Article

Studies in Mexican Grasshoppers: *Liladownsia fraile*, a new genus and species of Dactylotini (Acrididae: Melanoplinae) and an updated molecular phylogeny of Melanoplinae

DEREK A. WOLLER[1,3,4], PAOLO FONTANA[2,4], RICARDO MARIÑO-PÉREZ[1,4] & HOJUN SONG[1]

[1]*Department of Biology, University of Central Florida, 4000 Central Florida Blvd., Orlando, FL 32816-2368, U.S.A.*

[2]*Fondazione Edmund Mach - Centro Trasferimento Tecnologico – Protezione delle piante e biodiversità agroforestale, Via della Val, 2 - Loc. Costa di Casalino, I-38057 Pergine Valsugana, Italy*

[3]*Corresponding author. E-mail: asilid@gmail.com*

[4]*These authors participated equally*

Abstract

Liladownsia fraile **gen. nov. sp. nov.** Fontana, Mariño-Pérez, Woller & Song (Lila Downs' friar grasshopper) of the tribe Dactylotini (Orthoptera: Acrididae: Melanoplinae) is described from the pine-oak forest of the Sierra Madre del Sur Mountain Range in Oaxaca, Mexico. Taxonomic placement of this new genus is justified based on morphological characters as well as a molecular phylogeny. Information about the probable host plant, phenology, and known localities is also presented. We also present an updated molecular phylogeny of Melanoplinae, which includes representatives of five of the seven recognized tribes. The monophyly of the subfamily and the included tribes is tested and we find Dactylotini to be paraphyletic because of the placement of *Hesperotettix* Scudder, 1876. We also recover strong close relationships between the new genus and *Perixerus* Gerstaecker, 1873 and *Dactylotum* Charpentier, 1845.

Key words: Melanoplinae, Dactylotini, *Perixerus*, Oaxaca, *Salvia elegans*, aposematic

Introduction

The tribe Dactylotini is one of seven tribes into which the subfamily Melanoplinae is currently divided (Eades *et al.* 2013) and is presently composed of ten genera and 36 species with a distribution across the U.S.A. and Mexico. The first mention of the tribe, as Dactyloti, was by Scudder (1897), but Rehn and Randell (1963) were the first to formally describe Dactylotini. They included 12 genera as typical members of the tribe: *Aztecacris* Roberts, 1947, *Campylacantha* Scudder, 1897, *Chibchacris* Hebard, 1923, *Dactylotum* Charpentier, 1845, *Dasyscirtus* Bruner, 1908, *Dichroplus* Stål, 1873, *Hesperotettix* Scudder, 1876, *Oedomerus* Bruner, 1907, *Paraidemona* Brunner von Wattenwyl, 1893, *Paratylotropidia* Brunner von Wattenwyl, 1893, *Poecilotettix* Scudder, 1897, and *Perixerus* Gerstaecker, 1873, plus two atypical genera: *Gymnoscirtetes* Scudder, 1897 and *Meridacris* Roberts, 1937.

Of these original 14 genera, *Oedomerus* was transferred to the Conalcaeini tribe by Cohn and Cantrall (1974) and *Chibchacris*, *Dichroplus*, and *Meridacris* were transferred to Dichropli by Amédégnato (1977), leaving Dactyolini with its now-ten members. All the species in the tribe were described between 1843 and 1943 except for four species of the genus *Paraidemona* that were described recently: 1) *P. nuttingi* and 2) *P. olsoni* by Yin and Smith (1989) from Texas, USA and 3) *P. cohni* by Fontana and Buzzetti (2007) and 4) *P. ruvalcabae* by Buzzetti *et al.* (2010), both from Mexico.

Scudder (1897) employed the following characteristics to separate the members of Dactylotini from other tribes: hind tibiae with 6–8 spines only on the exterior margin, but lacking an apical spine on the outer side, face nearly vertical, fastigium of vertex not prolonged, apically obtuse, mesosternal lobes transverse or equally long and broad with the inner margin usually rounded. However, it should be noted, that due to the specific focus of his work, Scudder (1897) was relying chiefly upon his descriptions of only *Dactylotum*, but mentioned that he was also aware that Dactylotini was mainly a Central American group comprised of only two or three genera. Later, Roberts

(1947) suggested that Scudder's (1897) characterization of the tribe was not valid because he recognized that many Mexican melanoplines have 8–9 spines on the hind tibiae and *Oedomerus* and *Psilotettix* Bruner have 6–7 spines only. Furthermore, Roberts (1947) considered *Dactylotum* to be a member of Melanoplini based on the shape of the head and the male terminalia. Rehn and Randell (1963) redefined Dactylotini based on both external and internal characters, with an emphasis on the shape of the epiphallus (posterior process of the epiphallus showing a tendency toward reduction) and female genitalia (female internal genital armature with complex columellae, often with many supernumerary ones, or, alternately, with the columellae long, narrow and irregular in outline).

There have been four phylogenetic hypotheses for the subfamily Melanoplinae based on molecular data, focusing on tribal-level relationships. The first one was by Chapco *et al.* (2001), which included only 10 melanoplines from North America and Eurasia and did not include any member of Dactylotini. The second one, by Amédégnato *et al.* (2003), focused on the biogeographic origin of the subfamily, but, again, did not include any Dactylotini. The third one, by Chapco (2006), was the largest phylogeny of Melanoplinae to date and finally included members of Dactylotini, *Dactylotum* and *Hesperotettix*, but did not recover a monophyly of the tribe. The fourth, and latest study, by Chintauan-Marquier *et al.* (2011), also included *Dactylotum* and *Hesperotettix* and, like Chapco (2006), found the tribe to be paraphyletic. While important first steps, these previous studies lacked robust taxon and character sampling, and at this moment, the phylogenetic position of Dactylotini relative to other tribes still remains unclear.

In 2011, the first three authors embarked upon a December orthopterological expedition to Mexico and discovered a very colorful and amazing medium-sized grasshopper while in a mountainous locality. Based on the markedly reticulated tegmina, this new genus bears a strong resemblance to the genus *Perixerus*, but all of its other morphological features are unique in comparison, so it cannot be assigned to this or any other described genus or species. The second and third authors returned to the original locality (Fig. 1) in December of 2013 in the hopes of collecting additional specimens and managed to accomplish this goal as well as locate two more localities (Fig. 1C-2&3) not far (2–3 km) from the first (Fig. 1C-1). Additionally, during a recent trip to the Muséum national d'Histoire naturelle (MNHN) in Paris, France, the third author found a pair of specimens, which were collected only 4 km away from the other surveyed localities. Based on the series of newly collected specimens, we herein describe a new genus as the eleventh member of Dactylotini. The placement of the new genus into Dactylotini is justified based on morphological features as well as a molecular phylogenetic analysis, which we also present here.
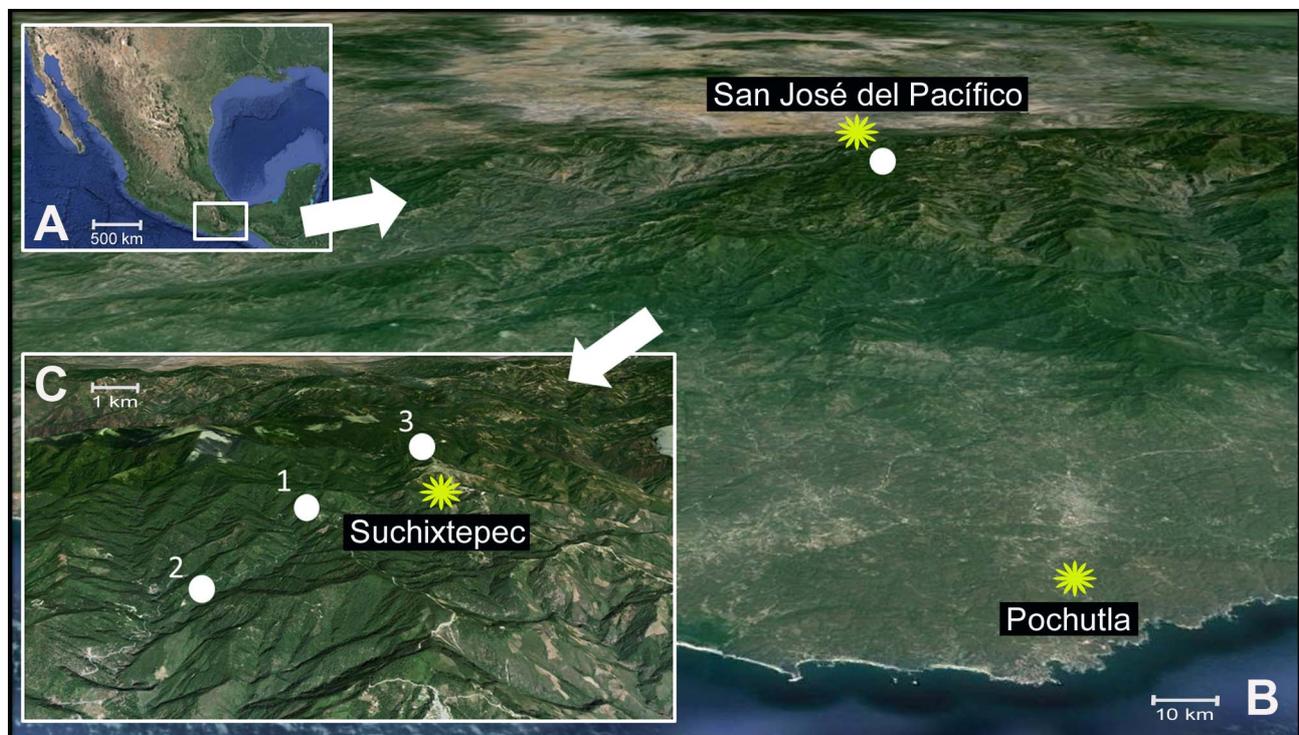
FIGURE 1. Distribution map of *Liladownsia fraile* **gen. nov. sp. nov.**: **A.** View of overall collection region within Oaxaca, Mexico. **B.** Relief map depicting specific site of the three known localities. **C.** Zoomed-in relief map displaying the three individual localities: **1)** holotype locality, 26 km after San José del Pacífico, **2)** 29 km after San José del Pacífico, and **3)** 1.3 km Northwest of Suchixtepec.

Material and methods

Descriptive taxonomy. All descriptions followed the terminology and style utilized by Otte (2007). The *Perixerus squamipennis* (Gerstaecker, 1873) specimens that were utilized for character comparisons came from a few sources, the main one being the Paolo Fontana Private Collection (CPF), which contains numerous specimens of this species from various collecting trips made prior to 2011. The 2011 Mexico expedition yielded much more material, all from Monte Albán in Oaxaca and the 2013 expedition to Oaxaca brought in even more material. In all cases, the second author was the primary identifier of the collected specimens to the species level.

Dissection and measurements. Male genitalia were extracted via the methods described by Hubbell (1932) in which a probe was inserted beneath the epiproct and removed fully from the body by using dissecting scissors to sever the tissue attachments. After taking photos, the excised genitalia were then cleared of all non-sclerotized portions by placing them into a 10% KOH solution combined with a warm water bath for about 20 minutes. After photographs were taken, they were then preserved in glycerin in genital vials pinned beneath the respective specimen. Anatomical measurements were made in the U.S.A. using a Reichert 570 Stereo Star Zoom (0.7x to 4.2x) microscope with a 50 micrometer lens inserted into the right eyepiece.

Photography. Photographs of all preserved specimens (Figs. 2–4) and associated genitalia characters (Figs. 5–8) were taken in the Song Laboratory of Insect Systematics and Evolution at the University of Central Florida (UCF) using a Visionary Digital BK Plus Imaging System in combination with a Canon EOS 7D camera (and either a 65mm or 100mm lens) to take multiple images at different focal lengths. Following this, Adobe Lightroom 3 (v.3.2) was used to import the photos and transform them from RAW files to TIFF's and then Zerene Stacker (v.1.02) was employed to stack the image slices into a single focused photo and then Adobe Photoshop CS5 Extended was utilized, when necessary, to adjust light levels, background coloration, sharpness, and to add an accurate scale bar. Photographs of the habitat (Fig. 9A&C), flower (Fig. 9B), and live specimens (Figs. 10 and 11) were taken using four types of cameras: a Nikon Coolpix S2, a Sony DSC-H5, a Canon IXUS 125 HS, and a Sony DSC-RX100 while on- site collecting the now-preserved specimens seen in Figs. 2–4.

Type material. Type material is deposited in the Stuart M. Fullerton Collection of Arthropods at the University of Central Florida, Orlando, Florida, USA (UCFC), the Colección Nacional de Insectos, Instituto de Biología at the Universidad Nacional Autónoma de México (CNIN-UNAM) in Mexico City, Mexico, the Muséum national d'Histoire naturelle (MNHN) in Paris, France, and in the Paolo Fontana Private Collection (CPF) at Fondazione Edmund Mach in Pergine Valsugana (TN), Italy.

Phylogenetic analysis. In order to test the hypothesis that the new genus belongs to Dactylotini, we reconstructed a phylogeny of Melanoplinae (Fig. 12) based on already available sequence data from GenBank as well as newly-generated sequence data. Specifically, our dataset consisted of two mitochondrial genes, cytochrome *c* oxidase I (COI) and cytochrome *c* oxidase II (COII) from a total of 42 taxa, including two non-melanopline outgroups and 40 melanoplines from across five tribes: Dactylotini, Dichroplini, Jivarini, Melanoplini, and Podismini (Table 1). In order to complement already existing sequence data, we generated COI and COII sequences for 10 new taxa, including three current members of Dactylotini (*Dactylotum bicolor bicolor* Charpentier, 1845, *Hesperotettix viridis* (Thomas, 1872), and *P. squamipennis*) as well as the new species. Specific details on DNA extraction, PCR profiles, primers, and sequencing reactions can be found in Leavitt *et al.* (2013), which we followed. The newly-generated sequences have been deposited on GenBank and the accession numbers are shown in Table 1.

For each gene, we first converted nucleotide sequences to amino acid sequences and aligned in MUSCLE (Edgar, 2004) using default parameters as implemented in MEGA 5 (Tamura *et al.*, 2011). We then back-translated the aligned dataset into nucleotide sequences, and then concatenated two gene alignments into a single matrix. We partitioned the data according to codon positions and used PartitionFinder (Lanfear *et al.*, 2012) to estimate the best-fit partition scheme as well as the best models of nucleotide substitution for each partition.

We analyzed our matrix using maximum likelihood (ML) and Bayesian inference methods. For ML analysis, we used RAxML 7.2.8 (Stamatakis *et al.*, 2008) on XSEDE (Extreme Science and Engineering Discovery Environment, https://www.xsede.org) through the CIPRES Science Gateway (Miller *et al.*, 2011). For each partition, we used the GTRCAT model and nodal support was evaluated using 5000 replications of rapid bootstrapping implemented in RAxML. For Bayesian analysis, we used MrBayes 3.2 (Huelsenbeck and Ronquist, 2001) with an appropriate model applied to each partition using default priors. We ran four runs with four chains

each for 20 million generations, sampling every 1000 generations. We plotted the likelihood trace for each run to assess convergence in Tracer 1.5.0 (Rambaut and Drummond, 2003–2009), and discarded 25% of each run as burn-in. Nodal support was assessed from posterior probabilities.

TABLE 1. Taxonomic information, GenBank accession numbers, and references for the taxa included in this study.

Taxa	Tribe	COI Accession #	COII Accession #	Reference
Coscineuta sp.	Outgroup	KJ531420	KJ531430	This study
Locusta migratoria (Linnaeus, 1758)	Outgroup	X80245	X80245	Flook et al. (1995)
Dactylotum bicolor bicolor Charpentier, 1845	Dactylotini	KJ531421	KJ531431	This study
Hesperotettix viridis (Thomas, 1872)	Dactylotini	KJ531422	KJ531432	This study
Liladownsia fraile sp. nov.	Dactylotini	KJ531423	KJ531433	This study
Perixerus squamipennis Gerstaecker, 1873	Dactylotini	KJ531427	KJ531437	This study
Atrachelacris unicolor Giglio-Tos, 1894	Dichroplini	AY014360	AY014358	Amedegnato et al. (2003)
Baeacris pseudopunctulatus (Ronderos, 1964)	Dichroplini	DQ083452	DQ083436	Colombo et al. (2005)
Chlorus bolivianus Bruner, 1913	Dichroplini	FJ829333	N/A	Dinghi et al. (2009)
Chlorus chiquitensis Cigliano & Lange, 2007	Dichroplini	FJ829340	N/A	Dinghi et al. (2009)
Dichromatos lilloanus (Liebermann, 1948)	Dichroplini	FJ829336	N/A	Dinghi et al. (2009)
Dichromatos schrottkyi (Rehn, 1918)	Dichroplini	FJ829339	N/A	Dinghi et al. (2009)
Dichroplus elongatus Giglio-Tos, 1894	Dichroplini	AF539856	AY014343	Amedegnato et al. (2003)
Dichroplus obscurus Bruner, 1900	Dichroplini	DQ083457	N/A	Dinghi et al. (2009)
Dichroplus patruelis (Stål, 1861)	Dichroplini	DQ083458	DQ083441	Colombo et al. (2005)
Dichroplus pratensis Bruner, 1900	Dichroplini	DQ389228	DQ083442	Chapco (2006); Colombo et al. (2005)
Digamacris amoena (Stål, 1878)	Dichroplini	AY014341	AY014339	Amedegnato et al. (2003)
Leiotettix flavipes Bruner, 1906	Dichroplini	FJ829337	N/A	Dinghi et al. (2009)
Ronderosia bergii (Stål, 1878)	Dichroplini	DQ083467	DQ083448	Colombo et al. (2005)
Ronderosia forcipatus (Rehn, 1918)	Dichroplini	DQ083468	DQ083449	Colombo et al. (2005)
Scotussa daguerrei Liebermann, 1947	Dichroplini	DQ083469	DQ083450	Colombo et al. (2005)
Jivarus americanus Giglio-Tos, 1898	Jivarini	DQ389233	DQ389220	Chapco (2006)
Jivarus ecuadorica (Hebard, 1924)	Jivarini	DQ389232	DQ389218	Chapco (2006)
Nahuelia rubriventris Liebermann, 1942	Jivarini	AF539840	AF539838	Amedegnato et al. (2003)
Hypochlora alba (Dodge, 1876)	Melanoplini	AF260548	AF260545	Chapco et al. (2001)
Melanoplus bivittatus (Say, 1825)	Melanoplini	KJ531424	KJ531434	This study
Melanoplus bruneri Scudder, 1897	Melanoplini	AF317189	AF145556	Chapco and Litzenberger (2002); Chapco et al. (1999)
Melanoplus differentialis (Thomas, 1865)	Melanoplini	KJ531425	KJ531435	This study
Melanoplus mexicanus (Saussure, 1861)	Melanoplini	KJ531426	KJ531436	This study
Phoetaliotes nebrascensis (Thomas, 1872)	Melanoplini	KJ531428	KJ531438	This study
Anapodisma miramae Dovnar-Zapolskij, 1932	Podismini	AY004204	AY004202	Litzenberger and Chapco (2001)
Bradynotes obesa (Thomas, 1872)	Podismini	KJ531419	KJ531429	This study
Fruhstorferiola omei (Rehn & Rehn, 1939)	Podismini	N/A	DQ099586	Ma and Huang (unpublished)
Kingdonella sp.	Podismini	N/A	GQ421444	Zhang et al. (2011)
Ognevia longipennis (Shiraki, 1910)	Podismini	EU914848	EU914848	Zhang and Huang (unpublished)
Pedopodisma sp.	Podismini	N/A	DQ099593	Ma and Huang (unpublished)
Prumna arctica (Zhang & Jin, 1985)	Podismini	GU294758	GU294758	Sun et al. (2010)
Sinopodisma tsinlingensis Zheng, 1974	Podismini	N/A	DQ099591	Ma and Huang (unpublished)
Apacris rubrithorax Ronderos, 1976	Unplaced	AF539848	AF539846	Amedegnato et al. (2003)
Neopedies brunneri (Giglio-Tos, 1894)	Unplaced	DQ389230	DQ389216	Chapco (2006)
Neopedies noroestensis Ronderos, 1991	Unplaced	AF539852	AF539850	Amedegnato et al. (2003)
Pseudoscopas nigrigena (Rehn, 1913)	Unplaced	AY014349	AY014347	Amedegnato et al. (2003)

Results

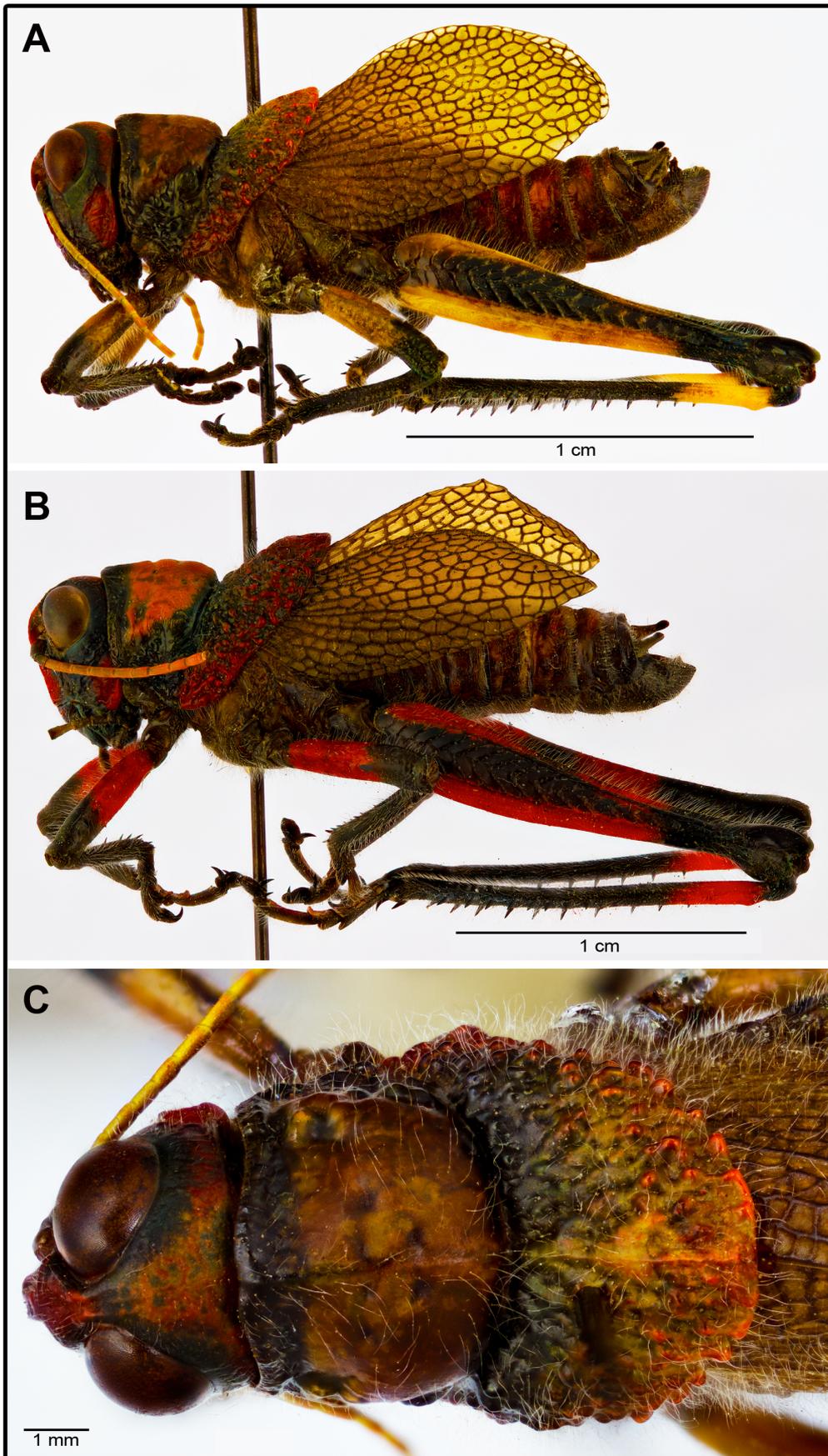### Taxonomic description

Subfamily Melanoplinae Scudder, 1897

Tribe Dactylotini Scudder, 1897

### *Liladownsia* gen. nov. Fontana, Mariño-Pérez, Woller & Song

http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:463900

Type species: *Liladownsia fraile* **sp. nov.** Fontana, Mariño-Pérez, Woller & Song, here designated.
http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:463901
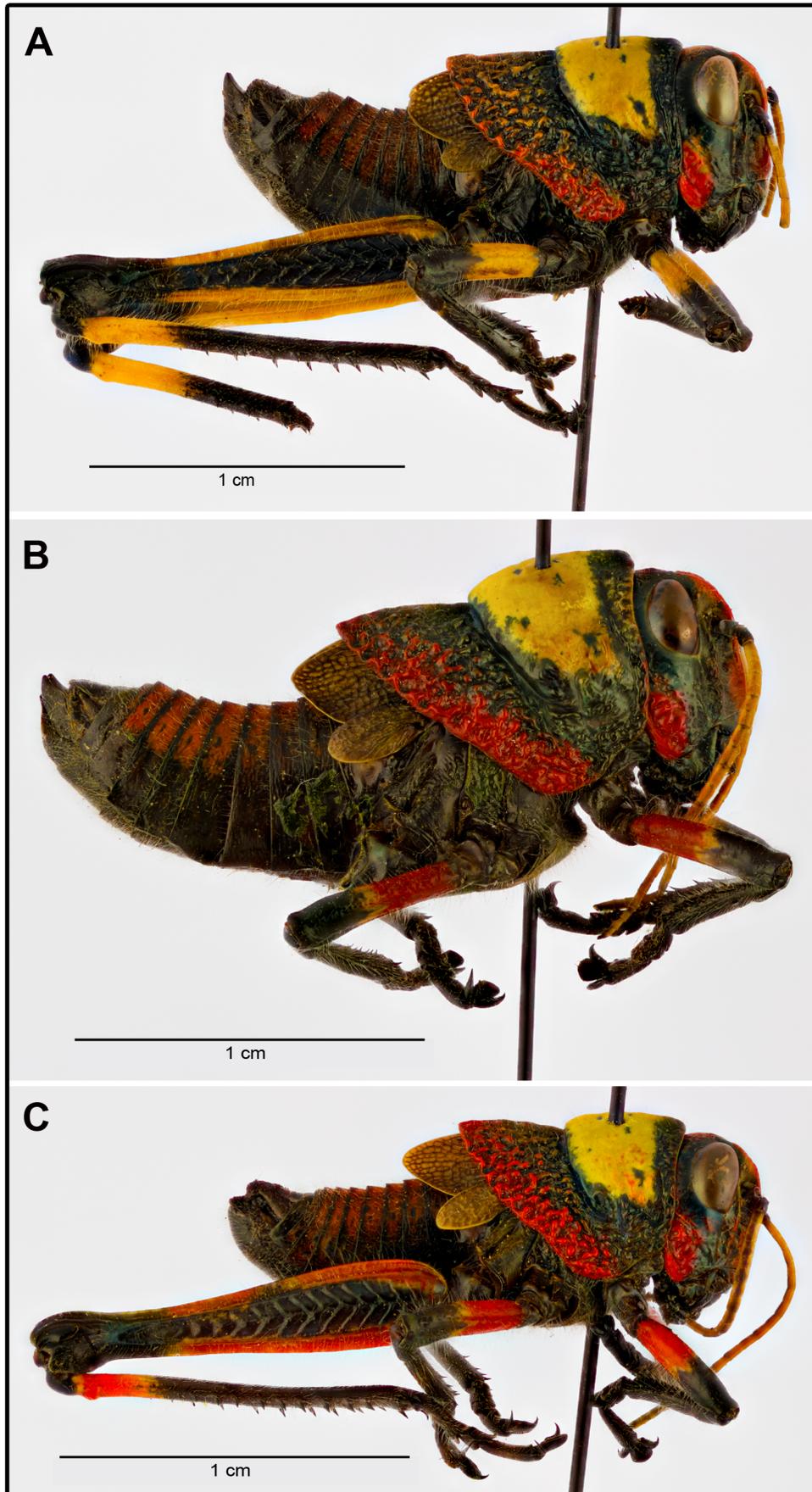
FIGURE 2. Photographs of both known color forms of male specimens of *Liladownsia fraile* **gen. nov. sp. nov.**: **A.** Holotype; lighter color form. **B.** Paratype; darker color form. **C.** Thoracic view of the holotype.
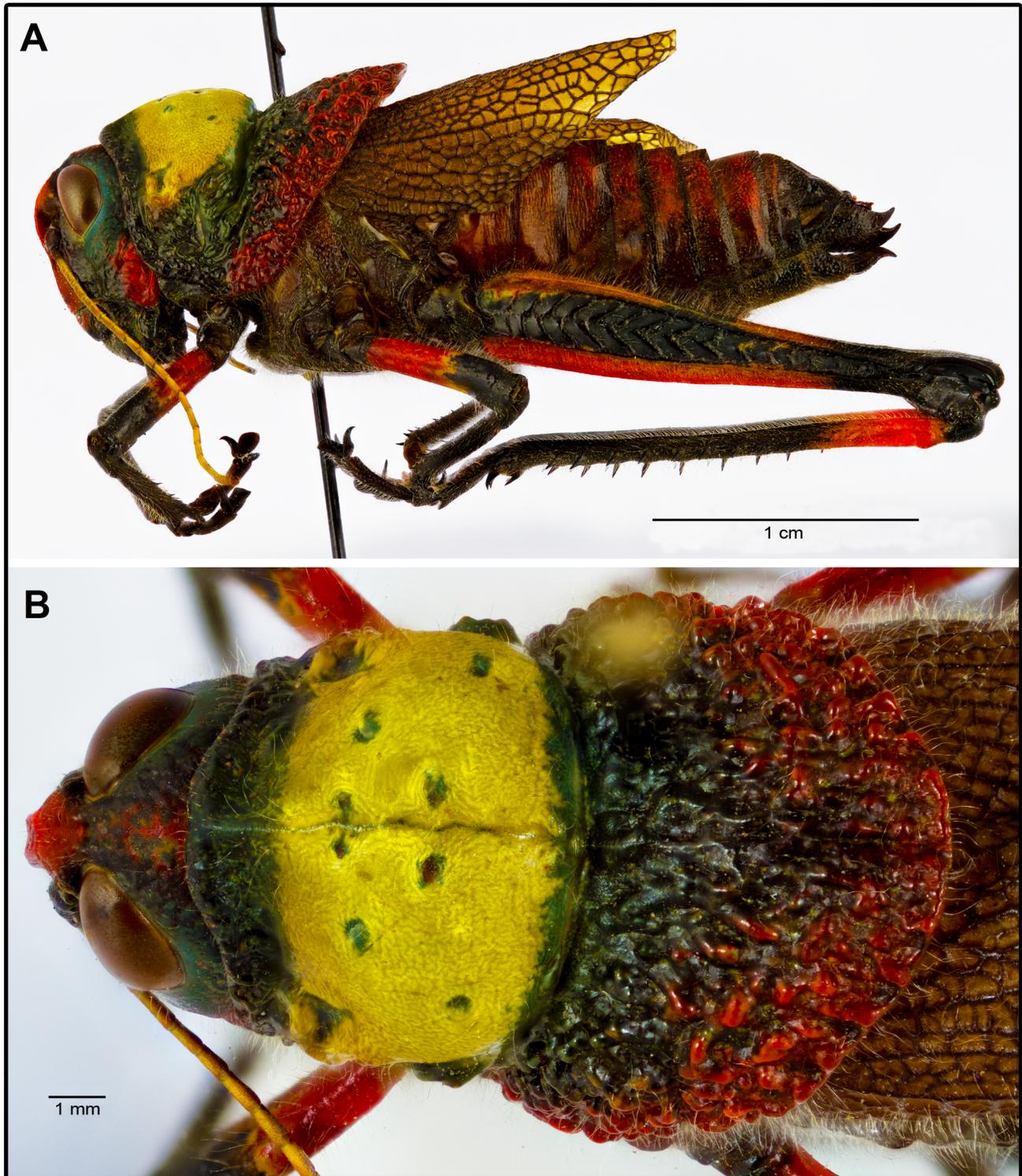
FIGURE 3. Photographs of the known color form of an adult female specimen (paratype) of *Liladownsia fraile* **gen. nov. sp. nov.**: **A.** Lateral view. **B.** Thoracic view.

General. Body stout; legs quite thin; bright colors with mixed combination of blackish-steel blue, red, yellow, and sometimes orange. Body surface heavily pubescent (Figs. 2A&B, 3A, and 4). Extremely peculiar pronotum shape with raised, swollen, and smooth prozona, and extremely rugose metazona. Sulcus very deep, lateral carinae absent (Figs. 2C and 3B). Tegmina brachypterous and tectiform, widely oval, densely-reticulated, covering 3/4 of male and 3/5 of female abdomen; overlapping partially on dorsum (Figs. 2A&B and 3A).

FIGURE 4. Photographs of known color forms of nymphal specimens of *Liladownsia fraile* **gen. nov. sp. nov.**: **A.** Female; lighter color form. **B.** Female; darker color form. **C.** Male; darker color form.
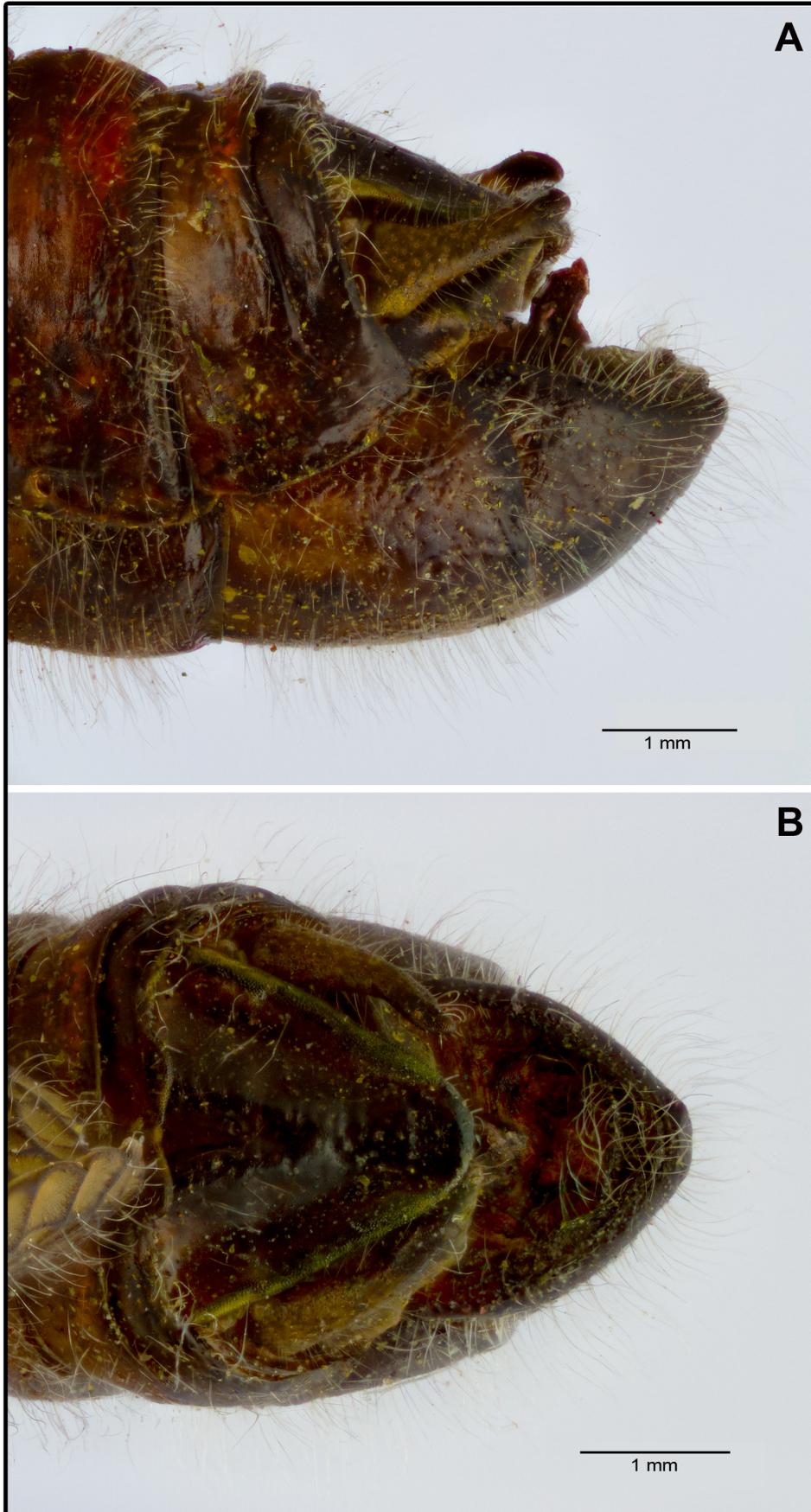
FIGURE 5. Close–up photographs of the external genitalia of the male holotype of *Liladownsia fraile* **gen. nov. sp. nov.**: **A.** Lateral view. **B.** Dorsal view.
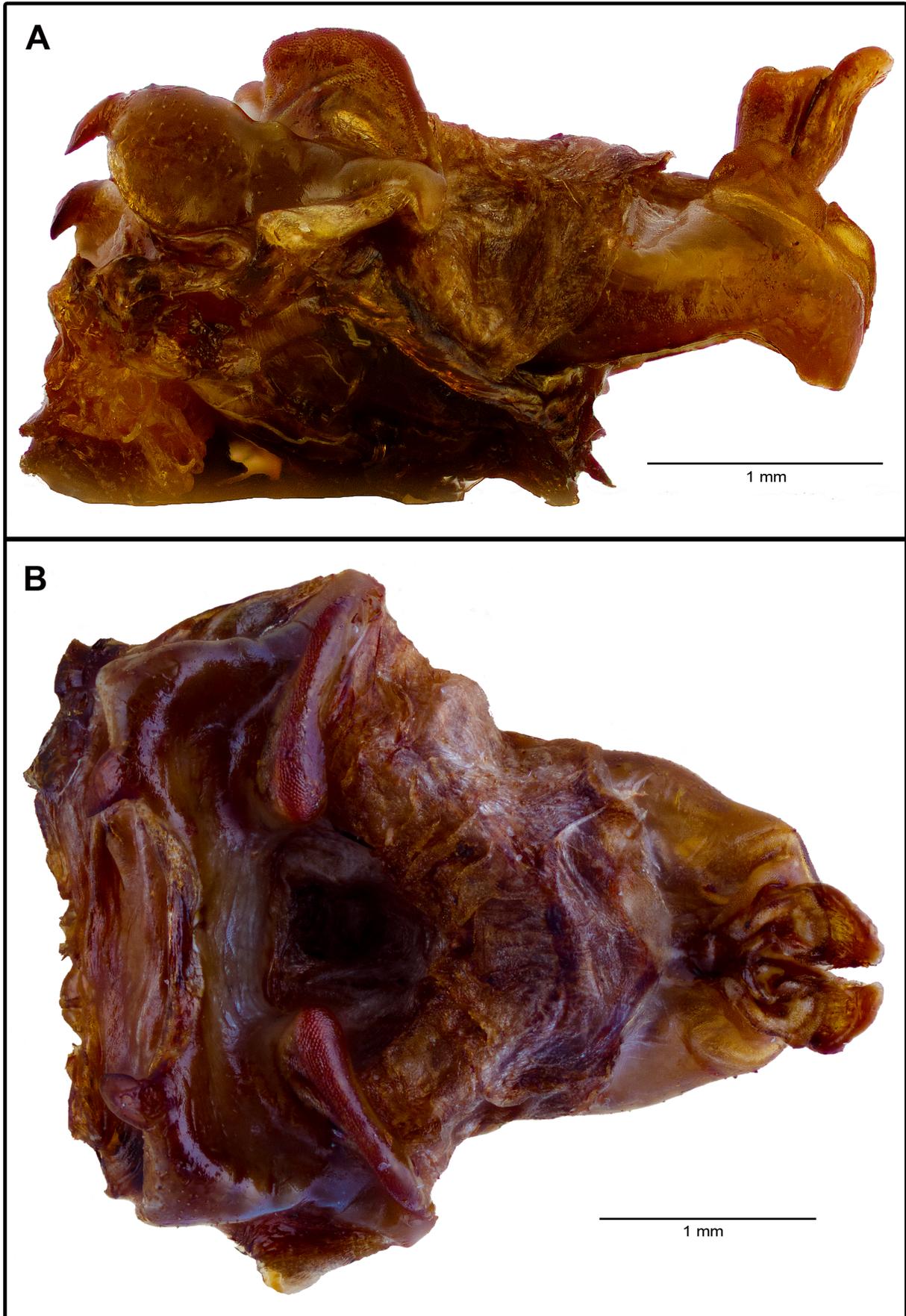
FIGURE 6. Photographs of the internal phallic complex of a male paratype of *Liladownsia fraile* **gen. nov. sp. nov.**: **A.** Lateral view. **B.** Dorsal view.
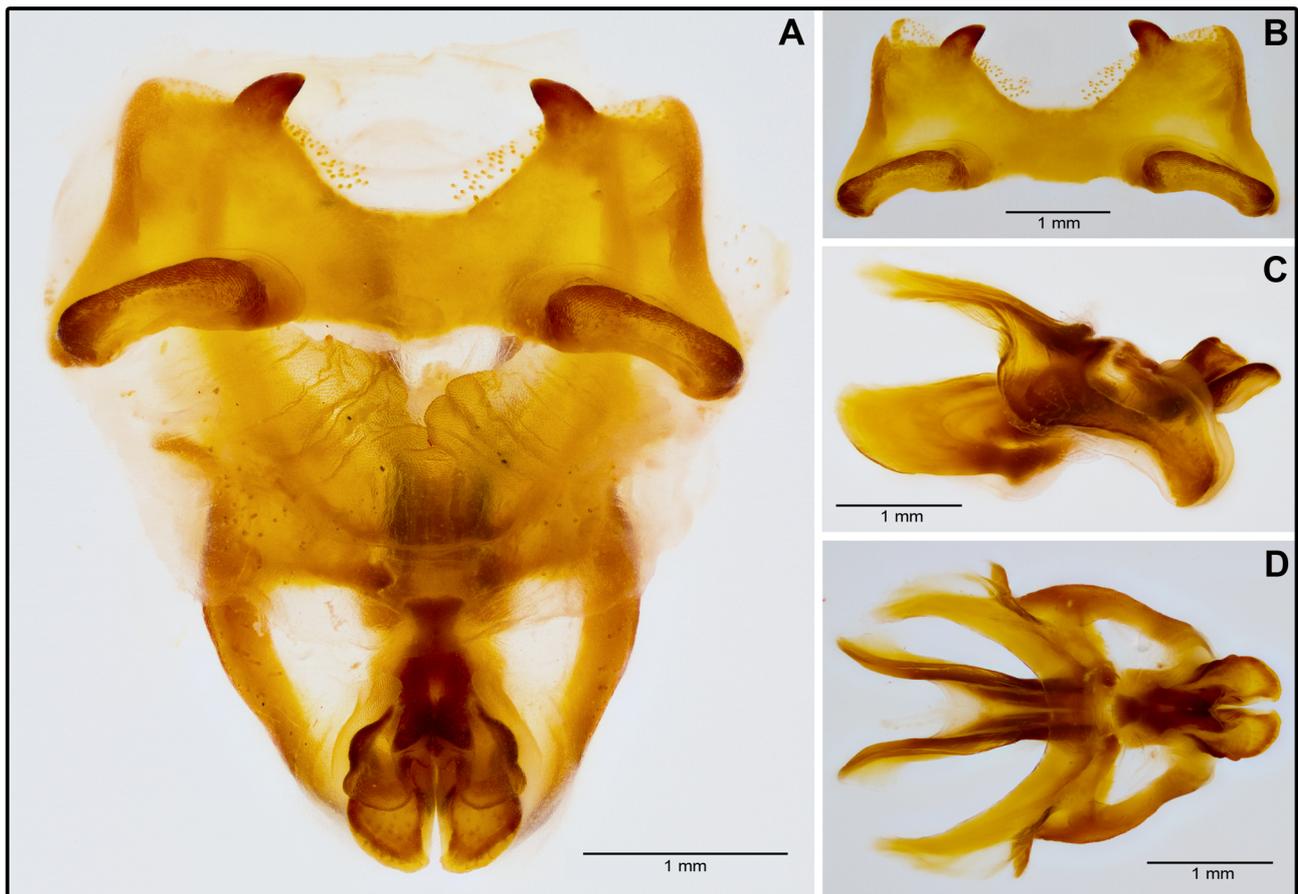
FIGURE 7. Photographs of the KOH-cleared internal phallic complex of a male paratype of *Liladownsia fraile* **gen. nov. sp. nov.**: **A.** Intact phallic complex. **B.** Epiphallus. **C.** Lateral view of the ecto/endophallus. **D.** Dorsal view of the ecto/endophallus.

Etymology. We are pleased to name the new genus in honor of the Mexican singer-songwriter and Grammy Award-winner, Ana Lila Downs Sánchez, whose stage name is Lila Downs. This taxon is dedicated to her for a number of reasons, such as the fact that she was born in the vicinity of the type locality and because she incorporates several indigenous tongues from Mexico into her musical style, including Mixteco and Zapoteco (the latter of which is spoken in the type locality). Additionally, Lila Downs has not only promoted the vast cultural diversity of Mexico worldwide via her music, but also through the use of bright colors, a staple of Mexican culture, and considering that this new genus is brightly-colored, we would like to recognize her efforts through the dedication of this new genus.

Diagnosis and Taxonomic affinity. Aside from its brilliant coloration, the shape and proportions of the respective parts of the body in *L. fraile* identify it as a unique grasshopper, one that is quite squat, relatively heavy, and also slow-moving, akin, in many ways, to the members of Romaleidae. A closer examination reveals the originality of the shape of the pronotum (Figs. 2C and 3B) (especially in females (Fig. 3 B)) and the frailty of the hind femora (Figs. 2A&B and 3A), a feature probably related to the slow and ponderous movements of this organism. Despite its superficial resemblance to a romaleid, the primary exterior aspect that makes this taxon more similar to some Dactylotini genera, like *Dactylotum* and *Perixerus*, is the short, highly-reticulated tegmina (Figs. 2A&B and 3A). In the genus *Dactylotum*, however, reticulation of the tegmina only exists in two dimensions with light color veins on a dark background. In *Perixerus*, reticulation is in the form of actual raised veins, which are either darker or similar in color to the tegmina. The tegmina of *L. fraile* exhibit a strong similarity to those of *Perixerus*, but are longer and clearly tectiform (Figs. 2A&B and 3A).

Other morphological characters that liken *L. fraile* to *Perixerus* are the dense hairs that cover the entire body (Figs. 2A&B and 3A) and the general structure of the internal genitalia of the males of each species (Figs. 6 and 7). There are, however, clear differences in these internal structures, such as the apical valves of the penis being far more sclerotized in *Liladownsia* compared to *Perixerus* (Figs. 6 and 7A,C, & D). Also, the fact that the apical

valves of the penis of *Perixerus*, in dorsal view, appear to emerge from a structure that is dilated and corrugated while, in *Liladownsia*, the general structure of the apical portion of the phallic complex appears to be more rounded and simple (Figs. 6B and 7A&D).

Liladownsia fraile sp. nov. Fontana, Mariño-Pérez, Woller & Song
http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:463901

Taxonomic description (of male except where specified). **General.** *Liladownsia fraile* is a medium-large showy grasshopper. Body is primarily colored with blackish-steel blue, yellow, red, and sometimes orange depending on color form (Figs. 2–4 and 10,11). Both sexes are very colorful, and are characterized by wrinkled teguments, reticulate tegmina, and diffuse hair on the body, which makes them appear almost silky (Figs. 2A&B, 3A, and 10). The shape of the pronotum (Figs. 2C and 3B) and hind femora is very peculiar. Prozona (especially in females) with a bulging appearance and almost smooth while metazona is markedly wrinkled and raised posteriorly. The overall look of the pronotum resembles the lowered hood of a monk/friar (*fraile* in Spanish) (Figs. 2–4 and 10). Hind femora are thin in comparison to body size and general body structure (Figs. 2A&B, 3A, and 10). Contrary to the generally more complicated structure of the overall exterior, the male genitalia are quite simple. The external genitalia do not have any special features with the cerci subconical, absent furcula, and the supra-genital plate subtriangular (Fig. 5). The internal phallic complex also lacks any peculiarities (Figs. 6 and 7).

Coloration. Two general color forms appear to exist across both sexes: a lighter color form with blackish-steel blue and yellow more dominant overall (Figs. 2A, 4A, 10B, and 11A&D) and a darker color form with blackish-steel blue, yellow, red, and sometimes orange more dominant overall (Figs. 2B, 3A, 4B&C, 10A, and 11 B,C,&E). Head blackish-steel blue with fastigium, vertex, frontal ridge, and cheeks red, yellow, or orange. Antennae yellow to orange with first two segments blackish (Figs. 2–4 and 10). Pronotum black on anterior margin, lateral sides of prozona, along and behind sulcus; prozona mainly red, orange, or yellow and metazona posteriorly red (Figs. 2C and 3B). Tegmina clear brown with blackish reticulation. Fore and middle femora red and/or yellow and blackish-blue steel apically. Fore and middle tibia blackish-blue steel, all tarsi blackish-blue steel. Hind femora with blackish medial area on external side and red or yellow-orange upper and lower marginal areas. Apical portion of hind femora and knees entirely blackish-blue steel; hind tibia blackish-blue steel with reddish-yellow or yellow basal portion. Thorax brownish; abdomen reddish brown and terminalia in both sexes blackish (Figs. 2A&B, 3A, and 10).

Head. Head short, fastigium projecting moderately from eyes, widely- rounded when viewed laterally; frontal ridge well-marked with almost parallel lateral keels. Antennae filiform, semi-flattened with parallel sides; about 24 segments, median segments about 2.5 times as long as wide. Eyes scarcely prominent in females, not spaced very far apart; in males, more prominent, larger, and closer together. Prosternal process cylindro-conical, slightly bent posteriorly (Figs. 2A&B, 3A, and 10).

Pronotum and wings. Pronotum with swollen prozona, more pronounced in female; metazona arising posteriorly from sulcus, posterior margin widely rounded. Prozona as long as metazona in both sexes. Aside from some setae, prozona smooth with some scattered indentations. Metazona wrinkled and highly rugose. Sulcus very deep; median carinae present on prozona, but more prominent anteriorly, and also present on metazona (Figs. 2C and 3B). Tegmina brachypterous, tectiform, and widely oval; homogeneously reticulated; longer than pronotum and reaching midpoint of hind femora in both sexes; partially overlapping on dorsum in both sexes. Hind wings vestigial and more or less half the length of the tegmina (Figs. 2A&B, 3A, and 10).

Legs. Fore tibia with 3–5 spines on both inner and outer lower margins. Middle tibia with 3–5 spines on both outer and inner lower margins. Upper margins of hind tibia with 11–12 spines on outer side and 10–11 on inner side. Hind femora thin in relation to body size: 5.45 times as long as high in males and 6.5 times in females (Figs. 2A&B, 3A, and 10).

Terminalia. Male. Furcula almost absent; only two vestigial protuberances present. Supra-anal plate subtriangular, with rounded apex and slightly convex lateral sides. Median impression and median keels hardly developed (Fig. 5B). Cerci subtriangular, gradually tapering from basal part; apex moderately flattened and rounded (Fig. 5). When viewed laterally (Fig. 5A), subgenital plate resembling 1/4 of a sphere, hemielliptical from above; apex truncated and barely concave.
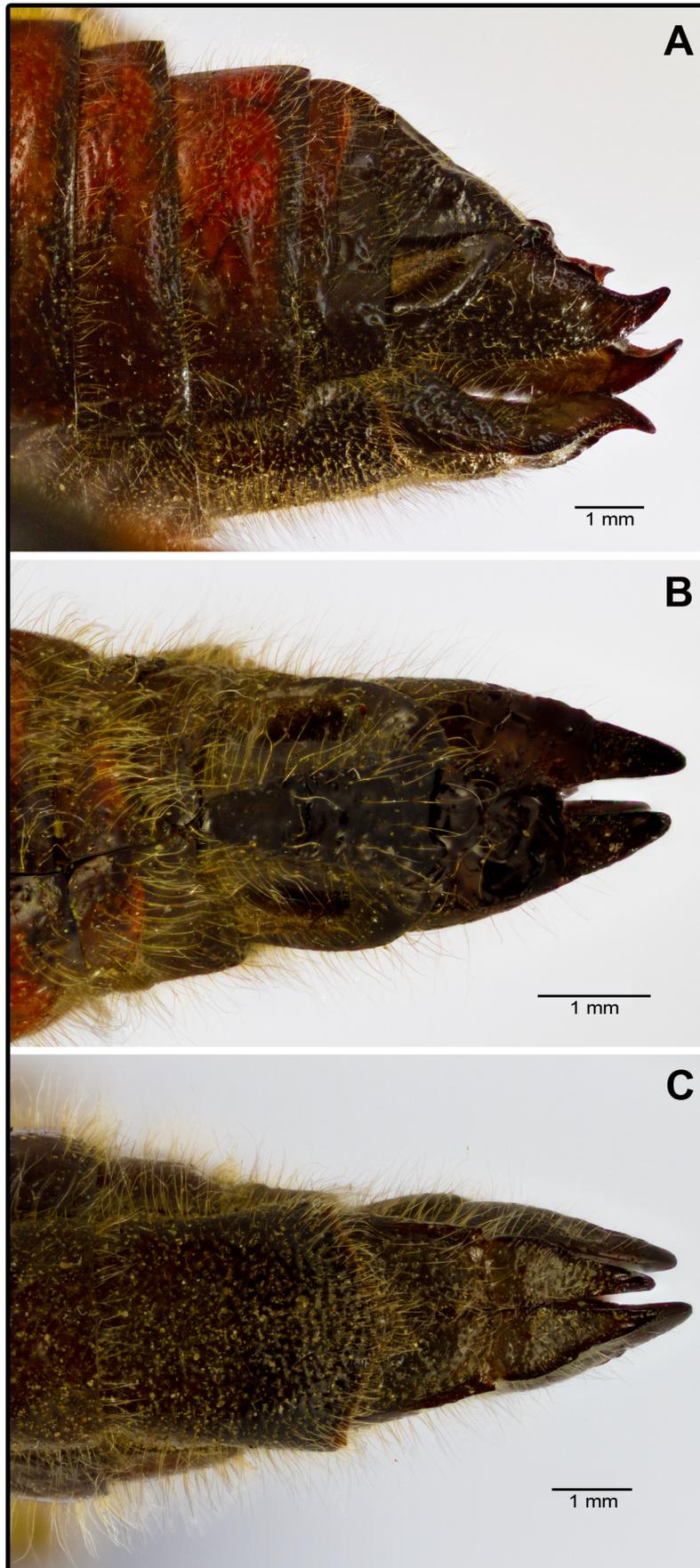
FIGURE 8. Close–up photographs of the external genitalia of a female paratype specimen of *Liladownsia fraile* **gen. nov. sp. nov.**: **A.** Lateral view. **B.** Dorsal view. **C.** Ventral view.

Female. Supra-anal plate subtriangular, apex rounded with concave lateral sides (Fig. 8B). Dorsal valvae of the ovipositor (Fig. 8A&B) almost twice as tall as ventral ones (Fig. 8A&C). Lower margin of ventral valvae uniformly sinuous without teeth or hooks (Fig. 8C). Subgenital plate with scarcely projecting subtriangular posterior margin and with concave lateral sides (Fig. 8C).

Phallic complex. Epiphallus well-sclerotized; anterior margin of bridge concave; anterior spines short, conical, directed inwards and downwards, arched lophi with superior margin almost straight (Figs. 6 and 7A&B); well-elevated over anterior processes from a lateral viewpoint (Fig. 6A). Valvae of penis short, subequal in length. Dorsal valvae subtrapezoidal; ventral valvae longer, transversally flattened (Figs. 6 and 7A,C,&D).

Etymology. This specific epithet comes from the common name used for this species by the local people of the type locality. In Spanish, "fraile" translates to monk or friar, referring to the swollen prozona, which resembles the hood of a monk's robe. For the same reason some locals also refer to it as "chapulín de capucho" (hooded grasshopper). Based on this, we propose the following common name for this amazing grasshopper: Lila Downs' friar grasshopper.

Male measurements (in mm) (n=4). Body length 24.09–29.49 (27.70 ± 2.49); pronotum length 7.15–7.88 (7.44 ± 0.35); prozona length 3.79–4.08 (3.97 ± 0.13); metazona length 3.21–3.79 (3.46 ± 0.24); hind femur length 13.87–15.33 (14.78 ± 0.69) and tegmina length 7.30–11.68 (10.18 ± 2.03).

Female measurements (in mm) (n=5). Body length 32.70–41.46 (37.23 ± 3.85); pronotum length 10.07–12.84 (11.53 ± 1.15); prozona length 5.54–6.71 (6.1 ± 0.44); metazona length 4.52–6.27 (5.4 ± 0.74); hind femur length 18.39–20.14 (19.27 ± 0.67) and tegmina length 10.07–12.99 (11.18 ± 1.19).

Holotype. Male. Mexico, Oaxaca, Near Suchixtepec. 26 km after San José del Pacífico. 16.0779500, -96.4945833 (WGS84). 2,321 m.a.s.l., edge of a pine forest. 10-XII-2011. (Paolo Fontana, Ricardo Mariño-Pérez, Derek A. Woller, and Paola Tirello) (Fig. 1B-1).

Additional specimens examined. Eight paratypes (three males and five females) with the same collecting information as the holotype (Fig. 1B-1); two paratypes (females): Mexico, Oaxaca, On Km 165, near Suchixtepec. 29 km after San José del Pacífico. 16.0586944, -96.4996667 (WGS84), 2127 m.a.s.l., pine-oak forest. 12-XII-2013. (Paolo Fontana, Ricardo Mariño-Pérez and Salomón Sanabria-Urbán) (Fig. 1C-2); two paratypes (one male and one female: 1.3 km Northwest of Suchixtepec. 16.104083, -96.471722 (WGS84). 2,663 m.a.s.l., pine-oak forest. 12-XII-2013. (Paolo Fontana, Ricardo Mariño-Pérez and Salomón Sanabria-Urbán) (Fig. 1C-3); two paratypes (one male and one female: 6 km Northeast of Suchixtepec at Rio Molino, Sierra del Sur, 2,591 m.a.s.l., 5-V-1962. (J. Stuart Rowley). Also, some nymphs were collected and examined from the holotype locality (Fig. 1C-1) and the locality 29 km after San José del Pacífico (Fig. 1C-2).

Type depository. Male holotype and five paratypes (one male and four females) at UCFC, five paratypes (two males and three females) at CNIN-UNAM, two paratypes (one male and one female) at MNHN, and two paratypes (one male and one female) at CPF.

Ecology. The habitat of the localities is in the boundaries of oak, pine-oak, and pine forests (1,900–3,000 m.a.s.l.) (Fig. 9C) within the southern parts of the Sierra Madre del Sur mountain range in Oaxaca, Mexico (Fig. 1). These vegetation types have been observed on diverse classes of rock: igneous, sedimentary and metamorphic, and do not tolerate draining deficiencies. Associated soil is of moderate acidity (pH 5.5–6.5) with abundant litter and organic matter in the superficial horizon and often in deeper horizons as well. Soil texture varies from clay to sand and the color is typically red, although sometimes it is also possible to find yellow, black, brown, or grey. According to the Köppen–Geiger climate classification system, the climate of the region in which these forests can be found is primarily *Aw* (equatorial, winter dry), but also: *Am* (equatorial, monsoonal), *Bsh* (arid, summer dry, hot arid), *Cfa* (warm temperate, fully humid, hot summer), *Cfb* (warm temperate, fully humid, warm summer), *Cwa* (warm temperate, winter dry, hot summer), and *Cwb* (warm temperate, winter dry, warm summer) (García, 1973; Kottek *et al.*, 2006). The mean precipitation per year ranges from 350 to over 2,000 mm, but is usually in the range of 600–1,200 mm. Temperatures vary from 10 to 26° C, but are quite often in the range of 12 to 20° C (Rzedowski, 1981).

The forests are comprised of various species of oaks (*Quercus conspersa*, *Q. laeta*, *Q. laurina*, *Q. rugosa,* and *Q. ocoteifolia* among others in addition to nunemrous species of pines (*Pinus)*, hornbeams (*Carpinus)*, *Styrax, and Ternstroemia*. All of these trees can range from 4 to 20 m in height, sometimes up to 30 m. The shrubby layer is comprised of the following genera: *Bejaria, Comarostaphylis, Gaultheria, Lyonia, Litsea, Myrica, Calliandra,* and *Symplocos* while herbaceous layer contains *Salvia, Arenaria, Lobelia,* and *Lupinus*. Climbing plants, epiphytes and rock-growers, are also quite common in these types of forests (Rzedowski, 1981).

During both collecting expeditions (2011 and 2013) we found adults (Figs. 2, 3, and 10), but also nymphs (Figs. 4 and 11) representing almost all developmental stages (Fig. 11), indicating that this species persists, at least, until the end of January, throughout some of the coldest times of the year in Mexico, which suggests, based on its size and overlapping presence of almost all life stages, that this grasshopper has a lifespan lasting several months. This idea was seemingly confirmed by the fact that the two adult specimens discovered in MNHN were collected in May. According to multiple conversations with local residents, this grasshopper is abundant and easy to find throughout the area. Based on the currently known localities (Fig. 1), it is possible that the geographic range of this grasshopper is confined to the southern parts of the Sierra Madre del Sur mountain range (Fig. 1C). Additionally, in 2013, a male and female were observed copulating in the typical manner of other Melanoplinae (Otte, 1970) while the pair was hanging from a shrubby plant in the Lamiaceae family about two meters from ground level.

In 2011, both nymph and adult specimens were collected on a single (possible) host plant, *Salvia elegans* (Pineapple sage) (Fig. 9A&B), which is also part of Lamiaceae, possesses showy red flowers, and is native to the pine-oak forests (Fig. 9C) of Mexico and Guatemala. During the 2013 expedition we collected further specimens of the new species in the same kind of habitat, but on a wider range of plants, mostly members of Lamiaceae as well.

Phylogenetic analysis. Our matrix based on COI and COII consisted of 2,289 aligned nucleotides and 42 taxa. The PartitionFinder analysis found that the best-fit data-partitioning scheme was partitioning the alignment into two subsets by treating the first codon position of COI and the third codon position as a single partition with the remainders combined as the second partition. For the Bayesian analysis, PartitionFinder recommended GTR+G as the best model of nucleotide substitution for the first partition, and GTR+I+G for the second partition.
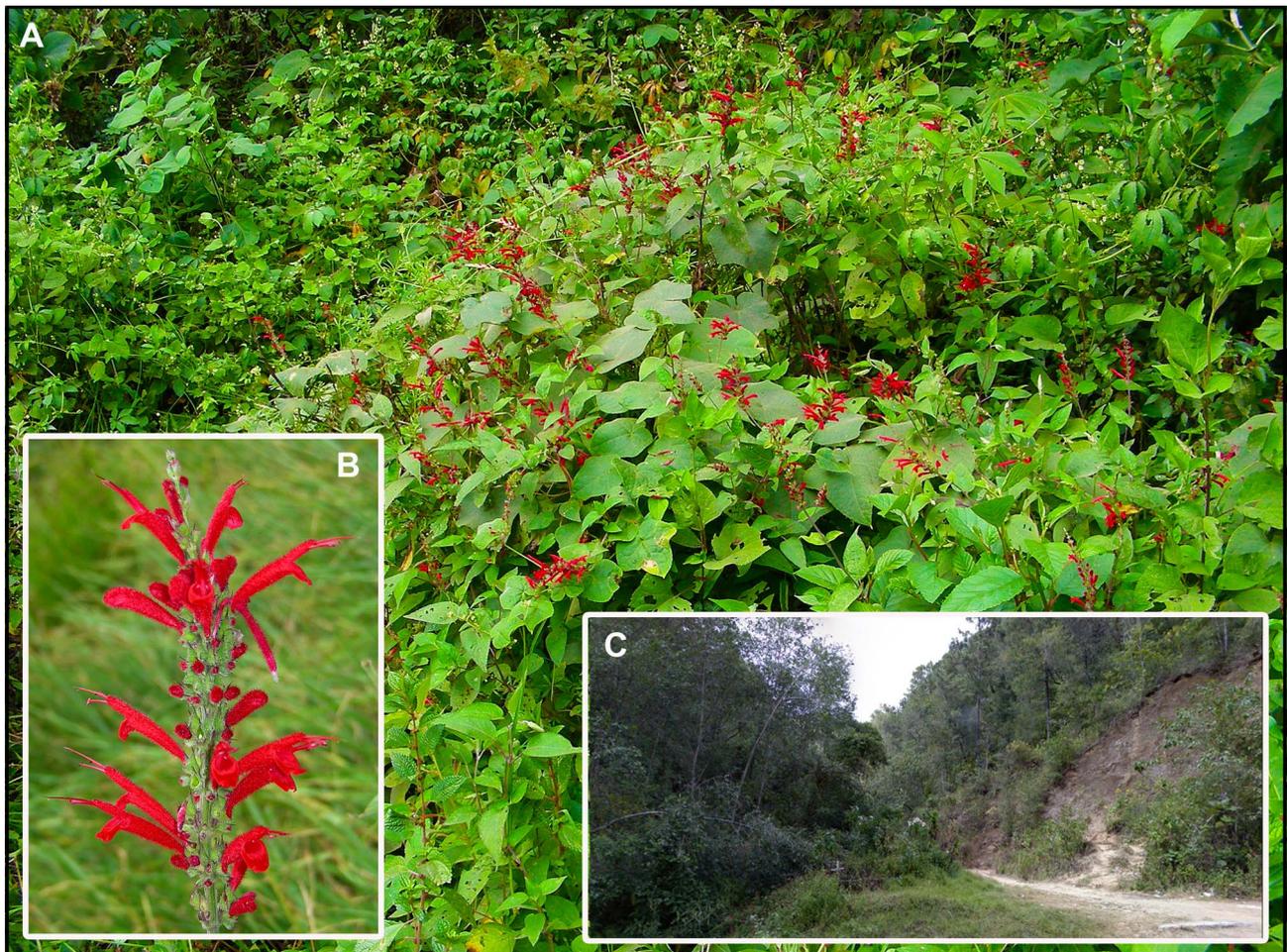
FIGURE 9. Photograph of the holotype locality for *Liladownsia fraile* **gen. nov. sp. nov.** at the edge of a pine forest in Oaxaca, Mexico, 26 km after San José del Pacífico: **A.** Large stand of the possible host plant, *Salvia elegans* (Pineapple sage). **B.** Close-up view of the plant and its brilliant red flowers. **C.** Full view of locality just off Highway 175.

FIGURE 10. Field photographs of both sexes of *Liladownsia fraile* **gen. nov. sp. nov.** from the type locality in Oaxaca, Mexico: **A.** Female. **B.** Male.

FIGURE 11. Field photographs of nymphs of *Liladownsia fraile* **gen. nov. sp. nov.** from across the three known localites in Oaxaca, Mexico: **A.** Most likely 2nd instar; lighter color form. **B.** Most likely 3rd instar; darker color form. **C.** Most likely 4th instar; darker color form. **D.** Most likely 5th instar; lighter color form. E. Most likely 5th instar; darker color form.

Both ML and Bayesian analyses recovered nearly identical topologies and we present the ML phylogram for discussion (Fig. 12). Nodal supports varied from weak to strong depending on the nodes. Monophyletic groups were recovered for the subfamily Melanoplinae overall as well as for four of the five included tribes: Jivarini, Podismini, Melanoplini, and Dichroplini. The analysis did not recover monophyly for Dactylotini because *H. viridis* was placed basally to Melanoplini. Additionally, the remaining three dactylotine taxa that were included, *D. bicolor bicolor*, *P. squamipennis*, and *L. fraile*, formed a clade and a sister relationship between *P. squamipennis*

and *L. fraile*. was robustly recovered. Based on this phylogenetic relationship, as well as the previous findings (Chapco 2006 and Chintauan-Marquier *et al.* 2011), we find that *Hesperotettix* does not belong to Dactylotini, but to Melanoplini. Thus, at the tribal level, the following relationships were recovered: ((Jivarini, ((Podismini, (Dactylotini, Melanoplini)), Dichroplini)).
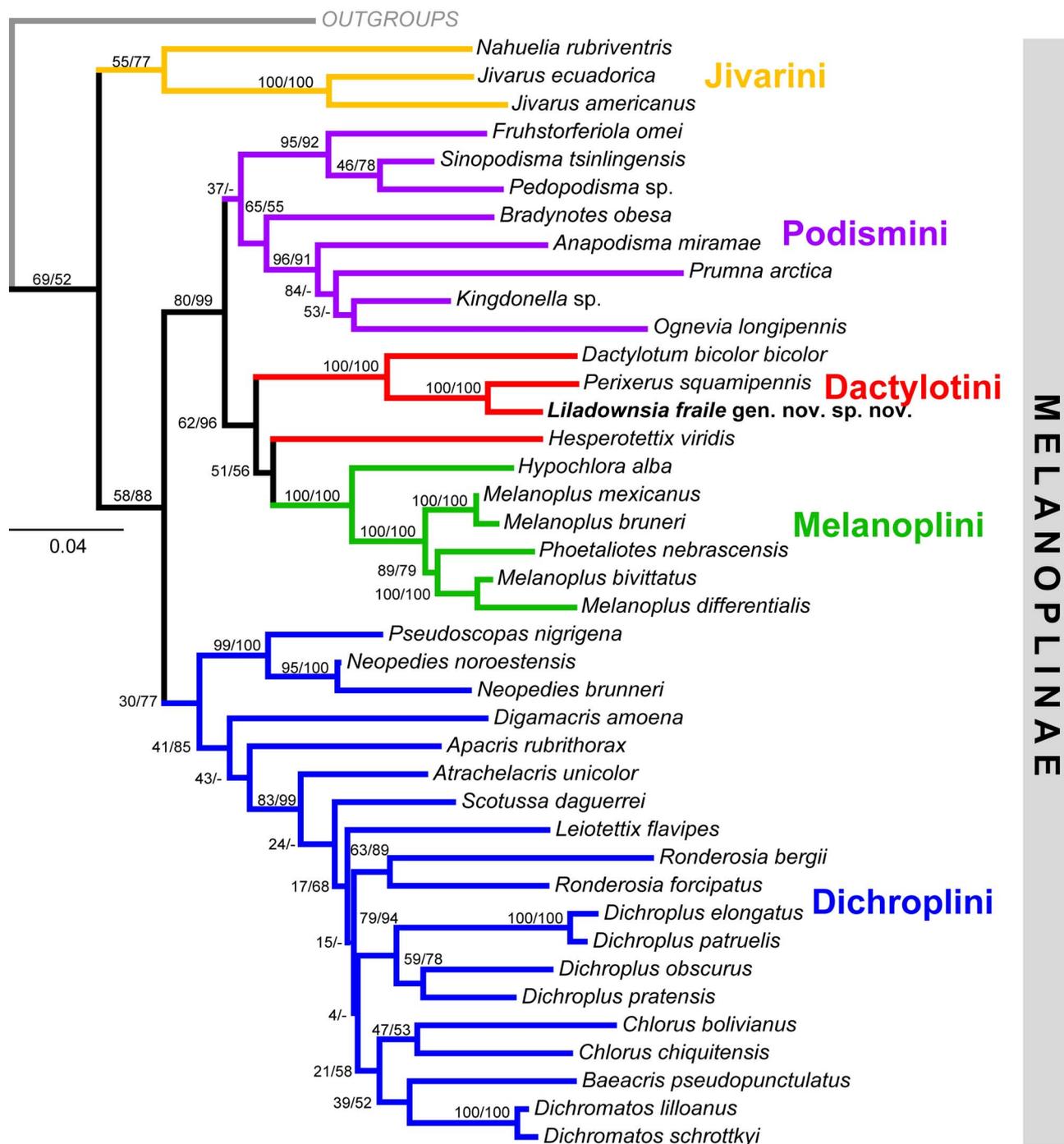
FIGURE 12. A phylogeny of Melanoplinae based on COI and COII genes. Shown here is the ML phylogram. Bootstrap support values/posterior probability values are shown on each node. Branches are color-coded by tribe and *Liladownsia fraile* **gen. nov. sp. nov.** is in bold.

Discussion

In this study, we have described a new grasshopper genus that is both colorful and charismatic from a relatively well-sampled region in Mexico. Although it is new to science, *L. fraile* is quite familiar to the local people who call

it "fraile" and "chapulín de capucho." Furthermore, the local people know much about its relative abundance, phenology, and specific microhabitat, which demonstrates the need to gather local knowledge when documenting biodiversity. Along the same lines, collaborative efforts between scientific institutions is also highly important; for example, the material from MNHN has resided there since 1962 and was enough to describe the new species, but obviously this never occurred. One possible solution is to increase the advertising, perhaps through the use of digital photography and the internet, of the myriad of interesting, yet unnamed, specimens housed within collections such as these as it can be crucial on their journey to becoming recognized by taxonomists as legitimate entities.

Based on our field observations and the information provided by the local people, *L. fraile* appears to be associated with the pineapple sage, *Salvia elegans* (Fig. 9A&B), both as nymphs and adults. However, it is not clear if the grasshopper is solely subsisting on this plant or if it simply has a preference for the plant, being polyphagous otherwise, like almost all acridids. Strict monophagy in grasshoppers is very rare and only known from two cases: *Schistocerca ceratiola* Hubbell & Walker, 1928, which solely subsists on Florida-rosemary (*Ceratiola ericoides*) (Hubbell and Walker 1928) and *Bootettix argentatus* Bruner, 1889, which feeds on creosote bush (*Larrea tridentata*) (Otte and Joern, 1977). More common are narrowly oligophagous species (Otte and Joern 1977; Smith and Capinera, 2005) or species that show ontogenetic specialization (Sword and Dopman, 1999). In North America, *D. bicolor* (Dactylotini) is known to specialize on Wright's baccharis (*Baccharis wrightii*) as early instars (Ball, 1936), but acquire a much larger diet breadth as adults (Joern, 1979). Therefore, it may be possible that *L. fraile* demonstrates host-plant specialization, at least at some life stage, as the phenomenon is being increasingly shown to be the case for some grasshopper species (Sword and Chapman, 1994).

The bright coloration of *L. fraile* deserves some more comments, especially because the members of Dactylotini are quite colorful, in general. For example, the common name of *D. bicolor* is the "painted grasshopper" due to its visually-striking mixture of blue, red, yellow, orange, and black. *P. squamipennis* is comprised of an unusually-appealing combination of blue, purple, yellow, and orange while *L. fraile* is similarly interesting with its remarkable hues of blackish-steel blue, red, yellow, and sometimes orange (Figs. 2–4 and 10,11). The combination of these bright colorations and short wings is highly suggestive of the possibility that the members of Dactylotini might be displaying aposematic coloration. In fact, Isley (1938) showed that several bird species would completely avoid *D. bicolor pictum* after they attempted to feed on the grasshopper and found them to be inedible. Neal *et al.* (1994) similarly found that *D. bicolor variegatum* was clearly aposematic against diurnal avian predators.

Although it needs to be experimentally demonstrated whether *L. fraile* is also aposematic, it is quite likely given the fact that both nymphs and adults share similar striking coloration, which is highly visible against their background. Their potential host plant, *Salvia elegans* (Fig. 9A&B), is known to be used as a traditional Mexican medicine for treating anxiety and insomnia (Herrera-Ruiz *et al.*, 2006). If *L. fraile* can sequester potentially toxic or harmful secondary compounds from the plant (or from other Lamiaceae containing essential oils), then its obvious coloration might be serving as aposematic coloration. There is still very much to learn about the biology of this fascinating grasshopper.

The main purpose of including a molecular phylogenetic analysis in the present work is to definitively place *Liladownsia* within Melanoplinae. As hypothesized based on morphological similarities with *P. squamipennis*, we found that *L. fraile* and *P. squamipennis* form a very strong sister relationship (Fig. 12). This clade is, in turn, sister to *D. bicolor bicolor* with strong nodal supports. However, we also discovered that Dactylotini is paraphyletic because one if its genera, *Hesperotettix,* represented by the species *H. viridis*, demonstrated strong affinity to Melanoplini (Fig. 12). This pattern is congruent with what Chapco (2006) and Chintauan-Marquier *et al.* (2011) reported and possibly suggests that *Hesperotettix* should be removed from Dactylotini and placed into Melanoplini. As our study only includes four out of eleven genera currently placed within Dactylotini, the results of our analysis on the matter are not conclusive, but it opens up the possibility that Dactylotini needs future refinement.

Incidentally, our phylogenetic analysis represents the most comprehensive study of Melanoplinae to date, despite the fairly small taxon and character sampling (Table 1). Although nodal supports are generally poor across the backbone nodes, most likely due to the fact that mitochondrial genes tend to evolve rapidly (Avise *et al.* 1987), there are some clear and interesting patterns we can deduce from our resulting phylogeny (Fig. 12). For instance, it appears that the earliest diverging lineage is the South American endemic Jivarini. The basal position of this tribe has been consistently found by the previous studies and we confirm their findings. The remaining melanoplines are

divided into two major clades, one solely consisting of the South American endemic Dichroplini and the other consisting of the Eurasian Podismini, the North American Dactylotini, and the North American Melanoplini. Based on the biogeographic distribution of the tribes, we hypothesize that Melanoplinae originated in South America, progressively diversified northward to Central and North America with one clade eventually colonizing Eurasia. This pattern is consistent with the "out-of-South America" hypothesis, put forth by both Amédégnato *et al.* (2003) and Chapco (2006).

The monophyly of Dichroplini was supported by Chapco (2006), but Chintauan-Marquier *et al.* (2011) found the tribe to be paraphyletic because *Neopedies* did not group with other dichropline species. Our phylogeny is congruent with Chapco (2006) and finds Dichroplini to be monophyletic. According to OSF (Eades *et al.*, 2014), *Apacris*, *Neopedies*, and *Pseudoscopas* are currently unplaced, although the latter two were assigned to Dichroplini by Ronderos (1991). Chapco (2006) found *Apacris* was closely related to other valid dichropline species. Our study finds that all three genera are found near the base of the clade forming Dichroplini, supporting the notion that they probably need to be assigned to Dichroplini. Mayer (2004) erected a new tribe called Prumnini purely based on nomenclatural grounds, but the nominal genus of the tribe, *Prumna,* is placed robustly within Podismini in our phylogeny, which provides no support for the validity of the Prumnini tribe concept.

In terms of classification, *Perixerus* is currently a monotypic genus and *Liladownsia* also appears to be monotypic at this point in time. Although the two genera share much in common, they also, as mentioned earlier, possess some differences, hence why we did not describe the new taxon under *Perixerus*. One of the main reasons is that some of the morphological characters, outlined earlier, that define *Perixerus* as a genus do not adequately describe the new taxon. Furthermore, *P. squamipennis* is known to occur in Puebla, Veracruz (Roberts, 1947), and Oaxaca (Fontana *et al.*, 2008) while *L. fraile* has only yet been found in southern Oaxaca within a habitat in which *P. squamipennis* does not typically live. However, it should be mentioned that during the 2013 expedition both species were collected within the same locality (29 km past San José del Pacífico, Fig. 1C-2), meters from one another, and in grasses, not far from *Salvia elegans* (Fig. 9A&B). Also, it should be noted that the range of *P. squamipennis* appears to be far greater.

We have demonstrated the validity of describing a new genus of Dactylotini based on several lines of evidence. There is still much to learn about this intriguing insect, especially in terms of aposematism and host-plant association. We think that the people of Oaxaca will be pleased to learn that their beautiful endemic grasshopper, the friar grasshopper, is now named after their beautiful endemic musician, Lila Downs.

Acknowledgments

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