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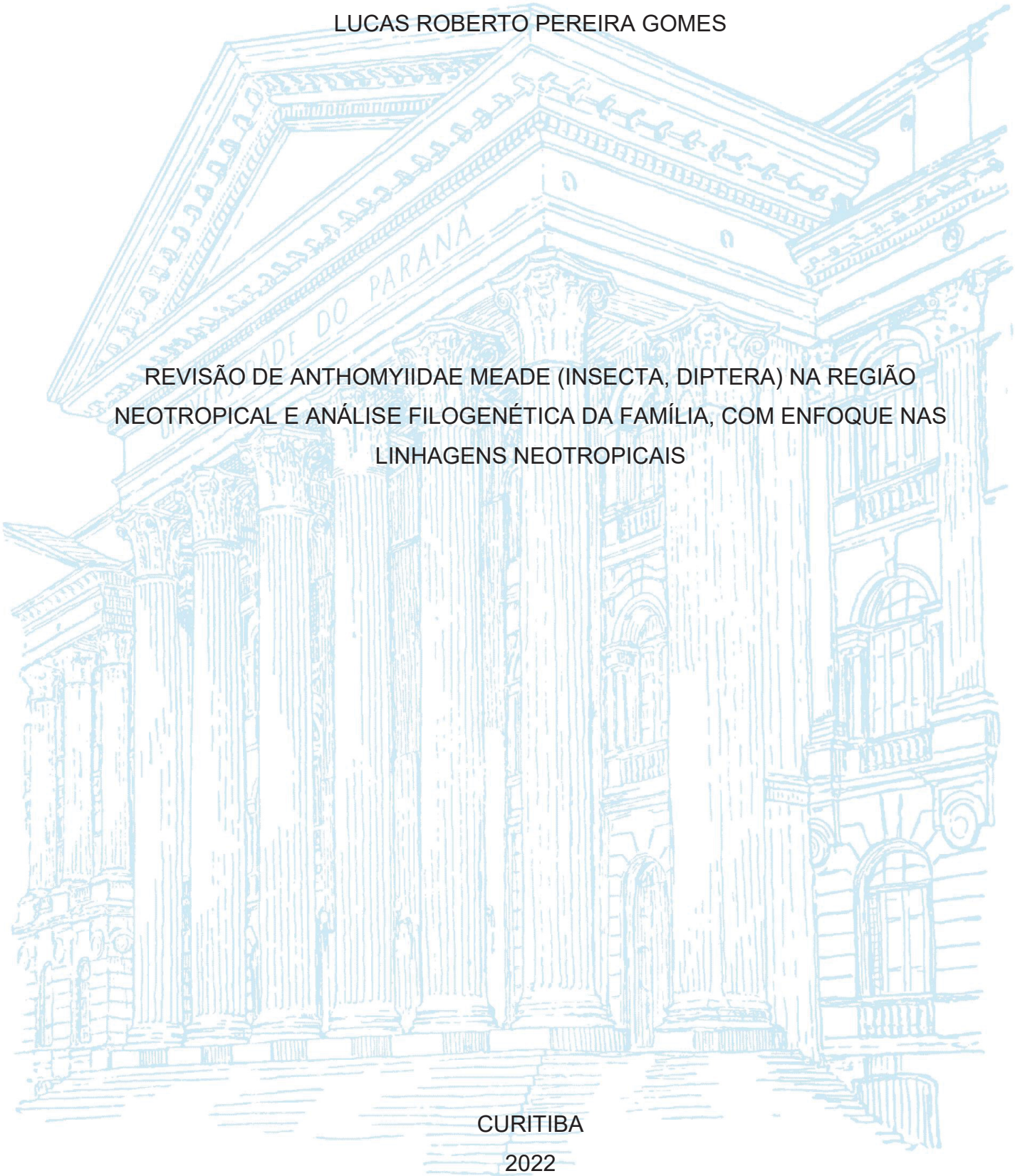

# REVISÃO DE ANTHOMYIIDAE MEADE (INSECTA, DIPTERA) NA REGIÃO NEOTROPICAL E ANÁLISE FILOGENÉTICA DA FAMÍLIA, COM ENFOQUE NAS LINHAGENS NEOTROPICAIS

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2022

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Orientador: Prof. Dr. Claudio José Barros de Carvalho

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# TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação CIÊNCIAS BIOLÓGICAS (ENTOMOLOGIA) da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de **LUCAS ROBERTO PEREIRA GOMES** intitulada: **Revisão de Anthomyiidae Meade (Insecta, Diptera) na Região Neotropical e análise filogenética da família, com enfoque nas linhagens neotropicais**, sob orientação do Prof. Dr. CLAUDIO JOSÉ BARROS DE CARVALHO, que após terem inquirido o aluno e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de doutor está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

CURITIBA, 28 de Janeiro de 2022.

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“The scientist does not study nature because it is useful. He studies it because he delights in it and he delights in it because it is beautiful”.

(Jules Henri Poincaré, 1854-1912)

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## RESUMO

Anthomyiidae (Insecta, Diptera) possui cerca de 2000 espécies e 49 gêneros distribuídos por todo o mundo. Na Região Neotropical, 108 espécies e 19 gêneros são conhecidos. Existem poucos estudos taxonômicos relacionados a fauna Neotropical e as relações filogenéticas entre os gêneros da família também são pouco conhecidas. Neste trabalho, são apresentados: a primeira análise filogenética da família com 56 terminais (11 Muscidae, 8 Oestroidea, 11 Scathophagidae, e 26 Anthomyiidae), baseada em dados moleculares (5 marcadores: 12S, COI, Cytb, 28S, EF1α) através de análise de Inferência Bayesiana e Máxima Verossimilhança, incluindo análise de tempos de divergência (Capítulo I); uma análise filogenética da família com 130 terminais (6 Scathophagidae, 10 Oestroidea, 114 Anthomyiidae) baseada em dados morfológicos (158 caracteres) através de análise de parcimônia, incluindo todos os gêneros neotropicais, além de gêneros de outras regiões biogeográficas (Capítulo II); uma análise filogenética de *Coenosopsia*, baseada em dados morfológicos (42 caracteres) através análise de parcimônia, incluindo a descrição de três novas espécies e análise biogeográfica (Capítulo III); novos registros de *Phaonantho* incluindo os primeiros registros do gênero na Bolívia, México, Paraguai e Peru; e novos registros para o Brasil (Capítulo IV); descrição de duas novas espécies neotropicais de *Calythea*, incluindo uma discussão sobre a morfologia da terminália do macho e da fêmea (Capítulo V); e descrição de três novas espécies de *Botanophila* do México, incluindo uma discussão sobre a morfologia da cabeça e distribuição das espécies (Capítulo VI).



Palavras-chave: América do Sul. Análise filogenética. Biogeografia. Filogenia. Taxonomia.

## ABSTRACT

Anthomyiidae (Insecta, Diptera) has about 2000 species and 49 genera worldwide distributed. On the Neotropical region, 108 species and 19 genera are known. There are few taxonomical studies about the Neotropical fauna and the phylogenetic relationship are few known. Herein, we present: the first phylogenetic analysis of Anthomyiidae, including 56 terminals (11 Muscidae, 8 Oestroidea, 11 Scathophagidae, and 26 Anthomyiidae), based on molecular data (5 molecular markers: 12S, COI, Cytb, 28S, EF1α), through Bayesian Inference and Maximum likelihood, including divergence times (Chapter I); a phylogenetic abalysis of Anthomyiidae with 130 terminals (6 Scathophagidae, 10 Oestroidea, 114 Anthomyiidae) based on morphological data (158 characters) through parsimony analysis, including all Neotropical genera, as well as genera from other biogeographical regions (Chapter II); a phylogenetic analysis of *Coenosopsia*, based on morphological data (42 characters) through parsimony, including description of three new species and biogeographical analysis (Chapter III); new records of *Phaonantho*, including the first record of the genus for Bolivia, Mexico, Paraguay and Peru; and new records for Brazil (Chapter IV); description of two new neotropical species of *Calythea*, including a discussion about male and female terminalia (Chapter V); and description of three new species of *Botanophila* from Mexico, including a discussion about head morphology and species distribution (Chapter VI).



Keywords: South America. Biogeography. Phylogenetic analysis. Phylogeny. Taxonomy.

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# PREFÁCIO

O objetivo desta tese foi propor, pela primeira vez, uma hipótese filogenética dos gêneros de Anthomyiidae (Insecta: Diptera), baseado em dados moleculares (Capítulo I) e morfológicos (Capítulo II), assim como revisar algumas linhagens neotropicais da família, como o gênero essencialmente neotropical *Coenosopsia* Malloch (Capítulo III), o gênero neotropical *Phaonantho* Albuquerque (Capítulo IV), e as espécies neotropicais do gênero *Calythea* Schnabl & Dziedzicki (Capítulo V). Além disso, foram descritas três novas espécies de *Botanophila* Lioy da Região de Transição Mexicana (Capítulo VI).

A ideia do projeto iniciou ainda no mestrado quando em uma conversa com meu orientador Dr. Claudio J. B. de Carvalho sobre continuar no laboratório durante o doutorado, ele sugeriu que eu começasse a pensar em algum grupo dentro de Muscidae que fosse pouco trabalhado num contexto filogenético mais amplo. Os Muscidae tem sido muito bem trabalhados recentemente por ex-integrantes do laboratório, como por exemplo, a tese de doutorado Kirstern Lica Follmann Haseyama, publicada em 2015. Assim, lembrei do grupo de moscas (Anthomyiidae) que sempre estavam misturadas aos Muscidae nas coleções e que durante minhas triagens eram rapidamente separadas e deixadas de lado, mas que ao mesmo tempo sempre despertaram curiosidade de conhecê-las melhor algum dia. Apresentei a ideia ao professor Claudio, que prontamente aprovou o projeto. E com isso, o grupo de estudo foi escolhido.

O objetivo do projeto foi realizar uma análise filogenética de Anthomyiidae, grupo pouco estudado na Região Neotropical e que necessita de uma revisão taxonômica. Além disso, buscamos revisar alguns grupos, inicialmente pensei em revisar o maior número de gêneros neotropicais possíveis, mesmo que não tenhamos conseguido trabalhar mais do que três gêneros, obtivemos resultados para publicar trabalhos futuramente com outros gêneros como *Anthomyia*, *Emmesomyia*, *Delia*, *Leucophora*, entre outros, incluindo diversos novos registros e algumas novas espécies.

Como resultado final da tese foi possível realizar a primeira análise filogenética com dados moleculares da família (Capítulo I), análise influenciada pela pandemia de duas formas contrastantes: a primeira negativa que impossibilitou a obtenção de mais material para ser utilizado na tese e a segunda fortemente

positiva, pois aproveitei os dois primeiros meses de isolamento social para trabalhar os dados exaustivamente, motivo que permitiu uma publicação antecipada do primeiro capítulo da tese, no princípio de 2021. Além disso, foi possível realizar uma análise morfológica com amostragem mais ampla (Capítulo II), mesmo sendo o capítulo mais afetado pela pandemia de Covid-19, que me impossibilitou de visitar mais coleções nos dois últimos anos do doutorado. Viagens que eram importantes no desenvolvimento do projeto e que inclusive já tinham data marcada e suporte financeiro aprovado para visitar instituições da Europa e Estados Unidos em 2020 e 2021. Também haviam visitas planejadas em outras coleções no Brasil e em outros países da América do Sul. Fora isso, o tempo de trabalho no laboratório para análise de material e levantamento de caracteres foi bastante reduzido nos primeiros meses de pandemia, mas que foi melhorando com a melhoria do controle da pandemia no Brasil.

Em relação a parte de revisão, foi possível trabalhar três gêneros, incluindo a análise filogenética com dados morfológicos de *Coenosopsia*, descrição de três novas espécies e diversos novos registros das espécies conhecidas (Capítulo III); novos registros de distribuição de *Phaonantho* (Capítulo IV); e revisão das espécies neotropicais de *Calythea* com a descrição de duas novas espécies (Capítulo V), além da descrição das três novas espécies de *Botanophila* da Zona de Transição Mexicana, sendo o primeiro registro do gênero para o México (Capítulo VI).

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# INTRODUÇÃO GERAL

Anthomyiidae (Insecta, Diptera) possui cerca de 2000 espécies e 49 gêneros distribuídos por todo o mundo (Michelsen, 2010; Evenhuis & Pape, 2021). Na Região Neotropical, 108 espécies e 19 gêneros são conhecidos (Pont, 1972, 1974; Pamplona, 1992b). A família é composta por moscas de tamanho pequeno a médio (2–12 mm) e podem ser identificadas principalmente pela presença de cerdas ventrais no ápice do escutelo (exceto *Coenosopsia* Malloch e *Fucellia* Robineau-Desvoidy)) e a veia $A_1$ alcançando a margem da asa (exceto em *Coenosopsia*) (Michelsen, 2010). Além dessas duas características principais, outras características estão presentes na maioria gêneros e podem auxiliar na identificação: presença de caliptra inferior desenvolvida, um par de cerdas interfrontais cruzadas nas fêmeas e presença de uma cerda ventral no basitarso da perna posterior (Michelsen, 2010).

As moscas desta família geralmente apresentam coloração castanha, cinza ou enegrecida, porém nunca metálicas; as asas são geralmente hialinas, mas podem apresentar máculas; e as pernas podem variar do amarelo ao preto (Huckett, 1987; Michelsen, 2010). O dimorfismo sexual é acentuado na maioria das espécies, os machos geralmente possuem o abdômen delgado, cilíndrico ou fortemente comprimido com o esternito 5, que é proeminente e em forma de “U”; o macho da maioria das espécies é holóptico e a fêmea é sempre dicóptica (Huckett, 1987).

A família ocorre em todas as Regiões biogeográficas, principalmente em áreas de clima temperado e ártico (Michelsen, 1991). As larvas têm hábitos alimentares variados, podem ser coprófagas, inquilinas, comensais, parasitas, fitófagas ou saprófagas, algumas espécies habitam ninhos de vespas solitárias, tocas de roedores e quelônios (Huckett, 1987). Entre as larvas fitófagas, destacam-se as larvas de algumas espécies dos gêneros *Delia* Robineau-Desvoidy e *Pegomya* Robineau-Desvoidy que são importantes pragas agrícolas, sendo encontradas em caules, raízes e partes aéreas de plantas de interesse econômico (Huckett, 1971, 1987; Evenhuis, 2007; Savage et al., 2016). Em relação aos adultos, as espécies de alguns gêneros são visitantes florais (e.g. *Anthomyia* Meigen, *Calythea* Schnabl & Dziedzicki e *Delia*) e desempenham papel importante como polinizadores em áreas temperadas, alimentando-se de néctar e pólen (Griffiths, 1986; Huckett, 1987; Rader et al., 2009; Savage et al., 2016). Outras espécies podem alimentar-se de matéria

orgânica animal ou vegetal em decomposição, sendo atraídas por frutas, seiva e vegetais fermentados, assim como por excretas e carcaças de animais (Huckett, 1987). Poucas espécies são sinantrópicas (Evenhuis, 2007).

Pouco se sabe sobre a fauna Neotropical de Anthomyiidae (Pont, 1974), os últimos estudos da família na região são principalmente taxonômicos, incluindo um estudo com a fauna do sul da América do Sul (Malloch, 1934), descrições e redescrições de *Coenosopsia* (Michelsen, 1991; Nihei & de Carvalho, 2004; Bortolanza et al., 2006) e *Anthomyia* (Albuquerque & Couri, 1979; Pamplona, 1992a), uma chave de identificação para os gêneros Neotropicais (Pamplona, 1992b) e análises cladísticas e biogeográficas de *Coenosopsia* (Nihei & de Carvalho, 2004; Bortolanza et al., 2006). No estudo mais recente, Gomes et al. (2019) listaram 12 espécies de sete gêneros de Anthomyiidae em uma unidade de conservação localizada no sul do estado do Paraná, apresentando uma chave para a identificação dos gêneros e diagnoses para as espécies.

Anthomyiidae pertence a superfamília “Muscoidea”, juntamente com Fanniidae, Muscidae e Scathophagidae. Inicialmente, todas as famílias de “Muscoidea” eram classificadas como Anthomyiidae (Stein, 1898, 1911, 1919). Malloch (1934) propôs que todos os Calyptratae com mero sem cerdas desenvolvidas deveriam ser classificados como subfamílias de Muscidae. Posteriormente, Roback (1951) propôs um conceito amplo de Anthomyiidae englobando Scathophagidae como subfamília, e indicou o grupo como irmão dos Muscoidea restantes e por fim, Hennig (1958, 1976) defendeu Anthomyiidae e Scathophagidae como famílias independentes, classificação utilizada atualmente.

Anos depois, alguns estudos buscaram elucidar o relacionamento entre os Muscoidea. McAlpine (1989) propôs Anthomyiidae como grupo irmão de Fanniidae + Muscidae, através de inferência filogenética. Posteriormente, Michelsen (1991) indicou Anthomyiidae como grupo irmão de Muscidae baseado principalmente em evidências morfológicas da genitália; e Lambkin et al. (2013) apresentou a única análise filogenética morfológica de Diptera que incluiu a superfamília (exceto Fanniidae), obtendo a topologia Scathophagidae + (Anthomyiidae + (Muscidae + Oestroidea)). Mais recentemente, diversas análises moleculares têm indicado um relacionamento próximo de Anthomyiidae com Scathophagidae (Bernasconi et al. 2000; Kutty et al. 2007, 2008, 2010, 2019; Wiegmann et al. 2011; Ding et al. 2015; Zhang et al. 2016; Junqueira et al. 2016; Cerretti et al., 2017; Buenaventura et al.

2021). É importante ressaltar que terminais neotropicais não foram incluídos em nenhuma dessas análises, tanto com dados morfológicos quanto moleculares. Gêneros neotropicais como *Coenosopsia* e *Phaonantho* possuem importância chave para entender a evolução de Anthomyiidae, considerando a hipótese de Michelsen (1991) de que esses dois gêneros formam o grupo irmão de todos os outros Anthomyiidae.

Anthomyiidae e Scathophagidae são morfologicamente semelhantes, sendo as únicas famílias dentro de Muscoidea com a veia anal alcançando a margem da asa (Vockeroth, 2010; Michelsen, 2010). Além disso, a ausência de cílios ventrais no ápice do escutelo, a calíptra inferior reduzida e os machos dicópticos são as principais características que permitem separar Scathophagidae de Anthomyiidae (Vockeroth, 1987, 2010), porém essas características também são encontradas em alguns gêneros de Anthomyiidae (*Coenosopsia*, *Fucellia* e *Myopinella* Michelsen) (Michelsen, 2010).

A monofilia de Anthomyiidae tem sido defendida por diversos autores (Hennig, 1976, McAlpine, 1989, Michelsen, 1991, Lambkin et al., 2013). Porém, Griffiths (1982), comentou que os limites da família Anthomyiidae como grupo monofilético necessitam de confirmação, pois a maioria dos caracteres que definem a família são plesiomórficos. Deste modo, a família pode ser composta por subgrupos de caliptrados com características primitivas e não por um grupo monofilético. Alguns estudos filogenéticos baseados em dados moleculares indicaram Anthomyiidae parafilético em relação a Scathophagidae (Kutty et al., 2007, 2008, 2010, 2019; Cerretti et al., 2017; Buenaventura et al., 2021), entretanto todos possuem uma amostragem pequena e sem nenhum representante neotropical.

Em relação a classificação, existiram tentativas de dividir a família em duas (Huckett, 1965) e três subfamílias (Michelsen, 2000), com Anthomyiinae concentrando a grande maioria dos gêneros em ambas classificações, enquanto Fucellinae (sensu Huckett, 1965), Pegomyiinae e Myopininae (sensu Michelsen, 2000) agrupam poucos gêneros. Porém essas tentativas de classificação não são utilizadas atualmente, principalmente por não serem baseadas em estudos filogenéticos e por desconsideram alguns gêneros, como por exemplos os gêneros neotropicais *Coenosopsia* e *Phaonantho.*

Anthomyiidae é uma família taxonomicamente desafiadora, pois a maioria dos caracteres diagnósticos estão presentes na genitália, inacessíveis sem

dissecção dos exemplares (Michelsen, 2010). Não existe nenhuma revisão ou guia de identificação para as espécies neotropicais de Anthomyiidae (Michelsen, 2010) e, a maioria dos exemplares-tipo das espécies neotropicais estão depositados na Europa e América do Norte (Pont, 1974).

Poucos estudos relacionados aos Anthomyiidae neotropicais foram feitos e provavelmente dezenas de espécies ainda são desconhecidas. Esse conhecimento incipiente torna de extrema necessidade estudos taxonômicos na região Neotropical. A grande similaridade morfológica entre algumas espécies, torna necessária a análise da genitália para uma correta identificação, porém muitas das descrições originais são antigas e carecem de informações diagnósticas importantes, inclusive de genitália. Michelsen (2010) apresentou uma chave de identificação para os gêneros neotropicais dos Anthomyiidae.

Considerando o presente cenário de conhecimento incipiente em relação a taxonomia e os relacionamentos filogenéticos de Anthomyiidae, este trabalho se justifica por propor: (I) uma análise filogenética de Anthomyiidae baseada em dados moleculares, com enfoque nas linhagens neotropicais; (II) uma análise filogenética morfológica incluindo representantes de todos os gêneros neotropicais, além de representantes de outras regiões biogeográficas; (III) descrição de três novas espécies de *Coenosopsia*, análise filogenética baseada em dados morfológicos e uma análise biogeográfica do gênero; (IV) novos registros de distribuição de *Phaonantho*; (V) descrição de duas novas espécies neotropicais de *Calythea*, incluindo uma discussão sobre a morfologia da terminália dos machos e das fêmeas; e (VI) descrição de três novas espécies de *Botanophila* da Zona de Transição Mexicana e uma discussão sobre a morfologia da cabeça dos machos e distribuição das espécies.

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# CAPÍTULO I

## FIRST INSIGHTS INTO THE EVOLUTION OF NEOTROPICAL ANTHOMYIID FLIES (DIPTERA: ANTHOMYIIDAE)

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# First insights into the evolution of Neotropical anthomyiid flies (Diptera: Anthomyiidae)

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ABSTRACT

Anthomyiidae is a family distributed worldwide comprising approximately 2,000 species, which, based on molecular analyses, belong to the Muscoidea grade. The phylogenetic data for this family are limited and the Neotropical lineages have never been studied at the molecular level. Herein, we present the first phylogenetic analyses of Anthomyiidae including Neotropical taxa. The resulting phylogenetic trees—inferred using maximum-likelihood and Bayesian criteria and based on two nuclear and three mitochondrial genes and 56 terminals, including 13 Neotropical anthomyiid species—confirmed Anthomyiidae as a monophyletic lineage and sister group of Scathophagidae, which is also monophyletic. The clade *Coenosopsia* + *Phaonantho* was not recovered as a sister group of the remaining anthomyiids, as

previously indicated by the results of morphological analyses. These and other generic relationships are discussed in the light of morphological data from previous studies. The divergence time estimation suggested that after a split from the Oestroidea clade approximately 51.7 Ma, the radiation of Anthomyiidae + Scathophagidae began during the Eocene, with the oldest common ancestor of both families living approximately 40.5 Ma and with the oldest anthomyiid ancestor living approximately 36.8 Ma. The split of the clade *Coenosopsia* + *Phaonantho* was dated to the Oligocene (*c*. 23 Ma). These results provide new insights into the timing and rate of anthomyiid and scathophagid fly evolution.

**Key words:** Calyptratae, Divergence time, Molecular analysis, Muscoidea, Oestroidea, Phylogenetic analysis.

## INTRODUCTION

The family Anthomyiidae (Diptera, Calyptratae) includes approximately 2,000 species and 40 genera distributed worldwide (Michelsen, 2010). Anthomyiids are found in all biogeographic regions, but mainly occur in areas with temperate and arctic climates, and 19 genera representing 108 species are reported for the Neotropical region (Pont, 1972, 1974; Michelsen, 1991; Pamplona, 1992; Michelsen 2010). Most of the adult Anthomyiidae flies are flower visitors because they feed on nectar or pollen, whereas in several species, their larvae are phytophagous, including some species that are known for their significance in agricultural environments (Huckett, 1987; Evenhuis, 2007; Rader *et al*., 2009; Michelsen, 2010; Savage *et al*., 2016).

Taxonomy of the anthomyiids is difficult because most of the generic diagnostic characters occur in the male genitalia and tend to be inaccessible without dissection (Michelsen, 2010). However, the family can be distinguished from other calyptrate flies by the presence of setulae on the ventral surface of the scutellum (only absent in *Coenosopsia* Malloch and *Fucellia* Robineau-Desvoidy) and by the long vein $A_1$ that reaches the wing margin (also absent in *Coenosopsia*) (Michelsen, 1991, 2010).

The relationships between Anthomyiidae and other families have varied according to each author's interpretation and evaluation of the characters. Formerly, all current Muscoidea families were classified in Anthomyiidae (Stein, 1898, 1911,

1919). Malloch (1934) proposed that all Calyptratae with bare meron should be classified as infrasubfamilial categories in Muscidae, including Anthomyiidae as a sister group of the remaining Muscidae. Subsequently, Roback (1951) proposed a classification in the broad sense for Anthomyiidae, including Scathophagidae as its subfamily, and suggested that the anthomyiids represented a sister group to the remaining Muscoidea families. Hennig (1958, 1976) recovered Anthomyiidae as an independent family of Scathophagidae based on the following putative synapomorphies: sclerotized connections established between male cerci and surstyli, surstyli distally biramous, scutellum beneath the apex bearing some fine setulae and pupal spiracles not forming respiratory horns dorsolaterally through the wall of the puparium.

The monophyly of Anthomyiidae and its validity as a family in Muscoidea have been strongly defended by several authors based on morphology (*e.g.*, Hennig, 1976; McAlpine, 1989; Michelsen, 1991; Lambkin *et al*., 2013). McAlpine (1989) considered Anthomyiidae as the sister to the remaining Muscoidea families (Fanniidae, Muscidae and Scathophagidae), whereas Michelsen (1991) considered Anthomyiidae as a sister group of Muscidae. Lambkin *et al*. (2013), in a phylogenetic analysis, recovered the clade Scathophagidae + (Anthomyiidae + (Muscidae + Oestroidea)).

The close relationship between Anthomyiidae and Scathophagidae has been repeatedly demonstrated by phylogenetic analyses using molecular data (Bernasconi *et al*., 2000; Wiegmann *et al*., 2011; Ding *et al*., 2015; Junqueira *et al*., 2016; Zhang *et al*., 2016) and numerous studies have recovered Anthomyiidae as a paraphyletic group, including Scathophagidae (Kutty *et al*., 2007, 2008, 2010, 2019; Cerretti *et al*., 2017; Buenaventura *et al*., 2020). However, no Neotropical taxon was included in these molecular analyses.

Morphologically, Anthomyiidae and Scathophagidae are quite similar; both families have anal veins reaching the wing edge. The main characters generally used in the literature to differentiate Scathophagidae from Anthomyiidae are the absence of ventral setulae on the apex of the scutellum (Vockeroth, 2010), the greatly reduced lower calypter and the broad frons in males (Vockeroth, 1987). However, these characters can also be found in some Anthomyiidae genera (*e.g.*, *Coenosopsia*, *Fucellia* and *Myopinella* Michelsen) (Michelsen, 2010).

A comprehensive classification for Anthomyiidae is lacking and no existing attempt to systematize the family has been founded on stringent cladistic argumentation (Michelsen, 2010). Huckett (1965) considered the genera *Fucellia* and *Circia* Malloch [=*Alliopsis* Schnabl & Dziedzicki] as a separate subfamily (Fucelliinae), whereas the remaining anthomyiids were classified as Anthomyiinae, which were divided into two tribes (Anthomyiini and Myopinini). Michelsen (2000) divided most anthomyiids into the subfamilies Myopininae, Pegomyinae and Anthomyiinae, leaving the genera from the Americas, *Coenosopsia* and *Phaonantho* Albuquerque, outside this classification.

Some explanations concerning the Neotropical distribution of *Coenosopsia* and *Phaonantho* have been proposed. Michelsen (1991) indicated a sister-group relationship between both genera and this lineage as a sister group to the remaining Anthomyiidae. However, this hypothesis has been contested by Nihei & de Carvalho (2004) and Bortolanza *et al*. (2006), who did not corroborate this sister-group relationship between these genera.

Thus, a pertinent issue in the systematics of Anthomyiidae is whether the clade *Coenosopsia* + *Phaonantho* is a sister group of the remaining family (Michelsen, 1991, 1996, 2000) or whether these two genera are sister groups and basal anthomyiid taxa (Nihei & de Carvalho, 2004; Bortolanza *et al*., 2006). Herein, we present the first phylogenetic molecular study of Anthomyiidae, including Neotropical taxa. Specifically, our goal is to assess the phylogenetic relationship within Anthomyiidae, focusing on Neotropical genera. We also aim to test Michelsen's (1991) hypothesis of the sister-group relationship between the *Coenosopsia* and *Phaonantho* clade and the remaining Anthomyiidae.

## MATERIAL AND METHODS

### Taxon sampling

Twenty-six species of Anthomyiidae were sampled from various biogeographic regions (Table 1). Additionally, 30 terminals were included as outgroups in the analyses, namely, representatives of Muscidae (11), Oestroidea (8) and Scathophagidae (11). Forty-one sequences of 12 Neotropical species of Anthomyiidae were newly generated for this study and 190 sequences were obtained from GenBank from previous studies (*e.g.*, Kutty *et al*., 2007, 2008, 2010; Wiegmann *et al*., 2011). Outgroups were chosen based on previous phylogenetic treatments for

Calyptratae, as provided by Bernasconi *et al*. (2000), Kutty *et al*. (2007, 2008, 2010, 2019), Wiegmann *et al*. (2011), Ding *et al*. (2015), Junqueira *et al*. (2016), Zhang *et al*. (2016), Cerretti *et al*. (2017) and Buenaventura *et al*. (2020). Trees were rooted in the Muscidae node.

### Laboratory procedures

DNA extraction was conducted by a non-destructive method, using the whole specimen with body perforations and the GenElute™ Blood Genomic DNA Kit, following the manufacturer's protocol. Following DNA extraction, each specimen was dry-mounted and labelled with a voucher number. Vouchered specimens were deposited in the Entomological Collection 'Padre Jesus Santiago Moure', Universidade Federal do Paraná (DZUP), in Curitiba, Brazil.

Phylogenetic inferences were based on five markers, including three mitochondrial gene regions—the short ribosomal RNA subunit (12S; 630 aligned positions), cytochrome c oxidase subunit 1 (COI; 658) and cytochrome b subunit (Cytb; 658)—and two nuclear markers—the large ribosomal RNA subunit (28S; 668) and elongation factor 1-alpha (Ef1α; 983). PCR amplifications of these fragments were performed using the kit MyTaq™ DNA Polymerase (Bioline Reagentes, Ltd., United Kingdom) in a total volume of 25 µL, consisting of 1 µL of genomic DNA, 5 µL 5× MyTaq Reaction Buffer (containing 15 mM $MgCl_2$ and 5 mM dNTPs), 0.5 µL of each 0.01 mM primer, 0.1 µL of MyTaq DNA Polymerase and 17.9 µL of sterilised ultrapure water. The primers used for PCR amplification are shown in Table 2.

PCR cycling conditions used for each marker were as follows: 12S (95 °C for 3 min; 35 cycles at 95 °C for 1 min, 50 °C for 1 min, 72 °C for 1.5 min; and a final extension at 72 °C for 5 min); COI (94 °C for 5 min; 40 cycles at 94 °C for 45 s, 51 °C for 50 s, 72 °C for 2 min; and a final extension at 72 °C for 10 min); Cytb (94 °C for 3 min; 35 cycles at 94 °C for 1 min, 55 °C for 1 min, 72 °C for 1.5 min; and a final extension at 72 °C for 5 min); 28S (95 °C for 3 min; 30 cycles at 95 °C for 1 min, 52 °C for 1.5 min, 72 °C for 2 min; and a final extension at 72°C for 7 min). The PCR products were visualized on 1.0% agarose gel and purified using 5 M ammonium acetate precipitation with isopropanol. Each PCR product was sequenced in both directions using the BigDye Terminator v3.1 technology (Applied Biosystems, Foster City CA, U.S.A.).

### Multiple sequence alignments and phylogenetic analyses

The multiple sequence alignments were produced including both new sequences generated in this study and sequences obtained from the NCBI GenBank database (Table 1). New sequences were manually edited and consensus sequences were generated using Geneious 9.1.3 (Biomatters Ltd.).

Alignment of the protein-coding genes (COI, Cytb and Ef1α) was performed in MAFFT v.7.222 (Katoh *et al*., 2002), using the G-INS-I algorithm with default parameters (gap open penalty = 1.53; offset value = 0.123), and the alignment was translated into amino acids to check for any translation problems. The alignment of the ribosomal genes (12S and 28S) was performed using MAFFT v.7 (Katoh & Standley, 2013) as implemented in the MAFFT server (http://mafft.cbrc.jp/alignment/server/), using the same parameters mentioned above for protein-coding genes, but employing the Q-INS-i algorithm (Katoh & Toh, 2008), which considers the secondary structure of the RNA to produce the alignment.

A data matrix combining the five markers was partitioned *a priori* considering each codon position separately in the case of protein-coding genes and single partitions for the ribosomal genes and analysed in Partitionfinder 2.1.1 (Lanfear *et al*., 2016) to identify the best-fitting substitution models for each partition, as well as the partition scheme under unlinked branch lengths and the Bayesian Information Criterion (Lanfear *et al*., 2012) (Table 3).

The maximum-likelihood (ML) analysis was performed in RAxML 7.2.6 (Stamatakis, 2006), using unlinked GTR + I + G nucleotide substitution models for each data partition (the only alternative allowed by RAxML). The consensus for the ML analysis was selected from 25 replicates of randomized maximum parsimony starting trees and branch support values were estimated from an independent bootstrap analysis based on 1,000 pseudoreplicates. Bayesian inference (BI) was performed in MrBayes 3.2.6 (Ronquist *et al*., 2012), using partitioned data with their corresponding best-fitting evolutionary model (Table 3) and two independent Markov chain Monte Carlo (MCMC) runs with eight chains of 100 million generations each, sampling trees every 1,000 generations. Convergence among BI runs was evaluated using Tracer 1.7.1 (Drummond & Rambaut, 2007) and the tree file resulting from each run was combined after discarding the output of the 25% initial generations. The maximum clade credibility tree was generated in TreeAnnotator 1.8.4 (Heled &

Bouckaert, 2013). All analyses were implemented in the CIPRES (Cyberinfrastructure for Phylogenetic Research) Science Gateway (Miller *et al*., 2010).

### Divergence time estimation

Molecular dating analysis was performed using a reduced dataset (56 taxa, 2929 positions), where the alignment of Ef1α was excluded from the matrix, aiming at maximum data completeness to avoid a negative effect on branch length estimation by missing data. Molecular clock analysis was conducted in BEAST 1.8.4 (Drummond *et al*., 2012), applying an uncorrelated lognormal relaxed clock (Drummond *et al*., 2006) to estimate the maximum clade credibility tree, with median node height and a 95% high posterior density (HPD) interval for each divergence. Tree searches consisted of a MCMC chain with 100 million generations, sampling every 1000$^{th}$ tree, under a Yule diversification model and unlinked substitution and clock models, and using GTR + I + G for each partition, as predefined in Partitionfinder 2.1.1, with default values for all model parameters.

Four fossil priors were used for tree calibration: (1) *Cuterebra ascarides* (Scudder, 1877), the oldest fossil known of Oestridae, from the Eocene (Ypresian/Lutetian) of the Green River formation in North America (50.3–46.2 Ma), assigned for the origin of Oestroidea; (2) *Protanthomyia minuta* Michelsen, 2000, a Baltic amber fossil from Russia, dated from the Eocene (Priabonian) (37.2–33.9 Ma), for the Anthomyiidae node; (3) *Coenosopsites poinari* Michelsen, 1996, from Miocene (Burdigalian/Langhian) Dominican amber from the Dominican Republic (20.4–13.6 Ma) (Michelsen, 1996), for the *Coenosopsia* + *Phaonantho* node; and (4) *Cordilura exhumata*, the oldest fossil of Scathophagidae, from the Eocene (Preabonian) of the Florissant Formation in North America (37.2–33.9 Ma), for the Scathophagidae node. Age ranges of fossils were obtained from the Fossilworks database (http://fossilworks.org/bridge.pl; accessed 20 May 2020).

## RESULTS

### Sequence data

In total, 26 sequences of Anthomyiidae were generated for this study, including the first DNA sequences for 12 Neotropical species in 7 genera (Table 1). The nucleotide data matrix used for the phylogenetic analyses consisted of 3,597

aligned sites for 56 taxa with 78.7% gene-by-taxa coverage and 30.7% GC frequency. The sequence summary statistics are given in Table 4.

### Phylogenetic analyses

Both BI and ML analyses (Fig. 1) produced congruent results when considering only supported nodes (posterior probability (PP) > 0.60 and bootstrap values (BS) > 60). Our analyses corroborate Anthomyiidae and Scathophagidae as sister groups (PP = 1.0; BS = 96) and both Anthomyiidae (PP = 0.81) and Scathophagidae (PP = 1.0) as monophyletic families.

The following genera were recovered as monophyletic in the phylogenetic analyses: *Anthomyia* Meigen, *Botanophila* Lioy, *Coenosopsia*, *Delia* Robineau-Desvoidy, *Lasiomma* Stein, *Pegoplata*, *Phaonantho*, *Taeniomyia* Stein and *Zaphne*. Among the generic relationships, *Hylemyza* Schnabl & Dziedzicki + *Botanophila* clade (PP = 1.0; BS = 74) was the sister group of the *Anthomyia* + *Lasiomma* clade (PP = 1.0; BS = 79). The clade *Zaphne caudata* + *Hydrophoria lancifer* was well supported (PP = 1.0; BS = 100). The clade formed by *Emmesomyia grisea* as a sister group of *Pegomya* species (PP= 0.97; BS= 88) + *Taeniomyia* species (PP = 1.0; BS = 100) was also well supported (PP = 1.0; BS = 99). Finally, the genus *Coenosopsia* was recovered as a sister group of *Phaonantho* (PP = 0.93; BS = 60).

The scathophagid species were recovered as monophyletic (PP = 1.0). *Americina adusta* was recovered as a sister to the remaining species of Scathophagidae, which clustered in four main clades: *Chaetosa punctipennis* + *Pogonota sahlbergi* (PP = 1.0; BS = 99), *Scathophaga* Meigen species (*S. furcata*, *S. litorea* and *S. stercoraria*) (PP = 0.97; BS = 82), *Gimnomera cerea* + *Acerocnema macrocera* (PP = 1.0; BS = 98) and *Cordilura* Fallén species (*C. atrata*, *C. ciliata* and *C. ontario*) (PP = 1.0; BS = 100).

### Divergence time estimation

The divergence time estimation topology is largely identical to the BI tree, differing only in some clades without support. Molecular dating based on our dataset (Fig. 2) suggested that the most recent ancestor of Oestroidea and Anthomyiidae + Scathophagidae existed *c.* 52 Ma (in the Early Eocene boundary; 49.02–54.78 Ma), whereas the crown group divergence of Anthomyiidae + Scathophagidae was dated to the Middle Eocene (*c.* 40 Ma; 37.39–43.71 Ma); the oldest anthomyiid ancestor

dated *c.* 37 Ma. Additionally, the divergence times of the following generic relationships were estimated: *Calythea* Schnabl & Dziedzicki and *Pegoplata* Schnabl & Dziedzicki *c.* 27 Ma (22.48–31.7 Ma); *Zaphne* Robineau-Desvoidy and *Hydrophoria* Robineau-Desvoidy *c*. 19 Ma (14.53–23.99 Ma); *Lasiomma* and *Anthomyia c.* 24 Ma (19.87–28.80 Ma); *Botanophila* + *Hylemyza c.* 17 (12.30–22.97 Ma); *Emmesomyia*, *Taeniomyia* and *Pegomya* Robineau-Desvoidy *c*. 27 Ma (23.83–31.88 Ma). Additionally, the origin of the genera *Coenosopsia* and *Phaonantho* was dated to the Oligocene/Miocene boundary (*c*. 23 Ma; 18.01–28.31 Ma) and the diversification of the *Coenosopsia* species occurred in the Miocene *c.* 16 Ma (11.47–21.68 Ma).

## DISCUSSION

### Monophyly of the Anthomyiidae

We present the first molecular phylogenetic hypothesis for Anthomyiidae including Neotropical taxa. Our results corroborate the close relationship between Anthomyiidae and Scathophagidae, as reported by previous molecular-based phylogenetic studies (Bernasconi *et al*., 2000; Kutty *et al*., 2007, 2008, 2010, 2019; Wiegmann *et al*., 2011; Ding *et al*., 2015; Junqueira *et al*., 2016; Zhang *et al*., 2016; Cerretti *et al*., 2017; Buenaventura *et al*., 2020).

Griffiths (1982) indicated that Anthomyiidae could be a non-monophyletic assemblage of primitive subgroups of Calyptratae, and some authors have indicated morphological evidence that supports the different relationships of Anthomyiidae within Muscoidea. McAlpine (1989) used larval (presence of parastomal bars and dorsal cornu flared with a fissure) and adult (vein $A_1$ continuing to wing margin and ventral surface of scutellum with setulae) characters to propose Anthomyiidae as the sister group of the remaining families (Fanniidae, Muscidae and Scathophagidae). Michelsen (1991) used the pair of crossed frontal setae (female) or setulae (male) inserted on the frontal vitta and male surstyli consisting of two articulating parts to propose Anthomyiidae as the sister group of Muscidae. Most of the morphological evidence does not support the evolutionary history and relationships among the muscoid families obtained by molecular data.

The paraphyly of Anthomyiidae with regard to Scathophagidae is indicated in different molecular studies (Kutty *et al*., 2007, 2008, 2010, 2019; Cerretti *et al*., 2017; Buenaventura *et al*., 2020). However, our analyses based on a more robust taxon

sampling of Anthomyiidae recovered both families as monophyletic. Nevertheless, a more complete analysis, including both more scathophagid and anthomyiid genera, is necessary to properly understand the relationships among these families.

## Generic relationships in the Anthomyiidae

Our analyses corroborate several hypotheses for generic relationships, some of which have been suggested previously, such as the relationship between *Calythea* and *Pegoplata* (Hennig, 1976; Michelsen, 1988), *Phaonantho* and *Coenosopsia* (Michelsen, 1991), *Anthomyia* and *Lasiomma* (Hennig, 1976), *Hydrophoria* and *Zaphne* (Griffiths, 1998), *Botanophila* and *Hylemyza* (Hennig, 1976) and *Emmesomyia* and *Pegomya* (Snyder, 1957; Hennig, 1976; Griffiths, 1982, 1984), and support several new hypotheses, which we will discuss below. It is important to highlight that some of the anthomyiid genera analysed, such as *Anthomyia*, *Botanophila* and *Delia*, are highly diverse (Evenhuis & Pape, 2020) and probably non-monophyletic.

### *Calythea* + *Pegoplata*

The genera *Calythea* and *Pegoplata*, together with *Enneastigma* Stein, *Nupedia* Karl [= *Pegoplata*] and *Myopina* Robineau-Desvoidy, form a morphologically well-defined lineage (*Nupedia*-group), which eventually deserves the status of subfamily or tribe (Michelsen, 1988). The monophyly of the clade formed by these genera is indicated by the remarkable distiphallus shape (Hennig, 1976), absence of accessory glands on the male reproductive system, insertion of the epandrium musculature on the apodemal process extending from the interior bases of the surstyli, female spermathecal ducts of equal diameter throughout and rather slender and male phallus more or less club-shaped and expanded at the distal part of the distiphallus (Michelsen, 1988). Additionally, Hennig (1976) considered the more differentiated balloon-like distiphallus of *Calythea* as a further development of the ground plan of this group. The relationship between *Calythea* and *Pegoplata*, in addition to morphological evidence (Hennig, 1976; Michelsen, 1988), is now supported by molecular data.

***Phaonantho + Coenosopsia***

Remarkably, *Coenosopsia* has no obvious characteristics that could indicate a close affinity to other anthomyiids (Michelsen, 1991; Nihei & de Carvalho, 2004). Michelsen (1991) indicated a sister-group relationship between *Phaonantho* and *Coenosopsia* based on the following putative synapomorphies: arista plumose, palpus dark with yellow apex, all elements of male terminalia (except surstylus) remarkably small, process longi (sternite 10) short and merging into anterobasal parts of surstyli, sperm pump sclerite vestigial and absence of a subapical seta on the pregonite. Michelsen (1991) also indicated two plesiomorphies that support *Phaonantho* + *Coenosopsia*: vein CuA+CuP strongly abbreviated, not reaching the wing edge and hind tibia with only one submedian posterodorsal seta. The remaining Anthomyiidae are characterized by two synapomorphies: CuA+CuP reaching the margin edge and tibia with two posterodorsal setae (Michelsen, 1991). The sister-group relationship between *Coenosopsia* and *Phaonantho*, in addition to morphological evidence (Michelsen, 1991), is now supported by molecular data. Nevertheless, Michelsen's (1991) hypothesis was only partially corroborated, because in our phylogenetic analysis, this lineage was not recovered as the sister group of all remaining Anthomyiidae.

***Anthomyia + Lasiomma***

There are no previous records in the literature indicating a close relationship between *Lasiomma* and *Anthomyia*. Hennig (1976) stated that *Anthomyia xanthopus* (Hennig) has a distiphallus similar to that of the genus *Lasiomma* and that some species of *Lasiomma* (*e.g.*, *L. longirostris* (Stein)) have surstyli remarkably similar to that of *Anthomyia*. These characters from male terminalia, in addition to our phylogenetic analyses, indicate that both genera (or at least some of their species) are closely related, but a more complete analysis, including more species and genera, is necessary to properly understand the relationship between *Anthomyia* and *Lasiomma*.

***Hydrophoria + Zaphne***

The genera *Hydrophoria* and *Zaphne* are closely related (Griffiths, 1998) and have already been considered in the wide concept of *Hydrophoria*. Michelsen (1985) proposed reinstating a pre-Hennig classification and divided *Hydrophoria* s. lat. into

two genera: *Hydrophoria* s. str. and *Zaphne*. These genera share some characteristics, such as antennae plumose, prementum shining, basal part of prosternum bare and abdomen without spots. The relationship between these morphologically similar genera is also supported by molecular data.

***Botanophila + Hylemyza***

Hennig (1976) commented that *Botanophila* probably forms a clade with *Circia* [= *Alliopsis*], *Fucellia*, *Pseudomyopina* Ringdahl [= *Botanophila*], *Pegohylemyia* Schnabl & Dziedzicki [= *Botanophila*], *Monochrotogaster* Ringdahl [= *Botanophila*], *Chirosiomima* Hennig and *Chiastocheta* Pokorny, but none of which were analysed here. Our analyses recovered *Botanophila* as a sister group of the monotypic genus *Hylemyza*, which has no specific information regarding its relationships.

***Emmesomyia + Pegomya + Taeniomyia***

The relationships between *Emmesomyia* s. lat. (including *Taeniomyia*) and *Pegomya* have been indicated by some authors (Snyder, 1957; Hennig, 1976; Griffiths, 1982) based on morphological characters. Hennig (1976) suggested that *Emmesomyia* s. lat. and *Pegomya*, together with *Mycophaga* Rondani, *Eutrichota, Eremomyioides* Malloch [= *Eutrichota*] and *Pegomyza* Schnabl [= *Eutrichota*], formed the '*Pegomya*-group'; he considered the apical division of the surstylus as a synapomorphic characteristic of the whole group (except *Mycophaga*). Griffiths (1982) considered the pregonite bilobate as a synapomorphy of *Emmesomyia* s. lat., *Eutrichota* and *Pegomya*.

Among these genera, *Emmesomyia* s. lat. and *Pegomya* have been indicated as the most closely related (Snyder, 1957; Griffiths, 1982, 1984). Snyder (1957) considered this relationship based on the presence of three anterodorsal and two posterodorsal setae on the hind tibia of both sexes and the absence of a complete or partial row of short posterior to posteroventral setae or setulae on the hind tibia of males. Griffiths (1982, 1984) considered sternite 5 largely covered by setae, the longest setae situated near the bases of the processes, basal to a median group of setule on the ventral surface of the pregonite and the apical division of surstylus as synapomorphies of both genera.

Michelsen (2010) proposed a division of *Emmesomyia* s. lat. in *Emmesomyia* s. str. and *Taeniomyia* Stein. Our analyses recovered *Taeniomyia* as more closely

related to *Pegomya* than to *Emmesomyia grisea*. Finally, the genera *Emmesomyia*, *Pegomya* and *Taeniomyia*, which have several lines of morphological evidence supporting their relationships (Snyder, 1957; Hennig, 1976; Griffiths, 1982, 1984), are now also supported by molecular data.

### Divergence time estimation

The estimated ages of some nodes in our analysis were earlier than those of previous studies using different datasets. However, our results are largely consistent with the estimates provided by Cerretti *et al*. (2017). For example, our results estimated the divergence between Oestroidea and Anthomyiidae + Scathophagidae at *c*. 51 Ma, which is in agreement with the Cerretti *et al*. (2017) estimate of *c*. 55 Ma, with both estimates much older than previous estimates that ranged between *c*. 34 and 43 Ma (Wiegmann *et al*., 2011; Ding *et al*., 2015; Junqueira *et al*., 2016). The same pattern emerged for the age of the clade Anthomyiidae + Scathophagidae and its subordinate lineages.

According to our results, the clade *Coenosopsia* + *Phaonantho* diverged at *c.* 23 Ma. Two main biogeographical hypotheses have been proposed to explain the Neotropical distribution of these taxa. Michelsen (1991) indicated this clade was a sister group of remaining anthomyiids, suggesting a North-to-South American dispersion in the Early Cenozoic (*c*. 65 Ma) when the first anthomyiids probably arrived in the Neotropics through the Proto-Greater Antilles, a Late Cretaceous to Early Cenozoic landmasses connection, which allowed biotic interchange between North and South America.

A second hypothesis was proposed by Nihei & de Carvalho (2004), who suggested that the first Neotropical anthomyiids originated from Africa during the Late Jurassic to Early Cretaceous, during the Gondwana period, when Africa and South America had just begun to separate (*c.* 135–106 Ma). This hypothesis was based on a biogeographic pattern in the Cretaceous indicated by Amorim & Pires (1996), who posteriorly modified the more probable events that generated the pattern that occurred during the Cenozoic (Amorim 2009). Bortolanza *et al*. (2006) and de Carvalho *et al*. (2016) indicated that pseudo-congruencies could be avoided by the inclusion of divergence times in the dating of the biogeographic analysis to *Coenosopsia*.

Our results showed that this Neotropical lineage, *Coenosopsia* + *Phaonantho*, arose much later than suggested by both Michelsen (1991) and Nihei & de Carvalho (2004) and occurred later than the emergence of the Proto-Greater Antilles in the Middle Eocene (*c.* 49 Ma; Graham, 2003). This estimation is more congruent with the GAARlandia (the Greater Antilles and Aves Ridge landspan) hypothesis (Iturralde-Vincent & MacPhee, 1999), a land bridge hypothesis that connected the Greater Antilles to South America during the Mid-Cenozoic (*c*. 32 Ma) and which may explain the early dispersal of some taxa between North and South America (Agnolin *et al*., 2019). Although there is no record of both genera in the islands from Central America, the extinct genus *Coenosopsites* from Dominican amber, which resembles *Coenosopsia* (Michelsen, 1996), is congruent with this hypothesis.

This study represents an important step in understanding the relationships and evolution of the Anthomyiidae clade. Currently, there is no classification of anthomyiid flies above the genus level and a full-scale cladistic analysis involving both morphological and molecular data is required to produce an appropriate classification hypothesis. We chose not to propose a new classification due to the low branches support among the main clades and the missing data of species of some genera in our analyses. Considering the generic relationships previously indicated by morphology (mainly terminalia), which were herein corroborated by molecular data, we highlight the importance of terminalia characters in understanding the relationships among Anthomyiidae genera. Additionally, we present a divergence time estimation hypothesis for Anthomyiidae, with the earliest ages, shedding light on the evolution and distributional pattern of the family.

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FIGURES

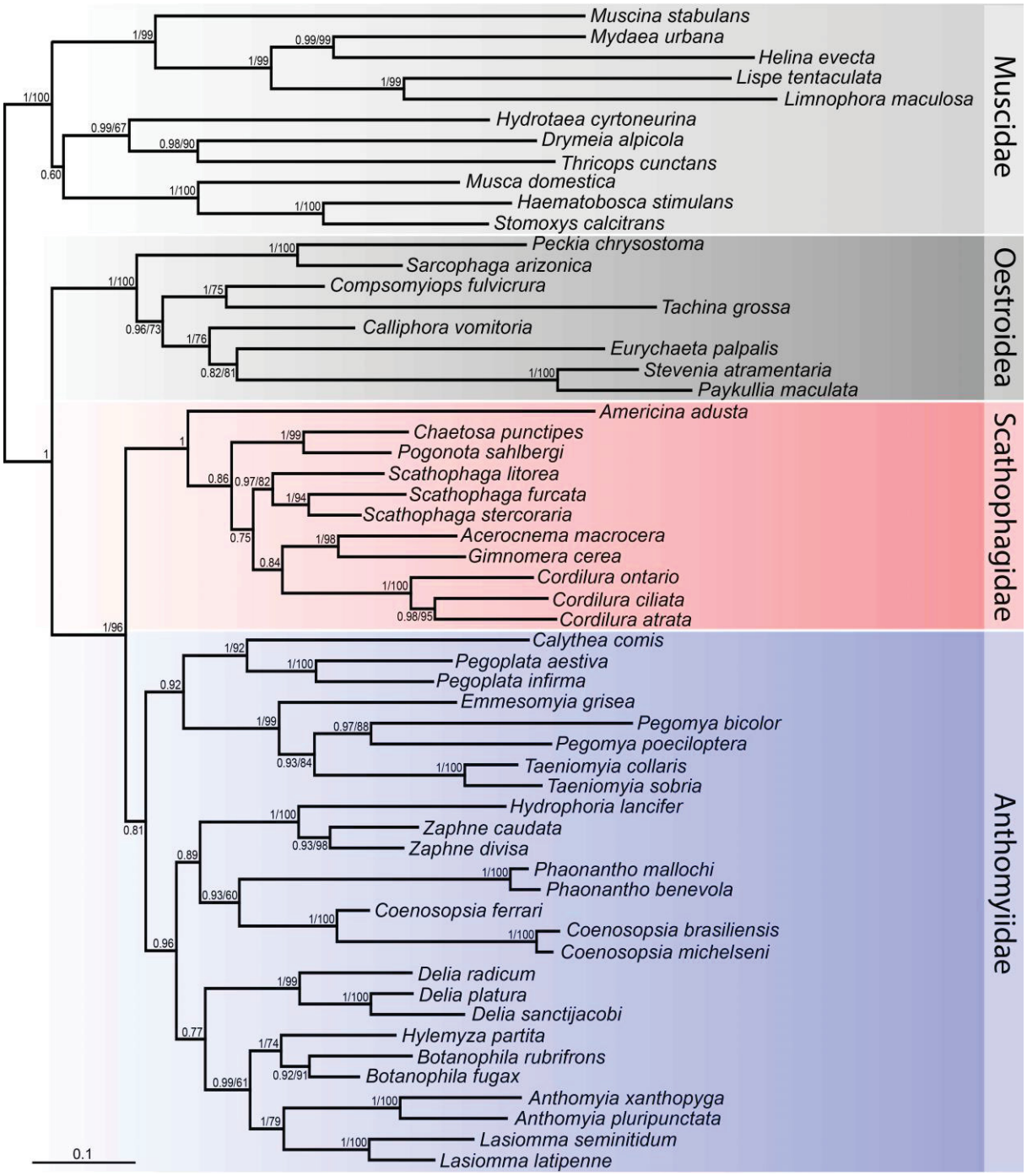


**Figure 1.** Phylogeny based on Bayesian Inference of the five-gene dataset, showing the relationships among species with both posterior probability support (PP) and maximum-likelihood bootstrap support (BS) (Bayesian posterior: >0.6/Bootstrap: >60).

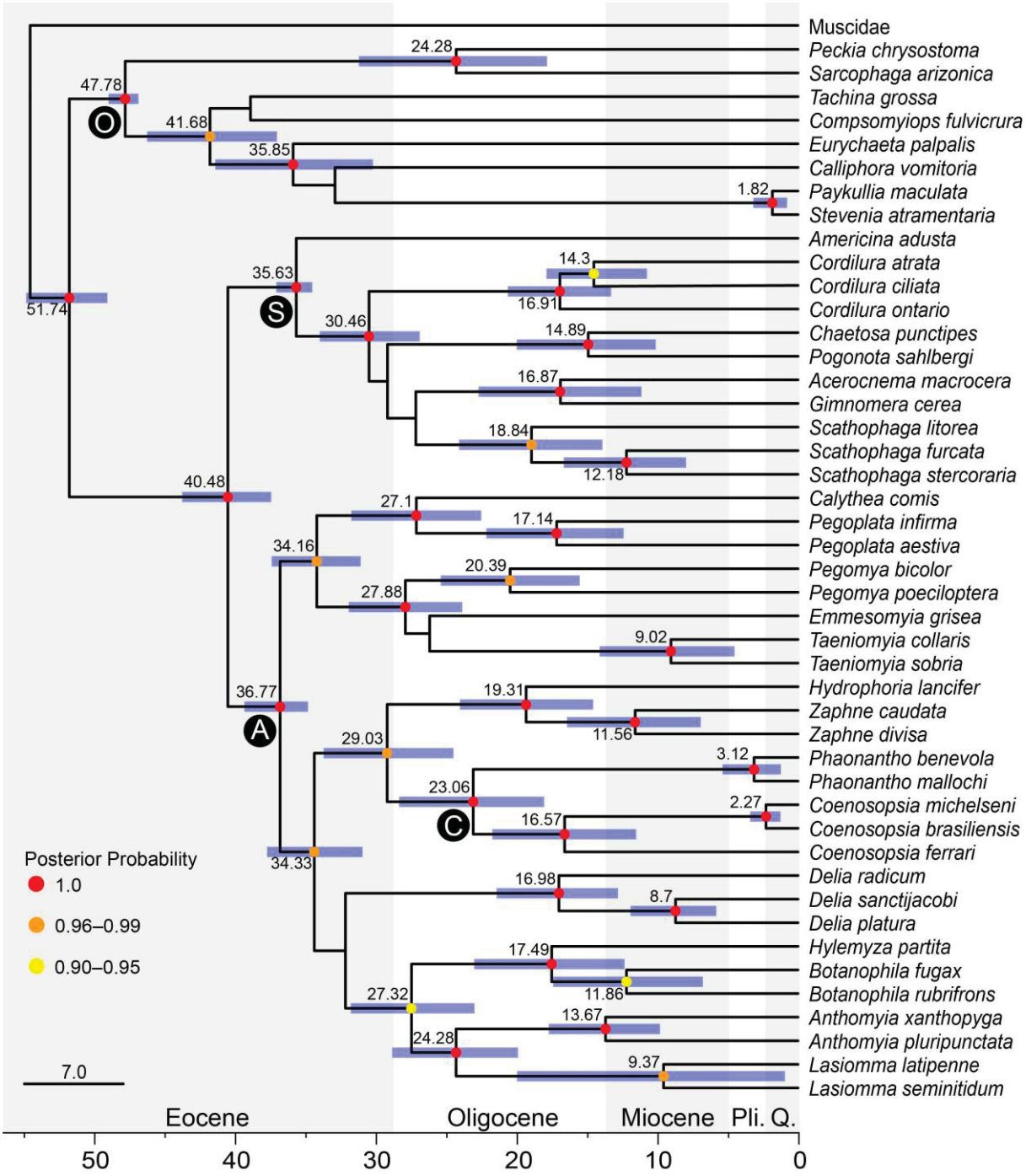


**Figure 2.** Bayesian inferred time-calibrated phylogeny of Anthomyiidae, Muscidae, Scathophagidae, and Oestroidea lineages from the analysis of the combined (12S, COI, Cytb, and 28S) dataset generated in BEAST v. 1.8.4. The blue bar length at nodes indicates a 95% high posterior density (HPD) interval at each divergence (only nodes with support >0.9 are shown). Fossil calibration points (black circle) for: O = Oestroidea crown; A = Anthomyiidae crown; S = Sarcophagidae crown; C = *Coenosopsia* + *Phaonantho* crown. Coloured circles indicate posterior probability (red = 1.0; orange = 0.96–0.99; yellow = 0.90–0.95). Time scale unit: 7 million years.

TABLES

**Table 1.** Taxon sampling of Anthomyiidae and outgroups used in the phylogenetic analyses. New sequences (*).

| Family | Species | 12S | COI | Cytb | 28S | EF1α | Voucher no. |
|---|---|---|---|---|---|---|---|
| Anthomyiidae | *Anthomyia pluripunctata* (Albuquerque, 1959)* | MT809147* | MT808059* | MT819969* | MT809163* | | DZUP2020A01 |
| Anthomyiidae | *Anthomyia xanthopyga* (Albuquerque, 1959)* | MT809148* | MT808060* | MT819970* | MT809164* | | DZUP2020A02 |
| Anthomyiidae | *Botanophila fugax* (Meigen, 1826) | MT410801 | MT410801 | MT410801 | DQ656967 | FJ025665 | |
| Anthomyiidae | *Botanophila rubrifrons* (Ringdahl, 1933) | FJ025364 | FJ025602 | | | | |
| Anthomyiidae | *Calythea comis* (Stein, 1911)* | MT809149* | MT808061* | MT819971* | MT809165* | | DZUP2020A03 |
| Anthomyiidae | *Coenosopsia brasiliensis* Michelsen, 1991* | MT809150* | MT808062* | MT819972* | MT809166* | | DZUP2020A04 |
| Anthomyiidae | *Coenosopsia ferrari* Nihei & Carvalho, 2004* | MT809151* | | MT819973* | MT809167* | | DZUP2020A05 |
| Anthomyiidae | *Coenosopsia michelseni* Nihei & Carvalho, 2004* | MT809152* | MT808063* | MT819974* | MT809168* | | DZUP2020A06 |
| Anthomyiidae | *Delia platura* (Meigen, 1826) | KP901268 | KP901268 | KP901268 | DQ656972 | | |
| Anthomyiidae | *Delia radicum* (Linnaeus, 1758) | KC177480 | HQ581775 | KC177595 | KC177819 | | |
| Anthomyiidae | *Delia sanctijacobi* (Bigot, 1885)* | MT809153* | MT808064* | MT819975* | | | DZUP2020A07 |
| Anthomyiidae | *Emmesomyia collaris* (Wulp, 1896)* | | MT808065* | | MT809169* | | DZUP2020A08 |
| Anthomyiidae | *Emmesomyia grisea* (Robineau-Desvoidy, 1830) | FJ025372 | FJ025610 | FJ025712 | FJ025510 | | |
| Anthomyiidae | *Emmesomyia sobria* (Albuquerque & Couri, 1981)* | MT809154* | MT808066* | MT819976* | MT809170* | | DZUP2020A09 |
| Anthomyiidae | *Hydrophoria lancifer* (Harris, 1780) | DQ656891 | HM386339 | DQ657058 | DQ656968 | FJ025677 | |
| Anthomyiidae | *Hylemyza partita* (Meigen, 1826) | | HM412433 | DQ657059 | DQ656969 | | |
| Anthomyiidae | *Lasiomma latipenne* (Zetterstedt, 1838) | | | | DQ656970 | FJ025683 | |
| Anthomyiidae | *Lasiomma seminitidum* (Zetterstedt, 1845) | | KR634383 | DQ657061 | DQ656971 | DQ657112 | |
| Anthomyiidae | *Pegomya poeciloptera* Malloch, 1921* | MT809156* | MT808068* | MT819978* | MT809172* | | DZUP2020A11 |
| Anthomyiidae | *Pegomya bicolor* (Wiedemann, 1817) | MT410802 | MT410802 | MT410802 | | | |
| Anthomyiidae | *Pegoplata aestiva* (Meigen, 1826) | FJ025407 | FJ025649 | FJ025745 | | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Anthomyiidae | *Pegoplata infirma* (Meigen, 1826) | MT410786 | MT410786 | MT410786 | FJ025554 | | |
| Anthomyiidae | *Phaonantho benevola* Couri, 1979* | MT809157* | MT808069* | | MT809173* | | DZUP2020A12 |
| Anthomyiidae | *Phaonantho mallochi* (Curran, 1934)* | MT809158* | MT808070* | | | | DZUP2020A13 |
| Anthomyiidae | *Zaphne caudata* (Zetterstedt, 1855) | DQ656888 | | DQ657055 | DQ656965 | | |
| Anthomyiidae | *Zaphne divisa* (Meigen, 1826) | MT628546 | MT628546 | MT628546 | | | |
| Calliphoridae | *Calliphora vomitoria* (Linnaeus, 1758) | KT444440 | FJ025603 | KT444440 | JQ307776 | JQ307782 | |
| Calliphoridae | *Compsomyiops fulvicrura* (Robineau-Desvoidy, 1830) | FJ025369 | FJ025607 | FJ025709 | FJ025504 | FJ025667 | |
| Calliphoridae | *Eurychaeta palpalis* (Robineau-Desvoidy, 1830) | FJ025374 | FJ025612 | KY749704 | FJ025512 | KY749862 | |
| Muscidae | *Drymeia alpicola* (Rondani, 1871) | FJ025370 | FJ025608 | FJ025710 | FJ025508 | FJ025669 | |
| Muscidae | *Haematobosca stimulans* (Meigen, 1824) | FJ025375 | FJ025615 | FJ025716 | FJ025518 | FJ025673 | |
| Muscidae | *Helina evecta* (Harris, 1780) | FJ025377 | FJ025619 | FJ025719 | FJ025522 | FJ025675 | |
| Muscidae | *Hydrotaea cyrtoneurina* (Zetterstedt, 1845) | FJ025380 | FJ025622 | FJ025721 | FJ025526 | FJ025678 | |
| Muscidae | *Limnophora maculosa* (Meigen, 1826) | FJ025385 | FJ025627 | FJ025726 | FJ025531 | FJ025685 | |
| Muscidae | *Lispe tentaculata* (De Geer, 1776) | FJ025388 | FJ025630 | FJ025729 | FJ025534 | FJ025687 | |
| Muscidae | *Musca domestica* Linnaeus, 1758 | DQ656896 | AF104622 | DQ657064 | DQ656974 | DQ657113 | |
| Muscidae | *Muscina stabulans* | FJ025396 | EF531210 | FJ025736 | EF531145 | FJ025689 | |
| Muscidae | *Mydaea urbana* (Meigen, 1826) | FJ025399 | FJ025641 | FJ025739 | FJ025548 | FJ025691 | |
| Muscidae | *Stomoxys calcitrans* (Linnaeus, 1758) | DQ656886 | DQ657039 | DQ657053 | DQ656963 | FJ025698 | |
| Muscidae | *Thricops cunctans* (Meigen, 1826) | FJ025418 | FJ025661 | FJ025753 | FJ025564 | FJ025700 | |
| Rhinophoridae | *Paykullia maculata* (Fallén, 1815) | FJ025404 | FJ025646 | FJ025742 | MK070751 | FJ025694 | |
| Rhinophoridae | *Stevenia atramentaria* (Meigen, 1824) | GQ409108 | | GQ409439 | GQ409281 | GQ409492 | |
| Sarcophagidae | *Peckia chrysostoma* (Wiedemann, 1830) | GQ409080 | AF259515 | GQ409411 | GQ409255 | | |
| Sarcophagidae | *Sarcophaga arizonica* (Townsend 1919) | FJ025413 | FJ025655 | FJ025749 | FJ025559 | FJ025696 | |
| Scathophagidae | *Acerocnema macrocera* (Meigen, 1826) | DQ656898 | | DQ657066 | DQ656976 | DQ657114 | |
| Scathophagidae | *Americina adusta* (Loew, 1863) | DQ656899 | HM413212 | DQ657067 | DQ656977 | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Scathophagidae | *Chaetosa punctipes* (Meigen, 1826) | DQ656916 | HM861616 | DQ657083 | DQ656994 | |
| Scathophagidae | *Cordilura atrata* Zetterstedt, 1846 | DQ656903 | JF867528 | DQ657071 | DQ656981 | DQ657116 |
| Scathophagidae | *Cordilura ciliata* (Meigen, 1826) | DQ656905 | EF531195 | DQ657073 | DQ656983 | |
| Scathophagidae | *Cordilura ontario* Curran, 1929 | DQ656908 | MF851933 | DQ657076 | DQ656986 | DQ657120 |
| Scathophagidae | *Gimnomera cerea* (Coquillett, 1908) | DQ656917 | | DQ657084 | DQ656995 | DQ657125 |
| Scathophagidae | *Pogonota sahlbergi* (Becker, 1900) | DQ656941 | KT782313 | DQ657108 | DQ657018 | |
| Scathophagidae | *Scathophaga furcata* (Say, 1823) | DQ656945 | HM413006 | AF180974 | DQ657022 | DQ657138 |
| Scathophagidae | *Scathophaga litorea* (Fallén, 1819) | DQ656948 | KT959998 | AF180983 | DQ657025 | DQ657139 |
| Scathophagidae | *Scathophaga stercoraria* (Linnaeus, 1758) | KM200724 | KM200724 | KM200724 | KC177825 | DQ657141 |
| Tachinidae | *Tachina grossa* (Linnaeus, 1758) | FJ222684 | | GQ409442 | KC177830 | GQ409494 |

**Table 2.** Primers used for PCR amplifications of the gene fragments used in this study.

| Gene fragment | Primer sequences | Reference |
|---|---|---|
| 12S | AAACTAGGATTAGATACCCTATTA | Simon *et al*. (1994) |
| | CCCTGATACACAAGGTA | Su *et al*. (2008) |
| COI | GGTCAACAAATCATAAAGATATTGG | Folmer *et al*. (1994) |
| | TAAACTTCAGGGTGACCAAAAAATCA | Folmer *et al*. (1994) |
| Cytb | TATGTTTTACCTTGAGGACAAATATC | Simon *et al*. (1994) |
| | AAATTCTATCTTATGTTTTCAAAAC | Simon *et al*. (1994) |
| 28S | AGCGGAGGAAAAGAAAC | Bertone *et al*. (2008) |
| | GCTATCCTGAGGGAAACTTCGG | Wiegmann *et al*. (2000) |

**Table 3.** Optimal partitioning scheme identified for the datasets of Anthomyiidae and outgroups sequences, as identified using Partitionfinder 2.1.1.

| Subset | Gene partition | Best scheme |
|---|---|---|
| 1 | 12S | TVM+I+G |
| 2 | COI (p.1) | HKY+G |
| 3 | COI (p.2) | TRN+I+G |
| 4 | COI (p.3) | F81+I |
| 5 | Cytb (p.1) | K81UF+I+G |
| 6 | Cytb (p.2) | HKY+I+G |
| 7 | Cytb (p.3) | K81UF+I+G |
| 8 | 28S | TVM+I+G |
| 9 | Ef1α (p.1) | K81+I+G |
| 10 | Ef1α (p.2) | GTR+G |
| 11 | Ef1α (p.3) | K81+I+G |

**Table 4.** Sequence statistic of Anthomyiidae and outgroup sampled in this study, based on the optimal alignment of each marker.

| Marker | N | Length | Aligned length | Variable sites | %AT |
|---|---|---|---|---|---|
| 12S | 52 | 328–630 | 630 | 252 | 78.7 |
| COI | 46 | 522–658 | 658 | 258 | 69.0 |
| Cytb | 51 | 554–658 | 658 | 334 | 74.7 |
| 28S | 50 | 634–983 | 983 | 306 | 69.9 |
| Ef1α | 29 | 468–668 | 668 | 215 | 47.4 |

# SUPPLEMENTARY MATERIAL

## **Table S1.** Script including molecular matrix used in the phylogenetic analyses.

#NEXUS

[Length of molecular markers in alignment: 12S (1-630); COI (631-1288); Cytb (1289-1946); 28S (1947-2929); Ef1a (2930-3597).]

begin taxa;

dimensions ntax=56;

begin characters;

dimensions nchar=3597;

format datatype=dna missing=N gap=-;

matrix

Acerocnema_macrocera

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NNNN

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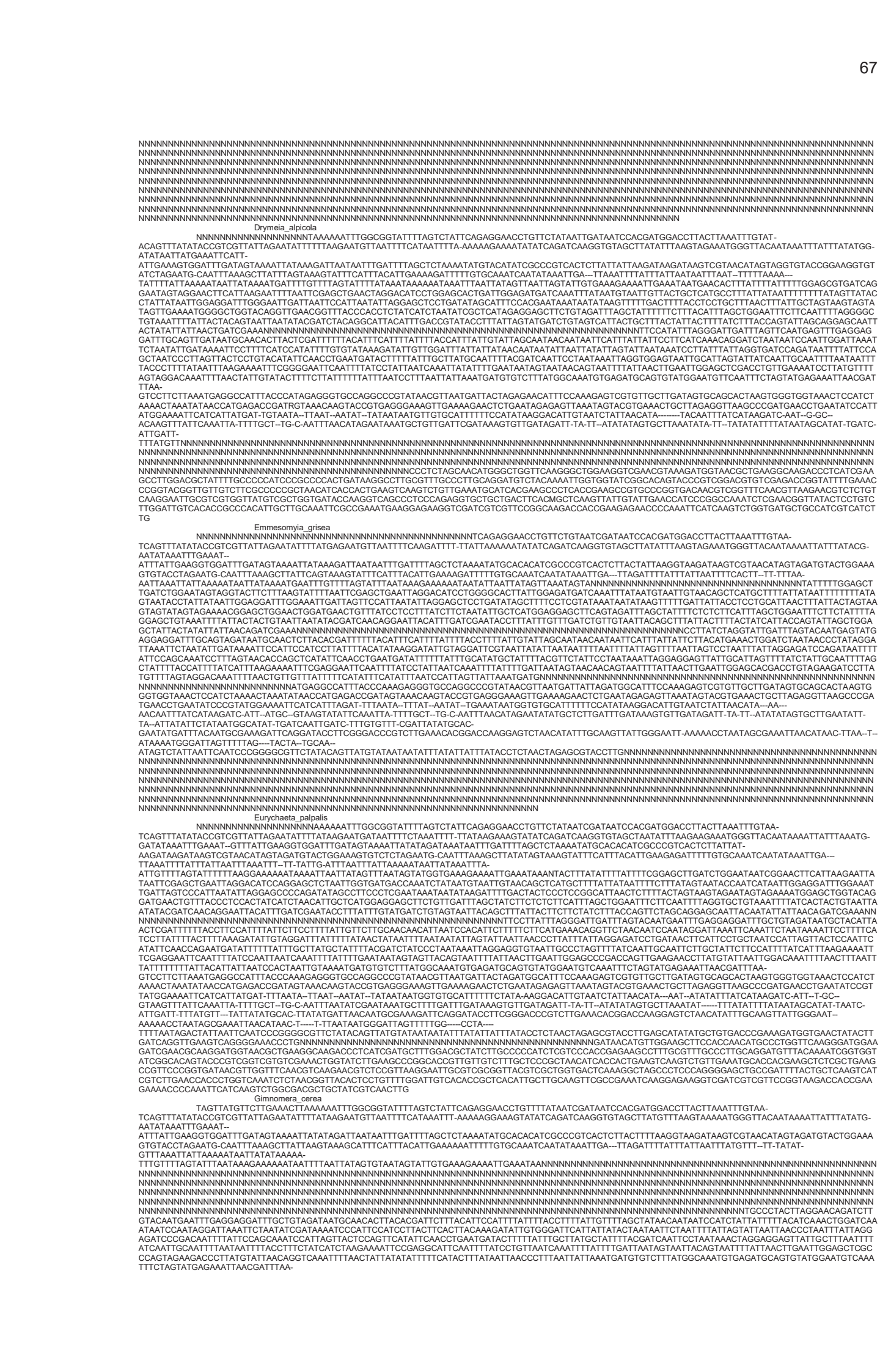

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Haematobosca_stimulans

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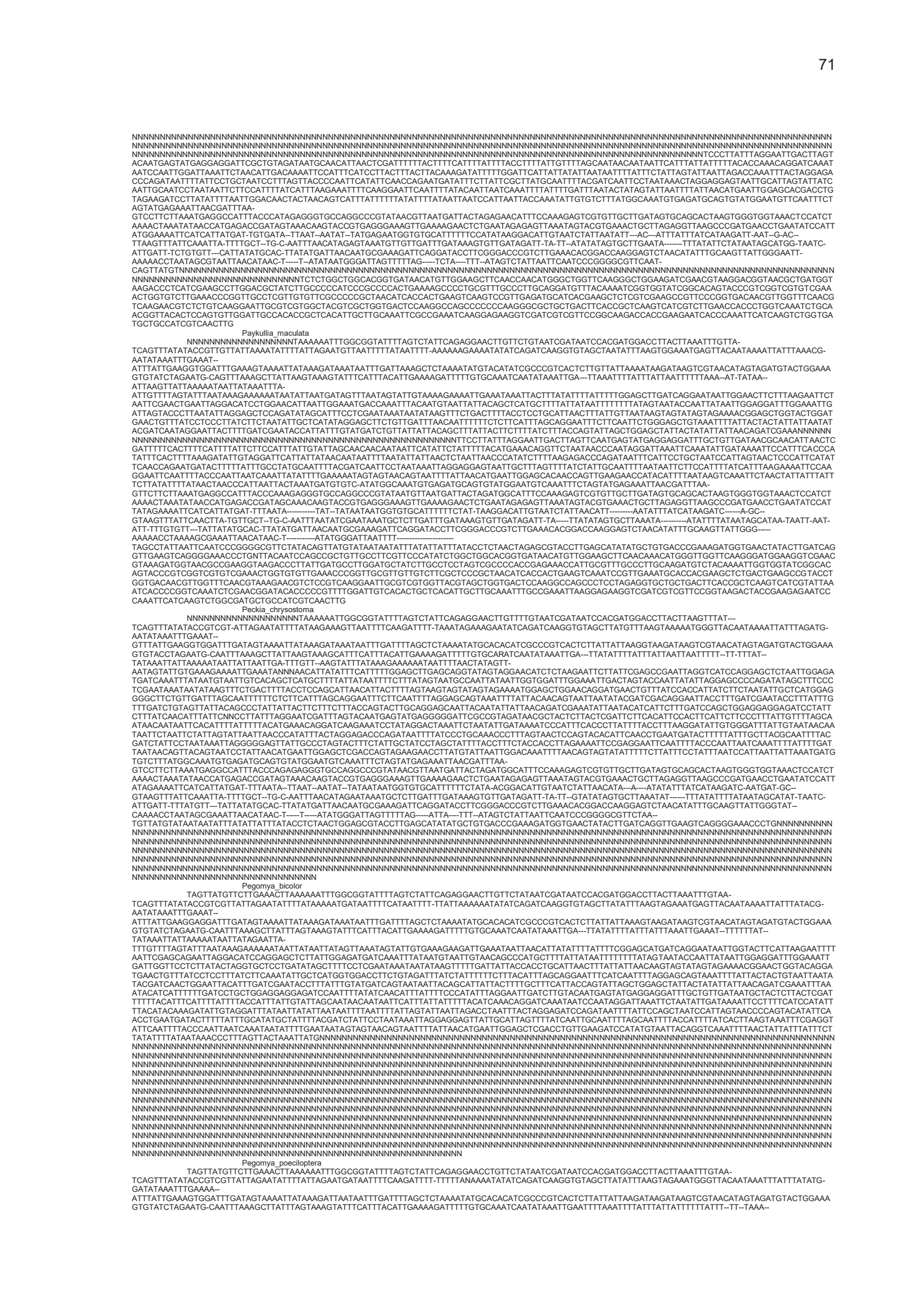

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Stevenia_atramentaria
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Tachina_grossa

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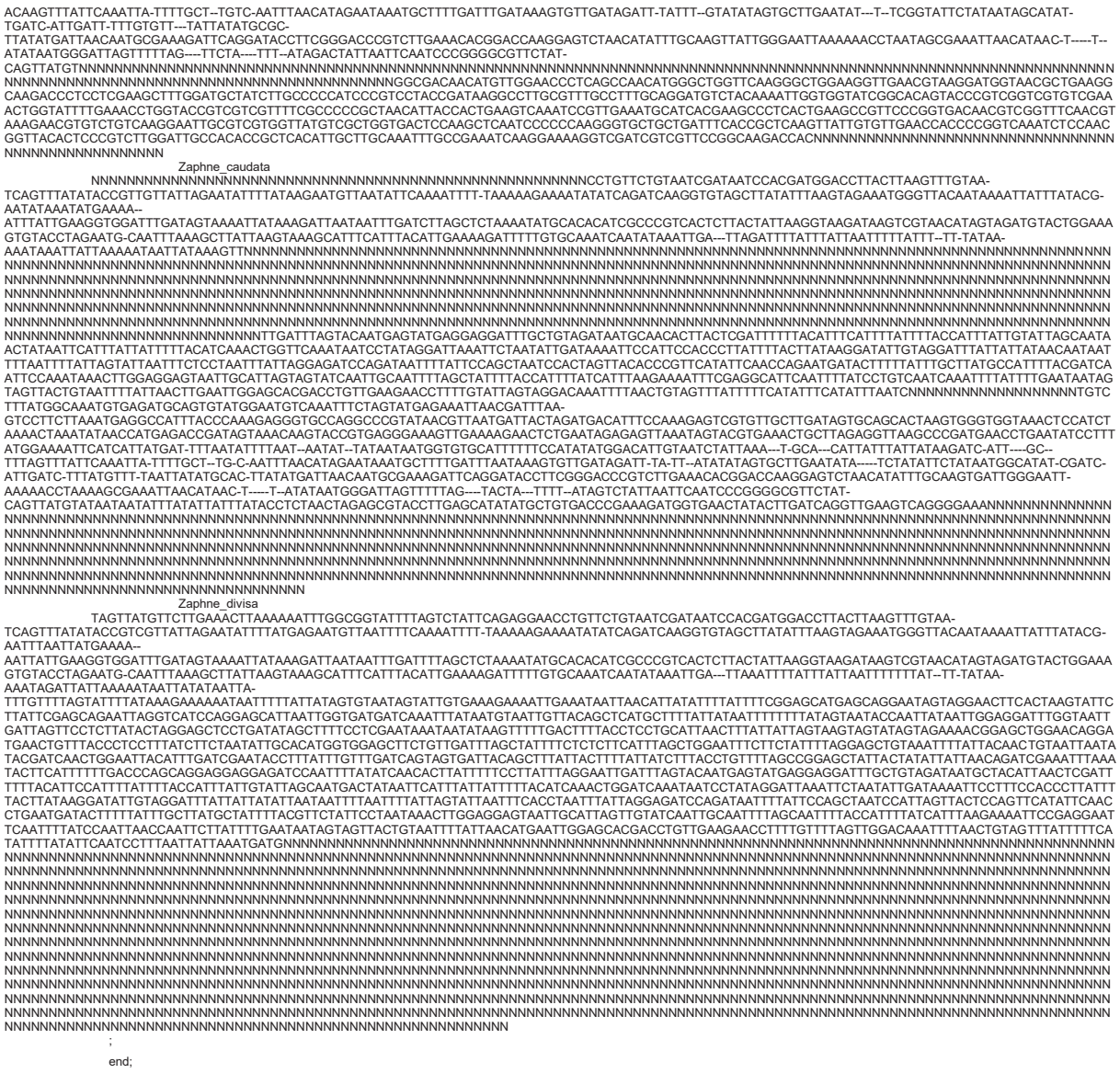
Zaphne_caudata
Zaphne_divisa
;
end;

# CAPÍTULO II

PHYLOGENETIC ANALYSIS OF ANTHOMYIIDAE BASED ON MORPHOLOGICAL EVIDENCE

# Phylogenetic analysis of Anthomyiidae (Insecta: Diptera) based on morphological evidence

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ABSTRACT

The Anthomyiidae comprises about 2,000 species and 49 genera worldwide distributed, occurring mainly in cold areas in both higher latitudes and higher altitudes. This family is taxonomically challenging, due to most generic diagnostic characters are in male terminalia and dissection is necessary to access them. A broad phylogenetic analysis aiming to understand the genera relationship was never performed and a generic classification covering all genera is absent. Herein, we present a morphological phylogenetic analysis based on parsimony, including 130 species of 44 genera of Anthomyiidae and 158 characters. Also, we discuss the relationship among some genera and propose a synonymy and a new combination to Neotropical species of *Anthomyia* Meigen. Almost all genera were recovered as monophyletic, except: *Botanophila* Lioy, *Emmesomyia* Malloch, *Hylemya* Robineau-Desvoidy, *Leucophora* Robineau-Desvoidy, and *Pegomya* Robineau-Desvoidy.

Key words: Calyptratae, flies, morphology, Muscoidea, systematics.

## INTRODUCTION

The Anthomyiidae (Diptera, Calyptratae) is a family with about 2,000 species and 49 genera worldwide distributed (Michelsen, 2010; Evenhuis & Pape, 2021). Most of the species are flower visitors, feeding on nectar or pollen, whereas larvae are usually phytophagous, including some species that can lead to significant damages in agriculture (Huckett, 1987; Evenhuis, 2007; Rader et al., 2009; Michelsen, 2010; Savage et al., 2016). The biodiversity of these flies is mainly distributed in cold areas of both higher latitudes and higher altitudes (Michelsen, 2010).

The taxonomy of anthomyiids is difficult, due to most of generic diagnostic characters are in male terminalia and dissection is necessary to access them (Michelsen, 2010). The family is distinguished from other calyptrate flies by presence of setulae on the ventral surface of scutellum and by the long vein $A_1$ reaching the wing margin (Michelsen, 1991, 2010), but these characteristics can be absent in some species and genera.

The monophyly of Anthomyiidae have been defended by several studies based on morphology (Hennig, 1976; McAlpine, 1989; Michelsen, 1991; Lambkin et al., 2013), while its position among the Muscoidea was controversial. The family has been considered as sister group of Muscidae (Michelsen, 1991), sister group of Muscidae + Oestroidea (Lambkin et al., 2013), and even as sister group to the remaining Muscoidea families (McAlpine, 1989). On the other hand, molecular data have been reached more congruent results, indicating Anthomyiidae as sister group of Scathophagidae (Bernasconi et al., 2000; Wiegmann et al., 2011; Ding et al., 2015; Junqueira et al., 2016; Zhang et al., 2016; Gomes et al., 2021), but some of them recovered Anthomyiidae as a paraphyletic group, including Scathophagidae (Kutty et al., 2007, 2008, 2010, 2019; Cerretti et al., 2017; Buenaventura et al., 2021).

Anthomyiidae and Scathophagidae are morphologically very similar families, the main characters used to differentiate Scathophagidae from Anthomyiidae are absence of ventral setulae on the apex of scutellum, lower calypter reduced, and broad frons in males (Vockeroth, 1987, 2010), but these characteristics are also observed in some Anthomyiidae genera (e.g, *Coenosopsia* Malloch, *Fucellia* Robineau-Desvoidy and *Myopinella* Michelsen) (Michelsen, 2010).

The Anthomyiidae has no comprehensive classification (Michelsen, 2010), even though some groupings of genera can be identified, it is still impossible to arrange all genera into a well-supported hierarchical system of subfamilies and tribes (Michelsen, 2000). Huckett (1965) and Michelsen (2000) presented classifications dividing the family in two and three subfamilies respectively, but without considering all known genera.

Huckett (1965) considered the genera *Fucellia* and *Circia* Malloch [=*Alliopsis* Schnabl & Dziedzicki] as a separate subfamily (Fucelliinae), whereas the remaining anthomyiids were classified as Anthomyiinae, which were divided into two tribes (Anthomyiini and Myopinini). Michelsen (2000) divided most anthomyiids into the

subfamilies Myopininae (*Enneastigma* Stein, *Calythea* Schnabl & Dziedzicki, *Pegoplata* Schnabl & Dziedzicki, and *Myopina* Robineau-Desvoidy), Pegomyinae (*Emmesomyia*, *Pegomya*, *Eutrichota* Kowarz, *Mycophaga* Rondani, *Paradelia* Ringdahl, *Alliopsis*, and *Myopella* Malloch [=*Myopinella* Michelsen]), and Anthomyiinae (almost all remaining anthomyiid genera).

Anthomyiidae has never been studied in a broad phylogenetic context. Some authors discussed the relationship among some genera (Snyder, 1957; Griffiths, 1982-2001; Hennig, 1976; Michelsen, 1985, 1988, 1991, 1996, 2000). However, the relationship among Anthomyiidae genera remain unclear. Herein, we present a broad phylogenetic study including 158 characters and 130 species of 44 genera. We aim to improve the phylogenetic understanding of Anthomyiidae using morphological data, presenting new characters and morphological evidence to support the relationship among some genera. A discussion about the phylogenetic relationships among the genera is provided.

## MATERIAL AND METHODS

### Taxon sampling

The material used in this study is deposited in the following institutions: Colección Nacional de Insectos, Ciudad de Mexico, Mexico (CNIN); Padre Jesus Santiago Moure Entomological Collection, Curitiba, Brazil (DZUP); Colección Entomológica del Instituto de Ecología, Xalapa, Mexico (IEXA); Fundación y Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina (IMLA); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Naturhistoriska Riksmuseet, Stockholm, Sweden (NHRS); National Museum of Natural History, Washington, USA (USNM).

The sampling (including outgroups) is based on previous studies (Bernasconi et al., 2000; Kutty et al., 2007, 2008, 2010, 2019; Wiegmann et al., 2011; Ding et al., 2015; Junqueira et al., 2016; Zhang et al., 2016; Cerretti et al., 2017; Buenaventura et al., 2021; Gomes et al., 2021). The phylogenetic analyses are based on a matrix composed by 130 terminals, including 114 Anthomyiidae (ingroup), six Scathophagidae (outgroup) and 10 Oestroidea (outgroup) (Table S1). Trees were rooted in the Oestroidea clade. We sampled representatives of 44 from the 49 valid

genera of Anthomyiidae, including the two known fossil genera. The complete information about the studied specimens are listed in Table S2.

Construction of the characters and terminology

The characters are based in analyses carried out by Couri & Pont (2000), Nihei & de Carvalho (2004), Nihei & de Carvalho (2007), Domínguez & Roig-Juñent (2008), Lambkin et al. (2013), and Gomes et al. (2020). The characters' construction follows Sereno (2007) and Brazeau (2011). The matrix was built in the software Mesquite 3.2 (Maddison & Maddison, 2011). The symbol "?" was used for unknown character state and "-" for inapplicable character (Table S1). The characters are listed in Table 1. The terminology follows Cumming and Wood (2017).

Phylogenetic analyses

The parsimony analyses were carried out on software TNT (Goloboff & Catalano, 2016). Characters were treated as unordered. The analyses were performed under equal weighting and implied weighting (Goloboff, 1993). The implied weighting was carried out using values of k (constant of concavity) from one to 30 (Table 2). The analyses were carried out using *New Technology* (*Sectorial Search*, *Ratchet*, *Drift* and *Tree Fusing*), with 9.999 trees in memory, random seed= 0 and the parameters in default mode, except: *Sectorial Search* with XSS activated; *Ratchet search* with total number of interactions= 200, *Drift search* with 200 cycles and Tree fusing with 100 rounds. Random seed 0, 1000 replications and 100 trees saved, and with the minimum tree length found 10 times. In order to ensure that the best tree was obtained, we repeated the analysis using the chosen k value (k= 10), but with the minimum tree length found 50 times, these analyses had 107.358.896.240 rearrangements. The characters' fast optimization was made in the software Winclada 1.61 (Nixon, 2002).

The Relative Bremer (Goloboff & Farris, 2001) and Bootstrap (Felsenstein, 1985) are presented as branches support and were performed in software TNT. The Relative Bremer was performed with suboptimal trees, length up to 10 additional steps stored. The Bootstrap was performed with 100 replications using New Technology (same parameters of the main analysis, except minimum tree length found 2 times). The trees were edited on Adobe Illustrator CS6.

## RESULTS

### List of characters

The matrix comprises 158 characters of adult male and female: 29 from the head, 31 from the thorax, 24 from the wings, 16 from the legs, 2 from abdomen, 48 from male terminalia, and 6 from female terminalia. Among the 158 characters, 111 are new and were built in this study.

### Phylogeny analyses

The parsimony analysis using implied weighting with *k*= 10, resulted in a most parsimonious tree with 1443 steps, CI= 17, RI= 63, same results obtained by k= 11 and 12. We choose this *k* value due to the smaller number of steps and trees if compared to trees obtained by lower *k* value; and due to the best resolution (number of clades) if compared to the trees with highest *k*. The number of steps, CI, RI, fit and number of trees of the analyses using *k* value of 1–30 are presented (Table 2). The Relative Bremer Support and the Bootstrap were plotted in the tree, indicated in gray and white boxes, respectively (Fig. 1). Branches without gray and/or white boxes were not supported.

The parsimony analysis supported Scathophagidae and Anthomyiidae as monophyletic. The Oestroidea clade was well supported by 13 synapomorphies: and 13 homoplasies, with the following topology: Rhinophoridae + (Mesembrinellidae + (Calliphoridae + (Tachinidae + Sarcophagidae))). The clade Anthomyiidae + Scathophagidae was well supported by three synapomorphies: fronto-orbital plate with setulae on its lower surface (12: 1), $A_1$ vein reaching the wing margin (80: 1), female sternite 8 completely divided longitudinally (158: 1); and eight homoplasies: male eyes separated by a distance of about three times the anterior ocellus length (19: 1), costal vein with a pair of setulae near subcostal connection two times longer than others costal setulae (75: 1), female fore tibia with one anterodorsal seta (87: 1), male hind tibia with one anteroventral seta (92: 1), Sternite 5 with lobus narrower than half of sternite 5 width (110: 1), male cerci as long as wide (116: 2), Surstyli curved on lateral view (128: 1), and pregonite with setae (137: 1).

The Scathophagidae clade was also well supported by two synapomorphies: abdomen sharped and distally enlarged (103: 2) and male cerci not forming a plate (117: 0); and five homoplasies: frons wider than long (22: 1), female palpi filiform (28:0), male abdomen sharped and apically enlarged (103: 2), sternite 5 rounded

(106: 2), male cerci not forming a plate (117: 0), pregonite with four setae (138: 3). The monophyly of Anthomyiidae was supported by 10 homoplasies: female interfrontal setae present (2: 1), male interfrontal setae present (3: 1), female fronto-orbital plate with setula on its lower surface (10: 1), arista pubescent (16: 1), katepisternum conformation 1+1 (47: 5), anterior seta of katepisternum similar to posterior seta (48: 1), apical setae of scutellum longer than subbasal setae (51: 2), presence of setulae on apex of scutellum (52: 1), costal vein with a pair of setulae near subcostal connection four times longer than others costal setulae (75: 2), presence of ventrobasal seta on hind tibia basitarso (100: 1), and surstyli apex narrower than proximal section (127: 0). The relationship among genera will be presented and discussed below (see Discussion).

## DISCUSSION

We present the most complete study to elucidate the phylogenetic relationship among Anthomyiidae genera based on morphological evidence. The tree generated by the implied weighting with *k*=10-12 (Fig. 1) presented a better resolution in topologies (forming more clades) than analysis under other *k* values and equal weighting (trees not shown). The obtained topology Oestroidea + (Anthomyiidae + Scathophagidae) (Fig. 1 (part 1)) is congruent with previous studies based on molecular evidence (Bernasconi et al., 2000; Kutty et al., 2007, 2008, 2010, 2019; Wiegmann et al., 2011, Ding et al. 2015, Junqueira et al., 2016; Zhang et al., 2016; Cerretti et al., 2017; Buenaventura et al., 2021; Gomes et al. 2021). Some of these molecular studies indicated Anthomyiidae as a paraphyletic group, including a monophyletic Scathophagidae nested (Kutty *et al*., 2007, 2008, 2010, 2019; Cerretti *et al*., 2017; Buenaventura *et al*., 2021). However, all these studies have a small sample of both Anthomyiidae and Scathophagidae and no Neotropical taxon was included in these analyses.

The monophyly of Anthomyiidae has been indicated by several studies based on morphology (Hennig, 1976; McAlpine, 1989; Michelsen, 1991; Lambkin et al., 2013), as well as in the broadest study based on molecular data, including 14 genera of Anthomyiidae (Gomes et al., 2021). Among the Anthomyiidae genera, the analyses corroborated 13 main clades, while the genera *Chirosiomima* Hennig was recovered as sister group of remaining Anthomyiidae, with the following next branches: *Fucellia*, *Boreophorbia* Michelsen, *Acklandia* Hennig, and *Chirosia*

Rondani. These branches were not well supported by Bremer and Bootstrap and future studies are necessary to understand the relationship among these genera.

The clade A is formed by *Leucophora*, *Oxyphorbia* Griffiths, *Myopina* and *Chiastocheta* Pokorny (Fig. 1 (part 2)). This clade is supported by a synapomorphy: presence of upcurved spines on female cerci (154: 1); and eight homoplasies: parafacial wider than pedicel on lateral view (1: 2), two proclinate orbital setae in female (6: 1), reclinate orbital setae absent in female (8: 0), gena three times longer than pedicel (13: 3), parafacial wider than postpedicel in lateral view (24: 3), apex of scutellum bare (55: 0), male cerci shorter than surstyli (119: 0), and phallapodema enlarged apically (152: 1).

*Leucophora* was recovered as paraphyletic, with one clade supported by a synapomorphy: arista very-long plumose (16: 4); and four homoplasies: male interfrontal setae shorter than frontal setae (4: 0), costal vein ventrally setulose (73: 1), male dm-m crossvein slightly curved (78: 1), and male hind tibia with a row of short erect posteroventral setae (98: 1). This clade is formed by Nearctic terminals: *Leucophora apivora*, which was described as *Pergandea* Aldrich; and *Leucophora* sp. 1 and *Leucophora* sp. 2, which resembles species of the genus *Ganperdea* Aldrich, and *Neohylemyia* Malloch, respectively. These three genera were synonymized under *Leucophora* (Evenhuis & Pape, 2021), and its species are morphologically similar, being represented by a large gena, and a long-plumose antenna with the base enlarged (Malloch, 1917; Aldrich, 1919, 1921), while most of the *Leucophora* species have a short-plumose or pubescent antenna. This Nearctic clade probably deserves be considered as a separated genus and future studies are necessary including more species of the genus representing the morphological diversity of *Leucophora*.

Also in clade A, our topology is incongruent with Hennig (1976) and Michelsen (2000) hypothesis that *Myopina* is close related to *Enneastigma*, *Calythea* and *Pegoplata* (clade C); and with Hennig (1976) hypothesis that *Chiastocheta* is close related to *Botanophila* (clade F and H), *Alliopsis* (clade L), *Fucellia* and *Chirosiomima*. Our analysis indicated *Myopina* as sister group of *Chiastocheta*, based on 10 homoplasies: parafacial narrower than pedicel (1: 0), proclinate orbital setae present in male (7: 1), male eyes dichoptic (18: 1), parafacial with about ¼ of postpedicel width (24: 0), anepisternum with a superior-anterior setae (42: 1), lower calypter shorter than upper one (85: 0), calcar twice longer than tibia width (96: 1),

ventrobasal seta on basitarso absent (100: 0), male cerci as long as wide (116: 2), and surstyli apex slightly curved (129: 1). *Chiastocheta* was recovered as monophyletic, based on five homoplasies: high of gena similar to pedicel (13: 1), post-pedicel twice longer than pedicel (14: 0), arista bare (16: 0), Katepisternum setae 2+2 (47: 1), and male pulville narrower than tarsomere width (101: 0).

The clade B (Fig. 1 (part 2)) is formed by the genus *Acridomyia* Stackelberg and the monophyletic genus *Myopinella,* based on two synapomorphies and 13 homoplasies, but the character information referent to *Acridomyia* is absent in all these characters, except the apical setae of scutellum similar to subbasal setae (51: 1), both genera are morphologically very distinct and the relationship between these genera have never been indicated. *Acridomyia* is a peculiar genus readily distinguished from all other genera by the absence of palpi and vibrissae (Snyder, 1940). Hennig (1976) indicated the possibility of *Acridomyia*, together with *Tettigoniomyia* Hennig and *Acyglossa* Rondani (both not included in the present analysis) form a monophyletic group, based on the palpi small (entirely absent in *Acridomyia*), the postgonite bare, surstyli weakly forked apically, and the fact of the larvae of probably all species are parasites of grasshopers. Due to the large number of missing data of *Acridomyia* in our analysis, we are unable to discuss about its phylogenetic position.

*Myopinella* is a genus with only two known species from Neotropics, easily distinguished by prosternum densely setulose, this genus resembles *Myopina* (clade A, Fig. 1 (part 2)), differing in having a pair of long presutural acrostichals, prosternum setulose and hind metarsus not modified in both sexes (Malloch, 1934). Michelsen (2000) classified *Myopinella* in the subfamily Pegomyinae together with *Paradelia*, *Mycophaga*, *Eutrichota*, *Emmesomyia*, *Taeniomyia* Stein, *Pegomya* and *Alliopsis*.

The clade C (Fig. 1 (part 2)) is formed by the extinct genus *Protoanthomyia* Michelsen as sister group of a clade formed by *Heterostylodes* Hennig, *Enneastigma*, *Calythea* and *Pegoplata*. This clade is supported by 10 homoplasies: proclinate orbital seta absent in female (5: 0), subcostal vein with a soft-angle (76: 0), male hind tibia with one anteroventral seta (92: 1), hind tibia with two setae (94: 2), male cerci as long as wide (116: 2), surstyli enlarged (124: 0), distiphallus covered by spines (147: 1), epiphallus similar to phallapodema length (149: 1), phalapodema shorter than pregonite (150: 0), and epiptroct as high as its wide (155: 2). The presence of

*Protoanthomyia* in this clade is uncertain. Even though external traits are abundant in this fossil, they are too variable to be phylogenetically informative and the information about male terminalia is inaccessible (Michelsen, 2000).

The next branch including *Heterostylodes*, *Enneastigma*, *Calythea* and *Pegoplata* is supported by seven homoplasies: post-pedicel three times longer than pedicel (14: 1), male palpi enlarged (26: 1), prealar longer than anterior notopleural seta (35: 2), katepimeron setulose (46: 1), costal vein with a pair of setulae near subcostal connection two times longer than others costal setulae (75: 1), abdomen dorsoventrally depressed (103: 0), and C-shape incision in sternite 5 (108: 0). The relationship among *Enneastigma*, *Calythea* and *Pegoplata* (also including *Myopina*) was previously indicated by Ackland (1968), Hennig (1976) and Michelsen (1988), based on the sclerotized and enlarged distiphallus (Hennig, 1976), reproductive system of male without accessory glands, epandrium musculature insertion on the apodemal process extending from the interior bases of the surstyli, spermathecal ducts slender and of equal diameter throughout, and phallus clubshaped and expanded at the distal part of the distiphallus (Michelsen, 1988). Additionally, Hennig (1976) considered the balloon-like distiphallus of *Calythea* as a further development of the ground plan of this group. The sister group relationship between *Calythea* and *Pegoplata* was also recovered by Gomes et al. (2021), in a phylogenetic study based on molecular data.

The clade D (Fig. 1 (part 3)) is formed by five *Delia* Robineau-Desvoidy species, this clade was supported by 10 homoplasies: male interfrontal seta absent (3:0), female reclinate orbital seta absent (8: 0), gena twice longer than pedicel (13: 2), first presutural dorsocentral seta shorter than the second one (58: 0), male *dm-m* crossvein slightly curved (78: 1), lower calypter slightly shorter than upper one (85: 1), female hind tibia with four posterodorsal setae (93: 4), male abdomen dorsoventrally depressed (103: 0), V-shape incision in sternite 5 (108: 2), and male cerci with a distal seta longer than cerci (122: 1). Gomes et al. (2021), based on molecular data, also recovered *Delia* as monophyletic. *Delia* is one of the most diverse genera in Anthomyiidae (Hennig, 1976; Evenhuis & Pape, 2021). Hennig (1976) indicated *Delia* as closely related to *Heterostylodes, Eustalomyia* Kowarz, *Leucophora*, *Botanophila*, *Phorbia* Robineau-Desvoidy, *Subhylemyia* Ringdahl, and probably *Hyporites* Pokorny, based on characters of male terminalia, as distiphallus elongated, epiphallus short and predominantly membranous, surstyli elongated and

firmly connected to the posterior epandrial arms. The present analysis is not enough to fully understand the relationship among *Delia* and other genera.

The clade E (Fig. 1 (part 3)) is formed by *Paradelia*, *Hyporites* and *Phorbia*, this clade is supported by a sinapomorphy: sternite 5 lobus with a tuft of spinulas on the inner border (114: 1); and three homoplasies: setulae on ventral surface of scutellum shorter than half length of setulae on lateral margin of scutellum (55: 0), sternite 5 with an anterior incision (107: 1), and sternite 5 lobus curved outside (111: 1). The genus *Phorbia* was recovered as monophyletic, based on two synapomorphies: female cerci long with a distal point dorsally directed (153: 2), hypoproct reduced to a narrow longitudinal plate (156: 3); and seven homoplasies: parafacial wider than pedicel width (1: 2), parafacial with about half width of postpedicel (24: 1), prealar longer than anterior notopleural seta (35: 2), female mid tibia with one anteroventral seta (88: 1), female hind tibia with one posteroventral seta (97: 1), pregonite longer than postgonite (134: 2), and pregonite bare (137: 0). The monophyly of *Phorbia* was also indicated by Hennig (1976).

Diverging from the result of the present analysis, Hennig (1976) indicated *Paradelia* as close related to *Alliopsis* (clade L), based on: proboscis sclerotized, probably reflecting a predacious habitus; basiphallus slanted and predominantly membranous; and the similarity in the distiphallus. Curiously, *Hyporites* was recovered as close related to *Paradelia* in our analysis and also has a proboscis sclerotized and predacious habitus (Suwa, 1974). The affinities of *Hyporites*, as well as *Phorbia* are unclear, but there is a possibility that both genera are related (Hennig, 1976), herein we present a probable relationship among these genera and *Paradelia*.

The clade F (Fig. 1 (part 3)) is formed by three species of *Botanophila*, supported by five homoplasies: first dorsocentral seta shorter than the second one (58: 0), female fore tibia without posterodorsal setae (87: 0), surstyli strongly curved (129: 1), postgonite long enlarged (139: 0), and phallapodeme curved (151: 1). This genus was not recovered as monophyletic and the remaining species were recovered in clade H (see below). *Botanophila* have 246 described species (Evenhuis & Pape, 2021; Gomes & de Carvalho, 2021) forming a large and morphologically diverse genus, containing several clusters of closely related species (Michelsen 2009, 2015). The genus is divided in 17 species groups based on characters of male terminalia and some of them may be monophyletic (Xue & Song, 2007).

The species in the clade F belong to three different groups of species (*fugax*-group, *biciliaris*-group and *brunneilinea*-group). Curiously, the other two species of the *brunneilinea*-group (*B. brunneilinea* and *B. subbrunneilinea*) were recovered in the clade H. We included a small sample of *Botanophila* species in our analysis, but our results indicated that the genus and the *brunneilinea*-group of species are probably non-monophyletic. Hennig (1976) indicated *Botanophila* as closely related to *Fucellia*, *Chirosiomima*, *Chiastocheta*, and *Circia* [=*Alliopsis*], even though he indicated several variations in male terminalia into species of the same genera and among these genera.

The clade G (Fig. 1 (part 3)) is formed by the genera *Karliella* Michelsen, *Ringdahlia* Michelsen and the mainly neotropical genera *Coenosopsia* and *Phaonantho* Albuquerque, in addition to the fossil genus *Coenosopsites* Michelsen. This clade is supported by seven homoplasies: anepisternum with more than one seta (44: 1), costal vein with a pair of setulae near subcostal connection two times longer than others costal setulae (75: 1), female mid tibia with one posterodorsal seta (89: 1), calcar twice longer than tibia width (96: 1), C-shape incision on sternite 5 (108: 0), surstyli wider than cerci on lateral view (123: 1), and surstyli bifurcated (130: 1).

The Palaeartic monotypic genus *Ringdahlia* has no obvious hints on relationship to existing anthomyiid genera (Michelsen, 2014). While the peculiar morphology of the monotypic Afrotropical genus *Karliella* makes it difficult to find a closer relationship to any particular genus or group of genera (Michelsen, 2013). Michelsen (2013) commented that *Karliella* is probably a relictual lineage, as well as the Neotropical *Coenosopsia* + *Phaonantho* lineage, and both share some probable homoplastic characters as the male terminalia and sternite 5 notably small. It is possible that *Karliella* and *Ringdahlia* were recovered in this clade based on homoplasies shared with *Coenosopsia* and *Phaonantho*.

The clade *Phaonantho* + (*Coenosopsites* + *Coenosopsia*) is supported by a synapomorphy: costal vein covered by long setae ventrally (74: 2); and 10 homoplasies: male interfrontal seta similar to frontal setae (4: 1), arista long-plumose (16: 3), prealar shorter than anterior notopleural seta (35: 0), costal vein with a pair of setulae near subcostal connection as long as the others costal setulae (75: 0), $A_1$ vein not reaching the wing margin (80: 0), female hind tibia with one posterodorsal seta (94: 1), male pulville narrower than tarsomere width (101: 0), postgonite long

enlarged (139: 0), distiphallus as long as phallapodeme (143: 1), and epiproct as high as its wide (155: 2).

The relationship between *Phaonantho* and *Coenosopsia* has been indicated based on morphological (Michelsen, 1991) and molecular data (Gomes et al., 2021) and the relationship *Phaonantho* + (*Coenosopsites* + *Coenosopsia*) was previously indicated by Michelsen (1991) based on phylogenetic inference. Michelsen (1991) indicated the following synapomorphies supporting *Coenosopsia* + *Phaonantho*: arista plumose, palpi dark with yellow apex, all elements of male terminalia (except surstyli) remarkably small, process longi (sternite 10) short and merging into anterobasal parts of surstyli, sperm pump sclerite vestigial, and absence of a subapical seta on the pregonite; and also indicated two plesiomorphies: vein $A_1$ strongly abbreviated, not reaching the wing edge and hind tibia with only one submedian posterodorsal seta. While the remaining Anthomyiidae are characterized by two synapomorphies: $A_1$ reaching the margin edge and tibia with two posterodorsal setae (Michelsen, 1991).

The clade H (Fig. 1 (part 4)) is formed by three species of *Botanophila,* this genus is not monophyletic, as indicated above. This clade is supported by seven homoplasies: scutum without longitudinal vittae (31: 0), katepisternum setae 2+1 (47: 4), lower calypter reduced to a linear fold (85: 0), V-shapped incision in Sternite 5 (108: 2), pregonite shorter than postgonite (134: 0), pregonite with one seta (138: 0), and postgonite long enlarged (139: 0).

The clade I (Fig. 1 (part 4)) is formed by *Mycophaga*, *Lasiomma* Stein, *Hylemya* and *Hylemyza* Schnabl & Dziedzicki, based on six homoplasies: arista long-plumose (16: 3), female fore tibia without setae (87: 0), male hind tibia with two anteroventral setae (92: 2), epiphallus shorter than phallapodeme (149: 1), and phallapodeme apically narrow (152: 0). Hennig (1976) indicated *Mycophaga* as belonging to the *Pegomya*-group (genera of this group were recovered mainly in the clade J, see below), due to bilobate pregonite and their connection with the postgonite, but this genus diverges from the genera of *Pegomya*-group due to the absence of the furcate surstyli. The relationship of *Lasiomma* is also still uncertain, Gomes et al. (2021) recovered this genus as sister-group of *Anthomyia*, and Hennig (1976) indicated similarities in the surstyli shape of some species of *Anthomyia* and *Lasiomma,* but future studies, including more species of both genera are necessary to fully understand its phylogenetic position.

The analysis indicated *Hylemyia* as paraphyletic in relation to *Hylemyza*, this topology was supported by three homoplasies: male cerci as long as wide (116: 2), male cerci shorter than surstyli (119: 0), and pregonite shorter than postgonite (134: 0). Griffiths (2001) indicated the separation between *Hylemya* and the monotypic genus *Hylemyza* as unnecessary. Gomes et al. (2021) recovered *Hylemyza* as sister group of *Botanophila*, also sharing a clade with *Anthomyia* and *Lasiomma*, but *Hylemya* was not included in this analysis. Based on morphological (Hennig, 1976) and molecular (Gomes et al. 2021) data, in addition to our analysis, is quite possible that *Lasiomma*, *Hylemyia* and *Hylemyza* are close related. Also, *Hylemyza* probably should be indicated as junior synonymy of *Hylemyia*. Future studies with a better sample of this genera are necessary to fully understand its phylogenetic position.

The clade J (Fig. 1 (part 4)) is formed by *Emmesomyia*, *Pegomya* and *Taeniomyia*, the relationship among these genera has been indicated by morphological (Snyder, 1957; Hennig, 1976; Griffiths, 1982) and molecular (Gomes et al. 2021) data. This clade is supported by a synapomorphy: sternite 6 and 7 with spinules (157: 1); and three homoplasies: post-pedicel twice longer than pedicel (14: 0), surstyli apex as wide as proximal section (127: 1), and distiphallus distally enlarged and wider than proximal section (145: 1). Hennig (1976) indicated that these three genera are also related to *Eutrichota* (clade K) and *Mycophaga* (clade I).

Griffiths (1982) considered the pregonite bilobate as a synapomoprhy of *Emmesomyia*, *Eutrichota* and *Pegomya*. Snyder (1957) and Griffiths (1982, 1984) indicated *Emmesomyia* and *Pegomya* as the most closely related genera. Snyder (1957) considered this relationship based on the presence of three anterodorsal and two posterodorsal setae on the hind tibia of both sexes and the absence of a complete or partial row of short posterior to posteroventral setae or setulae on the male hind tibia. Griffiths (1982, 1984) considered the sternite 5 largely covered by setae with the longest setae situated near the bases of the processes, a basal to median group of setule on the ventral surface of the pregonite, and the apical division of surstyli as synapomorphies of both genera. The genus *Taeniomyia* was considered as a subgenus of *Emmesomyia* during early studies (Michelsen, 2010).

The present analysis recovered *Pegomya* and *Emmesomyia* as paraphyletic, while the Neotropical *Taeniomyia* was recovered as monophyletic based on three homoplasies: arista not swollen basally (17: 0), costal vein with a pair of setulae near subcostal connection four times longer than others costal setulae (75: 2), and

postgonite with a distal seta (141: 1). The relationship among *Emmesomyia*, *Taeniomyia* and *Pegomya* is well known and supported by both molecular and morphological evidence, but the monophyly and phylogenetic position of these genera are still uncertain.

The clade K (Fig. 1 (part 4)) is formed by *Eutrichota*, *Adia* Robineau-Desvoidy, and *Paregle* Schnabl, it is supported by a synapomorphy: surstyli short bifurcated apically (131: 1); and three homoplasies: scutum without longitudinal vittae (31: 0), female mid tibia with one posterodorsal seta (89: 1), and pregonite longer than postgonite (134: 2). *Eutrichota* has been indicated as closely related to genera which were recovered in the clade J (Hennig, 1976; Griffiths, 1982). Hennig (1976) indicated *Paregle* as probably monophyletic, but with an uncertain phylogenetic position. The genus *Adia* has no information about its relationship (Griffiths, 2001).

The clade L (Fig. 1 (part 5)) is formed by *Hydrophoria* Robineau-Desvoidy, *Strobilomyia* Michelsen, *Subhylemyia*, *Alliopsis* and *Zaphne* Robineau-Desvoidy, based on six homoplasies: costal vein with a pair of setulae near subcostal connection as long as the others costal setulae (75: 0), female mid tibia with three posterodorsal setae (89: 3), male hind tibia with three anteroventral setae (92: 3), female hind tibia with two anteroventral setae (93: 2), surstyli apically straight on lateral view (128: 0), surstyli strongly curved on lateral view (129: 1), and pregonite with one seta (138: 0). *Hydrophoria* and *Zaphne* are closely related genera (Griffiths, 1998) and were recovered as sister groups in the molecular analysis performed by Gomes et al. (2021). Both genera share characters as antennae plumose, prementum shining, basal part of prosternum bare, and abdomen without spots (Xue et al., 2009). Griffiths (1998) indicated the monophyly between *Hydrophoria* + *Zaphne* based on lower calypter expanded, pregonite with a single apical/subapical setula, and distiphallus with strong sclerotization on dorsal surface.

*Hydrophoria* is a monophyletic group and one of the most diverse genus of the family, its monophyly is based on characters of male terminalia, as pregonite and postgonite shape, distiphallus elongated and reduced sclerotinization, and long connection between basiphallus and distiphallus (Hennig, 1976). Hennig (1976) proposed that *Hydrophoria* is probably closely related to *Alliopsis* and *Paradelia* (clade E) based on the sclerotized proboscis. We recovered *Hydrophoria* and *Alliopsis* at the same clade, but *Paradelia* was recovered in a different clade. Griffiths (1986) commented that the proposition of *Alliopsis* and *Paradelia* as close related,

indicated by Hennig (1976), is problematic because of the paraphyly of *Paradelia* in his sense.

Griffiths (1998) indicated the absence of evidence supporting the monophyly of *Subhylemyia*, but he also commented that the absence of free paraphallic processes in male terminalia may be a synapomorphy of *Subhylemyia* and *Hydrophoria* + *Zaphne.* Michelsen (1988) indicated *Strobilomyia* as closely related to *Chirosia*-group, composed by *Lasiomma*, *Chirosia*, *Egle* Robineau-Desvoidy and *Acklandia*, but he also comments that the monophyly of this group of genera is difficult to prove. The long, attenuate, basally compressed distiphallus with a petiole towards the basiphallus (except in *Egle*) is present to all these genera.

The relationship among genera as *Hydrophoria* and *Zaphne* has been nominated previously (Griffiths, 1998; Gomes et al., 2021), while the phylogenetic position of *Strobilomyia*, *Subhylemyia* and *Alliopsis* are still uncertain and future studies are necessary to fully understand the relationship among these genera, although the relationship of *Alliopsis* and *Subhylemyia* with *Hydrophoria* + *Zaphne* have also been indicated as probable in some studies (Michelsen, 1988; Griffiths, 1998).

The clade M (Fig. 1 (part 5)) is formed by *Anthomyia*, *Eustalomyia* and *Egle*, based on eight homoplasies: central vitta of scutum reaching the scutellum apex (32: 2), Scutellum bicolor (49: 1), lower calypter twice longer than upper calypter (85: 3), female mid tibia without posteroventral setae (90: 0), surstyli enlarged on dorsal view (124: 0), surstyli apex with similar width than proximal section (127: 1), surstyli bifurcated (130: 1), and hypoproct rectangular (156: 0). The relationship between *Eustalomyia* and *Egle* is supported by eight homoplasies: parafacial width similar to postpedicel (24: 2), length of palpi exceeding the apex of gena (25: 2), katepisternum setae 1+2 (47: 0), apex of scutellum bare (52: 0), setulae on ventral surface of scutellum short (55: 0), male hind tibia without anteroventral seta (92: 0), hind tibia with four posterodorsal setae (94: 4), and male pulville twice larger than tarsomere width (101: 2). Hennig (1976) proposed *Egle* as monophyletic and close related to *Anthomyia*, based on similarities on structure of aedeagus (basiphallus and distiphallus), but on the other hand, indicated *Eustalomyia* as closely related to *Leucophora*, based on parasitic larval habits. The relationship between *Eustalomyia* and *Egle* have never been proposed.

The *Anthomyia* was recovered as monophyletic based on seven homoplasies: arista short-plumose (16: 2), anterior katepisternal seta as long as the posterior one (48: 1), first dorsocentral presutural seta shorter than the second one (58: 0), female mid tibia with two posteroventral setae (90: 2), male abdomen depressed dorsoventrally (103: 0), sternite 5 lobus curved outside (111: 1), and presence of a proximal projection on surstyli (125: 1). According to Griffiths (2001) and Ackland (2001), the genus is defined based on characters of male terminalia, especially the quite characteristic surstyli, allowing an easy identification. The genus *Anthomyia* was recovered as sister group of *Lasiomma* based on molecular data (Gomes et al., 2021), while Hennig (1976) indicated similarities among some species of *Anthomyia* and *Lasiomma*, as basiphallus not abbreviated and distiphalus with similar shape.

*Anthomyia* is divided in six sections (*A. cannabina*, *A. mimetica*, *A. monilis*, *A. pluvialis*, *A. punctipennis*, and *A. xanthopus*). The species from Neotropics belong to *A. punctipennis* section, while the three species from Holarctics that we included in this analysis belong to *A. pluvialis* section (Griffiths, 2001). The neotropical species of *A. punctipennis* section can be easily identified based on presence of spots on transversal veins of wings. In addition, there are some terminalia characteristics as: postgonite constricted medially in lateral view (rather strongly in most species, and downcurved distally); cercus with a preapical bare path; distal section of aedeagus bearing a dorsal process somewhat removed from its base; acrophallus small and scarcely visible in lateral view; and female with only two spermathecae (Griffiths 2001).

The *Anthomyia* clade split in two main clades, one with the three Holoarctic species belonging to *A. pluvialis* section; and the other including 11 Neotropical species belonging to *A. punctipennis* section. Our analysis indicated that the Neotropical species of *Anthomyia* probably form a monophyletic group, as well as the species of the Holarctic clade. The Neotropical clade was supported by 10 homoplasies: male interfrontal setae present (3: 1), male interfrontal setae similar to frontal setae (4: 1), distance between male eyes three times wider than anterior ocellus (19: 1), prealar seta longer than anterior notopleural seta (35: 2), apical setae of scutellum similar to subbasal setae (51: 1), costal vein with a pair of setulae near subcostal connection four times longer than others costal setulae (75: 2), male *dm-m* straigth (78: 0), lower calypter slightly shorter than upper one (85: 1), female hind

tibia with two anteroventral setae (93: 2), and sternite 5 lobus with a ventral projection (112: 1). While the Holarctic clade was supported by four homoplasies: parafacial narrower than pedicel (1: 0), female palpi enlarged (28: 1), scutum without longitudinal vittae (31: 0), and anepisternum with one seta (44: 0).

The species *A. aurifacies* and *A. paulistensis* were described based on specimens from São Paulo state (Brazil) and only female and male are known respectively, both species were described in the same study by Albuquerque (1952). Both species have a similar distribution, occurring in other regions of Brazil and Bolivia (unpublished information). *A. paulistensis* has a wing spot pattern very distinguished from other species of the genus, what probably induced the author to describe it as a separated species. Considering the similarity among these species (head shape, chaetotaxy of head and legs), we propose *A. paulistensis* as new junior synonym of *A. aurifacies*.

The neotropical species *Pegomya bruchi* was nested in the *Anthomyia* clade. This species from Argentina, Brazil and Uruguay (Evenhuis & Pape, 2021), was described as *Hylemyia* (*Craspedocheta*) Macquart, 1850, currently junior synonyme of *Anthomyia*. Posteriorly, Malloch (1934) synonymized this species with *Pegomya poeciloptera* (Malloch). Albuquerque (1959) considered both as distinct and valid species, and in addition commented which this species is near to *Anthomyia punctipennis*. However, this species remained included in the genus *Pegomya*. It is quite obvious this species belongs to *Anthomyia* due to presence of interfrontal setae, triangular cercus, surstyllus bifurcated and with a proximal projection, pregonite with two long setulae and postgonite hooked tip. Based on these morphological indicatives and our phylogenetic analysis, we proposed this new combination: *Anthomyia bruchi* comb. nov.

The Anthomyiidae has no comprehensive classification (Michelsen, 2010), Huckett (1965) and Michelsen (2000) presented classifications hypothesis dividing the family in two and three subfamilies respectively, but without considering all known genera. Huckett (1965) considered the genera *Fucellia* and *Circia* Malloch [=*Alliopsis* Schnabl & Dziedzicki] as a separate subfamily (Fucelliinae), whereas the remaining anthomyiids were classified as Anthomyiinae, which were divided into two tribes (Anthomyiini and Myopinini). Michelsen (2000) divided most anthomyiids into the subfamilies Myopininae, Pegomyinae and Anthomyiinae.

Michelsen (2000) recognised four major subgroups of Anthomyiidae: (1) *Phaonantho* genus-group consisting of the genera *Phaonantho*, *Coenosopsites* and *Coenosopsia*; (2) Myopininae that include the genera *Enneastigma*, *Calythea*, *Pegoplata* and *Myopina*; (3) Pegomyinae containing the genera *Emmesomyia*, *Pegomya*, *Eutrichota*, *Mycophaga*, *Paradelia*, *Alliopsis*, and *Myopinella*; and (4) Anthomyiinae consisting of all remaining anthomyiid genera (Michelsen, 2000). We recovered *Phaonantho* genus-group as monophyletic, as well the genera of Myopininae group (except *Myopina*). On the other hand, the other groups and subfamilies were not recovered as monophyletic (Fig. 2).

Our results represent the most comprehensive phylogenetic study in Anthomyiidae under morphological evidence, an important step towards the understanding of the relationship among genera and a future classification. A next phylogenetic study involving more terminals and including more morphological data as female terminalia, biology and immatures, as well as molecular data, is necessary to reach a better understanding of relationship among anthomyiids genera, allowing a hypothesis of classification to the family.

The relationship among the main clades is not well supported in the present analysis and we are not able to discuss the relationship among the main clades, consequently not being possible to propose a new classification. On the other hand, we presented characters supporting the monophyly of some genera, as well as the relationship among some genera.

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FIGURES

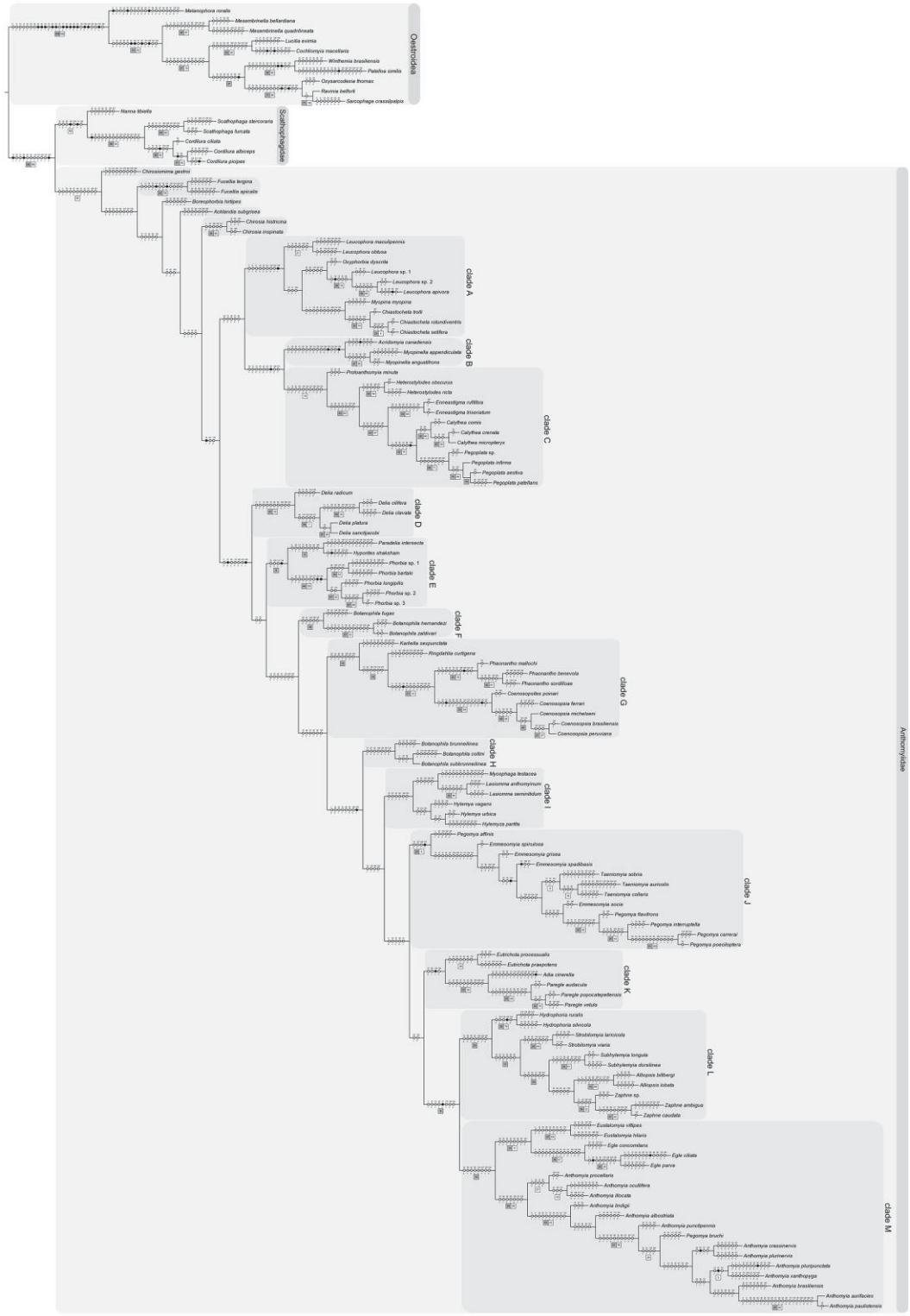


**Figure 1.** Most parsimonious tree obtained from the phylogenetic analysis of Anthomyiidae and outgroups, with implied weighting (k= 10), fast optimization. Relative Bremer support (gray box) and Bootstrap (white box) are indicated below each node. Homoplasies (clear circles) and synapomorphies (black circles) are shown in all branches.

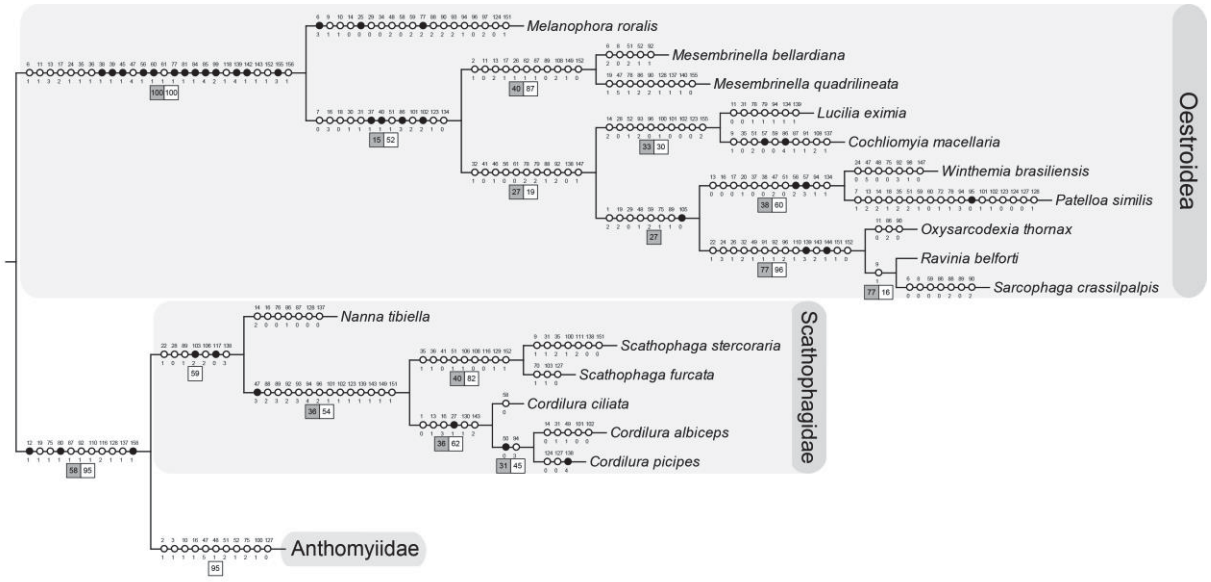


**Figure 1 (part 1).** Most parsimonious tree obtained from the phylogenetic analysis of Anthomyiidae and outgroups, with implied weighting (k= 10), fast optimization. Relative Bremer support (gray box) and Bootstrap (white box) are indicated below each node. Homoplasies (clear circles) and synapomorphies (black circles) are shown in all branches.

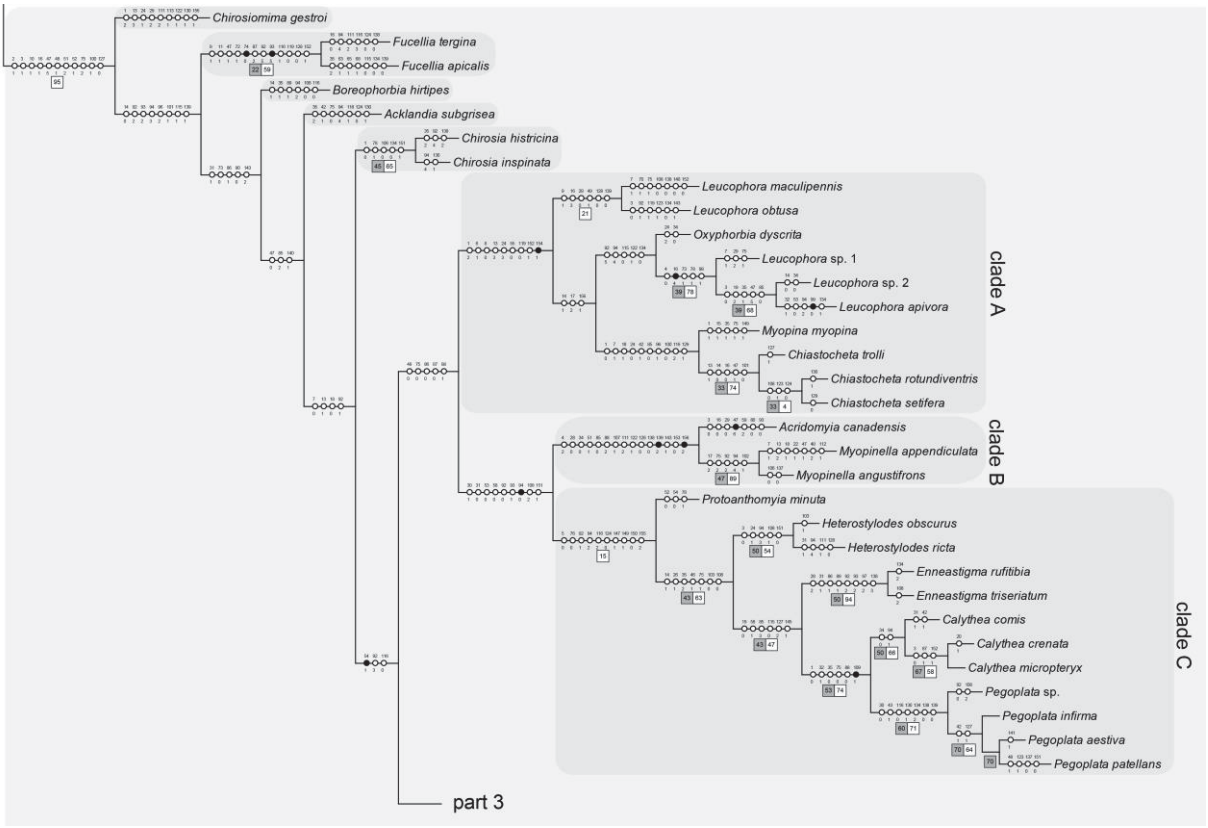


**Figure 1 (part 2).** Most parsimonious tree obtained from the phylogenetic analysis of Anthomyiidae and outgroups, with implied weighting (k= 10), fast optimization. Relative Bremer support (gray box) and Bootstrap (white box) are indicated below each node. Homoplasies (clear circles) and synapomorphies (black circles) are shown in all branches.

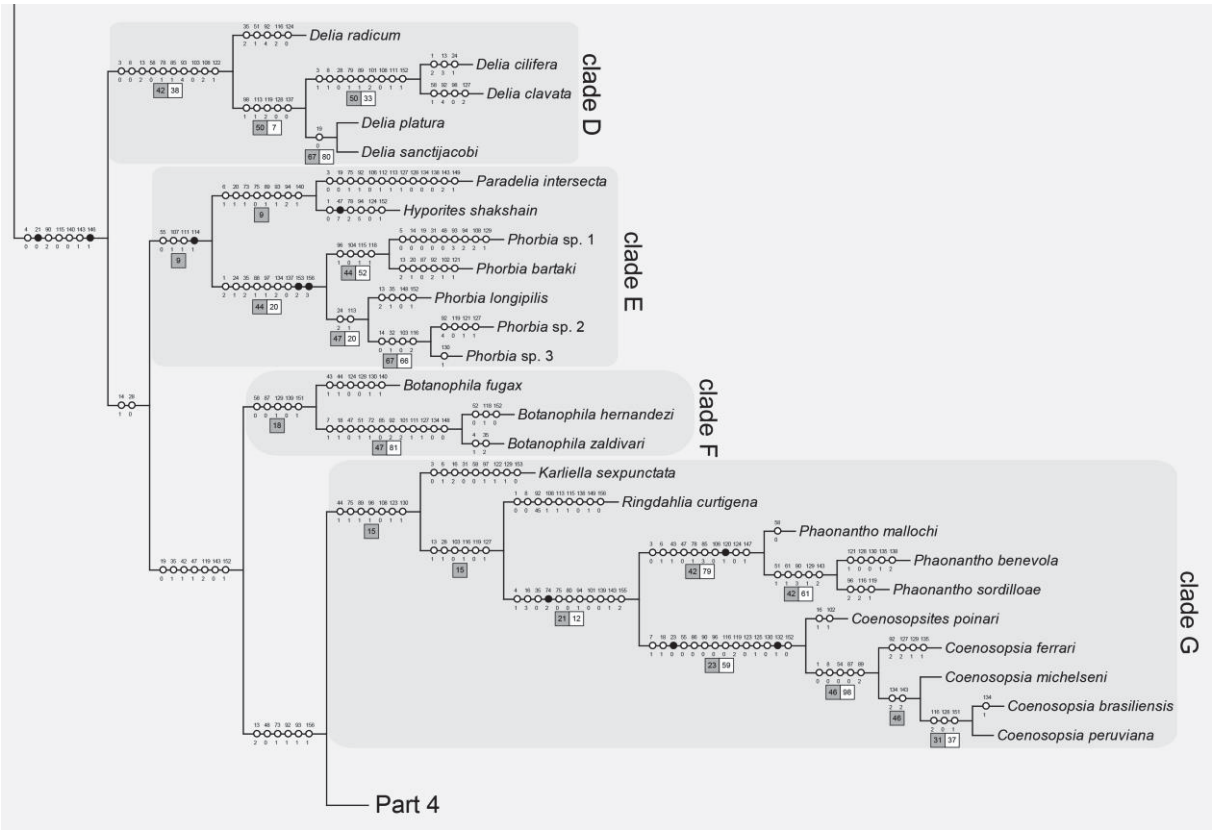


**Figure 1 (part 3).** Most parsimonious tree obtained from the phylogenetic analysis of Anthomyiidae and outgroups, with implied weighting (k= 10), fast optimization. Relative Bremer support (gray box) and Bootstrap (white box) are indicated below each node. Homoplasies (clear circles) and synapomorphies (black circles) are shown in all branches.

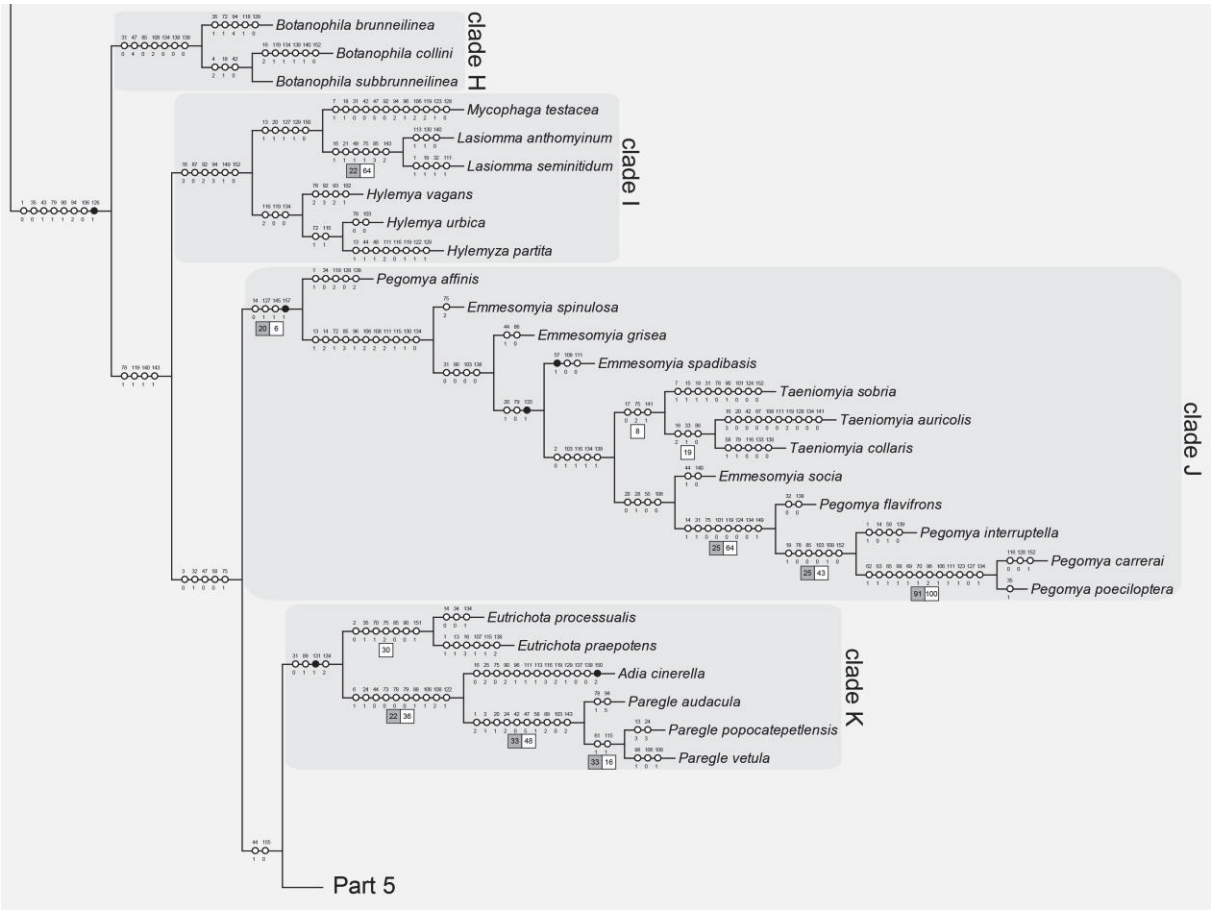


**Figure 1 (part 4).** Most parsimonious tree obtained from the phylogenetic analysis of Anthomyiidae and outgroups, with implied weighting (k= 10), fast optimization. Relative Bremer support (gray box) and Bootstrap (white box) are indicated below each node. Homoplasies (clear circles) and synapomorphies (black circles) are shown in all branches.

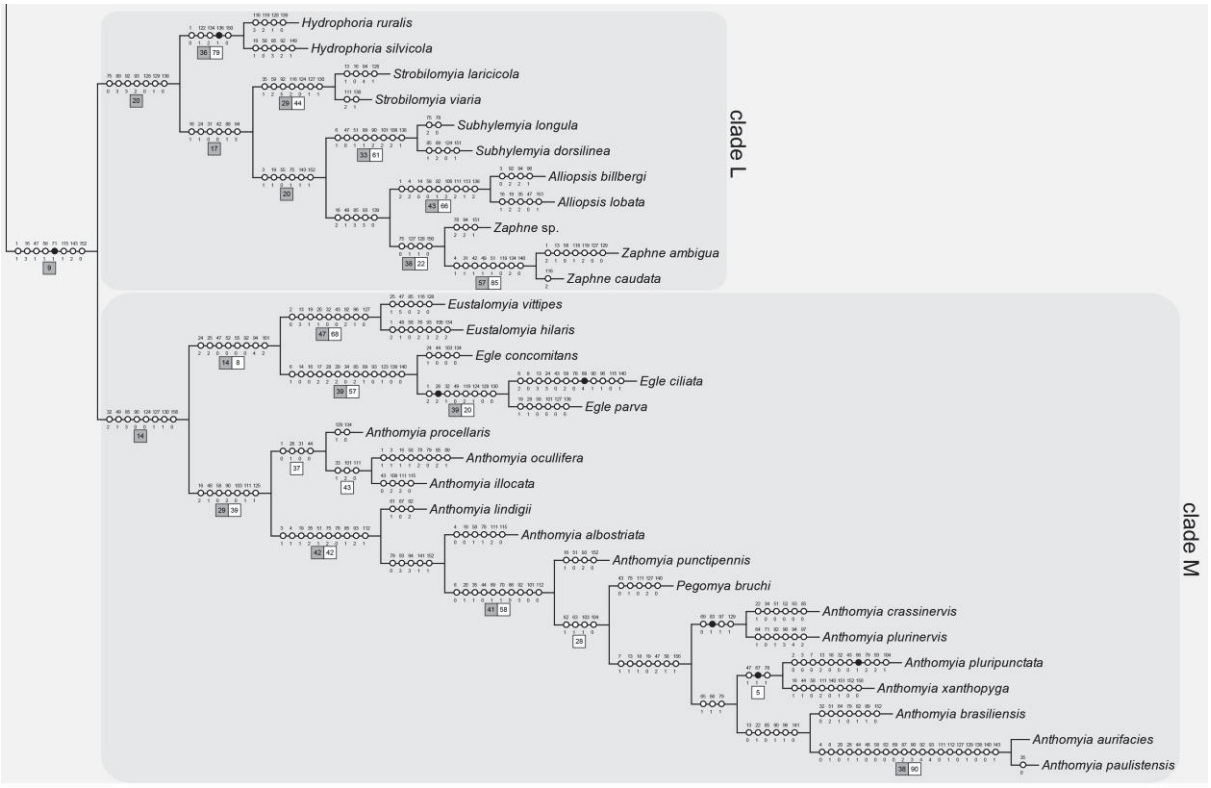


**Figure 1 (part 5).** Most parsimonious tree obtained from the phylogenetic analysis of Anthomyiidae and outgroups, with implied weighting (k= 10), fast optimization. Relative Bremer support (gray box) and Bootstrap (white box) are indicated below each node. Homoplasies (clear circles) and synapomorphies (black circles) are shown in all branches.

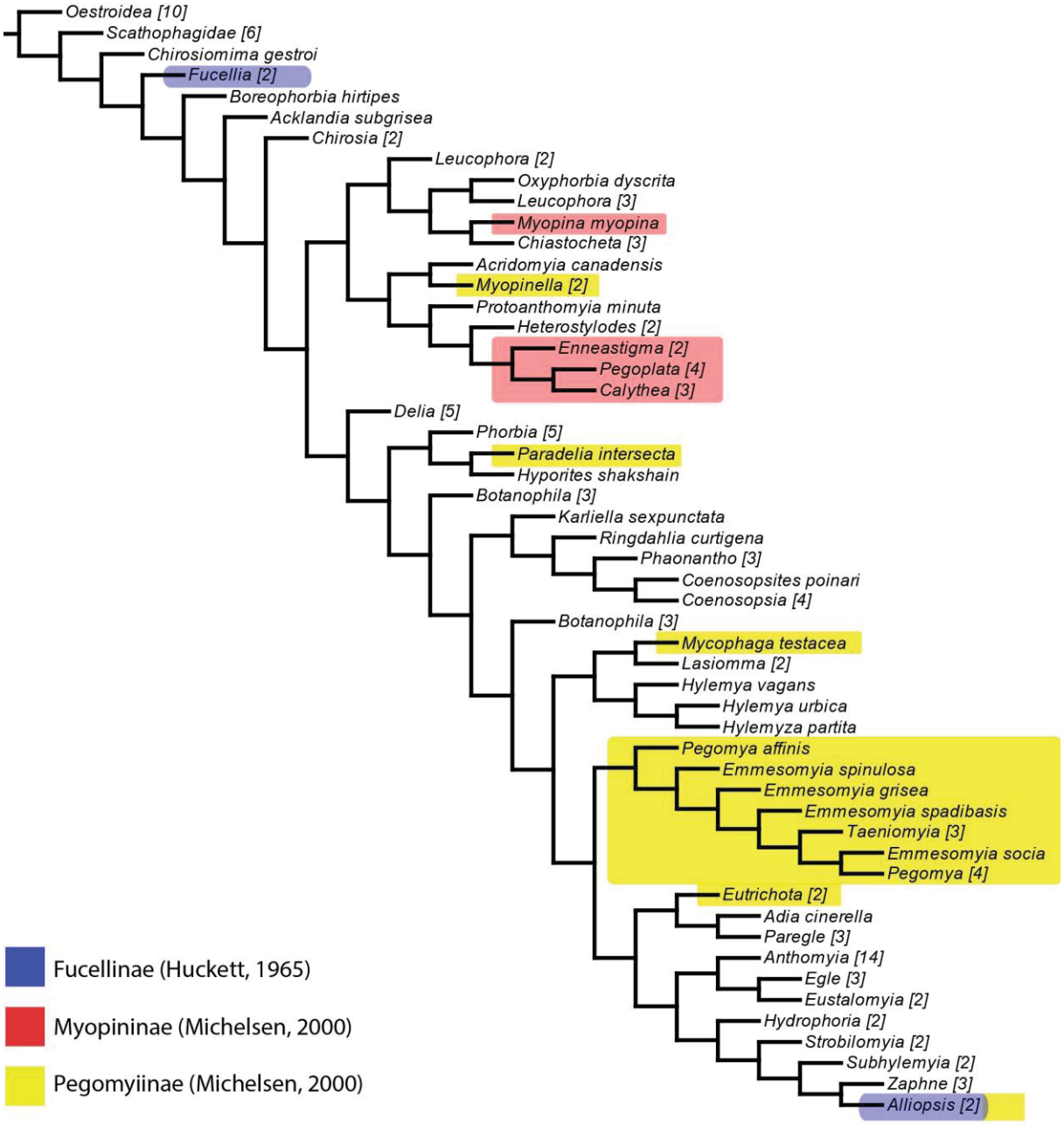


**Figure 2.** Most parsimonious tree obtained from the phylogenetic analysis of Anthomyiidae and outgroups, with implied weighting (k= 10), fast optimization. Monophyletic genera summarized, indicating the subfamilies, except Anthomyiinae (see Discussion).

TABLES

**Table 1.** List of characters and states. *characters based on Nihei & de Carvalho (2004); ** characters based on Nihei & de Carvalho (2007); *** characters based on Couri & Pont (2000); # Lambkin et al. (2013); ## Domínguez & Roig-Juñent (2008); ### Gomes et al. (2020).

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Head:

1. Parafacial (lateral view), width at antennal insertion: (0) narrower, (1) similar, or (2) wider, than pedicel width.
2. Interfrontal setae (female)*: (0) absent, (1) present.
3. Interfrontal setae (male)*: (0) absent, (1) present.
4. Interfrontal setae (male), length: (0) shorter, (1) similar, or (2) longer, than frontal setae.
5. Proclinate orbital setae (female)*: (0) absent, (1) present.
6. Proclinate orbital setae (female), number*: (0) 1, (1) 2, (2) 3, (3) 4.
7. Proclinate orbital setae (male)*: (0) absent, (1) present.
8. Reclinate orbital setae (female)*: (0) absent, (1) present.
9. Fronto-orbital plate, setulae (female)**: (0) absent, (1) present.
10. Fronto-orbital plate, setulae position (female)**: (0) on its entire extension, (1) on its lower half.
11. Fronto-orbital plate, setulae (male)**: (0) absent, (1) present.
12. Fronto-orbital plate, setulae position (male)**: (0) on its entire extension, (1) on its lower half.
13. Gena, high###: (0) narrower, (1) similar, (2) twice longer, or (3) three times longer, than pedicel.
14. Post-pedicel, length: (0) twice, (1) three times, or (2) four times, longer than pedicel.
15. Post-pedicel, width (male): (0) similar, or (1) twice longer than pedicel width.
16. Arista: (0) bare, (1) pubescent (barely exceeding greatest width of arista), (2) short-plumose (its longest cilia exceeding greatest width of palpi), (3) long-plumose (its longest cilia not longer than 1/4 of arista), or (4) very long-plumose (its longest cilia with half-length of arista).
17. Arista, basal width: (0) not swollen, (1) swollen, (2) very swollen (more than twice wider than width of the middle arista).
18. Eyes (male): (0) holoptic, (1) dichoptic.
19. Eyes (male), distance between eyes: (0) narrower than anterior ocellus, (1) about three times wider than anterior ocellus, (2) frons with 1/5 of head width.

20. Eyes, ciliation: (0) absent, (1) present.

21. Eyes, ciliation: (0) sparse and short, (1) long and dense.

22. Frons, width***: (0) as wide as long, (1) wider than long.

23. Parafrontal, width (female): (0) similar to ocelar width, (1) longer than ocelar width. Comments: the state 0 is a synapomorphy of *Coenosopsia*.

24. Parafacial (lateral view), width: (0) about ¼ of postpedicel width, (1) about half of postpedicel width, (2) similar to postpedicel width, (3) wider than postpedicel width.

25. Palpi, length: (0) short (not reaching the apex of gena, (1) long (reaching the apex of gena), (2) long (exceeding the apex of gena).

26. Palpi, shape (male): (0) filiform, (1) enlarged, (2) apically enlarged.

27. Pedicel, apical seta: (0) absent, (1) present.

28. Palpi, shape (female)*: (0) filiform, (1) enlarged, (2) apically enlarged.

29. Proboscis, prementum length: (0) shorter, (1) similar, (2) longer than gena.

Thorax

30. Prosternum, setulae*: (0) absent, (1) present.

31. Scutum, longitudinal vittae: (0) absent, (1) present.

32. Scutum, central vittae: (0) not reaching scutellum, (1) reaching scutellum base, (2) reaching the scutellum apex.

33. Scutum, transversal vitta: (0) absent, (1) present.

34. Prealar seta*: (0) absent, (1) present.

35. Prealar seta, length: (0) shorter, (1) similar, (2) longer, than anterior notopleural seta.

36. Anepimeron, setulae: (0) absent, (1) present.

37. Anatergite, setulae#: (0) absent, (1) present.

38. Metasternum, setulae#: (0) absent, (1) present.

39. Meron, row of setae: (0) absent, (1) present.

40. Metathoracic spiracle, posterior fringe#: (0) similar to anterior fringe, (1) operculum-shaped.

41. Anepisternum, setulae: (0) covering its entire surface, (1) anteroventral third bare.

42. Anepisternum, superior-anterior seta: (0) absent, (1) present.

43. Anepisternum, superior-anterior seta, length: (0) twice longer, (1) four times longer, than covered setulae.

44. Anepisternum, superior-anterior seta: (0) 1, (1) 2 or more.

45. Anepimeron, setae#: (0) absent, (1) present.

46. Katepimeron, setulae: (0) absent, (1) present.

47. Katepisternum, setae conformation: (0) 1+2, (1) 2+2, (2) 1+1+1, (3) 0+1, (4) 2+1, (5) 1+1, (6) 0+0, (7) 2+3.

48. Katepisternum, anterior seta###: (0) shorter, (1) similar, (2) longer, than posterior seta.

49. Scutellum, coloration: (0) uniform, (1) bicolor.

50. Scutellum, apical setae: (0) absent, (1) present.

51. Scutellum, apical setae length***: (0) shorter, (1) similar, (2) longer, than the subbasal setae.

52. Scutellum, setulae on apex: (0) absent, (1) present.

53. Scutellum, setulae on apex: (0) shorter, (1) similar, to the setulae on lateral margin of scutellum.

54. Scutellum, apex, setulae on ventral surface*: (0) absent, (1) presente.

55. Scutellum, apex, setulae on ventral surface, length: (0) short (shorter than half length of setulae on lateral margin of scutellum), (1) long (about half length of setulae on lateral margin of scutellum).

56. Subscutellum[#]: (0) slightly convex, (1) strongly convex (reaching less than half scutellum length), (2) very strongly convex (reaching more than half of scutellum length).

57. Dorsocentral setae, number of presutural setae: (0) 0, (1) 1, (2) 2, (3) 3.

58. Dorsocentral setae, first presutural seta[##]: (0) shorter, (1) similar, to the second presutural seta.

59. Dorsocentral setae, number of postsutural setae*: (0) 1, (1) 3, (2) 4.

60. Postalar wall, setulae[#]: (0) absent, (1) present.

Wing

61. Costal region, brownish: (0) absent, (1) present.

62. Vein $R_1$ and subcostal apex, maculae**: (0) absent, (1) present.

63. Vein $R_{2+3}$, maculae on the apex**: (0) absent, (1) present.

64. Vein $R_{2+3}$, maculae on the middle: (0) absent, (1) present.

65. Vein $R_{4+5}$, maculae on the apex: (0) absent, (1) present.

66. Vein $R_{4+5}$, maculae on the middle: (0) absent, (1) present.

67. Vein $R_{4+5}$, maculae on the base: (0) absent, (1) present.

68. Medial vein, maculae on the apex: (0) absent, (1) present.

69. Medial vein, maculae on the base: (0) absent, (1) present.

70. *dm-m* crossvein, maculae**: (0) absent, (1) present.

71. *dm-m* crossevein, number of maculae: (0) 1, (1) 2.

72. Costal vein, setulae length[#]: (0) all with same size, (1) alternating short and twice longer setulae.

73. Costal vein, ventrally setulose: (0) absent, (1) present.

74. Costal vein, setulae on ventral surface: (0) covered by long and sparse spinules on distal middle of the wing, (1) short-setulose (setulae shorter than costal setae), (2) covered by long setae (similar to costal setae).

Comments: The state 0 is a synapomorphy of *Fucellia* and the state 2 is a synapomoprhy of *Coenosopsia* + *Phaonantho*.

75. Costal vein, near the Subcostal connection, long pair of setulae, length: (0) as long as, (1) two times longer, (2) four times longer than others costal setulae.

76. Subcostal vein, curvature: (0) soft-angle (sigmoid), (1) sharp-angle (straight).

77. Medial vein, curvature#: (0) straight, (1) curved distally with an abrupt bend reaching the margin of the wing, (2) curved distally with an abrupt bend reaching $R_{4+5}$.

78. *dm-m* crossvein (male), curvature: (0) straight, (1) slightly curved (with a slight curvature in the middle), (2) strongly curved (with a curvature on the entire vein).

79. *dm-m* crossvein (female), curvature: (0) straight, (1) slightly curved (with a slight curvature in the middle), (2) strongly curved (with a curvature on the entire vein).

80. $A_1$ vein, length*: (0) not reaching the wing margin, (1) reaching the wing margin.

81. Rs node, setulose on dorsal surface: (0) absent, (1) present.

82. Vein $R_{2+3}$, recurrent branch: (0) absent, (1) present.

83. Vein $R_{2+3}$, number of recurrent branches: (0) 1, (1) 2.

84. Upper calypter, length#: (0) short (less than half length of scutellum), (1) very developed (as long as scutellum).

85. Lower calypter, length: (0) shorter than upper calypter (reduced to a linear folder), (1) slightly shorter than upper calypter (rounded); (2) as long as upper calypter, (3) twice longer than upper calypter, (4) three times longer than upper calypter.

Legs

86. Fore tibia (female), number of anterodorsal setae: (0) 0, (1) 1, (2) 2, (3) 3, (4) 4.

87. Fore tibia (female), number of posterodorsal setae: (0) 0, (1) 1, (2) 2.

88. Mid tibia (female), number of anteroventral setae: (0) 0, (1) 1, (2) 2.

89. Mid tibia (female), number of posterodorsal setae: (0) 0, (1) 1, (2) 2, (3) 3, (4) 4.

90. Mid tibia (female), number of posteroventral setae: (0) 0, (1) 1, (2) 2, (3) 3.

91. Hind coxa, setulae: (0) absent, (1) present.

92. Hind tibia (male), number of anteroventral setae**: (0) 0, (1) 1, (2) 2, (3) 3, (4) 4, (5) 5 or more.

93. Hind tibia (female), number of anteroventral setae**: (0) 0, (1) 1, (2) 2, (3) 3, (4) 4, (5) 5.

94. Hind tibia, number of posterodorsal setae: (0) 0, (1) 1, (2) 2, (3) 3, (4) 4, (5) 5.

95. Hind tibia, calcar: (0) absent, (1) present.

96. Hind tibia, length of calcar: (0) same length of tibia width, (1) twice longer than tibia width, (2) three times longer than tibia width.

97. Hind tibia (female), number of posteroventral setae: (0) 0, (1) 1, (2) 2.

98. Hind tibia (male), row of short erect posteroventral setae: (0) absent, (1) present.

99. Hind tibia (male), row of short erect posteroventral setae, length: (0) shorter, (1) similar, (2) longer, than tibia width.

100. Hind tibia, basitarso, ventrobasal seta*: (0) absent, (1) present.

101. Pulville (male), width###: (0) narrower than tarsomere width, (1) similar to tarsomere width, (2) twice larger than tarsomere width.

102. Pulville (female), width###: (0) narrower than tarsomere width, (1) similar to tarsomere width, (2) twice larger than tarsomere width.

Abdomen

103. Abdomen (male), lateral view, shape: (0) dorsoventrally depressed, (1) conical, (2) sharped and apically enlarged.

Comments: The state 0 is present in several anthomyiids and the state 2 is exclusive of some scathophagids.

104. Sternite 1, setulae: (0) absent, (1) present.

Male terminalia

105. Sternite 5, with an anterior region connecting the two lobes: (0) absent (sternite 5 reduced, only with the two lobes), (1) present.

106. Sternite 5, shape: (0) quadrangular, (1) rectangular, (2) rounded.

107. Sternite 5, anterior incision: (0) absent, (1) present.

108. Sternite 5, posterior incision, shape###: (0) C-shape, (1) U-shape, (2) V-shape.

109. Sternite 5, posterior incision, denticles: (0) absent, (1) present.

110. Sternite 5, lobus, width: (0) about half width of sternite width, (1) less than half of the sternite width.

111. Sternite 5, lobus: (0) straight, (1) curved outside, (2) curved inside.

112. Sternite 5, lobus, ventral projection: (0) absent, (1) present.

Commnets: This projection is present in some species of *Anthomyia* and *Myopinella appendiculata* and *Paradelia intersecta*.

113. Sternite 5, lobus, inner border, spinulas: (0) absent, (1) present.

114. Sternite 5, lobus, inner border, spinulas: (0) few spinulas, (1) a tuft of several spinulas.

115. Sternite 5, lobus, inner border, row of setulae: (0) absent, (1) present.

116. Cerci (male), shape*: (0) longer than wide, (1) wider than long, (2) as long as wide, (3) four times wider than long.

117. Cerci (male), fused forming a plate##: (0) absent, (1) present.

Comments: the state 1 is a synapomorphy of Scathophagidae.

118. Cerci (male), bifurcated anteriorly: (0) absent, (1) present.

119. Cerci (male), length: (0) shorter, (1) similar, (2) longer, than surstyli.

120. Cerci (male), width: (0) narrower than epandrium, (1) wider than epandrium.

Comments: The state 1 is a synapomorphy of *Phaonantho*.

121. Cerci (male), tuft of long setae (twice longer than cerci width): (0) absent, (1) present.

122. Cerci (male), distal setae longer than cerci: (0) absent, (1) present.

123. Surstyli, width lateral view: (0) similar, (1) wider, than cerci.

124. Surstyli, width dorsal view: (0) enlarged (at least half width of cerci), (1) narrow (narrower than half width of cerci).

125. Surstyli, proximal projection: (0) absent, (1) present.

126. Surstyli, proximal projection: (0) lameliform, (1) protruding.

Comments: state 0 is a synapomorphy of *Coenosopsia* and state 1 is present in some *Anthomyia*.

127. Surstyli, width of apex, (0) narrower, (1) similar, (2) wider than proximal section.

128. Surstyli, apex (lateral view): (0) straight, (1) curved.

129. Surstyli, apex, curvature (lateral view): (0) slightly curved, (1) strongly curved.

130. Surstyli, bifurcated: (0) absent, (1) present. Comments: The unforked surstyli is a primitive characteristic (Hennig, 1976).

131. Surstyli, apex short bifurcated: (0) absent, (1) present.

Comments: the state 1 is a synapomoprhy of the clade K (*Adia*, *Eutrichota* and *Paregle*).

132. Surstyli, asymmetrical*: (0) absent, (1) present.

Comments: the state 1 is a synapomorphy of *Coenosopsia*.

133. Surstyli, ventral projection on proximal section: (0) absent, (1) present.

Comments: present is some species of *Emmesomyia*.

134. Pregonite, length*: (0) shorter, (1) as long as, (2) longer, than postgonite.

135. Pregonite, distally setulose: (0) absent, (1) present.

136. Pregonite, spines: (0) absent, (1) present.

Comments: the state 1 is a synapomorphy of *Hydrophoria*.

137. Pregonite, setae: (0) absent, (1) present.

138. Pregonite, number of setae: (0) 1, (1) 2, (2) 3, (3) 4, (4) 5.

139. Postgonite, shape: (0) long enlarged (e. g. *Coenosopsia*), (1) narrow with one distal lobe, (2) triangular (e. g. *Myopella*), (3) enlarged and sclerotized (e. g. Sarcophagidae), (4) enlarged and curved (e. g. Tachinidae).

140. Postgonite, setae: (0) absent, (1) present.

141. Postgonite, distal seta: (0) absent, (1) present.

142. Postgonal podeme#: (0) absent, (1) present.

143. Distiphallus, length*: (0) shorter, (1) as long as, (2) longer, than phallapodeme.

144. Distiphallus, distally: (0) membranized, (1) sclerotized.

145. Distiphallus, distally, shape: (0) narrow, similar to proximal width, (1) enlarged, wider than proximal section.

146. Distiphallus, distally enlarged, shape: (0) quadrangular, (1) rounded.

147. Distiphallus, covered by spines: (0) absent, (1) present.

148. Epiphallus[#]: (0) absent, (1) present.

149. Epiphallus, length: (0) shorter, (1) similar, to phallapodeme length.

150. Phallapodeme, length: (0) shorter, (1) similar, (2) longer than pregonite.

151. Phallapodeme, shape: (0) straight, (1) curved.

152. Phallapodeme, apically: (0) narrow, (1) enlarged.

Female terminalia

153. Cerci, shape: (0) short and rounded, (1) long and slender, (2) long with a distal point dorsally directed.

Comments: The state 2 is a synapomporphy of *Phorbia*.

154. Cerci, upcurved spines: (0) absent, (1) present.

155. Epiproct, shape: (0) longer than its width, (1) wider than its length, (2) as high as its wide, (3) very reduced (only with two sclerotized dots with setulae.

156. Hypoproct, shape: (0) rectangular, (1) triangular, (2) reduced to a narrow transversal plate, (3) reduced to a narrow longitudinal plate.

Comments: The state 3 is a synapomporphy of *Phorbia*.

157. Sternite 6 and 7, spinules: (0) absent, (1) present.

158. Sternite 8: (0) undivided, (1) completely divided longitudinally.

**Table 2.** Constant of concavity (k) values applied in the phylogenetic analysis. L= length; CI= consistency index, RI= redention index, fit= fit value, # trees= number of threes generated.

| K | L | CI | RI | fit | # trees |
|---|---|---|---|---|---|
| - | 1414 | 17 | 63 | 71.33-72.57 | 80 |
| 1 | 1545 | 15 | 59 | 56.67492 | 2 |
| 2 | 1532 | 16 | 60 | 67.63203 | 2 |
| 3 | 1513 | 16 | 60 | 75.42075 | 2 |
| 4 | 1473 | 16 | 62 | 81.55525 | 1 |
| 5 | 1467 | 16 | 62 | 86.57454 | 1 |
| 6 | 1466 | 16 | 62 | 90.79960 | 1 |
| 7 | 1459 | 16 | 62 | 94.46949 | 1 |
| 8 | 1447 | 17 | 62 | 97.67569 | 5 |
| 9 | 1447 | 17 | 62 | 100.49883 | 5 |
| 10 | 1443 | 17 | 63 | 103.00900 | 1 |
| 11 | 1443 | 17 | 63 | 105.27170 | 1 |
| 12 | 1443 | 17 | 63 | 107.31516 | 1 |
| 13 | 1439 | 17 | 63 | 109.17325 | 1 |
| 14 | 1439 | 17 | 63 | 110.87468 | 1 |
| 15 | 1439 | 17 | 63 | 112.43757 | 1 |
| 16 | 1439 | 17 | 63 | 113.87942 | 1 |
| 17 | 1434 | 17 | 63 | 115.21559 | 1 |
| 18 | 1429 | 17 | 63 | 116.46728 | 1 |
| 19 | 1429 | 17 | 63 | 117.63449 | 1 |
| 20 | 1429 | 17 | 63 | 118.72498 | 1 |
| 25 | 1425 | 17 | 63 | 123.27221 | 1 |
| 30 | 1419 | 17 | 63 | 126.72620 | 1 |

SUPPLEMENTARY MATERIAL

**Table S1 (part 1a).** Matrix of morphological characters. Polymorphism: A= 0,1; B= 2,3; C= 3,4; D= 1,2; E= 4,5; F= 1,2,3; G= 1,2,3,4; H= 3,4,5.

| | 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 5 5 5 6 |
|---|---|
| | 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 |
| *Melanophora roralis* | 1 0 0 ? 1 3 1 1 1 1 1 0 3 0 0 2 2 1 ? 0 ? 0 1 1 0 0 0 ? 0 0 0 ? 0 0 ? 1 0 ? 1 0 1 0 ? ? 1 0 4 2 0 1 0 0 ? 0 ? 1 2 0 2 ? |
| *Ravinia belforti* | 2 0 0 ? 1 1 0 1 1 0 1 0 3 1 0 3 2 0 2 0 ? 1 1 3 1 1 0 1 0 1 1 2 0 1 1 1 1 1 1 1 0 0 ? ? 1 1 4 1 1 1 1 0 ? 0 ? 0 2 1 2 1 |
| *Sarcophaga crassilpalpis* | 2 0 0 ? 1 0 0 0 1 0 1 0 3 1 0 3 2 0 2 0 ? 1 1 3 1 1 0 1 0 1 1 2 0 1 1 1 1 1 1 1 1 0 0 ? ? 1 1 4 1 1 1 1 0 ? 0 ? 0 2 1 0 1 |
| *Oxysarcodexia thornax* | 2 0 0 ? 1 1 0 1 0 ? 0 ? 3 1 0 3 2 0 2 0 ? 1 1 3 1 1 0 1 0 1 1 2 0 1 1 1 1 1 1 1 0 0 ? ? 1 1 4 1 1 1 1 0 ? 0 ? 0 2 1 2 1 |
| *Winthemia brasiliensis* | 2 ? 0 ? ? ? 0 ? ? ? 1 0 0 1 0 0 0 0 2 1 1 0 ? 0 1 0 0 ? 0 1 1 1 0 1 1 1 0 0 1 1 0 0 ? ? 1 1 5 0 0 1 0 0 ? 0 ? 2 3 1 2 1 |
| *Patelloa similis* | 2 ? 0 ? ? ? 1 ? ? ? 1 0 2 2 0 0 0 1 ? 1 1 0 ? 1 1 0 0 ? 0 1 1 1 0 1 2 1 0 0 1 1 0 0 ? ? 1 1 2 1 0 1 2 0 ? 0 ? 2 3 1 1 0 |
| *Lucilia eximia* | 1 0 0 ? 1 1 0 1 0 ? 0 ? 3 2 0 3 2 0 0 0 ? 0 1 1 1 0 0 0 1 1 0 ? 0 1 1 1 1 1 1 1 0 0 ? ? 1 1 4 0 0 1 1 1 1 0 ? 0 2 1 1 1 |
| *Cochliomyia macellaria* | 1 0 0 ? 1 1 0 1 1 0 1 0 3 2 0 3 2 0 0 0 ? 0 1 1 1 0 0 0 1 1 1 ? 0 1 0 1 1 1 1 1 0 0 ? ? 1 1 4 0 0 1 2 1 1 0 ? 0 0 ? 0 1 |
| *Mesembrinella bellardiana* | 1 1 0 ? 1 2 0 0 0 ? 0 ? 2 1 0 3 1 0 0 0 ? 0 1 1 1 1 0 1 1 1 1 0 0 1 1 1 1 ? 1 1 1 0 ? ? 1 0 4 0 0 1 2 1 1 0 ? 1 2 1 1 1 |
| *Mesembrinella quadrilineata* | 1 1 0 ? 1 1 0 1 0 ? 0 ? 2 1 0 3 1 0 1 0 ? 0 1 1 1 1 0 1 1 1 1 0 0 1 1 1 1 ? 1 1 1 0 ? ? 1 0 5 0 0 1 1 0 ? 0 ? 1 2 1 1 1 |
| *Acridomyia canadensis* | 1 ? 0 ? ? ? 0 ? 0 ? 0 ? 1 0 0 0 1 0 ? ? ? 0 1 0 ? ? ? ? 0 ? 0 ? 0 ? ? 0 0 0 0 0 ? ? ? 0 0 6 ? 0 1 1 ? ? 1 ? 0 2 ? 2 0 |
| *Acklandia subgrisea* | 1 1 ? ? ? ? 1 ? 0 ? 0 ? 2 0 0 1 ? 1 ? ? ? 0 1 0 1 0 0 ? ? ? 1 ? 0 1 2 0 0 0 0 0 1 1 0 0 0 0 ? ? 0 ? ? ? ? 0 ? 0 ? ? ? 0 |
| *Chiastocheta trolli* | 0 1 1 1 ? ? 1 ? 0 ? 0 ? 1 0 0 0 2 1 ? ? ? 0 1 0 1 0 0 ? 1 ? ? ? 0 ? ? 0 0 0 0 0 1 1 0 0 0 ? 1 ? ? 1 ? ? ? ? 1 ? 0 ? ? ? 0 |
| *Chiastocheta rotundiventris* | 0 1 1 1 ? ? 1 ? 0 ? 0 ? 1 0 0 0 2 1 ? ? ? 0 1 0 1 0 0 ? 1 ? ? ? 0 ? ? 0 0 0 0 0 1 1 0 0 0 ? 1 ? ? 1 ? ? ? ? 1 ? 0 ? ? ? 0 |
| *Chiastocheta setifera* | 0 1 1 1 ? ? 1 ? 0 ? 0 ? 1 0 0 0 2 1 ? ? ? 0 1 0 1 0 0 ? 1 ? ? ? 0 1 0 0 0 0 0 0 1 1 0 0 0 ? 1 ? ? 1 ? ? ? ? 1 ? 0 ? ? ? 0 |
| *Chirosia histricina* | 0 1 1 ? ? ? ? ? 0 ? 0 ? 1 0 0 1 1 0 ? ? ? 0 ? 0 1 0 0 ? 1 ? 1 ? 0 1 2 0 0 0 0 0 1 ? ? ? 0 ? 0 ? ? ? ? ? ? 0 ? 0 ? ? ? 0 |
| *Chirosia inspinata* | 0 1 1 ? ? ? ? ? 0 ? 0 ? 1 0 0 1 1 0 ? ? ? 0 ? 0 1 0 0 ? 1 ? 1 ? 0 1 0 0 0 0 0 0 1 ? ? ? 0 ? 0 ? ? ? ? ? ? 0 ? 0 ? ? ? 0 |
| *Delia radicum* | 1 1 0 ? 1 0 0 0 0 ? 0 ? 2 0 0 1 1 0 1 0 ? 0 1 0 1 0 0 1 1 0 1 0 0 1 2 0 0 0 0 0 1 0 ? ? 0 0 0 1 0 1 1 1 1 1 1 0 2 0 1 0 |
| *Delia platura* | 1 1 0 ? 1 0 0 0 0 ? 0 ? 2 0 0 1 1 0 0 0 ? 0 1 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 0 1 0 1 2 1 1 1 1 0 2 0 1 0 |
| *Delia sanctijacobi* | 1 1 0 ? 1 0 0 0 0 ? 0 ? 2 0 0 1 1 0 0 0 ? 0 1 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 0 1 0 1 2 1 1 1 1 0 2 0 1 0 |
| *Delia cilifera* | 2 1 1 0 1 0 0 1 0 ? 0 ? 3 0 0 1 1 0 1 0 ? 0 1 1 1 0 0 0 1 0 1 0 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 0 A 0 1 2 1 1 1 1 0 2 0 1 0 |
| *Delia clavata* | 1 1 1 0 1 0 0 1 0 ? 0 ? 2 0 0 1 1 0 1 0 ? 0 1 0 1 0 0 0 1 0 1 0 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 0 1 0 1 2 1 1 1 1 0 2 1 1 0 |
| *Paradelia intersecta* | 1 1 0 ? 1 1 0 1 0 ? 0 ? 1 1 0 1 1 0 0 1 0 0 1 0 1 0 0 0 1 0 1 0 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 0 1 0 1 2 1 1 1 ? 0 2 1 1 0 |
| *Boreophorbia hirtipes* | 1 1 1 1 1 0 1 1 0 ? 0 ? 2 1 0 1 1 1 ? ? ? 0 1 0 1 0 0 ? 1 ? ? ? 0 1 1 0 0 0 0 0 1 ? ? ? 0 0 5 ? 0 1 ? ? ? 0 ? 0 ? ? ? 0 |
| *Phorbia* sp. 1 | 2 1 1 0 0 ? 0 1 0 ? 0 ? 1 0 0 1 1 0 0 0 ? 0 1 1 1 0 0 0 1 0 0 ? 0 1 2 0 0 0 0 0 1 0 ? ? 0 0 0 0 0 1 2 1 1 1 0 0 2 1 1 0 |
| *Phorbia* sp. 2 | 2 ? 1 0 ? ? 0 ? ? ? 0 ? 1 0 0 1 1 0 1 0 ? 0 ? 2 1 0 0 ? 1 0 1 1 0 1 2 0 0 0 0 0 1 0 ? ? 0 0 0 1 0 1 2 1 1 1 0 0 2 1 1 0 |
| *Phorbia* sp. 3 | 2 ? 1 0 ? ? 0 ? ? ? 0 ? 1 0 0 1 1 0 1 0 ? 0 ? 2 1 0 0 ? 1 0 1 1 0 1 2 0 0 0 0 0 1 0 ? ? 0 0 0 1 0 1 2 1 1 1 0 0 2 1 1 0 |
| *Phorbia bartaki* | 2 1 1 0 1 0 0 1 0 ? 0 ? 2 1 0 1 1 0 1 1 0 0 1 1 1 0 0 ? 1 ? 1 0 0 1 2 0 0 0 0 0 1 0 ? ? 0 0 0 1 0 1 2 1 1 1 0 0 2 1 1 0 |
| *Phorbia longipilis* | 2 1 1 0 ? ? 0 ? ? ? 0 ? 2 1 0 1 1 0 1 ? ? 0 ? 2 1 0 0 ? 1 ? 1 0 0 1 1 0 0 0 0 0 1 0 ? ? 0 0 0 1 0 1 2 1 1 1 0 0 2 1 1 0 |
| *Phaonantho benevola* | 1 1 0 ? 1 1 0 1 0 ? 0 ? 1 1 0 3 1 0 0 0 ? 0 1 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 0 0 1 1 1 1 0 0 0 0 0 1 1 1 1 1 1 0 2 1 1 0 |
| *Phaonantho mallochi* | 1 1 0 ? 1 1 0 1 0 ? 0 ? 1 1 0 3 1 0 0 0 ? 0 1 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 0 0 1 1 1 1 0 0 0 0 0 1 2 1 1 1 1 0 2 0 1 0 |
| *Phaonantho sordilloae* | 1 1 0 ? 1 1 0 1 0 ? 0 ? 1 1 0 3 1 0 0 0 ? 0 1 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 0 0 1 1 1 1 0 0 0 0 0 1 1 1 1 1 1 0 2 1 1 0 |
| *Coenosopsia brasiliensis* | 0 1 1 1 1 0 1 0 0 ? 0 ? 1 1 0 3 1 1 ? 0 ? 0 0 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 0 0 1 1 0 1 0 0 1 0 0 1 2 1 1 0 ? 0 2 1 1 0 |
| *Coenosopsia ferrari* | 0 1 1 1 1 0 1 0 0 ? 0 ? 1 1 0 3 1 1 ? 0 ? 0 0 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 0 0 1 1 0 1 0 0 1 0 0 1 2 1 1 0 ? 0 2 1 1 0 |
| *Coenosopsia michelseni* | 0 1 1 1 1 0 1 0 0 ? 0 ? 1 1 0 3 1 1 ? 0 ? 0 0 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 0 0 1 1 0 1 0 0 1 0 0 1 2 1 1 0 ? 0 2 1 1 0 |
| *Coenosopsia peruviana* | 0 1 1 1 1 0 1 0 0 ? 0 ? 1 1 0 3 1 1 ? 0 ? 0 0 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 0 0 1 1 0 1 0 0 1 0 0 1 2 1 1 0 ? 0 2 1 1 0 |
| *Protoanthomyia minuta* | 1 1 1 ? ? ? ? ? ? ? 0 ? 1 0 0 1 ? 0 1 0 ? 0 ? 0 1 0 0 ? 1 1 ? ? 0 1 0 0 0 0 0 1 0 ? ? 0 0 0 ? ? 1 ? 0 ? 0 ? 0 2 ? 1 0 |
| *Coenosopsites poinari* | 1 1 ? ? 1 0 ? 1 0 ? ? ? 1 1 0 1 1 ? ? ? ? 0 0 0 1 ? 0 1 1 0 1 0 0 1 0 0 0 0 0 0 1 1 ? ? 0 0 1 ? 0 1 ? 1 1 1 0 0 2 ? 1 0 |
| *Anthomyia pluripunctata* | 1 0 0 1 1 0 0 0 0 ? 0 ? 2 1 0 2 1 0 0 1 0 0 1 0 1 0 0 0 1 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 0 0 0 1 1 0 0 0 1 1 1 1 1 1 1 1 0 2 1 1 0 |
| *Anthomyia brasiliensis* | 1 1 1 1 1 0 1 0 0 ? 0 ? 0 1 0 2 1 1 ? 1 0 1 1 1 0 1 0 0 0 1 1 0 1 0 0 1 1 1 0 0 0 2 1 1 1 2 1 1 1 1 0 2 1 1 0 |
| *Pegomya bruchi* | 1 1 1 1 1 0 0 0 0 ? 0 ? 2 1 0 2 1 0 1 1 0 0 1 0 1 0 0 0 1 0 1 2 0 1 1 0 0 0 0 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 0 2 0 1 0 |
| *Anthomyia crassinervis* | 1 1 1 1 1 0 1 0 0 ? 0 ? 1 1 0 2 1 1 ? 1 0 1 1 0 1 0 1 0 0 0 1 0 1 2 0 0 ? 0 0 0 0 0 1 1 1 0 0 0 2 1 1 1 0 0 ? 1 1 0 2 1 1 0 |
| *Anthomyia ocullifera* | 1 1 1 0 1 0 0 1 0 ? 0 ? 2 1 0 1 1 0 0 0 ? 0 1 0 1 0 0 1 1 0 0 ? 1 1 0 0 0 0 0 1 1 1 0 0 0 1 1 1 2 1 1 1 1 0 2 1 1 0 |
| *Anthomyia illocata* | 0 1 0 ? 1 0 0 1 0 ? 0 ? 2 1 0 2 1 0 0 0 ? 0 1 0 1 0 0 1 1 0 0 ? 1 1 0 0 0 0 0 0 1 1 0 0 0 0 1 1 1 1 2 1 1 1 1 0 2 0 1 0 |
| *Anthomyia procellaris* | 0 ? 0 ? ? ? 0 ? ? ? 0 ? 2 1 0 2 1 0 0 0 ? 0 ? 0 1 0 0 1 1 0 0 ? 0 1 0 0 0 0 0 0 1 1 1 0 0 0 1 1 1 2 1 1 1 1 0 2 0 1 0 |
| *Anthomyia albostriata* | 1 1 1 0 1 0 0 1 0 ? 0 ? 2 1 0 2 1 0 0 0 ? 0 1 0 1 0 0 0 1 0 1 2 0 1 2 0 0 0 0 0 1 1 1 1 0 0 1 1 1 1 1 1 1 1 0 2 1 1 0 |
| *Anthomyia lindigii* | 1 1 1 1 1 0 0 1 0 ? 0 ? 2 1 0 2 1 0 1 0 ? 0 1 0 1 0 0 0 1 0 1 2 0 1 2 0 0 0 0 0 1 1 1 1 0 0 1 1 1 1 1 1 1 1 0 2 0 1 0 |
| *Anthomyia plurinervis* | 1 1 1 1 1 0 1 0 0 ? 0 ? 1 1 0 2 1 1 ? 1 0 0 1 0 1 0 0 0 1 0 1 2 0 1 1 0 0 0 0 0 1 1 1 0 0 0 2 1 1 1 1 1 1 1 1 0 2 1 1 0 |
| *Anthomyia punctipennis* | 1 1 1 1 1 0 0 0 0 ? 0 ? 2 1 0 1 1 1 0 0 1 0 1 0 0 0 1 0 1 2 0 1 1 0 0 0 0 0 1 1 1 0 0 0 1 1 1 1 0 1 1 1 1 0 2 1 0 |
| *Anthomyia xanthopyga* | 1 1 1 1 1 0 1 0 0 ? 0 ? 1 1 0 1 1 1 ? 1 0 0 1 0 1 0 0 0 1 0 1 2 0 1 1 0 0 0 0 0 1 1 1 1 0 0 1 1 1 1 1 1 1 1 0 2 0 1 0 |
| *Anthomyia aurifacies* | 1 1 ? ? 1 0 ? 1 0 ? ? ? 0 1 0 2 1 ? ? 0 ? 1 1 0 1 ? 0 1 1 0 1 2 0 1 1 0 0 0 0 0 1 1 1 1 0 0 2 0 1 1 1 1 1 1 1 0 2 0 1 0 |
| *Anthomyia paulistensis* | 1 ? 1 0 ? ? 1 ? ? ? 0 ? 0 1 0 2 1 1 ? 0 ? 1 1 0 1 0 0 ? 1 0 1 2 0 1 0 0 0 0 0 0 1 1 1 1 0 0 2 0 1 1 1 1 1 1 1 0 2 1 0 |
| *Taeniomyia auricolis* | 0 0 0 ? 1 0 0 1 0 ? 0 ? 1 2 0 3 0 0 0 0 ? 0 1 0 1 0 0 0 1 0 0 ? 1 1 0 0 0 0 0 0 1 0 ? ? 0 0 0 0 0 1 2 1 1 1 1 0 2 0 1 0 |
| *Taeniomyia sobria* | 0 0 0 ? 1 0 1 1 0 ? 0 ? 1 2 1 1 0 1 ? 1 0 0 1 0 1 0 0 0 1 0 1 ? 0 1 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 1 2 1 1 1 1 0 2 0 1 0 |
| *Taeniomyia collaris* | 0 0 0 ? 1 0 0 1 0 ? 0 ? 1 2 0 2 0 0 0 1 0 0 1 0 1 0 0 0 1 0 0 ? 1 ? 0 0 0 0 0 1 1 1 0 0 0 0 0 1 2 1 1 1 1 0 2 1 1 0 |
| *Emmesomyia socia* | 0 ? 0 ? ? ? 0 ? 0 ? 0 ? 1 2 0 1 1 0 0 ? ? 0 ? 0 1 0 0 ? 1 ? 0 ? 0 ? ? 0 0 0 0 0 1 1 1 1 0 0 0 0 0 1 ? ? ? 1 ? 0 2 0 1 0 |
| *Emmesomyia spinulosa* | 0 1 0 ? 1 0 0 1 0 ? 0 ? 1 2 0 1 1 0 0 0 ? 0 1 0 1 0 0 0 1 0 1 ? 0 1 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 1 2 1 1 1 1 0 2 0 1 0 |
| *Emmesomyia spadibasis* | 0 1 0 ? 1 0 0 1 0 ? 0 ? 1 2 0 1 1 0 0 1 0 0 1 0 1 0 0 0 1 0 0 ? 1 0 1 0 0 0 0 0 1 1 1 0 0 0 0 0 0 1 2 1 1 1 1 0 1 ? 1 0 |
| *Emmesomyia grisea* | 0 ? 0 ? ? ? 0 ? 0 ? 0 ? 1 2 0 1 1 0 0 0 ? 0 1 0 1 0 0 0 1 0 0 ? 1 ? 0 1 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 1 2 1 1 1 1 0 2 0 1 0 |
| *Fucellia tergina* | 1 1 1 1 1 0 1 1 1 1 1 1 2 0 0 0 1 1 ? 0 ? 0 1 0 1 0 0 1 1 0 0 ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 1 1 0 1 2 1 1 0 ? 0 2 1 1 0 |
| *Fucellia apicalis* | 1 1 1 1 1 0 1 1 1 ? ? ? 2 0 0 1 1 1 ? 0 ? 0 ? 0 1 ? 0 1 1 ? 0 ? 0 1 2 0 0 0 0 0 1 ? ? ? 0 0 1 1 0 1 2 ? ? ? 0 2 1 1 0 |
| *Leucophora maculipennis* | 2 1 1 1 1 1 1 0 1 1 0 ? 3 0 0 3 1 0 1 0 ? 0 1 3 1 0 0 0 1 0 1 0 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 0 0 1 2 1 1 1 0 0 2 1 1 0 |
| *Leucophora obtusa* | 2 ? 0 ? ? ? 0 ? ? ? 0 ? 3 0 0 ? 1 0 1 ? ? 0 1 3 1 0 0 0 1 0 ? ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 0 0 ? 1 ? ? ? 1 ? 0 2 1 ? 0 |
| *Leucophora* sp. 1 | 2 ? 1 0 ? ? 1 ? ? ? 0 ? 3 1 0 4 2 0 1 0 ? 0 ? 3 1 0 0 ? 2 0 1 0 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 0 0 0 1 2 1 1 1 0 0 2 1 1 0 |
| *Leucophora* sp. 2 | 2 ? 0 ? ? ? 0 ? ? ? 0 ? 3 0 0 4 2 0 2 0 ? 0 ? 3 1 0 0 ? 1 0 1 0 0 0 ? 0 0 0 0 0 1 0 ? ? 0 0 5 0 0 1 2 1 1 1 0 0 2 ? 1 0 |
| *Leucophora apivora* | 2 ? 0 ? ? ? 0 ? ? ? 0 ? 3 1 0 4 2 0 2 0 ? 0 ? 3 1 0 0 ? 1 0 1 1 0 1 1 0 0 0 0 0 1 0 ? ? 0 0 5 0 0 1 2 1 0 1 0 0 2 1 1 0 |
| *Pegomya carrerai* | 0 0 0 ? 1 0 0 1 0 ? 0 ? 1 1 0 1 1 0 1 0 ? 0 1 0 1 0 0 1 1 0 1 1 0 1 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 1 2 1 1 1 0 0 2 1 0 1 0 |
| *Pegomya poeciloptera* | 0 0 0 ? 1 0 0 1 0 ? 0 ? 1 1 0 1 1 0 1 0 ? 0 1 0 1 0 0 1 1 0 1 1 0 1 1 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 1 2 1 1 1 0 0 2 0 1 0 |
| *Pegomya flavifrons* | 0 ? 0 ? ? ? 0 ? ? ? 0 ? 1 1 0 1 1 0 0 0 ? 0 ? 0 1 0 0 ? 1 ? 1 0 0 1 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 1 2 1 1 1 0 0 2 0 1 0 |
| *Pegomya interruptella* | 1 ? 0 ? ? ? 0 ? ? ? 0 ? 1 0 0 1 1 0 1 0 ? 0 ? 0 1 0 0 ? 1 ? 1 1 0 1 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 1 2 1 1 1 0 0 2 1 1 0 |
| *Pegomya affinis* | 1 ? 0 ? ? ? 0 ? ? ? 0 ? 2 0 0 1 1 0 0 0 ? 0 ? 0 1 0 0 ? 1 0 ? ? 0 0 ? 0 0 0 0 0 1 1 1 0 0 0 0 0 0 1 2 1 1 1 1 0 2 0 1 0 |

**Table S1 (part 1b).** Matrix of morphological characters. Polymorphism: A= 0,1; B= 2,3; C= 3,4; D= 1,2; E= 4,5; F= 1,2,3; G= 1,2,3,4; H= 3,4,5.

| | 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 5 5 5 6 |
|---|---|
| | 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 |
| *Calythea comis* | 0 1 1 1 0 ? 0 1 0 ? 0 ? 1 1 0 1 1 0 0 0 ? 0 1 0 1 1 0 1 1 1 1 1 0 0 ? 0 0 0 0 0 1 1 0 0 0 1 0 0 0 1 2 1 0 1 1 0 2 1 1 0 |
| *Calythea crenata* | 0 1 0 ? 0 ? 0 1 0 ? 0 ? 1 1 0 1 1 0 0 1 1 0 1 0 1 1 0 1 1 1 0 ? 0 0 ? 0 0 0 0 0 1 0 ? ? 0 1 0 0 0 1 2 1 0 1 1 0 2 1 1 0 |
| *Calythea micropteryx* | 0 1 0 ? ? ? 0 ? ? ? 0 ? 1 1 0 1 1 0 0 0 ? 0 ? 0 1 1 0 1 1 1 0 ? 0 0 ? 0 0 0 0 0 1 0 ? ? 0 1 0 0 0 1 2 1 0 1 1 0 2 1 1 0 |
| *Heterostylodes obscurus* | 1 ? 0 ? ? ? 0 ? ? ? 0 ? 1 1 0 1 1 0 1 0 ? 0 ? 1 1 1 0 ? 1 ? 0 ? 0 1 2 0 0 0 0 0 1 0 ? ? 0 ? 0 0 0 1 ? ? ? 1 ? 0 2 0 1 0 |
| *Heterostylodes ricta* | 1 ? 0 ? ? ? 0 ? ? ? 0 ? 1 1 0 1 1 0 ? 0 ? 0 ? 1 1 1 0 ? 1 ? 1 ? 0 1 2 0 0 0 0 0 1 0 ? ? 0 ? 0 0 0 1 ? ? ? 1 ? 0 2 0 1 0 |
| *Enneastigma rufitibia* | 1 1 1 ? ? ? 0 ? 0 ? 0 ? 1 1 0 1 1 0 ? 0 ? 0 ? ? 1 1 0 2 1 ? 1 ? 0 1 2 0 0 0 0 0 1 ? ? ? 0 ? 0 ? ? 1 ? ? ? 1 ? 0 2 ? 1 0 |
| *Enneastigma triseriatum* | 1 1 1 ? ? ? 0 ? 0 ? 0 ? 1 1 0 1 1 0 ? 0 ? 0 ? ? 1 1 0 2 1 ? 1 0 0 1 2 0 0 0 0 0 1 ? ? ? 0 ? 0 ? ? 1 ? ? ? 1 ? 0 2 ? 1 0 |
| *Pegoplata aestiva* | 0 ? 1 1 ? ? 0 ? ? ? 0 ? 1 1 0 1 1 0 0 0 ? 0 ? 0 1 1 0 1 1 ? 0 ? 0 1 0 0 0 0 0 0 1 1 1 0 0 ? 0 0 0 1 2 1 0 1 1 0 2 1 1 0 |
| *Pegoplata infirma* | 0 ? 1 1 ? ? 0 ? ? ? 0 ? 1 1 0 1 1 0 0 0 ? 0 ? 0 1 1 0 1 1 ? 0 ? 0 1 0 0 0 0 0 0 1 1 1 0 0 ? 0 0 0 1 2 1 0 1 1 0 2 1 1 0 |
| *Pegoplata patellans* | 0 ? 1 1 ? ? 0 ? ? ? 0 ? 1 1 0 1 1 0 0 0 ? 0 ? 0 1 1 0 1 1 ? 0 ? 0 ? ? 0 0 0 0 0 0 1 1 1 0 0 ? 0 1 0 1 2 1 0 1 1 0 2 1 1 0 |
| *Pegoplata* sp. 1 | 0 ? 1 1 ? ? 0 ? ? ? 0 ? 1 1 0 1 1 0 0 0 ? 0 ? 0 1 1 0 1 1 0 0 ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 1 0 0 0 1 2 1 0 1 1 0 2 1 1 0 |
| *Myopina myopina* | 1 1 1 1 ? ? ? ? 0 ? 0 ? 3 1 1 1 2 1 ? ? ? ? 1 0 1 0 0 1 1 0 ? ? 0 1 1 0 0 0 0 0 1 ? ? ? 0 ? 0 ? ? 1 ? ? ? 1 0 0 2 1 1 0 |
| *Oxyphorbia dyscrita* | 2 1 1 1 ? ? 0 ? 0 ? 0 ? 3 1 0 1 2 0 1 0 ? 0 ? 2 1 0 0 ? 1 ? 1 0 0 0 ? 0 0 0 0 0 1 0 ? ? 0 0 0 0 0 1 2 1 1 1 ? 0 2 1 1 0 |
| *Subhylemyia longula* | 1 1 1 0 1 1 ? 1 0 ? 0 ? 2 1 0 1 1 0 1 0 ? 0 1 1 1 0 0 0 1 0 0 ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 0 0 0 1 1 ? ? 1 0 0 2 1 1 0 |
| *Subhylemyia dorsilinea* | 1 1 1 ? 1 1 ? 1 0 ? 0 ? 2 1 0 1 1 0 1 0 ? 0 1 ? 1 0 0 0 1 0 ? ? 0 1 0 0 0 0 0 0 1 ? ? ? 0 0 0 ? ? 1 1 ? ? 1 0 0 2 ? 1 0 |
| *Adia cinerella* | 0 1 0 ? 1 1 0 1 0 ? 0 ? 2 1 0 0 1 0 0 0 ? 0 1 1 2 0 0 0 1 0 0 ? 0 1 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 1 2 1 1 1 1 0 2 0 1 0 |
| *Eustalomyia vittipes* | 1 0 0 ? 1 0 0 1 0 ? 0 ? 3 1 0 3 1 0 1 1 0 0 1 2 1 0 0 0 1 0 1 ? 0 1 0 0 0 0 0 0 1 1 0 1 0 0 5 0 1 1 2 0 ? 1 0 0 2 1 1 0 |
| *Eustalomyia hilaris* | 2 0 0 ? 1 0 0 1 0 ? 0 ? 3 1 0 3 1 0 1 ? ? 0 1 2 2 0 0 0 1 ? 1 0 0 1 0 0 0 0 0 0 1 1 0 ? 0 0 0 1 1 1 2 0 ? 1 ? 0 2 0 1 0 |
| *Paregle popocatepetlensis* | 2 1 1 0 1 1 0 1 0 ? 0 ? 3 1 0 1 1 0 0 1 0 0 1 3 1 0 0 0 1 0 0 ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 5 0 0 1 2 1 1 1 1 0 2 1 1 0 |
| *Paregle vetula* | 2 1 1 0 ? ? ? ? 0 ? 0 ? 2 1 0 1 1 0 ? ? ? 0 1 2 1 0 0 0 1 ? 0 ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 ? ? 0 1 ? 1 1 1 1 0 2 1 1 0 |
| *Paregle audacula* | 2 1 1 0 ? ? ? ? 0 ? 0 ? 2 1 0 1 1 0 ? ? ? 0 1 2 1 0 0 0 1 ? 0 ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 ? ? 0 1 ? 1 1 1 1 0 2 1 1 0 |
| *Hyporites shakshain* | 0 ? 1 0 ? ? 0 ? ? ? ? ? ? ? 0 1 1 0 1 ? ? 0 ? ? 1 ? 0 ? 1 ? ? ? 0 1 ? 0 0 0 0 0 1 ? ? ? 0 ? 7 ? ? 1 ? ? ? ? 1 ? 0 ? ? ? 0 |
| *Hylemya urbica* | 0 1 1 0 1 0 0 1 0 ? 0 ? 2 1 0 3 1 0 0 0 ? 0 1 0 1 0 0 0 1 0 1 ? 0 1 0 0 0 0 0 1 1 1 0 0 0 1 0 0 1 2 1 1 1 1 0 2 1 1 0 |
| *Hylemya vagans* | 0 1 1 0 1 0 0 1 0 ? 0 ? 2 1 0 3 1 0 0 0 ? 0 1 0 1 0 0 0 1 0 1 0 0 1 0 0 0 0 0 1 1 1 0 0 0 1 0 0 1 2 1 1 1 1 0 2 1 1 0 |
| *Hylemyza partita* | 0 ? ? ? ? ? 0 ? ? ? 0 ? 1 1 0 3 1 0 0 0 ? 0 ? 0 1 0 0 ? 1 ? ? ? 0 1 0 0 0 0 0 0 1 1 1 1 0 0 1 1 0 1 2 1 1 1 ? 0 2 1 1 0 |
| *Myopinella appendiculata* | 1 1 1 2 1 0 1 1 0 ? 0 ? 2 0 0 1 2 1 ? 0 ? 1 1 0 1 0 0 0 1 1 0 ? 0 0 ? 0 0 0 0 1 0 ? ? 0 0 1 2 0 1 1 1 0 1 1 0 2 0 1 0 |
| *Myopinella angustifrons* | 1 ? 1 2 ? ? 0 ? ? ? 0 ? 1 0 0 1 2 0 1 0 ? 0 ? 0 1 0 0 0 1 1 0 ? 0 0 ? 0 0 0 0 0 1 0 ? ? 0 0 0 0 0 1 1 1 0 1 1 0 2 0 1 0 |
| *Chirosiomima gestroi* | 2 ? 1 ? ? ? 1 1 ? ? 0 ? 3 1 0 1 1 1 ? 0 ? 0 ? 1 1 0 0 1 2 ? 0 ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 5 1 0 1 ? ? ? 0 ? 0 ? ? ? 0 |
| *Ringdahlia curtigena* | 0 1 1 0 1 0 0 0 0 ? 0 ? 1 1 0 1 1 0 0 0 ? 0 1 0 1 0 0 ? 1 ? ? ? 0 1 1 ? 0 0 0 0 1 1 0 1 0 0 1 ? 0 1 ? ? ? ? ? 0 ? ? ? 0 |
| *Karliella sexpunctata* | 1 1 0 ? 1 1 0 1 0 ? 0 ? 2 1 0 2 1 0 0 0 ? 0 1 0 1 0 0 0 1 0 0 ? 0 1 1 0 0 0 0 0 1 1 ? ? 0 0 1 0 0 1 2 1 1 1 ? 0 2 0 1 0 |
| *Alliopsis billbergi* | 2 ? 0 ? ? 0 0 ? ? ? 0 ? 2 0 0 2 1 0 1 ? ? 0 ? 1 1 0 0 0 1 ? 0 ? 0 1 0 ? 0 0 0 0 1 0 ? ? 0 ? 1 1 0 1 2 ? ? 1 ? 0 2 0 1 0 |
| *Alliopsis lobata* | 2 ? 1 2 ? ? 0 ? ? ? 0 ? 2 0 0 1 1 0 2 ? ? ? 0 ? 1 1 0 0 0 1 0 ? ? 0 1 2 ? 0 0 0 1 ? ? ? 0 ? ? 0 1 2 ? ? 1 ? 0 ? ? ? 0 |
| *Egle ciliata* | 2 1 ? ? 1 2 0 0 0 ? 0 ? 3 0 0 0 2 0 0 0 ? 0 1 3 2 2 0 2 2 ? 1 1 0 0 ? ? 0 0 0 0 1 1 0 1 0 ? 0 0 0 1 2 ? ? 1 ? 0 2 1 2 ? |
| *Egle concomitans* | 1 ? ? ? ? ? 0 ? ? ? 0 ? 2 0 0 0 2 0 0 0 ? 0 1 2 0 0 ? 2 ? 1 2 0 0 ? ? 0 0 0 0 1 1 1 0 0 ? 0 0 1 1 2 0 ? 1 ? 0 2 1 1 ? |
| *Egle parva* | 2 1 ? ? 1 1 0 1 0 ? 0 ? 2 0 0 0 2 0 1 0 ? 0 1 2 2 2 0 2 1 ? 1 ? 0 0 ? ? 0 0 0 0 1 1 1 1 0 ? 0 0 1 2 ? ? 1 ? 0 2 0 1 ? |
| *Eutrichota processualis* | 0 0 0 ? 1 0 0 1 0 ? 0 ? 2 0 0 1 1 0 0 0 ? 0 1 0 1 0 0 0 1 0 0 ? 0 0 ? 0 0 0 0 0 1 1 1 1 0 0 0 0 0 1 2 1 1 1 1 0 2 0 1 0 |
| *Eutrichota praepotens* | 1 0 0 ? ? ? 0 ? 0 ? 0 ? 1 1 0 3 1 0 ? 0 ? 0 ? 0 1 0 0 ? 1 ? 0 ? 0 1 1 0 0 0 0 0 1 ? ? ? 0 0 0 ? 0 ? ? ? ? 1 ? 0 2 ? 1 0 |
| *Botanophila collini* | 0 ? 1 2 ? ? ? ? 0 ? 0 ? 2 1 0 2 1 1 ? 0 ? 0 ? 0 1 0 0 ? 1 ? ? ? 0 1 0 0 0 0 0 0 1 1 1 0 0 ? 0 ? 0 ? 4 ? 0 1 ? ? ? 1 ? 0 2 ? 1 0 |
| *Botanophila brunneilinea* | 0 ? 1 0 ? ? ? ? ? ? 0 ? 2 1 0 1 1 0 0 0 ? 0 ? 0 1 0 0 ? 1 ? 0 ? 0 1 1 0 0 0 0 0 1 1 1 0 0 ? ? ? 0 1 2 ? ? 1 ? 0 2 1 1 0 |
| *Botanophila fugax* | 1 ? 1 0 ? ? 0 ? ? ? 0 ? 1 1 0 1 1 0 0 0 ? 0 ? 0 1 0 0 0 1 0 1 1 0 0 1 1 0 0 0 ? 0 1 0 1 1 1 0 0 1 1 0 1 0 1 2 1 1 1 1 0 2 0 1 0 |
| *Botanophila subbrunneilinea* | 0 1 1 ? ? ? ? ? 0 ? 0 ? 2 1 0 1 1 1 ? 0 ? ? ? ? 1 0 0 ? 1 ? ? ? 0 ? ? 0 0 0 0 0 0 1 ? ? ? 0 0 ? ? ? 1 ? ? ? 1 ? 0 2 ? 1 0 |
| *Botanophila hernandezi* | 1 ? 1 0 ? ? 1 ? ? ? 0 ? 1 1 0 1 1 1 ? 0 ? 0 ? ? 1 0 0 ? 1 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 0 0 1 0 1 1 0 ? 1 1 0 2 0 1 0 |
| *Botanophila zaldivari* | 1 1 1 1 1 0 1 1 0 ? 0 ? 1 1 0 1 1 1 ? 0 ? 0 1 0 1 0 0 0 1 0 1 0 0 1 2 0 0 0 0 0 1 1 0 0 0 0 0 1 0 1 0 1 0 1 1 1 1 1 0 2 0 1 0 |
| *Zaphne ambigua* | 2 1 1 1 1 ? 0 1 0 ? 0 ? 1 1 0 2 1 0 1 0 ? 0 1 1 1 0 0 0 1 ? 1 1 0 1 0 0 0 0 0 1 1 1 1 0 0 1 1 1 1 1 1 1 1 ? 0 2 0 1 0 |
| *Zaphne caudata* | 1 1 1 1 1 0 0 1 0 ? 0 ? 2 1 0 2 1 0 1 0 ? 0 1 1 1 0 0 0 1 ? 1 1 0 1 0 0 0 0 0 1 1 1 1 0 0 1 1 1 1 1 1 1 1 ? 0 2 1 1 0 |
| *Zaphne* sp. 1 | 1 ? 1 0 ? ? 0 ? ? ? 0 ? 2 1 0 2 1 0 1 0 ? 0 ? 1 1 0 0 ? 1 0 0 ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 1 1 0 1 2 1 1 1 0 0 2 1 1 0 |
| *Lasiomma anthomyinum* | 0 ? ? ? ? ? 0 ? ? ? 0 ? 1 1 0 1 1 0 0 1 1 0 ? 0 1 0 0 0 1 ? 1 0 0 1 0 0 0 0 0 0 1 1 1 0 0 0 1 0 1 1 2 1 1 1 ? 0 2 1 1 0 |
| *Lasiomma seminitidum* | 1 ? ? ? ? ? 0 ? ? ? 0 ? 1 1 0 1 1 0 1 1 1 0 ? 0 1 0 0 0 1 ? 1 1 0 1 0 0 0 0 0 0 1 1 1 0 0 0 1 0 1 1 2 1 1 1 ? 0 2 1 1 0 |
| *Hydrophoria ruralis* | 0 1 0 ? 1 0 0 1 0 ? 0 ? 2 1 0 3 1 0 0 0 ? 0 1 0 1 0 0 0 1 0 1 1 0 1 0 0 0 0 0 0 1 1 1 1 0 0 1 0 0 1 2 1 1 1 1 0 2 1 1 0 |
| *Hydrophoria silvicola* | 0 ? 0 ? ? ? 0 ? ? ? 0 ? 2 1 0 3 1 0 1 0 ? 0 ? 0 1 0 0 0 1 ? 1 ? 0 1 0 0 0 0 0 0 1 1 1 1 0 0 1 0 0 1 2 ? ? 1 ? 0 2 0 1 0 |
| *Strobilomyia laricicola* | 1 ? 0 ? ? ? 0 ? ? ? 0 ? 1 1 0 0 1 0 0 0 ? 0 ? 1 1 0 0 0 1 ? 0 ? 0 ? ? 0 0 0 0 0 1 0 ? ? 0 0 1 0 0 1 2 1 1 1 1 0 2 ? ? 2 0 |
| *Strobilomyia viaria* | 1 ? ? ? ? ? 0 ? 0 ? 0 ? 2 1 0 1 1 0 ? 0 ? 0 ? 1 1 0 0 0 1 ? 0 ? 0 1 1 0 0 0 0 0 1 ? ? ? 0 0 1 0 0 1 ? ? ? 1 ? 0 ? ? ? 0 |
| *Mycophaga testacea* | 0 1 1 0 ? ? 1 1 ? ? 0 ? 1 1 0 3 1 1 ? 1 0 0 ? 0 1 0 0 0 1 ? 0 ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 5 0 0 1 2 1 1 1 ? 0 2 1 1 0 |
| *Scathophaga stercoraria* | 1 0 0 ? 1 0 1 1 1 0 0 ? 2 1 0 2 1 1 ? 0 ? 1 1 0 1 0 0 0 1 0 1 0 0 1 2 1 0 0 0 0 0 ? ? 0 0 3 ? 0 1 1 0 ? 0 ? 0 2 1 1 0 |
| *Scathophaga furcata* | 1 0 0 ? ? ? 1 ? 0 ? 0 ? 2 1 0 2 1 1 ? ? ? 1 1 0 1 0 0 0 1 ? 0 ? 0 1 1 1 0 0 0 0 0 ? ? 0 0 3 ? 0 1 1 0 ? 0 ? 0 2 1 1 0 |
| *Cordilura ciliata* | 0 0 0 ? 1 0 1 1 0 ? 0 ? 1 1 0 3 1 1 ? ? ? 1 1 0 1 0 1 0 1 ? 0 ? 0 ? ? ? 0 0 0 0 1 0 ? ? 0 0 3 ? 0 1 0 ? ? 0 ? 0 2 0 1 0 |
| *Cordilura albiceps* | 0 0 0 ? 1 0 1 1 0 ? 0 ? 1 0 0 3 1 1 ? 0 ? 1 ? 0 1 0 1 ? 1 ? 1 ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 3 ? 1 0 ? 0 ? 0 ? 0 ? ? 1 0 |
| *Cordilura picipes* | 0 0 0 ? 1 0 1 1 0 ? 0 ? 1 1 0 3 1 1 ? 0 ? 1 ? 0 1 0 1 ? 1 ? 0 ? 0 1 ? ? 0 0 0 0 1 0 ? ? 0 0 3 ? 0 0 ? 0 ? 0 ? 0 2 1 1 0 |
| *Nanna tibiella* | 1 0 0 ? 1 0 1 1 0 ? 0 ? 2 2 0 0 1 1 ? 0 ? 1 1 0 1 0 0 0 1 ? 0 ? 0 1 0 0 0 0 0 0 1 0 ? ? 0 0 0 0 0 1 0 ? ? 0 ? 0 ? 0 2 1 1 0 |

**Table S1 (part 2a).** Matrix of morphological characters. Polymorphism: A= 0,1; B= 2,3; C= 3,4; D= 1,2; E= 4,5; F= 1,2,3; G= 1,2,3,4; H= 3,4,5.

| | 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1

**Table S1 (part 2b).** Matrix of morphological characters. Polymorphism: A= 0,1; B= 2,3; C= 3,4; D= 1,2; E= 4,5; F= 1,2,3; G= 1,2,3,4; H= 3,4,5.

| | 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1

**Table S1 (part 3a).** Matrix of morphological characters. Polymorphism: A= 0,1; B= 2,3; C= 3,4; D= 1,2; E= 4,5; F= 1,2,3; G= 1,2,3,4; H= 3,4,5.

| | 1111111111111111111111111111111111111111111111<br>2222222222333333333344444444444555555555<br>1234567890123456789012345678901234567890123456789012345678 |
|---|---|
| *Melanophora roralis* | 00000?10?00001??40?1100?0101??0???? |
| *Ravinia belforti* | 00110?10?00000000?30?1?1??1??1??1??????? |
| *Sarcophaga crassilpalpis* | 00110?10?000000000?30?1?1??1??1??1???????0 |
| *Oxysarcodexia thornax* | 00110?10?000000000?30?121??1101101031??0 |
| *Winthemia brasiliensis* | 00110?10?00001000?40?1100?0101012?????? |
| *Patelloa similis* | 00000?0100000?1000?40?1100?1101012?????? |
| *Lucilia eximia* | 00010?10?00001000?10?1100?1101012?????? |
| *Cochliomyia macellaria* | 00010?10?000000001040?1100?1101011102??0 |
| *Mesembrinella bellardiana* | 00110?10?000000000?40?1100?0111001031??0 |
| *Mesembrinella quadrilineata* | 00110?1100000000011410?1100?0111001001??0 |
| *Acridomyia canadensis* | ???????????????????????????0?????????????? |
| *Acklandia subgrisea* | 0?000?0101?001001111002??0?0?0?????? |
| *Chiastocheta trolli* | 00010?1110000?100???100?0???1010?2?????1 |
| *Chiastocheta rotundiventris* | 00100?0111000?100???100?0???1010?2?????1 |
| *Chiastocheta setifera* | 00?00?0100000?100?????0?0?????????????1 |
| *Chirosia histricina* | 00010?0100000000012110?2??0?0110?2?????? |
| *Chirosia inspinata* | 00010?0101000000011110?2??0?0110?2?????? |
| *Delia radicum* | 01000?0100000?1001110?0100?0101001?01001 |
| *Delia platura* | 01010?00?0000?1000?10?0100?0101001?01001 |
| *Delia sanctijacobi* | 01010?00?0000?1000?10?0100?0101001?01001 |
| *Delia cilifera* | 01010?00?0000?1000?10?0100?0101011?1001 |
| *Delia clavata* | 01010?20?0000?1000?10?0100?0101011?1001 |
| *Paradelia intersecta* | 00010?10?000000001011002??0?1110010?1001 |
| *Boreophorbia hirtipes* | 0?010?0100000?1001110?0?2??0?0?0?0010?1001 |
| *Phorbia* sp. 1 | 00010?0110000?2000?10?0100?0?0?00?0130?1 |
| *Phorbia* sp. 2 | 10010?1100?00?2000?10?0100?0?0?00?0?????? |
| *Phorbia* sp. 3 | 00010?0101?00?2000?10?0100?0?0?00?0?????? |
| *Phorbia bartaki* | 10010?0100000?2000?10?0100?0?0?00?0130?1 |
| *Phorbia longipilis* | 00010?0100000?2000?10?0100?00??0?0?????? |
| *Phaonantho benevola* | 10100?10?0000?1101?00?0?2??1101??102101 |
| *Phaonantho mallochi* | 00100?1101000?1001100?0100?1101011102101 |
| *Phaonantho sordilloae* | 00100?1111000?1001100?0?2??1101011102101 |
| *Coenosopsia brasiliensis* | 00011010?00101001100?0?2??0?0?1101102101 |
| *Coenosopsia ferrari* | 00011021100?0?1101100?0?0?0?0?0?0?102101 |
| *Coenosopsia michelseni* | 00011011000?0?2001100?0?2??0?0?0?0?102101 |
| *Coenosopsia peruviana* | 00011010?00?0?2001100?0?2??0?0?1??102101 |
| *Protoanthomyia minuta* | 00?????????????????????????0?????????????? |
| *Coenosopsites poinari* | ???????????0?????????????0?????????102101 |
| *Anthomyia pluripunctata* | 00001111010001001111102??0?0?0?1100?01 |
| *Anthomyia brasiliensis* | 00001111010001001111002??0?0?0?0?0?01 |
| *Pegomya bruchi* | 00001121010001001110?0?2??0?0?0?1100001 |
| *Anthomyia crassinervis* | 00001111111000?1001111102??0?0?0?1100?01 |
| *Anthomyia ocullifera* | 00001111010001001111002??0?0?0?0?????? |
| *Anthomyia illocata* | 00001111010001001111002??0?0?0?0?????? |
| *Anthomyia procellaris* | 00001111111000000?111002??0?0?0?0?????? |
| *Anthomyia albostriata* | 00001111010001001111102??0?0?0?1?????? |
| *Anthomyia lindigii* | 00001111010001001111002??0?0?0?0?????? |
| *Anthomyia plurinervis* | 00001111111000?1001111102??0?0?0?1100?01 |
| *Anthomyia punctipennis* | 00001111010001001111102??0?0?0?0?0?01 |
| *Anthomyia xanthopyga* | 00001111010001001110?0?2??0?0?0?1?0001 |
| *Anthomyia aurifacies* | ???????????????????????0?0?????????????? |
| *Anthomyia paulistensis* | 00001101111000?1001010?0?0?0?0?0?1?????? |
| *Taeniomyia auricolis* | 00010?10?1001000?1111001?0?1?0?0?1?1111 |
| *Taeniomyia sobria* | 00000?1101001?1001111101?1?0?0?0?1?1111 |
| *Taeniomyia collaris* | 00010?1101000?1001?1?1?0?1?0?0?0?1?????1 |
| *Emmesomyia socia* | 00010?1101001?1001110?0?0?1?0?0?0?1?????? |
| *Emmesomyia spinulosa* | 00010?1101000000011110?0?1?0?0?0?1?????1 |
| *Emmesomyia spadibasis* | 00010?1101001?000?0?1?0?1?0?0?0?1?????1 |
| *Emmesomyia grisea* | 00010?1101000000?0?1?0?1?0?0?0?1?????? |
| *Fucellia tergina* | 00000?00?0000?1001?0?0000?0?0?0?1?????1 |
| *Fucellia apicalis* | 00010?00?000000000?100?0000?0?0?0?1?????? |
| *Leucophora maculipennis* | 00010?00?0000?1001000?0?2??0?0?0?1?1001 |
| *Leucophora obtusa* | 00110?00?000000001?0?0?100?0?0?0?1?????1 |
| *Leucophora* sp. 1 | 01010?0100000000011110?2??0?0?0?1?????? |
| *Leucophora* sp. 2 | 01010?0100000000011110?2??0?0?0?1?????? |
| *Leucophora apivora* | 01010?0100000?1001111?0?2??0?0?0?1111?01 |
| *Pegomya carrerai* | 00100?00?1001?00?1111?0?0?1?0?1?1?1?1?1 |
| *Pegomya poeciloptera* | 00100?0?0?0?0?1?0?1111?0?0?1?0?1?1?1?1 |
| *Pegomya flavifrons* | 00000?1101001?0?0?1?0?1?0?1?1?1?1?1?1?? |
| *Pegomya interruptella* | 00000?1101001?0?0?1?0?1?0?1?1?1?0?????? |
| *Pegomya affinis* | 00010?10?00001?0?1211?0?0?1?0?1?0?1?????? |

**Table S1 (part 3b).** Matrix of morphological characters. Polymorphism: A= 0,1; B= 2,3; C= 3,4; D= 1,2; E= 4,5; F= 1,2,3; G= 1,2,3,4; H= 3,4,5.

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**Table S2.** List of material examined for the phylogenetic analysis. Biogeographical regions: Afrotropical (AF); Australasian (AU); Mexican Transition Zone (MTZ); Nearctic (NE); Neotropical (NT); Oriental (OR); Palearctic (PA); *= new records.

| Family | Species | Label (Institution) or literature information | Distribution |
|---|---|---|---|
| Anthomyiidae | *Acklandia subgrisea* (Ringdahl, 1930) | Hennig (1976) | PA |
| Anthomyiidae | *Acridomyia canadensis* Snyder, 1940 | Snyder (1940); Griffiths (2001) | NE |
| Anthomyiidae | *Adia cinerella* (Fallén, 1825) | Mexico, Golfo de California, 6.ii.1986, F. Arias, 3♂♂ and 4♀♀ (CNIN; DZUP). | NE, PA |
| Anthomyiidae | *Alliopsis billbergi* (Zetterstedt, 1838) | http://www.spessart-fliegen.de/ | PA |
| Anthomyiidae | *Alliopsis lobata* Suwa, 2013 | Suwa (2013) | PA |
| Anthomyiidae | *Anthomyia albostriata* (Wulp, 1883) | Peru, Cuzco, Est. Biol. Wayqecha, 1-12.vi.2012, A. L. Norrbom et al., 3♂♂ and 3♀♀ (DZUP; USNM) | NT |
| Anthomyiidae | *Anthomyia aurifacies* (Albuquerque, 1952) | Brazil, São Paulo, São José dos Campos, H. S. Lopes, xii.1934, 1♀ (Holotype) (MNRJ); Paraná, Curitiba, 09.xii.2016, Vasconcelos & Wendt, 1♀ (DZUP) | NT |
| Anthomyiidae | *Anthomyia brasiliensis* (Albuquerque, 1949) | Brazil, São Paulo, São José dos Campos, H. S. Lopes, vii.1933, 1♂ (Holotype); xii.1934, 1♀ (Paratype) (MNRJ) | NT |
| Anthomyiidae | *Anthomyia bruchi* (Shannon & Del Ponte, 1926) **comb. nov.** | Brazil, Paraná, Curitiba, 28.v.1981, M. Britto, 1♂ and 1♀ (DZUP) | NT |
| Anthomyiidae | *Anthomyia crassinervis* (Albuquerque, 1959) | Brazil, Rio de Janeiro, 1.ii-8.iii.1957, D. Albuquerque, 1♂ (Holotype) (MNRJ); 1.xi.1937, 1♀ (Paratype) (MNRJ). | NT |
| Anthomyiidae | *Anthomyia illocata* Walker, 1856 | Brazil, Paraná, Rolândia, unknown date, R. C. Z. Carvalho, 1♂ (DZUP) | AU, NT*, NE, PA, OR |
| Anthomyiidae | *Anthomyia lindigii* Schiner, 1868 | Colombia, Boyaca, 31.viii-16.ix.2001, 2♂♂; 16.iv-2.v.2001, 1♀ (DZUP) | NT |
| Anthomyiidae | *Anthomyia ocullifera* Bigot, 1885 | Mexico, Veracruz, Apazapan, G. Quintero, 11.iii.1992, 1♂; 29.i.1992, 1♀ (IEXA) | NE, PA |
| Anthomyiidae | *Anthomyia paulistensis* (Albuquerque, 1952) **syn. nov.** | Brazil, São Paulo, J. Lam, xii.1930, 1♂ (Holotype) (MNRJ) | NT |
| Anthomyiidae | *Anthomyia plurinervis* (Albuquerque, 1958) | Brazil, Rio de Janeiro, Petrópolis, D. Albuquerque, 24.i-24.ii.1958, 1♂ (Holotype) (MNRJ); Paraná, Piraquara, 19.i.2000, C. J. B. de Carvalho, 1♀ (DZUP) | NT |
| Anthomyiidae | *Anthomyia pluripunctata* (Albuquerque, 1959) | Brazil, Santa Catarina, Nova Teutônia, v.1970, F. Plaumann, 1♂; viii.1967, 1♀ (MZUSP) | NT |
| Anthomyiidae | *Anthomyia procellaris* Rondani, 1866 | Great Britain, Oxon, Cothill, 25.vii.1992, C. Carvalho, 1♂ (DZUP) | NE, PA |
| Anthomyiidae | *Anthomyia punctipennis* Wiedemann, 1830 | Chile, Concepcion, Pinares, 9-13.xi.1970, T. Cekalovic, 1♂ (DZUP); Brazil, Paraná, 9-11.xi.2010, V. C. Silva, 1♀ (DZUP) | AF, AU, NT |
| Anthomyiidae | *Anthomyia xanthopyga* | Brazil, Paraná, Curitiba, 12.i.1984, M. | NT |

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|---|---|---|---|
| | (Albuquerque, 1959) | L. Pilloto & A. Carine, 1♂ (DZUP); 28-29.vi.1984, R. Zonta & M. Santos, 1♀ (DZUP) | |
| Anthomyiidae | *Boreophorbia hirtipes* (Stein, 1907) | Michelsen (1987) | NE, PA |
| Anthomyiidae | *Botanophila brunneillinea* (Zetterstedt, 1845) | Michelsen (2009) | PA |
| Anthomyiidae | *Botanophila collini* (Ackland, 1968) | Michelsen (2014) | PA |
| Anthomyiidae | *Botanophila fugax* (Meigen, 1826) | Lectotype images (MNHN); Great Britain, Norfolk, Hickling Broad, 24-25.viii.1992, C. Carvalho, 1♂; Oxon, Cothill, 25.vii.1992, C. Carvalho, 1♂ (DZUP) | PA |
| Anthomyiidae | *Botanophila hernandezi* Gomes & de Carvalho, 2021 | Mexico, Oaxaca, Concepción, G. Noguqiera, 9-10.vii.1997, 1♂ (IEXA) | MTZ |
| Anthomyiidae | *Botanophila subbruneilinea* (Ringdahl, 1934) | Michelsen (2009) | PA |
| Anthomyiidae | *Botanophila zaldivari* Gomes & de Carvalho, 2021 | Mexico, Tlaxcala, Nanacamilpa, Y. Marquez & A. Contreras, 01.viii-26.viii.2016, 1♂ (Holotype) (CNIN); 26.viii-4.x.2016, 1♀ (Paratype) (DZUP) | MTZ |
| Anthomyiidae | *Calythea comis* (Stein, 1911) | Chile, Valparaíso, x.1969, L. Peña, 2♂♂ and 2♀♀ (MZUSP) | NT |
| Anthomyiidae | *Calythea crenata* (Bigot, 1885) | Mexico, Tequesquinahuac, Cerro Tlaloc, 15.iv.1982, J. Butze, 1♂ and 1♀ (CNIN) | NE, NT |
| Anthomyiidae | *Calythea micropteryx* (Thomson, 1869) | United States, California, Kinb., 1♂ (Paralectotype) (NHRS); Mexico, Baja California, Golfo California, Isla Angel de la Guarda, 6.ii.1986, F. Árias, 1♀ (CNIN) | NE, NT |
| Anthomyiidae | *Chiastocheta trolli* (Zetterstedt, 1845) | Nartshuk et al. (2020) | PA |
| Anthomyiidae | *Chirosia histricina* (Rondani, 1866) | Suwa (1983) | PA |
| Anthomyiidae | *Chirosia inspinata* Suwa, 1983 | Suwa (1983) | PA |
| Anthomyiidae | *Chirosiomima gestroi* (Séguy, 1930) | Michelsen (2014) | AF, PA |
| Anthomyiidae | *Coenosopsia brasiliensis* Michelsen, 1991 | Brazil, Rio de Janeiro, Serviço Febre Amarela M. E. S. Bras., x.1938, 1♂ (Holotype) (MNRJ) and 1♀ (Paratype) (MNRJ) | NT |
| Anthomyiidae | *Coenosopsia ferrari* Nihei & Carvalho, 2004 | Brazil, Distrito Federal, 9.xii.1997, I. R. Diniz, 1♂ (Holotype) (DZUP) and 1♀ (Paratype) (DZUP) | NT |
| Anthomyiidae | *Coenosopsia michelseni* Nihei & Carvalho, 2004 | Brazil, Distrito Federal, 13.v.1997, I. R. Diniz, 1♂ (Holotype) (DZUP) and 1♀ (Paratype) (DZUP) | NT |
| Anthomyiidae | *Coenosopsia peruviana* Michelsen, 1991 | Brazil, Amazonas, Autaz-Mirim, 26.viii.1994, J. Vidal, 1♂ (INPA); Manaus, 09-16.iii.1989, Y. Camara & J. E. Binda, 1♀ (INPA) | NT |
| Anthomyiidae | *Coenosopsites poinari* Michelsen, 1996 | Michelsen (1996) | NT |
| Anthomyiidae | *Delia cilifera* (Malloch, | Mexico, Tlaxcala, La Malinche, | NE |

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|---|---|---|---|
| | 1918) | 10.vi.1984, E. Ramírez, 2♂♂ (CNIN) | |
| Anthomyiidae | *Delia clavata* Griffiths, 1993 | Mexico, Tlaxcala, La Malinche, 29.vii.1984, E. Ramírez, 2♂♂ (CNIN) | NT |
| Anthomyiidae | *Delia platura* (Meigen, 1826) | England, Oxford, Burguess Field Park, 23.viii.2003, S. S. Nihei, 2♂♂; Oxon, Henley, 18.vi.1992, C. Carvalho, 1♀ (DZUP) | AU, NE, NT, OR, PA |
| Anthomyiidae | *Delia radicum* (Linnaeus, 1758) | England, Oxford, Burguess Field Park, 14.ix.2003, 1♂ (DZUP) | NE, PA |
| Anthomyiidae | *Delia sanctijacobi* (Bigot, 1885) | Brazil, Paraná, Guarapuava, 03.ix.1986, Lev. PROFAUPAR, 2♂♂ and 2♀♀ (DZUP) | NT |
| Anthomyiidae | *Egle ciliata* (Walker, 1849) | http://www.spessart-fliegen.de/ | NE, PA |
| Anthomyiidae | *Egle concomitans* (Pandellé, 1900) | http://www.spessart-fliegen.de/ | NE, PA |
| Anthomyiidae | *Egle parva* Robineau-Desvoidy, 1830 | http://www.spessart-fliegen.de/ | PA |
| Anthomyiidae | *Emmesomyia grisea* (Robineau-Desvoidy, 1830) | Germany, Bavana, Schöngeising, vii.2010, W. Schacht, 1♂ (DZUP) | PA |
| Anthomyiidae | *Emmesomyia socia* (Fallén, 1825) | Griffiths (1984) | NE, PA |
| Anthomyiidae | *Emmesomyia spadibasis* Snyder, 1957 | Argentina, Tucuman, 21.xii.1950, R. Golbach, 1♂ (Holotype); 1♀ (Paratype) (IMLA) | NT |
| Anthomyiidae | *Emmesomyia spinulosa* Griffiths, 1984 | Mexico, Chiapas, 13-20.viii.2013, G. Melo, 2♂♂ and 2♀♀ (DZUP) | NE, NT |
| Anthomyiidae | *Enneastigma rufitibia* Michelsen, 1994 | Michelsen (1994) | PA |
| Anthomyiidae | *Enneastigma triseriatum* (Stein, 1900) | Michelsen (1994) | PA |
| Anthomyiidae | *Eustalomyia hilaris* (Fallén, 1823) | Hennig (1976) | PA |
| Anthomyiidae | *Eustalomyia vittipes* (Zetterstedt, 1845) | Great Britain, Oxon, Cothill, 25.vii.1992, C. Carvalho, 1♂ (DZUP) | NE, PA |
| Anthomyiidae | *Eutrichota praepotens* (Wiedemann, 1817) | Suwa (1974) | PA |
| Anthomyiidae | *Eutrichota processualis* Griffiths, 1984 | Mexico, Morelos, 18.iv.1982, C. B., 1♂ (CNIN); 8.xii.1978, 1♀ (CNIN) | NE |
| Anthomyiidae | *Fucellia apicalis* Kertész, 1908 | Suwa (1974) | AU, PA, OR |
| Anthomyiidae | *Fucellia tergina* (Zetterstedt, 1845) | Brazil, Rio de Janeiro, Angra dos Reis, H. S. Lopes, 23.vi.1972, 2♂♂; 27.vi.1972, 2♀♀ (DZUP) | AF, AU, NE, NT, PA |
| Anthomyiidae | *Heterostylodes obscurus* (Macquart, 1835) | http://www.spessart-fliegen.de/ | PA |
| Anthomyiidae | *Heterostylodes ricta* Ackland, 1971 | Ackland (1971) | PA |
| Anthomyiidae | *Hydrophoria ruralis* (Meigen, 1826) | England, Oxford, Brasenose Wood, 14.ix.2003, S. S. Nihei, 1♂ (DZUP) | NE, PA |
| Anthomyiidae | *Hydrophoria silvicola* (Robineau-Desvoidy, 1830) | http://www.spessart-fliegen.de/ | PA |
| Anthomyiidae | *Hylemya urbica* (Wulp, 1896) | Mexico, Tlaxcala, La Malinche, 21.x.1984, E. Ramírez, 1♂ (CNIN); 10.vi.1984, 1♀ (CNIN) | NE, PA |
| Anthomyiidae | *Hylemya vagans* | England, Oxford, Port Meadows, | PA |

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| | (Panzer, 1797) | 17.viii.2003, S. S. Nihei, 5♂♂; Burguess Field, 23.viii.2003, 5♀♀ (DZUP) | |
| Anthomyiidae | *Hylemyza partita* (Meigen, 1826) | Griffiths (2001) | NE, PA |
| Anthomyiidae | *Hyporites shakshain* Suwa, 1974 | Suwa (1974) | PA |
| Anthomyiidae | *Karliella sexpunctata* (Karl, 1935) | Michelsen (2013) | AF |
| Anthomyiidae | *Lasiomma anthomyinum* (Rondani 1866) | http://www.spessart-fliegen.de/ | PA |
| Anthomyiidae | *Lasiomma seminitidum* (Zetterstedt, 1845) | http://www.spessart-fliegen.de/ | PA |
| Anthomyiidae | *Leucophora apivora* (Aldrich, 1919) | Mexico, Veracruz, Miradores, 29.viii.1997, J. A. Gómez-Anaya, 1♂ (IEXA) | NE |
| Anthomyiidae | *Leucophora maculipennis* (Albuquerque, 1953) | Brazil, Paraná, São José dos Pinhais, 04.xi.1986, Lev. PROFAUPAR, 1♂; 31.x.1986, 1♀ (DZUP) | NT |
| Anthomyiidae | *Leucophora obtusa* (Zetterstedt, 1838) | http://www.spessart-fliegen.de/ | NE, PA |
| Anthomyiidae | *Leucophora* sp. 1 MEX long proboscis | Mexico, Morelos, Cañon de Lobos, 16.xi.1978, A. González, 1♂ (CNIN) | NT |
| Anthomyiidae | *Leucophora* sp. 2 MEX | Mexico, Veracruz, Miradores, 29.viii.1997, J. A. Gómez-Anaya, 1♂ (IEXA) | NT |
| Anthomyiidae | *Mycophaga testacea* (Gimmerthal, 1834) | http://www.spessart-fliegen.de/ | PA |
| Anthomyiidae | *Myopina myopina* (Fallén, 1824) | Hennig (1976); Griffiths (1986); Suwa (2013) | NE, PA |
| Anthomyiidae | *Myopinella angustifrons* (Malloch, 1934) | Chile, Magallanes, Laguna Parillar, 26.xi.2008, 1♂ (DZUP) | NT |
| Anthomyiidae | *Myopinella appendiculata* (Stein, 1904) | Peru, Cuzco, 28.i.2013, A. L. Norrbom, G. J. Steck & B. D. Sutton, 1♂ and 1♀ (USNM) | NT |
| Anthomyiidae | *Oxyphorbia dyscrita* Griffiths, 1996 | Fotos holotype (CNC); Griffiths (1996) | NE |
| Anthomyiidae | *Paradelia intersecta* (Meigen, 1826) | Michelsen (2007) | NE, PA |
| Anthomyiidae | *Paregle audacula* (Harris, 1780) | Griffiths (2001) | PA |
| Anthomyiidae | *Paregle popocatepetlensis* Griffiths, 2001 | Mexico, Mexico, Tequesquinahuac, 24.vi.1980, G. Sampedro, 1♂ (CNIN); J. Butze, 1♀ (DZUP) | NE |
| Anthomyiidae | *Paregle vetula* (Zetterstedt, 1838) | Griffiths (2001) | PA |
| Anthomyiidae | *Pegomya affinis* Stein, 1898 | United States, New York, Tompkins, Itahaca, 21.v.2007, K. Bayless, 1♂ (DZUP) | NE |
| Anthomyiidae | *Pegomya carrerai* Albuquerque, 1959 | Brazil, São Paulo, 16.x.1943, L. Travassos Filho, 1♂ (DZUP) | NT |
| Anthomyiidae | *Pegomya flavifrons* (Walker, 1849) | http://www.spessart-fliegen.de/ | NE, PA |
| Anthomyiidae | *Pegomya interruptella* (Zetterstedt, 1855) | http://www.spessart-fliegen.de/ | PA |
| Anthomyiidae | *Pegomya poeciloptera* Malloch, 1921 | Brazil, Rio Grande do Sul, Morro Redondo, 26.vii.2002, R. F. Krüger, 1♂ (DZUP); 09.v.2003, 1♀ (DZUP) | NT |
| Anthomyiidae | *Pegoplata aestiva* | http://www.spessart-fliegen.de/ | NE, PA |

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|---|---|---|---|
| | (Meigen, 1826) | | |
| Anthomyiidae | *Pegoplata infirma* (Meigen, 1826) | http://www.spessart-fliegen.de/ | NE, PA |
| Anthomyiidae | *Pegoplata patellans* (Pandellé, 1900) | https://www.discoverlife.org/ | NE, PA |
| Anthomyiidae | *Pegoplata* sp. 1 | Great Britain, Oxon, Henley, 18.vi.1992, C. Carvalho, 2♂♂ (DZUP) | PA |
| Anthomyiidae | *Phaonantho benevola* Couri, 1979 | Brazil, Mato Grosso, Sinop, x.1976, Alvarenga & Roppa, 1♂ (Holotype) (MNRJ); x.1975, 1♀ (Paratype) (MNRJ) | NT |
| Anthomyiidae | *Phaonantho mallochi* (Curran, 1934) | Brazil, Paraná, Jundiaí do Sul, 16.xi.1987, 1♂ (DZUP); 03.xi.1986, 1♀ (DZUP) | NT |
| Anthomyiidae | *Phaonantho sordilloae* Pamplona & Couri, 1993 | Brazil, Rio de Janeiro, xi.1988, C. M. O. Sordillo, 1♂ (Holotype) (MNRJ); 1♀ (Paratype) (MNRJ) | NT |
| Anthomyiidae | *Phorbia bartaki* Ackland & Michelsen, 1986 | http://www.spessart-fliegen.de/ | PA |
| Anthomyiidae | *Phorbia longipilis* (Pandellé, 1900) | http://www.spessart-fliegen.de/ | PA |
| Anthomyiidae | *Phorbia* sp. 1 | Great Britain, Norfolk, Hickling Broad, 24-25.viii.1992, C. Carvalho, 1♂ and 1♀ (DZUP) | PA |
| Anthomyiidae | *Phorbia* sp. 2 | Mexico, Tlaxcala, La Malinche, 10.vi.1984, E. Ramírez, 2♂♂ (CNIN) | NE |
| Anthomyiidae | *Phorbia* sp. 3 | Mexico, Tlaxcala, La Malinche, 10.vi.1984, E. Ramírez, 1♂ (CNIN) | NE |
| Anthomyiidae | *Protoanthomyia minuta* Michelsen, 2000 | Michelsen (2000) | NT |
| Anthomyiidae | *Ringdahlia curtigena* (Ringdahl, 1935) | Michelsen (2014) | PA |
| Anthomyiidae | *Strobilomyia laricicola* (Karl, 1928) | Michelsen (1988) | PA |
| Anthomyiidae | *Strobilomyia viaria* (Huckett, 1965) | Michelsen (1988) | NE |
| Anthomyiidae | *Subhylemyia dorsilinea* (Stein, 1920) | Griffiths (1998) | NE, PA |
| Anthomyiidae | *Subhylemyia longula* (Fallén, 1824) | Griffiths (1998) | NE, PA |
| Anthomyiidae | *Taeniomyia auricollis* Stein, 1918 | Brazil, Santa Catarina, Nova Teutônia, x.1967, F. Plaumann, 1♂ and 1♀ (MZUSP) | NT |
| Anthomyiidae | *Taeniomyia collaris* (Wulp, 1896) | Mexico, Veracruz, Teocelo, 12.viii.2004, V. Hernández, et. al., 1♂ (IEXA); 16.ii.2005, 1♀ (IEXA) | NE, NT |
| Anthomyiidae | *Taeniomyia sobria* (Albuquerque & Couri, 1981) | Brazil, Santa Catarina, Nova Teutônia, ii.1967, F. Plaumann (Paratype) (MNRJ); x.1967, 1♀ (MZUSP) | NT |
| Anthomyiidae | *Zaphne ambigua* (Fallén, 1823) | Griffiths (1998) | NE, PA |
| Anthomyiidae | *Zaphne caudata* (Zetterstedt, 1855) | http://www.spessart-fliegen.de/ | PA |
| Anthomyiidae | *Zaphne* sp. | Great Britain, Norfolk, Hickling Broad, 24-25.viii.1992, C. Carvalho, 1♂ (DZUP) | PA |
| Calliphoridae | *Cochliomyia macellaria* (Fabricius, 1775) | Brazil, Maranhão, Caxias, 06.iii.2006, J. O. A. Silva, 1♂ and 1♀ (DZUP) | NE, NT |
| Calliphoridae | *Lucilia eximia* (Wiedemann, 1819) | Brazil, Mato Grosso, Cáceres, 14.i.1985, C. Elias, 1♂ (DZUP); 24.xi.1984, 1♀ (DZUP) | NE, NT |

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|---|---|---|---|
| Mesembrinellidae | *Mesembrinella bellardiana* Aldrich, 1922 | Brazil, Rio de Janeiro, Comendador Levy, 30.x.2010, C. M. Maia & L. M. Santos, 1♂ and 1♀ (DZUP) | NT |
| Mesembrinellidae | *Mesembrinella quadrilineata* (Fabricius, 1805) | Brazil, Rondônia, 29.ix.1986, C. Elias, 1♂ and 1♀ (DZUP) | NT |
| Rhinophoridae | *Melanophora roralis* (Linnaeus, 1758) | http://www.spessart-fliegen.de/ | NE, NT, PA |
| Sarcophagidae | *Oxysarcodexia thornax* (Walker, 1849) | Souza et al. (2020) | NT |
| Sarcophagidae | *Ravinia belforti* (Prado & Fonseca, 1932) | 1♂ and 1♀ (DZUP) | NT |
| Sarcophagidae | *Sarcophaga crassipalpis* Macquart, 1839 | Bonacci et al. (2014) | AF, AU, NE, NT, OR, PA |
| Scathophagidae | *Cordilura albiceps* Fallen, 1819 | http://www.spessart-fliegen.de/ | PA |
| Scathophagidae | *Cordilura ciliata* (Meigen, 1826) | http://www.spessart-fliegen.de/ | PA |
| Scathophagidae | *Cordilura picipes* (Meigen, 1826) | http://www.spessart-fliegen.de/ | PA |
| Scathophagidae | *Nanna tibiella* (Zetterstedt, 1838) | Ozerov & Krivosheina (2015) | PA |
| Scathophagidae | *Scathophaga furcata* (Say, 1823) | http://www.spessart-fliegen.de/ | NE, PA |
| Scathophagidae | *Scathophaga stercoraria* (Linnaeus, 1758) | England, Oxford, 20.xii.1984, C. Elias, 1♂ and 1♀ (DZUP) | NE, NT, OR, PA |
| Tachinidae | *Patelloa similis* (Townsend, 1927) | Brazil, Paraná, Curitiba, xii.1986, M. Cruz, 1♂ and 1♀ (DZUP) | NT |
| Tachinidae | *Winthemia brasiliensis* (Townsend, 1927) | Brazil, Santa Catarina, Nova Teutônia, i.1965, F. Plaumann, 1♂ and 1♀ (DZUP) | NT |

# CAPÍTULO III

TAXONOMY, PHYLOGENY AND BIOGEOGRAPHY OF THE ABERRANT GENUS *Coenosopsia* Malloch (DIPTERA: ANTHOMYIIDAE)

***Artigo no formato da Invertebrates Systematics***

(Esse capítulo segue a recomendação da revista de indicar fêmeas com "@" e machos com "#")

# Taxonomy, Phylogeny and Biogeography of the aberrant genus *Coenosopsia* Malloch (Diptera: Anthomyiidae)

**Running title: Phylogeny and Biogeography of *Coenosopsia***

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**Summary:** *Coenosopsia* is a genus with eight described species, of which the main diagnostic characteristics of Anthomyiidae are absent. Some studies proposed biogeographical narratives to explain the mainly Neotropical distribution of the genus. Here, we describe three new species of *Coenosopsia*, update the distributional knowledge of all species of the genus, present a phylogenetic analysis based on morphological evidence, and present a biogeographical hypothesis based on ancestral reconstruction character and S-DIVA analyses.

ABSTRACT

*Coenosopsia* Malloch (Diptera, Anthomyiidae) has eight known species distributed from southern North America to southeastern South America. The species of the genus are morphologically very homogeneous, and the major differences remain in male terminalia. Remarkably, two of the main diagnostics characteristics of Anthomyiidae are absent in this genus: the setulae on the ventral surface of the scutellum and the vein $A_1$ reaching the wing margin. The genus has been indicated as closely related to the Neotropical genus *Phaonantho* Albuquerque, based on both morphological and molecular data. Some studies attempted to propose biogeographical narratives for the mainly Neotropical distribution of the genus. Herein, we describe three new species of *Coenosopsia* from northeastern Brazil, southern Brazil and central Mexico; and present an identification key. Also, we present a phylogenetic analysis based on morphological evidence and discuss its distribution based on ancestral reconstruction character and S-DIVA analyses. We recovered *Coenosopsia* as monophyletic and the sister group of *Phaonantho*, and

updated the previous biogeographical hypothesis, indicating a Mesoamerican origin of the genus with posterior dispersion to South America.

**Keywords:** ancestral distribution, biodiversity, morphology, Neotropical region.

## INTRODUCTION

*Coenosopsia* Malloch is a genus with eight described species, distributed from southern North America to southeastern South America (Bortolanza et al. 2006), occurring in the warm lowland forests, an unusual distribution for the family (Michelsen 1996). The species of the genus are morphologically very constant and homogeneous, there is very little sexual dimorphism in the external morphology and the major differences among the species remain on male terminalia (Nihei and de Carvalho 2004). Additionally, some of the main diagnostic characteristics of Anthomyiidae, as the presence of setulae on the ventral surface of the scutellum and the vein $A_1$ reaching the wing margin, are not observed in *Coenosopsia* (Michelsen 2010), which led to an original attribution to Muscidae (Michelsen 1996). There are a series of studies on *Coenosopsia*, including revisions (Michelsen 1991; Nihei and de Carvalho 2004) and phylogenetic and biogeographical hypotheses (Nihei and de Carvalho 2004; Bortolanza et al. 2006).

Remarkably, *Coenosopsia* has no obvious characteristics that could indicate a close affinity to other anthomyiids (Michelsen 1991; Nihei and de Carvalho 2004), but the genus has been indicated as the sister group of the Neotropical genus *Phaonantho* Albuquerque based on morphological (Michelsen 1991) and molecular evidence (Gomes et al. 2021). The origin of the clade *Coenosopsia* + *Phaonantho* was dated to the Oligocene/Miocene boundary (c. 23 Ma), and the diversification of the *Coenosopsia* species occurred in the Miocene (c. 16 Ma) (Gomes et al. 2021). Previously, Michelsen (1991) indicated the clade *Coenosopsia* + *Phaonantho* as the sister group of remaining Anthomyiidae, but this hypothesis was not corroborated in the lastest studies based on morphological (Nihei and de Carvalho 2004; Bortolanza et al. 2006) and molecular data (Gomes et al. 2021).

Here we describe three new species from northeastern Brazil, southern Brazil and central Mexico, and present an updated identification key. We performed a phylogenetic analysis of the genus based on morphological evidence and proposed a biogeographical hypothesis of *Coenosopsia* based on ancestral reconstruction character and S-DIVA analyses.

## MATERIAL AND METHODS

### Taxonomy

The material studied is deposited in the following institutions: Canadian National Collection of Insects, Ottawa, Canada (CNC); Colección Nacional de Insectos, Ciudad de Mexico, Mexico (CNIN); Coleção Zoológica do Maranhão, Caxias, Brazil (CZMA); Departamento de Zoologia, Universidade de Brasília, Brasília, Brazil (DBAI); Padre Jesus Santiago Moure Entomological Collection, Curitiba, Brazil (DZUP); Colección Entomológica del Instituto de Ecología, Xalapa, Mexico (IEXA); Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica (INBio); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); National Museum of Natural History, Washington, USA (USNM); Maurice T. James Entomological Collection, Pullman, USA (WSU).

For examination of the male and female terminalia, the abdomen was removed from a dry specimen and was placed in cold potassium hydroxide (KOH) 10% for 24h to soften and lighten the parts. The abdomen was transferred to acetic acid, and then to glycerin. The postabdomen structures were separated from the rest of the abdomen. Examination and illustration of the structures were done using a microscope and a stereomicroscope with a camera lucida attached to it. Dissected terminalia were placed in glycerin, inside microvials pinned beneath the respective specimens. The morphological terminology followed Cumming and Wood (2017).

### Images

Photographs of the habitus of the adult from the new species were obtained with sequential images mounted at different focal planes with a NIKON D610 digital camera coupled to a LEICA M165 C stereomicroscope. The images were stacked and edited using Adobe Photoshop CS6. Terminalia drawings were digitally inked using Adobe Illustrator CS6. The distribution map was produced using the software QGIS (available in: http://www.qgis.org/en/site/), with the shapefile of Löwenberg-Neto (2014) based on the biogeographical regionalization proposed by Morrone (2014). The literature distribution is based on Michelsen (1991), Nihei and de Carvalho (2004), Bortolanza et al. (2006) and Gomes et al. (2019).

### Phylogeny

The matrix is composed of 42 morphological characters, 18 of them adapted from Nihei and de Carvalho (2004), five adapted from Couri and Pont (2000), one character from Bortolanza et al. (2006) and 18 new characters (Table 1). The outgroup follows the current molecular analysis (Gomes et al. 2021), with a Scathophagidae rooting the tree and including 10 species of other Anthomyiidae genera aiming to have a wide sampling of the morphological diversity of the family (Table S1). The ingroup includes all the eight known species of *Coenosopsia* and the three new species described herein. We examined specimens of all species of *Coenosopsia*, including type material of five species (see below). We did not include the fossil species which resemble *Coenosopsia* (Michelsen 1996) due to the absence of male terminalia characters, crucial information to our analyses.

The characters were coded as binary, multistate or contingent and treated as unorded and non-additive. The description of the characters and their states follows the structural concepts proposed by Sereno (2007). In the results, the characters are followed by, between brackets, the character number and the state number of each character indicated in text. The phylogenetic hypothesis was constructed using parsimony. The data matrix (Table S2) was produced in Mesquite 3.6 (Maddison and Maddison 2018) and the parsimony analyses were performed in TNT 1.5 (Goloboff & Catalano 2016) through traditional search with 1,000 replications, 100 random-addition replicates and saving 100 trees per replication. The optimization of the characters was made in the software Winclada 1.61 (Nixon 2002) through fast optimization. The implied weighting was carried out using $k$ (constant of concavity) from one to 60 (Table S3). The topology produced by parsimony analyses using implied weighting with $6 \leq k \leq 60$ (Fig. 1) was chosen considering it resulted in one most parsimonious tree with 117 steps. The branch supports were also obtained in TNT. Bootstrap values were calculated from an independent analysis using 1,000 pseudoreplicates and Relative Bremer support was calculated with stored suboptimal trees with length up to 10 additional steps.

### Ancestral distribution

The ancestral distribution was inferred using parsimony ancestral state reconstruction performed in Mesquite 3.6 (Maddison and Maddison 2018). Also, the ancestral areas were estimated by S-DIVA (Statistical Dispersal-Vicariance Analysis)

(Yan et al. 2010), implemented in software RASP 4.2 (Reconstruct Ancestral State in Phylogenies) (Yu et al. 2020), using default. Both analyses are based on the topology obtained in the phylogenetic analysis. The areas implemented in the analyses are based on the dominions following the biogeographical regionalization proposed by Morrone (2014).

## RESULTS

### Taxonomy

#### Genus ***Coenosopsia*** Malloch

Type-species: *Coenosopsia prima* Malloch, 1924

**Diagnosis.** Both male and female dichoptic (Fig. 2*A*, 3*A*, *E*, 4*A*, *D*). Frons dark brown on upper half and orange-yellow on lower half. Ocellar triangle dark brown with silver pruinosity. Gena light brown with silver pruinosity. Proboscis and antennae brown. Antenna plumose. Palpus slightly spatulate on the apical half. Frons with one pair of interfrontal setae and 3 pairs of fronto-orbital setae (the lower most proclinate and other two reclinate). 3–4 pairs of frontal setae (two strong pairs, the lower one longer). Thorax dark brown with silver pruinosity. Calypters and halter whitish. Abdomen yellowish with brown maculae. Dorsocentral setae 2+3. Many short acrostichal setae, the prescutellar pair stronger. Prealar seta shorter than the posterior notopleural seta. Scutellum with some setulae laterally near the apex and bare ventrally. Prosternum bare, enlarged anteriorly. Katepisternal setae 1+2, the lower posterior seta shorter, and sometimes an additional lower anterior seta weaker than the lower posterior one. Tergites with marginal setae developed, the lateral ones longer. Sternite 1 setulose. Wing hyaline with brown veins, without spots (Fig. 2*C*, 3*G*, 4*C*, *F*). Veins bare, except for the presence of microtrichia, also present on the wing membrane. Vein A1 markedly short, not reaching the wing margin. Fore tibia with a submedian seta on posterior surface. Mid femur with a long median seta on anterior to anteroventral surface. Mid tibia with a long median seta on posterior surface; a short seta on apical third of posterodorsal to dorsal surface. Hind tibia with a seta inserted at the limit of the apical third of posterodorsal surface, as long as tibia width. Fore and hind basitarsus with a conspicuous ventrobasal seta. Male terminalia with asymmetrical surstyli (Fig. 5*B*, *G*, *L*); presence of a proximal projection on surstyli (Fig. 5*C*, *H*, *M*); two setae on pregonite (Fig. 5*E*, *J*, *O*). Female terminalia with tergites 6 and 7 weakly sclerotized longitudinally at median line; spiracles 6 and 7

conspicuous and both present on tergite 6; epiproct C-shaped; hypoproct subtriangular, twice longer than wide; cerci long and slender, twice longer than cerci length; three rounded spermathecae.

**Key to species of *Coenosopsia* Malloch (modified from Bortolanza *et al*. 2006)**

**1** Palpi entirely yellow … **2**

**-** Palpi entirely brown or brown with yellow apex … **4**

**2** Femora and tibiae completely brown (Fig. 3*D*, *G*) … *Coenosopsia limeirai* **sp. nov.**

**-** Femora and tibiae brown with yellow areas basally (Fig. 2*C*) … **3**

**3** All femora yellow on basal fifth (fore femur) to half (hind femur) (Mexico) … *C. mexicana* Michelsen, 1991

**-** Anterior femur completely brown; Mid femur with ⅕ basal yellow; Hind femur with ⅓ basal yellow (Fig. 2*C*) … *Coenosopsia azteca* **sp. nov.**

**4** Palpi entirely brown; pregonite setulose distally (Fig. 5*O*) … **5**

**-** Palpi brown with yellow apex [except in *C. prima*, which is entirely brown]; pregonite bare distally (Fig. 5*E*, *J*) … **7**

**5** Hind femur brown, lighter at base; abdomen dark brown; left surstylus distally narrower than the right one (see Bortolanza et al. 2006: Fig. 2); postgonite shorter than epiphallus (see Bortolanza et al. 2006: Fig. 11) (Brazil) … *C. albuquerquei* Bortolanza & de Carvalho 2006

**-** Hind femur brown; abdomen brown with yellow tergites 1+2; both surstyli with similar width distally (Fig. 5*L*); postgonite with almost the same length than epiphallus (Fig. 5*O*) … **6**

**6** Surstyli and cerci slightly curved (Fig. 5*M*, *N*) … *Coenosopsia ribeiroi* **sp. nov.**

**-** Surstyli and cerci strongly curved (see Nihei and de Carvalho 2004: Fig. 1B, C) (Brazil) … *C. ferrari* Nihei & de Carvalho, 2004

**7** Medial lobe of cerci with sub-parallel margins on dorsal view (Fig. 5*L*); left surstylus strongly curved on dorsal view (see Nihei and de Carvalho 2004: Fig. 1D) (Brazil) … *C. michelseni* Nihei & de Carvalho, 2004

**-** Medial lobe of cerci with margins converging from the base to a point on dorsal view (Fig. 5*B*); left surstylus not strongly curved on dorsal view (Fig. 5*C*, *H*, *M*) … **8**

**8** Palpi brown or brown with yellow apex; Proximal projection of surstyli exceeding the epandrium margin (Fig. 5*C*); Medial lobe of cerci with margins converging from the base gradually to a point on dorsal view (Fig. 5*B*) … **9**

**-** Palpi brown with yellow apex; Proximal projection of surstyli not exceeding the epandrium margin (Fig. 5*H*, *M*); Medial lobe of cerci with margins converging from the base abruptly to a point on dorsal view (see Michelsen 1991: Fig. 19, 20) … **10**

**9** Palpi brown; Cerci apex rounded (Fig. 5*L*); Right surstylus straight on lateral view (see Michelsen 1991: Fig. 24); Cerci long and enlarged, with apex as wide as surstyli apex (see Michelsen 1991: Fig. 19) (Belize, Costa Rica, Panama, Ecuador) … *C. prima* Malloch, 1924

**-** Palpi brown with yellow apex; Cerci apex narrow and sharped (see Michelsen 1991: Fig. 23); right surstylus strongly curved on lateral view (see Michelsen 1991: Fig. 28); cerci long and narrow, with apex narrower than surstyli apex (see Michelsen 1991: Fig. 23) (U.S.A., Mexico) … *C. floridensis* Michelsen, 1991

**10** Right surstylus enlarged proximally on lateral view, larger than on distal region (see Michelsen 1991: Fig. 26); Pregonite similar to postgonite length (Fig. 5*O*) (Brazil, Paraguay) … *C. brasiliensis* Michelsen, 1991

**-** Right surstylus narrowed proximally on lateral view, narrower than on distal region (see Michelsen 1991: Fig. 25); Pregonite longer than postgonite (Fig. 5*J*) (Peru, Brazil) … *C. peruviana* Michelsen, 1991

***Coenosopsia albuquerquei*** Bortolanza & de Carvalho

(Fig. 6*D*)

**Diagnosis.** Palpi brown. Legs brown, hind femur brown with basal fifth light brown. Male terminalia: Cerci triangular, as long as surstyli and narrow dorsally; apex narrow. Surstyli width with about ¼ of the epandrium width laterally; surstyli slightly curved laterally. Proximal projection of surstyli reaching epandrium margin. Pregonite longer than postgonite. Pregonite setulose distally. Phalapodema straight. This is the unique species with left surstylus conspicuously narrower than the right.

**Type-material examined.** Holotype. Male. Brazil. Paraná. Telêmaco Borba, Reserva Biológica Samuel Klabin [-24.297941, -50.618785], Malaise trap, Lev. Ent. PROFAUPAR, 25.vii.1988 (DZUP 245560). Paratypes 13##. Same data as holotype: 5## (DZUP 099282-86). Same data as holotype, except: 18.vii.1988, 2## (DZUP 099287-88); 11.vii.1988, 1# (DZUP 099289); 04.vii.1988, 1# (DZUP 099290); 31.viii.1987, 1# (DZUP 099291); Paraná, Ponta Grossa, Vila Velha (IAPAR) [-25.244012, -50.011530], Malaise trap, Ganho & Marinoni, 29.v.2000, 1# (DZUP 099292); same label information, except: 05.vi.2000, 2## (DZUP 099293-94).

**Material examined.** Brazil. Paraná. Guarapuava, Est. Águas Sta. Clara [-25.632814, -51.964977], Malaise trap, Lev. Ent. PROFAUPAR, 04.viii.1986, 1@ (DZUP 099396); same label information, except: 18.viii.1986, 1@ (DZUP 099397); 25.viii.1986, 1@ (DZUP 099398); Ponta Grossa, Vila Velha (IAPAR) [-25.244012, -50.011530], Malaise trap, Ganho & Marinoni, 08.xi.1999, 1@ (DZUP 099404); same label information, except: Lev. Ent. PROFAUPAR, 04.viii.1986, 1@ (DZUP 099399); 05.vi.2000, 2@@ (DZUP 099400-01); 04.x.1999, 1@ (DZUP 099402); 22.v.2000, 1@ (DZUP 099403); 17.vii.2000, 1@ (DZUP 099404); 29.v.2000, 1@ (DZUP); Telêmaco Borba, Reserva Biológica Samuel Klabin [-24.297941, -50.618785], Malaise trap, Lev. Ent. PROFAUPAR, 24.viii.1987, 7@@ (DZUP 099323-29); same label information, except: 07.ix.1987, 4@@ (DZUP 099330-33); 19.x.1987, 1@ (DZUP 099334); 11.vii.1988, 7@@ (DZUP 099335-41); 03.viii.1987, 6@@ (DZUP 099342-47); 17.viii.1987, 2@@ (DZUP 099348-49); 23.v.1988, 1@ (DZUP 099350); 07.ix.1987, 11@@ (DZUP 099351-61); 25.vii.1988, 20@@ (DZUP 099362-81); 31.viii.1987, 10@@ (DZUP 099382-91); 14.ix.1987, 3@@ (DZUP 099392-94); 18.vii.1988, 4@@ (DZUP 099395-98); 05.x.1987, 1@ (DZUP 099299); 18.vii.1988, 1@ (DZUP 099300); 24.viii.1987, 1@ (DZUP 099301); 05.x.1987, 2@@ (DZUP 099302-03); 07.ix.1987, 1@ (DZUP 099304); 19.x.1987, 1@ (DZUP 099305);

24.viii.1987, 2@@ (DZUP 099306-07); 07.ix.1987, 1@ (DZUP 099308); 24.viii.1987, 14@@ (DZUP 099309-22); 30.xi.1987, 1@ (DZUP 462917); 17.viii.1987, 3@@ (DZUP 462918-20); 27.vi.1988, 1@ (DZUP 462921); 17.viii.1987, 1@ (DZUP 462922); 30.v.1988, 1@ (DZUP 462923); 17.viii.1987, 2@@ (DZUP 462924-25); 27.vi.1988, 2@@ (DZUP 462926-27); 17.viii.1987, 1@ (DZUP 462928); 30.v.1988, 2@@ (DZUP 462929-30); 21.ix.1987, 2@@ (DZUP 462931-32); 31.viii.1987, 1@ (DZUP 462933); 30.v.1988, 1@ (DZUP 462934); 30.xi.1987, 1@ (DZUP 462935); 04.viii.1988, 1@ (DZUP 462936); 17.viii.1987, 1@ (DZUP 462937); 04.vii.1988, 1@ (DZUP 462938); 26.x.1987, 1@ (DZUP 462939); 20.vi.1988, 2@@ (DZUP 462940-41); 30.xi.1987, 1@ (DZUP 462942); 21.ix.1987, 1@ (DZUP 462943). Rio Grande do Sul. Arroio Grande, Distrito Mauá [-32.233483, -53.086682], Malaise trap, P. B. Ribeiro, 20.ix.2002, 1# (DZUP 099407); Morro Redondo, Santo Amor [-31.588260, -52.621141], R. F. Krüger, 23.viii.2002, 1# (DZUP 099414).

**Distribution.** Brazil (Paraná, Rio Grande do Sul)

**Remarks.** New record for Brazil (Rio Grande do Sul).

***Coenosopsia azteca****,* sp. nov.

(Fig. 2, 5*A*–*E*, 6*B*)

**Diagnosis.** Palpi yellow. Legs brown, mid femur brown with the basal fifth yellow, hind femur brown with basal third yellow, tibiae brown with basal half light brown (Fig. 2*C*). Male terminalia: Cerci triangular, shorter than surstyli and narrow dorsally; apex narrow (Fig. 5*B*). Surstyli width with about half of the epandrium width laterally (Fig. 5*C*); surstyli straight laterally. Proximal projection of surstyli exceeding epandrium (Fig. 5*C*). Pregonite longer than postgonite (Fig. 5*E*). Pregonite bare distally. Phalapodema straight. This species is very similar to *C. mexicana*, but can be distinguished by the right surstylus straight (Fig. 5*D*).

**Description.** Male. Body length: 3.0–3.5 mm. Wing length: 2.8–3.3 mm. Head: Postocellar setae divergent; inner vertical setae convergent and strong, twice longer than ocellar setae; outer vertical setae divergent, similar length to ocellar setae. Legs: Fore femur with a complete row of long setae on posterodorsal and posteroventral surfaces. Fore tibia with an apical seta on anterodorsal, dorsal and posteroventral surfaces. Midfemur with a row of short setae on anterodorsal, posteroventral (in both surfaces, setae longer on basal half) and anteroventral; an apical seta on anterodorsal; and 2 apical oblique setae on posterodorsal to posterior

surface. Midtibia with a median posterior seta; a submedian posterodorsal setae; and apical seta on anterodorsal, posterodorsal, posteroventral, ventral and anteroventral surfaces, the posteroventral and ventral twice longer than others. Hind femur with a row of fine and short setae on posteroventral surface; a row of long setae on apical half of anteroventral surface; a row of long setae on anterior to anterodorsal surfaces; an apical seta on anterodorsal, dorsal, posterodorsal to posterior, and posteroventral surfaces. Hind tibia with a submedian posterodorsal seta; 2 median anterodorsal; a submedian anteroventral; and preapical setae on anterodorsal, dorsal and ventral. Terminalia (Fig. 5*A*–*E*): Epandrium, in lateral view, with a set of setulae at lower anterior portion. Cerci with downwardly oriented median lobe narrow distally (Fig. 5*B*). Surstyli elongate, right surstylus narrower than the left one and slightly curved distally (Fig. 5*C*, *D*). Pregonite bare distally (Fig. 5*E*). Postgonite shorter than epiphallus (Fig. 5*E*). Phalapodema enlarged distally (Fig. 5*E*).

**Female.** Unknown.

**Etymology.** Name in apposition. The specific epithet, *azteca*, is in honor of the civilization which inhabited central Mexico and was destroyed after European occupation.

**Material examined.** Holotype. Male. Mexico. Morelos Km 58, Carretera Xochimilco Oaxtepec, 8. xii.1978, J. Butze (CNIN). Paratype. Mexico. Tequesquinahuac, C. Tlaloc, 16.iv.1982, A. Ibarra, 1# (CNIN).

**Distribution.** Mexico (Estado de Mexico, Morelos).

**Remarks.** This species is only known for the highlands of Mexican Transition Zone and in the Neotropical region, in the border between this region and the Mexican Transition Zone.

### ***Coenosopsia brasiliensis*** Michelsen

(Fig. 6*C*)

**Diagnosis.** Palpi brown with yellow apex. Legs brown. Male terminalia: Cerci triangular, shorter than surstyli and narrow dorsally; apex narrow. Surstyli width with about half of the epandrium width laterally; surstyli straight laterally. Proximal projection of surstyli reaching epandrium margin. Pregonite similar to postgonite length. Pregonite bare distally. Phalapodema curved. This is the unique species with left surstylus straight and thicker than the right one.

**Type-material examined.** Holotype. Male. Brazil. Rio de Janeiro. Serviço Febre Amarela M. E. S. Bras., x.1938 (MNRJ); Paratype. same as holotype: 1@ (MNRJ).
**Material examined.** Brazil. Bahia. Encruzilhada [-15.540277, -40.836666], 800m, Malaise trap, J. A. Rafael, P. C. Grossi & D. R. Parizotto, 10-12.xii.2007, 5## (INPA). Mato Grosso do Sul. Fazenda Guaiacurus Miranda [-20.109187, -56.651399], Koller, W. W., xii.2002, 2@@ (DZUP 099523; 099525); same label information, except: i.2003, 1@ (DZUP 099524). Mato Grosso. Cáceres [-16.084034, -57.675011], C. Elias, 17.xii.1984, 1@ (DZUP); Paraná. Antonina, Reserva Biol. Sapitanduva [-25.439498, -48.746125], Malaise trap, Lev. Ent. PROFAUPAR, 03.viii.1987, 1@ (DZUP 099518); same label information, except: 03.xi.1986, 1@ (DZUP 099519); 21.ix.1987, 1@ (DZUP); 16.v.1988, 1@ (DZUP 099444); Colombo, EMBRAPA, Br476, Km20 [-25.321620, -49.159959], Malaise trap, Lev. Ent. PROFAUPAR, 04.viii.1986, 1@ (DZUP 099521); same label information, except: 19.i.1987, 1@ (DZUP 099522); 03.xi.1986, 1# (DZUP 099531); 10.xi.1986, 1@ (DZUP 099437); 08.ix.1986, 1@ (DZUP 099438); 01.vi.1987, 1@ (DZUP 099439); Fênix, Reserva, Est. Vila Rica [-23.912610, -51.959757], Malaise trap, Lev. Ent. PROFAUPAR, 04.iv.1988, 1# (DZUP 099454); same label information, except: 21.iii.1988, 1# (DZUP 099455); 25.iv.1988, 2## (DZUP 099459-60); 02.v.1988, 1# (DZUP 099461); 18.iv.1988, 1# (DZUP 099462); 21.ix.1987, 2## (DZUP 099463-64); 06.vi.1988, 1# (DZUP 099465); 04.iv.1988, 1# (DZUP 099466); 17.xi.1986, 1# (DZUP 099467); 17.xi.1986, 1# (DZUP); 06.x.1986, 1@ (DZUP); 21.iii.1988, 1@ (DZUP 099515); 16.v.1988, 1@ (DZUP 099516); 01.ix.1986, 1@ (DZUP 099517); 28.iii.1988, 1# (DZUP 099548); 10.viii.1987, 1@ (DZUP 099431); 21.iii.1988, 1@ (DZUP 099432); 06.vi.1988, 1@ (DZUP 099433); Guarapuava, Est. Águas Sta. Clara [-25.632814, -51.964977], Malaise trap, Lev. Ent. PROFAUPAR, 24.xi.1986, 1@ (DZUP 099505); same label information, except: 10.xi.1986, 2@@ (DZUP); 27.vii.1987, 1@ (DZUP 099520); Jundiaí do Sul, Fazenda Monte Verde [-23.423531, -50.281910], Malaise trap, Lev. Ent. PROFAUPAR, 14.ix.1987, 1# (DZUP 099445); same label information, except: 09.xi.1987, 1# (DZUP 099446); 07.ix.1987, 1# (DZUP 099447); 11.iv.1988, 1# (DZUP 099448); 15.viii.1988, 1# (DZUP 099449); 14.ix.1987, 1# (DZUP 099473); 03.viii.1987, 1# (DZUP 099474); 14.ix.1987, 1# (DZUP 099475); 28.ix.1987, 1# (DZUP 099476); 10.viii.1987, 1# (DZUP 099477); 23.xi.1987, 2## (DZUP 099478-79); 24.viii.1987, 1@ (DZUP 099512); 02.xi.1987, 1@ (DZUP 099513); 09.xi.1987, 1@ (DZUP 099514); 19.x.1987, 1# (DZUP 099526); 07.ix.1987, 1# (DZUP 099527);

15.viii.1988, 1# (DZUP 099528) 2@@ (DZUP 099434-35); 07.ix.1987, 1# (DZUP 099529); 21.ix.1987, 1# (DZUP 099530); 16.xi.1987, 1@ (DZUP 099436); Telêmaco Borba, Reserva Biológica Samuel Klabin [-24.297941, -50.618785], Malaise trap, Lev. Ent. PROFAUPAR, 26.x.1987, 1# (DZUP 099450); same label information, except: 12.x.1987, 1# (DZUP 099451); 31.viii.1987, 1# (DZUP 099452); 26.x.1987, 1# (DZUP 099453); 02.xi.1987, 1# (DZUP 099468); same label information, except: 14.ix.1987, 1# (DZUP 099469); 30.xi.1987, 1# (DZUP 099470); 17.viii.1987, 1# (DZUP 099471); 25.i.1988, 1# (DZUP 099472); 11.vii.1988, 1@ (DZUP 099480); 04.vii.1988, 1@ (DZUP 099481); 20.vi.1988, 1@ (DZUP 099482); 16.v.1988, 1@ (DZUP 099483); 23.v.1988, 2@@ (DZUP 099484-85); 12.x.1987, 1@ (DZUP 099486); 04.vii.1988, 1@ (DZUP 099487); 31.viii.1987, 1@ (DZUP 099488); 07.iii.1988, 1@ (DZUP 099489); 09.v.1988, 1@ (DZUP 099490); 19.x.1987, 1@ (DZUP 099491); 26.x.1987, 1@ (DZUP 099492); 05.x.1987, 4@@ (DZUP 099493-96); 17.viii.1987, 1@ (DZUP 099497); 21.ix.1987, 1@ (DZUP 099498); 28.ix.1987, 1@ (DZUP 099499); 25.vii.1988, 1@ (DZUP 099500); 02.xi.1987, 1@ (DZUP 099501); 31.viii.1987, 1@ (DZUP 099502); 27.vii.1987, 1@ (DZUP 099504); 20.vi.1988, 1@ (DZUP 099507); 14.ix.1987, 1@ (DZUP 099508); 04.vii.1988, 1@ (DZUP 099509); 21.ix.1987, 3## (DZUP 099532-34); 14.ix.1987, 1# (DZUP 099535); 21.ix.1987, 1# (DZUP 099536); 25.vii.1988, 1# (DZUP 099537); 09.xi.1987, 1# (DZUP 099538); 05.x.1987, 1# (DZUP 099539); 02.xi.1987, 2## (DZUP 099540-41); 31.viii.1987, 1# (DZUP 099542); 19.x.1987, 1# (DZUP 099543); 31.viii.1987, 2## (DZUP 099544-45); 05.x.1987, 1# (DZUP 099546); 11.vii.1988, 1# (DZUP 099547); 19.x.1987, 1# (DZUP); 19.x.1987, 3@@ (DZUP 099420-22); 31.viii.1987, 2@@ (DZUP 099423-24); 17.viii.1987, 1@ (DZUP 099425); 02.xi.1987, 1# (DZUP 099427); 05.x.1987, 1@ (DZUP 099428); 12.x.1987, 1@ (DZUP 099429); 28.ix.1987, 1# (DZUP 099430); Palmas, Refúgio de Vida Silvestre dos Campos de Palmas [-26.533232, -51.599463], 1115m, Malaise trap, Adriana C. Pereira, 20.xi.2014, 1# (DZUP); same label information, except: 7.ii.2014, 1# (DZUP); 23.i.2014, 1# (DZUP); 16.i.2014, 1# (DZUP); Ponta Grossa, Vila Velha (IAPAR) [-25.244012, -50.011530], Malaise trap, Lev. Ent. PROFAUPAR, 02.ii.1987, 1# (DZUP 099456); same label information, except: 05.vi.2000, 1# (DZUP 099457); 17.xi.1986, 1# (DZUP 099458); Ganho & Marinoni, 22.v.2000, 1# (DZUP); Ganho & Marinoni, 12.v.2000, 1# (DZUP); 29.xii.1986, 1@ (DZUP 099503); 12.i.1987, 1@ (DZUP 099506); Ganho & Marinoni, 27.iii.2000, 1@ (DZUP 099510); 28.viii.2000, 1@

(DZUP 099511); 04.viii.1986, 1@ (DZUP 099440); 27.vii.1987, 1@ (DZUP 099441); 06.vii.1987, 1@ (DZUP 099442); 16.ii.1987, 1@ (DZUP 099443). Rio Grande do Sul. Arroio Grande, distrito de Mauá [-32.233483, -53.086682], Malaise trap, P. B. Ribeiro, 17.i.2003, 2## (DZUP 099410; 099415); same label information, except: R. F. Krüger, 15.xi.2002, 1# (DZUP 099411); R. F. Krüger, 07.iii.2003, 1# (DZUP 099416); 25.x.2002, 1# (DZUP 099417); R. F. Krüger, 21.ii.2003, 1# (DZUP 099418); 31.i.2003, 1@ (DZUP 099408); 22.xi.2002, 1@ (DZUP 099409); 31.i.2003, 2@@ (DZUP 099412-13); P. E. Itapuá, mata pequena pto2 [-30.284710, -51.015461], Malaise trap, R. F. K. & F. D. K., 20.i.2012, 1# (DZUP); Barra do Ribeiro, RPPN Barba Negra, mata da faxina, pto3 [-30.36447, -51.09595], Malaise trap, R. F. K. & F. D. K., 27.xi.2011, 1@ (DZUP); Quaraí [-30.384608, -56.448744], J. R. Cure, 21.xi.1985, 1@ (DZUP); Santa Catarina. Nova Teutônia [-27.161664, -52.416858], 300-500m, Fritz Plaumann, v.1970, 1@ (MZUSP); São Paulo. Ribeirão Preto, Campus USP, Secondary semideciduous forest [-21.1625, -47.86], Malaise trap, D. Amorim, 24.vi-24.vii.2017, 3# (DZUP2020A04; MZUSP) and 4@@ (DZUP; MZUSP); same label information, except: 16.vii-16.viii.2017, 2## (DZUP); 18.v-18.vi.2017, 1# (MZUSP); Sertãozinho, Res. Ecol. Augusto Ruschi, Frag. 2 [-21.181111, -48.096388], 529m, V. C. Silva, P. F. Danda & G. P. Ignácio, 16-30.vi.2010, 1@ (MZUSP); same label information, except: 13-28.vii.2010, 3@@ (DZUP; MZUSP); 30.vi-13.vii.2010, 1@ (MZUSP); 28.vii-11.viii.2010, 1@ (MZUSP); 25.v-08.vi.2011, 1@ (MZUSP); 09-22.ix.2010, 2@@ (DZUP; MZUSP). Paraguay. Amambay. P. N. Cerro Cora - Cerro Muralha [-22.652173, -56.025532], C. Aguilar J., 23.vii.1988, 1@ (DZUP); same label information, except: 27.vii.1988, 1@ (DZUP); Canindeyú. Reserva Natural Bosque Mbaracayú, Jejuí-mí, Bosque bajo [-24.122513, -55.446990], Malaise trap, A. C. F. Costa, 9-15.v.1996, 1# (DZUP 462944); same label information, except: 1-8.v.1996, 1# (DZUP 462945); 1-8.v.1996, 1# (DZUP); 2-10.iv.1996, 1@ (DZUP 462946); 9-15.v.1996, 1# (DZUP 462947); 17-23.iv.1996, 3## (DZUP 462948-50); 11-17.iv.1996, 1# (DZUP 462951).

**Distribution.** Brazil (Bahia, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, Mato Grosso, Mato Grosso do Sul) and Paraguay (Amambay, Canindeyú).

**Remarks.** New records for Brazil (Bahia, Mato Grosso, Mato Grosso do Sul, Rio Grande do Sul, São Paulo) and Paraguay (Amambay).

***Coenosopsia ferrari*** Nihei & de Carvalho

(Fig. 6*D*)

**Diagnosis.** Palpi brown. Legs brown, basal third of fore tibia light brown. Male terminalia: Cerci triangular, as long as surstyli and narrow dorsally; apex narrow. Surstyli width with about ¼ of the epandrium width laterally; surstyli slightly curved laterally. Proximal projection of surstyli reaching epandrium. Pregonite similar to postgonite length. Pregonite setulose distally. Phalapodema straight. This is the unique species with a strongly curved surstyli as long as cerci.

**Type-material examined.** Holotype. Male. Brazil. Distrito Federal. Brasília, Reserva Ecológica do IBGE [-15.948161, -47.878464], I. R. Diniz, 9.xii.1997 (DZUP 245561).Paratypes. 8## and 5@@. Same data as holotype: 1@ (DZUP 462958). Same data as holotype, except: 13.v.1997, 3## (DZUP 462952-54), 3@@ (DZUP 462956-57; 462961), 2## (MNRJ); 24.vi.1997, 2## (DZUP 462955; 462962) and 2@@ (DZUP 462959-60); 25.xi.1997, 1# (DBAI); 17.iii.1998, 1@ (DBAI).

**Material examined.** Brazil. Minas Gerais. Parque Nacional do Caparaó, Pico da Bandeira trail, WP243 [-20.41072, -41.83613], M. Savaris & A. L. Norrbom, 3.iii.2017, 1# (DZUP). Paraná. Palmas. Refúgio de Vida Silvestre dos Campos de Palmas [-26.533232, -51.599463], 1115m, Malaise trap, Adriana C. Pereira, 05.iii.2013, 12## and 3@@ (DZUP); same label information, except: Linha Alegre, Fazenda Cerro Chato [-26.50252, -51.67033], 1224m, M. Savaris & A. L. Norrbom, 3-4.iii.2015, 2## (DZUP).

**Distribution.** Brazil (Distrito Federal, Minas Gerais, Paraná)

**Remarks.** New record for Brazil (Minas Gerais).

***Coenosopsia floridensis*** Michelsen

(Fig. 6*B*)

**Diagnosis.** Palpi brown with yellow apex. Legs brown. Male terminalia: Cerci triangular, shorter than surstyli and narrow dorsally; apex narrow. Surstyli width with about 3/4 of the epandrium width laterally; right surstylus strongly curved laterally. Proximal projection of surstyli exceeding epandrium margin. Pregonite longer than postgonite. Pregonite bare distally. Phalapodema straight. This is the unique species with the proximal projection of surstyli strongly curved downwardly.

**Material examined.** Costa Rica. Guanacaste. Bagaces, P. N. Palo Verde, Sector Catalina, Fila Catalina [10.383874, -85.334288], 250m, Malaise trap, I. Jiménez, 8.i-

8.ii.2000, 1# (INBio); Valle la Estrella, R. B. Hitoy Cerere, Prov. Limón [9.759235, -83.032072], 100m, J. F. Quesada, vii.1994, 1@ (INBio). Mexico. Campeche, El Tormento [18.613176, -90.796948], A. Ibarra, 26.iii.1984, 1@ (CNIN); Jalisco, Estación de Biologia Chamela, Camino a Chachalaca [19.4959, -105.04202], 4013m, D. Perez, G. Aguilar & A. Zaldivar, 9-30.vi.2013, 1@ (DZUP); Veracruz. Est. Biol. Los Tuxtlas [18.584982, -95.073932], A. Ibarra, K. Ramírez & F. Sinaca, 17-18.iv.1986, 1# (CNIN); Córdoba, Cuauthemoc [18.909229, -96.960912], L. Delgado, 17.ii.1999, 1@ (IEXA); Teocelo, Finca Teocelo [19.393523, -96.980377], Malaise trap, S. Ibañez & F. A. Pech, 12.xi.2004, 1@ (IEXA); same label information, except: V. Hernandez, C. Deloya & F. A. Pech, 23.iv.2004, 1# (IEXA DIP_060474); Totutla, Finca La Vequia [19.210873, -96.961141], Malaise trap, V. Hernandez, C. Deloya & F. A. Pech, 21.iv.2004 (IEXA DIP_050336).

**Distribution.** Costa Rica (Guanacaste), Mexico (Campeche, Jalisco, Sinaloa, Tamaulipas, Veracruz), USA (Florida, Oklahoma, Texas).

**Remarks.** First record for Costa Rica (Guanacaste, Limón) and new records for Mexico (Campeche, Jalisco, Veracruz).

***Coenosopsia limeirai,*** sp. nov.

(Fig. 3, 5*F*–*J*, 6*C*)

**Diagnosis.** Palpi yellow (Fig. 3*A*). Legs brown, fore and mid tibia light brown on basal third (Fig. 3*D*). Male terminalia: Cerci triangular, very short, wider than long dorsally; apex narrow (Fig. 5*G*, *H*). Surstyli width with about half of the epandrium width laterally; surstyli straight laterally (Fig. 5*H*, *I*). Proximal projection of surstyli almost reaching epandrium margin (Fig. 5*H*). Pregonite longer than postgonite (Fig. 5*J*). Pregonite bare distally (Fig. 5*J*). Phalapodema curved (Fig. 5*J*). This is the unique species with the cerci very short and wider than long (Fig. 5*G*).

**Description.** Male. Body length: 2.8 mm. Wing length: 2.6 mm. Body morphology as *C. azteca* sp. nov., differing in terminalia (Fig. 5*F*, *J*): Epandrium, in lateral view, with a set of setulae at lower anterior portion (Fig. 5*H*). Cerci very short and narrow, wider than long, with about half length of surstyli (Fig. 5*G*, *H*). Surstyli elongated and straight (Fig. *H*, *I*). Pregonite bare distally (Fig. 5j). Postgonite similar to epiphallus length (Fig. 5*J*). Phalapodema enlarged distally (Fig. 5*J*).

**Female (n= 4).** (Fig. 3*E*–*G*) Body length: 2.5–3.5 mm. Wing length: 2.6–3.3 mm. Similar to male, except: abdomen widened; ovipositor as in the genus diagnosis.

**Etymology.** Name in apposition. This species is named in honor of Francisco Limeira-de-Oliveira, dipterist of the Universidade Estadual do Maranhão, Maranhão, Caxias, Brazil.

**Material examined.** Holotype. Male. Brazil. CE [Ceará], Ubajara, Parque Nac. de Ubajara, Cachoeira do Cafundó, 03º50'13''S/40º54'35''W, Armadilha Malaise, 18-30.xi.2012, F. Limeira-de-Oliveira, J. S. Pinto Júnior, cols. (CZMA). Paratype. Female. Same as holotype: 1@ (CZMA); same as holotype, except: 01-15.xii.2012, 2@@ (CZMA; DZUP); Piauí, Estação Ecológica Ecológica Uruçui, Município Ribeiro Gonçalves, Rio Uruçui [-7.241895, -44.553737], malaise trap, 17-23.v.1984, 1@ (DZUP).

**Distribution.** Brazil (Ceará, Piauí).

**Remarks.** The holotype has the antennae and legs broken, except the left fore leg. A fore, mid and hind leg are glued on the label.

***Coenosopsia mexicana*** Michelsen

(Fig. 6*B*)

**Diagnosis.** Palpi yellow. Legs brown, fore and mid femora brown with basal yellow; hind femur brown with basal ⅔ yellow, tibiae brown with basal half yellow. Male terminalia: Cerci triangular, shorter than surstyli and narrow dorsally; apex narrow. Surstyli width with about 3/4 of the epandrium width laterally; right surstylus strongly curved laterally. Proximal projection of surstyli exceeding epandrium margin. Pregonite longer than postgonite. Pregonite bare distally. Phalapodema straight. This species is very similar to *C. floridensis*, but can be distinguished by palpi yellow, right surstylus strongly curved with a longer apex, and proximal projection of surstyli not strongly curved downwardly.

**Material examined.** Mexico. Chiapas. Pto. 32 [16.322400, -91.791051], Malaise trap, G. Melo, 13-20.viii.2013, 6## (DZUP). Veracruz. Coatepec La Orduña, Finca Monges [19.452374, -96.936247], Malaise trap, S. Ibañez & F. A. Pech, 19.iii.2004, 1# and 2@@ (IEXA); Veracruz. Totutla, Finca La Vequia [19.210873, -96.961141], Malaise trap, V. Hernandez, C. Deloya & F. A. Pech, 21.iv.2004, 1# (IEXA).

**Distribution.** Mexico (Chiapas, Sinaloa, Veracruz)

**Remarks.** New record for Mexico (Veracruz).

***Coenosopsia michelseni*** Nihei & de Carvalho

(Fig. 6*B*)

**Diagnosis.** Palpi brown with yellow apex. Legs brown. Male terminalia: Cerci triangular, shorter than surstyli and narrow dorsally; apex rounded. Surstyli width with about 3/4 of the epandrium width laterally; right surstylus strongly curved laterally. Proximal projection of surstyli exceeding epandrium margin. Pregonite longer than postgonite. Pregonite bare distally. Phalapodema straight. This is the unique species with the left surstylus strongly curved on dorsal view.

**Type-material examined.** Holotype. Male. Brazil. Distrito Federal. Brasília, Reserva Ecológica do IBGE [-15.948161, -47.878464], I. R. Diniz, 13.v.1997 (DZUP 245562). Paratypes. 3## and 2@@. Same data as holotype, except: 29.iv.1997, 1# (DZUP 462963); 29.x.1997, 1@ (DZUP 462964); Pará. Serra Norte, Campo Canga [-6.084465, -50.176722], Pimentel, 10.vi.1983, 1# (MPEG).

**Material examined.** Brazil. Acre. Sen. Guiomard, F. E. Catuaba [-10.0744, -67.6166], Malaise trap, E. F. Morato & J. A. Rafael, viii-ix.2017, 1# (INPA); Distrito Federal. Brasília, Fazenda Água Limpa, Cerrado [-15.9594, -47.9328], Malaise trap, A. C. J. Aguiar, 20.xii.2012, 1# (DZUP2020A06); same label information, except: 26.xii.2012, 1# (DZUP); 30.iv.2011, 2## and 1@ (DZUP); 30.v.2011, 3## and 4@@ (DZUP); Goiás. Mineiros, Parque Nacional de Emas [-52.99575, -17.9111], Oliveira & Lopes, 19.iii-19.iv.2017, 1# (DZUP); same label information, except: Cerrado s.s. [-52.9890, -17.9124], Oliveira, Lopes & Fava, 17.xi-19.xii.2015, 1# (DZUP); Cerrado s.s. [-52.9957, -17.9111], Oliveira & Lopes, 12.vii-16.viii.2017, 1@ (DZUP); Maranhão. Mirador Parque Est. Mirador, Povoado Pindaíba [-6.662222, -45.026944], Malaise trap, F. Limeira-de-Oliveira, A. A. Santos & T. T. A. Silva, 01-05.vi.2011, 3## and 2@@ (CZMA; DZUP); Mirador Parque Est. Mirador, Base da Geraldina [-6.623611, -45.868888], Malaise trap, F. Limeira-de-Oliveira, L. L. M. Santos & L. S. Santos, 10-16.v.2013, 1# (CZMA); same label information, except: J. C. Silva & M. M. Abreu, 07.14.v.2010, 3## (CZMA); Mirador Parque Est. Mirador, Posto avançado do mel [-6.73, -45.006111], Malaise trap, F. Limeira-de-Oliveira & D. W. A. Marques, 18-25.iii.2012, 1@ (CZMA); Carolina PARNA Chapada das Mesas, Riacho Sucuruiu [-7.118194, -47.308777], 288m, Malaise trap, F. Limeira-de-Oliveira, T. L. Rocha & G. A. Reis, 20-31.viii.2014, 2@@ (CZMA). Minas Gerais. Santana do Riacho, Reserva Vellozia, WP 244 [-19.476111, -43.990833], 1134m, M. Savaris & A. L. Norrbom, 9-16.iii.2017, 1# (DZUP). Roraima. Amajari, Tepequém SESC [3.745833, -

61.728611], Malaise trap, R. Boldrini & J. A. Rafael, 1-15.iii.2016, 1# (INPA). São Paulo. Ribeirão Preto, Ribeirão Preto, Campus USP, Secondary semidecidous forest [-21.1625, -47.86], Malaise trap, D. Amorim, 16.vii-16.viii.2017, 1# (DZUP) and 2@@ (MZUSP); São Carlos, EMBRAPA [-21.954680, -47.847250], Malaise trap, Airton S. Soares, 11.v.2011, 1# (MZUSP); same label information, except: xii.2010, 1# (MZUSP).

**Distribution.** Brazil (Acre, Distrito Federal, Goiás, Maranhão, Minas Gerais, Pará, Roraima, São Paulo).

**Remarks.** New records for Brazil (Acre, Goiás, Maranhão, Minas Gerais, Roraima and São Paulo).

***Coenosopsia peruviana*** Michelsen

(Fig. 6*C*)

**Diagnosis.** Palpi brown with yellow apex. Legs brown. Male terminalia: Cerci triangular, shorter than surstyli and narrow dorsally; apex narrow. Surstyli width with about half of the epandrium width laterally; surstyli straight laterally. Proximal projection of surstyli reaching epandrium. Pregonite longer than postgonite. Pregonite bare distally. Phalapodema curved. This species is very similar to *C. brasiliensis*, but can be distinguished by the left surstylus narrower, similar to the right surstylus.

**Material examined.** Bolivia. Santa Cruz. 4km N of Bermejo, Refugio los Volcanes [-18.10429, -63.59870], 1058m, A. L. Norrbom, B. D. Sutton & E. Quiberth, 3-7.x.2014, 1# and 1@ (USNM); Brazil. Amazonas. Autaz-Mirim, Fazenda S. Lucas [-4.750523, -60.253709], Malaise trap, J. Vidal, 26.viii.1994, 1# (INPA); Manaus, R. Ducke [-2.999727, -59.939081], Y. Camara & J. E. Binda, 09-16.iii.1989, 1@ (INPA); Pará. Vitória do Xingu, Rio Xingu [-3.187426, -51.908433], Malaise trap, C. Maciel & J. Dias, 20-22.xi.2000, 1# (MPEG); same label information except: 14-16.xii.2000, 1@ (MPEG); R. Santos & J. Dias, 12.xii.2000, 1@ (MPEG); R. Santos & J. Dias, 28-30.xi.2000, 1@ (MPEG).

**Distribution.** Bolivia (Santa Cruz), Brazil (Amazonas, Pará), Peru (Cuzco, Quincemil, Madre de Dios).

**Remarks.** First record for Bolivia (Santa Cruz) and new record for Brazil (Pará).

***Coenosopsia prima*** Malloch

(Fig. 6*A*)

**Diagnosis.** Palpi brown. Legs brown. Male terminalia: Cerci triangular, shorter than surstyli and narrow dorsally; apex rounded. Surstyli width with about half of the epandrium width laterally; surstyli straight laterally. Proximal projection of surstyli exceeding epandrium margin. Pregonite longer than postgonite. Pregonite bare distally. Phalapodema straight. This species is very similar to *C. ribeiroi* sp. nov., but can be distinguished by the pregonite bare and surstyli straight laterally.

**Type-material examined.** Paratype. Panama. Canal Zone, Barro Colorado Is., 9.iii.1967, Roger D. Akre, 1@ (WSU); same label information, except: 4.iv.1967, 1@ (WSU).

**Material examined.** Brazil. Maranhão. Caxias [-4.865242, -43.362038], J. A. Silva & F. Limeira-de-Oliveira, 05-07.vi.2009, 1# (CZMA). Costa Rica. Puntarenas. Est. Aguias Send. Purruja [8.614016, -83.119355], 300m, M. Lobo, 3-6.v.1998, 1# (INBio); Costa Rica. Prov. Guanacaste, P. N. Rincón de la Vieja. Sector Santa Maria, Send. a las aguas termales [10.782311, -85.353613], 800m, D. Briceño, 7-8.xii.2001, 1@ [INB0003402712]. Mexico. Campeche, Grutas Ixta-Cumbilxunan [19.991024, -89.764204], F. Arias, 22.vi.1985, 3@@ (CNIN); Veracruz, Est. Biol. Los Tuxtlas [18.584982, -95.073932], P. Sinaca, 24.iv.1986, 1@ (CNIN); Totutla, Finca La Vequia [19.210873, -96.961141], S. Inañez & F. A. Pech, 13.vii.2004, 1@ (IEXA).

**Distribution.** Belize (British Honduras), Brazil (Maranhão), Costa Rica (Higuito), Ecuador (Pastaza, Pichincha), Mexico (Campeche, Veracruz), Panama (Alejuela, Canal Zone, Libéria and Puntarenas), USA (Florida).

**Remarks.** First record for Brazil (Maranhão); and new records for Mexico (Campeche) and Costa Rica (Libéria and Puntarenas).

***Coenosopsia ribeiroi,*** sp. nov.

(Fig. 4, 5*K*–*O*, 6*D*)

**Diagnosis.** Palpi brown. Legs brown, fore and mid tibiae brown with basal half light brown (Fig. 4*C*, *F*). Male terminalia: Cerci triangular, shorter than surstyli and narrow dorsally; apex rounded (Fig. 5*L*–*M*). Surstyli width with about half of the epandrium width laterally; surstyli slightly curved laterally (Fig. 5*M*, *N*). Proximal projection of surstyli reaching epandrium (Fig. 5*M*). Pregonite as long as postgonite (Fig. *O*). Pregonite setulose distally (Fig. *O*). Phalapodema straight (Fig. *O*). This species is

very similar to *C. prima*, but can be distinguished by the pregonite setulose distally and surstylus slightly curved laterally.

**Description.** Male. Body length: 3.0–3.2 mm. Wing length: 3.0–3.2 mm. Body morphology as *C. azteca* sp. nov. description, differing in terminalia (Fig. 5*K*–*O*): Epandrium, in lateral view, with a set of setulae at lower anterior portion (Fig. 5*M*). Cerci with downwardly oriented median lobe rounded distally (Fig. 5*L*, *M*). Surstyli elongate, right surstylus more markedly curved (Fig. 5*M*, *N*). Pregonite setulose distally (Fig. 5*O*). Postgonite similar to epiphallus length (Fig. 5*O*). Phalapodema straight and enlarged distally (Fig. 5*O*).

**Female (n= 1).** (Fig. 4*D*–*F*) Body length: 3.2 mm. Wing length: 3.0 mm. Similar to male, except: coxae and basal fifth of hind femur yellow; abdomen widened; ovipositor as in the genus diagnosis.

**Etymology.** Name in apposition. This species is named in honor of Paulo Bretanha Ribeiro, dipterist of Universidade Federal de Pelotas, Rio Grande do Sul, Brazil.

**Material examined.** Holotype. Male. Brazil, RS [Rio Grande do Sul], Arroio Grande, Distrito de Mauá, 30.viii.2002, Malaise, P. B. Ribeiro leg. (DZUP 099405); Paratype. same as holotype: 1# (DZUP 099419) and 1@ (DZUP 099406).

**Distribution.** Brazil (Rio Grande do Sul).

**Remarks.** This species is known only by the type locality.

## Phylogenetic analyses

According to the obtained topology (Fig. 1), the genus *Coenosopsia* was recovered as a monophyletic clade [Relative Bremer support (RB)= 63; Bootstrap support (BS)= 94]; sister group of the also monophyletic genus *Phaonantho* [RB= 80; BS= 99]; and both genera as sister group of *Hydrophoria ruralis*. The relationship between *Coenosopsia* and *Phaonantho* is supported by five synapomorphies (postpedicel four times longer than pedicel [2:2]; vein $A_1$ not reaching the wing margin [21:0]; cerci quadrangular [25:2]; cerci completely exceeding the surstyli [27:1]; and surstyli width with about half width of epandrium, [30:1]) and two homoplasies (postgonite quadrangular [39:1]; and absence of a long seta on postgonite [40:0]).

The monophyly of *Coenosopsia* is supported by five synapomorphies (length of calcar similar to the tibia width [23:0]; cerci short triangular, shorter than surstyli length [25:4]; cerci long and narrow, in lateral view, with medial and distal region with

similar width [28:1]; right and left surstyli asymmetrical [29:1]; presence of a proximal projection of surstyli [32:1]); and four homoplasies (presence of interfrontal setae on male [4:1]; presence of proclinate orbital setae on male [7:1]; male dichoptic [10:1]; apex of scutellum ventrally bare [17:0]).

We included the three known species of *Phaonantho* in the analysis and the monophyly of the genus is well supported (RB= 80; BS= 99) with three synapomorphies (two proclinate orbital seta on female [6:1]; two median setulae on pregonite [36:1]; and epiphallus absent [41:0]); and six homoplasies (one reclinate orbital seta on female [9:1]; prosternum narrow [12:0]; lower calypter longer than the upper one [22:3]; cerci distally with a quadrangular margin [26:2]; two long distal setulae on pregonite [34:1]; and pregonite as long as postgonite [37:0]).

Among the relationships of *Coenosopsia* species, *C. prima* was recovered as sister group of remaining species, which were recovered in two main clades. The first one composed by the three species from North America (*C. floridensis*, *C. mexicana*, *C. azteca*) and a species from South American (*C. michelseni*), this clade is supported by a synapomorphy: the cerci long and enlarged in lateral view [28: 2]. The second main clade is composed by the remaining species from South America, supported by a synapomorphy: proximal projection of surstyli reaching the epandrium margin [33:0]. This South american species clade is subdivided into two groups with three species each. The first clade including species from the north to south South America (*C. brasiliensis*, *C. peruviana*, and *C. limeirai*) is supported by one homoplasy: phalapodeme curved [42:1]; and the other clade including species from central, south and southeast Brazil (*C. albuquerquei*, *C. ferrari*, and *C. ribeiroi*), supported by a synapomorphy: pregonite setulose distally [38:1]; and two homoplasies: palpi entirely brown [11:1]; and surstyli slightly curved on lateral view [31:1].

### Distribution

Our study presents several new records of *Coenosopsia* in Americas, revealing a wide distribution of species as *C. floridensis* and *C. prima* which occurs in both Nearctic and Neotropical regions. We present new records for all species, including the first record of *C. floridensis* in Costa Rica, first record of *C. peruviana* in Bolivia, and the first record of *C. prima* in Brazil (Fig. 6). We carry out an ancestral area reconstruction based on parsimony, which indicates that the *Coenosopsia*

species ancestor probably occurred in Central America (specifically on the Mesoamerican Dominion), posteriorly originating a lineage which diverged in Central and North America (Fig. 7, clade A); and another lineage which diverged in South America (Fig. 7, clade B + C). The S-DIVA analysis revealed a nearly identical scenario with the ancestral reconstruction based on parsimony, but resulted in an inconclusive reconstruction of the ancestral distribution of some nodes, inclusive indicating several possibilities of distribution in the ancestral node of the genus.

The *Coenosopsia* had an early divergence, when the clade A, which is mainly distributed in the Nearctic region, Mexican Transition Zone and Central America split from the South American clade B+C. This pattern indicates an ancestral invasion in South America with posterior diversification of these two main clades: B) *C. limeirai*, *C. brasiliensis*, and *C. peruviana*; and C) *C. ribeiroi*, *C. albuquerquei*, and *C. ferrari*.

In the clade A, the South American distribution of *C. michelseni*, nested in a clade formed by Central and North American species, indicates an independent dispersion to South America. The clade B has species from north, northwest, northeast and southeast South America. While the clade C has species exclusively distributed in the southeast of South America (Chacoan and Parana Dominions). It is important to highlight that it is quite possible that the three new species herein described have a wider distribution.

In summary, considering the Mesoamerican origin of *Coenosopsia*, the analyses indicate at least two independent colonizations in South America, based on occurrence of *C. michelseni* and clade B+C in South America. Also, there was at least two events of colonization to the Nearctic region of North America, based on *C. prima* and *C. floridensis* distribution.

## DISCUSSION

### Phylogenetic analyses

Some studies aimed at elucidating the phylogenetic relationship of the aberrant genus *Coenosopsia* (Michelsen 1991, 1996; Nihei and de Carvalho 2004; Bortolanza et al. 2006; Gomes et al. 2021). The sister-group relationship between *Coenosospia* and the Neotropical genus *Phaonantho* was congruent with previous studies based on morphological (Michelsen 1991) and molecular data (Gomes et al. 2021). Michelsen (1991) indicated a sister-group relationship between *Phaonantho*

and *Coenosopsia* based on five synapomorphies: arista plumose, palpus dark with yellow apex, all elements of male terminalia (except surstylus) remarkably small, process longi (sternite 10) short and merging into anterobasal parts of surstyli, sperm pump sclerite vestigial and absence of a subapical seta on the pregonite; and two plesiomorphies: vein $A_1$ strongly abbreviated, not reaching the wing edge, and tibia with two posterodorsal setae. In addition to the vein $A_1$ not reaching the wing edge [21:0], also indicated by Michelsen (1991) as a character supporting *Coenosopsia* + *Phaonantho*, this relationship was supported by other six characters (see Results).

While the relationship *Coenosopsia* + *Phaonantho* seems to be well supported by both morphological and molecular data, the position of this clade within Anthomyiidae is still unclear. Michelsen (1991) proposed the clade *Coenosopsia* + *Phaonantho* as sister group of the remaining anthomyiids, but this relationship was not recovered by Gomes et al. (2021) based on molecular data. Our analyses have an insufficient sampling of anthomyiid genera, not allowing a deep discussion related to the position of *Coenosopsia* + *Phaonantho* within Anthomyiidae. However, it is important to highlight that these genera were not recovered as sister group of remaining anthomyiids and which *Hydrophoria*, present in the sister group of *Coenosopsia* + *Phaonantho* clade in the molecular analysis performed by Gomes et al. (2021), was also recovered as sister group of this clade.

The monophyly of *Coenosopsia* has been well supported by six characters in Bortolanza et al. (2006) analyses and by seven characters in Nihei and de Carvalho (2004) analyses, while our analysis indicated 10 characters supporting its monophyly. Some of those characters in our analyses are also presented in Nihei and de Carvalho (2004) and Bortolanza et al. (2006): presence of interfrontal setae on male [4:1], presence of proclinate fronto-orbital seta on male [7:1], male eyes dichoptics [10:1], ventral surface of scutellum bare [17:0], and surstyli asymmetrical [29:1]. In addition to the following new characters: calcar as long as tibia width [23:0]; cerci short triangular on dorsal view, shorter than surstyli length [25:4]; cerci narrow on lateral view, with medial and distal regions with similar width [28:1]; and presence of a proximal projection of surstyli [32:1].

The relationship among *Coenosopsia* species is partially congruent with previous studies, the clade with *C. floridensis*, *C. mexicana* and *C. michelseni* was also recovered by Nihei and de Carvalho (2004) and Bortolanza et al. (2006); while the close relationship between *C. albuquerquei* and *C. ferrari*; and between *C.*

*brasiliensis* and *C. peruviana* were recovered by Bortolanza et al. (2006). The main divergence among the topologies is related to *C. prima* position, which was recovered by Nihei and de Carvalho (2004) as sister group of the clade composed by *C. floridensis*, *C. mexicana* and *C. michelseni*; while Bortolanza et al. (2006) recovered *C. prima* in a polytomy with the clades *C. brasiliensis* + *C. peruviana*, and *C. michelseni* + (*C. floridensis* + *C. mexicana*). Gomes et al. (2021), based on molecular data, recovered the following topology: *C. ferrari* + (*C. brasiliensis* + *C. michelseni*), this closely relationship among *C. michelseni* and *C. brasiliensis* may be due to the inclusion of only three species of *Coenosopsia* in this analysis. Future molecular studies including more *Coenosopsia* species are necessary to fully understand the relationship among these species.

### Distribution

The ancestral distribution of *Coenosopsia* in Mesoamerican Dominion is congruent with Michelsen (1991) hypothesis that the ancestral range of the genus lies in the tropical realm of South or Central America and with the fossil of the extinct close related genus *Coenosopsites* from Dominican amber (Michelsen 1996). On the other hand, a wide ancestral distribution, as indicated by S-DIVA analysis, seems to be unrealistic, given the expected early origin of *Coenosopsia* (c. 23 Mya) (Gomes et al. 2021). Also, S-DIVA analysis method has a limitation in reconstructing ancestral areas correctly in cases that speciation was not driven only by vicariance (Kodandaramaiah 2010). Gomes et al. (2021), based on divergence time, indicated the GAARlandia (the Greater Antilles and Aves Ridge landspan) hypothesis (Iturralde-Vinent and MacPhee 1999), a land bridge hypothesis that connected the Greater Antilles to South America during the Mid-Cenozoic (c. 32 Ma), to explain the early dispersal of *Coenosopsia* to South America, but this hypothesis has been contested (Ali and Hedges 2021) and probably an over-water dispersion, facilitated by the low sea level which reduced the distance between Central America islands and South America, is the best explanation.

The previous biogeographical studies of *Coenosopsia* (Nihei and de Carvalho 2004; Bortolanza et al. 2006) also indicated a pattern (Caribbean component + (Northwestern component + Southeastern component)), but considering events from Cretaceous to explain this pattern. Among the biogeographical events indicated by Nihei and de Carvalho (2004), the formation of

an epicontinental sea formed by water invasion through the north, east and south (Paraná basin) in the Miocene, could explain the split between clade A and clade B+C (Fig. 7). Also, Nihei and de Carvalho (2004) and Bortolanza et al. (2006) proposed an ancestral distribution in the southern portion of South America with posterior dispersion to Central and North America, based on the split between the clade *C. ferrari* + *C. albuquerquei* and the remaining species, which was explained by a late vicariance event (the connection between the Parnaíba and Paraná basins, see Nihei and de Carvalho 2004: Fig. 6D). But the present hypothesis diverged from it, indicating a Central America origin and posterior dispersion to South America. Also, our analysis indicated *C. prima* and the next branch clade (clade A composed mainly by Central and North American species) as sister group of the remaining South America species, while Nihei and de Carvalho (2004) and Bortolanza et al. (2006) indicated the North American species (*C. floridensis* and *C. mexicana*) as a late divergence in the phylogenetic tree.

Nihei and de Carvalho (2004) inferred that *C. michelseni* could be more widespread than the known distribution in central and northern Brazil, considering its close relationship with species from Central and North America. Also, the authors discussed that this species probably has a distribution extending throughout northwestern South America mainly on regions covered by open vegetation. We found two new records in northwestern South America as predicted and also in open areas. We updated the distributional knowledge of this species, including a wide distribution in North, Northeast and Southeast Brazil (Fig. 6B).

The biogeographical pattern indicated in our analyses is also congruent with the general pattern proposed by Amorim and Pires (1996), who posteriorly updated the time of events that generated this pattern to Cenozoic (Amorim 2009), the same period estimated as the divergence time of *Coenosopsia* (Gomes et al. 2021). This pattern is fully or partially congruent in studies with other groups of Diptera (Manfrin et al. 2001; Gomes and de Carvalho 2018) and Coleoptera (Morrone 2002). Some of them (Manfrin et al. 2001; Morrone 2002) also indicated the early split between species from Mesoamerican Dominion and species from Chacoan + Paraná Dominions, with posterior diversification into other areas of South America. Some other studies with Coleoptera (Beza-Beza et al. 2021), Hymenoptera (Ceccarelli and Zaldívar-Riverón 2013; Rodríguez et al. 2014) and Lepidoptera (Matos-Maraví et al.

2021), also have indicated a Mesoamerican origin for its respective taxa with a posterior dispersion to South America in the Miocene.

Matos-Maraví et al. (2021) indicated several events of dispersion among Mesoamerica, Amazon and Atlantic Forest in the Miocene. These events probably were mainly driven by the extreme climatic changes during this period caused by global cooling with intermittent cycles of warming and cooling, which also explains why this pattern is observed in different taxonomic groups (Condamine et al. 2012). Also, Terra-Araujo et al. (2015) explained the relationship between species of Amazon and Atlantic Forest based on several events of connections through the dry corridor of open vegetation in central South America, which connected both evergreen forests environments several times in the evolutionary history of the groups, allowing some dispersal events and diversification in these forests. These events could explain the occurrence of *Coenosopsia* species from Amazon and from Atlantic forest occurring in the same clade and also species with a wide distribution ranging both environments.

*Coenosopsia* is a genus with recent diversification (Gomes et al. 2021), originating in Mesoamerica at Miocene with posterior diversification in South America. The dispersion events seem to have driven *Coenosopsia* species diversification, including dispersal events both to North and South America. A molecular study including more *Coenosopsia* species is necessary to properly understand the biogeography of this genus, with the divergence time of the subgroups in the genus.

## Conflicts of interest

The authors declare no conflicts of interest.

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FIGURES

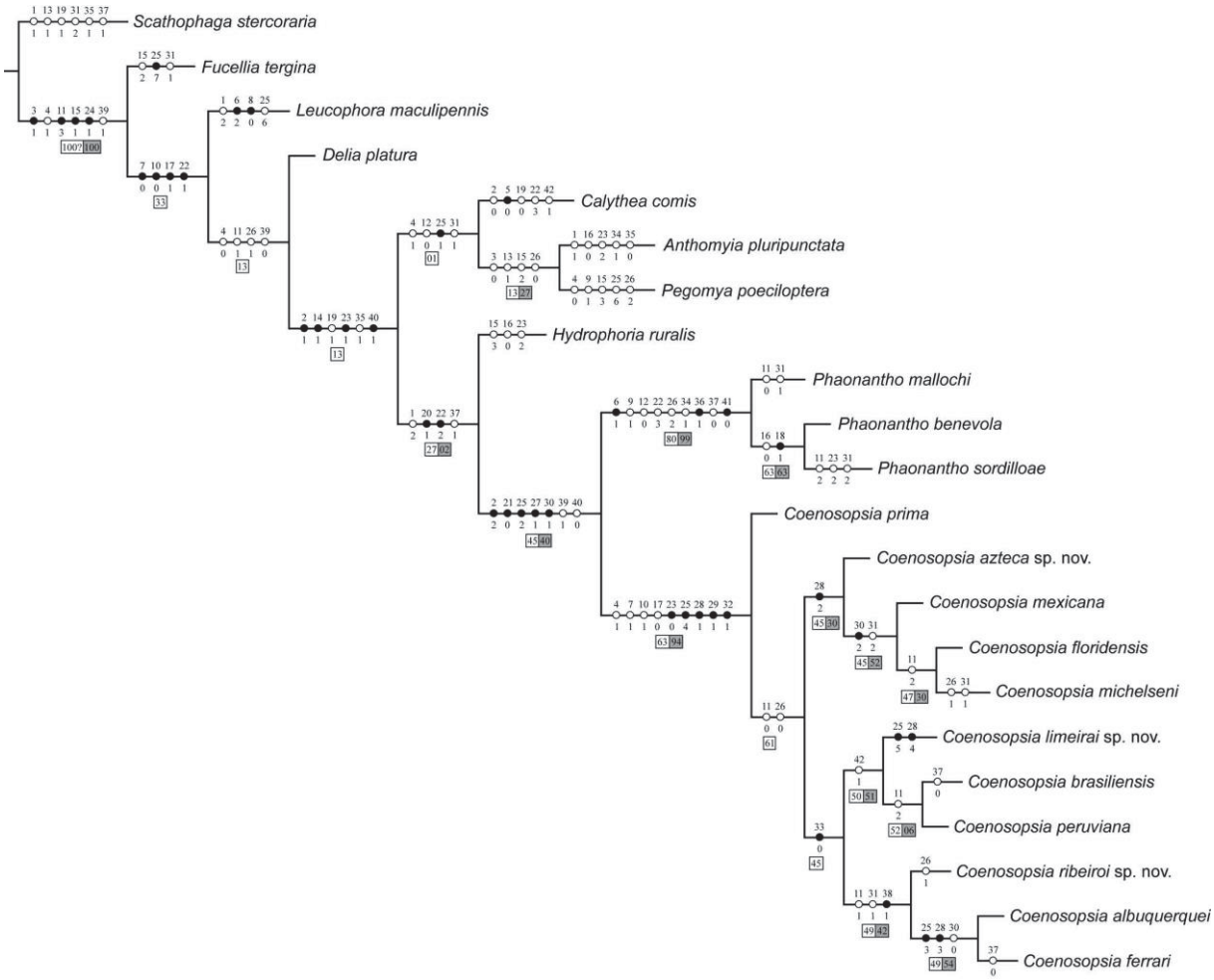


**Figure 1.** Most parsimonious tree for *Coenosopsia* species and outgroup generated from an analysis under implied weighting with k= 6. Character transformations are optimized under fast optimization. Solid black circles represent synapomorphies and white circles represent homoplasies. Relative Bremer (white box) and Bootstrap (gray box) supports are indicated below each branch.

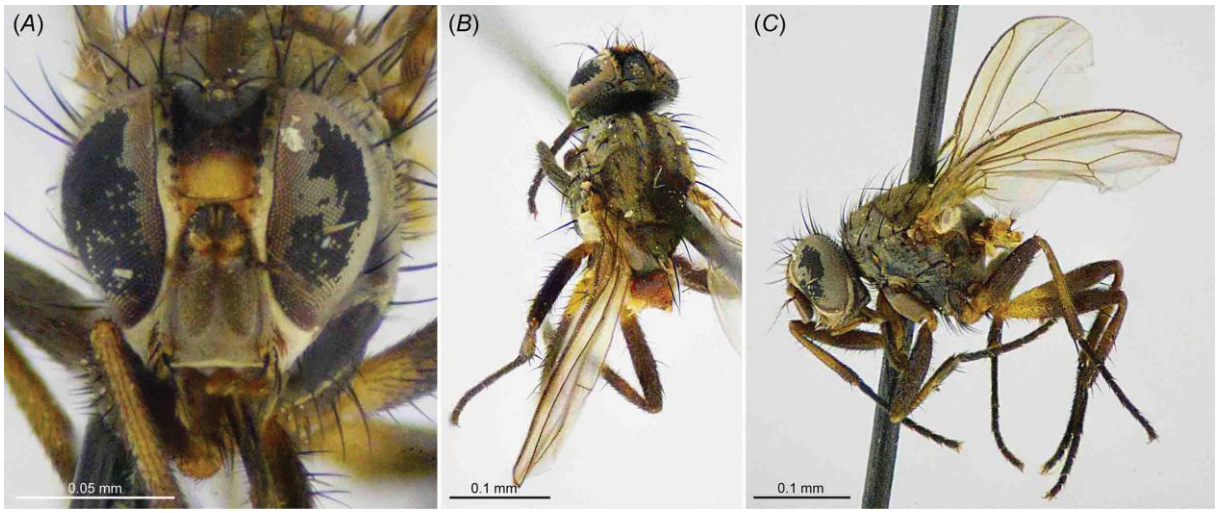


**Figure 2.** *Coenosopsia azteca* **sp. nov.** Male: head, frontal view (*A*); habitus, dorsal view (*B*); habitus, lateral view (*C*).

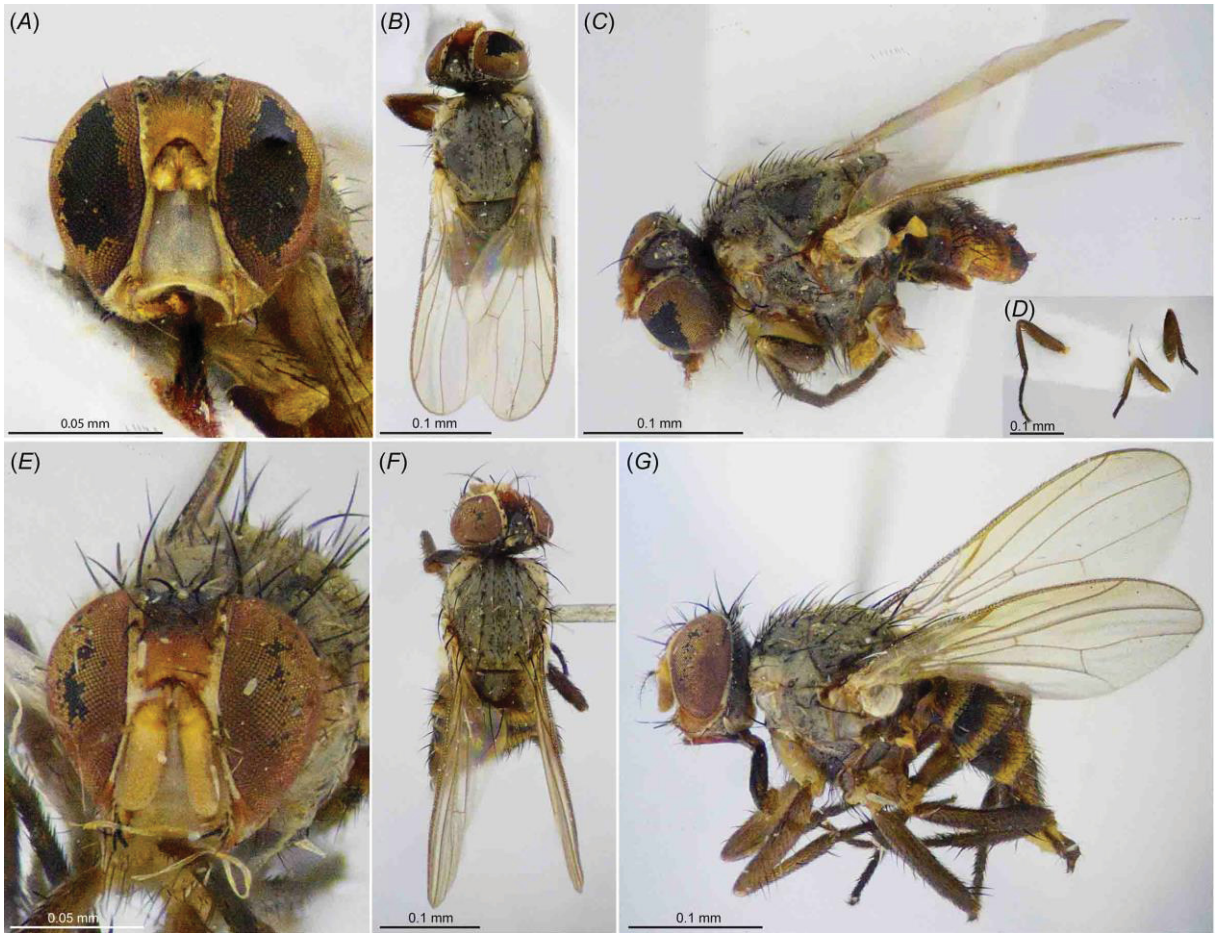


**Figure 3.** *Coenosopsia limeirai* **sp. nov.** Male: head, frontal view (*A*); habitus, dorsal view (*B*); habitus, lateral view (*C*); legs (*D*). Female: head, frontal view (*E*); habitus, dorsal view (*F*); habitus, lateral view (*G*).

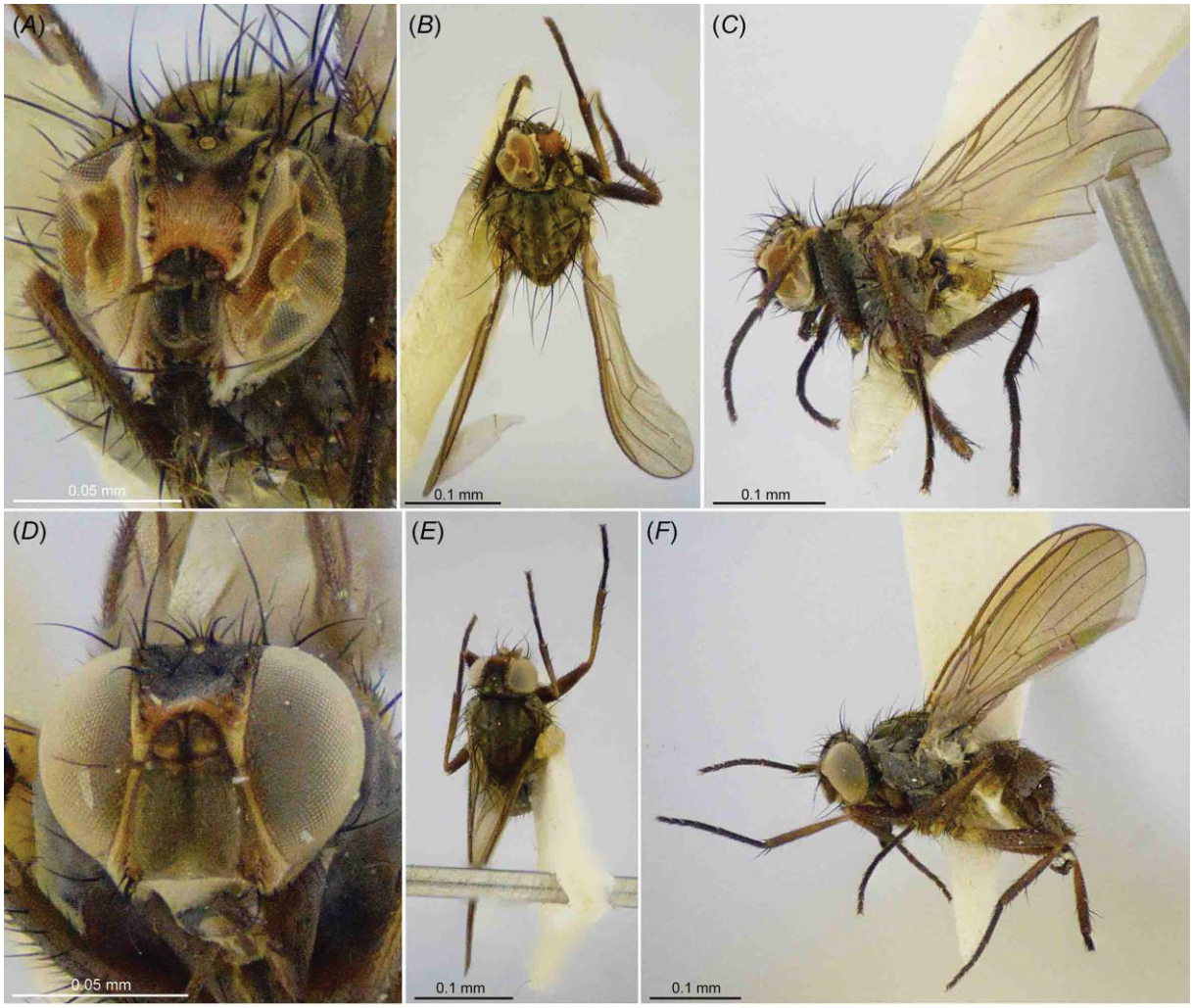


**Figure 4.** *Coenosopsia ribeiroi* **sp. nov.** Male: head, frontal view (*A*); habitus, dorsal view (*B*); habitus, lateral view (*C*). Female: head, frontal view (*D*); habitus, dorsal view (*E*); habitus, lateral view (*F*).

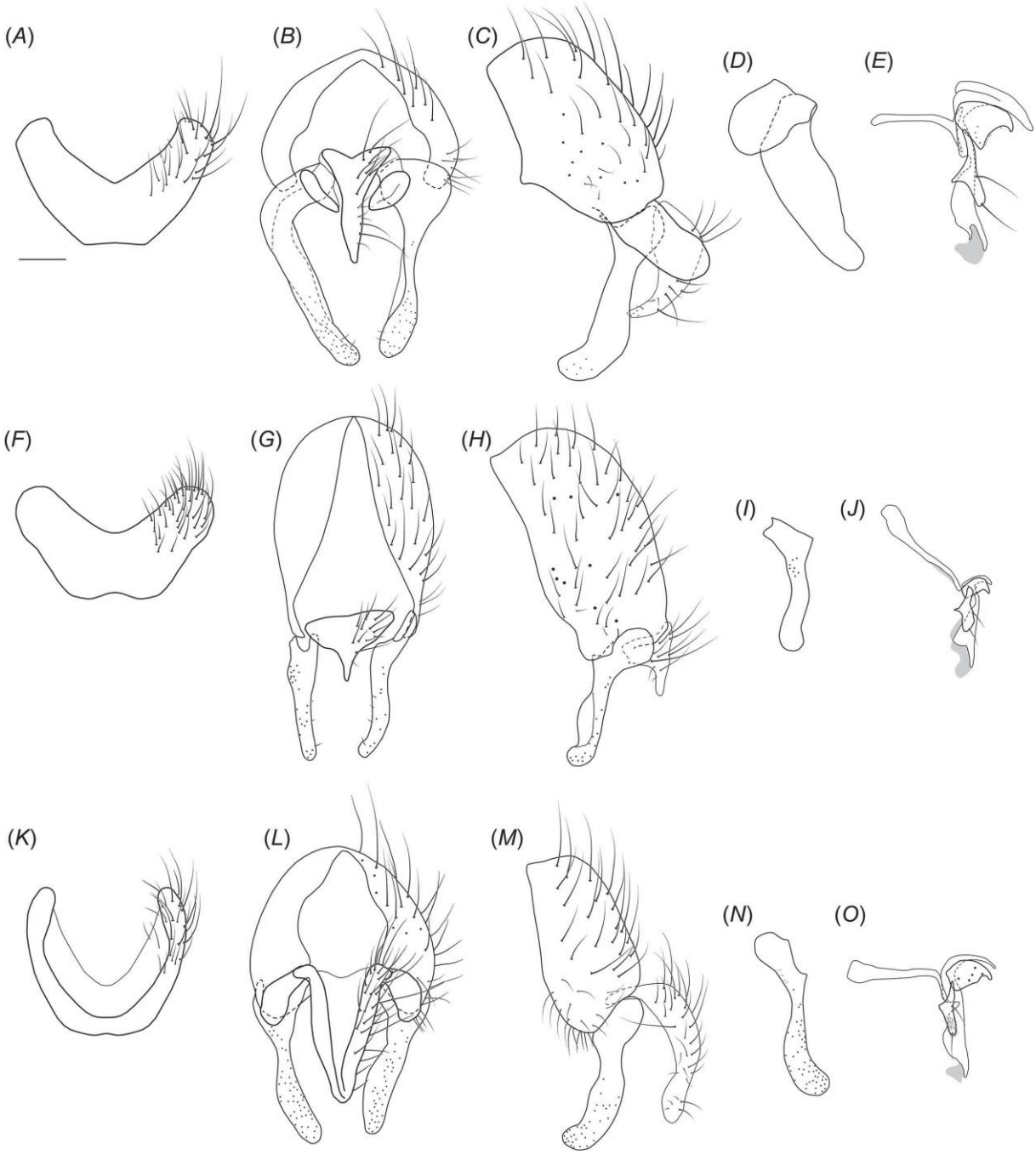


**Figure 5.** *Coenosopsia azteca* **sp. nov.**: sternite 5, dorsal view (*A*); epandrium, cerci and surstyli dorsal (*B*) and lateral view (*C*); right surstylus lateral view (*D*); aedeagus and associated structures, lateral view (*E*); *Coenosopsia limeirai* **sp. nov.**: sternite 5, dorsal view (*F*); epandrium, cerci and surstyli dorsal (*G*) and lateral view (*H*); right surstylus lateral view (*I*); aedeagus and associated structures, lateral view (*J*); *Coenosopsia ribeiroi* **sp. nov.**: sternite 5, dorsal view (*K*); epandrium, cerci and surstyli dorsal (*L*) and lateral view (*M*); right surstylus lateral view (*N*); aedeagus and associated structures, lateral view (*O*). Bar= 0.1 mm.

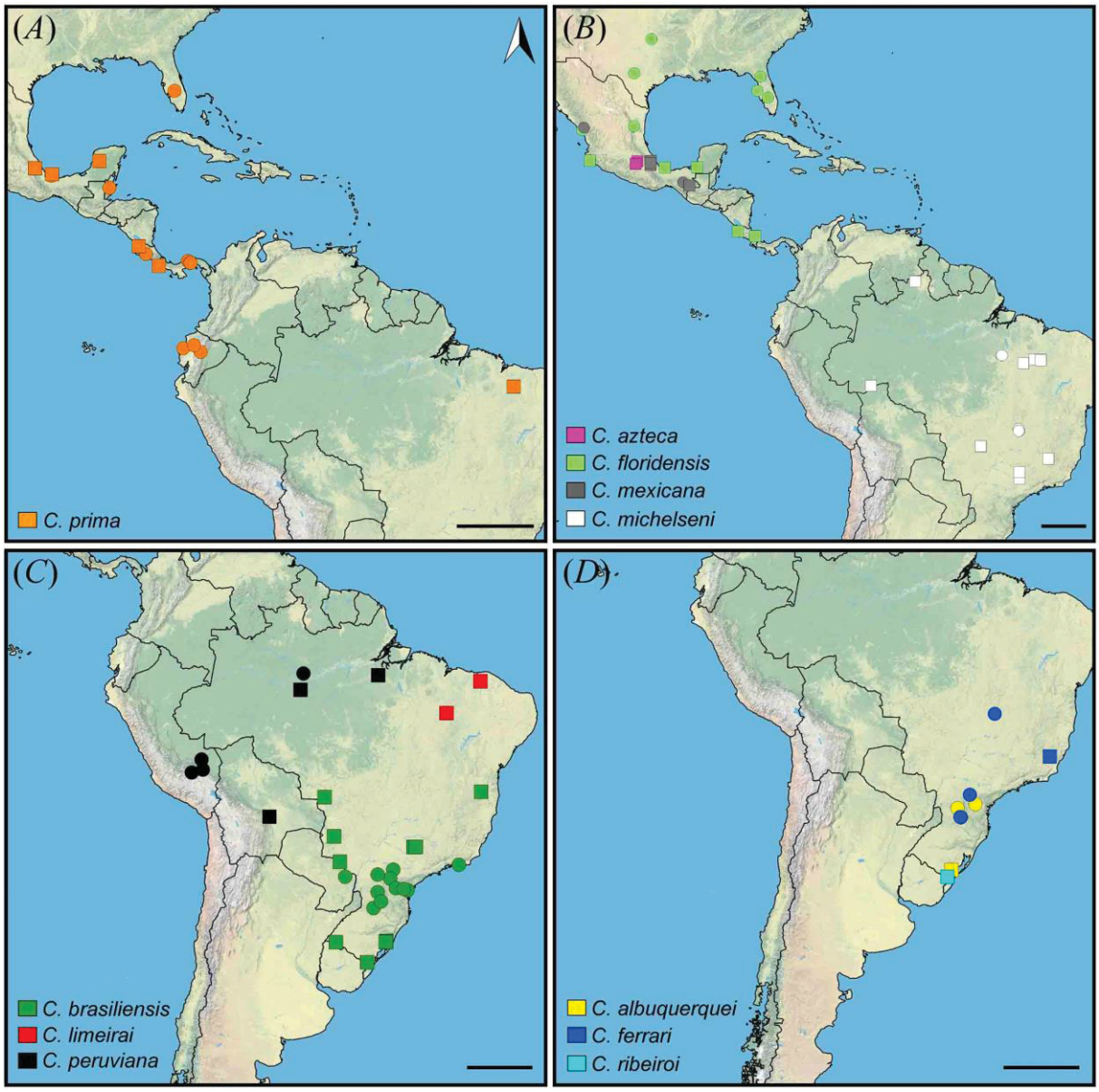


**Figure 6.** Map of *Coenosopsia* species: *C. prima* (*A*); *C. floridensis*, *C. mexicana*, *C. michelseni*, *C. azteca* [clade A] (*B*); *C. brasiliensis*, *C. peruviana*, *C. limeirai* [clade B] (*C*); *C. albuquerquei*, *C. ferrari*, *C. ribeiroi* [clade C] (*D*). Circles= literature records; square= new records.

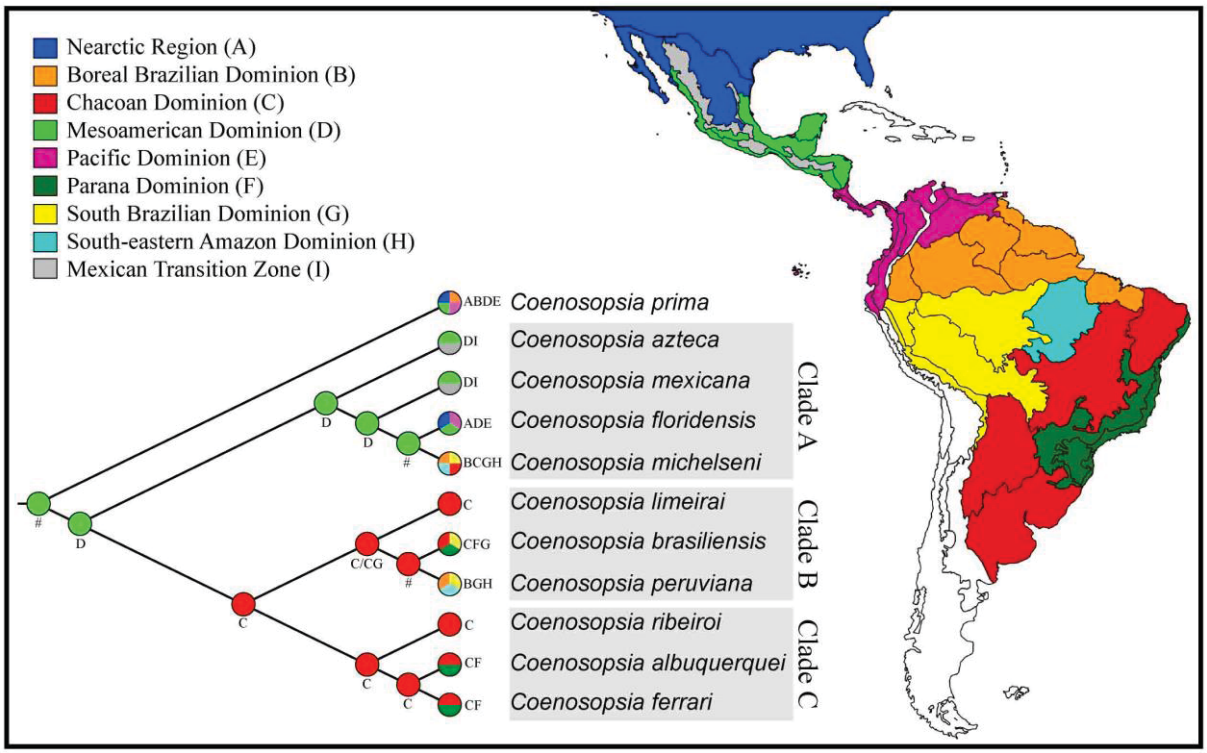


**Figure 7.** Ancestral reconstruction of the distribution of *Coenosopsia* species in biogeographical dominions, conducted for the most parsimonious tree using Mesquite Reconstruction of ancestral state (colored balls) and by Statistical Dispersal-Vicariance Analyses (S-DIVA) (uppercase letters). Map indicating the Neotropical Regionalisation, sensu Morrone (2014). #= inconclusive reconstruction or with more than five reconstruction options according to S-DIVA.

TABLES

**Table 1.** Characters and character states used in the cladistic analysis of *Coenosopsia* species and outgroup. L= Length; ci= consistency index; ri= retention index. Character based or modified from Couri & Pont (2000)= *; based or modified from Nihei & de Carvalho (2004)= **; based or modified from Bortolanza et al. (2006)= ***; new character= +.

**Head**

1. Antennae, arista, length of hairs: (0) short pubescent; (1) pubescent; (2) plumose.* [L: 4; ci: 50; ri: 50]

2. Antennae, postpedicel, length: (0) two times longer than pedicel; (1) three times longer than pedicel; (2) four times longer than pedicel. * [L: 3; ci: 66; ri: 83]

3. Interfrontal setae (female): (0) absent; (1) present. ** [L: 2; ci: 50; ri: 50]

4. Interfrontal setae (male): (0) absent; (1) present. ** [L: 5; ci: 20; ri: 33]

5. Proclinate fronto-orbital setae (female): (0) absent; (1) present. ** [L: 1; uninformative]

6. Proclinate fronto-orbital setae (female), number of setae: (0) 1; (1) 2; (2) 3. ** [L: 2; ci: 100; ri: 100]

7. Proclinate fronto-orbital setae (male): (0) absent; (1) present. ** [L: 2; ci: 50; ri: 87]

8. Reclinate fronto-orbital setae (female): (0) absent; (1) present. ** [L: 1; uninformative]

9. Reclinate fronto-orbital setae (female), number of setae: (0) two setae; (1) one seta. ** [L: 2; ci: 50; ri: 66]

10. Male eyes: (0) holoptic; (1) dichoptic. ** [L: 2; ci: 50; ri: 87]

11. Colour of palpi: (0) entirely yellow; (1) entirely brown; (2) brown with yellow apex; (3) yellow with brown apex. ** [L: 7; ci: 42; ri: 55]

**Thorax**

12. Prosternum, shape: (0) narrow; (1) anteriorly enlarged. ** [L: 2; ci: 50; ri: 80]

13. Prealar seta, length: (0) shorter than anterior notopleural seta; (1) similar to anterior notopleural seta; (2) longer than anterior notopleural seta. ** [L: 2; ci: 50; ri: 50]

14. Anepisternum, superior anterior seta: (0) absent; (1) presente. + [L: 1; ci: 100; ri: 100]

15. Katepisternum, setae conformation: (0) 0+1; (1) 1+2; (2) 2+2; (3) 1+1+1. * [L: 6; ci: 50; ri: 50]

16. Scutellum, apical scutellar setae, length: (0) similar to subbasal setae; (1) longer than subbasal setae. * [L: 3; ci: 33; ri: 33]

17. Scutellum, ventral surface: (0) bare; (1) setulose. ** [L: 2; ci: 50; ri: 87]

**Wing**

18. Wing, coloration: (0) hyaline; (1) brownish. + [L: 1; ci: 100; ri: 100]

19. Costal vein, ventrally: (0) bare; (1) setulose. + [L: 3; ci: 33; ri: 33]

20. Costal vein, setulose: (0) scattered setulose; (1) strongly setulose. + [L: 1; ci: 100; ri: 100]

21. $A_1$ vein, length: (0) not reaching the wing margin; (1) reaching the wing margin. ** [L: 1; ci: 100; ri: 100]

22. Lower calypter, length: (0) very short, reduced to a linear fold; (1) rounded and shorter than upper one; (2) same size than upper one; (3) longer than upper one. * [L: 4; ci: 75; ri: 85]

**Legs**

23. Hind tibia, median posterodorsal seta (calcar), length: (0) as long as tibia width; (1) twice longer than tibia width; (2) three times longer than tibia width. + [L: 5; ci: 40; ri: 66]

**Male terminalia**

24. Cerci, shape (dorsal view): (0) divided; (1) fused, forming a plate. + [L: 1; uninformative]

25. Cerci, shape of cerci as a unique plate (dorsal view): (0) rectangular; (1) triangular, forming an equilateral triangle; (2) quadrangular; (3) long triangular, similar to surstyli length (see Nihei & de Carvalho 2004: Fig. 1a); (4) short triangular, shorter than surstyli (Fig. 5b, l); (5) very short triangular, wider than long (Fig. 5g); (6) trapezoid; (7) wide and short, four times wider than its length. + [L: 8; ci: 87; ri: 83]

26. Cerci, distal region, shape (dorsal view): (0) thin (Fig. 5b); (1) round (Fig. 5l). + [L: 4; ci: 25; ri: 62]

27. Cerci, shape (lateral view): (0) narrow, only half the width exceeding the cerci; (1) enlarged, completely exceeding the cerci (Fig. 5c, h, m). + [L: 1; ci: 100; ri: 100]

28. Cerci, shape (lateral view): (0) short and rounded, as long as its wide (see Couri 1979: Fig. 3); (1) long and narrow, medial and distal region with similar width (Fig. 5m); (2) long and enlarged, medial region more than twice wider than distal region (Fig. 5c); (3) very long and narrow, cerci as long as surstyli (see Nihei & de Carvalho 2004: Fig. 1c); (4) very short and narrow (Fig. 5h). + [L: 4; ci: 100; ri: 100]

29. Surstyli, shape: (0) symmetrical; (1) asymmetrical. ** [L: 1; ci: 100; ri: 100]

30. Surstyli, width (lateral view): (0) about ¼ of the epandrium width (Fig. 5h); (1) about half of the epandrium width (Fig. 5m); (2) about ¾ of the epandrium width (Fig. 5d). + [L: 3; ci: 66; ri: 90]

31. Surstyli, shape (lateral view): (0) straight (Fig. 5h); (1) slightly curved (Fig. 5m); (2) strongly curved (see Michelsen 1991: Fig. 27). + [L: 8; ci: 25; ri: 40]

32. Surstyli, proximal projection (lateral view): (0) absent; (1) present (Fig. 5c, h, m). + [L: 1; ci: 100; ri: 100]

33. Surstyli, proximal projection, length (lateral view): (0) reaching the epandrium (Fig. 5m); (1) exceeding the epandrium (Fig. 5c). + [L: 1; ci: 100; ri: 100]

34. Pregonite, distal region, number of setulae: (0) 1; (1) 2. ** [L: 2; ci: 50; ri: 66]

35. Pregonite, medial region, setula: (0) absent; (1) present. ** [L: 3; ci: 33; ri: 33]

36. Pregonite, medial region, number of setulae: (0) 1; (1) 2. ** [L: 1; ci: 100; ri: 100]

37. Pregonite, length: (0) similar to postgonite; (1) longer than postgonite. ** [L: 5; ci: 20; ri: 60]

38. Pregonite, distal region: (0) bare (Fig. 5e, j); (1) covered by setulae (Fig. 5o). *** [L: 1; ci: 100; ri: 100]

39. Postgonite, shape: (0) triangular; (1) quadrangular (Fig. 5 e, j, o). + [L: 3; ci: 33; ri: 60]

40. Postgonite, long seta: (0) absent; (1) present. + [L: 2; ci: 50; ri: 66]

41. Epiphallus: (0) absent; (1) present. + [L: 1; ci: 100; ri: 100]

42. Phalapodema, shape: (0) straight; (1) curved. + [L: 2; ci: 50; ri: 66]

SUPPLEMENTARY MATERIAL

**Table S1.** List of material examined for the phylogenetic analysis.

| Family | Species | Label information |
|---|---|---|
| Anthomyiidae | *Anthomyia pluripunctata* (Albuquerque, 1959) | Brazil, Santa Catarina, Nova Teutônia, v.1970, F. Plaumann, 1#; viii.1967, 1@ (MZUSP) |
| Anthomyiidae | *Calythea comis* (Stein, 1911) | Chile, Valparaíso, x.1969, L. Peña, 2## and 2@@ (MZUSP) |
| Anthomyiidae | *Coenosopsia albuquerquei* Bortolanza et al., 2006 | Brazil, Paraná, Telêmaco Borba, 25.vii.1988, Lev. Ent. PROFAUPAR, 1# (Holotype) (DZUP); 24.vii.1987, 1@ (DZUP) |
| Anthomyiidae | *Coenosopsia azteca* sp. nov. | Mexico, Morelos, 8. xii.1978, J. Butze, 1# (Holotype) (CNIN). |
| Anthomyiidae | *Coenosopsia brasiliensis* Michelsen, 1991 | Brazil, Rio de Janeiro, Serviço Febre Amarela M. E. S. Bras., x.1938, 1# (Holotype) (MNRJ) and 1@ (Paratype) (MNRJ) |
| Anthomyiidae | *Coenosopsia ferrari* Nihei & de Carvalho, 2004 | Brazil, Distrito Federal, 9.xii.1997, I. R. Diniz, 1# (Holotype) (DZUP) and 1@ (Paratype) (DZUP) |
| Anthomyiidae | *Coenosopsia floridensis* Michelsen, 1991 | Mexico, Veracruz, Est. Biol. Los Tuxtlas, A. Ibarra et al., 17-18.iv.1986, 1# (CNIN); Córdoba, L. Delgado, 17.ii.1999, 1@ (IEXA) |
| Anthomyiidae | *Coenosopsia limeirai* sp. nov | Brazil, Ceará, Parque Nac. de Ubajara, 18-30.xi.2012, F. Limeira-de-Oliveira, et al., 1# (Holotype) (CZMA); 1@ (Paratype) (CZMA) |
| Anthomyiidae | *Coenosopsia mexicana* Michelsen, 1991 | Mexico, Veracruz. Coatepec, S. Ibañez & F. A. Pech, 19.iii.2004, 1# and 2@@ (IEXA) |
| Anthomyiidae | *Coenosopsia michelseni* Nihei & Carvalho, 2004 | Brazil, Distrito Federal, 13.v.1997, I. R. Diniz, 1# (Holotype) (DZUP) and 1@ (Paratype) (DZUP) |
| Anthomyiidae | *Coenosopsia peruviana* Michelsen, 1991 | Brazil, Amazonas, Autaz-Mirim, 26.viii.1994, J. Vidal, 1# (INPA); Manaus, 09-16.iii.1989, Y. Camara & J. E. Binda, 1@ (INPA) |
| Anthomyiidae | *Coenosopsia prima* Malloch, 1924 | Costa Rica. Puntarenas, M. Lobo, 3-6.v.1998, 1# (INBIO); Panama, Canal Zone, 9.iii.1967, Roger D. Akre, 1@ (Paratype) (WSU) |
| Anthomyiidae | *Coenosopsia ribeiroi* sp. nov. | Brazil,Rio Grande do Sul, Arroio Grande, 30.viii.2002, P. B. Ribeiro, 1# (Holotype) (DZUP); 1@ (Paratype) (DZUP) |
| Anthomyiidae | *Delia platura* (Meigen, 1826) | England, Oxford, Burguess Field Park, 23.viii.2003, S. S. Nihei, 2##; Oxon, Henley, 18.vi.1992, C. Carvalho, 1@ (DZUP) |

| | | |
|---|---|---|
| Anthomyiidae | *Fucellia tergina* (Zetterstedt, 1845) | Brazil, Rio de Janeiro, Angra dos Reis, H. S. Lopes, 23.vi.1972, 2##; 27.vi.1972, 2@@ (DZUP) |
| Anthomyiidae | *Hydrophoria ruralis* (Meigen, 1826) | England, Oxford, Brasenose Wood, 14.ix.2003, S. S. Nihei, 1# (DZUP) |
| Anthomyiidae | *Leucophora maculipennis* (Albuquerque, 1953) | Brazil, Paraná, São José dos Pinhais, 04.xi.1986, Lev. PROFAUPAR, 1#; 31.x.1986, 1@ (DZUP) |
| Anthomyiidae | *Pegomya poeciloptera* Malloch, 1921 | Brazil, Rio Grande do Sul, Morro Redondo, 26.vii.2002, R. F. Krüger, 1# (DZUP); 09.v.2003, 1@ (DZUP) |
| Anthomyiidae | *Phaonantho benevola* Couri, 1979 | Brazil, Mato Grosso, Sinop, x.1976, Alvarenga & Roppa, 1# (Holotype) (MNRJ); x.1975, 1@ (Paratype) (MNRJ) |
| Anthomyiidae | *Phaonantho mallochi* (Curran, 1934) | Brazil, Paraná, Jundiaí do Sul, 16.xi.1987, 1# (DZUP); 03.xi.1986, 1@ (DZUP) |
| Anthomyiidae | *Phaonantho sordilloae* Pamplona & Couri, 1993 | Brazil, Rio de Janeiro, xi.1988, C. M. O. Sordillo, 1# (Holotype) (MNRJ); 1@ (Paratype) (MNRJ) |
| Scathophagidae | *Scathophaga stercoraria* (Linnaeus, 1758) | England, Oxford, 20.xii.1984, C. Elias, 1# and 1@ (DZUP) |

**Table S2.** Matrix of characters of *Coenosopsia* species and outgroup. Non-applicability of characters to taxa is indicated by "–".

| Species | 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 4 4 4<br>1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 |
|---|---|
| *Scathophaga stercoraria* | 1 0 0 0 1 0 1 1 0 1 0 1 1 0 0 1 0 0 1 0 1 0 2 0 – 2 0 – 0 0 2 0 – 0 1 0 1 0 0 0 1 0 |
| *Anthomyia pluripunctata* | 1 1 0 1 1 0 0 1 0 0 1 0 1 1 2 0 1 0 1 0 1 1 2 1 1 0 0 – 0 0 1 0 – 1 0 – 0 0 0 1 1 0 |
| *Calythea comis* | 0 0 1 1 0 – 0 1 0 0 1 0 0 1 1 1 1 0 0 – 1 3 1 1 1 1 0 – 0 0 1 0 – 0 1 0 0 0 0 1 1 1 |
| *Delia platura* | 0 0 1 0 1 0 0 1 0 0 1 1 0 0 1 1 1 0 0 – 1 1 2 1 0 1 0 – 0 0 0 0 – 0 0 – 0 0 0 0 1 0 |
| *Fucellia tergina* | 0 0 1 1 1 0 1 1 0 1 3 1 0 0 2 1 0 0 0 – 1 0 2 1 7 2 0 – 0 0 1 0 – 0 0 – 0 0 1 0 1 0 |
| *Hydrophoria ruralis* | 2 1 1 0 1 0 0 1 0 0 1 1 0 1 3 0 1 0 1 1 1 2 2 1 0 1 0 – 0 0 0 0 – 0 1 0 1 0 0 1 1 0 |
| *Leucophora maculipennis* | 2 0 1 1 1 2 0 0 – 0 3 1 0 0 1 1 1 0 0 – 1 1 2 1 6 2 0 – 0 0 0 0 – 0 0 – 0 0 1 0 1 0 |
| *Pegomya poeciloptera* | 0 1 0 0 1 0 0 1 1 0 1 0 1 1 3 1 1 0 1 0 1 1 1 1 6 2 0 – 0 0 1 0 – 0 1 0 0 0 0 1 1 0 |
| *Phaonantho benevola* | 2 2 1 0 1 1 0 1 1 0 1 0 0 1 1 0 1 1 1 1 0 3 1 1 2 2 1 0 0 1 0 0 – 1 1 1 0 0 1 0 0 0 |
| *Phaonantho mallochi* | 2 2 1 0 1 1 0 1 1 0 0 0 0 1 1 1 1 0 1 1 0 3 1 1 2 2 1 0 0 1 1 0 – 1 1 1 0 0 1 0 0 0 |
| *Phaonantho sordilloae* | 2 2 1 0 1 1 0 1 1 0 2 0 0 1 1 0 1 1 1 1 0 3 2 1 2 2 1 0 0 1 2 0 – 1 1 1 0 0 1 0 0 0 |
| *Coenosopsia albuquerquei* | 2 2 1 1 1 0 1 1 0 1 1 1 0 1 1 1 0 0 1 1 0 2 0 1 3 0 1 3 1 0 1 1 0 0 1 0 1 1 1 0 1 0 |
| *Coenosopsia azteca* | 2 2 1 1 1 0 1 1 0 1 0 1 0 1 1 1 0 0 1 1 0 2 0 1 4 0 1 2 1 1 0 1 1 0 1 0 1 0 1 0 1 0 |
| *Coenosopsia brasiliensis* | 2 2 1 1 1 0 1 1 0 1 2 1 0 1 1 1 0 0 1 1 0 2 0 1 4 0 1 1 1 1 0 1 0 0 1 0 0 0 1 0 1 1 |
| *Coenosopsia ferrari* | 2 2 1 1 1 0 1 1 0 1 1 1 0 1 1 1 0 0 1 1 0 2 0 1 3 0 1 3 1 0 1 1 0 0 1 0 0 1 1 0 1 0 |
| *Coenosopsia floridensis* | 2 2 1 1 1 0 1 1 0 1 2 1 0 1 1 1 0 0 1 1 0 2 0 1 4 0 1 2 1 2 2 1 1 0 1 0 1 0 1 0 1 0 |
| *Coenosopsia limeirai* | 2 2 1 1 1 0 1 1 0 1 0 1 0 1 1 1 0 0 1 1 0 2 0 1 5 0 1 4 1 1 0 1 0 0 1 0 1 0 1 0 1 1 |
| *Coenosopsia mexicana* | 2 2 1 1 1 0 1 1 0 1 0 1 0 1 1 1 0 0 1 1 0 2 0 1 4 0 1 2 1 2 2 1 1 0 1 0 1 0 1 0 1 0 |
| *Coenosopsia michelseni* | 2 2 1 1 1 0 1 1 0 1 2 1 0 1 1 1 0 0 1 1 0 2 0 1 4 1 1 2 1 2 1 1 1 0 1 0 1 0 1 0 1 0 |
| *Coenosopsia peruviana* | 2 2 1 1 1 0 1 1 0 1 2 1 0 1 1 1 0 0 1 1 0 2 0 1 4 0 1 1 1 1 0 1 0 0 1 0 1 0 1 0 1 1 |
| *Coenosopsia prima* | 2 2 1 1 1 0 1 1 0 1 1 1 0 1 1 1 0 0 1 1 0 2 0 1 4 1 1 1 1 1 0 1 1 0 1 0 1 0 1 0 1 0 |
| *Coenosopsia ribeiroi* | 2 2 1 1 1 0 1 1 0 1 1 1 0 1 1 1 0 0 1 1 0 2 0 1 4 1 1 1 1 1 1 1 1 0 0 1 0 1 1 1 0 1 0 |

**Table S3.** Values of the constant of concavity (*k*) applied in the analysis with implied weighting with their respective number of steps (L), consistency index (IC), retention index (IR), fit value and number of trees generated.

| k | L | IC | IR | fit | trees |
|---|---|---|---|---|---|
| **-** | 117 | 54 | 74 | 29.44226 | 2 |
| **1** | 119 | 53 | 73 | 23.57500 | 2 |
| **2** | 118 | 54 | 74 | 27.36032 | 1 |
| **3** | 118 | 54 | 74 | 29.60714 | 1 |
| **4** | 118 | 54 | 74 | 31.09062 | 1 |
| **5** | 118 | 54 | 74 | 32.15278 | 1 |
| **6** | 117 | 54 | 74 | 32.95758 | 1 |
| **7** | 117 | 54 | 74 | 33.59452 | 1 |
| **8** | 117 | 54 | 74 | 34.10725 | 1 |
| **9** | 117 | 54 | 74 | 34.52942 | 1 |
| **10** | 117 | 54 | 74 | 34.88341 | 1 |
| **15** | 117 | 54 | 74 | 36.04568 | 1 |
| **20** | 117 | 54 | 74 | 36.69334 | 1 |
| **30** | 117 | 54 | 74 | 37.39480 | 1 |
| **60** | 117 | 54 | 74 | 38.15957 | 1 |

## CAPÍTULO IV

NEW RECORDS OF *PHAONANTHO* ALBUQUERQUE (DIPTERA: ANTHOMYIIDAE) FROM NEOTROPICAL REGION

***Capítulo no formato do Papéis Avulsos de Zoologia***

# New records of *Phaonantho* Albuquerque (Diptera: Anthomyiidae) from Neotropical region

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ABSTRACT

*Phaonantho* Albuquerque (Diptera, Anthomyiidae) is a Neotropical genus with three known species. The genus is characterized by antennae plumose; female with a pair of interfrontal setae; apex of scutellum setulose ventrally; vein $A_1$ short, not reaching the wing margin; lower calypter twice longer than the upper one; hind tibia with a submedian anteroventral seta, three anterodorsal setae, and a median posterodorsal seta (calcar) twice longer than tibia width. Herein, we update the distributional knowledge of the species of *Phaonantho*, including the first record of the genus in Bolivia, Paraguay, Peru and Mexico; and several new records for Brazil.

**Key words:** biodiversity, checklist, distribution, South America.

## INTRODUCTION

*Phaonantho* Albuquerque is a Neotropical genus comprising three described species (Pamplona & Couri, 1993), distributed from Central America to southern Brazil. This distributional pattern is an exception if compared with the distribuition of the most genera of neotropical anthomyiids, which are scarce or absent in the warm lowland forest (Michelsen, 1996). Albuquerque (1957) previously described *Phaonantho* as Muscidae, at that time the anthomyiid flies were considered a subfamily of Muscidae and he indicated the genus as an intermediary form between Phaoniinae (Muscidae) and Anthomyiinae. The cilia on ventral apex of scutellum, interfrontal setae on female, three anterodorsal setae on hind tibia and general aspect resemble Anthomyiidae; while the lower calypters longer than the upper one,

vein $A_1$ short, not reaching the wing margin, and posterodorsal calcar on hind tibia resemble Phaoniinae.

Few studies have been conducted regarding *Phaonantho* taxonomy (Curran, 1934; Albuquerque, 1957; Couri, 1979; Pamplona & Couri, 1993). The genus has been indicated as the sister group of *Coenosopsia* Malloch based on morphological (Michelsen, 1991; Gomes & de Carvalho, in progress) and molecular evidence (Gomes et al., 2021). The origin of the clade *Coenosopsia* + *Phaonantho* was dated to the Oligocene/Miocene boundary (circa 23 Ma), while the diversification of the *Phaonantho* species occurred in the Pliocene (circa 3 Ma) (Gomes et al., 2021). Also, Michelsen (1991) suggested the clade *Coenosopsia+Phaonantho* as the sister group of remaining Anthomyiidae, but this hypothesis has been contested based on phylogenetic analysis based on morphological (Nihei & de Carvalho, 2004; Bortolanza et al., 2006; Gomes & de Carvalho, in progress) and molecular data (Gomes et al. 2021).

Gomes & de Carvalho (in progress) indicated *Phaonantho* as monophyletic based on three synapomorphies: two proclinate orbital setae on female, two median setulae on pregonite, and epiphallus absent; and six homoplasies: one reclinate orbital seta on female, prosternum narrow, lower calypter longer than the upper one, cerci distally with a quadrangular margin, two long distal setulae on pregonite, and pregonite as long as postgonite.

Herein, we present a substantial contribution to the distributional knowledge of *Phaonantho* in the Neotropical region. Also, we present an updated identification key and discuss the collect methods and distribution of the genus.

## MATERIAL AND METHODS

The studied material is deposited in the following institutions: Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (CCT-UFMG); Colección Nacional de Insectos, Ciudad de Mexico, Mexico (CNIN); Coleção Zoológica do Maranhão, Caxias, Brazil (CZMA); Canadian National Collection of Insects, Ottawa, Canada (CNC); Padre Jesus Santiago Moure Entomological Collection, Curitiba, Brazil (DZUP); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP);

Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia (UASC); United States National Museum, Washington D.C., USA (USNM).

The morphological terminology followed Cumming & Wood (2017). For examination of the male and female terminalia, the abdomen was removed from a dry specimen and was placed in cold potassium hydroxide (KOH) 10% for 24h to soften and lighten the parts. The abdomen was transferred to acetic acid, and then to glycerin. The postabdomen structures were separated from the rest of the abdomen. Examination and illustration of the structures were done using a microscope and a stereomicroscope with a camera lucida attached to it. Dissected terminalia were placed in glycerin, inside microvials pinned beneath the respective specimens. Images of specimens were obtained with sequential images mounting at different focal planes with a NIKON D610 digital camera coupled to a LEICA M165 C stereomicroscope. The images were stacked and edited using Adobe Photoshop CS6. The distribution map was produced using the software QGIS (available in: http://www.qgis.org/en/site/), with the shapefile of Löwenberg-Neto (2014) based on the biogeographical regionalization proposed by Morrone (2014). The literature distribution is based on Curran (1934), Albuquerque (1957), Couri (1979), Linhares (1981), Oliveira (1986), D'Almeida (1992), Pamplona & Couri (1993), Nihei & de Carvalho (2004).

## RESULTS

### Taxonomy

***Phaonantho* Albuquerque, 1957**

Type-species. *Phaonantho devia* Albuquerque, 1957

**Diagnosis.** Male holoptic (Figs. 1A, 2A, 3A) and female dichoptic (Figs. 1D, 2D, 3D). Male frons at narrowest point with contiguous fronto-orbital plates (Figs. 1A, 2A, 3A). 2 pairs of frontal setae. Gena, proboscis and antennae light to dark brown. Antennae plumose. Palpi filiform. Female with a pair of interfrontal setae, two pairs of proclinate orbital seta (the upper one very short) and 1 pair of reclinate orbital seta (Figs. 1D, 2D, 3D). 1-2 anterior anepisternal setae. Prealar seta shorter than the posterior notopleural seta. Apex of scutellum setulose ventrally. Prosternum bare. Dorsocentral setae 2+3. Katepisternal setae 1+2, lower and upper katepisternal setae with similar length in males. Wing hyaline or brownish without spots. Veins

bare, except for the presence of microtrichia, also present on the wing membrane. Vein $A_1$ short, not reaching the wing margin (Figs. 1C, F). Lower calypter twice longer than the upper one. Male fore tibia with a median seta on posteroventral surface. Female fore tibia with a median seta on anterodorsal and posteroventral surface. Hind tibia with a submedian anteroventral seta, three anterodorsal setae, and a median posterodorsal seta (calcar) twice longer than tibia width. Fore and hind basitarsus with a conspicuous ventrobasal seta. Abdomen light brown, basally yellowish. Tergites with marginal setae developed, the lateral ones longer. Sternite 1 setulose. Male terminalia: surstyli bifurcated, shorter than cerci; cerci wide and rounded, as long as epandrium width on lateral view; pregonite covered by long setae.

**Key to *Phaonantho* species (updated from Pamplona & Couri, 1993)**

1. Thorax yellowish with golden pruinose (Figs. 2B, C, E, F); 5-6 posterior setae on anepisternum; wing hyaline … *P. mallochi* (Curran, 1934)

-. Thorax dark brown with gray pruinose (Figs. 1B, C, E, F; 3B, C, E, F); at most 4 posterior setae on anepisternum; wing brownish … 2

2. Palpi light brown; wing brownish, darker between $R_{4+5}$ and Costal vein (Figs. 1B, E); male with sternite 5 and cerci covered by several long setae … *P. benevola* Couri, 1979

-. Palpi yellow; wing slightly brownish, darker between $R_{4+5}$ and Costal vein (Fig. 3B), females usually have darker wings (Fig. 3E); male with sternite 5 and cerci not covered by several long setae … *P. sordilloae* Pamplona & Couri, 1993

***Phaonantho benevola* Couri, 1979**

(Figs. 1, 4)

*Phaonantho benevola* Couri, 1979:525, figs. 1-10 (Holotype male, MNRJ) (Paratypes male and female, MNRJ); Pamplona & Couri, 1993: 558

**Diagnosis.** Thorax dark brown with yellow pruinose (Figs. 1B, C, E, F). Palpi and antennae light brown (Figs. 1A, D). Wing brownish (Figs. 1B, C, E, F). Calypters dark brown. Cerci and sternite 5 covered by several long setae (male) (Fig. 1C).

**Type-material examined.** Holotype. Male. Mato Grosso, Sinop, 12° 31’ 55° 37’ W, BR 163, km 500–600, Alvarenga & Roppa, x.1975 (MNRJ). Paratypes. Same as holotype, except: iii.1976, 3♀♀ (MNRJ); x.1975, 1♂ (MNRJ).

**Additional material examined.** Bolivia. Cochabamba. San Antonio-Cotacajes [-16.85973, -66.75930], 900m, Pruett, Rogg & Cuellar, 26.viii.1992, 1♂ (DZUP); La Paz. Palos Blancos, Alto Beni [-15.583164, -67.252984], 600 m, L. E. Pena, 11-15.i.1976, 1♀ (DZUP); Santa Cruz. Ichilo, P. N. A. Río Cheio [-17.798140, -64.211760], 645 m, Paulo Bettella, 9.ii.1990, 1♀ (UASC); Potrerillo del Guenda, clearing [-17.67074, -63.45763], 401m, B. D. Sutton, A. L. Norrbom & E. Quisberth, 9-17.x.2014, 2♂♂ (DZUP, USNM) and 1♀ (USNM). Brazil. Acre. Bujari, FES Antimary [-9.333611, -68.321388], Malaise trap, E. F. Morato & J. A. Rafael, 18-31.vii.2017, 1♂ (DZUP); same label information, except: 22.ix-06.x.2016, 2♀♀ (INPA); Amazonas. Manaus [-2.999727, -59.939081], Shannon trap, M. C. Castilho & E. Bindá, 14-17.v.1988, 1♂ and 1♀ (INPA); Est. do Aleixo [-3.092208, -59.924512], E. V. Silva, 4.vii.1969, 1♀ (INPA); Barcelos, Rio Aracá, Comuni. Bacuquara [-0.154861, -63.1764440], S. S. Oliveira, J. T. Camara, J. A. Rafael & V. Linard, 12-14.vi.2010, 1♂ (DZUP); Rio Abacaxis, Flona P. Rosa [-5.2525, -58.6977], Light trap, J. A. Rafael, 29-29.v.2008, 2♀♀ (DZUP); Manaus, Reserva Ducke [-2.999727, -59.939081], Light trap, Norman Penny, 2.v.1978, 1♀ (DZUP); same label information, except: L. P. Albuquerque, 26.iv.1978, 1♂ (INPA); L. P. Albuquerque, 24.i.1978, 1♀ (INPA); L. P. Albuquerque, 11.iii.1978, 1♀ (INPA); J. A. Rafael & J. Vidal, 07-21.xi.1994, 1♀ (DZUP); C. Univers., Malaise trap, J. A. Rafael, 29.vi.1982, 1♀ (DZUP); A. Faustino, v.1968, 1♀ (INPA); A. Faustino, 29.vii.1970, 1♀ (INPA); AM 010, km31 [-2.999727, -59.939081], Shannon trap, L. Albuquerque & J. E. Binda, 2.i.1991 (INPA); Tefé, Terra Firme [-3.421944, -64.615055], Malaise trap, J. A. Oliveira, D. M. M. Mendes & J. A. Rafael, 20-31.xii.2016, 1♀ (INPA); same label information, except: 5-17.ix.2016, 1♂ (DZUP); Novo Airão, Rod. AM352, km-68, Igarapé Mato Grosso [-2.816111, -60.921666], J. A. Rafael & F. F. Xavier Fº, 3-17.vii.2017, 1♀ (INPA); Maranhão. Carolina PARNA Chapada das Mesas, Riacho Sucuruiu [-7.118222, -47.308777], 240 m, Malaise trap, J. A. Rafael et al., 01-10.i.2014, 1♂ and 1♀ (CZMA); same label information, except: 01-10.vii.2013, 4♀♀ (CZMA); 10-20.ix.2014, 1♀ (CZMA); Carolina PARNA Chapada das Mesas, Riacho Sucuruiu [-7.073388, -47.090333], 288 m, Malaise trap, J. A. Rafael et al., 20-30.vi.2014, 1♂ and 1♀ (CZMA); same label information, except: 20-31.viii.2014, 1♂ (CZMA); 10-20.vi.2014, 1♂ (CZMA); 01-10.ix.2014, 1♀ (CZMA); Carolina PARNA Chapada das Mesas, Riacho Sucuruiu [-7.118222, -47.308694], Malaise trap, F. Limeira-de-Oliveira, 1-10.iii.2014, 1♂ (DZUP); Carolina PARNA Chapada das Mesas,

Riacho Cancela [-7.112277, -47.299111], 225m, Malaise trap, J. A. Rafael & F. Limeira-de-Oliveira, 20-31.x.2013, 1♀ (CZMA); same label information, except: 14-30.vi.2013, 1♀ (CZMA); C. N. Maranhão REBIO - Res. Biol. Gurupi [-3.234722, -46.6833], F. Limeira-de-Oliveira & D. W. A. Marques, 01-06.iii.2011, 2♀♀ (CZMA); same label information, except: 07-15.i.2011, 1♂ (CZMA); Caxias, Zona Rural, Pov. Olho D'água das Moças [-4.661944, -43.053611], J. A. Rafael et al., 24.vii.2012, 1♂ and 2♀♀ (CZMA); Caxias, Caxias, Reserva Ecol. Inhamum [-4.906666, -43.438888], Malaise trap, F. Limeira-de-Oliveira et al., 10-20.ix.2017, 2♂♂ and 3♀♀ (CZMA); same label information, except: 20-30.vi.2017, 1♂ (CZMA); 20-28.ii.2017, 1♀ (CZMA); Mirador Parque Est. Mirador Base da Geraldina [-6.623611, -45.868888], Malaise trap, F. Limeira-de-Oliveira et al., 13-19.x.2012, 2♀♀ (CZMA); same label information, except: 14-18.viii.2012, 7♂♂ and 7♀♀ (CZMA); J. C. Silva & M. M. Abreu, 07-14.v.2010, 1♂ (CZMA); 02-26.x.2006, 1♀ (CZMA); Mirador Parque Est. Mirador Base da Geraldina [-6.808055, -45.109444], F. Limeira-de-Oliveira & D. W. A. Marques, 27.ix-02.x.2011, 1♂ (CZMA); Mato Grosso. Chapada dos Guimarães [-15.464939, -55.750653], Exc. Dep. Zool. UFPR, 06.xii.1983, 06.xii.1983, 1♀ (DZUP 099215); Pará. Belém, Mocambo [-2.234902, -53.854075], M. F. Torres, 21.iii.1978, 1♂ (MPEG); Belém, Bosque Rodrigues Alves [-1.430348, -48.456654], F. S. Carvalho-Filho, 30.x.2005, 1♂ and 1♀ (MPEG); Jacundá [-4.614514, -49.182549], 17.iii.1981, 1♂ (INPA); Monte Dourado [-0.868158, -52.538813], T. Gardner, v.2005, 1♂ (MPEG); Morro do Senador [-3.989722, -49.745833], Malaise trap, J. A. Rafael & J. Vidal, xii.2001, 1♂ (INPA); Novo Repartimento, Vicinal [-4.445, -49.906944], Malaise trap, J. A. Rafael & J. Vidal, 28.xi.2001, 1♂ and 1♀ (INPA); same label information, except: [-4.364166, -50.030277], 27.xi.2001, 4♂♂ and 4♀♀ (INPA); Tucuruí [-3.712826, -49.729370], Nunes de Mello, 6.viii.1980, 31 ♂♂ and 4♀♀ (INPA); same label information, except: 04.viii.1980, 4♂♂ and 4♀♀ (INPA); 17.viii.1980, 1♂ and 1♀ (INPA); Piauí. Piracuruca, P. N. de Sete Cidades, Posto do ICMBio [-4.099166, -41.709444], J. A. Rafael & F. Limeira-de-Oliveira, 19-24.iv.2012, 2♀♀ (CZMA); Rio de Janeiro. Petropolis [-22.420340, -43.162778], 900 m, E. G. I. & E. A. Munroe, xi.1971, 1♀ (CNC); Rondônia. Vilhena [-12.739081, -60.132936], C. Elias, 29.x.1986, 2♀♀ (DZUP 099216-17); same label information, except: 23.xi.1986, 2♀♀ (DZUP; DZUP 099218); 09.x.1986, 1♀ (DZUP); 15x.1986, 1♀ (DZUP); Roraima. Caracaraí, PARNA Viruá [1.489722, -61.003333], J. A. Rafael & R. Boldrini, 24.xii.2015, 1♂ (DZUP2020A12); Pacaraima [4.478494, -61.147079],

Shannon trap, J. A. Rafael, 5-8.iii.1988, 1♀ (DZUP); Rio Uraricoera, Ilha de Maraca [3.413441, -61.277408], J. A. Rafael & L. S. Aquino, 19-24.vii.1987, 1♀ (DZUP 463155); same label information, except: 18-28.viii.1987, 1♀ (INPA). Peru. Cusco, Estacion Biologica Villa Carmen [-12.894166, -71.403888], 540 m, A. L. Norrbom & B. D. Sutton, 12-14.xii.2013. 1♂ (USNM); Quincemil [-13.530514, -71.955476], 700 m, L. Pena, 1-15.xi.1962, 1♀ (CNC); Madre de Dios. Avispas [-12.163910, -70.896098], 400 m, L. Pena, 10-20.ix.1962, 1♂ (CNC); same label information, except: 400 m, L. Pena, 1-15.ix.1962, 1♀ (CNC); CICIA, Trail 2 [-12.56104, -70.10645], Malaise trap, 267m, T. Perez, 17-24.xii.2013, 1♂ (DZUP).

**Distribution.** Bolivia* (Cochabamba*, La Paz*, Santa Cruz*), Brazil (Acre*, Amazonas*, Maranhão*, Mato Grosso, Pará*, Piauí*, Rio de Janeiro, Rondônia*, Roraima*), Peru (Cusco*, Madre de Dios) (Couri, 1979; Nihei & de Carvalho, 2004). *= new records.

**Remarks.** Some specimens were collected with Malaise trap, Light trap, and Shannon trap, including dead fish and feces as bait.

***Phaonantho mallochi* (Curran, 1934)**

(Figs. 2, 4)

*Darwinomyia mallochi* Curran, 1934:468 (male Holotype, AMNH)

*Phaonantho devia* Albuquerque, 1957:191, figs. 1-12 (male Holotype, MNRJ) (Paratypes male and female) (synonymyzed by Couri, 1979:528); Pamplona & Couri 1993:558

**Diagnosis.** Thorax yellowish with silver pruinose (Figs. 2B, C, E, F). Palpi and antennae yellow (Figs. 2A, D). Wing hyaline (Figs. 2B, C, E, F). Calypters whitish. Cerci and sternite 5 not covered by several long setae (male) (Fig. 2C).

**Type-material examined.** Paratypes. Rio de Janeiro. Represa da Cabeça, Corcovado [-22.951993, -43.211569], D. Albuquerque, 28.vii.1946, 1♂ (MNRJ n°5212) and 1♀ (MNRJ n°5217).

**Additional material examined.** Brazil. Bahia. Una [-15.294652, -39.076150], Shannon trap, D. S. Amorim & C. Vasconcelos, 07-25.x.1986, 1♂ and 1♀ (DZUP); Espírito Santo. Ibitirama, Pq. Nac. Caparaó, Trilha da toca de São Jorge [-20.465833, -41.745], Malaise trap, C. O. Azevedo & F. B. Fraga, 16-23.iii.2013, 3♂♂ (DZUP L16; MZUSP); Goiás. Corumbá [-15.926315, -48.811015], M. F. Farretto, xi.1946, 1♀ (DZUP); Minas Gerais. Callado, Rio Doce [-19.336594, -41.232695], 12-

15.ii.1939, 1♀ (MNRJ n°5251); Cambuquira [-21.849743, -45.289764], Lopes & Soares, iii.1941, 1♀ (MNRJ n°5252); São Gonçalo do Rio Abaixo, Estação Ambiental de Peti [-19.880277, -43.368611], 603-808 m, Malaise trap, A. F. Kumagai, 21.vi.1987, 1♂ (CCT-UFMG IDI 1600459); same label information, except: 25.x-1.xi.2002, 2♀♀ (CCT-UFMG IDI 1701023; 1701052); 27.ix.2002, 1♀ (CCT-UFMG IDI 1702519); 17.i.2003, (CCT-UFMG IDI 1702569); [,-19.880277, -43.368333], 4.ix.2002, 3♀♀ (CCT-UFMG IDI 1702551; 1704050; 1702535); 17.i.2003, 1♀ (CCT-UFMG IDI 1702561); Belo Horizonte, Campus CCT-UFMG, Estação Ecológica [-19.875, -43.972222], 842 m, 5.v.1999, 1♀ (CCT-UFMG IDI 1701034); Viçosa [-20.754781, -42.878557], P. F. Ferreira, 19.xi.1984, 1♀ (DZUP 099214); same label information, except: 20.x.1984, 1♀ (DZUP 099238); Santa Catarina. Nova Teutônia [-27.183333, -52.383333], F. Plaumann, v.1967, 1♂ (MZUSP); same label information, except: xii.1967, 1♂ (MZUSP); xi.1970, 1♂ (MZUSP); São Paulo. Botucatu, Fundort [-22.887674, -48.445284], I. G. Gottsberger, 20.ix.1977, 1♂ and 1♀ (DZUP); [unknown locality and collector], 20.xii.1984, 1♀ (DZUP 099213); H. Florestal, Chapadão [-23.550130, -46.635242], F. Lane, viii.1946, 1♀ (MNRJ n°5223); Ilha Seca [-23.550130, -46.635242], Com. Inst. Osw. Cruz, 19-26.1940, 1♀ (MNRJ n°5250); Jundiaí, Serra do Japi [-23.230670, -46.955961], A. X. Linhares, 21.ii.1999, 1♀ (DZUP 159828); same label information, except: 24.ii.1999, 1♀ (DZUP); Peruíbe, Est. Ecol. Juréia-Itatins [-24.366666, -47.016666], Shannon trap, M. L. Cavallari, 03.v.2011, 2♀♀ (DZUP); Paraíba. João Pessoa, Mata do Buraquinho [-7.139444, -34.860277], R. C. A. P. Farias, 09.ix.2009, 1♂ (DZUP 463085); same label information, except: 10.ix.2009, 2♂♂ (DZUP 463086; 463092); 04.ix.2009, 1♂ (DZUP 463087) and 1♀ (DZUP 463095); 01.ix.2009, 2♂♂ (DZUP 463088-89) and 1♀ (DZUP 463097); 09.ix.2009, 2♂♂ (DZUP 463090-91); 07.ix.2009, 1♂ (DZUP 463093); 3.ix.2009, 2♀♀ (DZUP 463094; 463096); 11.iii.2010, 1♂ (DZUP); 19.viii.2010, 2♂♂ (DZUP); 05.ix.2009, 1♂ (DZUP); Paraná. Antonina, Reserva Sapitanduva [-25.439498, -48.746125], Light trap, Lev. Ent. PROFAUPAR, 03.xii.1986, 2♀♀ (DZUP); Reserva Natural da Guaricica [-25.313611, -48.704166], 244m, Entom. UFPR 2017, 27.x.2017, 1♀ (DZUP); Fênix, Reserva Est. ITCF [-23.912610, -51.959757], Malaise trap, Lev. Ent. PROFAUPAR, 06.ix.1986, 1♀ (DZUP 099163); same label information, except: 14.ix.1987, 1♀ (DZUP 099182); 20.vi.1988, 1♀ (DZUP 099183); 22.xii.1986, 1♀ (DZUP); 15.xii.1986, 1♀ (DZUP); Guarapuava, Est. Águas Sta. Clara [-25.632814, -51.964977], Malaise trap,

22.ix.1986, 3♀♀ (DZUP 099165-67); same label information, except: 06.iv.1987, 1♀ (DZUP 099168); 10.xi.1986, 1♀ (DZUP 099169); Jundiaí do Sul, Fazenda Monte Verde [-23.423531, -50.281910], Malaise trap, Lev. Ent. PROFAUPAR, 16.xi.1987, 1♂ (DZUP 159783) and 2♀♀ (DZUP 099180-81); same label information, except: 09.v.1988, 1♂ (DZUP 159784); 23.v.1988, 1♂ (DZUP 159785); 25.i.1988, 1♂ (DZUP 159786); 02.xi.1987, 1♂ (DZUP 159787); 24.xi.1986, 1♂ (DZUP 159788) and 1♀ (DZUP 099152); 08.ix.1986, 1♀ (DZUP 099157); 11.iv.1988, 1♀ (DZUP 099158); 09.xi.1987, 1♀ (DZUP 099159); 13.x.1986, 1♀ (DZUP 099160); 03.xi.1986, 2♀♀ (DZUP 099161-62); 25.viii.1986, 2♀♀ (DZUP 099153-54); 27.x.1986, 1♀ (DZUP 099155); 01.ix.1986, 1♀ (DZUP 099156); 12.x.1987, 1♀ (DZUP 463136); Telêmaco Borba, Res. Biol. Samuel Klabin [-24.297941, -50.618785], Malaise trap, Lev. Ent. PROFAUPAR, 26.x.1987, 1♂ (DZUP 159789); same label information, except: 03.viii.1987, 1♂ (DZUP 159790) and 3♀♀ (DZUP 159856-58); 24.viii.1987, 1♂ (DZUP 159791) and 1♀ (DZUP 099173); 02.xi.1987, 14♀♀ (DZUP 099178-79; 159793; 463121; 463124-33); 26.x.1987, 7♀♀ (DZUP 099170-71; 159794; 159849-51; 463098); 14.iii.1988, 1♀ (DZUP 159795); 08.ii.1988, 2♀♀ (DZUP 159796-97); 25.i.1988, 2♀♀ (DZUP 159798-99); 18.i.1988, 1♀ (DZUP 159800); 11.i.1988, 1♀ (DZUP 159801); 04.i.1988, 1♀ (DZUP 159802); 21.xii.1987, 3♀♀ (DZUP 159803-05); 14.xii.1987, 6♀♀ (DZUP 159806-11); 07.xii.1987, 7♀♀ (DZUP 159812-18); 12.x.1987, 6♀♀ (DZUP 099177; 159819; 159824-26; 159847); 30.xi.1987, 5♀♀ (DZUP 159820-23; 159848); 08.xii.1986, 1♀ (DZUP 159827); 05.x.1987, 6♀♀ (DZUP 159829; 159868-72); 04.vii.1988, 1♀ (DZUP 159830); 31.viii.1987, 1♀ (DZUP 159831); 19.x.1987, 15♀♀ (DZUP 159832-46); 07.ix.1987, 4♀♀ (DZUP 159852-55); 17.viii.1987, 8♀♀ (DZUP 099174-76; 159859-63); 14.ix.1987, 4♀♀ (DZUP 159864-67); 28.ix.1987, 1♀ (DZUP 099172); 07.ix.1987, 1♀ (DZUP 099426); 18.viii.1986, 2♀♀ (DZUP 159873-74); 29.ix.1986, 1♀ (DZUP 159875); 25.viii.1986, 1♀ (DZUP 159876); 03.xi.1986, 4♀♀ (DZUP 159877-80); 10.xi.1986, 3♀♀ (DZUP 159881-83); 24.xi.1986, 4♀♀ (DZUP 159884-86); 17.xi.1986, 4♀♀ (DZUP 159887-90); 01.xii.1986, 1♀ (DZUP 159891); 13.x.1986, 2♀♀ (DZUP 159892-93); 27.x.1986, 4♀♀ (DZUP 159894; 099147-49); 29.xi.1986, 1♀ (DZUP 099150); 20.x.1986, 1♀ (DZUP 099151); 21.ix.1987, 10♀♀ (DZUP 463099; 463102-04; 463111-13; 463116-18); 23.xi.1987, 6♀♀ (DZUP 463100; 463114; 463119-20; 463122-23); 16.xi.1987, 7♀♀ (DZUP 463101; 463105-07; 463109-10; 463115); 09.xi.1987, 1♀ (DZUP 463108); Colombo, EMBRAPA Br476 km20 [-25.321620, -49.159959], Malaise trap,

Lev. Ent. PROFAUPAR, 25.viii.1986, 1♂ (DZUP 159792); same label information, except: 18.viii.1986, 5♀♀ (DZUP 099184-88); 08.ix.1986, 2♀♀ (DZUP 099189-90); 20.x.1986, 1♀ (DZUP 099191); 01.ix.1986, 1♀ (DZUP 099192); 10.xi.1986, 1♀ (DZUP 099193); 11.viii.1986, 1♀ (DZUP 099194); 04.viii.1986, 1♀ (DZUP 099195); 06.x.1986, 1♀ (DZUP 099196); 08.ix.1986, 1♀ (DZUP); Rio de Janeiro. Mangui [-22.940901, -43.230452], C. L. de Paula, iv.1986, 2♂♂ (DZUP 099220-21); Nova Friburgo [-22.287228, -42.528854], 900m, Wygod., i.1946, 2♂♂ (MNRJ n°5213-5214); same label information, except: 1♂ (MNRJ nº5225); 5♀♀ (MNRJ); Rio de Janeiro [-22.932896, -43.222349], Serviço Febre Amarela, M. E. S., iv.1938, 1♂ (MNRJ nº5237); same label information, except: vi.1938, 2♂♂ (MNRJ nº5238-5239); 3♂♂ (MNRJ nº5240-5243); Rio de Janeiro, Grajaú [-22.928777, -43.269320], S. Lopes, 6.x.1939, 1♂ (MNRJ nº5245); same label information, except: 1.viii.1939, 1♂ (MNRJ nº5244); 22.ix.1937, 1♀ (MNRJ nº5249); Angra dos Reis [-22.987371, -44.294816], Travassos, vii.1934, 1♂ (MNRJ nº5216); Palmeiras [-22.760337, -43.018443], S. Lopes, 7.i.1939, 1♂ (MNRJ nº5246); Petrópolis, Alto da Mosela [-22.493368, -43.203059], D. Albuquerque, i.1956, 2♂♂ (MNRJ nº5247-5248); Porto Flores [-22.932896, -43.222349], Rlho Rllo, v.1944, 1♂ (MNRJ nº5215); Miguel Pereira [-22.459719, -43.481009], H. S. Lopes, v.1933, 1♀ (MNRJ nº5221); Rio Grande do Sul. Tenente Portela [-27.370133, -53.757764], J. R. Ipure, 02-05.xii.1985, 1♀ (DZUP 099164); São Paulo. Ribeirão Preto, Campus USP, Secondary semidecidous Forest [-21.1625, -47.86], Malaise trap, D. A. Amorim, 1-8.vii.2017, 1♀ (DZUP2020A13); Paraguay. Canindeyú. Reserva Natural del Bosque Mbaracayú, Jejuí-mí [-24.122513, -55.446990], Malaise trap, A. C. F. Costa, 18-28.vii.1996, 1♂ (DZUP 099222); same label information, except: 24-30.iv.1996, 2♂♂ (DZUP 099223-24); 17-23.iv.1996, 1♂ (DZUP 099225), 2♂♂ (DZUP), 2♀♀ (DZUP 099201; 099210) and 1♀ (DZUP); 29.v-11.vi.1996, 11♂♂ (DZUP 099226-36), 1♂ (DZUP) and 4♀♀ (DZUP 099200; 099202-04; 099211); 18-28.vii.1996, 1♂ (DZUP 463139) and 3♀♀ (DZUP 099212; 463137-38); 20-27.vi.1996, 2♂♂ (DZUP 463140-41); 11-18.vii.1996, 2♂♂ (DZUP 463143-44), 1♂ (DZUP); 12-19.vi.1996, 2♀♀ (DZUP 099197-98), 2♀♀ (DZUP); 1-15.v.1996, 2♀♀ (DZUP 099199; DZUP) and 1♀ (DZUP); 26.vii-8.viii.1996, 1♀ (DZUP 099205), 2♀♀ (DZUP); 1-8.v.1996, 1♀ (DZUP 099206); 9-15.v.1996, 1♀ (DZUP 099207); 12-19.vi.1996, 1♀ (DZUP 099208); 25.vii-8.viii.1996, 1♀ (DZUP 099209); 24-28.v.1996, 1♀ (DZUP 099212); 28.vi-3.vii.1996, 6♂♂ and 1♀ (DZUP); 25-30.iii.1996, 1♀ (DZUP); 04-18.vii.1996, 6♂♂ and 1♀

(DZUP); 29.iii-9.iv.1996, 1♀ (DZUP); 10-16.iv.1996, 1♀ (DZUP); 10-18.vii.1996, 1♀ (DZUP).

**Distribution.** Brazil (Bahia*, Espírito Santo*, Goiás*, Minas Gerais, Paraná*, Paraíba*, Rio de Janeiro, Rio Grande do Sul, Santa Catarina*, São Paulo), Panama (Canal Zone), Guyana (Cuyuni-Mazaruni), Paraguay* (Canindeyú*) (Curran, 1934; Albuquerque, 1957; Linhares, 1981; Oliveira, 1986; D'Almeida, 1992). *= new records.

**Remarks.** *Phaonantho devia* Albuquerque, is the junior synonym of *Phaonantho mallochi* (see Couri, 1979). Some specimens were collected with Malaise trap, Light trap, and Shannon trap, including garbage, feces and carcass of *Sus scrofa* as bait.

***Phaonantho sordilloae* Pamplona & Couri, 1993**

(Figs. 3, 4)

*Phaonantho sordilloae* Pamplona & Couri, 1993:37, figs. 1-11 (male holotype, MNRJ) (paratypes, MNRJ)

**Diagnosis.** Thorax dark brown with silver pruinose (Figs. 3B, C, E, F). Antennae yellow and palpi light brown with yellow apex (Figs. 3A, D). Wing brownish (Figs. 3B, C, E, F). Calypters light brown. Cerci and sternite 5 not covered by several long setae (male).

**Type-material examined.** Holotype. Male. Rio de Janeiro. Floresta da Tijuca [-22.950479, -43.291535], C. M. O. Sordillo, x.1988 (MNRJ). Paratypes. Same as holotype, except: Rio de Janeiro [-22.932896, -43.222349], xi.1988, 1♂ and 7♀ (MNRJ); ix.1988, 1♀(MNRJ); xii.1988, 1♀ (MNRJ); i.1989, 1♂ (MNRJ).

**Additional material examined.** Brazil. Acre. Sen. Guiomard, F. E. Catuaba [-10.074444, -67.616666], Malaise trap, REDE BIA, E. F. Morato & J. A. Rafael, 15-31.xii.2016, 1♂ (DZUP); same label information, except: 10-30.x.2016, 1♂ (DZUP); 6-26.ix.2016, 1♂ (DZUP) and 1♀ (INPA); 8-23.viii.2016, 1♀ (INPA); viii-ix.2017, 3♀♀ (INPA); Amazonas. Campus Universitário [-3.094779, -59.967742], Marcia Castilho & J. Elias Binda, 28,vii-05.viii.1988, 2♀♀ (INPA); Itacoatira [-3.134500, -58.438473], J. F. Vidal, 26.xi.1999, 1♀ (INPA); Manaus. R. Ducke [-2.999727, -59.939081], 24 m, Y. Camara & J. E. Binda, 06.x.1988, 1♂ (INPA); Marãa, R. Japurá, Manguari [-1.818081, -65.354387], J, Dias, 11-17.x.1988, 1♂ (MPEG); Goiás. SHMO, Mimoso [-15.037935, -48.183726], Bonaléia, M. P. S., 01.x,1986, 1♀ (UNB); Maranhão. Açailândia, Fazenda Itabaiana [-5.090833, -47.099444], J. A. Rafael & J. Vidal,

07.xii.2001, 1♀ (DZUP); Carolina, Pedra Caída [-7.043916, -47.44125], J. A. Rafael & J. T. Câmara, 10-13.vi.2013, 1♂ (DZUP) and 1♀ (INPA); Carolina, Rio Lages [-7.161955, -47.292480], Rafael, Oliveira & Vidal, xii.2001, 1♂ (DZUP); São Pedro da Água Branca [-5.118611, -48.255277], J. A. Rafael, F. Oliveira & J. Vidal, 06.xii.2001, 1♂ (INPA); Ribamar Fiquene, Rio Tocantins [-5.941388, -47.424166], J. A. Rafael & J. Vidal, 13.xii.2001, 1♀ (INPA); Mato Grosso. Cáceres, Polonoroeste [-16.084034, -57.675011], C. Elias, 3.xii.1984, 1♂ (DZUP 099219); same label information, except: 3.xii.1984, 1♀ (DZUP 099237); Chapada dos Guimarães. P. N. Chapada dos Guimarães [-15.406055, -55.835416], 788m, Malaise trap, Lamas, Nihei & eq., 01-22.xii.2011, 2♂♂ (MZUSP); Chapada dos Guimarães. P. N. Chapada dos Guimarães, Trilha Véu da Noiva [-15.409361, -55.831916], Patiu & Patiu, 19.i.2012, 1♂ and 2♀♀(MZUSP); Pará. Benevides [-1.362384, -48.256175], R. B. Neto, 18.ii.2001, 4♀♀ (MPEG); C. Araguaia [-9.501409, -50.809044], Malaise trap, J. A. Rafael, 19-31.i.1983, 1♂ (INPA); Paragaminas, Faz. Cachoeira do rio vermelho [-3.003606, -47.352915], J, Dias, 15-18.i.1991, 1♂ (MPEG); Parque Estadual do Utinga [-1.424356, -48.441683], S. L. Camargo, 07.x.2010, 1♂ (MPEG); Floresta Nacional de Caxiuanã [-1.954649, -51.683018], C. Esposito, 10.xi.1995, 1♂ (MPEG); same label information, except: iii.1996, 1♀ (MPEG); Jacundá, Ilha Maria Juriti [-4.614514, -49.182549], 17.iii.1981, 11♂♂ and 4♀♀ (INPA); Jacundá, Rio Tocantins, Ilha M. Juriti [-4.614514, -49.182549], J. A. Nunes de Melo, 17.iii.1981, 1♂ and 2♀♀ (INPA); same label information, except: 11-12.iv.1981, 1♀ (INPA); Repartimento, Vicinal 45 [-4.368611, -50.023611], Malaise trap, J. A. Rafael & J. Vidal, 29.xi.2001, 1♂ (INPA); Tucuruí [-3.712826, -49.729370], Nunes de Melo, 04.viii.1980, 1♂ and 5♀♀ (INPA); same label information, except: 06.viii.1980, 10♂♂ and 7♀♀ (INPA); Tucuruí, Vila Brava [-3.765058, -49.678289], Nunes de Melo, 27.vi.1980, 1♂ (INPA); Tucuruí, Lago do Pitinga [-3.755129, -49.701318], 10.iv.1981, 1♂ (INPA); Tucuruí, Morro do Senador [-3.989722, -49.745833], J. A. Rafael & J. Vidal, 01.xii.2001, 2♀♀ (INPA); Tucuruí, Ilha Chorona [-3.989722, -49.745833], 17.viii.1980, 1♀ (INPA); Paraíba. Cabaceiras (Fazenda Bravo) Caatinga de Lageiro [-7.490196, -36.287887], Light trap, D. S. Amorim & N. Stevaux, 28-29.vi.1986, 1♀ (DZUP).

**Distribution.** Brazil (Acre*, Amazonas*, Goiás*, Maranhão*, Mato Grosso*, Pará*, Paraíba*, Rio de Janeiro) (Pamplona & Couri, 1993). *= new records.

**Remarks.** Some specimens were collected with Malaise trap, Light trap, and Shannon trap, including fish, fruit and feces as bait.

***Phaonantho* sp.**

**Material examined.** Mexico. Veracruz. Est. Biol. de Los Tuxtlas [18.584982, -95.073932], A. Ibarra, 14.iv.1986, 1♀ (CNIN).

**Remarks.** This female specimen represents the first record of *Phaonantho* from Mexico. Its morphology resembles *P. benevola*, but considering its distribution and the fact of the main diagnostical characteristics are in male, we preferred indicated this specimen as a morphospecies.

### Distribution of *Phaonantho*

We update the distribution of the genus, with the first record of *Phaonantho* in Bolivia, Paraguay, Peru and Mexico; and the first records to the following Brazilian states: Amazonas, Bahia, Goiás, Maranhão, Pará, Paraíba, Paraná, Piauí, Rio Grande do Sul, Rondônia, Roraima, and Santa Catarina (Fig. 4). *Phaonantho benevola* and *P. sordilloae* have a main distribution in the Boreal Brazilian, Parana, Chacoan, South Brazilian, and South-eastern Amazonian dominions (sensu Morrone, 2014), both species co-occur in most regions where they have been recorded so far. While *P. mallochi* has a main distribution in Parana dominion, with few known records in Boreal Brazilian, Chacoan, and Pacific dominions (Fig. 5). Remarkable *P. mallochi* has a distribution in Panamá and Guyana (Curran, 1934), while the remaining records are exclusively from south, southeast and northeast Brazil and Paraguay, not occurring in Bolivia, Peru and Northern Brazil, regions where *P. benevola* and *P. sordilloae* have several records. We present several new records of *Phaonantho* species, but the distribution of these species probably is even wider.

## DISCUSSION

We observed a large number of specimens of the three known species of *Phaonantho*, and observed that some characters indicated in the Pamplona & Couri (1993) key vary, as the following: the number of posterior anepisternal setae ranging among 3-5 in *P. benevola* and *P. sordilloae*; the number of anterior anepisternal setae ranging between 1 and 2 in the three species; and hind femur ranging among 2 and 4 anterodorsal and anteroventral setae in the three species. Based on that, we updated the *Phaonantho* key removing these characters and including new information.

Some studies indicated *P. mallochi* as an asynanthropic species in Campinas (1981) and São Carlos (Oliveira, 1986), both in São Paulo state; and also, Rio de Janeiro (D'Almeida, 1992). Linhares (1981) collected *P. mallochi* with human feces and mouse carcass as bait. We analysed a large number of specimens of *Phaonantho* and according to the label information, these specimens have been collected mainly by Malaise, Light, and Shannon traps with several kinds of baits as fish, bovine lung, feces and pig carcass. In addition, *P. mallochi* was collected in *Aristolochia giberti* Hook. (Aristolochiaceae), the genus *Aristolochia* is known for being pollinated by several families of flies (Endress, 1994).

Gomes & de Carvalho (in progress) recovered the following topology: *P. mallochi* (*P. benevola* + *P. sordilloae*). This topology is in agreement with the distribution of these species, considering *P. benevola* and *P. sordilloae* co-occurring mainly in North of South America; and *P. mallochi* ocurring mainly in southeast South America.

Anthomyiidae has a distribution mainly concentrated in cold areas of high altitudes or latitudes (Michelsen, 2010), but *Phaonantho* (as well as *Coenosopsia*) species are an exception, occurring mainly in warm lowland forests of Central and South America (Michlesen, 1996). It is in agreement with the updated knowledge of *Phaonantho* distribution. Among the three species, *P. mallochi* is the species with the wider longitudinal distribution, reaching southern colder areas.

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FIGURES

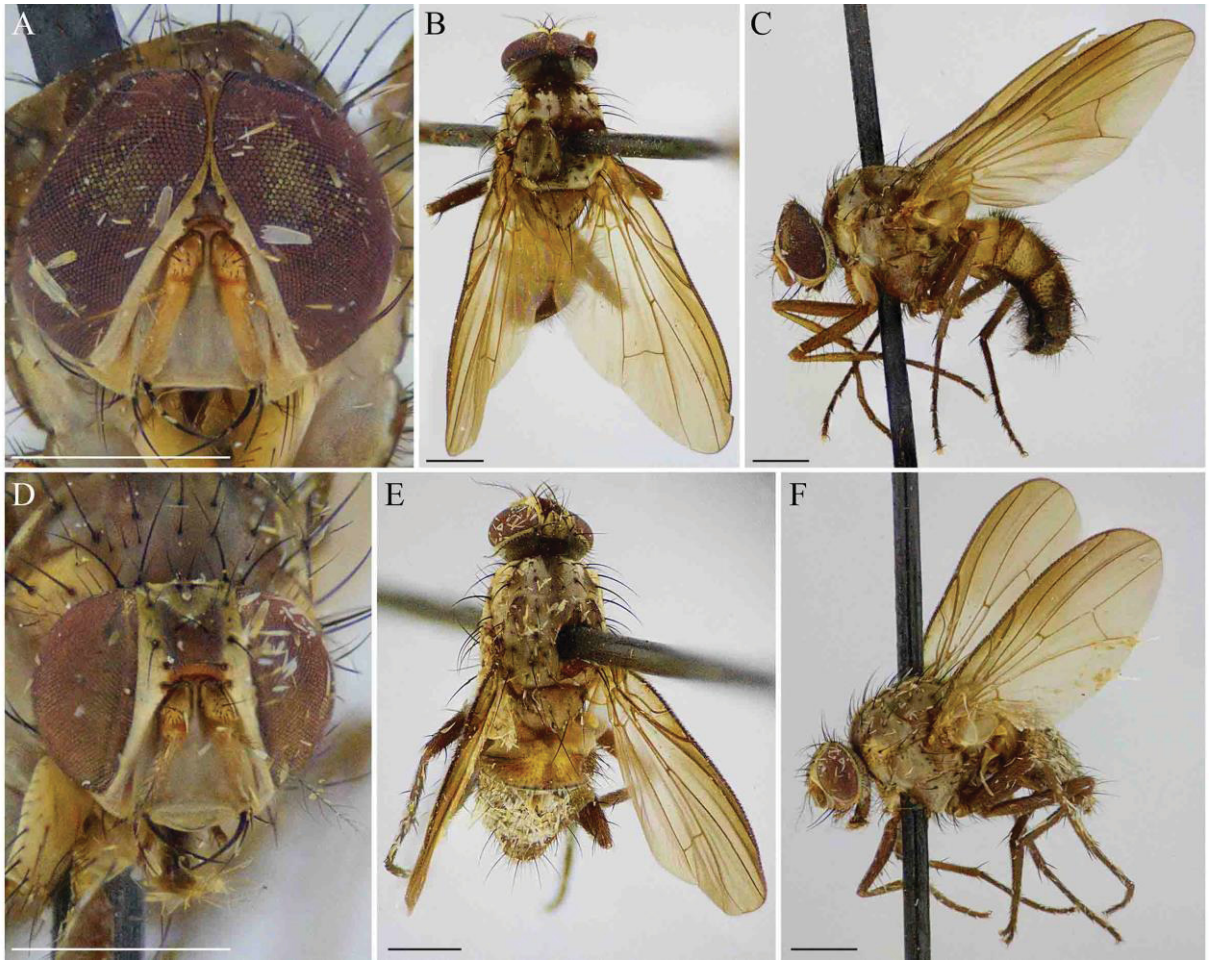


**Figure 1.** *Phaonantho benevola* Couri, 1979. Male: head, frontal view (A); habitus, dorsal view (B); habitus, lateral view (C). Female: head, frontal view (D); habitus, dorsal view (E); habitus, lateral view (F). Scale bar: 1.0 mm.

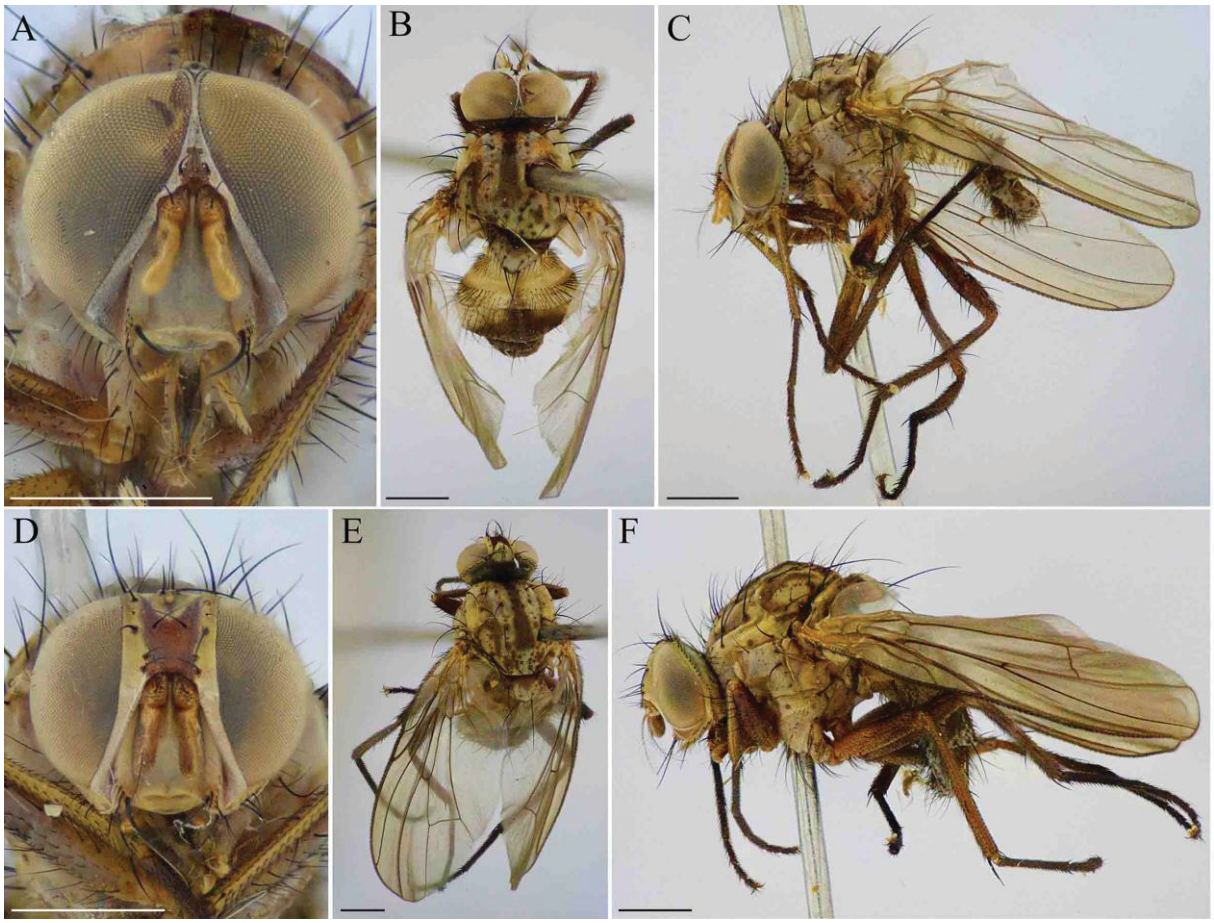


**Figure 2.** *Phaonantho mallochi* (Curran, 1934). Male: head, frontal view (A); habitus, dorsal view (B); habitus, lateral view (C). Female: head, frontal view (D); habitus, dorsal view (E); habitus, lateral view (F). Scale bar: 1.0 mm.

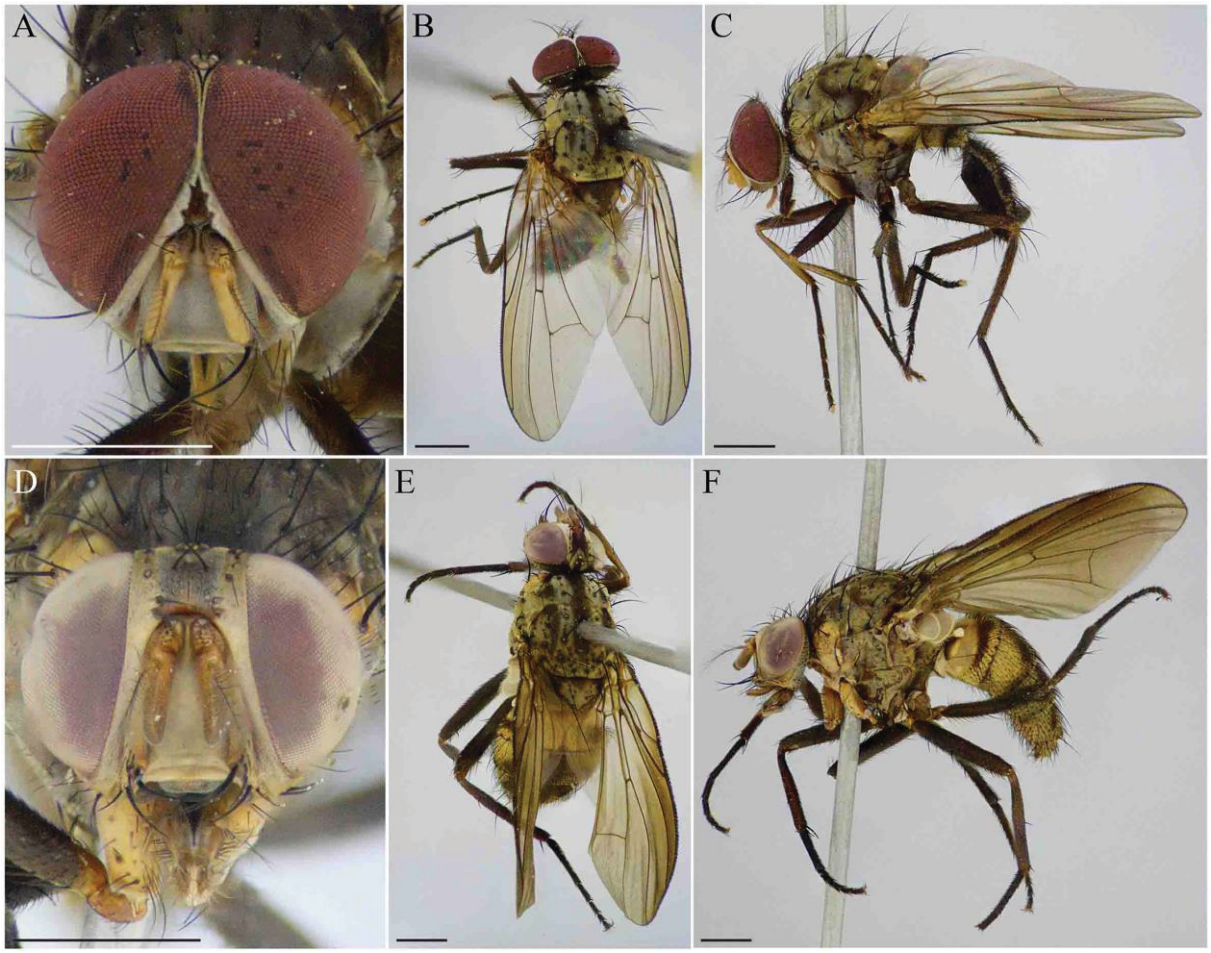


**Figure 3.** *Phaonantho sordilloae* Pamplona & Couri, 1993. Male: head, frontal view (A); habitus, dorsal view (B); habitus, lateral view (C). Female: head, frontal view (D); habitus, dorsal view (E); habitus, lateral view (F). Scale bar: 1.0 mm.

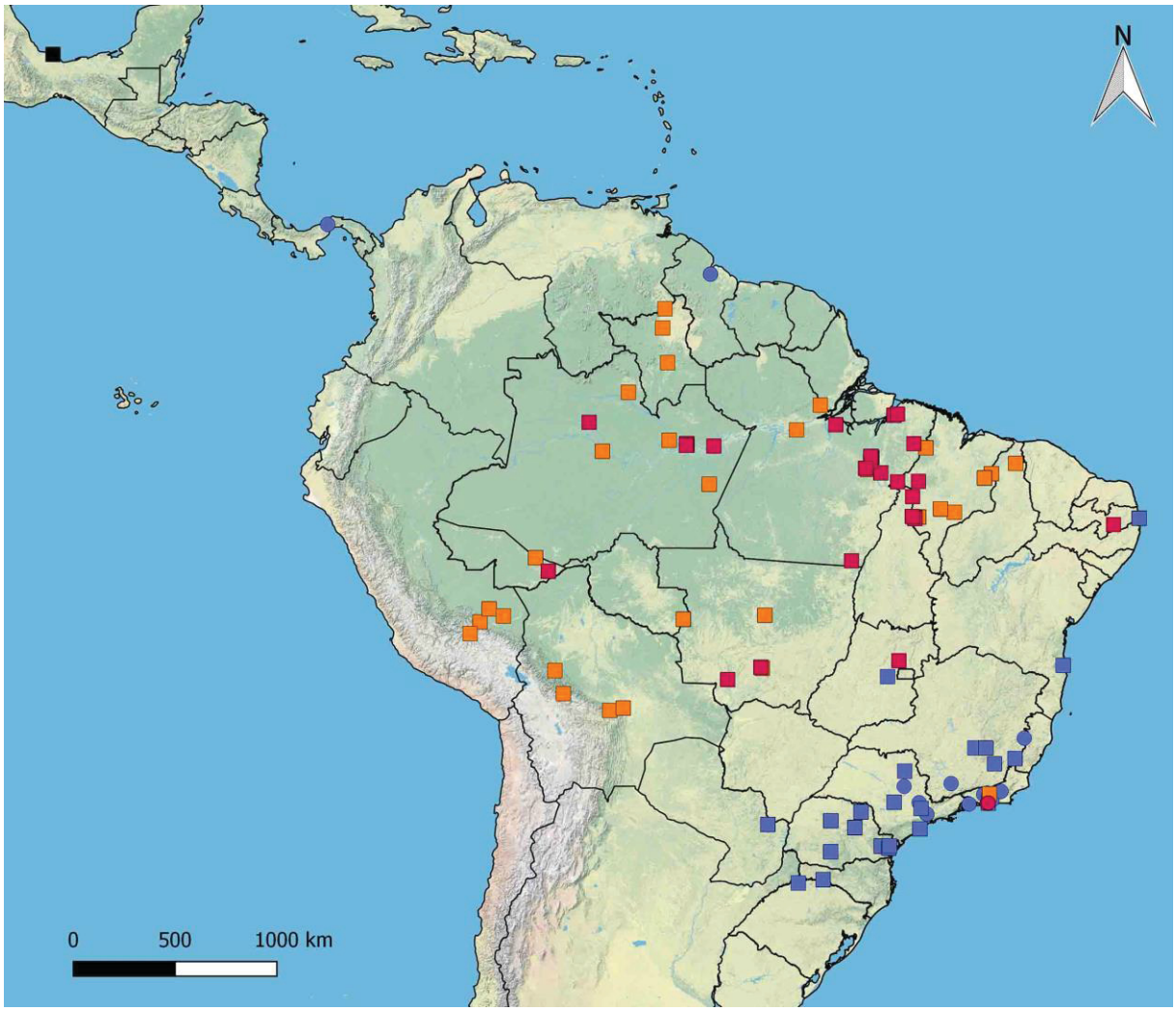


**Figure 4.** Map of *Phaonantho* species (geopolitical borders): *P. benevola* (orange); *P. mallochi* (blue); *P. sordilloae* (red); and *Phaonantho* sp. (black). Circles= literature records; square= new records.

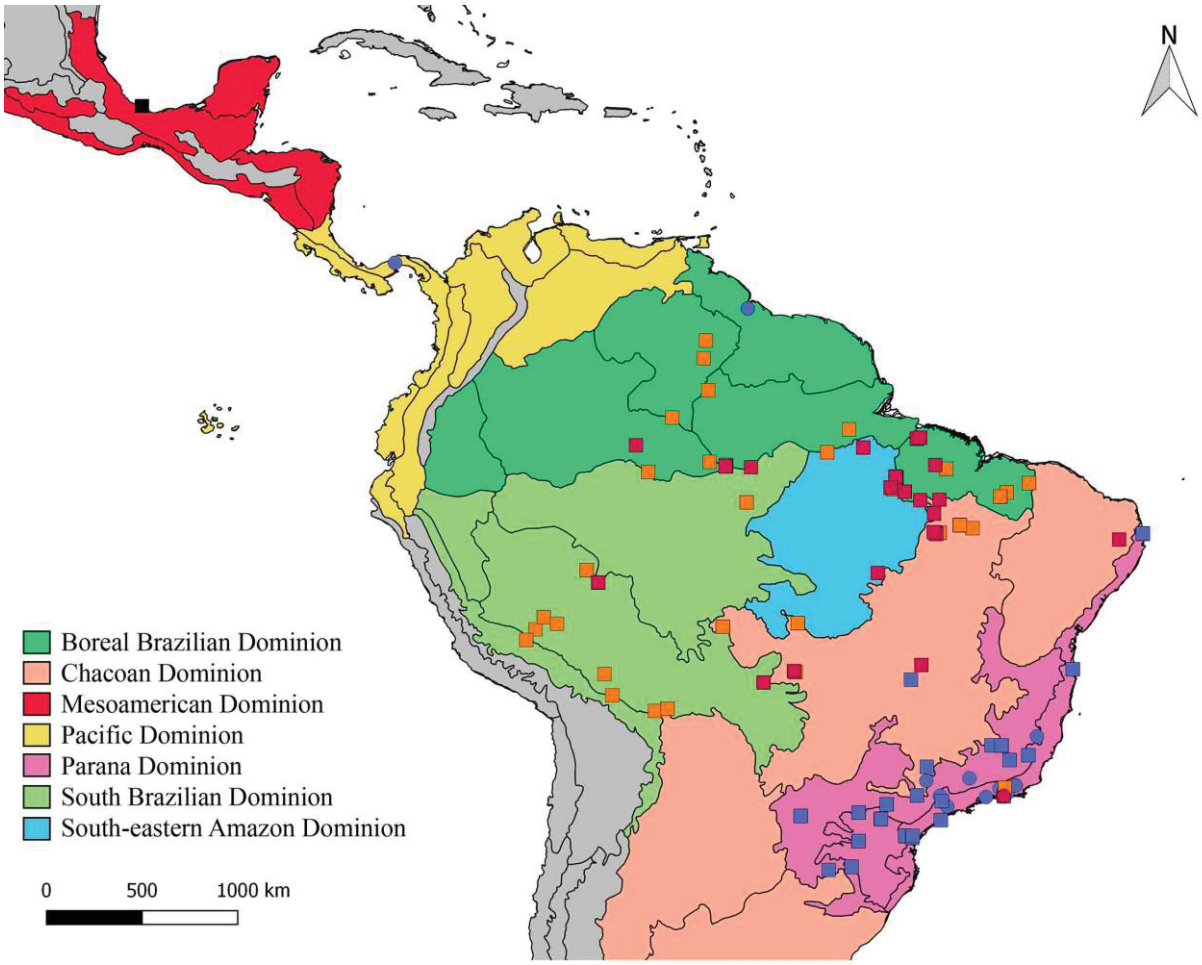


**Figure 5.** Map of *Phaonantho* species (biogeographical dominions, sensu Morrone, 2014): *P. benevola* (orange); *P. mallochi* (blue); *P. sordilloae* (red); and *Phaonantho* sp. (black). Circles= literature records; square= new records.

## CAPÍTULO V

# TAXONOMY OF THE NEOTROPICAL *Calythea* (ANTHOMYIIDAE: DIPTERA), WITH DESCRIPTION OF TWO NEW SPECIES FROM SOUTH AMERICA

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# Taxonomy of the Neotropical species of *Calythea* (Anthomyiidae: Diptera), with description of two new species from South America

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ABSTRACT

*Calythea* Schnabl & Dziedzicki has 15 known species distributed worldwide, including three species in the neotropics. The species of *Calythea* can be easily identified by having bright silvery grey-dusting on the thorax and abdomen, forming a contrasting pattern with the dark body. Herein, we describe two new species from the Neotropical region and present new records of the genus for Argentina, Brazil, Chile, Colombia, Ecuador and Peru. We also redescribe *Calythea comis* (Stein). In addition, we present an identification key for the Neotropical species and drawings of the terminalia and habitus images of the new species, *C. comis*, *C. crenata* (Bigot) and *C. micropteryx* (Thomson).

**Keywords**: biodiversity, identification key, morphology, new records.

## INTRODUCTION

*Calythea* Schnabl & Dziedzicki has 15 known species found in all biogeographical regions, including three species in the Neotropics (Griffiths 1986; Evenhuis and Pape 2021). Adults are floral visitors and larvae are known to eat mammalian faeces (Griffiths 1986). The genus is composed of small flies with wing less than 5 mm long. They can be easily confused with small muscids and fanniids upon superficial inspection in having the lower calypter enlarged and a distally faint anal vein (Griffiths 1986). The genus is very similar and closely-related to the more diverse genus *Pegoplata* Schnabl & Dziedzicki (Ackland, 1968; Griffiths 1986; Michelsen 1988; Gomes et al. 2021).

*Calythea* species can be recognized by a very characteristic bright silvery grey-dusting pattern on the thorax and abdomen, contrasting with the black body; the abdomen presents a transverse series of three basally connected black subtriangular marks at the anterior margin of each abdominal tergite (Malloch 1934; Griffiths 1986). The main characteristics of the genus are presence of interfrontal setae in females (also present in males of some species); female palpus enlarged; apex of scutellum ventrally setulose; scutellar apical setulae, when present, very fine, similar to the ventral setulae; a single long seta beyond middle of posterodorsal surface of hind tibia, and large lower calypter, about 1.5 times larger than the upper one (Malloch 1934; Griffiths 1986).

The Neotropical species belong to the *Calythea micropteryx* group of species (Griffiths 1986) and the species of this group are very similar to each other, being properly identified only by examination of the male terminalia. The few studies on the Neotropical fauna consist of taxonomic lists of species (Malloch 1934; Séguy 1934; Albuquerque 1953; Pont 1974; Griffiths 1986; Gomes et al. 2019).

Herein, we describe two new species of *Calythea*, one from Argentina and Brazil and the other from the Andean region of Colombia and Ecuador, including images and drawings. In addition, we present an identification key for Neotropical species.

## MATERIAL AND METHODS

We examined the type material of *Calythea micropteryx*; and non-type material from *C. comis*, *C. crenata*, and *C. micropteryx*. The material studied is deposited in the following institutions: Colección Entomológica de la Universidad de Antioquia, Medellín, Colombia (CEUA); Colección Nacional de Insectos, Ciudad de Mexico, Mexico (CNIN); Coleção Zoológica do Maranhão, Caxias, Brazil (CZMA); Padre Jesus Santiago Moure Entomological Collection, Curitiba, Brazil (DZUP); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); National Museum of Natural History, Washington, USA (USNM); Naturhistoriska Riksmuseet, Stockholm, Sweden (NHRS); Maurice T. James Entomological Collection, Pullman, USA (WSU).

The morphological terminology followed Cumming and Wood (2017). The following abbreviations were used in the diagnoses, key, descriptions and redescriptions: *a* – anterior surface, *ad* – anterodorsal surface, *av* – anteroventral surface, *d* – dorsal surface, *p* – posterior surface, *pd* – posterodorsal surface, *pv* – posteroventral surface, *v* – ventral surface.

For examination of the male and female terminalia, the abdomen was removed from a dry specimen and was placed in cold potassium hydroxide (KOH) 10% for 24h to soften and lighten the parts. The abdomen was transferred to acetic acid, and then to glycerin. The postabdomen structures were separated from the rest of the abdomen. Examination and illustration of the structures were performed using a microscope and a stereomicroscope with a camera lucida attached to it. Dissected terminalia were placed in glycerin, inside microvials pinned beneath the respective specimens.

Images of specimens were obtained with sequential images mounting at different focal planes with a NIKON D610 digital camera coupled to a LEICA M165 C stereomicroscope. The images were stacked and edited using Adobe Photoshop CS6. The distribution map was produced using the software QGIS (available in: http://www.qgis.org/en/site/).

## RESULTS

***Calythea*** Schnabl & Dziedzicki

***Calythea micropteryx*** species group

**Diagnosis.** Male holoptic. Body black in general color, bright silvery grey-dusting pruinosity on thorax and abdomen (Figs. 1–3). Frontal vitta, antenna and palp black. Gena and parafacialia black with silvery pruinosity (Figs. 1a, 2a, d, 3a, d, g). Anepimeron, anepisternum, and meron black, silvery pruinose (Figs. 2c, f). Prescutellar region, and postalar callus pruinose. Scutellum apically pruinose. Apical scutellar setae longer than basal and discal scutellar setae. Abdomen with 3 subtriangular dark spots basally connected on each abdominal tergite (Fig. 3c). Arista short pubescent. Presence of a keel on face, between antennae. Prosternum and katepimeron setulose. Meron bare or posteriorly setulose below spiracle. Katepisternum 1+2, covered by many long setae, including a differentiated seta discernible below the two posteriors one. Apex of scutellum ventrally setulose.

Prealar short or absent. 1 supra-alars. 2 intra-alars. 2 postalars. Wing hyaline. Lower calypter 1.5 times larger than upper one. Fore tibia with one *a* seta. Hind tibia with 1 *av* (submedian), 2 *ad* (supramedian and submedian), 1 *d* (preapical), and a long *pd* (submedian) seta. Pulville small, similar to tarsomere width. Subcostal vein evenly bowed towards the Costal vein, without any sinuosity. Vein dm-m straight. Palpi claviform. Sternite 1 setulose. Sternite 5 with a serrated edge on its posterior incision (Figs. 4a, e, i, m, q). Cerci triangular on posterior view (Figs. 4b, f, j, n, r). Pregonite with two long setae, postgonite with a median long seta and distiphallus very large and rounded (Figs. 4d, h, l, p, t). Female: Dichoptic; body dark brown, palpi claviform, twice enlarged than male; interfrontal setae present. Thorax with 3–5 longitudinal stripes. Katepisternum 1+2, without several long covered setae. Pulville smaller, about half of tarsomere width. Epiproct as long as its wide, tergite 6 and 7 T-shaped dorsally (Figs. 5b, e, h, k). Hypoproct longer than wide, sternite 6 and 7 trapezoid (Figs. 5c, f, i, l). Three spermathecae, one smaller with about half diameter of the others.

**Identification key to the males of *Calythea* Schnabl & Dziedzicki species from Neotropical Region**

The Palaearctic species *C. nigricans* Robineau-Desvoidy, 1830 was erroneously recorded from Neotropical Region (Pont 1974), and *C. monticola* Bigot, 1885 occurs in the Nearctic Region of Mexico and United States (Griffiths 1987). Both species were not included in the key. The species *C. costana* Séguy, 1934 is only known from its type-locality in Uruguay, this species probably is not an Anthomyiidae, due to male terminalia and dorsocentrals setae 2+4, and also was not included in the key.

**1.** Eyes setulose; thorax without pruinose near transversal suture (Fig. 3e); hind tibia with a *pd* seta 4 times longer than tibia width … *C. crenata* Bigot, 1885

**-.** Eyes bare; thorax with pruinose near transversal suture (Fig. 1b, 2b, 3a, 3h); hind tibia with a *pd* seta 2–3 times longer than tibia width … 2

**2 (1).** Face not projecting beyond frontal angle … 3

**-.** Face projecting beyond frontal angle… 4

**3 (2).** Palpi enlarged; frons with fronto-orbital plates separated by frontal vitta (Fig. 3a); anterior anepisternal seta twice longer than covered cilia; thorax pruinose from

transversal suture, with a forward projection, reaching the anterior dorsocentral presutural seta (Fig. 3b) … *C. comis* Stein, 1911

**-.** Palpi slightly enlarged; frons at narrowest point with contiguous fronto-orbital plates (Fig. 3g); anterior anepisternal seta slightly longer than covered cilia; thorax pruinose from transversal suture, without forward projection, reaching anterior dorsocentral presutural seta (Fig. 3h) … *C. micropteryx* (Thomson, 1869)

**4 (2).** margin of calypters brownish; setulae on sternite 1 twice longer than length of sternite; Postgonite distally not bilobate (Fig. 4d) … *C. andina* **new species**

**-.** margin of calypters whitish; setulae on sternite 1 slightly longer than length of sternite; Postgonite distally bilobate (Fig. 4h) … *C. cochlearis* **new species**

***Calythea andina* new species**

(Figs. 1, 4a–d, 6)

**Diagnosis.** *Calythea andina* **new species** can be separated from the other species of the genus in having the distance between the presutural acrostichal rows, at least the two first pairs of setae, similar to the distance to dorsocentral rows; calypters white, with apical half of upper calypter brownish, calypter margin basally brownish.

**Description.** Male holotype. Body length: 4.5 mm. Wing length: 4.5 mm.

Thorax black, silvery pruinose on postpronotal lobe and notopleuron; pronotum pruinose basally, parallel to notopleural suture and extending to transverse suture (Fig. 1b). Calypters white with basal edge brown and apical edge white. Halter basally brownish and yellow apically. Legs black with pulvillus yellowish. Abdomen black, silvery pruinose on tergites 2–5, forming two dorsal almost triangular spots, segments 3 and 4 with prolonged spots laterally and apically.

**Head.** Eyes bare. Frontal vitta very narrow, distance between eyes shorter than width of anterior ocellus (Fig. 1a). 4–5 pairs of frontal setae. Face projecting beyond frontal angle. Gena shorter than length of pedicel. Parafacialia very narrow, with about 1/5 of postpedicel width. Postpedicel twice longer than pedicel. Pedicel with long dorsal setae, shorter than pedicel.

**Thorax.** 2 postpronotals; dorsocentrals 2+3; acrostichals 4+8 setulae-like, with only prescutellar developed; prealar absent. Anepisternum with row of 4 posterior setae and upward anterior seta below anterior notopleural seta. Scutellum with a pair of

basal, preapical and apical setae; apical seta almost twice as long as basal seta. Meron with a tuft of 4–5 setulae. Katepimeron with 7–8 setulae.

**Legs.** Fore tibia with 1 submedian *p* seta; 1 preapical *d* seta, and 1 apical *pv*; fore pretarsus with 1 basal *v* seta. Mid femur with 4 *v* setae at base; and 2 *p* preapical setae; midtibia with 1 median *pv* seta, 1 submedian *p* seta; preapical seta on *av*, *d*, *pv*, and *v*. Hind femur with 2 *av* rows, 1 long and stout and 1 long fine; 2 *ad*, 2 *d,* and 1 *pd* preapicals; 1 *pv* row long and sparse setae; hind tibia with a submedian *av*, 1 supramedian and 1 submedian *ad*, and a long submedian *pd* seta three times longer than tibia width; preapical seta on *av* and *d*; hind pretarsus with 1 basal *v* seta.

**Abdomen.** with many covered setulae; sternite 1 setulose, setulae twice longer than length of sternite; tergite 3–5 with long median and lateral marginal seta, terminal segment with apical and discal setae; sternite 5 rectangular with a serrated edge on its posterior incision (Fig. 4a).

**Terminalia.** Cerci triangular from posterior view (Fig. 4b); surstyli, from posterior view, long and straight with rounded median projection on inner surface. (Fig. 4b), and from lateral view, slightly curved and slightly enlarged apically (Fig. 4c); Hypopygium on lateral view with phalapodema long and slightly curved, pregonite with two long setae, postgonite with median long seta and three apical setulae, epiphallus distally curved and as long as postgonite, distiphallus very large and rounded (Fig. 4d).

**Female.** Unknown.

**Etymology.** The specific epithet *andina* refers to the Andean distribution of this species. The specific epithet *andina* (nominative, adjective feminine) is derived from the Andes Mountains, where the specimens were collected. Gender female.

**Material examined.** Holotype. Male. Ecuador. Imbabura, N. Perueho. Otavalo [0.2360, -78.2622], 2000m, L. E. Peña, i.1971 (MZUSP). Paratypes (3♂♂). Colombia. Antioquia, Alejandría [6.3759, -75.1414], A. Vélez, ii.1972, #catal 2005 (CEUA); Ecuador. Imbabura, N. Perueho. Otavalo [0.2360, -78.2622], 2000m, L. E. Peña, i.1971, (DZUP); Loja, La Toma, W. de Loja [-4.0081, -79.2110], 1500m, L. E. Peña, xi.1970 (MZUSP).

**Distribution.** Colombia and Ecuador (Fig. 6).

**Remarks.** There are some male specimens from Costa Rica with 2–5 setulae on meron (V. Michelsen, pers. comm.).

***Calythea cochlearis* new species**

(Figs. 2, 4e–h, 5a–c, 6)

**Diagnosis.** *Calythea cochlearis* **new species** can be separated from the other species of the genus in having the distance between the presutural acrostichal rows, at least the two first pairs, longer than their distance to dorsocentral rows; postgonite bilobate.

**Description.** Male holotype. Body length: 4.2 mm. Wing length: 4.0 mm. Thorax black, silvery pruinose on postpronotal lobe and notopleuron; pronotum pruinose basally parallel to notopleural suture and extending to transverse suture (Fig. 2b). Calypters white with edge yellow. Halter basally brownish and yellow apically. Legs black with pulvillus yellowish. Abdomen black with silvery pruinose on tergites 2–5, forming two dorsal almost triangular spots, segments 3 and 4 with laterally and superiorly prolonged spots.

**Head.** Eyes bare. Frontal vitta very narrow, distance between eyes shorter than width of anterior ocellus (Fig. 2a). 6–7 pairs of frontal setae. Face projecting beyond frontal angle. Gena shorter than length of pedicel. Parafacialia very narrow, with about 1/5 of postpedicel width. Postpedicel twice longer than length of pedicel. Pedicel with a long dorsal seta, shorter than length of pedicel.

**Thorax.** 2 postpronotals; dorsocentrals 2+3; acrostichals 4+8 setulae-like, with only the prescutellar developed; prealar absent. Anepisternum with a row of 4 posterior setae and an upward anterior seta below anterior notopleural seta. Scutellum with a pair of basal, preapical and apical setae; the apical seta almost twice as long as basal seta. Meron with a tuft of 4–6 setulae, located posteriorly below spiracle. Katepimeron with 6–9 setulae.

**Legs.** Fore tibia with 1 submedian *p* seta; 1 preapical *d* seta, and 1 apical *pv*; fore pretarsus with 1 basal *v* seta. Mid femur with 4 *v* setae at base; and 2 *p* preapical setae; midtibia with 1 median *pv* seta, 1 submedian *p* seta; preapical seta on *av*, *d*, *pv*, and *v*. Hind femur with 2 *av* rows, 1 long and stout and 1 long fine; 2 *ad*, 2 *d,* and 1 *pd* preapicals; 1 *pv* row long and sparce setae; hind tibia with a submedian *av*, 1 supramedian and 1 submedian *ad*, and a long submedian *pd* seta three times longer than tibia width; preapical seta on *av* and *d*; hind pretarsus with 1 basal *v* seta.

**Abdomen.** with many covered setulae; sternite 1 setulose, setulae slightly longer than length of sternite; tergite 3–5 with long median and lateral marginal seta,

terminal segment with apical and discal setae; sternite 5 quadrangular with a serrated edge on its posterior incision (Fig. 4e).

**Terminalia.** Cerci triangular from posterior view (Fig. 4f); surstyli, from posterior view, long and straight with an acute median projection on inner surface (Fig. 4f), and from lateral view, slightly curved and enlarged apically (spoon-like) (Fig. 4g); Hypopygium on lateral view with phalapodema long and slightly curved, pregonite with two long setae, postgonite bilobate with a median long seta and two apical setulae, epiphallus as long as postgonite, distiphallus very large and rounded (Fig. 4h).

**Female.** Similar to male, except: Body length: 4.0–4.5 mm. Wing length: 3.8–4.0 mm. Thorax with 3 conspicuous dorsal stripes, the central stripe twice wider than the laterals and exceeding the line of acrostichal setae; and 2 dotted strips on dorsocentral setae region between the central stripe and the laterals (Fig. 2e). Scutellum fully covered by pruinose, except basally on lateral region and dorsally on the basal third. Anepisternum with a row of 3 posterior setae. Meron with a tuft of 3–4 setulae, located posteriorly below spiracle. Katepimeron with 4–5 setulae. Terminalia with cerci dilated distally, with long setae; epiproct subtriangular, as long as its wide; hypoproct subconical, twice longer than its wide; sternite 6 and 7 trapezoid; tergite 6 and 7 T-shaped dorsally; sternite 8 as long as tergite 8 (Fig. 5a–c).

**Etymology.** The specific epithet refers to the spoon-like shape of the surstyli in lateral view (latin word *cochlearis* = spoon). Gender neuter.

**Material examined.** Holotype. Brazil. Paraná. Jundiaí do Sul, Fazenda Monte Verde [-23.423531, -50.281910], Lev. Ent. PROFAUPAR, Malaise trap, 22.ix.1986 (DZUP 099249).

Paratypes (n= 55). Argentina: Tucumán, V. Padre Monti, Burruyacú [-26.4998, -64.7412], R. Golbach, 17.i–7.ii.1948, 1♂ (DZUP); Brazil: Maranhão. Parque Estadual Mirador, Base da Geraldina [-6.623888, -45.869166], J. A. Rafael & F. L. Oliveira, 28–30.ix.2006, 1♀ (INPA); Mato Grosso do Sul. Bodoquena Fazenda California [-20.698333, -51.881955], Van Someren modified, Lamas, C. J. E., 07–08.viii.2011, 1♀ (MZUSP); Minas Gerais. Araxá [-19.5934, -46.9411], C. T. & C. Elias, 22.xi.1965, 1♂ (DZUP 099242); Viçosa [-20.7536, -42.8761], G. R. Lima, 12.viii.1986 (Nº68), 1♂ (DZUP); Paraná. Guarapuava, Est.Sta. Clara [-25.632814, -51.964977], Lev. Ent. PROFAUPAR, 15.ix.1986, 1♀ (DZUP 099273); Jundiaí do Sul, Fazenda Monte Verde [-23.423531, -50.281910], Lev. Ent. PROFAUPAR, Malaise trap, 02.xi.1987, 1♀ (DZUP 099276); same label information, except: 22.ix.1986, 1♀ (DZUP 099280);

07.ix.1987, 1♀ (DZUP 099281); light trap, 04.x.1986, 2♂♂ (DZUP 099241; 099248); light trap, 02.ix.1986, 1♂ (DZUP 099243); Palmas, Linha Alegre, Fazenda Cerro Chato [-26.50252, -51.67033], Malaise, 1224m, M. Savaris & A. L. Norrbom, 3-4.iii.2015, 3♂♂ and 2♀♀ (DZUP); Ponta Grossa, V. Velha, IAPAR [-25.244012, -50.011530], Ganho & Marinoni, Malaise trap, 06.ix.1999, 1♀ (DZUP 099274); same label information, except: 10.vii.2000, 2♀♀ (DZUP 058573, 099275); 01.xi.1999, 1♀ (DZUP); 28.viii.2000, 1♀ (DZUP); Lev. Ent. PROFAUPAR, 18.viii.1986, 1♀ (DZUP 463152); Lev. Ent. PROFAUPAR, 01.x.1986, 1♀ (DZUP 058557); light trap, Lev. Ent. PROFAUPAR, 04.viii.1986, 1♀ (DZUP 099279); Lev. Ent. PROFAUPAR, 04.x.1986, 1♂ (DZUP 058550); Telêmaco Borba, Res. Biol. Klabin [-24.297941, -50.618785], Malaise trap, Lev. Ent. PROFAUPAR, 12.x.1987, 1♀ (DZUP 058495); Piauí. Guaribas, Parque Nacional Serra das Confusões, Andorinha; 09º08'27.8''S; 43º33'42.1''W, 515m, Malaise trap, J. A. Rafael & F. Limeira-de-Oliveira, 01–10.ix.2013, 1♂ (CZMA). Same label information, except: 11–20.viii.2013, 1♂ (CZMA); 20–31.viii.2013, 1♂ (DZUP); Piracuruca, P. N. de Sete Cidades, Posto ICMBio, 04º05'57''S; 41º42'34''W, F. Limeira-de-Oliveira & J. S. Pinto Júnior, 01–14.ii.2013, 1♂ (CZMA); Rio Grande do Sul. Quaraí [-30.384608, -56.448744], J. R. Cure, 21.xi.1985, 2♂♂ and 4♀♀ (DZUP 099239–40, 099269, 099277, 462901, 462909); Santa Catarina. Nova Teutônia [-27.1833, -52.3833], 300–500 m, Fritz Plaumann, 6.v.1961, 1♀ (MZUSP); São Paulo. São Carlos, EMBRAPA, Faz. Canchim [-21.954680, -47.847250], Airton S. Soares, xii.2010, 9♂♂ and 7♀♀ (MZUSP, DZUP); Sergipe. Canindé do São Francisco, Res. CHESF, Tabuleiro Argiloso Plano, área 1 [-9.6296, -37.8028], Malaise trap, Luciana Ianuzi, 14.ix.2000, 1♂ Projeto Xingó (DZUP).

**Non-type material.** Rio Grande do Sul. Quaraí [-30.384608, -56.448744], J. R. Cure, 19-20.xi.1985, 2♂♂ (DZUP 099251–52).

**Distribution.** Argentina (Tucumán) and Brazil (Mato Grosso do Sul, Minas Gerais, Paraná, Piauí, Rio Grande do Sul, Santa Catarina, São Paulo, Sergipe) (Fig. 6).

**Remarks.** Two male specimens from Quaraí (Rio Grande do Sul, Brazil) have the surstyli slightly narrower, this was considered as morphological variation and these specimens were not included as paratypes.

***Calythea comis* (Stein, 1911)**

(Figs. 3a–c, 4i–l, 5d–f, 6)

**Diagnosis.** *Calythea comis* can be separated from the other Neotropical species of the genus in the frons with fronto-orbital plates separated by frontal vitta (Fig. 3a); distance between presutural acrostichal rows, even anteriorly in the first pair, shorter than their distance to dorsocentral rows; and pattern of pruinosity, which extends forward covering the region of dorsocentral setae, forming an inconspicuous stripe (Fig. 3b).

**Redescription.** Male. Body length: 4.5–5.0 mm. Wing length: 4.0–4.5 mm.

Thorax black with silvery pruinose on postpronotal lobe and notopleuron; pronotum pruinose basally running parallel to the notopleural suture, extending to transverse suture with forward projection, reaching the anterior dorsocentral presutural seta (Fig. 3b). Calypters white with the edge yellow. Halter basally brownish and yellow apically. Legs black with pulvillus yellowish. Abdomen black with silvery pruinosity on tergites 2–5, forming two dorsal almost triangular spots, segments 3 and 4 with laterally and superiorly prolonged spots.

**Head.** Eyes bare. Frontal vitta narrow, distance between eyes subequal to width to anterior ocellus (Fig. 3a). 6–7 pairs of frontal setae. Face not projecting beyond frontal angle. Gena shorter than length of pedicel. Parafacialia relatively broad, with about 1/3 of postpedicel width. Postpedicel twice longer than pedicel. Pedicel with long dorsal setae, shorter than pedicel.

**Thorax.** 2 postpronotals; dorsocentrals 2+3; acrostichals 4+8 setulae-like, with only the prescutellar developed; prealar absent. Anepisternum with a row of 5 posterior setae and an upward anterior seta below anterior notopleural seta. Scutellum with a pair of basal, preapical and apical setae; the apical seta almost twice longer than the basal one. Meron with a tuft of 4–5 setulae, located posteriorly below spiracle. Katepimeron with 4–5 setulae.

**Legs.** Fore tibia with 1 submedian *p* seta; 1 preapical *d* seta, and 1 apical *pv*; fore pretarsus with 1 basal *v* seta. Mid femur with 4 *v* setae at base; and 2 *p* preapical setae; midtibia with 1 median *pv* seta, 1 submedian *p* seta; preapical seta on *av*, *d*, *pv*, and *v*. Hind femur with 2 *av* rows, 1 long and stout and 1 long fine; 2 *ad*, 2 *d,* and 1 *pd* preapicals; 1 *pv* row of long and sparse setae; hind tibia with a submedian *av*, 1 supramedian and 1 submedian *ad*, and a long submedian *pd* seta three times longer than tibia width; preapical seta on *av* and *d*; hind pretarsus with 1 basal *v* seta.

**Abdomen.** with many covered setulae; sternite 1 setulose, setulae twice longer than sternite length; tergite 3–5 with long median and lateral marginal seta, terminal segment with apical and discal setae; sternite 5 rectangular with a serrated edge on posterior incision (Fig. 4i).

**Terminalia.** Cerci triangular in posterior view (Fig. 4j); surstyli in posterior view long and straight, with proximal rounded incision (Fig. 4j), and in lateral view, slightly curved and slightly enlarged apically (Fig. 4k); Hypopygium in lateral view with phalapodema long and slightly curved, pregonite with two long setae, postgonite with a median long seta and two apical setulae, epiphallus as long as postgonite, distiphallus very large and rounded (Fig. 4l).

**Female.** Similar to male, except: Thorax with 3 conspicuous dorsal stripes, width of central stripe not exceeding the line of acrostichal setae; and 2 inconspicuous thin stripes close to central stripe, with about 1/5 the width of central stripe (Fig. 3c). Scutellum fully pruinose, except basally on lateral region. Anepisternum with a row of 3 posterior setae. Meron with a tuft of 3–5 setulae, located posteriorly below spiracle. Katepimeron with 3 setulae. Terminalia with cerci dilated distally, with long setae; epiproct subtriangular, as long as its wide; hypoproct subconical, 1.3 times longer than its wide; sternite 6 and 7 trapezoid; tergite 6 and 7 T-shaped dorsally; sternite 8 shorter than tergite 8 (Figs. 5d–f).

**Material examined.** Brazil: Paraná, Antonina, Reserva Sapitanduva [-25.439498, -48.746125], Lâmpada [light trap], Lev. Ent. PROFAUPAR, 02.xi.1986, 1♀ (DZUP 099272); Castro [-24.7978, -49.9976], S. Loroca, ix.1961, 3♂♂ (DZUP 099245–47); Curitiba [-25.4332, -49.2667], P. D. Hurd, xi.1959, 2♀♀ (DZUP 099270–71); same label information, except: 900m, Dept. Zoologia, 14.i.1986, 1♀ (DZUP 099278); Palmas [Palmas Grasslands Wildlife Refuge], 1115m, grasslands, -26.5025, -51.6755, A. C. Pereira, 9.xii.2013, 1♂ (DZUP); same label information except: 29.x.2014, 2♀♀ (DZUP); 28.iv.2014, 1♀ (DZUP); 16.i.2014, 1♂ (DZUP); 20.x.2014, 1♂ and 1♀ (DZUP); 29.x.2014, 1♀ (DZUP); inside forest, -26.5022, -51.6738, 12.vii.2014, 1♂ (DZUP); regeneration area, -26.5572, -51.5422, 03.xii.2013, 1♀ (DZUP); 21.ix.2012, 1♂ (DZUP); Tijucas do Sul, Morro do Araçatuba, -25.8997, -49.0096, 1200 m, P. C. Grossi, 01.xi.2010, 2♂♂ and 22 ♀♀ (DZUP); Rio Grande do Sul, Arroio Grande, Distrito Mauá [-32.233483, -53.086682], Malaise trap, R. F. Krüger, 22.xi.2002, 2♀♀ (DZUP 099253; 099256); same label information, except: P. B. Ribeiro, 6♀♀ (DZUP 099259–64); 15.xi.2002, 2♀♀ (DZUP 099254–55);

07.ii.2003, 1♀ (DZUP 099257); 31.i.2003, 1♀ (DZUP 099258); Santa Catarina, Itajaí, EMPASC [-26.9534, -48.7358], C. Paloschi, ix.1988, 1♂ (DZUP 099244); same label information except: xi.1989, 4♀♀ (DZUP 099265–68). Chile: Bío-Bío, Lag. Laja [-37.4042, -71.3415], Luis Peñas, 13.ii.1957, 1♂ (WSU); Los Lagos, Maullín, Llanquihue [-41.2675, -73.0240], Luis Peñas, 16–21.ii.1957, 2♂♂ (WSU); Valparaíso, Laguna Verde [-33.1054, -71.6676], L. E. Peña, x.1969, 15♂♂ and 6♀♀ (MZUSP).

**Distribution.** Argentina (Río-Negro), Brazil (Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul*, Santa Catarina), Chile (Bío-Bío*, Los Lagos, Valparaíso*) and Peru (Tacna) (Malloch 1934; Albuquerque 1953; Pont & Ackland 2009; Gomes et al. 2019) (Fig. 6). *= new records.

**Remarks.** The type-locality indicated as Tacna, Chile (Stein 1911; Pont & Ackland 2009) is a region that currently belongs to Peru. Some specimens from Chile have the body covered by pollen. There are some male specimens from Argentina, Brazil and Chile with 1–4 setulae on meron (V. Michelsen, pers. comm.).

***Calythea crenata* (Bigot 1885)**

(Figs. 3d–f, 4m–p, 5g–i, 6)

**Diagnosis.** *Calythea crenata* can be separated from the other species of the genus by the setulose eyes; face projecting beyond frontal angle; parafacialia very narrow, with about 1/5 of postpedicel width; thorax without pruinose near transversal suture; distance between presutural acrostichal rows twice longer than to dorsocentral rows; acrostichal setae thin, similar to covered setulae; hind tibia with a posterodorsal seta 4 times longer than tibia width.

**Description. Female.** Thorax with 1 dorsal stripe, covering the lines of acrostichal setae (Fig. 3f). Scutellum fully pruinose, except for a central triangle basally. Anepisternum with a row of 3 posterior setae. Meron with a tuft of 0–2 setulae, located posteriorly below spiracle. Katepimeron with 6–9 setulae. Terminalia with cerci dilated distally, with long setae; epiproct subtriangular, as long as wide; hypoproct subconical, twice longer than wide; sternite 6 and 7 trapezoid; tergite 6 and 7 subtriangular dorsally; sternite 8 slightly shorter than tergite 8 (Figs. 5g–i).

**Material examined.** Colombia: Boyacá, SFF [Santuario de Flora y Fauna] Iguaque Cabeña Chaina, 5.4166, -73.45, 2600m, P. Rema, 17.v–5.vi.2001, 1♂ (DZUP 099250); same label information, except: A. Roberto, 9–31.viii.2001, 1♂ (DZUP); A. Roberto, 31.viii–16.ix.2001, 1♀ (DZUP). Ecuador: Azuay, Portete de Tarqui, Sur de

Cuenca [-2.9012, -79.0070], L. E. Peña, xii.1970, 3♂♂ and 2♀♀ (MZUSP); 1♂ (DZUP 462892); Loja, La Toma, W. de Loja [-4.0081, -79.2110], 1500m, L. E. Peña, xi.1970, 4♂♂ and 4♀♀ (MZUSP); Saraguro [-3.6217, -79.2380], 2900m, L. E. Peña, xi.1970, 5♂♂ and 1♀ (MZUSP). Mexico: Chiapas, Pueblo Nuevo, Arroyo Grande [17.1582, -92.8972], F. Árias, 15.xii.1985, 1♂ and 1♀ (CNIN); Guerrero, Omiltemi [17.5564, -99.6869], F. Árias, 10.vii.1985, 2♂♂ and 7♀♀ (CNIN; DZUP); same label information, except: 11.vii.1985, 2♀♀ (CNIN; DZUP); Hidalgo, km 90, Pachuca-Tampico [20.7961, -98.7091], F. Árias & R. Medina, 14.iii.1986, 2♀♀ (CNIN; DZUP); Mexico, Dexcanic Alto [19.4306,-99.1342], F. Árias, 29.iii.1986, 1♀ (CNIN); km15 carretera Periferica Ajusco [19.2155, -99.2468], J. Butze, 1.v.1979, 1♂ (CNIN); Mexico D.F. km30 carretera Sn. Gregorio-Oaxtepec, [19.2084, -99.0688], 2750m, J. Butze, 7.xii.1979, 2♂♂ (CNIN; DZUP); Tequesquinahuac, C. Tlaloc [19.3987, -98.7085], J. Butze, 15.iv.1982, 1♂ and 1♀ (CNIN); Temascaltepec, Real de Arriba [19.0428, -100.2261], A. Cadena & L. Cervantes, 4.vi.1988, 1♀ (CNIN); Morelos, Huitzilac [19.0313, -99.2671], E. Olucra, 17.xi.1978, 1♂ (CNIN); same label information, except: E. Ramirez, 18.vii.1984, 1♂ (CNIN); E. Jimenez, 17.xi.1978, 1♀ (CNIN); 2km NW, Huitzilac [19.0313, -99.2671], 2750m, J. Butze & A. Ibarra, 18.vii.1984, 3♂♂ (CNIN; DZUP); same label information, except: J. Butze & E. Ramirez, 4♂♂ (CNIN; DZUP); J. Butze & V. Hernández, 2♂♂ (CNIN; DZUP); A. Ibarra, 1♀ (CNIN); km 58 Carretera Xochimilco-Caxtepec [19.0397, -98.9562], J. Butze, 8.xii.1978, 1♀ (CNIN); Nicolas Zapata [19.0375, -98.9115], J. Butze, 6.xii.1978, 1♀ (CNIN); Veracruz, km 120 Autopista Puebla Orizaba [18.8358, -97.1389], 2800m, J. Butze, 17.vii.1978, 2♂♂ (CNIN; DZUP). Peru: Cuzco, Est. Biol. Wayqecha, jct. Trochas Schefflera & Picaflor [-13.17385, -71.58808], 2905 m, A. L. Norrbom, B. D. Sutton & O. Quispe, 1–12.vi.2012, 2♀♀ (DZUP, USNM); same label information, except: Campo de Futbol [-13.17445, -71.5880], 2900m, 4-7.vii.2016, 3♂♂ and 7♀♀ (DZUP, USNM).

**Distribution.** Colombia (Boyacá*), Costa Rica, Ecuador (Azuay*, Loja* and Pichincha), Mexico (Durango, Estado de Mexico*, Guerrero, Hidalgo, Mexico, Morelos, Sinaloa, Veracruz), Puerto Rico, Peru (Arequipa, Chanchamayo, Cuzco*, Tarma) and Saint Thomas Island (Stein 1904, 1911; Curran 1928; Albuquerque 1953; Griffiths 1986; Michelsen 2010; Grisales et al. 2016) (Fig. 6). *= new records.

**Remarks.** Redescribed by Albuquerque (1953) and Griffiths (1986). The geographical information about the previous record from Colombia is only indicated

as Colombia's Cordillera (Stein 1904) and was not included in the map. The records from North America are based on Griffiths' (1986) map. There is morphological variation in the calypters, which range from light to dark brown.

***Calythea micropteryx* (Thomson 1869)**

(Figs. 3g–l, 4q–t, 5j–l, 6)

**Diagnosis.** *Calythea micropteryx* can be separated from the other species of the genus in having face not projecting beyond frontal angle; parafacialia very narrow, with about 1/5 of postpedicel width; distance between presutural acrostichal rows, except anteriorly in the first pair of setae, shorter than their distance to dorsocentral rows; hind tibia with a posterodorsal seta twice longer than tibia width. Also, this is the smaller neotropical species (body length: 3.3–3.5; wing length: 3.2–3.5).

**Type-material examined.** Paralectotypes. United States, California, Kinb., 3♂♂ (NHRS: 459 67; 464 67; 460 67).

**Material examined.** Mexico. Baja California, Golfo California, Isla Angel de la Guarda, Puerto Refugio [29.3407, -113.4311], F. Árias, 6.ii.1986, 1♂ and 1♀ (CNIN); Campeche, Grutas de Ixta, Cambilxunau [19.9911, -89.7642], F. Árias, 21.vi.1986, 1♂ (CNIN).

**Distribution.** Canada (Alberta, British Columbia, Manitoba); United States (Arizona, California, Colorado, Idaho, Montana, Nebraska, Nevada, New Mexico, Oregon, South Dakota, Texas, Utah, Washington, Wyoming); Mexico (Baja California Norte, Baja California Sur, Campeche*, Chihuahua, Hidalgo, Jalisco, Mexico, San Luis Potosí, Sonora, Zacatecas); Cuba, Dominican Republic (Griffiths 1986; Michelsen 2010) (Fig. 6). *= new record.

**Remarks.** Redescribed by Griffiths (1986). The records from North America are based on Griffiths (1986) map. The record from Costa Rica (Michelsen, 2010) is based on a misidentification (V. Michelsen, pers. comm.).

## DISCUSSION

The genera *Calythea*, *Pegoplata*, *Enneastigma* Stein, *Nupedia* Karl [= *Pegoplata*], and *Myopina* Robineau-Desvoidy, form a well-defined lineage known as *Nupedia*-group. The monophyly of this group is based mainly on characteristics of the male terminalia, as the club-shaped and distally expanded distiphallus. The

differentiated balloon-like distiphallus of *Calythea* is considered as being derived from the ground plan of this group (Hennig 1976; Michelsen 1988).

The short, but broad distiphallus, which is evenly sclerotized, with spinules on the distal region (Figs. 4d, h, l, p, t) and the surstyli short and spoon-like (Figs. 4c, g, k, o, s) are diagnostic of *Calythea*. The spoon-like surstyli are also present in few other species of the *Nupedia*-group (Hennig 1976). In the drawings published by Séguy (1934) for *C. costana*, the structures in the male terminalia are difficult to identify and this species probably it is not an Anthomyiidae due to dorsocentrals 2+4 and male terminalia shape. The main divergences we observed between those species and the Neotropical species we studied are in the shape of the surstyli in dorsal and lateral views (Fig. 4).

For the most part, while males can be identified based on their terminalia, the identification of females is more challenging, since the ovipositor is very similar among species. We observed differences in the sternite 8, which is shorter than tergite 8 in *C. comis* (Fig. 5d)*, C. crenata* (Fig. 5g) and *C. micropteryx* (Fig. 5j), while in *C. cochlearis* the sternite 8 is subequal in length to tergite 8 (Fig. 5a). The remaining sternites are rounded to trapezoid and we observed variations in different specimens of the same species even from the same locality. Tergites 6 and 7 form a T-shape pattern dorsally (Figs. 5b, e, h, k). The epiproct is very similar among *C. cochlearis*, *C. comis*, *C. crenata* and *C. micropteryx* (Figs. 5b, e, h, k), while the hypoprocts of *C. comis* and *C. micropteryx* (Figs. 5f, l) are wider than those of *C. crenata* and *C. cochlearis* (Figs. 5c, i).

Besides the terminalia, the species of *Calythea* present sexual dimorphism in the eyes and frons; and the pulvilli are slightly larger in males than in females (Griffiths 1986). In addition, the pruinose pattern of the thorax and abdomen differs between male and female, as well as the chaetotaxy of the katepimeron, katepisternum and meron. While the pruinosity of the thorax has some taxonomically important differences among species (see below), the abdomen of both male and female are very similar among species, without conspicuous differences that help in identification.

The pruinose pattern on the male thorax is similar among the studied species, with pruinosity on the notopleural region and two basal triangles on the posterior half of the dorsocentral setae region. While these basal triangles are connected in *C. andina* (Fig. 1b), *C. cochlearis* (Fig. 2b), and *C. micropteryx* (Fig. 3h),

they are not connected in *C. comis* (Fig. 3b) and *C. crenata* (Fig. 3e). The region separating the triangles is two times wider in *C. comis*. In addition, the only species without pruinosity on the transversal suture, intra-alar and postalar setae regions is *C. crenata* (Fig. 3e). *C. comis* is the only species with the pruinosity extending to the dorsocentral setae region (Fig. 3b).

The pruinosity on the female thorax also differs among the studied species. *C. crenata* and *C. cochlearis* have a wider central stripe (Figs. 2d, 3f), when compared with *C. comis* and *C. micropteryx* (Figs. 3c, i). In addition, *C. comis* has three dorsal stripes, with two inconspicuous stripes near to the central one (Fig. 3c), while all three dorsal stripes of *C. micropteryx* are inconspicuous (Fig. 3i). The pattern of *C. cochlearis* diverges from all the other species by two dotted lines on the region of the dorsocentral setae (Fig. 2e).

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FIGURES

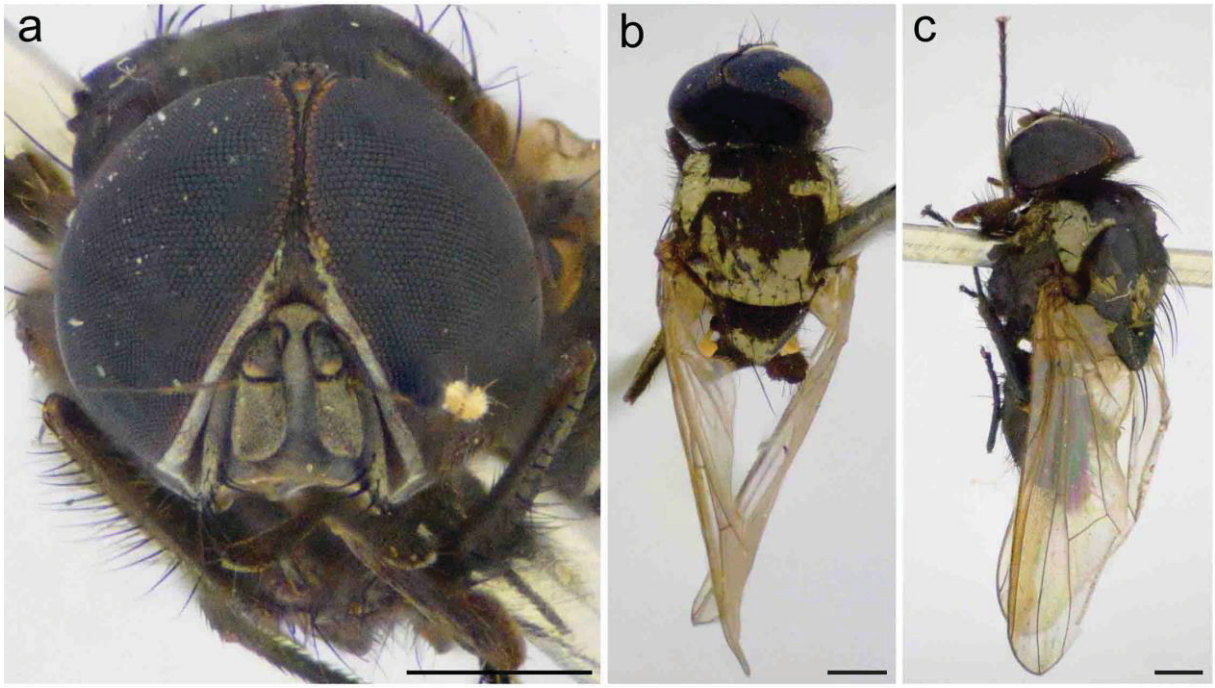


**Figure 1** *Calythea andina* **new species** Male: head, frontal view (a); habitus, dorsal view (b); habitus, lateral view (c). Bar= 0.5 mm.

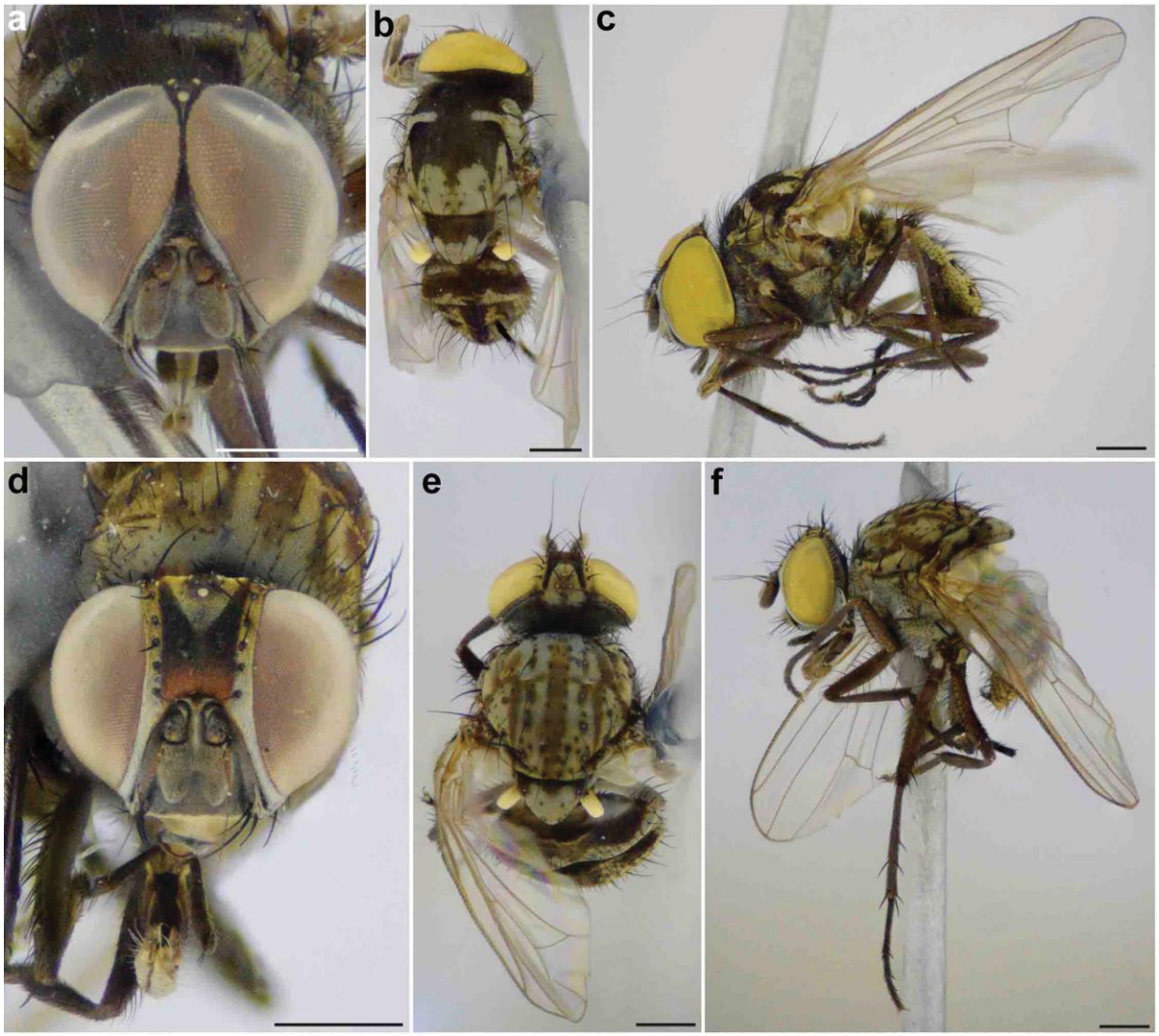


**Figure 2** *Calythea cochlearis* **new species** Male: head, frontal view (a); habitus, dorsal view (b); habitus, lateral view (c); Female: head, frontal view (d); habitus, dorsal view (e); habitus, lateral view (f). Bar= 0.5 mm.

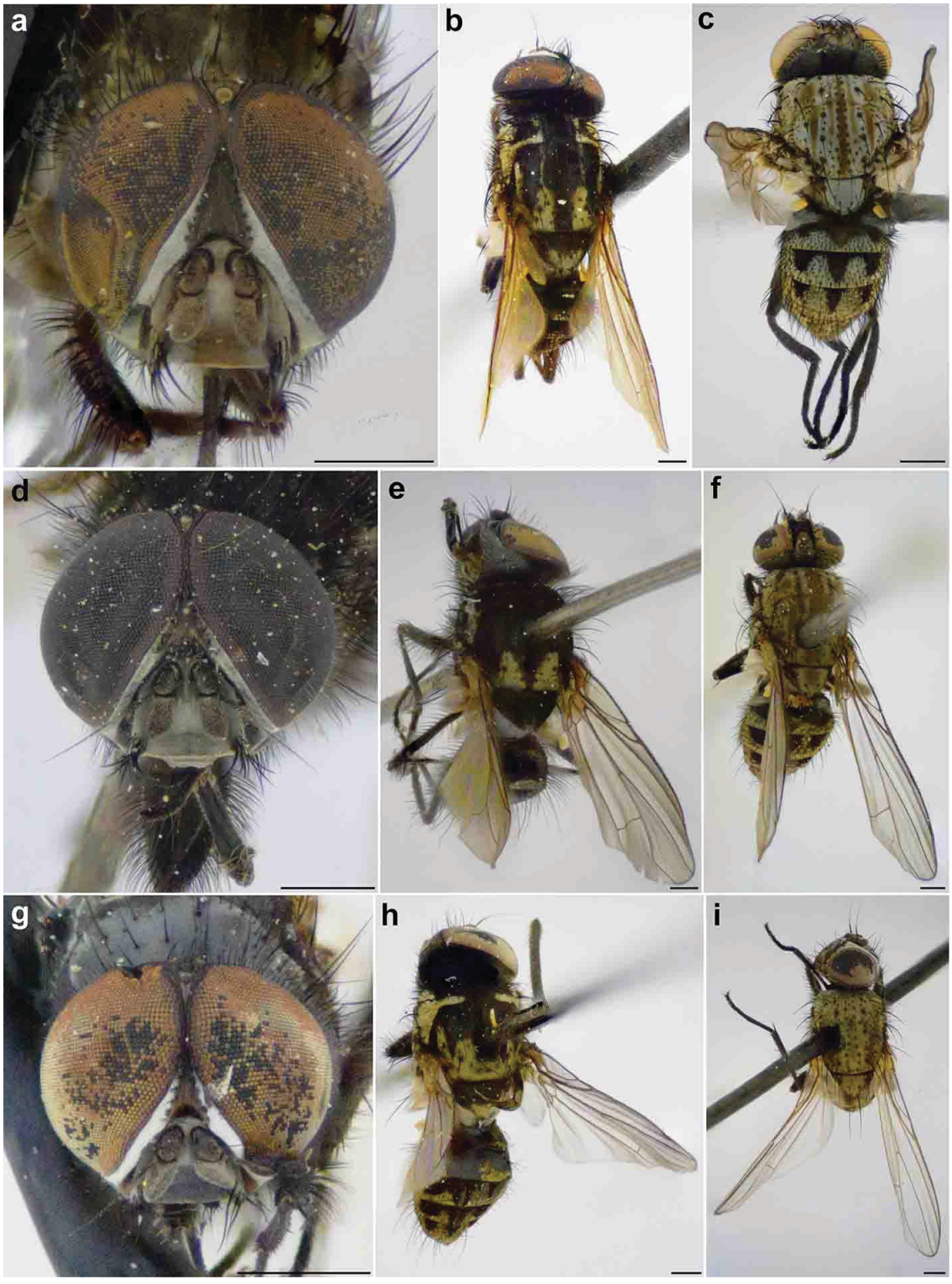


**Figure 3** *Calythea comis.* Male: head, frontal view (a); habitus, dorsal view (b); Female: habitus, dorsal view (c). *Calythea crenata.* Male: head, frontal view (d); habitus, dorsal view (e); Female: habitus, dorsal view (f). *Calythea micropteryx.* Male: head, frontal view (g); habitus, dorsal view (h); Female: habitus, dorsal view (i). Bar= 0.5 mm.

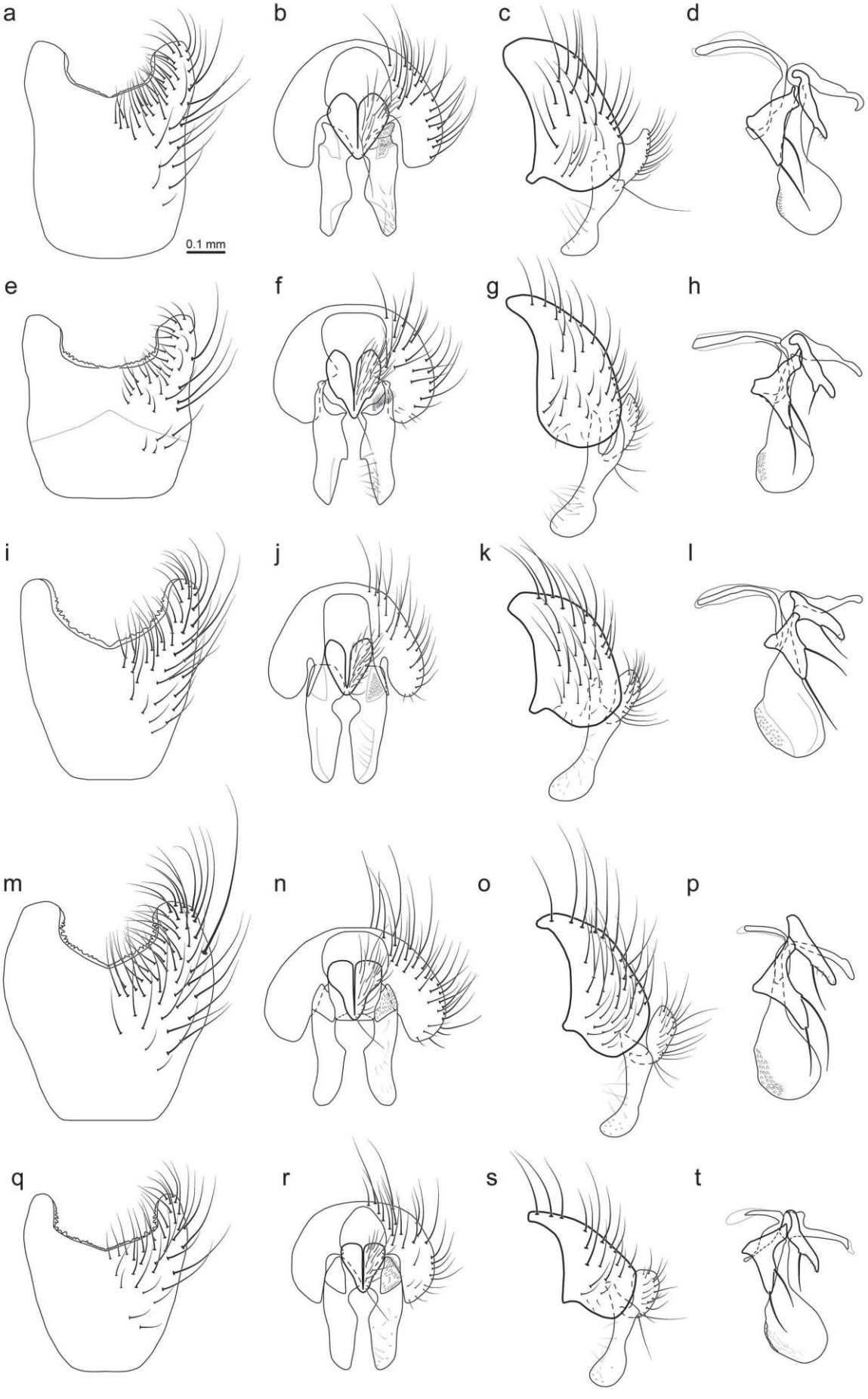
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**Figure 4** *Calythea* male terminalia: *C. andina* **new species**: sternite 5, dorsal view (a); epandrium, cerci and surstyli dorsal (b) and lateral (c) view; aedeagus and associated structures, lateral view (d). *Calythea cochlearis* **new species**: sternite 5, dorsal view (e); epandrium, cerci and surstyli dorsal (f) and lateral (g) view; aedeagus and associated structures, lateral view (h). *Calythea comis*: sternite 5, dorsal view (i); epandrium, cerci and surstyli dorsal (j) and lateral (k) view; aedeagus and associated structures, lateral view (l). *Calythea crenata*: sternite 5, dorsal view (m); epandrium, cerci and surstyli dorsal (n) and lateral (o) view; aedeagus and associated structures, lateral view (p). *Calythea micropteryx*: sternite 5, dorsal view (q); epandrium, cerci and surstyli dorsal (r) and lateral (s) view; aedeagus and associated structures, lateral view (t).

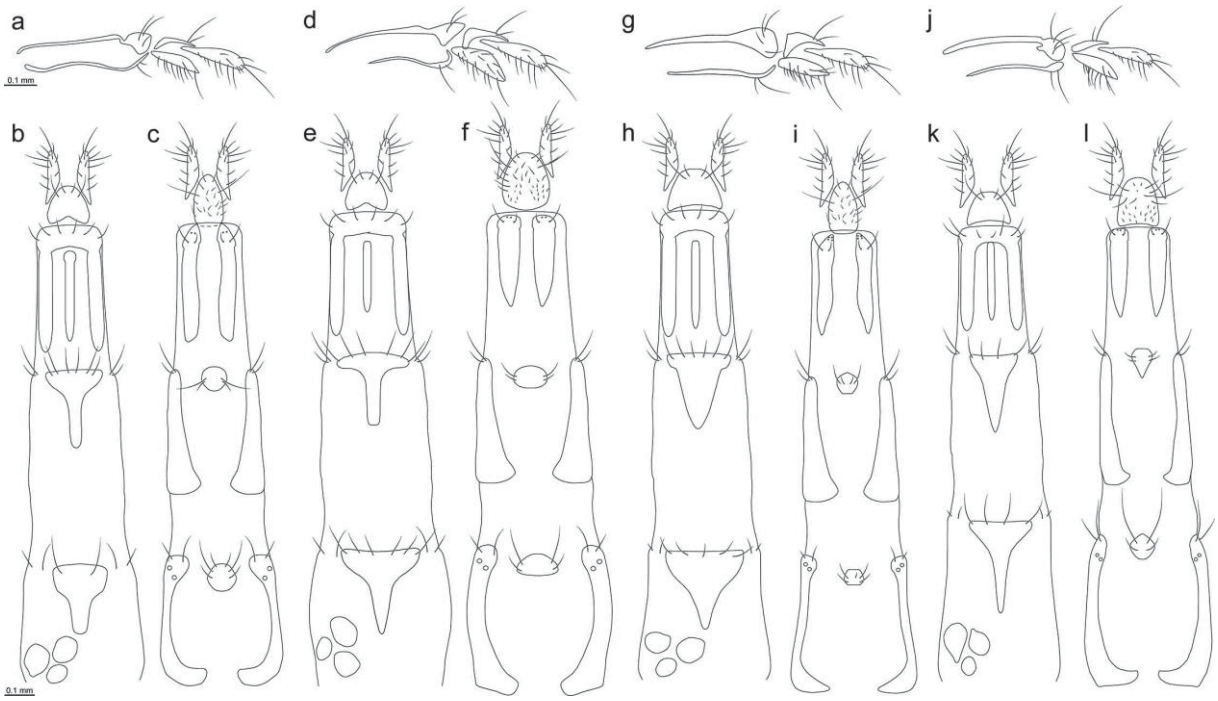


**Figure 5** Ovipositor *Calythea*. *C. cochlearis* **new species**: lateral view (a), dorsal view (b) and ventral view (c); *C. comis*: lateral view (d), dorsal view (e) and ventral view (f); *C. crenata*: lateral view (g), dorsal view (h) and ventral view (i); *C. micropteryx*: lateral view (j), dorsal view (k) and ventral view (l).

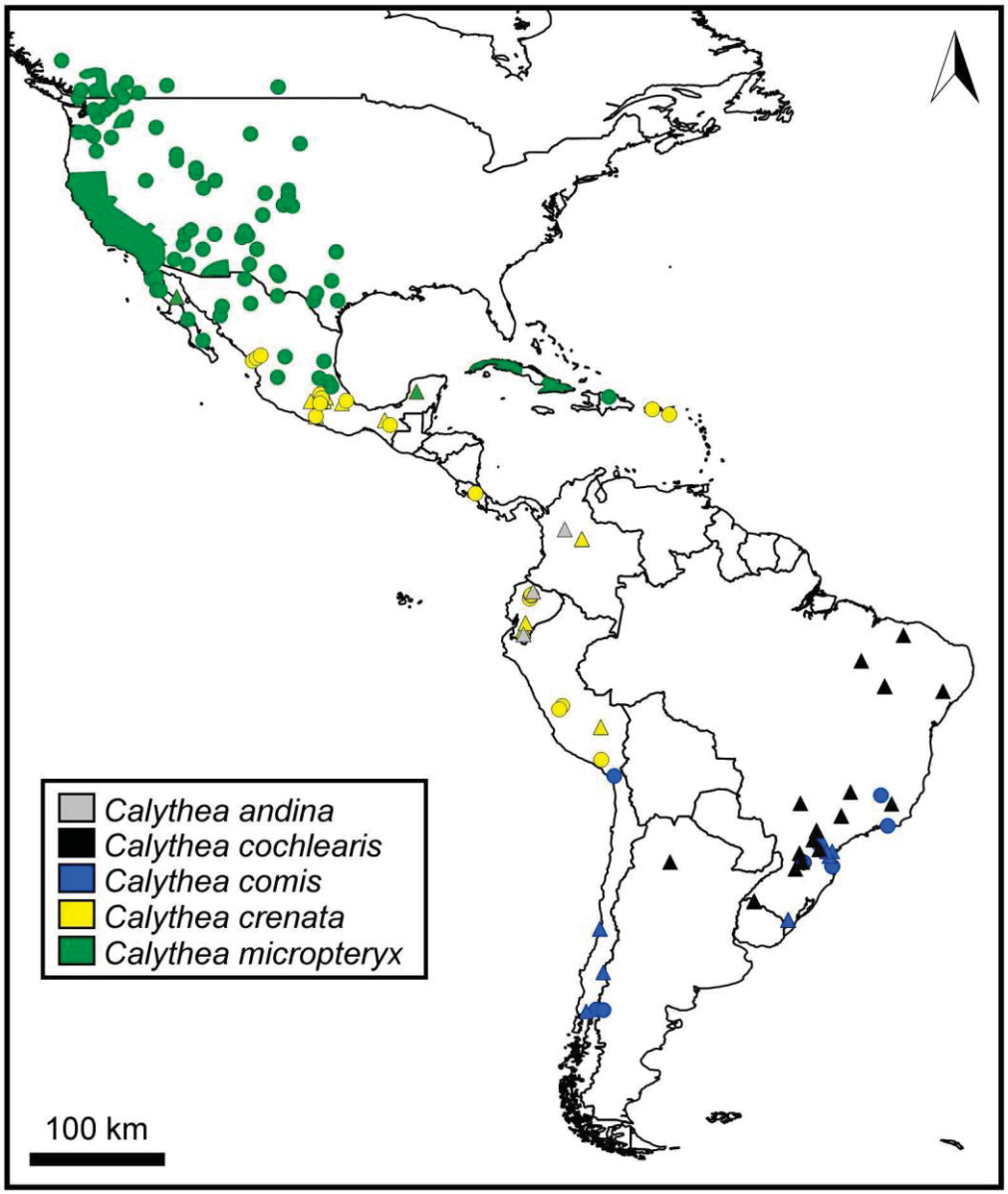


**Figure 6** Map of *Calythea* species from Neotropical region. Circles= literature records; triangle= new records.

## CAPÍTULO VI

# THREE NEW SPECIES OF *BOTANOPHILA* LIOY (DIPTERA: ANTHOMYIIDAE) FROM THE MEXICAN TRANSITION ZONE

***Artigo publicado na Zootaxa, 5005 (3): 317–328***
***(versão pré-publicação)***

# Three new species of *Botanophila* Lioy (Diptera: Anthomyiidae) from the Mexican Transition Zone

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Running title: New species of *Botanophila* from Mexico

ABSTRACT

The genus *Botanophila* Lioy has several species distributed in North America, but none had been recorded from Mexico. Here we describe three new species of *Botanophila* from the highlands of the Mexican Transition Zone. We include images of habitus, drawings of the terminalia and a key to facilitate the identification of species. Remarkably, the male of the new species has dichoptic eyes, an unusual characteristic in Anthomyiidae.

**Key Words:** biodiversity; highlands; Morphology; North America; taxonomy.

## INTRODUCTION

The genus *Botanophila* Lioy includes 243 described species. Among those, 65 species have been recorded from the Nearctic Region, excluding Mexico (Evenhuis and Pape 2020). The genus is distributed mainly in northern and high-altitude areas of North America and Eurasia (Michelsen 2015). Although many species are morphologically diverse, there are several assemblages of morphologically very similar and obviously closely-related species, and identification is primarily made using the male terminalia. (Michelsen 2009, 2015). The adults are mainly anthophilous, feeding on nectar (Michelsen 2015). The larvae of most *Botanophila* species are phytophagous, living in the capitulum inflorescence of various flowering plants (Pont and Ackland 1995). Some species are host-specific of invasive plants and have a potential to be used in biological control (Vitou *et al*. 2001).

It is unclear whether *Botanophila* is monophyletic, since there are no obvious diagnostic characters for the genus. Most, but not all species, share some characteristics, for instance interfrontal seta present, fronto-orbital seta absent, arista pubescent, prealar seta well developed, scutellum with two long marginal pairs of setae, a shorter discal pair, and fine pubescence on the ventral surface; male sternite 5 with submarginal series of spinules; pregonite very reduced with two robust setae; and distiphallus reduced (Huckett 1971; Hennig 1976; Suh and Kwon 2008).

Huckett (1924, 1929, 1947, 1965a, 1965b, 1966, 1971) worked extensively on the North American *Botanophila*, describing several species from Canada and the United States. Back in the time when Huckett was studying *Botanophila*, the genus was considered a subgenus of *Hylemya* Robineau-Desvoidy. It was only later that Hennig (1976) re-elevated *Botanophila* to full genus status. Following that, Michelsen (1983) proposed a broadened concept of *Botanophila*, with *Pegohylemyia* Schnabl as a junior synonym.

During the study of the muscoid material from Colección Nacional de Insectos (CNIN) of the Universidad Autónoma Nacional de México (UNAM), Ciudad de Mexico, D.F. and the Entomological Collection (IEXA) at the Instituto de Ecología (INECOL), Xalapa, Veracruz, we found some remarkable anthomyiids, with male eyes dichoptic, from the Mexican Transition Zone (MTZ), a highland area where the Nearctic and Neotropical regions overlap (Darlington 1957).

Herein, we described three new species from the Mexican transition zone, including images of habitus and drawings of the terminalia. In addition, the biology, distribution and morphology are discussed.

## MATERIAL AND METHODS

### Specimens

The material used on this study is based on seven males and two females from Colección Nacional de Insectos (CNIN), Instituto de Biología, Universidad Nacional Autónoma de México (UNAM) and one male from the Entomological Collection (IEXA) at the Instituto de Ecología (INECOL), Xalapa, Veracruz. Two males and one female paratypes of *Botanophila zaldivari* **sp. nov.** will be deposited at the Department of Zoology of the Universidade Federal do Paraná (DZUP). The holotype and remaining paratypes of *B. zaldivari* **sp. nov.** and the holotype and

paratype of *B. mayorgae* **sp. nov.** remain at CNIN. The holotype of *B. hernandezi* **sp. nov**. will be deposited at IEXA collection.

### Dissections and terminology

Specimens were examined under a stereomicroscope. The abdomen was removed from the specimens for the examination of the terminalia, which was cleared and softened in cold potassium hydroxide (KOH) 10% for 24 h, transferred to acetic acid, dehydrated in 70% alcohol and then placed in glycerin. In the transcription of the holotype label of the new species a backslash indicates the end of a line and a quotation mark indicates the beginning and the end of the label. The terminology follows Cumming and Wood (2017). The following abbreviations are used: *a*= anterior; *ad*= anterodorsal; *av*= anteroventral; *d*= dorsal; *p*= posterior; *pd*= posterodorsal; *pv*= posteroventral.

### Images and measurements

The images from specimens were obtained using an auto-montage setup acquired by the Taxonline project (UFPR – http://www.taxonline.ufpr.br/). Drawings of the terminalia were prepared using a Carl Zeiss ® Standard 20 microscope and were inked by Adobe Illustrator CS6. The map was generated using QGIS 2.18.28 (http://www.qgis.org/en/site/), the exact coordinates were not available and were estimated based on the label information of each specimen. We use the shapefile of the Mexican biogeographic provinces available in Morrone *et al*. (2017).

## RESULTS

### Taxonomy

***Botanophila*** Lioy, 1864

***Diagnosis.*** Male eyes usually holoptic; interfrontal seta present; fronto-orbital seta usually absent; arista pubescent; mid tibia with 1–3 posterodorsal seta; prealar seta well developed; scutellum with two long marginal pairs of setae and a shorter discal pair, and with fine pubescence on ventral surface; proepisternum, meron and anepimeron bare; pregonite small, and with two robust setulae; distiphallus reduced (adapted from Suh and Kwon 2008).

An unusual character of the species herein described is the male dichoptic eye, identical to female (Figs 1A, 2A, 3A), whereas the male terminalia is

*Botanophila*-type, with pregonite and distiphallus reduced, and the cercus long and apically furcated (Figs 4D, 5D, 6D). The new species belong to the *B. brunneilinea* species-group. This group is composed of relatively large and bristly species, which also present a long-pubescent arista, a long prealar seta, and numerous short *av* and *pv* setae but no apical *pd* seta on hind tibia (Michelsen 2009). The cercus of *brunneilinea*-group is long and narrowly separated in the distal part, forming two closely approximated halves of a more or less pointed cercus (Xue and Song 2007).

***brunneilinea*-group**

***Diagnosis.*** Sternite 5 processes with dense long lateral setae. Cercus large, distal margin reaching or nearly reaching the apex of surstyli, in the distal third or quarter narrowly separated and forming two points. (Xue and Song 2007).

**Key to *Botanophila* species from MTZ**

1 Interfrontal setae short, about half length of the frontal setae (Fig. 1A); arista pubescence with hairs longer than the greatest basal diameter of arista; median apical process on cercus absent (Fig. 4E) … *Botanophila hernandezi* **sp. nov.**

- Interfrontal setae long, similar to frontal setae (Figs 2A, 3A); arista pubescence with hairs of similar length to greatest basal diameter of arista; median apical process on cercus present (Figs 5E, 6E) … 2

2 (1) Tibiae dark brown (Fig. 2C); cercus quadrangular, as long as its width; surstylus slightly curved (Fig. 5C) … *Botanophila mayorgae* **sp. nov.**

- Tibiae light brown (Fig. 3C, F); cercus rectangular, longer than its width; surstylus strongly curved (Fig. 6C) … *Botanophila zaldivari* **sp. nov.**

***Botanophila hernandezi* sp. nov.**

(Figs 1, 4)

**Diagnosis:** Dichoptic. Interfrontal setae present (shorter than frontal setae). Prealar long. Katepisternals 1+2. Dorsocentrals 2+3. Hind tibia with 2 *av* seta (median and submedian), 4 *ad* setae, 3 *pd* setae, and 1 *pv* seta (supra median), apically with long and robust setae on *ad*, *av*, and *d*. Cercus on posterior view, enlarged and long,

twice longer than its width, slightly shorter than surstylus, apically rounded, without a median apical process.

**Description:** Male. Body length: 6.0 mm. Wing length: 6.2 mm.

**Color:** General coloration light brown with gray pruinosity. Frontal vitta dark brown with ochre yellow on the lower half, fronto-orbital plate, parafacial, and gena with gray pruinosity. Antennae and palpus dark brown. Three conspicuous brown stripes on the mesonotum. Calypter and halter white-yellowish. Legs light brown with gray pruinosity, tibiae yellow. Wing slightly brownish, with yellowish veins. Abdomen with a poorly delimited middorsal dark stripe, almost not visible on the posterior region of each tergite; syntergosternite 7 + 8 light brown with gray pruinosity.

**Head** (Fig. 1A): Dichoptic; parafacial in the middle, only half as wide as postpedicel; gena almost twice wider than pedicel, with a single row of robust setae; frons broad, frontal vitta with about 3/5 of the total frontal width, with strong inner and outer vertical setae (the inner vertical setae 2/5 longer than the outer), a pair of interfrontal setae, 3 orbital setae, and 4 frontal setae plus 4 frontal setulae. Antenna long; arista pubescence, hairs longer than the greatest basal diameter of arista. Proboscis short with labella larger than prementum width; prementum covered by short setulae, with a row of setulae on its margin and with a proximal pair longer than prementum width.

**Thorax** (Fig. 1C): Prosternum bare. Postpronotal lobe with covered setulae and 2 long setae (similar to notopleural setae). Acrostichal setae 0+1. Prealar seta longer than posterior notopleural seta. 2 proepisternal setae; 2 proepimeral setae, the upper one twice longer. Anepisternum with a row of 5 long posterior setae and covered by setulae in the upper posterior corner; with an anterior long setula, below anterior notopleural seta. Katepisternals 1+2. Dorsocentrals 2+3. Upper calypter with long setulae around the margin, with almost the same length of calypter width. Lower calypter reduced to an almost linear, narrow fold. Apical and basal scutellar setae long, twice longer than the scutellum length.

**Wing:** Vein C ventrally bar, just with some setulae apically, after subcostal vein; basal to costal break with slightly enlarged *av* spinules; subcostal break with 2 long spinules, 3 times longer than the other. Cross-vein dm–cu straight.

**Legs:** Fore femur covered by a long row of setae on *pd* to *pv* surface; fore tibia with 2 *ad* setae (median and submedian) and a median *pv* seta; apically only with a *pv* seta and a longer *d* seta. Mid femur basally with an *av* and *ad* rows of setae; mid tibia with 1 submedian *ad*, 2 *pd* setae (supramedian and submedian) and 2 *pv*

(supramedian and submedian), preapical setae on *p* and *pd* absent, long apical setae on *av*, *pv* and *v*, in addition to shorter setae on remaining surfaces. Hind femur with a row of robust *ad* and *av* setae, twice longer than the femur width; hind tibia with 2 *av* seta (median and submedian), 4 *ad* setae, 3 *pd* setae, and 1 *pv* seta (supra median), apically with long and robust setae on *ad*, *av*, and *d*. Pulvillus enlarged, longer than width of tarsomere.

**Abdomen** (Fig. 1B, C): All tergites with long lateral and median marginal setae, tergite 5 with discal setae. Tergite 6 exposed, bare. Sternite 1 setulose, with few lateral setulae; sternites 2–4 longer than width; sternite 5 (Fig. 4A) processes with long lateral setae on the outer margin and shorter setae on the inner margin.

**Terminalia** (Fig. 4): Cercus on posterior view, enlarged and long, twice longer than its width, slightly shorter than surstylus, apically rounded, without a median apical process (Fig. 4B). Surstylus long, narrow, slightly curved, and slightly enlarged apically. Hypopygium (Fig. 4D, E) of the *Botanophila*-type, i.e. pregonites reduced and shallow (strongly connected to distiphallus), presenting 2 long setae; pregonite firmly connected to the central plate of hypandrium; postgonite short, similar length to pregonite; epiphallus and distiphallus reduced, distiphallus distally membranized (Fig. 4D, E). Phallapodema enlarged on the dorsal view (Fig. 4E) and narrowed on the lateral view (Fig. 4D).

**Female:** unknown.

**Etymology:** Name in apposition. This species is named in honor of Vicente Hernández Ortiz, entomologist of the Instituto de Ecología, INECOL.

**Material examined:** Holotype. Male. “MEXICO: Oaxaca, Concepción \ Papalo. 2085 m. En \ coprotrampas \ 9 to 10-VII-1997. G. Nogueira col.” [17.842252; -96.881462] (IEXA).

**Distribution:** Mexico (Oaxaca).

**Remarks:** This new species is easily distinguished from the other known *Botanophila* species by the male head, which is fully feminized with dichoptic eyes, interfrontal setae and proclinate orbital setae developed. This species is morphologically very divergent from the other two new species, with frontal vitta dark brown with ochre yellow on the lower half, interfrontal setae shorter than frontal setae; inner vertical setae 2/5 longer than outer vertical setae; arista hairs longer than the greatest basal diameter of arista; sternite 1 setulose, with few lateral setulae; cercus without a median apical process; distiphallus positioned in the same direction as the

phallapodema; postgonite very reduced, subequal in length to pregonite; phallapodema dorsally enlarged, with the same width distally and proximally.

***Botanophila mayorgae* sp. nov.**

(Figs 2, 5)

**Diagnosis:** Dichoptic. Interfrontal setae present, similar to frontal setae. Prealar long. Katepisternals 1+2. Dorsocentrals 2+3. Pulvillus enlarged (male). Hind tibia with 2 *av* seta (median and submedian), 4 *ad* setae, 3 *pd* setae, and 1 *pv* seta (supra median), apically with long and robust setae on *ad*, *av*, and *d*. Cercus on posterior view, enlarged and long, twice longer than its width, shorter than surstylus, apically furcated, with an acutely pointed on each side and among them a median apical process.

**Description:** Male. Body length: 5.8 mm. Wing length: 6.0 mm.

**Color:** General coloration light brown with gray pruinosity. Frontal vitta dark brown with ochre yellow on the lower third, fronto-orbital plate, parafacial, and gena with gray pruinosity. Antennae and palpus dark brown. Three inconspicuous brown stripes on the mesonotum. Calypter and halter white-yellowish. Legs light brown with gray pruinosity, tibiae with the same femur coloration. Wing slightly brownish, with yellowish veins. Abdomen with a poorly delimited middorsal dark stripe, almost not visible on the posterior region of each tergite; syntergosternite 7 + 8 light brown with gray pruinosity.

**Head** (Fig. 2A): Dichoptic; parafacial in middle only half as wide as postpedicel; gena almost twice wider than pedicel, with a single row of robust setae; frons broad, frontal vitta with about 3/5 of the total frontal width, with strong inner and outer vertical setae (the inner vertical setae 1/5 longer than the outer), a pair of interfrontal setae, 2 orbital setae and 2 frontal setae plus 3 frontal setulae. Antenna long; arista pubescence, hairs with similar length to greatest basal diameter of arista. Proboscis short with labella larger than prementum width; prementum covered by short setulae, with a row of setulae on its margin and with a proximal pair longer than prementum width.

**Thorax** (Fig. 2B, C): Postpronotal lobe with covered setulae and 2 long setae (similar to notopleural setae). 3 acrostichal presutural setae, very short; the acrostichal postsutural setae not visible due to the pin. Prealar seta similar to posterior notopleural seta. 2 proepisternal setae; 2 proepimeral setae, the upper one twice

longer. Anepisternum with a row of 5 long posterior setae and covered by setulae in the upper posterior corner; with a long anterior setula, below anterior notopleural seta. Katepisternals 1+2. Dorsocentrals 2+3. Upper calypter with long setulae around the margin, with almost the same length of calypter width. Lower calypter reduced to an almost linear, narrow fold. Apical and basal scutellar setae long, twice longer than the scutellum length.

**Wing:** Vein C ventrally bar, just with some setulae apically, after subcostal vein; basal to costal break with slightly enlarged *av* spinules; subcostal break with 2 long spinules, 3 times longer than the other. Cross-vein dm–cu straight.

**Legs:** Fore femur covered by a long row of setae on *pd* to *pv* surface; fore tibia with a submedian *ad* seta and a median *pv* seta, apically only with a *pv* seta and a longer *d* seta. Mid femur with an *ad* and *av* row of setae and a long *pv* row of setae, long preapical setae on *p* and *pd*; mid tibia with 1 submedian *ad*, 2 *pd* setae (supramedian and submedian) and 2 *pv* (median and submedian), preapical setae on *p* and *pd* absent, apical long setae on *av*, *pv* and *v*, in addition to shorter setae on remaining surfaces. Hind femur with a row of robust *ad* and *av* setae, twice longer than the femur width; hind tibia with 2 *av* seta (median and submedian), 4 *ad* setae, 3 *pd* setae, and 1 *pv* seta (supra median), apically with long and robust setae on *ad*, *av*, and *d* seta. Pulvillus enlarged, longer than width of tarsomere.

**Abdomen** (Fig. 2B, C): All tergites with lateral and median marginal setae long, tergite 5 with discal setae. Tergite 6 exposed, bare. Sternite 1 setulose, with long setulae marginally. Sternites 2–4 longer than width; sternite 5 (Fig. 5A) processes with long lateral setae on the outer margin and shorter setae on the inner margin.

**Terminalia** (Fig. 5): Cercus on posterior view, enlarged and long, twice longer than its width and shorter than the surstylus, apically furcated, with an acutely pointed on each side and among them a median apical process (Fig. 5B). Surstylus long, narrow, and slightly curved. Hypopygium (Figs 5D, E) of the *Botanophila*-type, i.e. pregonites reduced and shallow, presenting 2 long setae; pregonite firmly connected to the central plate of hypandrium; postgonite twice longer than the pregonite; epiphallus and distiphallus reduced, distiphallus largely membranized except for a pair of anterobasal sclerotized rods (Fig. 5D, E). Phallapodema long and apically enlarged on dorsal (Fig. 5E) and lateral (Fig. 5D) view.

**Female:** unknown.

**Morphological variation:** (n=2). Body length: 5.4-5.8 mm. Wing length: 5.5-6.0 mm.

**Etymology:** Name in apposition. This species is named in honor of María Cristina Mayorga Martínez, entomologist of the Instituto de Biología, UNAM.

**Material examined:** Holotype. Male. "MEXICO Tlaxcala \ La Malinche \ alt. 3400m 16.VI.84 \ E. Ramírez" [19.238494; -98.031407] (CNIN). Paratype. 1 male, Mexico, Parque Nacional Zoquiapan, 3200 m, 31.vii.1980 [19.086448; -98.645898] (CNIN).

**Distribution:** Mexico (State of Mexico and Tlaxcala).

**Remarks:** This new species is easily distinguished from the other known *Botanophila* species by the male head fully feminized, with dichoptic eyes, interfrontal setae and proclinate orbital setae developed. It is very similar to *Botanophila zaldivari* **sp nov.**, but can be differentiated from it by the dark brown tibiae, shorter cercus and the slightly curved surstylus.

***Botanophila zaldivari* sp. nov.**

(Figs 3, 6)

**Diagnosis:** Dichoptic. Interfrontal setae present, similar to frontal setae. Prealar long. Katepisternals 1+2. Dorsocentrals 2+3. Hind tibia with 2 *av* seta (median and submedian), 4 *ad* setae, 3 *pd* setae, and 1 *pv* seta (supra median), apically with long and robust setae on *ad*, *av*, and *d*. Cercus on posterior view, enlarged and long, twice longer than its width, apically furcated, with an acutely pointed on each side and among them a median apical process. Epiproct semi-circular. Hypoproct suboval, twice as long as broad.

**Description:** Male. Body length: 5.3 mm. Wing length: 5.7 mm.

**Color:** General coloration light brown with gray pruinosity. Frontal vitta dark brown with ochre yellow on the lower third, fronto-orbital plate, parafacial, and gena with gray pruinosity. Antennae and palpus dark brown. Three inconspicuous brown stripes on the mesonotum. Calypter and halter white-yellowish. Legs light brown with gray pruinosity, tibiae lighter. Wing slightly brownish, with yellowish veins. Abdomen with a poorly delimited middorsal dark stripe, almost not visible on the posterior region of each tergite; syntergosternite 7 + 8 light brown with gray pruinosity.

**Head** (Fig. 3A): Dichoptic; parafacial in middle only half as wide as postpedicel; gena almost twice wider than pedicel, with a single row of robust setae; frons broad, frontal vitta with about 3/5 of the total frontal width, with strong inner and outer vertical setae (the inner vertical setae 1/5 longer than the outer), a pair of interfrontal setae, 3 orbital setae and 2 frontal setae plus 2 frontal setulae. Antenna long; arista

pubescence, hairs with similar length to greatest basal diameter of arista. Proboscis short with labella larger than prementum width; prementum covered by short setulae, with a row of setulae on its margin and with a proximal pair longer than prementum width.

**Thorax** (Fig. 3B, C): Postpronotal lobe with covered setulae and 2 long setae (similar to notopleural setae). Acrostichal setae 4+6, very short. Prealar seta longer than posterior notopleural seta. 2 proepisternal setae; 2 proepimeral setae, the upper one twice longer. Anepisternum with a row of 6 long posterior setae and covered by setulae in the upper posterior corner. Katepisternals 1+2. Dorsocentrals 2+3. Upper calypter with long setulae around the margin, with almost the same length of calypter width. Lower calypter reduced to an almost linear, narrow fold. Apical and basal scutellar setae long, about twice longer than the scutellum length.

**Wing:** Vein C ventrally bar, just with some setulae apically, after subcostal vein; basal to costal break with slightly enlarged *av* spinules; subcostal break with 2 long spinules, 3 times longer than the other. Cross-vein dm–cu straight.

**Legs:** Fore femur covered by a long row of setae on *pd* to *pv* surface; fore tibia with a submedian *ad* seta and a median *pv* seta; apically only with a *pv* seta and a longer *d* seta. Mid femur with a few *av* setae basally and some longish *pv* setae in basal half, long preapical setae on *p* and *pd*; mid tibia with 1 submedian *ad*, 2 *pd* setae (supramedian and submedian) and 2 *pv* (median and submedian), preapical setae on *p* and *pd* absent; long apical setae on *av*, *pv*, and *v*, in addition to shorter setae on remaining surfaces. Hind femur with a row of robust *ad* and *av* setae, twice longer than the femur width; hind tibia with 2 *av* seta (median and submedian), 4 *ad* setae, 3 *pd* setae, and 1 *pv* seta (supra median), apically with long and robust setae on *ad*, *av*, and *d* seta. Pulvillus enlarged, longer than width of tarsomere.

**Abdomen** (Fig. 3B, C): Sternite 1 setulose, with long setulae marginally. All tergites with lateral and median marginal setae long, tergite 5 with discal setae. Tergite 6 exposed, bare. Sternite 1 setulose; sternites 2–4 longer than width; sternite 5 (Fig. 6A) processes with long lateral setae on the outer margin and shorter setae on the inner margin.

**Terminalia** (Fig. 6): Cercus on posterior view, enlarged and long, twice longer than its width, almost with the same length of surstylus, apically furcated, with an acutely pointed on each side and among them a median apical process (Fig. 6B). Surstylus narrow and slightly curved (Fig. 6C). Hypopygium (Fig. 6D, E) of the *Botanophila*-

type, i.e. pregonites reduced and shallow, presenting 2 long setae; pregonite firmly connected to the central plate of hypandrium; postgonite twice longer than the pregonite; epiphallus and distiphallus reduced, distiphallus largely membranized except for a pair of anterobasal sclerotized rods (Fig. 6D, E). Phallapodema long and apically enlarged on dorsal (Fig. 6E) and lateral (Fig. 6D) view.

**Female:** Body length: 5.0 mm. Wing length: 5.3 mm. Similar to male, except: fore tibia with 2 median *ad* setae (lower one twice longer than the upper one), no *pv* seta. Hind tibia without 1 *pv* seta. Pulvillus reduced, not larger than width of tarsomere. Anepisternum with a long anterior setula, below anterior notopleural seta. Katepisternum with 5 setae forming a posterior row. Abdomen long-oviform (Fig. 3E, F). Spermathecae cylindrical, with surrounding grooves (Fig. 6H). Ovipositor long, sternite 6 and 7 rounded, sternite 8 long and narrow; tergite 6 and 7 enlarged, dorsally less sclerotized, tergite 8 forming a plate around the dorsal surface; epiproct semi-circular; hypoproct suboval, twice as long as broad (Fig. 6F, G).

**Morphological variation:** Male (n=5). Body length: 4.5-5.3 mm. Wing length: 4.6-5.7 mm. Female (n=2). Body length: 5.0-5.2 mm. Wing length: 5.2-5.5 mm. Prealar setae length range among similar to longer than posterior notopleural setae. The cercus length slightly varies among dissected specimens. The specimen from Ajusco has dark brown frons (without the yellow apex).

**Etymology:** Name in apposition. This species is named in honor of Alejandro Zaldívar Riverón, entomologist of the Instituto de Biología, UNAM.

**Material examined:** Holotype. Male. “Mexico: Tlaxcala, \ Nanacamilpa, Comunidad San \ Felipe Hidalgo, Ejido Los \ Bufalos, 2896 msnm, N 19º28' \ 14.8’’ O 98º35'17.1’’ T. \ Malaise 2. 01/viii-26/viii/2016 \ Bosque Pino-Encino. Col. Y. \ Marquez y A. Contreras” [19.470777; -98.588083] (CNIN). Paratypes. 1 female, same label information as the holotype (CNIN); 3 males and 1 female, same label information as the holotype, except: 2884 msnm, Malaise 1, 26/viii-4/x/2016 (CNIN, 2 males; DZUP, 1 male and 1 female); 1 male, Mexico, km 7 carretera Pedregal, Ajusco, México, D. F., 25.x.1974, J. Gutierrez [19.211298; -99.258872] (DZUP).

**Distribution:** Mexico (State of Mexico and Tlaxcala).

**Remarks:** This new species is easily distinguished from the other known *Botanophila* species by the male head, which is fully feminized, with dichoptic eyes, interfrontal setae and proclinate orbital setae developed. It is very similar to *Botanophila*

*mayorgae* **sp nov.**, but can be differentiated from it by the light brown tibiae, longer cercus and strongly curved surstylus.

## DISCUSSION

### Biology

According to Michelsen (2009) all members of the *Botanophila brunneilinea* species group have phytophagous larvae that feed on the developing rosettes of Asteraceae and, apparently, plants in the tribe Cardueae are potential host plants. Asteraceae is highly diverse in Mexico, including the highlands of MTZ, presenting a high level of endemism (Villaseñor 2018), which indicates that other unknown species of *Botanophila* could be found at the MTZ.

### Morphology

The species herein described have some characteristics found in most species of the genus: interfrontal seta present; fronto-orbital seta absent; arista pubescent; prealar seta well developed; scutellum with two long marginal pairs of setae, a shorter discal pair, and fine pubescence on the ventral surface; male sternite 5 with submarginal series of spinules; pregonite very reduced with 2 robust setae; and distiphallus reduced (Huckett 1971; Hennig 1976; Suh and Kwon 2008).

The three species belong to the *Botanophila brunneilinea* species-group. Species in this group are morphologically uniform, taxonomically complex and can only be identified through the male specimens after dissection and examination of the surstyli and cerci (Michelsen 2009). Furthermore, there are still many undescribed species in the group. The species found at MTZ have cercus enlarged and long, similar in length to surstylus, resembling other species, for example *Botanophila subbruneilinea* (Ringdahl, 1934). The terminalia of the latter was recently described by Michelsen (2009). The median apical process of the cercus present on *B. mayorgae* and *B. zaldivari*, however, is uncommon in other species of the *B. brunneilinea* group (Xue and Song 2007).

The male of *Botanophila* species usually presents holoptic eyes (Hennig 1976; Suh and Kwon 2008) and male of some species of the genus, like *B. brunneilinea*, have a partial broad-fronted head (Michelsen 2009), but not completely feminized (dichoptic) as the new species described herein. The head of the male of the *Botanophila* species from the MTZ is identical to the head of the female. The lack of

sexual dimorphism in the eyes, a plesiomorphic character in Calyptratae with several reversions on different lineages (Hennig 1965, 1973), is rare in Anthomyiidae.

Males with holoptic eyes are present in most species of calyptrate flies (Griffiths 1972), and are associated with swarming and aerial mating (McAlpine and Munroe 1968): the holoptic eyes make it easier for the male to visualize and pursue a potential mate (Perry and Desplan 2016). Additionally, *Botanophila* males usually have crossed interfrontal setae developed as a pair of short setulae at the tip of the ocellar triangle, and the proclinate orbital setae are only rarely developed (Hennig 1976), while in the new species both interfrontal setae and proclinate orbital setae are developed, similar to the condition found in the female (Figs 1A, 2A, 3A).

The female terminalia of *B. zaldivari* is very similar to the condition found in *B. brunneilinea*: both species present epiproct semi-circular; hypoproct suboval, twice as long as broad; tergites 6 and 7 dorsally poorly sclerotized centrally (horseshoe-shaped); sternite 8 consisting of two elongated, proximally tapered sclerites almost 4 times as long as broad; cercus slender; cercus and hypoproct with many long and strong setae (Komzáková and Rozkosný 2009); and can be differentiated by having sternite 6 and 7 rounded (Fig. 3G).

The morphological characteristics shared by *B. hernandezi, B. mayorgae* and *B. zaldivari*, clearly indicate that these species form a group of species within *B. brunneilinea* group, probably endemic from MTZ.

Distribution

The Mexican Transition Zone (MTZ) is a large overlap area between the Nearctic and Neotropical regions, extending from south of the United States to the plains of southern Nicaragua (Darlington 1957; Halffter and Morrone 2017). The MTZ has a high degree of endemic species and heterogeneity of environments (Halffter 1987). There have been only a few studies on the MTZ flies. Gomes *et al.* (2020) described a new genus of Muscidae from the same region, indicating the importance of taxonomic studies there MTZ.

*Botanophila mayorgae* and *B. zaldivari* occur in the Trans-Mexican Volcanic Belt (TMVB) (Fig. 7), a province that contains a series of mountain ranges and volcanoes that cross Mexico latitudinally (Ferrari *et al*. 2012), with a mean elevation of 2,300 m and reaching over 3,000 m in some peaks (Gérault *et al*. 2015).

*Botanophila hernandezi*, on the other hand, occurs in the Sierra Madre del Sur province (SMS) (Fig. 7), a mountain range parallel to the Mexican Pacific coast, situated in south-central Mexico and ranging from 1,000 and more than 3,500 m in altitude (Santiago-Alvarado *et al*. 2016; Morrone 2017). *Botanophila hernandezi* occurs specifically in the Eastern Sierra Madre del Sur subprovince, in Oaxacan Highlands districts (Morrone 2017). The Oaxacan Highlands is known as one of the most diverse areas in Mexico, with several endemic species (Flores-Villela and Gerez 1994; Morrone 2017) and species from the Nearctic and Neotropical biotas (León-Paniagua and Morrone 2009) that overlap. Curiously, the species here described belong to the *B. brunneilinea* species-group, which occurs primarily in the southern parts of the West Palaearctic subregion (Michelsen 2009).

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FIGURES

**Figure 1.** *Botanophila hernandezi* **sp. nov.** Male: head, frontal view (A); habitus, dorsal view (B); habitus, lateral view (C).

**Figure 2.** *Botanophila mayorgae* **sp. nov.** Male: head, frontal view (A); habitus, dorsal view (B); habitus, lateral view (C).

**Figure 3.** *Botanophila zaldivari* **sp. nov.** Male: head, frontal view (A); habitus, dorsal view (B); habitus, lateral view (C). Female: head, frontal view (D); habitus, dorsal view (E); habitus, lateral view (F).

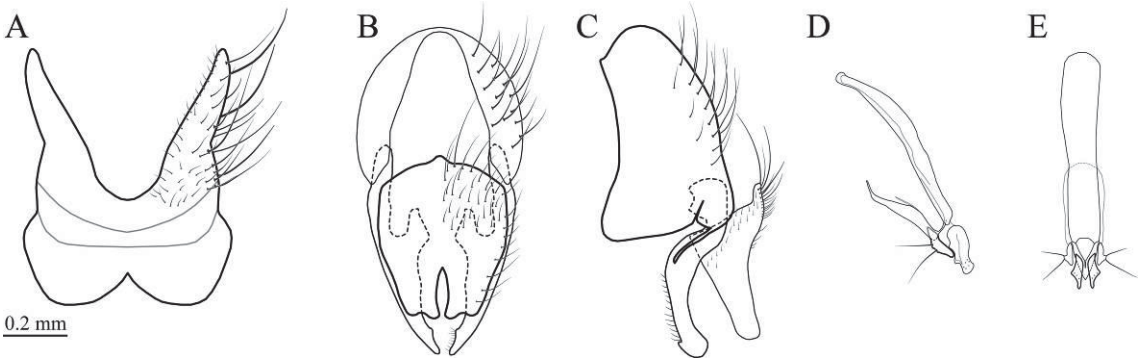


**Figure 4.** *Botanophila hernandezi* **sp. nov.** Male terminalia: (A) sternite 5, dorsal view; (B) epandrium, cercus and surstylus, posterior view; (C) epandrium, cercus and surstylus, lateral view; (D) aedeagus and associated structures, lateral view; (E) aedeagus and associated structures, dorsal view.

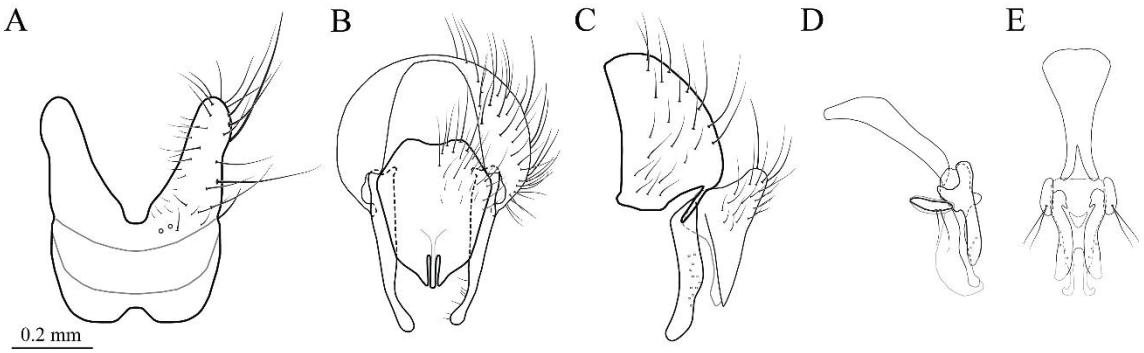


**Figure 5.** *Botanophila mayorgae* **sp. nov.** Male terminalia: (A) sternite 5, dorsal view; (B) epandrium, cercus and surstylus, posterior view; (C) epandrium, cercus and surstylus, lateral view; (D) aedeagus and associated structures, lateral view; (E) aedeagus and associated structures, dorsal view.

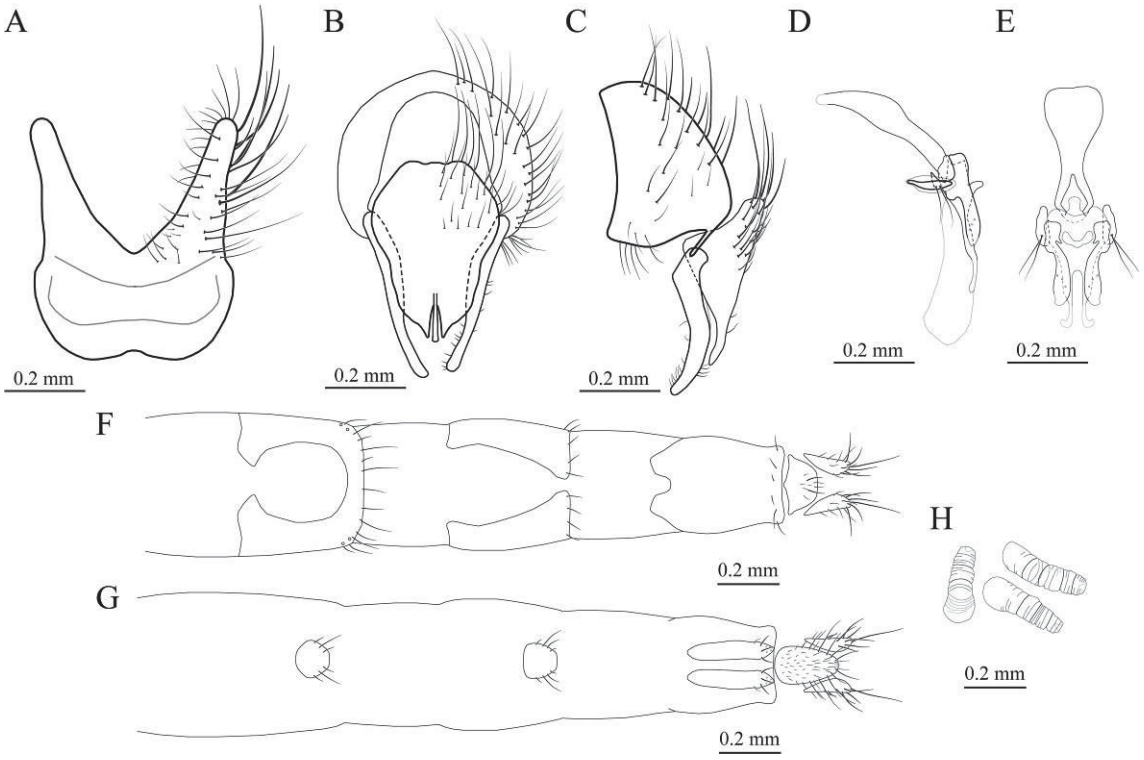


**Figure 6.** *Botanophila zaldivari* **sp. nov.** Male terminalia: (A) sternite 5, dorsal view; (B) epandrium, cercus and surstylus, posterior view; (C) epandrium, cercus and surstylus, lateral view; (D) aedeagus and associated structures, lateral view; (E) aedeagus and associated structures, dorsal view. Female terminalia: (F) ovipositor, dorsal view; (G) spermathecae; (H) ovipositor, ventral view.

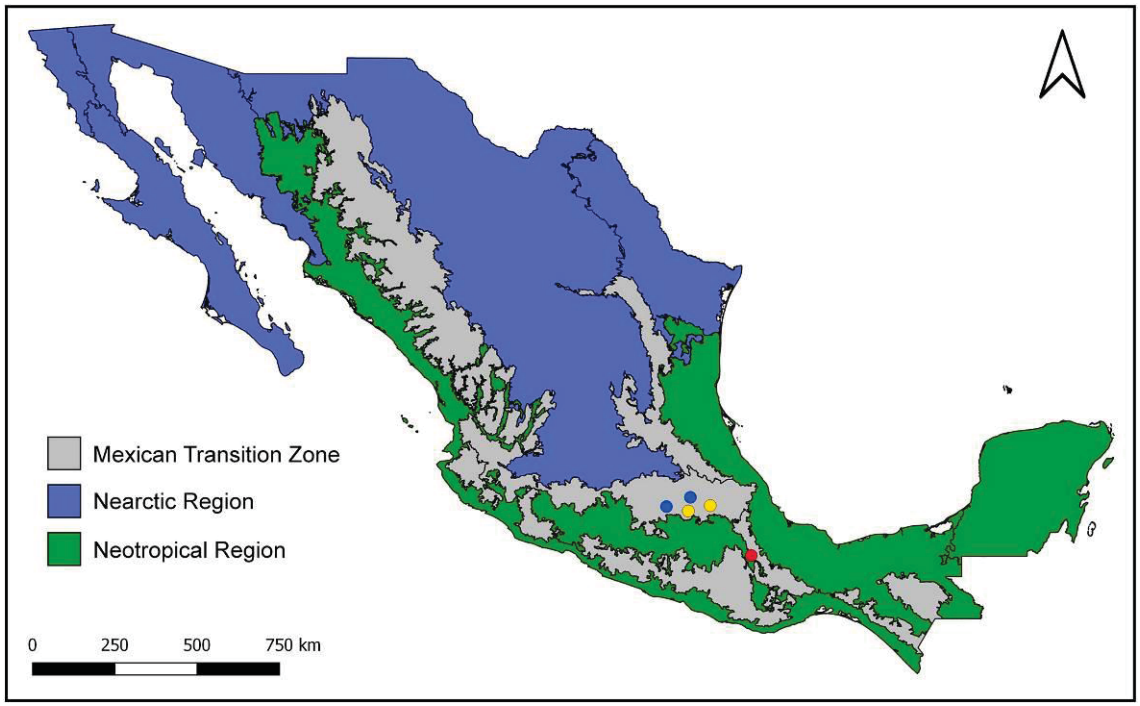


**Figure 7.** Map of Mexico and distribution of *Botanophila* species from Mexican Transitional Zone (MTZ). Circle: red= *B. hernandezi* **sp. nov.**; yellow= *B. mayorgae* **sp. nov.**; blue= *B. zaldivari* **sp. nov.**

## CONSIDERAÇÕES FINAIS

A tese de doutorado contém seis capítulos, dois deles já publicados, um submetido e três em formato de manuscrito para publicação (dois deles já no formato específico da revista). A estruturação da tese foi realizada a partir dos capítulos que apresentam análises filogenéticas com um contexto mais amplo dentro de Anthomyiidae, seguidos pelos quatro capítulos que focam em gêneros da família.

Entre os principais resultados da tese, apresentamos as primeiras hipóteses filogenéticas da família, as topologias obtidas suportam a monofilia de Anthomyiidae e o relacionamento entre alguns grupos de gêneros da família. Também apresentamos os tempos de divergência de Anthomyiidae, com uma estimativa da origem da família para cerca de 36,8 Ma no período Eoceno. Além disso, estimamos a origem da linhagem Neotropical *Coenosopsia* + *Phaonantho* para cerca de 23 Ma no Mioceno tardio, informação que permitiu atualizar as hipóteses biogeográficas de *Coenosopsia*. As topologias obtidas pelas análises morfológicas e moleculares foram congruentes. É importante ressaltar que a análise filogenética morfológica teve uma amostragem ampla, amostrando 89,8% dos gêneros da família, incluindo os dois gêneros fósseis conhecidos, assim como uma ampla amostragem de grupos neotropicais, nunca antes estudados em um contexto filogenético. Nesta filogenia apresentamos também uma série de caracteres morfológicos que suportam a monofilia de alguns gêneros e o relacionamento filogenético entre gêneros próximos.

Em relação aos capítulos seguintes com enfoque mais restrito em gêneros de Anthomyiidae, apresentamos a descrição de três novas espécies de *Coenosopsia* e atualizamos as hipóteses filogenética e biogeográfica; apresentamos diversos novos registros de *Phaonantho* para o Brasil, além dos primeiros registros para Bolívia, Paraguai, Peru e México; descrevemos duas novas espécies de *Calythea*, uma do Brasil e Argentina, e outra dos Andes da Colômbia e Equador; e apresentamos o primeiro registro de *Botanophila* para o México, através da descrição de três novas espécies da Zona de Transição Mexicana.

A presente tese buscou preencher a lacuna referente ao conhecimento filogenético de Anthomyiidae, assim como em relação a taxonomia dos grupos neotropicais. Esse trabalho representa um importante passo em direção a uma melhor compreensão da evolução de Anthomyiidae e melhora o conhecimento taxonômico de algumas linhagens neotropicais. Estudos futuros de grupos não trabalhados nessa tese são extremamente necessários, assim como estudos

filogenéticos utilizando um maior conjunto de dados, como dados morfológicos da terminália feminina e dos imaturos, e dados moleculares incluindo maior número de terminais e marcadores. Esses estudos permitirão entender melhor o relacionamento entre os grupos de gêneros de Anthomyiidae e consequentemente propor uma classificação para a família. Nós escolhemos não propor uma nova classificação baseda nas topologias obtidas em nossas análises, devido a falta de suporte entre os grandes clados e devido a quantidade de dados faltantes de alguns terminais que tiveram seus dados baseados exclusivamente em informações da literatura.

Os resultados apresentados (proposição de hipóteses filogenéticas, descrição de novas espécies, novos registros, proposição de chaves e discussões morfológicas e biogeográficas) são de extrema relevância para conhecermos melhor a fauna de Anthomyiidae da Região Neotropical, sua história evolutiva e biogeográfica.

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