

DISTRIBUTIONAL PATTERNS OF THE NEOTROPICAL MUSCIDAE (DIPTERA)

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Muscidae (Diptera) are worldwide in distribution with far more than 4000 described species (Pont, 1989; Carvalho *et al.*, 1993). They are known as common house flies and some species have a great medical and veterinary importance, acting as vectors of many diseases. However, most of the species have no contact with man or his anthropobiocenose because their habits. Adult Muscidae occur in many habitats, but they are less common in dry, open and exposed habitats, or where sandy or acidic soils prevail (Pont, 1986). They are rather common in higher altitudes. Muscidae are represented in the Neotropical region by 838 species in 84 recognized genera (Carvalho *et al.*, 1993; Carvalho and Couri, 2002a; Couri and Carvalho, 2002), about 20% of the world fauna.

Historical biogeographic studies on Muscidae are scarce (Carvalho, 1999), although they are increasing in recent years. A few papers have hypothesized on the distributional patterns of world Muscidae. In the Holarctic region, all taxa of the *Eudasyphora s.str.* Townsend are faunal elements of known dispersal centers. The speciation of these flies has been correlated with the history of the forest vegetation during the Pleistocene (Cuny, 1980).

The first analysis of the distributional patterns of South American Muscidae was made by Hennig (1965), with a clearly dispersalist approach. According to him, the first species occurring into the region came by dispersal from the North, at the beginning of latest Cretaceous or early Tertiary period. This biotic connection between North and South America could have resulted in a considerable amount of faunal interchange (Michelsen, 1991). On the other hand, Hennig (1965) considered that the marked differentiation of the groups in the southern South America could be a result of the long time of evolution of in the area. All those groups have originated from ancient lineages from the Northern Hemisphere, in several waves, being considered terminal of groups that suffered extinction in the northern lands.

Following this broad idea, Michelsen (1991) claimed that the occurrence of Anthomyiidae flies (the proposed sister group of Muscidae) in South America occurred by a first invasion of a lineage into the region from the Northern Hemisphere during the latest Cretaceous or early Tertiary period. From this lineage, evolved a clade comprising *Phaonantho Albuquerque plus Coenosopsites* Michelsen (fossil genus), with its sister group *Coenosopsia* Malloch, following an ancient vicariant event. These are currently understood as essentially Neotropical genera (Michelsen, 1991, 1996, 2000; also Nihei and Carvalho, in press).

In the recent years, other hypotheses have been proposed to explain the distribution of Muscidae in the region, mainly applying a cladistic approach (Carvalho, 1999; Couri and Carvalho, 2000, in press; Carvalho and Couri, 2002b), following a better biotic/geological understanding of the biogeographic evolution of the Neotropical region (Crisi *et al.*, 1991; Amorim and Pires, 1996; Marshall and Lieberr, 2000; Amorim, 2001).

Panbiogeographic analysis

The panbiogeographic approach was developed by Léon Croizat, in the 1950's, who established an objective method to represent the spatial component of biodiversity. Croizat's method consists basically in mapping the geographical distribution of the species and to connect that localities by an individual track. The congruence of two or more individual tracks indicates a generalized track, which indicates an ancestral biota distributed in the past and posteriorly fragmented (Craw *et al.*, 1999). The development of the panbiogeographic and cladistic meth-

ods emphasize that the Earth and its biota have evolved together showing a common history (see Morrone and Crisci, 1995 for a review).

Morrone (2001a) has recently suggested that the panbiogeographic method can be used in a first step to propose hypotheses of primary biogeographic homologies to refer to a common biogeographic history of the biota. In a second step, cladistic biogeography deals with secondary biogeographic homology, showing that a biogeographic analysis may include both approaches, in a two-stage analysis.

In spite of the increase in panbiogeographic studies in the Neotropical region, there is none using Muscidae flies. Within the six genera from the Neotropical region with known cladistic analysis (Carvalho, 1999; Pamplona, 1999; Couri and Motta, 2000; Carvalho and Couri, 2002b), we have chosen three genera to undertake a panbiogeographic analysis.

The sister groups *Cyrtoneurina* Giglio-Tos and *Cyrtoneuropsis* Malloch. The genera *Cyrtoneurina* and *Cyrtoneuropsis* are sister groups (Pamplona, 1999; Couri and Carvalho, in press) and both have species distributed in the Neotropical region. All their species were included in the present analysis, even the widespread ones, although they are less informative. On the other hand, there are no species of those genera occurring in southern South America (see Amorim and Pires, 1996 and Morrone, 2001c for a definition of this area).

Cyrtoneurina, a monophyletic genus, is comprised of nine species (Pamplona, 1999), distributed from Mexico to Brazil. Three species (*C. arleriopsis*, *C. cylindrica*, and *C. monstrata*), which are represented in only one or two localities, were not included in the analysis. The remaining six species, based on their distributional range, are shown by individual tracks in figure 1. Based on the species, basically four generalized tracks result, which are shown in figure 2 (tracks a-g). *C. geminata* and *C. uber* (tracks a, b, and d) compose a generalized track from the Caribbean to the Amazonian region, which is interrupted in northern Central America and northern South America. *C. confusa* and *C. uber* compose a generalized track in the southern Caribbean subregion (track c). *C. confusa* and *C. geminata* compose a track from southern of the Amazonian subregion to the Parana subregion, interrupted in the boundaries of northeastern/southeastern Brazil (tracks e and f). *C. biseta*, *C. geminata*, *C. costalis* and *C. crispaseta* are part of a generalized track in the Parana subregion (track g). These three latter species form a clade in Pamplona (1999) (Fig. 3). On the other hand, *C. uber* is a basal lineage of the remaining species and is distributed throughout the Neotropics (Fig. 1f), whereas *C. costalis*, one of the apical species, has a restricted occurrence (Fig. 1c).

The monophyletic genus *Cyrtoneuropsis* is abundant in the Neotropics, with 33 species ranging from Mexico to Argentina. There are 10 species (*C. brunnea*, *C. flaviantennata*, *C. fuscisquama*, *C. immunda*, *C. maculipennis*, *C. ocasionalis*, *C. pallipes*, *C. paraescita*, *C. similata*, and *C. varicolor*) ranged in only one or two localities, which were excluded from the analysis. Individual tracks of the remaining 23 species are shown in figure 4. The analysis resulted in 18 generalized tracks (Fig. 5), which are concentrated in the Caribbean subregion (a-h), where basically occur four tracks, one of them composed by several widespread species (tracks a, b, e, f, g) (Fig. 5). Tracks j and i are also present in this region. In the Amazonian subregion, there are eight tracks (k-s), where track m is basically the same as track k. In the Chacoan subregion there are only two tracks, one in the Caatinga province (track p) and another in the Cerrado province (track t). In

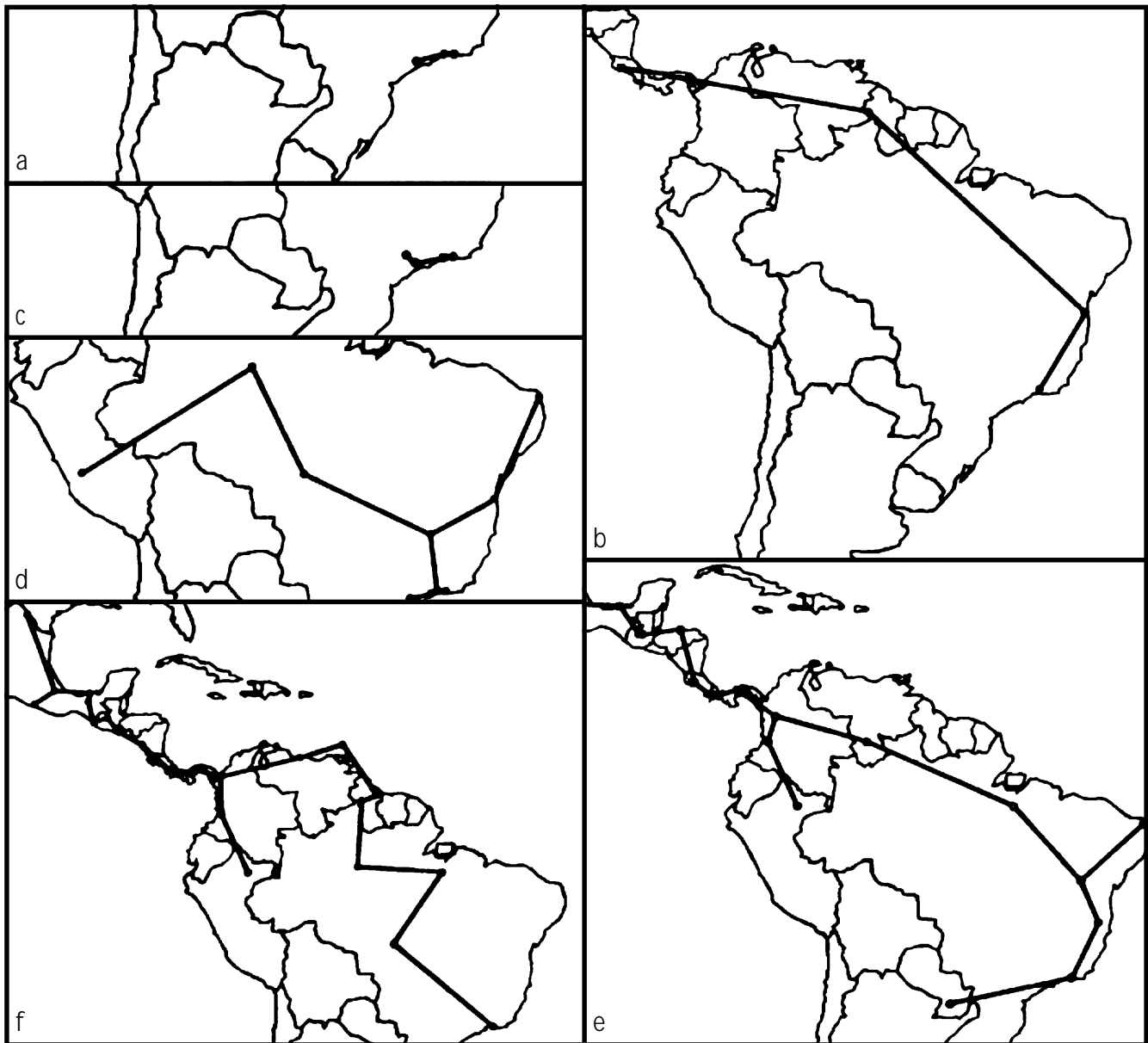


Fig. 1. Individual tracks of six species of *Cyrtoneurina*: a, *C. biseta*; b, *C. confusa*; c, *C. costalis*; d, *C. crispaseta*; e, *C. geminata*; f, *C. uber*.

the Parana subregion there are also two tracks (u and v), both in the Brazilian Atlantic Forest province. Three tracks are corroborated by Pamplona's (1999) cladogram (Fig. 6): track f, *C. polystigma*, *C. wulpi*, *C. inuber*, *C. veniseta*, these two last one are sister groups; track h, *C. mimica* and *C. multomaculata* are sister groups; and track p, *C. beebei* and *C. protosetosa* are probably sister groups. On the other hand, *C. armipes* forms a generalized track with *C. conspersa*, which also could indicate a phylogenetic pattern. As *Cyrtoneurina* and *Cyrtoneuropsis* are sister groups and occur in whole Neotropics, it is possible to infer that the distributional range of their common ancestral is in the tropics of Central or South America.

The monophyletic genus *Bithoracochaeta* Stein. *Bithoracochaeta* Stein is a monophyletic genus comprised of nine species (Motta and Couri, 1999), which has already studied through a cladistic analysis (Couri and Motta, 2000). Their species are distributed from Mexico to Argentina, with some widespread species (Couri and Carvalho, 2002). Although these widespread species are less informative, they were included in

the analysis. Four species (*B. equatorialis*, *B. nigricornis*, *B. maricaensis*, and *B. varicornis*) are represented by one or two localities and thus were not analyzed. Tracks of the remaining five species are shown in figure 7.

From these, basically three generalized tracks result (Fig. 8). *B. flavicoxa* and *B. leucoprocta* compose a generalized track in the Caribbean subregion (track a). In the Amazonian subregion, track b is composed by *B. flavicoxa* and *B. annulata*, that could probably be part of a larger track, which also includes the previous one. In the Parana subregion, there is one generalized track, composed by *B. annulata*, *B. atricornis*, and *B. leucoprocta* (track c) and another (track d and e) composed by *B. atricornis* and *B. leucoprocta* which is part of the previous one (Fig. 8).

Comparing the generalized tracks obtained with the cladogram of *Bithoracochaeta* proposed by Couri and Motta (2000) (Fig. 9), there is no corroboration. Therefore, we could argue there are no biogeographic homology, showing that the genus does not have a common history with the whole area.

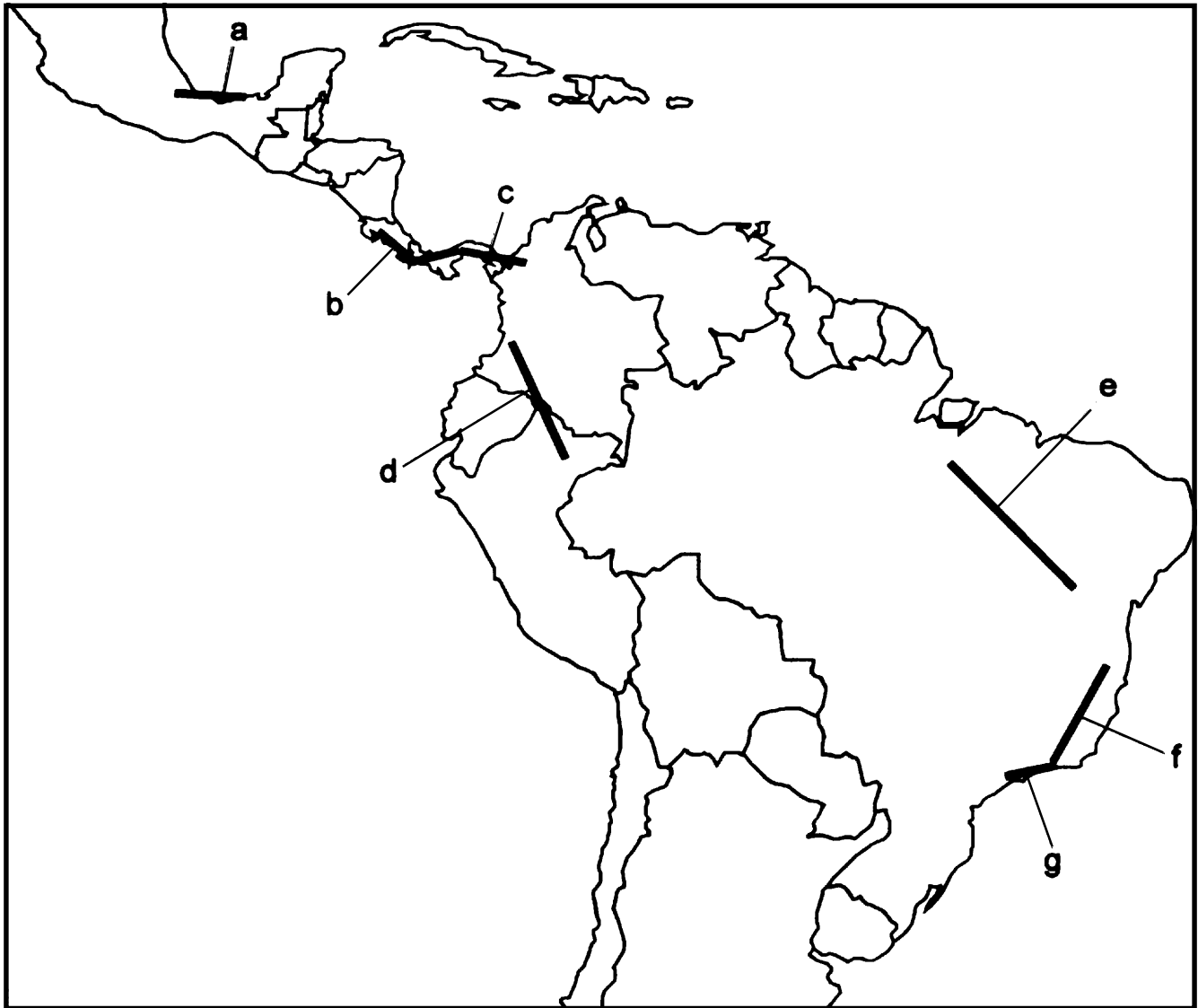


Fig. 2. Generalized tracks of *Cyrtoneurina*: a, b and d = *C. geminata* + *C. uber*; c, *C. confusa* + *C. uber*; e, *C. confusa* + *C. geminata*; f, *C. confusa* + *C. geminata*; g, *C. biseta* + *C. geminata* + *C. crispaseta* + *C. costalis*. See text for explanation.

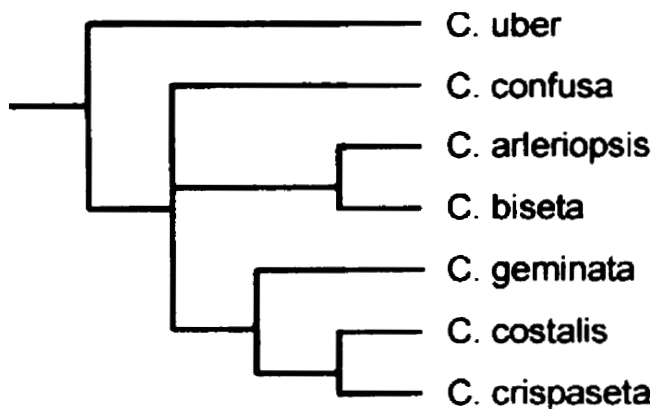


Fig. 3. Cladogram of the species of *Cyrtoneurina* (modified from Pamplona, 1999).

Parsimony Analysis of Endemicity (PAE)

The exclusive occurrence of taxa in the locality or a particular area (endemic taxa) has a strong significance. In PAE, the parsimony analysis is applicable to taxa which share localities, in order to postulate biotic relationships, by producing an area cladogram. In this sense, PAE classifies areas or localities (analogous to taxa) by their shared taxa (analogous to characters) in agreement with the most parsimonious solution. On the other hand, like systematics, an outgroup could be included to root the cladogram. Since it is difficult to infer the ancestral area, we included an area coded with zeros (Rosen and Smith, 1988; Morrone, 1994b; Morrone and Crisci, 1995; Luna-Vega *et al.*, 2001). Concerning the homology of areas, Craw *et al.* (1999) suggested that biogeographic homology could be recognized through PAE, which is equivalent to a generalized track (see also Morrone, 2001a).

In the present analysis, a map of southern South America was divided into quadrants of five grades of latitude x five grades of longitude

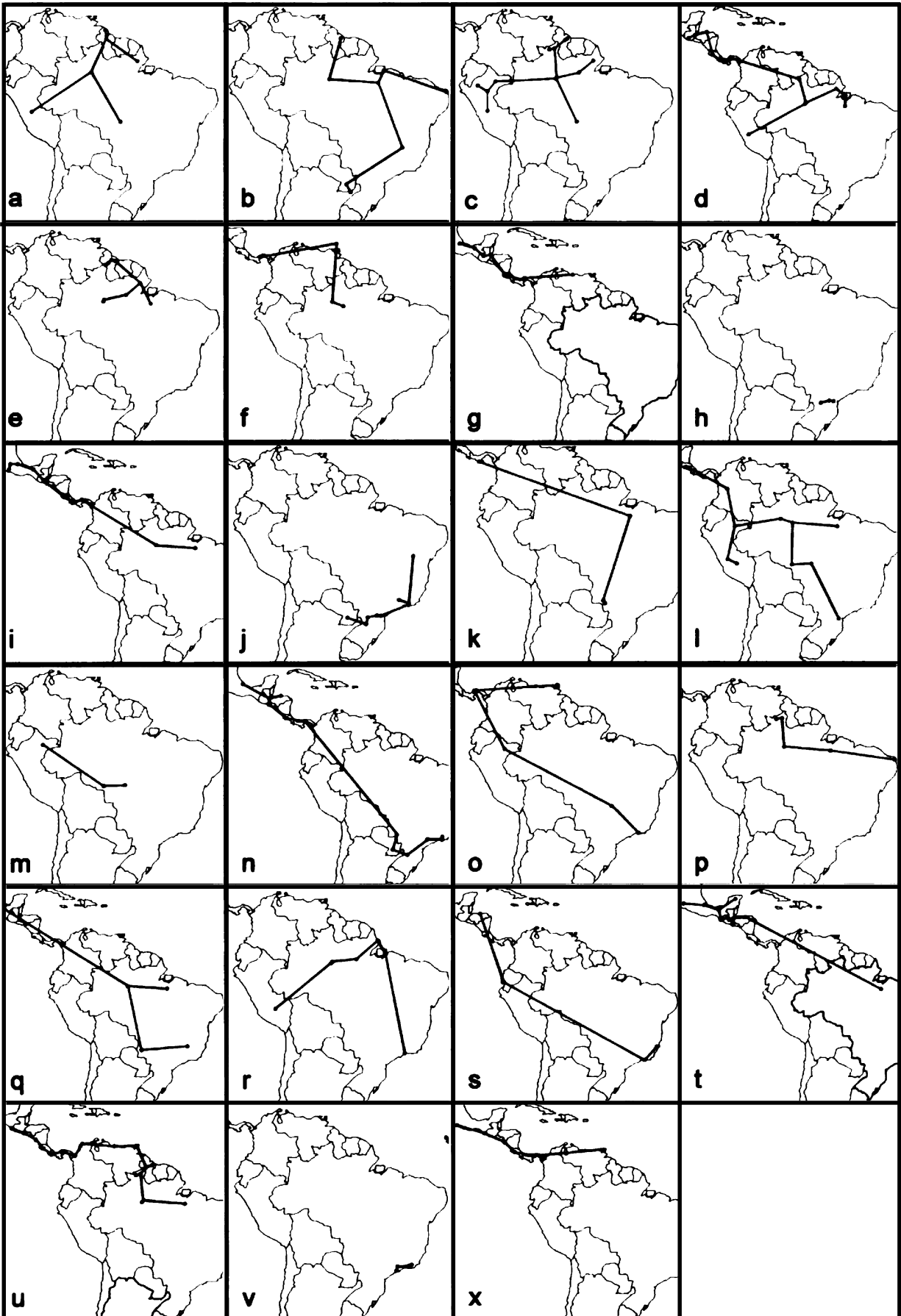


Fig. 4. Individual tracks of 23 species of *Cyrtoneuropsis*: a, *C. armipes*; b, *C. beebei*; c, *C. conspersa*; d, *C. dubia*; e, *C. fuscicosta*; f, *C. gemina*; g, *C. gluta*; h, *C. incognita*; i, *C. inuber*; j, *C. mellina*; k, *C. mimica*; l, *C. multomaculata*; m, *C. neotrita*; n, *C. polystigma*; o, *C. praenubila*; p, *C. protosetosa*; q, *C. rescita*; r, *C. seriata*; s, *C. spilopecta*; t, *C. steini*; u, *C. veniseta*; v, *C. walkeri*; x, *C. wulpi*.

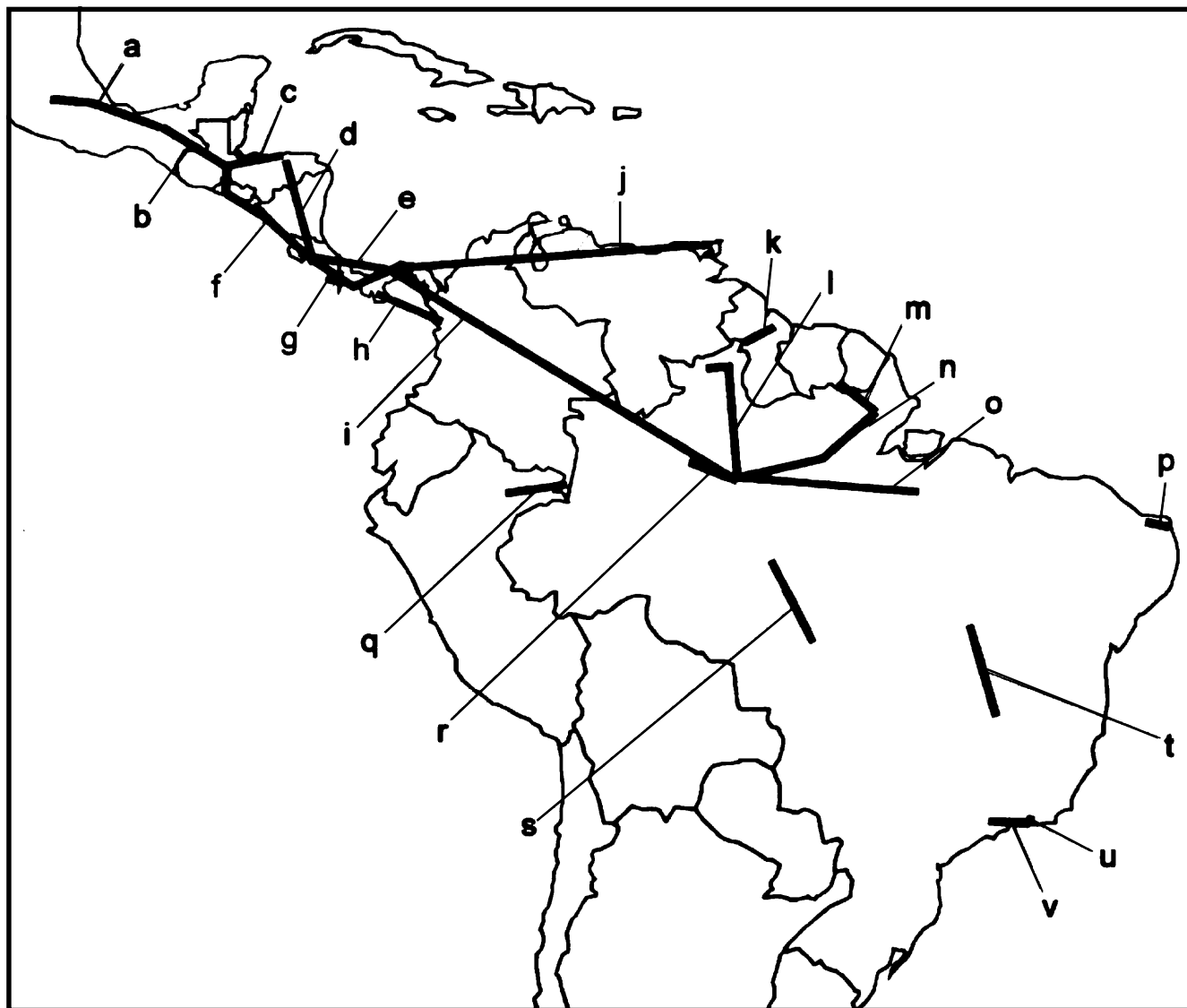


Fig. 5. Generalized tracks of *Cyrtoneuropsis*: a, *C. inuber* + *C. gluta* + *C. polystigma* + *C. steini*; b, *C. gluta* + *C. polystigma* + *C. rescita*; c, *C. dubia* + *C. polystigma* + *C. steini*; d, *C. spiloptera* + *C. dubia*; e, *C. gluta* + *C. polystigma* + *C. wulpi*; f, *C. inuber* + *C. polystigma* + *C. veniseta* + *C. wulpi*; g, *C. dubia* + *C. inuber* + *C. veniseta*; h, *C. mimica* + *C. multimaculata*; i, *C. rescita* + *C. inuber*; j, *C. gluta* + *C. praenubila* + *C. wulpi*; k, *C. armipes* + *C. fuscicosta* + *C. veniseta*; l, *C. conspersa* + *C. protosetosa* + *C. veniseta*; m, *C. armipes* + *C. fuscicosta*; n, *C. conspersa* + *C. fuscicosta*; o, *C. inuber* + *C. multimaculata* + *C. protosetosa* + *C. rescita*; p, *C. beebei* + *C. protosetosa*; q, *C. conspersa* + *C. multimaculata*; r, *C. gemina* + *C. multimaculata*; s, *C. armipes* + *C. conspersa*; t, *C. seriata* + *C. beebei*; u, *C. mellina* + *C. polystigma*; v, *C. polystigma* + *C. walkerii*. See text for explanation.

(Fig. 10). Based on 22 quadrants (A to V), a data matrix was constructed by coding 1 for presence and 0 for absence of species of the genera examined. The cladogram was constructed with WINCLADA (Nixon, 1999, version 0.9.9 beta) and NONA (Goloboff, 1993, version 2.0), through heuristic searches and, whenever necessary, a strict consensus cladogram was constructed.

The sister groups *Apsil* Malloch and *Reynoldsia* Malloch. *Apsil* Malloch and *Reynoldsia* Malloch are monophyletic genera and sister groups according to a cladistic analysis of the tribe Coenosini (Couri and Pont, 2000). They are endemic to Patagonia and southern Chile and were studied using cladistic methodology by Carvalho and Couri (2002b).

Apsil is comprised of 10 species (Couri and Carvalho, 2002); *A. diminuta* was not included in this analysis. The analysis of the data matrix yielded four trees (10 steps, CI = 90, RI = 66) and a strict consensus was constructed (Fig. 11). Two species, *A. biseta* and *A. maculipennis*, are synapomorphic for

the whole area, since they are widespread in the Subantarctic subregion (Morrone, 2001c). PAE also recognized a smaller area of endemism, defined by *A. apicata*, *A. dilatata*, *A. flavipalpis*, *A. pennata*, and *A. spatulata*. *Reynoldsia* is comprised of nine species (Couri and Carvalho, 2002); *R. robusta* and *R. trochanterata* were not included in the analysis. The analysis of the data matrix yielded a single tree (7 steps, CI = 100, RI = 100) (Fig. 12). PAE recognized only one area of endemism, defined by *R. aurifera*, *R. brevitarsis*, *R. coxata*, and *R. rufoapicata*.

According to Carvalho and Couri (2002b), distributional patterns of species of *Apsil* is more restricted than those of *Reynoldsia*. *A. atripes* is the only *Apsil* species occurring in the Central Chilean subregion (see Morrone *et al.*, 1997 and Posadas and Morrone, 2001 for a definition of this subregion). There are no *Reynoldsia* species in the Central Chilean subregion. On the other hand, the same area of endemism within the Subantarctic subregion was indicated by both genera. As they are sister groups, it is possible that the distributional range of its common ancestor is in the Chilean forests.

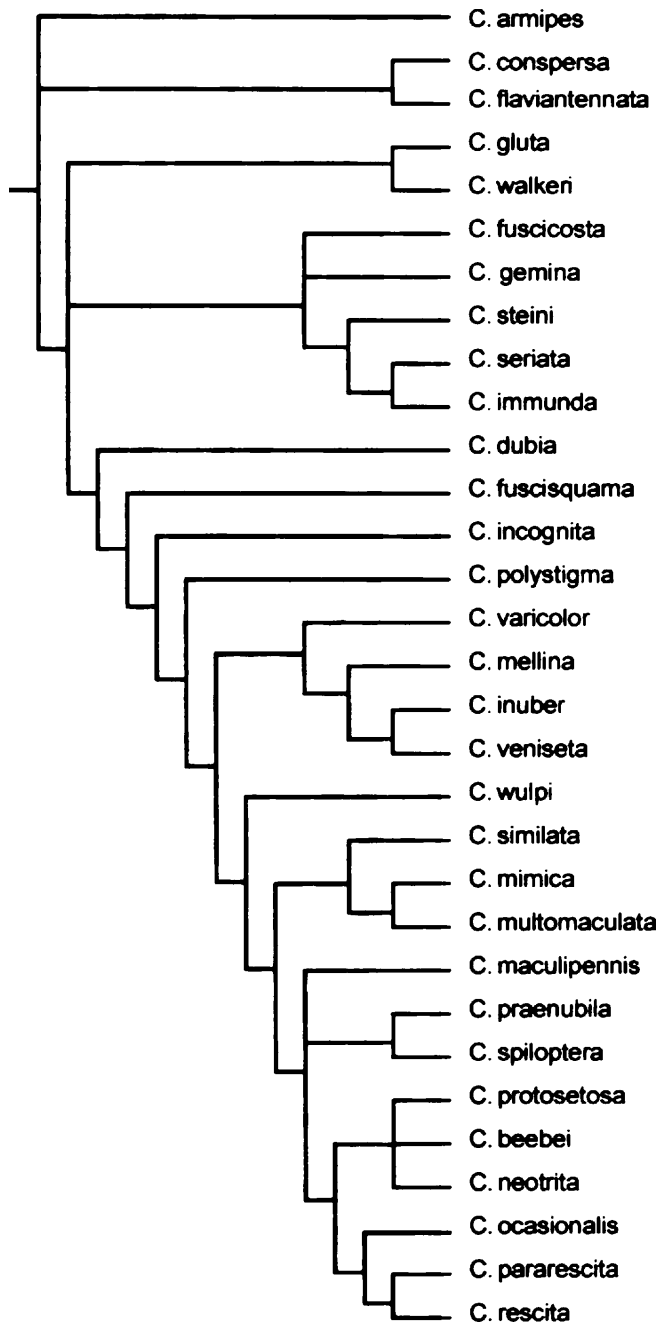


Fig. 6. Cladogram of the species of *Cyrtoneuropsis* (modified from Pamplona, 1999).

Palpibracus Rondani. *Palpibracus* is an endemic genus of Muscidae with 18 species distributed in the southern South America (Carvalho and Couri, 2002a); *P. carvalhoi* and *P. valdiviensis* were not included in the analysis. There is no cladistic study for its species (Carvalho, 1989). The analysis of the data matrix yielded a single tree (21 steps, CI = 76, RI = 72) (Fig. 13). PAE recognized two major areas of endemism: one, defined by *P. apicalis*, *P. fasciculatus*, *P. lancifer*, and *P. univittatus*, which is subordinated to a basal one, defined by *P. peruvianus*, *P. separatus*, *P. spicatus*, and *P. trivittatus*; and another defined by *P. pilosus* and *P. reynoldsi*.

Cladistic biogeography

The methodology of cladistic biogeography, by replacing the taxon names by the areas where they occur, generates biological area cladograms

(see Morrone and Crisci, 1995 for methodological procedures). The first study using a cladistic biogeographic approach to Muscidae flies in the Neotropical region was made by Carvalho (1999), with *Souzalopesmyia* Albuquerque, an unusual muscid genus. He argued that based on the position of the basal clade, *S. amazonica*, the genus may have had its ancestor back in the Late Cretaceous (Fig. 14). Amorim and Pires (1996), corroborated by other studies, argued that the first division in the continental Neotropical region occurred in the Late Cretaceous, suggesting a northwestern track against a southeastern track (Fig. 15).

Carvalho and Couri (2002b) compared the taxon area cladograms of *Apsil* Malloch and *Reynoldsia* Malloch with some biogeographic patterns of endemic taxa in southern South America (Crisci *et al.*, 1991; Morrone, 1993, 1994a; Morrone *et al.*, 1994a, 1997). They found a strong congruence, and hypothesized that those patterns were due to vicariance (Amorim and Pires, 1996; Morrone *et al.*, 1997). As it has been understood in the recent years, the Neotropical region seems to be composed by at least two different main biogeographic elements, each with different intercontinental relationships: the circumtropical and the circumtemperate components (Cabrera and Willink, 1973; Crisci *et al.*, 1991; Amorim and Tozoni, 1994; Amorim and Pires, 1996). Concerning to the circumtropical element, the eastern portion of South America is assigned to generalized tracks which connect it to the Tropics of the Old World (Morrone, 2001b,c); its northern limits are now understood since a better definition of the Mexican transition zone was recently presented (Marshall and Liebherr, 2000).

Areas of endemism in South America

Determining the distributional pattern of the species is first step of any biogeographic analysis; however, the main difficulty in undertaking biogeographic analyses is the definition of areas of endemism. To define these areas, it is necessary to use methods that generate hypotheses maximizing the consistency of distribution of the largest number of species. The delimitation of an area of endemism without taking the phylogeny into consideration, can result in erroneous relationships among the areas.

The areas of endemism of Muscidae, based on the analyzed genera, is basically coincident with the subregions and provinces found by Morrone (2001c). In the Caribbean subregion there are three generalized tracks (a-c); in the Amazonian subregion, there is only track d; and in the Parana subregion there is only track e (Fig. 16). In southern South America, there is a generalized track for Muscidae (tracks f-h), included in the Subantarctic subregion. This is one of the best studied subregions of the Neotemperate region (Amorim and Pires, 1996; Posadas and Morrone, 2001; see Morrone, 2001c for a review).

Age of the Muscidae

What is the age of the family Muscidae? There are only three ways to determine the age of any monophyletic group: the age of fossils and the distribution pattern of its species (Hennig, 1965) or, by molecular clocks. There are very few published molecular studies of Muscoidea (Vossbrinck and Friedmann, 1989; Bernasconi *et al.*, 2000), and none for Muscidae. Therefore, based on the increase of biogeographic studies, it is possible to indicate the probable age of the Muscidae, using the distributional patterns of their species. Couri and Carvalho (in press) found, based on a cladistic analysis, that *Philornis* Meinert and *Passeromyia* Rodhain and Villeneuve, genera whose its species parasite birds, belong to the same clade (Fig. 17). The biogeographic interpretation of this phylogenetic pattern resembles a Gondwanian pattern of distribution, also found in several basal or apical groups of Diptera (Papavero, 1977; Amorim and Tozoni, 1994), which could suggest that the common ancestor of those genera is older than what we have thought before. Perhaps it could have appeared before latest Cretaceous, the previous hypothetical age postulated for Muscidae (Hennig, 1965).

Other interesting relationship is shown by the clade (*Charadrella* (*Allaudinella* (*Aethiopomyia*, *Ochromusca*))) (Fig. 17). The former genus

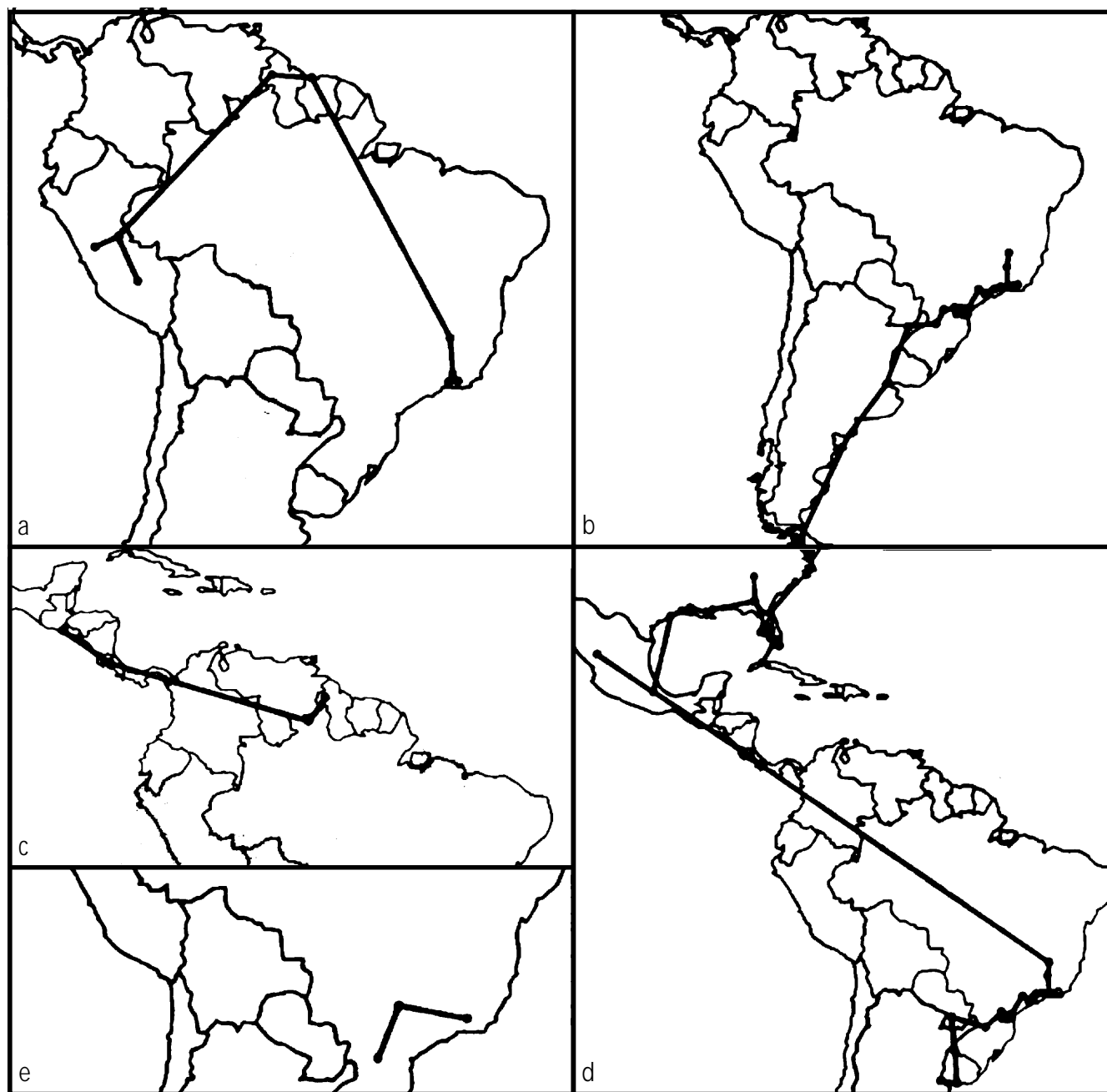


Fig. 7. Individual tracks of five species of *Bithoracochoeta*: a, *B. annulata*; b, *B. atricornis*; c, *B. flavicoxa*; d, *B. leucoprocta*; e, *B. plumata*.

occurs exclusively in the Neotropical region, whereas the others occur exclusively in the Afrotropical region (Couri and Carvalho, in press). Their cladistic relationships also corroborate a Gondwanian distribution, pushing the age of the clade back to middle or early Cretaceous. This would be the oldest hypothetical age for muscid flies, since Pont and Carvalho (1997) described the first three fossil amber muscids – two species included in *Phaonia* Robineau-Desvoidy, a recent genus, and another species included in *Archaeopolletes* Pont and Carvalho, an extinct taxon – known from Dominican amber (about 15–20 millions of years ago). Such amber age could be understood as the minimum age of Muscidae species (Couri and Carvalho, in press). Evenhuis (1994), however, found an Eocene fossil doubtly identified as Muscidae.

On the other hand, the age of Anthomyiidae could also reflect the age of Muscidae, as they are considered sister groups (Michelsen, 1991, 2000). Michelsen (2000) suggested a minimum age for Antho-

myiidae plus Muscidae of 40+ m.y.a. (Lower Eocene). As pointed above, based on the distribution patterns of some species, the oldest age (middle or early Cretaceous) is only a hypothesis since it was based on a partial phylogenetic analysis of the family, although some of the resulted monophyletic groups inside the family have corroborated the previously proposed classifications. The question if the break up of Gondwanaland could have been important to affect the pattern of distribution of these genera of Muscidae will still remains as an open question.

Therefore, the hypothetical age of this family still remains to be clearly defined while more historical biogeographic studies will be available, together with more fossil evidence. Grimaldi and Cumming (1999) recorded the oldest cyclorrhaphan larvae from Cretaceous amber, but they did not classified it into any family. However, according to them, calyptrates did not appear until Cenozoic.

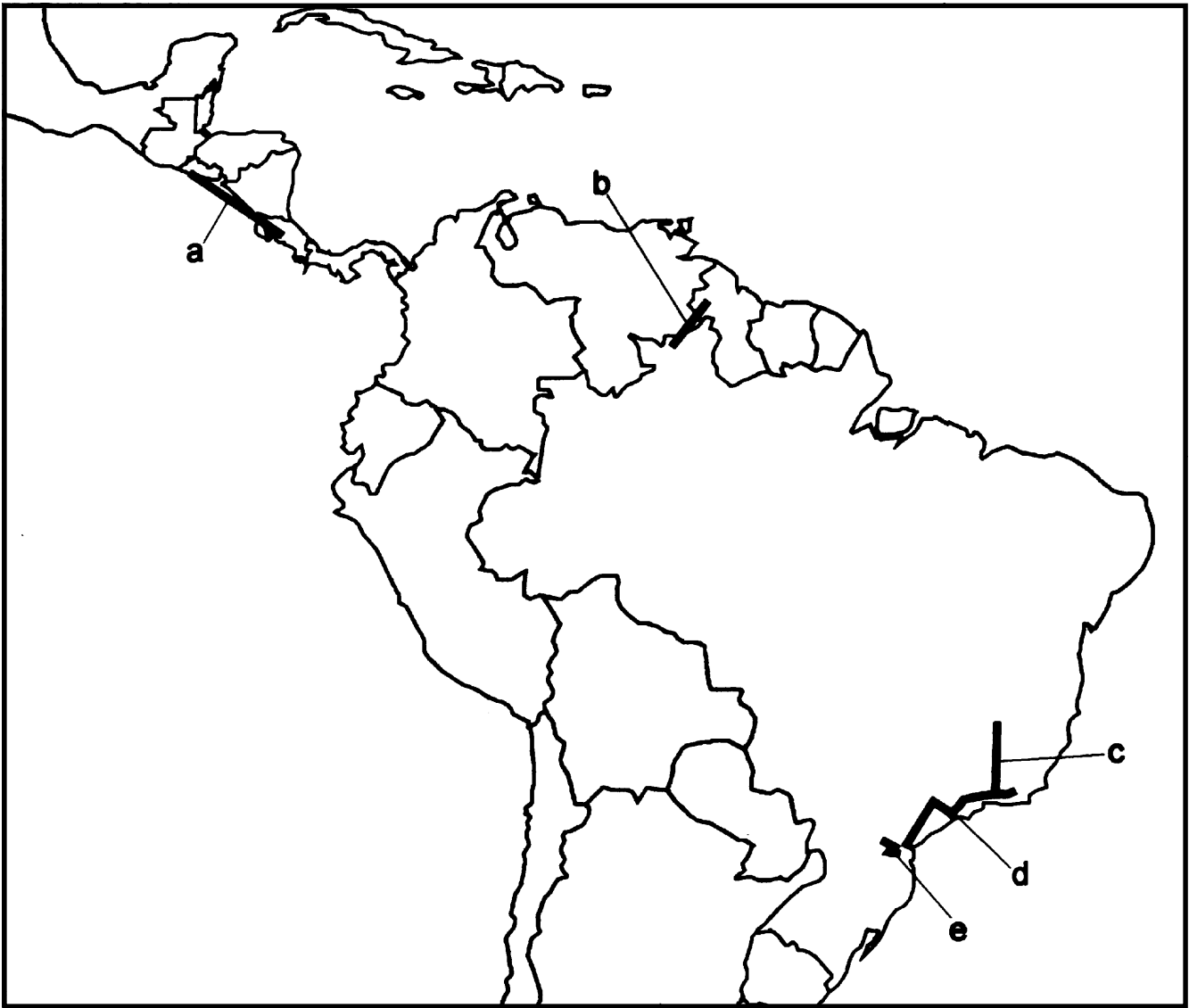


Fig. 8. Generalized tracks of *Bithoracochaeta*: a, *B. flavicoxa* + *B. leucoprocta*; b, *B. annulata* + *B. flavicoxa*; c, *B. annulata* + *B. atricornis* + *B. leucoprocta*; d and e, *B. atricornis* + *B. leucoprocta*. See text for explanation.

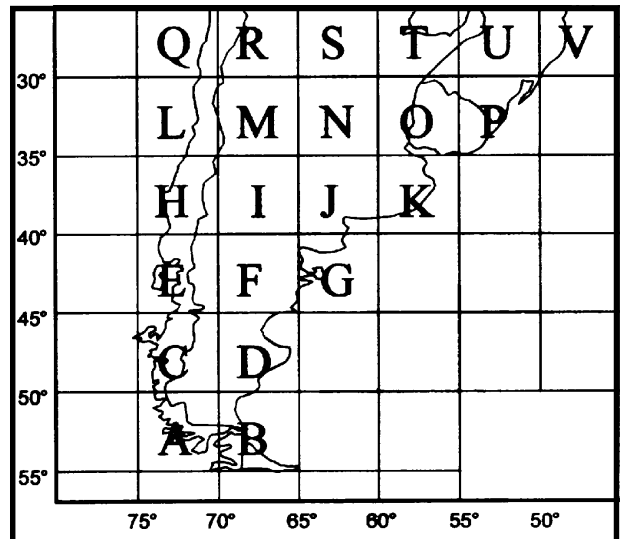
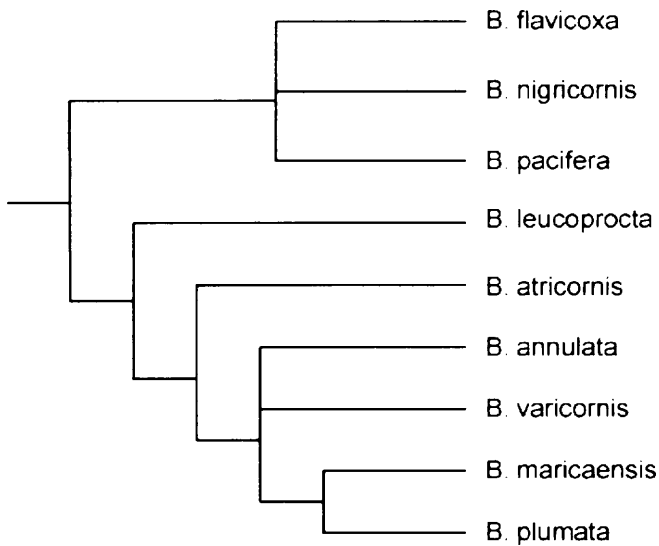


Fig. 9. Cladogram of the species of *Bithoracochaeta* (modified from Couri and Motta, 2000).

Fig. 10. Grid of southern South America with 22 quadrants (A-V) used in the PAE.

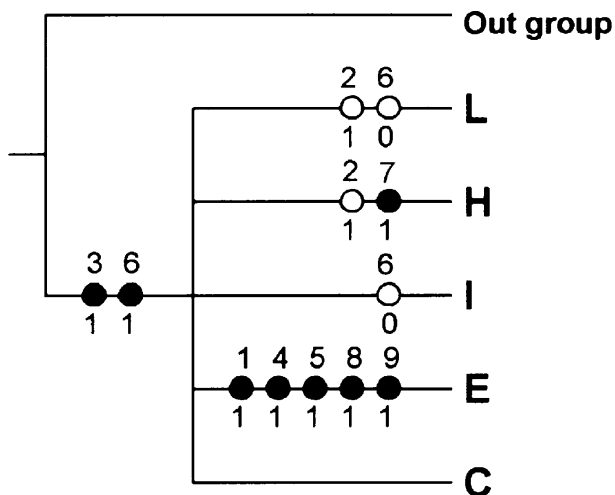


Fig. 11. Area cladogram of *Apsil*: 1, *A. apicata*; 2, *A. atripes*; 3, *A. biseta*; 4, *A. dilata*; 5, *A. flavipalpis*; 6, *A. maculipennis*; 7, *A. maculiventris*; 8, *A. pennata*; 9, *A. spatulata*. C, E, H, I, L = quadrants. See text for explanation.

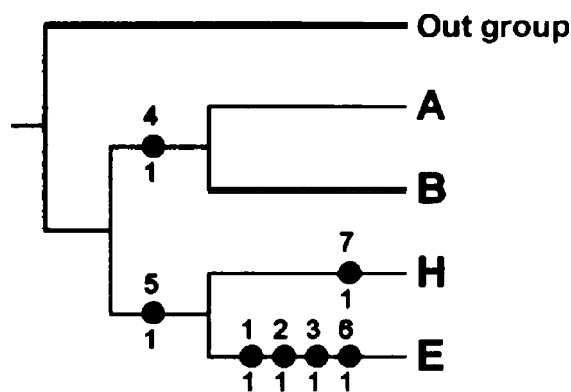


Fig. 12. Area cladogram of *Reynoldsia*: 1, *R. aurifera*; 2, *R. brevitarsis*; 3, *R. coxata*; 4, *R. pectinata*; 5, *R. pteropleuralis*; 6, *R. rufoapicata*; 7, *R. scutellata*. A, B, E, H = quadrants. See text for explanation.

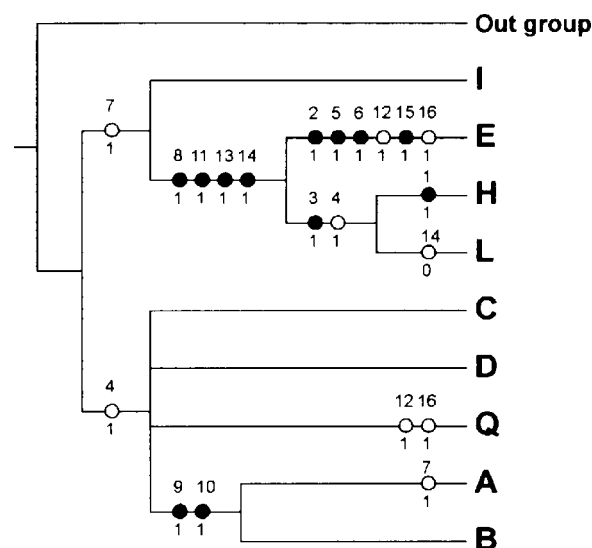


Fig. 13. Area cladogram of *Palpiacus*: 1, *P. albuquerquei*; 2, *P. apicalis*; 3, *P. chilensis*; 4, *P. confusus*; 5, *P. fasciculatus*; 6, *P. lancifer*; 7, *P. nigriventris*; 8, *P. peruvianus*; 9, *P. pilosus*; 10, *P. reynoldsi*; 11, *P. separatus*; 12, *P. similis*; 13, *P. spicatus*; 14, *P. trivittatus*; 15, *P. univittatus*; 16, *P. veneris*. A, B, C, D, E, H, I, L, Q = quadrants. See text for explanation.

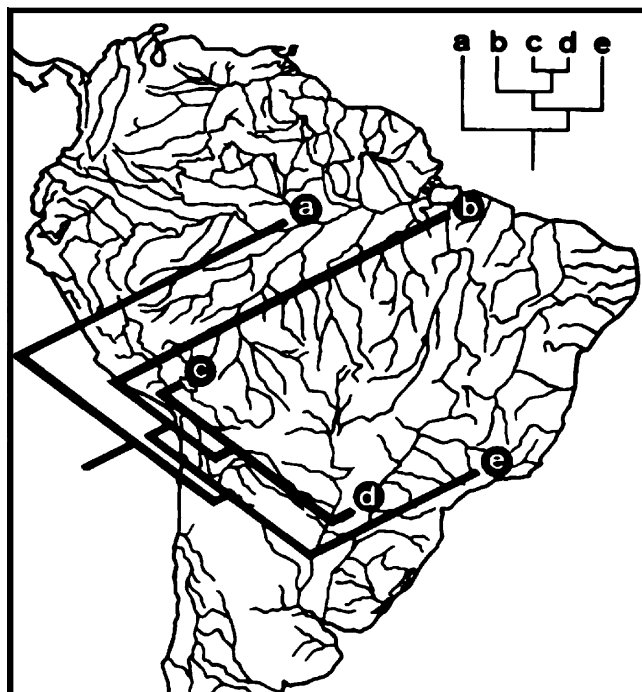


Fig. 14. Geographical distribution of species of *Souzalespesmyia*, with the taxon cladogram superimposed: a, *S. amazonica*; b, *S. paraensis*; c, *S. singularis*; d, *S. sulina*; e, *S. carioca* (from Carvalho, 1999).

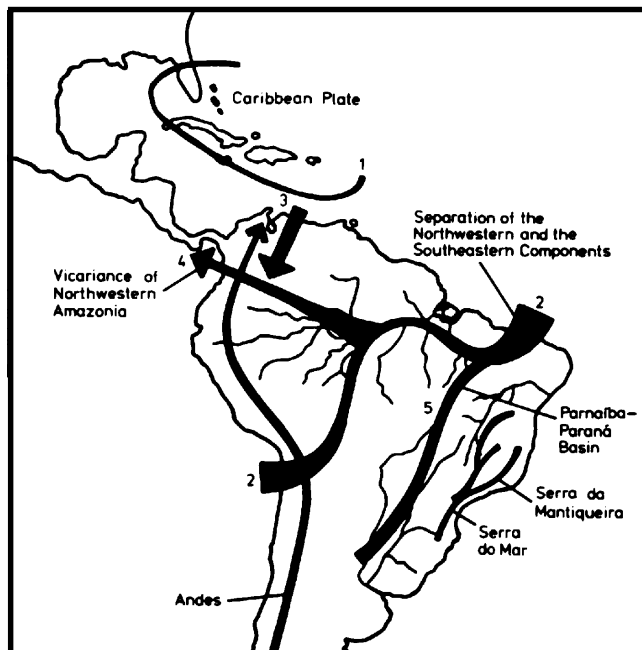


Fig. 15. Summary of the main vicariance barriers in the history of the Neotropical region. 1, Caribbean Plate detachment from the mainland; 2, separation between the northwestern and southeastern main components, the line along the rivers Amazonas/Madeira/Mamoré in the Amazonian basin; 3, epicontinental sea formation in the Maracaibo area; 4, a large division in northwestern Amazonia (not related to date to any geological event); 5, Middle to Late Cretaceous water connection between the Parnaíba and Paraná basins (redrawn from Amorim and Pires, 1996).



Fig. 16. Generalized tracks for Muscidae in the Neotropical region based on individual tracks of six genera of Muscidae; a, *Cyrtoneurina* + *Cyrtoneuropsis*; b, *Bithoracochoeta* + *Cyrtoneuropsis*; c, *Cyrtoneurina* + *Cyrtoneuropsis*; d, *Bithoracochoeta* + *Cyrtoneuropsis*; e, *Bithoracochoeta* + *Cyrtoneurina* + *Cyrtoneuropsis*; f, *Apsil* + *Palpibracus*; g, *Apsil* + *Palpibracus*; h, *Apsil* + *Palpibracus* + *Reynoldsia*.

Conclusions

It seems that the distributional patterns of the genera analyzed show congruence with the history of the Neotropics. From the analysis of the species, we found generalized tracks for *Cyrtoneurina* and *Cyrtoneuropsis*, which were corroborated by cladistic analysis. Using PAE of some genera from southern South America (*Apsil*, *Reynoldsia*, and *Palpibracus*) we found areas of endemism that were also corroborated by previous studies.

The congruence of the areas of endemism indicate that the patterns of distribution of Muscidae were due to vicariant events in the

past, however, there are much more to be done with Muscidae when more specimens are available. The analysis of other genera of the family is still required for a better understanding of the historical biogeography of Muscidae in the region.

The present study, based uniquely on biogeographic methods that reconcile both biogeographic and phylogenetic patterns of the biota, we suggest that the Muscidae age is back to middle or early Cretaceous. The biogeographic hypothesis herein proposed for the family will be more consistent when more evidence on distributional ranges and phylogeny is accumulated. We greatly hope that further studies using Neo-

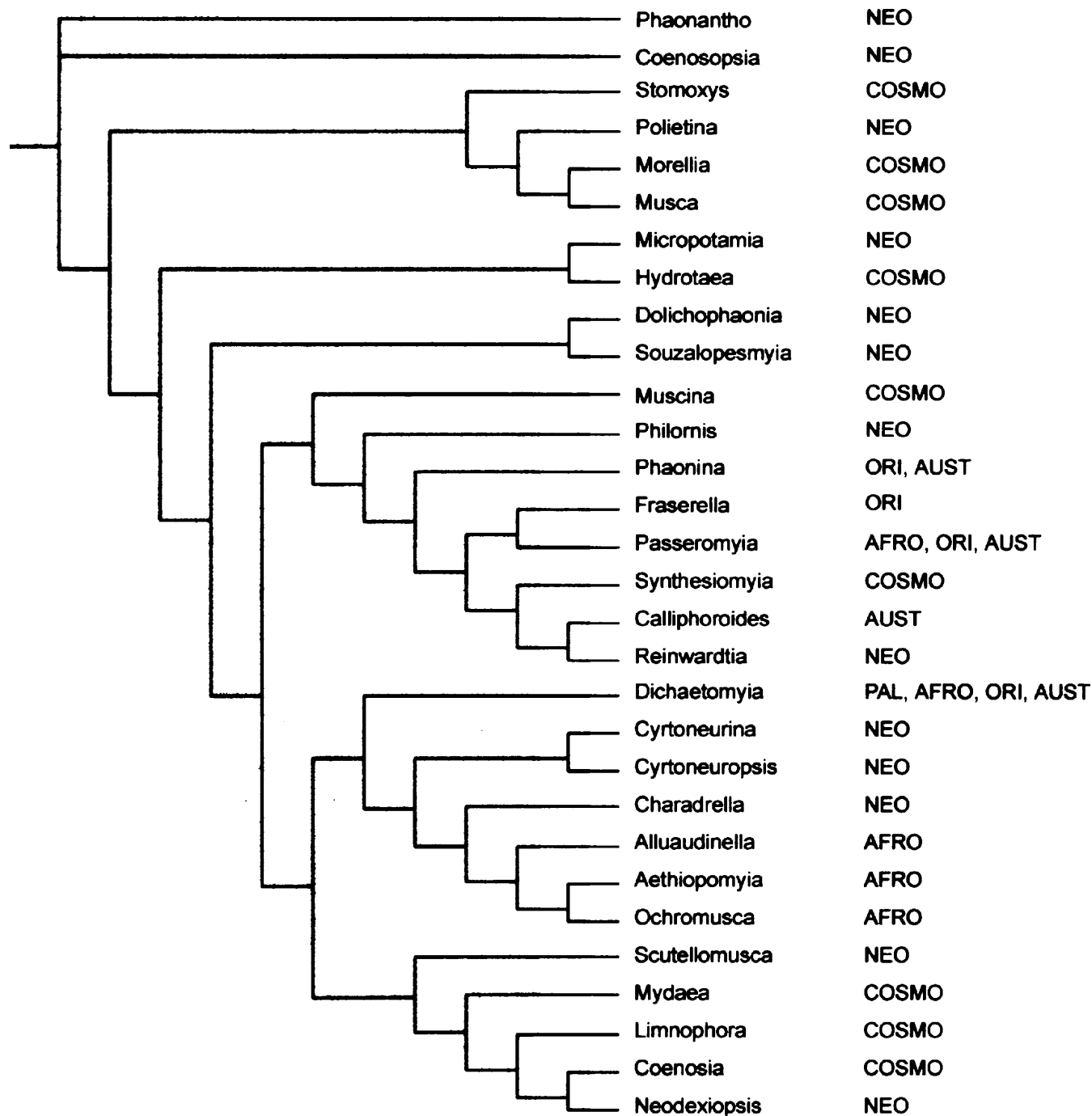


Fig. 17. Cladogram of selected genera of Muscidae. Abbreviations: AUST, Australian region; AFRO, Afrotropical region; COSMO, cosmopolitan; NEO, Neotropical region; ORI, Oriental region; PAL, Palearctic region (modified of Couri and Carvalho, in press).

tropical Muscidae flies as models be made in order to contribute to a better understanding of the evolution of the region.

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References

Amorim, D. de S. 2001. Dos Amazonas, pp. 245-255. In: Llorente Bousquets, J. and J. J. Morrone (eds.), *Introducción a la biogeografía*

- histórica en Latinoamérica: Teorías, conceptos, métodos y aplicaciones, Las Prensas de Ciencias, UNAM, México, D.F.
- Amorim, D. de S. and M.R.S. Pires. 1996. Neotropical biogeography and a method for maximum biodiversity estimation, pp. 183-219. In: Bicudo, C. E. M. and N. A. Menezes (eds.), *Biodiversity in Brazil, a first approach*, CNPq, São Paulo
- Amorim, D. de S. and S. N. S. Tozoni. 1994. Phylogenetic and biogeographic analysis of the Anisopodoidea (Diptera, Bibionomorpha), with an area cladogram for intercontinental relationships. *Rev. Bras. Ent.*, 38: 519-543.
- Bernasconi, M.V., C. Valsangiacomo, J. -C. Piffaretti, and P. I. Ward. 2000. Phylogenetic relationships among Muscoidea (Diptera: Calyptratae) based on mitochondrial DNA sequences. *Ins. Mol. Biol.*, 6: 67-74.
- Cabrera, A.L. and A. Willink. 1973. *Biogeografía de América Latina*. Monografía 13, Serie de Biología, OEA, Washington DC.
- Carvalho, C. J. B. de. 1989. Revisão das espécies e posição sistemática de *Palpibracus Rondani* (Diptera, Muscidae). *Rev. Bras. Zool.*, 6:325-376.
- Carvalho, C. J. B. de. 1999. Revision, cladistics and biogeography of the Neotropical genus *Souzalopesmyia* Albuquerque (Diptera: Muscidae). *Proc. Ent. Soc. Washington*, 101: 123-137.
- Carvalho, C. J. B. de and M.S. Couri. 2002a. Part I, Basal Muscidae, pp. 17-132. In: Carvalho, C.J.B. de (ed.), *Muscidae (Diptera) of the Neotropical region: Taxonomy*, Editora Universidade Federal do Paraná, Curitiba.
- Carvalho, C. J. B. de and M. S. Couri. 2002b. A cladistic and biogeographic analysis of *Apsil Malloch* and *Reynoldsia Malloch* (Diptera, Muscidae) of southern South America. *Proc. Ent. Soc. Washington*, 104: 309-317.
- Carvalho, C. J. B. De, M. S. Couri, A. C. Pont, D. Pamplona, and S. M. Lopes. 1993 Part II. Muscidae, pp. 1-201. In: Carvalho, C. J. B. de (ed.), *A catalogue of the Fanniidae and Muscidae (Diptera) of the Neotropical region*, Sociedade Brasileira de Entomologia, São Paulo.
- Couri, M.S. and C. J. B. de Carvalho. 2000. Recent advances on the Phylogeny and Biogeography of Muscidae (Diptera). Abstracts of the International Congress of Entomology, Book II, Foz do Iguaçu: 925.
- Couri, M.S. and C. J. B. de Carvalho. 2002. Part II, Apical Muscidae, pp. 133-259. In: de Carvalho, C. J. B. (ed.), *Muscidae (Diptera) of the Neotropical region: Taxonomy*, Editora Universidade Federal do Paraná, Curitiba.
- Couri, M.S. and C. J. B. de Carvalho. In press. Systematic relations among *Philornis Meinert*, *Passeromyia Rodhain* and *Villeneuve* and allied genera (Diptera, Muscidae). *Rev. Bras. Biol.*
- Couri, M.S. and H.C.G. da Motta. 2000. Análise cladística de *Bithoracochaeta Stein* (Diptera, Muscidae). *Rev. Bras. Ent.*, 44: 105-108.
- Couri, M.S. and A.C. Pont. 2000. Cladistic analysis of *Coenosia* (Diptera: Muscidae: Coenosinae). *Syst. Ent.*, 25: 373-392.
- Craw, R.C., J.R. Grehan, and M.J. Heads. 1999. *Panbiogeography: Tracking the history of life*. Oxford University Press, Oxford.
- Crisci, J. V., M. M. Gigliano, J. J. Morrone, and S. Roig-Juñent. 1991. Historical Biogeography of South America. *Syst. Zool.*, 40: 152-171.
- Cuny, R. 1980. Revision of the genus *Eudasyphora* Townsend (Diptera: Muscidae), and reflections on its evolution. *Can. Ent.*, 112: 345-373.
- Evenhuis, N. L. 1994. *Catalogue of the fossil flies of the world (Insecta: Diptera)*. Backhuys, Leiden.
- Goloboff, P. A. 1993. *NONA version 2.0. A tree searching program*. MS-DOS program and documentation, distributed by the author.
- Grimaldi, D. and J. Cumming. 1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the *Eremoneura*. *Bull. Amer. Mus. Nat. Hist.*, 239: 1-124.
- Hennig, W. 1965. Vorarbeiten zu einem phylogenetischen System der Muscidae (Diptera: Cyclorrhapha). *Stuttg. Beitr. Naturk.*, 141: 1-100.
- Luna-Vega, I., J. J. Morrone, O. Alcántara Ayala, and D. Espinosa Organista. 2001. Biogeographical affinities among Neotropical cloud forests. *Plant Syst. Evol.*, 228: 229-239.
- Marshall, C.J. and J.K. Liebherr. 2000. Cladistic biogeography of the Mexican Transition Zone. *J. Biogeogr.*, 27: 203-216.
- Michelsen, W. 1991. Revision of the aberrant New World genus *Coenosopsia* (Diptera: Anthomyiidae), with a discussion of anthomyiid relationships. *Syst. Ent.*, 16: 85-104.
- Michelsen, V. 1996. First reliable record of a fossil species of Anthomyiidae (Diptera), with comments on the definition of recent and fossil clades in phylogenetic classification. *Biol. J. Linn. Soc.*, 58: 441-451.
- Michelsen, V. 2000. Oldest authentic record of a fossil calyptrate fly (Diptera): a species of Anthomyiidae from early Cenozoic Baltic amber. *Stud. Dipterol.*, 7: 11-18.
- Morrone, J.J. 1993. Cladistic and biogeographic analyses of the weevil genus *Listroderes Schoenber* (Coleoptera: Curculionidae). *Cladistics*, 9: 397-411.
- Morrone, J.J. 1994a. Distributional patterns of species of Rhytirrhini (Coleoptera, Curculionidae) and the historical relationships of the Andean provinces. *Global Ecol. Biogeogr. Lett.*, 4: 188-194.
- Morrone, J.J. 1994b. On the identification of areas of endemism. *Syst. Biol.*, 43: 438-441.
- Morrone, J.J. 2001a. Homology, biogeography and areas of endemism. *Diver. Distrib.*, 7: 297-300.
- Morrone, J.J. 2001b. A proposal concerning formal definition of the Neotropical and Andean regions. *Biogeographica*, 77: 65-82.
- Morrone, J.J. 2001c. *Biogeografía de América Latina y el Caribe*. M and T – Manuales and Tesis SEA, vol. 3, Zaragoza.
- Morrone, J. J. and J. V. Crisci. 1995. Historical biogeography: Introduction to methods. *Annu. Rev. Ecol. Syst.*, 26: 373-401.
- Morrone, J. J., S. R. Juñent, and J.V. Crisci. 1994. South American Beetles. *Natl. Geogr. Res. Expl.*, 10: 104-115.
- Morrone, J. J., L. Katinas, and J.V. Crisci. 1997. A cladistic biogeographic analysis of Central Chile. *J. Comp. Biol.*, 2: 25-42.
- Motta, H.C.G. da and M.S. Couri. 1999. Revisão das espécies de *Bithoracochaeta Stein* (Diptera, Muscidae). *Rev. Bras. Zool.*, 16: 665-689.
- Nihei, S.S. and C. J. B. de Carvalho. In press. Cladistics and biogeography of *Coenosopsia Malloch* (Diptera, Anthomyiidae), with description of new species from Brazilian Cerrado. *Stud. Dipterol.*
- Nixon, K. C. 1999. *WINCLADA, Beta version 0.9.9*. Published by the author: L.H. Bailey Hortorium, Cornell University, Ithaca, New York.
- Pamplona, D. 1999. Nova caracterização de *Cyrtoneurina Gigliot*, 1893 e descrição de *Paracyrtoneurina* gen. nov. (Diptera, Muscidae). *Rev. Bras. Ent.*, 43: 9-24.
- Papavero, N. 1977. *The world Oestridae (Diptera), mammals and continental drift*. Junk, The Hague.
- Pont, A.C. 1986. Family Muscidae, pp. 57-215. In: Sóos, A. and L. Papp (eds.), *Catalogue of the Palearctic Diptera. Vol. 11*, Hungarian Natural History Museum, Budapest.
- Pont, A.C. 1989. Family Muscidae, pp. 675-699. In: Evenhuis, N. (ed.), *Catalog of the Diptera of the Australasian and Oceanian regions*, Bishop Museum Press, Honolulu and E.J. Brill, Leiden.
- Pont, A.C. and C. J. B. de Carvalho. 1997. Three species of Muscidae (Diptera) from Dominican amber. *Stud. Dipterol.*, 4: 173-181.
- Posadas, P. y J.J. Morrone. 2001. Biogeografía cladística de la subregión Subantártica: un análisis basado en taxones de la Familia Curculionidae (Insecta: Coleoptera), pp. 267-271. In: Llorente Bousquets, J. and J.I. Morrone (eds.), *Introducción a la biogeografía histórica en Latinoamérica: teorías, conceptos, métodos y aplicaciones*, Las Prensas de Ciencias, UNAM, México, D.F.
- Rosen, B. R. and A.B. Smith. 1988. Tectonics from fossils? Analysis of reef coral and sea Urchin distributions from late Cretaceous to Recent, using a new method. En: Audley-Charles, M.G. and A. Hallema (eds.), *Gondwana and Tethys*, Geol. Soc. Lond. Spec. Publ.
- Vossbrinck, C.R. and S. Friedmann. 1989. A 28s ribosomal RNA phylogeny of certain cyclorrhaphous Diptera based upon a hypervariable region. *Syst. Ent.*, 14: 417-431.