UNIVERSIDADE FEDERAL DE VIÇOSA

Revision and Phylogeny of Tupiperla Froehlich, 1969 (Plecoptera: Gripopterygidae) based on molecular and morphological data

Felipe Ribeiro Pereira Sarmento
Magister Scientiae

VIÇOSA - MINAS GERAIS
2026

FELIPE RIBEIRO PEREIRA SARMENTO

Revision and Phylogeny of Tupiperla Froehlich, 1969 (Plecoptera: Gripopterygidae) based on molecular and morphological data

Dissertation submitted to the Entomology Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Magister Scientiae*.

Adviser: Frederico Falcao Salles

Co-adviser: Daniela Maeda Takiya

VIÇOSA - MINAS GERAIS
2026

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

T

S246r
2026

Sarmento, Felipe Ribeiro Pereira, 1999-
Revision and phylogeny of Tupiperla Froehlich, 1969 (Plecoptera: Gripopterygidae) based on molecular and morphological / Felipe Ribeiro Pereira Sarmento. – Viçosa, MG, 2026.
137 f.: il. (algumas color.).

Inclui anexos.
Orientador: Frederico Falcão Salles.
Dissertação (mestrado) - Universidade Federal de Viçosa, Departamento de Entomologia, 2026.
Referências bibliográficas: f. 100-106.
DOI: https://doi.org/10.47328/ufvbbt.2026.088
Modo de acesso: World Wide Web.

1. Tupiperla Froehlich - Filogenia. 2. Tupiperla Froehlich -Morfologia. 3. Tupiperla Froehlich- Marcadores moleculares . I. Salles, Frederico Falcão, 1975-. II. Universidade Federal de Viçosa. Departamento de Entomologia. Programa de Pós-graduação em Entomologia. III. Título.

CDD 22. ed. 595.735

Bibliotecário(a) responsável: Advania Elza da Silva CRB-6/3263

FELIPE RIBEIRO PEREIRA SARMENTO

Revision and Phylogeny of Tupiperla Froehlich, 1969 (Plecoptera: Gripopterygidae) based on molecular and morphological data

Dissertation submitted to the Entomology Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Magister Scientiae*.

APPROVED: February 24, 2026.

Assent:

Felipe Ribeiro Pereira Sarmento
Author

Frederico Falcao Salles
Adviser

Dedico essa dissertação à minha avó Albertina Saraiva Sarmento (in memorian) por me mostrar a alegria de aprender. Me lembro muito bem de quando ela ouvia uma palavra nova e tentava escrever e ficava feliz quando conseguia, “Não tenha vergonha de não saber, tenha vergonha de não tentar aprender”

ACKNOWLEDGMENTS

Gostaria de agradecer primeiramente ao meu orientador, Frederico Falcão Salles, por ter acreditado em mim para desenvolver esta pesquisa. Sou muito grato por sua paciência durante as orientações, pela disposição constante em ensinar e compartilhar seu conhecimento em morfologia, e também por confiar no potencial da viagem de campo a Urubici. Deixo também um grande abraço à sua família, Marcela, Joaquim e Helena, por serem sempre pessoas tão incríveis e receptivas. Agradeço imensamente à minha coorientadora Daniela Maeda Takiya, pela paciência, disponibilidade e por sempre esclarecer minhas dúvidas, independentemente de quão pequenas ou grandes fossem. Obrigado por confiar em mim para desenvolver esta pesquisa e por todas as vezes que me recebeu no Rio de Janeiro. Estendo também meu carinho aos seus filhos, Sofia e Nicolas, sempre dispostos a brincar com o Tio Felipe.

À minha mãe, Ana Lúcia, ao seu marido Manoel Felipe e à minha madrinha Solange, agradeço por terem me criado e contribuído para que eu me tornasse a pessoa que sou hoje. Às minhas irmãs Thayna, Luany, Giovanna e Gabriela, obrigado por sempre me darem forças. Amo muito vocês e não há um dia em que não pense em nossa família.

Agradeço ao Tacio Duarte pela amizade e por ter sido fundamental na minha formação acadêmica, especialmente durante minha iniciação científica, quando me ensinou muito do que sei sobre morfologia de Gripopterygidae. À Fernanda Avelino-Capistrano, agradeço pela confiança e disponibilidade em me ajudar.

Ao Lucas (Prego), agradeço profundamente pela amizade, pelas coletas, conversas madrugada adentro e pelos ensinamentos em biologia molecular. Se hoje defendo esta dissertação, devo muito a você. À minha amiga Raquel, agradeço pelo presente que tornou este mestrado possível: o notebook que utilizei para realizar todas as minhas análises.

Aos meus grandes amigos Jefferson, Getulio, Fals e Paulo Naoto, obrigado por estarem sempre presentes em todos os momentos da minha vida. À minha companheira de longa data Milene Cristina Alves, agradeço pelo apoio durante minha graduação e mestrado.

À minha família em Viçosa, Ana Dária Viana, Victor Castro e Raul Viana Castro, agradeço por sempre me acolherem e me fazerem sentir em casa. Ao Rodrigo Braga Gastaldo, meu parceiro acadêmico durante o mestrado.

À minha querida família favorita, Pedro, Isabel e Aurora, agradeço pelo carinho e amizade. Aos amigos que Viçosa me proporcionou. Iâmara, João, Marielle, Mateus e Pedro, agradeço pelos momentos de convivência e descontração.

Agradeço também à equipe do Laboratório de Entomologia da UFRJ por sempre me receber de forma tão acolhedora. Um agradecimento muito especial ao André Antunes, por todo carinho, apoio e pelas conversas que marcaram essa fase da minha vida.

Agradeço ao Laboratório de Biologia Molecular de Insetos da UFV, especialmente ao professor Gustavo Martins e à técnica Renata, pelo suporte técnico. Ao professor Allan dos Santos (UniRio) e ao professor Leandro Dumas e à equipe do LABIA (UFRRJ), agradeço pelo acesso a materiais e infraestrutura, assim como à Marianna pela ilustração da capa.

Agradeço ao Programa de Pós-Graduação em Entomologia da UFV, em especial à secretária Eliane de Castro Silva e ao professor Og DeSouza pelo empréstimo de equipamentos. Também agradeço às instituições e pesquisadores que disponibilizaram imagens e materiais essenciais para este trabalho, incluindo o Natural History Museum Vienna e o Zentralmagazin Naturwissenschaftlicher Sammlungen.

This work has been sponsored by the following Brazilian research agencies: Coordination for the Improvement of Higher Education Personnel (CAPES; Financing code 001), Minas Gerais State Foundation for Research Aid (FAPEMIG) and National Council of Scientific and Technological Development (CNPq).

Quanto Mais Eu Como, Mais Fome Eu Sinto!
Gustavo “Djonga” Pereira Marques

ABSTRACT

SARMENTO, Felipe Ribeiro Pereira, M.Sc., Universidade Federal de Viçosa, February, 2026. **Revision and Phylogeny of Tupiperla Froehlich, 1969 (Plecoptera: Gripopterygidae) based on molecular and morphological data**. Adviser: Frederico Falcao Salles. Co-adviser: Daniela Maeda Takiya.

The genus Tupiperla Froehlich, 1969 represents one of the most diverse lineages of Neotropical Gripopterygidae (Insecta: Plecoptera), but its systematics has been hampered by taxonomic instability and the lack of a phylogenetic analysis involving its species. This study presents a comprehensive taxonomic revision and the first phylogenetic analysis with total evidence for the genus to assess its monophyly and evolutionary relationships among species. Phylogenetic hypotheses were reconstructed using a combined dataset of 2,082 characters, integrating external morphology with five molecular markers (28S, WING, H3, 16S, and COI) under the Maximum Likelihood and Bayesian Inference approaches. Parsimony analysis was performed for the morphological data. The results indicate a complex phylogenetic signal: while Guaranyperla was consistently recovered as a well-supported monophyletic clade, Tupiperla was recovered as paraphyletic in analyses that incorporated morphological data. This instability is attributed to the "Haeckelian deficit," a critical lack of nymph descriptions and taxon sampling. In contrast, concatenated molecular analysis recovered Tupiperla as a monophyletic entity, comprising four main lineages (Clades C, E, F, and G). Taxonomically, the genus is revised to include 33 species, including the description of eight new species and the diagnosis of the genus. Despite the conflict between the datasets, Guaranyperla is maintained as a valid genus.

Keywords: Total-evidence phylogeny; Maximum Likelihood and Bayesian inference; Neotropical stoneflies; Molecular markers (COI, 16S, 28S, H3, WING).

RESUMO

SARMENTO, Felipe Ribeiro Pereira, M.Sc., Universidade Federal de Viçosa, fevereiro de 2026. **Revisão e Filogenia de *Tupiperla* Froehlich, 1969 (Plecoptera: Gripopterygidae) com base em dados moleculares e morfológicos**. Orientador: Frederico Falcao Salles. Coorientadora: Daniela Maeda Takiya.

O gênero Tupiperla Froehlich, 1969 representa uma das linhagens mais diversas de Gripopterygidae neotropicais (Insecta: Plecoptera), porém sua sistemática tem sido dificultada pela instabilidade taxonômica e pela falta de uma análise filogenética envolvendo as suas espécies. Este estudo apresenta uma revisão taxonômica abrangente e a primeira análise filogenética com evidências totais do gênero para avaliar seu monofiletismo e relações evolutivas entre as espécies. As hipóteses filogenéticas foram reconstruídas utilizando um conjunto de dados combinado de 2.082 caracteres, integrando a morfologia externa com cinco marcadores moleculares (28S, WING, H3, 16S e COI) sob as abordagens de Máxima Verossimilhança e Inferência Bayesiana. Para os dados morfológicos foi feita análise de Parcimonia. Os resultados indicam um sinal filogenético complexo: enquanto Guaranyperla foi consistentemente recuperado como um clado monofilético bem suportado, Tupiperla foi recuperado como parafilético nas análises que incorporaram dados morfológicos. Essa instabilidade é atribuída à "deficit haeckeliano", uma carência crítica de descrições de ninfas e a defict de amostragem. Em contrapartida, a análise molecular concatenada recuperou Tupiperla como uma entidade monofilética, compreendendo quatro linhagens principais (Clados C, E, F e G). Taxonomicamente, o gênero é revisado para incluir 33 espécies, incluindo a descrição de oito novas espécies e o diagnóstico do gênero. Apesar do conflito entre os conjuntos de dados, Guaranyperla é mantido como um gênero válido.

Palavras-chave: Filogenia de evidência total; Inferência de máxima verossimilhança e bayesiana; Plecópteros neotropicais; Marcadores moleculares (COI, 16S, 28S, H3, WING).

ESTA DISSERTAÇÃO NÃO DEVE SER CONSIDERADA COMO UMA PUBLICAÇÃO NO SENTIDO DOS ARTIGOS 8 E 9 DO ICZN. PORTANTO, QUAISQUER NOMES OU ATOS NOMENCLATURAIS AQUI PROPOSTOS SÃO CONSIDERADOS NULOS PARA OS PRINCÍPIOS DE PRIORIDADE E HOMONÍMIA.

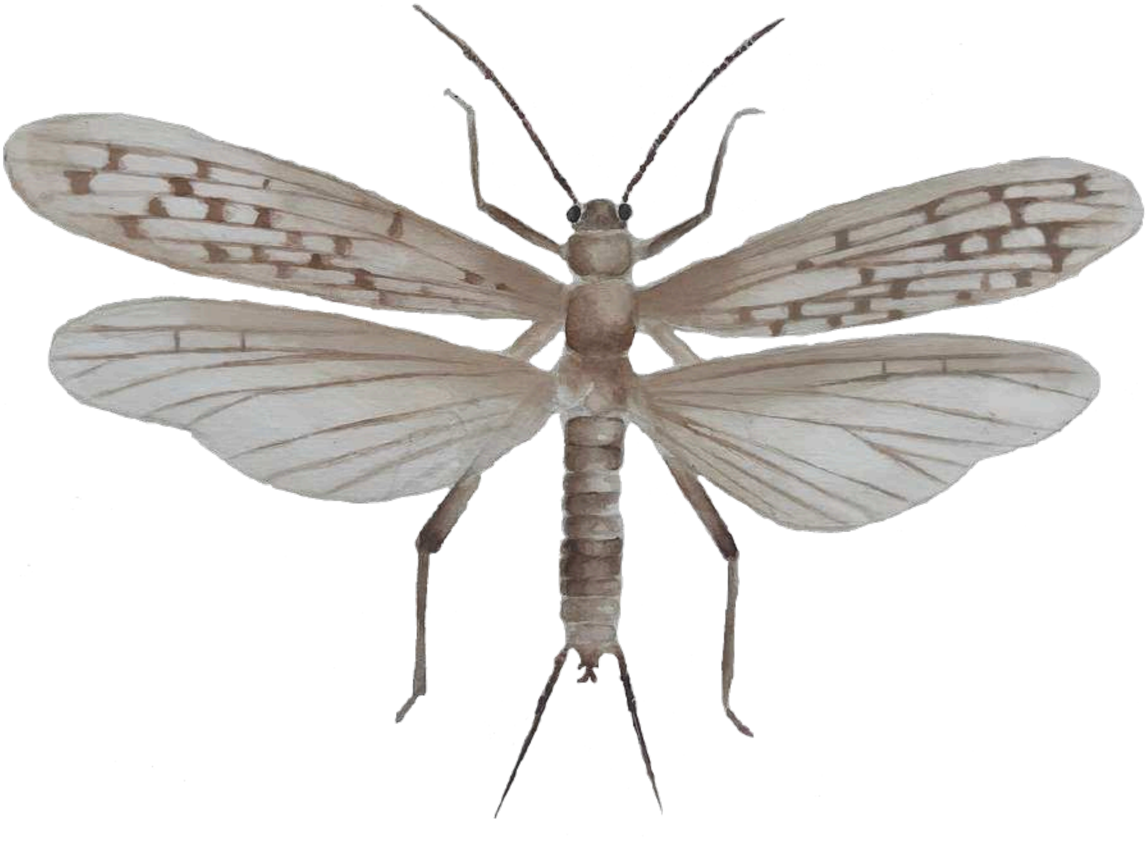


Illustration by

Marianna Medeiros de Andrade Laurindo

SUMÁRIO

INTRODUCTION

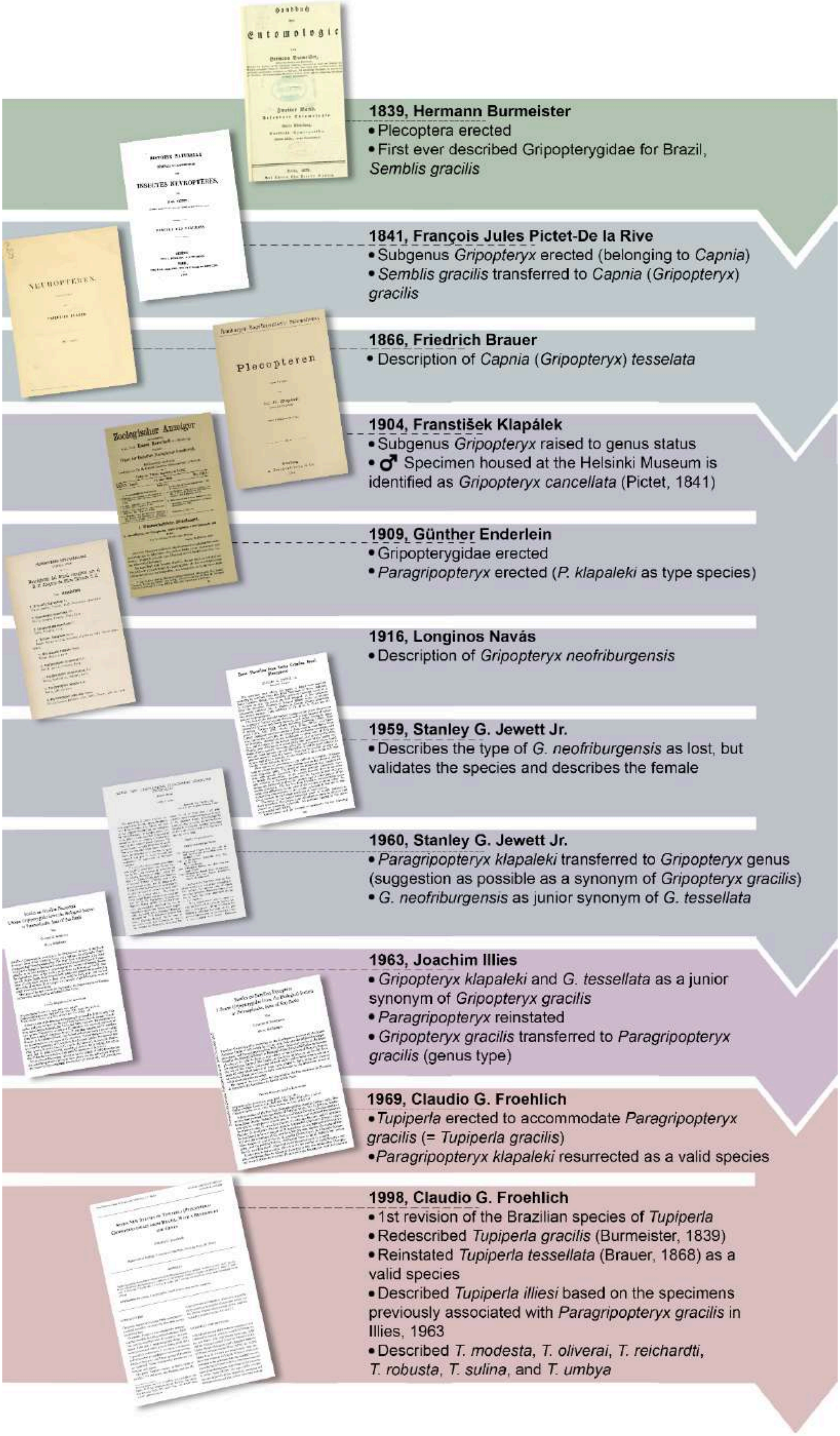
The Neotropical region harbors an invaluable reservoir of biological diversity, yet this richness faces numerous threats (Myers *et al.*, 2000; Antonelli & Sanmartín, 2011; Rull, 2011; Ulloa Ulloa *et al.*, 2017; Raven *et al.*, 2020). Despite considerable scientific efforts, a large portion of this biodiversity remains undocumented (e.g., Buck, 2006; van Nieukerken e*t al.*, 2016; Feitosa *et al.*, 2017). These knowledge gaps are especially evident in highly diverse groups such as insects, which represent one of the most species-rich lineages on Earth (Stork, 2018; Mayhew, 2007; Li & Wiens, 2023). Aquatic insects, a broad artificial assemblage that unifies several unrelated lineages, encompass approximately 100,000 described species across 12 orders (Balian *et al.*, 2008; Dijkstra *et al.*, 2014). Within this assemblage, Plecoptera Burmeister, 1839 is the third largest strictly aquatic order and currently comprises over 4,000 extant species in 17 families (DeWalt *et al.*, 2024). Despite their ecological and evolutionary significance, major gaps persist in our understanding of their diversity and phylogenetic relationships (Eichert *et al.*, 2025).

Taxonomic history of Grypopterygidae

Understanding the current diversity and evolutionary relationships of Plecoptera requires revisiting their taxonomic foundations. The genus *Tupiperla* Froehlich, 1969 is deeply rooted in the early development of plecopteran systematics, with its history extending nearly two centuries to the first modern treatments of the order. In 1839, Hermann Burmeister erected Plecoptera and described *Semblis gracilis* Burmeister, 1839, a species that later became central to the taxonomic history of Gripopterygidae and *Tupiperla*. Nineteenth-century contributions by Pictet (1841) and Brauer (1866) refined these early classifications, while the early twentieth century was marked by extensive taxonomic restructuring by Klapálek (1904), Enderlein (1909), and Navás (1916), who repeatedly elevated, synonymized, and redefined genera and families, often based on limited material. Mid-century revisions by Jewett (1959 and 1960) and Illies (1963) further modified these concepts, sometimes reversing earlier decisions and underscoring persistent uncertainty in species identities and generic limits. This complex trajectory culminated in Froehlich's late twentieth-century revisions (1969, 1998), which formally established *Tupiperla* as a distinct genus and redefined its species composition. Altogether, this nearly 187-year history reflects the gradual accumulation of taxonomic hypotheses shaped by shifting concepts, incomplete character sampling, and evolving taxonomic knowledge; a summary is presented in Figure 1, and further details are explored in the following section.

Plecoptera was originally described by Burmeister (1839) in the Entomologik Handbook, who characterized it as occupying an intermediate taxonomic position. Burmeister (1839) writes “Plecoptera are connected to Orthoptera by their chitinous, bidentate mandibles and to Trichoptera by wing morphology and venation, even though there are similarities in wing venation, important differences prevent their unification with Trichoptera”. So Burmeister (1839) adds “Plecoptera representatives have rigid mandibles, an expanded anal field on hind wings, and active nymphs, similar to Orthoptera. In contrast, Trichoptera possess membranous mouthparts in the adult stage and a quiescent pupa, traits shared with Neuroptera”. Then Burmeister (1839) concluded “This morphological and developmental dichotomy places Plecoptera closer to Orthoptera, justifying their separation from Trichoptera despite their closer evolutionary ties, aquatic life phase, compared with other insect orders in the knowledge of the time”.

Burmeister (1839) placed all known Plecoptera within the Perlidae Latreille, 1802 family and two genera: *Perla* Geoffroy, 1762 and *Sembilis* Fabricius, 1775. He distinguishes the two genera based on the following characteristics of the adults: *Perla* with membranous mouthparts and long maxillary palps, and *Sembilis* with sclerotic mouthparts and short maxillary palps. One new species from Brazil was described within the latter genus, *Sembilis gracilis* Burmeister 1839 (Figure 2). This species is distinguished from other congeners by its numerous transverse veins with broad brown margins, but also by its short cerci of 12 articles.



1839, Hermann Burmeister
- Plecoptera erected
- First ever described Gripopterygidae for Brazil, *Semblis gracilis*

1841, François Jules Pictet-De la Rive
- Subgenus *Gripopteryx* erected (belonging to *Capnia*)
- *Semblis gracilis* transferred to *Capnia* (*Gripopteryx*) *gracilis*

1866, Friedrich Brauer
- Description of *Capnia* (*Gripopteryx*) *tesselata*

1904, Franstišek Klapálek
- Subgenus *Gripopteryx* raised to genus status
- ♂ Specimen housed at the Helsinki Museum is identified as *Gripopteryx cancellata* (Pictet, 1841)

1909, Günther Enderlein
- Gripopterygidae erected
- *Paragripopteryx* erected (*P. klapaleki* as type species)

1916, Longinos Navás
- Description of *Gripopteryx neofriburgensis*

1959, Stanley G. Jewett Jr.
- Describes the type of *G. neofriburgensis* as lost, but validates the species and describes the female

1960, Stanley G. Jewett Jr.
- *Paragripopteryx klapaleki* transferred to *Gripopteryx* genus (suggestion as possible as a synonym of *Gripopteryx gracilis*)
- *G. neofriburgensis* as junior synonym of *G. tessellata*

1963, Joachim Illies
- *Gripopteryx klapaleki* and *G. tessellata* as a junior synonym of *Gripopteryx gracilis*
- *Paragripopteryx* reinstated
- *Gripopteryx gracilis* transferred to *Paragripopteryx gracilis* (genus type)

1969, Claudio G. Froehlich
- *Tupiperla* erected to accommodate *Paragripopteryx gracilis* (= *Tupiperla gracilis*)
- *Paragripopteryx klapaleki* resurrected as a valid species

1998, Claudio G. Froehlich
- 1st revision of the Brazilian species of *Tupiperla*
- Redescribed *Tupiperla gracilis* (Burmeister, 1839)
- Reinstated *Tupiperla tessellata* (Brauer, 1868) as a valid species
- Described *Tupiperla illiesi* based on the specimens previously associated with *Paragripopteryx gracilis* in Illies, 1963
- Described *T. modesta*, *T. oliverai*, *T. reichardti*, *T. robusta*, *T. sulina*, and *T. umbya*

Figure 1 - Timeline of the taxonomic research done in *Tupiperla* until 1998.

Pictet (1841) revised the family Perlidae, reinstaining old genera and creating new additional genera to replace the two genera system. He reassigned many species formerly placed in *Sembilis*. Pictet (1841) placed species without cerci in the reinstated *Nemura* Latreille, 1796, while those with long cerci were assigned to *Capnia* Pictet, 1841, a genus newly described in that work. *Capnia* was considered, by Pictet (1841), to have intermediate characteristics between *Perla* and *Nemura*. According to Pictet, *Capnia* possesses the cerci of *Perla* and the palpi of *Nemura*, thereby distinguishing it from both. However, it aligned more closely with *Nemura* because, following the taxonomic thoughts on the importance of characters discussed by Burmeister (1839), palpal characteristics outweighed the presence of cerci according to Pictet. Pictet (1841) also observed that all species in *Capnia* shared uniform black coloration and a posture and general appearance similar to those of *Nemura*. Some species, on the other hand, had short-winged males. The genus was subdivided into *Capnia* (*sensu stricto*), with forewings lacking transverse veins, and *Capnia* (*Gripopteryx*), with reticulated forewings containing numerous transverse veins (Pictet, 1841).

The subgenus *Gripopteryx* Pictet, 1841 was originally categorized based on wing characteristics, and the female's abdomen ending in a club-shaped subgenital plate on sternum 8. At that time, the subgenus contained two species with strong venational similarities: the type species, *Capnia* (*Gripopteryx*) *cancellata* Pictet, 1841 and *C.* (*Gripopteryx*) *gracilis* (Burmeister, 1839) (Figure 2). He remarked that *C.* (*Gripopteryx*) *gracilis* is much smaller and more slender than *C.* (*Gripopteryx*) *cancellata*. Incidentally, the abdomen was poorly preserved in the specimens examined by Pictet (1841) (Figure 2).

Later, Brauer (1866) described two new species: *Capnia* (*Gripopteryx*) *reticulata* Brauer, 1866 and *C.* (*Gripopteryx*) *tessellata* Brauer, 1866 (Figure 3). The latter was described based on a female, providing a more extensive description of the wings and veins. He pointed out that Pictet (1841) had confused the sexes of all species from the *Capnia* (*Gripopteryx*), probably because the males of *Capnia* (*Gripopteryx*), in contrast to the northern *Capnia* (*sensu stricto*) species, were also winged. Concerning the club-shaped organs attributed by Pictet (1841) to the female of *Gripopteryx*, Brauer (1866) stated, "I consider identical to these lobes (from males), and therefore Pictet's female *Gripopteryx* should be considered males". These lobes were probably the structures we now call paraprocts.

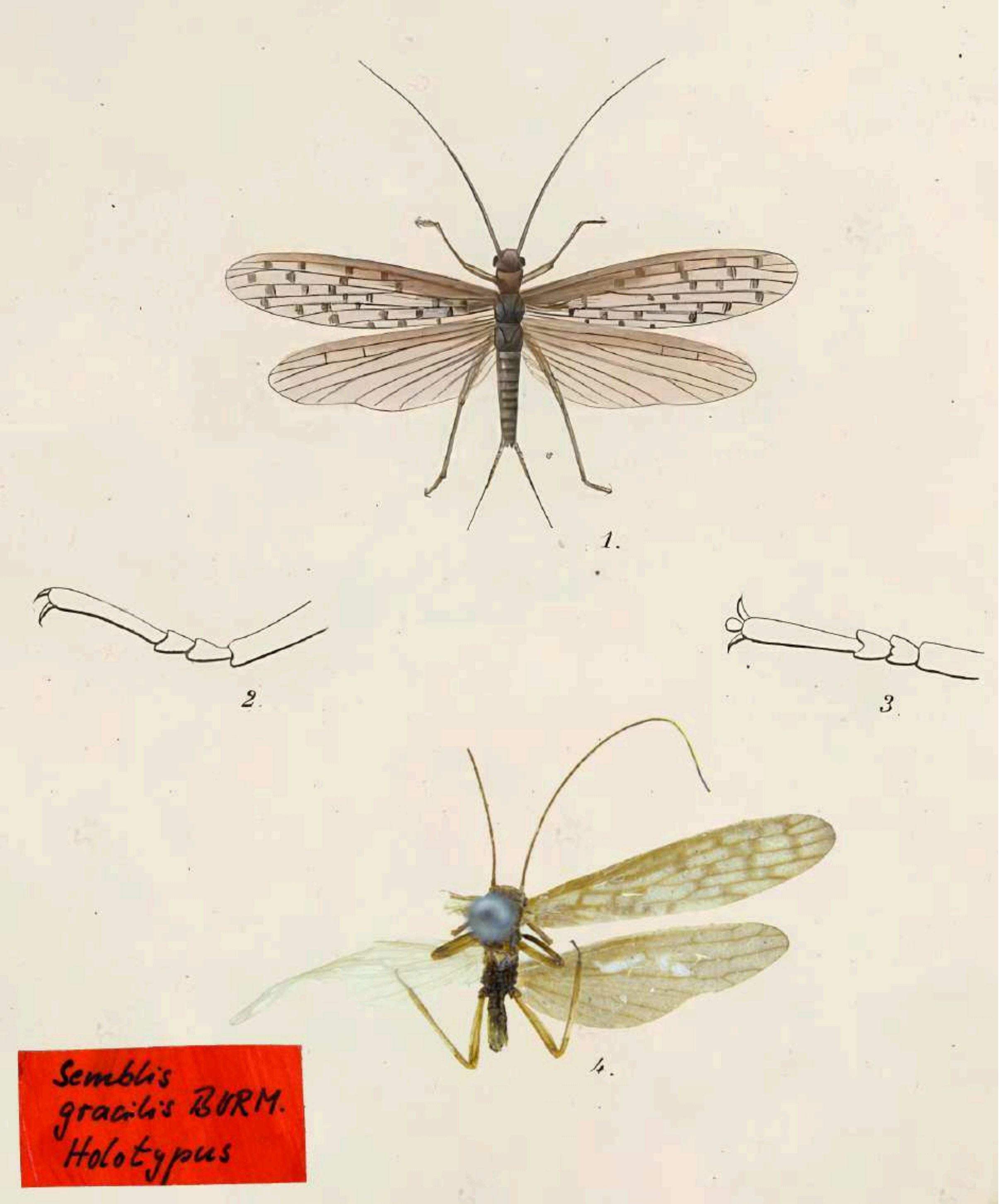


Figure 2 - Illustrations of the holotype of *Sembilis gracilis* Burmeister 1839 1 - Specimen described by Mr. Burmeister, 2 and 3. - Foreleg seen in lateral and dorsal view (Pictet 1841). 4. Holotype of *Sembilis gracilis* in dorsal view. © by Zentralmagazin Naturwissenschaftlicher Sammlungen / Natural Sciences Collections (ZNS) / Dr. Frank D. Steinheimer; photos by PD Dr. Hendrik Müller; published with permission.

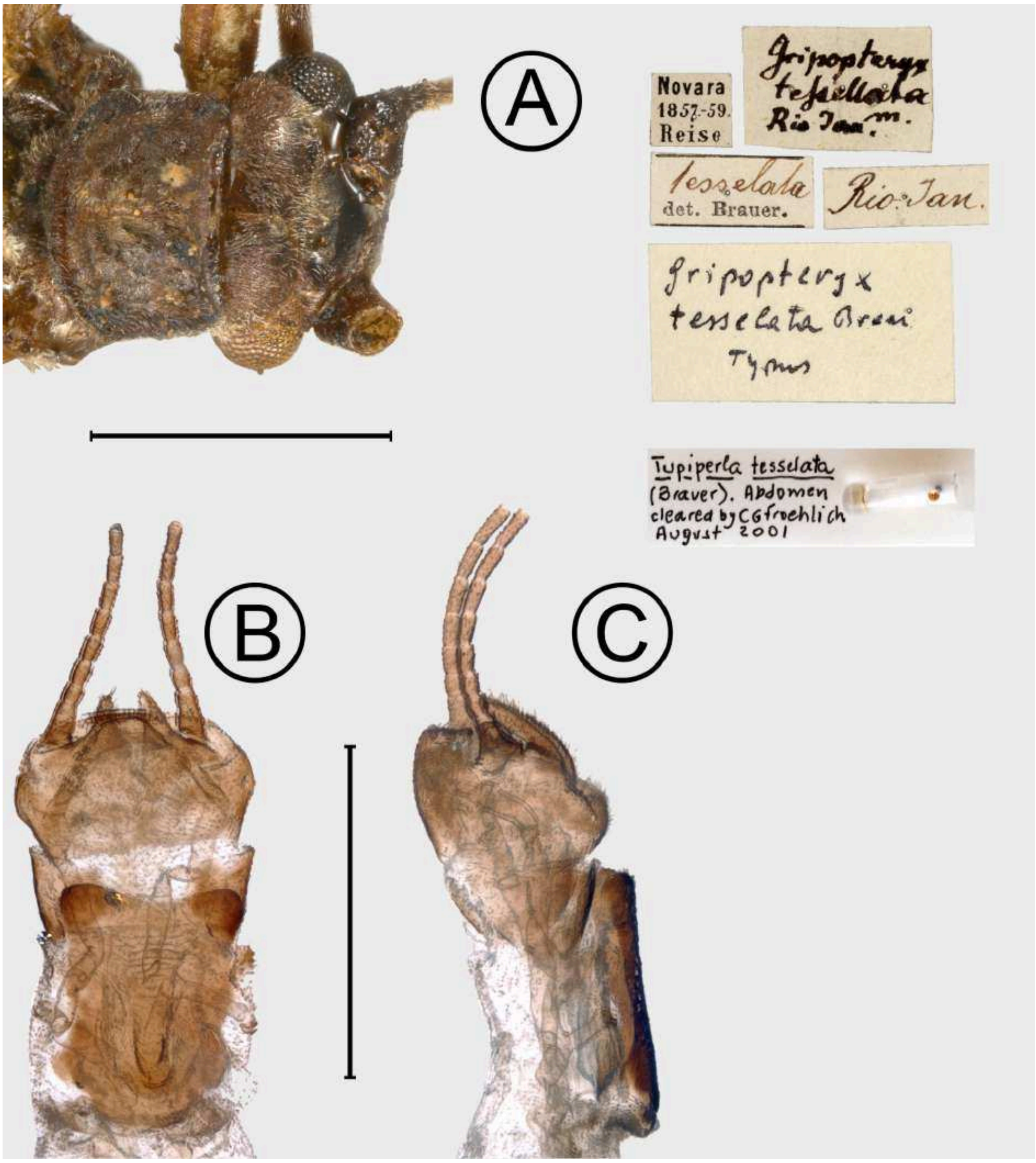


Figure 3 - Holotype of *Tupiperla tessellata* A - head and pronotum in dorsal view; B and C - terminalia in ventral and lateral views, respectively—scale bar: 1 mm. © by Natural History Museum Vienna, NOaS Image Collection / H. Bruckner; published with permission.

Klapálek (1904) elevated *Gripopteryx* to generic rank and provided the following diagnostic characteristics: “The numerous transverse veins at the wingtip were characterized by Pictet (1841), and this characteristic was so striking that it allowed us to easily recognize all the species belonging to it.” Among other features, “The filiform palps and the distinctly segmented, though shortened, cerci were very consistent. The relative length of the tarsal segments was quite variable, as in the genus *Capnia* (cf. *Capnia nigra* Pictet, 1841 and *Capnia pygmaea* Burmeister, 1839)".

The structure of the male genital appendages was described as "quite peculiar" and, according to Klapálek (1904), represented the "initial ancestral stage" of these organs for the entire Plecoptera group Filipalpia [first mention of a group that Klapálek would later establish (Klapálek, 1909), including families with fully functional mouthparts in the adult stage, in contrast to the group Subulipalpia (or Setipalpia)].

Klapálek (1904) gave the following description of the terminalia of *Gripopteryx*: "The ninth ventral arch was only slightly elongated and formed a short, rounded subgenital plate. The tenth ring narrowed towards the abdominal side and merged into two generally saber-shaped, upwardly curved extensions. The segment was more or less elongated dorsally and bore a robust, knob-shaped supraanal lobe." Below the supraanal lobe, Klapálek (1904) observed in the single alcohol specimen what he described as "a spoon-shaped appendage, also directed upward; without dissection of the specimen, it was impossible to determine whether this was formed," and, as Klapálek believed, "it was formed by the fused subanal flaps, the eleventh abdominal segment, or represented a process from the ventral surface of the supraanal lobe."

Klapálek (1904) also analyzed the five existing species and described two new ones. For this work, we will focus only on the complementary description of *Gripopteryx tessellata* (Brauer, 1866), which was based on two females. "The wings are narrow and brownish; the forewings have all the transverse veins widely infuscated, giving them a checkered and tessellated appearance, hence the very appropriate name tessellata," Klapálek (1904) also indicated. "There are no transverse veins outside the subcosta on the hindwing. In the female, the eighth segment is elongated into a long subgenital plate." For *G. gracilis*, Klapálek (1904) pointed out that the absence of transverse veins on the hind wings, as observed by Pictet (1841), distinguishes the species from all others".

Enderlein (1909), in his work "Klassifikation der Plecopteren sowie Diagnosen neuer Gattungen und Arten", described the new family Gripopterygidae to allocate the genus *Gripopteryx* and similar genera. The new family was established based on its southern distribution and the venation of the wings "Media of the forewing with a very long, narrow fork, of the hind wing unbifurcated. There are more or less numerous transverse veins in the forewing and hindwing. More than one branch or a forked branch branches off from the basal anal cell.". In this work, Enderlein (1909) divided the family into two subfamilies: Antarctoperlinae, with three genera, and Gripopteryginae, containing *Gripopteryx* and the newly described *Paragripopteryx* Enderlein, 1909. A new genus that differs in the presence of a crossvein in the pterostigma of the forewing and was described based on a single new species, *Paragripopteryx klapaleki* Enderlein, 1909.

In the following years, only a few minor contributions were made to the knowledge of neotropical Gripopterygidae. The first was the description of *Gripopteryx neofriburgensis* by Navás (1916), based on a male specimen. Jewett (1959) described the female of *G. neofriburgensis* and reported that the holotype designated by Navás had been lost. One year later, Jewett (1960) transferred the single species of *Paragripopteryx*, *P. klapaleki*, to the genus *Gripopteryx*, and suggests that it might be a synonym of *G. gracilis*. In the same work, he designated *G. neofriburgensis* as a junior synonym of *G. tessellata*.

Illies (1963) published the first major revision and comprehensive inventory of the South American Gripopterygidae fauna. By comparing all previously described species and examining type specimens, he clarified the taxonomy of most of the species recognized as valid up to that point; nearly half of which were classified under the genus *Gripopteryx*. Initially, 41 species were documented for South America, and after this taxonomic revision, they were reclassified into 10 distinct genera. Of these species, 23 were redescribed, while 18 were considered to be junior synonyms. Additionally, two new subfamilies, 11 new species, and 15 new genera were described, bringing the number of valid species of *Gripopteryx* to three (Illies, 1963).

Proposal of *Tupiperla* Froehlich, 1969

Illies (1963) transferred *Gripopteryx gracilis* to *Paragripopteryx*, and formalized it as a junior synonym of *G. tessellata* and also *G. klapaleki*, reinstating the genus *Paragripopteryx* and designating *Paragripopteryx gracilis* as its type species, instead of the *P. klapaleki* as it was previously designated because of the act of synonym. In his redescription, based on material from the Estação Biológica de Boracéia, São Paulo, Brazil, Illies pointed out that it is an extraordinarily variable species, represented by three morphotypes (Figure 4).

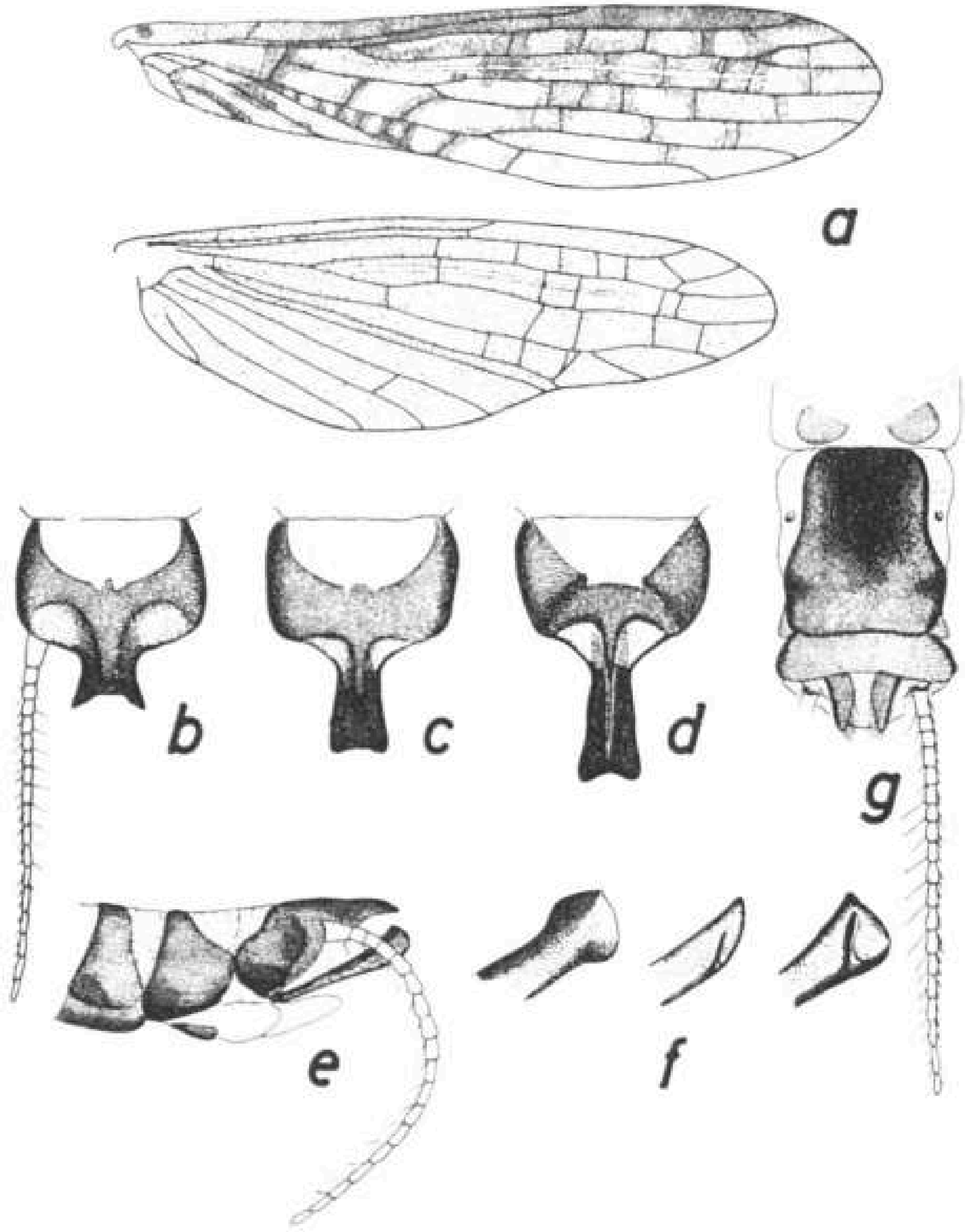


Figure 4 - The three morphotypes described by Illies 1963 for *Paragripopteryx gracilis*. Morphotype I (B and F1 form Illies, 1963); Morphotype II (C and F2 form Illies, 1963); Morphotype III (D, E and F3 form Illies, 1963).

Based on the specimens of *Paragripopteryx gracilis* described by Illies (1963), not the type material of *Semblis gracilis* Burmeister, 1839, Professor Claudio Gilberto Froehlich erected a new genus, *Tupiperla* Froehlich, 1969, 139 years after the Burmeister's original description of that species (Froehlich, 1969). Initially, *Tupiperla* was a monotypic genus. It was characterized in both adults and nymphs by a pronotum narrower than the head, presence of a distoventral spine on the femora, absence of a dorsal row of long hairs on the femora and tibiae, and absence of a row of spinules basal to the large apical teeth on the laciniae. Adults were further distinguished by the absence of an epiproct in males (Froehlich, 1969).

Froehlich (1969) mentioned that, in the field, adults of this species can be readily distinguished from those of *Paragripopteryx* by their longer antennae, lighter coloration, and the dark spots encircling most cross-veins in the forewings. When the wings are folded, this spot pattern resembles a mosaic, which justifies the specific name, *G. tessellata*, given by Brauer (1866). Among the specimens examined by Froehlich (1969), the shape of the posterior process of tergum 10 and the paraprocts of adult males remained constant, differing from the variation reported by Illies (1963).

In the 1990s Froehlich came back to the studies with Gripopterygidae. The first two with *Gripopteryx* (Froehlich, 1990, 1993), one with *Paragripopteryx* (Froehlich, 1994), and the last one the revision of *Tupiperla* (Froehlich, 1998). In this revision, Froehlich (1998) describes the male of *T. gracilis* based on the holotype (Figure 2) and the description made by Zwick (1972), including the probable collection site at Rio de Janeiro (Froehlich, 1998). The holotype was in relatively good condition at the time, and housed at the Burmeister collection of the Habsburg Museum. Froehlich (1998) also provides the first drawings of the terminalia of the type species (Figs. 1-3 in Froehlich, 1998).

Froehlich (1998) revalidates *Gripopteryx tessellata* (Brauer, 1866), previously synonymized under *Paragripopteryx gracilis* by Illies (1963) together with *Paragripopteryx klaplaleki*. Froehlich (1969) revalidated *P. klapaleki* and described *Tupiperla*, The only remaining junior synonym was *G. tessellata* for *Tupiperla gracilis*. However, based on the description of Brauer (1866), Forehlich proposed a new combination *T. tessellata,* for which the holotype is kept in the Vienna Museum (Figure 3). The curator of the museum examined it and states: “The type of *Gripopteryx tessellata* is in very bad condition and held together with a lot of glue, the abdomen is fixed obliquely and somewhat deformed” (Froehlich, 1998). There is one character in Brauer’s (1866) original description “...Antennae longer than the forewings” which the material analyzed by Froehlich (1998) conformed. *Tupiperla gracilis*, the only other species collected in the area, has antennae about as long as the forewings (Froehlich, 1998), this was sufficient evidence for the revalidation of *T. tessellata* for Froehlich (1998).

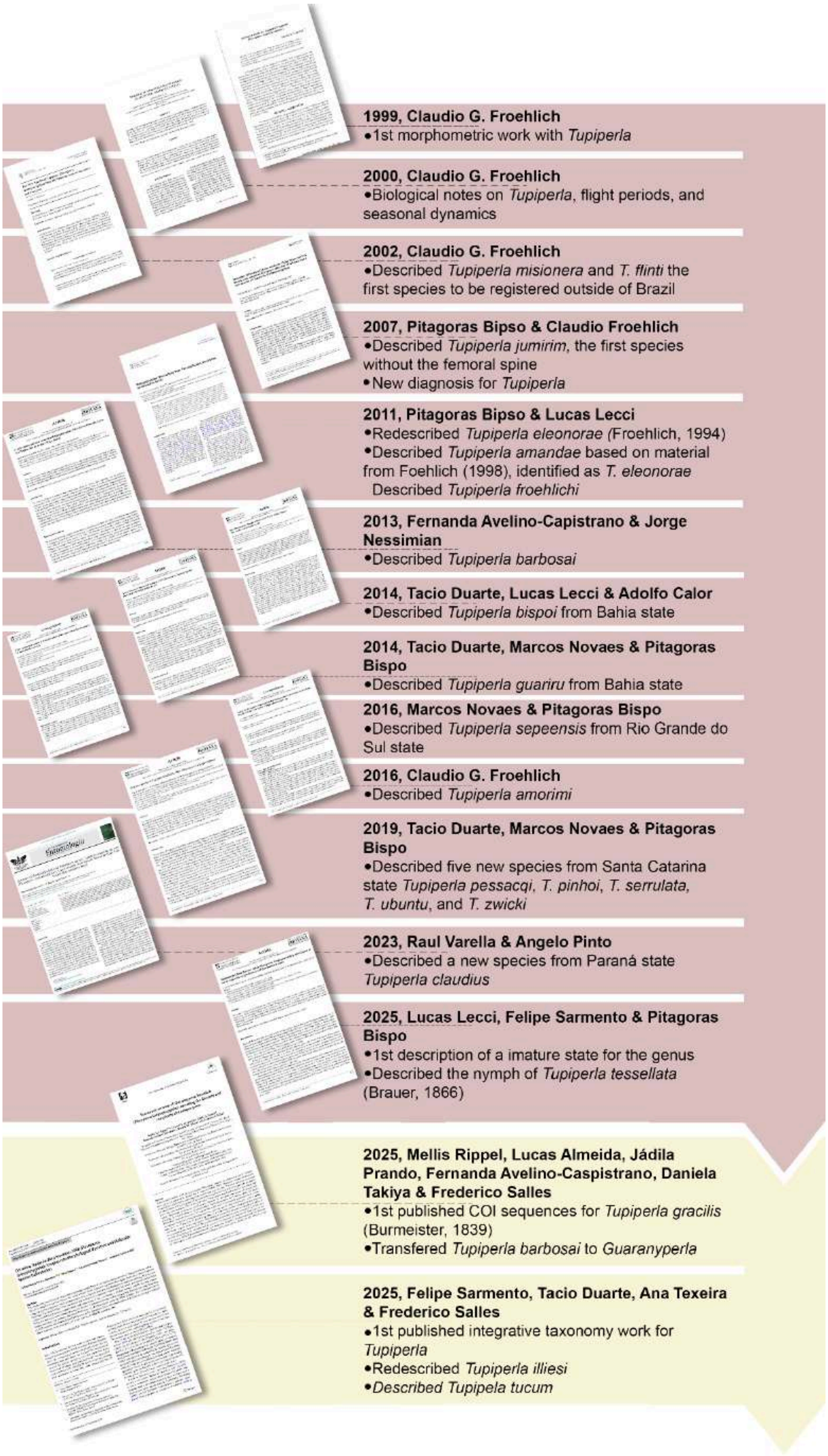
This difference in the proportion of the size of the antennae and the size of the wings, led to Froehlich’s (1998) decision to associate the sexes of *T. tessellata* and clarified that *G. neofriburgensis* Navás, 1916, a species described based on a male, was a synonym of *T.*

tessellata, a species described based on a female (Figure 3). This conclusion was based on the drawings of the male terminalia made by Navás (1916), as previously proposed by Jewett (1960). Froehlich examined the holotype of *T. tessellata* in 2001 and states "I succeeded in loosening the specimen from the card to which it was glued and cleared the terminalia. The shape of the female subgenital plate (Figure 3) confirmed my decision." (Froehlich, 2009).

Froehlich (1998) also transfers the species described by himself in 1994, *Paragripopteryx eleonorae* Froehlich, 1994 to *Tupiperla* and reported "The original description was based on teneral specimens, and a reexamination of the type series showed that it was misplaced generically" and makes new drawings of the species.

Froehlich (1998) also describes seven new species. One of these species, *Tupiperla illiesi* Froehlich, 1998, was described based on the specimens examined by Illies (1963) and Froehlich (1969) while treating *Paragripopteryx gracilis* and *Tupiperla gracilis* respectively. The drawings of *P. gracilis* (Illieis, 1963 Figure 16) and *T. gracilis* (Forehlich, 1969 Figure 26-28) in both papers are in fact this new species and no new drawings were made at the time of the description. Froehlich (1998) is a significant marker in the study of *Tupiperla* and the beginning of the modern era of taxonomic discussion. After this revision, all the subsequent works base the nomenclature of the structures on those used here. A timeline of important taxonomic studies after 1998 is summarized in Figure 5.

Later contributions expanded the genus to 26 valid species (Froehlich, 1999; 2000; 2002; 2016; Bispo & Froehlich, 2007; Bispo & Lecci, 2011; Avelino-Capistrano & Nessimian, 2013; Duarte, Lecci & Calor, 2014; Duarte, Bispo & Calor, 2014; Novaes & Bispo, 2016; Duarte, Novaes & Bispo, 2019; Varella & Pinto, 2023; Lecci, Sarmento & Bispo, 2025). It is noteworthy to mention that Bispo and Froehlich (2007) describes the first species of *Tupiperla* where the male specimens do not show the femur spine and the female show only a small spine. And in only recently a proper association between immatures and adult semaphoronts was published, the description of the nymph for *T. tessellata* (Lecci, Sarmento & Bispo, 2025).



1999, Claudio G. Froehlich
- 1st morphometric work with *Tupiperla*

2000, Claudio G. Froehlich
- Biological notes on *Tupiperla*, flight periods, and seasonal dynamics

2002, Claudio G. Froehlich
- Described *Tupiperla misionera* and *T. flinti* the first species to be registered outside of Brazil

2007, Pitagoras Bipso & Claudio Froehlich
- Described *Tupiperla jumirim*, the first species without the femoral spine
- New diagnosis for *Tupiperla*

2011, Pitagoras Bipso & Lucas Lecci
- Redescribed *Tupiperla eleonorae* (Froehlich, 1994)
- Described *Tupiperla amandae* based on material from Foehlich (1998), identified as *T. eleonorae*

Described *Tupiperla froehlichi*

2013, Fernanda Avelino-Capistrano & Jorge Nessimian
- Described *Tupiperla barbosai*

2014, Tacio Duarte, Lucas Lecci & Adolfo Calor
- Described *Tupiperla bispoi* from Bahia state

2014, Tacio Duarte, Marcos Novaes & Pitagoras Bispo
- Described *Tupiperla guariru* from Bahia state

2016, Marcos Novaes & Pitagoras Bispo
- Described *Tupiperla sepeensis* from Rio Grande do Sul state

2016, Claudio G. Froehlich
- Described *Tupiperla amorimi*

2019, Tacio Duarte, Marcos Novaes & Pitagoras Bispo
- Described five new species from Santa Catarina state *Tupiperla pessacqi*, *T. pinhoi*, *T. serrulata*, *T. ubuntu*, and *T. zwicki*

2023, Raul Varella & Angelo Pinto
- Described a new species from Paraná state *Tupiperla claudius*

2025, Lucas Lecci, Felipe Sarmento & Pitagoras Bispo
- 1st description of a imature state for the genus
- Described the nymph of *Tupiperla tessellata* (Brauer, 1866)

2025, Mellis Rippel, Lucas Almeida, Jádila Prando, Fernanda Avelino-Caspistrano, Daniela Takiya & Frederico Salles
- 1st published COI sequences for *Tupiperla gracilis* (Burmeister, 1839)
- Transfered *Tupiperla barbosai* to *Guaranyperla*

2025, Felipe Sarmento, Tacio Duarte, Ana Texeira & Frederico Salles
- 1st published integrative taxonomy work for *Tupiperla*
- Redescribed *Tupiperla illiesi*
- *Described Tupipela tucum*

Figure 5 - Timeline of the modern works done in *Tupiperla* after the revision of Froehlich (1998).

Currently, therefore, the genus is composed of 26 species (Duarte *et al.*, 2024 and Duarte *et al.*, in press), distributed in the mountainous areas of the Brazilian coast from south to the northeast regions, reaching inland areas of Brazil and northeastern Argentina (Duarte *et al.*, 2024). The nymph stage is only known for 2 species (Lecci *et al.*, 2025; Almeida *et al.*, in press), and the diagnosis is as follows: all developmental stages (males, females, and nymphs) share: (1) a pronotum narrower than the head and (2) the presence of a ventral spine on the femur (though this spine may be absent or reduced in some specimens of *T. jumirim*; Bispo & Froehlich, 2007). Adult-specific characters include: (1) the absence of pterostigmatic cross veins (though these cross veins may be present in *T. serrulata* Duarte *et al.*, 2019) and (2) forewings with a distinctive pattern of broad, squarish dark borders along most cross veins. Male-specific characters comprise: (1) the lack of a sclerotized epiproctum and (2) a relatively long extension of tergum 10, ending in two separate teeth (Froehlich, 1969; Bispo & Lecci, 2011; Duarte *et al.*, 2019).

Phylogenetic and taxonomic studies on Neotropical plecopterans

The first molecular phylogeny proposed for the order was the the six-gene Sanger dataset assembled by Terry (2003) (COII, 12S, 16S, 18S, 28S, and H3), which recovered several traditionally recognized groups, but also revealing instances of conflict with morphology, particularly in the placement and internal coherence of southern lineages. Subsequent studies, such as McCulloch *et al.* (2016), expanded taxon sampling within Antarctoperlaria using mitochondrial COI and nuclear 18S rRNA and H3, and obtained strong molecular support for the subdivision of this clade into Gripopterygoidea (Gripopterygidae + Austroperlidae), a result broadly congruent with morphological expectations but based on limited Neotropical representation (a single *Gripopteryx* species). More recent phylogenomic efforts using complete mitochondrial genomes (e.g., Ding *et al.*, 2019) further stabilized several deep nodes across Plecoptera and increased overall support values for interfamily relationships, yet continued to suffer from sparse sampling of Neotropical taxa, leaving the internal structure of Gripopterygidae and the placement of many Neotropical genera largely untested.

Recent research has ushered in a second renaissance in the taxonomic knowledge of *Tupiperla* with the works using molecular tools for integrative taxonomy, the delimitation of the two morphotypes of *T. illiesi* as two distinctive species (Sarmento *et al.*, 2025), the synonym of *T. amandae* under *T. eleonorae* with description of teneral stages (Duarte *et al.*, in press), description of the nymph and morphological variation in *T. gracilis* (Almeida *et al.*, in press), and the revision of the genus *Guaranyperla* and a new combination for *G. barbosai* that was previously under *Tupiperla* (Rippel *et al.*, 2025). These papers were crucial to delimit species boundaries within *Tupiperla* as of the morphological variation expected for the species of the genus.

However, key uncertainties persisted, particularly regarding the group's systematics. Since the description of the genus *Guaranyperla* Froehlich, 2001, the position and monophyly of *Tupiperla* have been the subject of ongoing discussion. Boundaries between the two genera remained narrow and indistinct, being more easily recognized in the immature stages. The only formal analyses addressing these relationships were the morphological phylogenies conducted by Duarte, one focused on *Tupiperla* (Duarte, 2014) and the other on the subfamily Gripopteryginae (Duarte, Bispo & Pessacq, 2025). In both studies, the genus *Tupiperla* was not recovered as a natural (monophyletic) group. In the first analysis, *Guaranyperla* was recovered as monophyletic, whereas *Tupiperla* appeared paraphyletic in relation to *Guaranyperla*. In the latter study, both genera were recovered in an unresolved polytomy.

OBJECTIVES

General

This dissertation addresses two primary questions: (i) Is *Tupiperla* monophyletic? and (ii) What is its relationship to *Guaranyperla*? In addition, it aims to clarify relationships among *Tupiperla* species and to examine the evolution of selected diagnostic morphological characters.

Specific

- To revise the genus *Tupiperla*, reevaluating its taxonomic status and that of all species currently included in the genus.
- To propose a phylogenetic hypothesis for *Tupiperla* species based on combined molecular and morphological data.
- To infer the phylogenetic placement of *Guaranyperla* and to test its monophyly.

MATERIAL AND METHODS

Taxon sampling

The ingroup taxa included 33 species, representing 15 described and eight new species assigned to *Tupiperla*. The following type species were included in the datasets, *Paragripopteryx klapaleki* Enderlein, 1909, *Guaranyperla guapiara* Froehlich, 2001, and *Tupiperla gracilis* (Burmeister, 1839). Sixteen terminal taxa were included as outgroups, representing Perlidae (used to root the trees) and Diamphonodea and other five genera of Gripopterygidae (*Aubertoperla*, *Gripopteryx*, *Guaranyperla*, *Paragripopteryx*, and *Teutoperla*). Undescribed species were included in the analyses due to the unavailability of representatives of formally described species or when significant morphological variations were observed compared to species nominally identified.

A complete list of specimens analysed to obtain morphological and molecular information is provided in Supplementary Material S1. The material examined belong to the following collections:

UFVB: Coleção do Museu de Entomologia da Universidade de Viçosa, Minas Gerais, Brasil.

CIACGF: Collection of Aquatic Insects "Prof. Dr. Cláudio Gilberto Froehlich" Laboratório de Biologia Aquática, Universidade Estadual Paulista (UNESP), Assis, São Paulo, Brasil.

DZRJ: Coleção Entomológica Prof. José Alfredo Pinheiro Dutra, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil.

MZUSP: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil.

Abbreviations

Abbreviations for morphological terms are as follows: AA1 –First anterior anal vein; AA2 –Second anterior anal vein; Ant–Antennae; Brls–Black rod-like setae; Cc–Cercus; CuA–Anterior cubitus vein; CuP–Posterior cubitus vein; Dt–Denticles; Ep–Epiproct; Fe–Femur; Hd–Head; M–Media vein; Ma–Membranous area; PC–Pterostigmatic cell; Pnt–Pronotum; Pp–Paraprocts; Ptc–Pterostigmatic crossvein; RA–Anterior radius vein; RP–Posterior radius vein; RPc–RP crossvein; Sat–Subapical tooth (paraprocts); Sc–Subcosta vein; Sp–Subgenital plate; T8 –Tergum 8; T9 –Tergum 9; T10 –Tergum 10; T10E –Tergum 10 extension; Tb–Tibia; Ts–Tarsi; Tth–Tooth.

Morphological data

The morphological terminology used largely follows that adopted by Froehlich (1969 and 1998) and was adapted from Duarte (2019, 2020, 2024, and 2025). Characters from head, thorax, and abdomen were analysed in individuals at both larval and adult stages. They were used to propose hypotheses of primary homology (De Pinna, 1991) and then coded in a character matrix in Mesquite v. 2.75 in Nexus format (Maddison & Maddison, 2011). The matrix was also exported to the format employed in the Tree analysis using New Technology software (TNT v. 1.5) (Goloboff & Catalano, 2015). Inapplicable characters were coded as (−), and applicable characters that could not be observed were coded as missing data (?). Contingent characters are represented with * when they are dependent on a previous character. Presentation of characters and their respective character states follow the format proposed by Sereno (2007). The character matrix is shown in Supplementary Material S2.

Descriptions of the immatures and adult females are scarce for most *Tupiperla* species. Although not informative for parsimony, autapomorphic characters were included in the matrix for their potential informativeness in probabilistic analyses (Lewis, 2001; Wright & Hillis, 2014), as well as for future taxonomic work on the group (Yeates, 1992).

Molecular data

Genomic DNA was extracted from specimens preserved in 96–100% ethanol collected between 2009 and 2025. Extractions were made with Qiagen® DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol, but with tissue lysis extended to 48 hours to avoid material maceration. Abdomen and wings were removed before the reactions. Body parts retained before and after extraction were combined in a tube with 100% ethanol and deposited in the original collection as vouchers. Table 1 provides voucher information and GenBank accession numbers from which nucleotide sequences were obtained.

Table 1. Specimens of *Tupiperla* and outgroups with DNA fragments sequenced and used in the analyses, with respective voucher codes, collection locality (in Brazil or Chile), and GenBank accession numbers.

Species	Voucher	Locality	16S	28S	COI	H3	WING
Anacroneuria debilis	ENT156	RJ: Macaé	X	X	X	X	

Aubertoperla illiesi	ENT2167	Chile	X	X	X	X	X
Diamphipnoa helgae	ENT2166	Chile	X	X	X	X	X
Gripopteryx flinti	ENT995	RJ: Macaé	X	X	X	X	X
Gripopteryx garbei	ENT254	RJ: Nova Friburgo	X	X			X
Gripopteryx maculosa	ENT569	ES: Santa Teresa	X	X	X	X	X
Gripopteryx reticulata	ENT564	RJ: Macaé	X			X	X
Gripopteryx reticulata	ENT588	MG: Alto Caparaó		X	X		
Guaranyperla barbosai	ENT292	RJ: Nova Friburgo	X	X	X	X	X
Guaranyperla guapiara	ENT6682	SP: Ribeirão Grande	X	X	X	X	X
Guaranyperla nitens	ENT6685	SP: Campos do Jordão	X	X	X	X	X
Guaranyperla puri	ENT6510	MG: Ervália	X	X	X	X	X
Paragripopteryx blanda	ENT3584	RJ: Itatiaia	X	X		X	X
Paragripopteryx klapaleki	ENT2179	MG: Alto Caparaó	X	X	X	X	X
Paragripopteryx sp.	ENT290	RJ: Nova Friburgo	X	X	X	X	X
Teutoperla rothi	ENT2168	Chile	X	X	X	X	X
Tupiperla bispoi	ENT1923	BA: Camacan	X	X			
Tupiperla claudius	ME44	PR: Morretes	X	X			
Tupiperla claudius	ME46	PR: Morretes				X	
Tupiperla eleonorae	TD14	SP: Ribeirão Grande	X	X	X	X	X
Tupiperla gracilis	TD105	SP: Campos do Jordão	X	X	X	X	X
Tupiperla illiesi	TD30	SP: Intervales	X		X		X
Tupiperla illiesi	S80	SP: Salesopolis		X		X	
Tupiperla misionera	ENT987	PR: Céu Azul		X		X	
Tupiperla misionera	TD75	PR: Foz do Iguaçu	X		X		X
Tupiperla oliveirai	MNG01	GO: Pirenópolis		X	X		
Tupiperla oliveirai	MNG02	GO: Pirenópolis	X			X	X
Tupiperla pessacqi	ME39	SC: Urubici	X	X	X	X	X
Tupiperla pinhoi	ME06	SC: Urubici	X	X	X	X	X
Tupiperla reichardt	MR02	MG: Poços de Caldas	X	X	X	X	X
Tupiperla robusta	ME58	SP: Campos do Jordão	X	X	X	X	X
Tupiperla sp. nov. 1	ENT599	RJ: Guapimirim	X	X			

Tupiperla sp. nov. 1	ENT7152	RJ: Cachoeira macacu			X	X	X
Tupiperla sp. nov. 2	ENT606	RJ: Macaé		X			X
Tupiperla sp. nov. 3	ENT1924	MG: São Roque de Minas				X	
Tupiperla sp. nov. 3	ENT1925	MG: São Roque de Minas	X	X	X		X
Tupiperla sp. nov. 4	ENT1057	MG: São José do Barreiro	X	X		X	
Tupiperla sp. nov. 5	ME02	MG: Lima Duarte	X	X	X	X	X
Tupiperla sp. nov. 6	ENT1056	MG: São José do Barreiro	X	X	X	X	X
Tupiperla sp. nov. 7	ENT597	RJ: Itatiaia	X	X			X
Tupiperla sp. nov. 8	ENT605	ES: Castelo	X	X	X	X	X
Tupiperla sulina	TD107	SC: Blumenau	X	X	X	X	X
Tupiperla tessellata	MNF07	SP: Jundiai	X	X	X	X	X
Tupiperla tucum	S199	SP: Salesopolis	X	X	X	X	X
Tupiperla umbya	ME34	SP: Ribeirão Grande	X	X	X	X	X

Molecular markers used were based on recent studies of orthopteroids (Mugleston *et al.*, 2017), Plecoptera (Terry, 2003), and other Gripopterygidae (McCulloch *et al.*, 2016), given their potential to resolve relationships within Gripopterygidae. Fragments of five genes were selected: mitochondrial cytochrome c oxidase subunit I (COI) and the ribosomal subunit 16S (16S) and the following nuclear wingless (WING), histone 3 (H3), and the ribosomal subunit 28S rRNA, domain 1 (28S-D1). Primers used for amplification and sequencing, with respective references, are listed in Tab. 2. The extracted DNA solution was subjected to polymerase chain reactions (PCR), using reactions of 25µl, which were composed of: 1µl of each primer, (10mM) 1-2µl extracted DNA, 5µl of Taq green buffer (Promega), 0.5µl dNTPs (10mM, Invitrogen), 4 µl MgCl2 (25mM, Promega), and 0.1µl Taq polymerase (5 U/µl, Promega) diluted in 11.5µl of H2O Milli-Q®. Fragments were amplified using PCR following, in general, these conditions: (1) initial denaturation at 94°C for 3 min; (2) 40 cycles of denaturation at 94°C for 1 min, annealing at 45–57°C for 1 min and extension at 72°C for 2 min; and (3) final extension at 72°C for 5 min. For more detailed protocol see Supplementary Material S3.

Table 2. Primers used for amplification and sequencing of markers sequenced for *Tupiperla* and outgroups, with respective references.

Gene	Primer	Sequence 5′–3′	Source
16S	LR-J-12887	CCGGTYTGAACTCARATCA	Takiya *et al.* 2006
	LR-N-13398	CRMCTGTTTAWCAAAAACAT	Takiya *et al.* 2006
28S	D1	GGAGGAAAAGAAACTAACAAGGATT	Kjer *et al.* 2001
	D1	CAACTTTCCCTTACGGTACT	Kjer *et al.* 2001
COI	LCO-1490	GGTCAACAAATCATAAAGATATTGG	Folmer *et al.* 1994
	C1-J-1718	GGAGGATTTGGAAATTGATTAGTTCC	Simon *et al.* 1994
	HCO-2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al.* 1994
H3	HexAF	ATGGCTCGTACCAAGCAGACGGC	Ogden & Whiting 2003
	HexAR	ATATCCTTGGGCATGATGGTGAC	Ogden & Whiting 2003
WING	Wg550F	ATGCGTCAGGARTGYAARTGYCAYGGYATGTC	Wild & Maddison, 2008
	WgAbRZ	CACTTNACYTCRCARCACCARTG	Wild & Maddison, 2008

PCR was verified through 1% agarose gel electrophoresis and products with positive responses were purified according to ExoSAP-IT™ (Thermo Fisher Scientific, Waltham, United States) protocol and sent to Macrogen Inc. (Seoul, Republic of Korea) or ACTGene Análises Moleculares Ltda. (Alvorada, Brasil) for sequencing. Forward and reverse electropherograms of DNA sequences were edited and combined into a consensus sequence using GeneStudio v2.2.0. These sequences were then compared with the NCBI nucleotide sequence database using the Basic Local Alignment Search Tool (BLAST) to confirm taxa and loci.

Sequence alignments for protein coding genes were performed using the Clustal W algorithm (Larkin *et al.*, 2007; Thompson *et al.*, 1994), implemented in MEGA 12 (Kumar *et al.*, 2024), using default gap opening and extension cost parameters and for the ribosomal genes, the MAFFT (Katoh *et al.*, 2013) using the algorithm Q-INS-i (Katoh *et al.*, 2019). Final editing was also performed in MEGA 12. The final alignment of COI was 567 bp long with 29 sequences (19 from *Tupiperla*), 16S was 426bp long (21 from *Tupiperla*), WING was 399bp long with 34 sequences (20 from *Tupiperla*), H3 was 345bp long with 29 sequences (16 from *Tupiperla*), and 28S was 297 bp long with 36 sequences (23 from *Tupiperla*). Complete information about sequences analyzed here are provided in Table 1.

Cladistic analysis

Parsimony analyses were run only on the morphological dataset, considering all characters as nonadditive (Fitch, 1971). It was analyzed using the "Traditional search" command in TNT software, with tree bisection reconnection (TBR) branch swapping, 10,000 replicates, 100 trees saved per replication, and collapsing trees after the search.

Analyses were implemented under an equal weights scheme and implied weighting (IW) against homoplastic characters (Goloboff, 1993; Goloboff *et al.*, 2008). According to Prendini (2003), under different weighting schemes, it is possible to recover more reliable relationships. Thus, we employed the scheme of concavity index variation (k = 3–15) to better understand the topological impacts of optimization and character changes in the most parsimonious trees.

Implied weighting, as introduced by Goloboff (1993), uses a concavity constant (k) to penalize homoplasious characters during tree search, with lower k values imposing harsher down-weighting and higher k values approaching equal weights. Among the values of k analyzed under implied weighting, k = 7 provided the most stable and informative topology. Lower values of k (3-5) produced trees susceptible to homoplastic characters. Higher values of k (13–15), in contrast, excessively down-weighted homoplastic characters, obscuring informative intermediate-level structure (Goloboff *et al.*, 2008; Goloboff, 2014; Ezcurra, 2024).

To estimate branch support, we employed Relative Bremer support (Goloboff and Farris 2001), utilizing 1,000 suboptimal trees up to five steps longer (obtained through the traditional search).

Probabilistic analyses

Maximum likelihood (ML) and Bayesian inference (BI) phylogenetic analyses were performed on four datasets: (1) independent alignments of genes; (2) a concatenated molecular dataset, partitioned by gene and codon position (for protein coding genes); (3) a combined dataset, including morphological characters and DNA sequences; and (4) a combined reduced dataset, excluding 10 species that only had morphological characters coded, to assess the potential effect of these missing data in the combined analyses.

ML analyses were performed locally in IQ-TREE v. 2.2.0 (Minh *et al.*, 2020) using the edge-linked partition model (Chernomor *et al.*, 2016) and the best-fitting substitution model for each partition selected by ModelFinder (Kalyaanamoorthy *et al.*, 2017), as detailed in Table 3. ML tree search was performed using 10 IQ-TREE runs per dataset. Branch support was assessed by ultrafast bootstrap (UFBoot, Hoang *et al.*, 2018) and Shimodaira-Hasegawa approximate likelihood ratio test (SH-aLRT, Guindon *et al.*, 2010), both with 10,000 replicates, also in IQ-TREE.

BI analyses were run in MrBayes v. 3.2.6 (Ronquist *et al.*, 2012) locally. All analyses were performed using four independent runs, each with four Markov chains, running for 10 million generations and sampling every 1,000 generations. Best-fitting models in BI analyses for each molecular partition were selected by PartitionFinder 2.3 (Lanfear *et al.*, 2016) (Tab. 3). Convergence and mixing of sampled parameters was assessed in Tracer v. 1.5 (Rambaut & Drummond, 2007) based on a unimodal posterior distribution and an effective sample size (ESS) higher than 200; the first 10% of trees and parameters were discarded as burn-in. Branch support was based on BI posterior probabilities (PP).

Table 3. Partitions included in the three datasets analysed, with respective numbers of taxa and characters, and evolutionary models implemented for BI and ML analyses. Models were selected based on BIC scores by ModelFinder in IQ-TREE.

Partitions	**Taxa**	**Characters**	**ModelFinder (ML)**	**PartitionFinder 2 (BI)**
Morphology	48	48	MK+ASC+G4	MKv
16S	36	426	TPM3u+F+I+R3	GTR+I+G
28S	36	297	TPM2u+I+G	GTR+I+G
COI	29	567	1st codon = TN+G4 2nd codon = TIM+I 3rd codon = TN+F+G4	1st codon = GTR+G 2nd codon = F81+I 3rd codon = GTR+G
H3	29	345	1st codon = TPM2u+I+G 2nd codon = TIM+I 3rd codon = GTR+F+I+G4	1st codon = GTR+I+G 2nd codon = JC+I 3rd codon = GTR+G
WING	34	399	1st codon = TPM2u+I+G 2nd codon = TIM+I 3rd codon = GTR+F+I+G4	1st codon = SYM+G 2nd codon = HKY+I 3rd codon = GTR+G
Concat.	48	2082	Partitioned as above	Partitioned as above

Ancestral character reconstruction

Unambiguous character-state changes were optimized under equal weights parsimony in WinClada (Nixon, 2002). Optimizations were performed on the strict consensus tree of the most-parsimonious trees obtained in TNT (Goloboff *et al.*, 2008) for each concavity constant (k) under implied weighting (Goloboff, 1993). Furthermore, using the command map common synapomorphies in TNT, we have ensured that inferred transformations reflected only relationships common to all MPTs for a given k value.

RESULTS

Phylogenetic relationships of *Tupiperla*

Morphological characters

A total of 10 nymphal and 38 male characters were scored. The list of characters and their respective states are given below; the coded data matrix is available in Supplementary Material S3. For characters obtained or reinterpreted from previous phylogenetic works, the reference is cited after the respective character.

Nymphs

Body

0. **Body, type of setae:** (0) setiform-like (Figure 2M in Duarte *et al.*, 2025); (1) vesicular-like (Figure 6 in Rippel *et al.*, 2025); (2) claviform-like (Figure 2B in Duarte *et al.*, 2025). — Froehlich (1969) described claviform setae in nymphs of *Paragripopteryx* species, whereas Froehlich (2001) described vesicular setae in nymphs of *Guaranyperla*. Adapted from Duarte *et al.*, 2025

1. **Pronotum, spines:** (0) absent; (1) present (Figure 2E in Duarte *et al.*, 2025). — Nymphs of *Ceratoperla* and *Gripopteryx* have spines or small warts on the thorax. Adapted from Duarte *et al.*, 2025

2. **Pronotum, broad paranota:** (0) absent; (1) present (Figure 9A, B in Rippel *et al.*, 2025). — Froehlich (2001) reported broad paranota in nymphs of *Guaranyperla*. Adapted from Duarte *et al.*, 2025

3. **Femur 1-3, dorsal (extensor margin) row of hairs:** (0) absent; (1) present (Figure 2F in Duarte *et al.*, 2025). — A dorsal row of long hairs is described for the femur and tibia in many species of Gripopterygidae. Adapted from Duarte *et al.*, 2025

4. **Terga 1–9, mid-dorsal row of spines:** (0) absent; (1) present (Figure 2B,C in Duarte *et al.*, 2025). — Illies (1963) described nymphs of some taxa, including *Ceratoperla* and *Gripopteryx*, with mid-dorsal spines on abdominal terga 1–9. The character state ranges from absent to one or two rows present. Adapted from Duarte *et al.*, 2025

5. **Pronotum, anterolateral projections (vestigial horns):** (0) absent; (1) present (Figure 4A in Rippel *et al.*, 2025). — Froehlich (2001) described projecting anterior corners on the pronotum of *Guaranyperla* species. Adapted from Duarte *et al.*, 2025

6. **Abdomen, distal margin of terga 1–9, type of setae:** (0) setiform; (1) stout setiform; (2) claviform; (3) vesicular. Adapted from Duarte *et al.*, 2025

7. **Metanotum, mid-distal margin (between wing pads), shape:** (0) circular or concave (Figure 2G in Duarte *et al.*, 2025); (1) angular or V-shaped (Figure 2J in Duarte *et al.*, 2025); (2) straight. Adapted from Duarte *et al.*, 2025

8. D**istal edge of T10, shape:** (0) rounded / without projection ; (1) with small swallow-shaped projection; (2) with pointed projection (Figure 5C in Rippel *et al.*, 2025); (3) with elongated projection (Figure 9C in Rippel *et al.*, 2025). Adapted from Duarte *et al.*, 2025

9. **Anal gills (gill rosette):** (0) absent; (1) present (Figure 2O in Duarte *et al.*, 2025). Adapted from Duarte *et al.*, 2025

10. **Ocelli, number:** (0) 2 ocelli; (1) 3 ocelli.

Adults

Body

11. **Forewings, pterostigmatic cell, crossveins:** (0) absent (Figure 2C in Duarte *et al.*, 2025); (1) present (Figure 10C in Rippel *et al.*, 2025). — The pterostigmatic crossvein occurs in *Guaranyperla*, *Paragripopteryx*, and some *Gripopteryx* species. Adapted from Duarte *et al.*, 2025

12. **Forewings, crossveins between C and Sc, number:** (0) one crossvein (Figure 5C in Duarte *et al.*, 2025); (1) more than one (Figure 3D in Duarte *et al.*, 2025). Adapted from Duarte *et al.*, 2025

13. **Femur, ventral femoral spine:** (0) absent (Figure 2L in Duarte *et al.*, 2025); (1) present (Figure 2R in Duarte *et al.*, 2025). — Froehlich (1969, 2001) described the ventral femoral spine in *Tupiperla* and *Guaranyperla*. Adapted from Duarte *et al.*, 2025

14. **Forewings, CuA vein, branching:** (0) unforked (Figure 2B in Pessacq *et al.*, 2020); (1) one fork (Figure 2A, C in Pessacq *et al.*, 2020); (2) two forks (Illies 1963; McLellan 1977). Adapted from Pessacq *et al.*, 2020.

15. **Hind wings, number of anal veins:** (0) fewer than six; (1) six anal veins; (2) more than six.

16. **Tibia, tibial spurs:** (0) absent; (1) present (Figure 2R in Duarte *et al.*, 2025). Adapted

from Duarte *et al.*, 2025

17. **Tarsi, hind tarsomeres, relative length proportions (tarsomeres I:II:III):** (0) 2:2:6; (1) 3:1:6 (Figure 2R in Duarte *et al.*, 2025); (2) 4:2:4 (In Illies 1963; Vera 2016). Adapted from Duarte *et al.*, 2025

Male Abdomen

18. **Sternite 9 (St9), subgenital plate, shape of posterior margin:** (0) oval/curved (Froehlich 1998: figs. 10, 22; Froehlich 2015: figs. 2, 7); (1) triangular/pointed (Froehlich 1969: Figure 27; Froehlich 1998: Figure 27; Bispo & Lecci 2011: Figure 23).

19. **Tergite 10 (T10), anterior sclerites relative to central sclerite, fusion:** (0) completely fused (Figure 15 A); (1) fused to but distinguishable by a suture; (2) separated by a narrow membrane (Figure 3A in Pessacq *et al.*, 2020).

20. **Abdomen; T10, conspicuous latero-dorsal clefts:** (0) absent (Froehlich 1998: figs. 1, 2); (1) present (Zwick 1972: Figure 1; Lecci & Froehlich 2011: Figure 10f; Froehlich 2015: Figure 6). — Species of *Gripopteryx* and *G. nitens* have a conspicuous latero-dorsal cleft on tergum 10.

21. **Abdomen; T10, distal margin of central sclerite, shape:** (0) not protruding Lecci & (Froehlich 2011: Figure 10f); (1) protruding (Figure).

22. Abdomen; T10E, posterior sclerite: (0) absent (Figure 30A); (1) present (Illies 1963: Figure 37e).

23. Sclerotized epiproct: (0) absent (Figure 28B); (1) present (Froehlich 1990: Figure 17). — Froehlich (1990) reported this distinct feature for *Gripopteryx* and *Paragripopteryx*.

24. Paraproct, paraproct length in relation to T9 length: (0) less than 2×; (1) 2×; (2) more than 2.5×; (3) 3×; (4) 3.5×; (5) more than 4×.

25. Paraproct, dorsal margin, row of spines: (0) absent (Figure 15B); (1) present (Figure 23C, C).

26*. **Paraproct, dorsal margin, position of serrated row:** (0) basal (Figure 30B); (1) apical (Figure 27B); (2) Whole margin (Figure 23B, C). *Dependent on previous character.*

27. Paraproct, lateral surface, preapical spine: (0) absent (Figure 15B); (1) present (Figure 39B).

28*. **Paraproct, lateral surface, apex of preapical spine, shape:** (0) rhomboid (Figure 39b); (1) acute (Figure 30B). *Dependent on previous character.*

29. Paraproct, lateral surface, medial lateral process: (0) absent (Figure 15 B); (1) present (Figure 36B).

30*. Paraproct, lateral surface, preapical lateral process apex, direction: (0) anterior (Figure 34B); (1) dorsal (Figure 35B). *Dependent on previous character.*

31. Paraproct, lateral surface, row of robust setae: (0) absent (Figure 15B); (1) present (Figure 25B).

32. Paraproct, ventral margin, preapical spine: (0) absent (Figure 17B); (1) present (Figure 38B).

33. Paraproct, ventral margin, median notch: (0) absent (Figure 15B); (1) present (Figure 24B).

34. Paraproct, ventral margin, lateral process: (0) absent (Figure 15B); (1) present (Figure 13B).

35*. **Paraproct, ventral margin, lateral process apex, shape:** (0) acute (Figure 33B); (1) rhomboid (Figure 13 B). *Dependent on previous character.*

36. Paraproct, apex, shape: (0) rounded (Figure 15B); (1) sharp/thin (Figure 30B).

37. Paraproct, apex, angulation (lateral view): (0) straight (Figure 37B); (1) acute (Figure 13B); (2) geniculate (90°) (Figure 21B).

38. Paraproct, base, direction (ventral view): (0) parallel (Figure 25A); (1) convergent (Figure 33A); (2) divergent (Figure 19A).

39. Paraproct, apex, direction (ventral view): (0) parallel (Figure 25A); (1) convergent (*T. eleonora*, *T. zwicki*); (2) divergent (*T. umbya*, *T. misionera*).

40. Paraproct, dorsal margin, preapical spine: (0) absent (Figure 15B); (1) present (Figure 37B).

41. T10E, apical teeth: (0) absent (Figure 4C); (1) present (Figure 25C). — Applies only to species with a protruding T10E.

42. T10e, lateral margins, direction (dorsal view) (0) parallel (*T. robusta*); (1) divergent (*T. misionera*, *T. umbya*); (2) divergent only in apical half (*T. froehlichi*); (3) convergent.

43. T10e, ratio of base (T10) to extension (T10e) size width: (0) 1×; (1) 2×; (2) 3×; (3) 4×; (4) 5×; (5) 9×.

44. T10e, length-to-maximum width ratio: (0) 0.5× (shorter than width, *T. robusta*); (1) 1×; (2) 1.5×; (3) 2×.

45. T10e, base-to-apex width ratio: (0) subequal (*T. robusta*, *T. gracilis*, *T. flinti*); (1) apex twice the base width (*T. amorimi*, *T. froehlichi*, *T. urubu*, *T. oliveira*); (2) apex half the base width; (3) apex one-third the base width; (4) apex less than one-third the base width.

46. T10e, median excavation: (0) absent (*T. robusta*, *T. sp. 7*, *T. sp. 8*); (1) present (*T. serrulata*, *T. tucum*, *T. froehlichi*, *T. oliveira*).

47*. T10e, median excavation depth: (0) shallow (*T. gracilis*, *T. eleonorae*, *T. sulina*); (1) swallow-tailed (almost half the total length) (*T. tessellata*, *T. illiesi*, *T. claudius*); (2) deep (more than half the total length, *T. oliveira*, *T. amorimi*, *T. froehlichi*). *Dependent on previous character.*

Phylogenetic analyses

Combined dataset

Results from the ML analysis of the combined dataset (Morphological, 28S, WING, H3, 16S and COI, 2082) are shown in Figure 6, including support values for clades also recovered in BI analysis with the same dataset. Results from the BI analysis are provided in Supplementary Material S4. BI and ML analyses of this dataset, recovered a strongly supported clade including *Tupiperla* and *Guaranyperla* species (Clade A, Figure 6, PP =0.99, UFBoot =100%, SH-aLRT =100%). However, *Tupiperla* was recovered as paraphyletic in relation to *Guaranyperla*, because of a *Tupiperla* clade (Clade C, Fig 6, PP =0.99, UFBoot =98%, SH-aLRT =99%) recovered more closely related to *Guaranyperla* (Clade B, Figure X, PP =0.99, UFBoot =99%, SH-aLRT =99%), but the support for this relationship is low in the ML analysis (UFBoot =75%, SH-aLRT =73%) and is not recovered in BI (Supplementary Material S4). *Guaranyperla* (Clade B, Figure 6, PP =0.99, UFBoot =100%, SH-aLRT =100%) was recovered in both ML and BI analyses as monophyletic with high support. Within *Tupiperla*, in both ML and BI analyses, seven clades were recovered with high support values. The first clade, referred herein as the *T. robusta* group (Clade C, Fig 6, PP =0.99, UFBoot =99%, SH-aLRT =98%), was composed of *T. robusta*, *Tupiperla* sp. 7, and *Tupiperla* sp. 8. The second clade (Clade D, Figure 6, PP =0.81, UFBoot =93%, SH-aLRT =98%) was composed of all *Tupiperla*, except *T. modesta*, *T. jumirim*, *T. robusta*, *Tupiperla* sp. 7, and *Tupiperla* sp. 8. The third clade (Clade E, Fig 6, PP =0.62; UFBoot =94%, SH-aLRT =99%) was composed of *T. tessellata*, *T. bispoi*, *T. tucum, T. illiesi*, *T. claudius*, *T. reichardti*, *T. serrulata*, *Tupiperla* sp. 1, *Tupiperla* sp. 2, *Tupiperla* sp. 5, and *Tupiperla* sp. 6. The fourth clade (Clade G, Figure 6, PP =0.99; UFBoot =99%, SH-aLRT =95%) was composed of *Tupiperla* sp. 4 + *T. sepeensis.* The fifth clade (Clade H, Figure 6, PP =0.70; UFBoot =71%, SH-aLRT =99%) was composed of *T. gracilis*, *T. oliverai*, and *T. amorimi*. The sixth clade (Clade I, Figure 6, PP =0.81; UFBoot =82%, SH-aLRT =99%) was composed of *T. sulina*, *T. eleonorae*, *T. misionera*, and *T. guariru*. Finally, the seventh clade (Clade J, Figure 6, PP =0.62; UFBoot =93%, SH-aLRT =77%) was composed of *T. modesta* + *T. jumirim*.

Another clade of interest (Clade F, Fig 6, UFBoot =60%, SH-aLRT =93%) was recovered only in ML analysis as the sister group of Clade E (Figure 6) and included *T. gracilis*. *T. oliverai*, *T. amorimi*, *Tupiperla* sp. 3, *T. sulina*, *T. eleonorae*, *T. misionera*, *T. guariru*, *T. umbya*, *T. pinhoi*, *T. pessacqi*, *T. flinti*, and *T. zwicki*.

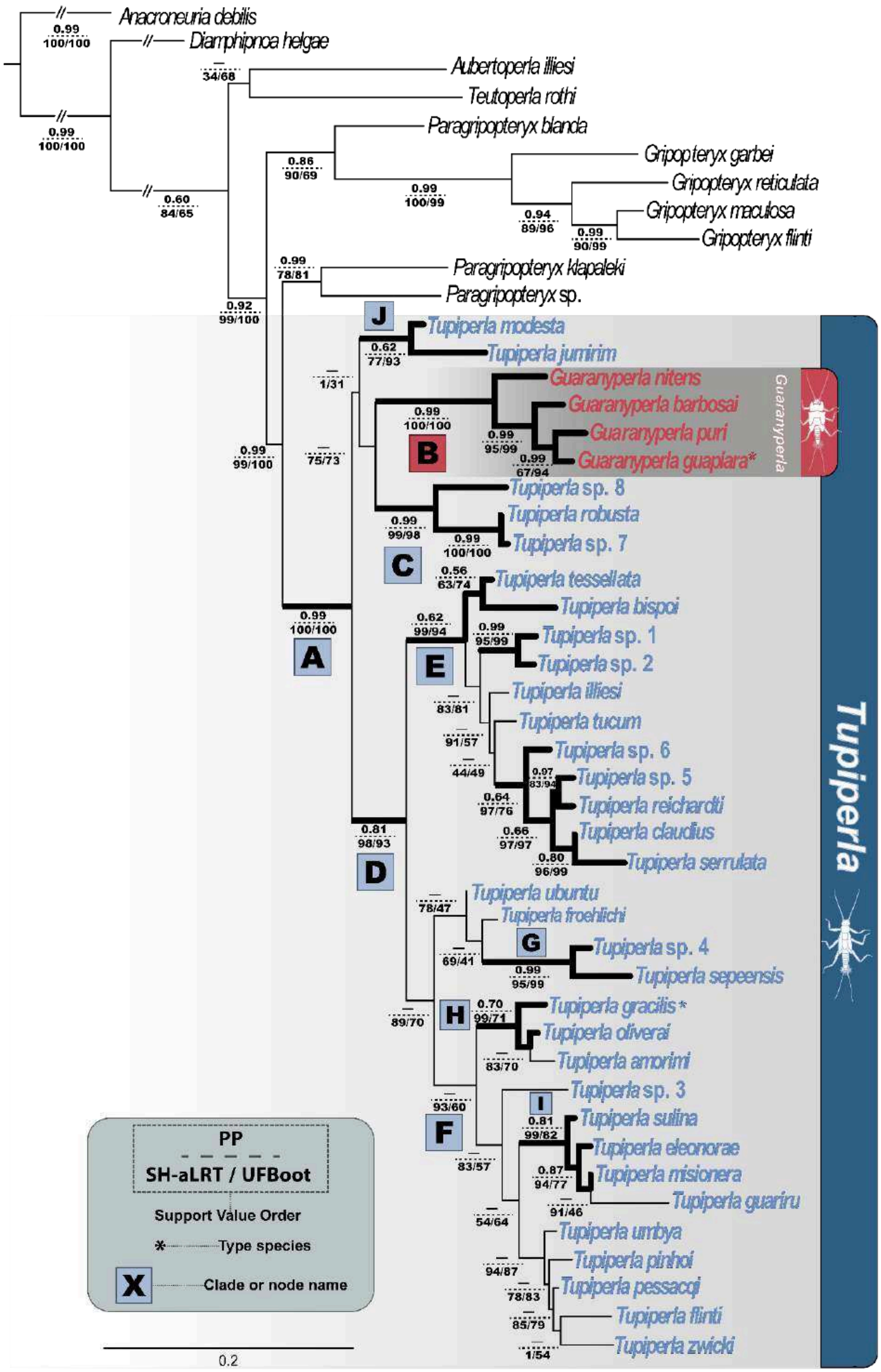

Anacroneuria debilis
Diamphipnoa helgae
Aubertoperla illiesi
Teutoperla rothi
Paragripopteryx blanda
Gripopteryx garbei
Gripopteryx reticulata
Gripopteryx maculosa
Gripopteryx flinti
Paragripopteryx klapaleki
Paragripopteryx sp.
Tupiperla modesta
Tupiperla jumirim
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla puri
Guaranyperla guapiara*
Guaranyperla
Tupiperla sp. 8
Tupiperla robusta
Tupiperla sp. 7
Tupiperla tessellata
Tupiperla bispoi
Tupiperla sp. 1
Tupiperla sp. 2
Tupiperla illiesi
Tupiperla tucum
Tupiperla sp. 6
Tupiperla sp. 5
Tupiperla reichardti
Tupiperla claudius
Tupiperla serrulata
Tupiperla ubuntu
Tupiperla froehlichi
Tupiperla sp. 4
Tupiperla sepeensis
Tupiperla gracilis*
Tupiperla oliverai
Tupiperla amorimi
Tupiperla sp. 3
Tupiperla sulina
Tupiperla eleonorae
Tupiperla misionera
Tupiperla guariru
Tupiperla umbya
Tupiperla pinhoi
Tupiperla pessacqi
Tupiperla flinti
Tupiperla zwicki
Tupiperla
0.99 100/100
0.99 100/100
34/68
0.60 84/65
0.86 90/69
0.99 100/99
0.94 89/96
0.99 90/99
0.99 78/81
0.92 99/100
0.99 99/100
0.62 77/93
1/31
75/73
0.99 100/100
0.99 95/99
0.99 67/94
0.99 99/98
0.99 100/100
0.99 100/100
0.56 63/74
0.62 99/94
0.99 95/99
83/81
91/57
44/49
0.97 83/94
0.64 97/76
0.66 97/97
0.80 96/99
0.81 98/93
78/47
69/41
0.99 95/99
89/70
0.70 99/71
83/70
93/60
0.81 99/82
83/57
0.87 94/77
91/46
54/64
94/87
78/83
85/79
1/54
J
B
C
A
E
D
G
H
F
I
PP
SH-aLRT / UFBoot
Support Value Order
* Type species
X Clade or node name
0.2

Figure 6 - Phylogenetic hypothesis of *Tupiperla* derived from maximum likelihood analysis of the combined dataset (28S, WING, H3, 16S and COI, 2034 bp, and 48 morphological characters). Thicker branches were also recovered in the Bayesian analysis. Support values as follows BI posterior probabilities (PP) over SH-like approximate likelihood ratio test (SH-aLRT) / Ultrafast bootstrap (UFBoot) from ML. Asterisks (*) indicate type species.

Concatenated dataset

Results from BI analyses of the genes separately (28S, WING, H3, 16S, and COI) are provided in Supplementary Material S5-S9. Results of the ML analysis of the concatenated dataset (total of 2034bp) are shown in Figure 7, including support values for clades also recovered in the BI analysis using the same dataset. Results from BI analysis are provided in Supplementary Material S10. BI and ML analyses of this dataset also recovered a strongly supported clade that included *Tupiperla* and *Guaranyperla* species (Clade A, Figure 7, PP =0.99, UFBoot =96%, SH-aLRT =95%). In both analyses, *Guaranyperla* was recovered as monophyletic (Clade B, Figure 7, PP =0.99, UFBoot =100%, SH-aLRT =100%), as well as *Tupiperla*, however with low clade support (PP =0.62, UFBoot =79%, SH-aLRT =38%).

Within *Tupiperla*, in both ML and BI analyses, six clades congruent to the combined analysis, although with smaller taxon sampling, were recovered with high support values (Figure 7): Clade C (PP =0.99, UFBoot =100%, SH-aLRT =99%; Clade D (PP =0.99, UFBoot =99%, SH-aLRT =95%); Clade E (PP =0.99; UFBoot =99%, SH-aLRT =99%); Clade F (PP =0.98; UFBoot =98%, SH-aLRT =95%); Clade H (PP =0.99; UFBoot =100%, SH-aLRT =100%); and Clade I (PP =0.99; UFBoot =99%, SH-aLRT =99%).

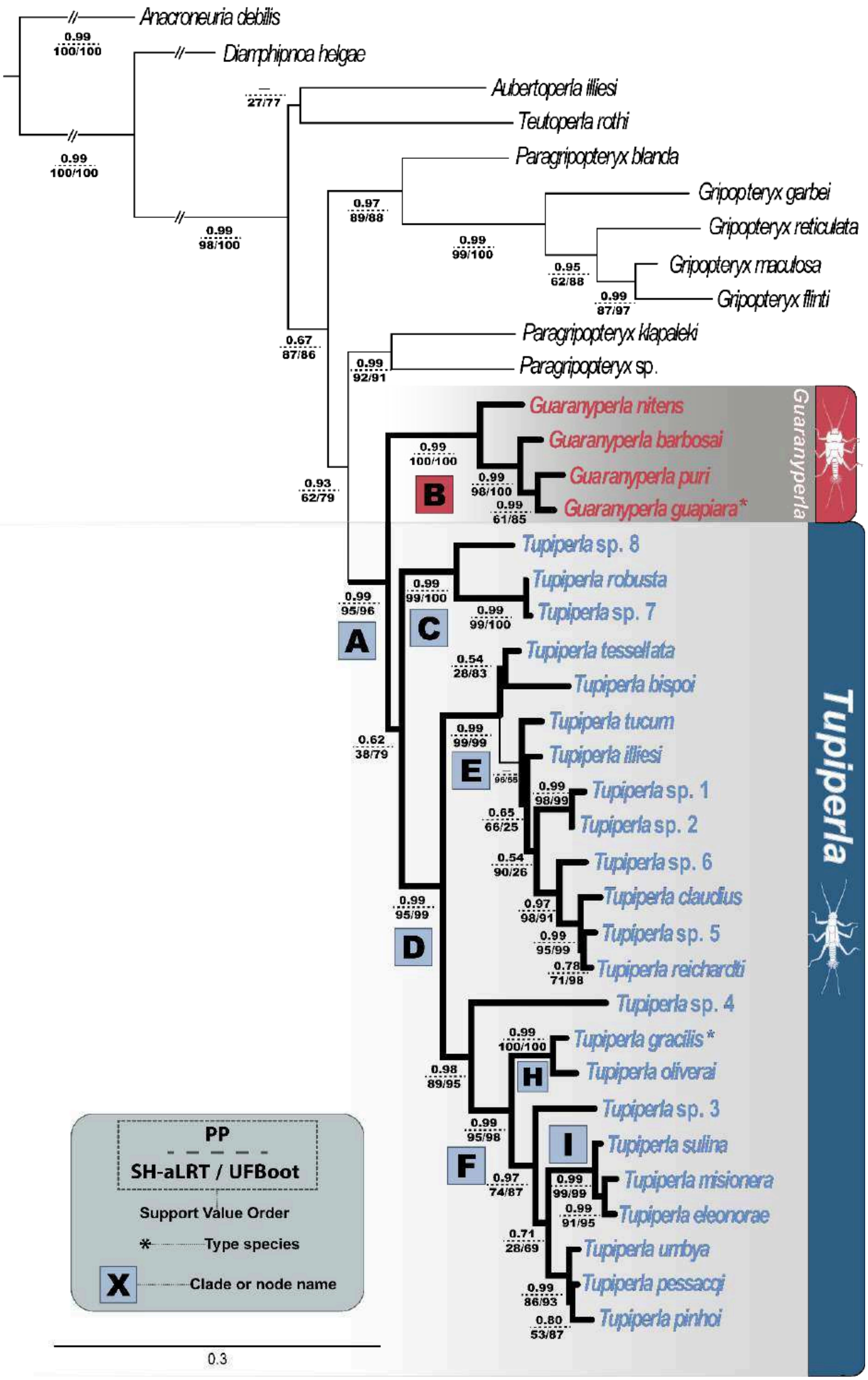

Anacroneuria debilis
0.99
100/100
Diamphipnoa helgae
0.99
100/100
Aubertoperla illiesi
Teutoperla rothi
—
27/77
Paragripopteryx blanda
Gripopteryx garbei
Gripopteryx reticulata
Gripopteryx maculosa
Gripopteryx flinti
0.97
89/88
0.99
99/100
0.95
62/88
0.99
87/97
0.99
98/100
Paragripopteryx klapaleki
Paragripopteryx sp.
0.67
87/86
0.99
92/91
0.93
62/79
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla puri
Guaranyperla guapiara*
0.99
100/100
B
0.99
98/100
0.99
61/85
Guaranyperla
Tupiperla sp. 8
Tupiperla robusta
Tupiperla sp. 7
0.99
99/100
0.99
99/100
C
0.99
95/96
A
Tupiperla tessellata
Tupiperla bispoi
0.54
28/83
Tupiperla tucum
Tupiperla illiesi
0.99
99/99
E
96/55
Tupiperla sp. 1
Tupiperla sp. 2
0.99
98/99
0.65
66/25
0.62
38/79
Tupiperla sp. 6
Tupiperla claudius
Tupiperla sp. 5
Tupiperla reichardti
0.54
90/26
0.97
98/91
0.99
95/99
0.78
71/98
0.99
95/99
D
Tupiperla sp. 4
Tupiperla gracilis*
Tupiperla oliverai
0.99
100/100
H
0.98
89/95
Tupiperla sp. 3
Tupiperla sulina
Tupiperla misionera
Tupiperla eleonorae
0.99
95/98
F
I
0.97
74/87
0.99
99/99
0.99
91/95
Tupiperla umbya
Tupiperla pessacqi
Tupiperla pinhoi
0.71
28/69
0.99
86/93
0.80
53/87
Tupiperla
PP
SH-aLRT / UFBoot
Support Value Order
* Type species
X Clade or node name
0.3

Figure 7 - Phylogenetic hypothesis of *Tupiperla* derived from maximum likelihood analysis of the concatenated dataset (28S, WING, H3, 16S and COI, 2034 bp). Thicker branches were also recovered in the Bayesian analysis. Support values as follows BI posterior probabilities (PP) over SH-like approximate likelihood ratio test (SH-aLRT) / Ultrafast bootstrap (UFBoot) from ML. Asterisks (*) indicate type species.

Morphological dataset

A total of 4,987 most parsimonious trees (S= 171, CI= 0.43, RI= 0.71) were found in the analysis of the morphological dataset under equal weights and were summarized in a strict consensus shown in Supplementary Material S11. Analyses of the morphological dataset under different values of k yielded differences in the number of trees retrieved and can be visualized in Table 4 with their Fit values. The strict consensus trees for each value of k, except for k7, are provided in Supplementary Material S12-S17. The analysis with k = 7 is believed to represent an optimal balance between being susceptible to homoplastic characters and excessively down-weighting homoplastic characters because it is an intermediate-level less prone to this effects (Goloboff *et al.*, 2008; Goloboff, 2014; Ezcurra, 2024). For these reasons, k = 7 was chosen as the reference analysis for interpreting the relationships within the group in Figure 8.

In all weighting schemes, Clade A was recovered including *Tupiperla* and *Guaranyperla* species. However, *Tupiperla* was recovered as paraphyletic in relation to *Guaranyperla*, in most of the weighting schemes because of the position of *T. modesta* and *T. jumirim* as more closely related to *Guaranyperla*, except in the values of k = 3-5 where Clade C (Figure 8) was found more closely related to *Guaranyperla*. Clade B composed of all the species of *Guaranyperla* was recovered as monophyletic in all the weighting schemes.

Within *Tupiperla*, other three clades were recovered in most to all weighting schemes and are also found congruent to the combined analysis. Clade D (Figure 8) was composed of all species of *Tupiperla*, excluding *Tupiperla modesta*, *Tupiperla jumirim*, *Tupiperla guariru*, *Tupiperla robusta*, *Tupiperla* sp. 7, and *Tupiperla* sp. 8. This clade was recovered in all of the weighting schemes. Clade D (Figure 8) was recovered in all weighting schemes, and within it, the following clades were always recovered: (*Tupiperla flinti*, *Tupiperla pessacqi*, and *Tupiperla zwicki*); ((*Tupiperla* sp 6, *Tupiperla illiesi*, and *Tupiperla tucum*) + (*Tupiperla pinhoi*, *Tupiperla serrulata*, and *Tupiperla claudius*)); (*Tupiperla* sp. 2, *Tupiperla reichardti*, and *Tupiperla* sp. 1); and Clade G (Figure 8) composed of *Tupiperla* sp. 4 and *Tupiperla sepeensis*. Finally Clade C (Figure 8) was found under equal weights and k = 7, 9, 11, 13, 15.

Table 4. Results obtained under different character-weighting schemes, showing the number of trees recovered and the presence or absence of the main clades identified in the analyses.

Weighting scheme	Equal	K3	K5	K7	K9	K11	K13	K15
Number of trees	4987	2	2	6	3	3	5	5
Score	171	10.85	8.7	7.29	6.29	5.53	4.94	4.46
Fit	29.13	30.14	32.29	33.70	34.70	35.46	36.05	36.53
Consistency Index	0.43	0.42	0.42	0.43	0.43	0.43	0.43	0.43
Retention Index	0.71	0.698	0.701	0.71	0.71	0.71	0.71	0.71
Clade A	yes	yes	yes	yes	yes	yes	yes	yes
Clade B	yes	yes	yes	yes	yes	yes	yes	yes
Clade C	yes	no	no	yes	yes	yes	yes	yes
Clade D	yes	yes	yes	yes	yes	yes	yes	yes
Clade E	no	no	no	no	no	no	no	no
Clade F	no	no	no	no	no	no	no	no
Clade G	yes	yes	yes	yes	yes	yes	yes	yes
Clade H	no	no	no	no	no	no	no	no
Clade I	no	no	no	no	no	no	no	no
Clade J	no	yes	yes	no	no	no	no	no

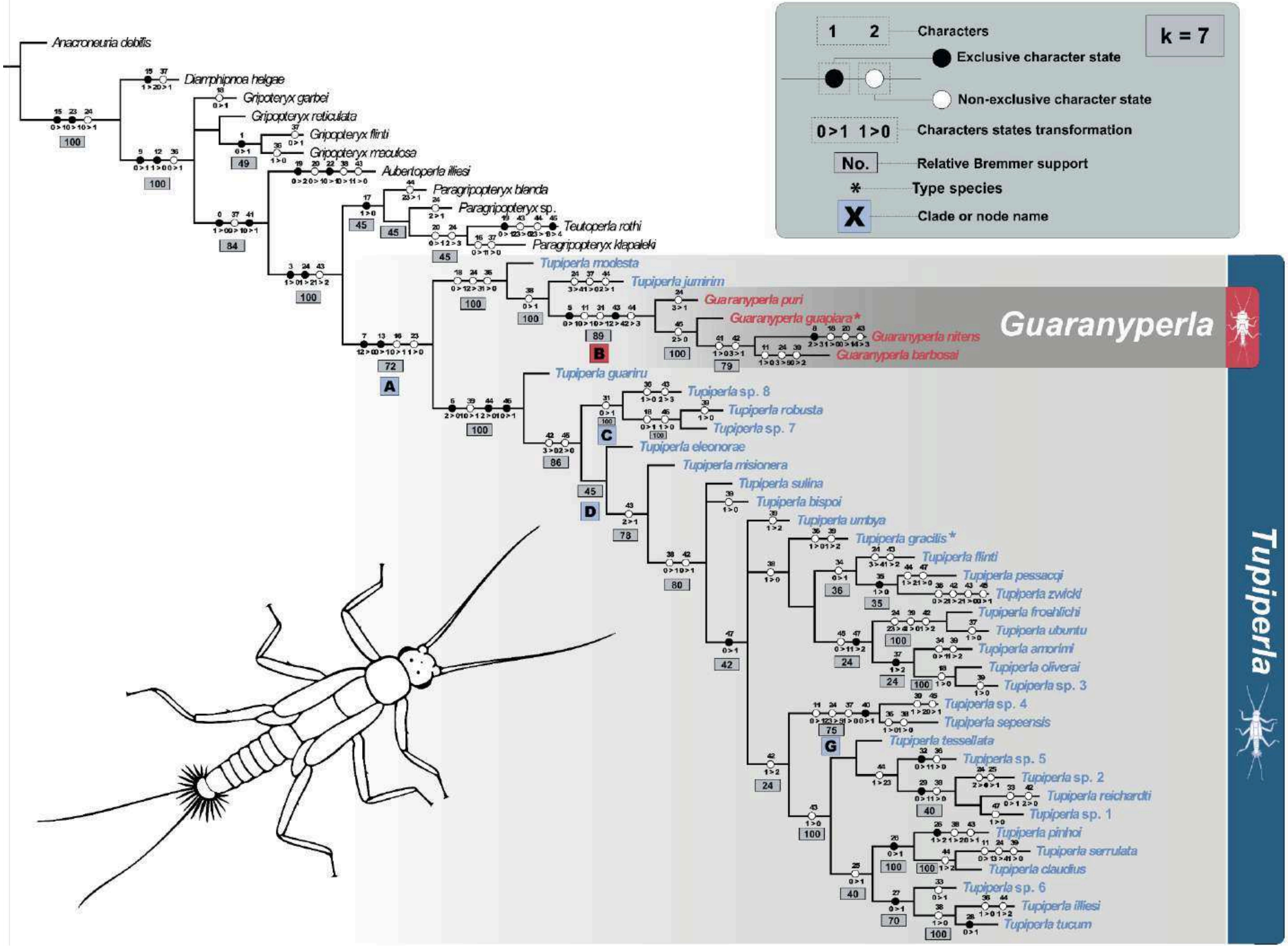

1 2
Characters
Exclusive character state
Non-exclusive character state
0>1 1>0
Characters states transformation
No.
Relative Bremmer support
*
Type species
X
Clade or node name
k = 7
Anacroneuria debilis
Diamphipnoa helgae
Gripopteryx garbei
Gripopteryx reticulata
Gripopteryx flinti
Gripopteryx maculosa
Aubertoperla illiesi
Paragripopteryx blanda
Paragripopteryx sp.
Teutoperla rothi
Paragripopteryx klapaleki
Tupiperla modesta
Tupiperla jurnirim
Guaranyperla puri
Guaranyperla guapiara*
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla
Tupiperla guariru
Tupiperla sp. 8
Tupiperla robusta
Tupiperla sp. 7
Tupiperla eleonorae
Tupiperla misionera
Tupiperla sulina
Tupiperla bispoi
Tupiperla umbya
Tupiperla gracilis*
Tupiperla flinti
Tupiperla pessacqi
Tupiperla zwicki
Tupiperla froehlichi
Tupiperla ubuntu
Tupiperla amorimi
Tupiperla oliverai
Tupiperla sp. 3
Tupiperla sp. 4
Tupiperla sepeensis
Tupiperla tessellata
Tupiperla sp. 5
Tupiperla sp. 2
Tupiperla reichardti
Tupiperla sp. 1
Tupiperla pinhoi
Tupiperla serrulata
Tupiperla claudius
Tupiperla sp. 6
Tupiperla illiesi
Tupiperla tucum
Tupiperla
A
B
C
D
G
100
100
49
84
100
45
45
45
100
72
100
100
89
100
79
100
86
45
78
80
42
36
35
100
24
24
100
75
24
40
100
100
100
40
70
100

Figure 8 - Phylogenetic hypothesis of *Tupiperla* (blue taxa) based on the strict consensus of six most parsimonious trees under k = 7 (fit = 34.70). Unambiguous character-state changes were optimized under maximum parsimony. Relative Bremer support values are indicated in gray below the clades.

Taxonomic treatment

Order Plecoptera Burmeister, 1839
Family Gripopterygidae Enderlein, 1909
Subfamily Gripopteryginae Enderlein, 1909

Tupiperla Froehlich, 1969

Paragripopteryx Illies, 1963 (nec Enderlein, 1909): 178.

Tupiperla Froehlich, 1969: 28 (Type species: *Semblis gracilis* Burmeister, 1839, by monotypy); McLellan, 1977: 121 (in Gripopteryginae); Froehlich, 1998: 34; Stark, Froehlich & Zuñiga, 2009: 96; Froehlich, 2010: 137; Duarte, Novaes & Bispo, 2019: 513.

Diagnosis. Adults with a spine at approximately midlength of inner margin of the femur; forewing pattern with most crossveins surrounded with brown; forewing pterostigmatic crossveins absent; in males, epiproct present without a ventral sclerotized projection, and a relatively long extension of tergum 10 (T10e) that ends in two separate teeth. Nymphs slender; femora, as in adults, provided with a spine at approximately midlength of inner margin; femora and tibiae lack a dorsal row of long hairs.

Distribution. Mountainous areas of the Brazilian coast from south to the northeast regions, reaching inland areas of Brazil and northeastern Argentina (Duarte *et al.*, 2024).

Species included. *Tupiperla amorimi* Froehlich, 2016; *T. bispoi* Duarte, Lecci & Calor, 2014; *T. claudius* Varella & Pinto, 2023; *T. eleonoroae* (Froehlich, 1994); *T. flinti* Froehlich, 2002; *T. froehlichi* Bispo & Lecci, 2011; ***T. gracilis** (Burmeister, 1839)**; *T. guariru* Duarte, Bispo & Calor 2014; *T. illiesi* Froehlich, 1998; *T. jumirim* Bispo & Froehlich, 2007; *T. misionera* Froehlich, 2002; *T. modesta* Froehlich, 1998; *T. oliveirai* Froehlich, 1998; *T. pessacqi* Duarte, Novaes & Bispo, 2019; *T. pinhoi* Duarte, Novaes & Bispo, 2019; *T. reichardti* Froehlich, 1998; *T. robusta* Froehlich, 1998; *T. sepeensis* Novaes & Bispo, 2016; *T. serrulata* Duarte, Novaes & Bispo, 2019; *T. sulina* Froehlich, 1998; *T. tessellata* (Brauer, 1866); *T. tucum* Sarmento, Duarte, Teixeira & Salles; *T. ubuntu* Duarte, Novaes & Bispo, 2019; *T. umbya*

Froehlich, 1998; *T. zwicki* Duarte, Novaes & Bispo, 2019; *Tupiperla* sp.1 **sp. nov.**; *Tupiperla* sp.2 **sp. nov.**; *Tupiperla* sp.3 **sp. nov.**; *Tupiperla* sp.4 **sp. nov.**; *Tupiperla* sp.5 **sp. nov.**; *Tupiperla* sp.6 **sp. nov.**; *Tupiperla* sp.7 **sp. nov.**; *Tupiperla* sp.8 **sp. nov.**

Tupiperla amorimi Froehlich, 2016

(Figure 9)

Tupiperla amorimi Froehlich 2016, p. 174; Pessacq, del Carmen Zúñiga & Duarte, 2019, p. 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 8 (Catalog.).

Diagnosis. The male of *Tupiperla amorimi* can be distinguished from other congeners by the following combination of characteristics: paraprocts elongated, geniculate with truncated enlarged apical region, spoon appearance; ventral margin of paraprocts with distinct upwards spinelike projection (Figure 9 B); Paraprocts, distally convergent, disto-lateral face concave (Figure 9 C); T10e shortened, lateral margins strongly divergent, apex V-shaped ending in two spine-like projections (Figure 9 A); subgenital plate basally oblique, apex round-triangular (Figure 9 C).

Comparative diagnosis. *Tupiperla amorimi* is most similar to *T. flinti*, *T. froehlichi*, and *T. oliverai* due to the shape of the paraproct and the strongly divergent, V-shaped, ending of the T10e. It can be distinguished from *T. oliverai* due to the shape of the apex of the paraprocts (upwards spinelike projection in *T. amorimi*, rounded in *T. oliverai*). In the case of the other similar species, it can be distinguished from them based on the median excavition of the T10e (deep in *T. amorimi* in shallow to *T. flinti*) or based on the shape of the T10e (V-shaped in *T. amorimi*, Y-shaped in *T. froehlichi*).

Distribution. Brazil, Minas Gerais. This species is known for its type locality in Cabo Verde and Botelhos, a few kilometers apart. No new records were made after the description of the species.

Type material. Holotype male: Brazil, Minas Gerais State, Cabo Verde, Fazenda da Cata, 21°27’09”S, 46°20’53”W, 598m, 11 August–13 October 2007, Malaise trap in forest, Amorim, Oliveira, Capellari. (MZUSP). [examined]

Figure 9 - *Tupiperla amorimi* adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla bispoi Duarte, Lecci & Calor, 2014

(Figure 10)

Tupiperla bispoi Duarte, Lecci & Calor 2014, p. 86; Pessacq, del Carmen Zúñiga & Duarte, 2019, p. 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 8 (Catalog.).

Diagnosis. Paraprocts directed toward T10e, distal region strongly curved laterally (Figure 10 B). Paraproct apex truncated, with lateral face slightly constricted distally, apex flat-curved (Figure 10 B). Paraprocts distally convergent, diso-latral face convex (Figure 10 C). T10e short, base narrower than apex (Figure 10 A), lateral margin concave, distal margin slightly curved, with pointed ventral spine-like process (Figure 10 B). Subgenital plate basally rhombic with pointed (Figure 10 C)

Comparative diagnosis. *Tupiperla bispoi* is most similar to *T. gracilis*, *T. misionera*, and *T. eleonorae* due to the medially bent paraproct in ventral view and the quadrangular T10e. It can be distinguished from *T. misionera* due to the shape of the apex of the paraprocts (a notch is present in the ventral edge in *T. bispoi*, while it is acuminate in *T. misionera*). In the case of the other similar species, it can be distinguished from them based on the length of the T10e (longer in *T. bispoi* in relation to *T. gracilis* and *T. eleonorae*) or based on the shape of the T10e (in *T. bispoi* the shape is more robust, while in *T. tessellata* it is thinner).

Distribution. Brazil, Bahia. This species is known only for its type locality in Serra Bonita, Camacan, Bahia. No new records were made after the description of the species.

Type material. Holotype, male: BRAZIL, Bahia: Camacan, Serra Bonita, 15°23'28"S, 39°33'56"W, 820 m, 31.vii.2008, Malaise trap, ARC, LSL, LCP and RAM. (MZUSP). [examined]

Figure 10 - *Tupiperla bispoi* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla claudius Varella & Pinto, 2023

(Figure 11)

Tupiperla claudius Varella & Pinto 2023, p. 2; Duarte, Froehlich & Bispo 2024, p. 8 (Catalog.).

Diagnosis. The male of *Tupiperla claudius* can be distinguished from other congeners by elongated paraprocts, apex curved downward, slightly hooked; dorsal margin with row of minute spine-like setae, ventral margin with medial notch (Figure 11 B). Paraprocts parallel outcurved, apex flattened (Figure 11 C). T10e elongated, apex with distinct shallow swallow-shaped median excavation (Figure 11 A). Antennae longer than forewings. Subgenital plate oblique, apex triangular (Figure 11 C).

Comparative diagnosis. *Tupiperla claudius* is most similar to *T. tessellata*, *T. tucum*, and *T. serrulata* due to the paraproct apex in lateral view and the elongated swallow-shaped T10e. It can be distinguished from *T. tessellata* due to the presence of minute spine-like setae in the dorsal margin of the paraprocts (present in *T. claudius*, absent in *T. tessellata*). It can be distinguished from *T. tucum* due to the presence or absence of a spine-like projection at the apex of the paraprocts (absent in *T. claudius*, present in *T. tucum*). In the case of the other similar species, it can be distinguished from them based on the width of the T10e apex (wider in *T. claudius* in relation to *T. tessellata*) or based on the median excavation depth of the T10e (shallow in *T. claudius*, while in deeper in *T. serrulata*).

Distribution. Brazil, Paraná. This species is known only for its type locality in Pico do Marumbi State Park, Piraquara. No new records were made after the description of the species.

Type material. Holotype, male: BRAZIL. Paraná State: Piraquara municipality, Pico do Marumbi State Park, Mananciais da Serra (SANEPAR), Caixa do Carvalho -25.4964, -48.9817, 1021 m a.s.l., light sheet, 20.I.2022, A.P. Pinto, J. Ehlert & L. Polizeli leg. (DZUP 287469). Paratype, male 1 male, same data but (UFVB PL656, ex-DZUP 287470); [examined]

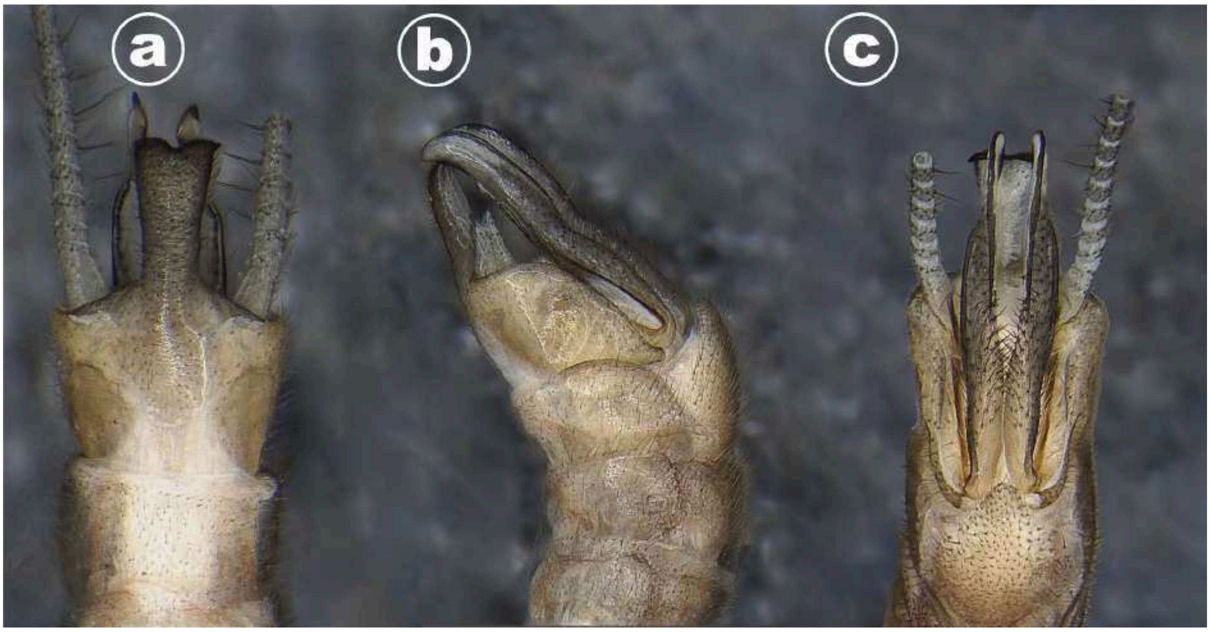


Figure 11 - *Tupiperla claudius* adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla eleonorae (Froehlich, 1994)

(Figure 12)

Paragripopteryx eleonorae Froehlich 1994, pp. 236–237. Aquatic Insects (description; figs. 22–25)

Tupiperla eleonorae – Froehlich 1998, pp. 23–24. Studies on Neotropical Fauna and Environment (redescription; figs. 8–12); Froehlich 2010, pp. 138. Illiesia (catalog); Bispo and Lecci 2011, pp. 380–381. Annales de Limnologie – International Journal of Limnologie (redescription; figs. 11–16)

Tupiperla amandae Bispo and Lecci 2011, pp. 381–383. Annales de Limnologie – International Journal of Limnologie (description; figs. 17–21).

Diagnosis. The male of *Tupiperla eleonorae* can be distinguished from other congeners by short paraprocts; dorsal margin straight, ventral margin convex, apex acuminate, blade-shaped (Cimitarra) (Figure 12 B). Paraprocts distally convergent, medially bent, disto-lateral face concave (Figure 12 C). T10e shortened, spatulate, lateral margins parallel, apex with small median excavation (Figure 12 A). Subgenital plate oval, central region more sclerotized, distal margin triangular (Figure 12 C).

Comparative diagnosis. *Tupiperla eleonorae* is most similar to *T. misionera*, *T. sulina*, and *T. umbya* due to the shape of the ventral margin and apex of the paraproct in lateral view and the quandragular-shape of the T10e. It can be distinguished from *T. sulina* due to the shape ventral margin and apex of the paraprocts (convex and acuminated, respectively, in *T. elonorae*, straight and truncated in *T. misionera*). It can be distinguished from *T. misionera* due to the width and shape of the paraprocts (wider and robust in *T. elonorae*, slender and sinuous in *T. misionera*). In the case of the other similar species, it can be distinguished from them based on length of the T10e (short in *T. elonorae*, longer in *T. umbya*).

Distribution. Argentina, Misiones; Brazil, São Paulo. This species is known for the type locality in Caverna Areias de Baixo (PETAR), Iporanga (Froehlich, 1994). This species occurs on coastal mountains of São Paulo State, especially in the south (PETAR, PEI) and in the north (Boracéia Biological Station in Salesópolis and Jaraguá Mountain in São Paulo) (Froehlich, 1998). Specimens from Misiones, Argentina, were determined as *T. amandae* Bispo & Lecci, 2011 by Manzo *et al.* (2014) and Romero (2017).

Remarks. This species recently became a senior synonym of *T. amandae* Bispo & Lecci, 2011 (Duarte *et al.*, in press).

Type material. Holotype, Male: SÃO PAULO, Iporanga, 21.IX.1991, S. Homem and N. Moracchioli (MZUSP); [examined]

Figure 12 - *Tupiperla eleonorae* adult male, terminalia in dorsal (A), lateral (B), and ventral views (C). Photograph of the holotype of Tupiperla amandae Bispo & Lecci, 2011.

Tupiperla flinti Froehlich, 2002

(Figure 13)

Tupiperla flinti Froehlich, 2002: 38; Froehlich, 2010: 138; Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla flinti* can be distinguished from other congeners by elongated paraprocts; lateral face concave, ventral edge outcurved dorsally, giving spoon appearance; dorsal margin contorted, ventral margin rounded, apex geniculate with distally acuminate projection (Figure 13 B). Paraprocts distally convergent; apex lateral face concave (Figure 13 C). T10e shortened, spatulate, lateral margins divergent, apex swallow-tailed with two spine-like projections (Figure 13 A). Subgenital plate oval, central sclerotization increased, distal margin triangular (Figure 13 C).

Comparative diagnosis. *Tupiperla flinti* is most similar to *T. gracilis*, *T. amorimi*, and *T. umbya* due to the concave disto-lateral face of the paraproct that resemble a spoon, and the quandragular-shape of the T10e. It can be distinguished from *T. gracilis* due to the shape of the apex of the paraprocts (distally pointed in *T. flinti*, enlarged and truncated in *T. gracilis*). It can be distinguished from *T. umbya* due to the shape of the ventral margin of the paraprocts (irregular contorted margin in *T. flinti*, sinuous in *T. umbya*). In the case of the other similar species, it can be distinguished from them based on the T10e apex (wider and robust projections in *T. flinti* in relation to the slender and smaller projections of *T. umbya*) or based on ratio of the base to the extension of the T10 (the base is 3x the extension in *T. flinti*, subequal in *T. amorimi*).

Distribution. Argentina, Misiones; Paraguay, Paraguarí; Brazil, Paraná. This species is known from the type locality in Province of Misiones, Argentina (Froehlich, 2002). This species occurs primarily in Paraguarí, Paraguay (Froehlich, 2002); Iguaçu National Park, Paraná State; and the municipality of Bom Jesus, Rio Grande do Sul State, Brazil. The Iguaçu National Park is a protected area shared between Brazil (Paraná State) and Argentina

(Misiones Province), situated along the border of these two countries, and located within the boundaries of the Atlantic Forest Biome (Duarte *et al.*, 2024).

Type material. Paratypes: ARGENTINA, Misiones, 18–19.XI.1973, 1; Arroyo Saura, 9 km N of L.N. Alem, 16 , 16 , 20.XI.1973, O.S. Flint, Jr. (MZUSP); [examined]

Figure 13 - *Tupiperla flinti* (Paratype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla froehlichi Bispo & Lecci, 2011

(Figure 14)

Tupiperla froehlichi Bispo & Lecci, 2011: p383; Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla froehlichi* can be distinguished from other congeners by elongated paraprocts, strong basal curvature posteriorly directed, boomerang-shaped; apex dorsally pointed, acuminated (Figure 14 B). Paraprocts parallel, flattened (Figure 14 C). T10e shortened, with short basal stem before divergence, Y-shaped, apex ending in two spine-like projections (Figure 14 A). Subgenital plate pentagonal with rounded corners (Figure 14 C).

Comparative diagnosis. *Tupiperla froehlichi* is most similar to *T. ubuntu*, *Tupiperla* sp. 4, *Tupiperla* sp. 7, and *T. robusta* due to dorsal angulation of the paraprocts in lateral view and the Y-shape T10e. It can be distinguished from *T. robusta* and *Tupiperla* sp. 7 based on the origin of the angulation of the paraprocts (the angulation originates medially in *T. froehlichi*, while originates distally in *T. robusta* and *Tupiperla* sp. 7). It can be distinguished from *T. ubuntu* due to the shape of the ventral margin of the paraprocts (convex margin in *T. froehlichi*, straight in *T. ubuntu*). In the case of the other similar species, it can be distinguished from them based on the width and shape of the T10e apex (smaller and slender in *T. froehlichi*, wider and robust in *T. ubuntu*) or based on shape of the T10e (Y-shaped in *T. froehlichi*, while heart-shaped in *Tupiperla* sp. 4).

Distribution. Brazil, São Paulo. This species is known for its type locality in Rio Betari, Parque Estadual Turístico do Alto Ribeira (PETAR), Iporanga. No new records were made after the description of the species.

Remarks. This species is only known by the holotype

Type material. Holotype. Brazil, Iporanga, PETAR, SP, Rio Betari: 1 male, 15.IX.2006. (MZUSP). [examined]

Figure 14 - *Tupiperla froehlichi* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla gracilis (Burmeister, 1839)

(Figure 15)

Semblis gracilis Burmeister, 1839, p. 876

Capnia (*Gripopteryx*) *gracilis*: Pictet, 1841, p. 330; Walker, 1852 p 175; Hagen, 1861 p. 303

Gripopteryx gracilis: Klapálek, 1904 p.10; Claassen, 1940, p. 31; Jewett, 1960 p.

Paragripopteryx gracilis: Illies, 1963, p. 179.

Tupiperla gracilis: Froehlich, 1969 p.29; Froehlich, 1998, p.20; Froehlich, 2010, p. 138; Bispo & Lecci, 2011, p. 379; Froehlich, 2011, p. 602; Avelino-Capistrano & Nessimian, 2013. p. 188; Novaes & Bispo, 2014, p. 439; Froehlich, 2016, p. 176; Goncalves, Novaes & Salles, 2017, p. 570; Novaes, Vilela, Lopez & Ferreira, 2018, p. 197; Pessacq, del Carmen Zúñiga & Duarte, 2019, p. 194; Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla gracilis* can be distinguished from other congeners by elongated paraprocts, apex enlarged and truncated, spatulate-shape (Figure 15 B). Paraprocts distally convergent, disto-lateral face concave spoon-shape (Figure 15 C). T10e shortened, lateral margins slightly divergent, apex superficial medial indentation (Figure 15 A). Subgenital plate oblique, apex round-triangular (Figure 15 C).

Comparative diagnosis. *Tupiperla gracilis* is most similar to *T. sulina*, *T. flinti*, and *T. amorimi* due to shape and apex of the paraprocts in lateral view and the quadrangular-shape T10e. It can be distinguished from *T. sulina* by the appearance of the paraprocts (elongated in *T. gracilis*, stout in *T. sulina*). It can be distinguished from *T. umbya* due to the shape of the ventral margin of the paraprocts (straight in *T. gracilis*, sinuous in *T. umbya*). In the case of the other similar species, it can be distinguished from them based on the shape of the T10e apex (quadrangular-shape in *T. gracilis*, V-shape in *T. amorimi*).

Distribution. This species has a uncertain type locality, as Burmeister (1839) only states Brazil, however the type locality is plausibly in the state of Rio de Janeiro as stated by Froehlich (1998), but without further explanation as to why. This species is one of most widely distributed species in the genus, occurring within the boundaries of the Atlantic Forest in the states of Minas Gerais (Froehlich 1998, 2016, Novaes & Bispo 2014), Espírito Santo (Gonçalves *et al.*, 2017), São Paulo (Froehlich 1969, 1998, Bispo & Lecci 2011), Rio de

Janeiro (Froehlich 1998, Nessimian *et al.*, 2009, Avelino-Capistrano & Nessimian 2013), and also Argentina, in the Misiones Province (Romero 2017).

Remarks. Holotype verified by pictures sent by the Zentralmagazin Naturwissenschaftlicher Sammlungen / Natural Sciences Collections (ZNS) Dr. Hendrik Müller (Figure 2). This species shows some variation in the torsion of the paraprocts as demonstrated by Almeida *et al.* (in press). They can be twisted and entangled, or be straight and flattened.

Type material. Holotype, Male: BRÉSIL. Museum Halle. [examined by photographs]

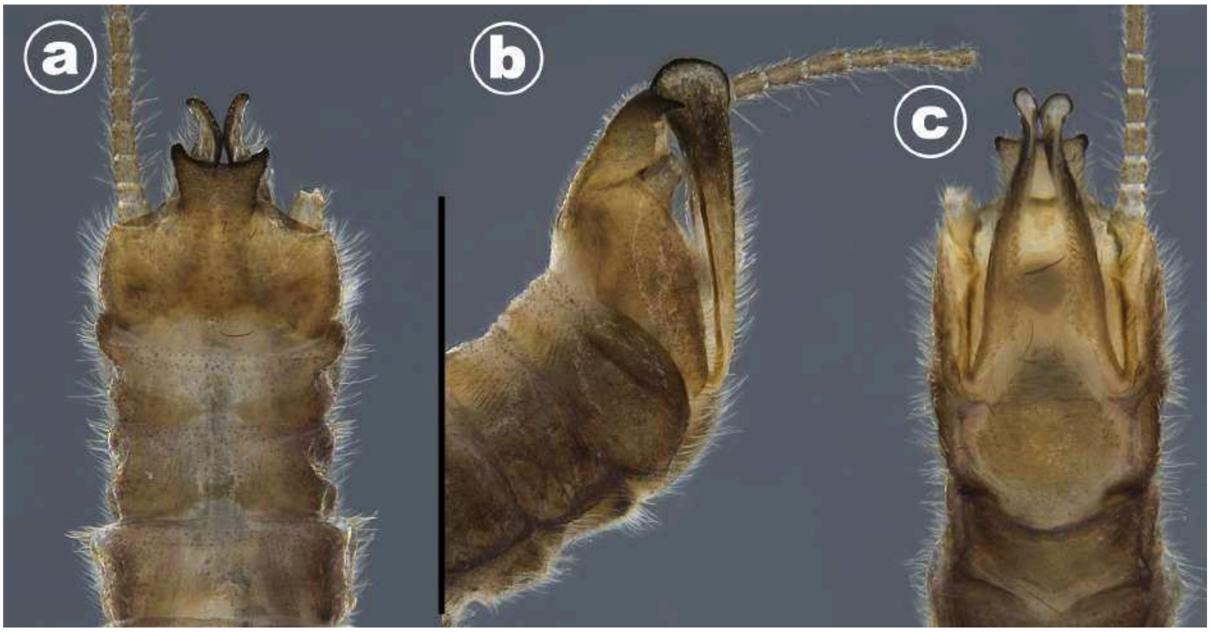


Figure 15 - *Tupiperla gracilis* adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla guariru Duarte, Bispo & Calor, 2014

(Figure 16)

Tupiperla guariru Duarte, Bispo & Calor, 2014: p141; Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla guariru* can be distinguished from other congeners by elongated paraprocts, apex enlarged and rounded, elliptical in shape, distal dorsal margin spine-like projection dorsally pointed (Figure 16 B). Paraprocts distally convergent, disto-lateral face concave (Figure 16 C). T10 extension short, lateral margins slightly conergent, apex superficial medial indentation (Figure 16 A). Subgenital plate oblique, apex round-triangular (Figure 16 C).

Comparative diagnosis. *Tupiperla guariru* is most similar to *T. modesta*, *T. jumirim*, and *T. gracilis* due to width and shape of the apex of the paraprocts in lateral view and the rectangular-shape of the T10e. It can be distinguished from *T. modesta* by the width of the paraprocts (gradually expanded apically in *T. guariru*, similar width throughout in *T. modesta*). It can be distinguished from *T. jumirim* due to the shape of the apex of the dorsal margin of the paraprocts (with a spine-like projection in *T. guariru*, rounded in *T. jumirim*). In the case of the other similar species, it can be distinguished from them based on the width of the T10e apex (slender in *T. guariu*, wider in *T. jumirim* and *T. modesta*) or based on shape of the T10e (rectangular in *T. guariru*, quadrangular in *T. gracilis*).

Distribution. Brazil, Bahia. This species is known from the type locality in Serra da Jiboia, Varzedo and one additional site in Amargosa, a few kilometers apart. No new records were made after the description of the species.

Type material. Holotype, male: BRAZIL: Bahia: Varzedo, Serra da Jibóia, Fazenda Baixa da Areia, Córrego Cai Camarão, 12°57'39.2"S, 39°26'53.7"W, 27.VIII.2013, light trap, Calor A.R., Gomes V. and Zanata A.M. (MZUSP). [examined]

Figure 16 - *Tupiperla guariru* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla illiesi Froehlich, 1998

(Figure 17)

Paragripopteryx gracilis Illies, 1963: 179 (in part).

Tupiperla gracilis Froehlich, 1969: 29 (in part).

Tupiperla illiesi Froehlich, 1998: 24; Froehlich, 2010: 138 (Catalog); Froehlich, 2011: 602; Pessacq, Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.); Sarmento, Duarte, Teixeira & Salles 2025, p. 5.

Diagnosis. *Tupiperla illiesi* can be distinguished from other congeners by the male with paraprocts elongated, apex truncated with a subapical spine-like process robust laterally positioned projecting dorsally (Figure 17 B). Paraprocts uniform width along most of length; dorsal margin serrated with minute spine-like setae (Figure 17 B). Paraprocts distally convergent, subapical spine-like projection outwards (Figure 17 C). T10 extension elongated, apex with median excavation (Figure 17 A). Antennae longer than forewings. The subgenital plate is obliquely shaped with a triangular rounded apex (Figure 17 C).

Comparative diagnosis. *Tupiperla illiesi* is most similar to *Tupiperla* sp. 6, *T. tucum*, and *T. claudius* due to the spine-like projection at the apex of the paraprocts in lateral view and the elongated swallow-tailed T10e. It can be distinguished from *Tupiperla* sp. 6 due to the presence, in this species, of a medial notch which is absent in *T. illiesi*. It can be distinguished from *T. tucum* due to the apex of the paraprocts (robust subapical spine-like process in *T. illiesi*, thin latero-distal spine-like process in *T. tucum*). In the case of the other similar species, it can be distinguished from them based on the depth of the median excavation of T10e (deeper in *T. illiesi*, shallower in *T. claudius*).

Distribution. Brazil, São Paulo. This species is known from the type locality in Estação Biológica de Boracéia, Salesópolis. This species occurs in the coastal mountains of São Paulo State in Reserva Biológica Alto da Serra de Paranapiacaba, Santo André; Parque Estadual Carlos Botelho, São Miguel Arcanjo; Parque Estadual Intervales, Iporanga; Parque Estadual Campos do Jordão, Campos do Jordão (Sarmento *et al.*, 2025).

Type material. Holotype, Male: BRAZIL, SÃO PAULO, Salesópolis, Estação Biológica de Boracéia, 12.IX.1988, C.G. Froehlich and O. Froehlich leg. (MZUSP). [examined]

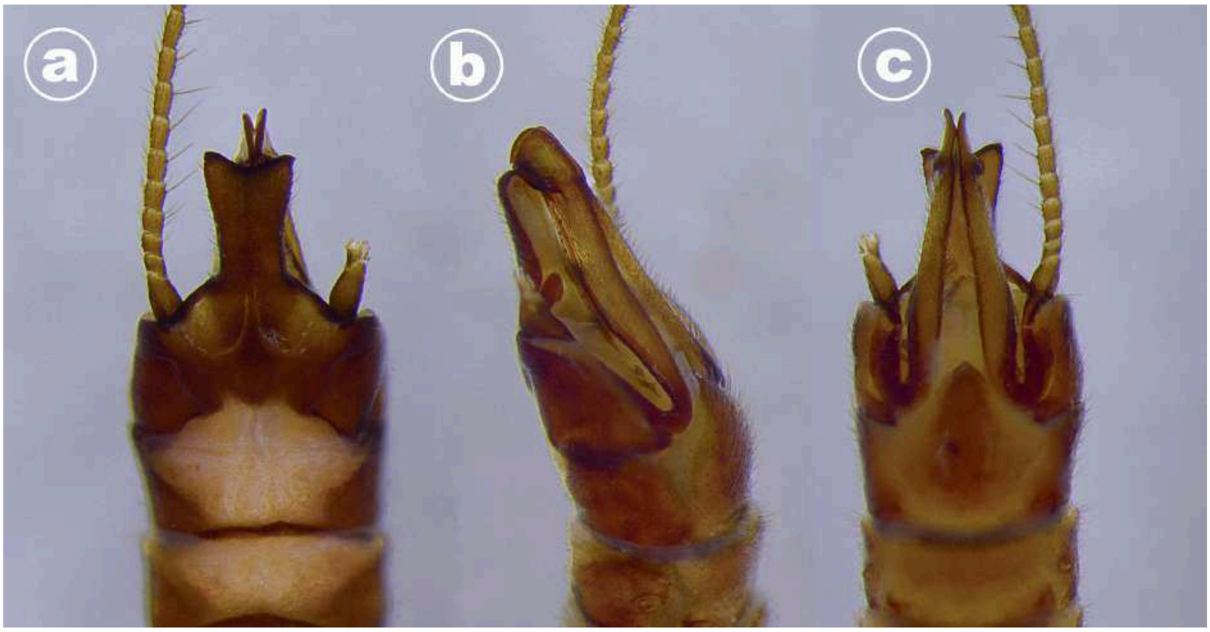


Figure 17 - *Tupiperla illiesi* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla jumirim Bispo & Froehlich, 2007

(Figure 18)

Tupiperla jumirim Bispo & Froehlich, 2007: 216; Froehlich, 2010: 138; Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla jumirim* can be distinguished from other congeners by the absence of the femoral spine; Paraprocts elongated, continuous margins, apex slightly curved dorsally (Figure 18 B). Paraprocts distally convergent, disto-lateral face slightly outcurved (Figure 18 C). T10 extension shortened, lateral margins slightly convergent, apex with ventrally projecting denticles (Figure 18 A). Subgenital plate oblique, apex round-triangular (Figure 18 C).

Comparative diagnosis. *Tupiperla jumirim* is most similar to *T. modesta*, *Tupiperla* sp. 8, and *T. guariru* due to the shape and short quadrangular-shaped T10e. It can be distinguished from

Tupiperla sp. 8 to the angulation of the paraprocts (straight in *T. jumirim*, with distally curved in *Tupiperla* sp. 8). It can be distinguished from *T. modesta* due to the shape of the ventral margin of the paraprocts (straight in *T. jumirim*, and sinuous in *T. modesta*). In the case of the other similar species, it can be distinguished from them based on lateral margins in T10e (parallel in *T. jumirim*, and convergent in *T. guariru*) or based on shape of the T10e (rectangular in *T. jumirim*, quadrangular in *Tupiperla* sp. 8).

Distribution. Brazil, Goiás. This species is only know for its type locality in Pouso Alto-Cruzeiro, National Park Chapada dos Veadeiros, Alto Paraíso. No new records were made after the description of the species.

Type material. Holotype Male: Brazil, Goiás State, Chapada dos Veadeiros, Alto Paraíso, Pouso Alto-Cruzeiro (138560 3700S; 478290 4100W), 18.xii.2006. (MZUSP). [examined]

Figure 18 - *Tupiperla jumirim* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla misionera Froehlich, 2002

(Figure 19)

Tupiperla misionera Froehlich, 2002: 38; Froehlich, 2010: 138 (Catalog); Novaes & Bispo, 2016; Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo, 2024; Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla misionera* can be distinguished from other congeners by shortened slender paraprocts; dorsal margin slightly straight, ventral margin convex, apex rounded and acuminate (Figure 19 B). Paraprocts basally parallel, medially convergent with gentle S-shaped curvature, apically realigned parallel (Figure 19 C). T10e shortened, lateral margins parallel, apex with small median excavation (Figure 19 A). Subgenital plate oval, central region more sclerotized, distal margin truncated (Figure 19 C).

Comparative diagnosis. *Tupiperla misionera* is most similar to *T. eleonorae*, *T. sulina*, and *T. umbya* due the shape of the ventral margin and apex of the paraproct in lateral view and the quandragular-shape T10e. It can be distinguished from *T. eleonorae* to the shape of the ventral margin of the paraprocts (sinuous in *T. misionera*, and dorsally curved, convex, in *T. eleonorae*). It can be distinguished from *T. sulina* due to the shape of the apex of the paraprocts (accuminated in *T. misionera*, and truncated in *T. sulina*). In the case of the other similar species, it can be distinguished from them based on lateral margins in T10e (parallel in *T. misionera*, and divergent in *T. umbya*) or based on width of the T10e (robust in *T. misionera*, and slender in *T. eleonorae*).

Distribution. Argentina, Misiones; Brazil, Rio Grande do Sul, Santa Catarina, Paraná This species is known from the type locality in 15 km E. of San José, Arroyo Coati (Foehlich, 2022). This species occurs especially in the south of South America: Santa Margarida do Sul; Orleans; São Francisco do Sul; Iguaçu National Park, Ceu Azul (Novaes & Bispo, 2016, Romero 2017, Duarte *et al.*, 2024).

Type material. Holotype: ARGENTINA, Misiones, Arroyo Coati, 15 km E. of San José, 18–19.XI.1973, O.S. Flint, Jr. (USNM).

Figure 19 - *Tupiperla misionera* adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla modesta Froehlich, 1998

(Figure 20)

Tupiperla modesta Froehlich, 1998: 26; Froehlich, 2010: 138 (Catalog); Froehlich, 2011: 603; Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla modesta* can be distinguished from other congeners by elongated; paraprocts continuous width, dorsal margin slightly sinuous and slightly curved dorsally, rounded apex (Figure 20 B). Paraprocts subparallel, disto-lateral face slightly flattened (Figure 20 C). T10 extension shortened, lateral margins slightly convergent, apex posteriorly projecting denticule (Figure 20 A). Subgenital plate oblique, apex round-triangular (Figure 20 C).

Comparative diagnosis. Comparative diagnosis. *Tupiperla modesta* is most similar to *T. jumirim*, *Tupiperla* sp. 8, and *T. guariru* due to the shape and short quadrangular-shaped T10e. It can be distinguished from *T. guariru* due to the projection on the distal-dorsal margin of the paraprocts (rounded, absent, in *T. modesta*, and a spine-like projection, in *T. guariru*). It can be distinguished from *T. jumimirm* due to the shape of the ventral margin of the paraprocts (straight in *T. jumirim*, and sinuous in *T. modesta*). In the case of the other similar species, it can be distinguished from them based on lateral margins in T10e (parallel in *T. modesta*, and convergent in *T. guariru*) or based on shape of the T10e (rectangular in *T. modesta*, quadrangular in *Tupiperla* sp. 8).

Distribution. Brazil, São Paulo. This species is only known for its type locality in Campos do Jordão State Park, Campos do Jordão, São Paulo State. No new records were made after the description of the species.

Type material. Holotype, Male: SÃO PAULO, Campos do Jordão, Parque Estadual, 26/XI/1986. (MZUSP). [examined]

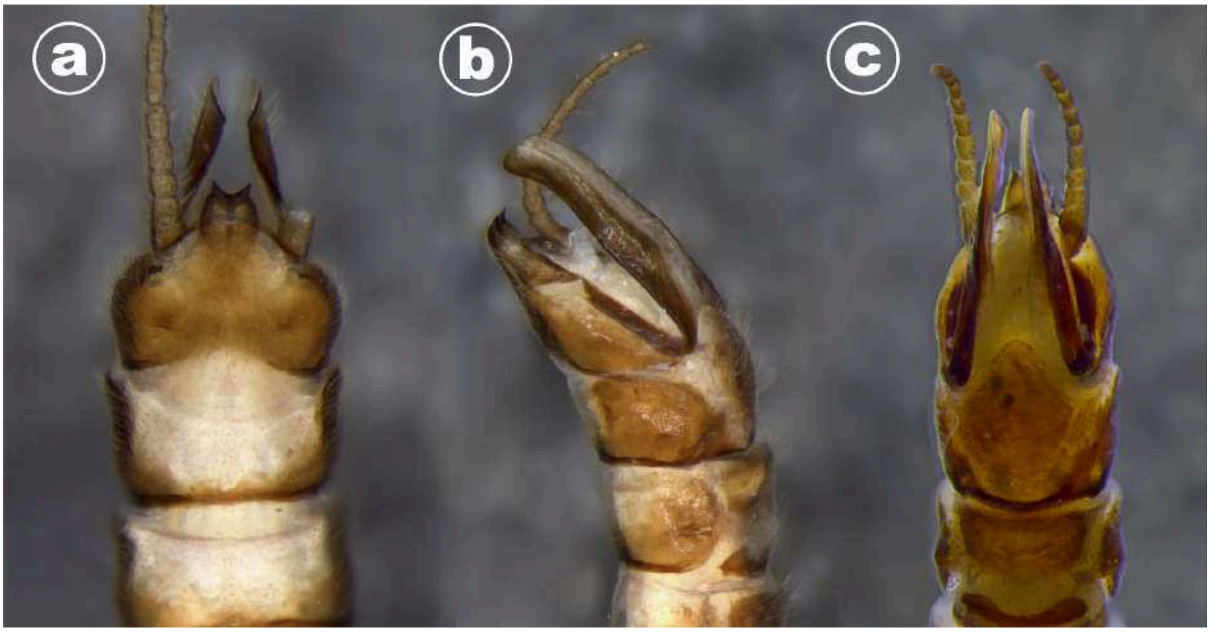


Figure 20 - *Tupiperla modesta* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla oliveirai Froehlich, 1998

(Figure 21)

Tupiperla oliveirai Froehlich, 1998: 38; Froehlich, 2010: 138 (Catalog); Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. Diagnosis. The male of *Tupiperla oliverai* can be distinguished from other congeners by elongated, dilated paraprocts with geniculated apex, forming inverted L-shape

(Figure 21 B). Dorsal margin medially dilated, apex rounded (Figure 21 B). Paraprocts subparallel, disto-lateral face slightly cylindrical (Figure 21 C). T10 extension shortened, lateral margins strongly divergent, apex V-shaped, ending in two spine-like projections (Figure 21 A). Subgenital plate oblique, apex round-triangular (Figure 21 C).

Comparative diagnosis. *Tupiperla oliveirai* is most similar to *Tupiperla* sp. 3, *T. amorimi*, and *T. flinti* due to the dilated paraprocts with geniculated apex in lateral view and the V-shape T10e. It can be distinguished from *Tupiperla* sp. 3 by the shape of the apex of the paraprocts (thin spine-like process in *Tupiperla* sp. 3, and rounded, in *T. oliveirai*). It can be distinguished from *T. amorimi* due to the apex of the paraprocts (dilated in *T. oliveirai*, and flattened, spoon-shaped, in *T. amorimi*). In the case of the other similar species, it can be distinguished from them based on the shape and width of the T10e (V-shape and robust in *T. oliveirai*, and short and shallow median excavation in *T. flinti*).

Distribution. Brazil, Goiás. This species is only known for its type locality in Córrego Inferno, Pirenópolis. No new records were made after the description of the species.

Type material. Holotype, Male: GOIÁS, Pirenópolis, Córrego Inferno, 13.I.1994, LGO. (MZUSP). [examined]

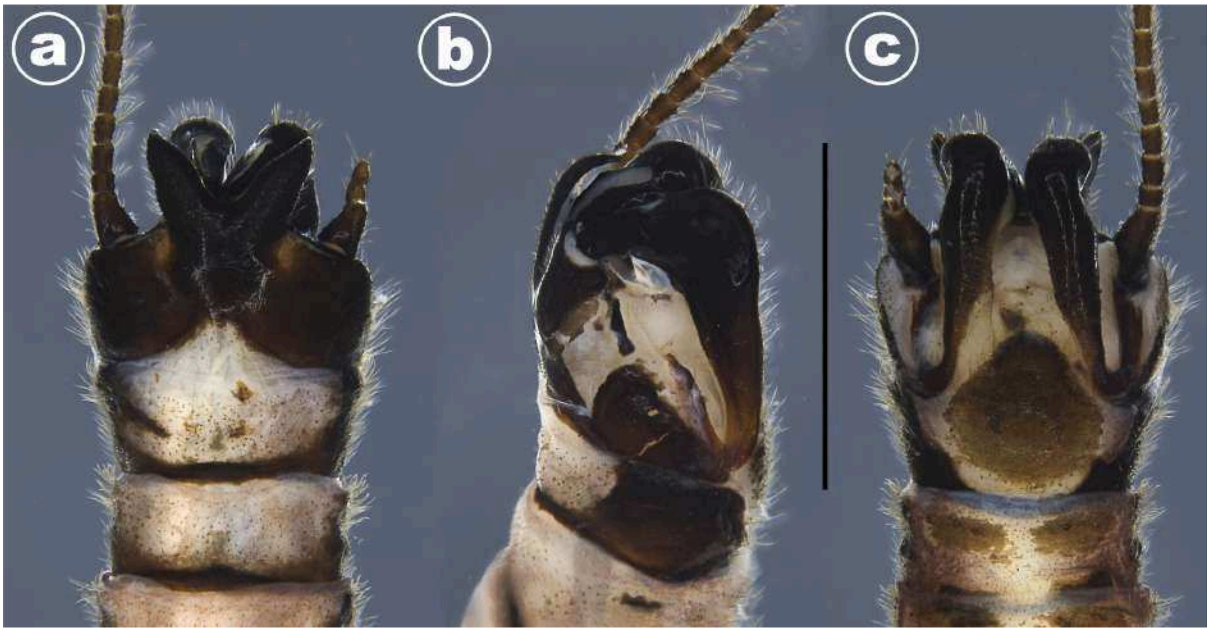


Figure 21 - *Tupiperla oliveirai* adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla pessacqi Duarte, Novaes & Bispo, 2019

(Figure 22)

Tupiperla pessacqi Duarte, Novaes & Bispo 2019, p518; Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla pessacqi* can be distinguished from other congeners by elongated paraprocts, ventral margin with subapical spine-like lateral process (flap), and a distal region acuminated, apex ending in an acute angle (Figure 22 B). Paraprocts are parallel, convergent distally, lateral process meeting distally, forming a kite-shape (Figure 22 C). The T10e is short, slender with an indention (Figure 22 A). The subgenital plate is obliquely shaped, with a round-triangular apex (Figure 22 C).

Comparative diagnosis. *Tupiperla pessacqi* is most similar to *T. zwicki*, *T. reichardti*, and *T. modesta* due to the shape of the ventral margin of the apex in lateral view and the short and slender rectangular shape of T10e. It can be distinguished from *T. reichardti* by the subapical lateral process (flap) in the ventral margin of the apex of the paraprocts (absent in *T. reichardti*, and present in *T. pessacqi*). It can be distinguished from *T. zwicki* due to the shape of the apex of the paraprocts (rounded in *T. zwicki*, and acuminated ending in an acute angle in *T. pessacqi*). In the case of the other similar species, it can be distinguished from them based on lateral margins in T10e (divergent only in the apical half in *T. zwicki*, and parallel in *T. pessacqi*) or based on the shape and width of the T10e (short and round in *T. modesta*, and longer and slender in *T. pessacqi*).

Distribution. Brazil, Santa Catarina. This species is known for its type locality in Cachoeira Avencal, Urubici and some few others located kilometers apart in the vicinity of the São Joaquim Nacional Park and the Serra Furada State Park on the municipalities of Urubici and Grão Pará. No new records were made after the description of the species.

Type material. Holotype. Male. Brazil: Santa Catarina: Urubici, Cachoeira Avencal, 1229 m.a.s.l., S28°02.798, W49°37.070, 08.i.2010, light trap, HF Mendes, LC Pinho & RA Moretto col. (MZUSP). [examined]

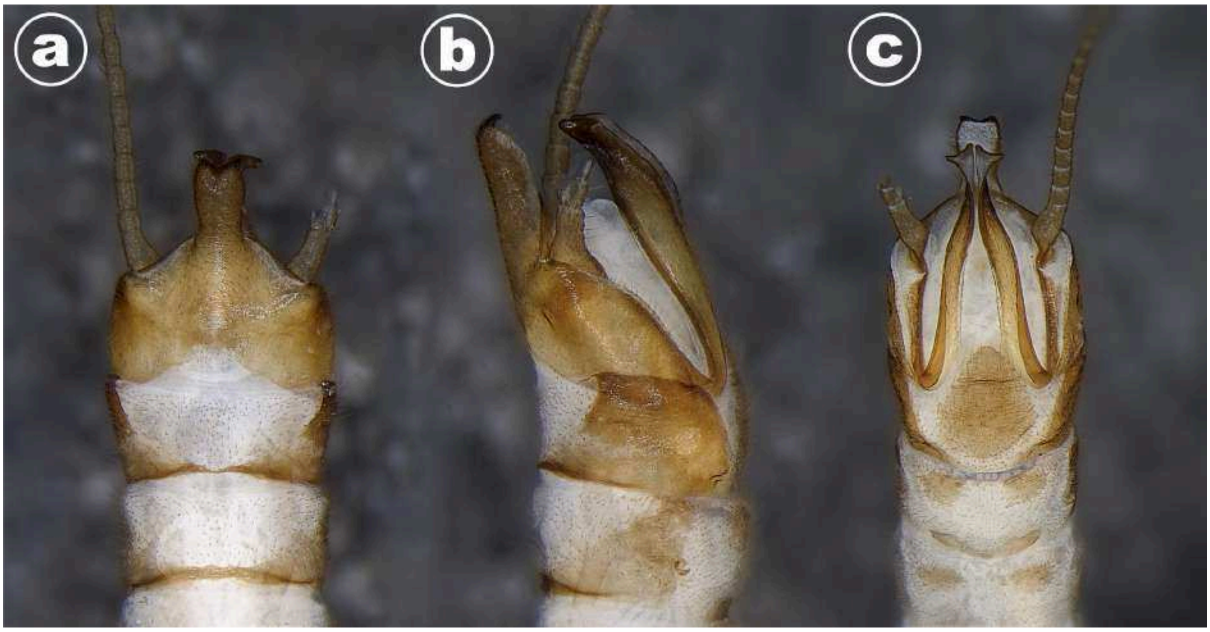


Figure 22 - *Tupiperla pessacqi* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla pinhoi Duarte, Novaes & Bispo, 2019

(Figure 23)

Tupiperla pinhoi Duarte, Novaes & Bispo 2019, p513; Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla pinhoi* can be distinguished from other congeners by elongated paraprocts with sinuous margins and apices curved downward in a hooked shape; dorsal margin from base to preapical bearing minute outward-pointing teeth (Figure 23 B). Paraprocts divergent at base, distally convergent, ventral margin distinctly serrated with spine-like setae (Figure 23 C). T10 extension elongated, apex with distinct swallow-shaped median excavation (Figure23 A). Subgenital plate oblique, apex rounded triangular (Figure 23 C).

Comparative diagnosis. *Tupiperla pinhoi* is most similar to *Tupiperla* sp. 2, *T. reichardti*, and *T. serrulata* due to the dorsal margin serrated with minute spine-like setae on the paraprocts in lateral view and the elongated swallow-shaped T10e. It can be distinguished from *T. serrulata* by the shape of the apex of the paraprocts (narrowing and rounded in *T. serrulata*, and curved downward in a hooked shape in *T. pinhoi*). It can be distinguished from *Tupiperla* sp. 2 due to the presence of subapical spine-like lateral process on the lateral face of the paraprocts (present in *T. zwicki*, and absent in *T. pessacqi*). In the case of the other similar species, it can be distinguished from them based on lateral margins in T10e (parallel in *T. reichardti*, and divergent in *T. pinhoi*) or based on the shape and width of the T10e (long and robust, heart-shaped, in *T. serrulata*, and stouter and teeth projected upwards in *T. pinhoi*).

Distribution. Brazil, Santa Catarina. This species is known only from the type locality in Cachoeira Avencal, Urubici. No new records were made after the description of the species.

Type material. Holotype. Male. Brazil: Santa Catarina: Urubici, Cachoeira do Avencal, 1229 m a.s.l., S28°02.798, W49°37.070, 08.i.2010, net, HF Mendes, LC Pinho & RA Moretto col. (MZUSP). [examined]

Figure 23 - *Tupiperla pinhoi* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla reichardti Froehlich, 1998

(Figure 24)

Tupiperla reichardti Froehlich, 1998: 28; Froehlich, 2010: 138 (Catalog.); Froehlich, 2011: p603; Novaes & Bispo, 2014: p440, Pessacq, del Carmen Zúñiga & Duarte, 2019: p194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla reichardti* can be distinguished from other congeners by elongated paraprocts, ventral notch, a subapical spine-like lateral process outward pointed; distal region curved downward, forming a slight hook-shaped (Figure 24 B). Paraprocts parallel, lateral process to project outward and anteriorly (Figure 24 C). T10 extension elongated, margins parallel, apex with superficial median excavation (Figure 24 A). Subgenital plate oblique, apex round-triangular (Figure 24 C).

Comparative diagnosis. *Tupiperla reichardti* is most similar to *Tupiperla* sp. 1, *Tupiperla* sp. 6, and *T. serrulata* due to the shape of the ventral margin and a lateral process of the paraprocts in lateral view, and the elongated swallow-shaped T10e. It can be distinguished from *Tupiperla* sp. 1 by the form of the ventral margin of the paraprocts (continuous in *Tupiperla* sp. 1, and medial notch in *T. reichardti*). It can be distinguished from *Tupiperla* sp. 6 due to the lateral process in the face of the paraprocts (absent in *Tupiperla* sp. 6, and present in *T. reichardti*). In the case of the other similar species, it can be distinguished from them based on the median excavation in T10e (deep in *T. serrulata*, and shallow in *T. reichardti*) or based on the lateral margins of the T10e (divergent, in *Tupiperla* sp. 6, and parallel in *T. reichardti*).

Distribution. Brazil, São Paulo; Minas Gerais. This species is known for its type locality in Campos do Jordão State Park, Campos do Jordão and some few others locaties kilometers apart in Serra do Japi, Jundiai and Poços de Caldas. No new records were made after the description of the species.

Type material. Holotype, Male: SÃO PAULO, Campos do Jordão, Parque Estadual, 22.XII.1986, CGF and M. Gimenes. (MZUSP). [examined]

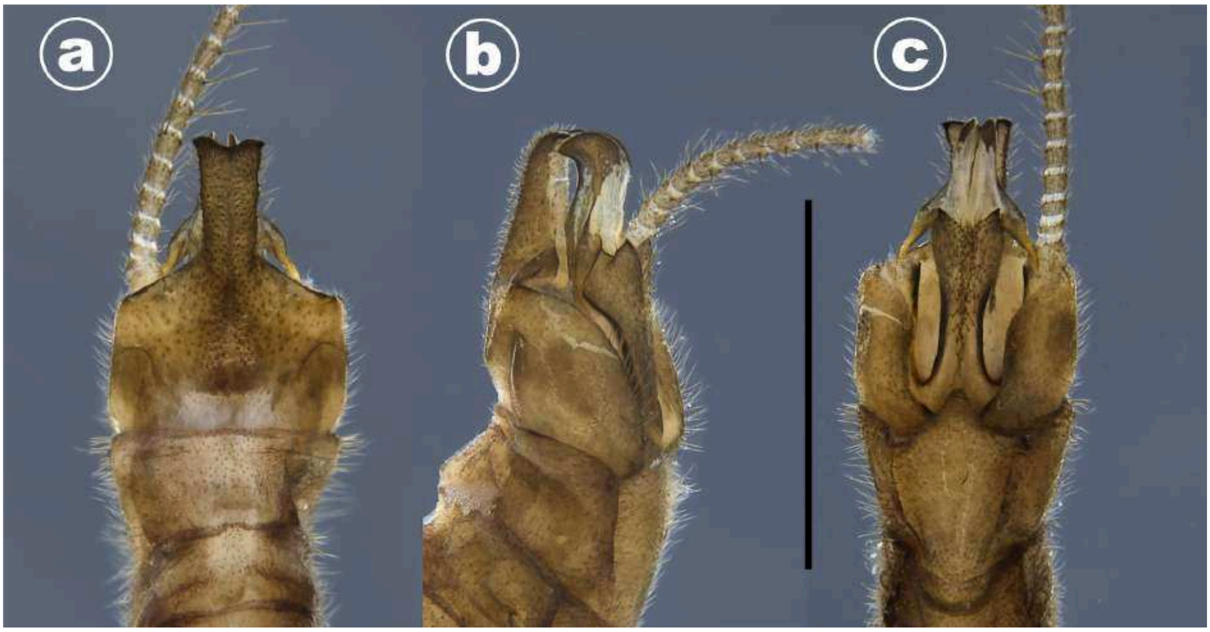


Figure 24 - *Tupiperla reichardti* adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla robusta Froehlich, 1998

(Figure 25)

Tupiperla robusta Froehlich, 1998: 29; Froehlich, 2010: 138 (Catalog.); Froehlich, 2011: p603; Pessacq, del Carmen Zúñiga & Duarte, 2019: p194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla robusta* can be distinguished from other congeners by its elongated paraprocts, base narrow and expand distally, dorsally pointed acuminated apex. Parprocts ventral margin bears a subapical, rounded, enlarged region that tapers into a narrowed apex (Figure 25 B). Paraprocts, subparallel distally (Figure 25 C). T10e short and broad, with parallel margins, two spine-like processes in the central region, and an almost straight apical margin (Figure 25 A). The subgenital plate is obliquely shaped with a rounded apex (Figure 25 C).

Comparative diagnosis. *Tupiperla robusta* is most similar to *Tupiperla* sp. 7, *Tupiperla* sp. 8, *T. guariru* and *T. jumirim* due to the shape of the apex, and ventral margin of the paraprocts in lateral view, and the short quandragular T10e. It can be distinguished from *Tupiperla* sp. 8 by the shape of the apex of the paraprocts (round and broad in *Tupiperla* sp. 8, and narrow, forming an acute projection in *T. robusta*). It can be distinguished from *Tupiperla* sp. 7 due to the relation of the ventral and dorsal margin of the paraprocts (subparallel, for most of its length, in *Tupiperla* sp. 7, and divergent, enlarging towards the apex, in *T. robusta*). In the case of the other similar species, it can be distinguished from them based on the shape of T10e (rectangular in *T. jumirim*, and quadrangular in *T. robusta*) or based on the lateral margins of the T10e (convergent, in *T. guariru*, and parallel in *T. robusta*).

Distribution. Brazil, São Paulo. This species is known for its type locality in Campos do Jordão State Park, Campos do Jordão. No new records were made after the description of the species.

Remarks. Holotype verified. This species was previously recorded from the state of Minas Gerais (Novaes & Bispo, 2014) and Espirito Santo (Goncalves, Novaes & Salles, 2017), however specimens identified previously do not belong to this species. This decision is based on additional material from Parque Nacional do Caparao.

Type material. Holotype, Male: SÃO PAULO, Campos do Jordão, Parque Estadual, 22/IV/1987, CGF and A.C.R. Ferreira. (MZUSP). [examined]

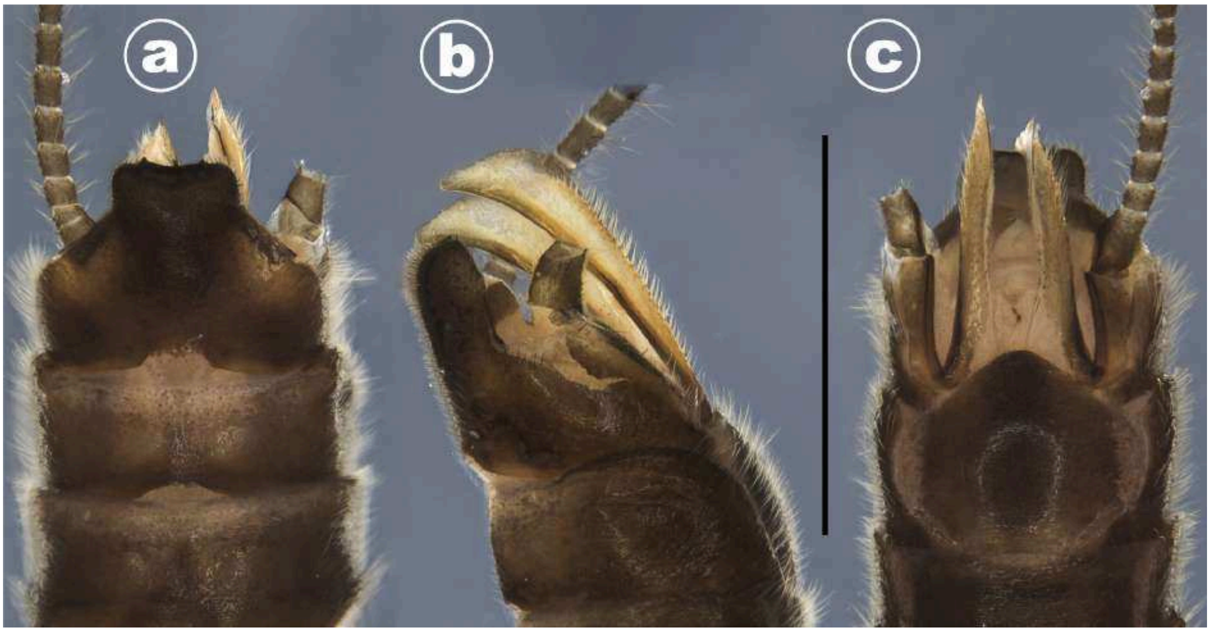


Figure 25 - *Tupiperla robusta* adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla sepeensis Novaes & Bispo, 2016

(Figure 26)

Tupiperla sepeensis Novaes & Bispo 2016, p513; Pessacq, del Carmen Zúñiga & Duarte, 2019: p194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. *Tupiperla sepeensis* can be distinguished from other congeners by the male paraprocts, elongated. The paraprocts maintain a constant width over most of their length and have a rounded distal region, dorsal margin with preapical spine-like projection (Figure 26 B). Paraprocts distally convergent, preapical dorsal margin spine-like process projecting outwards (Figure 26 C). The T10e is elongated, with an apical median excavation forming a swallow-tailed shape (Figure 26 A). Subgenital plate diamond-shape. (Figs. 26 C).

Comparative diagnosis. *Tupiperla sepeensis* is most similar to *Tupiperla* sp. 4, *T. ubuntu,* and *T. froehlichi*, due to the shape of the ventral margin and length proportions of the paraprocts in lateral view, and the elongated T10e. It can be distinguished from *T. ubuntu* by the shape of the apex of the paraprocts (truncated in *T. ubuntu*, and rounded in *T. sepeensis*). It can be distinguished from *T. froehlichi* due to the shape of the dorsal margin of the paraprocts (angulated, concave, in *T. froehlichi*, and a straight in *T. sepeensis*). In the case of the other similar species, it can be distinguished from them based on the width and shape of T10e (long and Y-shaped in *T. ubuntu*, and short, swallow-tailed shaped in *T. sepeensis*) or based on the lateral margins of the T10e (divergent in *Tupiperla* sp. 4, and parallel, in *T. sepeensis*).

Distribution. Brazil, Rio Grande do Sul. This species is known only for its type locality in São Sepé. No new records were made after the description of the species.

Remarks. Holotype, only known specimen, could not be located.

Type material. Holotype male: Brazil, Rio Grande do Sul State, São Sepé, July-August 2013, light trap in forest, M. R. Spies. (MZUSP).

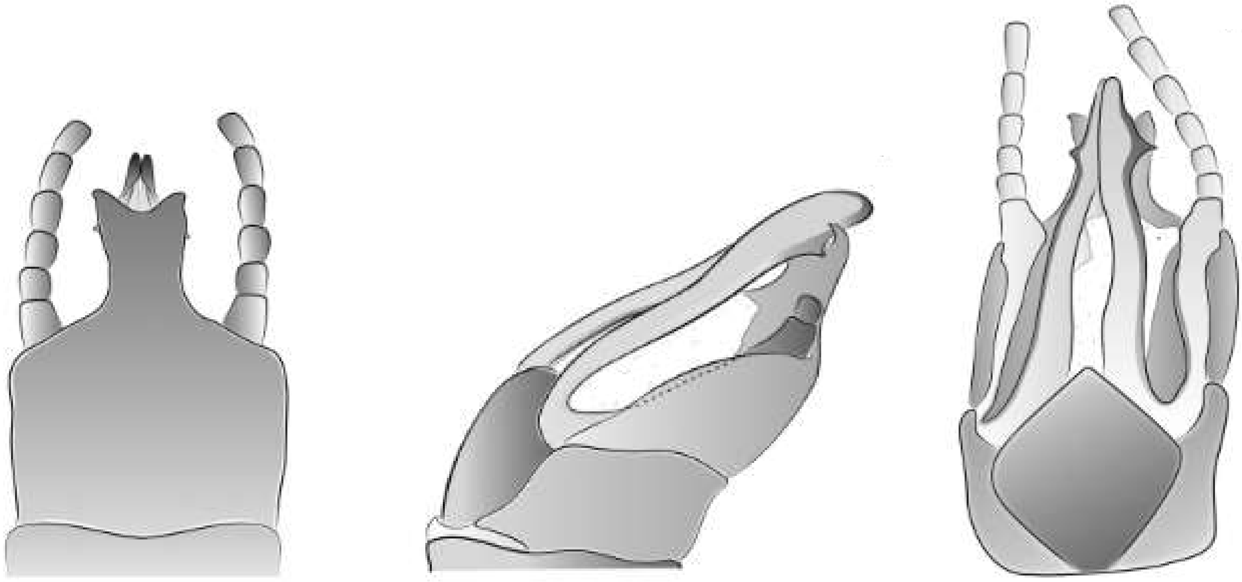


Figure 26 - *Tupiperla sepeensis* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C). (Figs. 1–3 Novaes & Bispo, 2016)

Tupiperla serrulata Duarte, Novaes & Bispo, 2019

(Figure 27)

Tupiperla serrulata Duarte, Novaes & Bispo, 2019, p517; Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla serrulata* can be distinguished from other congeners by its elongated paraprocts, constant width, acuminated apex, preapical dorsal margin with a row of minute spine-like setae (Figure 27 B). Paraprocts parallel, distally flattened (Figure 27 C). The T10e elongated, apex swallow-shape, deep median excavation (Figure 27 A). Forewing weak pterostigmatic crossvein, and antennae longer than the forewings. The subgenital plate is obliquely shaped with a triangular apex rounded (Figure 27 C).

Comparative diagnosis. *Tupiperla serrulata* is most similar to *T. claudius*, *T. pinhoi,* and *Tupiperla* sp. 4, due to presence of minute spine-like setae in the dorsal margin of the paraprocts in lateral view, and the elongated swallow-tailed T10e. It can be distinguished from *T. claudis* by the shape of the apex of the paraprocts (hook-shaped in *T. claudis*, and narrow, forming an acute angle in *T. serrulata*). It can be distinguished from *T. pinhoi* due to the region of the minute spine-like setae in the dorsal margin of the paraprocts (the base until the apex, in *T. pinhoi*, and at the apex in *T. serrulata*). In the case of the other similar species, it can be distinguished from them based on the shape of T10e (shorter and rounder in *Tupiperla* sp. 4, and longer and sharper in *T. serrulata*).

Distribution. Brazil, Santa Catarina. This species is known for its type locality in Serra Furada State Park, Grâo Pará and some few others localities kilometers apart in the vicinities of the São Joaquim National Park and the Serra Furada State Park on the municipalities of Urubici and Grão Pará. No new records were made after the description of the species.

Type material. Holotype, Male. Brazil: Santa Catarina: Grão Pará, Serra Furada State Park, S28°10'27", W49°23'38", 14.x-16.xi.2012, Malaise trap, LC Pinho, LC Gomes & AL Schlindwein col. (MZUSP). [examined]

Figure 27 - *Tupiperla serrulata* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla sulina Froehlich, 1998

(Figure 28)

Tupiperla sulina Froehlich, 1998: 29; Froehlich, 2010: 138 (Catalog.); Pessacq, del Carmen Zúñiga & Duarte, 2019: p194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla sulina* can be distinguished from other congeners by its paraprocts shortened, dorsal and ventral margin straight, terminating in a truncated apex (Figure 28 B). Paraprocts distally convergent, internal face concave (Figure 28 C). T10e shortened, spatulate, lateral margins parallel, apex with small median excavation (Figure 28 A). Subgenital plate oval, central region more sclerotized, distal margin triangular (Figure 28 C).

Comparative diagnosis. *Tupiperla sulina* is most similar to *T. eleonorae*, *T. misionera,* and *T. gracilis*, due to the ventral margin and apex of the paraprocts in lateral view, and the short quadrangular T10e. It can be distinguished from *T. eleonorae* by the apex of the paraprocts (acuminated in *T. eleonorae*, and truncated in *T. sulina*). It can be distinguished from *T. misionera* due to the ventral margin of the paraprocts (sinuous in *T. misionera*, and straight in *T. sulina*). In the case of the other similar species, it can be distinguished from them based on the width of T10e (wider and robust in *T. gracilis*, and thinner in *T. sulina*)

Distribution. Brazil, Santa Catarina. This species is known for its type locality in Spitzkopf Reserve (Serra do Itajaí National Park), Blumenau, and Morro do Baú, Ilhota, few kilometers apart. No new records were made after the description of the species.

Type material. Holotype, Male: SANTA CATARINA, Blumenau, Reserva Spitzkopf, 4.XII.1975, CGF, S.A. Vanin (MZUSP). [examined]

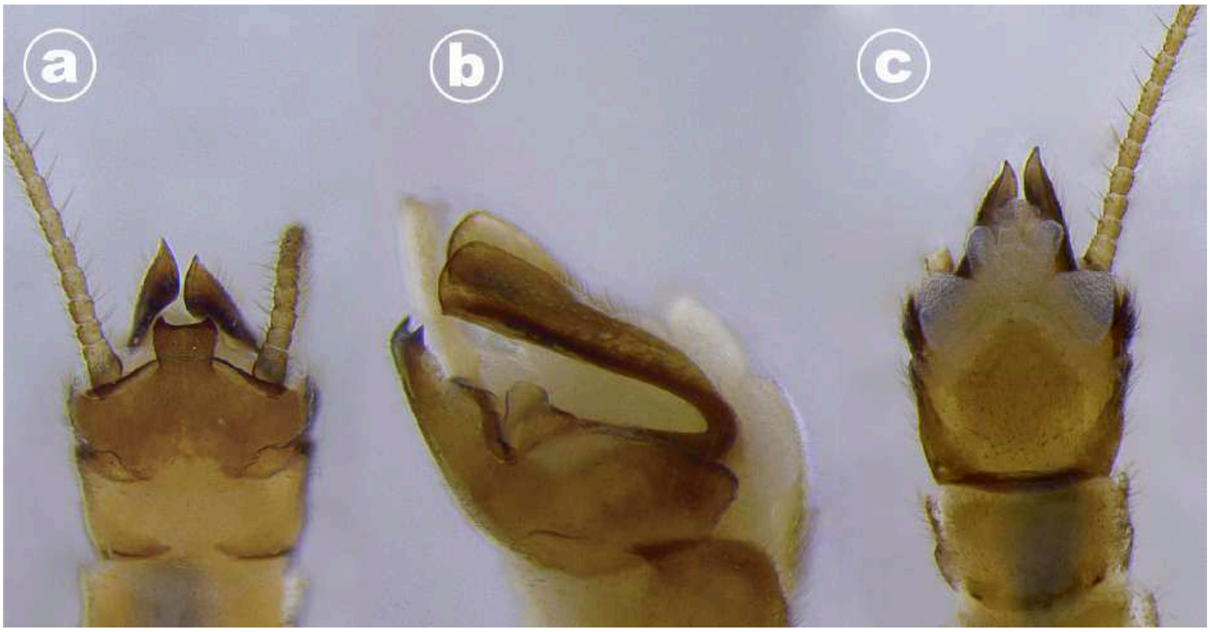


Figure 28 - *Tupiperla sulina* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla tessellata (Brauer, 1866)

(Figure 29)

Capnia (*Gripopteryx*) *tessellata* Brauer, 1866: 51;

Gripopteryx tessellata Klapálek, 1904, p. 9; Jewett, 1960: 172.

Gripopteryx neofriburgensis Navás, 1916: 27; Jewett, 1959: 150 (syn. fide Jewett, 1960).

Paragripopteryx gracilis Illies, 1963, p. 179.

Tupiperla tessellata Froehlich, 1998: p.20; Froehlich, 2008, p. 126; Stark *et al.*, 2009: 98; Froehlich, 2010: 139; Bispo & Froehlich, 2011, p. 139; Bispo & Lecci, 2011: 380; Avelino-Capistrano & Nessimian, 2013, p. 188; Avelino-Capistrano & Nessimian, 2014, p. 9; Duarte *et al.*, 2014, p. 86; Lecci *et al.*, 2014, p. 95; Novaes & Bispo, 2016, p. 488; Gonçalves *et al.*, 2017, p. 570; Pessacq *et al.*, 2019, p. 194.; Duarte & Lecci, 2024, p. e20230056; Varella & Parise, 2024, p. e20230072.; Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.); Lecci, Sarmento & Bispo, 2025, p. 552; Sarmento, Duarte, Teixeira & Salles 2025, p 4.

Diagnosis. The male of *Tupiperla tessellata* can be distinguished from other congeners by elongated paraprocts, dorsal and ventral margin uniform, apex curved downward in a slightly hooked-shape (Figure 29 B). Paraprocts, distally convergent (Figure 29 C). The T10e is elongated, apex bearing a distinct swallow-taillied, median excavation (Figure 29 A). Antennae are longer than the forewings. The subgenital plate is obliquely shaped with a triangular rounded apex (Fig 29 C).

Comparative diagnosis. *Tupiperla tessellata* is most similar to *T. claudius*, *T. tucum,* and *T. illiesi*, due to the shape of the apex of the paraprocts in lateral view, and the elongated and shallow-tailed T10e. It can be distinguished from *T. tucum* by the presence of a spine-like process in the apex of the paraprocts (present in *T. tucum*, and absent in *T. tessellata*). It can be distinguished from *T. claudius* due to the presence row of minute spine-like setae ventral margin of the paraprocts (present in *T. claudius*, and absent in *T. tessellata*). In the case of the other similar species, it can be distinguished from them based on the lateral margins of the T10e (divergent, in *T. illiesi*, and parallel in *T. tessellata*).

Distribution. Brazil. This species is know for the type locality in Rio de Janeiro (Brauer, 1866). This species, is the most well distributed, and occurs in the coastal mountains of Brazil, within the boundaries of the Atlantic Forest in the following states: Bahia (Duarte *et al.*, 2014a); Espírito Santo (Avelino-Capistrano & Nessimian 2014, Gonçalves et al. 2017); Minas Gerais (Froehlich 1998, Gonçalves *et al.*, 2017); Pernambuco (Lecci *et al.*, 2014); Rio de Janeiro (Brauer 1868*, Navás 1916, Jewett 1960, Froehlich 1998, Avelino-Capistrano & Nessimian 2013); Rio Grande do Sul (Novaes & Bispo 2016); Santa Catarina (Jewett 1959, 1960); São Paulo (Froehlich 1998, Bispo & Lecci 2011). *Tupiperla tessellata* represents the northernmost distributional record for the genus [Bonito-PE (Lecci *et al.*, 2014)], as well as the southernmost [São Sepe-RS (Novaes & Bispo 2016)].

Remarks. Holotype verified by pictures sent by the museum. The type is a female described by Brauer in 1868. Originally, the association of male and female was by the ratio of the length of antennae to the length of the posterior wing (Froehlich, 1998). Although this association was never contested, Sarmento *et al.* (2025) recently demonstrated a molecular association between the sexes, supporting Froehlich's (1998) and Jewett's (1960) earlier findings. It is valuable to remark that the type of *Gripopteryx neofriburguenses* Navás, 1916, a male adult, is lost however by the illustration and locality and is indeed a junior synonym of *T. tessellata* (Jewett, 1960; Froehlich, 1998; Sarmento *et al.*, 2025).

Type material. Holotype, Female: RIO DE JANEIRO, Naturhistorisches Museum, Vienna, Austria. [examined by photographs]

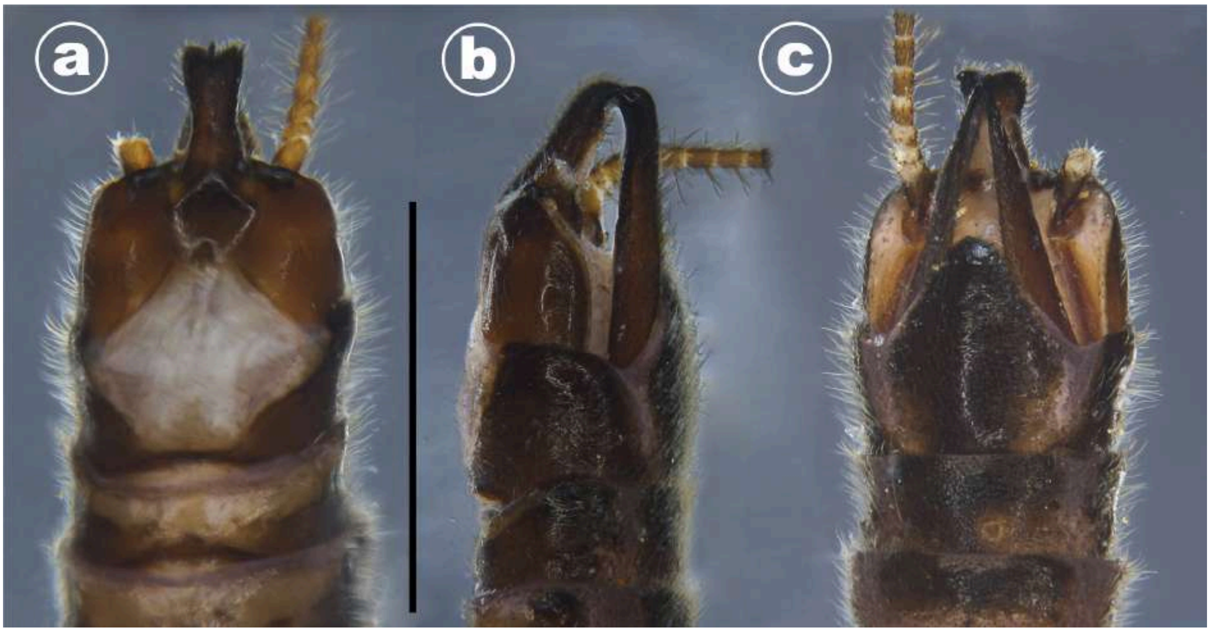


Figure 29 - *Tupiperla tessellata* adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla tucum Sarmento, Duarte, Teixeira & Salles 2025

(Figure 30)

Paragripopteryx gracilis Illies, 1963: 179 (in part.).

Tupiperla gracilis: Froehlich, 1969: 29 (in part.).

Tupiperla illiesi Froehlich, 1998: 24 (in part.); Froehlich, 2010: 138; Froehlich, 2011: 602; Pessacq, Zúñiga & Duarte, 2019: 194. Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Tupiperla tucum Sarmento, Duarte, Teixeira & Salles 2025, p 8.

Material examined. Holotype, Male: SÃO PAULO, Salesópolis, Estação Biológica de Boracéia, LED, 27.XI.2023, P.N. Taniguti and J.G. Lima leg. (S199) UFVB PL646

Diagnosis. The male of *Tupiperla tucum* can be distinguished from other congeners by elongated paraprocts, apex thin laterally positioned subapical spine-like process, distally curved downward in a slightly hooked shape (Figure 30 B). Paraprocts, dorsal margin with a row of minute spine-like setae (Figure 30 B). Paraprocts, distally convergent (Figure 30 C). T10e elongated, trapezoidal, apex deep median excavation (Figure 30 A). Antennae are longer than the forewings. The subgenital plate is obliquely shaped with a triangular rounded apex (Figure 30 C).

Comparative diagnosis. *Tupiperla tucum* is most similar to *T. claudius*, *Tupiperla* sp. 2*,* and *T. tessellata*, due to the spine-like projection at the apex of the paraprocts in lateral view, and the elongated and shallow-tailed T10e. It can be distinguished from *T. claudius* by the presence of the spine-like process on the apex of the paraprocts (absent in *T. claudius*, and present in *T. tucum*). It can be distinguished from *Tupiperla* sp. 2 due to the width of the paraprocts (broaded medially in *Tupiperla* sp. 2, and narrow in *T. tucum*). In the case of the other similar species, it can be distinguished from them based on the width of T10e (thinner in *T. tessellata*, and wider and robust in *T. tucum*)

Distribution. Brazil, São Paulo. This species is known for its type locality in Estação Biológica de Boracéia, Salesópolis. This species occurs on coastal mountains of São Paulo State in Reserva Biológica Alto da Serra de Paranapiacaba, Santo André and Parque Estadual Intervales, Iporanga.

Type material. Holotype, Male: SÃO PAULO, Salesópolis, Estação Biológica de Boracéia, LED, 27.XI.2023, P.N. Taniguti and J.G. Lima leg. (S199) UFVB PL646. (UFVB). [examined]

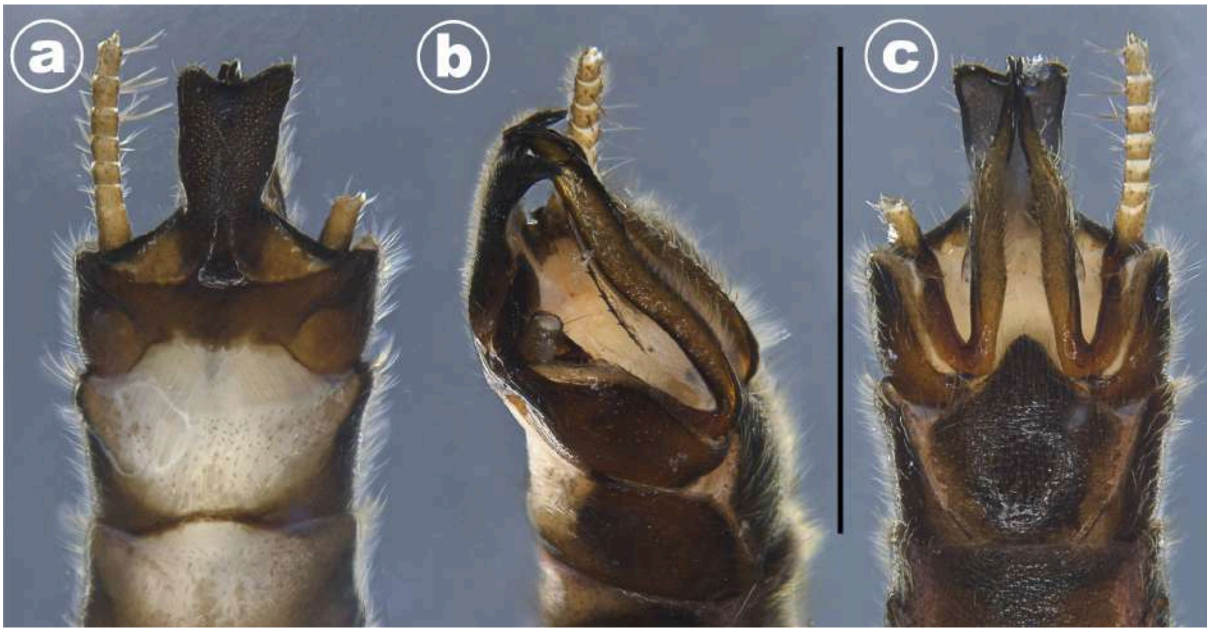


Figure 30 - *Tupiperla tucum* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla ubuntu Duarte, Novaes & Bispo, 2019

(Figure 31)

Tupiperla ubuntu Duarte, Novaes & Bispo, 2019, p520; Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. *Tupiperla ubuntu* can be distinguished from other congeners by elongated paraprocts, base narrow, expanding toward a truncated apex with sharp vertices (Figure 31 B). Paraprocts parallel, internal face concave (Figure 31 C). T10e elongated, small projection before the divergence of the arms, forming a Y-shape (Figure 31 A). The subgenital plate is brownish, darker centrally, rounded triangular, with the apex prolonged between the paraprocts (Figure 31 C).

Comparative diagnosis. *Tupiperla ubuntu* is most similar to *T. froehlichi*, *Tupiperla* sp. 4*,* and *T. sepeensis*, due to the shape of the ventral margin of the paraprocts in lateral view, and the elongated and Y-shaped T10e. It can be distinguished from *T. froehlichi* by the shape of the apex of the paraprocts (acuminated and acute in *T. froehlichi*, and truncated with sharp vertices in *T. ubuntu*). It can be distinguished from *Tupiperla* sp. 4 due to the presence of a preapical spine in the dorsal margin of the paraprocts (present in *Tupiperla* sp. 4, and absent in *T. ubuntu*). In the case of the other similar species, it can be distinguished from them based on the width and shape of T10e (slender and rectangular-shaped in *T. sepeensis*, and wider, robust, and Y-shaped in *T. ubuntu*)

Distribution. Brazil, Santa Catarina. This species is known for its type locality in Rio Minador, Orleans and some few others localities kilometers apart in the vicinity of the São Joaquim Nacional Park and the Serra Furada State Park on the municipalities of Orleans and Grão Pará. No new records were made after the description of the species.

Type material. Holotype. Male. Brazil: Santa Catarina: Orleans, Rio Minador, S28°10’24”, W49°24’37”, 19.viii-12.x.2013, Malaise trap, LC Pinho *et al.* col. (MZSP). [examined]

Figure 31 - *Tupiperla ubuntu* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla umbya Froehlich, 1998

(Figure 32)

Tupiperla umbya Froehlich, 1998: p. 31; Froehlich, 2010: p. 139 (Catalog.); Bispo & Lecci, 2011: p. 381; Froehlich, 2011: p. 603; Pessacq, del Carmen Zúñiga & Duarte, 2019: p. 194 (Catalog.).; Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla umbya* can be distinguished from other congeners by elongated paraprocts with a sinuous ventral margin, a distal spine-like process on the dorsal margin, apex ventral margin acuminated, twisted (Figure 32 B). Paraprocts convergent in the basal half and divergent distally, medially bent, disto-lateral face concave (Figure 32 C). The T10e is short, trapezoidal, with a shallow apical median excavation (Figure 32 A). Subgenital plate is obliquely shaped, with a round-triangular apex (Figure 32 C).

Comparative diagnosis. *Tupiperla umbya* is most similar to *T. misionera*, *T. pessacqi,* and *T. sulina*, due to the shape of the dorsal margin of the paraprocts in lateral view, and the short and quadrangular T10e. It can be distinguished from *T. misioneira* by the presence of a sharp subapical spine-like process on the dorsal margin of the apex of the paraprocts (absent and acute in *T. misionera*, and present in *T. umbya*). It can be distinguished from *T. sulina* due to the shape of the ventral margin of the paraprocts (straight in *T. sulina*, and sinuous in *T. umbya*). In the case of the other similar species, it can be distinguished from them based on the width and shape of T10e (slender and rectangular in *T. pessacqi*, and wider and trapezoidal in *T. umbya*)

Distribution. This species is known for its type locality in Intervales State Park, Iporanga, São Paulo State and one other locality kilometers apart in the Intervales State Park. This species was only recorded posteriorly from the same locality as the type material (Bispo & Lecci, 2011).

Type material. Holotype, Male: SÃO PAULO, Ribeirão Grande, Fazenda Intervales, 20/XI/1992, CGF and CMP. (MZUSP). [examined]

Figure 32 - *Tupiperla umbya* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla zwicki Duarte, Novaes & Bispo, 2019

(Figure 33)

Tupiperla zwicki Duarte, Novaes & Bispo, 2019, p522; Pessacq, del Carmen Zúñiga & Duarte, 2019: 194 (Catalog.); Duarte, Froehlich & Bispo 2024, p. 9 (Catalog.).

Diagnosis. The male of *Tupiperla zwicki* can be distinguished from other congeners by elongated paraprocts, ventral margin subapical spine-like lateral process (flap), distally slightly constricted, flattened curved apex (Figure 33 B). Paraprocts parallel, convergent distally, lateral process meeting distally, forming a hook-shape outwards (Figure 33 C). The T10e is elongated, with a distinct deep apical median excavation and divergent arms (Figure 33 A). The subgenital plate is obliquely shaped, with a round-triangular apex (Figure 33 C).

Comparative diagnosis. *Tupiperla zwicki* is most similar to *T. pessacqi*, *T. tessellata,* and *T. froehlichi*, due to the subapical spine-like lateral process on the ventral margin of the apex in lateral view and the elongated and swallow-tailed shape of T10e. It can be distinguished from *T. tessellata* by the presence of a subapical spine-like lateral process (flap) on the paraprocts (absent in *T. tessellata*, and present in *T. zwicki*). It can be distinguished from *T. froehlichi* due to the shape of the ventral margin of the paraprocts (concave in *T. froehlichi*, and sinuous in *T. zwicki*). In the case of the other similar species, it can be distinguished from them based on the shape of the T10e (rectangular in *T. pessacqi*, and long, trapezoidal in *T. zwicki*)

Distribution. Brazil, Santa Catarina. This species is known for its type locality in Rio Minador, Orleans and some few other localities kilometers apart in the vicinity of the São Joaquim Nacional Park and the Serra Furada State Park in the municipalities of Urubici and Orleans. No new records were made after the description of the species.

Type material. Holotype. Male. Brazil: Santa Catarina: Orleans, Rio Minador, S28°10’28”, W49°24’36”, 14.viii-12.x.2013, Malaise trap, LC Pinho *et al.* (MZUSP). [examined]

Figure 33 - *Tupiperla zwicki* (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla sp. 1

(Figure 34)

Holotype, Male: RIO DE JANEIRO, Guapimirim, PAC08. Parque Nacional da Serra dos Órgãos, sub-sede, Trilha das Ruínas, afluente do Rio Soberbo ("praia"), S 22° 29’45,00” W 42° 59’ 49,60”, 344m, 26.iii.2010, FAC Silva, JL Nessimian, LL Dumas, PM Souto. (DZRJ). Paratypes, 4 males: RIO DE JANEIRO, Rio de Janeiro, Cachoeira de Macacu, Parque Estadual Três Picos, Boca do Mato, afluente do Rio Macacu, S 22° 24’ 49,6” W 12° 36’ 50,8”, 494m, Malaise, 10.v-04.vi.2024, C.C.D. Corrêa, I.C. Gonçalves, M.D. Duarte, M.V.O. Duarte, N.O. Paiva & R. Canejo leg. (DZRJ)

Diagnosis. The male of *Tupiperla* sp. 1 can be distinguished from other congeners by paraprocts elongated, lateral face subapical spine-like lateral process downward pointed, apex dorsally angulated, rounded distally (Figure 34 B). Paraprocts parallel, lateral process outward and anteriorly pointed, resembling an arrowhead (Figure 34 C). T10e is elongated, trapezoidal, apex superficial apical median excavation (Figure 34 A). Antennae longer than the forewing. The subgenital plate is obliquely shaped, with a round-triangular apex (Figure 34 C).

Comparative diagnosis. *Tupiperla* sp. 1 is most similar to *T. reichardti*, *T. bispoi,* and *T. pessacqi*, due to the shape of the ventral margin of the paraprocts in lateral view, and the elongated swallow-shaped T10e. It can be distinguished from *T. bispoi* by the presence of a subapical spine-like lateral process of the paraprocts (absent in *T. bispoi*, and present in *Tupiperla* sp. 1). It can be distinguished from *T. reichardti* due to the shape of the ventral margin of the paraprocts (curved with a medial notch in *T. reichardti*, and straight in *Tupiperla* sp. 1). In the case of the other similar species, it can be distinguished from them based on the width and shape of T10e (short, slender, and rectangular in *T. pessacqi*, and long, wider and trapezoidal in *Tupiperla* sp. 1).

Description (male holotype). Medium-sized species (7,0 mm). General color brown. Head dark brown with a lighter area in front of coronal fork; ocelli and eyes light brown; anterior part of frons brown. Clypeus and labrum light to dark brown. Maxillary and labial palpi light brown. Antenna dark brown. Pronotum brown, squarish, with darker margins, and narrower than head. Legs: basal ⅔ of femur light brown, apical ⅓ dark brown; femur covered with thin bristles and with a spine at approximately midlength of inner margin; tibia with two spurs distally; tarsi with tarsomere 1 medium, tarsomere 2 short, and tarsomere 3 long (ou tarsus 3 > tarsus 2 > tarsus 1). Wings membranous light brown; forewing with a dark opaque pattern bordering veins and crossveins; a weak pterostigmatic crossvein present, RA unforked, RP forked, CuA long forked; hind wing with M3 + 4, near its separation from M1 + 2, fused with CuA in part of its length, CuA median forked, 6th anal vein fused with hind margin of wing. Abdomen. S1–S8 light brown, S9–10 dark brown. T10 dark brown, with a clear band at anterior border. T10e, in dorsal view, elongated, with base narrower than forked apex (Figure 34 A); in lateral view, straight dorsally, ending down-curved teeth (Figure 34 B). Paraprocts, in ventral view, thin and elongated, with a thin spine-like process in the subapical region (Figure 34 C); in lateral view, with a wide base narrowing along its length, dorsal edge with a row of diminute spine-like setae; distal region curved downwards with a latero-distal spine-like process originating from the ventral edge (Figure 34 B). Subgenital plate dark brown, oblique-shaped, with a triangular apex (Figure 34 C). Epiproct present without a ventral sclerotized projection.

Distribution. Brazil, Rio de Janeiro. This species is known for its type locality in Serra dos Órgãos National Park, Guapimirim and one other locality kilometers apart in the Três Picos State Park, Cachoeira de Macacu.

Etymology: UBA, Uyba correct spelling in Tupi, the arrow for the bow in the Tupi vernacular language (Sampaio, 1987). This name refers to how, when in ventral view, the paraprocts resemble the head of an arrow. Noun in apposition.

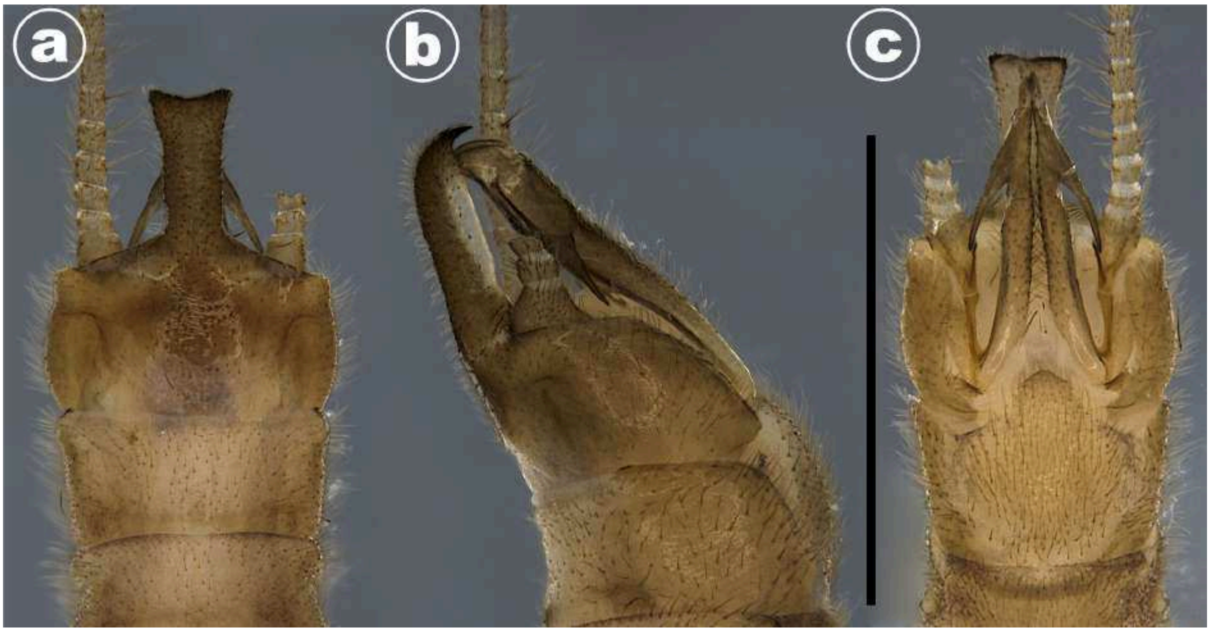


Figure 34 - *Tupiperla* sp. 1 (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla sp. 2

(Figure 35)

Holotype, Male: RIO DE JANEIRO, Macaé, SA08. Sana, Tributário de 2ª ordem do Córrego Alegre, S22° 15’ 26,60” W 42° 09’ 52,60”, 569m, 18.ii.2009, Sampaio, B.H.L, Jardim, G.A., Gonçalves, I., Alecrim, VP & Nessimian, JL. (DZRJ).

Diagnosis. The male of *Tupiperla* sp 2 can be distinguished from other congeners by paraprocts elongated, diminutive subapical spine-like lateral process on the lateral face, apex slightly hooked-shaped and acuminate (Figure 35 B). Paraprocts dorsal margin, preapical S-shaped expansion (Figure 35 B). Paraprocts parallel, thin spine-like lateral process dorsally pointed (Figure 35 C). T10e is elongated, apex deep median excavation, swallow-tailed (Figure 35 A). The subgenital plate is obliquely shaped, with a round apex (Figure 35 C).

Comparative diagnosis. *Tupiperla* sp. 2 is most similar to *T. reichardti*, *Tupiperla* sp. 1, and *T. pessacqi*, due to the shape of the ventral margin of the paraprocts in lateral view, and the elongated swallow-shaped T10e. It can be distinguished from *Tupiperla* sp. 1 by the shape of the apex of the paraprocts (rounded in *Tupiperla* sp. 1, and acuminated and hook-shaped in *Tupiperla* sp. 2). It can be distinguished from *T. reichardti* due to the shape of the ventral margin of the paraprocts (curved with a medial notch in *T. reichardti*, and straight in *Tupiperla* sp. 2). In the case of the other similar species, it can be distinguished from them based on the width and shape of T10e (short, slender, and rectangular in *T. pessacqi*, and long, wider and trapezoidal in *Tupiperla* sp. 2) or based on the lateral margins of the T10e (parallel, in *T. reichardti*, and divergent in *Tupiperla* sp. 2).

Description (male holotype). Medium-sized species (8,0 mm). General light brown. Pronotum brown, squarish, and narrower than head. Legs: basal ⅔ of femur light brown, apical ⅓ ligt brown; femur covered with thin bristles and with a spine at approximately midlength of inner margin; tibia with two spurs distally; tarsi with tarsomere 1 medium, tarsomere 2 short, and tarsomere 3 long (ou tarsus 3 > tarsus 2 > tarsus 1). Wings membranous light brown; forewing with a opaque pattern bordering veins and crossveins; RA unforked, RP forked, CuA long forked; hind wing with M3 + 4, near its separation from M1 + 2, fused with CuA in part of its length, CuA median forked, 6th anal vein fused with hind margin of wing. Abdomen. S1–S8 light brown, S9–10 light brown. T10 light brown, with a clear band at anterior border. T10e, in dorsal view, elongated, with base narrower than forked apex (Figure 35 A); in lateral view, straight dorsally, ending down-curved teeth (Figure 35 B). Paraprocts, in ventral view, thin and elongated, with a diminutive spine-like process in the subapical region (Figure 35 C); in lateral view, narrow base widening medially, dorsal margin sinouos; distal region curved downwards with a latero-distal spine-like process originating from the lateral face (Figure 35 B). Subgenital plate dark brown, oblique-shaped, with a rounded triangular apex (Figure 35 C). Epiproct present without a ventral sclerotized projection.

Distribution. Brazil, Rio de Janeiro. This species is known only for its type locality in Macae, a region that is not within a protected area.

Etymology: GRACIOSA, gra-ci-o-sa [grɐ.sjˈɔ.zɐ]. word in the vernacular language Portuguese meaning graceful. In honor of the most gracious Plecoptera researcher, Mellis Layra Soares Rippel, for always willing to talk about taxonomy and for noticing how unique the graceful curves of this species' paraproct are. Noun in apposition.

Remarks. The specimen is in a bad state of preservation and lost most of its coloration and the head.

Figure 35 - *Tupiperla* sp. 2 (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla sp. 3

(Figure 36)

Tupiperla oliverai Duarte, Froehlich & Bispo 2024, p. 17.

Holotype, Male: MINAS GERAIS, São Roque de Minas, CAN10. Serra da Canastra. Fazenda Velha. Corrego das Pombas, S 20° 14’ 56,6” W 46° 38’ 4,9”, 997m, 02.iv.2014, JL Nessimian, ALH Oliveira, LL Dumas, SP Gomes. (DZRJ3563).

Paratype, Male: MINAS GERAIS, São Roque de Minas, CAN10. Serra da Canastra. Fazenda Velha. Corrego das Pombas, S 20° 14’ 56,6” W 46° 38’ 4,9”, 997m, 02.iv.2014, JL Nessimian, ALH Oliveira, LL Dumas, SP Gomes. (DZRJ3564).

Diagnosis. The male of *Tupiperla* sp. 3 can be distinguished from other congeners by elongated, dilated paraprocts with geniculated apex, forming inverted L-shape (Figure 36 B). Paraprocts dorsal margin medially dilated, apex distal spine-like projecting anteriorly (Figure 36 B). Paraprocts subparallel, disto-lateral face slightly cylindrical (Figure 36 C). T10e elongated, with a distinct deep apical median excavation, V-shape (Figure 36 A). Subgenital plate is obliquely shaped, with a round apex (Figure 36 C).

Comparative diagnosis. *Tupiperla* sp. 3 is most similar to *T. oliverai*, *T. amorimi,* and *T. flinti*, due to the dilated paraprocts with a geniculated apex in lateral view and the V-shape T10e. It can be distinguished from *T. amorimi* by the shape of the distal dorsal margin of the paraprocts (ventral margin of with distinct upwards spinelike projection in *T. amorimi*, and a geniculated ending in a thin spine-like in *Tupiperla* sp. 3). It can be distinguished from *T. flinti* due to the dorsal margin of the paraprocts (almost straight in *T. flinti*, and an almost right angle (90°) in *Tupiperla* sp. 3). In the case of the other similar species, it can be distinguished from them based on the width and shape of T10e (short and with shallow bifurcation in *T. flinti*, and V-shape and robust in *Tupiperla* sp. 3).

Description (male holotype). Description (male holotype). Medium-sized species (7,0 mm). General color brown. Head dark brown with a lighter area in front of coronal fork; ocelli and eyes light brown; anterior part of frons brown. Clypeus and labrum light to dark brown. Maxillary and labial palpi light brown. Antenna dark brown. Pronotum brown, squarish, with darker margins, and narrower than head. Legs: basal ⅔ of femur light brown, apical ⅓ dark brown; femur covered with thin bristles and with a spine at approximately midlength of inner margin; tibia with two spurs distally; tarsi with tarsomere 1 medium, tarsomere 2 short, and tarsomere 3 long (ou tarsus 3 > tarsus 2 > tarsus 1). Wings membranous light brown; forewing with a dark opaque pattern bordering veins and crossveins; a weak pterostigmatic crossvein present, RA unforked, RP forked, CuA long forked; hind wing with M3 + 4, near its separation from M1 + 2, fused with CuA in part of its length, CuA median forked, 6th anal vein fused with hind margin of wing. Abdomen. S1–S8 light brown, S9–10 dark brown. T10 dark brown, with a clear band at anterior border. T10e, in dorsal view, elongated, with the base narrower than the deep forked apex forming a V-shape (Figure 36 A); in lateral view, straight dorsally, ending in two separated, down-curved teeth (Figure 36 B). Paraprocts, in ventral view, broad and elongated, cyllindrical (Figure 36 C); in lateral view, broaden distally, apex geniculate forming an inverted L-shape, distally spine-like process projecting anteriorly (Figure 36 B). Subgenital plate dark brown, oblique-shaped, with a rounded triangular apex (Figure 36 C). Epiproct present without a ventral sclerotized projection.

Distribution. Brazil, Minas Gerais. This species is known for its type locality in Serra da Canastra National Park, São Roque de Minas and one other locality kilometers apart in the RPPN Cachoeira do Campo, Serra do Salitre (Duarte *et al.*, 2024).

Etymology: URUBU, Urú-bú, common name for birds of the Cathartidae family in vernacular language Tupi de (Sampaio, 1987; Navarro & Suassuna, 2013), referring to how, when viewed from the side, the paraproct resembles the head of a vulture. Noted by researcher Rodrigo Braga Gastaldo and also named in his honor for the hours of discussions we had about morphology. Noun in apposition

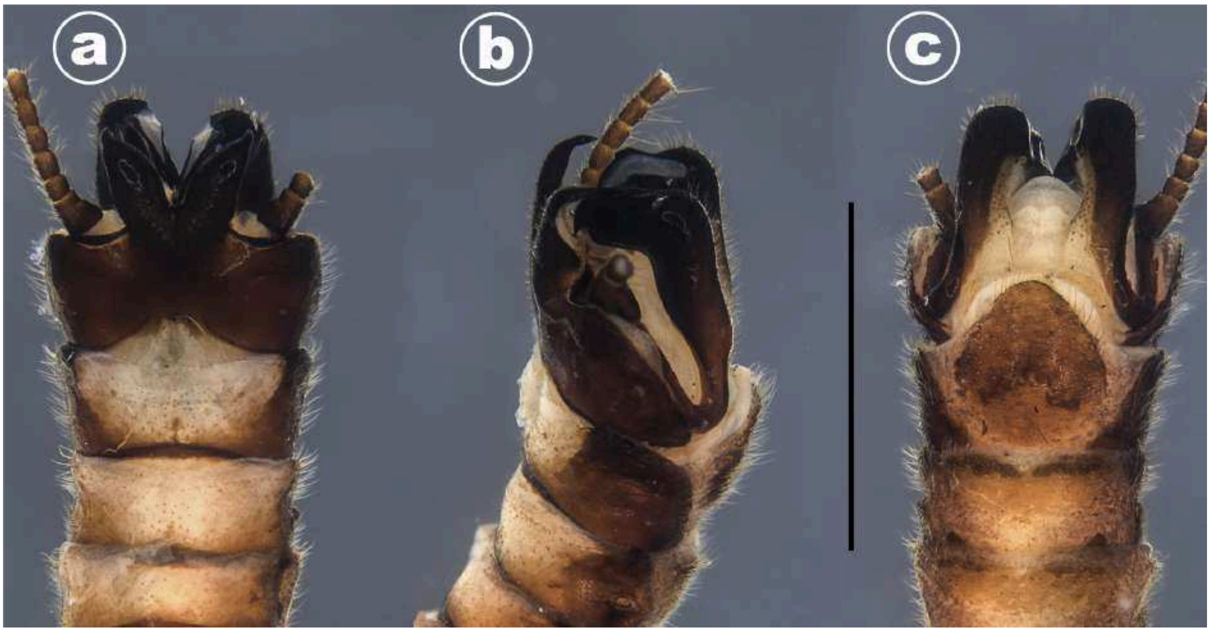


Figure 36 - *Tupiperla* sp. 3 (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla sp. 4

(Figure 37)

Holotype, Male: Brazil São Paulo. São José do Barreiro. Parque Nacional da Serra do Bocaina. Estrada para o Pico Tira Chapéu, Rio Mambucaba, 22°43'38"S 44°37'56.4"W. 1,529m. 09.xii.2010 Col. JL Nessimian, AL Henriques-Oliveira & PM Souto. (DZRJ 3372). Paratypes: Same as holotype, except 12.xii.2010. 5♂ (DZRJ 3397). Col. MR Souza, JL Nessimian, RA Carvalho, AL Henriques-Oliveira & LL Dumas.

Diagnosis. *Tupiperla* sp. 4 can be distinguished from other congeners by paraprocts elongated, one-third extending beyond the T10e (Figure 37 B). Paraprocts, constant width over most of their length, apex rounded distally, subapical dorsal margin bearing a spine-like projection (Figure 37 B). Paraprocts parallel, internal face concave (Figure 37 C). T10e elongated, apex median excavation heart-shape (Figure 37 A). Subgenital oblique-shaped, rounded triangular apex (Figure 37 C).

Comparative diagnosis. *Tupiperla* sp. 4 is most similar to *T. sepeensis*, *T. ubuntu,* and *T. froehlichi*, due to the ventral margin and length proportions of the paraprocts in lateral view, and the elongated and Y-shaped T10e. It can be distinguished from *T. ubuntu* by the apex of the paraprocts (truncated with sharp vertices in *T. ubuntu*, and rounded in *Tupiperla* sp. 4). It can be distinguished from *T. froehlich* due to the dorsal margin of the paraprocts (angulated, concave, in *T. froehlichi*, and a straight in *Tupiperla* sp. 4). In the case of the other similar species, it can be distinguished from them based on the width and shape of T10e (long and with sharp Y-shape in *T. ubuntu*, and short, round Y-shape in *Tupiperla* sp. 4) or based on the lateral margins of the T10e (parallel, in *T. sepeensis*, and divergent in *Tupiperla* sp. 4).

General description: General color brown. Head brown. Eyes brown. Lateral area of parietalia behind the eyes dark brown. Three ocelli. Depressed area between the paired ocelli lighter than surrounding areas of the head (Figure4). Antenna brown. Labrum yellowish brown. Pronotum brown, with rough surface; anterior and lateral margins dark brown. Longitudinal median line light brown,. Legs brown, dark brown at apex. Abdomen brownish.

Description (male holotype). Description (male holotype). Description (male holotype). Medium-sized species (7,5 mm). General color brown. Head dark brown with a lighter area in front of coronal fork; ocelli and eyes light brown; anterior part of frons brown. Clypeus and labrum light to dark brown. Maxillary and labial palpi light brown. Antenna dark brown. Pronotum brown, squarish, with darker margins, and narrower than head. Legs: basal ⅔ of femur light brown, apical ⅓ dark brown; femur covered with thin bristles and with a spine at approximately midlength of inner margin; tibia with two spurs distally; tarsi with tarsomere 1 medium, tarsomere 2 short, and tarsomere 3 long (ou tarsus 3 > tarsus 2 > tarsus 1). Wings membranous light brown; forewing with a dark opaque pattern bordering veins and crossveins; a weak pterostigmatic crossvein present, RA unforked, RP forked, CuA long forked; hind wing with M3 + 4, near its separation from M1 + 2, fused with CuA in part of its length, CuA median forked, 6th anal vein fused with hind margin of wing. Abdomen. S1–S8 light brown, S9–10 dark brown. T10 dark brown, with a clear band at anterior border. T10e, in dorsal view, elongated, small projection before the forked apex, heart-shape (Figure 37 A); in lateral view, straight dorsally, ending down-curved teeth (Figure 37 B). Paraprocts, in ventral view, thin and elongated, internal face concave (Figure 37 C); in lateral view, constant width over most of their length and have a rounded distal region bearing a spine-like projection on the dorsal margin at the base of the apex (Figure 37 B). Subgenital plate dark brown, oblique-shaped, with a rounded triangular apex (Figure 37 C). Epiproct present without a ventral sclerotized projection.

Distribution. Brazil, São Paulo. This species is known only for its type locality in Rio Mambucaba, Serra da Bocaina National Park, São José Barreiro.

Etymology: This species is named after Leandro Lourenço Dumas, in appreciation of his work in taxonomy and systematics of aquatic insects especially Trichoptera and his love for field work and expeditions.

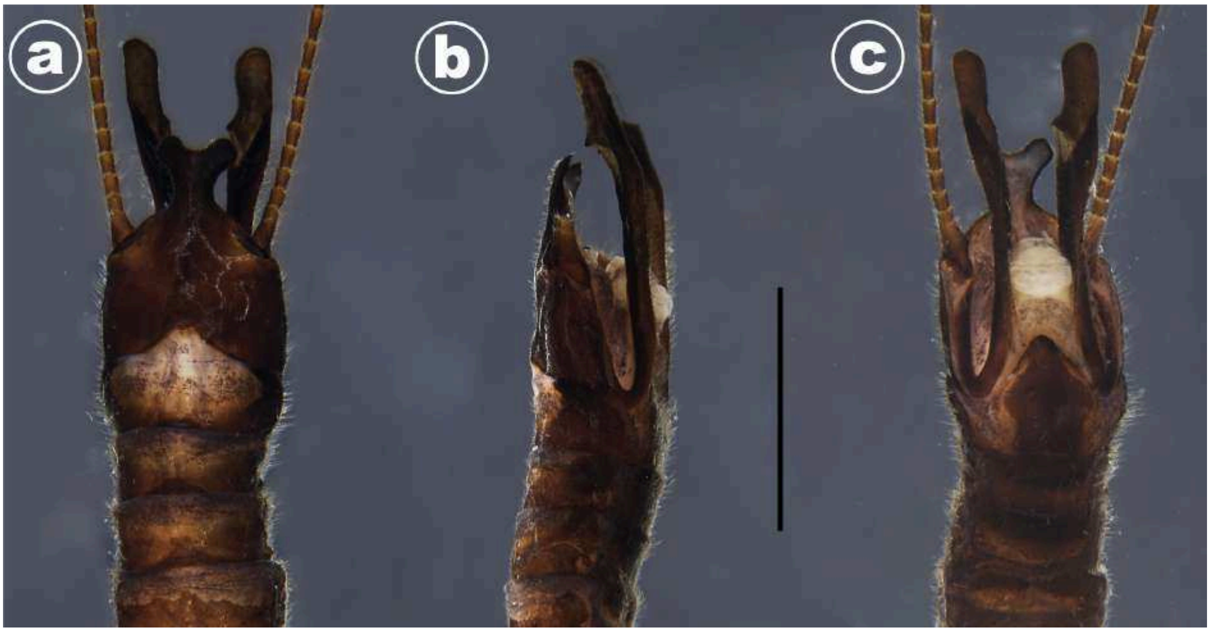


Figure 37 - *Tupiperla* sp. 4 (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla sp. 5

(Figure 38)

Holotype, Male: MINAS GERAIS, Lima Duarte, Conceição do Ibitipoca, Parque Estadual do Ibitipoca, prainha, 21° 42' 34" S 43° 53' 38" W, 1350m, 2022.x.25, lençol, FF Salles, JL Marulanda and MLS Rippel. (UFVB PL0036).

Diagnosis. *Tupiperla* sp. 5 can be distinguished from other congeners by Paraprocts elongated, dorsal margin medial robust spine-like process projecting dorsally (Figure 38 B). Paraprocts apex broad and rounded, ventral margin sinuous (Figure 38 B). Paraprocts parallel, lateral process to project outward and anteriorly (Figure 38 C). T10e elongated, apex deep median excavation (Figure 38 A). Antennae longer than the forewings, and numerous cercomeres. The subgenital plate is obliquely shaped with a triangular rounded apex (Figure 38 C).

Comparative diagnosis. *Tupiperla* sp. 5 is most similar to *T. gracilis*, *T. illiesi*, and *T. reichardti*, due to the dorsal margin and apex of the paraprocts in lateral view, and the elongated swallow-shaped T10e. It can be distinguished from *T. reichardti* by the apex of the paraprocts (acuminated and hook-shaped in *T. reichardti*, and rounded in *Tupiperla* sp. 5). It can be distinguished from *T. illiesi* due to the shape ventral margin of the paraprocts (straight in *T. illiesi*, and sinuous in *Tupiperla* sp. 5). In the case of the other similar species, it can be distinguished from them based on the width and shape of T10e (short and quadrangular in *T. gracilis*, long and swallow-tailed in *Tupiperla* sp. 5).

Description (male holotype). Description (male holotype). Medium-sized species (7,0 mm). General color brown. Head dark brown with a lighter area in front of coronal fork; ocelli and eyes light brown; anterior part of frons brown. Clypeus and labrum light to dark brown. Maxillary and labial palpi light brown. Antenna dark brown. Pronotum brown, squarish, with darker margins, and narrower than head. Legs: basal ⅔ of femur light brown, apical ⅓ dark brown; femur covered with thin bristles and with a spine at approximately midlength of inner margin; tibia with two spurs distally; tarsi with tarsomere 1 medium, tarsomere 2 short, and tarsomere 3 long (ou tarsus 3 > tarsus 2 > tarsus 1). Wings membranous light brown; forewing with a dark opaque pattern bordering veins and crossveins; a weak pterostigmatic crossvein present, RA unforked, RP forked, CuA long forked; hind wing with M3 + 4, near its separation from M1 + 2, fused with CuA in part of its length, CuA median forked, 6th anal vein fused with hind margin of wing. Abdomen. S1–S8 light brown, S9–10 dark brown. T10 dark brown, with a clear band at anterior border. T10e, in dorsal view, elongated, with base narrower than forked apex (Figure 38 A); in lateral view, straight dorsally, ending down-curved teeth (Figure 38 B). Paraprocts, in ventral view, thin and elongated, distally convergent, medially ventral pronjection pointed outwards (Figure 38 C); in lateral view, constant width over most of their length, sinouos ventral margin, medially ventral spine-like projection dorsally pointed (Figure 38 B). Subgenital plate dark brown, oblique-shaped, with a rounded triangular apex (Figure 38 C). Epiproct present without a ventral sclerotized projection.

Distribution. Brazil, Minas Gerais. This species is known only for its type locality in Ibitipoca State Park, Lima Duarte.

Etymology: DUARTEI, This species is named for Tacio Duarte, in appreciation of his work in taxonomy and systematics of Gripopterygidae.

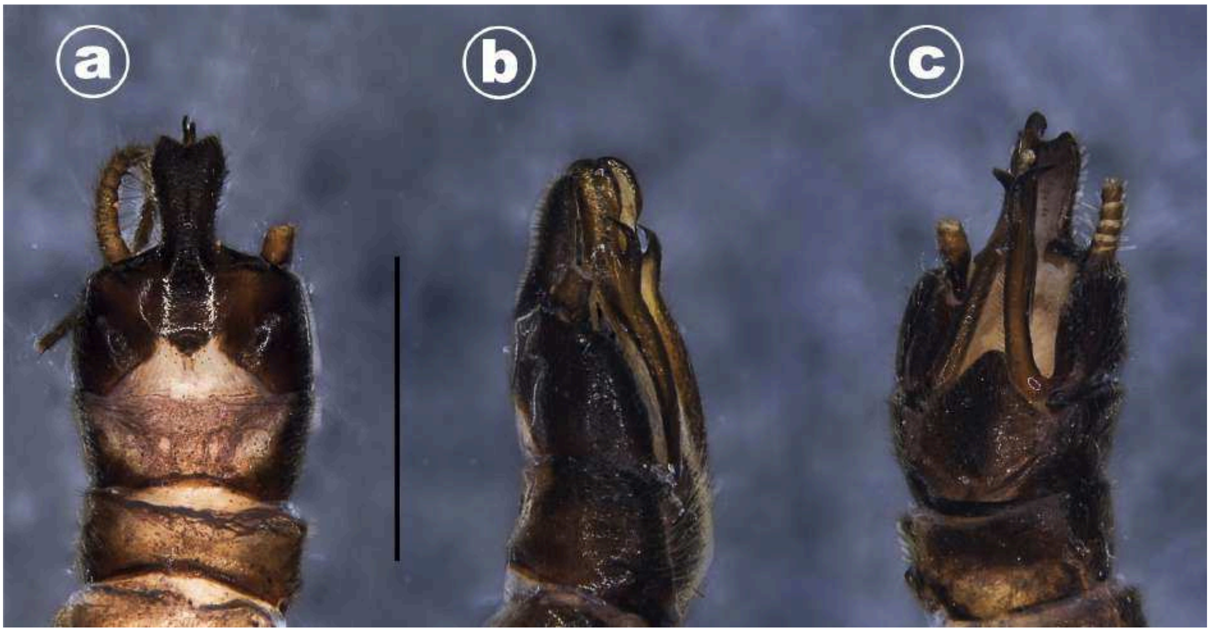


Figure 38 - *Tupiperla* sp. 5 (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla sp. 6

(Figure 39)

Holotype, Male: SÃO PAULO, São José do Barreiro, riacho de 1ª próximo a entrada do parque (antigo Pt 02), S 22°43'49,60" W 44° 37' 07,90" 1536m, 09.xii.2011, LL Dumas, GA Jardim, PM Souto, ALH Oliveira, JL Nessimian. (DZRJ3382).

Diagnosis. *Tupiperla* sp. 6 can be distinguished from other congeners by the male with paraprocts elongated, apex truncated with a subapical spine-like process robust laterally positioned projecting dorsally (Figure 39 B). Paraprocts, ventral medial notch, dorsal margin serrated with minute spine-like setae, apex broad and rounded (Figure 39 B). Paraprocts distally convergent, medial notch, subapical spine-like projection outwards (Figure 39 C). T10e elongated, trapezoidal, apex deep median excavation (Figure 39 A).. Antennae longer than the forewings. The subgenital plate is obliquely shaped with a triangular rounded apex (Figure 39 C).

Comparative diagnosis. *Tupiperla* sp. 6 is most similar to *Tupiperla* sp. 2, *T. illiesi,* and *T. reichardti*, due to the shape of the dorsal margin and apex of the paraprocts in lateral view, and the elongated swallow-shaped T10e. It can be distinguished from *Tupiperla* sp. 2 by the apex of the paraprocts (acuminated and hook-shaped in *Tupiperla* sp. 2, and truncated with a spine-like process in the lateral face in *Tupiperla* sp. 6). It can be distinguished from *T. illiesi* due to the shape of the ventral margin of the paraprocts (straight, in *T. illiesi*, and sinuous in *Tupiperla* sp. 6). In the case of the other similar species, it can be distinguished from them based on the lateral margins of the T10e (parallel, in *T. reichardti*, and divergent in *Tupiperla* sp. 6).

Description (male holotype). Description (male holotype). Medium-sized species (7,0 mm). General color brown. Head dark brown with a lighter area in front of coronal fork; ocelli and eyes light brown; anterior part of frons brown. Clypeus and labrum light to dark brown. Maxillary and labial palpi light brown. Antenna dark brown. Pronotum brown, squarish, with darker margins, and narrower than head. Legs: basal ⅔ of femur light brown, apical ⅓ dark brown; femur covered with thin bristles and with a spine at approximately midlength of inner margin; tibia with two spurs distally; tarsi with tarsomere 1 medium, tarsomere 2 short, and tarsomere 3 long (ou tarsus 3 > tarsus 2 > tarsus 1). Wings membranous light brown; forewing with a dark opaque pattern bordering veins and crossveins; a weak pterostigmatic crossvein present, RA unforked, RP forked, CuA long forked; hind wing with M3 + 4, near its separation from M1 + 2, fused with CuA in part of its length, CuA median forked, 6th anal vein fused with hind margin of wing. Abdomen. S1–S8 light brown, S9–10 dark brown. T10 dark brown, with a clear band at anterior border. T10e, in dorsal view, elongated, with base narrower than forked apex (Figure 39 A); in lateral view, straight dorsally, ending down-curved teeth (Figure 39 B). Paraprocts, in ventral view, thin and elongated, distally convergent, distally lateral spine-like projection pointed outwards (Figure 39 C); in lateral view, constant width over most of their length, sinouos ventral margin, ventral margin medial notch, apex spine-like projection dorsally pointed (Figure 39 B). Subgenital plate dark brown, oblique-shaped, with a rounded triangular apex (Figure 39 C). Epiproct present without a ventral sclerotized projection.

Distribution. Brazil, São Paulo. This species is known only for its type locality in Serra da Bocaina National Park, São José Barreiro.

Etymology: This species is named after Daniela (Dani) Maeda Takiya, in appreciation of her love and support of the insects and her job teaching a generation of entomologists.

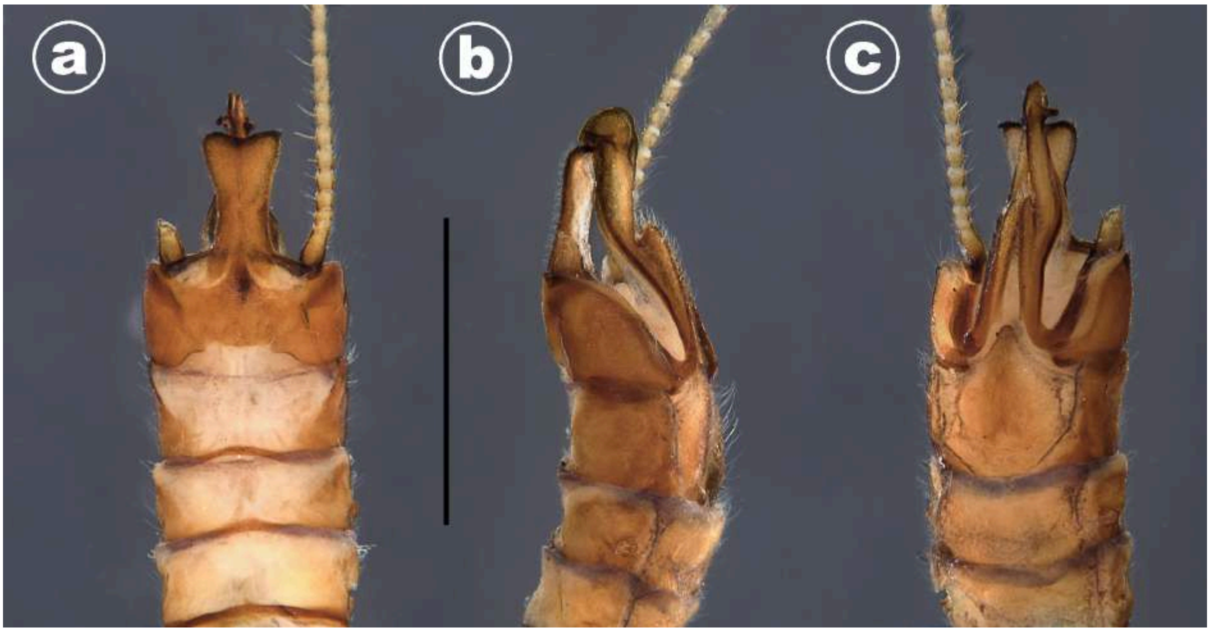


Figure 39 - *Tupiperla* sp. 6 (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla sp. 7

(Figure 40)

Holotype, Male: RIO DE JANEIRO, Itatiaia, Parque Nacional do Itatiaia, Piscina do Maromba, Rio Campo Belo, S 22°25'46,21" W 44°37'9,74", 957m, 16.iv.2007, LL Dumas *et al.* (DZRJ3176a). Paratype, Male: RIO DE JANEIRO, Itatiaia, Parque Nacional do Itatiaia, Piscina do Maromba, Rio Campo Belo, S 22°25'46,21" W 44°37'9,74", 957m, 16.iv.2007, LL Dumas *et al.* (DZRJ3176b)

Diagnosis. The male of Tupiperla sp. 7 can be distinguished from other congeners by elongated paraprocts, ventral margin subapically enlarged region, apex elongated narrowed dorsally angulated (Figure 40 B). Paraprocts distally convergent, flattened (Figure 40 C). T10e short and broad, with parallel margins, two spine-like processes in the central region, and an almost straight apical margin (Figure 40 A). The subgenital plate is obliquely shaped with a rounded apex (Figure 40 C).

Comparative diagnosis. *Tupiperla* sp. 7 is most similar to *T. robusta*, *Tupiperla* sp. 8, *T. guariru,* and *T. modesta* due to the shape of the apex and the ventral margin of the paraprocts in lateral view, and the short quandragular T10e. It can be distinguished from *Tupiperla* sp. 8 by the apex of the paraprocts (round and broad in *Tupiperla* sp. 8, and narrow, forming an acute projection in *Tupiperla* sp. 7) It can be distinguished from *T. robusta* due to the ventral and dorsal margin of the paraprocts (subparallel, for most of its length, in *Tupiperla* sp. 7, and divergent, enlarging towards the apex, in *T. robusta*). In the case of the other similar species, it can be distinguished from them based on the shape of T10e (rectangular in *T. modesta*, and quadrangular in *Tupiperla* sp. 7) or based on the lateral margins of the T10e (convergent, in *T. guariru*, and parallel in *Tupiperla* sp. 7).

Description (male holotype). Description (male holotype). Medium-sized species (9,8 mm). General color brown. Head dark brown with a lighter area in front of coronal fork; ocelli and eyes light brown; anterior part of frons brown. Clypeus and labrum light to dark brown. Maxillary and labial palpi light brown. Antenna dark brown. Pronotum brown, squarish, with darker margins, and narrower than head. Legs: basal ⅔ of femur light brown, apical ⅓ dark brown; femur covered with thin bristles and with a spine at approximately midlength of inner margin; tibia with two spurs distally; tarsi with tarsomere 1 medium, tarsomere 2 short, and tarsomere 3 long (ou tarsus 3 > tarsus 2 > tarsus 1). Wings membranous light brown; forewing with a dark opaque pattern bordering veins and crossveins; a weak pterostigmatic crossvein present, RA unforked, RP forked, CuA long forked; hind wing with M3 + 4, near its separation from M1 + 2, fused with CuA in part of its length, CuA median forked, 6th anal vein fused with hind margin of wing. Abdomen. S1–S8 light brown, S9–10 dark brown. T10 dark brown, with a clear band at anterior border. T10e, in dorsal view, short, with base subequal to apex, quandragular (Figure 40 A); in lateral view, straight dorsally, ending diminutive teeth (Figure 40 B). Paraprocts, in ventral view, thin and elongated, distally convergent, flattened (Figure 40 C); in lateral view, the ventral margin subapical enlarged region, apex elongated narrowed dorsally angulated (Figure 40 B). Subgenital plate dark brown, oblique-shaped, rounded apex (Figure 40 C). Epiproct present without a ventral sclerotized projection.

Distribution. Brazil, Rio de Janeiro. This species is known only for its type locality in Itatiaia National Park, Itatiaia.

Etymology: ITATIAIA, Itá-tiâi, the cliff full of spikes; the bristling crest (Sampaio, 1987) or from itá + atîaî/a (r,s) + -a: pointed stones (Navarro & Suassuna, 2013). It is the highest point of the system, in the Mantiqueira mountain range. São Paulo, Minas Gerais, and Rio de Janeiro (Sampaio, 1987). It refers to the type locality of the species as well as to the tip of its paraprocts, which are long and pointed resembling a pointed mountain. Noun in apposition.

Remarks. The specimen analyzed by Froehlich (1998: p. 29), identified as *T. robusta*, from Visconde de Mauá, Resende, Rio de Janeiro State could not be located. However, based on locality and some general similarities between *T. robusta* and *Tupiperla* sp. 7, it probably belongs to this new species.

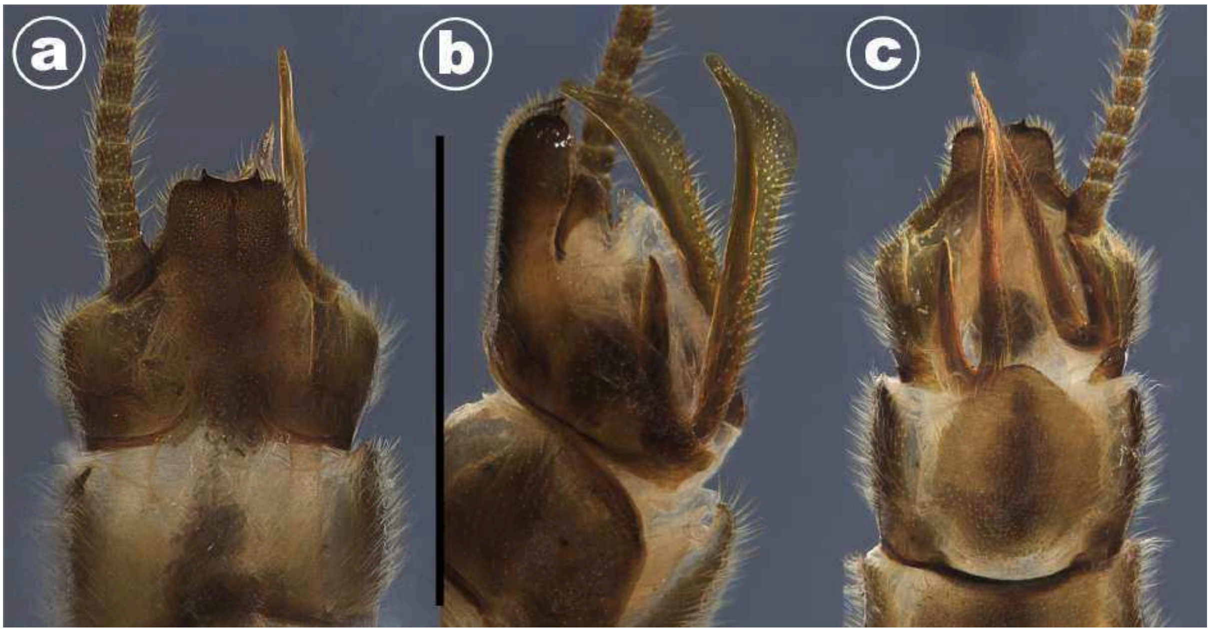


Figure 40 - *Tupiperla* sp. 7 (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

Tupiperla sp. 8

(Figure 41)

Holotype, Male: ESPÍRITO SANTO, ES36. Castelo, Forno Grande, Parque Estadual do Forno Grande, Afluente do Rio Caxixe, S 20° 31’ 05,60” W 41° 05’ 09,00”, 1156m 29.iii.11, GA Jardim, JL, Nessimian, LL Dumas, LFL Silveira, (ENT605).

Diagnosis. The male of *Tupiperla* sp. 8 can be distinguished from other congeners by elongated, paraprocts apex rounded dorsally angulated (Figure 41 B). Paraprocts distally convergent, flattened (Figure 41 C). T10e short and broad, with parallel margins, two spine-like processes in the central region, and an almost straight apical margin (Figure 41 A). The subgenital plate is obliquely shaped with a rounded apex (Figure 41 C).

Comparative diagnosis. *Tupiperla* sp. 8 is most similar to *T. robusta*, *Tupiperla* sp. 7, *T. guariru,* and *T. jumirim* due to the shape of the apex and the ventral margin of the paraprocts in lateral view, and the short quandragular T10e. It can be distinguished from *T. robusta* by the shape of the apex of the paraprocts (narrow, forming an acute projection in *T. robusta*, and round and broad in *Tupiperla* sp. 8). It can be distinguished from *Tupiperla* sp. 7 due to the ventral margin of the paraprocts (straight, angulate only at apex, in *Tupiperla* sp. 7, and angulated, convex, in *Tupiperla* sp. 8). In the case of the other similar species, it can be distinguished from them based on the shape of T10e (rectangular in *T. jumirim*, and quadrangular in *Tupiperla* sp. 8) or based on the lateral margins of the T10e (convergent, in *T. guariru*, and parallel in *Tupiperla* sp. 8).

Description (male holotype). Description (male holotype). Medium-sized species (8,0 mm). General color brown. Head dark brown with a lighter area in front of coronal fork; ocelli and eyes light brown; anterior part of frons brown. Clypeus and labrum light to dark brown. Maxillary and labial palpi light brown. Antenna dark brown. Pronotum brown, squarish, with darker margins, and narrower than head. Legs: basal ⅔ of femur light brown, apical ⅓ dark brown; femur covered with thin bristles and with a spine at approximately midlength of inner margin; tibia with two spurs distally; tarsi with tarsomere 1 medium, tarsomere 2 short, and tarsomere 3 long (ou tarsus 3 > tarsus 2 > tarsus 1). Wings membranous light brown; forewing with a dark opaque pattern bordering veins and crossveins; a weak pterostigmatic crossvein present, RA unforked, RP forked, CuA long forked; hind wing with M3 + 4, near its separation from M1 + 2, fused with CuA in part of its length, CuA median forked, 6th anal vein fused with hind margin of wing. Abdomen. S1–S8 light brown, S9–10 dark brown. T10 dark brown, with a clear band at anterior border. T10e, in dorsal view, short, with base subequal to apex, quandragular (Figure 41 A); in lateral view, straight dorsally, ending diminutive teeth (Figure 41 B). Paraprocts, in ventral view, Paraprocts distally convergent, flattened (Figure 41 C).; in lateral view, elongated, paraprocts apex rounded dorsally angulated (Figure 41 B). Subgenital plate dark brown, oblique-shaped, rounded apex (Figure 41 C). Epiproct present without a ventral sclerotized projection.

Distribution. Brazil, Espírito Santo. This species is known only for its type locality in Forno Grande State Park, Forno Grande, Castelo.

Etymology: ITAOKA : de ita + oka (r,s): stone house in the Tupi vernacular language (Navarro & Suassuna, 2013) in reference to the name of the type locality municipality Castelo-ES in the original language of the Puri people who originally inhabited the region. Noun in apposition

Figure 41 - *Tupiperla* sp. 8 (Holotype) adult male, terminalia in dorsal (A), lateral (B), and ventral views (C).

DISCUSSION

This study represents the first multigene approach to include multiple Gripopterygidae taxa from the Neotropical region, including *Gripopteryx*, *Paragripopteryx*, *Guaranyperla*, and *Tupiperla*. Across all analyses, *Guaranyperla* (Clade B) was consistently recovered as a well-supported monophyletic clade. In contrast, *Tupiperla* was paraphyletic relative to *Guaranyperla* in all analyses that incorporated morphological data, including both the parsimony and combined datasets. *Tupiperla modesta* and *T. jumirim* were not recovered in any of the analyses with the remaining species of *Tupiperla*. In the parsimony analysis, *T. modesta* and *T. jumirim* + *Guaranyperla* grouping was supported by three synapomorphies, although all were homoplastic. Importantly, these two species of *Tupiperla* were unavailable for molecular sequencing, preventing cross-validation of their placement.

In the combined dataset analysis (Figure 6), Clade C (*T. robusta*, *Tupiperla* sp. 7, and *Tupiperla* sp. 8) was recovered as the sister group to *Guaranyperla* (Clade B), though this relationship received low support (UFBoot = 73%; SH-aLRT = 75%). Conversely, the concatenated dataset analysis (Figure 7) placed Clade C as the sister group to the remaining *Tupiperla* species (Clade D), albeit also with weak support (PP = 0.62; UFBoot = 79%; SH-aLRT = 38%). The consistently low support values indicate that the monophyly of *Tupiperla* is uncertain, as different lineages are repeatedly recovered as sister to *Guaranyperla* depending on the analytical approach used.

The unstable placement of Clade C reflects broader issues in the morphological diagnosis of *Tupiperla*. Recent debate surrounding the taxonomic placement of *T. robusta* highlights overlap in diagnostic characters between *Tupiperla* and *Guaranyperla* (Rippel et al., 2025). While most *Tupiperla* species exhibit a rectangular or sub-quadrate pronotum with a head-to-pronotum width ratio exceeding 1.25, the reduced ratio reported for *T. aff. robusta* overlaps with values typical of *Guaranyperla*. However, the material examined by Rippel *et al.* (2025) originates from Serra do Brigadeiro (personal communication) and may represent an undescribed taxon not included in the present analyses. Measurements of the holotypes of *T. robusta*, *Tupiperla* sp. 7, and *Tupiperla* sp. 8 confirm that these species do not share this reduced ratio, suggesting that the condition may be autapomorphic.

Clade C can be easily recognised by the short protruding T10e sub-quadrate and robust with denticles in the medial region of the distal margin, which differs from all the other *Tupiperla*, where the denticles are found in the vertices of the T10e. The species of the

Clade C show very subtle morphological differences within these highly diagnostic regions, such as paraprocts that lack transformation in the dorsal or ventral margins, such as notches, outward processes, and spine-like setae, and the T10e that also lack transformations in shape. The synapomorphy of this group is the long setae found in the paraproct, a character also present in *Guaranyperla*. This shared trait further complicates generic boundaries when adult morphology alone is considered.

A close relationship between *Tupiperla* and *Guaranyperla* has been hypothesised since the original description of *Guaranyperla* (Froehlich, 2001). Both genera share a distinctive spine near the midlength of the inner margin of the femora, a feature absent in other Gripopterygidae. Additional characters are shared sporadically, including tessellated wings and the absence of a sclerotised epiproct projection, reinforcing the long-recognised morphological affinity between the two genera.

The first explicit cladistic test of the monophyly of Gripopteryginae recovered *Tupiperla* and *Guaranyperla* in an unresolved polytomy supported by nymphal synapomorphies, including hook-like body setae, a concave metanotal margin, a triangular distal margin of tergum 10, and a femoral spine (Duarte *et al.*, 2025). Except for the femoral spine, these characters are derived exclusively from immature stages, underscoring the importance of nymphal morphology in diagnosing relationships within the subfamily.

From a Hennigian perspective, classifications represent explicit translations of phylogenetic hypotheses, with taxa defined as monophyletic units supported by synapomorphies (Hennig, 1966). Central to this framework is the concept of the semaphoront, which recognises that characters are expressed at specific ontogenetic stages and that each developmental stage constitutes an independent source of phylogenetic information. To integrate these signals, characters from different semaphoronts must be coded independently and evaluated jointly within a single phylogenetic framework (Hennig, 1966).

Failure to achieve a holomorphological perspective biases classifications toward a single life-history stage, increasing susceptibility to homoplasy and obscuring deeper evolutionary signal (Sanderson and Donoghue, 1989; Carpenter, 1988; Meier and Lim, 2009). In insect systematics, this imbalance has often manifested as an overreliance on male genitalia, which, despite their diagnostic utility, may exhibit phylogenetic inertia and elevated homoplasy in species-specific traits of shape and size (Tuxen, 1970; Song, 2009; Song and Bucheli, 2010).

The evaluation of *Tupiperla* monophyly is critically limited by a pronounced Haeckelian deficit, defined as the absence of described semaphoronts across the life cycle

(Faria *et al.*, 2021). While nymphs are known for all described species of *Guaranyperla*, only two of the 33 recognised *Tupiperla* species, *T. tessellata* (Lecci et al., 2025) and *T. gracilis* (Almeida et al., in press), have formally described immature stages.

This imbalance is directly reflected in the morphological matrix, in which 64% of characters derive from male terminalia. As a consequence, morphological datasets are dominated by a single semaphoront and yield unstable and poorly resolved topologies, characterised by recurrent unresolved nodes and shifting placements of key lineages. These patterns do not represent methodological artifacts but instead reflect genuine conflict among character partitions, extensive homoplasy in adult traits, and the masking of deeper synapomorphies expected from immature stages (Meier and Lim, 2009).

Characters derived from immature stages are often more phylogenetically informative than adult traits, particularly in aquatic insects, where nymphs experience a broader range of ecological and selective pressures (Lee *et al.*, 2007; Meier and Lim, 2009). In contrast, adults represent a short-lived semaphoront primarily associated with reproduction. Phylogenetic studies integrating holomorphological datasets consistently recover improved resolution and topologies congruent with phylogenomic results (Lee *et al.*, 2005, 2007; Hayashi *et al.*, 2024). Within this context, the recurrent non-monophyletic configurations of *Tupiperla* recovered here are best interpreted as consequences of uneven character sampling rather than evidence against the genus itself.

Further sources of instability include incomplete and uneven taxon sampling. The absence of key species such as *T. jumirim* and *T. modesta* from molecular datasets, along with other taxa lacking sequence data, likely contributes to low support values and unstable intergeneric relationships. Phylogenetic accuracy depends not only on the number of taxa sampled but also on their composition, with balanced inclusion of slowly evolving lineages and closely related species being critical for resolving short internal branches (Hillis, 1998; Poe, 1998; Zwickl and Hillis, 2002; Hedtke et al., 2006; Pick et al., 2010).

Life-history traits may further exacerbate these patterns. In freshwater insects with synchronised emergence, including Plecoptera, diversification by temporal isolation can produce rapid radiations with short internal branches (Ribera *et al.*, 2001; Dijkstra et al., 2014). Such processes limit the accumulation of informative substitutions and increase rate heterogeneity among lineages, contributing to homoplasy and an ambiguous signal at deeper nodes. These dynamics may underlie the unstable backbone observed within *Tupiperla*.

Despite recurrent shifts in clade placement and low support at deeper nodes, Clade C is consistently recovered as a *Tupiperla* lineage across analyses. Collectively, *Tupiperla* comprises at least four major lineages (Clades C, E, F, and G), supported by three exclusive and one non-exclusive synapomorphies and recovered in the concatenated dataset. At present, these results provide provisional support for the monophyly of *Tupiperla*, albeit surrounded by significant uncertainty. Crucially, no robustly supported alternative hypothesis justifies the recognition of two distinct genera or the synonym of *Guaranyperla*. The observed paraphyly and instability are best explained by structural limitations of the available data, particularly the absence of immature characters, rather than by clear evolutionary discontinuities. Resolving the deep relationships within the *Tupiperla–Guaranyperla* lineage will require expanded taxon sampling and the integration of holomorphological datasets, including nymphal and internal anatomical characters.

CONCLUSIONS

The Neotropical Region harbors an invaluable diversity of aquatic insects, yet knowledge regarding their evolutionary relationships remains fragmented. The genus *Tupiperla* Froehlich, 1969, despite being one of the most representative within Gripopterygidae, lacked an integrative taxonomic revision and a robust phylogenetic hypothesis. This study sought to fill this gap by revising the taxonomy of the group and testing, for the first time, its monophyly through a total evidence approach, combining morphological and molecular data to elucidate the evolutionary history of these stoneflies.

Phylogenetic analyses, utilizing both maximum likelihood and Bayesian inference, revealed that *Tupiperla*, in its current circumscription, behaves as a paraphyletic group with respect to the genus *Guaranyperla*, albeit with low support. The recovery of *Guaranyperla* as a well-supported monophyletic clade, positioned as a sister group or nested within *Tupiperla* lineages (specifically the clade composed of *T. robusta* and related new species), challenges the traditional classification. Taxonomically, this study significantly expanded knowledge of the genus, now recognizing 33 species, of which eight are new to science (*Tupiperla* sp. 1 to sp. 8), in addition to redescribing and diagnosing previously known species. The analysis allowed for the identification of seven well-supported internal clades, although topological stability was affected by the reliance on adult characters.

Results obtained have profound implications for the systematics of Gripopterygidae. The low support found for *Tupiperla* monophyly suggests the need for a reevaluation of the generic limits between *Tupiperla* and *Guaranyperla*. However, we concluded by maintaining the validated *Tupiperla* and making an amended diagnosis for the genus composed of 33 species. Furthermore, this work highlights the impact of historical taxonomic bias focused on male terminalia, which comprises the vast majority (64%) of the available morphological matrix. This demonstrates that the evolution of male genitalia in *Tupiperla* may be subject to homoplasies or convergent evolution, complicating the recovery of deep relationships without the support of molecular data or other semaphoronts.

The main limitation identified refers to the "Haeckelian shortfall," specifically the critical scarcity of descriptions of immature stages. Of the 33 species treated, only one has a formally described nymph, which prevented the use of nymphal characters that could offer more conserved synapomorphies to resolve basal nodes. Another significant limitation was the absence of molecular data for key taxa such as *T. modesta* and *T. jumirim*, whose phylogenetic position remained unstable and dependent exclusively on adult morphology, resulting in groupings with *Guaranyperla* based on few homoplasies.

To overcome current impediments, it is imperative that future efforts focus on the association and description of the nymphs of *Tupiperla* species, allowing for a true "total evidence" analysis that includes all life stages. It is also recommended to perform molecular sequencing of rare or missing species (*T. modesta*, *T. jumirim*, and the new species described only based on morphological characters) to test the stability of the recovered clades. Studies focused on genitalia-function coevolution and the biogeography of the group need a robust phylogenetic framework and may clarify the processes that led to the current distribution and diversity of the genus in the Atlantic Forest and other regions.

This dissertation represents the most significant advance in the systematics of *Tupiperla* since its proposal, establishing a new benchmark for the study of Plecoptera in South America. Although questions regarding the monophyly of the genus remain, the integration of molecular tools and detailed morphological revision has provided the necessary foundation to transform *Tupiperla* from a taxonomically confusing taxon into a potential model for evolutionary studies in the Neotropical region.

REFERÊNCIAS

Almeida Navarro, E., & Suassuna, A. (2013). Dicionário tupi antigo: A língua indígena clássica do Brasil: Vocabulário português–tupi e dicionário tupi–português, tupinismos no português do Brasil, etimologias de topônimos e antropônimos de origem tupi. Global Editora.

Antonelli, A., & Sanmartín, I. (2011). Why are there so many plant species in the Neotropics? Taxon, 60, 403–414. https://doi.org/10.1002/tax.602010

Badano, D., Aspöck, U., Aspoeck, H., & Cerretti, P. (2017). Phylogeny of Myrmeleontiformia based on larval morphology (Neuropterida: Neuroptera). Systematic Entomology, 42(1), 94–117.

Balian, E. V., Lévêque, C., Segers, H., & Martens, K. (Eds.). (2008). Freshwater animal diversity assessment. Springer.

Carpenter, J. M. (1988). Choosing among multiple equally parsimonious cladograms. Cladistics, 4(3), 291–296.

Dijkstra, K. D. B., Monaghan, M. T., & Pauls, S. U. (2014). Freshwater biodiversity and aquatic insect diversification. Annual Review of Entomology, 59, 143–163.

Duarte, T., Lecci, L. S., & Calor, A. R. (2014). Stoneflies (Insecta: Plecoptera) from Serra Bonita, Bahia, Brazil: New species and updated records. Zootaxa, 3779(1), 81-92.

Duarte, T., Bispo, P. C., & Calor, A. R. (2014). A new species of Tupiperla Froehlich, 1969 (Plecoptera: Gripopterygidae) from Serra da Jibóia, Bahia, Brazil. Zootaxa, 3835(1), 140-144.

Duarte, T., Novaes, M. C., & Bispo, P. D. C. (2019). Five new species of Tupiperla Froehlich, 1969 (Plecoptera: Gripopterygidae). Zootaxa, 4671(4), zootaxa-4671.

Duarte, T., Calor, A. R., & Bispo, P. D. C. (2022). Systematic revision and phylogeny of Paragripopteryx Enderlein, 1909 (Plecoptera: gripopterygidae). PLoS One, 17(3), e0264264.

Duarte, T., & Lecci, L. S. (2023). A scientometric approach to the taxonomy of Brazilian Plecoptera: an overview of data. Revista Brasileira de Entomologia, 67(spe), e20230056.

Duarte, T., Froehlich, C. G., & Bispo, P. C. (2024). Neotropical species of gripopterygid stoneflies (Plecoptera: Gripopterygidae). Anais da Academia Brasileira de Ciências, 96(4), e20231362.

Duarte, T., Bispo, P. C., & Pessacq, P. (2025). What do morphological data tell us about the Andean-Neotropical Gripopteryginae (Plecoptera: Gripopterygidae) and related taxa?. Arthropod Systematics & Phylogeny, 83, 657-675.

Dunn, C. W., Hejnol, A., Matus, D. Q., Pang, K., Browne, W. E., Smith, S. A., … Giribet, G. (2008). Broad phylogenomic sampling improves resolution of the animal tree of life. Nature, 452(7188), 745–749.

Eichert, A., de Almeida, L. H., Du, Y. Z., Duarte, T., Fochetti, R., Hotaling, S., ... & Ware, J. (2025). Stonefly systematics: past, present, and future. Insect systematics and diversity, 9(4), 7.

Faria, R. R., Pie, M. R., Falcão Salles, F., & Della Giustina Soares, E. (2021). The Haeckelian shortfall or the tale of the missing semaphoronts. Journal of Zoological Systematics and Evolutionary Research, 59(2), 359–369.

Fleck, G., Brenk, M., & Misof, B. (2008). Larval and molecular characters help to solve phylogenetic puzzles in the highly diverse dragonfly family Libellulidae (Insecta:

Odonata: Anisoptera): The Tetrathemistinae are a polyphyletic group. Organisms Diversity & Evolution, 8(1), 1–16.

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

Goloboff, P. A. (1997). Self-weighted optimization: Tree searches and character state reconstructions under implied transformation costs. Cladistics, 13(3), 225–245.

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

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.

Hayashi, M., Kobayashi, T., Yoshitomi, H., & Sota, T. (2024). Molecular phylogeny of Old World Dryopoidea beetles (Coleoptera: Polyphaga: Elateriformia) based on ultraconserved elements of DNA sequence data from Japanese taxa. Insect Systematics and Diversity, 8(4), 5.

Hedtke, S. M., Townsend, T. M., & Hillis, D. M. (2006). Resolution of phylogenetic conflict in large data sets by increased taxon sampling. Systematic Biology, 55(3), 522–529.

Hedtke, S. M., Townsend, T. M., & Hillis, D. M. (2006). Resolution of phylogenetic conflict in large data sets by increased taxon sampling. Systematic Biology, 55(3), 522–529.

Hennig, W. (1966). Phylogenetic systematics. University of Illinois Press.

Hillis, D. M. (1998). Taxonomic sampling, phylogenetic accuracy, and investigator bias. Systematic Biology, 47(1), 3–8.

Huber, B. A., Rheims, C. A., & Brescovit, A. D. (2005). Two new species of litter-dwelling Metagonia spiders (Araneae, Pholcidae) document both rapid and slow genital evolution. Acta Zoologica, 86(1), 33–40.

Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K., Von Haeseler, A., & Jermiin, L. S. (2017). ModelFinder: fast model selection for accurate phylogenetic estimates. Nature methods, 14(6), 587-589.

Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution, 30(4), 772–780.

Katoh, K., Rozewicki, J., & Yamada, K. D. (2019). MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics, 20, 1160–1166.

Lawrence, J. F., Ślipiński, A., Seago, A. E., Thayer, M. K., Newton, A. F., & Marvaldi, A. E. (2011). Phylogeny of the Coleoptera based on morphological characters of adults and larvae. Annales Zoologici, 61(1), 1–217.

Lee, C. F., Sato, M., Shepard, W. D., & Jaech, M. A. (2007). Phylogeny of Psephenidae (Coleoptera: Byrrhoidea) based on larval, pupal and adult characters. Systematic Entomology, 32(3), 502–538.

Lecci, L. S., Sarmento, F. R. P., & Bispo, P. D. C. (2025). Tupiperla tessellata (Brauer, 1866)(Plecoptera: Gripopterygidae): description of the nymph with morphological and distributional notes. Zootaxa, 5642(6), 551-561.

Li, X., & Wiens, J. J. (2023). Estimating global biodiversity: The role of cryptic insect species. Systematic Biology, 72(2), 391–403.

Mayhew, P. J. (2007). Why are there so many insect species? Perspectives from fossils and phylogenies. Biological Reviews, 82(3), 425–454.

Meier, R., & Lim, G. S. (2009). Conflict, convergent evolution, and the relative importance of immature and adult characters in endopterygote phylogenetics. Annual Review of Entomology, 54(1), 85–104.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), 853–858. https://doi.org/10.1038/35002501

Peters, R. S., Meusemann, K., Petersen, M., Mayer, C., Wilbrandt, J., Ziesmann, T., … Misof, B. (2014). The evolutionary history of holometabolous insects inferred from transcriptome-based phylogeny and comprehensive morphological data. BMC Evolutionary Biology, 14(1), 52.

Pessacq, P., Duarte, T., & Epele, L. B. (2020). A first cladistic analysis of Antarctoperlinae (Plecoptera: Gripopterygidae) and a new micropterous species from Patagonia. Zoological Journal of the Linnean Society, 190(3), 771-787.

Pessacq, P., Zúñiga, M. D. C., & Duarte Simoes, T. (2019). An updated checklist of Neotropical Plecoptera.

Pick, K. S., Philippe, H., Schreiber, F., Erpenbeck, D., Jackson, D. J., Wrede, P., … Woerheide, G. (2010). Improved phylogenomic taxon sampling noticeably affects nonbilaterian relationships. Molecular Biology and Evolution, 27(9), 1983–1987.

Pick, K. S., Philippe, H., Schreiber, F., Erpenbeck, D., Jackson, D. J., Wrede, P., … Woerheide, G. (2010). Improved phylogenomic taxon sampling noticeably affects nonbilaterian relationships. Molecular Biology and Evolution, 27(9), 1983–1987.

Poe, S. (1998). The effect of taxonomic sampling on accuracy of phylogeny estimation: Test case of a known phylogeny. Molecular Biology and Evolution, 15(8), 1086.

Raven, P. H., Gereau, R. E., Phillipson, P. B., Chatelain, C., Jenkins, C. N., & Ulloa Ulloa, C. (2020). The distribution of biodiversity richness in the tropics. Science Advances, 6, eabc6228. https://doi.org/10.1126/sciadv.abc6228

Ribera, I., Barraclough, T. G., & Vogler, A. P. (2001). The effect of habitat type on speciation rates and range movements in aquatic beetles: Inferences from species‐level phylogenies. Molecular Ecology, 10(3), 721–735.

Rull, V. (2011). Neotropical biodiversity: Timing and potential drivers. Trends in Ecology & Evolution, 26, 508–513. https://doi.org/10.1016/j.tree.2011.05.011

Sanderson, M. J., & Donoghue, M. J. (1989). Patterns of variation in levels of homoplasy. Evolution, 43(8), 1781–1795.

Satô, M., Lawrence, J. F., & Lee, C. F. (2005). Description of a new species of Drupeus Lewis (Coleoptera: Ptilodactylidae), with a discussion of the systematic position of the genus based on larval, pupal, and adult characters. Insect Systematics & Evolution, 36(4), 371–393.

Sarmento, F. R. P., Duarte, T., Teixeira, A. C. P., & Salles, F. F. (2025). Decoding Tupiperla illiesi Froehlich 1998 (Plecoptera: Gripopterygidae): Insights into Morphological Variation and Molecular Species Delimitation: Felipe Ribeiro Pereira Sarmento. Neotropical Entomology, 54(1), 96.

Sharma, P. P., Clouse, R. M., & Wheeler, W. C. (2017). Hennig's semaphoront concept and the use of ontogenetic stages in phylogenetic reconstruction. Cladistics, 33(1), 93–108.

Simonsen, T. J., de Jong, R., Heikkilä, M., & Kaila, L. (2012). Butterfly morphology in a molecular age: Does it still matter in butterfly systematics? Arthropod Structure & Development, 41(4), 307–322.

Som, A. (2015). Causes, consequences and solutions of phylogenetic incongruence. Briefings in Bioinformatics, 16(3), 536–548.

Song, H. (2009). Species-specificity of male genitalia is characterized by shape, size, and complexity. Insect Systematics & Evolution, 40(2), 159–170.

Song, H., & Bucheli, S. R. (2010). Comparison of phylogenetic signal between male genitalia and non-genital characters in insect systematics. Cladistics, 26(1), 23–35.

Song, H., & Wenzel, J. W. (2008). Mosaic pattern of genital divergence in three populations of Schistocerca lineata Scudder, 1899 (Orthoptera: Acrididae: Cyrtacanthacridinae). Biological Journal of the Linnean Society, 94(2), 289–301.

Stork, N. E. (2018). How many species of insects and other terrestrial arthropods are there on Earth? Annual Review of Entomology, 63, 31–45. https://doi.org/10.1146/annurev-ento-020117-043348

Tuxen, S. L. (Ed.). (1970). Taxonomist's glossary of genitalia in insects. Scandinavian University Press.

Ulloa Ulloa, C., Acevedo-Rodríguez, P., Beck, S., Belgrano, M., Bernal, R., Berry, P. E., … Jørgensen, P. M. (2017). An integrated assessment of the vascular plant species of the Americas. Science, 358, 1614–1617. https://doi.org/10.1126/science.aao0398

Zwickl, D. J., & Hillis, D. M. (2002). Increased taxon sampling greatly reduces phylogenetic error. Systematic Biology, 51(4), 588–598.

ANEXOS

Supplementary Material S1. Additional material

Table with additional material - 🟩 Addicional Material S1 - Dissertação - Sarmento 2026

Supplementary Material S2. Morphological Matrix

Species	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
Anacroneuria debilis	?	0	0	?	0	0	?	?	0	0	1	?	1	0	?	0	0	?	0	?	0	0	0	0	0	0	-	0	-	0	-	0	0	0	0	-	0	0	?	?	0	0	-	-	-	-	-	-
Aubertoperla illiesi	0	0	0	1	0	0	2	2	0	1	0	?	0	0	1	1	0	?	0	2	1	1	1	1	1	0	-	0	-	0	-	0	0	0	0	-	1	1	1	0	0	1	3	0	3	3	0	-
Diamphipnoa helgae	?	0	0	1	0	0	?	?	0	0	0	1	1	0	2	2	0	?	0	?	0	0	0	1	1	0	-	0	-	0	-	0	0	0	0	-	0	1	0	2	0	0	-	-	-	-	-	-
Gripopteryx flinti	1	1	0	1	1	0	2	1	?	1	0	0	0	0	1	1	0	?	0	0	0	0	0	1	?	0	-	0	-	0	-	0	0	0	0	-	1	1	0	0	0	0	-	-	-	-	-	-
Gripopteryx maculosa	1	1	0	1	1	0	2	1	?	1	0	0	0	0	1	1	0	?	0	0	1	0	0	1	?	0	-	0	-	0	-	0	0	0	0	-	0	0	0	0	0	0	-	-	-	-	-	-
Gripopteryx reticulata	1	0	0	1	1	0	2	1	0	1	0	0	0	0	1	1	0	?	0	0	1	0	0	1	?	0	-	0	-	0	-	0	0	0	0	-	1	0	0	0	0	0	-	-	-	-	-	-
Gripopteryx garbei	1	0	0	1	1	0	2	1	0	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	?	0	-	0	-	0	-	0	0	0	0	-	1	0	0	0	0	0	3	1	3	1	0	-
Paragripopteryx blanda	0	0	0	0	0	0	2	2	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1	2	0	-	0	-	0	-	0	0	0	0	-	1	1	0	0	0	1	3	2	1	3	0	-
Paragripopteryx klapaleki	0	0	0	0	0	0	2	2	0	1	0	0	0	0	1	1	1	0	0	0	1	1	0	1	3	0	-	0	-	0	-	0	0	0	0	-	1	0	0	0	0	1	3	3	3	3	0	-
Paragripopteryx sp.	0	0	0	0	0	0	2	2	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	-	0	-	0	-	0	0	0	0	-	0	1	0	0	0	1	3	3	3	3	0	-
Guaranyperla barbosai	1	?	1	0	0	1	3	0	2	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	5	0	-	0	-	0	-	1	0	0	0	-	0	1	1	2	0	0	1	4	3	0	0	-
Guaranyperla guapiara	1	0	1	0	0	1	3	0	2	1	0	1	0	1	1	1	1	1	1	0	0	1	0	0	3	0	-	0	-	0	-	1	0	0	0	-	0	1	1	0	0	1	3	4	3	0	0	-
Guaranyperla nitens	1	0	1	0	0	1	3	0	3	1	0	1	0	1	1	1	1	1	0	0	1	1	0	0	3	0	-	0	-	0	-	1	0	0	0	-	0	1	1	0	0	0	1	3	3	0	0	-
Guaranyperla puri	1	0	1	0	0	1	3	0	2	1	0	1	0	1	1	1	1	1	1	0	0	1	0	0	1	0	-	0	-	0	-	1	0	0	0	-	0	1	1	0	0	1	3	4	3	2	0	-
Teutoperla rothi	0	0	0	0	0	0	2	2	0	1	0	?	0	0	1	1	0	?	0	1	1	1	0	1	3	0	-	0	-	0	-	0	0	0	0	-	0	1	0	0	0	1	3	0	1	4	0	-
Tupiperla amorimi	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	2	0	-	0	-	0	-	0	0	0	1	1	1	2	0	2	0	1	1	0	1	1	1	2
Tupiperla bispoi	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	2	0	-	0	-	0	-	0	0	0	0	-	1	1	1	0	0	1	1	1	1	0	1	0
Tupiperla claudius	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	3	1	1	0	-	0	-	0	0	0	0	-	1	1	1	1	0	1	2	0	2	0	1	1
Tupiperla eleonorae	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	1	0	-	0	-	0	-	0	0	0	0	-	1	1	0	1	0	1	0	2	1	0	1	0
Tupiperla flinti	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	4	0	-	0	-	0	-	0	0	0	1	1	1	1	0	1	0	1	1	2	1	0	1	1
Tupiperla froehlichi	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	4	0	-	0	-	0	-	0	0	0	0	-	1	1	0	0	0	1	2	1	1	1	1	2
Tupiperla gracilis	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	2	0	-	0	-	0	-	0	0	0	0	-	0	1	0	2	0	1	1	1	1	0	1	1
Tupiperla guariru	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	2	0	-	0	-	0	-	0	0	0	0	-	1	1	0	1	0	1	3	2	0	2	1	0
Tupiperla illiesi	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	3	1	0	1	0	0	-	0	0	0	0	-	0	1	0	1	0	1	2	0	2	0	1	1
Tupiperla jumirim	?	?	?	?	?	0	?	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	4	0	-	0	-	0	-	0	0	0	0	-	0	0	1	0	0	1	3	2	1	2	0	-
Tupiperla misionera	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	2	0	-	0	-	0	-	0	0	0	0	-	1	1	0	1	0	1	0	1	1	0	1	0
Tupiperla modesta	?	?	?	?	?	0	?	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	3	0	-	0	-	0	-	0	0	0	0	-	0	1	0	0	0	1	3	2	2	2	0	-
Tupiperla oliverai	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	2	0	-	0	-	0	-	0	0	0	0	-	1	2	0	1	0	1	1	0	1	1	1	2
Tupiperla pessacqi	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	3	0	-	0	-	0	-	0	0	0	1	0	1	1	0	1	0	1	1	1	2	0	1	0
Tupiperla pinhoi	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	3	1	2	0	-	0	-	0	0	0	0	-	1	1	2	1	0	1	2	1	1	0	1	1
Tupiperla reichardti	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	2	0	-	0	-	1	0	0	0	1	0	-	1	1	0	0	0	1	0	0	2	0	1	1
Tupiperla robusta	?	?	?	?	?	0	1	0	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0	-	0	-	0	-	1	0	0	0	-	1	1	0	0	0	1	0	2	0	0	0	-
Tupiperla sepeensis	?	?	?	?	?	0	0	?	?	1	0	1	0	1	1	1	1	1	1	0	0	1	0	0	5	0	-	0	-	0	-	0	0	0	0	-	0	0	0	1	1	1	2	1	1	0	1	1
Tupiperla serrulata	?	?	?	?	?	0	0	?	?	1	0	1	0	1	1	1	1	1	1	0	0	1	0	0	4	1	1	0	-	0	-	0	0	0	0	-	1	1	1	0	0	1	2	0	2	0	1	1
Tupiperla sulina	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	2	0	-	0	-	0	-	0	0	0	0	-	1	1	1	1	0	1	1	1	1	0	1	0
Tupiperla tessellata	0	?	?	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	2	0	-	0	-	0	-	0	0	0	0	-	1	1	1	1	0	1	2	0	1	0	1	1
Tupiperla tucum	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	2	1	0	1	1	0	-	0	0	0	0	-	1	1	0	1	0	1	2	0	1	0	1	1
Tupiperla ubuntu	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	4	0	-	0	-	0	-	0	0	0	0	-	1	0	0	0	0	1	2	0	1	1	1	2
Tupiperla umbya	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	3	0	-	0	-	0	-	0	0	0	0	-	1	1	1	2	0	1	1	1	1	0	1	1

Cont. Supplementary Material S3. Matrix morfológica

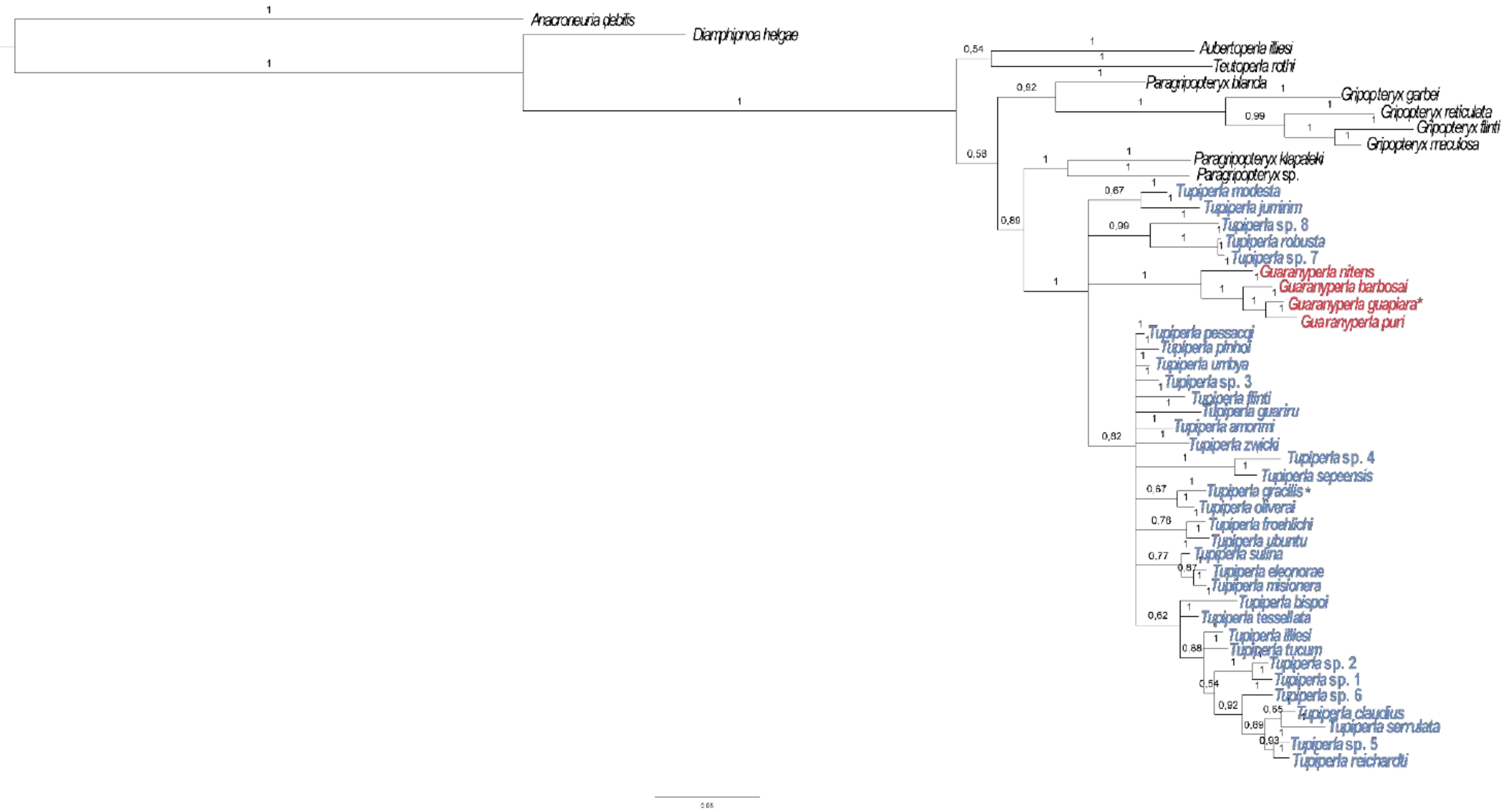
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**
Tupiperla zwicki	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	3	0	-	0	-	0	-	0	0	0	1	0	1	1	2	1	0	1	2	0	1	1	1	1
Tupiperla sp. 1	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	2	0	-	0	-	1	0	0	0	0	0	-	1	1	0	1	0	1	2	0	2	0	1	0
Tupiperla sp. 2	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	1	1	0	0	-	1	1	0	0	0	0	-	1	1	0	0	0	1	2	0	3	0	1	1
Tupiperla sp. 3	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	2	0	-	0	-	0	-	0	0	0	0	-	1	2	0	0	0	1	1	0	1	1	1	2
Tupiperla sp. 4	?	?	?	?	?	0	0	?	?	1	0	1	0	1	1	1	1	1	1	0	0	1	0	?	5	0	-	0	-	0	-	0	0	0	0	-	1	0	1	2	1	1	2	1	1	1	1	1
Tupiperla sp. 5	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	2	0	-	0	-	0	-	0	1	0	0	-	0	1	1	1	0	1	2	0	3	0	1	1
Tupiperla sp. 6	?	?	?	?	?	0	0	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	2	1	0	1	0	0	-	0	0	1	0	-	1	1	1	1	0	1	2	0	1	0	1	1
Tupiperla sp. 7	?	?	?	?	?	0	1	?	?	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0	-	0	-	0	-	1	0	0	0	-	1	1	0	1	0	1	0	2	0	0	0	-
Tupiperla sp. 8	?	?	?	?	?	0	1	?	?	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	1	0	-	0	-	0	-	1	0	0	0	-	0	1	0	1	0	1	0	3	0	0	1	0

Supplementary Material S3. Detailed PCR protocol

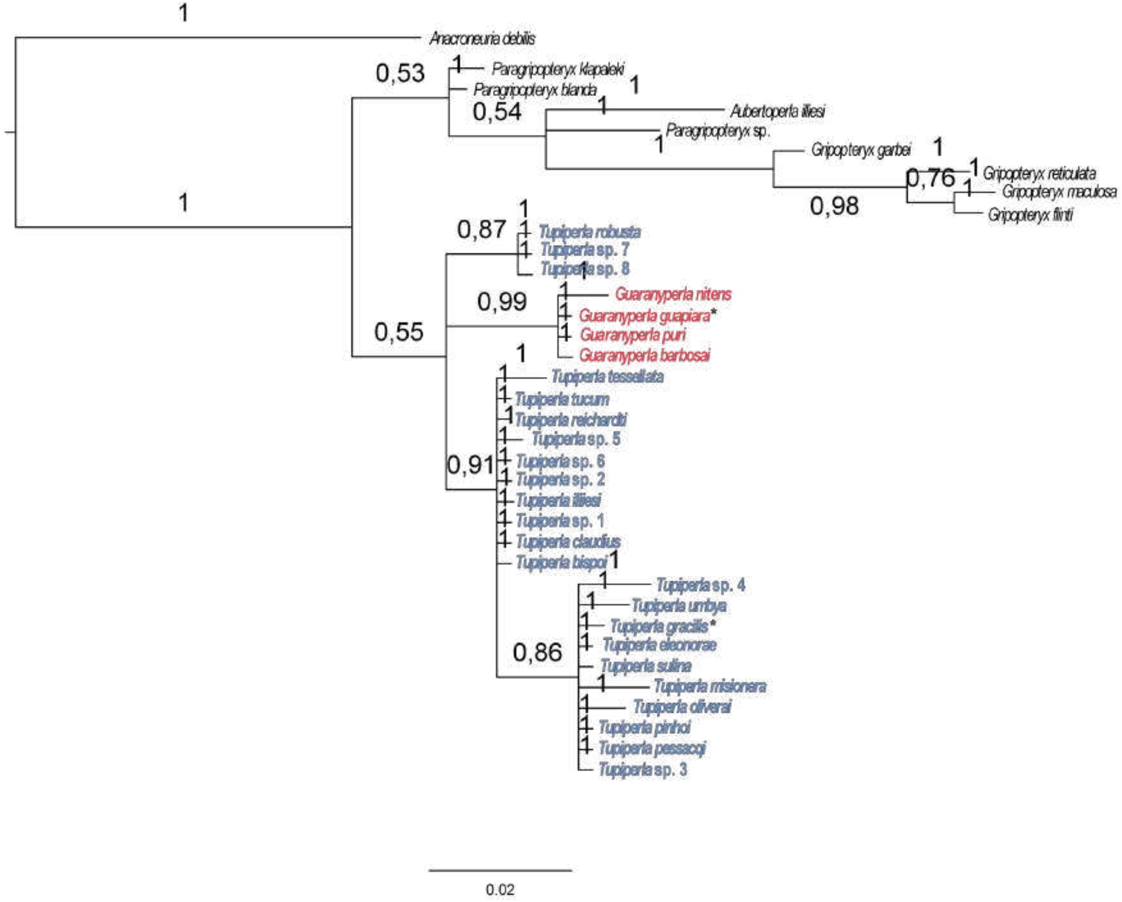
step	1	2	3	4	5	6	7	8	9	10	11
time (min)	02:00	01:00	01:00	02:00	go to step 2	01:00	01:00	02:00	go to step 6	05:00	infinity hold
temp °C (COI)	94	94	45	75	5x	94	50	75	35x	75	4

step	1	2	3	4	5	6	7
time (min)	02:00	01:00	01:00	02:00	go to step 2	05:00	infinity hold
temp °C (28S)	94	94	50	75	40x	75	4
temp °C (16S)	94	94	50	75	40x	75	4
temp °C (WING)	94	94	53	75	40x	75	4
temp °C (H3)	94	94	57	75	40x	75	4

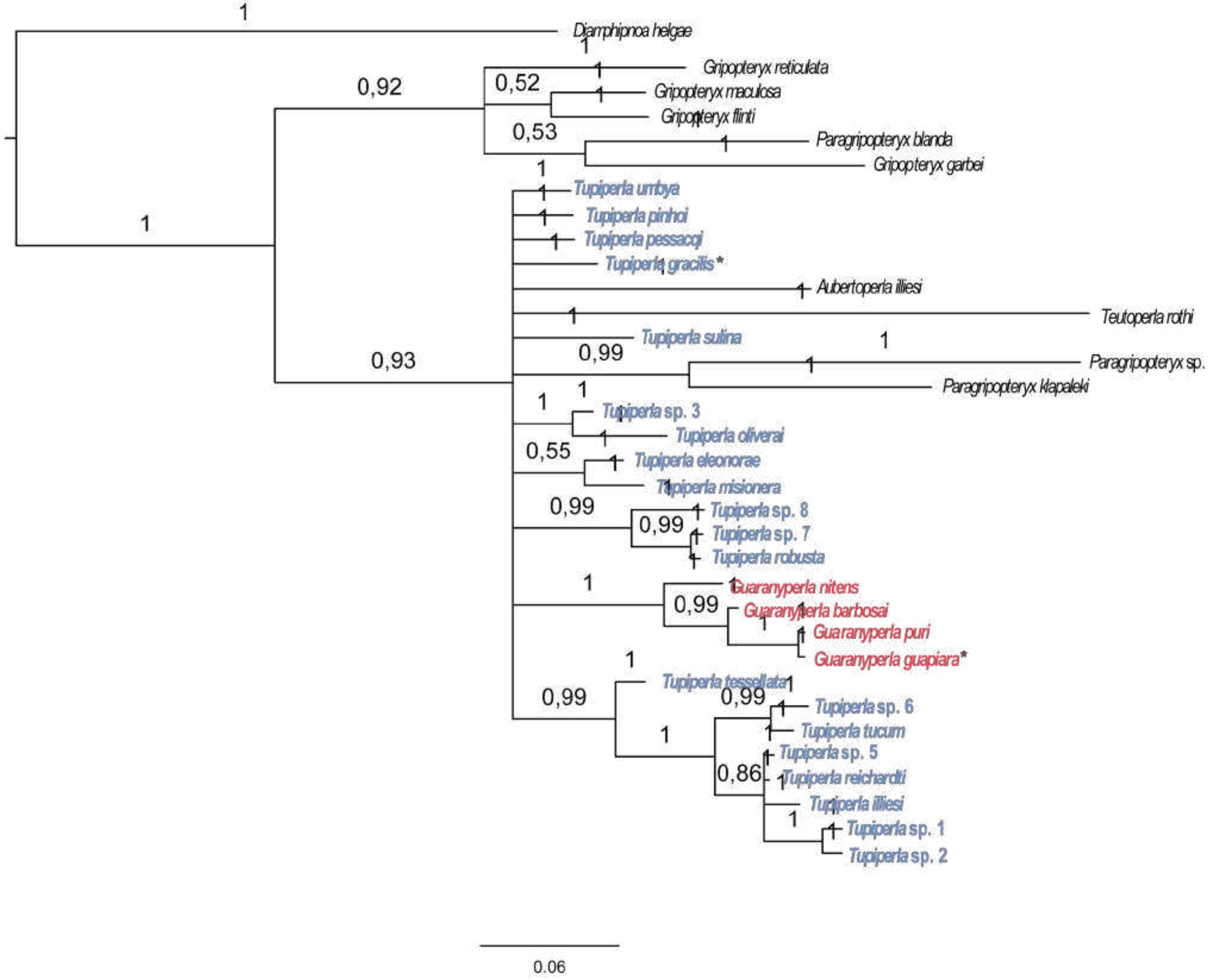
Supplementary Material S4. Phylogenetic hypothesis of *Tupiperla* derived from bayesian inference analysis of the (28S, WING, H3, 16S and COI, 2034 bp, and 48 morphological characters). Support values as posterior probabilities (PP). Asterisks (*) indicate type species.


Anacroneuria debilis
Diamphipnoa helgae
0,54
Aubertoperla illiesi
Teutoperla rothi
0,92
Paragripopteryx blanda
Gripopteryx garbei
0,99
Gripopteryx reticulata
Gripopteryx flinti
Gripopteryx maculosa
0,58
Paragripopteryx klapaleki
Paragripopteryx sp.
0,67
Tupiperla modesta
Tupiperla jurumim
0,89
0,99
Tupiperla sp. 8
Tupiperla robusta
Tupiperla sp. 7
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla guapiara*
Guaranyperla puri
Tupiperla pessacqi
Tupiperla pinhoi
Tupiperla umbya
Tupiperla sp. 3
Tupiperla flinti
Tupiperla guariru
Tupiperla amorimi
0,82
Tupiperla zwicki
Tupiperla sp. 4
Tupiperla sepeensis
0,67
Tupiperla gracilis *
Tupiperla oliverai
0,76
Tupiperla froehlichi
Tupiperla ubuntu
0,77
Tupiperla sulina
0,87
Tupiperla eleonorae
Tupiperla misionera
Tupiperla bispoi
0,62
Tupiperla tessellata
Tupiperla illiesi
0,88
Tupiperla tucum
Tupiperla sp. 2
0,54
Tupiperla sp. 1
Tupiperla sp. 6
0,92
0,55
Tupiperla claudius
0,69
Tupiperla serrulata
0,93
Tupiperla sp. 5
Tupiperla reichardti
0.05

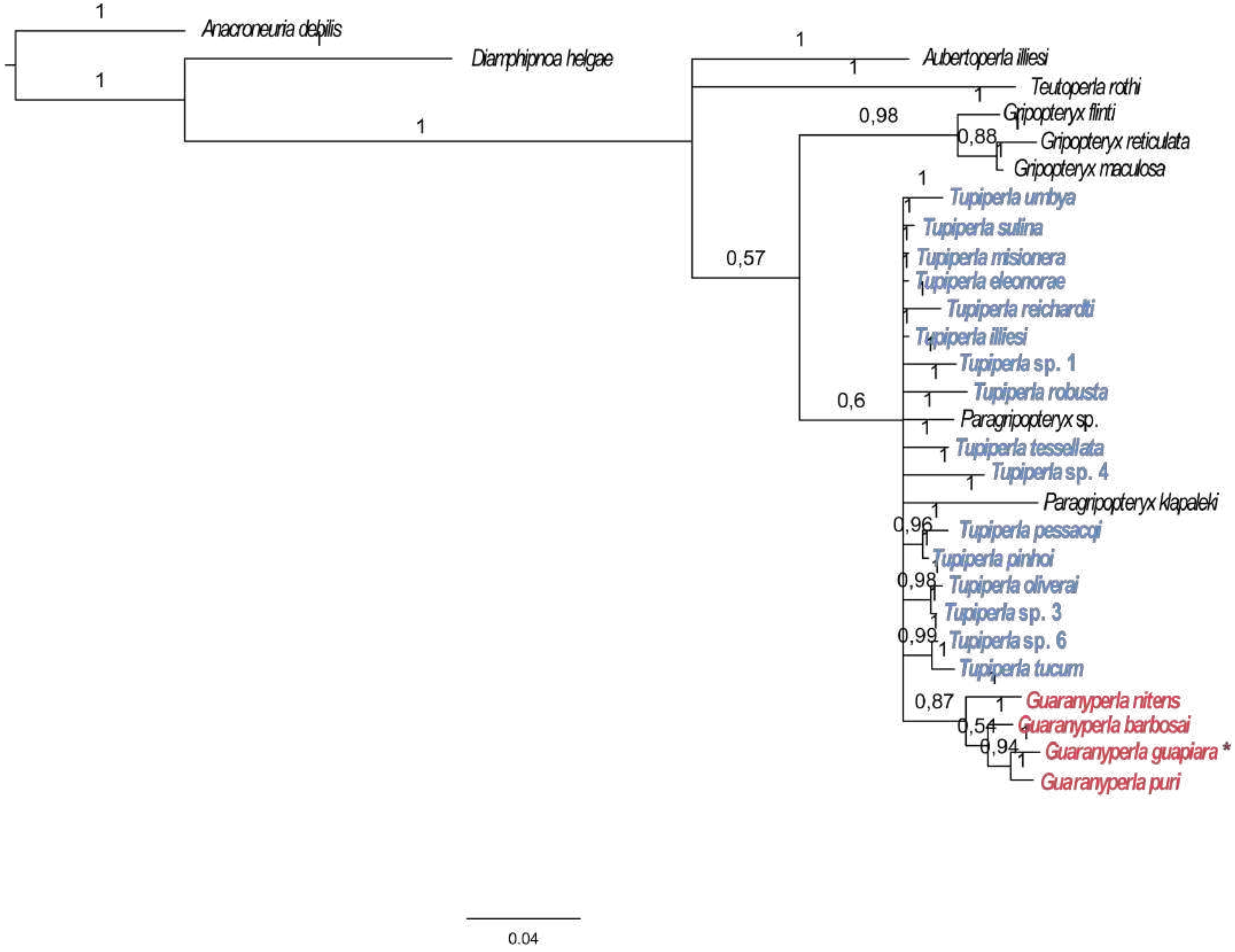
Supplementary Material S5. Phylogenetic hypothesis of *Tupiperla* derived from bayesian inference analysis of the 28S. Support values as posterior probabilities (PP). Asterisks (*) indicate type species.


1
Anacroneuria debilis
0,53
1
Paragripopteryx klapaleki
Paragripopteryx blanda
1
0,54
1
Aubertoperla illiesi
Paragripopteryx sp.
1
Gripopteryx garbei
1
1
Gripopteryx reticulata
0,76
1
Gripopteryx maculosa
0,98
Gripopteryx flinti
1
1
0,87
1
Tupiperla robusta
1
Tupiperla sp. 7
Tupiperla sp. 8
1
1
Guaranyperla nitens
0,99
1
Guaranyperla guapiara*
0,55
1
Guaranyperla puri
Guaranyperla barbosai
1
1
Tupiperla tessellata
1
Tupiperla tucum
1
Tupiperla reichardti
1
Tupiperla sp. 5
0,91
1
Tupiperla sp. 6
1
Tupiperla sp. 2
1
Tupiperla illiesi
1
Tupiperla sp. 1
1
Tupiperla claudius
Tupiperla bispoi
1
1
Tupiperla sp. 4
1
Tupiperla umbya
1
Tupiperla gracilis*
1
Tupiperla eleonorae
0,86
Tupiperla sulina
1
Tupiperla misionera
1
Tupiperla oliverai
1
Tupiperla pinhoi
1
Tupiperla pessacqi
Tupiperla sp. 3
0.02

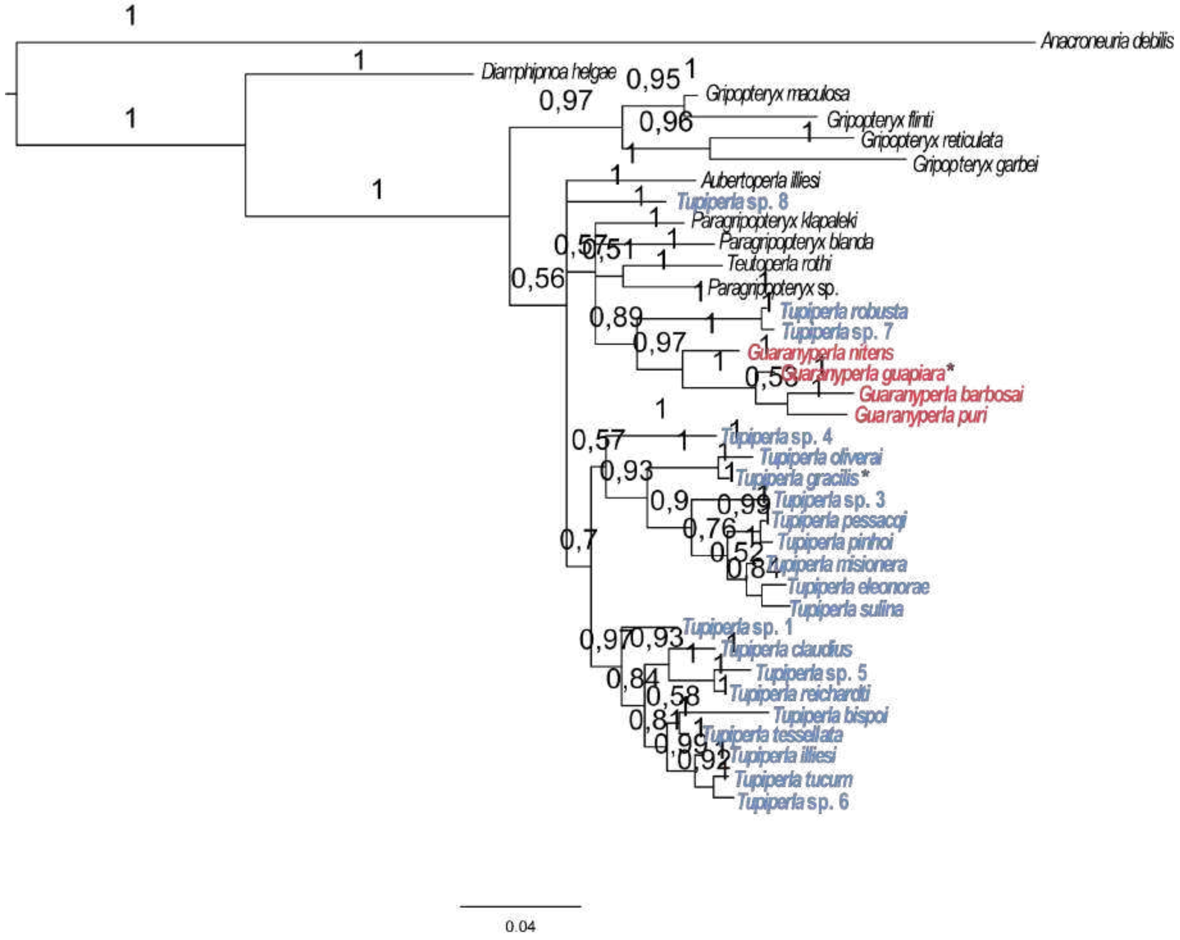
Supplementary Material S6. Phylogenetic hypothesis of *Tupiperla* derived from bayesian inference analysis of the WING. Support values as posterior probabilities (PP). Asterisks (*) indicate type species.


Diamphipnoa helgae
Gripopteryx reticulata
Gripopteryx maculosa
Gripopteryx flinti
Paragripopteryx blanda
Gripopteryx garbei
Tupiperla umbya
Tupiperla pinhoi
Tupiperla pessacqi
Tupiperla gracilis*
Aubertoperla illiesi
Teutoperla rothi
Tupiperla sulina
Paragripopteryx sp.
Paragripopteryx klapaleki
Tupiperla sp. 3
Tupiperla oliverai
Tupiperla eleonorae
Tupiperla misionera
Tupiperla sp. 8
Tupiperla sp. 7
Tupiperla robusta
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla puri
Guaranyperla guapiara*
Tupiperla tessellata
Tupiperla sp. 6
Tupiperla tucum
Tupiperla sp. 5
Tupiperla reichardti
Tupiperla illiesi
Tupiperla sp. 1
Tupiperla sp. 2
0,92
0,52
0,53
0,93
0,99
0,55
0,99
0,99
0,99
0,99
0,99
0,86
0.06

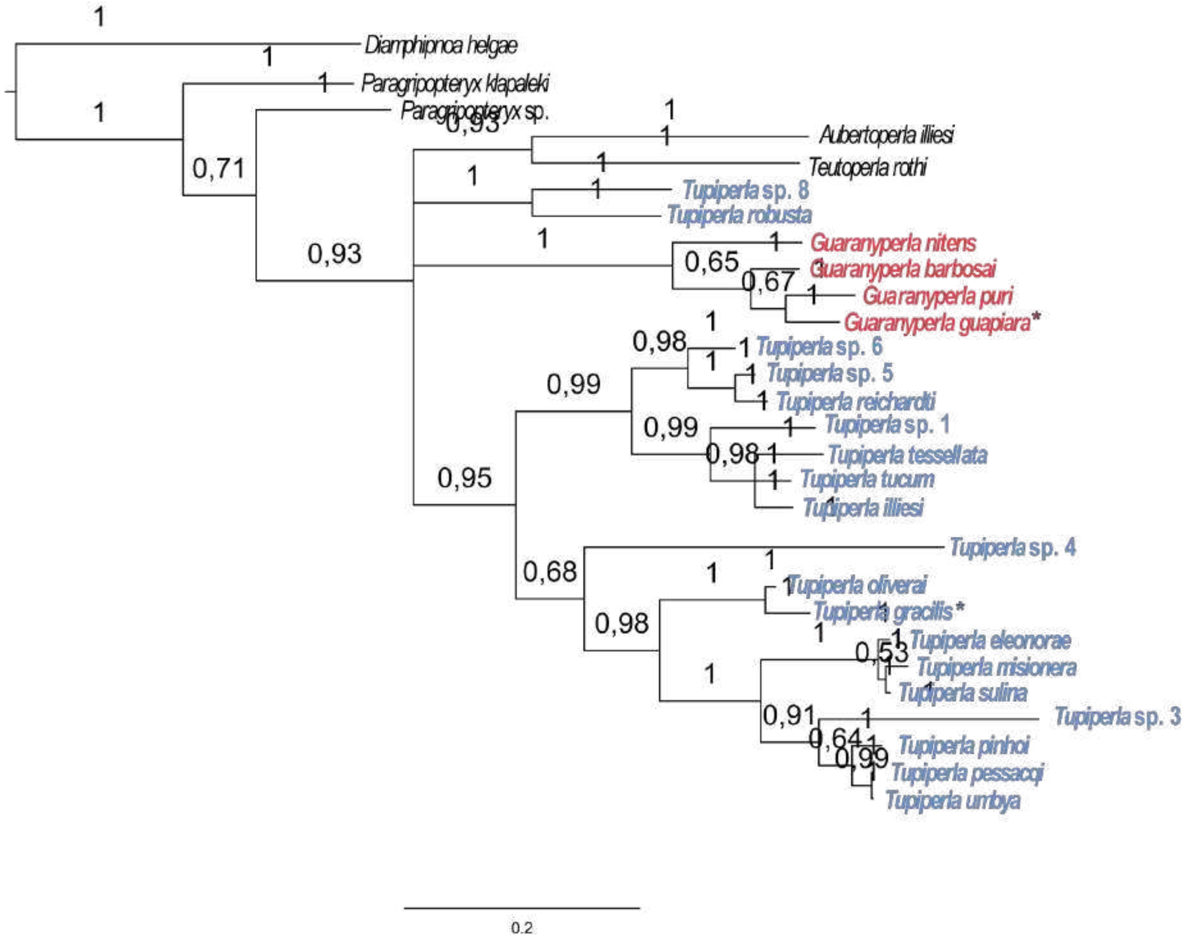
Supplementary Material S7. Phylogenetic hypothesis of *Tupiperla* derived from bayesian inference analysis of the H3. Support values as posterior probabilities (PP). Asterisks (*) indicate type species.


Anacroneuria debilis
Diamphipnoa helgae
Aubertoperla illiesi
Teutoperla rothi
Gripopteryx flinti
Gripopteryx reticulata
Gripopteryx maculosa
Tupiperla umbya
Tupiperla sulina
Tupiperla misionera
Tupiperla eleonorae
Tupiperla reichardti
Tupiperla illiesi
Tupiperla sp. 1
Tupiperla robusta
Paragripopteryx sp.
Tupiperla tessellata
Tupiperla sp. 4
Paragripopteryx klapaleki
Tupiperla pessacqi
Tupiperla pinhoi
Tupiperla oliverai
Tupiperla sp. 3
Tupiperla sp. 6
Tupiperla tucum
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla guapiara *
Guaranyperla puri
1
1
1
1
0,98
0,88
0,57
0,6
0,96
0,98
0,99
0,87
0,54
0,94
0.04

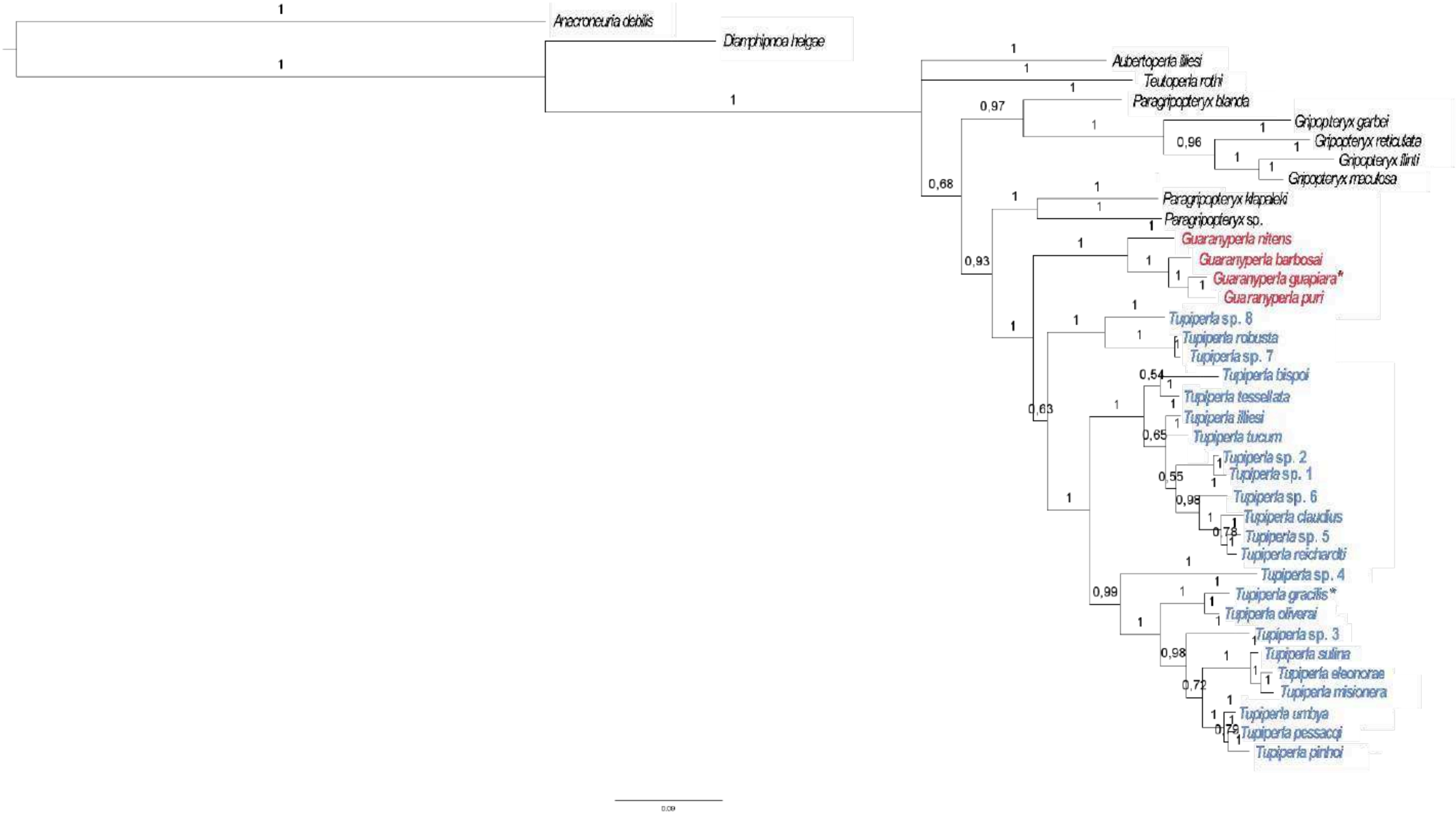
Supplementary Material S8. Phylogenetic hypothesis of *Tupiperla* derived from bayesian inference analysis of the 26S. Support values as posterior probabilities (PP). Asterisks (*) indicate type species.


Anacroneuria debilis
Diamphipnoa helgae
Gripopteryx maculosa
Gripopteryx flinti
Gripopteryx reticulata
Gripopteryx garbei
Aubertoperla illiesi
Tupiperla sp. 8
Paragripopteryx klapaleki
Paragripopteryx blanda
Teutoperla rothi
Paragripopteryx sp.
Tupiperla robusta
Tupiperla sp. 7
Guaranyperla nitens
Guaranyperla guapiara*
Guaranyperla barbosai
Guaranyperla puri
Tupiperla sp. 4
Tupiperla oliverai
Tupiperla gracilis*
Tupiperla sp. 3
Tupiperla pessacqi
Tupiperla pinhoi
Tupiperla misionera
Tupiperla eleonorae
Tupiperla sulina
Tupiperla sp. 1
Tupiperla claudius
Tupiperla sp. 5
Tupiperla reichardti
Tupiperla bispoi
Tupiperla tessellata
Tupiperla illiesi
Tupiperla tucum
Tupiperla sp. 6
1
1
1
1
0,95
0,97
0,96
0,56
0,57
0,51
0,89
0,97
0,53
0,57
0,93
0,9
0,99
0,76
0,52
0,84
0,7
0,97
0,93
0,84
0,58
0,81
0,99
0,92
0.04

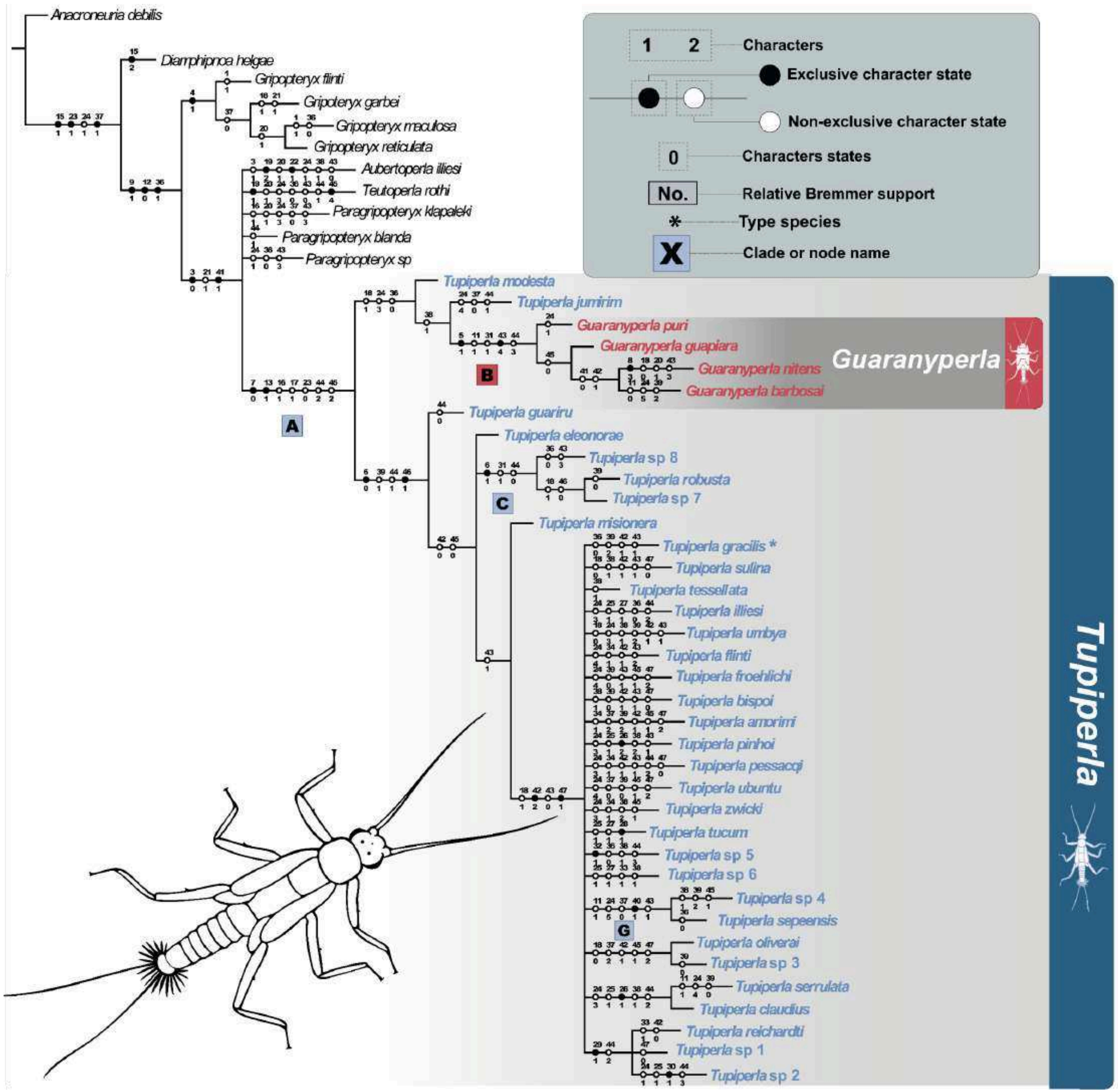
Supplementary Material S9. Phylogenetic hypothesis of *Tupiperla* derived from bayesian inference analysis of the COI. Support values as posterior probabilities (PP). Asterisks (*) indicate type species.



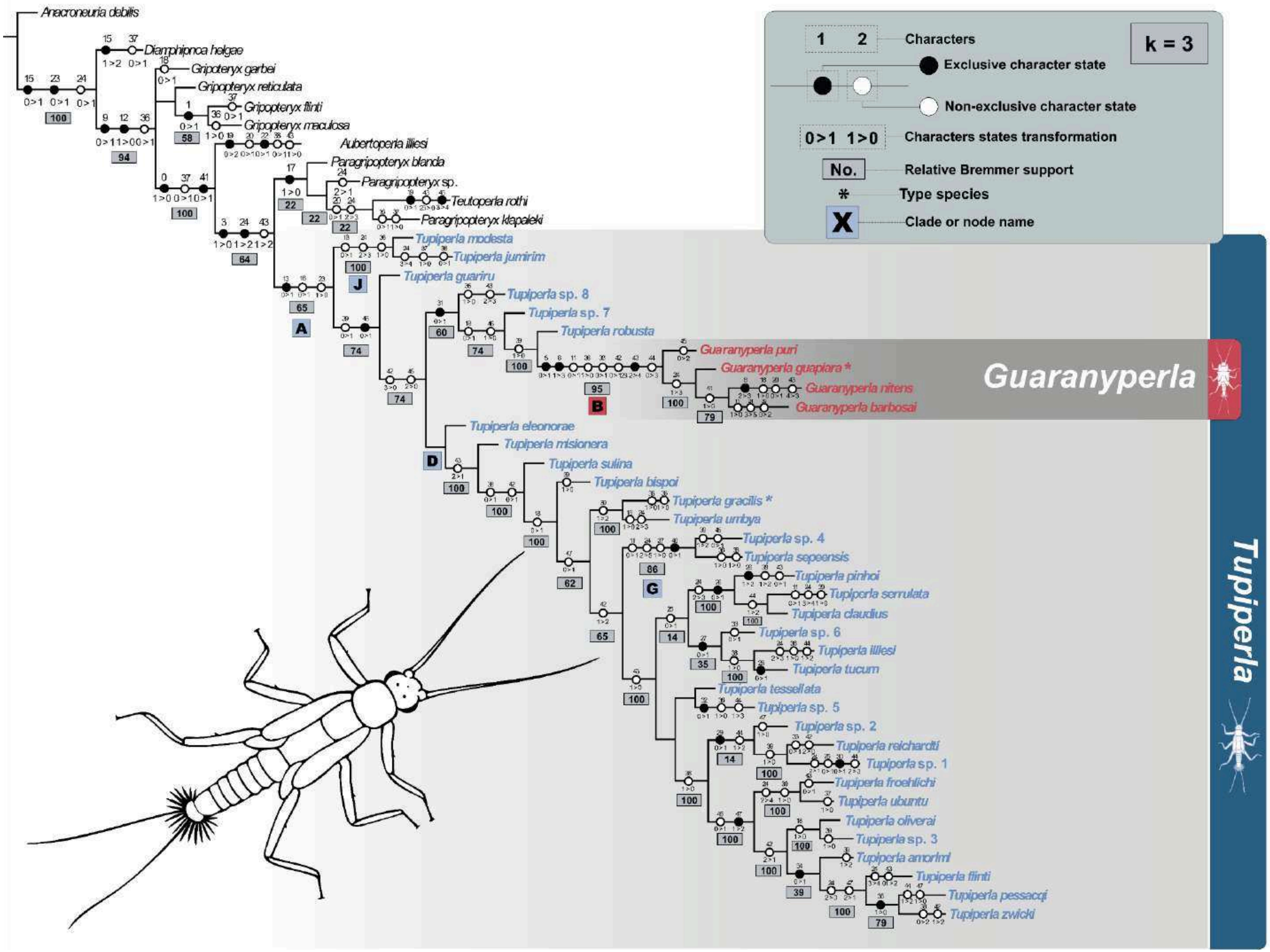
Supplementary Material S10. Phylogenetic hypothesis of *Tupiperla* derived from bayesian inference analysis of the (28S, WING, H3, 16S and COI, 2034 bp). Support values as posterior probabilities (PP). Asterisks (*) indicate type species.


1
1
1
Anacroneuria debilis
Diamphipnoa helgae
1
Aubertoperla illiesi
1
Teutoperla rothi
1
Paragripopteryx blanda
0,97
1
Gripopteryx garbei
1
0,96
Gripopteryx reticulata
1
1
Gripopteryx flinti
1
Gripopteryx maculosa
0,68
1
1
Paragripopteryx klapaleki
1
Paragripopteryx sp.
1
Guaranyperla nitens
1
0,93
1
Guaranyperla barbosai
1
Guaranyperla guapiara*
1
Guaranyperla puri
1
1
Tupiperla sp. 8
1
1
Tupiperla robusta
1
Tupiperla sp. 7
0,54
Tupiperla bispoi
1
Tupiperla tessellata
1
1
0,63
Tupiperla illiesi
1
0,65
Tupiperla tucum
Tupiperla sp. 2
1
Tupiperla sp. 1
0,55
1
Tupiperla sp. 6
1
0,98
Tupiperla claudius
1
1
0,78
Tupiperla sp. 5
1
Tupiperla reichardti
1
Tupiperla sp. 4
0,99
1
Tupiperla gracilis*
1
1
Tupiperla oliverai
1
1
Tupiperla sp. 3
1
0,98
Tupiperla sulina
1
1
Tupiperla eleonorae
1
0,72
Tupiperla misionera
1
Tupiperla umbya
1
1
0,79
Tupiperla pessacqi
1
Tupiperla pinhoi
0.09

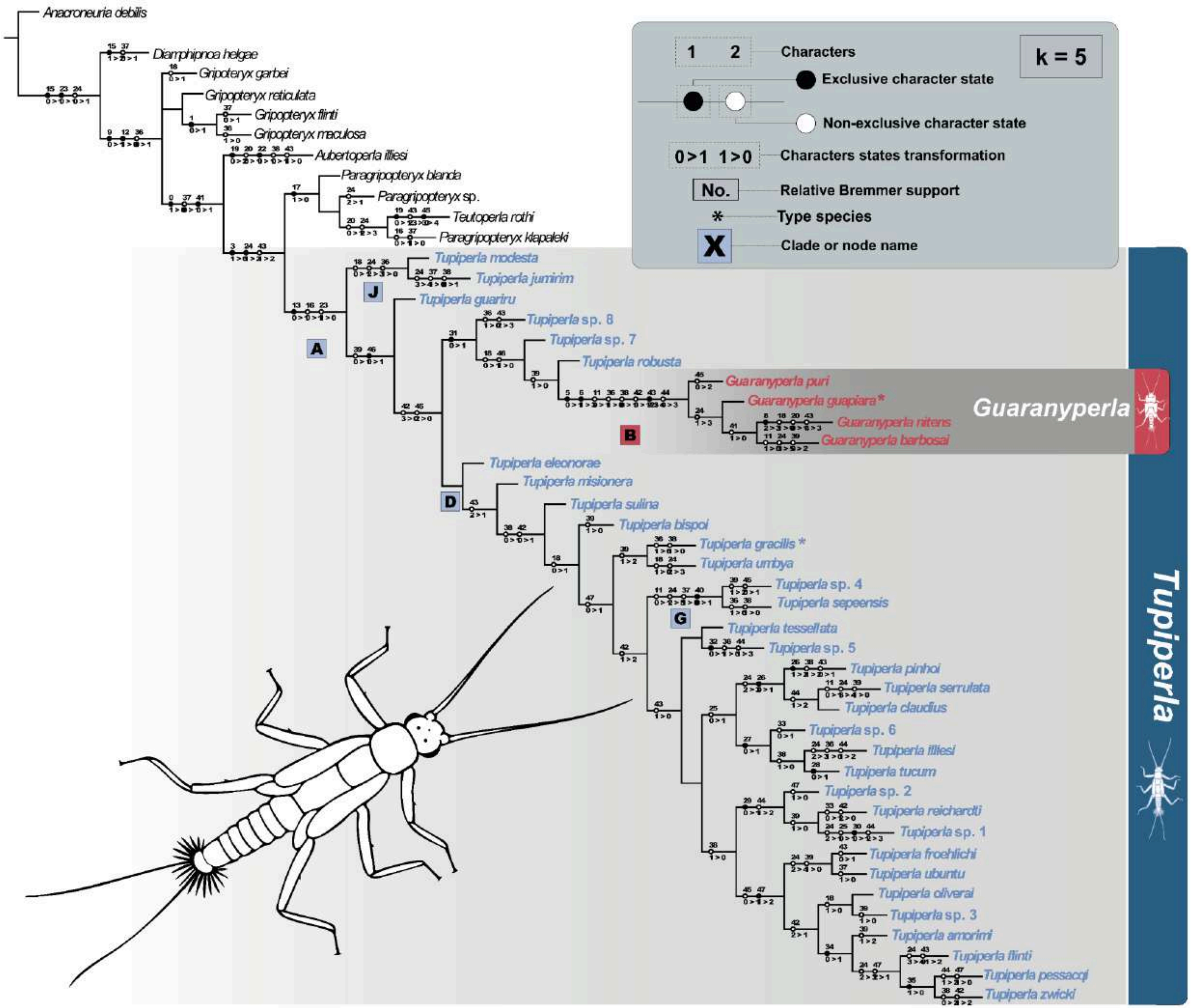
Supplementary Material S11. Phylogenetic hypothesis of *Tupiperla* (blue taxa) based on the strict consensus of 4987 most parsimonious trees.


1
2
Characters
Exclusive character state
Non-exclusive character state
0
Characters states
No.
Relative Bremmer support
*
Type species
X
Clade or node name
Anacroneuria debilis
Diamphipnoa helgae
Gripopteryx flinti
Gripoteryx garbei
Gripopteryx maculosa
Gripopteryx reticulata
Aubertoperla illiesi
Teutoperla rothi
Paragripopteryx klapaleki
Paragripopteryx blanda
Paragripopteryx sp
Tupiperla modesta
Tupiperla jurirrim
Guaranyperla puri
Guaranyperla guapiara
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla
B
A
Tupiperla guariru
Tupiperla eleonorae
Tupiperla sp 8
Tupiperla robusta
Tupiperla sp 7
C
Tupiperla misionera
Tupiperla gracilis *
Tupiperla sulina
Tupiperla tessellata
Tupiperla illiesi
Tupiperla umbya
Tupiperla flinti
Tupiperla froehlichi
Tupiperla bispoi
Tupiperla amorimi
Tupiperla pinhoi
Tupiperla pessacqi
Tupiperla ubuntu
Tupiperla zwicki
Tupiperla tucum
Tupiperla sp 5
Tupiperla sp 6
Tupiperla sp 4
Tupiperla sepeensis
G
Tupiperla oliverai
Tupiperla sp 3
Tupiperla serrulata
Tupiperla claudius
Tupiperla reichardti
Tupiperla sp 1
Tupiperla sp 2
Tupiperla

Supplementary Material S12. Phylogenetic hypothesis of *Tupiperla* (blue taxa) based on the strict consensus of two most parsimonious trees under k = 3 (fit = 30.14). Unambiguous character-state changes were optimized under maximum parsimony.

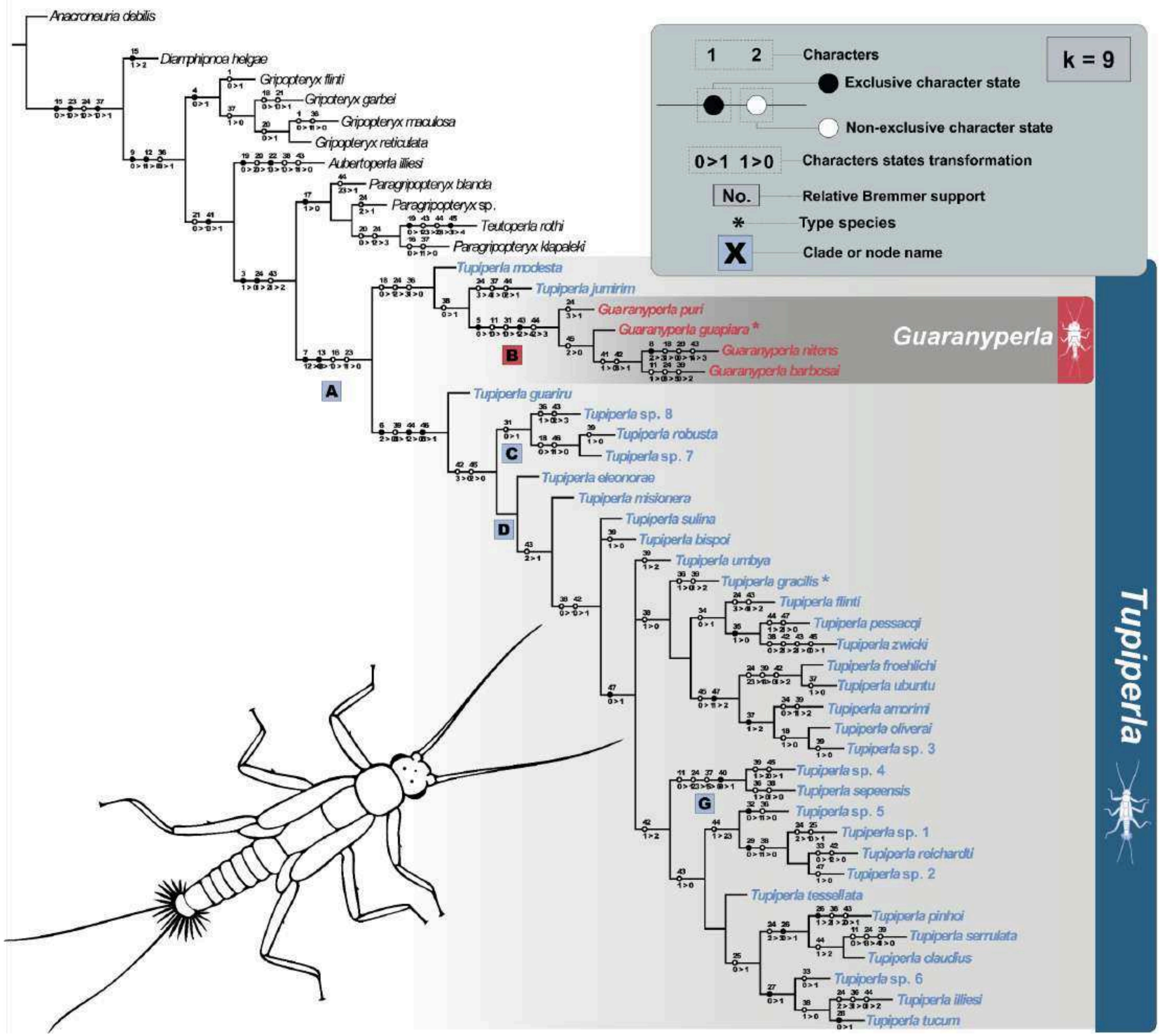

1 2 Characters
Exclusive character state
Non-exclusive character state
0>1 1>0 Characters states transformation
No. Relative Bremmer support
* Type species
X Clade or node name
k = 3
Anacroneuria debilis
Diamphipnoa helgae
Gripopteryx garbei
Gripopteryx reticulata
Gripopteryx flinti
Gripopteryx maculosa
Aubertoperla illiesi
Paragripopteryx blanda
Paragripopteryx sp.
Teutoperla rothi
Paragripopteryx klapaleki
Tupiperla modesta
Tupiperla jurimim
Tupiperla guariru
Tupiperla sp. 8
Tupiperla sp. 7
Tupiperla robusta
Guaranyperla puri
Guaranyperla guapiara *
Guaranyperla nitens
Guaranyperla barbosai
Tupiperla eleonorae
Tupiperla misionera
Tupiperla sulina
Tupiperla bispoi
Tupiperla gracilis *
Tupiperla umbya
Tupiperla sp. 4
Tupiperla sepeensis
Tupiperla pinhoi
Tupiperla serrulata
Tupiperla claudius
Tupiperla sp. 6
Tupiperla illiesi
Tupiperla tucum
Tupiperla tessellata
Tupiperla sp. 5
Tupiperla sp. 2
Tupiperla reichardti
Tupiperla sp. 1
Tupiperla froehlichi
Tupiperla ubuntu
Tupiperla oliverai
Tupiperla sp. 3
Tupiperla amorimi
Tupiperla flinti
Tupiperla pessacqi
Tupiperla zwicki
A
J
D
B
G
Guaranyperla
Tupiperla

Supplementary Material S13. Phylogenetic hypothesis of *Tupiperla* (blue taxa) based on the strict consensus of two most parsimonious trees under k = 5 (fit = 32.29). Unambiguous character-state changes were optimized under maximum parsimony.

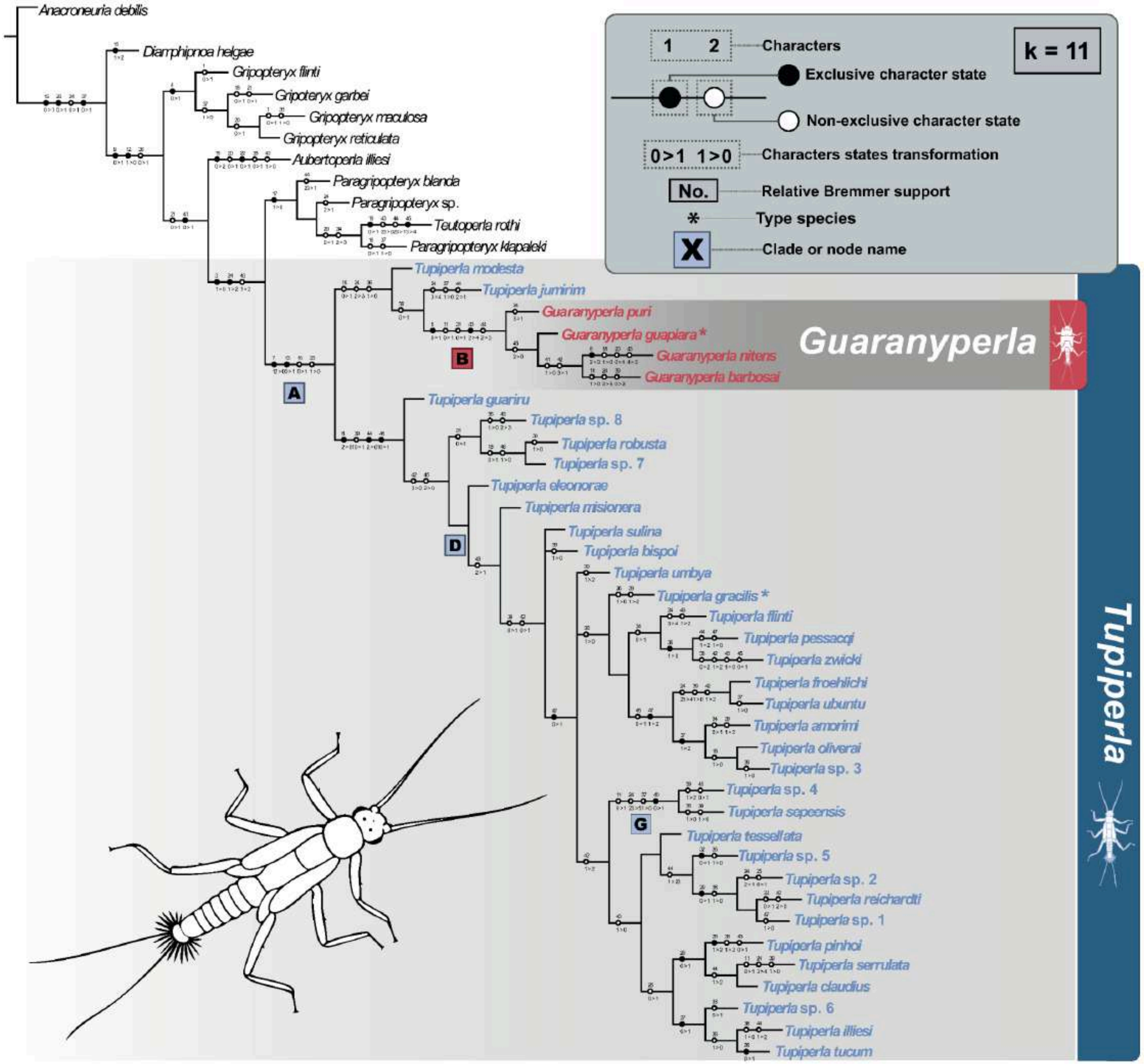


Characters
1 2
Exclusive character state
Non-exclusive character state
0>1 1>0
Characters states transformation
No.
Relative Bremmer support
*
Type species
X
Clade or node name
k = 5
Anacroneuria debilis
Diamphipnoa helgae
Gripopteryx garbei
Gripopteryx reticulata
Gripopteryx flinti
Gripopteryx maculosa
Aubertoperla illiesi
Paragripopteryx blanda
Paragripopteryx sp.
Teutoperla rothi
Paragripopteryx klapaleki
Tupiperla modesta
Tupiperla jurimirim
J
Tupiperla guariru
A
Tupiperla sp. 8
Tupiperla sp. 7
Tupiperla robusta
Guaranyperla puri
Guaranyperla guapiara*
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla
B
Tupiperla eleonorae
Tupiperla misionera
D
Tupiperla sulina
Tupiperla bispoi
Tupiperla gracilis *
Tupiperla umbya
Tupiperla sp. 4
Tupiperla sepeensis
G
Tupiperla tessellata
Tupiperla sp. 5
Tupiperla pinhoi
Tupiperla serrulata
Tupiperla claudius
Tupiperla sp. 6
Tupiperla illiesi
Tupiperla tucum
Tupiperla sp. 2
Tupiperla reichardti
Tupiperla sp. 1
Tupiperla froehlichi
Tupiperla ubuntu
Tupiperla oliverai
Tupiperla sp. 3
Tupiperla amorimi
Tupiperla flinti
Tupiperla pessacqi
Tupiperla zwicki
Tupiperla

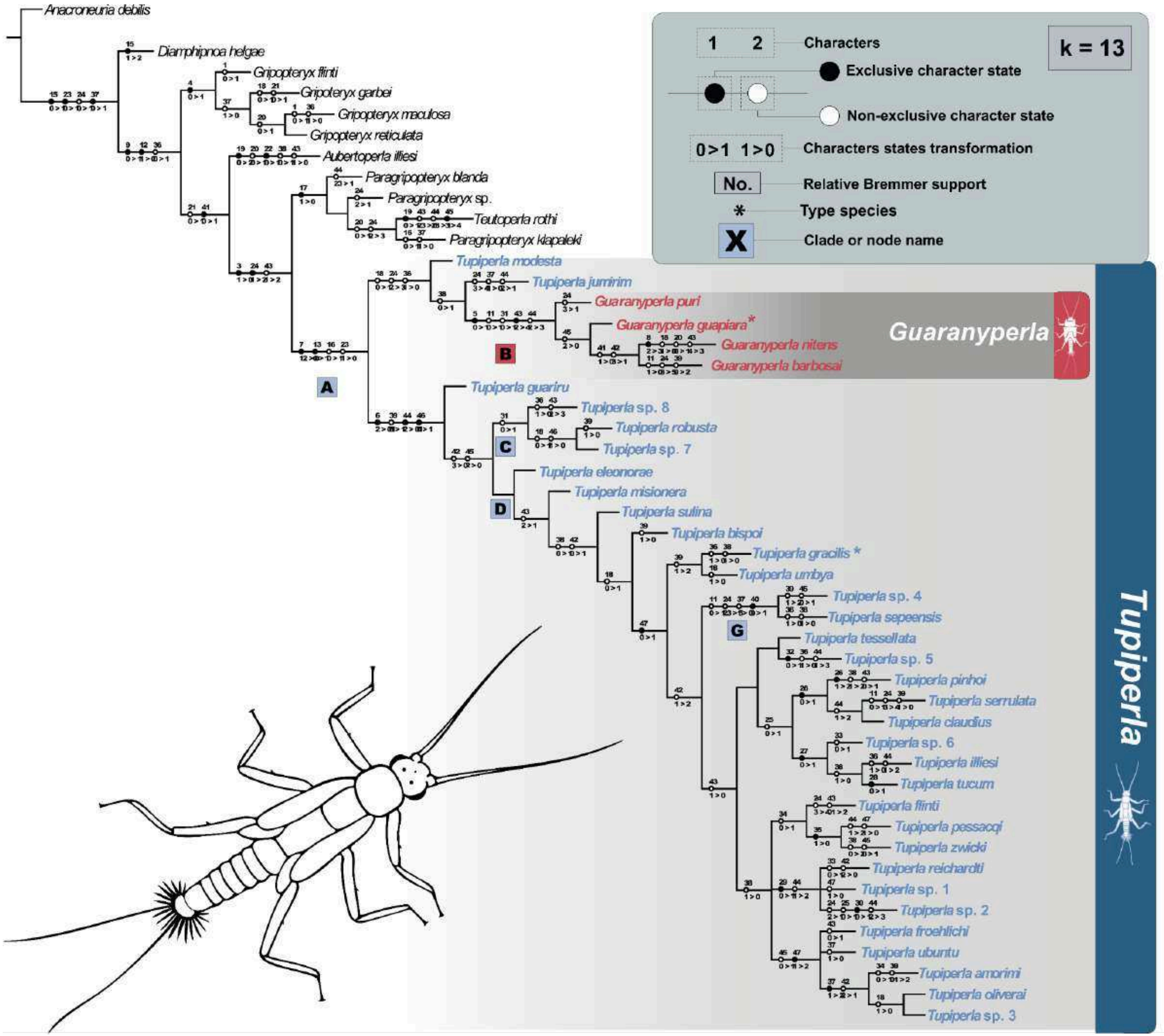
Supplementary Material S14. Phylogenetic hypothesis of *Tupiperla* (blue taxa) based on the strict consensus of three most parsimonious trees under k = 9 (fit = 34.70). Unambiguous character-state changes were optimized under maximum parsimony.


Anacroneuria debilis
Diamphipnoa helgae
Gripopteryx flinti
Gripopteryx garbei
Gripopteryx maculosa
Gripopteryx reticulata
Aubertoperla illiesi
Paragripopteryx blanda
Paragripopteryx sp.
Teutoperla rothi
Paragripopteryx klapaleki
Tupiperla modesta
Tupiperla jurirrim
Guaranyperla puri
Guaranyperla guapiara *
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla
A
B
Tupiperla guariru
Tupiperla sp. 8
Tupiperla robusta
Tupiperla sp. 7
C
Tupiperla eleonorae
D
Tupiperla misionera
Tupiperla sulina
Tupiperla bispoi
Tupiperla umbya
Tupiperla gracilis *
Tupiperla flinti
Tupiperla pessacqi
Tupiperla zwicki
Tupiperla froehlichi
Tupiperla ubuntu
Tupiperla amorimi
Tupiperla oliverai
Tupiperla sp. 3
Tupiperla sp. 4
Tupiperla sepeensis
G
Tupiperla sp. 5
Tupiperla sp. 1
Tupiperla reichardti
Tupiperla sp. 2
Tupiperla tessellata
Tupiperla pinhoi
Tupiperla serrulata
Tupiperla claudius
Tupiperla sp. 6
Tupiperla illiesi
Tupiperla tucum
Tupiperla
1 2 Characters
Exclusive character state
Non-exclusive character state
0>1 1>0 Characters states transformation
No. Relative Bremmer support
* Type species
X Clade or node name
k = 9

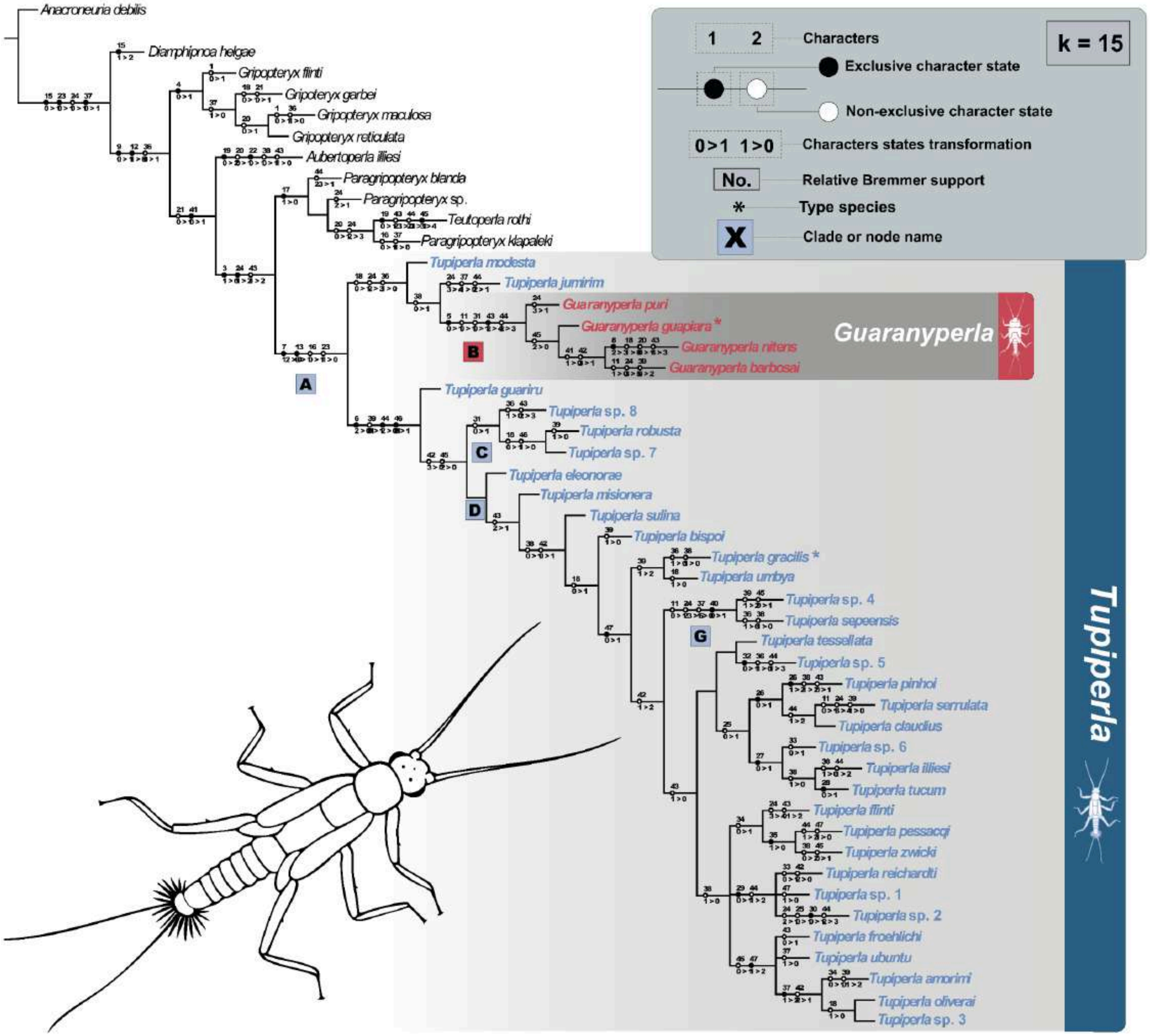
Supplementary Material S15. Phylogenetic hypothesis of *Tupiperla* (blue taxa) based on the strict consensus of three most parsimonious trees under k = 11 (fit = 35.46). Unambiguous character-state changes were optimized under maximum parsimony.


Characters
Exclusive character state
Non-exclusive character state
0>1 1>0
Characters states transformation
No.
Relative Bremmer support
* Type species
X
Clade or node name
k = 11
Anacroneuria debilis
Diamphipnoa helgae
Gripopteryx flinti
Gripopteryx garbei
Gripopteryx maculosa
Gripopteryx reticulata
Aubertoperla illiesi
Paragripopteryx blanda
Paragripopteryx sp.
Teutoperla rothi
Paragripopteryx klapaleki
Tupiperla modesta
Tupiperla jurumirim
Guaranyperla puri
Guaranyperla guapiara*
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla
A
B
Tupiperla guariru
Tupiperla sp. 8
Tupiperla robusta
Tupiperla sp. 7
Tupiperla eleonorae
D
Tupiperla misionera
Tupiperla sulina
Tupiperla bispoi
Tupiperla umbya
Tupiperla gracilis*
Tupiperla flinti
Tupiperla pessacqi
Tupiperla zwicki
Tupiperla froehlichi
Tupiperla ubuntu
Tupiperla amorimi
Tupiperla oliverai
Tupiperla sp. 3
Tupiperla sp. 4
Tupiperla sepeensis
G
Tupiperla tessellata
Tupiperla sp. 5
Tupiperla sp. 2
Tupiperla reichardti
Tupiperla sp. 1
Tupiperla pinhoi
Tupiperla serrulata
Tupiperla claudius
Tupiperla sp. 6
Tupiperla illiesi
Tupiperla tucum
Tupiperla

Supplementary Material S16. Phylogenetic hypothesis of *Tupiperla* (blue taxa) based on the strict consensus of five most parsimonious trees under k = 13 (fit = 36.05). Unambiguous character-state changes were optimized under maximum parsimony.


Anacroneuria debilis
Diamphipnoa helgae
Gripopteryx flinti
Gripopteryx garbei
Gripopteryx maculosa
Gripopteryx reticulata
Aubertoperla illiesi
Paragripopteryx blanda
Paragripopteryx sp.
Teutoperla rothi
Paragripopteryx klapaleki
Tupiperla modesta
Tupiperla jurririm
Guaranyperla puri
Guaranyperla guapiara*
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla
Tupiperla guariru
Tupiperla sp. 8
Tupiperla robusta
Tupiperla sp. 7
Tupiperla eleonorae
Tupiperla misionera
Tupiperla sulina
Tupiperla bispoi
Tupiperla gracilis *
Tupiperla umbya
Tupiperla sp. 4
Tupiperla sepeensis
Tupiperla tessellata
Tupiperla sp. 5
Tupiperla pinhoi
Tupiperla serrulata
Tupiperla claudius
Tupiperla sp. 6
Tupiperla illiesi
Tupiperla tucum
Tupiperla flinti
Tupiperla pessacqi
Tupiperla zwicki
Tupiperla reichardti
Tupiperla sp. 1
Tupiperla sp. 2
Tupiperla froehlichi
Tupiperla ubuntu
Tupiperla amorimi
Tupiperla oliverai
Tupiperla sp. 3
Tupiperla
A
B
C
D
G
1 2 Characters
k = 13
Exclusive character state
Non-exclusive character state
0>1 1>0 Characters states transformation
No. Relative Bremmer support
* Type species
X Clade or node name

Supplementary Material S17. Phylogenetic hypothesis of *Tupiperla* (blue taxa) based on the strict consensus of five most parsimonious trees under k = 15 (fit = 35.53). Unambiguous character-state changes were optimized under maximum parsimony.


Anacroneuria debilis
Diamphipnoa helgae
Gripopteryx flinti
Gripopteryx garbei
Gripopteryx maculosa
Gripopteryx reticulata
Aubertoperla illiesi
Paragripopteryx blanda
Paragripopteryx sp.
Teutoperla rothi
Paragripopteryx klapaleki
Tupiperla modesta
Tupiperla jumirim
Guaranyperla puri
Guaranyperla guapiara *
Guaranyperla nitens
Guaranyperla barbosai
Guaranyperla
B
A
Tupiperla guariru
Tupiperla sp. 8
Tupiperla robusta
Tupiperla sp. 7
C
Tupiperla eleonorae
Tupiperla misionera
D
Tupiperla sulina
Tupiperla bispoi
Tupiperla gracilis *
Tupiperla umbya
Tupiperla sp. 4
Tupiperla sepeensis
G
Tupiperla tessellata
Tupiperla sp. 5
Tupiperla pinhoi
Tupiperla serrulata
Tupiperla claudius
Tupiperla sp. 6
Tupiperla illiesi
Tupiperla tucum
Tupiperla flinti
Tupiperla pessacqi
Tupiperla zwicki
Tupiperla reichardti
Tupiperla sp. 1
Tupiperla sp. 2
Tupiperla froehlichi
Tupiperla ubuntu
Tupiperla amorimi
Tupiperla oliverai
Tupiperla sp. 3
Tupiperla
1 2 Characters
Exclusive character state
Non-exclusive character state
0>1 1>0 Characters states transformation
No. Relative Bremmer support
* Type species
X Clade or node name
k = 15