UNIVERSIDADE DE SÃO PAULO
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO
PROGRAMA DE PÓS-GRADUAÇÃO EM ENTOMOLOGIA

Systematics of Gripopterygidae Enderlein, 1909 (Insecta: Plecoptera): cladistic analyses
of Gripopteryginae with notes on Brazilian species and revision and phylogeny of

Paragripopteryx Enderlein, 1909

Sistemática de Gripopterygidae Enderlein, 1909 (Insecta: Plecoptera): análise cladística de
Gripopteryginae com notas sobre as espécies brasileiras e revisão e filogenia de *Paragripopteryx*

Enderlein, 1909

Tácio Vitor Duarte Simões

Tese apresentada à Faculdade de Filosofia,
Ciências e Letras de Ribeirão Preto da
Universidade de São Paulo, como parte das
exigências para obtenção do título de Doutor
em Ciências, obtido no Programa de Pós-
Graduação em Entomologia

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Orientador: Dr. Pitágoras da Conceição Bispo
Co-orientador: Dr. Adolfo Ricardo Calor

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Duarte, Tácio

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Aos Professores que me guiaram até aqui.

(...) caçamos dias melhores no breu

Nos que antecede o eu

Com os pés descalços, calçamos o chão (...)

Sant'Clair Araújo Alves de Souza

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Abstract

Gripopterygidae (Plecoptera) includes 54 genera and about 320 species, 100 of them recorded from South America. Although recent molecular analysis does not support all subfamilies, the family is traditionally divided into five subfamilies, being Gripopteryginae endemic to South America, comprising 15 genera and about 80 species. Among the genera of this subfamily, the Neotropical *Paragripopteryx* Enderlein currently comprises 14 species. The genus occurs along the coastal Brazilian mountains, from northeast of Bahia State to Rio Grande do Sul State, Brazil, while two species are restricted to Uruguay. According to traditional studies, the intergeneric relationships in Gripopterygidae and the delimitation of the current South American subfamilies (including Gripopteryginae) need to be reviewed. Considering *Paragripopteryx*, the genus has been defined based only on combination of morphological characters, without synapomorphies, therefore, the genus needs to be better delimited. As an attempt to understand the phylogenetic relationships in these two taxa (Gripopteryginae and *Paragripopteryx*), we performed two cladistic analyses based on morphological characters. As regards the Gripopteryginae, we used a dataset with 51 characters and 43 terminal taxa. In the case of *Paragripopteryx*, we used a dataset with 39 characters and 31 terminal taxa. We used Parsimony analysis with equal and implied weighting of characters (varying k-values: $k = 3-15$) and considered all characters as nonadditive. In the first approach, we recovered *Neopentura semifusca* outside the delimitation of Gripopteryginae and closer to Antarctoperlinae. Based on our results and considering the previous morphological analysis, we reclassified this genus in Antarctoperlinae. All other Gripopteryginae remained nested in a clade as sister of Australian Leptoperlinae, being this clade supported by a single synapomorphy: the sixth anal vein fused to wing margin in hind wings. Gripopteryginae taxa were supported by three synapomorphies: the CuA vein forked in forewings; distal margin of central sclerite in T10 protruding/coming out; and the absence of posterior sclerite in T10. Considering the analyses for *Paragripopteryx*, *P. munoai* was recovered outside the current delimitation of *Paragripopteryx*. For this reason, a new genus in Gripopteryginae is proposed to house this species. All other *Paragripopteryx* species remained nested in a clade supported by a single synapomorphy: the presence of pterostigmatic crossvein in forewings. In parallel to the phylogenetic study, we performed a revision of *Paragripopteryx* with the description of three new species and synonymy of *P. crassila* with *P. klapaleki*. Finally, we present an updated list of Brazilian Gripopterygidae with some notes, and the description of a new species of *Tupiperla*.

Key words: Aquatic insects, Morphological characters, Phylogenetic, Neotropical region, Stoneflies.

Resumo

Gripopterygidae (Plecoptera) compreende 54 gêneros e cerca de 320 espécies, das quais 100 são registradas na América do Sul. Embora análises moleculares recentes não suportem todas as subfamílias, Gripopterygidae tem sido tradicionalmente dividida em cinco subfamílias, sendo Gripopteryginae endêmica da América do Sul, compreendendo 15 gêneros e cerca de 80 espécies. Entre os Gripopteryginae, *Paragripopteryx* Enderlein compreende atualmente 14 espécies. O gênero ocorre ao longo das montanhas costeiras brasileiras, do nordeste da Bahia ao Rio Grande do Sul, sendo duas espécies restritas ao Uruguai. Estudos taxonômicos têm sugerido que as relações intergenéricas em Gripopterygidae e a delimitação das atuais subfamílias sul-americanas (incluindo Gripopteryginae) necessitam ser revistas. Quanto a *Paragripopteryx*, o gênero tem sido definido com base em combinação de caracteres morfológicos, sem sinapomorfias, portanto, o gênero precisa ser mais bem delimitado. Como tentativa de compreender as relações filogenéticas nestes dois táxons (Gripopteryginae e *Paragripopteryx*), realizamos duas análises cladísticas baseadas em caracteres morfológicos. Em relação a Gripopteryginae, uma matriz com 51 caracteres e 43 táxons terminais foi utilizada. No caso de *Paragripopteryx*, uma matriz com 39 caracteres e 31 táxons terminais foi utilizada. O critério de Parcimônia foi utilizado com pesagens iguais e implícitas dos caracteres (variando os valores de $k = 3-15$), sendo todos os caracteres considerados não-aditivos. Na primeira abordagem, *Neopentura semifusca* foi recuperada fora da delimitação de Gripopteryginae, sendo proximamente relacionada aos Antarctoperlinae. Com base em nossos resultados e considerando a análise morfológica prévia, *Neopentura* está sendo reclassificado em Antarctoperlinae. Todos os outros Gripopteryginae foram recuperados em um clado como grupo-irmão dos Leptoperlinae australianos. Esse grande clado foi suportado por uma sinapomorfia: sexta veia anal da asa posterior fusionada à margem da asa. Gripopteryginae foi suportado por três sinapomorfias: veia CuA bifurcada na asa anterior; margem distal do esclerito central no tergo 10 saliente/protuberante; e ausência de esclerito posterior no tergo 10. Em relação as análises de *Paragripopteryx*, *P. munoai* foi recuperada fora da delimitação atual do gênero. Assim, um novo gênero em Gripopteryginae é proposto para abrigar esta espécie. Todas os outros *Paragripopteryx* permaneceram em um clado suportado por uma sinapomorfia: presença de veias transversais na célula pterostigmática da asa anterior. Em paralelo ao estudo filogenético, foi realizada uma revisão de *Paragripopteryx* com a descrição de três novas espécies e a sinonímia de *P. crassila* com *P. klapaleki*. Por fim, apresentamos uma lista atualizada de Gripopterygidae do Brasil com notas sobre algumas espécies e a descrição de uma nova espécie de *Tupiperla*.

Palavras-chave: Insetos aquáticos, Caracteres morfológicos, Filogenética, Região Neotropical, Plecópteros.

General introduction

Plecoptera Burmeister, 1839

Plecoptera (Stoneflies) is an order of insects with aquatic nymphs and terrestrial winged adults. Exceptions to this pattern are rare (Stark *et al.*, 2009). The nymphs are mainly associated with clean, well-oxygenated and lower temperature streams (Froehlich, 1969; Pennak, 1978). In its environments, they can be found in boulder surfaces, among pebbles, tree trunks, moss and leaf packs (Froehlich & Oliveira, 1997; Diaz Villanueva & Albariño, 1999; Miserendino & Pizzolon, 2000; Wantzen & Wagner, 2006). Adults live on riparian vegetation or over rocks, closely associated with water bodies where the nymphs (immatures) live (Baumann, 1987; Theischinger, 1991; Froehlich, 2012). As in general the adults fly short distances (weak flying), the populations tend to be spatially structured (Schultheis *et al.*, 2002).

The life cycle duration and number of instars vary among the species of Plecoptera, and factors such as body size, temperature, food availability may affect the duration of the cycle. For example, according to Sephton & Hynes (1982), the number of instars for Australian groups are estimated between 10 to 14 instars. Considering Brazilian fauna, Froehlich (1969) estimated in laboratory 13 instars in about five months for *Paragripopteryx anga*, and Dorvillé & Froehlich (2001) estimated the maximum number of 34 instars for *Kempnyia tijucana*. Eggs deposition occurs most often during flight when the females plunge the terminal region of the abdomen into the water and disperse the eggs mass that attach to the substrate, remaining pooled until the hatching. Subsequently, the young nymphs pass through successive stages of growth and change until they become adults (Fig. 1). The newly emerged adults have a still soft and sclerotic body, a stage in which they can be easily predated (Duarte & Calor, 2017).

In general, the nymphs of Plecoptera are detritivores, shredders, scrapers or carnivorous (Hynes, 1976; Fuller & Stewart, 1977). In some cases, the feeding can change during stages of development, for example, several carnivorous species have their firsts instars detritivores (Stark *et al.*, 2009). As the nymphs live in fresh and cold water, where the dissolved oxygen concentration is high, most stoneflies species have high sensitivity to environmental changes. Thus, this group, together with Ephemeroptera and Trichoptera (E.P.T.), has been relevant in environmental impact assessment studies of the

water quality, mainly in North American and European countries (Rosenberg & Resh, 1993).

Figure 1. Hemimetabolous development scheme (life cycle) in Plecoptera (stonefly). The adult females plunge the terminal region of the abdomen into the water and disperse the mass of eggs that attach to the substrate. After the eggs hatching, the very young nymphs pass through successive stages of growth and change until they become adults. (Adapted from Duarte & Calor, 2017)

Several morphological characters are useful for identification of nymphs. The nymphs breathe through tracheobranchia present in the thoracic or abdominal segments, but also through the thin intersegmental membrane (Hynes, 1976; Pennak, 1978; Giller & Malmqvist, 1998; Zwick, 2000). The number and arrangement of gills have taxonomic relevance, since they allow identification at the family and genus levels (Stark *et al.*, 2009). In addition, other structures are also used in the taxonomy, such as the number of ocelli on the head; the shape of post-frontal line on the head; the types of bristles and their arrangements on the body; the presence, number and size of spines or processes on the thoracic and abdominal terga; the presence of spines in the femur; and the presence and number of tibial spurs (Olifiers, 2005).

In general, the adult stoneflies have two pairs of membranous wings; the forewings are elongated and narrow, while the hind wings are broader and have a well-developed anal lobe that fold when the insect is at rest (Fig. 2, Fig. 4A). From this character derives the name of the order, from the Greek, *pleco* and *ptera*, meaning folding/interlace and wing, respectively (Froehlich, 2012). Nevertheless, some genera of Plecoptera are brachypterous (*e.g.* *Notoperla* Enderlein, in part), micropterous or apterous (*e.g.* *Andiperla* Aubert, *Falklandoperla* McLellan, *Megandiperla* Illies, *Notoperla*, in part,

Rakiuraperla McLellan, 1977). The last three types usually have semi-terrestrial or terrestrial nymphs (Aubert, 1956; Illies, 1960, 1963; McLellan, 1967, 1977, 1983, 2001; Wisely, 1953) inhabiting alpine areas or zones of lower altitudes at higher latitudes, particularly where they are exposed to low temperatures and strong winds (Hynes, 1976; McLellan, 2001).

Figure 2. General diagram of Plecoptera (*Nemoura*). (A) an adult (reproductive stage) with folded wings at rest, (B) a nymph (immature) with wingpads (modified from Fochetti & Tierno de Figueroa, 2008).

The adults of some families, mainly Systellognatha (Pteronarcyidae, Peltoperlidae, Perlidae, Chloroperlidae and Perlodidae) have reduced mouthparts and do not feed in this stage. However, the water intake is common at this stage (Froehlich, 1969). Adults from other families feed on leaves, but the most common food is mosses over rocks or over tree barks and debris (Froehlich, 1969; Hynes, 1976).

The adults usually do not have showy colors, ranging from black to yellow-ocher. Few families, such as Chloroperlidae and representatives of Eustheniidae, have species with green, red, purple or black colors (Olifiers, 2005). The head and mouthparts are prognathous. The antennae are filiform and inserted laterally. Most species have two or

three ocelli (Lecci & Froehlich, 2006). In the thorax, the pronotum is subretangular or ellipsoid in shape, often with a rough surface (Stark *et al.*, 2009). The abdomen has 11 segments, with female subgenital plate in sternum VIII and male subgenital plate in sternum IX. Both the segments X and XI are characterized by the terminalia, being the segment XI modified in a pair of lateral paraprocts, a dorsal epiproct and a multisegmented cercus (except for Notonemouridae, unisegmented) (Stark *et al.*, 2009; Froehlich, 2012).

The terminalia, mainly of the males, have great taxonomic importance for adult identification. The morphological variations in male terminalia, like shape of penial armature, paraprocts, subgenital plate and tergum 10 are useful for identification of species. Additionally, characters such as wing venation and body size are also relevant in taxonomy.

Diversity and Classification of Plecoptera

Currently, the cosmopolitan order Plecoptera comprises about 3,500 species in 16 families (DeWalt *et al.*, 2019), being absent only in the Antarctic continent (Hynes, 1976; Zwick, 2000). The order is divided into two disjunct suborders, Arctoperlaria and Antarctoperlaria (Table 1). Arctoperlaria is classified in two infraorders, Euhognatha and Systellognatha, these composed by families of Laurasian origin, while the Antarctoperlaria is classified in two superfamilies, Eusthenioidea and Gripopterygoidea, represented by families of Gondwanan origin (Froehlich, 2012).

According to McCulloch *et al.* (2016), Arctoperlaria and Antarctoperlaria diverged 121 Ma. ago, succeeding the breaking of the supercontinent Pangea in Gondwana and Laurasia during the Jurassic. This hypothesis is in accordance with the suggested by Illies (1965) and Zwick (1990, 2000) of divergence of suborders by vicariance (McCulloch *et al.*, 2016). Additionally, the low dispersion capacity of stoneflies in relation to other insects (Brundin, 1967; Marden & Kramer, 1994; Thomas *et al.*, 2000; Zwick, 2000; Schultheis *et al.*, 2002; McCulloch *et al.*, 2009) may explain the role of vicariance suggested for these taxa.

The break of Gondwana probably was an important event for current distribution of Antarctoperlaria among the South America, Australia and New Zealand (Illies, 1965; Banareescu, 1990; Zwick, 2000, 2003; Fochetti & Tierno de Figueroa, 2008). Among the Antarctoperlarian families, Austroperlidae, Eustheniidae and Gripopterygidae have

representatives in these three land masses, while Diamphipnoidae is restricted to South America (Stark *et al.*, 2009). Gripopterygidae has a circum-Antarctic distribution with 14 genera occurring in Australia (plus *Nydyse, incertae sedis*), 12 in New Zealand and 28 in South America (Tables 3–4). The family is considered very diversified in number of genera in the south of South America (McLellan & Zwick, 2007). Currently, the number of described species of Gripopterygidae is about 320, with about 100 species recorded from South America (Froehlich, 2010; DeWalt *et al.*, 2019) (Table 3).

In South America two components of Gripopterygidae have been distinguished: The Neotropical taxa, represented by five genera of the subfamily Gripopteryginae, and the Andean taxa, represented by 23 genera belonging to all subfamilies (Pessacq *et al.*, 2019).

Table 1. Classification of Plecoptera and its distribution by Zoogeographical regions (modified from Stark *et al.*, 2009). (Abbreviations: Australia (A), Andean (An), Ethiopia (E), Holarctic (H), Palearctic East (EP), Madagascar (Ma), Nearctic (Na), Neotropical (Nt), New Zealand (NZ), Oriental (Or)).

Suborder	Infraorder/superfamily	Family	Distribution
Arctoperlaria	Euholognatha	Capniidae Banks, 1900	H, Or
		Leuctridae Klapálek, 1905	H, Or
		Nemouridae Billberg, 1820	H, Or
		Notonemouridae Ricker, 1950	A, An, E, Ma, Nt, NZ
		Taeniopterygidae Klapálek, 1905	H, Or
		Scopuridae Uéno, 1935	EP
	Systellognatha	Chloroperlidae Okamoto, 1912	H, Or
		Peltoperlidae Claassen, 1931	EP, Na, Or
		Perlidae Latreille, 1802	An, E, H, Nt
		Perlodidae Klapálek, 1909	H, Or
		Pteronarcyidae Newman, 1853	EP, Na
		Styloperlidae Wu, 1935	EP, Or
Antarctoperlaria	Eusthenioidea	Diamphipnoidae Ricker, 1950	An
		Eustheniidae Banks, 1913	A, An, Nt, NZ
	Gripopterygoidea	Austroperlidae Tillyard, 1921	A, An, Nt, NZ
		Gripopterygidae Enderlein, 1909	A, An, Nt, NZ

Gripopterygidae Enderlein, 1909

Gripopterygidae was erected by Enderlein (1909) which proposed its subdivision into two subfamilies, Gripopteryginae and Antarctoperlinae (Fig. 3; Table 2). In Gripopteryginae were grouped the genera *Eusthenia*, *Gripopteryx*, *Paragripopteryx* and

Stenoperla, while in Antarctoperlinae the genera *Antarctoperla*, *Notoperla* and *Paranotoperla* (Fig. 3; Table 2).

<p>392</p> <p>Gripopterygidae n.</p> <p>1. Radialramus im Vorder- und Hinterflügel lang bis kurz gegabelt. 1. Cubitalast im Vorderflügel lang, im Hinterflügel meist kurz gegabelt Gripopteryginae m. 2.</p> <p>Radialramus im Vorder- und Hinterflügel ungegabelt. 1. Cubitalast im Vorderflügel ungegabelt (höchstens Queradern hinter ihm), im Hinterflügel kurz gegabelt oder ungegabelt. Vor dem Medianstamm des Vorderflügels keine Queradern. Cubitalzelle (Cu_1) im Hinterflügel mit einer oder mehr Queradern Antarctoperlinae m. 5.</p> <p>2. Radialgabel sehr kurz. Gabel des 1. Cubitalastes im Vorderflügel sehr lang und schlank, im Hinterflügel ziemlich kurz. Queradern mäßig zahlreich. Pterostigma ohne Queradern oder mit 1 Querader. Von dem Medialstamm des Vorderflügels geht nach vorn keine oder nur eine Querader aus. Von der basalen Analzelle des Vorderflügels geht ein sichtsogleich gabelnder Ast ab, vor dessen vorderem Gabelast eine Querader. Cubitalzelle (Cu_1) im Hinterflügel nur mit einer Querader an der Basis und einer (selten zwei) Queradern an der Spitze. 3.</p> <p>Radialgabel sehr lang. Queradern im Vorder- und Hinterflügel sehr zahlreich. Pterostigma anscheinend mit Querader (oder Queradern). Von dem Medialstamm des Vorderflügels gehen nach vorn eine Reihe von Queradern aus. Cubitalzelle (Cu_1) im Hinterflügel mit einer Reihe Queradern 4.</p> <p>3. Pterostigma des Vorderflügels mit einer Querader. Vor dem Medialstamm des Vorderflügels eine Querader.</p> <p>Paragripopteryx nov. gen. [Typus: <i>P. ilopaki</i> nov. spec., Brasilien.]</p> <p>Pterostigma ohne Querader. Vor dem Medialstamm des Vorderflügels keine Querader. Gripopteryx Pict. 1841. [Typus: <i>G. cancellata</i> Pict. 1841 Brasilien.]</p> <p>4. Cerci lang Eusthenia Gray 1832. [Typus: <i>E. spectabilis</i> Gray 1832 Australien.]</p> <p>Cerci kurz. Stenoperla McLachl. 1866. [Typus: <i>St. prasina</i> (Newm. 1845) Neuseeland.]</p> <p>5. Cerci lang, vielgliedrig (bei den typischen Arten etwa 30–32 gliedrig). 6.</p> <p>Cerci sehr kurz, den Hinterleib wenig überragend; mit wenigen Gliedern (bei den beiden bekannten Arten 7–</p>	<p>I. Wissenschaftliche Mitteilungen.</p> <p>1. Klassifikation der Plekopteren, sowie Diagnosen neuer Gattungen und Arten.</p> <p>Von Dr. Günther Enderlein, Stettin.</p> <p>eingeg. 26. Februar 1909.</p> <p>Subordo: Holognatha { Fam. Gripopterygidae. Fam. Capniidae. Fam. Nemuridae.</p> <p>Subordo: Systellognatha { Fam. Pteronarcidae. Fam. Perlidae.</p> <p>393</p> <p>bzw. 8-gliedrig). Cubitus 1 im Hinterflügel mit kurzer Gabel. Von der basalen Analzelle geht im Vorderflügel hinten eine gegabelte Axillaris aus, dessen vorderer Ast keine Querader nach der Analis entsendet.</p> <p>Antarctoperla Enderl. 1905. [Typus: <i>A. anderssoni</i> Enderl. 1905 Feuerland.]</p> <p>6. Von der basalen Analzelle im Vorderflügel geht hinten eine gegabelte Axillaris aus, deren vorderer Ast keine Querader nach der Analis entsendet. Cubitus 1 im Hinterflügel mit kurzer Gabel. Notoperla nov. gen. [Typus: <i>N. fuegiana</i> Enderl. 1905 Feuerland.]</p> <p>Von der basalen Analzelle im Vorderflügel geht hinten eine gegabelte Axillaris aus, deren vorderer Ast eine Querader nach der Analis entsendet. Cubitus 1 im Hinterflügel ungegabelt. Paranotoperla nov. gen. [Typus: <i>M. australica</i> nov. spec. S. W. Australien.]</p>
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Figure 3. Pages 392–393 in Enderlein (1909) with the erection of the family Gripopterygidae and its subdivision in two subfamilies, Gripopteryginae and Antarctoperlinae.

Illies (1963) reviewed the Gripopterygidae and proposed a new division into five subfamilies: Andiperlinae, Antarctoperlinae, Gripopteryginae, Leptoperlinae and Paragripopteryginae (Table 2). This system was poorly inclusive due to anchoring of the taxa based on plesiomorphic characters (Zwick, 2000). Subsequently, McLellan (1977) reviewed Gripopterygidae and proposed the current classification, also with five subfamilies but with some changes (Table 3).

Table 2. First classifications of Gripopterygidae according to Enderlein (1909) and Illies (1963).

	Subfamilies	Genera	Distribution
Classification of Enderlein (1909)	Antarctoperlinae Enderlein, 1909	<i>Antarctoperla</i> Enderlein, 1905	South America
		<i>Notoperla</i> Enderlein, 1909	
		<i>Paranotoperla</i> Enderlein, 1909	Australia
	Gripopteryginae Enderlein, 1909	<i>Gripopteryx</i> Pictet, 1841	South America
		<i>Paragripopteryx</i> Enderlein, 1909	
		<i>Eusthenia</i> Westwood, 1832	Australia
Classification of Illies (1963)	Andiperlinae Illies, 1963	<i>Andiperla</i> Aubert, 1956	South America
		<i>Andiperlodes</i> Illies, 1963	
		<i>Megandiperla</i> Illies, 1960	
	Antarctoperlinae Enderlein, 1909	<i>Antarctoperla</i> Enderlein, 1905	South America
		<i>Araucanioperla</i> Illies, 1963	
		<i>Ceratoperla</i> Illies, 1963	
		<i>Chilenoperla</i> Illies, 1963	
		<i>Pelurgoperla</i> Illies, 1963	
		<i>Plegoperla</i> Illies, 1963	
	Gripopteryginae Enderlein, 1909	<i>Zelandobius</i> Tillyard, 1921	New Zealand
		<i>Gripopteryx</i> Pictet, 1841	South America
		<i>Notoperlopsis</i> Illies, 1963	
		<i>Trinotoperla</i> Tillyard, 1924	Australia
	Leptoperlinae Banks, 1913	<i>Megaleptoperla</i> Tillyard, 1923	New Zealand
		<i>Notoperla</i> Enderlein, 1909	South America
		<i>Senzilloides</i> Illies, 1963	
		<i>Leptoperla</i> Newman, 1839	Australia
		<i>Apteryoperla</i> Wisely, 1953	New Zealand
		<i>Aucklandobius</i> Enderlein, 1909	
		<i>Nesoperla</i> Tillyard, 1923	
	Paragripopteryginae Illies, 1963	<i>Zelandoperla</i> Tillyard, 1923	South America
		<i>Aubertoperla</i> Illies, 1963	
		<i>Claudioperla</i> Illies, 1963	
		<i>Jewettoperla</i> Illies, 1963	
		<i>Limnoperla</i> Illies, 1963	
		<i>Paragripopteryx</i> Enderlein, 1909	
		<i>Potamoperla</i> Illies, 1963	
		<i>Rhithroperla</i> Illies, 1963	
		<i>Teutoperla</i> Illies, 1963	
		<i>Dinotoperla</i> Tillyard, 1921	Australia

In McLellan's (1977) classification, the three genera belonging to Andiperlinae were allocated to Antarctoperlinae (*Megandiperla*) and Gripopteryginae (*Andiperla* and *Andiperlodes*), and the subfamily Paragripopteryginae (South American genera) was considered junior synonym of Gripopteryginae (Table 3). In addition, Dinotoperlinae and Zelandoperlinae subfamilies were created. The first, initially comprising the genera that occur in Australia and which were classified within Paragripopteryginae and Gripopteryginae. While the second, including genera that occur in New Zealand and

which were previously grouped in Griptopteryginae and Leptoperlinae, plus the South American *Notoperlopsis* (Table 3).

Table 3. Classification of Griptopterygidae according to McLellan (1977). (N° spp.: current number of species; Number between bars corresponding to the number of genera/number of species in each subfamily by region).

Subfamilies	Genera	N° spp.	Distribution
Antarctoperlinae Enderlein, 1909	<i>Antarctoperla</i> Enderlein, 1905	2	South America (9/17)
	<i>Araucanioperla</i> Illies, 1963	2	
	<i>Ceratoperla</i> Illies, 1963	2	
	<i>Chilenoperla</i> Illies, 1963	5	
	<i>Ericiataperla</i> Vera, 2016	1	
	<i>Megandiperla</i> Illies, 1960	1	
	<i>Pehuenioperla</i> Vera, 2009	1	
	<i>Pelurgoperla</i> Illies, 1963	1	
	<i>Plegoperla</i> Illies, 1963	2	
	<i>Vesicaperla</i> McLellan, 1967	7	
	<i>Zelandobius</i> Tillyard, 1921	30	New Zealand (2/37)
Dinotoperlinae McLellan, 1977	<i>Alfonsoperla</i> McLellan & Zwick, 2007	1	South America (1/1)
	<i>Dinotoperla</i> Tillyard, 1921	35	Australia (9/71)
	<i>Dundundra</i> Theischinger, 1982	1	
	<i>Eunotoperla</i> Tillyard, 1924	1	
	<i>Illiesoperla</i> McLellan, 1971	11	
	<i>Neboissoperla</i> McLellan, 1971	3	
	<i>Nescioperla</i> Theischinger, 1982	1	
	<i>Odontoperla</i> Mynott, Suter & Theischinger, 2017	2	
	<i>Oedemaperla</i> Mynott, Suter & Theischinger, 2017	2	
Griptopteryginae Enderlein, 1909	<i>Trinotoperla</i> Tillyard, 1924	15	South America (15/76)
	Table 4	76	
Leptoperlinae Banks, 1913	<i>Notoperla</i> Enderlein, 1909	7	South America (2/8)
	<i>Senzilloides</i> Illies, 1963	1	
	<i>Cardioperla</i> McLellan, 1971	8	Australia (5/69)
	<i>Kirrama</i> Theischinger, 1981	2	
	<i>Leptoperla</i> Newman, 1839	28	
	<i>Newmanoperla</i> McLellan, 1971	5	
	<i>Riekoperla</i> McLellan, 1971	26	
Zelandoperlinae McLellan, 1977	<i>Notoperlopsis</i> Illies, 1963	1	South America (1/1)
	<i>Acroperla</i> McLellan, 1977	5	
	<i>Apteryoperla</i> Wisely, 1953	6	New Zealand (10/37)
	<i>Aucklandobius</i> Enderlein, 1909	5	
	<i>Holcoperla</i> McLellan, 1977	3	
	<i>Nesoperla</i> Tillyard, 1923	3	
	<i>Rakiuraperla</i> McLellan, 1977	1	
	<i>Taraperla</i> McLellan, 1998	4	
	<i>Megaleptoperla</i> Tillyard, 1923	2	
	<i>Rungaperla</i> McLellan, 1977	2	
	<i>Zelandoperla</i> Tillyard, 1923	6	

Despite this classification, according to McLellan & Zwick (2007), intergeneric relationships in Gripopterygidae are still confusing, need the current subfamily concept and the delimitation of the current genera to be reviewed.

Most genera of Gripopterygidae have winged species, however, some genera occurring in the Alpine and Subantarctic regions are wingless. According to McLellan (1971), Gripopterygidae is characterized by the following characters: forewings with irregular number of crossveins from the distal half; M vein always forked; RA and CuA veins may be forked or not; anal region of the forewing with three longitudinal veins, thick vein between AA1 and AA2; wings with a row of hooked bristles in the hind margin between CuA and CuP. The hind wings resemble the forewings, but has the vein M3+4, close to its separation from M1+2, partially or completely fused to the CuA vein; anal lobe broad, with six longitudinal veins, usually without bifurcations or crossveins; sixth anal vein may be fused to the hind margin of wing (Fig. 4A). Male T10 modified, with anterior sclerites that may be dorsally fused or not; the posterior region of the tergite may be divided from the rest to form a separate sclerite (Fig. 4B). Paraprocts always present and usually sickle-shaped (Fig. 4C). Epiproct present in most genera and hook-shaped upwards (Fig. 4C). Female subgenital plate ovoid, usually short but may be long in some genera. Nymphs usually have a rosette of anal gills (Fig. 4D) (except for *Notoperla*) and a shortening of segment IV of the maxillary palp (McLellan, 1971). Excluding Antarctoperlinae, each abdominal dorsal nerve runs part way across the longitudinal muscle and then through it (Zwick, 1973).

Figure 4. Morphological characters of Gripopterygidae. (A) Forewing (above) and hind wing (below) of *Tupiperla* sp. highlighting the configuration of the longitudinal and crossveins, dashed line highlights the anal lobe of the hind wing. (B) Male terminalia; left, T10 with separation of the anterior, central and lateral sclerites in *Chilenoperla elongata*; right, T10 with fused sclerites in *Tupiperla modesta*. (C) Male terminalia; the paraprocts and the epiproct of *Gripopteryx elisae*. (D) Abdomen highlighting the anal gills of the nymph of *Paragripopteryx delicata*.

Gripopteryginae Enderlein, 1909

Gripopteryginae species occur only in South America (Froehlich, 2010; Table 4), from the high mountains of Colombia and Ecuador, passing through the Andes, Northeast and Central-West regions of Brazil to southern Argentina and Chile (Stark *et al.*, 2009). Currently, the subfamily comprises 15 genera and 76 species, most of them are endemic to the Andean region (Argentina and Chile), but other occur in subtropical and tropical areas such as Bolivia, Brazil, Colombia, Ecuador and Peru. In Brazil, 53 species belonging to four genera are recorded (Table 4).

According to McLellan (1977), Gripopteryginae is characterized by: 1) legs with a pair of distoventral spurs on each tibia; 2) forewings with a long CuA fork (Fig. 4A); 3) hind wings with the sixth anal vein fused to wing margin (Fig. 4A); 4) male genitalia with

epiproct tip not recurved (some genera with epiproct absent or very small); 5) tergite 10 (T10) sclerotized, and 6) posterior sclerite absent (Fig. 4B, right).

Table 4. South American Gripopteryginae (Froehlich, 2010; DeWalt *et al.*, 2019). (Abbreviations: N° spp.: number of species/genus. ARG, Argentina (CH: Chubut; IM: Malvinas Island; NQ: Neuquén; RN: Río Negro; SC: Santa Cruz; TF: Tierra del Fuego); BOL, Bolivia (LAP: La Paz); BRA, Brazil (BA: Bahia; ES: Espírito Santo; GO: Goiás; MG: Minas Gerais; PE: Pernambuco; RJ: Rio de Janeiro; RS: Rio Grande do Sul; SP: São Paulo; SC: Santa Catarina); COL, Colombia (NAR: Nariño); CHL, Chile (I: Tarapacá; II: Antofagasta; III: Atacama; VII: Maule; VIII: Biobío; IX: Araucanía; X: Los Lagos; XI: Aysén; XII: Magallanes; XIV: Los Ríos); ECU, Ecuador (AZU: Azuay); PRY, Paraguay (ITA: Itapúa; PRI: Paraguari); PER, Peru (CSC: Cusco; LIM: Lima; PUN: Puno); URY, Uruguay (FLO: Florida; LAV: Lavalleja; MAL: Maldonado)).

Genera	N° spp.	Records
<i>Andiperla</i> Aubert, 1956	1	ARG (SC); CHL (VI, XI, XII)
<i>Andiperlodes</i> Illies, 1963	2	ARG (SC), CHL (XII)
<i>Aubertoperla</i> Illies, 1963	2	ARG (CH, RN); CHL (VII, VIII, IX, X, XI, XII, XIV)
<i>Claudioperla</i> Illies, 1963	4	BOL (LAP); COL (NAR); CHL (I, II, III, XIV); ECU (AZU); PER (LIM, PUN)
<i>Falklandoperla</i> McLellan, 2001	1	ARG (IM)
<i>Gripopteryx</i> Pictet, 1841*	18	BRA (BA, ES, MG, RJ, RS, SC, SP); PRY (ITA); URY (FLO)
<i>Guaranyperla</i> Froehlich, 2001	3	BRA (ES, MG, RJ, SP)
<i>Limnoperla</i> Illies, 1963	1	ARG (CH, RN); CHL (IX, X, XI, XII, XIV)
<i>Neopentura</i> Illies, 1963	1	ARG (NQ, RN); CHL (IX, X, XI, XIV)
<i>Paragripopteryx</i> Enderlein, 1909	14	BRA (BA, ES, RJ, SP, SC); URY (LAV, MAL)
<i>Potamoperla</i> Illies, 1963	1	ARG (CH, NQ, RN); CHL (X, XI, XII, XIV) PER (CSC)
<i>Rhithroperla</i> Illies, 1963	2	ARG (CH, NQ, RN); CHL (X, XII, XIV)
<i>Teutoperla</i> Illies, 1963	4	ARG (RN); CHL (X, XIV)
<i>Tupiperla</i> Froehlich, 1969	20	ARG (MIS); BRA (BA, GO, MG, PE, RJ, SC, SP); PRY (PRI)
<i>Uncicauda</i> McLellan & Zwick, 2007	2	ARG (CH); CHI (IX, XI)
Total	76	

*Type genus.

***Paragripopteryx* Enderlein, 1909**

The genus *Paragripopteryx* was erected by Enderlein, 1909 (Fig. 5A) based on male specimen housed in “Helsinki Zoological Museum”, classified by Klapálek (1904), at the time, as *Gripopteryx cancellata* Pictet. After reviewing this specimen, Enderlein named it *Paragripopteryx klapaleki*, type species of *Paragripopteryx* (Froehlich, 1969).

Subsequently, Jewett (1960) discussed the status of *P. klapaleki* and transferred it to the genus *Gripopteryx* (= *G. klapaleki*). This species was synonymized with *G. gracilis* (= *Sembris gracilis* Burmeister, 1839). Illies (1963) reestablished *Paragripopteryx* and transferred *G. gracilis* (= *P. gracilis*) as type species of the genus (Figs. 5B–C). Then, Froehlich (1969) reviewed the Brazilian Gripopterygidae species, revalidated *P. klapaleki* and erected the genus *Tupiperla* for *P. gracilis* (= *T. gracilis*). At the same study, Froehlich described *P. anga* and *P. blanda* based on males, females and nymphs specimens, and transferred *Jewettoperla crassila* (Jewett, 1960) and *J. garbei* (Navás, 1960) to *Paragripopteryx* (*J. garbei* later was transferred to *Gripopteryx* by Froehlich (1990)). Posteriorly, Zwick (1973) combined *Jewettoperla munoai* in *Paragripopteryx* (= *P. munoai* (Benedetto, 1969)) and Benedetto (1983) described *P. baratinii*.

Figure 5. Cuttings from the works of Enderlein (1909) and Illies (1963). (A) Page 416 in Enderlein (1909) with the establishment of the genus *Paragripopteryx* based on specimen from “Helsinki Zoological Museum”; (B) page 178 and (C) page 179 in Illies (1963) with the reestablishment of *Paragripopteryx* and definition of *Gripopteryx gracilis* as the type species of the genus (*G. klapaleki* as synonym of *P. gracilis* = *Sembris gracilis* Burmeister, 1839).

Froehlich (1994) reviewed *Paragripopteryx* and described additional six species: *P. delicata*, *P. egena*, *P. guardae*, *P. hamata*, *P. merui* and *P. eleonora* (some of them subsequently transferred to *Tupiperla* by Froehlich, 1998). Finally, Bispo & Lecci (2011), described three additional species based on males: *P. intervalensis*, *P. kapilei* and *P. paranapiacabae*.

Figure 6. Map of *Paragripopteryx* records. BA (Chapada Diamantina; Wenceslau Guimarães; Camacan), ES (Espera Feliz; Santa Teresa), LAV (Aguas Blancas), MAL (Cerro de las Animas), RJ (Petrópolis), SC (Nova Teutônia), SP (Santo André; Salesópolis; Campos do Jordão; Iporanga; Ribeirão Bocaina; Ribeirão Grande; Umuarama).

Currently, *Paragripopteryx* comprises the species listed in Table 5. The genus has been recorded on the Atlantic Neotropical edge, from Uruguay, along the coastal mountains of south and southeastern Brazil to Bahia State (Benedetto, 1969, 1983; Bispo & Lecci, 2011), where two species were recorded (Fig. 6). *Paragripopteryx* can be recognized by the following combination of characters: nymphs with compact body;

absence of spines in both thoracic and abdominal terga; pronotum narrower than head (Bispo & Lecci, 2011); short legs without ventral femoral spine. Tergum 10 (T10) of male adults with an extension of medium length, ending in two denticles/teeth. Epiproct simple and small, inserted ventrally to the T10 extension (absent in *P. egena*). Forewings with 1–2 pterostigmatic crossvein (Stark *et al.*, 2009).

Table 5. *Paragripopteryx* species and its records and described stages. Scientific collections: CAS, California Academy of Sciences, United States; MZSP, Museu de Zoologia, Universidade de São Paulo, Brazil; UdelaR, Universidad de la República, Montevideo, Uruguay. BRA, Brazil (BA, Bahia; ES, Espírito Santo; RJ, Rio de Janeiro; SC, Santa Catarina; SP, São Paulo); URY, Uruguay (LAV, Lavalleja; MAL, Maldonado). N, nymphs; ♂, male; ♀, female.

	<i>Paragripopteryx</i> Enderlein, 1909	♂	♀	N	Scientific collections	Records
1	<i>P. anga</i> Froehlich, 1969	•	•	•	MZSP	BRA (SP)
2	<i>P. baratinii</i> Benedetto, 1983**	•	•	-	UdelaR	URY (LAV)
3	<i>P. blanda</i> Froehlich, 1969	•	•	•	MZSP	BRA (SP)
4	<i>P. crassila</i> (Jewett, 1960)***	•	•	-	CAS	BRA (SC)
5	<i>P. delicata</i> Froehlich, 1994	•	•	•	MZSP	BRA (SP)
6	<i>P. egena</i> Froehlich, 1994	•	•	•	MZSP	BRA (ES, SP)
7	<i>P. guardae</i> Froehlich, 1994	•	•	•	MZSP	BRA (SP)
8	<i>P. hamata</i> Froehlich, 1994	•	•	-	MZSP	BRA (SP)
9	<i>P. intervalensis</i> Bispo & Lecci, 2011	•	•	-	MZSP	BRA (ES, MG, SP)
10	<i>P. kapilei</i> Bispo & Lecci, 2011	•	-	-	MZSP	BRA (SP)
11	<i>P. klapaleki</i> Enderlein, 1909*	•	•	•	MZSP	BRA (ES, RJ, SP)
12	<i>P. merui</i> Froehlich, 1994	•	-	•	MZSP	BRA (SP)
13	<i>P. munoai</i> (Benedetto, 1969)	•	•	•	UdelaR	URY (MAL)
14	<i>P. paranapiacabae</i> Bispo & Lecci, 2011	•	-	-	MZSP	BRA (SP)

*Type species of *Paragripopteryx*; **Type series lost; ***Material analyzed by photos.

General objectives

The purpose of the present thesis is: 1) to test the monophyly of Gripopteryginae (Gripopterygidae); 2) to review, to test the monophyly and to infer the relationships among the species of *Paragripopteryx* (Gripopterygidae); 3) to provide an updated taxonomic account for the species of Gripopterygidae from Brazil. The thesis is structured in three chapters and its goals are specified below.

Chapter I:

The purpose of the first chapter was to provide the phylogenetic inference to the relationships in Gripopteryginae (Gripopterygidae) based on morphological characters in order to test: 1) the monophyly of Gripopteryginae; and 2) the characters proposed by McLellan (1977) under a phylogenetic perspective.

Chapter II:

The purpose of the second chapter was: 1) to provide a phylogenetic inference to the relationships in *Paragripopteryx* (Gripopterygidae) based on morphological characters; 2) to provide a taxonomical revision of *Paragripopteryx*; to describe three new species of *Paragripopteryx* based on males and females; 3) to describe the nymphs of the two species of *Paragripopteryx*; and 4) to provide an identification key for species of *Paragripopteryx*.

Chapter III:

The propose of the third chapter was: 1) to provide notes on the Brazilian Gripopterygidae; and 2) to describe a new species of *Tupiperla* based on males and females.

Chapter I: What morphological data tell us about the Neotropical Gripopteryginae (Plecoptera: Gripopterygidae)?

Full title:

What morphological data tell us about the South American Gripopteryginae (Plecoptera: Gripopterygidae)?

Running title:

South American Gripopteryginae (Plecoptera: Gripopterygidae)

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Abstract

Gripopterygidae (Plecoptera) includes 54 genera and about 320 species, 100 of them recorded from South America. Although recent molecular analysis does not support all subfamilies, the family is traditionally divided into five subfamilies, Gripopteryginae being endemic to South America. Members of this subfamily are characterized by legs with a pair of distoventral spurs on each tibia, forewings with a long CuA fork, hind wings with sixth anal vein fused to wing margin, epiproct absent or very small or with tip not recurved, tergite 10 sclerotized, and posterior sclerite absent in T10. A cladistic analysis of the subfamily based on 51 morphological characters for 40 terminal taxa of Gripopterygidae (32 genera) was performed, including 20 Gripopteryginae, seven Antarctoperlinae, eight Leptoperlinae, three Dinotoperlinae and two Zelandoperlinae taxa. We used a Parsimony analysis with equal and implied weighting of characters (varying k-values: k = 3–15) and considered all characters as nonadditive. For analysis, we used the “Traditional search” command with Tree Bisection Reconnection (TBR), 300 repls., 500 trees to save per replication. We recovered *Neopentura semifusca*, considered as a Gripopteryginae, outside the delimitation of the subfamily in all analyses, whether using EW or IW of characters. When we used EW, we recovered *N. semifusca* as sister of *Ceratoperla fazi* (Antarctoperlinae), and all other Gripopteryginae remained nested in

a poorly resolved consensus topology. On the other hand, when we vary the k-value in analyses using IW, we succeeded in finding well-resolved consensus topologies. *Neopentura semifusca* is recovered either as sister of *Pehuenioperla llaima* (Antarctoperlinae) ($k = 3$) or as sister of *Taraperla howesi* (Zelandoperlinae), *Antarctoperla michaelsoni* (Antarctoperlinae) at the base of this group ($k = 5-15$). All other taxa of the subfamily remained nested, as follows ($k = 3$): ((*Aubertoperla illiesi* ((*Gripopteryx cancellata*, *Gripopteryx liana*) (*Paragripopteryx munoai*, *Rhithroperla rossi* (*Paragripopteryx klapaleki*, *Paragripopteryx blanda*)))) (*Teutoperla maulina* (*Claudioperla tigrina* (*Potamoperla myrmidon* (*Andiperlodes tehuelche*, *Andiperla willinki*, *Falklandoperla kelper*, *Uncicauda testacea*, *Limnoperla jaffueli* (*Tupiperla gracilis*, *Tupiperla robusta* (*Guaranyperla guapiara*, *Guaranyperla nitens*)))))).

Key words: Andean Region, Neotropical Region, Phylogeny, Phylogenetic Relationships, Stoneflies.

Introduction

Plecoptera is an order of aquatic insects with more than 3,500 described species divided into 16 families, 12 in suborder Arctoperlaria and four in Antarctoperlaria. Antarctoperlaria includes the families: Austroperlidae, Diamphipnoidae, Eustheniidae and Gripopterygidae (Zwick, 2000; Fochetti & Tierno de Figueroa, 2008). This suborder has a circum-Antarctic distribution, including Australia and New Zealand (Australian Region), and South America (Andean and Neotropical regions + transition zones *sensu* Morrone, 2014). According to McCulloch *et al.* (2016), the divergence between the clades Diamphipnoidae + Eustheniidae and Austroperlidae + Gripopterygidae is estimated at approximately 70 Ma, while the divergence between Gripopterygidae and Austroperlidae is estimated at about 60 Ma between Paleocene and Eocene.

Currently, Gripopterygidae Enderlein, 1909 is the most diverse Antarctoperlarian family, comprising 54 genera and about 320 species (Pessacq *et al.*, 2019, in press), which are distributed in Australian Region and South America. The nymphs of Gripopterygidae are in general scraper or shredder and are mainly associated with lotic environments. They are mainly found on boulder surfaces, among pebbles, tree trunks, moss and leaf packs. The adults fly short distances and are found on riparian vegetation or rocks close to the water bodies (Brundin, 1967, 1972; Hynes, 1976; Zwick, 2000; McCulloch *et al.*, 2009).

In South America, Gripopterygidae is the dominant family in number of recorded genera (McLellan & Zwick, 2007). Illies (1963) reviewed the species of South American Gripopterygidae, and this paper is considered the starting point for the study of the family in South America. In his study, Illies erected several of the current genera (Table 1) and provided identification keys for most of them. Subsequent studies in Brazil, carried out mainly by Professor Claudio G. Froehlich in Southeast Region of the country, significantly increased the number of the Gripopterygidae species (Froehlich, 1969, 1990, 1993, 1994, 1998, 2001, 2002, 2015, 2016; Bispo & Lecci, 2011). As regards the Andean Region, McLellan and Zwick described some genera and species (McLellan, 2001; McLellan & Zwick, 2007); additional taxonomic studies, including descriptions of nymphs, have been performed by Alejandro Vera and Pablo Pessacq (*e.g.* Vera, 2005, 2006a, b, c, 2008, 2009, 2012, 2016; Pessacq, 2009, 2016). According to McLellan (1977), Gripopterygidae can be classified into five Gondwanian subfamilies (Table 1): Antarctoperlinae, Dinotoperlinae, Gripopteryginae, Leptoperlinae and Zelandoperlinae.

However, no phylogeny has yet been done in order to evaluate the monophyly of these subfamilies.

Gripopteryginae is restricted to South America (Table 1), comprising 15 genera and approximately 80 species (Pessacq *et al.*, in press). Most genera of Gripopteryginae are endemic to the Andean region (*Andiperla* Aubert, 1956, *Andiperlodes* Illies, 1963, *Aubertoperla* Illies, 1963, *Falklandoperla* McLellan, 2001, *Limnoperla* Illies, 1963, *Neopentura* Illies, 1965, *Rhithroperla* Illies, 1963, *Teutooperla* Illies, 1963, and *Uncicauda* McLellan & Zwick, 2007). *Potamoperla* Illies, 1963 has one record outside “Patagonia”, in Peru, but the genus is clearly Andean, and *Claudioperla* Illies, 1963 is distributed along the Andes from Colombia to Chile (Duarte *et al.*, 2019). Other four genera occur in subtropical and tropical areas, primarily from Brazil (*Gripopteryx* Pictet, 1841, *Guaranyperla* Froehlich, 2001, *Paragripopteryx* Enderlein, 1909, and *Tupiperla* Froehlich, 1969 (along the Brazilian Atlantic Forest and Cerrado to the northeastern of Argentina, Paraguay, and Uruguay).

According to McLellan (1977), Gripopteryginae is characterized by a combination of characters: (i) legs with a pair of distoventral spurs on each tibia, (ii) forewings with a long CuA fork, (iii) hind wings with 6th anal vein fused to wing margin, (iv) male genitalia with epiproct tip not recurved (some genera with epiproct absent or very small), (v) tergite 10 (T10) sclerotized, and (vi) posterior sclerite absent in T10.

According to McLellan & Zwick (2007), the intergeneric relationships in Gripopterygidae and the delimitation of the current South American subfamilies need to be reviewed. Here, our main objective was to infer the monophyly of Gripopteryginae. In order to achieve this objective, we propose a phylogeny based on morphology, including as many genera as possible of the five subfamilies of Gripopterygidae, among them all genera of Gripopteryginae.

Subfamilies	Genera	Nº spp.	Distribution
Antarctoperlinae Enderlein, 1909	<i>Antarctoperla</i> Enderlein, 1905	2	ARG, CHL
	<i>Araucanioperla</i> Illies, 1963	2	ARG, CHL
	<i>Ceratoperla</i> Illies, 1963	2	ARG, CHL
	<i>Chilenoperla</i> Illies, 1963	5	ARG, CHL
	<i>Ericiataperla</i> Vera, 2016	1	ARG, CHL
	<i>Megandiperla</i> Illies, 1960	1	ARG, CHL
	<i>Pehuenioperla</i> Vera, 2009	1	ARG, CHL
	<i>Pelurgoperla</i> Illies, 1963	1	ARG, CHL
	<i>Plegoperla</i> Illies, 1963	2	ARG, CHL
	<i>Vesicaperla</i> McLellan, 1967	7	
	<i>Zelandobius</i> Tillyard, 1921	30	NZL
Dinotoperlinae McLellan, 1977	<i>Alfonsoperla</i> McLellan & Zwick, 2007	1	ARG, CHL
	<i>Dinotoperla</i> Tillyard, 1921	35	
	<i>Dundundra</i> Theischinger, 1982	1	
	<i>Eunotoperla</i> Tillyard, 1924	1	
	<i>Illiesoperla</i> McLellan, 1971	11	
	<i>Neboissoperla</i> McLellan, 1971	3	AUS
	<i>Nescioperla</i> Theischinger, 1982	1	
	<i>Odontoperla</i> Mynott, Suter & Theischinger, 2017	2	
	<i>Oedemaperla</i> Mynott, Suter & Theischinger, 2017	2	
	<i>Trinotoperla</i> Tillyard, 1924	15	
Gripopteryginae Enderlein, 1909	<i>Andiperla</i> Aubert, 1956	1	ARG, CHL
	<i>Andiperlodes</i> Illies, 1963	2	ARG, CHL
	<i>Aubertoperla</i> Illies, 1963	2	ARG, CHL
	<i>Claudioperla</i> Illies, 1963	4	BOL, CHL, ECU, PER
	<i>Falklandoperla</i> McLellan, 2001	1	ARG (Falkland Islands)
	<i>Gripopteryx</i> Pictet, 1841	18	BRA
	<i>Guaranyperla</i> Froehlich, 2001	3	BRA
	<i>Limnoperla</i> Illies, 1963	1	ARG, CHL
	<i>Neopentura</i> Illies, 1965	1	ARG, CHL
	<i>Paragripopteryx</i> Enderlein, 1909	14	BRA, URY
	<i>Potamoperla</i> Illies, 1963	1	ARG, CHL
	<i>Rhithroperla</i> Illies, 1963	2	ARG, CHL
	<i>Teutoperla</i> Illies, 1963	4	ARG, CHL
	<i>Tupiperla</i> Froehlich, 1969	20	ARG, BRA, PRY
	<i>Uncicauda</i> McLellan & Zwick, 2007	2	ARG, CHL
Leptoperlinae Banks, 1913	<i>Notoperla</i> Enderlein, 1909	7	
	<i>Senzilloides</i> Illies, 1963	1	ARG, CHL
	<i>Cardioperla</i> McLellan, 1971	8	
	<i>Kirrama</i> Theischinger, 1981	2	
	<i>Leptoperla</i> Newman, 1839	28	AUS
	<i>Newmanoperla</i> McLellan, 1971	5	
	<i>Riekoperla</i> McLellan, 1971	26	
Zelandoperlinae McLellan, 1977	<i>Notoperlopsis</i> Illies, 1963	1	ARG, CHL
	<i>Acroperla</i> McLellan, 1977	5	
	<i>Apteryoperla</i> Wisely, 1953	6	
	<i>Aucklandobius</i> Enderlein, 1909	5	
	<i>Holcoperla</i> McLellan, 1977	3	
	<i>Nesoperla</i> Tillyard, 1923	3	
	<i>Rakiuraperla</i> McLellan, 1977	1	NZL
	<i>Taraperla</i> McLellan, 1998	4	
	<i>Megaleptoperla</i> Tillyard, 1923	2	
	<i>Rungaperla</i> McLellan, 1977	2	
	<i>Zelandoperla</i> Tillyard, 1923	6	

Material and Methods

We included several genera of Gripopterygidae in order to represent all subfamilies in the outgroup. We analyzed specimens in the *Centro de Investigación Esquel de Montaña y Estepa Patagónica* (CIEMEP), Esquel, Chubut, Argentina, where material of Andean and some Australian genera are housed (*e.g.* *Alfonsoperla* McLellan & Zwick, 2007, *Andiperlodes* Illies, *Antarctoperla* Enderlein, 1905, *Aubertoperla* Illies, *Ceratoperla* Illies, 1963, *Chilenoperla* Illies, 1963, *Dinotoperla* Tillyard, 1921, *Ericiataperla* Vera, 2016, *Klapopteryx* Navás, 1928, *Leptoperla* Newman, 1839, *Limnoperla* Illies, *Neopentura* Illies, *Notoperla* Enderlein, 1909, *Notoperlopsis* Illies, 1963, *Pehuenioperla* Vera, 2009, *Pelurgoperla* Illies, 1963, *Penturoperla* Illies, 1960, *Potamoperla* Illies, *Rhithroperla* Illies, *Riekoperla* McLellan, 1971, *Senzilloides* Illies, 1963, *Teutoperla* Illies, *Trinotoperla* Tillyard, 1924, *Uncicauda* McLellan & Zwick). We analyzed part of the Neotropical genera in the *Universidade Estadual Paulista*, Assis, São Paulo, Brazil (*Claudioperla* Illies, *Gripopteryx* Pictet, *Guaranyperla* Froehlich, *Paragripopteryx* Enderlein, and *Tupiperla* Froehlich). Five genera (*Andiperla* Aubert, *Cardioperla* McLellan, 1971, *Falklandoperla* McLellan, *Newmanoperla* McLellan, 1971, and *Taraperla* McLellan, 1998) were included in the analyses based on original descriptions. All the data of the material examined are in Table 1 in Supplementary material.

Our dataset includes 43 terminal taxa of which 40 species (32 genera) of Gripopterygidae (Tables 2–3) and three species (two genera) of Austroperlidae, family chosen as outgroup. According McCulloch *et al.* (2016), Austroperlidae and Gripopterygidae are sister-groups. From these 43 terminal taxa, we selected 51 characters with their respective states, mainly from nymphs and males; only two characters were related to the female terminalia (Table 2). We chose the characters used to define the subfamilies and genera, in addition to the characters defined in this work. The only genus of Gripopteryginae whose males have not yet been described is the monotypic genus *Falklandoperla* (*F. kelper* McLellan, 2001). This genus/species is described based on females and nymphs from Malvinas Island, Argentina. Thence, initially we performed two analyses, a first one including *F. kelper*, and a second, removing it from our dataset. The objective of these analyses is to understand how data behave in the presence/absence of this species, and to standardize our dataset.

The nomenclature for wing venation follows Béthoux (2005). We examined the external morphology of nymphs and adults on a Leica M205A stereomicroscope. In the matrix of morphological characters, we used “?” whenever that a character may not be observed in a given species, and we used “-” when a character was inapplicable for a given species. We used the Parsimony analysis (Fitch, 1971) and considered all characters as nonadditive. The parsimony seeks to minimize the total homoplasy of a dataset, but in the presence of characters with equal weights that infer contradictory groupings, it alone will not be able to decide in favor of any of them, generating a less solved final hypothesis. We search for characters with greater cladistic congruence, in detriment to those with a higher degree of homoplasy (Goloboff, 1997). Thus, in order to resolve conflicts between homoplastic characters distribution, and to determine the topology with the fewest *ad hoc* hypotheses, we used implied weights (Goloboff, 1993; Giribet, 2003), varying the k-values: $k = 3-15$.

The dataset was created using the *Nexus Data Editor*, NDE (Page, 2001), and cladistics analysis was performed under *Tree analysis using New Technology*, TNT (Goloboff *et al.*, 2008). The final topology was ready in software Adobe® Illustrator CC 2015. For analysis, we used the “Traditional search” command with Tree Bisection Reconnection (TBR), 300 repls., 500 trees to save per replication, and collapsing trees after the search. To estimate the branch support we used the Relative Bremer support (Goloboff & Farris, 2001), using 1000 suboptimal trees up to five steps longer (obtained using traditional search).

Table 2. List of morphological characters and states of Gripopteryginae (Gripopterygidae) used in phylogenetic inference (following the scheme proposed by Sereno, 2007).

Characters		Characters states
Nymphs – Body and head		
1.	Body; vesicular bristles	(0) absence; (1) presence (fig. 3–6 in Froehlich, 2001).
2.	Body; claviform bristles	(0) absence; (1) presence (fig. 8 in Froehlich, 1969).
3.	Head; antennae, fringe of bristles	(0) absence; (1) presence.
Nymphs – Thorax		
4.	Pronotum; cuticular structure	(0) without small projections; (1) with small projections (like spines or elevations) (fig. 36a in Illies, 1963; fig. 7a in Vera, 2006).
5.	Pronotum; anterior corners	(0) corners rounded (without forward expansion or horns) (fig. 27a in Illies, 1963); (1) with forward expansion or horns (fig. 3–6 in Froehlich, 2001).
6.	Metanotum; mid-distal margin (between wingpads), shape	(0) circular, concave; (1) circular, convex; (2) angular excised (^ pyramidal shaped); (3) angular (v shaped); (4) straight; (5) bilobated (w shaped).

7.	Coxae; procoxal projection/process	(0) absence; (1) presence (figs. 1–2 in McLellan <i>et al.</i> , 2005).
8.	Femora; extensor margin, fringe of bristles	(0) absence; (1) presence (fig. 12a in Illies, 1963; figs. 53–54 in McLellan & Zwick, 2007).
9.	Tibiae; extensor margin, fringe of bristles	(0) absence; (1) presence (fig. 12a in Illies, 1963; figs. 53–54 in McLellan & Zwick, 2007).
Nymphs – Abdomen		
10.	Abdomen; distal margin of terga, ring of bristles	(0) absence; (1) presence (fig. 39a in Illies, 1963).
11.	Abdomen; distal margin of terga 1–9, type of bristles	(0) setiform; (1) setiform stout; (2) spine form; (3) claviform; (4) vesicular.
12.	Abdomen; terga 1-9, row of mid-dorsal bristles	(0) absence; (1) presence.
13.	Abdomen; terga 1-9, row of mid-dorsal spines	(0) absence; (1) presence (fig. 5 in Froehlich, 1990).
14.	Abdomen; terga 1-9, number of rows of mid-dorsal spines	(0) 1 row (fig. 5 in Froehlich, 1990); (1) 2 rows (fig. 7a,b in Vera, 2006).
15.	Abdomen; T10, distal margin, shape	(0) curved/without projection; (1) trapezoid; (2) triangular; (3) spine form.
16.	Abdomen; anal gills	(0) absence; (1) presence (fig. 13 in Vera, 2009).
17.	Abdomen; epiproct and paraprocts modified as respiratory structures	(0) absence; (1) presence (fig. 8 in McLellan, 2001).
18.	Cerci; cercomeres, ring of small distal setae	(0) absence; (1) presence.
19.	Cerci, long bristles	(0) absence; (1) presence.
20.	Paraprocts; distal region (apex), spine	(0) without ornamentation/spine; (1) with a long spine (fig. 7a,b in Vera, 2006; fig. 20–21 in Vera, 2009).
Adults – Head		
21.	Ocelli	(0) absence; (1) presence.
22.	Head; maxillary palp, size of the 5 th segment in relation to the 3 rd	(0) subequal (nearly equal); (1) 2 times longer or more (fig. 18 in Vera, 2009).
Adults – Thorax		
23.	Wings (male)	(0) apterous; (1) brachypterous; (2) macropterous.
24.	Wings; staining pattern of fore and hind wings	(0) both wings without pigmentation; (1) forewing with pigmentation, hindwing without pigmentation; (2) both wings with pigmentation.
25.	Forewings; number of crossveins between C and Sc	(0) 1 crossvein (fig. 4 in Béthoux, 2005); (1) 2 or more crossveins (fig. 3 in Béthoux, 2005).
26.	Forewings; pterostigmatic crossveins	(0) absence; (1) presence (fig. 11 in Froehlich, 1969).
27.	Forewings; RP vein, shape	(0) unforked (fig. 4 in Béthoux, 2005); (1) forked (fig. 3 in Béthoux, 2005).
28.	Forewings; RP vein, number of forks	(0) 1 fork; (1) 2 forks (fig. 3 in Béthoux, 2005).
29.	Forewings; anterior fork of RP vein in relation to RA	(0) anterior fork of RP vein not joining RA (fig. 11 in Froehlich, 1969); (1) anterior fork of RP vein joining RA (fig. 1a in Vera, 2016).
30.	Forewings; CuA vein, shape	(0) unforked (fig. 1 in Vera, 2006); (1) forked (fig. 11 in Froehlich, 1969).

31.	Forewings; CuA vein, number of forks	(0) 1 fork; (1) 2 forks.
32.	Hind wings; inferior branch of M vein in relation to CuA	(0) unfused; (1) partially fused, separating near the wing margin (fig. 6 in McLellan & Zwick, 2007); (2) completely fused.
33.	Hind wings; 6 th anal vein, shape	(0) 6 th anal vein free of wing margin (fig. 6 in McLellan & Zwick, 2007); (1) 6 th anal vein fused to wing margin (fig. 11 in Froehlich, 1969).
34.	Femora; flexor margin, distal spine (spine disto-ventral)	(0) absence; (1) presence (fig. 32 in Froehlich, 1969).
35.	Tibiae; distal region, spurs	(0) absence; (1) presence (fig. 7 in Froehlich, 1969).
36.	Tarsi; basal tarsal segment in relation to apical segment	(0) much shorter than apical segment, 1/3 of the length; (1) shorter than apical segment, 1/2 of the length (fig. 5a in Vera, 2016); (2) subequal or equal to the apical segment (fig. 44g in Illies, 1963).
37.	Tarsi; narrow membranous band along the ventral side of the basal segment	(0) absence; (1) presence (fig. 3 in Vera, 2009).
Adults – Abdomen		
38.	Abdomen; T10, anterior sclerites, fusion (inner margin)	(0) completely fused (fig. 2 in Froehlich, 1998); (1) contacting in a small point or bridge (fig. 44c in Illies, 1963); (2) separated by a membrane (fig. 3b in Vera, 2006).
39.	Abdomen; T10, anterior sclerites in relation to central sclerite	(0) completely fused to central sclerite; (1) fused to central sclerite but distinguishable from it by a suture; (2) partially fused to central sclerite, with a lateral narrow cleft (considering the fusion of central and lateral sclerites); (3) separated from central sclerite by a membrane.
40.	Abdomen; T10, central sclerite, distal margin, shape	(0) not protruding; (1) protruding/coming out (fig. 18b,c in Illies, 1963).
41.	Abdomen; T10, central sclerite (distal margin), denticles/teeth	(0) absence; (1) presence (fig. 31 in Froehlich, 1998).
42.	Abdomen; T10, central sclerite on T10 (distal margin, extension), number of denticles/teeth (applicable only to 41 (1))	(0) 1; (1) 2 (fig. 31 in Froehlich, 1998).
43.	Abdomen; posterior sclerite (segment 11)	(0) absence (fig. 13 in Froehlich, 1994); (1) presence (fig. 3a,b in Vera, 2006).
44.	Abdomen; posterior sclerite (segment 11), shape	(0) small spine/knob; (1) elongated, digitiform; (2) large, rounded, (3) small, rounded.
45.	Abdomen; posterior sclerite (segment 11), position	(0) apical (fig. 3a,b in Vera, 2006); (1) ventral.
46.	Abdomen; upturned sclerotized epiproct	(0) absence; (1) presence (fig. 3a in Vera, 2006).
47.	Epiproct; ventro-basal region, lobe	(0) absence; (1) presence (fig. 44e in Illies, 1963).
48.	Epiproct; ventral region, keel	(0) absence; (1) presence (fig. 3a in Vera, 2006).
49.	Epiproct; row of dorsal denticles (dorsal teeth)	(0) absence; (1) presence (fig. 3b in Vera, 2006).
50.	Epiproct; row of dorsal denticles (dorsal teeth), number	(0) 1 row; (1) 2 rows (fig. 3b in Vera, 2006).
51.	Cerci; size	(0) short, less than 12 cercomeres (fig. 3b in Vera, 2006); (1) long, more than 12 cercomeres.

Table 3. Dataset of 51 morphological characters and state assignments for the species included in the cladistic analyses of Gripopteryginae. Characters 1–20: nymphs; 21–51: adults.

Taxa/Characters	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
<i>Penturoperla barbata</i>	0	0	0	0	1	0	0	0	0	1	1	0	0	-	0	0	1	1	0	0	1	0	2	2	1
<i>Klapopteryx armillata</i>	0	0	0	0	0	2	0	0	1	1	1	0	0	-	?	0	1	1	0	0	1	?	1	0	1
<i>Klapopteryx kuscheli</i>	0	0	0	0	0	4	0	1	1	1	1	0	0	-	2	0	1	1	0	0	1	0	1	0	1
<i>Alfonsoperla flinti</i>	0	0	0	1	0	1	0	1	1	0	-	0	0	-	2	1	0	1	0	0	1	-	2	1	0
<i>Dinotoperla serricauda</i>	0	0	0	0	0	1	0	1	1	1	?	0	0	-	0	1	0	1	0	0	1	1	2	1	0
<i>Trinotoperla irrorata</i>	0	0	1	0	0	1	0	1	1	1	?	1	0	-	2	1	0	1	1	0	1	0	2	1	1
<i>Cardioperla</i> sp.	0	0	0	0	0	?	0	1	1	1	?	0	1	0	2	1	0	?	0	0	1	0	2	1	0
<i>Leptoperla varia</i>	0	0	0	0	0	4	0	1	1	1	?	0	0	-	0	1	0	1	0	0	1	0	2	1	0
<i>Newmanoperla thoreyi</i>	?	?	1	0	0	?	0	1	1	1	?	1	0	-	0	1	0	1	1	?	1	?	2	0	0
<i>Notoperla fasciata</i>	0	0	1	0	0	4	1	1	1	1	?	1	0	-	2	0	0	1	1	0	1	0	1	0	0
<i>Notoperla magnaspina</i>	0	0	1	0	0	4	1	1	1	1	?	1	0	-	2	0	0	1	1	0	1	0	1	?	?
<i>Riekoperla karki</i>	0	0	0	0	0	1	0	1	1	1	?	0	0	-	0	1	0	1	0	0	1	1	2	0	0
<i>Riekoperla perkinsi</i>	0	0	0	0	0	?	0	1	1	1	?	0	1	0	2	1	0	1	0	0	1	1	2	0	0
<i>Senzilloides panguipullii</i>	0	0	0	0	0	4	0	1	1	1	3	0	1	0	2	1	0	1	0	0	1	0	2	1	0
<i>Notoperlopsis femina</i>	0	0	0	0	0	4	0	1	1	1	?	0	0	-	0	1	0	1	1	0	1	0	1	1	0
<i>Taraperla howesi</i>	?	?	0	0	1	4	0	0	0	1	?	0	0	-	0	1	0	?	0	0	1	?	2	0	0
<i>Antarctoperla michaelsoni</i>	0	0	0	0	1	4	0	0	0	1	1	0	0	-	0	1	0	1	0	0	1	1	2	0	0
<i>Ceratoperla fazi</i>	0	0	0	1	0	0	0	1	0	0	-	0	1	1	0	1	0	0	0	0	1	0	2	1	0
<i>Chilenoperla elongata</i>	0	0	1	0	0	1	0	1	1	1	1	0	0	-	0	1	0	1	0	0	1	1	2	2	0
<i>Chilenoperla puelche</i>	0	0	1	0	0	1	0	1	1	1	1	0	0	-	0	1	0	1	0	0	1	1	2	2	0
<i>Ericiataperla puerilis</i>	0	0	1	0	0	4	0	0	0	1	2	0	0	-	0	1	0	1	0	0	1	1	2	0	0
<i>Pehuenioperla llaima</i>	0	0	1	0	0	4	0	1	0	1	1	0	0	-	0	1	0	1	0	1	1	1	2	1	0
<i>Pelurgoperla personata</i>	0	0	1	0	0	4	0	1	1	1	1	0	0	-	0	1	0	0	0	0	1	0	2	1	0
<i>Andiperla willinki</i>	0	0	0	0	0	4	0	0	0	0	-	0	0	-	0	1	0	0	0	0	0	0	0	-	-
<i>Andiperlodes tehuelche</i>	0	0	1	0	0	4	0	0	0	0	-	0	0	-	2	1	0	1	0	0	1	1	0	-	-
<i>Aubertoperla illiesi</i>	0	1	0	0	0	4	0	1	1	1	3	0	0	-	0	1	0	1	0	0	1	1	2	0	0
<i>Claudioperla tigrina</i>	0	0	0	0	0	4	0	1	1	1	0	0	0	-	0	1	0	1	0	0	1	0	2	1	0
<i>Falklandoperla kelper</i>	0	0	0	0	0	1	0	0	0	?	?	0	0	-	2	1	0	1	0	0	1	0	?	?	?
<i>Gripopteryx cancellata</i>	0	1	0	1	0	3	0	1	1	1	3	0	1	0	1	1	0	1	0	0	1	0	2	0	0
<i>Gripopteryx liana</i>	0	1	0	1	0	3	0	1	1	1	3	0	1	0	3	1	0	1	0	0	1	0	2	1	0
<i>Guaranyperla guapiara</i>	1	0	0	0	1	0	0	1	0	1	4	0	0	-	2	1	0	0	0	0	1	0	2	0	0
<i>Guaranyperla nitens</i>	1	0	0	0	1	0	0	1	0	1	4	0	0	-	3	1	0	0	0	0	1	0	2	1	0
<i>Limnoperla jaffueli</i>	0	0	0	0	0	2	0	1	1	1	0	0	0	-	0	1	0	1	0	0	1	0	2	0	0
<i>Neopentura semifusca</i>	0	0	0	0	1	4	0	0	0	0	-	0	1	1	3	1	0	0	0	1	1	0	2	1	1
<i>Paragripopteryx klapaleki</i>	0	1	0	0	0	4	0	1	1	1	3	0	0	-	0	1	0	1	0	0	1	0	2	0	0
<i>Paragripopteryx blanda</i>	0	1	0	0	0	4	0	1	1	1	3	0	0	-	1	1	0	1	0	0	1	0	2	0	0
<i>Paragripopteryx munoai</i>	0	1	0	0	0	5	0	1	1	1	3	0	0	-	0	1	0	1	0	0	1	?	2	0	0
<i>Potamoperla myrmidon</i>	0	0	1	0	0	4	0	1	1	1	0	0	0	-	0	1	0	0	1	0	1	0	2	1	0
<i>Rhithroperla rossi</i>	0	1	0	0	0	?	0	1	1	1	3	0	0	-	0	1	0	1	0	0	1	0	2	0	0
<i>Teutoperla maulina</i>	0	0	0	0	0	4	0	1	1	1	?	0	0	-	1	1	0	1	0	0	1	1	2	0	0
<i>Tupiperla gracilis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	-	2	1	0	1	0	0	1	0	2	1	0
<i>Tupiperla robusta</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	-	2	1	0	1	0	0	1	0	2	1	0
<i>Uncicauda testacea</i>	0	0	0	0	0	2	0	0	0	1	0	0	0	-	2	1	0	1	0	0	1	?	2	0	0

Table 3 (Continuation). Dataset of 51 morphological characters and state assignments for the species included in the cladistic analyses of Gripopteryginae. Characters 1–20: nymphs; 21–51: adults.

Taxa/Characters	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	3 5	3 6	3 7	3 8	3 9	4 0	4 1	4 2	4 3	4 4	4 5	4 6	4 7	4 8	4 9	5 0	5 1
<i>Penturoperla barbata</i>	1	1	1	0	1	2	?	0	0	1	1	1	2	3	0	0	-	1	1	0	1	?	1	?	?	1
<i>Klapopteryx armillata</i>	1	1	1	0	?	?	?	0	0	1	1	1	2	3	0	0	-	1	1	0	1	?	1	0	-	1
<i>Klapopteryx kuscheli</i>	1	1	1	0	?	?	?	0	0	1	0	1	2	3	0	0	-	1	1	0	1	0	?	0	-	1
<i>Alfonsoperla flinti</i>	0	1	0	0	1	0	1	0	0	0	2	0	1	2	0	0	-	1	0	0	1	0	0	0	-	1
<i>Dinotoperla serricauda</i>	0	0	-	0	1	0	1	0	0	0	2	1	1	3	1	0	-	0	-	-	1	0	0	0	-	1
<i>Trinotoperla irrorata</i>	1	1	1	0	1	1	1	0	0	0	1	1	?	?	1	?	?	?	?	?	1	0	0	1	1	1
<i>Cardioperla</i> sp.	0	0	-	0	0	-	1	1	0	1	2	0	1	3	?	0	-	1	1	0	1	0	?	0	-	?
<i>Leptoperla varia</i>	0	0	-	0	0	-	2	0	0	0	2	0	2	3	0	0	-	1	1	0	1	0	0	?	?	1
<i>Newmanoperla thoreyi</i>	0	0	-	0	0	-	2	1	0	?	2	0	2	2	0	0	-	1	1	0	1	0	0	0	-	1
<i>Notoperla fasciata</i>	0	0	-	0	0	-	1	0	0	1	1	0	2	1	0	0	-	1	1	0	1	0	0	1	1	1
<i>Notoperla magnaspina</i>	?	?	?	?	0	-	?	?	0	?	?	?	2	1	0	0	-	1	3	0	1	0	?	1	1	1
<i>Riekoperla karki</i>	0	0	-	0	0	-	2	1	0	1	2	0	2	2	0	0	-	1	1	0	1	0	0	1	0	1
<i>Riekoperla perkinsi</i>	0	0	-	0	0	-	2	1	0	1	2	0	2	2	0	0	-	1	1	0	1	0	0	1	0	1
<i>Senzilloides panguipullii</i>	0	1	0	1	0	-	1	0	0	1	2	0	2	3	0	0	-	1	1	0	1	0	1	1	0	1
<i>Notoperlopsis femina</i>	1	1	0	0	0	-	1	0	0	0	1	0	2	2	0	0	-	1	3	0	1	0	1	1	1	1
<i>Taraperla howesi</i>	0	0	-	0	0	-	2	?	0	?	?	?	2	?	1	0	-	1	3	0	1	0	1	1	1	?
<i>Antarctoperla michaelsoni</i>	0	1	0	1	0	-	1	0	0	0	2	0	2	3	1	0	-	1	2	0	1	0	1	1	1	0
<i>Ceratoperla fazi</i>	0	0	-	1	0	-	1	0	0	0	2	0	2	3	1	0	-	1	0	1	1	0	1	1	1	0
<i>Chilenoperla elongata</i>	0	1	0	1	0	-	1	0	0	0	2	0	1	3	1	0	-	1	0	1	1	1	1	1	1	0
<i>Chilenoperla puelche</i>	0	1	0	1	0	-	1	0	0	0	2	0	1	3	1	0	-	1	0	1	1	0	1	1	1	0
<i>Ericiataperla puerilis</i>	0	1	0	1	0	-	1	0	0	0	2	0	1	3	1	0	-	1	1	1	1	0	1	1	1	0
<i>Pehuenioperla llaima</i>	0	1	0	0	0	-	1	0	0	0	2	0	2	3	1	0	-	0	-	-	1	0	1	1	1	0
<i>Pelurgoperla personata</i>	1	1	0	1	0	-	1	0	0	0	2	0	1	3	1	0	-	1	0	?	1	1	1	1	1	0
<i>Andiperla willinki</i>	-	-	-	-	-	-	-	-	0	1	0	0	2	0	0	0	-	0	-	-	0	-	-	-	-	1
<i>Andiperlodes tehuelche</i>	-	-	-	-	-	-	-	-	0	1	1	0	0	0	1	1	1	0	-	-	0	-	-	-	-	1
<i>Aubertoperla illiesi</i>	0	1	0	0	1	0	1	0	0	1	2	0	2	3	1	0	-	0	-	-	1	0	0	1	0	1
<i>Claudioperla tigrina</i>	0	1	0	0	1	0	1	1	0	1	1	0	2	1	1	1	1	0	-	-	1	0	0	1	0	1
<i>Falklandoperla kelper</i>	?	?	?	?	?	?	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Gripopteryx cancellata</i>	0	1	0	0	1	0	1	1	0	1	1	0	0	0	0	0	-	0	-	-	1	1	0	1	0	1
<i>Gripopteryx liana</i>	0	1	0	0	1	0	1	1	0	1	1	0	0	0	0	0	-	0	-	-	1	1	0	1	1	1
<i>Guaranyperla guapiara</i>	1	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	1	0	-	-	0	-	-	-	-	1
<i>Guaranyperla nitens</i>	1	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	1	0	-	-	0	-	-	-	-	1
<i>Limnoperla jaffueli</i>	0	0	-	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	-	-	1	0	1	1	0	1
<i>Neopentura semifusca</i>	1	1	0	0	0	-	2	0	0	0	1	0	2	3	1	0	-	1	1	0	1	0	1	1	1	0
<i>Paragripopteryx klapaleki</i>	1	1	0	0	1	0	1	1	0	1	1	0	0	0	1	1	1	0	-	-	1	0	0	1	0	1
<i>Paragripopteryx blanda</i>	1	1	0	0	1	0	1	1	0	1	1	0	0	0	1	1	1	0	-	-	1	0	0	1	0	1
<i>Paragripopteryx munoai</i>	0	1	0	0	1	0	1	1	0	1	1	0	0	0	1	1	1	0	-	-	0	-	-	-	-	1
<i>Potamoperla myrmidon</i>	0	1	0	0	1	0	1	1	0	1	1	0	2	0	1	1	1	0	-	-	0	-	-	-	-	1
<i>Rhithroperla rossi</i>	0	1	0	0	1	0	1	1	0	1	0	0	0	0	?	1	1	0	-	-	1	0	0	0	-	1
<i>Teutoperla maulina</i>	0	1	0	0	1	0	1	1	0	1	1	0	0	1	1	0	-	0	-	-	1	0	0	1	1	1
<i>Tupiperla gracilis</i>	0	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	1	0	-	-	0	-	-	-	-	1
<i>Tupiperla robusta</i>	0	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	1	0	-	-	0	-	-	-	-	1
<i>Uncicauda testacea</i>	0	1	0	0	1	0	1	1	0	1	1	0	0	2	1	1	0	0	-	-	0	-	-	-	-	1

Pylogenetic results

Different consensus topologies resulted from the different analyses proposed here: 1) including or not *Falklandoperla kelper*; 2) considering different weighting schemes (Figs. 1A–B, Figs. 1–6 in Supplementary material). In analysis under equal weighting of characters (EW), including *F. kelper* in the dataset, we obtained 86 most parsimonious trees whose Length (L) = 207, Consistency index (CI) = 0.335, and Retention index (RI) = 0.662. We retrieved a greater number of topologies when we removed *F. kelper* from the dataset in analysis under EW (120 MPTs, L = 206, CI = 0.337, and RI = 0.665). Whether we use *F. kelper* or not in the analysis under EW, we found similar consensus topologies, except for variation in the relationship between *Andiperlodes tehuelche* and *Andiperla willinki* (Figs. 1–2 in Supplementary material). We recovered *Neopentura semifusca* outside of Gripopteryginae delimitation, as sister of *Ceratoperla fazi* (Antarctoperlinae). The Gripopteryginae *Aubertoperla illiesi* was recovered in a polytomy along with taxa of Leptoperlinae, two taxa of Dinotoperlinae (*Alfonsoperla flinti* and *Dinotoperla serricauda*), plus a grouping with the majority of Gripopteryginae. This last group remained nested on delimitation of the subfamily, despite unresolved relationships among them (Figs. 1–2 in Supplementary material).

We used implied weighting of characters (IW) to evaluate potential topological changes (Goloboff, 1993; Giribet, 2003), and to resolve conflicts between homoplastic character distribution. Whether we vary the value of k (3, 5, 7, 9, 11, 13, and 15), and independently of the presence/absence of *Falklandoperla kelper* in the dataset, we succeeded in finding five well-resolved consensus topologies, except for small variations on taxa relationships. In all variations of k , *Neopentura semifusca* remained outside the Gripopteryginae delimitation, either as sister of *Pehuenioperla llaima* (Antarctoperlinae) ($k = 3$) or as sister of *Taraperla howesi* (Zelandoperlinae) ($k = 5–15$). All other taxa of Gripopteryginae remained nested within the delimitation of the subfamily (Fig. 1A, Figs. 3–6 in Supplementary material). According to Goloboff (1993), a low value of k (e.g. $k \sim 0–3$) strongly down weight homoplasy, and as it increases the value of k (typically larger than 3) up weight homoplasy in a phylogenetic inference. Below, we present the results obtained using $k = 3$ (Figs. 1A–B).

Family Gripopterygidae

In our analysis, which considered Austroperlidae as out-group (McCulloch *et al.*, 2016; Ding *et al.*, 2019), Gripopterygidae resulted monophyletic in all analyses (Relative Bremer support = 94), being supported by four synapomorphies: [16: 1] the anal gills in nymphs (reversed in *Notoperla* spp.); [17: 0] the epiproct and paraprocts of nymphs unmodified as respiratory structures; [35: 0] the lack of tibial spurs (reversed in some taxa of Leptoperlinae and Gripopteryginae); and [48: 0] the absence of keel in ventral region of epiproct (reversed in some taxa). Dinotoperlinae appeared as non-monophyletic, as its members appeared in the first three cladogenesis of the family. *Trinotoperla irrorata* followed by *Dinotoperla serricauda*, and *Alfonsoperla flinti* as sister taxa of all other Gripopterygidae (Fig. 1A). All taxa, except Dinotoperlinae, were nested in a polytomy supported by three synapomorphies: [6: 4] the straight shape of mid-distal margin (between wingpads) in metanotum (reversed in some taxa); [30: 0] the CuA vein unforked in forewings (reversed in some taxa); and [49: 1] the presence of row of dorsal denticles (dorsal teeth) in epiproct (a non-exclusive character state).

Leptoperla varia (Leptoperlinae) appeared separated from the remaining members of the polytomy. A first group of this polytomy included *Notoperlopsis femina* (Zelandoperlinae) as sister of *Notoperla* spp. (Leptoperlinae) and was supported by three synapomorphies: [19: 1] the presence of long bristles on cerci (a non-exclusive character state, shared with some taxa); [23: 1] the brachypterous shape of wings (males); and [36: 1] the basal tarsal segment shorter than apical segment in 1/2 of the length (a non-exclusive character state, shared with some taxa).

A second group comprised all taxa of Antarctoperlinae included in the analysis (*Pehuenioperla llaima*, *Antarctoperla michaelsoni*, *Ericiataperla puerilis*, *Chilenoperla elongata*, *Chilenoperla puelche*, *Ceratoperla fazi*, and *Pelurgoperla personata*), plus *Neopentura semifusca* (Gripopteryginae) and *Taraperla howesi* (Zelandoperlinae). Four synapomorphies supported this group: [9: 0] the absence of fringe of bristles on tibia extensor margin (a non-exclusive character state, shared with some taxa); [40: 1] the protruding distal margin in central sclerite of T10 (a non-exclusive character state, shared with some taxa); [48: 1] the presence of a keel in ventral region of epiproct (a non-exclusive character state, shared with some taxa); and [51: 0] the short cerci, less than 12 cercomeres. *Neopentura semifusca* and *Pehuenioperla llaima* were sister taxa supported by a single synapomorphy: [20: 1] the nymphs with a long spine in distal region (apex)

of paraprocts. On the other hand, *Taraperla howesi* was recovered as sister of all other Antarctoperlinae supported by a single synapomorphy: [24: 0] the absence of pigmentation of fore and hind wings (a non-exclusive character state, shared with some taxa).

The last group was composed by Leptoperlinae species (*Senzilloides panguipullii*, *Cardioperla* sp., *Riekoperla perkinsi*, *Riekoperla karki*, and *Newmanoperla thoreyi*) + all Griptopteryginae, except for *Neopentura semifusca*. This group was supported by three synapomorphies: [11: 3] the presence in nymphs of claviform bristles on distal margin of terga 1–9 (a character state modified in some taxa); [35: 1] the presence of distal tibial spurs (a non-exclusive character state, shared with some taxa); and [50: 0] the epiproct with one row of dorsal denticles (dorsal teeth) (a character state modified in some taxa).

Subfamily Griptopteryginae

Apart from *Neopentura semifusca*, all remaining Griptopteryginae taxa were nested in a large group (Relative Bremer support = 66) supported by three synapomorphies: [30: 1] the CuA vein forked in forewings; [40: 1] distal margin of central sclerite in T10 protruding/coming out; and [43: 0] the absence of posterior sclerite in T10.

Different from the other variation of k (k = 5–15; Figs. 3–6 in Supplementary material), where *Aubertoperla illiesi* was recovered at the first cladogenesis of the subfamily (*Neopentura semifusca* outside), when we used k = 3, two groups were recovered in Griptopteryginae (Fig. 1A). A first group comprises *Aubertoperla illiesi* as sister of the clade with *Griptopteryx* spp. (two species in a monophyletic clade) plus *Rhithroperla rossi* and three *Paragriptopteryx* species (paraphyletic) in a polytomy. These relationships were supported by a single synapomorphy: [2: 1] the presence in nymphs of claviform bristles on body. Relationships between *Rhithroperla rossi* and the paraphyletic *Paragriptopteryx* were supported by two synapomorphies: [38: 0] the inner margin of anterior sclerites in T10 completely fused to each other (a character state shared with some taxa); and [39: 0] the anterior sclerite in T10 completely fused to central sclerite (a character state shared with some taxa).

The second group in Griptopteryginae (Fig. 1A) comprised (*Teutoperla maulina* (*Claudioperla tigrina* (*Potamoperla myrmidon* (*Andiperlodes tehuelche*, *Andiperla willinki*, *Falklandoperla kelper*, *Uncicauda testacea*, *Limnoperla jaffueli* (*Tupiperla gracilis*, *Tupiperla robusta* (*Guaranyperla guapiara*, *Guaranyperla nitens*)))))).

Different from analyses using $k = 5-11$ (*Teutoperla maulina* + *Claudioperla tigrina*) and $k = 13-15$ (*Teutoperla maulina* + *Gripopteryx* spp.), when we used $k = 3$ (Fig. 1A) *Teutoperla maulina* was recovered as sister of a large group supported by a single synapomorphy: [39: 1] the anterior sclerite in T10 fused to central sclerite but distinguishable from it by a suture (reversed in some taxa). Subsequently, *Claudioperla tigrina* was recovered as sister of *Potamoperla myrmidon* + all other taxa, supported by a single synapomorphy: [41: 1] the presence of denticles/teeth on distal margin of central sclerite in T10 (a character state shared with *Paragripopteryx* spp., and *Rhithroperla rossi*, and modified in *Andiperla willinki*).

Potamoperla myrmidon + all other taxa were supported by two synapomorphies: [39: 0] the anterior sclerite in T10 completely fused to central sclerite (a character state shared with *Gripopteryx* spp., *Paragripopteryx* spp. and *Rhithroperla rossi*, and modified in *Uncicauda testacea*); and [46: 0] the absence of an upturned sclerotized epiproct (a character state modified in *Limnoperla jaffueli*). When we used $k = 3$, we recovered a collapsed polytomy comprising *Andiperlodes tehuelche*, *Andiperla willinki*, *Falklandoperla kelper*, *Uncicauda testacea*, *Limnoperla jaffueli* and a group with *Tupiperla* spp. + *Guaranyperla* spp. Except for *Limnoperla jaffueli*, this group was recovered well resolved in all other k schemes ($k = 5-15$) (Figs. 3–6 in Supplementary material). Four synapomorphies supported this group in analysis using $k = 3$: [8: 0] the absence of a fringe of bristles on femur extensor margin; [9: 0] the absence of a fringe of bristles on tibia extensor margin; [15: 2] the distal margin of T10 in nymphs triangular; and [38: 0] the anterior sclerite on T10 (inner margin), completely fused.

Tupiperla spp. + *Guaranyperla* spp. was supported by two synapomorphies: [6: 0] the circular, concave shape of mid-distal margin of metanotum (a non-exclusive character, shared with some taxa); and [34: 1] the presence of distal spine (spine disto-ventral) on femur flexor margin.

Discussion and taxonomical treatment

Implications of Neopentura placement

In our results, most Gripopteryginae genera nested together in a monophyletic clade, supporting the subfamily erected by Enderlein (1909) and endorsed by McLellan's review (1977). The only exception is the Andean *Neopentura semifusca* (Fig. 1A). This

monotypic genus was described by Illies (1965) in Penturoperlidae (now Austroperlidae) based on a single female specimen. Subsequently, Illies (1969) reviewed the family Austroperlidae and placed *Neopentura* in Gripopterygidae, within Gripopteryginae. McLellan (1977) studied Gripopterygidae subfamilies, however, disregarded *Neopentura* in his classification. Then, Vera (2006c) described the male, redescribed female and nymphs of *Neopentura semifusca*, and discussed several characters of the genus, and its classification within Gripopterygidae. According to Vera (2006c), several morphological characters distinguish *Neopentura* from the other South American Gripopterygidae, suggesting that the genus is more closely related with New Zealand *Zelandobius* (Antarctoperlinae). However, Vera did not formally propose reclassifying *Neopentura*; instead, this author performed an analysis of the characters shared between *Neopentura* and the Antarcticoperlinae. This reflected in Froehlich's Catalog of Neotropical Plecoptera (Froehlich, 2010), where this monotypic genus is still included in Gripopteryginae. Although we did not use *Zelandobius* species in our analysis, the morphological characters of *Neopentura semifusca* are recovered as closely related to the Antarcticoperlinae taxa (e.g. *Pehuenioperla llama*).

According to McLellan (1977), the following morphological characters are diagnostic for Gripopteryginae: (1) legs with a pair of distoventral spurs on each tibia; (2) forewings with a long CuA fork; (3) hind wings with sixth anal vein fused to wing margin; (4) male genitalia with epiproct tip not recurved; some genera with epiproct absent or very small; (5) T10 sclerotized; and (6) posterior sclerite absent in T10. All these characters were included in our analysis, and in general, they should be observed in *Neopentura semifusca* as a member of Gripopteryginae. However, except for the male genitalia with epiproct tip not recurved and the T10 sclerotized, *Neopentura* disagrees on all other characters, for example, in this species, there are no tibial spurs, the CuA vein are unforked in forewings, the sixth anal vein in hind wings is free, and the posterior sclerite is present in T10. All these characters are in accordance to the McLellan diagnosis for the subfamily Antarcticoperlinae. Thus, we are proposing the reclassification of *Neopentura*. Here, we include the monotypic genus *Neopentura* in Antarcticoperlinae, until a more comprehensive analysis, with additional characters and taxa is performed.

Gripopteryginae (sensu stricto) and related taxa

In accordance with McLellan's (1977) classification, our results support Gripopteryginae as a valid subfamily of Gripopterygidae after the reclassification of *Neopentura*. However, our results contrast in part with the results of McCulloch *et al.* (2016), which was based in a molecular analysis using the mitochondrial (COI) and nuclear (18S, H3) DNA, and that do not support the monophyly of the subfamily. In their study, seven taxa of Gripopteryginae were recovered as polyphyletic being more often related to the Australian and New Zealand taxa: *Limnoperla jaffueli* and *Teutopteryx auberti* as sister of Australian *Leptoperla* sp. (Leptoperlinae); *Gripopteryx* sp. as sister of New Zealand Zelandoperlinae; *Tupiperla* sp., *Andiperla* sp. and *Aubertoperla* sp. as sister of Australian Dinotoperlinae and Leptoperlinae; and *Claudioperla tigrina* nested with South American Antarctoperlinae (see fig. 3 in McCulloch *et al.*, 2016).

We examined many Australian taxa based on literature and in our analysis, *Leptoperla varia* (Kimmins, 1951; McLellan, 1971) has been recovered outside of Leptoperlinae and in a polytomy along with all other taxa, except for Dinotoperlinae (Fig. 1A). On the other hand, Gripopteryginae is recovered as sister of the most Australian Leptoperlinae, with South American *Senzilloides panguipullii* (Leptoperlinae) in the first cladogenesis of this group (Fig. 1A). Although Leptoperlinae appears as paraphyletic, the purpose of our analysis was not to test the monophyly of this subfamily and deeper analyses could change this outcome. In general, the placement of *Leptoperla varia* in a polytomy far from the other Australian taxa may be due to missing entries in important characters of the matrix, especially those characters supporting *Senzilloides panguipullii* as sister of the clade with Australian Leptoperlinae + Gripopteryginae (characters 11: type of bristles in distal margin of terga 1–9 in nymphs; and 50: number of rows of dorsal denticles in epiproct).

In the study of McCulloch *et al.* (2016) they proposed that many of the divergences between South American and Australian taxa of Gripopterygidae coincide with the opening of the Drake Passage 41 Ma during Oligocene and that the isolation of the South America and Australia continents may be responsible for these biogeographic disjunctions. In our analysis, the closer relationships recovered between Australian Leptoperlinae (except for *Leptoperla varia*) + Gripopteryginae was supported by the condition of the sixth anal vein fused to the wing margin in hind wings, which reinforces in part the results found by McCulloch *et al.* (2016). On the other hand, South American Leptoperlinae (*Senzilloides* and *Notoperla*) disagrees with Australian taxa of the same subfamily by having the sixth anal vein free of the wing margin in hind wings. These

characters are in accordance with the diagnosis proposed by McLellan (1977) for the two subfamilies.

According to McLellan (1977), Leptoperlinae and Griopteryginae also shared a third character state, the presence of tibial spurs (shared also with Dinotoperlinae), however these subfamilies can be morphologically distinguished by: (i) the CuA vein is forked in forewings in Griopteryginae (unforked in Leptoperlinae), and (ii) the absence in Griopteryginae and its presence in Leptoperlinae of a posterior sclerite in T10. These two characters plus a third character, (iii) the protruding distal margin of the central sclerite in T10, supported the relationships among the Griopteryginae taxa in our analysis (Fig. 1A).

Although the diagnosis of Griopteryginae as proposed by McLellan (1977) includes the condition of CuA vein forked and the absence of posterior sclerite in T10, these are non-exclusive characters, being shared with some Dinotoperlinae (the CuA vein forked in forewings; and the absence of posterior sclerite in T10) and *Pehuenioperla llaima* (the absence of posterior sclerite in T10).

Our results do not confirm the indications of non-monophyly of Griopteryginae suggested by the molecular analysis performed by McCulloch *et al.* (2016). Unlike McCulloch *et al.* (2016), we included representatives of all genera of Griopteryginae in our morphological analyses. As results, we recovered the monophyly of this subfamily (once *Neopentura* is removed from the subfamily) and a relatively well-resolved consensus topology under IW. In addition, regarding the characters used here, the subfamily has been divided in two large groups, although homoplastic characters support most of the internal relationships (Fig. 1A). Our results have confirmed the subfamily Griopteryginae, which has been redefined and now includes the following genera: *Andiperla*, *Andiperlodes*, *Aubertoperla*, *Claudioperla*, *Falklandoperla*, *Griopteryx*, *Guaranyperla*, *Limnoperla*, *Paragriopteryx*, *Potamoperla*, *Rhithroperla*, *Teutoperla*, *Tupiperla* and *Uncicauda*.

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Supplementary material. Material of Gripopterygidae examined.

Species	Material examined
<i>Alfonsoperla flinti</i>	El Comisario, 7.xii.2014, 1 nymph; El Comisario, 14.iii.2017, 2 nymphs; El Comisario, 7.ii.2010, 1 male; A° al sur de los Pumas, 20.i.011, copo, Pessacq, Omad, 1 male.
<i>Antarctoperla michaelsoni</i>	A° Blanco, Puente, 7.x.2006, Schiaffinni Leg., 3 nymphs; Arg DW 132 PL-L, PNNH, Ayo Totoral, 14.i.08, Kick, 1 nymph; Arg DW 105 PL-L+A, PNNH, Ayo Leon, 12.xii.07, Kick manual, 1 male, 4 nymphs; Baggilt, Dic. 2003, 1 male; La Hoya, 11.xii.07, 1 male, 2 females; A° en camping los Maitenes P. N., 3.xii.07, Pessacq Leg., 2 males; Corcovado, Pte Hierro, 7.xii.07, 14 males, 10 females.
<i>Aubertoperla illiesi</i>	Arg DWN-15/2, 4-25.i.2007, Malaise, PL-A, 1 male (frasco 7); La Hoya, 11.xii.07, 3 males, 1 female; Corcovado, Pte Hierro, 7.xii.07, 1 male.
<i>Aubertoperla kuscheli</i>	Arg DWN-15/2, 4-25.i.2007, Malaise, PL-A, 1 male (bottle 7).
<i>Cardioperla</i> sp.	Tasmania: Iris Creek at crossing on Cradle Mountain Road (C132), Middlesex. - 41.5515 145.96280, Date: 05 Jan 2012, Colls: J Mynott & M Shackleton, Field Code: 120105-4, 1 male, 1 female; Tasmania: O'Gradys Falls at footbridge, Pinnacle Road, Mt Wellington, Hobart, -42.90953 147.25378, Date: 13 Jan 2012, Colls: J Mynott & M Shackleton, Field Code: 120113-1, 2 nymphs.
<i>Ceratoperla fazi</i>	ARG, Chubut, A° El Comisario, Ruta Provincial 44, 25 km al sur del Corcovado, 21.i.07, Leg. Pessacq, 5 nymphs; A° El Comisario, 29.ii.08, 3 nymphs; A° El Comisario, 14.iii.08, 4 males; El Comisario, 14.iii.17, 1 male, 2 females; Comisario, 08, 1 male; Comisario, 010, 1 male; N13, 1 nymph; Arg DW 142 PL-L PNNH, Ayo Neuquenco, 23.i.08, Kick, 1 nymph.
<i>Chilenoperla elongata</i>	Arg DW 137 PL-L PNNH, Ayo Leon, 21.i.08, Kick, 5 nymphs; Vial 6. Argentina, Chubut Province, Rifleros River, 29 Sept 2004, L. Miserendino. Doesn't fit any of the 4 species in the keys in Nelson, 1973, 1 male.
<i>Chilenoperla puelche</i>	La Helad., 07, 1 male.
<i>Dinotoperla serricauda</i>	Tasmania: Flinders Island, Cronleys Creek on Big River Road, -40.24714 148.06625, Date 12.Dec.2011, J Mynott & M Carey, Field Code 111212-2, 4 nymphs; Tasmania: Hellyer River at Hellyer Gorge, -41.27291 145.61383, Date 04.Jan.2012, J Mynott & M Shackleton, Field Code 120104-1, 1 male, 1 female.
<i>Klapopteryx kuscheli</i>	1° A° despues de El Comisario, 16.xii.06, Pitfall trap, Pessacq Leg., 4 males, 4 females; A° Blanco, 9.x.17, RM LAB Adult, 8 nymphs.
<i>Klapopteryx armilata</i>	1° A° camino a QuilaQuina, Puente, 26.x.2017, 1 male, 2 nymphs.
<i>Leptoperla varia</i>	Tasmania, Lake St Clair, foreshore at viewing plataform, Visitor Centre, Cradle Mountain-Lake St Clair National Park, -42.11552 146.17325, Date 09.Jan.2012, J Mynott & M Shackleton, Field Code 120109-1, 1 male, 4 females; Tasmania, Lake St Clair, foreshore at viewing plataform, Visitor Centre, Cradle Mountain-Lake St Clair National Park, -42.11552 146.17325, Date 09.Jan.2012, J Mynott & M Shackleton, Field Code 120109-1, 2 nymphs.
<i>Limnoperla jaffueli</i>	Rio Grande, Pto. Cipres, 23.i.08, 2 males, 1 female; La Hoya, 23.xi.04(3), 2 males, 4 females; La Hoya, 20.xii.04(3), 1 male, 3 females; 1° A° camino a Quila Quina, puente, SMB, 26.x.17, 4 nymphs; Corcovado, Pte Hierro, 7.xii.07, 1 male.
<i>Neopentura semifusca</i>	S.N. Datos, 1 nymph; Arg-DWN-180, PL-L, 5.iii.08, Kick, 1 nymph; Arg-DWN-164, PL-L, 23.ii.08, Kick, 2 nymphs (frasco 11); Arg-DW-186, PL-L, PNNH Cantaros, 26.x.08, Colador, 1 nymph (pronotum different).
<i>Notoperla</i> sp.	Arg DW 128 PL-L PNNH, Rio Pedregoso, 14.i.08, Kick, 12 nymphs.

<i>Notoperla fasciata</i>	#3 Manso Superior, 1.xi.06, 7 nymphs; La Hoya, 21.ix.04, Pozón c/ arena (B)(1), nymphs; La Hoya, 21.ix.04, Pozón c/ arena (B), 10 nymphs; La Hoya, 25.i.05, 2 females; La Hoya, 25.i.05, 114 males; A° Blanco, Puente, 7.x.2006, Schiaffinn Leg., 1 nymph; Arg DW 142 PL-L PNNH, Ayo Neuquenco, 23.i.08, Kick, 2 nymph.
<i>Notoperla magnaspina</i>	Casc. Irigoyen, P.N. Los Alerces, 29.iii.07, Leg. Pessacq, 6 nymphs; La Hoya, 18.xii.04, 7 males; Rio Nilson "Nolsensein", 20.ii.07, Pessacq Leg., 1 nymph; C. Irigoyen, 3.iii.08, 1 nymph; La Hoya, 25.i.05, 1 female; La Hoya, 21.ix.04, Pozón c/ arena (B), 12 nymphs.
<i>Notoperlopsis femina</i>	Los Rifleros, Septiembre, 29.ix.04, 1 male, 4 females; Not. Fem., 07, 1 female; A° Esquel, 08.ix.08, 1 female; A° Rifleros, 23.x.07, 1 female, 3 exuviae; LEVA+GUALJAINA, 3 males; A° Blanco (INTA), Archangelsky leg, 17.x.05, 1 female; A° Rifleros, 7.x.06, Pessacq, 1 female (también: 1 male, 1 female <i>Limnoperla jaffueli</i> ; 1 female <i>A. illiesi</i>).
<i>Pehuenioperla llaima</i>	N14, 1 nymph.
<i>Pelurgoperla personata</i>	El Comisario, 16.iii.07, 1 male; A° Poncho Moro Puente, "Rio Corcovado ..., 30.iii.07", Pessacq Leg., 5 exuviae; Arg DW 141 PL-L, PNNH, Rio Pichi Trafal, 23.i.08, Kick, 2 nymphs; Arg DWN 183 PL-L, 06.iii.08, Kick, 1 nymph (Frasco 11); Arg DW 307 PL-L, PNNH A° Clau, 12.iii.09, Kick, Garre, 6 nymphs.
<i>Penturoperla barbata</i>	Pucon Pai, Nov.2016, 1 male; #29, A° Grande, 16.xii.06, Kick, 1 nymph; Arg, DW29 PL-A, PNNH, A° Grande, 41°02'21,6"S, 71°48'27"W, 763m, 4.ii.07-25.ii.07, "GARRE, M de oca"?, Malaise, 1 male.
<i>Potamoperla myrmidon</i>	S11, 1 female; A° R40, Caracoles-Perito, Santa Cruz, SCK 20.ii.17, 7 males, 5 females and 26 nymphs.
<i>Reikoperla karki</i>	Australia: New South Wales (NSW): Spencer's Creek, Kosciuszko National Park, 1.x.2009, 1 nymph.
<i>Reikoperla perkinsi</i>	Australia: New South Wales (NSW) ck at Polblue picnic ground -31.92583 151.38753, 24.ii.2011, 110224-2, 2 nymphs.
<i>Rhithroperla rossi</i>	A° Coronado, Lago Rivadavia, 12.iii.07, Pessacq Leg., 1 male (other 4 adults from hard identification).
<i>Senzilloides panguipullii</i>	A° al sur del Comisario, 7.iii.08, 1 nymph; El Comisario, 30.xi.07, 1 nymph; El Comisario, 14.iii.08, 1 nymph; C. Irigoyen, 3.iii.08, 4 nymphs, 5 exuviae; C. Irigoyen, 3.iii.08, 1 female, 1 exuviae; La Hoya, 28.iv.05 (C), 2 nymphs; La Hoya (1), 26.ii.05, 1 male, 1 female, 6 exuviae; La Hoya (B), 28.iv.05, 1 nymph; 1° A° desp. Comisario, 30.i.08, 1 male; A° Poncho Moro, Rta Corc Vintter, Pessacq Leg., 15.iii.07, 1 male; Casc. Irigoyen, P.N. Los Alerces, 27.iii.07, Pessacq Leg., 1 female; A° El Comisario, 30.iii.07, Pessacq Leg., 2 females, 1 nymph.
<i>Teutoperla</i> sp.	S.N. Datos, 1 nymph.
<i>Teutoperla brundini</i>	DWN-116, PL-A., 9-23.i.2008, Malaise, 1 male; DW 29 PL-A, PNNH Arroyo Grande, 41°02'21.6"S. 71°48'27"W, 763m, 4.ii.07-25.ii.07. Malaise Garré M.oca Leg., 1 male (<i>T. brundini</i> or <i>T. n. sp.</i>).
<i>Trinotoperla</i>	Tasmania, Bird River at Bird Bridge, Bird Track, Franklin-Wild Rivers National Park, -42.34311 145.59047, Date 07.Jan.2012, J Mynott & M Shackleton, Field Code 120107-3, 3 nymphs (<i>T. irrorata</i> ?); Australia: New South Wales: Small Creek crossing Thunderbolts Way, between Quarry Road and Topdale Road (south of Walcha), -31.37172 151.54803, Date 02.Nov.2011, J Mynott, P Suter & M Crump, Field code 111102-1, 1 male (<i>T. irrorata</i> ?); QLD, Stream on Tully Gorge rd 6.7km d\s of power station, -17.75599 145.62781, 8.May.2011, M Shackleton & J Mynott, 110508-3, 3 females (<i>Trinotoperla</i>).
<i>Trinotoperla irrorata</i>	VIC, White bridge on Mt Buller rd, -37.126775 146.438352, 24.jan.2012, M. Shackleton (120124-1), 2 females; VIC, White bridge on Mt Buller rd, -37.126775

	146.438352, 24.jan.2012, M. Shackleton (120124-1), 1 female; Victoria, Chalet Creek on Mt Buller Road (C320) at bend approximately 1300m., -37°08' 146°27', 24.March,2011, J Mynott, M Carey, Field Code 110324-1, 2 nymphs.
<i>Uncicauda testacea</i>	1° A° despues de A° El Comisario, 30.xi.07, Pessacq Leg., 2 males, 2 females.

Supplementary material. Cladograms.

Figure 1. Consensus strict for 86 trees under equal weighting scheme in Griptopterygidae (*F. kelper* present in analysis).

Figure 2. Consensus strict for 120 trees under equal weighting scheme in Gripoptyergidae (*F. kelper* absent in analysis).

Figure 4. Relationships between some genera of Gripoptyrigidae subfamilies. Consensus strict for three trees under implied weighting scheme ($k = 11$; *F. kelper* present in analysis).

Figure 5. Relationships between some genera of Griopterygidae subfamilies. One tree recovered under implied weighting scheme ($k = 13$; *F. kelper* present in analysis).

Figure 6. Relationships between some genera of Gripoptyerygidae subfamilies. One tree recovered under implied weighting scheme ($k = 15$; *F. kelper* present in analysis).

Chapter II: Revision and phylogenetic relationships of *Paragripopteryx* Enderlein, 1909 (Plecoptera: Gripopterygidae), including a new genus

Full title:

Revision and phylogenetic relationships of *Paragripopteryx* Enderlein, 1909 (Plecoptera: Gripopterygidae), including a new genus

Running title:

***Revision of Paragripopteryx* (Plecoptera: Gripopterygidae)**

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Abstract

Neotropical *Paragripopteryx* Enderlein currently comprises 14 species, two species being restricted to Uruguay and other 12 occurring along the coastal Brazilian mountains, from northeast of Bahia State to Rio Grande do Sul State, Brazil. The genus has been defined based only on combination of morphological characters, without synapomorphies, resulting in a tenuous line related to its status as a valid genus. We performed a cladistic analyses based on 39 morphological characters examined for 31 terminal taxa of Gripopterygidae. Among these species, 15 species (13 genera) representing outgroup species, and 16 species of *Paragripopteryx* (except for *P. baratinii*, and including the three new species described here). For analyses, we consider two datasets: (i) a complete dataset (31 species, 39 characters), and (ii) a reduced dataset, considering only species with known nymphs (24 species, 39 characters). The analyses were running under Parsimony with all characters as nonadditive. In all our analyses, *P. munoai* remained outside the current delimitation of *Paragripopteryx*. Consequently, a new genus in Gripopteryginae, *McLellanperla* **gen. nov.** is proposed to house *P. munoai*. All other *Paragripopteryx* species remained nested in a clade supported by a single synapomorphy in phylogenetic analysis: the presence of pterostigmatic crossvein in forewings (shared with *Guaranyperla* and some *Gripopteryx*). Considering the phylogenetic relationship

among the species of *Paragripopteryx*, based on characters shared by *P. crassila* and *P. klapaleki*, the synonymy of the first species under the second is proposed. Additionally, an identification key based on males of the genus is provided.

Key words: Aquatic insects, Morphological characters, Phylogenetic relationships, Stoneflies, Systematics.

Introduction

Gripopterygidae Enderlein, 1909 occurs in the Austral Hemisphere and comprise about 320 species in 54 genera (DeWalt *et al.*, 2019). Of these, 28 genera occur in Neotropical and Andean regions with about 100 species (Froehlich, 2010; Pessacq *et al.*, 2019, in press). Currently, four genera and 52 species of Gripopterygidae have been reported in Brazilian realm: 1) *Gripopteryx* Pictet, 1841 with 17 species (plus one restricted to Uruguay); 2) *Guaranyperla* Froehlich, 2001 with three species; 3) *Paragripopteryx* Enderlein, 1909 with 12 species (plus two restricted to Uruguay); and 4) *Tupiperla* Froehlich, 1969 with 20 species (Froehlich, 2010, 2015, 2016; Bispo & Lecci, 2011; Lecci & Froehlich, 2011; Avelino-Capistrano & Nessimian, 2013; Duarte *et al.*, 2014a, b; Novaes & Bispo, 2016; Gonçalves *et al.*, 2017).

Enderlein (1909) erected *Paragripopteryx* based on a single male specimen housed in the Zoological Museum of Helsinki (Finland), at that time classified as *Gripopteryx cancellata* Pictet by Klapálek (1904). After reviewing this specimen, Enderlein renamed it as *Paragripopteryx klapaleki*, the type species of the genus (Enderlein, 1909; Froehlich, 1969). Later, Jewett (1960) discussed the status of *P. klapaleki* and combined it in *Gripopteryx* (= *G. klapaleki*). Illies (1963) reinstated *Paragripopteryx* and allocated *Gripopteryx gracilis* as a type species of the genus (*G. klapaleki* as a synonym of *P. gracilis* = *Semblis gracilis* Burmeister, 1839). Then, Froehlich (1969) resurrected *P. klapaleki* as a valid species and created *Tupiperla* for *P. gracilis* (= *T. gracilis*). Froehlich (1969) also described *P. anga* and *P. blanda*, and established the new combinations for *Jewettoperla crassila* (Jewett, 1960) and *J. garbei* (Navás, 1936) under *Paragripopteryx* (the latter subsequently combined in *Gripopteryx* by Froehlich (1990)). Posteriorly, Zwick (1973) combined *Jewettoperla munoai* in *Paragripopteryx* (= *P. munoai* (Benedetto, 1969)) and Benedetto (1983) described *P. baratinii*.

Froehlich (1994) reviewed the Brazilian species of *Paragripopteryx* and described six species: *P. delicata*, *P. egena*, *P. guardae*, *P. hamata*, *P. merui*, and *P. eleonora* (the latter subsequently transferred to *Tupiperla* by Froehlich, 1998). Finally, Bispo & Lecci (2011) described three species based on male specimens: *P. intervalensis*, *P. kapilei*, and *P. paranapiacabae*. At the time, *Paragripopteryx* comprised 14 valid species.

Here, our main objectives are 1) to test the monophyly and the phylogenetic relationships among the species of *Paragripopteryx*; 2) delimit and review *Paragripopteryx*; and 3) to describe new species and semaphoronts of the genus. In order

to achieve these objectives, we reviewed and proposed the first phylogeny of *Paragripopteryx*; we provide the descriptions of three new species: *P. dasalmas* **sp. nov.** from Bahia State, and from Santa Catarina State, *P. convexa* **sp. nov.** and *P. ogum* **sp. nov.**; and we provide the descriptions of last instar exuviae of *P. intervalensis* and of the young nymph of *P. kapilei*. Additionally, we described a new genus, provided photos of the adults and nymphs for several species, and an identification key for *Paragripopteryx*.

Material and Methods

Taxa and cladistic

The specimens studied are from Museu de Zoologia, Universidade de São Paulo (MZSP), Brazil (*Paragripopteryx anga* Froehlich, *P. blanda* Froehlich, *P. delicata* Froehlich, *P. egena* Froehlich, *P. guardae* Froehlich, *P. hamata* Froehlich, *P. intervalensis* Bispo & Lecci, *P. kapilei* Bispo & Lecci, *P. klapaleki* Enderlein, *P. merui* Froehlich, *P. paranapiacabae* Bispo & Lecci, *Gripopteryx cancellata* (Pictet), *Guaranyperla guapiara* Froehlich, *G. nitens* Froehlich, *Tupiperla gracilis* (Burmeister), *T. robusta* Froehlich), Universidad de la República, Uruguay (*P. munoai* (Benedetto)), Centro de Investigación Esquel de Montaña y Estepa Patagónica (CIEMEP), Argentina (*Alfonsoperla flinti* McLellan & Zwick, *Aubertoperla illiesi* (Froehlich), *Ceratoperla fazi* (Navás), *Claudioperla tigrina* (Klapálek), *Limnoperla jaffueli* (Navás), *Potamoperla myrmidon* (Mabille), *Rhithroperla rossi* (Froehlich), and *Uncicauda testacea* (Vera)). Additional material was collected in Brazil, including the types of new species. Holotypes of the new species are housed in MZSP. Paratypes of the new species described here are housed in the entomological collection of the Laboratório de Biologia Aquática (UNESP/Assis, São Paulo State, Brazil). Paratypes of *Paragripopteryx dasalmas* **sp. nov.** (two males and two females) are housed in the entomological collection of the Museu de Zoologia, Universidade Federal da Bahia (Salvador, Bahia State, Brazil).

Paragripopteryx crassila was analyzed by means of the original description in Jewett (1960) and by photos of holotype sent us by Dr. Christopher Grinter at California Academy of Science (CAS), in the United States. Benedetto (1983) deposited the type specimens of *P. baratinii* in Universidad de la República in Montevideo, Uruguay. However, this material was not found in that institution (Dr. Enrique Morelli, personal communication). According to Benedetto (1983), two male paratypes were also sent to

the Max-Planck Institute in Schlitz, Germany. However, Dr. Peter Zwick (personal communication) stated that these specimens have never been in this institution. Unfortunately, the original description of *P. baratinii* is incomplete, and useless for the phylogenetic analyses. Thus, *P. baratinii* was not used in our study.

All other species were analyzed using a Leica M205A stereomicroscope. The following original papers were relevant for complementing the morphological characters and/or to help in the primary homology propositions: Illies (1963), Froehlich (1969, 1990, 1994, 1998, 2001, 2015) and Bispo & Lecci (2011). All material examined of *Paragripopteryx* is described in the Taxonomy section. The nomenclature for wing venation follows Béthoux (2005).

The phylogenetic dataset comprises 31 terminal taxa and 39 morphological characters (Tables 1–2). For it, we have included 15 outgroup species of 12 different South American genera and one Australian genus of Gripopterygidae. The criteria for choosing outgroup species were based on previous study (McCulloch *et al.*, 2016). The morphological characters for both nymphs and adults (males and females) were used, except for species without nymphs. Following Forey & Kitching (2000), the missing and inapplicable data were coded as “?” and “-”, respectively (Table 2).

Two different datasets were analyzed: 1) the complete dataset, comprising all the 31 species and 39 characters; and 2) a reduced dataset, considering only species with known nymphs, which excluded *P. dasalmas* **sp. nov.**, *P. crassila*, *P. convexa* **sp. nov.**, *P. egena*, *P. hamata*, *P. ogum* **sp. nov.**, and *P. paranapiacabae* (24 species and 39 characters).

The Parsimony analyses (Farris, 1983) were run considering all characters as nonadditive (Fitch evolution). Both datasets were analyzed using “Traditional search” command at the software *Tree analysis using New Technology*, TNT (Goloboff *et al.*, 2008), with Tree Bisection Reconnection (TBR), 300 repls., 500 trees to save per replication, and collapsing trees after the search.

Parsimony analyses were implemented under equal and implied weighting (Goloboff, 1993). The analyses under implied weighting were run with different values of *k* (3, 5, 7, 9, 11, 13, and 15) to evaluate potential topological changes. According to Prendini (2003), relationships recovered under different weighting schemes are more reliable than those recovered under fewer parameters. The Relative Bremer support (Goloboff & Farris, 2001) was used to estimate the branch support, with 1000 suboptimal trees up to five steps longer (obtained using traditional search).

Table 1. List of morphological characters used in phylogenetic inference of *Paragripopteryx* (following the scheme proposed by Sereno, 2007).

Characters	Characters States
Nymphs – Body, head and thorax	
1. Body; vesicular bristles	(0) absence; (1) presence (figs. 3–6 in Froehlich, 2001).
2. Thorax; claviform bristles	(0) absence; (1) presence (fig. 8 in Froehlich, 1969).
3. Pronotum; cuticular structure	(0) without small cuticular projections; (1) with small cuticular projections (like spines or elevations) (Illies, 1963).
4. Pronotum; paranota	(0) absence; (1) presence (fig. 3 in Froehlich, 2001).
5. Metanotum; mid-distal margin (between wingpads), shape	(0) circular, concave (fig. 4 in Froehlich, 2015); (1) circular, convex; (2) angular excised (^ pyramidal shaped) (Fig. 27a in Illies, 1963); (3) angular (v shaped); (4) straight (Fig. 12E); (5) bilobated (w shaped) (Fig. 3H).
6. Femur; extensor margin, fringe of bristles	(0) absence; (1) presence (Fig. 19B).
7. Tibia; extensor margin, fringe of bristles	(0) absence; (1) presence (Fig. 19B).
8. Tarsi; ventral face of 3 rd tarsal segment, type of bristles	(0) spinose/spine-like setae (fig. 14 in McLellan & Zwick, 2007); (1) setiform, small robust setae (Fig. 3I); (2) setiform, small thin setae (Fig. 17B).
Nymphs – Abdomen	
9. Abdomen; distal margin of terga 1–9, ring of bristles	(0) absence; (1) presence (Fig. 17C).
10. Abdomen; distal margin of terga 1–9, type of bristles	(0) setiform; (1) vesicular (Froehlich, 2001); (2) claviform (Fig. 17C).
11. Abdomen; terga 1–9, row of mid-dorsal spines	(0) absence; (1) presence (fig. 5 in Froehlich, 1990).
12. Abdomen; T10, distal margin, shape	(0) curved (Fig. 17C); (1) trapezoid (Fig. 12G); (2) triangular (fig. 11 in McLellan & Zwick, 2007); (3) spine form (fig. 3 in Froehlich, 2001).
13. Paraprocts; apex, general shape	(0) rounded; (1) squared; (2) triangular.
Adults – Thorax	
14. Forewings; pterostigmatic crossveins	(0) absence; (1) presence (Fig. 4C).
15. Forewings; RP vein, shape	(0) unforked; (1) forked (Fig. 4C).
16. Forewings; RP fork, crossveins	(0) absence; (1) presence.
17. Forewings; CuA vein, shape	(0) unforked; (1) forked (Fig. 4C).
18. Hind wings; inferior branch of M vein in relation to CuA vein, shape	(0) partially fused, separating near the wing margin (Fig. 4C); (1) completely fused.
19. Hind wings; 6 th anal vein, shape	(0) 6 th anal vein free of wing margin; (1) 6 th anal vein fused to wing margin (Fig. 4C).
20. Femur; flexor margin, distal spine (disto-ventral spine)	(0) absence; (1) presence (fig. 32 in Froehlich, 1969).
21. Tibia; distal region, spurs	(0) absence; (1) presence (fig. 7 in Froehlich, 1969).
22. Tarsi; basal tarsal segment in relation to apical segment	(0) shorter than apical segment, 1/2 of the length; (1) subequal or equal to the apical segment.
Adults – Abdomen	

23. Abdomen; T10, lateral clefts separating lateral sclerite from the anterior sclerite	(0) absence; (1) presence (Fig. 18B).
24. Abdomen; T10, anterior sclerites, fusion (inner margin)	(0) completely fused (Fig. 16B); (1) contacting in a small point or bridge (fig. 8 in McLellan & Zwick, 2007); (2) separated by a membrane (Illies, 1963).
25. Abdomen; T10, anterior sclerites in relation to central sclerite	(0) completely fused to central sclerite (Fig. 16B); (1) separated from central sclerite by a membrane (fig. 21f in Illies, 1963); (2) fused to central sclerite but distinguishable from it by a suture (fig. 8 in McLellan & Zwick, 2007).
26. Abdomen; T10, central sclerite, distal margin, condition	(0) not protruding; (1) protruding/coming out (Fig. 5A).
27. Abdomen; T10, central sclerite (extension), distal margin, shape	(0) not bilobated; (1) bilobated (Fig. 5A).
28. Abdomen; T10, central sclerite (distal margin), denticles/teeth	(0) absence; (1) presence (Figs. 5A, C).
29. Abdomen; T10, central sclerite (distal margin), number of denticles/teeth	(0) 1; (1) 2 (Fig. 5A).
30. Abdomen; posterior sclerite (segment 11)	(0) absence; (1) presence (Illies, 1963).
31. Epiproct	(0) absence (Fig. 13E); (1) presence (Fig. 15E).
32. Epiproct; general shape	(0) hook-shaped (tip facing outwards) (McLellan & Zwick, 2007); (1) hook-shaped (tip facing inwards) (Fig. 15E); (2) falciform (Fig. 9D); (3) shortened finger shape (fig. 22D in Illies, 1963); (4) elongated finger shape (fig. 3 in Bispo & Lecci, 2011); (5) spoon-shaped (Illies, 1963).
33. Epiproct; row of dorsal denticles (dorsal teeth)	(0) absence; (1) presence (Froehlich, 1994).
34. Paraprocts; distal third, narrowing (constricted)	(0) absence; (1) presence (Fig. 10C).
35. Paraprocts; distal third, black rod-like setae/bristles (stout setae)	(0) absence; (1) presence (Fig. 10C).
36. Paraprocts; distal margin, shape	(0) rounded (Fig. 13E); (1) almost pointed (Fig. 11C).
37. Subgenital plate (male); distal margin, shape	(0) general triangular, tip rounded; (1) trapezoid, tip slightly straight; (2) trapezoid, distal margin notched, (3) curved; (4) straight.
38. Subgenital plate (female); middle region, unsclerotized spot	(0) absence; (1) presence (Fig. 5D).
39. Subgenital plate (female); shape	(0) ovoid, distal margin cut/straight; (1) ovoid, distal margin rounded; (2) trapezoid, distal margin notched; (3) trapezoid, distal margin rounded; (4) squared, distal margin notched; (5) squared, distal margin slightly curved.

Table 2. Dataset of 39 morphological characters and state assignments for the species included in the cladistic analyses of *Paragripopteryx*. Characters 1–13 for nymphs; 14–39 for adults.

Taxa/Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Ceratoperla fazi</i>	0	0	1	0	0	1	0	0	0	-	1	0	0	0	1	0	0	0	0	0
<i>Alfonsoperla flinti</i>	0	0	1	0	1	0	0	1	0	-	0	2	2	0	1	0	1	0	0	0
<i>Riekoperla karki</i>	0	0	0	0	1	1	1	?	1	?	0	0	0	0	0	-	0	1	1	0
<i>Aubertoperla illiesi</i>	0	1	0	0	4	1	1	1	1	2	0	0	0	0	1	0	1	0	0	0
<i>Claudioperla tigrina</i>	0	0	0	0	4	1	1	1	1	0	0	2	2	0	1	0	1	0	1	0
<i>Limnoperla jaffueli</i>	0	0	0	0	2	1	1	2	1	0	0	0	2	0	0	-	1	1	1	0
<i>Potamoperla myrmidon</i>	0	0	0	0	4	1	1	2	1	0	0	0	1	0	1	0	1	0	1	0
<i>Rhithroperla rossi</i>	0	0	0	0	4	1	1	2	1	2	0	0	1	0	1	0	1	0	1	0
<i>Teutoperla rothi</i>	0	0	0	0	4	1	1	2	1	0	0	2	?	0	0	0	1	0	1	0
<i>Uncicauda testacea</i>	0	0	0	0	2	0	0	2	1	0	0	2	0	0	1	0	1	0	?	0
<i>Tupiperla gracilis</i>	0	0	0	0	0	0	0	2	1	0	0	2	0	0	1	0	1	0	1	1
<i>Tupiperla robusta</i>	0	0	0	0	0	0	0	2	1	0	0	2	0	0	1	0	1	0	1	1
<i>Guaranyperla guapiara</i>	1	0	0	1	0	1	0	2	1	1	0	2	0	1	1	0	1	0	1	1
<i>Guaranyperla nitens</i>	1	0	0	1	0	1	0	2	1	1	0	3	0	1	1	0	1	0	1	1
<i>Gripopteryx cancellata</i>	0	1	1	0	3	1	1	1	1	2	1	1	0	0	1	1	1	0	1	0
<i>Paragripopteryx dasalmas</i> sp. nov.	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	0	1	0
<i>Paragripopteryx anga</i>	0	1	0	0	4	1	1	2	1	2	0	0	0	1	1	0	1	0	1	0
<i>Paragripopteryx blanda</i>	0	1	0	0	4	1	1	2	1	2	0	1	0	1	1	1	1	0	1	0
<i>Paragripopteryx crassila</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	0	1	0
<i>Paragripopteryx convexa</i> sp. nov.	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	0	1	0
<i>Paragripopteryx delicata</i>	0	1	0	0	4	1	1	2	1	2	0	1	2	1	1	1	1	1	1	0
<i>Paragripopteryx egena</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	0	1	0
<i>Paragripopteryx guardae</i>	0	1	0	0	4	1	1	2	1	2	0	0	2	1	1	0	1	0	1	0
<i>Paragripopteryx hamata</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	0	1	0
<i>Paragripopteryx intervalensis</i>	0	1	0	0	4	1	1	2	1	2	0	0	0	1	1	0	1	0	1	0
<i>Paragripopteryx kapilei</i>	0	1	0	0	4	1	1	2	1	2	0	0	2	1	1	0	1	0	1	0
<i>Paragripopteryx klapaleki</i>	0	1	0	0	4	1	1	2	1	2	0	0	2	1	1	0	1	0	1	0
<i>Paragripopteryx merui</i>	0	1	0	0	4	1	1	2	1	2	0	0	2	1	1	0	1	0	1	0
<i>Paragripopteryx munoai</i>	0	1	0	0	5	0	0	1	1	2	0	0	0	0	1	0	1	0	*	0
<i>Paragripopteryx ogum</i> sp. nov.	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	0	1	0
<i>Paragripopteryx paranapiacabae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	0	1	0

Table 2 (Continuation). Dataset of 39 morphological characters and state assignments for the species included in the cladistic analyses of *Paragripopteryx*. Characters 1–13 for nymphs; 14–39 for adults.

Taxa/Characters	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
<i>Ceratoperla fazi</i>	0	1	0	2	1	1	0	0	-	1	1	5	1	0	0	0	3	0	0
<i>Alfonsoperla flinti</i>	0	?	0	1	2	0	-	0	-	1	1	0	0	0	0	1	?	?	4
<i>Riekoperla karki</i>	1	1	1	2	1	0	?	0	-	1	1	4	1	0	0	1	3	?	?
<i>Aubertoperla illiesi</i>	1	1	0	2	1	1	0	0	-	0	1	4	1	1	0	0	4	?	?
<i>Claudioperla tigrina</i>	1	0	0	2	0	1	0	1	1	0	1	3	1	0	0	0	3	0	5
<i>Limnoperla jaffueli</i>	1	0	1	0	0	1	0	1	0	0	1	5	1	0	0	1	3	1	4
<i>Potamoperla myrmidon</i>	1	0	0	2	0	1	1	1	1	0	0	-	-	0	0	0	3	1	4
<i>Rhithroperla rossi</i>	1	0	1	2	2	1	0	1	1	0	1	3	0	0	0	0	2	1	1
<i>Teutoperla rothi</i>	1	0	0	0	0	0	0	0	-	0	1	3	1	0	0	1	3	1	?
<i>Uncicauda testacea</i>	1	?	0	0	0	1	0	1	0	0	0	-	-	0	0	0	4	1	4
<i>Tupiperla gracilis</i>	1	0	0	0	0	1	1	1	1	0	0	-	-	0	0	0	0	0	5
<i>Tupiperla robusta</i>	1	0	0	0	0	1	0	1	1	0	0	-	-	0	0	1	0	0	4
<i>Guaranyperla guapiara</i>	1	0	0	0	0	1	0	1	1	0	0	-	-	0	0	0	3	1	4
<i>Guaranyperla nitens</i>	1	0	0	0	0	1	1	1	1	0	0	-	-	0	0	0	3	1	3
<i>Gripopteryx cancellata</i>	1	0	1	0	0	0	-	0	-	0	1	3	1	0	0	0	3	1	5
<i>Paragripopteryx dasalmas</i> sp. nov.	1	0	0	0	0	1	1	1	1	0	1	1	0	0	0	?	0	1	4
<i>Paragripopteryx anga</i>	1	0	0	0	0	1	1	1	1	0	1	1	0	1	1	0	0	1	4
<i>Paragripopteryx blanda</i>	1	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	0	0	5
<i>Paragripopteryx crassila</i>	1	0	0	0	0	1	0	1	1	0	1	2	?	1	0	0	3	1	5
<i>Paragripopteryx convexa</i> sp. nov.	1	0	0	0	0	1	1	1	1	0	1	1	0	1	1	0	3	?	?
<i>Paragripopteryx delicata</i>	1	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	1	5
<i>Paragripopteryx egena</i>	1	0	0	2	0	1	0	1	1	0	0	-	-	1	0	0	0	1	5
<i>Paragripopteryx guardae</i>	1	0	0	0	0	1	0	1	1	0	1	2	1	1	0	0	1	1	4
<i>Paragripopteryx hamata</i>	1	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	3	1	1
<i>Paragripopteryx intervalensis</i>	1	0	0	0	0	0	-	1	1	0	1	4	1	0	0	0	3	1	5
<i>Paragripopteryx kapilei</i>	1	0	1	0	0	1	1	1	1	0	1	1	0	1	1	0	0	?	?
<i>Paragripopteryx klapaleki</i>	1	0	0	0	0	1	0	1	1	0	1	2	1	1	0	0	3	1	5
<i>Paragripopteryx merui</i>	1	0	0	0	0	1	1	1	1	0	1	4	1	1	0	0	0	?	?
<i>Paragripopteryx munoai</i>	1	0	0	0	0	1	1	1	1	0	0	-	-	0	0	1	3	0	2
<i>Paragripopteryx ogum</i> sp. nov.	1	0	0	0	0	1	1	1	1	0	0	-	-	0	0	0	0	?	5
<i>Paragripopteryx paranapiacabae</i>	1	0	1	0	0	1	0	1	1	0	1	1	0	0	0	0	3	?	?

Phylogenetic results

In this study, the first phylogenetic relationships of *Paragripopteryx* species are presented. Our results recovered different consensus topologies from different analyses implemented, under equal weighting (EW) as well as implied weighting (IW) analyses, using different values of k .

The complete dataset analyzed under EW resulted in 10 most parsimonious trees (MPTs) whose Length (L) = 136, Consistency index (CI) = 0.445–0.449, and Retention index (RI) = 0.600–0.605. The consensus topology resulted poorly resolved for the most taxa, *Paragripopteryx* was recovered polyphyletic in a large polytomy along with the most genera of Gripopteryginae (Fig. 1A in Supplementary material). Likewise, the analyses using the reduced dataset under EW resulted in 15 MPTs and a consensus topology also poorly resolved (L = 128, CI = 0.477, and RI = 0.589) (Fig. 1B in Supplementary material).

Under IW approach, using variable k values to evaluate potential topological changes (Goloboff, 1993; Giribet, 2003), the analyses resulted in relatively well-resolved topologies for both complete and reduced datasets, despite some contrasting results.

The parsimony analyses with complete dataset under IW with variable values of k resulted in two different topologies. The first for values of k = 3–5, where most *Paragripopteryx* are nested, except for *Paragripopteryx munoai* (clade C; Fig. 1A). While in the second, for values of k = 7–15, the results are the same consensus for two topologies in each value of k ; the most *Paragripopteryx* are recovered nested in a well-resolved clade, except for *Paragripopteryx munoai* (Fig. 2 in Supplementary material).

Now, the analyses using the reduced dataset under IW resulted in two different topologies for different weighting schemes (Fig. 1B; Fig. 3 in Supplementary material). A single topology was recovered for k = 3, where most species of *Paragripopteryx* remained nested in a well-resolved clade, except for *P. munoai* (clade C; Fig. 1B). While for k = 5–15, we recovered also a single topology with *P. munoai* remaining outside of *Paragripopteryx* and other two species (*Paragripopteryx blanda* and *Paragripopteryx delicata*) nested with *Gripopteryx cancellata* in a group (Fig. 3 in Supplementary material).

In order to resolve conflicts between homoplastic characters distribution, Goloboff (1993), suggested that a low value of k (e.g. k ~ 0–3) strongly down weight homoplasy,

and as it increases the value of k (typically larger than 3) up weight homoplasy in a phylogenetic inference. Below, we present the results for the analyses under $k = 3$.

Independently of the values of k , *Paragripopteryx munoai* was always recovered outside the delimitation of *Paragripopteryx*. Considering the $k = 3$, *Paragripopteryx munoai* remained at the base of a large clade composed of Griptopteryginae species (except for *Aubertoperla illiesi* and *Griptopteryx cancellata*) and other species of *Paragripopteryx* (clade A; Figs. 1A–B). The clade A (*Paragripopteryx munoai* included) was supported by a single synapomorphy in both analyses using the complete and reduced datasets: [character 28: state 1] the presence of denticles/teeth in distal margin of central sclerite (Figs. 3D–F; 5C).

Similarly, whether using the complete or reduced dataset, a single synapomorphy supported the group including the species of Griptopteryginae + *Paragripopteryx* species (clade B; Figs. 1A–B): [8: 2] the ventral face of third tarsal segment in nymphs with setiform, small thin setae (Fig. 19B). In analyses under IW ($k = 3$), except for *P. munoai*, all other species of *Paragripopteryx* constitute a clade (clade C; Figs. 1A–B). In this case, in both datasets (complete and reduced), the clade C was supported in a single synapomorphy: [14: 1] the presence of pterostigmatic crossvein in forewings (Fig. 4C).

Considering the *Paragripopteryx* relationships (excluding *P. munoai*) in the topology A (Fig. 1A), there is a polytomy composed by *P. intervalensis* plus two clades, D and E. The clade D is composed by *P. merui* plus the clade F (*P. crassila*, *P. guardae* and *P. klapaleki*), and supported by two synapomorphies: [13: 2] the general triangular shape of apex of the paraprocts in nymphs (a non-exclusive character state, shared with *Claudioperla tigrina* and reversed in *P. anga* and *P. blanda*), and [34: 1] the narrowing (constricted) shape of distal third of the paraprocts in male adults (a character state shared with *Aubertoperla illiesi*, *Paragripopteryx egena* and the clade K) (Figs. 9D, F). Besides the unsolved relationships among the species of clade F, the relationships of this species were supported by a single synapomorphy: [32: 2] the falciform epiproct (Fig. 9D).

Figure 1. Phylogenetic relationships of *Paragripopteryx* (green) under IW ($k = 3$); most *Paragripopteryx* nested in a clade, except for *P. munoai*. (A) One tree resulting from the analysis of the complete dataset (31 species, 39 characters); (B) one tree resulting from the analysis of the reduced dataset (24 species, 39 characters). Relative Bremer support in grey below the clades.

The clade E includes all other species of *Paragripopteryx* and was supported by two synapomorphies: [32: 1] the epiproct hook-shaped (tip facing inwards) (Figs. 15E; 18B), and [33: 0] the absence of a row of dorsal denticles in the epiproct (a non-exclusive character state, shared with *Alfonsoperla flinti* and *Rhithroperla rossi*) (Figs. 15E; 18B). *Paragripopteryx hamata* and *P. paranapiacabae* compose a polytomy with the clade G, this last supported by a single synapomorphy: [37: 0] the general shape of distal margin of subgenital plate (male) triangular, tip rounded (a character state shared with *P. merui* and reversed in *P. convexa* **sp. nov.**) (Fig. 5B; Fig. 8B).

The clade G comprises the clade H (*P. blanda*, *P. delicata* and *P. egena*) and the clade I (*P. ogum* **sp. nov.**, *P. dasalmas* **sp. nov.**, *P. anga*, *P. convexa* **sp. nov.**, and *P. kapilei*). Two characters supported the monophyly of the clade H: [12: 1] the nymphs with distal margin of T10 trapezoid shape (Fig. 12G), and [16: 1] the presence of crossveins in RP fork of forewings (fig. 19 in Froehlich, 1969); both characters shared with *Gripopteryx cancellata*. While the relationships in the clade I were based on a single synapomorphy: [27: 1] the central sclerite (extension) in T10 with distal margin bilobed (Fig. 5A) (a non-exclusive character state, shared with *P. merui*, *P. munoai*, *Guaranyperla nitens*, *Tupiperla gracilis* and *Potamoperla myrmidon*). The clade J (*P. dasalmas* **sp. nov.** plus the clade K) was supported by a single synapomorphy: [39: 4] the subgenital plate (female) squared, distal margin notched (a non-exclusive character state, shared with *P. guardae*, *Alfonsoperla flinti*, *Limnoperla jaffueli*, *Potamoperla myrmidon*, *Uncicauda testacea*, *Tupiperla robusta* and *Guaranyperla guapiara*) (Fig. 5D). Finally, two synapomorphies supported the clade K (*P. anga*, *P. kapilei* and *P. convexa* **sp. nov.**): [34: 1] the narrowing (constricted) shape of distal third of the paraprocts in males (a character state shared with *Aubertoperla illiesi*, *Paragripopteryx egena* and the clade D) (Fig. 10C), and [35: 1] the presence of black rod-like setae/bristles (stout setae) in distal region of paraprocts (Fig. 10B–C).

Now, considering the relationships among the *Paragripopteryx* species that resulted from analysis with reduced dataset (Fig. 1B), *P. intervalensis* is also recovered as sister species of all other *Paragripopteryx*, that constitute the clade D. The clade D is composed by clades E and F, and was supported by two synapomorphies: [13: 2] the triangular general shape of paraprocts apex (a non-exclusive character state, shared with *Claudioperla tigrina* and reversed in *P. anga* and *P. blanda*), and [34: 1] the narrowing (constricted) shape of distal third of the paraprocts (a character state shared with *Aubertoperla illiesi* and reversed in *P. blanda* and *P. delicata*).

The clade E (*Paragripopteryx klapaleki* and *P. guardae*) was supported by a single synapomorphy: [32: 2] the epiproct falciform, as well as the clade F was supported by [37: 0] the general shape of distal margin of subgenital plate (male) triangular, tip rounded (a non-exclusive character state, shared with *Tupiperla* spp.).

The clade G is composed by clade H (*Paragripopteryx blanda* and *P. delicata*) and clade I (*P. anga* and *P. kapilei*), and was supported by two synapomorphies: [32: 1] the epiproct hook-shaped (tip facing inwards), and [33: 0] the absence of a row of dorsal denticles in the epiproct (a non-exclusive character state, shared with *Rhithroperla rossi* and *Alfonsoperla flinti*). Finally, the clade H was supported by three synapomorphies: [12: 1] the nymphs with distal margin of T10 trapezoid shape; [16: 1] the presence of crossveins in RP fork of forewings; and [34: 0] the distal third of paraprocts not narrowed (a reversed character state). While a single synapomorphy supported the clade I: [35: 1] the presence of black rod-like setae/bristles (stout setae) on distal region of paraprocts.

Discussion

Positioning of Paragripopteryx munoai and its implications

Benedetto (1969) described *Paragripopteryx munoai* in the genus *Jewettoperla* (= *Jewettoperla munoai* Benedetto, 1969). At the same time as Froehlich (1969) included *Jewettoperla crassila* (Jewett, 1960), the type species of *Jewettoperla*, in *Paragripopteryx*. Then, Zwick (1973) accepted the generic synonymy proposed by Froehlich (1969), and in his catalog transferred *Jewettoperla munoai* Benedetto to the genus *Paragripopteryx* (= *Paragripopteryx munoai* (Benedetto, 1969)). However, at the time, Zwick (personal communication) did not examine the material of *Jewettoperla munoai*, only fulfilled a formal nomenclatural issue.

Here, although our examination of the type series of *Paragripopteryx munoai* reveals some similar characters between this species and the other *Paragripopteryx*, such as the presence of claviform bristles on nymphs (also present in some *Gripopteryx* and *Aubertoperla illiesi*), there are some characters that differentiate *Paragripopteryx munoai* from the other species of *Paragripopteryx*. Beyond the difference in size of nymphs, our examination of all *Paragripopteryx* species and *Paragripopteryx munoai* revealed differences related to shape of mid-distal margin of metanotum. While in all other species of *Paragripopteryx* it is straight-shaped (Fig. 12E), in *Paragripopteryx munoai* it is

bilobated (w-shaped, Fig. 3H). Another constant character in *Paragripopteryx* species, and also in some genera of Gripopteryginae, is the presence of a fringe of long bristles on extensor margins of the femur and tibia. However, this fringe of long bristles are not present in *Paragripopteryx munoai*. In this species there are only small, sparse, almost imperceptible bristles. Additionally, the nymphs of *Paragripopteryx munoai* present setiform, small robust setae, on ventral face of the 3rd tarsal segment (Fig. 3I), similar to those of *Aubertoperla illiesi*; while all other species of *Paragripopteryx* have setiform, small thin setae, almost imperceptible.

Froehlich (1994) also discussed the different egg shapes in *Paragripopteryx* species. While the eggs presenting a simple hemispherical shape are characteristic of *P. munoai*, an elliptical shape in side view, provided by a differentiated chorion is the known pattern present in the congeners (*Paragripopteryx klapaleki*, *P. anga* and *P. blanda*) (Froehlich, 1994).

Related to adult characters, the absence of pterostigmatic crossveins in forewings (Fig. 3C) is a character state shared with some other genera/species of Gripopteryginae. Our examination of the type series of *Paragripopteryx munoai* also showed, in few specimens, the sixth anal vein partially fused to wing margin of hind wings (Fig. 3C). This condition has also been observed in *Aubertoperla illiesi*, but is a character state commonly observed in genera of Antartoperlinae, Dinotoperlinae, and Zelandoperlinae (McLellan, 1977).

Finally, Benedetto (1969) named and drew the T10 in *Paragripopteryx munoai* as “epiproct” (figs. 10–12 in Benedetto, 1969). As suggested by Froehlich (1994) and verified in the type material, an upturned sclerotized epiproct is lacking in this species (Fig. 3F). As regards the Benedetto’s scheme for *P. munoai*, the drawn structure is undoubtedly represented by a T10 extension (central sclerite) ending in two teeth. The T10 in this species is formed by the anterior and central sclerites completely fused to each other, and distally to it for two lateral sclerites separated from the anterior sclerite by a thin membrane (Fig. 3D).

Paragripopteryx munoai remained outside of *Paragripopteryx* delimitation as sister of the clade B (Figs. 1A–B) and sharing with them the presence of denticles/teeth on distal margin of central sclerite. Supported in the above discussion, we understand that *P. munoai* needs a new generic name, for which we propose *McLellanperla* **gen. nov.** (see section Taxonomic Treatment). In the future, it would be interesting to include other

sources of information to complement the morphological analyses, such as molecular and ultrastructural data (SEM), and provide additional support for the current proposal.

Phylogenetic relationships of Paragripopteryx (sensu stricto)

Phylogenetic hypothesis are important tools in understanding relationships between the taxa and the evolution of characters under a resulting topology(ies). Thus, considering a given dataset, we can tell a story about the possible phylogenetic relationships between species. *Paragripopteryx* has a quite confusing taxonomic history, and several synonyms and species combinations precede it (Jewett, 1960; Illies, 1963; Froehlich, 1969). Until now, there is no inference of the relationships on the genus, and in any level the species has been traditionally grouped based on combination of morphological characters (Froehlich, 1969, 1994; Bispo & Lecci, 2011). In the present contribution, our main aim is trying to understand how the phylogenetic relationships between species of *Paragripopteryx* are and, consequently, to check the status of this genus.

The clarification of the relationships in *Paragripopteryx* is not so simple. In the two analyses proposed here, *Paragripopteryx* (clade C; Figs. 1A–B) was supported by a single synapomorphy: the presence of pterostigmatic crossveins in forewings. This character state has been diagnostic for adults of all species of the genus (see section Taxonomic Treatment) and it is also shared with species of *Guaranyperla* and some *Gripopteryx* (Froehlich, 1993, 1994, 2001). However, our analyses showed that several diagnostic morphological characters are not shared among the last two genera and *Paragripopteryx*, such as the presence in *Guaranyperla* of the: 1) vesicular bristles and 2) the paranota in nymphs, and 3) the femoral spine in nymphs and adults (Froehlich, 1969, 1990, 1994, 2001).

Traditionally, the taxonomical studies of the Brazilian Gripopterygidae has treated *Paragripopteryx* as more closely related to *Gripopteryx* (Froehlich, 1990, 1994; Bispo & Lecci, 2011). Froehlich (1990), discussed the main morphological differences between these two genera and pointed the general shape of T10 and epiproct in males, the shape of abdominal terga in nymphs and the shape of eggs as important diagnostic characters in separating this one. In our analyses, we used all these characters discussed by Froehlich (except for the eggs shape) in order to test the close relationships between these two genera. *Paragripopteryx* species were recovered nested in a monophyletic clade with the exclusion of *Paragripopteryx munoai* (= *McLellanperla munoai* **comb. nov.**), while

Gripopteryx cancellata, the type species of *Gripopteryx*, has been recovered at the more inclusive clade A in Gripopteryginae.

According to the dataset analyzed, some internal relationships in *Paragripopteryx* still seem unresolved, as the polytomy among *Paragripopteryx intervalensis* and the clades D and E, when we consider the complete dataset (Fig. 1A). Despite this, some other clades have remained unchanged independently of the analysis, either by varying the dataset or the weighting scheme. This is true for the relationships recovered in the clade F (Fig. 1A), including *P. crassila*, *P. klapaleki* and *P. guardae*, that remained nested in the clade E (Fig. 1B) even with the exclusion of *P. crassila* from the analysis. The same happened for the clade H (Fig. 1A) with *P. blanda*, *P. delicata* and *P. egena*, nested in the clade H (Fig. 1B) even with the exclusion of *P. egena*. Finally, the same for the clade K (Fig. 1A) with *P. anga*, *P. convexa* **sp. nov.** and *P. kapilei*, nested in the clade I (Fig. 1B) even with the exclusion of *P. convexa* **sp. nov.**

Among the species of *Paragripopteryx* currently described, nine have known nymphs (Table 1). As a result, our complete dataset has many missing entries concentrated in characters of the nymphs of some species, an especially problematic approach (Prevosti & Chemisquy, 2010). According to Wiens (2003), the inclusion of many missing characters in phylogenetic analyses is a challenge since it can lead to poorly resolved consensus topologies. When we excluded the seven species of *Paragripopteryx* (without known nymphs), we find a well-resolved topology (Fig. 1B). Thus, our analyses suggest that an important discussion about the data refers to the importance of associations and descriptions of the nymphs of *Paragripopteryx*, since the characters of nymphs are phylogenetically and taxonomically relevant.

Synonymy in Paragripopteryx

In our phylogeny, in general, *Paragripopteryx guardae*, *Paragripopteryx crassila* and *Paragripopteryx klapaleki* form a monophyletic group. Although these three species form a polytomy, it is possible to separate morphologically *P. guardae* from other two species. However, in our examination of the material of *Paragripopteryx crassila* and *Paragripopteryx klapaleki*, we did not find enough characters to maintain the status of these two species as separate from each other. Besides the poor illustrations of *P. crassila* by Jewett (1960), the high-quality photographs sent us by Dr. Christopher Grinter (CAS) revealed a very similar morphological pattern between *P. crassila* and *P. klapaleki*. Thus,

we are proposing the synonymy of the first species with *Paragripopteryx klapaleki* based on morphology of the terminalia and by distributional evidences (see section Taxonomic Treatment).

Considerations

The phylogenetic analyses implemented here constitutes the first effort to understand the relationships among the *Paragripopteryx* species. Obviously, it is not a conclusive study of the genus, it creates the foundations to next steps. Our results encourage a more accurate approach using other sources of information (ultrastructure, molecules, and biogeography) in order to complement the current proposal. Here, in the phylogenetic context *Mclellanperla* **gen. nov.** is proposed to house *Paragripopteryx munoai* (Benedetto). Additionally, we synonymized *P. crassila* under *P. klapaleki*, based on morphological characters of the terminalia. Thus, *Paragripopteryx* now is represented by 15 species (Table 1).

Table 1. Currently valid species of *Paragripopteryx* and their respective records and described stages. Abbreviations: Country - Brazil (BRA), Uruguay (URY); State or Department - Bahia (BA), Espírito Santo (ES), Rio de Janeiro (RJ), Rio Grande do Sul (RS), Santa Catarina (SC), São Paulo (SP), Lavalleya (LAV), Maldonado (MAL); male (♂), female (♀), nymph (N).

<i>Paragripopteryx</i> : BRA (BA, ES, RJ, RS (Nymphs), SC, SP), URY (LAV)						
Nº	Species	Author, year	Papers record	Known life stages		
				♂	♀	N
1	<i>Paragripopteryx anga</i>	Froehlich, 1969	BRA (SP)	•	•	•
2	<i>Paragripopteryx baratinii</i> ^L	Benedetto, 1983	URY (LAV)	•	•	-
3	<i>Paragripopteryx blanda</i>	Froehlich, 1969	BRA (SP)	•	•	•
4	<i>Paragripopteryx delicata</i>	Froehlich, 1994	BRA (SP)	•	•	•*
5	<i>Paragripopteryx egena</i>	Froehlich, 1994	BRA (ES, SP)	•	•	-
6	<i>Paragripopteryx guardae</i>	Froehlich, 1994	BRA (SP)	•	•	•
7	<i>Paragripopteryx hamata</i>	Froehlich, 1994	BRA (SP)	•	•	-
8	<i>Paragripopteryx intervalensis</i> ⁺	Bispo & Lecci, 2011	BRA (ES, MG, SC, SP)	•	•	•*
9	<i>Paragripopteryx kapilei</i> ⁺	Bispo & Lecci, 2011	BRA (SP)	•	-	•
10	<i>Paragripopteryx klapaleki</i>	Enderlein, 1909	BRA (ES, RJ, SP)	•	•	•
11	<i>Paragripopteryx merui</i>	Froehlich, 1994	BRA (SP)	•	-	•*
12	<i>Paragripopteryx paranapiacabae</i>	Bispo & Lecci, 2011	BRA (SP)	•	-	-
New species described here						
13	<i>Paragripopteryx dasalmas</i> sp. nov.	In this paper	BRA (BA)	•	•	-
14	<i>Paragripopteryx convexa</i> sp. nov.	In this paper	BRA (SC)	•	-	-
15	<i>Paragripopteryx ogum</i> sp. nov.	In this paper	BRA (SC)	•	•	-
Synonymy						
	<i>Paragripopteryx crassila</i> ^S	(Jewett, 1960)	BRA (SC)	•	•	-
<i>Mclellanperla</i> gen. nov.						
	<i>Mclellanperla munoai</i> comb. nov.	(Benedetto, 1969)	URY (MAL)	•	•	•

⁺ Nymphs or exuviae described in the current study.

* Description based on last instar exuviae.

^L Lost material.

^S Synonym of *P. klapaleki*.

Distribution

Paragripopteryx occurs along the coastal Brazilian mountains, where 14 species has been recorded from northeast of Bahia State to Rio Grande do Sul State, Brazil, one species being restricted to Uruguay (Fig. 2, blue). *Mclellanperla* **gen. nov.** is restricted to Uruguay (Fig. 2, red).

Figure 2. Map of South America and partial map of Brazil highlighting the records of *Paragripopteryx* (blue) along the Brazilian coastal mountains, from the northeast of Bahia State to the southeast and south of Brazil, reaching the coast of Uruguay where *Mclellanperla gen. nov.* (red) is recorded.

Taxonomic Treatment

Genus *Mclellanperla* gen. nov.

Jewettoperla Benedetto, 1969, Beiträge zur Neotropischen Fauna, 6 (2): 145–151. Figs. 1–13.

Jewettoperla Benedetto, 1970, Limnologica, 7 (2): 383–389. Figs. 2, 4, 5.

Paragripopteryx Zwick, 1973, Das Tierreich, 94: 210. Comb. nov.

Paragripopteryx Froehlich, 2010, Illiesia, 6 (12): 136. Catalog.

Type species: *Mclellanperla munoai* (Benedetto, 1969), **comb. nov.**

Mclellanperla nymphs are slender; the body is covered by spaced claviform bristles; legs are long, flexor margin without femoral spine, extensor margin of femur and tibia lack a row of long hairs; meso and metanotum with mid-distal margin (between wingpads)

bilobated (w-shaped) (Fig. 3H); eggs simple hemispherical shape. The adults are characterized by the almost rounded wings (Fig. 3C); forewings without pterostigmatic crossveins, RA and CuA short fork; hind wings with inferior branch of M3+4 and CuA veins may be long forked (Fig. 3C). Male terminalia lack an upturned sclerotized epiproct.

Etymology. The specific name “*McLellanperla*” honors Prof. Dr. Ian D. McLellan, Auckland, New Zealand, for his numerous contributions to aquatic entomology, especially on the taxonomy of Plecoptera.

***McLellanperla munoai* (Benedetto, 1969), comb. nov.**

(Figs. 3A–J)

Jewettoperla munoai Benedetto, 1969, Beiträge zur Neotropischen Fauna, 6 (2): 145–151. ♂, ♀, nymphs, figs. 1–13.

Jewettoperla munoai Benedetto, 1970, Limnologica, Berlin, 7 (2): 383–389. Figs. 2, 4, 5.

Paragripopteryx munoai Zwick, 1973, Das Tierreich 94: 210. Comb. nov.

Paragripopteryx munoai Froehlich, 2010, Illiesia, 6 (12): 136. Catalog.

Type locality: Uruguay, Department of Maldonado, Cerro de las Animas.

Material examined: Holotype, male: Uruguay, Maldonado, Cerro de las Animas, 27.vii.1967, LCZ, EV, TR, FA, LB. Allotype, same data as holotype, except for: 1 female. Paratypes, same data as holotype, except for: 3 males, 3 females, 8 nymphs.

Redescription: *McLellanperla munoai* **comb. nov.** is a medium sized species of the genus. General color brown to dark brown. Head dark brown with a lighter-brown area between paired ocelli and coronal bifurcation, and two lighter brown bands from the lateral ocelli to the eyes; parietalia rough (Figs. 3A–B). Three ocelli and compound eyes black. Antennae brown. Labrum brown. Maxillary palps brown, 5-segmented; first, second and fourth segments short, third and fifth longer. Labial palps brown, 3-segmented. Thorax dark brown; pronotum rough, squared and with rounded corners; wings membranous, rounded shape; forewings slightly tinged with light brown, no pterostigmatic crossveins, RA unforked, RP and CuA forked (Fig. 3C); hind wing with M3+4, near its separation from M1+2, fused with CuA, its separate after the wing margin (fork may be short or long) (Fig. 3C); 6th anal vein fused with hind margin of wing (Fig. 3C), sometime not fused. Legs dark brown; tibia with a perpendicular suture in the proximal region and two

spurs at the distal region. Tarsi brown, tarsomere 1 medium, tarsomere 2 short and tarsomere 3 long. Cerci multisegmented, cercomeres covering by thin bristles.

Male. Abdomen dark brown, membranous pleura among the abdominal segments 2–9. In dorsal view, T10 dark brown, lateral sclerites separated from the anterior sclerite by a thin membrane; T10 extension short, with distal border M-shaped ending in two teeth (Fig. 3D). In ventral view, subgenital plate dark brown, robust and with rounded distal margin (Fig. 3E); paraprocts thin, directed to the T10 extension, epiproct absent. In lateral view, paraprocts dark brown, with four sharply angulated lobes, apex rounded (Fig. 3F).

Female. Abdomen brown with a pair of lateral and anterior spots dark brown; segments 9–10 forming complete rings. In dorsal view, T10 brown and with apex rounded. In ventral view, subgenital plate brown, produced posteriorly in a M-shaped, covering the gonopore (figs. 8–9 in Benedetto, 1969); paraprocts brown, covering by thin bristles and with apex rounded.

Nymphs. General color brown; head brown, antennae with scape and pedicel brown, flagellum light brown (Figs. G–H). Thorax brown and covered with spaced claviform bristles; pronotum rough, with margins slightly rounded; wing pads brown, distal margin between wing pads bilobated (w-shaped) (Fig. 3H). Femora thin, with some stouter short bristles. Tarsi with setiform, small robust setae in the ventral face (Fig. 3I). Abdominal terga dark brown, segments 2–7 separated by membranous pleura; segments 8–10 forming complete rings; distal margin of T10 rounded, with numerous stouter short bristles. Cerci brown. Gills light brown. Paraprocts robust, apex rounded.

Remarks: For taxonomy, see the subsection *Positioning of Paragripopteryx munoai and its implications* in the previous section Discussion.

Figure 3. *Mclellanperla munoai* (Benedetto, 1969) **comb. nov.** Adult male, head and pronotum in dorsal view (A). Paratype adult female, head and pronotum in dorsal view (B). Male, fore and hind wings (C). Male, terminalia in dorsal (D), ventral (E) and lateral views (F). Nymph, head and pronotum (G), meso- and metanotum in dorsal views (H), and detail of tarsi (I).

Genus *Paragripopteryx* Enderlein, 1909

Paragripopteryx Enderlein, 1909, Zoologischer Anzeiger, 34: 416. Type of the genus: *Paragripopteryx klapaleki* Enderlein, 1909 = *Gripopteryx cancellata* Klapálek, 1904 (nec Pictet, 1841), by original designation and monotype.

Gripopteryx Jewett, 1960, Arquivos do Museu Nacional, Rio de Janeiro, 50: 167–180. Synonymy.

Paragripopteryx Illies, 1963, Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 36: 178. Revalidates.

Jewettoperla Illies, 1963, Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 36: 184. Type of the genus: *Gripopteryx crassila* Jewett, 1960, by original designation. Synon. nov.

Paragripopteryx Froehlich, 1969, Studies on Neotropical Fauna and Environment, 6 (1): 17–39 (in Illies, 1966 after the manuscript in detail under Froehlich, 1964 included in the catalog).

Paragripopteryx Zwick, 1973, Das Tierreich, 94: 210. Comb. nov.

Paragripopteryx Froehlich, 1994, Aquatic Insects, 16 (4): 227–239. New species.

Paragripopteryx Bispo & Lecci, 2011, Annales de Limnologie - International Journal of Limnology, 47: 376–379. New species.

The genus *Paragripopteryx* is phylogenetically supported by the presence of pterostigmatic crossveins in forewings. Additional characters have been important as diagnostic for the genus: nymphs with body compact, pronotum narrower than head, short legs without femoral spine, dorsal row of long hairs and claviform hairs along femur and tibia can be present; no abdominal or thoracic spines (Bispo & Lecci, 2011). Male adults present a T10 extension that ends in two denticles/teeth; the latero-dorsal clefts are small or inconspicuous; the epiproct is compressed, thin and with apical point directed forward (absent in *P. ogum* **sp. nov.** and *P. egena*) (Froehlich, 1969, 1990, 1994); hind wings with inferior branch of M vein partially fused to CuA, and separating from it near the wing margin.

***Paragripopteryx dasalmas* sp. nov.**

(Figs. 4A–C, Figs. 5A–D)

Type material. Holotype, male: Brazil, Bahia, Wenceslau Guimarães, EEWG, Serra Grande Stream, waterfall, S13°35'34", W39°42'52", 10.x.2010, light pan trap, A.R. Calor, T. Duarte & E.S. Dias. Paratypes: same data as holotype, except for: 1 male, 1 female; same data, except for: 09.x.2010, 1 male, 4 females; same data, except for: 06.ix.2013, 1 female; same data, except for: 07.ix.2013, 2 males, 2 females; same data, except for: 06.ix.2013, light trap near the headquarter, 1 female; same data, except for: waterfall, S13°35'35.4", W39°42'51.2", 513m, 06.ix.2013, 1 female; same data, except for: 07.ix.2013, 1 female; same data, except for: 08.ix.2013, 1 male, 11 females; same data,

except for: 08.ix.2013, 1 male, 1 female; same data, except for: Patioba River, S13°34'50", W39°42'17", 09.x.2010, light pan trap, 2 females.

Measurements. Holotype, male: head width, 0.74 mm; pronotum width, 0.7 mm; pronotum length, 0.6 mm; forewing length, 6.6 mm; hind wing length, 5.2 mm; antennae length, 6.4 mm; 16 cercomeres; paratypes: males (n= 7): head width, 0.65–0.8 mm; pronotum width, 0.64–0.75 mm; pronotum length, 0.55–0.63 mm; forewing length, 6.4–6.9 mm; hind wing length, 5.4–5.8 mm; antennae length, 5–7.1 mm (incomplete in some specimens, maximum length 7.1 mm); 17–18 cercomeres; females (n= 25): head width, 0.8–0.83 mm; pronotum width, 0.76–0.77 mm; pronotum length, 0.55–0.7 mm; forewing length, 7.6–7.8 mm; hind wing length, 6.5–7 mm; antennae length, 7.85–7.95 mm; 18 cercomeres.

Description. *Paragripopteryx dasalmas* **sp. nov.** is a medium sized species. General color brown. Head brown with a lighter-brown area between paired ocelli and coronal bifurcation, parietalia rough (Figs. 4A–B). Ocelli and eyes black. Labrum light brown. Maxillary palps light brown, 5-segmented; first and fourth segments short, second, third and fifth longer. Labial palps light brown, 3-segmented. Antennae brown. Pronotum brown, squared with rounded edges and narrower than the head. Legs brown. Tibia with a perpendicular suture in the proximal region and two spurs at the distal region. Tarsi brown, legs with tarsomere 1 medium, tarsomere 2 short and tarsomere 3 long. Forewing membranous brown with darker patterns bordering veins and crossveins, 1–2 pterostigmatic crossveins present, RA unforked, RP and CuA forked. Hind wing with M3+4, near its separation from M1+2, fused with CuA in part of its length, CuA short forked, 6th anal vein fused with hind margin of wing (Fig. 4C).

Male. Abdomen brown with slightly clear band on abdominal terga 1–9. In dorsal view, T10 dark brown and with a proximal triangular clear band; T10 extension medium length, with distal border M-shaped ending in two teeth (Fig. 5A). In ventral view, subgenital plate brown with rounded base, distal margin triangular, tip slightly rounded (Fig. 5B); paraprocts thin, directed to the T10 extension and with clear area on the base; epiproct present and dark. In lateral view, paraprocts thick throughout its length; base covering by setae, apex with ventral curvature, dorsal margin straight, tip triangular (Fig. 5C); epiproct hook or sickle-shaped without denticles in dorsal margin and with pointed apex (Fig. 5C).

Female. Abdominal terga 1–9 light brown and mostly membranous. T10 brown and with apex rounded. St7 with two small, conspicuous spots. Subgenital plate squared and with

rounded corners; central area unpigmented; paraprocts small, covering by setae, and with apex truncated (Fig. 5D).

Nymphs. unknown.

Figure 4. *Paragripopteryx dasalmas* **sp. nov.** Holotype adult male, head and pronotum in dorsal view (A). Adult female, head and pronotum in dorsal view (B). Male Fore and hind wing (C). Scale bar: 0.5 mm. (Abbreviations: AA1, first anterior Analis; AA2, second anterior Analis; CuA, anterior cubitus; CuP, posterior cubitus; M, Media; PC, Pterostigmatic cell; RA, anterior Radius; RP, posterior Radius; Sc, Subcosta).

Remarks. *Paragripopteryx dasalmas* **sp. nov.** is the first species of the genus described and formally recorded for the Brazilian Northeastern. Silva & Hamada (2007) recorded only nymphs of *Paragripopteryx* sp. in the mountains of the Chapada Diamantina

National Park, in the central region of Bahia State. Duarte *et al.* (2014) also provided records of nymphs for the Serra Bonita Reserve, in the south of Bahia. However, none of the above-mentioned studies reached specific identification of the specimens. In the present study, we described *P. dasalmas* **sp. nov.** based on male and female specimens collected in Ecological Station of Wenceslau Guimarães, municipality of Wenceslau Guimarães, Bahia State. The species can be distinguished from the congeners by the shape of T10 and paraprocts in males. The T10 extension in males of *P. dasalmas* **sp. nov.** resembles in part to that of *P. merui* Froehlich, 1994; however, in *P. merui* this structure is wider and curved, while in *P. dasalmas* **sp. nov.** it is narrower and straight, ending in a pointed apex (Fig. 5A). The paraprocts in *P. dasalmas* **sp. nov.** are thick throughout its length, the apex has the dorsal margin angulated (Fig. 5C), while those of *P. merui* are narrow next to the apex, ending in a subapical tooth. The epiproct of two species are much different, *P. dasalmas* **sp. nov.** has a sickle-shaped epiproct without teeth on the inner margin, and the apex is pointed (Fig. 5C), while in *P. merui* the epiproct is long, provided with two rows of teeth on the inner margin. Additionally, *P. dasalmas* **sp. nov.** is darker than *P. merui*.

Etymology. The epithet “*dasalmas*” refers to the Das Almas River (Rio das Almas), municipality of Wenceslau Guimarães in Bahia State, Brazil.

Figure 5. *Paragripopteryx dasalmas* sp. nov. Holotype adult male terminalia in dorsal (A), ventral (B), and lateral views (C). Female terminalia in ventral view (D). Scale bar: 0.5 mm (A, B); 0.4 mm (C, D).

***Paragripopteryx convexa* sp. nov.**

(Figs. 6A–E)

Type material. Holotype, male: Brazil, Santa Catarina, Urubici, Serra do Panelão, 12.ix.2016, S27°54'04", W49°34'50", Pinho & Amaral, 1 male.

Measurements. Holotype, male: head width, 1.1 mm; pronotum width, 1.01 mm; pronotum length, 0.76 mm; forewing length, 7.9 mm; hind wing length, 6.8 mm; number of cercomeres, 16.

Description. *Paragripopteryx convexa* **sp. nov.** is a medium size species. General color brown. Head brown, ocelli and eyes black (Fig. 6A). Labrum light brown. Maxillary palps light brown, 5-segmented; first and fourth segments short, second, third and fifth longer. Labial palps light brown, 3-segmented. Antennae light brown. Pronotum light brown to brown; squarish with anterior margin rounded. Legs brown. Tibia with a perpendicular suture in the proximal region and with two spurs at the distal region. Tarsi brown, legs with tarsomere 1 medium, tarsomere 2 short and tarsomere 3 long. Forewing membranous with darker patterns bordering veins and crossveins weak; pterostigmatic crossveins present; RA unforked, RP and CuA forked. Hind wing with M3+4, near its separation from M1+2, fused with CuA in part of its length, CuA short forked, 6th anal vein fused with hind margin of wing (Fig. 6B).

Male. Abdomen light brown with brown band on distal margin of abdominal terga 1–9. In dorsal view, T10 brown, lateral region darker, latero-distal region with inconspicuous lateral clefts on each side (like a cleft, but not open); T10 extension medium length, base slightly constricted, latero-distal margin convex (curved), distal margin darker and forked, ending in two teeth (Fig. 6C). In ventral view, subgenital plate brown, ovoid (Fig. 6D); paraprocts thin. In lateral view, paraprocts elongated, mid-ventral region thick, ventral margin with a not sclerotized area, dorsal (inner) margin slightly curved (except for a dorsal membranous protuberance), ascending parts narrower but continuous, ends rounded (Fig. 6E); distal region provided with black rod-like setae (Fig. 6E); epiproct present, hook-shaped.

Female and nymphs. Unknown.

Remarks. *Paragripopteryx convexa* **sp. nov.** is based on a single male specimen collected in municipality of Urubici, Santa Catarina State. *Paragripopteryx convexa* **sp. nov.** has some characters resembling, in part, those of males of *P. anga* Froehlich, 1969 and *P. kapilei* Bispo & Lecci, 2011. In the phylogenetic analyses, *P. convexa* **sp. nov.** is closely related to these two species. However, the species can be distinguished from *P. anga* and *P. kapilei* by the curved shape of the latero-distal margin of T10 extension (Fig. 6C), while in *P. anga* is spatulate-shaped (fig. 12 in Froehlich, 1969), and in *P. kapilei* is elongated (like two finger-shaped processes, fig. 5 in Bispo & Lecci, 2011). The general shape of the paraprocts in both *P. convexa* **sp. nov.** and *P. anga* are more similar to each other than to *P. kapilei*. In *Paragripopteryx convexa* **sp. nov.** the ascending parts of paraprocts are narrow but continuous (Fig. 6E), while in *P. anga* there is a slightly strangled distal region (fig. 14 in Froehlich, 1969).

Etymology. The name “*convexa*” from Latin *convexus* “vaulted, arched”, curved like a circle or sphere when viewed from outside. Here, the name is a reference to the shape of latero-distal margin of T10 extension. The name is in apposition.

Figure 6. *Paragripopteryx convexa* **sp. nov.** Holotype adult male, head and pronotum in dorsal view (A). Male, fore and hind wings (B). Male, terminalia in dorsal (C), ventral (D) and lateral views (E).

***Paragripopteryx ogum* sp. nov.**

(Figs. 7A–C; Figs. 8A–D)

Type material. **Holotype, male:** Brazil, Santa Catarina, Orleans, Rio Minador, #72, S28°10'24"; W46°24'37", 12.x–10.xi.2013, Malaise, L.C. Pinho *et al.* Paratype: same data as holotype, except for: 1 female.

Measurements. Holotype, male: head width, 0.83 mm; pronotum width, 0.65 mm; pronotum length, 0.52 mm; forewing length, 6.8 mm; hind wing length, 5.7 mm; number of cercomeres, 16; Paratype: female (n= 1): head width, 0.88 mm; pronotum width, 0.73

mm; pronotum length, 0.53 mm; forewing length, 7.4 mm; hind wing length, 6.4 mm; number of cercomeres, 15.

Figure 7. *Paragripopteryx ogum* **sp. nov.** Holotype adult male, head and pronotum in dorsal view (A). Female, head and pronotum in dorsal view (B). Male, fore and hind wings (C). Scale bar: 0.5 mm.

Description. *Paragripopteryx ogum* **sp. nov.** is a medium sized species. General color light brown to yellowish. Head brown with a lighter-brown area between paired ocelli

and coronal bifurcation (Fig. 7A). Ocelli and eyes black. Labrum light brown. Maxillary palps light brown, 5-segmented; first and fourth segments short, second, third and fifth longer. Labial palps light brown, 3-segmented. Antennae brown. Pronotum brown, rough and squarish with subparallel margins (Fig. 7A). Legs brown. Tibia with a perpendicular suture in the proximal region and with two spurs at the distal region. Tarsi brown, legs with tarsomere 1 medium, tarsomere 2 short and tarsomere 3 long. Forewing membranous with darker patterns bordering veins and crossveins weak; pterostigmatic cell with white patches between pterostigmatic crossveins; RA unforked, RP and CuA forked (Fig. 7C). Hind wing with M3+4, near its separation from M1+2, fused with CuA in part of its length, CuA short forked, 6th anal vein fused with hind margin of wing (Fig. 7C).

Male. Abdomen light brown to ochraceous. In dorsal view, T10 light brown with a proximal clear band M-shaped; T10 extension long, with distal border M-shaped, darker and ending in two small teeth (Fig. 8A). In ventral view, subgenital plate ochraceous, apex rounded (Fig. 8B). In lateral view, paraprocts sword-shaped, ventrally curved, apex broader (Fig. 8C). Epiproct absent.

Female. Abdominal terga 1–9 light brown and mostly membranous. T10 light brown and with apex rounded. Subgenital plate squared and with rounded corners; central area unpigmented; paraprocts small, covering by setae, and with rounded apex (Fig. 8D).

Nymphs. Unknown.

Remarks. We are describing *Paragripopteryx ogum* **sp. nov.** based on a male and a female specimen collected in municipality of Orleans, Santa Catarina State. The T10 in *P. ogum* **sp. nov.** resembles, in part, that of male of *P. merui* Froehlich, 1994. However, the shape of paraprocts distinguished these two species. In *Paragripopteryx ogum* **sp. nov.** the distal third of paraprocts are broader (Fig. 8C), while in *P. merui* are narrowed.

Etymology. The specific name refers to the shape of male paraprocts that resembles the shortest form of the sword of the Orisha Ogum (Yoruba: Ògún, Portuguese: Ogum). In African traditions, Ogum is considered the great warrior, the first Orisha to descend into the realm of *Ile Aiye* ("Earth"), opening the way. The name is in apposition.

Figure 8. *Paragripopteryx ogum* sp. nov. Holotype adult male, terminalia in dorsal (A), ventral (B) and lateral views (C). Female, terminalia in ventral view (D).

***Paragripopteryx klapaleki* Enderlein, 1909**

(Figs. 9A–F)

Gripopteryx cancellata Klapálek, 1904 (nec Pictet, 1841), Ergebnisse der Hamburger Magalhaensischen Sammelreise, 7 (5): 8–9. ♂, figs. 3–5.

Paragripopteryx klapaleki Enderlein, 1909, Zoologischer Anzeiger, 34: 416. (Type: *Gripopteryx cancellata* Klapálek, 1904, Petrópolis, R.J., Brazil; probably lost, cf. Jewett, 1960: 170)

Gripopteryx klapaleki Jewett, 1960, Arquivos do Museu Nacional (Rio de Janeiro), 170. Notes.

Paragripopteryx klapaleki Froehlich, 1969, Studies on Neotropical Fauna and Environment, 6 (1): 19. ♂, ♀, nymphs, figs. 1–10.

Paragripopteryx klapaleki Froehlich, 1994, Aquatic Insects, 16 (4): 228. Review.

Paragripopteryx klapaleki Froehlich, 2010, Illiesia, 6 (12): 136. Catalog.

Paragripopteryx klapaleki Gonçalves *et al.*, 2017, Zootaxa, 4291 (3): 570. New record.

Type locality: Brazil, Rio de Janeiro, Petrópolis.

Material examined: Brazil, São Paulo, Biological Station at Paranapiacaba: Adults collected – 6.viii.63, 1 female (at light); same data, except for: 27.viii.63, 3 females; same data, except for: 5.xi.63, 2 females; same data, except for: 27.xi.63, 2 males, 2 females; same data, except for: 13.xii.63, 3 females (2 at light); same data, except for: 27.iii.64, 2 males, 1 female; same data, except for: 23.iv.64, 1 male; same data, except for: 20.v.64, 1 female; Adults emerged in the laboratory – 1962: viii, 1 male; ix, 1 female; 1963: iv, 1 male; vii, 3 males, 5 females; viii, 3 females; ix, 3 females; x, 1 male, females; 1964: vi, 2 males, 1 female; total, 8 males, 19 females. Cast exuviae (last nymphal instar) – 19.vii.63, 2 females; 15.x.63, 1 male, 2 females; 23.iv.64, 1 female; 20.v.64, 1 male, 1 female.

Diagnosis: *Paragripopteryx klapaleki* is a generally brown to dark brown species. Forewings of male with pterostigmatic crossvein (in some males it may be weak) (Figs. 9A–B). Male T10 extension forms a small process ending in two denticles close together (Figs. 9C, E). Male paraprocts elongated, narrow and almost straight, apical region narrower, ends rounded (Figs. 9D, F). Male epiproct bends upward, almost falciform (Fig. 9D). Female subgenital plate with a sclerotized band on each side and a central area not sclerotized. Female paraprocts pointed. Nymphs body hairs mostly short, claviform (fig. 8 in Froehlich, 1969). Dorsal row of long bristles of femora and tibia not thick; in tibia, accompanying row of long hairs, another of claviform ones (Froehlich, 1969).

Remarks: Enderlein (1909), described *Paragripopteryx klapaleki* after reviewing a single male specimen from the Zoological Museum of Helsinki (Finland) for that time classified as *Gripopteryx cancellata* Pictet by Klapálek (1904) (Froehlich, 1969). Later, Jewett (1960) discussed the status of *Paragripopteryx klapaleki* and combined it in *Gripopteryx* (= *Gripopteryx klapaleki*). Illies (1963) reinstated *Paragripopteryx* and allocated *Gripopteryx klapaleki* as a type species of the genus (*G. klapaleki* as a synonym of *P. gracilis* = *Semblis gracilis* Burmeister, 1839). Then, Froehlich (1969) revalidated *P. klapaleki* and redescribed the male and described the female and nymphs of this species and created *Tupiperla* for *P. gracilis* (= *T. gracilis*).

On the other hand, Jewett (1960) originally described *Paragripopteryx crassila* in the genus *Gripopteryx* (= *Gripopteryx crassila* Jewett, 1960) and based his description on a single male holotype and a female allotype from Nova Teutônia, Santa Catarina State, Brazil. So far, these are the only two known specimens of this species. Posteriorly, Illies (1963), created the genus *Jewettoperla* to include *Gripopteryx crassila* (= *Jewettoperla crassila* (Jewett, 1960)), the type of the genus, and Froehlich (1969) considered *Jewettoperla* as a synonym of *Paragripopteryx*.

We analyzed the material of *P. klapaleki* and compared it with the photos of *P. crassila* sent us by Dr. Christopher Grinter (CAS). We concluded that the terminalia of these two species are morphologically very similar. As regards to the general shape of T10 and paraprocts, the two species have a great similarity (Figs. 9C–F). In the original paper, Jewett (1960) described the paraprocts of *P. crassila* as a “pair of large subanal lobes that curve evenly upwards extend from median, posterior area”, while Froehlich (1969) redescribed the paraprocts of *P. klapaleki* as “long, almost straight in ascending part, apical part narrow, end rounded”. The analyses of fig. 3a in Froehlich (1969), the specimens of *P. klapaleki* and the photographs of *P. crassila* leave no doubts about the very similar morphology of these two nominal species.

In our phylogenetic analyses we found *P. crassila*, *P. klapaleki* and *P. guardae* in a polytomy supported by the falciform epiproct. However, *P. guardae* can be differentiated from the *P. crassila* and *P. klapaleki* by the shapes of T10, paraprocts and subgenital plate in males and by the subgenital plate in females.

Paragripopteryx klapaleki, originally described from Petrópolis, Rio de Janeiro State, Brazil, have been recorded in the border between Minas Gerais and Espírito Santo states (Gonçalves *et al.*, 2017), São Paulo State (Froehlich, 1969; Bispo & Lecci, 2011; Gonçalves *et al.*, 2017) and Santa Catarina State (material determined by Froehlich in

MZSP), in the same locality of *P. crassila*. In this contribution, considering the innumerable morphological evidences, we are proposing the synonymy of *P. crassila* with *P. klapaleki*. We are providing photos of the male wings and terminalia (Figs. 9A–F).

Figure 9. *Paragripopteryx klapaleki*, adult male, fore and hind wings (A). *Paragripopteryx crassila*, body and detail of the forewing left (B). *Paragripopteryx klapaleki*, male, terminalia in dorsal (C) and lateral views (D). *Paragripopteryx crassila*, male, terminalia in dorsal (E) and lateral views (F).

***Paragripopteryx anga* Froehlich, 1969**

(Figs. 10A–C)

Paragripopteryx anga Froehlich, 1969, Studies on Neotropical Fauna and Environment, 6 (1): 23. ♂, ♀, nymphs, figs. 11–18, 35.

Paragripopteryx anga Froehlich, 1994, Aquatic Insects, 16 (4): 228. Review.

Paragripopteryx anga Froehlich, 2010, Illiesia, 6 (12): 135. Catalog.

Paragripopteryx anga Bispo & Lecci, 2011, Annales de Limnologie - International Journal of Limnology, 47: 376–377.

Type locality: South America, Brazil, São Paulo, Paranapiacaba Biological Station.

Material examined: Holotype, male: Biological Station at Paranapiacaba, São Paulo, Brazil, 27.iii.1964. Allotype, female: same data as holotype, except for: 28.viii.1963. Paratypes: adults – same data, except for: 30.viii.62, 1 female; same data, except for: 12.iv.63, 1 male, 2 females; same data, except for: 5.vii.63, 1 male, 1 female; same data, except for: 19.vii.63, 1 male (at light); same data, except for: 6.viii.63, 3 male, 1 female; same data, except for: 27.viii.63, 3 males, 2 females (1 female at light); same data, except for: 17.ix.63, 1 male, 3 females; same data, except for: 15.x.63, 2 males, 1 female; same data, except for: 5.xi.63, 1 female; same data, except for: 27.xi.63, 1 male, 2 females; same data, except for: 28.xii.63, 2 males, 3 females; same data, except for: 17.i.64, 1 female; same data, except for: 27.iii.64, 1 male, 1 female; same data, except for: 23.iv.64, 1 male. Adults emerged in the laboratory – 1962: viii, 1 male, 1 female; ix, 3 males, 6 females; 1963: iv, 1 male, 1 female; v, 2 females; vii, 9 males, 5 females; viii, 10 males, 10 females; ix, 9 males, 22 females; x, 8 males, 8 females; xi, 3 males, 6 females; 1964: v, 1 female; vi, males, 4 females. Cast exuviae (last nymphal instar) – same data, except for: 23.vii.62, 1 male, 1 female; same data, except for: 12.iv.63, 1 female; same data, except for: 19.vii.63, 1 female; same data, except for: 27.viii.63, 2 males, 1 female; same data, except for: 15.x.63, 3 males, 2 females; same data, except for: 5.xi.63, 1 male; same data, except for: 27.xi.63, 3 females; same data, except for: 13.xii.63, 1 female; same data, except for: 17.i.64, 1 male; same data, except for: 27.iii.64, 1 male, 3 females; same data, except for: 23.iv.64, 1 female; same data, except for: 20.v.64, 2 males, 4 females; same data, except for: 10.vi.64, 2 females.

Diagnosis: *Paragripopteryx anga* is a generally brownish to ochraceous species (grey to brownish grey in life, Froehlich, 1969) (Fig. 10A). Forewing with pterostigmatic crossveins (fig. 11 in Froehlich, 1969); between RA-RP and M a light line present in both wings, inconspicuous in clear specimens. Male T10 extension spatulate, ending with two denticles separated by a rounded incision (Fig. 10B; fig. 12 in Froehlich, 1969). Male paraprocts elongated, thick basally, ascending parts narrower, ends rounded; distal region provided with black rod-like setae (Fig. 10C). Epiproct hook-shaped (Fig. 10C; fig. 14 in Froehlich, 1969). Female subgenital plate incised in distal edge, median area lighter (fig.

15 in Froehlich, 1969); paraprocts triangular, pointed. Nymphs with a dorsal row of bristles not dense on legs; tibia with both claviform and simple hairs (Froehlich, 1969). Nymphs without a light area in front of fork of epicranial suture; on T10, absence of dark spots and presence of two pairs of light spots, one of these at posterior margin of T10, or the spots on same side may join (fig. 18a–b in Froehlich, 1969).

Figure 10. *Paragripopteryx anga*, Paratype adult male, head and pronotum in dorsal view (A). Male, terminalia in dorsal (B) and lateral views (C).

Remarks: The male holotype of *Paragripopteryx anga* is in a good state of conservation, except for the thorax segments, crushed. It is possible to observe the main characters of holotype terminalia. The description of *P. anga* by Froehlich (1969) is well detailed and based on several males, females and nymphs collected in Paranapiacaba Biological Station, São Paulo State, Brazil. Froehlich provided figures of female wings, male and female terminalia, and the mouthparts, T10, and egg of nymphs (figs. 11–18, 35 in Froehlich, 1969). Froehlich (1969) also discussed the light spots pattern on T10 of advanced nymphs in this species. Froehlich compared *P. anga* with *P. klapaleki* and *P. blanda*, the only *Paragripopteryx* species described at the time. *Paragripopteryx anga* is distinguished from other species of the genus by male T10 extension spatulate and by the incised subgenital plate of the females. The general shape of the male paraprocts of *P. anga* resembles those of *P. kapilei* and *P. convexa* **sp. nov.**, which have the black rod-like setae in its distal region (Figs. 10B–C). However, it can be distinguished from this species by the spatulate shape of T10 extension (Fig. 10B).

***Paragripopteryx baratinii* Benedetto, 1983**

Paragripopteryx baratinii Benedetto, 1983, Studies on Neotropical Fauna and Environment, 18 (1): 19–23. ♂, ♀, figs. 1–7.

Paragripopteryx baratinii Froehlich, 2010, Illiesia, 6 (12): 135. Catalog.

Type locality: Uruguay, Department of Lavalleja, Aguas Blancas.

Remarks: Benedetto (1983) described *Paragripopteryx baratinii* based on three male specimens (one holotype and two paratypes) and a female paratype deposited at “Universidad de la República”, Uruguay (figs. 1–7 in Benedetto, 1983). A visit to this institution was held in order to examine the type of *P. baratinii*; however, the material was not found. Benedetto (1983), mentioned two male paratypes housed in the collection of the Limnological Station of the Max-Planck Institute, Schlitz, Germany. We contacted Dr. Peter Zwick (personal communication), former director of the station, who inform us that the material of *P. baratinii* never been in the in Max-Planck Institute collection. This situation leads us to conclude that the type series of *P. baratinii* is lost. We have some reasons to suspect that *P. baratinii* is not part of *Paragripopteryx*. As highlighted by Froehlich (1994), in the figures of *P. baratinii* by Benedetto there seems to be a posterior sclerite in the T10, a character uncommon in *Paragripopteryx* and other Gripopteryginae. Despite of this, we are maintaining *P. baratinii* in *Paragripopteryx* in the hope of collecting and examining this species in the future.

***Paragripopteryx blanda* Froehlich, 1969**

(Figs. 11A–D)

Paragripopteryx blanda Froehlich, 1969, Studies on Neotropical Fauna and Environment, 6 (1): 26–27. ♂, ♀, nymphs, figs. 19–25.

Paragripopteryx blanda Froehlich, 1994, Aquatic Insects, 16 (4): 228. Review.

Paragripopteryx blanda Froehlich, 2010, Illiesia, 6 (12): 135. Catalog.

Paragripopteryx blanda Bispo & Froehlich, 2011, Annales de Limnologie - International Journal of Limnology, 47: 377. New record.

Type locality: Brazil, São Paulo, Paranapiacaba Biological Station.

Material examined: Holotype, male: Biological Station at Paranapiacaba, São Paulo, Brazil, 17.ix.1963. Allotype, female: same data as holotype, except for: 27.iii.1964.

Paratypes: adults collected – same data, except for: 9.viii.62, 1 female; same data, except for: 30.viii.62, 1 female; same data, except for: 6.viii.63, 1 male (at light); same data, except for: 17.ix.63, 2 males; same data, except for: 15.x.63, 1 male; same data, except for: 27.xi.63, 2 males, 1 female; same data, except for: 13.xii.63, 1 male (at light), 1 female; same data, except for: 28.xii.63, 1 female; same data, except for: 17.i.64, 2 males, 1 female; same data, except for: 29.ii.64, 1 male; same data, except for: 27.iii.64, 1 male, 2 females; same data, except for: 23.iv.64, 1 female; same data, except for: 20.v.64, 1 male, 2 females. Adults emerged in the laboratory – 1963: iv, 1 female; vii, 1 male, 2 females; viii, 1 male, 1 female; x, 2 males; 1964: v, 1 male, 1 female; total, 5 males, 5 females. Cast exuviae (last nymphal instar) – same data, except for: 19.vii.63, 2 females; same data, except for: 5.xi.63, 1 female; same data, except for: 27.xi.63, 1 male; same data, except for: 13.xii.63, 1 male, 1 female; same data, except for: 28.xii.63, 1 female; same data, except for: 17.i.64, 1 male; same data, except for: 27.iii.64, 1 male, 1 female; same data, except for: 23.iv.64, 1 male, 1 female. **Brazil, Santa Catarina**, Serra Furada, 1 male.

Diagnosis: *Paragripopteryx blanda* is a generally dark brown species (dark brownish-grey in life, Froehlich, 1969) (Fig. 11A). Forewing with pterostigmatic crossveins (fig. 19 in Froehlich, 1969), sometimes bordered by darker spots; pterostigmatic cell occasionally violet; between RA-RP and M a light line present in both wings. Male T10 extension similar in part to those of *P. klapaleki*, *P. crassila* and *P. egena* (Fig. 11B). Male paraprocts are robust in basal half, narrowing towards apex, ending in a sharp point (Fig. 11C). Epiproct hook-shaped, without denticles. Female subgenital plate rounded; apex of paraprocts truncated (fig. 23b in Froehlich, 1969). Nymphs with a dorsal row of long hairs of femora and tibia dense (Fig. 11D); paraprocts with rounded apex, except for males, with an apical process (fig. 24 in Froehlich, 1969).

Remarks: Froehlich (1969) described male, female and nymphs of *Paragripopteryx blanda* from Paranapiacaba Biological Station, São Paulo, Brazil. We examined the type material of this species, which is in a good state of conservation. We are providing a new material of male collected in Serra Furada State Park (PAESF, Santa Catarina, Brazil). The description of *Paragripopteryx blanda* by Froehlich is complete, with figures of male wings, male and female terminalia, and mouthparts and T10 of nymphs (figs. 11–25 in Froehlich, 1969). Froehlich compared the male of this species, at the time, with the male of *P. klapaleki*. In our examination, we find a more pronounced similarity between the T10 in *P. blanda* and *P. egena*, except for the conspicuous lateral sclerite in it latter.

Additionally, these two species can be distinguished by the distal shape of paraprocts, narrower and pointed in *P. blanda*, and broadly rounded in *P. egena*, and by the presence of epiproct in *P. blanda*. As mentioned by Froehlich (1969), advanced nymphs of *P. blanda* are readily distinguished from those of *P. klapaleki* by the slenderer body, shorter paraprocts with rounded apices, and by the uniform color of T10.

Figure 11. *Paragripopteryx blanda*, holotype adult male, head and pronotum in dorsal view (A). Male, terminalia of the specimen from Santa Catarina in lateral view (C). Nymphs, body in dorsal view, detail of thorax and legs (D).

***Paragripopteryx crassila* (Jewett, 1960)**

Gripopteryx crassila Jewett, 1960, Arquivos do Museu Nacional (Rio de Janeiro), 169. ♂, ♀, figs. 1, 1A, 1B.

Jewettoperla crassila Illies, 1963, Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 36: 185. Synon. nov.

Paragripopteryx crassila Illies, 1966, 44.

Paragripopteryx crassila Froehlich, 1969, Studies on Neotropical Fauna and Environment, 6 (1): 19. Comb. nov.

Paragripopteryx crassila Zwick, 1973, Das Tierreich, 94: 210.

Paragripopteryx crassila Froehlich, 2010, Illiesia, 6 (12): 135. Catalog.

Type locality: Brazil, Santa Catarina, Nova Teutônia.

Material examined: Holotype, male: Brazil, Santa Catarina, Nova Teutônia, X/1956, Fritz Plaumann. Allotype, female: same data as holotype (both deposited in the collection of the California Academy of Sciences, material examined through the photos).

Remarks: Synonym of *Paragripopteryx klapaleki*.

***Paragripopteryx delicata* Froehlich, 1994**

(Figs. 12A–G)

Paragripopteryx delicata Froehlich, 1994, Aquatic Insects, 16 (4): 229–231. ♂, ♀, nymphs, figs. 1–5.

Paragripopteryx delicata Froehlich, 2010, Illiesia, 6 (12): 135. Catalog.

Type locality: Brazil, São Paulo, Campos do Jordão State Park.

Material examined: Adults. Holotype, male: São Paulo, Campos do Jordão, Parque Estadual, 1600 m, 26.xi.1986. Paratypes: same locality as holotype: 1 female, 11.XI.1985, CGF & LGO; 1 male, 2 females, 7.i.1986, CGF & LGO; same data, except for: 1 female, 3.x.1986, CGF & LGO; same data, except for: 2 females, 30–31.x.1986 (1 female, MNRJ); same data, except for: 2 males, 4 females, 26.xi.1986 (NMNH); same data, except for: 2 females, 21–23.xii.1986; same data, except for: 1 female, 20.i.1987, CGF & J. Furlan (LFSS); same data, except for: 1 female, 25.iii.1987, CGF & LGO; same data, except for: 3 males, 5 females, 17–20.xi.1987, CGF & LGO; same data, except for: 2 males, 4 females, 14–16.xii.1987, CGF & LGO (1 male, MNRJ; 1 female, NHMW); same data, except for: 1 female, 13.iii.1988, CGF & LGO (NHMW); same data, except for: 4 males, 7.xi.1990, CGF, LGO & MJNF (LFSS). Salesópolis, Estação Biológica de Boracéia, 850m: 1 male, 1 female, 12.x.1974; same data, except for: 1 male, 1 female + exuviae, 16.xi.1974, CGF & OF; same data, except for: 1 male, 2.xi.1975; same data, except for: 2 females, 22–24.x.1982, S.A. Vanin; same data, except for: 1 female, 12.ix.1988, CGF & OF (NMNH); same data, except for: 1 female, 22.ii.1990, CGF & LGO; same data, except for: 1 male, 3 females, 10–13.xi.1990, CGF, LGO & MJNF. Nymphs. Campos do Jordão, Umuarama: 1 n., 29.i.1959; Parque Estadual: 1 n., 9.xi.1985,

CGF & LGO; same data, except for: 11 n., 7.i.1986, CGF & LGO; same data, except for: 1 n., 4.iv.1986 (LFSS); same data, except for: 1 n., 21.x.1987. Salesópolis, Estação Biológica de Boracéia: 1 n., 17.ix.1965; same data, except for: 2 n., 16.xi.1974, CGF & OF; same data, except for: 2 n., 28.i.1983 (NMNH); same data, except for: 3 n., 22.ix.1987, CGF, OF & MS; same data, except for: 3 n., 11–12.viii.1988 (MNRJ); same data, except for: 3 n., 11.ix.1988, CGF & OF (LFSS); same data, except for: 1 n., 9.x.1988, CGF, OF & MS (NMHW).

Diagnosis: *Paragripopteryx delicata* is a generally brown species (Fig. 12A). Forewing pterostigmatic crossveins present, dark-bordered on either side (Fig. 12B). Male T10 extension triangular-shaped ending in two small denticles, very close together (Fig. 12C). Male paraprocts broad, may be broadest subapically, apex somewhat pointed (Fig. 12D; figs. 3–4 in Froehlich, 1994). Epiproct large, upturned and hook-shaped (Fig. 12D; fig. 3 in Froehlich, 1994). Female subgenital plate with pair of lateral sclerotizations, apex broad, margin almost straight. Paraprocts truncate in ventral view (fig. 5 in Froehlich, 1994). Nymphs with dorsal row of long bristles on femur and tibia. Wing pads with normal hairs, claviform bristles absent (Figs. 12E–F). Apex of T10 slightly truncate (Fig. 12G), surface covered by normal bristles, claviform bristles restricted to distal margin (Fig. 12G). Male nymphs with paraprocts upturned, apex pointed; female nymphs with paraprocts oval apically, and provided with thin subapical extensions appressed to base of cerci; elongate claviform hairs present on apical portions of paraprocts (Froehlich, 1994).

Remarks: Type material of *Paragripopteryx delicata* is in a good state of conservation, being possible to observe the main characters of terminalia. The description of *P. delicata* by Froehlich (1994) is well detailed and based on several material of male, female and nymphs collected in Campos do Jordão State Park and Boracéia Biological Station (São Paulo, Brazil). Froehlich (1994) provided good illustrations of the male and female adults, however, provided no figures of nymphs. In this study, we are providing photos of a male adult and a nymph (Figs. 12A–G). Froehlich discussed the morphological similarity between *P. delicata* and *P. blanda*, related to characters of T10 and paraprocts. In our analysis, these two species appeared as sister taxa in a collapsed clade (Figs. 1A–B).

Figure 12. *Paragripopteryx delicata*, holotype adult male, head and pronotum in dorsal view (A). Male, fore and hind wings (B). Male, terminalia in dorsal (C) and lateral views (D). Nymphs, body in dorsal view, details of thorax (E), hind leg (F) and distal abdomen (G).

***Paragripopteryx egena* Froehlich, 1994**

(Figs. 13A–E)

Paragripopteryx egena Froehlich, 1994, Aquatic Insects, 16 (4): 237–239. ♂, ♀, figs. 26–30.

Paragripopteryx egena Froehlich, 2010, Illiesia, 6 (12): 136. Catalog.

Paragripopteryx egena Bispo & Lecci, 2011, Annales de Limnologie - International Journal of Limnology, 47: 377.

Paragripopteryx egena Gonçalves *et al.*, 2017, Zootaxa, 4291 (3): 568. New record.

Type locality: Brazil, São Paulo, Ribeirão Grande, Intervales State Park.

Material examined: Holotype, male: Brazil, São Paulo, Ribeirão Grande, Fazenda Intervales, 18.xi.1992, CGF & CM. Polegatto. Paratypes: same data as holotype, except for: 3 males, 6 females, 19–20.xi.1992, CGF & CM. Polegatto (1 male, 2 females, LFSS; 1 male, 1 female, NMNH; 1 female, 1 male, NHMW). **Brazil, Santa Catarina**, Orleans, Minador Stream - #76, S28°10'28", W49°24'36", 10.xi–13.xii.2013, Malaise, L.C. Pinho *et al.*, 1 male; **Brazil, Santa Catarina**, Urubici, PARNA São Joaquim, PPBioMA, M1PR1 TN1200, S28°08'36", W49°38'13", 23.viii–05.ix.2014, Malaise, L.C. Pinho *et al.*, 1 male; **Brazil, Santa Catarina**, Urubici, #82, 09.xi–12.i.2014, 2 males, 6 females; **Brazil, Santa Catarina**, Urubici, RPPN Portal das Nascentes, #64, S28°03'12", W49°22'27", 19.viii–12.x.2013, Malaise, L.C. Pinho *et al.*, 1 male, 2 females; **Brazil, Santa Catarina**, Urubici, RPPN Portal das Nascentes, #68, S28°03'02", W49°22'44", 12.x–09.xi.2013, Malaise, L.C. Pinho *et al.*, 1 male, 3 females.

Diagnosis: *Paragripopteryx egena* is a generally brown to dark brown species (Figs. 13A–E). Forewing with pterostigmatic crossvein (Fig. 13C). Male T10 with pair of indentations on anterior margin; male T10 extension projected backwards, ending in two small denticles (Fig. 13D). Lateral sclerites in T10 well separated from central sclerite in dorsal view (Fig. 13D; fig. 26 in Froehlich, 1994). Paraprocts are thick, apical region narrowed, apex rounded in side view (Fig. 13E), epiproct absent (Froehlich, 1994). Female subgenital plate may be divided by a median pale band; apical margin from broadly rounded to shallowly emarginated (figs. 29–30 in Froehlich, 1994). Female paraprocts normal, apex slightly truncate (Froehlich, 1994).

Remarks: Type material of *Paragripopteryx egena* comes from Fazenda Intervales (currently, Intervales State Park), Ribeirão Grande, São Paulo, and it is in a good state of conservation. Froehlich (1994) described male and female adults of *P. egena* well

detailed. Until the date, the nymphs of this species are unknown. We are providing new records of this species from municipalities of Orleans and Urubici (Santa Catarina State, Brazil), and photos of male and female head, and male wings and terminalia. The main character distinguishing *P. egena* from the other species of the genus is the absence of epiproct but this state is shared with *P. ogum* **sp. nov.** *Paragripopteryx egena* together with *P. delicata* and *P. blanda* appeared as a sister in a collapsed clade in our analysis (Fig. 1A).

Figure 13. *Paragripopteryx egena*, holotype adult male, head and pronotum in dorsal view (A). Paratype adult female, head and pronotum in dorsal view (B). Male, fore and hind wings (C). Male, terminalia in dorsal (D) and lateral views (E). Scale bar: 0.5 mm.

***Paragripopteryx guardae* Froehlich, 1994**

(Figs. 14A–E)

Paragripopteryx guardae Froehlich, 1994, Aquatic Insects, 16 (4): 231–232. ♂, ♀, nymphs, figs. 6–12.

Paragripopteryx guardae Froehlich, 2010, Illiesia, 6 (12): 136. Catalog.

Type locality: Brazil, São Paulo, Campos do Jordão State Park.

Material examined: Holotype, male: Brazil, São Paulo, Campos do Jordão, Parque Estadual, 17.x.1985. Paratypes: same data as holotype, except for: 3 males, 4 females, 7 exuviae (4 males, 3 females), 18 nymphs, 17.x.1985; same data, except for: 2 nymphs, 9.xi.1985, CGF & LGO; same data, except for: 1 male + exuviae, 3 nymphs, 11.xi.1985, CGF & LGO (LFSS); same data, except for: 3 nymphs, 7.i.1986, CGF & LGO (NMNH); same data, except for: 1 male + exuviae, 3.x.1986, CGF & LGO (MNRJ); same data, except for: 1 male, 27.xi.1986 (NHMW); same data, except for: 3 females, 17–20.xi.1987, CGF, LGO, MJNF & G.M. Cavasin (2 females, MNRJ; 1 female, NHMW); same data, except for: 1 male, 3 females, 15–16.xii.1987, CGF & LGO (1 male, 1 female, NMNH; 2 females, LFSS); same data, except for: 1 male, 8.xi.1990, CGF, LGO & MJNF (LFSS).

Diagnosis: *Paragripopteryx guardae* is a generally ochraceous to yellowish species (Figs. 14A–D). Forewing pale brown, pterostigmatic crossveins present (Fig. 14B). Male T10 extension projected backwards, half-elliptical, ending in two small denticles (Fig. 14C). Lateral sclerites in T10 weak. Male paraprocts are thin, apical region narrower; epiproct small (Fig. 14D; figs. 6–8 in Froehlich, 1994). Female subgenital plate with lateral sclerotizations, apex notched; paraprocts thin (fig. 9 in Froehlich, 1994). Nymphs with numerous claviform bristles on wing pads (Fig. 14E). Leg fringe weak, femur with stouter short bristles along ventral ridges (fig. 12 in Froehlich, 1994). T10 covered with normal bristles and some claviform ones; posterior margin with numerous claviform bristles. Nymphs paraprocts long triangular, those of males longer; elongate claviform bristles present near apex (Froehlich, 1994).

Remarks: Type material of *Paragripopteryx guardae* comes from Campos do Jordão State Park (São Paulo, Brazil) and it is in a good state of conservation. The description of *P. guardae* by Froehlich (1994) is well detailed and based on males, females, and nymphs. Froehlich illustrated male and female terminalia, and details of femur and paraprocts of nymph. In his discussion, he compared this species with *P. klapaleki*. The two species differing for larger and rounded T10 extension in males of *P. guardae*. Nymphs of *P.*

guardae differ from those of *P. klapaleki* by the femur bearing stout short bristles on ventral side (Froehlich, 1994).

Figure 14. *Paragripopteryx guardae*, holotype adult male, head and pronotum in dorsal view (A). Male, fore and hind wings (B). Male, terminalia in dorsal (C) and lateral views (D). Nymphs, head and thorax in dorsal view (E).

***Paragripopteryx hamata* Froehlich, 1994**

(Figs. 15A–E)

Paragripopteryx hamata Froehlich, 1994, Aquatic Insects, 16 (4): 234–236. ♂, ♀, figs. 18–21.

Paragripopteryx hamata Froehlich, 2010, Illiesia, 6 (12): 136. Catalog.

Paragripopteryx hamata Bispo & Lecci, 2011, Annales de Limnologie - International Journal of Limnology, 47: 377. New records.

Type locality: Brazil, São Paulo, Boracéia Biological Station.

Material examined: Holotype, male: Brazil, São Paulo, Salesópolis, Estação Biológica de Boracéia, 850 m., 12.xi.1990, CGF, LGO & MJNF. Paratypes: same data as holotype, except for: 1 female, 26.i.1974, CGF & I.R. Ball; same data, except for: 1 male, 5–22.xii.1987, OF & MS; same data, except for: 1 female, 7.x.1988, CGF & OF (LFSS); same data, except for: 1 male, 3 females, 3.iii.1989, CGF & OF (1 male, 1 female, NMNH; same data, except for: 1 female, NHMW); same data, except for: 2 male, 12.xi.1990, CGF, LGO & MJNF (1 male, LFSS).

Diagnosis: *Paragripopteryx hamata* is a generally dark brown species (Figs. 15A–E). Forewings with paler pterostigmatic cell, crossvein present (Fig. 15B). Male T10 with pair of conspicuous bands not sclerotized in distal part (like clefts, but not open) (Fig. 15C); T10 extension projected backwards, distal margin rounded, ending in two small denticles very close together (Fig. 15C). Male subgenital plate rounded apically (Fig. 15D). Male paraprocts relatively narrow, apex rounded; epiproct hook-shaped (Fig. 15E; fig. 20 in Froehlich, 1994). Female with a relatively long subgenital plate, depigmented medially, apex rounded (fig. 21 in Froehlich, 1994). Nymphs unknown.

Remarks: Froehlich (1994) described the male and female of *Paragripopteryx hamata* from Boracéia Biological Station (São Paulo, Brazil). We examined the type material of this species, which is in a good state of conservation. Froehlich provided good illustrations of male and female terminalia (figs. 18–21 in Froehlich, 1994), and compared *P. hamata*, at the time, with *P. blanda*. In our analysis, *P. hamata* is in a polytomy along with *P. paranapiacabae* and the clade G (Fig. 1A). The rounded ends of T10 with a longitudinal membranous line in its species is very distinctive from the other species of the genus.

Figure 15. *Paragripopteryx hamata*, holotype adult male, head and pronotum in dorsal view (A). Male, fore and hind wings (B). Male, terminalia in dorsal (C), ventral (D) and lateral views (E).

***Paragripopteryx intervalensis* Bispo & Lecci, 2011**

(Figs. 16A–C; Figs. 17A–C)

Paragripopteryx intervalensis Bispo & Lecci, 2011, *Annales de Limnologie - International Journal of Limnology*, 47: 377–378. ♂, figs. 2–4.

Paragripopteryx intervalensis Gonçalves *et al.*, 2017, *Zootaxa*, 4291 (3): 568–569. ♀, figs. 7–9.

Type locality: Brazil, São Paulo, Intervales State Park.

Material examined: Holotype, male: Brazil, São Paulo, Iporanga, Parque Estadual Intervales, Chico Paes, 31.x.2002, ASM, RGA, PCB; same data, except for: Rib. Poços Altos, [1030C], 18.xi.1992, Froehlich, Polegatto, 1 male. **Brazil, Santa Catarina**, Serra Furada, 1 male; Malaise, Janela, #28, 16.xi–08.i.2013, 2 males. **Brazil, Minas Gerais**,

São Gonçalo do Rio Abaixo, [BR981117], Córrego, Burucutu, Estação Ambiental de Peti (CEMIG), S19°52.995', W43°22.757', Col. Paprocki, 1 male.

Figure 16. *Paragripopteryx intervalensis*, adult male from Serra Furada, Santa Catarina, male fore and hind wings (A), terminalia in dorsal (B) and lateral views (C).

Diagnosis: *Paragripopteryx intervalensis* is a generally brown species (Figs. 16A–C). Male forewing pterostigmatic crossvein present (Fig. 16A). Male T10 with distal region rounded and with two small denticles forming a tiny projection M-shaped at apex (Fig. 16B). Male subgenital plate rounded apically (fig. 4 in Bispo & Lecci, 2011). Male

paraprocts simple, apex rounded (Fig. 16C); epiproct elongated, sometimes surpassing the paraprocts (fig. 3 in Bispo & Lecci, 2011). Female with a relatively long subgenital plate, squared-shaped (fig. 7 in Gonçalves *et al.*, 2017).

Nymphal exuviae: General color brown to dark brown (Fig. 17A–C). Thorax provided with claviform bristles; pronotum squared, almost trapezoidal, corners rounded (Fig. 17A). Femora provided with normal and claviform bristles, some stouter short bristles along the ventral margin (Fig. 17B). Abdominal terga provided with both normal and claviform bristles; distal margin of T10 with numerous claviform bristles (Fig. 17C). Paraprocts with rounded apex.

Remarks: Bispo & Lecci (2011) described *Paragripopteryx intervalensis* based on a single male from Intervales State Park (São Paulo State, Brazil). Gonçalves *et al.* (2017) recorded the species for municipality of Santa Teresa (Espírito Santo State, Brazil) and described the female (figs. 7–9 in Gonçalves *et al.*, 2017). Here, we are providing the description of female exuviae from the material described by Gonçalves *et al.* (2017) (Figs. 17A–C). The stouter short bristles along the ventral margin of femur of the nymphal exuviae in *P. intervalensis* resembles that of *P. guardae*. Additionally, we are providing new records of this species from Serra Furada State Park (PAESF), Santa Catarina State (Brazil), and São Gonçalo do Rio Abaixo, Minas Gerais State (Brazil). The epiproct of the collected male differs in length from the type material, do not exceeding T10 (Fig. 16C).

Figure 17. *Paragripopteryx intervalensis*, nymphal exuviae, pronotum in dorsal view (A), detail of leg (B) and T10 (C).

***Paragripopteryx kapilei* Bispo & Lecci, 2011**

(Figs. 18A–B; Figs. 19A–D)

Paragripopteryx kapilei Bispo & Lecci, 2011, Annales de Limnologie - International Journal of Limnology, 47: 378. ♂, figs. 5–7.

Type locality: Brazil, São Paulo, Intervales State Park.

Material examined: Holotype, male: Brazil, São Paulo, Iporanga, Parque Estadual Intervales, Córrego Roda D'Água, 02.ii.2000, CGF, ASM, VRR, PCB. Paratype: same data, except for: 1 male, 10.v.2005, Mariano, R. **Brazil, Santa Catarina**, Blumenau, Spitzkopf, S27°00'22", W49°06'28", 28.xi.2003, CGF, RWH, ARC, 1 male, 1 nymph, exuviae [1453]; **Brazil, Santa Catarina**, Blumenau, Spitzkopf, Rib. do Ouro, S27°00'35", W49°06'69", 700m, 03.iii.1998, CGF, RWH, HP, 1 nymph [1293].

Diagnosis: *Paragripopteryx kapilei* is a generally ochraceous to yellowish species (Fig. 18A–B). Male forewings of male with one pterostigmatic crossvein. Male T10 with a conspicuous lateral cleft on each side (Fig. 18B; fig. 5 in Bispo & Lecci, 2011); T10 extension elongated, Y-shaped (Fig. 18B; fig. 5 in Bispo & Lecci, 2011). Male paraprocts elongated and with a small elevation medially, distal region before the apex narrow, apex rounded, stout setae present (Fig. 18B; fig. 6 in Bispo & Lecci, 2011). Epiproct hook-shaped (Fig. 18B). Female unknown.

Figure 18. *Paragripopteryx kapilei*, male from Santa Catarina, head and pronotum in dorsal view (A). Paratype male, terminalia in lateral view (B).

Description of nymphs: General color ochraceous to yellowish; head yellowish, antennae ochraceous; pronotum ochraceous, with rounded corners; meso- and metanotum ochraceous. Wing pads with numerous stouter short bristles (Fig. 19A). Femora robust, with some stouter short bristles; femur and tibia with a dorsal row of hair (Fig. 19B). Abdominal terga yellowish, covered with numerous stouter short bristles, distal margin of terga with a dark spot; posterior margin of T10 rounded, almost truncated, with numerous claviform hairs (Fig. 19C). Cerci ochraceous. Gills ochraceous. Ventral side lighter in color. Paraprocts elongated (Fig. 19D).

Remarks: Bispo & Lecci (2011) described *Paragripopteryx kapilei* based on two male specimens from Intervales State Park, São Paulo, Brazil. The type material is in good state of conservation, being possible the examination of main characters of wings and terminalia. The description of *P. kapilei* by Bispo & Lecci (2011) is good, and it presents details of the terminalia of species (figs. 5–7 in Bispo & Lecci, 2011). We examined a male and nymphs from municipality of Blumenau, Santa Catarina State (a new record). The material was reared by Dr. Claudio G. Froehlich and we are describing here (Figs. 19A–D). In our phylogenetic analyses, *P. kapilei* is close related to *P. anga* and *P. convexa* **sp. nov.** (Fig. 1A).

Figure 19. *Paragripopteryx kapilei*, young nymph, head and thorax in dorsal view (A), details of hind leg (B), and abdomen in dorsal (C) and ventral views (D). Scale bar: 0.5 mm.

***Paragripopteryx merui* Froehlich, 1994**

(Figs. 20A–C)

Paragripopteryx merui Froehlich, 1994, Aquatic Insects, 16 (4): 232. ♂, exuviae, figs. 13–17.

Paragripopteryx merui Froehlich, 2010, Illiesia, 6 (12): 135. Catalog.

Type locality: Brazil, São Paulo, Campos do Jordão State Park.

Material examined: Holotype, male: Brazil, São Paulo, Campos do Jordão, Parque Estadual, 20.xi.1987, CGF, LGO & MJNF; beating sheet. Paratypes: same data, except

for: 1 male + exuviae; same data, except for: 1 male, 16.xii.1987, CGF & LGO (LFSS). Additional material: Brazil, São Paulo, Campos do Jordão, Parque Estadual, light, Córrego Garalhada, Quiosque Viveiro, 02.xi.2005, MR Spies, 1 male.

Diagnosis: *Paragripopteryx merui* is a generally light brown species (Fig. 20A). Male forewings with pterostigmatic crossveins (Fig. 20B). Male T10 sclerotized, with a conspicuous light spot in central area, inconspicuous lateral clefts on each side of T10 (like a cleft, but not open) (Fig. 20C); Male T10 extension with a median notch, ending in two separated denticles, M-shaped (Fig. 20C). Paraprocts relatively thin, apex narrower, rounded, with a subapical anterior tooth (fig. 15 in Froehlich, 1994); epiproct robust, elongated and with two rows of denticles on inner area (fig. 16 in Froehlich, 1994). Nymphs with short stout bristles on femur. Pterothecae with claviform and few setiform hairs. Paraprocts triangular-shaped, with an apical rounded projection; claviform hairs subapically present. Female unknown.

Remarks: Froehlich (1994) described *Paragripopteryx merui* based on male specimens from Campos do Jordão State Park, São Paulo State, Brazil. The species has been recorded only in the type locality. The description and illustration of *P. merui* by Froehlich is detailed, and therefore does not require redescription.

Figure 20. *Paragripopteryx merui*, holotype adult male, head and pronotum in dorsal view (A). Male, fore and hind wings (B). Male, terminalia in dorsal view (C).

***Paragripopteryx paranapiacabae* Bispo & Lecci, 2011**

(Figs. 21A–B)

Paragripopteryx paranapiacabae Bispo & Lecci, 2011, Annales de Limnologie - International Journal of Limnology, 47: 379. ♂, figs. 8–10.

Type locality: Brazil, São Paulo, Iporanga, Intervalles State Park.

Material examined: Holotype, male: Brazil, São Paulo, Iporanga, Parque Estadual Intervales, Lago Negro, 19.xi.1992, CGF. Paratypes: same data as holotype, except for: 2 males, Ribeirão do Carmo (near Cachoeira das Pedrinhas), 01.xi.2002, ASM. São Paulo, Iporanga, PETAR, 1 male, 26–27.viii.2001, Galati, E.

Diagnosis: *Paragripopteryx paranapiacabae* is a generally ochraceous species (Fig. 21A). Forewings of male may not present pterostigmatic crossveins (Fig. 21B). Male T10 extension elongated, base constricted, apex ending in two teeth (fig. 8 in Bispo & Lecci, 2011). Paraprocts thick, L-shaped, apex rounded (fig. 9 in Bispo & Lecci, 2011). Epiproct short, hook-shaped (fig. 9 in Bispo & Lecci, 2011). Nymphs and females unknown.

Remarks: *Paragripopteryx paranapiacabae* was described based in male specimens from Intervales State Park, São Paulo State (Bispo & Lecci, 2011). The material is in good state of conservation. *Paragripopteryx paranapiacabae* description's is complete and therefore does not require redescription. One paratype of the species present the inferior branch of M vein completely fused to CuA vein. Here, we provided photos of the male.

Figure 21. *Paragripopteryx paranapiacabae*, holotype adult male, head and pronotum in dorsal view (A). Male, fore wing with pterostigmatic crossvein (B).

Identification key for male species of *Paragripopteryx*

1. Sclerotized epiproct absent. 2
- 1'. Sclerotized epiproct present (Fig. 5C). 4

- 2 (1). Forewings without pterostigmatic crossveins (Fig. 3C). Male subgenital plate robust, ending in a rounded apex (Fig. 3E). Paraprocts provided with four lobes (Figs. E–F). *Mclellanperla munoai* (Uruguay)
- 2'. Forewings with pterostigmatic crossveins. Male subgenital plate triangular, ending in a rounded apex. Paraprocts simple. 3

- 3 (2'). T10 anterior margin with a conspicuous pair of unsclerotized indentation (Fig. 13D); T10 extension protruding, but not bilobed, ending in two small teeth close together (Fig. 13D). Conspicuous lateral sclerites, lighter (Fig. 13D). Paraprocts thick with apical region narrowed and apex rounded (Fig. 13E). *Paragripopteryx egena*
- 3'. T10 with a proximal clear band M-shaped like *P. egena* but T10 extension bilobed, ending in two separated small teeth (Fig. 8A). Paraprocts expanded distally with dark distal margin and with concave shape (Fig. 8C). *Paragripopteryx ogum* **sp. nov.**

- 4 (1'). Posterior sclerite present (?).
..... *P. baratinii* (Uruguay) (Figs. 2, 4 in Benedetto, 1983)
- 4'. Posterior sclerite absent. 5

- 5 (4'). Distal region of paraprocts provided with black rod-like setae (Figs. 6E, 10C, 18B).
..... 6
- 5'. Distal region of paraprocts without black rod-like setae. 8

- 6 (5). T10 provided with conspicuous lateral clefts on each side; T10 extension very elongated, Y-shaped (ending in two well-separated processes finger shape) (Fig. 18B). Paraprocts elongated, narrowing in distal region, apex rounded. Epiproct hook-shaped (Fig. 18B). *Paragripopteryx kapilei*
- 6'. T10 with pair of conspicuous bands not sclerotized (like clefts, but not open); T10 extension medium sized, without elongated finger shape processes (Fig. 6C, 10B).
..... 7

- 7 (6'). T10 extension spatulate-shaped, ending with two denticles separated by a rounded incision (Fig. 10B; fig. 12 in Froehlich, 1969). Paraprocts elongated, thick basally, ascending parts narrower, slightly strangled, ends rounded (Fig. 10C). Epiproct smooth and pointed (Fig. 10C; fig. 14 in Froehlich, 1969). *Paragripopteryx anga*
- 7'. T10 extension curved shape in latero-distal margin (Fig. 6C). Paraprocts with a straight inner margin, ascending parts narrower but not strangled, ends rounded (Fig. 6E). *Paragripopteryx convexa* **sp. nov.**
- 8 (5'). Epiproct shorter, falciform or finger shaped (Fig. 9D, 14D). 9
- 8'. Epiproct not as above described. 10
- 9 (8). Subgenital plate trapezoidal (fig. 7 in Froehlich, 1994). Epiproct shortened finger shaped (Fig. 14D; fig. 8 in Froehlich, 1994). *Paragripopteryx guardae*
- 9'. Subgenital plate rounded (fig. 2 in Froehlich, 1969). T10 extension forms a small process ending in two denticles close together (Figs. 9C, E). Paraprocts elongated, narrow and almost straight, apex narrower (Figs. 9D, F). Epiproct bends upward, almost falciform (Fig. 9D). *Paragripopteryx klapaleki*
- 10 (8'). Epiproct elongated finger shaped, ends rounded (fig. 16 in Froehlich, 1994; fig. 3 in Bispo & Lecci, 2011). 11
- 10'. Epiproct elongated hook-shaped (tip facing inwards), ends pointed (Figs. 5C, 15E). 12
- 11 (10). T10 extension with a median notch, ending in two separated denticles (Fig. 20C). Paraprocts relatively thin, apex narrower, rounded, and with a subapical anterior tooth; epiproct robust and elongated, but not exceeding T10 extension, inner margin provided with two rows of tiny teeth (Fig. 20D; figs. 13–16 in Froehlich, 1994). *Paragripopteryx merui*
- 11'. T10 with distal region rounded, and two small denticles close, forming a tiny projection M-shaped at apex (Fig. 16B). Male subgenital plate rounded apically (fig. 4 in Bispo & Lecci, 2011). Paraprocts simple, apex rounded (Fig. 16C); epiproct elongated, sometimes exceed the T10 and paraprocts, inner margin without of tiny teeth. *Paragripopteryx intervalensis*

- 12 (10'). T10 with a pair of conspicuous bands not sclerotized on laterodistal region (like clefts, but not open); T10 extension projected backwards, distal margin rounded, ending in two small denticles very close together (Fig. 15C). Male subgenital plate rounded apically (Fig. 15D). Paraprocts relatively narrow, apex rounded (Fig. 15E; fig. 20 in Froehlich, 1994). *Paragripopteryx hamata*
- 12'. T10 without a pair of conspicuous bands not sclerotized on laterodistal region; T10 extension may or may not be bilobed. Paraprocts elongated, apex rounded or pointed. 13
- 13 (12'). T10 extension with apex bilobed (Fig. 5A). 14
- 13'. T10 extension with apex not bilobed (Fig. 12C). 15
- 14 (13). T10 with a pair of conspicuous lateral clefts on laterodistal margin; T10 extension elongated, base slightly strangled, apex bilobed (fig. 8 in Bispo & Lecci, 2011). Paraprocts thick in ventral and lateral views, L-shaped, apex rounded (fig. 9 in Bispo & Lecci, 2011). *Paragripopteryx paranapiacabae*
- 14'. T10 without a pair of conspicuous lateral clefts on laterodistal margin; T10 extension medium length, base not strangled, distal margin M-shaped (Fig. 5A). Paraprocts thin in ventral view (Fig. 5B), thick throughout its length in lateral view, apex with ventral curvature, dorsal margin straight, tip triangular (Fig. 5C). *Paragripopteryx dasalmas* **sp. nov.**
- 15 (13'). T10 extension extended posteriorly in a convex process ending in two small teeth close together (Fig. 11B) (similar in part to those of *P. klapaleki*, *P. crassila*, and *P. egena*). Paraprocts are robust in basal half, narrowing towards apex, ending in a sharp point (Fig. 11C). *Paragripopteryx blanda*
- 15'. T10 extension triangular-shaped ending in two small denticles, very close together (Fig. 12C). Paraprocts broad, may be broadest subapically, apex can be twisted, rounded (Fig. 12D; figs. 3–4 in Froehlich, 1994). *Paragripopteryx delicata*

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Supplementary material

Figure 1. Consensus topologies of *Paragripopteryx* obtained under EW. (A) Consensus strict from 10 trees using complete dataset, *Paragripopteryx* polyphyletic; (B) Consensus strict from 15 trees using reduced dataset, *Paragripopteryx* paraphyletic.

Figure 2. Consensus strict from two trees under IW (k = 7–15) using the complete dataset of *Paragripopteryx*.

Figure 3. Tree under IW (k = 5–15) using the reduced dataset of *Paragripopteryx*.

Chapter III: An overview of the species of Gripopterygidae (Plecoptera)
from Brazil: an updated list with a new species

Full title:

An overview of the species of Gripopterygidae (Plecoptera) from Brazil: an updated list with a new species

Running title:

Brazilian Gripopterygidae

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Abstract

The family Gripopterygidae occurs in the Austral Hemisphere and is composed by about 320 species in 55 genera. About 100 species in 29 genera occur in the Andean and Neotropical regions, and transition zones. Brazilian Gripopterygidae has been recorded in South, Southeast and mountain areas from Central and Northeast regions from Brazil. Four genera have been recorded in Brazil: 1) *Gripopteryx* Pictet with 18 described species; 2) *Guaranyperla* Froehlich with three species; 3) *Paragripopteryx* Enderlein with 14 species, and 4) *Tupiperla* Froehlich with 21 species, including a new species described in this contribution. Here, we studied the material from several Brazilian localities (Bahia, Minas Gerais, Paraná and Santa Catarina states). As result of this study, a new species, *Tupiperla furcata* **sp. nov.**, is described based on male and female specimens from Urubici, Santa Catarina State. In addition, a single male specimen, morphologically agreeing with *Gripopteryx elisae* Illies, 1964, was collected in Urubici, and we also supplemented the original description of this species adding pictures. Finally, we present an updated list with 55 Gripopterygidae species from Brazil (plus *G. serrei* and *P. baratinii* from Uruguay).

Key words: Aquatic insects – *Gripopteryx* – *Paragripopteryx* – Stoneflies – *Tupiperla*.

1. Introduction

The Gripopterygidae Enderlein, 1909 are associated with lotic environments like streams and waterfalls. The nymphs are scrapers or shredders and can be found in boulder surfaces, among pebbles, tree trunks, moss and leaf packs (Diaz Villanueva & Albariño, 1999; Miserendino & Pizzolon, 2000; Wantzen & Wagner, 2006). The adults can fly short distances, living on riparian vegetation or over rocks, closely associated with water bodies (Stark *et al.*, 2009).

The family occurs in Austral Hemisphere comprising about 320 species in 55 genera (Froehlich, 2010; DeWalt *et al.*, 2019; Duarte, Calor & Bispo). In Australia and New Zealand (Australian Region) occur 26 genera and about 200 species, while in South America (Andean and Neotropical regions *sensu* Morrone, 2014) occur 29 genera and about 110 species (Duarte, Calor & Bispo; Pessacq *et al.*, 2019, in press).

Illies (1963) is considered the starting point for the study of Gripopterygidae in South America, in his study the family was reviewed and most of the current genera were described. Several of them are monotypic or have few species (Tabela 1). Subsequent studies have added new genera and species of Gripopterygidae (Froehlich, 1969, 2001; McLellan, 2001; McLellan & Zwick, 2007; Vera, 2009), mainly in the southeastern of Brazil (Froehlich, 1969, 1990, 1993, 1994, 1998, 2001, 2002, 2015, 2016; Bispo & Lecci, 2011).

Currently, four Gripopterygidae genera have been reported in Brazil from the South, Southeast and mountain areas from Central and Northeast regions (Fig. 1): 1) *Gripopteryx* Pictet, 1841 with 18 described species (one species with occurrence restricted to Uruguay); 2) *Guaranyperla* Froehlich, 2001 with three species; 3) *Paragripopteryx* Enderlein, 1909 with 15 species (one species with occurrence restricted to Uruguay), and *Tupiperla* Froehlich, 1969 with 21 species (with species also recorded in Argentina and Paraguay), including a new species described in this contribution.

Table 1. Gripopterygidae genera from South America (Pessacq *et al.*, 2019). (Abbreviations: N° spp.: number of species by genus. ARG, Argentina; BOL, Bolivia; BRA, Brazil ; CHL, Chile; COL, Colombia; ECU, Ecuador; PRY, Paraguay; PER, Peru; URY, Uruguay).

	Genera	N° spp.	Distribution
1	<i>Alfonsoperla</i> McLellan & Zwick, 2007	1	ARG, CHL
2	<i>Andiperla</i> Aubert, 1956	1	ARG, CHL
3	<i>Andiperlodes</i> Illies, 1963	2	ARG, CHL
4	<i>Antarctoperla</i> Enderlein, 1905	2	ARG, CHL
5	<i>Aubertoperla</i> Illies, 1963	2	ARG, CHL
6	<i>Araucanioperla</i> Illies, 1963	2	ARG, CHL
7	<i>Ceratoperla</i> Illies, 1963	2	ARG, CHL
8	<i>Chilenoperla</i> Illies, 1963	5	ARG, CHL
9	<i>Claudioperla</i> Illies, 1963	4	ARG, BOL, COL, CHL, ECU, PER
10	<i>Erciataperla</i> Vera, 2016	1	ARG, CHL
11	<i>Falklandoperla</i> McLellan, 2001	1	ARG (Falkland Islands)
12	<i>Gripopteryx</i> Pictet, 1841	18	BRA, URY
13	<i>Guaranyperla</i> Froehlich, 2001	3	BRA
14	<i>Limnoperla</i> Illies, 1963	1	ARG, CHL
15	<i>Megandiperla</i> Illies, 1960	1	CHL
16	<i>McLellanperla</i> Duarte, Calor & Bispo	1	URY
17	<i>Neopentura</i> Illies, 1963	1	ARG, CHL
18	<i>Notoperla</i> Enderlein, 1909	7	ARG, CHL
19	<i>Notoperlopsis</i> Illies, 1963	1	ARG, CHL
20	<i>Paragripopteryx</i> Enderlein, 1909	15	BRA, URY
21	<i>Pehuenioperla</i> Vera, 2009	1	CHL
22	<i>Pelurgoperla</i> Illies, 1963	1	ARG, CHL
23	<i>Plegoperla</i> Illies, 1963	2	CHL
24	<i>Potamoperla</i> Illies, 1963	1	ARG, CHL, PER
25	<i>Rhithroperla</i> Illies, 1963	2	ARG, CHL
26	<i>Senzilloides</i> Illies, 1963	1	ARG, CHL
27	<i>Teutoperla</i> Illies, 1963	4	ARG, CHL
28	<i>Tupiperla</i> Froehlich, 1969	21	ARG, BRA, PRY
29	<i>Uncicauda</i> McLellan & Zwick, 2007	2	ARG, CHL
Total		106	

Duarte, Calor & Bispo in Chapter II.

In this paper, we present an updated list of Gripopterygidae (Table 3) and a discussion about the family in Brazil. A new species is described, *Tupiperla furcata* **sp. nov.** from Urubici, Santa Catarina State. A male specimen of *Gripopteryx elisae* was collected rediscovery in Santa Catarina. The morphological comparison between new species and congeners is done.

Figure 1. Distribution map of the four Gripopterygidae genera in Brazil.

2. Material and Methods

The new material studied comes from several localities of Brazil (States of Bahia, Minas Gerais, Paraná and Santa Catarina) and were collected along streams and waterfalls, mainly using light traps or manually. All material examined is preserved in 80% alcohol. For updating the list of Gripopterygidae, we used also data from published papers.

The photos of the morphological structures were taken with a Leica M205A stereomicroscope in Universidade Estadual Paulista (UNESP), Assis, São Paulo. The illustrations were prepared in a camera lucida and vectored in Adobe Illustrator CS5® editor. Types of the new species are deposited in the Zoological Museum, Universidade de São Paulo (MZSP). The nomenclature for wing venation follows Béthoux (2005).

Abbreviations on the text: Ecological Station of Wenceslau Guimarães (EEWG); Espírito Santo State (ES); Florida Department, Uruguay (FLO); Goiás State (GO); Lavalleja Department, Uruguay (LAV); Maldonado Department, Uruguay (MAL); Minas Gerais State (MG); Misiones Province, Argentina (MIS); Paraguairí Department, Paraguay (PRI); Paraguay (PRY); Paraná State (PR); Pernambuco State (PE); Rio de Janeiro State (RJ); Rio Grande do Sul State (RS); Santa Catarina State (SC); São Paulo State (SP); Uruguay (URY).

3. Taxonomic results

3.1. *Griopteryx*

3.1.1. *Griopteryx elisae* Illies, 1964

(Figs. 2A–H)

Material examined (new record). Brazil, Santa Catarina, Urubici, Rio Sete Quedas, 11.ix.2016, Pinho & Amaral, 1 male, 1 exuviae.

Measurements. *Griopteryx elisae* is a medium size species of the genus. Male: body size: 12,5 mm; head width, 1,1 mm; pronotum width, 0,9 mm; pronotum length, 1,0 mm; forewing length, 13 mm; hindwing length, 11 mm; antennae length, 1,1 mm; number of cercomeres, 21. Exuviae (n= 1): anterior wingpad length, 3,1 mm; antennae length, 7,1 mm; +50 cercomeres.

General color brown. Head dark brown, epicranial line lighter, darker area between the ocelli (Fig. 2A). Ocelli and eyes black. Clypeus brown, labrum light brown. Maxillary palps brown, 5-segmented, first, second and fourth segments short, third and fifth longer. Labial palps light brown, 3-segmented, third segment rounded. Antennae long, brown. Pronotum brown, trapezoidal with rugosities. Legs brown. Tibia with a perpendicular suture in the proximal region and two spurs at the distal region. Tarsi brown, legs with tarsomere 1 medium, tarsomere 2 short and tarsomere 3 long. Forewing membranous, pale brown (Fig. 2B) with a little spotted transversally between pterostigmatic cell and anal area, posterior area light brown; pterostigmatic crossveins absent; RA unforked; RP forked with two crossveins; CuA forked. Hind wing pale brown, with M3+4, near its separation from M1+2, fused with CuA, its separating near the hind margin of wing; 6th anal vein fused with hind margin of wing. Cerci multisegmented.

Figure 2A–H. *Griopteryx elisae*. Adult male, head and pronotum in dorsal view (A). Forewing of male (B). Adult male terminalia in lateral (C), dorsal (D), and ventral views (E). Epiproct of male in lateral view (F). Terminalia of exuviae in dorsal view (G). Paraproct of nymph in lateral view (H). Scale bar: 0,5 mm. (Abbreviations: AA1, first anterior Analis; AA2, second anterior Analis; CuA, anterior cubitus; CuP, posterior cubitus; M, Media; PC, Pterostigmatic cell; RA, anterior Radius; RP, posterior Radius; Sc, Subcosta).

Male. Abdominal segments 2–8 membranous, segment 9 laterally sclerotized (Fig. 2C). T10 wide, sclerotized, latero-posterior area rounded and median area curved downward (Figs. 2C–D). Sternum (St) 9 short, forming a trapezoidal subgenital plate, apex extending on 1/3 of St10 (Fig. 2E); latero-posterior corners with two dark brown strips (Fig. 2E). Paraprocts long and curved backwards of T10, relatively thin in width and with a row of bristles ventrally; apex rounded (Figs. 2C–D). Epiproct poorly developed, without small teeth (Figs. 2C, F).

Female. Unknown.

Exuviae. General color dark brown. Antennae dark brown. Pronotum brown, with a pair of discal elevations. Meso and metanotum with paired anterolateral and unpaired posterolateral small spines. Abdominal terga 1–9 with median-dorsal spines; T10 rounded, without a long ventrally curved spine (Fig. 2G).

Remarks. *Gripopteryx elisae* was described by Illies (1964) based on a newly emerged male, and additional material of three nymphs. In the present study, we are providing a single male specimen and an exuviae collected in Urubici, Santa Catarina State that constitutes a new record. The specimen is in accordance with characters of *G. elisae*, but a few variations in the body length, and shape of structures were observed (Table 2). Despite of this, we don't consider these variations as relevant to a new species description in *Gripopteryx*. Instead, we supplemented the Illies (1964) description and adding photos of the new specimen.

Table 2. Morphometric data of male specimens of *Gripopteryx elisae* from the municipalities of Bom Jesus, Rio Grande do Sul State, and Urubici, State of Santa Catarina, Brazil.

Locality	Sex	Body size (mm)	Forewing length (mm)	Number of cercomeres
Bom Jesus, RS (Illies, 1964)	Male	8,0	10,5	17
Urubici, SC (in this paper)	Male	12,5	13,0	21

The forewing of male adult of Illies (1964) shows two crossveins in RP-fork (Fig. 2B; fig. 1a in Illies), two long paraprocts ending in a rounded tip (Figs. 2C–E; fig. 1d in Illies) and a short epiproct toothless (Fig. 2C; fig. 1d in Illies) which are in accordance with our male specimen. However, the specimen of Illies (1964) is proportionally smaller than specimen collected in Urubici, including the body size, the forewing length and the

number of cercomeres (Table 2). Additionally, the shape of subgenital plate is slightly rounded in Illies' specimen while in our specimen it forms a trapezoidal plate with the apex extending on 1/3 of St10 (Fig. 2E). These variations in size of body and length of structures probably is related to specimens sclerotization, since the newly emerged adult, or teneral adult, is still weak and need to wait several hours before its body and structures become hard.

3.1.2. *Griopteryx garbei* Navás, 1936

Material examined. Brazil, Bahia, Wenceslau Guimarães, EEWG, Serra Grande Stream, S13°35'43", W39°43'12", 07.x.2010, A.R. Calor *et al.*, 1 male; same data, except for: 09.iii.2011-iv.2011, 1 male; same data, except for: S13°35'34", W39°42'52", 09.x.2010, light pan trap, A.R. Calor *et al.*, 1 male; same data, except for: waterfall, S13°35'35.4", W39°42'51.2", 513m, 06.ix.2013, light pan trap, A.R. Calor, T. Duarte & E.S. Dias, 2 males; same data, except for: 07.ix.2013, 6 males; same data, except for: 1 male; same data, except for: 1 male; same data, except for: 08.ix.2013, 2 males; same data, except for: 4 males.

Remarks. The type of this species comes from Serra de Macaé, Rio de Janeiro State. Material has been collected in several localities of Brazil (Table 3). Here, we report an additional record from Bahia State.

3.1.3. *Griopteryx pinima* Froehlich, 1993

Material examined. Brazil, Bahia, Wenceslau Guimarães, EEWG, Serra Grande Stream, headquarters, 10.x.2010, A.R. Calor *et al.*, 1 male, 1 female; same data, except for: waterfall, S13°35'35.4", W39°42'51.2", 10.x.2010, light pan trap, A.R. Calor *et al.*, 3 males; same data, except for: 1 male; same data, except for: 06.ix.2013, 3 males; same data, except for: 1 male; same data, except for: 07.ix.2013, 5 males; same data, except for: 08.ix.2013, 2 males, 1 female; same data, except for: 1 male; same data, except for: 1 male; same data, except for: 1 male, 1 female; same data, except for: light trap: 1 male; same data, except for: 1 male; same data, except for: 1 male.

Remarks. The type of this species comes from Biological Station of Boracéia, Salesópolis, São Paulo State. Material has been collected also in Serra Bonita Reserve, Bahia State, and Forno Grande State Park, Espírito Santo State (Froehlich, 1993; Lecci & Froehlich, 2011; Avelino-Capistrano & Nessimian, 2014). Here, we report an additional record for Bahia State.

3.2. *Tupiperla*

3.2.1. *Tupiperla flinti* Froehlich, 2002

Material examined (new record). Brazil, Paraná, Céu Azul, Parque Nacional Iguaçu, Azul Stream 3rd order, céu 04, #3435, S25°09'10.9", W53°43'44.9", 08.ix.2012, A.P.M. Santos, 1 male.

Remarks: The type of this species comes from Misiones Province, Argentina, and paratypes were collected also in Paraguairí, Paraguay (Froehlich, 2002). Here, we report a new record for the Brazilian part of Foz do Iguaçu, Paraná State, Brazil.

3.2.2. *Tupiperla misionera* Froehlich, 2002

Material examined (new record). Brazil, Santa Catarina, Orleans, Minador Stream - #63, S28°10'24", W49°24'37", 06.vii-19.viii.2013, Malaise, L.C. Pinho *et al.*, 2 males; same data, except for: #66, S28°10'28", W49°24'36", 14.viii-12.x.2013, Malaise, L.C. Pinho *et al.*, 4 males; same data, except for: #70, S28°10'35", W49°24'36", 12.x-10.ix.2013, Malaise, L.C. Pinho *et al.*, 1 male; Brazil, Paraná, Céu Azul, Manoel Ribas Stream, céu 04, #3490, 06.ix.2012, light trap, A.P.M. Santos, 2 males.

Remarks: Like *Tupiperla flinti*, this species was described by Froehlich (2002). The description was based on a single male specimen from Misiones Province, Argentina. Novaes & Bispo (2016) recorded the species from Santa Margarida do Sul, Rio Grande do Sul State, Brazil. Here we report the records to Santa Catarina and Paraná States, Brazil.

3.2.3. *Tupiperla oliveirai* Froehlich, 1998

Material examined (new record). Brazil, Minas Gerais, Serra do Salitre, RPPN Cachoeira do Campo, S19°10'06.3", W46°34'09.4", 11-15.x.2012, light trap, A.R. Lima leg. (UFMG IPL 1600023), 1 male; same data, except for: (UFMG IPL 1600026), 1 female; same data, except for: (UFMG IPL 1600027), 1 female.

Remarks. The type of this species comes from Pirenópolis, Goiás State, Brazil. We examined material from Serra do Salitre, Minas Gerais State, 580 km from Pirenópolis. This is a new record for the species.

3.2.4. *Tupiperla tessellata* (Brauer, 1866)

Material examined. Brazil, Minas Gerais, Nova Lima, woods, S19°58'7.4", W43°51'22.7", 20.ii.2016–13.iii.2016, Malaise, A.R. Lima leg. (UFMG IPL 1600017) 1 male; same data, except for: 7.ii.2016–22.ii.2016, Malaise, A.R. Lima leg. (UFMG IPL 1600011), 1 male; same data, except for: (UFMG IPL 1600013), 1 male.

Remarks. The type of this species comes from Atlantic Forest of the Rio de Janeiro State. Material has been collected in several localities of Brazil (Table 3). Here, we report an additional record from Minas Gerais State.

3.2.5. *Tupiperla furcata* sp. nov.

(Figs. 3A–C, Figs. 4A–E)

Type material. Holotype, male: Brazil, Santa Catarina, Urubici, Parque Nacional São Joaquim, S28°09'20", W49°38'47", 23.viii–05.ix.2014, Malaise, L.C. Pinho *et al.* Paratypes: same data as holotype, except for: 1 male, 2 females.

Measurements. Holotype, male: head width, 1.1 mm; pronotum width, 1.1 mm; pronotum length, 1.1 mm; forewing length, 9.0 mm; hindwing length, 8.0 mm; antennae length, 9 mm; number of cercomeres, 16; paratypes: male (n= 1): head width, 1.1 mm; pronotum width, 1.1 mm; pronotum length, 1.1 mm; forewing length, 8.5 mm; hindwing length, 7.5 mm; antennae length, 7.8 mm; number of cercomeres, 13; females (n= 2): head width, 1.2 mm; pronotum width, 1.2 mm; pronotum length, 1.2 mm; forewing length, 9.5–11.0 mm; hindwing length, 8.5–9.2 mm; antennae length, 8.5 mm (only one female); number of cercomeres, 14–15.

Figure 3A–C. *Tupiperla furcata* sp. nov. Holotype adult male, head and pronotum in dorsal view (A). Adult female, head and pronotum in dorsal view (B). Male Fore and hindwings (C). Scale bar: 0,5 mm. (Abbreviations: AA1, first anterior Analis; AA2, second anterior Analis; CuA, anterior cubitus; CuP, posterior cubitus; M, Media; PC, Pterostigmatic cell; RA, anterior Radius; RP, posterior Radius; Sc, Subcosta).

Description. *Tupiperla furcata* sp. nov. is a medium sized species. General color ochraceous to brownish. Head brown with a lighter area between paired ocelli, and two lighter bands from the lateral ocelli to the eyes, parietalia rough (Figs. 3A–B). Ocelli and eyes black. Labrum light brown, darker than clypeus. Maxillary palps ochraceous, 5-

segmented; first and fourth segments short, second, third and fifth longer; fifth segment slightly darker than the others. Labial palps ochraceous, 3-segmented; the last segment slightly darker than the other. Antennae brown. Pronotum square, light brown, with rough surface and narrower than the head. Legs light brown to ochraceous. Legs with a large disto-ventral spine on femur, distal region of spine darker. Tibia with a perpendicular suture in the proximal region and with two spurs at the distal region. Tarsi light brown, fore- and midlegs with tarsomere 1 medium, tarsomere 2 short and tarsomere 3 long; hind leg with tarsomeres 1 and 3 subequal and long; tarsomere 2 short. Forewing membranous light brown; inconspicuous darker pattern bordering veins and crossveins; pterostigmatic crossveins absent; 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 short forked, 6th anal vein may be fused with hind margin of wing (Fig. 3C).

Male. Abdomen brownish to ochraceous with slightly clear band on abdominal terga 1–9. In dorsal view, T10 ochraceous with clear band on anterior region; T10 extension brownish, large, Y-shaped and ending in two large down curved teeth (Fig. 4A). In ventral view, paraprocts thin, directed to the T10 extension. Subgenital plate ochraceous, triangular and with apex prolonged between the paraprocts (Fig. 4B). In lateral view, T10 extension is curved ventrally, ending in two large teeth; paraprocts deeply forked distally forming two thin bars; apex of dorsal bar slightly upcurved, apex of ventral bar slightly downcurved (Fig. 4C). Median epiproct absent.

Female. Abdomen membranous; brownish to ochraceous with slightly clear band on abdominal terga and with abdominal sterna darker; St7 with two small and inconspicuous sclerites; subgenital plate long with base broadest and reaching St10; a deep U-shaped notch medially dividing the plate (Figs. 4D–E); paraprocts thin and long compared to the other congeners; apex truncated. Nymphs unknown.

Etymology. The name “*furcata*” refers to forked shape of paraprocts in males and subgenital plate in females of this species.

Remarks. The new species described here, *Tupiperla furcata* **sp. nov.**, is based on two male and two female specimens collected in the mountains of National Park of São Joaquim, municipality of Urubici, Santa Catarina State. The area has a maximum altitude of 2,000 m a.s.l. and it is characterized by the Atlantic Forest vegetation cover. The species can be distinguished from the congeners by the complex paraprocts and the shape of T10 extension in males, and by the complex shape of subgenital plate in females. The T10 extension in males is large and forked, resembling a swallowtail shape as in *T.*

froehlichii Bispo & Lecci, 2011. On the other hand, the paraprocts of *T. furcata* **sp. nov.** are deeply forked forming two thin bars unique in Gripopterygidae (Fig. 4C). The subgenital plate of females is long and it has a deep medial notch also unique in Brazilian Gripopterygidae (Figs. 4D–E).

Figure 4A–E. *Tupiperla furcata* **sp. nov.** Holotype adult male terminalia in dorsal (A), ventral (B), and lateral views (C). Female terminalia in ventral (D) and ventro-lateral views (E). Scale bar: 0,5 mm.

4. Discussion

Distribution of Brazilian Gripopterygidae

Gripopteryginae comprises 16 South American genera, four of them recorded in Brazil: *Gripopteryx*, *Guaranyperla*, *Paragripopteryx* and *Tupiperla* (Table 1). Many species presented in Table 3 have been recorded only in Brazil, except for *Gripopteryx serrei* Navás, 1930 and *Paragripopteryx baratinii* Benedetto, 1983 both restricted to Uruguay, and *Tupiperla flinti* Froehlich, 2002 and *T. misionera* Froehlich, 2002 also recorded in Argentina and Paraguay (Fig. 1, Table 3).

The records of Gripopterygidae species by Brazilian political regions have been asymmetric in part in view of the size of country and, consequently, its differentiated biomes, altitudinal variations and the distributional pattern of species. Additionally, the research founts have been unevenly concentrated among the country's regions, with a higher concentration of research groups in the Southeast and South of the country.

Currently, there are no records of Gripopterygidae in the Northern Region. Since important research projects in the Amazon, especially regarding the INPA researchers, have been carried out there, probably this reflects the distribution of family. On the other hand, the largest number of species have been recorded in the Southeastern and South Brazilian states, 41 and 23 species by region, respectively (Table 3). In the Northeast Region, the records of species have increased in part due to the efforts concerning the Semi-Arid Biodiversity Research Program (semi-arid PPBio). There are eighth species recorded in the Northeast, while in the Center-West there are two records.

Concerning the number of records of species by genus by state, São Paulo State is the one which has the largest amount of records (Fig. 5). Until 2011 a total of 26 species of Gripopterygidae were registered in São Paulo (Froehlich, 2011). Most of these records are due to the efforts of Prof. Dr. Claudio G. Froehlich and other researchers involved in programs such as the BIOTA/FAPESP, that since 1999 has funding studies on fauna of São Paulo State. Currently, there are records of 10 species of *Gripopteryx*, two *Guaranyperla*, 11 *Paragripopteryx* and 10 *Tupiperla* in a total of 33 species recorded from São Paulo State (Fig. 5; Table 3).

Figure 5. Graph of Gripopterygidae genera recorded in Brazil by states and regions.

Santa Catarina State is the second in number of Gripopterygidae records in Brazil, 16 species in three genera: *Gripopteryx* with six species, *Paragripopteryx* with seven and *Tupiperla* with three records. Gripopterygidae records in this state were initially derived from the collection effort made by Fritz Plaumann between the beginning and middle of the twentieth century. Recently, the increase of records is a result of the collection effort of Dr. Luis Carlos de Pinho, Federal University of Santa Catarina, through projects linked to FAPESC and CNPq.

The Espírito Santo State followed by Minas Gerais and Rio de Janeiro states have 15, 14 and 14 records of Gripopterygidae, respectively. As regards to Espírito Santo, there are nine records of *Gripopteryx*, three of *Paragripopteryx* and three of *Tupiperla*, plus a record of *Guaranyperla* nymph. Until 2010, a single species (*Gripopteryx maculosa*) was recorded for the state (Froehlich, 2010). However, this scenario has been changing since later studies by Avelino-Capistrano & Nessimian (2014) and Gonçalves *et al.* (2017) that exponentially increased the records of species for Espírito Santo.

For Minas Gerais, at least four species have been recorded since Froehlich (2010). Currently, there are records of six species of *Gripopteryx*, one of *Guaranyperla*, one of

Paragripopteryx and six of *Tupiperla* in the state. On the other hand, for Rio de Janeiro at least three species have been recorded since 2010 with current records including seven species of *Gripopteryx*, one *Guaranyperla*, one *Paragripopteryx* and five *Tupiperla* (Fig. 5).

Finally, Gripopterygidae has been recorded, but in fewer number, in other five Brazilian states. In Bahia, there were no records of Gripopterygidae until 2011, when two species of *Gripopteryx*, *G. garbei* and *G. pinima* were recorded, and *G. clemira* was described in the south of the state (Lecci & Froehlich, 2011). Since then, plus three species records and two descriptions have been made (Duarte *et al.*, 2014a, b; Lecci *et al.*, 2014), mainly due to increased collection effort and the formation of the research groups coordinated by Dr. Adolfo R. Calor (UFBA) and Dr. Freddy R. Bravo Quijano (UEFS). Currently, eighth Gripopterygidae species are recorded in the state (four *Gripopteryx*, one *Paragripopteryx*, three *Tupiperla*), being the sixth state with the largest number of recorded species.

Rio Grande do Sul with seven species (four *Gripopteryx*, three *Tupiperla*), Paraná with two species (*Tupiperla*), Goiás with two species (*Tupiperla*) and Pernambuco with one species (*Tupiperla*) are the other states where the family is recorded (Fig. 5; Table 3).

Table 3. Gripopterygidae genera and species recorded in Brazil and surrounding, with respective known life stages. Published articles with the species records are given in the middle column.

N	Species	Author, year	Records	Known life stages		
Gripopteryx: BRA (BA, ES, MG, RJ, RS, SC, SP), URY (FLO)				♂	♀	N
1	G. brasiliensis	(Šámal, 1921)	SC (Šámal, 1921; Jewett, 1959; Lecci & Froehlich, 2011)	●	●	-
2	G. cancellata	(Pictet, 1841)	SC (Jewett, 1960); MG, RS (Froehlich, 1993); RJ (Froehlich, 1993; Lecci & Froehlich, 2011; Avelino-Capistrano & Nessimian, 2013); SP (Froehlich, 1993; Lecci & Froehlich, 2011); BA (Duarte et al., 2014a); ES (Gonçalves et al., 2017)	●	●	●
3	G. caparao	Gonçalves, Novaes & Salles, 2017	ES (Gonçalves et al., 2017)	●	-	-
4	G. clemira	Lecci & Froehlich, 2011	BA (Lecci & Froehlich, 2011)	●	●	-

5	<i>G. coruja</i>	Froehlich, 1993	SP (Froehlich, 1993; Bispo & Lecci, 2011; Illies, 1963); ES (Avelino-Capistrano & Nessimian, 2014)	•	•	•
6	<i>G. elisae</i>	Illies, 1964	RS (Illies, 1964); SC (Here)	•	-	•
7	<i>G. flinti</i>	Froehlich, 1993	RJ (Froehlich, 1993; Lecci & Froehlich, 2011); SP (Froehlich, 1993; Lecci & Froehlich, 2011; Bispo & Lecci, 2011); SC (Here)	•	•	-
8	<i>G. garbei</i>	Navás, 1936	RJ (Navás, 1936; Froehlich, 1990, 1993; Avelino-Capistrano & Nessimian, 2013); MG , SP (Froehlich, 1990, 1993); SC (Froehlich, 1993); BA (Lecci & Froehlich, 2011; Duarte <i>et al.</i> , 2014a; Here); ES (Avelino-Capistrano & Nessimian, 2014)	•	•	•
9	<i>G. japi</i>	Lecci & Froehlich, 2011	SP (Lecci & Froehlich, 2011)	•	•	•
10	<i>G. juetah</i>	Froehlich, 1990	SP , MG (Froehlich, 1990); ES (Gonçalves <i>et al.</i> , 2017)	•	•	•
11	<i>G. liana</i>	Froehlich, 1993	MG (Froehlich, 1993)	•	•	•
12	<i>G. maculosa</i>	Jewett, 1960	ES , RJ (Jewett, 1960)	•	•	-
13	<i>G. pardina</i>	Navás, 1936	RJ (Navás, 1936)	-	•	-
14	<i>G. pilosa</i>	Froehlich, 1990	MG , RJ , SP (Froehlich, 1990); RJ (Avelino-Capistrano & Nessimian, 2013); ES (Gonçalves <i>et al.</i> , 2017)	•	•	•
15	<i>G. pinima</i>	Froehlich, 1993	SP (Froehlich, 1993; Bispo & Lecci, 2011); BA (Lecci & Froehlich, 2011; Duarte <i>et al.</i> , 2014a; Here); ES (Avelino-Capistrano & Nessimian, 2013)	•	•	•
16	<i>G. reticulata</i>	Brauer, 1866	RJ (Brauer, 1866; Jewett, 1960; Froehlich, 1990, 1993; Avelino-Capistrano & Nessimian, 2013); MG (Froehlich, 1990, 1993); SP (Jewett, 1960; Froehlich, 1990, 1993; Bispo & Lecci, 2011); RS (Novaes & Bispo, 2016); ES (Gonçalves <i>et al.</i> , 2017)	•	•	•
17	<i>G. serrei</i>	Navás, 1930	FLO/URY (Navás, 1930)	-	•	-
18	<i>G. serrensis</i>	Froehlich, 1993	RS (Froehlich, 1993); SC (Lecci & Froehlich, 2011)	•	•	•*
Guaranyperla: BRA (ES (Nymphs), MG, RJ, SP)				♂	♀	N
1	<i>G. beckeri</i>	Froehlich, 2001	MG (Froehlich, 2001)	•	-	-

2	<i>G. guapiara</i>	Froehlich, 2001	SP (Froehlich, 2001, 2015); RJ (Avelino-Capistrano & Nessimian, 2013)	•	•	•
3	<i>G. nitens</i>	Froehlich, 2001	SP (Froehlich, 2001, 2015)	•	•	•
<i>Paragripopteryx</i>: BRA (BA, ES, RJ, RS (Nymphs), SC, SP), URY (LAV)				♂	♀	N
1	<i>P. anga</i>	Froehlich, 1969	SP (Froehlich, 1969, 1994; Bispo & Lecci, 2011)	•	•	•
2	<i>P. baratinii</i>	Benedetto, 1983	LAV/URY (Benedetto, 1983)	•	•	-
3	<i>P. blanda</i>	Froehlich, 1969	SP (Froehlich, 1969, 1994; Bispo & Lecci, 2011); SC (Duarte, Calor & Bispo)	•	•	•
4	<i>P. convexa</i>	Duarte, Calor & Bispo	SC (Duarte, Calor & Bispo)	•	-	-
5	<i>P. dasalmas</i>	Duarte, Calor & Bispo	BA (Duarte, Calor & Bispo)	•	•	-
6	<i>P. delicata</i>	Froehlich, 1994	SP (Froehlich, 1994)	•	•	•*
7	<i>P. egena</i>	Froehlich, 1994	SP (Froehlich, 1994; Bispo & Lecci, 2011); ES (Gonçalves <i>et al.</i> , 2017); SC (Duarte, Calor & Bispo)	•	•	-
8	<i>P. guardae</i>	Froehlich, 1994	SP (Froehlich, 1994)	•	•	•
9	<i>P. hamata</i>	Froehlich, 1994	SP (Froehlich, 1994; Bispo & Lecci, 2011)	•	•	-
10	<i>P. intervalensis</i>	Bispo & Lecci, 2011	SP (Bispo & Lecci, 2011); ES (Gonçalves <i>et al.</i> , 2017); SC, MG (Duarte, Calor & Bispo)	•	•	-
11	<i>P. kapilei</i>	Bispo & Lecci, 2011	SP (Bispo & Lecci, 2011); SC (Duarte, Calor & Bispo)	•	-	•
12	<i>P. klapaleki</i>	Enderlein, 1909	RJ (Enderlein, 1909); SP (Froehlich, 1969; Bispo & Lecci, 2011); ES (Gonçalves <i>et al.</i> , 2017); SC (Jewett, 1960; Duarte, Calor & Bispo)	•	•	•
13	<i>P. merui</i>	Froehlich, 1994	SP (Froehlich, 1994)	•	-	•*
14	<i>P. ogum</i>	Duarte, Calor & Bispo	SC (Duarte, Calor & Bispo)	•	•	-
15	<i>P. paranapiacabae</i>	Bispo & Lecci, 2011	SP (Bispo & Lecci, 2011)	•	-	-
<i>Tupiperla</i>: BRA (BA, ES, GO, MG, PE, RJ, RS, SC, SP), ARG (MIS), PRY (PRI)				♂	♀	N
1	<i>T. amandae</i>	Bispo & Lecci, 2011	SP (Bispo & Lecci, 2011)	•	•	-
2	<i>T. amorimi</i>	Froehlich, 2016	MG (Froehlich, 2016)	•	•	-
3	<i>T. barbosai</i>	Avelino-Capistrano & Nessimian, 2013	RJ (Avelino-Capistrano & Nessimian, 2013)	•	-	-
4	<i>T. bispoi</i>	Duarte, Lecci & Calor, 2014	BA (Duarte <i>et al.</i> , 2014a)	•	•	•
5	<i>T. eleonorae</i>	(Froehlich, 1994)	SP (Froehlich, 1994, 1998)	•	•	-
6	<i>T. flinti</i>	Froehlich, 2002	MIS/ARG, PRI/PRY (Froehlich, 2002); PR (Here)	•	•	-

7	<i>T. froehlichii</i>	Bispo & Lecci, 2011	SP (Bispo & Lecci, 2011)	•	-	-
8	<i>T. furcata</i> sp. nov.	<u>Here</u>	SC (<u>Here</u>)	•	•	-
9	<i>T. gracilis</i>	(Burmeister, 1939)	RJ (Burmeister, 1939); SP (Illies, 1963, in part); MG (Froehlich, 1998, 2016); ES (Gonçalves <i>et al.</i> , 2017)	•	•	•
10	<i>T. guariruru</i>	Duarte, Bispo & Calor, 2014	BA (Duarte <i>et al.</i> , 2014b)	•	•	-
11	<i>T. illiesi</i>	Froehlich, 1998	SP (Froehlich, 1998)	•	•	-
12	<i>T. jumirim</i>	Bispo & Froehlich, 2007	GO (Bispo & Froehlich, 2007)	•	•	-
13	<i>T. misionera</i>	Froehlich, 2002	MIS/ARG (Froehlich, 2002); RS (Novaes & Bispo, 2016); SC, PR (<u>Here</u>)	•	-	-
14	<i>T. modesta</i>	Froehlich, 1998	SP (Froehlich, 1998)	•	•	-
15	<i>T. oliveirai</i>	Froehlich, 1998	GO (Froehlich, 1998); MG (<u>Here</u>)	•	•	-
16	<i>T. reichardti</i>	Froehlich, 1998	MG, SP (Froehlich, 1998); RJ (Avelino-Capistrano & Nessimian, 2013)	•	•	-
17	<i>T. robusta</i>	Froehlich, 1998	RJ, SP (Froehlich, 1998); ES (Avelino-Capistrano & Nessimian, 2014); MG (Novaes & Bispo, 2014)	•	•	•
18	<i>T. sepeensis</i>	Novaes & Bispo, 2016	RS (Novaes & Bispo, 2016)	•	-	-
19	<i>T. sulina</i>	Froehlich, 1998	SC (Froehlich, 1998)	•	•	-
20	<i>T. tessellata</i>	(Brauer, 1866)	RJ (Brauer, 1866); SC (Jewett, 1960); MG (Froehlich, 1998; <u>Here</u>); SP (Froehlich, 1998); BA (Duarte <i>et al.</i> , 2014a); PE (Lecci <i>et al.</i> , 2014); ES (Avelino-Capistrano & Nessimian, 2014); RS (Novaes & Bispo, 2016)	•	•	-
21	<i>T. umbya</i>	Froehlich, 1998	SP (Froehlich, 1998)	•	•	-

Duarte, Calor & Bispo: in Chapter II; Duarte, Novaes & Bispo: in Annex I.

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