UNIVERSIDADE FEDERAL DE VIÇOSA

JHON FABER MARULANDA LOPEZ

SYSTEMATIC OF TERPIDINAE KLUGE (EPHEMEROPTERA: LEPTOPHLEBIIDAE)

VIÇOSA - MINAS GERAIS

2021

JHON FABER MARULANDA LOPEZ

SYSTEMATIC OF TERPIDINAE KLUGE (EPHEMEROPTERA: LEPTOPHLEBIIDAE)

Dissertation presented to the Universidade Federal de Viçosa, as part of the requirements of the Graduate Program in Entomology, to obtain the title of Magister Scientiae.

Adviser: Frederico Falcão Salles

VIÇOSA - MINAS GERAIS

2021

Ficha catalográfica elaborada pela Biblioteca Central da Universidade Federal de Viçosa - Campus Viçosa

T

M389s
2020

Marulanda Lopez, Jhon Faber, 1994-
Systematic of Terpidinae Kluge (Ephemeroptera: Leptophlebiidae) / Jhon Faber Marulanda Lopez. - Viçosa, MG, 2020.
120 f. : il. (algumas color.) ; 29 cm.

Inclui anexos.
Orientador: Frederico Falcão Salles.
Dissertação (mestrado) - Universidade Federal de Viçosa.
Inclui bibliografia.

1. Insetos - Morfologia. 2. Filogenia. 3. Taxonomia. 4. Castanophlebiinae. 5. *Fittkaulus*. I. Universidade Federal de Viçosa. Departamento de Entomologia. Programa de Pós-Graduação em Entomologia. II. Título.

CDD 22. ed. 595.734

JHON FABER MARULANDA LOPEZ

SYSTEMATIC OF TERPIDINAE KLUGE (EPHEMEROPTERA: LEPTOPHLEBIIDAE)

Dissertation presented to the Universidade Federal de Viçosa, as part of the requirements of the Graduate Program in Entomology, to obtain the title of *Magister Scientiae*.

APPROVED: July 17, 2020.

Assent:

Jhon Faber Marulanda Lopez

Jhon Faber Marulanda Lopez
Author

Frederico

Frederico Falcão Salles
Adviser

À minha família, e aos meus amigos por todo o apoio...

A todos os docentes que contribuíram no meu processo de formação...

ACKNOWLEDGMENTS

Inicialmente quero agradecer à minha família por me apoiar e me incentivar a estudar desde criança. De fato sempre foi e é uma prioridade para vocês meu processo de formação e vou valorizar isso a vida toda. Agradeço também por apoiar a minha decisão em vir estudar no Brasil, mesmo isso significando me afastar de vocês.

Aos meus amigos e companheiros do Museu de Entomologia que fizeram parte desse processo. Agradeço pelos trabalhos juntos durante as diferentes disciplinas. Também agradeço pelos bate papos e churrascos para dar uma relaxada e começar a próxima semana daquele jeito.

Estendo um agradecimento à UFV, ao Programa de Pós-Graduação em Entomologia e ao CNPq por me permitirem estudar nessa instituição e obter meu título. Também agradeço o fato de poder me apresentar no processo seletivo mesmo estando fora do Brasil, considero isso um ato de boa vontade. O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Código de Financiamento 001.

Quero também estender um agradecimento à Dra. Lucimar Gomes Dias, docente da Universidad de Caldas, orientadora da minha graduação, colega e amiga, por me ensinar o mundo dos Ephemeroptera e me incentivar a vir a estudar no Brasil. Também agradeço me apresentar aos seus amigos e especialistas em Ephemeroptera, como o Molineri, Domínguez e o meu atual orientador Fred, que contribuíram e ainda contribuem positivamente para o meu processo de formação.

Para finalizar, e não por isso menos importante, quero estender um especial agradecimento ao meu orientador Dr. Frederico Falcão Salles pela orientação, apoio e confiança. Muito obrigado Fred, o fato de conhecer você lá na Colômbia me incentivou ainda mais a vir ao Brasil e me formar. Agradeço por me aceitar como seu estudante, me ajudar a vir ao país e lembrá-lo que para mim é um prazer ser o seu orientado e seu amigo. Também quero agradecer por me incentivar a me tornar não só um excelente cientista, mas também uma pessoa melhor.

*“Nada em Biologia faz se*ntido exceto à luz da evolução".

(Theodosius Dobzhansky)

ABSTRACT

MARULANDA-LOPEZ, Jhon Faber, M.Sc., Universidade Federal de Viçosa, July, 2020. **Systematic of Terpidinae Kluge (Ephemeroptera: Leptophlebiidae)**. Adviser: Frederico Falcão Salles.

Leptophlebiidae is one of the most diversified groups of Ephemeroptera, both taxonomically as morphologically, and with a worldwide distribution with exception of Antarctica. Recently, Leptophlebiidae was divided into eight subfamilies, among them Terpidinae. Terpidinae is composed by the genera Terpides, Fittkaulus and Tikuna and its occurrence is restricted to the Neotropical region. Among the subfamilies of Leptophlebiidae, members of Terpidinae present particular morphological characteristics, as hypognathous mouthparts and presence of swimming setae in caudal filaments. The characters traditionally used in Terpidinae taxonomy are wing venation, shape of male genitalia in imagos, egg morphology, mouthparts morphology and type and disposition of setae, shape of the claws, abdominal color pattern, and shape of the gills in the nymphs. However, some species present the same abdominal color pattern and the morphology of the male genitalia is very conservative. In this context, additional morphological characteristics are necessary to complement the traditional characters used in the systematic of the subfamily. In addition, the subfamily was not proposed using a quantitative phylogenetic analysis and the phylogenetic relationships between Terpidinae species are unknown. The aim in this investigation is to test the current classification of Terpidinae using a morphology-based phylogenetic analysis. As a result, the monophyly of Terpidinae was recovered with good support. Castanophlebiinae was found to be the sister group of Terpidinae and Tikuna was recovered as sister group of Fittkaulus. The diagnosis of all genera and species of Terpidinae are presented and an interactive illustrated key for the identification of Terpidinae has also been proposed. Additionally, the evolution of some selected morphological characteristics used a priori in the classification of the group are discussed.

Keywords: Castanophlebiinae. Fittkaulus. Terpides lineage. Neotropic. Tikuna.

RESUMO

MARULANDA-LOPEZ, Jhon Faber, M.Sc., Universidade Federal de Viçosa, julho de 2020. **Sistemática de Terpidinae Kluge (Ephemeroptera: Leptophlebiidae)**. Orientador: Frederico Falcão Salles.

Leptophlebiidae é um dos mais diversificados grupos de Ephemeroptera, tanto taxonômica quanto morfologicamente, e com uma distribuição mundial com exceção da Antártica. Recentemente Leptophlebiidae foi dividida em oito subfamílias, entre elas Terpidinae. Terpidinae é composta pelos gêneros Terpides, Fittkaulus e Tikuna e sua ocorrência é restrita à região Neotropical. Entre as subfamílias de Leptophlebiidae, membros de Terpidinae apresentam características morfológicas particulares, como peças bucais hipognatas e a presença de cerdas natatórias nos filamentos caudais. Os caracteres usados tradicionalmente na taxonomia de Terpidinae são venação das asas, forma da genitália em imagos, morfologia dos ovos, morfologia das peças bucais e disposição e tipo de cerdas, forma das garras, padrão de cor abdominal e forma das brânquias nas ninfas. Contudo, algumas espécies apresentam o mesmo padrão de cor abdominal e a morfologia da genitália masculina é muito conservada. Neste contexto, características morfológicas adicionais são necessárias para complementar os caracteres tradicionais usados na sistemática da subfamília. Além disso, a subfamília não foi proposta usando uma análise filogenética quantitativa e as relações entre as espécies de Terpidinae são desconhecidas. O objetivo desta pesquisa é testar a classificação atual de Terpidinae usando uma análise filogenética baseada em dados morfológicos. Como resultado, foi recuperada a monofilia de Terpidinae com bom suporte. Castanophlebiinae foi agrupada como grupo irmão de Terpidinae e gênero Tikuna foi recuperado como grupo irmão de Fittkaulus. As diagnoses de todos os gêneros e espécies de Terpidinae são apresentadas, bem como uma chave ilustrada interativa para a identificação de Terpidinae. Além disso, a evolução de algumas características morfológicas selecionadas, usadas a priori na classificação do grupo são discutidas.

Palavras-chave: Castanophlebiinae. Fittkaulus. Linhagem Terpides. Neotropic. Tikuna.

LIST OF FIGURES

SUMMARY

DISSERTATION ORGANIZATION

Esse trabalho está dividido em um documento inicial e mais importante da dissertação, que aborda a sistemática de Terpidinae. Adicionalmente, são apresentados dois anexos que se referem a manuscritos desenvolvidos durante a dissertação já publicados: um na Revista Brasileira de Entomologia, que trata de registros históricos, adicionais e novos de Leptophlebiidae para Colômbia (DOI: 10.1590/1806-9665-rbent-2020-0063); e outro na Revista Zoologischer Anzeiger, o qual envolve um estudo oológico detalhado de algumas das espécies de Terpidinae (DOI: 10.1016/j.jcz.2021.02.010). As referências citadas ao longo de cada texto, bem como suas imagens, estão compiladas ao final de cada uma das três seções.

INTRODUCTION

General aspects of Ephemeroptera

Ephemeroptera is an order of living and extinct insects with discussed relationships, some authors favor its sister-group relationship with Odonata (Misof et al. 2014; Song et al. 2019), whereas others with Neoptera (Kristensen, 1991) or with Odonata+Neoptera (Wheeler et al. 2001). However, some authors proposed its relationships with the extinct order Coxoplectoptera Staniczek, Bechly & Godunko, 2011, in a clade named Heptabranchia (Sroka et al. 2015). Ephemeroptera are amphibiotic insects, nymphs can grow in aquatic environments and adults are winged and free-living. Nymphs are usually collectors, feeding on algae and detritus, while some species are predators.

Ephemeroptera are the only insects that have a sexually immature winged stage called subimago, before making one final molt and making them reproductively active imagos (Domínguez et al. 2006). Subimagos and imagos do not feed due the absence of functional mouthparts. They are important in the trophic chain as organic matter processors, as a source of energy for other aquatic organisms and as herbivores (Mol, 1986; Gattolliat & Sartori, 2000; Flowers & De la Rosa, 2010). The winged stages can live from a few hours to a few days (Flowers & De la Rosa, 2010). In the last stage, males and females perform a characteristic nuptial flight for each species, where females select males for breeding (Sartori & Britain, 2015). Ephemeroptera has a worldwide distribution, colonizing freshwater and brackish water environments on all continents except Antarctica. Their presence on islands is explained by vicariance or dispersal events (Sartori & Britain, 2015).

Ephemeroptera is currently composed of 42 families, 451 genera, and about 3500 species (Salles et al. 2018). Among these, 689 species in 115 genera and 14 families are recorded from South America (Domínguez et al. 2019). The lack of association between semaphoronts form different ontogenetic stages is one of the major taxonomic problems of the order. In this context, only 10% of South American species are known based on adults and nymphs (Domínguez et al. 2009). Ephemeroptera´s taxonomy is based on external anatomy, including the shape of mouthparts and setation, number and shape of denticles of tarsal claws in nymphs, and shape of male genitals and venation of the wings in adults (Godunko et al. 2017). Molecular characters, in turn, have been implemented allowing association of life stages (Dias et al. 2011; Salles et al. 2016), delimitation of species (Cardoni et al. 2015; Massariol et al. 2016), and phylogenetic analysis (Ogden & Whiting, 2005; Ogden et al. 2009, Dias et al. 2019; Massariol et al. 2019; Ogden et al. 2019; Monjardim et al. 2020; Salles et al. 2020). In addition, egg morphology has been shown to be a valuable source of taxonomic characters (Koss, 1968; Domínguez & Cuezzo, 2002; Ubero-Pascal, Fortuño & Puig, 2005).

Systematic of Leptophlebiidae

With over 643 species and 141 genera distributed worldwide, Leptophlebiidae is one of the most diverse groups of Ephemeroptera both taxonomically and ecologically (Sartori & Britain, 2015). In South America, Leptophlebiidae reaches its great diversity with 45 genera and almost 250 species (Domínguez et al. 2019). Currently there is a proposed classification for internal relationships in Leptophlebiidae provided by Kluge (1994; 2007; 2009; 2015; 2020). The author divided the family into six subfamilies: Leptophlebiinae, Atalophlebiinae s.str, Calliarcyinae, Habrophlebiinae, Castanophlebiinae, and Terpidinae. The author proposed Atalophlebiinae s.str + Castanophlebiinae as the sister group of Terpidinae in a clade named Atalophleboculata. Consecutively, Godunko et al. (2015) corroborated this classification through phylogenetic analysis using morphological data. In addition, the authors confirmed the placement of Leptophlebiinae as sister group of the remaining Leptophlebiidae and recovery Calliarcyinae as the sister group of Habrophlebiinae+Atalophlebiinae s.l. More recently, Monjardim et al. (2020), proposed a phylogeny and classification of Neotropical Leptophlebiidae using molecular data. The authors increased the number of subfamilies from six to eight, with Choroterpinae and Hagenulinae as new status. They also proposed new ranks for other groups and revised the concept of Atalophlebiinae, including genera with distribution in the Australasian and Neotropical regions.

Characters used in the systematic of the Leptophlebiidae

In addition to male genitalia and wing venation, external egg morphology has been implemented in taxonomic studies as source of characters (Towns & Peters 1978; Sivaramakrishnan 1984; Mazzini & Gaino 1985; Campbell & Peters 1986; Domínguez 1991; Gaino, Mazzini & Sartori 1993; Derka 2002; Derka et al. 2009; Godunko et al. 2015; Souto et al. 2016; Tiunova & Kluge 2016; Kluge, 2020). Additionally, oological characters have been used in phylogenetic studies of Hermanella complex, highlighting their importance in the hypothesis of phylogenetic relationships (Domínguez & Cuezzo, 2002). Egg morphology has also been important in the re-establishment of Tikuna Flowers, Savage & Porras 2005 and Fittkaulus Savage & Peters 1978 as genera (Kluge 2015).

Terpidinae

Terpides was proposed by Demoulin (1966) to include Terpides guyanensis, a species described based on nymphs collected in Suriname. Posteriorly, Savage & Peters (1978) described Fittkaulus and F. maculatus, a new genus and species, based on nymphs and imagos collected in Pará, northern Brazil.

As initially proposed by Peters (1980), Leptophlebiidae was divided into two distinct subfamilies, Leptophlebiinae and Atalophlebiinae. Atalophlebiinae included more than 100 genera and approximately 500 species (O´Donnel & Joackusch 2008) divided into distinct phyletic lineages (Peters, 1980). Among them, Savage, (1986) proposed the lineage Terpides to include Terpides Demoulin, 1966 and Fittkaulus Savage & Peters, 1978. Nymphs of Terpides lineage have peculiar characteristics in relation to other representatives of Leptophlebiidae, such as the presence of rows of setae in the caudal filaments and hypognathous mouthparts (Savage, 1986). Later, Tikuna was described in order to allocate Choroterpes atramentum Traver, 1947 and was also included in this lineage (Savage et al. 2005). The subfamily Terpidinae was proposed by Kluge (2009) to include the representants of the Terpides lineage, and the status of the genera Fittkaulus and Tikuna changed to subgenus. Posteriorly, after the description of the eggs, the subgenera Fittkaulus and Tikuna were again recognized as genera by the same author (Kluge, 2015).

Currently, Terpidinae contains 17 Neotropical species: nine Terpides spp. - Te. guyanensis Demoulin, 1966, (type species), Te. vinculum (Traver, 1947), Te. Jessiae Peters & Harrison, 1974, Te. diadema Lugo-Ortiz & McCafferty, 1996, Te. sooretamae Boldrini & Salles in Boldrini et al. (2009), Te. contamanensis Kluge, 2015, Te. echinovaris Kluge, 2015, Te. iguapoga Molineri, Domínguez & Zúñiga in Zúniga et al. (2015) and Te. ornatodermis Kluge, 2015; four Fittkaulus spp. - F. maculatus Savage & Peters, 1978 (type species), F. cuiabae Savage, 1986, F. cururuensis Savage 1986 and F. amazonicus Kluge, 2009; and four Tikuna spp. - Ti. bilineata (Needham & Murphy, 1924), Ti. atramentum (Traver, 1947) (type species), Ti. fusconotum Kluge, 2009 and Ti. nigrobulla Kluge, 2009.

Kluge (2009) suggested the following characteristics for the genera: Fittkaulus has a single apical segment on the forceps; in Tikuna the apex of the subcostal field of fore wings is yellow, and lateral projections are present on the apex of the ventral lamellae of gills II–VI; and Terpides has an enlarged apical denticle in the basal row of denticles of the tarsal claws. Posteriorly, Kluge (2015) presented a list of putative autapomorphies of Terpidinae, including a well-developed distal dentiseta, absence of the processes in the hypopharynx, and the absence of posterolateral projections in the abdominal segment VII.

Despite such advances, many species of Terpidiniae are still incompletely known. The morphology of the eggs, for example, was described for only five species (Te. contamanensis, Te. echinovaris, Te. ornatodermis, F. amazonicus, and Ti. bilineata) (Kluge, 2015). In addition, some species have the same hypodermal coloration (Kluge, 2015) and share a similar penis morphology, hampering their differentiation and pointing to the need of additional diagnostic characters. Furthermore, Savage (1986) and Kluge (2009) performed intuitive classification systems by proposing, respectively, the Terpides lineage and Terpidinae. Thus, the phylogenetic relationships are unknown among the species of the subfamily.

Objectives

General

Test the current classification of Terpidinae using a morphology-based phylogenetic analysis.

Specific

Propose additional morphological characters useful to support the phylogenetic hypotheses of the group;

Test the monophyly of Terpidinae and infer the phylogenetic relationships of the species of Terpidinae;

Present an illustrated interactive taxonomic key for the identification of the genera and species of Terpidinae.

MATERIALS AND METHODS

Material study and preparation

We revised the material deposited in the Museu de Entomologia (UFVB), Viçosa, Minas Gerais, Brazil; Colección Entomológica del Programa de Biología de la Universidad de Caldas (CEBUC), Colombia; and Universidade Federal de Rio de Janeiro. In addition, material from Laboratório de Entomologia da Universidade Federal de Roraima was also accessed.

We made the taxonomic identification of the specimens and the study of morphological characters with the aid of taxonomic keys and comparison with original descriptions (Needham & Murphy, 1924; Traver, 1947; Demoulin, 1966; Peters & Harrison, 1974; Savage & Peters, 1978; Savage, 1986; Lugo-Ortiz & McCafferty, 1996; Boldrini et al. 2009; Kluge, 2009; Kluge, 2015; Zúniga et al. 2015; Domínguez & Abdala, 2019). We examined the characters associated to the morphology of the male genitalia, oocytes in the females and venation of the wings in the adults. On the other hand, we examined the morphology of the mouthparts, gills and denticles in the tarsal claws in the nymphs (Boldrini et al. 2009; Domínguez & Cuezzo, 2002; Kluge, 2009; 2015; Godunko et al. 2015; Domínguez & Abdala, 2019). To standardize the study of such characters, we mouted them in permanent slides using Euparal®. The slides were visualized in microscope OLYMPUS CX31 and stereomicroscope LEICA M205 A and the structures were photographed using an coupled camera LEICA MC170 HD. In the study of oocytes morphology, we dissected the female abdomens with tweezers, removed the oocytes and transferred them to ethanol. The samples were incubated in Hexamethyldisilazane (HMDS) for 10 minutes and air dried. This samples were mounted on aluminum stubs, gold covered and analyzed with a LEO VP1430 Scanning Electron Microscope (SEM) at 15 kV at the Núcleo de Microscopia e Microanálise da Universidade Federal de Viçosa. We used the terminology proposed for Koss & Edmunds (1974) for the egg descriptions, and complemented them with oological descriptions published in the literature (Kluge, 2015).

Character coding

We constructed the characters statements following Sereno (2007). This author proposed the following components of a character statement: Character number. Locator (Ln), Variable (V), Variable qualifier (q), character state (vn). We elaborated the matrix of characters in the software Mesquite 3.6 (Maddison & Maddison, 2018). Of all 80 studied characters, 74 are binary and six multistate characters (8, 40, 42, 73, 78, 79), and multistate characters were treated as non-additive. The character states were scored as dashes (-) if not applicable and with question mark (?) for unknown.

Phylogenetic analysis

We analyzed the matrix in TNT v.1.5 (Goloboff & Catalano, 2016) under implied weighting (IW) (Goloboff, 1993). We reserved space for 90000 trees in memory. Tree searches were performed using ``New Technology Search´´ with the default algorithms (ratchet, sectorial searches, drifting and fusing) with 1000 random addition sequence replicates (Goloboff et al. 2008). Using implied weighting, decreases the impact of variable characters, depending on their homoplastic rate during the tree searches (Goloboff, 1993; 2014). Because homoplastic characters might or might not bear a phylogenetic signal, or are characters that evolve faster than non-homoplastic ones, down weighting them in respect to highly phylogenetically significant ones appears to be a plausible solution (Farris, 1969; Goloboff, 1993; Chippindale & Wiens, 1994). Indeed, has been shown that the inclusion of down weighted homoplastic characters increase phylogenetic accuracy both in simulations as with real morphological and molecular datasets (Chippindale & Wiens, 1994; Källersjö et al., 1998; Goloboff et al., 2008, 2018; Goloboff, 2014). The resultant most parsimonious trees were compared to determine the maximum total character fit, character fit was adjusted using a concavity constant (K) value, where k determines how much a character is down weighted based on its level of homoplasy (Legg et al. 2013). In this context, the implied weighting was suggested to improve continuous character scaling problems (Goloboff et al. 2006). In our analysis of implied weight a k = 3 value was used. We calculated the Relative Bremer support (RBS, Goloboff & Farris, 2001) as a measure of clade support using 3112 suboptimal trees obtained by Tree Bisection and Reconnection (TBR). Frequency differences (GC, Goloboff et al. 2003), using 100 replications of symmetric resampling was estimated. The consistency and retention indexes were calculated using the script Stats.run. The software Winclada (Nixon, 2002) was used to display the hypothesized tree and map the synapomorphies. We performed all analyses and explored the evolution of selected characters traditionally used in the classification of the group in the software TNT v.1.5.

Choice of terminals

To evaluate the monophyly of Terpidinae and its internal relationships, the following 16 of the 17 species of all genera of the subfamily were selected as in-group: eighth Terpides - Te. guyanensis, Te. Jessiae, Te. diadema, Te. sooretamae, Te. contamanensis, Te. echinovaris, Te. iguapoga and Te. ornatodermis; four Fittkaulus - F. maculatus, F. cuiabae, F. cururuensis and F. amazonicus; and four Tikuna - Ti. bilineata, Ti. atramentum, Ti. fusconotum and Ti. nigrobulla. The species Te. vinculum was not included in the final analysis because in a previous analysis this taxon fluted as wild-taxon, can be because it is only known based on the female imago and many missing entries were included in the matrix. We included in the ingroup the following species from six subfamilies of Leptophlebiidae: Castanophlebia calida Barnard, 1932 for Catanophlebiinae; Habrophlebia hassaine Benhadji, Hassaine & Sartori, 2018 for Habrophlebiinae; Calliarcys van Godunko & Bauernfeind, 2015 in Godunko et al. 2015 for Callyarcinae; Paraleptophlebia calcarica Robotham & Allen, 1988 for Leptophlebiinae; Massartella brieni Lestage, 1930 for Atalophlebiinae; and Thraulodes jones Gonçalves, Da-Silva & Nessimian, 2010 for Hagenulinae. The rooting was in P. calcarica, once Leptophlebiinae is considered the sister group of the remaining Leptophlebiidae (Godunko et al. 2015). A total of 22 terminals were used, six as outgroups and 16 for the in-group.

Occurrence maps

We elaborated a matrix containing all species of Terpidinae (i.e., collected and identified species, identified material from the collections and obtained data from the literature) and their respectives geographic coordinates. Based on this data, we confectioned the maps of occurrence in the Neotropical area with the software QGis, using a digital model of the elevation with countries delimitation in the Neotropic and the Amazon basin.

Taxonomic key

The interactive taxonomic key for the identification of the Terpidinae species was constructed and made available online in the Xper3 platform (http://www.xper3.fr/). The following species were included: Te. guyanensis, Te. Jessiae, Te. diadema, Te. sooretamae, Te. contamanensis, Te. echinovaris, Te. iguapoga, Te. ornatodermis; Te. vinculum; F. maculatus, F. cuiabae, F. cururuensis; F. amazonicus; Ti. bilineata, Ti. atramentum, Ti. fusconotum and Ti. nigrobulla.

In the key for the imagos, the species Te. diadema not was included because are unknown the winged stages. In the key for the nymphs, the species Te. vinculum, F. cuiabae and Ti. fusconotum were excluded because they are known only based on the imagos.

Twenty-one morphological characters (descriptors) base the imago matrix: (1) markings in the fore femur; (2) color pattern in femora of the mid and hind legs; (3) fork of vein MP in the fore wings; (4) coloration in the bulla of the vein Sc on fore wings; (5) trajectory of bulla; (6) coloration of C and Sc areas on fore wings; (7) maculae between RA and RS in fore wings; (8) macula in the fork of MA vein; (9) spots around cross veins in the fore wings; (10) shape of the costal projection of the hind wings; (11) shape of the hind wings; (12) number of apical segments in the forceps; (13) narrowing in distal part of the penes; (14) shape of the forceps; (15) penes shape; (16) shape of the base of the penes; (17) lateral projections in the penes; (18) color pattern in the abdominal tergites; (19) maculae near of the gonopore in the sternum VII of female; (20) shape of the eggs; and (21) chorionic ornamentation in the eggs. Characters 3 and 5 and 10–17 are best seen under high magnification as 200 and 400 x. Preparation of slides is recommended to permit visualizing the characters mentioned anteriorly. We recommend seeing the characters 20 and 21 in Scanning Electron Microscopy (SEM). The remaining characters are easily visualized under stereomicroscopes with magnification above 30 x.

The key matrix of nymphs is based on seventeen anatomical descriptors: (1) denticles in the anteromedian emargination of the labrum; (2) number of spines in the inner margin of labial palp segment II; (3) number of spine-like setae on inner margin of labial palp segment III; (4) color pattern in the fore femur; (5) presence of fine pectinate setae in the fore tibia; (6) shape of the denticles in the claws; (7) number of denticles in the basal set of the claws; (8) number of denticles in the distal set of the claws; (9) posterolateral projections on abdominal tergites; (10) shape of the dorsal lamella in the gills; (11) distal widening in the dorsal lamella of the gills; (12) trachea coloration on the gills; (13) denticles on posterior margin of abdominal tergites; (14) cuticular color pattern of the abdominal tergites; (15) hypodermal color pattern in the abdominal tergites; (16) chorionic ornamentation in the eggs; and (17) eggs shape. The characters 1–3, 5–8, 10–11 and 13 are best seen under high magnification as 200 and 400 x. Preparation of slides, therefore, is highly recommended. For the study of the characters 16 and 17 Scanning Electron Microscopy (SEM) are recommended and that oocyte extraction be performed of mature nymphs. The remaining characters are easily visualized under stereomicroscopes with magnification above 30 x.

To illustrate the states of taxonomic interest of the keys, we took imagens of specimens in alcohol with an Stereomicroscope LEICA M205 A with coupled camera LEICA MC170 HD. Living specimens were photographed in the field, in an acrylic aquarium, with a Nikon D800, a 105 mm objective, and a Nikon macro flash. We made line drawings on Adobe Illustrator CC® based on photographs and prepared based on Coleman (2003, 2006). For the oocyte micrographs, the samples of the oocytes were mounted on aluminum stubs, gold covered and analyzed with a LEO VP1430 Scanning Electron Microscope (SEM) a 15 kV at the Núcleo de Microscopia e Microanálise da Universidade Federal de Viçosa.

RESULTS

A total of 80 morphological characters were defined for males and females, and comprises 49 morphological characters of nymphs: head (1 character, 1.25%), labrum (6 characters, 7.5%), hypopharynx (1 character, 1.25%), maxillae (7 characters, 8.75%), mandible (6 characters, 7.5%), labium (6 characters, 7.5%), femora (4 characters, 5%), tibia (4 characters, 5%), tarsi (1 character, 1.25%), claws (4 characters, 5%), abdomen (4 characters, 5%), gills (4 characters, 5%), and caudal filaments (1 character, 1.25%). 31 of imagos: head (1 character, 1.25%), fore wings (10 characters, 12.5%), hind wings (3 characters, 3.75%), legs (2 characters, 2.5%), forceps (2 characters, 2.5%), male genitalia (6 characters, 7.5%). In addition, seven of eggs (8.75%). We presented illustrations of labium, hypopharynx, gills and caudal filaments in nymphs, and fore and hind wings, claws and genitalia in imagos (see below).

Characters statements

Nymph

Head

0. Head, mouthparts, orientation: prognathous (0), or hypognathous (1).

Labrum

1. Labrum, anteromedial emargination: absent (0), or present (1).

2. Labrum, anteromedial emargination, denticles: absent (0), or present (1).

3. Labrum, anteromedial emargination, number of denticles: 5 denticles (0), or 6 denticles (1).

4. Labrum, first row of fine simple setae: absent (0), or present (1).

5. Labrum, second row of fine simple setae: absent (0), or present (1).

6. Labrum, third row of setae: absent (0), or present (1).

Hypopharynx

7. Hypopharynx, lingua, lateral process: absent (0), present (1).

Maxilla

8. Maxilla, apex of galea-lacinia, dentisetae, number: 0 (0), 1 (1), 2 (2), or 3 (3).

9. Maxilla, apex of galea-lacinia, proximal dentiseta, shape: curved pectinate (0), curved not pectinate (1).

10. Maxilla, apex of galea-lacinia, row of simple setae: absent (0), or present (1).

11. Maxilla, inner apical margin, tusk: absent (0), or present (1).

12. Maxilla, palp, segment II / segment I, ratio: subequal (0), or >1.1 (1).

13. Maxilla, segment I of palp, thick blunt setae: absent (0), or present (1).

14. Maxilla, apical flange: absent (0), or present (1).

Mandible

15. Mandible, outer margin, shape: curved (0), or relatively straight (1).

16. Mandible, outer margin, setae: absent (0), or present (1).

17. Mandible, outer margin, setae, location: restricted to middle (0), or entire margin (1).

18. Right mandible, inner margin, distomedial row of simple setae: absent (0), or present (1).

19. Mandible, central area, row of setae: absent (0), or present (1).

20. Mandible, denticles on outer set of incisors, number: 2-3 denticles (0), or ≥ 4 denticles (1).

Labium

21. Labium, glossa, curved over ventrolaterally: not curved (0), or curved (1).

22. Labium, paraglossa, shape: broadly rounded laterally (0), or rounded laterally (1).

23. Labium, segment I of palp, spines on inner margin: absent (0), or present (1).

24. Labium, segment II of palp, spines on inner margin: absent (0), or present (1).

25. Labium, segment III of palp, spine-like setae on inner margin: absent (0), or present (1).

26. Labium, segments I-III of palp, simple setae on outer margin: absent (0), or present (1).

Femora

27. Fore femur, inner margin, stout setae: absent (0), or present (1).

28. Fore femur, dorsal surface, sub-marginal area, pectinate setae: absent (0), or present (1).

29. Middle and hind femora, dorsal surface, spines, shape: simple (0), or pectinate (1).

30. Middle and hind femora, dorsal surface, spines, location: near submarginal area (0), or near to middle (1).

Tibiae

31. Fore tibiae, dorsal setae: absent (0), or present (1).

32. Fore tibiae, inner margin, row of simple setae: 2 (0), ≥ 3 (1).

33. Fore tibiae, outer margin, row of simple setae: absent (0), or present (1).

34. Middle tibiae, patella-tibial suture: absent (0), or present (1).

Tarsi

35. Fore tarsi, inner margin, row of simple setae: one row (0), or two rows (1).

Claws

36. Claws, denticle in the middle: larger (0), or subequal (1).

37. Claws, denticles in the basal set, number: 2–4 denticles (0), or 5–6 denticles (1).

38. Claws, denticles in the distal set, number: 2–4 denticles (0), or 5–6 denticles (1).

39. Claws, shape: widened in proximal half (0), or entirely slender (1).

Abdomen

40. Abdomen, posterior margin of tergites, denticles: VI or VII–X (0), or IV or V–X (1) or I–X (2).

41. Abdomen, posterolateral projections on segment VII: absent (0), or present (1).

42. Abdomen, posterolateral projections absent on segments: I–II (0), I–IV or V (1), or I–VII (2).

43. Abdomen, terga, cuticular color pattern: similar on different segments (0), or different on different segments (1).

Gills

44. Gills II–VI, dorsal lamella, side projections: absent (0), or present (1).

45. Gills II–VI, ventral lamella, side projections: absent (0), or present (1).

46. Gills, wide/length, ratio: 3 to 4 times as long as wide (0), or ≥ 5 times as long as wide (1).

47. Gills, trachea, pigmentation: blackish (0), or dark with colorless area at middle (1).

Caudal filaments

48. Caudal filaments, proximal part, swimming setae: absent (0), or present (1).

Imago

Head

49. Eyes, facets, shape: hexagonal (0), or square (1).

Fore wings

50. Fore wings, bulla, breaking angle in R_{2+3}, direction: basal (0), or distal (1).

51 Fore wings, bulla, breaking angle in R_4, direction: basal (0), or distal (1).

52. Fore wings, bulla, trajectories, crossing the fork of vein MA: absent (0), or present (1).

53. Fore wings, bulla, dark dot: absent (0), or present (1).

54. Fore wings, C and Sc area, coloration: absent (0), or present (1).

55. Fore wings, RA and RS, macula: absent (0), or present (1).

56. Fore wings, fork of vein MA, macula: absent (0), or present (1).

57. Fore wings, cross veins, clouds: absent (0), or present (1).

58. Fore wings, vein MA, fork: symmetrical (0), or asymmetrical (1).

59. Fore wings, ICu_1, attachment: attached to CuA (0), or drop (1).

Hind wings

60. Hind wings, costal projection, shape: single (0), or bilobed (1).

61. Hind wings, costal projection, location: in basal 1/2 (0); or beyond basal 1/2 (1).

62. Hind wings, vein Sc, ending: in wing margin (0), or in cross vein or costal projection (1).

Legs

63. Legs, middle and hind femur, dark apical macula: absent (0), or present (1).

64. Legs, claws of a pair, shape: similar (0), or dissimilar (1).

Forceps

65. Abdomen, forceps, distal segments, number: one (0), or two (1).

66. Abdomen, forceps, segment I, shape: broader in basal 1/3-1/4 (0), or subcylindrical (1).

Penis

67. Penis, lateral projections: absent (0), or present (1).

68. Penis, fused: absent (0), or present (1).

69. Penis, fused, location: basal (0), or middle (1).

70. Penis, apices, apical projections: absent (0), or present (1).

71. Penis, base, abruptly swollen: absent (0), or present (1).

72. Penis, apex of lobes, shape: rounded (0), or rather straight, inner corner forming an acute angle (1).

Eggs

73. Eggs, fixation structures: chorionic plates (0), or chorionic projections (1) or adhesive layer (2).

74. Eggs, micropylar area, location: between free margins of chorionic plates (0), or between chorionic projections (1).

75. Eggs, micropylar area, number: one (0), or two or three (1).

76. Eggs, micropylar area, shape: irregular (0), or ring-like (1).

77. Eggs, surrounding area the micropylar area: not sieved (0), or sieved (1).

78. Eggs, chorion, ornamentation: hemispheric protuberances (0), or fibrillose units (1), or sculptured (2).

79. Eggs, shape; oval rounded in cross section (0), or bivalve shell (1) or fusiform (2).

Cladistic analysis

The New Technology Search analyses retrieved one most parsimonious tree (Figure 1), with tree length of 138 steps, consistency index (CI) of 0.587, and retention index (RI) of 0.725.

Monophyly of Terpidinae and sister group

We recovered Terpidinae as a well-supported monophyletic group (RBS = 72; GC = 97) (Figure. 1) and Castanophlebiinae as its sister group (RBS = 20; GC = 36). The subfamilies Atalophlebiinae and Hagenulinae were recovered as sister groups (RBS = 20; GC = 16) and clustered as sister groups of the clade Castanophlebiinae + Terpidinae (RBS = 39; GC = 54).

Phylogenetic relationships within Terpidinae

Terpidinae were subdivided into two monophyletic lineages corresponding to already recognized genera (Figure 1): a Terpides clade (RBS = 55; GC = 52) and a clade of two monophyletic genera (Tikuna + Fittkaulus) (RBS = 55; GC = 73). In the Terpides clade, one polytomy was recovered with the species Te. jessiae, Te. contamanensis and Te. sooretamae (RBS = 37; GC = 43). Terpides diadema and Te. ornatodermis were recovered as sister group (RBS = 36; GC = 45), and clustered as sister group of the polytomy (RBS = 19; GC = 1). The species Te. iguapoga was clustered as sister group of the clade that contains the polytomy and Te. diadema + T. ornatodermis clade (RBS = 36; GC = 9). In the Tikuna clade, Tikuna bilineata was recovered as sister group of Ti. fusconotum (RBS = 77; GC = 59). In addition, the species Ti. nigrobulla was clustered as sister group of Ti. bilineata + T. fusconotum clade (RBS = 50; GC = 32). The Fittkaulus clade was divided in two monophyletic lineages, the clade F. amazonicus + F. cururuensis (RBS = 58; GC = 23), and the clade F. maculatus + F. cuiabae (RBS = 60; GC = 66).

DISCUSSION

Monophyly of Terpidinae and subfamilies relationship

Among the character states proposed by Savage (1986) as diagnostic of the lineage, the following were recovered as synapomorphies that support the monophyly of Terpidinae: hypognathous mouthparts orientation (character 0-state 1); glossa curved over ventrolaterally (21-1); swimming setae in the proximal part of caudal filaments (48-1) (Fig. 7); presence of macula in RA and RS of fore wings (55-1); claws of a pair similar in legs of imagos (64-0); and penis lobes fused (68-1). In addition to these, Godunko et al. 2015 found as synapomorphy of the subfamily the presence of a third row of setae in the labrum (6-1). Ours results corroborated the subfamily-level category for this lineage as proposed by Kluge (2009). Kluge (2015) proposed the similar shape of the claws in Terpidinae as a plesiomorphic character state, repeatedly appearing in several mayfly taxa. In our phylogenetic analysis, this character state is apomorphic, and evolved convergently in Massartella and Terpidinae.

Castanophlebia, the single representative of Castanaophlebiinae, was recovery as the sister group of Terpidinae (Figure 1). Two synapomorphies supported the clade Castanophlebia + Terpidinae: the absence of lateral process in the lingua (7-0); and the location of the costal projection beyond basal 1/2 of the hind wings (61-1). Peters (1980) recognized the absence of lateral processes in the hypopharynx as shared character state for Castanophlebia, Terpides and Fittkaulus (Tikuna was unknown until 2005). In our phylogenetic analysis, this character state was recovered as a synapomorphy of Castanophlebiinae + Terpidinae, acquired by reversion in this clade and its presence in relation to Leptophlebiinae is homoplastic. Posteriorly, Peters (1997) proposed the Terpides lineage and Castanophlebia as sister groups and listed some synapomorphies to support this relationship, among them larval claws with large median denticle (36-0). However, in our phylogenetic analysis this character state evolved independently in the Castanophlebia and Terpides. Kluge (2009) considered Terpidinae as sister group of Atalophlebomaxillata (a clade comprising (Castanophlebiinae) + (Hagenulus/fg1 + Choroterpes/fg1 + cool adapted Leptophlebiidae)) supported by the presence of square facets in the upper portion of the male eyes and loss of stout setae on distal margin of labrum. On the other hand, Peters & Gillies (1995) proposed the presence of square facets in the dorsal male eyes of Atalophlebiinae as a derived character state. In our phylogenetic analysis, this characteristic (49-1), was recovered as a synapomorphy of the clade

Atalophleboculata sensu Kluge (2009), which includes Terpidinae, Atalophlebomaxillata, and Atalophlebolinguata. In addition, Monjardim et al. (2020) recovered Aprionyx as sister group of Terpidinae, but with low support. Aprionyx is distributed exclusively in the Afrotropical region and retain the distal dentiseta as in Terpidinae (Kluge, 2012). Unfortunately, Aprionyx was not included in our analysis. On the other hand, in Monjardim's classification, the clade Aprionyx + Terpidinae was grouped as sister group of Atalophlebolinguata (a clade comprising Atalophlebiinae, Choroterpinae, and Hagenulinae) with strong statistical Bremer support. Kluge (2015) suggested the absence of posterolateral projections on abdominal segment VII as the unique synapomorphy of Terpidinae. However, in our phylogenetic hypotheses, this character state is plesiomorphic in Leptophlebiidae, and the presence of these abdominal projections is apomorphic in Atalophlebiinae sensu Monjardim et al. (2020).

Monophyly and phylogenetic relationships among Terpidinae species

Terpidinae genera were grouped into two major monophyletic lineages, one including the genus Terpides and the other arranged as a clade of two monophyletic genera (Tikuna + Fittkaulus) (Figure 1). Demoulin (1966) proposed the absence of posterolateral projections on abdominal segment VII (42-2) and enlarged middle denticle in the claws of the nymphs (36-1) as diagnostic to diagnosis of the genus Terpides. On the other hand, Kluge (2015) proposed the shell-like egg (79-1) in the diagnosis of Terpides. In our phylogenetic analysis, chorionic plates as fixation structures in the eggs (73-0) were recovered as a synapomorphy of Terpides. Two additional synapomorphies supported the monophyly of this clade: two rows of simple setae in the inner margin of fore tarsi (35-1); and claws widened in the proximal half (39-0).

One polytomy was recovered with the species Te. jessiae, Te. contamanensis and Te. sooretamae. Kluge (2015) documented the relationship between these species and highlighted that these species have the same cuticular coloration, presence of posterolateral projections on abdominal segment VI, the absence of setae on the second segment of labial palp, and penis not narrowing in distal part. In our oologic study, the chorionic ornamentation in Te. contamanensis and Te. sooretamae was very similar (Figures. 18–19). In addition, these species are indistinguishable morphologically. Our results hipothetizate that these species are closely related and potentially could be synonyms. The sister group of this polytomy was a clade of the species Te. diadema and Te. ornatodermis. Kluge (2015) reported the relation of these species and documented the presence of setae on the inner margin of the second segment of labial palp

(24-1), and different abdominal color pattern on different segments (43-1) as shared characteristics among them. Our phylogenetic analysis is an additional evidence that these species are closely related and potentially could be synonyms. The species Te. echinovaris was recovered as the sister group of the remaining species of Terpides.

The eggs shape was proposed by Kluge (2015) in order to distinguished Terpides form the genera Tikuna and Fittkaulus, and in the present study, the oval rounded shape in cross section of the eggs (79-0) was recovered as synapomorphy of Tikuna + Fittkaulus. Domínguez & Abdala (2019) proposed the trajectory line of the bulla not crossing the fork of vein MA (52-0) as one synapomorphy of Tikuna, and independently acquired in other genera of Leptophlebiidae and, in this investigation, it was also recovered as synapomorphy of the Tikuna + Fittkaulus. Two additional synapomorphies supported this clade in our study, outer margin of mandibles relatively straight (15-1) and micropylar area of eggs ring-like (76-1). Kluge (2015) proposed the presence of side projections in the dorsal lamellae of gills in the diagnosis of Fittkaulus and Tikuna. This characteristic was recovered as apomorphic character state shared by these genera and the presence of this characteristic in Habrophlebiinae and Massartella genus was hypothesized as a convergence. Monjardim et al. (2020) using molecular characters recovered the monophyly of Terpidinae and Tikuna + Fittkaulus as monophyletic sister groups, just like in the present study.

Savage et al. (2005) reported that Tikuna is most closely related to Fittkaulus within the Terpides lineage. In the diagnosis of Tikuna, the authors highlighted the presence of mid-lateral margins of penis with projections in the diagnosis of genus. This character state (67-1) was recovered as a synapomorphy of this genus in our phylogenetic analysis. In the classification of Kluge (2009), Tikuna is characterized by yellow apex of subcostal field of fore wings and by the presence of projections by sides of terminal filament on ventral lamela of the gills II-VI. We recovered both characters as synapomorphies of this genus in the present phylogenetic analysis (54-1 and 45-1 respectively). In our analyses, the monophyly of Tikuna genus was supported by one additional synapomorphy, the presence of hemispheric protuberances distributed uniformly in the chorion surface of the eggs (78-0). On the other hand, the presence of side projections of ventral lamellae of gills in Tikuna and Habrophlebiinae evolved independently in both lineages.

The species Tikuna bilineata was recovered as sister group of the Ti. fusconotum and Kluge (2009) reported the presence of yellow stripe in distal part of the subcostal field as a shared character state in these species. The species type of the genus, Ti. atramentum, was recovered as the sister group of the remaining species of Tikuna.

Savage & Peters (1978) proposed Fittkaulus to be most closely related to Terpides, however, the Tikuna genus had not been described at time. The authors mentioned the presence of apical projection on dorsal lamella of the gills in the diagnosis of the genus. In the classification proposed by Kluge (2009), the author suggested that the genus Fittkaulus was characterized by the presence of a single apical segment of the forceps in contrast to Terpides and Tikuna, in which two apical segments are present. This character state (65-0) was recovered as the only synapomorphy that supports the monophyly of Fittkaulus in our study.

Fittkaulus was divided in two monophyletic lineages, the clade F. cuiabae + F. maculatus and the clade F. amazonicus + F. cururuensis. Kluge (2015) described the eggs of F. amazonicus and reported the presence of fibrillose units in the chorion sculpture. In our ootaxonomic study, fibrillose units uniformly distributed in the egg surface also characterized the chorion sculpture in the eggs of F. cururuensis. Our results are additional evidence of the closed relation of these species and potentially could be synonyms.

TAXONOMY

Terpidinae Kluge, 2009

In circumscription corresponds to “Terpides lineage” Savage, 1986: 255; Savage, 1987: 212; Peters, 1997: 452; Savage et al. 2005: 12; Terpides/fg1 or Terpidinae or Terpides s.l. Kluge, 2009: 244; Terpidinae Kluge, 2015: 152; Godunko et al. 2015: 277; Monjardim et al. 2020: 7.

Diagnosis.

Modified from Kluge, 2009 and 2015**.**

Imago. Claws of a pair similar (Fig. 14); tibiae of middle and hind legs retain patella-tibial suture; fork of vein MA asymmetric in fore wings (Fig. 8); vein Sc in hind wings terminates just distal of costal projection and far from apex (Figs. 9, 11, and 13); penes bears with a pair of thick sclerotized longitudinal bands located on ventral side and run along paired penial lobes (Fig. 16); distal segments of the forceps are smaller than the basal segment, in Fittkaulus the distal segments are fused forming a single segment (Figs. 15–17); and penis lobes fused (68-1).

Nymph. Hypognathous mouthparts orientation; labrum with presence of a third row of setae; hypopharynx without lateral projections (Fig. 3); maxilla has a pectinate proximal dentiseta and a simple distal dentiseta; glossa curved over ventrolaterally (Fig. 2); stout pointed spine-like setae on inner margin of segment III of labial palp forming an single regular longitudinal row; abdominal segment VII always lacks posterolateral projections; proximal part of caudal filaments with swimming setae (Fig. 7).

Composition. Terpides Demoulin, 1966: Te. guyanensis Demoulin 1966, (type species), Te. vinculum (Traver 1947), Te. jessiae Peters & Harrison 1974, Te. diadema Lugo-Ortiz & McCafferty 1996, Te. sooretamae Boldrini & Salles in Boldrini et al. (2009), Te. contamanensis Kluge 2015, Te. echinovaris Kluge 2015, Te. iguapoga Molineri, Domínguez & Zúñiga in Zúniga et al. (2015), and Te. ornatodermis Kluge 2015; Fittkaulus Savage & Peters, 1978: F. maculatus Savage & Peters 1978 (type species), F. cuiabae Savage 1986, F. cururuensis Savage 1986, and F. amazonicus Kluge 2009; Tikuna Savage, Flowers & Porras, 2005: Ti. bilineata (Needham & Murphy 1924), Ti. atramentum (Traver 1947) (type species), Ti. fusconotum Kluge 2009 and Ti. nigrobulla Kluge 2009.

Distribution. Restricted to the Neotropic (see below).

Terpides Demoulin, 1966

Terpides Demoulin, 1966: 15 (nymph); Peters & Harrison, 1974: 178 (adult); Orth et al. 2000: 33; Domínguez et al. 2001: 28, 37; Domínguez et al. 2002: 463; Domínguez et al. 2006: 486; subgenus Terpides s.s.; Kluge, 2009: 248; Terpides Zúñiga et al. 2014: 226; Terpides Gutiérrez & Dias, 2015: 16; Terpides s.s. Kluge, 2015: 155.

Type species: Terpides guyanensis Demoulin, original designation.

Diagnosis.

Modified from Demoulin, 1966 and Peters & Harrison, 1974.

Imago. Eyes of male with upper portion located on a short, wide stalk; trajectory of bullae crossing the fork of MA (Fig. 8); costal projection of hind wings blunt, and weakly developed

(Fig. 9); forceps with two distal segments (Fig. 15); penes short and tubular, fused basally, and without lateral projections (Fig. 15).

Nymph. Claws with enlarged apical denticle on inner row; dorsal and ventral lamellae of gills I–VII without side projections (Fig. 4); maxillary palp segment I shorter than the segment II; maxillary palp segment II with outer and inner margin with 9–12 and 5–7 simple setae respectively; maxillary palp segment III with outer margin with long row of 5–8 simple setae; tibiae of middle and hind leg with stout setae on outer margin; femur and tibia of hind legs without short pectinate setae on inner-posterior margin.

Composition. Te. guyanensis Demoulin 1966, Te. vinculum (Traver 1947), Te. jessiae Peters & Harrison 1974, Te. diadema Lugo-Ortiz & McCafferty 1996, Te. sooretamae Boldrini & Salles in Boldrini et al. (2009), Te. contamanensis Kluge 2015, Te. echinovaris Kluge 2015, Te. iguapoga Molineri, Domínguez & Zúñiga in Zúniga et al. (2015) and Te. ornatodermis Kluge 2015.

Distribution. Saint Vincent, Costa Rica, Colombia, Peru, French Guiana, and Brazil (Figs. 24–31 and 6D in annex I).

Terpides contamanensis Kluge, 2015

Terpides contamanensis Kluge, 2015: 175 (nymph, male, female and egg).

Diagnosis.

Modified from Kluge, 2015.

Imago. Fore wings with some or all cross veins in all fields bordered with brown (Fig. 4C in annex I); abdomen dark ocher-brown, terga II–VI with diffusive darker brown sublateral and submedian maculae near posterior margin; penes in ventral view narrow at base, widest in proximal part and gradually narrowed toward apex.

Nymph. Abdominal terga with small or large medio-posterior blackish markings; maxillary palp segment II with outer margin with 9–11 simple setae, and inner margin with 6–7 simple setae; labial palp segment II without simple setae on inner margin; posterolateral projections presents on abdominal segments II–VI or III–VI and VIII–IX.

Distribution. Peru: Ucayali province in the Loreto region (Fig. 24), and Colombia: Caldas and Tolima (Fig. 6D in annex I).

Terpides diadema Lugo-Ortiz & McCafferty, 1996

Terpides diadema Lugo-Ortiz & McCafferty, 1996: 9 (female nymph); McCafferty, 1996 & Lugo-Ortiz, 1996: 25.

Diagnosis.

Modified from Lugo-Ortiz & McCafferty, 1996.

Imago. Unknown.

Nymph. Inner margin of labial palp segment II with three simple setae; abdominal terga with color pattern different in each abdominal segment; abdominal segments VIII–IV with posterolateral projections.

Distribution. Costa Rica: Sinigri River on Putarenas province (Fig. 25).

Terpides echinovaris Kluge, 2015 (Fig. 4F in annex I)

Terpides echinovaris Kluge, 2015: 167 (nymph, male, female and egg).

Diagnosis.

Modified from Kluge, 2015.

Imago. Fore wings with some cross veins of costal, subcostal and first radial veins thickened, dark brown and narrowly bordered by brown; femora of mid and hind legs with proximal contrasting dark brown macula; penes with sharp narrowing in distal part (Figs. 77 and 78 in Kluge, 2015).

Nymph. Femora of mid and hind legs with proximal contrasting dark brown macula characteristic for winged stages; labial palp segment II without simple setae on inner margin (Fig. 51 in Kluge, 2015); abdomen with posterolateral projections on segments II–VI or III–VI and VII–IX.

Distribution. Peru: Satipo province in the Junin region (Fig. 26); and Colombia: Magdalena basin (Fig. 6D in annex I).

Terpides guyanensis Demoulin, 1966

Terpides guyanensis Demoulin, 1966: 17 (nymph); Hubbard, 1982: 266; Savage & Peters, 1978: 296; Boutonnet et al. 2004 (nymph complementary description); Domínguez et al. 2006: 487; Boldrini et al. 2009: 222 (male imago); Terpides (Terpides) guyanensis Kluge, 2009: 248; Terpides guyanensis Kluge, 2015: 155.

Diagnosis.

Modified from Demoulin, 1966, Boutnonnet et al. 2004 and Boldrini et al. 2009.

Imago. Male eyes with upper portion grayish brown (Figs. 36 and 37 in Boldrini et al. 2009); fore wings hyaline; genitalia with penes abruptly narrowing toward apex (Fig 41 in Boldrini et al. 2009).

Nymph. Anteromedial emargination of labrum with six large denticles; apex of fore tibia with a brown spot; fore femora with subapical brown spots; abdominal terga with two pairs of submedian spots; gills with tracheae blackish only in part; posterolateral projections in abdominal segments V–VI and VIII–IX.

Distribution. Brazil: Roraima; Surinam; and French Guyana (Fig. 27).

Terpides iguapoga Molineri, Domínguez & Zúñiga, 2015 in Zúñiga et al. 2015

Terpides iguapoga Molineri, Domínguez & Zúñiga, 2015: 283 (nymph, male and female).

Diagnosis.

Modified from Zúñiga et al. 2015

Imago. Male eyes with upper portion orangish white; fore wings with smoky areas around cross veins and marginal intercalary veins; hind wings with costal projection bilobed; penes abruptly thin in the distal third (Fig. 2E and F in Zúñiga et al. 2015).

Nymph. Anteromedial emargination of labrum with five blunt and rounded denticles; labial palp segment II with three stout spines on inner margin; fore trochanter and femur with row of strong spine-like setae on inner margin (Fig. 2A in Zúñiga et al. 2015); posterolateral projections in abdominal segments VI and VIII–IX.

Distribution. Colombia: Gorgona Island in the Colombian pacific (Fig. 28), Reserva Natural Ñambi, and Parque Nacional Natural Selva de Florencia (Fig. 6D in annex I).

Terpides jessiae Peters & Harrison, 1974

Terpides jessiae Peters & Harrison, 1974: 179 (nymph, male imago and female subimago); Boutonnet et al. 2004: 96 (complementary description of nymph and female imago); Terpides (Terpides) jessiae Kluge, 2009: 248; Terpides jessiae Kluge, 2015: 155.

Diagnosis.

Modified from Peters & Harrison, 1974 and Boutonnet et al. 2004.

Male imago. Male eyes with upper portion brown; femora of the prothoracic legs brown except a small paler area in the middle; some cross veins in anterior ½ of the fore wings surrounded with small dark brown clouds; penes widest in proximal part and gradually narrowed toward to apex (Fig. 5 in Peters & Harrison, 1974).

Nymph. Anteromedial emargination of labrum with six denticles; abdominal posterolateral projections occur on segments III–VI and VIII–IX; mesothoracic and metathoracic femora with median darker brown macula; abdominal tergites II–IX with darker brown, mesal color pattern (Fig. 20 in Peters & Harrison, 1974).

Distribution. Saint Vincent and Martinique in the West Indies (Fig. 29).

Terpides ornatodermis Kluge, 2015

Terpides ornatodermis Kluge, 2015: 157 (nymph, male, female and egg).

Diagnosis.

Modified from Kluge, 2015.

Imago. Fore wings with membrane by sides of most cross veins brown; femora of mid and hind legs with proximal and distal dark brown maculae; penes with narrowing in distal part and with angulate pedestal-like widening basally (Fig. 27 in Kluge, 2015).

Nymph. Labial palp segment II with 2–4 stout setae on inner margin; abdominal tergites with color pattern different on different segments (Fig. 7 in Kluge, 2015); abdomen with posterolateral projections only on segments VIII–IX; gills with tracheae blackish only in part (Fig. 36 in Kluge, 2015).

Distribution. Peru: Satipo province in the Junin region (Fig. 30); and Colombia: Tolima state (Fig. 6D in annex I).

Terpides sooretamae Boldrini & Salles, 2009

Terpides sooretamae Boldrini & Salles, 2009: 222 (nymph, male and female); Terpides (Terpides) sooretamae Kluge, 2009: 248; Salles et al. 2010: 306; Shimano et al. 2011: 250; Lima et al. 2012: 314; Brasil et al. 2013: 262 and 2014: 329; Angeli et al. 2015: 202; Terpides sooretamae Kluge, 2015: 155; Lima et al. 2015: 7.

Diagnosis.

Modified from Boldrini et al. 2009.

Imago. Male eyes with upper portion orange; cross veins of fore wings surrounded with small brown clouds (Fig. 8); genitalia with penes gradually narrowing toward apex (Fig. 15).

Nymph. Anteromedial emargination of labrum with six poorly defined denticles; posterolateral projections present on abdominal terga III–VI and VIII–IX; labial palp segment II without setae.

Distribution. Brazil: Espírito Santo, Rio de Janeiro, Minas Gerais, Mato Grosso, Mato Grosso do Sul, Alagoas and Pernambuco (Fig. 31).

Terpides vinculum (Traver, 1947)

Choroterpes vinculum Traver, 1947: 157 (female imago); Terpides (Terpides) vinculum Kluge, 2009: 248; Terpides vinculum Kluge, 2015: 155.

Diagnosis.

Modified from Traver, 1947.

Female imago. Body almost entire body very dark red-brown; humeral cross veins blackish browns; hind wings as Fig. 19 in Traver, 1947; on middle tergites indistinct paler submedian dashes at anterior margin and on some tergites traces of pale medial line in anterior half.

Nymph. Unknown.

Distribution. Costa Rica: Pedregoso River.

Tikuna Savage, Flowers & Porras, 2005

Choroterpes atramentum Traver, 1947: 156; genus Tikuna Savage et al. 2005: 2; Tikuna Domínguez et al. 2006: 511; Flowers & Ávila, 2006: 135; subgenus Tikuna of the genus Terpides Kluge, 2009: 248; Gutiérrez & Dias, 2015: 16; Tikuna genus Kluge, 2015: 182; Mosquera-Murillo & Córdoba-Aragón, 2017: 159.

Type species: Choroterpes atramentum Traver, original designation.

Diagnosis.

Modified from Savage et al. 2005, Domínguez et al. 2006 and Kluge, 2009, 2015.

Imago. Male eyes with upper portion very short and wide stalks; trajectory of bullae not crossing the fork of MA (Fig. 10); penes basal ½ fused, apical ½ unfused and mid-lateral margins with projections (Fig. 16), two apical segments in the forceps (Fig. 16); subcostal field of fore wings with yellow apex (Fig. 10); hind wings with costal projection prominent (Fig. 11).

Nymph. Claws with two rows of denticles similar in form and contiguous; gills II–VI with ventral lamellae with large inner and outer lobes in apical margin (Fig. 5); femur and tibia of hind legs with dense short pectinate setae on inner-posterior margin (Figs. 135 -137 in Kluge, 2015).

Composition. Ti. atramentum (Traver 1947), Ti. bilineata (Needham & Murphy 1924), Ti. fusconotum Kluge 2009, and Ti. nigrobulla Kluge 2009.

Distribution. Costa Rica; Colombia; Peru; Ecuador; Venezuela; Suriname; and Brazil (Figs. 32-35 and Fig. 6D in annex I).

Tikuna atramentum (Traver, 1947)

Choroterpes atramentum Traver, 1947: 156 (male and female subimagos); Tikuna atramentum Savage, Flowers, Porras, 2005: 4 (nymph, male, and female imagos); Flowers & Ávila, 2006: 133; Terpides (Tikuna) atramentum Kluge, 2009: 248; Tikuna atramentum Kluge, 2015: 182.

Diagnosis.

Modified from Traver, 1947 and Savage et al. 2005.

Imago. Abdominal tergites II–V with anterior and posterior, submedian, and spiracular brownish black marks and posterior marks absent in segment VII (Fig. 7 in Savage et al. 2005); genitalia with lateral pointed projections (Fig. 16); cross veins of R_1 cell of fore wing washed with brownish black (Fig. 1 in Savage et al. 2005).

Nymph. Anteromedial emargination of labrum well developed with six denticles; abdominal tergites I–VI and VIII with brownish black maculae as in male imago; submedian longitudinal brownish black stripes extended from anterior margin of pronotum to posterior mesonotum as in male imago.

Distribution. Costa Rica: Peninsulas of Santa Helena and Nicoya (Fig. 32); and Colombia: Magdalena basin in Caldas (Fig. 6D in annex I).

Tikuna bilineata (Needham & Murphy, 1924)

Choroterpes bilineata Needham & Murphy, 1924: 48 (male subimago and female imago); Traver, 1947: 156 (male and female); Choroterpes (Choroterpes) bilineata Hubbard, 1982: 264; Tikuna bilineata Peters et al. 2005: 52; Domínguez et al. 2006: 511; Flowers & Ávila, 2006: 135; Lopes et al. 2007: 143; Chacón et al. 2009: 728; Sweeney et al. 2009: 315; Boldrini et al. 2009: 225 (nymph and male imago); Terpides (Tikuna) bilineata Kluge, 2009: 254; Shimano et al. 2011: 250; Shimano et al. 2013: 36; Brasil et al. 2013: 262; Tikuna bilineata Kluge, 2015: 182 (egg); Angeli et al. 2015: 202; Boldrini & Krolow, 2017: 3; Raimundi, 2019: 40; Sousa-Nascimento et al. 2020: 587.

Diagnosis.

Modified from Needham & Murphy, 1924, Traver, 1947 and Boldrini et al. 2009.

Imago. Pronotum with longitudinal submedial black mark and mesonotum with longitudinal submedial black mark reaching posterior scutal protuberance; segments I–VII of abdominal tergites with longitudinal submedial black mark; fore wings with costal and posterior region of subcostal veins yellowish (Fig. 10); penes wanting apical spine.

Nymph. Pronotum with longitudinal submedial black mark and this mark is restricted to anterior half in the mesonotum and converging posteriorly; segments I–VIII of abdominal tergites with longitudinal submedial black mark; apex of tibiae with pectinate setae (Fig. 28 in Boldrini et al. 2009); posterolateral projections present on abdominal tergites VIII–IX.

Distribution. Brazil: Amazonas, Goiás, Mato Grosso, Pará, Tocantins, Espírito Santo, and Maranhão; Ecuador; Suriname; Venezuela; Peru; Colombia: Amazonas, Valle del Cauca, and Reserva Natural Rio Manso (Fig. 33 and Fig 6D in annex I).

Tikuna fusconotum (Kluge, 2009)

Terpides (Tikuna) fusconotum Kluge, 2009: 253 (male imago); Tikuna fusconotum Kluge, 2015: 185.

Diagnosis.

Modified from Kluge, 2009.

Imago. Abdominal tergites II–VII with paired dark maculae close to hind margins of terga; abdominal tergite VIII with and integral dark brown maculae instead of a pair of converging longitudinal strips; bulla of fore wings without brown dot (Fig. 24 in Kluge, 2009).

Nymph. Unknown.

Distribution. Peru: Province Maynas in the Loreto region (Fig. 34).

Tikuna nigrobulla (Kluge, 2009)

Terpides (Tikuna) nigrobulla Kluge, 2009: 251 (nymph and male subimago); Tikuna nigrobulla Kluge, 2015: 185.

Diagnosis.

Modified from Kluge, 2009.

Male subimago. Costal brace with cross portion colorless; fore wings with costal and radial fields without brown spots; bulla on subcostal field of fore wings with small dark brown dot (Fig. 21 in Kluge, 2009); penes with lobes fused in proximal half, divided in distal part and with pair of lateral sharp projections directed laterally-basally.

Nymph. Strips of anterior part of mesonotum diverging posteriorly; strips of abdominal tergites II–VII are progressively shorter; anterior parts of abdominal tergites with dark coloration; posterolateral projections only in abdominal segments VIII–IX.

Distribution. Peru: Loreto province and Satipo province in Junin region (Fig. 35).

Fittkaulus Savage & Peters, 1978

Fittkaulus Savage & Peters, 1978: 293; Savage, 1986: 257; 1987: 201; Orth et al. 2000: 30; Fittkaulus Domínguez et al. 2006: 377; Fittkaulus subgenus of Terpides, Kluge, 2009: 248; Fittkaulus genus Kluge, 2015: 180.

Type species: Fittkaulus maculatus Savage & Peters, original designation.

Diagnosis.

Modified from Savage & Peters, 1978, Savage, 1986, 1987 and Domínguez et al. 2006.

Imago. Male eyes with upper portion on tall stalk; trajectory of bullae not crossing the fork of MA (Fig. 12); hind wings with costal projection prominent (Fig. 13); forceps with only one distal segment (Fig. 17); penes short and tubular, fused in basal ⅔ and without projections.

Nymph. Dorsal lamella of gills II–VI with projections by sides of terminal point (Fig. 6); denticles of claws subequal; on hind leg femur and tibia without dense short pectinate setae on inner-posterior side.

Composition. F. maculatus Savage & Peters 1978, F. cuiabae Savage 1986, F. cururuensis Savage 1986, and F. amazonicus Kluge 2009.

Distribution. Peru: Province Maynas in Loreto region; Brazil: Amazonian basin (Pará and Roraima), Araguaia-Tocantins basin (Mato Grosso), Atlântico Sudeste basin (Espírito Santo), Pernambuco, Bahia and Maranhão; and Colombia: Orinoco basin (Figs. 36–39).

Fittkaulus amazonicus (Kluge, 2009)

Terpides (Fittkaulus) amazonicus Kluge, 2009: 248 (nymph, male and female imagos); Fittkaulus amazonicus Kluge, 2015: 181 (egg); Salinas-Jiménez et al. 2018: 98.

Diagnosis.

Modified from Kluge, 2009.

Imago. Male eyes with upper portion of not elongated; fore wings without dark macula on fork of MA (Fig. 12 in Kluge, 2009); penes with long pointed apical projections.

Nymph. Abdominal tergites with contrasting light brown marks and lighter blanks, repeated on segments III–VIII (Fig. 8 in Kluge, 2009); posterolateral projections present on abdominal segments II–VI and VIII–IX; claws with all denticles subequal.

Distribution. Peru: Province Maynas in Loreto region, and Amazon River; and Colombia: Orinoco basin (Fig. 36).

Fittkaulus cuiabae (Savage, 1986)

Fittkaulus cuiabae Savage, 1986: 265 (female imago); Domínguez et al. 2006: 380; Terpides (Fittkaulus) cuiabae Kluge, 2009: 248; Fittkaulus cuiabae Kluge, 2015: 180.

Diagnosis.

Modified from Savage, 1986.

Female imago. Fore wings with dark macula on fork of vein MA; hind wings with apex acute; apex of costal projection located less than 7/10 distance from base to apex; fore portion of lateral oviducts washed with brownish black forming submedian marks on sternum VII.

Nymph. Unknown.

Distribution. Brazil: Mato Grosso (Fig. 37).

Fittkaulus cururuensis (Savage, 1986)

Fittkaulus cururuensis Savage, 1986: 268 (female imago); Domínguez et al. 2002: 462; Domínguez et al. 2006: 380; Lopes et al. 2007: 141; Fittkaulus cururuensis Boldrini et al. 2009: 220 (nymph); Terpides (Fittkaulus) cururuensis Kluge, 2009: 248; Salles et al. 2010: 306; Lima et al. 2012: 309; Brasil et al. 2013: 262; 2014: 329; Shimano et al. 2013: 36; Fittkaulus cururuensis Kluge, 2015: 180; Costa et al. 2018: 4; Gama-Neto et al. 2018: 35; Sousa-Nascimento et al. 2020: 581.

Diagnosis.

Modified from Savage, 1986 and Boldrini et al. 2009.

Female imago. Eyes separated on meson of head by a distance of 2.8–3.0 times maximum width of an eye; abdominal sterna I–II with small posteromedial brownish black marks; fore wings without dark maculae on fork of vein MA (Fig. 12); coxae I and II or II and III with brown mark.

Nymph. Anteromedial emargination of labrum without denticles; coxae of middle and hind legs with brown mark; abdominal tergites II–VII with sublateral yellow mark and terga VIII with median area yellow (Fig. 31 in Boldrini et al. 2009); posterolateral projections present in abdominal segments II–VI and VIII–IX.

Distribution. Brazil: Araguaia-Tocantins basin (Mato Grosso), Amazon basin (Pará) e Atlântico Sudeste basin (Espírito Santo), Bahia, Pernambuco, Roraima, and Maranhão (Fig. 38).

Fittkaulus maculatus Savage & Peters, 1978

Fittkaulus maculatus Savage & Peters, 1978: 294 (male, female and nymph); Hubbard, 1982: 264; Savage, 1986: 262 (male, female and nymph); Domínguez et al. 2002: 462; Domínguez et al. 2006: 380; Terpides (Fittkaulus) maculatus Kluge, 2009: 248; Fittkaulus maculatus Kluge, 2015: 180; Costa et al. 2018; Gama-Neto et al. 2018: 35.

Diagnosis.

Modified from Savage & Peters, 1978 and Savage, 1986.

Male imago. Eyes with stalked turbinate portion long, pale yellow; fork of vein MA with brownish-black macula; costal projection of hind wings located approximately ¾ distance from base to wing margin; penes with basal ⅔ fused and without apical appendages; ninth sternum of female with a deep V-shaped cleft apically (Fig. 14 in Savage & Peters, 1978).

Nymph. Median area of metanotum with black triangular macula; claws with basal group of 5-8 short subequal denticles and distal set of unequal denticles; abdominal posterolateral projections present in segments IV–VI and XIII–IX.

Distribution. Brazil: Amazon basin in Pará, and Roraima states, Bahia, and Espírito Santo (Fig. 39).

Interactive keys

The interactive key of imagos and nymphs of Terpidinae species are available at following links:

http://www.xper3.fr/xper3GeneratedFiles/publish/identification/-5614202481360614904/

http://www.xper3.fr/xper3GeneratedFiles/publish/identification/157677526641953663/

Biology and ecology

Biological aspects and ecology of Terpidinae species remain poorly studied. However, Savage & Peters (1978) reported that nymphs of F. maculatus are collected in streams of 3–5 m of width, 20–50 cm of deep, with sandy bottoms and partly exposed bedrock. In turn, these authors collected many nymphs on leaves and other larger detrital fragments in areas of slow current. Savage et al. (2005) reported that all specimens of Tikuna atramentum collected during 2002 in Costa Rica came from seasonal streams in areas that experience a four to six-month dry season. Additionally, these authors highlighted that Ti. atramentum apparently has a long emergence period or is multigenerational and the adults of this species collected in Santa Elena peninsula where taken on a ridge of serpentine rock in a mixture of grasslands and fragments of dwarf forest. The specimens of Ti. atramentum recorded in Colombia in this work, were collected in pacific dominion proposed by Morrone (2014), in an affluent of Magdalena basin with bimodal climate regime, two marked periods of rain and two low water levels throughout the year (Pareja et al. 2014). Additionally, nymphs of Terpidinae species inhabit places with slow water current in warm tropical streams (Kluge, 2015). Future biological and ecological studies of Terpidinae species are required and species widely distributed as Ti. bilineata and

Te. sooretamae are interesting study models. To finalize, we propose future systematic studies using other type of characters as molecular information as geometric morphometry data as well and its relation with the evolution of anatomical characteristics.

ACKNOWLEDGEMENTS

We thank the Entomological Collection of the Biology Program of the University of Caldas, Colombia and Universidade Federal de Rio de Janeiro for facilitating a space to examine part of deposited material. We also thank Rafael Boldrini of Universidade Federal de Roraima for sending us some material of Terpidinae. We thank Dr. José Serrão, director of the Laboratorio de Ultraestructura Celular of the Universidade Federal de Viçosa, for his help in taking images at the Microscopy Electronic Scanning. We also thank Dr. Og DeSouza (Universidade Federal de Viçosa) for facilitating the use of optic equipment. This study was financed in part by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) to JFM (process # 162813/2018-0) and to FFS (processes # 305847/2015-5 and 309666/2019-8).

REFERENCES

Angeli, K. B., do Rozário, E. M. M., & Salles, F. F. (2015). Checklist of Ephemeroptera (Insecta) from São Mateus River Basin, Espírito Santo, Brazil. Revista Brasileira de Entomologia, 59(3), 197-204.

Barnard, K. H. (1932). South African may-flies (Ephemeroptera). Transactions of the Royal Society of South Africa, 20(3), 201-259.

Benhadji, N., Hassaine, K. A., & Sartori, M. (2018). Habrophlebia hassainae, a new mayfly species (Ephemeroptera: Leptophlebiidae) from North Africa. Zootaxa, 4403(3), 557-569.

Boldrini, R., Salles, F. F., & Cabette, H. R. (2009). Contribution to the taxonomy of the Terpides lineage (Ephemeroptera: Leptophlebiidae). In Annales de Limnologie-International Journal of Limnology, 45(4), 219-229.

Boldrini, R., & Krolow, T. K. (2017). New records of Ephemeroptera (Insecta) from Tocantins state, northern Brazil. Check List, 13(2), 2067.

Brasil, L. S., Shimano, Y., Batista, J. D., & Cabette, H. S. (2013). Effects of environmental factors on community structure of Leptophlebiidae (Insecta, Ephemeroptera) in Cerrado streams, Brazil. Iheringia. Série Zoologia, 103(3), 260-265.

Brasil, L. S., Juen, L., & Cabette, H. S. (2014). The effects of environmental integrity on the diversity of mayflies, Leptophlebiidae (Ephemeroptera), in tropical streams of the Brazilian Cerrado. In Annales de Limnologie-International Journal of Limnology (Vol. 50, No. 4, pp. 325-334). EDP Sciences.

Campbell, I. C., & Peters, W. L. (1986). Redefinition of Kirrara Harker with a redescription of Kirrara procera Harker (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). Aquatic Insects, 8(2), 71-81.

Cardoni, S., Tenchini, R., Ficulle, I., Piredda, R., Simeone, M. C., & Belfiore, C. (2015). DNA barcode assessment of Mediterranean mayflies (Ephemeroptera), benchmark data for a regional reference library for rapid biomonitoring of freshwaters. Biochemical Systematics and Ecology, 62, 36-50.

Chacón, M. M., Pescador, M. L., Hubbard, M. D., & Segnini, S. (2009). Mayflies (Insecta: Ephemeroptera) from Venezuela. Check List, 5(3), 723-731.

Chippindale, P. T., & Wiens, J. J. (1994). Weighting, partitioning, and combining characters in phylogenetic analysis. Systematic Biology, 43(2), 278-287.

Coleman, C. O. (2003). "Digital inking": How to make perfect line drawings on computers. Organisms Diversity and Evolution, 3(4), 303.

Coleman, C. O. (2006). Substituting time-consuming pencil drawings in arthropod taxonomy using stacks of digital photographs. Zootaxa, 1360(1), 61-68.

Costa, S. S., Souza, F. N., Nogueira, M. A. M., Santos, E. P. D., Sousa, M. M. L. D., Silva, V. D. A., ... & Mariano, R. (2018). Leptophlebiidae (Insecta: Ephemeroptera) from state of Bahia, Brazil. Biota Neotropica, 18(1).

Demoulin, G. (1966). Contribution à l'étude des Ephemeropteres du Surinam. Bull. Inst. R. Sci. Nat. Belg, 42, 1–22.

Derka, T. (2002). Massartella devani, a new mayfly species from Venezuela's Highlands (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). Aquatic Insects, 24(4), 309-316.

Derka, T., Svitok, M., & Schlögl, J. (2009). Massartella hirsuta sp. nov. (Ephemeroptera: Leptophlebiidae: Atalophlebiinae) and new data on mayflies of Guyana Highlands. Aquatic Insects, 31(1), 83-94.

Dias, L. G., Bacca, T., Navarro, L., Acevedo, F. E., Benavides, P. M., & Ferreira, P. S. F. (2011). Association of nymphs and adults of Ephemeroptera (Insecta) using the amplified fragment length polymorphism (AFLP) technique. In Annales de Limnologie-International Journal of Limnology (Vol. 47, No. 2, pp. 151-157). EDP Sciences.

Dias, L. G., Molineri, C., Takiya, D., Benavides, P., & Bacca, T. (2019). Phylogeny of Tricorythodes Ulmer (Leptohyphidae: Ephemeroptera) based on molecular and morphological evidence. Zoologischer Anzeiger, 278, 38-45.

Dominguez, E. (1991). The status of the genus Ulmeritus (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). In Overview and strategies of Ephemeroptera and Plecoptera.(Proc. Vlth Int. Ephemeroptera Cont. 24-28 July 1989 and Xth Int. Symp. on Plecoptera 27—30July 1989, Granada, Spain) (Vol. 157, p. 169).

Domínguez, E., Hubbard, M. D., Pescador, M. L., & Molineri, C. (2001). Ephemeroptera. Guía para la determinación de los artrópodos bentónicos sudamericanos (HR Fernandez & E. Domínguez, eds.). Editorial Universitária de Tucumán, Tucumán, 282p.

Domínguez, E., del Carmen Zúñiga, M., & Molineri, C. (2002). Status of the knowledge and distribution of the Ephemeroptera fauna (Insecta) in the Amazon region. Caldasia, 459-469.

Domínguez, E., & Cuezzo, M. G. (2002). Ephemeroptera egg chorion characters: a test of their importance in assessing phylogenetic relationships. Journal of Morphology, 253(2), 148-165.

Domínguez, E., Molineri, C., Pescador, M. L., Hubbard, M. D., & Nieto, C. (2006). Biodiversidad Acuática en América Latina Volumen 2 Ephemeroptera de América del Sur. Sofia– Moscow: PENSOFT.

Domínguez, E., Molineri, C., & Nieto, C. (2009). Ephemeroptera. En E. Domínguez, & H. R. Fernández, Macroinvertebrados bentónicos sudamericanos Sistemática y biología (págs. 55-95). San Miguel de Tucumán: Fundación Miguel Lillo.

Domínguez, E., & Abdala, V. (2019). Morphology and evolution of the wing bullae in South American Leptophlebiidae (Ephemeroptera). Journal of morphology, 280(1), 95-102.

Domínguez E., C. Molineri, C. Nieto., & Zúñiga, M. D. C. (2019). Lista de especies de Ephemeroptera Sudamericanos. http://ibn-conicet.gob.ar/ephemeroptera-sudamericanos/ (accessed 06 november 2019).

Farris, J. S. (1969). A successive approximations approach to character weighting. Systematic Biology, 18(4), 374-385.

Flowers, R. W., & Ávila, S. (2006). Biogeographical and ecological notes on the genus Tikuna Savage, Flowers, and Porras (Ephemeroptera: Leptophlebiidae) from Central and South America. Entomological news, 117(2), 133-138.

Flowers, R. W., & De La Rosa, C. (2010). Capítulo 4: Ephemeroptera. Revista de Biología Tropical, 58, 63-93.

Gaino, E., Mazzini, M., & Sartori, M. (1993). Comparative analysis of the chorionic pattern in Habroleptoides species (Ephemeroptera, Leptophlebiidae). Italian Journal of Zoology, 60(2), 155-162.

Gama-Neto, J. D. L. G., Passos, M. A. B., Cruz, J. A., & de Souza, N. T. (2018). New records of Ephemeroptera (Insecta) from Roraima State, Northern Brazil. EntomoBrasilis, 11(1), 33-40.

Gattolliat, J. L., & Sartori, M. (2000). Guloptiloides: an extraordinary new carnivorous genus of Baetidae (Ephemeroptera). Aquatic Insects, 22(2), 148-159.

Godunko, R. J., Sroka, P., Soldán, T., & Bojvoká, J. (2015). The higher phylogeny of Leptophlebiidae (Insecta: Ephemeroptera), with description of a new species of Calliarcys Eaton, 1881. Arthropod Systematics and Phylogeny, 73(2), 259-272.

Godunko, R. J., Soldán, T., & Staniczek, A. H. (2017). Baetis (Baetis) cypronyx sp. n., a new species of the Baetis alpinus species-group (Insecta, Ephemeroptera, Baetidae) from Cyprus, with annotated checklist of Baetidae in the Mediterranean islands. ZooKeys, 644, 1.

Goloboff, P. A. (1993). Estimating character weights during tree search. Cladistics, 9(1), 83-91.

Goloboff, P. A., & Farris, J. S. (2001). Methods for quick consensus estimation. Cladistics, 17(1), S26-S34.

Goloboff, P. A., Farris, J. S., Källersjö, M., Oxelman, B., Ramıacute, M. N. J., & Szumik, C. A. (2003). Improvements to resampling measures of group support. Cladistics, 19(4), 324-332.

Goloboff, P. A., Mattoni, C. I., & Quinteros, A. S. (2006). Continuous characters analyzed as such. Cladistics, 22(6), 589-601.

Goloboff, P. A., Carpenter, J. M., Arias, J. S., & Esquivel, D. R. M. (2008). Weighting against homoplasy improves phylogenetic analysis of morphological data sets. Cladistics, 24(5), 758-773.

Goloboff, P. A. (2014). Extended implied weighting. Cladistics, 30(3), 260-272.

Goloboff, P.A., & Catalano, S.A. (2016). TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics, 32, 221–238.

Goloboff, P. A., Torres, A., & Arias, J. S. (2018). Weighted parsimony outperforms other methods of phylogenetic inference under models appropriate for morphology. Cladistics, 34(4), 407-437.

Goncalves, I. C., Da-Silva, E. R., & Nessimian, J. L. (2010). A new species of Thraulodes Ulmer (Ephemeroptera: Leptophlebiidae) from Southeastern Brazil. Zootaxa, 2438(1), 61-68.

Gutiérrez, Y., & Dias, L. G. (2015). Ephemeroptera (Insecta) de Caldas-Colombia, claves taxonómicas para los géneros y notas sobre su distribución. Papéis Avulsos de Zoologia, 55(2), 13-46.

Hubbard, M. D. (1982). Catálogo abreviado de Ephemeroptera da América do Sul. Papéis Avulsos de Zoologia, 34(24), 257-282.

Källersjö, M., Farris, J. S., Chase, M. W., Bremer, B., Fay, M. F., Humphries, C. J., ... & Bremer, K. (1998). Simultaneous parsimony jackknife analysis of 2538rbcL DNA sequences reveals support for major clades of green plants, land plants, seed plants and flowering plants. Plant systematics and evolution, 213(3-4), 259-287.

Kluge, N. J. (1994). Habrophlebiinae subfam. n. with description of a new species of Habroleptoides from the Caucasus (Ephemeroptera: Leptophlebiidae). Zoosystematica Rossica, 3(1), 35-43.

Kluge, N. J. (2007). A new taxon Hermanellonota, or subtribe Hermanellini subtr. n. (Ephemeroptera: Leptophlebiidae: Hagenulini), with description of three new species from Peruvian Amazonia. Russian Entomological Journal, 16(4), 385-400.

Kluge, N. J. (2009). Higher system of Atalophlebiinae (Leptophlebiidae) with description of three new species of Terpides s.l. from Peruvian Amazonia. Russian Entomological Journal, 18(4), 243-256.

Kluge, N.J. (2012) Contribution to the knowledge of Choroterpes (Ephemeroptera, Leptophlebiidae). Russian Entomological Journal, 21, 273–306.

Kluge, N. J. (2015). Contribution to the knowledge of Terpidinae Kluge 2009 (Ephemeroptera: Leptophlebiidae). Zootaxa, 3999(2), 151-189.

Kluge, N. J. (2015a). Central Asian mountain Rhithrogenini (Ephemeroptera: Heptageniidae) with pointed and ephemeropteroid claws in the winged stages. Zootaxa, 3994(3), 301-353.

Kluge, N. J. (2020). Systematic position of Thraulodes Ulmer 1920 (Ephemeroptera: Leptophlebiidae) and descriptions of new and little-known species. Zootaxa, 4756(1), zootaxa-4756.

Koss, R. W. (1968). Morphology and taxonomic use of Ephemeroptera eggs. Annals of the Entomological Society of America, 61(3), 696-721.

Koss, R.W., & Edmunds, G.F. (1974). Ephemeroptera eggs and their contribution to phylogenetic studies of the order. Zoological Journal of the Linnean Society. 55(4), 267-349.

Kristensen, N. P. (1991). Phylogeny of extant hexapods. In The insects of Australia 2, 125–140. Melbourne University Publishing.

Laboratory of Informatics and Systematics of University Pierre et Marie Curie (Paris). Xper3. Version 3. Available in: <http://www.xper3.fr/>. Accessed in: December 2019.

Legg, D.A., Sutton, M.D., & Edgecombe, G.D. (2013). Arthropod fossil data increase congruence of morphological and molecular phylogenies. Nature Communications, 4, 2485.

Lestage, J. A. (1930). Notes sur le genre Massartella nov. gen. de la famille des Leptophlebiidae (Ephemeroptera) et le génotype Massartella brieni Lest. Une Mission Biologique Belge au Brésil, 2, 249-258.

Lima, L. R., Salles, F. F., & Pinheiro, U. (2012). Ephemeroptera (Insecta) from Pernambuco State, northeastern Brazil. Revista Brasileira de Entomologia, 56(3), 304-314.

Lima, L. R., Salles, F. F., & Pinheiro, U. (2015). New records of mayflies (Ephemeroptera: Insecta) from Pernambuco state, northeastern Brazil. Check List, 11(3), 1652.

Lopes, M. J. D. N., Ribeiro, J. M. F., & Peiró, D. F. (2007). Leptophlebiidae (Ephemeroptera) da Amazônia Brasileira. Acta Amazonica, 37(1), 139-145.

Lugo-Ortiz, C. R., & McCafferty, W. P. (1996). New species of Leptophlebiidae (Ephemeroptera) from México and Central America. Annales de Limnologie, 32(1), 3-18.

Maddison, W., & Maddison, D. (2018). Mesquite 2.75. [WWW document]. URLhttp://mesquiteproject.org/mesquite/mesquite.html.Version released 27.xii.2018.

Massariol, F. C., Paresque, R., & Salles, F. F. (2016). Species delimitation of Lachlania Hagen (Ephemeroptera: Oligoneuriidae) with description of two new species from Brazil. Zoosymposia, 11, 121-134.

Massariol, F. C., Takiya, D. M., & Salles, F. F. (2019). Global classification and evolution of brushlegged mayflies (Insecta: Ephemeroptera: Oligoneuriidae): phylogenetic analyses of morphological and molecular data and dated historical biogeography. Zoological Journal of the Linnean Society, 187(2), 378-412.

Mazzini, M., & Gaino, E. (1985). Fine structure of the egg shells of Habrophlebia fusca (Curtis) and H. consiglioi Biancheri (Ephemeroptera: Leptophlebiidae). International Journal of Insect Morphology and Embryology, 14(6), 327-334.

McCafferty, W. P., & Lugo-Ortiz, C. R. (1996). Los efemerópteros (Ephemeroptera) de América Central. Revista Nicaraguense de Entomologia, 35, 19-28.

Misof, B., Liu, S., Meusemann, K., Peters, R. S., Donath, A., Mayer, C., ... & Niehuis, O. (2014). Phylogenomics resolves the timing and pattern of insect evolution. Science, 346(6210), 763-767.

Mol, A. W. (1986). Harpagobaetis gulosus gen. nov., spec. nov., a new mayfly from Suriname (Ephemeroptera: Baetidae). Zoologische Mededelingen, 60(4), 63-70.

Molineri, C. (2006). Phylogeny of the mayfly family Leptohyphidae (Insecta: Ephemeroptera) in South America. Systematic Entomology, 31(4), 711-728.

Monjardim, M., Paresque, R., & Salles, F. F. (2020). Phylogeny and classification of Leptophlebiidae (Ephemeroptera) with an emphasis on Neotropical fauna. Systematic Entomology, 45(2), 415-429.

Morrone, J. J. (2014). Biogeographical regionalisation of the Neotropical region. Zootaxa, 3782(1), 1-110.

Mosquera-Murillo, Z., & Córdoba-Aragón, K. E. (2017). The first record of Tikuna Savage, Flowers y Porras (Ephemeroptera: Leptophlebiidae) for Chocó, Colombia. Boletín Científico. Centro de Museos. Museo de Historia Natural, 21(1), 157-161.

Needham, J. G., & Murphy, H. E. (1924). Neotropical mayflies. Bulletin of the Lloyd Library Number 24. Entomological Series, 4, 1-79.

Nixon, K.C., 2002. Winclada. Version 1.00.08. Published by the author, Ithaca, NY. [WWW document]. URL http://www.cladistics.com/ [accessed on 10 August 2012].

O'Donnell, B. C., & Jockusch, E. L. (2008). Phylogenetic relationships of leptophlebiid mayflies as inferred by histone H3 and 28S ribosomal DNA. Systematic Entomology, 33, 651–667.

Ogden, T. H., & Whiting, M. F. (2005). Phylogeny of Ephemeroptera (mayflies) based on molecular evidence. Molecular phylogenetics and evolution, 37(3), 625-643.

Ogden, T. H., Gattolliat, J. L., Sartori, M., Staniczek, A. H., Soldán, T., & Whiting, M. F. (2009). Towards a new paradigm in mayfly phylogeny (Ephemeroptera): combined analysis of morphological and molecular data. Systematic Entomology, 34(4), 616-634.

Ogden, T. H., Breinholt, J. W., Bybee, S. M., Miller, D., Sartori, M., Shiozawa, D., & Whiting, M. (2019). Mayfly phylogenomics: Initial evaluation of anchored hybrid enrichment data for the order Ephemeroptera. Zoosymposia, 16(1), 167-181.

Orth, K., Thomas, A., Dauta, C., Horeau, V., Brosse, S., & Ademmer, C. (2000). Les Ephémères de la Guyane Française. 1. Premier inventaire générique, a but de biosurveillance (Ephemeroptera). Ephemera, 2(1), 25-38.

Pareja Carmona, M. I., Jiménez Segura, L. F., & Ochoa Orrego, L. E. (2014). Variación espacio-temporal de las larvas de tres especies de peces migratorios en el cauce del río Magdalena (Colombia), durante el ciclo hidrológico 2006-2007.

Peters, W. L., & Harrison, A. D. (1974). Redescription of Terpides Demoulin from St. Vincent, West Indies (Ephemeroptera: Leptophlebiidae). Proceedings of the entomological Society of Washington, 76(2), 178-185.

Peters, W. L., & Gillies, M. T. (1995). Square facets in a hexagonal world. Current directions in research on Ephemeroptera. Canadian Scholars' Press, Toronto, 371-375.

Peters W.L. (1997) A redescription of the imago of Castanophlebia Barnard, 1932 from South Africa (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). Ephemeroptera & Plecoptera. Biology-Ecology Systematics. Landolt P;Sartori M. Mauron + Tinguely & Lachat, SA. Fribourg. pp 449-454.

Peters, J. G., Flowers, R. W., Hubbard, M. D., Domínguez, E., & Savage, H. M. (2005). New records and combinations for Neotropical Leptophlebiidae (Ephemeroptera). Zootaxa, 1054(1), 51-60.

Raimundi, E. A. (2019). Contribution to the knowledge of Ephemeroptera (Insecta) from Goiás state, Brazil. Journal of Insect Biodiversity, 12(2), 33-47.

Robotham, C. D., & Allen, R. T. (1988). Paraleptophlebia calcarica, n. sp. (Ephemeroptera: Leptophlebiidae) from western Arkansas. Journal of the Kansas Entomological Society, 317-320.

Salinas-Jiménez, L. G., Suárez-Mantilla, E. Y., Orejarena-Cuartas, J. A., & Torres-Mora, M. A. (2018). First record of the nymph of Fittkaulus amazonicus Kluge (Ephemeroptera-Leptophlebiidae) from Colombia and broadening of the distribution to the Orinoco river basin. Boletín Científico. Centro de Museos. Museo de Historia Natural, 22(1), 97-101.

Salles, F. F., Nascimento, J. M. C. D., Massariol, F. C., Angeli, K. B., Silva, P. B., Rúdio, J. A., & Boldrini, R. (2010). Primeiro levantamento da fauna de Ephemeroptera (Insecta) do Espírito Santo, sudeste do Brasil. Biota Neotropica, 10(1), 293-307.

Salles, F. F., Dominguez, E., Mariano, R., & Paresque, R. (2016). The imagos of some enigmatic members of the Hermanella complex (Ephemeroptera, Leptophlebiidae). ZooKeys, (625), 45-66.

Salles, F.F., Domínguez, E., Molineri, C., Boldrini, R., Nieto, C., & Dias, L.G. (2018). Order Ephemeroptera. in: Hamada, N., Thorp, J.H., Rogers, D.C. (Eds.), Thorp and Covich's Freshwater Invertebrates. Academic Press, pp. 61-117.

Salles, F. F., Nascimento, J. M. C., Monjardim, M., Paresque, R., Hamada, N., & Dominguez, E. (2020). Diamantina: An endemic new genus of Neotropical Atalophlebiinae (Ephemeroptera: Leptophlebiidae) evidenced by morphological and molecular data. Zoologischer Anzeiger, 284, 30-42.

Sartori, M., & Brittain, J. E. (2015). Order Ephemeroptera. En Thorp and Covich's Freshwater Invertebrates (Fourth Edition) (págs. 873-891). Oxford: Elsevier.

Savage, H. M. (1986). Systematics of the Terpides lineage from the Neotropics: Definition of the Terpides lineage, methods, and revision of Fittkaulus Savage & Peters. Spixiana, 9(3), 255-270.

Savage, H. M. (1987). Biogeographic classification of the Neotropical Leptophlebiidae (Ephemeroptera) based upon geological centers of ancestral origin and ecology. Studies on Neotropical Fauna and Environment, 22(4), 199-222.

Savage, H. M., & Peters, W. L. (1978). Fittkaulus maculatus a new genus and species from northern Brazil (Leptophlebiidae: Ephemeroptera). Acta Amazonica, 8(2), 293-298.

Savage, H. M., Flowers, R. W., & Porras, W. (2005). Rediscovery of Choroterpes atramentum in Costa Rica, type species of Tikuna new genus (Ephemeroptera: Leptophlebiidae: Atalophlebiinae), and its role in the" Great American Inter-change". Zootaxa, 932(1), 1-14.

Sereno, P. C. (2007). Logical basis for morphological characters in phylogenetics. Cladistics, 23(6), 565-587.

Shimano, Y., Salles, F. F., & Cabette, H. S. R. (2011). Ephemeroptera (Insecta) ocorrentes no Leste do Estado do Mato Grosso, Brasil. Biota Neotropica, 11(4), 239-253.

Shimano, Y., Juen, L., Salles, F. F., Nogueira, D. S., & Cabette, H. S. R. (2013). Environmental and spatial processes determining Ephemeroptera (Insecta) structures in tropical streams. In Annales de Limnologie-International Journal of Limnology (Vol. 49, No. 1, pp. 31-41). EDP Sciences.

Sivaramakrishnan, K. G. (1984). Description of female imago and eggs of Indialis badia Peters & Edmunds (Ephemeroptera: Leptophlebiidae). Oriental Insects, 18, 95-98.

Song, N., Li, X., Yin, X., Li, X., Yin, J., & Pan, P. (2019). The mitochondrial genomes of palaeopteran insects and insights into the early insect relationships. Scientific reports, 9(1), 1-11.

Sousa-Nascimento, S. R., Lima, L. R. C., & de Azevêdo, C. A. S. (2020). Leptophlebiidae Banks, 1900 (Insecta, Ephemeroptera) from Maranhão state, Brazil. Check List, 16, 579.

Souto, P. M., Da Silva, E. R., Nessimian, J. L., & Gonçalves, I. C. (2016). Two new species of Ulmeritoides Traver (Ephemeroptera: Leptophlebiidae) from Southeastern Brazil. Zootaxa, 4078(1), 127-136.

Sroka, P., Staniczek, A. H., & Bechly, G. (2015). Revision of the giant pterygote insect Bojophlebia prokopi Kukalová-Peck, 1985 (Hydropalaeoptera: Bojophlebiidae) from the Carboniferous of the Czech Republic, with the first cladistic analysis of fossil palaeopterous insects. Journal of Systematic Palaeontology, 13(11), 963-982.

Staniczek, A., Bechly, G., & Godunko, R. (2011). Coxoplectoptera, a new fossil order of Palaeoptera (Arthropoda: Insecta), with comments on the phylogeny of the stem group of mayflies (Ephemeroptera). Insect Systematics & Evolution, 42(2), 101-138.

Sweeney, B. W., Flowers, R. W., Funk, D. H., Ávila, S. A., & Jackson, J. K. (2009). Mayfly communities in two Neotropical lowland forests. Aquatic Insects, 31(sup1), 311-318.

Tiunova, T. M., & Kluge, N. J. (2016). Redescription of Paraleptophlebia falcula Traver 1934 with notes on status and composition of Paraleptophlebia Lestage 1917 and Neoleptophlebia Kluge 1997 (Ephemeroptera: Leptophlebiidae). Zootaxa, 4098(2), 369-382.

Towns, D. R., & Peters, W. L. (1978). A revision of genus Atalophlebioides (Ephemeroptera: Leptophlebiidae). New Zealand journal of zoology, 5(4), 607-614.

Traver, J. R. (1947) Notes on Neotropical mayflies. Part II. Family Baetidae, subfamily Leptophlebiinae. Revista de Entomologia, 18, 149-160.

Ubero-Pascal, N., Fortuño, J. M., & Puig, M. D. (2005). New Application of Air-Drying Techniques for Studying Ephemeroptera and Plecoptera Eggs by Scanning Electron Microscopy. Microscopy Research and Technique, 68(5), 264-271.

Wheeler, W. C., Whiting, M., Wheeler, Q. D., & Carpenter, J. M. (2001). The phylogeny of the extant hexapod orders. Cladistics, 17(2), 113-169.

Zúñiga, M. D. C., Cardona, W., Molineri, C., Mendivil, J., Cultid, C., Chará, A. M., & Giraldo, A. (2014). Entomofauna acuática del Parque Nacional Natural Gorgona, Pacífico colombiano, con énfasis en Ephemeroptera y Plecoptera. Revista de Biología Tropical, 62, 221-241.

Zúñiga, M. D. C., Molineri, C., Domínguez, E., & Cardona, W. (2015). Leptophlebiidae (Insecta: Ephemeroptera) from Gorgona Island National Natural Park (Tropical Eastern Pacific, Colombia) with the description of two new species. In Annales de Limnologie-International Journal of Limnology (Vol. 51, No. 4, pp. 281-296). Edp Sciences.

Legends and figures

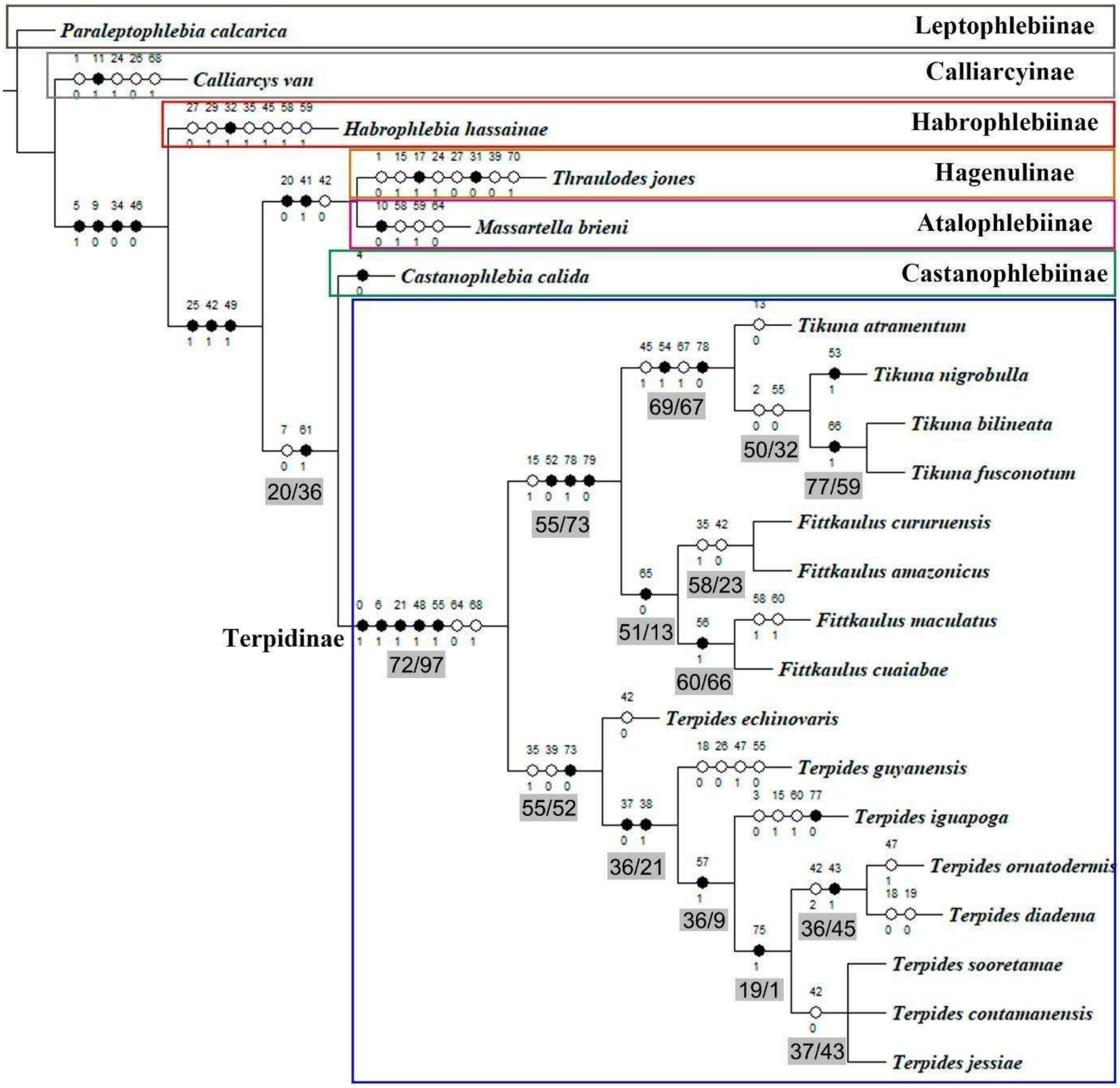
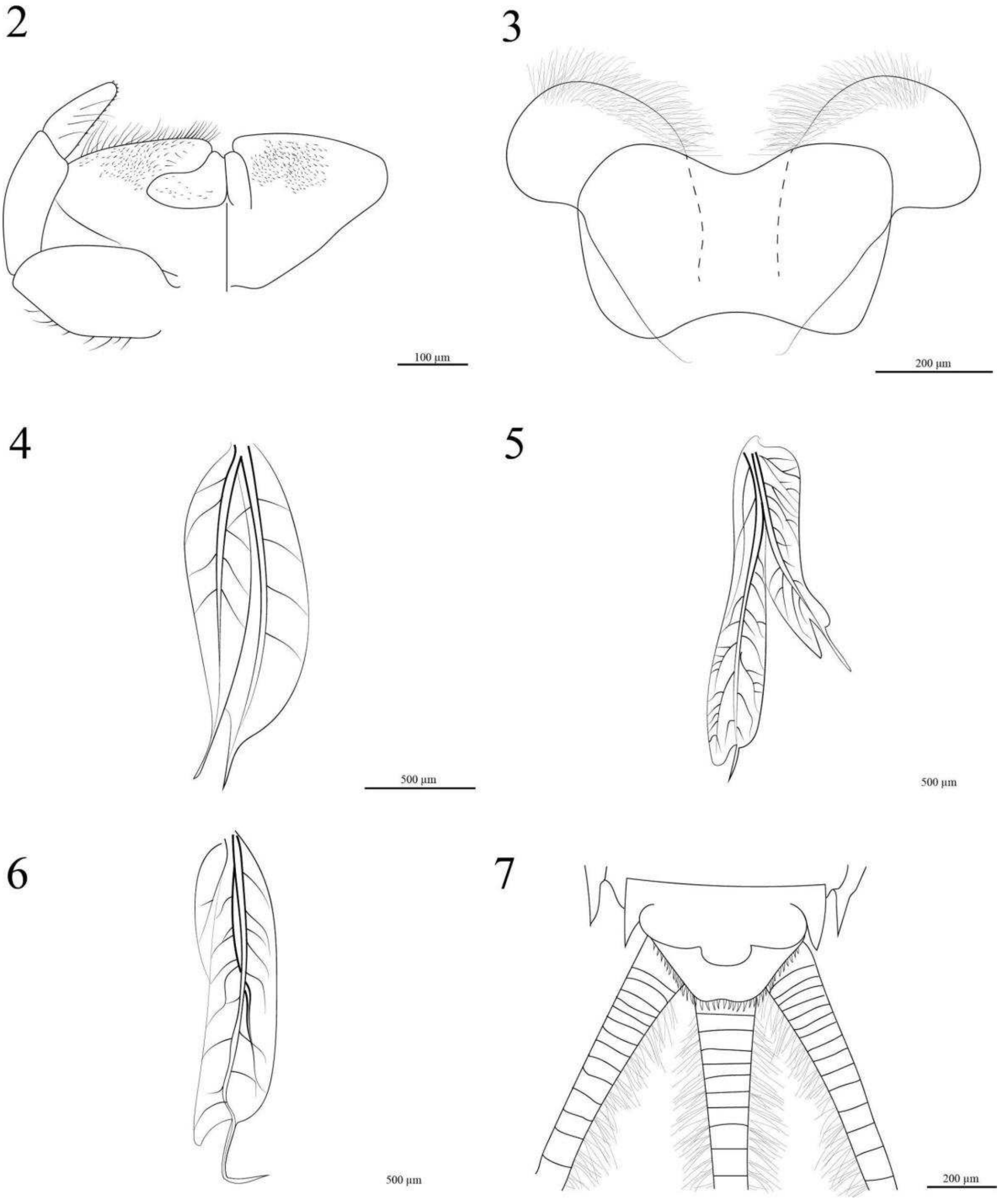
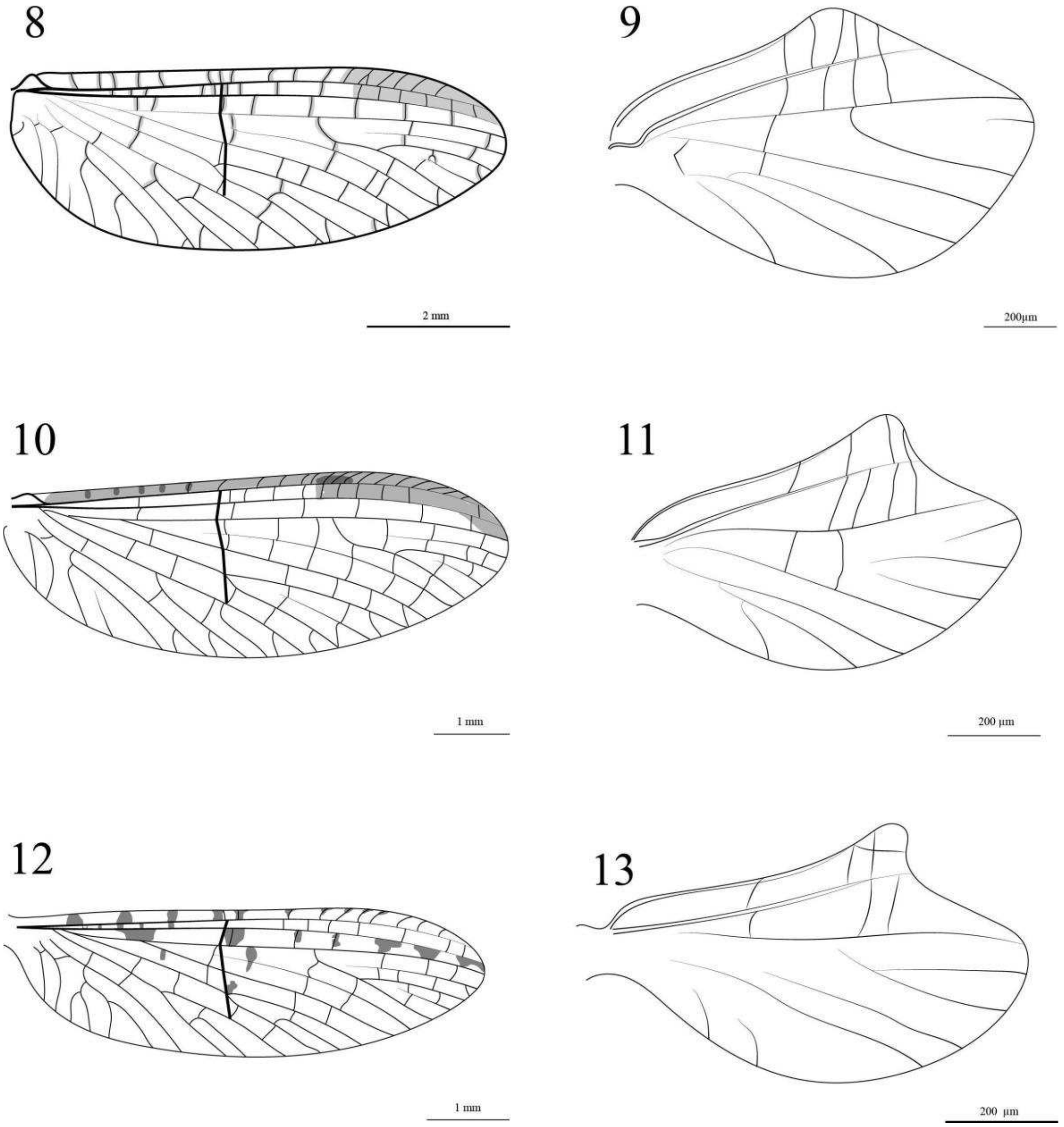


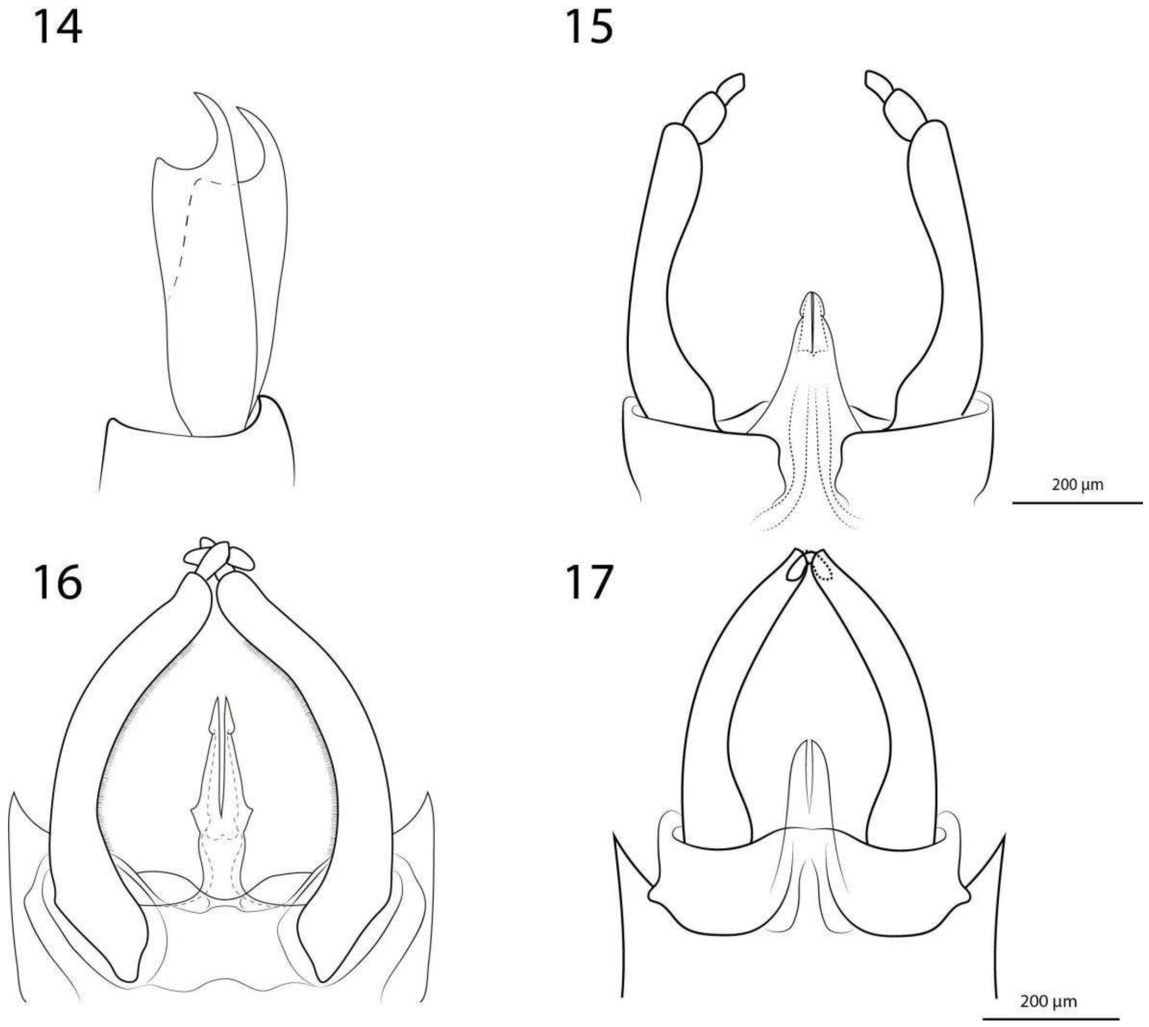
Figure 1. Phylogenetic hypothesis with supporting synapomorphies (circles) and group supports (grey rectangles: left Relative Bremer support, right GC values).



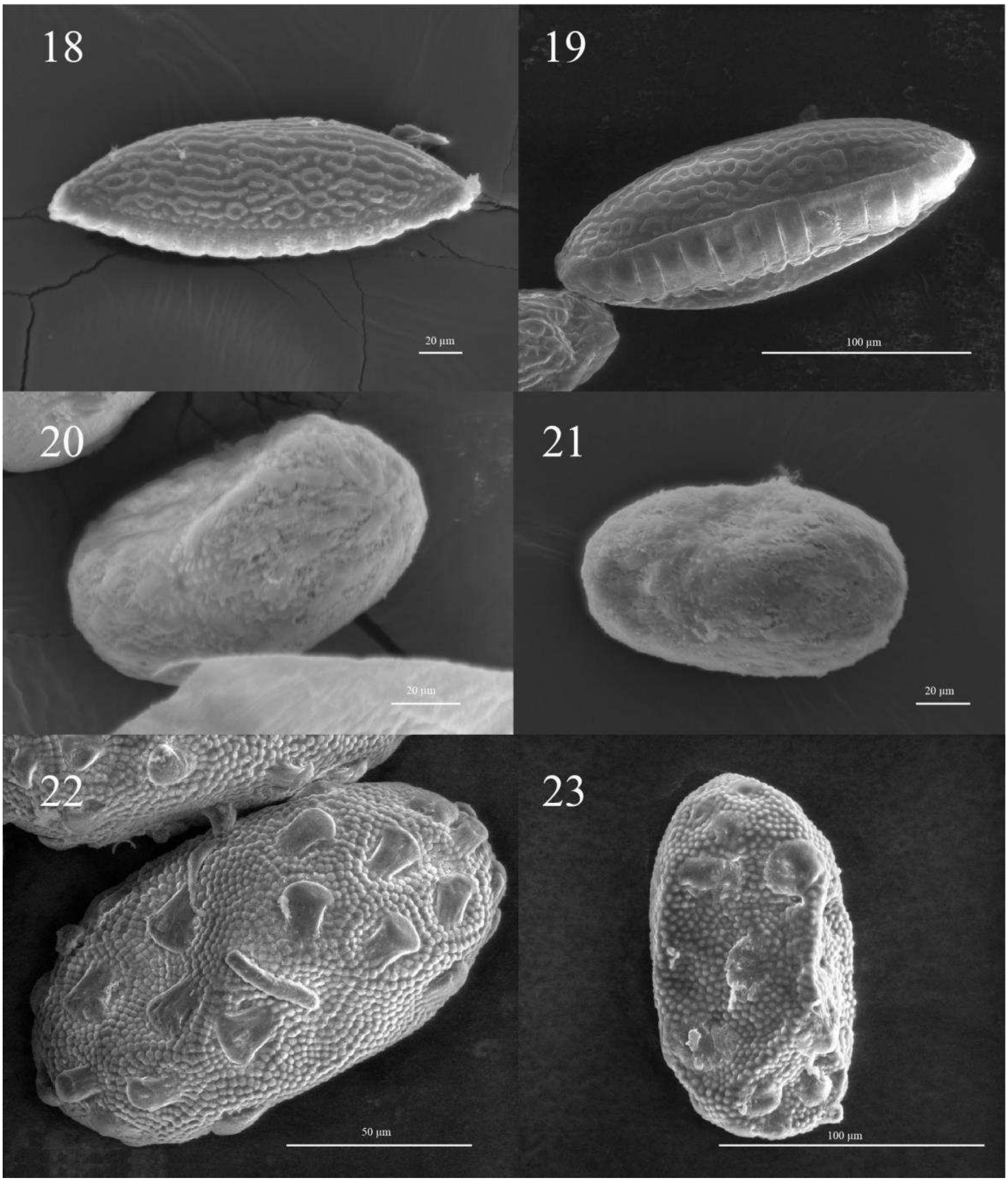
Figures 2-7. Larval characters of Terpidinae species: 2) labium of Terpides iguapoga; 3) hypopharynx of Terpides ornatodermis; 4) gill IV of Terpides sooretamae; 5) gill IV of Tikuna bilineata; 6) gill V of Fittkaulus cururuensis; 7) final abdominal tergites and caudal filaments of Tikuna bilineata.



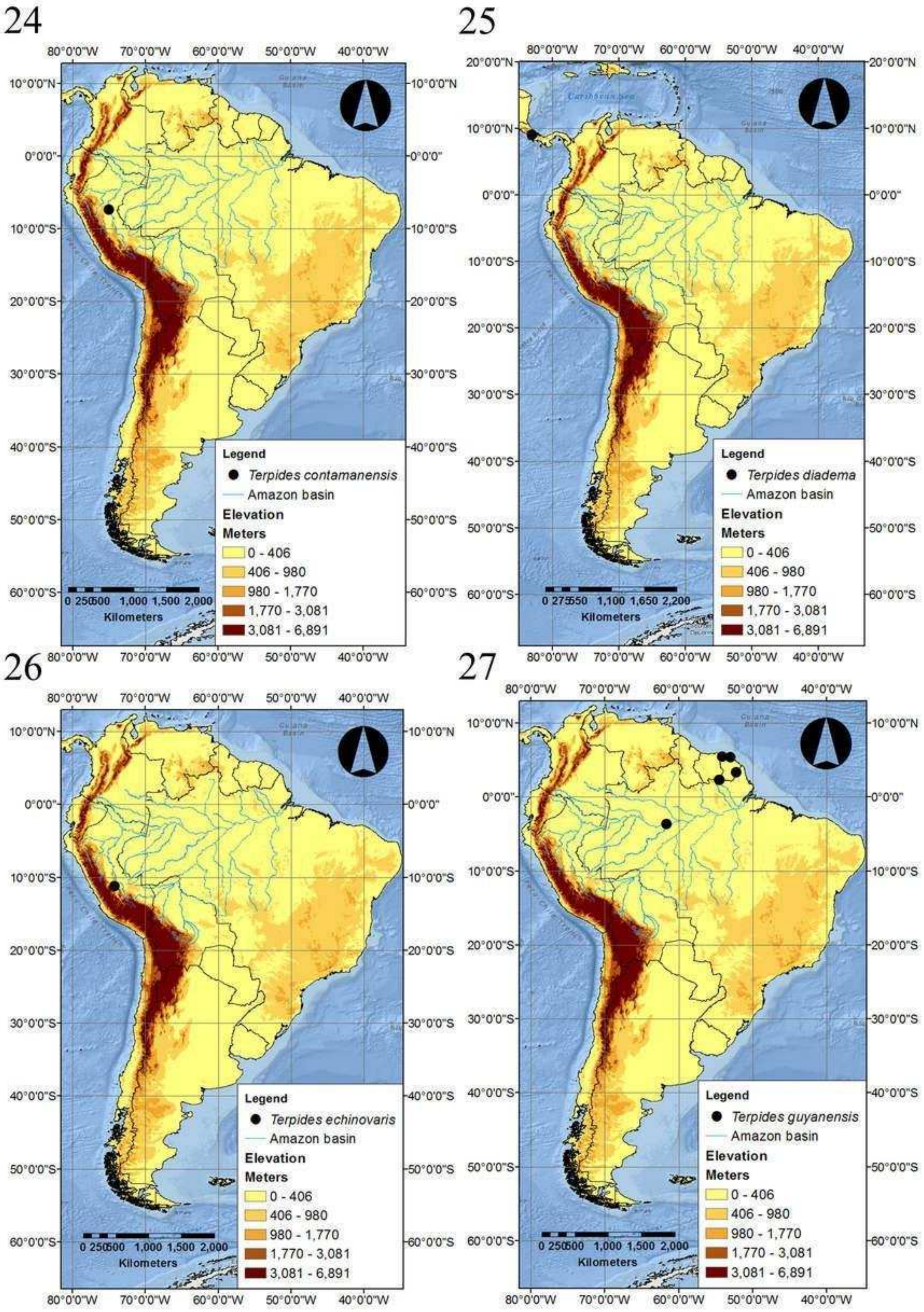
Figures 8-13. Fore and hind wings of Terpidinae species: 8-9) female imago of Terpides sooretamae; 10-11) female imago Tikuna bilineata; 12-13) female subimago of Fittkaulus cururuensis.



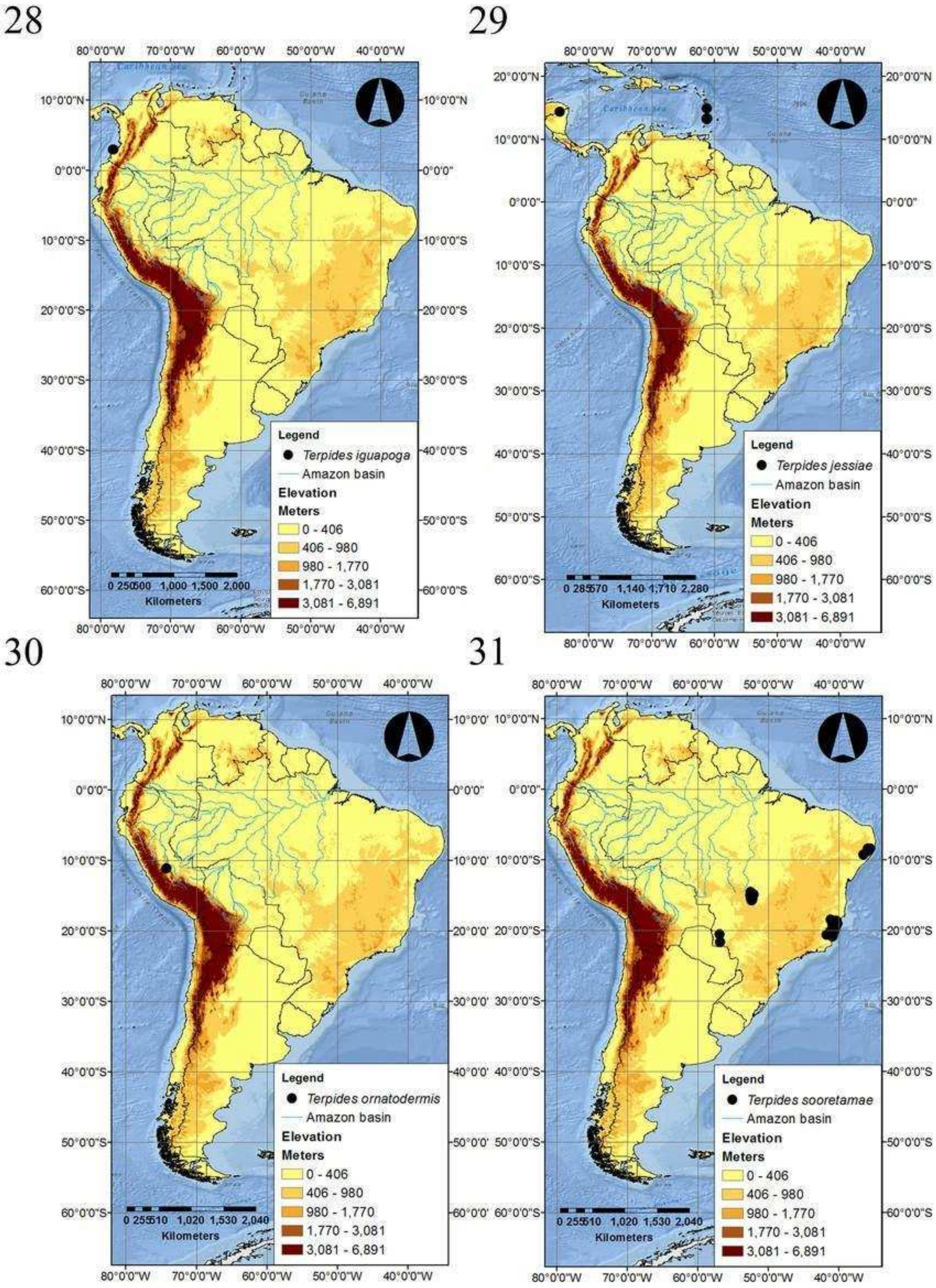
Figures 14-17. Male genitalia and claws imagos of Terpidinae species: 15) claws of Fittkaulus maculatus based of figure 5 on Savage & Peters, 1978; 15) genitalia Terpides sooretamae; 16) genitalia Tikuna atramentum; 17) genitalia Fittkaulus cuiabae.



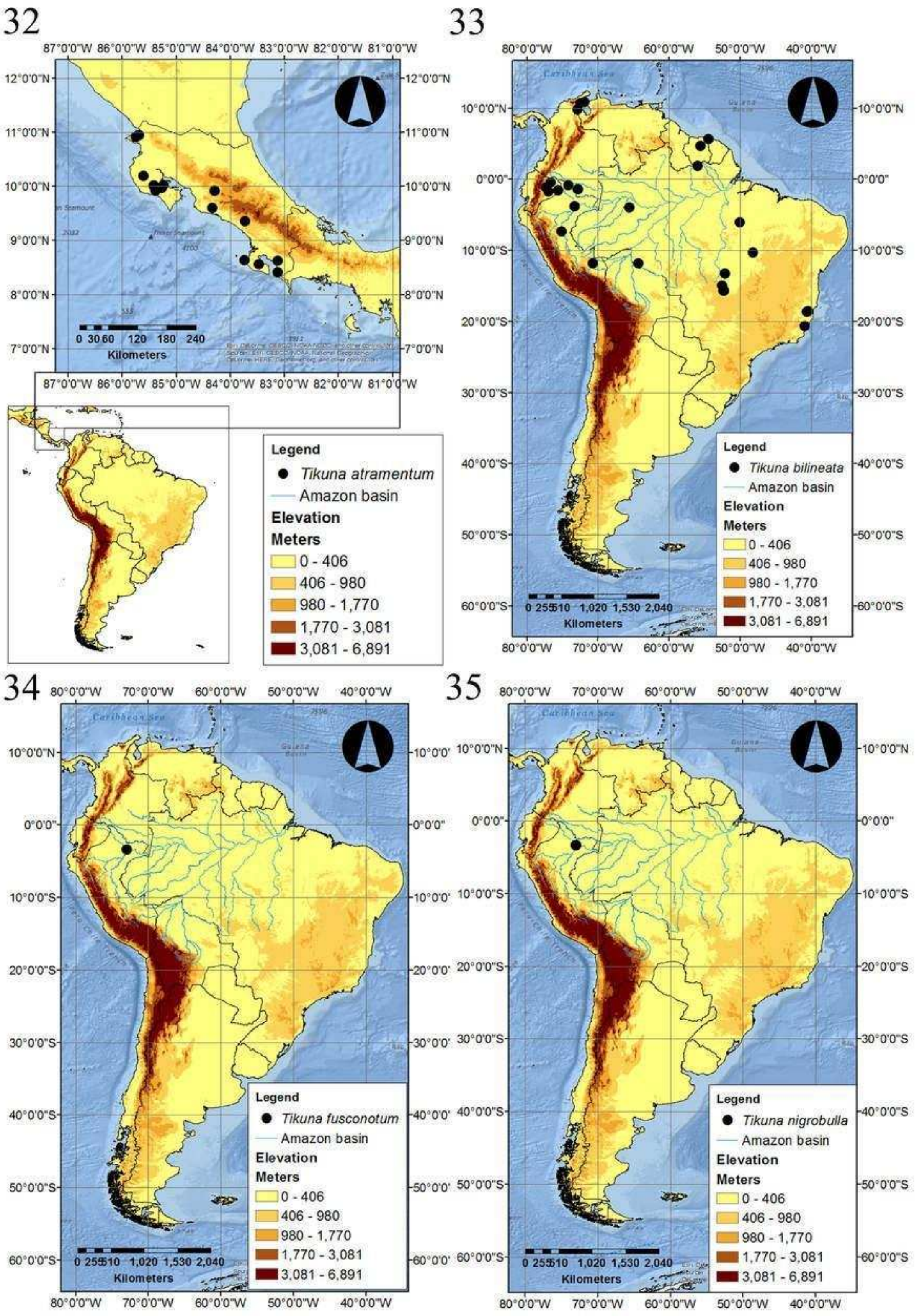
Figures 18-23. Eggs of female imagos of Terpidinae species: 18) Terpides sooretamae; 19) Terpides contamanesis; 20-21) Fittkaulus cururuensis; 22) Tikuna atramentum; 23) Tikuna bilineata.



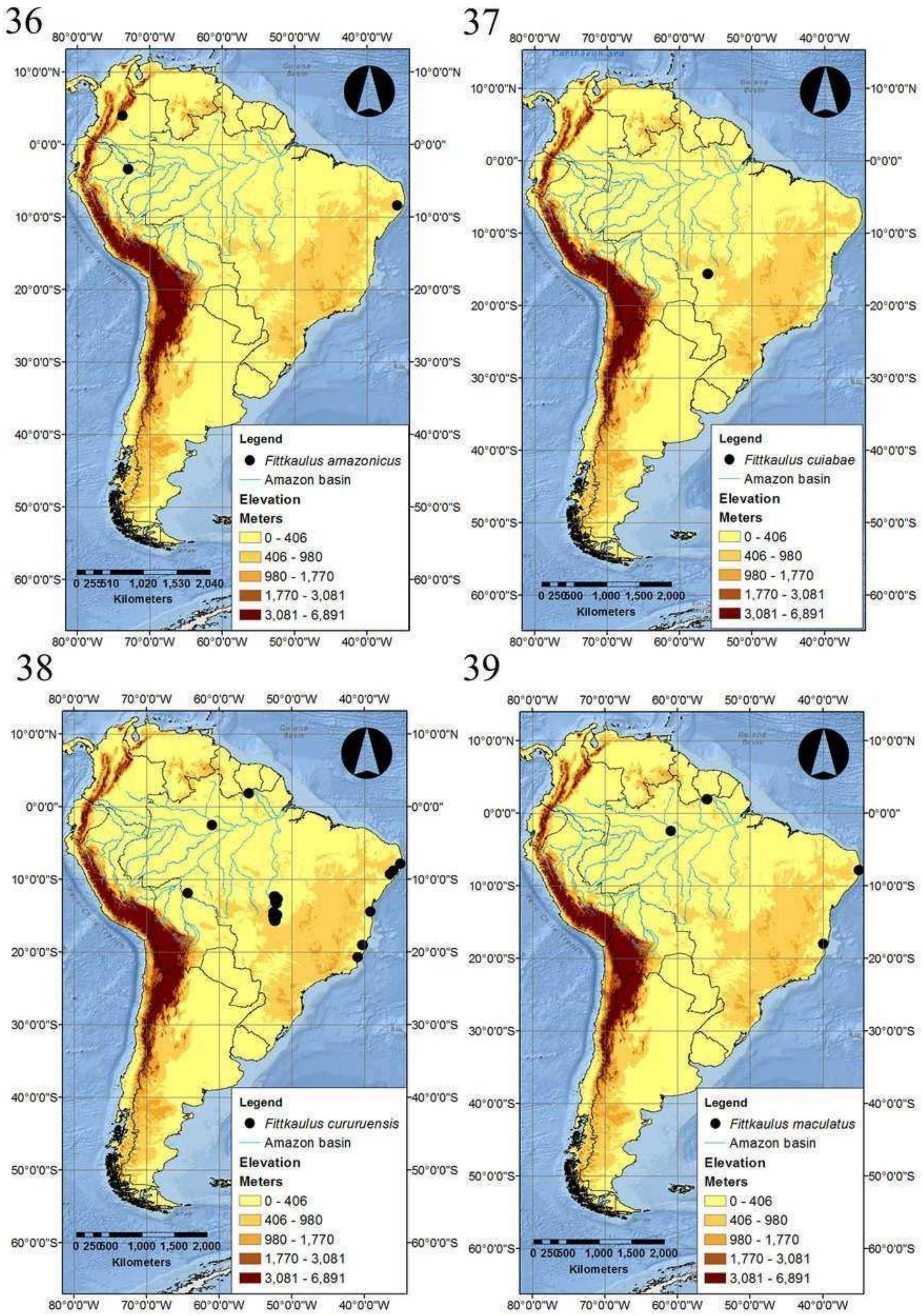
Figures 24-27. Partial maps of the Neotropical region showing the known distribution of selected species of Terpides: 24) Te. contamanensis; 25) Te. diadema; 26) Te. echinovaris; 27) Te. guyanensis.



Figures 28-31. Partial maps of the Neotropical region showing the known distribution of selected species of Terpides: 28) Te. iguapoga; 29) Te. jessiae; 30) Te. ornatodermis; 31) Te. sooretamae.



Figures 32-35. Partial maps of the Neotropical region showing the known distribution of species of Tikuna: 32) Ti. atramentum, 33) Ti. bilineata; 34) Ti. fusconotum; 35) Ti. nigrobulla.



Figures 36-39. Partial maps of the Neotropical region showing the known distribution of species of Fittkaulus: 36) F. amazonicus; 37) F. cuiabae; 38) F. cururuensis; 39) F. maculatus.

New, additional and historical records of Leptophlebiidae (Insecta, Ephemeroptera) from Colombia

Jhon Faber Marulanda Lopez[1,2,*]

[1]Museu de Entomologia, Departamento de Entomologia, Universidade Federal de Viçosa, 36570-900, Minas Gerais, Brazil.

[2]Grupo de Investigación Bionat, Facultad de Ciencias Exactas y Naturales, Universidad de Caldas, Manizales, Caldas, Colombia.

[*]Corresponding author. E-mail: jhon.lopez@ufv.br (J.F. Marulanda).

Orcid: 0000-0001-6539-3042.

Isabel Cristina Hernández[2]

[2]Grupo de investigación Bionat, Facultad de Ciencias Exactas y Naturales, Universidad de Caldas, Manizales, Caldas, Colombia.

E-mail: isabel.1711222177@ucaldas.edu.co.

Orcid: 0000-0001-9995-9139.

Lucimar Gomes Dias[2]

[2]Grupo de investigación Bionat, Facultad de Ciencias Exactas y Naturales, Universidad de Caldas, Manizales, Caldas, Colombia.

E-mail: lucimar.dias@ucaldas.edu.co.

Orcid: 0000-0001-6480-7688.

Frederico Falcão Salles[1]

[1]Museu de Entomologia, Departamento de Entomologia, Universidade Federal de Viçosa, 36570-900, Minas Gerais, Brazil.

E-mail: frederico.salles@ufv.br

Orcid: 0000-0001-8331-5929.

Abstract

In the Neotropical region, especially South America, Leptophlebiidae achieves its higher diversity, with 45 genera and almost 250 species. In Colombia, the diversity about this family is underestimated, with only 22 species reported so far. In order to contribute to the current knowledge of the Leptophlebiidae in Colombia we examined the adults of this family deposited at the Colección Entomológica del Programa de Biología, Universidad de Caldas. In addition to the historical records herein presented, nine species are registered for the first time from the country (Farrodes savagei, F. tepui, F. xingu, Hagenulopsis minuta, Terpides contamanensis, T. echinovaris, T. ornatodermis, Tikuna atramentum, and Ulmeritoides flavopedes). Besides that, additional records are presented for 12 species of the following genera: Askola, Farrodes, Simothraulopsis, Tikuna, Ulmeritoides, Hydrosmilodon, Terpides, Choroterpes, Paramaka, and Hagenulopsis. With these additional and new records, we update the list of Leptophlebiidae from Colombia to 33 species and 14 genera.

Keywords

Amazon, Andes, Diversity, Mayflies, Neotropical Region.

Introduction

Leptophlebiidae is one of the most diversified groups of mayflies (Ephemeroptera), both taxonomically and ecologically, with more than 640 species and 140 genera distributed worldwide (Sartori & Brittain, 2015). The family represents an important component of freshwater ecosystems, especially in the Southern Hemisphere (Savage, 1987).

Historically, the family was divided in two subfamilies, Leptophlebiinae Banks and Atalophlebiinae Peters (Peters, 1980). While Leptophlebiinae was represented by few genera and species mostly restricted to the Northern Hemisphere, Atalophlebiinae included more than 100 described genera and more than 500 species and presents a gondwanan distribution with some taxa spreading to the north (O´Donnell & Jockusch, 2008). Nowadays, however, the family is divided into eight subfamilies, due to the split of both Leptophlebiinae (in Leptophlebiinae s.s., Habrophlebiinae, and Calliarcyinae) and Atalophlebiinae (in Atalophlebiinae s.s., Terpidinae, Castanophlebiinae, Choroterpinae, and Hagenulinae) (Godunko et al., 2015; Kluge, 2009; Monjardim et al., 2020).

The Neotropics, especially South America, is where Leptophlebiidae achieves its higher diversity. In this region, more than 45 genera and 240 species are reported, belonging to Atalophlebiinae, Choroterpinae, Hagenulinae, and to the endemic Terpidinae (Domínguez et al., 2006; Kluge, 2015; Salles & Boldrini, 2019; Salles et al., 2020; Monjardim et al., 2020; Zúñiga et al., 2015). Nevertheless, the average of new species published every year is still high and many taxa remain to be described from the region.

Colombia is recognized as one of the most biodiversity rich countries in the Neotropic (Andrade, 2011). A huge variety of ecosystems, such as "tropical forests in the Amazon and Choco, mountain habitats like the Sierra Nevada and Andes, the grasslands of the plains and badlands, and islands like Gorgona in the Pacific and San Martin in the Caribbean", is the main reason for such biodiversity. Unfortunately, given the high rates of biodiversity loss, some areas in the country between them some hotspots for biodiversity in the World (Myers et al., 2000; Poveda et al., 2010).

Concerning mayflies, it is clear that the diversity in Colombia is underestimated. Currently, only 120 species are known: 32 species for Baetidae, eight for Caenidae, one for Coryphoridae, three for Ephemeridae, two for Euthyplociidae, 28 for Leptohyphidae, 22 for Leptophlebiidae, three for Oligoneuriidae, and 21 for Polymitarcyidae (Dias & Marulanda, 2019; Domínguez et al., 2019; Molineri et al., 2019; Salles et al., 2020). These numbers, especially for

Leptophlebiidae and Baetidae, are far from the actual number. In South American countries where the mayfly components have been studied more often, such as Brazil and Argentina, the number of species of this families surpasses one hundred and many species remain to be described.

Based on material collected by L.G. Dias team in the last years and deposited at the Entomological Collection of the Biology program of the Caldas University - CEBUC, our aim is to increase the knowledge of Leptophlebiidae from Colombia by presenting new and additional records of the family from the country.

Material & Methods

Identification

We examined and mounted the male genitalia and wings of imagos in permanent slides using Euparal®. For the identification of the collected insects taxonomic keys and original descriptions were used (Domínguez et al., 1996; Domínguez, 1999; Domínguez & Zúñiga, 2003; Domínguez et al., 2009; Eaton, 1883; Eaton, 1892; Flowers, 1987; Kluge, 2009; Kluge, 2015; Needham & Murphy, 1924; Peters et al., 2008; Salles et al., 2018; Savage & Peters, 1983; Savage, 1987a; Spieth, 1943; Traver, 1943; Traver, 1947; Traver & Edmunds, 1967; Walker, 1853; Zúniga et al., 2015).

Occurrence maps

We made the maps of occurrence in South America with the software ESRI® ArcMap 10.0, using a digital model of the elevation with countries delimitation in the Neotropic. Records from the literature were obtained from the following publications: Domínguez & Zúñiga (2003); Domínguez et al. (2009); Domínguez & Zúñiga (2009); Mosquera et al. (2001); Needham & Murphy (1924); Peters et al. (2008); Rozo & Salinas (2016); Salinas et al. (2013); Salinas et al. (2017); Salinas et al. (2018); Salles et al. (2018); Savage & Peters (1983); Traver & Edmunds (1967); Zúniga et al. (1997); Zúñiga et al. (2004); Zúniga et al. (2014); Zúniga et al. (2015).

Images

We took pictures of specimens deposited in alcohol using LEICA M205 A and LEICA M205 C stereo microscopes with LEICA MC170 HD digital cameras. Pictures of living specimens in the field were taken with a Nikon d800 camera, 105mm macro lens, a SB-5000 Nikon flash, and a small acrylic aquarium. Post-processing of pictures were made in Adobe Lightroom® and the final plates were prepared in Adobe Illustrator® and Adobe Photoshop®.

Deposition

We deposited the material in the Colección Entomológica del Programa de Biología, Universidad de Caldas (CEBUC), Manizales, Colombia, and at the Museu de Entomologia, Universidade Federal de Viçosa (UFVB), Viçosa, Brazil. In the case of Terpidinae, all specimens are temporarily deposited at the UFVB.

Results

Based on the specimens available at the CEBUC, we identified 21 species of Leptophlebiidae. Eleven of them (belonging to the genera Askola Peters, 1969; Farrodes Peters, 1971; Simothraulopsis Demoulin, 1966; Tikuna Savage, Flowers & Porras, 2005; Ulmeritoides Traver, 1959; Hydrosmilodon Flowers & Domínguez, 1992; Terpides Demoulin, 1966; and Hagenulopsis Ulmer, 1920), were already reported from Colombia and, thus, represent additional records for the country. Farrodes savagei Domínguez, 1999; F. tepui Domínguez, Molineri & Peters, 1996; F. xingu Domínguez, Molineri & Peters, 1996; Terpides contamanensis Kluge, 2015; T. echinovaris Kluge, 2015; T. ornatodermis Kluge, 2015; and Tikuna atramentum (Traver, 1947); Hagenulopsis minuta Spieth, 1943; and Ulmeritoides flavopedes (Spieth, 1943) represent new records for the country. We also present records for a new species of Choroterpes Eaton, 1881 and a new species of Paramaka Savage & Domínguez, 1992. With these new and additional records, we update the total number of Leptophlebiidae known from Colombia to 33 species and 14 genera. Importantly, given the diversity of Thraulodes in Colombia, the new species of this genus that were found in CEBUC will be treated elsewhere (Hernández in prep.).

We presented below s complete list of the species of Leptophlebiidae reported from Colombia. For species reported for the first time from the country, an asterisk succeeds the specific name (*).

Hagenulinae

Askola emmerichi Domínguez et al., 2009 (Figs. 1A and 5B)

Previous distribution: COLOMBIA: Amazonas department (Domínguez et al., 2009: 31); Venezuela: Bolivar state (Domínguez et al., 2014: 302); BRAZIL: Amazonas state (Nascimento et al., 2011: 200), Roraima state (Santos & Boldrini, 2016: 2), Bahia state (Costa et al., 2018: 4; Lima et al., 2016: 216), Pernambuco state (Campos et al., 2019: 36), Maranhão state (Nascimento et al., 2020: 581).

Additional records from Colombia: 2 male imagos, Putumayo department, Puerto Asís, Quebrada La Ventura (0°37’15.8’’N 76°34’33.6’’W), 19/xii/2015, light trap night, deposited at CEBUC; 88 male and 5 female imagos, Putumayo department, Puerto Asís, Quebrada Agua Negra (0°31’36.3’’N 76°31’38.3’’W), 17, 19 and 20/xii/2015, light trap night, deposited at CEBUC; 3 male imagos, Amazonas department, Leticia, 2017, light trap, deposited at CEBUC.

Atopophlebia caldasi Salles, Marulanda & Dias, 2018 (Figs. 1B and 4D)

Previous distribution: COLOMBIA, Caldas department, Norcasia and Samaná (Salles et al., 2018: 140).

Additional records from Colombia: 1 nymph, Tolima department, San Sebastián de Mariquita, Cataratas de Medina stream (5°14’41.09’’N 74°53’06.97’’W), 14/ii/2020, deposited at UFVB.

Atopophlebia fortunensis Flowers, 1987 (Fig. 5B)

Previous distribution: COLOMBIA, Valle del Cauca department, Pavas (Mosquera et al., 2001; Zúñiga et al., 1997); COSTA RICA: Cartago Province; (Flowers, 1987: 205); PANAMA: Chiriquí and Bocas del Toro Provinces (Flowers, 1980: 164, 1987:205).

Additional records from Colombia: none.

Atopophlebia pacis Salles, Marulanda & Dias, 2018 (Fig. 5B)

Previous distribution: COLOMBIA, Putumayo department, Mocoa and Puerto Asís (Salles et al., 2018: 139).

Additional records from Colombia: none.

Farrodes caribbianus (Traver, 1943) (Figs. 1C–D and 5C)

Previous distribution: COLOMBIA, Choco department, Acandí (Rozo & Jimenez, 2016: 8; Zúñiga et al., 2004: 36), Cauca department, Parque Nacional Natural Gorgona (Zúñiga et al., 2014: 234); COSTA RICA: Guanacaste Province (Domínguez, 1999: 159; Chacón et al., 2009: 726); VENEZUELA: Bolivar state (Domínguez, 1999: 159; Domínguez et al., 2014: 304; Chacón et al., 2009: 726); PANAMA: Canal de Panama (Domínguez, 1999: 159); NICARAGUA: Río San Juan department (Meyer et al., 2008: 140).

Additional records from Colombia: 3 male imagos, Tolima department, Armero Guayabal, Quebrada Santo Domingo - Granja Universidad del Tolima (5°00’06.0’’N 74°54’08.0’’W), 19/v/2017, light trap, deposited at CEBUC; 2 male imagos, Tolima department, Mariquita, Villa de los Caballeros (5°09’21.42’’N 74°53’58.32’’W), 21/v/2017, light trap, deposited at CEBUC; 2 male imagos, Tolima department, Mariquita, Villa de los Caballeros (5°09’21.42’’N 74°53’58.32’’W), 21/v/2017, light trap, deposited at UFVB.

Farrodes roundsi (Traver, 1947) (Figs. 1E and 5C)

Previous distribution: COLOMBIA: Nariño and Valle del Cauca departments (Zúñiga et al., 2004: 36), Pasto department, Reserva Natural La Planada (Domínguez & Zúñiga, 2009: 74), Cauca department, Parque Nacional Natural Gorgona (Zúñiga et al., 2014: 227; Zúñiga et al., 2015: 294); COSTA RICA: Guanacaste Province (Domínguez, 1999: 161); PANAMA: Chiriquí Province (Domínguez, 1999: 161).

Additional records from Colombia: 1 male imago, Nariño, Reserva Natural Río Ñambi (1°18’00’’N 74°04’58.79’’W), 01/iii/2013, light trap, deposited at CEBUC.

Farrodes savagei * Domínguez, 1999 (Figs. 1F and 5C)

Previous distribution: VENEZUELA: Zulia state (Domínguez et al., 1999: 164; Chacón et al., 2009: 726); NICARAGUA: Reserva de la Biosfera Bosawas (Meyer et al., 2008: 140).

New record from Colombia: 2 male imagos, Tolima department, Armero Guayabal, Quebrada Santo Domingo - Granja Universidad del Tolima (5°00’18.15’’N 74°54’24.78’’W), 19/xi/2017, light trap, deposited at UFVB; 1 male and 1 female imagos, same data, deposited at CEBUC.

Farrodes tepui * Domínguez, Molineri & Peters, 1996 (Figs. 1G–H and 5C)

Previous distribution: BRAZIL: Pernambuco (Lima et al., 2012: 309) and Bahia states (Lima et al., 2016: 217); VENEZUELA: Amazonas state (Domínguez et al., 1996: 98); FRENCH GUIANA: Amazonas state (Chacón et al., 2009: 726).

New record from Colombia: 3 male and 4 female imagos, Meta department, San Martín, Caño Camoa (3°41’24.72’’N 73°41’59.41’’W), 04/i/2015, light trap, deposited at UFVB; 4 male and 4 female imagos, same data, deposited at CEBUC.

Farrodes xingu * Domínguez, Molineri & Peters, 1996 (Figs. 2A–B and and 5C)

Previous distribution: BRAZIL: Pará state (Domínguez et al., 1996: 97), Mato Grosso state (Santos et al., 2019: 203); and Maranhão state (Nascimento et al., 2020: 581).

New record from Colombia: 10 male and 4 female imagos, Amazonas department, Leticia, Quebrada La Arenosa (4°12’11.39’’S 69°56’09.26’’W), 28/ix/2014, light trap, deposited at UFVB; 11 male and 5 female imagos, same data, deposited at CEBUC.

Hagenulopsis esmeralda Domínguez et al., 2009 (Figs. 4A–B and 5D)

Previous distribution: COLOMBIA: Cauca department, Parque Nacional Natural Gorgona (Zúñiga et al., 2014: 226; 2015: 294); ECUADOR: Esmeralda Province (Domínguez et al., 2009: 40).

Additional record from Colombia: 2 male imagos, Nariño department, Reserva Natural Río Ñambi (1°18’00’’N 74°04’58.79’’W), 01/iii/2013, light trap, deposited at CEBUC.

Hagenulopsis minuta * (Spieth, 1943) (Figs. 2C–D and 5D)

Previous distribution: BRAZIL: Roraima (Neto & Hamada, 2014: 279), and Bahia states (Lima et al., 2016: 217); SURINAME: Rio Marowijne (Peters & Domínguez, 2001: 354); VENEZUELA: Amazonas state (Chacón et al., 2009: 726; Peters & Domínguez, 2001: 354).

New record from Colombia: 6 male imagos, Putumayo department, Puerto Asís, Quebrada Agua Negra (0°31’36.3’’N 76°31’38.3’’W), 20/xii/2015, light trap, deposited at UFVB; 15 male imagos, same data: deposited at CEBUC; 60 male and 4 female imagos, same data, deposited at CEBUC.

Hagenulopsis zunigae Domínguez et al., 2009 (Fig. 5D)

Previous distribution: COLOMBIA: Valle del Cauca department, Parque Nacional Natural Farallones de Cali, Boyaca department, Arcabuco (Domínguez et al., 2009: 41), Cauca department, Parque Nacional Natural Gorgona (Zúñiga et al., 2014: 235).

Additional records from Colombia: none.

Hydrosmilodon primanus (Eaton, 1892) (Figs. 2E–F, 4E, and 5D)

Previous distribution: COLOMBIA: Tolima department, Mariquita (Salinas et al., 2013: 364), Meta department, Acacías (Salinas et al., 2017: 273); COSTA RICA: Guanacaste Province (Flowers & Domínguez, 1992: 660); MEXICO: Veracruz city and Tabasco state (McCafferty, 2011: 325); PANAMA: Bocas del Toro Province (Flowers & Domínguez, 1992: 660); HONDURAS: Comayagua, El Paraiso, Intibuca and Atlantida states (Flowers & Domínguez, 1992: 660).

Additional records from Colombia: 10 male and 5 female imagos, Tolima department, San Sebastián de Mariquita, Cataratas de Medina (5°14’41.09’’N 74°53’06.97’’W), 19/i/2016, light trap, deposited at CEBUC; 1 male imago and 10 nymphs, Caldas, Norcasia, Rio Manso, 15/ii/2020, light trap, male imago and 5 nymphs deposited at CEBUC, 5 nymphs at UFVB.

Miroculis (Atroari) colombiensis Savage & Peters, 1983 (Fig. 6A)

Previous distribution: COLOMBIA: Meta department, Puerto Lopez (Savage & Peters, 1983: 558).

Additional records from Colombia: none.

Miroculis (Miroculis) chiribiquete Peters, Domínguez & Dereser, 2008 (Figs. 2G–H and 6A)

Previous distribution: COLOMBIA: Caquetá department, Puerto Abeja (Peters et al., 2008: 296).

Additional records from Colombia: none.

Miroculis (Miroculis) nebulosus Savage, 1987 (Fig. 6A)

Previous distribution: COLOMBIA: Caquetá department, Puerto Abeja (Peters et al., 2008: 301); VENEZUELA: Amazonas state (Chacón et al., 2009: 727; Savage, 1987a: 104).

Additional records from Colombia: none.

Miroculis (Miroculis) wolverine Costa, Almeida & Salles, 2019 (Fig. 6A)

Previous distribution: COLOMBIA: Caldas department, Norcasia (Costa et al., 2019: 288).

Additional records from Colombia: none.

Paramaka sp. nov.* (Figs. 3A and 6B)

Previous distribution: none.

New records from Colombia: 1 male and 2 female imagos, Putumayo department, Puerto Asís, Quebrada Agua Negra (0°31’36.3’’N 76°31’38.3’’W), 17 and 20/xii/2015, light trap day, deposited at CEBUC; 1 male imago, Meta department, San Juan de Arama, Finca la Esmeralda (3°20’47.21’’N 73°53’21.87’’W), 16-17/v/2015, light trap, deposited at CEBUC; 15 male and 10 female imagos, Meta department, San Martín, Caño Camoa (3°41’24.72’’N 73°41’59.41’’W), 04/i/2015, light trap, deposited at CEBUC.

Simothraulopsis demerara (Traver 1947) (Figs. 3B and 6B)

Previous distribution: COLOMBIA: Amazonas department (Zúñiga et al., 2004: 36); BRITISH GUIANA: Demerara River; SURINAME: Brokopondo District; VENEZUELA:

Bolivar state (Domínguez et al., 2014: 313), Morichal District (Chacón et al., 2009: 728); FRENCH GUIANA: Sinnamary River; BRAZIL: Amazonas and Pará states (Domínguez et al., 1997:146), Tocantins state (Boldrini & Krolow, 2017: 3), Roraima state (Nieto & Hamada, 2014: 285; Raimundi et al., 2017: 581), Pernambuco state (Lima et al., 2015: 5), Bahia state (Campos et al., 2016: 310; Costa et al., 2018: 1; Lima et al., 2016: 217), Maranhão state (Nascimento et al., 2020: 584), São Paulo state (Mariano & Polegatto, 2011: 594), Espírito Santo state (Salles et al., 2010: 306), and Paraná state (Faria & Salles, 2019: 376).

Additional records from Colombia: 13 male and 4 female imagos, Amazonas department, Leticia, Reserva Natural Ágape, Quebrada La Arenosa (4°11’26.81’’S 69°56’11.94’’W), 28/ix/2014, light trap, deposited at CEBUC.

Thraulodes colombiae (Walker, 1853)

Previous distribution: COLOMBIA (Walker, 1853: 537).

Additional records from Colombia: none.

Thraulodes insular Domínguez, Molineri & Zúñiga, 2015 (Fig. 6B)

Previous distribution: COLOMBIA: Cauca department, Parque Nacional Natural Gorgona (Zúñiga et al., 2015: 288).

Additional records from Colombia: none.

Thraulodes laetus (Eaton, 1883)

Previous distribution: COLOMBIA (Eaton, 1883: 110).

Additional records from Colombia: none.

Thraulodes papilionis Traver & Edmunds, 1967 (Fig. 6B)

Previous distribution: COLOMBIA: Tolima department, Honda (Traver & Edmunds, 1967: 374).

Additional records from Colombia: none.

Ulmeritoides huitoto Domínguez & Zúñiga, 2003 (Figs. 3C–D and 6C)

Previous distribution: COLOMBIA: Amazonas department, Leticia (Domínguez & Zúñiga, 2003: 123).

Additional records from Colombia: 1 male and 1 female imagos, Amazonas department, Leticia, (2°14’43.03’’S 71°05’49.27’’W), 2017, light trap, deposited at CEBUC; 1 female imago and 2 female subimagos, Amazonas department, Leticia (4°12’21.75’’S 69°55’03.31’’W), 28/ix/2014, light trap, deposited at UFVB.

Ulmeritoides flavopedes * (Spieth, 1943) (Figs. 3E and 6C)

Previous distribution: SURINAME: Marowijne District (Domínguez, 1995: 19); BRAZIL: Mato Grosso state (Shimano et al., 2010: 304), Pernambuco state (Lima et al., 2015: 5), Tocantins state (Boldrini & Krolow, 2017: 3), Pará state (Shimano et al., 2018: 141), Maranhão state (Nascimento et al., 2020: 588).

New records from Colombia: 1 male imago, Meta department, San Juan de Arama, Finca la Esmeralda (3°20’47.21’’N 73°53’21.87’’W), 16-17/v/2015, light trap, deposited at CEBUC; 44 male and 4 female imagos, Putumayo department, Mocoa, Fin del Mundo (1°05’48.70’’N 76°36’12.13’’W), vii/2018, light trap, deposited at CEBUC; 1 male imago, Putumayo department, Puerto Asís, Quebrada Agua Negra (0°31’36.3’’N 76°31’38.3’’W), 20/xii/2015, light trap day, deposited at CEBUC.

Choroterpinae

Choroterpes sp. nov.* (Figs. 3F–G and 6C)

Previous distribution: none.

New record from Colombia: 4 male imagos, Caldas department, Norcasia, Reserva Natural Río Manso, Afluente Río Manso, (5°39’25.80’’N 74°51’44.66’’W), 04-05/iv/2017, light trap, deposited at CEBUC.

Terpidinae

Fittkaulus amazonicus Kluge, 2009 (Fig. 6D)

Previous distribution: COLOMBIA: Meta department, Acácias, Vereda La Esmeralda, Caño Seco stream (Salinas et al., 2018: 98); PERU: Loreto Region (Kluge, 2009: 248), Maynas Province (Kluge, 2015: 181).

Additional records from Colombia: none.

Terpides contamanensis * Kluge, 2015 (Figs. 4C and 6D)

Previous distribution: PERU: Loreto Region (Kluge, 2015; 175).

New records from Colombia: 2 female imagos, Caldas department, Norcasia, Reserva Natural Río Manso, Afluente Río Manso, (5°39’25.80’’N 74°51’44.66’’W), 05/iv/2017, light trap, deposited at UFVB; 1 male and 1 female imagos, Tolima department, Mariquita, Quebrada Granja Universidad del Tolima (5°00’06.2’’N 74°54’07.4’’W), 04/xi//2017, light trap, deposited at UFVB.

Terpides echinovaris * Kluge, 2015 (Figs. 4F and 6D)

Previous distribution: PERU: Satipo Province (Kluge, 2015: 167).

New record from Colombia: 3 male imagos, Caldas department, Norcasia, Reserva Natural Río Manso, Afluente Río Manso, (5°39’25.80’’N 74°51’44.66’’W), 05/iv/2017, light trap, deposited at UFVB.

Terpides iguapoga Molineri, Domínguez & Zúñiga, 2015 (Fig. 6D)

Previous distribution: COLOMBIA: Cauca department, Parque Nacional Natural Gorgona (Zúñiga et al., 2015: 283).

Additional records from Colombia: 1 male and 1 female imagos, Nariño department (Reserva Natural Ñambi) (1°18’00’’N 74°04’58.79’’W), iii/2013, light trap, deposited at UFVB; 1 male and 1 female imagos, Caldas department, Samaná (Parque Nacional Natural Selva de Florencia), Río San Antonio (5°30’31.7’’N 75°02’24.3’’W), 20/x/2017, light trap, deposited at UFVB.

Terpides ornatodermis * Kluge, 2015 (Fig. 6D)

Previous distribution: PERU: Satipo Province (Kluge, 2015; 157).

New record from Colombia: 1 male subimago, Tolima department, Mariquita, Villa de los Caballeros (5°09’21.42’’N 74°53’58.32’’W), 21/v/2017, reared, deposited at UFVB.

Tikuna atramentum * (Traver, 1947) (Figs. 3H and 6D)

Previous distribution: COSTA RICA: San Jose Province (Traver, 1947: 156), Guanacaste Province (Flowers & Ávila, 2006: 133; Savage, et al., 2005: 4).

New record from Colombia: 5 male and 1 female imagos, Caldas department, Norcasia, Reserva Natural Río Manso, Afluente Río Manso, (5°39’25.80’’N 74°51’44.66’’W), 05/iv/2017, light trap, deposited at UFVB.

Tikuna bilineata (Needham & Murphy, 1924) (Fig. 6D)

Previous distribution: COLOMBIA: Amazonas department, La Chorrera (Needham & Murphy, 1924: 48); SURINAME: Surinam River (Traver, 1947: 156); PERU and SURINAME (Hubbard, 1982: 264); BRAZIL: Pará state; ECUADOR: Pastaza Province; SURINAME: Wijne District and VENEZUELA: Zulia state (Chacón et al., 2009: 728; Peters et al., 2005: 52); PERU: Madre de Dios department, Ucayali Province, and Maynas Province (Kluge, 2015: 182; Sweeney et al., 2009: 315); BRAZIL: Mato Grosso and Pará states (Boldrini et al., 2009: 225; Brasil et al., 2013: 262; Shimano et al., 2011: 250; Shimano et al., 2013: 36), Espírito Santo state (Angeli et al., 2015: 202), Tocantins state (Boldrini & Krolow, 2017: 3), Goiás state (Raimundi, 2019: 40), and Maranhão state (Nascimento et al., 2020: 587).

Additional records from Colombia: 1 male imago, Caldas department, Norcasia, Reserva Natural Río Manso, Afluente Río Manso, (5°39’25.80’’N 74°51’44.66’’W), 05/iv/2017, light trap, deposited at UFVB; 1 female imago, Valle del Cauca department, Bajo Calima, Buenaventura, Quebrada La Larga (3°59’47’’N 76°58’28’’W), 12/xii/2017, light trap, deposited at UFVB.

Discussion

As expected, Hagenulinae is the most species-rich subfamily in Colombia, currently represented by 10 genera and 25 species. Among them, Farrodes (five species), Miroculis (four) and Thraulodes (four) stand out as the most diverse, closely followed by Atopophlebia and Hagenulopsis (three species each). In the case of Thraulodes, however, it should be noted, as previously stated, that additional species will be treated elsewhere. Terpidinae is represented by its three genera and seven species, while Choroterpinae is represented by a single new species of Choroterpes. Unidentified species of this genus have been previously reported from Colombia based on nymphs (García et al., 2013; Gutiérrez & Reinoso-Flórez, 2010; Peters et al., 2005), and for the first time adults were found. These are the only records of the world-widely distributed Choroterpinae in South America. The absence of Atalophlebiinae in Colombia, at least among the previous and new records, was somewhat expected. Members of this subfamily include cold-adapted mayflies (Dos Santos et al., 2018, Monjardim et al., 2020) that, in South America, are mostly restricted to Patagonia and some marginal areas along the southern portion of South American Transition Zone (Molineri et al., 2020) (the only exception is the genus Massartella Lestage, found in Brazil and Venezuela). It is very unlikely, therefore, that even additional collections in the Paramo, an area poorly represented at the CEBUC, would lead to the discovery of some Atalophlebiinae in the country.

Of the 33 species of Leptophlebiidae treated in this work, 14 are registered only to Colombia while 19 are present in other countries, such as Brazil (eight), Peru (five), Costa Rica (five), and Panama (four). Given the current distribution of these species, the fauna of Leptophlebiidae in Colombia seems to be a mosaic of elements from distinct biogeographic dominions (see Morrone, 2014). Some endemic, such as Atopophlebia fortunensis, Farrodes caribbianus, and Hydrosmilodon primanus (from the Pacific Dominion) or Askola emmerichi, Ulmeritoides flavopedes, and Hagenulopsis minuta (from the Boreal Brazilian Dominion). While others are present in more than one biogeographic dominion. For example, Fittkaulus amazonicus (northwestern portion of the South Brazilian dominion and Boreal Brazilian), and Terpides contamanensis and Terpides echinovaris (northwestern portion of the South Brazilian Dominion and Pacific).

The new and additional records presented in this work contribute significantly to our understanding of the knowledge of the order Ephemeroptera from Colombia. Furthermore, this work highlights the richness of the different biogeographical regions of Colombia and confirms that diversity in this country is underestimated. Our results also demonstrate the importance of biological collections as a depository of biodiversity and suggest that the knowledge of Ephemeroptera in Colombia could expand with the increase in the sampling effort, since many regions of the country have not been studied.

Acknowledgments

We thank the Universidad de Caldas for providing funds to LGD to conduct the sampling of Ephemeroptera in several projects. We also thank Dr. Tito Bacca (Universidad del Tolima), Milton Montaño, MSc Camilo Llano, MSc Ana Meza and students of the Laboratorio de Colecciones Biológicas of Universidad de Caldas for assistance with sampling specimens deposited in CEBUC collection. We thank ISAGEN for facilitating the sampling of macroinvertebrates in the east of the department of Caldas. We also thank Dr. Og DeSouza (Universidade Federal de Viçosa) for facilitating the use of optic equipment. This study was financed in part by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) to JFM (process # 162813/2018-0) and to FFS (processes # 305847/2015-5 and 309666/2019-8).

Conflicts of interest

The authors declare no conflict of interest.

Author contribution statement

LGD conceived the research, conducted the field work and take some imagens. FFS identified the species and elaborated the discussion. ICH obtained some imagens and produced the final plates, and included the world distribution of the lineages. JFM wrote the document and elaborated the maps. All authors critically reviewed the manuscript and approved the final version of this paper.

References

Andrade, M. G., 2011. Estado del conocimiento de la biodiversidad en Colombia y sus amenazas. Consideraciones para fortalecer la interacción ambiente-política. Rev. Acad. Colomb. Cienc, 35 (137), 491–507.

Angeli, K. B., do Rozário, E. M. M., Salles, F. F., 2015. Checklist of Ephemeroptera (Insecta) from São Mateus River Basin, Espírito Santo, Brazil. Revista Brasileira de Entomologia, 59 (3), 197–204. https://doi.org/10.1016/j.rbe.2015.06.004

Boldrini, R., Salles, F. F., Cabette, H. R., 2009. Contribution to the taxonomy of the Terpides lineage (Ephemeroptera: Leptophlebiidae). In Annales de Limnologie-International Journal of Limnology, 45 (4), 219–229.

https://doi.org/10.1051/limn/2009029

Boldrini, R., Krolow, T. K., 2017. New records of Ephemeroptera (Insecta) from Tocantins state, northern Brazil. Check List, 13 (2), 1–5.
https://doi.org/10.15560/13.2.2067

Brasil, L. S., Shimano, Y., Batista, J. D., Cabette, H. S., 2013. Effects of environmental factors on community structure of Leptophlebiidae (Insecta, Ephemeroptera) in Cerrado streams, Brazil. Iheringia. Série Zoologia, 103 (3), 260–265.

https://doi.org/10.1590/S0073-47212013000300008.

Campos, R., Mariano, R., Calor, A. R., 2016. Mayflies (Ephemeroptera) from Reserva Ecológica Michelin, Bahia, Brazil. Aquatic Insects, 37 (4), 303–315.

https://doi.org/10.1080/01650424.2016.1267769

Campos, R., Mariano, R., Calor, A. R., 2019. Askola Peters 1969 (Ephemeroptera: Leptophlebiidae: Atalophlebiinae): an updated review under cladistics approach. Zoologischer Anzeiger, 283, 69–92. https://doi.org/10.1016/j.jcz.2019.08.006

Chacón, M. M., Pescador, M. L., Hubbard, M. D., Segnini, S., 2009. Mayflies (Insecta: Ephemeroptera) from Venezuela. Check List, 5 (3), 723–731. https://doi.org/10.15560/5.3.723

Costa, S. S., Souza, F. N., Nogueira, M. A. M., Santos, E. P. D., Sousa, M. M. L. D., Silva, V. D. A., Almeida, E., Mariano, R., 2018. Leptophlebiidae (Insecta: Ephemeroptera) from state of Bahia, Brazil. Biota Neotropica, 18 (1). 1–6. https://doi.org/10.1590/1676-0611-bn-2017-0386

Costa, V., Almeida, T. B., Salles, F. F., 2019. Description of two related new species of Miroculis Edmunds, 1963 (Ephemeroptera: Leptophlebiidae) from Brazil and Colombia. Zootaxa, 4695 (3), 283–294. https://doi.org/10.11646/zootaxa.4695.3.3

Dias, L. G., Marulanda, J. F., 2019. First records of the genera Macunahyphes and Microphlebia (Insecta: Ephemeroptera) from Colombia. Boletín Científico Centro de Museos Museo de Historia Natural, 23 (2), 309–315.

https://doi.org/10.17151/bccm.2019.23.2.18.

Domínguez, E., 1995. Cladistic analysis of the Ulmeritus-Ulmeritoides group (Ephemeroptera, Leptophlebiidae), with descriptions of five new species of Ulmeritoides. Journal of the New York Entomological Society, 103 (1), 15–38.

Domínguez, E., Molineri, C., Peters, W. L., 1996. Ephemeroptera from Central and South America: New species of the Farrodes bimaculatus group with a key for the males. Studies on Neotropical Fauna and Environment, 31 (2), 87–101. http://dx.doi.org/10.1076/snfe.31.2.87.13325

Domínguez, E., Peters, W. L., Peters, J. G., Savage, H. M., 1997. The imago of Simothraulopsis Demoulin with a redescription of the nymph (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). Aquatic Insects, 19 (3), 141–150. https://doi.org/10.1080/01650429709361648

Domínguez, E., 1999. Systematics, cladistics and biogeography of the American genus Farrodes (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). Zoological Journal of the Linnean Society, 126 (2), 155–189. https://doi.org/10.1111/j.1096-3642.1999.tb00152.x.

Domínguez, E., Zúñiga, M. D. C., 2003. First generic record and description of a new species of Ulmeritoides (Ephemeroptera: Leptophlebiidae) from Colombia. Gaino, E. Research update on Ephemeroptera & Plecoptera. Bari, Università di Perugia, 123–125.

Domínguez, E., Molineri, C., Pescador, M. L., Hubbard, M. D., Nieto C., 2006.

Ephemeroptera of South America Aquatic Biodiversity of Latin America. Vol. 1. Pensoft, Sofia–Moscow.

Domínguez, E., Molineri, C., Mariano, R., 2009. Revision of the South American species of Hagenulopsis Ulmer and Askola Peters (Ephemeroptera: Leptophlebiidae) with description of six new species. Zootaxa, 2142 (1), 29–44.

Domínguez, E., Zúñiga, M. D. C., 2009. First description of the larva of Farrodes roundsi (Traver) (Ephemeroptera: Leptophlebiidae: Atalophlebiinae) with comments on its phylogenetic relationships. Aquatic Insects, 31 (1), 73–81. https://doi.org/10.1080/01650420802544297.

Dominguez, E., Grillet, M. E., Nieto, C., Molineri, C., Guerrero, E., 2014. Ephemeroptera from the Venezuelan Guayanass Uplands: Families Leptophlebiidae, Euthyplociidae and Oligoneuriidae. Zootaxa, 3827 (3), 301–317.

http://dx.doi.org/10.11646/zootaxa.3827.3.1

Domínguez, E., Molineri, C., Nieto, C., Zúñiga, M. D. C., 2019. Lista de especies de Ephemeroptera Sudamericanos. http://ibn-conicet.gob.ar/ephemeroptera-sudamericanos/ (Accessed 18 march 2020).

Dos Santos, D. A., Molineri, C., Nieto, C., Zuñiga, M. C., Emmerich, D., Fierro, P., ... Salles, F. F., 2018. Cold/Warm stenothermic freshwater macroinvertebrates along altitudinal and latitudinal gradients in Western South America: A modern approach to an old hypothesis with updated data. Journal of Biogeography, 45 (7), 1571–1581.

https://doi.org/10.1111/jbi.13234

Eaton, A. E., 1881. An announcement of new genera of the Ephemeridae. Entomol Mon Mag, 17, 191–197.

Eaton, A. E., 1883–1888. A revisional monograph of recent Ephemeridae or mayflies. T. Linnean Society of London, Second Series, Zoology, 2 (3), 1–352. https://doi.org/10.1111/j.1096-3642.1883.tb01550a.x.

Eaton, A. E., 1892. Fam. Ephemeridae. Biologia Centrali-Americana, 38, 1–16.

Faria, L. R., & Salles, F. F., 2019. An unexpected record of Simothraulopsis Demoulin, 1966 (Ephemeroptera, Leptophlebiidae) in the Paraná Basin, Brazil. Check List, 15, 375–378. https://doi.org/10.15560/15.3.375

Flowers, R. W., 1980. Atopophlebia fortunensis, a new genus and species from Panama (Leptophlebiidae: Ephemeroptera). Florida Entomologist, 63 (1), 162–165. https://doi.org/10.2307/3494670

Flowers, R. W., 1987. New species and life stages of Atopophlebia (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). Aquatic insects, 9 (4), 203–209. https://doi.org/10.1080/01650428709361297.

Flowers, R. W., Dominguez, E., 1992. New genus of Leptophlebiidae (Ephemeroptera) from Central and South America. Annals-Entomological Society of America, 85 (6), 655–655.

Flowers, R. W., Ávila, S., 2006. Biogeographical and ecological notes on the genus Tikuna Savage, Flowers, and Porras (Ephemeroptera: Leptophlebiidae) from Central and South America. Entomological news, 117 (2), 133–138. https://doi.org/10.3157/0013-872X(2006)117[133:BAENOT]2.0.CO;2

García, L. F., Hoyos, D. C., Dias, L. G., 2013. Primer reporte de Choroterpes (Ephemeroptera: Leptophlebiidae) para Caldas, Colombia. Revista Colombiana de Entomología, 39 (1), 164–165.

Godunko, R. J., Sroka, P., Soldán, T., Bojková, J., 2015. The higher phylogeny of Leptophlebiidae (Insecta: Ephemeroptera), with description of a new species of Calliarcys Eaton, 1881. Arthropod Systematics & Phylogeny, 73 (2), 259–279.

Gutiérrez, C., Reinoso-Flórez, G., 2010. Géneros de ninfas del orden Ephemeroptera (Insecta) del departamento del Tolima, Colombia: listado preliminar. Biota Colombiana, 11 (1 y 2), 23–32.

Hubbard, M. D., 1982. Catálogo abreviado de Ephemeroptera da América do Sul. Papéis Avulsos de Zoologia, 34 (24), 257–282.

Kluge, N. J., 2009. Higher system of Atalophlebiinae (Leptophlebiidae) with description of three new species of Terpides s.l. from Peruvian Amazonia. Russian Entomological Journal, 18 (4), 243–256.

Kluge, N. J., 2015. Contribution to the knowledge of Terpidinae Kluge 2009

(Ephemeroptera: Leptophlebiidae). Zootaxa, 3999 (2), 151–189. https://doi.org/10.11646/zootaxa.3999.2.1

Lima, L. R., Salles, F. F., Pinheiro, U., 2012. Ephemeroptera (Insecta) from Pernambuco State, northeastern Brazil. Revista Brasileira de Entomologia, 56 (3), 304–314. https://doi.org/10.1590/S0085-56262012005000043

Lima, L. R., Salles, F. F., Pinheiro, U., 2015. New records of mayflies (Ephemeroptera: Insecta) from Pernambuco state, northeastern Brazil. Check List, 11 (3), 1–7. https://doi.org/10.15560/11.3.1652

Lima, L. R. C., Knapp, W., Docio, L., 2016. New records of mayflies (Insecta: Ephemeroptera) from Bahia state, northeastern Brazil. Entomotropica, 31 (25), 212–220.

Mariano, R., Polegatto, C., 2011. Checklist de Ephemeroptera do Estado de São Paulo, Brasil. Biota Neotropica, 11(1a), 593–599. https://doi.org/10.1590/S1676-06032011000500025

McCafferty, W. P., 2011. New Mexican and Central American Ephemeroptera records, with first species checklists for Mexican states. Transactions of the American Entomological Society, 137 (3 & 4), 317–327. https://doi.org/10.3157/061.137.0310

Meyer, M. D., Baumgardner, D. E., McCafferty, W. P., 2008. The Ephemeroptera of Central America. Part 2: Nicaragua. Transactions of the American Entomological Society, 134 (1), 133–146.

https://doi.org/10.3157/0002-8320(2008)134[133:TEOCAP]2.0.CO;2

Molineri, C., Dias, L. G., Gonzalez, I., Nunez-Avellaneda, A., 2019. Nymphal description of Tricorythodes zagaia n. Comb. and Tricorythodes pemonensis n. Comb. (Ephemeroptera: Leptohyphidae) and first records from Colombia. Zootaxa, 4585 (2), 395–400. https://doi.org/10.11646/zootaxa.4585.2.13.

Molineri, C., Nieto, C., Dos Santos, D. A., Emmerich, D., Zúñiga, M. D. C., Fierro, P., ... Valdovinos Zarges, C., 2020. Do mayflies (Ephemeroptera) support a biogeographic transition zone in South America?. Journal of Biogeography. 1–14. https://doi.org/10.1111/jbi.13868

Monjardim, M., Paresque, R., Salles, F. F., 2020. Phylogeny and classification of Leptophlebiidae (Ephemeroptera) with and emphasis on Neotropical fauna. Systematic Entomology, 45 (2), 415–429. https://doi.org/10.1111/syen.12402.

Morrone, J. J., 2014. Biogeographical regionalisation of the Neotropical region. Zootaxa, 3782 (1), 1–110. https://doi.org/10.11646/zootaxa.3782.1.1

Mosquera, S., Zúñiga, M. D. C., Alba-Tercedor, J., 2001. Atopophlebia fortunensis Flowers (Ephemeroptera: Leptophlebiidae) and Caenis chamie, Alba-Tercedor and Mosquera (Ephemeroptera: Caenidae). Notes on Their Biology and Ecology, in: Springer, (Eds.), Trends in Research in Ephemeroptera and Plecoptera, Boston, MA, pp. 157–160. https://doi.org/10.1007/978-1-4615-1257-8_19

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature, 403 (6772), 853–858.

Nascimento, J. M. C. D., Barcelos-Silva, P., Salles, F. F., 2011. Two-winged Leptophlebiidae (Ephemeroptera) from Brazil: new species, records and stage description. Aquatic Insects, 33 (3), 191–201.

https://doi.org/10.1080/01650424.2011.597408

Nascimento, S. R., Lima, L. R. C., de Azevêdo, C. A. S., 2020. Leptophlebiidae Banks, 1900 (Insecta, Ephemeroptera) from Maranhão state, Brazil. Check List, 16 (3), 579–591. https://doi.org/10.15560/16.3.579

Needham, J. G., Murphy, H. E., 1924. Neotropical mayflies. Bulletin of the Lloyd Library Number 24. Entomological Series, 4, 1–79.

Neto, J. D. L. G., Hamada, N., 2014. Leptophlebiidae (Ephemeroptera) of the Serra do Tepequém, Roraima State, Brazil: new records and description of two new species. Zootaxa, 3900 (2), 279–286. http://dx.doi.org/10.11646/zootaxa.3900.2.8

O’Donnell, B. C., Jockusch, E. L., 2008. Phylogenetic relationships of leptophlebiid mayflies as inferred by histone H3 and 28S ribosomal DNA. Systematic Entomology, 33(4), 651-667. http://doi.org/10.1111/j.1365-3113.2008.00434.x.

Peters, W., 1980. Phylogeny of the Leptophlebiidae (Ephemeroptera): An Introduction, in: D. D. Williams (Ed.), Advances in Ephemeroptera Biology, New York, Plenum Press, pp. 33–43. https://doi.org/10.1007/978-1-4613-3066-0_3.

Peters, W. L., Domínguez, E., 2001. The identity of Hagenulopsis minuta Spieth (Leptophlebiidae: Atalophlebiinae). In Trends in research in Ephemeroptera and Plecoptera. Springer, Boston, MA. pp. 353–358.

https://doi.org/10.1007/978-1-4615-1257-8_40

Peters, J. G., Flowers, R. W., Hubbard, M. D., Domínguez, E., Savage, H. M., 2005. New records and combinations for Neotropical Leptophlebiidae (Ephemeroptera). Zootaxa, 1054 (1), 51–60. https://doi.org/10.11646/zootaxa.1054.1.6

Peters, J. G., Domínguez, E., Currea D. A., 2008. Species of Miroculis from the Serranía de Chiribiquete in Colombia. (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). International advances in Ecology, Zoogeography and Systematics of mayflies and stoneflies, 128, 295–305.

Poveda, G., Álvarez, D. M., Rueda, O. A., 2010. Hydro-climatic variability over the Andes of Colombia associated with ENSO: a review of climatic processes and their impact on one of the Earth's most important biodiversity hotspots. Climate Dynamics, 36 (11–12), 2233–2249. https://doi.org/10.1007/s00382-010-0931-y.

Raimundi, E. A., Nascimento, J. M. C. D., Barroso, P. C. S., Hamada, N., Boldrini, R., 2017. Three new species of Miroculis from the Serra da Mocidade National Park, Roraima State, Brazil, with new records and checklist of the Leptophlebiidae (Ephemeroptera). Zootaxa, 4317 (3), 573–583.

https://doi.org/10.11646/zootaxa.4317.3.8

Raimundi, E. A., 2019. Contribution to the knowledge of Ephemeroptera (Insecta) from Goiás state, Brazil. Journal of Insect Biodiversity, 12 (2), 33–47.

Rozo, M. P., Salinas-Jiménez, L. G., 2016. Inventario del orden Ephemeroptera (Insecta) en la quebrada Coquital, Serranía de Tripogadí, Departamento del Chocó, Colombia. Entomotropica, 31 (1), 1–13.

Salinas-Jiménez, L. G., Flowers, R. W., Dias, L. G., 2013. First record of Hydrosmilodon primanus (Eaton) (Ephemeroptera, Leptophlebiidae) from South America. Biota Neotropica, 13 (1), 363–365. https://doi.org/10.1590/S1676-06032013000100038.

Salinas-Jiménez, L. G., Rojas-Peña, J. I., Osorio-Ramírez, D. P., Caro-Caro, C. I., 2017. New records of Ephemeroptera from the Colombian Orinoco river basin of the Meta department. Revista Colombiana de Entomología, 44 (1), 147–147. http://dx.doi.org/10.25100/socolen.v43i2.5958.

Salinas-Jiménez, L. G., Suárez-Mantilla, E. Y., Orejarena-Cuartas, J. A., Torres-Mora, M., 2018. Primer registro de la ninfa de Fittkaulus amazonicus Kluge (Ephemeroptera, Leptophlebiidae) para Colombia y ampliación de la distribución a la cuenca del Río Orinoco. Boletín Científico Centro de Museos Museo de Historia Natural, 22 (1), 97–101. http://doi.org/10.17151/bccm.2018.22.1.8.

Salles, F. F., Nascimento, J. M. C. D., Massariol, F. C., Angeli, K. B., Silva, P. B., Rúdio, J. A., Boldrini, R., 2010. Primeiro levantamento da fauna de Ephemeroptera (Insecta) do Espírito Santo, sudeste do Brasil. Biota Neotropica, 10 (1), 293–307.

https://doi.org/10.1590/S1676-06032010000100025

Salles, F. F., Marulanda, J. F., Dias, L. G., 2018. Two new species of Atopophlebia Flowers, 1980 (Ephemeroptera, Leptophlebiidae) from Colombia. Zootaxa, 4446 (1), 138–150. http://dx.doi.org/10.11646/zootaxa.4446.1.10.

Salles, F. F., Boldrini, R., 2019. A new genus of the subtribe Hermanellina (Ephemeroptera: Leptophlebiidae: Atalophlebiinae) from Northern Brazil with accounts on the systematics of the group. Insect Systematics & Evolution, 1(aop), 1–17. https://doi.org/10.1163/1876312X-00002300.

Salles, F.F., Molineri, C., Nieto, C., Lima, L.R.C., Dias, L.G., Boldrini, R., Mariano, R. & Domínguez, E., 2020. Ephemeroptera da América do Sul. http://ephemeroptera.com.br/ (Accessed 08 August 2020).

Salles, F. F., Nascimento, J. M. C., Monjardim, M., Paresque, R., Hamada, N., Dominguez, E., 2020. Diamantina: An endemic new genus of Neotropical Atalophlebiinae (Ephemeroptera: Leptophlebiidae) evidenced by morphological and molecular data. Zoologischer Anzeiger, 284, 30–42. https://doi.org/10.1016/j.jcz.2019.10.005.

Santos, G. C., Boldrini, R., 2016. Askola emmerichi Domínguez, Molineri & Mariano, 2009 (Ephemeroptera: Leptophlebiidae), novo registro para o estado de Roraima, Brasil. Boletim do Museu Integrado de Roraima, 10 (1), 2317–5206.

Santos, R. P., Moreto, V., Mariano, R., 2019. Intersexuality in Farrodes Peters, 1971

(Ephemeroptera: Leptophlebiidae: Atalophlebiinae) from Brazil. Revista Brasileira de Entomologia, 63 (3), 202–204. https://doi.org/10.1016/j.rbe.2019.05.008

Sartori, M., Brittain, J. E., 2015. Order Ephemeroptera. In Thorp and Covich's freshwater invertebrates. Academic Press, pp. 873–891.

https://doi.org/10.1016/B978-0-12-385026-3.00034-6

Savage, H. M., Peters, W. L., 1983. Systematics of Miroculis and related genera from northern South America (Ephemeroptera: Leptophlebiidae). Transactions of the American Entomological Society, 108 (4), 491–600.

https://www.jstor.org/stable/25078309

Savage, H. M., 1987. Biogeographic classification of the Neotropical Leptophlebiidae (Ephemeroptera) based upon geological centers of ancestral origin and ecology. Studies on Neotropical Fauna and Environment, 22 (4), 199–222.

https://doi.org/10.1080/01650528709360734

Savage, H. M., 1987a. Two new species of Miroculis from Cerro de la Neblina, Venezuela with new distribution records for Miroculis fittkaui and Microphlebia surinamensis (Ephemeroptera: Leptophlebiidae). Aquatic Insects, 9 (2), 97–108. https://doi.org/10.1080/01650428709361279.

Savage, H. M., Dominguez, E., 1992. A new genus of Atalophlebiinae (Ephemeroptera: Leptophlebiidae) from northern South America. Aquatic Insects, 14 (4), 243–248. https://doi.org/ 10.1080/01650520500208481.

Savage, H. M., Flowers, R. W., Porras, W., 2005. Rediscovery of Choroterpes atramentum in Costa Rica, type species of Tikuna new genus (Ephemeroptera: Leptophlebiidae: Atalophlebiinae), and its role in the" Great American Inter-change". Zootaxa, 932 (1), 1–14. https://doi.org/10.11646/zootaxa.932.1.1

Shimano, Y., Cabette, H. S., Salles, F. F., Juen, L., 2010. Composição e distribuição da fauna de Ephemeroptera (Insecta) em área de transição Cerrado-Amazônia, Brasil. Iheringia. Série Zoologia, 100 (4), 301–308.

https://doi.org/10.1590/S0073-47212010000400004

Shimano, Y., Salles, F. F., Cabette, H. S. R., 2011. Ephemeroptera (Insecta) ocorrentes no Leste do Estado do Mato Grosso, Brasil. Biota Neotropica, 11 (4), 239–253.

https://doi.org/10.1590/S1676-06032011000400021

Shimano, Y., Juen, L., Salles, F. F., Nogueira, D. S., Cabette, H. S. R., 2013. Environmental and spatial processes determining Ephemeroptera (Insecta) structures in tropical streams. In Annales de Limnologie-International Journal of Limnology (Vol. 49, No. 1, pp. 31–41). EDP Sciences. https://doi.org/10.1051/limn/2013036

Shimano, Y., Cardoso, M., Juen, L., 2018. Estudos ecológicos com Ephemeroptera (Insecta): O esforço amostral pode ser reduzido sem perder informações ecológicas e taxonômicas?. Acta Amazonica, 48 (2), 137–145.

https://doi.org/10.1590/1809-4392201700583.

Spieth, H., 1943. Taxonomic studies on the Ephemeroptera. III. Some interesting Ephemerids from Surinam and other neotropical localities. Am. Mus. Novit, 1244, 1–13.

Sweeney, B. W., Flowers, R. W., Funk, D. H., Ávila, S. A., Jackson, J. K., 2009. Mayfly communities in two Neotropical lowland forests. Aquatic Insects, 31 (sup1), 311–318. https://doi.org/10.1080/01650420902833863

Traver, J. R., 1943. New Venezuelan mayflies. Boletín de Entomología Venezolana, 2, 49–57.

Traver, J. R., 1947. Notes on Neotropical Mayflies, Part II, Baetidae, Subfamily Leptophlebiinae. Revista de Entomología, 18, 149–160.

Traver, J. R., Edmunds J. G. F., 1967. A revision of the genus Thraulodes (Ephemeroptera: Leptophlebiidae). Miscellaneous Publication of the Entomological Society of America, 5 (8), 351–402.

Walker, F., 1853. Ephemerinae, in: London, (Eds.), Catalogue of the specimens of Neuropterus insects in the collection of the British Museum. Part III (Termitidae and Ephemeridaé). pp. 553–585.

Zúñiga, M. D. C., Hernández, A. M. R., Aguilera, S. M., 1997. Biological aspects of Ephemeroptera in rivers of southwestern Colombia (South America). Taller Internacional sobre sistemática y Ecología de Ephemeroptera como Bioindicador de

Calidad de Agua, 1–13.

Zúñiga, M. D. C., Molineri, C., Domínguez, E., 2004. El orden Ephemeroptera (Insecta) en Colombia (No. Doc. 21585) CO-BAC, Bogotá.

Zúñiga, M. D. C., Cardona, W., Molineri, C., Mendivil, J., Cultid, C., Chará, A .M., Giraldo, A., 2014. Entomofauna acuática del Parque Nacional Natural Gorgona, Pacífico colombiano, con énfasis en Ephemeroptera y Plecoptera. Rev. Biol. Trop, 62 (2), 221–241.

Zúñiga, M. D. C., Molineri, C., Domínguez, E., Cardona, W., 2015. Leptophlebiidae (Insecta: Ephemeroptera) from Gorgona Island National Natural Park (Tropical Eastern Pacific, Colombia) with the description of two new species. In Annales de Limnologie-International Journal of Limnology, 51 (4), 281–296. https://doi.org/10.1051/limn/2015026.

Figures

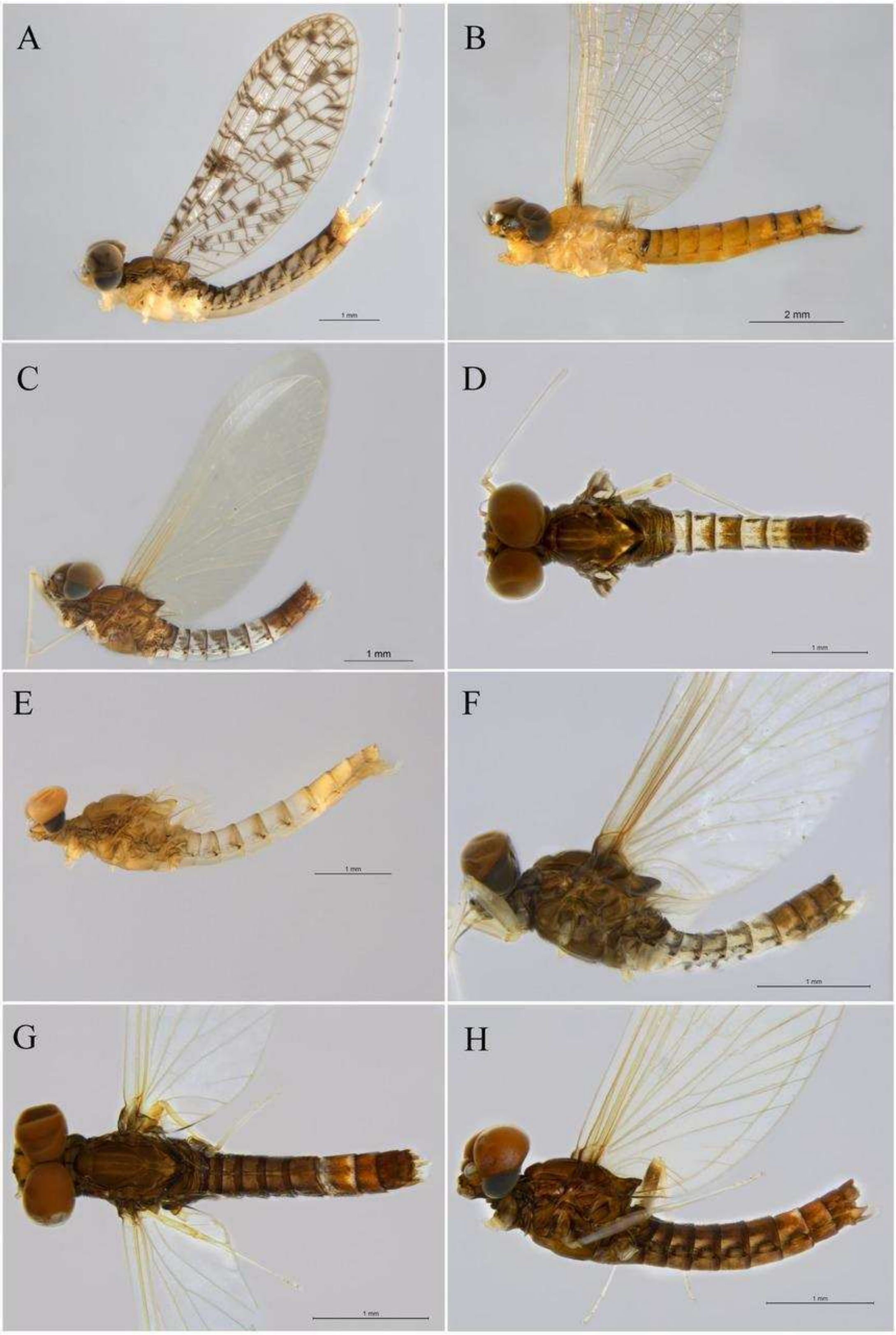


Figure 1. Habits of male imagos of Leptophlebiidae species: A) lateral view of Askola emmerichi; B) lateral view of Atopophlebia caldasi; C) lateral view of Farrodes caribbianus; and D) dorsal view of Farrodes caribbianus; E) lateral view of F. roundsi; F) lateral view of F. savagei; G) dorsal view of F. tepui; and H) lateral view of F. tepui.

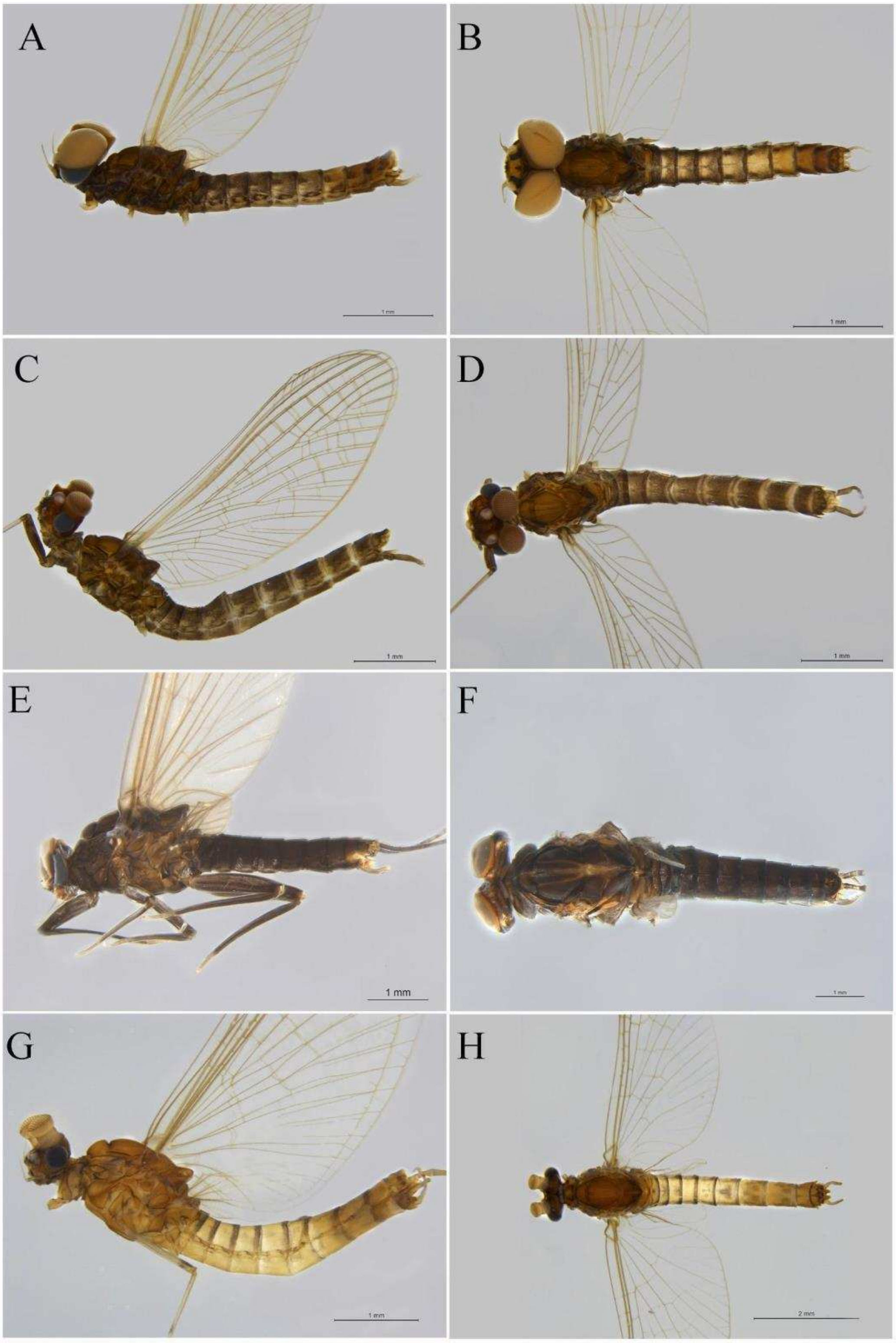


Figure 2. Habits of male imagos of Leptophlebiidae species: A) lateral view of Farrodes xingu; B) dorsal view of Farrodes xingu; C) lateral view of Hagenulopsis minuta; D) dorsal view of Hagenulopsis minuta; E) lateral view of Hydrosmilodon primanus; F) dorsal view of Hydrosmilodon primanus; G) lateral view of Miroculis (Miroculis) chiribiquete; H) dorsal view of Miroculis (Miroculis) chiribiquete.

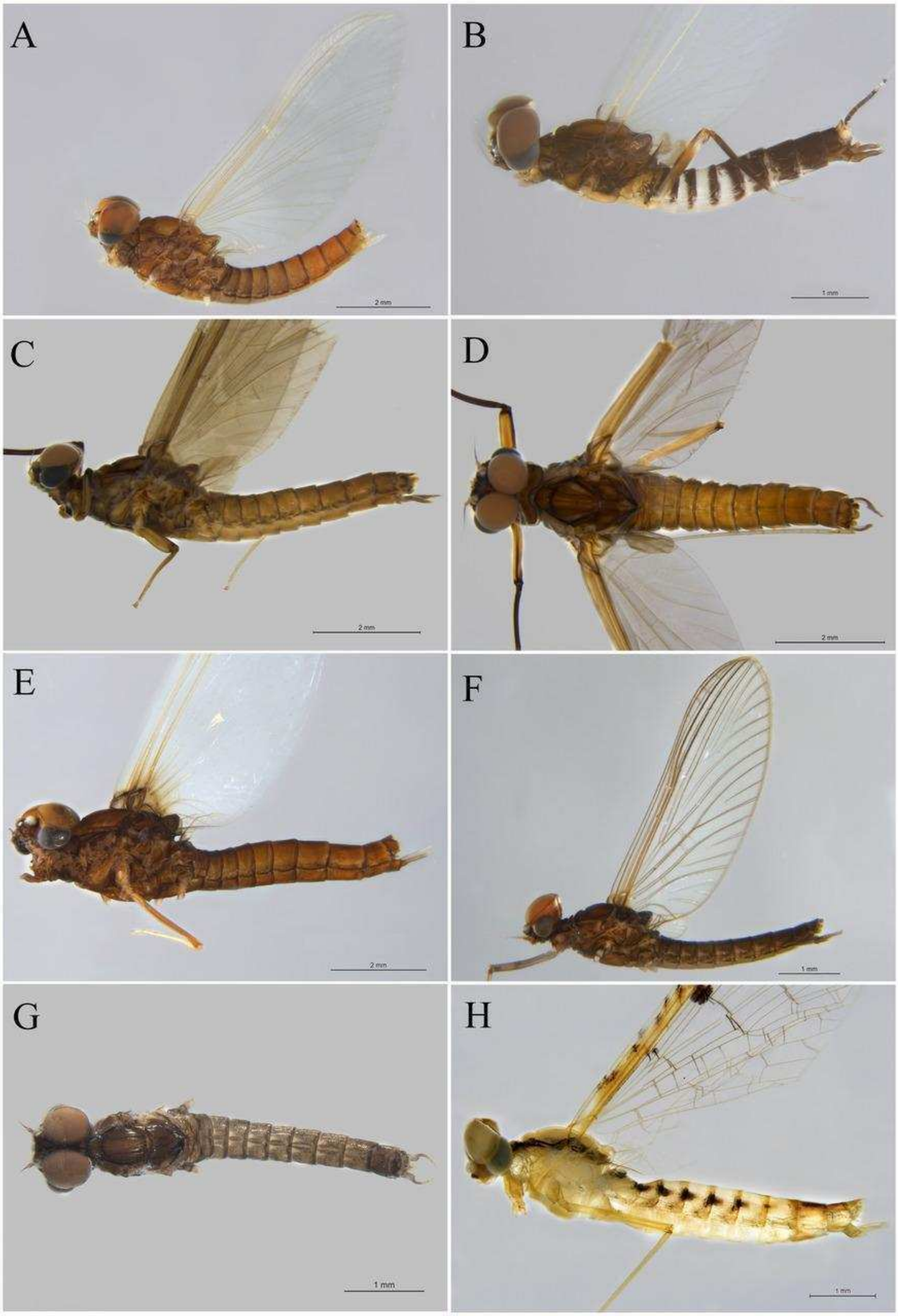


Figure 3. Habits of male imagos of Leptophlebiidae species: A) lateral view of Paramaka sp. nov.; B) lateral view of Simothraulopsis demerara; C) lateral view of Ulmeritoides huitoto; D) dorsal view of Ulmeritoides huitoto; E) lateral view of Ulmeritoides flavopedes; F) lateral view of Choroterpes sp. nov.; G) dorsal view of Choroterpes sp. nov.; H) lateral view of Tikuna atramentum.

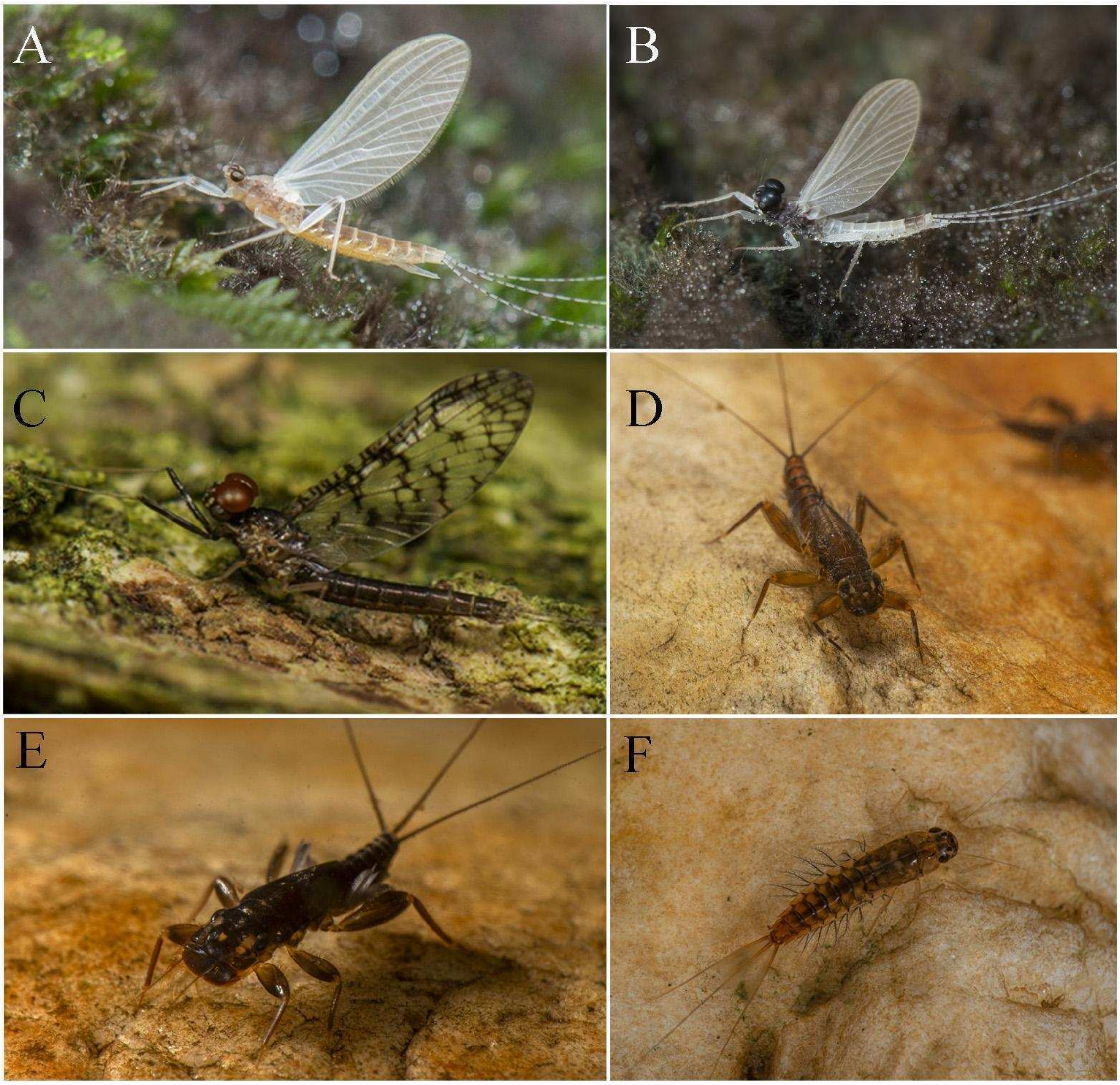


Figure 4. Habits of living specimens of Leptophlebiidae in the field: A) female lateral view of Hagenulopsis esmeralda; B) male lateral view of Hagenulopsis esmeralda; C) lateral view of Terpides contamanensis; D) dorsal view of the nymph of Atopophlebia caldasi; E) dorsal view of the nymph of Hydrosmilodon primanus; F) dorsal view of the nymph of Terpides echinovaris.

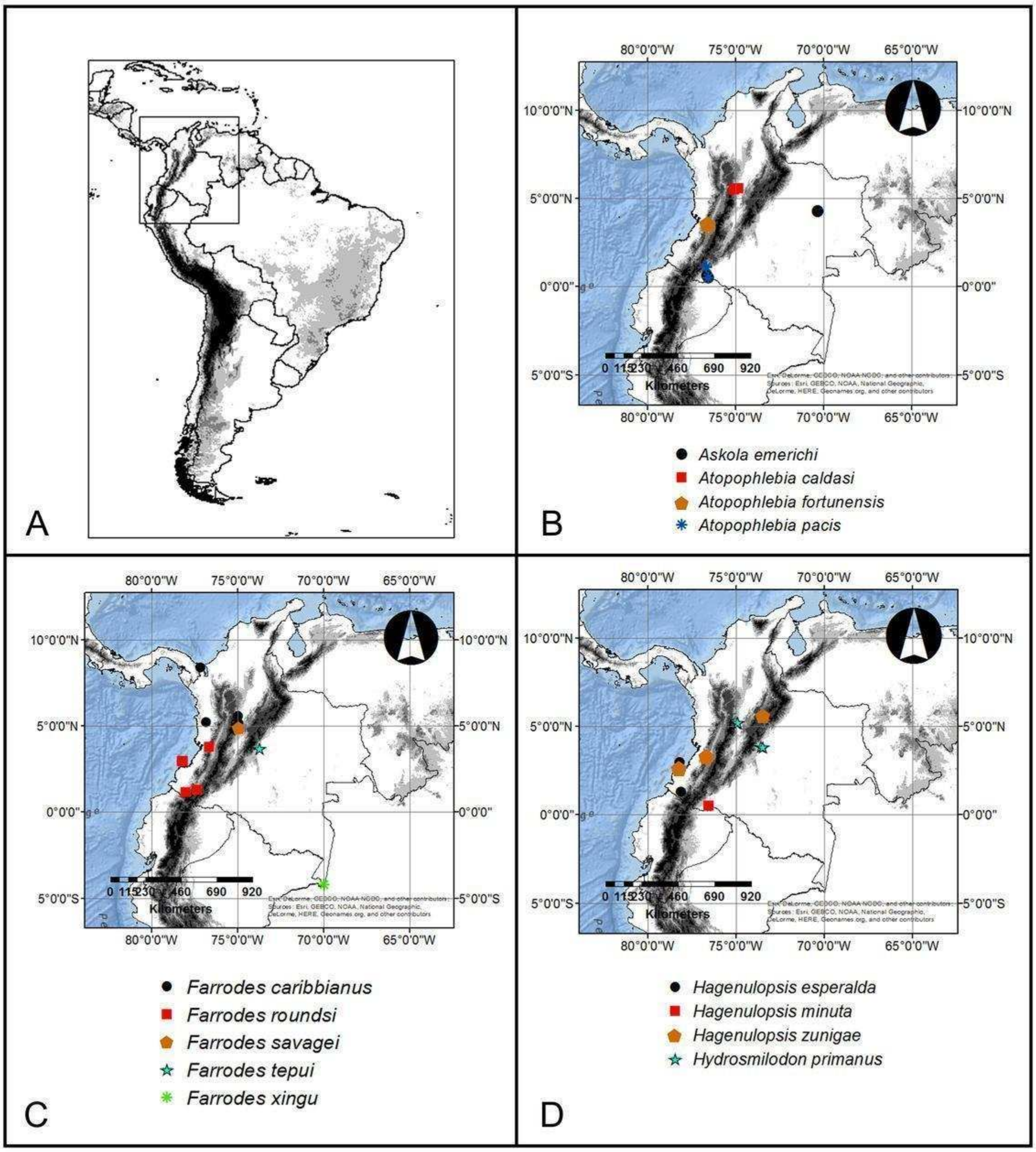


Figure 5. Maps of South America with detail of Colombia showing the distribution of the species of Leptophlebiidae: A) map of South America with detail of Colombia; B) Askola emerichi and Atopophlebia spp.; C) Farrodes spp.; D) Hagenulopsis spp. and Hydrosmilodon primanus.

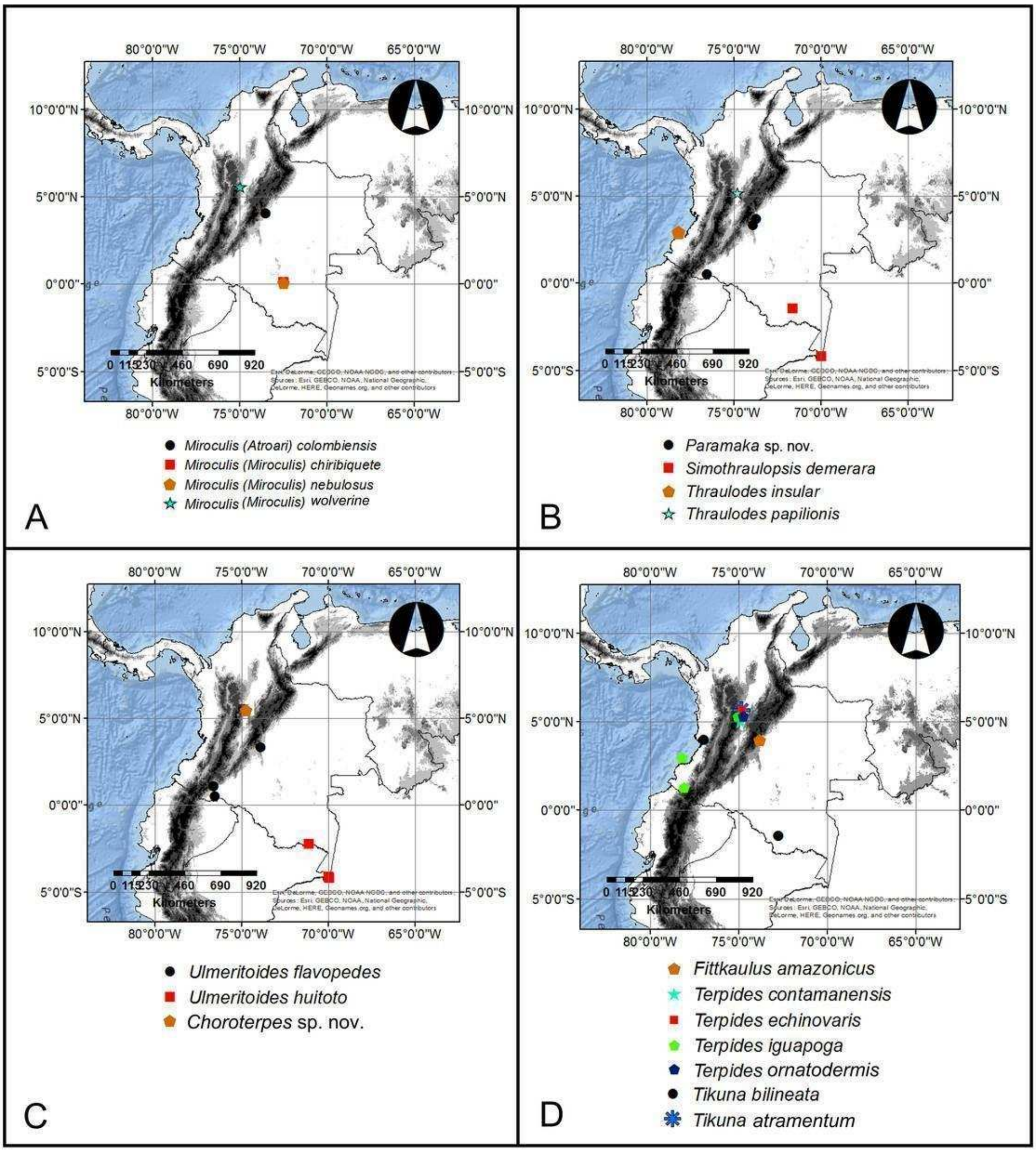


Figure 6. Maps of South America with detail of Colombia showing the distribution of the species of Leptophlebiidae: A) Miroculis spp.; B) Paramaka sp. nov., Simothraulopsis demerara and Thraulodes spp.; C) Ulmeritoides spp. and Choroterpes sp. nov.; D) Terpidinae.

The oology in taxonomic studies of Terpidinae Kluge (Ephemeroptera: Leptophlebiidae)

Jhon Faber Marulanda Lopez[1,2,*]

[1]Museu de Entomologia, Departamento de Entomologia, Universidade Federal de Viçosa, 36570-900, Minas Gerais, Brasil.

[2]Grupo de Investigación Bionat, Facultad de Ciencias Exactas y Naturales, Universidad de Caldas, Manizales, Caldas, Colombia.

[*]Corresponding author. E-mail: jhon.lopez@ufv.br (J.F. Marulanda).

Orcid: 0000-0001-6539-3042.

Jose Eduardo Serrão[3]

[3]Laboratório de Ultraestructura Celular, Universidade Federal de Viçosa, 36570-900, Minas Gerais, Brasil. E-mail: jeserrao@ufv.br.

Milena Oliveira Kalile[4]

[4]Pós-graduação em Entomologia, Universidade Federal de Viçosa, 36570-900, Minas Gerais, Brasil. E-mail: milenakalile@gmail.com.

Vinícius Moreira Marques[4]

[4]Pós-graduação em Entomologia, Universidade Federal de Viçosa, 36570-900, Minas Gerais, Brasil. E-mail: vmmufv@gmail.com.

Johana Quintero Cortes[4]

[4] Pós-graduação em Entomologia, Universidade Federal de Viçosa, 36570-900, Minas Gerais, Brasil. E-mail: joha_16ae@hotmail.com.

Frederico Falcão Salles[1]

[1] Museu de Entomologia, Departamento de Entomologia, Universidade Federal de Viçosa, 36570-900, Minas Gerais, Brasil. E-mail: ffsalles@gmail.com.

Abstract

Leptophlebiidae is a diverse family of mayflies (Ephemeroptera) and in Terpidinae the species identification is hard due to the similarity of male genitalia. In this study, we evaluated the chorion morphology of the eggs of 10 species of Terpidinae in different developmental stages, in order to explore the potential of the oocytes characteristics for the taxonomy of genus and species as well as species association. Eggs were analyzed with scanning electron microscope. The association of the nymph and adult using egg characters was possible for T. sooretamae and T. echinovaris. In the genera Terpides and Tikuna, variations in chorion sculpture allowed species differentiation, whereas in Fittkaulus amazonicus and F. cururuensis it was not possible. Egg features, including shape, chorion sculpture, location and number of micropylar areas, and attachment structures are useful characters to be also used in the taxonomy of these insects.

Key words: Attachment structures, Chorionic sculpture, Micropylar area, Neotropic, Oological characteristics.

Introduction

Mayflies (Insecta: Ephemeroptera) are amphibiotic aquatic insects with ca. 3500 species in 450 genera and 42 families (Salles et al., 2018). They often inhabit rivers and streams, but some species are also capable of inhabiting lentic environments. They are important in aquatic ecosystems' energy flow, since they feed on other animals, algae, detritus, and associated organisms, such as fungi and bacteria (Flowers & De la Rosa, 2010). These insects have also been historically used as bioindicators of water quality (Hellawell, 2012), because they may be sensitive to water pollution (Menetrey et al., 2007).

With more than 600 species and 130 genera distributed worldwide, Leptophlebiidae is one of the most diversified family of Ephemeroptera, both taxonomically and ecologically (Barber-James et al., 2008), mainly in South America, where Leptophlebiidae has the higher diversity with 250 species and 45 genera (Salles et al., 2020). Within Leptophlebiidae, Terpidinae was proposed by (Kluge, 2009) and includes three genera: Terpides (Demoulin, 1966), Fittkaulus (Savage & Peters, 1978) and Tikuna (Savage et al., 2005). Although the species differentiation of Ephemeroptera is historically based on penis morphology and wing venation (Domínguez et al., 2006), in Terpidinae representatives the penis morphology is very similar among the different genera, which difficult the species identification with the necessity for search additional morphological characters.

The external morphology of the egg has also been successfully used in taxonomic studies for Leptophlebiidae (Towns & Peters, 1978; Sivaramakrishnan, 1984; Mazzini & Gaino, 1985; Campbell & Peters, 1986; Domínguez, 1991; Gaino, Mazzini & Sartori, 1993; Derka, 2002; Derka et al. 2009; Godunko et al., 2015; Kluge, 2015; Souto et al. 2016; Tiunova & Kluge, 2016; Kluge, 2020). In the same way, oological characters have been used in phylogenetic analyses in some Leptophlebiidae, such as the Hermanella complex (or Hermanellognatha) (Domínguez & Cuezzo, 2002).

To date, Terpidinae encompasses 17 Neotropical species, but only for five of them, the egg morphology is known (Kluge, 2015, Zúñiga et al., 2015). The aim of this study was to characterize the chorion sculpture in eggs of Terpidinae representatives to explore its potential to associate developmental stages and discriminate species.

Methods

Eggs

The females were obtained from specimens kept in ethanol in the Museu de Entomologia (UFVB), of the Universidade Federal de Viçosa, Minas Gerais state, Brazil. The eggs were obtained dissecting the abdomen imagos and/or mature nymphs with iris-scissor and tweezers.

Identification

The taxonomic identification of the specimens was made with taxonomic keys and comparison with original descriptions (Needham & Murphy, 1924, Demoulin, 1966, Savage, 1986, Kluge, 2009, Kluge, 2015, Boldrini et al. 2009, Zúniga et al. 2015). The characters associated with the morphology of male genitalia and wings venation in adults were examined. In the nymphs, mouthparts, abdominal color pattern and gills were evaluated. In order to study the previously mentioned characters, morphological structures of taxonomic interest were mounted in permanent slides using Euparal®.

Scanning electron microscopy

After abdomen dissection such as aforementioned, the eggs were transferred to ethanol, to hexamethyldisilazane (HMDS) for 10 minutes and air-dried. The samples were mounted on aluminum stubs, gold covered (20 nm thick) and analyzed with a LEO VP1430 scanning electron microscope at 15 kV in the Núcleo de Microscopia e Microanálise da Universidade Federal de Viçosa. Some samples that were mounted on aluminum substrates were not dehydrated nor coated with gold, instead they were treated at a low vacuum pressure at 10 Kv and were photographed in an FEI QUANTA 250 scanning electron microscope in the Instituto de Investigaciones en Estratigrafía de la Universidad de Caldas, Colombia. The terminology of eggs structures followed Koss & Edmunds (1974) and Kluge (2015).

Results

The eggs of 10 species were evaluated in this study: Terpides sooretamae, Terpides contamanensis, Terpides iguapoga, Terpides echinovaris, Terpides guyanensis, Terpides ornatodermis, Fittkaulus cururuensis, Tikuna bilineata, Tikuna nigrobulla, and Tikuna atramentum. The main eggs characteristics of these specimens are described below.

Terpides sooretamae Boldrini & Salles, 2009 in Boldrini et al. 2009 (Fig. 1A, B).

(Extracted from female imago and nymph). Length 185–197 µm, width 62–73 µm. Shell-like. Chorion with relief formed by labyrinth-like ridges, with two longitudinal rows of 15–17 chorionic plates. Micropyle unknown. The eggs of the nymph and imago had the same shape and chorion sculpture.

Examined material: Imago, Brazil, Espírito Santo, Alfredo Chaves, Nova Mantova, 20°39’22’’ S, 40°50’13’’ W, 13/vii/2007, Boldrini, R & Salles, cols. Nymph, Brazil, Espírito Santo, Alfredo Chaves, Nova Mantova, 04/xi/2007, Boldrini, R cols.

Terpides contamanensis Kluge, 2015 (Fig. 1C, D).

The eggs of this species were previously described (Kluge, 2015).

(Extracted from female subimago). Length 190-206 µm, width 67-78 µm. Shell-like. Chorion with relief formed by labyrinth-like ridges. Two or three micropyles located in the equatorial region of the egg between the two longitudinal rows of 15 chorionic plates.

Examined material: Subimago, Colombia, Tolima, Mariquita, Río Lumbi, 5°09’2.05’’ N, 74°53’25.62’’ W,21/iii/2017, Dias, L & Marulanda, J cols.

Terpides iguapoga Molineri, Domínguez & Zúñiga, 2015 in Zúñiga et al. 2015 (Fig. 2A).

(Extracted from female imago). Length 120-133 µm, width 58-64 µm. Shell-like with two discontinue longitudinal rows of 8 chorionic plates. Chorion with circular projections distributed uniformly. One micropyle in the equatorial region of the egg between the two longitudinal rows of chorionic plates.

Examined material: Subimago, Colombia, Caldas, Samaná, Río San Antonio, 5°29’29.8’’ N, 75°02’45.6’’ W, 20/x/2017, Dias, L col.

Terpides echinovaris Kluge, 2015 (Fig. 2B).

The eggs of this species was previously described (Kluge, 2015).

(Extracted from female nymph). Length 149-151 µm, width 65-74 µm. Shell-like with two longitudinal rows of chorionic plates. Chorion with conic projections inclined toward poles. One micropyle in the equatorial region of the egg between the two longitudinal rows of chorionic plates (as in Fig. 82 in Kluge, 2015).

Examined material: Nymph, Colombia, Huila, San Agustín, Los Micos, 1°52’48.35’’ N, 76°16’2.69’’ W, v/2010, León, V col.

Terpides guyanensis Demoulin, 1966 (Fig. 2C).

(Extracted from female subimago). Length 116-156 µm, width 67-76 µm. Shell-like with two longitudinal rows of chorionic plates little differentiated. Chorion with longitudinal ridges and small hemispheric protuberances. Two circular micropylar areas located between chorionic plates and in the equatorial line of the egg.

Examined material: Subimago, Brazil, Roraima, Igarapé do Bananal, 3°37’14.43’’ N, 61°38’15.34’’ W, 22/x/2004, Salles, F. F col.

Terpides ornatodermis Kluge, 2015 (Fig. 2D).

The eggs of this species was previously described (Kluge, 2015).

(Extracted from female nymph). Length 115-123 µm, width 61-63 µm. Oval in shape. Chorion not visible due to follicular cells layer.

Examined material: Nymph, Colombia, Caldas, Samaná, La Selva, 5°30’52.0’’ N, 75°02’51,8’’ W, 19/x/2017, Dias, L col.

The eggs of this species were previously described (Kluge, 2015).

Fittkaulus cururuensis Savage, 1986 (Fig. 3A, B).

(Extracted from female imago and nymph). Length 100-142 µm, width 60-82 µm. Oval shape. Whole egg covered by a coat of oval fibrillose units, oriented along the egg and overlapping one another. Micropyle unknown.

Examined material: Imago, Brazil, Mato Grosso, Nova Xavantina, Córrego da Mata, 14°29’51.7’’ S, 52°28’42.6’’ W, 14/xi/2005, Salles, F col. Nymph, Brazil Espírito Santo, Sooretama, 20°39’22’’ S, 40°50’13’’ W, 16/vii/2008, Salles, F col.

Tikuna bilineata (Needham & Murphy, 1924) (Fig. 3C).

The eggs of this species were previously described (Kluge, 2015).

(Extracted from female imago). Length 127-139 µm, width 69-76 µm. Oval. Chorion with small hemispheric protuberances. One or two micropyles on one side at equator and two large projections between micropyle and poles. Each projection arises from shallow concavity, directed toward pole and bent, apically widened and pressed or stuck to egg surface (as in Fig. 124 in Kluge, 2015).

Examined material: Imago, Colombia, Valle del Cauca, Bajo Calima, La Larga, 3°59’53.60’’ N, 76°58’31.87’’ W, 12/xii/2017, Dias, L & Marulanda, J cols.

Tikuna nigrobulla Kluge, 2009 (Fig. 3D).

(Extracted from female nymph). Length 107-111 µm, width 55-64 µm. Oval in shape. Chorion not visible due to follicular cells layer.
Examined material: Nymph, Colombia, Caldas, Norcasia, Rio Manso, 5°39’25.80’’ N, 74°51’44.66’’ W, 13/ii/2012 Dias, L col.

Tikuna atramentum (Traver, 1947) (Fig. 3E, F).

(Extracted from female imago). Length 129-139 µm, width 70-79 µm. Shape oval. Small hemispheric protuberances of 2 µm in diameter uniformly distributed in the chorion. Chorionic projections uniformly distributed in the chorion with 15-16 µm of high and 12 µm in diameter with apical widening. Micropyle unknown.

Examined material: Imago, Colombia, Caldas, Norcasia, Rio Manso, 5°39’25.80’’ N, 74°51’44.66’’ W, 05/iv/2017, Dias, L & Marulanda, J cols.

Discussion

In this study, the association of nymphs and adults using eggs characters was possible for T. sooretamae and T. echinovaris, since both developmental stages have eggs with same shape and chorionic sculpture. Kluge (2015) described the eggs of adults of T. echinovaris with similar chorion sculpture as our results, but with bigger eggs. A similar association has been described in the Hermanella-complex indicating that the eggs are informative tools for the association of life stages (Domínguez & Cuezzo 2002). We consider that the eggs characters may complement the association of species using molecular (Hoyos et al., 2014; Salles et al., 2016) and rearing data (Boldrini & Cruz, 2013). Thus, our findings suggest the egg morpholgys contributes to solve one of the main taxonomic problems in Ephemeroptera, the association of life stages.

The eggs of Terpides spp. are characterized by bivalve shell shape and two rows of rectangular plates aligned along egg longitudinal axis. Micropyles are located between free margins of the plates in the equatorial region of the egg. In contrast to Terpides, eggs of Fittkaulus spp. and Tikuna spp. are oval, without the two rows of aligned plates (Kluge, 2015). The eggs of Tikuna are characterized by hemispheric protuberances uniformly distributed in the chorion, whereas those of Fittkaulus have fibrillose units uniformly distributed in the chorion. Therefore, after increasing the number of species evaluated, we agree with Kluge (2015) that the eggs shape is a reliable source for distinguishing the genera of Terpidinae.

Chorionic sculptures are different among T. echinovaris, T. iguapoga, T. ornatodermis, and T. sooretamae/T. contamanensis. Terpides sooretamae and T. contamanensis have the same chorionic sculpture and it is not possible to distinguish the eggs of these two mayflies. This finding is an additional evidence that they are closely related or even an indicative that they may represent the same species. The egg morphology of T. jessiae (Peters & Harrison, 1974), another species very similar to T. sooretamae and T. contamanensis, unfortunately remains unknown.

The variations in the eggs of Tikuna according to the species is characterized by the number of chorionic projections, with two in T. bilineata and many in T. atramentum. In Fittkaulus, the eggs of F. amazonicus, previously described (Kluge, 2015), and F. cururuensis have fibrillose units uniformly distributed in the chorion, so it is not possible differentiate them using egg morphology. Fittkaulus amazonicus and F. cururuensis are also similar species and may even represent synonymy.

Oology is a useful tool for the association of life stages of Terpides spp. and the discrimination of some Terpidinae species. The eggs characters, including shape, chorionic sculpture, location, and number of micropyles, and attachment structures, are characters that may complement those conventionally used in taxonomy and phylogeny of this subfamily. Our results suggest that in Terpidinae, eggs of females only in the final nymphal instars can be used for taxonomic differentiation of species, because in earlier stages, follicular cells are closely associated with the immature oocyte and the chorion synthesis is incomplete without evident final sculpture. Overall, we propose future taxonomic studies in order to evaluate if T. contamanensis and F. amazonicus are valid species or junior synonyms of T. sooretamae and F. cururuensis, respectively.

Declaration of competing interest

The authors declare that they have no known competing financial interest or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank the Laboratorio de Ultraestructura Celular of the Universidade Federal de Viçosa for the support in carrying out this research. We also thanks to Gustabo Bolaños Instituto de Investigaciones en Estratigrafía de la Universidad de Caldas for your asesory in the took of some SEM imagens. This work was conducted during a scholarship supported to first author by Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq (process # 162813/2018-0). Thanks to the National Counsel of Technological and Scientific Development from Brazil (CNPq) for a research productivity fellowship awarded to FFS.

References

Barber-James, H.M., Gattolliat, J.L., Sartori, M., Hubbard, M.D., 2008. Global diversity of mayflies (Ephemeroptera, Insecta) in freshwater. Hydrobiologia. 595, 339 –350. https://doi.org/10.1007/s10750-007-9028-y.

Boldrini, R., Salles, F.F., Cabette, H.R., 2009. Contribution to the taxonomy of the Terpides lineage (Ephemeroptera: Leptophlebiidae). Annales de Limnologie-International Journal of Limnology. 45, 219–229. https://doi.org/10.1051/limn/2009029.

Boldrini, R., Cruz, P.V., 2013. Criação e transporte de ninfas de Ephemeroptera (Insecta) em campo. EntomoBrasilis. 6, 168–170. https://doi.org/10.12741/ebrasilis.v6i2.281.

Campbell, I.C., Peters, W.L., 1986. Redefinition of Kirrara Harker with a redescription of Kirrara procera Harker (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). Aquatic Insects. 8, 71–81. https://doi.org/10.1080/01650428609361234.

Demoulin, G., 1966. Contribution à l'étude des Ephemeropteres du Surinam. Bulletin Institut Royal des Sciences Naturelles de Belgique. 42, 1–22.

Derka, T., 2002. Massartella devani, a new mayfly species from Venezuela's Highlands (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). Aquatic Insects. 24, 309–316. https://doi.org/10.1076/aqin.24.4.309.8241.

Derka, T., Svitok, M., Schlögl, J., 2009. Massartella hirsuta sp. nov. (Ephemeroptera: Leptophlebiidae: Atalophlebiinae) and new data on mayflies of Guyana Highlands. Aquatic Insects. 31, 83–94. https://doi.org/10.1080/01650420902811992.

Dominguez, E., 1991. The status of the genus Ulmeritus (Ephemeroptera: Leptophlebiidae: Atalophlebiinae), in: Overview and strategies of Ephemeroptera and Plecoptera. Proc. Vlth Int. Ephemeroptera Cont. 24–28 July 1989 and Xth Int. Symp. on Plecoptera 27–30 July 1989, Granada, Spain, pp. 169.

Domínguez, E., Gabriela Cuezzo, M., 2002. Ephemeroptera egg chorion characters: a test of their importance in assessing phylogenetic relationships. Journal of Morphology. 253, 148–165. https://doi.org/10.1002/jmor.1117.

Domínguez, E., Molineri, C., Pescador, M.L., Hubbard, M.D., Nieto, C., 2006. Biodiversidad Acuática en América Latina, Volumen 2 Ephemeroptera de América del Sur, Pensoft ed. Sofia-Moscow, Rusia.

Flowers, R.W., De la Rosa, C., 2010. Capítulo 4: Ephemeroptera. Revista de Biología Tropical. 58, 63–93.

Gaino, E., Mazzini, M., Sartori, M., 1993. Comparative analysis of the chorionic pattern in Habroleptoides species (Ephemeroptera, Leptophlebiidae). Italian Journal of Zoology. 60, 155–162. https://doi.org/10.1080/11250009309355805.

Godunko, R.J., Sroka, P., Soldán, T., Bojvoká, J., 2015. The higher phylogeny of Leptophlebiidae (Insecta: Ephemeroptera), with description of a new species of Calliarcys Eaton, 1881. Arthropod Systematics and Phylogeny. 73, 259–272.

Hellawell, J.M. 2012. Biological indicators of freshwater pollution and environmental management. Springer Science & Business Media.

Hoyos, D.C., García, L.F., Rivera, F.A., López, G.A., Zúñiga, M.D.C., & Dias, L.G., 2014. Contribution to the knowledge of Haplohyphes Allen (Insecta: Ephemeroptera: Leptohyphidae) from Colombia. Caldasia. 36, 125–138. https://doi.org/10.15446/caldasia.v36n1.43895.

Kluge, N.J., 2009. Higher system of Atalophlebiinae (Leptophlebiidae) with description of three new species of Terpides s.l. from Peruvian Amazonia. Russian Entomological Journal. 18, 243–256.

Kluge, N.J., 2015. Contribution to the knowledge of Terpidinae Kluge 2009 (Ephemeroptera: Leptophlebiidae). Zootaxa. 3999, 151–189. https://doi.org/10.11646/zootaxa.3999.2.1.

Kluge, N. J. (2020). Systematic position of Thraulodes Ulmer 1920 (Ephemeroptera: Leptophlebiidae) and descriptions of new and little-known species. Zootaxa, 4756, 001–142. https://doi.org/10.11646/zootaxa.4756.1.1.

Koss, R.W., Edmunds, G.F., 1974. Ephemeroptera eggs and their contribution to phylogenetic studies of the order. Zoological Journal of the Linnean Society. 55, 267–349. https://doi.org/10.1111/j.1096-3642.1974.tb01648.x.

Mazzini, M., Gaino, E., 1985. Fine structure of the egg shells of Habrophlebia fusca (Curtis) and H. consiglioi Biancheri (Ephemeroptera: Leptophlebiidae). International Journal of Insect Morphology and Embryology. 14, 327–334. https://doi.org/10.1016/0020-7322(85)90013-3.

Menetrey, N., Oertli, B., Sartori, M., Wagner, A., Lachavanne, J.B. 2007. Eutrophication: are mayflies (Ephemeroptera) good bioindicators for ponds?. In Pond Conservation in Europe Springer, Dordrecht, pp. 125–135.

Needham, J.G., Murphy, H.E., 1924. Neotropical mayflies. Bulletin of the Lloyd Library Number 24. Entomological Series. 4, 1–79.

Peters, W. L., Harrison, A. D., 1974. Redescription of Terpides Demoulin from St. Vincent, West Indies (Ephemeroptera: Leptophlebiidae). Proceedings of the Entomological Society of Washington, 76, 178–185.

Salles, F.F., Dominguez, E., Mariano, R., Paresque, R., 2016. The imagos of some enigmatic members of the Hermanella complex (Ephemeroptera, Leptophlebiidae). ZooKeys. 625, 45–66. https://doi.org/10.3897/zookeys.625.9874.

Salles, F.F., Domínguez, E., Molineri, C., Boldrini, R., Nieto, C., Dias, L.G., 2018. Order Ephemeroptera. in: Hamada, N., Thorp, J.H., Rogers, D.C. (Eds.), Thorp and Covich's Freshwater Invertebrates. Academic Press, pp. 61–117. https://doi.org/10.1016/B978-0-12-804223-6.00003-2.

Salles, F.F., Molineri, C., Nieto, C., Lima, L.R.C., Dias, L.C., Boldrini, R., Mariano, R., Domínguez, E. 2020. Ephemeroptera da América do Sul. Disponível em http://ephemeroptera.com.br/ (acessado em 09 outubro 2020).

Savage, H.M., 1986. Systematics of the Terpides lineage from the Neotropics: Definition of the Terpides lineage, methods, and revision of Fittkaulus Savage & Peters. Spixiana. 9, 255–270.

Savage, H.M., Peters, W.L., 1978. Fittkaulus maculatus a new genus and species from northern Brazil (Leptophlebiidae: Ephemeroptera). Acta Amazonica. 8, 293–298. https://doi.org/10.1590/1809-43921978082293.

Savage, H.M., Flowers, R.W., Porras, W., 2005. Rediscovery of Choroterpes atramentum in Costa Rica, type species of Tikuna new genus (Ephemeroptera: Leptophlebiidae: Atalophlebiinae), and its role in the" Great American Inter-change". Zootaxa. 932, 1–14. https://doi.org/10.11646/zootaxa.932.1.1.

Sivaramakrishnan, K.G., 1984. Description of female imago and eggs of Indialis badia Peters & Edmunds (Ephemeroptera: Leptophlebiidae). Oriental Insects. 18, 95–98. https://doi.org/10.1080/00305316.1984.10432199.

Souto, P.M., Da Silva, E.R., Nessimian, J.L., Gonçalves, I.C., 2016. Two new species of Ulmeritoides Traver (Ephemeroptera: Leptophlebiidae) from Southeastern Brazil. Zootaxa. 4078, 127–136. https://doi.org/10.11646/zootaxa.4078.1.11.

Tiunova, T.M., Kluge, N.J., 2016. Redescription of Paraleptophlebia falcula Traver 1934 with notes on status and composition of Paraleptophlebia Lestage 1917 and Neoleptophlebia Kluge 1997 (Ephemeroptera: Leptophlebiidae). Zootaxa. 4098, 369–382. https://doi.org/10.11646/zootaxa.4098.2.9.

Towns, D.R., Peters, W.L., 1978. A revision of genus Atalophlebioides (Ephemeroptera: Leptophlebiidae). New Zealand journal of zoology. 5, 607–614. https://doi.org/10.1080/03014223.1978.10423813.

Traver, J.R., 1947. Notes on Neotropical Mayflies, Part II, Baetidae, Subfamily Leptophlebiinae. Revista de Etologia. 18, 149–160.

Zúñiga, M.D.C., Molineri, C., Domínguez, E., Cardona, W., 2015. Leptophlebiidae (Insecta: Ephemeroptera) from Gorgona Island National Natural Park (Tropical Eastern Pacific, Colombia) with the description of two new species. Annales de Limnologie-International Journal of Limnology. 51, 281–296. https://doi.org/10.1051/limn/2015026.

List of figures

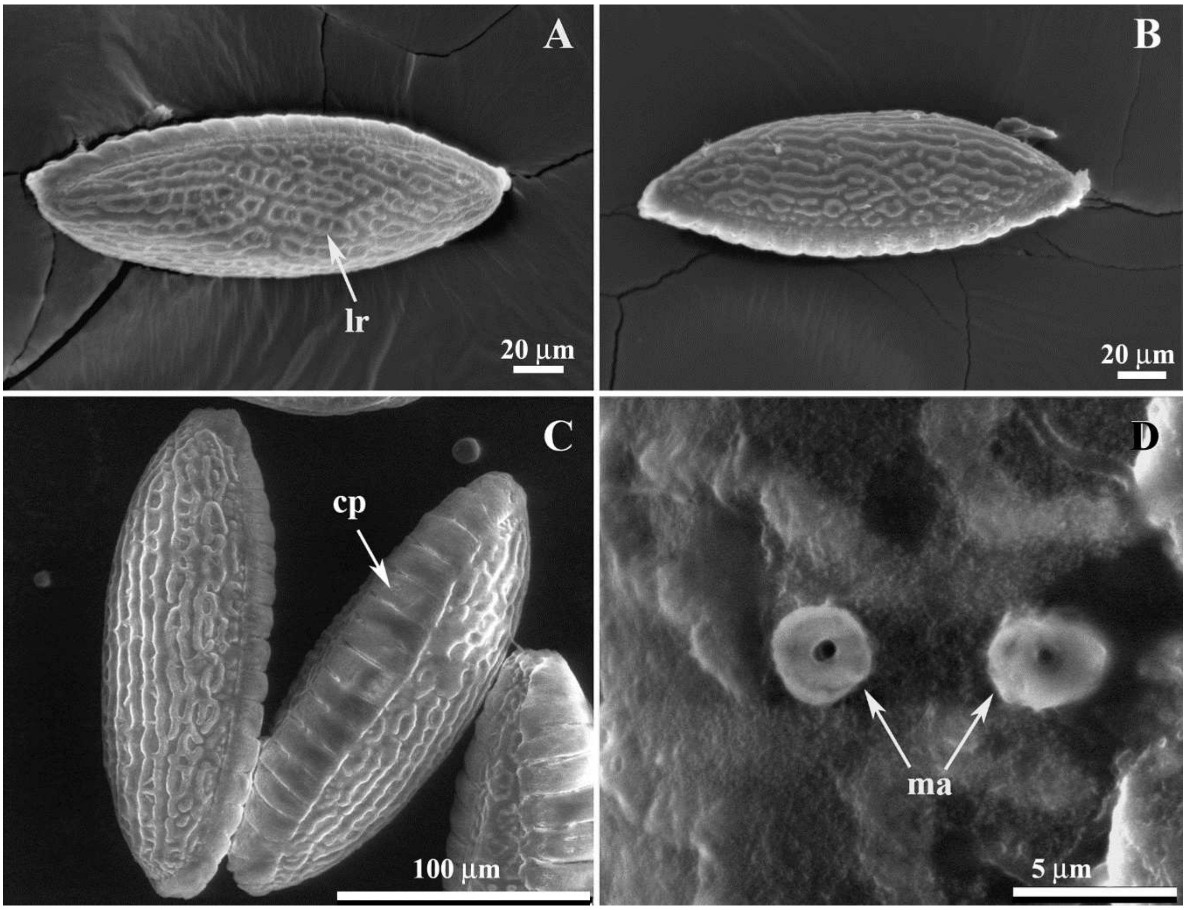


Fig. 1. Scanning electronic micrographs of Terpides sooretamae and Terpides contamanensis eggs: A. Female imago Te. sooretamae, general view; B. Female nymph Te. sooretamae, general view; C. Female Subimago Te. contamanensis; D. General view of micropylar area Te. contamanensis. lr: labyrinth-like ridges; cp: chorionic plates; ma: micropylar area.

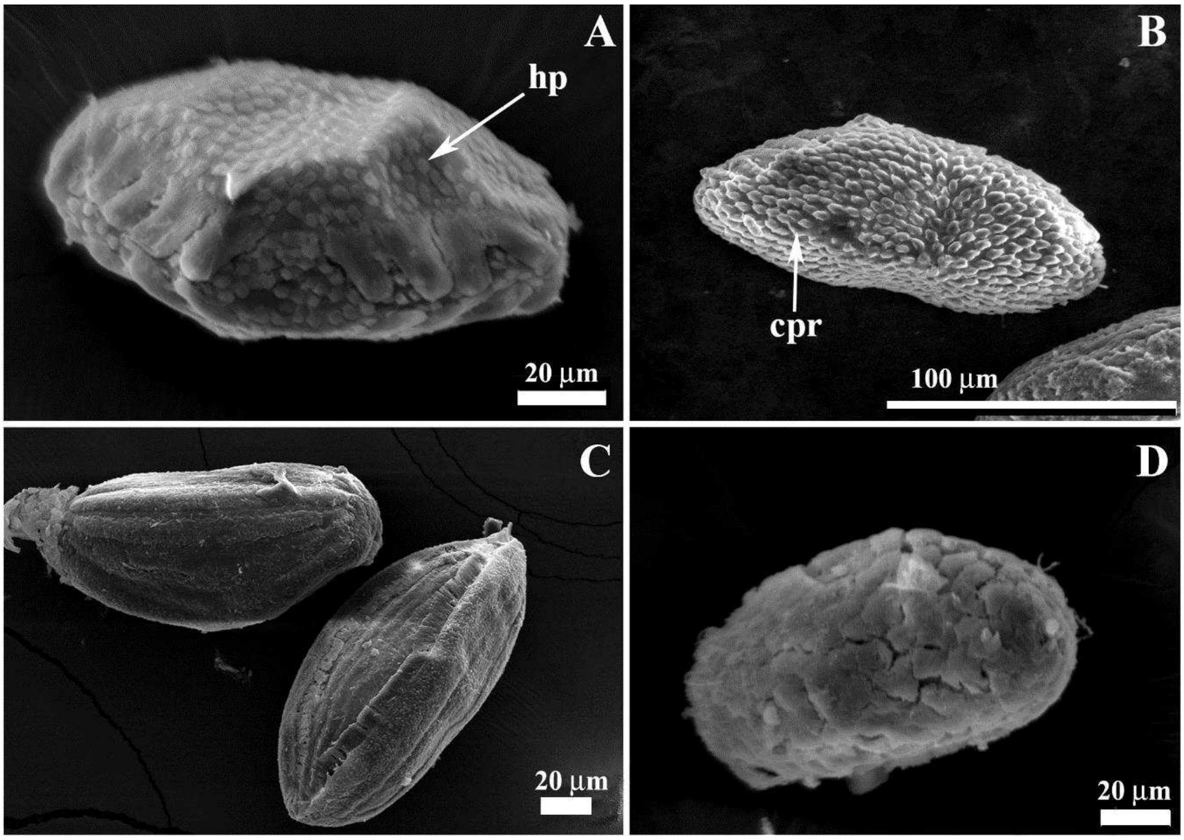


Fig. 2. Scanning electron micrographs of Terpides spp. eggs: A. General view of female imago of Te. iguapoga; B. General view of female nymph of Te. echinovaris; C. General view of female nymph of Te. guyanensis; D. General view of female nymph of Te. ornatodermis. hp: hemispheric protuberances; cpr: chorionic projections.

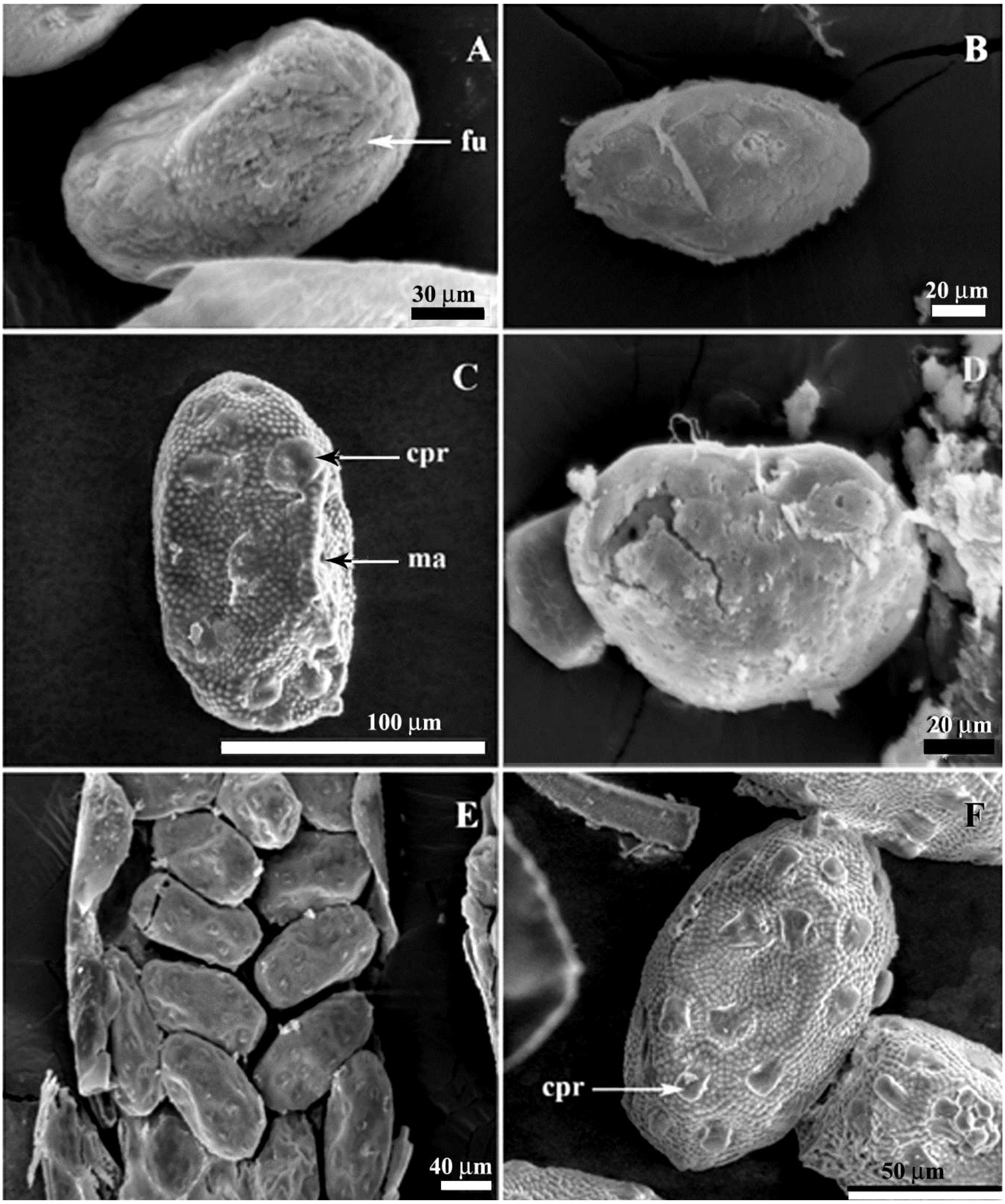


Fig. 3. Scanning electron micrographs of Fittkaulus cururuensis and Tikuna spp. eggs: A. General view of female imago of F. cururuensis; B. General view of female nymph of F. cururuensis; C. General view of female imago of Ti. bilineta; D. General view of female nymph of Ti. nigrobulla; E and F. General view eggs of female imago of Ti. atramentum. fu: fibrillose units; cpr: chorionic projections; ma: micropylar area.