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RESEARCH PAPER

Definition of the tribe Metrodorini (Orthoptera: Tetrigidae) with notes on biogeography and evolution of Metrodorinae and Cladonotinae

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Abstract. Both Metrodorinae and Cladonotinae are polyphyletic subfamilies of Tetrigidae and are thus in need of revision. This paper offers a key step toward this by defining the nominotypical tribe of Metrodorinae, Metrodorini Bolívar, 1887 that encompasses mostly apterous species with arcuate median carina of pronotum, laterally projecting lateral lobes of pronotum, and produced carinae of vertex forming horns. The tribe Metrodorini consists of the following genera: *Cota* Bolívar, 1887; *Hancockiella* Cadena-Castañeda & Cardona, 2015; *Metrodora* Bolívar, 1887; *Miriatra* Bolívar, 1906; *Antillotettix* Perez-Gelabert, 2003; *Armasius* Perez-Gelabert & Yong, 2014; †*Baeotettix* Heads, 2009; *Bahorucotettix* Perez-Gelabert, Hierro & Otte, 1998; *Cubanotettix* Perez-Gelabert, Hierro & Otte, 1998; *Cubonotus* Perez-Gelabert, Hierro & Otte, 1998; †*Electrotettix* Heads & Thomas, 2014; *Haitianotettix* Perez-Gelabert, Hierro & Otte, 1998; *Hottettix* Perez-Gelabert, Hierro & Otte, 1998; *Mucrotettix* Perez-Gelabert, Hierro & Otte, 1998; *Sierratettix* Perez-Gelabert, Hierro & Otte, 1998; *Tiburonotus* Perez-Gelabert, Hierro & Otte, 1998; and *Truncotettix* Perez-Gelabert, Hierro & Otte, 1998. The following new synonyms are recognized: Metrodorini = Miriatrini Cadena-Castañeda & Cardona, 2015, syn. nov. = Mucrotettigini Cadena-Castañeda & Silva, 2019, syn. nov. *Eleleus curtus* Bolívar, 1887 is excluded from Metrodorini and is left under Cladonotinae without tribal assignment. Biogeography, evolution, and taxonomies of Metrodorinae and Cladonotinae are briefly discussed.

Key words. Orthoptera, Tetrigidae, Cladonotini, Mucrotettigini, *Metrodora*, taxonomy, revision, Antilles, Caribbean, Neotropical Region

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Introduction

The Neotropical tetrigid fauna consists of five subfamilies encompassing more than 180 species (Cigliano et al. 2022). Among them, Metrodorinae and Cladonotinae both include very similar apterous species and their representatives were historically often confused with each other. For example, *Tylotettix* Morse, 1900 and *Platytettix* Hancock, 1906 were both described under Cladonotinae but they are in fact synonymous with the type genus of Metrodorinae, *Metrodora* Bolívar, 1887 (Cigliano et al. 2022). The definitions of both subfamilies are brief; Metrodorinae were historically defined by laterally projected lateral lobes and the first and third hind tarsal segments approximately equal in length, while the diagnostic characters of Cladonotinae were mostly the wide scutellum and the lack of wings (Bolívar 1887, Morse 1900, Hancock 1907, Bruner 1910, Pavón-Gozalo et al. 2012). These characters are unreliable by themselves, making the subfamilies polyphyletic in their current extent (Pavón-Gozalo et al. 2012, Zhang et al. 2020, Lu & Deng 2021). Both subfamilies require taxonomic revisions that will clearly define them as monophyletic.

The nominotypical tribus of Metrodorinae has, until now, remained undefined. Thus, the primary aim of this paper is to define the tribe Metrodorini Bolívar, 1887 by

conducting a detailed morphological analysis of the type genus and similar genera of the Neotropical Region. This will provide a crucial starting point for defining Metrodorinae as a whole and for resolving the complicated taxonomy of the subfamily. Additionally, by providing clear morphological characters that separate Metrodorini and Cladonotini, a baseline morphology is also established for Cladonotinae. Finally, some comments on the evolution and biogeography of the newly redefined tribe are presented, based on earlier literature.

Materials and methods

We conducted a comparative examination of photographs of the type specimens representing the extant and extinct genera and species belonging to the tribes Choriphyllini, Cladonotini sensu Storozhenko & Paik (2011) and Tumbrinck et al. (2020) (*Cladonotus* Saussure, 1862, *Deltonotus* Hancock, 1904, *Misythus* Stål, 1877), Miriatrini syn. nov., and Mucrotettigini syn. nov., the species belonging to the genera without tribal assignment within the subfamilies Metrodorinae and Cladonotinae, namely *Cota* Bolívar, 1887, *Hancockiella* Cadena-Castañeda & Cardona, 2015, as well as the type genus of Metrodorini, *Metrodora* Bolívar, 1887. In the case of *Metrodora*, all available type specimens were examined, except for *Metrodora rana* Bolívar, 1887 for which the type cannot be obtained at the moment. This species is, according to Günther (1939), similar to *Metrodora gibbosula* (Walker, 1871) and we thus find no reason to doubt the validity of the genus in the absence of a single species. The information on the types used and their depositories is summarised in Table 1.

The morphological examination was conducted on a set of characters that is widely used in descriptions and taxonomy of Tetrigidae (Tumbrinck 2014) and encompasses mostly the characters of the head and the pronotum. The terminology follows Tumbrinck (2014). Taxonomy and the data on type specimens follow Cigliano et al. (2022).

Results

Family Tetrigidae Rambur, 1838
Subfamily Cladonotinae Bolívar, 1887

Genus *Eleleus* Bolívar, 1887

We exclude the genus *Eleleus* from Mucrotettigini as well as Metrodorinae, and leave it without tribal placement under Cladonotinae. For more information see the species section below.

Eleleus curtus Bolívar, 1887

Eleleus curtus, the only species included in the genus, exhibits a shape of the pronotum similar to all other members of Mucrotettigini, which is also shared by many of the mainland members of the newly defined tribe Metrodorini, and by many species of Cladonotini. However, this species has the vertex bulging in the same way as in Cladonotini and Choriphyllini, without well-defined carinae of the vertex. This is in contrast to the rest of Mucrotettigini, which is why we exclude the monotypic genus *Eleleus* from that tribe and leave it without tribal placement under Cladonotinae.

Subfamily Metrodorinae Bolívar, 1887

Tribe Metrodorini Bolívar, 1887

Metrodorini Bolívar, 1887. Type genus: *Metrodora* Bolívar, 1887.
= Miriatrini Cadena-Castañeda & Cardona 2015, **syn. nov.** Type genus: *Miriatra* Bolívar, 1906; Storozhenko (2016); Silva et al. (2017)
= Mucrotettigini Cadena-Castañeda & Silva, 2019, **syn. nov.** Type genus: *Mucrotettix* Perez-Gelabert, Hierro & Otte, 1998

Composition and distribution. Widely distributed throughout the northern half of South America, including Central America, and the Caribbean. The following genera are present on the mainland: *Cota* Bolívar, 1887; *Hancockiella* Cadena-Castañeda & Cardona, 2015; *Metrodora* Bolívar, 1887; and *Miriatra* Bolívar, 1906. The following genera, formerly included in the tribe Mucrotettigini, are present in the Caribbean: *Antillotettix* Perez-Gelabert, 2003; *Armasius* Perez-Gelabert & Yong, 2014; †*Baeotettix* Heads, 2009; *Bahorucotettix* Perez-Gelabert, Hierro & Otte, 1998; *Cubanotettix* Perez-Gelabert, Hierro & Otte, 1998; *Cubonotus* Perez-Gelabert, Hierro & Otte, 1998; †*Electrotettix* Heads & Thomas, 2014; *Haitianotettix* Perez-Gelabert, Hierro & Otte, 1998; *Hottettix* Perez-Gelabert, Hierro & Otte, 1998; *Mucrotettix* Perez-Gelabert, Hierro & Otte, 1998; *Sierratettix* Perez-Gelabert, Hierro & Otte, 1998; *Tiburonotus* Perez-Gelabert, Hierro & Otte, 1998; and *Truncotettix* Perez-Gelabert, Hierro & Otte, 1998.

Diagnosis. The upper margin of the vertex is approximately at the level of the upper margin of the compound eyes. The eyes are set wide apart, i.e., the vertex is approximately two or more times wider than the eye. The carinae of the vertex are produced, with lateral carinae forming more or less pronounced horns and the medial carina visibly compresso-elevated, extremely so in *Miriatra*. In lateral view, the medial carina protrudes beyond the eyes and is at least slightly visible. The placement of the bifurcation of the frontal costa varies from around mid-level of the eyes to below the bottom margin of the eyes. The scutellum is usually wider than multiple widths of the scape, but there are rare exceptional species with a narrow scutellum. The upper margins of the antennal grooves are below the bottom margins of the eyes. Antennae are usually short, 10 to at least 15-segmented, but the precise upper boundary is hard to determine because the types usually lack antennae and the original descriptions do not describe them in detail. The median carina of the pronotum is arcuate, forming a more or less pronounced crest. The lateral lobes of the pronotum are usually projected outwards to varying degrees. The lateral lobes are occasionally in the form of sharp spines. Most species are apterous, except for the species of the genera *Electrotettix* and *Miriatra*.

Comparative notes. The main difference that separates Metrodorini from Cladonotini is the morphology of the head. In frontal view, Cladonotini have a smooth vertex that bulges upwards, while Metrodorini have the characteristic three protrusions formed by lateral and medial carinae of the vertex. In lateral view, the distant eye of Cladonotini

Table 1. Information pertaining to the type material examined for this study.

Subfamily	Tribe	Species	Type	Type locality	Depository
Metrodorinae	Metrodorini	*Metrodora acuta* Günther, 1939	holotype	Ecuador, Loja	Museum and Institute of Zoology, Warsaw (MZPW)
Metrodorinae	Metrodorini	*Metrodora arcuata* (Bruner, 1920)	holotype	French Guiana, Pied Saut, Oyapok River	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Metrodora colombiae* Günther, 1939	2 syntypes	Colombia, San Antonio/Tocoto	Staatliches Museum für Tierkunde, Dresden (SMTD)
Metrodorinae	Metrodorini	*Metrodora gibbinotus* (Bruner, 1910)	lectotype	Brazil, Brazil North, Pará	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Metrodora gibbosula* (Walker, 1871)	holotype	Brazil, Rio Negro	Natural History Museum, London (BMNH)
Metrodorinae	Metrodorini	*Metrodora harroweri* (Hebard, 1924)	holotype	Panamá, Gatún	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Metrodora lutosa* Bolívar, 1887	holotype	Brazil	Naturhistorisches Museum Wien (NHMW)
Metrodorinae	Metrodorini	*Metrodora pygmaea* (Roberts, 1937)	holotype	Venezuela, San Estaban	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Metrodora simplex* (Hebard, 1924)	holotype	Panamá, Porto Bello	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Metrodora sinuata* (Morse, 1900)	holotype	Nicaragua	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Metrodora uniformis* (Bruner, 1910)	lectotype	Brazil, Brazil North, Pará	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	†*Antillotettix electrum* Heads, 2009	holotype	Dominican Republic; Miocene: Burdigalian	American Museum of Natural History (AMNH)
Metrodorinae	Metrodorini	*Armasius iberianus* Perez-Gelabert & Yong, 2014	holotype	Cuba, Monte Iberia, Nibujón	Instituto de Ecología y Sistemática, La Habana (IES)
Metrodorinae	Metrodorini	†*Baeotettix lottiae* Heads, 2009	holotype	Dominican Republic, Hispaniola; Miocene: Burdigalian	American Museum of Natural History (AMNH)
Metrodorinae	Metrodorini	*Bahorucotettix larimar* Perez-Gelabert, Hierro & Otte, 1998	holotype	Dominican Republic, Eastern Sierra de Bahoruco	Florida State Collection of Arthropods (FSCA)
Metrodorinae	Metrodorini	*Cubanotettix turquinensis* Perez-Gelabert, Hierro & Otte, 1998	holotype	Cuba, Macizo del Turquino	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Cubonotus altinotatus* Perez-Gelabert, Hierro & Otte, 1998	holotype	Cuba, S side of Pico Turquino	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	†*Electrotettix attenboroughi* Heads & Thomas, 2014	holotype	Dominican Republic, near Santiago de los Caballeros, amber from La Toca region; Miocene: Burdigalian	Illinois Natural History Survey (INHS)
Metrodorinae	Metrodorini	*Haitianotettix tuberculatus* Perez-Gelabert, Hierro & Otte, 1998	holotype	Dominican Republic, 5 km NE of Los Arroyos, Western Sierra de Bahoruco	Carnegie Museum of Natural History, Pittsburgh (CM)
Metrodorinae	Metrodorini	*Hottettix haitianus* Perez-Gelabert, Hierro & Otte, 1998	holotype	Haiti, south slope of Morne Formon, Massif de la Hotte	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Mucrotettix gibbosus* Perez-Gelabert, Hierro & Otte, 1998	holotype	Dominican Republic, Santiago, Monte Diego de Ocampo	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Mucrotettix spinifer* Perez-Gelabert, Hierro & Otte, 1998	holotype	Dominican Republic, La Vega, Los Tablones, Parque Nacional J. A. Bermudez, Cordillera Central	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Sierratettix carinatus* Perez-Gelabert, Hierro & Otte, 1998	holotype	Dominican Republic, Barahona, Sierra De Bahorucco, on way to Cortico	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Tiburonotus peninsularis* Perez-Gelabert, Hierro & Otte, 1998	holotype	Haiti, La Hotte	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Truncotettix fronterizus* Perez-Gelabert, Hierro & Otte, 1998	holotype	Dominican Republic, Independencia, Los Pinos del Eden, Sierra de Neiba	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Truncotettix interruptus* Perez-Gelabert, Hierro & Otte, 1998	holotype	Dominican Republic, Monsenor Nouel Prov., Arroyo Toro Arriba, near Bonao, Cordillera Central	The Academy of Natural Sciences of Drexel University (ANSP)
Metrodorinae	Metrodorini	*Cota saxosa* Bolívar, 1887	holotype	Peru	Naturhistorisches Museum Wien (NHMW)
Metrodorinae	Metrodorini	*Hancockiella armata* Cadena-Castañeda & Cardona, 2015	holotype	Colombia, Amazonas, Parque Nacional Natural Amacayacu	Collection of Arthropods and other Invertebrates at the Francisco José de Caldas District University of Bogotá, Colombia (CAUD)
Metrodorinae	Metrodorini	*Miriatra boliviana* Günther, 1939	syntype	Bolivia, La Paz, Mapiri	Naturhistorisches Museum Wien (NHMW)
Metrodorinae	Metrodorini	*Miriatra chalazombra* Günther, 1939	holotype	Brazil, Pará	Museum and Institute of Zoology, Warsaw (MZPW)

(continues on the next page)

Table 1. Information pertaining to the type material examined for this study.

Subfamily	Tribe	Species	Type	Type locality	Depository
Metrodorinae	Metrodorini	*Miriatra producta* (Bolívar, 1887)	syntype	Peru, Alto Amazonas	Museo Nacional de Ciencias Naturales, Madrid (MNCN)
Cladonotinae		*Eleleus curtus* Bolívar, 1887	holotype	Brazil	Naturhistorisches Museum Wien (NHMW)
Cladonotinae	Cladonotini	*Cladonotus humbertianus* Saussure, 1862	holotype	Sri Lanka, Peradeniya	Muséum d'histoire naturelle de Genève (MHNG)
Cladonotinae	Cladonotini	*Cladonotus bhaskari* Tumbrinck, Deranja, Adžić, Pavlović & Skejo, 2020	holotype	Sri Lanka, Sabaragamawa, Sinharaja Rainforest	National Museum of Colombo, Sri Lanka (CNMS)
Cladonotinae	Cladonotini	*Deltonotus subcucullatus* (Walker, 1871)	unspecified primary type	Sri Lanka	Natural History Museum, London (BMNH)
Cladonotinae	Cladonotini	*Misythus cristicornis* (Walker, 1871)	holotype	Philippines	Natural History Museum, London (BMNH)
Cladonotinae	Cladonotini	*Misythus rectangularis* Hebard, 1923	holotype	Philippines, Luzon, Imugan	The Academy of Natural Sciences of Drexel University (ANSP)
Cladonotinae	Cladonotini	*Misythus securifer* (Walker, 1871)	holotype	Philippines	Natural History Museum, London (BMNH)
Cladonotinae	Cladonotini	*Misythus tectatus* Hebard, 1923	holotype	Philippines, Ripang	The Academy of Natural Sciences of Drexel University (ANSP)
Cladonotinae	Choriphyllini	*Choriphyllum plagiatum* Walker, 1871	holotype	Jamaica	Natural History Museum, London (BMNH)
Cladonotinae	Choriphyllini	*Choriphyllum saussurei* Bolívar, 1887	2 syntypes	Cuba	Muséum d'histoire naturelle de Genève (MHNG)
Cladonotinae	Choriphyllini	*Phyllotettix compressus* (Thunberg, 1815)	holotype	Jamaica	Universitets Zoologiska Institutionen Uppsala, Sweden (UZIU)
Cladonotinae	Choriphyllini	*Phyllotettix foliatus* (Hancock, 1902)	holotype	Jamaica	The Academy of Natural Sciences of Drexel University (ANSP)
Cladonotinae	Choriphyllini	*Phyllotettix rhombeus* (Felton, 1765)	holotype	Jamaica	Natural History Museum, London (BMNH)

is obscured by the bulging part of the vertex, while the distant eye of Metrodorini is either visible or obscured by the thin elevated medial carina. The tribe Choriphyllini, the only true Caribbean cladonotines, have a highly specialized leaf-like morphology and are thus both easy to differentiate from and difficult to compare to the other taxa present in the region.

Compared to Batrachideinae (Tumbrinck 2014), Metrodorini and Cladonotini are not as robustly defined but the herein presented diagnosis offers several independent characters that should mitigate the confusion of classifying similar genera in the future. A visual comparison of the heads of Metrodorini, Cladonotini, and Choriphyllini is available in Fig. 1.

The original diagnosis by Silva et al. (2019) compares the tribe Mucrotettigini only to the tribe Choriphyllini, noting that they are easily separated because the latter tribe exhibits leaf-like morphology. That diagnosis does not take into account the type specimens of either Metrodorinae or Cladonotinae and thus fails to provide evidence for the subfamilial classification of Mucrotettigini. The original description of Mucrotettigini for the most part fits with the herein presented diagnosis of Metrodorini, differing only in its description of the length of the pronotum and the shape of the legs as important characters. We expand the definition of the tribe by not considering the latter two characters diagnostic. The reasoning for this decision is provided in the Discussion.

Discussion

Metrodorinae and Cladonotinae have already been shown to be polyphyletic, with Metrodorinae encompassing a wide array of morphologies, while Cladonotinae are comprised mostly of apterous species with a wide scutellum (Pavón-Gozalo et al. 2012, Zhang et al. 2020, Cigliano et al. 2022). The definition of Cladonotinae is especially problematic as the value of characters such as the lack of wings and a wide scutellum is invalidated by the very existence of the genus *Metrodora*, the type genus of an entire subfamily. Publications regarding Cladonotinae often do not thoroughly discuss their justification for placing a taxon within the subfamily (Pérez-Gelabert et al. 1998, Heads et al. 2014, Silva et al. 2019). This adds to the confusion about the identity of Cladonotinae as it adds more material without addressing the underlying problem. The changes we propose are not meant to be final but are simply to set up a workable taxonomic environment. The definition of Mucrotettigini, syn. nov. is inseparable from that of Metrodorini, so the act of synonymization is performed. Changes to the taxonomy of Metrodorini can be expected when the taxonomy of Cladonotinae of Africa and Asia gets revised. Only a robust phylogenetic analysis coupled with morphology will be able to bring us closer to the reliable solution.

The newly defined tribe Metrodorini is widespread in the northern half of South America, including Central America, and the type genus *Metrodora* is present in most of the range, represented by 13 species, as currently recognized. The only member of Cladonotinae present on the mainland is *Eleleus curtus,* known only from a single specimen (Cigliano et al. 2022). Considering that South America and the Greater Antilles were connected as late as the Eocene-Oligocene transition (35–33 Mya) (Iturralde-Vinent & MacPhee 1999), it is quite likely that some of the South American fauna migrated to the Caribbean during that time (Marivaux et al. 2020). It could be expected to find taxa related to the widespread genus *Metrodora* in the Antilles, and yet, all of the apterous species inhabiting the islands

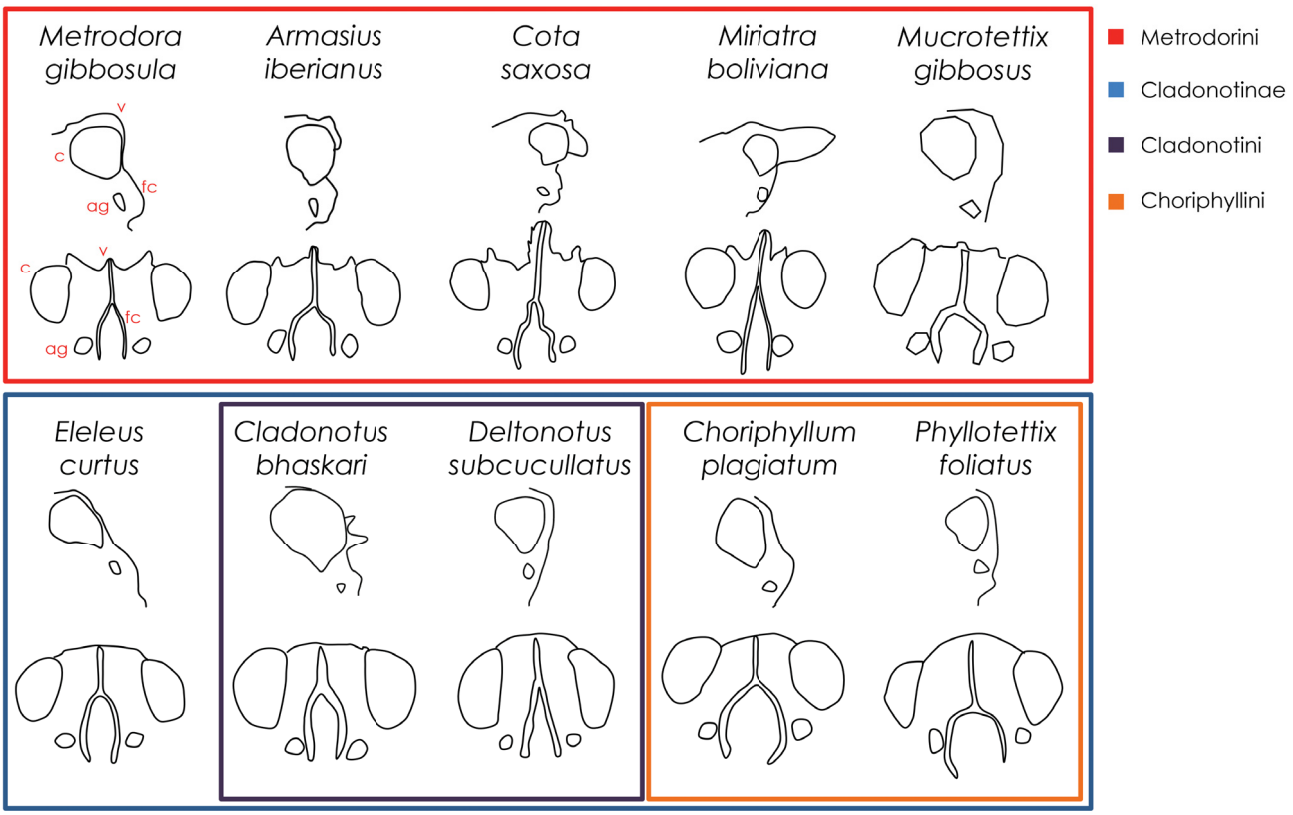

Fig. 1. A comparison of drawings traced over the type specimens of the species representing the tribes Metrodorini, Cladonotini, Choriphyllini, and a single species placed under Cladonotinae without tribal assignment: *Eleleus curtus* Bolívar, 1887. The drawings represent the key morphological features of the head, namely the compound eye (c), the position of the antennal groove (ag), the shape of the vertex (v), and the facial carinae (fc). The drawings were adapted after the photographs taken by Josef Tumbrinck, Daniela Silva, and Marcelo Pereira, available in the Orthoptera Species File (Cigliano et al. 2022).

have until now been considered to belong to Cladonotinae.

A comparative examination of the Caribbean tribes Choriphyllini and Mucrotettigini, both until now considered Cladonotinae, showed that there are considerable differences in head morphology between them. The shape of the vertex and its carinae proved to be a stable character for differentiating the tribe Metrodorini from the tribes Cladonotini and Choriphyllini. This character is effectively the same in the tribe Cladonotini, genera *Cladonotus* Saussure, 1862 (Sri Lanka), *Misythus* Stål, 1877 (Southeast Asia), and *Holoarcus* Hancock, 1909 (Australia), in the tribe Choriphyllini (Caribbean), and in the genus *Eleleus* (South America). In contrast to this, the same character in Mucrotettigini appears very close to what is present in the genus *Metrodora* and other genera included in the tribe Metrodorini. The previously mentioned geological history of the region coupled with clear differences in morphology prompted us to propose an alternative hypothesis outlined in the Results. *Eleleus curtus* remains a curiosity, as it is the only currently known mainland member of Cladonotinae and the only Neotropical cladonotine that does not exhibit leaf-like morphology. Unfortunately, it is known only from a single specimen (Cigliano et al. 2022). This enigmatic taxon could in time prove to be an important "piece of the puzzle" in resolving the true nature of Cladonotinae.

It has been observed that the Caribbean tetrigid diversity of Cladonotinae is a product of numerous vicariant events with dispersion limited by the lack of wings (Pérez-Gelabert et al. 1998, Heads 2009, Heads et al. 2014). Since most of those species now belong to Metrodorini, an interesting new implication can be extracted. *Electrotettix attenboroughi* Heads & Thomas, 2014 is an extinct genus and species from the Early Miocene described from Dominican amber and was considered a part of Mucrotettigini. It is remarkable for its possession of wings and tegmina, which are unusual even for Metrodorini which include only one winged genus, *Miriatra*. The clade comprising Mucrotettigini is characterized by many similarities, which could point out to it being monophyletic. If that is the case, it is possible that within the subfamily Metrodorinae wings were lost at least twice just in this region.

Lastly, we present observations regarding some recognizable morphological characters. The genus *Metopomystrum* Günther, 1939 is not included in Metrodorini although it has a "horn-like" vertex. The morphology of the vertex in that genus is not homologous to that of Metrodorini as it lacks clearly visible carinae; the vertex as a whole is expanded.

The genus *Chiriquia* Morse, 1900 is not included in Metrodorini even though it exhibits most of the characters that define that tribe. This genus does not have the medial carina of the vertex as strongly expressed to fit the diagnosis, and its pronotum is not arcuate as in many species belonging to Metrodorini. Otherwise, it appears similar to *Miriatra* and is likely related to it. Another similar genus

is *Trigonofemora* Hancock, 1906 which is excluded for the same reasons as *Chiriquia*, but shows some other interesting characters. The leg morphology of *Trigonofemora*, i.e., long and slim legs, femora with tubercles and lappets, fit with the diagnostic characters described for Mucrotettigini (Silva et al. 2019). Most notably, it has slender hind femora as well, making it closely resemble *Haitianotettix tuberculatus* Perez-Gelabert, Hierro & Otte, 1998, in particular. Both genera have an elevation of the median carina in the prozona but *Trigonofemora* does not have an arcuate pronotum. Both genera have elevated carinae of the vertex, but in *Trigonofemora* they are very low, while in *Haitianotettix* they are well developed. This could imply that these genera are related, but such a conclusion cannot be made based solely on leg morphology, especially considering that there are different combinations of this feature in Mucrotettigini. In most cases, the legs of Mucrotettigini members are long and tuberculated, just as in Metrodorini, but there are many exceptions with smooth or short legs, suggesting that those characters are not so well constrained as the facial morphology.

To summarize the morphological considerations, we define the tribe Metrodorini as narrowly as possible, excluding the similar genera that include *Chiriquia* and *Trigonofemora*. A systematic revision of South American Tetrigidae is needed, which should result in more tribes being defined, alongside more precise hypotheses regarding their evolutionary history.

Most of the species of Mucrotettigini have the hind margin of the pronotum truncated, forming a variety of shapes. This is a character often seen in Cladonotini and is absent in mainland Metrodorini. We do not consider it taxonomically viable at the level of subfamilies as it is probably not evolutionary constrained. We hypothesize that, following the loss of wings, selective pressure acting upon the shape of the hind margin of the pronotum ceases as its role in the protection of wings is lost. The subsequent changes to this trait are thus likely to be the result of genetic drift and may appear independently in wingless taxa. An example of this can be found in *Austrohancockia* Günther, 1938, a genus that exhibits a variety of shapes of the hind margin of the pronotum. It is currently assigned to Cladonotinae but molecular analyses place it close to the subfamily Scelimeninae, where it could easily be included following some morphological studies (Zhang et al. 2020). This shows that, just like winglessness, this character has appeared multiple times in the evolutionary history of Tetrigidae. On the other hand, it is difficult to speculate about the reason for the high similarity of the general shape of the pronotum among most of the genera included in this study. Whether this is due to evolutionary constraints following the loss of wings, inheritance from a common ancestor, a mutation connected to an essential metabolic pathway, or some other reason, future studies tackling these problems will most likely shed some much-needed light on the taxonomy of Tetrigidae.

With this paper, we have made a stride towards a natural classification of genera within Metrodorinae and Cladonotinae of South America. By defining the tribe Metrodorini, we have set a foundation upon which our understanding of the subfamily can be built. The value of the new tribe lies in its function as a taxonomic and evolutionary hypothesis that can be tested and amended. For an underfunded field such as tetrigidology, it will surely take some time to widely adopt molecular studies, that would provide new insights into the matter. Until then, the best we can do is to consider the available data and extract all we can from it.

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