

SYSTEMATIC RELATIONS AMONG *Philornis* MEINERT, *Passeromyia* RODHAIN & VILLENEUVE AND ALLIED GENERA (DIPTERA, MUSCIDAE)

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(With 1 figure)

ABSTRACT

Passeromyia Rodhain & Villeneuve and *Philornis* Meinert are the only known Muscidae whose larvae are parasites of birds. *Passeromyia* is known from the Old World and *Philornis* from the New World. Opinions on the relations between these two genera and their systematic positions among the Muscidae have varied. This survey aims to clear the discussion on the relations of *Passeromyia*, *Philornis*, and of some allied genera and give an overview of the classification of the Muscidae based on cladistic methodology. Thirty-two terminal taxa (2 of them outgroups) were analysed based on 54 characters. The cladistic analysis, carried out using Hennig86, resulted in 1 minimal tree (length 373), with a consistency index of 71 and a retention index of 85. *Philornis* and *Passeromyia* belong to a monophyletic group, supported by a synapomorphy, the presence of a cocoon, enclosing the pupa. The phylogenetic relationships found in this group are: (*Muscina* (*Philornis* (*Phaonina* ((*Fraserella*, *Passeromyia*) (*Synthesiomia* (*Calliphoroides*, *Reinwardtia*)))))). Other probable monophyletic muscid groups, like Muscinae (with Stomoxyini and Muscini) and Coenosiinae (with Limnophorini and Coenosiini) are also discussed. Phylogenetic patterns within Reinwardtinae and Dichaetomyiinae could be explained by a Gondwana distribution.

Key words: Muscidae, *Passeromyia*, *Philornis*, cladistics, biogeography.

RESUMO

Relações sistemáticas entre *Passeromyia* Rodhain & Villeneuve, *Philornis* Meinert e gêneros relacionados (Diptera, Muscidae)

Passeromyia Rodhain & Villeneuve e *Philornis* Meinert são os únicos gêneros de Muscidae cujas larvas são parasitas de aves. *Passeromyia* é conhecido do Velho Mundo e *Philornis*, do Novo Mundo. Opiniões sobre as relações entre esses dois gêneros e suas posições sistemáticas entre os Muscidae têm variado. Este trabalho tem por objetivo esclarecer as relações de *Passeromyia*, *Philornis* e de alguns gêneros relacionados com eles e dar uma visão da classificação de Muscidae com base na metodologia cladística. Foram analisados 32 táxons terminais (2 deles como grupos externos), com base em 54 caracteres. Na análise cladística foi utilizada o Hennig86. A análise resultou em uma árvore de menor comprimento (373), com índice de consistência 71 e índice de retenção 85. *Philornis* e *Passeromyia* pertencem ao mesmo grupo monofilético, suportado por uma sinapomorfia – presença de um casulo envolvendo a pupa. As relações filogenéticas encontradas neste grupo são: (*Muscina* (*Philornis* (*Phaonina* ((*Fraserella*, *Passeromyia*) (*Synthesiomia* (*Calliphoroides*, *Reinwardtia*)))))). Outros prováveis grupos monofiléticos de muscídeos, como Muscinae (com Stomoxyini e Muscini) e Coenosiinae (com Limnophorini e Coenosiini), também são discutidos. Os padrões filogenéticos dentro de Reinwardtinae e Dichaetomyiinae podem ser explicados por uma distribuição Gondwana.

Palavras-chave: Muscidae, *Passeromyia*, *Philornis*, cladística, biogeografia.

INTRODUCTION

Passeromyia Rodhain & Villeneuve and *Philornis* Meinert are two of the most interesting muscid genera, found in larvae. Biology present knowledge shows that the larvae are parasites of birds, associating with them in ways ranging from scavenging in their nests to subcutaneous bloodfeeding. Pont (1974) revised *Passeromyia* and provided data on the biology of the species. Couri (1999) and Teixeira (1999) summarized the available data on *Philornis* relations with birds. Carvalho & Couri (2002a) presented a key to species, modified from Couri (1999).

Passeromyia is distributed throughout the Old World, Afrotropical and Oriental regions, Australasia, and the Western Pacific (Pont, 1974) and *Philornis* is known from the New World, mainly in the Neotropical region, with 2 species occurring in the southern United States. Besides larval behaviour similarities, both genera also share some morphological characters like the presence of a tuft of bristles on the post-alar wall (present in all *Philornis* species and in some *Passeromyia*) and very similar ovipositor morphology.

Opinions on the systematic position of both genera among the Muscidae have varied, especially regarding *Passeromyia*, for which Pont (1974) presented those of many authors. Malloch (1925, 1928), Séguéy (1937), Hardy (1937), and Emden (1939) placed the genus among the Muscinae, based on the upward curvature of vein M and the truncated lower squama. Townsend (1935, 1937) considered *Passeromyia* in the tribe Hemichlorini, together with *Ornithomusca* Townsend, *Hemichlora* Wulp, *Ochromusca* Malloch, and *Synthesiomyia* Brauer & Bergenstamm. Emden (1965) and Hennig (1965) considered *Passeromyia* close to other Old World genera such as *Muscina* Robineau-Desvoidy, *Synthesiomyia* Brauer & Bergenstamm, *Calliphoroides* Malloch, *Fraserella* Steyskal, *Phaonina* Emden, and *Phaonidia* Emden. Emden (*op. cit.*) included these genera in the Phaoniini, Phaoniinae, while Hennig (*op. cit.*) included them in the Muscinae (tribe Hydrotaeini), a subfamily he considered paraphyletic. Vockeroth (1972) included the genus in the Muscinae: "Whilst the male aedeagus places the genus in Hennig's group Muscinae + Phaoniinae, the female ovipositor supports assignment in the Muscinae whilst the absence of proclinate ors on the female frons indicates the Phaoniinae". Pont (*op. cit.*) also

mentioned the similarity between *Passeromyia* and *Philornis* (= *Neomusca* Malloch), which differ chiefly by the presence of hairs on the anepimeron of all *Philornis* species. Pont (1972) placed *Philornis* in the subfamily Cyrtoneurinae which according to him (Pont, 1974), is a paraphyletic group.

More recent publications and catalogues also show divergence on the *Passeromyia* systematic position. Pont (1980, 1989) placed the genus among the Muscinae, tribe Hydrotaeini and Reinwardtiini, respectively.

In the Skidmore (1985) classification, *Passeromyia* and *Philornis* are placed in the tribe Reinwardtiini, subfamily Reinwardtiinae, together with *Ochromusca*, *Alluaudinella* Giglio-Tos, *Aethiopomyia* Malloch, *Charadrella* Wulp, *Muscina* Robineau-Desvoidy, *Synthesiomyia*, and *Calliphoroides*. He also mentioned that the close parallels between *Passeromyia* and *Philornis* in larval morphology also suggest that they may be closely related.

Carvalho (1989) in his classification of the family Muscidae based on cladistic analysis, placed *Philornis* among the Reinwardtiini, tribe of Azeliinae, together with *Dalcyella* Carvalho, *Reinwardtia* Brauer & Bergenstamm, *Brachygasterina* Macquart, *Palpibracus* Rondani, and *Psilochaeta* Stein. Carvalho *et al.* (1993) and Carvalho & Couri (2002a) followed this classification, placing *Philornis* among the Reinwardtiini, subfamily Azeliinae. None of these papers included the genus *Passeromyia* in their studies.

Passeromyia is known from 5 described species: *P. heterochaeta* (Villeneuve), *P. indecora* (Walker), *P. steini* Pont, *P. longicornis* (Macquart), and *P. veitchi* Bezzi. The larvae of these species are known to be scavengers in bird nests (*P. steini*); external parasites of nestlings, remaining on the body surface and piercing the skin to suck blood (*P. heterochaeta*); or subcutaneous parasites of the nestlings (*P. indecora*). In the last case, if the host dies the subcutaneous larvae can feed on the carcass until ready to pupate (Pont, 1974). The life history of *P. longicornis* and *P. veitchi* is unknown.

Philornis is a bigger genus, known from 50 species (Dodge, 1955; Carvalho *et al.*, 1993), the majority of them described in the sixties by Dodge (1963, 1968) and Dodge & Aitken (1968) and in the eighties by Couri (1983, 1984). The same range of larval habits found in *Passeromyia*, is also found in *Philornis*: free-living larvae in bird nests, with coprophagous habits (*P. aitkeni* Dodge and *P. rufoscutellaris* Couri); free-living in nests, semi-

hematophagous (*P. downsi* and *P. falsifica*); and subcutaneous bloodfeeders (the majority of the species, with known larval biology).

The main objectives of this paper are to clarify the relations of *Passeromyia* and *Philornis* and the discussion on the evolutionary line of larvae habits (see also Dodge, 1971) based on cladistic methodology.

MATERIAL AND METHODS

The material used in this study belongs to Museu Nacional, Rio de Janeiro, Brazil; The Natural History Museum, London; Canadian National Collection of Insects, Ottawa; and the Australian National Insect Collection, Canberra.

The terminal taxa are represented by *Philornis*, *Passeromyia* and the following related genera considered by different authors as in different positions among the Muscidae, but close to those two: *Aethiopomyia*, *Alluaudinella*, *Calliphoroides*, *Charadrella*, *Fraserella*, *Muscina*, *Ochromusca*, *Phaonina*, *Reinwardtia*, and *Synthesiomyia*.

Besides these, other muscid genera were added to the analysis: *Coenosia* Meigen; *Cyrtoneurina* Giglio-Tos; *Cyrtoneuropsis* Malloch [= *Paracyrtoneurina* Pamplona (Pamplona, 1999; Pont & Pamplona, 2000)]; *Dichaetomyia* Malloch; *Dolicophaonia* Carvalho; *Hydrotaea* Robineau-Desvoidy; *Limnophora* Robineau-Desvoidy; *Micropotamia* Carvalho; *Mydaea* Robineau-Desvoidy; *Morellia* Robineau-Desvoidy; *Musca* Linnaeus; *Neodexiopsis* Malloch; *Polietina* Schnabl & Dzedzicki; *Scutellomusca* Townsend; *Souzalopesmyia* Albuquerque; and *Stomoxys* Geoffroy. Each genus is represented by one species, except for *Philornis* and *Passeromyia*, represented by two species, one with coprophagous and the other with hematophagous larvae. The scanty information on *Phaonidia* Emden, also referred to by some authors as being close to *Passeromyia*, made it impossible to consider this genus in the analysis.

The cladistic analysis was carried out using Hennig86, version 1.5 (Farris, 1988), running in "Tree Gardener", version 2.2 (Ramos, 1997), a program designed for running Hennig86 in a Windows environment. Minimum-length trees were calculated using the options "mhennig" associated with "successive weighting".

Thirty-two terminal taxa were analyzed based on 54 characters. Characters were polarized by the outgroup method (Watrous & Wheeler, 1981; Maddison *et al.*, 1984). The outgroups were

represented by two Anthomyiidae genera: *Coenosopia* Malloch and *Phaonantho* Albuquerque. These two genera are the only ones among the Anthomyiidae where the anal vein does not reach the wing margin (as found in Muscidae). Michelsen (1991) proposed Anthomyiidae as the sister-group of the Muscidae.

Characters were coded as binary and multistate. The latter was considered as additive or non-additive, depending on available information on the contiguity of states in the outgroups. Information not available was coded as a question mark (?). The character distributions were examined using Tree Gardener and Clados (Nixon, 1995).

Table 1 shows the matrix and the characters used in the analysis.

RESULTS AND DISCUSSION

The cladistic analysis resulted in 1 minimal length (373) tree, with a consistency index of 71 and retention index of 85 (Fig. 1). The monophyly of the Muscidae was confirmed by the loss of the postabdominal spiracles in the female, as pointed out by Hennig (1965, 1973). Among the Muscidae, only *Acanthiptera* Rondani and *Cariocamyia* Snyder have independently re-acquired spiracle 6 (Carvalho & Couri, 2002a).

The classification shows that *Philornis* and *Passeromyia* belong to a monophyletic group supported by one synapomorphy, the presence of a cocoon, enclosing the pupa. This clade includes the following genera: *Muscina*, *Philornis*, *Phaonina*, *Fraserella*, *Passeromyia*, *Synthesiomyia*, *Calliphoroides*, and *Reinwardtia*.

Skidmore (1985) placed *Philornis* close to *Passeromyia* because, according to him, "it appears inconceivable that many similarities between these two genera should be due merely to convergence. The same range of larval habits is found in both genera, but elsewhere in the Muscidae parasitism of birds is known except in *Muscina* and *Synthesiomyia* where it is of purely casual nature". The present analysis shows this character (larvae associated with birds) as having appeared independently in both genera.

Muscina also has different positions among the Muscidae, according to different authors: Phaoniinae (Collin, 1948), Muscinae (Hennig, 1965). According to Skidmore (*op. cit.*) there can be no doubt about the close affinity between *Muscina*, *Synthesiomyia*, and *Passeromyia*.

TABLE 1 (Continued.)

10. Secondary cilia/plumes at arista: (0) absent (1) present [ci: 50; ri: 75; weight: 3; steps: 2]
11. Remarkably short stubby spines on the upper side of the palpi [ci: 100; ri: 100; weight: 10; steps: 1]
12. Cilia at eyes: (0) absent or very short (1) numerous [ci: 50; ri: 66; weight: 3; steps: 2]
13. Shape of labellum: (0) not reduced (1) reduced [ci: 100; ri: 100; weight: 10; steps: 1]
14. Prestomal teeth: (0) absent (1) present [ci: 50; ri: 66; weight: 3; steps: 2]
15. Cilia at facial ridge: (0) absent (1) present [ci: 50; ri: 83; weight: 4; steps: 2]
16. Prealar seta: (0) present (1) absent [ci: 100; ri: 100; weight: 10; steps: 1]
17. Cilia at prosternum (0) absent (1) present [ci: 20; ri: 63; weight: 1; steps: 5]
18. Color of prosternum: (0) not glossy (1) glossy [ci: 33; ri: 0; weight: 0; steps: 3]
19. Lower proepimeral seta: (0) upcurved (1) downcurved [ci: 100; ri: 100; weight: 10; steps: 1]
20. Cilia at anepimeron: (0) absent (1) present [ci: 33; ri: 83; weight: 2; steps: 3]
21. Setae at margins of posterior spiracle: (0) absent (1) present [ci: 16; ri: 16; weight: 0; steps: 6]
22. Setae at post-alar declivity: (0) absent (1) present as a tuft [ci: 33; ri: 33; weight: 1; steps: 3]
23. Setulae on lateral margins of scutellum: (0) absent (1) present [ci: 33; ri: 81; weight: 2; steps: 3]
24. Length of inferior calypter related to the superior one: (0) at most twice as long as (1) enlarged, more than three times [ci: 25; ri: 80; weight: 2; steps: 4]
25. Acrostichal post-sutural setae: (0) differentiated (1) not differentiated [ci: 14; ri: 57; weight: 0; steps: 7]
26. Number of dorso-central post-sutural setae: (0) 3 (1) 4 [ci: 12; ri: 36; weight: 0; steps: 8]
27. Arrangement of katepisternals: (0) 1:2 (1) 1:1 (2) 1:1:1 (3) 0:1 [ci: 100; ri: 100; weight: 10; steps: 3]
28. Length of anterior katepisternal related to posterior one: (0) almost as long as (1) shorter [ci: 33; ri: 66; weight: 2; steps: 3]
29. Inferior calypter darker and with hairs: (0) absent (1) present [ci: 50; ri: 50; weight: 2; steps: 2]
30. Cilia on inferior portion of scutellum: (0) present (1) absent [ci: 100; ri: 100; weight: 10; steps: 1]
31. Calcar: (0) present long (1) present short (2) absent [ci: 20; ri: 69; weight: 1; steps: 5]
32. Subcostal vein: (0) smooth (1) sinuose [ci: 50; ri: 50; weight: 2; steps: 2]
33. Cilia on apical dorsal section of stem vein (0) absent (1) present [ci: 50; ri: 50; weight: 2; steps: 2]
34. Cilia at both surfaces of R4+5: (0) absent (1) present [ci: 33; ri: 50; weight: 1; steps: 3]
35. Course of M1+2 at end: (0) nearly straight or very weakly bowed upwards (1) strongly bowed upwards (2) divergent [ci: 33; ri: 63; weight: 2; steps: 6]
36. Length of anal vein: (0) long (1) short [ci: 100; ri: 100; weight: 10; steps: 1]
37. Cilia at sternite 1: (0) present (1) absent [ci: 33; ri: 66; weight: 2; steps: 3]
38. Spined process on ventral surface of cercal plate (0) absent (1) present [ci: 100; ri: 100; weight: 10; steps: 1]
39. Small spinules on juxta on male distiphallus: (0) absent (1) present [ci: 100; ri: 100; weight: 10; steps: 1]
40. Shape of male hypandrium: (0) plate-like (1) tubular [ci: 100; ri: 100; weight: 10; steps: 1]
41. Shape of female hypoproct: (0) not modified, with setae (1) elongated and with spines [ci: 50; ri: 50; weight: 2; steps: 2]
42. Ovipositor: (0) straight (1) curve [ci: 50; ri: 50; weight: 2; steps: 2]
43. Ovipositor: (0) long (1) medium [ci: 25; ri: 57; weight: 1; steps: 4]
44. Shape of the tergites: (0) large (1) fine to medium (2) anchor-type [ci: 40; ri: 62; weight: 2; steps: 5]
45. Bristles on sternite 8: (0) not strong (1) strong [ci: 100; ri: 100; weight: 10; steps: 1]
46. Spicules at membranae of the segment 8 of the ovipositor: (0) absent (1) present [ci: 50; ri: 50; weight: 2; steps: 2]
47. Length of cerci at ovipositor: (0) long (1) short (not surpassing hypoproct) [ci: 33; ri: 33; weight: 1; steps: 3]
48. Setae at cerci: (0) on both surfaces (1) only on external surface [ci: 100; ri: 100; weight: 10; steps: 1]
49. Spiracle 6 of the ovipositor: (0) present (1) absent [ci: 100; ri: 100; weight: 10; steps: 1]
50. Larval habits: (0) not parasite (1) parasite, associated with snails (2) parasite, associated with birds [ci: 66; ri: 80; weight: 5; steps: 3]
51. Larval feeding habitus: (0) saprophagous/coprophagous (1) carnivorous (2) hematophagous [ci: 33; ri: 55; weight: 1; steps: 6]
52. Cocoon: (0) absent (1) present [ci: 100; ri: 100; weight: 10; steps: 1]
53. Egg type: (0) *Musca* (1) *Phaonia* (2) *Mydaea* [ci: 50; ri: 66; weight: 3; steps: 4]
54. Viviparity: (0) does not occur (1) occurs [ci: 25; ri: 0; weight: 0; steps: 4]

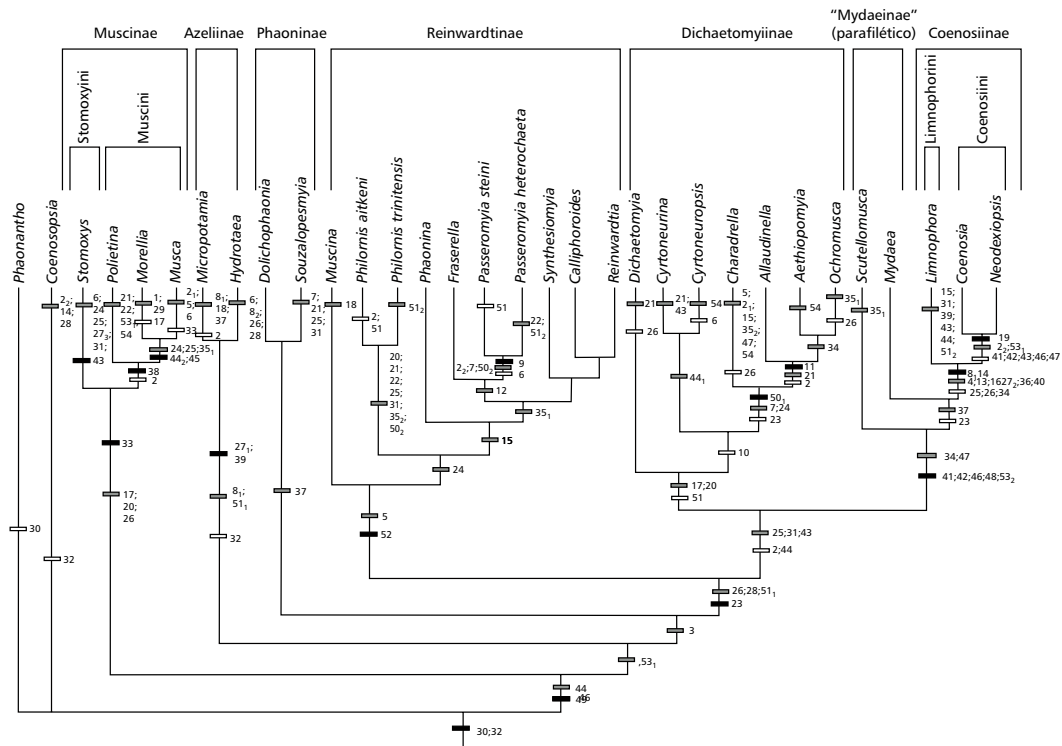


Fig. 1 — Cladogram depicting the phylogenetic relationships among the species of some Muscidae genera. Length: 373; ci: 71; ri: 85. Black boxes, synapomorphies; stippled boxes, homoplasies; clear boxes, reversals.

Unfortunately little information was available on *Phaonina* and *Fraserella*. *Phaonina*, according to Skidmore (1985) “has many unusual features which render its true affinities uncertain”. He placed this genus among the “aberrant Reinwardtinae” and in the tribe Hemichlorini, together with *Cyrtoneurina*, *Neomuscina* Townsend, *Polietina* Schnabl & Dziedzicki, and *Metopomyia* Malloch. In the present analysis they appear closely related to *Passeromyia* in a monophyletic group also formed by *Synthesiomyia*, *Calliphoroides*, and *Reinwardtia*.

The close relations between *Calliphoroides* and *Reinwardtia*, corroborated in this analysis, were long discussed by Hennig (1965) who placed them among the Muscinae. The strong curvature at the end of the vein M, used by many authors to characterize this subfamily, was a homoplastic character state in this analysis. Hennig (*op. cit.*) also approximated *Calliphoroides* to *Muscina* and *Synthesiomyia*.

In this analysis, *Alluadinella*, *Aethiopomyia*, and *Ochromusca* appear to form a monophyletic group, defined by the presence of remarkably short stubby spines on the upper side of the palpi. Pont (1980) following Hennig (1965) considered *Ochromusca*, *Aethiopomyia*, and *Alluadinella* in the *Dichaetomyiini*. Emden (1939) placed them in the Muscinae based on their *Musca*-type thoracic calypter. Skidmore (1985) mentioned that the larval mouthparts and larval spiracle of *Ochromusca* suggest a close relationship with *Muscina* and *Synthesiomyia*. According to Skidmore (*op. cit.*) these three genera are clearly closely related. The larva of *Ochromusca* and *Alluadinella* feed on dead snails and, although the larval habits of *Aethiopomyia* are not known, the final larval instar of *Aethiopomyia* closely resemble those of *Ochromusca*, *Alluadinella*, *Synthesiomyia*, and *Muscina* (Skidmore, 1985).

Charadrella appears as the sister group of (*Alluaudinella* (*Aethiopomyia*, *Ochrhomusca*)) forming with them a monophyletic group based on the association of their larvae with snails. Skidmore (1985) considered that, although it shares with the three previously mentioned genera an unusual mode of life and some structural affinity, it may not be particularly closely related to them nor to *Muscina* and *Synthesiomia*. Skidmore (*op. cit.*) provisionally placed *Charadrella* close to *Ochrhomusca* on the strength of their biology. A more complete analysis will certainly better define this relation. *Charadrella* together with the three preceding genera were considered to be in Reinwardtiini (Reinwardtinae) by Skidmore (*op. cit.*).

Cyrtoneurina and *Cyrtoneuropsis* appeared close to these groups of genera. Skidmore (1985) examined *Cyrtoneuropsis gemina* Wiedemann in his study, considering it as a Hemichlorini (Reinwardtiinae). He mentioned that the species is apparently "archaic combining some features of the Reinwardtinae, Muscinae and Azeliinae".

The paleotropical genus *Dichaetomyia* (two species in the Palearctic, Skidmore, 1985), seems closely related to this group in the analysis. According to Skidmore (1985) *Dichaetomyia* appears to be closely related to *Phaonia*, "but further work may reveal that some of the species included under this genus belong to the *Ochromusca* group".

Although using few genera representing the other muscid subfamilies, the resulted cladogram corroborated the data in the literature, showing some monophyletic muscid groups such as Muscinae. This subfamily appears in the base of the cladogram and is here represented by *Stomoxys*, *Polietina*, *Morellia*, and *Musca*. The "Azeliini" (as termed by Carvalho, 1993) was represented by *Micropotamia* and *Hydrotaea*. The genus *Micropotamia* was constructed by Carvalho (1993) who also presented a discussion of some character-states of phylogenetic importance to Azeliini (as termed by Carvalho, 1989), a tribe in which *Micropotamia* was included. Carvalho (*op. cit.*) called attention to the striking configuration of the male distiphallus, with juxta spinulose, shared by the Azeliini genera. He also mentioned that although there is no published phylogenetic hypothesis for intergeneric relationships in Azeliini, there is evidence that the tribe is monophyletic (Michelsen, 1978; Carvalho, 1993).

The other monophyletic group, and one of the most solidly based among the Muscidae – Mydaeinae +

Coenosiinae (Hennig, 1965; Carvalho, 1989; Couri & Pont, 2000) appears at the apex of the cladogram supported by five sinapomorphies. *Scutellomusca* and *Mydaea*, considered today among the Mydaeinae, did not form a monophyletic group. The Coenosiinae represented by *Limmophora*, *Coenosia*, and *Neodexiopsis* confirmed their monophyly (six sinapomorphies). The last two genera, known as well as the tribe Coenosiini, also confirmed their monophyly, supported by one sinapomorphy (see also Couri, 2000).

BIOGEOGRAPHICAL ANALYSIS

Historical biogeographical studies on the Muscidae family are few, and rare are the hypotheses about the distribution patterns of the muscid species. In the sixties, Hennig (1965) explained such patterns of some muscid species based exclusively on dispersion. Carvalho (1999) and Carvalho & Couri (2002b) analyzed distribution patterns of muscid species using vicariance, but both studies were based on genera occurring exclusively in the Neotropical region. Although Hennig (1965) theorized on this subject, nothing is actually known about the transoceanic patterns of relationships of muscid species. On the other hand, the intercontinental relationships of the basic groups of Diptera are well known (for a summary, see Amorim & Tozoni, 1994). At the same time, few papers exist on Schizophora (Griffiths, 1972; Papavero, 1977; Matthis, 1977, 1978; Barnes, 1981; Cortéz, 1983).

Using the methodology of cladistic biogeography, by replacing the taxa nomenclature with names of areas where the species occur, a biological area cladogram can be generated (for methodological procedures, see Morrone & Crisci, 1995). Based on this, sister group relationships of some genera could be analyzed based on vicariance biogeography.

The distribution pattern of the species among the genera of Reinwardtiinae (Fig. 1) resembles a Gondwana pattern, suggesting that the ancestor of these genera could have appeared before the Upper Cretaceous, the hypothetical age previous to Muscidae (Hennig, 1965). As pointed out in this paper, the breakup of the Gondwana could have strongly affected the pattern distribution of these genera, suggesting an older age for this family.

Pont & Carvalho (1997) described the first muscids, found in Dominican amber (about 15-20

million years ago, the minimum age of those species). Evenhuis (1994) identified a muscid fossil from the Eocene, and Grimaldi & Cumming (1999) recorded the oldest definitive cyclorrhaphan larvae in Cretaceous amber, but did not position them in a family (uncertain family).

On the other hand, the distribution pattern here shown for another monophyletic group within the Dichaetomyiinae subfamily formed by *Charadrella* + *Alluaudinella* + *Aethiopomyia* + *Ochromusca* (Fig. 1) (the first, an exclusively Neotropical genus and

the three others Afrotropical) also corroborates a hypothetical older age for the Muscidae.

This older age for Muscidae, as here suggested, is hypothesized to be based on a partial phylogenetic analysis of this family, although some of the resulting monophyletic groups inside this family corroborated previous classifications. Therefore, the hypothetical age of this family remains undefined and more fossil evidence and historic biogeographic studies are required. The geographical distribution of the genera included in this analysis is shown in Table 2.

TABLE 2
Geographical distribution of the analyzed genera.

Genus name	Geographical distribution
<i>Phaonantho</i>	Neotropical
<i>Coenosopsia</i>	Nearctic, Neotropical
<i>Alluaudinella</i>	Afrotropical
<i>Aethiopomyia</i>	Afrotropical
<i>Calliphoroides</i>	Australasian
<i>Charadrella</i>	Neotropical
<i>Coenosia</i>	Cosmopolitan
<i>Cyrtoneurina</i>	Neotropical
<i>Cyrtoneuropsis</i>	Neotropical
<i>Dichaetomyia</i>	Essentially Afrotropical, Oriental, Australasian
<i>Dolichophaonia</i>	Essentially Neotropical
<i>Hydrotaea</i>	Cosmopolitan
<i>Fraserella</i>	Oriental
<i>Limmophora</i>	Cosmopolitan
<i>Micropotamia</i>	Afrotropical
<i>Morellia</i>	Cosmopolitan
<i>Musca</i>	Cosmopolitan
<i>Muscina</i>	Holarctic (predominantly), Nearctic, Neotropical
<i>Mydaea</i>	Cosmopolitan
<i>Neodexiopsis</i>	Nearctic, Neotropical
<i>Ochromusca</i>	Afrotropical
<i>Passeromyia</i>	Mainly tropical-South Africa to east Asia, eastwards to Australia and the West Pacific
<i>Phaonina</i>	Oriental-Australasian
<i>Philornis</i>	Essentially Neotropical
<i>Polietina</i>	Neotropical
<i>Reinwardtia</i>	Neotropical
<i>Scutellomusca</i>	Neotropical
<i>Souzalopesmyia</i>	Neotropical
<i>Stomoxys</i>	Cosmopolitan
<i>Synthesiomyia</i>	Tropicopolitan

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REFERENCES

- AMORIM, D. de O. & TOZONI, S. H. S., 1994, Phylogenetic and biogeographic analysis of the Anisopodoidea (Diptera, Bibionomorpha), with an area cladogram for intercontinental relationships. *Revta. Bras. Ent.*, 38: 517-543.
- BARNES, J. K., 1981, Revision on the Helosciomyzinae (Diptera). *J. R. Soc. N. Z.*, 11: 45-72.
- CARVALHO, C. J. C., 1989, Classificação de Muscidae (Diptera): uma proposta através da análise cladística. *Revta. Bras. Zool.*, 6: 627-648.
- CARVALHO, C. J. B., 1993, *Micropotamia*, gen. n. of neotropical Muscidae (Diptera, Azeliinae), with comments on allied Azeliini genera. *Revta. Bras. Zool.*, 9(1992): 241-246.
- CARVALHO, C. J. B., 1999, Revision, cladistics and biogeography of the neotropical Genus *Souzalopesmyia* Albuquerque (Diptera: Muscidae). *Proc. Entomol. Soc. Wash.*, 101: 123-137.
- CARVALHO, C. J. B. & COURI, M. S., 2002a, Part I. Basal Groups, pp. 17-132. In: C. J. B. Carvalho (ed.), *Muscidae (Diptera) of the neotropical region: taxonomy*. Editora Universidade Federal do Paraná, Curitiba, 287p.
- CARVALHO, C. J. B. & COURI, M. S., 2002b, A cladistic and biogeographic analysis of *Apsil* Malloch and *Reynoldsia* Malloch (Diptera, Muscidae) of southern South America. *Proc. Ent. Soc. Wash.*, 104: 309-317.
- CARVALHO, C. J. B., COURI, M. S., PONT, A. C., PAMPLONA, D. & LOPES, S. M., 1993, Part II. Muscidae, 201p. In: C. J. B. Carvalho (ed.), *A catalogue of the Fanniidae and Muscidae (Diptera) of the neotropical region*. Sociedade Brasileira de Entomologia, São Paulo, 201p.
- COLLIN, J. E., 1948, On the classification of the genera allied to *Musca* L. (Dipt.). *Proc. Royal. Ent. Soc. London*, 17: 125-127.
- CORTÉS, R., 1983, First record of transantarctic relationships in the Tachinidae (Diptera, Muscoidea, Calyptratae). *Revta. Bras. Zool.*, 1: 419-420.
- COURI, M. S., 1983, Descrição de seis espécies novas de *Philornis* Meinert, 1890 (Diptera, Muscidae, Cyrtoneurinae). *Revta. Bras. Zool.*, 43: 297-309.
- COURI, M. S., 1984, Notes and descriptions of *Philornis* flies (Diptera, Muscidae, Cyrtoneurinae). *Revta. Bras. Ent.*, 28: 473-490.
- COURI, M. S., 1999, Myiasis caused by obligatory parasites. Ia. *Philornis* Meinert (Muscidae), pp. 51-70 In: J. H. Guimarães & N. Papavero (eds.), *Myiasis in man and animals in the Neotropical Region. Bibliographic database*. Editora Pleaide, FAPESP, São Paulo, 308p.
- COURI, M. S., 2000, A new species of *Philornis* Meinert from Galapagos Islands. *Bol. Mus. Nac., Rio de J. (Zoologia)*, 414: 1-16.
- COURI, M. S. & PONT, A. C., 2000, A cladistic analysis on Coenosiinae (Diptera, Muscidae). *Syst. Ent.*, 25: 373-392.
- DODGE, H. R., 1955, New Muscid flies from Florida and the West Indies (Diptera, Muscidae). *Florida Entomologist*, 38: 147-151
- DODGE, H. R., 1963, A new *Philornis* with coprophagous larva, and some related species (Diptera, Muscidae). *Journal Kansas Ent. Soc.*, 36: 239-247.
- DODGE, H. R., 1968, Some new and little-known species of *Philornis* (Diptera, Muscidae). *Journal Kansas Ent. Soc.*, 41: 155-164.
- DODGE, H. R., 1971, Revisional studies of flies of the genus *Philornis* (Diptera, Muscidae). *Studia Ent.*, 14: 458-459.
- DODGE, H. R. & AITKEN, T. H. G., 1968, *Philornis* flies from Trinidad (Diptera, Muscidae). *Journal Kansas Ent. Soc.*, 41: 134-154.
- EMDEN, F. I. Van., 1939, *Muscidae, A: Muscinae and Stomoxydinae. Ruwenzori Expedition. 1934-5*. British Museum (Natural History), London, v. 2, pp. 49-89.
- EMDEN, F. I. Van., 1965, *Diptera 7, Muscidae, Part I. The fauna of India and the adjacent countries*. Government of India, Delhi, xiv + 647p.
- EVENHUIS, N. L., 1994, *Catalogue of the fossil flies of the world (Insect: Diptera)*. Backhuys, Leiden, 600p.
- FARRIS, J. S., 1988, *Hennig 86, version 1.5*. Published by the author, Port Jefferson, New York, 18p.
- GRIFFITHS, G. C. D., 1972, The phylogenetic classification of Diptera Cyclorhapha. In: Dr. W. Junk N.V. (ed.), *The Hague*, 340p. (Series Entomologica, vol. 8).
- GRIMALDI, D. & CUMMING, J., 1999, Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bull. Amer. Mus. Nat. Hist.*, 239: 124.
- HARDY, G. H., 1937, Notes on Australian Muscoidea, II. Subfamily Muscinae. *Proc. R. Soc. Qd.*, 48: 22-29.
- HENNIG, W., 1965, Vorarbeiten zu einem phylogenetischen System der Muscidae (Diptera, Cyclorhapha). *Stuttg. Beitr. Naturkd.*, 141: 100.
- HENNIG, W., 1973, Diptera. In: W. Kukenthal (ed.), *Handbuch der Zoologie, IV: Arthropoda de Gruyter*. New York, pp. 1-337.
- MADDISON, W. P., DONOGHUE, M. J. & MADDISON, D. R., 1984, Outgroup analysis and parsimony. *Syst. Zool.*, 33: 83-103.
- MALLOCH, J. R., 1925, Notes on Australian Diptera. n. V. *Proc. Linn. Soc. N. S. W.*, 50: 35-46.

- MALLOCH, J. R., 1928, Fauna sumatrensis (Beitra Nr. 56). Family Muscidae (Dipt.). *Ent. Mitt.*, 17: 290-303, 310-336.
- MATTHIS, W. N., 1977, Key to the Neotropical genera of Parydrinae, with a revision of the genus *Eleleides* Cresson (Diptera: Ephydrinae). *Proc. Biol. Soc. Wash.*, 90: 553-565.
- MATTHIS, W. N., 1978, A synopsis of the Neotropical *Eleleides* Cresson (Diptera: Ephydridae). *Proc. Biol. Soc. Wash.*, 80: 465-472.
- MICHELSSEN, V., 1978, *Cryptophyra lundbecki*, n. gen. and n. sp. From North Europe, with some notes on hydrotaeinae genera (Diptera, Muscidae). *Entomol. Scand.*, 9: 85-92.
- MICHELSSEN, V., 1991, Revision of the aberrant New World genus *Coenosopsia* (Diptera, Anthomyiidae), with a discussion of anthomyiid relationships. *Syst. Ent.*, 16: 85-105.
- MORRONE, J. J. & CRISCI, J. V., 1995, Historical biogeography: introduction to methods. *Annu. Rev. Ecol. Syst.*, 26: 373-401.
- NIXON, K., 1995, *Clados*, ver. 1.49. Program and documentation. Trumansburg, New York.
- PAMPLONA, D., 1999, Nova caracterização de *Cyrtoneurina* Giglio-Tos, 1983 e descrição de *Paracyrtoneurina* gen. n. (Diptera, Muscidae). *Revta. Bras. Ent.*, 43: 9-24.
- PAPAVERO, N., 1977, *The world Oestridae (Diptera), mammals and continental drift*. W. Junk, The Hague, 249p.
- PONT, A. C., 1972, Family Muscidae. In: *A catalogue of the Diptera of the Americas South of the United States*. Museu de Zoologia, Universidade de São Paulo, São Paulo, v. 97, p. 111.
- PONT, A. C., 1974, A revision of the genus *Passeromyia* Rodhain & Villeneuve (Diptera, Muscidae). *Bull. Brit. Mus. (Nat. Hist.)*, 30: 339-372.
- PONT, A. C., 1980, Family Muscidae, pp. 721-761. In: R. W. Crosskey (ed.), *Catalogue of the Diptera of afrotropical region*, British Museum (Natural History), London, 1437p.
- PONT, A. C., 1989, Family Muscidae, pp. 675-699. In: N. L. Evenhuis (ed.), *Catalog of the Diptera of the australasian and oceanian regions*. Special Publications of the Bernice Pauahi Bishop Museum, 1155p.
- PONT, A. C. & CARVALHO, C. J. B., 1997, Three new species of Muscidae (Diptera) from Dominican amber. *Studia dipterologica*, 4: 173-181.
- PONT, A. C. & PAMPLONA, D., 2000, A note on the genus *Paracyrtoneurina* Pamplona, 1999 (Diptera, Muscidae). *Studia dipterologica*, 7. Heft 1: 213-223.
- RAMOS, T. C., 1997, *Tree Gardner 2.2*. Privately distributed by Thiago Courrol Ramos, Museu de Zoologia, Universidade de São Paulo, Brasil.
- SÉGUY, E., 1937, Diptera, family Muscidae. In: P. Wystmann (ed.), *Genera Insectorum*, Bruxelles, 205: 604.
- SKIDMORE, P., 1985, *The biology of the Muscidae of the world*. Junk, Dordrecht. Series entomologica, 29, xiv + 550p.
- TEIXEIRA, D. M., 1999, Myiasis caused by obligatory parasites. Ib. General observations on the biology of the species of the genus *Philornis* Meinert, 1890 (Diptera, Muscidae). In: J. H. Guimarães & N. Papavero (eds.), *Myiasis in man and animals in the neotropical region. Bibliographic database*. Editora Pleaide, FAPESP, São Paulo, 308p.
- TOWNSEND, C. H. T., 1935, *Manual of myiology in twelve parts. Part II. Muscoid classification and habits*. Charles Townsend & Filhos, Itaquaquecetuba, Brazil, 296p., 9 pls.
- TOWNSEND, C. H. T., 1937, *Manual of Myiology in twelve parts. Part V. Muscoid generic diagnoses data, Glossinini to Agrinini*. Charles Townsend & Filhos, Itaquaquecetuba, Brazil, 234p.
- VOCKEROTH, J. R., 1972, *A review of the world genera of Mydaeinae, with a revision of the species of New Guinea and Oceania (Diptera: Muscidae)*. Pacific Insects, Monographs, 29: 1-134.
- WATROUS, L. E. & WHEELER, Q. D., 1981, The outgroup comparison method of character analysis. *Syst. Zool.*, 30: 1-11.