Article

A new discovery of a long-winged form of Mexican endemic grasshopper *Melanotettix dibelonius* Bruner, 1904 (Orthoptera: Acrididae: Gomphocerinae) and notes on wing polymorphism and geographic distribution

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Abstract

The species *Melanotettix dibelonius* Bruner, 1904 was previously recorded from Michoacán and Guerrero states in Mexico. This species is characterized by its tegmina, which are always shorter than head and pronotum together and sometimes shorter than the pronotum. After recent field expeditions (2015-2019) and an extensive review of museum specimens from the most important Orthoptera collections in Mexico and USA (291 specimens), we discovered a long-winged form of this species south of its previous known range, which effectively expanded its distribution range into Oaxaca state. We discuss some aspects regarding the patterns of geographic distribution and morphological variation among the long-winged and short-winged morphs. We conduct statistical analyses and observed that on average, the tegmina of long-winged individuals (both females and males) are slightly longer than twice the length of pronotum; whereas in short-winged individuals the tegmina are nearly as long or slightly longer than the length of the pronotum. Moreover, on average, females appear to have longer tegmina than males in both morphotypes. We provide photographic records of both forms live and mounted, the most comprehensive distribution map to date and a discussion of evolutionarily interesting patterns found in this species.

Key words. Gomphocerinae, short-winged form, long-winged form, extension range

Introduction

The genus *Melanotettix* Bruner, 1904 (Orthoptera: Acrididae: Gomphocerinae) is a monotypic genus, which was described by Bruner in 1904 based on a single short-winged male specimen collected in October in Acahuizotla, Guerrero, Mexico at 1000 masl. The overall body color of the type species, *M. dibelonius*, is coal-black, hence the name of the genus, and Bruner (1904, p. 91) speculated that "judging from its general obscure colouring if not a denizen of the forest, it must be confined in its distribution to shady localities." Later, Jago (1971) in a taxonomic review of the subfamily Gomphocerinae examined the specimens of *M. dibelonius* and commented that the species "seems to represent a brachypterous, flightless isolate of *Fenestra*, found in Mexico." However, the genus *Fenestra* Brunner von Wattenwyl, 1895 is confined to South America (Brazil, Paraguay, Argentina, Uruguay and Ecuador) and has never been reported from Mexico. Otte (1981) disregarded its resemblance with *Fenestra* and discussed its possible affinities with the *Aulocara* genus group, from which it differs by the absence of stridulatory teeth (pegs),

and decided to erect the tribe Melanotettigini to place this genus and species. *Melanotettix* was tentatively placed in Gomphocerinae because of its external morphology more resembling Gomphocerinae than Acridinae, and currently it is considered a member of Gomphocerinae (Cigliano et al., 2020). Otte (1981) made an extensive description of both males and females of *M. dibelonius*, and regarding tegmina, he stated that they are always shorter than head and pronotum together, and sometimes shorter than the pronotum. Concerning its distribution range, it was reported to be found in Michoacán and Guerrero States in Mexico.

During recent expeditions to southwestern Mexico (2015-2019), we found new populations that would expand the geographic range of *M. dibelonius*. We also found a previously unreported long-winged form ~100 km southeast of the species' known range. Here, we aim to update our knowledge on the geographic distribution of this species and describe a new form identified within the species based on a thorough examination of museum specimens and recently collected material. Moreover, we discuss some aspects regarding the patterns of geographic distribution and morphological variation among the morphotypes recognized within *M. dibelonius*.

Material and Methods

Acquisition of specimens

We use material of *M. dibelonius* collected during the last five years currently deposited in the Texas A&M University Insect Collection (TAMUIC) and Colección de Artrópodos de la Facultad de Estudios Superiores Iztacala, UNAM (CAFESI). Additionally, we conducted a thorough search of *M. dibelonius* specimens in the following collections: University of Michigan Museum of Zoology in Ann Arbor (UMMZ), Academy of Natural Sciences of Drexel University in Philadelphia (ANSP), California Academy of Sciences in San Francisco (CAS), and Colección de Insectos del Instituto de Biología, UNAM (CNIN-IBUNAM).

Acquisition of images

Images of mounted material were taken at the Song Laboratory of Insect Systematics and Evolution in the Department of Entomology at Texas A&M University using a Visionary Digital imaging system equipped with a Canon EOS 6D DSLR camera combined with a 100mm/65mm lens (the latter often coupled with a 2x magnifier) to take multiple images at different focal lengths. The resulting files were converted from RAW to TIFF format using Adobe Lightroom (v.4.4), stacked into a single composite image using Zerene Stacker (v.1.04), and then Adobe Photoshop CS6 Extended was used to adjust light levels, background coloration, and sharpness as needed. In addition, during our expeditions we were able to take images of live individuals of the species with the following cameras: Samsung Galaxy S8, Sony DSC HX60v and Nikon Coolpix B700.

Geographic distribution maps

In order to update the information about the geographic distribution of *M. dibelonius*, we used georeferenced data obtained from our own expeditions as well as from the collecting labels from the museum specimens. The majority of museum specimens were collected without georeferenced data, but fortunately the label information allowed us to determine coordinates with a high level of accuracy. In most cases, as usual with grasshopper expeditions, the localities were next to roads and provided altitude data that matched the altitude information associated with the coordinates. We used the program QGIS 2.18 to visualize all obtained georeferenced data and for generating a geographic distribution map of *M. dibelonius* morphotypes.

Morphological analysis

We used the previous taxonomic studies in the species (Bruner, 1904; Otte, 1981) to ensure taxonomic identification

of the analyzed specimens, as well as to investigate if morphological traits other than wing length were different among the identified morphs. In addition, we measured three external traits from the specimens of both morphotypes (LW: long-winged; SW: short-winged) of *M. dibelonius*: dorsal length of pronotum (PnL), length of hind femora from the base to the apex of the knee (HfL), and length of tegmina along the main vein from its base to its apex, (TgL). The measurements of PnL and TgL are commonly considered as proxies of body size in grasshoppers (e.g. Sanabria-Urbán et al., 2015) and we considered TgL as a proxy of wing length because we observed that the apex of the wings always reached the tegmina apex. Measurements were taken by using a digital calliper (Mitutoyo Corp., Tokyo, Japan). Moreover, we also estimated the proportion of wing size within each sex and morphotype, by dividing the TgL over the PnL. We averaged the values of these three morphological traits considering the total number of individuals per sex and morph.

We used these measurements to analyze if females and males differed in wing size within each morphotype and if the body size of both sexes were different between the two morphotypes. For these analyses, we $\log_{10}$-transformed all measurements to improve linear fits. We observed a positive and significant correlation between wing length and body size in both morphotypes (correlation between TgL and PnL: LW morph: $R^2 = 0.56$, *d.f.* = 35, $p = 0.0001$; SW morph $R^2 = 0.94$; *d.f.* = 45; $p = 0.0001$; correlation between TgL and HfL: LW morph: $R^2 = 0.91$, *d.f.* = 35, $p = 0.0001$; SW morph $R^2 = 0.89$; *d.f.* = 45; $p = 0.0001$). Therefore, to evaluate the effect of body size on wing size, we used the residuals of these two regressions (TgL vs PnL and TgL vs HfL) for analyzing the differences in wing size between the sexes in both morphotypes by conducting separate two-way analysis of variance (ANOVA), one considering the PnL and the other considering the HfL. To test if there were differences in body size between the two morphotypes in both females and males, we also conducted two-way ANOVA, one using the PnL and the other using the HfL. In all ANOVA, we specified as factors the sex, the morph and their interaction. All analyzes were conducted on the program JMP v15 (SAS Corp).

Examined material

UMMZ (102 specimens). **Short-winged form. MEXICO:** Michoacán, 3 rd. mi. SW. Arteaga church (0.1 mi E. Hwy. 37) (2460 ft) 3-XI-1974, T.J. & J.W. Cohn #122 (9♂; 7♀). Michoacán, 7.2 mi NE Playa Azul (on hwy 37) 2.8 mi La Mira Jct (700 ft) 6-XI-1974, T.J. & J.W. Cohn #123 (6♂; 1♀). Michoacán, 7.8 mi NE Playa Azul, 2-XI-1977, T.J. & J.W. Cohn #144 (2♂). Michoacán, 1.6 mi S Arteaga (on Hwy 37) 16-XII-1972, J.C. Lee #59 (1♂; 2♀). Guerrero, Acapulco, 10-VIII-1955, A.K. Hooper (5♂; 6 nymphs). Guerrero, 14 mi S Chilpancingo, 4200 ft, 19-IX-1959, Cantrall & Cohn #146 (5♂; 3♀). Guerrero, 4.3 mi E Petaquillas (1.3 mi E Tepechicotlán) 3800 ft, 19-IX-1959, Cantrall & Cohn #149 (1♂). Guerrero, 8 rd mi S Petaquillas, 13-XII-1958, 3900 ft, Cohn #375 (1♂; 3♀). Guerrero, 22 rd mi NE of Arcelia, 9-XII-1958, 4000 ft, Cohn #362 (2♂; 1♀). Guerrero, 15 mi N Tecpan, 100 ft, 24-VIII-1950, J. Peters (1♀). Guerrero, 2 mi S Tierra Colorada (km 335 on Hwy 95) 1400 ft, 19-IX-1959, Cantrall & Cohn #148 (30♂; 16♀).

CAFESI (53 specimens). **Short-winged form. MEXICO:** Guerrero, Carr. 134 Km 2, rumbo a Vallecitos, 440m, 23-IX-2017, Sanabria-Urbán S., L111-2017 (1♂; 2♀); Guerrero, Carr. 134 pasando Vallecitos, 1145m, 23-IX-2017, Sanabria-Urbán S., L112-2017 (1 nymph); Guerrero, Guamu Sierra de Atoyac, Km 19-Carr Acapulco-Zihuatanejo, 49m, 13-X-2018, S. Sanabria-Urbán, R. Palacios & V. H. Jiménez-Arcos, L01-2018 (1♂); Guerrero, Tehuacalco, 471m, 14-X-2018, S. Sanabria-Urbán, R. Palacios & V. H. Jiménez-Arcos, L08-2018 (5♂; 3♀); Guerrero, Tehuacalco, entrada a sitio arqueológico, 17.1880779974162N, -99.5049679744988W, 605m, 7-X-2018, S. Sanabria-Urbán, O Barrera, F. Soto & V. Ruiz Valdez #L02-2019 (3♂; 1♀). **Long-winged form. MEXICO:** Oaxaca, El Tapanco antes de Santa María Zacatepec, 361m, 31-X-2018, S. Sanabria-Urbán & V.H. Jiménez-Arcos, L24-2018 (1♀); Guerrero, Barrio Nuevo, sobre carretera Las Cruces-Pinotepa Nal., 16.604869030416N, -98.75047297216965W, 96m, 8-X-2018, S. Sanabria-Urbán, O Barrera, F. Soto & V. Ruiz Valdez #L03-2019 (18♂; 3♀); Guerrero, Ca. Huajintepec sobre camino a San Juan Cacahuatepec, 16.6143799759447N, -98.2519189640879W, 309m, 8-X-2018, S. Sanabria-Urbán, O Barrera, F. Soto & V. Ruiz Valdez #L04-2019 (3♂; 1♀); Guerrero, San Miguel Re'ediin, San Luis Acatlán, 16.94901N, -98.68518W, 674m, 5-IX-2018, R. Palacios-Aguilar #L16-2019 (8♂; 1♀); Guerrero, Arroyo del Coral, Río Santiago; Mpo. Atoyac de Álvarez, 17.25069N, -100.32047W, 679m, 8-IX-2018, R. Palacios-Aguilar #L17-2019 (1♂).

ANSP (125 specimens). **Short-winged form**. **MEXICO:** Michoacán, few mi N Arteaga, dry forest on mountain slope, 8-ix-1981, D. Otte, # 58 (1♂; 1♀). Michoacán, 15 mi W Caleta de Campos (W Playa Azul) remains of

lowland tall forest, 10.ix.1981, Otte #62 (1♂; 2♀). Michoacán, btw. Tzitzio & Capullo, S.E. Morelia, 3000-4000 ft, VIII.14.1940, H.R. Roberts (1 nymph). Guerrero, Km 234 between Iguala and R. Balsas 2000ft, ix-13-1940, C. Bolívar and H.R. Roberts (8♂; 5♀). Guerrero, Btw Tierra colorada and R Papagayo, 1000ft, ix-16-1940, C. Bolívar and H.R. Roberts (3♂; 5♀). Guerrero, Km 335, 16 mi S Chilpancingo, 4000ft, ix-14-1940, C. Bolívar and H.R. Roberts (3♂; 1 nymph). Guerrero, 19 mi S Chilpancingo, oak and pine open forest, tall grass, 4.ix.1981, Otte, Azuma, Newlin, #51 (3♂; 1♀). Guerrero, 14 mi S Chilpancingo, brushy pasture, forest on hillside, 4.ix.1981, Otte, Azuma, Newlin, #52 (7♂; 5♀). Guerrero, 5 mi N Acapulco, 15-ix-1940, C. Bolívar and H.R. Roberts (4♂; 7♀). Guerrero, Acapulco, 12-viii-1935, H.R.Roberts (3♂; 2♀; 1 nymph). Guerrero, Acapulco, 10-viii-1936, H.R.Roberts (9♂; 2♀; 1 nymph). Guerrero, 9 mi W of Acapulco, 11-viii-1962, Marstonn, Naumann, Ordway, Roberts (8♂; 1♀; 2 nymphs). Guerrero, Acapulco, Agassiz (4♂; 2♀). Guerrero, Agua de Obispo 30 mi S Chilpancingo, 400ft, 7-viii-1940 (2 nymphs). Guerrero, Río Balsas, 600 ft, 8-VIII-1936, H.R.Roberts (2 nymphs). Guerrero, Btw Tixtla and Chilpancingo, 31-VIII-1940, 6500 ft, H.R.Roberts (1 nymphs). Guerrero, ridge, 2mi N of Acapulco, IX-15-1940, H.R. Roberts (1♂; 1♀). Guerrero 16-20 km NE Rt 200, Ixtapa-Altamirano Rd, mountain forest, 9.ix.1981, Otte #60 (2♂). Guerrero, Zihuatanejo lowland scrub forest, 9.ix.1981, D. Otte #61 (1♂; 1♀). **Long-winged form. MEXI-CO:** Oaxaca, 24-25 mi N Pto Escondido, rd to Oaxaca, mountain national forest, roadside, 2.ix.1981, Otte, Azuma, Newlin, #45 (10♂; 7♀). Oaxaca, few mi E Pinotepa Nacional, thorn forest, 3.ix.1981, Otte, Azuma, Newlin, #43 (1♀). Oaxaca, Lagunillas N of Pinotepa Nacional, Tow forest with surrounding torn scrub, 3.ix, 1981, Otte, Azuma, Newlin, #48 (1♂; 2♀).

TAMUIC (10 specimens). **Short-winged form**. **MEXICO:** Guerrero, Tlahuacalco Arqueological Site, 25-X-2017, RMP, SSU, BF, MEP (3♂; 2♀). **Long-winged form. MEXICO:** Oaxaca, Km 16 Near Pie del Cerro, 22-X-2017, RMP, SSU, BF, MEP (2♂; 3♀).

CNIN-IBUNAM (11 specimens). **Long-winged form. MEXICO:** Oaxaca, Km 156 carretera 175 a Puerto Ángel, 21-X-1982 (1♂). Oaxaca, 45 km antes de Pinotepa Nacional, 6-IX-1982 (1♂). Oaxaca, Arroyo Cruz, 24-X-2008 (4♂; 2♀). Oaxaca, Santa María Huatulco, 24-X-2008 (2♂; 1♀).

Results

Material examined

Overall, we were able to examine 291 specimens of which 221 corresponded to the short-winged morph and 70 to the long-winged form. These specimens were collected from 47 localities, of which 36 localities only contained short-winged individuals and 11 contained only long-winged individuals. Short-winged and long-winged morphs were never encountered on the same location. Eleven localities corresponded to new records for the species, five of long-winged individuals and six of short-winged individuals.

Description of the long-winged morphotype

After a careful inspection between the two morphs of *M. dibelonius,* we did not identify any consistent differences other than the length of wings between the two morphotypes (Figs. 1 & 2). In live specimens of both forms, it is possible to see a bright blue coloration in the hind tibiae (Fig. 1). This coloration vanishes in mounted material.

Geographic distribution

Melanotettix dibelonius is distributed across southwestern Mexico in the states of Michoacán, Guerrero, and Oaxaca. Within the geographic range of the species, the two morphotypes appear to be restricted to different geographic areas (Fig. 3). The short-winged morphotype occupies the northern portion of the species' range and has been collected across the coastal plains, the mountain ranges and basins of Michoacán and Guerrero, in elevations ranging from the sea level to 1,981 masl (Fig. 3). On the other hand, the long-winged morphotype occupies the southern portion of the species' range, from southern Guerrero to southcentral Oaxaca. This morphotype has been collected

in elevations ranging from 96 up to 2,423 masl mainly across the coastal plains and the external slope of the Sierra Madre del Sur across mountain range (Fig. 3).

Some aspects of its ecology and biology

Across their distribution, the two morphotypes of *M. dibelonius* can be found in open woodlands of tropical deciduous forests and pine-oak forests. Although we did not observe the grasshopper's feeding behavior, most of the individuals we collected were found on dicotyledonous herbs, suggesting that this kind of plants could be an important part of their diet. Other gomphocerine genera adapted to forest habitats, such as *Silvitettix* Bruner, 1904 found in Costa Rica, are known to feed on forest-dwelling bambusoid grasses (Rowell, 2013), so it is also possible that *M. dibelonius* feeds on forest grasses.
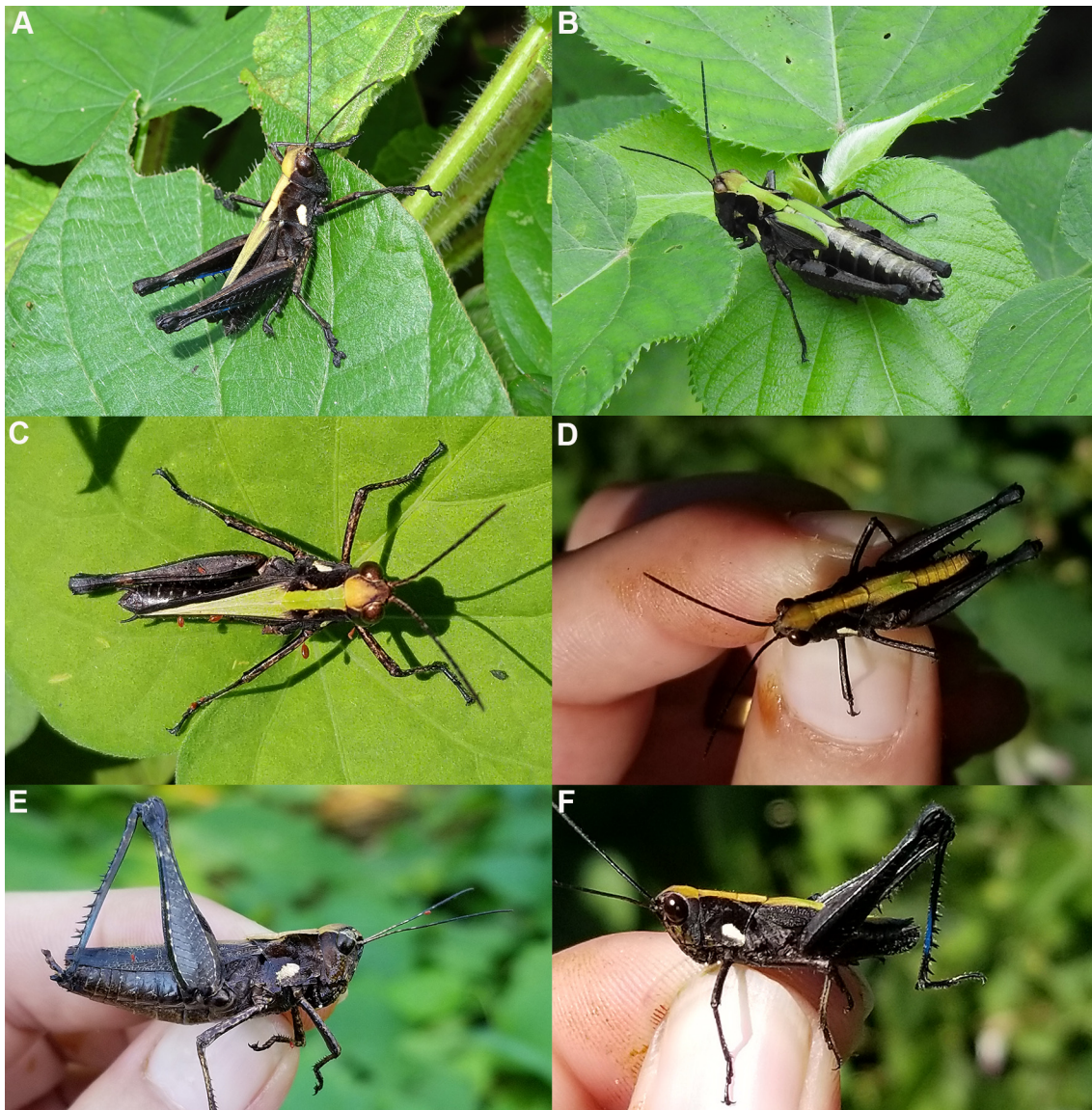

FIGURE 1. Images of live individuals of *Melanotettix dibelonius*. **A.** Long-winged male. **B.** Short-winged female. **C.** Long-winged male (parasitized with acari). **D.** Short-winged male. **E.** Long-winged female. **F.** Short-winged male. Photos by SSU, BF & MEP.

Among the material examined, most nymphs were collected in August and a few of them in September; whereas most of the adult specimens were collected from September to December. During our field expeditions conducted in September and October in 2017, 2018, and 2019, we observed that most adult individuals were males; whereas the observed nymphs were mainly females. Together, these observations suggest the possibility of protandry within

the species, in which males might complete their development by the end of the rainy season, around September; whereas females might mature later in the following months.

During our fieldwork, we also observed that long-winged individuals, especially males, were able to fly or glide at least for short distances (< 10 m) at low height (< 3 m) when we tried to capture them. Although it is unknown whether long-winged individuals are able to sustain long-distance flight, it is possible that the flying capacity in this morph still plays an important role in avoiding predators. Incidentally, we detected Acari (at least seven individuals) associated to a long-winged male. These ectoparasites were found attached to the three pairs of legs and tegmina (Fig. 1c).
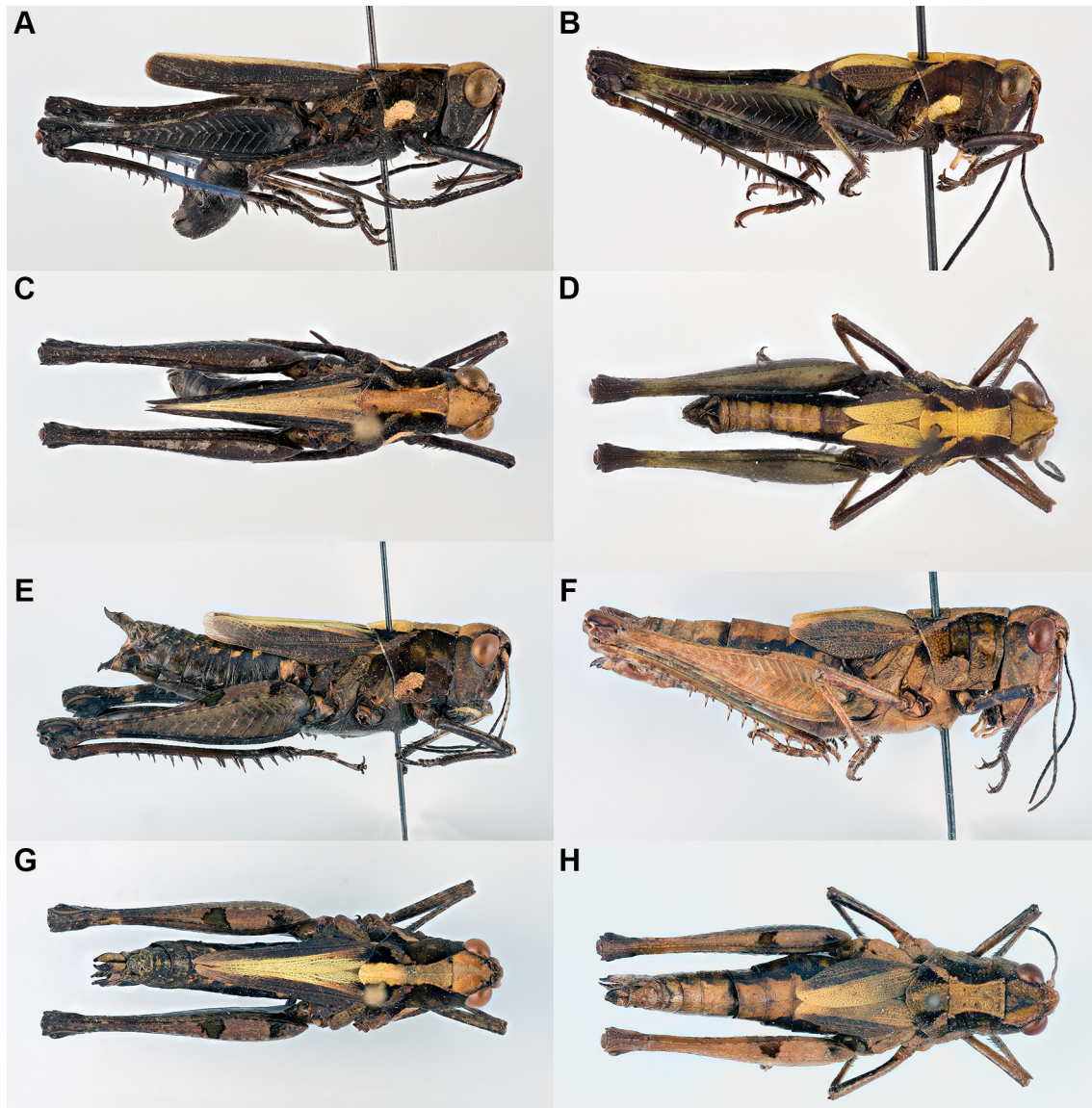

FIGURE 2. Images of mounted individuals of *Melanotettix dibelonius*. **A.** Long-winged male lateral. **B.** Short-winged male lateral. **C.** Long-winged male dorsal. **D.** Short-winged male dorsal. **E.** Long-winged female lateral. **F.** Short-winged female lateral. **G.** Long-winged female dorsal. **H.** Short-winged female dorsal.

Morphological analyses

We were able to measure 82 specimens of *M. dibelonius* (36 long-winged and 46 short-winged individuals) from 11 different sampling localities (five for the long-winged morphotype and six for the short-winged morphotype) (see Fig. 3 for the geographic locations of these localities). Means and standard deviations per morphotype and sex of each morphological trait measured are shown in Table 1.

On average, females and males of the short-winged morphotype seem to have a longer pronotum than the long-winged individuals. Also, the hind femur shows a trend towards being longer in short-winged individuals than in long-winged individuals for males, while the opposite was observed for females (Table 1). However, none of these differences was statistically significant when tested with an ANOVA (data not shown). Only significant differences were found in these two body size measurements between females and males within the two morphotypes (ANOVA results: PnL: $d.f. = 81$, *Sum of squares* $= 0.59$, $p < 0.001$; HfL: $d.f. = 81$, *Sum of squares* $= 0.31$, $p < 0.001$), indicating a marked sexual size dimorphism biased toward females in the species.

We also observed that on average, the tegmina of long-winged individuals (both females and males) are slightly longer than twice the length of pronotum (TgL/PnL ratio > 2); whereas in short-winged individuals the tegmina are nearly as long as or slightly longer than the length of the pronotum (TgL/PnL ratio $\gtrsim$ 1) (see Table 1). Moreover, on average, females appear to have longer tegmina than males in both morphotypes, either when considering absolute values or when considering its size relative to the pronotum length (Table 1). However, these differences were not significant in our ANOVA analyses (data not shown).

TABLE 1. Measurements of morphologic traits of the two morphotypes recognized in *M. dibelonius*.

Morphotype	Sex	Sample size	PnL Mean ± SD (mm)	HfL Mean ± SD (mm)	TgL Mean ± SD (mm)	TgL/PnL ratio Mean ± SD
Long-winged	Females	7	6.93 (±0.91)	18.57 (±1.78)	15.67 (±2.12)	2.29 (±0.38)
	Males	29	4.85 (±0.63)	13.84 (±0.92)	10.68 (±0.92)	2.22 (±0.25)
Short-winged	Females	21	7.05 (±0.36)	18.4 (±1.03)	8.78 (±0.8)	1.24 (±0.07)
	Males	25	4.95 (±0.41)	14.49 (±0.94)	5.09 (±0.48)	1.02 (±0.06)

PnL, dorsal length of pronotum; HfL, length of hind femur; TgL, length of tegmina; SD, standard deviation.
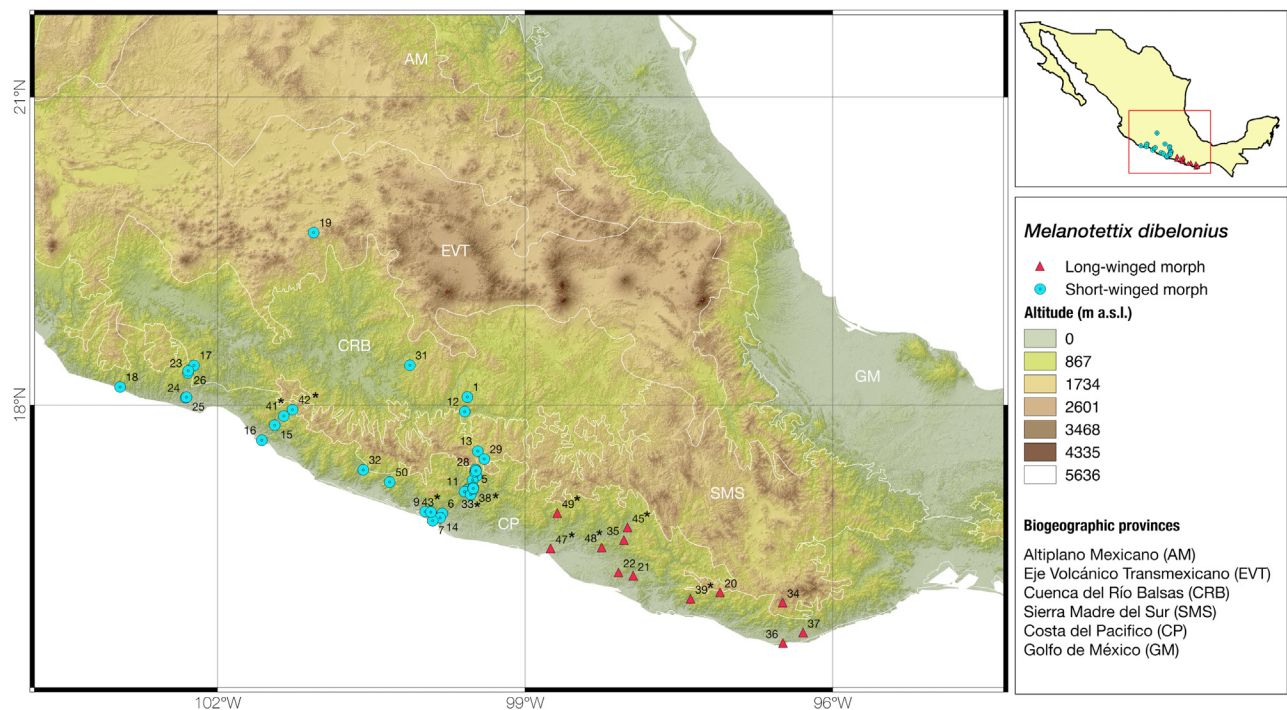

FIGURE 3. Updated geographic distribution of *Melanotettix dibelonius* and its two morphotypes identified (red triangle = long-winged form; blue circle = short-winged form). Numbers beside the symbols indicate the locality number. *Asterisk denotes localities from which specimens were measured for the morphological analyses.

Discussion

In this study, we describe a long-winged form within the Mexican endemic species *M. dibelonius* for the first time, providing information about the differences between this new morph and the previously recognized short-winged form within the species, as well as general information about the distribution ranges, ecology, and general biology of these grasshoppers. Among the museum material examined, the first records of the long-winged morph of *M. dibelonius* dated back to 1981 by Otte, Azuma and Newlin, who extensively conducted fieldwork in Mexico. However, no formal description or mention of this morph was made until now.

Taxonomic considerations

Coloration traits are commonly used to differentiate species in the subfamily Gomphocerinae. Moreover, within this subfamily, different species can be distinguished by their wing length but usually in association with other morphological differences, as intra-specific wing-length polymorphism is relatively common in gomphocerines (Otte, 1979 ; 1981). In this study, we did not identify differences in coloration or external morphology between the short-winged and long-winged individuals of *M. dibelonius*, except in the length of tegmina and the geographic distribution of these two forms. Therefore, we recognized all the long-winged individuals as only representing a morphotype within the species. Moreover, similar patterns of intraspecific geographic variation in wing length have been documented within other North American Gomphocerinae, in which, long-winged and short-winged forms occur in different portions of the species' geographic ranges (e.g. *Ageneotettix deorum, Horesidotes cinereus, Opeia obscura* and *Dichromorpha* spp.) (Otte 1979 and 1981). For example, in *Dichromorpha viridis* forewings are longer in populations from Western Mexico than in populations from Eastern Mexico and USA (Otte 1981). Regarding the Old World Gomphocerinae, *Pseudochorthippus parallelus*, *Pseudochorthippus montanus*, and *Chrysochraon dispar* are all usually in the short-winged morph but occasionally found in the long-winged form in short-winged populations (Massa et al., 2012).

   Nevertheless, we do not reject the possibility that the two recognized morphotypes might represent separate species or genetically distinct populations within the genus *Melanotettix*. The geographic distribution patterns of the morphotypes provide support for this idea. The two morphotypes were found in different geographic areas within the species' range, roughly the short-winged morphotype ranged from central Michoacán to central Guerrero and the long-winged morphotype from the southern Guerrero to central Oaxaca. Interestingly, this pattern, in which parapatric and closely related lineages encounter their contiguous distribution limits around the southern coastal plains of Guerrero has been observed in other taxa. For example, in *Sphenarium* grasshoppers (Pyrgomorphidae), two sister species, *S. occidentalis* and *S. histrio*, reach their contiguous distribution limits nearly at the same area and they were only recognized as independent species after analyzing their genetic differences (Sanabria-Urbán et al., 2015, 2017). Similarly, a clear phylogeographic break, in which intraspecific genetic lineages form Guerrero separate from those from Oaxaca has been documented in *Trimorphodon biscutatus* lyre snakes (Devitt, 2006), *Azteca pittieri* ants (Pringle et al., 2012), and *Tlacuatzin canescens* opossums (Arcangeli et al., 2019). All these studies suggest that a common historic event in southern costal Guerrero could have caused the vicariance of ancestral populations of taxa distributed across southwestern Mexico, such as *M. dibelonius*. Therefore, further genetic analysis might find that the two morphotypes of the species represent independent lineages.

Comments on the wing variation

The North American and European Gomphocerinae show an extensive variation at inter and intraspecific levels in wing morphology associated with their flight capacities. This variation ranges from flying species with fully developed wings to non-flying species with reduced or lost wings (e.g. species in the genera *Silvitettix, Phaneroturis, Orphulella, Opeia, Eritettix, Ageneotettix, Psoloessa, Boopedon* and *Achurum*). Moreover, between these extremes, there are many facultative flying species involving cases in which just one sex, some individuals of both sexes or some populations are capable of flight (Otte, 1979). This makes Gomphocerinae a very interesting group for studying the evolution of flightlessness and wing reduction.

   Fully developed and functional wings can increase the dispersal and survival capabilities of individuals that

possess them, reducing the risk of population extinction due to environmental variation (Roff, 1990; Denno et al., 2001). However, the development and functioning of wings is energetically expensive, regardless of their use, and can reduce egg production and development rates of individuals as a result of life history trade-offs (Roff, 1990). Thus, when flight is not crucial for the individuals' fitness, natural selection can favor the reduction or loss of wings if the energy invested on wings and flight is redirected to other important components of fitness of individuals, such as fecundity and mating success (Roff, 1990; 1994). Generally, fecundity and reproduction successes increase when body size increases in many organisms, including grasshoppers (Whitman, 2008). Therefore, as a consequence of the trade-off between wing development and fecundity (or mating success), flying species or morphs can be expected to have smaller body sizes than non-flying species or morphs. For instances, Köning and Krauss (2019) found that two species of Palearctic gomphocerines (*Chorthippus biguttulus* and *Gomphocerippus rufus*) exhibited a larger body size in areas where plenty of suitable habitat was present, while a smaller body size and longer wings was observed in areas where suitable habitat was highly fragmented.

Consistent with this hypothesis, we observed that in *M. dibelonius* long-winged individuals (females and males) were, on average, smaller than the short-winged individuals. However, these differences were not statistically significant, which can be explained by the relatively small sample size in our analyses. Further studies including more individuals of both morphotypes and sexes might add further support to the observed body size differences between the two morphotypes of *M. dibelonius*. Interestingly, we also observed that, on average, females have larger wings than males in both morphotypes, both in absolute value and relative to the pronotum length. This pattern is opposite to what has been commonly reported in other Gomphocerinae species, in which males quite consistently have larger wings than females (e.g. *Barracris petraea, Pseudochorthippus curtipennis, Silvitettix communis, S. salinus, Ageneotettix brevipennis, Psoloessa brachyptera, P. microptera, Boopedon diabolicum, B. gracile, B. flaviventris, B. nubilum* and *Achurum minimipenne*). However, these differences observed in *M. dibelonius* were again not statistically significant. If future analyses with a larger sample size obtain significant results for these same differences, it would suggest that females can experience a stronger selection for locomotor capacity than males (Roff, 1986).

Despite the fact that the two morphotypes showed marked differences on their average wing proportion, we also observed considerable variation in this ratio, especially in the long-winged morphotype (see SD values on Table 1). Our data did not allow us to determine if this variation correlates with a geographic cline, as has been observed in other gomphocerine species. Further analyses studying a greater number of localities across the distribution range of the species can determine if such a cline exists in *M. dibelonius*. This work is the basis for further studies in *M. dibelonius*, involving different aspects of the species' general biology, ecology and evolution. We consider that it is imperative to continue reporting natural history observations, especially in grasshoppers, in this era of "omics" because it is precisely the natural history that we are studying, and these type of reports are the foundations of new sets of questions such as: Do the two morphotypes represent different or incipient species? How important has natural selection been on wing size, through local adaptation, in generating the differences between these two morphotypes? Why does the short-winged form have the broadest and more northern distribution? Is there an area where both forms co-occur?

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