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Biogeographical History of the Neotropical and Neantarctic Simuliidae (Diptera)

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Abstract: Using the lineages of taxa and their distribution on different areas of endemism, and by cladistic methodology applied to biogeography, we try to define the biotic history of the areas of endemism based on Neotropical and Neantarctic Simuliidae. Using the information of the cladograms of nine Central and South American monophyletic supraspecific taxa of Simuliini and 16 areas of endemism, we perform a Component Analysis with component 1.5, using the assumption 2. A second analysis was made using Biogeographic Parsimony Analysis; the data matrix was analyzed with the program NONA. The cladograms obtained show the possible sequence of historic separation of areas of endemism, evidencing the presence of two large biotas: the austral (Neantarctic) and the tropical (Neotropical), that were maintained in partial isolation. The areas of endemism of the austral biota are: Subantarctic, Central Chile, Patagonian, Puna, Monte and Pampean; those of the tropical biota are: Amazonia, Southeastern Brazil Mountains, Cerrado, Guiana, Caribbean, Yungas, Norandean, Pacific and Mesoamerican Mountains. It was not possible to assign the Desert to any of these biotas. The principal vicariant events that affected the Simuliidae are sea ingressions, the emergence of the Andes and climatic changes.

Key words: Neotropical Region, Neantarctic Region, blackflies, cladistic biogeography, areas of endemism, biogeographic history

The similitude between biotas from different areas has called the attention of naturalists, who have tried to explain their probable relations with a number of hypotheses. Many of the biogeographic schemes are based on the comparison between different biotas of the world, proposing dispersion hypotheses to explain the observed similitude (Wallace, 1876; Simpson, 1964; Darlington, 1965; Raven & Axelrod, 1975).

The use of cladistic methodology in systematics (Hennig, 1965) and its application in biogeography (Brundin, 1966; Hennig & Wydozinsky, 1966; Rosen, 1978) have provided an operational tool to analyze the distribution patterns (Platnick & Nelson, 1978; Nelson & Platnick, 1981; Humphries & Parenti, 1986).

Cladistic biogeography assumes a correspondence between the phylogenetic relations of the taxa and the relations of the areas they occupy, and that organisms have evolved together with the Earth. This would be why the "history of the areas of endemism" can be inferred starting from the cladistic analyses of the several taxa composing a biota.

This contribution uses the information available on Simuliidae (Diptera). The Simuliidae is a well represented group in the Central and South America, with 12 genera and approximately 340 species (Crosskey & Howard, 1997), most of which are endemic to this region (Coscarón & Coscarón Arias, 1995). The Simuliidae occur in Central and South America from southern Mexico to Tierra del Fuego. They are distributed in a large number of environments ranging from sea level to 4700 meters of altitude.

Numerous phylogenetic studies of the Central and South American Simuliidae have been made in the last years (Coscarón & Coscarón-Arias, 1996, 1997; Coscarón & Miranda-Esquivel, 1998; Coscarón *et al.*, 1996, 1999), where possible biogeographic inferences are discussed for each one of the groups analyzed. Coscarón & Coscarón-Arias (1995) identified the areas of endemism for the Neotropical and Neantarctic Simuliidae which are used in this work, together with the Simuliidae phylogenetic analyses, to obtain hypotheses on the biogeographic history of this family in Central and South America.

MATERIAL AND METHODS

Selection of the areas

The area under study comprises the Neotropical Region and the Neantarctic Region of Central and South America. These two regions are considered by many authors (Ringuelet, 1961; Fittkau, 1969; Müller, 1973) as only one region, the Neotropical. Nevertheless there are two biotas with very dissimilar affinities (Jeannel, 1942; 1967; Monrós, 1958; Kuschel, 1969; Halfter, 1974; Porter, 1991; Roig-Juñent, 1992) which occupy areas that have been considered as different biogeographic regions. One of them is the tropical biota called Guiano-Brazilian (or Jeannel´s Inabresic, 1942, or Kuschel´s Brasilic, 1969) tha taxa of which are phylogenetically related with other taxa from the tropical African regions. The other biota in South America is the Patagonian (or Jeannel´s Paleantarctic, 1942, or Monrós´ Neantarctic, 1958) with taxa more closely related to the taxa from other austral areas, such as Australia, New Zealand, South Africa, and numerous subantarctic islands. The region occupied by this austral biota of South America differs greatly according to the different authors. Monrós (1958) considered only the area occupied by *Nothofagus* forests. Most of the authors considered that it constituted all the area south of 30° S latitude (Jeannel, 1967; Porter, 1991; Crisci *et al.*, 1991). A third position (Morrone, 1996) regards it as the areas south of 30° S latitude, including also the Andean regions north of this latitude up to Colombia (Páramo).

The 16 areas of endemism proposed (Fig. 1) have been delimited by Coscarón & Coscarón-Arias (1995) based on the distribution of the species of Simuliidae (*Simulium* and eight of the genera of *Prosimuliini*). The acronyms of the areas and their location are given in Figure 1.

1. **Amazonia (AM):** it is a large area representing the Amazon basin. It corresponds to the rain forest. It is constituted by a series of recent fluvial sediments and the remnants of the mountains of the Brazilian and Guiana shields (Cabrera & Willink, 1980).

2. **Northern Andes (NA):** this is the biogeographic province named Páramo by Cabrera & Willink (1980), located in the Andean region of Venezuela, Perú, Colombia and Ecuador between 2500 and 3500 meters.

3. **Caribbean (CA):** this area occupies the plains and mountain ranges of northern Colombia and of Venezuela north of the Orinoco, and the Lesser Antilles. It comprises different environments with xerophytic vegetation, and jungle in the humid galleries and piedmonts. It corresponds partly to the biogeographic provinces named Sabana, Guajira, and Venezolana by Cabrera and Willink (1980). Its their fauna is related to that of the Guiana and Yungas areas.

4. **Cerrado (CE)**: it is a large, diagonally disposed area in South America, located between Amazonia and the Mountains region of the Brazilian southeast. It corresponds to what Cabrera and Willink (1980) called Caatinga, Chaco, Cerrado, and part of the Espinal. It is a tropical arid area with shrubby vegetation and xeric forests of *Prosopis* ('algarrobos') and *Aspidosperma* ('quebracho'). It constitutes a rich area of endemism for insects (Roig-Juñent, 1998) related to the tropical fauna of South America.

5. **Central Chile (CH)**: it includes the Chilean area from Coquimbo to Concepción (between 30° and 37° S latitude). In its septentrional part the aridity conditions are higher (Coquimbo region of Roig-Juñent, 1994), with small forests along the creeks close to the coast. The meridional part is characterized by shrubby vegetation (Cabrera & Willink, 1980). Within this Central Chilean area there are relicts of subantarctic forests (Mt. Campana) showing that the Antarctandean forest was much more extended.

6. **Desert (DE)**: this area extends along the Pacific coast from 5° S latitude in Ecuador to 30° S latitude in Chile. The precipitation is scarce, getting to zero in Arica and Iquique (Cabrera & Willink, 1980). It has a warm climate and the vegetation on the coast is almost null, with some vegetation on the Andean slopes or bordering the watercourses descending from the mountains. The region possesses numerous endemisms adapted to the extreme aridity conditions. Its fauna is quite related to that of Central Chile and of the Puna. The same as in the Central Chile area, there are relicts of the Antarctandean forest like that of Fray Jorge.

7. **Guiana (GU)**: this area includes the Guianan massif, with the Roraima and Parima Tepuis, together with the Orinoco plains (Coscarón & Coscarón-Arias, 1995). It is an undulated plain alternating with plateaus reaching almost 1600 meters of altitude, with nearly vertical walls. The vegetation is characterized by savanna and gallery forests along the rivers. The fauna of the region has been considered by some authors as very ancient (Jeannel, 1942, 1967); it was called by Ihering (1927) the Archiguyana Region.

8. **Mesoamerican Mountains (MM)**: it comprises the highland forests of the Mexican and Central American mountains as far south as

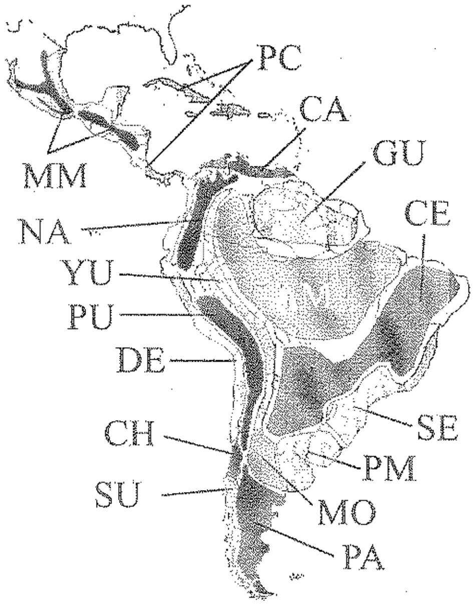


Fig. 1. Areas of endemism: AM, Amazonia; NA, Northern Andes; CA, Caribbean; CE, Cerrado; CH, Central Chile; DE, Desert; Gu, Guiana; MM, Mesoamerican Mountains; MO, Monte; PC, Pacific; PM, Pampean; PA, Patagonian; PU, Puna; SE, Mountainous Region of the Brazilian Southeast; SU, Subantarctic; YU, Yungas.

Panamá. It coincides with the biogeographic province called Mesoamericana de Montañas by Cabrera & Willink (1980). The fauna of the area has three types of elements: endemic, neotropical, and nearctic (Halffter, 1964), of which the most ancient elements would be from the beginning of the Cenozoic.

9. **Monte (MO)**: this area is located in west-central Argentina, from the south of Mendoza and northeast of La Pampa to the south of Catamarca. The area here considered does not include the austral part of the Monte of Cabrera & Willink (1980). It is a semiarid area with temperate climate and shrubby vegetation. The fauna is closely related to that of the Chaco (Stange *et al.*, 1976).

10. **Pacific (PC)**: includes the peripheral lowlands under 1000 meters of altitude in Mexico, Central America, Antilles and a western strip of Colombia and Ecuador. It is a rainforest and coincides with the provinces Pacifica and Caribe of Cabrera & Willink (1980). It is one of the most humid regions of the planet and the temperature is constant almost all year-round.

11. **Pampean (PM)**: this is a plain with a few hills, with steppe vegetation, and moderate precipitation diminishing toward the west. It corresponds to the biogeographic provinces of the Pampa and part of the Espinal of Cabrera & Willink (1980). Its fauna is considered to be closely related to that of the Brazilian southeast (Ringuelet, 1961).

12. **Patagonian (PA)**: it comprises the austral part of Argentina, from the Río Colorado to Tierra del Fuego. The Patagonian area as it is here considered includes the meridional part of the Monte of Cabrera & Willink (1980) and their biogeographic province of Patagonia (Coscarón & Coscarón–Arias, 1995). The steppe is the prevailing vegetation and the precipitation is diminished by the Andes mountains. The climate is temperate cold. Several elements of the fauna are related, like those of the Subantarctic area, with taxa from Australia and New Zealand. Nevertheless, in contrast to what occurs in the Subantarctic area, the taxa present in Patagonian in many cases reach the Pampean, Puna, and Monte areas.

13. **Puna (PU)**: it is located in the Altoandean plateau of Argentina, Chile, Bolivia and Perú, between 3000 and 5000 meters of altitude. It is a strip that extends from 10º S latitude (Perú) to 33 º S in province of Mendoza (Argentina). It is a terrain of xeric conditions, with a marked thermal amplitude. The vegetation is that of the steppe. The area here considered includes the Puneña, Prepuneña and Altoandina biogeographic provinces of Cabrera & Willink (1980), since none of the species of Simuliidae shows the division proposed by these authors (Coscarón & Coscarón-Arias, 1995). The Puna fauna has great affinity with the Patagonian (Morrone, 1996).

14. **Mountainous Region of the Brazilian Southeast (SE)**: it is distributed in Argentina (Misiones), east of Paraguay and southeast of Brazil. It comprises a large region of the Planalto and of the Sierras of the Brazilian Atlantic coast. The vegetation are savannas and tropical forests. It coincides with the Paranense and Atlantica biogeographic provinces of Cabrera & Willink (1980).

15. **Subantarctic (SU)**: it corresponds to the area of distribution of the *Nothofagus* forests extending from Concepción (37° S) to Tierra del Fuego, including the oriental flank of the Patagonian Andes of Argentina. The climate is cold temperate with great humidity. The taxa from this area have the greatest affinity with those from Australia and New Zealand (Morrone

et al., 1994; Roig-Juñent, 1994) and in America they are restricted only to this region (Roig-Juñent, 1998).

16. **Yungas (YU)**: it lies on the oriental slope of the Oriental Andes between 500 and 3000 meters of altitude. It is limited by the Amazonia and Cerrado areas to the west, extending from Colombia to the province of Catamarca in Argentina. It coincides with the area proposed by Cabrera & Willink (1980) for the homonymous biogeographic province. It is characterized by a cloudy forest, with a temperate climate which turns cold in the highest zones.

Selection of the taxa

Nine monophyletic taxa of Simuliidae for which there exist phylogenetic analyses have been chosen. One of them is a tribe (Prosimuliini) (Coscarón & Miranda-Esquivel, 1998) and the remaining eight are subgenera of *Simulium* (Coscarón & Coscarón-Arias, 1996, 1997; Coscarón *et al.*, 1996, 1999). The cladograms have been selected according to the criteria proposed by Humphries (1981). Therefore the cladograms of the chosen areas have to comply with the following: a) at least three should have areas of endemism from the studied area; b) at least one of the terminal taxa in the area should be endemic of one area. This is because if all the taxa occupy two or more areas of endemism, the information provided by the cladogram is irrelevant.

For each lineage a cladogram of the fundamental areas was obtained, the terminal taxa being replaced by the area(s) of endemism they occupy (Figs. 2, 4, 6, 8, 10, 12, 14, 16, and 18). In some cases the area cladograms have been simplified, as for example in *Simulium (Psilopelmia),* which has entire clades occupying only one area and provide the same information.

1. **Prosimuliini** (Coscarón & Miranda-Esquivel, 1998). Three genera endemic to South and Central America, comprising 74 species, are considered here (Coscarón & Coscarón-Arias, 1995). The tribe includes *Cnesia* Enderlein (restricted to the *Nothofagus* forests), *Pedrowygomya* Coscarón & Miranda-Esquivel (distributed in the Puna), and *Gigantodax* Enderlein (distributed from southern USA to the south of Patagonia). The terminal units for the genus *Gigantodax* used by Coscarón and Miranda-Esquivel (1998) correspond to the four species of the *Gigantodax cortesii* group and one species from each of the remaining groups of species. Cladogram of areas, Fig. 2.

2. ***Simulium (Pternaspatha)*** Enderlein (Coscarón & Coscarón-Arias, 1996). This is a subgenus with 27 species, distributed from southern Patagonia to Ecuador through the Puna. Some species also occur west of the southern Andes, as in the Subantarctic, Central Chile, and Desert areas. This subgenus is largely sympatric with the Prosimuliini. Cladogram of areas, Fig. 4.

3. ***S. (Hemicnetha)*** Enderlein (Coscarón, unpublished). This subgenus comprises 20 species distributed mostly in Mesoamerica, the Caribbean and tropical regions of South America, excepting Amazonia (Coscarón & Coscarón-Arias, 1995). Cladogram of areas, Fig. 6.

4. ***S. (Psaroniocompsa)*** Enderlein (Coscarón & Coscarón-Arias, 1997). It includes 15 species, distributed in disjunct areas: one austral area from the Brazilian southeast to Patagonia, another area in Guiana and the Caribbean, and a third one in the Pacific region, from Panama to Ecuador. Cladogram of areas, Fig. 8.

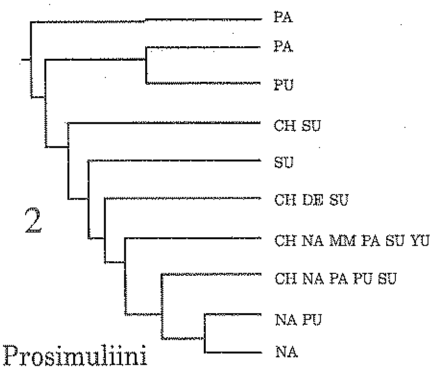
5. ***S. (Inaequalium)*** Coscarón & Wygodzinsky (Coscarón & Coscarón-Arias, 1997). This subgenus has 13 species. Its distribution area has the shape of an arc, from Panama and Venezuela to the Brazilian southeast and northeast of Argentina, very similar to that of *S. (Psaroniocompsa),* but without reaching Patagonia. Cladogram of areas, Fig. 10.

6. ***S. (Chirostilbia)*** Enderlein (Coscarón & Coscarón-Arias, 1997). There are 12 species in this subgenus, most of them in the Brazilian southeast, although its distribution reaches out of this area and is similar to that of *S. (Inaequalium).* Cladogram of areas, Fig. 12.

7. ***S. (Ectemnaspis)*** Enderlein (Coscarón, unpublished). It comprises 39 species (Coscarón & Coscarón-Arias, 1995) which are widely distributed in South America, and on a smaller scale in Central America, from the Pacific and the Caribbean to Patagonian. Cladogram of areas, Fig. 14.

8. ***S. (Psilopelmia)*** Enderlein (Coscarón *et al.*, 1996). It comprises 21 species distributed from Mexico to the north of Colombia, Venezuela, Guyana, Suriname and French Guiana (Coscarón & Coscarón-Arias, 1995). One species (*S. (P.) escomeli* Roubaud) is distributed in the coastal desert of Peru and north of Chile. Cladogram of areas, Fig. 16.

9. ***S. (Simulium)*** Latreille (Coscarón *et al.*, 1999). This cosmopolitan subgenus has 25 neotropical species that constitute a monophyletic group (*Aspathia* Enderlein), and are distributed in Central America, the Caribbean and the septentrional region of South America (Coscarón & Coscarón-Arias, 1995), with a species endemic



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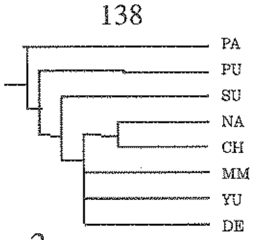

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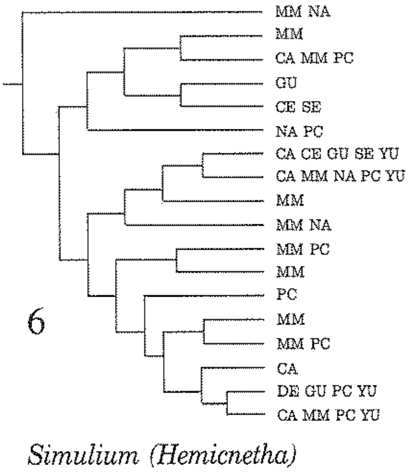

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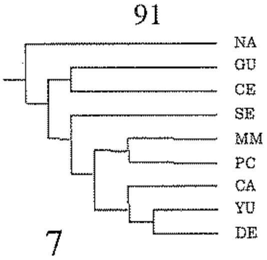

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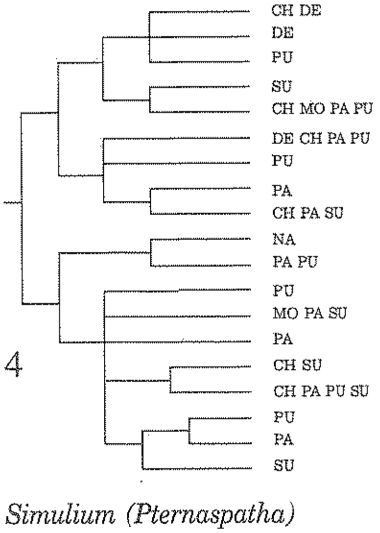

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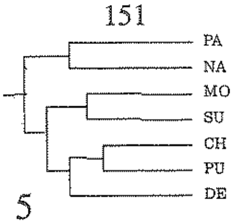

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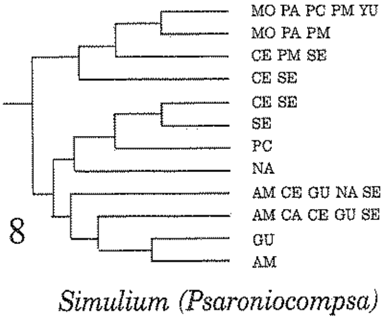

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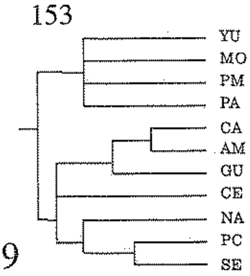

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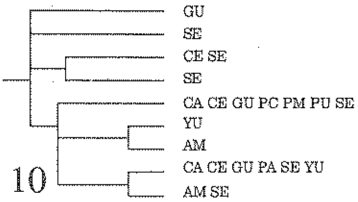
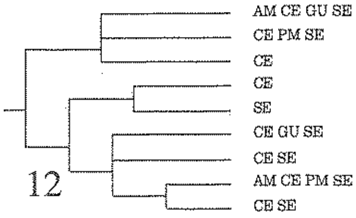
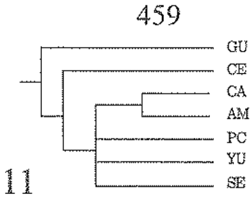
Figs. 2-9. Figs. 2-3, Prosimuliini: 2, fundamental area cladogram; 3, Nelson consensus tree from the 138 resolved area cladograms. Figs. 4-5, *Simulium (Pternaspatha)*: 4, fundamental area cladogram; 5, Nelson consensus tree from the 151 resolved area cladograms. Figs. 6-7, *Simulium (Heminecta)*: 6, fundamental area cladogram; 7, Nelson consensus tree from the 91 resolved area cladograms. Figs 8-9, *Simulium (Psaroniocompsa)*: 8, fundamental area cladogram; 9, Nelson consensus tree from the 153 resolved area cladograms.

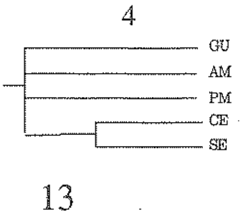


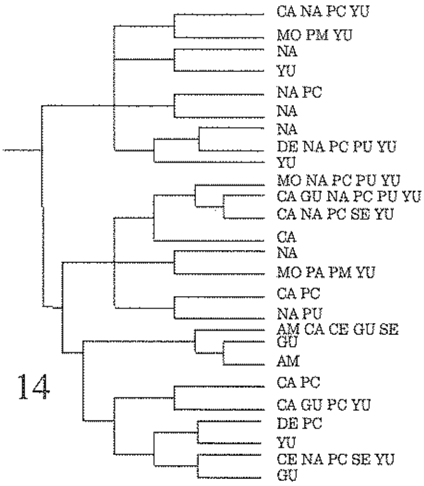
Simulium (Inaequalium)



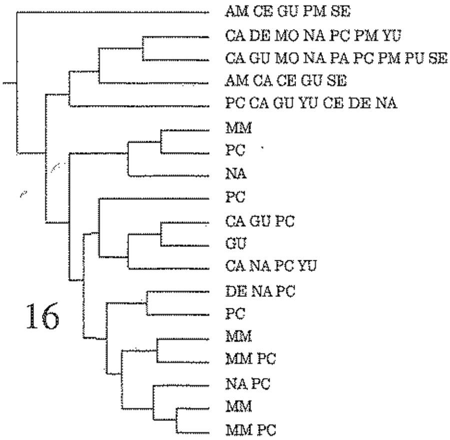
Simulium (Chirostilbia)



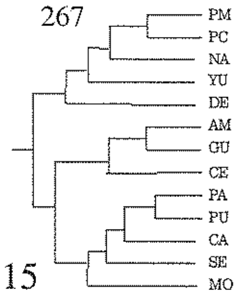


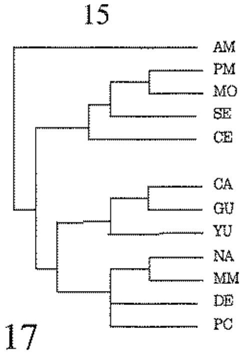


Simulium (Ectemnaspis)

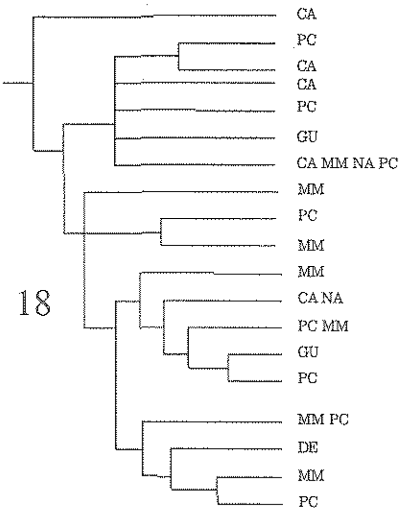


Simulium (Psilopelmia)





Figs. 10-17. Figs. 10-11, *Simulium (Inaequalium)*: 10, fundamental area cladogram; 11, Nelson consensus tree from the 459 resolved area cladograms. Figs. 12-13, *Simulium (Chirostilba)*: 12, fundamental area cladogram; 13, Nelson consensus tree from the 4 resolved area cladograms. Figs. 14-15, *Simulium (Ectemnaspis)*: 14, fundamental area cladogram; 15, Nelson consensus tree from the 267 resolved area cladograms. Figs. 16-17, *Simulium (Psilopelmia)*: 16, fundamental area cladogram; 17, Nelson consensus tree from the 15 resolved area cladograms.



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Simulium (Simulium)

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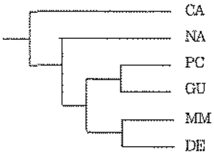

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Figs. 18-19. *Simulium (Simulium)*: 18, fundamental area cladogram; 19, Nelson consensus tree from the 32 resolved area cladograms.

to the Desert area. Cladogram of areas, Fig. 18.

Data analysis

Two different techniques were used to obtain the general cladogram of areas. All the resolved area cladograms were obtained under assumption 2 from the essential area cladograms (Figs. 2, 4, 6, 8, 10, 12, 14, 16 and 18) using the program Component 1.5 (Page, 1989). The sets of resolved area cladograms are represented through Nelson consensus trees (Figs. 3, 5, 7, 9, 11, 13, 15, 17, and 19; the number of cladograms obtained is indicated above each figure). The resolved area cladograms were compared to obtain general cladograms of areas through intersection, that is to say shared cladograms of areas (Crisci *et al.*, 1991).

A second method used was Wiley´s (1988) Biogeographic Parsimony Analysis, where a data matrix is built based on all the essential area cladograms. For this, each component is turned into binary numbers. The absent areas have been neutrally treated, as non-comparable and not as absent, as proposed by Wiley (1988). For each essential area cladogram each component has been codified only once, although it may be present more than once. The basal component is not considered in the matrix when it replicates a component already codified in the cladogram. These matrices have been analyzed with the Wagner algorithm using the program NONA (Goloboff, 1993).

RESULTS

From the analysis of the different sets of resolved area cladograms it was not possible to obtain a cladogram shared by all the cladograms. Likewise, it was not possible to obtain a general cladogram of areas shared by more than two or three lineages. Nevertheless, eight of the treated lineages (exception made of *S.* (*Ectemnaspis*)) shared a reduced area cladogram (Fig. 20), with only eight of the 16 treated areas. Two reduced cladograms of 11 areas shared by six lineages were also found (Fig. 21). The impossibility of finding shared area cladograms is mainly due to the different position presented by certain areas of endemism in the resolved area cladograms, as for example Desert (DE), Yungas (YU), Cerrado (CE), Caribbean (CA), and Northern Andes (NA).

The codification of the components of the essential area cladograms permitted the obtention of a basic data matrix (17 areas by 115 components) (Table 1). Its analysis resulted in a cladogram (Fig. 22) 233 steps long, with a consistency index of 48 and a retention index of 56. This cladogram is compatible with that obtained through the intersection of eight of the nine lineages used (Fig. 20).

The three general area cladograms (Figs. 20-22) show the possible sequence of the historical separation of the areas of endemism in South America. The discussion of the relations between areas will be mainly based on the general cladogram of areas obtained through parsimony (Fig. 22), but will also take into account the two cladograms obtained through intersection (Figs. 20-21). The separation sequence of the areas is represented graphically in Figure 23.

In the cladogram obtained by parsimony the first area to be separated is the Desert. The second separation clearly marks a division between the Neotropical and the Neantarctic Regions (Fig. 23b), which is also shown by the general cla-

Table 1. Data matrix of 17 areas and 115 components extracted from phylogenies of Simuliidae.

	Prosimuliini	*S.(Pternaspatha)*	*S.(Hemicnetha)*	*S.*	*S.*	*S.*	*S.*	*S.*	*S.*
				(Psaroniocompsa)	*(Inaequalium)*	*(Chirostilbia)*	*(Ectemnaspis)*	*(Psilopelmia.)*	*(Simulium)*
AN	0000000	0000000000000000	00000000000000	000000000000	000000	000000	0000000000000000000000000000000	00000000000000	000000000
MM	0011010	????????????????	11110010000000	????????????	??????	??????	???????????????????????????????	01100111101011	011011101
PC	???????	????????????????	11011111110110	000011110011	100010	??????	1111111100111111001011110101111	11110110101011	111011101
CA	???????	????????????????	00001111111110	011000100001	111010	??????	0000011110101111001011110100001	01111110111011	000110101
NA	1111010	0000000001000011	01110111110110	001001100001	??????	??????	1001100100111111010111110111111	00000111100001	000110101
YU	0011010	????????????????	00000111010110	001000110011	111010	??????	1011101100111111111000111110111	11101110110000	?????????
AM	???????	????????????????	00000000001101	111000100001	001110	010110	0000000011100000000000100000000	??????????????	?????????
GU	???????	????????????????	00001010111111	111000100001	111010	001110	0001101111101011000001100000000	10101010100000	101010100
CE	???????	????????????????	00000000001111	011111100111	111011	111111	1001100110100111000001100000000	00001010100111	?????????
SE	???????	????????????????	00000000111101	011111100111	111111	111111	1001100110100000000000100000000	00001010100111	?????????
PU	1101011	0111101111101011	00000000110100	????????????	100010	??????	0000000000011011000111100000000	??????????????	?????????
MO	???????	0011100000000111	00000001110100	000000011011	??????	??????	0000000000010001110001101100001	??????????????	?????????
PM	???????	????????????????	00000001110101	000000011111	100010	010101	0000000000000000110001101100001	??????????????	?????????
PA	0111011	0011111111101111	00000000110100	000000011011	011010	??????	0000000000000000110001100000000	??????????????	?????????
DE	0000110	1100101100000001	00110011010110	????????????	??????	??????	0110100100100000000000100000011	10100000100000	000001100
CH	0111110	1111111100011011	??????????????	????????????	??????	??????	???????????????????????????????	??????????????	?????????
SU	0111110	0001110100111111	??????????????	????????????	??????	??????	???????????????????????????????	??????????????	?????????

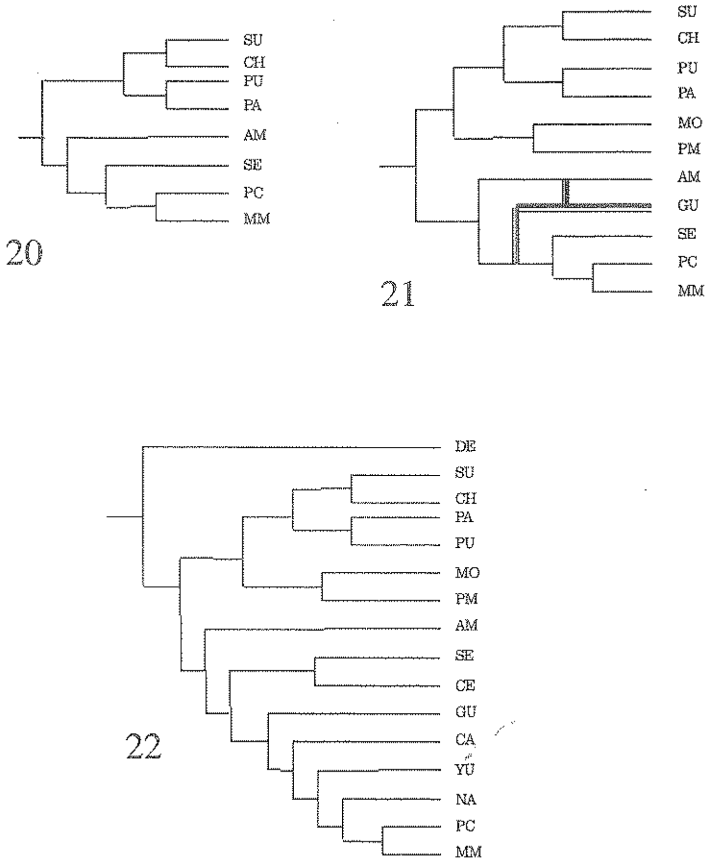
dograms of areas obtained through intersection (Figs. 20-21). The cladograms obtained through intersection and that obtained by parsimony are totally congruent regarding the separation of austral areas (Neantarctic). The sequence shows a first separation of the clade (PM, MO) (Fig. 23c) and later the separation of the remaining areas in two clades (PA, PU) and (CH, SU) (Fig. 23d).

The first Neotropical area to separate in the three general cladograms of areas (Figs. 20-22) is Amazonia (Fig. 23e). The subsequent separation sequence in the cladogram obtained by parsimony is the following: first the two more austral areas (CE, SE) separate (Fig. 23f) from the other septentrional areas, the Guiana area follows (Fig. 23g), then the Caribbean area, and finally the Yungas area separates from the septentrional areas (Fig. 23h). For the Neotropical areas, one of the cladograms obtained by intersection (Fig. 21) does not present the same separation sequence, as in this cladogram the Guiana area may be the sister area of Amazonia, or be the second to separate.

DISCUSSION

The close relations of some groups of *Simulium* species and of Prosimuliini with taxa from other continents show that these Diptera were already present and widely distributed in Gondwana before its fragmentation. The existence of fossils gives evidence that some genera already existed at least in the Middle Jurassic in Asia and at the beginning of the Cretacic in Australia (Crosskey, 1991). This wide distribution has been also stated for other insects like Ichneumonidae (Porter, 1991) and Carabidae (Roig-Juñent, 1998). During this period of the Mesozoic the climate was warm and not seasonal; this climatic uniformity would have allowed a wide distribution of organisms in the Gondwana (Porter, 1991).

The general cladogram of areas shown in figure 22 shows the possible sequence of vicariant events undergone by this Gondwanic biota. Nevertheless, it is very difficult to try to relate the known geological events that may have had vicariant effects with the sequence of the cladogram (Fig. 22). In the case of insular isolations (for example, New Zealand) it is easier to assign a vicariance, as the possibilities for dispersion are reduced. In continental areas it becomes much more difficult. The vicariant effects within continents may finish when barriers disappear. There can occur cycles when the vicariance of widely distributed species first takes place, fol-



Figs. 20-22. General area cladograms. 20, reduced general area cladogram of eigth areas of endemism shared by eigth lineages. 21, reduced general area cladogram of 11 areas of endemism shared by six lineages. 22, general area cladogram obtained by parsimony.

lowed by the establishment of new endemic species in more restricted areas; should barriers disappear, the dispersion of the descendant species would occur to produce forms again widely distributed, that would be affected by other vicariances (Roig-Juñent & Flores, in press).

This is what has happened in South America, because since the Cretacic the continental area has undergone large transformations (Tarling, 1980; Uliana & Biddle, 1988). During this period there were great climatic changes. Subtropical forests existed in the Paleocene in Santa Cruz (Argentina), with a climate that remained warm temperate in the Eocene, temperate during the Oligocene and Miocene, and turned to cold in the Pliocene, especially when a cold water current started in the circumantarctic sea, producing the cooling of South America and an expansion of open environments such as savannas and pastures. Plate tectonics connected South America with North America and separated it from Antarctica. The rising of mountain chains, mainly the Andes, caused lower precipitation regimes (Shmida, 1985). Finally, this period was characterized by numerous marine regressions and transgressions (Volkheimer, 1971) that in many cases occupied most of the austral region of South America.

The analysis of the distribution of the species of the treated groups shows that redundant distributions exist in many cases. They might be owed to the installation of barriers that later on disappeared, thus allowing for a new cosmopolitism of the newly formed groups. This would not be strange for South America, as most of the barriers from the end of the Mesozoic and from the Cenozoic were continental seas that underwent great oscillations (ingressions and regressions) through time (Volkheimer, 1971), causing a new cosmopolitism of the species when they disappeared.

Considering the above, we try to correlate a geological event with a vicariant event shown by the three general area cladograms (Figs. 20-22). This separation involves the two large Gondwanic biotas of South America, the Neotropical and the Neantarctic. The division of the Gondwanic biota has been proposed for the Upper Cretacic (Jeannel, 1942, 1967; Halffter, 1974), when a marine ingression occurred during the Maastrichtian and lasted until the Paleogene, separating South America in two parts (Uliana & Biddle, 1988) (Fig. 23b). This sea made its entrance through eastern Argentina and reached Bolivia. Another sea tongue was a narrow Patagonic sea connecting the Atlantic and the Pacific, thus isolating the Austral and Principal Cordilleras until the Miocene (Camacho, 1967). South America was thus divided in two, one austral region connected with Australia by way of Antarctica, and a tropical region intermittently connected with North America, and connected to a lesser extent with the African tropical region. This vicariant event between the two regions of South America explains that austral groups like the Prosimuliini are closely related to the taxa of the remaining austral areas (Wygodzinsky & Coscarón, 1962; Coscarón, 1985) and not to the other South American Simuliidae. The Maastrichtian vicariant event also affected the genus *Simulium,* widely distributed in the Gondwana, separating *Simulium (Pternaspatha)* and the *Simulium "blancasi* group", with a neantarctandean distribution, from the remaining subgenera with a Neotropical distribution. Most of the other subgenera of *Simulium* are Neotropical and have a closer relation to Ethiopic taxa like *S. (Thyrsopelma), S. (Anasolen), S. (Ectetemnaspis)* and *S. (Pomeroyellum)* (Crosskey, 1991). There also exists a relation to some subgenera of *Simulium* from the Nearctic region, like *S. (Hearlea), S. (Psilopelmia), S. (Simulium),* and the *S. (Ectemnaspis) dinellii* group, all of them largely developed in Mexico and Central America, and which through transitional bridges passed to South America and/or viceversa, as it is known that has occurred in other groups of insects (Halffter, 1976).

These two faunal groups, the Neotropical and the Neantarctic, were not only separated by geographic barriers but, like vertebrates and other organisms, continued isolated even though the barriers, like epicontinental seas, had disappeared. It has been postulated that for the Eocene there existed in austral South America two biogeographic units that evolved under different climatic conditions according to their different latitudinal locations (Pascual & Ortiz-Jaureguizar, 1990; Pascual *et al.*, 1996), one located north and the other Patagonic, connected to Australia. The latter union lasted probably until the Middle Eocene when Antarctica underwent a great cooling process with the formation of the ice cap, and Drake´s passage opened (Pascual, 1984). Later on, during the Middle Tertiary the rising of the Andes and the consequent desertification, plus the marine Paranense ingression of the Middle Miocene kept the Neantarctic region isolated from the Brazilian region along the east and the north (Porter, 1991).

Even though the separation mentioned above is clearly shown by the three cladograms (Figs. 20-22), the first area to be separated in the cladogram obtained by parsimony is the Desert (Figs. 22 and 23a). There are no geologic data that permit the supposition of a very early separation of this area with respect to the rest of South America. Roig-Juñent & Flores (in press), in their analysis of the eremic areas of austral South America, postulate that the area of the Atacama desert is one of the first to separate from the remaining arid areas, even though its age would be between the end of the Eocene and the beginning of the Oligocene (37 Mya). This would contradict what has been obtained through the parsimony analysis (Fig. 22), according to which the Desert would have to be earlier than the Maastrichtian sea from the Cretacic. Even though Shmida (1985) proposes that the Atacama is an ancient desert because of its high diversity of unique forms, he does not consider it to be of Mesozoic origin but from the Cenozoic. The origin of this desertic region constitutes an enigma. In some groups like the Ichneumonidae there occur Nearctic elements and there is no endemism of Neantarctic groups (Porter, 1991). This is not the case for the Simuliidae, where in the Atacama region there appear Neantarctic endemisms as well as Neotropical or Nearctic elements that could have arrived before North America separated from South America in the Cretacic, coinciding with the rupture of Gondwana and the separation of Africa.

It is possible, nevertheless, that the basal location of the Desert (DE) in the parsimony analysis could be owed to a methodological error. Six from the nine analyzed taxa of Simuliidae have

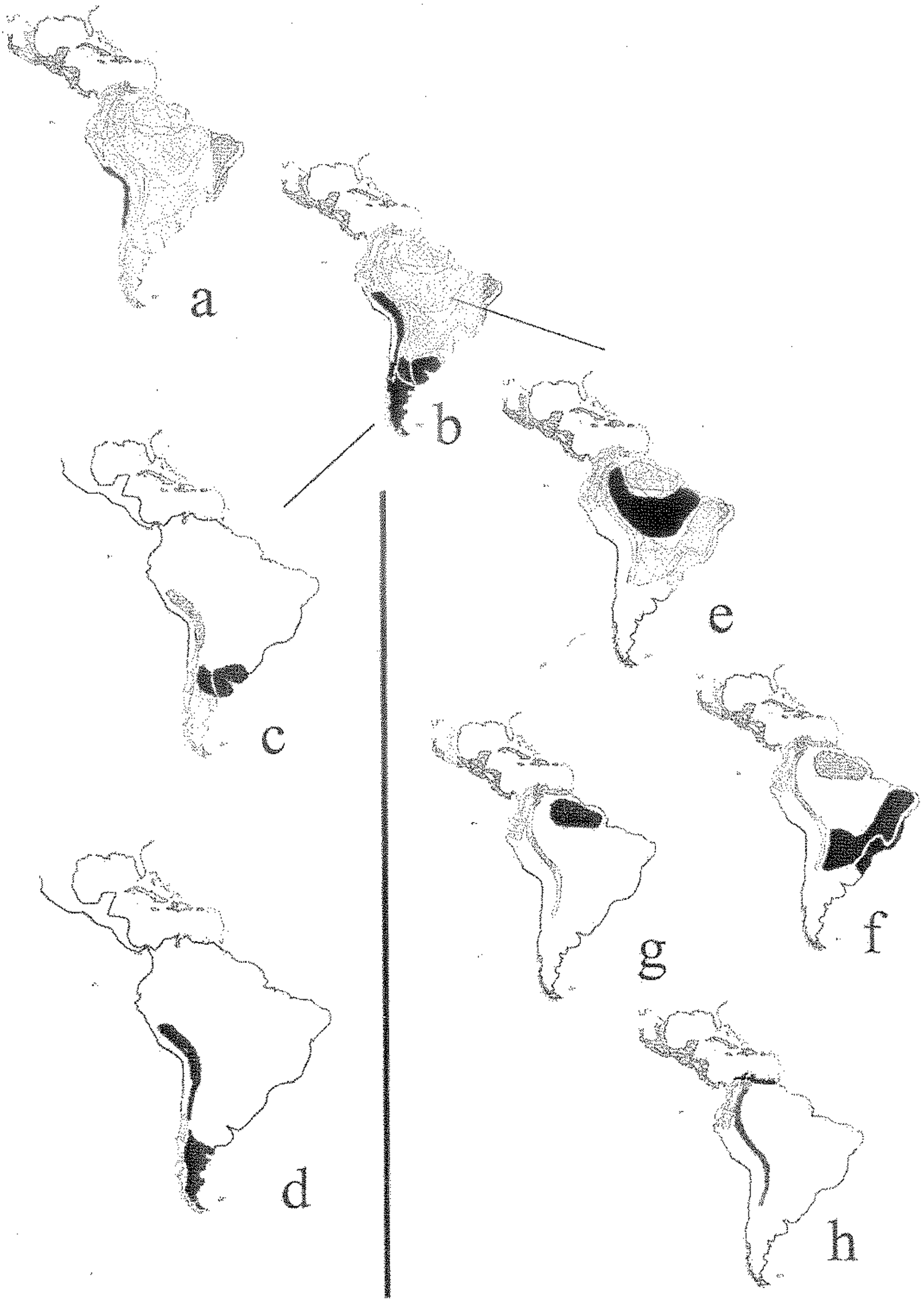


Fig. 23. Sequency of vicariant events. a) separation of Desert; b) separation of Neantarctic and Neotropical biotas; c) separation of Pampean and Monte areas; d) separation of Patagonian and Puna from Subantarctic and Central Chile areas; e) separation of Amazonia; f) separation of Cerrado and Mountainous region of the Brazilian Southeast; g) separation of Guiana; h) separation of Yungas and Caribbean from the remainig Neotropical areas.

species distributed in this area. None of the essential cladograms show the Desert area as a basal one (Figs. 2, 4, 6, 14, 16, and 18). The resolved area cladograms of these taxa show that in most cases the location is apical (Figs. 3, 5, 7, 17, and 19). Differences are in that the Neantarctic taxa from the Desert are more closely related to austral taxa (Figs. 3 and 5), while the Neotropical taxa from the Desert (Figs. 7, 17, and 19) are more closely related to taxa with higher diversity in septentrional areas from the Neotropic. When codifying the components between Neantarctic and Neotropical taxa they would be contradictory, therefore the simplest position is the basal.

Evolution of the Austral Areas (Neantarctic)

The area considered as Neantarctic coincides greatly with that proposed by Jeannel (1967) and by Crisci *et al.* (1991). Many of the areas of endemism presently considered as Neantarctic, especially those in southeastern Argentina, were occupied by the Neotropical biota until the Eocene (55-50 Mya) with a subtropical warm temperate climate (Volkheimer, 1971). Until that period the Neantarctic biota was restricted to the austral region of Patagonia. It was only in the Middle Eocene (40-45 Mya) that the expansion of the Neantarctic elements occured, up to latitude 25°-30° S, in Sierra do Mar in Brazil, and ascending through the Andes up to Ecuador (Volkheimer, 1971). This was probably caused by a climatic change, with a lowering of the temperature (Axelrod *et al.*, 1991; Pascual, 1984) because of the opening of a passage south of Tasmania that produced a glaciation, thus causing in South America the displacement of the subtropical forests to the north, dismembering the Protochaco. Therefore, the vicariant events that separated the austral areas must have occured after the Eocene, since when they have occupied all the area where they are presently found.

The first separation (Figs. 20-22, 23c) is the clade formed by the Monte and the Pampean areas. This would not be strange, as the central part of Argentina has been isolated repeatedly by marine ingressions. During the last ingression in the Lower Miocene (20 Mya) the southern Buenos Aires province and the central part of Argentina constituted large islands surrounded by an epicontinental sea (Uliana & Biddle, 1988). This ingression totally isolated these two areas from the rest. During this same period, Lower Miocene (25-15 Mya), the Patagonian vertebrate fauna was connected with that from Central Chile and the two were very much alike (Volkheimer, 1971), thus showing that the other Neantarctic areas were still connected. This early separation of areas east of the Andes would be in agreement with that proposed by Axelrod *et al.* (1991) for the Monte, which would have originated in the Miocene. In spite of this origin in the Middle Miocene, the existence of a semiarid biota has been mentioned for west central Argentina for the end of the Eocene (Volkheimer, 1971; Axelrod *et al.*, 1991). The separation of the areas belonging to this first clade, Monte and Pampean, could be owed to the rising of the Andes (reaching 2000-3000 meters of altitude) that created the arid conditions that originated the Monte (Axelrod *et al.*, 1991).

The rising of the Andes also isolated the clade formed by the Puna and Patagonian areas from the clade formed by the Central Chile and Subantarctic areas. As mentioned before, in the Lower Miocene the fauna of Patagonia and Chile was the same (Pascual *et al.*, 1996). In the Middle Miocene the most important Quechua phase occurs (14/15 Mya); it had already begun at the end of the Lower Miocene with the rising of the Puna, reaching an altitude of 3000 meters. This rising of the Andes together with the desertification of the oriental areas was the vicariant event that separated geographically and climatically the Chilean areas from the Puna and Patagonian areas. According to Jeannel (1967) the subantarctic forest was distributed to the east over most of Patagonia until the Miocene, and suffered a great regression because of the conditions of aridity.

The separation between the Patagonian and Puna areas was caused by the progressive rising of the latter. In the Upper Miocene, Puna and the Sierras Pampeanas, the mountains presently limiting the occidental border of the Chaco plain, began to rise (Harrington, 1968). The rising produced and arid region west of the Sierras Pampeanas and sierras subandinas, region which at that time showed conditions similar to the present Chaco forests (Pascual *et al.*, 1996).

With regard to the separation of the Central Chile area from the *Nothofagus* forests (Subantarctic), a very recent division (Quaternary) has been proposed, caused by the Bio Bio Barrier (Solervicens, 1987). There exist relictual areas in Central Chile with *Nothofagus* forests (La Campana) and other subantarctic species in the Coquimbo region (Fray Jorge), proving that the distribution of the Neantarctic forests has undergone a large retraction. It is very probable that the conformation of the biota of central Chile can be explained by arid conditions produced by the installation of Humboldt´s cold current, which impedes precipitation in the continent (Porter, 1991). This would be coetaneous with the Quechua phase (14/15-11 Mya) and would not be as recent as proposed by Solervicens (1987).

Evolution of the septentrional areas of endemism (Neotropic)

The sequence of the separation of areas in the Neotropical region as per the cladograms is very different from that posed by Cracraft & Prum (1988). For these authors the first separation is constituted by the Mesoamerican region (Choco and Central America) from the South American Neotropical areas. In our case this separation is among the last ones. Other information also points toward a later formation of the Mesoamerican fauna. Haffer (1967a, b, 1969, and 1975) poses that a biota exchange occurred around the northernmost regions of the Colombian Andes, where during the Quaternary glaciations the lowering of the sea level gave way to an exchange. Halffter (1978) considers that an earlier exchange, that permitted the entry of South American fauna to Central America, occurred during the Miocene. Later, but in the same period, a most generalized faunal exchange between Central and South America occured, especially through the lowlands (PC), after the formation of the Tehuantepec isthmus, and the more recent formation of the Panama isthmus.

According to our study the first area to separate is Amazonia (Figs. 20-22, 23e). It is not possible to assign a vicariant event for the isolation of this area from the others. The separation of Guiana from the other areas is conflictive. This area could have separated as a clade together with Amazonia (Fig. 21), and would be the sister area to the remaining Neotropical areas (Fig. 21). Or perhaps it separated later with Cerrado and the Brazilian Southeast (CE and SE). Jeannel (1942) and Halffter (1974) proposed that Guiana is one of the three biotic units of the Upper Cretacic. This assumption would be consistent if Guiana were a basal area like Amazonia (Fig. 21). It is very probable that this area has a very ancient origin, as there were marine ingressions from the Lower Eocene (Senonian, Marajo-Blen trench) to the Lower Miocene (Paramaiba Basin) that totally isolated the Guiana area from the Brazilian northeast (Harrington, 1968). The vicariant role could be assigned to the hypothetical Amazonas lake that formed when the connection with the Pacific through Ecuador was closed at the time of the rise of the Andes in the Middle Miocene. This lake occupied all the Amazonas and Orinoco basins and persisted until the Pleistocene (Frailey *et al.*, 1988).

The areas of Cerrado and the Brazilian Southeast have kept in contact for a longer time and in many cases there exist large transition areas among them, owed in many cases to the riparian forest entering from the Brazilian Southeast to the Cerrado. It is very likely that these two areas have undergone repeated size fluctuations, changing their boundaries because of climatic changes. Coscarón & Coscarón-Arias (1997) proposed a vicariant event for the Cerrado-Sierras of the Brazilian southeast because of the change in sea level in the Lower Oligocene, when the sea level rose more than 200 m, as well as in the Miocene when it rose more than 100 m.

The separation of the remaining areas must have been caused by the progressive rise of the Andes and the lowland areas east of the Andes and north of the Bolivar Geosyncline. The Caribbean (Fig. 23h) was the first area to separate. This area was occupied during long periods by marine facies, from the Eocene to the Lower Oligocene, and increased in surface and altitude during the Upper Oligocene and Miocene, but remained isolated from the rest of South America (Raven & Axelrod, 1975). The rising of the Sierra de Perija, the Oriental Cordillera in Colombia and the Cordillera de Merida in Venezuela, occurring at the end of the Oligocene and the Miocene, must have had a vicariant role between Guiana and the Caribbean (Cracraft & Prum, 1988).

From the remaining areas the next to separate was the Yungas area. This was largely owed to the rise of the Andes and to the appearance of environmental conditions favorable to the cloudy forest. Hence, an ecological factor has been the vicariant element. This oriental region of the Andes had a humid, yungas type forest already during the Tertiary from Ecuador to Chile (Porter, 1991). This area surely has had an important role in the dispersion of the Central American faunas toward the south. The rise of the Andes also created the separation of the other areas, one with extreme conditions due to altitude, the Northen Andes (NA), from the plains of the Pacific area and from the Mesoamerican Mountains.

CONCLUSIONS

The entire analysis of the phylogenies of the different groups of Simuliidae clearly shows that the fauna existing in South America during the Cretacic suffered a main vicariant event. This event can be correlated with a large marine ingression.This event split the ancestral biota in two large biotas with different affinities, the Neotropical related to tropical African fauna, and the Neantarctic related to austral biotas from Australia, New Zealand and others austral areas. Nevertheless, in spite of the forming of these two biotas in South America during the Cenozoic there existed a hybridization partly because of the rise of the Andes. This last event gave place to the conditions for an expansion of the austral fauna, as well as causing the plains to turn into arid lands, that allowed an exchange principally in southern South America (Rappoport, 1968). But in spite of the hybridizations, the repeated marine transgressions that joined the Pacific with the Atlantic in the Miocene, the rise of the Andes, and the climatic conditions, allowed these biotas to evolve like independent units under different climatic regimes.

Of all the recognized areas of endemism for South America, the only area that could not be assigned to either of the two biotas was the Desert. Further studies could provide new data to elucidate its origin.

From the Neantarctic areas, the Pampean area (Fig. 1, PM) does not fit with the affinities proposed by Ringuelet (1961) as this author atributes it to the Guiano-Brazilian region. He considers that the Pampean area has close relations with the Brazilian Southeast or with the Monte. Our analysis shows a clear affinity of the Pampean area with the Monte, but both closely related to the austral areas. All the present biogeographic schemes also consider the Pampean area as part of the Austral Region, in spite of the great contribution from the Brazilian fauna.

Another austral area that does not match previous schemes is the Puna. Müller (1973) proposes that the Puna is closely related to the North Andean region and to Patagonia, while in this study the North Andean region is less related to Puna than to the septentrional areas.

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