










Article

Integrative Taxonomy of Costa Rican Tetrigidae (Orthoptera) Reveals Eight New Species [†]

Niko Kasalo ^{1,*}, Daniel H. Janzen ², Winnie Hallwachs ², Allison Brown ³, Martin Husemann ⁴, Mathias Vielsäcker ⁴, Tomislav Domazet-Lošo ^{1,5}, Damjan Franjević ⁶, Madan Subedi ⁷, Domagoj Bogić ⁶ and Josip Skejo ^{6,*}

¹ Laboratory of Evolutionary Genetics, Ruđer Bošković Institute, Bijenička cesta 54, HR-10000 Zagreb, Croatia

² Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

³ Centre for Biodiversity Genomics, University of Guelph, Guelph, ON N1G 2W1, Canada

⁴ Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstraße 13, 76133 Karlsruhe, Germany

⁵ School of Medicine, Catholic University of Croatia, Ilica 242, HR-10000 Zagreb, Croatia

⁶ Evolution Lab, Department of Biology, Faculty of Science, University of Zagreb, Horvatovac 102a, HR-10000 Zagreb, Croatia

⁷ Agriculture Science Center, Directorate of Research and Extension, Agriculture and Forestry University, Ghyalchok, Gorkha 34000, Nepal

* Correspondence: nkasalo@irb.hr (N.K.); jskejo@biol.pmf.hr (J.S.)

[†] urn:lsid:zoobank.org:pub:28AB3A25-6582-436C-AEF0-101AD9F062A8;

urn:lsid:zoobank.org:act:32C4D9BE-A27A-4921-834D-80A753B4F4D7;

urn:lsid:zoobank.org:act:A9EC48E6-5EF5-448A-9F35-BE061B8D5360;

urn:lsid:zoobank.org:act:B057ACBB-1D2D-4717-9AE5-17E53EBDA685;

urn:lsid:zoobank.org:act:7D883D7C-9FCF-4119-8BCF-698F0583CB46;

urn:lsid:zoobank.org:act:41F84B6E-BBB7-430C-9943-57965B0B74E8;

urn:lsid:zoobank.org:act:CD81B685-240A-4F6B-B143-EA4DBD65FA67;

urn:lsid:zoobank.org:act:07A3D89E-8911-4F09-8734-B528C4990E5C;

urn:lsid:zoobank.org:act:F5D46CE2-7D9F-4B35-9E84-B45C1F66AFBB.

Abstract: Tetrigidae is one of the largest orthopteran families, but very few studies so far have integrated molecular and morphological data. Unsurprisingly, few species have been DNA barcoded, and the unresolved taxonomy makes Tetrigidae a difficult group to work with. Here, we examined a sample of 90 specimens collected as a part of the Costa Rican DNA barcoding project and identified 20 species assigned to 24 BINs, among which are 8 newly described species: *Scaria bimaculata* sp. nov., *Lophotettix semicristatus* sp. nov., *Otumba auricarinata* sp. nov., *Otumba tenuis* sp. nov., *Otumba ignicula* sp. nov., *Metrodora mollilobata* sp. nov., *Metrodora ala* sp. nov., and *Platythorus inabsolutus* sp. nov. We found that coloration and lateral lobe shape are species-specific among the examined species of Batrachideinae and Metrodorinae and that Lophotettiginae and *Metrodora* might be more closely related than previously assumed.

Keywords: DNA barcoding; pygmy grasshopper; Neotropics; COI; BOLD systems



Academic Editor: Luc Legal

Received: 17 February 2025

Revised: 25 February 2025

Accepted: 3 March 2025

Published: 6 March 2025

Citation: Kasalo, N.; Janzen, D.H.; Hallwachs, W.; Brown, A.; Husemann, M.; Vielsäcker, M.; Domazet-Lošo, T.; Franjević, D.; Subedi, M.; Bogić, D.; et al. Integrative Taxonomy of Costa Rican Tetrigidae (Orthoptera) Reveals Eight New Species. *Diversity* **2025**, *17*, 190. <https://doi.org/10.3390/d17030190>

Copyright: © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Tetrigidae, commonly known as pygmy grasshoppers, is one of the most speciose orthopteran families numbering just over 2000 species, with more being continuously described [1–3]. Although a lot of work is being conducted on tetrigid taxonomy, it is still predominantly morphology-based; only a few studies dealing with molecular data exist [4–15]. Many species of Tetrigidae still lack clear morphological diagnoses and many subgroups lack good identification keys, making pygmy hoppers difficult to identify [16–19].

The simplest genetic data is the DNA barcode. DNA barcoding using a 658 bp segment of the Cytochrome oxidase subunit I gene (COI) was proposed as a way to help identify animal species, thus addressing the limitation of pure morphology [20]. DNA barcoding has become a widely used tool [21–23] and has even been utilized to fast-track species descriptions [24,25], which has been criticized on the grounds of instability of clustering algorithms (e.g., Barcode Index Number (BIN) system) and superficial treatment of morphology [26–29]. There is clearly a need to develop novel, fast, and precise taxonomic protocols for megadiverse taxa without sacrificing precious information [26,30] and this is an important issue to be resolved. In the context of Tetrigidae, DNA barcoding has only been used once to assist in species descriptions, resulting in the recognition of two sympatric species [7].

Tetrigidae is not a megadiverse taxon, and it is still possible (albeit increasingly difficult) to define each species with morphologic characters. As we showed previously, the availability of tetrigid COI sequences is low, and many existing sequences belong to poorly, if at all, identified specimens [31]. Here, we present the first large-scale integrative characterization of Tetrigidae species, combining morphology and DNA barcoding data generated after extensive sampling in Costa Rica. We relate BIN clusters to species, revise the taxonomic placement of certain species and groups, and describe eight new ones based on conservative molecular and morphologic criteria. We conduct taxonomic revisions only where strictly necessary as many taxa require extensive work before confident classifications—and by extension identification keys—can be made.

2. Materials and Methods

2.1. The Origin of Specimens

The Costa Rican specimens were collected between 2012 and 2021 as a part of the BioAlfa DNA barcoding project of the Guanacaste Dry Forest Conservation Fund (GDFCF) based in Área de Conservación Guanacaste (ACG) and led by some of the authors of this study (DJ and WH). The specimens were collected using malaise traps and were deposited at the Centre for Biodiversity Genomics, Canada (BIOUG), where they were sequenced. The data pertaining to around 1500 tetrigid specimens from BIOUG are publicly available through the BOLD Systems website. A sample of 90 specimens representing all the BINs identified in this collection was loaned to NK for morphological examination and analysis. The specimens were selected so that each BIN was represented by non-damaged specimens, ideally a male and a female. Full specimen data are available at <https://dx.doi.org/10.5883/DS-CRTET> (accessed on 16 November 2024). The DNA analysis methods follow those used by Kasalo et al. [31].

The holotypes are housed at the Staatliches Museum für Naturkunde Karlsruhe (SMNK), while the other specimens remain at BIOUG. The collection localities of examined specimens are shown in distribution maps in Figure 1. The distribution maps were generated in QGIS (Geographic Information System, QGIS Association. <http://www.qgis.org>, accessed on 16 November 2024).

2.2. Phylogenetic and Clustering Analyses

The COI sequences of the 90 Costa Rican specimens were initially screened. The sequence representing the BIN AEI8939 (Process ID PLBDH006-20) is likely a result of contamination since NCBI BLAST (version + 2.15.0) showed that it is highly similar to lepidopteran sequences, so it was removed. We further used the coil R package [32] to screen the barcodes for stop codons, insertions, and deletions and found them all to be clear. Some shorter sequences which could have impacted the analysis were removed (Process IDs: GMAAJ013-16—*Metrodora mollilobata*; PLEDB2783-20—*Tettigidea* cf. *bruneri*

Morse, 1900; CRSIA47828-22 and CRSIA47831-22—*Teredorus aztecus* (Saussure, 1861) [33]; CRCEA42890-22 and GMABQ013-16—*Chiriquia serrata*). Longer sequences representing all of the mentioned BINs and species remained in the analysis, so the exclusion of these sequences did not impact the analysis. Sequences of *Tettigonia viridissima* (Linnaeus, 1758) [34] (Ensifera) (BOLD ID: NOORT142-13) and *Myrmeleotettix maculatus* (Thunberg, 1815) [35] (Caelifera) (BOLD ID: FBORT260-09) were added to serve as outgroups. In total, 85 sequences were analyzed.

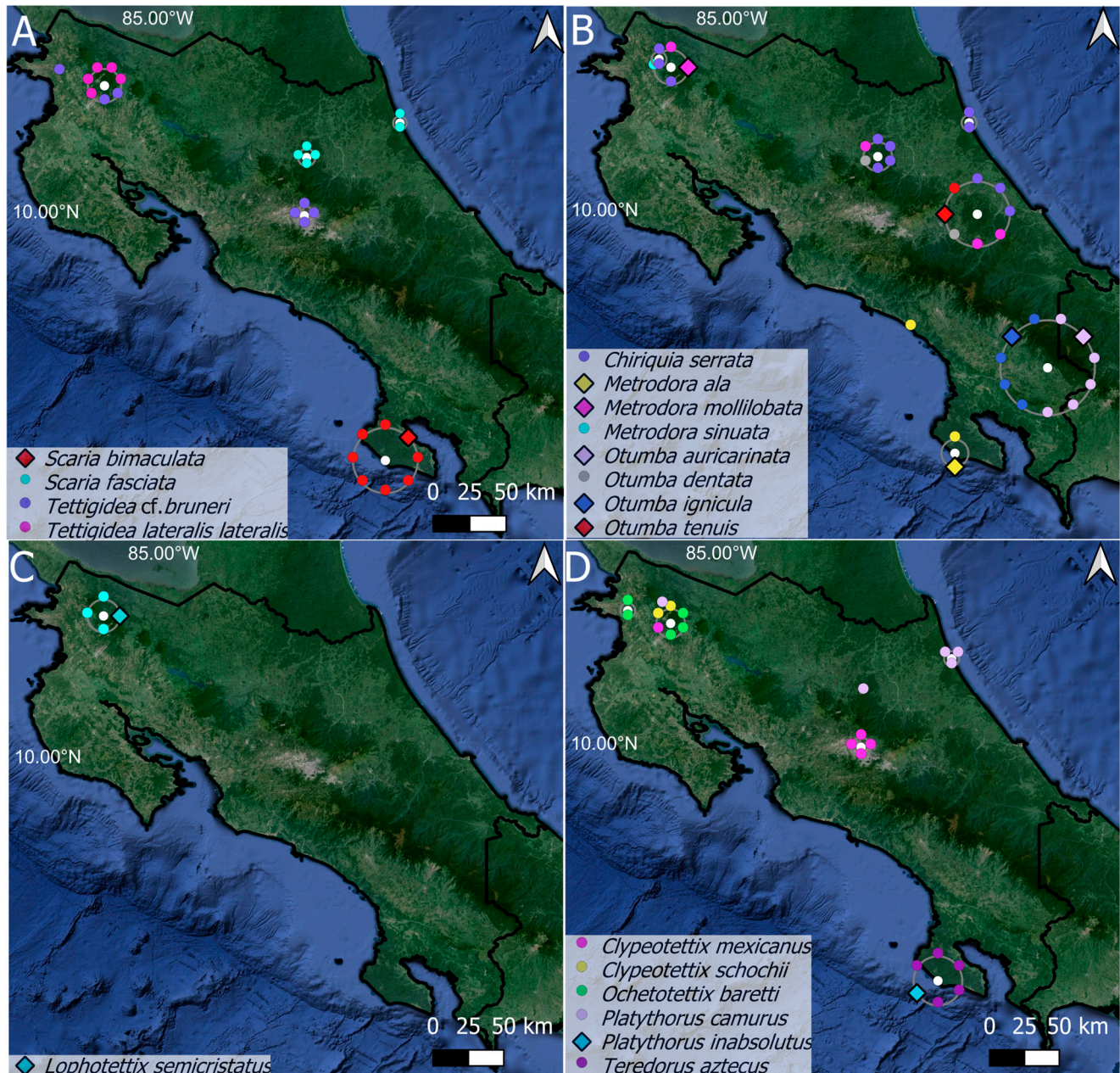


Figure 1. Collection localities of the examined specimens from Costa Rica. The rhomboid shapes represent type localities. Where multiple specimens were collected from a single locality, this locality is denoted by a white dot encircled by the specimens found there. (A) Batrachideinae; (B) Metrodorinae; (C) Lophotettiginae; (D) Tetriginae.

The sequences were aligned using the MAFFT (Multiple Alignment using Fast Fourier Transform) algorithm (<https://www.ebi.ac.uk/Tools/msa/mafft/>, accessed on 16 November 2024). The aligned sequences were trimmed using the BioEdit program [36]. The

trimmed alignment was 564 bp long. The appropriate model for the Maximum Likelihood (ML) analysis was determined using IQ-TREE's ModelFinder function [37,38]. The best-fit model according to the BIC criterion was found to be TIM2+F+R3. Using this model, an ML phylogenetic analysis was conducted in IQ-TREE using the ultrafast bootstrap method [39] with 10,000 replicates and the SH-like approximate likelihood ratio test (SH-aLRT) with 1000 replicates. The visual representation of the tree was generated using FigTree v1.4.4 [40].

The Assemble Species by Automatic Partitioning (ASAP) clustering analysis was performed to delimit groups independently of BOLD's own algorithm. We used Kimura's two-parameter substitution model at ts/tv 1.5 with other settings default. We performed ASAP on the full set of sequences from this project, numbering 1187 after screening for length. We also calculated the pairwise distances between barcode sequences using the K80 model implemented in the R package ape [41].

2.3. Taxonomy, Nomenclature, and Measurements

Taxonomy follows Cigliano et al. (2024). Morphological terminology follows previously established conventions [18,42–45], as do measurements [18,46,47]. Nomenclature is in accordance with the International Code of Zoological Nomenclature [48]. The photographs of holotypes were taken by MV at SMNK using a Canon EOS R5 with either a Canon EF 100MM F/2.8L MACRO IS USM for the dorsal, ventral, and lateral images, or a Laowa 25 mm f/2.8 Ultra Macro 2.5–5× for the images of smaller details. Stacked imaging was performed using a WeMacro rail. Images were then stacked using Helicon Focus. The photographs of other specimens were photographed by BIOUG as a part of the data curation process, and all photographs are available at: <https://dx.doi.org/10.5883/DS-CRTET>, accessed on 16 November 2024.

The following measurements were made and are labeled in the text as indicated: Body length—BL; Vertex width—VW; Eye width—EW; Scutellum width—SW; Pronotum length—PL; Pronotum lobe width—PLW; Pronotum height—PH; Tegmen length—TL; Tegmen width—TW; Alae length—AL; Fore femur length—FFL; Fore femur width—FFW; Mid femur length—MFL; Mid femur width—MFW; Post femur length—PFL; Post femur width—PFW; Hind tibia length—HTL; First tarsal segment (basal) length—FTL; Third tarsal segment (apical) length (without claws)—TTL; Subgenital plate length—SPL; Subgenital plate width—SPW; Ovipositor dorsal valve length—ODL; Ovipositor dorsal valve width—ODW; Ovipositor ventral valve length—OVL; Ovipositor ventral valve width—OVW

The measurements were made using the ImageJ 1.53t software [49].

The differentiation of species is based on the following criteria. For two species to be considered separate, they must (i) belong to separate clusters (BINs, ASAP clusters), (ii) have a high pairwise genetic distance (taken here to be around 10% following [7]), and (iii) be definable by at least one clearly visible and stable morphologic character.

In accordance with Article 13 of the ICZN [48], each new species is defined by a set of characters that differentiate it from its closely related species, which we here refer to as a "diagnosis". The degree of detail provided in diagnoses varies according to the difficulty of identification. Alongside diagnosis, a "general description" is provided, including characters important for characterizing the species within its group, but which are not necessarily unique to it. The already-described species are also accompanied by a diagnosis. Each genus or species group is accompanied by a diagnosis or a general description, as necessary, which includes characters shared by all members of the group. These descriptions fully apply to the lower taxonomic levels, making it unnecessary to repeat those characters in species descriptions and diagnoses. Our naming of the different categories of morphological descriptions was chosen for its intuitiveness and does not imply that the characters that were not mentioned were not examined, but that they were not found to be informative.

The style of the description does not impact the validity of the taxonomic act if the intent to differentiate taxa is clearly demonstrated [48].

Zoobank publication ID is LSID urn:lsid:zoobank.org:pub:28AB3A25-6582-436C-AEF0-101AD9F062A8.

3. Results

3.1. Phylogenetic and Clustering Analyses

A Maximum Likelihood (ML) tree of barcode sequences belonging to the examined specimens is shown in Figure 2. When deeper branches are considered, some notable observations can be made. The subfamily Batrachideinae is, with maximum support, separated from all the other taxa, i.e., it is recovered as holophyletic. This is not the case with Metrodorinae and Tetrigenae, which are part of a single clade with many unresolved basal nodes, demonstrating the common observation that COI is insufficient for higher classification. Interestingly, the genus *Otumba* is reconstructed as the sister clade of this Metrodorinae-Tetrigenae-Lophotettiginae clade and this branching is highly supported (97.1/99). The species of the same genus are reconstructed together, but intergeneric relationships within subfamilies remain unclear. The most interesting is the grouping of *Metrodora ala* and *Lophotettix semicristatus* with high statistical support (96/97), which implies a close relationship between Lophotettiginae and at least some Metrodorinae.

Among the examined sequences, BOLD's BIN system recognizes 24 different BINs (BIN AEI8939 excluded due to contamination). When these sequences are analyzed using the ML method, the sequences of the same BIN group together in all cases with high statistical support (UFbootstrap $\geq 99\%$) (Figure 2). A heatmap showing clear and large gaps in genetic identity between sequences belonging to the same species is presented in Figure 3.

BINs largely correspond to species, with only two exceptions. First, the *Otumba dentata* cluster consists of two BINs (AEY6158, AEU1829). The specimens to which these sequences belong cannot be morphologically differentiated so they are considered to represent the same species. Second, the *Chiriquia serrata* complex consists of four BINs (AEU8363, ACY3240, ADL7675, AEO7600). Each of these *C. serrata* clusters is highly supported. When genetic distances are considered (Figure 3), the two *O. dentata* BINs differ by about 3.5%, while the distances between some *C. serrata* BINs surpass 10%, indicating that both of these groups could harbor cryptic species. In the *C. serrata* group, there are no clear morphological differences between the specimens, with the exception of some specimens having slightly different crest heights. All of this, taken together, does not allow for a meaningful specific diagnosis, so all four BINs are reported under a single species.

Another worthwhile exception is *Scaria bimaculata* sp. nov., to which we assign two BINs which differ by around 8%. Although they could represent separate species, one of the BINs (AER7428) is composed exclusively of nymphs so diagnostic characters could not be determined for this BIN. We report those specimens under *Scaria bimaculata* sp. nov. since they cluster most closely with its representatives.

When the ASAP clustering is performed on the whole database, the most likely partitioning (asap-score 5.00, p -value = 10^{-5}) corresponds almost exactly to the groups outlined above, with a few exceptions: all four *C. serrata* BINs are grouped together, and all *Otumba* sequences except for *O. tenuis* are grouped together as well. On the other hand, the second-best partitioning (asap-score 6.0, p -value = 10^{-5}) separates the *Otumba* species well while keeping both *O. dentata* BINs together, but it separates the *C. serrata* BIN AEU8363 from other *C. serrata* sequences. This approach thus differentiates between 18 and 21 species, but we remain with the above-explained interpretation of 20 species. Therefore, it seems

that BOLD's BIN system corresponds well to species but neither BOLD nor ASAP are able to perfectly delimit groups.

In conclusion, we recognize 20 different species assigned to 24 BINs.

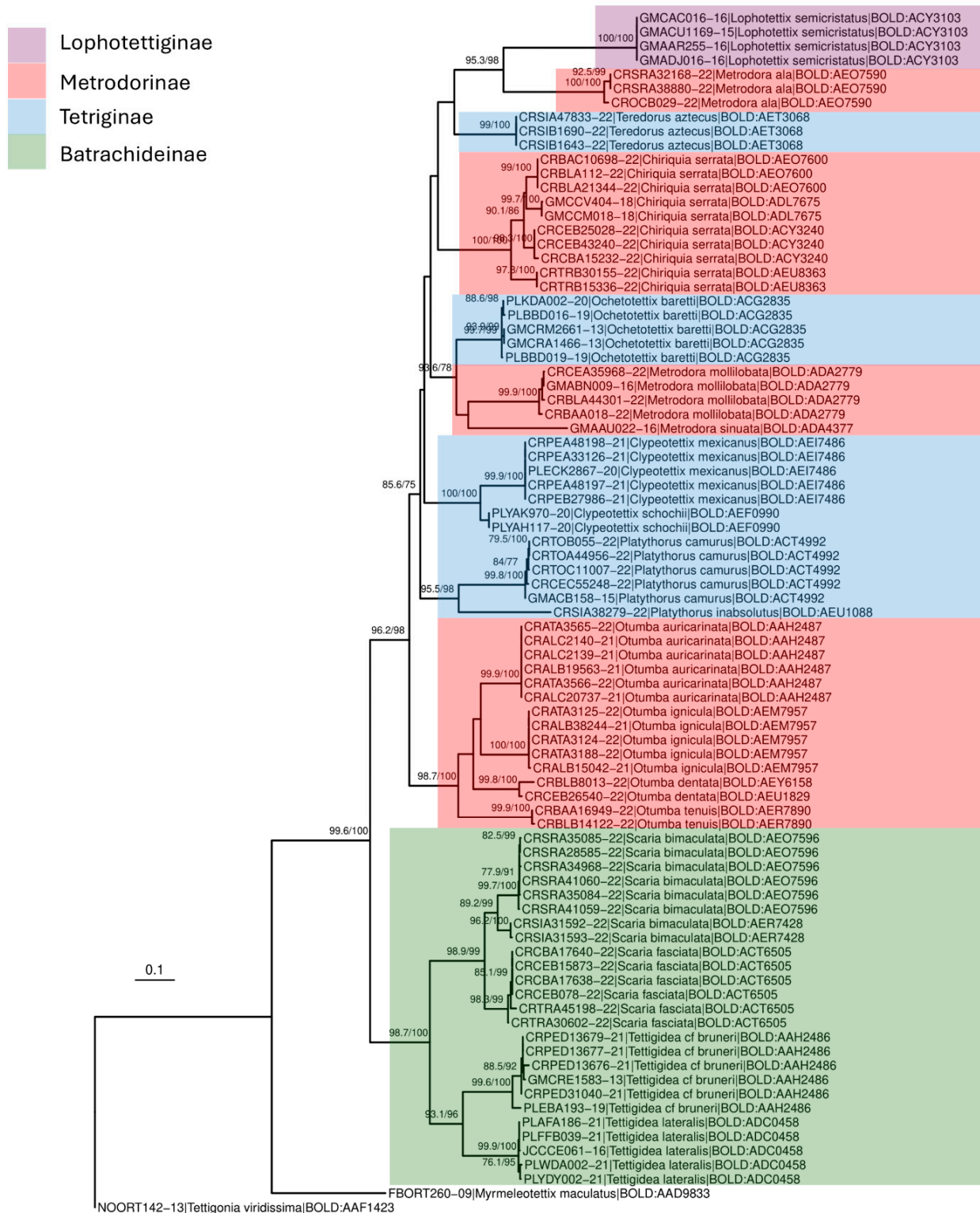


Figure 2. Maximum Likelihood tree of 85 tetrigid COI sequences with 10,000 bootstrap replicates. Each node is labeled with the SH-aLRT (first number) and bootstrap (second number) values; only values larger than 70 are shown. Each sequence is identified by the BOLD Process ID, species name, and BIN. Taxa are colored according to the subfamily they belong to; unassigned taxa and outgroups are colored black. Branch lengths represent substitutions per site.

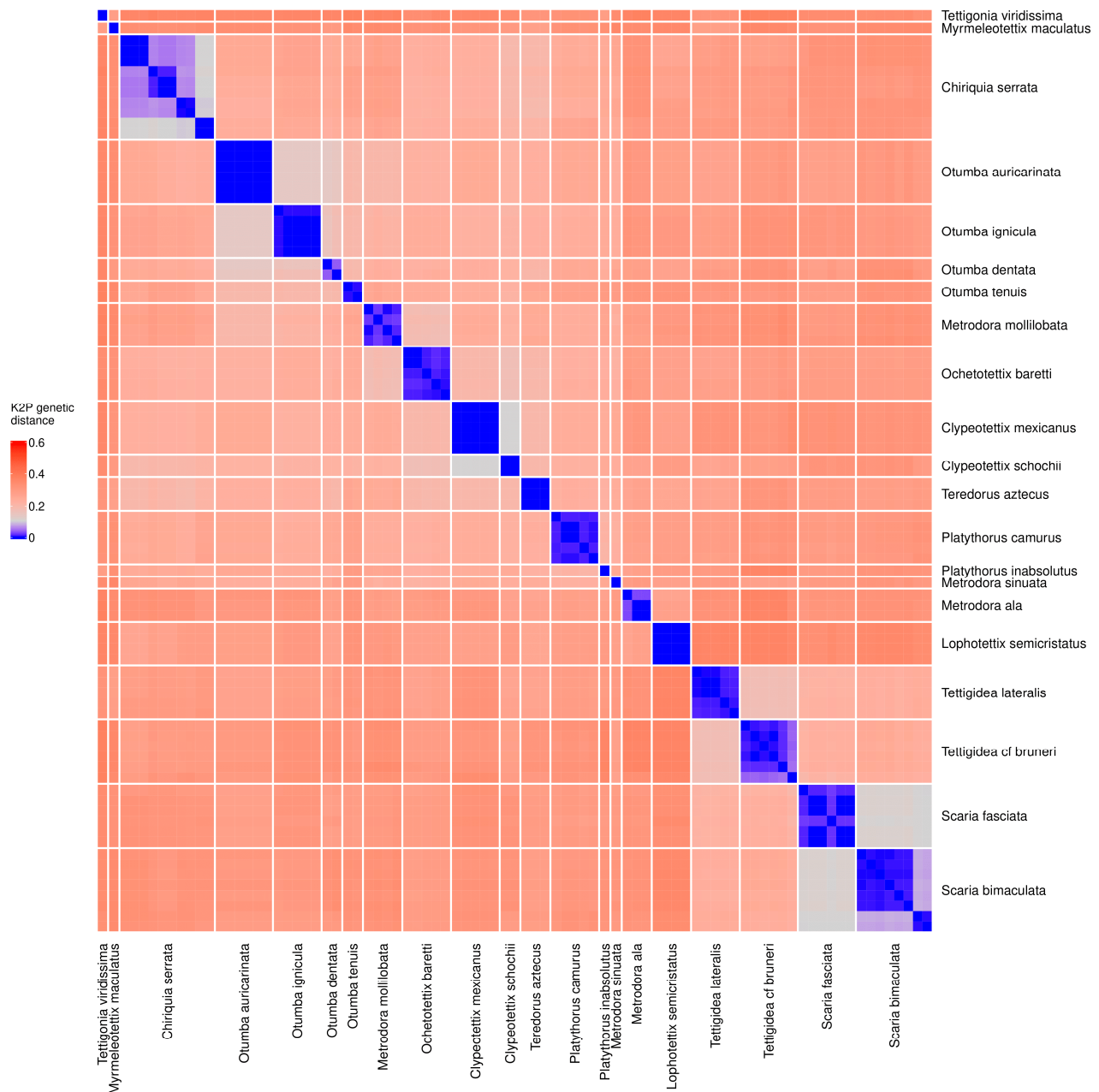


Figure 3. Heatmap of genetic distances. Distances were calculated using the K80 model. Sequences are grouped according to our species classification.

3.2. Taxonomy

Family Tetrigidae Rambur, 1838 [50]

Subfamily Batrachideinae Bolívar, 1887 [51]

Tribe Batrachideini Bolívar, 1887 [51]

Genus *Scaria* Bolívar, 1887 [51]

Diagnosis. The body is slender. The pronotum and wings are long. The tegmina is black and usually maculated. The vertex is lowered between the eyes. The anterior margin of the vertex does not reach the anterior margin of the eyes. The anterior margin of the pronotum is in the form of a slim spine. The preceding diagnosis is based on recent literature [17,52,53] and is expected to be refined in the upcoming revisions.

Type species. *Scaria hamata* [54]

Composition. A total of 16 described species [1,53] and one undescribed [55].

Distribution. Central and South America [56].

Scaria (lineata) species group (sensu Cadena-Castañeda et al. 2019) [52]
Species *Scaria fasciata* Hancock, 1907 [57] (Figure 4)



Figure 4. A female specimen of *Scaria fasciata* (BIOUG77732-G05) belonging to the BIN ACT6505.

Diagnosis. Differentiated from all other members of the *S. (lineata)* species group by the following characters. The postocular stripe is strongly expressed. The anterior margin of the pronotum forms a slim spine that reaches past the middle of the eye length in dorsal view. The median carina forms a small hump at the posterior end of the prozona. The pronotum does not have a distinct dorsal line. The tegmina has an apical macula.

Distribution. Northeastern part of Southern America and Central America [58,59]. The previous records should be revisited to separate *S. fasciata* from the newly described species, as it seems that *S. fasciata* does not inhabit Puntarenas and San José regions in Costa Rica, where a new species, described below, is present.

BOLD Systems BIN. ACT6505

Species *Scaria bimaculata* Kasalo & Skejo sp. nov. (Figure 5)

ZooBank ID: LSID urn:lsid:zoobank.org:act:32C4D9BE-A27A-4921-834D-80A753B4F4D7

Diagnosis. Very similar to *S. fasciata*. Differentiated by the tegmina, which have both a basal and an apical macula.

General description. Frontal costa bifurcation at the top of the face. The bottom margin of the antennal groove is a little below the bottom margin of the eye. The anterior margin of the vertex does not reach the anterior margin of the eye. The anterior margin of the pronotum forms a slim spine that reaches past the middle of the eye length in dorsal view. The prozonal carinae are long and parallel. The median carina is well-expressed and continuous. Median carina forming a small hump at the posterior end of the prozona. Alae surpasses the apex of the pronotum. Tegmina oval with basal and apical macula. Fore and middle femora are smooth and slender. The first segment of the fore tarsi is long, with three pulvilli. Hind femora smooth; antegenicular tooth small and sharp, genicular tooth imperceptible. The first and third segments of the hind tarsus are equally long. The first segment of the hind tarsus with three rounded pulvilli, all of the same size.

Type series. Costa Rica 1 ♀holotype; Puntarenas, Area de Conservacion Osa, Parque Nacional Corcovado, Sector Sirena; 8.483, -83.591; 22.VIII.2020; D. Janzen, W. Hallwachs, A. Azofeifa A leg; SMNK. 1 ♂paratype; idem; 21.III.2020; BIOUG.

Type locality. Parque Nacional Corcovado, Sector Sirena.

Measurements (in mm). HT: BL 9.98; VW 0.61; EW 0.65; SW 0.2; PL 12.5; PLW 3.19; PH 2.33; TL 1.52; TW 0.68; AL 11.42; FFL 2.52; FFW 0.47; MFL 2.29; MFW 0.52; PFL 6.29; PFW 1.73; HTL 4.83; FTL 0.75; TTL 0.63; ODL 1.63; ODW 0.28; OVL 1.59; OVW 0.22.

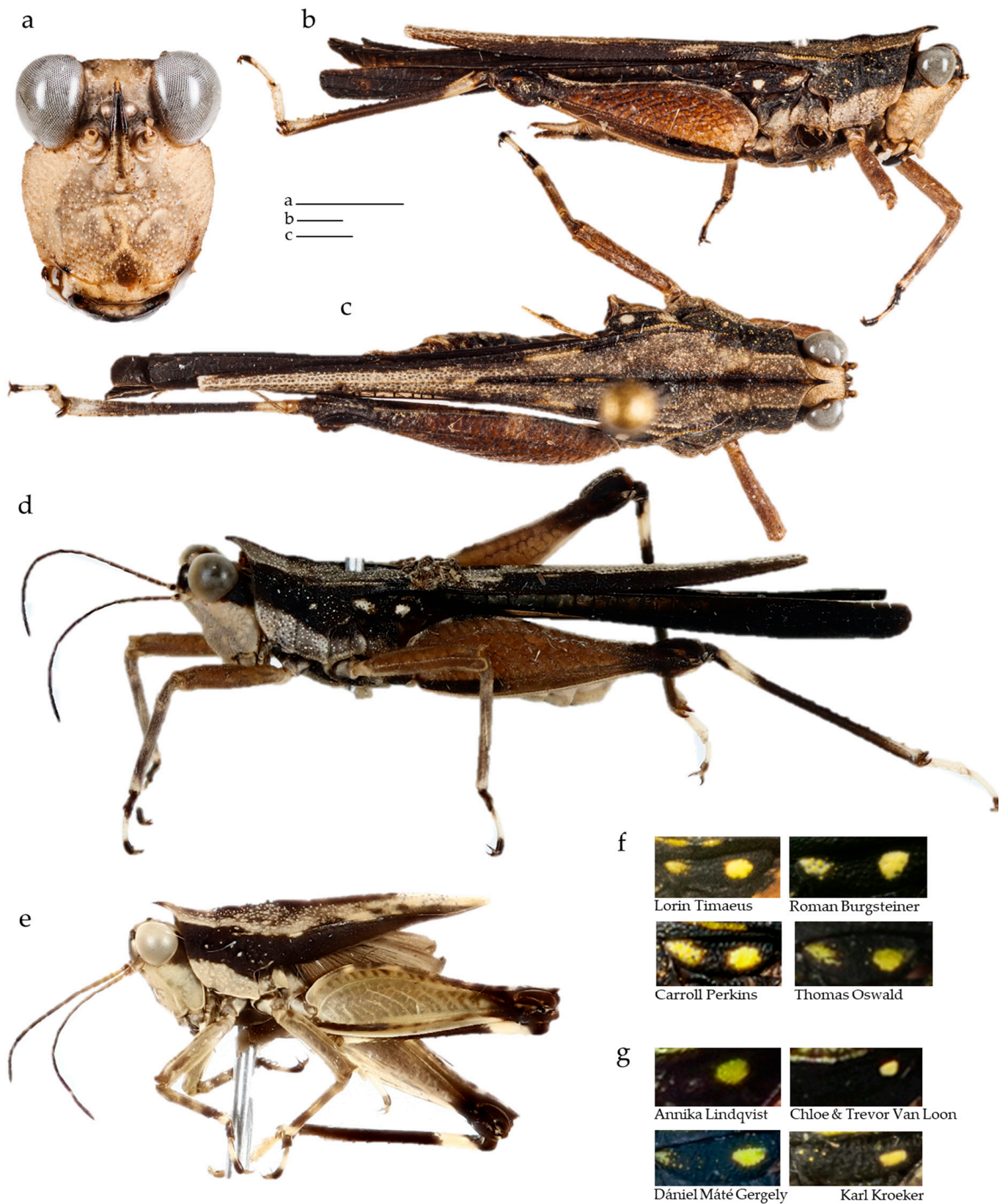


Figure 5. The female holotype (a–c), male paratype (d) and a potential nymph (e) of *Scaria bimaculata* sp. nov. Each scale bar is 1 mm. (a) Head in frontal view. (b) Body in lateral view. (c) Body in dorsal view. (d) Male paratype in dorsal view. (e) Nymph, (f) bimaculated tegmina of *Scaria bimaculata* individuals from iNaturalist (observations 201087251, 20952601, 263007986, and 203374879), (g) unimaculated tegmina of Costa Rican *S. fasciata* from iNaturalist.

PT: BL 8.71; VW 0.48; EW 0.64; SW 0.17; PL 11.37; PLW 2.51; PH 2.07; TL 1.53; TW 0.59; AL 10.4; FFL 2.42; FFW 0.47; MFL 2.37; MFW 0.49; PFL 5.36; PFW 1.41; HTL 4.18; FTL 0.67; TTL 0.62; SPL 0.48; SPW 0.28

Distribution. Endemic to the Pacific side of Costa Rica, SW of Cordillera Talamanc. For now, it is known only from the Puntarenas and San José regions in Costa Rica. The previous records of *S. fasciata* should be revisited since they are likely to hide records of the new species. Namely, 16 observations identified in iNaturalist as *Scardia fasciata* in fact belong to this species (observations 20952601, 67748490, 67821547, 68065127, 74669830, 108217693, 122554371, 131653486, 138424668, 151336734, 178609597, 190317031, 201087251, 203374879, 206313045, 263007986).

Etymology. The specific epithet is the Latin adjective “bimaculata” in the nominative case, meaning “two-spotted”. The name refers to the two white spots on the tegmina.

BOLD Systems BINs. AEO7596; AER7428

Type series Sample IDs. HT: BIOUG77727-A04; PT: BIOUG70307-B11.

Note. The specimens belonging to the BIN AER7428 are nymphs (Figure 5e) that differ from the BIN assigned to the type specimen by about 8%, making it possible that this is yet another undescribed species. Adult specimens will have to be found in order to resolve the identity of this group.

Genus *Tettigidea* Scudder, 1862 [60]

Diagnosis. Eyes are tear-shaped and elongated, slanting toward each other anteriorly. The anterior margin of the pronotum protrudes in the form of a spine or rounded. Usually fully winged. Macro- or brachypronotal.

Type species. *Tettigidea lateralis* (Say, 1824) [61]

Composition. A total of 21 species with many synonyms and nomina dubia.

Distribution. North and South America [56].

Note. *Tettigidea* is a difficult genus to define due to its complicated history and a number of unresolved problems [16,17]. Before large revisions can be made, it will be necessary to track down and reexamine the type specimens, especially those of synonyms to determine if there are some valid species among them. The identifications provided below are not final and should be reexamined once more material is available.

***Tettigidea lateralis lateralis* (Say, 1824) [61] (Figure 6)**



Figure 6. A male specimen of *Tettigidea lateralis lateralis* (BIOUG59944-G08) belonging to the BIN ADC0458.

Diagnosis. The anterior margin of the vertex is a little wider than the eye in the dorsal view. The anterior margin of the pronotum is rounded. The median carina is slightly and uniformly elevated throughout its length. The tegmen has an apical dot or uneven spot. The pronotum and alae surpass the tip of the abdomen.

Distribution. Northern America and Central America [62].

BOLD Systems barcode. ADC0458

Species *Tettigidea* cf. *bruneri* Morse, 1900 [63] (Figure 7)



Figure 7. A female specimen of *Tettigidea* cf. *bruneri* (BIOUG48901-H05) belonging to the BIN AAH2486.

Diagnosis. Similar to *T. lateralis lateralis*. Tip of pronotum at approximately the same level as tip of abdomen (surpassing abdomen in *T. l. lateralis*). Alae invisible (fully developed in *T. lateralis lateralis*).

Distribution. Described from Mexico. No further distribution records.

BOLD Systems BIN. AAH2486. The BIN AEI8939 is assigned to the singular specimen of this morphospecies in the examined collection, but this one was excluded from the analysis since NCBI BLAST showed around 90% compatibility with some Lepidoptera sequences and no matches with other *Tettigidea* sequences. It is clear that this sequence has been contaminated in some way and the BIN itself is not reliable.

Note. The identification of this species is based on its high similarity with *T. lateralis lateralis* and its short pronotum and wings [63]. However, there are a lot of synonyms of *T. lateralis* that could fit this diagnosis as well, but their types are not available for examination.

Subfamily Lophotettiginae Hancock, 1909 [64]

Genus *Lophotettix* Hancock, 1909 [64]

Diagnosis. Wide head with wide scutellum. Antennae are composed of around 11 antennomeres. Antennomeres flattened. Median carina forming a crest. Femora with teeth and lappets. The genus and its species were reviewed in [53,65,66].

General description. Antennae are composed of around 11 antennomeres, apical two segments white. The vertex is around two times wider than the eye. The vertex is a little lowered between the eyes. The frontal costa bifurcation is a little above half of eye height. Scutellum rectangular. Paired ocelli are a little below frontal costa bifurcation. Antennal grooves below the bottom margin of the eyes. Vertex rectangular in dorsal view. Deep fossulae extend throughout the length of the vertex. The carinae of the vertex is short, occupying the anterior quarter of eye length in dorsal view. The prozonal carinae strongly converge caudally. Median carina forming foliaceous or triangular crest. The surface of the pronotum is strongly carinulated. Macropronotal and fully winged. Femora tuberculated. The first segment of the fore tarsus is short. The first segment of the hind tarsus has two small proximal pulvilli and one large distant pulvillus. The first and third segments of the hind tarsus are approximately equal in length.

Type species. *Lophotettix brevicristatus* Hancock, 1909 [64]

Composition. A total of 6 species, including the herein-described one.

Distribution. Central and South America [1].

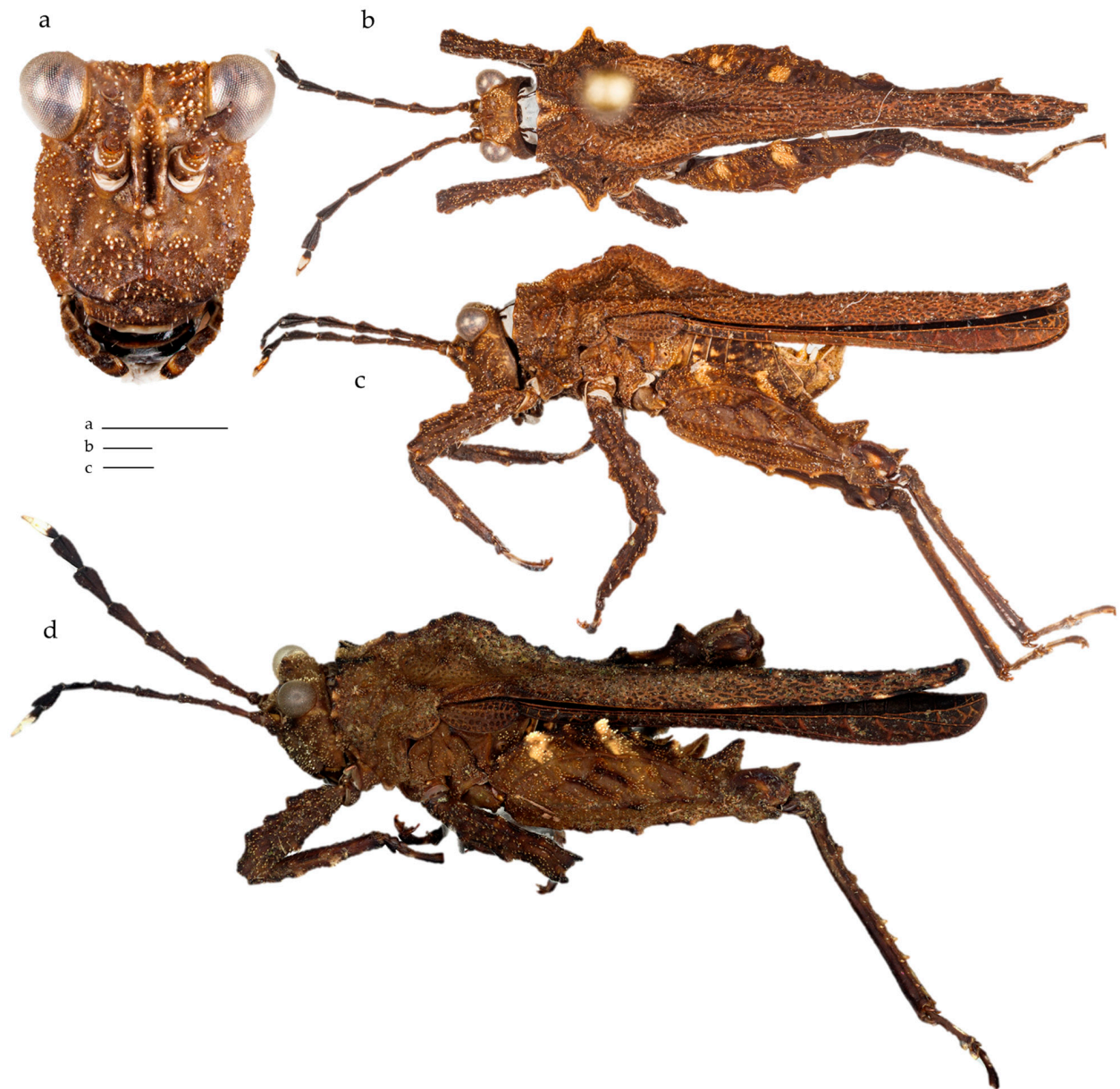
Species *Lophotettix semicristatus* Kasalo & Skejo sp. nov. (Figure 8)

Figure 8. The male holotype (a–c) and the male paratype (d) of *Lophotettix semicristatus* sp. nov. Each scale bar is 1 mm. (a) Head in frontal view. (b) Body in dorsal view. (c) Body in lateral view. (d) Male paratype.

ZooBank ID: LSID urn:lsid:zoobank.org:act:A9EC48E6-5EF5-448A-9F35-BE061B8D5360

Diagnosis. Currently, the species does not have a subgenus placement as it is rather different from its congeners. Crest triangular; climbs up starting in prozona, reaches the highest point at the level of tegmen, and lowers up to the proximal third of the hind femur. Tips of lateral lobes strongly bilobate, projected outward.

Type series. Costa Rica 1 ♂ holotype; Guanacaste, Area de Conservacion Guanacaste, Sector San Cristobal, Estacion San Gerardo; 10.88, -85.389; 27.IV.2015; D. Janzen, W. Hallwachs leg; SMNK. 1 ♂ paratype; idem; 19.V.2014; BIOUG.

Type locality. Area de Conservacion Guanacaste, Sector San Cristobal, Estacion San Gerardo.

Measurements. HT: BL 8.24; VW 0.96; EW 0.56; SW 0.27; PL 11.94; PLW 4.01; PH 3; TL 1.66; TW 0.63; AL 9.79; FFL 2.49; FFW 0.81; MFL 2.71; MFW 0.82; PFL 5.42; PFW 1.91; HTL 4.47; FTL 0.91; TTL 0.63; SPL 0.89; SPW 0.37

PT: BL 8.05; VW 0.92; EW 0.54; SW 0.29; PL 10.87; PLW 3.71; PH 2.82; TL 1.42; TW 0.55; AL 9.49; FFL 2.3; FFW 0.79; MFL 2.66; MFW 0.73; PFL 5.18; PFW 1.75; HTL 4.09; FTL 0.9; TTL 0.57; SPL 0.84; SPW 0.26

Distribution. Known only from Costa Rica.

BOLD Systems BIN. ACY3103

Type series Sample IDs. HT: BIOUG28111-G01; PT: BIOUG25179-B12.

Etymology. The specific epithet is the Latin adjective “semicristatus” in the nominative case, meaning “half-crested”. The name refers to the fact that this species has a much lower crest than its congeners.

Note. The specimen from Costa Rica previously reported as *L. brevicristatus* is here found to represent a new morphologically distinct species, *L. semicristatus* [65].

Note. The sequences attributed to *L. (A.) semicristatus* sp. nov. and *Metrodora ala* sp. nov. are grouped closely together (SH-aLRT/UFbootstrap: 96/97). These two species belong to different subfamilies and their general morphologies differ significantly, but it has been hypothesized that Lophotettiginae and Metrodorinae might be closely related [67], based on facial morphology and the placement of the pronotal crest. These results are based only on a single gene fragment and some important species have not been sampled so a full interpretation is impossible at this point, but there is now a clear indication that Lophotettiginae and Metrodorinae are connected. Future research may show that Metrodorinae and Lophotettiginae are synonymous, but a lot more work is needed to establish the identity of Metrodorinae. The problem is illustrated by the fact that these two species are grouped together but other *Metrodora* species are not clustering in the same clade.

Subfamily Metrodorinae Bolívar, 1887 [51]

Tribe unassigned

Genus *Otumba* Morse, 1900 [63]

Diagnosis. The frontal costa bifurcation is a little above half of eye height. The top margin of the antennal groove is a little above the bottom margin of the eye. Antennae have around 14 visible antennomeres. The vertex is slightly lowered between the eyes. The head is exserted above the level of the pronotum. The carinae of the vertex is short, occupying the anterior quarter of eye length in dorsal view. The median carina is generally low, sometimes forming a single low hump. The lateral lobes are projected outward, and are either rectangular or bilobate. The lateral lobes, carinae, and head often have bright yellow details. The third segment of the hind tarsus is longer than or equal to the first.

Type species. *Otumba scapularis* Morse, 1900 [63]

Composition. A total of 13 species following the taxonomic acts under the *Chiriquia* section of this paper, including the newly described species. Further revision is required.

Distribution. Central and South America [1].

Note. The provided diagnosis has been made expansive in an attempt to limit the genus to a group of relatively uniform morphologies, but a more thorough revision is required. There is a large variation in lateral lobe shapes among the *Otumba* species, which can generally be split into those with simple rectangular lateral lobes, and those with bilobate and sharp lateral lobes. It should be examined whether this character has a phylogenetic value. The following descriptions of new species are based on simple diagnoses, with the omitted characters fitting the above diagnosis.

Species *Otumba dentata* Hancock, 1907 [68] (Figure 9)



Figure 9. A female specimen of *Otumba dentata* (BIOUG85510-B08) belonging to the BIN AEY6158. Additional specimens can be examined in [1].

Diagnosis. The vertex is wide or a little wider than the eye. The median forms a very low elevation past the prozona. The lateral lobe is bilobate, with both forks pointing backward, the outer one is moderately sharp and the inner one is blunt. The bottom part of the lateral lobe is distinctly yellow. The prozonal carinae barely diverge caudad. The prozona is as long as the eye in the dorsal view. The pronotum is light-brown with yellow carinae. The tegmina is very small.

Distribution. Known only from Costa Rica.

BOLD Systems BINs. AEU1829, AEY6158. This species is represented by two BINs that cluster closely together. No morphological differences are apparent between the specimens of these BINs.

Species *Otumba tenuis* Kasalo & Skejo sp. nov. (Figure 10)

ZooBank ID: LSID urn:lsid:zoobank.org:act:B057ACBB-1D2D-4717-9AE5-17E53EBDA685

Diagnosis. Similar to *O. dentata*. The vertex is a little narrower than the eye. The median carina forms a very low elevation past the prozona. The lateral lobe is bilobate, with both forks pointing backward, the outer one is very thin and sharp and the inner one is moderately sharp to blunt. The bottom part of the lateral lobe is a washed-out yellow. The prozonal carinae barely converge caudad. The prozona is shorter than the eye in the dorsal view. The pronotum is dark-brown with yellow carinae. The tegmina is of normal size.

Type series. Costa Rica 1 ♀holotype; Limon, Area de Conservacion La Amistad Caribe, Parque Nacional Barbilla; 9.969, -83.449; 2.VIII.2020; D.Janzen, W.Hallwachs, M.Obando leg; SMNK. 1 ♂paratype; idem; 31.V.2020; BIOUG.

Type locality. Parque Nacional Barbilla.

Measurements. HT: BL 8.66; VW 0.43; EW 0.56; SW 0.15; PL 12.45; PLW 3.86; PH 1.83; TL 1.39; TW 0.55; AL 10.78; FFL 1.9; FFW 0.4; MFL 1.96; MFW 0.46; PFL 5.48; PFW 1.72; HTL 4.43; FTL 0.63; TTL 0.74; ODL 1.47; ODW 0.31; OVL 1.27; OVW 0.19

PT: BL 7.93; VW 0.41; EW 0.52; SW 0.12; PL 10.99; PLW 3.2; PH 1.74; TL 1.26; TW 0.51; AL 10.09; FFL 1.81; FFW 0.33; MFL 1.95; MFW 0.4; PFL 5.08; PFW 1.53; HTL 4.01; FTL 0.61; TTL 0.65

Distribution. Known only from Costa Rica.

Etymology. The specific epithet is the Latin adjective “tenuis” in the nominative case, feminine gender, meaning “thin”. The name refers to the species’ elongated and gracile appearance.

BOLD Systems BIN. AER7890

Type series Sample IDs. HT: BIOUG85491-G12; PT: BIOUG73630-D05



Figure 10. The female holotype (a–c) and the male paratype (d) of *Otumba tenuis* sp. nov. Each scale bar is 1 mm. (a) Head in frontal view. (b) Body in dorsal view. (c) Body in lateral view. (d) Male paratype.

Species *Otumba auricarinata* Kasalo & Skejo sp. nov. (Figure 11)

ZooBank ID: LSID urn:lsid:zoobank.org:act:7D883D7C-9FCF-4119-8BCF-698F0583CB46

Diagnosis. The vertex is distinctly wider than the eye. The apical antennomere is black. The median carina forms a small but distinct hump at the end of the prozona. The lateral lobe is weakly bilobate, with both forks pointing backward and both are moderately sharp. The lateral lobe is framed in yellow. The prozonal carinae are semicircular and divergent in the middle part. The prozona is as long as the eye in the dorsal view. The pronotum is dark-brown with yellow carinae. The tegmina is very small.



Figure 11. The female holotype (a–c) and the male paratype (d) of *Otumba auricarinata* sp. nov. Each scale bar is 1 mm. (a) Head in frontal view. (b) Body in dorsal view. (c) Body in lateral view. (d) Male paratype.

Type series. Costa Rica 1 ♀holotype; Puntarenas, Area de Conservacion La Amistad-Pacifico, Estacion Biologica Altamira; 9.016, -83.004; 18.VIII.2019; D. Janzen, W. Hallwachs, J. Porras Quiros leg; SMNK. 1 ♂paratype; idem; BIOUG.

Type locality. Area de Conservacion La Amistad-Pacifico, Estacion Biologica Altamira.

Measurements. HT: BL 8.93; VW 0.66; EW 0.57; SW 0.26; PL 8.47; PLW 4.19; PH 2.08; TL 1.2; TW 0.44; AL 6.41; FFL 2.06; FFW 0.56; MFL 1.92; MFW 0.44; PFL 5.27; PFW 1.76; HTL 4.63; FTL 0.52; TTL 0.56; ODL 1.36; ODW 0.35

PT: BL 6.67; VW 0.55; EW 0.49; SW 0.21; PL 7.2; PLW 3.3; PH 1.86; TL 1; TW 0.34; AL 5.51; FFL 1.78; FFW 0.43; MFL 1.84; MFW 0.5; PFL 4.53; PFW 1.34; HTL 3.61; FTL 0.56; TTL 0.62; SPL 0.57; SPW 0.31

Distribution. Known only from Costa Rica.

Etymology. The specific epithet is a Latin adjective in the nominative case coined from the Latin words “aurum” (gold) and “carinata” (keeled, carinated). The name refers to the carinae which are interspersed with yellow patches.

BOLD Systems BIN. AAH2487

Type series Sample IDs. HT: BIOUG91407-E03; PT: BIOUG91407-E04.

Species *Otumba ignicula* Kasalo & Skejo sp. nov. (Figure 12)



Figure 12. The female holotype (a–c) and the male paratype (d) of *Otumba ignicula* sp. nov. Each scale bar is 1 mm. (a) Head in frontal view. (b) Body in lateral view. (c) Body in dorsal view. (d) Male paratype.

ZooBank ID: LSID urn:lsid:zoobank.org:act:41F84B6E-BBB7-430C-9943-57965B0B74E8

Diagnosis. The vertex is distinctly wider than the eye. The apical and basal six antennomeres are white. The median carina forms a small hump at the end of the prozona. The lateral lobe is strongly bilobate, with both forks pointing backward, the outer one is sharp and long and the inner one is moderately sharp and short. The lateral lobe is framed in yellow. The prozonal carinae barely converge caudad. The prozona is as long as the eye in the dorsal view. The pronotum is dark-brown with yellow carinae. The tegmina is small.

Type series. Costa Rica 1 ♀holotype; Puntarenas, Area de Conservacion La Amistad-Pacifico, Estacion Biologica Altamira; 9.015, -83.004; 13.IV.2020; D. Janzen, W. Hallwachs leg; SMNK. 1 ♂paratype; idem; 10.VI.2020; D. Janzen, W. Hallwachs, J. Porrás Quiros leg; BIOUG.

Type locality. Area de Conservacion La Amistad-Pacifico, Estacion Biologica Altamira.

Measurements. HT: BL 11; VW 0.82; EW 0.61; SW 0.26; PL 9.87; PLW 5.16; PH 2.13; TL 1.18; TW 0.51; AL 7.62; FFL 2.17; FFW 0.56; MFL 2.47; MFW 0.56; PFL 5.66; PFW 2.11; HTL 5.03; FTL 0.58; TTL 0.85; ODL 1.82; ODW 0.4; OVL 1.89; OVW 0.24

PT: BL 8.23; VW 0.67; EW 0.54; SW 0.23; PL 8.54; PLW 4.27; PH 2.09; TL 0.87; TW 0.34; AL 6.22; FFL 2.1; FFW 0.49; MFL 1.86; MFW 0.55; PFL 5.24; PFW 1.82; HTL 4.16; FTL 0.64; TTL 0.75

Distribution. Known only from Costa Rica.

Etymology. The specific epithet is derived from the Latin diminutive noun “igniculus” (little fire), used here as a feminine adjective in the nominative case. The name refers to the brown-orange coloration that resembles a burning fire.

BOLD Systems BIN. AEM7957

Type series Sample IDs. HT: BIOUG64451-E01; PT: BIOUG89948-D07

Genus *Chiriquia* Morse, 1900 [63]

Diagnosis. The frontal costa bifurcation is a little below half of the eye height. The top margin of the antennal groove is visibly below the bottom margin of the eye. The antennae have around 13 visible antennomeres. The entire vertex lowers between the eyes and the middle part lowers further. The head is dorsoventrally elongated. The head is exerted above the level of the pronotum. The scutellum is vase-shaped. The carinae of the vertex is short, occupying the anterior third of eye length in the dorsal view. The median carina generally forms two humps anteriorly and sometimes several small ones posteriorly. The lateral lobes are projected outward and either smooth or sharp. The third segment of the hind tarsus is approximately equal to the first.

Type species. *Chiriquia serrata* Morse, 1900 [63]

Composition. Six species, counting the herein proposed taxonomic acts.

Distribution. Central and South America [69].

Note. *Chiriquia spinifrons* (Stål, 1861) [70] comb. resurr. and *Chiriquia concinna* (Bolívar, 1887) comb. resurr. are transferred here to *Chiriquia* from *Otumba*. Both have historically been shuffled between these two genera [1,71], but we find that they fit the above diagnosis and differ significantly from the diagnosis of *Otumba*. While *C. spinifrons* comb. resurr. has only one pronotal hump instead of two, its head morphology completely matches that of *C. serrata*. The head is identical in *C. concinna* as well.

Species *Chiriquia serrata* Morse, 1900 [63] (Figure 13)



Figure 13. A male specimen of *Chiriquia serrata* (BIOUG77759-C05) belonging to the BIN ACY3240.

Diagnosis. The vertex is nearly two times wider than the eye. The lateral carinae of the vertex forms low horns. The median carina forms two crests, the anterior one is medium-sized, the posterior one is small, and several small humps are caudad.

Distribution. Known only from Costa Rica.

BOLD Systems BIN. ACY3240, ADL7675, AEO7600, AEU8363

Note. Although the specimens of this species are assigned to several BINs, there are no significant morphological differences between them. These BINs group closely together in the cluster analysis; hence, we refrain from describing more species until further research can be conducted.

Tribe Metrodorini Bolívar, 1887 [51]

Genus *Metrodora* Bolívar, 1887 [51]

Diagnosis. The vertex is rectangular in the dorsal view and wider than the eye. The frontal costa bifurcation is at the middle of the eye height or lower. The median carina forms a hump or slight arcuation. The femora is tuberculated. The lateral lobes are projected sideways. Apterous.

Type species. *Metrodora rana* Bolívar, 1887 [51]

Composition. A total of 15 species including the herein described two.

Distribution. Central and South America [1].

Note. This genus is notoriously difficult to define. At the moment it includes many vaguely similar apterous species from mainland Latin America, while the Caribbean species are separated into multiple genera. For now, we place the new species in *Metrodora*, but a revision is required. For a detailed discussion of this problem see Kasalo et al. (2023d).

Species *Metrodora mollilobata* Kasalo & Skejo sp. nov. (Figure 14)

ZooBank ID: LSILSID urn:lsid:zoobank.org:act:CD81B685-240A-4F6B-B143-EA4DBD65FA67

Diagnosis. Most similar to *Metrodora gibbosula* [72], *Metrodora gibbinota* [73], and *Metrodora arcuata* [74].

Differentiated from *M. gibbosula* by: (i) medial carina moderately protruding in front of eyes (slightly in *M. gibbosula*); (ii) lateral lobe rounded (weakly bilobate, sharp in *M. gibbosula*); (iii) pronotal apex blunt triangular (very sharp in *M. gibbosula*).

Differentiated from *M. gibbinota* by: (i) medial carina moderately protruding in front of eyes (not protruding in *M. gibbinota*); (ii) pronotal hump nearly rectangular (rounded in *M. gibbinota*); (iii) fore and middle femora strongly tuberculated (weakly tuberculated in *M. gibbinota*).

Differentiated from *M. arcuata* by: (i) medial carina moderately protruding in front of eyes (slightly in *M. arcuata*); (ii) pronotal hump nearly rectangular (strongly sloping anteriorly in *M. arcuata*); (iii) lateral lobe rounded (weakly bilobate, sharp in *M. arcuata*); (iv) pronotal apex blunt triangular (very sharp in *M. arcuata*).

General description. The base of the vertex is approximately at the level of the top margin of the eyes in frontal view, and the medial carina is distinctly raised. The frontal costa bifurcation is at the middle of the eye height. The scutellum is vase-like. The paired ocelli are a little above the bottom margin of the eyes. The antennal grooves are below the bottom margin of the eyes. The vertex is more than two times wider than the eye. The carinae of the vertex is short, occupying the anterior third of eye length in dorsal view. The prozonal carinae are short and slightly converge caudally. The pronotum is raised in the anterior part, forming a nearly rectangular hump. Posterior to hump, pronotum rugose. The pronotal apex is blunt and triangular. The infrascapular area is long, moderately wide in the anterior half, and very narrow in the posterior half. The lateral lobes are projected outward and rounded. The anterior and middle femora are tuberculated. The first segment of the anterior tarsus is short. The hind femur is tuberculated, with large antegenicular and

genicular teeth. The first segment of the hind tarsus has two small sharp proximal pulvilli and one large sharp distal pulvillus. The first and third segments of the hind tarsus are equal in length.



Figure 14. The female holotype (a–c) and the male paratype (d) of *Metrodora mollilobata* sp. nov. Each scale bar is 1 mm. (a) Head in frontal view. (b) Body in dorsal view. (c) Body in lateral view. (d) Male paratype.

Type series. Costa Rica 1 ♀ holotype; Guanacaste, Area de Conservacion Guanacaste, Sector San Cristobal, Estacion San Gerardo; 10.88, -85.389; 24.XI.2014; D. Janzen, W. Hallwachs leg; SMNK. 1 ♂ paratype; Heredia, Area de Conservacion Central, Parque Na-

cional Braulio Carrillo, Sector El Ceibo; 18.V.2020; 10.327, -84.079; D.Janzen, W.Hallwachs, J. A. Solano leg; BIOUG.

Type locality. Area de Conservacion Guanacaste, Sector San Cristobal, Estacion San Gerardo.

Measurements. HT: BL 7.49; VW 0.85; EW 0.44; SW 0.49; PL 6.56; PLW 3.47; PH 2.77; FFL 1.43; FFW 0.68; MFL 2.04; MFW 0.73; PFL 4.22; PFW 1.79; HTL 3.68; FTL 0.48; TTL 0.41; ODL 0.88; ODW 0.28; OVL 0.55; OVW 0.15

PT: BL 7.3; VW 0.81; EW 0.41; SW 0.43; PL 6.84; PLW 3.24; PH 2.85; FFL 1.39; FFW 0.64; MFL 1.73; MFW 0.88; PFL 3.76; PFW 1.6; HTL 3.24; FTL 0.4; TTL 0.37

Distribution. Known only from Costa Rica.

Etymology. The specific epithet is a Latin compound adjective in the nominative case coined from the Latin words “mollis” (soft, delicate) and “lobata” (lobed). The name refers to the species’ rounded lobes that differentiate it from other similar species.

BOLD Systems BIN. ADA2779

Type series Sample IDs. HT: BIOUG27762-D11; PT: BIOUG73029-F11

Species *Metrodora sinuata* (Morse, 1900) [63] (Figure 15)



Figure 15. A female specimen of *Metrodora sinuata* (BIOUG28273-F09) belonging to the BIN ADA4377.

Diagnosis. The entire vertex protrudes far past the anterior margin of the eyes. The median carina is slightly elevated in the anterior third. The pronotal apex is narrow but blunt. The fore and mid femora are tuberculated.

Distribution. Nicaragua [75], Costa Rica.

BOLD Systems BIN. ADA4377

Species *Metrodora ala* Kasalo & Skejo sp. nov. (Figure 16)

ZooBank ID: LSID urn:lsid:zoobank.org:act:07A3D89E-8911-4F09-8734-B528C4990E5C

Diagnosis. Most similar to *Metrodora uniformis* (Bruner, 1910) [73]. Differentiated by: (i) apex and base of antenna white (small white patches near apex and base in *M. uniformis*); (ii) lateral lobe bilobate, outer fork sharp, inner fork blunt (rounded lateral lobe in *M. uniformis*); (iii) pronotum raised in anterior third, forming low, long, and slightly wavy hump (hump not wavy in *M. uniformis*).

General description. The base of the vertex is approximately at the level of the top margin of the eyes in the frontal view, with medial and lateral carinae distinctly raised. The frontal costa bifurcation is at the middle of the eye height. The scutellum is vase-like. The paired ocelli are a little above the bottom margin of the eyes. The antennal grooves are below the bottom margin of the eyes. The vertex is around two times wider than the eye. The carinae of the vertex is short, occupying the anterior third of eye length in the dorsal view. The prozonal carinae are short and parallel. The pronotum is raised in the anterior

third, forming a low, long, and slightly wavy hump. Posterior to hump, pronotum rugose. The pronotal apex is narrow and sharp. The infrascapular area is long, wide in the anterior third, and progressively narrowing caudad. The lateral lobes are projected outward and bilobate, the outer fork is sharp and the inner fork is blunt. The anterior and middle femora are strongly tuberculated. The first segment of the anterior tarsus is short. The hind femur is tuberculated, with large antegenicular and genicular teeth. The first segment of the hind tarsus has three sharp pulvilli of approximately the same size. The first and third segments of the hind tarsus are equal in length.



Figure 16. The male holotype (a–c) and the male paratype (d) of *Metrodora ala* sp. nov. Each scale bar is 1 mm. (a) Head in frontal view. (b) Body in lateral view. (c) Body in dorsal view. (d) Male paratype.

Type series. Costa Rica 1 ♂holotype; Puntarenas, Area de Conservacion Osa, Parque Nacional Corcovado, Sector Sirena; 8.483, -83.591; 20.VI.2020; D. Janzen, W. Hallwachs, A. Azofeifa A leg; SMNK. 1 ♂paratype; Puntarenas, Area de Conservacion Pacifico Central, Savegre, Quepos; 26.V.2020; 9.263, -83.871; D. Janzen, W. Hallwachs, S. Stroud leg; BIOUG.

Type locality. Parque Nacional Corcovado, Sector Sirena.

Measurements. HT: BL 6.6; VW 0.63; EW 0.36; SW 0.3; PL 5.75; PLW 4.08; PH 1.94; FFL 1.57; FFW 0.69; MFL 2.01; MFW 0.7; PFL 3.88; PFW 1.79; HTL 2.98; FTL 0.42; TTL 0.4; SPL 0.58; SPW 0.25

PT: BL 6.54; VW 0.64; EW 0.38; SW 0.3; PL 6.21; PLW 4.27; PH 2.08; FFL 1.67; FFW 0.72; MFL 1.99; MFW 0.69; PFL 4.04; PFW 1.53; HTL 2.99; FTL 0.42; TTL 0.31; SPL 0.54; SPW 0.37

Distribution. Known only from Costa Rica.

Etymology. The specific epithet is the Latin word “ala” (wing) in apposition. The name refers to the fact that the lateral lobes of this species are spread out like wings when seen from above.

BOLD Systems BIN. AEO7590

Type series Sample IDs. HT: BIOUG77726-F05; PT: BIOUG76527-G11.

Subfamily Tetriginae Rambur, 1838 [50]

Tribe Tetrigini Rambur, 1838 [50]

Genus *Clypeotettix* Hancock, 1902 [76]

Diagnosis. Similar to *Paratettix*. Differentiated from it by: (i) bifurcation of frontal costa in the upper third of eye height (upper quarter in *Paratettix*); (ii) middle femora very robust with a strong tooth in the middle of bottom margin (fore and middle femora approximately equally robust in *Paratettix*); (iii) third segment of hind tarsus approximately equal to first (third segment shorter in *Paratettix*); (iv) median carina reaching anterior margin of pronotum (not reaching in *Paratettix*).

Note. This genus might be synonymous with *Paratettix*, and is at least very closely related to it. More data on the American Tetriginae is necessary to resolve this issue.

Type species. *Clypeotettix schochii* (Bolívar, 1887) [51]

Composition. *C. schochii*, *C. mexicanus* comb. nov., *C. zonata* (Walker, 1871) comb. nov.

Distribution. North, Central, and South America [77,78].

Note. The morphologies of *Paratettix zonata* (Walker, 1871) and *Paratettix mexicanus* completely fit with the diagnosis of *Clypeotettix* and are thus placed in this genus, resulting in the new combinations *C. zonata* comb. nov. and *C. mexicanus* comb. nov.

Species *Clypeotettix schochii* (Bolívar, 1887) [51] (Figure 17)



Figure 17. A female specimen of *Clypeotettix schochii* (BIOUG55327-A01) belonging to the BIN AEF0990.

Diagnosis. Wide humeral angles. Tectate pronotum. The middle femur is very robust with a triangular tubercle in the middle of the bottom margin.

Distribution. North America (including Central America).

BOLD Systems BIN. AEF0990

Species *Clypeotettix mexicanus* (Saussure, 1861) [33] **comb. nov.** (Figure 18)



Figure 18. A male specimen of *Clypeotettix mexicanus* (BIOUG73008-B12) belonging to the BIN AEI7486.

Diagnosis. Normal humeral angles. Tectate pronotum. The middle is femur robust with a rounded tubercle in the middle of the bottom margin.

Distribution. North America (including Central America) [79].

BOLD Systems BIN. AEI7486

Note. Both the morphology and molecular data point to this species being closely related to *C. schochii* so we transfer it from *Paratettix* to *Clypeotettix*. The relationship with other Tetrigini genera remains to be determined.

Genus *Platythorus* Morse, 1900 [63]

Diagnosis. The frontal costa bifurcation is near the top of the face. Paired ocelli at around middle of eye height. The midline of antennal grooves at the level of the bottom margin of the eyes. The vertex is as wide as the eye or wider. The lateral carinae of the vertex forms U-shapes. The prozonal carinae converge caudally. The median carina reaches the anterior margin of the pronotum. The median carina forms a small hump at the end of the prozona. The middle femora is robust but has no strongly expressed tubercles. The third segment of the hind tarsus is usually barely shorter than the first.

Type species. *Platythorus camurus* Morse, 1900 [63]

Composition. *P. camurus*, *P. toltecus* comb. nov., *P. inabsolutus* sp. nov.

Distribution. North and South America [1].

Note. This genus has until now been assigned to Metrodorinae, but it is unlikely that it is closely related to *Metrodora*. Due to the high placement of facial features and its similarity with *Paratettix* and *Clypeotettix*, the genus is transferred to Tetriginae.

Note. This genus is similar to *Paratettix*, *Clypeotettix*, *Allotettix* Hancock, 1899 [80], and *Crimisus* Bolívar, 1887. However, the median carina in *Platythorus* is uninterrupted, the lateral carinae of the vertex are U-shaped, and the prozonal carinae are convergent and longer than in *Paratettix*. *Paratettix* is a large genus in need of revision, so many more changes to its taxonomy are expected [81]. The most notable similarity with *Clypeotettix* is the presence of a hump in the anterior part of the pronotum and laterally projected lateral lobes. The main differences between *Platythorus* and *Clypeotettix* are the lower pronotal hump, middle femora without tubercles, and higher placement of frontal costa bifurcation

in *Platythorus*. *Allotettix* and the macropronotal species herein treated as *Platythorus* are exceptionally similar with a few key differences: higher pronotal hump, more robust middle femora, and higher placement of frontal costa bifurcation in *Platythorus*. Finally, the main differences between *Crimisus* and *Platythorus* are higher placement of facial features and smoother anterior femora in *Platythorus*. At least some of these prevalent similarities could be due to shared ancestry, but the currently available molecular data is insufficient to resolve even intrageneric relationships [82]. Additionally, these genera have not even been well sorted out morphologically [17].

Species *Platythorus camurus* Morse, 1900 [63] (Figure 19)



Figure 19. A female specimen of *Platythorus camurus* (BIOUG77724-F12) belonging to the BIN ACT4992.

Diagnosis. The vertex is 1.5 times wider than the eye. The prozonal carinae moderately converge caudally. Apterous species. The anterior and middle femora have strong tubercles on the ventral margin.

Distribution. Central America [1].

BOLD Systems BIN. ACT4992

Species *Platythorus toltecus* (Saussure, 1861) [33] comb. nov.

Diagnosis. The vertex is about 1.5 times wider than the eye. The prozonal carinae barely converge caudally. The pronotum reaches up to the level of the hind knees. The alae are a little shorter than the pronotum. The third segment of the hind tarsus is shorter than the first.

Distribution. Widely distributed in North and South America, but some of the synonyms of this species may represent separate species.

Note. The above diagnosis is based on the holotype only since specimens of many different morphologies are currently assigned to this species. This species has until now been assigned to *Paratettix*, but is found here to be more similar to the other *Platythorus* species. However, more data is needed to confidently systematize the American Tetriginæ.

Species *Platythorus inabsolutus* Kasalo & Skejo sp. nov. (Figure 20)

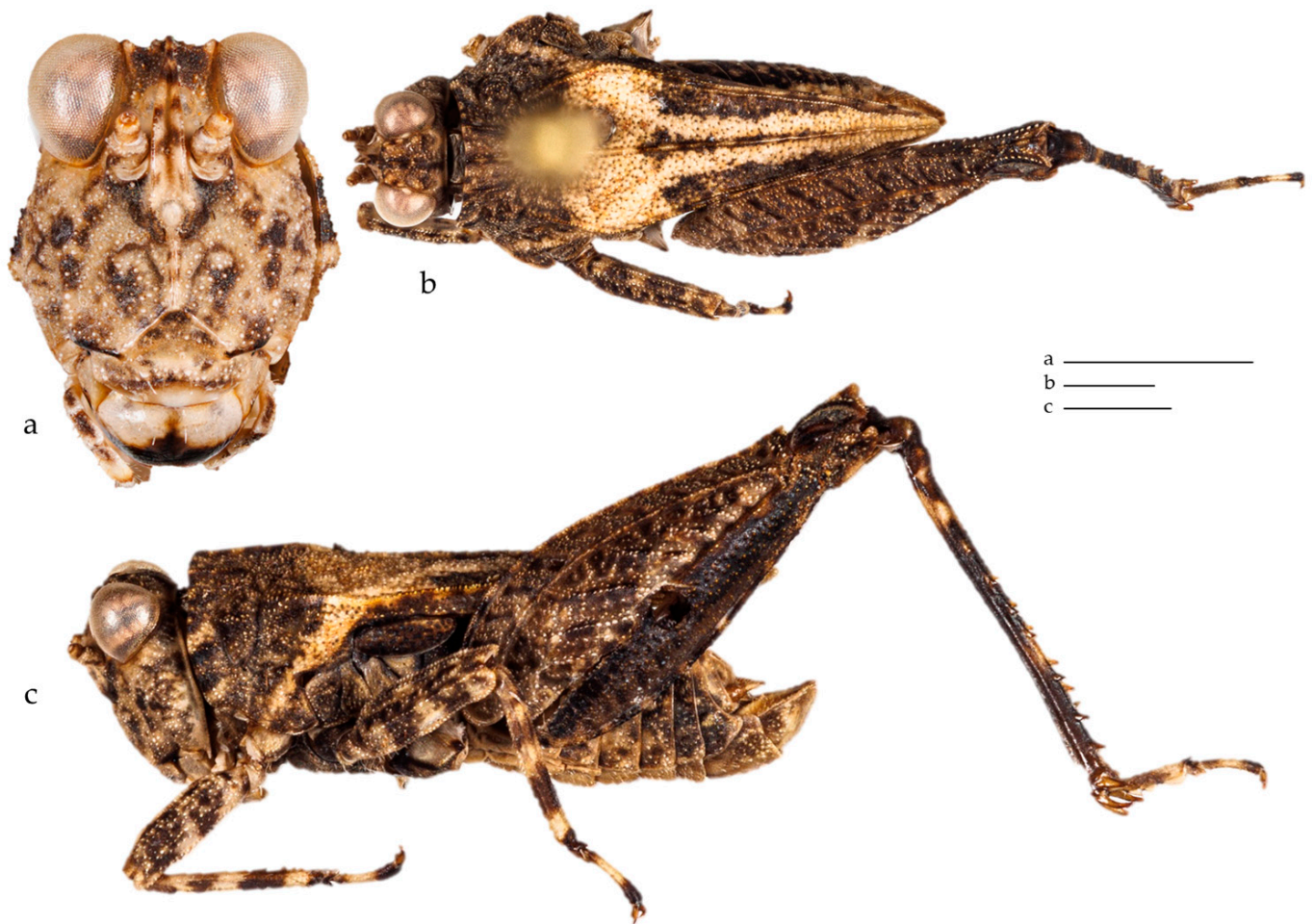


Figure 20. The male holotype of *Platythorus inabsolutus* sp. nov. Each scale bar is 1 mm. (a) Head in frontal view. (b) Body in dorsal view. (c) Body in lateral view.

ZooBank ID: LSID urn:lsid:zoobank.org:act:F5D46CE2-7D9F-4B35-9E84-B45C1F66AFBB

Diagnosis. The vertex is as wide as the eye. Very small tegmina, alae absent or invisible. The third segment of the hind tarsus is barely shorter than the first.

General description. The frontal costa bifurcation near the top of the face. The paired ocelli are at half of the eye height. The midline of antennal grooves is at the bottom margin of the eyes. The vertex is approximately as wide as the eye. The lateral carinae of the vertex is U-shaped. The prozonal carinae are short, converging caudally. The lateral lobes are moderately projected outward. The median carina forms a small hump at the end of the prozona. Brachypronotal. The pronotal apex is narrow and blunt. The tegmina is very small, and the alae are invisible. The fore and middle femora are robust with wavy margins. The first segment of the anterior tarsus is short, with three pulvilli. The hind femur is robust with a black bottom half. The first segment of the hind tarsus has two small sharp proximal pulvilli and one large sharp distal pulvillus. The third segment of the hind tarsus is barely shorter than the first.

Type specimen. Costa Rica 1 ♂ holotype; Puntarenas, Area de Conservacion Osa, Parque Nacional Corcovado, Sector Sirena; 8.478, -83.593; 29.III.2020; D. Janzen, W. Hallwachs, A. Azofeifa A leg; SMNK.

Type locality. Parque Nacional Corcovado, Sector Sirena.

Measurements. HT: BL 6.72; VW 0.47; EW 0.56; SW 0.23; PL 5.57; PLW 2.87; PH 2.03; TL 0.97; TW 0.39; FFL 1.39; FFW 0.5; MFL 1.63; MFW 0.56; PFL 4.63; PFW 1.74; HTL 3.94; FTL 0.66; TTL 0.58; SPL 0.68; SPW 0.36

Distribution. Known only from Costa Rica.

Etymology. The specific epithet is the Latin adjective “absolutus” (unfinished, incomplete) in the nominative case. The name refers to the fact that the species lacks alae and is thus incomplete.

BOLD Systems BIN. AEU1088

Type series Sample IDs. HT: BIOUG73625-D09.

Genus *Ochetotettix* Morse, 1900 [63]

Diagnosis. The frontal costa bifurcation is at the upper third of the eye height. The vertex is two times wider than the eye. The median carina forms a medium-high crest in the anterior quarter. Fully winged.

Type species. *Ochetotettix barretti* (Hancock, 1899) [80]

Composition. Monotypic.

Distribution. Mexico and Central America [83].

Note. *Ochetotettix* was up to now not classified in any of the Tetriginæ tribes. Here, we place it in Tetrigini due to the elevation of its median costa, and the width and the shape of the vertex which are all reminiscent of the genus *Tetrix*.

Species *Ochetotettix barretti* (Hancock, 1899) [80] (Figure 21)



Figure 21. A female specimen of *Ochetotettix barretti* (BIOUG48915-D04) belonging to the BIN ACG2835.

Diagnosis. Indistinguishable from the generic diagnosis.

BOLD Systems BIN. ACG2835

Tribe unassigned

Genus *Teredorus* Hancock, 1907 [68]

Diagnosis. Extremely narrow vertex.

Type species. *Teredorus stenofrons* Hancock, 1907 [68]

Composition. Only two American species, *T. stenofrons* and *T. aztecus*.

Distribution. North and South America [17].

Note. Devriese and Husemann (2023) [84] proposed for the narrow-vertex Tetriginæ genera to be differentiated by the region they inhabit, i.e., *Teredorus* is present only in the Americas. This approach is preliminary but is practical until the many Asian species can be reviewed and systematized. This approach is followed here as well.

Species *Teredorus* cf. *aztecus* (Saussure, 1861) [33] (Figure 22)



Figure 22. A male specimen of *Teredorus aztecus* (BIOUG73628-D07) belonging to the BIN AET3068.

Diagnosis. The vertex is extremely narrow. The pronotal surface is flat. The dorsal margin of the anterior femora is semi-elliptical.

Note. Differences between *T. aztecus* and *T. stenofrons* are not completely clear, which is made more problematic by the numerous synonyms of *T. aztecus* that need to be reviewed. It seems that *T. aztecus* has a more northern distribution than *T. stenofrons*.

Distribution. North America and the extreme north of South America [1].

BOLD Systems BIN. AET3068

4. Discussion

As previously established [31], the tetrigid COI barcodes carry an insufficient phylogenetic signal to reconstruct most of the relationships above the generic level. The only exception is the position and status of the subfamily Batrachideinae, which is strongly supported as basal and monophyletic. In this study, the genera *Scaria*, *Tettigidea*, *Otumba*, *Clypeotettix*, and *Platythorus* are reconstructed as monophyletic, while most of the others are represented by only a single species. The genus *Metrodora* is not resolved in our analysis, which might be due to the low resolution of the marker, but might also imply that it could be split into several genera since there are several distinct morphologies included in *Metrodora* [67]. Most notably, *Lophotettix semicristatus* sp. nov. and *Metrodora ala* sp. nov. are grouped together with high support. This is supported by their morphological similarity as well [67], which suggests that the subfamilies Metrodorinae and Lophotettiginae need to be completely reevaluated.

We have expanded the genera *Clypeotettix* and *Platythorus* by new combinations and *Platythorus* by new species. *Clypeotettix mexicanus* comb. nov., *Clypeotettix zonata* comb. nov., and *Platythorus toltecus* comb. nov. had all previously been assigned to *Paratettix*. Both morphology and barcoding data point to close relationships between the species within the mentioned genera, giving us an opportunity to better define the American Tetriginae. *Paratettix* is a cosmopolitan genus with a very poor diagnosis [81]. It seems likely that this genus actually encompasses many smaller geographically constrained genera which are very similar to each other [81,85]. To address the problem of *Paratettix*, we have reassigned some of the *Paratettix* species according to their similarity with the type species of *Clypeotettix* and *Platythorus*, but this is only the first step towards a more concrete solution. All of these genera, together with *Crimisus* Bolívar, 1887 need to be reassessed in detail to understand the relationships between the American Tetriginae.

Integrative taxonomy is an important tool in elucidating the true diversity of insects, especially those in diverse regions and groups [86–88]. Until now, the only other instance of DNA barcoding data being used to supplement species descriptions was the discovery of two new sympatric species of *Eucriotettix* [7]. The genetic distance between these two

species is nearly 13% despite them having very few morphological differences [7]. This level of divergence between species for the COI marker is extremely high, as the intraspecific genetic distances in insects have been found to generally be around 3% [89–91]. It should be noted that large-scale analyses have identified a subset of species with larger intraspecific genetic variation [91]. This could be the result of several cryptic species being grouped under a single morphospecies but describing every bearer of a divergent COI sequence as a new species without further molecular or morphologic evidence would result in impractical species inventories [20,90,92].

We thus opted to use conservative criteria for species delimitation, insisting on both 10% genetic distances and clearly identifiable morphological differences. Even so, the diversity of the Costa Rican fauna of Tetrigidae was underestimated [93,94], in part because previous morphological studies defined species more broadly [17,69,95]. A notable example is the high molecular and low morphological difference between *Scaria fasciata* and *S. bimaculata* sp. nov. Since relatively few characters are currently recognized as useful for species differentiation [18], further studies might identify many more cryptic or nearly cryptic species. It should also be noted that a single molecular marker such as COI cannot offer all answers by itself. The question of the level of separation between *Chiriquia serrata* populations should be resolved using more molecular data. The same is true for the phylogenetic relationships between genera and higher taxonomic categories.

This study enabled us to understand the variability of Tetrigidae a little better. While some evolutionarily younger taxa can have high variation in lateral lobe shape [47,96], this character has shown itself to be an important one for species delimitation within Metrodorinae. Similarly, coloration in Tetriginae and Thoradontini is highly variable [47,97–101], but in Metrodorinae and Batrachideinae it seems to have value for species identification as it is very consistent among specimens from different localities. Unfortunately, molecular data on tetrigids in most of the world is scarce [102]; hence, the taxonomy of this group will remain based mostly on morphology until projects addressing this gap are undertaken. Generating more DNA barcodes and assigning them to well-described morphologies will speed up further research and make this group much more accessible.

The work on Neotropical Tetrigidae is far from over. Although many revisions were conducted in recent years on many higher taxonomic groups, a large number of genera and species remain ill-defined and unclearly classified, which will likely preclude the production of a high-confidence general identification key in the foreseeable future [17,52,65,66,95,103,104].

Author Contributions: Conceptualization, N.K. and J.S.; Data curation, N.K., M.H. and D.B.; Formal analysis, N.K.; Investigation, N.K., D.H.J., W.H., M.S. and D.B.; Methodology, N.K., D.H.J., W.H., A.B., M.H. and M.V.; Resources, D.H.J., W.H., T.D.-L. and D.F.; Software, N.K.; Supervision, M.H., T.D.-L., D.F. and J.S.; Validation, N.K., D.H.J., W.H., A.B., M.H., M.V., T.D.-L., D.F., M.S. and J.S.; Visualization, N.K., M.V. and J.S.; Writing—original draft, N.K.; Writing—review & editing, D.H.J., W.H., A.B., M.H., M.V., M.S., D.B. and J.S. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: Full specimen data, including DNA sequences, photographs, and localities, is available at <https://dx.doi.org/10.5883/DS-CRTET>, accessed on 16 November 2024.

Acknowledgments: Thanks to Filipa Burul for taking preliminary photographs of some species and to Bože Kokan for handling specimen shipment. Thanks to Maja Kovačević for reading an early version of this manuscript and providing feedback. All ACG specimens were collected, exported and DNA barcoded under Costa Rican government permits issued to BioAlfa (Janzen and Hallwachs 2019) (R-054-2022-OT-CONAGEBIO; R-019-2019-CONAGEBIO; National Published Decree #41767), JICA-

SAPI #0328497 (2014) and DHJ and WH (ACG-PI-036-2013; R-SINAC-ACG-PI-061-2021; Resolución N°001-2004 SINAC; PI-028-2021).

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Cigliano, M.M.; Braun, H.; Eades, D.C.; Otte, D. Orthoptera Species File. Available online: <https://orthoptera.speciesfile.org/> (accessed on 16 November 2024).
2. Tan, M.K.; Tumbrinck, J.; Rivera, R.R.; Nuñez, O.M. A New Genus and a New Species of Cladonotinae (Orthoptera: Tetrigidae) from Mindanao, Philippines. *Zootaxa* **2024**, *5506*, 194–204. [[CrossRef](#)] [[PubMed](#)]
3. Luo, J.; Zhang, R.; Deng, W. First Mitogenomic Characterization of *Macromotettixoides* (Orthoptera, Tetrigidae), with the Descriptions of Two New Species. *ZooKeys* **2024**, *1195*, 95–120. [[CrossRef](#)] [[PubMed](#)]
4. Guan, D.-L.; Chen, Y.-Z.; Qin, Y.-C.; Li, X.-D.; Deng, W.-A. Chromosomal-Level Reference Genome for the Chinese Endemic Pygmy Grasshopper, *Zhengitettix transpicula*, Sheds Light on Tetrigidae Evolution and Advancing Conservation Efforts. *Insects* **2024**, *15*, 223. [[CrossRef](#)] [[PubMed](#)]
5. Li, R.; Ying, X.; Deng, W.; Rong, W.; Li, X. Mitochondrial Genomes of Eight Scelimeninae Species (Orthoptera) and Their Phylogenetic Implications within Tetrigoidea. *PeerJ* **2021**, *9*, e10523. [[CrossRef](#)]
6. Qin, Y.-C.; Liu, J.; Li, X.-D.; Chen, Y.-Z.; Deng, W.-A. On the Specific Status of *Scelimena spicupennis* and a New Record of *S. discalis* from China with Mitochondrial Genome Characterization (Orthoptera, Tetrigidae). *ZooKeys* **2023**, *1185*, 83–104. [[CrossRef](#)]
7. Tan, M.K.; Storozhenko, S.Y.; Hwang, W.S.; Meier, R. Integrative Taxonomy Reveals Two Sympatric Species of the Genus *Eucriotettix* Hebard, 1930 (Orthoptera: Tetrigidae). *Zootaxa* **2017**, *4268*, 377–394. [[CrossRef](#)]
8. Guan, D.-L.; Huang, C.-M.; Deng, W.-A. Reassessment of the Phylogenetics of Two Pygmy Grasshopper Generic Groups *Tetrix* and *Systolederus* through Mitochondrial Phylogenomics Using Four New Mitochondrial Genome Assemblies. *Insects* **2024**, *15*, 174. [[CrossRef](#)]
9. Li, X.; Lin, C.; Wang, L.; Gao, Z.; Zhu, T.; Lin, L. Mitogenomic Characterization and Phylogeny of *Scelimena melli* Günther (Orthoptera: Tetrigoidea: Scelimeninae). *Mitochondrial DNA Part B* **2021**, *6*, 3021–3022. [[CrossRef](#)]
10. Wei, C.-M.; Chen, Y.-Z.; Liu, J.; Deng, W.-A.; Li, X.-D. Mitochondrial genome characteristics and phylogenetic analysis of *Thoradonta yunnana* (Orthoptera: Tetrigoidea). *J. South. Agric.* **2023**, *54*, 1303–1316. [[CrossRef](#)]
11. Zhang, R.-J.; Xin, L.; Deng, W.-A. Characterization of the Complete Mitochondrial Genome of *Tripetaloceroides tonkinensis* (Orthoptera: Tetrigoidea) from China and Its Phylogenetic Analysis. *Mitochondrial DNA Part B* **2021**, *6*, 1990–1991. [[CrossRef](#)]
12. Liu, Y.; Li, X.; Lin, L. Transcriptome of the Pygmy Grasshopper *Formosatettix qinlingensis* (Orthoptera: Tetrigidae). *PeerJ* **2023**, *11*, e15123. [[CrossRef](#)] [[PubMed](#)]
13. Li, R.; Qin, Y.; Rong, W.; Deng, W.; Li, X. Chromosome-Level Genome Assembly of the Pygmy Grasshopper *Eucriotettix oculatus* (Orthoptera: Tetrigoidea). *Sci. Data* **2024**, *11*, 431. [[CrossRef](#)] [[PubMed](#)]
14. Li, X.-D.; Jiang, G.-F.; Li, R.; Bai, Y.; Zhang, G.-S.; Xu, S.-J.; Deng, W.-A. Molecular Strategies of the Pygmy Grasshopper *Eucriotettix oculatus* Adapting to Long-Term Heavy Metal Pollution. *Ecotoxicol. Environ. Saf.* **2024**, *276*, 116301. [[CrossRef](#)] [[PubMed](#)]
15. Song, H.; Amédégno, C.; Cigliano, M.M.; Desutter-Grandcolas, L.; Heads, S.W.; Huang, Y.; Otte, D.; Whiting, M.F. 300 Million Years of Diversification: Elucidating the Patterns of Orthopteran Evolution Based on Comprehensive Taxon and Gene Sampling. *Cladistics* **2015**, *31*, 621–651. [[CrossRef](#)]
16. Itac-Bruneau, R.; Doucet, G. Contribution à La Connaissance Des Tetrigidae (Orthoptera) de Guyane. *Zoosystema* **2022**, *44*, 405–421. [[CrossRef](#)]
17. Kasalo, N.; Naskrecki, P.; Rebrina, F.; Skejo, J. Central American Tetrigidae Rambur, 1838 (Orthoptera): A Preliminary Catalogue. *Zoosystema* **2023**, *45*, 177–212. [[CrossRef](#)]
18. Tumbrinck, J. 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. In *Biodiversity, Biogeography and Nature Conservation in Wallacea and New Guinea*; Entomological Society of Latvia: Riga, Latvia, 2014; Volume 2, pp. 345–396. ISBN 978-9984-9768-7-7.
19. Long, Y.; Teng, C.; Huang, C.; Zhang, R.; Deng, W.; Lin, L. Twenty-Three New Synonyms of the Eastern Common Groundhopper, *Tetrix japonica* (Bolivar, 1887) (Orthoptera, Tetrigidae). *ZooKeys* **2023**, *1187*, 135–167. [[CrossRef](#)]
20. Hebert, P.D.N.; Cywinska, A.; Ball, S.L.; deWaard, J.R. Biological Identifications through DNA Barcodes. *Proc. R. Soc. Lond. B* **2003**, *270*, 313–321. [[CrossRef](#)]
21. DeSalle, R.; Goldstein, P. Review and Interpretation of Trends in DNA Barcoding. *Front. Ecol. Evol.* **2019**, *7*, 302. [[CrossRef](#)]
22. Fišer Pečnikar, Ž.; Buzan, E.V. 20 Years since the Introduction of DNA Barcoding: From Theory to Application. *J. Appl. Genetics*. **2014**, *55*, 43–52. [[CrossRef](#)]

23. Antil, S.; Abraham, J.S.; Sripoorna, S.; Maurya, S.; Dagar, J.; Makhija, S.; Bhagat, P.; Gupta, R.; Sood, U.; Lal, R.; et al. DNA Barcoding, an Effective Tool for Species Identification: A Review. *Mol. Biol. Rep.* **2023**, *50*, 761–775. [[CrossRef](#)] [[PubMed](#)]
24. Sharkey, M.J.; Janzen, D.H.; Hallwachs, W.; Chapman, E.G.; Smith, M.A.; Dapkey, T.; Brown, A.; Ratnasingham, S.; Naik, S.; Manjunath, R.; et al. Minimalist Revision and Description of 403 New Species in 11 Subfamilies of Costa Rican Braconid Parasitoid Wasps, Including Host Records for 219 Species. *ZooKeys* **2021**, *1013*, 1–665. [[CrossRef](#)] [[PubMed](#)]
25. Slater-Baker, M.-R.; Fagan-Jeffries, E.P.; Oestmann, K.J.; Portmann, O.G.; Bament, T.M.; Howe, A.G.; Guzik, M.T.; Bradford, T.M.; McClelland, A.R.; Woodward, A.; et al. DNA Barcoding, Integrative Taxonomy, Citizen Science, and Bush Blitz Surveys Combine to Reveal 34 New Species of *Apanteles* (Hymenoptera, Braconidae, Microgastrinae) in Australia. *ZooKeys* **2025**, *1227*, 1–128. [[CrossRef](#)]
26. Zamani, A.; Fric, Z.F.; Gante, H.F.; Hopkins, T.; Orfinger, A.B.; Scherz, M.D.; Bartoňová, A.S.; Pos, D.D. DNA Barcodes on Their Own Are Not Enough to Describe a Species. *Syst. Entomol.* **2022**, *47*, 385–389. [[CrossRef](#)]
27. Zamani, A.; Dal Pos, D.; Fric, Z.F.; Orfinger, A.B.; Scherz, M.D.; Bartoňová, A.S.; Gante, H.F. The Future of Zoological Taxonomy Is Integrative, Not Minimalist. *Syst. Biodivers.* **2022**, *20*, 1–14. [[CrossRef](#)]
28. Huber, B.A.; Szymański, H.; Bennett-West, A. Progress or Burden? Formal Description of Every Apparently New Species Available in Collections Is Neither Necessary nor Useful. *ZooKeys* **2024**, *1214*, 77–90. [[CrossRef](#)]
29. Meier, R.; Blaimer, B.B.; Buenaventura, E.; Hartop, E.; Von Rintelen, T.; Srivathsan, A.; Yeo, D. A Re-analysis of the Data in Sharkey et al.'s (2021) Minimalist Revision Reveals That BINs Do Not Deserve Names, but BOLD Systems Needs a Stronger Commitment to Open Science. *Cladistics* **2022**, *38*, 264–275. [[CrossRef](#)]
30. Sharkey, M.J.; Brown, B.; Baker, A.; Mutanen, M. Response to Zamani et al. (2020): The Omission of Critical Data in the Pursuit of “Revolutionary” Methods to Accelerate the Description of Species. *ZooKeys* **2021**, *1033*, 191–201. [[CrossRef](#)]
31. Kasalo, N.; Skejo, J.; Husemann, M. DNA Barcoding of Pygmy Hoppers—The First Comprehensive Overview of the BOLD Systems’ Data Shows Promise for Species Identification. *Diversity* **2023**, *15*, 696. [[CrossRef](#)]
32. Nugent, C.M.; Elliott, T.A.; Ratnasingham, S.; Adamowicz, S.J. Coil: An R Package for Cytochrome *c* Oxidase I (COI) DNA Barcode Data Cleaning, Translation, and Error Evaluation. *Genome* **2020**, *63*, 291–305. [[CrossRef](#)]
33. Saussure, H. Orthoptera Nova Americana (Diagnoses Praeliminares). *Revue Mag. Zool.* **1861**, *2*, 126–130, 156–164, 313–324, 397–402.
34. Linnaeus, C. *Systema Naturae per Regna Tria Naturae: Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis*; Laurentii Salvii: Stockholm, Sweden, 1758.
35. Thunberg, C.P. Hemipterorum Maxillosorum Genera Illustrata Plurimisque Novis Speciebus Ditata Ac Descripta. In *Mémoires de l’Académie Impériale des Sciences de St. Pétersbourg*; Académie impériale des sciences: St. Petersburg, Russia, 1815; Volume 5, pp. 211–301.
36. Hall, T.A. BioEdit: A User-Friendly Biological Sequence Alignment Editor and Analysis Program for Windows 95/98/NT. *Nucleic Acids Symp. Ser.* **1999**, *41*, 95–98.
37. Kalyaanamoorthy, S.; Minh, B.Q.; Wong, T.K.F.; von Haeseler, A.; Jermini, L.S. ModelFinder: Fast Model Selection for Accurate Phylogenetic Estimates. *Nat. Methods* **2017**, *14*, 587–589. [[CrossRef](#)]
38. Nguyen, L.-T.; Schmidt, H.A.; von Haeseler, A.; Minh, B.Q. IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. *Mol. Biol. Evol.* **2015**, *32*, 268–274. [[CrossRef](#)] [[PubMed](#)]
39. Hoang, D.T.; Chernomor, O.; von Haeseler, A.; Minh, B.Q.; Vinh, L.S. UFBoot2: Improving the Ultrafast Bootstrap Approximation. *Mol. Biol. Evol.* **2018**, *35*, 518–522. [[CrossRef](#)]
40. Rambaut, A. FigTree v1.4.4. Available online: <https://github.com/rambaut/figtree/releases> (accessed on 16 November 2024).
41. Paradis, E.; Blomberg, S.; Bolker, B.; Brown, J.; Claramunt, S.; Claude, J.; Cuong, H.S.; Desper, R.; Didier, G.; Durand, B.; et al. Ape: Analyses of Phylogenetics and Evolution. *Bioinformatics.* **2004**, *20*, 289–290. [[CrossRef](#)]
42. Devriese, H. Contribution à l’étude Des Tetrigidae de Madagascar (Orthoptera). *Bulletin et Annales de la Société Royale Belge d’Entomologie* **1991**, *127*, 119–131.
43. Devriese, H. Révision Des Xerophyllini d’Afrique (Orthoptera Tetrigidae). *Belg. J. Entomol.* **1991**, *1*, 21–99.
44. Devriese, H. Bijdrage Tot de Systematiek, Morfologie En Biologie van de West-Palearktische Tetrigidae. *Nieuwsbrief/Lettre de contact Saltabel* **1996**, *15*, 2–38.
45. Storozhenko, S.Y.; Kim, T.W.; Jeon, M.J. *Monograph of Korean Orthoptera*; National Institute of Biological Resources: Incheon, Republic of Korea, 2015.
46. Storozhenko, S.Y.; Pushkar, T.I. A New Genus of Pygmy Locusts (Orthoptera: Tetrigidae: Metrodorinae) from Vietnam. *Ann. Zool.* **2015**, *65*, 65–69. [[CrossRef](#)]
47. Subedi, M.; Kasalo, N. *Aryalidonta itishreea*, a New Genus and Species of Thoradontini (Orthoptera, Tetrigidae) from Nepal Honors the Emperor of Laughter. *J. Orthoptera Res.* **2023**, *32*, 63–80. [[CrossRef](#)]
48. ICZN. *International Code of Zoological Nomenclature*, 4th ed.; International Trust for Zoological Nomenclature: London, UK, 1999.

49. Schneider, C.A.; Rasband, W.S.; Eliceiri, K.W. NIH Image to ImageJ: 25 Years of Image Analysis. *Nat. Methods* **2012**, *9*, 671–675. [[CrossRef](#)] [[PubMed](#)]
50. Rambur, J.P. Orthoptères. *Faune Entomologique de l'Andalousie* **1838**, *2*, 12–94.
51. Bolívar, I. Essai Sur Les Acridiens de La Tribu Des Tettigidae. *Ann. Soc. Ent. Belg.* **1887**, *31*, 175–313.
52. Cadena-Castañeda, O.J.; De Mello Mendes, D.M.; Silva, D.S.M.; Granda, J.M.C.; García, A.G.; Tumbrinck, J. Systematics and Biogeography of the Genus *Scaria* Bolívar, 1887 (Orthoptera: Tettigidae: Batrachideinae). *Zootaxa* **2019**, *4675*, 1–65. [[CrossRef](#)]
53. Itrac-Bruneau, R.; Doucet, G. Apport Des Collections Du Muséum National d'Histoire Naturelle et de Didier Morin à La Connaissance Des Batrachideinae et Lophotettiginae (Orthoptera, Tettigidae) de Guyane. *Zoosystema* **2023**, *45*, 601–634. [[CrossRef](#)]
54. De Geer, C. *Mémoires Pour Servir à l'Histoire des Insectes*; Pierre Hasselberg: Stockholm, Sweden, 1773; Volume 3.
55. Kasalo, N.; Deranja, M.; Adžić, K.; Sindaco, R.; Skejo, J. Discovering Insect Species Based on Photographs Only: The Case of a Nameless Species of the Genus *Scaria* (Orthoptera: Tettigidae). *J. Orthoptera Res.* **2021**, *30*, 173–184. [[CrossRef](#)]
56. Grant, H.J. A Revision of the Subfamily Batrachideinae (Orthoptera; Tettigidae). Ph.D. Thesis, University of Colorado, Boulder, CO, USA, 1962.
57. Hancock, J.L. XII. Studies of the Tettigiae (Orthoptera) in the Oxford University Muscum. *Trans. Ent. Soc. Lond.* **1907**, *55*, 213–244. [[CrossRef](#)]
58. Buzzetti, F.M.; Devriese, H. Tettigidae from Ecuador (Orthoptera Caelifera Tetrigoidea). *Atti Della Accademia Roveretana Degli Agiati* **2007**, *7*, 41–54.
59. Hebard, M. Studies in the Dermaptera and Orthoptera of Colombia. Third Paper. Orthopterous Family Acrididae. *Trans. Am. Entomol. Soc.* **1923**, *49*, 165–313.
60. Scudder, S.H. Materials for a Monograph of the North American Orthoptera. *Boston J. Nat. Hist.* **1862**, *7*, 409–480. [[CrossRef](#)]
61. Say, T. *American entomology, or Descriptions of the insects of North America, illustrated by coloured figures from original drawings executed from nature*; Augustus Mitchell; Philadelphia Museum: Philadelphia, PA, USA, 1824.
62. Rehn, J.A.G.; Grant, H.J. The Batrachideinae (Orthoptera; Acridoidea; Tettigidae) of North America. *Trans. Am. Entomol. Soc.* **1958**, *84*, 13–103.
63. Morse, A.P. The Acrididae. Subfamily Tettiginae. In *Biologia Centrali-Americana. Insecta. Orthoptera*; Porter, R.H., Ed.; Dulau and Co.: London, UK, 1900; Volume 2, pp. 3–19.
64. Hancock, J.L. XIX. Further Studies of the Tettiginae (Orthoptera) in the Oxford University Museum. *Trans. R. Entomol. Soc. Lond.* **1909**, *56*, 387–426. [[CrossRef](#)]
65. Kasalo, N.; Bertner, P.; de Rueda, J.A.G.; Skejo, J. The True Nature of the Genus *Lophotettix* Hancock, 1909 (Orthoptera: Tettigidae): A Brief Taxonomic Revision. *Ann. Zool.* **2022**, *72*, 223–234. [[CrossRef](#)]
66. Silva, D.S.M.; Cadena-Castañeda, O.J.; Pereira, M.R.; De Domenico, F.C.; Sperber, C.F. Review of *Lophotettix*, the Sole Member of the Subfamily Lophotettiginae Hancock, 1909 (Insecta: Orthoptera: Caelifera: Tettigidae). *Zootaxa* **2019**, *4686*, 346–360. [[CrossRef](#)]
67. Kasalo, N.; Husemann, M.; van de Kamp, T.; Skejo, J. Description of *Phelene reinschmidti* from Ecuador with Notes on the Subfamily Lophotettiginae (Orthoptera, Tettigidae). *Evol. Syst.* **2024**, *8*, 119–125. [[CrossRef](#)]
68. Hancock, J.L. Orthoptera Fam. Acridiidae. Subfam. Tettiginae. In *Genera Insectorum*; V. Verteneuil & L. Desmet: Bruxelles, Belgium, 1907; Volume 48, pp. 1–79.
69. Günther, K. Revision Der Acrydiinae (Orthoptera), III. Sectio Amorphopi (Metrodorae Bol. 1887, Aut.). *Abhandlungen und Berichte aus den Staatlichen Museen für Tierkunde und Völkerkunde in Dresden (Ser. A Zool.) (N.F.)* **1939**, *20*, 16–335.
70. Stål, C. Orthoptera Species Novas Descripsit. In *Kongliga Svenska Fregatten Eugenies Resa Omkring Jorden (Zoologi)*; P.A. Norstedt and Soner: Stockholm, Sweden, 1861; Volume 2, pp. 299–350.
71. Cadena-Castañeda, O.J. *Introducción a Los Saltamontes de Colombia: Orthoptera: Caelitera, Acridomorpha, Tetrigoidea & Tridactyloidea*; Lulu: Research Triangle, NC, USA, 2015; ISBN 978-1-329-39264-9.
72. Walker, F. *Catalogue of the Specimens of Dermaptera Saltatoria in the Collection of the British Museum*; The Trustees of the British Museum: London, UK, 1871.
73. Bruner, L. South American Tettigidae. *Ann. Carnegie Mus.* **1910**, *7*, 89–143. [[CrossRef](#)]
74. Bruner, L. Saltatorial Orthoptera from South America and the Isle of Pines. *Ann. Carnegie Mus.* **1920**, *13*, 5–91. [[CrossRef](#)]
75. Maes, J.-M. Catálogo de Los Tettigidae, Rhipipterygidae y Tridactylidae (Orthoptera) de Nicaragua. *Revista Nicaraguense de Entomología* **1989**, *6*, 49–53.
76. Hancock, J.L. *Tettigidae of North America*; The Lakeside Press, R.R. Donnelley & Sons Company: Chicago, IL, USA, 1902.
77. Rehn, J.A.G. A Contribution to the Knowledge of the Orthoptera of Mexico and Central America. *Trans. Am. Entomol. Soc.* **1903**, *29*, 1–34.
78. Rehn, J.A.G.; Grant, H.J. *A Monograph of the Orthoptera of North America (North of Mexico)*; Monographs of the Academy of Natural Sciences of Philadelphia; Literary Licensing, LLC: Whitefish, MT, USA, 1961; Volume 1.

79. Rehn, J.A.G.; Grant, H.J. The Genus *Paratettix* as Found in North America (Orthoptera: Tettigoniidae). *Proc. Acad. Nat. Sci. Phila.* **1957**, *109*, 247–319.
80. Hancock, J.L. Some Tettigian Studies. *Entomol. News* **1899**, *10*, 275–282.
81. Devriese, H.; Nguyen, E.; Husemann, M. An Identification Key to the Genera and Species of Afrotropical Tetrigini (Genera *Paratettix*, *Leptacrydium*, *Hedotettix*, *Rectitettix* Nov. Gen., and *Alienitettix* Nov.Gen.) with General Remarks on the Taxonomy of Tetrigini (Orthoptera, Tetrigidae). *Zootaxa* **2023**, *5285*, 511–556. [[CrossRef](#)]
82. Pavon-Gozaló, P.; Manzanilla, J.; Garcia-Paris, M. Taxonomy and Morphological Characterization of *Allotettix simoni* (Bolívar, 1890) and Implications for the Systematics of Metrodorinae (Orthoptera: Tetrigidae). *Zool. J. Linn. Soc.* **2012**, *164*, 52–70. [[CrossRef](#)]
83. Rehn, J.A.G.; Grant, H.J. A Review of the Genus *Neotettix* (Orthoptera: Acridoidea, Tetrigidae). *Trans. Am. Entomol. Soc.* **1957**, *82*, 217–250.
84. Devriese, H.; Husemann, M. *Afrosystolederus garmisi* (Orthoptera, Tetrigidae), a New Genus and Species from Mount Gibi (Liberia) with Remarks on *Systolederus*, *Pseudosystolederus* and *Teredorus*. *Zootaxa* **2023**, *5258*, 331–341. [[CrossRef](#)]
85. Tumbrinck, J. Taxonomic and Biogeographic Revision of the Genus *Lamellitettigodes* (Orthoptera: Tetrigidae) with Description of Two New Species and Additional Notes on *Lamellitettix*, *Probolotettix*, and *Scelimena*. *J. Orthoptera Res.* **2019**, *28*, 167–180. [[CrossRef](#)]
86. Lamarre, G.P.A.; Decaëns, T.; Rougerie, R.; Barbut, J.; Dewaard, J.R.; Hebert, P.D.N.; Herbin, D.; Laguerre, M.; Thiaucourt, P.; Bonifacio Martins, M. An Integrative Taxonomy Approach Unveils Unknown and Threatened Moth Species in Amazonian Rainforest Fragments. *Insect. Conserv. Divers.* **2016**, *9*, 475–479. [[CrossRef](#)]
87. Hlebec, D.; Harms, D.; Kučinić, M.; Harvey, M.S. Integrative Taxonomy of the Pseudoscorpion Family Chernetidae (Pseudoscorpiones: Cheliferoidae): Evidence for New Range-Restricted Species in the Dinaric Karst. *Zool. J. Linn. Soc.* **2024**, *200*, 644–669. [[CrossRef](#)]
88. Chung, F.-Y.; Hsu, P.-W.; Hsu, F.-C.; Lin, C.-C. A New Genus in a Hyperdiverse Ant Lineage (Hymenoptera: Formicidae: Myrmicinae) Revealed by Integration of Morphological and Molecular Evidence. *Myrmecol. News* **2025**, *35*, 29–60. [[CrossRef](#)]
89. Jung, S.; Duwal, R.K.; Lee, S. COI Barcoding of True Bugs (Insecta, Heteroptera). *Mol. Ecol. Resour.* **2011**, *11*, 266–270. [[CrossRef](#)] [[PubMed](#)]
90. Ma, Z.; Ren, J.; Zhang, R. Identifying the Genetic Distance Threshold for Entiminae (Coleoptera: Curculionidae) Species Delimitation via COI Barcodes. *Insects* **2022**, *13*, 261. [[CrossRef](#)]
91. Zhang, H.; Bu, W. Exploring Large-Scale Patterns of Genetic Variation in the COI Gene among Insecta: Implications for DNA Barcoding and Threshold-Based Species Delimitation Studies. *Insects* **2022**, *13*, 425. [[CrossRef](#)] [[PubMed](#)]
92. Astrin, J.J.; Stüben, P.E.; Misof, B.; Wägele, J.W.; Gimnich, F.; Raupach, M.J.; Ahrens, D. Exploring Diversity in Cryptorhynchine Weevils (Coleoptera) Using Distance-, Character- and Tree-Based Species Delineation. *Mol. Phylogenetics Evol.* **2012**, *63*, 1–14. [[CrossRef](#)]
93. Barranco, P. Ortópteros de La Reserva Biológica Alberto Manuel Brenes (Costa Rica) II. Orthoptera: Caelifera. *Boletín de la Sociedad Entomológica Aragonesa* **2010**, *47*, 21–32.
94. Hebard, M. Studies in the Acrididae of Panama (Orthoptera). *Trans. Am. Entomol. Soc.* **1924**, *50*, 75–140.
95. Silva, D.S.M.; Cadena-Castañeda, O.J.; Pereira, M.R. Batrachideinae (Orthoptera: Caelifera: Tetrigidae): An Overview of the Most Diverse Tetrigids of the Neotropical Region. *Zootaxa* **2021**, *4946*, 1–84. [[CrossRef](#)]
96. Zha, L.-S.; Sheng, M.; Wen, T.; Hyde, K. A New Species and a Revised Key of the Genus *Thoradonta* (Orthoptera, Tetrigidae). *ZooKeys* **2016**, *607*, 69–79. [[CrossRef](#)]
97. Hochkirch, A.; Deppermann, J.; Gröning, J. Phenotypic Plasticity in Insects: The Effects of Substrate Color on the Coloration of Two Ground-Hopper Species. *Evol. Dev.* **2008**, *10*, 350–359. [[CrossRef](#)]
98. Zhao, L.; Ling, L.-L.; Zheng, Z.-M. DNA Barcoding Reveals Polymorphism in the Pygmy Grasshopper *Tetrix bolivari* (Orthoptera, Tetrigidae). *ZooKeys* **2016**, *582*, 111–120. [[CrossRef](#)]
99. Nabours, R.K. The Genetics of the Tettigidae (Grouse Locusts). *Bibliogr. Genet.* **1929**, *5*, 27–104.
100. Neo, I.; Tan, M.K.; Cho, T.J.Y.; Yeo, D.C.J. A Faunistic Study and Taxonomic Account of Species of Pygmy Grasshoppers (Orthoptera: Tetrigidae) from Singapore’s Last Freshwater Swamp Forest. *J. Asia-Pac. Biodivers.* **2024**, *17*, 87–116. [[CrossRef](#)]
101. Adžić, K. Pygmy Grasshoppers (Orthoptera: Tetrigidae) of Peninsular Malaysia. Master Thesis, University of Zagreb, Zagreb, Croatia, 2021.
102. Hawlitschek, O.; Morinière, J.; Lehmann, G.U.C.; Lehmann, A.W.; Kropf, M.; Dunz, A.; Glaw, F.; Detcharoen, M.; Schmidt, S.; Hausmann, A.; et al. DNA Barcoding of Crickets, Katydid and Grasshoppers (Orthoptera) from Central Europe with Focus on Austria, Germany and Switzerland. *Mol. Ecol. Resour.* **2017**, *17*, 1037–1053. [[CrossRef](#)] [[PubMed](#)]

103. Kasalo, N.; Yong, S.; Rebrina, F.; Skejo, J. Definition of the Tribe Metrodorini (Orthoptera: Tetrigidae) with Notes on Biogeography and Evolution of Metrodorinae and Cladonotinae. *Acta Entomol. Musei Natl. Pragae* **2023**, *63*, 187–193. [[CrossRef](#)]
104. Kasalo, N.; Buzzetti, F.M.; Stancher, G.; Cambra, R.A.; Skejo, J. Contribution to the Knowledge of Batrachideini (Orthoptera: Tetrigidae): Description of Two New Flightless Genera, *Naskreckiana* and *Procellator*, and Revision of the Status of *Eotetrix*. *Acta Entomol. Musei Natl. Pragae* **2023**, *63*, 279–292. [[CrossRef](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.