

# First natural history observations of the canyon pygmy mole cricket, *Ellipes monticolus* (Orthoptera: Tridactylidae)

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Academic editor: *Maria-Marta Cigliano* | Received 28 January 2019 | Accepted 26 June 2019 | Published 10 January 2020

<http://zoobank.org/F83876E3-4588-4353-9769-BF72BB5229E6>

Citation: Woo B (2020) First natural history observations of the canyon pygmy mole cricket, *Ellipes monticolus* (Orthoptera: Tridactylidae). *Journal of Orthoptera Research* 29(1): 1–7. <https://doi.org/10.3897/jor.29.33413>

## Abstract

The first live photos of the canyon pygmy mole cricket, *Ellipes monticolus* Günther, are presented, with preliminary observations on the habitat and behavior of populations in the Chiricahua Mountains of southeastern Arizona. The species was previously known solely from the original description in 1977, which included only drawings of the structure of the genitalia and almost no natural history information. This paper provides the first look at this species' biology and provides a framework for future studies on Tridactylidae of the southwestern United States.

## Keywords

Arizona, Caelifera, Chiricahua Mountains, photographs, Sky Islands, Tridactylinae

## Introduction

The Chiricahua Mountains of southeastern Arizona, USA, are well known as part of the Madrean Pine-Oak Woodlands biodiversity hotspot (Mittermeier et al. 2004). Among the vertebrates, about 80 species of mammals and 400 birds (Brown and Peters 2014) are known from the area. Add to this the 619 species of native plants that occur in Chiricahua National Monument (McLaughlin 1994), and you start to get an idea of the incredible biological diversity of the region. The diversity of insect species is even higher. This biodiversity is due to the confluence of several factors: the varied elevations from 1097 m to 2975 m and resulting weather and habitat conditions at those elevations, the Chiricahuas' position at the edges of both the Sonoran and Chihuahuan deserts, and the intrusion of both Nearctic species from the USA and Neotropical species from Mexico (Brown and Peters 2014). The Orthoptera (grasshoppers, crickets, and katydids) are well represented in the Chiricahuas, with over 100 species in 10 families based on specimen records in the collection of the Southwestern Research Station (SWRS). The grasshopper *Melanoplus chiricahuae* Hebard, 1922 and the camel cricket *Ceuthophilus chiricahuae* Hubbell, 1936 are endemic to the Chiricahuas (Hebard 1922, Hubbell 1936).

The Tridactylidae (Orthoptera: Caelifera: Tridactyloidea), commonly known as pygmy mole crickets, is a family of small, burrowing orthopterans distributed worldwide (Deyrup and Eisner 1996). They are well adapted to living in wet, sandy areas and can burrow, swim, and fly (with the exception of a few flightless species) with ease. Algae growing in moist habitats is their preferred food (Deyrup and Eisner 1996). There are about seven species in the USA with four recorded in Arizona (Günther 1975, 1977). Two of these, *Neotridactylus apicalis* (Say, 1825) and *Ellipes minuta* (Scudder, 1862), are widespread across the continent. A third species, *Ellipes gurneyi* Günther, 1977, is found in northern Mexico and in the western and southern United States.

The fourth species from Arizona, *Ellipes monticolus* Günther, 1977, is apparently endemic to the southwestern United States; it is also recorded from Utah, New Mexico, and western Texas. In Arizona it is known from Patagonia in Santa Cruz County, Wickensburg in Yavapai County, and from the SWRS in Cochise County (Günther 1977). The SWRS is owned by the American Museum of Natural History and is located in Cave Creek Canyon in the Chiricahua Mountains. In Günther (1977)'s original description of *E. monticolus*, which appears in his revision of the genus, the only natural history information given is that the species "...seems to populate the mountainous southwestern states of the USA". Since Günther's revision, *E. monticolus* has been mentioned only once, in a catalog of Tridactyloidea that simply refers the reader back to the 1977 revision (Günther 1980). No other pertinent natural history or biological work has been done with the species, nor have any images (drawings or photos) appeared in print or online, except for Günther (1977)'s figures depicting the terminalia and internal genitalia of the species. The North American Orthoptera fauna has been comparatively well-studied, so for such an animal to have so little known about it is unique. This is likely due to the fact that the Tridactylidae are tiny and have no economic importance and thus do not draw much attention. The goal of this work is to provide preliminary natural history observations and images of *E. monticolus* and to suggest avenues for future, more in-depth studies of southwestern Tridactylidae.

## Methods

*Field searching and observations.*—In March and April 2018, I stayed at the SWRS and searched likely habitats for tridactylids. On March 17, 2018, a tridactylid population was discovered on a sandy bank of Cave Creek (Fig. 1A). The site (31.906528, -109.152389) is on private property and was accessed with the owner's permission; it is also accessible by walking upstream from downtown Portal. Three nymphs were photographed in situ and one adult was collected, but several other nymphs and adults were seen. I returned to the site on March 23, 2018 and collected four adults. Three nymphs and three additional adults were also photographed in situ on this date, and two other populations were located a few yards upstream in similar habitat. On April 11, I walked upstream checking for tridactylids starting at the Portal Library and discovered no populations until reaching the original site. One adult was collected on this date.

On April 24, 2018, a second tridactylid population was discovered along the north fork of Cave Creek, along 42 Forest Road about 1.1 mi north of the SWRS (31.892667, -109.212111). This site is located within the Coronado National Forest and consists of a sandy bend of the creek with a much larger open shoreline than the first site (Fig. 1B). Numerous adult tridactylids (but no nymphs) were seen; two were photographed in situ, and two others were collected. All collected specimens were first flushed from their burrows by splashing the bank with creek water and then captured in vials.

During each of the four dates mentioned above, approximately two hours were spent collecting and observing the tridactylids, as well as photographing and collecting any insects and spiders that occurred in the same habitat.

*Determination.*—Adult specimens were identified using the keys and figures of Günther (1975, 1977). Species of the genus *Ellipes*,

including *E. monticolus*, are distinct from the two other North American tridactylid genera by the near absence of the hind tarsi (Fig. 2A), which have been reduced to a tiny flap concealed between the hind tibial spurs. The collecting locations, near one of the original paratype localities, as well as the pronotal and hind femur pattern (Fig. 2B, C) all pointed to *E. monticolus*. The terminalia of both males and females matched up to Günther (1977)'s description and figures (Figs 3, 4). Nymphs were identified based on their association with adults and the absence of any other tridactylid species among the adults seen. Specimens are deposited in the Cornell University Insect Collection (Ithaca, NY), and the author's personal collection (Rochester, NH). Determinations of associated grasshoppers (gomphocerines and oedipodines) were made using Otte (1981) and Otte (1984). Other associated arthropods were identified via images posted to BugGuide.net (see Table 1), by the BugGuide editors noted in acknowledgements.

*Photographs.*—Nymphs and adults were photographed in situ using a Canon EOS Rebel T3 with an 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). Collected adults were photographed in a whitebox studio setup using the same equipment, with the addition of Canon extension tubes (EF25 and EF12 II) to the camera. Associated arthropods were photographed using the same setup. Images of the habitat and burrows were taken with an iPhone.

Images of the terminalia and stridulatory apparatus were made using a Canon EOS 6D with an attached 10X zoom lens and Macro Twin Lite MT-24EX flash on a Cognisys Stackshot 3X system. Images were stacked using Zerene Stacker v.1.04 (Zerene Systems LLC, Richland, WA). All images were processed using Adobe Lightroom CC to crop and adjust the white balance.

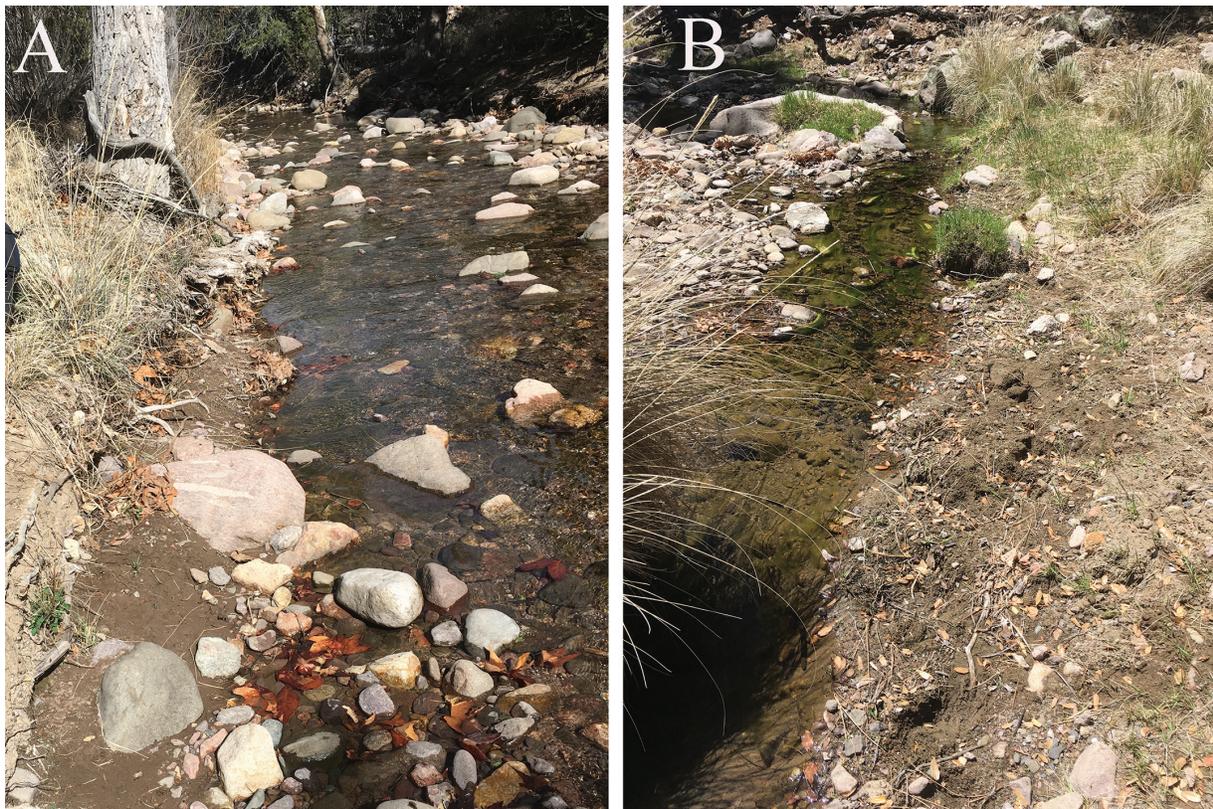


Fig. 1. A. Habitat at the Portal site. B. Habitat at the North Fork Cave Creek site.

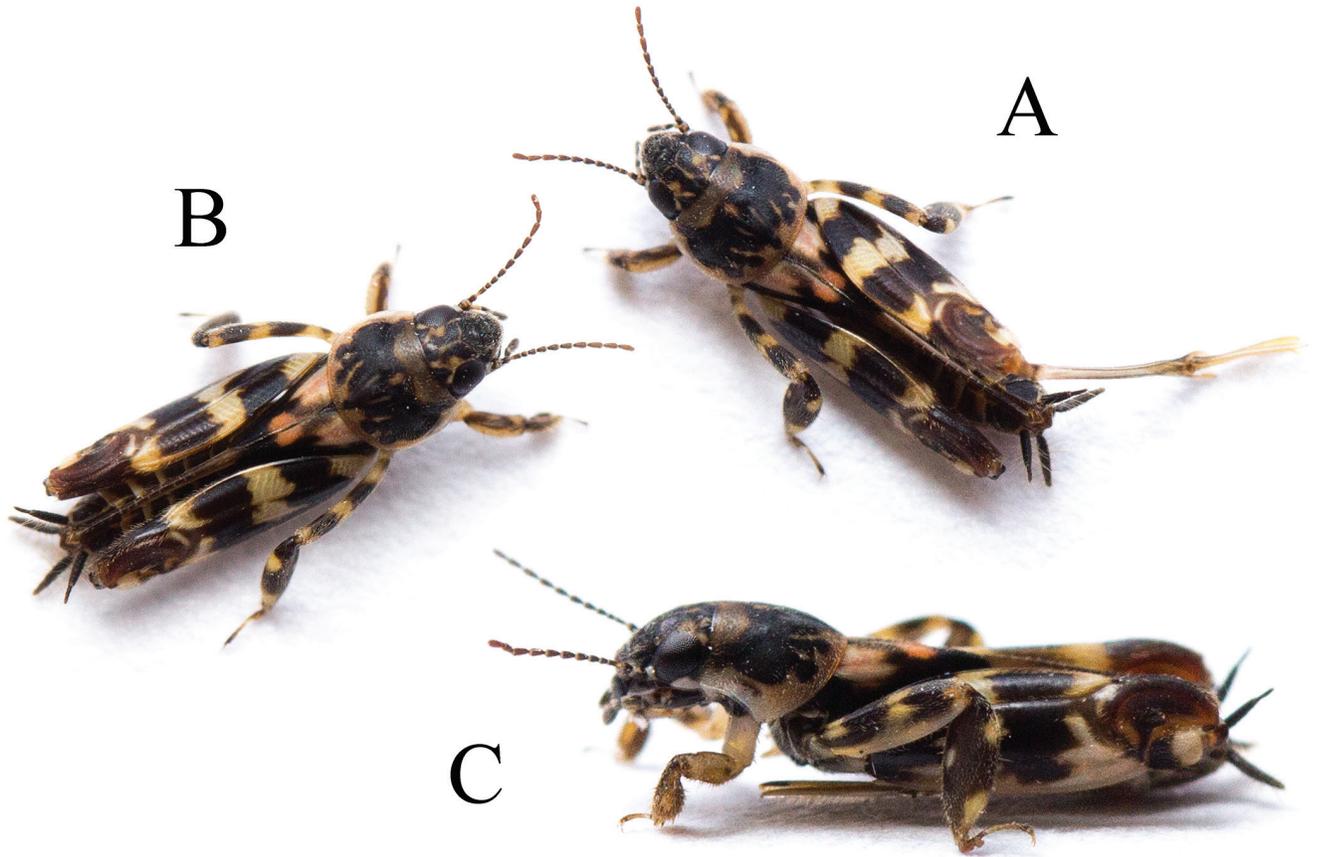


Fig. 2. A. Adult female *Ellipes monticolus* from the Portal site with right hind leg outstretched, showing lack of a tarsus. B. Dorsal view of same. C. Lateral view of same.

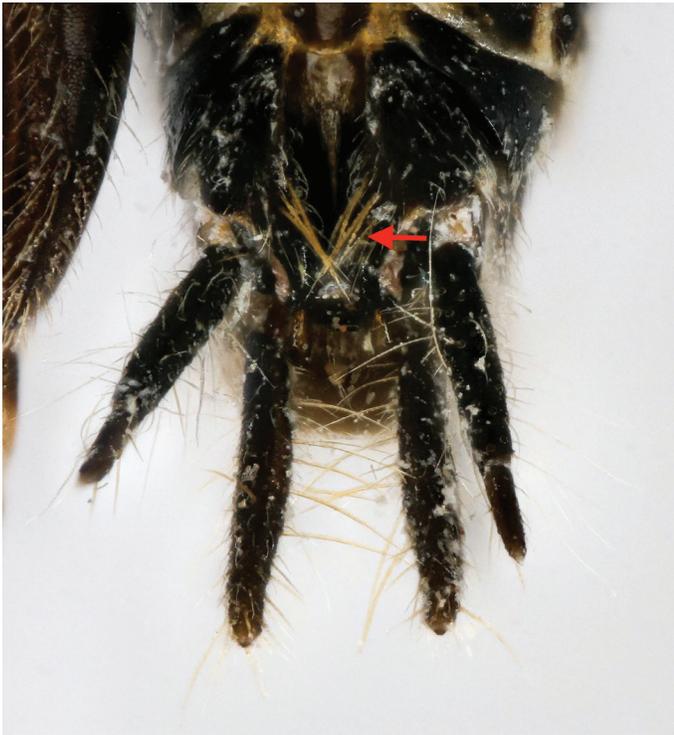


Fig. 3. Terminalia (dorsal view) of male *Ellipes monticolus*. Arrow denotes the elongate golden setae tufts above the epiproct, which no other local tridactylid species possesses.



Fig. 4. Subgenital plate (ventral view) of female *Ellipes monticolus*. Arrow denotes the diagnostic short, broad protrusion at the median of the caudal margin.

Table 1. Associated arthropod fauna.

Species	Order: Family	Site	Status	BugGuide image link
<i>Allocosa</i> sp.	Araneae: Lycosidae	North Fork Cave Creek site	~5 individuals on shoreline	<a href="https://bugguide.net/node/view/1513577">https://bugguide.net/node/view/1513577</a>
<i>Pardosa</i> sp.	Araneae: Lycosidae	both sites	over 20 individuals at both sites, on shoreline	<a href="https://bugguide.net/node/view/1517656">https://bugguide.net/node/view/1517656</a>
<i>Salina mulcahyae</i> Christiansen & Bellinger, 1980	Entomobryomorpha: Paronellidae	North Fork Cave Creek site	~10 individuals on shoreline	<a href="https://bugguide.net/node/view/1513579">https://bugguide.net/node/view/1513579</a>
<i>Paratettix aztecus</i> (Saussure, 1861)	Orthoptera: Tetrigidae	Portal site	over 20 individuals on shoreline; 2 collected	<a href="https://bugguide.net/node/view/1501617">https://bugguide.net/node/view/1501617</a>
<i>Paratettix mexicanus</i> (Saussure, 1861)	Orthoptera: Tetrigidae	both sites	over 20 individuals at both sites on shoreline; 1 collected	<a href="https://bugguide.net/node/view/1513582">https://bugguide.net/node/view/1513582</a>
<i>Achurum sumichrasti</i> (Saussure, 1861)	Orthoptera: Acrididae	Portal site	~5 individuals in dry grass adjacent to creek; 2 collected	<a href="https://bugguide.net/node/view/1503655">https://bugguide.net/node/view/1503655</a>
<i>Aidemona azteca</i> (Saussure, 1861)	Orthoptera: Acrididae	Portal site	1 individual in oak leaf litter adjacent to creek	<a href="https://bugguide.net/node/view/1517670">https://bugguide.net/node/view/1517670</a>
<i>Amblytropidia mysteca</i> (Saussure, 1861)	Orthoptera: Acrididae	Portal site	~10 individuals in dry grass adjacent to creek	<a href="https://bugguide.net/node/view/1517666">https://bugguide.net/node/view/1517666</a>
<i>Tomonotus ferruginosus</i> Caudell, 1905	Orthoptera: Acrididae	Portal site	~5 individuals in oak leaf litter adjacent to creek; 1 collected	<a href="https://bugguide.net/node/view/1509152">https://bugguide.net/node/view/1509152</a>
<i>Gelastocoris rotundatus</i> Champion, 1901	Hemiptera: Gelastocoridae	Portal site	~10 individuals on sandy shoreline; 1 collected	<a href="https://bugguide.net/node/view/1501615">https://bugguide.net/node/view/1501615</a>
<i>Saldula</i> sp.	Hemiptera: Saldidae	Portal site	1 individual on sandy shoreline, collected	<a href="https://bugguide.net/node/view/1517684">https://bugguide.net/node/view/1517684</a>
<i>Chlaenius leucoscelis</i> Chevrolat, 1834	Coleoptera: Carabidae	Portal site	~10 individuals under rocks on shoreline; 1 collected	<a href="https://bugguide.net/node/view/1501616">https://bugguide.net/node/view/1501616</a>
<i>Elaphropus</i> sp.	Coleoptera: Carabidae	Portal site	1 individual on sandy shoreline, collected	<a href="https://bugguide.net/node/view/1517685">https://bugguide.net/node/view/1517685</a>
<i>Anthicus bellulus</i> LeConte, 1851	Coleoptera: Anthicidae	Portal site	1 individual on sandy shoreline, collected	<a href="https://bugguide.net/node/view/1517683">https://bugguide.net/node/view/1517683</a>
<i>Limnichites</i> sp.	Coleoptera: Limnichidae	Portal site	1 individual on sandy shoreline, collected	<a href="https://bugguide.net/node/view/1501613">https://bugguide.net/node/view/1501613</a>
<i>Erynnis</i> sp.	Lepidoptera: Hesperidae	Portal site	~3 individuals puddling on sandy shoreline	N/A
Calliphoridae undet. spp.	Diptera: Calliphoridae	both sites	over 20 individuals puddling on sandy shoreline at both sites	N/A
<i>Apis mellifera</i> Linnaeus, 1758	Hymenoptera: Apidae	Portal site	~5 individuals puddling on sandy shoreline	N/A
<i>Osmia</i> sp.	Hymenoptera: Megachilidae	Portal site	~3 individuals puddling on sandy shoreline	<a href="https://bugguide.net/node/view/1503634">https://bugguide.net/node/view/1503634</a>
<i>Formica gnava</i> Buckley, 1866	Hymenoptera: Formicidae	Portal site	~10 individuals present at any given time on shoreline, 1 collected	<a href="https://bugguide.net/node/view/1517691">https://bugguide.net/node/view/1517691</a>
<i>Dorymyrmex smithi</i> Cole, 1936	Hymenoptera: Formicidae	Portal site	1 on shoreline, collected	<a href="https://bugguide.net/node/view/1517688">https://bugguide.net/node/view/1517688</a>
<i>Nylanderia bruesii</i> (Wheeler, 1903)	Hymenoptera: Formicidae	Portal site	1 on shoreline, collected	<a href="https://bugguide.net/node/view/1517687">https://bugguide.net/node/view/1517687</a>
<i>Monomorium</i> sp.	Hymenoptera: Formicidae	Portal site	1 on shoreline, collected	<a href="https://bugguide.net/node/view/1517692">https://bugguide.net/node/view/1517692</a>

## Results

**Habitat.**—Both sites are riparian areas in oak–pine–juniper woodland in Cave Creek Canyon. The Portal site was at about 1463 m elevation and the North Fork Cave Creek site was at about 1706 m elevation. The creek at both sites has patches of sandy shoreline interspersed with rocks and gravelly mixes of rock and sand; tridactylid populations were observed only in the pure sandy shores. Populations were generally found on the sunny side of the creek, possibly as a result of their algal food source being located in places with optimal sunlight. Associated plants at the Portal site were: alligator juniper (*Juniperus deppeana* Steudel), Arizona cypress (*Cupressus arizonica* Greene),

Arizona sycamore (*Platanus wrightii* Watson), Fremont's cottonwood (*Populus fremontii* Watson), Arizona walnut (*Juglans major* (Torr.) A. Heller), oaks (*Quercus* spp.), mesquite (*Prosopis* sp.), Arizona grape (*Vitis arizonica* Engelm), clover (*Trifolium* sp.), bull grass (*Muhlenbergia emersleyi* Vasey), and unidentified sedges. Associated plants at the North Fork Cave Creek site were: alligator juniper (*Juniperus deppeana* Steudel), Arizona sycamore (*Platanus wrightii* Watson), oaks (*Quercus* spp.), yellow monkeyflower (*Erythranthe guttata* (Fisch. DC.) G.L.Nesom), and unidentified sedges.

**Associated arthropod fauna (Table 1).**—Other arthropods were found to share the habitat of *E. monticolus*. Alongside the tridactylids on the

sandy shorelines there were two species of wolf spiders (Lycosidae), two species of pygmy grasshoppers (Tetrigidae), toad bugs (Gelastocoridae), shore bugs (Saldidae), two species of ground beetles (Carabidae), ant-like flower beetles (Anthicidae), minute marsh-loving beetles (Limnichidae), and four species of ants (Formicidae). Puddling on these shorelines were skippers (Hesperiidae), blow flies (Calliphoridae), and bees (Apidae and Megachilidae). In the dry grass and oak leaf litter directly adjacent to the creek shorelines, four grasshopper (Acrididae) species were common (Table 1).

*Tridactylid behavior and burrows.*—Burrows appeared as small raised piles of sand, slightly drier (thus of a lighter color) than the surrounding sand (Fig. 5). When these burrows were splashed with water, anywhere from one to five individual tridactylids would appear. If more than one tridactylid inhabited a burrow, they would usually all spring away immediately, but single individuals would sometimes remain in place or jump a short distance. When tridactylids landed on the sand, they would often remain there for several minutes, allowing for close-up photos. Individuals that landed on leaves or rocks would stand on those surfaces for a moment before attempting to locate sand (Fig. 6A, B). After two or three minutes had passed, tridactylids on sand would usually burrow back into the substrate, using their mouthparts and forelegs to move sand particles and create their raised tunnels (Fig. 6C). Some nymphs, upon digging a short burrow, would remain with their terminalia poking out of the burrow for almost ten minutes.

One adult tridactylid was observed creating a new burrow after it had been splashed out of the old burrow and stood on the sand for a few minutes. It grasped sand grains in its mouthparts and placed them around itself, creating a sort of small archway that gradually became a raised tunnel as construction continued.



Fig. 5. *Ellipes monticolus* raised burrows at the North Fork Cave Creek site.



Fig. 6. Three individuals of *Ellipes monticolus* in situ at the Portal site. A. Adult on a rock next to the creek. B. Nymph on a rock next to the creek. C. Nymph burrowing in substrate.

Larger sand grains were grasped with the mouthparts and set in place with the forelegs. Within about 10 minutes, the whole insect fit inside the tunnel and was hidden from view.

No predation of tridactylids was observed. One ant (species unidentified) was seen to come into contact with a tridactylid nymph standing on the substrate, which immediately sprung away. However, once a tridactylid had successfully created a burrow and hidden inside, ants would run right over the burrows, apparently not noticing the potential food item underneath their feet.

At the Portal site, both nymphs of various instars and adults were present at each visit, with nymphs somewhat outnumbering the adults. At the second site, only adults were present. Photographs of nymphs and adults of *E. monticolus* from both localities are posted by the author to BugGuide.net for public viewing, at <https://bugguide.net/node/view/1501623/bgimage>.

## Discussion

The observations of *E. monticolus* presented here are generally in line with what is already known about tridactylid biology. The species occurs in moist sandy habitats along water, creates feeding burrows, and is a prodigious jumper, just like most known members of the family. However, there are a few factors that set it apart from related species. It appears to be restricted to waterways within canyons, and in southeastern Arizona is thus presumably restricted to the Madrean Sky Islands. Its habitats are ephemeral and prone to high levels of disturbance or destruction because of flooding during the monsoon season. As with most tridactylids, *E. monticolus* is fully winged and can presumably fly to new areas if its habitat is destroyed; however, the presence of suitable habitat is strongly correlated with the canyon structure. The stream edge habitats that it occupies are only found in canyon bottoms, and if individuals venture too far down the canyon, they could end up in the hot, dry desert scrub where they would certainly perish. It is unknown how high in elevation the species occurs. Food availability could also restrict the dispersal of *E. monticolus*. In central Florida, the tridactylid *Neotridactylus archboldi* Deyrup & Eisner, 1996 was shown to feed on blue-green algae (Deyrup and Eisner 1996). It would be interesting to see if *E. monticolus* shares this

food preference, and, if so, what species of algae are consumed and how the tridactylids locate algal populations along the creeks. Long-term study could shed light on these and other questions.

Other arthropods present in the tridactylid habitat were mostly typical of shore-inhabiting fauna. The pygmy grasshoppers *Paratettix mexicanus* (Saussure, 1861) and *P. aztecus* (Saussure, 1861) occurred in the sandy shoreline patches along with *E. monticolus* and also along other stream edges where there were only rocks. *P. mexicanus*, along with carabid beetles and ants, is known to feed on algae (Bastow et al. 2002). There are many places where tetrigrads and tridactylids co-occur (pers. obs.), but no work has been done to understand possible competitive effects between these orthopterans or between the orthopterans and the presumably more efficient, but also more generalist, feeding ants.

Several potential predators of *E. monticolus* were observed. Toad bugs are known predators of tridactylids (Blatchley 1920); the species *Gelastocoris rotundatus* Champion, 1901 was observed in the same habitat but was not seen to approach tridactylids. Two different wolf spider species were common in the same habitats as the tridactylids, but these did not approach tridactylids either. Several species of sphecid wasps are known to hunt tridactylids (Evans and Hook 1984), but these probably emerge later in the year. Sustained observation would probably reveal one or more of these potential predators feeding on *E. monticolus*.

Many tridactylids have a stridulatory apparatus in the male, comprised of a scraper on the underside of the tegmen and a file on the fourth abdominal tergite. *E. monticolus* possesses such a structure (Fig. 7), but almost nothing is known of the nature or function of the calls they may produce. Deyrup and Eisner (1996) speculated that song could be an important isolating mechanism in tridactylids, but no attempts have been made to record the calls of any species of pygmy mole cricket.

The canyon pygmy mole cricket is likely more widespread than currently known, given the widely spaced localities where it has been collected. More extensive sampling would probably extend the range of this species to other mountain ranges in Arizona and in other southwestern states, as well as in northern Mexico. As mentioned previously, the species seems to only occur in the pure sandy shores of canyon creeks, at least in the Chiricahua

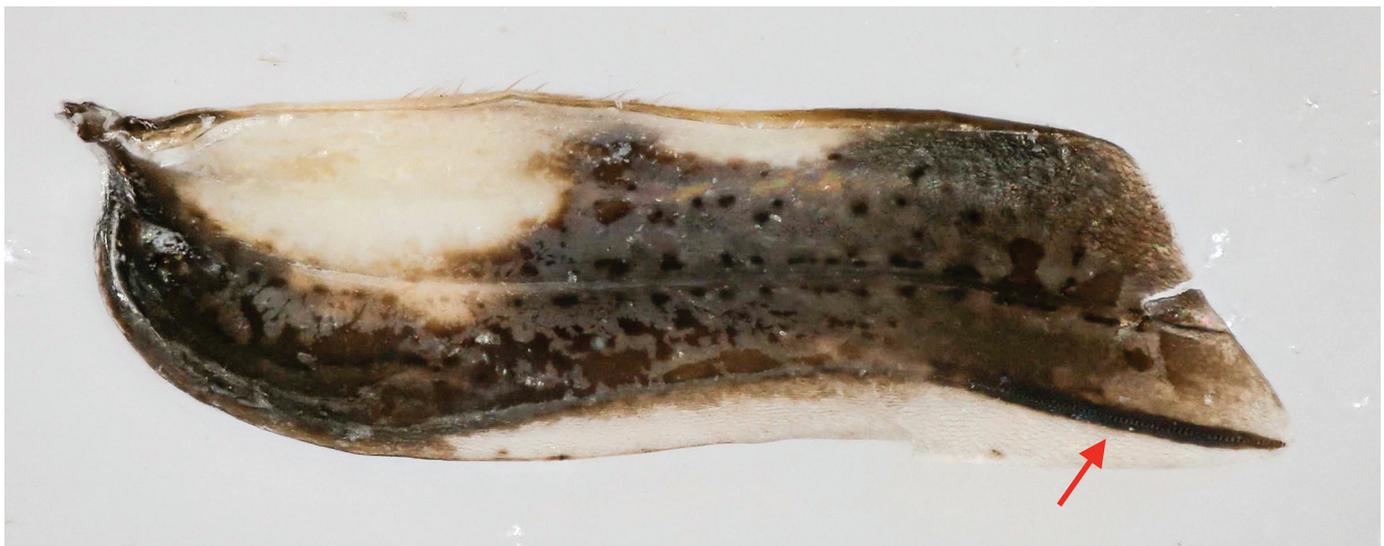


Fig. 7. Underside of right tegmen of male *Ellipes monticolus*, showing stridulatory apparatus (scraper).

Mountains. Burrows are easily detected if one is familiar with their appearance. Individuals are easily scared out from burrows but extreme speed must be exercised when collecting them as they spring away remarkably fast. This paper only scratches the surface of canyon tridactylid biology; there is much more to be learned.

### Acknowledgements

I thank the staff of the Southwestern Research Station for providing food and housing, as well as encouragement and potential tridactylid localities. Thanks are also due to the Downers who allowed me access to the Portal site through their property. I thank Stacey Weiss for alerting me to the presence of sandy banks of Cave Creek which turned out to be the second site. Thanks to Alina Downer for determining the plants. Several BugGuide editors helped with associated insect and spider determinations; thanks are due to Vassili Belov, Blaine Mathison, Curt Harden, and Donald Chandler (beetles and shore bug), James C. Trager, Seth Burgess, and Steven Wang (ants), Ken Wolgemuth (toad bug), John S. Ascher (bees), Laura P. (spiders), and Frans Janssens (springtail). Thanks to Silas Bossert for help with translating Günther's work, and to Kyhl Austin for assistance with the Cognisys focus-stacking system and zoom lens. Jason Dombroskie reviewed the original manuscript and encouraged my studies of these little-known insects. I also thank María Marta Cigliano, Pedro Souza Dias, and Tony Robillard for reviewing the manuscript.

### References

- Bastow JL, Sabo JL, Finlay JC, Power ME (2002) A basal aquatic-terrestrial trophic link in rivers: Algal subsidies via shore-dwelling grasshoppers. *Oecologia* 131: 261–268. <https://doi.org/10.1007/s00442-002-0879-7>
- Blatchley WS (1920) Orthoptera of Northeastern America, with Special Reference to the Faunas of Indiana and Florida. Nature Publ. Co., Indianapolis, 784 pp. <https://doi.org/10.5962/bhl.title.37901>
- Brown W, Peters R (2014) Cave Creek Canyon: Revealing the heart of Arizona's Chiricahua Mountains. ECO Wear & Publishing, Rodeo.
- Deyrup M, Eisner T (1996) Description and natural history of a new pygmy mole cricket from relict xeric uplands of Florida (Orthoptera: Tridactylidae). *Memoirs of the Entomological Society of Washington* 17: 59–67.
- Evans HE, Hook AW (1984) Nesting behavior of a *Lyroda* predator (Hymenoptera: Sphecidae) on *Tridactylus* (Orthoptera: Tridactylidae). *Australian Entomological Magazine* 11: 16–18.
- Günther KK (1975) Das Genus *Neotridactylus* Günther, 1972 (Tridactylidae, Saltatoria, Insecta). *Zoosystematics and Evolution* 51: 305–365. <https://doi.org/10.1002/mmz.4830510208>
- Günther KK (1977) Revision of the genus *Ellipes* Scudder, 1902 (Saltatoria, Tridactylidae). *German Entomological Journal* 24: 47–122. <https://doi.org/10.1002/mmnd.4800240104>
- Günther KK (1980) Katalog der Caelifera–Unterordnung Tridactyloidea [Catalogue of the Caelifera–Subordo Tridactyloidea] (Insecta), *Deutsche Entomologische Zeitschrift* 27: 149–178. <https://doi.org/10.1002/mmnd.4810270114>
- Hebard M (1922) New genera and species of Melanopli found within the United States and Canada (Orthoptera: Acrididae): Part IV. *Transactions of the American Entomological Society (1890-)* 48: 49–66.
- Hubbell TH (1936) A monographic revision of the genus *Ceuthophilus* (Orthoptera, Gryllacrididae, Rhaphidophorinae) (Vol. 2, No. 1). The University of Florida.
- McLaughlin SP (1994) An overview of the flora of the Sky Islands, southeastern Arizona: Diversity, affinities, and insularity. In: DeBano LH, Ffolliott PH, Ortega-Rubio A, Gottfried GJ, Hamre RH, Edminster CB (Eds) *Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico*, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, 60–70.
- Mittermeier RA, Robles-Gil P, Hoffmann M, Pilgrim JD, Brooks TB, Mittermeier CG, Lamoreux JL, Fonseca GAB (2004) Hotspots Revisited: Earth's Biologically Richest and Most Endangered Ecoregions. CEMEX, Mexico City, 390 pp.
- Otte D (1981) *The North American Grasshoppers*. Vol. 1, Acrididae: Gomphocerinae and Acridinae. Harvard University Press.
- Otte D (1984) *The North American Grasshoppers*. Vol. 2, Acrididae: Oedipodinae. Harvard University Press.



# Acridid ecology in the sugarcane agro-ecosystem in the Zululand region of KwaZulu-Natal, South Africa

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Academic editor: Michel Lecoq | Received 8 April 2019 | Accepted 17 June 2019 | Published 10 January 2020

<http://zoobank.org/77D0467F-09AA-40E1-A354-46E48924B24D>

Citation: Bam A, Addison P, Conlong D (2020) Acridid ecology in the sugarcane agro-ecosystem in the Zululand region of KwaZulu-Natal, South Africa. Journal of Orthoptera Research 29(1): 9–16. <https://doi.org/10.3897/jor.29.34626>

## Abstract

Grasshoppers and locusts are well known crop and pasture pests throughout the world. Periodically they cause extensive damage to large areas of crops and grazing lands, which often exacerbate food shortage issues in many countries. In South Africa, acridid outbreaks rarely reach economic proportions, but in sugarcane plantations, localized outbreaks of native acridid species have been reported for the last eight years with increasing frequency and intensity in certain areas. This study was undertaken from May 2012 to May 2013 to identify the economically important acridid species in the sugarcane agroecosystem in these outbreak areas, to monitor seasonal activity patterns, to assess sampling methods, and to determine the pest status of the major species through damage ratings. Five acridid species of particular importance were identified: *Nomadacris septemfasciata* (Serville), *Petamella prosternalis* (Karny), *Ornithacris cyanea* (Stoll), *Cataloipus zuluensis* Sjötedt, and *Cyrtacanthacris aeruginosa* (Stoll). All species are univoltine. *Petamella prosternalis* was the most abundant species and exhibited a winter egg diapause, while *N. septemfasciata*, the second most abundant species, exhibited a winter reproductive diapause. *Petamella prosternalis* and *N. septemfasciata* were significantly correlated with the damage-rating index, suggesting that these two species were responsible for most of the feeding damage found on sugarcane. This study, for the first time, identified the acridid species complex causing damage to sugarcane in the Zululand area of KwaZulu-Natal, South Africa, and documented their population characteristics and related damage. These data are important information on which to base sound integrated pest management strategies.

## Keywords

*Cataloipus zuluensis*, *Cyrtacanthacris aeruginosa*, damage rating, management, *Nomadacris septemfasciata*, *Ornithacris cyanea*, outbreaks, *Petamella prosternalis*, population surveys

## Introduction

Grasshoppers and locusts (Orthoptera: Acrididae) attack sugarcane in various parts of the world, such as Indonesia (Lecoq and

Sukirno 1999), West Africa (Maiga et al. 2008), India (Easwaramoorthy et al. 1989), and Africa (Whellan 1968, Bakker 1999, Price and Brown 1999). These insects defoliate plants, thereby reducing their photosynthetic capabilities (Williams et al. 1969, Easwaramoorthy et al. 1989). In southern Africa, three major plagues of the red locust, *Nomadacris septemfasciata* (Serville) (Orthoptera: Acrididae: Cyrtacanthacridinae), have occurred in recent history (Bahana 1999). The last one, between 1929 and 1944, affected most of Africa south of the equator. During this plague, the northern part of KwaZulu-Natal Province of South Africa was heavily invaded and, in 1934, cost the sugarcane industry approximately £1 million (De V. Minnaar 1990). This report has been, so far, the only documented acridid pest attack on sugarcane in South Africa. Locust outbreaks on other crops and pastures remain a serious problem in the southern African region, especially outbreaks of brown locust, *Locustana pardalina* (Walker) (Acrididae: Oedipodinae), and *N. septemfasciata*, which still threaten sustainable agricultural production to this day (Lomer et al. 1999, Price and Brown 1999). In South Africa, sugarcane-growing areas lie within the invasion area of these two aforementioned locust species (Whellan 1968). Although there are no recognized red locust outbreak areas in South Africa (Bahana 1999), it is mentioned as an occasional problematic species along the eastern seaboard of KwaZulu-Natal (Faure 1935, Picker et al. 2004). There have been no major outbreaks since 1944, possibly because of our improved knowledge of locust outbreak dynamics, insecticide technology, application techniques, and intervention strategies (Whellan 1968, Price and Brown 1999, Bahana 1999, Lecoq et al. 2011).

Grasshopper outbreaks, on the other hand, have occurred sporadically in southern Africa and, apart from the elegant grasshopper *Zonocerus elegans* Thunberg (Orthoptera: Pyrgomorphidae), which attacks a wide range of wild and crop plants (Nyambo 1991), little information is available for other species. Grasshoppers do not have gregarious habits and therefore do not swarm and migrate even in years of mass outbreaks. They remain pests of purely local importance with no immediate threat to neighboring districts

(Uvarov 1928). Grasshoppers also feed on the leaves of sugarcane, thereby affecting the photosynthetic capability of the plant (Easwaramoorthy et al. 1989). When infestations are high, defoliation may be so serious that only the mid-rib of the plant is left.

Population surveys have generally been used to estimate animal numbers in the field for conservation purposes (Gardiner et al. 2002) but also for studies relating to pest species (O'Neill et al. 2003). In South African sugarcane, population densities and related damage have been reported based on qualitative visual estimates and opinions, rather than quantitative data. Quantitative population surveys based on rigorous capture methods are therefore needed to gain an accurate understanding of pest ecology (Clarke 1948, Southwood and Henderson 2000). However, over the last ten years sugarcane has increasingly come under attack by what was locally referred to as "grasshoppers" in the northern parts of KwaZulu-Natal, generally referred to as "Zululand". Control measures applied against them during this period were ineffective and the identity of the species was unknown, nor was their population phenology. Furthermore, a quantified measurement of actual crop damage was not known. This paper aims to address these shortcomings and provide data on which to base a structured Integrated Pest Management (IPM) program.

## Methods

*Site descriptions.*—Population surveys took place in the Empangeni region of KwaZulu-Natal, South Africa (28°44'56.74"S; 31°53'59.24"E) from 30<sup>th</sup> May 2012 until 30<sup>th</sup> May 2013. Four farms, which previously reported significant damage and high population densities, were chosen as study sites. Magazulu farm (Tedder) (28°44'9.54"S, 31°52'16.60"E) is situated within 2 km of Empangeni town and was the most southerly site surveyed. GSA farms (28°40'54.94"S, 31°54'51.98"E) and Crystal Holdings (28°40'0.50"S, 31°54'47.37"E) are situated close to each other, roughly 8 km from Empangeni town, and Jengro (28°37'30.84"S, 32°0'52.68"E) was the most northerly site, situated roughly 18 km from Empangeni town.

*Sampling methods.*—Population surveys were completed on each farm once a week from May 2012 to May 2013. When the sugarcane was young (3–6 months old), conventional sweep netting was used as it allowed the standard 180° sweep to be done (see Gardiner et al. 2005). However as the sugarcane got taller (above hip height) standard sweep netting became impractical and this method was adapted to drive netting. Drive netting entailed driving at a standard speed (20 km/hour) along the edges of sugarcane plantations while holding an insect net (Bugdorm cages and traps: 60 cm diameter, Product # DC0005, Taiwan) parallel to the soil surface, 1.5 m off the ground, out the window of the vehicle for five minutes and along a specific route (Fig. 1). From May 2012, drive netting was used to catch adult fliers. Mean sugarcane age at the start of the survey (May 2012) was five months.

The route (Fig. 1) consisted of five 100 m transects completed on each farm. This method was used because tall sugarcane forms dense stands and has a closed canopy which makes conventional sweep netting within the sugarcane field impossible as movement of the net is restricted (Bomar 2001). Due to sugarcane harvesting operations, which started in July 2012, drive netting was not possible because acridid populations dispersed more widely over the more open survey area. A visual line transect method was used in the harvested sugarcane in order to maintain sampling accuracy.

**Table 1.** Summary of survey methods used to measure acridid abundances during population surveys on four sugarcane sites and associated natural habitats from May 2012 to May 2013.

Sampling method	Period of sampling (start and end date)		Age of cane
Drive netting	30-May-12	12-Sep-12	8 months
Visual transects	20-Sep-12	03-Dec-12	12 months
Sweep netting	21-Nov-12	10-Jan-13	3 months
Drive netting	17-Jan-13	15-May-13	5 months

This method was used from the beginning of August until the end of November 2012 and involved walking five 100 m transects per farm, which were measured using a Garmin global positioning system (GPS). Line transects were completed as close as reasonably possible to drive netting transects. A single transect involved walking 100 m between a sugarcane row while counting each acridid that was disturbed in the row in which the counter was walking and the rows on either side of the counter (i.e., three rows – a width of approximately 3 m). A handheld tally counter (Ugreen counters, UK) was used to record the number of grasshoppers disturbed per transect, which was then added to the total amount for all five transects per farm. At the beginning of November 2012, a new generation of hoppers started to emerge and sweep netting was done along the same walked transects as noted above during visual transects, as described in Gardiner et al. (2005) (Table 1).

*Data collection.*—During each field trip, rainfall and temperature were recorded for that day. An attempt was made to conduct field trips only during sunny, dry days in order to minimize sample bias due to climatic factors. One area on each farm where acridid population densities were high was selected as the designated survey site for that farm. Acridids obtained from sweep netting were stored separately per site and brought back to the laboratory alive for identification and counting. Once in the laboratory, they were either killed by freezing or 'cooled' to aid counting. For visual transects, disturbed individuals were identified and recorded without being caught. Collected individuals were sorted into morphologically similar groups, and reference material was identified by a specialist (Corinna S. Bazelet).

*DNA Extraction.*—The acridid species identified using morphological characters were molecularly DNA barcoded (using the CO1 gene) in the biotechnology section at the South African Sugarcane Research Institute (SASRI). DNA was extracted from the muscle of the hind femur, using the KAPA Express Extract DNA Extraction kit (Kapa Biosystems, South Africa) according to the manufacturer's instructions.

*PCR using Cytochrome Oxidase gene primers.*—PCR amplification was conducted using the KAPA 2G Robust PCR Kit (Kapa Biosystems, South Africa) with 1 µl DNA template. The final reaction conditions were as follows: 1X Kapa2G Buffer A, 0.2 mM dNTP mix, 0.5 µM each COI Forward and COI Reverse primer and 0.5 units Kapa2G Robust DNA Polymerase.

The DNA primer sequences were:

COI Forward – 5'AATTGGGGGGTTTGAAATG3'

COI Reverse – 5'GCTCGTGTATCAACGTCIATTC3'

PCR reactions were conducted in an Applied Biosystems Veriti Thermal Cycler using the following thermal cycling profile: 94°C for 2 min, followed by 35 cycles of 94°C for 30 sec, 55°C for 50 sec, and 72°C for 90 sec. Final extension was at 72°C for 10 min. PCR products were purified using the DNA Clean and Concentrator kit (Zymo Research, USA) according to the manufacturer's instructions.

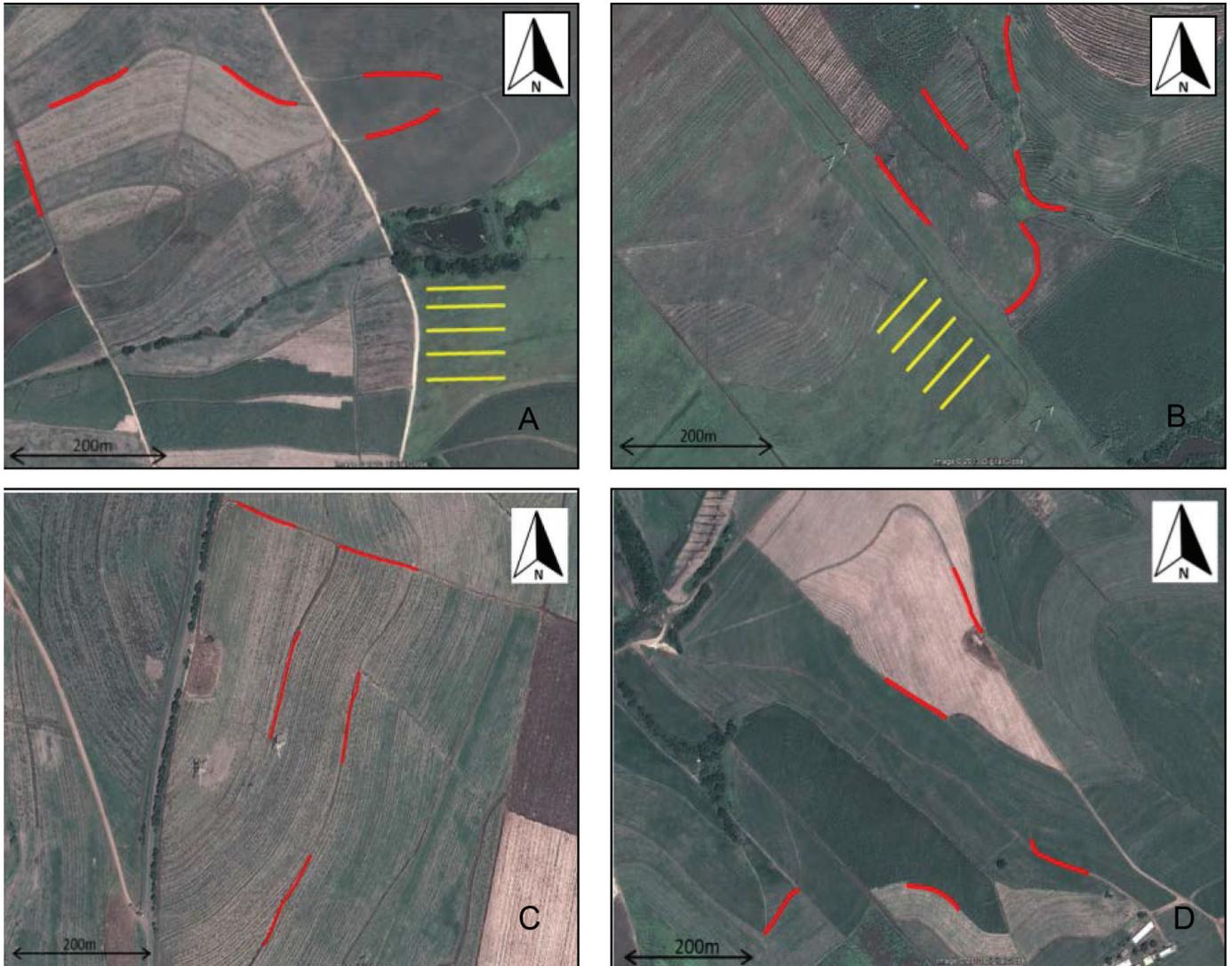


Fig. 1. Aerial view of four farms where surveys took place indicating the five 100 m transects per farm (red lines). Yellow lines indicate the two survey areas in natural habitats. A. Tedder (Magazulu) farm; B. Crystal Holdings; C. GSA farm; and D. Jengro.

DNA sequencing was conducted using the BigDye Terminator v3.1 Cycle Sequencing kit (Applied Biosystems, USA) according to the manufacturer’s instructions. Sequencing reactions were conducted in an Applied Biosystems Veriti Thermal Cycler using the BigDye Terminator v3.1 kit recommended thermal cycling profile. Sequencing products were purified using the BigDye XTerminator Purification Kit (Applied Biosystems) according to manufacturer’s instructions.

*Uploading of DNA sequences to online databases.*—After obtaining good CO1 sequences, a search on two DNA barcoding websites, namely, BOLD systems ([www.boldsystems.org](http://www.boldsystems.org)) and the National Centre for Biotechnology Information ([www.ncbi.nlm.nih.gov](http://www.ncbi.nlm.nih.gov)) indicated that none of the species’ DNA had been submitted to these databases. The sequences were thus submitted to BOLD systems and Genbank.

*Damage rating estimate.*—The level of leaf damage due to grasshopper feeding was estimated on a weekly basis to generate a damage-rating index for the period of May 2012–May 2013. During weekly population surveys, five random sugarcane stools (the un-

derground stubble from which the plant is grown) within the sugarcane survey sites were chosen and a damage rating from 1–5 was estimated as the percentage of leaf area eaten on the youngest top five green leaves of a randomly chosen stalk in the stool (Table 2).

Rating	% damage rating
0/5:	0
1/5:	1–20
2/5:	21–40
3/5:	41–60
4/5:	61–80
5/5:	81–100

The five values per transect were then averaged to get a mean damage rating per farm. The four mean weekly damage ratings were combined and averaged to get a monthly damage-rating index and then plotted against the other farms over the entire year.

*Acridid surveys in surrounding grassland (natural habitat).*—Grassland surveys were completed as a means of comparing grasshopper population densities and species composition in grassland sites compared to sugarcane survey sites. Four sites of natural grassland adjacent or nearby to each of the sugarcane survey sites (approximately 1 km from the sugarcane sites) on each farm were sampled for five months from October 2012 to February 2013. Due to unforeseen circumstances, two of the grassland survey sites had to be abandoned, therefore only two grassland sites remained from 21 November to 17 January (seven weeks). During this period, all acridid species sampled were in the hopper stage. Grassland surveys were completed using the same sweep net method as in the sugarcane study sites. Five 100 m transects were walked per site while sweeping the net over the top half of the grass sward in an 180° arc. Captured specimens were placed in separately marked tubs and brought back to the laboratory for identification and counting.

*Data analysis.*—Rank abundance curves were plotted, calculating a log abundance value that designated each species a ranking from 1–5 according to their total abundance in sugarcane sites. Monthly relative abundance (total count for all species by individual count for each species) was calculated as a percentage in order to correlate the relative abundance of acridid population densities with observed damage. Gamma rank correlation analysis was performed, which is preferable over the Spearman's R analysis as the data contained many tied observations, which the Gamma analysis explicitly accounts for. Where a correlation between species abundance and the damage-rating index was found, a pairwise comparison was conducted. All analyses were completed in Statistica 11.0 (StatSoft Inc., Tulsa, OK, USA). To compare whether farms were associated with any particular species of grasshopper, a simple correspondence analysis, with grasshopper species as column variables and farms as row variables, was used. Likewise, a simple correspondence analysis was also used to compare habitat type (sugarcane vs. grassland) with grasshopper species over a seven-week sampling period with habitat type as column variables and species as row variables. No supplementary row variables were used in either analysis. The analyses were conducted in Statistica 11.0.

## Results and discussion

*Species assemblage.*—A total of seven acridid species were recorded during one year of sampling, including the less abundant *Orthochthya* sp. (Orthoptera: Acrididae) and *Z. elegans*. Five species, however, were of particular concern due to their high population densities (Fig. 2). The rank abundance plot indicates that *P. prosternalis* had the highest overall abundance over a one-year period, followed by *N. septemfasciata*. The extremely mobile nature of the latter species (Faure 1935) and particularly clumpy distribution (Rainey et al. 1957) meant that sampling might have underestimated their abundance in relation to *P. prosternalis*. The other species, *C. zuluensis*, *C. aeruginosa*, and *O. cyanea*, were more evenly distributed over the sampling areas and generally easier to catch during the drive-netting period of sampling. Acridid species always occurred as a species assemblage. It was never observed that only one species occurred in a particular area, although species densities varied.

*Molecular identification.*—None of the species' DNA matched the sequences previously loaded onto GenBank or the BOLD websites

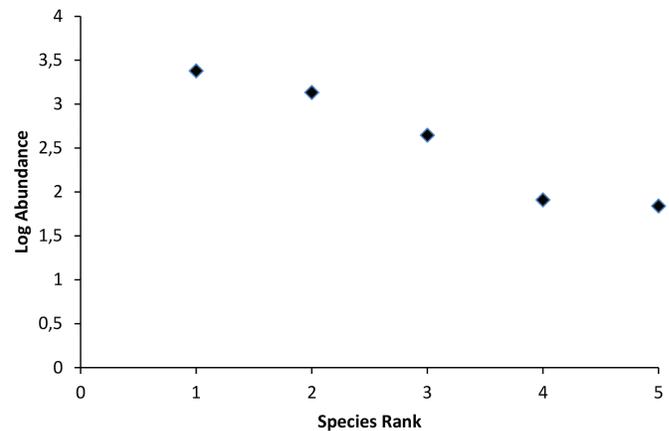


Fig. 2. Rank abundance plot of the five most prominent acridid species found in sugarcane in Zululand, South Africa (1: *Petamella prosternalis*; 2: *Nomadacris septemfasciata*; 3: *Cataloipus zuluensis*; 4: *Cyrtacanthacris aeruginosa*; 5: *Ornithacris cyanea*), based on population surveys carried out from May 2012 to May 2013 in four study sites.

accurately. All five specimen sequences were submitted to BOLD systems, as well as Genbank. The Genbank accession numbers are as follows:

*Nomadacris septemfasciata*: BankIt1690897 SASRI1001-13. COI-5P KJ130657

*Cyrtacanthacris aeruginosa*: Bank1t1690897 SASRI1002-13. COI-5P KJ130656

*Petamella prosternalis*: Bank1t1690897 SASRI1003-13. COI-5P KJ130659

*Cataloipus zuluensis*: Bank1t1690897 SASRI1004-13. COI-5P KJ130655

*Ornithacris cyanea*: Bank1t1690897 SASRI1005-13. COI-5P KJ130658

*Population surveys and damage rating.*—From the start of the surveys in May 2012, populations fluctuated, alternating between a high relative abundance of *P. prosternalis* in summer, and a high relative abundance of *N. septemfasciata* and *O. cyanea* in winter (Fig. 3).

At the beginning of August, only *N. septemfasciata* and *O. cyanea* individuals were still present as adults; this continued until October 2012, when the next generation of hoppers of all species emerged in a fairly synchronized manner. According to Bazelet (2011), who worked in natural veld sites in the Zululand region, *O. cyanea* is a univoltine species, which mates, lays eggs, and dies before the onset of cold, dry weather in winter. This is contrary to the findings of our study. Hoppers were present for roughly 3 months until about January 2012. During this period, *N. septemfasciata* and *P. prosternalis* were the dominant species while *C. zuluensis* made up roughly 20% of the hoppers collected. Hoppers of *C. aeruginosa* and *O. cyanea* were found in very low numbers. *Cyrtacanthacris aeruginosa* was further found to have an egg diapause, which substantiates the findings of Jago (1968).

During the period of May 2012 to May 2013, the damage-rating index fluctuated substantially, indicating that damage varies in relation to population density and possibly the season and growth stage of the sugarcane plant (Fig. 3). Damage was initially at 1.4 on the damage-rating index but started to increase as the season progressed into winter. Thereafter damage started to decrease to a level of 1, roughly at the same period of *P. prosternalis* numbers de-

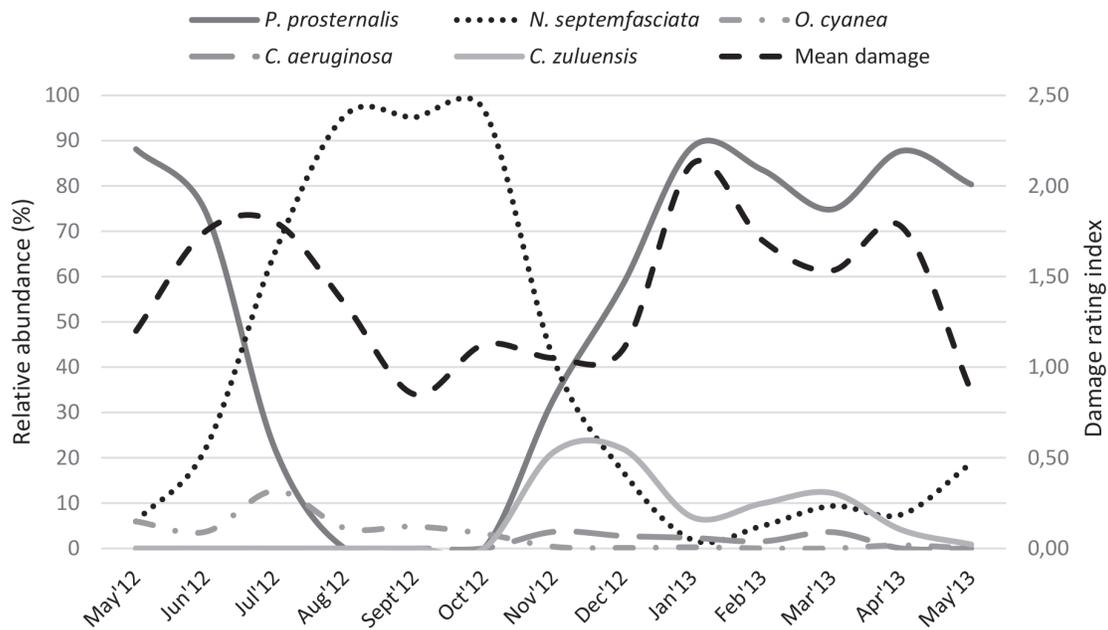


Fig. 3. Population survey showing the relative abundance of the five most prominent acridid species in sugarcane in relation to the damage rating index on the secondary y axis.

creasing. Damage remained fairly low and constant until mid-November, possibly due to the hopper populations. As they grew into 3<sup>rd</sup> and 4<sup>th</sup> instar, and therefore increased in body size, adults fed more, which would explain the increase in damage over this time (Fig. 3). The population dynamics of *N. septemfasciata* observed in our sugarcane study site was comparable with the findings of Lecoq et al. (2006, 2011) in Madagascar. Both of these studies defined three different geographical areas where *N. septemfasciata* populations migrated to and from as a result of seasonal climatic changes, and the term 'main rainy season breeding zone' was suggested.

The Empangeni area (Zululand region of KwaZulu-Natal, South Africa) would qualify as such a breeding zone, as high *N. septemfasciata* numbers were only found in this region of the province. In Madagascar, long range migrations of *N. septemfasciata* have been proven to occur (Lecoq et al. 2006) while in South Africa, this has not yet been shown. The likelihood of significant *N. septemfasciata* migrations occurring in the Zululand region, however, are slim given the fact that the current population surveys have shown that adults remain in the vicinity throughout the dry winter period. These findings contradict those of Faure (1935) that "South Africa does not serve as a permanent breeding ground of the *N. septemfasciata* in its solitary phase". Lecoq et al. (2011) found that during an eight-year study, the biological cycle of *N. septemfasciata* repeated with regularity, although the diapause cycles of all species in the current study generally coincide with the change in seasons and onset of summer rains – thus causing early researchers to presume rainfall was the main factor involved (see: Robertson 1958, Franc and Luong-Skovmand 2009). It has recently been found that the photoperiod is the factor that is responsible for initiation and cessation of diapause (Lecoq et al. 2011). This finding could possibly explain why initiation and cessation of diapause is earlier in South African *N. septemfasciata* populations compared to those in Madagascar.

Damage reached a peak at the end of January 2013, which was when grasshopper population density was the greatest as most in-

dividuals had undergone their final molt to become adults and the effects of natural mortality over time were small.

The damage rating index was significantly correlated with the fluctuations of *P. prosternalis* and *N. septemfasciata* (Table 3), indicating the close relationship between *P. prosternalis* population density and damage to sugarcane (Fig. 3, Table 3).

These results suggest that the combination of *P. prosternalis* and *N. septemfasciata* currently pose the greatest risk to South African sugarcane in terms of crop damage. A shortcoming of the damage rating index is that it does not take into account the growth rate of the plant being analyzed over time. Three of the four survey sites were dryland sugarcane farms; therefore, a decrease in rainfall over winter may slow down plant recovery after feeding and cause damage to be overestimated during winter months.

**Seasonal life cycle.**—Population surveys and personal observations by AB indicated that the five main species in sugarcane are all univoltine (completing one generation per year). All species had a diapause period although the life stage that entered into diapause differed between the species (Table 4). *Nomadacris septemfasciata* and *O. cyanea* overwintered as the adult stage. The immature adults entered a reproductive diapause at the onset of the dry season, only becoming reproductively active five or six months later

Table 3. Relationship between acridid species abundance and damage rating in four sugarcane study sites in Zululand, KwaZulu-Natal.

Species	Damage rating (gamma statistic)
<i>P. prosternalis</i>	0.429143*
<i>N. septemfasciata</i>	0.250408*
<i>O. cyanea</i>	0.111739
<i>C. aeruginosa</i>	-0.190004
<i>C. zuluensis</i>	0.152348

\*indicates species with population densities that were significantly ( $P < 0.05$ ) correlated with observed damage estimates.

at the onset of the rainy season (October). *Petamella prosternalis*, *C. aeruginosa*, and *C. zuluensis* exhibited a different overwintering strategy whereby the adults mated and then the females laid their eggs and died before the onset of the dry season in April or May. The eggs then lay dormant in the soil for up to 7 months until rains began towards October (Table 4).

**Species composition.**—Figure 4 illustrates the mean abundance of six species found at the four sugarcane study sites and the two grassland study sites. Species abundance, diversity, and composition differed between the six study sites, with *N. septemfasciata* being the most abundant on GSA and Crystal Holdings. Very few *N. septemfasciata* individuals were recorded in grassland sites. *P. prosternalis* was most abundant on GSA and Jengro during this period while in grassland sites, very few individuals were recorded. *Orthochtha* species had higher

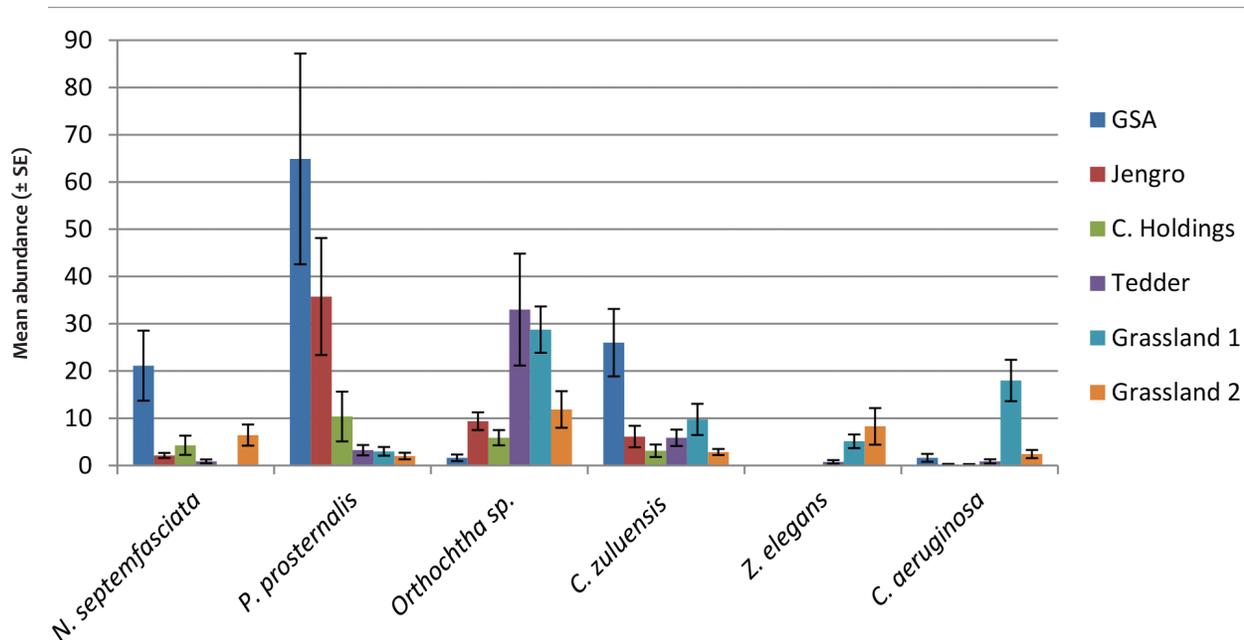
abundance levels in the grassland sites compared to sugarcane. *Cataloipus zuluensis* was equally abundant in sugarcane as in grassland sites, acting as a generalist feeder. *Zonocerus elegans* was almost exclusively found in grassland sites indicating this habitat as being preferable. *Cyrtacanthacris aeruginosa* was recorded in low numbers everywhere except one of the grassland sites where high numbers were counted. Bazelet (2011) recorded no *Orthochtha* sp., one *C. aeruginosa*, and two *Z. elegans* individuals during her study in the Zululand region in semi-natural habitat.

Grassland sites were more similar in acridid assemblage structure, the species occurring there falling mostly to the right of the graph, while sugarcane sites were also more similar but with a different acridid assemblage structure, falling to the left of the graph (Fig. 5). *Zonocerus elegans*, *Orthochtha* sp., and *C. aeruginosa* were closely associated with grassland sites with dimension 1 accounting for 46.62% of the inertia. Dimension 2 (whilst only capturing 23.82% of inertia) indicated that *N. septemfasciata* is closely associated with sugarcane sites at a high order of magnitude, and, similarly, *P. prosternalis* shows a strong association with sugarcane sites but at a low order of magnitude. In a study by Bazelet (2011) in natural grasslands in the Zululand region, over two years, no *N. septemfasciata* and only 22 individuals of *P. prosternalis* were caught in her sites. This indicates that these two species prefer sugarcane to grasslands in this area as a habitat. Michelmore (1947) and Burnett (1951) found that hoppers and adults of *N. septemfasciata* in the Rukwa Valley, Tanzania, showed a marked preference for tall dense grass. Lea and Webb (1939) also found that *N. septemfasciata* hoppers, when disturbed in short grass, would shelter in tall clumps of grass. Generally, sugarcane gets much taller than surrounding natural grasslands, especially over winter in our study areas, which could explain why *N. septemfasciata* preferred tall sugarcane over shorter grassland areas.

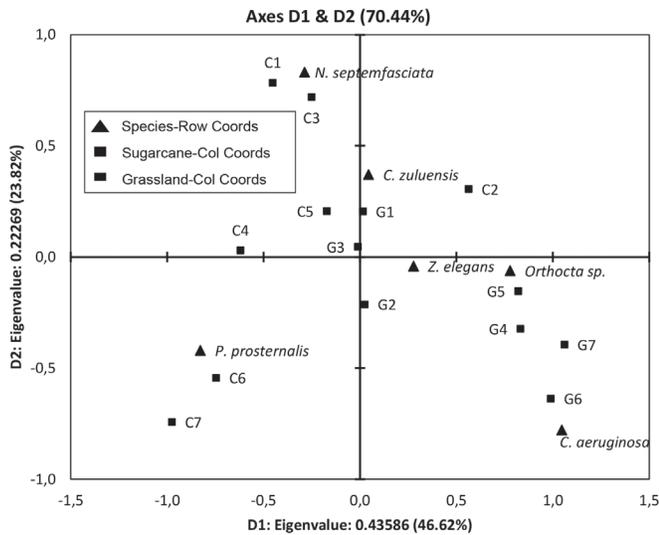
*Nomadacris septemfasciata* are capable, over time, of covering distances of over 1000 miles or more (Rainey et al. 1957) but during the study period, all species including *N. septemfasciata* were confined to relatively small areas in Empangeni. Sugarcane, espe-

**Table 4.** Simplified summary of the two diapause strategies observed within the grasshopper assemblage attacking South African sugarcane. Bold rows indicate southern hemisphere winter months.

Month	Egg diapause present	Reproductive diapause present
	<i>P. prosternalis</i> , <i>C. aeruginosa</i> , <i>C. zuluensis</i>	<i>N. septemfasciata</i> , <i>O. cyanea</i>
January	Hoppers	Hoppers
February	Hoppers	Hoppers
March	Mating/oviposition	Hoppers
April	Mating/oviposition	Reproductive diapause
May	Mating/oviposition	Reproductive diapause
<b>June</b>	<b>Egg diapause</b>	<b>Reproductive diapause</b>
<b>July</b>	<b>Egg diapause</b>	<b>Reproductive diapause</b>
<b>August</b>	<b>Egg diapause</b>	<b>Reproductive diapause</b>
September	Egg diapause	Reproductive diapause
October	Egg diapause	Mating/oviposition
November	Hoppers	Mating/oviposition/Hoppers
December	Hoppers	Mating/oviposition/Hoppers



**Fig. 4.** Mean abundance (± SE) of six species of grasshoppers surveyed at the four sugarcane sites and the two grassland sites for the period 21 November 2012–19 February 2013.



**Fig. 5.** Association between grasshopper species and habitat. Correspondence analysis showing the association between grasshopper species in relation to sugarcane and grassland survey sites sampled over a seven-week period from 21 November 2012–19 February 2013.

cially irrigated, may be the factor causing *N. septemfasciata* populations to remain quite sedentary in the study area, contrary to their mobile nature (Lea 1935). Grasshoppers will always remain pests of local importance, and currently it seems the locust *N. septemfasciata* could remain a pest of local importance. However, the potential for population upsurges of this species resulting in significant outbreaks should not be underestimated.

## Conclusion

Species identification and their population dynamics are the first steps in developing an integrated pest management plan. Population surveys have shown that *P. prosternalis* is the most abundant species in sugarcane in the Zululand region, followed by *N. septemfasciata*. These two species should, therefore, be considered as the primary targets for IPM. The other three species—*C. zuluensis*, *C. aeruginosa*, and *O. cyanea*—are found at lower but appreciable numbers and therefore should not be ignored as their potential for population increase is not well known but certainly possible. All species studied are univoltine, which means that to correlate population fluctuations with weather variables as done in previous literature (see Chiconela et al. 2003), surveys will have to be completed over a longer period in order to determine the significant effect of climate on acridid populations. The findings further show that the distribution of species among farms and natural habitat areas is not uniform, some species being found at higher densities on certain farms or in certain habitats. These findings provide important information for managers and growers in that they enable the development of a more species-specific management plan.

## Acknowledgements

The following staff from SASRI were instrumental in the success of the project: Angela Walton, Denise Gillespie, and all insect rearing staff for assisting with the colonies in the Insect Rearing Unit (IRU). Nelson Muthusamy, for always lending an extra hand with all rearing issues; the late Mike Way, for advice and help in

photographing the research specimens; Keshia Pather from GIS for help in the map constructions in the paper, and Deborah Sweby from Biotechnology for the enthusiastic molecular identifications of the locust and grasshopper species found during the study. Special thanks are given to Tom Fortmann, SASRI's Extension Specialist for the affected area, and the growers who willingly allowed the use of their farms for the research. SASRI provided the funding to complete the research, for which they are thanked, and additional funding was obtained from the National Research Foundation of South Africa [Grant specific unique reference number (UID) 71909; P Addison].

## References

- Bahana JW (1999) Studies on the red locust, *Nomadacris septemfasciata* (Serville) (Acrididae: Cyrtacanthacridinae): Bibliography for the period 1940–1998. *Insect Science and its Application* 19: 377–397. <https://doi.org/10.1017/S1742758400019007>
- Bakker H (1999) *Sugar Cane Cultivation and Management*. Kluwer Academic/Plenum Publishers. Dordrecht, the Netherlands, 642 pp. [https://doi.org/10.1007/978-1-4615-4725-9\\_12](https://doi.org/10.1007/978-1-4615-4725-9_12)
- Bazelet CS (2011) *Grasshopper Bioindicators of Effective Large-Scale Ecological Networks*. Unpublished PhD Thesis, University of Stellenbosch, Stellenbosch.
- Bomar CR (2001) Comparison of grasshopper (Orthoptera: Acrididae) communities on remnant and reconstructed prairies in western Wisconsin. *Journal of Orthoptera Research* 10: 105–112. [https://doi.org/10.1665/1082-6467\(2001\)010\[0105:COGOAC\]2.0.CO;2](https://doi.org/10.1665/1082-6467(2001)010[0105:COGOAC]2.0.CO;2)
- Burnett GF (1951) Field observations on the behaviour of the red locust (*Nomadacris septemfasciata* Serville) in the solitary phase. *Anti-Locust Bulletin* 8: 1–37.
- Chiconela T, Chongo D, D'uamba P, Ngazero A, Santos L (2003) Predicting the occurrence of red locust outbreaks in Mozambique. *African Crop Science Conference Proceedings* 6: 224–230.
- Clarke EJ (1948) Studies in the ecology of British grasshoppers. *Transactions of the Royal Entomological Society of London* 99: 173–222. <https://doi.org/10.1111/j.1365-2311.1948.tb01235.x>
- De V, Minnaar A (1990) In Natal: The locust invasion of 1933–1937. *Natal Society Foundation* 20: 30–42.
- Easwaramoorthy S, David H, Kurup NK (1989) Studies on the feeding potential of two species of grasshoppers infesting sugarcane. *Sugarcane Breeding Convention* 52: 169–171.
- Faure JC (1935) The life history of the red locust (*Nomadacris septemfasciata* (Serville)). *Bulletin No. 144 Union Department of Agriculture*. Pretoria, 30 pp.
- Franc A, Luong-Skovmand MH (2009) Life cycle, reproductive maturation, and wing colour changes in *Nomadacris septemfasciata* (Orthoptera: Acrididae) in Madagascar. *Environmental Entomology* 38: 569–576. <https://doi.org/10.1603/022.038.0308>
- Gardiner T, Hill J, Chesmore D (2005) Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems. *Journal of Insect Conservation* 9: 151–173. <https://doi.org/10.1007/s10841-005-2854-1>
- Gardiner T, Pye M, Field R, Hill J (2002) The influence of sward height and vegetation composition in determining the habitat preferences of three *Chorthippus* species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. *Journal of Orthoptera Research* 11: 207–213. [https://doi.org/10.1665/1082-6467\(2002\)011\[0207:TIOSHA\]2.0.CO;2](https://doi.org/10.1665/1082-6467(2002)011[0207:TIOSHA]2.0.CO;2)
- Jago ND (1968) New East African taxa in the genus *Gymnobothroides* (Acridinae; Acrididae; Orthoptera). *Notulae Naturae* 417: 1–14.
- Lea A (1935) The red locust in Natal. Life history and habits – Control measures Important Series of Investigations. *The South African Sugar Journal* 4: 1–14.
- Lea A, Webb D van V (1939) Field observations on the Red Locust at Lake Rukwa in 1936 and 1937. *Science Bulletin, Union of South Africa Department of Agriculture and Forestry* 189: 1–84.

- Lecoq M, Chamouine A, Luong-Skovmand MH (2011) Phase dependent color polyphenism in field populations of red locust nymphs (*Nomadacris septemfasciata* Serv.) in Madagascar. *Psyché Special Issue on Locusts and Grasshoppers: Behaviour, Ecology, and Biogeography 2011*: 1–12. <https://doi.org/10.1155/2011/105352>
- Lecoq M, Franc A, Luong-Skovmand MH, Raveloson A, Ravelombony V (2006) Ecology and migration patterns of solitary red locusts, *Nomadacris septemfasciata* (Serville) (Orthoptera: Acrididae) in south-western Madagascar. *Annales de la Société Entomologique de France* 42: 197–205. <https://doi.org/10.1080/00379271.2006.10700623>
- Lecoq M, Sukirno (1999) Drought and an exceptional outbreak of the oriental migratory locust, *Locusta migratoria manilensis* (Meyen 1835) in Indonesia (Orthoptera: Acrididae). *Journal of Orthoptera Research* 8: 153–161. <https://doi.org/10.2307/3503438>
- Lomer CJ, Bateman RP, Dent D, De Goote H, Douro-Kpindou OK, Kooyman C, Langewald J (1999) Development strategies for the incorporation of biological pesticides into the integrated management of locusts and grasshoppers. *Agricultural and Forest Entomology* 1: 71–88. <https://doi.org/10.1111/j.1461-9563.1999.tb00001.x>
- Maiga IH, Lecoq M, Kooyman C (2008) Ecology and management of the Senegalese grasshopper *Oedaleus senegalensis* (Krauss 1877) (Orthoptera: Acrididae) in West Africa: Review and prospects. *Annales de la Société Entomologique de France* 44: 271–288. <https://doi.org/10.1080/00379271.2008.10697563>
- Michelmore APG (1947) The habits and control of the red locust in outbreak areas and elsewhere. *Bulletin of Entomological Research* 37: 331–379. <https://doi.org/10.1017/S0007485300030431>
- Nyambo BT (1991) The pest status of *Zonocerus elegans* (Thunberg) (Orthoptera: Acridoidea) in Kilosa district in Tanzania with some suggestions on control strategies. *Insect Science and its Application* 12: 132–236. <https://doi.org/10.1017/S1742758400020749>
- O'Neill KM, Olson BE, Rolston MG, Wallander R, Larson DP, Seibert CE (2003) Effects of livestock grazing on rangeland grasshopper (Orthoptera: Acrididae) abundance. *Agricultural Ecosystems & Environment* 97: 51–64. [https://doi.org/10.1016/S0167-8809\(03\)00136-1](https://doi.org/10.1016/S0167-8809(03)00136-1)
- Picker M, Griffiths C, Weaving A (2004) *Field Guide to Insects of South Africa*. Struik Publishers, Cape Town, 444 pp.
- Price RB, Brown HD (1999) A century of locust control in South Africa. Workshop on Research Priorities for Migrant Pests of Agriculture in Southern Africa, Plant Protection Research Institute, Pretoria, 37–49.
- Rainey RC, Waloff Z, Burnett GF (1957) The behaviour of the red locust (*Nomadacris septemfasciata* Serville) in relation to the topography, meteorology and vegetation of the Rukwa Rift Valley, Tanganyika. *Anti-Locust Bulletin* 26. Anti-locust Research Centre, London, 96 pp.
- Robertson IAD (1958) The reproduction of the red locust, *Nomadacris septemfasciata* (Serv.) (Orthoptera, Acrididae), in an outbreak area. *Bulletin of Entomological Research* 49: 479–496. <https://doi.org/10.1017/S0007485300053797>
- Southwood TRE, Henderson PA (2000) *Ecological Methods* (3<sup>rd</sup> edn). Wiley-Blackwell, New Jersey, 524 pp.
- Uvarov BP (1928) *Locusts and Grasshoppers. A Handbook for Their Study and Control*. London. William Clowes and Sons, 170–217.
- Whellan JA (1968) Locusts in relation to sugar cane. *Proceedings of the South African Sugar Technologists' Association*, 1–5.
- Williams JR, Metcalfe JR, Mungomery RW, Mathes R (1969) *Pests of Sugarcane*. Elsevier, Amsterdam.

# *Mopla guttata* (Acrididae: Catantopinae) rediscovered in the Western Ghats, Kerala, India

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Academic editor: Daniel Petit | Received 23 April 2019 | Accepted 17 June 2019 | Published 10 January 2020

<http://zoobank.org/1603537E-2A31-446F-8CC4-79E333EB0F9E>

Citation: Bhaskar D, Easa PS, Rowell CHF (2020) *Mopla guttata* (Acrididae: Catantopinae) rediscovered in the Western Ghats, Kerala, India. Journal of Orthoptera Research 29(1): 17–23. <https://doi.org/10.3897/jor.29.35664>

## Abstract

The endemic Catantopinae genus *Mopla* was described by Henry in 1940 from the Malabar region of South India. Henry described two species under this genus, *M. guttata* and *M. rubra*. The female type specimens of *Mopla* are deposited in the Natural History Museum, London, UK. There have been no further records of these two species since their description. Seventy-six years later, the first male specimen of the genus *Mopla* was discovered in the Western Ghats, Kerala, India, in 2016. This paper describes the specimen, thought to be of *Mopla guttata*, and reconsiders its systematic placement.

## Keywords

endemism, first male of genus, grasshopper, systematics, tropical forest

## Introduction

Most of the 1033 known Indian grasshopper species were described by foreign researchers (Chandra et al. 2010). In modern India, grasshoppers are considered agricultural pests, hence research publications are confined to agricultural universities and regional pest research centers (Priya and Narendran 2003, Chandra et al. 2010, Nayeem and Usmani 2012). The Western Ghats region, a biodiversity hotspot, is the type locality for some endemic grasshoppers (Cigliano et al. 2018). Most of the 790 species mentioned in the Faunal Diversity in India by Tandon and Hazra (1998) are from biodiversity hotspots such as Western Ghats.

Henry (1940) collected many Catantopinae from southern India as part of a joint expedition of the British Museum and the Colombo Museum from 1936 to 1938. He recorded the exact collection locations for future researchers and explorers; as he mentioned, this was to facilitate further work on the Orthoptera fauna of India. In Henry's (1940) publication he described some very interesting Catantopinae species including *Tinnevellia andrewi*, *Bambusacris travancora*, *Siruvania dimorpha*, *Naraikadua charmichae-lae*, *Palniacris maculatus*, *Coniocara rubropicta*, *Mopla guttata*, and

*Mopla rubra*. Most of these need further investigation. However, these diversity-rich highlands were never revisited for grasshoppers after the departure of the foreign researchers. Bhaskar et al. (2018) reported 130 species of Orthoptera from the Kerala part of Western Ghats. From 2015 onwards we started searching for grasshoppers in protected areas of the State of Kerala, part of the Western Ghats. In September 2016, we came across a completely unfamiliar grasshopper in the Parambikulam Tiger Reserve (PKMTR), Kerala. Unfortunately, we have since failed to find any further specimens. Later the specimen was found to be very close to the type-specimens of *Mopla* that DB had photographed previously at the Natural History Museum, London, UK (NHMUK). Our male specimen was at first misidentified as *Mopla rubra* and illustrations were provided on the sample page of the proposed field guide to Indian Orthoptera (Bhaskar et al. 2018).

*Mopla* are small brachypterous catantopine grasshoppers with distinctive coloration of bright yellow stripes and spots on a dark brown background (Fig. 1). Morphologically, the genus is notable for: A) its very abbreviated frontal ridge that forms a short narrow rostrum that is lamelliformly compressed between the antennae, but becomes obsolete immediately below the antennal bases; B) the absence of visible ocelli, both medial and lateral; and C) the terminal segment of the maxillary palp is laterally expanded, forming a pale-colored broadly elliptical surface (Fig. 2). These modified palps are probably used in intraspecific communication; a similar structure is found in several other tropical forest acridid taxa, such as *Ateliacris* or *Silvitettix*.

Henry (1940) erected the genus *Mopla* with two species: *guttata*, the type of the genus, and *rubra*. The two species were described from two female grasshoppers from the forests of the Western Ghats Mountains of southern India, in what are now the states of Tamil Nadu and Kerala. Henry (1940) named this genus for the Muslim community inhabiting the Malabar region of South India; the Muslims of this region are locally called "Mapla" in the Malayalam language of Kerala. The type specimen of *Mopla guttata* was collected from Top Slip, Anamalai Tiger Reserve, Tamil Nadu, and that of *Mopla rubra* was collected from Nilambur, Kerala. To our

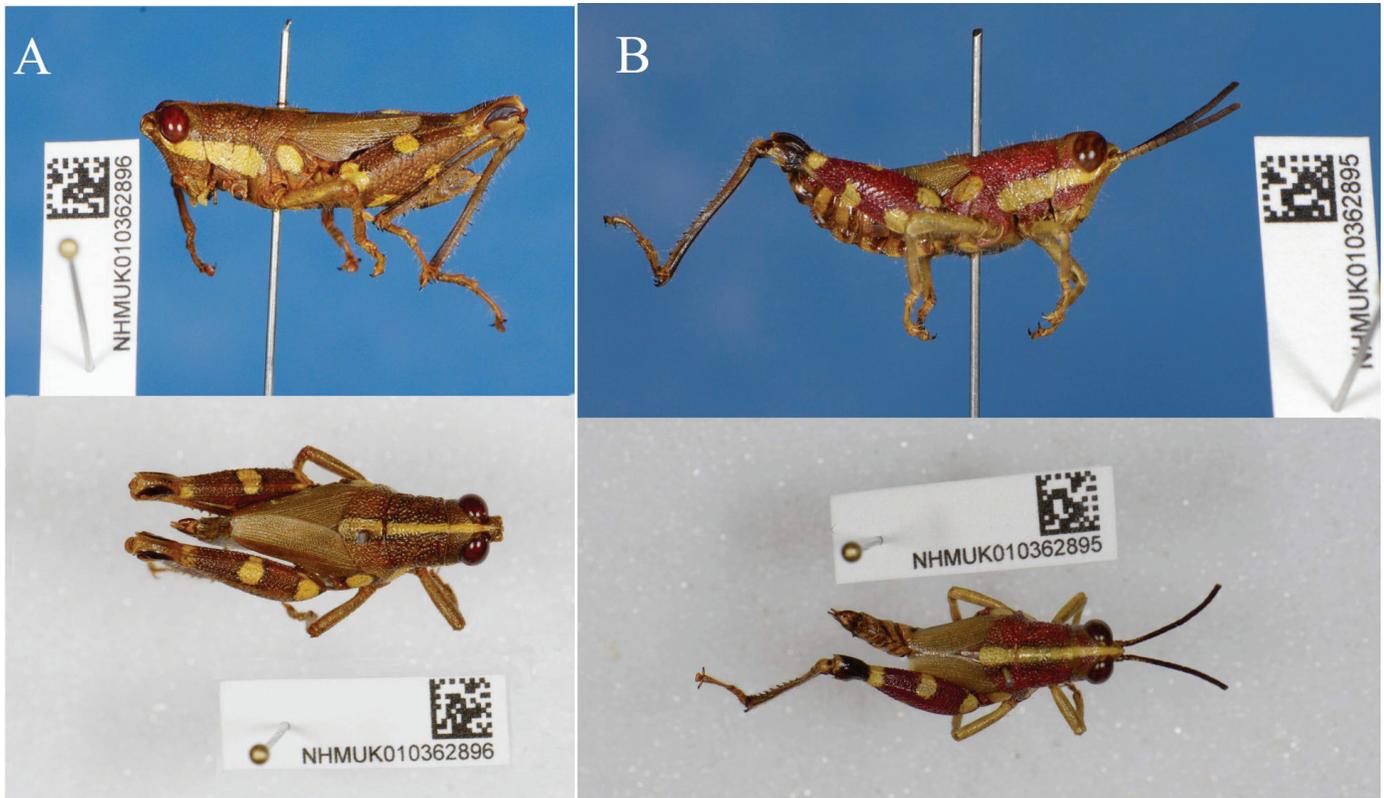


Fig. 1. A. *Mopla guttata*, holotype female (NHMUK); B. *Mopla rubra*, holotype female (NHMUK). Photo credit: D. Bhaskar.

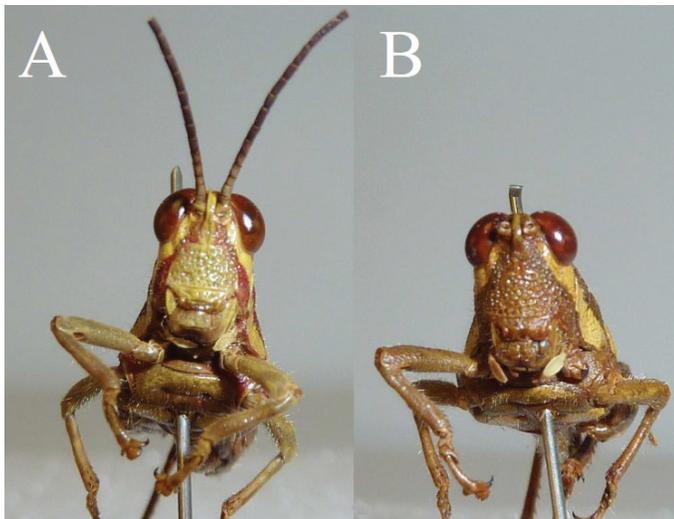


Fig. 2. Facial coloration of the female holotypes of A. *Mopla rubra* and B. *M. guttata*, showing the expanded terminal segments of the labial palps, and the difference in structure of the frontal ridges. The frontal ridge of *guttata* is almost devoid of medial sulcus, only a trace at the extreme ventral margin is apparent. In *rubra* there is a faint sulcus over the entire length. Photo credit: L.D.C. Fishpool.

knowledge, there has been no further record of this taxon since the original publication, and no male has been described.

We now report the capture of the first male of this genus. Its identification and description necessarily require reconsideration of Henry (1940)'s publication and of the type material.

## Methods

**Study area.**—Parambikulam Tiger Reserve (PKMTR) of Kerala is one of the richest wildernesses in the Western Ghats of India. PKMTR (10° 20'–10° 32'N, 76° 35'–76° 5'E) is situated between Anamalai and Nelliampathi hill ranges in the Palakkad District, Kerala, India. PKMTR has an area of 643.662 km<sup>2</sup> and extends over an altitude ranging from 460 m to 1439 m asl. The vegetation types include evergreen, semi-evergreen, teak, moist deciduous, and riparian forests.

Grasshopper diversity of PKMTR was documented from 2015 to 2018. We collected and recorded the diversity of grasshoppers by using sweep netting and hand-picking of specimens. Standard Orthoptera taxonomy was followed using the Orthoptera Species File (Cigliano et al. 2018). The pinned specimens were deposited at the Kerala Forest Research Institute (KFRI) entomology museum.

The male *Mopla* specimen was relaxed in water to dissect the phallic complex. The phallic complex was extracted after treating the last abdominal segments with 10% KOH that loosened the attached muscles and membranes. This procedure unfortunately destroyed the tergites and sternites of these segments, which are therefore missing from the final specimen. The components of the phallic complex were separated and sorted in vials with 70% alcohol. The phallic complex was then verified by CHFR. The complex was stained using acid fuchsin and differentiated in water. Dimensions were measured using a graticule eyepiece in the stereo microscope and a digital stage reading to 0.01 mm to move the pinned specimen under an appropriate magnification (between 6 and 50 times, depending on the size of the structure being measured). Drawings were made under the stereo microscope and edited using Photoshop CS5 (Adobe Systems Inc.). Specimens were imaged

using digital camera DFC 295 attached to a Leica S8AP0 stereomicroscope and processed using software LAS V3.8. Image editing was accomplished using Adobe Photoshop CS4.

#### Abbreviations of depositories:

NHMK Natural History Museum, London, United Kingdom.  
KFRI Kerala Forest Research Institute, Kerala, India.

#### Results

*Comparison of M. guttata and M. rubra.*—Henry's (1940) two specimens are almost identical superficially and obviously congeneric (Fig. 1A, B). When describing the second specimen as *M. rubra*, Henry (1940) wrote: "Very near to *M. guttata*, of which it will probably eventually be regarded as a subspecies; it differs from the latter, however, in so many minor points that I feel the only satisfactory course is to treat it as a full species". These "minor points" of difference were listed as follows: "Slightly smaller than *M. guttata*, with relatively shorter antennae; shorter and less well-developed tegmina, which are much more widely separated at their bases and are not so distinctly divided into two planes at vein M; frontal ridge feebly constricted opposite antennal scrobes; below this point, irregularly sulcate to a point half-way to the clypeal suture; fastigium of vertex more evenly declivent, less tumescent than in *M. guttata*; puncturation of face, occiput, pronotum and pleurae less coarse than in the latter; pronotum with the angle of posterior margin rounded". Henry also noted differences in coloration, which are discussed later below.

We have examined and photographed the type specimens of both *guttata* and *rubra* (both in NHMK), and have attempted to confirm these reported differences.

**Size:** Henry (1940) provided measurements of both specimens (Table 1), and there seems to be no reason to doubt his accuracy:

It is noteworthy, however, that Henry (1940) stressed that both body length measurements were uncertain, although he ultimately suggested the same value (20 mm) for both. All the other measurements show that *guttata* is 10–20% larger than *rubra*, except for length of the tegmen (T), where that of *guttata* is apparently 40% longer than *rubra*. The slightly larger size of *guttata* is apparent when the two types are compared (Fig. 3).

After normalizing for the difference in size of the two species by dividing each value by the length of the pronotum (P), the ratio of *guttata* to *rubra* values is close to unity ( $\leq 10\%$  difference) throughout, indicating that the relative sizes of different body parts are identical in the two specimens. Henry (1940) was therefore incorrect in stating that the antennae of *rubra* are "relatively shorter". The antennae are broken on both the types, and Henry's (1940) measurements cannot be checked. The exception to the above is the length of the tegmen (T), which is 20% longer in *guttata* even after normalization. Presumably this is the basis of Henry's (1940) statement that the tegmina of *rubra* are "shorter and less well-developed". We have checked this by recalculating the ratio T/P from photographs of the two specimens, yielding new values of  $T = 1.24P$  for *guttata*, and  $T = 1.12P$  for *rubra*. This reduces the normalized *guttata/rubra* ratio to  $1.24/1.12 = 1.11$ , in line with that of all the other body measurements. We conclude, therefore, that Henry's (1940) tegmen measurement for *guttata* was somewhat too large, and that all the morphometric ratios of the two type specimens are within 10% of each other.

**Table 1.** Measurements of female *Mopla guttata* and *M. rubra* (Henry 1940).

Measurements (mm)	<i>guttata</i> female	<i>rubra</i> female
Length of body	20.0	ca. 20.0
Length of antenna	13.0	11.0
Width of head, across eyes	4.5	4.1
Length of pronotum	7.0	6.0
Greatest width of pronotum	6.25	5.3
Length of tegmen	9.0	6.4
Length of fore femur	4.2	3.7
Length of hind femur	12.3	10.3



**Fig. 3.** Female holotypes of *Mopla guttata* (bottom) and of *M. rubra* (top), showing the slightly smaller size and distinctly redder ground coloration of *M. rubra*. Photo credit: L.D.C. Fishpool.

**Separation of the wing bases:** Henry's (1940) claim that *M. rubra*'s wing bases are "much more widely separated" than those of *M. guttata* is unconvincing. In photographs of the types (Fig. 1), there seems to be merely a difference in the extent of overlap of the trailing edges of the tegmina, which could be influenced by the position of the tegmina or variation in their width.

**Posterior angles of the pronotum:** We traced the outlines of the pronotum in lateral photographs of the types and superimposed them. We found a slight difference as noted by Henry (1940), in that the posterior angle of the *rubra* type is indeed somewhat more smoothly rounded than that of *guttata*.

The remaining morphological criteria (slope and convexity of the fastigium, puncturation of the integument) cannot be examined critically in the available photographs.

In summary, the differences in morphology claimed by Henry (1940) are only partially supported on reexamination. The confirmed differences are slight, and alone are possibly insufficient for a specific separation, as Henry (1940) remarked.

*Biogeography of the Mopla species.*—As mentioned above, the *guttata* and *rubra* type localities are both located in the Western Ghats and are relatively close to each other. Significantly, however, they are separated by a prominent geographical feature, the 30–40 km Palghat Gap (Myers et al. 2000), which is the only significant break in the chain of the Ghats. The Palghat Gap is known to be a major biogeographic barrier for numerous plant (Bahulikar et al. 2004, Apte et al. 2006) and vertebrate (Vidya et al. 2005, Gunawardene et al. 2007, Robin et al. 2010, Van Bocxlaer et al. 2012, Ram et al. 2015, Vijayakumar et al. 2016) species, and could very well interrupt gene flow between populations of flightless grasshoppers such as *Mopla*. It is therefore quite plausible that the slight differences seen between *guttata* and *rubra* derive from genetic differences and represent at least incipient speciation.

*Is the newly captured male rubra or guttata?*—Our male *Mopla* specimen was collected in the Anamalai Hills, only 3 km from the *guttata* type locality. If the Palghat Gap is suspected of being a boundary between the two populations of *Mopla*, this alone suggests that the male belongs to *guttata*. At least two morphological findings strengthen this hypothesis:

1. The detailed structure of the frontal ridge is very similar in our male and in the *guttata* female type (compare Figs 2 vs. 4). In both, the narrow rostral part of the ridge terminates just above the point where the medial ocellus would be expected, and at that point the ridge suddenly becomes sulcate for a very short distance immediately before its disappearance. This results in a small “fishtail” structure at the lower end of the frontal ridge, seen in both specimens. The faint suggestion of a longitudinal sulcus, seen in the holotype of *rubra*, is absent from both the female and the putative male of *guttata*.
2. The ratio T/P can be calculated from dorsal photos of the male as previously described for the female types. This produces a value of T/P = 1.28, much closer to the female *guttata* value (1.24) than to the female *rubra* value (1.12). It is not unusual in grasshoppers for males to have relatively longer tegmina than females.

Henry (1940) further noted a difference in coloration between his two specimens. While both have a similar pattern of yellow markings on a brown background, in the female *rubra* he reported that much of the brown area was suffused with crimson (hence his specific name). This is not visible in the 80-year old type today, and has probably been lost by fading over time, but the *rubra* holotype is still distinctly more reddish brown than the olive-brown *guttata* holotype (Fig. 3). Significantly, however, the freshly caught male (Fig. 4) also shows no crimson coloration. This too supports the hypothesis that the male is *guttata* and not *rubra*, although sexual dimorphism in coloration is, of course, possible.

Henry (1940) also noted, but did not stress, a difference in facial coloration. Comparison of recent photographs of the holotypes (Fig. 2) shows that the frons of *rubra* is predominantly yellow, while that of *guttata* is dark brown. Our male has the latter coloration, as expected of *guttata*, at least in the absence of sexual dimorphism.

With a genus known from only three specimens, it is impossible to be sure of a specific determination as the range of intraspecific variation is unknown. However, all the available evidence (geographical, morphological, and coloration) suggest that we are dealing with the previously unknown male of *Mopla guttata*.

*Material examined and depository.*—Allotype: Adult male (opposite sex to the holotype) (Fig. 4): INDIA: Kerala: Palakkad district: Parambikulam Tiger Reserve: Sungum range, coordinates 10°41'93.40"N, 076°72'12.40"E. 28.09.2016 (leg. D. Bhaskar). Specimen number OR0024 (KFRI).

Size: Table 2. Medium, L (length from fastigium to tip of subgenital plate) = 17.82 mm.

*Description of the male of M. guttata.*—Integument rugose, coarsely punctate, with numerous short white hairs. Antennae filiform, 22 segments, longer than head and pronotum together. Flagellum long and thick, black, flattened towards the tip with a light brown-yellow terminal segment (Fig. 4). Head with rounded occiput, fastigium of the vertex triangular, wider at its base than long, extending slightly beyond the anterior margins of the antennal



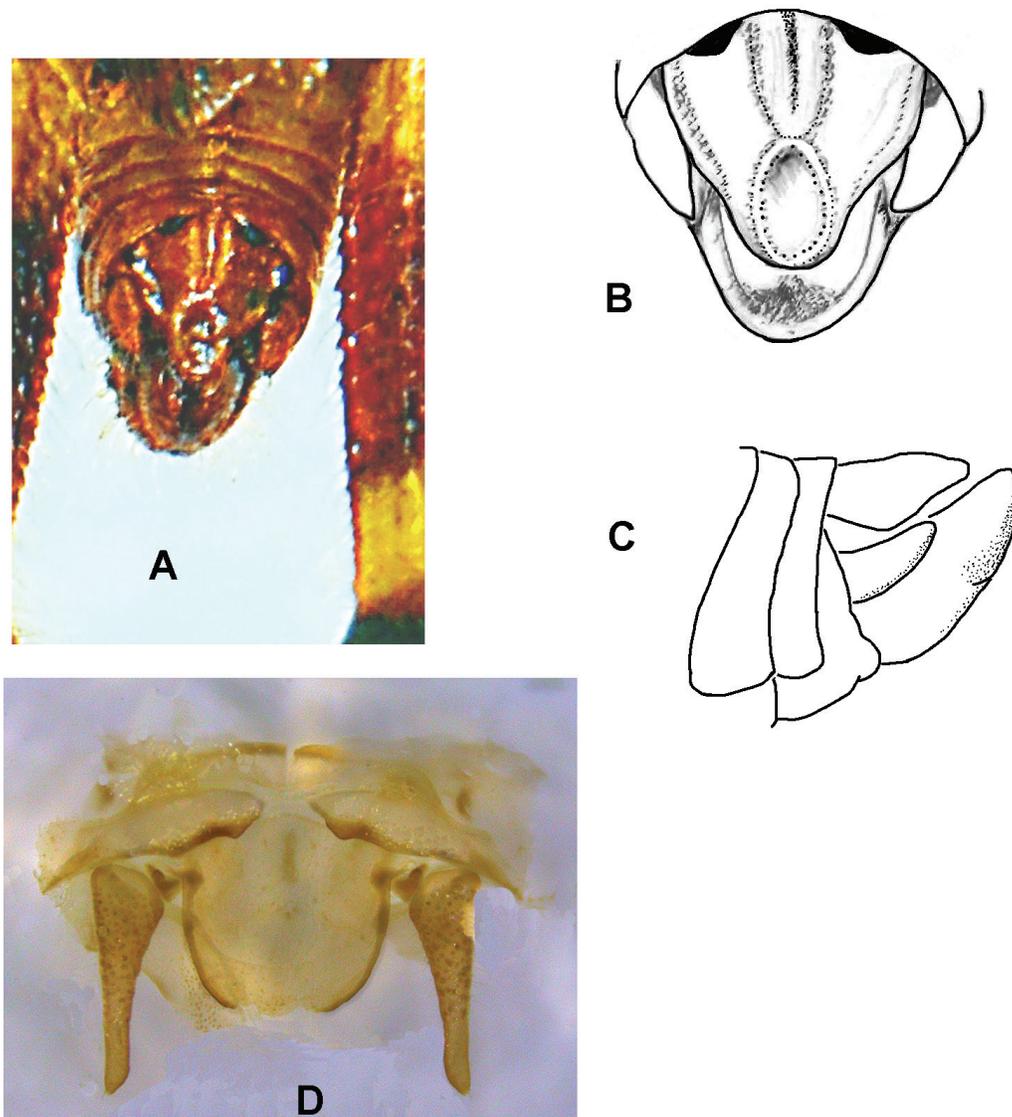
Fig. 4. *Mopla guttata*, male. A. Whole animal alive; the odd position of the right tibia is due to specimen being injured in capture. B. Oblique frontal view to show frontal ridge, for comparison with Fig. 2. Photo credit: D. Bhaskar and L.D.C. Fishpool.

**Table 2.** Measurements of male *Mopla guttata* (specimen OR0024-KFRI).

Character	Code	Length (mm)
Length from fastigium to tip of subgenital plate	L	17.82
Length of elytron	E	5.51
Length of antenna	Ant	31.89
Length of pronotum in the dorsal midline	P	4.47
Head and pronotum (combined length)	H+PN	7.43
Length of hind femur	F	12.64
Depth of femur (the maximum width of the hind femur)	FD	3.68
Length of hind tibia	Tib	10.21
Length of the most proximal tarsal segment	T1	1.01
Length of the second tarsal segment	T2	0.75
Length of the distal tarsal segment	T3	2.49
Total length of the three tarsal segments	T1-T3	4.25
Foot formula ratio 0.23 (T1/T1-3)		
0.17 (T2/T1-3)		
0.58 (T3/T1-3)		

scape segments, the tip bluntly rounded, dorsal surface finely punctate, devoid of lateral or medial carinae. Fastigial foveolae absent. Frontal ridge lamelliformly compressed, developed only between the antennal sockets, obsolete below; extends as a very thin semicircular rostrum between the antennal scapes; anterior surface smooth, not sulcate, over most of its length, but minutely sulcate and divergent just at its ventral extremity (Fig. 4). Compound eyes large, globular and protuberant, interocular space narrow, less than width of antennal scape. Medial and lateral ocelli apparently obsolete.

Pronotum transversely rounded, medial carina scarcely visible, lateral carinae absent; front margin broadly rounded, hind margin obtuse-angulate, with a rounded tip. Metazona much shorter than prozona, its margins diverging strongly towards the rear. Disc of pronotum coarsely rugoso-punctate, deeply incised by the principal (most posterior) sulcus, and very weakly by one or two more anterior sulci. Prosternal tubercle short, vertical, slender and



**Fig. 5.** Male terminalia of *Mopla guttata*. A. Dorsal aspect of pinned specimen; B. Interpretive drawing of A; C. Lateral view; and D. Cleared preparation of abdominal tergites 10 and 11. Note that the terminal lobe of the supraanal plate is missing; compare with A and B. Furcula and the obliquely truncate cerci are clearly shown.

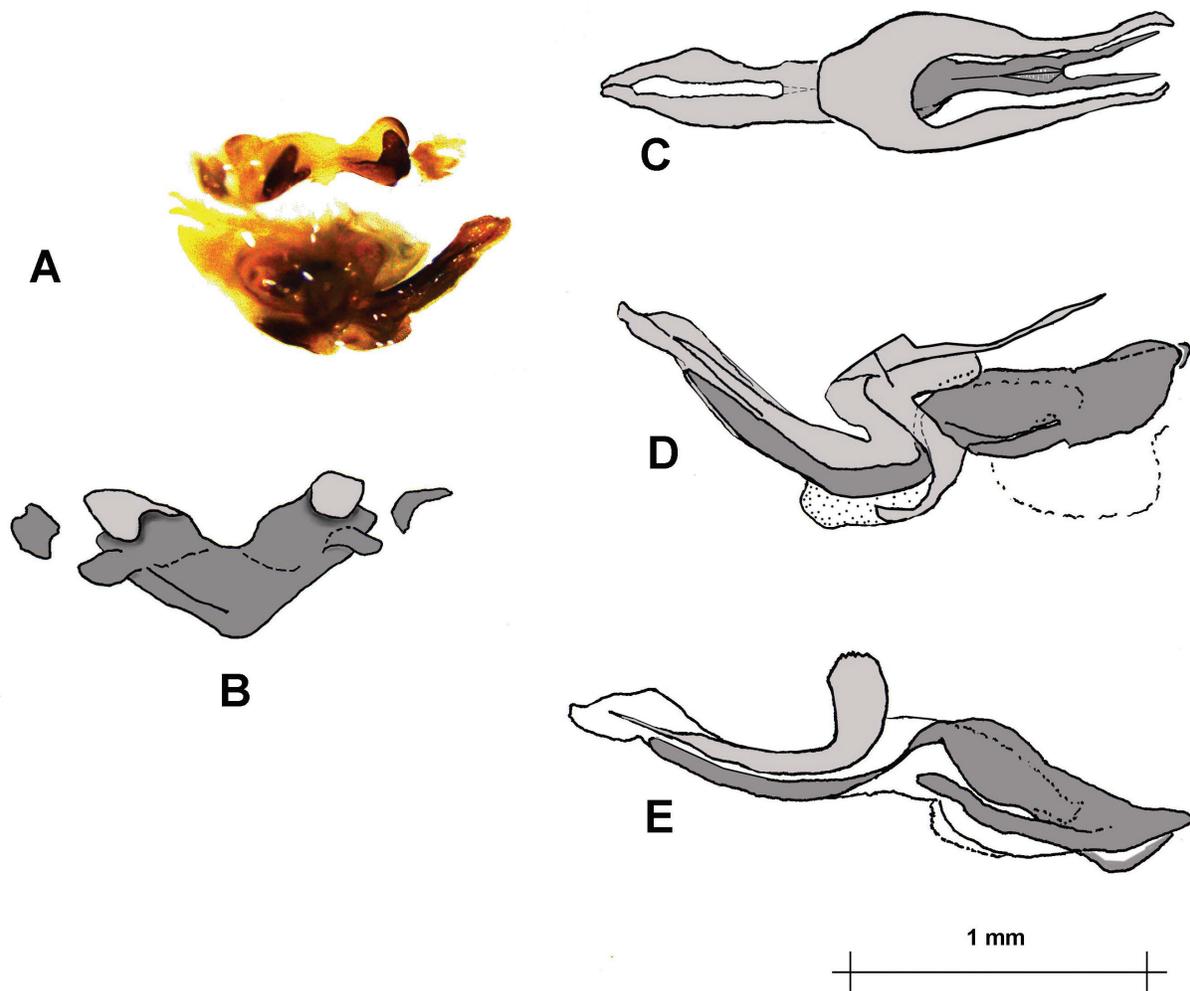


Fig. 6. *Mopla guttata*, phallic structures. A. Oblique posterior view of phallic complex before preparation and dissection; B. Epiphallus, anterior view; C. Dorsal and D. Lateral views of phallic complex with epiphallus, epiphallic, and ectophallic membranes removed; and E. Endophallus, arch sclerite, and ectophallic aedeagal valves, after removal of remaining ectophallic structures. In C-E the endophallus is in a darker shading, the ectophallus in lighter shading. The broken line in D indicates the presumed position of the ejaculatory sac, missing from this preparation. Spermatophore sac stippled.

pointed. Brachypterous; tegmina overlap dorsally and extend only to 7<sup>th</sup> abdominal tergite, with rounded tips. Wings: tegmen 5.51 mm long, olive brown in color. Legs: Pro- and mesothoracic legs stout, femora widened and nearly cylindrical, fore and middle tibiae rounded, with numerous small hairs, punctured. Hind femur stout, strongly rounded, thick, exceeds both abdomen and the elytra in length, coarsely punctured; dorsal and ventral longitudinal carinae weakly serrate. External face of femur with prominent chevron patterning marked by rows of strong punctures. Hind knees with medial dorsal tooth, ventral lobes slightly downwardly curved, pointed, but not spinous. Hind tibia stout with 8 external and 10 internal spines, inner spines are slightly longer than the external spines; external apical spine present. Hind tibia (10.21 mm) 2.40 times as long as hind tarsus (4.25 mm). Third segment of hind tarsus longer than the first two segments together, foot formula 0.23, 0.17, 0.58; arolia well developed. For the foot formula, the value for each tarsal segment is obtained by expressing its length as a percentage of the sum of the three tarsal segmental lengths; e.g., the value for T2 is  $T2/(T1 + T2 + T3)$ . This formulation allows the feet of different species of different sizes to be compared with each other.

**Abdomen:** Short, conical and compressed, tenth abdominal tergite divided, with a weak furcula (Fig. 5). Supra-anal plate roughly triangular, with a rounded tip. Male cerci fairly short, straight, tapering to an obliquely truncate tip (Fig. 5). Male sub-genital plate rather short, apex smoothly rounded in lateral view.

**Phallic complex:** (Fig. 6). Elongate and slender, aedeagus equal in length to the more proximal parts of the phallus. Epiphallus: bridge shaped, broad, undivided medially, with short hooked ancorae and large tapering lobe-shaped lophi that are curved over at their tips. Lateral lobes weakly differentiated. Oval sclerites present, of irregular shape. Ectophallic apodemes long and slender, tapering, more or less parallel; zygoma rounded, rami slender, running rearwards at their tips, and giving rise to an extensive ectophallic sheath surrounding the dorsal aedeagal valves. Arch sclerite large, supporting long spatulate dorsal aedeagal valves that exceed the ventral valves in length. Endophallus slender, gonopore processes present and elongate, extending ventrally almost to the flexure. Flexure slender, ventral aedeagal valves tapering but not pointed. Endophallic apodemes small and narrow, not inflected laterally. Ejaculatory sac apparently

lost in dissection, spermatophore sac lies ventrally, between and below the ventral aedeagal valves.

**Biology.**—Practically nothing is known of the way of life of this genus. The male specimen was caught on low bushes at a forest verge with predominantly herbaceous vegetation. Henry's (1940) holotypes were caught "in rain-forest", with no further details provided. The hind foot formula, with a short second tarsal joint, suggests a life on herbaceous plants rather than an arboreal one, and the large arolia rules out a terrestrial way of life.

## Discussion

Henry (1940) tentatively placed *Mopla* in the Catantopinae; his reservations were based on the lack of a precise diagnosis of this subfamily. Dirsh (1961) later described the Catantopinae as a subfamily with no exclusive diagnosis; historically the subfamily has been used as a depository for forms that do not fit the criteria for other Old-World subfamilies (Akite and Rowell 2013). The present description shows that *Mopla* has a typically catantopine phallic complex with a long sheathed aedeagus, the sheath being derived from the ectophallus, very reminiscent of that seen in e.g., the African Serpusiinae (Rowell et al. 2018).

Henry (1940) mentioned a discussion he had with Uvarov regarding an alleged similarity of *Mopla* to Neotropical grasshoppers and its differences from other Old-World grasshoppers. Some characters of *Mopla*, especially the structure of the head and the unique bold spotting and banding all over the body including on the femora, apparently caused Henry to perceive a faint affinity of this genus to the Neotropical group Tropinoti. It is not clear what characters could have led Uvarov or Henry to this speculation; *Tropinotus* Serville 1831 is now considered a junior synonym of *Xyleus*, a large macropterous Romaleinae savanna grasshopper, completely different from *Mopla* in both habitus and ecology. *Mopla* seems to be well placed in the Catantopinae as currently understood and has morphology typical of tropical forest light-gap species worldwide, with brightly contrasting coloration, prominent eyes, and diminished flight ability (Rowell 1978).

## Acknowledgements

We are thankful to the Director, Dr. Sreejith KA, Dr. Sajeer TV, (scientists) and the scientific community of Kerala Forest Research Institute (KFRI) for facilitating the study. Financial support from the Orthoptera Species File (OSF) to DB made the visit to European museums possible for verifying the type specimens. We are thankful to Maria Marta Cigliano and Holger Braun of the OSF for their wholehearted support during the study. We especially thank Dr. Judith Marshall of the NHMUK for access to the type specimens of *Mopla*, and Dr. L.C.D. Fishpool for taking photographs of them at our request. We acknowledge the Parambikulam Tiger Conservation Foundation of Kerala Forest and Wildlife Department along with our field assistants, Bagyaraj and Sreenivasan. Thanks to Mr. Subin KK and Mr. Bharath for assistance with Photoshop. We acknowledge the skills of Mr. Shiju (driver KFRI) in driving through the forests.

## References

Akite P, Rowell CHF (2013) *Oshwea dubiosa* rediscovered in Uganda. *Journal of Orthoptera Research* 22: 45–49. <https://doi.org/10.1665/034.022.0107>

- Apte GS, Bahulikar RA, Kulkarni RS, Lagu MD, Kulkarni BG, Suresh HS, Rao PSN, Gupta VS (2006) Genetic diversity analysis in *Gaultheria fragrantissima* Wall. (Ericaceae) from the two biodiversity hotspots in India using ISSR markers. *Current Science* 91: 1634–1640.
- Bahulikar RA, Lagu MD, Kulkarni BG, Pandit SS, Suresh HS, Rao MKV, Ranjekar PK, Gupta VS (2004) Genetic diversity among spatially isolated populations of *Eurya nitida* Korth. (Theaceae) based on inter-simple sequence repeats. *Current Science* 86: 824–831.
- Bhaskar D, Easa PS, Hochkirch A (2018) Digitalisation of Indian Orthoptera types deposited in British Natural History Museum, London (NHM UK) and a checklist to Orthoptera of Kerala, India. *Metalepeta* 38: 18–23.
- Chandra K, Gupta SK, Shoshodia MS (2010) A checklist of Orthoptera (Insecta) of India. *Zoological Survey of India (M.P.)*, 1–57.
- Cigliano MM, Braun H, Eades DC, Otte D (2018) Orthoptera Species File. Version 5.0/5.0. <http://orthoptera.speciesfile.org> [accessed Nov 2018]
- Dirsh VM (1961) A preliminary revision of the families and subfamilies of Acridoidea (Orthoptera, Insecta). *Bulletin of the British Museum of Natural History (Entomology)* 10: 349–419. <https://doi.org/10.5962/bhl.part.16264>
- Gunawardene NR, Dulip Daniels AE, Gunatilleke IAUN, Gunatilleke CVS, Karunakaran PV, Geetha Nayak K, Prasad S, Puyravaud P, Ramesh BR, Subramanian KA, Vasanthi G (2007) A brief overview of the Western Ghats-Sri Lanka biodiversity hotspot. *Current Science* 93: 1567–1572.
- Henry GM (1940) New and little known South Indian Acrididae (Orthoptera). *Transactions of the Royal Entomological Society of London* 90: 497–540. <https://doi.org/10.1111/j.1365-2311.1940.tb01033.x>
- Nayeem R, Usmani K (2012) Taxonomy and field observations of grasshopper and locust fauna (Orthoptera: Acridoidea) of Jharkhand, India. *Munis Entomology and Zoology* 7: 391–417.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–857. <https://doi.org/10.1038/35002501>
- Priya AV, Narendran TC (2003) A key and a checklist of the genera of short-horned grasshoppers (Orthoptera: Acridoidea) of Kerala. *Entomon* 28: 223–230.
- Ram MS, Marne M, Gaur A, Kumara HN, Singh M, Kumar A, Umapathy G (2015) Pre-historic and recent vicariance events shape genetic structure and diversity in endangered lion-tailed macaque in the Western Ghats: Implications for conservation. *PLoS ONE* 10: e0142597. <https://doi.org/10.1371/journal.pone.0142597>
- Robin VV, Sinha A, Ramakrishnan U (2010) Ancient geographical gaps and paleo-climate shape the phylogeography of an endemic bird in the sky-islands of Southern India. *PLoS ONE* 5: e13321. <https://doi.org/10.1371/journal.pone.0013321>
- Rowell CHF (1978) Food-plant specificity in neotropical rain forest acridids. *Entomologia Experimentalis et Applicata* 24: 651–662.
- Rowell CHF, Jago ND, Hemp C (2018) Revision of *Aresceutica* (Orthoptera: Acrididae: Catantopinae) with comments on related genera. *Journal of Orthoptera Research* 27: 107–118.
- Tandon SK, Hazra AK (1998) Orthoptera. In: *Faunal Diversity in India*. ENVIS Centre, Zoological Survey of India, Calcutta, 184–188.
- Van Bocxlaer I, Biju SD, Willaert B, Giri VB, Shouche YS, Bossuyt F (2012) Mountain-associated clade endemism in an ancient frog family (Nyctibatrachidae) on the Indian subcontinent. *Molecular Phylogenetics and Evolution* 62: 839–847. <https://doi.org/10.1016/j.ympev.2011.11.027>
- Vidya TNC, Fernando P, Melnick DJ, Sukumar R (2005) Population differentiation within and among Asian elephant (*Elephas maximus*) populations in southern India. *Heredity* 94: 71–80. <https://doi.org/10.1038/sj.hdy.6800568>
- Vijayakumar SP, Menezes RC, Jayarajan A, Shanker K (2016) Glaciations, gradients, and geography: multiple drivers of diversification of bushfrogs in the Western Ghats Escarpment. *Proceedings of the Royal Society B: Biological Sciences* 283(1836): 20161011. <https://doi.org/10.1098/rspb.2016.1011>



# Effect of anthropogenic pressure on grasshopper (Orthoptera: Acridomorpha) species diversity in three forests in southern Cameroon

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Academic editor: Alina Avanesyan | Received 25 January 2019 | Accepted 4 May 2019 | Published 3 February 2020

<http://zoobank.org/0AB48AF9-C0D3-408A-87A2-F7148C727C6C>

Citation: Oumarou Ngoute C, Kekeunou S, Lecoq M, Nzoko Fiemapong AR, Um Nyobe PCA, Bilong Bilong CF (2020) Effect of anthropogenic pressure on grasshopper (Orthoptera: Acridomorpha) species diversity in three forests in southern Cameroon. Journal of Orthoptera Research 29(1): 25–34. <https://doi.org/10.3897/jor.29.33373>

## Abstract

Grasshoppers are highly diversified in tropical rainforests and considered of both ecological and conservation importance. The population dynamics of central African grasshoppers, however, and the structure of their communities remain poorly studied. We report here on the impact of human activities on the diversity of grasshopper species from three localities in southern Cameroon: Ongot, more anthropized forest; Zamakoe, moderately anthropized forest; and Ngutadjap, less anthropized forest. Data were collected using sweep nets, quadrats, and pitfall traps. We analyzed how pressures from human activities affected the grasshopper species compositions using five statistical methods: (1) two non-parametric estimators for specific richness, (2) abundance, (3) abundance distribution model, (4)  $\alpha$  diversity index, and (5)  $\beta$  diversity index. The results showed no significant differences in species richness between the sites (nine species at Zamakoe, seven each at Ongot and Ngutadjap). Among these species, one was specific to Ongot and Zamakoe, while one, two, and three species, respectively, were found only in Ongot, Ngutadjap, and Zamakoe. Abundance and species diversity of grasshoppers increased with anthropogenic pressure on the forests. We noticed a great similarity between the grasshopper communities of the two localities under the greatest anthropogenic pressure (Ongot and Zamakoe) compared to that of the less anthropized locality of Ngutadjap. The most common grasshopper species, *Mazea granulosa*, was most abundant where deforestation was highest. Species diversity was highest in the more and moderately anthropized forests, and the diversity index showed greater similarity between these two grasshopper communities compared with that of the less anthropized forest. This work enables us to better understand how the parameters of these insect communities reflect the degree of forest degradation in southern Cameroon.

## Keywords

biodiversity, degradation rate, grasshopper communities, tropical rainforest

## Introduction

Tropical rainforests shelter an important part of the world's biodiversity and represent an important stake for all countries, in

particular with regard to the effects of anthropogenic disturbances and climate change. Forest biodiversity remains poorly studied throughout the African continent (Basset et al. 2001), where these ecosystems are heavily deforested, particularly in the Congo Basin. The rate of deforestation doubled in the Congo Basin between 1990 and 2005 (Tchatchou et al. 2015). These forests are subject to growing anthropogenic pressures leading to their fragmentation and progressive destruction (de Wasseige et al. 2012). The direct causes of deforestation include intensification of mining, population expansion, intensive agricultural practices, and construction of dams that severely alter the structure of the forest and its dependent biodiversity. As the primary means of livelihood for semi-subsistence farmers in the Congo Basin, shifting cultivation uses forest resources for agricultural production and as a source of non-wood products (Brown 2006). Cameroon loses about 140,000 hectares of forest per year (Ndoye and Kaimowitz 2000). In its southern part, industrial wood production has increased from 2.3 million m<sup>3</sup> in 1991 to more than 3 million m<sup>3</sup> in 2000 (de Wasseige et al. 2012). The destruction of these forests has altered the biophysical structure of the natural environment and leads to the breakdown of ecosystem equilibrium and the extinction of species as well as the modification of the structure of floral and faunal communities. The faunal composition is known to be negatively affected by this clearing, with reduction of canopy cover being the major factor of these losses (Scott et al. 2006, Steer et al. 2009). The habitat loss is predicted to greatly impact invertebrates' species diversity (Chinery 1993); these organisms are less mobile than vertebrates, have short life cycles, and are more specialized in micro-habitats due to their specificity to host plants.

Grasshoppers are a common and diverse invertebrate group worldwide (Gangwere et al. 1997, Song 2010, Zhang 2011). They are a dominant group of herbivorous insects with up to 20–30% of all arthropod biomass (Soliman et al. 2017) and occasionally constituting as much as half of the biomass in an environment (Gillon 1983). This group plays an important role in terrestrial

food webs and is known to be a good source of protein for other animals such as amphibians, small reptiles, birds, and small mammals; therefore, their scarcity may disturb the trophic structure in an ecosystem (Schmidt et al. 1991, Soliman et al. 2017). Grasshoppers are important bioindicators of threatened environments because of their specific microhabitat preferences, functional importance in ecosystems, sensitivity to the modification of biotic and abiotic factors of their habitats, and the ease with which they can be sampled (Armstrong and van Hensbergen 1997, Samways 1997, Andersen et al. 2001, Guido and Gianelle 2001, Soliman et al. 2017). Diversity and community structure of grasshoppers as they relate to anthropogenic activities, types of vegetation, and climate change have been studied in many regions of the world (Otte 1976, Kemp et al. 1990, Clayton 2002, Torrusicio et al. 2002, Gebeyehu and Samways 2003, Steck et al. 2007, Saha and Haldar 2009, Sirin et al. 2010, Branson 2011, Chen et al. 2011, Kekeunou et al. 2017). However, despite the high rate of deforestation observed, the bioindicator potential of grasshoppers in the Congo Basin area, and particularly in Cameroon, has been largely neglected. Apart from the recent works of Seino et al. (2013) and Kekeunou et al. (2017) on the diversity of acridoids in higher mountains in West Cameroon, abundance and grasshopper diversity have been poorly studied. The present article is a contribution to the understanding of the effect of anthropogenic pressure and forest degradation on the abundance and diversity of grasshopper species in southern Cameroon.

## Materials and methods

**Study sites.**—Grasshoppers were collected over a year in three localities (Ongot, Zamakoe, and Ngutadjap; Fig. 1) in the forest area located on the margins of southern Cameroon plateau (3° 27'N, 11° 32'E and 4° 10'N, 11° 49'E). This area, about 650–700 m in elevation, is a part of the plateau that forms the northern and western edges of the Congo Basin (Westphal et al. 1981). The climate

is typical of the Guinean zone with four seasons comprised of a long dry season (mid-November to mid-March), a short rainy season (mid-March to June), a short dry season (July to mid-September), and a long rainy season (mid-September to mid-November). Precipitation ranges from 1500–2000mm per year (Amou'ou et al. 1985, Santoir and Bopda 1995). The southern Cameroonian forest is dominated by Sterculiaceae and Ulmaceae, and its undergrowth is made up of herbaceous plants such as Maranthaceae and Acanthaceae (Westphal et al. 1981). In this ecosystem, the natural vegetation is regularly degraded by the economic exploitation of wood and the practice of slash-and-burn agriculture (Santoir and Bopda 1995). The resulting bushy vegetation after degradation is less diversified and dominated by *Chromolaena odorata*, *Ageratum conizoides*, *Synedrella nodiflora*, and *Imperata cylindrica*. Plantain, cassava, yam, maize, and groundnut are the main food crops, while industrial crops include cocoa, coffee, sweet banana, and palm oil.

Grasshoppers were sampled in three forest ecosystems, each with different levels of anthropogenic pressure and degradation: Ongot forest, 14 to 88 inhabitants/km<sup>2</sup> located in the division of Mefou and Akono, near Yaoundé; Zamakoe forest, 10 to 41 inhabitants/km<sup>2</sup> in the division of Nyong and So'o, near Mbalmayo; and Ngutadjap forest, 2 to 15 inhabitants/km<sup>2</sup> in the division of Ntem Valley, near Ebolowa (Gockowski 1996). Plant species richness is higher in the less degraded Ngutadjap forest, lower in the Zamakoe forest, and lowest in the Ongot forest (Suppl. material 1). Gockowski (1996) showed that the residents of Ongot draw more income from paid work and extensive agriculture. In Ngutadjap, people depend more on hunting and fishing activities, while Zamakoe is a transition zone between the conditions of Ongot and Ngutadjap forests.

**Grasshopper sampling.**—The grasshopper species were sampled every month from the forests of Ongot, Zamakoe, and Ngutadjap using sweep nets, quadrats, and pitfall traps. Samples by net were made randomly for 30 min; grasshoppers were also captured by hand on the litter in 22 movable iron quadrats of 1 m<sup>2</sup> each.

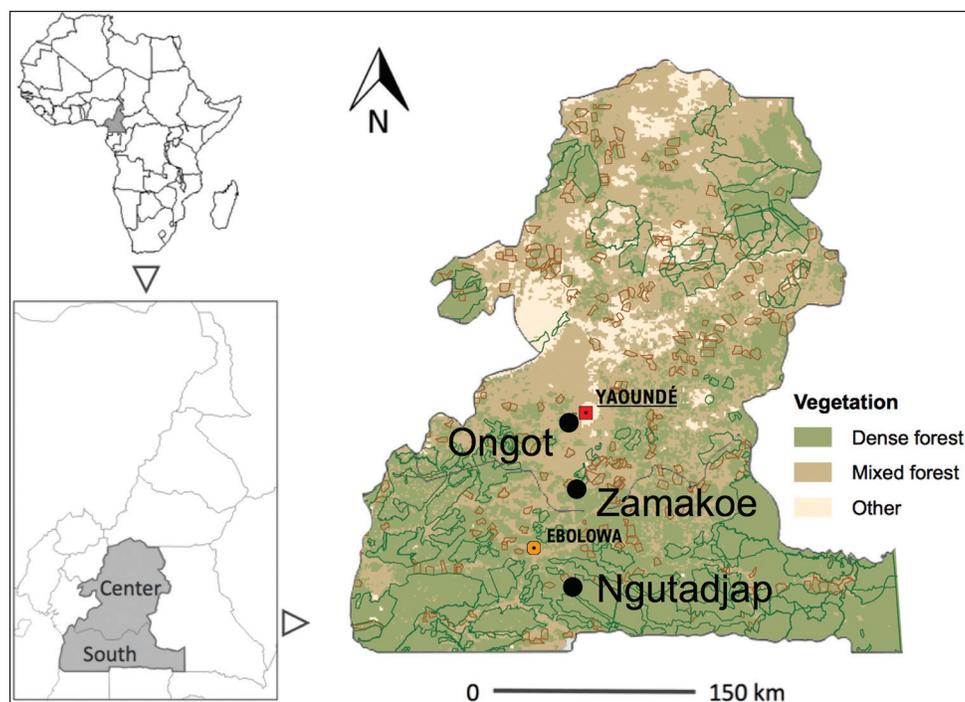


Fig. 1. Study sites in relation to vegetation types in Cameroon (see Mertens et al. 2012).

These quadrats were placed every 10m, on two parallel transects of 110m, separated from each other by 10m. Other specimens were collected in 10 pitfall traps (of 8cm diameter each), 1/3 filled with 5% formalin as a preservative; each trap was laid every 20m in the same transects after quadrat exploration.

*Grasshopper identification.*—The collected specimens were identified using keys from Dirsh (1956, 1961, 1965, 1966, 1970), Jago (1967), Kevan (1975), Hollis (1975), and Lecoq (1980).

### Data analysis

*Species richness, sampling efforts and species accumulation curves.*—Species richness (S) is the number of species reported from each sampling site. We have estimated these theoretical values by the non-parametric estimators *viz.*, Chao1 and Abundance-based Coverage Estimator (ACE) (Marcon 2015) using the software EstimateS (Colwell 2013). The plots of cumulative species number per sample were generated using the same software with data randomized 100 times. We estimated the sampling effort as the ratio of observed species richness to theoretical species richness. Average efforts were compared using a Kruskal-Wallis H-test in the software PAST (Hammer et al. 2001).

*Relative abundances.*—The average relative abundances (Marcon 2015) were calculated using the following formula:

$$fx = \frac{\sum nx1 + nx2 + \dots + nx17}{N} \times 100$$

$\sum nx1 + nx2 + \dots + nx17$  is the sum of abundances of species  $x$  from the first to the seventeenth month in a given site;  $N$  is the sum of abundances of all the species in the three sites. Mean abundance between the different sites and between species were compared by the Kruskal-Wallis H-test while comparisons of mean abundances for two samples were made by the Wilcoxon W-test using PAST.

*Abundance distribution models.*—The abundance distributions of the reported species were compared to the geometric distribution

model of Motomura, the broken stick model of Mac-Arthur, and the log series model of Fisher (Carlo et al. 1998, Cielo Filho et al. 2012, Havyarimana et al. 2013, Marcon 2015) to find the one that fits most to our dataset. These models provide information on how species are distributed and on how they share the available resources in the ecosystem (Havyarimana et al. 2013). PAST software automatically generates the results from the row data. The  $\chi^2$  test was used in PAST to compare the observed abundance distribution to the expected for the three types of theoretical distributions tested.

*Diversity.*—Species diversity of grasshoppers was calculated in PAST and expressed as dominance (D), Shannon diversity (H), and evenness (H/Hmax) indexes (Carlo et al. 1998, Tadu et al. 2013, Marcon 2015, Kekeunou et al. 2017, Mbenoun Masse et al. 2017, Raghavender and Vastrad 2017). The Shannon index for two samples were compared using the Student t-test (Hutcheson 1970).

*Similarity.*—Similarities between the grasshopper communities were assessed by the Bray Curtis index ( $C_n$ ) (Bray and Curtis 1957, Tadu et al. 2013, Tadu and Djiéto-Lordon 2014, Raghavender and Vastrad 2017) and the correspondence analysis of the species to the different communities (Yelland 2010). Cluster analysis was performed using the Paired Group Method (UPGMA) in PAST. PAST graphically generates the Euclidean distances between rows (species) and columns (sites/forests) for the correspondence analysis.

### Results

*Species richness.*—A total of 12 grasshopper species were identified belonging to two families: Pyrgomorphidae (two species) and Acrididae (10 species) (Fig. 2A). The subfamily Catantopinae was the most diverse with six species following by the Oxyinae and Pyrgomorphinae (two species each), and Acridinae and Coptacrinae with only one species each (Fig. 2B).

Ten of the 12 identified species were collected by net, six species were collected in quadrats, and only two species in pitfalls (Table 1). Two species were collected only from the least disturbed forest of Ngutadjap (*Gemeneta opilionoides* and *Parapetasia femorata*).

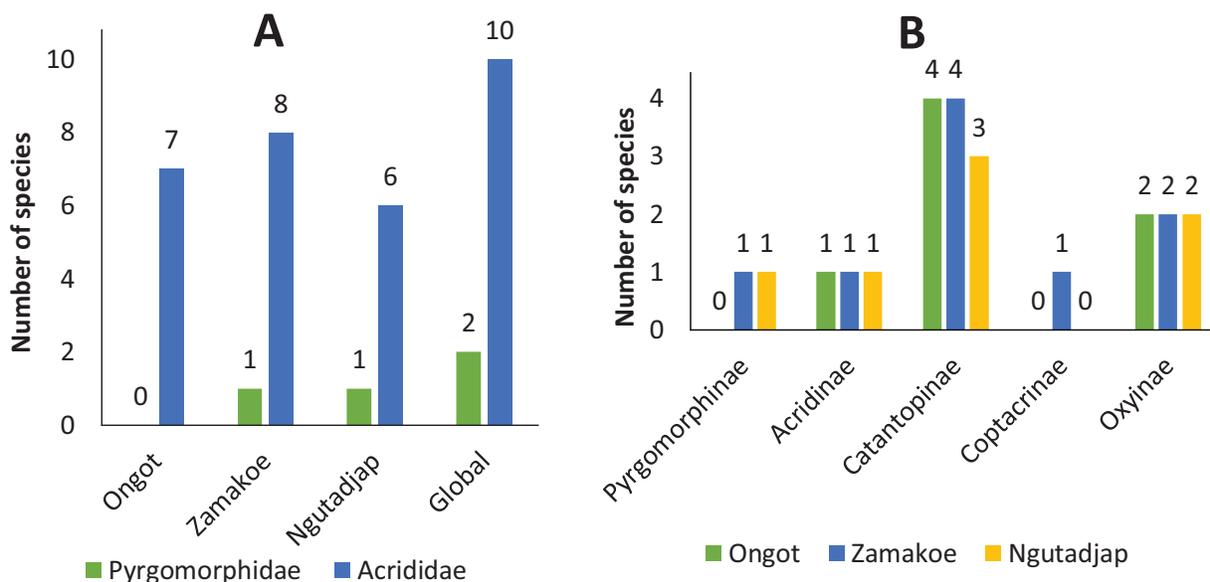


Fig. 2. Species richness from each study site. A. Families; B. Subfamilies.

**Table 1.** Species richness according to the different sampling methods in the forests.

Family	Subfamily	Species	Ongot			Zamakoe			Ngutadjap			
			net	quadrat	pitfall	net	quadrat	pitfall	net	quadrat	pitfall	
Acrididae	Acridinae	<i>H. gerstaeckeri</i>	+	+		+	+		+			
		Catantopinae	<i>A. degener</i>	+	+							
	<i>G. opilionoides</i>								+			
	<i>G. terrea</i>		+			+						
	<i>M. granulosa</i>		+	+	+	+	+	+	+	+	+	
	<i>P. carnapi</i>					+						
	<i>S. opacula</i>		+				+	+	+			
	Coptacrinae		<i>C. hopei</i>				+					
			Oxyinae	<i>D. fasciata</i>	+			+	+			+
	<i>P. apicalis</i>	+		+			+					
Pyrgomorphidae	Pyrgomorphinae	<i>P. femorata</i>							+			
		<i>T. ferruginea</i>				+						
Number of taxa			7	4	1	7	5	2	6	2	1	

+ indicates the presence of the species at the site for the collection method used.

*Gemeneta terrea* was collected from the two more disturbed forests of Ongot and Zamakoe, while *Apoboleus degener* was collected only from the most disturbed forest of Ongot. *Pteropera carnapi*, *Cyphocerastis hopei*, and *Taphronota ferruginea* were collected only from the moderately anthropized forest of Zamakoe (Table 1). The remaining five species were common to all three localities.

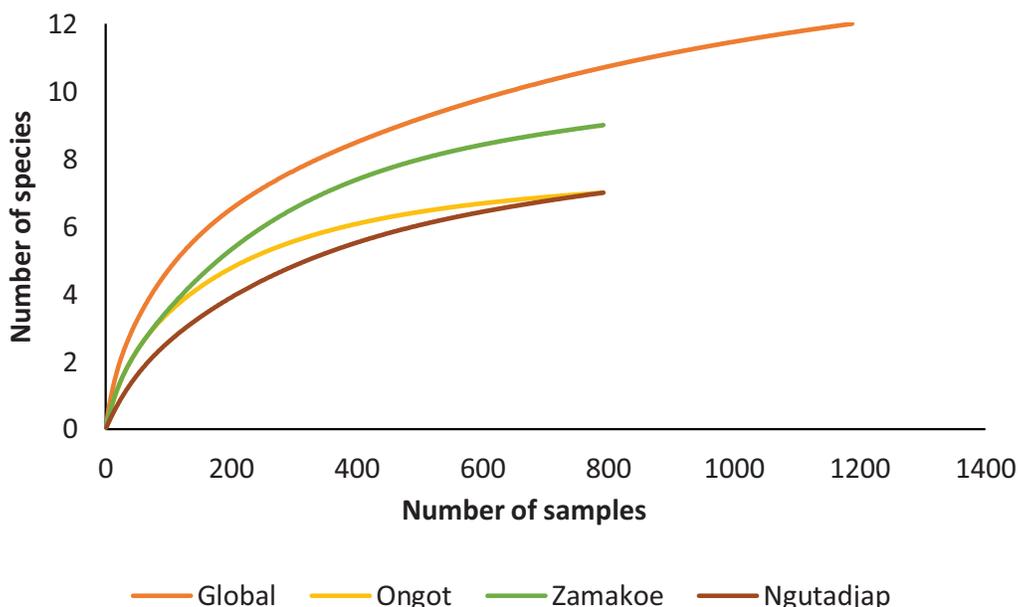
**Sampling effort and species accumulation curves.**—Sampling captured almost the entire estimated species assemblage ( $95.3 \pm 1.42\%$ ). No significant difference ( $H = 2, P = 0.36$ ) was observed between the localities: Ngutadjap ( $97.0 \pm 3\%$ ), Ongot ( $96.5 \pm 3.5\%$ ), and Zamakoe ( $92.5 \pm 2.5\%$ ) (Table 2). The species accumulation curve of each forest started to flatten out towards the end of the sampling period (Fig. 3).

**Relative abundance.**—A total of 465 individuals were collected from the target localities (Appendix 1). We did not observe great differences in abundance between seasons (Appendix 1). Among these

**Table 2.** Sampling effort and diversity of grasshopper species from the study sites. The values in brackets represent the theoretical species richness; a and b: the results of Shannon diversity index test for two samples.

Diversity/Estimator	Ongot	Zamakoe	Ngutadjap
Taxa S	7	9	7
Individuals	167	226	72
Dominance D	0.54	0.71	0.47
Shannon H	0.97 <sup>ab</sup>	1.18 <sup>b</sup>	0.73 <sup>a</sup>
Evenness H/Hmax	0.38	0.23	0.46
ACE	93% (7.52)	90% (10.00)	94% (7.40)
Chao1	100% (7.00)	95% (9.47)	100% (7.00)
Mean of Estimators	96.5±3.5% (7.26±0.26)	92.5±2.5% (9.73±0.26)	97±3% (7.2±0.2)

The same letter between two sites shows no significant difference between the values.

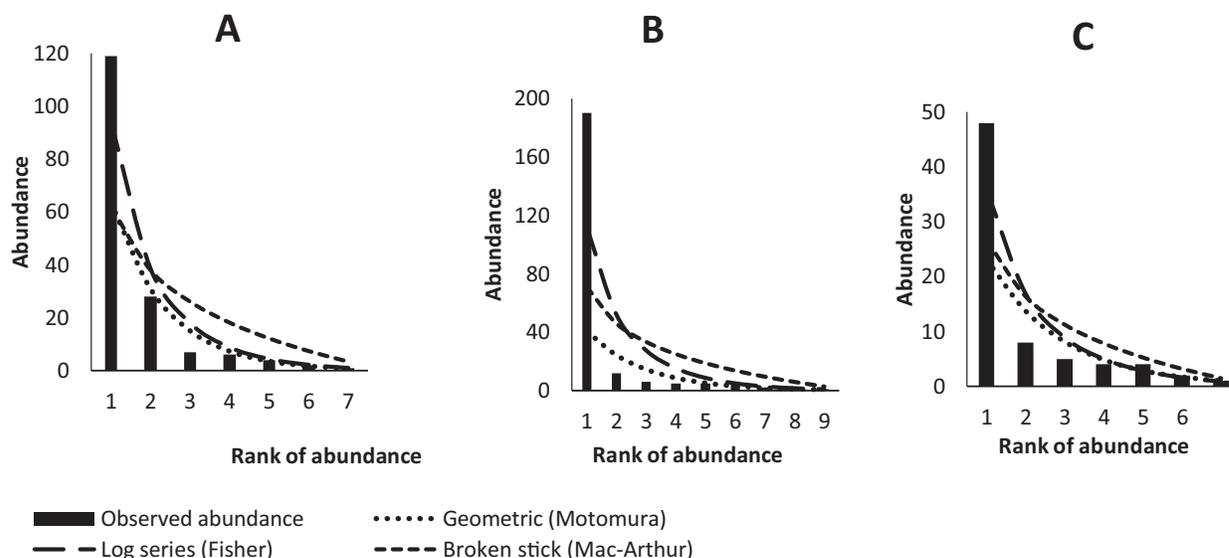


**Fig. 3.** Species accumulation curves of the study sites.

**Table 3.** The mean relative abundance (%) of species between the different study sites. Each value is: mean  $\pm$  standard error; H-value: Kruskal Wallis test; P-value: probability; a, b and c: the results of the comparisons, with the Wilcoxon test, for two samples.

Family	Subfamily/ Species	Ongot	Zamakoe	Ngutadjap	H- value	P-value	Total
Acrididae	Acridinae						
	<i>H. gerstaeckeri</i>	1.1 $\pm$ 0.4	2.07 $\pm$ 0.9	1.65 $\pm$ 0.8	0.14	0.91	4.82 $\pm$ 1.7
	Catantopinae						
	<i>A. degener</i>	0.44 $\pm$ 0.2	0	0	0.64	0.13	0.44 $\pm$ 0.29
	<i>G. opilionoides</i>	0	0	0.45 $\pm$ 0.4	0.16	0.36	0.45 $\pm$ 0.45
	<i>G. terrea</i>	0.17 $\pm$ 0.1	0.45 $\pm$ 0.3	0	0.51	0.32	0.62 $\pm$ 0.03
	<i>M. granulosa</i>	26.44 $\pm$ 2.3 <sup>b</sup>	41.05 $\pm$ 3.2 <sup>c</sup>	11.66 $\pm$ 2.2 <sup>a</sup>	22.02	<0.0001	79.15 $\pm$ 3.1
	<i>P. carnapi</i>	0	0.77 $\pm$ 0.4	0	1.45	0.05	0.77 $\pm$ 0.4
	<i>S. opacula</i>	4.8 $\pm$ 1.9 <sup>ab</sup>	0.82 $\pm$ 0.3 <sup>b</sup>	1.2 $\pm$ 0.6 <sup>a</sup>	5.28	0.03	6.82 $\pm$ 1.8
	Coptacrinae						
	<i>C. hopei</i>	0	0.37 $\pm$ 0.3	0	0.16	0.36	0.37 $\pm$ 0.3
Oxyinae							
<i>D. fasciata</i>	0.85 $\pm$ 0.4	1.14 $\pm$ 0.6	0.35 $\pm$ 0.3	0.65	0.51	2.34 $\pm$ 0.09	
<i>P. apicalis</i>	1.7 $\pm$ 0.6	0.86 $\pm$ 0.4	0.92 $\pm$ 0.4	0.76	0.56	3.48 $\pm$ 1.07	
Pyrgomorphidae	Pyrgomorphinae						
	<i>P. femorata</i>	0	0	0.57 $\pm$ 0.4	0.64	0.12	0.57 $\pm$ 0.4
	<i>T. ferruginea</i>	0	0.17 $\pm$ 0.1	0			0.17 $\pm$ 0.1
H-value		62.5	50.02	37.62			85.58
P-value		<0.0001	<0.0001	<0.0001			<0.0001
Total		35.5 $\pm$ 2.8 <sup>b</sup>	47.7 $\pm$ 3.0 <sup>c</sup>	16.8 $\pm$ 2.3 <sup>a</sup>	23.49	<0.0001	100

The same letter between two sites shows no significant difference between the values.

**Fig. 4.** Abundance distribution model of species in the different forests. A. Ongot; B. Zamakoe; C. Ngutadjap.

465 individuals, 72 (16.8  $\pm$  2.3%) were collected from the low anthropized forest of Ngutadjap, 167 (35.5  $\pm$  2.8%) from the more anthropized forest of Ongot, and 226 (47.7  $\pm$  3.0%) from the moderately anthropized forest of Zamakoe (Table 3). The mean abundances were significantly higher (H = 23.49, P < 0.0001) in the grasshopper community from Zamakoe, and significantly lower in that of Ngutadjap. *Mazea granulosa* reported from all localities was the most abundant species (79.2%) (Table 3). The abundance of this species significantly differed among the three sites (H = 22.02, P < 0.0001): 11.7% in Ngutadjap, 26.4% in Ongot, and 41.1% in Zamakoe (Table 3). The common species *Holopercna gerstaeckeri* and *Serpusia opacula* were less abundant than *M. granulosa*. All other species were present with very low abundances in the different sites studied (Table 3).

**Abundance distribution models.**—The grasshopper species collected during this study were distributed into seven abundance ranks in the Ongot and Ngutadjap forests and in nine abundance ranks in Zamakoe forest. The distribution models of species abundance from the target localities were very different from the geometric model of Motomura: Ongot ( $\chi^2 = 53.3$ ; P < 0.001; Fig. 4A), Zamakoe ( $\chi^2 = 562.2$ ; P < 0.001; Fig. 4B), and Ngutadjap ( $\chi^2 = 30.6$ ; P < 0.001; Fig. 4C); the broken stick of MacArthur model: Ongot ( $\chi^2 = 88.6$ ; P < 0.001; Fig. 4A), Zamakoe ( $\chi^2 = 290.8$ ; P < 0.001; Fig. 4B), and Ngutadjap ( $\chi^2 = 27.4$ ; P < 0.001; Fig. 4C). All the observed abundance distribution models were closer to, though slightly different from, Fisher' log-series distribution model: Ongot ( $\chi^2 = 17.1$ ; P = 0.002; Fig. 4A), Zamakoe ( $\chi^2 = 110.5$ ; P < 0.001; Fig. 4B), and Ngutadjap ( $\chi^2 = 11.1$ ; P = 0.011; Fig. 4C). The rare

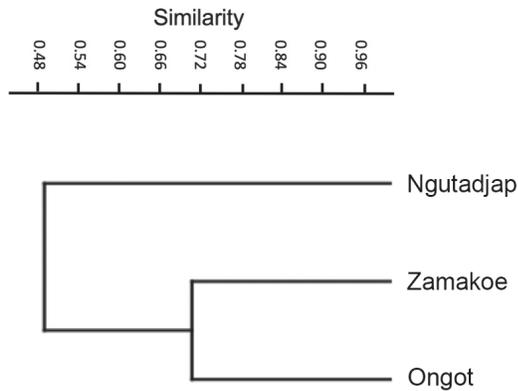


Fig. 5. Similarity between the different forest grasshopper communities using the Bray-Curtis index.

species (average relative abundance <1%) accounted for 58% of the species collected in all three of the studied forests.

**Diversity.**—The dominance index showed that there are fewer dominant species in Zamakoe (0.71) than in Ongot (0.54) and Ngutadjap (0.47) (Table 2). The Shannon diversity index (H) was higher at Zamakoe (H = 1.18, H/Hmax = 0.23) followed by Ongot (H = 0.97, H/Hmax = 0.38) and lower at Ngutadjap (H = 0.73, H/Hmax = 0.46) (Table 2). The Shannon diversity index of grasshopper communities of Zamakoe and Ngutadjap forests were significantly different (t = 14.3, P = 0.005) (Table 2). All the above shows that the species diversity has increased with the level of forest degradation in the study site.

**Similarity.**—The cluster analysis based on species composition performed on the basis of Bray-Curtis index revealed that the grasshopper communities of Zamakoe and Ongot forests are more similar to each other (Fig. 5). The disposition of species by cor-

respondence analysis shows that most of the species studied were closer to these two most degraded forests of Ongot and Zamakoe (Fig. 6). *A. degener* was specific to Ongot; *P. carnapi*, *C. hopei*, and *T. ferruginea* were specific to Zamakoe; and *G. opilionoides* and *P. femorata* were specific to Ngutadjap (Fig. 6).

**Discussion**

**Species richness and sampling effort.**—The sampling efforts were high, varying between 87% and 93% in the forests studied, with no significant difference, which is consistent with the statement of Branson (2011) that evaluation and comparison of grasshopper diversities requires that all regions and ecosystems be studied in the same way. The species accumulation curve of each forest started to flatten out towards the end of the sampling period; this shows that almost all the species had been collected: all the common species were sampled. The missing species are likely to be all rare taxa corresponding to the expected low abundance nature of tropical forest faunas.

Overall, 12 species were identified: seven in Ngutadjap and Ongot and nine in Zamakoe. Seino et al. (2013) and Kekeunou et al. (2017) have identified, respectively, 28 and 27 species in the mountainous area of West Cameroon. This considerable difference in species richness can be explained by the fact that (1) previous studies collected grasshoppers in both fallows and forests and (2) the works cited were conducted in the upland area of western Cameroon with two climatic seasons, while we carried out the present work in the southern Cameroon plateau with four climatic seasons. The structure, biology, and ecology of the grasshopper communities are logically expected to be different in the two different habitats.

Grasshoppers are indeed recognized as abundant insects in open environments, which may explain the low species richness observed in our work. Joubert et al. (2016) recently reported that grasshoppers constitute a significant proportion of invertebrate diversity in grasslands; their abundance increases with burning, cattle grazing, and short vegetation. Spungis (2007) and Arya et

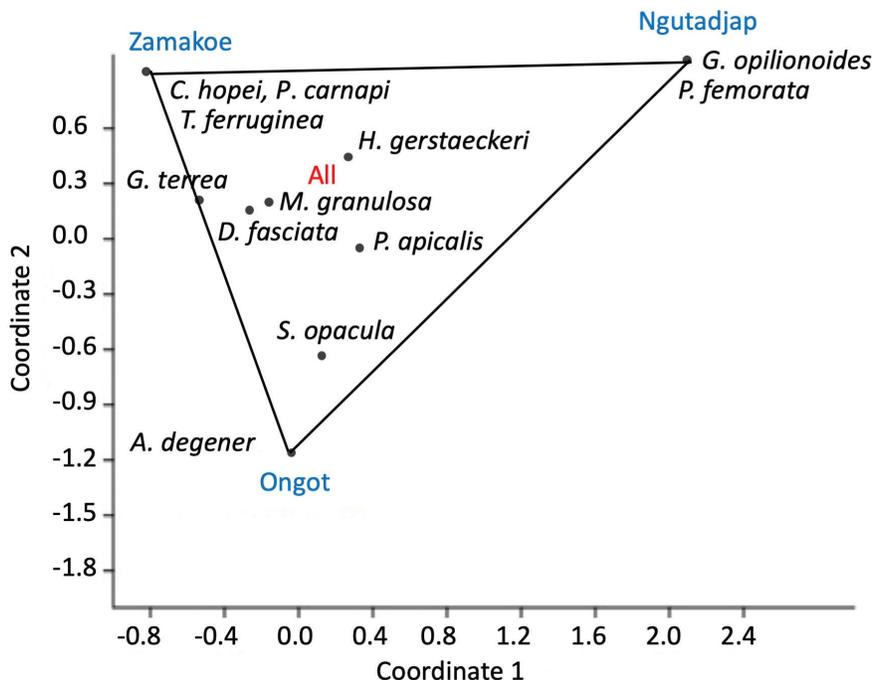


Fig. 6. Disposition of species between the different study sites using correspondence analysis.

al. (2015) also carried out studies in forests and found 14 and 12 species of grasshoppers identified, respectively, in the Western Himalaya in India and in the Ziemupe Nature Reserve forest in Latvia; the number of species of grasshoppers collected in these studies are similar to ours. Nevertheless, Raghavender and Vastrad (2017) report a high species richness, 30 species, in the forest of Dharwad in India. This difference may be explained by differences in the climate, types of vegetation, and grasshopper communities between southern Cameroon and the Dharwad region in India. In our study, the families were Acrididae (10 species) and Pyrgomorphidae (two species). Dirsh (1965, 1966, 1970) and Mestre and Chiffaud (2009) showed that these two taxa are the main acridid families in the fauna of both Cameroon and Congo Basin.

In the same way, Seino et al. (2013) and Kekeunou et al. (2017) found that Acrididae (18 and 22 species, respectively) and Pyrgomorphidae (four and six species, respectively) are the more speciose families in West Cameroon. The same results were given by Almeida and Câmara (2008) in Brazil, and by Arya et al. (2015), More and Nikam (2016), and Raghavender and Vastrad (2017) in India. The Catantopinae was the richest subfamily in the study areas with three species in Ngutadzap and four species in Zamakoe and Ongot. Seino et al. (2013) reported this subfamily as most speciose in West Cameroon. After the Oedipodinae, the Catantopinae was also the richest subfamily in both agriculture and forest ecosystems of Dharwad, India (Raghavender and Vastrad 2017). The above results are consistent with the findings by Dirsh (1965) more than fifty years ago in Cameroon and in Africa.

*Relative abundance and abundance distributions.*—The abundance of grasshoppers in the three study sites increased with human pressure. In fact, it is already known that grasshopper abundance increases in dry grassland habitats and forests used by humans (Latchininsky and Gapparov 1996, 2011, Spungis 2007, Latchininsky 2008). These results contrast with those of Soliman et al. (2017) who reported higher species richness, abundance, and diversity in the less disturbed sites in South Cairo, Egypt. We can therefore assume that the behavior of grasshoppers in response to the environmental disturbances is influenced by the eco-climatic zone and the structure of plant and even animal communities.

In fact, ecosystem changes strongly affect behavior, especially of poikilotherms such as grasshoppers that feed on plant materials (Bronwyn 2013). The increase in abundance as the forest is opened up by human agency that was observed in our work is not due to an invasion by grassland or forest edge species, but of forest forms due to increased light penetration and, thus, a change in understory vegetation. The positive correlations that exist between the population density of grasshoppers and plant species diversity can be explained by both feeding and sheltering requirements of grasshoppers (Spungis 2007).

Disturbed and new habitats can be important for the spreading of some grasshopper forms (Samways et al. 1997, Sergeev 1998, Latchininsky et al. 2011). At the same time, some grasshopper species are threatened by anthropogenic pressures, such as overgrazing and ploughing (Latchininsky and Gapparov 1996, 2011, Sergeev 1998). The abundance distribution of the species observed in this work were most similar to, though slightly different from, Fisher' log-series distribution model. Therefore, species with low abundance were the most numerous in the forests studied compared to the most abundant ones or those with intermediate abundance (Havyarimana et al. 2013). This distribution model shows that although they had different levels of utilization and degradation,

these three forest ecosystems are disturbed by human activities (Hughes 1986). Under these conditions, the available resources may be immobilized by a small number of species that develop strategies of resistance to human disturbances (Ramade 2009, Cielo Filho et al. 2012, Havyarimana et al. 2013); this was the case of *M. granulosa*, *S. opacula*, and *H. gerstaeckeri* in the forests studied. The other species are relegated to the unfavorable areas (Ramade 2009), as was the case with *G. opilionoides* and *P. femorata*, two very rare species found only in the less degraded forest of Ngutadzap. It therefore seems necessary to reconstitute and conserve these different ecosystems in order to protect this forest biodiversity and its trophic structure.

*Diversity and similarity.*—In this work, species diversity increased with the level of human activity and use of forest resources: it was higher in the more anthropized forests of Zamakoe and Ongot and lower in the less anthropized forest of Ngutadzap. This result is presented by our cluster analysis based on species composition. Steer et al. (2009) also observed an increase in the invertebrate diversity, especially of diurnal Lepidoptera, with the level of forest degradation in Madagascar. Recently, Soliman et al. (2017) also reported significant differences between grasshopper community structures in moderately and highly disturbed sites in India, using one-way analysis of similarity. We therefore assume that invertebrate communities, especially of insects, are strongly influenced by increased human activities in forest ecosystems around the world; these invertebrates are recognized worldwide as indicative of the levels of natural habitat degradation (Clayton 2002, Gebeyehu and Samways 2003, Steck et al. 2007, Sirin et al. 2010, Chen et al. 2011).

## Acknowledgements

This work was financially supported by a Rufford Small Grant (ID application: 19665-1) from the Rufford Foundation. We thank Dr. C.H.F. Rowell for proofreading the manuscript.

## References

- Almeida AV, Câmara CAG (2008) Distribution of grasshoppers (Orthoptera: Acridoidea) in the Tapacurá ecological station (São Lourenço da Mata, PE/Brazil). *Brazilian Journal of Biology* 68: 21–24. <https://doi.org/10.1590/S1519-69842008000100004>
- Amou'ou JP, Melingui A, Mounkam J, Tchepannou A (1985) *Le Cameroun*. Armand Colin, Paris.
- Andersen AN, Ludwig JA, Lowe LM, Rentz DCF (2001) Grasshopper biodiversity and bioindicators in Australian tropical savannas: Responses to disturbance in Kakadu National Park. *Austral Ecology* 26: 213–222. <https://doi.org/10.1046/j.1442-9993.2001.01106.x>
- Armstrong AJ, van Hensbergen HJ (1997) Evaluation of afforestable montane grasslands for wildlife conservation in the north-eastern Cape, South Africa. *Biological Conservation* 81: 179–190. [https://doi.org/10.1016/S0006-3207\(96\)00034-1](https://doi.org/10.1016/S0006-3207(96)00034-1)
- Arya M K, Joshi PC, Vinod PB (2015) Species composition, abundance, density and diversity of grasshoppers (Insecta: Orthoptera) in a protected forest ecosystem in the Western Himalayas, India. *International Journal of Fauna and Biological Studies* 2: 42–46. <http://www.faunajournal.com/vol2Issue5/pdf/2-5-6.1.pdf>
- Basset Y, Aberlenc HP, Barrios H, Curletti G, Berenger JM, Vesco JP, Causse PA, Haug A, Hennion AS, Lesobre L, Marques F, O'Meara R (2001) Stratification and diel activity of arthropods in a lowland rainforest in Gabon. *Biological Journal of the Linnean Society* 72: 585–607. <https://doi.org/10.1111/j.1095-8312.2001.tb01340.x>
- Branson DH (2011) Relationships between plant diversity and grasshopper diversity and abundance in the Little Missouri National Grassland. *Psyche* 2011: 748635. <https://doi.org/10.1155/2011/748635>

- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* 27: 325–349. <https://doi.org/10.2307/1942268>
- Bronwyn AE (2013) Culturally and Economically Significant Insects in the Blouberg Region, Limpopo Province, South Africa. Dissertation, University of Limpopo, South Africa. <http://hdl.handle.net/10386/1002>
- Brown DR (2006) Personal preferences and intensification of land use: Their impact on southern Cameroonian slash-and-burn agroforestry systems. *Agroforestry Systems* 68: 53–67. <https://doi.org/10.1007/s10457-006-0003-9>
- Carlo HR, Help P, Herman MJ, Soetaert K (1998) Indices of diversity and evenness. *Oceanis* 24: 61–87.
- Chen Y, Li Q, Chen Y, Chen Z (2011) Effects of different land use on grasshopper diversity in lac agroecosystems. *Terrestrial Arthropod Reviews* 4: 255–269. <https://doi.org/10.1163/187498311X601704>
- Chinery M (1993) *Insects of Britain and Northern Europe*. Harper Collins Publishers, New York.
- Cielo Filho R, Martins FR, Gneri MA (2012) Fitting abundance distribution models in tropical arboreal communities of SE Brazil. *Community Ecology* 3: 169–180. <https://doi.org/10.1556/ComEc.3.2002.2.4>
- Clayton JC (2002) The effects of clear cutting and wildfire on grasshoppers and crickets (Orthoptera) in an intermountain forest ecosystem. *Journal of Orthoptera Research* 11: 163–167. [https://doi.org/10.1665/1082-6467\(2002\)011\[0163:TEOCAW\]2.0.CO;2](https://doi.org/10.1665/1082-6467(2002)011[0163:TEOCAW]2.0.CO;2)
- Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. <http://viceroy.eeb.uconn.edu/estimates>
- de Wasseige C, de Marcken P, Bayol N, Hiol Hiol E, Mayaux Ph, Desclée B, Nasi R, Billand A, Defourny P, Eba'a Atyi R (2012) Les Forêts du Bassin du Congo – État des Forêts 2010. Office des publications de l'Union européenne, Luxembourg. <https://doi.org/10.2788/48830>
- Dirsh VM (1956) The phallic complex in Acridoidea (Orthoptera) in relation to taxonomy. *Transactions of the Royal Entomological Society of London* 108: 223–356. <https://doi.org/10.1111/j.1365-2311.1956.tb02270.x>
- Dirsh VM (1961) A preliminary revision of the families and subfamilies of Acridoidea (Orthoptera, Insecta). *Bulletin of the British Museum (Natural History) Entomology* 10: 351–419. <https://doi.org/10.5962/bhl.part.16264>
- Dirsh VM (1965) *The African Genera of Acridoidea*. Cambridge University Press, Cambridge.
- Dirsh VM (1966) Acridoidea of Angola. *Publicações Culturais da Companhia de Diamantes de Angola* 74: 1–727.
- Dirsh VM (1970) Acridoidea of the Congo (Orthoptera). *Annales du Musée Royal d'Afrique Centrale, Tervuren, Serie in-8-Science Zoologiques-n° 182*: 1–605.
- Gangwere SK, Muralirangan MC, Muralirangan M (1997) *The Bionomics of Grasshoppers, Katydid and Their Kin*. CAB International, Wallingford.
- Gebeyehu S, Samways MJ (2003) Responses of grasshopper assemblages to long-term grazing management in a semi-arid African savanna. *Agriculture, Ecosystems & Environment* 95: 613–622. [https://doi.org/10.1016/S0167-8809\(02\)00178-0](https://doi.org/10.1016/S0167-8809(02)00178-0)
- Gillon Y (1983) The invertebrates of the grass layer. In: Bourlière F (Ed) *Ecosystems of the World (Vol. 13). Tropical Savannas*. Elsevier, Amsterdam, 289–311. <http://www.documentation.ird.fr/hor/fdi:17364>
- Gockowski JJ (1996) Quelques données de l'enquête agricole dans les villages de recherche. Programme EPHTA en collaboration avec l'IRAD/ASB. IITA-Yaoundé, Cameroon.
- Guido M, Gianelle D (2001) Distribution patterns of four Orthoptera species in relation to microhabitat heterogeneity in an ecotonal area. *Acta Oncologica* 22: 175–185. [https://doi.org/10.1016/S1146-609X\(01\)01109-2](https://doi.org/10.1016/S1146-609X(01)01109-2)
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 1–9. [http://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm)
- Havyarimana F, Bigendako MJ, Masharabun T, Bangirirama F, Lejoly J, Barima YSS, De Cannière C, Bogaert J (2013) Diversité et distribution d'abondances des plantes d'un écosystème protégé dans un paysage anthropisé: cas de la Réserve Naturelle Forestière de Bururi, Burundi. *Tropicultura* 31: 28–35. <http://hdl.handle.net/2268/160257>
- Hollis D (1975) A review of the subfamily Oxyinae (Orthoptera: Acridoidea). *Bulletin of the British Museum (Natural History) Entomology* 31: 189–234. <https://doi.org/10.5962/bhl.part.29486>
- Hughes RG (1986) Theories and models on species abundance. *The American Naturalist* 128: 879–899. <https://doi.org/10.1086/284611>
- Hutcheson K (1970) A test for comparing diversities based on the Shannon formula. *Journal of Theoretical Biology* 29: 151–154. [https://doi.org/10.1016/0022-5193\(70\)90124-4](https://doi.org/10.1016/0022-5193(70)90124-4)
- Jago ND (1967) A key to the grasshopper species (Orthoptera: Acridoidea) recorded from Ghana. *Transactions of the Royal Entomological Society of London* 119: 235–266. <https://doi.org/10.1111/j.1365-2311.1967.tb00511.x>
- Joubert L, Pryke JS, Samways MJ (2016) Positive effects of burning and cattle grazing on grasshopper diversity. *Insect Conservation and Diversity* 9: 290–301. <https://doi.org/10.1111/icad.12166>
- Kekeunou S, Membou DT, Tamesse JL, Oumarou Ngoute C (2017) Acrididae diversity in degraded areas of higher mountains in West Cameroon. *African Entomology* 25: 239–243. <https://doi.org/10.4001/003.025.0239>
- Kemp WP, Harvey SJ, O'Neill KM (1990) Patterns of vegetation and grasshopper community composition. *Oecologia* 83: 299–308. <https://doi.org/10.1007/BF00317552>
- Kevan DKM (1975) A revision of the genus *Taphronota* Stål, 1873 (Orthoptera: Acridoidea; Pyrgomorphidae). *Publicações Culturais da Companhia de Diamantes de Angola* (1974) 88: 79–150.
- Latchinsky AV (2008) Grasshopper outbreak challenges conservation status of a small Hawaiian Island. *Journal of Insect Conservation* 12: 343–357. <https://doi.org/10.1007/s10841-008-9143-8>
- Latchinsky A, Gapparov FA (1996) Les conséquences du dessèchement de la mer d'Aral sur la situation acridienne dans la région. *Sécheresse* 7: 109–113.
- Latchinsky A, Sword GA, Sergeev MG, Cigliano MM, Lecoq M (2011) Locusts and grasshoppers: Behavior, ecology and biogeography. *Psyche* 2011: 578327. <https://doi.org/10.1155/2011/578327>
- Lecoq M (1980) Clés de détermination des acridiens des zones sahélienne et soudanienne en Afrique de l'Ouest. *Bulletin de l'Institut Fondamental d'Afrique Noire* (1979) 41/A/3: 531–595.
- Marcon E (2015) Mesures de la biodiversité. UMR Écologie des forêts de Guyane, Kourou. <http://hal-agroparistech.archives-ouvertes.fr/cel-01205813v4>
- Mbenoun Masse PS, Nzoko Fiemapong AR, VandenSpiegel D, Golovatch IS (2017) Diversity and distribution of millipedes (Diplopoda) in the Campo Ma'an National Park, southern Cameroon. *African Journal of Ecology* 56: 73–80. <https://doi.org/10.1111/aje.12418>
- Mertens B, Neba SG, Steil M, Tessa B, Mendo B, Leach A, Mboua D, Mboua P, Feuzing A, Methot P, Minnemeyer S, Douard P, Ngilambi H (2012) *Atlas Forestier Interactif du Cameroun*. World Resources Institute, Washington DC.
- Mestre J, Chiffaud J (2009) Acridiens du Cameroun et de République centrafricaine (Orthoptera Caelifera). *Supplément au catalogue et atlas des acridiens d'Afrique de l'Ouest*. <http://acrida.info/PDF2009/Catalogue-Acridiens-2009.pdf>
- More SV, Nikam KN (2016) Studies on grasshoppers (Orthoptera) in Tilar forest, Chandgad, Kolhapur district of Maharashtra (India). *International Journal of Recent Scientific Research* 7: 9457–9460. [http://www.recentscientific.com/sites/default/files/4578\\_0.pdf](http://www.recentscientific.com/sites/default/files/4578_0.pdf)
- Ndoye O, Kaimowitz D (2000) Macro-economics, markets and the humid forests of Cameroon, 1967–1997. *Journal of Modern African Studies* 38: 225–253. <https://doi.org/10.1017/S0022278X00003347>
- Otte D (1976) Species richness patterns of new world desert grasshoppers in relation to plant diversity. *Journal of Biogeography* 3: 197–209. <https://doi.org/10.2307/3038010>

- Raghavender B, Vastrad AS (2017) Changing scenario of short horned grasshopper diversity in agriculture and forest ecosystems in Dharwad. *Journal of Entomology and Zoology Studies* 5: 268–272. <http://www.entomoljournal.com/archives/2017/vol5issue2/PartD//5-1-138-321.pdf>
- Ramade F (2009) *Eléments d'écologie: Ecologie fondamentale* (4<sup>th</sup> edn). Dunod.
- Saha HK, Haldar P (2009) Acridids as indicators of disturbance in dry deciduous forest of West Bengal in India. *Biodiversity and Conservation* 18: 2343–2350. <https://doi.org/10.1007/s10531-009-9591-9>
- Samways MJ (1997) Conservation biology of Orthoptera. In: Gangwere SK, Muralirangan MC, Muralirangan M (Eds) *The Bionomics of Grasshoppers, Katydid and their Kin*. CAB International, Wallingford, 481–496.
- Santoir C, Bopda A (1995) *Atlas régional Sud-Cameroun*. Orstom/Minrest, Paris/Yaoundé. <http://www.documentation.ird.fr/hor/fdi:010004189>
- Schmidt GH, Ibrahim NM, Abdallah MD (1991) Toxicological studies on the long-term effects of heavy metals (Hg, Cd, Pb) in soil on the development of *Aiolopus thalassinus* (Fabr.) (Saltatoria: Acrididae). *Science of the Total Environment* 107: 109–133. [https://doi.org/10.1016/0048-9697\(91\)90254-C](https://doi.org/10.1016/0048-9697(91)90254-C)
- Scott DM, Brown D, Mahood S, Denton B, Silburn A, Rakotondraparany F (2006) The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar. *Biological Conservation* 127: 72–87. <https://doi.org/10.1016/j.biocon.2005.07.014>
- Seino RA, Dongmo TI, Ghogomu RT, Kekeunou S, Chifon RN, Manjeli Y (2013) An inventory of short horn grasshoppers in the Menoua Division, West Region of Cameroon. *Agriculture and Biology Journal of North America* 4: 291–299. <https://doi.org/10.5251/abjna.2013.4.3.291.299>
- Sergeev MG (1998) Conservation of orthopteran biological diversity relative to landscape change in temperate Eurasia. *Journal of Insect Conservation* 2: 247–252. <https://doi.org/10.1023/A:1009620519058>
- Sirin D, Eren O, Çiplak B (2010) Grasshopper diversity and abundance in relation to elevation and vegetation from a snapshot in Mediterranean Anatolia: Role of latitudinal position in altitudinal differences. *Journal of Natural History* 44: 1343–1363. <https://doi.org/10.1080/00222930903528214>
- Soliman MM, Haggag AA, El-Shazly MM (2017) Assessment of grasshopper diversity along a pollution gradient in the Al-Tebbin region, South Cairo, Egypt. *Journal of Entomology and Zoology Studies* 5: 298–306.
- Song H (2010) Grasshopper systematics: Past, present and future. *Journal of Orthoptera Research* 19: 57–68. <https://doi.org/10.1665/034.019.0112>
- Spungis V (2007) Fauna and ecology of grasshoppers (Orthoptera) in the coastal dune habitats in Ziemupe Nature Reserve, Latvia. *Latvian entomologists* 44: 58–68. <http://leb.daba.lv/44-sp1.pdf>
- Steck CE, Bürgi M, Bolliger J, Kienast F, Lehmann A, Gonseth Y (2007) Conservation of grasshopper diversity in a changing environment. *Biological Conservation* 138: 360–370. <https://doi.org/10.1016/j.biocon.2007.05.001>
- Steer MD, Vater A, McCann-Wood S (2009) The effect of forest degradation on the species richness and diversity of a diurnal Lepidoptera community in Northern Madagascar. *Frontier – Madagascar Environmental Research, Report 22*. The Society for Environmental Exploration, London. [http://frontier.ac.uk/Publications/Files/2010\\_11\\_23\\_13\\_51\\_51\\_235.pdf](http://frontier.ac.uk/Publications/Files/2010_11_23_13_51_51_235.pdf)
- Tadu Z, Djiéto-Lordon C, Babin R, Yede, Messop-Youbi EB, Fomena A (2013) Influence of insecticide treatment on ant diversity in tropical agroforestry system: Some aspect of the recolonization process. *International Journal of Biodiversity and Conservation* 5: 832–844. [https://agritrop.cirad.fr/572130/1/document\\_572130.pdf](https://agritrop.cirad.fr/572130/1/document_572130.pdf)
- Tadu Z, Djiéto-Lordon C (2014) Ant diversity in different cocoa agroforest habitats in the centre region of Cameroon. *African Entomology* 22: 388–404. <https://doi.org/10.4001/003.022.0219>
- Tchatchou B, Sonwa DJ, Ifo S, Tiani AM (2015) Deforestation and Forest Degradation in the Congo Basin: State of Knowledge, Current Causes and Perspectives. Occasional paper 144, Center for International Forestry Research, Bogor. <https://doi.org/10.17528/cifor/005894>
- Torrusio S, Cigliano MM, De Wysiecki ML (2002) Grasshopper (Orthoptera: Acridoidea) and plant community relationships in the Argentine pampas. *Journal of Biogeography* 29: 221–229. <https://doi.org/10.1046/j.1365-2699.2002.00663.x>
- Westphal E, Embrechts J, Mbouemboue P, Westphal-Stevens JMC, Mouzong-Boyomo (1981) L'agriculture autochtone au Cameroun; les techniques culturelles, les séquences de culture, les plantes alimentaires et leur consommation. *Miscellaneous papers 20-Landbouwhogeschool, Wageningen*.
- Yelland PM (2010) An Introduction to Correspondence Analysis. *The Mathematica Journal* 12: 1–23. <https://doi.org/10.3888/tmj.12-4>
- Zhang ZQ (2011) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa* 3148: 1–237.

#### Supplementary material 1

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Data type: plant species richness

Explanation note: Effect of anthropogenic pressures on floristic composition from the forests of three localities of southern Cameroon.

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Link: <https://doi.org/10.3897/jor.29.33373.suppl1>

## Appendix 1

Species composition and abundance of the grasshopper species in different seasons (Srs: Short rainy season; Sds: Short dry season; Lrs: Long rainy season; Lds: Long dry season).

Taxon	Srs (n = 2)	Sds (n = 2)	Lrs (n = 1)	Lds (n = 1)	Total
Caelifera					
Acridoidea					
Acridomorpha					
Acrididae					
Acridinae					
<i>Holopercna gerstaeckeri</i> (Bolivar, 1980)	9	13	3	1	26
Catantopinae					
<i>Apoboleus degener</i> Karsch, 1891	0	0	2	0	2
<i>Gemeneta opilionoides</i> (Bolivar, 1905)	0	0	2	0	2
<i>Gemeneta terrea</i> Karsch, 1892	1	1	1	0	3
<i>Mazaea granulosa</i> Stål, 1876	93	71	89	104	357
<i>Pteropera carnapi</i> Ramme, 1929	0	4	1	0	5
<i>Serpusia opacula</i> Karsch, 1891	8	15	8	7	38
Coptacrinae					
<i>Cyphocerastis hopei</i> Brunner, 1920	1	0	0	0	1
Oxyinae					
<i>Digentia fasciata</i> Ramme, 1929	5	1	3	2	11
<i>Pterotiltus apicalis</i> Bolívar, 1905	6	4	0	5	15
Pyrgomorphidae					
Pyrgomorphinae					
<i>Parapetasia femorata</i> Bolivar, 1884	3	1	0	0	4
<i>Taphronota ferruginea</i> (Fabricius, 1791)	0	1	0	0	1
Site					
Ongot	39	47	34	47	167
Zamakoe	58	49	64	55	226
Ngutadjap	29	15	11	17	72
<b>Total</b>	<b>126</b>	<b>111</b>	<b>109</b>	<b>119</b>	<b>465</b>

n indicates the number of seasons sampled.

# Mating behavior of the Persian boxer mantid, *Holaptilon brevipugilis* (Mantodea: Mantidae)

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Academic editor: *Matan Shelomi* | Received 21 June 2019 | Accepted 7 July 2019 | Published 13 March 2020

<http://zoobank.org/5F48711C-1B2D-421F-826E-C07AE90CB62D>

Citation: Kolnegari M (2020) Mating behavior of the Persian boxer mantid, *Holaptilon brevipugilis* (Mantodea: Mantidae). Journal of Orthoptera Research 29(1): 35–39. <https://doi.org/10.3897/jor.29.37595>

## Abstract

The Persian boxer mantid, *Holaptilon brevipugilis*, is the mantid most recently described from Iran. Here, I present some aspects of the courtship display and mating behavior of this species. I conducted 28 mating trials, quantified the relative frequency of all mating behaviors, and estimated the pre-copulation, copulation, and post-copulation periods. I also compared the effects of frontal vs. lateral approaches of the male for mating success, since frontal approach increases the risk that the male will be seen and cannibalized by the female. In 64% of trials, the male approached the female immediately, regardless of whether the female could see him or not. Copulation was successful in 61% of trials. Male courtship consisted of dorsoventral bending of the male's abdomen and occurred in 10% of all trials, but only when the female was facing the male. In contrast, trembling of the forelimbs was not associated with copulation, occurred in 10% of all trials, and was always followed by the male moving away from the female. I observed one female cannibalizing a male post-copulation. The Persian boxer mantid might be sexually cannibalistic, but confirming this hypothesis would require further studies, including a focus on female hunger level as a determining factor in sexual cannibalism and in male courtship behaviors.

## Keywords

courtship, deimatic behavior, experiment, forelimb trembling, Iran, sexual cannibalism

## Introduction

Descriptions of courtship displays and their prevalence are relatively rare for Mantodea (Battiston 2008). The mating behavior of mantids can be divided into two main categories: male-originated mating behavior, or courtship; and female-originated mating behavior, or sexual cannibalism. These two types are interconnected. A higher likelihood of sexual cannibalism can increase the rate of courtship and, consequently, courting decreases the probability of sexual cannibalism (Maxwell 1998, Lelito and Brown 2006, Barry et al. 2008b, Jayaweera et al. 2015, Kadoi et al. 2017). The structure of courtship and the frequency of sexual cannibalism were the subjects of a few research studies (Edmunds 1975, Loxton 1979,

Liske and Davis 1987, Battiston 2008). Male-originated courtship often includes movement of body parts when approaching the female. Some of these courtship movements include “boxing” of the prothoracic legs by *Oxyphilus hamatus* Roy (Edmunds 1975), “semaphore” and “stamping” with the metathoracic legs by *Ephestiasula amoena* (Bolivar) (Loxton 1979) and *Acontiothespis multicolor* (Saussure) (Quesnel 1967), “pumping” and “weaving” of the abdomen by *Tenodera aridifolia sinensis* (Saussure) (Liske and Davis 1987), and “trembling” by *Oligonyx insularis* Bonfils (Bonfils 1967). Female attacks on a male can occur before, during, and after copulation (Lelito and Brown 2006, Jayaweera et al. 2015). The frequency of sexual cannibalism differs from one species to another (Maxwell 1999) and can be affected by factors such as female hunger levels and the approach direction of the males (Maxwell 1998, Barry et al. 2008a).

In this study, I focused on courtship and sexual cannibalism in a recently described mantid species, *Holaptilon brevipugilis* Kolnegari, or the Persian boxer mantid. *H. brevipugilis* belongs to a rare genus, having just one identified congeneric species with a small distribution range (Beier 1964, Abu-Dannoun and Katbeh-Bader 2007, Kolnegari and Vafaei-shoushtari 2018). This wingless species, which was recently discovered in the center of Iran, is one of the smallest mantids in the world with a body size range of 1.2–1.6 cm (Roy 1999, Kolnegari and Vafaei-shoushtari 2018). The name of the species comes from the occasional trembling movement of its oversized grasping forelimbs. Such behavior was observed in both males and females, though it is apparently more frequent in males (Kolnegari and Vafaei-shoushtari 2018). The behavior was observed in the laboratory mostly during encounters with other individuals (different- or same-sex), and rarely arose before hunting prey (e.g., housefly). In addition, numerous males and females were observed performing characteristic forelimb movement during specimen collection from their wild habitat, but this behavior was not associated with escape from collectors nor encounters with other mantids or prey.

The main question of this study is whether foreleg trembling has a determinative function in the mating process of the mantid as a possible courtship display (Bonfils 1967, Edmunds 1975, Battiston 2008). Additional questions include whether or not, and how frequently, female-originated sexual cannibalism occurs in

boxer mantids. Elucidating the behavioral complexities of mating in this species could help to inform the systematic position and evolutionary history of this rare genus.

## Materials and methods

I collected adult individuals of *Holoptilon brevipugilis* from their only known habitat around Arak City, Iran, during June–July 2017. I collected 28 males and 28 females and reared them on a diet of one small housefly (*Musca domestica*) three times a week. Animals were kept individually within well-ventilated, 30-cm-diameter opaque plastic containers in the laboratory, at a temperature of 20–22°C. The same conditions were used for 28 staged mating trials that allowed an observation of general male mating behavior. I paid particular attention to behaviors such as courtship display, approach pattern, jumping distance, male mating success, and copulation duration.

Habitat structure, particularly the type of flora, can impact mating behavior based on the objects the mantids are situated on (Younes 2007, Battiston 2008). The boxer mantid in the wild resides in a stony habitat covered with low vegetation. Fortunately, I was able to easily rebuild this environment in the laboratory. Following Liske and Davis (1987), I illuminated the mating arena in an otherwise darkened room. This enabled me to observe the behaviors without disturbing or stressing the mantids. Since hungry females are more likely to cannibalize males than well-fed females (Liske and Davis 1987, Hurd et al. 1994, Kadoi et al. 2017), I provided a satiating diet for females. Experimental pairs were randomly chosen for copulation three hours after feeding; therefore, females were not hungry during the mating experiments. Pairs were excluded after each trial, so each pair was used only once.

Approximately 30 min after the initial introduction of a female, a male was placed into the container at least 20 cm away from the female. If an interaction did not occur within three hours, the trial was terminated. Alternatively, if courtship and copulation occurred, then the male approach conditions and duration of mating were recorded. I examined the effects of two orientations of encounter on courtship behavior according to previous studies (Lelito and Brown 2006, Barry et al. 2008b, Battiston 2008). The approach orientations were 'frontal', where males approached the female from the front and faced her within her visual field of not more than 80°, and 'lateral', where the male approached from completely outside the female's visual field towards the rear of the female. These were established by placing the male in the container either in front of or laterally and somewhat behind the female. For each approach orientation, 14 trials were carried out.

I used a Canon SX240HS digital camera to record all trials, and a professional camera, Canon 7D (Mark 2), to take high-resolution photos of any notable behaviors. The variables measured included the distance from the female at detection, how the male detected the female (based on signs of abundant antennal movements or visual fixation), male jumping distance, pre-copulation duration, copulation duration, and post-copulation duration. I also paid attention to possible courtship behaviors as previously reported from other mantodeans, such as lateral swaying, abdomen bending, and rhythmic movements of legs. Due to possible directional changes by the sexes during the encounters, I considered the resulting direction instead of initial direction for jumping. I recorded pre-copulatory mounting duration as the time from mounting to the genital linkage, copulation duration as the time from linkage to separation of the genitalia, and post-copulation duration as the time from the end of intromission until the male leaped off the

female (according to Lelito and Brown 2006). I used multivariate ANOVA to analyze the data with SAS software (version 9.1). Mean and standard deviation were calculated with Microsoft Excel.

## Results

Components of male sexual behavior typically included the following: oscillation of antennae, visual fixation on the female, quick running, cessation of movement, repeated downward and upward bending of the abdomen, and jumping on the female's back from 2.2±0.4 cm away. The dorsoventral rhythmic movement of the male's abdomen was typical of courtship and started slightly downward (plantar flexion), then continued with an upward variable bending (dorsiflexion) at an angle of 0° to 90° (Fig. 1). The male sexual behavior was comprised of three phases.

*Phase 1: Male orientation.*—The initial approach occurred when a male sensed a female and began abundant antennal movements and prolonged viewing of her. These behaviors occurred within 15±1.9 cm of the females with no significant difference between frontal and lateral male release ( $F = 2.68$ ,  $df = 1, 22$ ,  $p = 0.4$ ). In five of the 28 trials (one frontal and four lateral), the males did not interact with the females within three hours; these were excluded from the dataset. Lateral swaying was not observed in any intersexual approaches during this experiment. Seventy-eight percent of males that noticed a female moved quickly toward the female. Sixty-seven percent of these moving males mounted without courtship. Twenty-two percent of males that noticed a female were motionless until the female began to advance. This behavior occurred more frequently in frontal encounters than lateral encounters (Fig. 2). Thirty-eight percent of initially frontal encounters changed to lateral encounters as males changed their approach route. Meanwhile, 20% of lateral encounters became frontal encounters because of female awareness and subsequently turning to face the male. Flexion of the abdomen and forelimb waving occurred only when males and females were facing each other. Regardless of initial approach, 21% of the trials ( $n = 6$ ) resulted in face-face encounters, which led males to display one of these rhythmic movement. While abdomen bending was a typical form of courtship, forelimb waving was not followed by mounting in the study.

Among frontal encounters ( $n = 13$ ), five males started to move then changed their orientation from frontal to lateral and stopped within 2.2±0.4 cm of females (i.e., "jumping distance"). Two males demonstrated flexion of the abdomen seven and eight times in 10 and 11 seconds, respectively, in what could be considered courtship behavior (Fig. 1), then reached the jumping point. Another two males responded to the female by trembling their forelimbs, displaying the patterned interior faces and waving them in slow arcs, before moving away from the female. Therefore, forelimb trembling did not seem to be a component of courtship. Four males did not move but waited for the female to approach to jumping distance.

Among lateral encounters ( $n = 10$ ), one male did not move and waited for the female to approach to jumping distance. Nine males moved towards the females. Two of these moving males faced the females frontally because she changed her direction. One of these two males demonstrated flexion of abdomen (six times in 11 seconds) and reached the jumping point, the other male trembled his forelegs before moving away from the female who followed after him (Fig. 3). The seven remaining males reached jumping distance and did not show rhythmic movement.

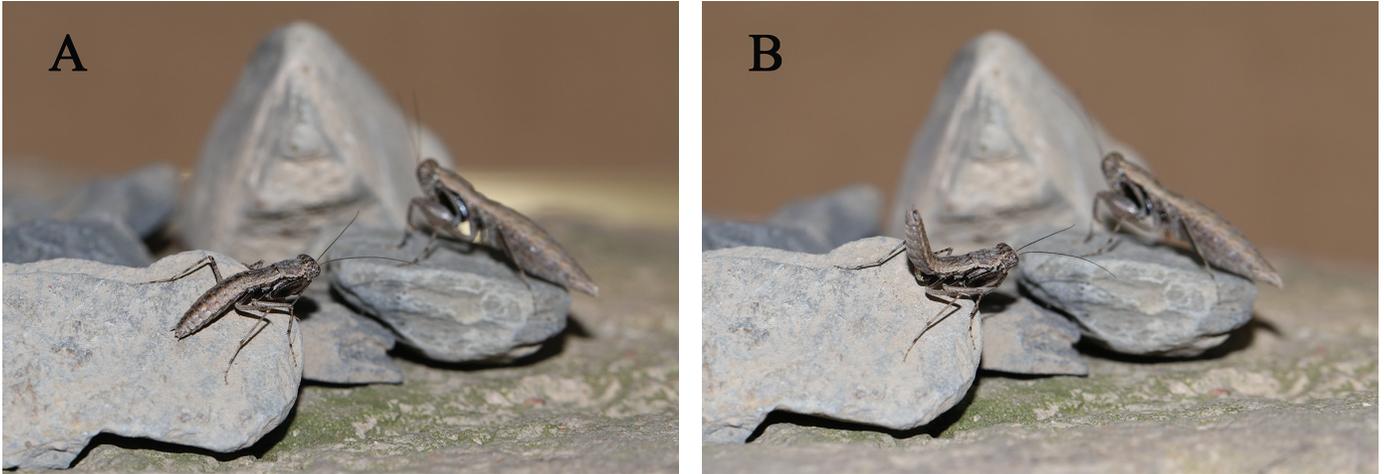


Fig. 1. Orientation of male *Holaptilon brevipugilis* abdomen in a frontal encounter with a female prior to copulation. A. Plantar flexion and B. Dorsiflexion of the abdomen. The male is in the foreground on the left and the female is to the rear and to the right of the male.

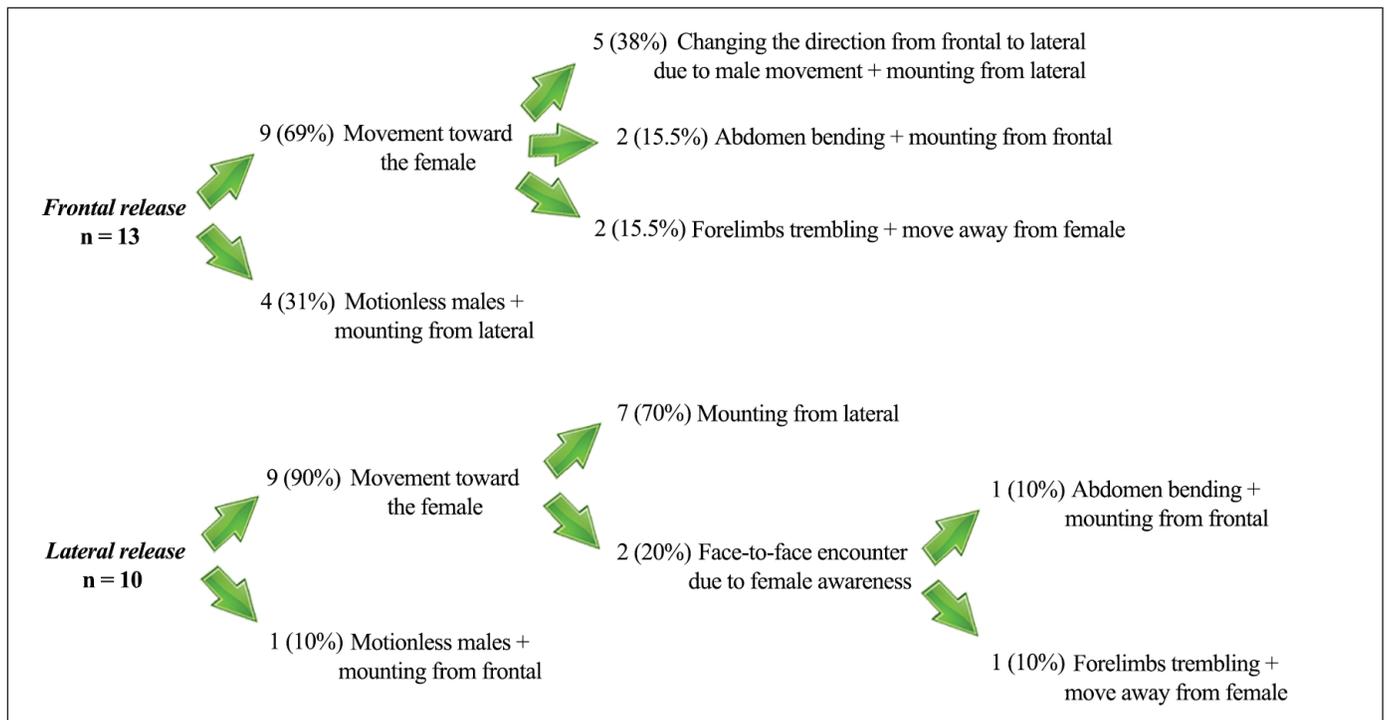


Fig. 2. The sequence of mating behavior of *Holaptilon brevipugilis* showing the number and the percentage of males at each stage. One frontal encounter and four lateral encounters did not lead to any interaction between males and females, so they were excluded from the dataset.

**Phase 2: Male mounting.**—This phase was characterized by males jumping onto the female for copulation (mounting) from a distance of  $2.2 \pm 0.4$  cm from the female. Nine males that initially encountered females laterally and eleven males that initially encountered females from a frontal position entered the mounting phase. Sixty percent of these males mounted the female from a lateral position and 40% mounted from a frontal (face-to-face) position. Almost all males leaped successfully, with just one male with a frontal orientation miscalculating the distance and lying under the female after jumping (Fig. 4A). The orientation prior to the jump had a significant effect on jumping distance ( $F = 8.43$ ,

$df = 1, 19, p = .017$ ), so males mounting from a frontal position leapt from greater distances than males mounting females from a lateral position.

**Phase 3: Copulation.**—As soon as the male mounted the female, he began the characteristic, approximately  $45^\circ$  angle S-bending mating movements of his abdomen similar to those described for *Tenodera aridifolia sinensis* (Liske and Davis 1987, Lelito and Brown 2006). There was an interesting bias in abdomen S-bending direction not mentioned in prior literature, as males preferred to bend the abdomen from the left side in 95% of trials (Fig. 4B).



Fig. 3. Trembling and showing the shiny colored surface of forefemora by a *Holaptilton brevipugilis* male during a frontal encounter with a female.



Fig. 4. Copulation behavior in *Holaptilton brevipugilis*. A. Male mounting failure. Male is underneath the female. B. Copulation. Smaller male is on top of the larger female.

Sixteen of the 28 trials led to copulations that occurred 5–28 seconds after mounting. One trial in which the male mounted in a reverse position delayed this pre-copulation period for more than four minutes. I terminated two trials after males mounted for 20–24 minutes but did not successfully contact the female's genitalia. Body measurement confirmed those two males (with 1.05 and 1.07 cm body length) were among the smallest males, while those two females (with 1.77 and 1.86 cm body length) were larger than the average female (1.6 cm body length).

Copulation lasted  $5.76 \pm 1.06$  hours and post-copulation duration was  $9.88 \pm 1.4$  minutes. Neither copulation duration nor post-copulation duration differed significantly between frontal and lateral encounters ( $F = 44.2$ ,  $df = 1, 17$ ,  $p = 0.71$  and  $F = 9.6$ ,  $df = 1, 17$ ,  $P = 0.26$ ).

I recorded just one case of cannibalism, which occurred after mating when a male separated from the female.

## Discussion

The male mantid presents a complicated series of mating behaviors, which can differ between species. These behaviors induce behavioral isolation as a barrier to mating with other species (reviewed in Gray 2005). Adult male Persian boxer mantids in this study performed a rather simple mating pattern that included

moving closer to the female and leaping onto her back from a conserved distance. Males most frequently mounted females from a lateral approach, consistent with the idea that males try to reduce the probability that they will be cannibalized during intersexual encounters by avoiding the visual field of females (Liske and Davis 1987, Maxwell 1998). However, in face-to-face encounters, males lifted and bent their abdomens, which may be a form of courtship. Male courtship frequency was inconsistent, which we would expect if males adjust their behaviors in ways that minimize the chance of being attacked (Jayaweera et al. 2015).

In this study, female *H. brevipugilis* rarely performed sexual cannibalism, though future studies could examine the effect of female hunger level on this behavior. *H. brevipugilis* nymphs did not have any cannibalistic activity (personal observation), and so it is possible that *H. brevipugilis* is an infrequently cannibalistic mantid. On the other hand, hungry females might not be able to easily consume males during copulation because of considerable sexual dimorphism, although this conclusion needs further investigation.

Orientation of approach had a significant effect on the Persian boxer mantid males' jumping distance, while Lelito and Brown (2006) found that factor did not have a significant effect on Chinese mantid (*Tenodera aridifolia sinensis* (Saussure)) male jumping distance. Increased male jumping distance decreases the likelihood of cannibalism (Lelito and Brown 2006), so future studies

on Persian boxer mantid should investigate the correlation of female hunger levels to male jumping distance. However, both the frequency of female-on-male cannibalism and the jumping distance of males in the Persian boxer mantid could be dependent on female hunger level and changeable under different conditions.

I did not identify when and why males and females of Persian boxer mantids performed foreleg trembling, but I concluded that this is not related to mating behavior because males that displayed this behavior tended to move away from the female rather than mating with her. However, forelimb trembling could demonstrate threat posture, which has been known as “deimatic behavior” in mantodeans (Maldonado 1970, Umbers et al. 2015) and could explain why this behavior was observed when specimens were being field collected. By contrast, males of *Ephestiasula amoena* (Bolivar) move their forelimbs to expose a bright pattern on the inside face of the expanded, plate-like forefemora before mating (Loxton 1979). Flexion of the abdomen, another rhythmic movement of Persian boxer mantid, is more likely associated with mating. Bending of the abdomen in *H. brevipugilis* follows a different pattern from *Hestiasula major* (Beier), which moves the abdomen laterally (personal observation). Additionally, the Persian boxer mantid male starts this rhythmic motion with a slightly downward movement (Fig. 1A), unlike *Pseudomantis albofimbriata* (Barry et al. 2008b) and *Tenodera sinensis* (Liske and Davis 1987) that show only upward abdomen bending.

I did not observe any lateral swaying or side-to-side movement in the boxer mantid, while this behavior is a component of *Pseudomantis albofimbriata* males’ sexual behavior (Barry et al. 2008b). The Persian boxer mantid’s flexion of the abdomen only occurred in some frontal encounters; however, Lelito and Brown (2006) observed this behavior in lateral encounters of *Tenodera aridifolia sinensis*, although they provided evidence that frontal encounters induced Chinese mantid males to bend their abdomens with a greater angle. In fact, both above-mentioned studies showed that frontal encounters increase the degree of the male’s movements.

In a broader context, courtship display has some correlations with taxonomic categories. “Abdomen movement” has been observed in all four studied species in the Mantidae family (*Holaptilon brevipugilis*, *Tenodera aridifolia*, *Ameles decolor*, *Pseudomantis albofimbriata*) and only one third of the studied species in the Hymenopodidae family (*Hestiasula major*) (Liske and Davis 1987, Barry et al. 2008b, Battiston 2008). The similarity of courtship behavior in such taxonomically distant species of praying mantids may suggest this behavior is quite old, and could have been present in a common ancestor. Of course this might also be explained as convergence, but using the same structures to signal in the same way would seem an improbable result of separate evolution (Battiston 2008). Though we now know the courtship displays of the Persian boxer mantid, we need to study such behaviors in other members of the Mantidae in general and, more specifically, the Amelinae subfamily, to understand their evolutionary history.

## Acknowledgements

I would like to thank Dr. Matan Shelomi and Dr. Saeed Alaei for English improvement of the manuscript, as well as Ms. Mandana Hazrati and Mr. Reza Babaei-pour for their help in the field survey and laboratory trials.

## References

- Abu-Dannoun O, Katbeh-Bader A (2007) Mantodea of Jordan. *Zootaxa* 1617: 43–56. <https://doi.org/10.11646/zootaxa.1617.1.2>
- Barry KL, Holwell GI, Herberstein ME (2008a) Female praying mantids use sexual cannibalism as a foraging strategy to increase fecundity. *Behavioural Ecology* 19: 710–715. <https://doi.org/10.1093/behco/arm156>
- Barry KL, Holwell GI, Herberstein ME (2008b) Male mating behaviour reduces the risk of sexual cannibalism in an Australian praying mantid. *Journal of Ethology* 27: 377–383. <https://doi.org/10.1007/s10164-008-0130-z>
- Battiston R (2008) Mating behaviour of the mantid *Ameles decolor* (Insecta, Mantodea): Courtship and cannibalism. *Journal of Orthoptera Research* 17: 29–33. [https://doi.org/10.1665/1082-6467\(2008\)17\[29:MBOTMA\]2.0.CO;2](https://doi.org/10.1665/1082-6467(2008)17[29:MBOTMA]2.0.CO;2)
- Beier M (1964) Ein neues mantiden-genus aus Israel. *Israel Journal of Zoology* 13: 184–186.
- Bonfils J (1967) Contribution à l’étude des orthoptéroïdes des Antilles 111. Une espèce nouvelle du genre *Oligonyx* Saussure: description et notes biologiques (dig.). *Bulletin de la Société Entomologique de France* 72: 243–248.
- Edmunds M (1975) Courtship, mating, and possible sex pheromones in three species of Mantodea. *Entomologist’s Monthly Magazine* 111: 53–57.
- Gray DA (2005) Does courtship behaviour contribute to species-level reproductive isolation in field crickets? *Behavioural Ecology* 16: 201–206. <https://doi.org/10.1093/behco/arl144>
- Hurd LE, Eisenberg RM, Fagan WF, Tilmom KJ, Snyder WE, Vandersall KS, Datz SG, Welch JD (1994) Cannibalism reverses male-biased sex ratio in adult mantids: female strategy against food limitation? *Oikos* 69: 193–198. <https://doi.org/10.2307/3546137>
- Jayaweera A, Rathnayake DN, Davis KS, Barry KL (2015) The risk of sexual cannibalism and its effect on male approach and mating behaviour in a praying mantid. *Animal Behaviour* 110: 113–119. <https://doi.org/10.1016/j.anbehav.2015.09.021>
- Kadoi M, Morimoto K, Takami Y, Ethol J (2017) Male mate choice in a sexually cannibalistic species: Male escapes from hungry females in the praying mantid *Tenodera angustipennis*. *Journal of Ethology* 37: 177–185. <https://doi.org/10.1007/s10164-017-0506-z>
- Kolnegari M, Vafaei-shoushtari R (2018) The first Persian boxer mantid, a new species of *Holaptilon* Beier, 1964 from Haftad-gholeh Protected Area, Iran (Mantodea, Mantidae). *Journal of Entomological Research* 10: 9–17.
- Lelito JP, Brown WD (2006) Complicity or conflict over sexual cannibalism? Male risk taking in the praying mantis *Tenodera aridifolia sinensis*. *The American Naturalist* 168: 263–269. <https://doi.org/10.1086/505757>
- Liske E, Davis WJ (1987) Courtship and mating behaviour of the Chinese praying mantis, *Tenodera aridifolia sinensis*. *Animal Behaviour* 35: 1524–1537. [https://doi.org/10.1016/S0003-3472\(87\)80024-6](https://doi.org/10.1016/S0003-3472(87)80024-6)
- Loxton RG (1979) On display behaviour and courtship in the praying mantis *Ephestiasula amoena* (Bolivar). *Zoological Journal of the Linnean Society* 65: 103–110. <https://doi.org/10.1111/j.1096-3642.1979.tb01083.x>
- Maldonado H (1970) The deimatic reaction in the praying mantis *Stagmatoptera biocellata*. *Zeitschrift für vergleichende Physiologie* 68: 60–71. <https://doi.org/10.1007/BF00297812>
- Maxwell MR (1998) Lifetime mating opportunities and male mating behaviour in sexually cannibalistic praying mantids. *Animal Behaviour* 55: 1011–1028. <https://doi.org/10.1006/anbe.1997.0671>
- Maxwell MR (1999) Mating behavior. In: Prete FR, Wells H, Wells PH, Hurd LE (Eds) *The Praying Mantids*. Johns Hopkins University Press, Baltimore, 62–99.
- Quesnel VC (1967) Observations on the reproductive behaviour of the mantis *Acontiothespis multicolor*. *Journal Trinidad and Tobago Field Naturalist’s Club* 1967: 53–56.
- Roy R (1999) Morphology and Taxonomy. In: Prete FR, Wells H, Wells PH, Hurd LE (Eds) *The Praying Mantids*. Johns Hopkins University Press, Baltimore, 19–41.
- Umbers KDL, Lehtonen J, Mappes J (2015) Deimatic displays. *Current Biology* 25: 58–59. <https://doi.org/10.1016/j.cub.2014.11.011>
- Younes A (2007) Laboratory study of cannibalism in *Sphodromantis viridis* Forskal (Mantodea: Mantidae): Effects of prey availability, habitat structure, and predator density. *Egyptian Journal of Pest Control* 17: 57–63.



# Squatting (squatter) mantis man: A prehistoric praying mantis petroglyph in Iran

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Academic editor: *Michel Lecoq* | Received 24 August 2019 | Accepted 2 October 2019 | Published 13 March 2020

<http://zoobank.org/9B604BFF-3954-4DB1-82C1-E60992218182>

Citation: Kolnegari M, Naserifard M, Hazrati M, Shelomi M (2020) Squatting (squatter) mantis man: A prehistoric praying mantis petroglyph in Iran. *Journal of Orthoptera Research* 29(1): 41-44. <https://doi.org/10.3897/jor.29.39400>

## Abstract

A 14-cm motif of a six-legged creature with raptorial forearms was discovered in the Teymareh rock art site in central Iran (Markazi Province) during a 2017 and 2018 survey of petroglyphs or prehistoric stone engravings. In order to identify it, entomologists and archaeologists compared the motif to local insects and to similar motifs and geometric rock art from around the world. The inspected motif resembles a well-known "squatter man" motif based on aurora phenomena and found all over the world, combined with a praying mantid (Mantodea), probably a local species of *Empusa*. The petroglyph proves that praying mantids have been astounding and inspiring humans since prehistoric times.

## Keywords

archaeology, cultural entomology, Mantodea, paleoart, rock art

## Introduction

Rock art is visible in much of the world and is an integral part of the history of humankind, serving as a form of nonverbal and visual communication (Fossati et al. 1990). Petroglyphs (engraved rock art, from the Greek *petra* meaning "stone", and *glypho* meaning "carve") have been used since prehistory to express feelings and opinions. Petroglyphs often appear in similar contexts, such as on the walls of caves and rocky shelters or on freestanding outdoor rocks (Bradley et al. 1994). The engraved images are diverse and depict everything from simple geometric shapes (lines, circles, triangles, or squares) to more or less recognizable representations of creatures or elements from the local environment, such as humans, animals, plants, or tools (van der Sluijs and Peratt 2010). Scholars studying the cultures of the past examine stone art as an important source of data and try to describe them by visual comparison (Burno and Lourandos 1998, Deufemia and Paolino 2014). Understanding the meaning of petroglyphs carved into stone thousands of years ago is highly challenging. The task is

similar to a game of Pictionary, albeit without the artist on hand to say whose guess is correct (van der Sluijs and Peratt 2010).

Zoomorphic petroglyphs comprise a considerable amount of rock art and attract zoologists' attention throughout the world. Ira et al. (1994) divided zoomorphic petroglyphs into four categories: 1) animals hunted for food, 2) domesticated animals (for food, work, or pets), 3) animals with ritualistic symbolism (shamanism, sorcery), and, finally, 4) purely artistic motifs (animals depicted only for artistic purposes). As hunter-gatherers, early humans depicted mostly the large-sized animals (mostly mammals) that they preyed upon or that were threatening their lives. The numerous ancient rock arts with invertebrate motifs are less easily explained. Several prehistoric images from around the world have been identified as invertebrates, such as a cave cricket motif carved into a bison bone in the Magdalenian epoch (Chopard 1928), and more are continuously being discovered (Loring and Loring 1996, Amador Bech 2015).

In Iran, zoomorphic petroglyphs are found in mountainous regions that were inhabited by nomadic tribes (Kazemi et al. 2016). As invertebrate motifs in the country have been rather understudied, with many of them unidentified or interpreted as geometrics (Naserifard 2009, 2017), a team of local entomologists and archaeologists conducted a survey in 2017 and 2018 to identify several arthropod-like petroglyphs found in Iran in 2017. Consequently, some amazing motifs were discovered and/or their likely identity determined, and one such motif is presented here. The aim of this article is to present a new type of invertebrate-morph petroglyph from Iran, and to put it in context.

## Materials and methods

An engraved, arthropod-like image with a length of 14 cm and a width of 11 cm (Fig. 1A) was found on a 30-degree sloped boulder in the vicinity of Sarkubeh Village in the Teymareh Region of Markazi Province in the Islamic Republic of Iran (Fig. 2).

The petroglyph was made using hammering and engraving techniques. International sanctions preclude the use of radiocarbon dating methods to precisely date the petroglyphs, but a chronological survey estimated the petroglyphs in the region were created in the range of 40,000–4,000 years ago (Samuels 2016).

To identify the depicted organism, taxonomic methods were used. In particular, we analyzed morphological characters and compared the petroglyph to arthropods known to be distributed in this area and their behavioral characteristics. The motif was also compared with ancient anthropomorphs and anthropomorphized animal images in Iran and other countries to find possible similarities. The comparisons were independent of scale and rotation.

## Results

The inspected petroglyph represents a six-legged creature with grasping forelegs, and so was identified as a praying mantid (Mantodea). Characteristics of the petroglyph are a large triangular head equipped with a vertical extension, large eyes, opened forelegs, intermediately looped mid-legs, and curved hind-legs (Fig. 1A, B). The motif seems to have raised and opened its forelegs laterally, so it may depict a menacing mantid. This posture is typically seen in various mantid species during intra- and/or inter-specific encounters (Bonfils 1967, Edmunds 1975, Yamawaki 2011, Kolnegari 2020) (Fig. 3A, B). Although the position of the forelegs brings to mind the frightening pose (i.e., deimatic reaction) of a mantid, this type of depiction might be due to the constraints of two-dimensional rock art. The upper, linear part of the motif symbolizes the head extension, which is comparable with some mantid species. Among Iran's mantodeans, *Empusa* spp. have similar head shapes as the motif with an expanded vertex typical of the Empusini, although one can perceive variations in form and size of the extension in

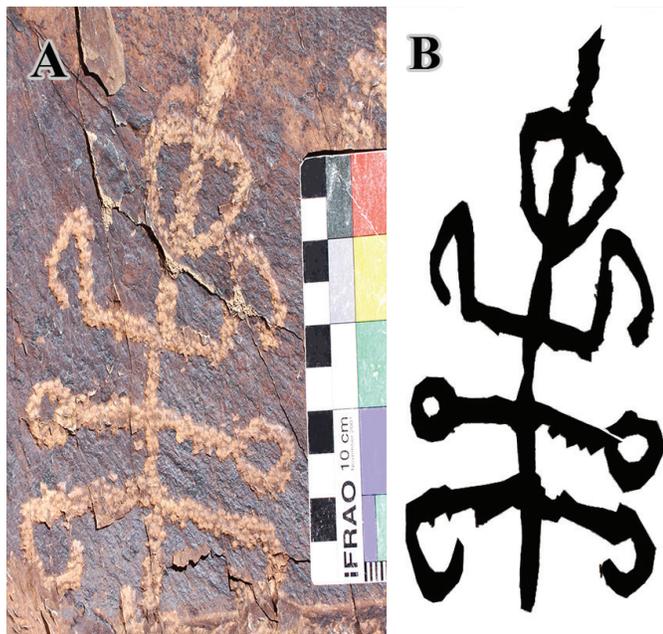


Fig. 1. "Squatting mantis man" petroglyph. A. The inspected petroglyph, located in Teymareh Region, Khomein County, Markazi Province, Iran. IFRAO (International Federation of Rock Art Organizations) Standard Scale: 10 cm from end to end. Photo credit: M. Naserifard. B. Black and white drawing of the motif (illustration by M. Kolnegari).

different species of the genus (Battiston et al. 2010) (Fig. 3C, D). *Empusa* spp. live in warm and dry environments like the Teymareh Region of Iran, thus the same biota could have been present in the area at the time the petroglyphs were carved. Theoretically, the large "head" could instead depict the large pronotum of some mantid species, such as *Idolomantis* or other species that lived in this region in prehistory but are not present today. The unrelated insects, called mantid lacewings (Neuroptera: Mantispidae), also have grasping forelegs, but they are quite a bit smaller than mantids and have no head expansion, so are unlikely to have inspired this motif.

The specific shape of the mid-legs and hind legs are the deceptive parts of the motif that could mislead the identification process. In fact, the entire appearance of the motif is comparable with particular anthropomorphs that show a man-like figure having two dots on either side of the midsection: e.g., fig. 14 in Peratt (2003). The symbol is named "squatting man" ("squatting man"), and some archaeologists believe that the motif is associated with aurora phenomenon due to plasma discharge, specifically a "Z-pinch instability" (Scott and Peratt 2003, Peratt 2004). This anthropomorph has been discovered in several regions including northern Arizona, Tucson, Arizona, New Mexico, Armenia, Spain, Tyrolian Alps, Italy, United Arab Emirates, Guyana, and Venezuela (Peratt 2003). Alternatively, in some ancient depictions, it represents a human shape holding a circular object in the hand (Lahafian 2013). The Iranian motif seems to be a combination of "praying mantis" and "squatting (squatting) man," so it is hereby named "squatting (squatting) mantis man."

## Discussion

While it is difficult to interpret prehistoric petroglyphs, morphological similarity and distinct features suggest the inspected petroglyph likely symbolizes a praying mantid. Mantid-like motifs have been found in several regions around the world—some were even considered as alien symbols (Davidson 2015)—but humanity's interest in the praying mantis can be dated to prehistoric times. Praying mantids had great value to the Mesopotamian people who established the first civilization (Panayotov et al. 2018). In the Egyptian Book of the Dead (written on papyrus, 1555–1350 B.C.), praying mantids appear as the aby-t-bird (bird-fly or bird-dancer), a smaller divinity of the underworld and a guide that accompanies the dead along their path in the Royal Palace of the great divine spirits (Prete et al. 1999). Praying mantids also had a hieroglyphic symbol, named "qdtm" (Evans 2004).

The main question is why prehistoric man was fascinated by mantids as far back as at least 4,000 years ago, and, consequently, why did they start scratching their images into solid rocks? Might it be related to Lewis-Williams and Dowson's (1988) controversial hypothesis that connects ancient rock art to using hallucinogenic plants? Exaggeration and mysticism are seen in much prehistoric rock art within and outside of Iran (Loring and Loring 1996, Sanders 2014, Sabzi and Hemati Azandaryani 2017). Mantids may also have been depicted for their hunting ability, perhaps as inspiration to prehistoric human hunters. The praying mantids have always fascinated, scared, and astonished mankind with their camouflage and mimicry ability, their skills in hunting and capturing prey, and for their bizarre sexual behaviors (Battiston et al. 2010).

Unlike large mammals with practical connections to humans, such as those hunted or domesticated, arthropods are more rarely depicted in ancient petroglyphs. The useless but astonishing praying mantids could have merited petroglyphs of their forms by be-

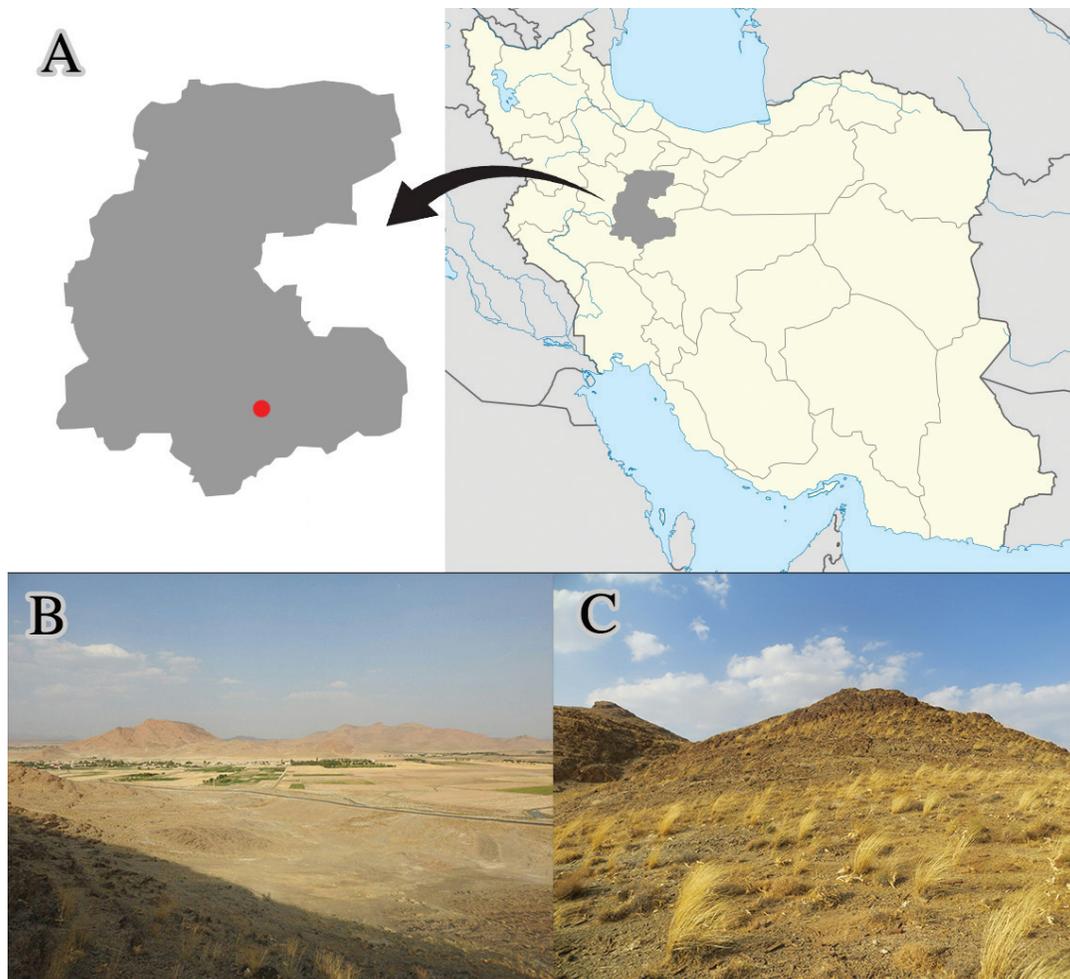


Fig. 2. Locality of the "squatting mantis man" petroglyph. A. Map of Iran with Markazi Province highlighted and the location of the Teymareh petroglyph site labeled on the insert in red (illustration by M. Kolnegari). B. Sarkubeh Village as seen from the petroglyph site. C. The Teymareh petroglyph locality. Photo credit: M. Kolnegari.

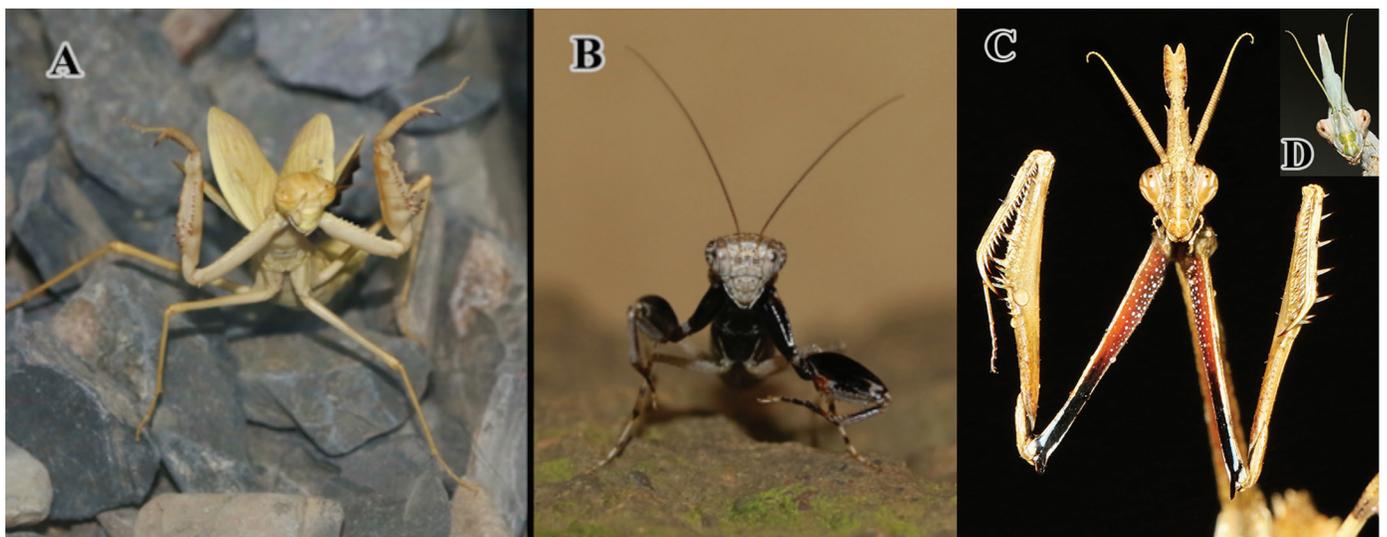


Fig. 3. Praying mantids with records in Iran. A. Adult *Bolivaria brachyptera* Pallas, 1773, with raised and opened forelimbs in a deimatic display. B. Adult *Holaptilon brevipugilis* Kolnegari, 2018. C. *Empusa hedenborgii* Stal, 1877, with opened forelimbs. D. Conehead mantis *Empusa pennicornis* (Pallas, 1773). Photo credit: M. Kolnegari.

ing part of ancient religions, fears, or admirations. The praying mantis has since ancient times been a symbol for the supernatural, or that which stands between “the world of men and gods” (Battiston et al. 2010). An example includes several prehistoric pictographs in southern Africa representing “mantis people” with half-mantid bodies (Davidson 2015). These, and the Iranian mantid petroglyph, bear witness that in prehistory, almost as today, praying mantids were animals of mysticism and appreciation.

### Acknowledgements

The authors are thankful for the support of the Orthopterists' Society. We would also like to thank the people of Khomein city who make efforts to protect ancient petroglyphs.

### References

- Amador Bech J (2015) Animal mythic symbolism in the rock art of the Sonoran desert. *Diseño de Metodologías y Técnicas de Registro, de Diagnóstico de Conservación y de Estrategias de Preservación y Protección del Patrimonio Rupestre de México*.
- Battiston R, Picciau L, Fontana P, Marshal J (2010) Mantids of the Euro-Mediterranean area. *World Biodiversity Association (WBA-Handbooks 2)*, Verona, Italy, 240 pp.
- Bonfils J (1967) Contribution à l'étude des orthoptéroïdes des Antilles 111. Une espèce nouvelle du genre *Oligomyx* Saussure: description et notes biologiques (digit.). *Bulletin de la Société Entomologique de France* 72: 243–248.
- Bradley R, Boado FC, Valcarce RF (1994) Rock art research as landscape archaeology: a pilot study in Galicia, NW Spain. *World Archaeology* 25: 374–390. <https://doi.org/10.1080/00438243.1994.9980252>
- Burno D, Lourandos H (1998) Rock art and socio demography in north-eastern Australian prehistory. *World Archaeology* 30: 193–219. <https://doi.org/10.1080/00438243.1998.9980407>
- Chopard L (1928) Sur une gravure d'insecte de l'époque magdalénienne. *Comptes Rendus de la Société de Biogéographie* 1928: 64–67.
- Davidson J (2015) The mysterious mantis people. <https://www.linkedin.com/pulse/mysterious-mantis-people-james-g-davidson/> [Accessed on 14.08.2019]
- Deufemia D, Paolino L (2014) Segmentation and recognition of petroglyphs using generic Fourier descriptors. In: Elmoataz A, Lezoray O, Nouboud F, Mamass D (Eds) *Image and Signal Processing. ICISP 2014. Lecture Notes in Computer Science 8509*. Springer, Cham. [https://doi.org/10.1007/978-3-319-07998-1\\_56](https://doi.org/10.1007/978-3-319-07998-1_56)
- Edmunds M (1975) Courtship, mating, and possible sex pheromones in three species of Mantodea. *Entomologist's Monthly Magazine* 111: 53–57.
- Evans L (2004) The praying mantis in Egypt. *The Bulletin of the Australian Centre for Egyptology* 15: 7–18.
- Fossati A, Jaffe L, De Abreu MS (1990) Rupestrian archaeology. Techniques and terminology. A methodological approach: Petroglyphs. In: Jaffe L, Ronayne D (Eds) *Ricerche Archeologiche*, Vol. 1. Cooperativa archeologica Le orme dell'uomo, Italy, 51–58.
- Ira G, Gonsalves J, Mundy P (1994) Animal diversity in prehistoric rock art. In: *Biodiversity in the Western Ghats, Information Kit*. World Wide Fund for Nature, India. Chapter 8–5, 1–4.
- Kazemi M, Naseri Soomeh H, Tahmasebi F (2016) Study of dash complex, petroglyphs in Meshginshahr, northwest of Iran. *International Journal of Science and Research Methodology: Human* 5: 317–328.
- Kolnegari M (2020) Mating behavior of the Persian boxer mantid *Holaptilon brevipugilis* (Mantodea: Mantidae). *Journal of Orthoptera Research* 29: 35–39. <https://doi.org/10.3897/jor.29.37595>
- Lahafian J (2013) Rock art in Kurdistan Iran. *Arts* 2: 328–349. <https://doi.org/10.3390/arts2040328>
- Lewis-Williams D, Dowson T (1988) The signs of all times: Entopic phenomena in Upper Palaeolithic Art. *Current Anthropology* 29: 201–245. <https://doi.org/10.1086/203629>
- Loring JM, Loring L (1996) *Pictographs and petroglyphs of the Oregon county, parts I and II*. University of California Press, USA, 293 pp.
- Naserifard M (2009) *Iran petroglyphs ideogram symbol*. Khomein Press. 444 pp.
- Naserifard M (2017) *Iran petroglyphs universal common language*. Vasef Publisher, 530 pp.
- Panayotov SV, Vacin L, Trabich G (2018) *Mesopotamian Medicine and Magic: Studies in Honor of Markham J. Geller*. Brill, 968 pp. <https://doi.org/10.1163/9789004368088>
- Peratt AL (2003) Characteristics for the occurrence of a high-current, Z-pinch aurora as recorded in antiquity. *IEEE Transactions on Plasma Science* 31: 1192–1214. <https://doi.org/10.1109/TPS.2003.820956>
- Peratt AL (2004) Orientation of intense Z-pinch instabilities from an intense aurora as recorded in antiquity: Western USA. In: *The 31<sup>st</sup> IEEE International Conference on Plasma Science, 2004. ICOPS 2004. IEEE Conference Record-Abstracts*, 426. <https://doi.org/10.1109/PLASMA.2004.1340222>
- Prete FR, Wells H, Wells PH, Hurd LE (1999) *The praying mantids*. Johns Hopkins University Press, Baltimore, 400 pp.
- Sabzi M, Hemati Azandaryani E (2017) Bichoun: newfound rock art at Boroujerd, Lorestan province, western Iran. *Rock Art Research* 34: 1.
- Samuels G (2016) 'World's oldest rock drawings' uncovered in Iran by archaeologist. *The Independent*, 12 December. <https://www.independent.co.uk/news/world/middle-east/world-oldest-rock-drawings-archaeologist-iran-khomeyn-mohammed-naserifard-a7470321.html> [Accessed on 14.08.2019]
- Sanders T (2014) *Jeffers Petroglyphs: A recording of 7000 years of North American history*. Minnesota Historical Society, 52 pp. [http://www.mnhs.org/sites/default/files/jefferspetroglyphs/learn/archaeology/jeffers-petroglyphs\\_history.pdf](http://www.mnhs.org/sites/default/files/jefferspetroglyphs/learn/archaeology/jeffers-petroglyphs_history.pdf) [Accessed on 14.08.2019]
- Scott D, Peratt AL (2003) The origin of petroglyphs – Recordings of a catastrophic aurora in human prehistory? In: *The 30<sup>th</sup> International Conference on Plasma Science, 2003. ICOPS 2003. IEEE Conference Record-Abstracts*, 143.
- van der Sluijs MA, Peratt AL (2010) Astronomical petroglyphs; Searching for rock art evidence for an ancient super aurora. *Expedition [University of Pennsylvania Museum of Archeology and Anthropology]* 52: 33–42.
- Yamawaki Y (2011) Defence behaviours of the praying mantis *Tenodera aridifolia* in response to looming objects. *Insect Physiology* 57: 1510–1517. <https://doi.org/10.1016/j.jinsphys.2011.08.003>

# Review of the tribe Amorphopini (Orthoptera: Tetrigidae: Metrodorinae): Pygmy moss-lichen tetrigids from the Amazon rainforest

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Academic editor: C.S. Bazelet | Received 9 February 2019 | Accepted 11 July 2019 | Published 30 March 2020

<http://zoobank.org/647877CD-F043-4952-8419-20D0F18EA28C>

Citation: Cadena-Castañeda OJ, Silva DSM, Mendes DMM, Pereira MR, Domenico FC, Sperber CF (2020) Review of the tribe Amorphopini (Orthoptera: Tetrigidae: Metrodorinae): Pygmy moss-lichen tetrigids from the Amazon rainforest. Journal of Orthoptera Research 29(1): 45–62. <https://doi.org/10.3897/jor.29.33717>

## Abstract

The tribe Amorphopini Günther, 1939 is reviewed. It consists of two genera: *Amorphopus* Seville, 1838 and *Eomorphopus* Hancock, 1907 with three Neotropical species: *Amorphopus notabilis* Serville, 1838, *Eomorphopus antennatus* (Bolívar, 1887), and *Eomorphopus granulatus* Hancock, 1907. Two species are transferred from *Amorphopus* to the genera *Metrodora* Bolívar, 1887 and *Crimisus* Bolívar, 1887, and two new combinations are proposed: *Metrodora gibbosula* (Walker, 1871), **comb. nov.** and *Crimisus humeralis* (Walker, 1871), **comb. nov.** New synonyms are proposed: *Amorphopus notabilis* Serville, 1838 = *Amorphopus griseus* Bolívar, 1887, **syn. nov.**; *Metrodora gibbosula* (Walker, 1871) = *Platyttix reticulatus* Hancock, 1906, **syn. nov.**; and *Crimisus humeralis* (Walker, 1871) = *Allotettix bolivianus* Brunner, 1913, **syn. nov.** Neotypes of *Amorphopus notabilis* and *Eomorphopus antennatus* as well as the lectotype of *E. granulatus* are designated. The description of *Amorphopus testudo* Saussure, 1861 is based on an immature specimen and we considered it as *nomen dubius* and the type depository of *Eomorphopus purpurascens* is unknown so we considered it, too, as *nomen dubius*. The tribe Amorphopini and all included taxa were redescribed and illustrated. A key to the genera and species is provided. Data on distribution, behavior, camouflage with lichens, polychromy, as well as ecological aspects of the species are reported.

## Keywords

behavior, camouflage, chromatic variation, lectotype, neotype, redescription

## Introduction

Metrodorinae is a cosmopolitan subfamily currently composed of five tribes (Cleostratini Bolívar, 1887; Amorphopini Günther, 1939; Clinophaestini Storozhenko, 2013; Miriatriini Cadena-Castañeda & Cardona-Granda, 2015; and Ophiotettigini Tumbrinck & Skejo, 2017) and about 70 genera of uncertain placement (Cigliano et al. 2019). The tribe Amorphopini Günther, 1939 [*sensu* Cadena-Castañeda and Cardona-Granda (2015)] is exclusive to the New World and

includes three genera: *Amorphopus* Serville, 1838 and *Eomorphopus* Hancock, 1907 from the northern region of South America (Cigliano et al. 2019), and *Platythorus* Morse, 1900 from Central America (Brunner et al. 1900–1909, Cigliano et al. 2019). Among the Amorphopini, *Amorphopus* is morphologically similar to *Eomorphopus* but can be easily distinguished by the enlarged fore and mid-legs (Buzzetti and Devriese 2007, Cadena-Castañeda and Cardona-Granda 2015).

*Amorphopus* was described by Serville (1838) and it is distinguished by its flattened (depressed) body dorsoventrally, fore and middle femur strongly carinate, shield-like shape, and ovoid tegmina (Hancock 1907, Günther 1939, Cadena-Castañeda and Cardona-Granda 2015). Currently *Amorphopus* includes five species: *A. notabilis* Serville, 1838 (type species); *A. testudo* Saussure, 1861; *A. gibbosulus* Walker, 1871; *A. humeralis* (Walker, 1871); and *A. griseus* Bolívar, 1887 (Cigliano et al. 2019).

*Eomorphopus* was defined by Hancock (1907) and was characterized by a strongly depressed body, granulose surface, oblique face, vertex truncated anteriorly, frontal costa compresso-elevated, moderately sulcate, between the antennae; pronotum anteriorly truncated and posteriorly acuminate, tegmina oval sublanceolate; fore femur strongly carinate (but not shield-like as in some *Amorphopus*), with the superior carinae often bi- or tri-undulate and inferior carina with only one lobe, middle femur clypeated and foliaceous (see Hancock 1907, Cadena-Castañeda and Cardona-Granda 2015). Similarly, to *Amorphopus*, the genus *Eomorphopus* is distributed only within South America and includes three species: *E. purpurascens* (Olivier, 1791), *E. antennatus* (Bolívar, 1887), and *E. granulatus* Hancock, 1907 (Cigliano et al. 2019). The monotypic genus *Platythorus* was described by Morse (1900) and is found in Nicaragua and Costa Rica. *Platythorus* lacks wings, the body is not flattened as in the other genera and, unlike *Amorphopus* or *Eomorphopus*, it lacks expanded or carinate fore or mid femora (Hancock 1907, Cadena-Castañeda and Cardona-Granda 2015).

In the present study, we review the tribe Amorphopini and its species, study the status of the genera and species and their ecological associations and behaviors, and provide an updated identification key. Additionally, we also present updated distribution maps for all known Amorphopini species. This paper is part of the cooperative study of Neotropical Tetrigidae led by Daniela Santos Martins Silva and Oscar J. Cadena-Castañeda.

## Material and methods

**Specimen preparation.**—The studied specimens were deposited in the following institutions: Colección de Artrópodos y otros Invertebrados de la Universidad Distrital Francisco José de Caldas, Bogotá, Colombia (CAUD), Academy of Natural Sciences, Philadelphia, Pennsylvania, USA (ANSP), Naturhistoriska Riksmuseet, Sweden, Stockholm (NHRS), The Natural History Museum [formerly British Museum (Natural History)], London, England (BMNH), Naturhistorisches Museum Wien, Vienna, Austria (NMW), Museo Natural de Ciencias Naturales, Madrid, Spain (MNCN), and Coleção de Invertebrados do Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA).

Specimen photos were taken with a Leica DFC295 attached to a stereomicroscope M205. The photographs of ANSP types were taken in a photo lightbox with a Canon EOS T3i digital camera equipped with a EF 100mm f/2.8 L macro lens. Photographs of living specimens were taken using a Nikon D7100 digital camera, with a 60 mm 2: 8 lens. The illustrations were made using Adobe Illustrator CS6 and Adobe Photoshop CS6.

Terminology and measurements follow Devriese (1996) and Tumbrinck (2014). The measures that most discriminated Amorphopini species were the following: Body length from the tip of the fastigium projection to the posterior tip of the pronotum (CFP); pronotum length (PL); pronotum lateral lobes maximal width (PLB); fore femur length (FF); fore tibia length (FL); middle femur length (MFL); middle tibia length (MTL); hind femur length (HL); hind femur maximal width (HW); and hind tibia length (HL).

**Maps and distribution data.**—Maps were drawn with Simplemapp (Shorthouse 2010). Data included in the maps were collected from the studied specimens and from visits to the different collections previously mentioned, and maps are intended to correct erroneous or doubtful records in the literature. Distribution data of photographed specimens were also recorded and identifications could be reliably made from photographs.

## Results and discussion

### Tribe Amorphopini Günther, 1939

**Taxa included.**—The type genus *Amorphopus* Serville, 1838 and *Eomorphopus* Hancock, 1907.

**Diagnosis.**—Small to medium size, robust insects with the body depressed dorso-ventrally (Figs 1A, 2A, 6A, 8A, 9A). Vertex does not project between the eyes, slightly tapering, truncate anteriorly; the median carina is short and distinct, the lateral carinae slightly more elevated than the median one, fossulae and supraocular tubercle absent. Facial carinae significantly pronounced between the antennae, with variable width from very narrow to form a scutellum. Eyes globose in lateral and frontal view. Antennae of moderate length with 15 filiform segments, originating

at the mid-point frontal costa, lateral ocelli present between the eyes and the frontal costa bifurcated initially (Figs 1B, 2B, 6B, 8B, 9B). Tegmina and wings always present on the known genera (Figs 1C, 2C, 6C, 8C, 9C). Pronotum granulated and surpassing the abdomen apex, anterior margin truncated, lateral lobe projecting sideways, prozonal carina slightly developed, midline from mesozona to the apex. Fore femur carinated and middle femur strongly expanded (Figs 1E, 2E, 6E, 8E, 9E); dorsal and ventral margin of middle femur lobed or foliaceous (Figs 1F, 2F, 6F, 8F, 9F), hind femur with antegenicular tooth, transversal ridge (or “chevrons”) between the dorso and ventro external carinae, and transversal ridge between the dorsal margin of the hind femur and dorso-external carina.

**Comments.**—Amorphopini was erected as a tribe by Cadena-Castañeda and Cardona-Granda (2015) to contain three genera: *Amorphopus*, *Eomorphopus*, and *Platythorus*. This tribe was characterized by globose eyes in lateral view (Figs 1C, 2C, 6C, 8C, 9C); body strongly flattened (Figs 1A, 2A, 6A, 8A, 9A); fore femur carinated and middle femur strongly expanded; dorsal and ventral margin of middle femur lobed or foliaceous (Figs 1E, F, 2E, F, 6E, F, 8E, F, 9E, F); and body camouflage frequently resembling lichens or bryophytes (Fig. 3) (Cadena-Castañeda and Cardona-Granda 2015) since *Amorphopus* and *Eomorphopus* are found in humid environments such as rivers and lakes (Amédégato and Devriese 2008). In addition to the previously mentioned characters, Amorphopini differs from the tribes established to date in Metrodorinae by lacking a prolonged vertex (which is common in Clinophaestini, Cleotrastini *sensu* Storozhenko 2016, and Miriatriini *sensu* Cadena-Castañeda and Cardona-Granda 2015), and by having filiform antennae. Clinophaestini and some Ophiotettigini, have widened antennal segments.

*Platythorus* is monotypic with only one female type, *Platythorus camurus* Morse, 1900, and occurs in Nicaragua and Costa Rica (Bruner et al. 1900–1909). This genus is easily distinguished from other Amorphopini by the lack of tegmina and wings and the middle femur that is not strongly expanded. This genus has morphology rather different from Amorphopini and is placed out of Amorphopini, as a Metrodorinae genus without tribal placement.

**Distribution.**—The Amorphopini species, as well as other species in South America, exhibit a very peculiar geographical distribution (see Silva et al. 2017, Cadena-Castañeda et al. 2019). There is a large area in the north region of South America (mainly Amazon Forest) where these genera are not known to occur (Figs 12–14). In addition, there is only one record for an *Eomorphopus* species that probably refers to the Atlantic Forest of Bahia State (Brazil), but Günther (1939) did not provide an exact location. *Eomorphopus* probably does occur in those areas, but its species haven't been sampled or identified due to limited zoological expeditions and taxonomic effort focused on tiny litter insects.

### Key to genera and species of the tribe Amorphopini

- 1 Body moderately depressed (Figs 6A, D, 8A, D). Scutellum narrow (Figs 6B, 8B), only middle femora flattened (Figs 6F, 8F), the fore femur is carinated (Figs 6E, 8E), tegmina sublanceolate (Figs 6C, 8C) .....2
- Body strongly depressed (Figs 1A, D, 2A, D). Scutellum wide (Figs 1B, 2B), fore and middle femora flattened, foliaceous and clypeate (Fig. 1E, F), tegmina ovoid (Figs 1C, 2C) .....*Amorphopus notabilis* Serville, 1838

- 2 Mid-sized (♀ 19–19.5 mm, ♂ 18 mm). Apex of the lateral lobe of the pronotum (sideway projection) triangular shaped and moderately sharp (Figs 8D, 9D). Body granulose, prozona with rounded sculpturing..... *Eomorphopus antennatus* (Bolivar, 1887)
- Small sized (♀ 16.5–17.5 mm, ♂ 15–16 mm). Apex of the lateral lobe of the pronotum (sideway projection) rounded (Figs 4C, 5C, 6D). Body mostly smooth and slightly granulose, prozona without sculpturing..... *Eomorphopus granulatus* Hancock, 1907

*Amorphopus* Hancock, 1907

*Type species.*—*Amorphopus notabilis* Serville, 1838.

*Diagnosis.*—Body strongly depressed dorsoventrally and minutely granulate (Figs 1A, 2A, 3). Eyes globose, not prominent; vertex anteriorly truncated; face very distinctly oblique; frontal costa with a wide scutellum between the lower part of the eyes, slightly compressed-elevated, sinuate below (Figs 1B, 2B). Lateral lobes of pronotum outwardly ampliate with both margins undulate. Tegmina oval and wings to the pronotum apex (Figs 1C, 2C). Legs short, fore and middle femora flattened, foliaceous and clypeate (Figs 1E, F, 2E, F), antegenicular tooth of the hind femur slightly developed, hind tibia very sparingly spinose, minutely serrulate; the first and third articles of the hind tarsi equal in length.

*Amorphopus notabilis* Serville, 1838

Figs 1, 2, 3, 12

*Neotype.*—COLOMBIA • ♀; Amazonas, PNN Amacayacu; 03°44'19"S, 70°13'7"W; C. Rodríguez leg (CAUD).

*Description.*—**Head.** Not protruding from the body; face very distinctly oblique (Fig. 1B, C); antennae filiform with 15 segments, inserted below the eyes; vertex anteriorly truncated and equal in width to one of the eyes; frontal costa with a wide scutellum between the lower part of the eyes, slightly compressed-elevated, sinuate below; eyes globose, not prominent; posterior ocelli placed between the inferior part of the eyes (Fig. 1B). **Thorax.** Meso-pleura expanding to the sides and covering the coxae in dorsal view. **Pronotum.** Macropronotal and strongly depressed dorso-ventrally. Lateral view. Median carina slightly undulated on prozona and extended to pronotal disc apex, prozonal carina and humero-apical carina visible, reaching the sulci; tegminal and ventral sinus present; length of the infrascapular area mid-sized covering to first abdominal tergite; humeral angles obtuse (Fig. 1A). Dorsal view. anterior and posterior margins truncated, also the first one undulated; prozonal carina visible; lateral lobes of pronotum ampliate and projected sideways, with the margins undulated and with a blunt spine (Fig. 1D). **Wings.** Tegmina and hind wings developed; tegmina ovoid, hind wings as long as the pronotum apex, opaque with the apical veins between the C and Sc yellowish. **Legs.** Fore and middle femora rectangular, longer than wide and with margins undulated (Fig. 1E, F), fore and middle tibiae narrow and short. Hind femur with the pre-genicular tooth slightly developed, small foliose plate present between the ventro and dorso-external carinae (Fig. 1D), hind tibia narrow and with few spines on the meso-distal portion. **Abdomen.** Narrow and slim, subgenital plate with the distal edge wavy with a rounded prolongation in the middle (Fig. 1G); ovipositor with narrow valves and with denticulations of moderate size (Fig. 1H).

**Male.** Similar to the female, except for the post-abdomen characters (Fig. 2A–F). Subgenital plate moderately prolonged, with

the dorsal edge straight and the apex rounded (Fig. 2G), conical and robust cerci (Fig. 2H).

**Coloration.** Predominantly white with scattered gray spots. Face and ventral surface of the body black with scattered whitish bands; pronotal disc from the level of the third pair of coxae with gray stripes, which extend and alternate towards the posterior area of the pronotum; fore femur white, fore tibia black with a white ring in the mesal region; femur and mid tibia, as well as the basal half of the hind femur, light pink, distal half of the hind femur white with gray stripes in similar appearance to the pronotal disc (Fig. 3).

*Variations.*—The margin undulations of the fore and mid femora may be more conspicuous in some specimens and the lateral lobes with the posterior angles may have sinuato-dentate or serrato-crenate margins.

*Measurements (in mm).*—**Female.** CFP: 14.0–15.5; PL: 13.6–14.2; PLB: 5.5–5.9; FF: 2.6–2.8; FL: 2.1–2.3; MFL: 2.7–3.0; MTL: 2.6–2.9; HL: 6.0–6.2; HW: 1.7–1.9; HL: 4.3–4.6. **Male.** CFP: 11.5–12.2; PL: 11.2–11.5; PLB: 4.8–5.1; FF: 2.3–2.5; FL: 2.0–2.1; MFL: 2.9–3.1; MTL: 2.0–2.2; HL: 5.1–5.5; HW: 1.8–2.0; HL: 3.9–4.1.

*Specimens examined.*—**Museum specimens.** BRAZIL • 1♀. Amazonas, Manaus, Reserva Adolpho Ducke; 02°55'49"S, 59°58'31"W; 14–18 Apr. 2010, Rede entomológica, V. Linard leg.; AM-010, km 26 • 2♀♀; same collection data as for preceding; Coleta manual, D.M.M. Mendes leg. • 1♂. Amazonas, Manaus. ZF2, km 14; 02°35'21"S, 60°04'55"W; 1–15 Apr. 2016, Malaise grande no chão, J.A. Rafael and F.F. Xavier F leg. • 1♀. Amazonas, Tefé, Terra Firme; 03°25'19"S, 64°37'05"W; 10–26 Jun. 2016, malaise, J.A. Oliveira, D.M.M. Mendes and J.A. Rafael leg. (INPA). **Photographic records.** ECUADOR • Sumaco NP, Bigal River Forest Reserve (Arthur Anker). PERU • Huánuco, Tingo María (Huamán Cuespán et al. 2014).

*Comments.*—Currently *A. notabilis* has two synonyms: *Tetrix cnemidotus* Burmeister, 1838 and *Amorphopus caiman* Saussure, 1861, both synonymized by Günther (1939). *A. testudo* Saussure, 1861 is an immature specimen (Günther 1939) and currently the type depositary is unknown (Hollier 2013); this specimen could possibly be an immature of *A. notabilis*, but we kept it as *nomen dubius*.

Bruner (1910) separated *A. griseus* Bolívar, 1887, *A. notabilis* Serville, 1838, *A. cnemidotus* (Burmeister, 1838), and *A. caiman* by the size of the females and the coloration of the specimens. The size and coloration in this species may vary, depending on the area, availability of resources, and camouflage strategies (Cadena-Castañeda 2011a, b, 2013a, b, c). Moreover, colors of specimens preserved in museums may vary by virtue of the preservation method used, such as storage in alcohol, which usually makes the specimens lose its color (Cadena-Castañeda 2012, Cadena-Castañeda and Páez 2013). By studying the type specimens, the synonymy of these species is confirmed, and we propose that *Amorphopus griseus* Bolívar, 1887 **syn. nov.**, be considered as a new synonym under *A. notabilis*.

To the two remaining species of the genus, the following nomenclatural acts are proposed: 1. *A. gibbosulus* Walker, 1871 is transferred to *Metrodora* Bolívar, 1887, and it is synonymized with *Metrodora reticulata* (Hancock, 1906) **syn. nov.** (originally described as *Platyettix reticulatus* Hancock, 1906) under *Metrodora gibbosulus* (Walker, 1871) **comb. nov.** This synonym is proposed by comparison of the type specimens of both species. It is observed that there is no variation in the shape of the fastigium of

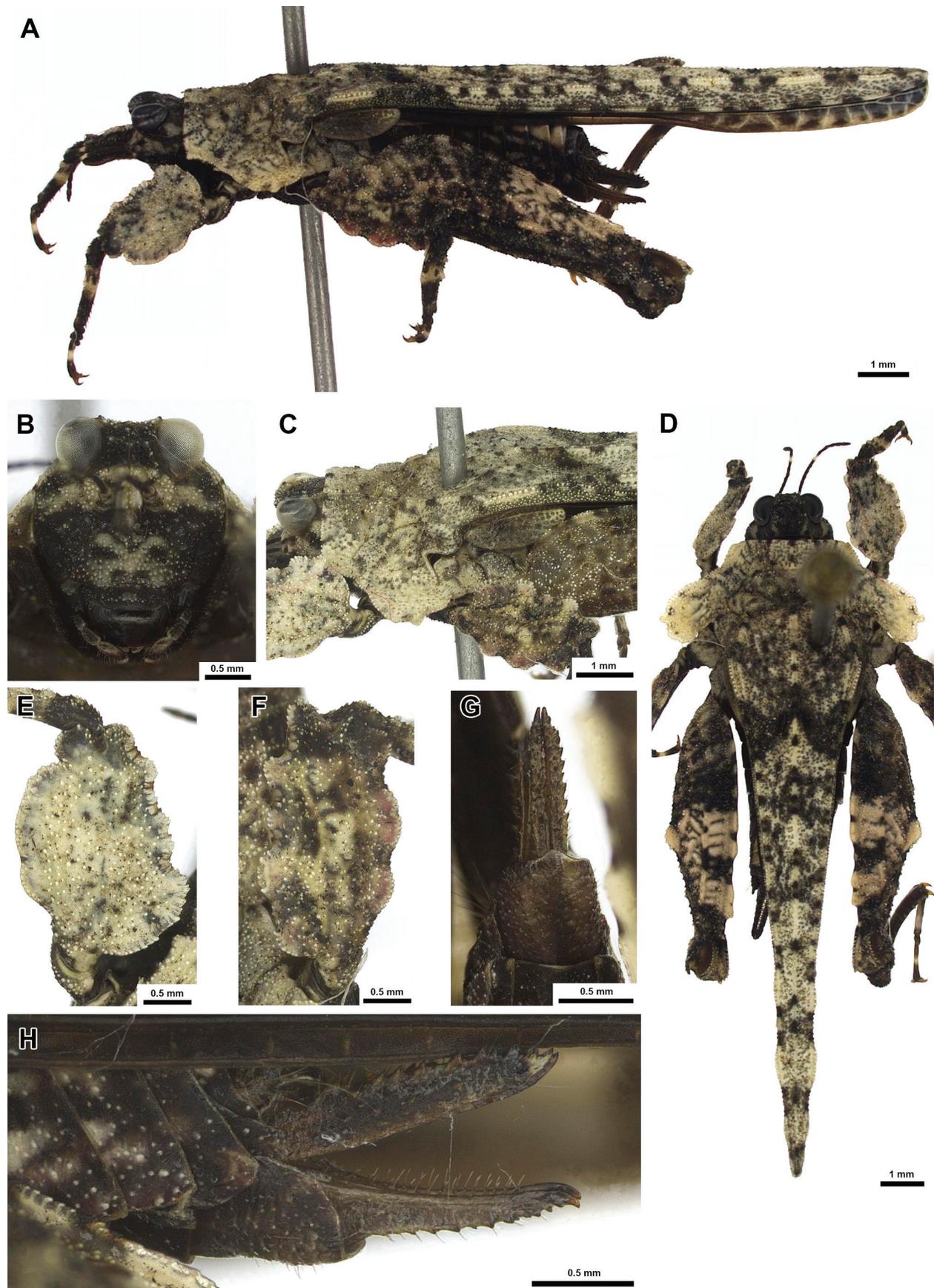


Fig. 1. *Amorphopus notabilis* (female). A. Habitus in lateral view; B. Frons; C. Head, lateral lobes of pronotum and tegmina in lateral view; D. Habitus in dorsal view; E. Fore-femur; F. Mid-femur; G. Terminalia in ventral view; and H. In lateral view.

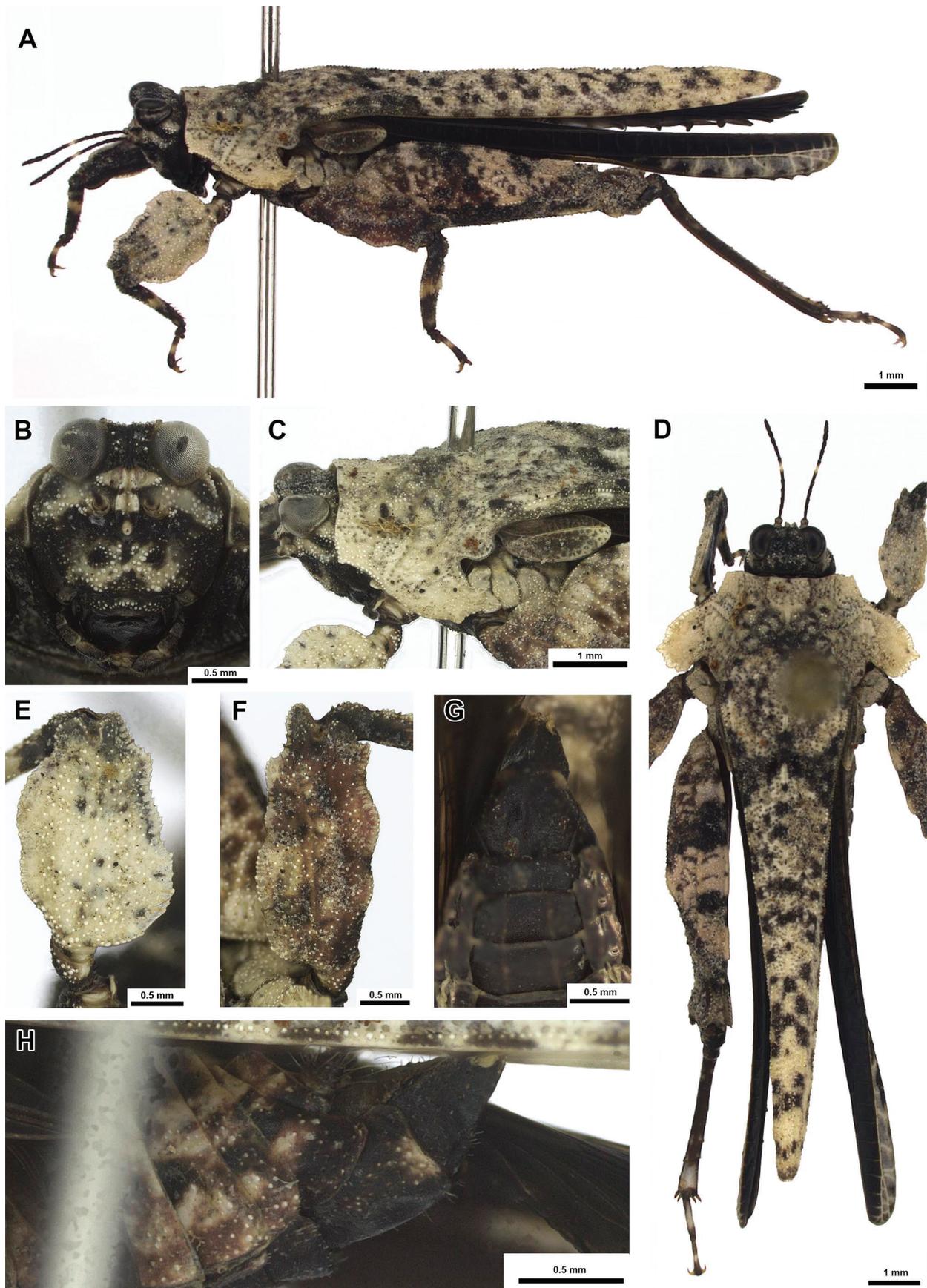


Fig. 2. *Amorphopus notabilis* (male). A. Habitus in lateral view; B. Frons; C. Head, lateral lobes of pronotum and tegmina in lateral view; D. Habitus in dorsal view; E. Fore-femur; F. Mid-femur; G. Terminalia in ventral view; and H. In lateral view.



Fig. 3. Live *Amorphopus notabilis* from Brazilian Amazon.

the vertex, since both species have a broad frontal costa, similar to the species of the subfamily Cladonotinae. The pronotum has a curvature in the prozone that rises significantly; the apex of the pronotum is curved slightly upwards and the lateral lobes of the pronotum project towards the sides, with the inferior margin triangular in shape. Since these diagnostic characters are present in specimens of both species, they cannot be maintained as separate specific entities, much less belonging to different genera.

2. Similarly, *A. humeralis* (Walker, 1871) (= *Tettix humeralis*) is transferred to *Crimisus* Bolívar, 1887, and it is synonymized with *Crimisus bolivianus* (Bruner, 1913), **syn. nov.** (originally described as *Allotettix bolivianus* Bruner, 1913) under *Crimisus humeralis* (Walker, 1871), **comb. nov.** The type specimens of both species are females, but, unfortunately, the legs in the holotype of *A. humeralis* are missing, so the legs were not compared. Nevertheless, both species share the same characteristics: narrow frontal costa, lower margins of the pronotal lobes rounded, without projecting to the sides as in the previous case, subgenital plate triangular, with a small prolongation at the apex. The aforementioned characters are observed in the type specimens of both species, indicating that they belong to a single species. Since they do not have expanded anterior and middle femora, it is ruled out that they belong to the *Amorphopini* tribe, fitting better in the genus *Crimisus*.

The two species described by Walker (1871), *A. gibbosulus* and *A. humeralis*, were not studied again and were not included in the Orthoptera Species File until Dr. J. Tumbrinck photographed the specimens and updated the information. If historical authors like Hancock and Günther had access to those specimens, for example, certainly they would have considered them to be synonyms. The nomenclatural acts were carried out by comparing the type specimens and their photographs; *A. gibbosulus* and *A. humeralis* do not meet the diagnostic characteristics to be included in *Amorphopus*, but they are similar to

*Metrodora reticulata* **syn. nov.** (now *Metrodora gibbosulus*) and *Crimisus bolivianus* **syn. nov.** (now *Crimisus humeralis*), respectively, in diagnostic structures such as pronotum structure, face, and terminalia shape.

Finally, the genus *Amorphopus* is kept monotypic and its known distribution is extended through the Amazonian slope, similarly to *Pterochroza ocellata* (Linnaeus, 1758), a species that was once considered several different species, but is now known to be a single, very variable species (Xiberras and Ducaud 2004).

A neotype specimen is designated as the carrier-name of the species and is supported by the following reasons (ICZN 1999 Art. 75): 1. The location of the only type specimen is unknown. It was deposited in NHRS, but Josef Tumbrinck visited that collection and did not find the type specimen (pers. comm.) "Some of the types of Serville are lost. Some of them are in Paris. But Josip Skejo did not find *Amorphopus notabilis* in Paris. So - today - the type is lost". The holotype female specimen has as type locality "Brazil, Para". This specimen could not be traced from its original description (Arts. 75.3.1., 75.3.4.), but the author provided figures, and when compared with the neotype specimen here designated, it agrees with the drawings by Serville (1838). 2. Not having specimens from the type locality, a female from a nearby and available locality of similar geological characteristics was designated (Arts. 75.3.5, 75.3.6; recommendation 75A ICZN). 3. A detailed description is written of the neotype that is in agreement with the general idea of the identity of this species, differentiating itself from other taxa, ensuring the recognition of the designated specimen, and conveying a consensus in identifications and wide distribution that characterizes the species, ensuring that most identifications from the past are correct (Arts. 75.3.2, 75.3.3, 75.3.5; recommendation 75B). 4. The neotype is deposited in CAUD, a collection of a recognized scientific institution, which maintains adequate facilities to preserve the types and makes them accessible for study (Art. 75.3.7).

**Behavioral notes.**—The Brazilian specimens were collected only in non-flooded ombrophilous forests (Terra Firme). In this environment they are usually found on the trunk and branches of fallen trees, where, due to their coloration and flattened body, they are easily confused with the tree's bark. Once physically stimulated, the specimens exhibited thanatosis behavior, where the individual remained immobile, leaving its femurs parallel to the body, with the lobes of the femora that mimic foliage lying alongside the body and the tibia folded against the femora. Thus, the body of the insect is very similar to a small fragment of bark, and it remains in this position for several minutes even on physical stimulation. Only after several minutes did the observed specimens leave the thanatosis behavior and move (D. Mello Mendes pers. obs.).

#### *Eomorphopus* Hancock, 1907

**Type species.**—*Eomorphopus antennatus* (Bolívar, 1887).

**Description.**—Body moderately depressed dorsoventrally (Figs 4A, 5A), granulate and moderately rugose. Eyes slightly conical with a flattened base; vertex narrowed forward, truncate anteriorly, not advancing beyond the eyes; frontal costa with a narrow scutellum between the antennae and moderately sulcate (Figs 4D, 5D), lateral lobes outwardly dilated below, the posterior angles oblong (Figs 4C, 5C, 6D) or acute (Figs 8D, 9D). Tegmina sublanceolate and wings surpassing the pronotum apex (Figs 4A, 8A). Fore femur strongly carinate, but not entirely clypeate (Figs 6E, 8E, 9E); mid femur flattened, margins above sub-straight, below strongly foliaceous-expanded, often sinuate toward the apices (Figs 6F, 8F, 9F); antegenicular tooth of hind femur developed; the first and third articles of the hind tarsi equal in length.

**Comments.**—For a long time, *Eomorphopus* species were described as *Amorphopus*, except for *E. purpurascens*, which was originally described as *Acrydium purpurascens* by Olivier (1791) and is still almost unknown, without photos and with scant morphological information. Additionally, some of the available morphological information on *E. purpurascens* is non-traditional, such as the description of the coloration used by Oliver (1791). Characteristics of this kind can be lost over time (e.g., wings with purplish coloration). Furthermore, the type species was not defined in the original description and the depository is unknown. The distribution is known only for Trinidad Island (Olivier 1791). For that reason, we propose as *nomen dubius* this species, and *Eomorphopus* only contains two valid species: *E. granulatus* and *E. antennatus*.

**Behavioral notes.**—The Brazilian specimens were collected in lowland floodplains in areas of the Solimões River and non-flooding ombrophilous forests (Terra Firme). They are commonly found in litter on the ground and occasionally on trunks of fallen trees. They are usually found in the same environment with other pygmy grasshoppers, such as *Scaria* (Cadena-Castañeda et al. 2019). They are easily unnerved and usually jump when approached.

#### *Eomorphopus granulatus* Hancock, 1907

Figs 4–7, 13

*Eomorphopus granulatus* Hancock 1907: 38 [general description], lectotype female (ANSP) and paralectotype male designated, Plate 4, figs 35–35a; type-locality: "Dutch Guiana, S. America". Kirby 1910: 22 [synonymic catalogue of Orthoptera]. Bruner 1910 [key, new localities]. Rehn 1913: 82 [New localities "Suriname"] Rehn

1916: 268 [new localities]. Rehn 1918: 167 [new localities]. Bruner 1919–1922: 8 [new localities]. Günther 1939: 263 [new localities]. Liebermann 1955: 331 [catalogue of Brazilian Orthoptera]. Otte D. 1979 (1978): 39 [catalogue of primary types at ANSP].

**Type material.**—Lectotype female, by present designation, deposited at ANSP and labeled as follows: "*Eomorphopus granulatus* Hancock H573 [handwritten] TYPE [printed, red label]/Hancock's [printed] Type *Eomorphopus granulatus* [handwritten, white label]/Dutch Guiana [handwritten, white label]". Conservation status. Bad condition, both antennae missing; specimen glued on card and remnants of fungi on body. Paralectotype male, by present designation, deposited at ANSP and labeled as follows: "*Eomorphopus granulatus* Allotype Hancock ♂ [handwritten] PARATYPE HEBARD CLN [printed, yellow label]/Dutch Guiana [handwritten, white label]". Conservation status. Bad condition, both antennae missing; right fore and middle tarsi missing; specimen glued on card and remnants of fungi on body.

**Redescription (Female lectotype, Fig. 4).**—Body surface granulated. **Head.** Lateral view (Fig. 4A, B): protuberant and slightly conical eyes with a flattened base; vertex and fastigium visible between eyes; antennal groove situated between lower margin of compound eyes; frontal costa elevated. Frontal view (Fig. 4D). Fastigium of vertex slightly conic; frontal costa bifurcation placed between compound eyes with narrow scutellum; fascial carinae between both superior ocelli; median ocelli placed between fascial carinae and frontal carina, but not touching on the base by frontal carina; antennal groove situated between lower margin of compound eyes and medial ocelli. Dorsal view (Fig. 4C). Vertex with distance between eyes as long as horizontal diameter of eyes; medial carina conspicuous and continuing towards frontal costa; area of fastigium to occiput granulated; occipital area visible and anterior margin of pronotum distant from the eyes. **Pronotum.** Macropronotal and flattened dorso-ventrally. Lateral view (Fig. 4A, B). Anterior margin of pronotum truncated and slightly elevated; median carina slightly undulated, prozonal carina and humero-apical carina visible and short, not reaching the sulci; extralateral carina inconspicuous; ventral sinus present; lateral lobe with anterior margin truncated and without spine; tegminal sinus present; length of infrascapular area shorter than length of fore tibiae; two deep sulci between prozona and humero-apical carina; paranota granulated and triangularly shaped; humero-apical carina continuous to external lateral carina and both parallel to median carina. Frontal view (Fig. 4D). Lateral lobes of pronotum projected and directed sideways. Dorsal view (Fig. 4C). Dorsum granulated; prozonal carina visible and short, not reaching the sulci; median carina continuous; humero-apical carina conspicuous; anterior and posterior margin of pronotum truncated; lateral lobe directed sideways. **Sternonotum.** The sternonotum could not be checked due to it being glued on card. **Wings.** (Fig. 4A, B). Tegmina and hindwings visible; tegmina oval, sublanceolated shape; hindwings dark brown and surpassing pronotum apex. **Legs.** Fore legs (Fig. 4A, B, D). Fore femur flattened laterally, dorsal and ventral margins of femur carinated with three undulations in the dorsal margin and one in ventral margin; tibia as long as femur. Middle legs (Fig. 4A–C). Middle femur shieldlike shape, flattened laterally and strongly foliaceous; dorsal and ventral margin slightly undulated; ventral margin expanded, with rounded teeth (crenated) near tibia; femur longer than tibia. Hind legs (Fig. 4A, B). Dorsal-external and ventro-external of femur granulated; antegenicular tooth conspicuous; dorso-external carina and ventro-external carina conspicuous; transversal ridges visible on external surface; tibia not

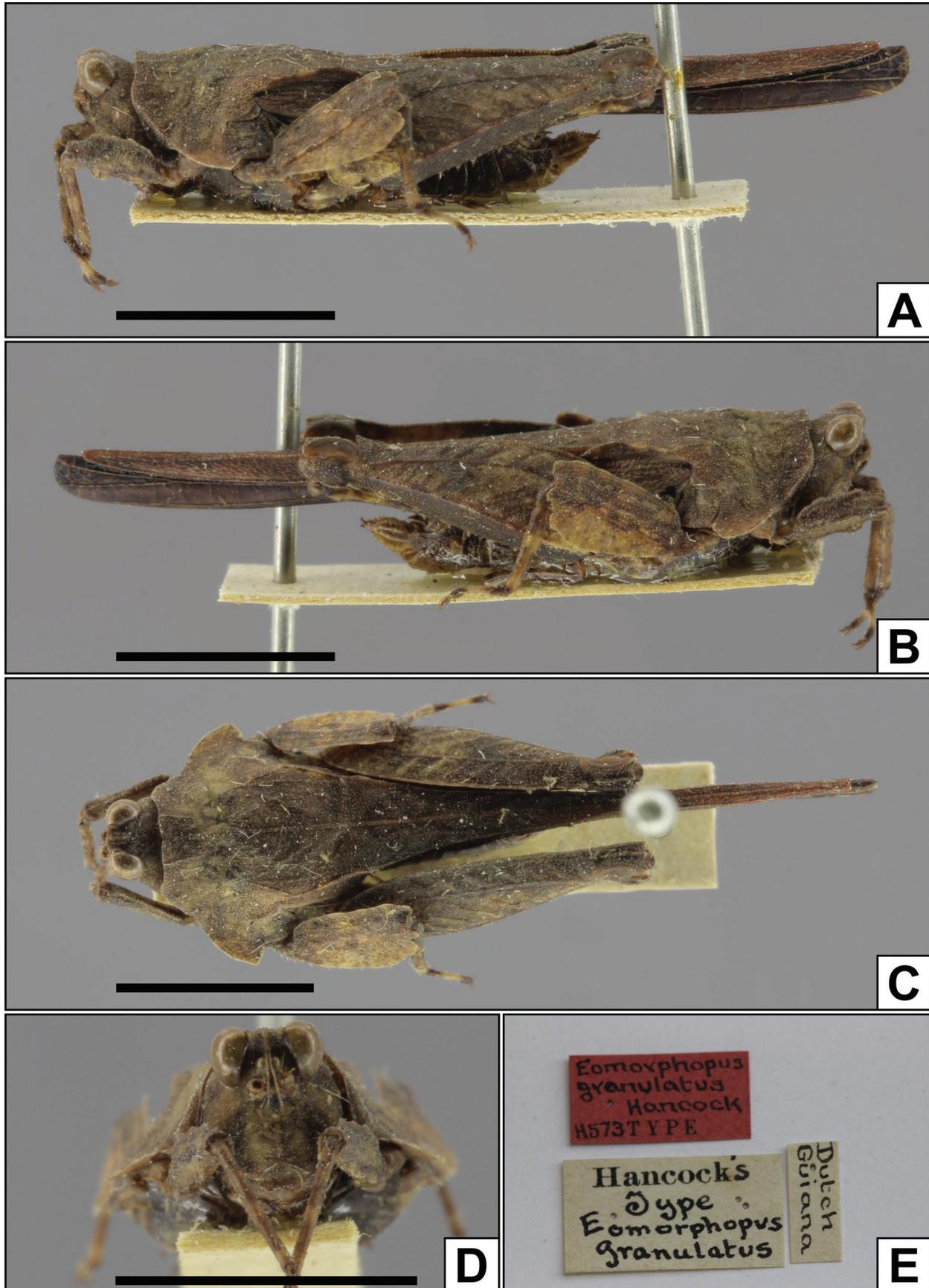


Fig. 4. *Eomorphopus granulatus* (female lectotype) A. Lateral left habitus; B. Lateral right habitus; C. Dorsal view; D. Head details in frontal view; and E. Labels. Scale bars: 5 mm.

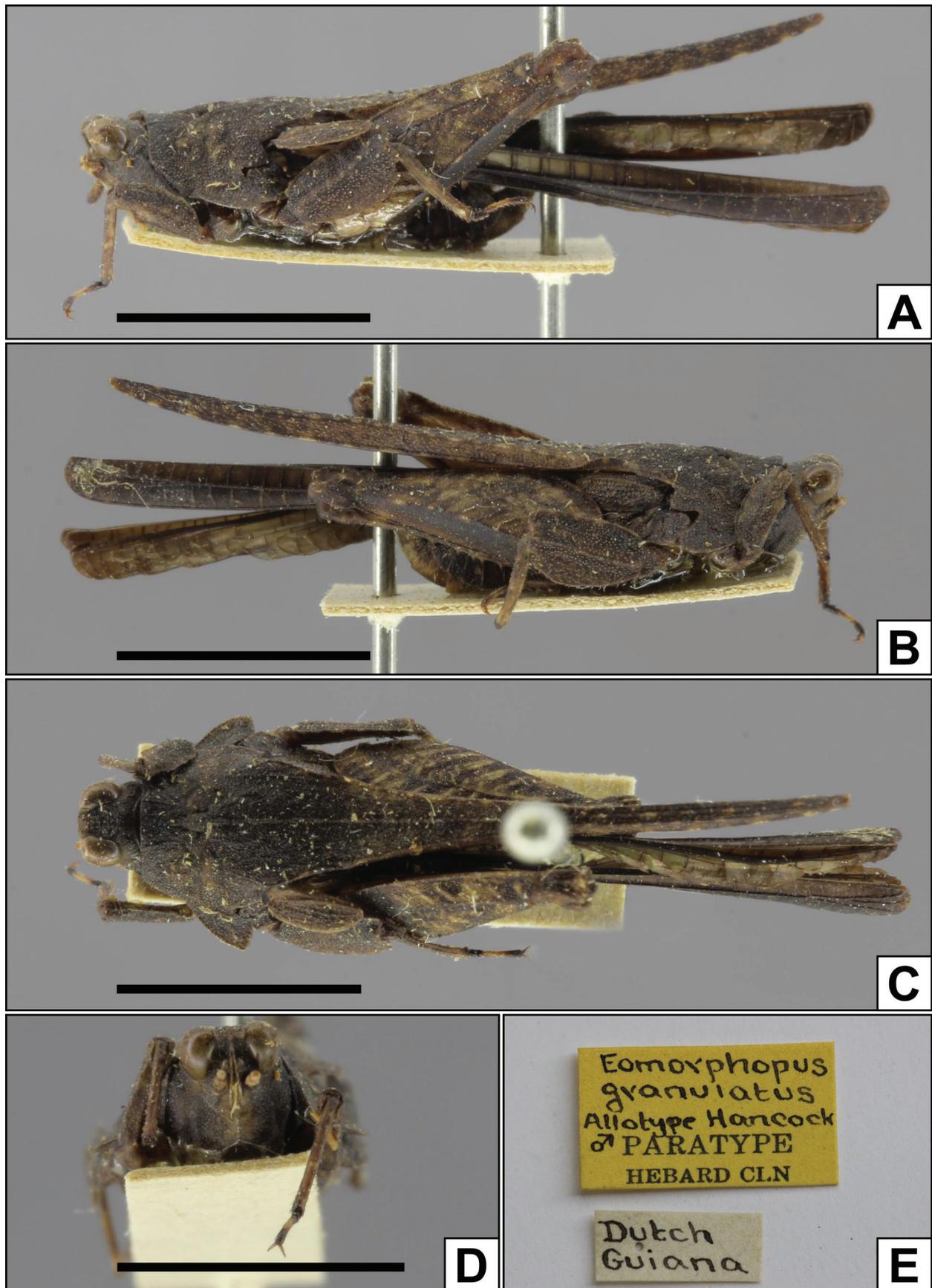


Fig. 5. *Eomorphopus granulatus* (male paralectotype) A. Lateral left habitus; B. Lateral right habitus; C. Dorsal view; D. Head details in frontal view; and E. Labels. Scale bars: 5 mm.



Fig. 6. *Eomorphopus granulatus* (male not a type) A. Habitus in lateral view; B. Frons; C. Head, lateral lobes of pronotum and tegmina in lateral view; D. Habitus in dorsal view; E. Fore-femur; F. Mid-femur; G. Terminalia in ventral view; and H. In lateral view.



Fig. 7. Live *Eomorphopus granulatus* from Brazilian Amazon.

visible and hidden behind the femur. **Abdomen.** (Fig. 4A, B). Sternites not visible due to specimen glued on card; ovipositor valves short and robust, superior margin of dorsal and ventral valve with teeth. Measurements (in Hancock, 1907). Total length of female body: 16.5 mm; pronotum: 14.5 mm; hind femur: 7 mm.

**Male (paralectotype, Fig. 5).**—Similar to female, except: **Head.** Frontal view (Fig. 5D). Fastigium straight. **Pronotum.** Lateral view (Fig. 5A, B). Humero-apical carina not continuous to external lateral carina. Measurements (in Hancock 1907). Total length of male body: 15 mm; pronotum: 13 mm; hind femur: 6 mm.

**Measurements (from additional specimens studied; in mm).**—**Female.** CFP: 18; PL: 15.2; PLB: 5.8; FF: 3; FL: 3.2; MFL: 3.5; MTL: 3.7; HL: 8; HW: 2.4; HL: 7.2. **Male.** CFP: 16.5–17.4; PL: 15.0–16.0; PLB: 5.0–5.2; FF: 2.2–2.5; FL: 2.8–3.0; MFL: 3.0–3.1; MTL: 3.1–3.2; HL: 7.0–7.5; HW: 2.0–2.2; HL: 6.4–6.6.

**Specimens examined.**—COLOMBIA • 1♀; Putumayo, Puerto Asis, Vda. Nariño, Nariño; 0°29'20.9"N, 76°24'23.6"W; 273 m; 25 Mar. 2015; N. Jimenez leg. • 1♂; Caquetá, Florencia, Corregimiento Venecia, Vereda Balcanes, Granja Agroecológica Balcanes de la Universidad de la Amazonia; 01°25'34.7"N, 75°30'58.6"W; 266 m; 21 Sep. 2017; D. Cabra leg. (CAUD). BRAZIL • 1♂; Amazonas, Uarini, Boca do Mamirauá; 03°07'29.4"S, 64°47'32.1"W; 5 Sep. 2018; D.M.M. Mendes, J.C. Oliveira and J. Oliveira leg (INPA).

**Comments.**—*Eomorphopus granulatus* Hancock 1907 has been recorded from Guyana, French Guyana, Suriname, and Brazil. *E. granulatus* is the only species of *Eomorphopus* with type species housed at

ANSP. Both specimens of the museum have labels, with the female labeled as "Type" and the male labeled as "Allotype"/"Paratype". As the author did not designate the holotype in the original description, we designated the female as the lectotype and, consequently, the male specimen became the paralectotype. We believe that this redescription will facilitate species recognition in the future. In his description, Hancock (1907) indicated that the body was subtly granulated and cinereous or fuscus-cinereous (ash-colored; gray tinged with blackish), see Smith (1906). Actually, this type has overall brownish-yellow and brown color.

*Eomorphopus antennatus* Bolívar, 1887

Figs 8–11, 14

**Neotype.**—COLOMBIA • ♀; Amazonas, San Juan de Loreto Yacu; 03°37'0"S; 70°33'59.3"W; 180 m; N. Ruiz leg. (CAUD).

**Description.**—**Female.** This species is very similar to *E. granulatus*, but *E. antennatus* is larger. Furthermore, it is differentiated by the following characters: Body surface more granulated than *E. granulatus* (Fig. 8A). Eyes globose and prominent, fastigium visible between the eyes, median carina slightly developed and continuing towards frontal costa; area of fastigium to occiput abundantly granulated (Fig. 8B). Pronotum with rounded sculpturing on prozona, median carinae undulate at level of humeral sinus, length of infra-scapular area as long as fore femur (Fig. 8C); prolongation of the pronotum constricting and resuming its thickness rapidly, close to the distal third, apex of the lateral lobe of the side projection triangular shaped and moderately sharp; anterior and posterior margin of pronotum truncated; lateral lobes directed sideways (Fig. 8D).

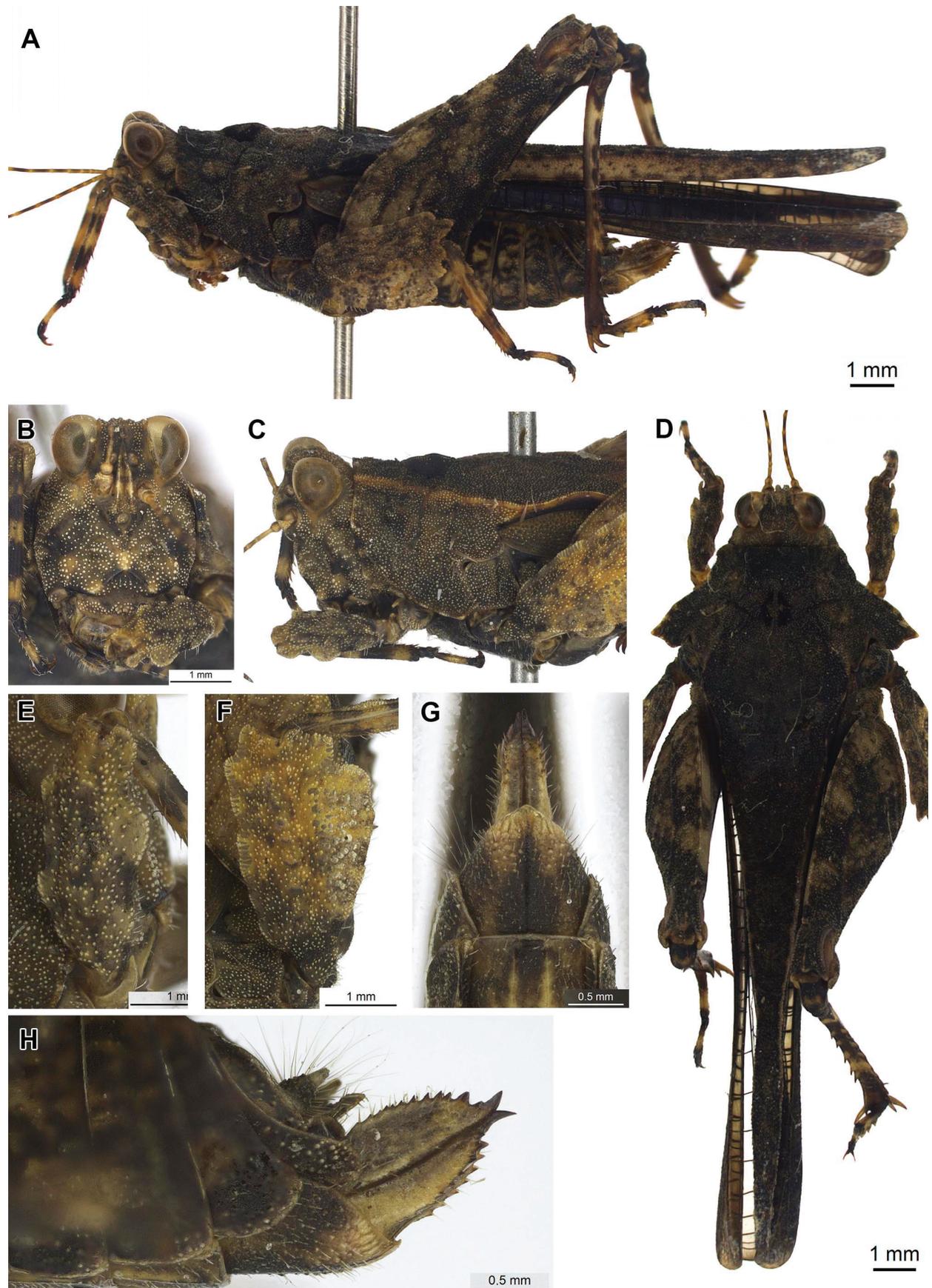


Fig. 8. *Eomorphopus antennatus* (female) A. Habitus in lateral view; B. Frons; C. Head, lateral lobes of pronotum and tegmina in lateral view; D. Habitus in dorsal view; E. Fore-femur; F. Mid-femur; G. Terminalia in ventral view; and H. In lateral view.

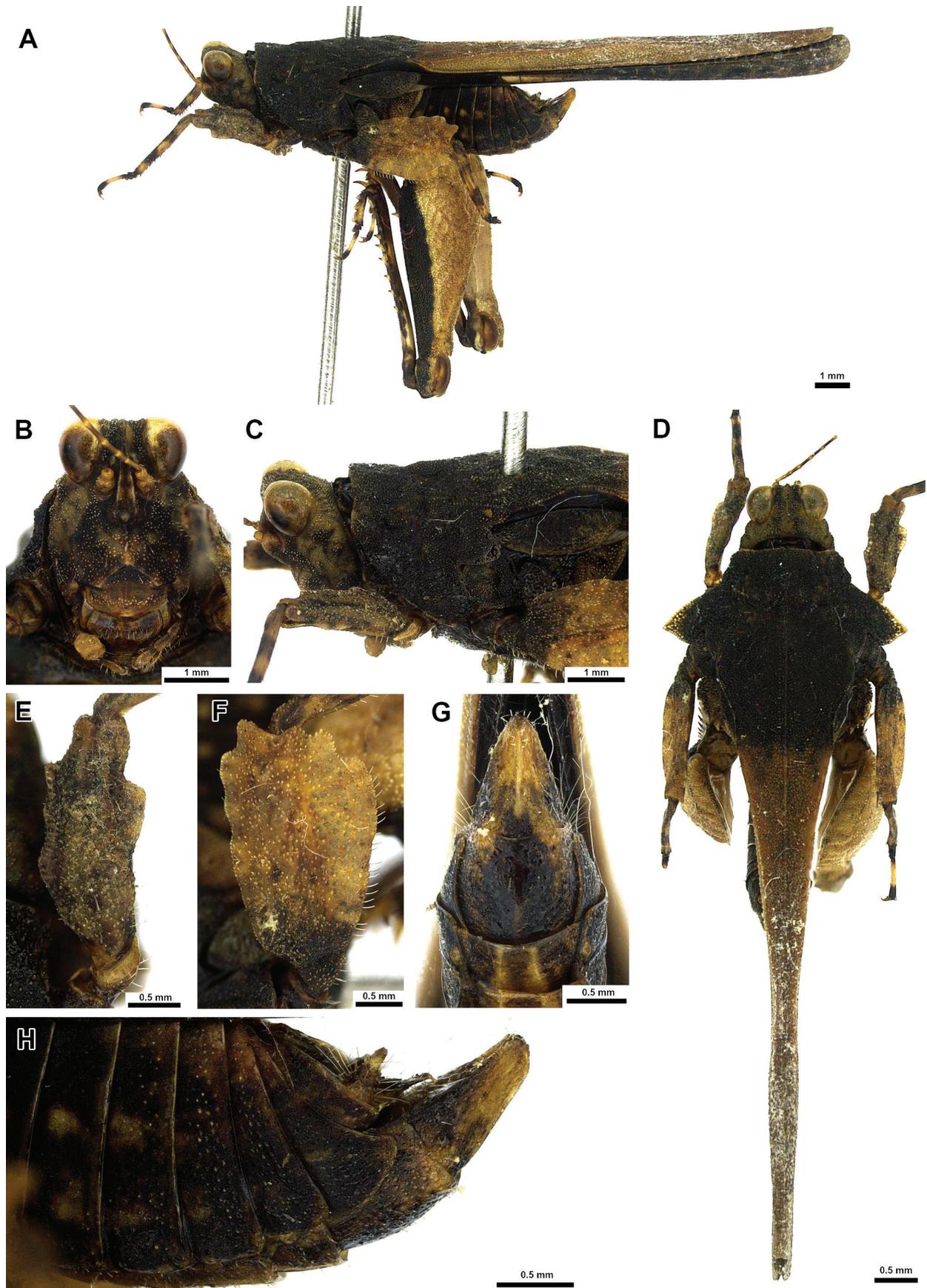


Fig. 9. *Eomorphopus antennatus* (male) A. Habitus in lateral view B. Frons; C. Head, lateral lobes of pronotum and tegmina in lateral view; D. Habitus in dorsal view; E. Fore-femur; F. Mid-femur; G. Terminalia in ventral view; and H. In lateral view.



Fig. 10. Live *Eomorphopus antennatus* female from Brazilian Amazon.



Fig. 11. Live *Eomorphopus antennatus* male from Brazilian Amazon.

Fore femur flattened laterally, dorsal and ventral margins carinated with two or three undulations in the dorsal margin and one or two in ventral margin (Fig. 8E); middle femur shield like in shape, flattened laterally and strongly foliaceous (mid-femur notably wider than *E. granulatus*), dorsal and ventral margin slightly undulated; ventral margin expanded, with rounded teeth in the apex (Fig. 8F). Subgenital plate triangular shaped, slightly longer than wide, with a small mid triangular tooth (Fig. 8G).

**Male.** Similar to the female, distinguished by the ambisexual characters (Fig. 9A–F): subgenital plate prolonged, in ventral view triangular shaped and with rounded apex (Fig. 9G), cerci cylindrical, slightly reducing in thickness from the base to the apex (Fig. 9H).

**Variations.**—The main variations observed in this species are related to the coloration, that will be detailed later. Morphologically, the undulations of the middle and anterior femur may be more conspicuous in some individuals than others, although it was observed that they are more conspicuous in males than in females. Moreover, the undulations of the dorsal margin of the anterior femur can vary from two, three, or four, distorting the use of this character to separate the two species of *Eomorphopus*. (Bruner (1910) suggested that *E. granulatus* had three undulations and *E. antennatus* had two).

**Measurements (in mm).**—**Female.** CFP: 19.4–19.5; PL: 17.4–17.9; PLB: 5.5–5.9; FF: 3.4–3.6; FL: 2.7–3; MFL: 3.3–3.4; MTL: 3–3.3; HL: 7.1–7.3; HW: 1.9–2.2; HL: 6.7–6.8. **Male.** CFP: 18.3; PL: 16.4; PLB: 5.5; FF: 2.8; FL: 2.7; MFL: 3.6; MTL: 2.8; HL: 7.4; HW: 2.3; HL: 6.1.

**Specimens examined.**—**Museum specimens.** COLOMBIA • 1♀; same data as neotype • 1♀; Amazonas, Leticia; 27 Oct. 1996. • 1♀; La Pedrera; 100 m; 18 May. 2011; C. Linares. • 1♂; Caquetá, Florencia, Vda. La Victoriosa, Centro de Investigaciones Amazónicas CIMAZ, Macagal. 01°30'37"N, 75°40'29"W; 233 m.; 20 Sep. 2017; A. Quiroga leg. • 1♂; Meta, San Juan de Arama, Bosque de Galería, Caño Curia; 24 Sep. 1987. (CAUD). BRAZIL, • 1♀1♂; Amazonas, Manaus, Bosque da Ciência, INPA; 1–20 May. 2010; J.T. Câmara leg. • 1♀; same data collection data as for preceding; 22 May. 2009; coleta manual, T. Mahlmann leg. • 1♀; Amazonas, Rio Abacaxis; 05°15'09"S, 58°41'52"W; 35m; 27–29 May. 2008; Armadilha luz sobre o barco, J.A. Rafael e equipe leg. • 1♂; Amazonas, Manaus, Reserva Adolpho Ducke, km 26; 02°55'49"S, 59°58'31"W; 30 Apr. – 4 May. 2014; Coleta manual, K.F.S. Cezar leg. • 2♀; Amazonas, Tefé, Lago Tefé, Ilha em frente de Tefé; 03°19'55"S, 64°41'11.9"W; 1 Sep. 2018; Coleta em floresta de várzea, D.M.M. Mendes, J.C. Oliveira and J. Oliveira leg. • 1♂; Amazonas, Uarini, Boca do Mamirauá; 03°07'29.4"S, 64°47'32.1"W; 5 Sep. 2018; Coleta em floresta de várzea, D.M.M. Mendes, J.C. Oliveira and J. Oliveira leg. • 1♀; Amazonas, Careiro Castanho, BR-319, km 181, Sítio São Paulo; 04°12'48"S, 60°49'04"W; 24 Mar. 2017; J.A. Rafael and F.F. Xavier F. leg. **Photographic records.** PERU, • 1♀; Loreto Tamshiyacu-Tahuayo Reserve.

**Comments.**—*Eomorphopus antennatus* was described by Bolívar (1887) as *Amorphospus*, and in 1907, Hancock reallocated this species to the new genus *Eomorphopus*. *E. antennatus* is very similar to *E. granulatus* but is distinguished by the biundulated fore femur dorsal margin vs. the triundulated fore femur dorsal margin in *E. granulatus* (Bruner 1910). *E. antennatus* has several records: Peru, Guyana, Venezuela, Ecuador, Suriname, Brazil, and

Trinidad Island. Currently, the depository of the primary type is unknown (Cigliano et al. 2019) and there is a female from Alto Amazonas in Bolívar's Tétrigoidea collection, housed at the National Museum of Natural History, Madrid, Spain (MNCN) (Paris 1993–1994).

A neotype specimen is designated as the carrier-name of the species and is supported by the following reasons (ICZN 1999) Art. 75) 1. The status of the only type specimen is lost. It was deposited in MNCN, but this specimen could not be traced from its original description (Arts. 75.3.1., 75.3.4.). 2. The type female specimen has as type locality Peru, Upper Amazonas, but not having specimens from the same locality, a female from a nearby and available locality of similar geological characteristics was designated (Arts. 75.3.5, 75.3.6; recommendation 75A ICZN). 3. A detailed description is written for the neotype that is in agreement with the general idea of the identity of this species, differentiating it from other taxa, ensuring the recognition of the designated specimen, and conveying a consensus in identifications and wide distribution that characterizes the species, ensuring that most identifications from the past are correct (Arts. 75.3.2, 75.3.3, 75.3.5; recommendation 75B). 4. The neotype is deposited in CAUD, a collection of a recognized scientific institution, which maintains adequate facilities to preserve the types and makes them accessible for study (Art. 75.3.7).

### Amorphopini camouflage

The species of this tribe have the peculiarity of camouflaging themselves among lichens and bryophytes in humid environments of the Amazon (Cadena-Castañeda and Cardona-Granda 2015). When the Amorphopini feel threatened, they take positions to go unnoticed, placing themselves flattened on the substrate to ensure their camouflage with the environment. The front legs are extended towards the front and the middle and the rear legs remain next to the pronotum.

The most striking case is of *A. notabilis*. The individuals of this species exhibit a peculiar design that simulates the surface of trees or rocks covered by diverse lichen and bryophyte communities (Fig. 3). Its whitish coloration simulates foliose lichen (Parmeliaceae and Lobariaceae) or scabby/crustacean lichen (Stereocaulaceae and Roccellaceae), and the reddish to pink coloration of the middle and half of the basal surface of the posterior femur resembles the scabby lichens of the family Arthoniaceae. The gray stripes and other greenish ones give the appearance of surrounding bryophytes mainly of the families Plagiochilaceae and Leucobryaceae. They are usually observed covered by a green dust that consists of microalgae.

### Polychromy in Amorphopini species

Color variation is more conspicuous in *Eomorphopus* species. The individuals of this genus are bluish black, yellowish with brown spots of different shades, light or dark brown (Fig. 7); parts of the body are light or dark brown, with or without stripes (Figs 10, 11). These color variations do not define geographic populations, can occur in specimens from the same locality, and the function of the color variation is still unknown but it may be linked to the microenvironments that individuals inhabit. In *A. notabilis*, the variations are very subtle and are restricted to the intensity of the gray stripes on the body and the reddish color of the middle and hind legs.

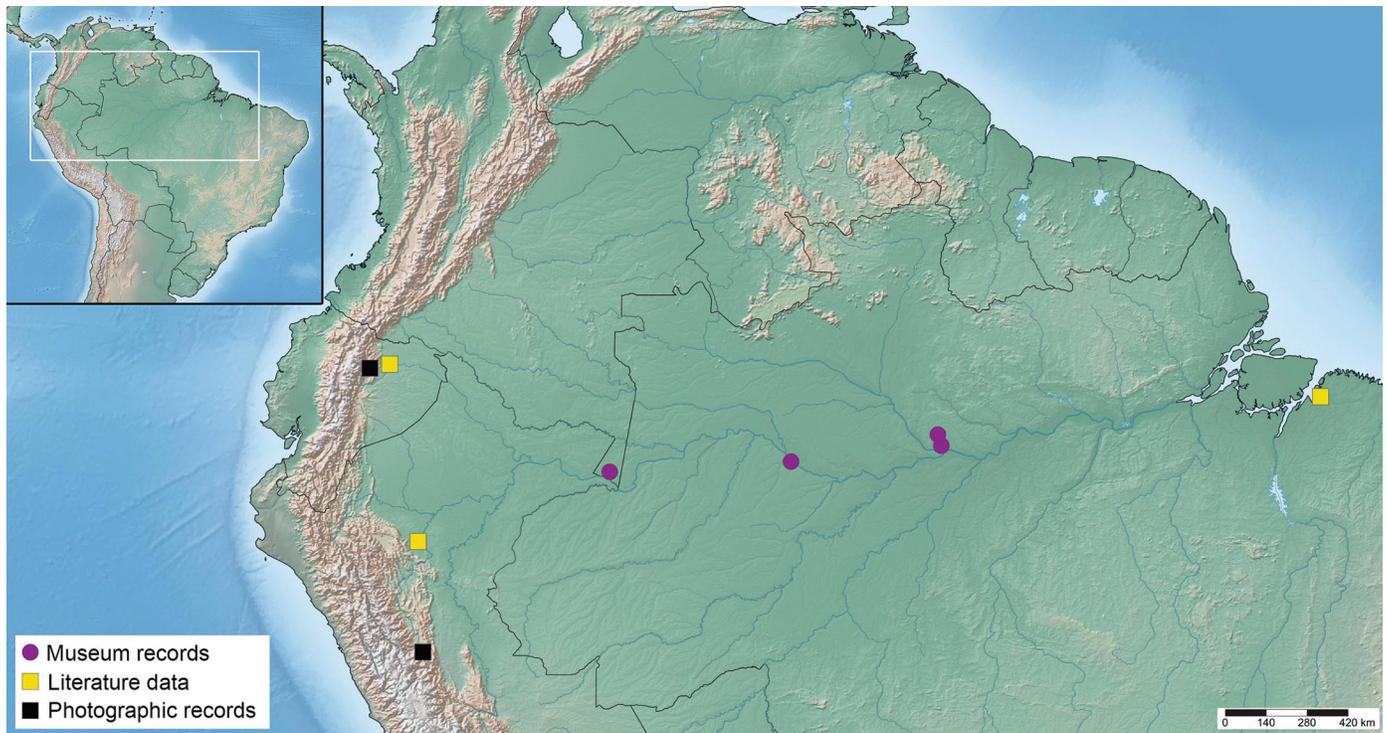


Fig. 12. *Amorphopus notabilis* distribution.

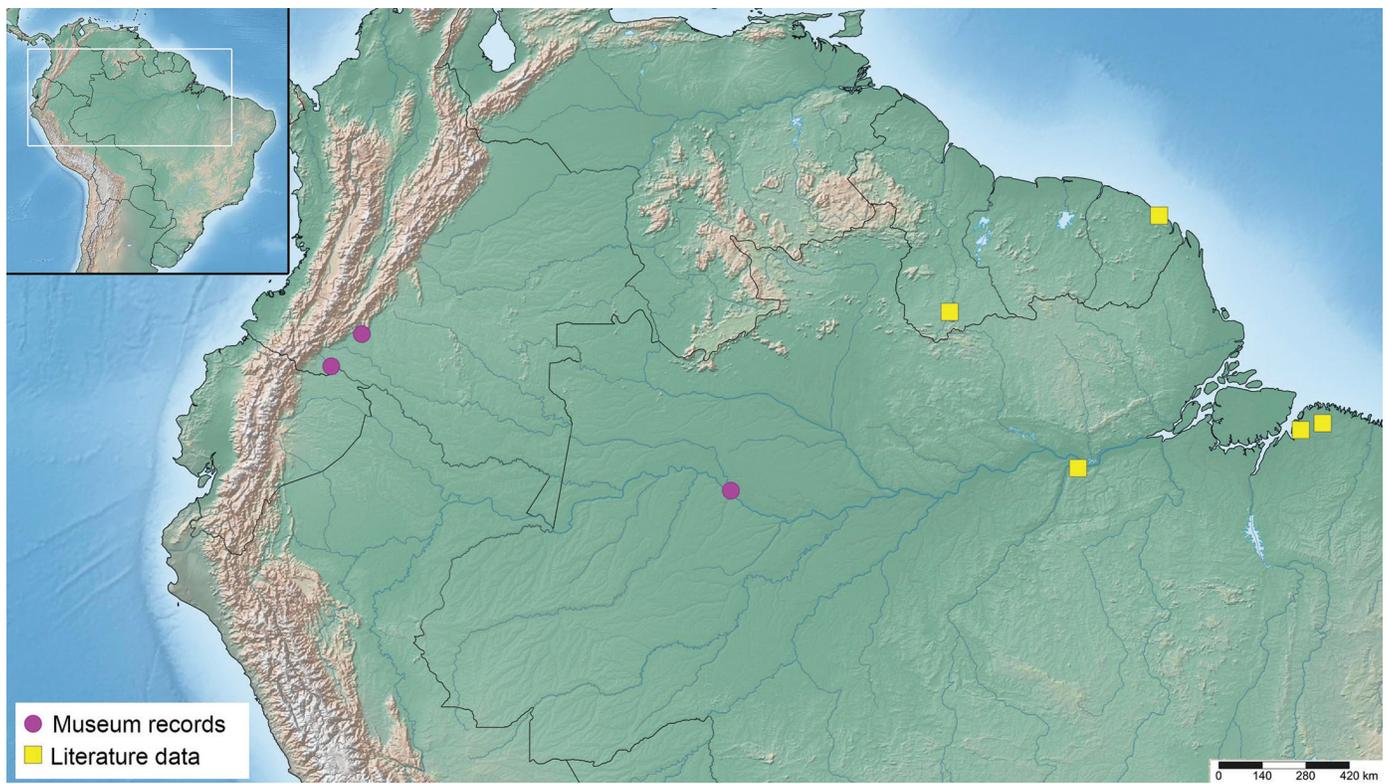


Fig. 13. *Eomorphopus granulatus* distribution.

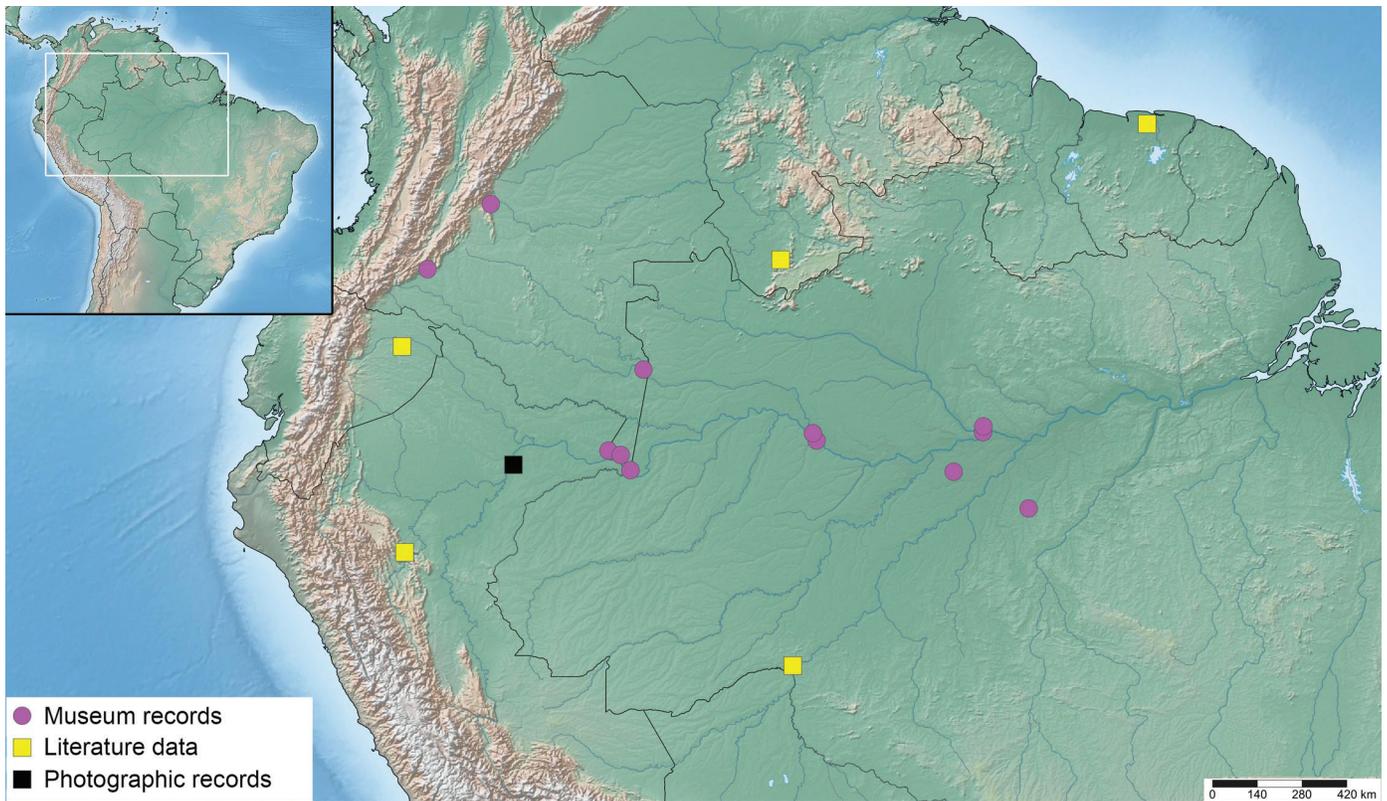


Fig. 14. *Eomorphopus antennatus* distribution.

## Acknowledgements

The study has benefited with grants and facilities from CNPq/Programa SISBIOTA Brasil (Edital MCT/CNPq/MMA/MEC/CAPES/FNDCT e FAPEMIG-Ação Transversal/FAPs 166 n° 47/2010, Proc. n° 563360/2010-0), PROTAX/CNPq/FAPEMIG (Proc. n° 440664/2015-2 and APQ - 04154-15), and FAPEMIG APQ-04154-15. We especially thank Jason Weintraub and Daniel Otte for allowing access to type material of Orthoptera deposited at the Academy of Natural Sciences of Drexel University (ANSP). Fundação de Amparo à Pesquisa do Estado do Amazonas - FAPEAM provided a grant for master studies to DMMM (Edital 016/2006, Proc. 1437/2007). Jonas Alves de Oliveira and Jomara Cavalcante Oliveira provided support during field work and João Rafael Alves-Oliveira helped in revising the manuscript. Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), provided funding and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided a research grant (Process: 300019/2017-3). The photographs of types were taken during the execution of the projects: "The Neotropical Tetrigidae (Caelifera: Tetrigoidea) deposited in the Academy of Natural Sciences of Drexel University, Philadelphia, USA" and "Photographic, sound and distributional data to some Neotropical Orthoptera Groups and Colombian Phasmatodea" financed by The Orthopterists' Society. Finally, we thank Dr. Josef Tumbrinck for his important comments on the manuscript.

## References

- Amédégno C, Devriese H (2008) Global diversity of true and pygmy grasshoppers (Acridomorpha, Orthoptera) in freshwater. *Hydrobiologia*. 595: 535–543. <https://doi.org/10.1007/s10750-007-9132-z>
- Bolívar I (1887) Essai sur les Acridiens de la tribu des Tettigidae. *Annales de la Société Entomologique Belgique* 31: 175–313.
- Bruner L (1910) South American Tetrigidae. *Annals of the Carnegie Museum* 7: 89–143.
- Bruner L (1919–1922) Saltatorial Orthoptera from South America and the Isle of Pines. *Annals of the Carnegie Museum* 13: 5–91.
- Bruner L, Morse AP, Shelford, R (1900–1909) *Biologia Centrali-Americana. Insecta. Orthoptera. Vol. II*, Pub. for the editors by R. H. Porter: London, 379 pp.
- Buzzetti FM, Devriese H (2007) Tetrigidae from Ecuador (Orthoptera Caelifera Tetrigoidea). *Accademia Roveretana degli Agiati* 8: 41–54.
- Cadena-Castañeda OJ (2011a) El género *Adeclus* (Orthoptera: Tettigoniidae): Claves, distribución y notas biológicas. *Journal of Orthoptera Research* 20: 43–49. <https://doi.org/10.1665/034.020.0104>
- Cadena-Castañeda OJ (2011b) La tribu Dysoniini parte I: el complejo *Dysonia* (Orthoptera: Tettigoniidae) y su nueva organización taxonómica. *Journal of Orthoptera Research* 20: 51–60. <https://doi.org/10.1665/034.020.0105>
- Cadena-Castañeda OJ (2012) La tribu Viadaniini n. trib. (Orthoptera: Tettigoniidae): primer aporte a la organización supra-genérica de los faneropterinos neotropicales. *Journal of Orthoptera Research* 21: 25–43. <https://doi.org/10.1665/034.021.0102>
- Cadena-Castañeda OJ (2013a) Revisión de la tribu Dysoniini (Orthoptera: Tettigoniidae: Phaneropterinae) sistemática, filogenia, biogeografía, adaptaciones liquenomórficas y nuevos taxones. Undergraduate Thesis, 250 pp.

- Cadena-Castañeda OJ (2013b) The tribe Dysoniini part II: The genus *Markia* (Orthoptera: Tettigoniidae; Phaneropterinae), new species and some clarifications. *Zootaxa* 3599: 501–518. <https://doi.org/10.11646/zootaxa.3599.6.1>
- Cadena-Castañeda OJ (2013c) La tribu Dysoniini parte III: Adiciones a los géneros *Apolinaria*, *Lichenodraculus*, *Machimoides* y *Markia* (Orthoptera: Tettigoniidae). *Journal of Orthoptera Research* 22: 101–23. <https://doi.org/10.1665/034.022.0202>
- Cadena-Castañeda OJ, Cardona-Granda JM (2015) Introducción a los Saltamontes de Colombia (Orthoptera: Caelífera, Acridomorpha, Tetrigoidea and Tridactyloidea). Lulu press. North Carolina, 534 pp.
- Cadena-Castañeda OJ, Mendes DMM, Silva DSM, Cardona-Granda JM, García García A, Tumbrinck J (2019) Systematics and biogeography of the genus *Scaria* Bolívar, 1887 (Orthoptera: Tetrigidae: Batrachideinae). *Zootaxa* 4675: 1–65. <https://doi.org/10.11646/zootaxa.4675.1.1>
- Cadena-Castañeda OJ, Páez MA (2013) Estudios sobre el comportamiento de los Ortópteros Neotropicales. *Bioma* 14: 53–64.
- Cigliano MM, Braun H, Eades DC, Otte D (2019) Orthoptera Species File. Version 5.0/5.0. <http://Orthoptera.SpeciesFile.org> [visited July 2019]
- Devriese H (1996) Bijdrage tot de systematiek, morfologie en biologie van de West-Palearktische Tetrigidae. *Nieuwsbrief / Lettre de contact Saltabel* 15: 2–38.
- Günther K (1939) Revision der Acrydiinae (Orthoptera), III. Sectio Amorphopi (Metrodora Bol. 1887, aut.). *Abhandlungen und Berichte aus den Staatlichen Museen für Tierkunde und Völkerkunde in Dresden (Ser. A: Zool.) (N.F.)* 20: 335 pp.
- Hancock JL (1907) Orthoptera Fam. Acridiidae. Subfam. Tetriginae. *Genera Insectorum* 48: 1–79.
- Hollier JA (2013) An annotated list of the Orthoptera (Insecta) species described by Henri de Saussure, with an account of the primary type material housed in the Muséum d'histoire naturelle de Genève. Part 4: The Acridomorpha excluding the superfamily Acridoidea. *Revue Suisse de Zoologie* 120: 203–219.
- Huamán L, Westerduijn R, Cadena-Castañeda OJ (2014) Common Orthoptera from Tinga María, Huánuco-Peru. *Field Museum Guides* 1–6.
- ICZN (1999) International Code of Zoological Nomenclature, Fourth Edition, adopted by the International Union of Biological Sciences. International Trust for Zoological Nomenclature, London, xxix + 306 pp.
- Kirby WF (1910) A Synonymic Catalogue of Orthoptera (Orthoptera Saltatoria, Locustidae vel Acridiidae) 3: 674 pp.
- Liebermann J (1955) Primeira relação sistemática dos Acridoideos do Brasil. *Memórias do Instituto Oswaldo Cruz* 53: 329–344. <https://doi.org/10.1590/S0074-02761955000200011>
- Morse AP (1900) Orthoptera. The Acrididae. Subfamily Tettiginae. *Biologia Centrali-Americana* 2: 3–9.
- Olivier GA (1791) *Encyclopédie méthodique. Histoire naturelle. Insectes.* Paris, 6, 702 pp.
- Otte D (1979[1978]) The primary types of Orthoptera (Saltatoria, Blattoidea, Phasmatodea, and Mantodea) at the Academy of Natural Sciences of Philadelphia. *Proceedings of the Academy of Natural Sciences of Philadelphia* 130: 26–87.
- Paris M (1993–1994) *Catálogo de tipos de Ortopteroides (Insecta) de Ignacio Bolívar, I: Blattaria, Mantodea, Phasmoptera y Orthoptera (Stenopelmatoidea, Rhaphidophoroidea, Tettigoniodea, Grylloidea, Tetrigoidea).* *Eos, Revista Española de Entomología* 69: 143–264.
- Rehn JAG (1913) Descriptions and records of South American Orthoptera, with the description of a new subspecies from Clarion Island. *Proceedings of the Academy of Natural Sciences of Philadelphia* 65: 82–113.
- Rehn JAG (1916) The Stanford Expedition to Brazil, 1911 – Dermaptera and Orthoptera I. *Transactions of the American Entomological Society* 42: 251–308.
- Rehn JAG (1918) On a collection of Orthoptera from the State of Pará, Brazil. *Proceedings of the Academy of Natural Sciences of Philadelphia* 70: 146–236.
- Serville JGA (1838) *Histoire naturelle des insectes. Orthoptères.* i–xviii, 776 pp.
- Shorthouse DP (2010) SimpleMappr, an online tool to produce publication-quality point maps. <http://www.simplemappr.net> [visited July 2019]
- Silva DSM, Skejo J, Pereira MR, De Domenico FC, Sperber CF (2017) Comments on the recent changes in taxonomy of pygmy unicorns, with description of a new species of *Metopomystrum* from Brazil (Insecta, Tetrigidae, Cleostratini, Miriatriini). *ZooKeys* 702: 1–18. <https://doi.org/10.3897/zookeys.702.13981>
- Smith JB (1906) Explanation of terms used in entomology. *Brooklyn Entomological Society, Brooklyn*, 154 pp.
- Storozhenko SY (2016) Review of the pygmy grasshoppers of the tribe Cleostratini (Orthoptera: Tetrigidae). *Far Eastern Entomologist* 326: 1–44.
- Tumbrinck J (2014) Taxonomic revision of the Cladonotinae (Orthoptera: Tetrigidae) from the islands of South-East Asia and from Australia, with general remarks to the classification and morphology of the Tetrigidae and descriptions of new genera and species from New Guinea and New Caledonia. *Biodiversity, Biogeography and Nature Conservation in Wallacea and New Guinea* 2: 345–396.
- Walker F (1871) *Catalogue of the Specimens of Dermaptera Saltatoria in the Collection of the British Museum* 5: 811–850.
- Xiberras S, Ducaud P (2004) Sauterelles-feuilles de Guyane: révision du genre *Pterochroza* (Orthoptera: Tettigoniidae: Pseudophyllinae: Pterochrozini). *Lambillionea* 104: 1–38.

# Influence of cold temperature and exposure time on egg overwintering survival in the white-whiskered grasshopper (Orthoptera: Acrididae)

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Academic editor: Ludivina Barrientos-Lozano | Received 30 September 2019 | Accepted 18 November 2019 | Published 14 May 2020

<http://zoobank.org/FEB0C705-B05F-448C-8C3B-6E87DA5AE7EC>

Citation: Branson DH (2020) Influence of cold temperature and exposure time on egg overwintering survival in the white-whiskered grasshopper (Orthoptera: Acrididae). Journal of Orthoptera Research 29(1): 63–65. <https://doi.org/10.3897/jor.29.46967>

## Abstract

The effect of cold temperatures and exposure time on egg survival and hatching success were examined in the white-whiskered grasshopper, *Ageneotettix deorum*. Temperature treatments ranged from 4°C to -35°C, with treatment times ranging from 48 to 240 hours. Both decreasing temperatures and exposure time negatively affected egg survival, with a temperature below -25°C being lethal. Similar lethal temperatures are known for several North American grasshopper species. The relatively shallow location of *A. deorum* egg pods would result in increased vulnerability of eggs to cold temperatures in the absence of snow.

## Keywords

*Ageneotettix*, egg pods, hatching success, lethal temperature

## Introduction

Cold winter air temperatures and snow cover have been assumed to play an important role in grasshopper overwintering egg survival in northern latitudes in North America, but the exact role cold temperatures have on egg survival and population dynamics remains poorly understood (Riegert 1967, Pickford 1970, Mukerji and Braun 1988, Qi et al. 2007). Mukerji and Braun (1988) conducted the only North American quantitative study on grasshopper egg survival and found significant mortality occurred only with temperatures below -15°C for three *Melanoplus* spp. and *Camnula pellucida*. Snow cover generally reduces the impact of cold temperatures on below-ground overwintering insects (Somme 1999, Irwin et al. 2003, Marshall and Sinclair 2012), and few grasshoppers hatched following a winter with temperatures below -30°C and little snow cover in Saskatchewan, Canada (Riegert 1967). Although Mukerji and Braun (1988) argued that cold air temperatures rarely affect egg survival due to insulation from snow, climate change is predicted to result in reduced snow cover duration at northern latitudes while periods of extreme cold will continue (Marshall and Sinclair 2012).

Investigations of chill injury and death can improve the understanding of how extreme cold weather events affect overwin-

tering egg survival (Pang et al. 2014). Cold temperature exposure time, along with super cooling points, is frequently used to assess cold hardiness and mortality of insect eggs (Somme 1999, Pang et al. 2014). In this study, cold temperature effects on egg survival were examined in the white-whiskered grasshopper, *Ageneotettix deorum*, a species that lays egg pods parallel to the soil surface and in the top 0.6 cm (Onsager and Mulhern 1963, Branson 2006). The white-whiskered grasshopper is a widely distributed egg-overwintering grasshopper typically not found at higher elevation sites, with its northern distribution reaching central Alberta and Saskatchewan (Pfadt 2002). The experiment was conducted to determine if eggs of the white-whiskered grasshopper are more vulnerable to temperature extremes than species that lay deeper egg pods or if selection for cold hardiness has reduced vulnerability to temperature extremes, both of which could influence population dynamics (Jing and Kang 2003, Branson and Vermeire 2007).

## Materials and methods

Adult grasshoppers were caught in the field and placed in insect rearing cages containing oviposition trays with a mix of soil, vermiculite, and sand. Cages were maintained at 30°C with a naturally varying light/dark cycle at the USDA Agricultural Research Service Lab in Sidney, Montana, USA (47°43'33"N, 104°9'4"W). Grasshoppers were fed wheat seedlings and wheat bran *ad libitum*, with romaine lettuce added as a supplement. A given set of oviposition trays remained in a cage for ~2.5 weeks starting on August 10<sup>th</sup>, August 27<sup>th</sup>, and September 16<sup>th</sup>, 2010. Trays were then kept at 30°C for two additional weeks to promote egg development. The egg pods were then removed from the trays and 16 egg pods were placed in cups with vermiculite; there were an equal number of egg pods from each removal date and eight replicates per treatment. Environmental test chambers (Model SD-505, Associated Environmental Systems, Ayer, MA, USA) were utilized for temperature treatments, with temperatures verified using dataloggers. Temperature treatments were 4°C (control), -20°C, -25°C, -30°C, and -35°C, with exposure times of 48, 120, and 240 hours. Temperatures and exposure times were chosen based on Parker (1930), with the lowest (-35°C) temperature treatment

chosen specifically due to the shallow egg pod depth in this species. Cups were incubated at cold temperatures for a minimum of 4 months to break obligate diapause (Henry 1985), with cups initially placed in a refrigerator maintained at 4°C, moved to test chambers for cold temperature treatments, and then returned to 4°C. Egg pods in the control treatment remained at a constant 4°C. After egg cups were placed in a test chamber, the chamber was held at 4°C for 48 hours before ramping to the desired treatment temperature over a 15-minute period and then maintained at a constant temperature until the end of the exposure time. Cold treatments began on February 16<sup>th</sup> and March 2<sup>nd</sup> using half of the replicates for each treatment on each date. On March 28<sup>th</sup>, water was added to all cups and cups were then placed at 30°C to begin a 16h:8h (light:dark) cycle. Plastic cages with a wire mesh top were placed on each cup and hatching grasshoppers were counted and removed daily. Egg pods were removed and dissected once no hatching had occurred for 10 days.

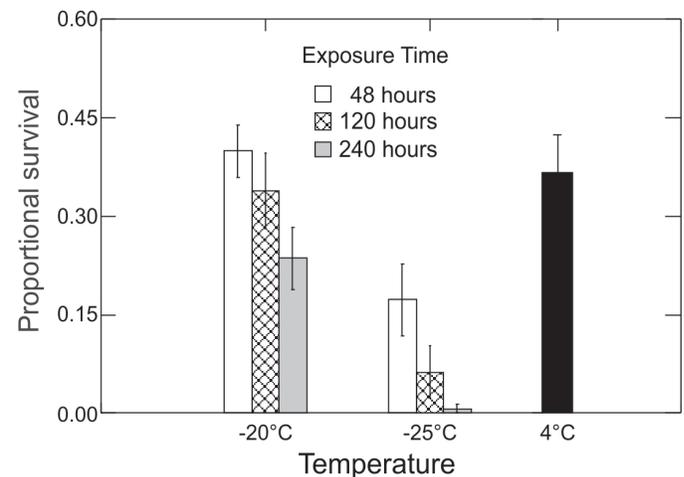
The proportion of eggs hatched was used for statistical analysis after arcsine transformation of the proportion data. As no eggs survived in any exposure time treatment at -30°C and -35°C, those temperatures were not statistically analyzed. For -20°C and -25°C treatments, analysis of variance was used to examine if temperature and exposure time significantly affected the proportion of eggs that hatched. A split plot analysis was used to account for the replicates being evenly divided into separate temperature exposure chamber runs. Additional pairwise comparisons were used to examine treatment differences using Tukey's test. Additional pre-planned pairwise comparisons were used to examine if hatching was reduced in cold temperature treatments relative to the control (4°C) treatment using Tukey's test. Statistical analyses were conducted using Systat 13 (Systat Software 2009).

## Results and discussion

Both temperature and exposure time significantly affected egg survival in the -20°C and -25°C treatments, with the temporally separated chamber runs accounting for very little variation in hatching (Table 1, Fig. 1). For both temperatures, the proportion of eggs hatching decreased with time of exposure (Table 1), with only 3 eggs hatching in the 240 hour -25°C treatment. Survival was lower in the 120 hour exposure than in the 48 ( $P = 0.035$ ), lower in the 240 hour exposure than in the 48 ( $P < 0.001$ ), and lower in the 240 hour exposure than in the 120 ( $P = 0.04$ ). No eggs hatched in any time exposure treatments at -30°C and -35°C, indicating 100% egg mortality occurred at those temperatures. Egg survivorship did not differ significantly between the control (4°C) treatment and 48 hours at -20°C ( $P > 0.3$ ), trended towards sig-

**Table 1.** Results from an ANOVA model examining the effect of temperature and exposure time on proportion of eggs hatching for the -20°C and -25°C treatments, using a split plot analysis to account for treatment replicates being divided between two chambers (Block). Proportion data was arcsine transformed prior to analysis.

ANOVA source	SS	df	F-Ratio	P value
Time	0.651	2	12.63	$P < 0.001$
Temperature	1.791	1	69.54	$P < 0.001$
Time*Temperature	0.076	2	1.48	$P = 0.240$
Block	0.004	1	0.17	$P = 0.680$
Error	1.061	41		



**Fig. 1.** Proportional survival (mean  $\pm$  SE) of white-whiskered grasshopper eggs by temperature (-20°C, -25°C, and 4°C control) and exposure time (48, 120, and 240 hours) treatments (8 replicates with 16 egg pods per replicate). No eggs survived in any exposure time treatment at -30°C and -35°C.

nificance at 120 hours at -20°C ( $P = 0.09$ ), and was significantly lower at 240 hours at -20°C ( $P < 0.01$ ) where survival was reduced by 51%. Egg survival was significantly lower in all three exposure times at -25°C compared to the 4°C control ( $P < 0.001$ ). Egg survival was reduced by 18% with a 48 hour exposure to -20°C relative to 4°C, while survival was reduced by nearly 65% with a 48 hour exposure to -25°C. As no eggs hatched at -30°C, the lethal low temperature for eggs exposed to 48 hours of low temperatures was between -25 and -30°C.

In contrast to the shallow depth egg pods laid by *A. deorum*, *Melanoplus sanguinipes*, examined in cold temperature studies by Parker (1930), Riegert (1967), and Mukerji and Braun (1988), oviposits vertical egg pods with a midpoint depth of  $\sim 2$  cm. Sub-surface temperatures were found to be colder at the depth of *A. deorum* egg pods (0.6 cm) than at the depth of species such as *M. sanguinipes* that lay vertically oriented egg pods, during a cold winter period when snow and litter were removed from the soil surface (Branson unpublished data). Thus, white-whiskered grasshopper eggs would be exposed to colder minimum temperatures than many other grasshoppers when snow cover is limited (Marshall and Sinclair 2012). Mukerji and Braun (1988) tested low temperature impacts on egg mortality in three *Melanoplus* species and *C. pellucida*, but the lowest temperature they tested was -18°C. In a less rigorous study, Parker (1930) found that *M. sanguinipes* and *C. pellucida* egg hatching declined at -25°C, while 100% mortality occurred with varying exposure times at -30°C. Thus, the eggs of several grasshopper species laying egg pods at a range of depths in North America have similar lethal temperatures of -25°C to -30°C, indicating that sustained extremely cold temperatures are required to significantly reduce grasshopper egg survival. Although temperatures were kept constant in this study, winter air temperatures fluctuate and repeated cold exposure events have been shown to modify temperature impacts on eggs (Colinet et al. 2018, Marshall and Sinclair 2018). Due to its shallow egg pod location, the white-whiskered grasshopper may have an increased vulnerability to extreme cold temperature events that could contribute to its northern distribution boundary.

## Acknowledgements

Nicole Davidson caught grasshoppers, coordinated the laboratory work, and collected data.

## References

- Branson DH (2006) Life-history responses of *Ageneotettix deorum* (Scudder) (Orthoptera: Acrididae) to host plant availability and population density. *Journal of the Kansas Entomological Society* 79: 146–155. <https://doi.org/10.2317/0501.11.1>
- Branson DH, Vermeire LT (2007) Grasshopper egg mortality mediated by oviposition tactics and fire intensity. *Ecological Entomology* 32: 128–134. <https://doi.org/10.1111/j.1365-2311.2006.00847.x>
- Colinet H, Rinehart JP, Yocum GD, Greenlee KJ (2018) Mechanisms underpinning the beneficial effects of fluctuating thermal regimes in insect cold tolerance. *Journal of Experimental Biology* 221: jeb164806. <https://doi.org/10.1242/jeb.164806>
- Henry JE (1985) *Melanoplus* spp. In: Singh P, Moore RF (Eds) *Handbook of Insect Rearing*. Elsevier Science Publishers B.V., Amsterdam, 451–464.
- Irwin JT, Lee J, Richard E (2003) Cold winter microenvironments conserve energy and improve overwintering survival and potential fecundity of the goldenrod gall fly, *Eurosta solidaginis*. *Oikos* 100: 71–78. <https://doi.org/10.1034/j.1600-0706.2003.11738.x>
- Jing XH, Kang L (2003) Geographical variation in egg cold hardiness: A study on the adaptation strategies of the migratory locust *Locusta migratoria* L. *Ecological Entomology* 28: 151–158. <https://doi.org/10.1046/j.1365-2311.2003.00497.x>
- Marshall KE, Sinclair BJ (2012) Threshold temperatures mediate the impact of reduced snow cover on overwintering freeze-tolerant caterpillars. *Naturwissenschaften* 99: 33–41. <https://doi.org/10.1007/s00114-011-0866-0>
- Marshall KE, Sinclair BJ (2018) Repeated freezing induces a trade-off between cryoprotection and egg production in the goldenrod gall fly, *Eurosta solidaginis*. *Journal of Experimental Biology* 221: jeb177956. <https://doi.org/10.1242/jeb.177956>
- Mukerji MK, Braun MP (1988) Effect of low temperatures on mortality of grasshopper eggs (Orthoptera, Acrididae). *Canadian Entomologist* 120: 1147–1148. <https://doi.org/10.4039/Ent1201147-12>
- Onsager JA, Mulkern GB (1963) Identification of eggs and egg-pods of North Dakota grasshoppers (Orthoptera: Acrididae). *North Dakota Agricultural Experiment Station Bulletin No. 446*: 3–47.
- Pang BP, Li N, Zhou XR (2014) Supercooling capacity and cold hardiness of band-winged grasshopper eggs (Orthoptera: Acrididae). *Journal of Insect Science* 14: 1–289. <https://doi.org/10.1093/jisesa/ieu151>
- Parker JR (1930) Some effects of temperature and moisture upon *Melanoplus mexicanus mexicanus* Saussure and *Camnula pellucida* Scudder (Orthoptera). *University of Montana Agricultural Experiment Station Bulletin* 223: 1–132.
- Pfadt RE (2002) *Field Guide to Common Western Grasshoppers* (3<sup>rd</sup> edition). Wyoming Agricultural Experiment Station Bulletin, 912 pp.
- Pickford R (1970) The effects of climatic factors on egg survival and fecundity in grasshoppers. In: Hemming CF, Taylor THC (Eds) *International Study Conference on the Current and Future Problems of Acridology*. London Centre for Overseas Pest Research, London, 257–260.
- Qi XL, Wang XH, Xu HF, Kang L (2007) Influence of soil moisture on egg cold hardiness in the migratory locust *Locusta migratoria* (Orthoptera: Acrididae). *Physiological Entomology* 32: 219–224. <https://doi.org/10.1111/j.1365-3032.2007.00564.x>
- Riegert PW (1967) Association of subzero temperatures, snow cover, and winter mortality of grasshopper eggs in Saskatchewan. *The Canadian Entomologist* 99: 1000–1003. <https://doi.org/10.4039/Ent991000-9>
- Somme L (1999) The physiology of cold hardiness in terrestrial arthropods. *European Journal of Entomology* 96: 1–10.
- Systat Software (2009) *Systat 13: Statistics*. Systat Software, Richmond.



# Grasshopper populations respond similarly to multiple moderate intensity livestock grazing treatments

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Academic editor: Maria-Marta Cigliano | Received 30 September 2019 | Accepted 21 November 2019 | Published 14 May 2020

<http://zoobank.org/BB3F6B96-BA16-47F2-96F0-103FA9FE87B8>

Citation: Branson DH (2020) Grasshopper populations respond similarly to multiple moderate intensity livestock grazing treatments. *Journal of Orthoptera Research* 29(1): 67–69. <https://doi.org/10.3897/jor.29.46966>

## Abstract

Livestock grazing frequently affects grasshopper populations, but no prior studies have simultaneously examined a wide range of moderate intensity livestock grazing treatments in the Northern Great Plains. Grasshopper densities varied significantly between years, but five moderate grazing treatments, including both rotational and continuous grazing treatments, did not differentially affect grasshopper densities or species composition. Grasshopper populations appear resilient to different types of moderate grazing at this Northern Great Plains mixed-grass prairie site.

## Keywords

Acrididae, continuous grazing, grasshopper density, Great Plains, mixed prairie, rangeland, rotational grazing

## Introduction

Grasshoppers are frequently the most abundant herbivore in North American grasslands, often consuming more vegetation than livestock during outbreaks and can be in competition with livestock (Branson et al. 2006, Branson and Haferkamp 2014). Grasshopper responses to livestock grazing vary across western U.S. ecosystems (Branson et al. 2006). Livestock grazing can reduce food availability for grasshoppers, modify plant species composition, and impact habitat structure (Fielding and Brusven 1996, Onsager 2000, Branson et al. 2006, O'Neill et al. 2010, LeGall et al. 2019). Species specific responses to livestock grazing are common, with many pest grasshoppers in the Northern Great Plains thriving in open microhabitats (Onsager 2000, Joern 2004, 2005, Joern and Laws 2013).

Relatively few studies in the Northern Great Plains have assessed how grazing intensity or treatments with a similar grazing intensity affect grasshopper populations (Onsager 2000, Branson and Sword 2010, Branson and Haferkamp 2014, Branson and Vermeire 2016). Certain moderate intensity livestock grazing systems appear to have potential for use as a vegetation habitat manipulation tool in managing grasshoppers, with continuous and twice-over rotational livestock management systems differentially affecting grasshopper populations in the Northern Great Plains (Onsager 2000, Branson et al. 2006). No previous studies have

examined impacts of many moderate grazing intensity treatments on grasshopper populations in the Northern Great Plains. The objective of this study was to examine grasshopper density and community composition responses to five moderate intensity livestock grazing treatments, as part of a study examining vegetation responses to grazing (Vermeire et al. 2008).

## Materials and methods

The experiment was conducted on the USDA, ARS, Fort Keogh Livestock and Range Research Laboratory near Miles City, Montana, USA (46° 19' 25" N, 105° 49' 36" W). The study site and experimental design are fully described in Vermeire et al. (2008). Vegetative biomass was dominated by perennial grasses, with blue grama-needlegrass-wheatgrass the dominant rangeland vegetation type (Vermeire et al. 2008). Five grazing treatments with an identical moderate cattle grazing rate of 28.8 animal unit days ha<sup>-1</sup> year<sup>-1</sup> were compared. These covered a wide range of livestock grazing management approaches used in the region of the study site. Technical details of the grazing treatments are fully described in Vermeire et al. (2008). The five grazing treatments were: season-long continuous livestock grazing; high-intensity, low-frequency grazing with a 24-day graze followed by a 706-day rest period; short-duration grazing with a three-day graze followed by a 42-day rest period; three-pasture winter rotation grazing; and three-pasture summer, twice-over rotation grazing with 15- and 30-day graze periods (Vermeire et al. 2008). Treatments were randomly assigned to two replicate 6.1 ha pastures. Vegetation responses including biomass and composition were measured (Vermeire et al. 2008). Grazing treatments were initiated in 1997 and grasshopper sampling occurred from 1997 to 2000. Grasshopper densities were assessed between June and early September each year, with ten samples in 1997 and 1998, eight in 1999, and four in 2000. In each replicate pasture, 40 rings of 0.1 m<sup>2</sup> were permanently placed in four transects located approximately 5–10 m from each other, and the number of grasshoppers flushed from each ring were counted. Random sweep net samples were collected to assess grasshopper species composition on July 13<sup>th</sup> and 23<sup>rd</sup>, 1999, and July 12<sup>th</sup> and August 1<sup>st</sup> of 2000.

As grasshoppers in the study area are univoltine and sampling efforts varied, density samples were averaged within each year.

Treatment differences in densities over four years were assessed using a repeated-measures ANOVA model. A permutational distance-based MANOVA (PERMANOVA), using a Bray-Curtis (Sorensen) distance measure, was used to assess treatment differences in grasshopper community composition (Anderson 2001, 2017). Species that occurred in only one plot were deleted prior to analysis (McCune and Grace 2002). As the number of species present in at least two plots varied between years, community composition was analyzed separately for 1999 and 2000. Due to the low replication, a significance level of 0.1 was deemed appropriate *a priori*. Systat 13 was used for the repeated measures analysis and PC-ORD 6.22 was used for PERMANOVA analyses.

## Results and discussion

Grasshoppers were generally abundant during the study, with relatively stable densities during the last three years (Fig. 1). The grasshopper community was dominated by two Gomphocerinae (slantfaced) species, *Opeia obscura* and *Ageneotettix deorum*, and two Melanoplineae (spurthroated) species, *Phoetaliotes nebrascensis* and *Melanoplus sanguinipes* (Table 1). Three of these species feed primarily on grasses and sedges, while *M. sanguinipes* is a generalist, mixed grass and forb feeder. Community composition did not differ between grazing treatments in either 1999 or 2000 (Table 2). There were also no significant grasshopper density differences between the moderate grazing rate treatments, although densities differed between years (Table 2). Study replication was low, but there was no indication that moderate grazing treatments differentially affected grasshoppers as treatments explained very little of the variation in densities (Table 2). The lack of density and species composition differences between moderate intensity grazing treatments parallels the vegetation results of Vermeire et al. (2008). Standing vegetation biomass and functional composition were largely resistant to moderate grazing systems, with similar results between rotational and continuous grazing strategies (Vermeire et al. 2008).

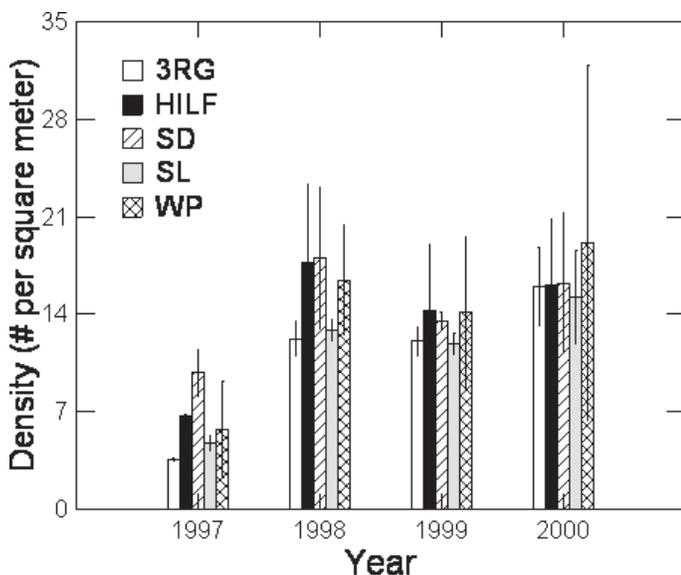


Fig. 1. Average grasshopper density (# per m<sup>2</sup>, mean ± SE) from 1997 through 2000 for each treatment. (3RG: three-pasture, twice-over rotational grazing; HILF: high-intensity low-frequency grazing; SD: short-duration grazing; SL: season-long continuous grazing; and WP: three-pasture winter rotation).

Table 1. Average grasshopper species composition from sweep net samples at the site in 1999.

Species	% of total caught
<i>Opeia obscura</i>	25.3
<i>Ageneotettix deorum</i>	25.1
<i>Phoetaliotes nebrascensis</i>	22.1
<i>Melanoplus sanguinipes</i>	16.9
<i>Trachyrhachys kiowa</i>	3.1
<i>Eritettix simplex</i>	1.7
<i>Encoptolophis costalis</i>	1.3
<i>Mermiria bivittata</i>	1.1

Table 2. Statistical results from A. Repeated measures ANOVA model examining grazing treatment effects on average grasshopper density across all years; B. Permutational multivariate analysis of variance examining treatment effects on grasshopper community composition in 1999 with analysis based on Bray-Curtis dissimilarities; and C. Permutational multivariate analysis of variance examining treatment effects on grasshopper community composition in 2000 with analysis based on Bray-Curtis dissimilarities.

	Factor	df	SS	F	P
A.	Year	3	660.881	39.554	0.000
	Year*Grazed	12	48.661	0.728	0.707
	Error	15	83.543		
B.	Grazed	4	0.360	1.277	0.280
	Residual	5	0.353		
	Total	9	0.713		
C.	Grazed	4	0.338	1.319	0.319
	Residual	5	0.321		
	Total	9	0.659		

The season-long continuous and three-pasture, twice-over summer rotation grazing treatments in this study were similar to treatments shown to impact grasshopper microhabitat availability and developmental rates in a study in western North Dakota, USA (Onsager 2000). Grasshopper densities in that study averaged six times higher under continuous grazing compared to twice-over rotational grazing during a two-year period with outbreak densities, which was hypothesized to result from increased ground cover from grass tillering and reduced habitat quality for grasshoppers in the rotational grazing system. In contrast to the results in North Dakota, most replicate pastures in this study had abundant bare ground and low vegetation ground cover, which would reduce the potential impacts of grass tillering. In addition, the below-average spring precipitation observed during three of the four study years likely constrained vegetation responses, as plant biomass production in the study area is closely linked to April and May precipitation (Vermeire et al. 2008). Branson and Sword (2010) also examined the impact of rotational versus continual grazing and found relatively weak effects of grazing during a five-year study when grasshopper densities were low. The results of this study conducted during a period of high grasshopper densities, combined with the results of Branson and Sword (2010), indicate that grasshopper populations may commonly be resilient to moderate grazing in the Northern Great Plains. Given the variable results between the three studies to date, additional experiments examining how grasshoppers respond to differing moderate intensity livestock grazing treatments are needed.

## Acknowledgements

Jerry Onsager, Jeff Holmes, Sarah Bucklin-Comiskey, and Mitch Faulkner assisted in field work.

## References

- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Anderson MJ (2017) Permutational Multivariate Analysis of Variance (PERMANOVA). In: Balakrishnan N, Colton T, Everitt B, Piegorsch W, Ruggeri F, Teugels JL (Eds) *Wiley StatsRef: Statistics Reference Online*. <https://doi.org/10.1002/9781118445112.stat07841>
- Branson DH, Haferkamp MA (2014) Insect herbivory and vertebrate grazing impact food limitation and grasshopper populations during a severe outbreak. *Ecological Entomology* 39: 371–381. <https://doi.org/10.1111/een.12114>
- Branson DH, Joern A, Sword GA (2006) Sustainable management of insect herbivores in grassland ecosystems: New perspectives in grasshopper control. *Bioscience* 56: 743–755. [https://doi.org/10.1641/0006-3568\(2006\)56\[743:SMOIHJ\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[743:SMOIHJ]2.0.CO;2)
- Branson DH, Sword GA (2010) An experimental analysis of grasshopper community responses to fire and livestock grazing in a northern mixed-grass prairie. *Environmental Entomology* 39: 1441–1446. <https://doi.org/10.1603/EN09378>
- Branson DH, Vermeire LT (2016) Grasshopper responses to fire and postfire grazing in the Northern Great Plains vary among species. *Rangeland Ecology and Management* 69: 144–149. <https://doi.org/10.1016/j.rama.2015.10.005>
- Fielding DJ, Brusven MA (1996) Livestock grazing and grasshoppers: An interregional perspective. *University of Idaho College of Agriculture Bulletin* 786: 1–12.
- Joern A (2004) Variation in grasshopper (Acrididae) densities in response to fire frequency and bison grazing in tallgrass prairie. *Environmental Entomology* 33: 1617–1625. <https://doi.org/10.1603/0046-225X-33.6.1617>
- Joern A (2005) Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology* 86: 861–873. <https://doi.org/10.1890/04-0135>
- Joern A, Laws AN (2013) Ecological mechanisms underlying arthropod species diversity in grasslands. *Annual Review of Entomology* 58: 19–36. <https://doi.org/10.1146/annurev-ento-120811-153540>
- Le Gall M, Overson R, Cease A (2019) A global review on locusts (Orthoptera: Acrididae) and their interactions with livestock grazing practices. *Frontiers in Ecology and Evolution* 7: 1–263. <https://doi.org/10.3389/fevo.2019.00263>
- McCune B, Grace JB (2002) *Analysis of Ecological Communities*. MJM Software Design, Gleneden Beach.
- O'Neill KM, Olson BE, Wallander R, Rolston MG, Seibert CE (2010) Effects of livestock grazing on grasshopper abundance on a native rangeland in Montana. *Environmental Entomology* 39: 775–786. <https://doi.org/10.1603/EN09173>
- Onsager JA (2000) Suppression of grasshoppers in the Great Plains through grazing management. *Journal of Range Management* 53: 592–602. <https://doi.org/10.2307/4003152>
- Vermeire LT, Heitschmidt RK, Haferkamp MR (2008) Vegetation response to seven grazing treatments in the Northern Great Plains. *Agriculture, Ecosystems and Environment* 125: 111–119. <https://doi.org/10.1016/j.agee.2007.12.003>



# Consequences of advanced maternal age on reproductive investment by male offspring

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Academic editor: Kevin Judge | Received 19 August 2019 | Accepted 31 October 2019 | Published 14 May 2020

<http://zoobank.org/3CA3669E-085A-444D-87C5-DD8469E6662C>

Citation: Wilson JD, Anner SC, Murphy SM, Tinghitella RM (2020) Consequences of advanced maternal age on reproductive investment by male offspring. Journal of Orthoptera Research 29(1): 71–76. <https://doi.org/10.3897/jor.29.39228>

## Abstract

Maternal age can have contrasting effects on a variety of offspring fitness traits. While the effects of maternal age on offspring traits that are not sex-specific, such as body size and growth rate, as well as on traits specific to females, have been well researched, traits that are specific to male offspring have been understudied. Across taxa, male reproductive investment is a particularly salient component of fitness, especially when females mate with several males. We tested whether maternal age affects the reproductive traits of their male offspring by comparing the investment made by male field crickets, *Teleogryllus oceanicus*, from 'young' and 'old' maternal age treatments. Female *T. oceanicus* mate with several males, and sperm competition is a fair lottery, so male reproductive investment is important for fitness in this system. After two generations of mating young and old females, we measured the testes mass, spermatophore mold mass, and sperm viability of their male offspring. Despite differences in maternal and grand-maternal age and the demonstrated effects of advanced maternal age on egg number and offspring immunocompetency in this system, the male offspring of young and old females did not differ in reproductive tissues and sperm viability. This study is one of the first to examine the effect of maternal age on fitness-related traits specific to male offspring, and we encourage future research that tests the effects of maternal age on male offspring in other species.

## Keywords

aging, aging theory, life history theory, male fitness, maternal effect, sperm viability

## Introduction

Intrinsic characteristics of parents and their experiences through life can have profound effects on offspring traits through parental effects (reviewed in Badyaev and Uller 2009). Age is a particularly important component of a parent's condition that impacts offspring traits ranging from disease resistance to growth in numerous taxa including insects (Bloch Qazi et al. 2017), fish (Berkeley et al. 2004, Hansen et al. 2015), mammals (Descamps

et al. 2008), and birds (Asghar et al. 2014). However, the effects of parental age on the traits of the offspring are not consistent across studies and can be positive, negative, or neutral. The effects of advanced parental age on offspring fitness typically support one of two major bodies of literature: life history theory or aging theory. One component of life history theory—the terminal investment hypothesis—predicts that at later stages in life, selection will favor life histories that invest heavily in reproduction because the need to invest in survival and future reproduction is minimal at that stage (Trivers 1974, Partridge and Harvey 1988); terminal investment, then, has the potential to increase the fitness of aging parents (with all else equal). Aging theory predicts that older parents are unable to make reproductive investments late in life or that such investments are poor due to the detrimental effects of senescence (Nussey et al. 2013, Lemaitre and Gaillard 2017); if so, offspring born to old females may be less fit than offspring born to young females. Even if females of advanced age invest heavily in their offspring (terminal investment), consistent with life-history theory, limited resources late in life may mean that that investment is lower than investments made at younger ages. An alternative, of course, is that there may simply be no change in maternal investment with maternal age. Both the terminal investment literature and aging literature have traditionally focused on the effects of advanced parental age on traits that are relevant to both sexes (such as body size or growth rate) or investigated fitness effects only for female offspring.

Male fitness is often determined, to some extent, by the investment made in postcopulatory reproductive traits (Harcourt et al. 1981, Taborsky 2002, Parker 2015). Though males invest less in individual gametes than females, males are limited in the amount of sperm they can allocate to each reproductive opportunity (Wedell et al. 2002). Males can optimize investment in reproductive bouts by adjusting the size or contents of their ejaculate to match perceived levels of mate availability and sperm competition (Simmons 2003, Reinhardt et al. 2011, Vahed et al. 2011). Little work has linked maternal age to investment in traits specific to male offspring, though

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research has found that older female seed beetles had male offspring with longer sperm (Dowling et al. 2007, Gay et al. 2009); the fitness consequences of sperm length for males were, however, unclear in these studies. In other studies, no link was found between maternal age and the fitness of their male offspring (Mossman et al. 2019).

In crickets, females mate with multiple males and store sperm in a round spermatheca, leading to a fair 'lottery' in determining which sperm fertilize available eggs (Larson et al. 2012). Therefore, in crickets, male investment in reproductive traits, such as sperm volume and sperm viability, are particularly important determinants of paternity, more so than other factors like mating order (Sakaluk and Eggert 1996, Simmons 2003, Bretman et al. 2009). We studied the Pacific field cricket, *Teleogryllus oceanicus*. In this species, females mate with multiple males, and males that invest more in postcopulatory reproductive traits (such as sperm viability) tend to father more offspring (Garcia-Gonzalez and Simmons 2005). Male investment in reproductive somatic tissue is particularly plastic in *T. oceanicus*, changing, for instance, in response to rearing environments that mimic a high density of males (Bailey et al. 2010, Gray and Simmons 2013). We tested if maternal age influences male reproductive traits, given that 1) male investment in reproductive traits can be adjusted through plasticity, 2) male investment in reproductive traits is important for male fitness, 3) quality-related traits of offspring are sometimes dependent on parental age (e.g., Bloch Qazi et al. 2017), and 4) maternal age has been found to have an impact on daughters' traits in this species (unpublished results).

We investigated the effects of advanced maternal age on male reproductive investment by measuring the testes mass, spermatophore mold mass, and sperm viability of male offspring following two generations of mating females at either a young or old age (Fig. 1). We had two questions: 1) does maternal age affect the reproductive investment of male offspring and, if so, 2) does the effect of maternal age on male reproductive investment support the predictions of life history theory or aging theory? In the broadest sense, support for life history theory would come from male offspring of older mothers and grandmothers having greater (or equal) reproductive investment as compared with male offspring of younger mothers and grandmothers. Alternatively, if male offspring of older mothers and grandmothers show lower reproductive investment than male offspring of younger mothers and grandmothers, this would support aging theory.

## Methods

**Study system and design.**—To study the effects of maternal age on male reproductive investment, we used the Pacific field cricket, *T. oceanicus*, because they live a relatively long time for an insect and male reproductive investment is easily measured using established methods. Female *T. oceanicus* mate throughout their life and with multiple males (Simmons 2003), a breeding system that should lead to selection on postcopulatory reproductive traits of males (Simmons 2001). Additionally, testes mass is a well-established measure of male reproductive investment in this cricket (Bailey et al. 2010, Gray and Simmons 2013).

The *T. oceanicus* individuals that we used in this study were from a laboratory colony established from animals collected at the University of California's Gump Field Station on the Polynesian island of Mo'orea in 2014. A colony typically contains approximately 100 breeding adults. We randomly chose 10 females from the colony to serve as our founding females in April of 2017. We mated the 10 founding females at 7 days post-eclosion (DPE) and then started mating their female offspring at either a young age (young treat-

ment) or an old age (old treatment) for two generations (Fig. 1). We mated females in the young treatment at 7 DPE and females in the old treatment at 25 DPE, which is close to the natural adult lifespan of about one month. Thus, we had two treatments: one in which we mated both the grandmother and mother of our study males at a young age (young treatment), and the other in which we mated both the grandmother and the mother at an old age (old treatment). This experiment is part of a larger fully factorial experiment in which all combinations of old and young mothers and grandmothers are included. We chose to investigate the effects of maternal age on male sexual traits in the two treatments in which we expected to see the greatest potential effect of maternal age; this means that we cannot differentiate maternal from grandmaternal effects in this experiment. To mate each female, we placed her in a 0.5 L deli cup with an unrelated colony male for a 4-hour period over multiple consecutive days (7 days for founding females and 3 days for both subsequent generations). To reduce the possible effects of paternal age, all males used for matings were 5–10 DPE.

**Rearing.**—We kept all crickets in temperature-controlled (27°C) Percival incubators (model I36VLC8) on a 12h:12h light:dark schedule throughout the experiment. We housed juvenile crickets in family groups inside 0.5 L deli cups and supplied them with Fluker's High Calcium Cricket Chow, part of an egg carton for shelter, and moist cotton for water. We checked for eclosions daily and separated males and females immediately (<24 hours from eclosion). We housed all females that were to be mated individually in 0.5 L deli cups provisioned with Kaytee Rabbit Chow, egg carton for shelter, and moist cheese cloth for water and egg deposition. After eclosion, we housed all male crickets in individual 118 mL Ziploc containers provisioned similarly to the females.

**Male reproductive investment.**—For the male crickets that we studied, we measured three aspects of male reproductive investment: testes mass, spermatophore mold mass, and sperm viability. We measured male reproductive investment on males that were 1–22 DPE. After collecting a fresh spermatophore from each male for sperm viability testing, we euthanized males by freezing and stored them dry in individual, sterile 1.5 mL microcentrifuge tubes at -20°C between March and April of 2018. We thawed the males to dissect fully intact reproductive tissues from them: the testes (which generate sperm) and the spermatophore mold (which holds and shapes the sperm containing packet before it exits the male's body; Khalifa 1949). We were unable to dissect out the accessory glands (which are responsible for producing seminal fluid) because they had partially disintegrated while the male was frozen. We dissected the testes and the spermatophore mold from all males from both treatments at one of two times: July of 2018 (young treatment, n = 7 individuals, and old treatment, n = 48 individuals) and April of 2019 (young treatment, n = 38 individuals, and old treatment, n = 28 individuals). Hereafter, we refer to the dataset that consists of males we dissected in July 2018 as the 'early' dataset and the dataset that consists of males we dissected in April 2019 as the 'late' dataset. We refer to the dataset that includes all males as the complete dataset.

To test sperm viability, we used a ThermoFisher LIVE/DEAD sperm viability kit and established methods (Garcia-Gonzalez and Simmons 2005). The ThermoFisher LIVE/DEAD kit stains live sperm green and dead sperm red. Immediately after staining, we imaged all sperm samples using a Leica M165FC scope with an EC3 camera on a computer running LAS X imaging software. We captured two images from the same view window of each sample:

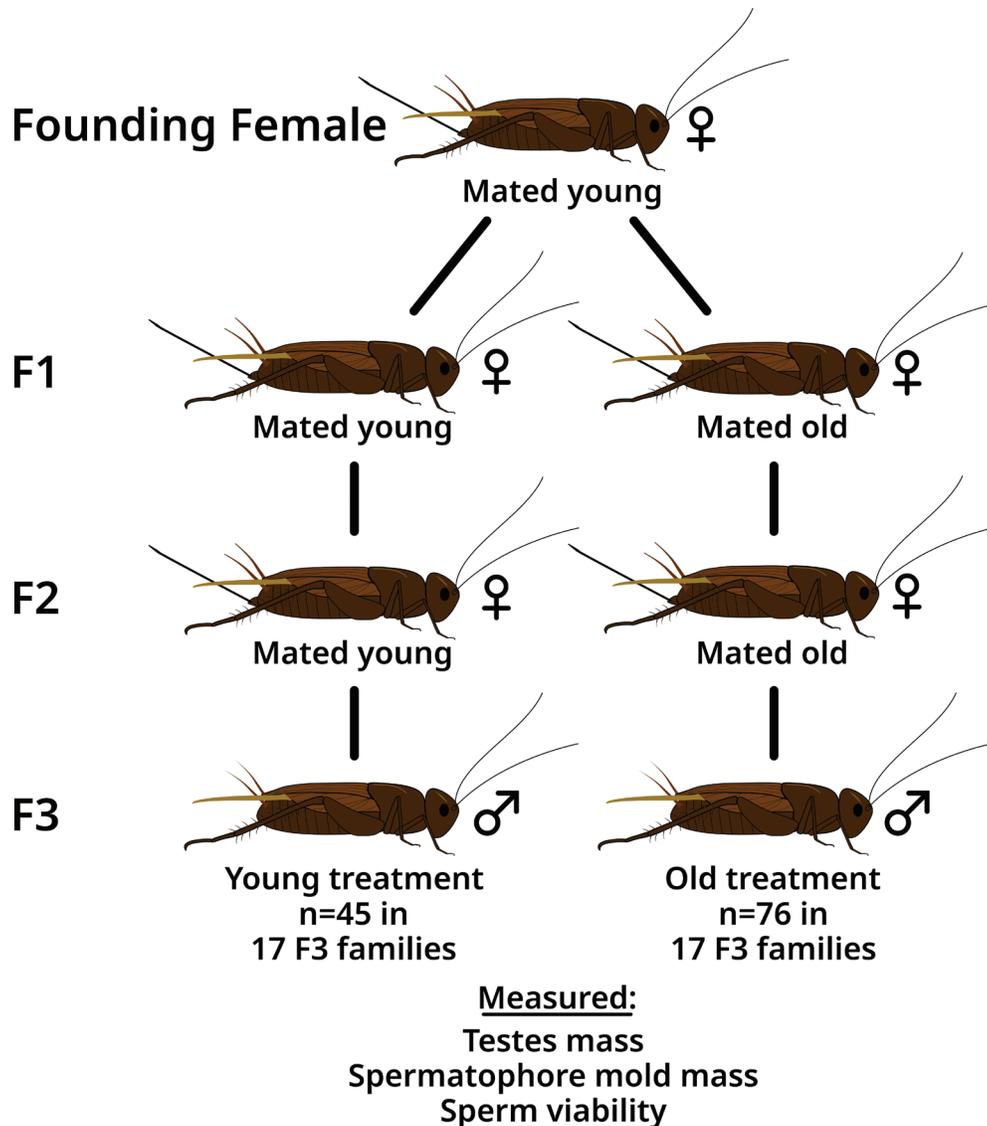


Fig. 1. A diagram of our experimental mating design. We mated females at either a young age (7 days after eclosion to adulthood) or an old age (25 days after eclosion to adulthood) for two subsequent generations, then measured three proxies of reproductive investment in males of the F3 generation. The F3 families from the Old treatment were the offspring of 8 founding females and the F3 families from the Young treatment were the offspring of 7 founding females.

one image using a FITC excitation filter (for the green-stained, live sperm) and one image using a TRITC excitation filter (for the red-stained, dead sperm). After imaging, we overlaid a  $36 \times 24$  grid on both images from each sample using Inkscape (a vector graphics editing program) to facilitate counting of sperm cells. We counted 25% of each image (or 216 grid squares) by haphazardly choosing an evenly spaced subset of grid rows and counting those same rows in each image. We counted live and dead images separately and recorded any sperm cells that fell within the counted area, including those that landed on the top or bottom line. We recorded sperm viability as the proportion of total counted sperm that were alive. Due to the inherent difficulties of rearing two generations of crickets at different mating ages, the majority of young treatment males were euthanized by the time we started collecting sperm viability data. Therefore, we only have sperm viability for 7 males in the young treatment and 48 males in the old treatment; these are the same males from the early dataset described above.

*Statistical analysis.*—We used a linear mixed model to test the effect of maternal age treatment on testes mass and spermatophore mold mass using the complete dataset. We transformed spermatophore mold mass using a cube-root transformation to meet assumptions of normality and equal variance. We had two response variables: testes mass and spermatophore mold mass. We included *maternal age treatment* as a fixed effect and *age of the male* when euthanized and *pronotum width* (a measure of size) as covariates. We included male age as a covariate in our models because male age impacts sperm viability in *T. oceanicus* (Garcia-Gonzalez and Simmons 2005, Dowling and Simmons 2012). We included *dissection date* as a fixed effect in the model because we noticed that tissue dissected at the later date was generally smaller than tissue dissected at the earlier date, likely due to the extra time that the tissue spent in the freezer. We included the *maternal line* of each male as a random effect that accounted for the identity of the founding female, grandmother, and mother of each male and also any variation in rearing environments among

families. We also initially included the interaction between *dissection date* and *maternal age treatment*, but the interaction was not significant so we removed it from the model. Therefore, our final model included *maternal age treatment*, *age of the male*, *pronotum width*, and *dissection date* as fixed effects and *maternal line* as the random effect.

We also tested the effect of maternal age treatment on testes mass and spermatophore mold mass using only the individuals from the late dataset because this dataset had a more balanced sample size (young treatment  $n = 38$ , and old treatment  $n = 28$ ) than the early dataset and the complete dataset. We ran the same statistical model described above for both testes mass and transformed spermatophore mold mass, but because these males were all from a single dissection date, we removed *dissection date* as a fixed effect. Thus, our final model included *maternal age treatment*, *age of the male*, and *pronotum width* as fixed effects and *maternal line* as the random effect.

We used one additional linear mixed model to test the effect of maternal age on the sperm viability of male offspring. We checked the sperm viability data for equality of variance and normality before proceeding with analysis. We only measured sperm viability for males from the early dataset and, thus, our sample size was unbalanced (young treatment  $n = 7$ , and old treatment  $n = 48$ ). Our statistical model included *maternal age treatment*, *age of the male*, and *pronotum width* as fixed effects and *maternal line* as the random effect.

We used post-hoc power analyses to confirm we had sufficient sample size for any non-significant results and to guard against making a type II error, and we compared our effect sizes to effect sizes in the literature where possible. We were not able to run power analyses on the linear mixed models described above, so we used models that did not include the random effect accounting for the *maternal line* of each cricket but verified beforehand that the results of these models aligned with the results of the linear mixed models. We used JMP Pro version 13.0.0 for all analysis.

## Results

We found that *maternal age treatment* did not affect the reproductive traits of male offspring. In the complete dataset *maternal age treatment* did not have a significant effect on either testes mass ( $F_{1,41.76} = 0.11$ ,  $p = 0.74$ ; Fig. 2A) or transformed spermatophore mold mass ( $F_{1,32.5} = 0.99$ ,  $p = 0.32$ ; Fig. 2B). Our power analysis showed that with our means and variance, we would need 47,396 observations of testes mass and 556 observations of spermatophore mold mass to detect a significant difference in these variables between the maternal age treatments. In our old treatment, males had testes that were 2% larger than the testes of young-treatment males, which is much smaller than the difference of 10% that Bailey et al. (2010) found when assessing plasticity in the reproductive organs of the same crickets in response to song heard during development. Older and smaller males from the late dataset had significantly smaller testes masses than younger and larger males from the early dataset (*age of the male*:  $F_{1,114.8} = 9.85$ ,  $p = 0.002$ ; *pronotum width*  $F_{1,114.5} = 7.04$ ,  $p = 0.009$ ; and *dissection date*  $F_{1,114.7} = 31.81$ ,  $p < 0.0001$ ). Males that we dissected from the late dataset had significantly smaller spermatophore molds (*dissection date*:  $F_{1,115.9} = 20.77$ ,  $p < 0.0001$ ), but there was no significant difference among males of different ages (*age of the male*:  $F_{1,115.3} = 0.67$ ,  $p = 0.42$ ) or of different sizes (*pronotum width*:  $F_{1,110.2} = 0.83$ ,  $p = 0.36$ ).

In our analysis of only the late dataset, we found no significant effect of *maternal age treatment* on testes mass ( $F_{1,18.99} = 0.04$ ,  $p = 0.8$ ) or spermatophore mold mass ( $F_{1,29.98} = 3.59$ ,  $p = 0.07$ ). Our power analysis showed that with our means and variance, we

would need 3,539 observations of testes mass and 83 observations of spermatophore mold mass to detect a significant difference in these variables between maternal age treatments.

In our analysis of sperm viability data, we found no significant effect of *maternal age treatment* ( $F_{1,29.04} = 0.82$ ,  $p = 0.37$ ; old treatment:  $0.67 \pm 0.03$ , young treatment:  $0.76 \pm 0.09$ ). Sperm viability did not differ among males of different ages ( $F_{1,45.18} = 0.44$ ,  $p = 0.51$ ) or different sizes ( $F_{1,47.52} = 0.49$ ,  $p = 0.49$ ). Our power analysis showed that we would need 284 observations of sperm viability to detect a significant difference between maternal age treatments. Though not significant, young treatment males had 13% higher sperm viability than old treatment males; this difference is larger than the 7% difference induced by experience with song during development in Gray and Simmons (2013).

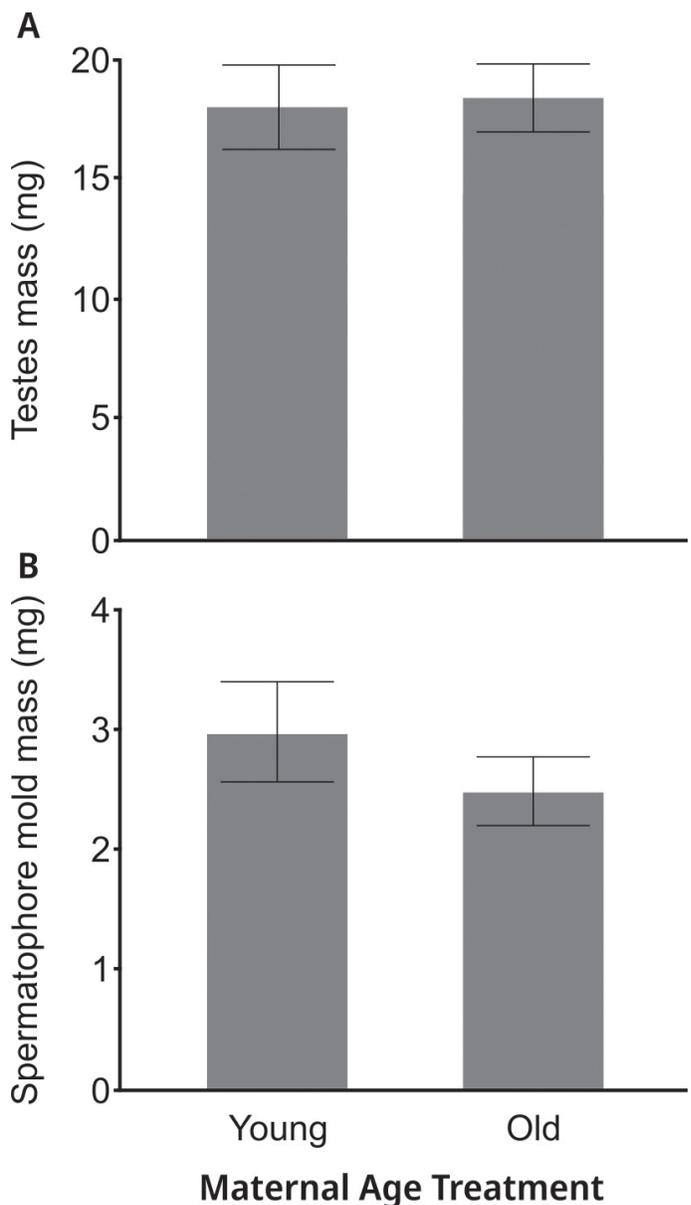


Fig. 2. Reproductive investment of male offspring by treatment. For all male offspring from both maternal age treatments: A. Testes mass; B. Spermatophore mold mass. There were no significant differences between treatments for either measure. Bars represent least square means  $\pm$  SE.

## Discussion

Maternal age can have complex and contrasting influences on a number of offspring traits (Berkeley et al. 2004, Hansen et al. 2015). We asked whether advanced maternal age influenced the reproductive traits of male offspring and found no influence of maternal age treatment on testes mass, spermatophore mold mass, or sperm viability; however, our sperm viability results should be viewed cautiously due to our unbalanced sample size for that portion of the experiment. Given that we did not find differences in male reproductive traits between the young and old treatments, we conducted power analyses and comparisons of effect sizes that largely supported and validated our null results. For one measure—spermatophore mold mass in the males that we dissected later (late dataset)—the power analysis suggests we may need a larger sample size to definitively conclude that there was no effect from maternal age. For the measure of sperm viability, our comparison of effect sizes showed that the difference in sperm viability between groups may warrant further exploration in future experiments.

Both life history theory and aging theory have been used to explain the impacts of advanced maternal age on offspring fitness. In the most general sense, finding that the offspring of older mothers are less fit than the offspring of younger mothers would support aging theory (Nussey et al. 2013, Lemaitre and Gaillard 2017), but mothers making terminal investments can increase offspring fitness (Williams 1966, Trivers 1974). We found no differences in the reproductive traits of males belonging to old and young mothers; there are several reasons this might be the case. First, there could simply be no link between maternal age and the reproductive investment of male offspring. We know that male postcopulatory traits (such as sperm viability and accessory gland mass) are plastic in *T. oceanicus* (Bailey et al. 2010, Gray and Simmons 2013), but we do not know all of the conditions under which that plasticity is released. Second, there may be other unmeasured constraints on male reproductive investment, or the traits measured may be pleiotropically linked with others. Third, it is possible that the pattern we found may, indeed, result from mothers of advanced maternal age making a terminal investment, but, because of the costs of aging, that terminal investment is still less than the investment made by younger mothers. Finally, it is possible that males differentially allocate resources depending on the age of their mate. If this effect counteracts age-dependent differential investment made by mothers, this could lead to no overall difference in the fitness of sons. A deeper understanding of the underlying mechanisms and drivers of both male and female reproductive investment and resource allocation would elucidate the patterns.

Testes size is often highly variable within populations and increased size is associated with an increased risk of sperm competition (Merila and Sheldon 1999, Simmons 2001), including in this species (Bailey et al. 2010). In many taxa, this pattern is the result of selection; males in species with a higher risk of sperm competition often have much larger testes than males in closely related species with a lower risk of sperm competition (Merila and Sheldon 1999). Testes size can also be plastic depending on perceived level of sperm competition during rearing (Bailey et al. 2010, Fisher and Hook 2018). In our analysis, we found that testes size is correlated with pronotum width, dissection date, and age of the male. We would expect testes size to covary with the size of the male (pronotum width) due to allometry, and differences associated with dissection date are likely a result of tissue degradation. We found that older males had smaller testes, but, to our knowledge, the existing literature does not suggest that testes shrink with age.

In many species, older males have larger testes because they have reached sexual maturity, and there is also some evidence for an increase in asymmetry between testes with age (Merila and Sheldon 1999, Brown and Brown 2003, Abdul-Rahman et al. 2018). Perhaps the pattern of old males having smaller testes reflects a trade-off between reproduction and longevity (Austad and Hoffman 2018); if older males have invested more resources in survival and maintenance than younger males, this investment could come at the expense of reproductive somatic tissue.

We measured the effect of advanced maternal age on traits specific to male offspring, and we suggest that researchers begin to include these male traits in studies of fitness to gain a more comprehensive view of fitness measures. In an unpublished study, we measured the effects of one generation of advanced maternal age on offspring size, survival to adulthood, and immunocompetency in *T. oceanicus*, finding results that support either life history theory or aging theory, depending on the fitness measure assessed. Notably, young mothers had more offspring, but there was no difference between old and young mothers in number of offspring that reached adulthood, and offspring of old mothers had higher measures of immunocompetency. Alongside the current results, our unpublished work demonstrates that life history theory and aging theory can predict the effects of maternal age on different traits. Depending on which trait is measured, advanced maternal age may have positive, negative, or neutral effects. Our work is among the first to consider the effects of maternal age on traits specific to male offspring, and we encourage other researchers to include male offspring fitness in a comprehensive suite of fitness measures of offspring in aging studies.

## Acknowledgements

We thank the University of Denver Ecology and Evolutionary Biologists group for valuable feedback on previous versions of this manuscript. We thank Dr. Cathy Durso for help with our statistical analysis and Dr. Erich Kushner for allowing us to use a dissection microscope in his lab. We also deeply appreciate all of the help from Claudia Hallagan, who not only offered invaluable input on the manuscript, but also started the larger scale experiment of which our study was a part. Our research was supported by funding from the Knoebel Institute for Healthy Aging at the University of Denver awarded to RT and SM, a summer research grant from the University of Denver Undergraduate Research Center awarded to SA, as well as a University of Denver Shubert Grant and an Orthopterists' Society Research Grant awarded to JW.

## References

- Abdul-Rahman II, Obese FY, Robinson JE (2018) Testis size and asymmetry in the guinea fowl (*Numida meleagris*): A test of the compensation hypothesis. *Avian Biology Research* 11: 123–131. <https://doi.org/10.3184/175815618X15203333340470>
- Asghar M, Bensch S, Tarka M, Hansson B, Hasselquist D (2014) Maternal and genetic factors determine early life telomere length. *Proceedings of the Royal Society B: Biological Sciences* 282: 20142263–20142263. <https://doi.org/10.1098/rspb.2014.2263>
- Austad SN, Hoffman JM (2018) Is antagonistic pleiotropy ubiquitous in aging biology? *Evolution, Medicine, and Public Health* 2018: 287–294. <https://doi.org/10.1093/emph/eoy033>
- Badyaev AV, Uller T (2009) Parental effects in ecology and evolution: Mechanisms, processes and implications. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364: 1169–1177. <https://doi.org/10.1098/rstb.2008.0302>

- Bailey NW, Gray B, Zuk M (2010) Acoustic experience shapes alternative mating tactics and reproductive investment in male field crickets. *Current Biology* 20: 845–849. <https://doi.org/10.1016/j.cub.2010.02.063>
- Berkeley SA, Chapman C, Sogard SM (2004) Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* 85: 1258–1264. <https://doi.org/10.1890/03-0706>
- Bloch Qazi MC, Miller PB, Poeschel PM, Phan MH, Thayer JL, Medrano CL (2017) Transgenerational effects of maternal and grandmaternal age on offspring viability and performance in *Drosophila melanogaster*. *Journal of Insect Physiology* 100: 43–52. <https://doi.org/10.1016/j.jinsphys.2017.05.007>
- Bretman A, Fricke C, Chapman T (2009) Plastic responses of male *Drosophila melanogaster* to the level of sperm competition increase male reproductive fitness. *Proceedings of the Royal Society B: Biological Sciences* 276: 1705–1711. <https://doi.org/10.1098/rspb.2008.1878>
- Brown CR, Brown MB (2003) Testis size increases with colony size in cliff swallows. *Behavioral Ecology* 14: 569–575. <https://doi.org/10.1093/beheco/arg030>
- Descamps S, Boutin S, Berteaux D, Gaillard J (2008) Age-specific variation in survival, reproductive success and offspring quality in red squirrels: Evidence of senescence. *Oikos* 117: 1406–1416. <https://doi.org/10.1111/j.0030-1299.2008.16545.x>
- Dowling DK, Nowostawski AL, Arnqvist G (2007) Effects of cytoplasmic genes on sperm viability and sperm morphology in a seed beetle: Implications for sperm competition theory? *Journal of Evolutionary Biology* 20: 358–368. <https://doi.org/10.1111/j.1420-9101.2006.01189.x>
- Dowling DK, Simmons LW (2012) Ejaculate economics: Testing the effects of male sexual history on the trade-off between sperm and immune function in Australian crickets. *PLoS ONE* 7: e30172. <https://doi.org/10.1371/journal.pone.0030172>
- Fisher HS, Hook KA (2018) Sibling rivalry: Males with more brothers develop larger testes. *Ecology and Evolution* 8: 8197–8203. <https://doi.org/10.1002/ece3.4337>
- García-González F, Simmons LW (2005) Sperm viability matters in insect sperm competition. *Current Biology* 15: 271–275. <https://doi.org/10.1016/j.cub.2005.01.032>
- Gay L, Hosken DJ, Vasudev R, Tregenza T, Eady PE (2009) Sperm competition and maternal effects differentially influence testis and sperm size in *Callosobruchus maculatus*. *Journal of Evolutionary Biology* 22: 1143–1150. <https://doi.org/10.1111/j.1420-9101.2009.01724.x>
- Gray B, Simmons LW (2013) Acoustic cues alter perceived sperm competition risk in the field cricket *Teleogryllus oceanicus*. *Behavioral Ecology* 24: 982–986. <https://doi.org/10.1093/beheco/art009>
- Hansen ØJ, Puvanendran V, Bangera R (2015) Do maternal age and experience contribute to better growth, survival and disease resistance of offspring in Atlantic cod (*Gadus morhua*)? *Aquaculture International* 23: 1157–1164. <https://doi.org/10.1007/s10499-014-9872-5>
- Harcourt AH, Harvey PH, Larson SG, Short RV (1981) Testis weight, body weight and breeding system in primates. *Nature* 293: 55–57. <https://doi.org/10.1038/293055a0>
- Khalifa A (1949) The mechanism of insemination and the mode of action of the spermatophore in *Gryllus pennsylvanicus*. *Quarterly Journal of Microscopical Science* 90: 281–292.
- Larson EL, Hume GL, Andres JA, Harrison RG (2012) Post-mating prezygotic barriers to gene exchange in hybridizing field crickets. *Journal of Evolutionary Biology* 25: 174–186. <https://doi.org/10.1111/j.1420-9101.2011.02415.x>
- Lemaitre JF, Gaillard JM (2017) Reproductive senescence: New perspectives in the wild. *Biological Reviews* 33: 2182–2199. <https://doi.org/10.1111/brv.12328>
- Merila J, Sheldon BC (1999) Testis size variation in the green finch *Carduelis chloris*: Relevance for some recent models of sexual selection. *Behavioral Ecology and Sociobiology* 45: 115–123. <https://doi.org/10.1007/s002650050545>
- Mossman JA, Mabeza RMS, Blake E, Mehta N, Rand DM (2019) Age of both parents influences reproduction and egg dumping behavior in *Drosophila melanogaster*. *Journal of Heredity* 110: 300–309. <https://doi.org/10.1093/jhered/esz009>
- Nussey DH, Froy H, Lemaitre JE, Gaillard JM, Austad SN (2013) Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews* 12: 214–225. <https://doi.org/10.1016/j.arr.2012.07.004>
- Parker GA (2015) The evolution of expenditure on testes. *Journal of Zoology* 298: 3–19. <https://doi.org/10.1111/jzo.12297>
- Partridge L, Harvey PH (1988) The ecological context of life history evolution. *Science* 241: 1449–1455. <https://doi.org/10.1126/science.241.4872.1449>
- Reinhardt K, Naylor R, Siva-Jothy MT (2011) Male mating rate is constrained by seminal fluid availability in bedbugs, *Cimex lectularius*. *PLoS ONE* 6: e22082. <https://doi.org/10.1371/journal.pone.0022082>
- Sakaluk SK, Eggert AK (1996) Female control of sperm transfer and intraspecific variation in sperm precedence: Antecedents to the evolution of a courtship food gift. *Evolution* 50: 694–703. <https://doi.org/10.1111/j.1558-5646.1996.tb03879.x>
- Simmons LW (2001) *Sperm Competition and its Evolutionary Consequences in the Insects*. Princeton University Press, Princeton, 456 pp. <https://doi.org/10.1515/9780691207032>
- Simmons LW (2003) The evolution of polyandry: Patterns of genotypic variation in female mating frequency, male fertilization success and a test of the sexy-sperm hypothesis. *Journal of Evolutionary Biology* 16: 624–634. <https://doi.org/10.1046/j.1420-9101.2003.00572.x>
- Taborsky M (2002) The evolution of bourgeois, parasitic, and cooperative reproductive behaviors in fishes. *Journal of Heredity* 92: 100–110. <https://doi.org/10.1093/jhered/92.2.100>
- Trivers RL (1974) Parent-offspring conflict. *American Zoologist* 14: 249–264. <https://doi.org/10.1093/icb/14.1.249>
- Vahed K, Parker DJ, Gilbert DJG (2011) Larger testes are associated with a higher level of polyandry, but a smaller ejaculate volume, across bushcricket species (Tettigoniidae). *Biology Letters* 7: 261–264. <https://doi.org/10.1098/rsbl.2010.0840>
- Wedell N, Gage MJG, Parker GA (2002) Sperm competition, male prudence and sperm-limited females. *Trends in Ecology and Evolution* 17: 313–320. [https://doi.org/10.1016/S0169-5347\(02\)02533-8](https://doi.org/10.1016/S0169-5347(02)02533-8)
- Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist* 100: 687–690. <https://doi.org/10.1600/036364411X583510>

# Microhabitats of planted sea wall strips used by pollinators and Orthoptera

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Academic editor: Corinna S. Bazelet | Received 11 March 2019 | Accepted 19 February 2020 | Published 14 May 2020

<http://zoobank.org/96BFEAE3-6444-4DA6-8EF3-B2583558B641>

Citation: Gardiner T, Fargeaud K (2020) Microhabitats of planted sea wall strips used by pollinators and Orthoptera. Journal of Orthoptera Research 29(1): 77–82. <https://doi.org/10.3897/jor.29.34452>

## Abstract

As part of an Urban Buzz scheme, strips of teasel (*Dipsacus fullonum*) and greater knapweed (*Centaurea scabiosa*) have been established along a sea wall flood defense in the UK to provide a corridor of flower-rich habitat for pollinators such as bees and butterflies. The cutting of tall grassland and planting of dicotyledons also created a suitable short sward environment (c. 30 cm height) for Orthoptera nymphs in the establishment year (2018). However, by 2019, the grassland in the pollinator strips was taller (c. 75 cm) and suboptimal for grasshoppers; in contrast to Roesel's bush-cricket (*Roeseliana roeselii*), which inhabited the taller vegetation in greater abundance. The progression to established grassland with flowering *D. fullonum* saw the pollinator strips attract significantly higher numbers of bees and butterflies than the floristically poor control strips. This small-scale study illustrates that pollinator strips can have multi-functional benefits for ecosystems beyond pollination, with Orthoptera of tall grassland (*R. roeselii*) likely to persist alongside planted wildflowers.

## Keywords

bumblebee, bush-cricket, butterfly, conservation, dicotyledon, grasshopper, flood defense

## Introduction

The loss of 97% of wildflower-rich meadows in the UK has necessitated conservation interventions to restore essential ecosystem services such as pollination (Blowers et al. 2017, Cresswell et al. 2018, Gardiner and Fargeaud 2018a). Sea wall flood defenses often have the last remnants of unimproved meadow in lowland areas (Gardiner et al. 2015), which can be important habitats for bumblebees (Gardiner and Fargeaud 2018b) and Orthoptera (Gardiner and Charlton 2012, Fargeaud and Gardiner 2018) largely due to the varied sward structure and microhabitats. In response to the decline in urban pollinator populations in the UK, Buglife, the Invertebrate Conservation Trust, led an Urban Buzz project with Ipswich as one of the focus towns in eastern England (Buglife 2018). As part of the scheme, strips of wildflowers have been established along an urban fringe sea wall flood defense in Ipswich

to provide a corridor of flower-rich habitat for pollinators. It is the aim of this short communication to ascertain the incidental benefits of the pollinator strip microhabitats for Orthoptera.

## Methods

As part of the Urban Buzz project, the Environment Agency (EA) was given wildflower plugs (small-sized seedlings grown in trays) to plant in spring 2018. The Wherstead sea wall that runs under the Orwell Bridge towards Fox's Marina (Ordnance Survey grid reference start: TM169410, end: TM166414) was selected due to the good opportunities for enhancement. Rank grassland on the folding (flat area between borrowdyke and landward slope) was chosen as being suitable for planting after consultation with engineers at the EA. The grassland was mainly composed of coarse grasses such as cock's-foot (*Dactylis glomerata*), occasional reed (*Phragmites australis*), and hemlock (*Conium maculatum*). The diversity of the flora was low and plants providing pollen and nectar for bees were virtually absent over much of the flood defense apart from scattered creeping thistle (*Cirsium arvense*) and teasel (*Dipsacus fullonum*) plants. Locally scarce plants found on the flood bank included three orchids: pyramidal orchid (*Anacamptis pyramidalis*), common-spotted orchid (*Dactylorhiza fuchsia*), and bee orchid (*Ophrys apifera*). Two Nationally Scarce species were recorded: dittander (*Lepidium latifolium*) and annual beard-grass (*Polypogon monspeliensis*), the former in some abundance, the latter on one small patch of disturbed ground.

The vegetation of seven strips (strip length x width in m, 1: 15x1, 2: 10x1, 3: 17x1, 4: 15x1, 5: 5x1, 6: 10x1, 7: 6x1) within the 1 km long sea wall folding was cut by hand (with shears to avoid mechanical mortality of orthopteran nymphs) to a height of 20 cm in early April 2018 to create favorable planting conditions for the plugs. Strips were separated by at least 10 m from each other by a buffer of uncut grassland. On 18 and 19 April, 300 greater knapweed (*Centaurea scabiosa*) and 200 teasel were planted into a strip of 1 m wide grassland in each strip (plugs of both species intermingled during planting; planted at a density c. 6.4 plants per m<sup>2</sup>), 2–3 m away from the landward slope to avoid machinery

tracking over them during subsequent management of the flood defense. These two plant species were chosen because they have been recorded in the Ipswich area and could be considered locally native and suitable for clay soil. They are also excellent species for foraging pollinators (Rollin et al. 2016, Nichols et al. 2019). Stakes were used to mark out each section for ease of location in the field. On the 14 May 2018, vegetation was again cut to a height of 20 cm in the planted strips to aid establishment. In April 2019, the sward was cut to a height of 20 cm for pollinator plants and Orthoptera.

*Orthoptera sampling.*—In each pollinator strip and an adjacent unplanted/uncut control strip, a 1-m-wide transect (the same length as each pollinator strip and control) was established closely following the methodology of Gardiner et al. (2005) and Gardiner and Hill (2006). The pollinator and control strips were parallel to each other and at least 3 m apart due to space limitations on the folding. The vegetation of the pollinator and control strips were both selected for this study due to their homogeneity in vegetation composition/structure and overall similarity in environmental characteristics. Each transect was walked at a slow strolling pace (2 km/hr) in early June and July of 2018 and 2019 (four surveys in total). During the June surveys, only nymphs flushed from a 1 m wide band (using a 1-m-long pole swept back and forth in a 180° arc) in front of the observer were recorded. The June surveys were undertaken when the vegetation was sufficiently short (<50 cm) to minimize the possibility of overlooking nymphs in the tall grass (Gardiner et al. 2005). Adults were not recorded in the June surveys due to their low abundance at this stage of the season. With practice, it was relatively easy to ascertain the species of each orthopteran without capture. During the July surveys, only adults were recorded as nymphs were in low abundance by this time in the summer (most had matured). The weather conditions on all survey days were favorable for insect activity, being largely sunny and warm (>17°C).

*Pollinator sampling.*—In the pollinator strips and sea wall grassland (control), transects were established (a total of seven transects each for the pollinator and control strips, the same length as the strips). The methodology for surveying bees (Hymenoptera) and butterflies (Lepidoptera) followed that of Carvell et al. (2007). Surveys were undertaken between 10:00 and 17:00 h, when weather conditions conformed to the following criteria for the UK Butterfly Monitoring Scheme: 1) transects are not walked when the temperature is below 13°C; 2) between 13–17°C, a transect may be walked providing there is at least 60% sun; 3) above 17°C, a transect may be walked in any conditions, providing it is not raining; 4) when wind speeds are above 5 on the Beaufort scale, transects should not be walked (Pollard and Yates 1993). Seven surveys of the transects were undertaken in 2019 from early June to mid-July. Bee and butterfly species were only recorded if they visited flowering plants (either natural or planted).

*Sward height and rabbit droppings.*—Ten sward heights were recorded at random positions using a meter rule in each pollinator and control strip in early July 2018 and 2019 (70 heights for pollinator and control strips in each year). In addition, during the sward height surveys, the number of wild rabbit (*Oryctolagus cuniculus*) (Lagomorpha: Leporidae) droppings (dung balls) were counted for each transect (in 1 m band for entire length of strips) in each year to ascertain the level of grazing pressure on each strip (Wood 1988, Gibb and Fitzgerald 1998, Millett and Edmondson 2013).

*Statistical analysis.*—To correct for non-normality, the data were square-root transformed (Heath 1995). The mean density of *C. scabiosa* and *D. fullonum* plants were compared between the pollinator and control strips in both years using a two-way ANOVA in the online VassarStats package (Lowry 2020). A paired samples t-test was used to compare the mean number of pollinators/100 m and the mean pollinator species richness/strip in 2019 between pollinator and control strips.

Only grasshopper (all Acrididae species combined) and Roesel's bush-cricket (*Roeseliana roeselii* Hagenbach) nymphs were in high enough abundance from the Orthoptera to allow meaningful analysis. The mean nymphs and adults of both, overall species richness, rabbit droppings, and sward height were compared between the pollinator and control strips in both years using a two-way ANOVA (Heath 1995). To further investigate the influence of variables (sward height, height variance (standard deviation of sward height), rabbit grazing pressure) on nymph (grasshopper and *R. roeselii*) and adult abundance, a Principal Components Analysis (PCA) was undertaken for the combined 2018 and 2019 data using ClustVis software (Metsalu and Vilo 2015).

## Results

*Pollinator plants.*—Of the 300 *C. scabiosa* planted, only 24 were left (8%) in the strips by September 2018. The plant species experienced significant damage by grazing rabbits, with defoliation and digging up of newly planted plugs. This significant decline continued into 2019 (t-test: 5.09,  $P = 0.002$ ), with only 7 plants (2%) surviving into July (Table 1). Contrastingly, *D. fullonum* fared better with 56 (28%) surviving into July 2019 and no significant decline noted (t-test: 1.9,  $P = 0.1$ ). Only one *D. fullonum* flowered in 2018, whereas 44 *D. fullonum* flowered in July 2019, providing numerous flowers for pollinators to utilize.

*Pollinators.*—Fourteen species of pollinator were recorded on the planted strips, composed of common species of bee: buff/white-tailed bumblebee (*Bombus terrestris/lucorum*), common carder bee (*Bombus pascuorum*), and red-tailed bumblebee (*Bombus lapidarius*); 63, 17, and 16 workers, respectively. Other pollinators included butterfly species such as peacock (*Aglais io*) and Essex skipper (*Thymelicus lineola*); 8 and 7 butterflies, respectively. The UK 'priority' species, small heath (*Coenonympha pamphilus*), was seen on the pollinator strips, although it did not visit the flower-

**Table 1.** Recorded variables for the pollinator strips and control.

	Pollinator 2018	Pollinator 2019	Control 2018	Control 2019	P v C sig.
Orthoptera					
Grasshopper nymphs/m <sup>2</sup>	1.4 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	**
<i>R. roeselii</i> nymphs/m <sup>2</sup>	0.1 ± 0.0	0.9 ± 0.3	0.1 ± 0.1	0.3 ± 0.2	NS
Grasshopper adults/m <sup>2</sup>	0.4 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	NS
<i>R. roeselii</i> adults/m <sup>2</sup>	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	NS
No. species/strip	2.3 ± 0.4	0.7 ± 0.4	1.9 ± 0.7	0.0 ± 0.0	NS
Habitat characteristics					
Rabbit droppings/m <sup>2</sup>	6.1 ± 2.0	1.1 ± 0.5	0.9 ± 0.5	0.1 ± 0.1	**
Sward height (cm)	29.0 ± 3.7	74.4 ± 7.7	94.4 ± 8.2	113.0 ± 7.2	**
Pollinators/plants					
No. pollinators/100 m	–	17.1 ± 8.2	–	0.4 ± 0.3	*
No. pollinator species/strip	–	4.3 ± 1.5	–	0.4 ± 0.3	*
<i>Dipsacus fullonum</i> density/m <sup>2</sup>	1.0 ± 0.7	0.7 ± 0.2	–	–	–
<i>Centaurea scabiosa</i> density/m <sup>2</sup>	0.6 ± 0.2	0.2 ± 0.1	–	–	–

\*  $P < 0.05$ , \*\*  $P < 0.01$

ing *D. fullonum*. Only three pollinator species were recorded on the control strips. Species richness was significantly higher on the pollinator strips (t-test: 3.01,  $P = 0.02$ ) as was the mean number of pollinators (t-test: 2.74,  $P = 0.03$ ) (Table 1).

**Orthoptera.**—Grasshopper (143 individuals, 55% of total number) and *R. roeselii* (110 individuals, 42%) nymphs were abundant, with *Conocephalus fuscus* Fabricius (4 individuals) and slender groundhopper (*Tetrix subulata* L., 2 individuals) extremely scarce. The latter species was only seen on a damp, mossy patch between tall *Phragmites australis* on a pollinator strip in 2019.

For grasshopper nymphs, there was a significantly higher density on the pollinator strips compared to the control strips ( $F = 12.32$ ,  $P = 0.002$ ), where the swards were shorter ( $F = 63.20$ ,  $P < 0.001$ ) and rabbit droppings more evident ( $F = 16.47$ ,  $P = 0.001$ ). This overall trend in numbers was reflected in a significantly higher grasshopper nymph density on the pollinator strips in 2018 ( $F = 6.52$ ,  $P = 0.017$ ) where sward height was lower around the establishing plants ( $F = 8.07$ ,  $P = 0.009$ ) (Table 1). The density of *R. roeselii* nymphs did not differ between pollinator and control strips in either year.

Overall, there were significantly lower numbers of grasshopper nymphs in 2019 ( $F = 43.57$ ,  $P < 0.001$ ), which contrasted with *R. roeselii* nymphs that were higher ( $F = 5.27$ ,  $P = 0.031$ ). Sward height increased on all strips ( $F = 26.95$ ,  $P = 0.001$ ) with a concomitant decline in rabbit droppings ( $F = 14.93$ ,  $P = 0.001$ ). Grasshopper nymphs decreased significantly on the pollinator strips in 2019 as sward height increased around the planted flowers ( $F = 8.07$ ,  $P = 0.009$ ), despite early cutting.

Adults of six Orthoptera species were recorded on both the pollinator strips and controls. Numbers were generally low (only 76 adults recorded), the most abundant being the meadow grasshopper (*Pseudochorthippus parallelus* Zetterstedt), lesser marsh grasshopper (*Chorthippus albomarginatus* De Geer), and *R. roeselii* (a total of 25, 22, and 20 adults, respectively, for both strips combined). Rare species (<10 adults) in the survey included field grasshopper (*Chorthippus brunneus* Thunberg), long-winged conehead (*Conocephalus fuscus* Fabricius), and dark bush-cricket (*Pholidoptera griseoptera* De Geer). However, species richness did not differ significantly between pollinator or control strips, but did decline in 2019 ( $F = 13.84$ ,  $P = 0.001$ ).

Overall, there were significantly lower numbers of grasshopper adults in 2019 ( $F = 23.36$ ,  $P < 0.001$ ) and there was a higher density on the pollinator strips compared to the control strips ( $F = 4.61$ ,  $P = 0.042$ ). The density of *R. roeselii* adults did not differ between pollinator and control strips in either year or vary between years.

The PCA for nymphs revealed that PC1 and PC2 accounted for 60.9% and 25.3% of the variance in the dataset, respectively (Fig. 1). Component loadings for PC1 revealed the importance of sward height (coefficient -0.61), while *R. roeselii* nymph density (coefficient 0.99) was a major factor in PC2. For adults, PC1 and PC2 accounted for 57.9% and 25.5% of the variance in the dataset, respectively (Fig. 2). Similar to nymphs, component loadings for PC1 revealed the importance of sward height (coefficient -0.58), while *R. roeselii* adult density (coefficient 0.76) was a major factor in PC2.

## Discussion

Vegetation structure is a key factor for grassland fauna (Duffey et al. 1974, Morris 2000), particularly for Orthoptera. Clarke (1948) and Gardiner and Hassall (2009) noted that vegetation

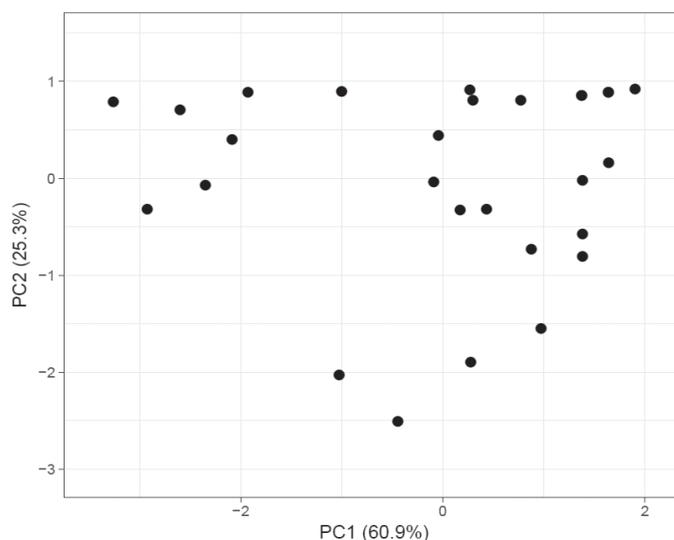


Fig. 1. Principal components for the nymph (grasshopper and *R. roeselii*), sward height/variability, and rabbit grazing data. PC1 represents sward height, PC2 represents *R. roeselii* nymph density.

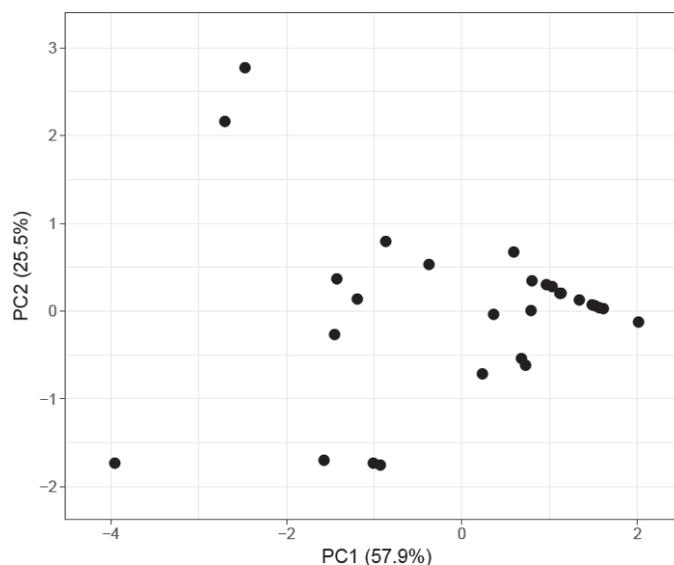


Fig. 2. Principal components for the adult (grasshopper and *R. roeselii*), sward height/variability, and rabbit grazing data. PC1 represents sward height, PC2 represents *R. roeselii* adult density.

height/density is the most important habitat factor for grasshoppers, particularly in respect to the influence on microclimate. Vegetation which is dense and tall is not readily warmed by the sun or cooled by free circulation of air, in contrast to sparser vegetation which provides better conditions for diurnal activity (Clarke 1948, Gardiner and Hassall 2009). Dense vegetation with high percentage cover, however, provides abundant food sources (Bernays and Chapman 1970a, b). Therefore, Orthoptera may be abundant in habitats which possess both dense vegetation and areas of sparser vegetation, and such local differentiation of sward structure may be important (Richards and Waloff 1954, Gardiner et al. 2002).

In the current study, the shorter vegetation of the pollinator strips due to vegetation cutting in spring 2018 (Fig. 3) led to their favorability for grasshopper nymphs perhaps because of warmer microclimatic temperatures more conducive to development



Fig. 3. Pollinator strip with a short sward ideal for Orthoptera nymphs being planted with plugs by the second author in April 2018. Photo credit: T. Gardiner.

(Gardiner and Hassall 2009). Grazing animals also play a part in reducing vegetation height and cover (Gardiner 2018). On the Ipswich sea wall, rabbit grazing was more intensive on the pollinator strips than in the control strips in 2018 (Table 1), with a significant impact on sward height. Sward height was confirmed as a significant influence in this study, particularly in respect of *R. roeselii* nymph and adult density (Figs 1, 2).

Clarke (1948) suggested that excessive grazing by rabbits promoted sparser vegetation comprised of less vigorous grass species such as sheep's fescue (*Festuca ovina*), which was consequently more favorable to grasshoppers. A study at Flatford Mill (Bhadresa 1987) concluded that the diet of wild rabbits consisted mainly of grasses. In another study on a heavily rabbit-grazed grassland, *C. brunneus* was more abundant within an enclosure than on the surrounding grazed grassland (Grayson and Hassall 1985). The authors of that study suggested that the taller vegetation in the enclosure provided better cover from vertebrate predators and higher quality food resources for grasshopper nymphs than the shorter grazed vegetation. Intensive grazing by wild rabbit populations in Epping Forest in the UK, led to the extirpation of the locally scarce common green grasshopper (*Omocestus viridulus* L.), a species with a preference for tall grassland (Gardiner 2010). The grazing created a very homogeneously short grassland sward resembling a 'lawn' (Crofts 1999), which may not have provided the necessary shelter or 'cool' microclimate for *O. viridulus*.

In the current study, the cutting of tall grassland and planting of wildflowers for pollinators appears to have created a suitable short sward environment (c. 30 cm height) in 2018 for nymphs but not adults, which may have migrated into the taller vegetation of the control strips (Gardiner and Hill 2004, Gardiner 2009). The cutting of the pollinator strips allowed wild rabbits to graze the

closed grassland, further reducing grass growth (Isermann et al. 2010) and creating patches of exposed soil due to their burrowing activities, which may be favorable for basking nymphs (Gardiner et al. 2002). Grasshoppers have been found in higher densities (2.9 adults/m<sup>2</sup>) on rabbit-grazed sea walls in Essex when compared with mown flood defenses (0.7 adults/m<sup>2</sup>) due to the shorter swards created by lagomorphs (Fargeaud and Gardiner 2018).

Vegetation structure may also influence egg development (van Wingerden et al. 1991a). Tall vegetation could lead to lower maximum temperatures in the soil surface and consequently delay hatching of eggs laid in the soil (Waloff 1950, Choudhuri 1958), resulting in a loss of some mesophilous grasshopper species (van Wingerden et al. 1991b). Such tall grasslands may be described as 'cold', whilst those with shorter, sparse vegetation are 'warm' (van Wingerden et al. 1991b). The 'warm' grasslands of the pollinator strips post-planting may have contributed to the early hatching of nymphs compared to the controls.

In 2019, the pollinator strips had progressed to a taller sward (c. 75 cm) with less rabbit grazing; consequently, the colder microclimate was unfavorable for grasshopper nymphs and adults that prefer grassland of 10–20 cm in height (Gardiner et al. 2002). The tall sward species, *R. roeselii*, appeared to benefit from this transition to longer grassland on the pollinator strips and controls (Fig. 4). It appears that despite the decline in species richness in 2019, the pollinator strips can support up to seven species of Orthoptera including more localized insects such as the groundhopper *Tetrix subulata* (Ling 2000).

The pollinator strips were also effective at attracting over ten species of insect to the *D. fullonum* flowers (Fig. 5). The abundance of pollinators in 2019 illustrates the success of the strips with common grassland bee (such as *B. pascuorum* and *B. vestalis*) and but-



Fig. 4. Roesel's bush-cricket (*Roeseliana roeselii*) nymph on a plant-teasel (*Dipsacus fullonum*) leaf in 2019. Photo credit: T. Gardiner.



Fig. 5. A teasel (*Dipsacus fullonum*) flowerhead visited by the tree bumblebee (*Bombus hypnorum*) in 2019. Photo credit: T. Gardiner.

terfly (*Pyronia tithonus* and *T. lineola*) species utilizing the flowers. The abundance of grass species should also be favorable for egg-laying and larval feeding of the grassland butterflies (e.g., meadow brown, *Maniola jurtina*) in successive years.

The multifunctional nature of the pollinator strips, which supported foraging bees, nectaring butterflies, and populations of

Orthoptera, particularly in their nymphal stages, indicates that if carefully managed, these habitats can be beneficial to several orders of insect. The early season cutting (1–2 cuts) of the pollinator strips with hand tools, to avoid any mortality that may occur during mechanized cutting (Gardiner 2009), should continue in future years to ensure that a suitable warm microclimate is maintained for basking nymphs. Cutting by hand is possible on small sea wall strips (c. 78 m<sup>2</sup> of pollinator strips in this study), as it is in churchyards where scythes are used to cut flower-rich grassland (Gardiner 2011). The absence of mechanized cutting may be a significant factor in the persistence of Orthoptera on the pollinator strips.

### Acknowledgements

We would like to thank David Dowding of Buglife's Urban Buzz Project for supplying us with the wildflowers and Mark Durrell of the EA for helping us set up the sea wall planting areas. We are also grateful for constructive comments on the manuscript by an anonymous reviewer, Corey Bazelet, and Zoltán Kenyeres.

### References

- Bernays EA, Chapman RF (1970a) Experiments to determine the basis of food selection by *Chorthippus parallelus* (Zetterstedt) (Orthoptera: Acrididae) in the field. *Journal of Animal Ecology* 39: 761–776. <https://doi.org/10.2307/2866>
- Bernays EA, Chapman RF (1970b) Food selection by *Chorthippus parallelus* (Zetterstedt) (Orthoptera: Acrididae) in the field. *Journal of Animal Ecology* 39: 383–394. <https://doi.org/10.2307/2977>
- Bhadresa R (1987) Rabbit grazing: Studies in a grassland community using faecal analysis and exclosures. *Field Studies* 6: 657–684.
- Blowers CJ, Cunningham HM, Wilcox A, Randall NP (2017) What specific plant traits support ecosystem services such as pollination, bio-control and water quality protection in temperate climates? A systematic map protocol. *Environmental Evidence* 6: 1–3. <https://doi.org/10.1186/s13750-017-0081-3>
- Buglife (2018) Urban Buzz Hub. <https://www.buglife.org.uk/urban-buzz> [accessed 31 October 2018]
- Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology* 44: 29–40. <https://doi.org/10.1111/j.1365-2664.2006.01249.x>
- Choudhuri JCB (1958) Experimental studies on the choice of oviposition sites by two species of *Chorthippus* (Orthoptera: Acrididae). *Journal of Animal Ecology* 27: 201–215. <https://doi.org/10.2307/2239>
- Clarke EJ (1948) Studies in the ecology of British grasshoppers. *Transactions of the Royal Entomological Society of London* 99: 173–222. <https://doi.org/10.1111/j.1365-2311.1948.tb01235.x>
- Cresswell CJ, Cunningham HM, Wilcox A, Randall NP (2018) What specific plant traits support ecosystem services such as pollination, bio-control and water quality protection in temperate climates? A systematic map. *Environmental Evidence* 7: 1–2. <https://doi.org/10.1186/s13750-018-0120-8>
- Crofts A (1999) Grazing. In: Crofts A, Jefferson RG (Eds) *The Lowland Grassland Management Handbook* (2<sup>nd</sup> edn). English Nature/The Wildlife Trusts, Peterborough, 5(1–5), 84.
- Duffey E, Morris MG, Sheail J, Ward LK, Wells DA, Wells TCE (1974) *Grassland Ecology and Wildlife Management*. Chapman and Hall, London.
- Fargeaud K, Gardiner T (2018) The response of Orthoptera to grazing on flood defense embankments in Europe. *Journal of Orthoptera Research* 27: 53–61. <https://doi.org/10.3897/jor.27.25183>
- Gardiner T (2009) Hopping Back to Happiness? Conserving Grasshoppers on Farmland. VDM Verlag, Saarbrücken.

- Gardiner T (2010) Precipitation and habitat degradation influence the occurrence of the common green grasshopper *Omocestus viridulus* in southeastern England. *Journal of Orthoptera Research* 19: 315–326. <https://doi.org/10.1665/034.019.0219>
- Gardiner T (2011) Grasshoppers sing the praises of long grass on sacred sites. *The Lychgate* 20: 1–2.
- Gardiner T (2018) Grazing and Orthoptera: A review. *Journal of Orthoptera Research* 27: 3–11. <https://doi.org/10.3897/jor.27.26327>
- Gardiner T, Charlton P (2012) Effects of seawater flooding on Orthoptera and the yellow meadow ant *Lasius flavus* during New Zealand pygmy weed *Crassula helmsii* eradication at Old Hall Marshes, Essex, England. *Conservation Evidence* 9: 50–53.
- Gardiner T, Fargeaud K (2018a) Build it and they will come: Grasshoppers check-in to a grassland bee hotel. *Journal of Orthoptera Research* 27: 159–161. <https://doi.org/10.3897/jor.27.28385>
- Gardiner T, Fargeaud K (2018b) The effect of late cutting on bumblebees (*Bombus* spp.) in sea wall grassland. *Aspects of Applied Biology* 139: 43–50.
- Gardiner T, Hassall M (2009) Does microclimate affect grasshopper populations after cutting of hay in improved grassland? *Journal of Insect Conservation* 13: 97–102. <https://doi.org/10.1007/s10841-007-9129-y>
- Gardiner T, Hill J (2004) Directional dispersal patterns of *Chorthippus parallelus* (Orthoptera: Acrididae) in patches of grazed pastures. *Journal of Orthoptera Research* 13: 135–141. [https://doi.org/10.1665/1082-6467\(2004\)013\[0135:DDPOCP\]2.0.CO;2](https://doi.org/10.1665/1082-6467(2004)013[0135:DDPOCP]2.0.CO;2)
- Gardiner T, Hill J (2006) A comparison of three sampling techniques used to estimate the population density and assemblage diversity of Orthoptera. *Journal of Orthoptera Research* 15: 45–51. [https://doi.org/10.1665/1082-6467\(2006\)15\[45:ACOTST\]2.0.CO;2](https://doi.org/10.1665/1082-6467(2006)15[45:ACOTST]2.0.CO;2)
- Gardiner T, Hill J, Chesmore D (2005) Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems. *Journal of Insect Conservation* 9: 151–173. <https://doi.org/10.1007/s10841-005-2854-1>
- Gardiner T, Pilcher R, Wade M (2015) *Sea Wall Biodiversity Handbook*. RPS, Cambridge.
- Gardiner T, Pye M, Field R, Hill J (2002) The influence of sward height and vegetation composition in determining the habitat preferences of three *Chorthippus* species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. *Journal of Orthoptera Research* 11: 207–213. [https://doi.org/10.1665/1082-6467\(2002\)011\[0207:TIOSHA\]2.0.CO;2](https://doi.org/10.1665/1082-6467(2002)011[0207:TIOSHA]2.0.CO;2)
- Gibb JA, Fitzgerald BM (1998) Dynamics of sparse rabbits (*Oryctolagus cuniculus*), Orongorongo Valley, New Zealand. *New Zealand Journal of Zoology* 25: 231–243. <https://doi.org/10.1080/03014223.1998.9518153>
- Grayson FWL, Hassall M (1985) Effects of rabbit grazing on population variables of *Chorthippus brunneus* (Orthoptera). *Oikos* 44: 27–34. <https://doi.org/10.2307/3544039>
- Heath D (1995) *An Introduction to Experimental Design and Statistics for Biology*. CRC Press, London. <https://doi.org/10.1201/b12546>
- Isermann M, Koehler H, Mühl MJ (2010) Interactive effects of rabbit grazing and environmental factors on plant species-richness on dunes of Norderney. *Coastal Conservation* 14: 103–114. <https://doi.org/10.1007/s11852-009-0056-9>
- Ling SJ (2000) Orthoptera of Suffolk. *Transactions of the Suffolk Naturalists' Society* 36: 53–60.
- Lowry R (2020) VassarStats. <http://vassarstats.net/>
- Metsalu T, Vilo J (2015) ClustVis: A web tool for visualizing clustering of multivariate data using Principal Component Analysis and heatmap. *Nucleic Acids Research* 43: 566–570. <https://doi.org/10.1093/nar/gkv468>
- Millett J, Edmondson S (2013) The impact of 36 years of grazing management on vegetation dynamics in dune slacks. *Journal of Applied Ecology* 50: 1367–1376. <https://doi.org/10.1111/1365-2664.12113>
- Morris MG (2000) The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biological Conservation* 95: 129–142. [https://doi.org/10.1016/S0006-3207\(00\)00028-8](https://doi.org/10.1016/S0006-3207(00)00028-8)
- Nichols RN, Goulson D, Holland JM (2019) The best wildflowers for wild bees. *Journal of Insect Conservation* 23: 819–830. <https://doi.org/10.1007/s10841-019-00180-8>
- Pollard E, Yates T (1993) *Monitoring Butterflies for Ecology and Conservation*. Chapman and Hall, London.
- Richards OW, Waloff N (1954) Studies on the biology and population dynamics of British grasshoppers. *Anti-Locust Bulletin* 17: 1–182.
- Rollin O, Benelli G, Benvenuti S, Decourtye A, Wratten SD, Canale A, Desneux N (2016) Weed-insect pollinator networks as bio-indicators of ecological sustainability in agriculture. A review. *Agronomy for Sustainable Development* 36: 1–22. <https://doi.org/10.1007/s13593-015-0342-x>
- Van Wingerden WKRE, Musters JCM, Kleukers RMJC, Bongers W, van Biezen JB (1991a) The influence of cattle grazing intensity on grasshopper abundance (Orthoptera: Acrididae). *Proceedings of the Experimental and Applied Entomology Section, N.E.V. Amsterdam* 2: 28–34.
- Van Wingerden WKRE, Musters JCM, Maaskamp FIM (1991b) The influence of temperature on the duration of egg development in west European grasshoppers (Orthoptera: Acrididae). *Oecologia* 87: 417–423. <https://doi.org/10.1007/BF00634600>
- Waloff N (1950) The egg pods of British short-horned grasshoppers (Acrididae). *Proceedings of the Royal Entomological Society of London, Series A* 25: 115–126. <https://doi.org/10.1111/j.1365-3032.1950.tb00088.x>
- Wood DH (1988) Estimating rabbit density by counting dung pellets. *Australia Wildlife Research* 15: 665–671. <https://doi.org/10.1071/WR9880665>

# Bioecological aspects of the common black field cricket, *Gryllus assimilis* (Orthoptera: Gryllidae) in the laboratory and in *Eucalyptus* (Myrtaceae) plantations

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Academic editor: Ludivina Barrientos-Lozano | Received 1 December 2019 | Accepted 1 February 2020 | Published 29 May 2020

<http://zoobank.org/D69058BA-4EC5-41D7-B319-82251D38493D>

Citation: Masson MV, Tavares WS, Alves JM, Ferreira-Filho PJ, Barbosa LR, Wilcken CF, Zanuncio JC (2020) Bioecological aspects of the common black field cricket, *Gryllus assimilis* (Orthoptera: Gryllidae) in the laboratory and in *Eucalyptus* (Myrtaceae) plantations. Journal of Orthoptera Research 29(1): 83–89. <https://doi.org/10.3897/jor.29.48966>

## Abstract

The common black field cricket, *Gryllus assimilis* (Orthoptera: Gryllidae), damages young plants of red cedar, *Juniperus virginiana* (Cupressaceae); strawberry, *Fragaria × ananassa* (Rosaceae); sugarcane, *Saccharum officinarum* (Poaceae); teak, *Tectona grandis* (Lamiaceae); upland cotton, *Gossypium hirsutum* (Malvaceae); and, mainly, *Eucalyptus* spp. (Myrtaceae). The objective of this study was to investigate the biological and behavioral parameters of this insect in the laboratory and in *Eucalyptus* spp. plantations in Inhambupe, Bahia State, Brazil. The incubation period and the viability of *G. assimilis* eggs were 11.87 days and approximately 22%, respectively. The duration of the nymphal stage was 62.34 days with approximately 60% of the nymphs obtained in the laboratory being females. The average number of egg batches per female, eggs per female, and eggs per batch per female of this insect were 25.50, 862.17, and 34.65, respectively. *G. assimilis* females lived for 76.50 days in the adult stage, and 138.34 days in total, from egg through nymph to adult. Males produced three characteristic sounds: one for the marking of territory, one for courtship, and one when alone. *G. assimilis* fed primarily on weeds but, in their absence, it damaged young *Eucalyptus* spp. plants. This paper presents important data on the biology and behavior of *G. assimilis*; this information may encourage additional biological research, laboratory rearing, and integrated management of this pest.

## Keywords

bioecology, field observation, forest pest, Gryllides, Grylloidea, laboratory rearing

## Introduction

The common black field cricket, *Gryllus assimilis* (F., 1775) (Orthoptera: Gryllidae), is a pest of *Eucalyptus* spp. (Myrtaceae) (Severin 1926, Barbosa et al. 2009, Silva et al. 2013). Adults and

nymphs commonly damage outdoor plants, mainly nursery seedlings and young plants in the field (Spann 1934, Barbosa et al. 2009, Weissman et al. 2009). Occasional damage to seeds shortly after sowing and in adult *Eucalyptus* spp. trees has been reported (Grodzki 1972, Barbosa et al. 2009, Silveira et al. 2014). Damage by nymphs and adults (Hutchins and Langston 1953) may necessitate the replanting of *Eucalyptus* spp. to maintain the desired number of plants per hectare (Folsom 1931, Thomas and Reed 1937, Doggett et al. 1980). *G. assimilis* has been reported from Canada to Argentina and from the Atlantic to the Pacific Oceans (Rehn and Hebard 1915, Alexander and Walker 1962, Weissman et al. 1980, 2009).

*Eucalyptus* spp. planting is done in the months prior to and during the rainy season in Brazil when irrigation is, generally, not necessary (Stape et al. 2001, Sampaio et al. 2016), making conditions favorable for *G. assimilis*, which prefers moist soil and a dark environment (Grodzki 1972, David et al. 2003, Barbosa et al. 2009). Nymphs and adults of this pest feed on the stem, leaves, roots, and branches of young *Eucalyptus* spp. plants during the night and remain hidden during the day in holes or between clods of earth and vegetation on the ground (Grodzki 1972, David et al. 2003, Barbosa et al. 2009). Damage by *Gryllus* sp. adults was recorded only on the lower third of *Eucalyptus grandis* seedlings in a laboratory in Brazil, and damage was greater to plants on the ground than in those grown in raised beds in a nursery (Barbosa et al. 2009), probably due to this insect's inability to jump or fly to elevated heights (Guerra and Pollack 2007).

Management strategies for *G. assimilis* in *Eucalyptus* spp. and other forest trees in the nursery and the field depend on studies of the biology and behavioral aspects of this insect (Mello et al. 1980, Hall 1988, Bertram and Rook 2012). An online system for rapid identification of insect pests in commercial teak plantations,

*Tectona grandis* (Lamiaceae), including *G. assimilis*, using smartphones as the inference mechanism, was developed (Nascimento et al. 2016). *G. assimilis* was found to inflict damage to *E. grandis* seedlings up to 40 days after planting, and this damage was lower in plantations near native forest areas (Barbosa et al. 2009), probably due to the presence of *G. assimilis* predators in the forest areas (Severin 1926). The objective of the present study was to evaluate the biology and behavior of *G. assimilis* in the laboratory and *Eucalyptus* spp. plantations in Inhambupe, Bahia State, Brazil.

## Material and methods

**Study site.**—The study was carried out in the Laboratório de Proteção Florestal (LPF) at  $26.5 \pm 0.5^\circ\text{C}$ ,  $61.0 \pm 0.5\%$  RH, and 12h:12h (L:D) photoperiod, and in *Eucalyptus* spp. plantations ( $11^\circ 47'S \times 38^\circ 21'W$ , 292 m above sea level) of Bracell Ltd. in Inhambupe, Bahia State, Brazil, with a temperature and RH of  $26.5 \pm 0.5^\circ\text{C}$  and  $62 \pm 15\%$ , respectively. Meteorological data were obtained from the company weather station located about 5 km from the study site. The municipality is located on the northern coast of Bahia State, where *Eucalyptus* spp. are planted for the production of special soluble cellulose (basically two types: rayon-grade and specialty-grade) with  $\alpha$ -cellulose content above 98.5%. *Eucalyptus* spp. pests, including *G. assimilis*, have been reported in Inhambupe and in another 20 municipalities of Bahia State (Masson et al. 2017a, b).

**Collecting insects of the parental generation in the field.**—*G. assimilis* adults were collected from the study site at night during outbreaks on recently planted *Eucalyptus* spp. seedlings and brought to the laboratory in individual plastic containers (500 mL) lined with hydrophilic cotton. For mating, each pair was placed in a glass container (1.5 L) closed with polyvinyl chloride (PVC) fabric. Into each glass container was placed a plastic container (4 mL) with freshly harvested, crushed *Brassica oleracea* group *acephala* (Brassicaceae) leaves as food, another container (4 mL) with hydrophilic cotton soaked in distilled water as a moisture source, and a third container (60 mL) with oviposition substrate (3 cm of sieved and sterilized fine sand) (Mello et al. 1980). This sand was sieved using a Granutest n° 35 sieve (São Paulo State, Brazil). Corrugated and perforated cardboard was also placed in the container for shelter and shade (Mello et al. 1980), an important addition for *G. assimilis* as it is nocturnal (Ackert and Wadley 1921) as well as cannibalistic and an omnivore (Blatchley 1901).

**Insect identification.**—*G. assimilis* was identified by Dr. Evoneo Berti Filho of the Departamento de Entomologia e Acarologia at the Universidade de São Paulo in Piracicaba, São Paulo State, Brazil. Five adult males and five adult females collected in *Eucalyptus* spp. plantations in Inhambupe were identified by comparing external morphology with that described in Weissman et al. (1980).

**Rearing eggs, nymphs, and adults of the F1 generation.**—*G. assimilis* eggs obtained from adults collected in the field were placed in Petri dishes (9 cm diameter) lined with sterilized fine sand. Nymphs obtained from these eggs were each put in separate Petri dishes (15 cm diameter) using a fine-tipped brush. The nymphs were given the same food and moisture source as the adults were given.

Forty healthy *G. assimilis* adults (20 males and 20 females) of a larger size were selected from the nymphs reared in the laboratory, which were in turn obtained from individuals collected in the field and mated as described. The mating and maintenance of

adults and the collection and maintenance of *G. assimilis* eggs were performed as for the parental generation. If one half a pair died, it was replaced with a healthy individual of the same sex.

**Biological evaluations of the F2 generation nymphs in the laboratory.**—*G. assimilis* nymphs were obtained from eggs laid by the F1 generation adults in the laboratory. First-instar nymphs were kept individually in Petri dishes (15 cm diameter) until the end of the last instar. The number of instars and the duration of the nymph stage (days) were quantified by counting the number of exuviae observed on the base of the rearing containers during daily evaluations.

**Behavioral assessments of nymphs in the laboratory (F2 generation) and field.**—The behavioral aspects of *G. assimilis* were determined via visual observation throughout the insects' life cycle in the laboratory, as well as day and night visits (two visits per month in the morning, afternoon, and night periods for 12 months) and notes in the field. The following behavioral parameters were measured and basic statistics obtained: beginning, ending, and hatching peaks of the nymphs; the dispersal behavior of the nymphs shortly after hatching in the rearing containers; their coloration two hours after hatching and the changes in coloration with development; their feeding start time; and the acts of cannibalism and the percentage of each body part attacked. The percentage of first instar nymphs adhered to eggshells and the percentage of these nymphs that died were quantified. The percentage of nymphs that fed on their exuviae was also assessed.

In the field, the depth (cm) of galleries with aggregated first instar nymphs, and the nymphs' dispersion characteristics, according to their development, were registered from 20 randomly selected galleries excavated between 04:00 and 08:00 AM, which is the period of greatest occurrence of this insect in *Eucalyptus* spp. plantations.

**Bioecological evaluations of F2 generation adults and their eggs in the laboratory.**—The sex ratio (females: males) was evaluated with the females identified by the ovipositor at the abdomen extremity (Weissman et al. 1980). Copulation was reported and described. The number of copulations per couple and the copula time (h) were obtained daily by visual observations during the adult stage. The period (days) of pre-oviposition, oviposition, and post-oviposition, the number of egg batches (eggs laid per oviposition act) and eggs per female, the number and viability (%) of eggs per batch, and the incubation period (days) of eggs laid per female were evaluated. Adult female longevity (days) and the duration (days) of the full life cycle (from egg oviposition to death of the F2 generation females) were also evaluated. The duration (min) of the oviposition period and oviposition behavior, considering egg batch oviposition, the introduction of the ovipositor in the rearing container sand (depth in cm), and the distance (mm) between eggs of the same batch were evaluated in five randomly selected females. The geometric shape and the egg diameter (mm) were measured. The egg diameter was measured in five randomly selected eggs per female from egg batches laid at the intermediate time. The color of the newly deposited eggs, those close to hatching, and of the unviable eggs were also evaluated.

**Sound observations under laboratory conditions.**—The number and types of sounds, the sex of individuals emitting them, and the reaction of conspecific males and females when hearing these sounds were registered. Three trials were set for mating males and females in three different combinations and appraising the

sounds emitted in each situation. The first trial consisted of four crickets: two males and two females. The second trial consisted of one male and one female, and the third trial consisted of a single individual male. In all trials, only two-day-old virgin crickets were used. The largest and healthiest F1 and F2 generation insects from the laboratory colony were chosen for the sound tests. Three replicates per trial were conducted, and the crickets' behavior in each trial was observed and recorded for 24 hours. Each trial was conducted in one of three glass containers, each at the far end of an insect rearing room (25 m<sup>2</sup>) to minimize the possibility of trials interfering with each other. The containers were placed on a bench at a height of 1.5 m, 26.5 ± 0.5 °C, 61.0 ± 0.5% RH, and 12h:12h (L:D) photoperiod.

*Host plants in the field.*—Plants preferred by *G. assimilis* nymphs and adults for feeding, including *Eucalyptus* spp. and weeds, were evaluated visually in two commercial plots of *Eucalyptus* in Inhambupe, one without weed removal and another with manual weed removal at plots establishment. *Eucalyptus* spp. and weeds were examined daily for damage from planting to 30 days.

## Results and discussion

*Biological evaluations of F2 generation nymphs in the laboratory.*—*G. assimilis* nymphs passed through five instars in 53 to 66 days (average 62.34 days) (Table 1). These results are similar to previous reports on *Gryllus abbreviatus* Serville, 1838, in Illinois (McNeill 1891) and the fall field cricket, *Gryllus pennsylvanicus* Burmeister, 1838, in Indiana, USA (Blatchley 1901). However, our results differed from those found in other studies of *G. assimilis*. For example, *G. assimilis* from *Eucalyptus saligna* plantations in Brazil also had five instars but spent three to five weeks as nymphs (Grodzki 1972); *G. assimilis* collected in *T. grandis* plantations (Silva et al. 2013) and those collected in *Eucalyptus* spp. plantations in Piracicaba, São Paulo State, Brazil (Mello et al. 1980), both spent 45 days as nymphs. These differences may be due to variation in RH in the laboratories (61.0 ± 0.5% in this study vs. 70.0 ± 10.0% in the others).

*Behavioral assessment of nymphs in the laboratory (F2 generation) and field.*—In the laboratory, *G. assimilis* nymphs emerged between 05:00 and 10:00 AM, with a peak around 06:00 AM (Table 1). This time corresponds to sunrise in Inhambupe, with milder temperatures and rains or dew during the rainy season. The newly emerged, yellowish-white *G. assimilis* nymphs, which spread through the rearing container shortly after hatching in the laboratory, turned brown after about two hours and then turned darker brown to black as they developed. Cannibalism was observed only on moribund or dead nymphs in both the absence and presence of food and a moisture source; the abdomen of the victim was the most attacked body part. First and second instar nymphs are more agile than the other instars. During the daytime, nymphs remained in dark places and began foraging in the rearing containers at about 05:00 PM. No preferential feeding time was observed. About 2% of the nymphs were trapped in the eggshell and died, probably from injuries to their bodies. The nymphs fed on their exuviae after molting making it difficult to evaluate the number of exuviae. Cannibalism behavior on weak or dying individuals had rarely been observed among laboratory-living individuals (Ackert and Wadley 1921).

In the laboratory, *G. assimilis* eggs were laid in the container provided with sterilized fine sand as oviposition substrate. Females

leaned on their anterior legs and lowered their abdomen, introducing the ovipositor in the sand to a depth of up to 1.5 cm. During the oviposition process, females moved the abdomen down and upwards rapidly several times in a single location. In an egg batch, the distance between each egg was about 1 mm. The number of eggs laid was lower on drier substrates, and no eggs were laid on very moist substrates. The oviposition period was 5 min per egg batch, and a higher number of eggs were laid at night. Feeding habits of adults were similar to that of the nymphs, with cannibalism on dying or dead individuals being observed regardless of the lack or presence of food and a moisture source. As cannibalism was performed, aggressiveness among individuals was observed.

In the field, first instar nymphs were observed aggregated in the interior of galleries they excavated. These nymphs separated from each other according to their development and remained in the galleries at an average depth of 20 cm. This depth probably increases according to nymphs' development and soil moisture, which are important parameters for nymph hatching and development during the rainy season.

*Bioecological evaluations of F2 generation adults and their eggs in the laboratory.*—The *G. assimilis* female: male ratio was 6:4. Copula occurred during the daytime (04:30 AM to 04:00 PM), coinciding with a reduction in foraging activity (Table 1). The number of copulations per couple varied from zero to four (average 1.34). The pre-oviposition, oviposition, and post-oviposition periods ranged from 16 to 37, 11 to 66, and from 0 to 12 days with averages of 35.20, 36.80, and 4.50 days, respectively (Fig. 1). The number of egg batches, total eggs, and eggs per batch per female ranged from 8 to 55 (average 25.50), 260 to 1,918 (average 862.17), and 23.64 to 46.13 (average 34.65 eggs), respectively. Egg viability was 8 to 38% (average 22%). The egg incubation period ranged from 11.38 to 12.40 days (average 11.87). The F2 adult females' longevity ranged from 27 to 115 days (average 76.50 days); while the entire F2 adult females' life cycle duration (from the egg stage to death) was 138.34 days (Table 1).

Our results generally agreed with earlier works. For example, Veazey et al. (1976) indicate that between 30 to 80% of the total individuals are males for *Gryllus* spp. in the field in Florida, USA. Variation from zero to four in the copulation number per *G. assimilis* couple confirms the fact that multiple mating is frequent and

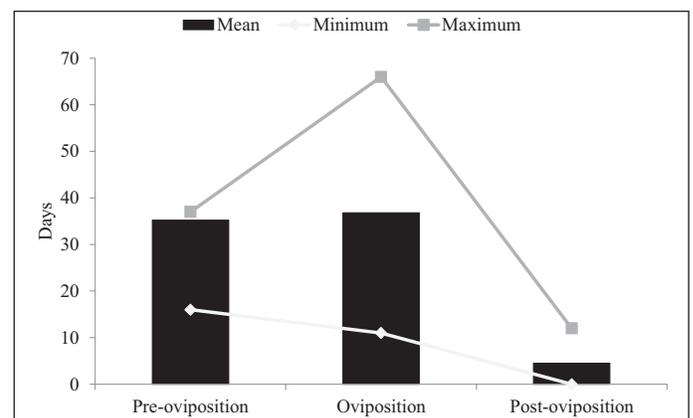


Fig. 1. Minimum, maximum, and mean duration of the pre-oviposition, oviposition, and post-oviposition periods of *Gryllus assimilis* (Orthoptera: Gryllidae) in the laboratory (N = 50 couples).

**Table 1.** *Gryllus assimilis* biological and behavioral parameters under laboratory conditions: minimum (Min.), maximum (Max.), mean (Mean), total (Total), and sample size (N).

Parameters	Min.	Max.	Mean	Total	N
Number of instars	–	–	–	5	500
Duration nymphal stage (days)	53	66	62.34	–	500
Sex ratio females: males	–	–	–	6:4	100
Number of copulations per couple	0	4	1.34	–	50*
Time at copulation	04:30 AM	04:00 PM	–	–	50*
Number of egg batches per female	8	55	25.50	–	50*
Total number of eggs per female	260	1,918	862.17	–	50*
Eggs per batch per female	23.64	46.13	34.65	–	50*
Viability of eggs (%)	8.40	38.24	22.37	–	20**
Incubation period of eggs (days)	11.38	12.40	11.87	–	20**
Longevity of adult females (days)	27	115	76.50	–	50*
Female life cycle duration (egg, nymph, and adult) (days)	–	–	138.34	–	50*
Egg diameter (mm)	2.8	3.2	3.0	–	250
Time of nymph emergence	05:00 AM	10:00 AM	06:00 AM	–	20***
Dead nymphs adhered to egg shell (%)	–	–	–	2	20***
Cannibalism on abdomen (%)	–	–	–	100	20***
Time nymphs began foraging	–	–	–	05:00 PM	20***
Depth of galleries excavated by nymphs (cm)	–	–	20	–	20
Depth of ovipositor introduction into the sand (cm)	–	1.5	–	–	10****
Distance between eggs in the same batch (mm)	–	–	1.0	–	2*****
Duration of egg batch oviposition (min)	–	–	5	–	2*****

\* Number of couples, \*\* number of eggs per first, intermediate, and final egg batch laid per couple, \*\*\* number of nymphs obtained from eggs per first, intermediate, and final batch per couple, \*\*\*\* number of ovipositor introductions per first, intermediate, and final batch per couple, and \*\*\*\*\* number of egg batches for first, intermediate, and final batch laid per couple.

beneficial for female crickets (Arnqvist and Nissson 2000). The female Mediterranean field cricket, *Gryllus bimaculatus* De Geer, 1773 (Bretman and Tregenza 2005), and the tropical house cricket, *Gryllobates sigillatus* Walker, 1869 (Orthoptera: Gryllidae) (Sakaluk et al. 2002), can mate up to 7 and 15 times, respectively. The number of matings increases fecundity and the number of eggs produced by vocal field cricket females, *Gryllus vocalis* Scudder, 1901 (Gershman 2009). Regarding the number of eggs laid per female, we found a higher number than Mello et al. (1980), who worked on a population of *G. assimilis* females collected in a *Eucalyptus* sp. plantation and subsequently reared in the laboratory in Piracicaba, São Paulo State, Brazil. Nonetheless, egg viability was higher (86%) in the Piracicaba population than in our present study (22%). This variation may be attributed to differences in the rearing environment, e.g., RH. The low viability of the eggs may be associated with a failure in copulation and the rejection of the female by the second male after the exchange of the first one due to its premature death; i.e., non-mating females may lay infertile eggs. Eggs from the first and final batches laid showed variable viability, while batches laid at the intermediate time had the most fertile eggs. This suggests that females require periodic copulations to maintain the viability of their eggs. It was noticed that in those females that laid a low number of eggs, the eggs had high viability, suggesting a negative correlation between the total number of eggs laid per female and their viability. Out of the viable eggs laid within a single batch, 95% hatched within 24 h.

We found a similar incubation period of *G. assimilis* eggs compared with the population from *Eucalyptus* spp. plantations in Piracicaba, São Paulo State, Brazil (Mello et al. 1980). However, in a study in Manhattan, Kansas, USA, Ackert and Wadley (1921) found that the incubation period of eggs from young *G. assimilis* females mated in the field and brought to the laboratory was three weeks. The longevity of *G. assimilis* females in this study was higher than the longevity of the same species of undetermined

sex from the study of Silva et al. (2013), which was about 60 days, and higher than those of undetermined sex from the study by Mello et al. (1980), of about 45 days. The complete life cycle of *G. assimilis* females (from the egg stage to the females' death) was 138.34 days, suggesting the potential of two or three generations per year in Inhambupe, Bahia State, Brazil. However, two is more likely because the rainy season in this municipality lasts about five months. In contrast, the life cycle of *G. assimilis* individuals collected on *E. saligna* plantations in Brazil was about three months in summer and shorter in winter (Grodzki 1972).

*G. assimilis* eggs were rod-shaped and  $3.0 \pm 0.2$  mm diameter. Eggs were white-opaque soon after oviposition, becoming straw-yellow except for the apex, which darkened as it neared hatching. Inviolate eggs were translucent white soon after deposition, making it easier to distinguish them. Some viable eggs became dark yellow and wrinkly at low RH, rendering them inviolate.

**Sound observations.**—*G. assimilis* males emitted three types of sound. These sounds were emitted at different times in the laboratory, each during a specific situation. The first sound was for marking territory, the second for courtship, and the third could be heard when the insect was alone. Each sound provoked a particular reaction in both conspecific females and males. The sound for marking territory was emitted intensely by the males in containers with two female and two male individuals, indicating territorial disputes. The wings were quickly raised, and the characteristic sound was emitted. One male retreated from the other and returned or not to the dispute after a few minutes, ending with the death or injury of the smaller, weaker insect. In most cases, the winner changed his song to courtship.

The sound for courtship was alternating, soft, strident, low frequency, and was done while the male slowly walked behind the female and turned his back to her. Then, the male lowered his abdomen to the female, which mounted the male, then lowered her

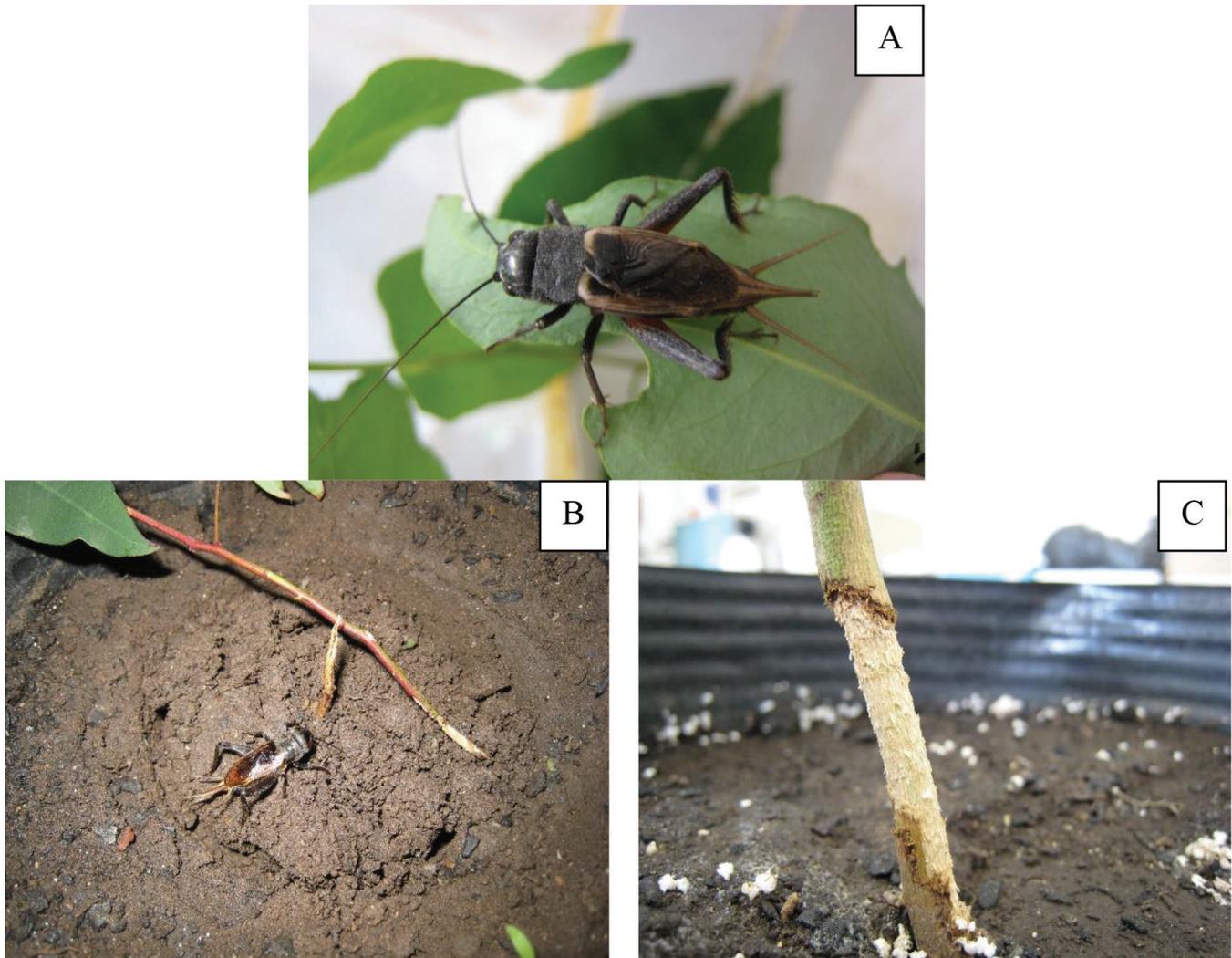


Fig. 2. *Gryllus assimilis* (Orthoptera: Gryllidae). A. Adult; B, C. Damage to *Eucalyptus* sp. (Myrtaceae).

abdomen for the male to introduce his copulatory organ into her genital opening, remaining in this position for less than a minute. Noises caused by equipment and people in the laboratory caused the female to dismount from the male several times with both returning to the mating position. Courtship lasted for up to one hour and the copulation period lasted about eight minutes. The spermatophore was observed at the insertion of the genital opening of copulated *G. assimilis* females. The calling sound emitted by individuals alone in the laboratory rearing container was continuous, strident, and often attracted sexually receptive females.

Sound production by resting *G. assimilis* males is a common behavior of *Gryllus* spp. The sound is produced by a structure called the pars stridens composed of small teeth on the ventral region of the right tegmen that are scraped by a "scraper" on the border of the left tegmen (portion of the anal edge), similar to a "washboard". These teeth generally present a triangular, uniform, and sloping morphology and gradually decrease in size at both ends (David et al. 2003). The sound may be indicative of cricket species, but *G. assimilis* individuals emitted different sounds in the field in North Carolina, USA (Fulton 1932). After the emission of territorial marking sounds, disputes between *Gryllus* spp. males and females are aggressive, but females do not necessarily mate with the winning male (Loranger and Bertram 2016). Vigorous

males of *Gryllus* spp. win more competitions with rivals for territory and mating (Bertram and Rook 2012). The *G. assimilis* courtship sound has two components: "chirps" and "ticks". "Chirps" are groups of low amplitude and frequency sound pulses and "ticks" are single pulses of greater amplitude with a high dominant frequency. Although variable, a cricket sound consists of five "chirps" followed by two "ticks" (Vedenina and Pollack 2012). The *Gryllus* spp. courtship sound forms the basis for sexual choice (Rebar et al. 2009). The calling sound is less complex with only one element, while the courtship call has two which differ in time and frequency (Elsner and Popov 1978). The sound of *G. assimilis* has been registered in oscillograms by Weissman et al. (2009), Shestakov and Vedenina (2012), and Pacheco et al. (2013).

*Host plants in the field.*—*Eucalyptus* spp. seedlings were more damaged by *G. assimilis* nymphs and adults after the manual removal of weeds (Fig. 2). This suggests that the weeds are preferred food for this insect. In this study, damage by *G. assimilis* was mainly observed on rass-jack weeds, *Bidens pilosa* (Asteraceae), native to the Americas (Rejmánek et al. 2017); lilac tassel flower, *Emilia sonchifolia* (Asteraceae), native to Asia (Sheikh and Dixit 2017); *Solanum* sp. (Solanaceae); and amaranth, *Amaranthus hybridus* (Amaranthaceae), native to North America

(Iamónico and El Mokni 2017). *G. assimilis* fed on weeds of *M. sativa*; Kentucky bluegrass, *Poa pratensis*; bindweed species, *Convolvulus* (Convolvulaceae); crabgrass, *Syntherisma sanguinale*; Dulac and Bermuda grass, *Capriola dactylon* (Poaceae) as well as decomposing bodies of its own species and animal carcasses in areas near Manhattan, Kansas, USA (Ackert and Wadley 1921), confirming the polyphagous habits of this insect.

## Acknowledgements

We would like to thank Dr. Phillip John Villani (University of Melbourne, Australia) for revising and correcting the English language used in an early version of this manuscript. We also thank the laboratory and field staff of Bracell Ltd. for their help in this research. Funding was provided by the following Brazilian institutions: Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Finance code 001, Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG), Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), and Programa Cooperativo sobre Proteção Florestal (PROTEF) of the Instituto de Pesquisas e Estudos Florestais (IPEF).

## References

- Ackert JE, Wadley FM (1921) Observations on the distribution and life history of *Cephalobium microbivorum* Cobb and of its host, *Gryllus assimilis* Fabricius. *Transactions of the American Microscopical Society* 40: 97–115. <https://doi.org/10.2307/3221581>
- Alexander RD, Walker TJ (1962) Two introduced field crickets new to Eastern United States (Orthoptera: Gryllidae). *Annals of the Entomological Society of America* 55: 90–94. <https://doi.org/10.1093/aesa/55.1.90>
- Arnqvist G, Nissson T (2000) The evolution of polyandry: Multiple mating and female fitness in insects. *Animal Behaviour* 60: 145–164. <https://doi.org/10.1006/anbe.2000.1446>
- Barbosa LR, Iede ET, Santos F (2009) Characterization of mischief of *Gryllus* spp. in plants of eucalyptus, in laboratory. *Pesquisa Florestal Brasileira* 30: 63–68. <https://doi.org/10.4336/2009.pfb.59.63>
- Bertram SM, Rook V (2012) Relationship between condition, aggression, signaling, courtship, and egg laying in the field cricket, *Gryllus assimilis*. *Ethology* 118: 360–372. <https://doi.org/10.1111/j.1439-0310.2011.02019.x>
- Blatchley WS (1901) *The Orthoptera of Indiana: An Illustrated Descriptive Catalogue of the Species Known to Occur in the State, with Bibliography, Synonymy and Descriptions of New Species*. Indiana Department of Geology and Natural Resources Press, Indianapolis, IN, USA. <https://doi.org/10.5962/bhl.title.8712>
- Bretman A, Tregenza T (2005) Measuring polyandry in wild populations: A case study using promiscuous crickets. *Molecular Ecology* 14: 2169–2179. <https://doi.org/10.1111/j.1365-294X.2005.02556.x>
- David JAO, Zefa E, Fontanetti CS (2003) Cryptic species of *Gryllus* in the light of bioacoustic (Orthoptera: Gryllidae). *Neotropical Entomology* 31: 75–80. <https://doi.org/10.1590/S1519-566X2003000100010>
- Doggett CA, Hawley V, Norris W (1980) Cricket damage to red cedar seedlings. *Tree Planters' Notes* 31: 18.
- Elsner N, Popov A (1978) Neuroethology of acoustic communication. *Advances in Insect Physiology* 13: 229–335. [https://doi.org/10.1016/S0065-2806\(08\)60267-2](https://doi.org/10.1016/S0065-2806(08)60267-2)
- Folsom JW (1931) Damage to cotton by crickets. *Journal of Economic Entomology* 24: 807–815. <https://doi.org/10.1093/jee/24.4.807>
- Fulton BB (1932) North Carolina's singing Orthoptera. *Journal of the Elisha Mitchell Scientific Society* 47: 55–69.
- Gershman SN (2009) Large numbers of matings give female field crickets a direct benefit but not a genetic benefit. *Journal of Insect Behavior* 23: 59–68. <https://doi.org/10.1007/s10905-009-9195-y>
- Grodzki RM (1972) *Gryllus assimilis*: Danos causados e métodos de combate. *Revista Floresta* 4: 34–37. <https://doi.org/10.5380/rf.v4i2.5754>
- Guerra PA, Pollack GS (2007) A life history trade-off between flight ability and reproduction behavior in male field crickets (*Gryllus texensis*). *Journal of Insect Behavior* 20: 377–387. <https://doi.org/10.1007/s10905-007-9084-1>
- Hall DG (1988) Insects and mites associated with sugarcane in Florida. *Florida Entomologist* 71: 138–150. <https://doi.org/10.2307/3495361>
- Hutchins RE, Langston JM (1953) An unusual occurrence of the field cricket. *Journal of Economic Entomology* 46: 169–169. <https://doi.org/10.1093/jee/46.1.169>
- Iamónico D, El Mokni R (2017) *Amaranthus palmeri*, a second record for Africa and notes on *A. sonoriensis* nom. nov. *Bothalia* 47: 1–4. <https://doi.org/10.4102/abc.v47i1.2100>
- Loranger MJ, Bertram SM (2016) The effect of male dominance on female choice in a field cricket (*Gryllus assimilis*). *Animal Behaviour* 114: 45–52. <https://doi.org/10.1016/j.anbehav.2016.01.020>
- Masson MV, Tavares W de S, Lopes F de A, de Souza AR, Ferreira-Filho PJ, Barbosa LR, Wilcken CF, Zanuncio JC (2017a) *Selitrichodes neseri* (Hymenoptera: Eulophidae) recovered from *Leptocybe invasa* (Hymenoptera: Eulophidae) galls after initial release on *Eucalyptus* (Myrtaceae) in Brazil, and data on its biology. *Florida Entomologist* 100: 589–593. <https://doi.org/10.1653/024.100.0316>
- Masson MV, Tavares W de S, Pereira DWV, Matos WC, Lopes F de A, Ferreira-Filho PJ, Wilcken CF, Zanuncio JC (2017b) Management of *Hylesia nanus* (Lepidoptera: Saturniidae) on *Eucalyptus* (Myrtaceae) plantations. *Florida Entomologist* 100: 380–384. <https://doi.org/10.1653/024.100.0239>
- McNeill J (1891) A list of the Orthoptera of Illinois. I. *Psyche* 6: 3–9. <https://doi.org/10.1155/1891/35871>
- Mello AMLT, Silveira Neto S, Parra JRP (1980) Fertility and life expectancy table for *Gryllus assimilis* (Fabricius, 1775) (Orthoptera, Gryllidae) in the laboratory. *Anais da Sociedade Entomológica do Brasil* 9: 133–141.
- Nascimento DA, Anuniação Jr RM, Arnhold A, Ferraz Filho AC, dos Santos A, Zanuncio JC (2016) Expert system for identification of economically important insect pests in commercial teak plantations. *Computers and Electronics in Agriculture* 121: 368–373. <https://doi.org/10.1016/j.compag.2015.12.024>
- Pacheco K, Dawson JW, Jutting M, Bertram SM (2013) How age influences phonotaxis in virgin female Jamaican field crickets (*Gryllus assimilis*). *PeerJ* 1: e130. <https://doi.org/10.7717/peerj.130>
- Rebar D, Bailey NW, Zuk M (2009) Courtship song's role during female mate choice in the field cricket *Teleogryllus oceanicus*. *Behavioral Ecology* 20: 1307–1314. <https://doi.org/10.1093/beheco/arp143>
- Rehn JAG, Hebard M (1915) The genus *Gryllus* (Orthoptera) as found in America. *Proceedings of the Academy of Natural Sciences of Philadelphia* 67: 293–322.
- Rejmánek M, Huntley BJ, Le Roux JJ, Richardson DM (2017) A rapid survey of the invasive plant species in western Angola. *African Journal of Ecology* 55: 56–69. <https://doi.org/10.1111/aje.12315>
- Sakaluk SK, Schaus JM, Eggert AK, Snedden WA, Brady PL (2002) Polyandry and fitness of offspring reared under varying nutritional stress in decorated crickets. *Evolution* 56: 1999–2007. <https://doi.org/10.1111/j.0014-3820.2002.tb00126.x>
- Sampaio TE, Dalcin TE, Bogiani JC, Mori ES, Guerrini IA (2016) Selection of *Eucalyptus* clones and adjustment of potassium doses for extended drought in Bahia savanna. *Revista Árvore* 40: 1031–1039. <https://doi.org/10.1590/0100-67622016000600008>
- Severin HC (1926) The common black field cricket, *Gryllus assimilis* (Fab.) and its control. *Journal of Economic Entomology* 19: 218–227. <https://doi.org/10.1093/jee/19.2.218>
- Sheikh DK, Dixit AK (2017) Occurrence of invasive plant in three phytogeographical region of Bilaspur district of Chhattisgarh. *Annals of Plant Sciences* 6: 1872–1878. <https://doi.org/10.21746/aps.2017.6.12.13>
- Shestakov LS, Vedenina VY (2012) A problem of taxonomic status of “banana cricket” from culture of the Moscow Zoo insectarium. *Entomological Review* 92: 262–270. <https://doi.org/10.1134/S0013873812030025>

- Silva CVM, Yamaki KY, Silva AG (2013) Identification and characterization of insect fauna on teak plantation (*Tectona grandis*). *Nucleus* 10: 207–218. <https://doi.org/10.3738/1982.2278.879>
- Silveira JA, Souto HN, Miranda Filho R, Ferreira QC, Ribeiro FA (2014) Levantamento preliminar qualitativo das ordens e das espécies de invertebrados em diferentes estágios de crescimento de eucalipto *Eucalyptus grandis*, no município de Monte Carmelo – MG. *Revista GETEC* 3: 74–82.
- Spann L (1934) Studies on the reproductive systems of *Gryllus assimilis* Fabr. *Transactions of the Kansas Academy of Science* 37: 299–341. <https://doi.org/10.2307/3625312>
- Stape JL, Gonçalves JLM, Gonçalves AN (2001) Relationships between nursery practices and field performance for *Eucalyptus* plantations in Brazil. *New Forests* 22: 19–41. <https://doi.org/10.1023/A:1012271616115>
- Thomas WA, Reed LB (1937) The field cricket as a pest of strawberries and its control. *Journal of Economic Entomology* 30: 137–140. <https://doi.org/10.1093/jee/30.1.137>
- Weissman DB, Rentz DCF, Alexander RD, Loher W (1980) Field crickets (*Gryllus* and *Acheta*) of California and Baja California, Mexico (Orthoptera: Gryllidae: Gryllinae). *Transactions of the American Entomological Society* 106: 327–356.
- Weissman DB, Walker TJ, Gray DA (2009) The field cricket *Gryllus assimilis* and two new sister species (Orthoptera: Gryllidae). *Annals of the Entomological Society of America* 102: 367–380. <https://doi.org/10.1603/008.102.0304>
- Veazey JN, Kay CAR, Walker TJ, Walker WHW (1976) Seasonal abundance, sex ratio, and macroptery of field crickets in Northern Florida. *Annals of the Entomological Society of America* 69: 374–380. <https://doi.org/10.1093/aesa/69.2.374>
- Vedenina VY, Pollack GS (2012) Recognition of variable courtship song in the field cricket *Gryllus assimilis*. *Journal of Experimental Biology* 215: 2210–2219. <https://doi.org/10.1242/jeb.068429>



# *Oecanthus salvii* sp. nov. (Orthoptera: Gryllidae: Oecanthinae): A new tree cricket species from Modoc County in northeast California

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Academic editor: Klaus-Gerhard Heller | Received 22 January 2020 | Accepted 8 March 2020 | Published 29 May 2020

<http://zoobank.org/28C1635B-B0D0-40A8-AEC1-495BD49D724A>

Citation: Collins N, Schneider KR (2020) *Oecanthus salvii* sp. nov. (Orthoptera: Gryllidae: Oecanthinae): A new tree cricket species from Modoc County in northeast California. Journal of Orthoptera Research 29(1): 91–99. <https://doi.org/10.3897/jor.29.50400>

## Abstract

A new species of *Oecanthus* is described from extreme northeast California. *Oecanthus salvii* sp. nov. is currently known only from Lake Annie in Modoc County, California, and occurs on sagebrush (*Artemisia*) and rabbitbrush (*Ericameria*). It has the narrow tegmina, antennal markings, metanotal gland configuration, and trilling song found in the *Oecanthus nigricornis* species group. Song details and morphology, including the shape of the subgenital plate and copulatory blades, are provided in this paper. This new species has been given the common name of sage tree cricket.

## Keywords

Lake Annie, rabbitbrush, sage tree cricket, sagebrush, setae, subgenital plate

## Introduction

*Oecanthus* Serville, 1831 is the only genus of Oecanthinae that occurs in the western U.S. (Cigliano et al. 2020, SINA 2020b). The 19 species of *Oecanthus* reported in the United States are divided into four main groups: *nigricornis*, *niveus*, *rileyi*, and *varicornis* (Walker 1962, 1963, Walker and Collins 2010). These groups can be distinguished by characteristics including song pattern (chirping vs. trilling and continuous vs. intermittent); song pulse or chirp rate at given temperatures; regular vs. irregular pattern of pulses or chirps; coloration of the antennae, head, pronotum, and abdomen; antennal markings on the pedicel and scape; and tegminal width.

Photographs posted on BugGuide (2020) by KS at Lake Annie in Modoc County, California, led to the investigation of this new species (Figs 1, 2). The green coloring, narrow tegmina, and the configuration and shapes of the antennal markings matched the *nigricornis* species group. Three tree crickets in the *nigricornis* species group are known to occur in the western United States: *Oecanthus argentinus* Saussure, 1874, *O. quadripunctatus* Beutenmüller, 1894, and *O. walkeri* Collins & Symes, 2012.

These tree crickets found at Lake Annie had unusual coloring and an unusual upper outer marking on the scape. Photographs taken during two visits by KS in 2017 and 2018 show tree crickets

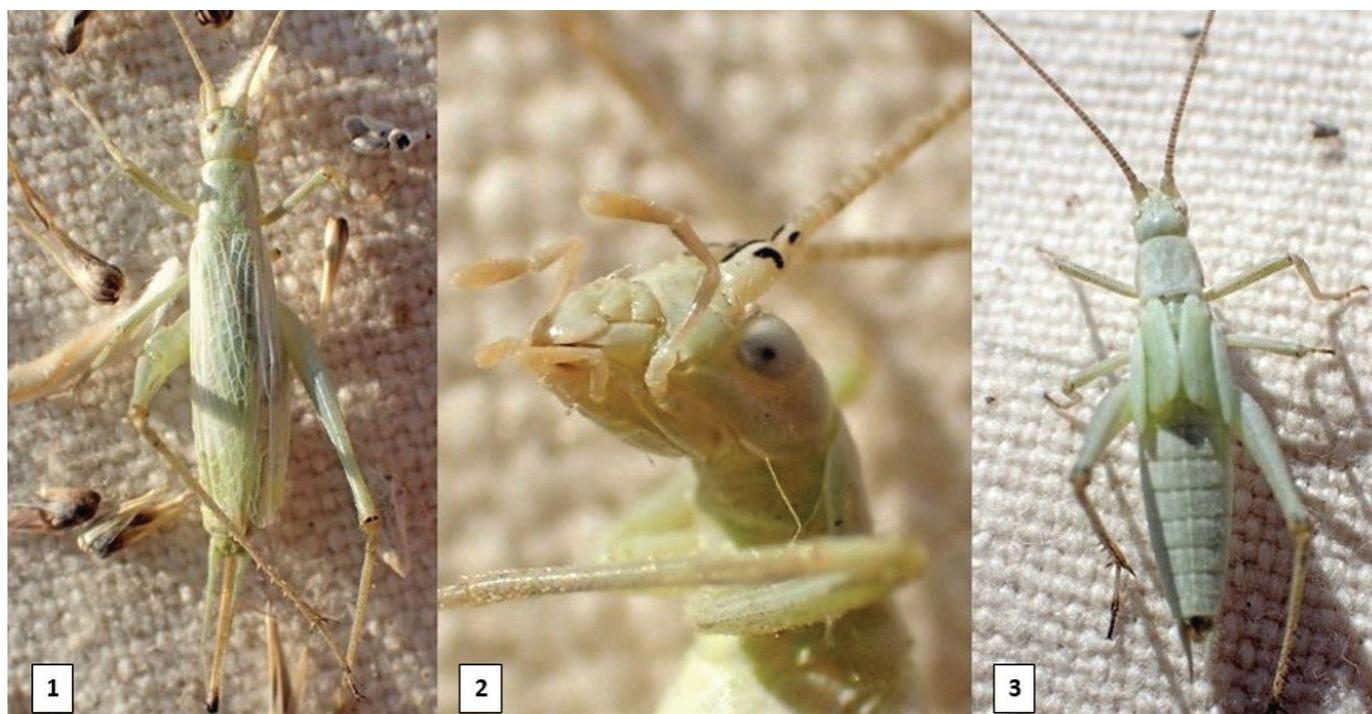
with a milky pale green color. The 2018 male photographed was a 5<sup>th</sup> stage instar, thus no song recordings were possible (Fig. 3). The upper-outer black mark on the first antennal segment (scape) is in an upward arch shape, and the two marks on the second segment (pedicel) are of medium width and separated by a width greater than either of the marks.

## Materials and methods

**Collection methods.**—Photographs of sweep-netted individuals were taken by KS in July 2017 and July 2018 using an Olympus TG-4 camera in macro mode. A subsequent visit to the area was made by NC in July 2019, and a total of seven individuals were captured with a sweep net: two adult males, two male nymphs, and three female nymphs. Photographs of these seven tree crickets were taken with a Canon S5 IS. The area was not visited at night; thus recordings of captive males were made indoors. The vegetation on the south end of Lake Annie was sweep-netted and tree crickets were collected into hand-held plastic containers. The key from Walker (1967) was used to verify the genus. Specimens were examined for the presence/absence of spines on the hind tibiae.

**Acoustics.**—Songs were recorded using a Canon S5 IS. Adult males were recorded while singing in captivity at different temperatures, with the thermometer probe placed as close as possible to the tree cricket. The temperature when the tree crickets were singing indoors in captivity was measured using a LaCrosse Technology dual channel digital thermometer. Additional recordings from the Macaulay Library (Cornell Lab 2020) and data from SINA (2020c) were used for the preparation of graphs that compared pulse rate vs. temperature and frequency vs. pulse rate of other species in the *nigricornis* group. DoremiSoft AVI to WAV Converter was used to convert AVI files to WAV files. Raven Lite 2.0 was used to create waveforms for counting the pulses per second and spectrograms to determine dominant frequency. Graphs were created using Excel 2010.

**Morphological measurements.**—Measurements were made after the specimens were euthanized in 91% ethyl alcohol. The total length



Figs 1–3. Sage tree cricket. 1. Adult female; 2. Antennal markings; and 3. Male 5<sup>th</sup> instar nymph.

refers to the midline length from the tip of the labrum to the apex of the subgenital plate, not including antennae, tegmina, limbs, or cerci. The tegminal width was measured at the widest section, while the tegmina rested atop the abdomen of the male. Pronotal length was measured along the medial line of the pronotum, and the width was measured at the widest section. The female ovipositor was measured from the base at the distal end of the abdomen to the tip. Photographs and measurements of the ovipositor, cerci, and metanotal gland, as well as counts of the stridulatory teeth, were made using a Canon PowerShot S5 IS in the AV setting in the macro mode through the eyepiece of a My First Lab microscope, model USB, magnification 4 $\times$ .

**Genitalia.**—Extracted male genitalia were photographed through the eyepiece of a My First Lab microscope at 4 $\times$  using a Canon PowerShot S5 IS in the AV setting in macro mode. The resulting photographs were then cropped and enlarged. Copulatory blades project from the internal genitalia complex and are situated just above the subgenital plate (Fulton 1915). These internal genitalia structures have also been referred to as pseudepiphallus (Chopard 1961, 1969), lophi medians [middle lobes] (Desutter 1987), or main lobe of pseudepiphallus (Zefa et al. 2012).

**Comparison with congeneric species.**—*O. argentinus* and *O. quadripunctatus* are the only two members of the *nigricornis* species group that are known to occur in northern California. Out of an abundance of caution, we decided to compare our new species with all eight species in the *nigricornis* species group, regardless of distribution range, in order to rule out these tree crickets being a color form of a known species with a range extension or a displaced population. Therefore, the new species was compared with *O. celerinictus* T. Walker, 1963, *O. forbesi* Titus, 1903, *O. laricis* T. Walker, 1963, *O. nigricornis* F. Walker, 1869, *O. pini* Beutenmüller, 1894, and *O. walkeri* Collins & Symes, 2012.

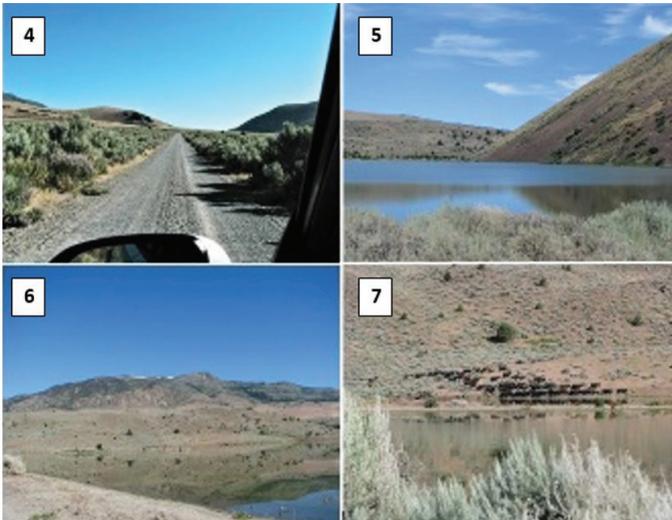
## Results

**Location.**—Lake Annie, in the extreme northeast corner of Modoc County, is located approximately five miles west of Nevada and five miles south of Oregon. The lake lies on the northern end of the Surprise Valley, at the western edge of the Great Basin and just east of the Warner Mountains range. It sits on the western edge of Lake Annie Mountain, a summit with an elevation of 1830 m. The elevation of the lake is 1530 m. Areas searched were no more than 4 m above the level of the lake at the following coordinates: 41°54'24"N, 120°06'31"W.

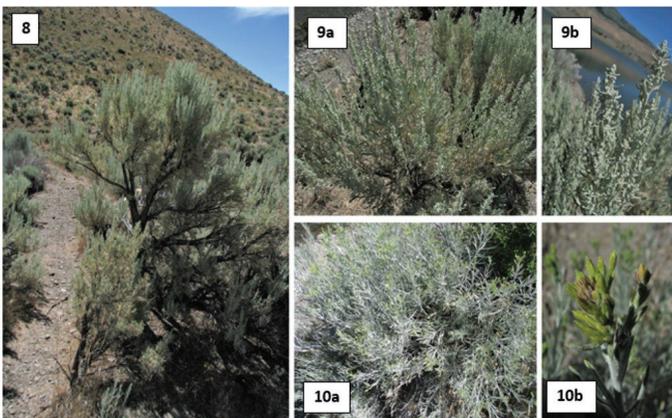
**Habitat.**—The majority of the area surrounding the lake was dotted with sagebrush (*Artemisia* spp.) and rabbitbrush (*Ericameria* spp.) shrubs that were 1 m tall. Bare ground was common, and the soil was fine and light greyish brown in color (Figs 4–6). A herd of cattle grazing on the surrounding vegetation was not uncommon on the edge of the lake (Fig. 7). Host plants identified in the tree cricket search area included big sagebrush (*Artemisia tridentata* ssp. *tridentata*), mountain sagebrush (*Artemisia tridentata* ssp. *vaseyana*), and rubber rabbitbrush (*Ericameria nauseosa*) (Figs 8–10).

**Climate.**—According to the University of California Agriculture and Natural Resources (2020), climate variables in 2019 for Cedarville, 22 miles (35 km) south of Lake Annie, were highest temperature (July) 91°F (32.8°C); lowest temperature (December) 15°F (-9.4°C); highest low (July) 58°F (14.4°C); and lowest high (December) 35°F (1.7°C). The total precipitation for 2019 was less than 15 in (381 mm).

**Morphology.**—These tree crickets at Lake Annie were a pastel, milky-green color and had pale pedicels and scapes, narrow tegmina, and



Figs 4–7. Location of *Oecanthus salvii* sp. nov. discovery. 4. Road to Lake Annie; 5. Eastern edge of lake with foot of Lake Annie Mountain; 6. Western edge of lake; and 7. Cattle drive along western shore.

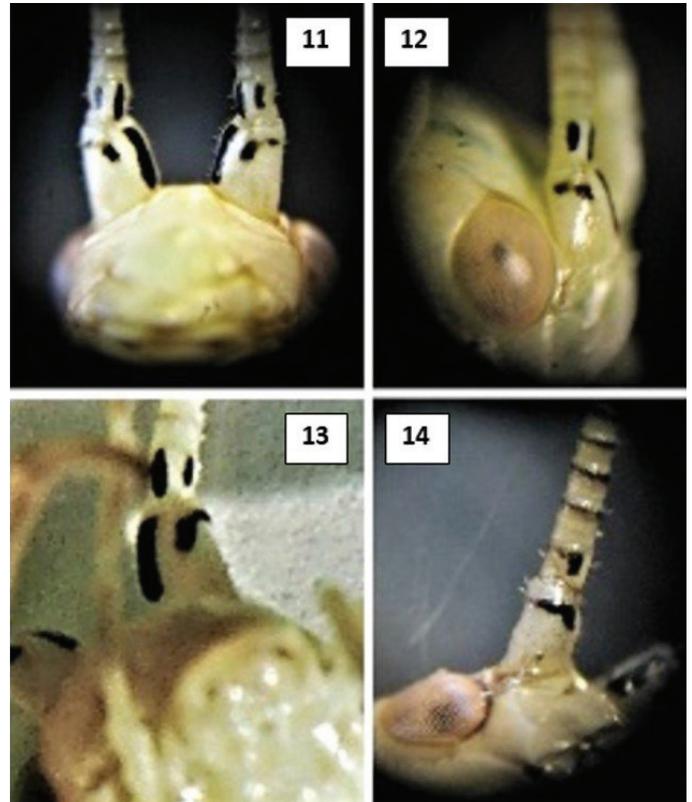


Figs 8–10. Host plants at Lake Annie. 8. Big sagebrush; 9a. Mountain sagebrush; 9b. Mountain sagebrush inflorescences; 10a. Rubber rabbitbrush; 10b. Rubber rabbitbrush inflorescences.

a continuous trilling song. Black antennal markings were visible on the ventral surface of the pedicel and the scape (Figs 11–14), and there were visible greyish brown rings of various degrees of darkness on the pale antennae filaments (Figs 11, 14).

Nymphs of instar stages four and five (Figs 15–17) and adults (Figs 18–20) were encountered on various sagebrush and rabbitbrush plants during July. The 4<sup>th</sup> stage instar and one 5<sup>th</sup> stage instar died prior to reaching the next stage. Adults retained a milky-green color and had a white abdomen (Fig. 21). Dark black setae caused a speckling effect on the limbs, especially on the hind limbs (Fig. 22). Black markings were visible on the hind femoral-tibial joints, with a whitish field on the ventral surface (Fig. 23). Two blackish horizontal lines were situated on the tibia just distal to the femoral-tibial joints (Fig. 24).

**Song analysis.**—Analysis of waveforms confirmed a continuous trilling pattern with a rate of 41 pulses per second at 24.8°C (Fig. 25). Dominant frequency 3.5 kHz at 24.8°C (Fig. 26). The song pulse rate of the sage tree cricket was compared to seven other



Figs 11–14. Antennal markings and dark rings of sage tree cricket.

species (Fig. 27), and the frequency vs. pulse rate was compared to five species (Fig. 28). A recording of two sage tree cricket males in separate netted containers within two feet of each other shows various patterns of synchrony and opposition (Figs 29, 30).

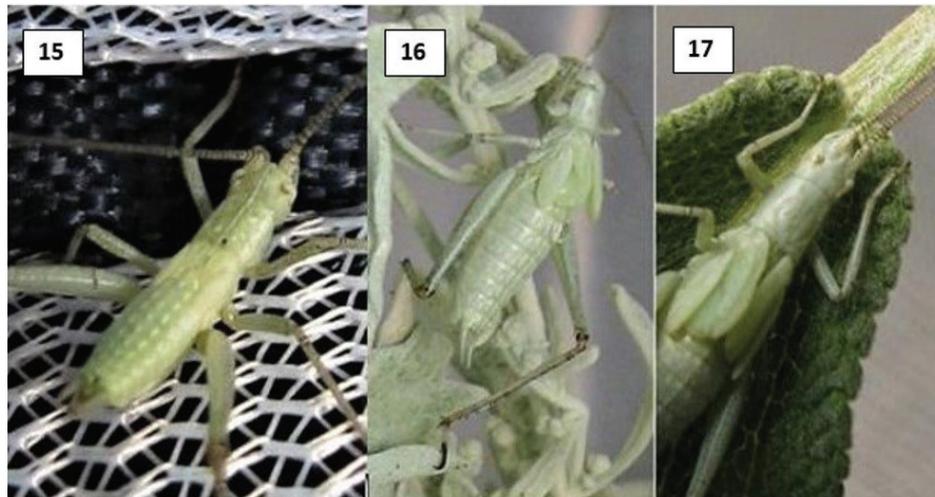
*Oecanthus salvii* Collins, sp. nov.

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**Etymology.**—Specific epithet after Lodovico (Ludovico) Salvi, an Italian philosopher and theologian, who included illustrations of a male tree cricket, a female tree cricket, and a stem with oviposition holes, in his article published 270 years ago (Salvi 1750). In *Voices of a Summer Night* (Lioy 1866), Salvi was recognized as being the first person to publish an article about a tree cricket. His 1750 article was published 13 years before the first tree cricket was officially described (*Oecanthus pellucens* Scopoli, 1763). The common name, sage tree cricket, is given because these tree crickets have similar coloration to the sagebrush host plants at Lake Annie.

**Type verification.**—The genus *Oecanthus* was determined as the specimens had spines on the hind tibiae.

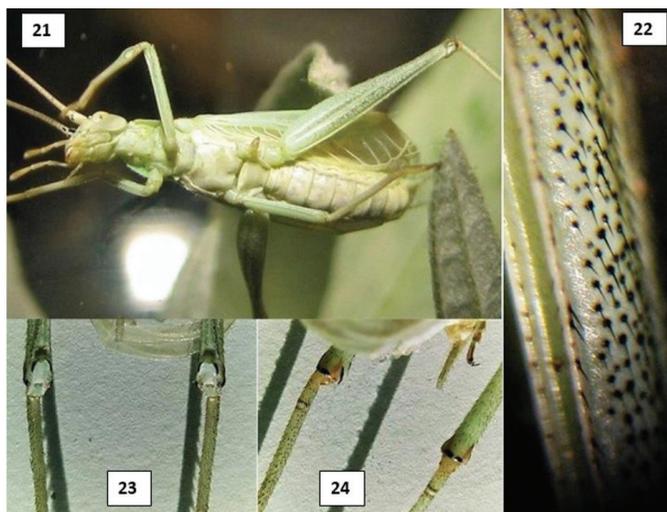
**Type-specimen.**—Holotype ♂, alcohol vial. Lake Annie, Modoc County, California, USA, 41°54'24"N, 120°06'31"W, elevation ca. 1530 m, arid, sagebrush, N. Collins leg., 25 July 2019. Body length (in mm) 15.4; tegminal length 11.0; tegminal width 5.0; pronotal length 2.2; distal pronotal width 2.0; hind femur length 8.0; cerci 5.4. Four antennal markings per side with two vertical black antennal markings on the pedicel, and one each vertical and horizontal black mark on the scape. Deposited at California Academy of Sciences (CAS).



Figs 15–17. Nymphs. 15. 4<sup>th</sup> instar; 16, 17. 5<sup>th</sup> instar.



Figs 18–20. Sage tree cricket. 18. Adult male; 19. Adult female; 20. Raised tegmina of male preparing to sing.

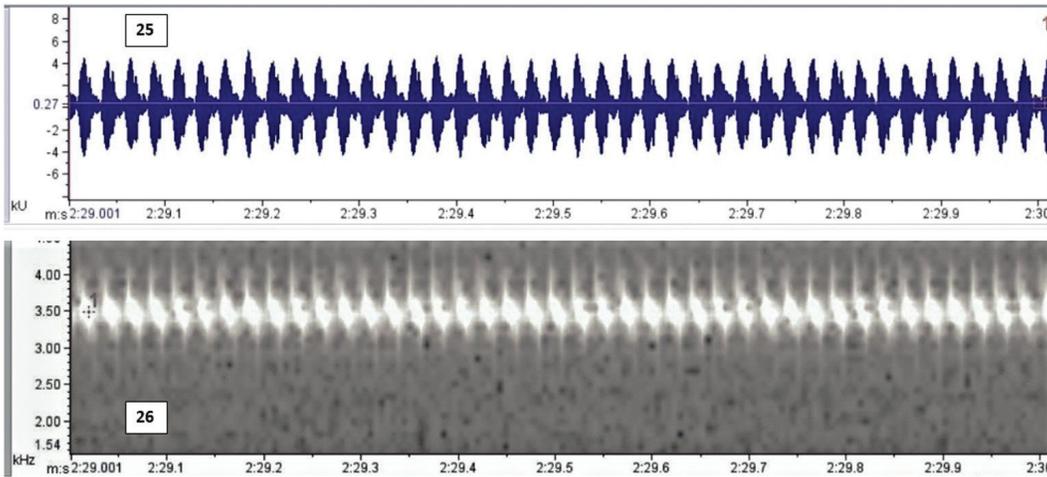


Figs 21–24. Adult sage tree cricket male abdomen, limb setae coloring, and hind femoral-tibial joints. 21. Creamy white ventral abdomen; 22. Dark black setae on limbs; 23. Ventral view of joints; and 24. Dorsal view of joints and two horizontal black lines on tibiae.

*Paratypes*.—3 ♂ and 1 ♀. Located in same area as holotype, 24–25 July 2019. 1 ♂ and 1 ♀ deposited at CAS, 1 ♂ Academy of Natural Sciences of Philadelphia, and 1 ♂ Florida State Collection of Arthropods. Two nymphs retained by NC for possible future DNA analysis.

*Description*.—Face creamy white to faint yellowish. Pedicel with two unequal-sized vertical lines, and scape with one vertical black line medially and one horizontal arched or right-angled black mark near the top of the segment. Remainder of antennae segments tan with darker brown or grey rings. Eye color whitish to dark cream. Palpi translucent pale tan. Pronotum light green. Tympanal membrane on fore tibiae whitish. Wing color of both sexes pale greenish. Ventral abdomen whitish or pale tan. Tibiae and femora translucent pale green with black setae. Cerci straight and pale green.

*Male* ( $N=4$ ).—Hind wings do not extend beyond distal edge of tegmina; cerci do extend beyond the tegmina. Metanotal gland with bilateral horizontal structures with tiny bristles situated mid-line in the triangular-shaped gland opening as in Fig. 51. Copulatory blades slender with a deep notch between them as in Fig. 41. Subgenital plate with pointed distal tip as in Fig. 43.



Figs 25, 26. One-second trilling of male sage tree cricket at 24.8°C. 25. 41 pulses per second; 26. Dominant frequency 3.5 kHz.

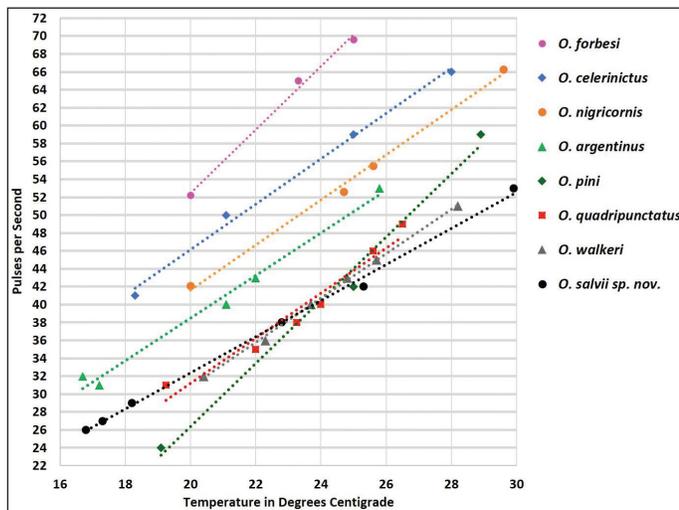


Fig. 27. Song pulse rates of *Oecanthus salvii* sp. nov., *O. forbesi*, *O. celerinictus*, *O. nigricornis*, *O. argentinus*, *O. quadripunctatus*, *O. walkeri*, and *O. pini* (data in Suppl. materials 1, 2).

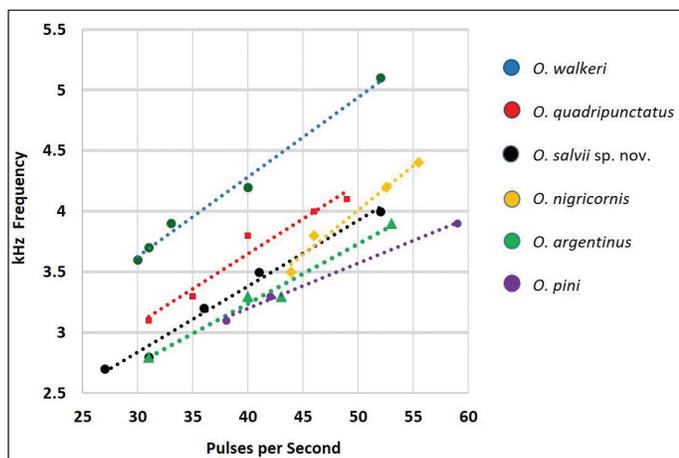


Fig. 28. Dominant frequency vs. pulses per second of *Oecanthus salvii* sp. nov. compared to other members of the *nigricornis* species group: *O. walkeri*, *O. quadripunctatus*, *O. nigricornis*, *O. argentinus*, and *O. pini* (data in Suppl. materials 1,2).

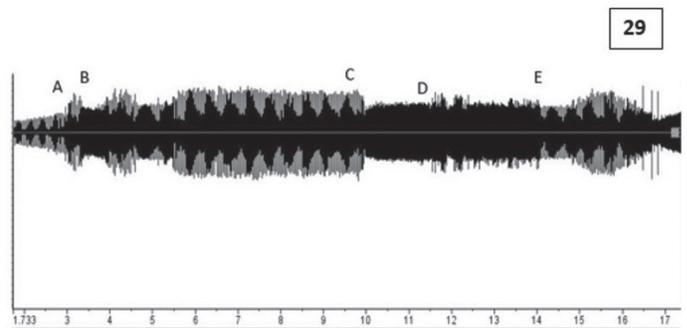


Fig. 29. Seventeen-second waveform of two male sage tree crickets at 17.3°C. Areas of interest shown in Fig. 30a–e.

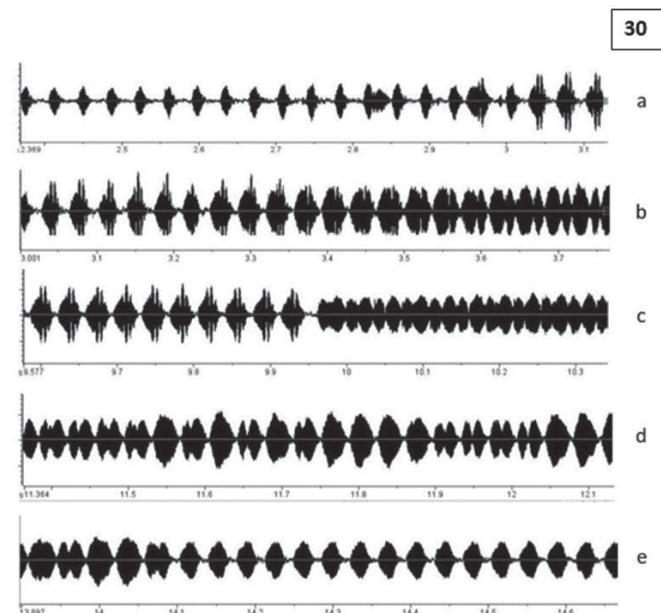


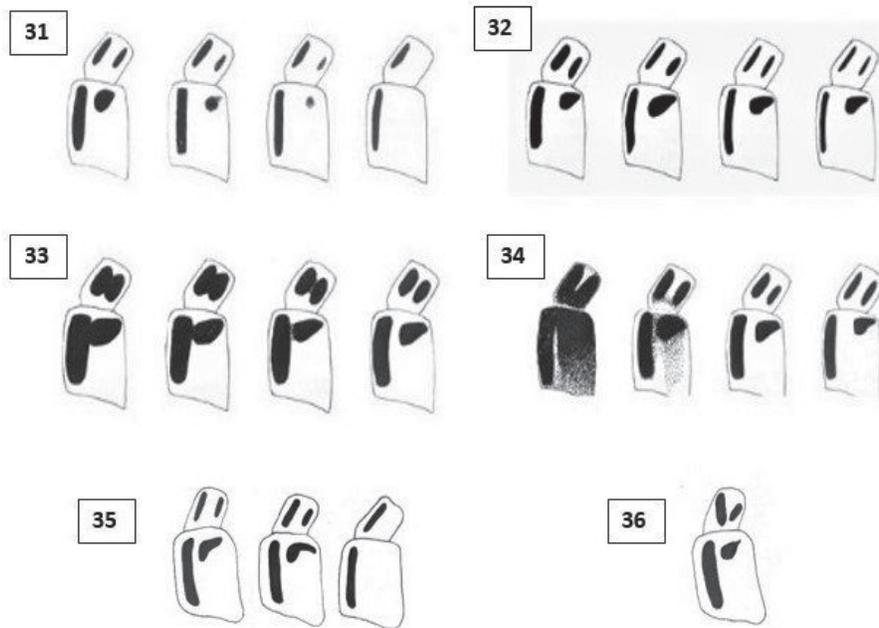
Fig. 30. Waveform sections from Fig. 29. a. Single male then joined by another male; b. The same two males in imperfect synchrony evolving into opposition; c. The same two males in near synchrony, pausing, then in opposition; d. The same two males in various degrees of synchrony; e. The same two males achieving synchrony.

*Measurements (in mm).*—Body length 15.4–16.8; tegminal length 11.0–11.5; tegminal width 5.0–5.5; pronotal length 2.2–2.6; distal pronotal width 2.0–2.2; hind femur length 8.0–9.0; cerci 5.2–5.6; stridulatory file 0.8 (N=2). Right tegminal stridulatory teeth 50–51 (N=2).

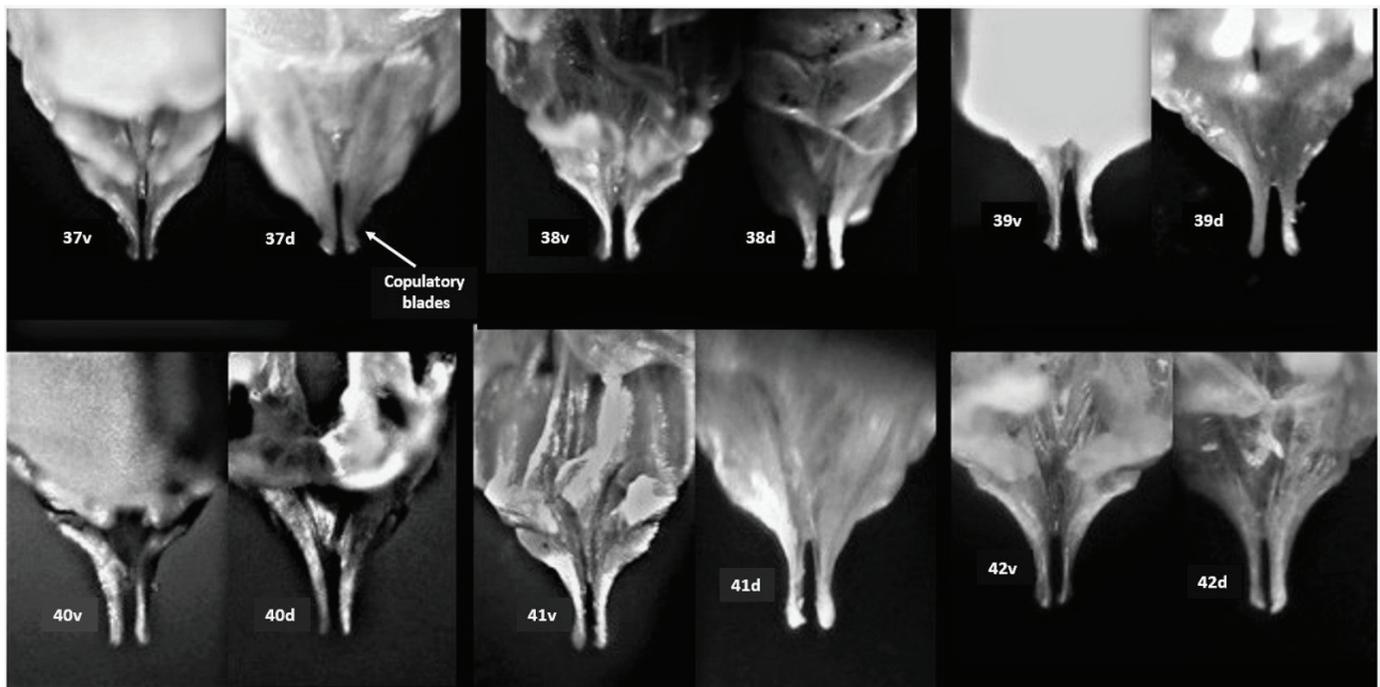
*Female (N=1).*—Latticed vein pattern on translucent greenish wings. The tip of the ovipositor extends to the tips of the cerci.

*Measurements (in mm).*—Body length 17.0; pronotal length 2.3, distal pronotal width 2.0; hind femur length 9.0; cerci 5.2; ovipositor length 5.5.

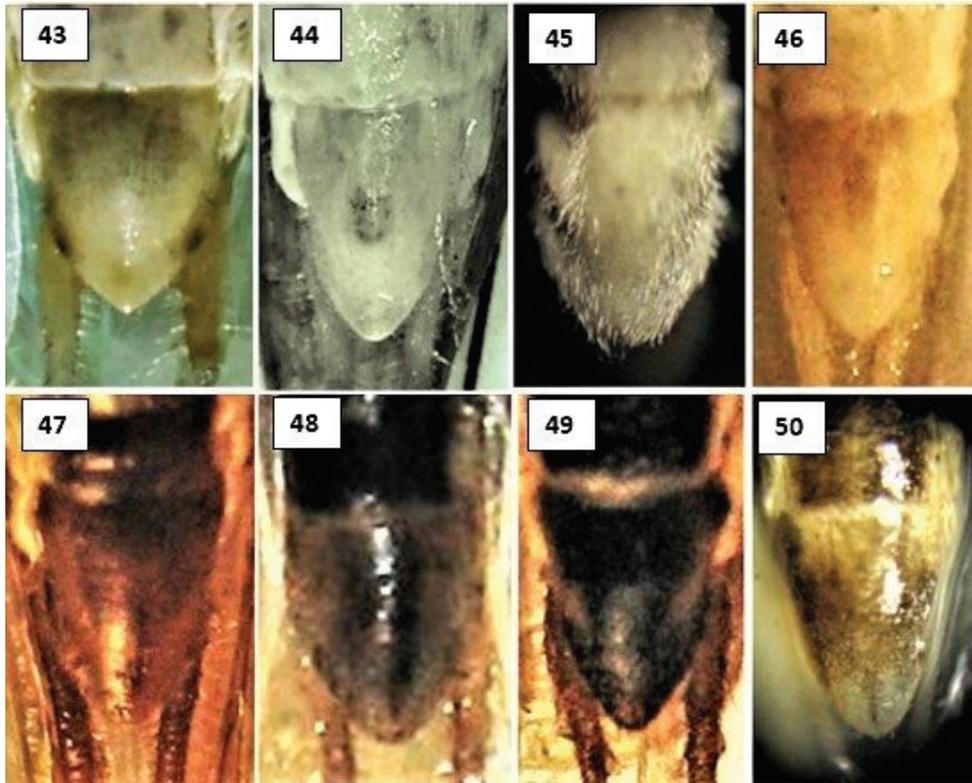
*Behavior.*—The Lake Annie area was not explored after dark when it is expected these tree crickets would be singing in the wild. No singing was detected during the daytime by either KS on two occasions or by NC on two consecutive days. In captivity, males did



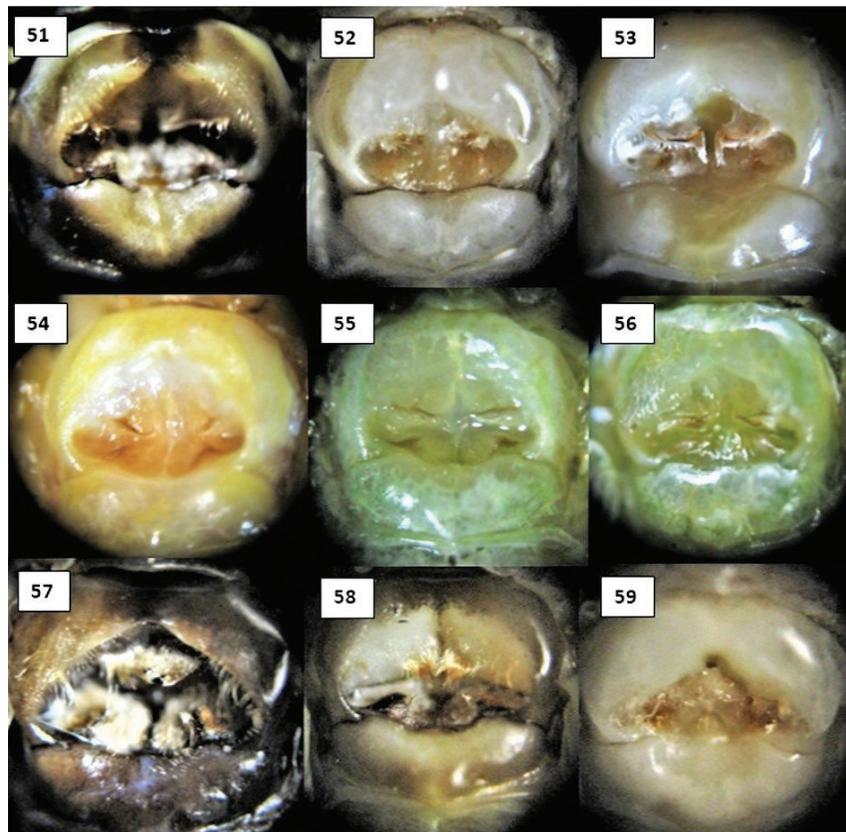
Figs 31–36. Drawings showing variations of antennal markings. 31. *Oecanthus quadripunctatus*; 32. *O. celerinictus*; 33. *O. argentinus*; 34. *O. nigricornis/O. forbesi*; 35. *O. pini*; and 36. *O. walkeri*.



Figs 37–42. Shapes of copulatory blades in (v)-ventral and (d)-dorsal views. 37. *Oecanthus walkeri*; 38. *O. nigricornis*; 39. *O. quadripunctatus*; 40. *O. argentinus*; 41. *O. salvii* sp. nov.; and 42. *O. celerinictus*.



Figs 43–50. Male subgenital plates. 43. *Oecanthus salvii* sp. nov.; 44. *O. walkeri*; 45. *O. celerinictus*; 46. *O. quadripunctatus*; 47. *O. pini*; 48. *O. nigricornis*; 49. *O. forbesi*; and 50. *O. argentinus*.



Figs 51–59. Metanotal glands comparisons. 51. *Oecanthus nigricornis*; 52. *O. argentinus*; 53. *O. celerinictus*; 54. *O. forbesi*; 55. *O. salvii* sp. nov.; 56. *O. quadripunctatus*; 57. *O. laricis*; 58. *O. pini*; and 59. *O. walkeri*.

not start singing until dusk or later. The color of sage tree crickets allows them to blend remarkably well with the rabbitbrush and sage shrubs they inhabit. Shrubs were intensely visually scoured by NC, but no tree crickets were detected. Only with the use of sweep netting were tree crickets found by both KS and NC.

**Discussion**

We describe a new species of *Oecanthus* that falls into the *nigricornis* species group. While *O. salvii* sp. nov. has some degree of song and morphological similarities to the eight known members of the *nigricornis* group, each of those species also has characters that do not match. The characters most unique for *O. salvii* sp. nov. are an upper outer mark on the scape in the shape of a horizontal arch or right angle, and a distinct pointed tip on the male's subgenital plate.

*Comparisons.*—The ten known members of the *rileyi*, *niveus*, and *varicornis* species groups in the United States can be ruled out because of having different song types, tegminal widths, antennal markings, or antennal coloring. The eight members of the *nigricornis* species group have many similarities to each other. Table 1 shows our results for comparing eleven of the characters presented in this paper for *O. salvii* sp. nov. to the eight known species in the *nigricornis* group. We were able to rule out *O. salvii* sp. nov. as displaced *O. laricis* or *O. pini* because they are conifer dwellers with a rust or dark brown head. *Oecanthus walkeri* was ruled out as it has two thick markings on the pedicel in the shape of a 'v' that touch or nearly touch at the bottom, and the frequency vs. pulse rate results are too high. *Oecanthus celerinictus* and *O. forbesi* do not match as they have pulse rates over 55 pulses per second at 25.0°C, whereas *O. salvii* sp. nov. has a rate below 45.

Although *O. nigricornis* is considered an eastern US species, there are two photographs on BugGuide of females from California which cannot be ruled out as *O. nigricornis/forbesi*: images 561469 and 325581 (BugGuide 2020). While the frequency of the male's song of *O. nigricornis* is essentially identical to that of *O. salvii* sp. nov., the song rate, metanotal gland, and subgenital plate do not match.

*Oecanthus argentinus* has seven matching or similar characters to *O. salvii* sp. nov., but it is ruled out as a match as it has two thick pedicel markings that are separated by less than one width of one of the markings, and the male has a longer subgenital plate with no point at the tip.

*Oecanthus quadripunctatus* is a match or similar to *O. salvii* sp. nov. in six categories. It does not, however, match in the categories of the antennal markings, horizontal black lines on the limbs, and dark black setae on the limbs.

We compared the antennal markings to drawings of *O. quadripunctatus* (Fig. 31), *O. celerinictus* (Fig. 32), *O. argentinus* (Fig. 33), and *O. nigricornis/forbesi* (Fig. 34), from the Singing Insects of North America website (SINA 2020a). We also provide examples of the antennal markings of *O. pini* (Fig. 35) and *O. walkeri* (Fig. 36). The upper outer marking on the first antennal segment of *O. pini* varies, including some individuals with no upper outer mark and some individuals with arched upper outer marks similar to that of *O. salvii* sp. nov. (Figs 11–14).

The copulatory blades of five members of the *nigricornis* species group were compared to those of *O. salvii* sp. nov. (Figs 37–42). We could see no major differences in the sizes or shapes of the blades and the notch between them. We also compared the distal tip of the subgenital plate of *O. salvii* sp. nov. to seven other species (Figs 43–50). The plate of *O. salvii* sp. nov. tapers to a distinct point, which the other species lack. The metanotal glands for members of the *nigricornis* species group are quite similar (Figs 51–59). The prominent feature of the gland of *O. salvii* sp. nov. is the near meeting of the horizontal tapered structures projecting from the lateral sides of the cavity.

*Oecanthus walkeri* has not been documented west of Arizona, and the markings on the pedicel do not match that of *O. salvii* sp. nov. Despite the close match of the upper outer mark on the scape of *O. pini*, that species and *O. laricis* have not been documented west of the Continental Divide and are both conifer dwellers.

*Oecanthus quadripunctatus* and *O. argentinus* have several similarities to *O. salvii* sp. nov., and both occur in northern California. However, both have character differences to *O. salvii* sp. nov. *O. quadripunctatus* does not have dark black setae

**Table 1.** Comparisons of *Oecanthus salvii* sp. nov. characters to the eight members of the *nigricornis* species group. M: Match; S: Similar; P: Possible; D: Different; N: Not included; I: Intermittently matches; U: Undetermined.

Characters of <i>O. salvii</i> sp. nov.	<i>O. quadripunctatus</i>	<i>O. argentinus</i>	<i>O. walkeri</i>	<i>O. celerinictus</i>	<i>O. nigricornis</i>	<i>O. forbesi</i>	<i>O. pini</i>	<i>O. laricis</i>
<b>Pulses per second</b> – 41 pulses per second at 24.8°C.	M	S	M	D	D	D	M	N
<b>Metanotal gland</b> – Horizontal tapered structures projecting from the lateral sides of the cavity and nearly touching at the center.	M	D	D	S	S	S	S	D
<b>Distribution</b> – California or western region states.	M	M	D	D	U	U	D	D
<b>Black setae</b> – Numerous present on pale green limbs.	D	M	D	D	D	D	D	D
<b>Limb lines</b> – Two parallel horizontal lines present on pale green tibiae.	D	I	D	M	I	I	D	D
<b>Subgenital plate</b> – Roundish shape that tapers to a distinct pointed tip.	D	D	S	D	D	D	D	N
<b>Antennal markings</b> – Pedicel: Two vertical black lines separated by more than width of one of the lines. Scape: Upper outer mark in shape of upright arch or right angle.	D	D	D	S	S	S	I	D
<b>Frequency</b> – 3.5 kHz at 24.8°C.	S	S	D	N	M	N	S	N
<b>Copulatory blades</b> – Long and slender with deep round-topped notch between them.	S	S	S	S	S	N	N	N
<b>Coloring</b> – Pale green with white abdomen.	S	S	S	S	D	D	D	D
<b>Host plants</b> – Sagebrush, rabbitbrush.	P	P	P	N	N	D	D	D

on the limbs or horizontal black lines on the limbs, and the subgenital plate of the male of *O. argentinus* is rounded at the distal end. Additionally, *O. quadripunctatus* has no or a mostly round upper outer antennal marking on the scape, and *O. argentinus* has two thick lines on the pedicel that are positioned more closely to each other.

Further study of this new species is needed to determine its potential range beyond Modoc County and whether it dwells on plants other than sagebrush and rabbitbrush. More in-depth investigation of this species' life cycle and singing/mating behavior is also needed. The remote location makes investigating this species more challenging.

## Acknowledgements

We are grateful to Iowa State University's Department of Entomology for maintaining BugGuide.net, a website that allows scientists and the general public to post photographs of insects from the continental United States and Canada. Kevin McKereghan was tremendously helpful to NC during her field work. We appreciate Thomas J. Walker, Professor Emeritus, University of Florida, for the wealth of knowledge he generously shares. Dr. Walker has long been a proponent of the open access of articles and recordings that were of immense assistance in our investigation of this new species. An Orthoptera Species File grant for "Oecanthines of high interest in the United States" provided financial support for NC's field trip. The Orthopterists' Society provided free publication of this paper. We thank Holger Braun, Zhu Qing He, and Klaus-Gerhard Heller for their constructive suggestions on improving this manuscript.

## References

- BugGuide (2020) BugGuide.net. <https://bugguide.net> [Accessed August 2019]
- Chopard L (1961) Les divisions du genre *Gryllus* basées sur l'étude de l'appareil copulateur (Orth. Gryllidae) EOS: Revista Española de Entomología 37: 267–287. <http://hdl.handle.net/10261/157258>
- Chopard L (1969) The Fauna of India and Adjacent Countries, Orthoptera Vol. 2. Baptist Mission Press, 421 pp. [http://faunaofindia.nic.in/php/fi\\_books\\_toc.php?book\\_id=003&type=fi&book\\_title=Orthoptera-Grylloidea](http://faunaofindia.nic.in/php/fi_books_toc.php?book_id=003&type=fi&book_title=Orthoptera-Grylloidea)
- Cigliano MM, Braun H, Eades DC, Otte D (2020) Orthoptera Species File, Version 5.0/5.0. <http://Orthoptera.SpeciesFile.org> [Accessed August 2019]
- Cornell Lab (2020) Macaulay Library. <https://search.macaulaylibrary.org/catalog?view=List&searchField=animals> [Accessed January 2020]
- Desutter L (1987) Structure et évolution du complexe phallique des Grylloidea (Orthoptères) et classification des genres Nétropicaux de Grylloidea. Première Partie. Annales de la Société Entomologique de France 23: 213–239. <https://gallica.bnf.fr/ark:/12148/bpt6k6139207n/f3.image>
- Fulton BB (1915) The tree crickets of New York: Life history and bionomics. New York Agricultural Experiment Station Technical Bulletin 42: 3–47. <http://entomology.ifas.ufl.edu/walker/buzz/s5761f15.pdf>
- Lioy P (1866) Voci di notte estive [Voices of a summer night]. Nuova antologia di scienze, lettere ed arti. Quarta serie, 148: 325–335. <https://archive.org/details/nuovaantologiadi148unse/page/326/mode/2up>
- Salvi L (1970) Memorie intorno le locuste grillajole. Verona, 14 pp. [https://archive.org/details/bub\\_gb\\_HsEz9uP2LzWC/page/n5/mode/2up](https://archive.org/details/bub_gb_HsEz9uP2LzWC/page/n5/mode/2up)
- SINA (2020a) Genus *Oecanthus* common tree crickets. Singing Insects of North America: Crickets and Katydid. <http://entnemdept.ufl.edu/walker/buzz/g576a.htm> [Accessed January 2020]
- SINA (2020b) Key to genera of tree crickets (Oecanthinae). Singing Insects of North America: Crickets and Katydid. <http://entnemdept.ifas.ufl.edu/walker/buzz/g576k.htm> [Accessed August 2019]
- SINA (2020c) List of Species. Singing Insects of North America: Crickets and Katydid. <http://entnemdept.ufl.edu/walker/buzz/cricklist.htm#oecanthinae> [Accessed January 2020]
- SINA (2020d) Black-horned tree cricket (Excel worksheet). <http://entnemdept.ufl.edu/walker/buzz/589a.htm> [Accessed January 2020]
- SINA (2020e) Forbes' tree cricket (Excel worksheet). <http://entnemdept.ufl.edu/walker/buzz/594a.htm> [Accessed January 2020]
- University of California Agriculture and Natural Resource (2020) <http://ipm.ucanr.edu/calludt.cgi/WXDESCRIPTION?STN=ALTURAS.C> [Accessed January 2020]
- Walker TJ (1962) The taxonomy and calling songs of United States tree crickets (Orthoptera: Gryllidae: Oecanthinae). I. The genus *Neoxabea* and the *niveus* and *varicornis* groups of the genus *Oecanthus*. Annals of the Entomological Society of America 55: 303–322. <https://doi.org/10.1093/aesa/55.3.303>
- Walker TJ (1963) The taxonomy and calling songs of United States tree crickets (Orthoptera: Gryllidae: Oecanthinae). II. The *nigricornis* group of the genus *Oecanthus*. Annals of the Entomological Society of America 56: 772–789. <https://doi.org/10.1093/aesa/56.6.772>
- Walker TJ (1967) Revision of Oecanthinae (Orthoptera: Gryllidae) of America south of the United States. Annals of the Entomological Society of America 60: 784–796. <https://doi.org/10.1093/aesa/60.4.784>
- Walker TJ, Collins NJ (2010) New world thermometer crickets: The *Oecanthus rileyi* species group and a new species from North America. Journal of Orthoptera Research 19: 371–376. <https://doi.org/10.1665/034.019.0227>
- Zefa E, Neutzling AS, Redü DR, Oliveira LG, Martins LP (2012) A new species of *Oecanthus* and *Oecanthus lineolatus* Saussure, 1897 from southern Brazil: Species description, including phallic sclerites, metanotal glands and calling song (Orthoptera: Gryllidae: Oecanthinae). Zootaxa 3360: 53–67. <https://doi.org/10.11646/zootaxa.3360.1.2>

## Supplementary material 1

Author: Nancy Collins, Ken R. Schneider

Data type: Number of pulses per second vs. temperature in Centigrade

Explanation note: Resources used for creating the figure showing the number of pulses per second vs. temperature in Centigrade of several species in the *nigricornis* group.

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Link: <https://doi.org/10.3897/jor.29.50400.suppl1>

## Supplementary material 2

Author: Nancy Collins, Ken R. Schneider

Data type: Song frequency vs. pulses per second

Explanation note: Resources used for creating a graph showing frequency vs. pulses per second of several species in the *nigricornis* group.

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Link: <https://doi.org/10.3897/jor.29.50400.suppl2>



# Studies on neotropical Phasmatodea XXII: Two new species of *Taraxippus* (Phasmatodea: Cladomorphinae: Hesperophasmatini) and the first record of the genus from Central America

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Academic editor: Matan Shelomi | Received 20 February 2020 | Accepted 6 March 2020 | Published 29 May 2020

<http://zoobank.org/BB2E7A21-C67E-444D-941A-E77CBBABAF71>

Citation: Conle OV, Hennemann FH, Valero P (2020) Studies on neotropical Phasmatodea XXII: Two new species of *Taraxippus* (Phasmatodea: Cladomorphinae: Hesperophasmatini) and the first record of the genus from Central America. Journal of Orthoptera Research 29(1): 101–114. <https://doi.org/10.3897/jor.29.51328>

## Abstract

Two new species of *Taraxippus* Moxey, 1971 are described and illustrated: *T. samarae* sp. nov. from Costa Rica and Panama and *T. perezgelaberti* sp. nov. from the Dominican Republic. Both sexes and the previously unknown eggs are described. The genus is recorded from Central America for the first time. A distribution map and a discussion of the distributional pattern of *Taraxippus* are provided.

## Keywords

Costa Rica, Dominican Republic, Hispaniola, morphology, Panama, phasmids, stick insects, taxonomy

## Introduction

Phasmatodea is one of the few insect orders that still lack a robust higher-level phylogeny. The relationships between many New World taxa in particular are still speculative. Numerous genera are only known from a few specimens and sometimes only from one sex. One of these seldom encountered genera is *Taraxippus* Moxey, 1971, a member of the predominantly Caribbean tribe Hesperophasmatini (subfamily Cladomorphinae). The intergeneric relationships and the definitions of some of the genera of this particular tribe are still insufficient, and further work is needed to clarify relationships within Hesperophasmatini.

This is the 22<sup>nd</sup> part of an on-going study of New World Phasmatodea and describes two new species of the very distinctive and stunning genus *Taraxippus* Moxey, 1971. Until now, this genus was known only from the type species, *Taraxippus paliurus* Moxey, 1971, which was only known from a unique female specimen from Haiti. A male described by Pérez-Gelabert (1999) from the Dominican Republic was proven to represent an unknown species that is here described as a new species. A further new species is described from Costa Rica and Panama and is the first record of this peculiar genus from outside the Caribbean. The eggs of *Taraxippus* are described and illustrated for the first time.

A survey of Hispaniolan orthopteroid insects was carried out by the Hispaniolan Orthopteroids Project from 2002 through 2004 in the Dominican Republic. Besides many interesting Orthoptera, a large number of Phasmatodea were collected that significantly increase the number of Phasmatodea species known from Hispaniola. Almost all regions and habitats of the island still harbor many undescribed taxa. In several previous papers, the authors have dealt with the material collected by the Hispaniolan Orthopteroids Project and described four new genera and 17 new species (Conle et al. 2006, 2008, 2014, Hennemann et al. 2016, in press).

## Material and methods

The material for this study is exclusively dried and pinned. Insects and eggs were examined using an entomological lens with 4× magnification and a stereoscope (Zeiss Stemi SV 6). Eggs were examined at 10× magnification. Measurements were taken using a long ruler or a digital caliper and are given to 0.1 mm. Average measurements are given. Eggs were examined fully developed after they were laid. The terminology used for the descriptions of external and internal egg structures follows that of Sellick (1997). Photos were taken using either a Nikon D7100 camera with a AF-S Nikkor 60 mm f/2.8 G ED lens, or, for the eggs, a Sony A7RIII with a Tamron 90 mm f/2.8 DI VC USD MACRO and Raynox DCR-250. Lighting was produced with a Nikon SU-800 dual speed light system and background lighting provided by a 18W 6000K LED panel light plate. Depositories of specimens and type status are abbreviated as follows:

- INBIO Instituto Nacional de Biodiversidad, Costa Rica.
- USNM United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.
- ZSMC Zoologische Staatssammlung München, Germany.
- FH Personal collection of Frank H. Hennemann, Bad Homburg, Germany.
- OC Personal collection of Oskar V. Conle, Duisburg, Germany.
- HT, PT holotype, paratype.

## Results

## Phasmatidae: Cladomorphinae: Hesperophasmatini

*Taraxippus* Moxey, 1971

Figs 1–8

*Type-species.*—*Taraxippus paliurus* Moxey, 1971: 67, by original designation.

*Comments.*—The genus comprises three species including the two new species described here. It is so far recorded from Hispaniola Island (Haiti and Dominican Republic), Costa Rica, and Panama.

*Diagnosis of genus.*—Medium to small member of the tribe Hesperophasmatini (body length ♀♀ including subgenital plate 39.8–71.1 mm, ♂♂ 38.2–54.2 mm), body prominently spinose and mesonotum with a prominent hump-like median swelling (more pronounced in females). Females apterous, males either winged or apterous. Body in both sexes all over armed with distinct spines, bulges, and/or irregular foliaceous lobes. Head with vertex strongly conically raised and armed with spines, higher than long; no ocelli. Antennae filiform; longer than head, pro-, and mesothorax combined. Antennomeres considerably longer than wide and gradually shortening in apical portion, more or less club-like in females. Scapus with spines on outer lateral margin. Mesothorax >2.5× longer than prothorax, strongly widened and deflexed medially; mesonotum prominently swollen and hump-like in central portion (females in particular). Metapleurae with a distinct multispinose supracoxal projection. Tegmina in males ovoid and with a fairly pointed central projection. Anal region of alae translucent greyish. Abdomen excluding median segment slightly longer than head and thorax combined. In females, segment VII longest segment, II quadrate, and II–VII wider than long; abdomen swollen and broadened medially. In males, all segments longer than wide and roughly uniform in width. Abdominal tergum VII in both sexes strongly deflexed laterally; III–VI and VIII occasionally with lateral lobes. Praeopercular organ on abdominal sternum VII of females distinct and positioned a considerable distance anterior to posterior margin. Epiproct of females scale-like and noticeably projecting over posterior margin of anal segment. Subgenital plate shovel-like and projecting notably beyond apex of abdomen; the apical portion more or less decidedly narrowed. Anal segment of males slightly convex and notched medially; the outer posterior angles set with a variable number of minute teeth ventrally. Vomer well developed, principally triangular in shape and with a single fairly acute terminal hook. Poculum (= subgenital plate) cup-shaped, strongly convex, and conical in center, and the posterior margin more or less labiate. Cerci laterally compressed in females, lancet-like, circular in cross-section in males, with tipped apex, projecting over the anal segment. All legs slender and bearing spines and/or variably sized and shaped foliaceous lobes; all femora shorter (females) or longer (males) than pro- and mesothorax combined. Profemora almost straight and just slightly compressed basally. Femora with medioventral carina almost obsolete and armed with a variable number of medium-sized spines. Tarsi elongated with basitarsus longer than following two tarsomeres combined.

*Eggs:* Capsule flattened laterally; the anterior, posterior, and lateral margins set with rows of long fringes. Lateral surfaces more or less flattened and rugulose. Micropylar plates less than half as long as capsule, spear-shaped, and roughly placed in center of dorsal capsule surface. Operculum oval, flat; outer margin with long setae or fringes.

*Differentiation:* This very distinctive genus is well differentiated from other members of the tribe Hesperophasmatini by the

extremely prominent body armature and almost straight profemora. Females further differ from all other known genera of the tribe by the strongly swollen and hump-like median portion of the mesonotum and males by having a very large pair of antler-like, median projections on the mesonotum. The eggs are very distinctive, being laterally flattened and somewhat angular and having the anterior, posterior, and lateral margins set with rows of long fringes.

*Comments:* This previously monotypic genus currently comprises three species including the two new species described herein. It is so far recorded from the Caribbean island of Hispaniola (Haiti and Dominican Republic) as well as Central America (Costa Rica and Panama). The disjunct distribution of *Taraxippus* is remarkable and may be subject to speculation on the mechanisms and reasons that led to the distributional pattern now seen. Very few phasmid genera are known to have representatives in both the Caribbean and in Central America; e.g., *Pterinoxylus* Serville, 1838 (Hennemann et al. 2016). But while *Pterinoxylus* is found throughout various altitudinal ranges including coastal lowland forests, *Taraxippus* seems to be confined to mountainous habitats. This would suggest a relict distribution for *Taraxippus*, meaning that the genus or its direct ancestors might once have had a considerably larger range but has subsequently become locally extinct in most areas.

*Distribution.*—Hispaniola, Costa Rica, and Panama.

*Species included.*—

*Taraxippus paliurus* Moxey, 1971: 70, figs 2, 5. [Hispaniola: Haiti]  
*Taraxippus perezgelaberti* sp. nov. [Hispaniola: Dominican Republic]  
*Taraxippus samarae* sp. nov. [Costa Rica and Panama]

Keys to species of *Taraxippus* Moxey, 1971

♂♂\*

- 1 Apterous. Hispaniola..... *T. perezgelaberti* sp. nov.  
 – Winged. Costa Rica and Panama..... *T. samarae* sp. nov.

♀♀

- 1 Armature of head and mesonotum formed by acutely pointed spines or multispinose processes. Lateral lobes of abdominal tergum VII larger than all preceding. Sternum VII armed with at least six distinct spines. Hispaniola ..... 2  
 – Armature of head and mesonotum with blunt apices. Lateral lobes of abdominal tergites V and VI largest. Sternum VII unarmed. Costa Rica and Panama ..... *T. samarae* sp. nov.  
 2 Small (body length <52 mm). Mesonotum medially armed with a transverse row of four very large, laterad directed, multispinose, antler-like processes..... *T. perezgelaberti* sp. nov.  
 – Larger (body length 57 mm). Mesonotum very prominently raised and swollen medially and armed with several simple spines ..... *T. paliurus*

Eggs\*\*

- 1 Capsule roughly rectangular in cross-section with lateral surfaces flattened and distinctly rugulose; dull. Marginal fringes setae-like, long and slender, usually branched and free at apex. Micropylar plate surrounded by a row of fringes. Costa Rica and Panama..... *T. samarae* sp. nov.  
 – Capsule trapezoidal in cross-section with lateral surfaces gently convex and weakly coriaceous; glossy. Marginal fringes irregularly branched and net-like. Micropylar plate not surrounded by fringes. Hispaniola..... *T. perezgelaberti* sp. nov.

\* Males of *Taraxippus paliurus* are unknown.\*\* Eggs of *Taraxippus paliurus* are unknown.

*Taraxippus perezgelaberti* sp. nov.

<http://zoobank.org/A2D89729-BEC4-42F9-BB2F-58256292C70C>

Figs 1–3b, e, h, 4d–f

*Taraxippus paliurus* Pérez-Gelabert, 1999: 23, figs 1, 2.

**Differentiation.**—Females can easily be distinguished from the two other species in the genus by the armature of the mesonotum and the more elongate subgenital plate (ratio length/max. width >3; Fig. 3). Males are readily differentiated from those of *T. samarae* sp. nov. by the lack of wings (Fig. 1). Eggs differ from those of *T. samarae* sp. nov. by their triangular cross-section, gently concave lateral margins, glossy surface, and strongly branched, net-like marginal fringes (Fig. 4).

**Type material and specimens examined.**—

- HT**, ♂: DOMINICAN REPUBLIC, RD-043, on Trail Arroyazo to La Sal, Reserva Científica Ebano Verde (RCEV), La Vega Prov., on path between 19°02.374'N, 70°32.684'W, 1249 m and 19°02.021'N, 70°32.584'W, 1102 m, 10.vii.2002, D. E. Pérez-Gelabert (DEPG), B. Hierro (BH), R. Bastardo (RB) [USNM].
- PT**, ♀: DOMINICAN REPUBLIC, Parque Nacional Armando Bermúdez (PNAB), Los Tablones, La Vega Prov., 1250 m, 4.ix.1997, DEPG, K. Grasela (KG) [USNM].
- PT**, ♀: DOMINICAN REPUBLIC, La Sal, RCEV, La Vega Prov., 21.v.1992, S. Navarro [USNM].
- PT**, nymph ♀: DOMINICAN REPUBLIC, PNAB, Arroyo Gurabo, Santiago Prov., 13.iii.1999, A. del Monte [USNM].
- PT**, ♂: DOMINICAN REPUBLIC, PNAB, Los Tablones, La Vega Prov., 1250 m, 4.ix.1997, DEPG, KG [USNM].
- PT**, ♀: DOMINICAN REPUBLIC, PNAB, in bamboo forest approx. 400 m from park entrance, La Vega Prov., 9.i.1986, S. Larcher, DEPG [USNM].
- PT**, ♂: DOMINICAN REPUBLIC, PNAB, Jamamucito, dentro de yagua, Santiago Prov., 10.iv.1999, night, RB [USNM].
- PT**, 4 ♂♂, nymph ♂, nymph ♀: DOMINICAN REPUBLIC, RD-043, on Trail Arroyazo to La Sal, RCEV, La Vega Prov., on path between 19°02.374'N, 70°32.684'W, 1249 m and 19°02.021'N, 70°32.584'W, 1102 m, 10.vii.2002, DEPG, BH, RB [USNM].
- PT**, 3 ♂♂: DOMINICAN REPUBLIC, RD-042, Arroyazo, RCEV, La Vega Prov., 19°01.945'N, 70°32.593'W, 1066 m, 9–10.vii.2002, DEPG, BH, RB [USNM].
- PT**, 5 ♂♂, 3 ♀♀, nymph ♀: DOMINICAN REPUBLIC, RD-044, La Sal, RCEV, La Vega Prov., 19°04.101'N, 70°34.089'W, 1043 m, 11–12.vii.2002, DEPG, BG, RB [USNM].
- PT**, 2 ♂♂: DOMINICAN REPUBLIC, RD-128, PNAB, around ca-seta La Sierrecita, Santiago Prov., 19°14.889'N, 71°04.735'W, 752 m, 9.iv.2003, DEPG, BH, RB [USNM].
- PT**, ♂, ♀: DOMINICAN REPUBLIC, RD-149, Loma La Golondrina, RCEV, La Vega Prov., 19°03.498'N, 70°32.670'W, 11.vii.2003, day and night, DEPG, RB, BH, ex coll USNM [OC, No. 0535-2, 3].
- PT**, 2 ♀♀: DOMINICAN REPUBLIC, RD-043, on Trail Arroyazo to La Sal, RCEV, La Vega Prov., on path between 19°02.374'N, 70°32.684'W, 1249 m and 19°02.021'N, 70°32.584'W, 1102 m, 10.vii.2002, DEPG, BH, RB [USNM].
- PT**, 3 ♀♀: DOMINICAN REPUBLIC, RD-128, PNAB, around ca-seta La Sierrecita, Santiago Prov., 19°14.889'N, 71°04.735'W, 752 m, 9.iv.2003, DEPG, RB, BH [USNM].
- PT**, ♀: DOMINICAN REPUBLIC, RD-218, 1 km ESE Cortico, Barahona Prov., 18°06.520'N, 71°12.898'W, 1347 m, 9–10.iv.2004, day and night, DEPG, BH, RB [USNM].

- PT**, 2 ♂♂: DOMINICAN REPUBLIC, RD-157, PNAB, Los Tablones, La Vega Prov., 19°03.308'N, 70°53.049'W, 1270 m, 23.vii.2003, night, DEPG, RB, BH [USNM].
- PT**, ♀: DOMINICAN REPUBLIC, RD-148, ~100 m up from El Sitio del Agua, cloud forest, N Los Bolos, Sierra de Neiba, Independencia Prov., 18°39.339'N, 71°39.279'W, 1520 m, 9.vii.2003, day and night, DEPG, RB, BH [USNM].
- PT**, 4 ♂♂: DOMINICAN REPUBLIC, RD-023, Loma Casabito, RCEV, La Vega Prov., 340–522 m E 2106-146 m N, 1390 m, 31.i.2002, RB, BH, DEPG [USNM].
- PT**, 6 ♂♂, 2 ♀♀, 3 nymph ♀♀: DOMINICAN REPUBLIC, RD-022, La Sal, RCEV, La Vega Prov., 19°04.42'N, 70°34.18'W, 1010 m, 28–30.i.2002, RB, BH, DEPG [USNM].
- PT**, nymph ♂: DOMINICAN REPUBLIC, RD-021, Arroyazo, RCEV, La Vega Prov., 19°02.27'N, 70°32.64'W, 990 m, 26–27.i.2002, RB, BH, DEPG [USNM].
- PT**, ♂, ♀: DOMINICAN REPUBLIC, RD-025, Km 10 on Rd to Los Anones, S Ocoa, San José de Ocoa Prov., 347–605 m E 2052-511 m N, 1070 m, 1–2.ii.2002, RB, BH, DEPG [USNM].
- PT**, ♀: DOMINICAN REPUBLIC, near Los Tablones River, W La Ciénaga de Manabao, E Pico Duarte, Cordillera Central, La Vega Prov., ca. 1200 m asl, 28.vi.2012, C. Vogt [OC, No 0535-4].
- PT**, nymph ♀: DOMINICAN REPUBLIC, RD-043, on Trail Arroyazo to La Sal, RCEV, La Vega Prov., on path between 19°02.374'N, 70°32.684'W, 1249 m and 19°02.021'N, 70°32.584'W, 1102 m, 10.vii.2002, DEPG, BH, RB [USNM].
- PT**, nymph ♀: DOMINICAN REPUBLIC, RD-128, PNAB, around caseta La Sierrecita, Santiago Prov., 19°14.889'N, 71°04.735'W, 752 m, 9.iv.2003, DEPG, RB, BH [USNM].
- PT**, 4 eggs: DOMINICAN REPUBLIC, RD-149, Loma La Golondrina, RCEV, La Vega Prov., 19°03.498'N, 70°32.670'W, 11.vii.2003, day and night, DEPG, RB, BH [USNM].
- PT**, 2 eggs: DOMINICAN REPUBLIC, RD-149, Loma La Golondrina, RCEV, La Vega Prov., 19°03.498'N, 70°32.670'W, 11.vii.2003, day and night, DEPG, RB, BH, ex coll USNM [OC, No 0535-1].
- PT**, ♀: DOMINICAN REPUBLIC, RD-151, La Sal, RCEV, La Vega Prov., 19°04.101'N, 70°34.089'W, 1043 m, 12.vii.2003, night, DEPG, RB, BH, ex coll USNM [FH, No 1220-1].
- PT**, ♂: DOMINICAN REPUBLIC, RD-149, Loma La Golondrina, RCEV, La Vega Prov., 19°03.498'N, 70°32.670'W, 11.vii.2003, day and night, DEPG, RB, BH, ex coll USNM [FH, No 1220-2].
- PT**, egg: DOMINICAN REPUBLIC, RD-14, Loma La Golondrina, RCEV, La Vega Prov., 19°03.498'N, 70°32.670'W, 11.vii.2003, day and night DEPG, RB, BH, ex coll USNM [FH, No 1220-E].

**Distribution.**—So far only known from the provinces of La Vega, Santiago, Barahona, Independencia, and San José de Ocoa in Dominican Republic (Fig. 9).

**Etymology.**—This species is dedicated to Dr. Daniel E. Pérez-Gelabert (USNM) who collected the type specimens and provided specimens for the present study.

**Description.**—♀♀ (Figs 2, 3b, e, h). Small for the genus (body length 39.8–50.5 mm). Apterous. General color variable and more or less lichenose to moss-like; various shades of brown and green. Eyes dark brown with a yellowish-green reticulate pattern.

**Head:** Slightly longer than wide, broadest at the eyes and slightly narrowed towards the posterior. Vertex strongly raised, rounded, convex, and armed with a crown-like ornamentation formed by six prominent and acute spines and four dentate foliaceous projections.



Fig. 1. Male (HT) of *Taraxippus perezgelaberti* sp. nov. Habitus: a. Dorsal; b. Lateral; c. Ventral. Head and thorax: d. Dorsal; e. Lateral; f. Ventral. End of the abdomen: g. Dorsal; h. Lateral; i. Ventral.



Fig. 2. Female (PT) of *Taraxippus perezgelaberti* sp. nov. Habitus: a. Dorsal; b. Lateral; c. Ventral. Head and thorax: d. Dorsal; e. Lateral; f. Ventral. End of the abdomen: g. Dorsal; h. Lateral; i. Ventral.



Fig. 3. Comparison of females of *Taraxippus*. Note: (d–i) not in scale. Habitus in lateral view: a. *Taraxippus paliurus* Moxey, 1971; b. *Taraxippus perezgelaberti* sp. nov.; c. *Taraxippus samarae* sp. nov. Head, pro-, and mesothorax in lateral view: d. *Taraxippus paliurus* Moxey, 1971; e. *Taraxippus perezgelaberti* sp. nov.; f. *Taraxippus samarae* sp. nov. End of the abdomen in ventral view: g. *Taraxippus paliurus* Moxey, 1971; h. *Taraxippus perezgelaberti* sp. nov.; i. *Taraxippus samarae* sp. nov.

Genae usually with a pale cream longitudinal postocular line. Eyes prominent, almost spherical and their length about 2× that of genae. Antennae filiform, reaching to abdominal segment IV. Scapus slightly compressed dorsoventrally, constricted at base, about 2× longer than wide and with a distinct dorsal spine towards apex. Pedicellus cylindrical and somewhat constricted towards apex.

**Thorax:** Pronotum slightly wider than long and the transverse median sulcus distinctly impressed; entire surface irregularly granulated. Four enlarged spines in posterior half, two towards the lateral and two towards the dorsolateral. Mesonotum 3.7× longer than pronotum; distinctly swollen premedially, densely granulate and with irregular spines; at widest area with four dorsal distinctly outward-directed, multispinose processes, two towards the lateral and two dorsolateral, larger, and somewhat pointing towards the anterior; two dorsal, smaller ones close to the posterior margin. Mesosternum rough, with small spines along the lateral margins. Metanotum widened towards the posterior; sculptured with two distinct, dorsal, multispinose projections medially, slightly pointing towards the posterior; 0.5× longer than mesonotum. Metapleurae with large supracoxal multispinose projection near the base, supplied with several shorter spines.

**Abdomen:** Median segment almost half the length of metanotum. Abdomen excluding median segment almost as long as head and thorax combined. Segments III–IV slightly increasing in width, V widest segment (2× wider than long), VI–VII tapered towards the posterior. Terga III–VIII with the lateral margins posteriorly expanded into a small dentate and dorsally carinate lobe; the smallest in tergum III, larger and almost equal in size in terga IV–VI, which projects laterally by less than one-third the width of segment; the largest in tergum VII, which projects laterally by more than half the width of segment. All abdominal terga with two irregular and sub-parallel longitudinal median carinae; along each of them, with one medium to large multispinose process per segment (II–VI); very small in VII. In VIII–IX, with expanded dentate lobes pointing towards the posterior, the biggest in VIII. Praeopercular organ formed by several concentric circular carinae, surrounded by eight small spines. Anal segment 0.7× longer than tergum IX, tectiform, broadened basally with expanded dentate lobes pointing towards the posterior; posterior margin with acute spines. Supranal plate weakly developed, tectiform, triangular, and pointed at apex; slightly projecting over the anal segment and never reaching the end of the subgenital plate. Cerci usually green, long, and flattened, projecting over the anal segment. Subgenital plate slightly convex, shovel-like, widened medially, and strongly compressed towards the posterior third; granulated, with a median keel; ratio length/max. width ≈ 3×, posterior margin rounded at apex.

**Legs:** Profemora slightly compressed basally. Dorsal and ventral carinae of all femora, as well as dorsal carinae of all tibiae, armed with some irregular dentate foliaceous lobes. Tarsi elongated and slender.

♂♂ (Fig. 1). Small for the genus (body length 38.2–45.0 mm). Apterous. Generally similar to female but much more slender. Color similar to female except for the yellowish green markings along the lateral margins of pro-, meso-, and metathorax as well as abdominal terga II–VI.

**Head:** Similar to female except for the narrowed and more acute dorso-laterally directed and multispinose antler-like projections. Antennae filiform, long, slightly longer than the entire body.

**Thorax:** Meso- and metasternum with irregular spines. Pronotum similar to female. Mesonotum 3.7× longer than pronotum; slightly swollen premedially, densely granulate and with irregular spines; at widest area with two small spines towards the lateral

and two dorsal distinctly outward-directed, multispinose processes (composed of less spines than in females); two dorsal, small spines close to the posterior margin. Mesosternum rough, with small spines. Metanotum 0.6× longer than mesonotum, roundly constricted medially and widened towards the posterior; sculptured with two distinct, dorsal, multispinose projections medially, slightly pointing towards the posterior. Metapleurae with large supracoxal spine near the base, supplied with several shorter spines.

**Abdomen:** Median segment almost half the length of metanotum, with two small spines close to the posterior margin. Abdomen excluding median segment slightly longer than head and thorax combined. Segments II–VI almost equal in length. Sterna II–VI armed with two ventral small spines medially and two tiny spines close to the posterior margin. Terga II–IV (sometimes even V) armed with two dorsal pairs of spines close to the posterior margin and joined at base; each pair of spines consists of a small one pointing towards the anterior and a larger one (at least 2× in length) pointing towards the posterior. VI only with a pair of spines close to the posterior margin. The size of the spines on the terga decreases towards the posterior. Tergum VII with the lateral margins deflexed into a prominent, irregularly denticulate lobe, which laterally projects by more than one-third the width of segment. Anal segment 1.4× longer than tergum IX, tectiform, broadened basally, strongly narrowed medially, with a rounded incision at apex. Cerci brown, long, and narrowed towards the apex, projecting over the anal segment. Vomer triangular, widened at base, and acute at apex. Poculum strongly convex, the posterior portion granulated, with an irregular median keel; posterior margin rounded.

**Legs:** Profemora slightly compressed basally. Dorsal and ventral carinae of all femora, as well as dorsal carinae of all tibiae, armed with some irregular dentate foliaceous lobes. Tarsi elongated and slender.

*Measurements (in mm).*—♂, HT: Body 42.5, head 4.2, pronotum 2.1, mesonotum 9.7, metanotum 5.6, median segment 1.5, profemora 14.0, mesofemora 10.9, metafemora 14.2, protibia 14.7, mesotibia 12.2, metatibia 16.3, antennae >40.0.

♂♂, PT: Body 38.2–45.0, head 4.3–4.5, pronotum 2.3–2.5, mesonotum 8.3–10.6, metanotum 5.2–6.0, median segment 1.6–2.3, profemora 12.1–14.8, mesofemora 9.9–11.9, metafemora 12.8–15.2, protibia 12.7–16.2, mesotibia 10.9–13.2, metatibia 13.8–18.2, antennae >28.8.

♀♀, PT: Body 39.8–50.5, head 5.2–6.4, pronotum 2.8–3.0, mesonotum 8.7–10.9, metanotum 5.6–6.8, median segment 2.3–3.3, profemora 9.5–11.6, mesofemora 7.3–9.7, metafemora 9.9–13.3, protibia 9.1–12.0, mesotibia 9.0–10.7, metatibia 11.4–15.1, antennae >29.0.

**Egg:** (Fig. 4d–f) General color various shades of brown. Capsule 2× longer than wide and 1.6× longer than high. General shape of capsule triangular prism, with the lateral surfaces slightly convex and the dorsal surface almost flat. Lateral longitudinal carinae set with a net-like structure of branched and tangled fringes, without free standing apices. Lateral surfaces wavy and glossy. Dorsal surface of egg without a longitudinal median row of hairy structures. Micropylar plate positioned in the anterior half in the dorsal egg surface and roughly half the length of capsule; shape spearhead-like pointing towards anterior; surface unarmed and outer margin set with moderately long hairy structures. Micropylar cup placed almost in posterior margin of plate. Median line pale brown, not reaching the posterior pole. Operculum oval, slightly convex; surface variable from smooth to rough, with a raised concentric central plateau from whose

margin a network of fringes is born and connects with that of the lateral margins of the capsule, intertwining with each other; between the central plateau and the margin of the operculum a crown-like ornamentation is present, formed by sets of multispinose processes.

*Measurements (in mm).*—Egg, **PT**: length 3.1, width 1.4, height 2.0, length of micropylar plate 1.4.

*Comments.*—The male of this new species was mistaken for *T. paliurus* Moxey, 1971 by Pérez-Gelabert (1999), who provided a description and illustrations of the terminalia.

***Taraxippus samarae* sp. nov.**

<http://zoobank.org/400FD424-309B-41D6-ADF5-8A2FF0C37B08>

Figs 3c, f, i, 4a–c, 5–8

*Differentiation.*—Males are readily differentiated from those of *T. perezgelaberti* sp. nov. by being winged. Furthermore, they differ from that species by bearing distinct lateral foliaceous projections on abdominal segments V–VII and having the apex of the antler-like mesonotal processes bifurcate (Figs 5, 6). Females differ from the other two known species of the genus by the broadened subgenital plate, apically bifurcate antler-like processes of the mesonotum, and unarmed abdominal sternum VI (at best tiny granules) and terga (Fig. 3). Eggs readily differ from those of *T. perezgelaberti* sp. nov. by their rectangular cross-section, flattened lateral surfaces, setae-like long, slender marginal fringes that usually are free at the apex, as well as having fringes along the outer margin of the micropylar plate (Fig. 4).

*Type material and specimens examined.*—

**HT**, ♂: COSTA RICA, Siquirres, Limón Prov., 10°03'17.1"N, 83°33'05.6"W, 610 m, iii.2018, J. Sommerhalder [ZSMC].

**PT**, ♀: COSTA RICA, Siquirres, Limón Prov., 10°03'17.1"N, 83°33'05.6"W, 610 m, iii.2018, J. Sommerhalder [ZSMC].

**PT**, 2 ♂♂, 2 ♀♀, ♀ **nymph**: COSTA RICA, Siquirres, Limón Prov., 10°03'17.1"N, 83°33'05.6"W, 610 m, iii.2018, J. Sommerhalder [OC, No. 0536-(3–7)].

**PT**, ♀: COSTA RICA, Pocaá, Finca INBio, Bosque Lluvioso, Limón Prov., 200–300 m, 22.ix.2004, night, J. Mata, Colecta Libre, L\_N\_241740\_S51770, #95228; INB0004179712, INBIOCRI COSTA RICA; DNA Barcoding E. Ulate, CCDB-15936 D04 [INBIO].

**PT**, ♀, **15 eggs**: PANAMA, Parque Nacional General de División Omar Torrijos Herrera, Coclé Prov., 8°40'5.53"N, 80°35'33.48"W, vii.2019, O. Conle, P. Valero [OC, No. 0536-1, 2].

**PT**, **11** ♂♂, **10** ♀♀, **12 eggs**: COSTA RICA, Siquirres, Limón Prov., iii.2018, J. Sommerhalder, Ex Zucht B.Kneubühler 2019, F1 [OC, No. 0536-(8-29)].

**PT**, ♂, ♀, **egg**: COSTA RICA, Siquirres, Limón Prov., iii.2018, J. Sommerhalder, Ex Zucht B. Kneubühler 2019, F1 [FH, No. 1200-1, 2 and E].

*Distribution.*—So far only known from Costa Rica (Limón Province: Siquirres and Pocaá) and Panama (Coclé Province, Parque Nacional General de División Omar Torrijos Herrera) (Fig. 9).

*Etymology.*—This stunning new species is named after Samara, the daughter of Jürg Sommerhalder (Switzerland), who found the holotype and several paratypes in March 2018 in Costa Rica.

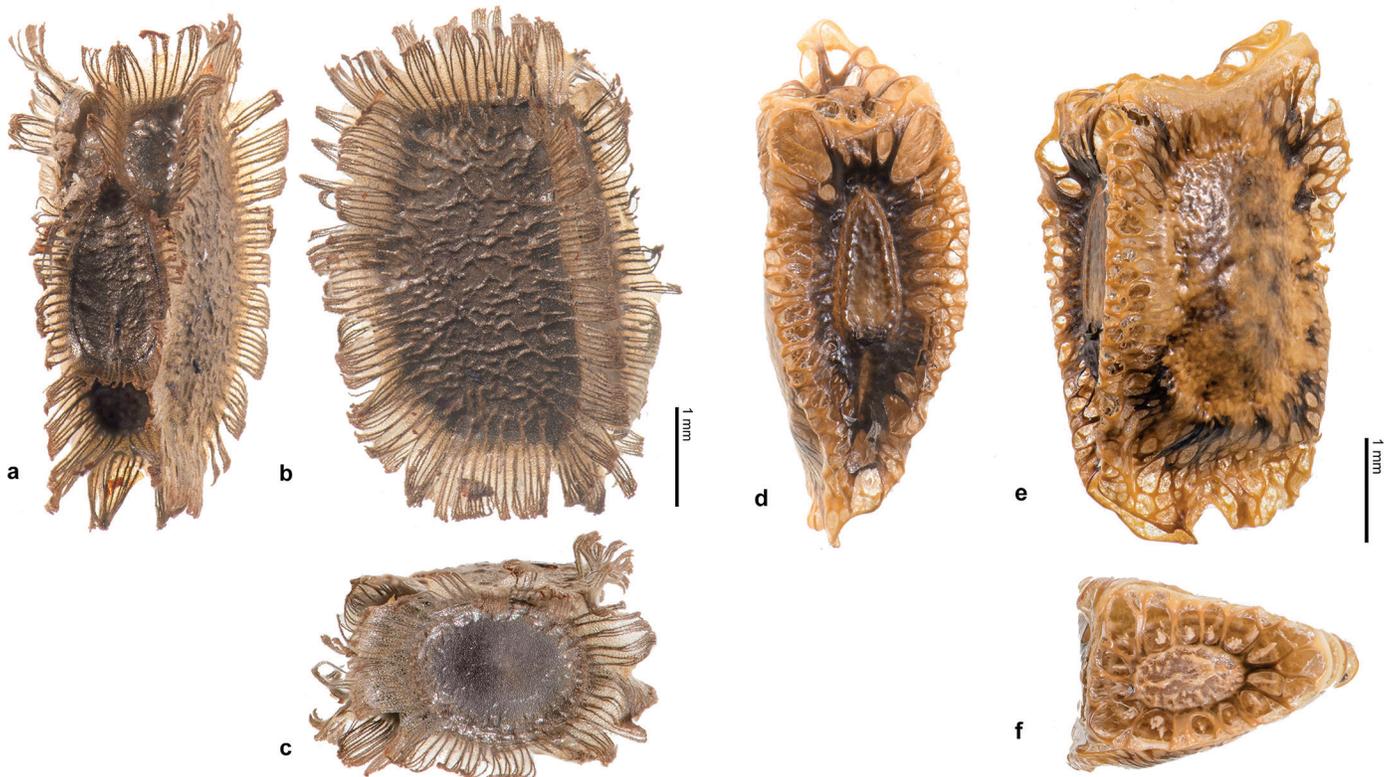


Fig. 4. Comparison of eggs: *Taraxippus samarae* sp. nov.: a. Dorsal; b. Lateral; c. Frontal. *Taraxippus perezgelaberti* sp. nov.: d. Dorsal; e. Lateral; f. Frontal.



Fig. 5. Male (HT) of *Taraxippus samarae* sp. nov. Habitus: a. Lateral; b. Dorsal.



Fig. 6. Male (PT) of *Taraxippus samarae* sp. nov. Habitus: a. Dorsal; b. Lateral; c. Ventral. Head and thorax: d. Dorsal; e. Lateral; f. Ventral. End of the abdomen: g. Dorsal; h. Lateral; i. Ventral.

*Description.*—In this species, all spines and multispinose processes have blunt apices.

♀♀ (Figs 3c, f, i, 7, 8a–c). Medium to large for the genus (body length 54.7–71.1 mm). Apterous. General color various shades of brown, usually with green markings (especially in foliaceous projections) and a dorsal longitudinal pale cream stripe from the head to the end of the abdomen. Eyes dark brown with a yellowish-green reticulate pattern. Entire body (including antennae) setose.

**Head:** Slightly longer than wide, broadest at the eyes and slightly narrowed towards the posterior. Vertex slightly raised, rounded, convex, and armed with a crown-like ornamentation formed by eight prominent antler-like projections, with reddish brown and blunt apex. Genae with a pale cream longitudinal postocular carina that ends in a small spiniform tubercle. Eyes prominent, almost spherical, and their length about 2× that of genae. Antennae filiform, reaching to median segment. Scapus compressed dorsoventrally, about 2× longer than wide and with two exterior foliaceous projections towards apex. Pedicellus cylindrical and somewhat constricted towards apex.

**Thorax:** Pronotum slightly wider than long and the transverse median sulcus distinctly impressed, expanding over the entire width of segment; entire surface irregularly granulated. Four enlarged, spiniform tubercles in posterior half, two towards the lateral and two towards the dorsal. Mesonotum 3.2× longer than pronotum; distinctly swollen premedially, densely granulate and with irregular spiniform tubercles; at widest area with two dorsal distinctly outward-directed, multispinose processes bifurcated at apex; two smaller dorsal multispinose projections towards the posterior margin; lateral margins bearing multispinose projections, increasing in size towards the widest area. Mesosternum rough, with small spiniform tubercles along the lateral margins. Metanotum widened towards the posterior, roundly constricted medially; sculptured with four dorsal small multispinose projections, two medially and two close to the posterior margin; 0.5× longer than mesonotum. Meso- and metapleurae granulated and with a marginal row of small spiniform tubercles.

**Abdomen:** Median segment almost half the length of metanotum, usually with two dorsal multispinose projections towards the posterior, variable in size. Abdomen excluding median segment almost equal in length to head and thorax combined. Segments III–IV strongly increasing in width, V widest segment (2.5× wider than long), VI–VII narrowing towards the posterior. Terga II–VIII with the lateral margins posteriorly expanded into a dentate and foliaceous projection; this strongly increasing in size from II–VI and decreasing in size towards VII. All terga with two irregular and sub-parallel longitudinal median carinae, usually with expanded foliaceous projections, distinctly large in VIII–IX. Praeopercular organ formed by a small dark blunt tubercle close to the posterior margin of sternum VII. Anal segment 0.8× longer than tergum IX, tectiform, broadened basally; posterior margin rounded. Supraanal plate well developed, tectiform, slightly longer than wide, projecting over the anal segment and almost reaching the end of the subgenital plate to form a beak-like structure. Cerci green, long, laterally compressed, with tipped apex, projecting over the anal segment. Subgenital plate slightly convex, shovel-like, with a median keel, ratio length/max. width ≈ 1.8×, posterior margin narrowed but not acute and usually not projecting over the anal segment.

**Legs:** Profemora slightly compressed basally. Dorsal and ventral carinae of all femora, as well as dorsal carinae of all tibiae, armed with some irregular dentate lobes. Tarsi elongated and slender.

♂♂ (Figs 5, 6, 8d). Medium to large for the genus (body length 45.8–54.2 mm) and fully winged. General color various shades

of brown, usually with irregular green markings (especially in foliaceous projections and tegmina). Anal area of the wings greyish brown, translucent. Eyes dark brown with a yellowish-green reticulate pattern. Entire body (including antennae) setose.

**Head:** Slightly longer than wide, broadest at the eyes and slightly narrowed towards the posterior. Vertex slightly raised, rounded, convex, and armed with a crown-like ornamentation formed by eight prominent antler-like projections, with reddish brown and blunt apex. Genae with a longitudinal postocular carina that ends in a small spiniform tubercle. Eyes prominent, almost spherical and their length about 2× that of genae. Antennae reaching to abdominal segment V. Scapus compressed dorsoventrally, about 2× longer than wide and with two exterior foliaceous projections towards apex. Pedicellus cylindrical and somewhat constricted towards apex.

**Thorax:** Pronotum slightly wider than long and the transverse median sulcus distinctly impressed, expanding over the entire width of segment; entire surface irregularly granulated. Four enlarged, spiniform tubercles in posterior half, two towards the lateral and two towards the dorsal. Mesonotum 2.8× longer than pronotum; swollen premedially, densely granulate and with irregular spiniform tubercles; at widest area with two dorsal distinctly outward-directed, multispinose processes bifurcated at apex; two smaller dorsal multispinose projections towards the posterior margin; lateral margins bearing spines, increasing in size towards the widest area. Mesosternum rough, with small, spiniform, pale cream tubercles along the lateral margins. Metanotum slightly widened towards the posterior; 0.7× longer than mesonotum. Meso- and metapleurae granulated and with a marginal row of small spiniform tubercles. Tegmina not reaching the posterior margin of metanotum and with a fairly acute central spine; the basal portion notably narrowed and the posterior margin rounded. Alae reaching to abdominal segment VII.

**Abdomen:** Unarmed. Median segment about one-quarter the length of metanotum. Abdomen excluding median segment slightly longer than head and thorax combined. Segments II–VII almost equal in length and width. Terga III–IV with the lateral margins deflexed into a tiny irregularly foliaceous projection. Terga V–VIII with the lateral margins deflexed into a prominent irregularly foliaceous projection, which projects laterally by more than two-thirds the width of segment in V–VII and one-third in VIII. Anal segment 0.7× longer than tergum IX, tectiform, broadened basally; posterior margin rounded. Cerci green, long, and almost cylindrical, projecting over the anal segment. Vomer triangular, widened at base, and acute at apex. Poculum strongly convex, the posterior portion granulated, with an irregular median keel; posterior margin rounded.

**Legs:** Profemora slightly compressed basally. Dorsal and ventral carinae of all femora, as well as dorsal carinae of all tibiae, armed with some irregular dentate lobes. Tarsi elongated and slender.

*Measurements (in mm).*—♂, HT: Body 47.3, head 3.6, pronotum 2.3, mesonotum 7.8, metanotum 7.2, median segment 1.8, profemora 11.4, mesofemora 9.1, metafemora 10.7, protibia 10.2, mesotibia 10.3, metatibia 12.8, tegmina 6.4, alae 30.1, antennae >27.0.

♂♂, PT: Body 45.8–54.2, head 3.8–4.5, pronotum 1.9–3.0, mesonotum 7.3–7.9, metanotum 6.4–7.9, median segment 1.5–1.9, profemora 10.3–12.3, mesofemora 9.1–10.7, metafemora 11.4–12.7, protibia 10.2–12.2, mesotibia 10.2–11.4, metatibia 12.2–15.2, tegmina 6.4–7.1, alae 27.5–31.1, antennae >30.0.

♀♀, PT: Body 54.7–71.1, head 6.6–7.8, pronotum 3.7–4.7, mesonotum 11.5–14.8, metanotum 6.3–8.5, median segment



Fig. 7. Female (PT) of *Taraxippus samarae* sp. nov. Habitus: a. Dorsal; b. Lateral; c. Ventral. Head and thorax: d. Dorsal; e. Lateral; f. Ventral. End of the abdomen: g. Dorsal; h. Lateral; i. Ventral.



Fig. 8. Living specimens of *Taraxippus samarae* sp. nov. a. Adult female from Cope, Panama, in its natural habitat; b, c. Adult females from Siquirres, Costa Rica, showing intraspecific variability in the coloration; d. Adult male from Siquirres, Costa Rica.

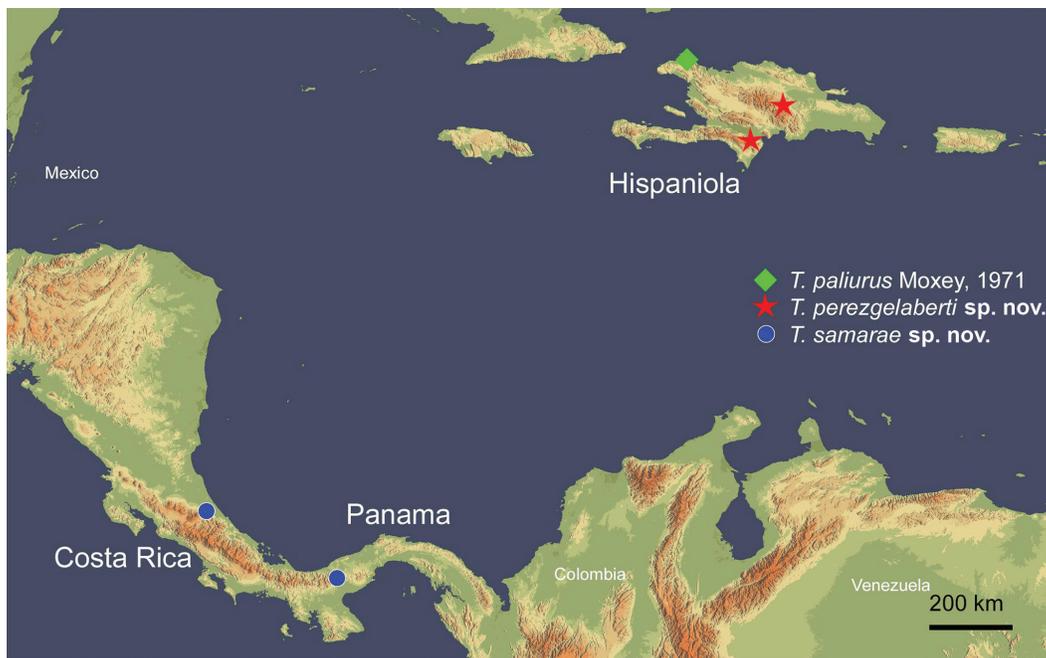


Fig. 9. Distribution map of all known *Taraxippus* species.

2.2–2.7, profemora 11.4–14.9, mesofemora 9.7–13.2, metafemora 11.5–16.0, protibia 11.3–15.2, mesotibia 11.1–14.4, metatibia 14.4–18.6, antennae >26.0.

**Egg** (Fig. 4a–c): General color chestnut brown. Capsule 2.6× longer than wide and 1.6× longer than high. General shape of capsule cuboid, with the lateral surfaces flattened and almost parallel and the dorsal surface slightly convex. In lateral aspect, slightly widened medially. Lateral longitudinal carinae set with a row of long and slender fringes, usually branched and somewhat connected laterally by a kind of brownish translucent membrane. Lateral surfaces with a reticulate pattern of carinae. Dorsal and ventral surfaces of egg each with a longitudinal median row of hairy structures. Micropylar plate positioned medially on the dorsal egg surface and roughly half the length of capsule; shape spearhead-like and pointed towards anterior; surface unarmed and outer margin set with moderately long hairy structures. Micropylar cup small and placed in posterior one-quarter of plate. Operculum oval, flat, and with the outer margin set with a row of the same long feather-like fringes seen along the longitudinal outer carinae of the egg-capsule; no capitulum.

**Measurements (in mm).**—Egg, PT: length 3.6, width 1.2, height 2.3, length of micropylar plate 1.9.

### Acknowledgments

Our appreciation to all the biologists from the Dominican Republic who contributed to the successful expeditions of the Hispaniolan Orthopteroids Project (Daniel E. Pérez-Gelabert, Ruth H. Bastardo, Brígido Hierro, and others). The Ministerio de Medio Ambiente y Recursos Naturales (then Secretaría) en Santo Domingo, graciously provided collecting and export permits. The Ministerio de Ambiente, Panamá, and Dr. Roberto A. Cambra (Universidad de Panamá - Museo de Invertebrados G. B. Fairchild, Panama City) are kindly thanked for collecting and export permits. Jürg Sommerhalder (Switzerland) collected *Taraxippus samarae* sp. nov. in Costa Rica and kindly contributed his specimens together with detailed information about the type locality. Dr. Bruno Kne-

bühler (Luzern, Switzerland) kindly provided a culture stock of *Taraxippus samarae* sp. nov.

### References

- Conle OV, Hennemann FH, Pérez-Gelabert DE (2006) Studies on neotropical Phasmatodea III: A new species of *Anisomorpha* Gray, 1835 (Phasmatodea, Pseudophasmatidae, Pseudophasmatinae) from Hispaniola. *Proceedings of the Entomological Society of Washington* 108: 885–891.
- Conle OV, Hennemann FH, Pérez-Gelabert DE (2008) Studies on neotropical Phasmatodea II: Revision of the genus *Malacomorpha* Rehn, 1906, with the descriptions of seven new species (Phasmatodea: Pseudophasmatidae: Pseudophasmatinae). *Zootaxa* 1748: 1–64. <https://doi.org/10.11646/zootaxa.1748.1.1>
- Conle OV, Hennemann FH, Pérez-Gelabert DE (2014) Studies on neotropical Phasmatodea XV: A remarkable new stick insect from highly montane habitats of Hispaniola (Pseudophasmatidae: Xerosomatinae: Hesperophasmatini). *Novitates Caribaea* 7: 28–36. <https://doi.org/10.33800/nc.v0i7.57>
- Hennemann FH, Conle OV, Pérez-Gelabert DE (2016) Studies on neotropical Phasmatodea XVI: Revision of Haplopodini Günther, 1953 (rev. stat.), with notes on the subfamily Cladomorphinae Bradley & Galil, 1977 and the descriptions of a new tribe, four new genera and nine new species (Phasmatodea: “Anareolatae”: Phasmatidae: Cladomorphinae). *Zootaxa* 4129: 1–211. <https://doi.org/10.11646/zootaxa.4128.1.1>
- Hennemann FH, Conle OV, Valero P (in press) Studies on neotropical Phasmatodea XXI: *Sigaruphasma* gen. nov., a new genus of Hesperophasmatini Bradley & Galil, 1977 from Hispaniola with the descriptions of two new species (Phasmatodea: Cladomorphinae). *Novitates Caribaea*.
- Moxey CF (1971) Notes on the Phasmatodea of the West Indies: Two new genera. *Psyche* 78: 1–67. <https://doi.org/10.1155/1971/927579>
- Pérez-Gelabert DE (1999) *Taraxippus paliurus* (Phasmatodea: Phasmatidae) en República Dominicana: Primera cita y descripción del macho. *Cocuyo* 9: 22–24.
- Sellick JTC (1997) Descriptive terminology of the phasmid egg capsule, with an extended key to the phasmid genera based on egg structures. *Systematic Entomology* 22: 97–122. <https://doi.org/10.1046/j.1365-3113.1997.d01-30.x>