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Sistemática e biogeografia de Helicopsychidae do Novo Mundo (Trichoptera): desafios no enfretamento dos déficits de conhecimento da biodiversidade

Salvador
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Rafael Pereira da Silva

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“A educação não transforma o mundo. Educação muda pessoas. Pessoas transformam o mundo!

(Paulo Freire 1979, p. 84)

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Índice

Resumo

Helicopsychidae é uma das famílias mais facilmente reconhecíveis, principalmente pelo singular formato helicoidal dos abrigos larvais, que se assemelham às conchas de moluscos gastrópodes. Atualmente, 304 espécies estão descritas em dois gêneros, *Rakiura* McFarlane, monotípico e endêmico da Nova Zelândia, e *Helicopsyche* von Siebold. *Helicopsyche* apresenta 303 espécies e distribuição em todas as regiões biogeográficas, exceto Antártica. A maior diversidade deste gênero é encontrada nos trópicos. Os estudos taxonômicos sobre os Helicopsychidae iniciaram-se no século XIX a partir de uma má interpretação dos abrigos larvais. Somente em 1856 o gênero *Helicopsyche* foi descrito com base em abrigos larvais de três espécies. Posteriormente, Hagen transferiu outras quatro espécies para *Helicopsyche*. Os erros de interpretação só foram resolvidos com a publicação de *Genera Insectorum* por Ulmer, com o reconhecimento do gênero como pertencente à ordem Trichoptera. As relações filogenéticas do grupo foram inferidas primeiramente por Schmid e, posteriormente, por Johanson. Em um trabalho recente de inferências filogenéticas e biogeográficas para Sericostomatoidea, as hipóteses precedentes foram refutadas e foi recuperada uma relação entre os subgêneros Neotropicais *Feropsyche* Johanson e *Cochliopsyche* Müller. *Feropsyche*, o subgênero mais rico em espécies (127 espécies), foi revisado em 2002 e desde então ca. 50 espécies foram descritas. Porém, padrões de distribuição, conhecimento de semaforontes e de aspectos biológicos ainda permanecem pouco explorados. Na contramão, *Cochliopsyche*, endêmico da região Neotropical e com apenas 17 espécies, foi revisado em 2003 e desde então apenas registros de distribuição e descrição de uma única espécie foram feitos. Neste contexto, ambos os grupos, *Cochliopsyche* em especial, apresentam déficits de conhecimento da biodiversidade relacionados ao conhecimento das espécies (Déficit Linneano), padrões de distribuição (Déficit Wallaceano), de conhecimento dos semaforontes (Déficit Haeckeliano) e de conhecimento da evolução dos grupos (Déficit Darwiniano). Assim, a presente tese objetiva fornecer uma ampliação do conhecimento de Helicopsychidae na região Neotropical com descrição de novas espécies e dos padrões distribucionais. Para tanto, uma revisão sistemática de *Cochliopsyche* foi feita, assim como estudos filogenéticos e biogeográficos para a família. Como resultados temos a descrição de quatro novas espécies de *H.* (*Feropsyche*) e estabelecimento dos padrões biogeográficos, mapas de distribuição potencial e construção de base de dados com informações sobre este subgênero. Os representantes do âmbar Dominicano são retirados deste grupo com base em inferências filogenéticas. Também são aventadas hipóteses que o subgênero forme uma linhagem junto ao subgênero australasiano *Saetotrichia*. *Cochliopsyche* é reerigido ao status de gênero com base em inferências filogenéticas e biogeográficas, como grupo irmão dos *H.* (*Petrotrichia*) com alto suporte. Adicionalmente é fornecida uma revisão sistemática de *Cochliopsyche*, com fornecimento de descrição padronizada para todas as espécies e descrição de cinco espécies novas. Para além dos grupos Neotropicais, uma proposta filogenética entre os grupos viventes e fósseis de Helicopsychidae, assim como a reconstrução de área ancestral para o grupo. Como legado do trabalho temos o combate aos déficits de conhecimento Linneano, Wallaceano e Darwiniano para os grupos Neotropicais. A hipótese filogenética apresentada sugere que os subgêneros restantes de *Helicopsyche* constituam linhagens independentes, porém devido ao baixo suporte e amostragem taxonômica, seremos conservativos, apenas indicamos a necessidade de trabalhos mais abrangentes que testem essa hipótese, preferindo, assim, não realizar mudanças taxonômicas para além do escopo deste trabalho.

Palavras-chave. *Cochliopsyche*, *Feropsyche*, inferências filogenéticas, *Helicopsyche*, modelagem de distribuição, novas espécies.

Abstract

Helicopsychidae is one of the most easily recognizable families, mainly due to the unique helical shape of the larval case, which resembles the shells of gastropod mollusks. Currently, 304 species are described in two genera, *Rakiura* McFarlane, monotypic and endemic to New Zealand, and *Helicopsyche* von Siebold. *Helicopsyche* has 303 species and a distribution in all biogeographic regions except Antarctica, with the greatest diversity found in the tropics. Taxonomic studies on the Helicopsychidae date back to the 19th century due to a misinterpretation of larval case. Only in 1856 the genus *Helicopsyche* was described based on the larval case of three species. Subsequently, Hagen transferred another four species to *Helicopsyche*. Misinterpretations were only resolved with the publication of *Genera Insectorum* by Ulmer, recognizing the genus as belong to the order Trichoptera. The phylogenetic relationships of the group were inferred by Schmid and, later, by Johanson with a large sample size. In a recent phylogenetic and biogeographic study on Sericostomatoidea, the previous hypotheses were refuted, and the relationship was proposed for the Neotropical subgenera *Feropsyche* Johanson and *Cochliopsyche* Müller. *Feropsyche*, the richest subgenus in species (127 species), was revised in 2002 and since then ca. 50 species have been described. However, distribution patterns, knowledge of semaphoronts and biological aspects remain poorly explored. On the other hand, *Cochliopsyche*, endemic to Neotropics and with only 17 species, was revised in 2003 and since then only distribution records and the description of one species have been made for the group. In this context, both groups, especially *Cochliopsyche*, have shortfalls in biodiversity knowledge related to species (Linnean shortfall), distribution patterns (Wallacean shortfall), knowledge of semaphoronts (Haeckelian shortfall) and knowledge of the evolution of the groups (Darwinian shortfall). In this context, this thesis aims to expand the knowledge of Helicopsychidae in the Neotropical region by describing new species and distributional patterns. In addition, a systematic revision of *Cochliopsyche* was performed, as well as the phylogenetic and biogeographic studies on the family. The results include the description of four new species of *H.* (*Feropsyche*) and the establishment of biogeographic patterns, potential distribution maps and the construction of a database with information on the group. The representatives of Dominican amber are removed from this subgenus based on phylogenetic results. Hypothesis are presented that the subgenus *Feropsyche* forms a lineage with the Australasian subgenus *Saetotrichia*. *Cochliopsyche* is resurrected to genus status based on phylogenetic and biogeographic results, and *H.* (*Petrotrichia*) as its sister group, with high support. In addition, a systematic revision of *Cochliopsyche* is provided, including standardized descriptions for all described species and description of five new species. In addition to Neotropical taxa, a phylogenetic proposal is presented for living and fossil species of Helicopsychidae, as well as a reconstruction of the ancestral area for the group. The legacy of this work is to be facing the shortfalls in Linnean, Wallacean and Darwinian knowledge of Neotropical taxa. The phylogenetic hypothesis presented suggests that the remaining subgenera of *Helicopsyche* form independent lineages, but due to the low support and taxon sampling, we are conservative and only indicate the need for more comprehensive work to test this hypothesis, preferring not to make taxonomic changes beyond the scope of this work.

Keywords: *Cochliopsyche, Feropsyche*, phylogenetic inferences, *Helicopsyche,* distribution modelling, new species.

Introdução Geral

Os insetos constituem o grupo mais diversificado e rico em espécies dentre a macrofauna da Terra, com ca. 50–70% do total de espécies descritas (Stork 2018). Nos ecossistemas continentais e aquáticos, esses animais desempenham papéis essenciais para a manutenção da biodiversidade e dos processos ecossistêmicos (Dangles & Casas 2019). Para além disso, a manutenção de populações viáveis, a conservação das espécies e a proteção dos seus habitats permitem que os insetos continuem atuando nos serviços essenciais para a manutenção do bom funcionamento dos ambientes, assim como a subsistência humana através dos seus serviços de provisão, suporte e regulação, tão necessários para manutenção da vida como um todo (Dangles & Casas 2019). Por outro lado, as ações antropogênicas nos ecossistemas do mundo têm contribuído para elevados declínios das populações de insetos, levando a extinções locais e regionais de espécies menos tolerantes (Vogel 2017; Eisenhauer et al. 2019; Boyes et al. 2021 Bowler 2022).

Em termos de unidade ecológicas, os ecossistemas de águas continentais constituem as unidades mais ricas e diversas, abrigando ca. 10% da biodiversidade mundial em uma área de menos de 1% da superfície do planeta (Tickner et al. 2020). Os ecossistemas dulcícolas se destacam por sua elevada biodiversidade, mas, também, por serem particularmente suscetíveis às interferências antrópicas (Dijkstra et al. 2014). Tais ambientes fornecem uma gama diversificada de serviços ecossistêmicos essenciais para manutenção da vida e, em particular, da civilização humana (Culhane et al. 2019). Em contraponto, esses ecossistemas têm sofrido alterações devido aos processos de urbanização, agropecuária, poluição, desmatamento e mudanças climáticas, principalmente nos últimos 50 anos (Wagner 2019; Wagner et al. 2021).

A biodiversidade dulcícola experimenta declínios populacionais muito maiores quando comparados aos ecossistemas terrestres e marinhos (MEA 2005). Estimativas recentes indicam que o declínio populacional de espécies de insetos é duas vezes maior que o de vertebrados, assim como as taxas de extinção locais são oito vezes maiores para insetos do que para vertebrados (Sánchez-Bayo & Wyckhuys 2019). Atualmente, 33% das espécies de insetos aquáticos estão ameaçadas de extinção e, a cada ano, cerca de 1% de todas as espécies têm sido adicionadas a essa lista, resultando numa taxa de extinção média (espécies não observadas em 50 anos) de 6,8–9% para alguns grupos (Sánchez-Bayo & Wyckhuys 2019).

Dentre os organismos dulcícolas, os insetos aquáticos têm recebido bem menos atenção que plantas e vertebrados em estudos relacionados a conservação (Contrador et al. 2012), apesar de serem essenciais para a estrutura e funcionamento adequados dos ecossistemas de água doce (Bowles & Courtney 2018). Além de importantes componentes desses ecossistemas (Dijkstra et al. 2014; Morse et al. 2019), os insetos aquáticos são bons bioindicadores em estudos de avaliação da saúde ambiental, devido ao seu amplo gradiente de sensibilidade às alterações na integridade dos ambientes (Akamagwuna & Odume 2020). Portanto, conhecer e conservar a biodiversidade, assim como os processos ecossistêmicos envolvidos nos ambientes dulcícolas constituem grandes desafios para a limnologia (Poff et al. 2012).

As estratégias de conservação da biodiversidade são limitadas pelo conhecimento escasso da biodiversidade (Galetti et al. 2021). Para insetos aquáticos, cerca de 80% das espécies estimadas permanecem desconhecidas (Mora et al. 2011). Além disso, das espécies formalmente descritas, menos de 10% apresentam mais de 20 registros de distribuição, em contraste com outros grupos que apresentam de 20% a 80% das espécies com mais de 20 registros (crustáceos e peixes, respectivamente) (Troudet et al. 2017). Esses déficits de conhecimento da biodiversidade não estão limitados ao desconhecimento das espécies (Déficit Linneano) e de sua distribuição (Déficit Wallaceano), mas também às interações biológicas (Déficits Eltoniano e Raunkiærano) e tolerâncias das espécies (Déficits Hutchinsoniano), ao conhecimento de diferentes estágios de vida (Déficit Haeckeliano) e à evolução dos grupos (Déficit Darwiniano) (Hortal et al. 2015; Faria et al. 2020).

Dentre as ordens de insetos aquáticos bioindicadores, Trichoptera Kirby se destaca por constituir a mais diversificada, taxonomicamente e em termos de características funcionais (Morse et al. 2019) e por fornecer uma diversa gama de serviços ecossistêmicos. Estes organismos desempenham papéis essenciais nas cadeias alimentares, atuando na engenharia de seus habitats, servindo de alimento para vertebrados aquáticos e terrestres, na conversão de partículas orgânicas para fragmentos menores, no monitoramento biológico da qualidade da água, assim como o uso de sua seda em trabalhos de biotecnologia de materiais ou de seu emprego em questões forenses (Holzer 1936; Wallace & Webster 1996; Ashton et al. 2012; Morse et al. 2019).

Os Trichoptera constituem a ordem originalmente aquática com maior riqueza de espécies, com 61 famílias, 765 gêneros e cerca de 16.800 espécies (Morse 2019). A ordem compreende duas subordens, Annulipalpia e Integripalpia, estabelecidas por Martynov (1924), posteriormente modificadas por Ross (1967), que podem ser reconhecidas com base na morfologia dos segmentos do palpo maxilar dos adultos e morfologia e características comportamentais dos imaturos. Essas subordens têm sido recuperadas nas análises filogenéticas mais recentes como monofiléticas, a exemplo de Thomas et al. (2020).

Os Annulipalpia apresentam larvas que constroem retiros fixos de detritos e/ou fragmentos minerais, mantidos juntos por meio da seda produzida por essas larvas. Os retiros são fixados ao substrato e as “redes” formada de seda geralmente utilizadas para captura de material orgânica particulada e outros invertebrados (Thomas et al. 2020).

Já os Integripalpia (*sensu* Ross) são divididos em dois grupos. O primeiro é formado por organismos de vida livre ou que produzem abrigos próximo ao estágio de pupa (anteriormente classificados como Spicipalpia). Enquanto o segundo, Phryganides, é constituído por organismos cujas larvas são construtoras de abrigos portáteis, geralmente tubulares, feitas de uma grande variedade de materiais encontrados no habitat larval, mantidos juntos também por meio da seda produzida por essas larvas (Thomas et al. 2020).

Diversos estudos buscaram entender a origem e dispersão dos Trichoptera, o que gerou diversas estimativas de datação dos grupos, desde as focadas no grupo (Ivanov & Sukatsheva 2002; Malm et al. 2013) até estimativas mais gerais dentro de Hexapoda (e.g., Misof et al. 2014). Na maioria destes, a origem de grupos cosmopolitas está datada de um período posterior à divisão da Pangeia (195–165 Ma), implicando em um forte poder de dispersão (Thomas et al. 2020). Já a proposição da Thomas et al. (2020) indica uma origem mais antiga para o grupo, tendo a Pangeia como área de origem e diversificação dos grupos mais inclusivos, seguida de diversificação e dispersão local de clados menos inclusivos. O que parece ser biologicamente mais consistente, dada a associação de estágios imaturos com os corpos d’água e uma baixa capacidade de dispersão em longas distâncias dos adultos (Holzenthal et al. 2015; Thomas et al. 2020).

O estudo de Thomas et al. (2020) conta até então com a maior amostragem em termos de táxons e caracteres dentre as inferências disponíveis para a ordem, neste trabalho estimou-se a origem da ordem Trichoptera entre 253–298 Ma. O ancestral comum mais recente dos Annulipalpia [Hydropsychoidea (143–217 Ma), Psychomyioidea (157–201 Ma) e Philopotamoidea (183–203 Ma)], e dos Integripalpia [(152–195 Ma), Hydroptilidae (181–247 Ma) e Glossosomatidae (153–224 Ma)] provavelmente tiveram origem anterior a divisão da Pangeia, em Laurásia e Gondwana (195–165 Ma) (McIntyre et al. 2017; Thomas et al. 2020). Isso é consistente com a vicariância como uma explicação para as distribuições atuais da maioria dos grandes grupos de Trichoptera (Thomas et al. 2020).

Esse cenário mais geral parece não se ajustar às famílias Rhyacophilidae (85–106 Ma) e Hydrobiosidae (60–121 Ma) (Thomas et al. 2020). Os Rhyacophilidae apresentam distribuição exclusiva no hemisfério norte, enquanto Hydrobiosidae apresenta distribuição no hemisfério sul com poucos representantes viventes e fósseis no hemisfério norte, porém com origem datada entre o Cenozóico e Cretáceo, após a divisão de Pangeia (Wichard 2013; Thomas et al. 2020). Os grupos caule das duas famílias são estimados para entre 190–195 Ma, desta forma, as duas famílias deveriam ter distribuição cosmopolita na Pangeia com extinção diferenciais em cada hemisfério, o que não tem evidências no registro fóssil (Thomas et al. 2020)

Já os Phryganides, formadores de abrigos portáteis tubulares, são datados no registro fóssil para o Jurássico médio (163–174 Ma) (Sukatsheva 1985), consistente com Thomas et al. (2020), que estimaram a origem do grupo entre 152–194 Ma. Nesse cenário, os Integripalpia teriam surgido e se diversificado na Pangeia e as linhagens das infraordens de Phryganides, Plenitentoria e Brevitentoria, teriam se irradiado após a divisão da Pangeia.

Os Plenitentoria, encontrados predominantemente no hemisfério norte e com origem aproximada de 127–165 Ma, se diversificaram na Laurásia, com posterior dispersão para hemisfério sul (e.g., Phryganoidea). Enquanto os Brevitentoria, são encontrados predominantemente no hemisfério sul e com origem aproximada de 135–174 Ma, se diversificaram na Gondwana, com posterior dispersão para hemisfério norte (e.g., Sericostomatoidea) (Thomas et al. 2020) ambos os padrões coerentes com o registro fóssil (Morse 2023).

Após a divisão da Pangeia, a fragmentação da Gondwana constitui um segundo período de origem de linhagens, o que é evidenciado pelo compartilhamento de fauna entre os continentes e/ou biorregiões que formavam esse supercontinente (e.g., Regiões Neotropical, Afrotropical, Antarctica, Indiana e Australasiana). Essas relações podem ser evidenciadas pelos Protoptilinae do sudeste asiático e da região Neotropical, os Tasimiidae distribuídos no sul da Região Neotropical (*Trichovespula*) e Australasiana (*Tasimia*) (Thomas et al. 2020), os subgêneros de *Helicopsyche* (Helicopsychidae) na Região Neotropical [*H.* (*Cochliopsyche*) e *H.* (*Feropsyche*)] e Afrotropical [*H.*

(*Petrotrichia*)] (Johanson 1998), entre tantos outros grupos com distribuição disjunta em áreas que foram componentes da Gondwana.

Levando em consideração a ampla definição do que é a biogeografia, todos os trabalhos que envolvem distribuição de espécies (e.g., descrição de novas espécies, registros de distribuição, listas e inventários), até os que se ocupam com os padrões e processos envolvidos na configuração dessa distribuição, podem ser alocados dentro desta disciplina. Vertentes como biogeografia evolutiva, por sua vez, usa dados distribucionais, filogenéticos, moleculares e fósseis para avaliar eventos históricos que produziram os padrões bióticos atuais (Morrone 2008), mas biogeografia pode também ser entendida como campo de estudos integradores que conecta conceitos e informações de ecologia, biologia evolutiva, taxonomia, geologia, geografia física, paleontologia e climatologia (Cox & Moore 2010).

Desta forma, trabalhos envolvendo discussões acerca dos padrões biogeográficos dos grupos presentes na Região Neotropical estão geralmente associados a inferências gerais acerca da distribuição dos grupos no globo (e.g., Johanson 1998; Wahlberg & Johanson 2014). Alguns trabalhos que buscam discutir os padrões de distribuição dos táxons na região utilizam geralmente uma abordagem descritiva (e.g., Ross & King 1952; Flint 1974; Robertson & Holzenthal 2005). Por fim, há trabalhos centrados em discutir os padrões e processos relacionados à distribuição ancestral e atual das espécies, porém geralmente estes carecem de uma abordagem analítica para embasar suas inferências (e.g., Ross & King 1952; Hamilton 1982; Holzenthal 1986a, b; Calor et al. 2006; Holzenthal & Blahnik 2010). Assim, são necessários esforços que visem a confecção de hipóteses de biogeografia interpretativa, possibilitando a diminuição de déficits relacionados à distribuição e a evolução dos grupos no espaço e tempo (Hortal et al. 2015).

Os Trichoptera apresentam 18 autapomorfias que os diferenciam das demais ordens de Amphiesmenoptera (Mey et al. 2017). O casulo pupal com parede semipermeável é a autapomorfia mais notável de Trichoptera, essa característica possivelmente permitiu que o grupo caule da ordem invadisse o ambiente aquático tornando Trichoptera, a única ordem de holometábolos conhecida com estágio pupal aquático (Morse 1997). Os Trichoptera historicamente contemplam duas subordens monofiléticas, Annulipalpia (=Vericloaca) e Integripalpia (=Dicloaca) (Thomas et al. 2020). Embora haja um terceiro grupo de quatro famílias que ora foi tratado como subordem Spicipalpia, ora foi incluído em Annulipalpia ou Integripalpia (Thomas et al.

2020). Atualmente as famílias "spicipalpianas" estão incluídas em Integripalpia e as inferências baseadas em dados moleculares suportam essa classificação (Thomas et al. 2020).

O entendimento das relações filogenéticas e a classificação da ordem foram mudando ao longo do tempo (Figura 1), as proposições mais recentes recuperaram Annulipalpia como composto por três superfamílias e nove famílias e Integripalpia composto pelas famílias spicipalpianas [Ptilocolepidae (Martynov), Hydroptilidae Stephens, Glossosomatidae Wallengren, Hydrobiosidae Ulmer, Rhyacophilidae Stephens] e por um grupo formado por produtores de abrigos portáteis, os Phryganides, composto por quatro superfamílias e 46 famílias (Thomas et al. 2020).

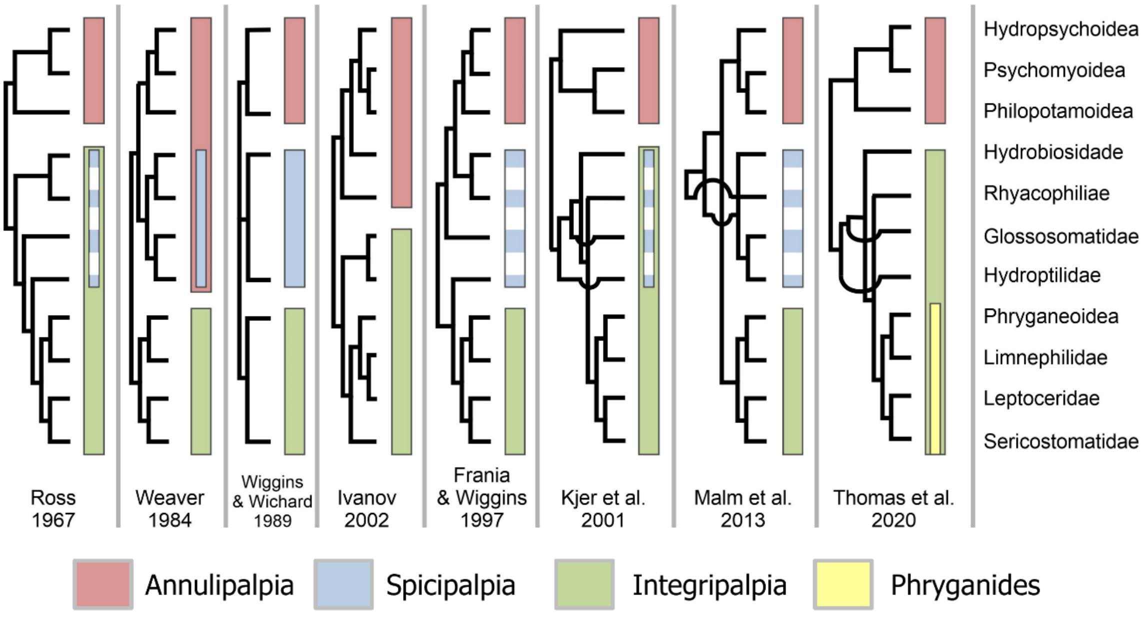

Figura 1. Proposições de relações filogenéticas de Trichoptera

A ordem apresenta elevados déficits de conhecimento da biodiversidade relacionados ao conhecimento das espécies, com estimativas que indicam que existam pelo menos 50.000 espécies de Trichoptera no mundo, sendo que boa parte dessa fauna deve estar em regiões tropicais como a Região Neotropical (de Moor & Ivanov 2008). A Região Neotropical compreende a área desde o sul do México até o sul da América do Sul, podendo ser dívida em províncias biogeográficas (*sensu* Morrone 2014) e ecoregiões (*sensu* Olson et al. 2001; Abell et al. 2008). Estas classificações em unidades menores são amplamente utilizadas em estudos de ecologia, sistemática e biogeografia (Bowles & Courtney 2018).

Dentre as regiões biogeográficas propostas por de Moor & Ivanov (2008) para Trichoptera, há um destaque para Região Oriental, com maior número de espécies, e a Região Neotropical, com segunda maior fauna em termos de riqueza, mas apontada como com grande potencial para descoberta de novos táxons, devido à diversidade encontrada para outros grupos nesta região, além das lacunas de amostragem para as regiões biogeográficas menos inclusivas desta região (de Moor & Ivanov 2008; Holzenthal & Calor 2017).

A Região Neotropical é conhecida por apresentar vastas florestas tropicais, sistemas fluviais e grande diversidade de fauna e flora, assim como pelo maior número de espécies dentre as regiões biogeográficas (Tundisi & Matsumura-Tundisi 2008). Também apresenta um elevado grau de perturbações antropogênicas, que ameaçam a integridade dos seus ecossistemas e sua biodiversidade (MEA 2005; Cayuela et al. 2012). Em especial a fauna de invertebrados, que permanece em grande parte desconhecida, com distribuição negligenciada e com uma parcela significativa ameaçada de extinção local e global (Stork 2018; Cardoso et al. 2020).

Nos ecossistemas Neotropicais se destacam os Integripalpia, que apresentam a maior diversidade entre os Trichoptera, representado por 18 das 26 famílias, ca. 75% dos gêneros e ca. 60% das espécies neotropicais, com uma infinidade de formas e funções entre os ecossistemas aquáticos continentais (Holzenthal & Calor, 2017; Morse et al. 2019). Entre os Phryganides, estão os Helicopsychidae Ulmer, uma das famílias mais facilmente reconhecíveis, principalmente pelo singular formato helicoidal dos abrigos larvais, torcidos dextralmente, se assemelhando a conchas de moluscos gastrópodes (Johanson 1998).

Em uma série de trabalhos, Johanson estabeleceu a base do conhecimento para os Helicopsychidae [Johanson 1995 (catálogo), Johanson 1997 (padrões zoogeográficos e mapa de distribuição) e Johanson 1998 (inferências filogenéticas e biogeográficas)]. A família apresenta dois gêneros, *Rakiura* McFarlane, 1973 (monoespecífico, endêmico da Nova Zelândia) e *Helicopsyche* von Siebold, 1856, com 304 espécies, seis subgêneros e distribuição cosmopolita, exceto Antártica (Morse 2023; Santos et al. 2023). Na Região Neotropical, há 144 espécies válidas de *Helicopsyche* (Holzenthal & Calor 2017; Morse 2023; Santos et al. 2023), distribuídas em dois subgêneros: *Helicopsyche* (*Cochliopsyche*) Müller, 1885 (17 espécies) e *H.* (*Feropsyche*) Johanson, 1998 (127 espécies, sendo três do registro fossilífero) (Holzenthal & Calor 2017; Morse 2023; Santos et al. 2023).

Dos subgêneros ocorrentes na Região Neotropical, *H.* (*Feropsyche*) foi revisado por Johanson (2002) e tem sido tratado em vários trabalhos nos últimos anos, especialmente com descrições de espécies (e.g., Souza et al. 2017; Vilarino & Calor 2017; Dumas & Nessimian 2019; Gama-Neto et al. 2019; Cavalcante-Silva et al. 2022). Por outro lado, *H.* (*Cochliopsyche*) não tem recebido a mesma atenção, por exemplo, nas análises filogenéticas para a família (Johanson 1998), apenas uma espécie do subgênero [*H.* (*Cochliopsyche*) *vazquezae* (Flint, 1986)] foi considerada e, após o trabalho de revisional de Johanson (2003), nenhuma espécie foi descrita.

O subgênero *Cochliopsyche* foi estabelecido por Müller sem a designação de espécies. Posteriormente, Ulmer (1905) descreveu a primeira espécie do subgênero [*Helicopsyche* (*Cochliopsyche*) *clara* (Ulmer, 1905)]. Flint (1972; 1983; 1986) adicionou três espécies [*H.* (*C.*) *opalescens* Flint 1972, *H.* (*C.*) *lobata* Flint 1983 e *H.* (*C.*) *vazquezae* Flint, 1986], enquanto Monson et al. (1988) apresentaram a descrição de estágios imaturos de *H.* (*C.*) *vazquezae* (Flint, 1986). Mais recentemente, Johanson (2003) realizou a revisão do grupo descrevendo outras 12 espécies apenas com base nos machos adultos, além da descrição e ilustração de fêmea de *H.* (*Cochliopsyche*) *clara*, única conhecida para o grupo. Assim, pode-se entender que os *Cochliopsyche* têm recebido menos atenção na taxonomia de Helicopsychidae, fato reforçado pelo número de espécies reconhecidas como novas, aguardando descrição depositadas em museus e coleções nacionais e internacionais.

Considerando os déficits de conhecimento da biodiversidade (Hortal et al. 2015), nosso entendimento acerca dos Helicopsychidae pode ser entendido como deficitário através de diferentes nuances: (i) déficit Linneano: muitas espécies, especialmente do subgênero *Cochliopsyche* apresentam a serem descritas, pode-se ainda atentar para o fato que algumas espécies apresentam descrições antigas e imprecisas, resultando em circunscrição frágil, além de contarmos com cinco espécies descritas apenas com base em abrigos larvais; (ii) déficit Wallaceano: quase a metade (ca. 45%) das espécies têm seu registro de distribuição restrito a localidade tipo ou localidades adjacentes; (iii) déficit Haeckeliano: os imaturos (ovos, larvas e pupas) e adultos (fêmeas) da maioria das espécies ainda são desconhecidos (estágios imaturos de apenas apenas 18 espécies e fêmeas de 26 espécies das 131 viventes foram descritos) (dados não publicados). Como dito, há cinco espécies descritas exclusivamente com base em estágios imaturos e duas com base nas fêmeas, as quais podem ser (ou não) sinônimos de outras espécies; (iv) e, também, pelo déficit Darwiniano (escassez de conhecimento acerca da evolução dos grupos), pois as relações filogenéticas entre os subgêneros de *Helicopsyche,* estabelecidas por Johanson (1998), são conflitantes com as relações recuperadas por Johanson et al. (2017), e, além disso, não há hipóteses acerca das relações filogenéticas entre as espécies nos subgêneros e tampouco inferências biogeográficas considerando os subgêneros.

Assim, pretende-se reduzir esses déficits através de critérios de delimitação de espécies com base no conceito morfológico de espécies (*sensu* Cronquist 1978) e a partir de descrições abrangentes e padronizadas das espécies fornecendo circunscrições mais robustas. Para além disso pretende-se fornecer uma ampliação do conhecimento dos padrões distribucionais. Adicionalmente, realizar uma revisão sistemática e construção de hipóteses filogenéticas e biogeográficas com ênfase no *H.* (*Cochliopsyche*). Os dados gerados fornecerão informações para o melhor entendimento da biodiversidade, das relações entre as espécies e da evolução do grupo. Conhecimento esse que já pode ser considerado consolidado para alguns grupos mais inclusivos da ordem, porém, poucas hipóteses filogenéticas têm sido propostas para grupos menos inclusivos (Thomas et al. 2020). Além disso, a extrapolação de dados fornecerá um melhor entendimento dos padrões de distribuição e histórico biogeográfico do grupo.

Diante do cenário apresentado, a presente tese tem como objetivo geral realizar um estudo de sistemática e biogeografia de Helicopsychidae do Novo Mundo, tendo como objetivos específicos:

I. Identificar e descrever padrões biogeográficos de *Helicopsyche* (*Feropsyche*)
II. Descrever novas espécies e realizar novos registros de distribuição de *Helicopsyche*
III. Propor hipóteses filogenéticas e biogeográficas para *Helicopsyche* (*Cochliopsyche*)
IV. Realizar revisão sistemática de *Helicopsyche* (*Cochliopsyche*)

Buscando responder aos objetivos estabelecidos, a presente tese está estruturada em quatro capítulos (manuscritos), sendo eles:

Capítulo 1 (Manuscrito I) – *Helicopsyche* (*Feropsyche*) Johanson, 1998 (Trichoptera) from Northeastern Mata Atlântica Freshwater ecoregion: integrating taxonomy and niche modelling. Aceito no periódico Anais da Academia Brasileira de Ciências.

Capítulo 2 (Manuscrito II) – Biodiversity shortfalls and challenges revealed by a biogeographic study with New World snail-case caddisflies (Trichoptera, Helicopsychidae). Submetido ao periódico PlosOne.

Capítulo 3 (Manuscrito III) – Resurrection of the long-horned snail case caddisflies *Cochliopsyche* Müller (Trichoptera, Helicopsychidae) based in phylogenetic and biogeographic analyses. Com provável submissão ao periódico Zoological Journal of the Linnean Society.

Capítulo 4 (Manuscrito IV) – Systematics revision of Neotropical long horned snail-case caddisflies *Cochliopsyche* Müller, 1885 (Trichoptera, Helicopsychidae). Com provável submissão ao periódico Insect Systematics & Evolution.

Capítulo I

Título: *Helicopsyche* (*Feropsyche*) Johanson, 1998 (Trichoptera) from Northeastern Mata Atlântica Freshwater ecoregion: integrating taxonomy and niche modelling

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Helicopsyche (*Feropsyche*) Johanson, 1998 (Trichoptera) from Northeastern Mata Atlântica Freshwater ecoregion: integrating taxonomy and niche modelling

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Keywords: Atlantic Forest, biodiversity shortfalls, potential distribution, Helicopsychidae, snail-case caddisflies.

***Helicopsyche* (*Ferosyche*) from NMAF**

Section: Ecosystems

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Abstract

The Northeastern Mata Atlântica Freshwater ecoregion (NMAF) is part of the 25 worlds biodiversity hotspots. It comprises the Central Atlantic Forest Ecological Corridor and Chapada Diamantina Complex (in part), including high rates of endemism in coastal freshwater ecosystems. However, estimates indicate a high population decline in Freshwater ecosystems. Trichoptera are the most affected insect order, with average extinction rates of ~9% and many unknown species (e.g., estimates are around 50% in Brazil and Ecuador). This crisis can be aggravated by gaps in the knowledge of species (Linnean shortfall) and their distribution (Wallacean shortfall), caused mainly by a lack of investment in extensive fauna inventories and human resources related to systematics. Thus, to face these shortfalls in NMAF, we describe four new species of *H.* (*Feropsyche*) and provide new distribution records. In addition, we perform niche modeling based on the species distributions of the group to identify areas with high environmental suitability to direct biodiversity research efforts on NMAF, a highly endemic and underexplored ecoregion. We increased the number of known species of NMAF from seven to 16 species. The niche modeling pointed to two areas as priorities to guide the strategies to reduce shortfalls in the NMAF.

Keywords: Atlantic Forest, biodiversity shortfalls, potential distribution, Helicopsychidae, snail-case caddisflies.

Introduction

Freshwater ecosystems cover around 1% of Earth's land surface but comprise ca. 10% of all known species (Strayer & Dudgeon 2010), with a high rate of endemism (Watson et al. 2018). These species have experienced significant population declines compared to terrestrial and marine ecosystems (MEA 2005). Due to these characteristics, freshwater ecosystems have the most acute biodiversity crisis among ecosystems (Tickner et al. 2020). In addition, biodiversity knowledge shortfalls on freshwater ecosystems are pronounced as the result of several factors such as neglected large areas, few comprehensive inventories, and lack of specialized human resources and/or investment in biodiversity research, especially in developing countries (Kier et al. 2005; Collen et al. 2008; Ely et al. 2013; Yang et al. 2013; Oliveira et al. 2016).

Tropical freshwater ecosystems house rich biodiversity, with faunal components more susceptible to impacts related to the degradation of the forests, pollution of freshwater environments, and climate change (Tewksbury et al. 2008; Senior et al. 2019). Recent estimates indicate that the population decline of aquatic insect species is twice that of vertebrates, and local extinction rates are eight times greater for insects than for vertebrates (Sánchez-Bayo & Wyckhuys 2019). Currently, 33% of aquatic insect species are threatened with extinction, and each year about 1% of all species have been added to the list, resulting in an average extinction rate (species not observed in >50 years) of 9% for some groups, such as Trichoptera (Sánchez-Bayo & Wyckhuys 2019). Additionally, the uncertainty about the extinction of insect species is standard because rare or highly threatened species are intrinsically difficult to detect (Ladle et al. 2011), which can be exacerbated by biodiversity shortfalls (Mulieri et al. 2022).

Some solutions are presented for better use of research funding and biodiversity shortfalls, such as using tools like niche modeling to identify areas of high environmental suitability (Guisan & Zimmermann 2000). Identifying these areas with a high probability of potential distribution can analyze the material deposited in museums and collections [e.g., around 26 million specimens were deposited in Brazilian scientific collections (Joly et al. 2011)]. Allowing the use of already collected material (Joly et al. 2011) and optimizing resources for focal collections in freshwater areas with high environmental suitability and without or scarce distributional records. These areas with low Trichoptera distribution records are mainly concentrated in the northeastern Atlantic Forest and dry diagonal (Santos et al. 2020).

Trichoptera comprises the most-rich order of aquatic insects (ca. 16.800 valid species) (Morse et al. 2023) and constitutes an essential component of freshwater ecosystems, contributing with diverse ecosystem services, including its contribution to nutrients cycling, decomposition processes, trophic network, with ecosystem engineering and biological monitoring of water quality (Morse 2013; Morse et al. 2019). Besides its relevance, the knowledge of Brazilian species is biased, with all kinds of biodiversity deficits, specially Linnean and Wallacean shortfalls (*sensu* Hortal et al. 2015). Santos et al. (2020) recently indicated that only ca. 50% of the Brazilian caddisfly species are known. Some ecoregions, especially those located in the Northeastern of Brazil, such as the Northeast Mata Atlântica Freshwater ecoregion (NMAF), present more pronounced knowledge deficits about other ecoregions with high richness (e.g., Amazon, Parana, Southeastern Atlantic Forest ecoregions). However, with substantial advances in species knowledge in the NMAF in recent years, going from about ten species (Paprocki et al. 2004) to the fourth ecoregion with the most species (137 valid species) and third with a rate of endemic species (38.7% of record species are endemic) (Santos et al. 2020), but with still a lot to be explored.

Among the Trichoptera occurring in the NMAF, the cosmopolitan genus *Helicopsyche* von Siebold, 1856 is virtually found in the various freshwater ecosystems (Johanson 2002). There are two subgenera, *H.* (*Cochliopsyche*) Müller, 1885 with one species, and *H.* (*Feropsyche*) Johanson, 1998 with seven species (Santos et al. 2023). The two subgenera can be differentiated by the tibial spur formula [1, 2, 2 in *H.* (*Cochliopsyche*) *versus* 2, 4, 4 in *H.* (*Feropsyche*)] and relative antennae/body length [>1.2 in *H.* (*Cochliopsyche*) *versus* ≤1.2 in *H.* (*Feropsyche*)] (Johanson 2002). Of the seven species of *Helicopsyche* (*Feropsyche*) recoding in NMAF (Tab. 1), six of them were described or recorded in the last two decades (Johanson & Holzenthal 2004; Johanson & Malm 2006; Holzenthal et al. 2016; Souza et al. 2017; Vilarino & Calor 2017), many of which have a restricted distribution in the NMAF.

Within this context, we can observe that the knowledge shortfalls related to species recognition and distribution (Linnean and Wallacean shortfalls) are accentuated mainly for the freshwater taxa, including *Helicopsyche* (*Feropsyche*) subgenus. Thus, here we describe and illustrate four new species of *H.* (*Feropsyche*) and provide new distribution records. In addition, we perform niche modeling based on the species distributions of the group to identify areas with high environmental suitability (high potential distribution) to direct future biodiversity research efforts on the NMAF, a highly endemic and underexplored ecoregion in Brazil.

Material and methods

Study area

Abell et al. (2008) classified the freshwater environments into ecoregions, among then it stands out the “*Northeastern Mata Atlântica Freshwater*" ecoregion (NMAF, number 328), which comprises all coastal drainages from the Sergipe River in the north to the Itabapoana river in the south. It is west-bordered by the São Francisco Freshwater ecoregion in Northeast Brazil. NMAF comprises a mosaic of landscapes from mountains and valleys to sandstone plateaus with elevations from the flat coastal plain up to 2,890 m a.s.l. (Pico da Bandeira at Serra do Caparaó, the third highest peak of Brazil), and includes diverse phytophysionomies from the Atlantic Forest, Caatinga, and Cerrado domains (Hales & Petry, 2013).

Along with other freshwater environments, the drainages of the NMAF form a series of isolated hydrographic basins, which are separated by the scarped, mountainous landscapes of the eastern margin of the Brazilian crystalline shield (Ribeiro 2006). Resulting in a complex biogeographical history, with the hydrographic systems (e.g., Paraguaçú, Contas, Jequitinhonha, Doce, Paraíba do Sul), as well as several other more minor adjacent drainages, demonstrating a high rate of endemism (Ribeiro 2006).

NMAF is part of the 25 world hotspots of biodiversity, with highlighted importance for providing water and resource for the population, conservation of habitats, and maintenance of biodiversity (Mayers et al. 2000). Beside the Central Atlantic Forest Ecological Corridor (CAFEC), the ecoregion comprises part of the Chapada Diamantina Complex (CDC), and Serra do Espinhaço, recognized regions with environmental heterogeneity and high biodiversity (Santos et al. 2003; Silva & Castelletti, 2005; Oliveira et al. 2015; Fricke et al. 2020; Santana et al. 2020), including high rates of endemism of several taxa (e.g., Camelier & Zanata 2014 for fishes; Duarte et al. 2014 for stoneflies; Araujo et al. 2015 for beetles; Vilarino & Calor 2017 for caddisflies; SOS Mata Atlântica and INPE, 2017 for plants; Cavarzere et al. 2019 for birds).

Systematics

The material examined comprises 50 localities of the NMAF (Fig. 1). Methods used in the preparation, examination, and illustration followed Blahnik et al. (2003) and Blahnik & Holzenthal (2004). The terminology applied to the morphological structures followed Johanson (2002), except for inferior appendage (rather than gonocoxite), as suggested by Holzenthal et al. (2016) (Fig. 2).

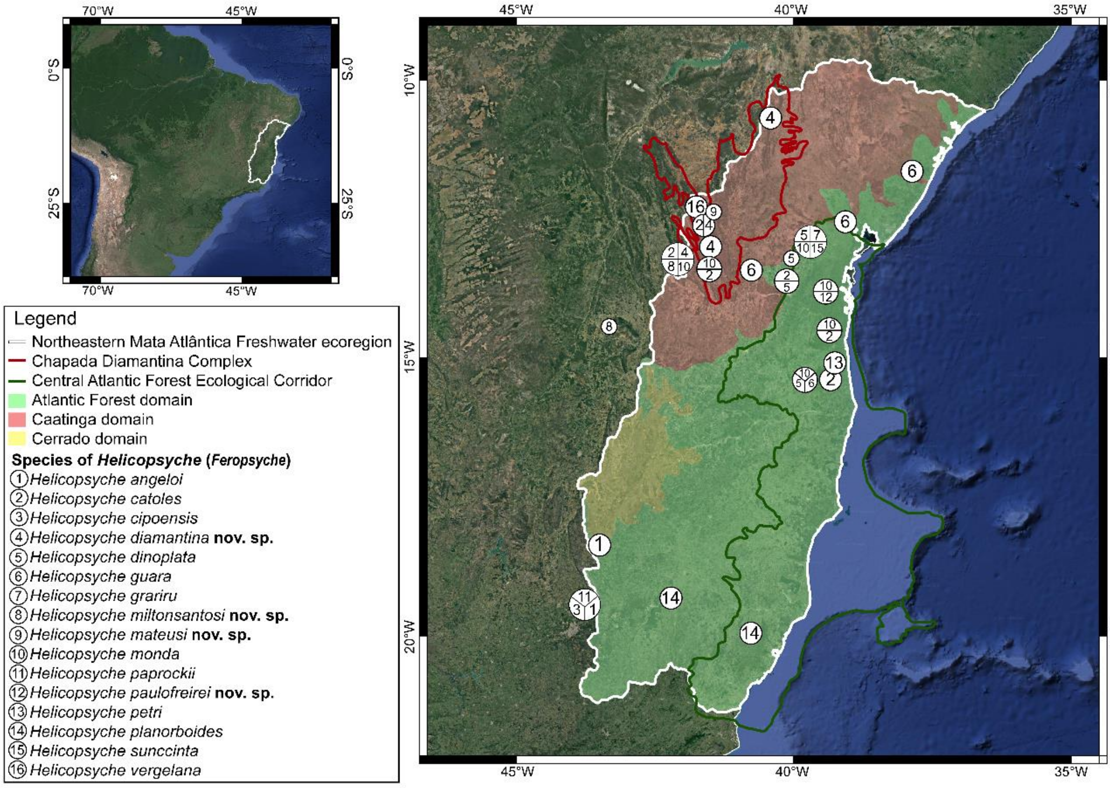

Figure 1. Map with *Helicopsyche* (*Feropsyche*) distribution from Northeastern Mata Atlântica Freshwater ecoregion, Brazil.

The illustrations were made with a microscope equipped with a camera lucida, scanned, and finalized in Adobe® Illustrator® CS5. Microphotographs were made using a Leica stereoscope equipped with a digital camera, Nikon model DS-Fi1 and finalized in Adobe® Illustrator® CS5. Map was made using QGIS 3.10.10 (QGIS Development Team) and finalized with Adobe® Illustrator® CS5.

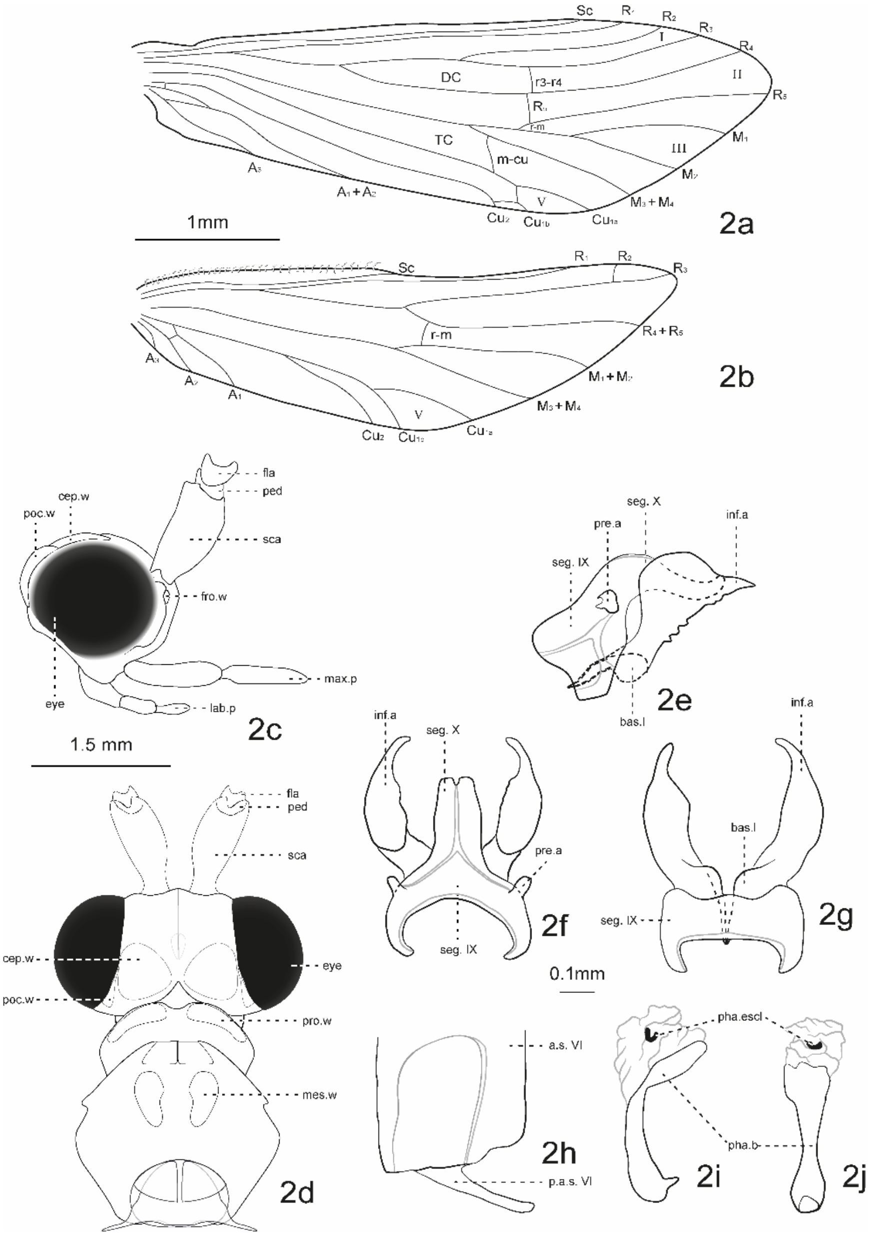

Figure 2. *Helicopsyche* (*Feropsyche*) *diamantina* **sp. nov.** schematic illustration of wings, head, thorax and gelitalia characters. **2a**, forewing; **2b**, hind wing; **2c**, head, lateral view; **2d**, head and thorax, dorsal view; **2e**, genitalia, lateral view; **2f**, genitalia, dorsal view; **2g**, genitalia, ventral view; **2h**, sternum VI, lateral view; **2i**, phallus, left lateral view; **2j**, phallus, ventral view. Abbreviations: Sc = subcostal vein; R = radial vein; M = medial vein; Cu = cubital vein; A = anal vein; DC = discoidal cell; TC = tiridial cell; fla = flagellomere; ped = pedicel; sca = scape; fro.w = frontal wart; cep.w = cephalic warts; poc.w = posterocular warts; max.p. = maxillary palp; lab.p. = mandibular palp; seg. IX = abdominal segment IX; pre.a = preanal appendage; seg. X = abdominal segment X; inf.a = inferior appendage; bas.l = basomesal lobe; a.s. VI = abdominal sternum VI; p.a.s. VI = process of abdominal sternum VI pha.b = phallobase; pha.scl. = phallotremal sclerite.

Type material will be deposited at Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZSP) and Museu de História Natural da Bahia, Bahia, Salvador, Brazil (UFBA), as indicated in the material examined. Additional material will be deposited at UFBA.

The distribution of caddisfly species through terrestrial ecoregions was used to estimate the number of unknown species in the NMAF using non-parametric estimators. Estimators were calculated based on incidence data (presence-absence only), using Brazilian phytogeographic domains as sampling unities, with the function specpool from the vegan package (Oksanen et al. 2019) in software R. This function calculates three estimators: CHAO2, first-order jackknife (JACK1) and second order jackknife (JACK2). These non-parametric estimators of species richness help estimate a potential number of unobserved species based on incidence data as those available here. They have performed better than model-based or asymptotic estimators (Palmer 1990; Hortal et al. 2006).

Niche modelling

Assumed there is a scarce number of records of species of the subgenus and that they present similar niches, areas, and feeding behavior. The species' complete set of distributional records was used to understand the subgenus's potential distribution in the NMAF. For this purpose, a database was compiled through the primary literature (species description and distributional records), Global Biodiversity Information Facility (GBIF; https://www.gbif.org), SpeciesLink (http://www.splink.org.br/), and original data from UFBA. Gazetteers and Google Maps© were used to register localization without coordinates. The centroid of the least comprehensive location was used. After the data compilation, a two steps filtering process was performed, (1) manual selection of the data with determined locality and species level; and (2) selection from the RStudio program (RStudio Team), discarding points that can generate an analysis bias (e.g., with equal coordinates or marine areas). After filtering, the database (Table S1, Supplementary material) was used as input for niche modelling and to make a species distribution map.

Environmental data were obtained from monthly climate data for minimum, mean, and maximum temperature, precipitation, solar radiation, wind speed, water vapor pressure, and for total precipitation, 19 “bioclimatic” variables, and elevation on a scale of 30 arc seconds, available in the online database WorldClim version 2.1 (https://www.worldclim.org/data/worldclim21.html). After obtaining the data, in the RStudio program, a correlation analysis was performed using the Spearman method, the 'correlate' function of the 'corrr' package (Kuhn et al. 2022). This procedure allows the selection of uncorrelated variables (correlation <30%) and avoids overweighing in the analyses.

Predictive distribution models are influenced by choice of modelling technique and the settings chosen by the researcher, summing up various uncertainties related to data quality and quantity, sample size, sampling bias, and spatial resolution (Zhang et al. 2015). To address these issues and improve distribution model performance, the use of an ensemble of algorithms, which address the results of multiple models in a single estimation, results in more accurate predictions than single model methods (Turner et al. 2018). Moreover, this methodology allows the identification of consensus forecasts by determining the level of agreement/disagreement between individual models, thus mapping model uncertainty (Araújo and New 2007).

Thus, we use at least one representative of the three main types of modelling algorithms to determine the level of agreement/disagreement between the different individual models building a more precise consensus. Four correlative modelling algorithms were used: two environmental distance models, the Bioclim (Nix 1986) and Domain (Carpenter et al. 1993); a regression-based model, the Generalized Linear Model (GLM; Nelder & Wedderburn 1932), and a machine learning model the Vector Support Machine (SVM; Tax & Duin 2004).

To generate the absence points, not available for the species used, we randomly generated 72 pseudo-absence points (1:1 ratio for the occurrence points) through the 'randomPoints' function of the 'dismo' package (Hijmans et al. 2017) in the RStudio program. Data partitioning was randomly performed in 30% for training and 70% for testing the models. The repeatability of the models used to increase the robustness of the result was 200 times. Only models with Area Under Curve (Hanley & McNeil 1982) superior to 80% were considered for constructing suitability maps, using default limits of presence and absence.

Results

Systematics

Family Helicopsychidae Ulmer, 1906

Genus *Helicopsyche* von Siebold, 1956

Subgenus *Helicopsyche* (*Feropsyche*) Johanson, 1998

Helicopsyche (*Feropsyche*) *diamantina* **nov. sp.**

(Figs. 2–4)

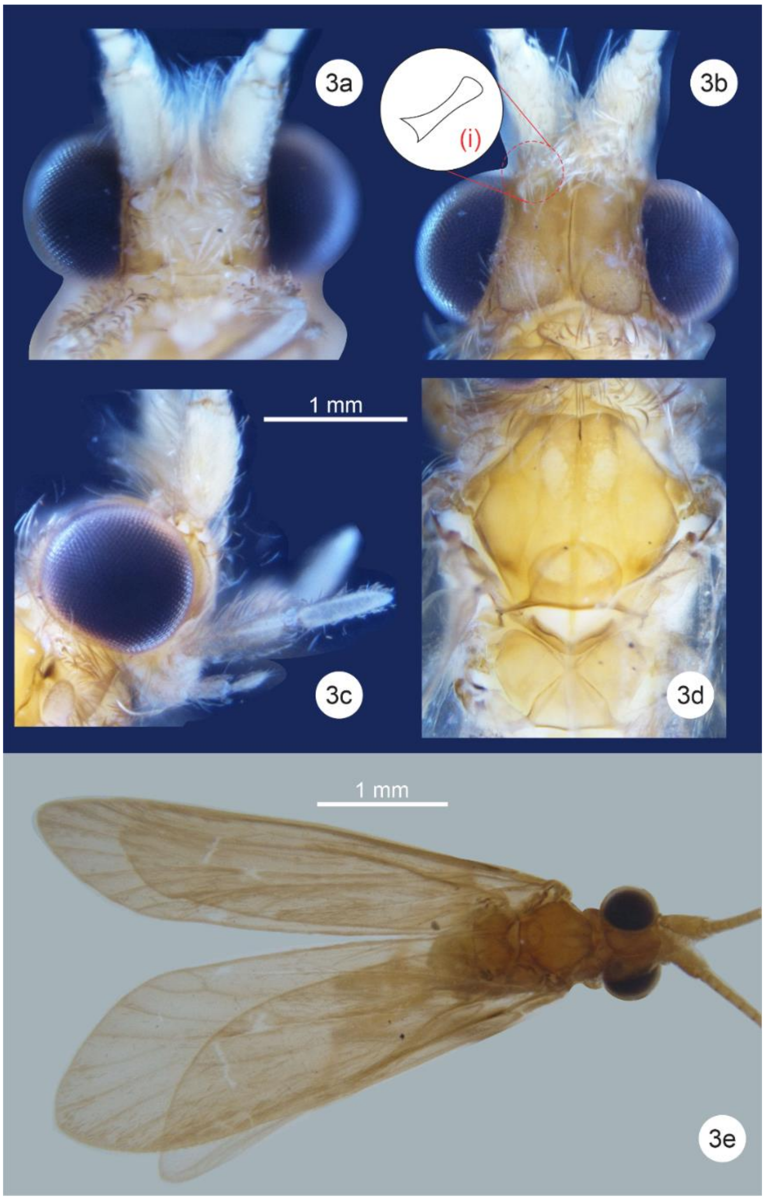

Figure 3. *Helicopsyche* (*Feropsyche*) *diamantina* **nov. sp.** male**. 3a**, head, frontal view; **3b**, head, dorsal view, (i) detail of interantennal warts; **3c**, head, lateral view; **3d**, thorax, dorsal view; **3e**, habitus, dorsal view

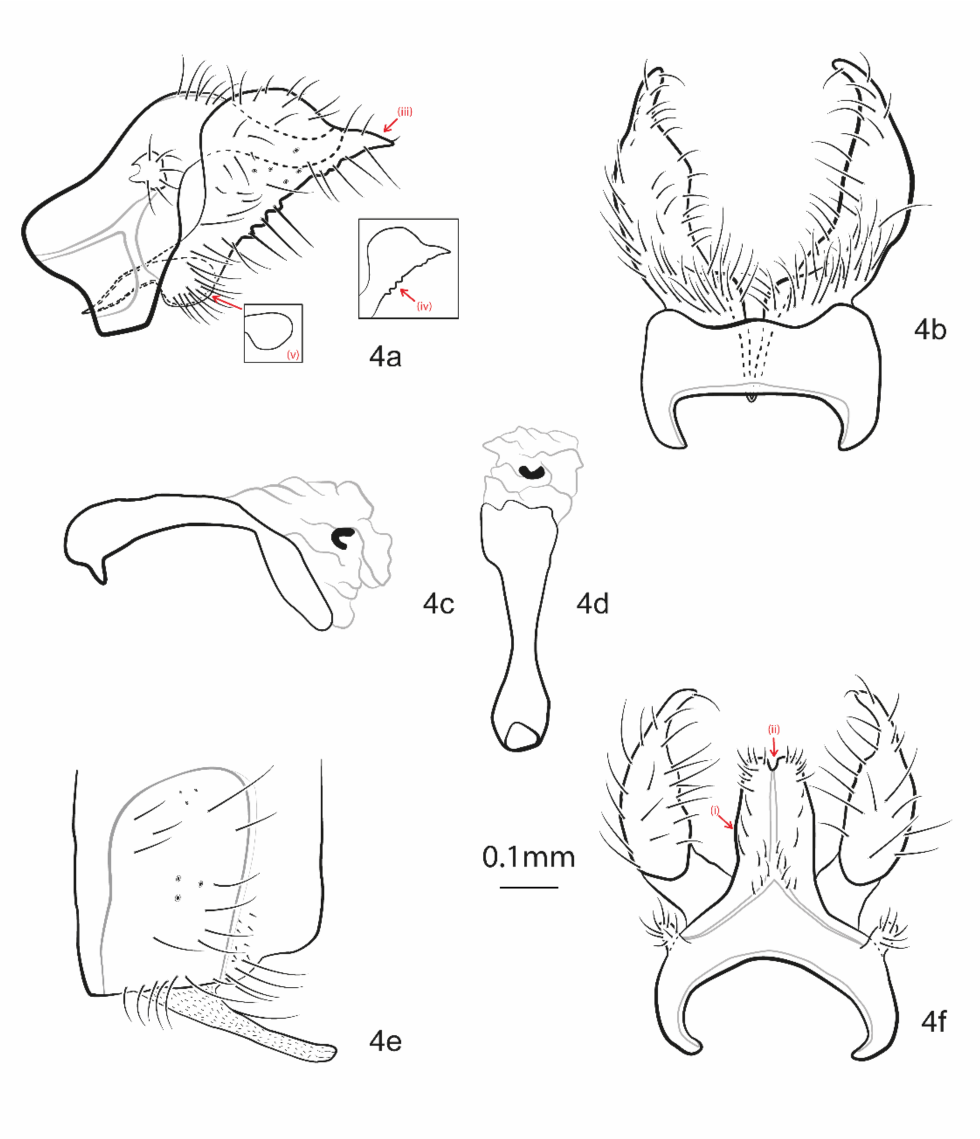

Figure 4. *Helicopsyche* (*Feropsyche*) *diamantina* **nov. sp.** male. **4a** genitalia, left lateral view, red arrows point diagnostic characters iii–v; **4b**, genitalia, ventral view; **4d**, Phallus, left lateral view; **4e**, Phallus, ventral view; **4f**, sternum VI; **4g**, genitalia, dorsal view, red arrows point diagnostic characters i–ii.

Diagnosis. The new species is distinguished from all congeners by the following set of male characters: (i) abdominal segment X long and narrow, with convex lateral margins, and (ii) apex with a short, shallow cleft U-shaped, in dorsal view (Fig. 4f); (iii) inferior appendage with acuminated posterior projection, (iv) ventral margin with medial small setose projection, in lateral view (Fig. 4d), and (v) basomesal lobe of inferior appendage rounded, without a distinct protuberance or projection, in ventral view (Fig. 4b). The new species is morphologically similar to *H. mateusi* **nov. sp.**, *H. monda* Flint, 1983 and *H. obscura* Rueda Martín & Isa Miranda, 2015 by general shape of abdominal segment X in dorsal view, and basomesal lobe in ventral view, but differs from them by abdominal segment X with apex upcurved, in lateral view (Fig. 4a) (posteriorly oriented in all others), and apex with short, shallow apical cleft forming two lobes covered by setae, in dorsal view (Fig. 4f) (apical cleft absent in *H. mateusi* **nov. sp.** and *H. obscura*, and present, but without lobes in *H. monda*); The new species and *H. monda* share the inferior appendage medial region slightly constricted, in lateral view (wide in *H. mateusi* **nov. sp.** and *H. obscura*), but the new species differs from *H. monda* by the posteroventral margin of inferior appendage, new species with medial small setose projection *versus* without setose projection in *H. monda*, and by the basomesal lobe with posterior margin wide with rounded apex, in lateral view (Fig. 4a) (globose with short distal projection in *H. mateusi* **nov. sp.**, subtriangular in *H. monda*, and unseen in *H. obscura*).

Description. Overall color yellowish brown (in alcohol, n=10). Forewing length 3.37–4.74 mm (n = 10), forks I, II, III and V present, with discoidal and thyridial cells, without medial cell (Fig. 2a). Hind wing forks I and V present, without discoidal and thyridial cells (Fig. 2b). Head: antennae around ≤1.4x forewing length, scape longer, length around half of head, covered by long setae (Fig. 3a); dense set of interantennal setae (Fig. 3b); interantennal warts finger-shaped with medial constriction with around 1/3 of head length; cephalic warts subtriangular covered by long setae (Fig. 2d, 3b); postocular warts subtriangular with wide base, covered by long setae (Fig. 2d, 3b);

maxillary palps 2-segmented, covered by long setae (Fig. 3c); labial palps 3-segmented, covered by long setae (Fig. 2c, 3c). Thorax: pronotum bearing setal warts, digitated, with long and ferruginous setae; mesoscutum diamond-shaped, setal warts bean shaped covered by small setae, with 1/3 of mesoscutum length; mesoscutellum with setal warts subtriangular with small setae (Fig. 2d, 3d); legs with tibial spur formula 2, 2, 4. Abdomen: abdominal sternum VI process present, about 2/3 of the segment length (Fig. 2h, 4e).

Male genitalia. Abdominal segment IX anterior lobe rounded projection, located ventrally on segment, anterodorsal, and anteroventral margin concave, in lateral view (Fig. 2e, 4a); posterior lobe convex, basal plate V-shaped, in ventral view (Fig. 2g, 4b). Preanal appendages globose, in lateral view (Fig. 2e, 4a), digitated, short, in dorsal view (Fig. 2f, 4f). Abdominal segment X base wider than the apex; apex slightly rounded, upcurved, in lateral view (Fig. 2e, 4a); rectangular, with convex lateral margins, and apex with short, slightly deep apical cleft forming two lobes covered by setae, in dorsal view (Fig. 2f, 4f). Inferior appendage clavate, acuminated in anterior region, medial region slightly constricted, posterodorsal margin smooth and convex, posteroventral margin slightly concave with medial small setose projection, posterior region of appendage with acuminated projection, in lateral view (Fig. 2e, 4a); base wide, median constriction, apex wide, without apical tooth and inner face margin containing rows of long setae, in ventral view (Fig. 2b, 4b); basomesal lobe of inferior appendage globose covered by long setae, in lateral view (Fig. 2e, 4a), and wide rounded, slightly projected, covered by long setae, in ventral view (Fig. 2g, 4d). Phallus tubular, phallobase constricted medially (Figs. 2i, j, 4c, d), posterior region wide and rounded, in lateral view (Fig. 2i, j, 4c, d); phallotremal sclerite single, U-shaped, in ventral view (Fig. 4f).

Type material. Holotype: Brazil, Bahia, Complexo da Chapada Diamantina, Lençóis, Rio Mucugezinho, 12°23'44"S, 41°25'01"W, 306 m a.s.l., UV light pan trap, 1 ♂, 29.x.2013, Calor, Dias and Campos cols. (MZUSP). Paratypes: Brazil, Bahia, Complexo da Chapada Diamantina, Abaíra, Serra do Barbado, Tijuquinha abaixo, 13°11'56.3"S, 41°53'21.5"W, UV light pan trap, 2 ♂, 05.xi.2013, Calor, Dias and Campos cols. (MZUSP); same data, except 2 ♂, (UFBA); same data, except Igatú, Rio Coisa Boa, 12°53'23.3"S, 41°19'0.0"W, 633 m a.s.l., UV light pan trap, 1 ♂, 12.v.2010 (MZUSP); same data, except 9 ♂ (UFBA); same data, except Andaraí, Rio Piaba, 12°59’34”S, 41°20’23”W, 25♂, 22.i.2018, Calor et al. cols. (UFBA); same data, except Mucugê, Parque Municipal de Mucugê, Córrego Bandeira, 12°59'56.8"S, 41°19'53.8"W, 958 m a.s.l., UV light sheet attraction, 1 ♂, 01.vi.2019, Calor et al. cols. (UFBA); Córrego Boiadeiro, 2 ♂, 10.i.2015, Dias and Campos cols. (UFBA); same data, except, Rio Mucugê, 12°53'1.8"S, 41°16'33"W, 993 m a.s.l., UV light pan trap, 6 ♂, 25.xi.2018, Calor et al. cols. (MZUSP); same data, except, Rio Piabinha, 12°59'34"S, 41°20'23"W, 921 m a.s.l., UV light pan trap Branca/UV, 4 ♂, 25.vii.2010, Calor, Lecci Quinteiro, França, Arantes and Camelier cols. (UFBA); same data, except, Rio Tiburtino, 12°59'53"S, 41°20'50"W, 909 m a.s.l., UV light pan trap, 8 ♂, 13.v.2015, Calor et al. cols. (UFBA); same data, except Rio Cumbuca, 12°59'51"S, 41°20'56"W, UV light pan trap, 14 ♂, 23.vii.2010, Calor, Lecci Quinteiro, França, Arantes and Camelier cols. (UFBA); same data, except Palmeiras, Vale do Capão, riachinho (ponte), 12°34'19.2"S, 41°30'52.5"W, 918 m a.s.l., UV light pan trap, 1 ♂, 25.vi.2011, Calor, Camelier and Burguer cols. (UFBA); Piatã, Cachoeira do Patrício (embaixo), 13°05'12"S, 41°51'12"W, Light, 1 ♂, 29.x–03.xi.2013, Menezes cols. (MZUSP); Brazil, Bahia, Complexo da Chapada Diamantina, Pindobaçu, Cachoeira da Fumaça, 10°28'43"S, 40°12'23"W, 13 ♂, 13.xii.2009, Zacca, T. cols. (UFBA)

Distribution. NMAF (CDC) [Brazil (Bahia state)].

Remarks. This new species belongs to the *Helicopsyche monda* complex.

Etymology. The specific name, a noun in apposition, refers to the Chapada Diamantina Complex, a mountain range of the Caatinga domain and central region of Bahia State, Brazil, which is the type locality of new species. The specific name "diamantina" in Portuguese means "diamantiferous" and is an allusion to the large diamond reservoirs in the region.

Helicopsyche (*Feropsyche*) *mateusi* **nov. sp.**

(Figs. 5, 6)

Diagnosis. The new species is distinguished from all congeners by the following set of male characters: (i) abdominal segment X quadrangular, with parallel lateral margins, (ii) apex slightly undulated not forming lobes, in dorsal view (Fig. 6f); (iii) inferior appendage with ventral margin substraight with mesal setose projections, and (iv) basomesal lobe globose with short distal projection, in lateral view (Fig. 6a); (v) inferior appendage with inner face bearing set of projections with spine-like setae, in ventral view (Fig. 6b). The new species is morphologically similar to *Helicopsyche alajuela* Johanson & Holzenthal, 2010, *H. diamantina* **nov. sp.** and *H. monda* by general shape of inferior appendage in lateral view, and basomesal lobe in ventral view, but differs from them by the inner face of the inferior appendage bearing projections with spine-like setae (projections absent in all, except sometimes present in *H. diamantina* **nov. sp.**), and by the presence of basomesal lobe with posterior region wide, with acuminated apex, in lateral view (absent in *H. alajuela*, and with rounded apex in *H. diamantina* **nov. sp.**, with pointed apex in *H. monda*).

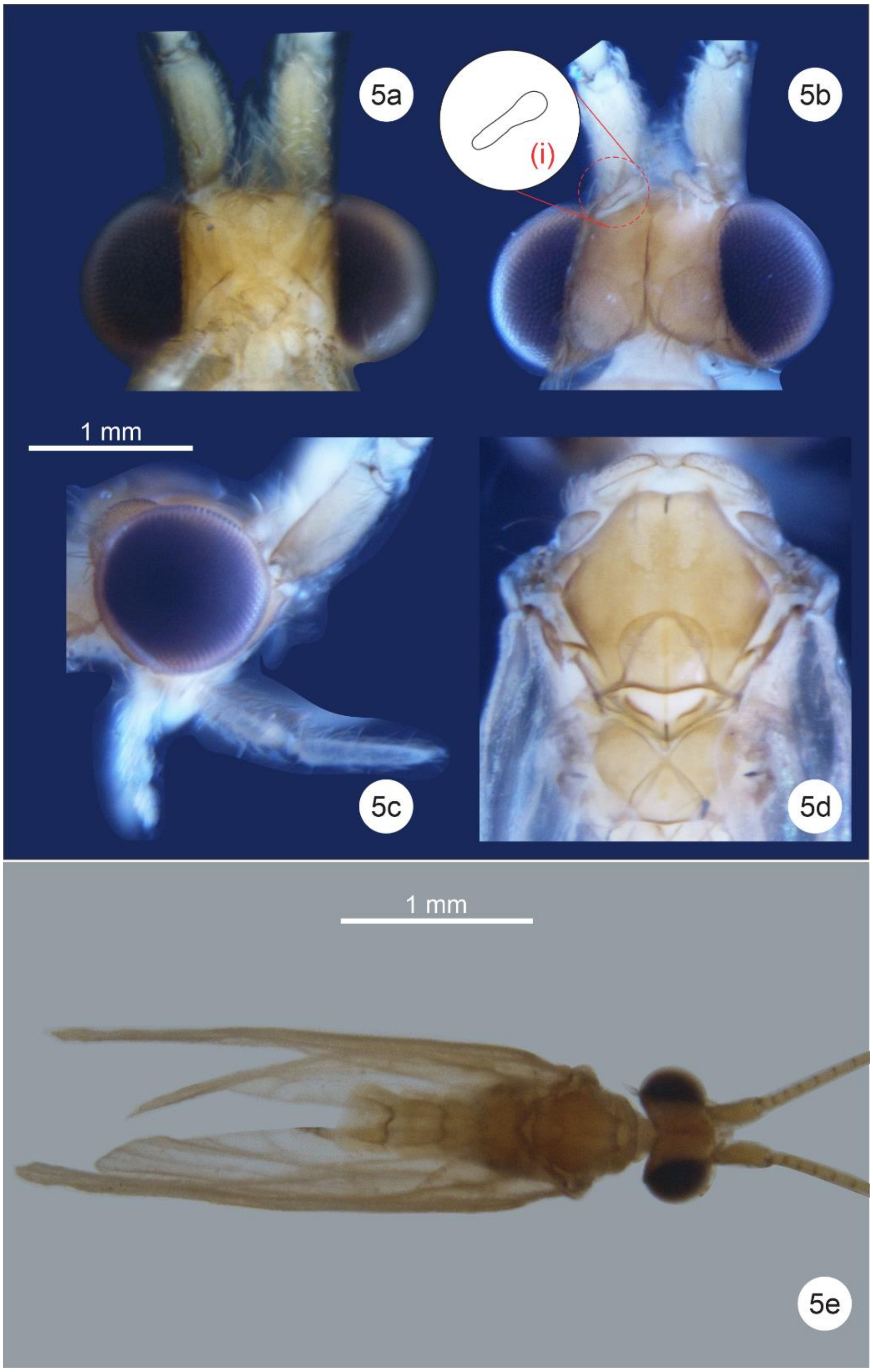

Figure 5. *Helicopsyche* (*Feropsyche*) *mateusi* **nov. sp.** male. **5a**, head, frontal view; **5b**, head, dorsal view, (i) detail of interantennal warts; **5c**, head, lateral view; **5d**, thorax, dorsal view; **5e**, habitus, dorsal view.

Description. Overall color yellowish brown (in alcohol). Forewing length 2.98–3.92 mm (n = 8), forks I, II, III, and V present, with discoidal and thyridial cells, without medial cell. Hind wing forks I and V present, without discoidal and thyridial cells. Head: antennae around ≤1.2x forewing length, scape longer, length subequal to head, with a dense set of interantennal setae (Fig. 5b); interantennal warts club-shaped with apex globose and around 1/3 of head length; cephalic warts subtriangular covered by long setae (Fig. 5b); postocular warts mid-moon shaped with wide base, covered by long setae (Fig. 5b); maxillary palps 2-segmented, covered by long setae (Fig. 5c); labial palps 3-segmented, covered by long setae (Fig. 5c). Thorax: pronotum bearing setal warts, digitated, with small setae; mesoscutum diamond-shaped, setal warts bean shaped covered by small setae, with 1/3 of mesoscutum length; mesoscutellum with setal warts subtriangular with small setae (Fig. 5d); legs with tibial spur formula 2, 2, 4. Abdomen: abdominal sternum VI process present, about half the segment length (Fig. 6e).

Male genitalia. Abdominal segment IX anterior lobe rounded projection, located midway on segment, anterodorsal margin sub-straight, anteroventral margin concave, in lateral view (Fig. 6a), posterior margin convex, basal plate V-shaped, in ventral view (Fig. 6b). Preanal appendages globose, in lateral view (Fig. 6a), digitated, in dorsal view (Fig. 6f). Abdominal segment X base wider than the apex, apex rounded, slightly upcurved, in lateral view (Fig. 6a); quadrangular, with parallel lateral margins, and apex slightly undulated, in dorsal view (Fig. 6e). Inferior appendage clavate, acuminated in anterior region, medial region wide; ventral margin substraight with medial setose projections, posterior region of appendage with finger shape projection, in lateral view (Fig. 6a); base wide, narrowing towards the acuminated apex and inner face margin of the inferior appendage containing projections with spine-like setae, in ventral view (Fig. 6b); basomesal lobe globose with short distal projection, in lateral view (Fig. 6a); wide, triangular, slightly projected, covered by long setae, in ventral view (Fig. 6b). Phallus tubular, phallobase constricted medially (Figs. 6c, d), acuminated in posteroventral region, slightly downcurved, in lateral view (Fig. 6c); phallotremal sclerite single, comma shaped, in ventral view (Fig. 6d).

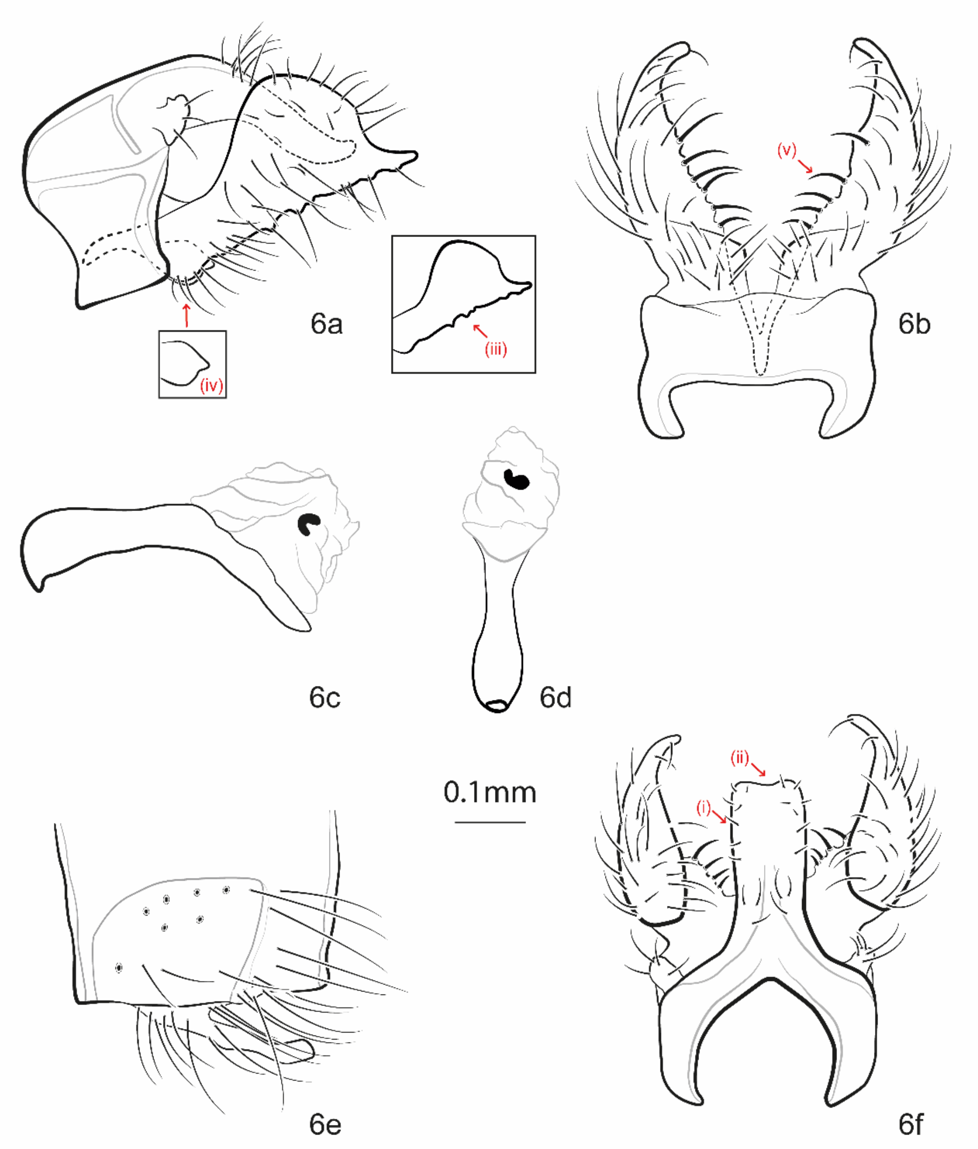

Figure 6. *Helicopsyche* (*Feropsyche*) *mateusi* **nov. sp.** male. **6a**, genitalia, left lateral view, red arrows point diagnostic characters iii–iv; **6b**, genitalia, ventral view, the red arrow points diagnostic character v; **6c**, phallus, left lateral view; **6d**, phallus, ventral view; **6e**, sternum VI; **6f**, genitalia, dorsal view, red arrows point diagnostic characters i–ii.

Type material. Holotype: Brazil, Bahia, Complexo da Chapada Diamantina, Lençóis, Rio Mucugezinho, 12°23'44"S, 41°25'1"W, 306 m a.s.l, 1 ♂, 29.x.2013, UV light pan trap, Calor AR, Dias ES, and Campos R cols. (MZUSP). Paratypes. same data Holotype, except 3 ♂ (UFBA); same data, except 1 ♂ (MZUSP); same data, except 12°23'45"S, 41°24'56"W, 305 m a.s.l, 1 ♂, 01.viii.2010, UV light pan trap, Calor AR, Camelier P, Lecci L, Arantes T, and França D cols. (MZUSP); same data, except Complexo da Chapada Diamantina, Rio Ribeirão, 12°35'13.0"S, 41°22'96.3"W, 361 m a.s.l), 1 ♂, 23.x.2008, UV light pan trap, Calor AR, Mariano R, and Mateus S cols.; same data, except 1 ♂ (UFBA).

Distribution. NMAF (CDC) [Brazil (Bahia State)].

Remarks. This new species belongs to the *Helicopsyche monda* complex.

Etymology. The specific name is in honor of the eminent German scientist Dr. Sidnei Mateus (USP, Ribeirão Preto), an honorable citizen of Pedregulho municipality, for his friendship and contribution to several aquatic insects' fieldwork.

Helicopsyche (*Feropsyche*) *miltonsantosi* **nov. sp.**

(Figs. 7, 8)

Diagnosis. The new species is distinguished from all congeners by the following set of male characters: (i) Abdominal segment X subquadrangular, with parallel lateral margins, and (ii) apex with shallow concavity, in dorsal view (Fig. 8f); and (iii) inferior appendage ventral margin strongly sinuous with medial setose projections, in lateral view (Fig. 8a); (iv) and with inner face bearing set of projections with spine-like setae, in ventral view (Fig. 8b); (v) basomesal lobe triangular, well projected, covered by long setae, in ventral view (Fig. 8b).

Figure 7. *Helicopsyche* (*Feropsyche*) *miltonsantosi* **nov. sp.** male. **7a**, head, frontal view; **7b**, head, dorsal view, (i) detail of interantennal warts; **7c**, head, lateral view; **7d**, thorax, dorsal view; **7e**, habitus, dorsal view.

The new species is morphologically similar to *H. catoles* Souza, Gomes & Calor, 2017, *H. mateusi* **nov. sp.** and *H. paprockii* Johanson & Malm, 2006 by general shape of abdominal segment X, in dorsal view, and inferior appendage, in lateral view, but it differs from them by inferior appendage with basomesal lobe well projected, in ventral view (Fig. 8a) (slightly projected in *H. catoles* and *H. paprockii*, and not projected in *H. mateusi* **nov. sp.**). The new species and *H. paprockii* share the basomesal lobe of the inferior appendage triangular, in lateral view (globose in *H. catoles* and *H. mateusi* **nov. sp.**), but the new species differs from the *H. paprockii* by the distal region of inferior appendage (digitated in new species *versus* truncated in *H. paprockii*).

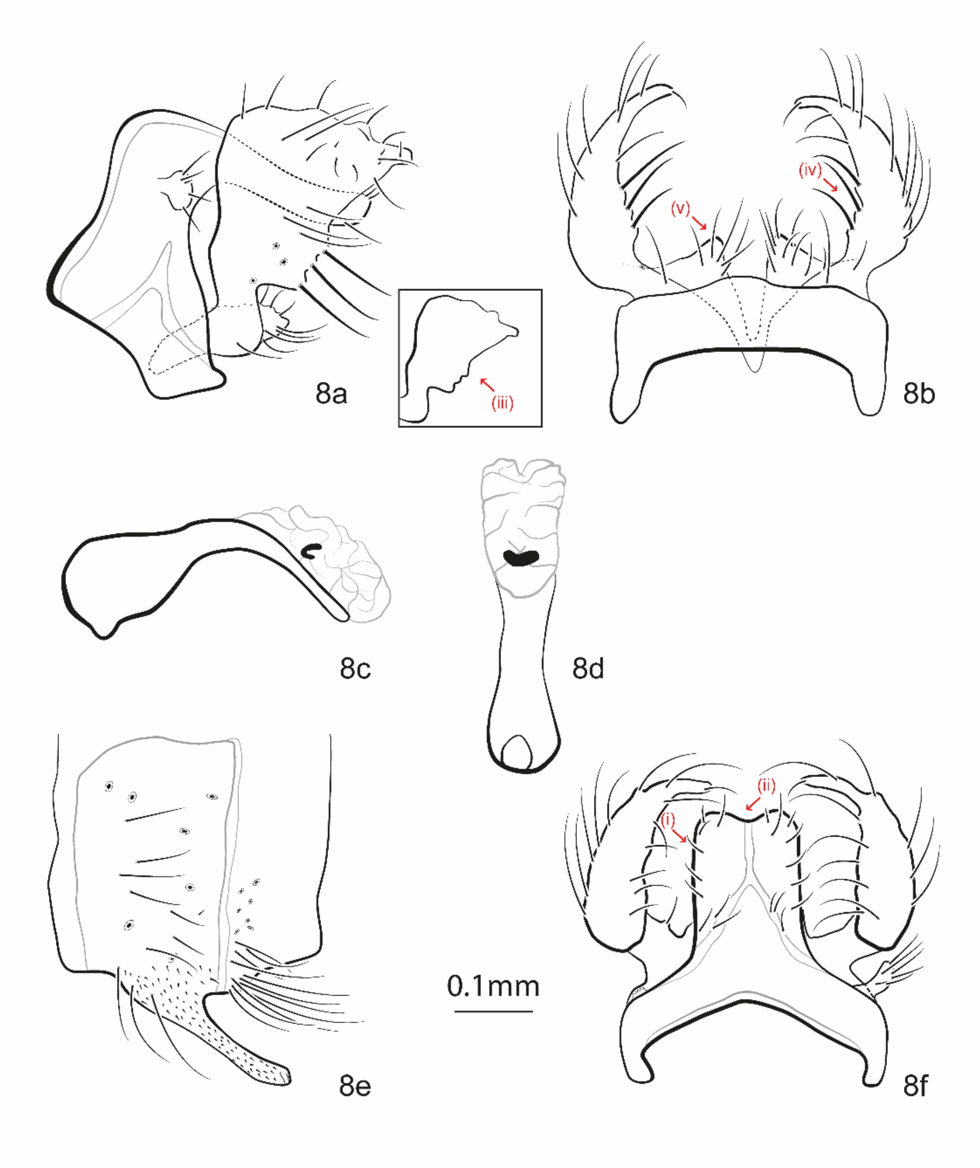

Figure 8. *Helicopsyche* (*Feropsyche*) *miltonsantosi* **nov. sp.** male. **8a**, genitalia, left lateral view, red arrow points diagnostic character iii; **8b**, genitalia, ventral view; **8c**, phallus, left lateral view, red arrows point diagnostic characters iv–v; **8d**, Phallus, ventral view; **8e**, sternum VI; **8f**, genitalia with left preanal appendage lost, dorsal view, red arrows point diagnostic characters i–ii

Description. Overall color yellowish brown (in alcohol). Forewing length 3.06–3.63 mm (n = 10), forks I, II, III, and V present, with discoidal and thyridial cells, without medial cell. Hind wing forks I and V present, without discoidal and thyridial cells. Head: antennae around ≤1.2x forewing length, scape longer, length subequal to head, with a set of interantennal setae (Fig. 7b); interantennal warts filiform around half of head length; cephalic warts globose covered by long setae (Fig. 7b); postocular warts mid-moon shaped with wide base, covered by long setae (Fig. 7b); maxillary palps 2-segmented, covered by long setae (Fig. 7c); labial palps 3-segmented, covered by small and ferruginous setae (Fig. 7c). Thorax: pronotum bearing setal warts, oval-shaped, with small setae; mesoscutum diamond-shaped, setal warts bean shaped covered by small setae, with 1/4 of mesoscutum length; mesoscutellum with setal warts subtriangular with small setae (Fig. 7d); legs with tibial spur formula 2, 2, 4. Abdomen: abdominal sternum VI process present, about half the segment length (Fig. 8e).

Male genitalia. Abdominal segment IX anterior margin with rounded projection, located ventrally on segment, anterodorsal, and anteroventral margin concave, in lateral view (Fig. 8a); posterior margin convex, basal plate V-shaped, in ventral view (Fig. 8b). Preanal appendages clavate, in lateral view (Fig. 8a), digitated, in dorsal view (Fig. 8f). Abdominal segment X base wider than the apex, without basal projection, apex truncated, without curvature, in lateral view (Fig. 8a), abdominal segment X subquadrangular, with parallel lateral margins and apex with shallow concavity, in dorsal view (Fig. 8f). Inferior appendage clavate, rounded in anterior region; medial region constricted and bent 90°; ventral margin strongly sinuous with medial setose projections, posterior region of appendage with short finger shape projection, in lateral view (Fig. 8a); base and apex with subequal width, apex without apical tooth, and inner face margin of the inferior appendage containing medial projections with spine-like setae in ventral view (Fig. 8b); basomesal lobe subtriangular, in lateral view (Fig. 8a); and triangular, well projected, covered by long setae, in ventral view (Fig. 8b). Phallus tubular, phallobase slightly constricted medially (Figs. 8c, d), posteroventral region acuminated, slightly downcurved, in lateral view (Fig. 8c); phallotremal sclerite single, U-shaped, in ventral view (Fig. 8d).

Type material. Holotype: Brazil, Bahia, Sebastião Laranjeiras, Riacho Mandiroba, 14°22'34.5"S, 43°02'18.9"W, 1 ♂, 5.v.2013, UV light pan trap, Nogueira M.A.M. col. (MZUSP). Paratypes: Brazil, Bahia, Sebastião Laranjeiras, Riacho Mandiroba, 14°22'34.5"S, 43°02'18.9"W, 8 ♂, 5.v.2013, UV light pan trap, Nogueira M.A.M. col. (UFBA); same data, except 6 ♂ (MZUSP), same data, except Abaíra, Distrito Catolés, 13°18'33.6"S, 41°51'62.9"W, 1263 m a.s.l., UV light pan trap, 1, 30.x.2013, Calor, Dias and Campos cols. (MZUSP); same data, except Piatã, Rio Toboró, 13°13'31"S, 41°44'43"W, 860 m a.s.l., 1 ♂, 28.vii.2010, UV light pan trap, Calor, França, Quinteiro, Lecci, Camelier, and Arantes cols (UFBA).

Distribution. SFF and NMAFs (CDC) [Brazil (Bahia State)].

Etymology. This species is named in memory of Milton Almeida dos Santos (1926–2001), a Brazilian geographer, writer, scientist, journalist, lawyer, and university professor. Considered one of the most renowned intellectuals in Brazil in the twentieth century, he was one of the great names of the renovation of geography in Brazil that took place in the 1930s (Elias 2002). Although he graduated in Law, he stood out for his works in several areas of geography, especially in studies of Third World urbanization and for his works on globalization in the 1990s (Elias 2002). His work was characterized by a critical position on the capitalist system and its theoretical assumptions, dominant in the geography of his time (Elias 2002). Thus, we used the specific name *miltonsantosi* as a tribute to the honorable citizen of the municipality of Brotas de Macaúbas in the Chapada Diamantina Complex region.

Helicopsyche (*Feropsyche*) *paulofreirei* **nov. sp.**

(Figs. 9, 10)

Diagnosis. The new species is distinguished from all congeners by the following set of male characters: (i) abdominal segment X trapezoid with convex lateral margins, (ii) apex with shallow concavity, not forming lobes, in dorsal view (Fig. 10f); (iii) inferior appendage subtriangular, medial region constricted; (iv) with posterior region wide, elongated with rounded apex, in lateral view (Fig. 10a); and (v) basomesal finger shaped, well developed, base 1.5x as wide as apex and apex covered by setae, in ventral view (Fig. 10b). The new species is morphologically similar to *Helicopsyche cipoensis* Johanson & Malm, 2006 and *H. guara* Holzenthal, Blahnik & Calor, 2016 by general shape of abdominal segment X and inferior appendage in lateral view, but differs from them by abdominal segment X trapezoid, apex with shallow concavity, not forming lobes, in dorsal view (Fig. 10f) (rectangular, with apex rounded in *H. cipoensis*, and subtriangular, with apex with very short, deep apical cleft forming two lobes covered by setae in *H. guara*); and basomesal lobe of inferior appendage base 1.5x as wide as apex, apex wide and truncated, in ventral view (Fig. 10b) (base and apex same width, apex wide and rounded in *H. cipoensis* and base 2x as wide as apex, apex narrow and finger shaped).

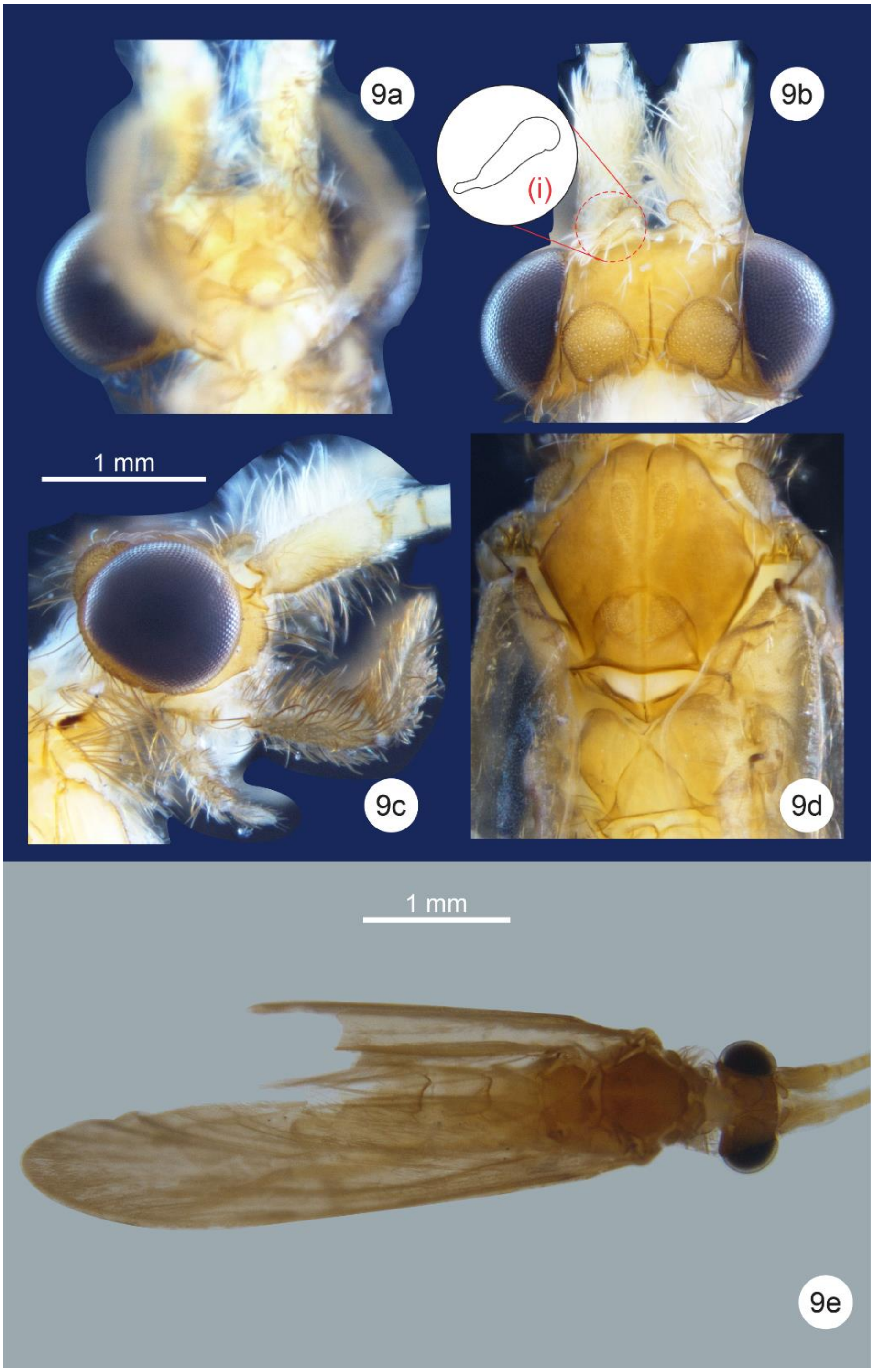

Figure 9. *Helicopsyche* (*Feropsyche*) *paulofreirei* **nov. sp.** male. **9a**, head, frontal view; **9b**, head, dorsal view, (i) detail of interantennal warts; **9c**, head, lateral view; **9d**, thorax, dorsal view; **9e**, habitus, dorsal view

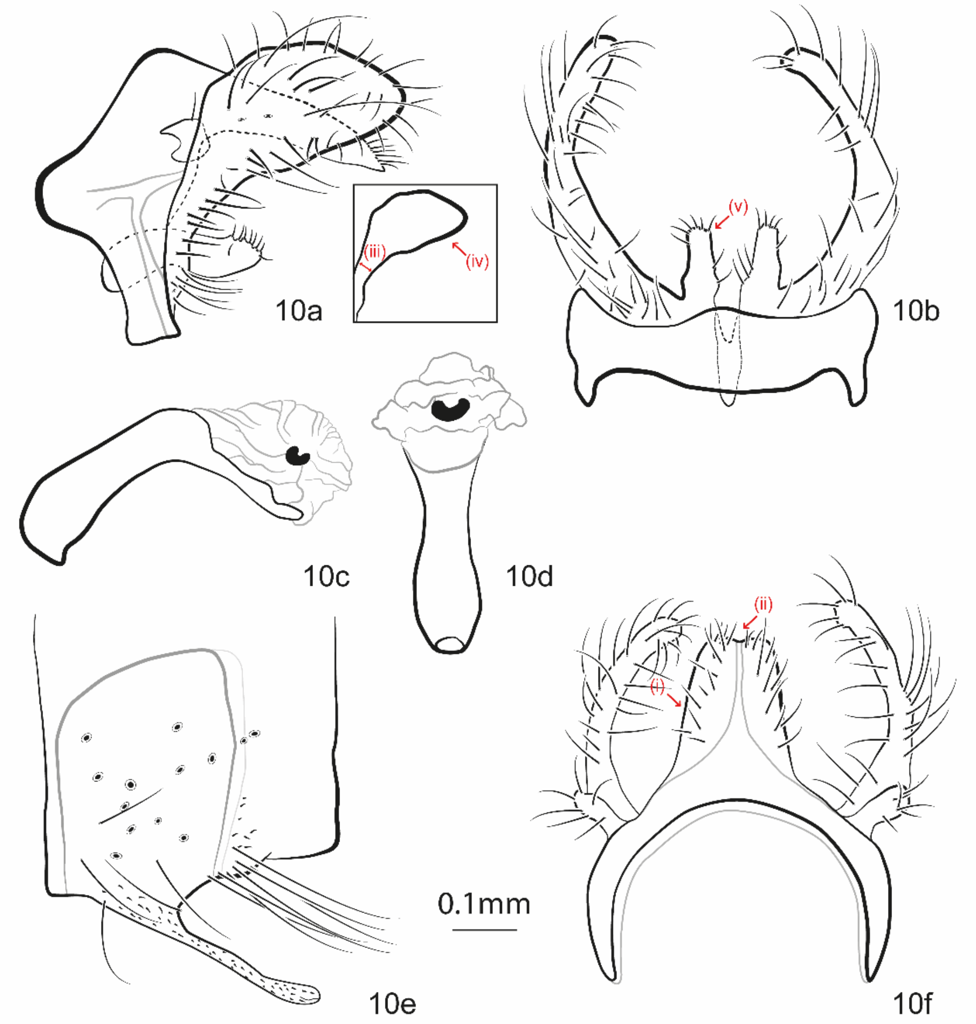

Figure 10. *Helicopsyche* (*Feropsyche*) *paulofreirei* **nov. sp.** male. **10a**, genitalia, left lateral view, red arrows point diagnostic characters iii–iv; **10b**, genitalia, ventral view, the red arrow points diagnostic character v; **10c**, phallus, left lateral view; **10d**, phallus, ventral view; **10e**, sternum VI; **10f**, genitalia, dorsal view, red arrows point diagnostic characters i–ii

Description. Overall color yellowish brown (in alcohol). Forewing length 3.32–4.87 mm (n = 10), forks I, II, III, and V present, with discoidal and thyridial cells, without medial cell. Hind wing forks I and V present, without discoidal and thyridial cells. Head brownish; antennae around ≤1.2x forewing length, scape longer, length subequal to head, covered by long setae; with a dense set of interantennal setae; interantennal warts club-shaped, anterior region projected, posterior region wide and globose, around half of head length (Fig. 9b); cephalic warts subquadrangular margins with long setae (Fig. 9b); postocular warts subtriangular with wide base, covered by long setae (Fig. 9b); maxillary palps brown, 2-segmented, covered by long, ferruginous setae; labial palps brown, 3-segmented, covered by long, ferruginous setae (Fig. 9c). Thorax: pronotum brown, with setal warts, digitated, covered by long, ferruginous setae; mesoscutum brown, with setal warts, bean-shaped, covered by small, ferruginous setae; mesoscutellum brown, with setal warts, globose, covered by small, ferruginous setae (Fig. 9d); legs yellowish brown, tibial spur formula 2, 2, 4. Abdomen: yellowish brown; abdominal sternum VI process present, about two-thirds of the segment length (Fig. 10e).

Male genitalia. Abdominal segment IX anterior lobe rounded projection, located ventrally on segment, anterodorsal and anteroventral margins concave, in lateral view (Fig. 10a), posterior lobe convex, basal plate U-shaped, in ventral view (Fig. 10b). Preanal appendages globose, in lateral view, digitated, in dorsal view (Fig. 10f). Abdominal segment X base wider than the apex, apex pointed, in lateral view (Fig. 10a), lateral margin convex, with a pair of little apical projections, U-shaped apex cleft, weakly notches, with a row of setae near lateral margin and a set of setae at the apex, in dorsal view (Fig. 10f). Inferior appendage clavate, widest apically, rounded in posterior region, anterior margin convex, with margin smooth, ventral margin weakly sinuous, without notches, containing a row of setae near the margin, in lateral view (Fig. 10a); inner face margin of the inferior appendage covered with rows of long setae, base and apex with equal width, apex without apical tooth, in ventral view (Fig. 10b); basomesal lobe of inferior appendage digitated, well-developed, with posterodorsal region rounded, with a set of setae on the basomesal margin, a subapical spine-like setae and an apical set of short spine-like setae, in lateral view (Fig. 10a), digitated, covered of few short spine-like setae on margin, projected posteriad, with length 1/3 of inferior appendage, in ventral view (Fig. 10b). Phallus tubular, phallobase slightly constricted medially (Figs. 10c, d), acuminated in posteroventral region, downcurved, in lateral view (Fig. 10c); phallotremal sclerite single, U-shaped, in ventral view (Fig. 10d).

Type material. Holotype: Brazil, Bahia, Igrapiúna, Reserva Michelin, Trilha do Guigó, 1ª ponte, 13°49'21"S, 39°12'12"W, 1 ♂, 26.ix.2013, UV light pan trap 4, Equipe PARFOR (MZUSP). Paratypes: Brazil, Bahia, Igrapiúna, Reserva Michelin, Trilha do Guigó, 1ª ponte, 13°49'21"S, 39°12'12"W, UV light pan trap 4, 3 ♂, 26.ix.2013, Equipe PAFOR cols. (UFBA); same data, except, Córrego próximo ao alojamento, 13°49'23"S, 39°10'21"W, UV light pan trap, 1 ♂, 19.ix.2012, Equipe LEAq cols. (MZUSP); same data, except Córrego das Matas, Trilha do Guigó, 13°49'25.4"S, 39°12'10.8"W, 120 m a.s.l., 2 ♂, 22.ix.2012, UV light pan trap, Calor et al. cols. (UFBA)

Distribution. NMAF (CAFEC) [Brazil (Bahia State)].

Etymology. This species is named in memory of Paulo Reglus Neves Freire (1921–1993), a Brazilian educator and philosopher. He is considered one of the most remarkable thinkers in world pedagogy and the Patron of Brazilian Education (Ferreira & Wiggers, 2018). His didactic practice was based on the premise that the student would assimilate the object of study by using a dialectic practice with reality (Ferreira & Wiggers, 2018). Thus, we used the specific name *paulofreirei* as a tribute to all the educators who participated in fieldwork at the Reserva Ecológica Michelin during the biology undergraduate course in the context of *Plano Nacional de Formação de Professores da Educação Básica* (PARFOR).

New distributional records

Helicopsyche (*Feropsyche*) *dinoprata* Dumas & Nessimian, 2019

[Type locality: Brazil, Rio de Janeiro, Santa Maria Madalena, Parque Estadual do Desengano, Morumbeca dos Marreiros, afluente do Ribeirão Macapá, 21°52’39.0” S, 41°54’55.3” W, 1,110 m; DZRJ; ♂].

Distribution. Northeastern Mata Atlântica, Paraíba do Sul, and Ribeira de Iguape Freshwater ecoregions [Brazil (Bahia and Rio de Janeiro states)].

Material examined. Brazil, Bahia, Amargosa, Faz. Sr. Alcides, Boqueirão, Colonha, 13°08'11"S, 39°39'46"W, 544 m, UV light pan trap, 1 ♂, 18.vii.2009, Calor and Lecci cols. (UFBA); same data, except Faz. Sr. Alcides, Boqueirão, Colonha, 13°08'11"S, 39°39'46"W, 544 m, UV light pan trap, 1 ♂, 18.vii.2009, Calor and Lecci cols. (UFBA); same data, except Camacan, Fazenda Waldemar da Farmácia, 15°25'13"S, 39°34'01"W, 310 m, UV light pan trap, 1 ♂, 28.iii.2011, Calor, Quinteiro, França and Barreto cols. (UFBA); same data, except, Wenceslau Guimarães, EEEWG, Riacho Dr. Germano, afluente Riacho Patioba, 13°34'50"S, 39°42'13"W, UV light pan trap, 1 ♂, 03.ix.2013, Calor, Duarte and Dias cols. (UFBA); same data, except Elísio Medrado, Serra da Jiboia, Reserva Jequitibá, 12°52'13"S, 39°28'36.8"W, 493 m, Malaise trap, 5 ♂, 05.iii.2013, Calor et al. cols. (UFBA)

Remarks. New record for the NMAF (CAFEC), as well as for the Brazilian Northeast region.

Helicopsyche (*Feropsyche*) *guara* Holzenthal, Blahnik & Calor, 2016

[Type locality: Brazil, Santa Catarina, [Blumenau] Rio Caeté, at the entrance to Parque Ecológico Spitzkopf, 23°00.350’S, 49°06.650’W, el. 92 m; MZUSP; ♂; ♀].

Distribution. São Francisco, Northeastern Mata Atlântica, and Southeastern Mata Atlântica Freshwater ecoregions [Brazil (Bahia, Minas Gerais, Santa Catarina, Rio de Janeiro states)].

Material examined. Brazil, Bahia, Cachoeira, Fazenda Villa Real, mata sede, 12°35'41"S, 38°53'58"W, 1 ♂, 15.vi.2003, Alvim, Souza, Silva, and Monteiro cols. (UFBA); same data, except Camacan, Fazenda Waldemar da Farmácia, 15°25'13"S, 39°34'01"W, 310 m a.s.l., UV light pan trap, 1 ♂, 28.iii.2011, Calor, Quinteiro, França and Barreto cols. (UFBA); same data, except UV light pan trap, 1 ♂, 28.iii.2011, Calor, Quinteiro, França and Barreto cols. (UFBA); same data, except Jandaíra, Reserva COPERN, 11°36'51.9"S, 33°38'46.9"W, UV light pan trap, 3 ♂, 11.x.2016, Kiszewski, Silva, Dias and Campos cols. (UFBA); same data, except Maracás, Milagres, MAMI 25AMA, 13°22’33.9"S, 40°29’22.0"W, 858 m a.s.l., UV light pan trap, 1 ♂, 25.iii.2012, PPBIO cols. (UFBA).

Remarks. New record for the NMAF (CAFEC), as well as for the Brazilian Northeast region.

Helicopsyche (*Feropsyche*) *monda* Flint, 1983

[Type locality: Paraguay, Depto. Alto Paraná, Salto del Monday, near Puerto Presidente Franco; NMNH; ♂].

Distribution. Orinoco Llanos, Northeastern Mata Atlântica, Paraíba do Sul, Lower Uruguay, Upper Uruguay, Upper Paraná and Lower Paraná Freshwater ecoregions

[Argentina, Brazil (Bahia, Ceará, Minas Gerais, Paraná, Rio de Janeiro, Santa Catarina, São Paulo states), Paraguay, Venezuela].

Material examined. Brazil, Bahia, Camacan, RPPN Serra Bonita, córrego em frente ao barranco desmoronando, 15°23'13.6"S, 39°33'56.3"W, 333 m a.s.l., UV light pan trap, 2 ♂, 13.xi.2011, Quinteiro, Dias and Duarte cols. (UFBA); same data, except Córrego Itauna, 15°23'35"S, 39°33'50"W, 330 m a.s.l., UV light pan trap, 2 ♂, 29.iii.2011, Quinteiro, França and Barreto cols. (UFBA); same data, except córrego próximo ao alojamento, 13°49'24.6" S, 39°10'19.9" W, 63 m a.s.l., 2 ♂, 29.xii.2011, Quinteiro, Duarte and Dias cols. (UFBA); same data, except Complexo da Chapada Diamantina, Abaíra, Catolés de cima, Riacho da Forquilha (porteira), 13°13’28.3”S, 41°54’02.3”W, 1603 m a.s.l., 8 ♂, 02.xi.2013, Calor, Dias and Campos cols. (UFBA); same data, except Cachoeira do Guarda Mó, 13°19'35"S, 41°19'35"W, 126 m a.s.l., UV light pan trap, 1 ♂, 30.x.2013, Calor, Dias and Campos cols. (UFBA); same data, except Piatã, Rio de Contas, Cachoeira das Deusas, Fazenda Oshoki, 13°06'33.1"S, 41°50'20.6"W, UV light trap, 5 ♂, 05.xi.2013, Menezes col. (UFBA); same data, except Santa Teresinha, Pedra Branca, Serra da Jiboia, Riacho das Torres, 12°51’00”S, 39°28’48”W, 638 m a.s.l., UV light pan trap, 8 ♂, 24.xi.2010 (UFBA); same data, except Serra da Jiboia, 80 m abaixo da cachoeira, 12°51'00"S, 39°28'48"W, 638 m a.s.l., Malaise trap, 1 ♂, 08.viii–28.xi.2009, Calor and Lecci cols. (UFBA); same data, except Uruçuca, Serra Grande, Parque Estadual Serra do Conduru, Cachoeira da Trilha Principal, 14°29'48.5"S, 39°03'53.1"W, 223 m a.s.l., UV light pan trap (branca), 3 ♂, 13.i.2014, Dias and Pereira cols. (UFBA).

Remarks. New record for NMAF (CAFEC and CDC), Brazil.

***Helicopsyche* (*Feropsyche*) *petri* Dumas & Nessimian, 2019**

[Type locality: Brazil, Rio de Janeiro, Rio das Ostras, Reserva Biológica União, Trilha Interpretativa do Pilão, riacho, 22°25’29.2” S, 42°02’21.2” W; DZRJ; ♂].

Distribution. Northeastern Mata Atlântica, Paraíba do Sul, and Fluminense Freshwater ecoregions [Brazil (Bahia and Rio de Janeiro states)]

Material examined. Brazil, Bahia, Una, REBIO Una, 15°10'16.3"S, 39°03'40.5"W, 141 m a.s.l.) 2 ♂, 04.viii.2013, UV light pan trap, Dias, Campos, Laurindo, and Gudim cols. (UFBA)

Remarks. New record for NMAF (CAFEC), as well as for the Brazilian Northeast region.

***Helicopsyche* (*Feropsyche*) *vergelana* Ross, 1956**

[Type locality: Mexico, Chiapas, Finca Vergel; INHS; ♂].

Distribution. Rio San Juan (Mexico), West Texas Gulf, Sorona, Rio Balsas, Papaloapan, Grijalva - Usumacinta, Chiapas - Fonseca, Quintana Roo - Motagua, Estero Real - Tempisque, San Juan (Nicaragua/Costa Rica), Chagres, Rio Tuira, North Andean Pacific Slopes - Rio Atrato, Magdalena - Sinu, South American Caribbean Drainages - Trinidad, Orinoco Piedmont, Orinoco Delta & Coastal Drainages, Essequibo, Guianas, Amazonas Guiana Shield, Madeira Brazilian Shield, Northeastern Caatinga & Coastal Drainages, Northeastern Mata Atlântica and Central Andean Pacific Slopes Freshwater ecoregions [Belize, Brazil (Bahia, Ceará, Maranhão, Pernambuco, Piauí states), Costa Rica, Grenada, Guatemala, Honduras, Mexico, Nicaragua, Panama, Paraguay, Peru, Suriname, Tobago, Trinidad, Venezuela].

Material examined. Brazil, Bahia, Iraquara, Pratinha, Rio Pratinha, abaixo da queda d'água, 12°21′10″S, 41°32′24″W, 642 m a.s.l., 2 ♂, 28.xi.2015, UV light pan trap, Queiroz, Santana, Mugnai, Ribeiro, Silva, and Cardoso cols. (UFBA)

Remarks. New record for NMAF (CDC), Brazil.

The four new species described here, and the new distribution records for five species (*H. dinoplata*, *H. guara*, *H. monda*, *H. petri*, and *H. vergelana*), increase from seven to 16 the known species in the NMAF. Our estimates indicate the existence of between 25 to 49 species of *H.* (*Feropsyche*) in the NMAF, based on the estimators of JACK1 (25 species), JACK2 (30 species), and CHAO2 (49 species).

Niche modelling

Sixteen species (twelve recorded and four new species) are used for modelling using distributional literature records, an online database, material examined, and data on UFBA (Table I). After correlation testing, seven raster variables were found to be uncorrelated, belonging to four groups, as arranged in Table II (more details Table S2 and Fig. S1, Supplementary material). Of the four algorithms tested, three (Bioclim, GLM, and SVM) presented AUC values higher than the cut-off value, and these were used to elaborate the subgenus environmental suitability maps (Fig. S2, Supplementary material).

Table I. Species of *Helicopsyche* (*Feropsyche*) from Northeastern Mata Atlântica Freshwater ecoregion, known semaphoronts and ID ecoregion (based on Abell et al. 2008) and distribution.

Species	**KS**	**ID ecoregion - Distribution**
H. angeloi Holzenthal, Blahnik and Calor	♂	328, 330, 344, 352 - BRA (MG; RJ; SP)
H. catoles Souza, Gomes and Calor	♂	328, 329, 352 - BRA (BA; RJ)
H. cipoensis Johanson and Malm	♂	323 - BRA (MG)
H. diamantina **nov. sp.**	♂	328 - BRA (BA)
H. dinoprata Dumas and Nessimian*	♂	328, 329, 330 - BRA (BA; RJ)
H. guara Holzenthal, Blahnik and Calor*	♂	323, 328, 331 - BRA (BA; MG; SC)
H. guariru Vilarino and Calor	♂	328, 329 - BRA (BA; MG)
H. mateusi **nov. sp.**	♂	328 - BRA (BA)
H. miltonsantosi **nov. sp.**	♂	323, 328 - BRA (BA)
H. monda Flint*	♂	303, 328, 329, 332, 333, 344, 345 - ARG; BRA (BA; MG; RJ; SC); PRY; VEN
H. paprockii Johanson and Malm	♂	323, 328 - BRA (MG)

H. paulofreirei **nov. sp.**	♂	328 - BRA (BA)
H. petri Dumas and Nessimian*	♂	328, 329, 352 - BRA (BA; RJ)
H. planorboides Machado	all	328, 329 - BRA (ES; MG; RJ)
H. succincta Johanson and Holzenthal	♂	314, 328 - BRA (BA); VEN
H. vergelana Ross*	all	138, 139, 160, 169, 131, 133, 201, 202, 204, 205, 209, 210, 301, 302, 304, 306, 309–311, 315, 321, 326, 328, 336 - BLZ; BRA (BA; PE; RO); COL; CRI; ECU; GTM; MEX; NIC; PAN; PER; SUR; TRI; VEN

KS = known semaphoronts; ♂ = male; ♀ = female; L = larva; P = pupa; *New distributional records; Ecoregion ID: 138 = Rio San Juan (Mexico), 139 = West Texas Gulf, 160 = Sorona, 169 = Rio Balsas, 131 = Papaloapan, 133 = Grijalva - Usumacinta, 201 = Chiapas - Fonseca, 202 = Quintana Roo - Motagua, 204 = Estero Real - Tempisque, 205 = San Juan (Nicaragua/Costa Rica), 209 = Chagres, 210 = Rio Tuira, 301 = North Andean Pacific Slopes - Rio Atrato, 302 = Magdalena - Sinu, 304 = South American Caribbean Drainages - Trinidad, 306 = Orinoco Piedmont, 303 = Orinoco Llanos, 309 = Orinoco Delta & Coastal Drainages, 310 = Essequibo, 311 = Guianas, 314 = Rio Negro, 315 = Amazonas Guiana Shield, 321 = Madeira Brazilian Shield, 326 = Northeastern Caatinga & Coastal Drainages, 323 = São Francisco, 328 = Northeastern Mata Atlântica, 329 = Paraíba do Sul, 330 = Ribeira de Iguape, 331 = Southeastern Mata Atlântica, 332 = Lower Uruguay, 333 = Upper Uruguay, 336 = Central Andean Pacific Slopes, 344 = Upper Paraná, 345 = Lower Paraná, 352 = Fluminense; countries acronym: ARG = Argentina, BLZ = Belize, BRA = Brazil, COL = Colombia, CRI = Costa Rica, ECU = Ecuador, GTM = Guatemala, MEX = Mexico, NIC = Nicaragua, PAN = Panama, PER = Peru, PRY = Paraguay, SUR = Suriname, TRI = Trinidad, VEN = Venezuela; Brazilian states: BA = Bahia, ES = Espírito Santo, MG = Minas Gerais, PE = Pernambuco, RJ = Rio de Janeiro, RO = Rondônia, SC = Santa Catarina, SP = São Paulo.

The distribution records of the present study are concentrated in the central and southern regions of the NMAF. Results point to high environmental suitability in two main areas of the NMAF region (Fig. 11a). The first area corresponds to the south of CDC, mainly in areas of high altitude (Fig. 11a), and the second is with high environmental suitability is the coastal drainages inserted in north of CAFEC (Fig. 11a). The other areas in the north and south of the NMAF show low environmental suitability (<0.5) (Fig. 11a).

Table II. Environmental variables were used for niche modelling, using a 35% correlation cut-off.

Variables group	**WorldClim Code**	**Variables**
Bioclimatic	Bio_2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
	Bio_3	Isothermality (BIO2/BIO3) (×100)
	Bio_4	Temperature Seasonality (standard deviation ×100)
	Bio_8	Mean Temperature of Wettest Quarter
Precipitation	Prec_05 and 10	Precipitation (mm)
Temperature	Tmax_09	Maximum temperature (°C)

Discussion

Although *H.* (*Feropsyche*) is highly rich and virtually distributed in all freshwater ecosystems (Johanson 2002; Johanson & Malm 2006), its distributional range is poorly known, and its diversity may be underestimated, as evidenced by the richness estimates of the NMAF. The subgenus *Feropsyche* is usually sampled in small and medium-sized streams (Flint 1991). Despite the wide distribution and number of species in Brazil (23 species), only seven species of *H.* (*Feropsyche*) were known in the NMAF (Santos et al. 2020), three of them known only from the type or adjacent locality. Despite slight differences, male genital structures have been remarkably useful for differentiating species in *H.* (*Feropsyche*). The shape and projections of the abdominal segment X, the inferior appendage, and the basomesal lobe have more useful characters in differentiating species. However, we observed differences in setal warts, especially of the head, when comparing species from different regions. These may indicate these as good characters for separating species groups in *H.* (*Feropsyche*).

Two species described here are part of what we designated, the *Helicopsyche monda* complex, a group of species with very similar genitalia morphology to *H. monda*. *Helicopsyche monda* was described by Flint (1983) from a series of specimens from Paraguay (holotype), Argentina, and Brazil (Santa Catarina state) (Flint, 1983), currently recorded from Northwestern (Oniroco Llanos Freshwater ecoregion, Venezuela) to Southeastern South American (Lower Uruguay Freshwater ecoregion, Argentina) (Holzenthal & Calor 2017). The original description by Flint (1983) shows divergence regarding the basomesal lobe of the inferior appendage when compared to the redescription and reillustration provided by Johanson (2002). In the ventral view, basomesal lobe of inferior appendage, according to Flint (1983), is slightly projected posteriad and subtriangular, although according to Johanson (2002), the basomesal lobe is absent. However, no comment was made about the morphological differences.

Here we use Flint's (1983) original description for comparison in differential diagnosis. However, all specimens morphologically identical to *H. monda sensu* Flint (1983) or Johanson (2002) were designated as *H. monda*. These identifications indicate that what we know as *H. monda* is a complex of species, evidencing the need for a reanalysis of the type series and additional material to resolve this taxonomic problem.

Since the present work, 16 species have been recorded for the NMAF, including four new species and five new distribution records. Of these ten species are recorded from the Caatinga domain (only *H. miltonsantosi* does not occur in the CDC), six are recorded from the Atlantic Forest domain (all occurring in CAFEC and only *H. guara* and *H. planorboides* with records outside), and two are recorded from the Cerrado domain (*H. angeloi* and *H. cipoensis*) (Fig. 1). The distribution records are mainly centered in easily accessible areas and protected areas, indicating that the same bias found for terrestrial organisms (i.e., Oliveira et al. 2016), seems to apply for aquatic insects.

These results and richness estimates evidence the biodiversity deficits, especially Linnean and Wallacean shortfalls, in the NMAF and the Brazilian Northeast region. Given the vastness of the ecoregion, the limited number of distributional records and species reveal knowledge deficits in the north and south of the NMAF. Therefore, we pointed out two main areas, south of CDC and north of CAFEC (Fig. 11), that have high environmental suitability (high potential distribution) and with piecemeal collection efforts in sparse areas, which highlights that these areas prioritized for research’s efforts as pointed out in results of the niche modelling.

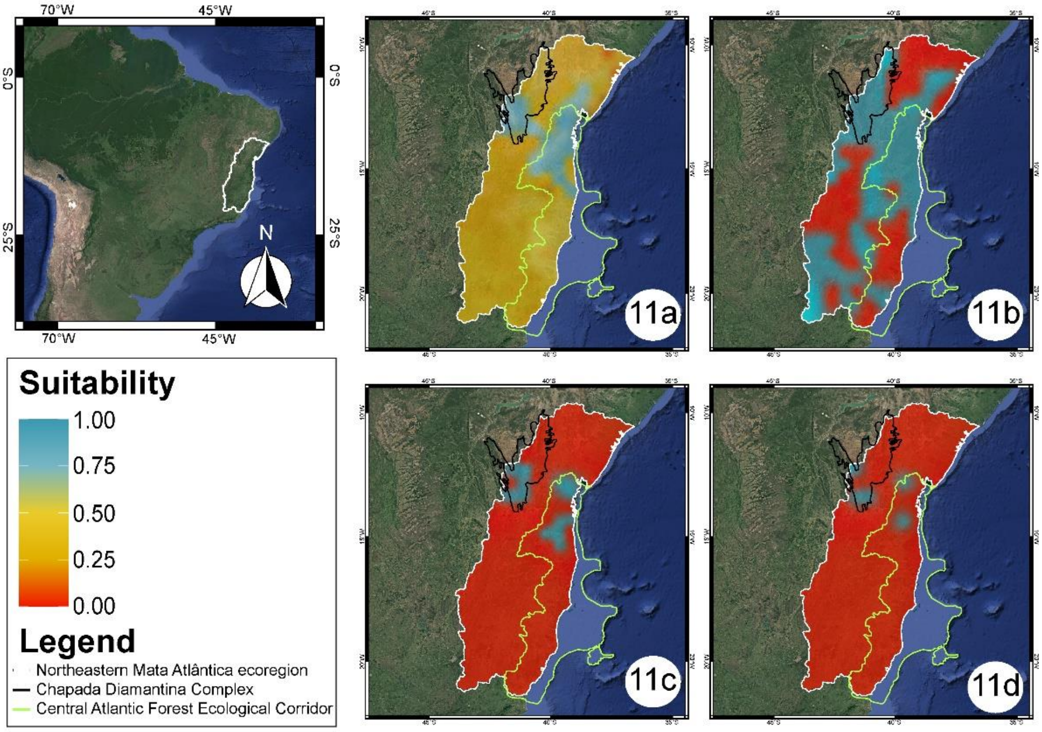

Figure 11. Environmental suitability map for *Helicopsyche* (*Feropsyche*) from Northeastern Mata Atlântica Freshwater ecoregion, Brazil. **11a**, Environmental suitability map (weighted average); **11b**, Environmental suitability map (minimum cut-off); **11c**. Environmental suitability map (50% cut-off); **11d**, Environmental suitability map (75% cut-off).

The CDC presents a vegetation mosaic composed of Caatinga, Cerrado, and Campo Rupestres, among others (Velloso et al. 2002), and has essential springs of streams and rivers in the region (Juncá et al. 2005; Santos et al. 2020). The region presents a high biodiversity of several groups, including Trichoptera. The CDC is where the most significant number of Trichoptera records are found in the NMAF, as well as the highest species richness and abundance (Santos et al. 2020). CDC has received attention in the last decade (e.g., Research Program of Biodiversity in Semiarid region), resulting in many specimens housed at UFBA (and other biological collections in the Brazilian Northeast region). Besides, CDC presents several unexplored areas north and south of the ecoregion.

The second area of the NMAF with high environmental suitability is CAFEC, composed of a mosaic of Atlantic Forest with low- and high-altitude coastal regions (0 to 2868 m a.s.l.). Regarding land use, CAFEC presents ca. 41% occupied by forest, ca. 57% by some farming activity, and 2% formed by natural non-forest formation, non-vegetated areas, water bodies, and unobserved (Santana et al. 2020). The Atlantic Forest is the richest forest domain in Brazil, with 495 species of Trichoptera, of which 137 species are recorded for the NMAF (Santos et al. 2020). However, despite being in the Atlantic Forest domain, CAFEC is mainly located in the Northeast region, with the most significant deficit of biodiversity knowledge and great potential to harbor new taxa (Santos et al. 2020). Here are increased from three to nine known species, but according to estimates and models presented, there is still much to be known, especially in the north of CAFEC, which has a larger area of forest cover and more outstanding environmental suitability for *H.* (*Feropsyche*).

Despite our work's contributions that increase the known species from seven to 16, distribution records are still concentrated and scarce for most of the NMAF. Thus, we consider that this ecoregion should be prioritized for research efforts given the high environmental suitability (high potential distribution) for *H.* (*Feropsyche*) species and the diversity estimates that indicate that there is still much to be recorded and between 36–67% of species awaiting description. As priority areas within the ecoregion, we highlight the CDC and CAFEC.

Conclusion

This work is the first study to use distribution modeling tools for the order Trichoptera in the Neotropics. It provides essential data that help to reduce the knowledge of biodiversity shortfalls. It also points to ways that can help select areas for research efforts in the NMAF. Our data, although important, are still the first step in the direction of understanding the biodiversity of the ecoregion, so future studies and databases can provide data that help in a better understanding of the distribution of *H*. (*Feropsyche*), as well as a better resolution of the potential distribution models of species.

The main conclusions of the paper are (i) the need for collection and analysis of material in areas of high environmental suitability and without or scarce distributional records, optimizing the use of resources in taxonomic research; and (ii) the need for a detailed reanalysis of what becomes known as the *Helicopsyche monda* complex, to face the Linnean shortfall and solve this taxonomic problem.

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Author contributions

ARC and RP conceived the design, main conceptual ideas, and overall manuscript format. RP performed the preparation, analysis of the biological material, and construction of the models and maps with ARC supervision, suggestions, and correction. RP wrote the manuscript with input and corrections from ARC. All authors interpreted and discussed the results of the manuscript.

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Capítulo II

Título: Biodiversity shortfalls and challenges revealed by a biogeographic study with New World snail-case caddisflies (Trichoptera, Helicopsychidae)

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Biodiversity shortfalls and challenges revealed by a biogeographic study with New World snail-case caddisflies (Trichoptera, Helicopsychidae)

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[a]This author contributed to the conception of the project, the main conceptual ideas, and the general format of the manuscript. He carried out the preparation, analysis of the biological material and construction of the models and maps. In addition, he wrote the manuscript and interpreted and discussed the results of the manuscript.

[b]This author also contributed to the conception, main conceptual ideas, and general format of the manuscript. He supervised, made suggestions and corrections, and interpreted and discussed the results of the manuscript. In addition to assisting in the writing and finalization of the manuscript.

Abstract

The biodiversity knowledge shortfalls (BKS) notably difficult the design of data-base conservation strategies. Some tools such as bioregionalization, distribution modelling and richness estimates can help identifying knowledge gaps and address these shortfalls. Among the continental ecosystems, freshwater environments constitute biodiversity hotspots that harbour about 10% of the world's highly endemic continental species. However, we know less than 20% of the freshwater species, 27% of them are threatened, with aquatic insects being the most affected. About 30% of aquatic insects are threatened, with some groups, e.g., Trichoptera, presenting a high extinction rate [6.8% of valid species not collected in 50 years]. Among the components of the order Trichoptera, the subgenus *Helicopsyche* (*Feropsyche*), stands out for its wide distribution and occurrence in different ecosystems and its high richness comprising 128 valid species, representing a good biological model for distribution pattern studies. The present work provides a synthesis of knowledge of *H.* (*Feropsyche*) with the description of biogeographic patterns, distribution hotspots, richness estimate, potential distribution, highlighting BKS as well as ways to face them. As for the BKS, estimates indicate the existence of 200–225 species, of which 129 are described, indicating a Linnean shortfall of around 40% of the species. As for semaphoronts, only 19 immature stages and 28 adult females are known (Haeckelian shortfall). Phylogenetic hypotheses are conflicting and biogeographic inferences have only been provided for more inclusive groups and more general biogeographic units, making it difficult to understand species relationships and the biogeographic history of the group (Darwinian shortfall). Here 684 (1,023 before filtration) distribution records are provided to 18 bioregions. The biodiversity hotspots are located on the central region of Antilles, northwest and north of Neotropical region, Bahia state in Brazil, and Southeast Brazil (between Rio de Janeiro and Minas Gerais states). Our results highlighted large BKS of the group. Besides advances in the last 20 years, which have been responsible for describing around 40% of the current fauna, the number of described semaphoronts is not increasing in the same way, thus the association immature-adults, with descriptions of females and immatures need to be made always as possible. Distribution modelling indicates that inventories and studies of specimens in the areas of Atlantic Forest and Caatinga in Brazil and east of the Andes (Chaco and Pantanal domain) should be prioritized because these areas have high environmental suitability and scarcity of data. Finally, we report the relevance of focused studies in the subgenus Helicopsyche, including comprehensive revision, phylogenetic hypothesis proposal and biogeographic inferences. Our work highlights the major BKS and provides a pathway to face these gaps. Here is compiled information published to date on the group, elevating it to a new status of knowledge, which can stimulate and drive the next research proposals.

Keywords. Biodiversity hotspots, distribution modelling, Haeckelian and Darwinian shortfalls, Linnean and Wallacean shortfalls, regionalization.

Introduction

Areas with “assemblages of geographically distinct species and communities” [98], also known as bioregions, ecoregions, or biogeographic regions, are a central concept in biogeography [32,48]. These areas delimitations are very important for ecological and evolutionary studies, in addition to serving as a base for establishing global conservation agreements [49]. The identification of these biogeographic units was generally made using taxonomic turnover or using grouping of endemic taxa [16]. Recent biogeographic regionalization proposals have been based on a broad dataset and using analytical methods at the local [e.g., 12,31], continental [16,21,51] and global level [13,22,98]. These inferences, provided by delimited methods and verifiable data, lead to reproductible results and testable corollaries [51,98]. It can be replicated with a wide range of taxonomic groups, seeking to identify and understand factors that determine shared distribution patterns among the diverse groups [18,98].

The biogeographic patterns generally used the distribution of known species as a proxy [16], and, consequently, they are strongly related to collection efforts, which are biased [67]. There are huge gaps in biodiversity knowledge related to areas neglected in terms of collection effort, fauna inventories, taxonomists, and investment in research, especially in developing countries [19,67]. These factors cause collection bias and directly affected the biodiversity knowledge [11,45,103].

In this context, some authors conceptualized the BKS to face them as research programs. The gap of species knowledge (Linnaean shortfall), poorly known species geographic distribution (Wallacean shortfall), shortfall of knowledge about semaphoronts of species (Haeckelian shortfall), and evolution of groups (Darwinian shortfall) [20,38].

Among the tools available to face the knowledge deficits, distribution modelling can identify areas with a high probability of potential distribution [environmental suitability] [3]. The generated models can help to prioritizing of the resources and efforts in areas with probability of potential distribution [88].

Anthropogenic actions have caused planetary-scale changes, which have caused the sixth mass extinction [10] with critical loss of biodiversity as faster than our ability to catalog it [38,55]. Among the ecosystems, freshwater environments cover only 1% of Earth’s land surface, but comprise around 10% of all species [85]. Levels of endemism in these environments are remarkably high, and about 20% in the New World (NW) species are threatened *sensu* IUCN [100]. Due to these characteristics, freshwater environments have the most acute biodiversity crisis among ecosystems [90]. The formulation of strategies based on large datasets is urgent to protect species as also the priority areas [30,51,90], and consequently reduce [or reverse] the decline of freshwater biota as much as possible [90].

Several insect orders have species with life stages occurring in freshwater ecosystems, but some orders and families stand out as having primarily aquatic origins (e.g., Trichoptera) [59]. Among these amphibiotic orders, the caddisflies stand out as having the greatest richness and diversity of functional trophic groups [59]. Despite recent advances in caddisfly taxonomy and phylogeny, the order is underexplored and poorly known in several aspects [14,59,60,89]. Knowledge about species, distribution ranges and biogeographic patterns for Trichoptera are scarce, especially in the Neotropical region (NT) [14,74,82]. Additionally, the regionalization of the NW based on the distribution of the order is limited to a classification in five regions [14], which forces the use of bioregions established based on other groups or limits the detail on biogeographic patterns of species and the relationship between areas [e.g., 6,28,22, 34,75,79].

Among the caddisflies, Helicopsychidae is represented by two genera, the monotypic *Rakiura* McFarlane, 1973 (endemic of New Zealand), and *Helicopsyche* von

Siebold, 1856 (circum-global distribution) [41]. *Helicopsyche* comprises 298 valid species in six subgenera, *H*. (*Cochliopsyche*) Müller, 1885, *H*. (*Feropsyche*) Johanson, 1998, *H*. (*Galeopsyche*) Johanson, 1998, *H*. (*Helicopsyche*) von Siebold, 1856, *H*. (*Petrotrichia*) Ulmer, 1910, *H*. (*Saetotricha*) Brauer, 1865 [56,61,66].

Biogeographical knowledge related to Helicopsychidae is limited, and phylogenetic hypotheses proposed are conflicting [e.g., 41,44]. Phylogenetic hypothesis pointed *H*. (*Feropsyche*) as more related to *H*. (*Saetotricha*) and *H*. (*Helicopsyche*), forming a sister group to all remain subgenera (Figure 1A) [41]. Biogeographic hypotheses are provided only for subgenera level, using more inclusive biogeographic units (e.g., NT) [41]. In opposite, recent proposal with basis a molecular data indicate which the *H*. (*Feropsyche*) as more related to *H*. (*Cochliopsyche*) forming a sister group with *H*. (*Saetotricha*) and *H*. (*Helicopsyche*) (Figure 1B) [44]. The taxa sample of this propose was reduced because their focus on Sericostomatoidea, and the biogeographical inferences comprise only the family level [44].

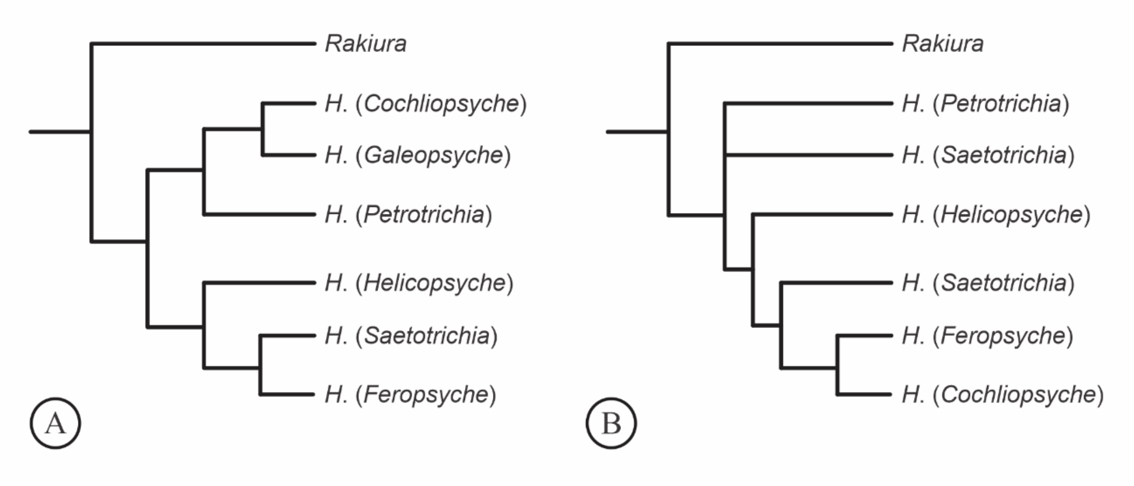

Fig. 1. Phylogenetic hypotheses of Helicopsychidae or more inclusive groups. A. Proposed by Johanson (1998); B. Proposed by Johanson et al. (2017), thin line represents clade with weak support

In the NW, we have 145 valid species in two subgenera, *H.* (*Cochliopsyche*), with 17 Neotropical species, and *H.* (*Feropsyche*), with 128 species (including three fossil species from the Dominican Republic) widely distributed throughout the NW [Nearctic region (NA) with 13 and NT with 125 valid species] [61,83]. *Helicopsyche* is a genus recognized by larval cases built with sand grains, helically organized, and resemble snail shells [35]. As other caddisflies, the immature stages live in freshwater ecosystems and, after completing the metamorphosis, they emerge in winged adults associated with riparian forests [89].

Helicopsyche (*Feropsyche*) has recently been revised [42]. Further studies are related to species descriptions and/or new distribution records [e.g., 9,17,25,56,94]. The taxonomic literature on *Helicopsyche* reveals a male bias [35,42]. Species descriptions based only on male adults is a very common practice in caddisfly taxonomy [82], as in some other insect orders [107]. For most of Neotropical caddisflies, immature stages and females are unknown [an average of <15% of the immatures are known, and in 41 Neotropical genera the immature stages are unknown [72], demonstrating a knowledge gap related to other semaphoronts. In addition, *H.* (*Feropsyche*) species are mainly reported exclusively from type localities and/or adjacent localities (like same district) [e.g., 17, 25, 36, 84, 94]. The combination of these two factors inevitably leads to knowledge shortfalls [38].

Due to its wide distribution and occurrence in different freshwater environments of the NW [42], *H.* (*Feropsyche*) represents a good biological model for studies that seek to identify and define distributional patterns of amphibiotic insects' groups. Furthermore, understanding how these species are distributed and grouped can provide subsidies for the identification of under-sampled areas. This information can help to direct attention to neglected areas regarding the collection effort. In this context, the present work aims to provide an updated synthesis of knowledge of *H*. (*Feropsyche*), with the description of distributional patterns, and to propose a biogeographic regionalization. In addition, we provide a distribution modelling to evidence potential distribution areas and indicate neglected areas to receive attention.

Material and methods

Study area

The NW comprises two regions, the NA and NT. Having in Mexico, a transition zone in western and eastern Sierra Madre provides routes linking elements of Nearctic and Neotropical fauna [57]. The NA *sensu* Wallace [99] is divided into four subregions: (i) Californian, (ii) Rocky Mountain, (iii) Alleghany, and (iv) Canadian sub-regions. As for NT *sensu* Wallace [99] is divided into four subregions: (i) Chilian, (ii) Brazilian, (iii) Mexican, and (iv) Antillean sub-regions. However, this delimitation applies mainly to vertebrate biogeographic studies, and several phylogeographers and zoogeographers (of invertebrates) have adapted this definition of the Neotropical region, excluding the southern portion and the Andean area of South America, which have a greater relationship with the Australasian region and forms the Andean region (AN) [57].

The NT corresponds to central and southern Mexico, the Antilles and most of South America, with three sub-regions (Antillean, Brazilian and Chacoan), two transition zones the Mexican transition zone overlaps NA-NT, while the South American transition zone overlaps NT-AN, and 54 provinces [58]. The AN corresponds to all South America below 26S latitude, adding the Andean highlands north of this latitude, with three sub-regions (Central Chilean, Subantarctic, Patagonian), South American transition zone overlaps NT-AN, and 15 provinces [58].

Recent proposal divides aquatic environments based on fish distribution, dividing NA into North America (with 76 ecoregions) and NT into Central America (with 17 ecoregions) and South America (with 52 ecoregions) [1]. Using amphibians as a model to test a network analysis algorithm were delimited for NA five bioregions and for NT 12 ecoregions [97].

Ross [76, 78] and Wiggins [102], based on caddisflies fauna sharing, divided the NA fauna into three biogeographic elements, one comprising the Rocky Mountains fauna forming the Nearctic East subregion, the fauna to the east forming the Nearctic West subregion and the fauna to the north with a greater relationship with the Palaearctic region forming the Beringian subregion. Flint (1983), also based on caddisflies fauna, divided the NT into two subregions, Chilean sub-region, that includes all of Chile and much of western and southern Argentina (northern boundary Rio Negro and its northern tributary, Rio Neuquén), and Brazilian sub-region, that covers the rest of the Neotropical region bounded to the north by the Isthmus of Tehuantepec in Mexico and including the Antilles. However, he makes it clear that there is no uniformity of components, presenting divisions generally related to topography and rainfall [24].

Following these delimitations in a work on global diversity of Trichoptera de Moor & Ivanov [14] delimit NA in three sub-regions: (i) Nearctic East (=Californian+Rocky Mountain), (ii) Nearctic West (=Alleghany), and (iii) Beringian (=Canadian) (14). NT caddisflies fauna, divided in two subregions Brazilian (=Brasilian+Mexican+Antillean) and Patagonian (=Chilean) [14]. Apart from these, all other proposals for bioregionalization for aquatic insects have been made with too large divisions [e.g., 96], making it difficult to use in efforts to plan for area protection and species conservation.

Distributional data and richness estimates

The distribution database was compiled through the primary literature [description and record of the occurrence of species], the database of Global Biodiversity Information Facility (GBIF, https://www.gbif.org) and SpeciesLink [http://www.splink.org.br/], original data from collections at the Museu de História Natural da Bahia, Universidade Federal da Bahia (UFBA), and the Laboratório Citotaxonomia e Insetos Aquáticos do Instituto Nacional de Pesquisa da Amazônia (LACIA-INPA). We use gazetteers and Google Maps© to register localization without coordinates, the centroid of the less comprehensive location was used. After the data compilation, two-stage filtering process was performed, (i) manual selection of the data, discarding points without coordinate information, generic data of locality (e.g., only state), or with the indeterminacy of the species (e.g., identification only to the genus level), and (ii) selection in R environment, discarding points that can generate an analysis bias (e.g., points localized at the centroid of the capital areas and/or with same coordinates or in marine areas). Species distribution map and heatmap (Kernel density) were prepared using QGIS v. 3.10.10.

Distribution of *H*. (*Feropsyche*) species through terrestrial ecoregions were used, as distinct datasets, to estimate the number of unknown species in the NW using non-parametric estimators. Estimators were calculated based on incidence data [presence-absence only], using bioregions as sampling unities, with the function ‘specpool' from ‘vegan’ package [65] in R environment. This function calculates two estimators of species richness: CHAO2, second order jackknife (JACK2) [46]. These non-parametric estimators are useful to estimate a potential number of unobserved species based on incidence data as those available here, and they have shown better performance than model-based or asymptotic estimators [37,68].

Biogeographic patterns

To obtain bioregion delimitation, a network approach developed was used, integrated with the web application Infomap Bioregions [18]. Species distribution was used with an adaptative resolution method in spatially explicit grade cells, to reflect differences in data density [18]. After this stage, a bipartite network was generated between the species and the cells, resulting in bioregion delimitation through the theoretical information clustering algorithm, named Infomap [80]. This algorithm is more efficient than others network grouping algorithms for the best resolution, and also for the possibility of self-adjusting the grid to the dataset [2,50].

The analyses followed the parameters, (i) large size between 1° to 8°, given the amplitude of the region of interest and the average distance between the points, (ii) maximum cell capacity = 100 and minimum cell capacity = 10, which defines the limits for the adaptive resolution algorithm to operate, (iii) the number of attempts = 10 and the cost of the cluster = 1.0. As an output file we obtained the map of the bioregions and as the most indicative species (EMI) of each bioregion (defined as the ratio between the frequency of species in a bioregion against all bioregions). After bioregion delimitation, composition, and EMI results, the maps were made using QGIS v. 3.10.10 and CorelDraw 2020 to adjust the images.

Distribution Modelling

Environmental data were obtained from monthly climate data for minimum, mean, and maximum temperature, precipitation, solar radiation, wind speed, water vapor pressure, and for total precipitation, 19 “bioclimatic” variables, and elevation on a scale of 5 arc minutes, all environmental variables obtained in WorldClim version 2.1 [https://www.worldclim.org/data/worldclim21.html]. The resolutions of these environmental variables were kept avoiding the loss of information or the impossibility of modelling. After obtaining the data, a correlation analysis between the variables was performed with the Spearman method using the 'correlate' function of the 'corrr' package [https://cran.r-project.org/package=corrr], in R environment. This correlation analysis permitted to select uncorrelated variables and consequently to avoid overweighing in the models. Variables with correlation values greater than 80% were considered as correlated.

Four correlative modelling algorithms were used: Bioclim [64], Domain [8], Generalized Linear Model (GLM) [63], and the Vector Support Machine (SVM) [87]. To generate the absence points, not available for the species used, we randomly generated 684 pseudo-absence points (1:1 ratio for the occurrence points), through the 'randomPoints' function of the 'dismo' package [https://cran.r-project.org/package=dismo] in R environment. Data partitioning was randomly performed in 70% for training and 30% for testing the models. The repeatability of the models (100 times) was used to increase the robustness of the result. After, the models were evaluated using the Area Under the Curve (AUC) [29] method, from which only models with values of AUC >75% for construction of suitability maps. Finally, we used default limits of presence and absence for the construction of the suitability maps.

Results

Synthesis of knowledge of subgenus, shortfalls, and challenges

Helicopsyche (*Feropsyche*) comprises 129 valid species, and is a subgenus widely distributed in the NT and some species distributed in NT. The greatest species richness is found in NT, especially in the Brazilian subregion with 127 valid species (Table 1).

Table 1. Species of *Helicopsyche* (*Feropsyche*) and information of known semaphoronts, distribution, and collections with deposited material. KS = Known semaphoronts; ♂ = Male; ♀ = Female; L = Larvae; P = Pupa; Collections that house type material in bold; *semaphoronts present in material examined of the publications, but not formally described

Species	**KS**	**Museum**	**Distribuition**
H. alajuela Johanson & Holzenthal, 2010	♂	**NMNH;** COZEM	CRI; PAN
H. altercoma Botosaneanu & Flint, 1991	♂♀	**NMNH**; CMNH; FSCA; ZMUA	DOM
H. angeloi Holzenthal, Blahnik & Calor, 2016	♂♀*	**MZUSP**; UFBA; UMSP	BRA
H. angulata Flint, 1981	♂♀	**USNM**; UMSP; NRM	COL; ECU; VEN
H. apicauda Flint, 1968	all	**USNM;** NMNH	DMA; GUA
H. auroa Johanson & Holzenthal, 2004	♂♀*	**UMSP**; NMNH	VEN
H. bendego Dumas & Nessimian, 2019	♂♀*	**DZRJ**	BRA
H. blancasi Schmid, 1958	♂♀*	**NMNH**	PER
H. blantoni Johanson & Malm, 2006	♂	**NMNH;** NRM	PAN
H. borealis (Hagen, 1861)	all	**MCZ**; UMSP; NMNH; TAMU; USNM	CAN; CRI; GTM; HND; MEX; NIC; PAN; USA
H. braziliensis (Swainson, 1840)	C	-	BRA
H. breviterga Flint, 1991	♂♀*	**UMSP**; COZEM; UMSP; NRM	COL; PAN; VEN
H. caligata Flint, 1967	♂	**NMNH**	CHI
H. camuriensis Johanson & Holzenthal, 2004	♂♀*	**UMSP**	VEN
H. carajas Gama Neto, Ribeiro & Passos, 2019	♂	**MPEG**	BRA
H. catoles Souza, Gomes & Calor, 2017	♂♀*	**MZUSP**; UFBA; UFRJ	BRA
H. centrocubana Botosaneanu & Flint, 1991	♂L	**ZMUA**	CUB
H. chilensis Flint, 1983	♂♀*	**NMNH**	CHI
H. chiriquensis Johanson & Malm, 2006	♂♀*	**NMNH**; UMSP; INBIO	CRI; PAN
H. cipoensis Johanson & Malm, 2006	♂	**NMNH**	BRA
H. circulata Johanson & Holzenthal, 2004	♂	**UMSP**	VEN
H. cochleara Johanson, 1999	♂	**NMNH**	ECU

H. colombiensis von Siebold, 1856	C	-	COL;VEN
H. comosa Kingsolver, 1964	♂♀	**INHS**; ZMUA; NMNH; MCZ	CUB
H. cotopaxi Botosaneanu & Flint, 1982	♂♀*L*P*C	**USNM**; ZMUA	ECU
H. cubana Kingsolver, 1964	all*	**INHS**; NHMJ; ZMUA	CUB; JAM
H. curvipalpia Johanson & Malm, 2006	♂♀*	**INHS**; NRM	MEX
H. dampfi Ross, 1956	♂♀*P*	**INHS**; CNHM; NMNH; UMSP; INBIO; MEL	CRI; GTM; MEX; NIC
H. daome Dumas & Nessimian, 2019	♂♀*	**DZRJ**	BRA
H. diamantina Pereira & Calor, 2023	♂	**MZUSP; UFBA**	BRA
H. dinoprata Dumas & Nessimian, 2019	♂♀*	**DZRJ**; MZUSP	BRA
H. disjuncta Johanson & Holzenthal, 2004	♂	**NMNH**	VEN
H. dominicana Botosaneanu & Flint, 1991	♂♀	**USNM; CMNH; CNHM; FSCA; NMNH; ZMUA**	DOM
H. dorsocurvata Johanson & Holzenthal, 2010	♂	**UMSP**	CRI
† *H. electra* Johanson & Wichard, 1996	♂	Collection Wichard	DOM
H. extensa Ross, 1956	♂♀*	**INHS**; UMSP	PER; VEN
H. falcigona Botosaneanu & Flint, 1991	♂♀*L	**ZMUA**; USNM; MCZ	CUB
H. fistulata Flint, 1991	♂♀*	**USNM**	COL; VEN
H. flinti Johanson, 1999	♂	**BMNH**	BRA
H. fridae Johanson, 2003	♂♀*	**NMNH**; UCD	PAN
H. golfitoensis Johanson & Holzenthal, 2010	♂	**NMNH**	CRI
H. granpiedrana Botosaneanu & Sykora, 1973	♂	**ZMUA**	CUB
H. grenadensis Flint & Sykora, 1993	♂♀*	**FSCA**; NMNH; UMSP; NRM	GRE; VEN
H. guadeloupensis Malicky, 1980	all	**CM**; ZMUA; MHNH; CMNH; MNNM; MNHM	DMA; GUA; LCA; MTQ
H. guara Holzenthal, Blahnik & Calor, 2016	♂♀*	**MZUSP**; UMSP; UFBA	BRA

H. guariru 94	♂	**MZUSP**; UMSP; UFBA	BRA
H. hageni Banks, 1938	all	**MCZ**; ZMUA	CUB; DOM
H. haitiensis Banks, 1938	♂	**MCZ**	HTI
H. helicoidella (Vallot, 1855)	C	-	BRA
H. incisa Ross, 1956	♂♀*	**INHS**; UMSP; INBIO; NMNH; NRM	CRI; MEX; NIC; PAN
H. johansoni Moreno, Desidério, Pes & Hamada, 2023	♂	**INPA; DZRJ; MNRJ; UFBA**	BRA
H. inflata Gama Neto, Ribeiro & Passos, 2019	♂	**MPEG**	BRA
H. kalaom Botosaneanu, 1996	♂♀*	**ZMUA**; FSCA; NMNH; CMNH	DOM
H. kingstona Johanson, 2003	♂	**UCD**	JAM
H. lambda Flint, 1983	♂	**NMNH**	ARG
H. laneblina Johanson & Holzenthal, 2004	♂	**NMNH**	VEN
H. lara Johanson & Holzenthal, 2004	♂♀*	**UMSP**; IZAM; NRM	VEN
H. lazzariae Holzenthal, Blahnik & Calor, 2016	♂	**MZUSP**	BRA
H. lewalleni Denning & Blickle, 1979	♂♀	**CAS**; INBIO; UMSP	CRI; ELS
H. limnella Ross,1937	♂	**INHS**	**USA**
H. linabena Johanson & Holzenthal, 2004	♂♀*	**NMNH**	VEN
H. linguata Johanson & Malm, 2006	♂	**NMNH**	PAN
H. lutea [Hagen], 1961	♀	**MCZ**	DOM
H. luziae 17	♂♀*	**DZRJ**	BRA
H. maculisternum Botosaneanu, 1993	♂♀*	**ZMUA**	VEN; TRI
H. manaos Moreno, Desidério, Pes & Hamada, 2023	♂	**NMNH**; ZMUA; CMNH; FSCA	DOM
H. melanochaeta Flint & Sykora, 2004	♂♀*	**INPA; DZRJ; MNRJ; UFBA**	BRA
H. merida Botosaneanu & Flint, 1982	♂♀*L*P*C	**NMNH**; ZMUA; UMSP	VEN
H. mexicana Banks, 1901	♂♀	**MCZ;** INHS; NMNH; USNM; CAS; OSU; UCR	CRI; MEX; USA
H. minima von Siebold, 1856	all	**USNM**; ZMUA	NIC; PRI

H. minuscula Martynov, 1912	♀	**PAN**	PER
H. molesta Botosaneanu, 1998	♂	**ZMUA**	JAM
H. mateusi Pereira & Calor, 2023	♂	**MZUSP;** **UFBA**	BRA
H. miltonsantosi Pereira & Calor, 2023	♂	**MZUSP;** **UFBA**	BRA
H. monda Flint, 1983	♂	**USNM**; DZRJ; NMNH	ARG; BRA; PRY; VEN
H. montana Felber, 1912	LPC	**NMB**	MEX
H. muelleri Banks, 1920	♂♀*LPC	**MCZ**; IRSNB	ARG; BRA; PER
H. neblinensis Johanson & Holzenthal, 2004	♂♀*	**NMNH**; IZAM; NRM	VEN
H. nigrisensilla Botosaneanu & Flint. 1991	♂♀	**USNM;** **ZMUA**	DOM
H. obscura Rueda Martín & Isa Miranda, 2015	♂LPC	**IBN**	ARG
H. occidentale Botosaneanu & Flint, 1991	♂L	**USNM;** **ZMUA**	CUB
H. ochthephila Flint, 1968	all	**NMNH**	JAM
H. paprockii Johanson & Malm, 2006	♂	**NMNH**	BRA
H. parahageni Flint & Sykora, 2004	♂♀	**NMNH;** CMNH; FSCA	DOM
H. paralimnella Hamilton, 1989	♂	**CUEC**	USA
H. paucispina Botosaneanu & Flint, 1991	♂	**ZMUA**	CUB
H. perija Johanson & Holzenthal, 2004	♂	**UMSP**	VEN
H. peruana Banks, 1920	♂	**MCZ**	PER
H. paulofreirei Pereira & Calor, 2023	♂	**MZUSP;** **UFBA**	BRA
H. petri Dumas & Nessimian, 2019	♂	**DZRJ;** **MZUSP**	BRA
H. pietia Denning, 1964	♂♀	**CAS**; INHS; NRM	MEX; USA
H. piroa Ross, 1944	♂♀*	**INHS**; TAMU; USNM	CRI; MEX; NIC; USA
H. planata Ross, 1956	♂	**INHS**; CNIN; CUEC	NIC; MEX
H. planorboides Machado, 1957	all	**DZRJ**	BRA
H. poliochaeta Flint & Sykora, 2004	♂♀	**NMNH**; FSCA	DOM
H. propinqua Botosaneanu & Flint, 1991	♂	**NMNH**	PRI
H. quadrosa Ross, 1956	♂	**INHS**	MEX
H. ralphi Cavalcante-Silva, Pereira & Calor, 2022	all	**MZUSP**; INPA; UFBA; UFRJ	BRA
H. ramosi Flint, 1964	all	**NMNH**; ZMUA	PRI
H. rentzi Denning & Blickle, 1979	♂♀	**CAS**; INBIO; UMSP; USNM	CRI

H. sanblasensis Johanson & Malm, 2006	♂	**NMNH**	PAN
H. scalaris Hagen, 1864	C	-	VEN
† *H. electra* Johanson & Wichard, 1996	♂	Collection Wichard	DOM
H. selanderi Ross, 1956	♂♀*	**INHS**; NMNH; UMSP	CRI; MEX; VEN
H. septifera Flint & Sykora, 2004	♂♀	**NMNH**; CMNH; ZMUA	DOM
H. shaamunensu 17	♂	**DZRJ**	BRA
H. sigillata Botosaneanu & Flint, 1991	♂♀	**NMNH; ZMUA**	CUB
H. singulare Botosaneanu & Flint, 1991	♂	**NMNH**; USNM; ZMUA	PRI
H. sinuata Denning & Blickle, 1979	♂	**UCD**; NMNH	MEX; USA
H. succincta Johanson & Holzenthal, 2004	♂	**NMNH**; UFBA	BRA; VEN
H. sucrensis Johanson & Holzenthal, 2004	♂	**UMSP**	VEN
H. tachira Johanson & Holzenthal, 2004	♂	**UMSP**	VEN
H. tapadas Denning, 1966	♂	**CAS**; UFBA	BRA; VEN
H. temora Denning & Blickle, 1979	♂	**UCD**	MEX
H. thelidomus Hagen, 1864	C	-	VEN
H. timbira Silva, Santos & Nessimian, 2014	♂♀*	**DZRJ; MNRJ; INPA**	BRA
H. truncata Ross, 1956	♂	**INHS;** UMSP; USNM	CRI; MEX; PAN
H. turbida Navás, 1923	all	**MZBS**; NMNH; IBN; USNM	ARG
H. tuxtlensis Bueno-Soria, 1983	♂♀*	**IBUNAM**; UCD; USNM	GTM; MEX; PAN
H. umbonata Hagen, 1864	all	**USNM**; MCZ; AMNH; USNM	JAM
H. valligera Flint, 1983	♂♀*	**NMNH**; USNM	ARG; BRA
H. venezuelensis Johanson & Holzenthal, 2004	♂	**UMSP**	VEN
H. vergelana Ross, 1956	all	**INHS**; NMNH; NRM; UCD; UFPE; UMSP; USNM	BLZ; BRA; COL; CRI; ECU; GTM; GUY; MEX; NIC; PAN; PER; SUR; TRI; VEM
H. villegasi Denning & Blickle, 1979	♂	**UCD**	MEX
† *H. voigti* Johanson & Wichard, 1996	♂	Collection Wichard	DOM
H. woldai Johanson, 2003	♂	**NMNH**; UCD	PAN

H. woytkowskii Ross, 1956	♂♀*	**INHS**; NRM; UMSP	PAN; PER; VEN

Among the species of the subgenus, ca. 40% were described in the last 20 years, corresponding to an average of five species/year, while between 1840-1999 we have an average of two species/year (Table 1). Estimates indicate from 200 (Jacknife2, error = 20.6) to 225 (Chao2, error = 48.6) species for the NW, indicating that ca. 40% of the species remain unknown. Considering the distribution, ca. 45% of species have records restricted to type localities or type localities and adjacent areas (e.g., same stream).

As for the knowledge of semaphoronts, the larva/pupa and female adults are still unknown in most species [7,35,61]. Only 19 immature stages and 28 adult females are described to valid species of *H.* (*Feropsyche*) (Table 1). Additionally, five species are described exclusively based on immature stages [*H. braziliensis* (Swainson, 1840), *H. colombiensis* von Siebold, 1956, *H. helicoidella* (Vallot, 1855), *H. minima* von Siebold, 1956, *H. scalaris* Hagen, 1864, *H. thelidomus* Hagen, 1864, and *H. umbonata* Hagen, 1864] and two for adult females [*H. lutea* (Hagen, 1861) and *H. minuscula* Martynov, 1912].

Bioregions and biodiversity hotspots

A total of 684 (1,023 with redundances and unspecific localities) distributional records of all *H.* (*Feropsyche*) species were compiled, except *H. braziliensis* because its type-location is vague (Figure 2). This database is the result of a survey of 84 publications, online databases (GBIF and SpeciesLink), and original data (UFBA and INPA). For the formation of a bioregion a minimum of 10 clustered occurrence records is required, because of these 22 species used in the analysis are not placed in any bioregion.

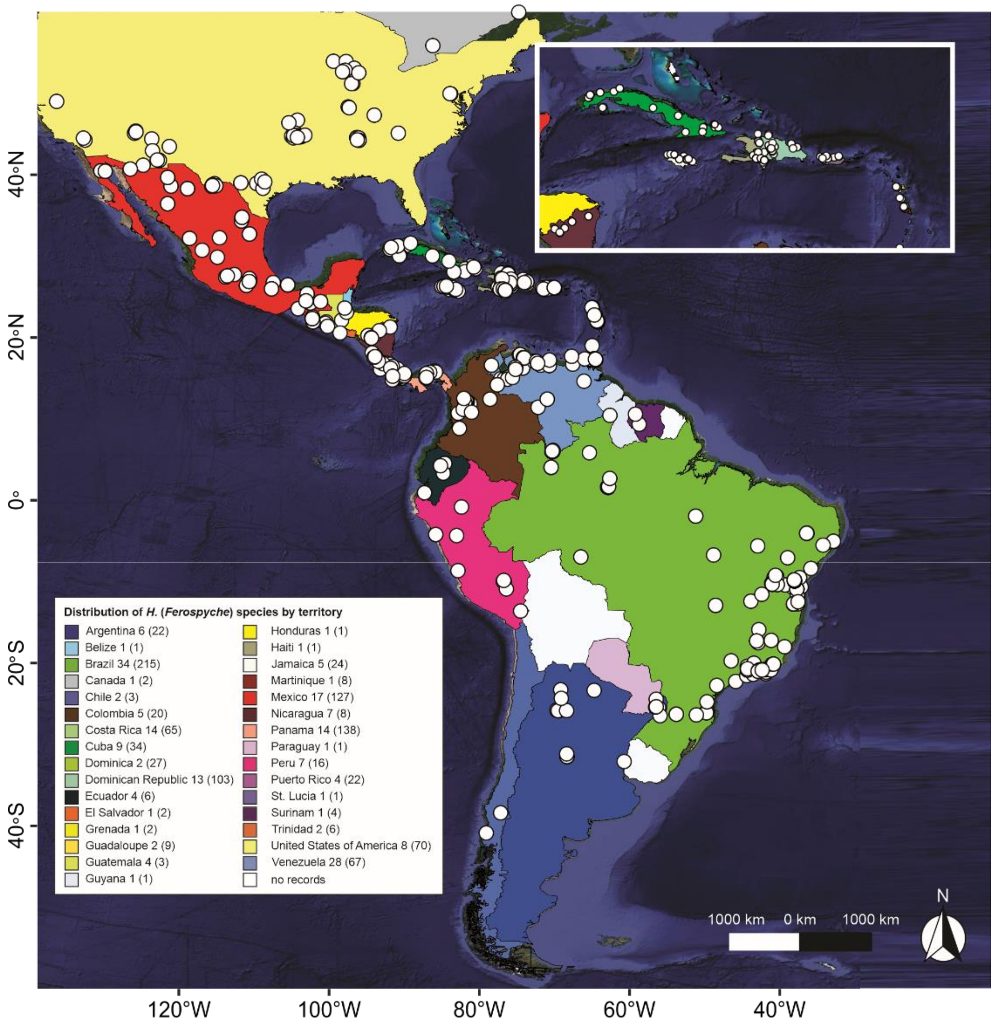

Fig. 2. Distribution records of *Helicopsyche* (*Feropsyche*) species with number of species recorded and exclusive species in brackets per territory

Analyses resulted in 18 bioregions (BR1–BR18), four in NA and 15 in NT (one in both) (Figure 3). The highest number of bioregions was found in “Brazilian subregion” *sensu* de Moor & Ivanov [14] (in Central America, north-western and east of South America).

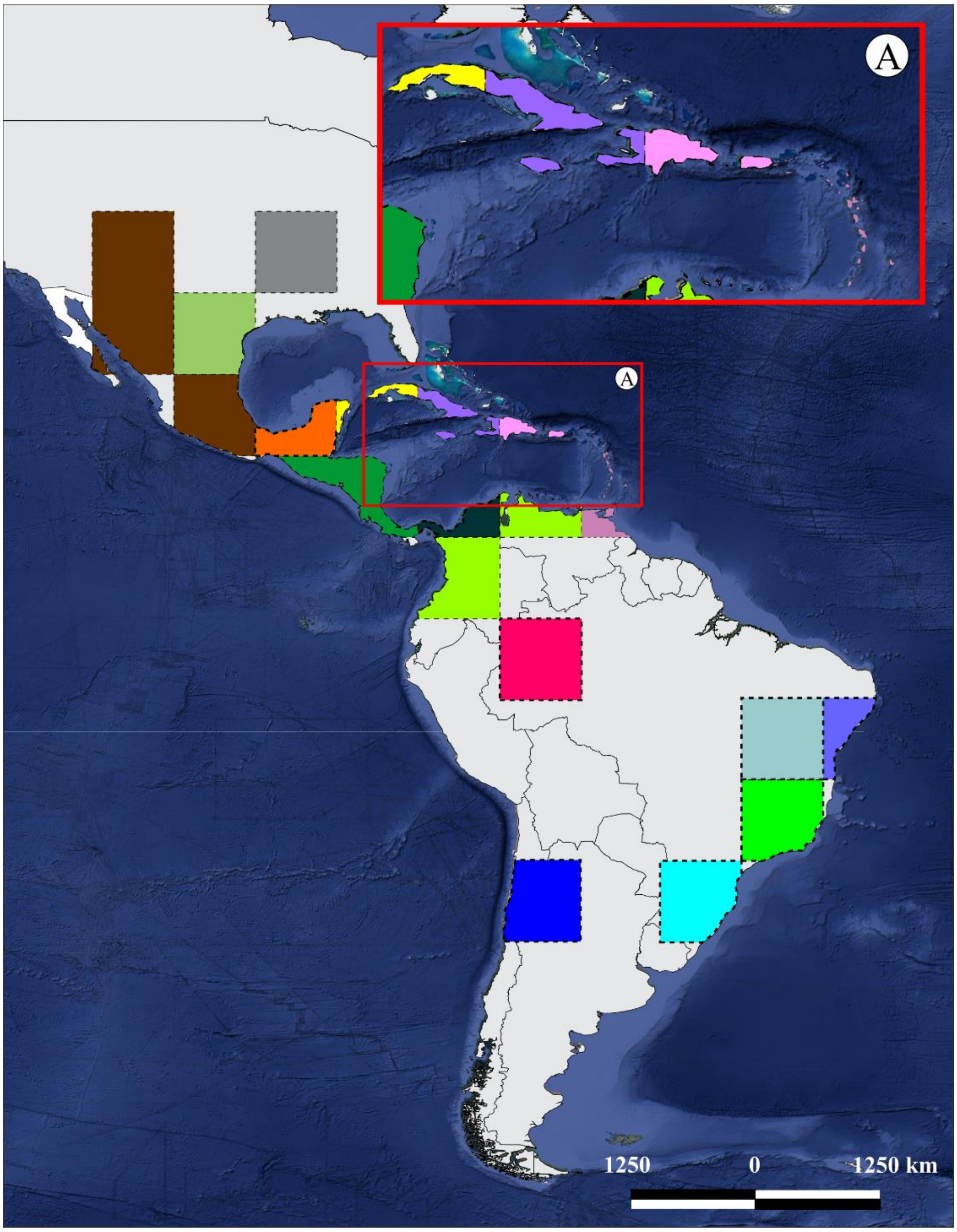

Fig. 3. Bioregions of the Nearctic and Neotropical regions for distributional records of *Helicopsyche* (*Feropsyche*)

The BR9 has the highest species richness with 21 species, followed by the BR11 region (17 species) and BR16 region (15 species) (Table 2). The BR8 with 119 species records, followed by the BR9 (117 species records) and BR10 (110 species records) have the highest number of records (Table 2). *H. vergelana* Ross, 1956 presents the highest number of distribution records (66 records in 5 mi km^2), followed by *H. borealis* (Hagen, 1861) (59 records in 3 mi km^2) (S1 Table).

Table 2. Summary of species richness data, distribution records, most common species [MCS]; most indicative species [MIS] from each bioregion of Nearctic and Neotropical regions

Bioregion	**Records**	**Species**	**MCS (records)**	**MIS (score)**
Bioregion 1	13	3	*H. limnella* (9)	*H. limnella* (7.33)
Bioregion 2	23	3	*H. piroa* and *H. borealis* (9)	*H. piroa* (4.40)
Bioregion 3	76	12	*H. mexicana* (40)	*H. temora, H. villegasi, H. montana* and *H. curvipalpia* (1.65)
Bioregion 4	13	3	*H. pietia* (9)	*H. pietia* (5.08)
Bioregion 5	33	7	*H. quadrosa, H. truncata, H. tuxtlensis* and *H. planata* (6)	*H. quadrosa* (11.00)
Bioregion 6	17	5	*H. falcigona* (5)	*H. comosa, H. occidentale* and *H. paucispina* (13.20)
Bioregion 7	41	10	*H. umbonata* (12)	*H. umbonata, H. cubana, H. ochthephila, H. granpiedrana, H. sigillata, H. molesta, H. kingstona* (5.50)
Bioregion 8	119	14	*H. dominicana* (28)	*H. ramosi, H. nigrisensilla, H. kalaom, H. singulare, H. propinqua, H. haitiensis* (2.36)
Bioregion 9	117	21	*H. incisa* (27)	*H. dampfi, H. chiriquensis, H. rentzi , H. lewalleni, H. alajuela, H. linguata, H. golfitoensis, H. dorsocurvata* (2.4)
Bioregion 10	110	4	*H. fridae* (43)	*H. fridae* (1.535)
Bioregion 11	72	17	*H. angulata* and *H. fistulata* (15)	*H. fistulata , H. merida, H. lara, H. camuriensis, H. auroa, H. venezuelensis, H. colombiensis, H. circulata, H. tachira* (4.40)
Bioregion 12	50	8	*H. apicauda* (26)	*H. disjuncta* and *H. sucrensis* (2.538)
Bioregion 13	12	1	*H. neblinensis* (12)	*H. neblinensis* (5.5)
Bioregion 14	48	9	*H. diamantina* (15)	*H. diamantina, H. miltonsantosi, H. mateusi, H. helicoidella* (4.4)
Bioregion 15	54	10	*H. guariru* (8)	*H. succincta* (2.87)
Bioregion 16	63	15	*H. bendego* (11)	*H. bendego, H. angeloi, H. planorboides, H. shaamunensu, H. paprockii, H. cipoensis, H. daome, H. luziae* (6)
Bioregion 17	20	7	*H. guara* (8)	*H. lambda, H. lazzariae, H. flinti* (8.25)
Bioregion 18	16	3	*H. turbida* (12)	*H. obscura* (5.5)

The areas with the highest number of distributional records are: central region of Antilles (bioregion 8 - Haiti and Dominican Republic, with 106 records of 11 species), northwest of NT (bioregions 9 and 10 - Costa Rica, south Nicaragua, and west Panama, with 205 records of 20 species), north of NT (bioregion 11 - northwest Venezuela, with 36 records of 12 species), and two localities of east of NT (bioregions 14 and 15 - Bahia state in Brazil, with 94 records of 13 species, and bioregion 16 - southeast region of Brazil, Rio de Janeiro State, southeast Minas Gerais State, and east São Paulo State, with 54 records of 12 species) (Figure 4).

Distribution modelling

After correlation testing, nine raster variables were found to be uncorrelated, belonging to five groups (bioclimatic, elevation, precipitation, solar radiation and wind speed), as arranged in Table 3 (more details, S2 Table). Of the four algorithms tested, all presented AUC values higher than the cut-off value, and these were used to elaborate the subgenus environmental suitability maps (S1 Fig.).

Table 3. Environmental variables used for species modelling, using 80% correlation cut-off

Variables group	**Code**	**Variables**
Bioclimatic	Bio_7	Temperature Annual Range [Annual Precipitation- Min Temperature of Coldest Month]
	Bio_12	Annual Precipitation
Elevation	Elev	Elevation
Precipitation	Prec_07	Precipitation (mm)
Solar radiation	Srad_03, 04, 07 and 08	Solar radiation (kj m-2 day-1)
Wind speed	Wind_01	Wind speed (m s-1)

Helicopsyche is one of the more representative genera of the NW with 128 valid species and wide distribution in the region [61]. Specimens show little variation in length and shape but are distributed in various types of freshwater ecosystems from small lentic to large lotic environments [43].

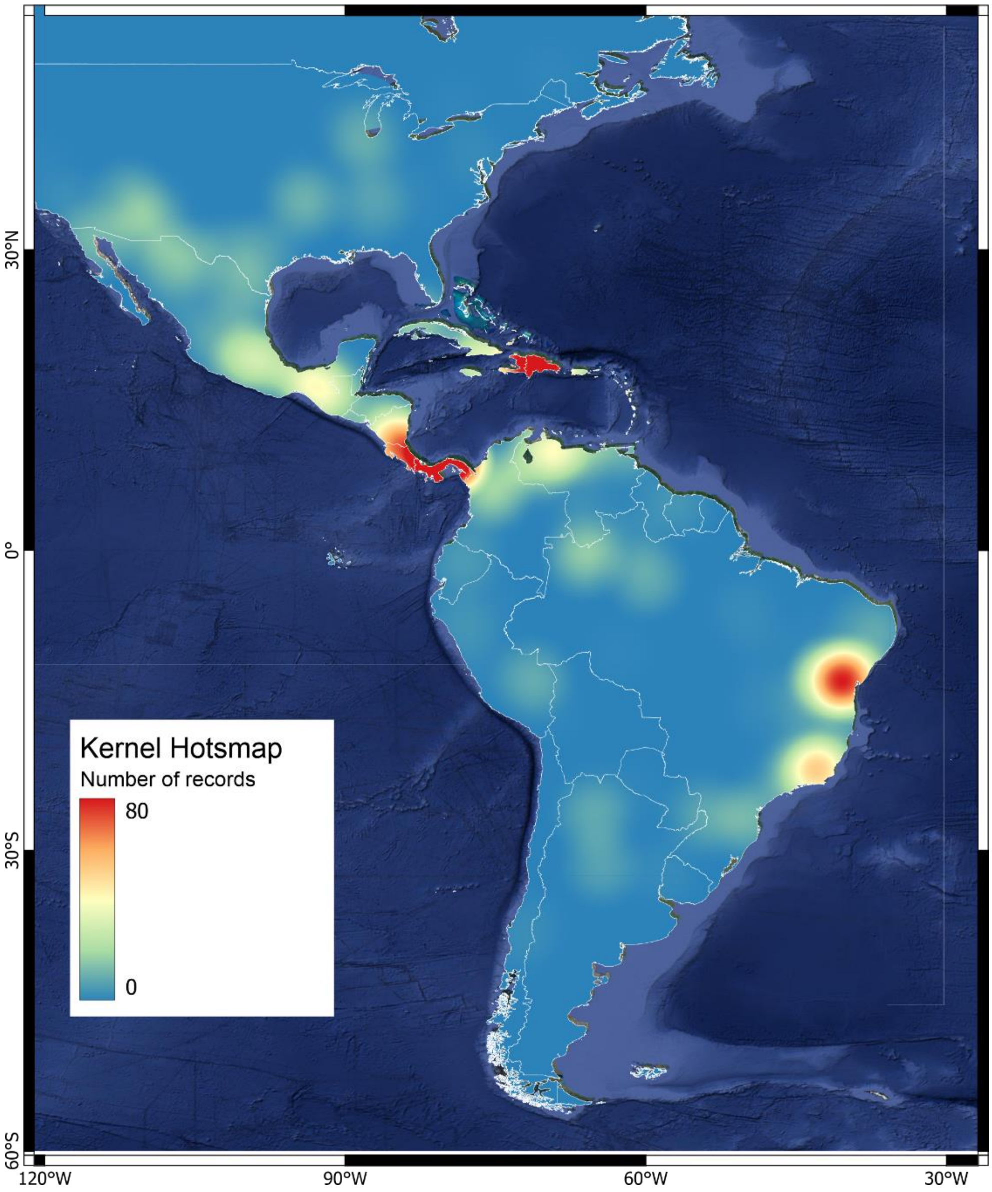

Fig. 4. Heatmap representing distributional records of *Helicopsyche* (*Feropsyche*) species in Nearctic and Neotropical region

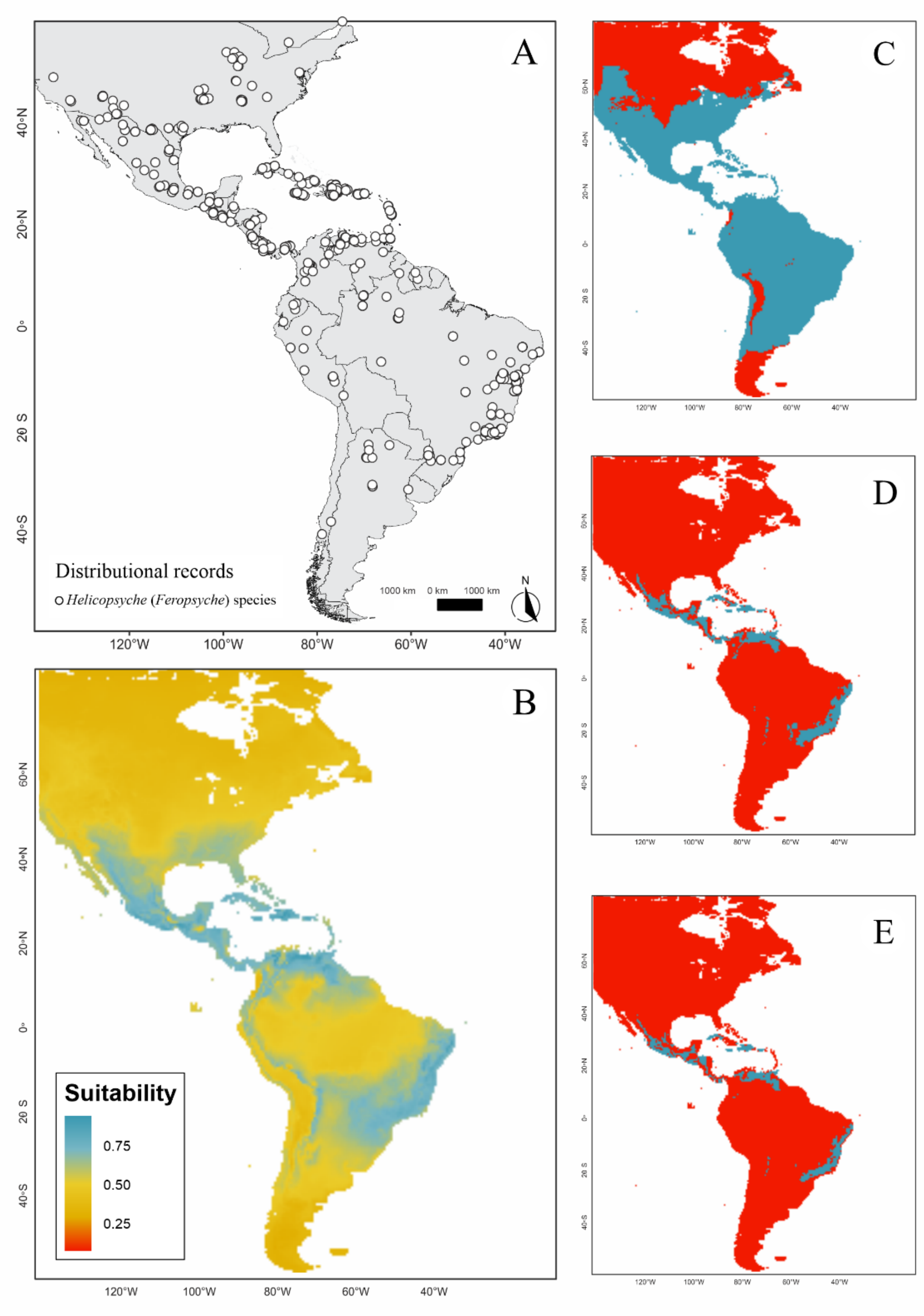

Fig. 5. Environmental suitability map for the species of the subgenus *Helicopsyche* (*Feropsyche*). A. Distributional records map; B. Environmental suitability map (weighted average); C. Environmental suitability map (minimum cut-off); D. Environmental suitability map (30% cut-off); E. Environmental suitability map (50% cut-off)

Our results show higher environmental suitability of *H.* (*Feropsyche*) species in NA in three areas: (i) Temperate coniferous forests (bioregion 1), (ii) temperate grassland, savannah, and shrublands forests (bioregion 2), (iii) desert and xeric shrublands, and mediterranean forests, woodlands, and scrub (bioregions 3 and 4) of USA (Figure 5). In the NT, five areas also show high environmental suitability: (i) almost the entire Central America continental (bioregions 3, 5, 6 and 9), (ii) Greater and Lesser Antilles (bioregions 6–8 and 12), (iii) northwestern South America (except the llanos of Colombia and Venezuela) (bioregions 10–12), (iv) east of the Andes from montane grasslands and shrublands and Chaco and Pantanal domain (without bioregions because the low species records), and (v) southeastern of Cerrado domain and tropical forests of eastern and southern Brazil (bioregions 14–17) (Figure 5). In other hand, three areas (Brazilian Amazon region, the Cerrado domain, and the Patagonian subregion) show low environmental suitability.

Discussion

Our results demonstrate the clear increment of species descriptions and cataloguing of distributional records, mainly in under-explored areas of the NT. This increase can be related with the development of trichopterology in the NW [e.g., 35,83], cooperation among researchers of NT with other researchers' groups [e.g., 36], the establishment of research groups in different countries of the NT [e.g., 25,81].

After Johanson [39–44], who stablished the panorama of Helicopsychidae taxonomy in the NW, several contributions have been made by local researchers [e.g., 9,17,25,56,70,81,84,94].

The richness estimates results are coherent with previous diversity estimates in the NT, which indicate around 40% unknown fauna and numerous unexplored areas [74,82, both with around 50% of species unknown]. In the same way, the Wallacean shortfalls are expressed in scarce data on the species distribution [67]. The distributional information is centred on the type locality or adjacent localities [91], which also appears in our results from *Helicopsyche* (*Feropsyche*), demonstrating the need for increase the effort to implement faunistic surveys in unexplored areas, and to analyse the material deposited in collections [data not public]. These actions will provide description of taxa not known to science, and better knowledge about the species distribution, combating the gap of knowledge related to Linnean and Wallacean shortfalls, respectively [38].

Inventories, checklists, descriptions of new species and new distribution records are the first step in addressing BKS [7]. However, other aspects such as ecology, biology, phenology, and ethology are extremely important to guide biodiversity conservation policies and the consequences of anthropogenic interventions (e.g., climate change, suppression of riparian vegetation) [74]. In the caddisfly life cycle, the most period is comprised by immature stages, but the adult males are the most abundant specimens in the collections because the insect taxonomy, particularly in Trichoptera, is strongly based on its semaphoronts [7].

Immature and female semaphoronts are known for the most caddisfly families and genera, but these semaphoronts have been described for a small number of species [7,35]. For *H.* (*Feropsyche*), 36 species have adult females known and undescribed, and four species (*H. cotopaxi* Botosaneanu & Flint, 1982, *H. cubana* Kingsolver, 1964, *H. merida* Botosaneanu & Flint, 1982, and *H. dampfi* Ross, 1956) have immature stages known and undescribed besides present in literature (Table 1) [4, 47, 77], showing that there is material for the description of other stages.

Haeckelian shortfall is common among the genera of Neotropical Trichoptera, despite recent efforts employed in some groups such as *Smicridea* [e.g., 15], *Plectromacronema* [e.g., 69], *Macrostemum* [e.g., 71], *Phylloicus* [e.g., 73] and *Helicopsyche* [e.g., 9], there is still much to be explored. In *H.* (*Feropsyche*), at least 65 valid species have females and 21 have at least one immature stage deposited in collections (Table 1). Despite this, only 28 adult females and 19 immature stages have been described [35, 42], demonstrating the great potential of the material to be described, which has already been collected and identified and is just waiting to be described. The description of these semaphoronts can contribute to a better circumscription of the species, the correction of possible taxonomic errors and the formation of a complementary database for studies related to the understanding of relationships [20], the same can be applied to *Helicopsyche*.

A total of 18 bioregions were found, with 13 of them located at the Brazilian sub-region, which can be explained by its territorial extension, high species richness and wide distribution of *H.* (*Feropsyche*). The bioregions with the highest concentration of species are in the areas near the Equator line, between 0° to 25°N, which is coherent with zoogeographic proposal of Johanson [40]. Ten bioregions have at least one part at these latitudes, with also is true to other animal groups [e.g., 1,18,98], reenforcing the complex biogeographic history of the area.

In general, the bioregions recovered here show similarities to amphibian regionalization proposals [98], particularly in the bioregions of the Yucatan Peninsula (bioregion 5), Orinoco Delta National Park (bioregion 12), and between northern Chile and northwestern Argentina (bioregion 18), as well as four bioregions in eastern Brazil (bioregions 14–17) with almost overlapping boundaries. This similarity may be mainly related to the amphibiotic life cycles, with complete dependence on aquatic and terrestrial environments, like amphibians. In opposite, the flying ability of caddisflies could explain some differences in the distribution patterns in relation to terrestrial or aquatic groups [14].

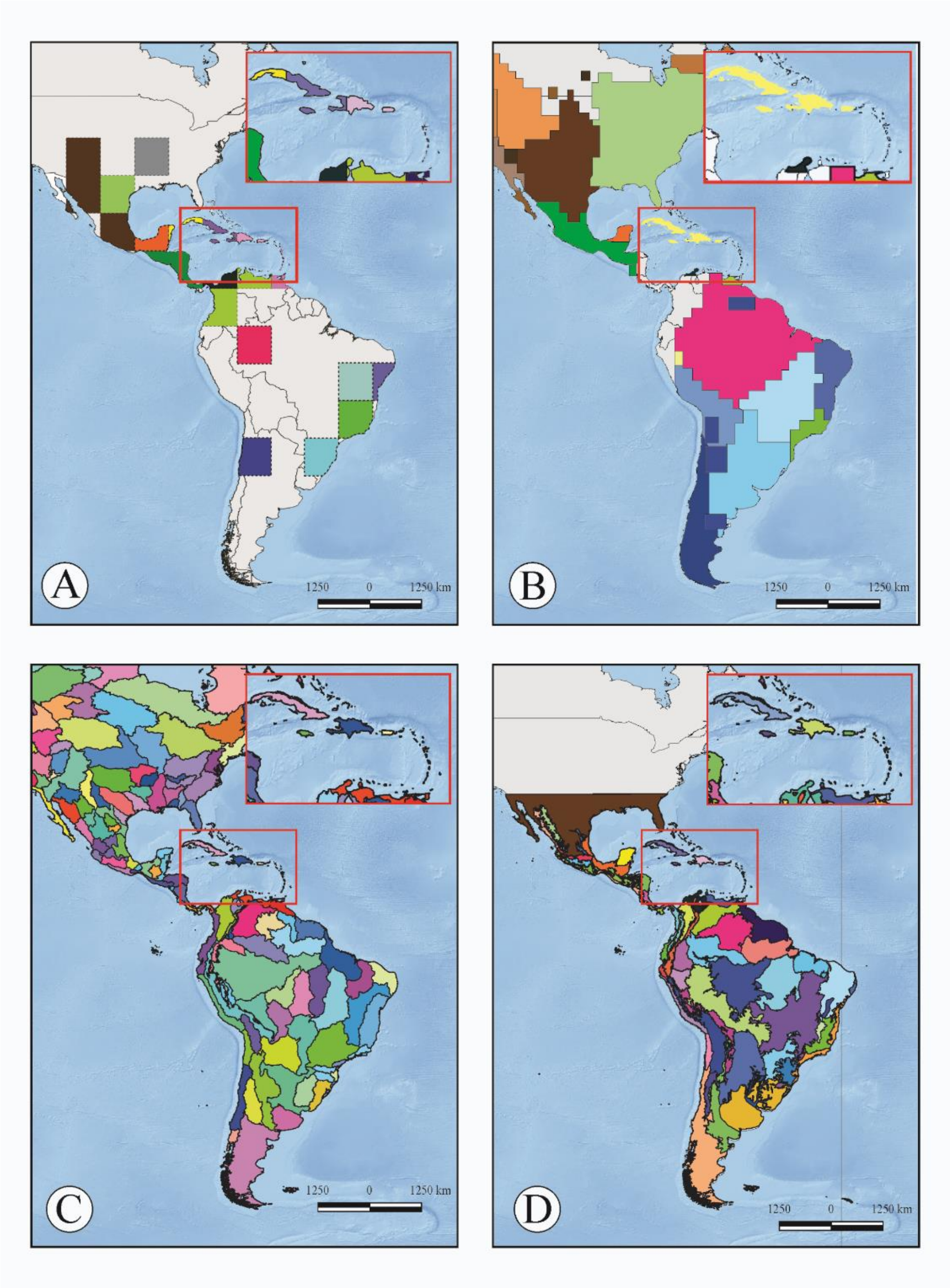

Fig. 6. Bioregions proposals for A. aquatic insects, *H.* (*Feropsyche*) (Trichoptera, Helicopsychidae), original data; B. amphibian (based on Vilhena & Antonelli 2015); C. fish (based on Abell et al., 2008) and D. terrestrial organisms (based on Morrone et al. 2022)

In this way, our results are less comparable to the patterns from fishes [1] or terrestrial organisms [compiled for 58] (Figure 6). Despite having a large database, the bioregions proposed here constitute the primary hypothesis to caddisflies distribution in NW, which need to be tested with biggest datasets and more taxa.

Despite the large number of species, our results indicate that there is still much to be explored, with several new species to be described and catalogued. Eight areas showed high environmental suitability for *H.* (*Feropsyche*), three in NA and five in NT.

In NA, bioregions 1-4 (Figure 4) show high environmental suitability with low richness but wide distribution, possibly due to tropical environments and well-sampled areas (Figure 5). In NA, almost the entire northern part of the United States and all of Canada have low environmental suitability, as these areas are well explored in terms of Trichoptera sampling and may not have suitable conditions for the group.

In NT, all bioregions except bioregions 13 and 18 (Figure 4), as well as areas not covered by bioregions such as the eastern part of the Andes, the Chaco and Pantanal domains, the south-eastern Cerrado and the northern Caatinga show high environmental suitability (Figure 5). The high suitability in these areas may be related to the abundance of lower order freshwater environments in tropical and subtropical areas where *H.* (*Feropsyche*) biodiversity is generally high [40, 42].

On the other hand, the Cerrado domain, Chihuahua Desert and Patagonian environments show low environmental suitability. In these areas, data on Trichoptera, particularly the Helicopsychidae fauna, are scarce [35, 82], which is the most likely explanation. Like these areas, the Brazilian Amazon also shows low suitability, but there are a high number of records of *H.* (*Cochliopsyche*) [43], which rules out low sampling. A possible explanation could be the preference of *H.* (*Feropsyche*) for low order freshwater environments such as springs, streams, and lakes [103].

Areas with high environmental suitability and not covered by bioregions (east of the Andes and Chaco and Pantanal domain, as well as Atlantic Forest, and Caatinga domains) are regions with low sampling and high distribution potential for *H.* (*Feropsyche*) species. They should therefore be treated as highly relevant for research efforts in the NT. Our results indicate that there are large BKS and distribution of the group, mainly in areas of the northern Atlantic Forest domain, eastern Caatinga domain, Chaco and Pantanal domain that have high environmental suitability and scarcity of data on species and species distribution.

Conclusion

Based on the results at different analyses, efforts should be made to carry out material analysis and inventories of the Tropical Forest and Savannas of Paraguay, Venezuela and central west of Brazil, Atlantic Forest and Caatinga domains. Other initiatives should be taken to describe available and already identified semaphoronts deposited in museums, besides the recommendation that descriptions of new species should include, when possible, all semaphoronts to reduce BKS.

For a long time, the biogeographic units used for studies related to amphibiotic taxa, such as Trichoptera, followed the same units for vertebrate and terrestrial arthropods groups proposed by Wallace [99]. In the absence of proposals for less inclusive biogeographic units using the distribution of amphibiotic insects, the use of regionalization proposals established for other groups may not ideally reflect the distribution patterns of amphibian insects. Studies defining these biogeographic units are needed for better understanding and delineation of the distribution patterns of these insects, and result in primary hypothesis to be tested with other groups and large databases.

Until now, discussion about the caddisfly biogeographic patterns is generally associated with general commentaries about the distribution [e.g., 41, 98], generally using a descriptive approach [e.g., 23,75,79]. Other studies focused on discussing the patterns and processes related to the ancestral and current distribution of species, but these generally lack a testable analytical approach to support their inferences [e.g., 6,28,33,34,79]. Thus, efforts aimed at making interpretive biogeographic hypotheses are needed, enabling the reduction of deficits related to the distribution and evolution of groups in space-time [38].

Finally, we report the relevance of focused studies in the subgenus *Feropsyche*, including comprehensive revision, phylogenetic hypothesis proposal and biogeographic inferences. Our work highlights the major BKS and provides a pathway to face these gaps. Here is compiled information published to date on the group, elevating it to a new status of knowledge, which can stimulate and drive the next research proposals.

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Capítulo III

Título: Resurrection of long-horned snail case caddisflies *Cochliopsyche* Müller (Trichoptera, Helicopsychidae): based in phylogenetic and biogeographic analyses

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Resurrection of the long-horned snail case caddisflies *Cochliopsyche* Müller (Trichoptera, Helicopsychidae) based in phylogenetic and biogeographic analyses

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ABSTRACT

Phylogenetic and biogeographic relationships of the Helicopsychidae were inferred by Schmid and by Johanson, who based their analyses on a large sample of taxa and morphological data. Recent studies using molecular data and focus on Sericostomatoidea inferred the relationships among the Helicopsychidae groups. Results from morphological and molecular studies are uncongruent. We aim to carry out a study of the systematics and biogeography of Helicopsychidae, with focus on the subgenus *Cochliopsyche*. Phylogenetic relationships and divergence time estimates were inferred simultaneously using Bayesian inference. Dating analysis was performed using relaxed morphological clock. Biogeographic patterns were investigated using the best-fit model Dispersal-Extinction-Cladogenesis (S-DEC). Our results support Helicopsychidae and *Helicopsyche* as monophyletic and non-monophyletic group, respectively. Subgenera of *Helicopsyche* was recovered with other genera inside (†*Electrohelicopsyche* and †*Palaeohelicopsyche*). The subgenera of *Helicopsyche* are recovered as monophyletic, except for *Feropsyche*. *Feropsyche* and *Saetotrichia* are recovered as sister groups with high support. Helicopsychidae was estimated at around 157 Ma with the split of the stem †*Cretahelicopsyche*; followed by the split of *Rakiura* at around 148 Ma; and the first split of fossil *Helicopsyche* species plus †*Electrohelicopsyche,* and †*Palaeohelicopsyche* at around 140 Ma. The results indicated the dispersal to the West Palaearctic at around 157 Ma, a common pattern for several groups of Sericostomatoidea. *Cochliopsyche* is resurrected as a genus and the Dominican amber species are removed from *Feropsyche*. Except for *Feropsyche* and *Saetotrichia,* the remaining subgenera of *Helicopsyche* are putative monophyletic and can also be interpretated as genus status. We also point out the need for a systematic revision of *Cochliopsyche* with the description of the putative species present here and for a better delimitation and circumscription of the species.

Keywords: Aquatic insects, evolution, *Helicopsyche,* Sericostomatoidea, systematics.

INTRODUCTION

Helicopsychidae was erected as a subfamily of Sericostomatidae Stephens, 1836 by Ulmer (1906), and received the status of family by Ross (1944). The early described species, (*Helicopsyche scalaris* Hagen, 1864; *H. thelidomus* Hagen, 1864 and *H. umbonata* Hagen, 1864), were classified in Phryganidae Leach, 1815, in the subfamily Sericostomatinae Stephens, 1836 by Hagen (1864).

The phylogenetic and biogeographic relationships of Helicopsychidae were firstly provided by Schmid (1993), who established *Cochliophylax* Schmid, 1993 as the crown group of Helicopsychidae, in addition to the relationship between the *Helicopsyche* von Siebold, 1856 of the New World and the *Cochliopsyche* Müller, 1885 (as genus). After, that Johanson (1995; 1997; 1998), presented a catalog, phylogenetic, and biogeographic inferences for Helicopsychidae.

Johanson (1998) divided the species into two genera, the monotypic *Rakiura* McFarlane, 1973, and its sister group, *Helicopsyche*, with *Helicopsyche* being composed by six subgenera. The recognized genera *Cochliophylax* and *Cochliopsyche* (now considered subgenus) were synonymized under *Helicopsyche*. The subgenus *H.* (*Galeopsyche*) Johanson, 1998 was proposed for *H. koreana* Mey, 1991 and *H. khemoiensis* Schefter & Johansson, 2001. The other Eastern and Palearctic species were included in the subgenus *H.* (*Helicopsyche*) von Siebold,

1856. The species distributed in Australia, New Zealand and New Caledonia were grouped in the subgenus *H*. (*Saetotricha*) Brauer, 1865. Afro-tropical species were included in the subgenus *H*. (*Helicopsyche*). The species of the Seychelles, Madagascar and East Africa were assigned to the subgenus *H*. (*Petrotrichia*) Ulmer, 1910. The American species were divided in the subgenera *H*. (*Cochliopsyche*) Müller, 1885, and *H*. (*Feropsyche*) Johanson, 1998.

Helicopsyche comprises two subgenera clades: (*Petrotrichia*, (*Galeopsyche*, *Cochliopsyche*)), and (*Helicopsyche*, (*Saetotrichia*, *Feropsyche*)) (Johanson 1998). Relationships between fossil species are uncertain as well as the position of the fossil genera *Palaeohelicopsyche* Ulmer, 1912 and *Electrohelicopsyche* (Pictet, 1856) (Johanson, 1998).

A Gondwanan origin of Helicopsychidae has been established from the biogeography hypothesis of the group, which is represented by groups with distribution in Africa, northern South America and throughout Gondwana, except India and Madagascar (Johanson 1998). A Gondwanan origin of the family is consistent with hypotheses for the Sericostomatoidea (Johanson et al. 2017). According to Johanson (1998), the stem groups of the clade formed by subgenera (*Petrotrichia*, (*Galeopsyche*, *Cochliopsyche*)) were distributed between the Afrotropical region and South America, while *Rakiura* and the stem groups of (*Helicopsyche*, (*Saetotrichia*, *Feropsyche*)) were distributed between Antarctica and Australasia (Johanson 1998).

With the separation of the African continent, the stem species of the subgenus *Petrotrichia* were isolated from the rest of the family (Johanson 1998). The subgenera *Galeopsyche* and *Helicopsyche* evolved after vicariance events during the separation of the Palearctic and the rest of Gondwana (Johanson 1998). The isolation of *Rakiura* in New Zealand, and the subgenus *Saetotricha* in New Caledonia from species of *Helicopsyche* + *Feropsyche* species are consequences of the formation of an epicontinental sea between and the Patagonian subregion and Brazilian subregion of Neotropical region, and between New Zealand and the remaining part of Gondwana (Johanson 1998). Subsequently, the stem species of *Saetotricha* subgenus became isolated in New Caledonia by the separation of New Caledonia-Australia (Johanson 1998). The fossils were considered *incertae sedis* by Johanson (1998).

There are currently 304 extant and 13 fossil species of Helicopsychidae Ulmer, 1906, including the endemic to New Zealand, *Rakiura vernale*, and the cosmopolitan *Helicopsyche* von Siebold, 1856, with 303 species subdivided into six subgenera: *Cochliopsyche* Müller, 1885 (17 species, endemic of Neotropical region); *Feropsyche* Johanson, 1998 (127 species, distributed in the Neotropical and Nearctic regions); *Galeopsyche* Johanson, 1998 (two species, distributed in the Oriental and

West Palearctic regions); *Helicopsyche* von Siebold, 1856 (72 species, distributed in the Oriental and West Palearctic regions); *Petrotrichia* Ulmer, 1910 (17 species, endemic of Afrotropical region) and *Saetotricha* Brauer, 1865 (52 species, endemic of Australasian region) (Holzenthal & Calor, 2017; Morse, 2023; Souza & Santos, 2023). The greatest diversity of *Helicopsyche* is found between the coordinates of 5–30°N and 15–45°S in the tropics (Johanson, 1997).

Johanson et al. (2017) provided phylogenetic hypothesis for superfamily Sericostomatoidea Stephens, 1836, establishing Chathamiidae Tillyard, 1925 and Antipodoeciidae Ross, 1967 (as Anomalopsychidae Flint, 1981) as the closest families of Helicopsychidae. Comparing the results with Johanson (1998) proposal, there is a highly congruent pattern, with the main difference being the clade formed by the subgenera *Cochliopsyche* and *Feropsyche* (Johanson et al. 2017).

Within this context, we aim to carry out a study of the systematics and biogeography of Helicopsychidae, with an emphasis on the subgenus *Cochliopsyche*, testing the following hypotheses: (i) Helicopsychidae, including extant and fossil groups, constitutes a monophyletic group; (ii) *Helicopsyche* and its subgenera constitutes a monophyletic group; (iii) species from the Dominican amber are members of *H*. (*Feropsyche*); and (iv) Helicopsychidae have a Gondwana origin with later dispersal to Laurasia consistent with the pattern found in Sericostomatoidea.

MATERIAL AND METHODS

TAXON SAMPLING

The material analyzed includes 982 specimens from the Museu de História Natural da Universidade Federal da Bahia (UFBA, 544 specimens); Instituto Nacional de Pesquisa da Amazônia, Manaus, Amazonas, Brazil (INPA, 381 specimens); Museum of Comparative Zoology, Harvard University (MCZ, 11 specimens); University of Minnesota Insect Collection, St. Paul, Minnesota (UMSP, 22 specimens); National Museum of Natural History, Washington (NMNH-USNM, 24 specimens). Additional information was gathered from primary literature on the descriptions and illustrations of the species (McFarlane, 1973; Flint, 1981; Mey, 1991; Johanson, 1995a; b; Johanson & Wichard, 1996; Johanson, 1998; Johanson, 1999; Johanson & Schefter, 1999; Johanson, 2002; Johanson, 2003a; b; Wichard, 2013; Wichard et al., 2018; Oláh & Oláh, 2022; Moreno et al., 2023).

The ingroup were composed by *Helicopsyche* species, putative new taxon of this group. The outgroups were composed by type species of other genus, including fossil species of all Helicopsychidae groups, and members of Sericostomatoidea [i.e., *Anomalopsyche minuta* (Antipodocidae), *Chathamia integripennis* (Chathamiidae)] (Table 1). *Anomalopsyche* *minuta* (Schmid, 1957) was fixed for character polarization and rooting of trees, totalling 51 taxa in the analysis.

Table 1. Species included in the phylogenetic analyses, with respective indication of locality, depository collection (or literature source).

Species	Distribution	Collection / Source	Sex
Anomalopsyche minuta	CHI	Flint, 1981	♂
Chatamia integripenis	NZE	USNM	♂
†*Cretahelicopsyche liuyani*	Burmese Ambar	Wichard et al. 2018	♂
†*Electrohelicopsyche taeniata*	Baltic Ambar	Wichard, 2013	♂
†*Paleohelicopsyche serriconis*	Baltic Ambar	Wichard, 2013	♂
Rakiura vernale	NZE	McFarlane, 1973	♂
†*Helicopsyche confluens*	Baltic Ambar	Wichard, 2013	♂
†*Helicopsyche cona*	Baltic Ambar	Wichard, 2013	♂
†*Helicopsyche damseni*	Baltic Ambar	Wichard, 2013	♂
†*Helicopsyche scapi*	Baltic Ambar	Wichard, 2013	♂
†*Helicopsyche typica*	Baltic Ambar	Wichard, 2013	♂
†*H.* (*Feropsyche*) *electra*	Dominican Ambar	Johanson & Wichard, 1996; Wichard, 2013	♂
†*H.* (*Feropsyche*) *scaloida*	Dominican Ambar	Johanson & Wichard, 1996; Wichard, 2013	♂
†*H.* (*Feropsyche*) *voigti*	Dominican Ambar	Johanson & Wichard, 1996; Wichard, 2013	♂
H. (*Petrotrichia*) *barbata*	TZA	Johanson, 2003	♂
H. (*Petrotrichia*) *giboni*	MDG	USNM	♂
H. (*Petrotrichia*) *palpalis*	SYC	USNM01866356	♂
H. (*Saetotrichia*) *albescens*	NZE	Johanson, 1999	♂
H. (*Saetotrichia*) *petersorum*	NZE	USNM	♂
H. (*Saetotrichia*) *ptychopteryx*	AUS	Johanson, 1995a	♂
H. (*Helicopsyche*) *crispata*	ITA, CHE	Johanson, 1995b	♂
H. (*Helicopsyche*) *shuttleworthi*	CHE	Johanson, 1995b	♂
H. (*Galeopsyche*) *coreana*	PRK	Mey, 1991; Johanson, 1998	♂
H. (*Galeopsyche*) *khemoiensis*	VNM	Johanson & Schefter, 1999	♂
H. (*Feropsyche*) *angulata*	COL, ECU, VEN	Johanson, 2002	♂
H. (*Feropsyche*) *borealis*	CAN, CRI, GUA, MEX, NIC, PAN, USA	Johanson, 2002	♂
H. (*Feropsyche*) *diamantina*	BRA	UFBA	♂
H. (*Feropsyche*) *fridae*	PAN	Johanson, 2002	♂
H. (*Feropsyche*) *johansoni*	BRA	Moreno et al. 2023	♂
H. (*Cochliopsyche*) *amazona*	BRA	USNM01883588	♂

H. (*Cochliopsyche*) *amica*	BRA, GUY, VEN	MCZ	♂
H. (*Cochliopsyche*) *blahniki*	BRA, COL, ECU, GUY, PER, VEN	UMSP000172442	♂
H. (*Cochliopsyche*) *brazilia*	BRA	UFBA	♂
H. (*Cochliopsyche*) *chocoensis*	BRA, COL	USNM00948790	♂
H. (*Cochliopsyche*) *clara*	ARG, BRA, ECU	UMSP00082731	♂
H. (*Cochliopsyche*) *holzenthali*	VEN	UMSP00042366	♂
H. (*Cochliopsyche*) *lobata*	ARG, BRA, PER	UMSP00029965, USNM01866353, MCZ	♂
H. (*Cochliopsyche*) *napoa*	ECU	UMSP000502144, USNM00948792	♂
H. (*Cochliopsyche*) *nyurga*	ECU	Oláh & Oláh, 2022	♂
H. (*Cochliopsyche*) *ocosingua*	BRA, MEX	USNM	♂
H. (*Cochliopsyche*) *opalescens*	ARG, BRA, ECU, GUY, PAR, PER, SUR, URU, VEN	UMSP000120885	♂
H. (*Cochliopsyche*) *pandeirosa*	BRA	UMSP000080979	♂
H. (*Cochliopsyche*) *paraguaiensis*	PAR	USNM01883559	♂
H. (*Cochliopsyche*) *puyoa*	BRA, ECU	UMSP01866351	♂
H. (*Cochliopsyche*) *vazquezae*	BOL, COR, ECU, MEX, VEN	USNM01866348, USNM01866349	♂
H. (*Cochliopsyche*) *xinguensis*	BRA	UMSP000070788	♂
H. (*Cochliopsyche*) **sp. 1**	BRA	UFBA	♂
H. (*Cochliopsyche*) **sp. 2**	BRA	UFBA	♂
H. (*Cochliopsyche*) **sp. 3**	BRA	UFBA	♂
H. (*Cochliopsyche*) **sp. 4**	BRA	UFBA	♂
H. (*Cochliopsyche*) **sp. 5**	BRA	USMP	♂

The final phylogenetic dataset comprised 51 taxa (22 ingroup taxa, 29 outgroup) with 117 morphological characters (Table 2). The data matrix was built using Mesquite (Maddison & Maddison, 2023). The symbols "?" and "-" were used for missing and non-applicable data, respectively. The characters and character states were elaborated following Sereno (2007) (Table 2). Most characters were binary (70) and all multi-state characters (46) were treated as unordered. The characters were coded from direct observation of 24 species (20 based on type specimens), and the others based on literature (Table 1).

Table 2. Morphological data matrix. ‘?’ represents missing data; ‘–’ represents inapplicable characters.

Taxon	**Characters**																													
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
Anomalopsyche minuta	0	1	0	3	1	0	0	1	5	1	-	-	1	0	4	1	0	4	0	0	0	0	2	2	0	0	1	1	0	0	1
Chatamia integripenis	0	1	3	4	0	5	0	1	0	1	-	-	1	0	2	0	1	?	0	0	0	0	2	2	0	0	1	1	0	0	0
†*Cretahelicopsyche liuyani*	?	1	1	2	1	?	?	?	?	1	-	-	?	?	?	?	?	?	?	?	0	0	3	2	0	0	0	1	0	0	1
†*Electrohelicopsyche taeniata*	?	1	1	1	1	5	1	?	?	1	-	-	1	0	2	1	0	1	0	1	1	0	0	1	0	0	2	0	0	0	1
†*Paleohelicopsyche serriconis*	?	1	2	1	1	5	1	?	?	0	3	1	1	0	2	1	0	1	0	0	1	0	0	2	0	0	2	0	0	0	1
Rakiura vernale	1	1	3	1	1	6	0	1	5	1	-	-	1	0	2	1	0	2	0	1	0	0	0	1	1	?	0	1	0	0	1
†*Helicopsyche confluens*	?	1	2	1	1	?	?	?	?	1	-	-	1	?	?	?	?	?	?	0	1	0	1	1	0	0	0	1	0	1	0
†*Helicopsyche cona*	?	1	1	1	1	?	1	?	?	0	2	2	1	0	3	1	0	3	0	0	1	0	0	2	0	0	2	1	1	0	?
†*Helicopsyche damseni*	?	1	1	2	1	?	?	?	?	0	4	3	1	?	?	?	?	?	?	0	1	1	2	2	0	0	0	1	1	1	?
†*Helicopsyche scapi*	?	1	1	1	1	5	1	?	?	1	-	-	2	?	?	?	?	?	?	1	0	1	0	1	0	0	0	1	0	1	1
†*Helicopsyche typica*	?	1	2	1	1	?	1	?	?	1	-	-	1	0	0	1	?	?	?	1	1	0	2	1	0	0	1	1	0	0	1
†*H.* (*Feropsyche*) *electra*	?	1	1	1	1	6	1	?	?	1	-	-	1	0	3	1	0	3	0	0	1	0	1	3	0	0	0	0	0	0	1
†*H.* (*Feropsyche*) *scaloida*	?	1	1	1	1	5	0	0	1	1	-	-	1	0	3	1	0	3	0	0	1	0	1	2	0	0	0	1	0	1	1
†*H.* (*Feropsyche*) *voigti*	?	1	1	1	1	5	?	?	?	1	-	-	1	0	?	1	0	?	0	0	1	0	0	3	0	0	1	1	0	0	1
H. (*Petrotrichia*) *barbata*	1	1	2	1	1	6	0	1	5	1	-	-	1	1	-	0	0	0	0	1	1	0	3	2	0	0	0	1	0	1	1
H. (*Petrotrichia*) *giboni*	1	0	0	1	1	5	0	1	5	1	-	-	1	1	-	0	0	0	0	1	1	0	0	3	0	0	1	1	0	1	1
H. (*Petrotrichia*) *palpalis*	1	0	2	2	1	6	0	1	5	1	-	-	1	1	-	0	1	0	0	1	1	0	2	3	0	0	1	1	0	1	0
H. (*Saetotrichia*) *albescens*	1	1	0	1	1	6	0	0	1	1	-	-	1	0	3	1	0	5	0	1	1	0	0	2	0	0	1	1	0	0	1
H. (*Saetotrichia*) *petersorum*	1	1	0	1	1	6	0	1	?	1	-	-	1	0	3	1	0	5	0	0	1	1	1	2	0	0	1	1	0	0	1
H. (*Saetotrichia*) *ptychopteryx*	1	1	0	1	0	6	0	1	?	1	-	-	1	0	3	1	0	5	0	1	1	0	1	2	0	0	1	1	1	0	1
H. (*Helicopsyche*) *crispata*	1	1	0	1	1	6	0	1	6	1	-	-	1	0	?	1	0	?	1	0	1	0	1	2	0	0	2	1	0	0	0
H. (*Helicopsyche*) *shuttleworthi*	1	1	1	1	1	6	0	1	5	1	-	-	1	0	?	1	0	?	1	0	1	0	1	2	0	0	1	1	0	0	0
H. (*Galeopsyche*) *coreana*	1	1	1	1	1	5	0	1	2	0	0	0	1	0	?	1	1	?	0	1	1	1	0	2	0	1	0	1	0	0	1
H. (*Galeopsyche*) *khemoiensis*	1	1	0	1	1	5	0	1	6	1	-	-	1	0	?	1	1	?	0	1	1	0	1	2	0	0	0	1	0	0	1
H. (*Feropsyche*) *angulata*	1	1	1	1	1	5	0	0	1	1	-	-	1	0	2	1	0	0	0	1	1	0	0	2	0	0	1	1	0	0	1
H. (*Feropsyche*) *borealis*	1	1	1	1	1	4	0	0	2	1	-	-	1	0	2	1	0	5	0	0	1	0	0	2	0	0	1	1	0	0	1
H. (*Feropsyche*) *diamantina*	1	1	1	1	1	4	0	0	1	1	-	-	1	0	0	1	0	2	0	0	1	0	1	2	0	0	0	1	0	0	1
H. (*Feropsyche*) *fridae*	1	1	1	1	1	5	0	0	1	1	-	-	1	0	?	1	0	?	0	0	1	0	1	2	0	0	1	1	0	0	1

Taxon	**Characters**																														
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
H. (*Feropsyche*) *johansoni*	1	1	1	1	1	4	0	0	1	1	-	-	1	0	0	1	0	2	0	0	1	0	1	2	0	0	1	1	0	0	1
H. (*Cochliopsyche*) *amazona*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	3	3	0	0	0	1	0	0	0
H. (*Cochliopsyche*) *amica*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	1	2	0	0	0	1	0	0	0
H. (*Cochliopsyche*) *blahniki*	1	1	2	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	2	3	0	0	0	1	0	0	0
H. (*Cochliopsyche*) *brazilia*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	2	3	0	0	0	1	0	0	0
H. (*Cochliopsyche*) *chocoensis*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	0	1	0	2	2	0	0	0	1	0	0	1
H. (*Cochliopsyche*) *clara*	1	1	3	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	2	3	0	0	0	1	0	0	0
H. (*Cochliopsyche*) *holzenthali*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	1	2	0	0	1	1	0	0	0
H. (*Cochliopsyche*) *lobata*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	0	1	0	2	2	0	0	0	1	0	0	1
H. (*Cochliopsyche*) *napoa*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	0	2	0	1	0	1	0	0	1
H. (*Cochliopsyche*) *nyurga*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	2	3	0	0	0	1	0	0	?
H. (*Cochliopsyche*) *ocosingua*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	0	1	0	1	2	0	0	0	1	0	0	1
H. (*Cochliopsyche*) *opalescens*	1	1	1	1	1	7	1	1	5	1	-	-	2	1	-	0	0	0	0	0	1	0	3	3	0	0	0	1	0	0	1
H. (*Cochliopsyche*) *pandeirosa*	1	1	2	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	0	1	0	2	3	0	0	0	1	0	0	1
H. (*Cochliopsyche*)*paraguaiensis*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	0	1	0	2	3	0	0	0	1	0	0	1
H. (*Cochliopsyche*) *puyoa*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	2	3	0	0	1	1	0	0	0
H. (*Cochliopsyche*) *vazquezae*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	0	1	0	1	2	0	0	0	1	0	0	0
H. (*Cochliopsyche*) *xinguensis*	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	1	2	0	0	0	1	0	0	1
H. (*Cochliopsyche*) **sp. 1**	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	2	2	0	0	0	1	0	0	1
H. (*Cochliopsyche*) **sp. 2**	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	2	2	0	0	0	1	0	0	1
H. (*Cochliopsyche*) **sp. 3**	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	0	1	0	1	2	0	0	1	1	0	0	1
H. (*Cochliopsyche*) **sp. 4**	1	1	1	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	2	3	0	0	0	1	0	0	1
H. (*Cochliopsyche*) **sp. 5**	1	1	2	1	1	7	0	1	5	1	-	-	2	1	-	0	0	0	0	1	1	0	2	3	0	0	1	1	0	0	1

Taxon	**Characters**																													
	31	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**
Anomalopsyche minuta	0	1	2	1	1	0	1	0	1	1	1	0	0	1	0	1	?	?	?	?	0	1	1	0	2	0	1	1	?	?
Chatamia integripenis	-	0	2	1	1	0	1	0	1	1	1	0	0	1	1	1	?	?	?	?	0	1	2	0	2	0	1	1	?	?
†*Cretahelicopsyche liuyani*	0	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	2	1	0	1	?	?	?	?	?	?	?	?	?	?
†*Electrohelicopsyche taeniata*	1	0	1	1	1	0	0	0	1	1	0	0	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	0	1	2
†*Paleohelicopsyche serriconis*	1	0	1	1	1	0	0	0	1	1	1	0	0	1	0	0	2	1	1	1	?	?	?	?	?	?	?	0	1	2
Rakiura vernale	0	1	1	1	0	0	0	1	0	1	1	0	0	1	0	0	?	?	0	?	0	1	1	0	0	0	1	1	?	?
†*Helicopsyche confluens*	-	1	1	0	1	0	0	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Helicopsyche cona*	1	0	3	?	1	?	?	0	1	0	1	0	1	?	0	0	2	1	1	1	?	?	?	?	?	?	?	?	?	?
†*Helicopsyche damseni*	1	1	?	?	?	?	?	?	?	?	?	?	1	?	0	1	?	?	?	?	?	?	?	?	?	?	?	0	1	1
†*Helicopsyche scapi*	1	0	?	?	?	?	?	?	?	1	0	?	?	?	?	0	3	0	0	2	?	?	?	?	?	?	?	0	1	1
†*Helicopsyche typica*	0	1	2	1	1	0	0	0	1	1	0	0	?	?	?	0	1	0	0	1	?	?	?	?	?	?	?	1	?	?
†*H.* (*Feropsyche*) *electra*	0	0	2	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	2	?	?	?	?	?	?	?	1	?	?
†*H.* (*Feropsyche*) *scaloida*	0	1	3	?	1	0	0	1	1	0	1	0	0	1	0	0	0	0	1	1	?	?	?	?	?	?	?	1	?	?
†*H.* (*Feropsyche*) *voigti*	0	0	2	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	2	2	?	?	?	?	?	?	?	1	?	?
H. (*Petrotrichia*) *barbata*	0	1	2	1	1	0	1	0	1	1	1	1	0	1	0	0	1	2	1	1	0	1	1	0	2	1	1	0	1	1
H. (*Petrotrichia*) *giboni*	0	1	3	1	1	0	1	1	1	1	1	1	0	1	0	0	2	2	2	0	1	?	?	0	0	0	0	0	1	1
H. (*Petrotrichia*) *palpalis*	-	1	3	1	1	0	1	1	1	1	1	1	1	?	0	0	0	2	1	2	0	0	1	0	0	1	1	0	0	1
H. (*Saetotrichia*) *albescens*	0	1	2	1	1	0	1	0	1	1	1	0	0	0	0	1	?	?	?	?	0	1	1	0	2	0	1	1	?	?
H. (*Saetotrichia*) *petersorum*	1	1	2	1	1	0	1	0	1	1	1	1	0	0	0	0	2	2	0	1	0	1	0	0	1	0	0	1	?	?
H. (*Saetotrichia*) *ptychopteryx*	0	1	2	1	1	0	1	0	1	1	1	0	0	1	0	1	?	?	?	?	0	1	0	0	2	0	0	1	?	?
H. (*Helicopsyche*) *crispata*	-	1	2	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	2	2	1	1	0	1	2
H. (*Helicopsyche*) *shuttleworthi*	-	0	2	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	1	1	1	1	0
H. (*Galeopsyche*) *coreana*	1	0	2	1	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	2	1	0	0	1	0
H. (*Galeopsyche*) *khemoiensis*	1	0	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	2	0	1	1	?	?
H. (*Feropsyche*) *angulata*	0	0	2	1	1	0	1	0	1	1	1	0	0	1	0	0	2	1	2	1	0	1	1	0	0	0	0	1	?	?
H. (*Feropsyche*) *borealis*	0	0	2	1	1	1	1	0	1	1	1	0	0	1	0	0	2	0	1	1	0	1	1	0	2	0	0	1	?	?
H. (*Feropsyche*) *diamantina*	0	0	2	1	1	0	1	0	1	1	1	0	0	1	0	0	2	1	2	1	0	1	2	2	2	0	0	0	1	1
H. (*Feropsyche*) *fridae*	0	0	2	1	1	0	1	0	1	1	1	0	0	1	0	0	2	2	2	0	0	0	0	0	2	0	0	1	?	?

Taxon	Characters																													
	31	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**
H. (*Feropsyche*) *johansoni*	0	0	2	1	1	0	1	0	1	1	1	0	0	1	0	0	2	2	2	0	0	1	1	0	2	0	0	0	1	0
H. (*Cochliopsyche*) *amazona*	-	0	2	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	1	-	-	0	0	1	1	0	0	1
H. (*Cochliopsyche*) *amica*	-	0	2	1	1	0	0	0	1	1	1	0	0	0	1	1	-	-	-	-	0	0	1	0	0	1	1	0	1	2
H. (*Cochliopsyche*) *blahniki*	-	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	1	1	0	0	1
H. (*Cochliopsyche*) *brazilia*	-	0	2	1	1	0	0	0	1	1	1	0	0	0	1	1	-	-	-	-	0	1	1	2	0	1	1	0	0	1
H. (*Cochliopsyche*) *chocoensis*	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	1	-	-	-	-	0	1	0	0	0	1	1	0	1	0
H. (*Cochliopsyche*) *clara*	-	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	1	1	0	2	1	1	0	1	1
H. (*Cochliopsyche*) *holzenthali*	-	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	2	1	0	0	2	0	0	1	1	0	1	0
H. (*Cochliopsyche*) *lobata*	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	2	0	0	1	0	0	1	0	0	0	0	0	1	0
H. (*Cochliopsyche*) *napoa*	0	0	2	1	1	0	1	0	1	1	1	0	0	0	1	0	0	0	2	2	0	1	1	0	2	1	1	0	0	1
H. (*Cochliopsyche*) *nyurga*	?	0	?	1	1	0	0	1	1	1	1	0	0	0	1	0	0	0	1	1	0	1	1	0	2	1	1	0	0	1
H. (*Cochliopsyche*) *ocosingua*	0	0	2	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	1	1	0	1	1	0	0	1	1	0	0	0
H. (*Cochliopsyche*) *opalescens*	0	0	2	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	2	0	0	1	0	0	0	0
H. (*Cochliopsyche*) *pandeirosa*	0	0	2	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0
H. (*Cochliopsyche*)*paraguaiensis*	0	1	1	1	1	0	0	0	1	1	1	0	0	0	1	1	-	-	-	-	0	1	0	0	0	1	1	0	0	0
H. (*Cochliopsyche*) *puyoa*	-	0	2	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	2
H. (*Cochliopsyche*) *vazquezae*	-	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	2	0	1	0	0	2	1	0	0	0	0
H. (*Cochliopsyche*) *xinguensis*	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	1	-	-	-	-	0	0	1	0	0	1	1	0	0	0
H. (*Cochliopsyche*) **sp. 1**	0	0	2	1	1	0	0	0	1	1	1	0	0	0	1	0/1	0	0	0	1	0	1	1	0	0	1	1	0	0	1
H. (*Cochliopsyche*) **sp. 2**	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	1	-	-	0	0	1	1	0	0	0
H. (*Cochliopsyche*) **sp. 3**	0	0	2	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0
H. (*Cochliopsyche*) **sp. 4**	0	0	2	1	1	0	0	0	1	1	1	0	0	0	1	1	-	-	-	-	0	1	1	0	0	1	1	0	1	1
H. (*Cochliopsyche*) **sp. 5**	0	0	2	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	1	1	0	1	1	0	2	1	1	0	0	1

Taxon	**Characters**																													
	61	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**
Anomalopsyche minuta	1	?	1	?	?	2	1	1	0	5	2	0	6	7	2	3	0	0	2	1	1	1	1	0	0	1	1	1	1	1
Chatamia integripenis	0	1	1	?	?	2	0	1	1	?	?	?	?	?	?	0	1	0	0	1	0	1	1	1	1	-	1	1	1	1
†*Cretahelicopsyche liuyani*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	0	0	3	?	?	1	1
†*Electrohelicopsyche taeniata*	1	?	1	?	?	0	1	?	0	5	4	0	6	4	2	0	1	0	2	?	?	?	?	?	?	?	?	0	?	?
†*Paleohelicopsyche serriconis*	1	?	1	?	?	0	0	?	0	5	4	0	6	1	4	2	1	0	2	0	0	1	1	1	1	-	1	1	1	1
Rakiura vernale	1	?	1	?	?	2	0	?	0	5	4	0	6	4	4	0	0	0	0	0	0	1	1	1	1	-	1	1	1	1
†*Helicopsyche confluens*	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Helicopsyche cona*	?	?	1	?	?	?	?	?	0	5	4	0	6	?	4	4	1	0	0	?	?	0	1	0	?	?	?	0	?	?
†*Helicopsyche damseni*	1	?	1	?	?	?	?	?	0	5	4	0	6	?	2	3	1	0	2	?	?	?	?	?	?	?	0	0	0	1
†*Helicopsyche scapi*	1	?	1	?	?	?	0	1	0	5	4	0	6	?	3	0	1	0	2	2	?	1	1	1	1	-	?	?	?	?
†*Helicopsyche typica*	1	?	1	?	?	?	0	1	1	?	?	?	?	?	4	2	1	0	2	1	0	0	1	0	0	0	1	1	1	0
†*H.* (*Feropsyche*) *electra*	1	?	1	?	?	0	0	?	0	4	2	0	6	3	2	4	1	0	2	0	2	1	0	0	0	0	1	1	0	1
†*H.* (*Feropsyche*) *scaloida*	1	?	1	?	?	0	0	?	0	4	2	0	6	3	2	0	1	0	2	0	1	1	1	1	0	0	1	1	0	1
†*H.* (*Feropsyche*) *voigti*	1	?	1	?	?	0	0	?	0	5	4	0	6	3	3	0	1	0	0	1	?	1	1	1	1	-	1	1	0	1
H. (*Petrotrichia*) *barbata*	1	?	1	?	?	0	2	1	1	?	?	?	?	?	3	0	1	0	2	0	1	1	1	0	1	-	1	1	1	0
H. (*Petrotrichia*) *giboni*	1	?	1	?	?	?	?	?	0	6	3	0	7	3	2	0	1	0	2	0	?	1	?	?	?	?	?	?	?	0
H. (*Petrotrichia*) *palpalis*	1	?	1	?	?	0	2	1	1	?	?	?	?	?	4	5	1	0	2	1	1	1	0	0	0	2	1	1	1	0
H. (*Saetotrichia*) *albescens*	1	?	1	?	?	0	1	0	0	1	0	0	5	1	4	2	0	0	1	1	1	0	0	0	0	0	1	0	0	1
H. (*Saetotrichia*) *petersorum*	1	?	0	0	0	2	0	0	0	6	4	0	6	4	4	2	1	1	2	0	0	0	0	0	0	3	0	0	0	0
H. (*Saetotrichia*) *ptychopteryx*	1	?	0	0	1	?	?	?	0	6	1	0	7	1	1	2	1	1	2	0	0	1	0	0	0	2	0	0	0	1
H. (*Helicopsyche*) *crispata*	1	?	1	?	?	2	1	1	0	6	4	0	6	4	4	2	1	0	0	1	2	1	1	0	0	2	1	0	1	1
H. (*Helicopsyche*) *shuttleworthi*	1	?	1	?	?	2	1	?	0	6	4	0	6	3	2	0	1	0	0	0	1	1	1	0	0	3	1	0	1	1
H. (*Galeopsyche*) *coreana*	1	?	1	?	?	2	1	1	0	1	0	0	5	2	3	0	1	0	0	1	1	1	1	0	0	0	1	0	1	1
H. (*Galeopsyche*) *khemoiensis*	1	?	1	?	?	2	0	?	0	6	2	0	6	4	4	2	1	0	2	0	2	1	1	0	0	1	1	0	0	1
H. (*Feropsyche*) *angulata*	1	?	1	?	?	0	0	0	0	1	0	0	5	0	2	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1
H. (*Feropsyche*) *borealis*	1	?	1	?	?	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	1	1	1	0	0	0	0	1	0	1
H. (*Feropsyche*) *diamantina*	1	?	1	?	?	2	2	0	0	1	0	0	5	0	2	2	1	0	0	0	1	1	1	0	0	0	0	0	0	1
H. (*Feropsyche*) *fridae*	1	?	1	?	?	2	0	0	0	1	0	0	3	0	3	2	1	0	2	0	0	1	1	1	1	-	0	0	0	1

Taxon	**Characters**																													
	61	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**
H. (*Feropsyche*) *johansoni*	1	?	1	?	?	0	1	1	0	2	1	0	7	2	2	4	1	0	0	0	0	1	1	0	0	0	0	0	0	1
H. (*Cochliopsyche*) *amazona*	0	1	1	?	?	2	0	1	0	0	0	0	0	1	2	6	0	0	0	1	0	1	0	0	0	0	1	0	0	1
H. (*Cochliopsyche*) *amica*	0	1	0	0	1	2	1	1	0	2	1	0	5	1	2	3	1	0	1	1	0	1	1	0	0	0	1	0	0	1
H. (*Cochliopsyche*) *blahniki*	1	?	1	?	?	0	0	0	0	4	1	0	1	1	2	3	0	0	1	0	2	1	0	0	0	0	0	0	0	1
H. (*Cochliopsyche*) *brazilia*	0	1	1	?	?	1	1	1	0	0	1	0	3	1	2	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1
H. (*Cochliopsyche*) *chocoensis*	0	1	1	?	?	0	1	1	0	2	1	0	2	1	0	0	0	1	0	1	2	1	0	0	0	0	0	0	0	1
H. (*Cochliopsyche*) *clara*	1	?	1	?	?	2	1	1	0	0	0	0	5	1	2	0	1	1	1	1	0	1	0	0	0	0	1	0	0	1
H. (*Cochliopsyche*) *holzenthali*	1	?	1	?	?	0	1	2	0	0	1	0	1	1	2	6	0	0	2	0	0	0	1	0	0	0	0	0	0	1
H. (*Cochliopsyche*) *lobata*	1	?	1	?	?	2	1	1	0	2	1	0	3	1	2	3	0	1	1	1	2	1	0	0	0	0	0	0	0	1
H. (*Cochliopsyche*) *napoa*	0	1	0	0	1	0	1	0	0	4	1	0	0	1	1	3	0	1	1	0	2	1	0	0	0	0	0	0	0	1
H. (*Cochliopsyche*) *nyurga*	1	?	0	0	1	2	1	1	0	0	1	0	3	1	1	0	1	0	0	0	0	1	1	1	1	-	0	0	0	1
H. (*Cochliopsyche*) *ocosingua*	1	?	1	?	?	2	1	1	0	1	1	0	2	1	2	0	1	1	0	1	2	1	0	0	0	0	0	0	0	1
H. (*Cochliopsyche*) *opalescens*	1	?	0	0	1	1	1	1	0	1	1	0	5	2	1	0	1	1	2	1	0	1	1	1	1	-	1	0	0	1
H. (*Cochliopsyche*) *pandeirosa*	0	1	1	?	?	2	1	1	0	1,3	1	1	3,4	1	1	3	1	1	1	1	0	0	1	1	1	-	0	0	0	1
H. (*Cochliopsyche*)*paraguaiensis*	0	1	0	1	0	2	1	1	0	0	1	0	3	0	2	0	1	1	2	1	0	1	1	1	0	0	1	0	0	1
H. (*Cochliopsyche*) *puyoa*	1	?	1	?	?	0	1	1	0	3	0	0	2	1	2	0	1	1	0	0	0	1	1	0	0	0	0	0	0	1
H. (*Cochliopsyche*) *vazquezae*	1	?	1	?	?	0	1	0	0	4	1	0	1	1	2	6	0	1	0	2	2	1	0	0	0	0	0	0	0	1
H. (*Cochliopsyche*) *xinguensis*	1	?	1	?	?	0	0	1	0	0	1	0	1	1	2	3	1	1	0	2	0	1	0	0	0	0	0	0	0	1
H. (*Cochliopsyche*) **sp. 1**	1	?	1	?	?	2	1	1	0	1	0	0	5	0	2	6	1	1	0	1	0	1	1	1	0	0	1	0	0	1
H. (*Cochliopsyche*) **sp. 2**	0	0	1	?	?	0	1	1	0	0	1	0	5	1	1	0	1	1	0	0	0	1	1	1	1	-	1	1	1	1
H. (*Cochliopsyche*) **sp. 3**	0	0	0	1	0	2	1	2	0	1	0	0	4	1	2	0	0	1	2	2	0	1	1	1	1	-	1	0	0	1
H. (*Cochliopsyche*) **sp. 4**	0	1	1	?	?	1	1	1	0	0	0	0	0	1	2	3	0	0	1	1	1	1	0	0	0	0	0	0	0	1
H. (*Cochliopsyche*) **sp. 5**	1	?	1	?	?	2	1	1	0	0	1	0	1	1	2	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1

Taxon	Characters																									
	91	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**
Anomalopsyche minuta	1	-	1	1	0	1	-	1	-	1	-	0	0	1	-	1	-	1	-	-	1	-	-	-	1	-
Chatamia integripenis	1	-	0	1	1	1	-	1	-	1	-	1	-	1	-	1	-	1	-	-	1	-	-	-	1	-
†*Cretahelicopsyche liuyani*	1	-	-	1	1	1	-	1	-	1	-	1	-	1	-	1	-	1	-	-	0	2	4	4	1	-
†*Electrohelicopsyche taeniata*	0	1	1	1	1	1	-	0	0	1	-	0	0	1	-	1	-	1	-	-	0	0	2	1	1	-
†*Paleohelicopsyche serriconis*	1	-	1	1	1	1	-	0	0	1	-	0	0	1	-	1	-	0	-	1	0	3	2	2	1	-
Rakiura vernale	1	-	1	0	1	1	-	1	-	1	-	1	-	1	-	1	-	1	-	-	0	3	4	0	0	0
†*Helicopsyche confluens*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
†*Helicopsyche cona*	0	3	1	1	-	1	-	1	-	1	-	1	-	1	-	1	-	1	-	-	0	4	-	-	1	-
†*Helicopsyche damseni*	1	-	0	0	-	1	-	1	-	1	-	1	-	1	-	1	-	1	-	-	0	2	2	2	1	-
†*Helicopsyche scapi*	0	3	1	1	1	1	-	0	0	1	-	1	-	0	0	0	0	1	-	-	0	4	-	2	1	-
†*Helicopsyche typica*	1	-	2	1	1	1	-	1	-	1	-	1	-	0	0	0	1	1	-	-	0	4	3	2	1	-
†*H.* (*Feropsyche*) *electra*	1	-	0	0	0	1	-	1	-	1	-	1	-	1	-	1	-	0	1	0	1	-	-	-	1	-
†*H.* (*Feropsyche*) *scaloida*	1	-	0	2	1	1	-	1	-	1	-	1	-	1	-	1	-	0	1	0	0	4	4	4	1	-
†*H.* (*Feropsyche*) *voigti*	1	-	0	0	1	1	-	1	-	1	-	1	-	1	-	1	-	0	1	0	0	2	4	4	1	-
H. (*Petrotrichia*) *barbata*	1	-	1	2	0	1	-	0	0	1	-	0	0	1	-	1	-	1	-	-	0	5	0	0	1	-
H. (*Petrotrichia*) *giboni*	1	-	0	0	0	1	-	1	-	1	-	1	-	1	-	1	-	1	-	-	1	-	-	-	1	-
H. (*Petrotrichia*) *palpalis*	1	-	1	0	2	1	-	0	0	1	-	1	-	1	-	1	-	1	-	-	1	-	-	-	1	-
H. (*Saetotrichia*) *albescens*	1	-	1	0	1	1	-	1	-	1	-	0	0	1	-	1	-	1	-	-	0	2	1	0	1	-
H. (*Saetotrichia*) *petersorum*	0	1	1	0	1	1	-	1	-	1	-	1	-	1	-	0	0	1	-	-	0	2	4	4	1	-
H. (*Saetotrichia*) *ptychopteryx*	1	-	0	1	-	1	-	1	-	1	-	0	0	1	-	1	-	1	-	-	0	1	3	3	1	-
H. (*Helicopsyche*) *crispata*	1	-	1	0	0	1	-	1	-	1	-	1	-	1	-	1	-	0	1	0	0	0	4	1	0	2
H. (*Helicopsyche*) *shuttleworthi*	0	1	1	0	1	1	-	1	-	1	-	1	-	1	-	1	-	1	-	-	0	0	0	0	0	1
H. (*Galeopsyche*) *coreana*	0	1	0	2	0	1	-	1	-	1	-	1	-	1	-	1	-	0	1	0	0	5	2	0	1	-
H. (*Galeopsyche*) *khemoiensis*	1	-	0	0	0	1	-	1	-	1	-	0	0	1	-	1	-	0	1	0	0	2	4	2	1	-
H. (*Feropsyche*) *angulata*	1	-	1	0	0	0	0	1	-	1	-	1	-	0	0	1	-	0	1	0	0	0	3	0	1	-
H. (*Feropsyche*) *borealis*	1	-	0	2	1	1	-	1	-	1	-	1	-	1	-	1	-	1	-	-	0	3	1	1	1	-
H. (*Feropsyche*) *diamantina*	1	-	0	2	1	1	-	1	-	1	-	0	2	0	0	1	-	1	-	-	0	0	0	1	1	-
H. (*Feropsyche*) *fridae*	1	-	0	2	0	1	-	1	-	1	-	0	0	1	-	1	-	1	-	-	0	0	3	1	1	-

Taxon	**Characters**																									
	91	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**
H. (*Feropsyche*) *johansoni*	1	-	0	2	1	1	-	1	-	1	-	0	0	0	0	1	-	0	1	0	0	2	1	1	1	-
H. (*Cochliopsyche*) *amazona*	1	-	0	2	1	1	-	1	-	1	-	1	-	1	-	1	-	0	1	1	1	-	-	-	1	-
H. (*Cochliopsyche*) *amica*	1	-	0	2	1	1	-	1	-	0	1	1	-	0	1	1	-	0	1	0	1	-	-	-	1	-
H. (*Cochliopsyche*) *blahniki*	1	-	0	2	2	1	-	0	1	0	0	0	1	1	-	1	-	0	0	0	1	-	-	-	1	-
H. (*Cochliopsyche*) *brazilia*	1	-	0	2	0	1	-	0	0	1	-	0	1	1	-	1	-	0	0	0	1	-	-	-	1	-
H. (*Cochliopsyche*) *chocoensis*	1	-	0	2	0	1	-	0	0	0	1	0	1	1	-	1	-	0	0	0	1	-	-	-	1	-
H. (*Cochliopsyche*) *clara*	1	-	0	2	1	1	-	0	0	0	1	0	0	1	-	1	-	0	0	1	1	-	-	-	1	-
H. (*Cochliopsyche*) *holzenthali*	1	-	0	2	0	1	-	0	1	0	1	0	1	1	-	1	-	0	1	1	1	-	-	-	1	-
H. (*Cochliopsyche*) *lobata*	1	-	0	2	0	1	-	0	0	0	1	1	-	0	0	1	-	0	1	1	1	-	-	-	1	-
H. (*Cochliopsyche*) *napoa*	1	-	0	2	0	1	-	0	0	0	0	0	1	1	-	0	2	0	0	0	1	-	-	-	1	-
H. (*Cochliopsyche*) *nyurga*	1	-	0	2	0	1	-	0	0	0	0	1	-	1	-	1	-	0	1	1	1	-	-	-	1	-
H. (*Cochliopsyche*) *ocosingua*	1	-	0	2	1	1	-	0	0	0	1	1	-	0	0	1	-	0	1	1	1	-	-	-	1	-
H. (*Cochliopsyche*) *opalescens*	1	-	0	2	2	1	-	0	0	1	-	1	-	0	1	1	-	0	0	0	1	-	-	-	1	-
H. (*Cochliopsyche*) *pandeirosa*	1	-	0	2	1	1	-	0	0	1	-	0	1	1	-	0	0	0	0	0	1	-	-	-	1	-
H. (*Cochliopsyche*)*paraguaiensis*	1	-	0	2	0	1	-	0	0	0	1	1	-	0	1	1	-	0	0	1	1	-	-	-	1	-
H. (*Cochliopsyche*) *puyoa*	1	-	0	2	0	1	-	0	1	0	1	1	-	1	-	1	-	0	0	0	1	-	-	-	1	-
H. (*Cochliopsyche*) *vazquezae*	1	-	0	2	0	1	-	0	0	1	-	0	0	1	-	1	-	0	0	1	1	-	-	-	1	-
H. (*Cochliopsyche*) *xinguensis*	1	-	0	2	1	1	-	0	0	0	1	1	-	0	1	0	0	0	0	0	1	-	-	-	1	-
H. (*Cochliopsyche*) **sp. 1**	1	-	0	2	1	1	-	0	0	0	0	1	-	1	-	1	-	0	0	1	1	-	-	-	1	-
H. (*Cochliopsyche*) **sp. 2**	1	-	0	2	0	1	-	0	0	1	-	0	0	1	-	1	-	0	1	1	1	-	-	-	1	-
H. (*Cochliopsyche*) **sp. 3**	1	-	0	2	0	1	-	0	0	0	-	0	0	1	-	1	-	0	1	1	1	-	-	-	1	-
H. (*Cochliopsyche*) **sp. 4**	1	-	0	2	2	1	-	0	0	0	2	1	-	1	-	1	-	0	0	1	1	-	-	-	1	-
H. (*Cochliopsyche*) **sp. 5**	1	-	0	2	0	1	-	0	0	1	-	1	-	1	-	0	0	0	0	1	1	-	-	-	1	-

PHYLOGENETIC ANALYSIS

The phylogenetic analysis was performed using Bayesian inference in CIPRES. We used the strategy presented by Rosa et al. (2019) for modelling morphological character, which uses the Mk model (Lewis 2001) with partitions based on homoplasy, estimated from consistency indices generated in parsimony analysis with implicit weighting performed in TNT (Goloboff et al. 2008). A traditional search was performed, with 10.000 TBR replications, ten trees saved per replication. The implied weighting K values were adjusted as implemented in TNT, so that weight ratio between no homoplasy and maximum possible steps is in the ratio 1 to 10,000 (k-value calculated was 12.46), making the generated results comparable with other matrices of different sizes. The adjusted values of homoplasy (consistency index) of each character were combined into more inclusive intervals resulting in eight morphological partitions (Table 3). These morphological character partitions were then used in the Bayesian analyses.

DIVERGENCE-TIMES ESTIMATION

We used the morphological data to estimate the divergence times in a tip-dating approach using the Fossilized-Birth-Death model (FBD, Heath et al., 2014) generated together with the phylogenetic analyses implemented in MrBayes (3.2.7a). The FBD model allows the insertion of fossils as terminals in the analysis, considering the uncertainty in the phylogenetic positioning of the fossil and using morphological information in the time estimation. A relaxed morphological clock was used with independent gamma rate (IGR) (Lepage et al., 2007). The tree age prior was based on the estimated divergence of Sericostomatoidea (~220-200 Ma) (Thomas et al. in press). Fossil species of Helicopsychidae were used for temporal calibration as terminal taxa. The FBD model was used with diversity sampling strategy. Parameters of speciation, extinction, and fossil discovery rate were set according to Zhang (2019). The living sample proportion parameter was adjusted between the number of the extant terminals taxa and the number of known extant species of Helicopsychidae (Morse et al., 2019). Two runs were performed, a first analysis was made without dating to infer the clades relationship, and a second one was ran adding some clade constraints to the dating analysis so to help the tree to converge adequately. Clades with low support (<50) were allowed to float. The matrix with the MrBayes parameters block were uploaded to the CIPRES online cluster (Miller et al., 2010).

Table 3. Morphological partitions used for Bayesian inferences. The partitions were established based on its levels of homoplasy obtained from the adjusted homoplasy of a phylogenetic analysis under implied weight. Individual values were combined into more inclusive classes.

Partition	Adjusted homoplasy	Characters
1	0	1, 2, 14, 19, 41, 63, 65, 106
2	0.04	5, 8, 13, 16, 18, 21, 26, 28, 29, 36, 40, 43, 44, 46, 66, 93, 100, 104, 116, 4, 7, 9, 10, 15, 17, 42, 52, 55, 91, 102
3	0.08–0.12	22, 32, 57, 69, 70, 99, 112, 6, 30, 38, 39, 45, 48, 79, 90, 110
4	0.15–0.24	59, 62, 64, 83, 87, 92, 101, 115, 49, 58, 60, 88, 89, 107, 109, 111
5	0.27–0.33	31, 54, 56, 84, 94, 95, 114, 33, 51, 53, 67, 105, 61, 68, 85, 86, 113, 47, 72, 75
6	0.35–0.42	20, 27, 50, 78, 103, 3, 34, 71, 96, 24, 74, 81, 82
7	0.43–0.5	77, 80, 76, 23
8	-	11, 12, 25, 35, 37, 73, 97, 98, 108, 117

At CIPRES online cluster (Miller et al., 2010), a tree search was carried out using the Markov Chain Monte Carlo (MCMC) algorithm, analysis was run for 50,000,000 generations, sampled every 1000 generations, in two analyses in parallel with four Markov chains each (three hot, one cold), and discarding 25% of initial trees retained (burn-in). Convergence between analysis was verified in TRACER (Rambaut et al. 2018). The statistical support of the branches was measured by posterior probability values generated in the analysis. The trees were visualized and edited in FigTree 1.4.3 (Rambaut 2016) and in WinClada 1.00.08 (Nixon 2002), the final phylogeny was edited in Adobe Illustrator® CS6.

BIOGEOGRAPHICAL ANALYSIS

The consensus cladogram resulting from Bayesian analysis was used for historical biogeography analyses. The biogeographic model was estimated using the Akaike information criterion (AIC) using the R package, BioGeoBEARS (Matzke, 2013). The selected best-fit model was Dispersal-Extinction-Cladogenesis (S-DEC) (Ree & Smith, 2008), it was used for the biogeographic analysis in RASP v.4.0 (Yu et al. 2020). The analysis sought to understand a broader biogeographical relationship using the entire data set (51 taxa) to reconstruct the ancestral area of Helicopsychidae. For this purpose, we used the bioregions of de Moor & Ivanov (2008): Afrotropical, Australasian, Eastern and Western Palearctic, Nearctic, Neotropical and Oriental, additionally we included an Antillean region.

RESULTS AND DISCUSSION

Characters and states for phylogenetic analysis

The morphological characters and their respective states obtained from the analysis of type and additional material and/or from the literature are listed below and the resulting matrix is shown in Table 2 (Figure 1)

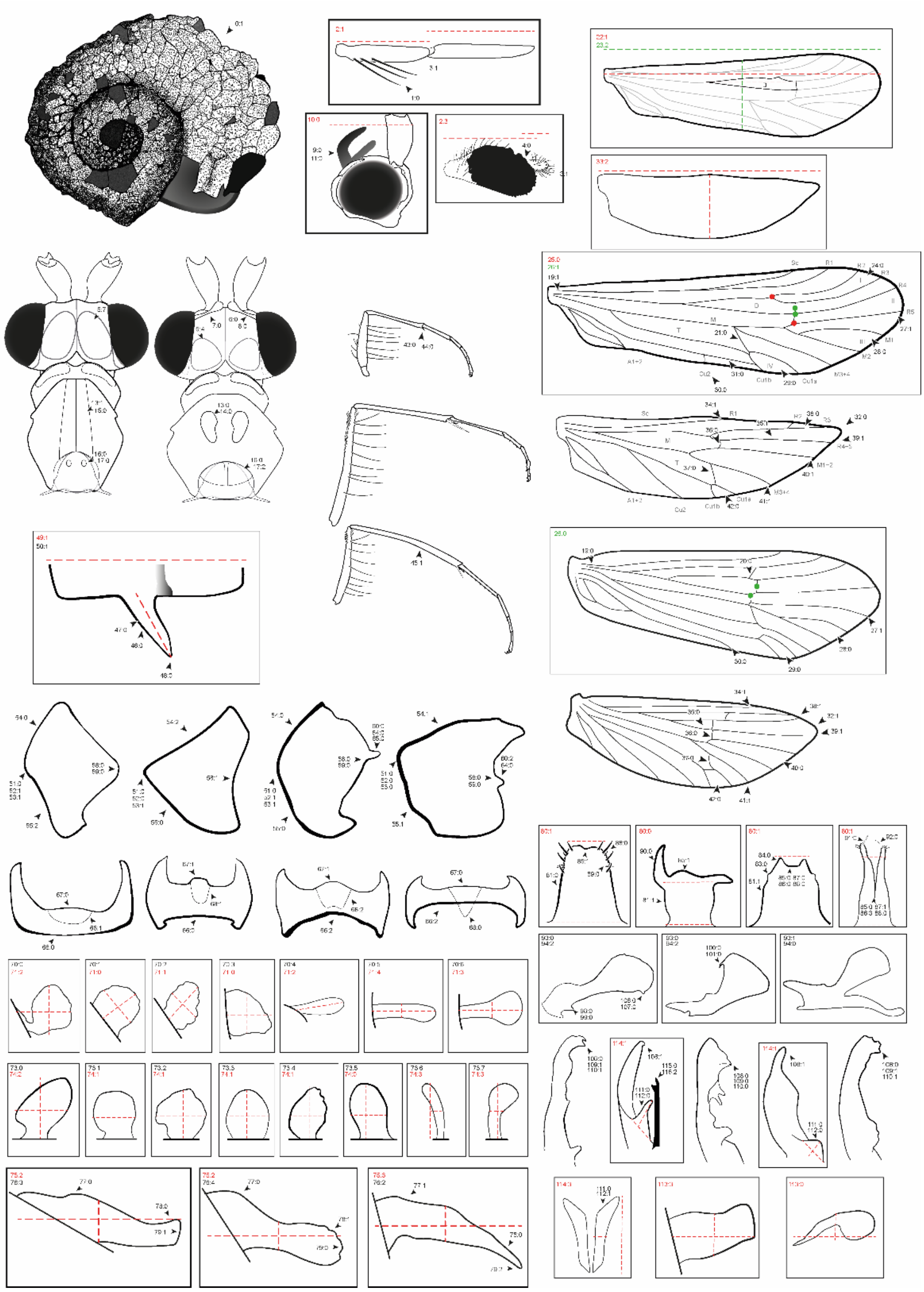

Figure 1: Morphological characters coded for Helicopsychidae and related taxa *Anomalopsyche* and *Chathamia*.

List of morphological characters

1. Larva case, shape: [0] helicoidal, [1] not helicoidal.
2. Male Head, Maxillary palp (basal article), occurrence, long and stout median setae: [0] present, [1] absent.
3. Male Head, Maxillary palp, length, distal article for basal article: [0] length less than or subequal, [1] length greater than 1x and less than 1.5x, [2] length between 1.5x and less than 2x, [3] length 2x or greater.
4. Male Head, Maxillary palp, number, article: [0] one, [1] two, [2] three, [3] four, [4] five.
5. Male Head, Maxillary palp, location, inserted of last article: [0] before apex, [1] in apex.
6. Male Head, Cephalic warts, form: [0] subtriangular, [1] bean shaped, [2] digitiform, [3] trapezoid, [4] subrectangular, [5] globose, [6] pyriform, [7] ovoid.
7. Male Head, Interantennal warts, occurrence: [0] present, [1] absent.
8. Male Head, Interantennal warts, form: [0] projected, [1] unprojected.
9. Male Head, Interantennal warts, form: [0] subtriangular, [1] club-shaped, [2] digitiform, [3] trapezoid, [4] subrectangular, [5] globose, [6] ovoid.

10. Male Head, androconial organs, occurrence: [0] present, [1] absent.
11. Male Head, androconial organs, length, organ length in relation of head: [0] length less than or subequal, [1] length greater than 1x and less than 1.5x, [2] length between 1.5x and less than 2x, [3] length between 2x and less than 2.5x, [4] length 2.5x or greater.
12. Male Head, androconial organs, form, in dorsal view: [0] bifid, [1] club-shaped, [2] cone-shaped, [3] cylindrical-shaped.
13. Male Head, Antennae length, length, in relation to the body: [0] length less than half the body, [1] length between half and less than 1.2x, [2] length 1.2x or greater.
14. Male Thorax, Mesoscutal setal warts, occurrence: [0] present, [1] absent.
15. Male Thorax, Mesoscutal setal warts, shape: [0] been-shaped, [1] subrectangular, [2] ovoid, [3] globose, [4] pyriform.
16. Male Thorax, Mesoscutal longitudinal subrcetangular pale band, occurrence: [0] present, [1] absent.
17. Male Thorax, Mesoscutellar setal warts, occurrence: [0] present, [1] absent.
18. Male Thorax, Mesoscutellar setal warts, width: [0] width less than 5x, [1] width between less than 5x and 6x, [2] width between less than 6x and 7x, [3] width between less than 7x and 8x, [4] width between less than 8x and 9x, [5] width less than more 9x

19. Male Thorax, Metascutellum posteriorly, form: [0] not extended, [1] extended.
20. Male Wings, Forewing Subcostal vein, origin: [0] independent, [1] originates from the R branch.
21. Male Wings, Forewing transversal vein R1-R2, occurrence: [0] present, [1] absent.
22. Male Wings, Forewing Thyridial cell, form: [0] closed, [1] open.
23. Male Wings, Forewing length over discoidal cell length, length: [0] less than 3x, [1] between 3x and less than 4x, [2] between 4x and less than 5x, [3] less than 5x or more.
24. Male Wings, Forewing, length, in relation to height: [0] length between 1x and less than 2x height, [1] length between 2x and less than 3x height, [2] length between 3x and less than 4x height, [3] length 4x or more height.
25. Male Wings, Forewing fork I, occurrence: [0] present, [1] absent.
26. Male Wings, Forewing fork I, position: [0] anteriorly to basal branch R5, [1] on-line or after basal branch R5.
27. Male Wings, Forewing R5 originates proximally, position, in relation of wings crossvein R3-R4: [0] anteriorly to crossvein R3-R4, [1] on-line or after crossvein R3-R4, [2] posteriorly to crossvein R3-R4.

28. Male Wings, Forewing R5, position, in relation of wings margin: [0] ends before the wings margin, [1] ends in wings margin.
29. Male Wings, Forewing fork III, occurrence: [0] present, [1] absent.
30. Male Wings, Forewing fork V, occurrence: [0] present, [1] absent.
31. Male Wings, Forewing Cu2, position: [0] ends in Cu1b, [1] ends in wings margin.
32. Male Wings, Forewing crossvein Cu1-Cu2, occurrence: [0] present, [1] absent.
33. Male Wings, Hind wing apex, form: [0] slightly pointed, [1] rounded.
34. Male Wings, Hind wing, length, in relation to height: [0] length between 1x and less than 2x height, [1] length between 2x and less than 3x height, [2] length between 3x and less than 4x height, [3] length 4x or more height.
35. Male Wings, Hind wing R1 vein, position: [0] ends in R2 vein, [1] ends in wings margin.
36. Male Wings, Hind wing Discoidal cell, form: [0] closed, [1] open.
37. Male Wings, Hind wing Medial cell, form: [0] closed, [1] open.
38. Male Wings, Hind wing Thyridial cell, form: [0] closed, [1] open.
39. Male Wings, Hind wing fork I, occurrence: [0] present, [1] absent.
40. Male Wings, Hind wing fork II, occurrence: [0] present, [1] absent.
41. Male Wings, Hind wing fork III, occurrence: [0] present, [1] absent.

42. Male Wings, Hind wing fork IV, occurrence: [0] present, [1] absent.
43. Male Wings, Hind wing fork V, occurrence: [0] present, [1] absent.
44. Male Legs, Foreleg apical spur, occurrence: [0] present, [1] absent.
45. Male Legs, Foreleg apical spur, number: [0] one, [1] two.
46. Male Legs, Hind leg preapical spur, occurrence: [0] present, [1] absent.
47. Male Abdomen, Sternal VIth process, occurrence: [0] present, [1] absent.
48. Male Abdomen, Sternal VIth process, form, lateral view: [0] subtriangular, [1] club-shaped, [2] digitiform, [3] filiform.
49. Male Abdomen, Sternal VIth process, form, apex of process: [0] acute, [1] truncated, [2] rounded.
50. Male Abdomen, Sternal VIth process, length, in relation to abdominal segment: [0] length less than 1/3 height of abdominal segment IX, [1] length from 1/3 to less than 2/3 of the height of abdominal segment IX, [2] length from 2/3 to equal of the height of abdominal segment IX, [3] length greater than the height of abdominal segment IX.
51. Male Abdomen, Sternal VIth process, position, in relation to abdominal segment: [0] inserted between the anterior margin and the first third of the segment, [1] inserted after first third until second

third of the segment, [2] inserted after second third until posterior margin of the segment.

52. Male Genitalia, Abdominal segment IX, form, anterior lobe, lateral view: [0] projected, [1] unprojected.
53. Male Genitalia, Abdominal segment IX, form, anterior lobe, lateral view: [0] with acuminated projection, [1] with rounded projection.
54. Male Genitalia, Abdominal segment IX, position, anterior lobe, lateral view: [0] positioned dorsally on segment, [1] positioned midway on segment, [2] positioned ventrally on segment.
55. Male Genitalia, Abdominal segment IX, form, anterodorsal margin, lateral view: [0] substraight, [1] convex, [2] concave.
56. Male Genitalia, Abdominal segment IX, form, anteroventral margin, lateral view: [0] substraight, [1] convex, [2] concave.
57. Male Genitalia, Abdominal segment IX, occurrence, median apodeme, lateral view: [0] present, [1] absent.
58. Male Genitalia, Abdominal segment IX, occurrence, dorsomedian apodeme, lateral view: [0] present, [1] absent.
59. Male Genitalia, Abdominal segment IX, form, posterior lobe, lateral view: [0] projected, [1] unprojected.
60. Male Genitalia, Abdominal segment IX, form, posterior lobe, lateral view: [0] with acuminated projection, [1] with rounded projection.

61. Male Genitalia, Abdominal segment IX, position, posterior lobe, lateral view: [0] positioned dorsally on segment, [1] positioned midway on segment, [2] positioned ventrally on segment.
62. Male Genitalia, Abdominal segment IX, occurrence, posterior lobe, lateral view: [0] with set of setae, [1] without set of setae.
63. Male Genitalia, Abdominal segment IX, length, posterior lobe, lateral view: [0] short setae, not exceeding the segment margin, [1] long setae, exceeding the segment margin.
64. Male Genitalia, Abdominal segment IX, occurrence, posterior lobe projection, lateral view: [0] present, [1] absent.
65. Male Genitalia, Abdominal segment IX, length, posterior lobe projection, lateral view: [0] slightly projected, [1] well-projected.
66. Male Genitalia, Abdominal segment IX, form, posterior lobe projection, lateral view: [0] digitated, [1] subtriangular.
67. Male Genitalia, Abdominal segment IX, form, anterior margin, ventral view: [0] substraight, [1] convex, [2] concave.
68. Male Genitalia, Abdominal segment IX, form, central posterior lobe, ventral view: [0] substraight, [1] convex, [2] concave.
69. Male Genitalia, Abdominal segment IX, form, basal plate, ventral view: [0] V-shaped, [1] U-shaped, [2] W-shaped.
70. Male Genitalia, Preanal appendage, occurrence: [0] present, [1] absent.

71. Male Genitalia, Preanal appendage, form, lateral view: [0] boxing glove shaped, [1] globose, [2] ovoid, [3] pyriform-shaped, [4] thumb-shaped, [5] digitated; [6] club shaped.
72. Male Genitalia, Preanal appendage, length, lateral view: [0] length and width subequal size, [1] length between more than one to two times the width, [2] length between more than two to three times the width, [3] length between more than three to four times the width, [4] length more than four times the width, [5] width between more than one to two times the length, [6] width between more than two to three times the length, [7] width between more than three to four times the length, [8] width more than four times the length.
73. Male Genitalia, Preanal appendage, form, dorsal view: [0] subequal shape, [1] different shape.
74. Male Genitalia, Preanal appendage, form, dorsal view: [0] boomerang-shaped, [1] boxing glove shaped, [2] globose, [3] ovoid, [4] pyriform, [5] thumb-shaped, [6] digitated, [7] club shaped.
75. Male Genitalia, Preanal appendage, length, dorsal view: [0] length and width subequal size, [1] length between more than one to two times the width, [2] length between more than two to three times the width, [3] length between more than three to four times the width, [4] length more than four times the width, [5] width between more than one to two times the length, [6] width between more than two to

three times the length, [7] width between more than three to four times the length, [8] width more than four times the length.

76. Male Genitalia, Abdominal segment X, length, in relation to height, lateral view: [0] length and width subequal size, [1] length between more than one to two times the width, [2] length between more than two to three times the width, [3] length between more than three to four times the width, [4] length more than four times the width, [5] width between more than one to two times the length, [6] width between more than two to three times the length, [7] width between more than three to four times the length, [8] width more than four times the length.
77. Male Genitalia, Abdominal segment X, form, lateral view: [0] subtriangular, [1] club-shaped, [2] filiform, [3] subrectangular, [4] cylinder shape, [5] S-shaped, [6] digitated.
78. Male Genitalia, Abdominal segment X, occurrence, anterodorsal projection, lateral view: [0] present, [1] absent.
79. Male Genitalia, Abdominal segment X, form, posterodorsally margin, lateral view: [0] smooth, [1] sinuous.
80. Male Genitalia, Abdominal segment X, form, apex, lateral view: [0] rounded, [1] truncated, [2] acuminated.

81. Male Genitalia, Abdominal segment X, length, dorsal view: [0] width of base subequal to apex, [1] base wider than apex, [2] apex wider than base.
82. Male Genitalia, Abdominal segment X, form, lateral margin, dorsal view: [0] substraight, [1] convex, [2] concave.
83. Male Genitalia, Abdominal segment X, occurrence, median projection, dorsal view: [0] present, [1] absent.
84. Male Genitalia, Abdominal segment X, occurrence, subapical projection, dorsal view: [0] present, [1] absent.
85. Male Genitalia, Abdominal segment X, occurrence, apical projection, dorsal view: [0] present, [1] absent.
86. Male Genitalia, Abdominal segment X, occurrence, apical evagination, dorsal view: [0] present, [1] absent.
87. Male Genitalia, Abdominal segment X, form, depth of invagination, dorsal view: [0] less than 1/5 of abdominal segment length X, [1] between more than 1/5 and 1/3 abdominal segment X length, [2] between more than 1/3 and half the length of the abdominal segment X, [3] longer than half of the abdominal segment X.
88. Male Genitalia, Abdominal segment X, occurrence, central apodeme, dorsal view: [0] present, [1] absent.
89. Male Genitalia, Abdominal segment X, occurrence, apical set of setae, dorsal view: [0] present, [1] absent.

90. Male Genitalia, Abdominal segment X, occurrence, lateral row of setae, dorsal view: [0] present, [1] absent.
91. Male Genitalia, Abdominal segment X, form, apical ornamentations, dorsal view: [0] present, [1] absent.
92. Male Genitalia, Abdominal segment X, form, apical spines like mega setae, dorsal view: [0] present, [1] absent.
93. Male Genitalia, Abdominal segment X, number, apical spines like mega setae, dorsal view: [0] one, [1] two, [2] three, [3] four, [4] five.
94. Male Genitalia, Inferior appendage, form, lateral view, unique: [0] bifid, [1] trifid.
95. Male Genitalia, Inferior appendage, length, lateral view, width of base subequal to apex: [0] base wider than apex, [1] apex wider than base.
96. Male Genitalia, Inferior appendage, length, ventral view, width of base subequal to apex: [0] base wider than apex, [1] apex wider than base.
97. Male Genitalia, Inferior appendage, occurrence, anterodorsal process: [0] present, [1] absent.
98. Male Genitalia, Inferior appendage, form, anterodorsal process, lateral view: [0] unique, [1] bifid, [2] trifid.
99. Male Genitalia, Inferior appendage, occurrence, anteroventral process: [0] present, [1] absent.

100. Male Genitalia, Inferior appendage, form, anteroventral process, lateral view: [0] unique, [1] bifid, [2] trifid.

101. Male Genitalia, Inferior appendage, occurrence, mediodorsal process: [0] present, [1] absent.

102. Male Genitalia, Inferior appendage, form, mediodorsal process, lateral view: [0] unique, [1] bifid, [2] trifid.

103. Male Genitalia, Inferior appendage, occurrence, medioventral process: [0] present, [1] absent.

104. Male Genitalia, Inferior appendage, form, medioventral process, lateral view: [0] unique, [1] bifid, [2] trifid.

105. Male Genitalia, Inferior appendage, occurrence, posterodorsally process: [0] present, [1] absent.

106. Male Genitalia, Inferior appendage, form, posterodorsally, process, lateral view: [0] unique, [1] bifid, [2] trifid.

107. Male Genitalia, Inferior appendage, occurrence, posteroventral: [0] present, [1] absent.

108. Male Genitalia, Inferior appendage, form, posterodorsally process, lateral view: [0] unique, [1] bifid, [2] trifid.

109. Male Genitalia, Inferior appendage, occurrence, subapical teeth on inner face, ventral view: [0] present, [1] absent.

110. Male Genitalia, Inferior appendage, form, subapical teeth on inner face, ventral view: [0] sclerotized, [1] unsclerotized.

111. Male Genitalia, Inferior appendage, number, subapical teeth on inner face, ventral view: [0] a tooth, [1] two teeth, [2] three teeth.

112. Male Genitalia, Inferior appendage, occurrence, basomesal lobe: [0] present, [1] absent.

113. Male Genitalia, Inferior appendage, form, basomesal lobe, ventral view: [0] subtriangular, [1] club-shaped, [2] digitiform, [3] subretangular, [4] filiform, [5] trapezoid

114. Male Genitalia, Inferior appendage, length, basomesal, lateral view: [0] length and width subequal size, [1] length between more than one to two times the width, [2] length between more than two to three times the width, [3] length between more than three to four times the width, [4] length more than four times the width, [5] width between more than one to two times the length, [6] width between more than two to three times the length, [7] width between more than three to four times the length, [8] width more than four times the length.

115. Male Genitalia, Inferior appendage, length, basomesal lobe, ventral view: [0] length and width subequal size, [1] length between more than one to two times the width, [2] length between more than two to three times the width, [3] length between more than three to four times the width, [4] length more than four times the width, [5] width between more than one to two times the length, [6] width

between more than two to three times the length, [7] width between more than three to four times the length, [8] width more than four times the length.

116. Male Genitalia, Inferior appendage, occurrence, inner face branch: [0] present, [1] absent.

117. Male Genitalia, Inferior appendage, form, inner face branch: [0] S-shaped, [1] digitiform, [2] spear-shaped.

The maximum credibility Bayesian tree obtained from the morphological characters (Figure 2) recovered the Helicopsychidae family as monophyletic including both extant and fossil representatives, supported by the characters: Forewing R5 vein originates anteriorly to crossvein R3-R4, presence of abdominal sternum VI process, presence of basomesal lobe and others (posterior probability value, PP = 80). With †*Cretahelicopsyche* as the sister group to all other Helicopsychidae (PP = 67), with the second cladogenesis within the family separating *Rakiura* from *Helicopsyche* + †*Eletrohelicopsyche* + †*Palaeohelicopsyche* with low support (PP = 17). *Helicopsyche* was not recovered as monophyletic, having parts grouped with *Electrohelicopsyche* + *Paleohelicopsyche*. Except for the subgenus *Feropsyche*, all other subgenera were recovered as monophyletic with high support (Figure 2).

The clade formed by *Helicopsyche* + †*Eletrohelicopsyche* + †*Paleohelicopsyche* is divided into two clades. **Clade A** is composed of the fossil representatives of *Helicopsyche*, together with †*Eletrohelicopsyche*, †*Palaeohelicopsyche*, *H*. (*Feropsyche*) and *H*. (*Saetotrichia*) with low support (PP = 14); and **Clade B** comprised *H*. (*Galeopsyche*), *H*. (*Helicopsyche*), *H*. (*Petrotrichia*) and *Cochliopsyche* with low support (PP = 14) (Figure 2).

The **Clade A** comprises four clades: **clade A1** formed by representatives †*E*. *taeniata*, †*P*. *serricornis* and †*H*. *scapi*, †*H*. *confluens* and †*H*. *typica*, all from Baltic amber (PP = 45); **clade A2** (PP = 37) is composed by †*H*. *cona*, †*H*. *damseni*, both from Baltic amber, and three species from Dominican amber (PP = 51); and **clade A3** which is composed by representatives of *H*. (*Ferospyche*) and *H*. (*Saetotrichia*) (PP = 90) (Figure 2).

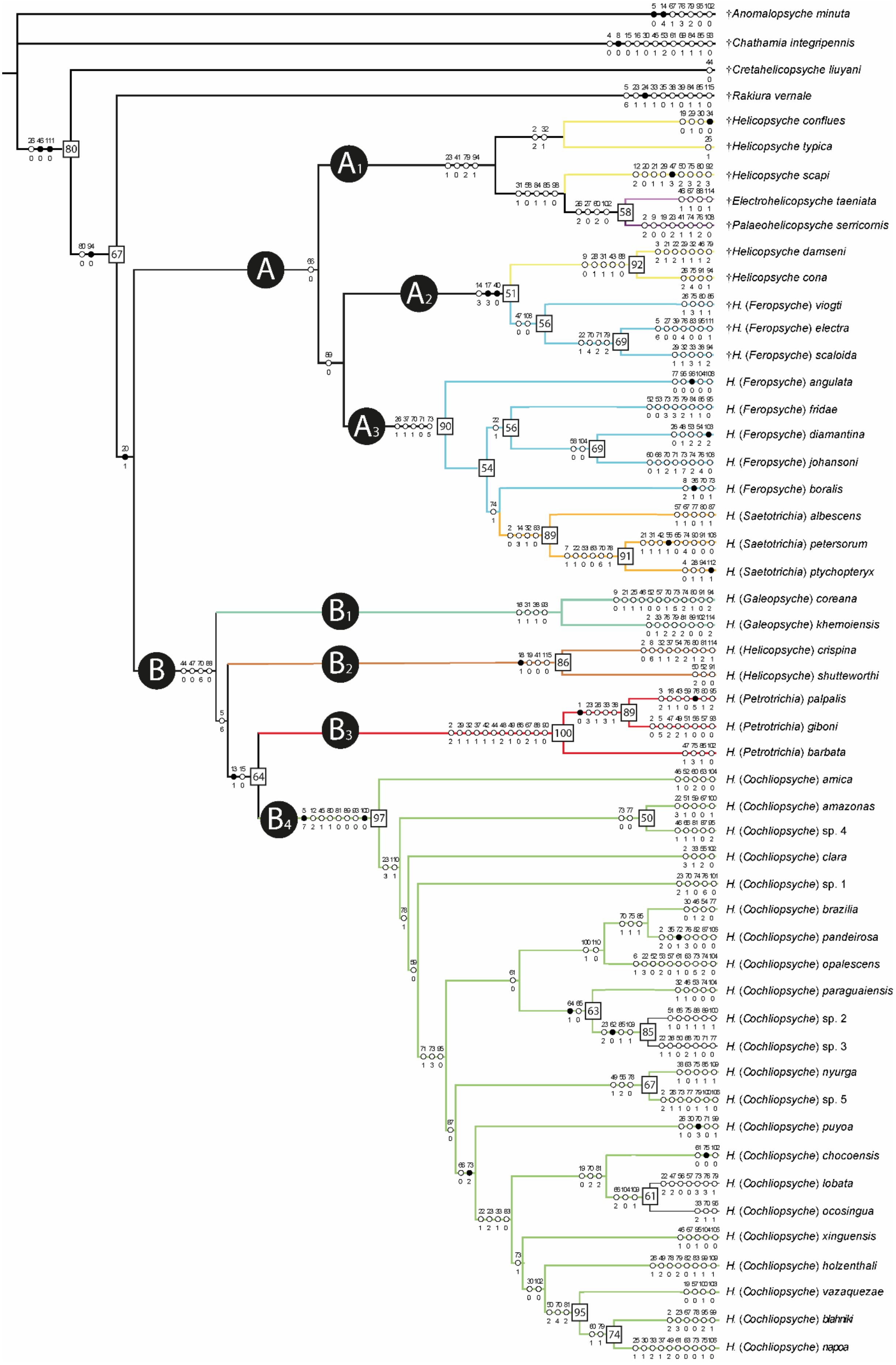
†Anomalopsyche minuta
†Chathamia integripennis
†Cretahelicopsyche liuyani
†Rakiura vernale
†Helicopsyche conflues
†Helicopsyche typica
†Helicopsyche scapi
†Electrohelicopsyche taeniata
†Palaeohelicopsyche serricornis
†Helicopsyche damseni
†Helicopsyche cona
†H. (Feropsyche) viogti
†H. (Feropsyche) electra
†H. (Feropsyche) scaloida
H. (Feropsyche) angulata
H. (Feropsyche) fridae
H. (Feropsyche) diamantina
H. (Feropsyche) johansoni
H. (Feropsyche) boralis
H. (Saetotrichia) albescens
H. (Saetotrichia) petersorum
H. (Saetotrichia) ptychopteryx
H. (Galeopsyche) coreana
H. (Galeopsyche) khemoiensis
H. (Helicopsyche) crispina
H. (Helicopsyche) shutteworthi
H. (Petrotrichia) palpalis
H. (Petrotrichia) giboni
H. (Petrotrichia) barbata
H. (Cochliopsyche) amica
H. (Cochliopsyche) amazonas
H. (Cochliopsyche) sp. 4
H. (Cochliopsyche) clara
H. (Cochliopsyche) sp. 1
H. (Cochliopsyche) brazilia
H. (Cochliopsyche) pandeirosa
H. (Cochliopsyche) opalescens
H. (Cochliopsyche) paraguaiensis
H. (Cochliopsyche) sp. 2
H. (Cochliopsyche) sp. 3
H. (Cochliopsyche) nyurga
H. (Cochliopsyche) sp. 5
H. (Cochliopsyche) puyoa
H. (Cochliopsyche) chocoensis
H. (Cochliopsyche) lobata
H. (Cochliopsyche) ocosingua
H. (Cochliopsyche) xinguensis
H. (Cochliopsyche) holzenthali
H. (Cochliopsyche) vazaquezae
H. (Cochliopsyche) blahniki
H. (Cochliopsyche) napoa
A
A1
A2
A3
B
B1
B2
B3
B4
80
67
58
92
51
56
69
90
56
69
54
89
91
86
89
100
64
97
50
63
85
67
61
95
74

Figure 2: Consensus cladogram of the Bayesian tree obtained from 117 morphological characters coded for Helicopsychidae and related taxa *Anomalopsyche* and *Chathamia* (all compatible groups are shown).

Morphological character states shown in boxes refer to unambiguous transformations, black symbols indicate unique character changes, posterior probability support values are shown in boxes at branch nodes, and clades are marked in round boxes. the colored branch indicates the terminals of each subgenus or genus of Helicopsychidae

The **Clade B** is composed by three clades: **clade B1** is formed by two species of *H.* (*Helicopsyche*), (*H. crispina* and *H. shuttleworthi*); **clade B2** is formed by two species of *H.* (*Galeopsyche*), (*H. coreana* and *H. khemoiensis*) (PP = 45); **clade B3** is formed by three species of *H.* (*Petrotrichia*), (*H. barbata*, *H. giboni* and *H. palpalis*) (PP = 100); and the **clade B4** which is formed for all species of *Cochliopsyche* and five putative new species (PP = 97) (Figure 2).

In response to the hypotheses raised in this study, Helicopsychidae forms a monophyletic group including extant and fossil genera. The genus *Helicopsyche* was not recovered as a monophyletic group since there are species [e.g., *H.* (*Feropsyche*) and *H.* (*Galeopsyche*)] more closely related to fossil species placed in another genera (i.e., †*Electrohelicopsyche* and †*Palaeohelicopsyche*). The hypothesis that *H*. (*Cochliopsyche*) as a monophyletic group was corroborated (PP = 97). The subgenera *Galeopsyche* (PP = 45), *Helicopsyche* (PP = 86), *Petrotrichia* (PP = 100), and *Saetotrichia* (PP = 89) were also recovered as monophyletic (Figure 2), except for *Feropsyche* (polyphyletic with a distinct clade including fossil species of Dominican amber grouped with representatives of the Baltic amber and with *H. borealis* forming with low support a group with the *Saetotrichia*) (Figure 2). *Feropsyche* and *Saetotrichia* form a single lineage with high support (PP = 90).

Among the *Cochliopsyche*, five clades are supported: the first includes *C. amazonas* and *Cochliopsyche* sp. 4; the second with *C. paraguaiensis*, *Cochliopsyche* sp. 2 and *Cochliopsyche* sp. 3; the third comprises *C. nyurga* and *Cochliopsyche* sp. 5; the fourth with *C. lobata* and *C. oconsigua*; and the fifth with *C. blahniki* and *C. napoa* (Figure 2). However, more general relationships are weakly supported and do not allow for further explanation. This is possibly due to the low variability in the morphological characteristics of the species.

SYSTEMATICS

Based on the taxa sampling, the high support, the age of the clade and the fact that it forms a monophyletic group, we have resurrected

Cochliopsyche to genus status. Additionally, based on our phylogenetic results, we propose the removal of the fossil representatives from Dominican amber from the subgenus *Feropsyche* (i.e., †*Helicopsyche voigti* Johanson & Wichard, 1996; †*Helicopsyche scaloida* Johanson & Wichard, 1996; †*Helicopsyche electra* Johanson & Wichard, 1996).

†*Helicopsyche* (*incertae sedis*) *voigti* Johanson & Wichard, 1996 **stat. nov.**

†*Helicopsyche* (*Feropsyche*) *voigti* Johanson & Wichard, 1996 – Johanson, 1998

†*Helicopsyche* (*incertae sedis*) *scaloida* Johanson & Wichard, 1996 **stat. nov.**

†*Helicopsyche* (*Feropsyche*) *scaloida* Johanson & Wichard, 1996 – Johanson, 1998

†*Helicopsyche* (*incertae sedis*) *electra* Johanson & Wichard, 1996 **stat. nov.**

†*Helicopsyche* (*Feropsyche*) *electra* Johanson & Wichard, 1996 – Johanson, 1998

Cochliopsyche Müller, 1885 **stat. nov.**

Helicopsyche (*Cochliopsyche*) Müller, 1885 – Johanson, 1998

Diagnosis of genus Cochliopsyche

The species of this genus can be differentiated from others Helicopsychidae' genus by set of characters (characters from other genera are presented in parentheses):

1. Antennae more than 1.2–3x body length (versus antennae less than 1.2x body length)

2. Tibial spurs formula 1,2,2 (versus tibial spurs formula 2,2,4 or 1,2,4)

High support argues that subgenera *Petrotrichia*, *Galeopsyche* and a group formed by *Feropsyche* + *Saetotrichia* form monophyletic groups and possibly in the future be elevated to genus status. However, due to the reduced taxa sampling for these subgenera and low value of support, we decided out of caution not to make any more changes to the classification of *Helicopsyche* based in phylogenetic analysis. However, there is the need for a comprehensive study to understand the relationships between the different subgenera. So, as the representatives of †*Electrohelicopsyche* and †*Palaeohelicopsyche* seem to be related to species from the fossiliferous record grouped in *Helicopsyche*, but studies focusing on these species and other putative Helicopsychidae fossil representatives are also needed.

DIVERGENCE TIMES AND BIOGEOGRAPHY

The origin of the Sericostomatoidea dates back 200 Ma, preceding the Pangea split (Thomas et al. 2020). The first stage of the sea floor spreading separating the northern (Laurasia) and southern (Gondwana) parts occurred at 190–180 Ma (Veevers 2012). The origin of the family

Helicopsychidae was estimated at around 157 Ma with the split of †*Cretahelicopsyche*, followed by the split of *Rakiura* at around 148 Ma, and the first splits of fossil species of *Helicopsyche* ~140 Ma.

The fossil impression of †*Archotaulius bavaricus* Handlirsch (1906) from the late Triassic (~155Ma), attributed to Helicopsychidae (Johanson et al. 2017, Carpenter 1932) agrees with this ancient origin. The fossil †*Cretahelicopsyche* is from the mid-Cretaceous Burmese amber, and the Burma Terrane was connected to Australia before the Indian plate start to detach from Gondwana (Bolotov et al. 2022). Therefore, the recovered ancestral area including the Oriental, Australasian and Neotropical regions is in fact Gondwana (Australasia and Neotropics).

The results indicated the dispersal to the West Palaearctic at around 157 Ma (Figure 3). It is indicated that there was a connection until around 100 Ma, as in the clade showing the close relationship of certain Eocene fossil species from Europe (†*H. cona,* †*H. damseni*) and Miocene fossil species from the Antilles (~100 Ma), and the clade including the subgenera *H*. (*Galeopsyche*) and *H.* (*Helicopsyche*) from Eurasia and *H.* (*Petrotrichia*) and *Cochliopsyche* from Africa and the Americas (~118 Ma).

Despite Africa do not appear in the earlier ancestral range reconstructions it was part of Gondwana until mid-Cretaceous and was the main connection route with the West Palaearctic. Dispersals between

Africa and Laurasia were common during the Cretaceous and Paleogene, with evidence dating back to the early Cretaceous or possibly the Late Jurassic, with a discontinuous route through the Mediterranean Tethyan Sill regulated by sea-level changes (Gheerbrant & Rage 2006).

This route through Africa would explain better the occurrence of the West Palearctic species range. The relationship of the Antillean Miocene species and the European Eocene fossil species with the divergence at around 100 Ma is quite curious, the Greater Antilles arc was formed during the Cretaceous (~135 Ma) (Riel et al. 2023) and the analysis suggest a vicariant between the clades, what is clearly misleading, but even a dispersal event would be intriguing. However, a similar event also was reported to a Cretaceous praying mantis lineage that dispersed from Africa to the Antilles around 107 Ma, with a subsequent extinction in the Old World (Svenson & Rodrigues 2017). A similar event may have occurred with this *Helicopsyche* fossil lineage, and fossils of the same lineage could also be found in Africa.

The sea floor spreading between Africa and South America began at 130 Ma (Veevers 2012) and may have maintained continental connections or proximity of southern Africa and South America until around 105 Ma (McLoughlin 2001). The results indicate the split between the Neotropical *H.* (*Cochliopsyche*) and the Afrotropical *H.* (*Petrotrichia*) at around 104 Ma, which is close to the minimum date of the connection.

The Australasian *H*. (*Saetotrichia*) and the Neotropical and Nearctic *H*. (*Feropsyche*) are indicated as diverging during the late Cretaceous (~76 Ma). Until the end of the Paleocene (56 Ma), South America was still connected to Antarctica and Australia via the Patagonian region (Reguero et al. 2014). Since nodes with low support were not constrained in the dating results, *H*. (*Feropsyche*) *borealis* was grouped with other Neotropical *Feropsyche* species, but *H. borealis* is distributed in the Nearctic and Neotropics (Canada to northern South America) and can be the result from an earlier Neotropical radiation, which can expand their range and disperse northward.

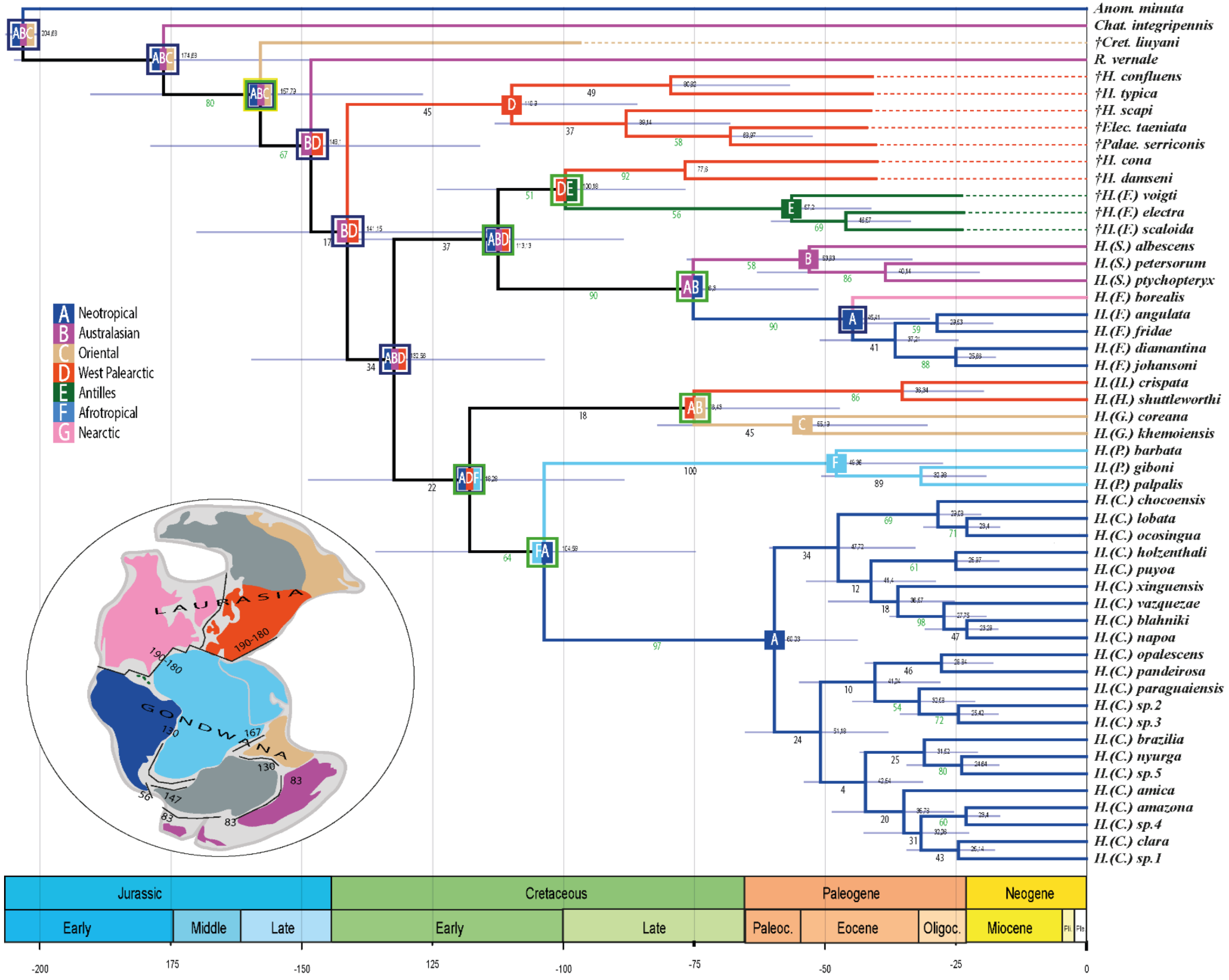

Figure 3. Chronogram resulting from Bayesian analysis employing a relaxed clock. Most likely ancestral distribution recovered in DEC analysis and estimated mean age are displayed at the nodes. Dispersal events are indicated as blue boxes, vicariant events as green boxes, extinctions as yellow boxes, as recovered in the biogeographic analysis. Highest posterior density (HPD) 95% intervals for the ages of the nodes are indicated by light blue bars. Clade posterior probabilities are shown below the branches, supports higher than 50% are highlighted in green.

From Gondwanan origin, the first *Helicopsyche* split was the dispersal to Laurasia (now fossil species in the West Palearctic) during the early Cretaceous (~140 Ma). It is followed by the cladogenesis of two main clades at around 132 Ma, which can indicate a dispersal back to South America (western Gondwana) after the lineage had become extinct in the region around 157 Ma. In these two main clades the early splits also were from clades in the Laurasia [*H.* (*Helicopsyche*), *H.* (*Galeopsyche*), and fossil species], while the later splits were within Gondwana of lineages in Africa and South America [*Cochliopsyche* + *H.* (*Petrotrichia*)], and Australasia and South America (*Saetotrichia* + *Feropsyche*). All the subgenera were already formed at the end of Cretaceous, and most of the species' radiation occurred in the Paleogene. Despite only one lineage currently occurs in the Afrotropical region, it is evident through the Palearctic clades the former occurrence of lineages in Africa during the early Cretaceous.

CONCLUSION

Helicopsychidae is a monophyletic group, including taxa in the fossil record and extant species. However, phylogenetic analysis refutes the hypothesis that the genus *Helicopsyche* is a monophyletic group. Based on the results, we removed the Dominican amber species from the subgenus *Feropsyche*. The origin and reconstruction of biogeographic patterns of

Helicopsychidae are consistent with those established for the Sericostomatoidea groups and the relationships between taxa from the Gondwana regions with taxa from the western Palearctic appear to be consistent in dates and geological events and follow patterns presented for other groups. However, more comprehensive studies focusing on other subgenera and fossil taxa are needed to see if the hypotheses presented here hold up.

We are conservative in proposing changes to the classification beyond the scope of the work because our data are not representative of all subgenera (except *Cochliopsyche*) and the support values are not high. However, based on our data, we suggest that the other subgenera of *Helicopsyche* form independent lineages with high support, except for *Saetotrichia* and *Feropsyche*, which appear to form a single lineage.

Finally, *Cochliopsyche* is resurrected to a genus status and has morphological characteristics that make it very different from its sister groups. Characters of the genital apparatus are not very variable between species and the descriptions provided rely almost substantially on the description of this genital apparatus. In addition, there are at least five putative new species used in this study that need to be described. In this context, a systematic review of the group is necessary with the aim of providing more detailed descriptions, describing alar venation, the pattern of setal warts and so on. Now, we are facing the Darwinian shortfall and a revision of *Cochliopsyche* could allow a better circumscription and delimitation, as well as facing the Linnean and Wallacean deficits.

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Supplementary material

Table S1. Results of the RASP model test. In bold the model with best Akaike information criterion test corrected for small sample sizes (AICc)

Model	LnL	numparams	d	e	j	**AICc weight**
DEC	**-43,81**	**2**	**0,0017**	**0,2**	**0**	**0,70**
DEC+J	-46,84	3	0,0008	0,13	0,017	0,01
DIVALIKE	-46,97	2	0,001	0,014	0	0,03
DIVALIKE+J	-44,92	3	0,0014	0,058	1,00E-05	0,08
BAYAREALIKE	-45,45	2	0,0013	0,046	0	0,14
BAYAREALIKE+J	-45,38	3	0,0011	0,061	0,006	0,05

Capítulo IV

Título: Systematics revision of resurrected long horned snail-case caddisfly genus *Cochliopsyche* Müller, 1885 (Trichoptera, Helicopsychidae)

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Systematics revision of resurrected long horned snail-case caddisfly genus *Cochliopsyche* Müller, 1885 (Trichoptera, Helicopsychidae)

Insect Systematics & Evolution

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Abstract

The *Cochliopsyche* Müller are a group of long horn snail-case caddisflies described by Müller in 1885 as helicopsychids with long wings and antennae. The genus was named without a formal species description after the reallocation of *Tetonema clarum* Ulmer [=*Cochliopsyche clara* (Ulmer)] and the subsequent description of three species by Flint (*C. lobata* Flint, *C. opalescens* Flint and *C. vazquezae* Flint) during the 1990s. After 12 years and a revision of the family, *Cochliopsyche* was positioned as a subgenus under *Helicopsyche* von Siebold. In 2003 the subgenus was revised, including the description of 12 species, then, after 19 years, a new species (*C. nyurga* Oláh & Oláh) was described. Lastly, *Cochliopsyche* was restored to genus level under a phylogenetic framework. Now, it comprises 17 species distributed from southern Mexico to southern Uruguay. Species in this genus are difficult to distinguish due to their similar genitalia morphology. In addition, several biodiversity knowledge shortfalls are related to the group, especially Linnean and Wallacean. This study aims to carry out a systematic revision of *Cochliopsyche*, with the description of five new species and new distribution records. In addition, a standardized description of the genus, with illustrations of all species and identification keys for Neotropical helicopsychid genera and *Cochliopsyche* species are included. *Cochliopsyche mulleri* **sp. n.**, *C. kjelli* **sp. n.,** *C. maierae* **sp. n.,** *C. uwape* **sp. n.** and *C. boraceia* **sp. n.** are described and illustrated, expansion of distributional ranges and new records for three species for Brazil (*C. chocoensis* Johanson, *C. ocosingua* Johanson, and *C. puyoa* Johanson) are presented. This paper addresses the biodiversity knowledge shortfalls in terms of knowledge of species (Linnean shortfall) and distribution (Wallacean shortfall), making it easier to identify the species in the group by providing an identification key and a detailed description of its species.

Keywords. Aquatic insects, biodiversity shortfalls, new species, Sericostomatoidea, taxonomy

Introduction

Helicopsychidae Ulmer, 1906 is a family of caddisflies characterized by the fact that the larvae build helicoidal, snail shell-like cases (Johanson, 1998). There are currently 304 valid species, grouped in three genera (Morse 2023): *Cochliopsyche* Müller, 1885, with 17 valid species endemics to the Neotropical region (Pereira & Calor, *in prep*.), *Helicopsyche* von Siebold, 1856 with 286 species distributed in all biogeographic regions except Antarctica, with the greatest diversity found in the tropics (Johanson, 1997), and *Rakiura* McFarlane, 1973, a monotypic genus endemic to New Zealand (Johanson, 1997).

Taxonomic studies on Helicopsychidae initiated by description of species in pulmonated mollusk like the misinterpretation of a larval case from the XIX century (Johanson et al., 2017). *Paludina lustrica* Say, 1821 [now synonym of *Helicopsyche* (*Feropsyche*) *borealis* (Hagen, 1861)] was described based on the larval case in the genus *Paludina* Férussac, 1812, a group of pulmonated mollusks (Johanson, 1998). Subsequently, some authors treated the species as *Amnicola lustrica* (e.g., Haldeman, 1840), another pulmonated mollusk (Fischer 1970). Only in 1856, three species of *Helicopsyche* were described based on larvae, *H. shuttleworthi* von Siebold, 1856, *H. minima* von Siebold, 1856, and *H. colombiensis* von Siebold, 1856, as caddisflies.

Later, Hagen (1864; 1865; 1866) transferred four other species (*Notidobia borealis* Hagen, 1961, *Notidobia lutea* Hagen, 1961, *Phryganea helicoidella* Vallot, 1855, *Thelidomus brasiliensis* Swainson, 1840) to *Helicopsyche*. This error was clarified with the publication of *Genera Insectorum* by Ulmer (1907), where the genus was finally recognized as belonging to the order Trichoptera (Johanson, 1998).

Cochliopsyche was described based on the helicoidal shaped larval cases and recognized as a helicopsychid by Müller (1885), and differenciated from its congeners based on adult characters (Müller, 1885). The adults have exceptionally long, delicate, multi-segmented antennae and a tibial spur formula 1,1,2, two features that distinguish them from the other Helicopsychidae (short antennae and tibial spur formula 2,2,4 or 1,2,4) (Johanson, 2003).

Ulmer (1912) described the first fossil species to the family from Baltic amber dating to the late Eocene. Two monotypic new genera, *Electrohelicopsyche* Ulmer, 1912 and *Paleohelicopsyche* Ulmer, 1912, and two *Helicopsyche* species (*Helicopsyche confluens* Ulmer, 1912 and *Helicopsyche typica* Ulmer, 1912) were assigned to the family based on wing venation and the reduced number of palpomeres (Ulmer, 1912).

Later, *Rakiura* was described from New Zealand with a unique species, *R. vernale* McFarlane, 1973. The restricted distribution led to the hypothesis that the species could be a remnant from the glacial age that was able to survive in cold springs at an inadequate latitude (Michaelis, 1973).

The fourth extant genera, *Cochliophylax* Schmid, 1993, was described by Schmid (1993). The author described 12 species of *Cochliophylax* and 16 species of *Helicopsyche*, from India, Nepal, and Ceylon (Schmid, 1993). In addition, morphological, phyletic, and zoogeographical considerations were made about the family, and *Cochliophylax* was presented as a sister group to all other helicopsychid genera (Schmid, 1993).

Johanson (1995) published the first world catalogue of the Helicopsychidae, which included 168 species in the four extant (*Cochliophylax*, *Cochliopsyche*, *Helicopsyche* and *Rakiura*), and the two known fossil genera (*Palaeohelicopsyche*

Ulmer, 1912 and *Electrohelicopsyche* Ulmer, 1912). Further fossil species from Dominican amber and from the Miocene were later described by Johanson & Wichard (1996). Then, Johanson (1998) published a systematic and zoogeographical work that established the group's knowledge base for extant and fossil taxa of Helicopsychidae.

Cochliophylax and *Cochliopsyche* were synonymized under *Helicopsyche* by Johanson (1998), who proposed six subgenera for *Helicopsyche* [*H.* (*Cochliopsyche*), *H.* (*Feropsyche*), *H.* (*Galeopsyche*) Johanson, 1998, *H.* (*Helicopsyche*) von Siebold, 1856, *H.* (*Petrotrichia*) Ulmer, 1910 and *H.* (*Saetotrichia*) Brauer, 1865]. In this paper, a single, non-type species of the *Cochliopsyche* was considered, *C. vazquezae*. In addition, the species from Dominican amber were positioned in the Neotropical subgenus *H.* (*Feropsyche*), besides the phylogenetic framework (Johanson, 1998).

After that, many extant species have been described (e.g., Mey & Freitag, 2019; Oláh & Oláh, 2022; Bonfá-Neto et al., 2023), some fossil species and a new fossil genus (Wichard, 2013; Wichard et al., 2018). These extant species were generally classified in subgenera, but the three fossil *Helicopsyche* species were not classified in subgenera (Morse, 2023).

Johanson et al. (2017) implemented a phylogenetic and biogeographic study on Sericostomatoidea, with the relationships among the Helicopsychidae species diverging from the previous hypotheses. Besides the limited taxon sampling, the topology presented a clade with the Neotropical species of the family.

Pereira & Calor (*in prep.*) implemented a phylogenetic study using a broad taxon sampling of *Cochliopsyche* to understand the species relationships of this genus and the other Helicopsychidae, as well as proposed a biogeographic hypothesis. As a result, *Cochliopsyche* was resurrected to genus level, and the terminal taxa were presented as putative new species. In addition, the need for a comprehensive revision of *Helicopsyche* subgenera was suggested because they weren't recovered as monophyletic groups (Pereira & Calor, *in prep*.).

Cochliopsyche is endemic to the Neotropical region and distributed from southern Mexico to southern Uruguay, with 17 valid species (Holzenthal & Calor, 2017; Olah & Olah, 2022). Adults can be distinguished by the formula of the tibial spurs 1,2,2 and by the antennae longer than the body (Johanson, 2003). All species are known from adult males, females are only known for 11 species [only *Cochliopsyche clara* (Ulmer, 1905) has a description and illustrations of the female genitalia], and only one species have its immature stages described (*Cochliopsyche vazquezae* Flint, 1986).

The species identification of *Cochliopsyche* is considered a difficult task because they show slight variations in male genitalia, wing length, color and pattern (Johanson, 2003). After Johanson's (2003) revision, the taxonomic knowledge of *Cochliopsyche* stagnated, without new species descriptions or assignment of immature stages, except for the description of *C. nyurga* and some new distribution records (e.g., Souza et al. 2013; Desidério et al. 2017).

This study provides a systematic review of the genus *Cochliopsyche,* presenting characters to facilitate the diagnosis, delimitation, and identification of known and new species. It also presents new distributional records (localities and freshwater ecoregions), altitudinal distributional ranges and morphological variations of species. All this with the aim of facing the biodiversity knowledge shortfalls of this group.

Material and methods

The material analyzed includes 976 specimens from the Museu de História Natural da Universidade Federal da Bahia (UFBA, 544 specimens); Instituto Nacional de Pesquisa da Amazônia, Manaus, Amazonas, Brazil (INPA, 381 specimens); Museum of Comparative Zoology, Harvard University (MCZ, 11 specimens); University of Minnesota Insect Collection, St. Paul, Minnesota (UMSP, 22 specimens); National Museum of Natural History, Washington (NMNH-USNM, 18 specimens). Distributional records are presented to ecoregions *sensu* Abell et al. (2008), and more precise as possible for Brazil.

The morphological terminology for male adults was herein proposed as presented in Figure 1. The collection, preparation and examination methods of the species followed Calor & Mariano (2012), Blahnik et al. (2007) and Blahnik & Holzenthal (2004), respectively. The illustrations were made using a microscope equipped with a camera lucida and then edited and finalized in Adobe Illustrator CS6 ®.

The localities of the holotypes and type series are given in each description in the section ‘Material analyzed’. In the present study, a comprehensive description of all described and undescribed species is provided, aiming to avoid errors in species identification due to the high degree of similarity of genitalia. These descriptions were created using the DELTA software (Coleman et al. 2010). The taxonomic keys were created using the *Intkey* package for DELTA (Coleman et al. 2010) aiming to increase the consistency and accuracy of the keys, and manual adjusts were made to avoid redundances.

Abbreviations for institutions: **INHS:** Illinois Natural History Survey, Champaign, Illinois, USA; **INPA:** Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil; **MCZ:** Museum of Comparative Zoology, Harvard University, Cambridge, USA; **MNRJ:** Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **MVC:** Maracay Venez private collection, Macay, Venezuela; **MZUSP:** Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; **USNM (NMNH):** National Museum of Natural History, Washington, D.C., USA; **UFBA:** Museu de História Natural da Bahia, Universidade Federal da Bahia, Bahia, Brazil; **UMSP:** University of Minnesota Insect Collection, St. Paul, Minnesota, USA.

Abbreviations for countries: **ARG**: Argentina; **BOL**: Bolivia; **BRA**: Brazil; **COL**: Colombia; **ECU**: Ecuador; **GUY**: Guyana; **MEX**: Mexico; **PER**: Peru; **PRY**: Paraguay; **SUR**: Suriname; **URY**: Uruguay; **VEN**: Venezuela.

Abbreviations for States of Brazil: **AM**: Amazonas; **BA**: Bahia; **MG**: Minas Gerais; **MT**: Mato Grosso; **PA**: Pará; **PE**: Pernambuco; **PR**: Paraná; **RO**: Rondônia; **SC**: Santa Catarina; **SP**: São Paulo.

Results

Systematics

Family Helicopsychidae Ulmer, 1906

Genus *Cochliopsyche* Müller, 1885

Type species: *Cochliopsyche clara* (=*Tetanonema clarum*) (Ulmer, 1905)

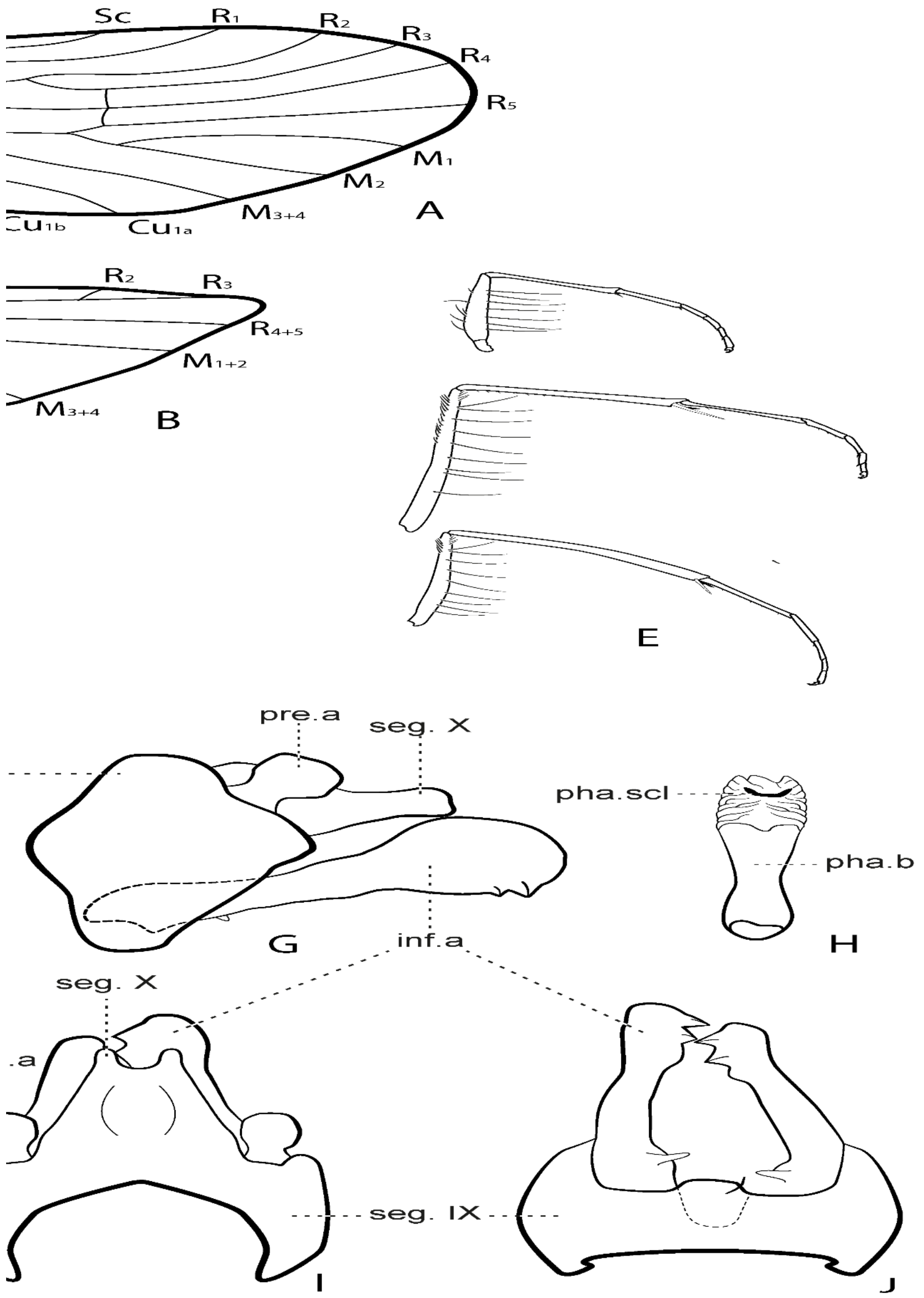

Figure 1. *Cochliopsyche* schematic illustration of wings, head, thorax, and genital characters. A. Forewing; B. Hind wing; C. Head, lateral view; D. Head and thorax, dorsal view; E. Legs, lateral view; F. Abdominal sternum VI; G. Genitalia, lateral view; H. Phallus, ventral view; I. Genitalia, dorsal view; J. Genitalia, ventral view. Abbreviations: Sc = Subcostal vein; R1-5 = Radial veins; M1-4 = Medial veins; Cu1-2 = Cubital veins; A1+2 = Anal vein 1+2; D = Discoidal cell; M = Median cell; T = Thyridial cell; fla = flagellomere; ped = pedicel; sca = scape; fro.w = frontal wart; cep.w = cephalic warts; poc.w = posterocular warts; max.p. = maxillary palp; lab.p. = labial palp; pro = pronotum; pro.w = pronotum warts; mes = mesonotum; mes.p.b. = mesonotum pale band; mss = mesoscutum; mss.w = mesoscutal warts; a.s. VI = abdominal sternum VI; p.a.s. VI = process of abdominal sternum VI; seg. IX = abdominal segment IX; seg. X = abdominal segment X; inf.a = inferior appendage; pha.b = phallobase; pha.scl. = phallotremal sclerite.

Diagnosis of genus <u>Cochliopsyche</u>

The species of this genus can be differentiated from others Helicopsychidae' genus by set of characters (characters from other genera are presented in parentheses):

1. Antennae more than 1.2–3x body length (versus antennae less than 1.2x body length)

2. Tibial spurs formula 1,2,2 (versus tibial spurs formula 2,2,4 or 1,2,4)

Description of genus <u>Cochliopsyche</u>

Larva. see Monson et al. (1988:154).

Larval case. see Monson et al. (1988:154).

Pupa. see Monson et al. (1988:154).

Adult. Forewing length 5–7.5 mm (median 6.05 mm, n = 30); forks I, II, III and V present; discoidal, medial, thyridial cells closed (Figure 1A). Hind wing length 3.2–4.8 mm (median 3.6 mm, n = 30), slightly pointed; forks I and V present; discoidal cell open (except in *C. pandeirosa*); medial and thyridial cells closed (Figure 1B). Head. Antennae more than 1.2–3x body length, scape bearing long setae, barrel shaped (Figure

1C), antennomeres 4x longer than thick. Cephalic warts ovoid with long setae, covering almost all dorsum of head (Figure 1D). Postocullar warts half-moon shaped, bearing long setae (Figure 1D). Maxillary palps 2-segmented, distal article 1.5–2x the length of basal article, with long setae (Figure 1C). Labial palps 3-segmented, with long setae (Figure 1C). Thorax. Pronotum with a pair of long, oval setal warts, with long setae (Figure 1D). Mesoscutum diamond-shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts, bearing long setae (Figure 1D). Legs tibial spur formula 1,2,2 (Figure 1E). Abdomen. Abdominal sternum VIth process generally present (Figure 1F).

Male genitalia (Figure G–J). Abdominal segment IX longer compared to abdominal segment VIII, without marginal or lateral horizontal thickening. Abdominal segment X large and long with lateral and apical projections; posteromedian evagination and in with sets of setae. Preanal appendages generally developed and globose. Inferior appendages simplified, consisting of a large anterior branch in a globose posterior region with sinuous, sometimes with teeth. Phallic apparatus small, tubular, generally with sclerite and without parameres.

Female genitalia. See Johanson (2003:386).

Distribution. The genus is currently made up of 17 species, and this study added the description of five more species, making a total of 22 species (Table 1). All males of the species are known and described, 11 species have known females, but only one species has larva, pupa and case described. The species are distributed from southern Mexico (Grijalva - Usumacinta freshwater ecoregion) to southern Uruguay (Lower Uruguay freshwater ecoregion). The distribution is restricted to the Brazilian subregion of the Neotropical region and is present in practically all freshwater ecoregions included in this subregion. The species altitudinal range is 5–2,121 m a.s.l. with records in 1st to

9th order freshwater environments. *Cochliopsyche* inhabit snail-like case and show a typically curled pupal abdomen (like other Helicopsychidae) (Flint, 1983). Adults are usually attracted to lights near large rivers and streams in lowland areas, which seems to be the preferred habitat of the genus (Flint, 1983).

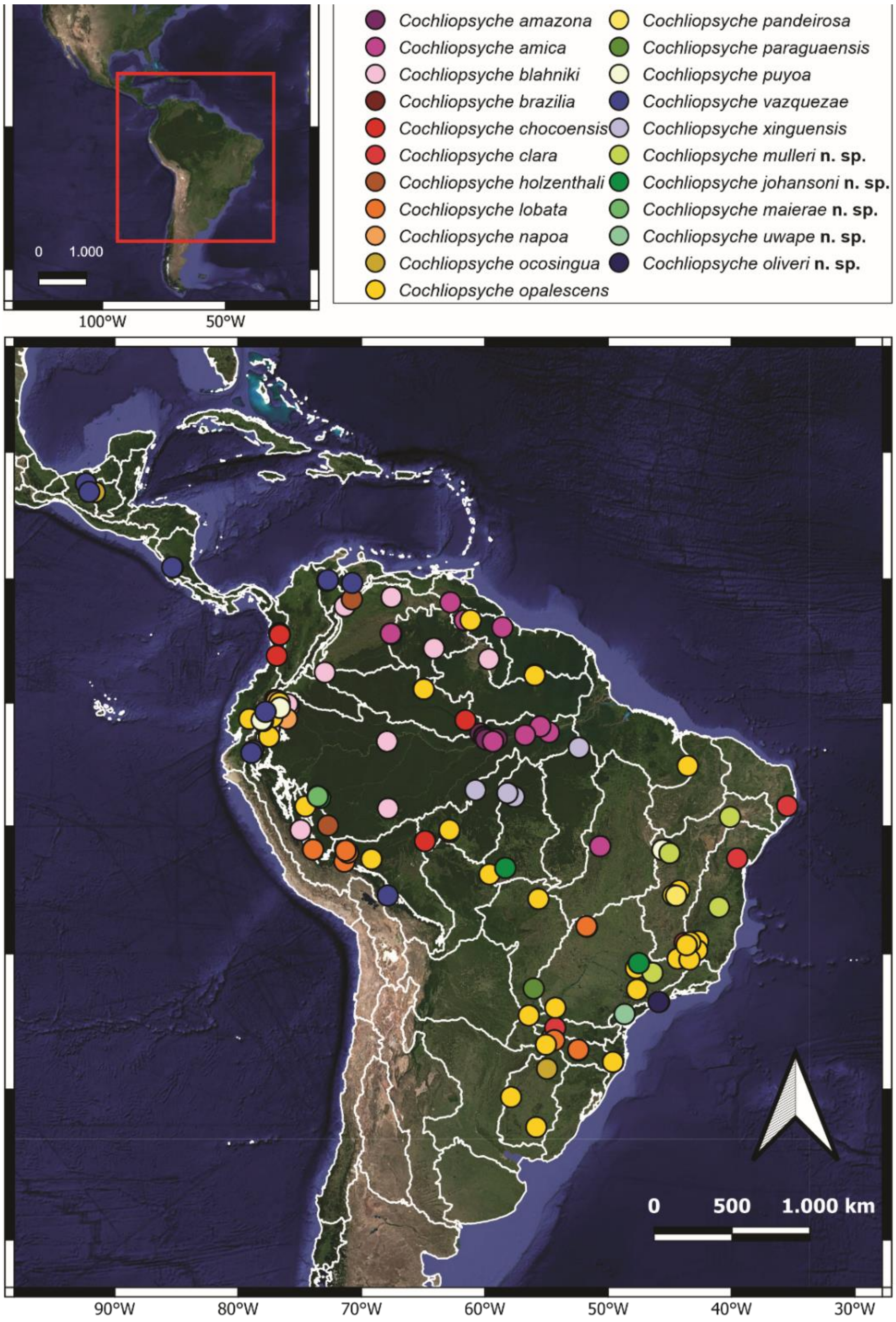

Figure 2. Distribution map of *Cochliopsyche* species in freshwater ecoregions of the Neotropical region.

Table 1. *Cochliopsyche* species, known semaphoronts, collections with deposited material and known distribution. KS = Known semaphoronts; ♂ = Male; ♀ = Female; L = Larvae; P = Pupa; *known semaphoronts, but not formally described; New distributional records in bold.

Species	KS	Collections	Known distribution
C. amazona Johanson, 2003	♂	USNM, NRM	BRA (AM)
C. amica Johanson, 2003	♂, ♀*	MVC, USNM, ISNB, MCZ	BRA (AM, PA, **TO**), GUY, VEN
C. blahniki Johanson, 2003	♂, ♀*	UMSP, CIUC, FMNH, MVC, USNM NRM	BRA (AM, **RO**), COL, ECU, GUY, PER, VEN
C. brazilia Johanson, 2003	♂, ♀*	MZUSP, USNM, MRM	BRA (MG)
C. chocoensis Johanson, 2003	♂, ♀*	USNM	**BRA (AC, AM, RO)**, COL
C. clara (Ulmer, 1905)	♂, ♀	MCZ, MZUSP, UMSP, USNM	ARG, BRA (AM, **BA**, MG, PE, SC, **SP**), ECU
C. holzenthali Johanson, 2003	♂, ♀*	UMSP, USMN	VEN
C. lobata Flint, 1983	♂	MCZ, MZUSP, UMSP, USNM	ARG, BRA (DF, **GO**, MG, SC) PER
C. napoa Johanson, 2003	♂, ♀*	USNM, USNM	ECU
C. ocosingua Johanson, 2003	♂, ♀*	INHS, NRM	**BRA (RS)**, MEX
C. opalescens Flint, 1972	♂	FNMH, MZUSP, UMSP, USNM	ARG, BRA (AM, **BA**, MA, MG, MT, PA, PR, RO, RR, SC, SP), ECU, GUY, PAR, PER, SUR, URU, VEN
C. pandeirosa Johanson, 2003	♂, ♀*	MZUSP, UMSP, NRM, USNM	BRA (MG)
C. paraguaiensis Johanson, 2003	♂	USNM	PAR
C. puyoa Johanson, 2003	♂, ♀*	USNM, UMSP	**BRA (BA)**, ECU
C. vazquezae Flint, 1986	♂, L, P, C	INHS, UMSP, USNM	BOL, COR, ECU, MEX, VEN
C. xinguensis Johanson, 2003	♂, ♀*	MZUSP, USNM, UMSP	BRA (AM, PA)
C. mulleri **n. sp.**	♂	MZUSP, UFBA	BRA (BA, MG, MT)
C. kjelli **n. sp.**	♂	MZUSP, UFBA	BRA (AC, MT, SP)

C. maierae **n. sp.**	♂	MZUSP, UFBA	BRA (AC)
C. uwape **n. sp.**	♂	MZUSP, UFBA	BRA (SP)
C. boraceia **n. sp.**	♂	UMSP	BRA (SP)

Phylogenetic relationships.

According to Pereira et al. (*in prep*) *Cochliopsyche* forms a monophyletic group, with the sister group *H*. (*Petrotrichia*) (Afrotropical group). Among the groups most closely related to this clade are *H*. (*Galeopsyche*) (Oriental group) and *H*. (*Helicopsyche*) (Western Palearctic group) with low support. The origin of Helicopsychidae was inferred to the Gondwana (late Jurassic, ~157 Ma). With the split between the stem group of *Cochliopsyche* and *H*. (*Petrotrichia*) around 104 Ma, seafloor spreading between Africa and South America began at 130 Ma (Veevers 2012) and may have maintained the continental connections or proximity of southern Africa and South America until ~105 Ma (McLoughlin 2001).

Cochliopsyche mulleri **n. sp. Pereira & Calor**

(Figure 3)

–Pereira & Calor, *in prep* [as *Cochliopsyche* sp. 1].

Diagnosis. The species can be differentiated from congeners by the following set of male characters: (i) abdominal segment X subquadrangular with a long and very shallow apical U-shaped invagination; (ii) inferior appendages with wide rounded median projection towards abdominal segment X, in dorsal view (Figure 3G); and (iii) apex of inferior appendages rounded with two pointed, subapical teeth on the inner face, in ventral view (Figure 3H).

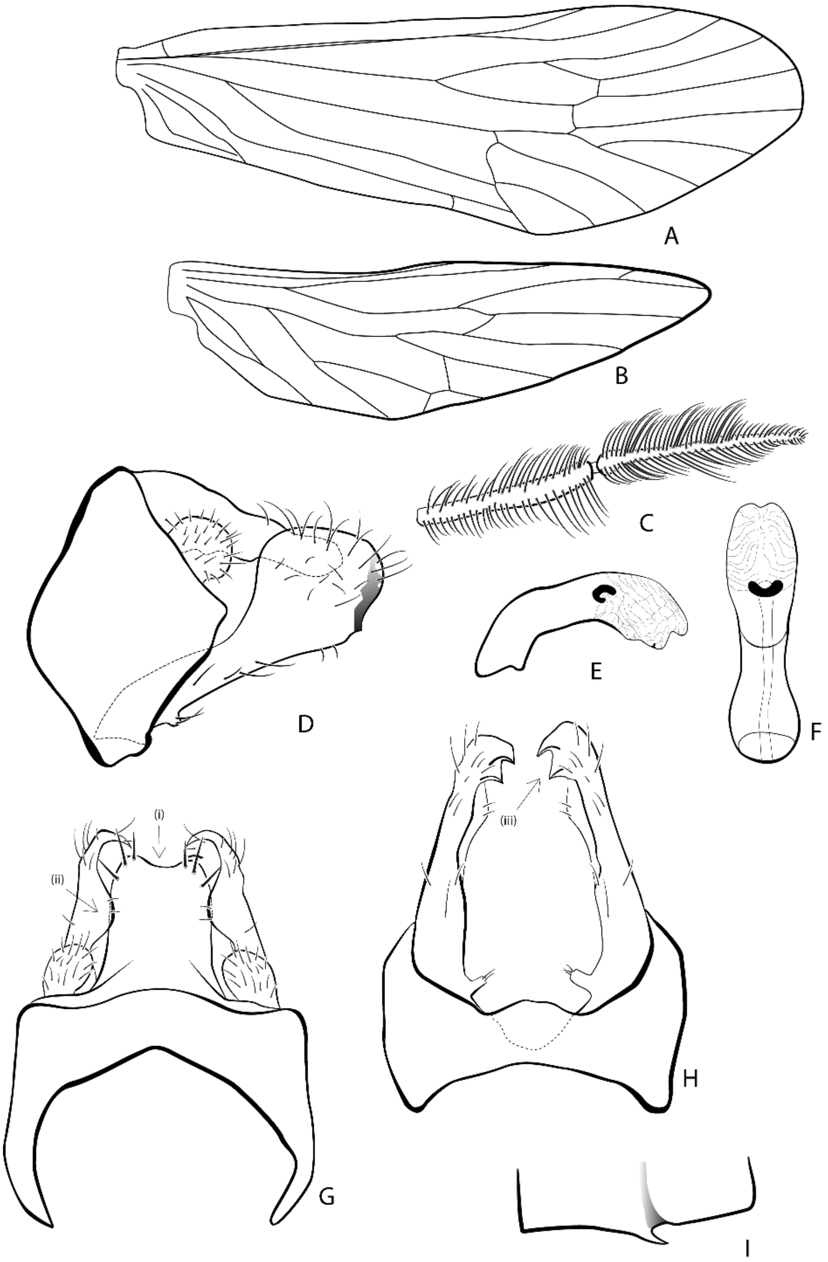

Figure 3. *Cochliopsyche mulleri* **n. sp.**: Male, A. Forewing; B. Hind wing; C. Maxillary palp; D. Genitalia, lateral view; E. Phallus, lateral view; F. Phallus, ventral view; G. Genitalia, dorsal view; H. Genitalia, ventral view; I. Abdominal segment VI, lateral view. Diagnostic characters indicated with arrows.

The new species is similar to *C. holzenthali* and *C. paraguaiensis* by having inferior appendages with long and narrow proximal region, in lateral view (Figure 3D), and apex rounded with two subapical teeth on the inner face, in ventral view (Figure 3H). But the new species can be distinguished from these congeners by the presence of abdominal segment X with wide and shallow apical invagination, in dorsal view (Figure 3G) (short and deep apical invagination in *C. holzenthali* and without apical invagination in *C. paraguaiensis*); and the inferior appendages rounded median projection towards abdominal segment X, in dorsal view (Figure 3G) (finger-shaped median projections towards abdominal segment X in *C. holzenthali* and without median projection in *C. paraguaiensis*).

Description. Forewing length 6.2–6.7 mm (n = 5); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 3A). Hind wing length 3.1–3.8 mm, slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 3B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts covering almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint more than 2x basal joint length, with long setae (Figure 3C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond-shaped, with a pair of longitudinal subtriangular pale bands with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur formula 1,2,2. Abdomen. Abdominal sternum VI process small (Figure 3I).

Male genitalia. Abdominal segment IX anterior lobe rounded, positioned ventrally on segment, anterodorsal and anteroventral margins substraight with posterobasally acuminated slightly projected, in lateral view (Figure 3D). Posterior lobe acuminated, positioned midway on segment, without set of setae, in lateral view (Figure 3D); anterior margin concave, central posterior lobe convex, and basal plate U-shaped, in ventral view (Figure 3H). Preanal appendages globose, in lateral view (Figure 3D); thumb-shaped, in dorsal view (Figure 3G). Abdominal segment X digitiform with sinuous margins, apex rounded with setae, in lateral view (Figure 3D); subquadrangular with lateral margins substraight, rounded apical projections and a long and very shallow apical invagination U-shaped, in dorsal view (Figure 3G). Inferior appendages pipe shaped, proximal region subquadrangular shaped, length 2.2x width, distal region ovoid, same length and width, with anteroventral projection finger-shaped well-projected, and a posteroventral projection present, slightly and subtriangular with sclerotized area, in lateral view (Figure 3D); base slightly wide than apex, with basomesal setose projections, and two subapical teeth sclerotized and apex rounded, in ventral view (Figure 3H); with inner face median projection rounded, in dorsal view (Figure 3E). Phallus with phallobase calyx-shaped, wide base, with a median constriction and slightly widening towards apex, and with a small phallotremal sclerite U-shaped in lateral and ventral views (Figures 3E; F).

Holotype. 1 #Male, Brazil: Bahia, Barreiras, Pousada Buritis, Rio de Ondas (-2.146666, -45.016972), 15.X.2008, Luz, Calor, A., Matheus, S. & Mariano, R. [MZUSP].

Paratypes. same holotype data, except 5 #Males Brazil: Bahia, Curaçá, Rio São Franscisco, 06.v.2011, Bandeja, França, D. col. [UFBA]; same data, except 2 #Males, Mato Grosso, Rio Papagaio (-13.32111, -58.33330), 31.x.2012, Hamada, N., Nascimento, J. (cols.) [INPA]; same data, except 3 #Males, Minas Gerais, Cabo Verde, Pedregol (-21.4683333, -46.4036111), 02-05.xi.2006, Amorim, D. Falaschi R. & Oliveira, S. (cols.) [UFBA]; 2 #Males, same data, except Jequitinhonha, Córrego Mata Escura (-16.406611, -41.023888), 14.viii.2017, Dias, E. Silva, F. & Campos, R. [UFBA].

Remarks. The new species shows morphological variations in some specimens such as apical invagination of segment X slightly deeper, and inner median face projections less developed, in dorsal view. This species is proposed based on only male known semaphoronts, with distribution records in Northeastern Mata Atlântica, São Francisco, Tapajos - Juruena, and Upper Parana freshwater ecoregions, in altitudinal range from 402–935 m a.s.l., and in 1st, 2nd, and 4th order freshwater environments.

Etymology. The specific name is a tribute in memoriam to the honored German-Brazilian naturalist Johann Friedrich Theodor Müller, better known as Fritz Müller, who was one of the pioneers on Trichoptera studies in Brazil (with publications between 1879 and 1921). Müller made important contributions on other Brazilian fauna and to support the evolution theory, especially with the book *Für Darwin* in 1864 (Papavero, 2003).

Distribution. BRA (BA, MG, MT).

Cochliopsyche kjelli **n. sp. Pereira & Calor**

(Figure 4)

–Pereira & Calor, *in prep* [as *Cochliopsyche* sp. 2].

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subquadrate with lateral and apical margins substraight, except for median apex slightly notched; (ii) inferior appendages with basomesal projections; (iii) proximal region narrow, apex wide globose, with a subapical invagination and two slightly subapical teeth on the inner face, in ventral view (Figure 4H).

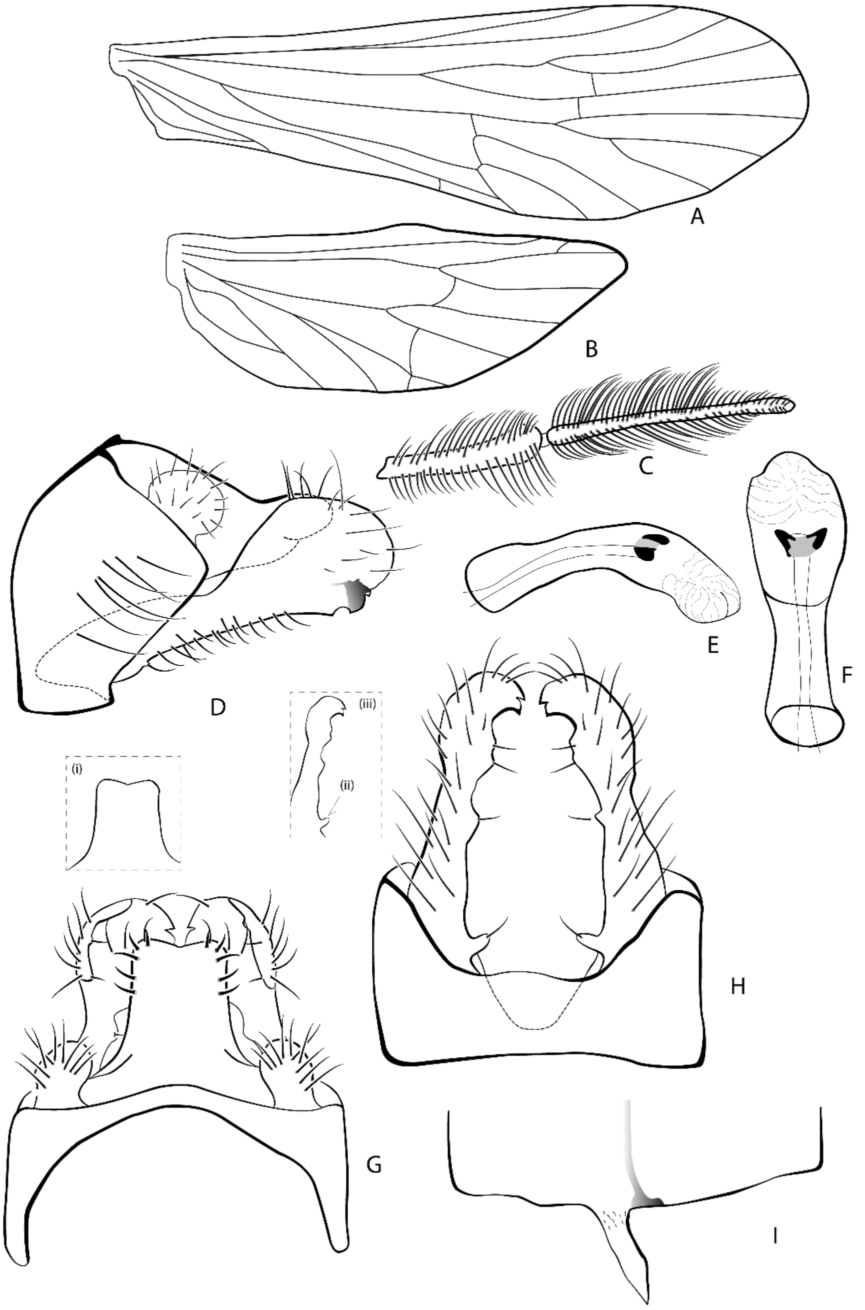

Figure 4. *Cochliopsyche kjelli* **n. sp.**: Male, A. Forewing; B. Hind wing; C. Maxillary palp; D. Genitalia, lateral view; E. Phallus, lateral view; F. Phallus, ventral view; G. Genitalia, dorsal view; H. Genitalia, ventral view; I. Abdominal segment VI, lateral view. Diagnostic characters indicated with dashed lines and arrows.

Cochliopsyche kjelli **n. sp.** is similar to *C. opalescens* and *C. puyoa* by having abdominal segment X subquadrate, in dorsal view (Figure 4G); inferior appendages with long proximal region more than 2 time the width, and distal region ovoid, in lateral view (Figure 4D). The new species can be distinguished from these species by the presence of abdominal segment IX with anterior lobe unprojected, in lateral view (Figure 4D) (with anterior lobe acuminated and projected in *C. opalescens* and *C. puyoa*); and the inferior appendages with, a subapical invagination and two slightly subapical teeth on the inner face, in ventral view (Figure 4H) (without, a subapical invagination and a slightly subapical tooth on inner face in *C. opalescens* and *C. puyoa*).

Description. Forewing length 6.0–6.5 mm (n = 5); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 4A). Hind wing length 2.9–3.8 mm slightly pointed; forks I and V present; discoidal cell opens, medial and thyridial cells closed (Figure 4B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts covering almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal article less than 1.5x basal article length with long setae (Figure 4C). Labial palps 3-segmented, with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond-shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process subtriangular, shorter than 1/3 segment length(Figure 4I).

Male genitalia. Abdominal segment IX anterior lobe unprojected, anterodorsal and anteroventral margins substraight with posterobasal acuminated slightly projected, in lateral view (Figure 4D). Posterior lobe with acuminated projection, positioned dorsally on segment, bearing set of long setae, in lateral view (Figure 4D); anterior margin substraight, central posterior lobe slightly convex, and basal plate U-shaped, in ventral view (Figure 4H). Preanal appendages boxing gloves shaped, in lateral view (Figure 4D); thumb-shaped, in dorsal view (Figure 4G). Abdominal segment X subtriangular with smooth margins, apex rounded with setae, in lateral view (Figure 4D); subquadrangular with lateral margins substraight, and a very short and shallow apical cleft, in dorsal view (Figure 4G). Inferior appendages club-shaped; proximal region subquadrangular, length 2.5x width; distal region ovoid, length 1.3x width, with anteroventral projection finger-shaped, posteroventral projection small, subtriangular, with sclerotized area, in lateral view (Figure 4D); base wider than apex, base with basomesal setose projections, inner face with setose median and subapical projections, , apex bent inwards, with two small apical teeth in ventral view (Figure 4H). Phallus with phallobase calyx-shaped, narrow base, with a median constriction and widening towards apex, and with a small bifid phallotremal sclerite V-shaped (Figures 4E; F).

Holotype. 1 #Male, Brazil, Acre, Mâncio Lima, P. N. Serra do Divisor, Igarapé da Cobra (-7.57722222, -73.573611), 18.iii.2006, Calor, A. col. [MZUSP].

Paratypes. same holotype data, except 2 #Males [UFBA]; same data, except 3 #Males Mato Grosso, Rio Papagaio, 31.x.2012, Hamada, N. & Nascimento, J. (cols.) [INPA]; same data, except 2 #Males São Paulo, Restinga, Fazenda Conquista (20°43’28”S, 47°30’56”W, 663 m a.s.l., 21.iii.2008, Amorim, D., Rafael, J.A., Falaschi, R. & Capellari, R. (cols.)

Remarks. The new species shows morphological variations in some specimens such as basomesal projections of inferior appendages with apex rounded or truncated. This species is proposed based only on male known, and presents distribution records in Amazonas Lowlands, Tapajos - Juruena, and Upper Parana freshwater ecoregions, in altitudinal range from 217–699 m a.s.l., with records in 1st to 7th order freshwater environments.

Etymology. The specific name is a tribute to the honored Swedish trichopterologist Dr. Kjell Arne Johanson, who has laid the foundation for currently knowledge of Helicopsychidae (Johanson, 1997; 1998 2002; 2003).

Distribution. BRA (AC, MT, SP).

Cochliopsyche maierae **n. sp. Pereira & Calor**

(Figure 5)

–Pereira & Calor, *in prep* [as *Cochliopsyche* sp. 3].

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subrectangular with lateral margins substraight, apex rounded with apical cleft, in dorsal view (Figure 5G); (ii) inferior appendages long, narrow with inner face sinuous, a subapical invagination and two small apical teeth, in ventral view (Figure 5H). *Cochliopsyche maierae* **n. sp.** is similar to *C. nyurga* and *C. paraguaensis* by having abdominal segment X with lateral margin substraight, in dorsal view (Figure 5G); inferior appendages long and narrow, and inner face with a small projections and with two apical teeth, in ventral view (Figure 5H).

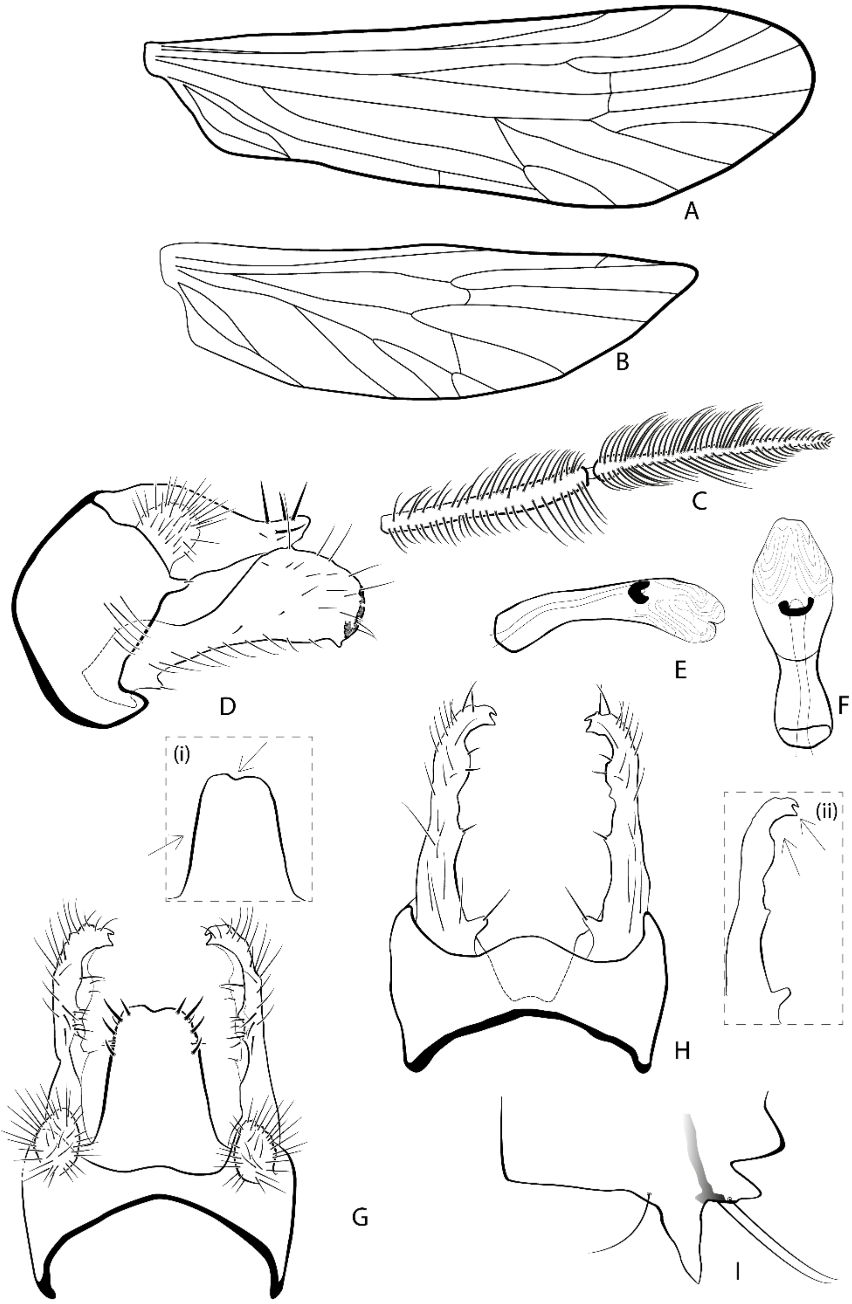

Figure 5. *Cochliopsyche maierae* **n. sp.**: Male, A. Forewing; B. Hind wing; C. Maxillary palp; D. Genitalia, lateral view; E. Phallus, lateral view; F. Phallus, ventral view; G. Genitalia, dorsal view; H. Genitalia, ventral view; I. Abdominal segment VI, lateral view. Diagnostic characters indicated with dashed lines and arrows.

But the new species can be distinguished from these species by the presence of abdominal segment X subrectangular, apex rounded with shallow apical cleft, in dorsal view (Figure 5G) (with abdominal segment X subrectangular, apex truncated without cleft in *C. nyurga* and with abdominal segment X subquadrate, apex rounded with small apical cleft in *C. paraguaensis*); and the inferior appendages with inner face margins sinuous with small projections, in ventral view (Figure 5H) (with inner face margins non sinuous and a median subtriangular projection in *C. nyurga* and face margins non sinuous with two median subtriangular projections in *C. paraguaensis*).

Description. Forewing length 5.8–6.4 mm (n = 3); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 5A). Hind wing length 2.8–3.3 mm slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 5B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covering almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint shorter than 1.5x basal joint length, with long setae (Figure 5C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond-shaped, with a pair of longitudinal subtriangular pale bands with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur formula 1,2,2. Abdomen. Abdominal sternum VI process subtriangular, shorter than 1/3 segment length (Figure 5I).

Male genitalia. Abdominal segment IX anterior lobe rounded positioned midway on segment, anterodorsal and anteroventral margins substraight with posterobasally rounded well-projected, in lateral view (Figure 5D). Posterior lobe with acuminated projection, positioned dorsally on segment with set of long setae, and posterior finger shape projection, in lateral view (Figure 5D); anterior margin concave, central posterior lobe convex, and basal plate W-shaped, in ventral view (Figure 5H). Preanal appendages globose, in lateral view (Figure 5D); pyriform, in dorsal view (Figure 5G). Abdominal segment X subtriangular, with sinuous dorsal and ventral margins, and a small anterodorsal projection, apex acuminated with setae, in lateral view (Figure 5D); subrectangular with lateral margins substraight, and a very short and shallow apical cleft, in dorsal view (Figure 5G). Inferior appendages club-shaped, proximal region subquadrangular, length 1.8x width, distal region ovoid, length 1.5x width, with anteroventral projection finger-shaped, well-projected, and a posteroventral projection present, small and subtriangular with sclerotized area, in lateral view (Figure 5D); base wide narrowing to apex, base with basomesal setose projections, inner face with setose median and subapical projections, apex bent inwards and with two small apical teeth, in ventral view (Figure 5H). Phallus with phallobase calyx-shaped, wide base, with a median constriction and widening towards apex, and with a broad phallotremal sclerite U-shaped (Figures 5E; F).

Holotype. 1 #Male, Brazil, Acre, Mâncio Lima, P. N. Serra do Divisor, Igarapé Amor, Calor, A. [MZUSP].

Paratypes. same holotype data, except 3 #Males [UFBA].

Remarks. This species is proposed based on only male, and presents distribution records in Amazon Lowlands freshwater ecoregion, in altitudinal range around 251 m a.s.l. with records in 2nd order freshwater environments.

Etymology. The specific name is a tribute to the honored North American entomologist Dr. Crystal A. Maier, Curatorial Associate of the Entomology Collection at the Museum of Comparative Zoology, Harvard University, Cambridge, MA. For his help during the visit to the MCZ to analyze the type specimens, which contributed substantially to the content of this work.

Distribution. BRA (AC).

Cochliopsyche uwape n. sp. Pereira & Calor

(Figure 6)

–Pereira & Calor, *in prep* [as *Cochliopsyche* sp. 4]

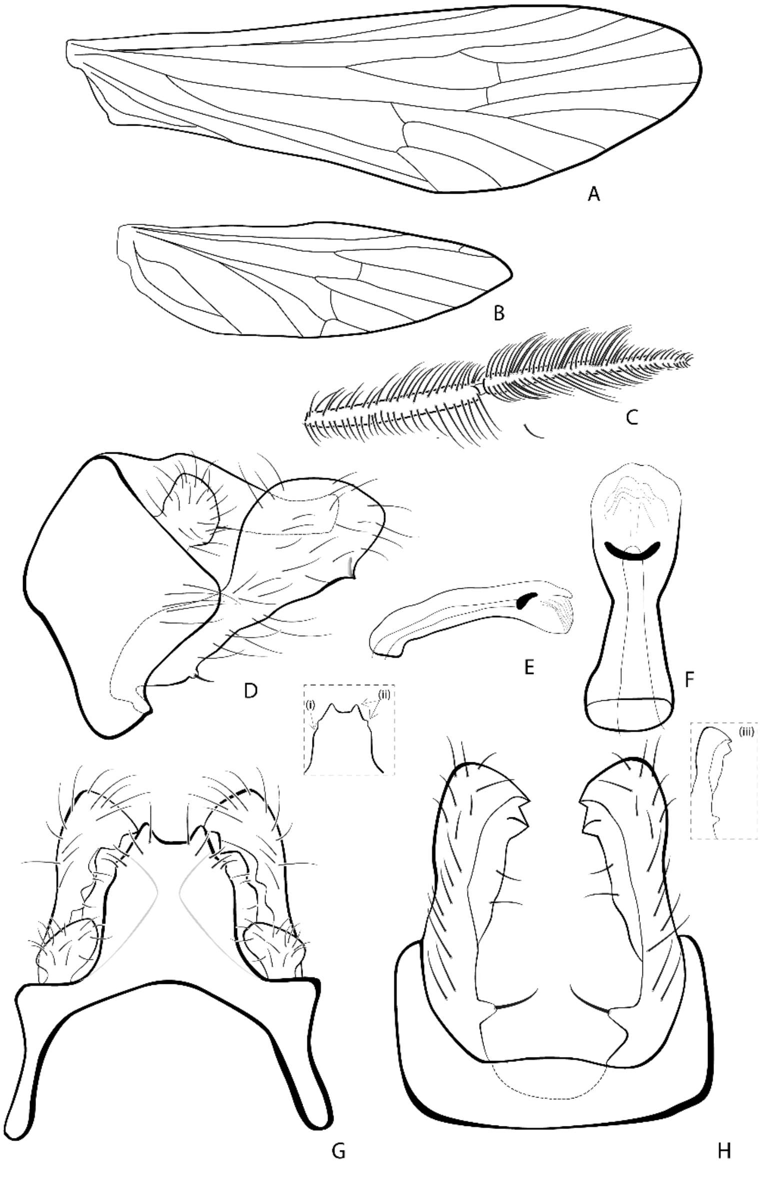

Figure 6. *Cochliopsyche uwape* **n. sp.**: Male, A. Forewing; B. Hind wing; C. Maxillary palp; D. Genitalia, lateral view; E. Phallus, lateral view; F. Phallus, ventral view; G. Genitalia, dorsal view; H. Genitalia, ventral view. Diagnostic characters indicated with dashed lines and arrows.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subquadrate with margins convex; (ii) with two subapical pointed projections and two well-developed lateroapical subtriangular projections, in dorsal view (Figure 6G); and (iii) inferior appendages widening towards the distal region, with inner basomesal projections, ,apex wide, globose and with two inner face small subapical teeth, in ventral view (Figure 6H). *Cochliopsyche uwape* **n. sp.** is similar to *C. opalescens* and *C. kjelli* by having abdominal segment X subquadrate, in dorsal view (Figure 6G); inferior appendages with long proximal region longer than 2x width, and distal region ovoid, in lateral view (Figure 6D). But the new species can be distinguished from these species by the presence of abdominal segment X with a wide and deep invagination, in dorsal view (Figure 6G) (without and with slightly short and shallow invagination, respectively in *C. opalescens* and *C. kjelli*); and inferior appendages with the median region projected mesally, forming a flap, in ventral view (Figure 6H) (without ou with slightly median projection never as a flap in *C. opalescens* and *C. kjelli*).

Description. Forewing length 5.6–6.1 mm (n = 3), forks I, II, III and V present, discoidal, medial, and thyridial cells closed (Figure 6A). Hind wing length 2.8–3.3 mm slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 6B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covering almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 6C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond-shaped, with a pair of longitudinal subtriangular pale bands with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur formula 1,2,2. Abdomen. Abdominal sternum VIth process absent.

Male genitalia. Abdominal segment IX anterior lobe rounded, positioned midway on segment, anterodorsal margin substraight and anteroventral margins slightly concave, in lateral view (Figure 6D). Posterior lobe rounded, positioned midway on segment with set of long setae, in lateral view (Figure 6D); anterior margin slightly convex, central posterior lobe slightly convex, and basal plate U-shaped, in ventral view (Figure 6H). Preanal appendages boxing glove shaped, in lateral view (Figure 6D); boomerang shaped, in dorsal view (Figure 6G). Abdominal segment X subrectangular with smooth margins, with small anterodorsal projection, apex truncated with setae, in lateral view (Figure 6D); subquadrangular with lateral margins convex, subtriangular subapical and lateroapical projections, and a short and deep apical invagination U-shaped, in dorsal view (Figure 6G). Inferior appendages club-shaped, proximal region subquadrangular, length 2x width, distal region ovoid, length 1.2x width, with anteroventral projection finger-shaped, and a posteroventral projection present, small and subtriangular with sclerotized area, in lateral view (Figure 6D); apex wider than base, base with basomesal setose projections, inner face with setose subapical projections, two small subapical teeth, and apex rounded, in ventral view (Figure 6H). Phallus with calyx shaped phallobase, wide base, with a median constriction and widening towards apex, and with a broad phallotremal sclerite U-shaped (Figures 6E; F).

Holotype. 1 #Male, Brazil, São Paulo, Iporanga, PETAR, Rio Betari [MZUSP].

Paratypes. same holotype data, except 3 #Males [UFBA].

Remarks. This species is proposed based on only male. Presents distribution records in Ribeira de Iguape freshwater ecoregion, in altitudinal range around 410 m a.s.l. inhabiting 1st order freshwater environments.

Etymology. U'wape (from the indigenous Tupi-Guarani language, "iguape" in the Portuguese language) has the following spelling and meaning: u'wa = inlet, bay, river basin, lagoon + pe = in, derived from Ribeira do Iguape freshwater ecoregion, where the type locality is located.

Distribution. BRA (SP).

Cochliopsyche boraceia **n. sp. Pereira & Calor**

(Figure 7)

–Pereira & Calor, *in prep* [as *Cochliopsyche* sp. 5]

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subtriangular with lateral margins substraight, in dorsal view (Figure 7G); (ii) abdominal segment X with apical, long and deep evagination U-shaped, in dorsal view (Figure 7G); (iii) inferior appendages with basomesal projections and two inner face subapical teeth, in ventral view (Figure 7H).

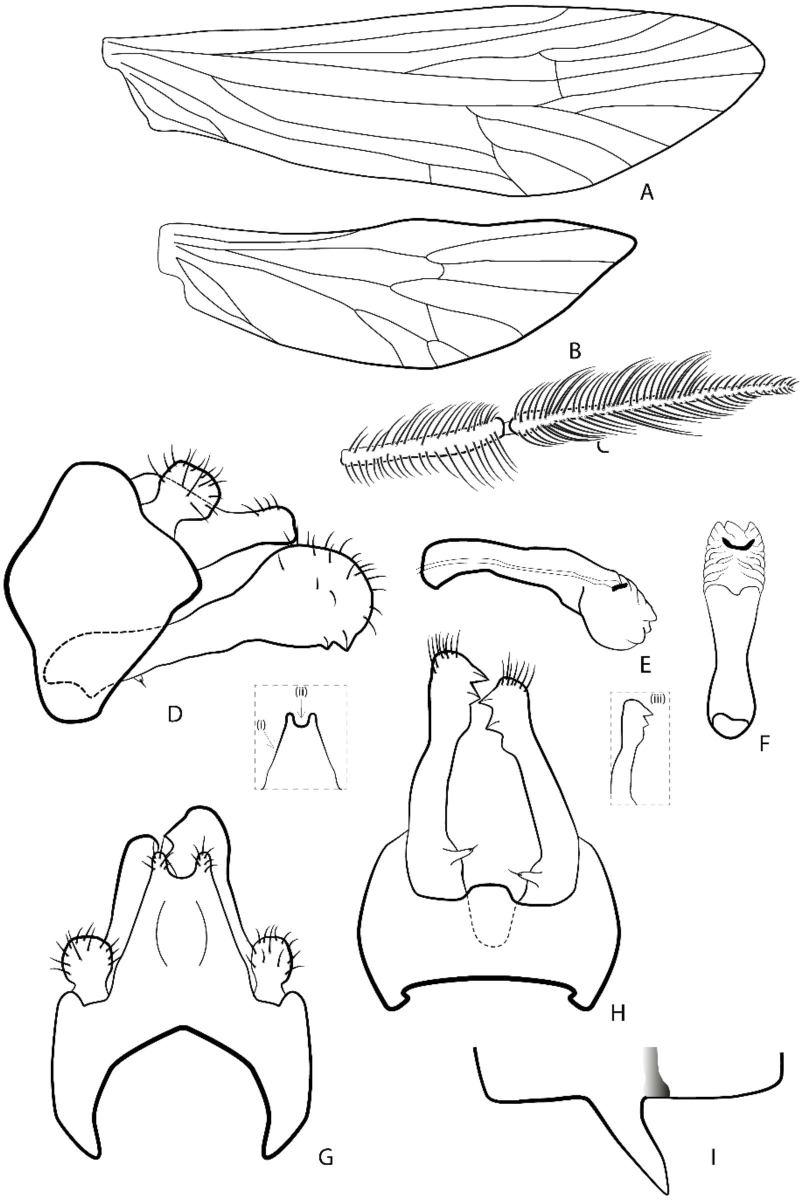

Figure 7. *Cochliopsyche boraceia* **n. sp.**: Male, A. Forewing; B. Hind wing; C. Maxillary palp; D. Genitalia, lateral view; E. Phallus, lateral view; F. Phallus, ventral view; G. Genitalia, dorsal view; H. Genitalia, ventral view; I. Abdominal segment VI, lateral view. Diagnostic characters indicated with dashed lines and arrows.

Cochliopsyche boraceia **n. sp.** is similar to *C. vazquezae* and *C. mulleri* **n. sp.** by having abdominal segment IX with posterior lobe acuminated, in lateral view (Figure 7D);

inferior appendages with apex rounded and two subapical teeth on the ventral margin, in lateral view (Figure 7D). But the new species can be distinguished from these species by the (i) abdominal segment X subtriangular (with abdominal segment X subquadrate in *C. vazquezae* and *C. mulleri* **n. sp.**) and (ii) with apical invagination wide and deep, forming well-projected, rounded apicolateral lobes, in dorsal view (Figure 7G) (with long and shallow apical invagination forming subtriangular slightly projected lobes in *C. vazquezae* and long and shallow apical invagination without lobes in *C. mulleri* **n. sp.**)

Description. Forewing length 4.6–5.5 mm (n = 3); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 7A). Hind wing length 3.05–3.73 mm, slightly pointed; forks I and V present; discoidal cell open; medial and thyridial cells closed (Figure 7B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covering almost all dorsal region of head, ovoid, with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 7C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond-shaped, with a pair of longitudinal subtriangular pale bands with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur formula 1,2,2. Abdomen. Abdominal sternum VI process subtriangular, shorter than 1/3 segment length (Figure 7I).

Male genitalia. Abdominal segment IX anterior lobe rounded, positioned midway on segment, anterodorsal and anteroventral margins slightly concave, in lateral view (Figure 7D). Posterior lobe acuminated, positioned midway on segment, without set of setae, in lateral view (Figure 7D); anterior margin slightly concave, central posterior lobe convex, and basal plate U-shaped, in ventral view (Figure 7H). Preanal appendages boxing glove shaped, in lateral and dorsal views (Figures 7D; G). Abdominal segment X subtriangular with smooth lateral margins, with small anterodorsal projection, apex truncated with setae, in lateral view (Figure 7D); subtriangular with lateral margins substraight, with two apicolateral projections, and a wide and deep, U-shaped apical invagination, in dorsal view (Figure 7G). Inferior appendages club-shaped, proximal region subquadrangular, length 3.9x width, distal region globose, length 1.2x width, with a posteroventral projection present, small and subtriangular, with sclerotized area, in lateral view (Figure 7D); base slightly wider than apex, base with basomesal setose projections, and two subapical, sclerotized teeth, apex rounded, in ventral view (Figure 7H). Phallus with phallobase calyx-shaped, wide base, with a median constriction and widening towards apex, and with a broad phallotremal sclerite U-shaped (Figures 7E; F).

Holotype. 1 #Male, Brazil: São Paulo, E. E. Boracéia, Rio Claro, ponte (23°39.002' S, 45°54.889' W, 815 m a.s.l.) [UMSP].

Paratype. same holotype data, except #2 Males [UMSP].

Remarks. This species is proposed based only on male, and presents distribution records in Ribeira de Iguape freshwater ecoregion, in altitudinal range around 851 m a.s.l., inhabiting 2nd order freshwater environments.

Etymology. The specific name, a noun in apposition, refers to the Estação Ecologia de Boraceia, which is the type locality of new species.

Distribution. BRA (SP).

***Cochliopsyche amazona* (Johanson, 2003):409** [Brazil: Amazonas; Manaus area; Rio Branquinho; Lager Tapiri, #Male, USNM].

Helicopsyche (*Cochliopsyche*) *amazona* Johanson, 2003

(Figure 8)

–Paprocki & França 2014:16 [checklist]. –Holzenthal & Calor 2017 [catalog].

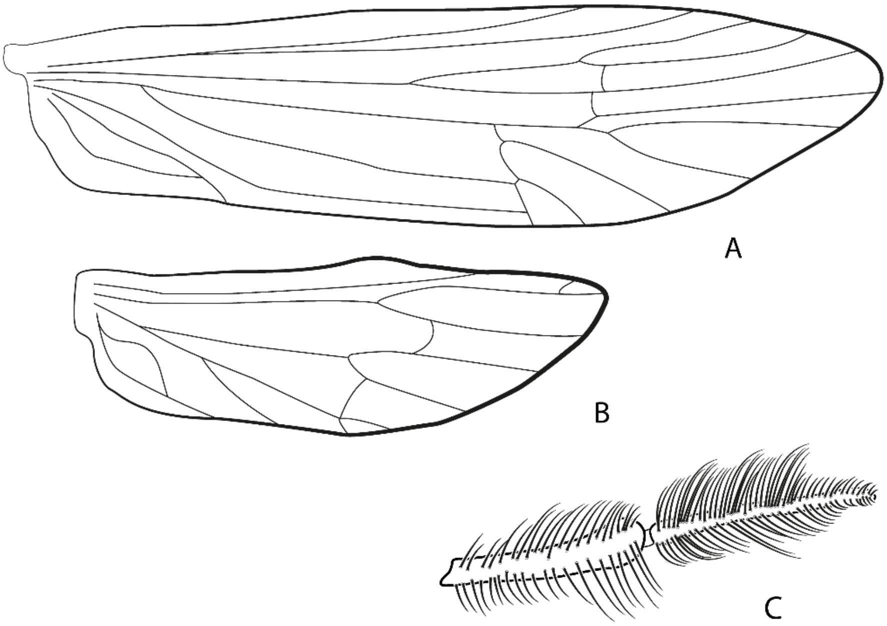

Figure 8. *Cochliopsyche amazona* (Johanson, 2003): Male, A. Forewing; B. Hind wing; C. Maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) apex of abdominal segment X trapezoidal; and (ii) inferior appendages more than 1.5x abdominal segment X length, in dorsal view (Figure 83 in Johanson, 2003); and (iii) with widened median region, in ventral view (Figure 84 in Johanson, 2003). *Cochliopsyche amazona* is similar to *C. paragueiensis* and *C. maierae* by having abdominal segment X with lateral margin substraight, in dorsal view (Figure 83 in Johanson, 2003); inferior appendages long and filiform, and inner face with a small basal projections and with two apical teeth, in ventral view (Figure 84 in Johanson, 2003). *Cochliopsyche amazona* can be distinguished from these species by the abdominal segment X with apex rounded, in lateral view (Figure 82 in Johanson, 2003), with subapical projection, and wide and shallow U shaped invagination, in dorsal view (Figure 83 in Johanson, 2003) (with apex of abdominal segment X subtriangular, without subapical projections, and a small apical cleft in *C. paraguaiensis* and *C. maierae*); and the preanal appendages boomerang shaped, in dorsal view (Figure 83 in Johanson, 2003) (with preanal appendages globose and ovoid, respectively in *C. paraguaiensis* and *C. maierae*).

Description. Forewing length 5.0 mm (n = 1); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 8A). Hind wing length 3.4 mm (n = 1) slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 8B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covering almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 8C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale bands with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur formula 1,2,2. Abdomen. Abdominal sternum VI process present, less than 1/3 segment length and filiform (Figure 81 in Johanson, 2003).

Male genitalia. Abdominal segment IX anterior lobe unprojected, anterodorsal and anteroventral margins substraight, in lateral view (Figure 82 in Johanson, 2003). Posterior lobe acuminated, positioned midway on segment with set of long setae, in lateral view (Figure 82 in Johanson, 2003); anterior margin slightly concave, central posterior lobe substraight, and basal plate U shaped, in ventral view (Figure 84 in Johanson, 2003). Preanal appendages boxing glove shaped, in lateral view (Figure 82 in Johanson, 2003); boomerang shaped, in dorsal view (Figure 83 in Johanson, 2003). Abdominal segment X digitiform with smooth margins, with slightly anterodorsal projection, apex rounded with setae, in lateral view (Figure 82 in Johanson, 2003); subrectangular with lateral margins substraight, rounded subapically, with a wide and very shallow, U shaped, apical invagination, with two lateroapical projections, ,in dorsal view (Figure 83 in Johanson, 2003). Inferior appendages pipe shaped, proximal region subquadrangular, length 2.3x width, distal region globose, same length and width, with posteroventral small invagination and distal margin sclerotized, in lateral view (Figure 82 in Johanson, 2003); base wider than apex, and with subbasal expansion, base with basomesal setose projections, distal part bent inwards bearing two apical teeth, in ventral view (Figure 84 in Johanson, 2003). Phallus with calyx shaped phallobase, narrow base, with a subbasal constriction and widening towards apex, and with a wide, U shaped phallotremal sclerite (Figures 86;87 in Johanson, 2003).

Material examined. 1 #Male, Brazil: Amazonas, Manaus, Reserva Ducke, Igarapé Ipiranga (AC) 02°58'53.6"S, 59°54'24.4"W, 30.vi-02.vii.2015, Pes, A.M., Desidério, G.R., Barcelos-Silva, P. & Xavier, W. col. [INPA]; same data, except 1 #Male, BR174, KM18, 30.xii.2013, LACIA-INPA col., [INPA]; same data, except 1 #Male, Rio Branquinho, Lager Tapiri, 22.vii.1961, Fittkau, F.J., col. [USNM01883588, Holotype]

Collections. **USNM**; NRM; INPA; UFBA.

Remarks. This species has only male known semaphoronts, and presents distribution records in Amazon Lowlands and Rio Negro freshwater ecoregions, in altitudinal range from 10–77 m a.s.l. with records in 1st, 2nd, 3rd, and 4th order freshwater environments.

Distribution. BRA (AM).

***Cochliopsyche amica* (Johanson, 2003):395** [Venezuela; TFA; Puerto; Ayacucho, M/F, MCV].

Helicopsyche (*Cochliopsyche*) *amica* Johanson, 2003

(Figure 9)

–Holzenthal & Calor 2017 [catalog].

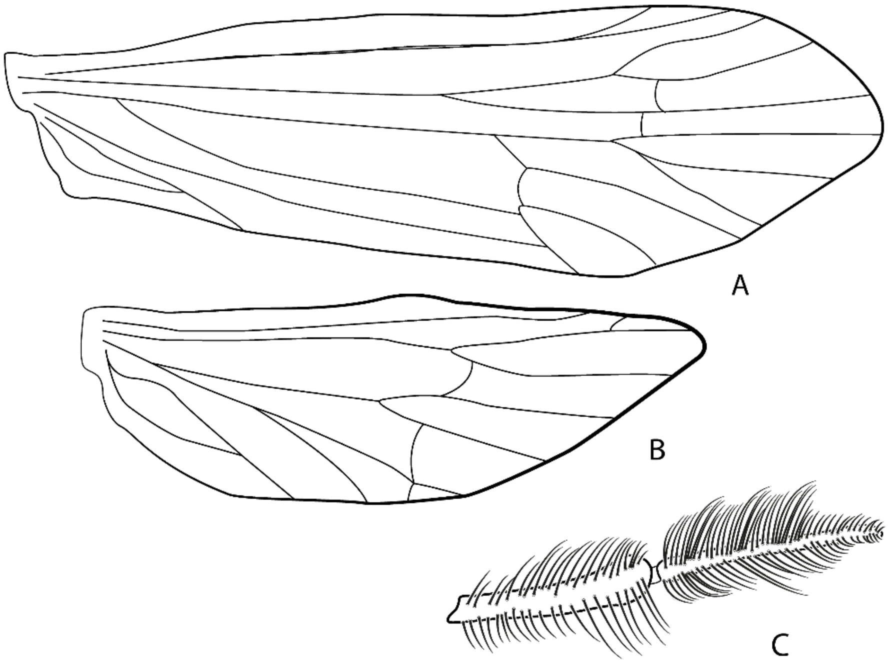

Figure 9. *Cochliopsyche amica* (Johanson, 2003): Male, A. Forewing; B. Hind wing; C. Maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subtriangular with base wide and narrowing towards to apex, in dorsal view (Figure 30 in Johanson, 2003); (ii) inferior appendages with mediodorsal finger shaped projection, in lateral view (Figure 29 in Johanson, 2003); and (iii) subtriangular with base and median region wide and narrowing towards apex, in ventral view (Figure 31 in Johanson, 2003). *Cochliopsyche amica* is similar to *C. chocoensis* and *C. xinguensis* by having inferior appendages with a finger shaped mediodorsal projection, in lateral view (Figure 29 in Johanson, 2003), and apex pointed and bent inwards, in ventral view (Figure 31 in Johanson, 2003). *Cochliopsyche amica* can be distinguished from these species by the (i) abdominal segment X subtriangular with apex about 2 times base width and without subbasal projections, in dorsal view (Figure 30 in Johanson, 2003) (base subequal or slightly wider than apex, and with subtriangular subapical projections in *C. chocoensis* and *C. xinguensis*); and the (ii) inferior appendages with median withing, and apex pointed and bent inwards in ventral view (Figure 31 in Johanson, 2003) (without median withing, and a broad and subtriangular inner face tooth in *C. chocoensis* and *C. xinguensis*).

Description. Forewing length 7.4 mm (n = 1); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 9A). Hind wing length 4.8 mm (n = 1) slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 9B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covering almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 9C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur formula 1,2,2. Abdomen. Abdominal sternum VI process absent.

Male genitalia. Abdominal segment IX anterior lobe acuminated, positioned ventrally on segment, anterodorsal and anteroventral margins substraight, in lateral view (Figure 29 in Johanson, 2003). Posterior lobe rounded, positioned ventrally on segment with set of long setae and posterior small projection, in lateral view (Figure 29 in Johanson, 2003); anterior margin concave, central posterior lobe slightly convex, and basal plate U shaped, in ventral view (Figure 31 in Johanson, 2003). Preanal appendages ovoid, in lateral view (Figure 29 in Johanson, 2003); thumb shaped, in dorsal view (Figure 30 in Johanson, 2003). Abdominal segment X subrectangular with smooth margins, apex truncated with setae, in lateral view (Figure 29 in Johanson, 2003); subtriangular with lateral margins substraight, with two rounded lateroapical projections, and a narrow and very shallow U shaped apical invagination, in dorsal view (Figure 30 in Johanson, 2003). Inferior appendages club shaped, proximal region subtriangular, same length and width, distal region subtriangular, length 1.2x width, with a mediodorsal finger-shaped projection, in lateral view (Figure 29 in Johanson, 2003); base and median region wide, and narrowing toward apex, base with basomesal setose projections, inner face with setose median projections, an apical tooth sclerosed and apex truncated, in ventral view (Figure 31 in Johanson, 2003). Phallus with calyx shaped phallobase, narrow base, with a subbasal constriction and widening towards apex, and with a small phallotremal sclerite S shaped, in ventral view (Figures 32; 33 in Johanson, 2003).

Material examined. 2# Males, Brazil: Pará, Óbidos, [Rio Amazonas], 19.viii.1949, Parish col., [MCZ0001, Paratype]; same data, except 1 #Male, 18.viii.1949, Parish col., [MCZ0003, Paratype]; same data, except 1 #Male, 13.ix.1949, Parish, col., [MCZ0002]; same data, except 1 #Male, Paritins, [Rio Amazonas], 2.x.?, Parish, col., [MCZ0004, Paratype]; same data, except 4 #Males, Roraima, #08, 7-8.vii.2018, LACIA-INPA, col., [INPA; UFBA]; same data, except 1#Male, Tocantins, Rio Araguaia, 08.v.2017, Hamada, N., Amora, G., col., [INPA].

Collections. **MCZ**; INPA; ISNB; UFBA; USNM.

Remarks. The new species shows morphological variations in some species such as abdominal segment X, in dorsal view, with apex not as narrow as holotype, and inferior appendage, in ventral view, with a slightly narrower median region than the holotype. This species has male, female (undescribed) known semaphoronts. Presents distribution records in Amazon Lowlands, Esequibo, Oniroco Guiana Shield, Orinoco Llanos, Tapajos - Juruena, and Tocantins - Araguaia freshwater ecoregions, in altitudinal range from 5–194 m a.s.l. with records in 1st, 2nd, 8th, and 9th order freshwater environments.

Distribution. BRA (AM; PA, **TO**); GUY; VEN.

Cochliopsyche blahniki **(Johanson, 2003):401** [Venezuela; Guarico; Hato Masuguaral; 45 km S Calabozo; 8.57°N; 67.58°W; el. 75 m, #Male#Female, UMSP].

Helicopsyche (*Cochliopsyche*) *blahniki* Johanson, 2003

(Figure 10)

–Paprocki & França 2014:16 [checklist]. –Holzenthal & Calor 2017 [catalog].

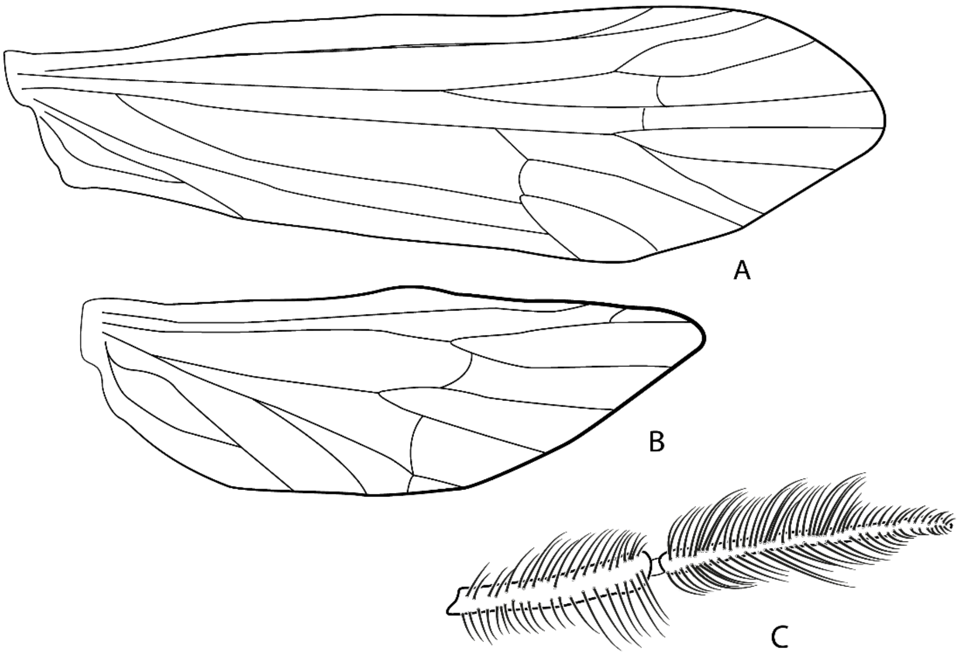

Figure 10. *Cochliopsyche blahniki* (Johanson, 2003): Male, A. Forewing; B. Hind wing; C. Maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) apex of abdominal segment X with acuminated subapical and apical projections; and (ii) inferior appendages with same length of abdominal segment X, in dorsal view (Figure 52 in Johanson, 2003); and (iii) a subtriangular, pointed inner subapical tooth, in ventral view (Figure 53 in Johanson, 2003). *Cochliopsyche blahniki* is similar to *C. chocoensis* and *C. napoa* by having inferior appendages with a finger shaped mediodorsal projection, in lateral view (Figure 51 in Johanson, 2003), and with wide subapical inner face tooth, in ventral view (Figure 53 in Johanson, 2003). *Cochliopsyche blahniki* can be distinguished from these species by the abdominal segment X with subapical and apical acuminated projections, in dorsal view (Figure 52 in Johanson, 2003) (with rounded subapical and apical projections, forming two rounded lobes in *C. chocoensis* and *C. napoa*); and the inferior appendages with apex globose, a subapical inner small tooth well pointed, and small median projections, in ventral view (Figure 53 in Johanson, 2003) (with apex subtriangular and projected, a subapical inner wide bifid tooth, and bifid median projection in *C. chocoensis* and with apex truncated and sinusous, with a wide, subapical internal tooth, and median finger-like projection in *C. napoa*).

Description. Forewing length 6.5 mm (n = 1); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 10A). Hind wing length 3.6 mm (n = 1) slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 10B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covering almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint about 1.5x basal joint length with long setae (Figure 10C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VI process present, less than 1/3 segment length and subtriangular (Figure 50 in Johanson, 2003).

Male genitalia. Abdominal segment IX anterior lobe rounded, positioned dorsally on segment, anterodorsal margin substraight, anteroventral margin slightly concave, in lateral view (Figure 51 in Johanson, 2003). Posterior lobe acuminated, positioned midway on segment, without setae, in lateral view (Figure 51 in Johanson, 2003); anterior margin substraight, central posterior lobe substraight, and basal plate V shaped, in ventral view (Figure 53 in Johanson, 2003). Preanal appendages thumb shaped, in lateral view (Figure 51 in Johanson, 2003); boxing glove shaped, in dorsal view (Figure 52 in Johanson, 2003). Abdominal segment X subrectangular with smooth margins, with small anterodorsal projection, apex truncated with setae, in lateral view (Figure 51 in Johanson, 2003); subquadrangular with lateral margins concave, subtriangular subapical and apical projections, and a wide and shallow U shaped apical invagination, in dorsal view (Figure 52 in Johanson, 2003). Inferior appendages pipe shaped, proximal region subquadrangular, length 1.6x width, distal region globose, width 1.3x length with anteroventral and mediodorsal projection finger shaped, posteroventral projection present, small and rounded with sclerotized area, in lateral view (Figure 51 in Johanson, 2003); base wider than apex, base with basomesal setose projections, inner face with setose median and subapical projections, and a well-projected subapical tooth sclerosed and apex rounded, in ventral view (Figure 53 in Johanson, 2003). Phallus with calyx shaped phallobase, wide base, with a subbasal constriction and slightly widening towards apex, and with a small phallotremal sclerite U shaped, in ventral view (Figure 53 in Johanson, 2003).

Material examined. 4 #Males, Brazil: Roraima, Guajará-Mirim confluência Rio Pacaás Novos com Rio Negro Ocaia (okawa) prainha, 6-8.ix.1999, Hamada, N., Barbosa, U., col., [INPA; UFBA]. 1 #Male, Venezuela: Guarico, Hato, Masaguaral, 45kmS Calabozo (8.57N, 67.85W, 75 m [a.s.l.]) Savanna#1, 4-6.iv.1988, Spstein, M. & Blahnik, R., col., [UMSP000042387, Holotype]; same data, except 1 #Male, Savanna#16, 6-8.v.1988, Spstein, M. & Blahnik, R., col. [UMSP0000172441]; same data, except 1 #Male, Garry Forest#20, 4-6.iv.1988, Spstein, M. & Blahnik, R., col. [UMSP0000172442]

Collections. **UMSP**; CIUC; FMNH; INPA; MVC; UFBA; USNM; NRM

Remarks. The new species shows morphological variations in some species such as basomesal projections of inferior appendage, in ventral view, with one projection, with a bifid projection and with two projections as a holotype. This species has male and female (undescribed) known. Presents distribution records in Amazonas Guiana Shield, Amazonas High Andes, Amazon Lowlands, Madeira Brazilian Shield, North Andean Pacific Slopes - Rio Atrato, Orinoco Guiana Shield, Orinoco Llanos, Orinoco Piedmont, Ucayali - Urubamba Piedmont, and Western Amazon Piedmont freshwater ecoregions, in altitudinal range from 29–944 m a.s.l. with records in 1st, 2nd, 3rd, 4th, 5th, 6th, and 8th order freshwater environments.

Distribution. BRA (AM); COL; ECU; GUY; PER; VEN.

***Cochliopsyche brazilia* (Johanson, 2003)**:410 [Brazil: Minas Gerais; confluence Rio Peixe & Rio Preto do Itambe; 19°17.525'S; 43°15.457'W; el. 500 m, #Male, #Female, MZUSP].

Helicopsyche (*Cochliopsyche*) *brazilia*

–Paprocki & França 2014:16 [checklist]. –Holzenthal & Calor 2017 [catalog].

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) segment abdominal X subrectangular with lateral margins substraight, rounded apical projections; (ii) a short and deep apical invagination U shaped, in dorsal view (Figure 88 in Johanson, 2003); and (iii) inferior appendages with projected and rounded apex, and an inner face small tooth sclerosed, in ventral view (Figure 89 in Johanson, 2003). *Cochliopsyche brazilia* is similar to *C. puyoa* and *C. mulleri* **n. sp.** by having abdominal segment X slightly shorter than inferior appendages, in dorsal view (Figure 88 in Johanson, 2003), and with base wide than apex, and small inner face subapical tooth, in ventral view (Figure 89 in Johanson, 2003). But the new species can be distinguished from these species by the inferior appendages with apex projected, rounded, in ventral view (Figure 89 in Johanson, 2003) (with unprojected, truncated apex in *C. puyoa* and with apex unprojected, rounded apex in *C. mulleri* **n. sp.**); and the small subapical inner face sclerosed tooth, in ventral view (Figure 89 in Johanson, 2003) (with a small subapical inner face tooth in *C. puyoa* and with two broads subapical sclerosed inner face teeth in *C. mulleri* **n. sp.**).

Description. Forewing length 5.2 mm (n = 1), forks I, II, III and V present, discoidal, medial, and thyridial cells closed. Hind wing length 3.5 mm (n = 1) slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed. Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae. Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process absent.

Male genitalia. Abdominal segment IX anterior lobe with rounded projection positioned midway on segment, anterodorsal concave and anteroventral margins substraight, in lateral view (Figure 87 in Johanson, 2003). Posterior lobe with acuminated projection, positioned midway on segment with set of long setae, in lateral view (Figure 87 in Johanson, 2003); anterior margin slightly convex, central posterior lobe slightly convex, and basal plate U shaped, in ventral view (Figure 89 in Johanson, 2003). Preanal appendages boxing glove shaped, in lateral view (Figure 87 in Johanson, 2003); ovoid, in dorsal view (Figure 88 in Johanson, 2003). Abdominal segment X subtriangular with sinuous posterodorsally margins, with anterodorsal projection, apex rounded with setae, in lateral view (Figure 87 in Johanson, 2003); subrectangular with lateral margins substraight, rounded apical projections, and a short and deep apical invagination U shaped, in dorsal view (Figure 88 in Johanson, 2003). Inferior appendagesclub shaped, proximal region subquadrangular shaped, length 3.5x width, distal region ovoid, length 1.2x width, with anteroventral projection finger shaped, in lateral view (Figure 87 in Johanson, 2003); base wide than apex, base with basomesal setose projections, and a slightly subapical tooth sclerosed and apex rounded, in ventral view (Figure 89 in Johanson, 2003). Phallus with calyx shaped phallobase, wide base, with a median constriction and widening towards apex, and with a small bifid phallotremal sclerite U shaped, and membranous ornamentation on the apex (Figures 90;91 in Johanson, 2003).

Collections. **MZUSP**; USNM; MRM

Remarks. This species has Male, Female (undescribed) known semaphoronts. Presents distribution records in Northeastern Mata Atlântica freshwater ecoregion, in altitudinal range around 595 m a.s.l. with records in 2nd and 3rd order freshwater environments.

Distribution. BRA (MG).

***Cochliopsyche chocoensis* (Johanson, 2003):401** [Colombia: Choco; Rio Atrato; Yuto, M/F, USNM].

Helicopsyche (*Cochliopsyche*) *chocoensis* Johanson, 2003

(Figure 11)

–Holzenthal & Calor 2017 [catalog].

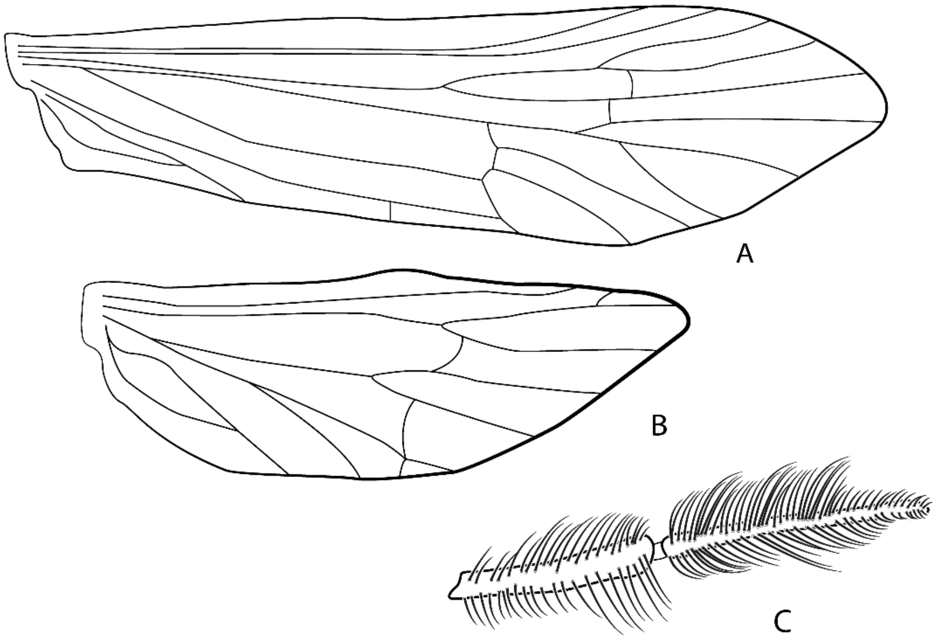

Figure 11. *Cochliopsyche chocoensis*: Male, A. Forewing; B. Hind wing; C. Maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) apex of abdominal segment X with rounded subapical and apical projections, in dorsal view (Figure 46 in Johanson, 2003); (ii) inferior appendages with mediodorsal bifid finger shaped projection, in lateral view (Figure 45 in Johanson, 2003); and (iii) a subtriangular, pointed inner subapical tooth, in ventral view (Figure 47 in Johanson, 2003). *Cochliopsyche chocoensis* is similar to *C. blahniki* and *C. napoa* by having inferior appendages with a finger shaped mediodorsal projection, in lateral view (Figure 45 in Johanson, 2003), and with wide subapical inner face tooth, in ventral view (Figure 47 in Johanson, 2003). But the new species can be distinguished from these species by the abdominal segment X subquadrate with rounded subapical projection, in dorsal view (Figure 46 in Johanson, 2003) (with abdominal segment X subquadrate with acuminated subapical projection *C. blahniki* and with abdominal segment X subrectangular with rounded subapical projection *C. napoa*); and the short and deep apical evagination, in dorsal view (Figure 46 in Johanson, 2003) (with long, shallow apical evagination in *C. blahniki* and with long, deep apical evagination in *C. napoa*).

Description. Forewing length 6.0 mm (n = 1), forks I, II, III and V present, discoidal, medial, and thyridial cells closed (Figure 11A). Hind wing length 3.3 mm (n = 1) slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 11B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae. Labial palps 3-segmented with long setae (Figure 11C). Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process absent (in holotype), when present less than 1/3 segment length and subtriangular.

Male genitalia. Abdominal segment IX anterior lobe with rounded projection positioned dorsally on segment, anterodorsal substraight and anteroventral margins slightly concave, in lateral view (Figure 45 in Johanson, 2003). Posterior lobe with rounded projection, positioned dorsally on segment with set of long setae, in lateral view (Figure 45 in Johanson, 2003); anterior margin substraight, central posterior lobe convex, and basal plate U shaped, in ventral view (Figure 47 in Johanson, 2003). Preanal appendages appendages ovoid, in lateral view (Figure 45 in Johanson, 2003); globose, in dorsal view (Figure 46 in Johanson, 2003). Abdominal segment X subtriangular with sinuous posterodorsally margins, with anterodorsal projection, apex rounded with setae, in lateral view (Figure 45 in Johanson, 2003); subquadrangular with lateral margins concave, rounded subapical and subtriangular apical projections, and a short and deep apical invagination U shaped, in dorsal view (Figure 46 in Johanson, 2003). Inferior appendages pipe shaped, proximal region subtriangular shaped, length 1.7x width, distal region globose, same length and width, with anteroventral projection finger shaped, and with a mediodorsal projection finger shaped, and a posteroventral projection present, slightly and subtriangular with sclerosed area, in lateral view (Figure 45 in Johanson, 2003); base and apex wide, with median constriction, base with basomesal setose projections, inner face with setose median projections, and a well-projected subapical tooth sclerosed and apex projected and subtriangular, in ventral view (Figure 47 in Johanson, 2003). Phallus with calyx shaped phallobase, narrow base, with a subbasal constriction and widening towards apex, and with a small phallotremal sclerite B shaped (Figure 48;49 in Johanson, 2003).

Material examined. 1#Male, Colombia: Choco, Yuto, Rio Atrato, 18.ii.1983, Flint, O.S. Jr., col. [USNM948790, Holotype]; same data, except 1#Male, Valle, Municipio de Buenaventura, Rio Escalarete frente à casa de ""AcuaValle"" - 15km SE Cordoba (3°49'38"N, 76°52'15"W, 200 m [a.s.l.]), 1.xii.1997, Muñoz-Quesada, F.J., col. [UMSP000114690]; #1Male, Brazil: Acre, Mâncio Lima, P.N.Sa Divisor, Rio Azul, 15.III.2006, Calor, A. col. [UFBA]; same data, except #1 Amazonas, Barcelos, Miranda, Rio Jauari, 21.vii.2099, Pes, A.M. [INPA; UFBA] ; same data, except #1 Roraima, 09.vii.2018 [INPA].

Collections. **USNM**, INPA, UFBA.

Remarks. The new species shows morphological variations in some species such as abdominal sternum VIth process present in some specimens and basomesal projections of inferior appendage, in ventral view, with a bifid projection or one projection as a holotype. This species has Male, Female (undescribed) known semaphoronts. Presents distribution records in Amazon Lowlands, Madeira Brazilian Shield, North Andean Pacific Slopes - Rio Atrato, and Rio Negro freshwater ecoregions, in altitudinal range from 30–217 m a.s.l. with records in 3rd, 4th, and 7th order freshwater environments.

Distribution. BRA(**AC**, **AM**, **RO**); COL.

Cochliopsyche clara **Ulmer, 1905:18** [Brazil: Santa Catarina, #Male, MCZ].

Tetanonema clarum Ulmer, 1905

Helicopsyche (*Cochliopsyche*) *clara* Johanson, 2003

(Figure 12)

–Flint 1966:12 [♂; lectotype]. –Johanson 1995:107 [catalog]. –Johanson 1998:128 [status; phylogeny]. –Johanson 2003:388 [♂; ♀; redescription; distribution]. –Blahnik et al. 2004:4 [distribution]. –Paprocki et al. 2004:6 [checklist]. –Calor 2011:320 [checklist]. –Souza et al. 2013:3 [distribution]. –Paprocki & França 2014:17 [checklist]. –Holzenthal & Calor 2017 [catalog].

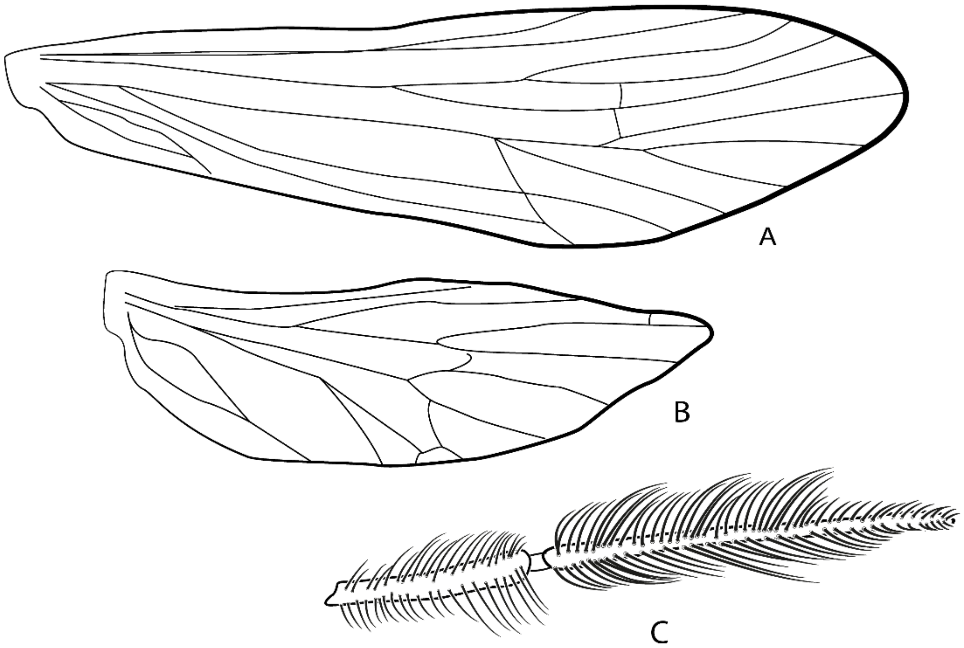

Figure 12. *Cochliopsyche clara*: Male, A. Forewing; B. Hind wing; C. Maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subrectangular with slightly pair of subtriangular apical projections, in dorsal view (Figure 7 in Johanson, 2003); (ii) inferior appendages with base wide than apex with basomesal finger shaped setose projection; and (iii) apex projected, truncated and with two small sclerosed inner face teeth, in ventral view (Figure 8 in Johanson, 2003). *Cochliopsyche clara* is similar to *C. vazquezae* and *C. uwape* **n. sp.** by having inferior appendages with a finger shaped basomesal projection, in ventral view (Figure 8 in Johanson, 2003), and two inner face subapical tooth, in ventral view (Figure 8 in Johanson, 2003). But the new species can be distinguished from these species by the (i) abdominal segment X with lateral margins substraight and only small subtriangular apical projections, in dorsal view (Figure 7 in Johanson, 2003) (with lateral margins concave and wide subtriangular subapical and apical projections in

C. vazquezae and with lateral margins convex and small subtriangular subapical and apical projections in *C. uwape* **n. sp.**); and the (ii) inferior appendages proximal region with same length and width, and distal region globose, in lateral view (Figure 6 in Johanson, 2003) (with inferior appendages proximal region with length about 2 times the width, and distal region ovoid in *C. vazquezae* and *C. uwape* **n. sp.**).

Description. Forewing length 6.3 mm (n = 1), forks I, II, III and V present, discoidal, medial, and thyridial cells closed (Figure 12A). Hind wing length 4.2 mm (n = 1) slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 12B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint more than 2x basal joint length with long setae (Figure 12C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process absent (in holotype), when present less than 1/3 segment length and subtriangular.

Male genitalia. Abdominal segment IX anterior lobe with rounded projection positioned midway on segment, anterodorsal margin substraight and anteroventral margin concave, with posterobasally acuminated slightly projected, in lateral view (Figure 6 in Johanson, 2003). Posterior lobe with rounded projection, positioned midway on segment, without set of setae, in lateral view (Figure 6 in Johanson, 2003); anterior margin concave, central posterior lobe convex, and basal plate U shaped, in ventral view (Figure 8 in Johanson, 2003). Preanal appendages boxing glove shaped, in lateral view (Figure 6 in Johanson, 2003); thumb shaped, in dorsal view (Figure 7 in Johanson, 2003). Abdominal segment X subtriangular with sinuous posterodorsally margins, apex truncated with setae, in lateral view (Figure 6 in Johanson, 2003); subrectangular with lateral margins substraight, a slightly subtriangular apical projections, and a long and shallow apical invagination U shaped, in dorsal view (Figure 7 in Johanson, 2003). Inferior appendages pipe shaped, proximal region subquadrangular shaped, same length and width, distal region globose, same length and width, with anteroventral projection finger shaped, and a posteroventral slightly evagination and distal area sclerosed, in lateral view (Figure 6 in Johanson, 2003); base wide than apex, base with basomesal setose projections, inner face with setose subapical projections and two slightly subapical teeth sclerosed and apex truncated, in ventral view (Figure 8 in Johanson, 2003). Phallus with calyx shaped phallobase, narrow base, with a subbasal constriction and widening towards apex, and with median membranous ornamentation and large phallotremal sclerite U shaped (Figure 9;10 in Johanson, 2003).

Material examined. 1#Male, Brazil: Santa Catarina [MCZ, Holotype]; same data, except Minas Gerais, Santana do Riacho, Rio Paraúna, 3kmS (19°10.986'S, 43°485'W, 650 m [a.s.l.]), 11.ix.2001, Holzenthal, R., Paprocki, H., Blahnik R. & Amarante M.C., col., [UMSP000082731]; same data, except 1#Female, [UMSP000082759]; same data, except 1#Male, Bahia, Rio de Janeiro, Captação EMBASA, Rio Paraguaçu 12°33'52.4"S, 39°32'24.4"W, 26.iii.2012, Quinteiro, Duarte & Gracia, col., [UFBA]

Collections. **MCZ**; MZUSP; UFBA; UMSP; USNM

Remarks. The new species shows morphological variations in some species such as abdominal sternum VIth process present in some specimens. This species has Male, Female known semaphoronts. Presents distribution records in Iguassu, Lower Parana, Northeastern Caatinga & Coastal Drainages, Northeastern Mata Atlântica, Ribeira de Iguape, Rio Negro, São Francisco, Upper Uruguay, and Western Amazon Peidmont freshwater ecoregions, in altitudinal range from 154–913 m a.s.l. with records in 1st, 2nd, 3rd, 6th, and 7th order freshwater environments.

Distribution. ARG; BRA (AM; MG; SC; SP; PE); ECU.

***Cochliopsyche holzenthali* (Johanson, 2003):403** [Venezuela: Barinas; Rio Singüis in Cano Grande; 8°24.00'N; 70°46.45'W; el. 520 m, #Male#Female, UMSP].

Helicopsyche (*Cochliopsyche*) *holzenthali* Johanson, 2003

(Figure 13)

–Holzenthal & Calor 2017 [catalog].

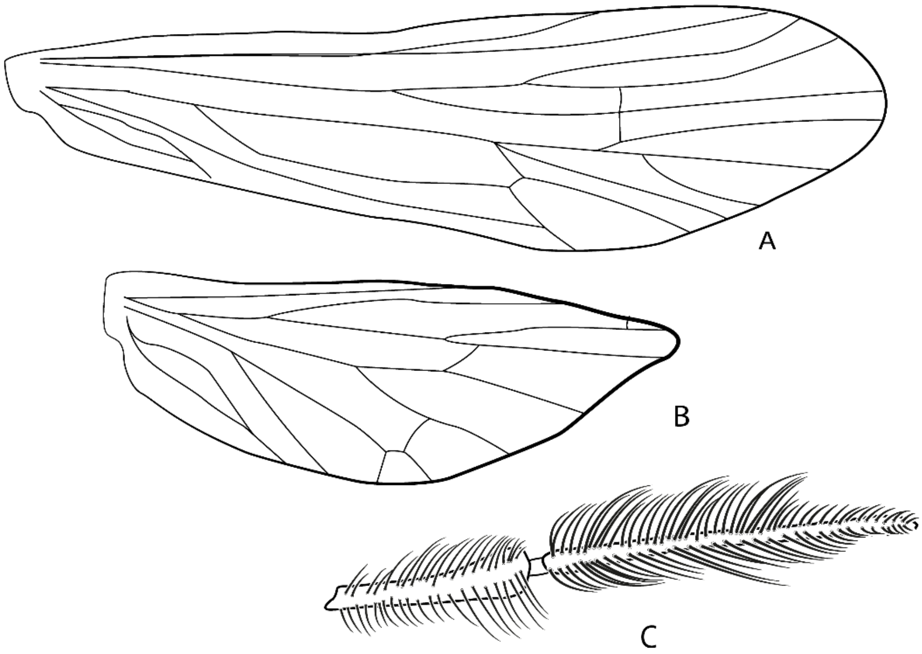

Figure 13. *Cochliopsyche holzenthali*: Male, A. Forewing; B. Hind wing; C. Maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subquadrangular with slightly median projections, well rounded apical projections, and a short and deep apical evagination, in dorsal view; and (ii) inferior appendages with bifid mediodorsal projections finger shaped, in dorsal view (Figure 58 in Johanson, 2003); (iii) anteroventral rounded projection, in lateral view (Figure 57 in Johanson, 2003). *Cochliopsyche holzenthali*is similar to *C. paraguaiensis* and *C. mulleri* **n. sp.** by having inferior appendages with long and narrow proximal region, in lateral view (Figure 57 in Johanson, 2003), and apex rounded with two inner face subapical tooth, in ventral view (Figure 59 in Johanson, 2003). But the new species can be distinguished from these species by the (i) abdominal segment X invagination deep, forming two rounded lobes, in dorsal view (Figure 58 in Johanson, 2003) (with slightly apical cleft and shallow apical evagination, that do not form well-projected lobes in *C. paraguaiensis* and *C. mulleri* **n. sp.**); and the (ii) inferior appendages with inner face median projections, well-projected and finger shaped, in ventral view (Figure 59 in Johanson, 2003) (without median inner face projections in *C. paraguaiensis* and *C. mulleri* **n. sp.**).

Description. Forewing length 6.3 mm (n = 1), forks I, II, III and V present, discoidal, medial, and thyridial cells closed (Figure 13A). Hind wing length 3.9 mm (n = 1) slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 13B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae.

Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 13C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process present, more than 2/3 segment length and subtriangular.

Male genitalia. Abdominal segment IX anterior lobe with acuminated projection positioned ventrally on segment, anterodorsal and anteroventral margins substraight, in lateral view (Figure 57 in Johanson, 2003). Posterior lobe with rounded projection, positioned dorsally on segment, without set of setae, in lateral view (Figure 57 in Johanson, 2003); anterior margin substraight, central posterior lobe slightly convex, and basal plate W shaped, in ventral view (Figure 59 in Johanson, 2003). Preanal appendages boxing glove shaped, in lateral view (Figure 57 in Johanson, 2003); boxing glove shaped, in dorsal view (Figure 58 in Johanson, 2003). Abdominal segment X digitiformwith sinuous posterodorsally and ventral margins, with medioventral projection, apex acuminated with setae, in lateral view (Figure 57 in Johanson, 2003); subquadrangular with lateral margins substraight and median slightly projection, rounded apical projections and a short and deep apical invagination U shaped, in dorsal view (Figure 58 in Johanson, 2003). Inferior appendages pipe shaped, proximal region subquadrangular shaped, length 3x width, distal region ovoid, length 1.2x width, with anteroventral projection rounded, and with a mediodorsal projection finger shaped, in lateral view (Figure 57 in Johanson, 2003); base slightly wide than apex, base with basomesal setose projections, inner face with setose subapical projections and two slightly subapical teeth and apex rounded, in ventral view (Figure 59 in Johanson, 2003). subrectangular phallobase, narrow base and widening towards apex, and with a small phallotremal sclerite U shaped (Figure 60;61 in Johanson, 2003).

Material examined. 1 #Male, Venezuela: Zulia, [Liberdad], Rio Yasa ca. 3km (air) E Kasmera (Est. Biológica) (9.941°N, 72.720°W, 150 m [a.s.l.]), 14.i.1994, Holzenthal, R., Cressa, *C*. & Ricon, M.E., col., [UMSP000042366]; same data, except 1 #Female, Venezuela: Barinas, [Andrés Bellos], Rio Sinlgüis in Caño Grande (8°24.00'N, 70°46.45'W) 520 m [a.s.l.], 22.iii.1997, Holzenthal, R., col., [UMSP000042384, Paratype]

Collections. **UMSP**; USNM.

Remarks. The new species shows morphological variations in some species such as basomesal projection of inferior appendage, in ventral view, with a bifid projection or one projection as a Paratype. This species has Male, Female (undescribed) known semaphoronts. Presents distribution records in Amazon Lowlands, Maracaibo, and Orinoco Piedmont freshwater ecoregions, in altitudinal range from 310–544 m a.s.l. with records in 1st, 2nd, and 3rd order freshwater environments.

Distribution. VEN.

***Cochliopsyche lobata* Flint, 1983:95** [Argentina: Pcia. Misiones; Arroyo Piray Guazú; N San Pedro, #Male, USNM].

Helicopsyche (*Cochliopsyche*) *lobata* Johanson, 2003

(Figure 14)

–Johanson 1995:107 [catalog]. –Johanson 1998:128 [status; phylogeny]. –Johanson 2003:391 [♂; redescription; distribution]. –Blahnik et al. 2004:4 [distribution]. –

Paprocki et al. 2004:6 [checklist]. –Manzo et al. 2014:167 [distribution]. –Paprocki & França 2014:17 [checklist].

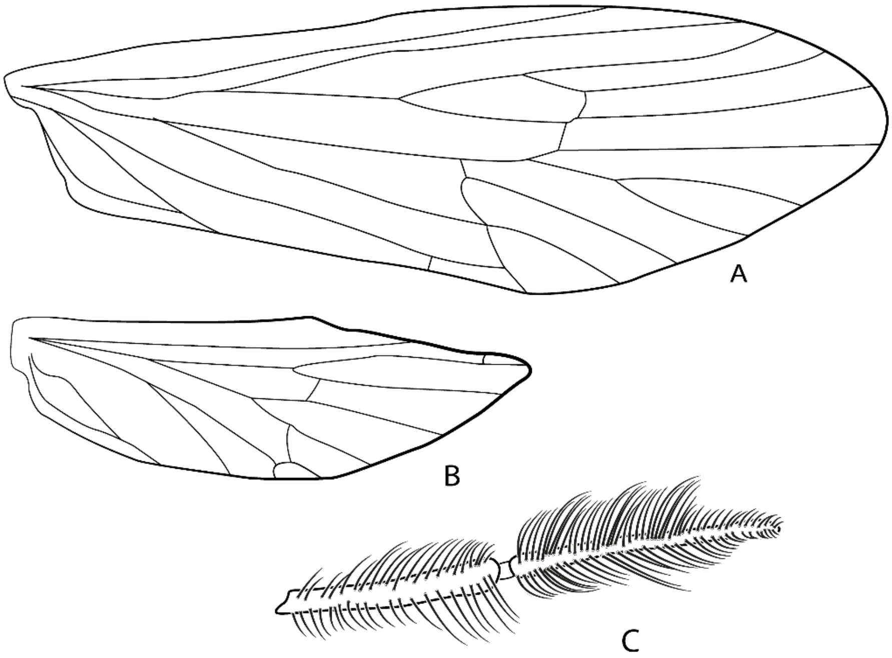

Figure 14. *Cochliopsyche lobata*: Male, A. Forewing; B. Hind wing; C. maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) Inferior appendages with a mediodorsal projection, in lateral view (Figure 12 in Johanson, 2003); (ii) basomesal projection wide and rounded; and (iii) apex truncated with subapical subquadrate projection, in ventral view (Figure 14 in Johanson, 2003). *Cochliopsyche lobata*is similar to *C. ocosingua* and *C. xinguensis* by having abdominal segment X with slightly rounded apical projections, in dorsal view (Figure 13 in Johanson, 2003), and inferior appendages with median inner face projections, in dorsal view (Figure 13 in Johanson, 2003). But the new species can be distinguished from these species by the (i) abdominal segment X with lateral margins convex and slightly apical projections, in dorsal view (Figure 13 in Johanson, 2003) (with lateral margins substraight and subapical and apical projections in *C. ocosingua* and *C. xinguensis*); and the (ii) inferior appendages with wide rounded basomesal projections and apex truncated with inner face subquadrate projection, in ventral view (Figure 14 in Johanson, 2003) (with slightly and subtriangular basomesal projection and apex truncated with inner face acuminated projection in in *C. ocosingua* and with slightly and rounded basomesal projection, and apex subtriangular with inner face pointed projection in *C. xinguensis*).

Description. Forewing length 7.1 mm (n = 1), forks I, II, III and V present, discoidal, medial, and thyridial cells closed (Figure 14A). Hind wing length 4.6 mm (n = 1) slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 14B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 14C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process present, less than 1/3 segment length and filiform (Figure 11 in Johanson, 2003).

Male genitalia. Abdominal segment IX anterior lobe with acuminated projection positioned midway on segment, anterodorsal and anteroventral margins substraight, in lateral view (Figure 12 in Johanson, 2003). Posterior lobe with rounded projection, positioned dorsally on segment, without set of setae, in lateral view (Figure 12 in

Johanson, 2003); anterior margin concave, central posterior lobe slightly convex, and basal plate U shaped, in ventral view (Figure 14 in Johanson, 2003). Preanal appendages ovoid, in lateral view (Figure 12 in Johanson, 2003); ovoid, in dorsal view (Figure 13 in Johanson, 2003). Abdominal segment X subrectangular with sinuous posterodorsally margins, with slightly anterodorsal projection, apex truncated with setae, in lateral view (Figure 12 in Johanson, 2003); subquadrangular with lateral margins convex, rounded apical projections and a short and shallow apical invagination U shaped, in dorsal view (Figure 13 in Johanson, 2003). Inferior appendages pipe shaped, proximal region subquadrangular shaped, length 1.6x width, distal region globose, same length and width, and with a mediodorsal projection finger shaped, in lateral view (Figure 12 in Johanson, 2003); base wide than apex, base with basomesal setose rounded area, inner face with setose subapical projections, subapical subquadrate projection and apex truncated, in ventral view (Figure 14 in Johanson, 2003). subrectangular phallobase, widening median region, and narrowing towards apex, and with a small phallotremal sclerite U shaped, and membranous ornamentation on the subapical and apical (Figure 15;16 in Johanson, 2003).

Material examined. 6#Male, Argentina: Misiones, Ao. Piray Guazú No., São Pedro, 22.xi.1973, Flint, O.S. Jr., col., [USNM01866353, Paratype]. 4#Male, Brazil: Goiás, Jataí, Fazenda Nova Orlandia, i.1964, Martins, Morgante & Silva, col., [USNM01866352]; same data, except 1#Male, Santa Catarina, Nova Teutônia, 4.x.1932, Plaumann, F., col., [MCZ0006]; same data, except 1#Male,Urubici, Cachoeira Avencal (28°02.839"S, 49°36.997"W, 1260 m [a.s.l.]), 6.iii.1998, Holzenthal, R., Foehlich, *C.* & Paprocki, H., col., [UMSP000029965]; same data, except 1#Male, [UMSP000029968]; same data, except 1#Male, Hagen col., [MCZ0005]. 1#Male, Peru: Junin Prov. Mission, Cutivireni, at. Rio Mamiri, 6-25.iii.1985, Savage, H.M., col., [USNM01866343]; same data, except 2#Male, Madre de Dios, Manu, Pakitza, (11°56'S, 71°18'W, 250 m [a.s.l.]), 17-20.ix.1989, Adams, N. et al., col., [UNSM01866345]

Collections. **USNM**; MCZ; MZUSP; UMSP.

Remarks. The new species shows morphological variations in some species such as basomesal projection of inferior appendage, in ventral view, some specimens show setose sinuous margin of projection. This species has only male known semaphoronts. Presents distribution records in Lower Parana, Mamore - Madre de Dios Piedmont, Northeastern Mata Atlântica, Ucayali - Urubamba Peidmont, Upper Parana, and Uruguay freshwater ecoregions, in altitudinal range from 220–1281 m a.s.l. with records in 1st, 2nd, 3rd, 4th, 5th, 6th, and 7th order freshwater environments.

Distribution. ARG, BRA (DF, **GO,** MG, SC), PER.

Cochliopsyche napoa **(Johanson, 2003):398** [Ecuador: Napo; Lago Agrio, M/F, USNM].

Helicopsyche (*Cochliopsyche*) *napoa* Johanson, 2003

(Figure 15)

–Holzenthal & Calor 2017 [catalog]. –Olah & Olah 2022 [distribution].

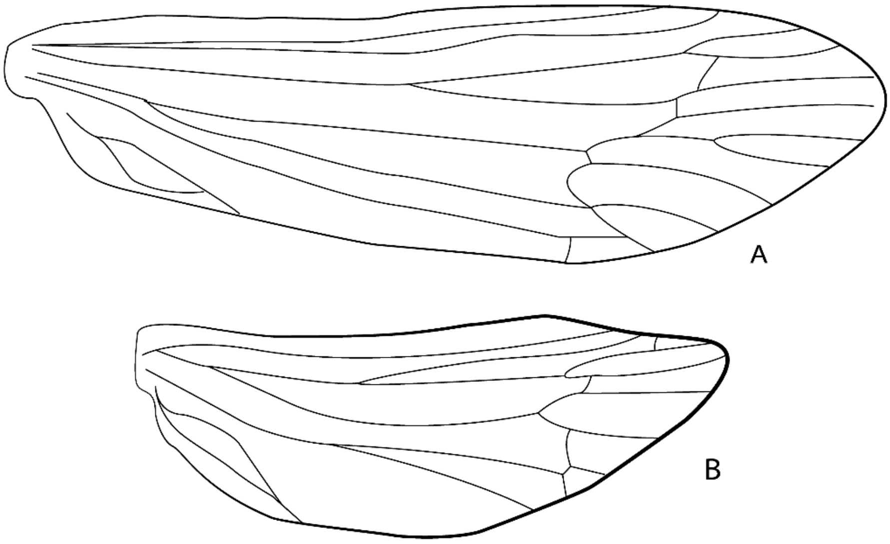

Figure 15. *Cochliopsyche napoa*: Male, A. Forewing; B. Hind wing; C. Maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subrectangular with slightly subapical projections, and well-rounded apical projections, with a long and deep apical evagination; and (ii) preanal appendages boomerang shaped, in dorsal view; (iii) inferior appendages with inner face wide and pointed apical tooth, in ventral view (Figure 42 in Johanson, 2003). *Cochliopsyche napoa*is similar to *C. blahniki* and *C. chocoensis* by having inferior appendages with a finger shaped mediodorsal projection, in lateral view (Figure 40 in Johanson, 2003), and with wide subapical inner face tooth, in ventral view (Figure 42 in Johanson, 2003). But the new species can be distinguished from these species by the abdominal segment X subrectangular with a long and deep apical evagination, in dorsal view (Figure 41 in Johanson, 2003) (both subquadrangular segment; and respectively with apical long and shallow and short and deep evagination in *C. chocoensis* and *C.*

napoa); and the inferior appendages with apex truncated and sinuses, with a subapical inner wide, and median projection well-projected, in ventral view (Figure 42 in Johanson, 2003) (with apex globose, a subapical inner small tooth well pointed and slightly median projections in *C. blahniki* and with apex subtriangular and projected, a subapical inner wide tooth bifid, and bifid median projection well-projected in *C. chocoensis*).

Description. Forewing length 6.0 mm (n = 1), forks I, II, III and V present, discoidal, medial, and thyridial cells closed (Figure 15A). Hind wing length 3.4 mm (n = 1) slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 15B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 15C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process present, 2/3 segment length and subtriangular (Figure 39 in Johanson, 2003).

Male genitalia. Abdominal segment IX anterior lobe with rounded projection positioned midway on segment, anterodorsal margin substraight and anteroventral margins slightly concave, in lateral view (Figure 40 in Johanson, 2003). Posterior lobe with acuminated projection, positioned midway on segment with set of long setae, and posterior slightly projection, in lateral view (Figure 40 in Johanson, 2003); anterior margin substraight, central posterior lobe slightly convex, and basal plate V shaped, in ventral view (Figure 42 in Johanson, 2003). Preanal appendages thumb shaped, in lateral view (Figure 40 in Johanson, 2003); boomerang shaped, in dorsal view (Figure 41 in Johanson, 2003). Abdominal segment X subrectangular with sinuous posterodorsally and ventral margins, with anterodorsal projection, apex truncated with setae, in lateral view (Figure 40 in Johanson, 2003); subrectangular with lateral margins concave, rounded apical projections and a long and deep apical invagination U shaped, in dorsal view (Figure 41 in Johanson, 2003). Inferior appendages pipe shaped, proximal region subquadrangular shaped, length 1.8x width, distal region globose, same length and width, with a mediodorsal projection finger shaped, and a posteroventral projection present, slightly and subtriangular with sclerosed area, in lateral view (Figure 40 in Johanson, 2003); base wide than apex, base with basomesal setose projections, inner face with setose median and subapical projections, and a well-projected subapical tooth sclerosed and apex rounded, in ventral view (Figure 42 in Johanson, 2003). Phallus with calyx shaped phallobase, narrow base, with a median constriction and widening towards apex, and with a small phallotremal sclerite V shaped (Figures 43; 44 in Johanson, 2003).

Material examined. 1#Male, Ecuador: Napo, Lagoa Angrio, 16.viii.1975, Langley, A., col., [USNM948792, Holotype]

Collections. **USNM**

Remarks. This species has Male, Female (undescribed) known semaphoronts. Presents distribution records in Amazonas Lowlands and Western Amazon Piedmont freshwater ecoregions, in altitudinal range from 200–321 m a.s.l. with records in 1st, 2nd, 3rd, and 4th order freshwater environments.

Distribution. ECU.

Cochliopsyche nyurga **(Olah & Olah, 2022):220** [Ecuador: Amazonian Lowland; Terra Firme; Gareno lodge; near Puerto Napo; 400 m, #Male, OPC].

Helicopsyche (*Cochliopsyche*) *nyurga* Olah & Olah, 2022

–Olah & Olah 2022 [distribution].

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subrectangular with lateral margins substraight and apex truncated, in dorsal view (Figure 24 in Olah & Olah, 2022); (ii) inferior appendages with median inner face subtriangular projection, and (iii) apex rounded with two inner face slightly subapical teeth, in ventral view (Figure 25 in Olah & Olah, 2022). *Cochliopsyche nyurga* is similar to *C. paraguaiensis* and *C. maierae* by having abdominal segment X with lateral margin substraight, in dorsal view (Figure 24 in Olah & Olah, 2022); inferior appendages long and narrow, and inner face with a slightly projections and with two subapical teeth, in ventral view (Figure 25 in Olah & Olah, 2022). But the new species can be distinguished from these species by the abdominal segment X with apex truncated, in dorsal view (Figure 24 in Olah & Olah, 2022) (with apex rounded and a slightly apical cleft in *C. paraguaiensis* and *C. maierae*); and the inferior appendages without basomesal projection, and a median inner face subtriangular projection, in ventral view (Figure 25 in Olah & Olah, 2022) (with basomesal projection and two median inner face projection in *C. paraguaiensis* and both with basomesal projection and slightly median projection in *C. maierae*).

Description. Forewing length 5.0 mm (n = 1), forks I, II, III and V present, discoidal, medial, and thyridial cells closed. Hind wing slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed. Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae. Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process present, 2/3 segment length and subtriangular (Figure 27 in Olah & Olah, 2022).

Male genitalia. Abdominal segment IX anterior lobe with rounded projection positioned midway on segment, anterodorsal and anteroventral margins substraight with posterobasally rounded slightly projected, in lateral view (Figure 23 in Olah & Olah, 2022). Posterior lobe with acuminated projection, positioned midway on segment, without set of setae, and posterior slightly projection, in lateral view (Figure 23 in Olah & Olah, 2022); anterior margin slightly concave, central posterior lobe slightly convex, and basal plate U shaped, in ventral view (Figure 25 in Olah & Olah, 2022). Preanal appendages boxing glove shaped, in lateral view (Figure 23 in Olah & Olah, 2022); ovoid, in dorsal view (Figure 24 in Olah & Olah, 2022). Abdominal segment X subtriangular with smooth margins, apex rounded with setae, in lateral view (Figure 23 in Olah & Olah, 2022); subrectangular with lateral margins substraight, without apical invagination, in dorsal view (Figure 24 in Olah & Olah, 2022). Inferior appendages club shaped, proximal region subquadrangular shaped, length 2.1x width, distal region ovoid, length 1.6x width, with anteroventral projection finger shaped and a posteroventral projection present, slightly and subtriangular with sclerosed area, in lateral view (Figure 23 in Olah & Olah, 2022); base slightly wide than apex, inner face with setose subapical projections and two slightly subapical tooth and apex rounded, in ventral view (Figure 25 in Olah & Olah, 2022). subrectangular phallobase, narrow base and widening towards apex, and with a small phallotremal sclerite U shaped, in ventral view (Figure 26 in Olah & Olah, 2022).

Collections. **OPC**

Remarks. The description and illustration do not provide many details about the head, thorax, wing, and genitalia in ventral view, so it is necessary to illustrate and describe these characters for a better circumscription of the species. This species has only Male known semaphoronts. Presents distribution records in Amazon Lowlands freshwater ecoregions, in altitudinal range about 400 m a.s.l. with records in 5th order freshwater.

Distribution. ECU.

***Cochliopsyche ocosingua* (Johanson, 2003)**:405 [Mexico: Chiapas; Ocosingo Valley; Monte Finca Libano, M/F, INHS].

Helicopsyche (*Cochliopsyche*) *ocosingua* Johanson, 2003

–Holzenthal & Calor 2017 [catalog].

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) inferior appendages with inner face bifid and spine-like median projection, in dorsal view (Figure 64 in Johanson, 2003); (ii) with wide base and narrowing towards to apex; and (iii) a slightly subtriangular basomesal projection, in ventral view (Figure 65 in Johanson, 2003). *Cochliopsyche ocosingua* is similar to *C. lobata* and *C. xinguensis* by having abdominal segment X with slightly rounded apical projections, in dorsal view (Figure 64 in Johanson, 2003), and inferior appendages with median inner face projections, in dorsal view (Figure 64 in Johanson, 2003). But the new species can be distinguished from these species by the (i) abdominal segment X with a long and deep evagination, in dorsal view (Figure 64 in Johanson, 2003) (with short and deep evagination in *C. lobata*, and with short and shallow evagination in *C. xinguensis*); and the (ii) inferior appendages with wide subtriangular basomesal projections and apex truncated with inner face acuminated projection, in ventral view (Figure 65 in Johanson, 2003) (with wide rounded basomesal projections and apex truncated with inner face subquadrate projection in *C. lobata*, and with slightly and rounded basomesal projection, and apex subtriangular with inner face pointed projection in *C. xinguensis*).

Description. Forewing length 5.6 mm (n = 1), forks I, II, III and V present, discoidal, medial, and thyridial cells closed. Hind wing length 3.5 mm (n = 1) slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed. Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 16C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process absent.

Male genitalia. Abdominal segment IX anterior lobe with rounded projection positioned midway on segment, anterodorsal and anteroventral margins substraight, in lateral view (Figure 63 in Johanson, 2003). Posterior lobe with acuminated projection, positioned dorsally on segment, without set of setae, in lateral view (Figure 63 in

Johanson, 2003); anterior margin concave, central posterior lobe convex, and basal plate U shaped, in ventral view (Figure 65 in Johanson, 2003). Preanal appendages globose, in lateral view (Figure 63 in Johanson, 2003); globose, in dorsal view (Figure 64 in Johanson, 2003). Abdominal segment X subtriangular with sinuous posterodorsally and ventral margins, apex rounded with setae, in lateral view (Figure 63 in Johanson, 2003); subquadrangular with lateral margins substraight, rounded subapical and apical projections, and a long and shallow apical invagination U shaped, in dorsal view (Figure 64 in Johanson, 2003). Inferior appendages pipe shaped, proximal region subquadrangular shaped, length 2.5x width, distal region globose, same length and width, and a posteroventral slightly evagination and distal area sclerosed, in lateral view (Figure 63 in Johanson, 2003); base wide than apex, base with basomesal setose subtriangular projections, inner face with setose subapical projections, apical subrectangular projection and apex truncated, in ventral view (Figure 65 in Johanson, 2003). Phallus with calyx shaped phallobase, wide base, with a median constriction and slightly widening towards apex, and with a broad phallotremal sclerite U shaped (Figure 66;67 in Johanson, 2003).

Material examined. Brazil: Rio Grande do Sul, Bossoroca, Barra do Angico, Rio Piratinim (28°32’5.53”S, 54°57’30.05”W, 131 m a.s.l.), 11.ii.2014, Pes, A.M.O. col. [UFBA].

Collections. **INHS**; NRM; UFBA

Remarks. The species has a disjunct distribution record with occurrences in Chiapas, Mexico and now in Rio Grande do Sul, Brazil. Despite this, the characteristics of the head, wings and genitalia remain consistent between the Mexican specimens (holotype) and the Brazilian specimens (new record), and it is possible that the species has a wide distribution that is not yet known. This species has Male, Female (undescribed) known semaphoronts. Presents distribution records in Lower Uruguay and Upper Usumacinta freshwater ecoregions, in altitudinal range from 138–631 m a.s.l. with records in 5th order freshwater environments.

Distribution. BRA(**RS**), MEX.

Cochliopsyche opalescens **Flint, 1972:245** [Argentina; Misiones; Puerto Rico, #Male, USNM].

Helicopsyche (*Cochliopsyche*) *opalescens* Johanson, 2003

(Figure 16)

–Flint 1974:145 [♂; distribution]. –Flint 1992:81 [distribution]. –Johanson 1995:107 [catalog]. –Flint 1996:428 [distribution]. –Johanson 1998:128 [status phylogeny]. –Johanson 2003:393 [♂; redescription; distribution]. –Blahnik et al. 2004:4 [distribution]. –Cohen 2004:77 [distribution]. –Paprocki et al. 2004:6 [checklist]. –Dumas et al. 2009:372 [distribution]. –Calor 2011:320 [checklist]. –Paprocki & França 2014:17 [checklist]. –Holzenthal & Calor 2017 [catalog].

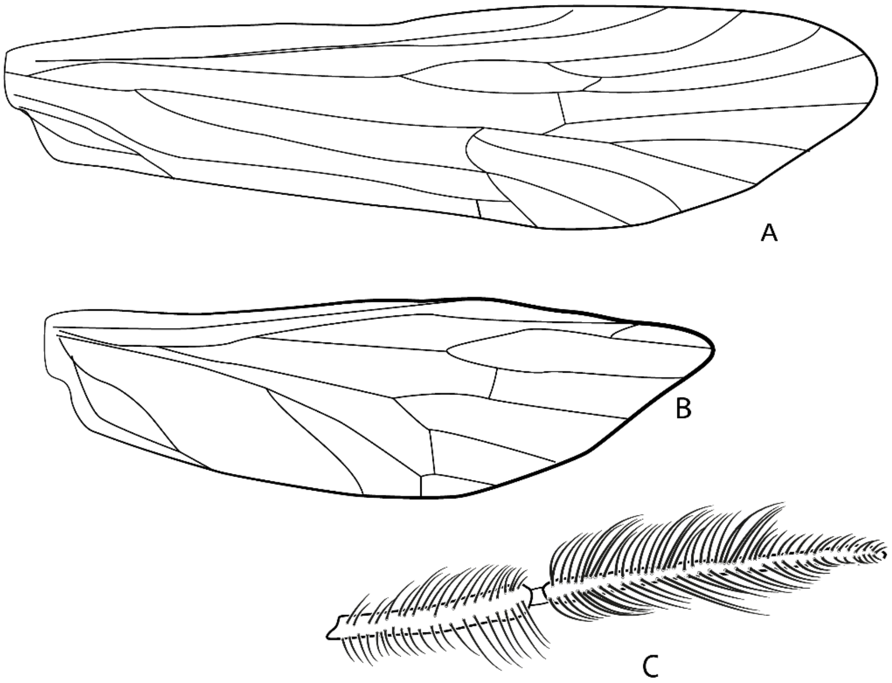

Figure 16. *Cochliopsyche xinguensis*: Male, A. Forewing; B. Hind wing; C. Maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subquadrate with apex rounded and slightly apical cleft, in dorsal view (Figure 25 in Johanson, 2003); (ii) inferior appendages with basomesal projections; (iii) proximal region narrow, apex wide globose and an inner face slightly subapical tooth, in ventral view (Figure 26 in Johanson, 2003). *Cochliopsyche opalescens* is similar to *C. kjelli* and *C. uwape* **n. sp.** by having abdominal segment X subquadrate, in dorsal view (Figure 25 in Johanson, 2003); inferior appendages with long proximal region more than 2 time the width, and distal region ovoid, in lateral view (Figure 24 in Johanson, 2003). But the new species can be distinguished from these species by the abdominal segment X with rounded apex and without subapical and apical projection, in dorsal view (Figure 25 in Johanson, 2003) (with apex truncated and slightly apical projection in *C. kjelli* and with apex trapezoid, and apical and subapical projection in *C. uwape* **n. sp.**); and the inferior appendages with an inner face sclerosed subapical tooth, in ventral view (Figure 26 in Johanson, 2003) (both with two inner face sclerosed subapical teeth in *C. kjelli* and *C. uwape* **n. sp.**).

Description. Forewing length 4.9–5.5 mm (n = 2), forks I, II, III and V present, discoidal, medial, and thyridial cells closed (Figure 16A). Hind wing length 3.2 mm (n = 1) slightly pointed; forks I and V present; discoidal cell open, medial and thyridial cells closed (Figure 16B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 16C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process present, less than 1/3 segment length and subtriangular (Figure 23 in Johanson, 2003).

Male genitalia. Abdominal segment IX anterior lobe with acuminated projection positioned ventrally on segment, anterodorsal and anteroventral margins substraight, in lateral view (Figure 24 in Johanson, 2003). Posterior lobe with acuminated projection, positioned dorsally on segment, without set of setae, and posterior slightly projection, in lateral view (Figure 24 in Johanson, 2003); anterior margin slightly convex, central posterior lobe convex, and basal plate U shaped, in ventral view (Figure 26 in Johanson, 2003). Preanal appendages globose, in lateral view (Figure 24 in Johanson, 2003); thumb shaped, in dorsal view (Figure 25 in Johanson, 2003). Abdominal segment X subtriangular with sinuous posterodorsally and ventral margins, apex acuminated with setae, in lateral view (Figure 24 in Johanson, 2003); subquadrangular with lateral margins substraight, and a very short and shallow apical cleft, in dorsal view (Figure 25 in Johanson, 2003). Inferior appendages club shaped, proximal region subquadrangular shaped, length 2.6x width, distal region ovoid, length 1.2x width, with anteroventral projection finger shaped, and, and a posteroventral projection present, slightly and subtriangular with sclerosed area, in lateral view (Figure 24 in Johanson, 2003); apex wide than base, base with basomesal setose projections, and a slightly subapical tooth sclerosed and apex rounded, in ventral view (Figure 26 in Johanson, 2003). Phallus with calyx shaped phallobase, wide base, with a subbasal constriction and slightly widening towards apex, and with a broad phallotremal sclerite U shaped (Figures 27; 28 in Johanson, 2003).

Material examined. 3#Male, Brazil: Bahia, Barreiras, Cachoeira Redondo 11°53'S, 45°25'W, 573, 5.vi.2008, Bravo, Menezes, Alvim & Silva-Neto, col., [UFBA]; same data, except 1#Male, Cachoeira Acaba Vidas, 14.x.2008, Coleta 2, col., [UFBA]; same data, except 1#Male, Maranhão, Caxias, Igarape Ponti, 19.x.2015, Desidério, G.R., col., [INPA]; same data, except 14#Male, Mato Grosso, Rio Arica, Km 391 on Cuiaba-Rondonopolis Rd., 22.iv.1981, Wojcik, D.P., col., [USNM01866346]; same data, except 2#Male, Rio Papagaio, 31.X.2012, 31.x-01.xi.2012, Hamada, N., Nascimento, J., col., [INPA]; same data, except 1#Male, Minas Gerais, PN Peruaçu, Rio Peruaçu (15°06.674'S, 44°14.487'W, 590 m [a.s.l.]), 16.xi.2001, Holzenthal, R., Paprocki, H. & Amarante M.*C*., col., [UMSP000082806]; same data, except 11#Male, Rondonia, Creek 8km S. Cacaulandia, 21.xi.1991, D. Petr, col., [USNM01866357]; same data, except 1#Male, São Paulo, Piracicaba, 20.i.1965, Triplehorn, *C*.A., col., [USNM01866341]; same data, except 1 #Male, 11.xi.1965, Triplehorn, *C*.A., col., [USNM01866340]; same data, except 1 #Male, Altinópolis, Cachoeira dos Macacos (20°55.380'S, 47°22.758'W, 759 m [a.s.l.]), 18.xi.2003, Holzenthal, R., Paprocki, H. & Calor, A., col., [UMSP0000120885]; same data, except 1 #Male, Riberão Preto, ponte velha sentido Jardinópolis, Rio Pardo, 6.ix.2008, Calor, A., col., [UFBA]. 2 #Males, Paraguay: Ao. Tapiracuay, San Estenislao, 27.xi.1973, Flint, O.S. Jr., col., [USNM01866339]. 7 #Males, Uruguay: Antigas, San Grogorio, 29.xi.1959, Carbunell, C.S., Mesa A. & San Martin, P.R., col., [USNM01866344]. 10 #Males, Venezuela: Bolivar, Anacoco, R. Cuyuni, 10-23.viii.1979, Exp. La Salle, col. [USNM01866342]

Collections. **USNM**; FNMH; MZUSP.

Remarks. The new species shows morphological variations in some species such as basomesal projection of inferior appendage, in ventral view, with a bifid projection or one projection (most common). The most widely distributed species in the genus, it has morphological characteristics very similar to other species described here, such as *C. kjelli* **n. sp.** and *C. uwape* **n. sp.** Therefore, it is necessary to analyze the material already identified as *C. opalescens* and not analyzed in this study in order to confirm the identifications and delimit the species' more accurately distribution range. This species has only male known semaphoronts. Presents distribution records in Amazon Estuary & Coastal Drainages, Amazon Guiana Shield, Amazon Lowlands, Essequibo, Guapore - Itenez, Lower Parana, Lower Uruguay, Madeira Brazilian Shield, Mamore - Madre de Dios Piedmont, Noth Andean Pacific Slopes - Rio Atrato, Northeastern Mata Atlântica, Paraguay, Rio Negro, São Francisco, Upper Parana, Upper Uruguay, Western Amazon Piedmont, and Xingu freshwater ecoregions, in altitudinal range from 36–2121 m a.s.l. with records in 1st to 9th order freshwater environments.

Distribution. ARG; BRA (AM; **BA**, DF; MA; MG; MT; PA; PR; RJ; RO; RR; SC; SP); ECU; GUY; PRY; PER; SUR; URY; VEN.

***Cochliopsyche pandeirosa* (Johanson, 2003):407** [Brazil: Minas Gerais: Rio Pandeirosa in Pandeiros; ca. 50 km W Januária; 15°30.727'S; 44°30.255'W; el. 495 m, #Male #Female, MZUSP].

Helicopsyche (*Cochliopsyche*) *pandeirosa* Johanson, 2003

(Figure 17)

–Paprocki & França 2014:17 [checklist]. –Holzenthal & Calor 2017 [catalog].

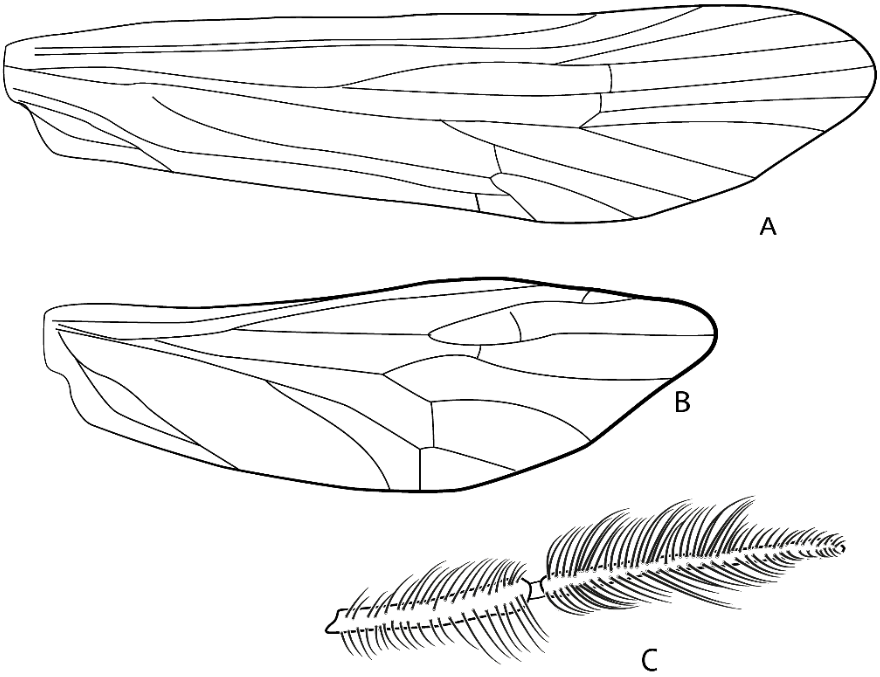

Figure 17. *Cochliopsyche pandeirosa*: Male, A. Forewing; B. Hind wing; C. Maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subquadrate with apex rounded and slightly apical cleft; (ii) preanal appendages with different shape, in dorsal view (Figure 77 in Johanson, 2003);

(iii) inferior appendages narrow, long with subtriangular apex and slightly subapical sclerosed tooth, in ventral view (Figure 78 in Johanson, 2003). *Cochliopsyche pandeirosa* is similar to *C. paraguaiensis* and *C. maierae* by having abdominal segment X with apical slightly cleft, in dorsal view (Figure 77 in Johanson, 2003); inferior appendages long and filiform, and inner face with a slightly projections and with subapical tooth, in ventral view (Figure 78 in Johanson, 2003). But the new species can be distinguished from these species by the inferior appendages curved 35° in relation to the main axis of abdominal segment IX, in ventral view (Figure 78 in Johanson, 2003) (curvatures never greater than 10° in *C. paraguaiensis* and *C. maierae*); and the inferior appendages with a slightly sclerosed subapical tooth, in ventral view (Figure 78 in Johanson, 2003) (both with two inner face sclerosed subapical teeth in *C. paraguaiensis* and *C. maierae*).

Description. Forewing length 6.1 mm (n = 1); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 17A). Hind wing length 4.0 mm (n = 1) slightly pointed; forks I and V present; discoidal, medial and thyridial cells closed (Figure 17B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint about 1.5x basal joint length with long setae (Figure 17C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process present, less than 1/3 segment length and subtriangular (Figure 74 in Johanson, 2003).

Male genitalia. Abdominal segment IX anterior lobe with rounded projection positioned midway on segment, anterodorsal and anteroventral margins substraight, in lateral view (Figure 75 in Johanson, 2003). Posterior lobe with acuminated projection, positioned dorsally on segment with set of long setae, in lateral view (Figure 75 in Johanson, 2003); anterior margin concave, central posterior lobe convex, and basal plate U shaped, in ventral view (Figure 78 in Johanson, 2003). Preanal appendages right pyriform shaped and left globose, in lateral view (Figure 75 in Johanson, 2003); left ovoid and right pyriform, in dorsal view (Figure 77 in Johanson, 2003). Abdominal segment X subrectangular with sinuous posterodorsally and ventral margins, apex truncated with setae, in lateral view (Figure 75 in Johanson, 2003); subquadrangular with lateral margins substraight, and a very short and shallow apical cleft, in dorsal view (Figure 77 in Johanson, 2003). Inferior appendages club shaped, proximal region subquadrangular shaped, length 3.3x width, distal region ovoid, same length and width, with anteroventral projection finger shaped well-projected, and, and a posteroventral projection present, slightly and subtriangular with sclerosed area, in lateral view (Figure 75 in Johanson, 2003); base wide than apex, base with basomesal setose projections, inner face with setose median and subapical projections, and a slightly subapical tooth sclerosed and apex subtriangular, in ventral view (Figure 78 in Johanson, 2003). subrectangular phallobase, wide median region, and narrowing towards apex, and with a broad phallotremal sclerite U shaped (Figure 79;80 in Johanson, 2003).

Material examined. 1 #Male, Brazil: Minas Gerais, Pandeirosa, Rio Pandeirosa ca. 50km W Januária (15°30.727'S, 44°30.225'W, 495 m [a.s.l]), 17.xi.2001, Holzenthal, R. & Amarante, M.C., col., [UMSP000080979, Paratype]; same data, except 1 #Female, [UMSP000080993, Paratype].

Collections. **MZUSP**; UMSP; NRM; USNM .

Remarks. This species has male and female (undescribed) known, and presents distribution records in São Francisco freshwater ecoregion, in altitudinal range around 546 m a.s.l. with records in 2nd order freshwater environments.

Distribution. BRA (MG).

***Cochliopsyche paraguaiensis* (Johanson, 2003):413** [Paraguay: Rio Aquidaban; Cerro Cora, #Male, USNM].

Helicopsyche (*Cochliopsyche*) *paraguaiensis* Johanson, 2003

–Holzenthal & Calor 2017 [catalog].

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subquadrate with apex rounded and slightly apical cleft; and (ii) inferior appendages with distal region subtriangular, in lateral view (Figure 93 in Johanson, 2003); and (iii) with two inner face median projection and apical t**ee**th, in ventral view (Figure 95 in Johanson, 2003). *Cochliopsyche paraguaiensis* is similar to *C. nyurga* and *C. maierae* by having abdominal segment X with lateral margin substraight, in dorsal view (Figure 94 in Johanson, 2003); inferior appendages long and narrow, and inner face with a slightly projections and with two subapical teeth, in ventral view (Figure 95 in Johanson, 2003). But the new species can be distinguished from these species by the abdominal segment X subquadrate with apical cleft, in dorsal view (Figure 94 in Johanson, 2003) (subrectangular without apical cleft in *C. nyurga* and subrectangular with apical cleft in *C. maierae*); and the inferior appendages with inner face bifid median projections, slightly projected and subtriangular, in ventral view (Figure 95 in Johanson, 2003) (with inner face unique median projections, well-projected and subtriangular in *C. nyurga* and without inner face median projections in *C. maierae*).

Description. Forewing length 5.2 mm (n = 1); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 92 in Johanson, 2003). Hind wing length 3.4 mm (n = 1) slightly pointed; forks I and V present; discoidal cell opens, medial and thyridial cells closed (Figure 92 in Johanson, 2003). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae. Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process absent.

Male genitalia. Abdominal segment IX anterior lobe unprojected, anterodorsal margin substraight and anteroventral margins slightly concave, in lateral view (Figure 93 in Johanson, 2003). Posterior lobe with acuminated projection, positioned dorsally on segment with set of long setae, and posterior finger shape projection, in lateral view (Figure 93 in Johanson, 2003); anterior margin concave, central posterior lobe convex, and basal plate U shaped, in ventral view (Figure 95 in Johanson, 2003). Preanal appendages boxing glove shaped, in lateral view (Figure 93 in Johanson, 2003); ovoid, in dorsal view (Figure 94 in Johanson, 2003). Abdominal segment X subtriangular with sinuous posterodorsally margins, apex acuminated with setae, in lateral view (Figure 93 in Johanson, 2003); subquadrangular with lateral margins substraight, and a very short and shallow apical cleft, in dorsal view (Figure 94 in Johanson, 2003). Inferior appendages club shaped, proximal region subquadrangular shaped, length 2.2x width, distal region subtriangular, length 1.3x width, with anteroventral projection finger shaped well-projected, and, and a posteroventral projection present, slightly and subtriangular with sclerosed area, in lateral view (Figure 93 in Johanson, 2003); base slightly wide than apex, base with basomesal setose projections, and two slightly subapical tooth and apex projected and subtriangular, in ventral view (Figure 95 in Johanson, 2003). Phallus with calyx shaped phallobase, narrow base, with a median constriction and widening towards apex, and with a small phallotremal sclerite U shaped (Figures 96; 97 in Johanson, 2003).

Material examined. 1#Male, Paraguay: Cerro Cora, Rio Aquidaban, 29.nov.1973, Flint, O.S. Jr., col., [USNM01883589, Holotype]

Collections. **USNM**.

Remarks. This species has only male known, and presents distribution records in Paraguay freshwater ecoregion, in altitudinal range around 263 m a.s.l. with records in 2nd order freshwater environments.

Distribution. PRY.

***Cochliopsyche puyoa* (Johanson, 2003):406** [Ecuador: Past. Puyo 22 km W, #Male #Female, USNM].

Helicopsyche (*Cochliopsyche*) *puyoa* Johanson, 2003

(Figure 18)

–Holzenthal & Calor 2017 [catalog].

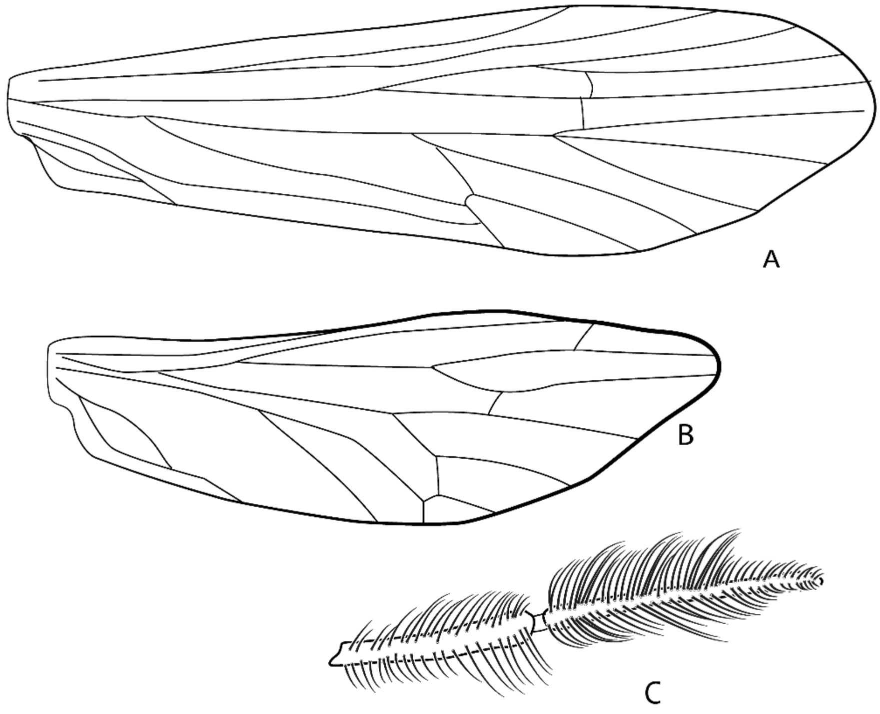

Figure 18. *Cochliopsyche puyoa*: Male, A. Forewing; B. Hind wing; C. Maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subrectangular with apical long and deep evagination, in dorsal view (Figure 70 in Johanson, 2003); (ii) inferior appendages with two slightly basomesal projections; (iii) proximal region narrow, distal region wide apex and an inner face slightly tooth, in ventral view (Figure 71 in Johanson, 2003). *Cochliopsyche puyoa* is similar to *C. vazquezae* and *C. uwape* **n. sp.** by having inferior appendages with a finger shaped basomesal projection, and inner face sclerosed subapical tooth, in ventral view (Figure 71 in Johanson, 2003). But the new species can be distinguished from these species by the abdominal segment X subrectangular without subapical projections and apical projections rounded, in dorsal view (Figure 70 in Johanson, 2003) (with abdominal segment X subquadrangular with subapical projections and apical projections acuminated in *C. vazquezae* and *C. uwape* **n. sp.**); and the inferior appendages with two slightly basomesal projections and a subapical tooth, in ventral view (Figure 71 in Johanson, 2003) (with two basomesal finger shaped projections and two subapical teeth in *C. vazquezae* and *C. uwape* **n. sp.**).

Description. Forewing length 6.5 mm (n = 1); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 18A). Hind wing length 4.7 mm (n = 1) slightly pointed; forks I and V present; discoidal cell opens, medial and thyridial cells closed (Figure 18B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 18C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process subtriangular, shorter than 1/3 segment length (Figure 68 in Johanson, 2003).

Male genitalia. Abdominal segment IX anterior lobe with acuminated projection positioned dorsally on segment, anterodorsal margin substraight and anteroventral margins slightly concave, in lateral view (Figure 69 in Johanson, 2003). Posterior lobe with rounded projection, positioned ventrally on segment, without set of setae, in lateral view (Figure 69 in Johanson, 2003); anterior margin substraight, central posterior lobe convex, and basal plate U shaped, in ventral view (Figure 71 in Johanson, 2003). Preanal appendages pyriform shaped, in lateral view (Figure 69 in Johanson, 2003); globose, in dorsal view (Figure 70 in Johanson, 2003). Abdominal segment X subtriangular with sinuous posterodorsally margins, apex rounded with setae, in lateral view (Figure 69 in Johanson, 2003); subrectangular with lateral margins substraight, rounded apical projections and a short and deep apical invagination U shaped, in dorsal view (Figure 70 in Johanson, 2003). Inferior appendages club shaped, proximal region subquadrangular shaped, length 1.9x width, distal region ovoid, length 1.4x width, with anteroventral projection rounded, and, and a posteroventral projection present, slightly and subtriangular with sclerosed area, in lateral view (Figure 69 in Johanson, 2003); base wide than apex, base with basomesal setose projections, and a subapical tooth sclerosed and apex projected and subtriangular, in ventral view (Figure 71 in Johanson, 2003). Phallus with calyx shaped phallobase, wide base, with a subbasal constriction and slightly widening towards apex, and with a broad phallotremal sclerite U shaped (Figures 72; 73 in Johanson, 2003).

Material examined. 4 #Males, Ecuador: Napo, Limoncocha, 16.vi.1977, Spangler, P. & Givens, D.R., col. [USNM01866351, Paratype]; same data, except 1 #Male, Ecuador: Pastaza, unnamed stream, trib. to Rio Anzu, Sacha Yachak (1.40601°S, 78.08759°W, 2,539 m [a.s.l.]), 23.ix.2021, Ríos-Touma, B., Holzenthal, R., Frandsen, P., Errigo, I. & Amigo, X., col. [UMSP000502144]; same data, except 1 #Female, [UMSP000502145]; same data, except 1 #Male, Brazil: Bahia, MAMI 24LEN, 24.iii.2012, Calor, A., col., [UFBA]

Collections. **USNM**; UFBA; UMSP.

Remarks. The new species shows morphological variations in some species such as abdominal sternum VIth process, some specimens do not show anterior constriction as seen in the Paratype. This species has Male, Female (undescribed) known semaphoronts. Presents distribution records in Amazonas High Andes, São Francisco, and Western Amazon Piedmont freshwater ecoregions, in altitudinal range from 259–1458 m a.s.l. with records in 1st, 2nd, and 4th order freshwater environments.

Distribution. ECU.

***Cochliopsyche vazquezae* Flint, 1986:214** [Mexico: Chiapas; Río Tulijá; 48 km south of Palenque, #Male, USNM].

Helicopsyche (*Cochliopsyche*) *vazquezae* Johanson, 2003

–Holzenthal 1988:75 [distribution]. –Monson et al. 1988:154 [larva; pupa; biology; distribution]. –Johanson 1995:107 [catalog]. –Johanson 1998:129 [status phylogeny]. –Muñoz-Quesada 2000:275 [checklist]. –Johanson 2003:392 [♂; redescription; distribution]. –Bueno-Soria & Barba-Álvarez 2011:354 [checklist]. –Holzenthal & Calor 2017 [catalog]. Barba-Álvarez et al. 2019:85 [checklist].

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X subquadrangular with trapezoid apex; (ii) apical evagination V shaped with sinuous margins, in dorsal view; (iii) inferior appendages with distal region wide and projected towards inner face with two slightly sclerosed subapical teeth, in ventral view (Figure 20 in Johanson, 2003). *Cochliopsyche vazquezae* is similar to *C. puyoa* and *C. kjelli* by having inferior appendages club shaped, in lateral view (Figure 18 in Johanson, 2003), proximal region narrows and distal region wide, in ventral view (Figure 20 in Johanson, 2003), and inner face sclerosed subapical tooth, in ventral view (Figure 20 in Johanson, 2003). But the new species can be distinguished from these species by the abdominal segment X with subapical projections and apex with V shaped evagination, in dorsal view (Figure 19 in Johanson, 2003) (without subapical projection and apex with U shaped evagination in *C. puyoa* and without subapical projection and apical evagination in *C. kjelli*); and the inferior appendages with truncated apex and projected towards inner face with two slightly sclerosed subapical teeth, in ventral view

(Figure 20 in Johanson, 2003) (with truncated apex and unprojected towards inner face with a slightly sclerosed subapical tooth in *C. puyoa* and with rounded apex and slightly projected towards inner face with two slightly sclerosed subapical teeth in *C. kjelli*).

Description. Forewing length 5.6 mm (n = 1); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 21B in Johanson, 1998). Hind wing length 3.8 mm (n = 1) slightly pointed; forks I and V present; discoidal cell opens, medial and thyridial cells closed (Figure 21B in Johanson, 1998). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 12B in Johanson, 1998). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process subtriangular, shorter than 1/3 segment length (Figure 17 in Johanson, 2003).

Male genitalia. Abdominal segment IX anterior lobe with rounded projection positioned dorsally on segment, anterodorsal margin substraight and anteroventral margins slightly concave, in lateral view (Figure 18 in Johanson, 2003). Posterior lobe with acuminated projection, positioned dorsally on segment, without set of setae, in lateral view (Figure 18 in Johanson, 2003); anterior margin substraight, central posterior lobe convex, and basal plate V shaped, in ventral view (Figure 20 in Johanson, 2003). Preanal appendages thumb shaped, in lateral view (Figure 18 in Johanson, 2003); boxing glove shaped, in dorsal view (Figure 19 in Johanson, 2003). Abdominal segment

X digiteform with sinuous posterodorsally margins, with slightly anterodorsal projection, apex rounded with setae, in lateral view (Figure 18 in Johanson, 2003); subquadrangular with lateral margins concave, subtriangular apical projections and a long, deep with sinuous margin apical invagination V shaped, in dorsal view (Figure 19 in Johanson, 2003). Inferior appendages club shaped, proximal region subquadrangular shaped, length 2x width, distal region ovoid, length 1.4x width, with anteroventral projection finger shaped, and, and a posteroventral projection present, slightly and subtriangular with sclerosed area, in lateral view (Figure 18 in Johanson, 2003); base wide than apex, base with basomesal setose projections, inner face with setose subapical projections and two slightly subapical tooth sclerosed and apex truncated, in ventral view (Figure 20 in Johanson, 2003). Phallus with calyx shaped phallobase, wide base, with a median constriction and widening towards apex, and with a small ovoid phallotremal sclerite U shaped, and membranous ornamentation on the apex (Figures 21; 22 in Johanson, 2003).

Material examined. 1 #Male, Colombia: Antioquia, Rio Claro, 3.v.1984, Matthias, U., col., [USNM01866349, Paratype]. 1 #Male, Honduras: Rio Humuya, NW. Comayagua, 3.viii.1967, Flint, O.S. Jr., col., [USNM01866348, Paratype]. 10 #Males, Mexico: Chiapas, Rio Tulija, 48km S. Palenque, 17.v.1981, C.M. & Flint, O.S. Jr., col., [USNM01866350]. 1 #Male, Brazil: Pará, Rio Xingu camp (52°22'W, 3°39'S) ca. 60km S Altamira, 1-7.x.1986, Spangler, P. & Flint, O.S. Jr., col. [UMSP000070788, Paratype].

Collections. **USNM**; INHS; UMSP; USNM.

Remarks. This species has male, larva, pupa, and case known. It presents distribution records in Amazonas High Andes, Grijalva - Usumacinta, Mamore - Madre de Dios Piedmont, Maracaibo, San Juan (Nicaragua/Costa Rica), and Upper Usumacinta freshwater ecoregions, in altitudinal range from 8–1164 m a.s.l. with records in 1st to 5th order freshwater environments.

Distribution. BOL.

***Cochliopsyche xinguensis* (Johanson, 2003):397** [Brazil: Pará; Rio Xingu Camp; 3°39'S; 52°22'W; ca. 60 km S Altamira, #Male#Female, MZUSP].

Helicopsyche (*Cochliopsyche*) *xinguensis* Johanson, 2003

(Figure 19)

–Paprocki & França 2014:17 [checklist]. –Holzenthal & Calor 2017 [catalog].

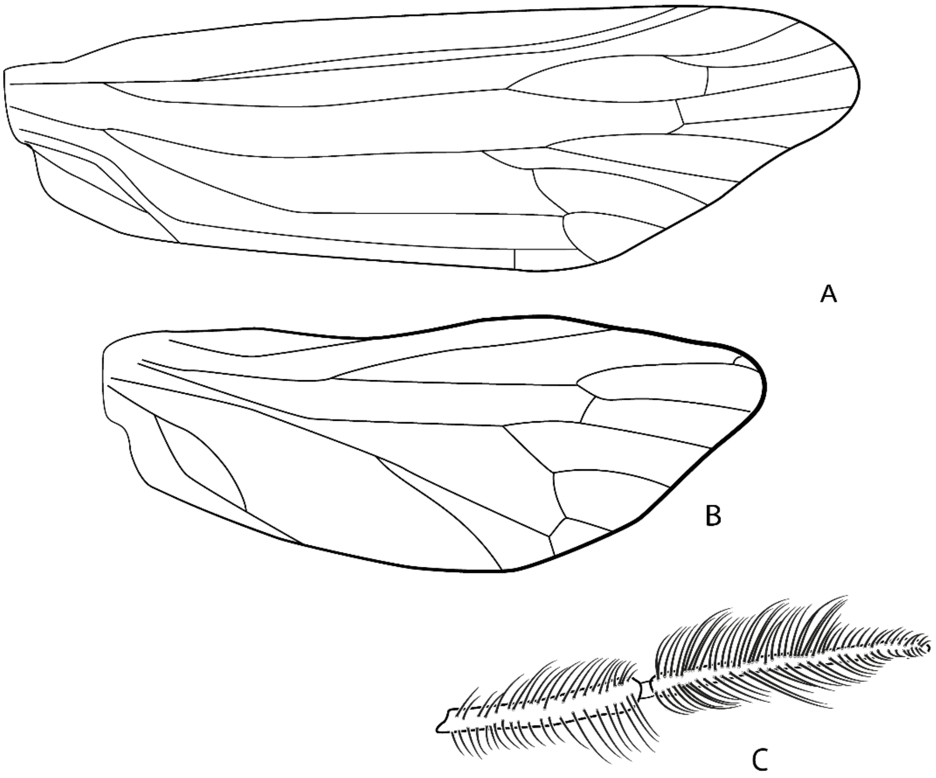

Figure 19. *Cochliopsyche xinguensis*: Male, A. Forewing; B. Hind wing; C. Maxillary palp.

Diagnosis. The species can be differentiated from congeners by set of male characters: (i) abdominal segment X with apical and subapical projection well-projected forming a two diamond shaped lobe; and (ii) inferior appendages with mediodorsal wide and bifid projection, in lateral view (Figure 34 in Johanson, 2003); (iii) inferior appendages with apex subtriangular projected towards inner face with subapical very pointed tooth, in ventral view (Figure 36 in Johanson, 2003). *Cochliopsyche xinguensis* is similar to *C. lobata* and *C. ocosingua* by having abdominal segment X with slightly rounded apical projections, in dorsal view (Figure 35 in Johanson, 2003), and inferior appendages with median inner face projections, in dorsal view (Figure 35 in Johanson, 2003). But the new species can be distinguished from these species by the abdominal segment X with subapical projection well-projected with apex acuminated, in dorsal view (Figure 35 in Johanson, 2003) (both with subapical slightly rounded projection in *C. lobata* and *C. ocosingua*); and the inferior appendages with mediodorsal projection wide and with apex bifid, in dorsal view (Figure 35 in Johanson, 2003), and apex projected towards inner face with a subtriangular subapical tooth, in ventral view (Figure 36 in Johanson, 2003) (with mediodorsal projection narrow and finger shaped apex projected towards inner face with a subquadrangular subapical projection in *C. lobata* and with mediodorsal spine like projection, and apex projected towards inner face with a slightly acuminated subapical projection in *C. ocosingua*).

Description. Forewing length 7.5 mm (n = 1); forks I, II, III and V present; discoidal, medial, and thyridial cells closed (Figure 19A). Hind wing length 4.6 mm (n = 1) slightly pointed; forks I and V present; discoidal cell opens, medial and thyridial cells closed (Figure 19B). Head. Antennae more than 1.2x body length, scape with long setae, barrel shaped. Cephalic warts present covers almost all dorsal region of head, ovoid with long setae. Postocullar warts present, half-moon shaped with long setae. Maxillary palps 2-segmented, distal joint less than 1.5x basal joint length with long setae (Figure 19C). Labial palps 3-segmented with long setae. Thorax. Pronotum with single pair of long and oval setal warts with setae. Mesoscutum diamond shaped, with a pair of longitudinal subtriangular pale band with long setae; mesoscutellum subtriangular with long setae, with a pair of globose setal warts with long setae. Legs tibial spur form 1,2,2. Abdomen. Abdominal sternum VIth process absent.

Male genitalia. Abdominal segment IX anterior lobe with acuminated projection positioned midway on segment, anterodorsal and anteroventral margins substraight, in lateral view (Figure 34 in Johanson, 2003). Posterior lobe with acuminated projection, positioned dorsally on segment, without set of setae, in lateral view (Figure 34 in Johanson, 2003); anterior margin substraight, central posterior lobe substraight, and basal plate U shaped, in ventral view (Figure 36 in Johanson, 2003). Preanal appendages boxing glove shaped, in lateral view (Figure 34 in Johanson, 2003); boxing glove shaped, in dorsal view (Figure 35 in Johanson, 2003). Abdominal segment X subtriangular with sinuous posterodorsally margins, apex rounded with setae, in lateral view (Figure 34 in Johanson, 2003); subtriangular with lateral margins substraight, subtriangular subapical and apical projections, and a short and shallow apical invagination V shaped, in dorsal view (Figure 35 in Johanson, 2003). Inferior appendages pipe shaped, proximal region subquadrangular shaped, length 1.7x width, distal region subtriangular, same length and width, with anteroventral projection rounded, and with a mediodorsal projection finger shaped, and a posteroventral projection present, slightly and subtriangular with sclerosed area, in lateral view (Figure 34 in Johanson, 2003); base wide and narrowing toward apex, base with basomesal setose projections, inner face with setose median projections, an apical well projected tooth and apex subtriangular, in ventral view (Figure 36 in Johanson, 2003). subrectangular phallobase, wide base, with a slightly median constriction, and narrowing towards apex, and with a small phallotremal sclerite trapezoid, in ventral view (Figures 37; 38 in Johanson, 2003).

Material examined. 1 #Male, Brazil: Pará, Rio Xingu camp (52°22'W, 3°39'S) ca. 60km S Altamira, 1-7.x.1986, Spangler, P. & Flint, O.S. Jr., col., [UMSP000070788, Paratype]; same data, except 1 #Male, [UMSP000070789, Paratype].

Collections. **MZUSP**; USNM; UMSP.

Remarks. This species has male and female (undescribed) known. Presents distribution records in Madeira Brazilian Shield, Tapajos - Juruena, and Xingu freshwater ecoregions, in altitudinal range from 34–129 m a.s.l. with records in 3rd, 4th, and 7th order freshwater environments.

Key to Neotropical Helicopsychidae genera

1. Larva with large postgenal concavity patch of 8-10 setae in vicinity of head setae 9 and 10 positions; pupa with anterior hooks of segments III-VI with one tooth; adults with formula of tibial spurs 1,2,2, antennae for 1.2x to 3x body length … *Cochliopsyche*

   Larva with single setae each at 9 and 10 positions; pupa with anterior hooks of segments III-VI with two or more teeth; adults with formula of tibial spurs 2,2,4, antennae less than 1.2x body length… *Helicopsyche*

***Key to Cochliopsyche* species based on adult male**

1. Inferior appendages with a mediodorsal projection, in lateral view…2

   Inferior appendages without mediodorsal projection, in lateral view…15
2. Abdominal segment X with apical invagination, in dorsal view…3

   Abdominal segment X without apical invagination, generally with slightly apical cleft, in dorsal view…10
3. Abdominal segment X with substraight lateral margins, without lateral projections, in dorsal view…4

   Abdominal segment X with lateral projections, in dorsal view…8
4. Inferior appendages with two subapical teeth on the inner face, in ventral view…5

   Inferior appendages with one sclerosed inner face subapical tooth, in ventral view…7
5. Abdominal segment X subtriangular, with a short and deep apical invagination, in dorsal view… *Cochliopsyche flinti* **n. sp.**

   Abdominal segment X subrectangular, with a long and shallow apical invagination, in dorsal view…6
6. Inferior appendages with median inner face rounded well projected in front of the abdominal segment X, and apex rounded, in dorsal view, without tooth on the inner face…*C. mulleri* **n. sp.**

   Inferior appendages without median inner face projection, and apex truncated with two subapical teeth on the inner face… *C. clara*
7. Inferior appendages with apex projected, rounded and with small subapical inner face sclerosed tooth, in ventral view…*C. brazilia*

   Inferior appendages with apex truncated wide unprojected and with subapical tooth on inner face, in ventral view…*C. puyoa*

8. Preanal appendages of segment abdominal IX boxing glove shaped; abdominal segment X apex invagination V-shaped with sinuous margins, in dorsal view…*C. vazquezae*

   Preanal appendages of segment abdominal IX boot shaped; abdominal segment X apex invagination U-shaped, in dorsal view…9

9. Inferior appendages more than 1.5 times abdominal segment X length, in dorsal view… *C. amazona*

   Inferior appendages less than 1.5 times abdominal segment X length, in dorsal view…*C. uwape* **n. sp.**

10. Inferior appendages long narrow with sinuosity on inner face margin, in ventral view…11

    Inferior appendages with subequal length of abdominal segment X with a slightly sinuous inner margin and an expanded, rounded apex, in ventral view…14

11. Abdominal segment X subrectangular, in dorsal view…12

    Abdominal segment X subquadrangular, in dorsal view…13

12. Abdominal segment X with apex truncated; inferior appendages without basomesal projection, with a median inner face subtriangular projection, in dorsal view… *C. nyurga*

    Abdominal segment X with apex rounded; inferior appendages with basomesal projection, with a slightly median inner face projection, in dorsal view … *C. maierae*

13. Inferior appendages curved 35° in relation to the main axis of abdominal segment IX, with a slightly sclerosed subapical tooth, in ventral view…*C. pandeirosa*

Inferior appendages curvature never greater than 10° in relation to the main axis of abdominal segment IX, with two inner face sclerosed subapical teeth, in ventral view…*C. paraguaiensis*

14. Abdominal segment X with rounded apex, in dorsal view; inferior appendages with a subapical, sclerosed tooth on the inner face…*C. opalescens*

    Abdominal segment X with truncated apex, in dorsal view; inferior appendages with two subapical teeth on the inner face, in ventral view …*C. kjelli* **n. sp.**

15. Inferior appendages with apex truncated, and narrow projections or two teeth on the inner face, in ventral view…16

    Inferior appendages with apex rounded, with a wide subtriangular subapical with a single tooth on the inner face, in ventral view…20

16. Segment abdominal X with base with width subequal to apex, in dorsal view; inferior appendages globose or ovoid, in lateral view...17

    Segment abdominal X with base wider than apex, in dorsal view; inferior appendages with distal region subtriangular, in lateral view…19

17. Abdominal segment X with margins convex, in dorsal view; inferior appendages with basomesal projection wide and rounded, in ventral view…*C. lobata*

    Abdominal segment X with margins substraight, in dorsal view; inferior appendages with basomesal projection finger shaped, in ventral view…18

18. Abdominal segment X with median sightly cleft, apical invagination forming two rounded lobes, in dorsal view; inferior appendages with two subapical teeth on the inner face…*C. holzenthali*

    Abdominal segment X without cleft with subapical projections, apical invagination forming two subtriangular lobes, in dorsal view; inferior appendages with an internal projection pointed well projected…*C. ocosingua*

19. Inferior appendages with median widening, with an apical, narrow, pointed tooth on the inner face , in ventral view…*C. amica*

    Inferior appendages without median widening, with a broad and subtriangular tooth on the inner face, in ventral view…*C. xinguensis*

20. Abdominal segment X with subapical and apical projections acuminated; inferior appendages with subequal length to abdominal segment X, in dorsal view…*C. blahniki*

    Abdominal segment X subapical and apical when present rounded; inferior appendages with more than length to abdominal segment X, in dorsal view…21

21. Preanal appendages boomerang-shaped; abdominal segment X subrectangular without subapical projections, with a long and deep apical invagination, in dorsal view…*C. napoa*

22. Preanal appendages globose; abdominal segment X subquadrangular with subapical projections, with a shallow and deep apical invagination, in dorsal view…*C. chocoensis*

Discussion

The monophyly of *Cochliopsyche* was well supported by a total of eight unambiguous characters (Pereira et al. *in prep.*), the most notable are cephalic warts ovoid, antennae length 1.2x body length, hind leg preapical spur present (Figure 1). Adding previous diagnostic characters from Monson et al. (1988) and Flint (1986), Pereira et al. (*in prep.*) the diagnostic characters of the genus are (*Helicopsyche* characters in parenthesis):

1. Patch of 8–10 setae in vicinity of head setae 9 and 10 positions (single seta each at positions 9 and 10)

2. Antennal position at anterior edge of head capsule, adjacent to frontoclypeal apotome (antenna midway between eye and anterior edge of head capsule)
3. Pupa with anterior hooks of segments III-VI with one tooth (pupa with anterior hooks of segments III-VI with two or more teeth)
4. Three setae in vicinity of head seta 16 position (single seta at position 16)
5. Cephalic warts ovoid (Cephalic warts of other forms)
6. Antennae more than 1.2–3x body length (Antennae less than 1.2x body length)
7. Tibial spur form 1,2,2 (tibial spur form 2,2,4 or 1,2,4)

The group forms a clade with the *Helicopsyche* (*Petrotrichia*) (Afrotropical) which possibly split after the connection between the Neotropical and Afrotropical regions was broken at 130Ma (Pereira & Calor, *in prep*). The following synapomorphies absence of mesoscutal setal warts and mesoscutal longitudinal subretangular pale bands, support this clade.

After this work, we increased the number of known species by ca. 25%, totaling 21 species for the genus, which are widely distributed in the Neotropical Region. The group occurs most commonly in rivers and large lakes (Flint, 1983), but they are also recorded in first and second-order streams (Table 1). Some authors point out that most *Cochliopsyche* species are difficult to distinguish from each other because they show slight variations in genitalia, wing length, and minor differences in wing color and pattern (Johanson, 2003; Olah & Olah, 2022). Here, we also present intraspecific variations that should be considered when identifying and delimiting *Cochliopsyche* species.

Characters such as (i) presence or absence of the projection of the abdominal sternum VI, (ii) width of the mesonotum pale band, and (iii) shape of the basomesal projections of the inferior appendages seem to vary within species and are not recommended as diagnostic characters in future descriptions. Characters related to abdominal segment X and the inferior appendages are the most recommended for the identification and description of *Cochliopsyche* species, as they show little or no variation between the specimens analyzed.

We have herein established a recommendation for the terminology of morphological characters for the group to standardized the descriptions with what is applied to recent descriptions within Helicopsychidae in the Neotropical region (e.g., Vilarino & Calor, 2017; Dumas & Nessimian, 2019; Cavalcante-Silva et al., 2022; Bonfá-Neto et al., 2023).

The shortfalls in knowledge of the evolution (Darwinian shortfall) of the group were addressed by Pereira & Calor (*in prep*), who established hypotheses for the relationship of this genus with the other representatives of Helicopsychidae and stablished a biogeographical hypothesis for the group. In addition, the deficits in knowledge about species (Linnean shortfall) and their distribution (Wallacean shortfall) are herein addressed with the description of five new species and standardized descriptions of already described species, as well as new distributional records.

In addition, there is still a significant deficit in the knowledge of the different semaphoronts, Haeckelian shortfalls (mainly adult females and immature stages) that needs to be addressed in future work to understand better the biology, ecology, and evolution of this idiosyncratic group of long-horned snail-case caddisfly genus *Cochliopsyche*.

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Considerações Finais

Na presente tese apresentamos uma visão geral das espécies de Helicopsychidae da Região Neotropical. Para *Helicopsyche* (*Feropsyche*) são estabelecidas bases de dados distribucionais, taxonômicos e biológicos com a descrição de quatro espécies e estabelecimento de padrões de distribuição e indicação de áreas de distribuição potencial para o subgênero no Novo Mundo, combatendo os déficits de conhecimento Linneano e Wallaceano e dimensionando os demais déficits de conhecimento da biodiversidade para o subgênero. Os resultados relacionados a relações filogenéticas e inferências biogeográficas indicam que os representantes do Âmbar Dominicano não formam um grupo monofilético com *Feropsyche* e portanto esses são retirados do grupos, assim como que os represntes viventes de *Feropsyche* possivelmente compõem um linhagem junto as espécies classificadas no subgênero *Saeotrichia*, porém devido ao baixo suporte e a reduzida amostragem para esses grupos propomos apenas a hipótese dessa relação para que seja testada futuramente com conjunto de dados mais robusto para os subgêneros. Assim, deixamos como legado informações que podem ser utilizadas na proposição de novos estudos e projetos com foco nesse importante grupo de Helicopsychidae.

Cochliopsyche a partir do presente trabalho passa a ser novamente um gênero com base nas inferências filogenéticas que recuperam os representantes como um grupo monofilético, baseado em oito caracteres e com alto suporte de ramo. Para além, é fornecida uma revisão sistemática com a adição de descrição padronizada e amplas das espécies já descrição e proposição de cinco novas espécies, além de informações relacionadas variações morfológicas, distribuição em ecoregião de água doce (*sensu* Abell et al. 2008), gradiente de altitude e ordem de riachos. Combatendo assim os déficits de conhecimento Linneano, Wallaceano e Darwiniano e fornecendo subsídios para melhor circunscrição e futura delimitação de novos táxons. Deixando como legado uma maior consistência nas diagnoses e descrição, chaves de identificação para o gênero e bases de dados de distribuição.

Assim, a presente tese fornece base de dados e hipóteses que auxiliam no melhor entendimento das espécies, padrões distribucionais, biogeografia e relações filogenéticas atingindo o objetivo de combater e/ou dimensionar os déficits de conhecimento da biodiversidade para Helicopsychidae do Novo Mundo.

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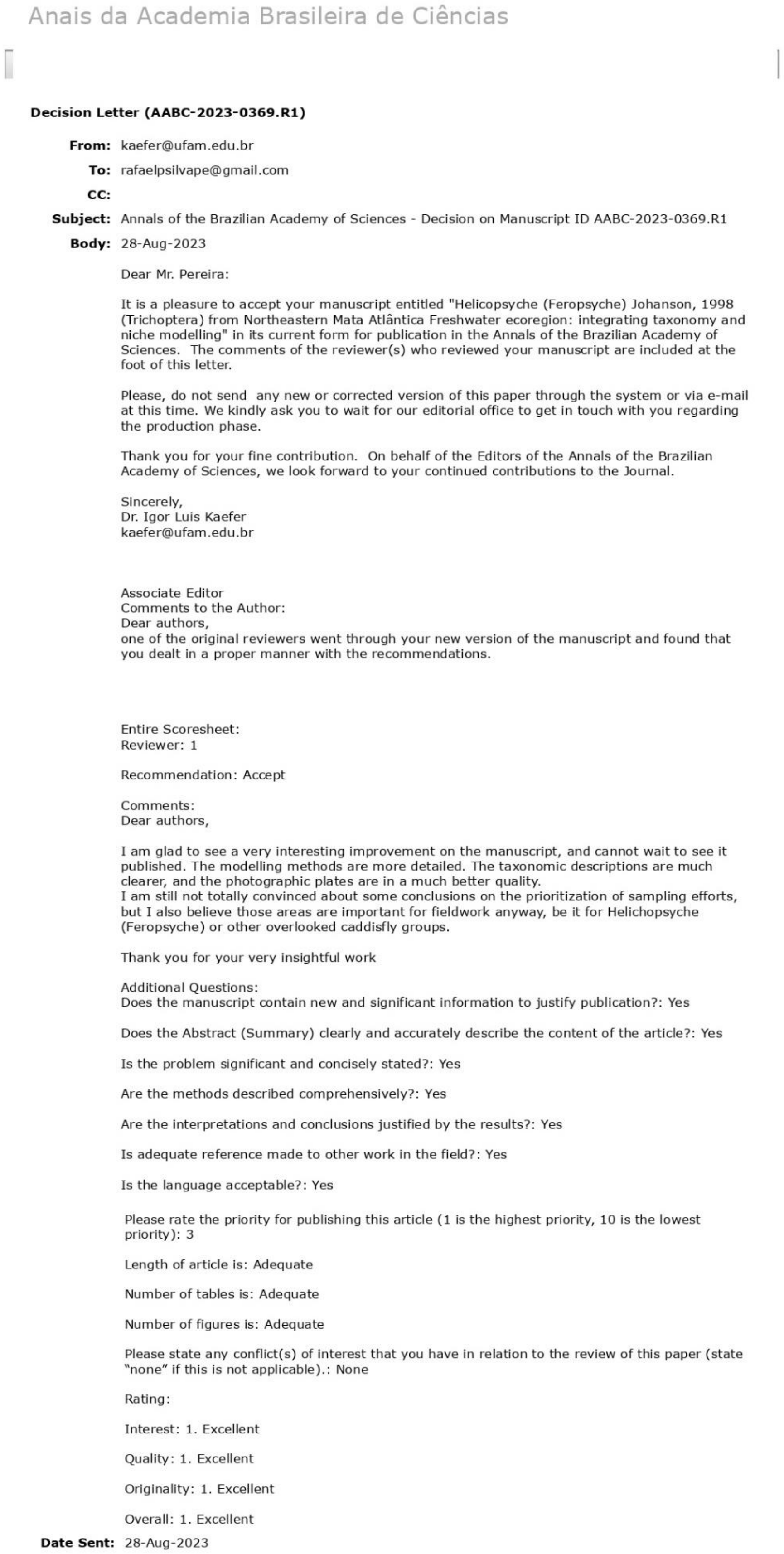
Anexos



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From: kaefer@ufam.edu.br
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Subject: Annals of the Brazilian Academy of Sciences - Decision on Manuscript ID AABC-2023-0369.R1
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Dear Mr. Pereira:

It is a pleasure to accept your manuscript entitled "Helicopsyche (Feropsyche) Johanson, 1998 (Trichoptera) from Northeastern Mata Atlântica Freshwater ecoregion: integrating taxonomy and niche modelling" in its current form for publication in the Annals of the Brazilian Academy of Sciences. The comments of the reviewer(s) who reviewed your manuscript are included at the foot of this letter.

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Sincerely,
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Associate Editor
Comments to the Author:
Dear authors,
one of the original reviewers went through your new version of the manuscript and found that you dealt in a proper manner with the recommendations.

Entire Scoresheet:
Reviewer: 1

Recommendation: Accept

Comments:
Dear authors,

I am glad to see a very interesting improvement on the manuscript, and cannot wait to see it published. The modelling methods are more detailed. The taxonomic descriptions are much clearer, and the photographic plates are in a much better quality.
I am still not totally convinced about some conclusions on the prioritization of sampling efforts, but I also believe those areas are important for fieldwork anyway, be it for Helichopsyche (Feropsyche) or other overlooked caddisfly groups.

Thank you for your very insightful work

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