

# Taxonomy, cladistics and biogeography of *Coenosopsia* Malloch (Diptera, Anthomyiidae) and its significance to the evolution of anthomyiids in the Neotropics

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**Abstract.** The anthomyiid fly genus *Coenosopsia* Malloch contained five species geographically restricted to the forests of the New World, from southern U.S.A. to southeastern Brazil and Paraguay. Two new species are described here from the Brazilian Cerrado: *C. ferrari* sp.n. and *C. michelseni* sp.n. Viviparity in *C. brasiliensis* Michelsen and *C. peruviana* Michelsen is reported and discussed. A cladistic analysis of the genus was performed using *Fannia bahiensis* Albuquerque (Fanniidae), *Polietina orbitalis* (Stein) (Muscidae), *Anthomyia pluripunctata* (Albuquerque), *Delia platura* (Meigen) and *Phaonantho benevola* Couri (Anthomyiidae) as outgroups. The analysis was carried out using three character weighting schemes: equal, successive and implied weighting. In the phylogenetic relationship ((*C. ferrari*, *C. brasiliensis*) (*C. peruviana* (*C. prima* (*C. michelseni* (*C. floridensis*, *C. mexicana*))))), two major clades were found, one distributed mainly in southeastern South America and the other from northwestern South America to southern North America. Reconciling the phylogeny with the available distributional data, a biogeographical analysis of the genus is proposed and discussed. The pattern found for *Coenosopsia* corroborated a previously proposed model of vicariance events for the Neotropical region. Although the presence of anthomyiid fauna in the region was explained previously on the basis of the North-to-South America dispersal, we suggest an alternative hypothesis, that of a Gondwanan origin for the Neotropical anthomyiids.

## Introduction

The anthomyiid fly genus *Coenosopsia* Malloch is endemic to the New World and is found from southern North America to southeastern South America. Malloch (1924) described the genus based on a single species, *C. prima* Malloch, 1924 and included it in the family Muscidae, tentatively referred to Phaoniinae. Subsequent authors assigned it to different groups. Séguy (1937) suggested an uncertain position among Coenosiinae, whereas

Albuquerque (1953) maintained it in its original placement, although he considered it an atypical Phaoniini. However, Hennig (1965), in discussing the phylogeny of Muscidae, argued about a possible placement of *Coenosopsia* in his tribe Hydrotaeini of Muscinae. Thereafter, Pont (1972) followed Hennig's view in his Neotropical Muscidae catalogue. Based upon the presence of the sixth and seventh pairs of spiracles in the female terminalia, a feature not noticed by previous authors, Hockett (1987), in the *Manual of Nearctic Diptera*, first referred *Coenosopsia* to Anthomyiidae.

More recently, Michelsen (1991) revised the genus, adding four new species, namely *C. brasiliensis* Michelsen, *C. floridensis* Michelsen, *C. mexicana* Michelsen and *C. peruviana* Michelsen. In this revision, Michelsen preliminarily discussed the phylogenetic and biogeographical hypothesis of *Coenosopsia*, suggesting a sister-group

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relationship with the Neotropical genus *Phaonantho* Albuquerque, 1956. Subsequently Michelsen (1996, 2000) proposed that both genera comprise a basal lineage forming the sister group of all other lineages within Anthomyiidae.

The five described species are confined to forested areas, either in Central/South American tropical forests (*C. brasiliensis*, *C. peruviana* and *C. prima*) or in southeastern North American subtemperate forests (*C. floridensis* and *C. mexicana*) (Michelsen, 1991). In this study, we found two new species from nonforested, open areas in the Brazilian Central Cerrado, and carried out a cladistic analysis of *Coenosopsia* including the five known species and the two new species. The resulting phylogenetic pattern forms the basis for the biogeographical hypothesis presented herein. The biogeographical pattern found, with *Coenosopsia* species and some closely related anthomyiid genera (including *Coenosopsia* and *Phaonantho*), is discussed on the basis of the reconciliation of the available phylogenetic and distributional patterns, and the geological knowledge accumulated for the West Indies and Central and South America.

Thus, here we describe two new species from Brazilian Cerrado and present a generic characterization as well as a key to the species. We then present a cladistic analysis of the species of *Coenosopsia* and analyse the distributional pattern of its species.

## Materials and methods

The studied material is deposited at the following institutions: Canadian National Collection, Ottawa, Canada (CNC); Coleção Entomológica, Departamento de Zoologia, Universidade de Brasília, Brasília, Brazil (DBAI); Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (DZUP); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); Museu Nacional, Rio de Janeiro, Brazil (MNRJ); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Maurice T. James Entomological Collection, Washington State University, Pullman, U.S.A. (WSU).

The adult morphological terminology follows McAlpine (1981) and Hockett & Vockeroth (1987) with some exceptions noted in de Carvalho (1989), and larval morphological terminology follows Ferrar (1987).

In addition to *C. ferrari* sp.n. and *C. michelseni* sp.n. studied with the listed type material, material for the other species included in the cladistic analysis is listed in Appendix 1. All species were examined through specimens of both sexes, except *C. prima*, for which male specimens are unavailable, and so male characters were obtained from the literature.

### Cladistic analysis

In the cladistic analysis the following species were included in the ingroup as terminal taxa: *C. prima*, *C. peruviana*, *C. brasiliensis*, *C. floridensis*, *C. mexicana*, *C. ferrari* sp.n. and *C. michelseni* sp.n. The outgroup taxa

were chosen based on previous phylogenetic hypotheses proposed for Muscoidea (Vossbrinck & Friedman, 1989; Michelsen, 1991) which approximate Muscidae and Anthomyiidae, and suggest a more basal position for Fanniidae within the Muscoidea. Hence, the terminal taxa included in the outgroup were *Anthomyia pluripunctata* (Albuquerque, 1959), *Delia platura* (Meigen, 1826) and *Phaonantho benevola* Couri, 1979 from Anthomyiidae; *Polietina orbitalis* (Stein, 1904) from Muscidae; and *Fannia bahiensis* Albuquerque, 1954 from Fanniidae.

The analysis was based exclusively on adult characters. All multistate characters were treated as unordered. The characters used in the analysis are presented in Appendix 2, and the data matrix with the terminal taxa and character distribution is described in Appendix 3. The program NEXUS version 0.5.0 (Page, 2001) was used for data matrix editing and the cladistic analysis was carried out using the program PAUP version 4.0b10 (Swofford, 2001). The tree search was performed using the branch-and-bound command, and character optimization using ACCTRAN.

In addition to the analysis carried out using equally weighted characters, we carried out other analyses with weighted characters to examine the consistency of the results under more than one weighting approach (Carpenter *et al.*, 2000). Thus, we applied the successive weighting approach (Farris, 1969), an iterative weighting scheme which gives different weights to characters according to their performance or fitness (interpreted as phylogenetic reliability by Carpenter, 1994) in the initial analysis with equal weights. Character performance can be quantified by several character indexes, for example, consistency index (CI), retention index (RI) or rescaled consistency index (RCI). In using the program PAUP, we defined CI (using their maximum values) as the parameter that maximizes the phylogenetic reliability of the characters.

We also used implied weighting (Goloboff, 1993, 1997) which gives weights to characters simultaneously with tree reconstruction, i.e. it does not depend on any previous analysis, as does the former approach. Weights are determined by the character fit in each given tree, not including any other tree (as occurs when one uses successive weighting, which determines the weight for a character according to some index calculated over all sets of equally parsimonious trees resulting from an initial analysis with equal weights). Character fit depends strongly on the value previously defined for the concavity constant  $k$  (see Turner & Zandee, 1995 for a discussion). In our analysis, we used different values for  $k$  to examine its impact on the number of resulting cladograms. The values were within the range from 2 (the PAUP default) up to 10 000.

### Taxonomy

#### *Coenosopsia Malloch, 1924*

A comprehensive characterization of the genus was given by Michelsen (1991) in the genus revision. Therefore, for

instance, we provide below a generic characterization presenting some diagnostic features that can distinguish *Coenosopsia* from other anthomyiid genera. Both generic characterizations, namely that of Michelsen (1991) and ours, should be consulted.

**Generic characterization.** *Head:* Both male and female dichoptic. Frons with 1 pair of interfrontal setae and 3 pairs of fronto-orbital setae (the lowermost proclinate and the other 2 reclinate); 3–4 pairs of frontal setae (2 strong pairs, the lowermost longer). Gena with a strong vibrissa and uniserial subvibrissal setae, 1 of which is upwardly directed. Antenna with plumose arista, with cilia at most the width of first flagellomere. *Thorax:* Humeral setae 2; posthumeral seta 1; dorsocentral setae 2:3; many short acrostichal setae, the pre-scutellar pair stronger; postsutural intra-alar setae 2; prealar seta shorter than posterior notopleural seta; supra-alar seta 1; postalar setae 2, the posteriormost longer; notopleural setae 2, the anteriormost longer. Notopleuron and postalar callus with no coverage setulae. Proepisternum with 2 setae (the uppermost about twice the length of the shorter) and bare on upper portion. Scutellum with a long basal, a short preapical (discal) and a long apical pair of setae; with some setulae laterally near the apex and bare ventrally. Prosternum bare, enlarged anteriorly. Proepimeron with 2 setae (the uppermost about twice the length of the shorter). Katepisternal setae 1:2, the lower posterior seta shorter, and sometimes an additional lower anterior seta weaker than the lower posterior seta. Anepimeron, katepimeron, meron, katatergite and anatergite bare. Suprasquamal ridge and postalar wall bare. *Wings:* Wing hyaline, without spots. Veins bare, except for the presence of microtrichia, also present on the wing membrane. Vein A1 markedly short, with no fold extending to wing margin. Lower calypter slightly larger than the upper. *Legs:* Fore tibia with a submedian seta on posterior surface. Midfemur with a long median seta on anterior to anteroventral surface. Midtibia with a long median seta on posterior surface; a short seta on apical third of posterodorsal to dorsal surface. Hind tibia with 2 setae on median third of anterodorsal surface; a long seta inserted at the limit of the apical third of posterodorsal surface; a submedian seta on anteroventral surface; an apical seta on anterodorsal, posterodorsal and anteroventral surfaces.

#### *Key to Coenosopsia species*

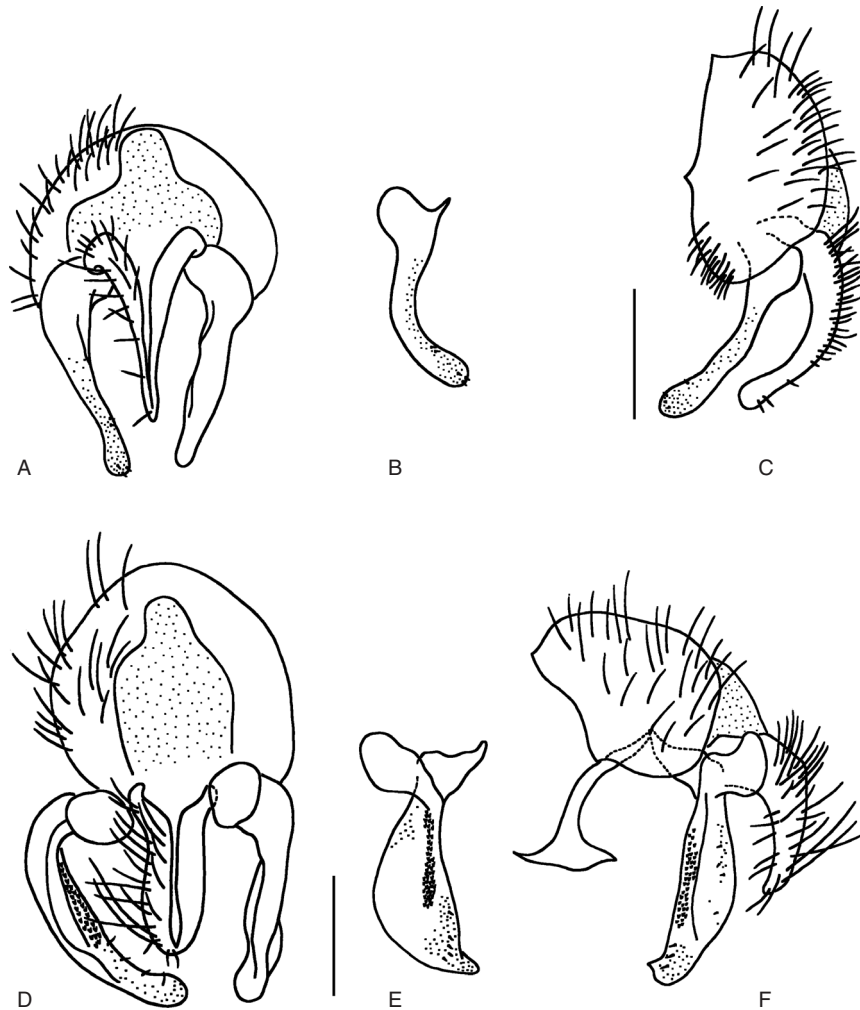
The *Coenosopsia* species are morphologically very constant and homogeneous, and the major differences remain on male genitalia structure. Facing this problem, unfortunately it is impossible to provide an identification key using only external features which can be easily and promptly examined. Therefore, in the key provided below we have included many diagnostic features from the male genitalia structure.

1. Palpus entirely yellow (Mexico).....  
.....*C. mexicana* Michelsen, 1991
- Palpus not entirely yellow, at least with the basal half brown ..... 2

2. Palpus brown with yellow apex ..... 3
- Palpus entirely brown ..... 4
3. Medium lobe of cercal plate with subparallel margins (Fig. 1D) (Brazil).....*C. michelseni* sp.n.
- Medium lobe of cercal plate with margins converging gradually to a point since the base (as in Fig. 1A) (Belize, Costa Rica, Panama, Ecuador).....  
.....*C. prima* Malloch, 1924
4. Medium lobe of cercal plate with margins converging abruptly to a point since the base (see Michelsen, 1991: figs 20, 21); basal width of cercal plate with the same length as the medium lobe (see Michelsen, 1991: figs 20, 21)..... 5
- Medium lobe of cercal plate with margins converging gradually to a point since the base (as in Fig. 1A); basal width of cercal plate conspicuously shorter than the length of the medium lobe (as in Fig. 1A, D)..... 6
5. Gonopod as long as paramere (Brazil, Paraguay).....  
.....*C. brasiliensis* Michelsen, 1991
- Gonopod longer than paramere (Peru, Brazil) .....  
.....*C. peruviana* Michelsen, 1991
6. Gonopod as long as paramere; aedeagus as long as aedeagal apodeme (Brazil).....*C. ferrari* sp.n.
- Gonopod longer than paramere; aedeagus longer than aedeagal apodeme (U.S.A., Mexico).....  
.....*C. floridensis* Michelsen, 1991

#### ***Coenosopsia ferrari* Nihei & Carvalho, sp.n.** (Figs 1A–C, 2A, 3A, B)

*Male. Measurements:* 2.0–2.3 mm (body length), 2.0–2.3 mm (wing length). *Colour:* Frons dark brown on upper half; lower half orange-yellow. Ocellar triangle dark brown with silver pollinosity. Gena yellow with silver pollinosity. Palpus, proboscis and antenna brown. Thorax dark brown to black with silver pollinosity. Wing hyaline, without spots. Legs brown, lighter at junction of fore femora and tibia, and base of fore. Abdomen yellowish with brown maculae (colour pattern of abdomen similar to Michelsen, 1991: fig. 13). Calypters and halter whitish. *Head:* Postocellar setae divergent; inner vertical setae convergent and strong, twice length of postocellar setae and outer vertical setae, latter pair divergent. Palpus slightly spatulate on apical half. *Legs:* Fore femur with a complete row of long setae on posterodorsal and posteroventral surfaces. Fore tibia with an apical seta on anterodorsal, dorsal and posteroventral surfaces. Midfemur with a row of short setae on anterodorsal, posteroventral (in both surfaces, setae longer on basal half) and anteroventral; an apical seta on anterodorsal; and 2 apical oblique setae on posterodorsal to posterior surface. Midtibia with an apical seta on anterodorsal, posterodorsal (both short), posteroventral, ventral (very long) and anteroventral surfaces. Hind femur with a row of fine and short setae on posteroventral surface; a row of long setae on apical half of anteroventral surface; a row of long setae on anterior to anterodorsal surfaces; an apical seta on anterodorsal, dorsal, posterodorsal to posterior, and



**Fig. 1.** Male terminalia. A, *Coenosopsia ferrari* Nihei & Carvalho, dorsal view; B, same species, terminalia, right surstylus, lateral view; C, same species, terminalia, lateral view; D, *C. michelseni* Nihei & Carvalho, terminalia, dorsal view; E, same species, right surstylus, lateral view; F, same species, terminalia, lateral view (scale bars: 0.1 mm).

posteroventral surfaces. First tarsomere of the fore and hind legs with a conspicuous ventrobasal seta. *Abdomen*: Tergites with marginal setae developed, the lateral ones longer. Sternite 1 setulose with robust setulae. *Terminalia* (Figs 1A–C, 2A): Epandrium, in lateral view, with a dense set of robust setulae at lower anterior portion. Cercal plate with median lobe (downward projected) tapering to a point until the apex. Surstyli elongate, right surstylus more markedly curved. Aedeagus and associated structures as in Fig. 2A.

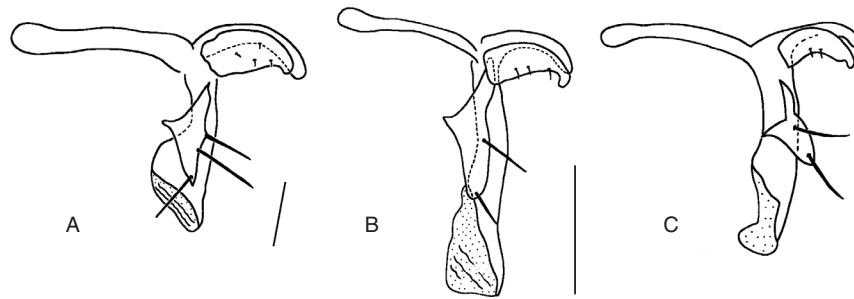
*Female. Measurements*: 2.8–2.9 mm (body length), 2.8–3.5 mm (wing length). There is very little sexual dimorphism in the external morphology. Dimorphism is restricted to the more widened abdomen on the females (when viewed dorsally) and to the features of terminalia (see below). No conspicuous differences were noted on the body chaetotaxy and colour. *Terminalia* (Fig. 3A, B): Tergites 6 and 7 weakly sclerotized longitudinally at median line; spiracles 6 and 7 conspicuous

and both present on tergite 6. Tergite 8 with an additional median plate, distinctly thin. Three rounded spermathecae.

*Material examined. Holotype*: ♂, BRAZIL: Distrito Federal, Brasília, Reserva Ecológica do I.B.G.E., 9.xii. 1997 (*I.R. Diniz*) (DZUP). *Paratypes*: same locality data as holotype, but 5♂, 1♀, 13.v. 1997 (DZUP, MNRJ); 1♂, 3♀, 24.vi. 1997 (DZUP); 1♂, 25.xi. 1997 (DBAI); 1♂, 9.xii. 1997 (DZUP); 1♀, 17.iii. 1998 (DBAI).

*Etymology*. The species name is dedicated to Paul Ferrar, from the Australian Centre for International Agricultural Research (Canberra, Australia), for his valuable contributions to the knowledge of muscoid biology.

*Geographical distribution*. Brazil.



**Fig. 2.** Male aedeagus and associated structures, lateral view. A, *Coenosopsia ferrari* Nihei & Carvalho; B, *C. michelseni* Nihei & Carvalho; C, *C. brasiliensis* Michelsen (scale bars: 0.1 mm).

***Coenosopsia michelseni* Nihei & Carvalho, sp.n.**  
(Figs 1D–F, 2B)

*Measurements.* Male: 2.5 mm (body length), 2.5 mm (wing length). Female: 3 mm (body length), 3 mm (wing length).

*Remarks.* Differs from *C. ferrari* sp.n. in the following: antenna light brown to yellow (except for brown arista); palpus brown with yellow apex; apical half of palpus more cylindrical (unlike the enlarging observed in *C. ferrari*); fore coxa brownish (yellowish in the paratypes). The male ter-

minalia is quite different (Figs 1D–F, 2B): epandrium without setulae at lower anterior portion; median lobe of cercal plate with margins subparallel to rounded apex; surstyli more elongate, with apical half widened, right surstylus conspicuously widened; aedeagus and associated structures as in Fig. 2B. The female terminalia is very similar in both species, thus the terminalia of *C. michelseni* was not illustrated. As occurs with *C. ferrari*, the female specimens are very similar to the male, differing only in the shape of the abdomen.

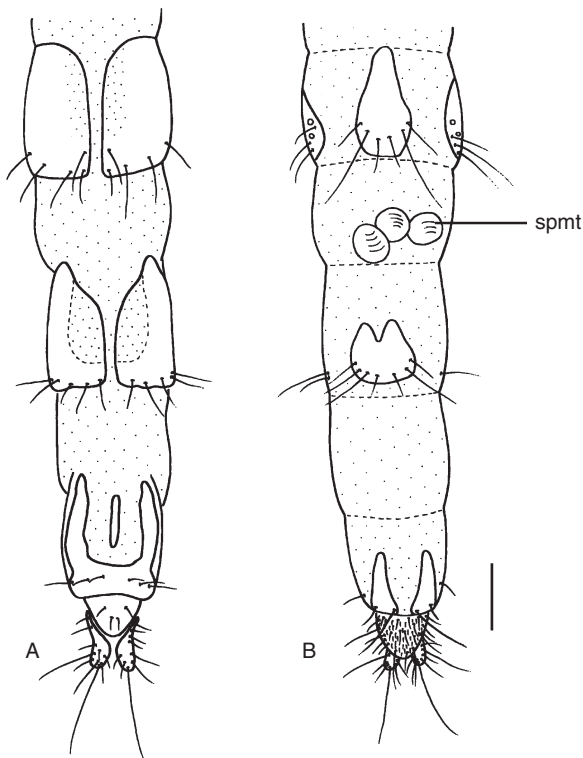
*Material examined.* Holotype: ♂, BRAZIL: Distrito Federal, Brasília, Reserva Ecológica do I.B.G.E., 13.v. 1997 (*I.R. Diniz*) (DZUP). Paratypes, 1♂, same locality data as holotype, but 29.iv. 1997 (DZUP); 1♀, same locality data, but 29.x. 1997 (DZUP); 1♂, Pará, Serra Norte, Campo Canga, 10.x. 1983 (*Pimentel*) (MPEG).

*Etymology.* The species name is dedicated to Verner Michelsen, from the Zoological Museum, University of Copenhagen, Denmark, for his valuable contributions to the study of world-wide Anthomyiidae systematics.

*Geographical distribution.* Brazil.

*Comments on species habitat*

The two new species were collected from the Reserva Ecológica do IBGE, near Brasília, with coordinates 15°56'S 47°53'W. This national conservation unit is characterized mainly by Cerrado vegetation (Pereira *et al.*, 1989). These two new species are the only species in this genus associated with Cerrado, and whereas *C. ferrari* is known only from the type locality, *C. michelseni* has also been found in northern Brazil (State of Pará, also in a region of Cerrado vegetation (Ana Y. Harada, MPEG, pers. commun.)). The other species of *Coenosopsia* are associated with forests, either in Central/South American tropical forests (*C. brasiliensis*, *C. peruviana* and *C. prima*) or in southeastern North American subtropical forests (*C. floridensis* and *C. mexicana*) (Michelsen, 1991).



**Fig. 3.** *Coenosopsia ferrari* Nihei & Carvalho, female terminalia. A, Dorsal view; B, ventral view. spmt = spermathecae (scale bar: 0.2 mm).

### Reproductive biology

Very little is known about the reproductive biology of *Coenosopsia* species. In the only information available, Michelsen (1991) reports larviparity followed by a brief discussion. However, in reporting larviparity in *C. floridensis* and *C. peruviana*, Michelsen (1991) mentions only the presence of differentiated eggs containing first instar larvae inside the abdomen. However, this cannot confirm larviparity because the female can retain mature eggs inside her abdomen until finding a suitable substrate to deposit them, and consequently an egg can develop to the first instar larva inside the female.

Here, we report a similar occurrence in *C. brasiliensis* of an egg containing a first instar larva inside the female (as in Michelsen, 1991). Moreover, we also report larviparity in *C. peruviana* from a remnant moult of a second instar head skeleton inside the female abdomen. By examination and morphological characterization of the latter, we inferred biological aspects of the larval feeding habits of *C. peruviana*.

In a gravid female of *C. brasiliensis* collected from Reserva Mbaracayú, Paraguay (collected using a Malaise trap), we found forty-six mature eggs, one containing a first instar larva. This egg was found next to the female terminalia with the head of the larva opposite the tip of the terminalia. The larva examined was similar morphologically to *C. peruviana* and *C. floridensis* (see Michelsen, 1991: figs 4, 5).

In a dissected female of *C. peruviana* from Reserva Ducke (26 km northeast of Manaus, Amazonas, Brazil) we found a remnant moult of a head skeleton of a second instar larva inside its abdomen. The remaining moult was badly preserved, and, for this reason, although the instar number determination was possible, a satisfactory morphological characterization was not. Because of the lack of posterior spiracles, the instar determination was possible only through the examination of the moult's cephalopharyngeal skeleton. The observed morphological features were compared with first instar larvae of *C. peruviana* and *C. floridensis* (illustrated in Michelsen, 1991) and with the general characterization of anthomyiid larvae given in Ferrar (1987).

In general aspect, the remnant head skeleton is more developed and sclerotized than that of the first instar; mouthhooks are paired and symmetrical, with both hooks apparently entirely separate from each other; the intermediate sclerite is present and well developed, distinctly separate from the pharyngeal sclerite; the ventral cornua of the pharyngeal sclerite is developed and stout, the dorsal cornua was not recognized.

Some care is needed in the interpretation of the moult characterization above. Particularly because it may have been posteriorly deformed or modified (e.g. by the abdomen clarification process under KOH solution). However, at least one important observation should be considered regarding its life habits and the larval head skeleton morphology. Ferrar (1987) argued that most anthomyiid saprophagous species possess the intermediate sclerite

separate from the pharyngeal sclerite. If our characterization is correct, it would be reasonable to assume that at least *C. peruviana* presents saprophagous habits in the larval stage. Another feature frequently present in saprophagous species of cyclorrhaphous dipterans is the presence of pharyngeal ridges (Keilin & Tate, 1930; Skidmore, 1973; Ferrar, 1979, 1987), but unfortunately we could not recognize these in the remnant skeleton.

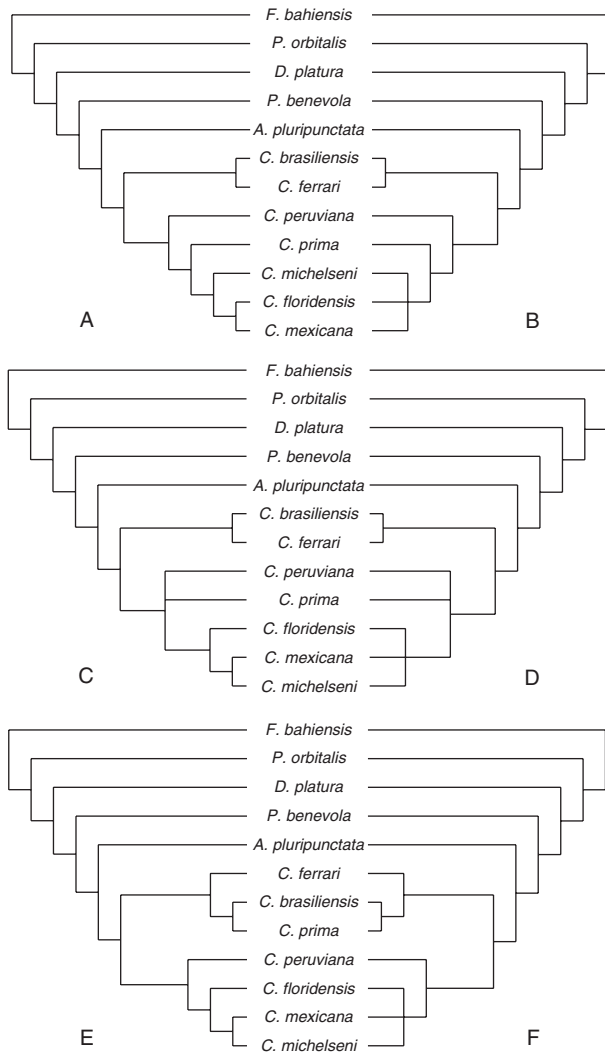
Neither the remnant moult of the first instar nor the chorion were found, from which we can infer that they had been expelled along with the mature larva during its deposition in the outside media. This was observed in the field by Ferrar (1975) in the larviposition behaviour of *Musca fergusonii* Johnson & Bancroft, 1920, whose female can extrude the larva immediately followed by the chorion.

As demonstrated above, further investigations are needed to accurately discuss the reproductive biology of *Coenosopsia* species, including breeding habits and female reproductive behaviour. Except for some economically important species, basic knowledge about the biology and ecology of all anthomyiid fauna is scarcely known, with very few data available in the literature.

### Cladistics

The analysis using all characters, equally weighted, resulted in forty-four most parsimonious cladograms with length = 54 steps, CI = 0.70, RI = 0.67 and fitness values varying among -16.300, -16.200 or -16.100. In the strict consensus tree, *Coenosopsia* appears as a monophyletic group which includes all species in a large polytomic clade with no internal resolution. After applying successive and implied weighting schemes, better resolved topologies were obtained. Using successive weighting, the analysis yielded six most parsimonious cladograms (Fig. 4A-F) with length = 54 steps, CI = 0.77, RI = 0.75 and fitness = -12.638.

In the implied weighting analysis, we applied different values for the concavity constant ( $k$ ) to examine the influence of that constant on the number of resulting topologies. Using  $k = 2$  (the PAUP default) and  $k = 3$ , the analysis yielded thirty-two cladograms with length = 55 steps and fitness -16.350 (when  $k = 2$ ) and -17.010 ( $k = 3$ ). These thirty-two cladograms resulted in an unresolved consensus tree regarding the *Coenosopsia* species. However,  $k > 4$  yielded only six most parsimonious cladograms identical to those cladograms obtained under successive weighting, with the same length (= 54 steps) but higher fitness (-17.476, when  $k = 4$ ). The same six cladograms resulted with  $k = 4-1400$ . Using  $k = 1500$ , the number of cladograms increased to fourteen, and with higher  $k$ -values (up to 10 000) the number of cladograms increased, resulting in less resolved consensus trees. The cladograms resulted from analysis under implied weighting and using  $k = 4$  were preferred, because this analysis provided the shortest (at least equally parsimonious to those from equal weighting) and fittest trees.



**Fig. 4.** The six most parsimonious cladograms resulting from analysis under both successive and implied weighting (applying  $k=4$ ). Trees obtained under successive weighting presented length = 54, consistency index (CI) = 0.77, retention index (RI) = 0.75, fitness = -12.638, and under implied weighting, length = 54, CI = 0.70, RI = 0.67, fitness = -17.476.

The six most parsimonious cladograms (Fig. 4A–F) support the monophyly of *Coenosopsia*. The major difference in their topologies was regarding the position of *C. prima*. In cladograms A–D (Fig. 4), this species is included in the lineage comprising *C. peruviana* + *C. michelseni* + *C. floridensis* + *C. mexicana* with the support of the synapomorphic character 25 (cladograms A–D) and additionally by the synapomorphic character 10 (cladograms A and B). On the other hand, in cladograms E and F, *C. prima* appears included in the lineage comprising *C. brasiliensis* + *C. ferrari*, although supported by a synapomorphy (character 1) and a homoplasy (character

17). In spite of being equally parsimonious, cladograms A–D have stronger character support to explain the position of *C. prima* than cladograms E and F. Therefore, among the six phylogenetic hypotheses, we preferred cladogram A (Fig. 4), due to the character transformation and interpretation, and character support for the branches. In Fig. 5, this cladogram is shown with optimized characters. In this cladogram, *Coenosopsia* monophyly is supported by four synapomorphies: interfrontal setae on male (character 3), male eyes dichoptic (character 8), asymmetrical surstyli (character 21) and gonopod with one median sensilla (character 24). Another three characters were interpreted as homoplasies, but we suspect that they could be true synapomorphies for the genus in a higher-level analysis. Character 5, proclinate fronto-orbital setae on male, also appears in the muscid *Polietina orbitalis*. Anterior enlargement of the prosternum (character 11), although present in *Delia platura*, is absent in the more closely related anthomyiids. Character 14, the ventral surface of the scutellum, appears as setulose in the anthomyiid clade comprising *Delia platura*, *Phaonantho benevola*, *Anthomyia pluripunctata* and *Coenosopsia* spp. However, there is a reversal in the *Coenosopsia* spp. clade and the scutellum is bare ventrally.

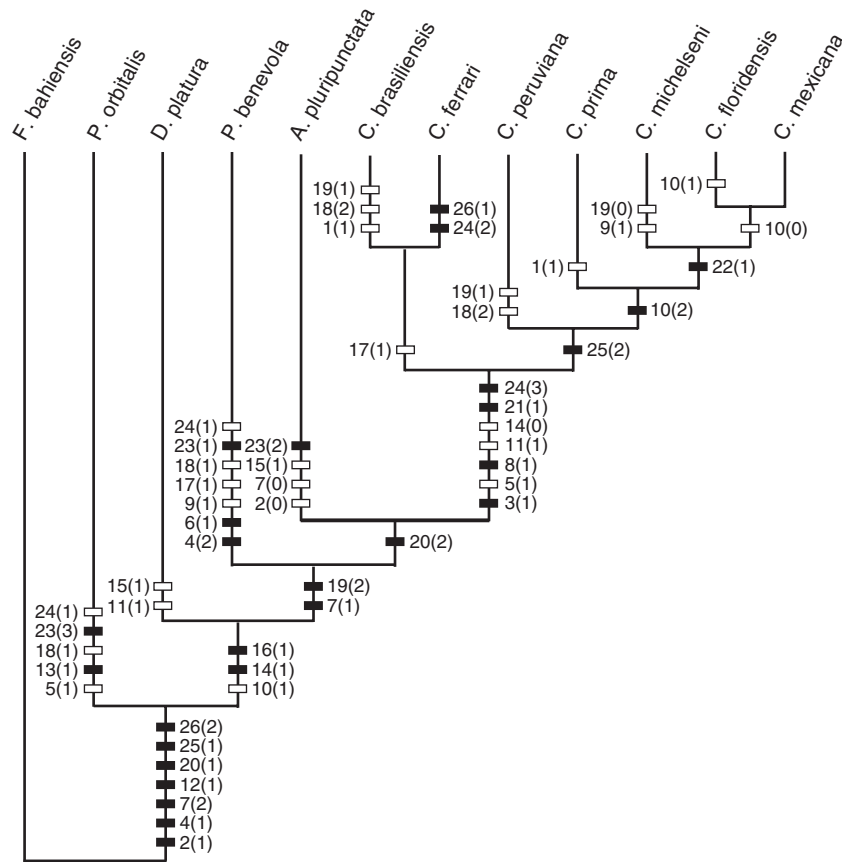
Among the four synapomorphies for *Coenosopsia* from our analysis, three (characters 3, 8 and 21) were proposed previously and discussed by Michelsen (1991). Moreover, the author also considered the homoplastic characters 11 and 14 as generic synapomorphies.

Two major groups within the genus *Coenosopsia* were found (Fig. 5): one small clade including *C. brasiliensis* and *C. ferrari*, and a larger clade including *C. peruviana*, *C. prima*, *C. michelseni*, *C. floridensis* and *C. mexicana*. The sister groups *C. brasiliensis* and *C. ferrari* are supported uniquely by character 17, a homoplastic trait that is also present in *Phaonantho benevola*. The larger clade of five species is supported by one apomorphic trait (character 25).

Although not the purpose of our study, some interesting secondary observations arose. Regarding the relationship between *Coenosopsia* and other anthomyiid genera in this analysis (Fig. 5), a sister-group relationship is not indicated between *Coenosopsia* and *Phaonantho*, as suggested by Michelsen (1991, 1996). The suggested sister group for *Coenosopsia*, *Anthomyia pluripunctata*, belongs to the large cosmopolitan genus *Anthomyia* Meigen, 1803. However, these data are inconclusive and the sister group of *Coenosopsia* remains uncertain.

Another interesting point is the relationship Muscidae + Anthomyiidae denoted in all six cladograms obtained (Fig. 4A–F). Michelsen (1991) formally proposed this close kinship on the basis of morphological characters, also suggested by Vossbrinck & Friedman (1989) based on molecular characters from 28S ribosomal RNA and by Pont & de Carvalho (in preparation) using morphological characters. This view is contrary to the traditional view in which Anthomyiidae is considered the sister group of the clade Muscidae + Fanniidae (Hennig, 1965; McAlpine, 1989). A phylogenetic study of Muscoidea performed by Bernasconi





**Fig. 5.** One of the six most parsimonious cladograms (the same as Fig. 4A) with character optimization. Synapomorphies are indicated by solid black rectangles; homoplasies by blank rectangles.

*et al.* (2000), based on molecular data from mitochondrial DNA, has not presented conclusive data, arguing that the relationships among Muscoidea still remain unclear, needing further investigation.

We also believe our observations are inconclusive, as the main purpose herein was to study the internal relationships among *Coenosopsia* species. To obtain consistent and reliable hypotheses on which to postulate the sister group of *Coenosopsia* or to clarify the relationships of Anthomyiidae within the Muscoidea, further higher-level studies with a larger number of genera are required.

### Biogeography

Prior to discussing the biogeographical patterns found, a tentative reconstruction of ancient vicariance events in the Neotropics is presented (Fig. 6). This reconstruction was based initially on a vicariance model (Amorim & Pires, 1996), modified and complemented with additional data: the detachment of the Caribbean plate follows Pitman *et al.* (1993), the Andes uplift from Lundberg *et al.* (1998),

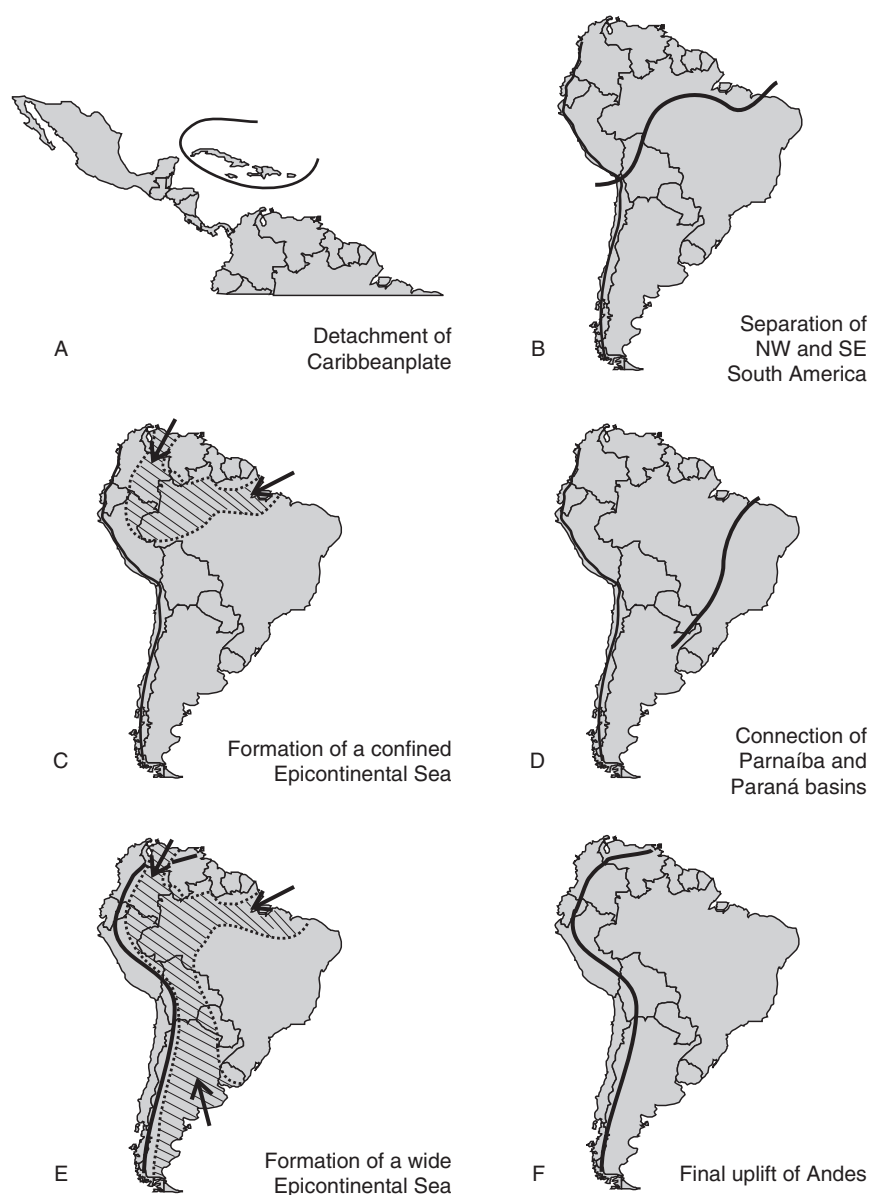
the Epicontinental sea formation during the Late Tertiary from Frailey (2002) and general geological data from Petri & Fúlvaro (1983).

### Origin of the Neotropical anthomyiids

A working hypothesis for the presence of anthomyiid taxa in the Neotropical region is the North-to-South America dispersal proposed by Michelsen (1991). The first invasion of anthomyiids into the region must have come from North America during the Latest Cretaceous and Earliest Coenozoic, when the latest biotic connection between North and South America existed. From this lineage, following an ancient vicariance event, evolved a clade formed by the sister groups *Coenosopsia* and *Phaonantho* (Michelsen, 1991, 1996, 2000).

According to Pitman *et al.* (1993), during the interval between Early Cretaceous (Valanginian, 130 Ma) and Late Cretaceous (Santonian to Campanian, 84 Ma), the biotic interchange was only possible through an island-arc system (the Proto-Greater Antilles) which would have been a filter bridge. Then, about 80 Ma (Briggs, 1994), the Caribbean





**Fig. 6.** Maps showing the reconstruction of ancient vicariance events in the Neotropics (original reconstruction from Amorim & Pires, 1996; but modified and complemented here). A, Detachment of the Caribbean plate from the continental mainlands beginning in the Late Cretaceous and finishing in the Miocene–Middle Pliocene; B, separation between the northwestern and southeastern Neotropical components in the Late Cretaceous due to a lake formation along the rivers Amazon, Madeira and Mamoré; the Andes began its uplift in the Middle Cretaceous; C, Epicontinental sea formation by water invasion through the north (Maracaibo) and east (Amazon basin) portal seaways (the dashed line demarcates the sea boundaries); D, connection between the Parnaíba and Paraná basins existing in the Middle to Late Cretaceous; E, Epicontinental sea formation by water invasion through the north, east and south (Paraná basin) portal seaways in the Miocene; F, Andes uplift in an advanced stage; F, Andes uplift in its final stage, reaching the current conformation in the Miocene–Pliocene.

plate initiated its eastward movement in opposition to the westward movement of the North and South American plates. This process finished in the Late Tertiary (Miocene to Middle Pliocene, 20–3 Ma), when the Caribbean plate reached its modern position and the Isthmus of Panama was established (Pitman *et al.*, 1993). During this process, contact between North and South America eventually

occurred (e.g. the Noah's arc in the Late Oligocene, 30 Ma). With north-to-south dispersal, the first anthomyiids must have arrived in the Neotropics through the Proto-Greater Antilles during the Late Cretaceous.

Despite scarce fossil records for the family (Amorim & Silva, 2002), a new extinct genus from Dominican amber was described recently and named *Coenosopsites* due to its



**Fig. 7.** Geographical distribution of the genera *Coenosopsia* Malloch (●), *Phaonantho* Albuquerque (■) and †*Coenosopsites* Michelsen (▲) with the superimposed cladogram denoting their phylogenetic relationship according to the proposal of Michelsen (1996). The circled question marks are additional records for *Phaonantho* spp. in Bolivia, Ecuador and Costa Rica (personal observation of Michelsen, 1996), but without exact geographical data (latitude and longitude).

resemblance to *Coenosopsia* (Michelsen, 1996). Also, Michelsen (1996) proposed a generic relationship as follows: (*Phaonantho* + (*Coenosopsia* + *Coenosopsites*)). On this basis, we superimposed this phylogenetic relationship on a map showing their known geographical distributions (Fig. 7). Thus, the minimum age indicated for *Coenosopsites* is about 25 Ma (Michelsen, 1996), although the amber of Dominican assemblages dates from 15 to 20 Ma in the Early to Middle Miocene (Iturralde-Vinent & MacPhee, 1996; Pont & de Carvalho, 1997). During that time period, the Caribbean plate almost reached its current position.

If it is possible to postulate the detachment of the Caribbean plate as the vicariance event responsible for the origin of *Coenosopsites*, then its age must be older than 20 Ma, lying within the interval 25 and 80 Ma, during the plate detachment process. The exact ageing of *Coenosopsites* is very important to determine the age of Neotropical anthomyiids and their history in the region.

A competing hypothesis is that the first anthomyiids originated during the Gondwanan period. The separation of the Gondwanan landmasses (South America, Africa, Madagascar, India, Antarctica, and Australia) began in the Late Jurassic to Early Cretaceous, and the separation between South America and Africa occurred during its final phase, from Valanginian (135 Ma) to Albian (106 Ma) (Pitman *et al.*, 1993). Possibly the first Neotropical anthomyiids came from Africa when the two landmasses were connected. Couri & de Carvalho (2003) argued about a Gondwanan origin to some Muscidae genera, showing a close relationship and each one distributed exclusively on Neotropical or Afrotropical domains.

This question remains until we clarify the sister group of the lineage which originated the Neotropical clade *Phaonantho* + *Coenosopsia* + *Coenosopsites*. The two possibilities concerning the biogeographical origin of the Neotropical anthomyiids are based on probable relationships with faunal elements either from the Nearctic or from

Gondwana. (However, with regard to the modern Neotropical anthomyiids, they are surely not monophyletic and should be related to both domains.) In explaining the biogeographical pattern of the Neotropical muscids, de Carvalho *et al.* (2003) discuss the Gondwanan distributional pattern presented by some closely related genera and infer the age of the family Muscidae to the Middle or Early Cretaceous. Therefore, if the Muscidae and Anthomyiidae really are sister groups, they must be the same age. On the other hand, the oldest fossil records available for both taxa do not indicate such an age: a Baltic amber fossil of Anthomyiidae dating about 40 Ma (Michelsen, 2000) and Dominican amber fossils of Muscidae dating about 15–20 Ma (Pont & de Carvalho, 1997).

In addition, the Antarctic fossil puparium reported by Ashworth & Thompson (2003) represents the most recent advance regarding fossil Diptera research. The puparium assigned to *Cyclorrhapha Schizophora* dates from Middle Pliocene (about 3–17 Ma) and, based on its finding, the authors raised two opposing questions: whether the fossil is originally from South America and colonized Antarctica

posteriorly during a warmer period, or the fossil is originally Antarctic and derived from a Gondwanan relict.

The fossil record does not indicate a precise taxonomic ageing, as the presence of a taxon in a given assemblage shows only that the clade including that taxon already existed but cannot refute the hypothesis that the clade could have existed earlier (Amorim & Silva, 2002). Unlike palaeontology, which provides minimum age estimates, vicariance-based estimates suggest absolute ages because they are linked to process-related events (Lundberg, 1998). Therefore, despite existing fossil evidence, either the North-to-South America dispersal or the Gondwanan origin can be regarded as reasonably plausible and consistent with the biogeographical data discussed above.

#### *Biogeographical hypothesis for Coenosopsia species*

The ancestral range of *Coenosopsia* species probably lies in the tropical realm of South or Central America (Michelsen,



**Fig. 8.** Geographical distribution of *Coenosopsia* species, with the selected cladogram superimposed. Legends: *C. brasiliensis* Michelsen (◆), *C. ferrari* Nihei & Carvalho (⊛), *C. floridensis* Michelsen (■), *C. mexicana* Michelsen (□), *C. michelseni* Nihei & Carvalho (★), *C. peruviana* Michelsen (⊙), *C. prima* Malloch (●).

1991). A cladogram superimposed on the species distribution map (Fig. 8) could precede the hypothesis of origin and evolution of the genus as some conclusions can be deduced from the analysis of species distribution. The individual pattern of *Coenosopsia* was compared with the general biogeographical pattern proposed by Amorim & Pires (1996) (Fig. 6).

Two major groups are recognized in the cladistic analysis: the clade *C. brasiliensis* + *C. ferrari* restricted to southeastern South America, and the large clade comprising the remaining species restricted mainly to northwestern South America up to southern North America. The vicariance event proposed (see Fig. 6B) for this basal divergence between the two groups is the separation of northwestern and southeastern South American components in the Late Cretaceous through the formation of a lake along the rivers Amazonas, Madeira and Mamoré (Amorim & Pires, 1996; see also Petri & Fúlvaro, 1983 for geological details). Thence, the two clades diverged. This basal divergence corroborates the general area cladogram (Fig. 9) proposed by Amorim & Pires (1996), in particular with regard to the dichotomy between the northwestern and southeastern components.

Within the northwestern clade, *C. peruviana* was probably distributed in the southern portion of the then available landmass, in opposition to the ancestral taxon of the remaining clade which is presumed to have been restricted to the extreme northwest of South America next to Central America. It is thought that precisely in that region is the ancestral area of *C. prima* currently known from Ecuador to southern Central America. Thus, the incursion of *C. prima* into Central America would have been through a posterior reconnection between the Central and South American mainlands.

The apical clade composed of the most septentrional species, *C. floridensis* and *C. mexicana* from North America, and *C. michelseni* from the Brazilian Cerrado, are included within the northwestern component (Fig. 9). Michelsen (1991) called attention to the fact that *C. floridensis* and *C. mexicana*, found outside the tropics of Central and South America, would be apical in the genus. A probable explanation of their occurrence in such a septentrional position could be due to the formation of Noah's arc connecting North and South America during the Late Oligocene about 30 Ma.

However, *C. michelseni* is restricted to the Brazilian Central Cerrado, extending from Brasilia (central Brazil) to



**Fig. 9.** A map showing the three main components of the Neotropical region and its proposed general area cladogram (redrawn from Amorim & Pires, 1996).

northern Pará state (Fig. 8). This distribution is not incongruent with the northwestern component composition, as this component also comprises the Lower Amazon basin region (Fig. 9). Thus, we can infer that *C. michelseni* could be more widespread than we currently know, with its range probably extending throughout northwestern South America mainly on regions covered by open vegetation. A similar distributional pattern is observed for many South American birds endemic to dry forests (Silva, 1995). To explain these patterns, Silva (1995) hypothesized ancient connections (dry forest corridors along the Amazon borders) between the Brazilian Cerrado and other savannahlike regions, such as the Llanos (in Venezuela and Colombia) and the Grã-Sabana (in Venezuela, Guyana, Surinam and French Guyana). However, Silva (1995) discussed these ancient connections as Quaternary. Using a botanical perspective, Rizzini (1979) commented on the similarity (in structure, physiognomy and shared species) between the Cerrado and the Surinam savannah. The distribution hypothesized herein for *C. michelseni* will be corroborated if collecting efforts confirm its presence throughout other regions of northeastern South America covered by open vegetation. Unfortunately, these regions are poorly represented in zoological collections.

The individual biogeographical pattern of *Coenosopsia* corroborated the general pattern proposed by Amorim & Pires (1996), including both vicariance event sequences (Fig. 6) and the general area cladogram (Fig. 9). Such congruence can also be completely or partially seen in other works. For example, the individual patterns presented by de Carvalho (1999), de Carvalho *et al.* (2003) and Manfrin *et al.* (2001) with dipterans, Grazia (1997) with heteropterans, Rodríguez & Campos (1998) with freshwater decapods, and Morrone (2002) with coleopterans, show some congruence with the general area cladogram from Amorim & Pires (1996) (Fig. 9). Moreover, even without a phylogenetic framework, some studies analysing animal and plant species distributional patterns through a panbiogeographical approach also support the northwestern and southeastern Neotropical components as historical units (Cortés & Franco, 1997; Franco & Berg, 1997; Morrone, 2000a, b, 2003; Franco, 2001).

General biogeographical patterns will be more informative and detailed as more individual patterns are proposed and corroborated/refuted. Therefore, further investigations which focus on phylogenetic and distributional patterns of Anthomyiidae genera occurring in the Neotropical region are clearly required to understand better their origins in this region. Also required are studies which test whether the areas of endemism proposed for the region actually represent historical units. Because a major classification and division of the Neotropical region (in subregions and provinces) proposed by Morrone (2001) is partially incongruent with the pattern found by Amorim & Pires (1996) and which was corroborated herein, we emphasize this exciting frontier for better understanding the biogeographical patterns of the Central/South American biota.

## Acknowledgements

We are deeply grateful to Ivone R. Diniz (Departamento de Zoologia, Universidade de Brasília) who kindly provided the described material and to the following curators for the loan of material: Ana Y. Harada (MPEG), Jeffrey M. Cumming (CNC), José A. Rafael (INPA), José R. Pujol-Luz (DBAI), Márcia S. Couri (MNRJ) and Richard S. Zack (WSU). We would like to thank Walter A. Boeger (Departamento de Zoologia, Universidade Federal do Paraná), Juan J. Morrone (Facultad de Ciencias, Universidad Nacional Autónoma de México), and Paul Ferrar (Australian Centre for International Agricultural Research) for valuable comments on the manuscript, to James J. Roper for revising the English, and to Adrian Pont (Oxford University Museum of Natural History) and one anonymous referee for comments and suggestions. Thanks are also due to Ana Y. Harada (MPEG) who provided us with the vegetational characterization and geographical data of Serra Norte (Pará). This study was supported by grants of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), process numbers 141.936/2000–2 (SSN) and 304.148/2002–4 (CJBC). This is contribution number 1364 of the Departamento de Zoologia, Universidade Federal do Paraná.

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Accepted 13 October 2003

## Appendix 1

Examined material of taxa included in the cladistic analysis.

- Coenosopsia brasiliensis*: BRAZIL: 1 ♀, 1 ♂, Rio de Janeiro, x. 1938 (*Serviço Febre Amarela M.E.S. Bras.*) (MNRJ). PARAGUAY: 1 ♀, Canindeyú, Reserva Natural Bosque Mbaracayú, 02–10.iv. 1996 (*A.C.F. Costa*) (DZUP); 1 ♂, same locality, 11–17.iv. 1996 (*A.C.F. Costa*) (DZUP); 2 ♂, same locality, 17–23.iv. 1996 (*A.C.F. Costa*) (DZUP); 1 ♂, same locality, 01–08.v. 1996 (*A.C.F. Costa*) (DZUP); 2 ♂, same locality, 09–15.v. 1996 (*A.C.F. Costa*) (DZUP); 1 ♂, same locality, 16–23.v. 1996 (*A.C.F. Costa*) (DZUP).
- Coenosopsia floridensis*: U.S.A.: 1 ♂ paratype, Florida, Highlands Co., Archbold Biol. Sta., 23.iv. 1967 (*B.V. Peterson*) (CNC). MEXICO: 1 ♀, Sin. 20 mi. E. Concordia, 04.viii. 1964 (*W.R.M. Mason*) (CNC).
- Coenosopsia mexicana*: MEXICO: 1 ♂ paratype, Chis. San Cristóbal de Las Casas, 27.v. 1969 (*B.V. Peterson*) (CNC); 1 ♀ paratype, same locality, 03–07.vi. 1969 (*B.V. Peterson*) (CNC).
- Coenosopsia peruviana*: PERU: holotype ♂, Quincemil, Cuzco, 01–15.xi. 1962 (*L. Pena*) (CNC); 1 ♀ paratype, Avispas, Madre de Dios, 10–20.ix. 1962 (*L. Pena*) (CNC). BRAZIL: 1 ♀, Amazonas, Manaus, Reserva Ducke, 09–16.iii. 1989 (*Y. Camara & J.E. Binda*) (INPA).
- Coenosopsia prima*: PANAMA: 1 ♀, Canal Zone, Barro Colorado Is., 09.iii. 1967 (*Roger D. Akre*) (WSU); 1 ♀, same locality, 04.iv. 1967 (*Roger D. Akre*) (WSU).
- Anthomyia pluripunctata*: BRAZIL: 2 ♀ Paraná: Curitiba, viii. 1980 (*C.B. Jesus*) (DZUP); 1 ♂, same locality, x. 1980 (*C.B. Jesus*) (DZUP); 1 ♂, São José dos Pinhais, 23–30.vii. 1984 (*C.I.I.F.*) (DZUP); 2 ♀, same locality, 24.iv–01.x. 1984 (*C.I.I.F.*) (DZUP); 3 ♂, 1 ♀, same locality, 01–08.x. 1984 (*C.I.I.F.*) (DZUP); 1 ♂, 1 ♀, same locality, 08–19.x. 1984 (*C.I.I.F.*) (DZUP); 1 ♂, same locality, 16.x. 1984 (*C.I.I.F.*) (DZUP); 1 ♀, same locality, 05–12.xi. 1984 (*C.I.I.F.*) (DZUP).
- Fannia bahiensis*: BRAZIL: 1 ♂, 8 ♀, Bahia, Anajé, 15–24.v. 1975 (*C. & P. Elias*) (DZUP).
- Delia platúra*: UNITED KINGDOM: 1 ♀, Oxon, Henley, 18.vi. 1992 (*C. Carvalho*) (DZUP). AUSTRIA: 1 ♂, Matri, Osttirol, 2 km east of Zedlach, 1320 m, 07.viii. 1967 (*Wright & Pont*) (DZUP); 1 ♂, Matri, Hildenberg, 1050–1150 m, 14.viii. 1967 (*Wright & Pont*) (DZUP). MOROCCO: 1 ♀, Atlas, Jb. Ayachi, R. Jaffar, 800–1500 m, 25.vii. 1963 (*A.C. Pont*) (DZUP); 1 ♀, Atlas, Jb. Ayachi, Mikdane, Stream III, 17.vii. 1963 (*A.C. Pont*) (DZUP). BRAZIL: 3 ♂, 1 ♀, Paraná, Colombo, 02.xi. 1986 (*Lev. Ent. Profaupar*) (DZUP); 2 ♀, Paraná, Curitiba, vii. 1980 (*C.B. Jesus*) (DZUP); 2 ♂, 2 ♀, same locality, x. 1980 (*C.B. Jesus*) (DZUP); 2 ♂, Paraná, Guarapuava, 31.x. 1986 (*Lev. Ent. Profaupar*) (DZUP); 3 ♀, same locality, 02.xi. 1986 (*Lev. Ent. Profaupar*) (DZUP); 4 ♂, 4 ♀, Paraná, Ponta Grossa, 31.x. 1986 (*Lev. Ent. Profaupar*) (DZUP).
- Phaonantho benevola*: PERU: 1 ♂, Madre de Dios, Avispas, 400 m, 10–20.ix. 1962 (*L. Pena*) (DZUP). BRAZIL: 1 ♀, Rio de Janeiro, Petrópolis, 900 m, xi. 1971 (*E.G., I. & E.A. Munroe*) (DZUP); 1 ♀, Mato Grosso, Cáceres, 13.xi. 1984 (*Buzzi, Mielke, Elias & Casagrande*) (DZUP).
- Polietina orbitalis*: BRAZIL: 3 ♀, São Paulo: Araçatuba, x. 1961 (*Lane & Rabello*) (MZSP); 7 ♂, 11 ♀, São Paulo, Assis, 12.ii. 1993 (*V. Silva*) (DZUP); 4 ♂, 3 ♀, same locality, 10.iii. 1993 (*V. Silva*) (DZUP); 1 ♂, 2 ♀, same locality, 29.iv. 1993 (*V. Silva*) (DZUP); 1 ♀, Paraná: Antonina, 22.xii. 1986 (*Lev. Ent. Profaupar*) (DZUP); 1 ♀, same locality, 29.xii. 1996 (*Lev. Ent. Profaupar*) (DZUP); 4 ♀, Paraná, Colombo, 04.viii. 1986 (*Lev. Ent. Profaupar*) (DZUP); 6 ♀, same locality, 11.viii. 1986 (*Lev. Ent. Profaupar*) (DZUP); 1 ♂, 2 ♀, Paraná, Engenheiro Beltrão, 25–26.xii. 1983 (*J.A. Rafael*) (DZUP); 9 ♀, Paraná, Guarapuava, 04.viii. 1986 (*Lev. Ent. Profaupar*) (DZUP). 1

## Appendix 2

Characters and character states used in the cladistic analysis of *Coenosopsia*.

1. Female orbital facial in profile view: (0) completely visible; (1) partly visible.



2. Interfrontal setae on female: (0) absent; (1) present.
3. Interfrontal setae on male: (0) absent; (1) present.
4. Proclinate fronto-orbital setae on female: (0) absent; (1) present, 1 seta; (2) present, 2 setae.
5. Proclinate fronto-orbital setae on male: (0) absent; (1) present.
6. Reclinate fronto-orbital setae on female: (0) 2 setae; (1) 1 seta.
7. Gena with upward directed seta: (0) absent; (1) present, 1 seta; (2) present, many setae.
8. Male eyes: (0) holoptic; (1) dichoptic.
9. Shape of female palpus: (0) spatulate at the apical half; (1) filiform.
10. Colour of palpus: (0) entirely yellow; (1) entirely brown; (2) brown, with yellow apex.
11. Shape of prosternum: (0) narrow; (1) enlarged anteriorly.
12. Prealar seta: (0) undeveloped; (1) developed.
13. Postsutural dorsocentral setae: (0) 3; (1) 4.
14. Ventral surface of scutellum: (0) bare; (1) setulose.
15. Length of vein A1: (0) not reaching the wing margin; (1) reaching the wing margin.
16. Ventrobasal seta on hind basitarsus: (0) absent; (1) present.
17. Epandrium setulosity at the lower anterior portion: (0) bare; (1) with developed setulae.
18. Cercal plate: (0) longer than wide; (1) wider than long; (2) as wide as long.
19. Median lobe of the cercal plate: (0) margins subparallel; (1) margins converging abruptly to the apex from the median portion; (2) margins converging gradually to the apex since the base.
20. Upper incision of the median lobe of the cercal plate: (0) reaching near beyond half the median lobe length; (1) not reaching half the median lobe length; (2) almost reaching the apex.
21. Right and left surstyli asymmetrical: (0) absent; (1) present.
22. Right surstylus in profile with the apical portion enlarged (hooklike): (0) absent; (1) present.
23. Apical sensilla on gonopod: (0) present, only 1; (1) present, numerous; (2) present, 2; (3) absent.
24. Median sensilla on gonopod: (0) absent; (1) present, numerous; (2) present, 2; (3) present, only 1.
25. Gonopod length: (0) shorter than paramere; (1) as long as paramere; (2) longer than paramere.
26. Aedeagus length: (0) shorter than aedeagal apodeme; (1) as long as aedeagal apodeme; (2) longer than aedeagal apodeme.

**Appendix 3.** Data matrix (?, missing data; –, inapplicable characters).

Taxa	Characters																										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
<i>F. bahiensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. orbitalis</i>	0	1	0	1	1	0	2	0	0	0	0	1	1	0	0	0	0	1	–	1	0	0	3	1	1	2	
<i>A. pluripunctata</i>	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	2	2	0	0	2	0	0	1	2	
<i>D. platura</i>	0	1	0	1	0	0	2	0	0	1	1	1	0	1	1	1	0	0	1	0	0	0	0	0	1	2	
<i>P. benevola</i>	0	1	0	2	0	1	1	0	1	1	0	1	0	1	0	1	1	1	–	1	0	0	1	1	1	2	
<i>C. brasiliensis</i>	1	1	1	1	1	0	1	1	0	1	1	1	0	0	0	1	1	2	1	2	1	0	0	3	1	2	
<i>C. ferrari</i>	0	1	1	1	1	0	1	1	0	1	1	1	0	0	0	1	1	0	2	2	1	0	0	2	1	1	
<i>C. floridensis</i>	0	1	1	1	1	0	1	1	0	1	1	1	0	0	0	1	0	0	2	2	1	1	0	3	2	2	
<i>C. mexicana</i>	0	1	1	1	1	0	1	1	0	0	1	1	0	0	0	1	0	0	2	2	1	1	0	3	2	2	
<i>C. michelseni</i>	0	1	1	1	1	0	1	1	1	2	1	1	0	0	0	1	0	0	2	1	1	0	3	2	2	2	
<i>C. peruviana</i>	0	1	1	1	1	0	1	1	0	1	1	1	0	0	0	1	0	2	1	2	1	0	0	3	2	2	
<i>C. prima</i>	1	1	1	1	1	0	1	1	0	2	1	1	0	0	0	1	?	0	2	2	1	0	0	3	2	2	