

DISTRIBUTION OF NEOTROPICAL SIMULIIDAE (INSECTA, DIPTERA) AND ITS AREAS OF ENDEMISM

por

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Resumen

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Se presenta un estudio biogeográfico de la fauna de simúlidos neotropicales considerando 340 especies incluidas en 26 taxa supraespecíficos. Se analiza e indica la distribución de cada género, subgénero y grupo de especies. Se obtuvieron 16 áreas de endemismo con más de 9 taxa endémicos en relación con los campos biogeográficos conocidos. Se describe una diagnosis corta de las áreas endémicas con sus taxon y se señalan las especies monocéntricas y policéntricas. Se incluyen 6 mapas con la distribución de especies y uno con las áreas de endemismo.

Palabras clave: Simuliidae, Región neotropical, Distribución, Areas de endemismo.

Abstract

Biogeographic study on Neotropical black fly fauna, on 340 species included in 26 supraespecific taxa is made. Each genus, subgenus, or species group is analyzed indicating its distribution. Sixteen black fly areas of endemism having more than nine endemic taxa, were obtained in reference to known biogeographical realm. A short endemic area diagnosis and its taxa are described, and a number of monocentric and polycentric species are pointed out. Additionally six maps with species distributions and a map of areas of endemism are included.

Key words: Simuliidae, Neotropical Region - Distribution - Areas of endemism.

Introduction

Most researchers working in taxonomy like to explore biogeographic relationships. But when the study includes a biote fauna with a high diversity as that of the Neotropical Region, the curiosity on possible biogeographic relationships becomes stronger. This region has the richest fauna in the world, with the largest number of supraspecific taxa and primitive endemism (Crosskey 1981; 1991). Based on the present distribution of species, their taxonomy and paleogeographic information, it is possible to infer biotic evolution. A

complete knowledge of species distribution results fundamental to reach this objective. According to this reason, we intend to gather here the dispersed information about the corology of black flies, published elsewhere, and new unpublished records. New records in a relatively unknown area as the Neotropical realm will help to understand its biogeography. Also, we wish to establish the distribution of different black fly taxa and compare them with known biogeographic realm in order to obtain a map of areas of endemism not reported before. This information will be also useful for future historical analysis applying vicariance biogeography.

Black flies are man and animal parasites and pathogenic vector species (Coscarón 1971, Shelley 1988). We consider then that this black fly distribution information can be useful in future epidemiology and sanitary studies.

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We are aware of scarce information on records in the vast Neotropical realm, stretching from Southern United States and Northern Mexico to the southern end of the continent. On the other hand, distribution includes some not well explored areas, and some other with collections made in trips during only one season of the year, which gives then partial information. Besides, there is a lack of an updated revision of the subgenus *Simulium* (*Simulium*), with about 25 species mentioned for this realm.

In the present report, we review and update available records of Neotropical black flies and we analyze whether it is possible to outline a geographic distribution and to differentiate areas of endemism. Although black fly biology requires strictly freshwater (rivers and creeks) for development of larval instars, we analyze how far this distribution corresponds to a general faune pattern which is generally related to a floristic range.

Material and methods

Corological information was obtained from authors cited by Coscarón (1987), Coscarón 1990, 1991, Coscarón *et al.* (1991), Coscarón *et al.* (inedit), Coscarón & Takaoka (1989), Ibáñez Bernal (1992), Muñoz de Hoyos (1994), Py-Daniel (1987, 1988, 1989a, 1989b, 1990), Py-Daniel & Moreira (1988), Ramírez Pérez *et al.* (1984, 1986, 1988), Shelley (1988), Shelley *et al.* (1989), Takaoka & Takahasi (1982), Vargas & Ramírez Pérez (1988), Wygodzinsky & Coscarón (1989). The information was summarized and depicted on maps. Areas of endemism were obtained by overlapping taxonomic distributions on maps of biogeographic realms according to Cabrera & Willink (1973). Areas with less than 9 reported species were discarded. Areas smaller than those considered by Cabrera & Willink (1973), Müller (1973), or special areas cited by Peña (1966) for Chile or by Roig (1990), Morrone (1991), were not considered in the present report. Nomination of areas of endemism and acronymus used for their individualization are summarized in figure 7.

Generic names are based on Wygodzinsky & Coscarón (1973) and subgenera of *Simulium* on Coscarón (1987). Maps presented here correspond only to unpublished distribution maps. References about published subgeneric taxa maps are added to each taxa description.

I. Diversity of Neotropical Simuliidae

Up to now, Neotropical Simuliidae fauna has 11 genera. Ten out of them can be considered as a practical but not phylogenetic group described by Wygodzinsky & Coscarón (1973) the Prosimuliini, an endemic primitive taxa with about 90 species. The remaining genus is the cosmopolitan genus *Simulium*, with over 250 species grouped in 18 neotropical supraspecific taxa.

The genus *Gigantodax* is the largest Prosimuliini taxon, comprising 68 species. Together with *Cnesia*, they have been reported to be a monophyletic group, and gave rise to the first clado in Neotropical Simuliidae cladogram analysis (Py-Daniel, 1990).

Gigantodax is widespread along mesoamerican mountains and the Andes Range, from Central Mexico to Tierra del Fuego the southernmost continental region.

This genera is the largest latitudinally extended taxa in the world. Most of its breeding places are located in small fairly torrential streams.

According to the species groups proposed by Wygodzinsky & Coscarón (1989) the first is called "cortesi group" (3 spp), which has a distribution restricted to the peruvian-bolivian-chilean-argentinean area so-called "Puna". The "igniculus group" (2 spp) is distributed on the South Andes slopes with an altitude range from about 800 to 1.600 meters in Central Chile up to sea level in Tierra del Fuego. The "minor group" (3 spp) lives in the Andean *Nothofagus* forest, from 43° of latitude up to the desertic area in the northern Central Chile. Another species of uncertain taxonomic location and endemic of bolivian Puna should be added to this group. The "multifilis group" (1 spp) is restricted to the ecuatorial Andes. The "brophyi group" (18 spp) has a distribution from North Colombia and Venezuela up to Tierra del Fuego. It is composed by two subgroups: the northern one, spread on the Andes of Venezuela, Colombia and Ecuador has also two isolated species in the peruvian plateau. The southern subgroup lives in the chilean *Nothofagus* forest, located from the parallel 30° up to the end of the continent. The "cilicinus group" (10 spp) is widespread from northern Venezuela to the parallel 40° on the South. The "cormonsi group" distribution extends from central Colombia to north Chile and overlaps "cilicinus" group's. The "wrighti group" (17 spp) has the largest distribution occupying an area extended from Central Mexico up to Tierra del Fuego (Fig. 6).

Taking into account that the most generalized species are distributed in the south of the continent, it seems that the dispersion to the North should have followed the Andean Range. It should not have been necessary during Andes rise, because this area had already emerged in the Upper Cretacic (Cracraft & Prum, 1988). A continental facies has been present since the Lower Tertiary at least, on a stripe over the eastern border of the Andes, from Venezuela and Colombia to southern Perú. During the Middle Eocene and the Upper Oligocene it reached northern Argentina and later between the Upper and Middle Miocene this continental area reached Mendoza province (Argentina). Finally on the Pliocene it reached Patagonia (Harrington, 1968).

Cnesia is represented by three species allocated from Central Chile to the southern extremity of the continent along the *Nothofagus* forest. *Cnesia* has the same distribution area of *Cnesiamima* and *Paraustrosimulium* both monospecific genera (Fig. 1). These genera show an interesting similarity with Australian black flies which is considered as an evidence of their filogenetic relationship.

There are two other southern monoespecific genera located in Central Chile (Fig. 1). *Araucnephia* a peculiar genus presumed to be opposite to other similar Simuliinae (Py-Daniel, 1990). *Araucnephioides* constitutes with four other Holartic genera, a monophyletic group (Py-Daniel, 1990). According to this, it can be suggested that the ancestor of this genera lived in the American continent at the beginning of the Tertiary.



Figure 1: Distribution of genera *Tlalocomyia*, *Mayacnephia*, *Araucnephia*, *Araucnephioides*, *Cnesia*, *Cnesiamima*, *Paraustrosimulium*, *Lutzsimulium* and *Kempfsimulium*.

Tlalocomya with *Mayacnephia* and *Lutzsimulium* form another monophyletic clado (Py-Daniel, 1990). The presence of apomorphic characters shared with South American taxa would indicate a gondwanic ancestor. *Tlalocomya* and *Mayacnephia* are both mesoamerican genera and form a monophyletic group. *Tlalocomya* is a monospecific genus endemic in Central Mexico mountains (Fig. 1).

Mayacnephia has 9 mesoamerican species known, spread from Mexico to Panamá plus another two species in West U.S.A. and Canada (Fig. 1).

Lutzsimulium with 3 described species, has a distribution restricted to southeastern Brazilian mountains. Together with *Kempfsimulium* they are the only two genera living in the East of South America at the Brazilian shield (Fig. 1). *Kempfsimulium* is monospecific and reaches the southern border of Amazonia.

Simulium is a cosmopolitan genus represented in the Neotropical realm by 17 supraspecific taxa. We will mention here the subgenera and species groups following the order as it was proposed by the author in 1987, in his hypothetical cladogram. We do not take account of the distribution of *Eusimulium*, *Byssodon* and *Psilozia*, although there are species present in northern Mexico, because these genera are considered Holarctic.

Simulium (*Pternaspatha*) is a typical austral genus distributed to the West, from Ecuador to Tierra del Fuego. It has two monophyletic groups: *nigristrigatum* (11 spp) and *memorale* (16 spp). These two groups spread in both watershed of Andean Cordillera from southern Peru to Tierra del Fuego. Puna and Patagonia realms seemed to be the most important diversity centers. This genus has an endemic species in Ecuador (Coscarón and Coscarón-Arias ined.), and show sympatry with *Gigantodax* and *Cnesia* genera. It competes with *Cnesia* in the southern torrential rivers.

Simulium "blancasi group" (3 spp) is an unnominated taxon with subgenus rank. It shows high affinity with *S. Pternaspatha*, which is considered its sister group. It breeds in the Peruvian and Chilean desert. Some species reach the Andean slopes near the Puna plateau (Fig. 3).

Simulium (*Notolepria*) (6 spp) is the sister group of the clado integrated by *S. (Inaequalium)*, *S. (Psaroniocompsa)*, *S. (Cerqueirellum)* and *S. (Coscaroniellum)*. It is distributed in Mesoamerica and northwestern South America on both Andean watershed, being northwestern Argentina its austral limit. The tropical eastern region of South America is scarcely occupied, but *Simulium* (*Notolepria*) is absent in Amazonia. This taxa has high antropophilic species, reported as onchocercosis vector (Fig. 3).

Simulium (*Inaequalium*) (15 spp) is a subgenus predominant in the southeastern Brazilian mountains, reaching Venezuela and Panamá to the North and Northwest of Argentina (Coscarón and Coscarón-Arias ined.).

Simulium "quadrivittatum group" is a monospecific taxon of subgeneric rank distributed on northwestern South America, Antilles and lowlands of Mesoamerica.

Simulium (*Psaroniocompsa*) (16 spp) is a typical subgenus of southeastern Brazilian mountains, mostly overlapping *Inaequalium* distribution but extending to south reaching Central Patagonia (Coscarón and Coscarón-Arias ined.).

Simulium (*Cerqueirellum*) (14 spp) has the largest distribution area along the basin of bigger warm rivers of South America such as: Amazonas, Orinoco, Paraná, Uruguay and Magdalena. It is important to point out that each river seems to have developed its own fauna because each one has its peculiar species.

S. (Cerqueirellum) characterizes the Amazonia realm, occupying a huge area of eastern tropical land and reaching up to Buenos Aires province (Argentina) to the South (Fig. 3).

There is one species breeding in the Magdalena valley (Colombia) and a peculiar species has been reported for North Mexico at San Luis Potosí (Coscarón and Ibañez Bernal, in press).

Simulium (*Coscaroniellum*) (4 spp) shows nearly the same distribution area as *S. (Cerqueirellum)* (Fig. 2).

Simulium (*Chirostilbia*) (12 spp) is characteristic of southeastern Brazilian mountains with a distribution pattern that resembles *S. (Inaequalium)*'s (Coscarón and Coscarón-Arias, ined.).

Simulium "oviedoi group" is an unnominated taxon constituted by 2 species from Andes to Mérida (Venezuela). They have a very generalized morphology, despite some autoapomorphies that support its subgeneric category.

Simulium (*Ectemnaspis*) provisionally includes 4 species groups that probably will obtain a subgeneric category in future. The first group, with more generalized characters is "bicoloratum group" (14 spp) with the largest spread in the northern Andes of Venezuela, Colombia and Ecuador reaching southern Andes oriental slopes up to northwestern Argentina. One species has been observed in Sierra de la Ventana (Coscarón, 1991) at southern Pampas steppe (Argentina).

The "romanai group" (8 spp) distribution area mostly overlaps "bicoloratum group"'s but it is wider to the North along Caribbean realm and Roraima reaching southeastern Brazilian mountains and stretching away across northern Patagonia (Coscarón, 1991).

The "perflavum group" (7 spp) spreads over Guiana suggesting that diversification could have taken place at this old shield. Its distribution is similar to that of *S. (Chirostilbia)*, but it extends longer in northern Colombia. The "perflavum group" is a peculiar inhabitant of tropical reddish soil areas.

The "dinellii group" (10 spp) shows an opposite distribution to "perflavum group", both considered sister groups (Coscarón, 1987). It spreads along the circumcaribbean area, including northern Venezuela, Antillas and the lowlands of Mesoamerica. In South America there is one species breeding in the southeastern



Figure 2: Distribution of *Simulium (Notolepria)* and *S. (Coscaroniellum)*.

Brazilian mountains, and some other species are present in an occidental stripe which stretches to northwestern Argentina (Coscarón, 1991).

Simulium (Psilopelmia) (27 spp including 5 nearctic species restricted to U.S.A.) (Peterson, 1993) shows the largest endemism in Mexico and Guatemala. Three species of North Mexico were found in western U.S.A. and one was collected in Canada. On the other hand four species are shared with northern South America. Finally two others are endemic of South America, one of them spreads in the West up to northern Chile and the other one breeds in Guayana (Coscarón et al, in press).

Simulium (Simulium) (25 spp) shows a distribution similar to *S. (Psilopelmia)*, being Mesoamerica the principal diversification area. Besides it extends to Antilles, northern South America, and to the West it reaches its farthest southern distribution at North Chile (Fig. 6).

Simulium (Hearlea) (20 spp) is restricted to the Mesoamerican mountains (exception made of one species found in West Canada) (Fig. 4). *S. (Hearlea)* is probably an ancient taxon diversified in this biogeographic area, unable to cross the Isthmus of Panama (emerged at the end of the Tertiary).

Simulium (Hemicnetha) (20 spp) is the sister group of *S. (Hearlea)* (Coscarón, 1987), showing the greatest distribution in the highlands of Mesoamerica, reaching northern South America.

It shows a high dispersion capacity which has allowed it to reach the southeastern Brazilian mountains and northwestern Argentina.

This subgenus is also present in the Nearctic realm with three species distributed in western U.S.A. and Canada. Two species were cited also for Palearctic realm (Rubtsov, 1940). This subgenus has three species groups:

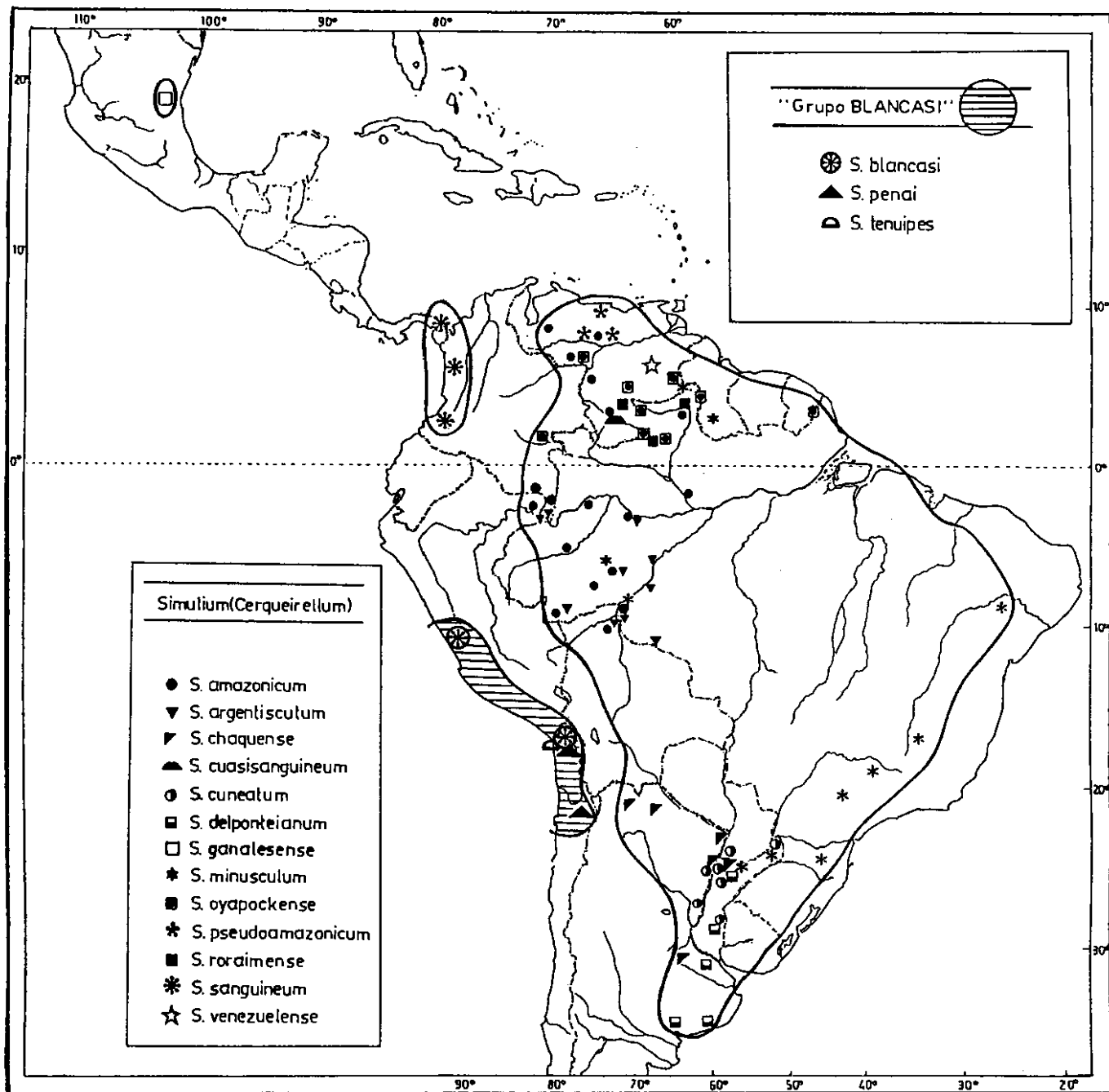


Figure 3: Distribution of *Simulium* (*Cerqueirellum*) and *Simulium* "blancasi group".

"*brachycladum*", "*mexicanum*" and "*paynei*" and it has the largest distribution in Mesoamerica (Fig. 5).

The "*brachycladum* group" (5 spp), has three species present in Mesoamerica. The other two species are endemic of Roraima and southeastern Brazil respectively.

The "*paynei* group" (5 spp) has four mesoamerican species. One of them reaches northwestern South America and the other four are endemic of South America (from Venezuela to southeastern Brazil).

The "*mexicanum* group" (11 sp) is the most diversified one. Ten species are mesoamerican and the remaining one is located from North to West in South America (absent in the Southeast).

Some species have a wide distribution such as *seriatum* (which spreads from Mexico to Venezuela and Northwest Argentina) and *paynei* (breeding from Mexico

to Central Perú). They demonstrate a surprising lack of diversification associated to a high adaptability to different environments.

Simulium (*Grenieriella*) (7 spp) considered the sister group of *S. (Hemicnetha)* is therefore morphologically very close to it. It has three species groups (Coscarón, 1987). The distribution is restricted to a stripe along North of Venezuela and Colombia up to Central Argentina. Only one species stretches to southeastern Brazil (Fig. 4). *S. (Grenieriella)* has a similar distribution to that of *S. "romanai* group".

Simulium (*Thyrsopelma*) (8 spp) is a monophyletic taxon with three species groups. The widest distribution takes place at the southeastern Brazilian mountains, but stretching away across Cerrado realm is also present in the circumamazonicum shield (Roraima, South Venezuela). Some species breeds in the rivers coming from

Tandilia shield up to Necochea (Buenos Aires province) in the South of Pampas region (Fig. 6).

This taxon points out an affinity with the ethiopic *S. (Anasolen)* by the presence of similar tegumentary scales in larval body. The hypothesis of a filogenetic relationship is reinforced by the fact that the two present day distribution where both these taxa breeds (*S. (Thyrsopelma)* in Brazilian shield, and *S. (Anasolen)* in Ethiopic region) belonged to the paleocontinent of Gondwana.

II.- Areas of endemism in Neotropical realm

Through the analysis of taxa distribution and its relationships with classical biogeographic areas, it is

possible to outline 16 different areas of endemism of black fly (Fig. 7).

1.- Subantarctic (SU).

Location: Long stripe from Concepción (37° lat. S) in Chile to Tierra del Fuego in western Argentina.

Climate: Temperate and humid, with rains all the year.

Monocentric species: Total : 14 species. *Cnesiamima* (1 sp.), *Lutzsimulium* (1 sp.), *Cnesia* (2 spp.), *Gigantodax*: "igniculus gr." (2 spp.), "minor gr." (1 sp.), "brophyi gr." (4 spp.), "wrighti gr." (1 sp.), *Simulium (Pternaspahta)* "nigristrigatum gr." (1 sp.) and "nemorale gr." (1 sp.)



Figure 4: Distribution of Simulium (Hearlea) and S. (Grenierella).

Polycentric species: Total: 13 species. *Araucnephia* (1 sp.), *Cnesia* (1 sp.), *Gigantodax* (7 spp.), *S. (Pternaspatha)* (4 spp.).

Description: This area is very close to the homonymous province of **Cabrera and Willink** (1973), the "*Nothofagus* Center" of Müller, or "Araucanian Subregion" of **Monrós** (1958). It is a realm of forests and meadows, with many endemic species. Tropical taxa are absent. Subantarctic fauna shows some relationships with australian fauna. It remains isolated from the rest of American continent due to the barriers formed by the Andean Cordillera and the semidesertic Patagonian

steppe in the East, and the Chilean desert towards the North. During the Upper Cretacic and the Tertiary a narrow patagonic sea connected Atlantic and Pacific oceans and isolated Cordillera Austral and Principal at the Miocene (**Camacho**, 1967). This sea could have been an effective barrier.

The four polycentric species of *S. (Pternaspatha)* are shared with Central Chile realm (12 spp.) and Patagonia (5 spp.). The presence of some relict species as *G. chilensis* in Valcheta (Río Negro) and *G. marginalis* in Piedra del Aguila (Neuquén) in Patagonia, far away from the present limit of the Subantarctic realm, suggests



Figure 5: Distribution of *Simulium (Hemicnetha)*.

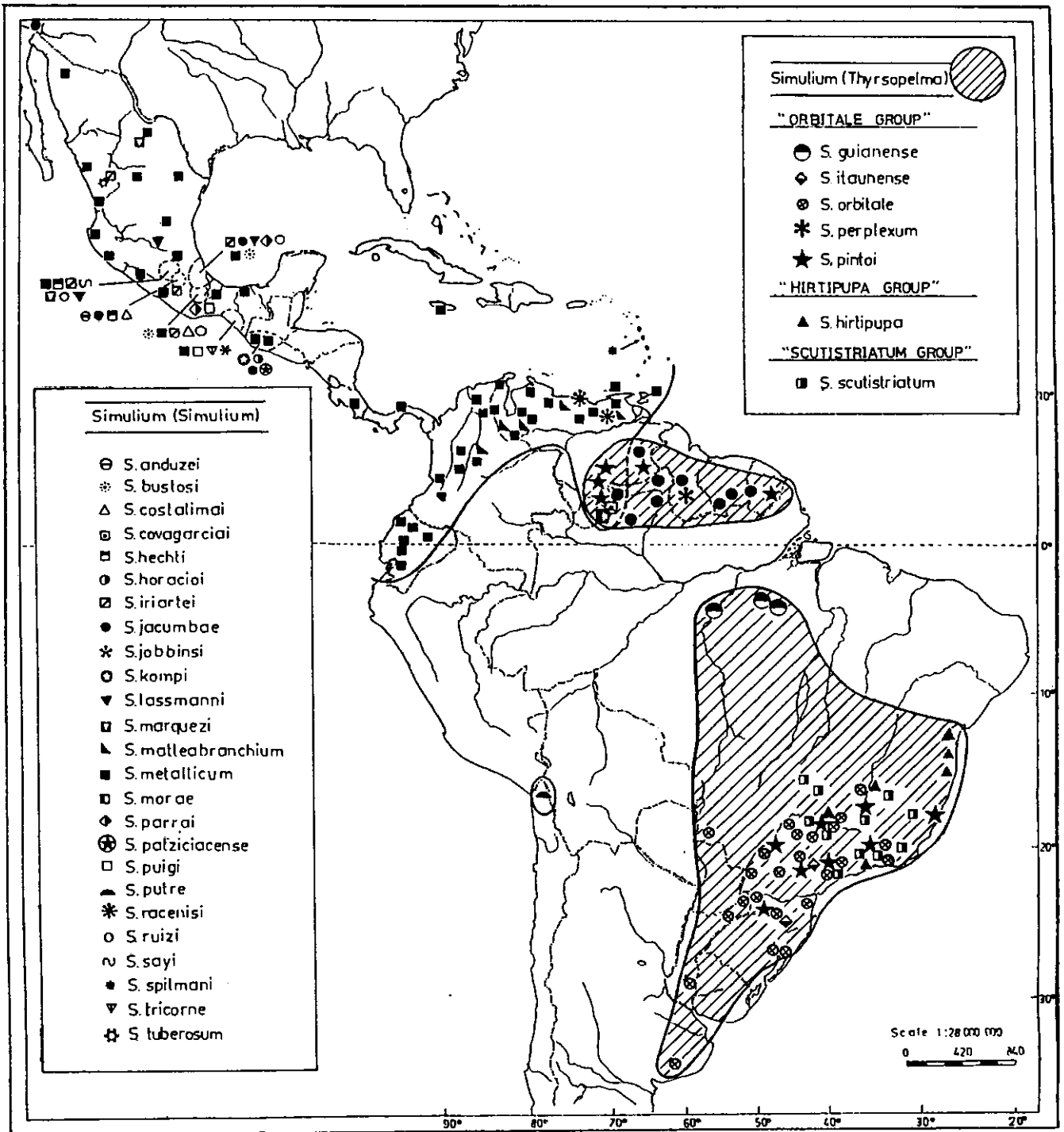


Figure 6: Distribution of *Simulium (Simulium)* and *S. (Thyrsopelma)*.

that in the past this area was larger than nowadays, specially towards the East.

2.- Central Chile (CH)

Location: From Coquimbo to Concepción (between 30° to 37° lat. South).

Climate: Temperate mediterranean

Monocentric species: Total : 3 species. *Araucnephioides* (1 sp.), *Gigantodax "brophyi gr."* (2 spp.)

Polycentric species: Total : 13 species. *Araucnephia* (1 sp.), *Cnesia* (1 sp.), *Gigantodax* (7 spp.), *S. (Pternaspatha)* (4 spp.).

Description: It corresponds approximately to the "Coquimbo desert" region of Peña (1966) or to the "Chilean province" of Cabrera and Willink (1973).

This region shows small forests and chaparral. It shares species specially with the Subantarctic realm and a few ones with the Desert and Patagonian regions.

3.- Desert (DE)

Location: Long occidental stripe between the Pacific coast and the Andes Range from Central Chile to South Ecuador including Chilean-peruvian desert.

Climate: desertic temperate, very dry without rains.

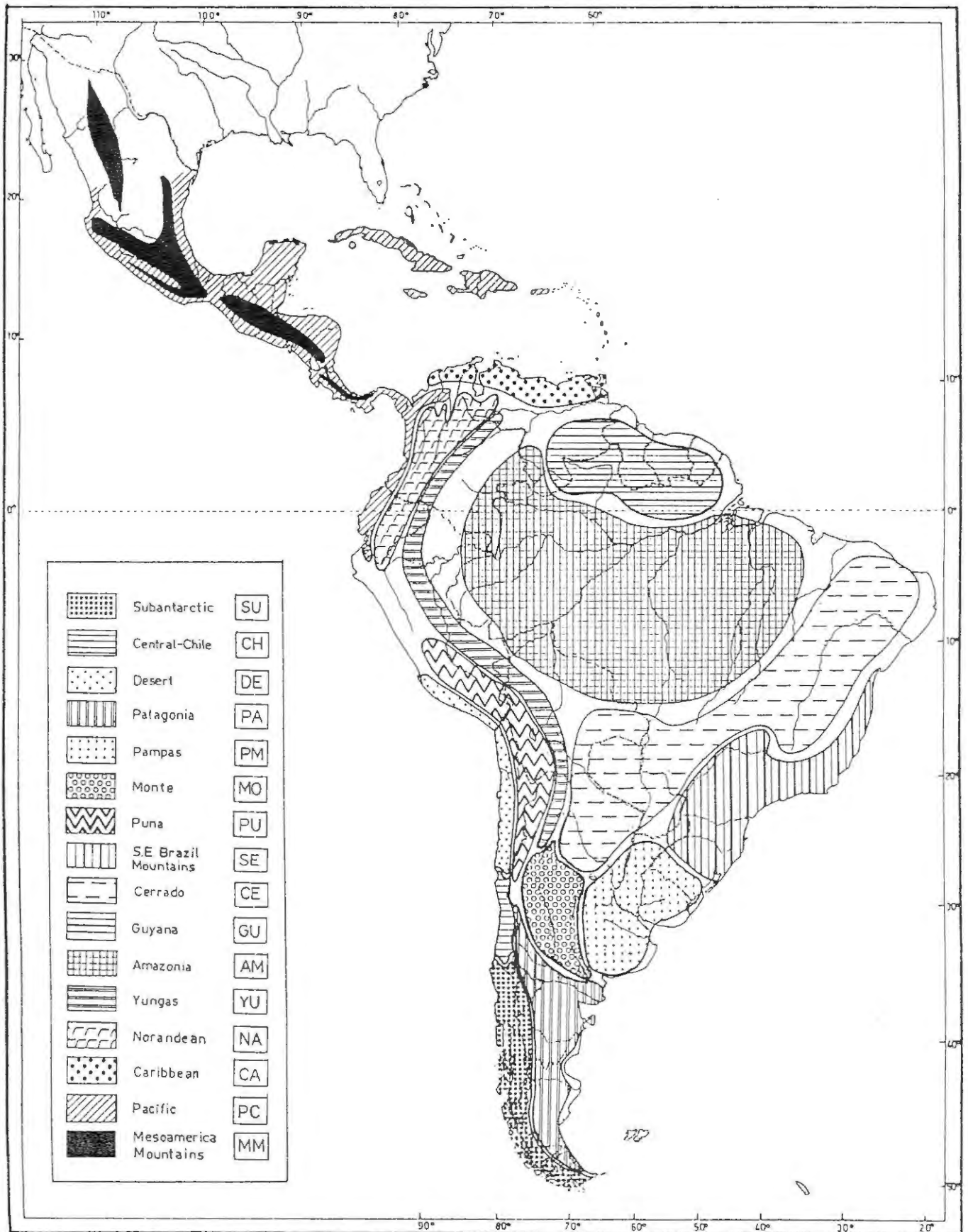


Figure 7: Neotropical Simuliidae endemism areas.

Monocentric species: Total: 6 species. The innominated peculiar *Simulium* subgenus, the "blancasi group" (2 spp.), *Gigantodax* "minor gr." (1 sp.), *S. (Pternaspatha)* "nemorale gr." (1 sp.), *S. (Notolepria)* (1 sp.), *S. (Ectemnaspis)* "dinellii gr." (1 sp.).

Polycentric species: Total: 9 species. *S. (Pternaspatha)* (1 sp.), *S. "blancasi gr."* (1 sp.), *S. (Notolepria)* (1 sp.), *S. (Ectemnaspis)* "bicoloratum gr." (1 sp.), *S. "romanai gr."* (2 spp.), *S. (Psilopelmia)* (1 sp.), *S. (Hemicnetha)* (1 sp.), *S. (Grenieriella)* (1 sp.).

Description: Biota with scarce diversity which it is confined to the small freshwater currents flowing from Andean Cordillera. Black fly fauna is shared with Central Chile, Puna and the Norandean area.

4.- Puna (PU)

Location: Peru, Bolivia, Chile and Argentina plateau. A stripe in the Andean Range with altitudes of 3.000 to 4.500 m. North boundary is the Pisco-Jurua fault, which crosses the Andes north of Lima.

Climate: Cold to temperate with high daily thermal amplitude, summer rains and xerofitic vegetation.

Monocentric species: Total: 30 species. *Gigantodax* "cortesi gr." (4 spp.), "minor gr." (1 sp.), "brophyi gr." (2 spp.), "cilicinus gr." (4 spp.), "cormonsi gr." (3 spp.), "wrighti gr." (1 sp.), *S. (Pternaspatha)* "nigristrigatum gr." (2 spp.), "nemorale gr." (9 spp.), *S. (Ectemnaspis)* "romanai gr." (1 sp.), *S. (Simulium)* (1 sp.), *S. (Grenieriella)* (2 spp.).

Polycentric species: Total: 10 species. *Gigantodax* (3 spp),

Simulium "blancasi gr." (1 sp.), *S. (Inaequalium)* (1 sp.), *S. (Ectemnaspis)* "romanai gr." (2 spp.), *S. (Grenieriella)* (3 spp.).

Description: Puna realm corresponds to the "Puneña", "Prepuneña" and part of "Altoandina" provinces of Cabrera and Willink (1973). The last one is not considered separately here, because the highest altitude at which black flies were found breeding is 4.700 m (Wygodzinsky & Coscarón, 1989).

It has a rich variety in its fauna with 40 species. Which is explained by the presence of emerged areas since the Cretacic with a differential ascension in the Upper Miocene. Glacial and interglacial periods at the end of the Tertiary and during the Cuaternary should have helped the increase of the biodiversity in the area.

Black fly fauna of Puna shows similitude with Monte (4 species shared) and Patagonia (2 species shared).

5.- Patagonia (PA)

Location: Southeastern Argentina, from the Colorado River to Tierra del Fuego. The west boundary is Subantarctic realm and the Andean range reaching Puna on the northwest.

Climate: Dry cold temperate with strong western winds.

Monocentric species: Total: 5 species. *S. (Pternaspatha)* "nigristrigatum gr." (4 spp.), "nemorale gr." (1 sp.).

Polycentric species: Total: 10 species. *Gigantodax* "brophyi gr." (2 spp.), *S. (Pternaspatha)* (5 spp.), *S. (Psaroniocompsa)* (2 spp), *S. (Ectemnaspis)* "romanai gr." (1 sp.).

Description: It corresponds to the "Patagonic dominion" of Ringuet (1961), the limnological "Extraandina Patagonia" region of Drago (1990) and to the homonymous province including southern area of "Monte province" of Cabrera and Willink (1973).

Malvinas (Falkland) Islands are not included in this realm because of the apparent absence of black flies (black flies were not found by Coscarón in December, 1974, field trip to Port Stanley (Puerto Argentino) and Malo river in the East Island. Nevertheless, the role of a fossil fauna of Malvinas in the constitution of Patagonia realm fauna can not be ruled out.

Patagonia is an undulating steppe without high elevations with chaparral in the North. Fauna is relatively poor, most probably due to the Andes range elevation which developed the Patagonia desertization (Pascual, 1984). Afterwards this process was emphasized by the continental glaciation and the opening of the Drake Strait.

This region shows a vast extension without freshwater currents, and the best breeding places are the allocthonous rivers running West to East and draining andean lakes in the Atlantic ocean.

The closer relationships of patagonian black fly fauna are observed with Puna, Subantarctic and Pampas realms.

6.- Monte (MO)

Location: Central Argentina. Limited by Patagonia in the South and Southwest and with Yungas and Chaco-Cerrado in the Northwest. Pampas is the east boundary.

Climate: Dry, temperate in the South and warm in the North with xerofitic vegetation.

Monocentric species: No monocentric species.

Polycentric species: Total: 9 species. *S. (Pternaspatha)* (2 spp.), *S. (Psaroniocompsa)* (2 spp.), *S. (Ectemnaspis)* "bicoloratum group" (1 sp.), "romanai gr." (2 spp.) and *S. (Grenieriella)* (2 spp.).

Description: It corresponds to the homonymus province of Cabrera and Willink (1973), but slightly reduced in the South.

It has an endorrheic fluvial system with few freshwater currents mostly in flat lands.

The fauna of Simulids is poor with only nine polycentric species. Apparently it is mainly composed of a stenoic fauna of Yungas and Pampas.

7.- Pampas (PM)

Location: Southern Brasil, Uruguay and eastern Argentina. It is limited to the north by the southeastern Brazilian mountains and Chaco-Cerrado realms, to the west by the Monte realm and to the southeast by the Atlantic ocean.

Climate: humid temperate

Monocentric species: Total : 1 monocentric species. *S. (Cerqueirellum)* (1 sp.).

Polycentric species: Total : 15 species. *S. (Psaroniocompsa)* (5 spp.), *S. (Cerqueirellum)* (3 spp.), *S. (Inaequalium)* (2 spp.), *S. (Chirostilbia)* (2 spp.), *S. (Ectemnaspis) "bicoloratum gr."* (1 sp.), "*romanai gr.*" (1 sp.), and *S. (Thyrsopelma)* (1 sp.).

Description: It corresponds approximately to the "Espinal" and "Pampeana" provinces of **Cabrera and Willink**, and to the "Pampas" and "Uruguay" endemic centers of **Müller** (1973). It has steppe vegetation in lowlands with scarce hills and low mountains. Black fly fauna is relatively poor and has a strong influence from the southeastern Brazilian mountains and Yungas fauna. The presence of isolated populations of black fly species in the hilly areas of Sierra de la Ventana and Tandilia (southeast of Buenos Aires province) which came from distant distribution centers indicate that those elevated areas were a refuge during marine transgressions that took place in the Miocene and interglacial periods of the Pliocene and the Pleistocene. Marine transgressions covered large areas hindering by that time, terrestrial contact with southern Brazil, northwest Argentina and Patagonia.

8. Southeastern Brazil Mountains (SE)

Location: its limits are to the South: Misiones province (Argentina), to the West: the eastern bank of Paraguay river, to the East: Atlantic Ocean, and to the North: the central part of Bahia State (Brazil).

Climate: subtropical warm and humid with rain forests.

Monocentric species: Total : 17 species. *Lutzsimulium* (3 spp.), *S. (Inaequalium) "inaequale gr."* (4 spp.), "*botulibranchium gr.*" (3 spp.), *S. (Psaroniocompsa)* (3 spp.), *S. (Chirostilbia) "pertinax gr."* (3 spp.), *S. (Thyrsopelma) "orbitale gr."* (1 sp.).

Polycentric species: Total : 29 species. *S. (Notolepria)* (1 sp.), *S. (Inaequalium)* (4 spp.), *S. (Psaroniocompsa)* (4 spp.), *S. Cerqueirellum* (2 spp.), *S. (Chirostilbia)* (8 spp.), *S. (Ectemnaspis) "romanai gr."* (1 sp.), "*perflavum gr.*" (1 sp.), "*dinellii gr.*" (1 sp.), *S. (Hemicnetha)* (2 spp.), *S. (Grenieriella)* (1 sp.), *S. (Thyrsopelma)* (4 spp.).

Description: Extense and undulated area with savanna and tropical forests very close to "Atlantica" and "Paranense" provinces of **Cabrera and Willink** (1973). To this realm belongs one of the richest Neotropical black fly fauna. A diversity such as the Brazilian oriental shield is the result of a long lasting emerged area where some valley and highlands were isolated during marine transgressions. There are a lot of species in Sierra do Mar area, but fauna becomes poorer to the periphery towards Cerrado and Pampas realms, which represent continental boundary.

9. Cerrado (CE)

Location: Extense region lying diagonally among southeastern Brazilian mountains, Pampas, Monte and Yungas in the South and West, and Amazonia in the North.

Climate: arid and warm, with a dry season and xerofitic vegetation.

Monocentric species: Total : 3 species. *S. (Coscaroniellum)* (1 sp.), *S. (Chirostilbia) "pertinax gr."* (1 sp.), *S. (Inaequalium) "subpallidum gr."* (1 sp.).

Polycentric species: Total : 24 species. *S. (Notolepria)* (1 sp.), *S. (Inaequalium)* (3 spp.), *S. (Psaroniocompsa)* (5 spp.), *S. Cerqueirellum* (3 spp.), *S. (Chirostilbia)* (4 spp.), *S. (Ectemnaspis) "perflavum gr."* (1 sp.), "*dinellii gr.*" (1 sp.), *S. (Hemicnetha)* (2 spp.), *S. (Grenieriella)* (1 sp.), *S. (Thyrsopelma)* (3 spp.).

Description: It corresponds mostly to "Caatinga", "Cerrado", "Chaco" and part of "Monte" and "Espinal" of **Cabrera and Willink** (1973). Cerrado is a xerofitic area alternating chaparral with savanna, and gallery forests along rivers and creeks. It shows a strong influence of southeast Brazilian mountains and Amazonia fauna.

10. Amazonia (AM)

Location: It is a huge area corresponding approximately to the Amazonas basin.

Climate: Humid warm with rain forests.

Monocentric species: Total: 7 species. *Kempfsimulium* (1 sp.), *S. (Inaequalium)* (1 sp.), *S. (Psaroniocompsa)* (3 spp.), *S. (Cerqueirellum)* (2 spp.).

Polycentric species: Total: 15 species. *S. (Inaequalium)* (1 spp.), *S. (Psaroniocompsa)* (2 spp.), *S. (Cerqueirellum)* (3 spp.), *S. (Coscaroniellum)* (3 spp.), *S. (Chirostilbia)* (2 spp.), *S. (Ectemnaspis) "perflavum gr."* (2 spp.), *S. (Hemicnetha)* (1 sp.), *S. (Thyrsopelma)* (1 sp.).

Description: It closely corresponds to Cabrera and Willink's homonymous province. It occupies a recent fluvial system and rest of hills of central Brazilian's and southern Guiana's shields. Lowlands represent an ancient lake fulfilled by Pliocene sediments (**Frayley et al.**, 1988). Consequently jungle is pretty young.

Amazonia is considered the richest faunistical realm of America (**Halffter**, 1974), nevertheless only 22 species of black flies have been reported. A similar situation has been observed for other insect taxa, as Ichneumonidae (**Porter**, 1980). One possible but speculative explanation for this fact is that Amazonia is a huge land extension with relatively homogeneous environmental characteristics, specially high humidity and warm rivers which wouldn't be suitable for Simuliidae speciation.

11. Guyana (GU)

Location: Includes Guyana shield, the Roraima and Parima Mountains, and Orinoco plains.

Climate: tropical with dry season alternating steppes with forests.

Monocentric species: Total: 15 species. *S. (Inaequalium)* (2 spp.), *S. (Psaroniocompsa)* (1 sp.), *S. (Cerqueirellum)* (3 spp.), *S. (Ectemnaspis) "perflavum gr."*

(3 spp.), "*dinellii* gr." (2 spp.), *S. (Psilopelmia)* (1 sp.), *S. (Simulium)* (2 spp.), *S. (Hemicnetha)* (1 sp.).

Polycentric species: Total: 22 species. *S. (Notolepria)* (1 sp.), *S. (Inaequalium)* (2 spp.), *S. (Psaroniocompsa)* (3 spp.), *S. (Cerqueirellum)* (2 spp.), *S. (Coscaroniellum)* (3 spp.), *S. (Chirostilbia)* (2 spp.), *S. (Ectemnaspis)* "*romanai* gr." (1 sp.), "*perflavum* gr." (2 spp.), "*dinellii* gr." (2 spp.), *S. (Psilopelmia)* (1 sp.), *S. (Hemicnetha)* (1 sp.), *S. (Thyrsopelma)* (2 spp.).

Description: It corresponds to Müller centers of "Roraima", "Pantipuy" and "Guiana". It is a hilly area with peaks of 1600 meters high. The savanna is interrupted by gallery forests and humid premountain forests.

12. Caribbean (CA)

Location: North of Colombia and northern Orinoco (Venezuela), West Indies (Trinidad, Tobago, Jamaica and Bahamas)

Climate: dry warm to moderate humid in accordance to the season.

Monocentric species: Total : 4 species. *S. (Cerqueirellum)* (1 sp.), *S. (Ectemnaspis)* "*romanai* gr." (1 sp.), *S. (Simulium)* (1 sp.), *S. (Hemicnetha)* (1 sp.).

Polycentric species: Total : 26 species. *S. (Notolepria)* (1 sp.), *S. (Inaequalium)* (2 spp.), *S. (Psaroniocompsa)* (2 spp.), "*quadrivittatum* gr." (1 sp.), *S. (Cerqueirellum)* (1 sp.), *S. (Chirostilbia)* (1 sp.), *S. (Ectemnaspis)* "*bicoloratum* gr." (1 sp.), "*romanai* gr." (3 spp.), "*perflavum* gr." (1 sp.), "*dinellii* gr." (3 spp.), *S. (Psilopelmia)* (2 spp.), *S. (Simulium)* (2 spp.), *S. (Grenieriella)* (1 sp.), *S. (Hemicnetha)* (5 spp.).

Description: The name comes from Ramírez Pérez (1983), corresponding to the "Subregion of Caribe", and to "Guajira", "Venezolana", and "Sabana" provinces of Cabrera and Willink (1973) classification. Caribbean has heterogeneous environments including xerofitic vegetation mixed with gallery forests and humid premountain climate. Simuliidae fauna shares common taxa with Guiana, southeastern Brazilian mountains, Yungas and Pacific realms.

13. Norandean (NA)

Location: Andean region of Venezuela and Colombia among the Mérida, Oriental and Occidental Ranges, extending over the mountainous area up to South Ecuador.

Climate: Temperate to alpine

Monocentric species: Total : 44 species. *Gigantodax multifilis* gr. (1 sp.), "*brophyi* gr." (7 spp.), "*cilicinus* gr." (5 spp.), "*cormonsi* gr." (7 spp.), "*wrighti* gr." (8 spp.), *S. (Pternaspatha)* (1 sp.), *S. (Psaroniocompsa)* (1 sp.), *Simulium "oviedoi* gr." (2 spp.), *S. (Ectemnaspis)* "*bicoloratum* gr." (9 spp.), "*romanai* gr." (1 sp.), *S. (Grenieriella)* (3 spp.).

Polycentric species: Total : 9 species. *S. (Ectemnaspis)* "*bicoloratum* gr." (3 spp.), "*romanai* gr." (4 spp.), "*dinellii* gr." (1 sp.), *S. (Hemicnetha)* (1 sp.).

Description: It corresponds partially to the "Páramo province" of Cabrera and Willink (1973) and to the endemic centers of "Magdalena", "Cauca", "Colombian mountain forests" and "Norandean" considered by Müller (1973).

Norandean is a large area located about 2.500-3.000 meters high with a lot of intermountainous valleys that aid allopatric speciation. Nowadays the realm has the highest faunistic diversity in South America with 44 monocentric species out of 53 species living in it.

14. Yungas (YU)

Location: It is a relatively narrow stripe on the oriental Andean slope between 500 to about 3.000 meters high, which extends from the proximity of Caribbean sea up to Catamarca province in Argentina (about 30° South latitude)

Climate: Temperate to warm, very humid.

Monocentric species: Total : 2 species. *Gigantodax "wrighti* gr." (1 sp.), *S. (Ectemnaspis)* "*bicoloratum* gr." (1 sp.)

Polycentric species: Total : 24 species. *Gigantodax* (1 sp.), *S. (Notolepria)* (1 sp.), *S. (Inaequalium)* (2 spp.), *S. (Psaroniocompsa)* (1 sp.), *S. (Cerqueirellum)* (1 sp.), *S. (Ectemnaspis)* "*bicoloratum* gr." (4 spp.), *S. "romanai* gr." (4 spp.), "*dinellii* gr." (3 spp.), *S. (Psilopelmia)* (1 sp.), *S. (Simulium)* (1 sp.), *S. (Hemicnetha)* (3 spp.), *S. (Grenieriella)* (2 spp.).

Description: It has nearly the same extension given by Cabrera and Willink to the homonymous province, but larger than Müller's "Yungas center" which reaches only up to Ucayali river. It is a humid region with peculiar fogged forests. The great latitudinal extension that characterizes the realm probably facilitates the species dispersion along the occidental part of the South American continent, specially in the North-South direction as it happened with *S. (Ectemnaspis)*, *S. (Psilopelmia)*, *S. (Grenieriella)* and *S. (Hemicnetha)*.

15. Mesoamerican Mountains (MM)

Location: It includes the high forest from Mexico and Central America to Panama, and the intermountainous area about 2.000 meters over sea level reaching up to Paramo mountains.

Climate: Cold to temperate relatively humid on the mountains and dry on intermountainous lands.

Monocentric species: Total : 49 species. *Tlalocomyia* (1 sp.), *Mayacnephia* (9 spp.), *Gigantodax* (4 spp.), *S. (Hearlea)* (20 spp.), *S. (Psilopelmia)* (2 spp.), *S. (Simulium)* (9 spp.), *S. (Hemicnetha)* (4 spp.).

Polycentric species: Total: 20 species. *S. (Notolepria)* (1 sp.), *S. (Psilopelmia)* (7 spp.), *S. (Simulium)* (4 spp.), *S. (Hemicnetha)* (8 spp.).

Description: Most of "Mexican xerofitic province" of Cabrera and Willink (1973) is included here. The Mesoamerican mountains realm has a record of 69 species of Neotropical black fly fauna with 49 monocentric

species. There are relicts of an old faunistic stock such as the primitive "Prosimuliini": *Tlalocomyia* (1 sp.), *Mayacnephia* (9 spp.) which has two species breeding in East U.S.A. and Canada, and *Gigantodax* (4 spp.) likely to be a southern migrant diversified lately here. *Simulium* has an endemic subgenus *S. (Hearlea)* with twenty species and only two out of them are present in the Holarctic realm. No special Neartic fauna is present, while in the lower northeast Mexican xerofitic area this fauna is a common element.

16. Pacific (PC)

Location: It includes the peripheral lowlands and intermountainous valleys of Mexico, Central America, Antillas, and an occidental stripe of Colombia and Ecuador.

Climate: Warm and very humid.

Monocentric species: Total: 14 species. *S. (Notolepria)* (2 spp.), *S. (Psaroniocompsa)* (1 sp.), *S. (Cerqueirellum)* (1 sp.), *S. (Ectemnaspsis)* "dinellii gr." (2 spp.), *S. (Psilopelmia)* (2 spp.), *S. (Simulium)* (5 spp.), *S. (Hemicnetha)* (1 sp.).

Polycentric species: Total: 37 species. *S. (Notolepria)* (2 spp.), *S. (Inaequalium)* (1 sp.), *S. (Psaroniocompsa)* (1 sp.), *S. "quadrivittatum gr."* (1 sp.), *S. (Cerqueirellum)* (1 sp.), *S. (Ectemnaspsis)* "bicoloratum gr." (3 spp.), "romanai gr." (4 spp.), "dinellii gr." (3 spp.), *S. (Psilopelmia)* (8 spp.), *S. (Simulium)* (5 spp.), *S. (Hemicnetha)* (8 spp.).

Description: It coincides with the homonymus province of **Cabrera and Willink** (1973). It is a humid forest area. Delimitation of the realm, specially in valleys with medium altitude on mountain slopes, is difficult to perform.

III.- General Conclusions

The analysis of the above mentioned information allow us to state that:

I) The realms determined using the black fly fauna distribution eventhough this fauna is strictly related to freshwater currents, responds to the pattern obtained from general biota distribution identifying biogeographical realms in the Neotropical region.

II) It is possible to observe a significant arrangement of taxa distribution:

a.- *Cnesia*, *Cnesiamina*, *Paraustrosimulium* and *Gigantodax* "igniculus group" and mostly "brophyi group" have a peculiar Subantarctic realm distribution.

b.- *Tlalocolmyia*, *Mayacnephia* and *Simulium (Hearlea)*, are restricted to Mesoamerican Mountains, with the exception of two species of the last two taxa, reaching West U.S.A. and Canada.

c.- *Simulium (Inaequalium)*, *S. (Psaroniocompsa)*, *S. (Chirostilbia)*, and *S. (Thyrsopelma)*, are characteristic taxa of southeastern Brazilian mountains, with some species reaching the North of South America. *S. (Ectemnaspsis)* "perflavum group" has the widest distribution in northern South America but it is more restricted in the South.

d.- *Simulium (Psilopelmia)* and *S. (Simulium)* show a predominant distribution in Mesoamerica (lowlands and mountains as well) and Antilles, but they are also well represented in northern South America, reaching West at North Chile.

e.- *Simulium (Hemicnetha)*, *S. (Ectemnaspsis)* "dinellii group" and *S. (Notolepria)* (this last one in a lesser degree) have similar distribution as described before in (d), but they reach southeastern Brazilian mountains.

f.- *Simulium (Ectemnaspsis)* "bicoloratum and romanai groups" and *S. (Grenieriella)* are distributed predominantly in the Andean region from Venezuela to northern Argentina, reaching southeastern Brazilian mountains.

g.- *Simulium (Cerqueirellum)* and *S. (Cosconiellum)* are related to big tropical river basins of eastern South America.

III) Some taxa predominate in determinate realms.

a.- *Prosimuliini* are mostly restricted to the Andean Range and Mesoamerican mountains, having 8 genera including 84 species, while only two genera with 4 species breed in Brazilian shield.

b.- *Simuliini* has only one cosmopolitan genus called *Simulium* which is represented in Neotropic with 14 nominated subgenera and likely 5 more unnominated subgenera. *Simulium* is a taxa exclusive of tropical extraandean region. Only *S. (Pternaspatha)* is peculiar of cold to temperate areas of southwestern South America, restricted to the Andes and showing no evident affinities with tropical *Simulium*, exception made of *S. "blancasi group"* present in western South America and considered as "sister group" of *S. (Pternaspatha)*.

IV) Some realms own a highly diversified black fly fauna. From South to North we found:

| Realm | Species (total) | Monocentric species | Observations |
|----------------|-----------------|---------------------|---------------------|
| Subantarctic | 28 | 14 | 5 primitive genera |
| Puna | 30 | 10 | G. "cortesi group" |
| S.E. Brazil | 46 | 17 | One primitive genus |
| Guyana | 37 | 15 | |
| Norandean | 55 | 44 | |
| Mesoam. Mounts | 69 | 49 | 2 primitive genera |
| Pacific | 51 | 14 | |

V) On the other hand some other realms are faunistically poor. They probably represent transition areas such as Monte, Pampas, Cerrado and the northern area of Mexican plateau corresponding to "Chihuahuano district" of **Cabrera and Willink** (1973), and "Mexican transition" of **Halffter** (1962).

VI) Comparing the relationships among black fly fauna and their distribution, it is possible to identify four major groups:

a.- *Neantarctic*: including Subantarctic, Central Chile, and Desert. To this group belong ancient gondwanic genera: *Paraustrosimulium*, *Cnesiamima*, *Cnesia*, and *Gigantodax*, which have strong affinities with Australian fauna. There are also some old elements not difficult to relate with other paleogondwanic genera as *Araucnephia* and *Araucnephioides* (with some resemblance of Nearctic fauna) and *Simulium* (*Pternaspatha*) and *S.* "blancasi group".

b.- *Andine-Patagonic*: formed by Patagonia, Puna and Monte realms. It has an old temperate gondwanic fauna related neither with foreign nor with tropical fauna as *Gigantodax* and *Simulium* (*Pternaspatha*) and a few species of *Simulium* sugenera as recent settlers coming from Brazil, Norandean region and Mesoamerica.

c.- *Guiane-Brazilian*: it includes by southeastern Brazilian mountains, Pampas, Cerrado, Amazonas and Guiana. The fauna is represented by ancient gondwanic genera as *Lutzsimulium* and *Kempfsimulium* (with some resemblance of other southern *Prosimuliini*) and several young diversified taxa typical from South America: *Simulium* (*Inaequalium*), *S.* (*Psaroniocompsa*), *S.* (*Cerqueirellum*), *S.* (*Chirostilbia*), *S.* (*Coscaroniellum*), *S.* (*Ectemnaspis*) "perflavum group", and a peculiar *S.* (*Thyrsopelma*) with affinities to Ethiopic fauna.

d.- *Mesoamerica and northern South America*: composed of Mesoamerican Mountains, Pacific, Norandean, Yungas and Caribbean realms. Eventhough this region possesses two different interrelated fauna, it should be pointed out that Mesoamerica black fly fauna shows a stronger affinity with Neotropical than with Nearctic fauna. Similar results have been previously reported by Halffter (1962) for insects, by Hershkovitz (1968) for mammals and by Fitkau (1974) for the fauna in general.

It developed a rich endemism as a result of the great isolation that took place during the Tertiary. Only South and North American fauna might have got in contact through volcanic islands (Raven & Axelrod, 1975). The intensive connection between North and South America must have started after Andes ascension on the Lower Pliocene and ended three million years ago when Isthmus of Panama emerged (Marshall et al., 1979).

Mesoamerican Mountains have three *Prosimuliini* paleogondwanic genera *Tlalqcomyia*, *Mayacnephia* and *Gigantodax* (this last one was probable native from South America). Also *Simulium* is present with the peculiar *S.* (*Hearlea*), *S.* (*Hemicnetha*) and *S.* (*Simulium*) with wide distribution in northwestern South America. Some taxa have crossed the isthmus and colonized the lowlands as happened with *Simulium* (*Notolepria*), *S.* "quadrivittatum group", *S.* (*Ectemnaspis*) "dinellii gr." and *S.* (*Psilopelmia*).

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