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

Small sparking flies: systematics of *Pholeomyia* Bilimek, 1867 (Diptera: Milichiidae: Milichiinae)

Pequenas moscas brilhantes: sistemática de *Pholeomyia* Bilimek, 1867 (Diptera: Milichiidae: Milichiinae)

Heloísa Fernandes Flores

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

Ribeirão Preto - SP
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Orientador: Dalton de Souza Amorim

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New taxonomic names as well as nomenclatural changes proposed in this thesis are provisional and are not to be considered as validly published according to the rules of the International Code of Zoological Nomenclature (ICZN 1999[1]: Articles 8–10). Names and taxonomic acts herein established shall, therefore, be considered **invalid** within the meaning of the Code (ICZN 1999) and **shall not be cited and/or reproduced.**

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[1] ICZN [International Commission of Zoological Nomenclature] (1999). International Code of Zoological Nomenclature, 4th edition. ITZN, London, 1–306.

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Abstract

Milichiidae (Diptera: Schizophora) is a family of acalyptratae flies known for the fascinating kleptoparasitic biology of most of the species. Within the family, Milichiinae is the subfamily with the largest number of described species. The males of many species of the subfamily have silvery pilosity dorsally in the abdomen that makes them “flash”, reflecting small beams of light when they swarm early in the morning. Several aspects of the systematics of the group need to be properly understood, including questions about the phylogenetic relationships between genera. Within the subfamily, *Pholeomyia* Bilimek has 39 described species, of which 27 occur in the Neotropical Region. The genus has not been completely reviewed so far in literature, and there are no studies establishing the phylogenetic relationships between the species or even hypotheses of monophyly of the genus based on non-homoplastic synapomorphies. Also, questions on the synonymy of *Pseudomilichia* with *Pholeomyia* still remain. Here, the evolution of Milichiinae is discussed, and a phylogenetic hypothesis of *Pholeomyia* based on male morphology is presented. The phylogenetic analysis included 72 terminal taxa (57 ingroup and 15 outgroup species) and used 67 morphological characters, resulting in a single most parsimonious tree under implied weights. The monophyly of *Pholeomyia* is recovered, and the new cladogram for the subfamily highlights the relationships between the milichiines. Our results also corroborate that *Pseudomilichia* is synonymous with *Pholeomyia*. The cladogram obtained with 57 species of the genus show four main clades, which position and species composition may find some level of adjustment with the addition of male abdomen information in the data matrix for 12 of the species included as terminals in the analysis.

Resumo

Milichiidae (Diptera: Schizophora) é uma família de moscas acaliptradas conhecidas pelo fascinante hábito cleptoparasita da maioria das espécies. Dentro da família, Milichiinae é a subfamília com o maior número de espécies descritas. Os machos de muitas espécies da subfamília apresentam pilosidade prateada dorsalmente no abdômen que os faz “relampejar”, refletindo pequenos raios de luz quando enxameiam no início da manhã. Vários aspectos da sistemática do grupo precisam ser devidamente compreendidos, incluindo questões envolvendo as relações filogenéticas entre os gêneros. Dentro da subfamília, *Pholeomyia* Bilimek, 1867 possui 39 espécies descritas, das quais 27 ocorrem na região Neotropical. O gênero não foi completamente revisto na literatura até o momento, e não há estudos que estabeleçam as relações filogenéticas entre as espécies ou mesmo hipóteses de monofilia do gênero baseadas em sinapomorfias não homoplásticas. Além disso, questões relacionadas a sinonímia de *Pseudomilichia* com *Pholeomyia* ainda permanecem. Aqui, a evolução de Milichiinae é discutida e uma hipótese filogenética de *Pholeomyia* baseada na morfologia de machos é apresentada. A análise filogenética incluiu 72 táxons terminais (57 espécies no grupo interno e 15 do grupo externo) e usou 67 caracteres morfológicos, resultando em uma única árvore mais parcimoniosa sob pesagem implícita. A monofilia de *Pholeomyia* é recuperada e o novo cladograma para a subfamília destaca as relações entre os gêneros de Milichiinae. Nossos resultados também corroboram que *Pseudomilichia* é sinônimo de *Pholeomyia*. O cladograma obtido com 57 espécies do gênero mostra quatro clados principais, cuja posição e composição de espécies podem encontrar algum nível de ajuste com a adição de informações do abdômen masculino na matriz de dados para 12 das espécies incluídas como terminais na análise.

1. INTRODUCTION

1.1. The family Milichiidae

Milichiidae (Diptera: Schizophora), popularly known as 'jackal flies' due to the kleptoparasitism habit of most of the species, includes approximately 417 extant and ten fossil species described in 20 genera in the world (Brake, 2000; Swann, 2016). Compared to other fly families, the jackal flies are not particularly species-rich. Nevertheless, considering the undescribed specimens in collections around the world, the number of species to be described may move the diversity of the group to over 1,000.

Milichiids are small flies, ranging in length from 1 to 6 mm. The coloration of most species varies from light brown to black. Males of some genera, as *Pholeomyia* Bilimek, *Milichiella* Giglio-Tos and some others, may have silvery abdominal tergites. The family has a rather broad spectrum of morphological variation, and some species may resemble in some extent other families, as carnids, agromyzids, chloropids and even tachinids (Brake, 2000). This can make it difficult for non-trained entomologists to identify milichiids in collections around the world. Some morphological characters may help in separating the jackal flies from these families, such as the presence of a geniculate proboscis, the presence of both humeral and subcostal breaks, the closed cup cell, and the absence of the postgonites (Brake, 2000; Swann, 2010).

Descriptions of the natural history of the jackal flies demonstrate that they are also ecologically diverse (Brake, 2000) (Figure 1). There are reports of saprophagous, necrophagous and coprophagous larvae (Sabrosky, 1977; Ferrar, 1987; Papp & Wheeler, 1998; Brake, 2000). Coprophagy is a habit present in adults of some species too (Sabrosky, 1959). At least seven genera have been documented to feed on nectar of *Aristolochia* flowers (Brantjes, 1980; Wolda & Sabrosky, 1986).

Within the spectrum of sources of food for adults, one of them stands out: the kleptoparasitism. Kleptoparasitic interactions occur at least in eight genera. Adults feed on the preys of a variety of species of spiders or insects (Reduviidae, Asilidae, Mantidae, among others) (Robinson & Robinson, 1977; Sivinski & Stowe, 1980; Eisner, Eisner & Deyrup, 1991; Sivinski, Marshall & Petersson, 1999; Brake, 2000; Swann, 2008). In almost all cases, only females are kleptoparasites (Sivinski & Stowe, 1980; Eisner, Eisner & Deyrup, 1991) and it is hypothesized that kleptoparasitism provides an extra source of protein for egg maturation (Robinson & Robinson, 1977; Brake, 2000). Kleptoparasitism may be related to the morphological diversity and to the geographical distribution of the family (Brake, 2000), providing an interesting model for understanding the transition of different life histories across time and space.

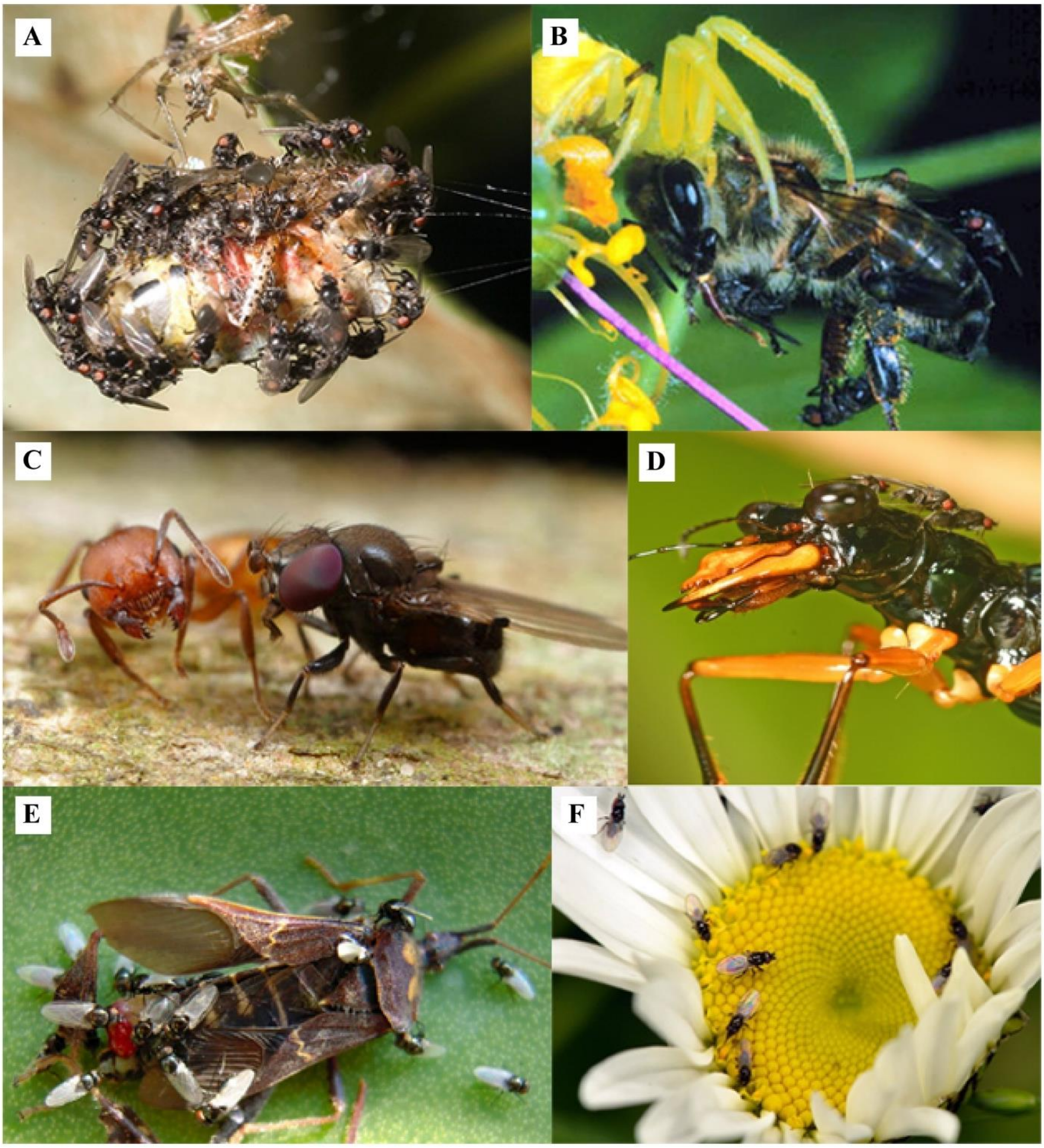


Figure 1. Illustrations of some jackal fly biologies. (A) *Paramyia* sp. feeding on the captured stink bug prey of a spider, photo by Steve A. Marshall. (B) *Desmometopa* sp. feeding on the bee prey of a crab spider, photo by Robert Copeland. (C) *Milichia patrizii* Hennig trying to trigger regurgitation of a *Crematogaster* ant, photo by Alex Wild. (D) *Therates labiatus* (Fabricius) with phoretic *Paramyia* sp., photo by Steve A. Marshall. (E) *Milichiella lacteipennis* (Loew) attracted to freshly killed female *Leptoglossus zonatus* (Dallas), photo by Takumasa Kondo. (F) Flowering plant visited by *Paramyia* sp., photo by Steve A. Marshall

It is considerably well established in the literature that Milichiidae is the sister group of Chloropidae within the Carnoidea. This is supported by some synapomorphies, as the lacinia of maxillae strongly reduced, the proboscis slightly elongated and geniculate, a bare anepisternum, the distiphallus short and glabrous, and the pocket-like ventral receptacle of the female terminalia. There is no dispute that the jackal flies are monophyletic. The most conspicuous synapomorphies of the clade are: upper orbital seta lateroclinate, middle orbital seta lateroclinate, lower orbital seta lateroclinate, two medioclinate frontal setae, presence of a proclinate setula between supra-antennal seta and eye margin, presence of a pair of setulae on the lunula, presence of four pseudotrachea, and absence of postgonites (Brake, 2000).

In older classifications, the milichiids were divided into the subfamilies Madizinae and Milichiinae. Hennig (1958) pointed out that Madizinae could be paraphyletic. Brake (2000), in fact, recovered in her phylogenetic analysis of the family a paraphyletic Madizinae. She subdivided the Madizinae *sensu lato* into the subfamilies Madizinae and Phyllomyzinae, and recovered Madizinae *sensu stricto* as the sister group of Milichiinae (Figure 2).

Swann (2010) disagreed with the subdivision of Madizinae *s.l.* into two subfamilies. He argued that Brake's (2000) analysis missed information on some characters for several terminals, which ended up as synapomorphies for several Phyllomyzinae taxa. Brake's (2000)

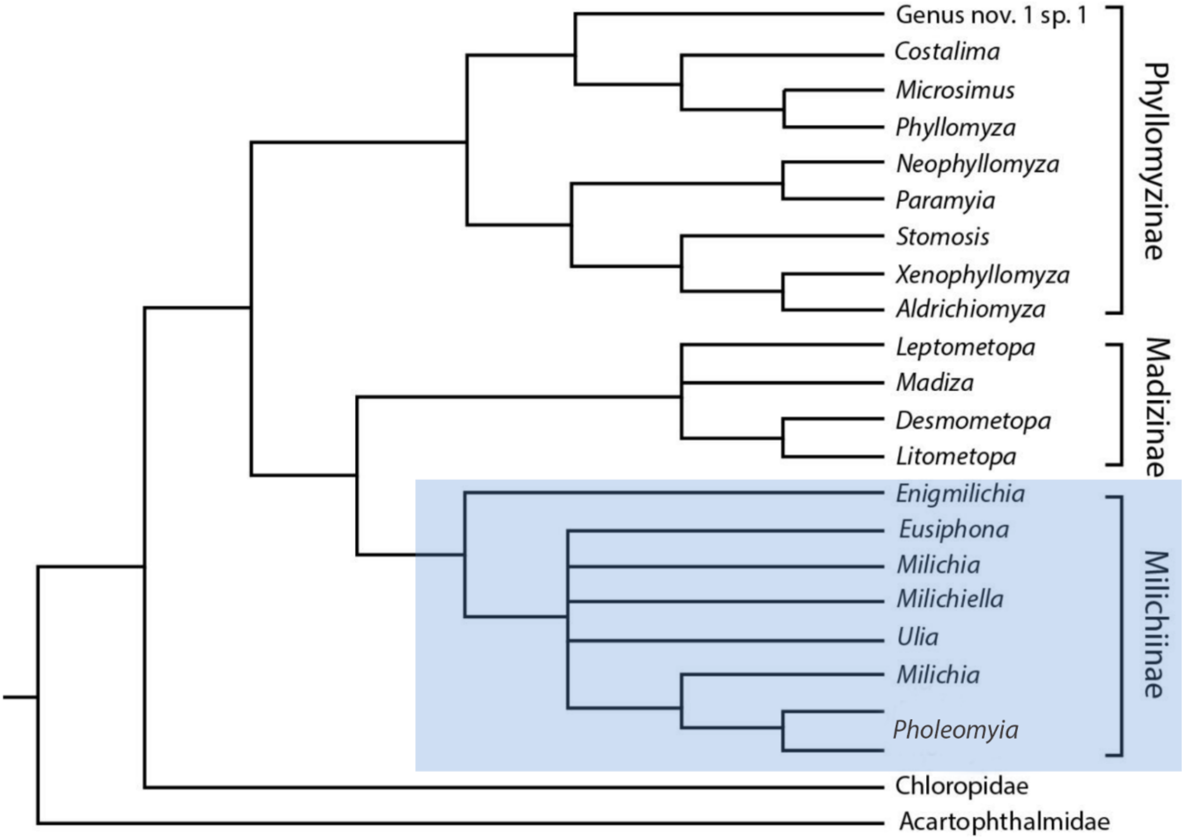


Figure 2. Brake's (2000) phylogenetic hypothesis for Milichiidae based on morphological characters.

study is the only formal phylogenetic analysis of the relationships between the milichiid genera. Swann's (2010) comments are helpful as an analysis of the Brake's (2000) study, but are not a formal reanalysis of the group.

Brake (2000) brought a significant advance in the understanding of the evolution of morphological characters in the family, clarifying the phylogenetic relationship between some milichiid genera, but many questions still remain to be solved. Several genera need careful revisions and there are different pending issues on homology in the family, especially of mouthparts and male terminalia sclerites.

1.2. The subfamily Milichiinae

Milichiinae — the milichiid subfamily with largest number of described species — comprises 226 extant species described in five genera in the world (Table 1). It includes the genera *Enigmilichia* Deeming, *Eusiphona* Coquillett, *Milichia* Meigen, *Milichiella* Giglio-Tos and *Pholeomyia* Bilimek (Brake, 2000) (Figure 3). The subfamily also has the largest number of described fossil species: seven *Milichiella* species from Dominican amber (Brake, 2006). In the other subfamilies, only two Phyllomyzinae fossils from Baltic amber and Mexican amber (Hennig, 1967; Sabrosky, 1963) and one Madizinae species from Baltic amber are known (Hennig, 1971).

Table 1. Diversity and geographic distribution of extant milichiines. Abbreviations: AF, Afrotopical; AU, Australia; NE, Nearctic; NT, Neotropical; PA, Palearctic; OR, Oriental.

Táxon	Nº of species	AF	AU	NE	NT	PA	OR
Milichiinae	**203**						
Enigmilichia Deeming, 1981	1	1					
Eusiphona Coquillett, 1897	4			3	1		
Milichia Meigen, 1830	39	21	4			10	6
Milichiella Giglio-Tos, 1895	120	20	14	23	47	6	11
Pholeomyia Bilimek, 1867	39			27	12		

The subfamily is considered monophyletic, a hypothesis supported by the following synapomorphies: enlarged eyes, obsolescent vibrissal angle, vibrissa above lower margin of eye, frons in males narrower than in females, and distal margin of anal cell meeting the anal vein at an acute angle (Brake, 2000). The group has been recovered as monophyletic, but the question of the relationships between the genera and the monophyly of the genera still demand investigation (Figure 2). *Milichia* and *Pholeomyia* are likely to be paraphyletic and the status of some genera previously described within the subfamily and later synonymized (as *Pseudomilichia* Becker) still remains controversial. It is necessary to increase the taxonomic sampling of all five milichiine genera to properly check their monophyly and address the internal relationships within the subfamily.

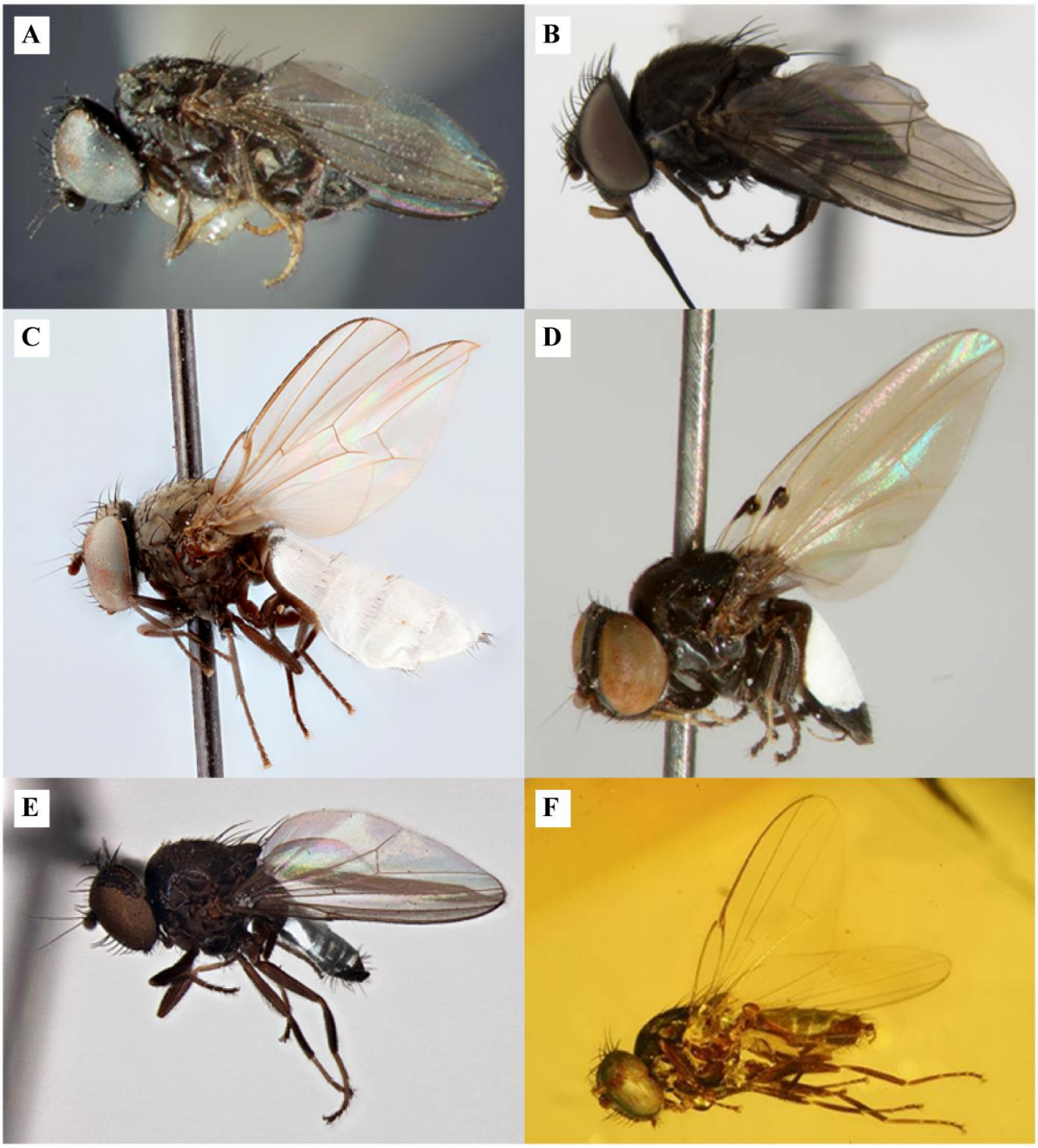


Figure 2. Representative species of the Milichiinae genera. (A) *Enigmilichia dimorphica* Deeming, Nigeria, photo by Irina Brake. (B) *Eusiphona vittata* Sabrosky, Brazil, photo by Heloísa Flores. (C) *Pholeomyia vockerothi* Sabrosky, United States, photo by Daniel Whitmore. (D*) Milichia formicophila* Deeming, Nigeria, photo by Irina Brake. (E) *Milichiella* sp., Brazil, photo by Heloísa Flores. (F) *Milichiella margaretae* Brake, Dominican Republic amber, photo by Irina Brake.

1.3. The genus *Pholeomyia* Bilimek, 1867

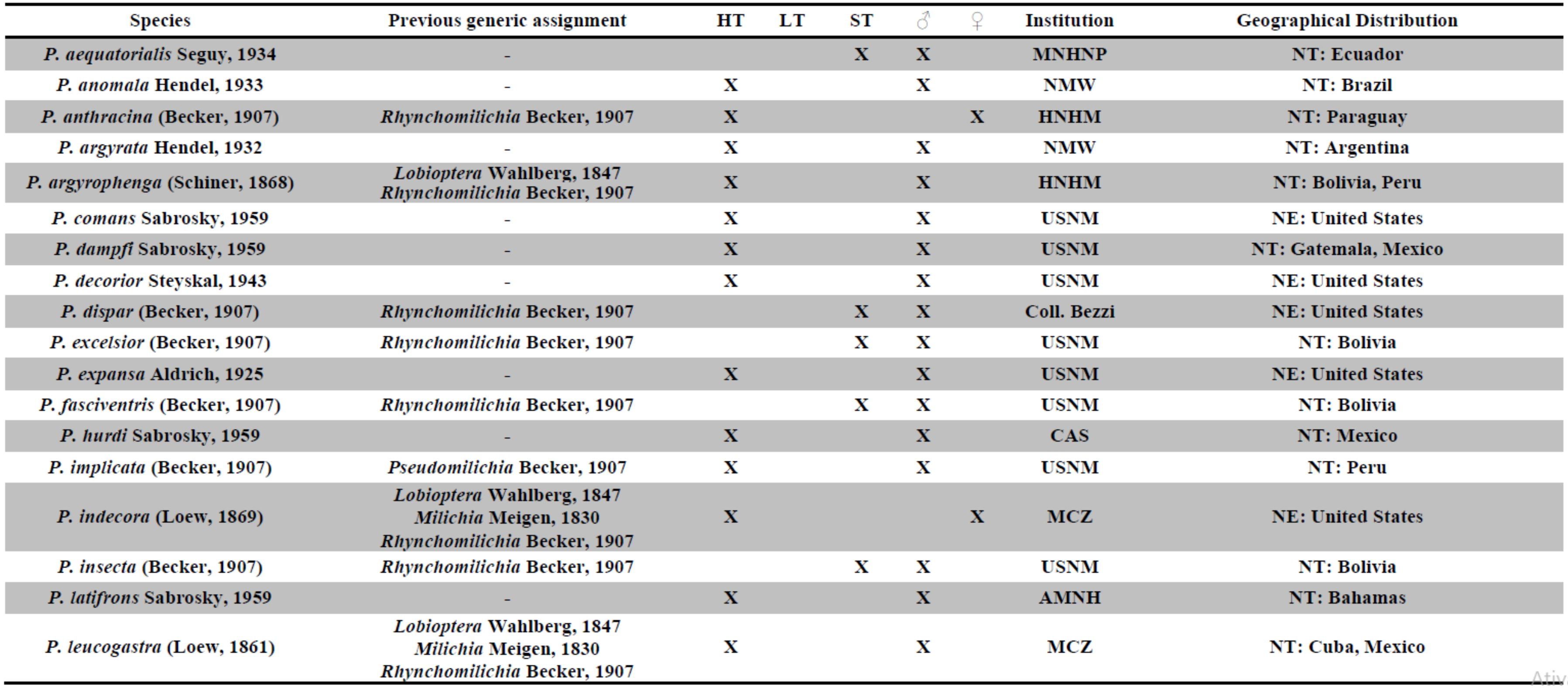
According to the world catalog of the family (Brake, 2000), there are 39 species described in *Pholeomyia* (Table 2). The genus is mostly Neotropical, with 11 species known from the Nearctic region. Most *Pholeomyia* species were described by Becker (1907), Hendel (1932), and Sabrosky (1959). The only taxonomic review for the genus in the literature was provided by Sabrosky (1959), which includes all Nearctic and seven of the Neotropical species. Sabrosky (1959) study is the most recent paper to providing descriptions of new species in the genus—no *Pholeomyia* species have been described along the last 60 years.

Adults and larvae of *Pholeomyia* have an interesting biology. Males of most (but not all) of the species of the genus have silvery abdominal tergites, which reflect light while swarming, what allows them to be spotted over long distances (Sabrosky, 1973; Monteith, 1982; Swann, 2010). *Pholeomyia* larvae have been found in nests of *Atta texana*, where they feed on fungal garden debris (Sabrosky, 1959). Larvae of *Pholeomyia* have also been reported in nests of the Megachilidae bee (Sabrosky, 1955).

Brake (2000) recovered *Pholeomyia* as monophyletic in her cladistic analysis of the family, obtaining as synapomorphies the presence of more than one postprotonal setae, the presence of three fronto-orbital setae, and the presence of three or four strong anepisternal setae. Brake (2000) did not include *Pseudomilichia* species as terminal taxa, but synonymized *Pseudomilichia* with *Pholeomyia*. She justified that the three synapomorphies defining *Pholeomyia sensu stricto* would also apply to all *Pseudomilichia* species, and that the emarginate eye of *Pseudomilichia* would be an insufficient character to define the genus.

Pseudomilichia was a small genus with only two described species (*Pseudomilichia implicata* Becker, 1907 and *Pseudomilichia schnusei* Becker, 1907), defined mainly by the combination of the presence of an emarginate eye and the presence of three or four strong anepisternal setae. The genus had already been synonymized with *Pholeomyia* by Hendel (1932), but his nomenclatural change was ignored by further authors—e.g., Hennig (1939). Instead, Hennig (1939) synonymized *Macromilichia* Hendel with *Pseudomilichia*. He also suggested that *Macromilichia nigricosta* Hendel, 1932 might be synonymous with *Pseudomilichia schnusei*, a pair of species that Brake (2000) accepted as valid. In the same study, Hennig synonymized *Rhynchomilichia* Hendel with *Pholeomyia*. After the synonymy proposed by Brake (2000), all *Macromilichia*, *Rhynchomilichia* and *Pseudomilichia* species have been included in *Pholeomyia*. It seems well established that *Macromilichia* and *Rhynchomilichia* would be synonymous of *Pholeomyia*, but questions about *Pseudomilichia* still remain.

Table 2. Described species of *Pholeomyia* Bilimek, with the corresponding depository institutions of their types. Acronyms for institutions are explained in Material and Methods. Abbreviations: HT, holotype; LT, lectotype, NE, Nearctic; NT, Neotropical; ST, sintype; ♀, female; ♂, male.



Species	Previous generic assignment	HT	LT	ST	♂	♀	Institution	Geographical Distribution
P. aequatorialis **Seguy, 1934**	-			X	X		MNHNP	NT: Ecuador
P. anomala **Hendel, 1933**	-	X			X		NMW	NT: Brazil
P. anthracina **(Becker, 1907)**	***Rhynchomilichia*** **Becker, 1907**	X				X	HNHM	NT: Paraguay
P. argyrata **Hendel, 1932**	-	X			X		NMW	NT: Argentina
P. argyrophenga **(Schiner, 1868)**	***Lobioptera*** **Wahlberg, 1847** ***Rhynchomilichia*** **Becker, 1907**	X			X		HNHM	NT: Bolivia, Peru
P. comans **Sabrosky, 1959**	-	X			X		USNM	NE: United States
P. dampfi **Sabrosky, 1959**	-	X			X		USNM	NT: Gatemala, Mexico
P. decorior **Steyskal, 1943**	-	X			X		USNM	NE: United States
P. dispar **(Becker, 1907)**	***Rhynchomilichia*** **Becker, 1907**			X	X		Coll. Bezzi	NE: United States
P. excelsior **(Becker, 1907)**	***Rhynchomilichia*** **Becker, 1907**			X	X		USNM	NT: Bolivia
P. expansa **Aldrich, 1925**	-	X			X		USNM	NE: United States
P. fasciventris **(Becker, 1907)**	***Rhynchomilichia*** **Becker, 1907**			X	X		USNM	NT: Bolivia
P. hurdi **Sabrosky, 1959**	-	X			X		CAS	NT: Mexico
P. implicata **(Becker, 1907)**	***Pseudomilichia*** **Becker, 1907**	X			X		USNM	NT: Peru
P. indecora **(Loew, 1869)**	***Lobioptera*** **Wahlberg, 1847** ***Milichia*** **Meigen, 1830** ***Rhynchomilichia*** **Becker, 1907**	X				X	MCZ	NE: United States
P. insecta **(Becker, 1907)**	***Rhynchomilichia*** **Becker, 1907**			X	X		USNM	NT: Bolivia
P. latifrons **Sabrosky, 1959**	-	X			X		AMNH	NT: Bahamas
P. leucogastra **(Loew, 1861)**	***Lobioptera*** **Wahlberg, 1847** ***Milichia*** **Meigen, 1830** ***Rhynchomilichia*** **Becker, 1907**	X			X		MCZ	NT: Cuba, Mexico

Table 2. Continued.

P. leucozoma **Bilimek, 1867**	-		**X**		**X**		**NMW**	**NT: Mexico**
P. longifacies **Hendel, 1933**	-			**X**	**X**	**X**	**NMW**	**NT: Brazil, Paraguay**
P. longiseta **(Becker, 1907)**	***Milichia*** **Meigen, 1830**	**X**				**X**	**HNHM**	**NT: Argentina, Paraguay, Nicaragua**
P. myopa **Melander, 1913**	-	**X**			**X**		**USNM**	**NT: Bolivia, Brazil, Costa Rica, Mexico, Panama, Venezuela**
P. nigricosta **(Hendel, 1932)**	***Macromilichia*** **Hendel, 1932** ***Pseudomilichia*** **Becker, 1907**	**X**				**X**	**SMNS**	**NT: Bolivia**
P. nitidula **Sabrosky, 1959**	-	**X**			**X**		**USNM**	**NE: United States**
P. obscura **Sabrosky, 1959**		**X**			**X**		**USNM**	**NE: United States**
P. palparis **(Becker, 1907)**	***Rhynchomilichia*** **Becker, 1907**	**X**				**X**	**HNHM**	**NT: Paraguay**
P. pectoralis **Hendel, 1932**	-	**X**			**X**		**SMNS**	**NT: Bolivia**
P. politifacies **Sabrosky, 1959**	-	**X**				**X**	**USNM**	**NT: Brazil, Colombia, Costa Rica, El Salvador, Mexico, Panama**
P. praeocellaris **Hendel, 1932**	-			**X**	**X**	**X**	**SMNS**	**NT: Bolivia**
P. praesecta **(Becker, 1907)**	***Rhynchomilichia*** **Becker, 1907**			**X**	**X**		**USNM**	**NT: Peru**
P. prominens **(Becker, 1907)**	***Rhynchomilichia*** **Becker, 1907**			**X**	**X**		**USNM**	**NT: Bolivia, Peru**
P. pseudodecora **(Becker, 1907)**	***Rhynchomilichia*** **Becker, 1907**			**X**	**X**	**X**	**Coll. Bezzi**	**NE: United States**
P. quadrifasciata **Hendel, 1932**	-	**X**			**X**		**SMNS**	**NT: Bolivia**
P. robertsoni **(Coquillett, 1902)**	***Milichia*** **Meigen, 1830** ***Rhynchomilichia*** **Becker, 1907**	**X**			**X**		**USNM**	**NE: United States**
P. schineri **(Hendel, 1932)**	***Rhynchomilichia*** **Becker, 1907**			**X**	**X**		**NMW**	**NT: Argentina, Brazil, Paraguay**
P. schnusei **(Becker, 1907)**	***Pseudomilichia*** **Becker, 1907**			**X**	**X**		**USNM**	**NT: Bolivia, Peru**
P. sororcula **(Becker, 1907)**	***Rhynchomilichia*** **Becker, 1907**			**X**	**X**		**HNHM**	**NT: Bolivia, Peru**
P. texensis **Sabrosky, 1959**	-	**X**			**X**		**USNM**	**NE: United States**
P. vockerothi **Sabrosky, 1961**	-	**X**			**X**		**CNC**	**NE: United States**

Swann (2010) disagreed from Brake's (2000) synonymy and suggested that her synapomorphies for *Pholeomyia* would be homoplastic features evolving inside and outside Milichiinae. He mentioned, for example, that the presence of three or four strong anepisternal setae is also known to occur in some *Eusiphona* species. Following Swann (2000) and Sabrosky (1955), the presence of anepisternal setae may indicate a close relationship between *Eusiphona* and *Pholeomyia*, and even unite *Eusiphona*, *Pholeomyia*, and *Pseudomilichia*. Swann (2010) also points out that the presence of three frontal setae, considered by Brake (2000) as a synapomorphy of the genus, actually corresponds to a range of three to six frontal setae in *Pholeomyia sensu stricto*. Although it is not a unique condition within the subfamily, Swann (2010) considered *Pseudomilichia* a valid genus and the emarginated eye would be one of its defining features.

Brake’s (2000, 2009) studies were a major step forward towards resolving the phylogenetic relationships within Milichiinae. Brake (2000) recovered *Pholeomyia* as sister of one of the branches of a paraphyletic *Milichia*. In Brake’s (2009) taxonomic review and cladistics analysis of *Milichiella*, the *Pholeomyia* species included was recovered as sister group of *Milichiella*. As both analyses had limited number of species of *Pholeomyia*, a new cladistic reanalysis of the group with a wider taxonomic sampling may bring some shift to the conclusions on the monophyly of the genus and to its position in the system of the Milichiinae.

To properly address Brake’s (2000) inferences for *Pholeomyia*, hence, it is necessary to broaden the sampling of species of the genus and properly sampling other Milichiinae genera to root the analysis and test the monophyly of *Pholeomyia*. Also, a detailed study of the male terminalia sclerites would highlight several unsolved questions in the evolution of the terminalia in milichiids. Finally, advances in the understanding of the phylogenetic relationships of the jackal flies shall provide an important background to future studies of evolutionary biology investigating the fascinating life histories of the family.

2. GOALS

The main objective of this dissertation is to discuss the monophyly of *Pholeomyia* Bilimek, the phylogenetic position of the genus and the relationships between the species of the genus. A null hypothesis to be considered is that *Pseudomilichia* Becker would be a synonymous of *Pholeomyia*, in such a way that *Pholeomyia* would be monophyletic—this is the position supported by the synapomorphies recovered by Brake (2000) and the perspective of many of the taxonomic studies working with the genus.

More precisely, this research intends to answer the following questions:

(I) Is the genus monophyletic?

(II) Is *Pseudomilichia* a synonymous of *Pholeomyia*, i.e., is *Pseudomilichia* a smaller clade nested within *Pholeomyia*?

(III) What are the phylogenetic relationships between the known species of the genus?

(IV) How did the morphology modify along the evolution of *Pholeomyia*?

(V) How is this taxon phylogenetic related to other milichiines?

3. MATERIAL AND METHODS

3.1. Taxon sampling

Taxon sampling is linked to the objectives of the research (Young & Gillung, 2020), so the choice of terminal taxa was based on the questions addressed in this study. Specimens of 27 described species of *Pholeomyia* were included in our analysis, representing almost 70% of the species known in the genus. We could not examine the types of all described *Pholeomyia* species. When the original description was insufficient to provide a secure identification, we identified as morphospecies (e.g., *Pholeomyia* sp.1, *Pholeomyia* sp.2, etc.), most of which shall be new species to be described: additional 30 *Pholeomyia* species were added as terminals in the analysis. Two of the morphospecies in the ingroup correspond to "*Pseudomilichia*", what allows to test the position of the clade in the study and the synonymy assumed by Brake (2000). The ingroup, therefore, consists of 57 terminal taxa, providing a broad taxonomic coverage of the genus and allows addressing, besides the phylogenetic relationships between the species, a number of aspects of the evolution of the morphology.

In order to test the monophyly of *Pholeomyia* and its relationship with the other milichiines, representatives of all genera of Milichiinae were included—five species of *Milichiella*, three species of *Milichia*, two species of *Eusiphona* and one species of *Enigmilichia*. One species of Madizinae and two species of Phyllomyzinae were also included. To root the entire analysis, the root was placed between a chloropid (using a species of *Apotropina* Hendel) and the group with all jackal flies. All taxa used in the analysis are listed in Table 3.

The specimens analyzed are deposited in the institutions below (museum acronyms follow Evenhuis, 2014). Information of the specimens analyzed, such as the transcription of the labels, the number of specimens and the institution to which they belong, are summarized in Table A1 at the Appendix.

CAS	California Academy of Science, São Francisco, California, United States
CDFA	California Department of Agriculture and Food, Sacramento, California, United States
CNC	Canadian National Collection of Insects, Arachnids, and Nematods, Ottawa, Ontario, Canada
ESSIG	Essig Museum of Entomology, Berkeley, California, United States
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazônia, Brazil
LACM	Natural History Museum of Los Angeles, Los Angeles, California, United States

LMED	Laboratório de Morfologia e Evolução de Diptera, FFCLRP, Universidade de São Paulo, Ribeirão Preto, São Paulo, Brazil
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, United States
MPEG	Museu Paraense Emílio Goeldi, Belém, Pará, Brazil
MZUSP	Museu de Zoologia da Universidade de São Paulo, Universidade de São Paulo, São Paulo, São Paulo, Brazil
SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Baden-Württemberg, Germany
USNM	Smithsonian National Museum of Natural History, New York, New York, United States

Some terminals were studied based on photos, illustrations and original descriptions. This information is summarized in table A1 at the Appendix. As many milichiine females are unknown and those known from different species at this stage are hard to distinguish from each other (Brake, 2009), we decided to include only males (and male characters) in our taxon study. Females were included only when they were the only sex known to the species. As most descriptions point out that sexual dimorphism is concentrated in the abdomen, we had some security to codify the other characters for these species.

Table 3. Taxon sampling for the analysis. Abbreviations: NE, Nearctic; NT, Neotropical; PA, Palearctic; OR, Oriental.

Taxon	**Distribution**
Chloropidae	
Apotropina sp.1	NT: Brazil
Milichiidae: Phyllomyzinae	
Costalima myrmicola Sabrosky, 1953	NT: Brazil
Phyllomyza sp.1	NT: Brazil
Milichiidae: Madizinae	
Madiza glabra Fallén, 1810	NE: United States, PA: widespread
Milichiidae: Milichiinae	
Enigmilichia dimorphica Deeming, 1981	AF: Nigeria
Eusiphona mira Coquillett, 1897	NE: United States
Eusiphona vittata Sabrosky, 1982	NT: Argentina, Brazil
Milichia myrmecophila de Meijeri, 1909	OR: Indonesia
Milichia speciosa Meigen, 1830	PA: Israel, Marroco, southern Europe
Milichia sp.1	NT: Mexico
Milichiella cavernae Brake, 2009	NT: Trinidad and Tobago
Milichiella circularis Aldrich, 1981	NE: Hawaii
Milichiella faviformis Brake, 2009	NE: United States

Table 3. Continued.

Milichiella sumptuosa de Meijeri, 1911	OR: Indonesia
Milichiella sp.1	NT: Brazil
Pholeomyia aequatorialis Seguy, 1934	NT: Ecuador, Brazil
Pholeomyia anomala Hendel, 1933	NT: Brazil
Pholeomyia anthracina (Becker, 1907)	NT: Paraguay
Pholeomyia argyrata Hendel, 1932	NT: Argentina
Pholeomyia argyrophenga (Schiner, 1868)	NT: Bolivia, Peru
Pholeomyia comans Sabrosky, 1959	NE: United States
Pholeomyia dampfi Sabrosky, 1959	NT: Guatemala, Mexico
Pholeomyia decorior Steyskal, 1943	NE: United States
Pholeomyia dispar (Becker, 1907)	NE: United States
Pholeomyia expansa Aldrich, 1925	NE: United States
Pholeomyia hurdi Sabrosky, 1959	NT: Mexico, Brazil
Pholeomyia indecora (Loew, 1869)	NE: United States
Pholeomyia latifrons Sabrosky, 1959	NT: Bahamas
Pholeomyia leucogastra (Loew, 1861)	NT: Cuba, Mexico
Pholeomyia leucozoma Bilimek, 1867	NT: Mexico, Brazil
Pholeomyia longiseta (Becker, 1907)	NT: Argentina, Paraguay, Nicaragua
Pholeomyia myopa Melander, 1913	NT: Bolivia, Brazil, Costa Rica, Mexico, Panama, Venezuela
Pholeomyia nigricosta (Hendel, 1932)	NT: Bolivia
Pholeomyia nitidula Sabrosky, 1959	NE: United States
Pholeomyia palparis (Becker, 1907)	NT: Paraguay
Pholeomyia pectoralis Hendel, 1932	NT: Bolivia
Pholeomyia praeocellaris Hendel, 1932	NT: Bolivia
Pholeomyia praesecta (Becker, 1907)	NT: Peru
Pholeomyia quadrifasciata Hendel, 1932	NT: Bolivia
Pholeomyia schineri (Hendel, 1932)	NT: Argentina, Brazil, Paraguay
Pholeomyia sororcula (Becker, 1907)	NT: Bolivia, Peru
Pholeomyia vockerothi Sabrosky, 1961	NE: United States
Pholeomyia sp.1	NT: Paraguay
Pholeomyia sp.2	NT: Honduras
Pholeomyia sp.3	NT: Bolivia
Pholeomyia sp.4	NT: Peru
Pholeomyia sp.5	NT: Ecuador
Pholeomyia sp.6	NT: El Salvador
Pholeomyia sp.7	NT: Ecuador
Pholeomyia sp.8	NT: Costa Rica
Pholeomyia sp.9	NT: Costa Rica
Pholeomyia sp.10	NT: Bolivia
Pholeomyia sp.11	NT: Brazil
Pholeomyia sp.12	NT: Brazil
Pholeomyia sp.13	NT: Brazil
Pholeomyia sp.14	NT: Brazil
Pholeomyia sp.15	NT: Brazil

Table 3. Continued.

Pholeomyia sp.16	NT: Brazil
Pholeomyia sp.17	NT: Brazil
Pholeomyia sp.18	NT: Brazil
Pholeomyia sp.19	NT: Brazil
Pholeomyia sp.20	NT: Brazil
Pholeomyia sp.21	NT: Brazil
Pholeomyia sp.22	NT: Venezuela
Pholeomyia sp.23	NT: Argentina
Pholeomyia sp.24	NT: Argentina
Pholeomyia sp.25	NT: Paraguay
Pholeomyia sp.26	NT: Mexico
Pholeomyia sp.27	NT: Brazil
Pholeomyia sp.28	NT: Brazil
Pholeomyia sp.29	NT: Brazil
Pholeomyia sp.30	NT: Brazil

3.2. Specimen preparation and documentation

Specimens were illustrated with photographs in several views (habitus lateral, dorsal view of head, lateral view of head, face, dorsal view of thorax, and dorsal view of the abdomen). The photographs were taken using a Leica DC500 camera attached to a Leica MZ16 stereomicroscope or a Leica MC170HD camera coupled to a Leica M205C stereomicroscope. Stacking was made using the software Helicon Focus 6.3.0. Photos were edited with the Adobe Photoshop CS6 software.

The male terminalia and the wing were also studied. Dry specimens were placed in a wet chamber and rehydrated prior to the preparation of slide mountings of the male terminalia and the wing. The following procedure was used for dissection of the male terminalia: removal of the abdomen; immersion in 10% KOH for approximately 1-2 hours (according to the degree of sclerotization) at 60 °C; immersion in 100% glacial acetic acid; dissection of the terminalia; transfer to a temporary slide mounting with glycerin jelly. The entire abdomen was removed in order to study the sternites 4 and 5. Drawings of the male terminalia were performed with a camera lucida coupled to a compound microscope, later scanned for vectorization in Adobe Illustrator CS6. The dissected terminalia was stored in vials with glycerin. Permanent slide mountings of the wing were prepared with Euparal. The vial with the terminalia and the slide of the wing were added to the pin of their respective specimens.

Classification, names and authorship for subfamilies, genera and species follow Brake (2000). The morphological terminology used follows Cumming & Wood (2017). Abbreviations for the morphological structures are given in the legend of each figure.

3.3. Phylogenetic analysis

The character matrix was built and edited in WinClada ver. 1.0 (Nixon, 2002). Most characters previously proposed in the literature for Milichiidae were included, although sometimes using a slightly different delimitation of character states and/or coding. When the character was based in the literature, the source was indicated. New characters were built, especially from the head and the male terminalia. All characters were considered non-additive. Missing data were scored with a question mark, '?', and inapplicable data with a hyphen, '-'. Character states were optimized on a maximum parsimonious tree (MPT) using Winclada ver. 1.0 (Nixon, 2002), showing only unambiguous changes. The full list of characters and the data matrix were provided in the section 'Results'.

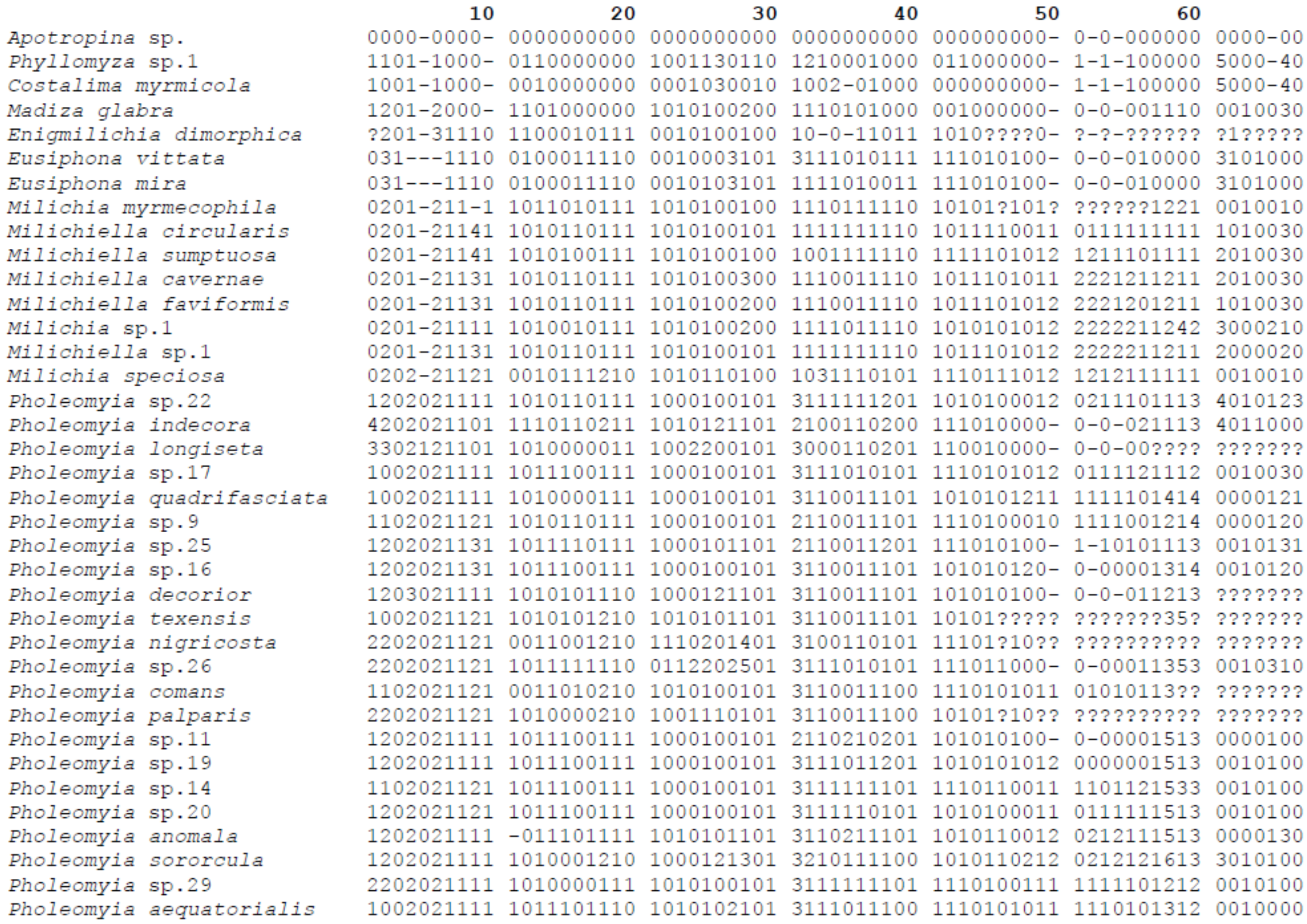
Parsimony analyses were performed with TNT ver. 1.1 using both equal and implied weight schemes (Goloboff, 1993; Goloboff, Farris & Nixon, 2008). To define the constant 'k', the script 'setk.run' (available from Salvador Arias, unpublished data) was used to calculate within the TNT a value of k based on the dataset itself. The tree searches strategies were conducted with the Traditional search and New Technology search options. The Traditional searches were performed setting with 900 replicates, tree bisection–reconnection (TBR), branch swapping, saving 45 trees per replicate and the random seed was set to 0. The New Technology searches were carried out under the following parameters: random seed 0, level 75, initial addseqs = 5, find minimum tree length 10 times, and default values for Drift, Ratchet, Sectorial search and Tree fusing. The most parsimonious trees (MPTs) were saved and summarized in a strict consensus tree using Winclada ver. 1.0 (Nixon, 2002). The trees were exported as a .svg file and edited using Adobe Illustrator CS6.

4. RESULTS

The matrix consisted of 67 morphological characters for 72 terminal taxa (Table 4). A total of 36 of the characters are binary and 31 multistate. The characters were built using information from different parts of the adult body: 27 from the head, 16 from the thorax, and 24 from the male terminalia.

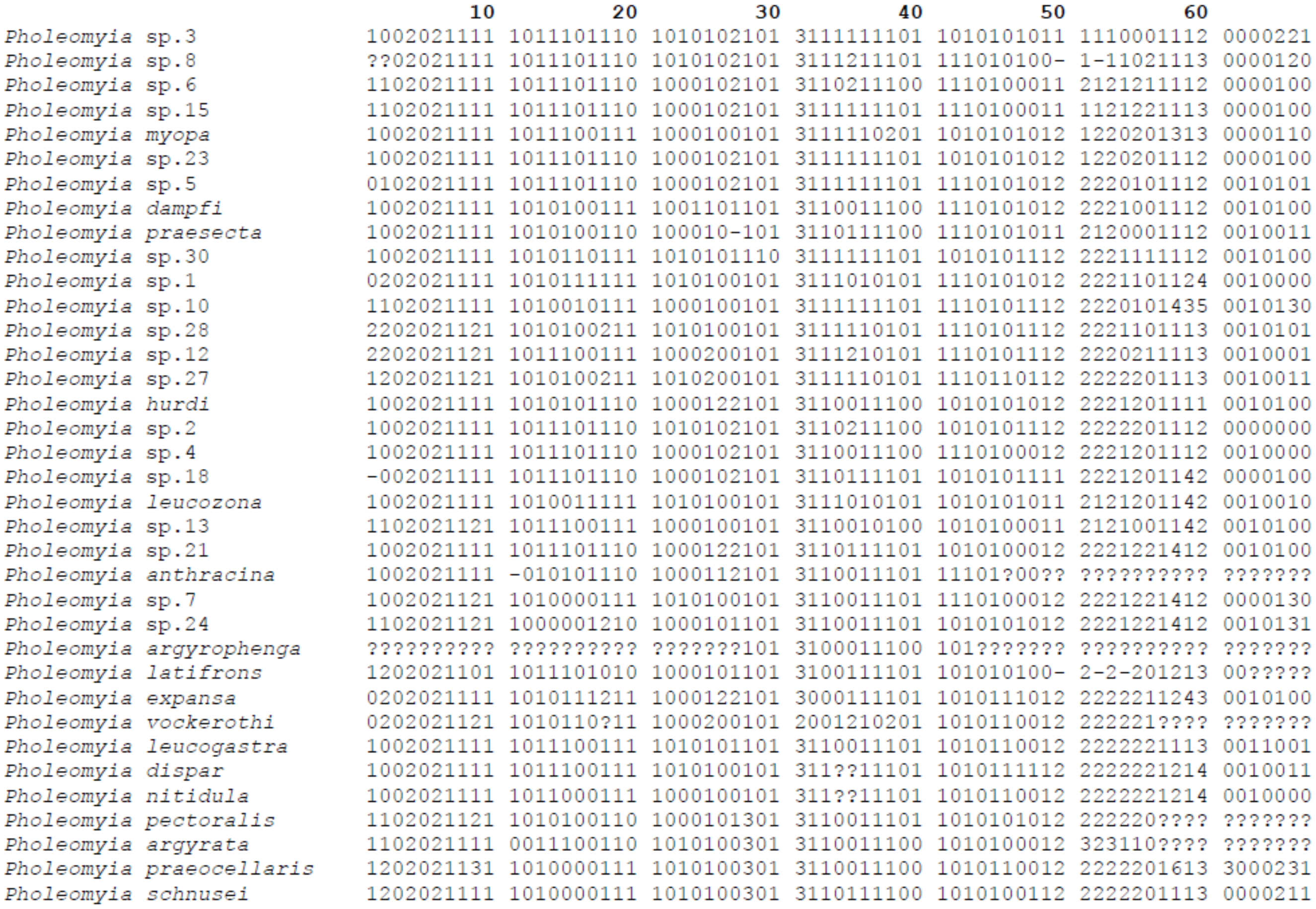
Several of the characters included in this study were made available in the literature in distinct contexts—*e.g.*, Brake (2000), for high-level relationships in milichiids and Brake (2009), for relationships in *Milichiella*. In most of the cases, the coding system used was modified from the original character construction, including additional character states. Consistency and retention indices were also used to address the meaning of the characters in the evolution of the group.

Table 4. Morphological data matrix. Abbreviations: ?, missing data; -, inapplicable characters.



	10	20	30	40	50	60	
Apotropina sp.	0000-0000-	0000000000	0000000000	0000000000	000000000-	0-0-000000	0000-00
Phyllomyza sp.1	1101-1000-	0110000000	1001130110	1210001000	011000000-	1-1-100000	5000-40
Costalima myrmicola	1001-1000-	0010000000	0001030010	1002-01000	000000000-	1-1-100000	5000-40
Madiza glabra	1201-2000-	1101000000	1010100200	1110101000	001000000-	0-0-001110	0010030
Enigmilichia dimorphica	?201-31110	1100010111	0010100100	10-0-11011	1010????0-	?-?-??????	?1?????
Eusiphona vittata	031---1110	0100011110	0010003101	3111010111	111010100-	0-0-010000	3101000
Eusiphona mira	031---1110	0100011110	0010103101	1111010011	111010100-	0-0-010000	3101000
Milichia myrmecophila	0201-211-1	1011010111	1010100100	1110111110	10101?101?	??????1221	0010010
Milichiella circularis	0201-21141	1010110111	1010100101	1111111110	1011110011	0111111111	1010030
Milichiella sumptuosa	0201-21141	1010100111	1010100100	1001111110	1111101012	1211101111	2010030
Milichiella cavernae	0201-21131	1010110111	1010100300	1110011110	1011101011	2221211211	2010030
Milichiella faviformis	0201-21131	1010110111	1010100200	1110011110	1011101012	2221201211	1010030
Milichia sp.1	0201-21111	1010010111	1010100200	1111011110	1010101012	2222211242	3000210
Milichiella sp.1	0201-21131	1010110111	1010100101	1111111110	1011101012	2222211211	2000020
Milichia speciosa	0202-21121	0010111210	1010110100	1031110101	1110111012	1212111111	0010010
Pholeomyia sp.22	1202021111	1010110111	1000100101	3111111201	1010100012	0211101113	4010123
Pholeomyia indecora	4202021101	1110110211	1010121101	2100110200	111010000-	0-0-021113	4011000
Pholeomyia longiseta	3302121101	1010000011	1002200101	3000110201	110010000-	0-0-00????	???????
Pholeomyia sp.17	1002021111	1011100111	1000100101	3111010101	1110101012	0111121112	0010030
Pholeomyia quadrifasciata	1002021111	1010000111	1000100101	3110011101	1010101211	1111101414	0000121
Pholeomyia sp.9	1102021121	1010110111	1000100101	2110011101	1110100010	1111001214	0000120
Pholeomyia sp.25	1202021131	1011110111	1000101101	2110011201	111010100-	1-10101113	0010131
Pholeomyia sp.16	1202021131	1011100111	1000100101	3110011101	101010120-	0-00001314	0010120
Pholeomyia decorior	1203021111	1010101110	1000121101	3110011101	101010100-	0-0-011213	???????
Pholeomyia texensis	1002021121	1010101210	1010101101	3110011101	10101?????	??????35?	???????
Pholeomyia nigricosta	2202021121	0011001210	1110201401	3100110101	11101?10??	??????????	???????
Pholeomyia sp.26	2202021121	1011111110	0112202501	3111010101	111011000-	0-00011353	0010310
Pholeomyia comans	1102021121	0011010210	1010100101	3110011100	1110101011	01010113??	???????
Pholeomyia palparis	2202021121	1010000210	1001110101	3110011100	10101?10??	??????????	???????
Pholeomyia sp.11	1202021111	1011100111	1000100101	2110210201	101010100-	0-00001513	0000100
Pholeomyia sp.19	1202021111	1011100111	1000100101	3111011201	1010101012	0000001513	0010100
Pholeomyia sp.14	1102021121	1011100111	1000100101	3111111101	1110110011	1101121533	0010100
Pholeomyia sp.20	1202021121	1011100111	1000100101	3111110101	1010100011	0111111513	0010100
Pholeomyia anomala	1202021111	-011101111	1010101101	3110211101	1010110012	0212111513	0000130
Pholeomyia sororcula	1202021111	1010001210	1000121301	3210111100	1010110212	0212121613	3010100
Pholeomyia sp.29	2202021111	1010000111	1010100101	3111111101	1110100111	1111101212	0010100
Pholeomyia aequatorialis	1002021111	1011101110	1010102101	3111011100	1110101011	1110101312	0010000

Table 4. Continued.



	10	20	30	40	50	60	
Pholeomyia sp.3	1002021111	1011101110	1010102101	3111111101	1010101011	1110001112	0000221
Pholeomyia sp.8	??02021111	1011101110	1010102101	3111211101	111010100-	1-11021113	0000120
Pholeomyia sp.6	1102021111	1011101110	1000102101	3110211100	1110100011	2121211112	0000100
Pholeomyia sp.15	1102021111	1011101110	1000102101	3111111101	1110100011	1121221113	0000100
Pholeomyia myopa	1002021111	1011100111	1000100101	3111110201	1010101012	1220201313	0000110
Pholeomyia sp.23	1002021111	1011101110	1000102101	3111111101	1010101012	1220201112	0000100
Pholeomyia sp.5	0102021111	1011101110	1000102101	3111111101	1110101012	2220101112	0010101
Pholeomyia dampfi	1002021111	1010100111	1001101101	3110011100	1110101012	2221001112	0010100
Pholeomyia praesecta	1002021111	1010100110	100010-101	3110111100	1110101011	2120001112	0010011
Pholeomyia sp.30	1002021111	1010110111	1010101110	3111111101	1010101112	2221111112	0010100
Pholeomyia sp.1	0202021111	1010111111	1010100101	3111010101	1110101012	2221101124	0010000
Pholeomyia sp.10	1102021111	1010010111	1000100101	3111111101	1110101112	2220101435	0010130
Pholeomyia sp.28	2202021121	1010100211	1010100101	3111110101	1110101112	2221101113	0010101
Pholeomyia sp.12	2202021121	1011100111	1000200101	3111210101	1110101112	2220211113	0010001
Pholeomyia sp.27	1202021121	1010100211	1010200101	3111110101	1110110112	2222201113	0010011
Pholeomyia hurdi	1002021111	1010101110	1000122101	3110011100	1010101012	2221201111	0010100
Pholeomyia sp.2	1002021111	1011101110	1010102101	3110211100	1010101112	2222201112	0000000
Pholeomyia sp.4	1002021111	1011101110	1000102101	3110011100	1110100012	2221201112	0010000
Pholeomyia sp.18	-002021111	1011101110	1000102101	3110111101	1010101111	2221201142	0000100
Pholeomyia leucozona	1002021111	1010011111	1010100101	3111010101	1010101011	2121201142	0010010
Pholeomyia sp.13	1102021121	1011100111	1000100101	3110010100	1010100011	2121001142	0010100
Pholeomyia sp.21	1002021111	1011101110	1000122101	3110111101	1010100012	2221221412	0010100
Pholeomyia anthracina	1002021111	-010101110	1000112101	3110011101	11101?00??	??????????	???????
Pholeomyia sp.7	1002021121	1010000111	1010100101	3110011101	1110100012	2221221412	0000130
Pholeomyia sp.24	1102021121	1000001210	1000101101	3110011101	1010101012	2221221412	0010131
Pholeomyia argyrophenga	??????????	??????????	???????101	3100011100	101???????	??????????	???????
Pholeomyia latifrons	1202021101	1011101010	1000101101	3100111101	101010100-	2-2-201213	00?????
Pholeomyia expansa	0202021111	1010111211	1000122101	3000111101	1010111012	2222211243	0010100
Pholeomyia vockerothi	0202021121	1010110?11	1000200101	2001210201	1010110012	222221????	???????
Pholeomyia leucogastra	1002021111	1011100111	1010101101	3110011101	1010110012	2222221113	0011001
Pholeomyia dispar	1002021111	1011100111	1010100101	311??11101	1010111112	2222221214	0010011
Pholeomyia nitidula	1002021111	1011000111	1000100101	311??11101	1010110012	2222221214	0010000
Pholeomyia pectoralis	1102021121	1010100110	1000101301	3110011101	1010101012	222220????	???????
Pholeomyia argyrata	1102021111	0011100110	1010100301	3110011100	1010100012	323110????	???????
Pholeomyia praeocellaris	1202021131	1010000111	1010100301	3110011100	1010110012	2222201613	3000231
Pholeomyia schnusei	1202021111	1010000111	1010100301	3110111100	1010100112	2222201113	0000211

The analysis under equal weighting using Traditional search generated 16 trees (length = 657, CI = 19, RI = 55). The results of this search are presented in a consensus tree (length = 714, CI = 18, RI = 51). The searches using New Technology search under equal weighting resulted in 8 trees (length = 657, CI = 19, RI = 55). The results of this search are also presented in a consensus tree (length = 714, CI = 18, RI = 51; Figure 4). As often happens with equal weight analyses, there is collapse of many nodes into large polytomies.

The cladistic analysis under implied weight with the value of k = 22.919922 returned a single maximum parsimonious tree (MPT) for both Traditional and New Technology searches, with a total of 664 steps, consistency index of 19 and retention index of 55. This tree was used in our discussion (Figures 5-6). The list of synapomorphies supporting each clade is given in Figures 6.

Number of trees, length (L), consistency index (CI) and retention index (RI) obtained for each parsimony analysis are summarized below (Table 5).

Table 5. Number of trees, length (L), consistency index (CI) and retention index (RI) obtained for each parsimony analysis.

Search	Schemes	Script	K value	Nº of trees	Consensus?	L	CI	RI
Traditional search	Equal weight	-	-	16	No	657	19	55
Traditional search	Equal weight	-	-	16	Yes	714	18	51
New Technology search	Equal weight	-	-	8	No	657	19	55
New Technology search	Equal weight	-	-	8	Yes	714	18	51
Traditional search	Implied weight	setk.run	22.919922	1	No	664	19	55
New Technology search	Implied weight	setk.run	22.919922	1	No	664	19	55

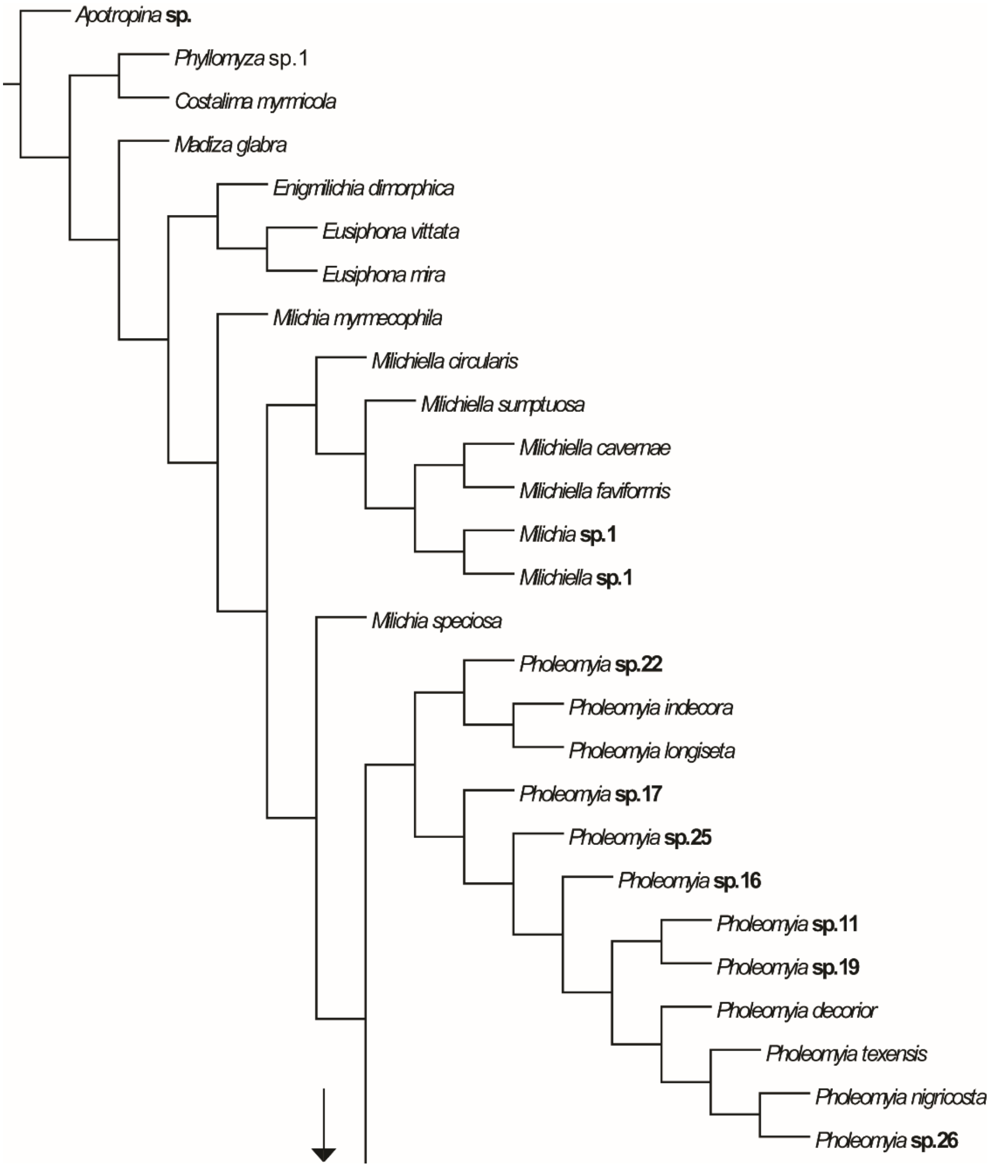


Figure 4. Strict consensus tree of the 8 most parsimonious trees (L = 714, CI = 18, RI = 51) under equal weighting scheme using New Technology search.

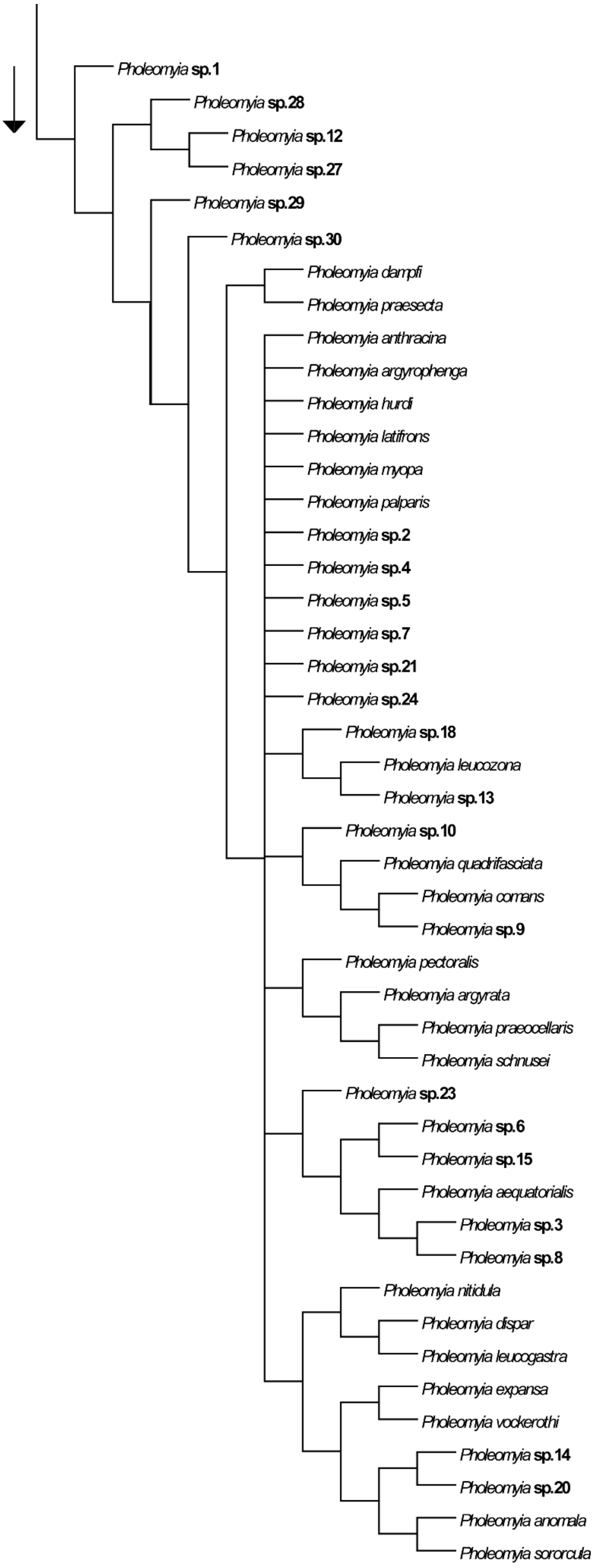


Figure 4. Continued.

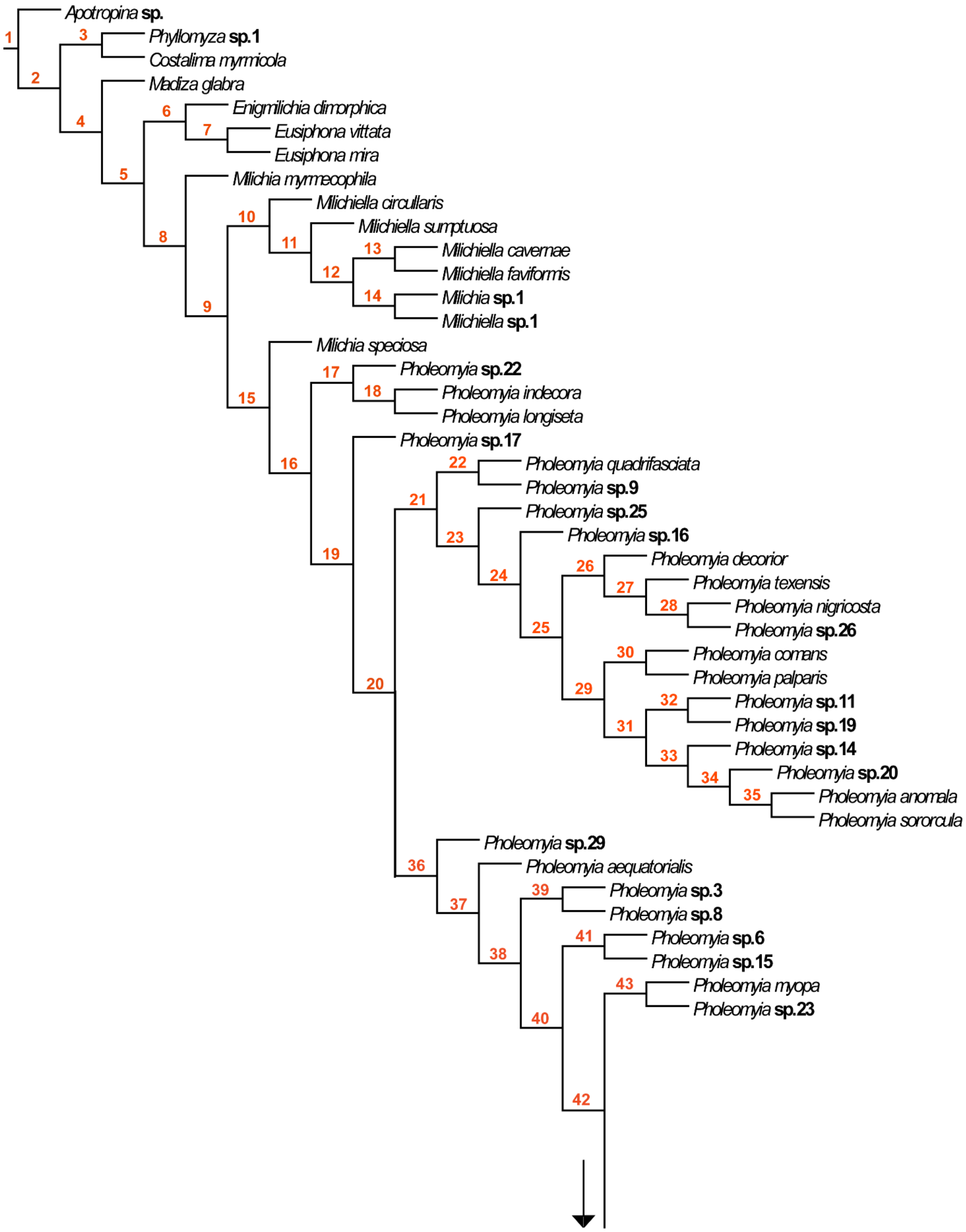


Figure 5. Most parsimonious tree (L = 664, CI = 19, RI = 55) under implied weighting scheme. Values on branches are clade numbers.

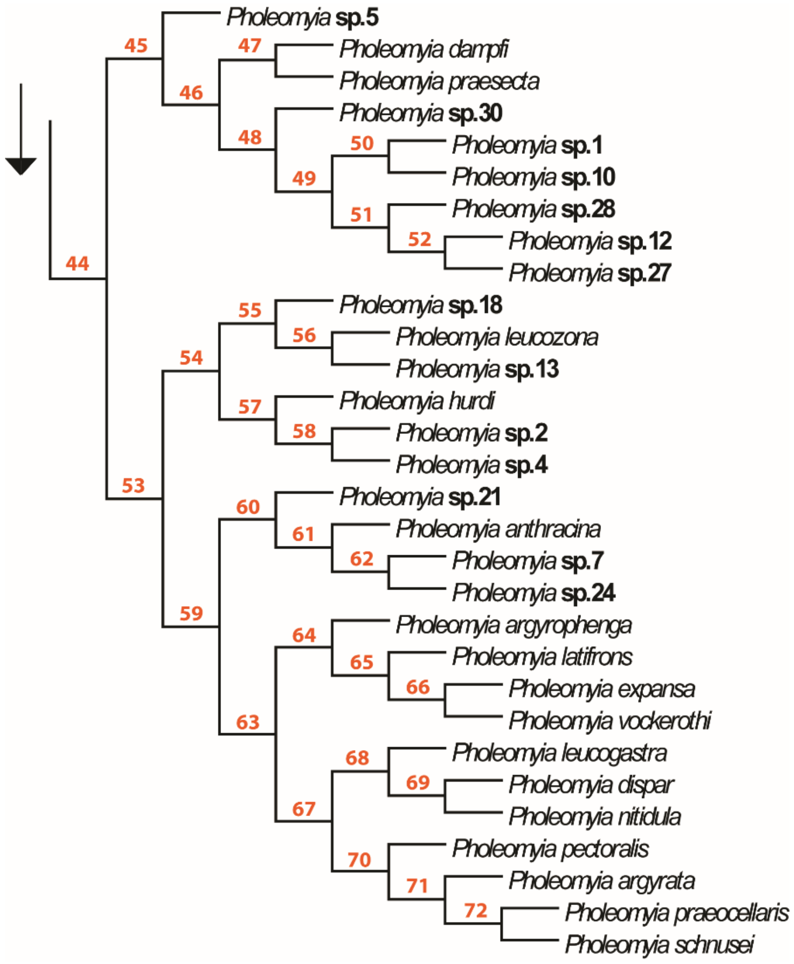


Figure 5. Continued.

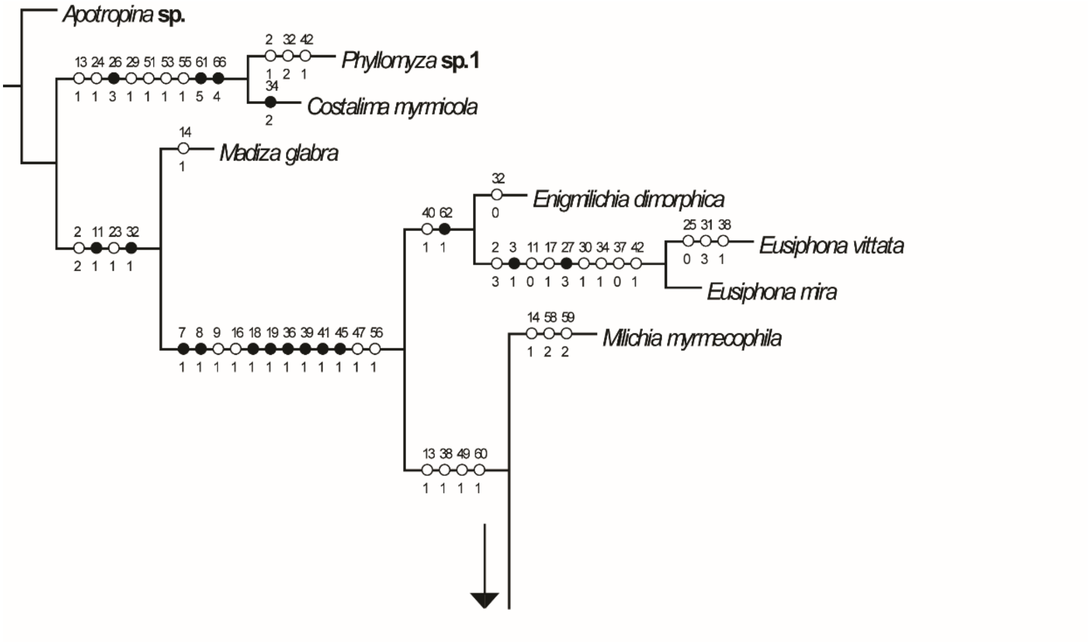


Figure 6. Most parsimonious tree (L = 664, CI = 19, RI = 55) under implied weighting scheme with unambiguous apormorphies mapped on branches. White circles, homoplastic synapomorphies; full black circles, non-homoplastic synapomorphies.

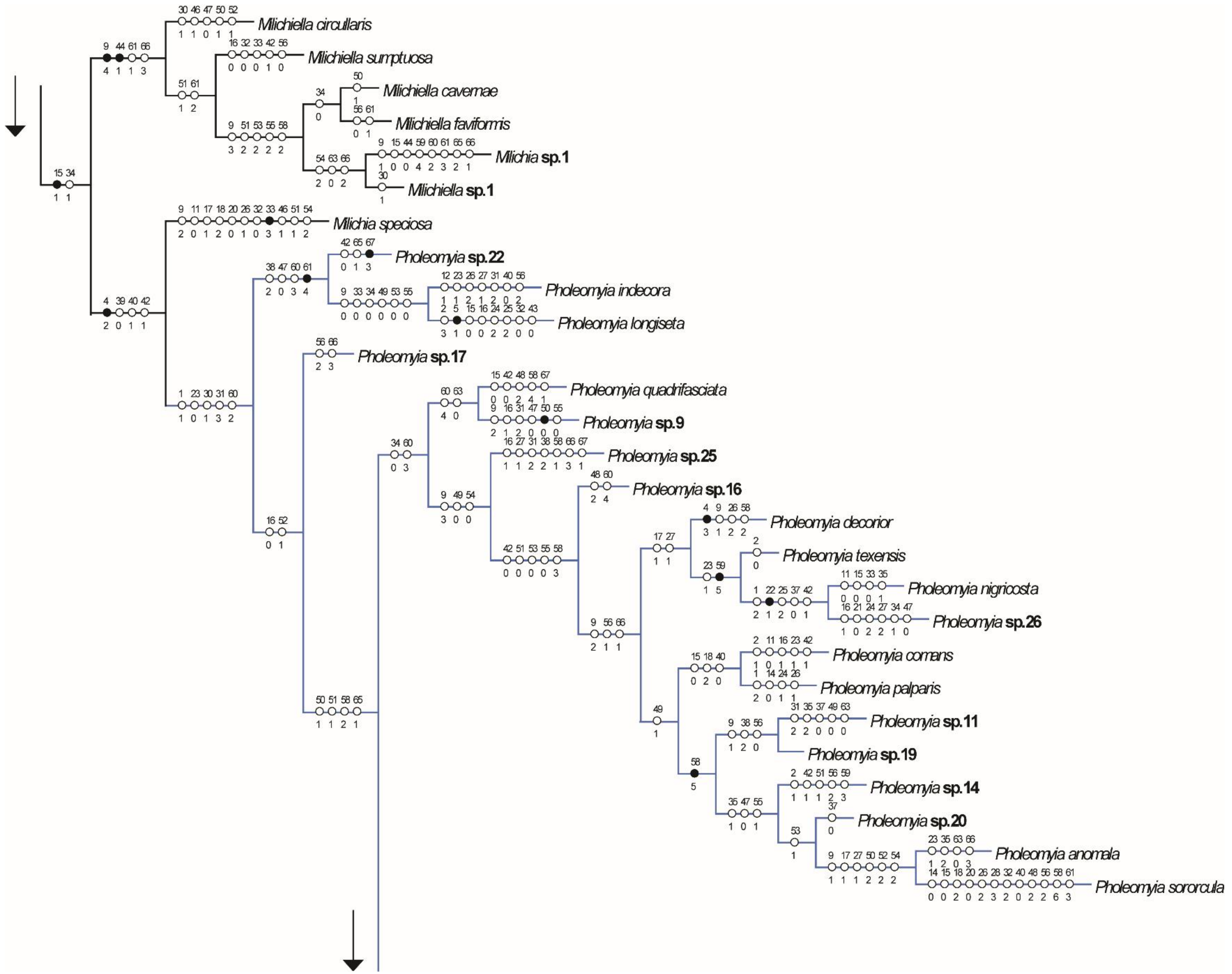


Figure 6. Continued.

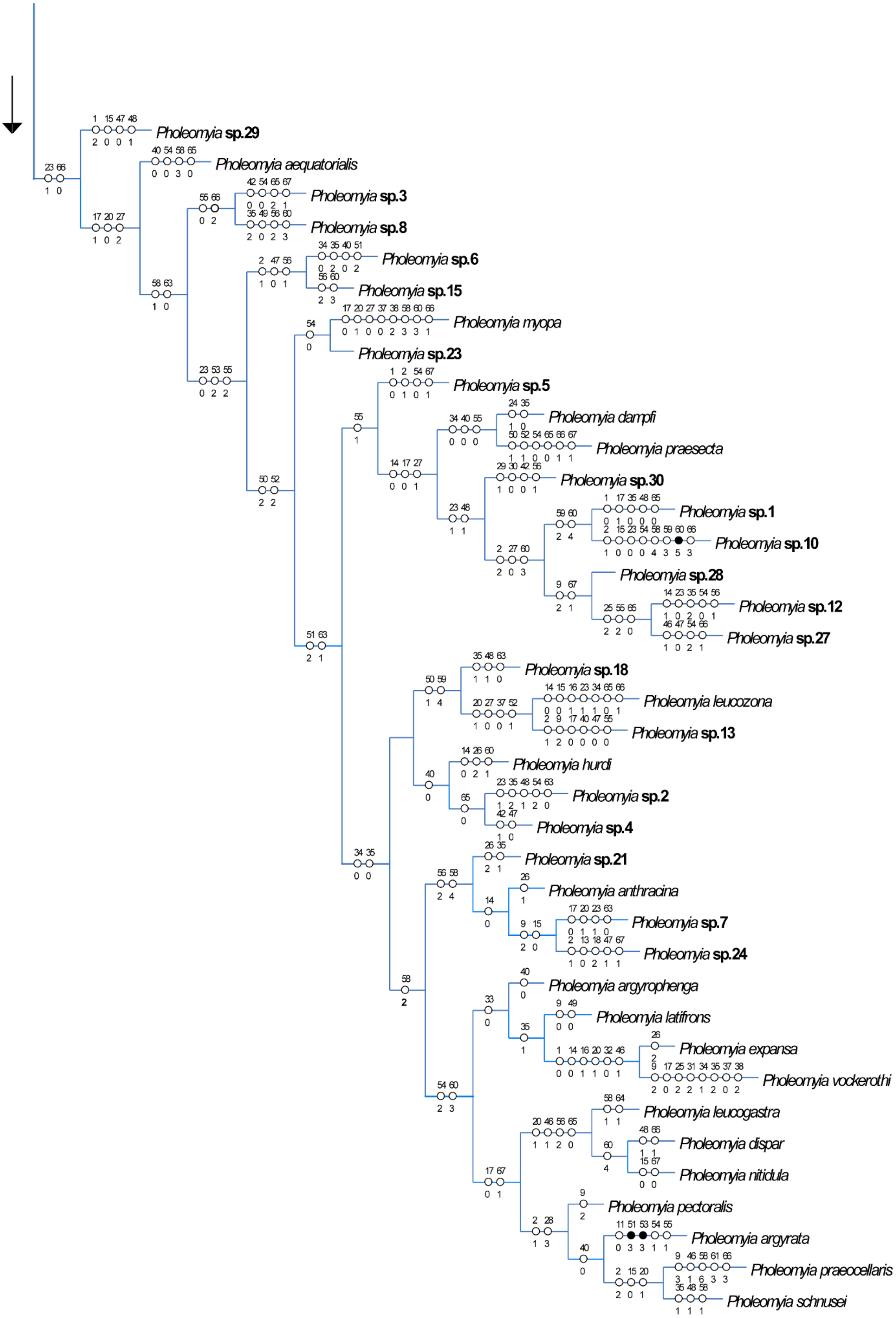


Figure 6. Continued.

Characters

Head

1. Length of the outer vertical seta: (0) present, as long as the inner vertical seta; (1) present, half of the inner vertical seta; (2) present, 1/3 of the inner vertical seta; (3) present, longer than inner vertical seta; (4) absent. L = 13, CI = 30, RI = 52.

The character state (1) was obtained as a homoplastic synapomorphy for *Pholeomyia*. This character also occurs in other milichiids, as *Phyllomyza*, *Costalima* and *Madiza*. Some changes occurred in few species of the genus. The character state (2) is a homoplastic apomorphy for *Pholeomyia* palparis, *Pholeomyia* sp. 29 and the node 28. The character state (3) is present only in *Pholeomyia longiseta*. Supporting the node 66 is the character state (0). This condition is also present in *Pholeomyia* sp. 1 and *Pholeomyia* sp. 5. In *Pholeomyia indecora*, the outer vertical seta is absent (character state 4). This absence is associated with sexual dimorphism: it is absent in males and present in females.

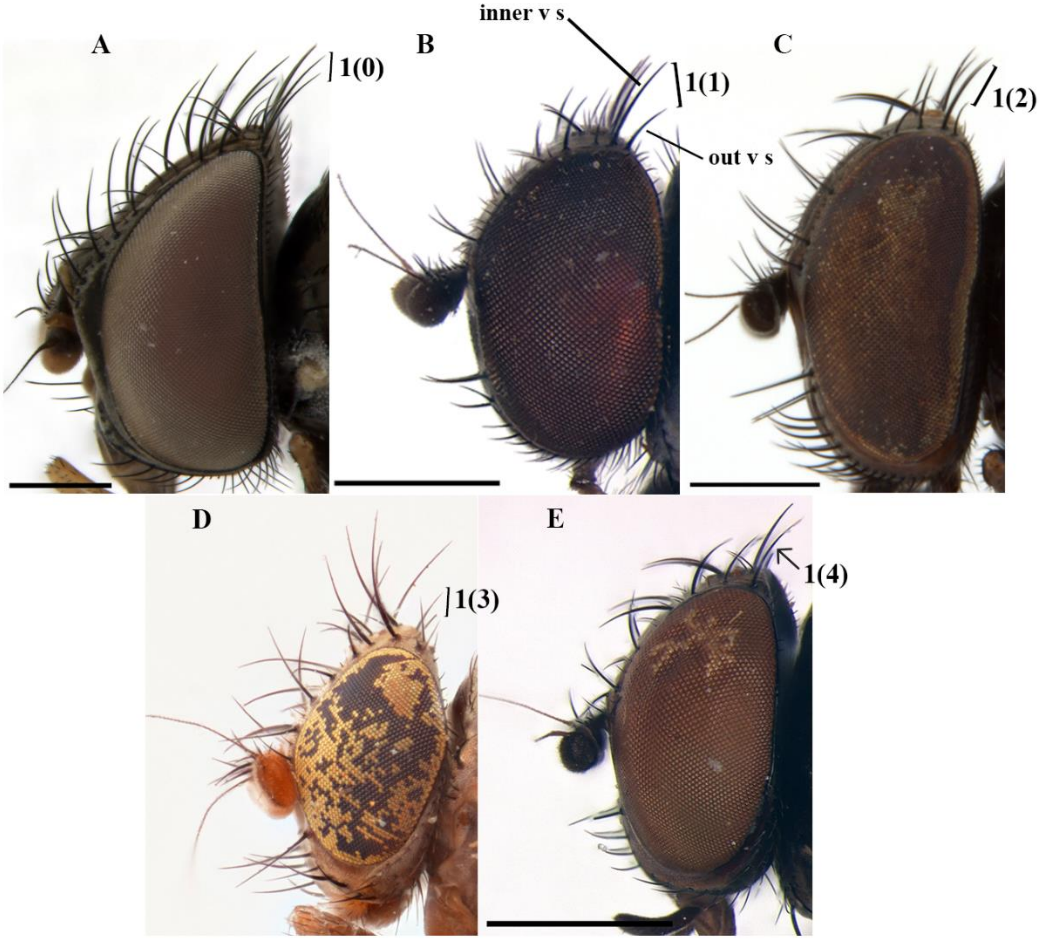


Figure 7. Character 1 (length of the outer vertical seta). **A.** *Eusiphona vittata*. **B.** *Pholeomyia praeocellaris*. **C.** *Pholeomyia* sp. 27. **D.** *Pholeomyia longiseta* (female), photo by Zoltán Soltész. **E.** *Pholeomyia indecora*. Abbreviations: inner v s, inner vertical seta; out v s, outer vertical seta. Scale bar, 0.5 mm.

2. Position of the postocellar seta (modified from Brake, 2000): (0) cruciate; (1) convergent; (2) parallel; (3) divergent. L = 20, CI = 15, RI = 51.

The parallel postocellar (character state 2) is a homoplastic synapomorphy that supports Madizinae (represented by *Madiza glabra*) and Milichiinae (node 5) as sister group. Within *Pholeomyia*, other conditions evolved: cruciate (character state 0), convergent (character state 1) and divergent (character state 3). The evolution of this character within the node 20 has ambiguous interpretation. One of the scenarios is the change of a parallel to a cruciate postocellar in the node 19, with reversions to the parallel condition in node 23, *Pholeomyia* sp. 29, node 49, node 65 and node 72. The other scenario is the change of a parallel to a cruciate postocellar in *Pholeomyia* sp. 17, *Pholeomyia quadrifasciata*, *Pholeomyia texensis* and node 37.

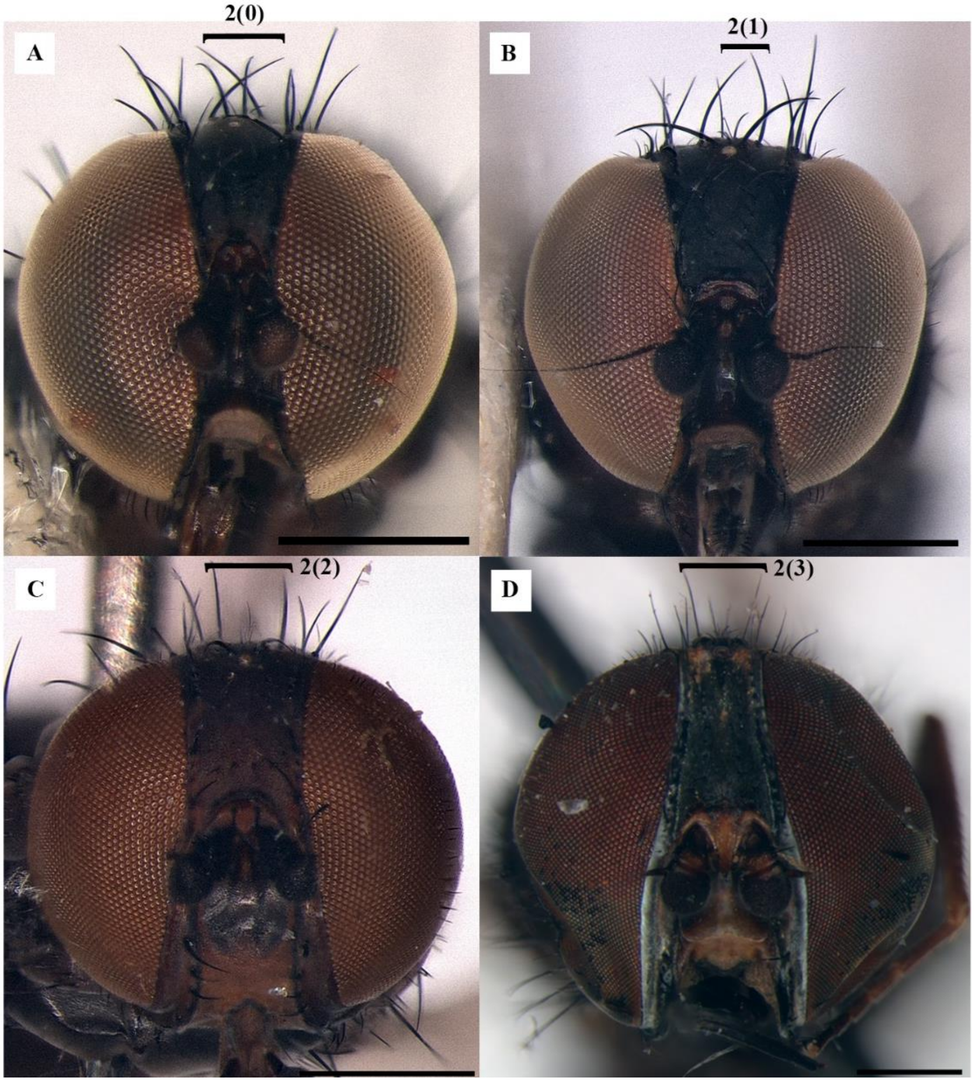


Figure 8. Character 2 (position of the postocellar seta). **A.** *Pholeomyia* sp. 23. **B.** *Pholeomyia* sp. 5. **C.** *Pholeomyia indecora*. **D.** *Eusiphona mira.* Scale bar, 0.5 mm.

The convergent condition is present in *Pholeomyia* sp. 9, *Pholeomyia comans*, *Pholeomyia* sp. 14, node 41, *Pholeomyia* sp. 5, *Pholeomyia* sp. 10, *Pholeomyia* sp. 13, *Pholeomyia* sp. 24 and node 70. This condition is also present in *Phyllomyza* sp. 1. Within *Pholeomyia*, Only *Pholeomyia longiseta* has the divergent condition. *Eusiphona* also share this character state. Although considerably plastic, the retention index demonstrates it brings some structure to the tree, and supports some clades within *Pholeomyia*.

3. Fronto-orbital and orbital seta (modified from Brake, 2000): (0) distinct; (1) indistinct. L = 1, CI = 100, RI = 100.

In *Eusiphona*, the configuration of orbital and frontal setae differs from all other Milichiidae: all the setae together form a uniform row of 8-10 reclinate setae. This is a synapomorphy for the genus, as already demonstrated by Brake (2000).

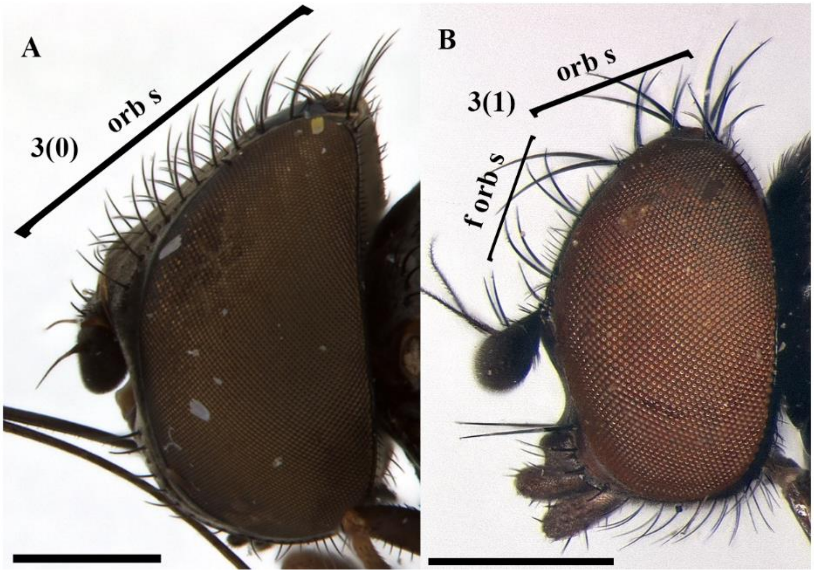


Figure 9. Character 3 (fronto-orbital seta and orbital seta). **A.** *Eusiphona mira.* **B.** *Pholeomyia praesecta*. Abbreviations: f orb s, fronto-orbital seta; orb s, orbital seta. Scale bar, 0.5 mm.

4. Number of fronto-orbital setae (modified from Brake, 2000): (0) 0; (1) 2; (2) 3; (3) 4. L = 3, CI= 100, RI = 100.

This character is inapplicable to *Eusiphona*. Within Milichiinae, the presence of three frontal setae was recovered as a synapomorphy for (*Pholeomyia* + *Milichia speciosa*). In *Pholeomyia decorior*, this condition evolved for the presence of four fronto-orbital setae.

5. Position of third fronto-orbital seta: (0) reclinate; (1) lateroclinate. L = 1.

This character is applicable only for *Pholeomyia* and *Milichia speciosa*. The lateroclinate third fronto-orbital seta is an apomorphy for *Pholeomyia longiseta*.

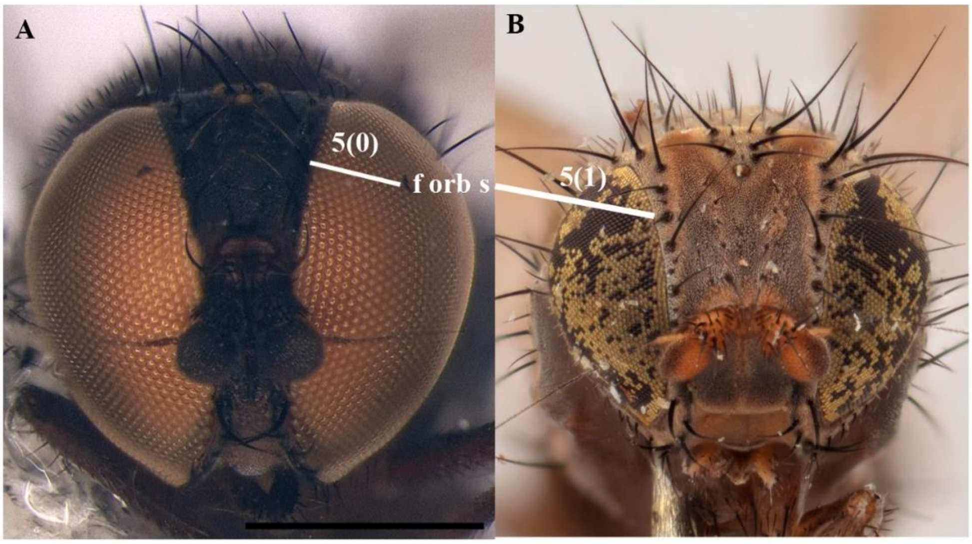


Figure 10. Character 5 (position of third fronto-orbital seta). **A.** *Pholeomyia* sp. 1. **B.** *Pholeomyia longiseta* (female), photo by Zoltán Soltész. Abbreviations: f orb s, fronto-orbital seta. Scale bar, 0.5 mm.

6. Position of the upper orbital seta (modified from Brake, 2000): (0) present, latero-reclinate; (1) present, lateroclinate; (2) present, medio-reclinate; (3) absent. L = 3, CI = 100, RI = 100.

This character also is inapplicable to *Eusiphona*. The upper orbital seta medio-reclinate is a synapomorphy for the clade Milichiinae + Madizinae, as already shown by Brake (2000). Within Milichiinae, this seta is absent only in *Enigmilichia*.

7. Eye (modified from Brake, 2000): (0) up to 1.5x as high as wide; (1) more than 1.5x as high as wide. L = 1, CI = 100, RI = 100.

The character state (1) is a synapomorphy for Milichiinae. Madizinae and Phyllomyzinae species have eyes more or less circular in lateral view. Milichiines have eyes enlarged in width and mainly in height. This character state is associated with the swarming behavior.

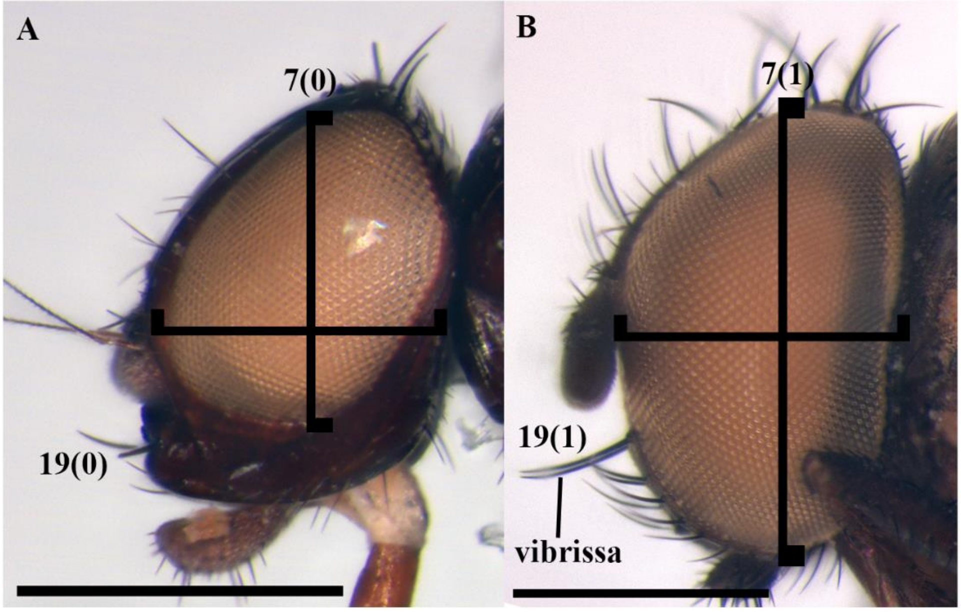


Figure 11. Characters 7 (eye) and 19 (position of vibrissa). **A.** *Madiza glabra.* **B.** *Pholeomyia* sp. 1. Scale bar, 0.5 mm.

8. Frons in males (modified from Brake, 2000): (0) as wide as in females; (1) narrower than in females. L = 1, CI = 100, RI = 100 (see figure 10).

Although we did not include females in the analysis, we studied several female specimens that corroborate the hypothesis that male milichiines have narrower frons. Brake (2000) had already codified this character and obtained the state 1 as a synapomorphy for Milichiinae. This character state is an example of sexual dimorphism, and probably is connected to the swarming behavior in males: it seems to be an adaptation to the recognition and capture of females in flight (Downes, 1969).

9. Posterior eye margin (modified from Brake, 2000): (0) broad emargination, as a right triangle; (1) straight, without notch or emargination; (2) narrow emargination; (3) narrow notch [1–3om]; (4) broad notch [>3om]. L = 19, CI = 21, RI = 46.

These character states have been used for several decades as diagnostic features to separate milichiines into genus: the notch is absent in *Pholeomyia* and *Milichia*, and it is present in *Pseudomilichia* and *Milichiella*. Brake (2000) had already discussed that this character is not informative to separate the genera due to its plasticity. This hypothesis was corroborated by Brake (2009) when she demonstrated that there are transitional stages between notch, emargination, and a straight eye margin in *Milichiella*. After studying several *Pholeomyia* species, we concluded that the same scenario occurs in the genus, and these conditions seems to have evolved multiple times within the genus. Despite that, the different states are informative for some nodes within *Pholeomyia*. Most of these homoplasies supports several small nodes with two or three species, and two bigger nodes (23 e 25). Within the nodes 23 and 25, at least three reversions probably occurred.

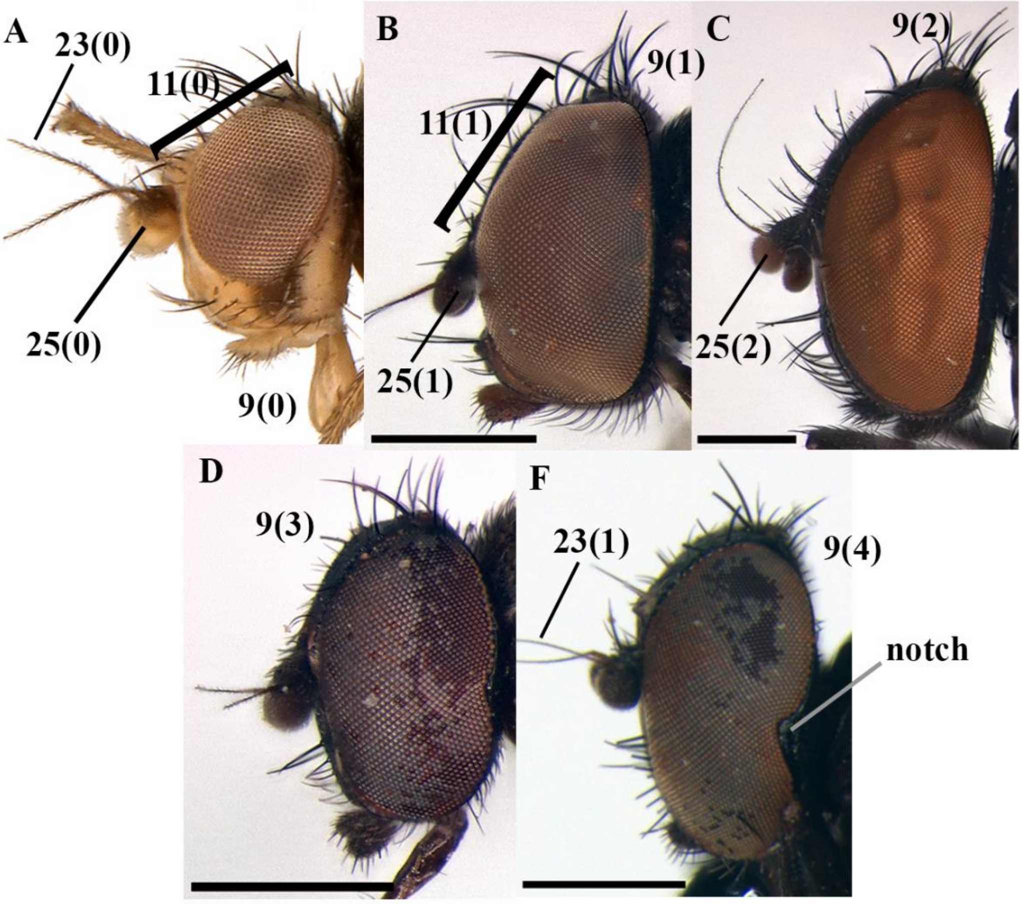


Figure 12. Characters 9 (posterior eye margin), 11 (angled frons in lateral view), 23 (arista pilosity arrangement) and 25 (color of first flagellomere). **A.** *Apotropina* sp.1, photo by Paula Riccardi. **B.** *Pholeomyia* sp. 15. **C.** *Pholeomyia* sp. 12. **D.** *Pholeomyia* sp. 16. **E.** *Milichiella circullaris*. Scale bar, 0.5 mm.

10. Shape of frons: (0) trapezium; (0) inverted trapezium. L = 1, CI = 100, RI = 100.

This character is applicable only for milichiines due to the presence of narrower frons in males of this subfamily. This condition differs between the milichiines. In *Milichia*, *Milichiella* and *Pholeomyia*, the narrowing of the frons assumes a trapezoid shape. In the node (*Enigmilichia* + *Eusiphona*), the frons is presented as an inverted trapezium. As both nodes were recovered as sister group, and the genera outside Milichiinae do not have narrower frons, the plesiomorphic condition of this character has ambiguous interpretation.

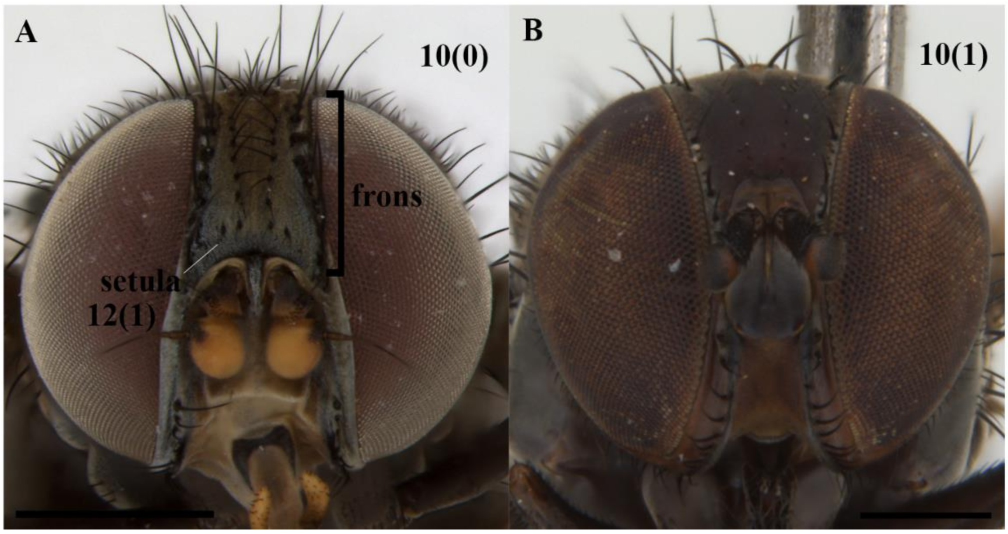


Figure 13. Characters 10 (shape of frons) and 12 (proclinate setula between supra-antennal seta and eye margin). **A.** *Eusiphona vittata*. **B.** *Pholeomyia* sp. 28. Scale bar, 0.5 mm.

11. Angled frons in lateral view: (0) present (1) absent. L = 6, CI = 16, RI = 37 (see figure 12).

The absence of a frons with angle was obtained as a synapomorphy for Madizinae + Milichiinae. Within Milichiinae, some reversions in *Eusiphona* and *Pholeomyia* (for example, *Pholeomyia nigricosta*, *Pholeomyia comans*, *Pholeomyia argyrata*) probably occurred.

12. Proclinate setula between supra-antennal seta and eye margin: (0) absent; (1) present. L = 4, CI = 25, RI = 40 (see figure 13).

A pair of proclinate setula between supra-antennal seta and the eye margin is absent in most milichiines, with the exception of the genera *Eusiphona* and *Enigmilichia*. In Brake (2000), the absence of the proclinate setula was obtained as a synapomorphy for Milichiidae, which probably evolved secondarily in some genera of the family, such as *Costalima* and *Microsimus*.

13. Lunule seta: (0) absent; (1) present. L = 3, CI = 33, RI = 60.

The presence of one pair of setae on the lunule has been indicated in the literature as an apomorphic condition in Milichiidae. In Brake's (2000) analysis, this character was codified as present for *Enigmilichia* and *Eusiphona*. We did not identify the lunule seta in our specimens. Therefore, we codified this character as absent for these genera. Brake (2000) also points out the absence of the lunule seta in *Pholeomyia nigricosta*. After studying the holotype, we concluded that the seta is present in the species.

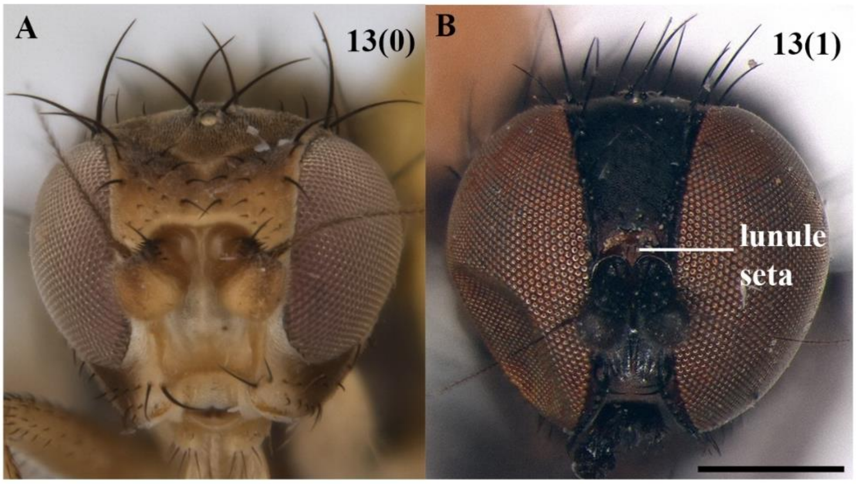


Figure 14. Character 13 (lunule seta). **A.** *Apotropina* sp.1, photo by Paula Riccardi. **B.** *Pholeomyia* sp. 19. Scale bar, 0.5 mm.

14. Lunule: (0) not shiny; (1) shiny. L = 17, CI = 5, RI = 48.

In some *Milichia* and *Pholeomyia* species, the frons is shiny. Although considerably plastic, as can be seen by the low consistency index, this character supports some clades within *Pholeomyia*.

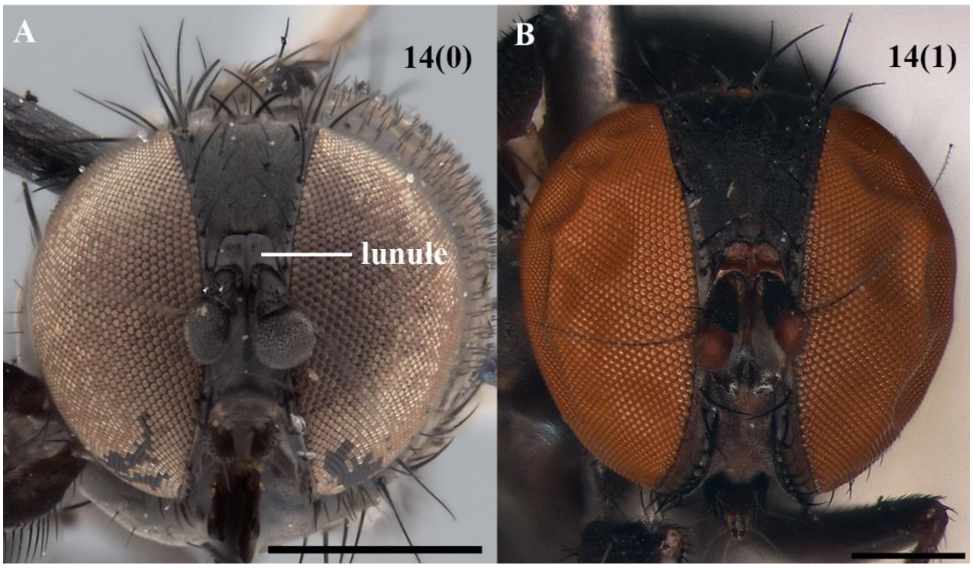


Figure 15. Character 14 (lunule). **A.** *Pholeomyia hurdi*. **B.** *Pholeomyia* sp. 12. Scale bar, 0.5 mm.

15. Height of lunule: (0) narrow; (1) high, almost the length of the first flagellomere. L = 13, CI = 7, RI = 45.

Although the presence of a large lunule was recovered as a synapomorphic condition for the node that includes *Milichia speciosa*, *Milichia* sp. 1, *Milichiella* and *Pholeomyia*, this structure is well developed in most Milichiidae (Brake, 2000). Therefore, this result is probably an artifact of the low sampling of Phyllomyzinae and Madizinae genera. If we adopt the scenario that a developed lunule is synapomorphic in Milichiidae, it is most parsimonious to consider as reversions the cases where the lunule is narrow. Within *Pholeomyia*, the nodes 30 and 72, and the species *Pholeomyia longiseta*, *Pholeomyia quadrifasciata*, *Pholeomyia nigricosta*, *Pholeomyia sororcula*, *Pholeomyia* sp. 29, *Pholeomyia* sp. 10, *Pholeomyia leucozona*, *Pholeomyia* sp. 7, *Pholeomyia* sp. 24 and *Pholeomyia nitidula* have a narrow lunule.

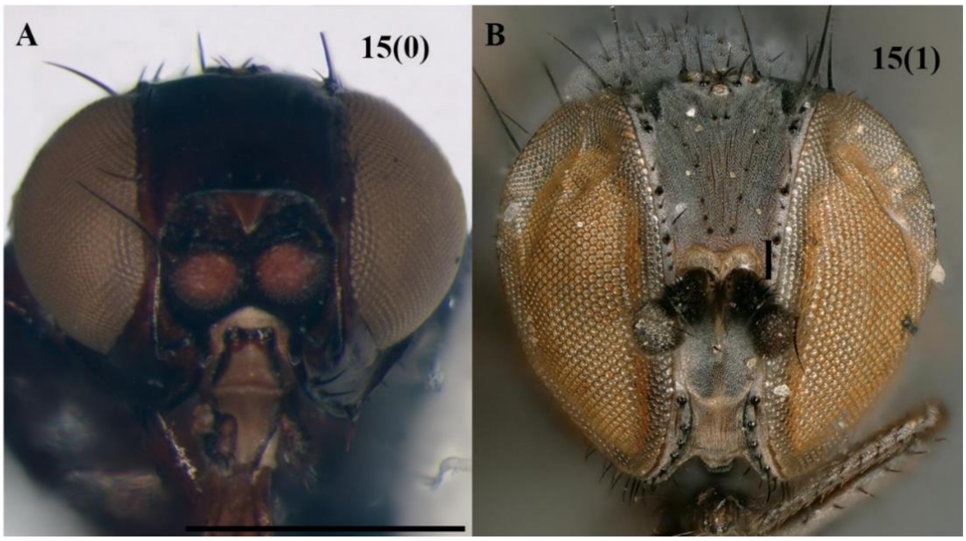


Figure 16. Character 15 (lunule). **A.** *Madiza glabra.* **B.** *Pholeomyia praeocellaris*, photo by Daniel Whitmore. Scale bar, 0.5 mm.

16. Shape of lunule: (0) rectangular; (1) rounded. L = 12, CI = 8, RI = 47.

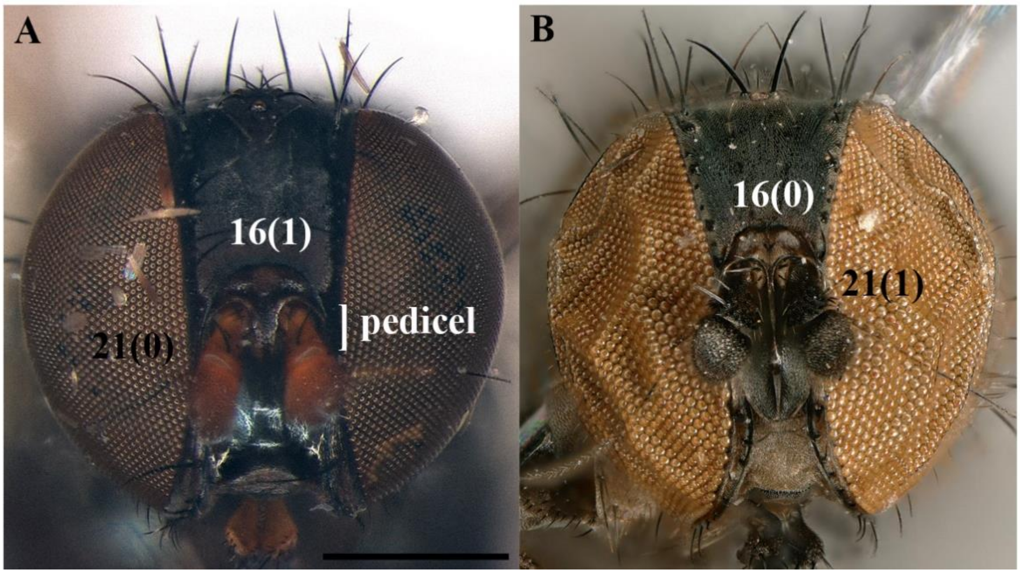


Figure 17. Characters 16 (shape of lunule) and 21 (pedicel pilosity arrangement). **A.** *Pholeomyia* sp. 26. **B.** *Pholeomyia argyrata*, photo by Daniel Whitmore. Scale bar, 0.5 mm.

The rounded condition was obtained as a homoplasy for Milichiinae. The rectangular lunule is present in several *Pholeomyia* species. The presence of a rounded lunule supports the node (*Pholeomyia expansa* + *Pholeomyia vockerothi*), two Nearctic species, and probably corresponds to a reversion within the genus. This character state also occurs in *Pholeomyia indecora*, *Pholeomyia* sp. 9, *Pholeomyia* sp. 25 and *Pholeomyia* sp. 26.

17. Epistoma in lateral view: (0) not prominent; (1) prominent. L = 12, CI = 8, RI = 57.

The character state (1) probably evolved independently in *Eusiphona* and *Pholeomyia*, since this condition was not recovered as a shared feature between milichiines. Within *Pholeomyia*, a prominent epistoma evolved in clades 26, 35 and 37. In these clades, several reversions probably occurred to condition (0), as in the node 46, *Pholeomyia myopa*, *Pholeomyia* sp. 7 and *Pholeomyia vockerothi*.

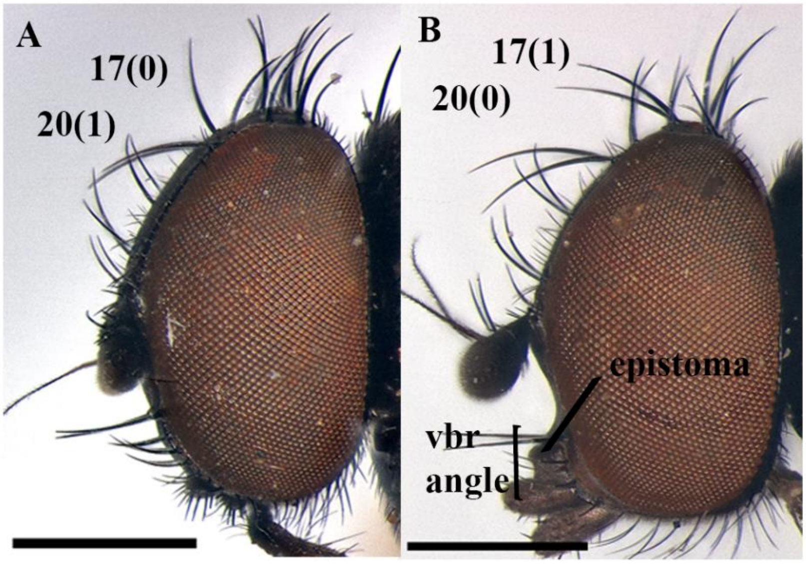


Figure 18. Characters 17 (epistoma in lateral view) and 21 (vibrissal angle). **A.** *Pholeomyia* sp. 19. **B.** *Pholeomyia praesecta*. Abbreviations: vbr angle, vibrissal angle. Scale bar, 0.5 mm.

18. Height of gena: (0) broad, equal or more than the height of the first flagellomere; (1) narrow, almost inconspicuous; (2) narrow, but conspicuous (see *Pholeomyia indecora* in figure 7). L = 13, CI = 15, RI = 26.

In Milichiinae, correlated with the enlargement of the eyes, the gena are often narrow and the eyes take up nearly the whole lateral side of the head (Brake, 2000). This is a synapomorphy for Milichiinae. In *Milichia speciosa* and a few *Pholeomyia* species, a narrow, but conspicuous gena probably evolved multiple times.

19. Position of vibrissa (modified from Brake, 2000): (0) below or at level of lower margin of eye; (1) above lower margin of eye. L = 1, CI = 100, RI = 100 (see figure 11).

The vibrissa above the lower margin of the eye is a synapomorphy for Milichiinae. This condition is probably associated with the enlargement of the eyes in the subfamily.

20. Vibrissal angle: (0) present; (1) absent. L = 15, CI = 6, RI = 54 (see figure 18).

Most milichiines, especially *Milichiella*, have an obsolescent vibrissal angle. This is probably the plesiomorphic condition in *Pholeomyia*. The presence of a small vibrissal angle occurs in several species of the genera and supports clade 37. Within this clade, several species probably returned to an obsolescent vibrissal angle, as *Pholeomyia myopa*, *Pholeomyia leucozona*, *Pholeomyia* sp. 13, node 58, *Pholeomyia* sp. 7, node 68 and node 72.

21. Pedicel pilosity arrangement: (0) scattered small setulae; (1) scattered strong setulae. L = 4, CI = 25, RI = 40 (see figure 17).

The presence of scattered strong seta is consistent in *Milichia*, *Milichiella* and *Pholeomyia*. The only reversion to character state (0) occurred in *Pholeomyia longiseta*.

22. Pedicel: (0) short; (1) long. L = 1, CI = 100, RI = 100.

The long pedicel is a synapomorphic condition shared between only two species: *Pholeomyia nigricosta* and *Pholeomyia* sp. 26.

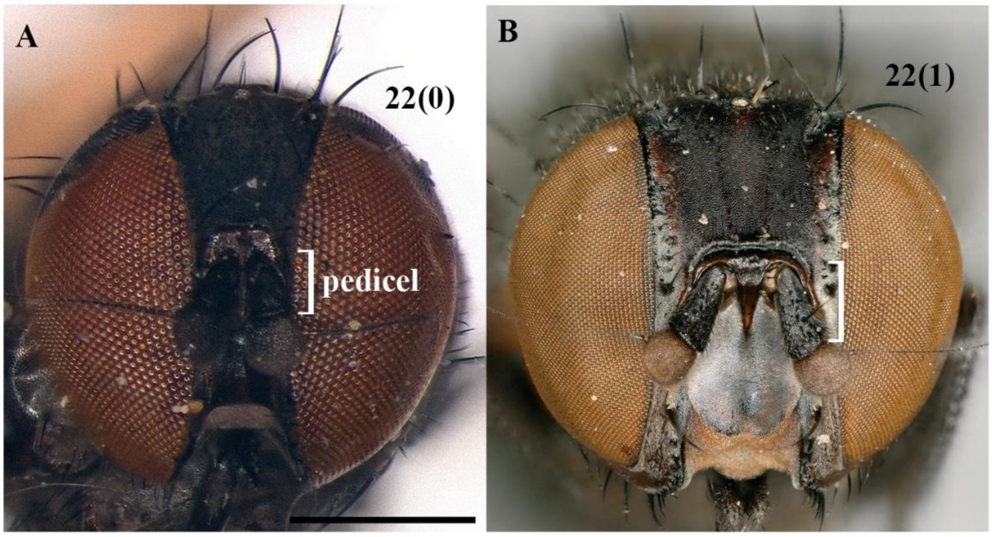


Figure 19. Character 22 (pedicel). **A.** *Pholeomyia* sp. 15. **B.** *Pholeomyia nigricosta* (female), photo by Daniel Whitmore. Scale bar, 0.5 mm.

23. Arista pilosity arrangement: (0) pubescent; (1) micropubescent. L = 17, CI = 5, RI = 51 (see figure 12).

The micropubescent arista probably is the plesiomorphic condition in Milichiinae. Between milichiines, the pubescent condition appears in *Pholeomyia* and multiple reversions to a micropubescent arista have taken place across the genus.

24. Shape of first flagellomere: (0) rounded, small; (1) rounded, enlarged; (2) oval. L = 5, CI = 40, RI = 25.

Most milichiines have a rounded and small first flagellomere. The character states (1) and (2) probably evolved independently in *Pholeomyia dampfi*, and *Pholeomyia longiseta* and *Pholeomyia* sp. 26, respectively.

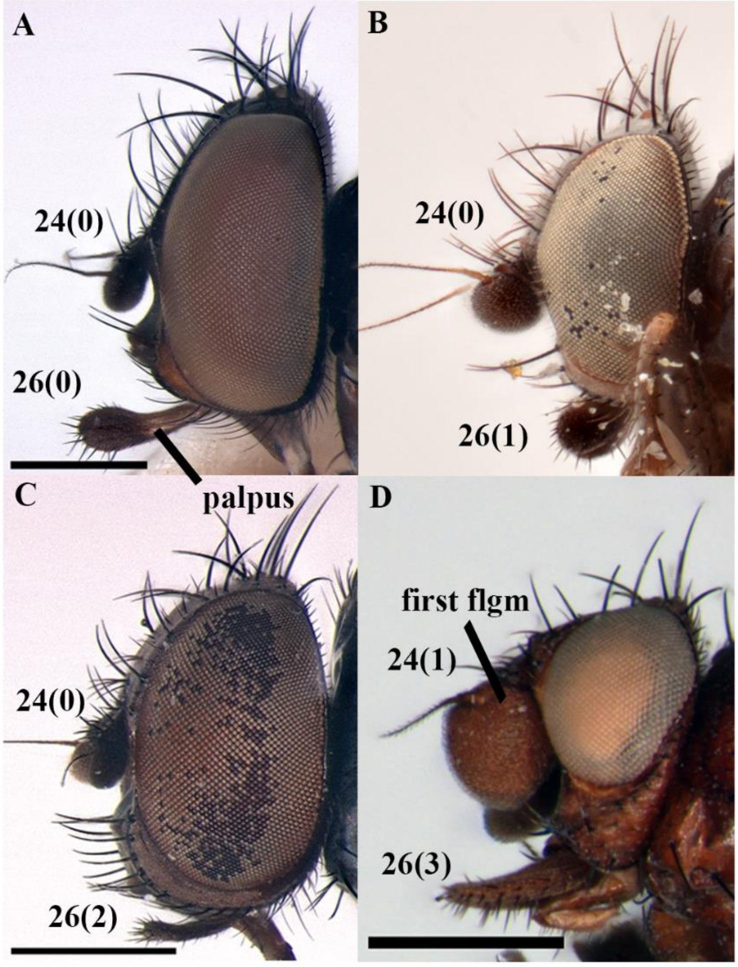


Figure 20. Characters 24 (shape of first flagellomere) and 26 (shape of palpus). **A.** *Pholeomyia* sp. 5. **B.** *Pholeomyia palparis* (female). **C.** *Pholeomyia schnusei*. **D.** *Phyllomyza* sp.1. Abbreviations: first flgm, first flagellomere. Scale bar, 0.5 mm.

25. Color of first flagellomere: (0) yellow with dark base; (1) brown with golden pruinosity; (2) orange. L = 7, CI = 28, RI = 28 (see figure 12).

The character state (2) occurs in most milichiines. The orange condition evolved in a few *Pholeomyia* species and supports some small clades, as (*Pholeomyia* sp. 12 + *Pholeomyia* sp. 27) and (*Pholeomyia nigricosta* + *Pholeomyia* sp. 26). This condition is also present in *Pholeomyia longiseta*.

26. Shape of palpus (modified from Brake, 2000): (0) short and clavate; (1) short, clavate and enlarged; (2) short, not clavate and thin; (3) long and thick. L = 10, CI = 30, RI = 12 (see figure 20).

Most milichiines have a short and clavate palpus. The character states (1) and (2) probably evolved independently in some *Pholeomyia* species. The character state (1) occurs in *Pholeomyia palparis* and *Pholeomyia anthracina*. The condition (2) occurs in *Pholeomyia indecora, Pholeomyia decorior, Pholeomyia sororcula, Pholeomyia hurdi, Pholeomyia* sp. 21 *and Pholeomyia expansa.*

27. Proboscis length: (0) short, distal section much shorter than head; (1) short, distal section half the length of head; (2) elongated, distal section slightly longer than length of head; (3) very elongated, distal section much longer than length of head. L = 18, CI = 16, RI = 44.

The character state (3) is a synapomorphy for *Eusiphona*. The conditions (1) and (2) evolved within *Pholeomyia*. The presence of an elongated proboscis is a condition that supports one of the largest clades in *Pholeomyia*: the node 37. Although several species have this condition, multiples reversions to character state (1) occurred.

Thorax

28. Color of scutellum (modified from Brake, 2009): (0) yellow microtomentose; (1) brown microtomentose; (2) shiny or subshiny; (3) grey or silvery microtomentose; (4) black micromentose; (5) metallic. L = 10, CI = 50, RI = 37.

The plesiomorphic condition in Milichiinae is a brown microtomentose scutellum. In *Pholeomyia*, a few changes evolved. *Pholeomyia nigricosta* has a black microtomentose scutellum. In *Pholeomyia* sp. 26, the scutellum is metallic. A grey or silvery microtomentose scutellum is a homoplastic condition that supports a clade with four Neotropical species (node 70).

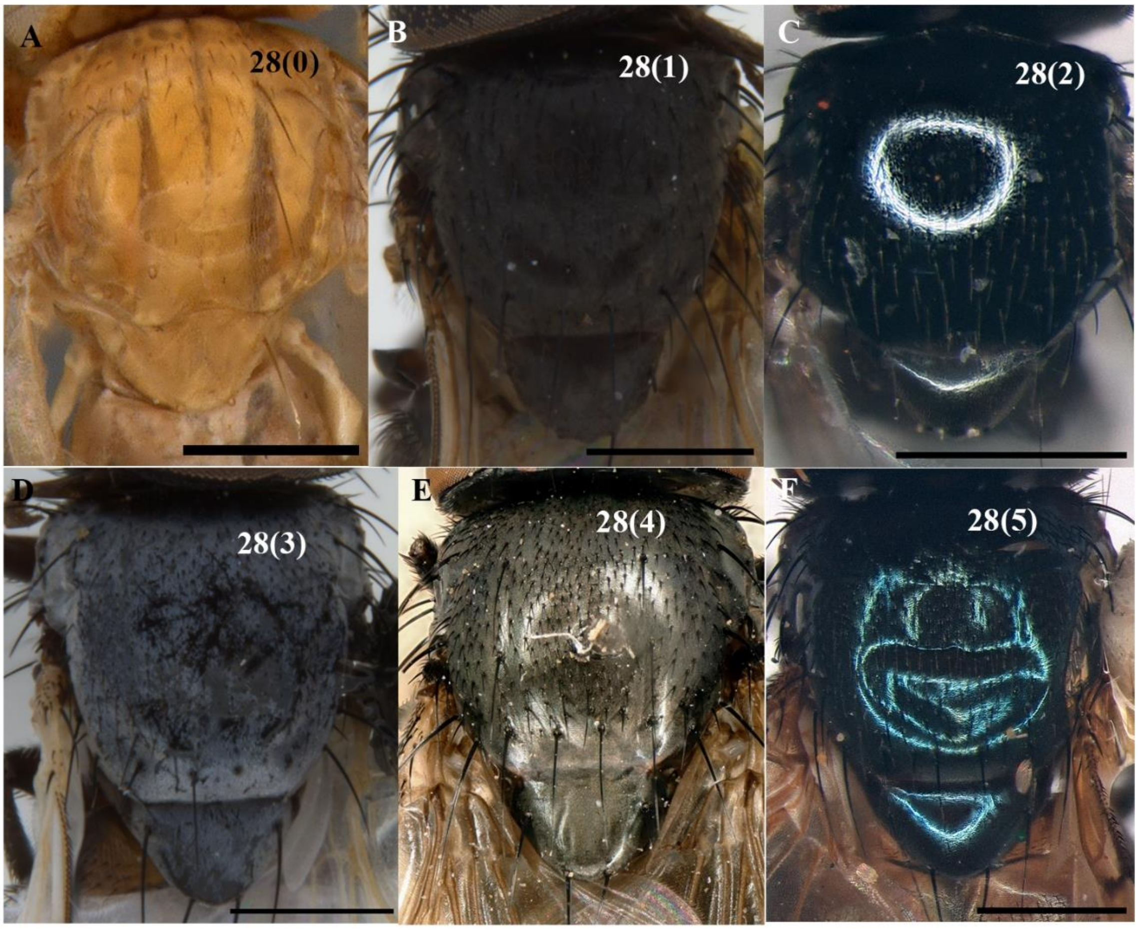


Figure 21. Character 28 (color of scutellum). **A.** *Costalima myrmicola*. **B.** *Pholeomyia leucozona*. **C.** *Milichia* sp.1. **D.** *Phoelomyia praeocellaris*. **E.** *Pholeomyia nigricosta* (female), photo by Daniel Whitmore. **F.** *Phoelomyia* sp. 26. Scale bar, 0.5 mm.

29. Proepimeral seta: (0) absent; (1) present. L = 2, CI = 50, RI = 50.

The absence of the proepimeral seta is a homoplastic condition that supports the close relationship of Madizinae and Milichiinae.

30. Number of postpronotal seta (modified from Brake, 2000): (0) one; (1) more than one. L = 5, CI = 20, RI = 63.

The plesiomorphic condition in Milichiinae is the presence of only one postpronotal seta. In *Pholeomyia*, more than one postpronotal seta is a homoplastic synapomorphy for the genus. This character state also occurs in *Eusiphona*, *Milichiella circularis* and *Milichiella* sp. 1.

31. Anepisternum (modified from Brake, 2000): (0) covered with hairs; (1) bare; (2) with three setae; (3) with four setae. L = 8, CI = 37, RI = 68.

Sabrosky (1955) and Swann (2010) were of the opinion that the presence of anepisternal setae and a costal notch in *Eusiphona cooperi* indicated a close relationship between *Eusiphona* and *Pholeomyia* (Brake, 2000). Brake (2000) did not analyse *Eusiphona cooperi*, but following the description of the species, she concluded that the setation on the anepisternum in *Pholeomyia* and *Eusiphona cooperi* was probably not homologous. We did not access *Eusiphona cooperi*, but we analyzed a very close species, *Eusiphona vittata*. After studying the anepisternal setae, we concluded that this feature could be homologous with the one present in *Pholeomyia*. However, our cladogram indicates that this character state probably evolved independently in these genera, and therefore did not have a single origin to be considered homologous. In *Eusiphona*, it is most parsimonious to adopt a scenario where the absence of anepisternal setae is the plesiomorphic condition and the presence of four setae evolved only in some species, such as *Eusiphona vittata* and *Eusiphona cooperi*. Within *Pholeomyia*, the reduction to three setae occurred independently in some species, as *Pholeomyia indecora*, *Pholeomyia* sp. 9, *Pholeomyia* sp. 25, *Pholeomyia* sp. 11 and *Pholeomyia vockerothi*.

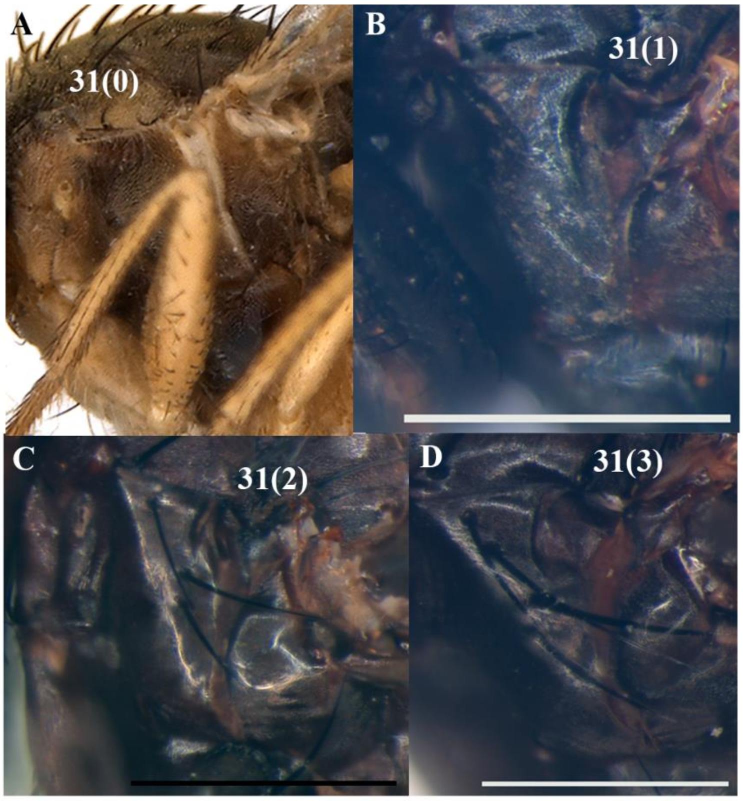


Figure 22. Character 31 (anepisternum). **A.** *Apotropina* sp. 1, photo by Paula Riccardi. **B.** *Milichiella circullaris.* **C.** *Pholeomyia indecora*. **D.** *Phoelomyia* sp. 19. Scale bar, 0.5 mm.

32. Number of postsutural dorsocentral seta: (0) three; (1) two; (2) one. L = 8, CI = 25, RI = 25.

The presence of two postsutural dorsocentral seta was obtained as a synapomorphy for Madizinae + Milichiinae. A few *Pholeomyia* species secondarily evolved three postsutural dorsocentral seta, as *Pholeomyia longiseta*, *Pholeomyia expansa* and *Pholeomyia vockerothi*.

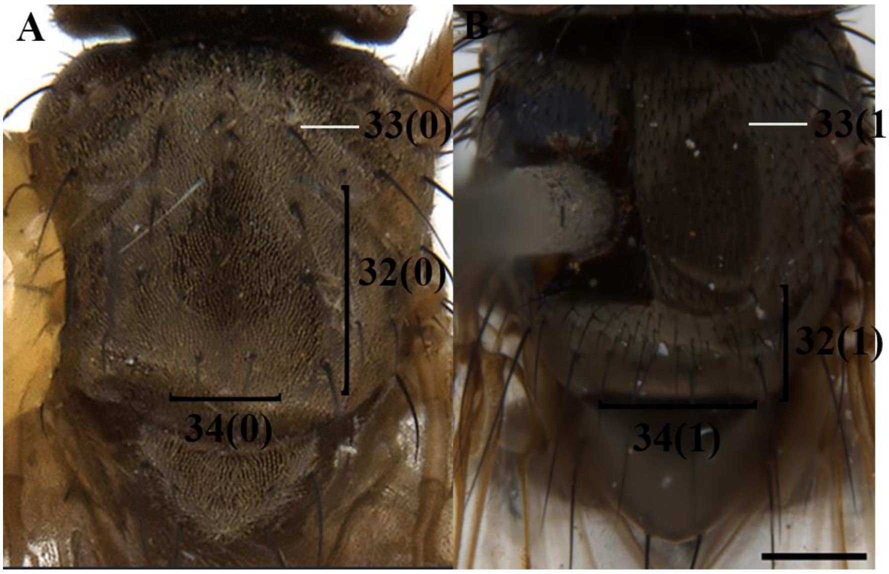


Figure 23. Characters 32 (number of postsutural dorsocentral seta), 33 (presutural dorsocentral seta) and 33 (number of prescutellar seta). **A.** *Apotropina* sp. 1, photo by Paula Riccardi. **B.** *Pholeomyia* sp. 28. Scale bar, 0.5 mm.

33. Presutural dorsocentral seta: (0) present; (1) absent. L = 7, CI = 28, RI = 44 (see figure 23).

The absence of the presutural seta is the plesiomorphic condition in Milichiinae. In *Milichiella* and *Pholeomyia*, a few species have this seta and this condition supports two small *Pholeomyia* clades: nodes 18 and 64.

34. Number of prescutellar seta: (0) one; (1) two; (2) absent. L = 15, CI = 13, RI = 53 (see figure 23).

The presence of two pairs is a homoplasy for the node 9, which includes *Milichia*, *Milichiella* and *Pholeomyia*. Within Milichiinae, this condition also evolved in *Eusiphona*. Multiple reversions to the presence of only one pair of prescutellar seta have taken place across *Pholeomyia* and are homoplastic synapomorphies for some clades, as nodes 18, 21, 47 and 53.

35. Length of prescutellar seta: (0) less than 0.8x of the last dorsocentral length; (1) about as long as the last dorsocentral length. (2) longer than the last dorsocentral length. L = 23, CI = 8, RI = 38.

36. Shape of wing (modified from Brake, 2000): (0) oval; (1) triangular. L = 1, CI = 100, RI = 100 (see figure 25).

The triangular wing is a synapomorphic condition for Milichiinae.

37. Color of wing: (0) brownish; (1) hyaline. L = 12, CI = 8, RI = 35.

Few species evolved secondarily a brownish wing within *Phoelomyia*, which was recovered as homoplastic synapomorphies for some small clades within the genus.

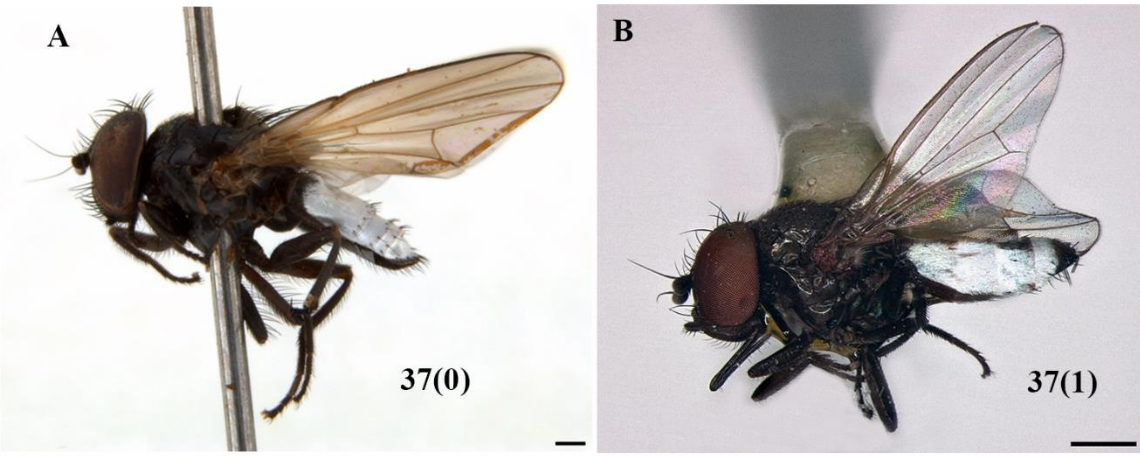


Figure 24. Character 37 (color of wing). **A.** *Pholeomyia* sp. 28. **B.** *Pholeomyia* sp. 6. Scale bar, 0.5 mm.

38. Subcostal break (modified from Brake, 2000): (0) normal, not developed into a notch; (1) developed into a notch; (2) developed into a deep notch. L = 7, CI = 28, RI = 58 (see figure 25).

Our analysis showed that the subcostal break developed into a notch in the node including *Milichia*, *Milichiella* and *Pholeomyia*. This notch can be quite deep in some *Pholeomyia* and *Milichia* species (Brake, 2009), as *Pholeomyia* sp. 25, *Pholeomyia* sp. 32, *Pholeomyia myopa*, *Pholeomyia vockerothi* and node 17. In *Eusiphona*, the costal notch is secondarily developed in some species, as *Eusiphona vittata*.

39. R_{4+5} and M_l (modified from Brake, 2000): (0) parallel; (1) convergent. L = 2, CI = 50, RI = 88.

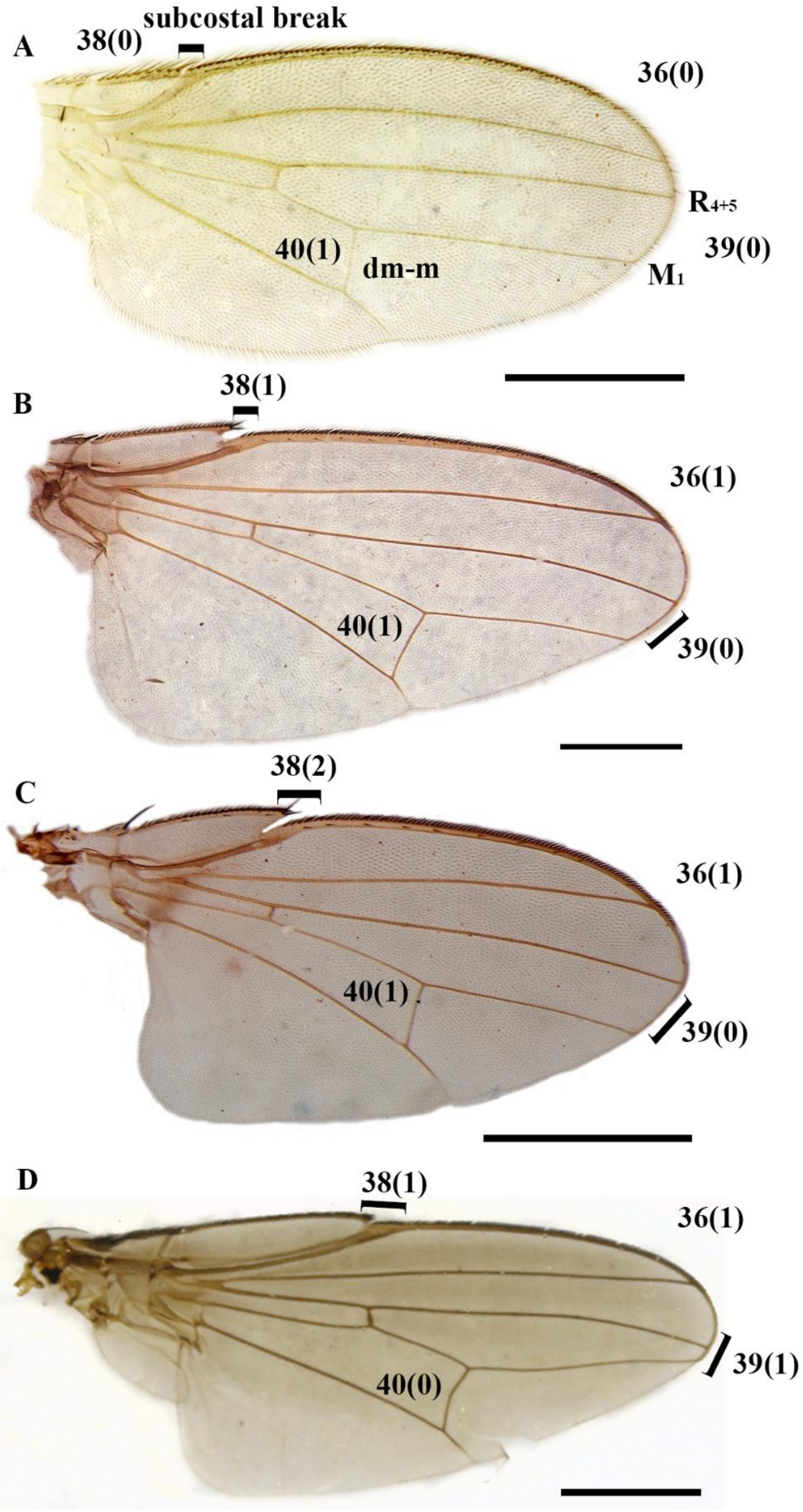


Figure 25. Characters 36 (shape of wing), 38 (subcostal break), 39 (R_{4+5} and M_1) and 40 (dm-m). **A.** *Costalima myrmicola*. **B.** *Pholeomyia* sp. 17. **C.** *Pholeomyia* sp. 25. **D.** *Eusiphona vittata*. Scale bar, 0.5 mm.

We got the same results as Brake (2000) for this character. The R_{4+5} and M_1 strongly converging at tip is a synapomorphy for Milichiinae. The parallel condition evolved secondarily in (*Milichia speciosa* + *Pholeomyia*).

40. dm-m: (0) curved; (1) straight. L = 12, CI = 8, RI = 57 (see figure 25).

The straight condition is a homoplastic synapomorphy for (*Milichia speciosa* + *Pholeomyia*). Within *Pholeomyia*, multiple reversions to the curved state probably occurred, as in *Pholeomyia indecora*, node 30, *Pholeomyia sororcula*, *Pholeomyia aequatorialis*, *Pholeomyia* sp. 6, node 47, node 54, *Pholeomyia* sp. 13, *Pholeomyia argyrophenga* and node 71.

41. Distal margin of anal cell (CuA_2) (modified from Brake, 2000): (0) rounded; (1) CuA_2 meets anal vein in an acute angle. L = 1, CI = 100, RI = 100.

The character state (1) is a synapomorphy for Milichiinae.

42. Color of calypter margin: (0) white to light brown; (1) dark brown or black. L = 17, CI = 5, RI = 44.

The dark brown condition is a homoplastic synapomorphy for (*Milichia speciosa* + *Pholeomyia*). Within *Pholeomyia*, multiple reversions to the white or light brown state occurred. Although considerably plastic, the retention index demonstrates it brings some structure to the tree, and supports some big clades within *Pholeomyia*, as node 24.

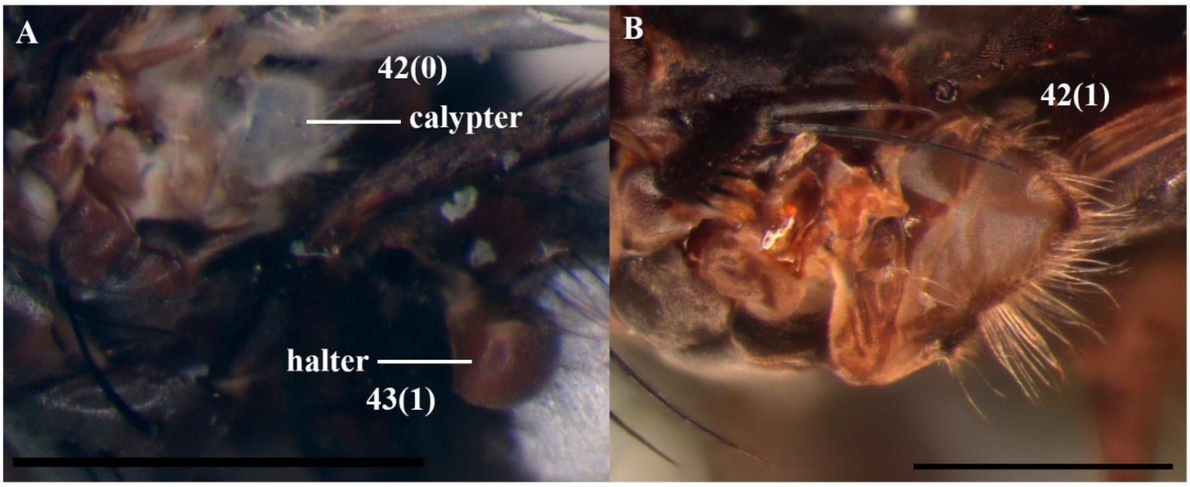


Figure 26. Characters 42 (color of calypter margin) and 43 (color of halter). **A.** *Pholeomyia* sp. 24. **B.** *Pholeomyia* sp. 17. Scale bar, 0.5 mm.

43. Color of halter: (0) light brown, yellow; (1) black. L = 3, CI = 33, RI = 0 (see figure 26).

Most milichiids have a black halter, which explains the low retention index. We use this character as an effort to understand the position of *Pholeomyia longiseta* within *Pholeomyia,* one of the most conspicuous species with the genus. The character state (0) is a homoplastic apomorphy for this species, occurring also in *Costalima* and *Apotropina*.

Abdomen

44. T1 with abdominal triangle (modified from Brake, 2009): (0) absent; (1) present. L = 2, CI = 50, RI = 75.

The presence of a medial projection of T1 was recovered as a synapomorphy for *Milichiella*.

45. Tergites bent at the sides (modified from Brake, 2000): (0) absent; (1) present. L = 1, CI = 100, RI = 100.

In *Eusiphona*, *Milichia*, *Milichiella* and *Pholeomyia*, the lateral margins of the tergites of the males are strongly bent under the abdomen. It was not possible to verify if this condition occurs in *Enigmilichia*.

46. T3+T4 lateral crease (modified from Brake, 2009): (0) absent; (1) present. L = 9, CI = 11, RI = 33.

In some *Milichiella*, *Pholeomyia*, and *Milichia* species there is even a crease in the tergites at the site of the bend. In this case, the dorsal side of the abdomen is flat, so that the silvery surface reflects light optimally (Brake, 2000).

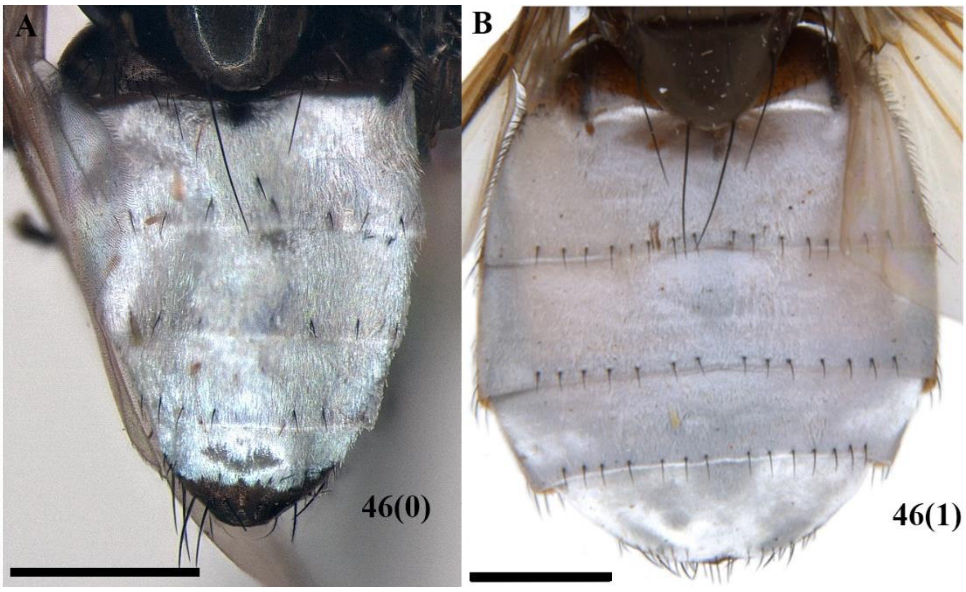


Figure 27. Character 46 (T3+T4 lateral crease). **A.** *Pholeomyia* sp. 21. **B.** *Pholeomyia* sp. 27. Scale bar, 0.5 mm.

47. Length of T2: (0) as long as T3; (1) double of T3. L = 17, CI = 5, RI = 42.

The T2 twice the size of T3 is a homoplastic synapomorphy for Milichiinae. Within *Pholeomyia*, multiple reversions occurred and some of them are probably homoplastic synapomorphies for the nodes.

48. Length of T3: (0) as long as T4; (1) double of T4. L = 13, CI = 15, RI = 21.

49. Color of T2-T5 (modified from Brake, 2000): (0) not silvery microtomentose; (1) completely or partly silvery microtomentose. L = 7, CI = 14, RI = 60.

In males of most species of *Milichia*, *Milichiella* and *Pholeomyia*, T2-5 are partly or completely silvery microtomentose. Within these genera, multiple reversions occurred. The light-reflecting abdomen could be an adaptation for swarming behavior, so that males swarming in sunlight can be seen from a long distance (Brake, 2000).

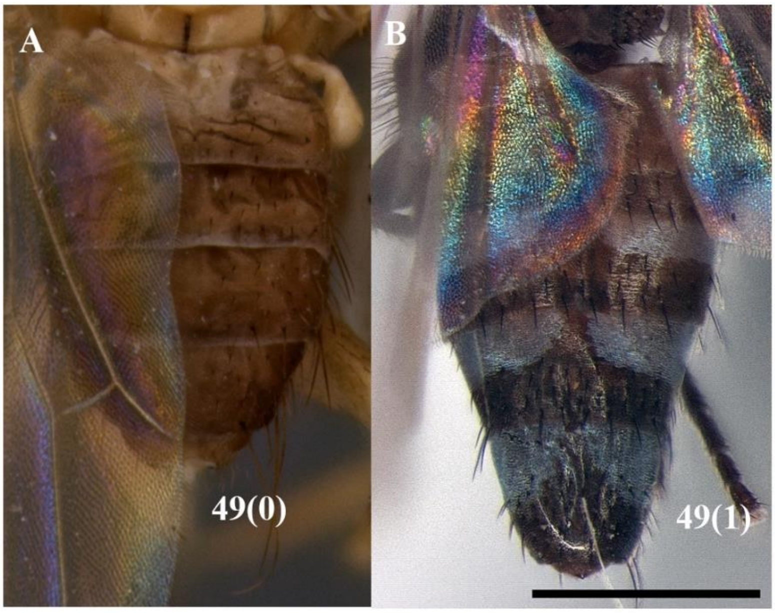


Figure 28. Character 49 (color of T2-T5). **A.** *Costalima myrmicola*. **B.** *Pholeomyia quadrifasciata*. Scale bar, 0.5 mm.

50. Color of T2 (modified from Brake, 2009): (0) brown microtomentose; (1) partly silvery microtomentose; (2) completely silvery microtomentose. L = 9, CI = 22, RI = 53.

The characters 49, 51 and 53 are applicable only for species codified with state 1 of the character 48. The decision of codifying the tergites separately was an effort to minimize the number of states, since there are different combinations of patterns between the tergites. Brake (2009) also used the color of T2 as a character. However, she coded each variation in T2 in detail. After analyzing a large number of *Pholeomyia* specimens, we decided that it would be better to construct more embracing states for this character, since some patterns may correspond to intraspecific variations. In Milichiinae, the plesiomorphic condition is a completely silvery microtomentose T2.

51. Chaetotaxy of T2: (0) densely setulose; (1) scattered setulae; (2) one row of setae along posterior margin. L = 10, CI = 30, RI = 85.

52. Color of T3-T4 (modified from Brake, 2009): (0) brown microtomentose; (1) partly silvery microtomentose; (2) completely silvery microtomentose. L = 7, CI = 28, RI = 66.

53. Chaetotaxy of T3-T4: (0) densely setulose; (1) scattered setulae; (2) one row of setae along posterior margin. L = 8, CI = 37, RI = 87.

54. Color of T5: (0) brown microtomentose; (1) partly silvery microtomentose; (2) completely silvery microtomentose. L = 17, CI = 11, RI = 42.

55. Chaetotaxy of T5: (0) densely setulose; (1) setulae along posterior margin; (2) setulae absent. L = 15, CI = 13, RI = 69.

56. Shape of T5: (0) densely setulose; (1) scattered setulae; (2) one row of setae along posterior margin. L = 23, CI = 8, RI = 46.

57. Width of S4 (modified from Brake, 2000): (0) wider than high; (1) higher than wide. L = 2, CI = 50, RI = 75.

58. Shape of S5 (modified from Brake, 2009): (0) rectangular, wider than high; (1) rectangular, higher than wide; (2) roughly sickle moon shaped; (3) rectangular shape, widest in middle; (4) roundish shape, widest in middle; (5) rectangular, with a lobe projection in the middle; (6) rectangular, with two sclerotized lobes. L = 29, CI = 20, RI = 66.

S5 is considerably sclerotized in *Milichia*, *Milichiella* and *Pholeomyia* species with silvery abdominal tergites. In this way, the male genitalia are protected by a strong chitinous ring, probably an adaptation to the swarming behavior in sunlight (Brake, 2000). The shape of S5 is very variable between species and a good character for identification at a specific level.

59. Shape of S4: (0) rectangular, wider than high; (1) rectangular, higher than wide; (2) rectangular shape, widest in middle; (3) bifurcated; (4) rectangular, very thin; (5) square. L = 20, CI = 25, RI = 48.

60. Chaetotaxy of S4: (0) scarce to medium setulose, scattered setulae; (1) scarce setulose, with two rows of scattered setulae; (2) medium setulose, with two rows with setulae; (3) medium setulose with dense row of setulae along posterior margin; (4) strongly setulose with short setae; (5) strongly setulose, with tuft of longer setae posterolaterally. L = 16, CI = 31, RI = 78.

61. Shape of surstylus: (0) rounded, thin and with narrow tip; (1) spoon-shaped; (2) rectangular and large; (3) rounded, large and with narrow tip; (4) notched. L = 22, CI = 22, RI = 52.

62. Indentation on surstyli: (0) absent; (1) present. L = 1, CI = 100, RI = 100.

The presence of indentation on surstyli is a synapomorphy for (*Enigmilichia* + *Eusiphona*).

63. Pregonite: (0) short; (1) long. L = 12, CI = 8, RI = 47.

64. Hypandrial arms: (0) short; (1) long. L = 3, CI = 33, RI = 33.

A long condition is present in most *Pholeomyia* species.

65. Phallapodemic sclerite: (0) convex, covering the phallapodeme; (1) concave, V-shape; (2) concave, U-shape. L = 15, CI = 20, RI = 53.

66. Shape of basiphallus: (0) ring shape; (1) two short parallel sclerites; (2) two long parallel sclerites; (3) dome shape. L = 39, CI = 10, RI = 43.

67. Phallapodeme: (0) straight; (1) with apical dilatation; (2) bifurcated at tip. L = 12, CI = 25, RI = 30.

5. DISCUSSION

The discussion below addresses four aspects of the phylogenetic hypothesis: (i) relationships within Milichiinae; (ii) monophyly of *Pholeomyia*, and the question of *Pseudomilichia*; (iii) relationships within *Pholeomyia*; and (iv) the opportunities of study with the small sparking flies.

5.1. Relationships within Milichiinae

The main focus of the analysis are the relationships between the species of *Pholeomyia*. Hence, the sampling effort to clarify the relationships between the genera of Milichiinae was less extensive than characters for interspecific relationships. Still, there is interesting signal coming out from the tree.

A monophyletic Milichiinae was recovered in the analysis. Brake (2000) had already demonstrated the monophyly of this group. The clade is supported by several synapomorphies, such as: enlarged eyes [character 7(1)], a narrow frons in males [character 8(1)], a narrow gena [character 18(1)], the vibrissa above the lower margin of the eye [character 19(1)], R_{4+5} and M_1 converging at tip [character 39(1)], distal margin of anal cell meeting anal vein in a sharp angle [character 31(1)], a triangular shape of the wing [character 36(1)], and tergites 2-5 bent laterally [character 45(1)]. Four homoplastic conditions also support the milichiines: absence of a notch or emargination on posterior margin of the eye [character 9(1)], a rounded lunule [character 16(1)], T2 twice the size of T3 [character 47(1)], and rectangular T5 [character 56(1)]. These four homoplastic features are somewhat plastic and multiple reversions have taken place across the subfamily.

Within the Milichiinae, our results have a better resolution for the phylogenetic relationships between genera than Brake (2000) obtained in her analysis (Figure 3). The first point is the clade (*Enigmilichia* + *Eusiphona*), recovered here as the sister group of the node with *Milichia*, *Milichiella* and *Pholeomyia* species. In Brake (2000), *Enigmilichia* was sister to the remainder of the subfamily.

The clade (*Enigmilichia* + *Eusiphona*) is supported by two homoplasies (absence of the lunule seta [character 13(0)] and dm-m straight [character 40(1)]), and one synapomorphy (presence of an indentation on the surstyli [character 62(1)]). A more detailed study of the male terminalia of *Enigmilichia* (which we did not have access for dissection) might result in more characters supporting this relationship. This result confirms Brake's (2000) hypothesis that the anepisternal setae present in all *Pholeomyia* and in some species of *Eusiphona* is not homologous (see discussion for character 31). Thus, the discussion raised by Sabrosky (1955) and Swann (2010) indicating a close relationship between *Eusiphona* and *Pholeomyia* do not find much support in our data. *Enigmilichia* is an Afrotopical genus, while *Eusiphona* is known for the Nearctic and Neotropical regions.

The node including *Milichia*, *Milichiella* and *Pholeomyia* species is supported by three homoplastic characters: subcostal break developed into a notch [character 38(1)], tergites 2-5 completely or partly silvery microtomentose [character 49(1)], and S4 scarce setulose, with two rows of scattered setulae [character 60(1)]. In Brake's (2000) tree for the subfamily these three genera come out in a polytomy. Indeed, the use of three species of *Milichia* rendered a hypothesis that the genus is not monophyletic. *Milichia myrmecophila* is sister of the node with *Milichiella* and *Pholeomyia*; *Milichia* sp. 1 fits the generic delimitation of the genus, but phylogenetically came out within *Milichiella*; and *Milichia speciosa* is sister of *Pholeomyia*. This should not be a surprise. As the genotype of the family, *Milichia* is still a genus comprising species showing great morphological variation. It has been traditionally characterized only by plesiomorphic characters, i.e., the absence of the conditions seen in *Milichiella* and *Pholeomyia* as a posterior eye margin entire (in contrast to *Milichiella*) and anepistemum bare (in contrast to *Pholeomyia*) (Brake, 2000). A careful taxonomic revision of the genus is necessary to bring order to this grade, showing how the groups of species in the genus are related to these other two milichiine genera.

The clade including *Milichiella*, *Milichia* sp.1, *Milichia speciosa* and *Pholeomyia* is supported by one synapomorphy and one homoplasy: the elevated lunule [character 15(1)] and the presence of two prescutellar seta [character 34(1)], respectively. The arched lunule might not be a synapomorphic condition for the node, as discussed in the character 15. *Milichiella* is supported by the presence of a broad notch [character 11(4)], the T1 with an abdominal triangle [character 44(1)], spoon shaped surstyli, about as long as epandrium high [character 61(1)], and dome shaped phallus [character 66(3)]. The features recovered for *Milichiella* in this study is different from the ones obtained by Brake (2009) because of our lower taxonomic sample compared to the number of species used in her analysis. The presence of *Milichia* sp.1 within *Milichiella* might corroborate the plasticity of the posterior eye margin in the subfamily (see discussion for character 11).

Brake (2000) and Brake (2009) also recovered *Milichia speciosa* as the sister group of all *Pholeomyia*. In our cladogram, this relationship is supported by the presence of three fronto orbital setae [character 4(2)], the parallel R_{4+5} and M_1 [character 39(0)], the dark brown calypter margin [character 42(1)], and the straight dm-m [character 40(1)]. The last three conditions originate more than once in the tree. Characters 41 and 43 probably reverted to condition 0 several times along the evolution of *Pholeomyia*. In Brake's (2000) study, she obtained two homoplastic conditions for this clade: the absence of the proclinate setulae between supra-antennal seta and eye margin, and the parallel R_{4+5} and M_1. In our analysis, the first feature was lost in the node including *Milichia*, *Milichiella* and *Pholeomyia*.

5.2. Monophyly of *Pholeomyia*, and the question of *Pseudomilichia*

In our analysis, *Pholeomyia* was recovered as monophyletic and the clade is supported by five characters with homoplastic evolution within the family: inner vertical seta twice the size of the outer vertical seta [character 1(1)], a pubescent arista [character 23(0)], the presence of two postpronotal setae [character 30(1)], the presence of four anepisternal setae [character 31(3)], and S4 with two rows of scattered setulae [character 60(2)]. Brake (2000) obtained two synapomorphies (presence of three frontal setae, and three or four anepisternal setae), and one homoplasy (more than one postpronotal seta) for *Pholeomyia* in her analysis.

For an unknown reason, Brake (2000) codified the number of frontal seta (our character 4) as zero in *Milichia speciosa*. Studying photographs of the lectotype, we observed the presence of three frontal seta. This excludes the scenario where this condition is a unique feature in *Pholeomyia*. At the same time, it raises questions about the placement of this species. Should *Milichia speciosa* be considered a *Pholeomyia*? *Milichia speciosa* indeed shares several features with the species of *Pholeomyia*. Actually, if we ignore the absence of anepisternal setae in the species, it would be easy to fit *Milichia speciosa* among the *Pholeomyia* species. The presence of anepisternal setae is a condition present in all known *Pholeomyia*, so including *M. speciosa* in *Pholeomyia* would demand an important, apparently undesirable modification of the diagnosis of the genus. We do not forward any taxonomic change here. We presently considered that *M. speciosa* should be outlimits of *Pholeomyia* and any generic status to this species needs to be given within the frame of a phylogenetic study of *Milichia*.

To address the question of the synonymy of *Pseudomilichia* with *Pholeomyia*, we had to include in our sampling species that have been ascribed to *Pseudomilichia*. We did not have access the types or other specimens of *Pholeomyia implicata* (Becker, 1907) and *Pholeomyia schnusei* (Becker, 1907). We could include, nevertheless, two morphospecies that share the diagnostic features of *Pseudomilichia* (*Pholeomyia* sp. 16 and *Pholeomyia* sp. 25), so for the first time we can address this discussion from a phylogenetic perspective. Our results corroborate the synonymy proposed by Hendel (1932) and Brake (2000), since both these species came out as subclades of *Pholeomyia*. This confirms the observations from Hendel (1932) and Brake (2000) that the shape of the posterior margin of the eye is plastic and does not establish a sister-group relationship between *Pseudomilichia* or between *Pseudomilichia* and a higher clade. In our tree, these two species did not compose a clade, but a small grade at the base of one of the large groups of species of *Pholeomyia*. A larger sampling of species that have been included in *Pseudomilichia* in the analysis would bring further clarification on the evolution of the shape of the eye margin and on the nature of this group of species. We did not find any additional feature that could provide support for *Pseudomilichia* as a separate genus. We therefore accept here *Pseudomilichia* as a junior synonymous of *Pholeomyia*.

5.3. Relationships within *Pholeomyia*

In cladograms, clades correspond to particular hypotheses of relationships, meaning that the strength of a hypothesis does not necessarily merit other parts of the phylogeny. Terminals with too much missing data, particular characters with high plasticity (especially if the overall total number of nested characters is not high), and taxonomic under sampling use to influence global results of a data matrix. The use of implicit weighting is able to reduce the influence of incongruent (or highly plastic) characters over nested characters in the analysis.

The fact that we have about 70% of the described species of the genus included in the analysis suggest that under sampling is not an issue in our study. Our data matrix, however, has several terminals that could not have the male abdomen dissected and appear in the matrix with 5 to 20 characters missing information for the abdomen. This may account for the low support of some of the nodes along the backbone and for some of the clades to group of morphologically rather distinct species. This means that some of the species gathered in smaller clades in our tree may be analytical artifacts and that the species composition of these clades and their relationships are subject to revision.

Four main clades can be recognized in our tree. One of them includes *Pholeomyia indecora*, *P. longiseta* and *Pholeomyia* sp. 22; a second higher level clade has only one species, *Pholeomyia* sp. 17; a third clade include *P. quadrifasciata* and other described and undescribed species; the fourth, large clade includes, e.g., *P. aequatorialis*, *P. myopa* and a number of other described and undescribed species.

The first of these clades, which appears as sister of the remainder of the genus, seems pretty well supported. Its position in the phylogeny of the genus seems reliable, since it is plesiomorphic for features of the backbone that gather the other three larger clades, the characters supporting each of these clades etc. The position of *Pholeomyia* sp. 17 is subject to review, but it is quite distinctive from the other clades. The node gathering the two larger clades of *Pholeomyia* has reasonable support, with four features that have parallel evolution in the tree. Anyway, these features seem to define the bulk of the diversification of the genus.

Each of the two larger clades, however, have low support. This means that the composition of the clade may change (i.e., some of the species now present in these clades may shift out of the clade) and the internal backbone of these two clades still has low support, meaning possible change of the relationships within these clades. These general issues, however, do not disqualify the underlying hypothesis that two large groups of species of *Pholeomyia* with that basic composition assemble as separated clades within the evolution of the genus.

The group including *Pholeomyia quadrifasciata* also includes the species that fit into the diagnosis of *Pseudomilichia*, showing that they are deeply nested in the cladogram of *Pholeomyia*. Some of the smaller nodes in this clade seem reliable. The other group has a sequence of species or small clades branching before the separation between two still large subclades. This is the most species-rich, relatively more recent clade of *Pholeomyia*, and seems to correspond to the bulk of the diversification of the genus.

5.4. Small sparking flies: hidden gems waiting to be studied

The only published taxonomic review of *Pholeomyia* is Sabrosky's (1959) study, with a partial sampling of the species known at that time. No additional *Pholeomyia* species have been described along the last 60 years. It should also be considered that large areas in South America were never sampled for the family diversity. The lack of detailed descriptions, illustrations, keys and other taxonomic tools to properly identify milichiid species and make easier the recognition of undescribed species is a problem for the development of the knowledge of the family.

Despite not having a formal taxonomic revision of the genus, this study raises some relevant advances in the taxonomy of *Pholeomyia*. Several species used here as terminals were collected in areas very poorly explored. Only five species of *Pholeomyia* have been described so far for Brazil, while this study recognizes 15 additional undescribed species for the country.

This taxonomic gap, of course, is not unique to *Pholeomyia* in the Milichiidae. Brake (2009) demonstrated that what we know of Milichiinae diversity is only the tip of the iceberg. In her taxonomic review of *Milichiella*, Brake (2009) described 69 new species from different parts of the world. There are no described species of Neotropical *Milichia*, but in our sorting of milichiids in Malaise trap samples from Brazil we found several species of the genus.

With the improvement in our knowledge of Milichiidae phylogeny along the last two decades, now some patterns can be grasped. It is well known that several milichiines interact with ants either as adults or as larvae. One of the most interesting interactions occurs with myrmecophilous species of the genus *Milichiella* Giglio-Tos. These flies feed on food regurgitated by ants of the genus *Crematogaster* Lund. The antennae of these species of flies have morphological modifications capable of immobilizing the ants and, after immobilization, the flies insert the proboscis into the oral apparatus of the ants, forcing regurgitation (Wild & Brake, 2009).

Aerial swarms are also a conspicuous behavior in many milichiine species. We have observed swarms of at least three *Pholeomyia* species in the Amazon rainforest and in urbanized areas in southeastern Brazil. Part of morphology patterns of these species seems to be linked to sexual selection, raising several evolutionary questions on biology and behavior. The silvery setation on the abdomen of males appears in our analysis as shared by the species of the clade gathering *Milichia*, *Milichiella* and *Pholeomyia*. Not all species of these genera, however, have this feature. This points to a complex evolution system of the morphology, not a single-step process of acquisition of the silvery reflex by males. When information on swarming, mating behavior and morphology become available, it will be easier to understand how this evolved along the second half of the Cenozoic.

6. CONCLUSIONS

This study adressed the systematics of *Pholeomyia*, one of the most distinctive jackal fly genera, with a phylogenetic hypothesis for the genus. The taxonomic sampling of analysis was considerably extensive, allowing to further discuss the monophyly of *Pholeomyia*, the relationships within the genus, and the relationships between milichiine species.

Our results corroborate the hypothesis of a monophyletic *Pholeomyia* including the species assigned to *Pseudomilichia*. The sampling of the genus *Milichia* also reinforces the idea that this genus is paraphyletic in relation to *Milichiella* and to *Pholeomyia*. Our analysis increased the resolution of the relationships within Milichiinae. This study also highlights the gap in the knowledge of *Pholeomyia* diversity, with up to 30 potentially undescribed species that would add to the 28 described Neotropical species. The phylogeny obtained with 57 species of the genus show four main clades, which position and species composition may find some level of adjustment with the addition of male abdomen information in the data matrix for 12 of the species included as terminals in the analysis.

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Table A1. Taxon sampling for the morphological analysis with label information.

Taxon	Information
Costalima myrmicola Sabrosky, 1953	1♂ BRASIL, Nova Iguaçu, Tinguá, REBIO Tinguá, 13.ix.2016, LLD JL Nessimian JFB, Pensilvania (TIN 03) (MNRJ).
Phyllomyza sp.1	1♂ BRASIL, AM, Manaus, ZF2, km-14, 2°35'21"S-60°06'65"W, 11-15.ix.2016, Malaise grande, 34m na torre, J.A. Rafael & F.F. Xavier (INPA)
Madiza glabra Fallén, 1810	1♂ Morroco, Marrakech, Imlil S'Asni, C.F. Kassebeer coll., 26.iv.1994 (LACM)
Enigmilichia dimorphica Deeming, 1981	♂, photos and illustrations (Brake, 2000), original description
Eusiphona mira Coquillett, 1897	1♂, Moscow, Idaho, July 28.1925, C.L. Fox Collector (ESSIG)
Eusiphona vittata Sabrosky, 1982	1♂ BRASIL: Goiás, Mineiro, Malaise 2, Parcela 4CSS, -52.9890689174 -17.9124731055, 12.viii.2018-09.ix.2018, Oliveira & Lopes (MZUSP)
Milichia myrmecophila de Meijeri, 1909	♂ holotype, photos and illustrations by Irina Brake
Milichia speciosa Meigen, 1830	♂ holotype, photos and illustrations by Irina Brake
Milichia sp.1	1♂, Mex: Baja Cal Sur, 2mi N Todos Santos, 23.46869 110.23993, 10.X.2016, P. Rude (ESSIG)
Milichiella cavernae Brake, 2009	♂ holotype, photos and illustrations by Irina Brake
Milichiella circularis Aldrich, 1981	1♂, HAWAII, Oahu, Honolulu, 20 Jun – 5 Jul 84, G.E. Bohart (LACM)
Milichiella faviformis Brake, 2009	♂ holotype, photos and illustrations by Irina Brake
Milichiella sumptuosa de Meijeri, 1911	♂ holotype, photos and illustrations by Irina Brake
Milichiella sp.1	1♂, Capanema, Pará, Brasil, H.S. Lopes, 12-7-65 (MZUSP)
Pholeomyia aequatorialis Seguy, 1934	1♂, BRAZIL, Rondonia, 62km SE Ariquemes, 22-31 Oct 1997, W.J. Hanson (LACM)
Pholeomyia anomala Hendel, 1933	1♂, BOLIVIA: Santa Cruz, Santa Cruz, IX-28-72, G.E. Bohart (LACM)
Pholeomyia anthracina (Becker, 1907)	1♀, Brasil: Amazonas, 30 km W Itaquatiara, Rio Urubu, 13.I.1981, Ekis & Davidson (INPA) / ♀ holotype, photos by Zoltán Soltész
Pholeomyia argyrata Hendel, 1932	♂, holotype, photos by Daniel Whitmore (SMNS)
Pholeomyia argyrophenga (Schiner, 1868)	♂, holotype, photos by Irina Brake (NMW)
Pholeomyia comans Sabrosky, 1959	♂, holotype, photos by Irina Brake (USNM)
Pholeomyia dampfi Sabrosky, 1959	1♂, MEX: Oaxaca, 5km NE Valle Nacional, VII-22-90, J. Doyen, ex.bat cave (ESSIG) / ♂, holotype, photos by Irina Brake (USNM)
Pholeomyia decorior Steyskal, 1943	♂, holotype, photo by Irina Brake (USNM)
Pholeomyia dispar (Becker, 1907)	1♂, Orlando, Fla., Mar 1944, R & G. Bohart (CAS)
Pholeomyia expansa Aldrich, 1925	♂, lectotype, photos by Heloísa Flores (CAS)
Pholeomyia hurdi Sabrosky, 1959	1♂, Óbidos, PA, 11.i.1958, E.P.A. (MZUSP) / ♂, holotype, photos by Rachel Diaz-Bastin (CAS)
Pholeomyia indecora (Loew, 1869)	1♂, Scotia Barrens, Centre Co., Pa. 19 July 1973, D. Dee Wilder (CAS) / ♀, holotype, photos by MCZ
Pholeomyia latifrons Sabrosky, 1959	♂, holotype, photos by Irina Brake (USNM)
Pholeomyia leucogastra (Loew, 1861)	1♂, Havana, Cuba, Becker (LACM) / ♂, holotype, photos by MCZ
Pholeomyia leucozoma Bilimek, 1867	1♂, COSTA RICA, S.J., Escazu, 8 Feb 1987, G.E. Bohart (LACM)
Pholeomyia longiseta (Becker, 1907)	♀, holotype, photos by Zoltán Soltész (HNHM)
Pholeomyia myopa Melander, 1913	1♂, MEXICO: Sonora: Alamos, 5-I-1971, P.H. & M. Arnaud collectors (CAS)

Pholeomyia nigricosta (Hendel, 1932)	♀, holotype, photos by Daniel Whitmore (SMNS)
Pholeomyia nitidula Sabrosky, 1959	1♂, Atascosa Mt., Sta. Cruz Co. Ari., viii-16-50, R.S. Beal Collector (ESSIG)
Pholeomyia palparis (Becker, 1907)	♀, holotype, photos by Zoltán Soltész (HNHM)
Pholeomyia pectoralis Hendel, 1932	♂, holotype, photos by Daniel Whitmore (SMNS)
Pholeomyia praeocellaris Hendel, 1932	1♂, BOLIVIA: Santa Cruz, Santa Cruz, IX-28-72, G.E. Bohart / ♂, lectotype, photos by Daniel Whitmore (SMNS)
Pholeomyia praesecta (Becker, 1907)	1♂, PERU: Monson Valley, Tingo Maria, XI-29-1954, E.I. Schlinger & E.S.Ross collectors (CAS)
Pholeomyia quadrifasciata Hendel, 1932	1♂, ARG: Catamarca, Andalgala, XI-4-72, G.E. Bohart (LACM) / ♂, holotype, photos by Daniel Whitmore (SMNS)
Pholeomyia schineri (Hendel, 1932)	1♂, Salvador-Bahia, Brasil, 20-XI-85, H.S. Lopes (MZUSP)
Pholeomyia sororcula (Becker, 1907)	1♂, BOLIVIA, Prov. La Paz, Mapiri, 680m, 11.IV.2004, 15°18'48"S, 68°13'27"W, leg. S.D. Gaimari, ex. swarm (CDFA)
Pholeomyia vockerothi Sabrosky, 1961	♂, holotype, photos by Jeff Skevington (CNC)
Pholeomyia sp.1	1♂, PARAGUAY: San Pedro, Cororo-Rio Ypane, XII-5/9-1983, Malaise Trap, M. Wasbauer coll. (CDFA)
Pholeomyia sp.2	1♂, HONDURAS: 30km. SE Siguatepeque, VIII-11-12-1978, J.A. Chemsak, E.G. & J.M.Linsley (ESSIG)
Pholeomyia sp.3	1♂, BOLIVIA, Prov. La Paz Cumbre Alto Beni, vicinity of Caranavi, 1685m, 19.IV.2004, 15°40'19"S, 67°29'35"W leg S.D. Gaimari (CDFA)
Pholeomyia sp.4	1♂, PERU: Madre de Dios, Rio Tambopata Reserve, 30 air km SW of Puerto Maldonado, 290m, November 1-26.1982, Edward S. Ross (CAS)
Pholeomyia sp.5	1♂, ECUADOR: Napo Prov. Huahua Sumaco km 45 on Hollin Loreto rd XII-18-1989, malaise trap, M&J. Wasbauer, H. Real (CDFA)
Pholeomyia sp.6	1♂, El Salvador: Quezaltepeque, 500 meters, VI-19-1963, D.Q. Cavagnaro & M.E.Irwin Collectors (CAS)
Pholeomyia sp.7	1♂, ECUADOR Pich. E. Sto. Domingo 8-14 May 1988 Hanson & Bohart (LACM)
Pholeomyia sp.8	1♂, Costa Rica: Heredia 3km S. Puerto Viejo, III-14-78, P.A. Opler Collec. (ESSIG)
Pholeomyia sp.9	1♂, COSTA RICA S.J. Escazu, 21-27 Mar 1988 F. D. Parker (LACM)
Pholeomyia sp.10	1♂, BOLIVIA, Prov. La Paz Cumbre Alto Beni, vicinity of Caranavi, 1685m, 19.IV.2004, 15°40'19"S, 67°29'35"W leg S.D. Gaimari (CDFA)
Pholeomyia sp.11	1♂, Paquetã – GO Brasil, 7.II.68, H.S. Lopes (MZUSP)
Pholeomyia sp.12	1♂, Juruti, PA, Brasil, IX.1969, Exp. Perm. Amz. (MZUSP)
Pholeomyia sp.13	1♂, Brasilien, Nova Teutonia, 27°11'B. 52°23'L, Fritz Plaumann, VI.1970, 300-500m (MZUSP)
Pholeomyia sp.14	1♂, Brasilien, Nova Teutonia, 27°11'B. 52°23'L, Fritz Plaumann, VII.1970, 300-500m (MZUSP)
Pholeomyia sp.15	1♂, Baixo Guandu, E.S., X. 1970, P.C. Elias col. (MZUSP)
Pholeomyia sp.16	1♂, 10.II.63, Barra da Tijuca, Rio de Janeiro, Brasil, H.S.Lopes (MZUSP)
Pholeomyia sp.17	1♂, Taquara, Petropolis, E. do Rio, Brasil, H.S.Lopes, 12.XII.70 (MZUSP)
Pholeomyia sp.18	1♂, Cambé Vigia, 28/5/1967, Brasil, PA, T. Pimentel (MPEG)
Pholeomyia sp.19	1♂, Baixo Guandu, E.S., IX. 1970, P.C. Elias col. (MZUSP)
Pholeomyia sp.20	1♂, Brasil: SP: Butantan, v.1991, R. L. Baptista col. (MZUSP)
Pholeomyia sp.21	1♂, Brazil, Rondonia, 62km SE, Ariquemes, 13-25 Apr 1992, W.J. Hanson (LACM)
Pholeomyia sp.22	1♂, VENEZUELA: Guanare, estado Portuguesa, IX-10 to 13-1957, Borys Malkin Collector (CAS)
Pholeomyia sp.23	1♂, ARGENTINA: Salta Rosario de Lerma, XII-24/27-1983, M. Wasbauer coll, malaise trap (CDFA)

Pholeomyia sp.24	1♂, ARGENTINA: Salta Rosario de Lerma, XI-10/14-1983, M. Wasbauer coll, malaise trap (CDFA)
Pholeomyia sp.25	1♂, PARAGUAY: San Pedro, Cororo-Rio Ypane XII-5/9-1983, Malaise Trap, M. Wasbauer coll. (CDFA)
Pholeomyia sp.26	1♂, MEX: Nayarit, 24 mi. SE. Tepica, VIII-16-60, P.H. Arnaud, E.D. Ross, D.C. Rentz (CAS)
Pholeomyia sp.27	1♂, Capanema, Pará, Brasil, H.S. Lopes, 12-7-65 (MZUSP)
Pholeomyia sp.28	1♂, Córrego Azul, Araçatuba, SP, Brasil, III-1947, M.P. Barreto col. (MZUSP)
Pholeomyia sp.29	1♂, BRASIL, AM, Manaus, ZF2, km-14, 2°35'21"S-60°06'65"W, 11-15.ix.2016, Malaise grande, 34m na torre, J.A. Rafael & F.F. Xavier
Pholeomyia sp.30	1♂, Horto 2 Irmãos, Recife, Brasil, Pernambuco, IX.69, H.S. Lopes (MZUSP)