific areas. If the value of a species is predictable, according to the development of the market, specific measures can be taken to protect individual species.

At the present time, the market for insects as domestic pets is almost completely unregulated, and its future is difficult to forecast. On one hand, awareness toward a free market and of the biological needs, threats, and impacts on the species being sold should be promoted. Good conservation legislation should support this development, not general and uncritical replications of the legislation designed for vertebrates, on invertebrates, something that has already started to seriously hinder scientific research (Prathapan et al. 2018, Britz et al. 2020, Williams et al. 2020). Future regulations must allow adjustments for specific species and situations, in accordance with the scientific community.

On the other hand, this market is nearly the only source of information on insects whose biology and ecology are still poorly known and that are difficult to study. This point is reinforced by the status of previously assessed mantis species in the IUCN Red List of Threatened Species, where most mantis species are listed as Data Deficient. Of course, knowledge alone is not enough to save these species from extinction, but it is a valuable foundation. The lack of data on mantises hampers implementation of effective conservation measures (Hochkirch et al. 2021). The community around the mantis pet market is already large and active (Durrant 2003, Maxwell 2011), giving it the potential to be a strong ally in efforts to fill this gap. For this reason, efforts should be made to encourage this community to stay active and work with the scientific community. The value of such collaboration is exemplified by the countless number of scientific papers published using citizen-science data (e.g., Battiston et al. 2021, Moulin 2020) or observations on the biology of wild or

Fig. 4. Stocks of oothecae sold through social media (Facebook groups related to mantis enthusiasts). *Idolomantis diabolica* (Saussure, 1869) from Tanzania (left) and *Stagmomantis carolina* (sold as *Tenodera*) from the United States (right).

reared specimens (e.g., Battiston and Carolo 2018). Improving this relationship will help to identify target species and promote their study, which are important steps toward obtaining more information on their conservation status.

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Citizen scientists track a charismatic carnivore: Mapping the spread and impact of the South African Mantis (Miomantidae, *Miomantis caffra*) in Australia

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Abstract

The recent integration of citizen science with modern technology has greatly increased its applications and has allowed more people than ever to contribute to research across all areas of science. In particular, citizen science has been instrumental in the detection and monitoring of novel introduced species across the globe. This study provides the first records of *Miomantis caffra* Saussure, 1871, the South African Mantis, from the Australian mainland and uses records from four different citizen science and social media platforms in conjunction with museum records to track the spread of the species through the country. A total of 153 wild mantises and oothecae were observed across four states and territories (New South Wales, Norfolk Island, Victoria, and Western Australia) between 2009 and 2021. The large number of observations of the species in Victoria and the more recent isolated observations in other states and territories suggest that the species initially arrived in Geelong via oothecae attached to plants or equipment, likely from the invasive population in New Zealand. From there it established and spread outwards to Melbourne and eventually to other states and territories, both naturally and with the aid of human transport. We also provide a comparison of *M. caffra* to similar native mantises, specifically *Pseudomantis albofimbriata* (Stål, 1860), and comment on the potential impact and further spread of the species within Australia. Finally, we reiterate the many benefits of engaging directly with citizen scientists in biodiversity research and comment on the decision to include them in all levels of this research investigation.

Keywords

citizen science, geographic distribution, introduced species, iNaturalist, Mantodea, ootheca, *Pseudomantis*

Introduction

Citizen science has always provided important contributions to research, but with the integration of modern technology, particularly social media and communication networks, the types of data that can be collected, the potential applications, and the number of people who can participate have increased dramatically (Silvertown 2009, Larson et al. 2020). Of particular importance are broad-scale citizen science projects such as iNaturalist (https://www.inaturalist.org 2021), eBird (https://ebird.org, Sullivan et al. 2009), and QuestaGame (https://questagame.com 2015) that collect and aggregate large amounts of data in the form of species observations from users spread across the world. These observations are a valuable resource to biodiversity and conservation researchers and are increasingly being utilized in conjunction with more traditional data sources for a wide variety of purposes. They provide researchers with an easy and effective way to collect data across a much broader spatial and temporal scale than would be possible with traditional fieldwork alone (Lodge et al. 2006, Silvertown 2009). In just the last four years, these citizen-science projects have been used to discover and describe new species (Winterton 2020, Collins and Velazco-Macias 2021), map the distributions of poorly known species (Skejo et al. 2020), confirm the continued existence of rare threatened species (Wilson et al. 2020), supplement natural history collections with digital data (Heberling and Isaac 2018), reconstruct plant phenology patterns and record anomalous flowering times (Barve et al. 2020), record both pollination (Saul-Gershenz et al. 2020) and herbivory interactions (Gazdic and Groom 2019) between insects and plants, inform conservation regulation decisions for at-risk species (Young et al. 2019), track and monitor urban biodiversity (Callaghan et al. 2020), and rapidly map biodiversity responses after large-scale disturbances (Kirchhoff et al. 2021). However, social media-based citizen science is still very much in its infancy when compared with other research techniques, and many aspects remain largely unexploited.

One of the most important applications of citizen science is the detection and monitoring of introduced species (Groom et al. 2019, Johnson et al. 2020, Larson et al. 2020). In particular, citizen science has been instrumental in the early detection of many introduced species, principally due to the large number of observations produced by members of the public over a wide geographic spread (Lodge et al. 2006, Silvertown 2009, Larson et al. 2020). Citizen scientists can be quickly and easily trained to identify alien species with a high degree of accuracy (Delaney et al. 2008) or to undertake standardized surveys to estimate abundance (Anderson et al. 2017) and can use these skills to collect data over large areas, including on private property (Andow et al. 2016). In addition to these focused citizen-science initiatives, broad-scale citizen-science projects can help to detect introduced species via a more passive approach, with project users uploading observations that can then be identified by experts. These observations have been instrumental in both detecting new introductions of species (Maistrello et al. 2016, Walther and Kampen 2017, Hiller and Haelewaters 2019, Walker et al. 2020) and in documenting range expansions of already-established species (Bowles 2018, Liebgold et al. 2019, Lanner et al. 2021). Citizen science has the capacity to detect introduced species earlier and more frequently than traditional methods (Scyphers et al. 2015), increasing the potential for a successful rapid management response where needed. Furthermore, research has also repeatedly shown that citizen scientists benefit greatly from feedback from experts and the knowledge that their efforts are making a meaningful difference (Geoghegan et al. 2016, Domroese and Johnson 2017, Peters et al. 2017). This has the potential to greatly improve both the quality and quantity of data by retaining existing participants and attracting new ones (Grese et al. 2000, Domroese and Johnson 2017) while increasing the outreach of invasive species management campaigns (Davis et al. 2018).

Although praying mantises are comparatively rare among insect introductions (Nisip et al. 2019), their large size and charismatic appearance means that they are frequently observed and photographed by citizen scientists, enabling novel introductions to be relatively well-documented (Schwarz and Ehrmann 2018, Battiston et al. 2020, Moulin 2020). Mantodean introductions have significantly increased in the past decade (Shcherbakov and Govorov 2020), particularly in Europe (Marabuto 2014, Fernández and Santaeufemia 2016, Moulin 2020, Zlatkov et al. 2020) where the situation has been further complicated by range expansions of native mantises (Schwarz and Ehrmann 2018). These introductions have likely been facilitated by the inadvertent transport of both mantises and oothecae via railways and other commercial routes (Battiston et al. 2020), and it is expected that these will remain important introduction pathways into the future. Recent alien mantis introductions have been less well-documented elsewhere in the world but have been no less pervasive. Within Oceania, for example, at least seventeen species have been introduced outside their historical ranges (*Brunneria borealis* Scudder, 1896; *Hierodula majuscula* (Tindale, 1923); *H. patellifera* (Serville, 1839); *Kongobatha diademata* Hebard, 1920; *Mantis religiosa* (Linnaeus, 1758); *Miomantis caffra* Saussure, 1871; *Orthodera burmeisteri* Wood-Mason, 1889; *O. ministralis* (Fabricius, 1775); *Polyspilota aeruginosa* (Goeze, 1778); *Pseudomantis albofimbriata* (Stål, 1860); *Sibylla pretiosa* Stål, 1856; *Statilia maculata* (Thunberg, 1784); *S. pallida* Werner, 1922; *Tenodera angustipennis* Saussure, 1869; *T. australasiae* (Leach, 1814); *T. sinensis* Saussure, 1871; *Tropidomantis tenera* (Stål, 1860)), particularly in Hawaii, and yet less than a quarter of these have been extensively documented and only three quarters have been documented in the literature at all (Swezey 1921, 1933, Williams 1934, Pemberton 1952, Chong 1965, Joyce 1969, Beier 1972, Mau 1976, Ramsay 1990, Kevan and Vickery 1997, Ramage and Roy 2014, Fearn 2018). The remainder are known only from citizen science observations posted to iNaturalist, where several new introductions have been recorded since 2020 (Britstra 2020, Fitzgerald 2020, Li 2020, Klein 2021).

The most notable Oceanian mantodean introduction has been that of the South African Mantis (*Miomantis caffra*) in New Zealand. A hardy and adaptable species, *M. caffra* has also been introduced elsewhere in the world, including in Portugal (Marabuto 2014) and California (Anderson 2018). In New Zealand, *M. caffra* was first found in Auckland in 1978 (Ramsay 1984) and subsequently expanded its range to Kaitaia in the north and Waiuku in the south by the late 1980s (Ramsay 1990). It has now spread throughout the entire North Island and has been found as far south as Christchurch on the South Island (Bowie 2017). *Miomantis caffra* is not known to be a pest in its native range; however, in New Zealand it is displacing the native *Orthodera novaezealandiae*

(Colenso, 1882) (Ramsay 1990, Fea et al. 2013). In addition to producing many more offspring than *O. novaezealandiae* (Ramsay 1990) and being able to reproduce parthenogenetically (Walker and Holwell 2016), female *M. caffra* also produce pheromones that inadvertently attract male *O. novaezealandiae*, frequently resulting in the deaths of the native males (Fea et al. 2013).

In this study, we present the first formal records of *M. caffra* from mainland Australia. The species was first recorded in Geelong, Victoria, in 2015 (Walker 2015), but photographic records of the species extend back as far as 2009, and it has been known from Norfolk Island since 2014 (Australian Government Department of Agriculture 2015, Maynard et al. 2018). Records from the citizen science platforms iNaturalist (https://www.inaturalist.org, 2021), QuestaGame (https://questagame.com, 2015), and BowerBird (http://bowerbird.org.au, no longer accessible, Walker 2014) and the social media site Facebook (https://www.facebook.com) were used in conjunction with museum specimens and records directly from the field to map the spread of *M. caffra* in Australia over the past decade. Additionally, we discuss the potential negative effects of *M. caffra* on the native Australian fauna, provide information on identifying the species with reference to similar Australian mantises, and outline the many benefits of engaging directly with citizen scientists.

Materials and methods

Online citizen science and social media.—Observations of *Miomantis caffra* were located on iNaturalist (https://www.inaturalist.org 2021) by manually screening all Australian observations of Mantodea. These included observations transferred from the now-defunct citizen science platform BowerBird (http://bowerbird.org.au, no longer accessible, Walker 2014) and observations from QuestaGame (https://questagame.com, 2015), another broad-scale citizen-science project. The Atlas of Living Australia (ALA) (https://www.ala.org.au 2010) was also manually searched for records of Australian Mantodea with images. Records from all ALA data sources except iNaturalist were viewed to find observations of *M. caffra*. Additionally, manual photo searches were conducted on the photograph-sharing website Flickr (https://www.flickr.com) using the search terms "Mantis", "Mantid", "Mantodea", and "Miomantis". Sightings of *M. caffra* were also searched for in the Facebook groups Amateur Entomology Australia (https://www.facebook.com/groups/AmateurEntomologyAustralia, no longer accessible), Amateur @ Professional Australian Entomology (https://www.facebook.com/groups/1158046414207850), Australian Marsupials, Reptiles, Amphibians, Invertebrates and Plants (https://www.facebook.com/groups/144261675750262), Australian Native Animals (https://www.facebook.com/groups/401945966623460), Australian Praying Mantis Group (https://www.facebook.com/groups/319900008113408), Field Naturalists Club of Victoria (https://www.facebook.com/groups/191099460990243), and Insect Identification Australia – Pest or Friend (https://www.facebook.com/groups/476897096018877, now renamed), using the search terms "Miomantis caffra" and "South African Mantis". All searches were conducted in March 2021 and were updated with additional observations from iNaturalist and Facebook until October 2021. All sightings were annotated with a life stage (ootheca, nymph, or adult), and all nymphs and adults were sexed if the photographs were detailed enough to do so. Information from observations was copied manually to ensure uniformity across data sources, and records from different platforms were compared to ensure the removal of duplicates.

Field collection and museum specimens.—To enable a detailed description of the species, oothecae were collected from the field by Matthew G. Connors in October 2020, and oothecae and an adult were collected by MGC and Brendan Wallis in May 2021. *Miomantis caffra* specimens held by the Museum of Victoria (MV) (Melbourne, Victoria) and specimens in the personal collection of Honglei Chen were also inspected. Specimens from Norfolk Island referenced in Maynard et al. (2018), held in the Australian National Insect Collection (ANIC) (Canberra, Australian Capital Territory), and three additional specimens from the collection were also included. Due to the ongoing COVID-19 pandemic, the specimens held in MV and ANIC were not inspected in person; however, detailed collection information on them was available. The specimens held by the former were identified by G. Milledge (Australian Museum, Sydney, Australia) (S. Hinkley, pers. comm. 2020), and the specimens held by the latter were identified by F. Wieland (Palatinate Museum of Natural History, Bad Dürkheim, Germany) (A. Broadley, pers. comm. 2021), so their identity is not in question. The lengths of all specimens collected by MGC, HC, and BW (including oothecae laid in captivity) were measured using digital calipers to the nearest 0.05 millimeters. Specimens of *Pseudomantis albofimbriata* held by MGC were also inspected to enable a comprehensive comparison between the two species. Foreleg spination formulae and the names and descriptions of morphological structures follow Brannoch et al. (2017).

Figures.—Maps were created using ggplot implemented in the R package ggplot2 (Wickham 2016) and ggmap implemented in the R package ggmap (Kahle and Wickham 2013), with base maps sourced from OpenStreetMap and OpenStreetMap Foundation (https://www.openstreetmap.org/copyright, OpenStreetMap Contributors 2021). Graphs were created using plot in the R Base package (R Core Team 2013). Figures and plates were edited with GIMP (The GIMP Development Team 2019).

Data reporting.—The novel reporting tool Standardised Data on Initiatives: Beta Version (STARDIT) (Nunn et al. in press) was used to report on the data shared as part of this research; data about this article can be found in a STARDIT Beta version report, located here: https://www.wikidata.org/wiki/Q110597302

Results

A total of 112 observations of *M. caffra* were recorded from online citizen-science and social media platforms, comprising a total of 113 mantises and 14 oothecae. These included 64 observations from iNaturalist, 14 observations from BowerBird via iNaturalist, one observation from BowerBird via the ALA, eight observations from QuestaGame via iNaturalist, two observations from QuestaGame via the ALA, and 23 observations from Facebook. No additional records were located on Flickr. Nine oothecae were collected by MGC in October 2020, three of which hatched over the following three days, producing 298 total offspring. Two oothecae and one adult female were collected by MGC and BW in May 2021. An ootheca produced by this adult in captivity in May 2021 was also inspected. Thirteen specimens were collected by HC between 2017 and 2021, six of which are also recorded on iNaturalist. One ootheca laid in captivity by one of these specimens was also inspected. Additionally, seven specimens were located in ANIC, and one ootheca and three adult specimens were located in MV. One of the specimens held by the former was too young to be accurately sexed, and two others did not have precise locality data ("Norfolk Island"). Of the MV specimens, two were captive-bred and the ootheca also has a record on iNaturalist, so these records were excluded from the analyses. One of the iNaturalist sightings, an ootheca laid by a captive female, and the captive-laid oothecae in MGC and HC's collections were also excluded for these reasons. Two sightings of nymphs were unable to be sexed from the photographs provided and they, along with the specimen held by ANIC, were excluded from the analysis comparing male and female observations. Additionally, the specimens held by ANIC that did not have precise locality information were excluded from the spatial analysis. In total, 129 mantises and 24 oothecae were observed in the wild across four states and territories (New South Wales, Norfolk Island, Victoria, and Western Australia).

Miomantis caffra was observed in three different states (Victoria, New South Wales, and Western Australia) and one external territory (Norfolk Island) over a period of 13 years (2009–2021). The majority of observations are from Victoria (131 individuals and oothecae), where the species has been present since at least 2009. Of the remaining observations, nine are from New South Wales, eight are from Norfolk Island, and five are from Western Australia. These observations provide a clear view of *M. caffra*'s spread through Australia over time (Fig. 1). First appearing in southern Geelong (Victoria) in 2009, there are no mainland sightings outside this region until 2015, when the species was observed in Fitzroy North,

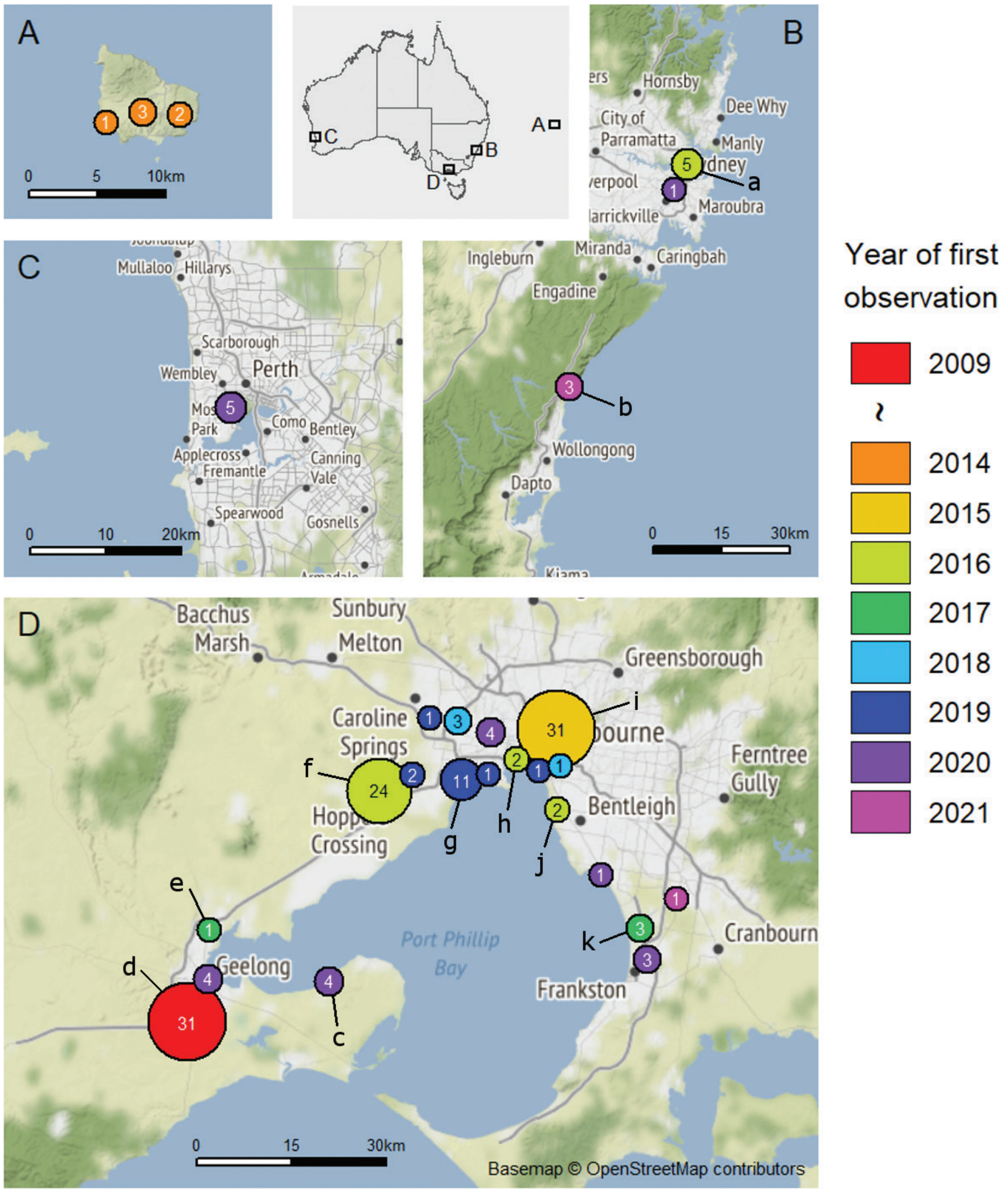

Fig. 1. Map of all known wild *Miomantis caffra* observations in Australia, including oothecae and live mantises from both citizen science and museum records. Circle colors represent the year of the first observation of the species at that locality, and the total number of observations at each locality is represented by both the size of the circles and the numbers indicated on them. **A.** Norfolk Island; **B.** Sydney and Wollongong in New South Wales; **C.** Perth in Western Australia; **D.** Melbourne and Geelong in Victoria. Localities referred to in the text are indicated with lowercase letters: **a** = Kirribilli, **b** = Northern Wollongong, **c** = Clifton Springs, **d** = Geelong and surrounding suburbs, **e** = Corio, **f** = Werribee and surrounding suburbs, **g** = Altona, **h** = Port Melbourne, **i** = Fitzroy North and surrounding suburbs, **j** = Brighton, **k** = Patterson Lakes.

more than 70 km away. Prior to this, in 2014, *M. caffra* was recorded from several localities on Norfolk Island. By 2016, the species had spread further and was observed in Werribee, Brighton, and Port Melbourne (Victoria), as well as in Kirribilli in Sydney (New South Wales), over 700 km away. In 2017, *M. caffra* was observed for the first time in Corio near Geelong, as well as further southeast in Patterson Lakes near Frankston (both Victoria). Between 2018 and 2020, *M. caffra* was observed in many further locations around Geelong, Melbourne (including around Frankston), and Sydney, notably in the vicinity of Altona in Melbourne's west and in Clifton Springs on the Bellarine Peninsula, and was additionally observed for the first time in Perth (Western Australia), more than 2500 km away. Finally, in 2021, the species was observed for the first time in northern Wollongong (New South Wales) and in Victoria for the first time in additional locations around Frankston.

Live mantises were observed in all months except September. Observations of *M. caffra* were much more frequent during summer and autumn than during winter and spring, with approximately three-quarters of all sightings occurring between January and April and more than 40% of all sightings occurring in April. Males and females displayed a similar pattern in the timing of observations, with the only significant difference being that some females survived over winter and the following spring, whereas no males were observed after June (Fig. 2A). Although adult *M. caffra* were observed in every month except September and November, nymphs were only observed between October and April. The highest number of nymphs observed was during January (*n* = 11), and the highest number of adults observed was during April (*n* = 48) (Fig. 2B).

In this study, 15 adult mantises and 13 oothecae were examined. A detailed description and taxonomic account were provided by Ramsay (1990), and thus the specimens will only be briefly described here. Adult males observed in this study were slender green or rarely brown with a conspicuous pinkish posterior portion of the pronotum, a yellow dorsal abdominal surface, tegmina that exceed the end of the abdomen, and greenish, mostly hyaline hind wings (Fig. 3C, D). The studied specimens range in body length from 32.15–37.65 mm (μ = 34.84 mm, *n* = 11) and range in tegmen length from 25.60–30.80 mm (μ = 26.25 mm, *n* = 11). Adult females are much more robust, lack pink markings on the pronotum, have tegmina that just reach or do not quite reach the end of the abdomen, and have yellow hind wings, but are otherwise similar (Fig. 3A, B, E–I). The studied specimens range in length from 32.80–43.80 mm (μ = 38.34 mm, *n* = 4) and range in tegmen length from 17.80–22.20 mm (μ = 20.89 mm, *n* = 4). The foreleg spination formula for both sexes is F = 4DS/13–14AvS/4Pvs; T = 12–13AvS/6–8PvS, and the forefemoral anteroventral spines alternate in size from large to small in the following formation: iIiIiIiIiIii(i)I. The forecoxa has 5–7 large spines interspersed with several small spines and a row of 4–6 raised black, brown, or orange spots on the inner surface (very rarely only three spots are present). The inner surface of the forefemur may also have 1–3 small black dots near its base, and adults of both sexes have the underside of the foretibiae bright yellow (Figs 3F, H, I; 4F, H; 5A). In both sexes, the vertex is distinctly elevated; this is especially obvious in females (Figs 3E, H, I; 4G). Oothecae are elongate, pale, and conspicuously foamy, with one or both ends pointed (Fig. 4I, J). They range in length from 15.80–26.45 mm (μ = 21.35 mm, *n* = 13), in width from 8.55–12.10 mm (μ = 11.07 mm, *n* = 13), and in height from 6.05–8.55 mm (μ = 6.95 mm, *n* = 13). Older, hatched oothecae frequently lack foam and are brown with distinctly concave sides (Fig. 4L). First instar nymphs measure 5.15–6.15 mm (μ = 5.58 mm, *n* = 10) and are pale with dark stripes

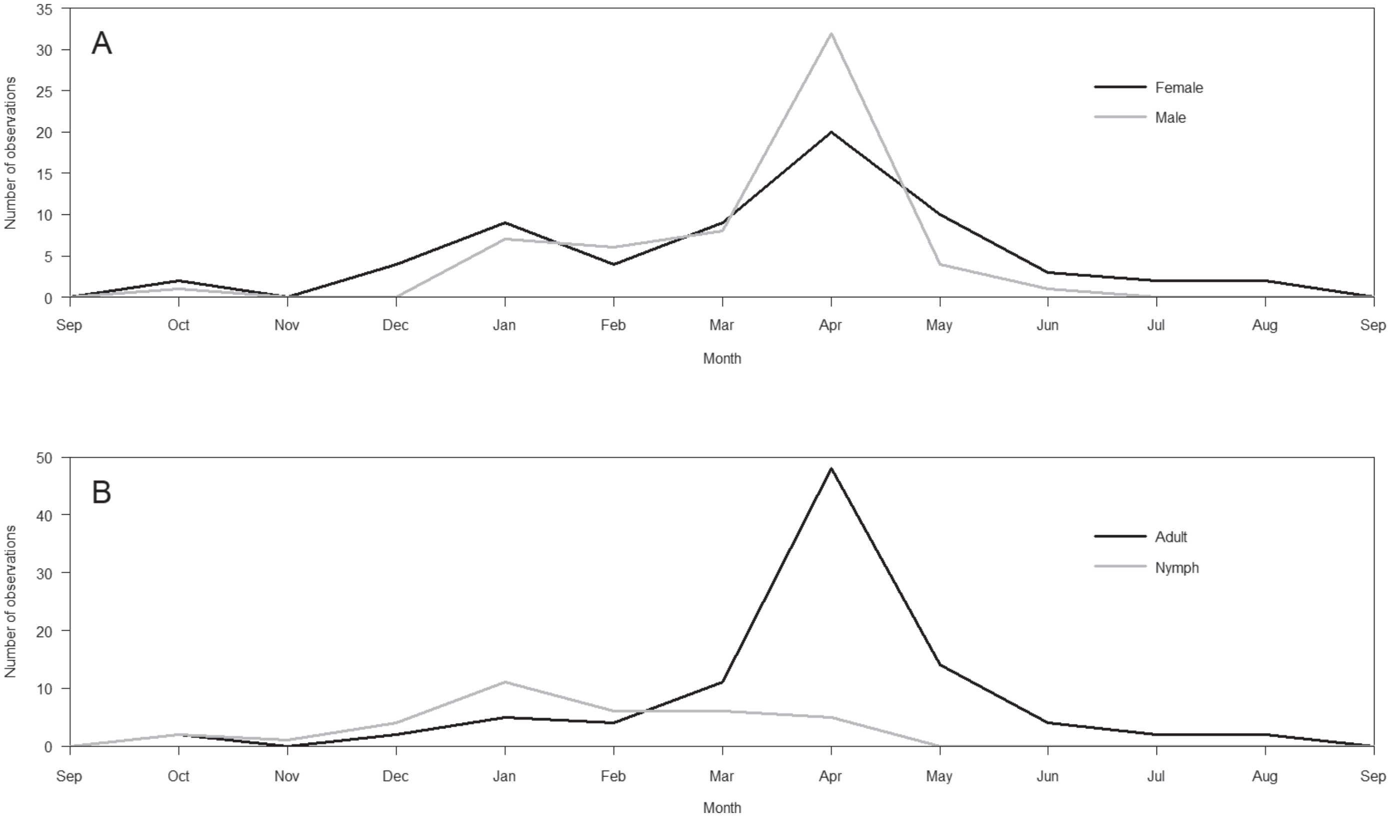

Fig. 2. Observations of live *Miomantis caffra* individuals by month. September is duplicated on both the left and right sides for clarity. **A.** Comparison of female and male observations; **B.** Comparison of adult and nymph observations.

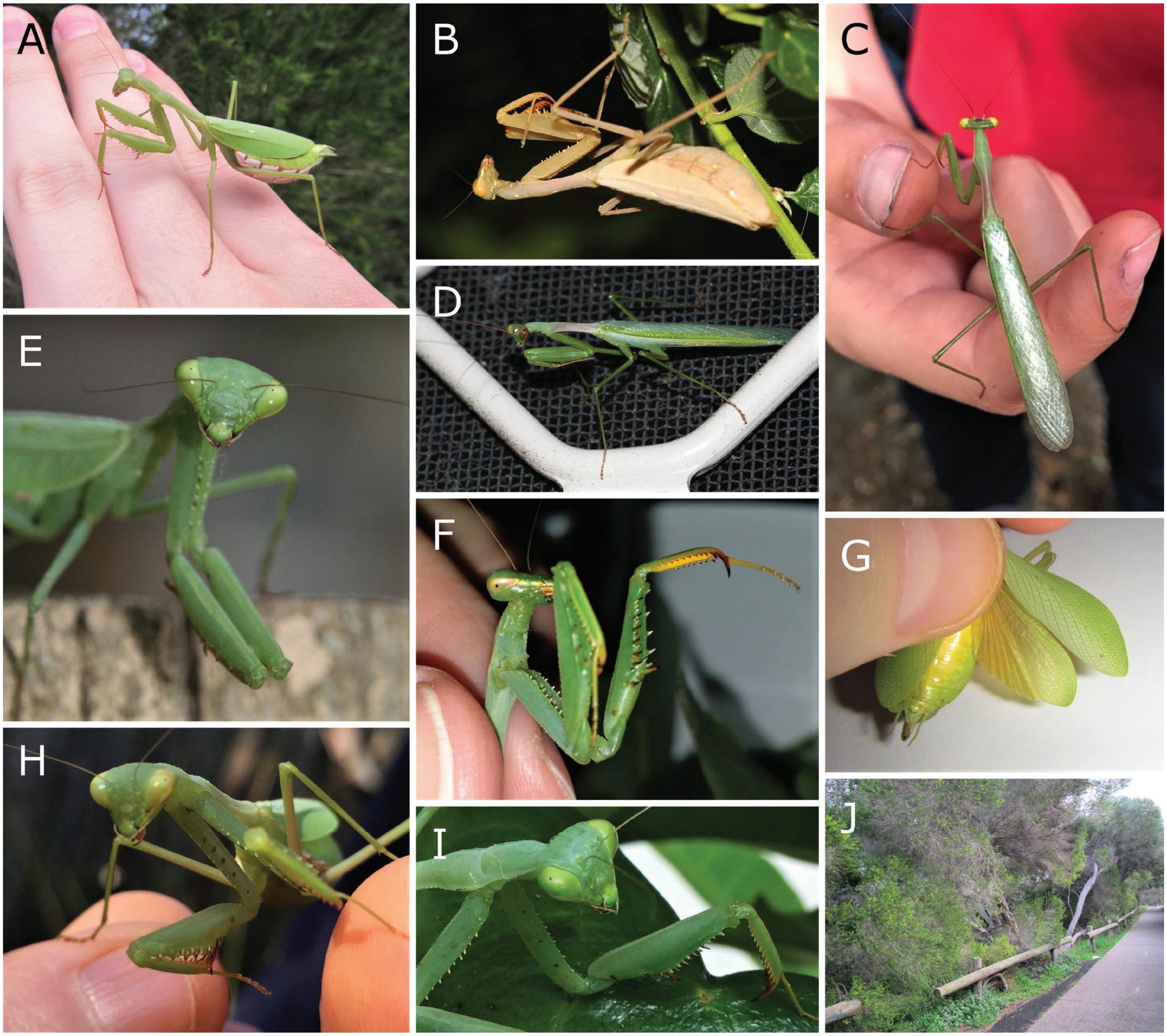

Fig. 3. Live *Miomantis caffra* adults and habitat. **A.** Adult female, green form (Merri Creek, Victoria); **B.** Adult female, brown form (Grovedale, Victoria); **C.** Adult male, yellow-eyed form (Fairfield, Victoria); **D.** Adult male, dark-eyed form (Grovedale, Victoria); **E.** Adult female showing head and forelegs (Grovedale, Victoria); **F.** Adult female showing forelegs (Werribee, Victoria); **G.** Adult female showing wings and abdomen (Merri Creek, Victoria); **H.** Adult female showing head and forelegs (Brunswick, Victoria); **I.** Adult female showing head and forelegs with atypical spot pattern on coxa (Ball Bay Reserve, Norfolk Island); **J.** Typical habitat of *Miomantis caffra*, suburban parkland at Merri Creek, Victoria. **A**, **G**, **J.** Taken by Matthew G. Connors; **B**, **D**, **E.** Taken by Adam Edmonds; **C.** Taken by Bastian A. Menz; **F.** Taken by Kenneth L. Walker; **H.** Taken by Katrina Sandiford; **I.** Taken by Harvey D. Perkins.

on the head, legs, and abdomen (Fig. 4K). Older nymphs of both sexes are green or brown, often with stripes along the dorsal surface of the abdomen (males) or a mottled base to the abdomen (both sexes) and are otherwise similar to adults (Fig. 4A–H).

Discussion

Australia has a long history of both accidental and deliberate alien introductions (West 2018), and there are still many pathways through which a foreign species can enter the country (Early et al. 2016). Being large, charismatic, and relatively easy to care for, mantises are common in the exotic pet trade (Marabuto 2014), and many species are likely already illegally present in captivity in Australia (Alacs and Georges 2008, C. Lambkin, pers. comm. 2020). It is possible that *Miomantis caffra* was deliberately smuggled into the country and then accidentally escaped into the wild. A much more likely method of entry, however, is the accidental transportation of *M. caffra* oothecae attached to plants, gardening tools, and other objects. Mantis oothecae are often deposited in well-concealed places and are extremely hardy in comparison to

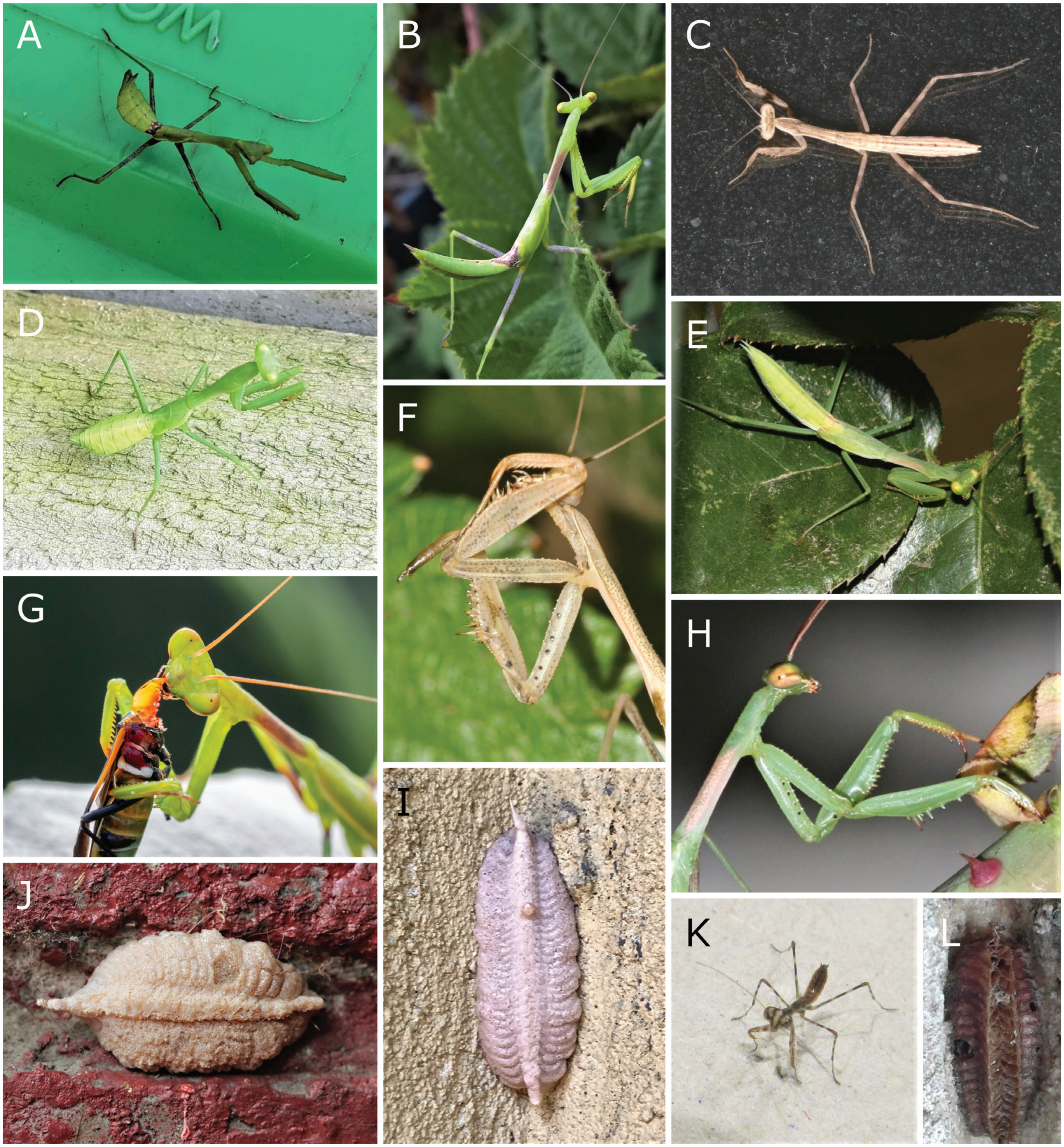

Fig. 4. *Miomantis caffra* oothecae and live nymphs. **A.** Female nymph, green and brown form (Wollongong, New South Wales); **B.** Male nymph, green and brown form (Shenton Park, Western Australia); **C.** Male nymph, brown form (Grovedale, Victoria); **D.** Female nymph, green form (Frankston North, Victoria); **E.** Male nymph, green form (Grovedale, Victoria); **F.** Male nymph showing forearm (Grovedale, Victoria); **G.** Male nymph feeding on the native Australian hemipteran *Dindymus versicolor* (Clifton Springs, Victoria); **H.** Male nymph showing forearm (Grovedale, Victoria); **I.** Live ootheca (Brunswick East, Victoria); **J.** Live ootheca (Brighton, Victoria); **K.** First instar nymph (Merri Creek, Victoria); **L.** Hatched, degraded ootheca (Kirribilli, New South Wales). **A.** Taken by Luke N. Quinane; **B.** Taken by Kimberley A. Smith; **C**, **E**, **F**, **H.** Taken by Adam Edmonds; **D.** Taken by Brendon Quan; **G.** Taken by Kelly Clitheroe; **I.** Taken by mtreikoy; **J.** Taken by Kenneth L. Walker; **K.** Taken by Matthew G. Connors; **L.** Taken by Ishbel Morag Miller. Image **I** courtesy of iNaturalist user mtreikoy, CC BY-NC 4.0 (original available at https://www.inaturalist.org/observations/54795470).

live insects. They are frequently transported because of this (Harris 2007, Fearn 2018, Battiston et al. 2020) and, because potentially hundreds of eggs are contained within each ootheca (Ramsay 1990), the accidental translocation of even a single ootheca can result in the establishment of a new population. Several recent mantis introductions have been attributed to this pathway, including that of *M. caffra* in New Zealand (Ramsay 1990), and it is likely that the species entered Australia in the same way. Many goods are frequently shipped between Australia and New Zealand (Davis 2009), and it is almost certain that the Australian populations of *M. caffra* originated from New Zealand's alien population rather than directly from their native range in southern Africa.

The first known observation of *M. caffra* in Australia is from Geelong in 2009. From here, they have spread further through both natural and anthropogenic means. There is a notable and significant lag period between this first sighting and observations of *M. caffra* from elsewhere in Australia, which did not occur until 2015, six years later. Although this may simply be due to lack of observations, a similar time discrepancy is seen in the New South Wales observations, with four years between the initial sighting (2016) and sightings from other locations (2020). The observations from Western Australia are so far only known from a single location, but this population may show similar patterns of dispersal in the future. In 2015, *M. caffra* appeared for the first time in suburban Melbourne, and then in 2016 was observed in three further locations around Melbourne. The closest of these locations is almost 40 km from Geelong and, similar to their arrival in Australia, the most probable method for the spread of *M. caffra* over this distance is the accidental transportation of oothecae attached to plants and other goods. From 2017 onwards, most of the additional localities at which *M. caffra* has been observed in Victoria have been relatively close to the locations in which the species had been sighted previously, and so likely represent mostly natural dispersal. Interstate dispersal over distances of more than 600 km undoubtedly represents human-aided travel, and notably the spread of the species to Western Australia occurred despite strict quarantine and biosecurity arrangements in that state. The origin of the remote Norfolk Island population is unknown, but the relatively early arrival and the proximity of Norfolk Island to New Zealand suggests a possible second invasion event from New Zealand rather than dispersal from the mainland Australian population. The ability of *M. caffra* to use both anthropogenic and natural means to expand its range allows them to readily colonize new areas, but accidental anthropogenic transport of mantises within Australia has also occurred in multiple native species. iNaturalist observations suggest that both *Hierodula majuscula* (Britstra 2020) and *Kongobatha diademata* (Li 2020) have been transported south of their native range to Gladstone (Queensland) and Melbourne (Victoria), respectively. *Pseudomantis albofimbriata* has established a population in Launceston (Tasmania) (Fearn 2018), and iNaturalist observations also indicate the presence of populations in Adelaide (South Australia) (O'Neill 2020) and Albany (Western Australia) (Kurniawan 2020). There is also some evidence that the expansive Victoria population of *P. albofimbriata* represents an introduced population from further north (Fearn 2018). As Australian towns and cities become more interconnected, further inadvertent transport of both native mantises and *M. caffra* appears inevitable.

The very recent appearance of *M. caffra* in Wollongong and the slow but steady spread of the species in New Zealand provide strong evidence that *M. caffra* will continue to disperse throughout urban areas of southern Australia. In addition to dispersing more extensively through Perth, Sydney, and Wollongong, it seems likely that *M. caffra* will spread to other towns and cities. Based on the available evidence, likely places for future introductions are cities and towns along the New South Wales coast, Adelaide, and possibly Tasmania and Southeast Queensland. The presence of *M. caffra* on Norfolk Island also suggests that it should be monitored for on Lord Howe Island and other offshore territories. *Miomantis caffra* appears to be limited to temperate climates; none of the introduced populations are at latitudes lower than 29° (Norfolk Island) (Ramsay 1990, Marabuto 2014, Anderson 2018). The exception is a single photographic record of the species in southern New Caledonia (22°S) in 2017 (Galois 2021). There are no further records from the island, however, suggesting that the species did not establish a population. Due to this apparent intolerance of tropical climates, the species is unlikely to establish itself in the northern half of Australia. Despite its strong dispersal capabilities, *M. caffra* has so far only been collected from suburbia in Australia, particularly in parks and gardens, and has not been recorded in unmodified native habitats. This is in direct contrast to the species' range in New Zealand, where it is common in a variety of modified and unmodified habitats. The native habitats adjacent to known Australian populations of *M. caffra* are well surveyed both by researchers and by citizen scientists and are populated by several native mantis species, so it is unclear why *M. caffra* has ostensibly not dispersed into these areas.

A clear seasonal pattern can be observed from the temporal distribution of *M. caffra* observations in Australia. The available data suggests that nymphs begin emerging in mid to late spring and adults first appear in early summer, and that all nymphs reach adulthood before the onset of winter. This well-defined seasonality contrasts with observations in New Zealand, where very young nymphs have been recorded in June and August and some nymphs take many months to mature (Ramsay 1990). The reason for this discrepancy is unknown. Prior to April, both sexes were observed in similar numbers. Many of these observations are of nymphs, suggesting that nymphs have a similar chance of survival regardless of their sex. In April, however, males were observed far more frequently than females, and from May onwards the reverse was observed. Although females cannot fly, adult male *M. caffra* are volant and are often attracted to artificial lights (Ramsay 1990), providing a possible explanation of the sex ratio observed in April. Female *M. caffra* are highly aggressive towards males and frequently consume potential mates, leading to the rapid decline of males observed from May onwards (Ramsay 1990, Walker and Holwell 2016). By contrast, females in New Zealand commonly overwinter and may survive for more than 10 months (Ramsay 1990), agreeing well with the Australian observations.

Miomantis caffra is morphologically very similar to several native Australian mantises, making it difficult for inexperienced members of the public to distinguish between them. In particular, adult males and larger nymphs of both sexes are similar to *Pseudomantis* species, including the widespread and common False Garden Mantis (*P. albofimbriata*). The most reliable distinguishing feature of *M. caffra* is the row of 3–6 raised dots on the inner surface of the forecoxa, which is absent from all native Australian mantises (Figs 3H, I; 4F, H; 5). These dots are always present (although they can vary in color from black to orange) on all except the youngest *M. caffra* nymphs. Some specimens also have 1–3 black dots on the inner surface of the forefemur, a feature also present in some larger native mantises that are otherwise unlikely to be confused with *M. caffra*. Aside from these foreleg markings and the obvious differences in abdomen breadth and wing length in adult females

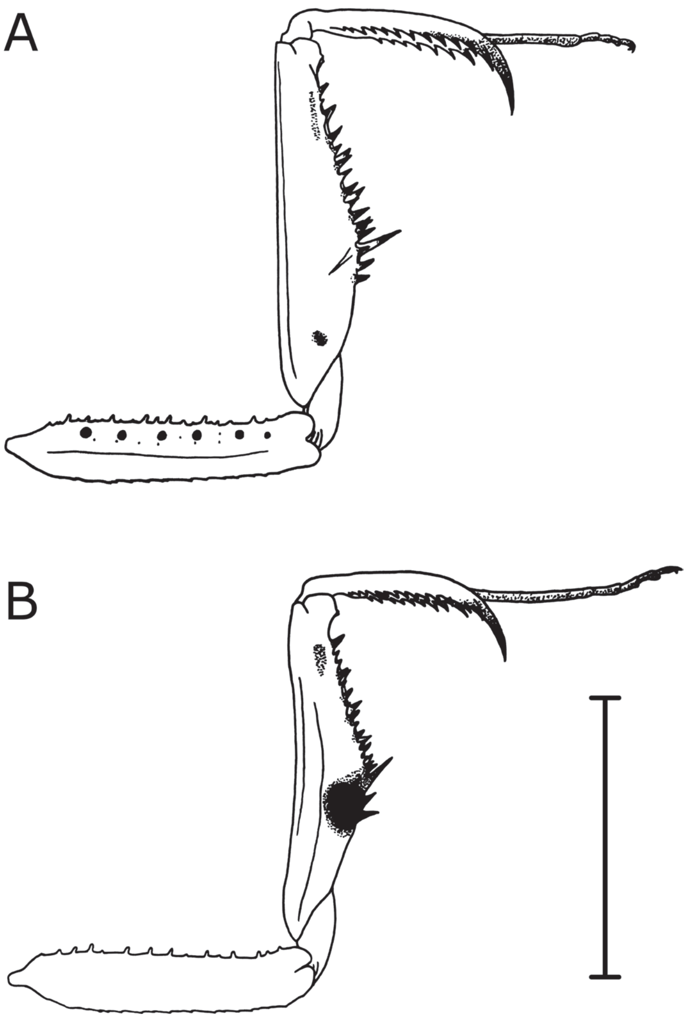

Fig. 5. Internal (ventral) surface of the foreleg of **A.** Adult female *Miomantis caffra*; **B.** Adult female *Pseudomantis albofimbriata*. Scale bar: 10mm.

(Fig. 3A, B), other more subtle features of *M. caffra* that are useful in differentiating it from *P. albofimbriata* include the strongly elevated vertex of the female (Fig. 3E, H–F), the frequently yellow eyes (Figs 3C; 4B, E) and pinkish posterior half of the pronotum (Figs 3C, D; 4B, E, G, H) of adult males, the more angulate pronotum of males (Fig. 3C), the comparatively broader and straighter forefemur, especially in females (in *M. caffra*, approximately 4.6 and 5.6 times as long as broad in females and males, respectively, and in *P. albofimbriata*, approximately 4.9 and 5.9 times as long as broad in females and males, respectively) (Figs 3H, I; 4F, H; 5), the slightly lower number of spines on the forefemur and foretibia (Figs 3F, 5), and the bright yellow underside of the foretibia in adults of both sexes (Fig. 3F). Larger nymphs share many of these features but also frequently exhibit patterning not seen in native Australian mantises, namely a brownish base to the abdomen (Fig. 4A, B) and longitudinal striping on the abdomen (Fig. 4C). First instar *M. caffra* nymphs are unlike any native Australian mantis, being primarily pale with prominent dark stripes on the head, abdomen, and legs (Fig. 4K). Unhatched oothecae are also relatively easy to distinguish from those of native mantises. *Miomantis caffra* oothecae are conspicuously pale and foamy and are laid directly onto a surface (frequently fences, walls, and plants). They are relatively elongated (average 21 mm long, 11 mm wide, and 7 mm high) and are pointed at one or both ends (Fig. 4I, J). Native Australian mantises produce oothecae that are either much larger or smaller, are brown and not conspicuously foamy, or are not elongated and pointed at one end. Hatched, degraded oothecae can be more difficult to identify as the foam often disintegrates over time, exposing the brown interior (Fig. 4L). These features are summarized in Table 1.

A key question that arises from the introduction of *M. caffra* into Australia is that of detrimental effects on native species. Introduced species may be either invasive or adventive; invasive species negatively impact native species within their introduced range, whereas adventive species do not (Walker et al. 2020). Despite being present in some areas for more than a decade, there has so far been no observed negative impact on any native mantises or other wildlife in the areas where *M. caffra* has been introduced. Native mantises remain common in the areas inhabited by *M. caffra*, and it is not unusual to find both native and introduced mantises living in the same park or garden (M. Connors and H. Chen, unpublished data). Geelong, the area with the highest number of *M. caffra* sightings, is home to abundant numbers of both *P. albofimbriata* and *Orthodera ministralis*, another common native, and there has been no noticeable decline in their numbers as *M. caffra* has become more common. *Miomantis caffra* is both more fecund and more aggressive than these native species (Ramsay 1990, Barry et al. 2008, Walker and Holwell 2016, M. Connors pers. obs.), so it is possible that this will give it a competitive advantage as it continues to spread. Both the lack of an observed decline in native species and the apparent absence of the species outside of suburbia, however, suggests that it is not negatively affecting native mantises. This is in stark contrast to New Zealand, where *M. caffra* is displacing the native *Orthodera novaezealandiae* in both modified and unmodified habitats (Ramsay 1990). In addition to being more aggressive and more fecund than *O. novaezealandiae* (Ramsay 1990, Walker and Holwell 2016), *M. caffra* females also unintentionally attract and then consume *O. novaezealandiae* males (Fea et al. 2013). A possible explanation for this difference in impact is the great difference in mantis diversity between the two countries. Australia is home to upwards of 100 native mantis species, including many that occur in the regions where *M. caffra* has been introduced (Balderson 1984), whereas *O. novaezealandiae* is New Zealand's only native mantis. Australia's mantises must not only compete with each other but must be able to distinguish between the pheromones of conspecific and heterospecific females, and it is not uncommon for several closely related species to occur in the same region (Tindale 1923, Balderson 1984). By contrast, male *O. novaezealandiae* faced no such challenges before the introduction of *M. caffra*, and there was no evolutionary pressure on male *O. novaezealandiae* to distinguish between mantis pheromones of any kind. Over time they may have lost this ability, and when *M. caffra* arrived in New Zealand the native males would have been unable to distinguish between the pheromones of the two species. The presumed specificity in pheromone attraction present in males of native Australian mantises would suggest that they are not attracted to female *M. caffra*, and hence that they are not being displaced in this way. Pheromone attraction studies between *M. caffra* and native mantises similar to those conducted by Fea et al. (2013) between *M. caffra* and *O. novaezealandiae* would help to confirm this hypothesis. If true, this may indicate that native mantises will not be impacted even if *M. caffra* spreads into undisturbed habitats. However, it remains to be seen whether the high fecundity and parthenogenetic ability of *M. caffra* will give them a competitive

Table 1. Summary of distinguishing features between *Miomantis caffra* and *Pseudomantis albofimbriata*.

Feature	*Miomantis caffra*	*Pseudomantis albofimbriata*
Inner surface of forecoxa	With 3–6 raised black, brown, or orange spots	Without markings
Inner surface of forefemur	Sometimes with 1–3 black dots near base	With large black (rarely orange) mark surrounding claw groove
Female tegmina	Covering or almost covering the entire abdomen	Covering approximately half to two-thirds of the abdomen
Female abdomen	Very broad, robust, and rounded	Slender and somewhat flattened
Vertex	Strongly elevated, especially in female	Not strongly elevated
Male eyes	Usually yellow or concolorous with head, rarely pink	Usually pink or concolorous with head
Male pronotum	Usually with pinkish posterior half and angulate corners	Usually unicolorous and with rounded corners
Forefemur shape	Approximately 4.6 (females) or 5.6 (males) times as long as broad, with straight anterior edge	Approximately 4.9 (females) or 5.9 (males) times as long as broad, with slightly concave anterior edge
Underside of adult foretibia	Bright yellow	Concolorous with upper side
Foreleg spination formula	F = 4DS/13–14AvS/4Pvs; T = 12–13AvS/6–8PvS	F = 4DS/15–16AvS/4Pvs; T = 13AvS/9PvS
Patterning of large nymphs	Often with brownish base to abdomen and/or longitudinal stripes on abdomen	Without brownish base to abdomen, usually without obvious longitudinal stripes on abdomen
Patterning of first instar nymphs	Pale with prominent dark stripes on head, abdomen, and legs	Dark with some pale markings on head and legs
Unhatched oothecae	Pale and conspicuously foamy, with one or both ends pointed	Brown and not foamy, with one or neither end pointed
Hatched, degraded oothecae	With concave sides	With parallel or convex sides

advantage into the future. Despite the lack of evidence for a significant impact on native species, we still strongly recommend that any wild *M. caffra* individual or ootheca encountered should be removed in order to contain current populations and limit further spread. In particular, removing *M. caffra* during the initial "lag period" following their colonization of a new area may be an effective way of preventing the establishment of new populations.

This detailed information about the arrival and spread of *M. caffra* in Australia would not be possible without the use of citizen science. Citizen scientists are increasingly becoming one of the first lines of defense against novel alien species (Maistrello et al. 2016, Johnson et al. 2020, Larson et al. 2020), and recent reports of new introductions have occurred across multiple citizen-science platforms (Baumann et al. 2016, Encarnação et al. 2021). Aside from the benefits of being able to provide much more surveying power than researchers, both in terms of the amount of data that can be collected and in the geographic area that can be surveyed (Lodge et al. 2006, Silvertown 2009, Larson et al. 2020), citizen scientists also provide many other benefits. Importantly, citizen scientists have intimate knowledge of their local wildlife (Kobori et al. 2015) and can regularly and repeatedly survey areas that would be inaccessible or unaffordable to normal researchers (Tulloch et al. 2013, Andow et al. 2016). The majority of *M. caffra* individuals observed in this study were sighted on private property, and almost all were observed in urban areas typically not surveyed by researchers. By contrast, citizen scientists frequent these areas, and many of our coauthors were aware that their sighting represented a species they had not seen before in the area. Without citizen scientists, we might still be completely unaware of *M. caffra*'s presence in Australia.

The benefits of citizen science can be enhanced even further if researchers engage directly with citizen scientists. Most Australian studies that utilize broad-scale citizen-science projects extract spatiotemporal data but do not make use of any secondary data, usually because it is more difficult to do so. This secondary information—information about sex, age, color, and other phenotypic, phenological, and behavioral factors—represents a vast expanse of untapped resources, and the use of sex and age data in this study represents only the beginning of its exploitation (Mesaglio and Callaghan 2021). Engaging directly with the citizen scientists who create these sightings, however, can increase the research value of secondary data even further. If asked, the majority of observers are more than happy to provide additional photos and information surrounding the circumstances of their sightings. This qualitative information—information on how an organism was encountered—can be invaluable not only in monitoring and controlling introduced species, but in all aspects of biodiversity research. Importantly, it can provide data on life histories, ecological interactions, microhabitat preference, and many other aspects beyond the presence of a species (Tulloch et al. 2013, Mesaglio and Callaghan 2021). Citizen scientists also potentially help to control invasive species by removing individual organisms, both providing important scientific specimens and aiding in their eradication (Anderson et al. 2017).

A further value of citizen science is the benefit to the citizen scientists themselves. Research has repeatedly shown that volunteers are strongly motivated both by the learning opportunities offered by citizen science and by the knowledge that their effort is contributing to something meaningful, both of which are enhanced when scientists directly communicate and collaborate with citizen scientists (Johnson et al. 2014, Geoghegan et al. 2016, Domroese and Johnson 2017, Steven et al. 2019). For example, the most successful iNaturalist projects are often those with strong communities centered around helping and teaching volunteers (Mesaglio and Callaghan 2021). If experts engage with citizen scientists by sharing their expertise and showing volunteers that their observations are having a tangible impact, the community of contributors will be strengthened greatly, and the benefits will be reaped by researchers and volunteers alike (Grese et al. 2000, Peters et al. 2017, Groom et al. 2019). It is for these reasons that all of the citizen scientist volunteers who contributed observations of *M. caffra* from around Australia were invited to be directly involved in this study. Among our authors are not only researchers, but students, teachers, and other enthusiastic citizen scientists. They include a ten-year-old boy, an interior designer, a special needs teacher, a ranger at a childcare center, a software engineer, and many others, all united by a love of the natural world and a desire to contribute to science and conservation. Many are members of their local nature clubs, notably the Geelong Field Naturalists Club, and all have contributed to citizen science programs, well and truly proving that anyone can be a scientist in the twenty-first century.

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Research Article Journal of Orthoptera Research 2022, 31(1): 83–89

Description of two new species of Turanogryllini crickets (Orthoptera, Gryllidae, Gryllinae) from Cameroon, with identification keys for African species

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Abstract

During a Gryllidae survey in the Southern Cameroonian Plateau, two new species of the tribe Turanogryllini Otte, 1987 were discovered and described, namely *Turanogryllus zamakoensis* Um Nyobe, Kekeunou & Bilong Bilong **sp. nov.** and *Neogryllopsis gorochovi* Um Nyobe, Kekeunou & Ma **sp. nov.** This finding extends the known distribution of the genera *Turanogryllus* Tarbinsky, 1940 and *Neogryllopsis* Otte, 1983. New environments are also recorded for these crickets, and an identification key for African species is proposed for these two genera.

Résumé

Au cours d'une étude des Gryllidae dans le Plateau Sud Camerounais, deux nouvelles espèces de la tribu Turanogryllini Otte, 1987 ont été découvertes et décrites, à savoir *Turanogryllus zamakoensis* Um Nyobe, Kekeunou & Bilong Bilong **sp. nov.** et *Neogryllopsis gorochovi* Um Nyobe, Kekeunou & Ma **sp. nov.** Cette découverte élargie l'aire de répartition connue des genres *Turanogryllus* Tarbinsky, 1940 et *Neogryllopsis* Otte, 1983. De nouveaux environnements ont été également signalés pour ces grillons et une clé de détermination est proposée pour les espèces africaines de ces deux genres.

Keywords

bioecology, Central Africa, taxonomy, Turanogryllini

Mots clés

bioecologie, Afrique Centrale, taxonomie, Turanogryllini

Introduction

Despite its central role in ecosystem functioning, biological diversity remains poorly known in some regions, especially for non-emblematic species such as orthoptera. In Cameroon, no detailed taxonomic study of crickets has been performed. Yet, crickets play several ecosystemic roles and are suitable bioindicators of the assessment of habitat quality and environmental change (Anso 2016). They form a major component of food webs (Capinera 2011, Wellstein et al. 2011), and some crickets are food for humans and some pets (Lavalette 2013, Rumpold and Schlüter 2013). Crickets can also be harmful to the environment (Bellmann and Luquet 2006). They attack most plants, but they are mostly seen on young plants that are not resistant to their injuries (Valdeyron 1955, Sikirou et al. 2018).

Crickets from the tribe Turanogryllini Otte, 1987 belong to the field cricket subfamily Gryllinae Laicharting, 1781 (Chopard 1967, Tae-Woo 2012). This tribe includes four genera: *Podogryllus* Karsch, 1893; *Turanogryllus* Tarbinsky, 1940; *Afrogryllopsis* Randell, 1964; and *Neogryllopsis* Otte, 1983. Its monophyly, however, has not been confirmed by the recent phylogenetic study of Chintauan-Marquier et al. (2016). Their taxonomy and distribution have yet to be clearly established, and several new species remain undescribed.

The genus *Podogryllus* is known from Africa (16 spp.) and Saudi Arabia (3 spp.) (Cigliano et al. 2021). According to Otte (1987), *Afrogryllopsis* is a synonym of *Podogryllus*; a taxonomic revision is required for these two genera. The genus *Turanogryllus* is mainly characterized by the presence of styli on the external apical corners of the epiphallus (*sensu* Randell 1964). According to Cigliano (2021), 36 species have been described from Eurasia (Afghanistan, Arabia, China, Iran, Israel, and Russia), Indo-Malaysia (India, Laos, Nepal, and Pakistan), and Africa (Angola, Egypt, Guinea, Kenya, Sierra Leonne, Zaire, and Zambia). Currently, 10 species in this genus are known from Africa: *T. niloticus* (Saussure, 1877); *T. scenicus* (Gerstacker, 1869); *T. machadoi* Chopard, 1961; *T. flavolateralis* (Chopard, 1934); *T. microlyra* (Chopard, 1938); *T. vicinus* (Chopard, 1967); *T. nimba* Otte, 1987; *T. kitale* Otte, 1987; *T. sombo* Otte, 1987, and *T. mau* Otte, 1987 (Cigliano et al. 2021). The last genus of the tribe, *Neogryllopsis*, is mainly characterized by a sharp virga (*sensu* Randell 1964) without spines along edges

(Otte 1983). It is known from southern Malawi, Zimbabwe, and South Africa. It currently includes 20 species (Otte et al. 1988, Gorochov 1988), all from Africa. Otte et al. (1988) provided a key for males and defined five species groups of Southern African species: *Jordani*, *Pundae*, *Sabianus*, *Kuhlgatzi*, and *Ohopohoi*.

In the current study, we update the taxonomic information on *Turanogryllus* and *Neogryllopsis* genera by describing two new species from Cameroon and providing identification keys to males of both genera.

Materials and methods

This study was conducted in closed (forests) and open (fields and/or fallows) environments of three localities in the southern Cameroonian plateau: Zamakoe, Ongot, and Ngutadjap (Fig. 1). The characteristics of each study locality can be found in the publication of Um Nyobe et al. (2021). In these habitats, crickets were captured from March 2014 to September 2015 using pitfalls and quadrats, according to the methodology described in Um Nyobe et al. (2021).

The captured specimens were stored in 70% ethanol and transported to the zoology laboratory of the University of Yaoundé I for further studies.

Observations of morphological characters were performed using a binocular magnifier (Leica) connected to an Amscope camera (Heerbrugg brand). Pictures of the external morphology of specimens immersed in 70% ethanol were taken using an LCD Digital Microscope connected to a computer. Measurements were taken using a NEIKO electronic caliper. Male genitalia were dissected and then cleaned with 5% KOH and ethanoic acid for 8 hours and 30 minutes, respectively (Vasanth 1993, Um Nyobe et al. 2021). Imaging of male genitalia was made using an AmScope MU1000 digital camera or a Canon EOS 40D Digital SLR camera. To highlight the structural components of male genitalia, a water solution containing a drop of JBL Punktol was used. To fix orientations and stabilization of genitalia for photography, a clear and viscous hand sanitizer was used, following Su (2016).

Abbreviations used in morphological identification.—General morphology: FI, FII, FIII, fore, mid, hind femora, respectively; FW, forewing; TI, TII, TIII, fore, mid, hind tibia, respectively. Terminology of forewing venation follows Desutter-Grandcolas et al. (2017) and Schubnel et al. (2019): cubital vein, *cu.v.*; anal vein, *a. v.* (= postcubital vein, *Pcu*); median vein, *m.v.*; radial vein, *r.v.*; subcostal vein and its branches, *sc.v.*; oblique vein, *o.v.*; diagonal vein, *d.v.*; anal node, *a.n.*; mirror, *m.*; harp, *h.*; cord, *c.*; anal field, *a.f.*; apical field, *ap.f.*; lateral field, *l.f.*

Abbreviations used for the measurements.—Measurements were recorded in millimeters (mm) following Otte (1985): BL, body length; FL, hind femora length; TL, hind tibia length; FWL, forewing length; PL, pronotal length; ML, mirror length; MW, width of the mirror; OL, ovipositor length; CL, cercal length.

Abbreviations used in genitalia identification.—Desutter (1987), Randell (1964), and Otte et al. (1988) used different terms for the same genital structures. Although we realize that there is a need to have a unified terminology system that does not currently exist, we chose to use the terminology for male genitalia adapted from Randell (1964) and Otte et al. (1988) because they explicitly described the structure of the male genitalia of the type species of the genera *Turanogryllus* and *Neogryllopsis*, which allows direct comparisons between the new species and the other species previously described in these genera. We indicate the terms corresponding to the terminology from Desutter (1987) in brackets, as presented in the following list of abbreviations for male genitalia: epiphallus, *epi*.; ectoparameres, ect.; endoparameres, *end*.; ramus, *r*; virga, *v*. (ectophallic fold *sensu* Desutter); posterior emargination of epiphallus, *p.e.e*.; stylus, *sty*.; lateral lobe of epiphallus, *l.l.e*. (median lophi of pseudepiphallus

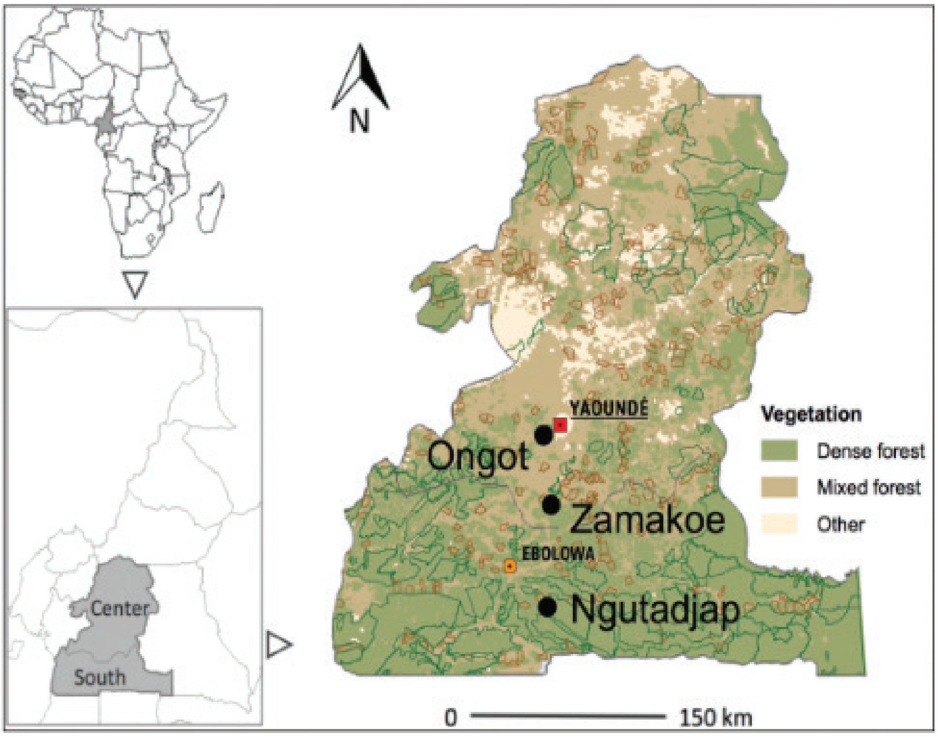

Fig. 1. Study localities in relation to vegetation types in Cameroon (see Oumarou et al. 2020).

sensu Desutter); dorsal lobe of ectoparamere, *d.l.ect.* (lateral lophi of pseudepiphallus *sensu* Desutter); ventral lobe of ectoparamere, *v.l.ect.* (pseudepiphallic parameres *sensu* Desutter).

Results

Taxonomy

Order Orthoptera Olivier, 1789
Family Gryllidae Laicharting, 1781
Subfamily Gryllinae Laicharting, 1781
Tribe Turanogryllini Otte, 1987

Diagnosis of tribe Turanogryllini Otte (1987)

Inner tympanum small, present, or absent on TI. Outer tympanum present, large. TIII 0.68–0.86 times as long as FIII. Male stridulum with small, short setae arranged in ventral view. Harp with three or more oblique veins connected indirectly to the stridulatory file through small veins. Mirror with one dividing vein. Male genitalia large, epiphallus relatively short, and the entire structure is dominated by huge and sometimes elaborate ectoparameres that form spikes and may present prominent serrations. Virga usually stout, narrowing at point; endoparamers joining posteriorly to form a large muscle attachment plate.

Genus *Turanogryllus* Tarbinsky, 1940

Type species.—*Gryllus lateralis* Fieber, 1853

Diagnosis.—Head globose, body cylindrical. Male tegmina well developed. Male subgenital plate concave or deeply notched; dorsal lobes of ectoparameres externally visible; styli present on the posterolateral corners of epiphallus. Female tegmina reduced to small pads; ovipositor straight, slender, needle-shaped.

Turanogryllus zamakoensis Um Nyobe, Kekeunou & Bilong Bilong, sp. nov.

http://zoobank.org/DFD1267F-4E26-47D6-8C38-DADE761156E1

Material examined.—**Holotype:** CAMEROON • ♂; Center Region, Zamakoe; 3°33'816"N, 11°31'913"E; 14 February 2015; in crops field, quadrat trap; P. Um Nyobe & team leg.; MNHN-EO-ENSIF1749. **Allotype:**—CAMEROON • ♀; Center Region, Zamakoe; 3°33'816"N, 11°31'913"E; 21 March 2015; in crops field, quadrat trap; P. Um Nyobe & team leg.; MNHN-EO-ENSIF1713.

Etymology.—The species epithet *zamakoensis* refers to the type locality.

Diagnosis.—*Turanogryllus zamakoensis* sp. nov. is distinguished from congeners by light brown coloration, male genitalia provided with a large dorsal lobe of ectoparamere, and with micropptereous FWs; the other species are either brachypetereous or macropetereous. In addition, it has only one outer tympanum while the other species have tympana on external and internal side.

Description.—(Figs 2, 3) **Male.** Size average, brown, lighter than other species. Head dark brown with four pale stripes on occiput, not extending over vertex (Fig. 2A); cheeks pale (Fig. 2B); ocelli large; face entirely pale below median ocellus and below level of antennae (Fig. 2C). Pronotum covered with very fine pubescence, without bristles; dorsum dark brown, muscle attachment plates pale brown (Fig. 2A); lateral lobes ivory, becoming dark brown at upper margin (Fig. 2B). TI and TII ivory-colored; TI with a large outer tympanum. Hindlegs: f FIII pale brown with faintly darker oblique stripes on outer surface; darker around knees, especially on inner surface; TIII pale brown with 6 inner and 7 outer subapical spurs. FWs with square base, reaching abdomen mid-length; its length to pronotal length ratio ca. 2.5; dorsum brown; lateral field pale, dark brown between upper three veins. Stridulatory file with 156 teeth; harp with 3 oblique veins; mirror oval, with one dividing vein (Fig. 2E). Hind wings short, hidden by FWs. Abdomen dorsum dark brown; venter pale; cerci pale. Male genitalia (Fig. 3): lateral lobes of epiphallus with styli at their posterior extremities, and these styli are provided with bristles;

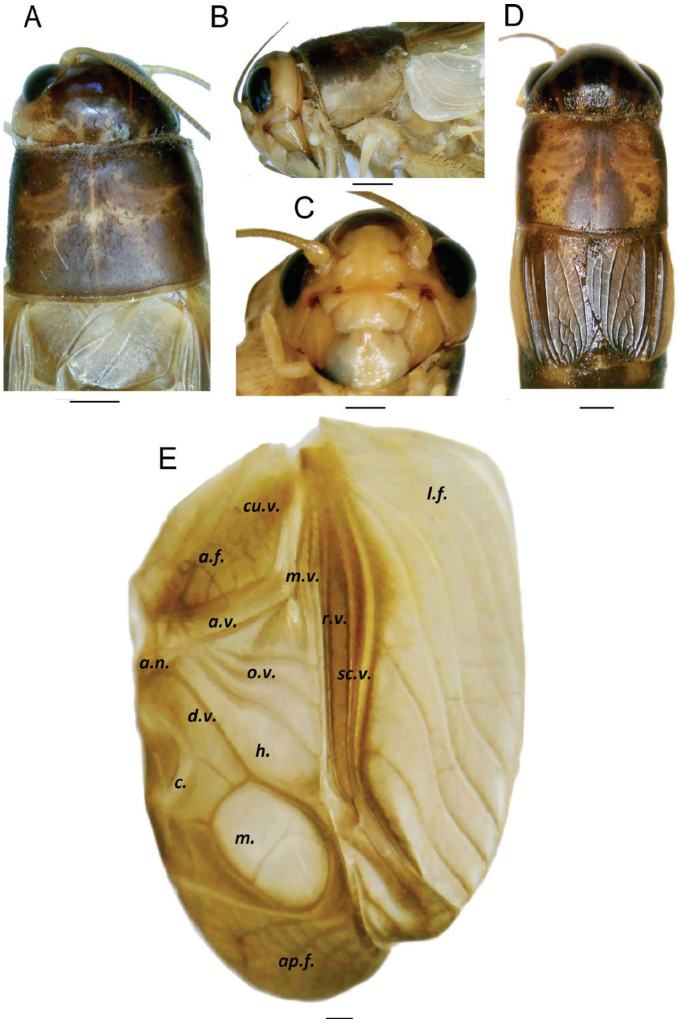

Fig. 2. Morphology of *Turanogryllus zamakoensis* sp. nov. **A.** Male head and pronotum; **B.** Male lateral view of head and pronotum; **C.** Male face; **D.** Female head, pronotum, and FWs; **E.** Male FW. Scale bars: 10 mm (**A**); 8 mm (**B, C**); 7 mm (**D**); 5 mm (**E**). Abbreviations: cubital vein, *cu.v.*; anal vein, *a.v.* (postcubital vein, *Pcu*); median vein, *m.v.*; radial vein, *r.v.*; subcostal vein and its branches, *sc.v.*; oblique vein, *o.v.*; diagonal vein, *d.v.*; anal node, *a.n.*; mirror, *m.*; harp, *h.*; cord, *c.*; anal field, *a.f.*; apical field, *ap.f.*; lateral field, *l.f.*

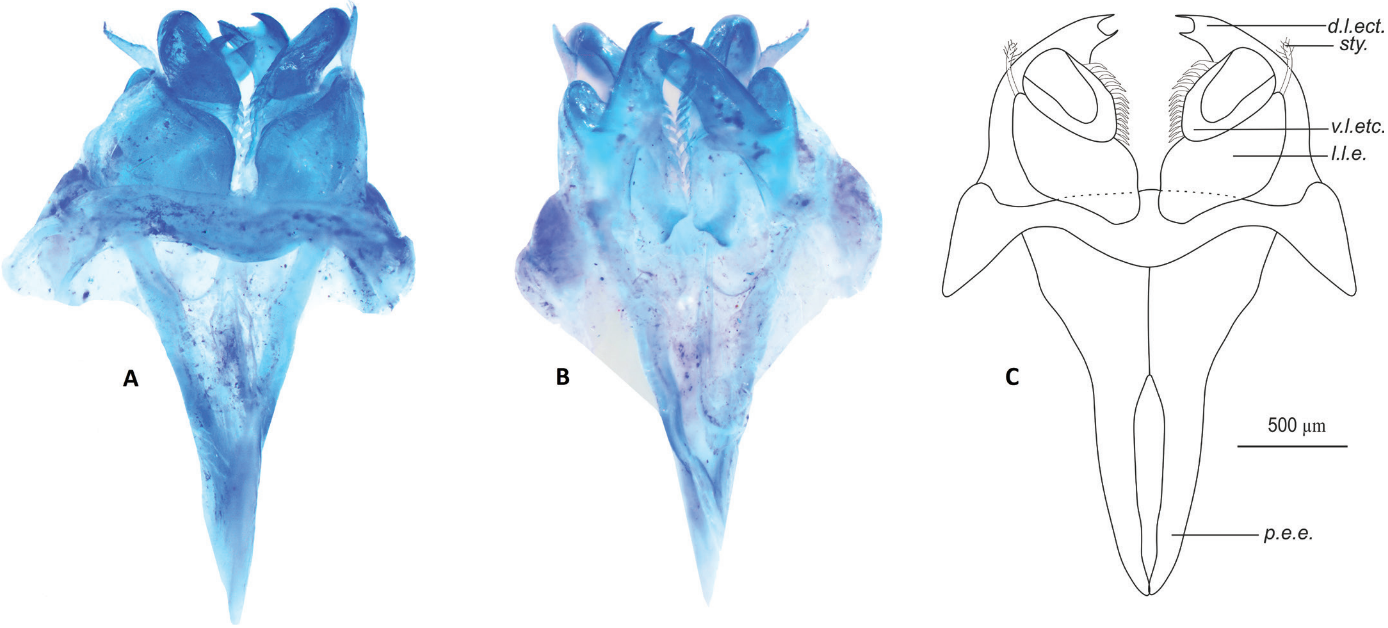

Fig. 3. Male genitalia of *Turanogryllus zamakoensis* sp. nov. **A**. Dorsal view; **B**. Ventral view; **C**. Drawing. Scale bar: 500 µm. Abbreviations: posterior emargination of epiphallus, *p.e.e.*; stylus, sty.; lateral lobe of epiphallus, *l.l.e.*; dorsal lobe of ectoparamere, *d.l.ect.*; ventral lobe of ectoparamere, *v.l.ect.*

dorsal lobes of ectoparameres lamelliform, curved dorsally in its posterior half; ventral lobes of ectoparameres digitiform, sigmoidally curved; dorsal lobes of ectoparameres enlarged above ventral lobes of ectoparameres.

Female. Similar to male but occiput with 6 fine, well-individualized brown stripes; FWs short, overlapping slightly and with rounded ends (Fig. 2D).

Male measurements (holotype, in mm).—BL, 18.37; PL, 3.83; PW, 4.07; FWL, 9.41; CL, 9.00; FL, 12.18; FW, 4.25; TL, 8.61. Stridulatory file with 156 teeth.

Key to males of African species of *Turanogryllus*

1 Pronotum dark brown or black 2
– Pronotum light brown 10
2 Vertex unbanded .... *Turanogryllus flavolateralis* (Chopard, 1934)
– Vertex banded 3
3 Occiput without stripe .... *Turanogryllus kitale* Otte, 1987
– Occiput with stripe 4
4 Occiput with one thin medium pale stripe .... *Turanogryllus microlyra* (Chopard, 1938)
– Occiput with four distinct longitudinal stripes 5
5 FWs with a small mirror and long apical field .... *Turanogryllus nimba* Otte, 1987
– FWs with a large mirror and short apical field 6
6 TIII armed with 5:5 subapical spurs 7
– TIII armed with more than 5:5 subapical spurs 8
7 FWs covering the abdomen; 4 oblique veins; the first cord sending one venule to the anterior inner edge of the mirror; dorsal lobes of ectoparamers located below the ventral ones .... *Turanogryllus niloticus* (Saussure, 1877)
– FWs covering less than half of the abdomen; 3 oblique veins; the first cord sending two venules to the anterior inner edge of the mirror; dorsal lobes of ectoparamers located above the ventral ones .... *Turanogryllus zamakoensis* sp. nov.
8 Dorsal lobe of ectoparameres lamelliform, curved dorsally in its posterior part like claws with more than two fingers .... *Turanogryllus scenicus* (Gerstacker, 1869)
– Dorsal lobe of ectoparameres lamelliform, curved dorsally in its posterior part like claws with one or two fingers 9
9 Dorsal lobe of ectoparameres with one finger .... *Turanogryllus mau* Otte, 1987
– Dorsal lobe of ectoparameres with two fingers .... *Turanogryllus sombo* Otte, 1987
10 Short diagonal vein and large apical field .... *Turanogryllus vicinus* (Chopard, 1967)
– Long diagonal vein and short apical field .... *Turanogryllus machadoi* Chopard, 1961

Genus *Neogryllopsis* Otte, 1983

Type species.—*Neogryllopsis zomba* Otte, 1983.

Diagnosis.—**Males.** Head and pronotum orange-brown on dorsum, ivory-colored on sides and venter, abdomen banded with dark brown and ivory on dorsum. Dorsum of head without longitudinal stripes, sometimes with transverse light and dark bands. Face and cheeks ivory colored. FWs: Dorsum brown to gray-brown, lateral field pale; vein 1A strongly raised above level of stridulum; harp with 5 or 6 veins (rarely 4); harp veins attached indirectly to the distal half of the stridulum through a series of small veinlets; stridulum with small short setae arranged along both sides of the file; diagonal vein bent close to chords. Hind wings absent in males. Abdomen medium to dark brown, with pale segmental margins, and tergites becoming pale on sides of body. Inner tympanum absent on TI; outer tympanum present, large. FIII with distinct or indistinct oblique rows of medium brown spots in middle of inner and outer surfaces. TIII 0.63–0.68 times as long as FIII; with 4 or 5 inner and 4 to 6 outer subapical spurs. Cerci very pale.

Females. Similar in coloration to males. Apterous. Ovipositor as long as or longer than FIII.

Neogryllopsis gorochovi Um Nyobe, Kekeunou & Ma, sp. nov.

http://zoobank.org/50C1C458-BB47-4C8B-A7D6-BA3583D1D599

Material examined.—**Holotype:** CAMEROON • ♂; Center Region, Ongot; 3°33'816"N, 11°31'913"E; 23 November 2014; secondary forest, pitfall trap; P. Um Nyobe & team leg.; MNHN-EO-ENSIF1727. **Paratypes:** CAMEROON • 1♀; same information as holotype; MNHN-EO-ENSIF1751 • 5♂, 12♀; Center Region, Zamakoe; 3°33'816"N, 11°31'913"E; 19 October 2014; 16 November 2014; 13 December 2014; crops field and forest, pitfall and quadrat traps; MNHN • 4♂, 9♀; Ongot; 3°85'786"N, 11°38'333"E; 27 Sepptember 2014; 26 October 2014; 28 March 2015; 21 April 2015; 23 August 2015; secondary forest, pitfall traps; P. Um Nyobe & team leg.; MNHN • 2♂, 7♀; Ngutadjap; 02°42'N, 011°03'E; 07 December 2014; 14 February 2015, 14 March 2015, 11 June 2015, 09 May 2015, 12 June 2015; secondary forest, pitfall traps; P. Um Nyobe & team leg.; MNHN.

Etymology.—The species is dedicated to Dr. Andrej V. Gorochov for his background work on the taxonomy of crickets in general and of *Neogryllopsis* species in particular.

Diagnosis.—Characters of the male genitalia of *Neogryllopsis gorochovi* Um Nyobe, Kekeunou & Ma **sp. nov.** grouped it in the ***Sabianus* group** made up of two species, namely *Neogryllopsis sabianus* Otte, Toms & Cade, 1988 and *Neogryllopsis limpopensis* Otte, Toms & Cade, 1988. *Neogryllopsis gorochovi* can be differentiated from these species by its male genitalia with ectoparamere without setae, short epiphallus, and FW with an undivided round mirror.

Description.—(Figs 4, 5, Table 1) **Male.** Medium size, pale orange-brown. Dorsum of head without a transverse pale band across vertex (Fig. 4A); top of head without dark markings along inner margins of eyes; forehead dark brown, without white stripe between lateral ocelli; cheeks pale brown (Fig. 4B) and face brown before epistomal suture and pale after this suture (Fig. 4C). Pronotum red-brown without ivory-colored band along margins (Fig. 4A). TI and TII pale, somewhat orange. Hindlegs: FIII with distinct oblique brown stripes on outer surface; TIII pale brown with 5 inner and 5 outer subapical spurs. FWs: dorsum grayish brown, lighter on lateral field; FW length to pronotal length ratio c. 2.3 mm; stridulatory file with 86 teeth; harp with 4 oblique veins; mirror round without a dividing vein; apical field very small (Fig. 4E). Hind wings absent. Abdomen: Tergites dark brown, with pale posterior margins; venter light brown; cerci dark brown. Male genitalia (Fig. 5): Epiphallus well developed but short; lobes of epiphallus in posterior view long, tapering, two points closely apposed, separated by a deep cleft; lateral lobe of epiphallus with long setae near base and without spines; ectoparamere without setae.

Female. Similar to male in color. Size range extends considerably above that of male (Table 1). FWs very short, sometimes just visible under edge of pronotum (Fig. 4D).

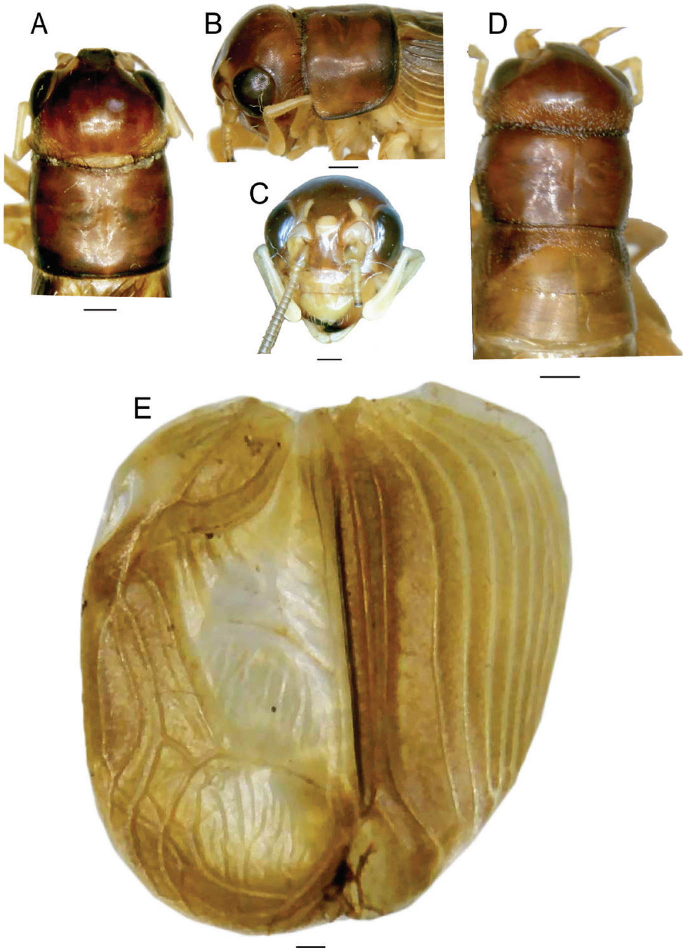

Fig. 4. Morphology of *Neogryllopsis gorochovi* sp. nov. **A.** Male head and pronotum; **B.** Male lateral view of head and pronotum; **C.** Male face; **D.** Female head, pronotum, and FWs; **E.** Male FW. Scale bars: 7 mm (**A**); 6 mm (**B, E**); 5 mm (**C**); 8 mm (**D**).

Male measurements (holotype, in mm).—BL, 15.03; PL, 2.60; PW, 4.12; FWL, 6.02; CL, 10.33; FL, 11.82; FW, 3.83; TL, 9.49. Stridulatory file with 86 teeth.

Key to males of African *Neogryllopsis* species of *Sabianus* group

1 FWs without a dividing vein in mirror; harp with 4 oblique veins; less than 200 stridulatory file teeth; ectoparamere without setae .... *Neogryllopsis gorochovi* sp. nov.

– FWs with a dividing vein in mirror; harp with 5 oblique veins; more than 200 stridulatory file teeth; ectoparamere with setae 2

2 Stridulatory file with 200 to less than 270 teeth; presence of white stripe between lateral ocelli and pale band across vertex; pronotum reddish brown, unbanded .... *Neogryllopsis sabianus* Otte, Toms & Cade, 1988

– Stridulatory file with more than 270 teeth; absence of white stripe between lateral ocelli and pale band across vertex; pronotum reddish brown but with a distinct ivory-colored band along all margins.................. *Neogryllopsis limpopensis* Otte, Toms & Cade, 1988

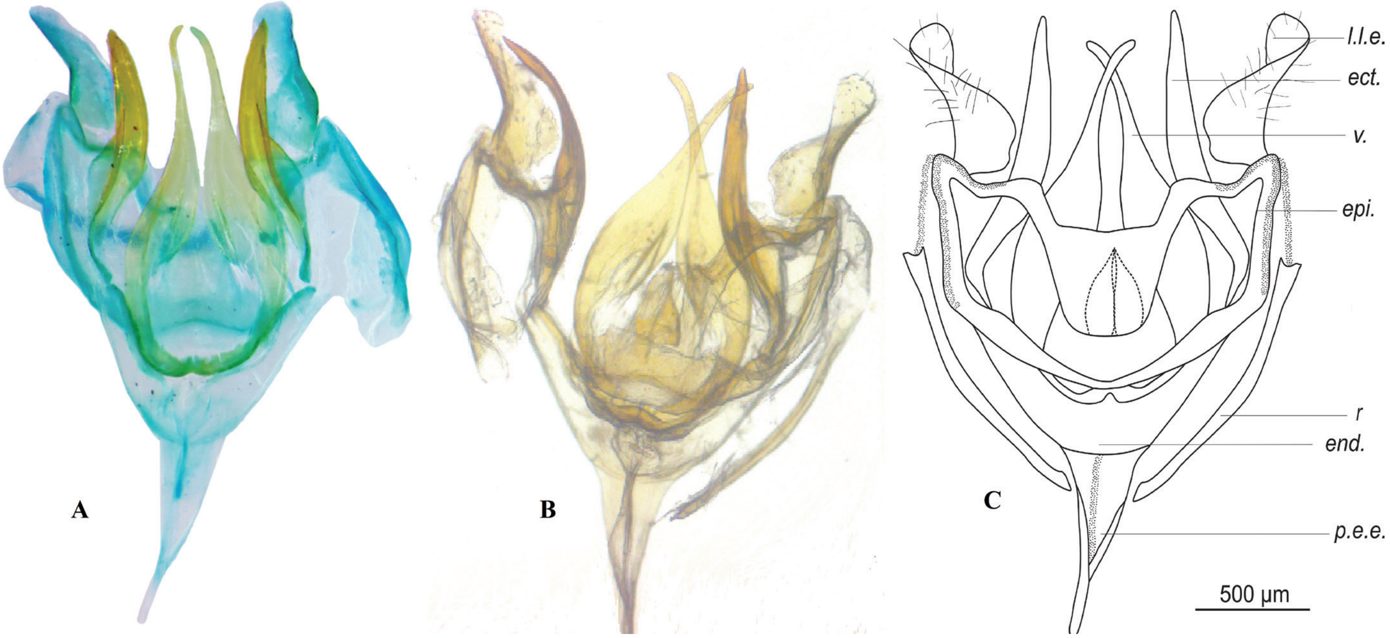

Fig. 5. Male genitalia of *Neogryllopsis gorochovi* sp. nov.; **A**. Dorsal view; **B**. Ventral view; **C**. Drawing. Scale bar: 500 µm. Abbreviations: epiphallus, *epi*.; ectoparameres, *ect*.; endoparameres, *end*.; ramus, *r*; virga, *v*.; posterior emargination of epiphallus, *p.e.e.*

Table 1. Measurements in mm: average ± standard error (minimum–maximum) total abundance.

Feature	Male	Female	t Value	P Value
BL	15.77 ± 0.48 (14.10–19.84) 12	17.43±0.34 (14.64–21.10) 29	2.70	0.01
PL	2.93 ± 0.08 (2.40–3.23)12	3.26±0.06 (2.62–4.45)29	3.25	0.002
PW	3.95 ± 0.03 (3.77–4.12)12	4.23±0.06 (3.16–4.68)29	2.63	0.01
FWL	5.17 ± 0.22 (3.99–6.10)12	–	–	–
CL	9.15 ± 0.87 (8.27–11.58) 11	11.00±0.32 (6.83–14.24)29	2.49	0.017
FL	12.32 ± 0.11 (11.60–12.92)12	12.73±0.13 (10.43–13.8)29	1.85	0.07
FW	3.92 ± 0.10 (3.43–4.61)12	4.19±0.06 (3.33–4.67)29	2.47	0.018
TL	9.88 ± 0.23 (7.88–10.62)12	10.34±0.16 (8.45–11.48)29	1.62	0.11
OL	–	9.30±0.28 (7.52–13.89)29	–	–
FWL/PL	1.78 ± 0.09 (1.31–2.32) 12	–	–	–
CL/FL	0.74± 0.07 (0.67–0.93) 11	0.86±0.02 (0.65–1.24)29	2.14	0.039
OL FL	–	0.74±0.03 (0.59 –1.15)29	–	–

Discussion

We described two new species belonging to the genera *Turanogryllus* and *Neogryllopsis*, respectively. Both are newly recognized for Cameroonian fauna; they increase the number of African species of *Turanogryllus* to 11 and of *Neogryllopsis* to 21.

These species, namely *Turanogryllus zamakoensis* Um Nyobe, Kekeunou & Bilong Bilong sp. nov. and *Neogryllopsis gorochovi* Um Nyobe, Kekeunou & Ma sp. nov., are characterized by comparatively low numbers of teeth on the stridulatory file, i.e., 156 and 86 teeth, respectively, while the other known species belonging to the genera *Turanogryllus* and *Neogryllopsis* have stridulatory files with more than 200 teeth (Otte 1994, Otte et al. 1988).

It is worth noting that all species of the genus *Turanogryllus* have TI with small inner and large outer tympanum (Tarbinsky 1940), while those of the genus *Neogryllopsis* have divided mirrors (Otte 1987). Nevertheless, *T. zamakoensis* sp. nov. has only one outer tympanum, and *N. gorochovi* sp. nov. has an undivided mirror as found in *Neogryllopsis storozhenkoi* Gorochov, 1988 (Otte et al. 1988).

The description of these two new species of Turanogryllini from Central Africa (more precisely, from Cameroon), extends the known range for both genera. In addition, they were previously known as field crickets (Randell 1964, Otte 1983, Otte 1987, Otte et al. 1988) but in the current work, *T. zamakoensis* sp. nov. was captured in a forested area,while *N. gorochovi* sp. nov. was found in both open and closed environments. It is possible that *T. zamakoensis* and *N. gorochovi* also occur in open areas near forests. To better characterize the species' living environments, additional studies are needed.

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Relationships among body size components of three flightless New Zealand grasshopper species (Orthoptera, Acrididae) and their ecological applications

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Abstract

Body size is perhaps the most fundamental property of an organism and is central to ecology at multiple scales, yet obtaining accurate estimates of ecologically meaningful size metrics, such as body mass, is often impractical. Allometric scaling and mass-to-mass relationships have been used as alternative approaches to model the expected body mass of many species. However, models for predicting body size in key herbivorous insects, such as grasshoppers, exist only at the family level. To address this data gap, we collected empirical body size data (hind femur length and width, pronotum length, live fresh mass, ethanol-preserved mass, and dry mass) from 368 adult grasshoppers of three flightless species at Hamilton Peak, Southern Alps, New Zealand. We examined the relationships among body size components across all species using linear and non-linear regression models. Femur length and preserved mass were robust predictors of both fresh mass and dry mass across all species; however, regressions using preserved mass as a predictor always showed higher predictive power than those using femur length. Based on our results, we developed species-specific statistical linear mixed-effects models to estimate the fresh and dry masses of individual grasshoppers from their preserved mass and femur length. Including sex as an additional co-variate increased model fit in some cases but did not produce better estimates than traditional mass-to-mass and allometric scaling regressions. Overall, our results showed that two easy-to-measure, unambiguous, highly repeatable, and non-destructive size measures (i.e., preserved mass and femur length) can predict, to an informative level of accuracy, fresh and dry body mass across three flightless grasshopper species. Knowledge about the relationships between body dimensions and body mass estimates in these grasshoppers has several important ecological applications, which are discussed.

Keywords

allometric scaling, body mass, linear body dimension, mass-to-mass relationships, predictive models

Introduction

Organism body size is one of the most important axes in ecology, as it is related to nearly all biological processes, from individual performance to ecosystem function (Whitman 2008, Chown and Gaston 2010). In insects, body size is closely linked to physiological rates (e.g., metabolic and growth), life-history traits (e.g., longevity and fecundity), and ecological attributes, such as abundance, range size, and dispersal (Peters 1983, Siemann et al. 1996, Whitman 2008, Chown and Gaston 2010, Ehnes et al. 2011, Stevens et al. 2012). Moreover, arthropod body size is central to the contribution of individuals and communities to key ecosystem processes and services, such as decomposition, carbon cycling, primary productivity, pollination, predation, and herbivory (Cízek 2005, Barnes et al. 2018, Kendall et al. 2019). Therefore, changes in the body size of a taxon reflect changes in resources that may cascade across all levels of biological organization. For example, body size differences are usually associated with individual survival and fecundity, and changes in body size might alter ecological processes, including trophic interactions, plant–animal interactions, and food web connectivity (Peters 1983, Stang et al. 2009, DeLong et al. 2015, Horne et al. 2018).

Adult body size in Orthoptera is generally expressed in terms of length and mass, each of which is controlled by both genetic and environmental factors that operate through molecular and physiological mechanisms (Nijhout 2003, Whitman 2008, Chown and Gaston 2010). Although length and mass are often correlated, each captures a different aspect of an organism's size and is subject to different selective pressures during an organism's lifespan (Gaston and Blackburn 2000). Insect structural body size (e.g., length dimensions) is determined during development by gene–environment interactions, whereas adult body mass additionally varies through time depending on environmental factors, for example, reproductive phase and nutritional status (Whitman 2008, Chown and Gaston 2010, Knapp and Knappová 2013). Despite this fact, body mass- and linear-based estimates are often used interchangeably as measures of adult body size in ecological research (Chown and Gaston 2010). Decisions on the body size measure used in a particular study should be made cautiously and considering the research question and species (Gaston and Blackburn 2000, Moretti et al. 2017).

Body mass is the most meaningful size metric, as it is directly linked with metabolic rate and is affected by environmental conditions (Gaston and Blackburn 2000, Sohlström et al. 2018). Therefore, fresh (live) mass is preferred to relate body size to a range of functional and ecological attributes, such as metabolism, movement, and abundance (e.g., Chown and Steenkamp 1996, Meehan 2006, Ehnes et al. 2011, Hirt et al. 2017). In some instances, however, dry mass is recorded to estimate, for example, organism biomass, since variation from water content is reduced (e.g., Sage 1982, Cressa 1999, Sabo et al. 2002, Gilbert 2011, Penell et al. 2018). While body mass is a useful predictive trait for many ecosystem processes, measuring individual arthropod body mass is a time-consuming and tedious process (Johnston and Cunjak 1999, Eklöf et al. 2017, Sohlström et al. 2018, Kendall et al. 2019). Moreover, collection and storage methods often prevent the direct determination of mass estimates, especially when specimens are damaged (e.g., loss of appendages) or when subject to chemical preservation that causes unpredictable mass change (Johnston and Cunjak 1999, Wetzel et al. 2005, Chown and Gaston 2010, Moretti et al. 2017). As a result, most ecological studies on insects rely on more easily measured body dimensions (e.g., body length) as proxies for body size (Chown and Gaston 2010). Many insect collections are composed of specimens preserved in ethanol, and these collections provide an important source of information about organismal change over time if we can convert preserved mass to biologically meaningful measures.

Allometric scaling rules applied to co-varying traits can be used to predict an organism's body mass based on an easy-to-obtain body length measurement, thus avoiding the use of problematic body mass estimators (Johnston and Cunjak 1999, Moretti et al. 2017, Pennell et al. 2018, Kendall et al. 2019). Scaling equations have proven to be powerful tools for the prediction of body mass for a wide range of insect taxa based on different linear metrics (e.g., Rogers et al. 1977, Schoener 1980, Johnston and Cunjak 1999, Sabo et al. 2002, García-Barros 2015, Kendall et al. 2019). These equations rely on regression parameters estimated for length–mass relationships, which are often subject to intersexual allometric differences (Hagen and Dupont 2013, Kendall et al. 2019). Incorporating sexual size dimorphism data into scaling relationships, and thus their regression parameters, is crucial to overcome this limitation (e.g., Kendall et al. 2019). Despite the broad application of allometric scaling in ecological research, there are surprisingly few studies providing regression parameters for estimating the body mass of key herbivorous taxa, such as grasshoppers (but see Schoener 1980, Sabo et al. 2002 for allometric equations at the ordinal level).

Short-horn grasshoppers (Orthoptera: Acrididae) are among the most diverse (> 6,700 described species) and ubiquitous fauna of grassland ecosystems around the world (Uvarov 1966, Latchininsky et al. 2011, Song et al. 2018) contributing, in some cases, to more than half of the total above-ground arthropod biomass (Gillon 1983, Song et al. 2018). The endemic short-horn grasshoppers of Aotearoa New Zealand occur widely, but are especially abundant in alpine habitats (Bigelow 1967, Trewick 2001, Trewick 2008, Trewick and Morris 2008, Koot et al. 2020). As major invertebrate herbivores in native grassland ecosystems (Batcheler 1967, White 1975), these grasshoppers might play a major role in structuring plant communities and regulating ecosystem function via plant productivity, competition, and nutrient cycling (Olff and Ritchie 1998, Belovsky and Slade 2000, Moretti et al. 2013, Deraison et al. 2015). Given the ecological importance of grasshoppers, the determination of allometric scaling relationships provides an opportunity to explore ecologically important traits and variations that are otherwise difficult to measure.

Body size data have been accumulated for New Zealand grasshoppers mostly as linear dimensions: hind femur length and width, and pronotum length (e.g., Batcheler 1967, Staples 1967, Bigelow 1967, Mason 1971; but see Dowle et al. 2014, Carmelet-Rescan et al. 2021). However, the suitability of these measures as predictors of body size and their relationship with other body mass estimates have not been tested. A key feature of grasshoppers is the use of jumping in locomotion and predator avoidance (Queathem 1991), and this is especially true for flightless species such as those found in New Zealand. Therefore, the size of the hind jumping leg may be closely related to other size components and, thus, to overall body size. The marked sexual size dimorphism of most grasshoppers might compound intraspecific differences in the relationships among body size components. Here, we examined these relationships focusing on three brachypterous and flightless species of the endemic alpine radiation of Kā Tiritiri-o-te-moana, the Southern Alps (Bigelow 1967, Trewick and Morris 2008, Koot et al. 2020; Fig. 1A–C): *Brachaspis nivalis* (Hutton, 1987), *Paprides nitidus* Hutton, 1987, and *Sigaus australis* (Hutton, 1987). First, we quantified the effects of short-term ethanol preservation by describing the weight change over 120 days. Then, we examined scaling ratios to assess the predictive power of preserved mass for both fresh and dry masses. We also analyzed intraspecific length–mass relationships over an elevation gradient to account, at least partially, for environmental variation in body size. Based on our results, we developed species-specific statistical models to estimate the fresh and dry mass of individual grasshoppers from their preserved mass and hind femur length. Overall, our models showed high predictive power such that body mass estimates derived from them can be used to test mechanistic hypotheses for shifts in morphological and ecological traits related to body size.

Materials and methods

Specimen collection and measurements.—A total of 368 complete adult specimens (no missing appendages) representing three grasshopper species (*B. nivalis* 61♂, 71♀; *P. nitidus* 73♂, 73♀; *S. australis* 42♂, 48♀) were collected on Hamilton Peak in the Craigieburn Range, New Zealand (-43.129, 171.688; WGS84). Sampling was done by hand, capturing grasshoppers disturbed by walking at five sites at ~100 m elevation intervals (BR1 to BR5) from 1,383 to 1,817 m asl, to capture as much local variation in body size as possible. Species and sex were recorded from live specimens in the field and were later corroborated upon processing based on morphological features (e.g., body color pattern, pronotum shape, and body shape and size) following Bigelow (1967). Maturity and sex were determined using the size and shape of the tegmina and terminalia (Bigelow 1967).

Grasshoppers were weighed alive after cooling to 4 °C, then frozen overnight before being preserved in 95% ethanol for DNA preservation. Specimens were weighed using a Sartorius Quintix35–1S digital scale (Sartorius Lab Instruments GmbH & Co, Goettingen, Germany) accurate to 0.001 g. We measured the left hind femur length (hereafter femur length) and width (hereafter femur width), and pronotum length of specimens (Fig. 1D) using an Olympus SZX7 stereomicroscope with Olympus SC100 image capture and Olympus cellSens Dimension v1.6 software (Olympus Corporation, Tokyo, Japan). These measures were chosen because they are commonly used proxies for body size in grasshoppers (e.g., Bigelow 1967, Mason 1971, Harris et al. 2012, Yadav et al. 2018).

To quantify the effects of our preservation method on body mass estimates, we remeasured the body mass of all specimens after two and four months of storage in ethanol. Once all other measurements were completed, a random subsample of 50 specimens of each species (25 males and 25 females) were dried in an

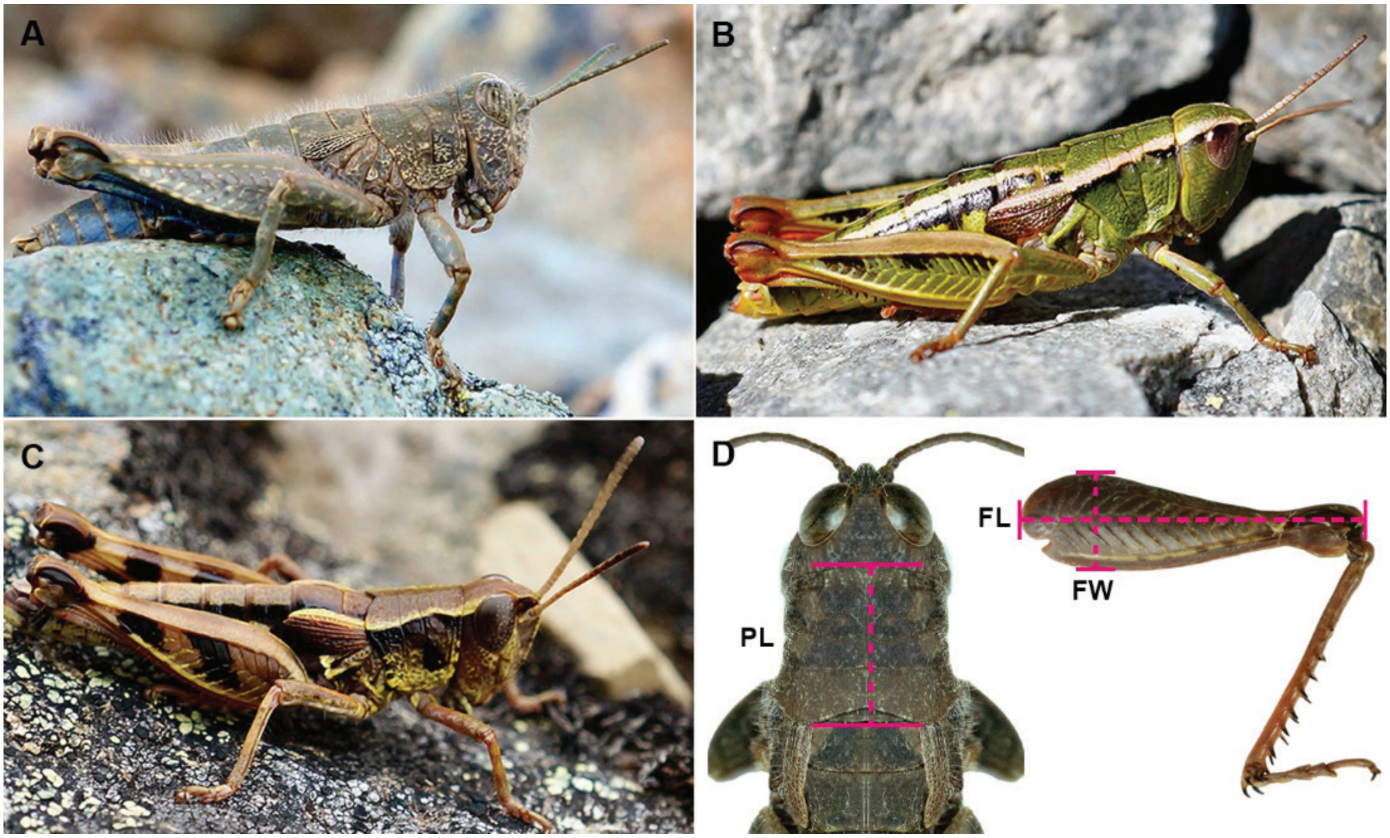

Fig. 1. Adult endemic, brachypterous, and flightless grasshopper species from Hamilton Peak in the Southern Alps, New Zealand. **A.** *Brachaspis nivalis* female; **B**. *Paprides nitidus* female; **C**. *Sigaus australis* male; **D**. Body dimensions used as proxies of overall body size in this study: morphometric data were collected for hind femur length (FL), hind femur width (FW), and pronotum length (PL).

oven at 60°C for at least 96 h, until their mass ceased to change, and were then weighed. To assess measurement repeatability, we randomly selected five males and five females of each species and remeasured and reweighed them three times in random order.

Data analysis and model structures.—Repeatability (R) was calculated independently for species and sexes with the R package rptR (Stoffel et al. 2017), using specimen as a grouping term. The ratio of intra-observer variance (i.e., R) was calculated as the among-group variance (VG) over the sum of group-level and within-group (residual) variance (VR): R = VG / (VG + VR). Confidence intervals (95%) around repeatability values were estimated using 1,000 parametric bootstrap iterations. The effect of preservation in 95% ethanol on specimen body mass was examined by comparing the mass of individuals when live (fresh mass) and after ethanol preservation for two and four months. We also examined the frequency distributions of differences in body mass before and after preservation for each species. As the shape of the size–frequency distribution was almost identical for both preserved states (Fig. 2), we used a Wilcoxon signed-rank test to analyze overall and sex-specific differences between fresh mass and preserved mass after four months of preservation (hereafter preserved mass), pooling data from all species. For these analyses, a non-parametric approach was preferred, as mass difference between live and 4-month preserved specimens was not normally distributed when considered together. Statistical tests were implemented using the R package rstatix version 0.7.0 (Kassambara 2021).

We explored mass-to-mass ratios between ethanol preserved mass (after four months of preservation, **PM**), and both fresh mass (**FM**) and dry mass (**DM**) for each species, using model II regressions with standardized major axis (SMA) in the R package smatr version 3.4-8 (Warton et al. 2012). We performed SMA regressions by (i) including an intercept term (i.e., not forced through the origin) under the robust outlier option and (ii) assuming that changes in any body mass metric is reflected in the other metric, as measurements came from the same specimens ($y = 0$ when $x = 0$), and forcing the intercept through the origin (i.e., zero-intercept). We also tested for a common slope between sexes and among sites (i.e., elevation) with an ANCOVA-like test, using the slopes estimated in SMA regressions (Warton et al. 2012). Since preserved mass was closely related to the other measures of mass ($R^2 \geq 0.913$, $p < 0.001$; for additional details see Results), we specified a series of species-specific linear mixed-effects (LMM) models to predict **FM** and **DM** as a function of **PM** using the R package lme4 version 1.1-27.1 (Bates et al. 2015). This approach allowed us to account for sex- and site-specific differences in body mass by including sex as an additional fixed effect and as an interaction term with preserved mass, elevation as a random intercept, and preserved mass as a random slope.

We used ordinary least squares (OLS) regressions in R base (R Core Team 2020) to compare body dimensions (femur length = **FL**, femur width = **FW**, and pronotum length = **PL**) as predictors of body mass components (i.e., **FM** and **DM**) using log-transformed data. For each species, we estimated and compared the slopes of fitted lines between sexes using the R package emmeans version 1.6.2-1 (Lenth 2021). As the strength of relationships varied between sexes and in some instances presented apparent deviations from linearity (see Results), we fitted sex-specific non-linear mod-

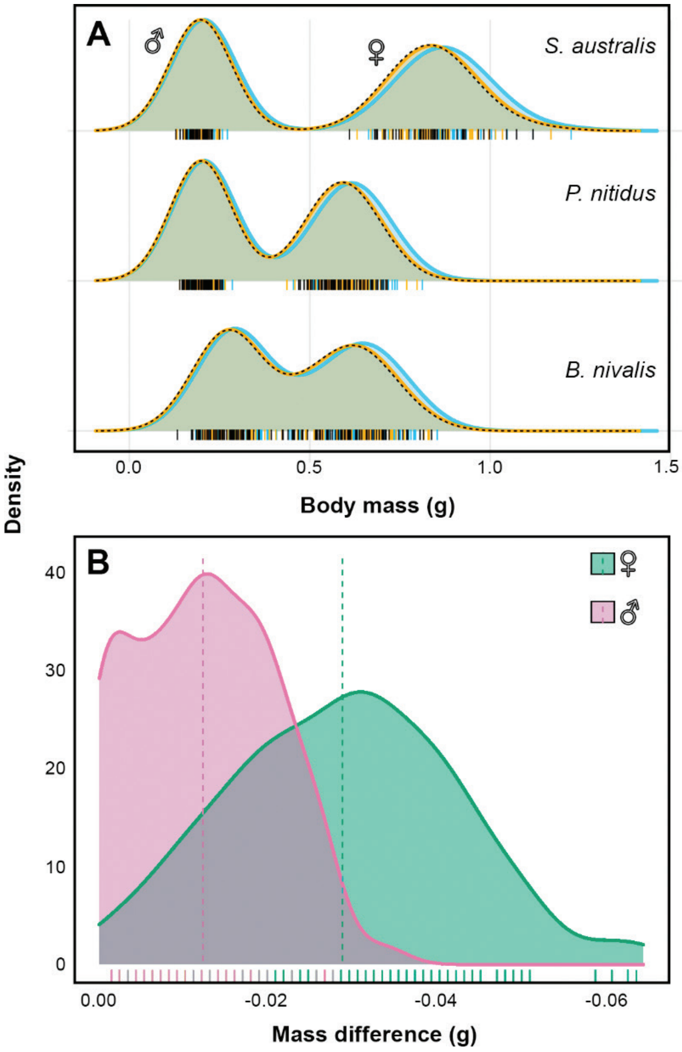

Fig. 2. A. Density distributions of body mass in three flightless New Zealand grasshopper species when alive (turquoise) and after ethanol-preservation for two (dark yellow) and four months (black); **B.** The distribution of the difference in mass between live and 4-month preserved specimens pooled for all three species and partitioned by sex. Mean values for male (-0.012 g) and females (-0.029 g) are indicate by dashed lines. Marginal rug indicates individual observations of body mass.

els (Knell 2009) to analyze the shape of the scaling relationship. Five models were compared using Akaike's Information Criteria (AIC): (i) quadratic, (ii) logistic, (iii) four-parameter logistic, (iv) Weibull growth function, and (v) power function models. Models were fitted on untransformed variables (Packard 2011) using base R (R Core Team 2020) and the R package aomisc version 0.647 (Onofri 2020). We chose femur length for the following analyses because it was highly correlated with all other body dimensions (Pearson's R > 0.924, $p < 0.001$) and easier to measure consistently, as indicated by our repeatability analysis (Suppl. material 1: Appendix 1).

We further explored scaling relationships between **FL** and both **FM** and **DM** using model II regressions SMA including only an intercept term (i.e., not forced through the origin), as the femur length of adult insects does not change in response to changes in body mass (Whitman 2008, Chown and Gaston 2010, Bailey et al. 2020). We also specified LMMs using **FL** as a predictor of both **FM** and **DM**, using homologous model structures as defined previously for mass-to-mass modeling, to account for sex- and site-specific differences in trait variability. These approaches were chosen because sex-specific linear models generally performed as well as or better than non-linear models ($\Delta AIC \leq 1.95$), although when predicting dry mass for females of *B. nivalis,* the quadratic model performed slightly better than the linear model ($\Delta AIC = 2.61$). For model formulation, we used log-transformed values because static allometric relationships explored here are generally well-described by a power function ($y = ax^b$), which is linearized when log-transformed: $\ln(y) = \ln(\alpha) + \beta \times \ln(x) + e$, where y = dry mass, α = intercept, β = allometric coefficient, and x = linear size proxy.

The best-fitted models (both allometric and LMMs) were selected using Akaike's information criterion corrected for sample size (AICc) and Akaike weight (wi) using the R package AICcmodavg version 2.3-1 (Mazerolle 2020). Models with $\Delta AICc < 2$ were considered equally supported by the data, while models with $\Delta AICc > 2$ were considered to show substantial differences (Burnham and Anderson 2002). The Akaike weight (wi) was interpreted as the probability that model i was the best model given all evaluated models and data available (Burnham and Anderson 2002). For all models, the goodness of fit was examined by calculating conditional R^2 using the R package MUMIn version 1.43.17 (Barton 2020). The statistical significance of fixed and random effects was examined for the best-fitted models using the R package lmerTest version 3.1-3 (Kuznetsova et al. 2017). Assumptions of model fit were met for all models as indicated by diagnostic plots of residuals.

Testing model accuracy.—We predicted fresh and dry body mass for 368 grasshopper specimens using mass-to-mass ratios, scaling regressions, and parameters from the best-fitted LMMs. We then tested the relationship between measured and predicted values using model II regressions with a major axis approach using the R package lmodel2 version 1.7-3 (Legendre 2018). This method is appropriate when comparing empirical observations to model predictions (Legendre and Legendre 2012). The statistical significance of relationships was tested using one-tailed permutation tests (with 1,000 permutations), and the strengths of the relationships were determined by model R^2 values. Observed relationships were also compared to the ideal $x = y$ association where estimated = measured by calculation of 95% confidence intervals around the estimated slope. The accuracy of our predictions was also estimated using the root-mean-square error (RMSE) between the observed and predicted values, using the R package Metrics version 0.1.4 (Hamner and Frasco 2018). All analyses were performed using R 4.0.3 (R Core Team 2020).

Results

We found high measurement consistency (R > 0.970), although the degree of repeatability differed among body size proxies, species, and sexes, reflecting the relative size of the values (Suppl. material 1: Appendix 1). The highest mean repeatability was recorded for the larger traits (femur length R = 0.9990 ± 0.0001 SD, preserved mass R = 0.9985 ± 0.0001 SD), the larger species (*B. nivalis* R = 0.9941 ± 0.0082 SD and *S. australis* R = 0.9941 ± 0.0094 SD compared to *P. nitidus* R = 0.9912 ± 0.0147 SD), and the larger sex (females R = 0.9953 ± 0.0068 SD compared to males R = 0.9907 ± 0.0148 SD). Overall, grasshopper specimens weighed significantly less after four months in ethanol than when they were alive (Wilcoxon's test $p < 0.001$; Fig. 2A), although differences were small (4.606% ± 2.705 SD). On average, the larger female specimens lost more weight than the male specimens (Wilcoxon's test $p < 0.001$; Fig. 2B; see Suppl. material 1: Appendix 2 for species details).

There were strong and significant relationships between preserved mass (**PM**) and both fresh mass (**FM**, $R^2 \geq 0.997$, $p < 0.001$) and dry mass (**DM**, $R^2 \geq 0.913$, $p < 0.001$) in all species (Fig. 3; Suppl. material 1: Appendix 3). No significant differences in slopes were indicated by the ANCOVA-like test for the two sexes, but site differences were found when predicting **DM** as a function of **PM** in *S. australis* (Suppl. material 1: Appendix 3). Estimated ratios of preserved to fresh mass (mean ratio = 1.041 ± 0.005 SD) and preserved to dry mass (mean = 0.310 ± 0.008 SD) were similar for all species (Table 1). All LMMs including co-variables exhibited similar overall predictive power as judged by their fitting scores (Table 2). When predicting fresh mass as a function of preserved mass, the **PM**-only fixed-effect model incorporating site as a random effect (**FM**~**PM**+(1|Site)) outperformed other models for all species, except *B. nivalis* (Table 2a). For this species, one of the models accounting for sexual dimorphism exceeded the baseline model (i.e., **FM**~**PM**+(1|Site)) in terms of AICc (ΔAICc = 3.47, Δwi = 0.54) but not R^2 ($\Delta R^2 = 0.001$). In contrast, when predicting dry mass, one of the models accounting for sexual dimorphism and site differences (**FM**~**PM**+Sex+(**PM**|Site)) surpassed other models for all species (Table 1b) except *B. nivalis*. In this species, the **PM**-only fixed-effect model outperformed models including sex in terms of AICc (ΔAICc = 2.47, Δwi = 0.51) but not R^2 ($\Delta R^2 = 0.000$). Fixed effects were significant in all best-fitted models ($p > 0.001$), yet the random effect (i.e., site) was only significant when predicting **FM** for *S. australis* ($p > 0.001$; Suppl. material 1: Appendix 4). All LMMs outperformed the null models (i.e., **FM**~1+(1|Site) and **DM**~1+(1|Site)) in their predictive power (Table 2).

As expected, there was a strong and significant correlation (Pearson's R ≤ 0.893, $p < 0.001$) among all body size measures, with pairwise comparisons involving femur length (**FL**) having the highest correlation coefficients (Pearson's R > 0.924, $p < 0.001$; Suppl. material 1: Appendix 5). All body dimensions exhibited strong and significant linear relationships with both fresh mass ($R^2 \geq 0.938$, $p < 0.001$) and dry mass ($R^2 \geq 0.887$, $p < 0.001$), although the strength of these relationships differed between sexes and, in some cases, appeared nonlinear (Suppl. material 1: Appendix 5). Differences in slopes between sexes were subtle for all species, and a significant difference was only detected when predicting **FM** in the function of pronotum length (**PL**) for *S. australis* ($p = 0.007$, Suppl. material 1: Appendix 5). Comparisons of sex-specific models showed that, in most cases, linear models performed as well as or better than alternative non-linear models. However, slight deviation from linearity was detected when predicting **DM** for female *B. nivalis*, where an allometric quadratic model performed marginally better than a linear model for females (ΔAIC = 2.61), although both models were comparable for males (ΔAIC = 1.88). Scaling relationships between body mass estimates and femur length were generally well-described by a power function (Suppl. material 1: Appendix 6). The coefficients from SMA regressions were similar for all species

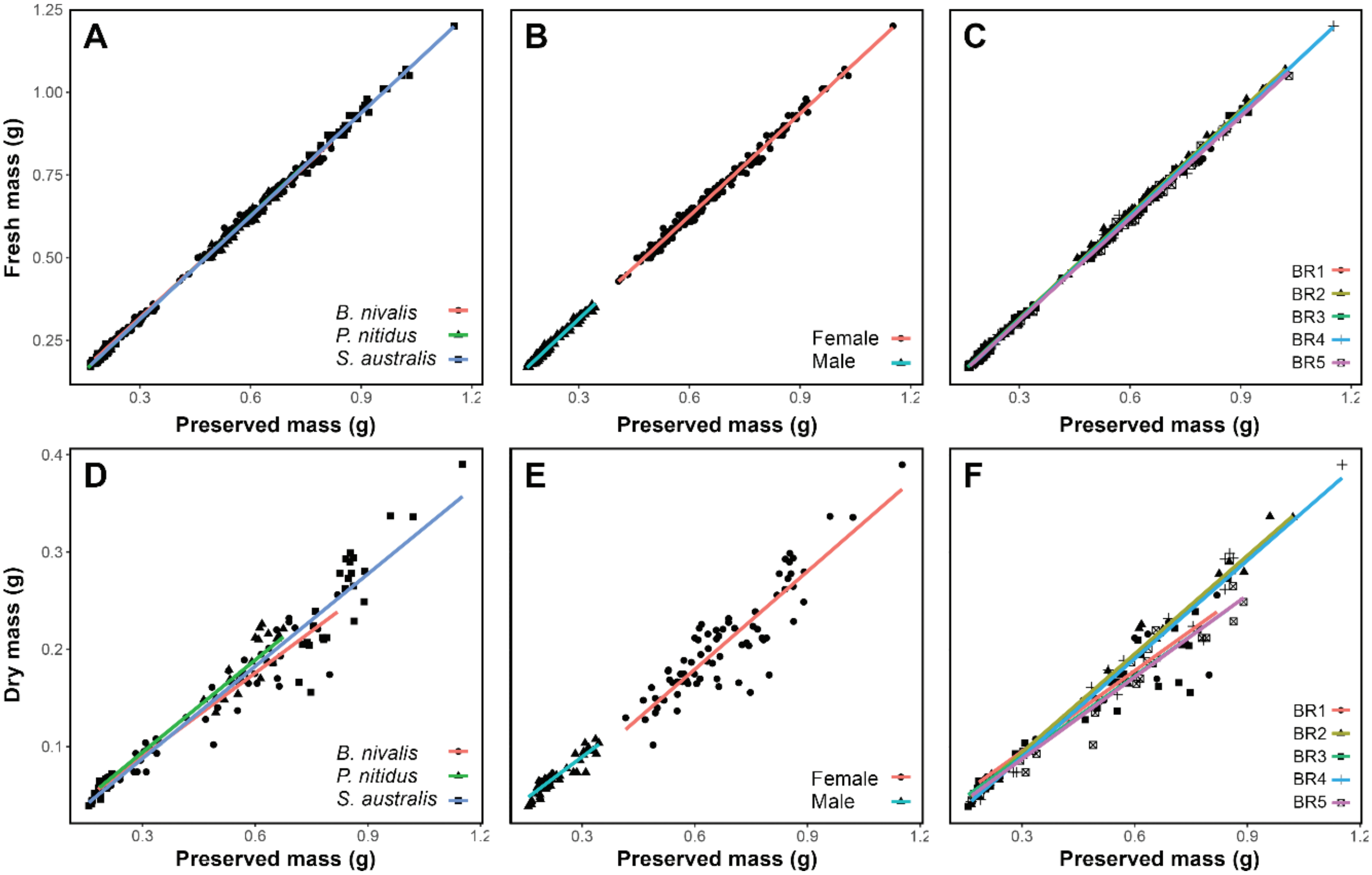

Fig. 3. Mass-to-mass relationships in three flightless New Zealand grasshopper species showing the influence of elevation and sexual dimorphism. Fresh mass–preserved mass (**A–C**) and dry mass–preserved mass (**D–F**). Sample sites (BR1 to BR5) indicating five sites in ~100-m elevation intervals from 1,383 to 1,817 m asl. Lines represent the best-fit from standardized major axis regressions. Credible intervals are omitted for clarity. Some regression lines overlie each other.

Table 1. Mass-to-mass ratios for predicting both fresh and dry mass from preserved mass in three flightless New Zealand grasshopper species. Regression parameters based on standardized major axis regressions and their confidence intervals (95% CI) are shown.

Species	SMA	Intercept$_{(CI)}$	Slope$_{(CI)}$	R^2	p-value	Ratio
(a) Preserved mass to fresh mass (PM:FM)						
Brachaspis nivalis	0-intercept	0.000	$1.045_{(1.041,\ 1.050)}$	0.999	< 0.001	FM=1.045PM
Brachaspis nivalis	intercept	$0.009_{(0.004,\ 0.013)}$	$1.030_{(1.021,\ 1.039)}$	0.997	< 0.001	FM=1.030PM
Paprides nitidus	0-intercept	0.000	$1.045_{(1.041,\ 1.049)}$	0.999	< 0.001	FM=1.045PM
Paprides nitidus	intercept	$0.000_{(-0.003,\ 0.003)}$	$1.045_{(1.038,\ 1.052)}$	0.998	< 0.001	FM=1.045PM
Sigaus australis	0-intercept	0.000	$1.042_{(1.038,\ 1.045)}$	0.999	< 0.001	FM=1.042PM
Sigaus australis	intercept	$0.002_{(-0.001,\ 0.006)}$	$1.039_{(1.033,\ 1.045)}$	0.998	< 0.001	FM=1.039PM
(b) Preserved mass to dry mass (PM:DM)						
Brachaspis nivalis	0-intercept	0.000	$0.296_{(0.286,\ 0.306)}$	0.986	< 0.001	DM=0.296PM
Brachaspis nivalis	intercept	$-0.004_{(-0.014,\ 0.005)}$	$0.308_{(0.289,\ 0.330)}$	0.913	< 0.001	DM=0.308PM
Paprides nitidus	0-intercept	0.000	$0.316_{(0.308,\ 0.323)}$	0.993	< 0.001	DM=0.316PM
Paprides nitidus	intercept	$0.001_{(-0.004,\ 0.006)}$	$0.310_{(0.297,\ 0.324)}$	0.969	< 0.001	DM=0.310PM
Sigaus australis	0-intercept	0.000	$0.308_{(0.298,\ 0.319)}$	0.987	< 0.001	DM=0.308PM
Sigaus australis	intercept	$-0.009_{(-0.019,\ 0.001)}$	$0.321_{(0.304,\ 0.338)}$	0.959	< 0.001	DM=0.321PM

Table 2. Model selection showing the best-fitted models (AICc in bold) for predicting both fresh mass and dry mass from preserved mass in three New Zealand flightless grasshopper species. Abbreviations: K = number of parameters, AICc = Akaike's information criterion corrected for sample size, wi = Akaike weight, LL = Log-Likelihood, R^2 = marginal R^2. Model parameters of the best-fitting models (ΔAICc < 2) used for predictions are shown in Suppl. material 1: Appendix 4.

Species	Model formulae	K	AICc	ΔAICc	wi	LL	R^2
(a) fresh mass (FM) as a function of preserved mass (PM)							
Brachaspis nivalis	**FM**~**PM**+Sex+(1|Site)	5	**-808.58**	0.00	0.66	409.53	0.997
	FM~**PM**+Sex+(**PM**|Site)	7	**-807.01**	1.57	0.23	410.96	0.997
	FM~**PM***Sex+(1|Site)	6	-806.38	2.20	0.22	409.53	0.997
	FM~**PM**+(1|Site)	4	-805.11	3.47	0.12	406.71	0.996
	FM~1+(1|Site)	3	-64.11	744.47	0.00	35.15	0.112
Paprides nitidus	**FM**~**PM**+(1|Site)	4	**-937.02**	0.00	0.67	472.65	0.998
	FM~**PM**+Sex+(1|Site)	5	-934.87	2.14	0.23	472.65	0.998
	FM~**PM***Sex+(1|Site)	6	-933.26	3.75	0.10	472.93	0.998
	FM~**PM**+Sex+(**PM**|Site)	7	-931.53	5.49	0.04	473.17	0.998
	FM~1+(1|Site)	3	-35.70	901.31	0.00	20.94	0.000
Sigaus australis	**FM**~**PM**+(1|Site)	4	**-566.34**	0.00	0.50	288.35	0.999
	FM~**PM**+Sex+(1|Site)	5	**-565.69**	0.65	0.36	287.41	0.999
	FM~**PM***Sex+(1|Site)	6	-563.69	2.65	0.13	288.20	0.999
	FM~**PM**+Sex+(**PM**|Site)	7	-561.04	5.31	0.03	288.20	0.999
	FM~1+(1|Site)	3	69.40	635.75	0.00	-31.56	0.000
(b) dry mass (DM) as a function of preserved mass (PM)							
Brachaspis nivalis	**DM**~**PM**+(1|Site)	4	**-259.16**	0.00	0.73	134.03	0.915
	DM~**PM**+Sex+(1|Site)	5	-256.70	2.47	0.21	134.03	0.915
	DM~**PM***Sex+(1|Site)	6	-254.14	5.02	0.06	134.05	0.915
	DM~**PM**+Sex+(**PM**|Site)	7	-251.39	7.77	0.01	134.03	0.915
	DM~1+(1|Site)	3	-139.34	119.82	0.00	72.93	0.000
Paprides nitidus	**DM**~**PM**+Sex+(**PM**|Site)	7	**-300.56**	0.00	0.67	158.65	0.981
	DM~**PM**+Sex+(1|Site)	5	-298.31	2.25	0.22	154.85	0.976
	DM~**PM***Sex+(1|Site)	6	-296.03	4.53	0.07	155.02	0.976
	DM~**PM**+(1|Site)	4	-294.75	5.81	0.04	151.83	0.972
	DM~1+(1|Site)	3	-125.73	174.83	0.00	66.13	0.000
Sigaus australis	**DM**~**PM**+Sex+(**PM**|Site)	7	**-258.46**	0.00	0.59	137.53	0.979
	DM~**PM**+Sex+(1|Site)	5	**-257.21**	1.25	0.31	134.27	0.974
	DM~**PM***Sex+(1|Site)	6	-254.85	3.62	0.10	134.38	0.974
	DM~**PM**+(1|Site)	4	-241.01	17.46	0.00	124.94	0.964
	DM~1+(1|Site)	3	-78.24	180.22	0.00	42.38	0.000

when scaling the relationship between **FL** and both **FM** and **DM** (Table 3; Fig. 4). Most LMMs including co-variables displayed comparable overall predictive ability as judged by their fitting scores (Table 4). In general, models accounting for sexual dimorphism outperformed other models for all species, although in a few cases, parameters from equally supported baseline models (e.g., **FL**-only fixed-effect, ΔAICc < 2) led to more accurate body mass predictions (Table 4). Fixed effects were significant in all best-fitted models (in all cases $p > 0.001$, but $p = 0.048$ when predicting fresh mass for *B. nivalis*), but the random effect (i.e., site) was not significant for any model ($p > 0.001$; Suppl. material 1: Appendix 4). All formulated LMMs outperformed the null models (i.e., ln(**FM**)~1+(1|Site) and ln(**DM**)~1+(1|Site)) in their predictive power.

We found that predicted body mass (both fresh and dry mass) was significantly correlated with empirical measurements; however, using **PM** as a predictor led to the most accurate estimates (Fig. 5). In all cases, the relationship between estimated and measured body mass was not significantly different from a 1:1 relationship, with > 89% of the variation explained (Table 5). The range of prediction error (RMSE) was near identical for body mass predictions obtained from mass-to-mass ratios, scaling regressions, and LMMs. When using **PM** as a predictor, **FM** estimates from **PM**:**FM** ratios were marginally more accurate than those from LMMs (RMSE = 0.011 g and 0.012 g, respectively). In contrast, LMMs were slightly more accurate than **PM**:**DM** ratios when predicting **DM** (RMSE = 0.014 g and 0.017 g, respectively). However, the range of prediction error was considerably higher when using **FL** as a predictor. For **FM** estimates, predictions based on SMA scaling relationships were marginally more accurate than those from LMMs (RMSE = 0.048 g and 0.050 g, respectively), but when predicting **DM,** prediction errors were identical using both methods (RMSE = 0.025 g).

Discussion

A key source of variation in morphological traits is measurement repeatability, which is inherently related to the statistical power of analyses based on those measurements (Bailey and Byrnes 1990, Wylde and Bonduriansky 2021). We found the highest repeatability for larger traits compared to smaller traits (e.g., femur length vs femur width), and the larger sex (female vs male) when pooling values for all size proxies and species. The effect of sex on repeatability was less clear when considering individual traits, suggesting that measurement repeatability in these species depends on other factors such as species size, trait size, and their interactions rather than sex alone. As noted by Bigelow (1967), measurement repeatability in these grasshoppers decreases in traits with rounded boundaries, such as femur width, and in traits where margins are highly variable in shape, such as pronotum length.

Table 3. Length–mass scaling coefficients for predicting both fresh and dry mass from femur length in three flightless New Zealand grasshopper species. Regression parameters based on standardized major axis regressions and their confidence intervals (95% CI) are shown.

Species	Model formulae	$\text{Intercept}_{(CI)}$	$\text{Slope}_{(CI)}$	R^2	p-value
(a) fresh mass (FM) as a function of femur length (FL)					
Brachaspis nivalis	ln(FM)~ln(FL)	$-7.754_{(-7.937, -7.571)}$	$2.696_{(2.625, 2.768)}$	0.965	< 0.001
Paprides nitidus	ln(FM)~ln(FL)	$-8.914_{(-9.085, -8.743)}$	$3.090_{(3.024, 3.157)}$	0.976	< 0.001
Sigaus australis	ln(FM)~ln(FL)	$-9.584_{(-9.783, -9.385)}$	$3.315_{(3.241, 3.391)}$	0.982	< 0.001
(b) dry mass (DM) as a function of femur length (FL)					
Brachaspis nivalis	ln(DM)~ln(FL)	$-9.234_{(-9.747, -8.721)}$	$2.778_{(2.585, 2.986)}$	0.898	< 0.001
Paprides nitidus	ln(DM)~ln(FL)	$-10.077_{(-10.504, -9.650)}$	$3.071_{(2.908, 3.242)}$	0.953	< 0.001
Sigaus australis	ln(DM)~ln(FL)	$-11.423_{(-11.919, -10.927)}$	$3.539_{(3.357, 3.731)}$	0.939	< 0.001

In addition, the orientation of specimens to the focal plane of the microscope can result in parallax error that is expected to be more pronounced for small structures that are difficult to measure (e.g., Wylde and Bonduriansky 2021). We found larger traits, such as femur length, could be measured with relatively little error compared to smaller features (femur width and pronotum length) that were subject to more parallax error. Measurement repeatability was also higher for the larger body mass measures (fresh and preserved mass) compared to dry specimens (dry mass), which had small values that were sensitive to variation in humidity. Dried specimens become slightly hydrated during weighing, resulting in increased errors in measurement. Body length is a widely used linear metric, but we found it unreliable in grasshoppers, as abdomen size varied considerably with body condition, including reproductive state (Hochkirch and Gröning 2008, García-Navas et al. 2017). Furthermore, the extent of telescoping of abdominal segments (Bigelow 1967) and distortion during preservation are additional sources of measurement error (García-Barros 2015).

Collecting and storing insects in chemical fluids, such as ethanol, has the potential to alter their body mass (Moretti et al. 2017, Penell et al. 2018), thus limiting their use in ecological studies that require accurate body mass data (Leuven et al. 1985, Chown and Gaston 2010). We found that the weight loss of 95% ethanol-preserved specimens was largely restricted to the first two months of preservation after which weight stabilized, and only minimal differences were recorded (Suppl. material 1: Appendix 2). The high ethanol concentration (i.e., 95%) used here to also protect DNA could explain these results, as it would speed the leaching of water from tissues. Studies of aquatic insects show similar responses, with weight loss mostly limited to the first four weeks after preservation (e.g., Stanford 1973, Leuven et al. 1985, Cressa 1999, Wetzel et al. 2005). The degree of weight loss during preservation is a function of specimen size, which probably explains different responses to preservation of sexes. In absolute terms (g), larger specimens (females) lost more mass than smaller ones (males), yet the proportional difference (%) was negligible (Suppl.

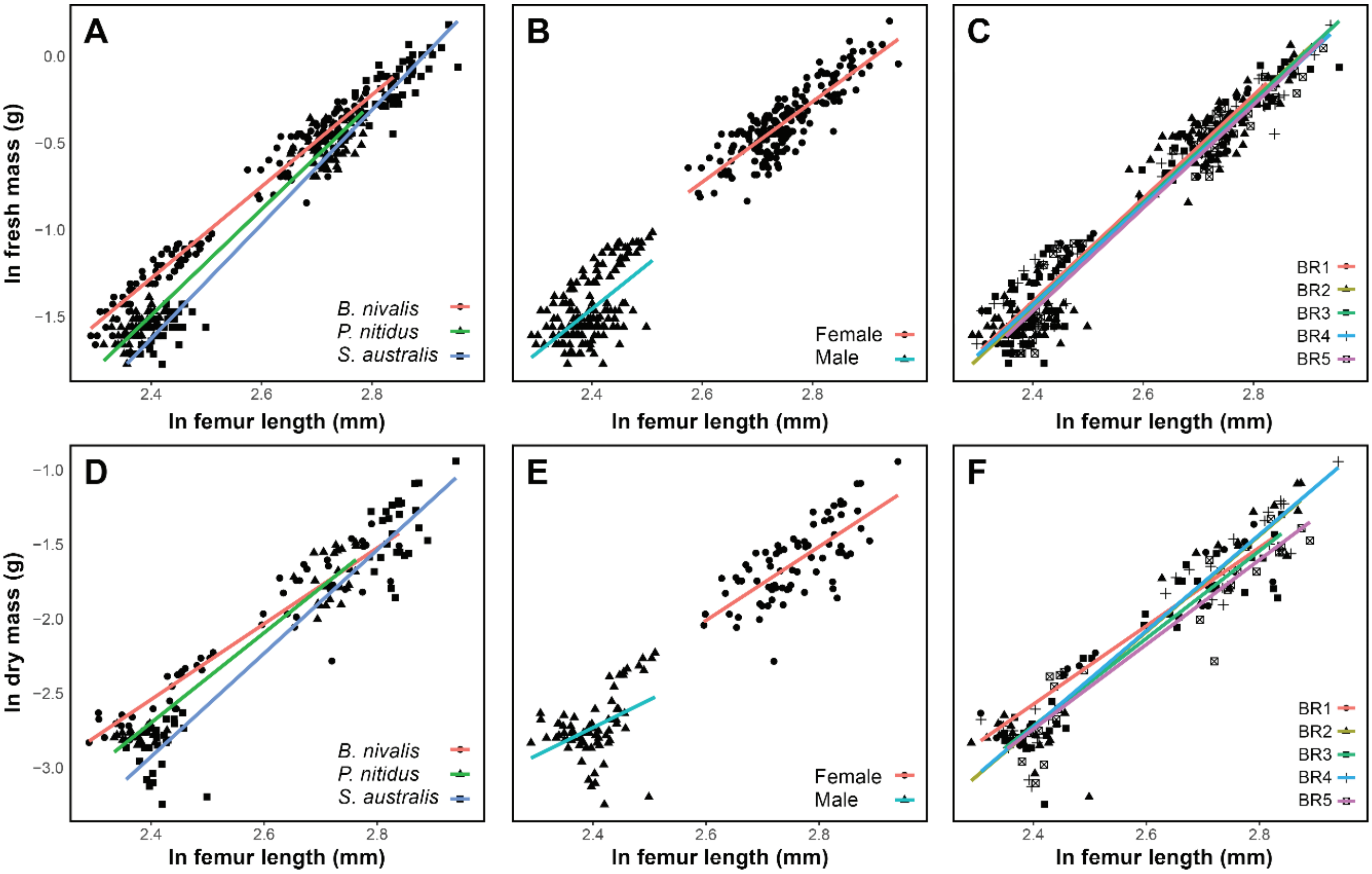

Fig. 4. Length-to-mass relationships in three flightless New Zealand grasshopper species showing the influence of elevation and sexual dimorphism. Fresh mass–femur length (**A–C**) and dry mass–femur length (**D–F**). Length–mass relationships are shown on natural logarithmic axes (ln). Sample sites (BR1 to BR5) indicating five sites in ~100-m elevation intervals from 1,383 to 1,817 m asl. Lines represent the best-fit from standardized major axis regressions. Credible intervals are omitted for clarity. Some regression lines overlie each other.

Table 4. Model selection showing the best-fitted models (AICc in bold) for predicting both fresh mass and dry mass from femur length in three flightless New Zealand grasshopper species. Abbreviations: K = number of parameters, AICc = Akaike's information criterion corrected for sample size, wi = Akaike weight, LL = Log-Likelihood, R^2 = marginal R^2. Model parameters of the best-fitting models (ΔAICc < 2) used for predictions are shown in Suppl. material 1: Appendix 4.

Species	Model formulae	K	AICc	ΔAICc	wi	LL	R^2
(a) fresh mass (FM) as a function of femur length (FL)							
Brachaspis nivalis	ln(**FM**)~ln(**FL**)*Sex+(1|Site)	6	**-284.34**	0.00	0.44	148.51	0.968
	ln(**FM**)~ln(**FL**)+Sex+(ln(**FL**)|Site)	7	**-283.44**	0.90	0.28	149.18	0.969
	ln(**FM**)~ln(**FL**)+Sex+(1|Site)	5	**-283.22**	1.12	0.25	146.85	0.967
	ln(**FM**)~ln(**FL**)+(1|Site)	4	-278.56	5.78	0.02	143.44	0.965
	ln(**FM**)~1+(1|Site)	3	149.94	434.28	0.00	-71.88	0.111
Paprides nitidus	ln(**FM**)~ln(**FL**)+(1|Site)	4	**-328.73**	0.00	0.64	169.58	0.976
	ln(**FM**)~ln(**FL**)+Sex+(1|Site)	5	**-327.15**	1.58	0.29	169.88	0.981
	ln(**FM**)~ln(**FL**)*Sex+(1|Site)	6	-324.43	4.30	0.07	169.62	0.981
	ln(**FM**)~ln(**FL**)+Sex+(ln(**FL**)|Site)	7	-296.49	32.24	0.00	152.38	0.981
	ln(**FM**)~1+(1|Site)	3	247.53	576.26	0.00	-120.68	0.000
Sigaus australis	ln(**FM**)~ln(**FL**)+Sex+(1|Site)	5	**-180.21**	0.00	0.65	95.46	0.987
	ln(**FM**)~ln(**FL**)+(1|Site)	4	**-178.53**	1.68	0.28	95.77	0.982
	ln(**FM**)~ln(**FL**)*Sex+(1|Site)	6	-175.85	4.36	0.07	95.61	0.987
	ln(**FM**)~ln(**FL**)+Sex+(ln(**FL**)|Site)	7	-156.20	24.01	0.00	82.34	0.987
	ln(**FM**)~1+(1|Site)	3	204.43	384.63	0.00	-99.07	0.000
(b) dry mass (DM) as a function of femur length (FL)							
Brachaspis nivalis	ln(**DM**)~ln(**FL**)+(1|Site)	4	**-45.22**	0.00	0.48	27.05	0.904
	ln(**DM**)~ln(**FL**)+Sex+(1|Site)	5	**-44.42**	0.80	0.32	27.89	0.902
	ln(**DM**)~ln(**FL**)*Sex+(1|Site)	6	-43.14	2.08	0.17	28.55	0.904
	ln(**DM**)~ln(**FL**)+Sex+(**FL**|Site)	7	-39.14	6.08	0.02	27.90	0.903
	ln(**DM**)~1+(1|Site)	3	66.45	111.67	0.00	-29.96	0.000
Paprides nitidus	ln(**DM**)~ln(**FL**)+Sex+(1|Site)	5	**-69.02**	0.00	0.53	40.21	0.962
	ln(**DM**)~ln(**FL**)*Sex+(1|Site)	6	**-68.45**	0.57	0.40	41.23	0.964
	ln(**DM**)~ln(**FL**)+(1|Site)	4	**-67.97**	1.05	0.03	35.94	0.955
	ln(**DM**)~ln(**FL**)+Sex+(ln(**FL**)|Site)	7	-63.98	5.04	0.04	40.13	0.963
	ln(**DM**)~1+(1|Site)	3	85.46	154.48	0.00	-39.46	0.000
Sigaus australis	ln(**DM**)~ln(**FL**)+(1|Site)	4	**-28.96**	0.00	0.65	18.93	0.955
	ln(**DM**)~ln(**FL**)+Sex+(1|Site)	5	-26.75	2.21	0.21	19.06	0.955
	ln(**DM**)~ln(**FL**)+Sex+(ln(**FL**)|Site)	7	-24.78	4.19	0.08	20.72	0.960
	ln(**DM**)~ln(**FL**)*Sex+(1|Site)	6	-24.27	4.70	0.06	19.11	0.956
	ln(**DM**)~1+(1|Site)	3	120.31	149.28	0.00	-56.90	0.000

material 1: Appendix 2). These results agree with previous studies (e.g., Wetzel et al. 2005, Paxton 2013); however, additional factors, such as surface area–volume ratio, environmental conditions, and concentration and volume of preservative, may also influence the leaching process (Leuven et al. 1985, Paxton 2013).

Studies of the mass-to-mass relationships of terrestrial insects are scarce (e.g., Edwards 1996, Penell et al. 2018). Here, we found that preserved mass was a prime predictor of body mass across all three grasshopper species, especially when predicting fresh mass (Tables 1, 2). Inter-individual differences during the drying process seemed to challenge model accuracy and fit when predicting dry mass. Visual inspection of dry mass–preserved mass regressions indicates unexplained size-related variance, meaning higher residual error in large individuals across all species. This suggests that inter-individual differences in body composition (e.g., water, carbohydrates, protein, and fat content) and condition (nutritional and reproductive status) may be important factors explaining such variance.

The choice of a robust linear size trait is an important consideration for accurate mass estimates when applying allometric scaling regressions (Gaston and Blackburn 2000, Moretti et al. 2017). Here, we showed that femur length strongly correlates with other body dimensions and body mass measures in all three grasshopper species, having by itself a high predictive power when estimating body mass at the species level, especially when predicting fresh mass (Tables 3, 4). Femur length has previously been shown to have a linear relationship to body length in one of these species, which is in turn linearly related to body mass (Batcheler 1967). However, in all cases, body mass predictions based on preserved mass were substantially more accurate (Table 5), with prediction errors < 0.018 g (against < 0.050 g for predictions based on femur length). Thus, it seems sensible to use preserved mass as a predictor when basic knowledge of the effects of preservation method on body mass is available. Otherwise, femur length is the metric to be used, as more than 90% of the variance in body mass was described by this trait in all cases (Tables 3, 4). The addition of alternative body dimensions during the modeling process would result in marginal improvement of prediction accuracy but would substantially increase the time needed for processing samples (e.g., Sohlström et al. 2018).

As expected, sex was sometimes retained as an informative predictor of body mass when used in addition to or as an interaction with femur length. This is not surprising given that adult females of these grasshopper species are approximately three times as heavy as adult males. Including sex generally increased model fit (Tables 2, 4); however, its inclusion did not produce better estimates than traditional mass-to-mass and allometric scaling regressions (Table 5; Fig. 5). Similar allometric relationships have been found in bees and hoverflies (Kendall et al. 2019) where sex was influential in the fit of the models but not in their predictive power. Likewise, the use of sex-specific regressions did not produce better mass estimates than simple regressions for

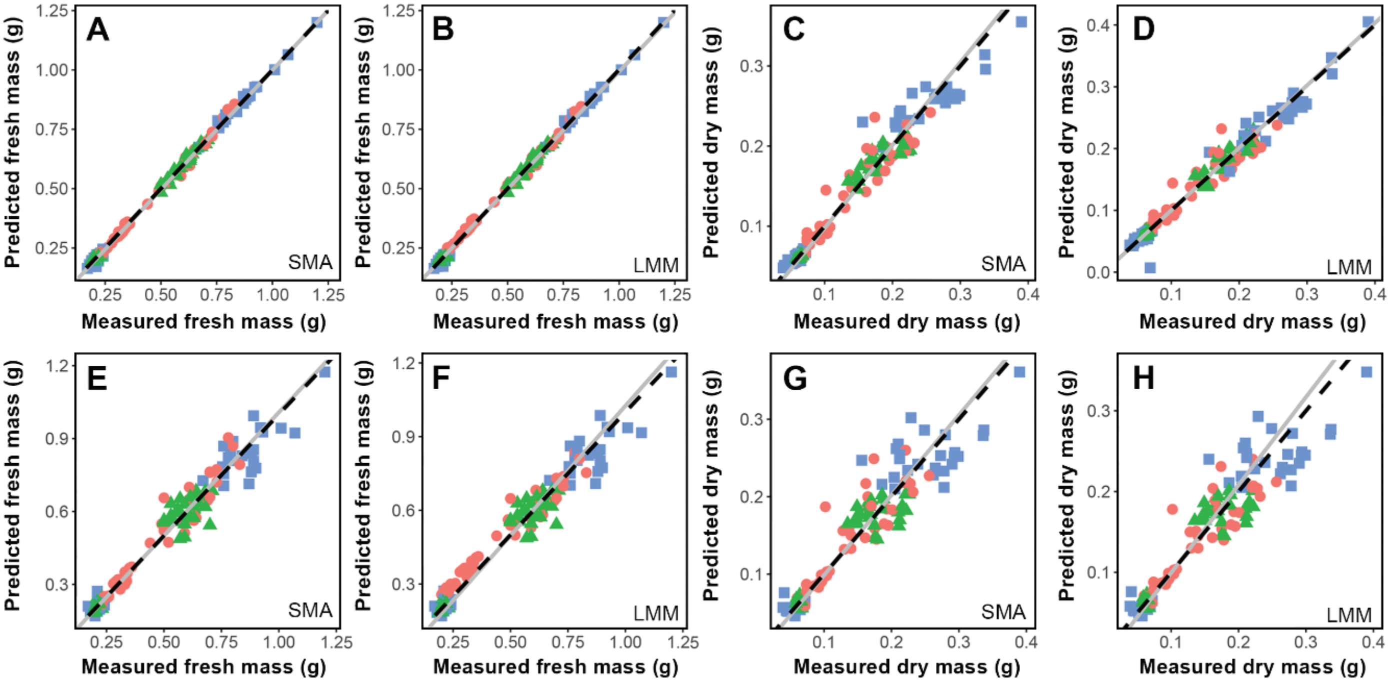

Fig. 5. High predictability observed when comparing measured and predicted body mass using type-II linear regression with a major axis approach. Predictions based on preserved mass (**A–D**) and femur length (**E–H**) pooling data from three flightless New Zealand grasshopper species: *Brachaspis nivalis* (pink circles), *Paprides nitidus* (green triangles), and *Sigaus australis* (blue squares). The expected $x = y$ relationship is shown in dashed black line, and the observed is shown in solid grey line. Predictions from standardized major axis regressions (SMA) and linear mixed-effects models (LMM) are shown. Note that in most cases fitting lines overlap.

European spiders (Penell et al. 2018). Although the use of models accounting for sexual size dimorphisms is desirable, it seems that, at least for our dataset, general regressions led to better estimates than more complex models. While femur length was an accurate predictor of body mass across species, it became less reliable when comparing sexes within a given species, which can be related to the fact that, contrary to body mass, femur length remains fixed throughout adult life. Adult body size variation in structural linear traits is affected by environmental factors during development (Davidowitz et al. 2004). Therefore, intraspecific changes in the average value of adult structural size traits will require changes in size and structure at the population level (Bailey et al. 2020).

The difficulty of accurately predicting intraspecific body size variation based on co-varying linear traits is not new. The lack of predictive power has previously been explained in terms of traits varying in response to environmental conditions during development (Hagen and Dupont 2013, Kendall et al. 2019). Thus, decomposing a multidimensional trait, such as body size, into linear measures seems insufficient to capture intraspecific body size variation. Indeed, body size in the broadest sense is closely linked to the volume of an organism, which in linear terms is described by length, width, and height (Moretti et al. 2017, Sohlström et al. 2018). With this in mind, predictions based on models incorporating complementary morphological traits directly related to width and/or height (e.g., femur length in addition to pronotum width) would improve intraspecific body mass prediction accuracy, and thus the applicability of allometric scaling for exploring the ecological implications of widespread phenomena, such as sexual size dimorphism. Given that the sexes commonly respond differently to environmental shifts, a considerable amount of the unexplained intraspecific variation observed here may be related to sexual differences in body size plasticity (e.g., Stillwell et al. 2010).

Table 5. Details of statistical models (type II linear regression with a major axis) testing the relationships between predicted and measured body mass in three flightless New Zealand grasshopper species. Predictions are based on mass-to-mass ratios and scaling parameters from standardized major axis regressions (SMA) and linear mixed-effects models (LMM). The R^2 values, estimated intercept, and slope (95% confidence intervals) are given.

Model	Sample size	R^2	Intercept$_{(CI)}$	Slope$_{(CI)}$	p-value
(a) Preserved mass to fresh mass					
PM:FM ratio	368	0.998	0.004$_{(0.002–0.006)}$	0.993 $_{(0.989–0.998)}$	< 0.001
LMM	368	0.998	-0.004$_{(-0.006--0.002)}$	1.005 $_{(1.004–1.010)}$	< 0.001
(b) Preserved mass to dry mass					
PM:DM ratio	150	0.957	-0.006$_{(-0.011–0.001)}$	1.035 $_{(1.000–1.071)}$	< 0.001
LMM	150	0.958	-0.004$_{(-0.009–0.001)}$	1.032 $_{(0.997–1.068)}$	< 0.001
(c) femur length to fresh mass					
SMA	368	0.965	-0.006 $_{(-0.021–0.009)}$	1.013 $_{(0.982–1.045)}$	< 0.001
LMM	368	0.963	-0.031 $_{(-0.048--0.016)}$	1.056 $_{(1.023–1.091)}$	< 0.001
(d) femur length to dry mass					
SMA	150	0.898	-0.004$_{(-0.013–0.002)}$	1.034 $_{(0.979–1.092)}$	< 0.001
LMM	150	0.901	-0.009$_{(-0.018–0.002)}$	1.088 $_{(1.031–1.148)}$	< 0.001

The slope parameter β (power coefficient) of our femur length regressions ranged between 2.152 and 3.293 for fresh mass and between 2.544 and 3.425 for dry mass, thus being close to 3 as expected for animals with isometric growth (Suter and Stratton 2011). These values are higher than those from pre-existing allometric models (Schoener 1980) for tropical orthopterans (β = 1.65–1.96 for dry mass estimates), further supporting differences in slopes between insects from different climatic zones: tropical insects usually have smaller gradients than temperate ones (Schoener 1980). Interestingly, the slopes of temperate grasshoppers from North America

(Sabo et al. 2002) are around the lower limit of those reported here for New Zealand grasshoppers (β = 2.274 for dry mass estimates). However, regression parameters for North American grasshoppers were obtained using body length as a co-variable, thus preventing reliable comparison, as allometric relationships often differ between traits. As noted above, the use of body length in allometric studies on grasshoppers is not recommended, as this trait is difficult to measure accurately, thus jeopardizing model predictive power. Therefore, we expect our regressions to be highly applicable to ecological studies on New Zealand grasshoppers.

One source of potential error in our models is intraspecific regional variation in body size. This limitation can be problematic because scaling relationships in terrestrial insects, and thus, their regression parameters, are likely to vary geographically if populations' body size evolve independently of one another depending on local conditions (e.g., Johnston and Cunjak 1999, Sohlström et al. 2018, Kendall et al. 2019). New Zealand grasshoppers exhibit variations in body size among populations inhabiting elevational and latitudinal gradients (Bigelow 1967, Staples 1967, Mason 1970). By including size data from specimens collected on an elevational gradient in our models, we expect to have improved model robustness and reduced, at least in part, the effects of geographic size variation on their predictive power (Figs 3, 4). Variation in response to sampling season is expected to represent an additional source of error in our models, as average body size can change from year to year at the same site due to differences in environmental conditions (Bigelow 1967). Therefore, the performance of our models could be affected when predicting mass estimates from individuals with size measures far outside the trait ranges reported here.

Ecological applications.—Here we show that, for New Zealand grasshoppers, two easy-to-measure, non-destructive, and highly repeatable size estimates (i.e., preserved mass and femur length) are good predictors of other difficult-to-measure but ecologically meaningful size traits, such as fresh and dry mass. Many ecological disciplines typically require body mass data to relate body size to a range of ecological attributes. For example, body mass has been proposed as a suitable metric for testing ecogeographic patterns, such as Bergmann's rule (Blackburn et al. 1999). Since body mass is universally comparable, it is the metric of choice in macroecological studies interested in body size variation or size-dependent ecological processes (Gaston and Blackburn 2000). Body size estimates for New Zealand grasshoppers are more frequently available as body size dimensions (but see Batcheler 1967), making mass-to-mass and length–mass regression models useful for increasing our ability to further explore the ecological implications of body size.

Body mass estimates from scaling regressions have proven useful for studying aspects shaping arthropod communities including biomass production (e.g., Eklöf et al. 2017, Penell et al. 2018, Kinsella et al. 2020) and abundance (White et al. 2007). Traditionally, size–abundance relationships rely on fresh body mass of organisms (White et al. 2007, Sohlström et al. 2018), which is not available for most species. Thus, mass estimates from scaling regressions will alleviate this limitation. Given the apparent linear relationship between body size and consumption rate in the grasshopper species we examined (White 1975), indirect body mass estimates from length–mass regressions could also be used to predict herbivore impact on plant communities. For example, grasshopper dry mass correlates negatively with plant biomass in the field (Moretti et al. 2013), providing a potential trait for predicting plant consumption (Deraison et al. 2014).

Recently, declines in body size have been proposed as a general response to anthropogenic climate change in both endothermic and ectothermic animals (Gardner et al. 2011). Examining trends in body size requires the use of consistent size measures, and unfortunately, data often come as different size proxies, thereby hindering comparisons (Bailey et al. 2020). Body mass estimates from scaling regressions have helped to overcome this limitation by providing a tool for making size metrics from different sources (e.g., museum specimens, published datasets, and fresh sampling) comparable, so that tests of body size responses to climate change and warming temperatures can be performed (e.g., Tseng et al. 2018). This approach has proven useful for studying the trends and drivers of the change in the biomass of flying insects over time and space (e.g., Macgregor et al. 2019, Kinsella et al. 2020) and can now be used to estimate the body mass of New Zealand grasshoppers from historical abundance datasets (e.g., White 1975, White and Sedcole 1991).

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Supplementary material 1

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Data type: docx file

Explanation note: **Appendix 1.** Measurement repeatability based on repeated measures of body size traits from the same specimens in three New Zealand grasshopper species. **Appendix 2.** Effect of the preservation method (i.e., 95% ethanol) on body mass by comparing mass estimates between live (fresh mass) and preserved states (preserved mass after two and four months of preservation) in three New Zealand grasshopper species. **Appendix 3.** Intraspecific relationships between preserved mass and both fresh and dry mass in three New Zealand grasshopper species. **Appendix 4.** Regression parameters for the best-fitted linear mixed-effect models for body mass prediction based on preserved mass (Table 2) and femur length (Table 4) in three New Zealand grasshopper species. **Appendix 5.** Relationships between mass estimates (g) and body dimensions (mm) in three New Zealand grasshopper species. **Appendix 6.** Non-linear models fitted to describe intraspecific allometric relationships between mass estimates (FM and DM) and femur length (FL) in three New Zealand grasshopper species.

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