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# Cladistic analysis of the subgenera *Inaequalium, Psaroniocompsa,* and *Chirostilbia* of the genus *Simulium*, with comments on their distribution (Diptera: Simuliidae)

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☐ **ABSTRACT.** *Inaequalium, Psaroniocompsa,* and *Chirostilbia* are subgenera of *Simulium,* characteristic of the tropical area from southeastern Brazil. They form monophyletic groups, composed of 12, 15, and 13 species, respectively. Morphological characters of larvae, pupae and imagos were used in the cladistic analysis of each subgenus. Character polarity was based on the outgroup comparison method, using *Notolepria* for the first subgenus and *Inaequalium* for the other two subgenera. Performing option ie* of Hennig86 for *Inaequalium,* 12 parsimonious trees, each with 28 steps and a CI and RI of 1 were obtained. Pee-wee program was used intenting to reduce the trees number; using option amb- were produced three trees with length = 28, and CI and RI = 1. Each tree shows only two well defined clades, that represent the *S. botulibranchium* and *S. inaequale* species groups. The strict consensus cladogram, although well defined for the *S. botulibranchium* species group as a clade, is not fully resolved for the *S. inaequale* species group. Applying the ie* option for *Psaroniocompsa* one parsimonious tree was obtained, with a length of 42 and CI and RI of 0.92. In *Chirostilbia*, 24 trees with 38 steps and CI and RI of 0.89 were obtained. Using Pee-wee / Nona 2 trees were obtained with a length of 33 and CI and RI of 1. Strict consensus tree defines two monophyletic clades that support the *S. subpallidum* and *S. pertinax* species groups of Coscarón (1987). Maps of distribution are included, covering all tropical South America, except the lowland Amazonian valley and the west Andean area south of Ecuador. The Amazonian barrier was surpassed and species of the three subgenera are distributed in Guianas and towards the south they reach the Pampas. *Inaequalium* and *Psaroniocompsa* reach the Pacific, northern Andes, and the Yungas areas. The presence of the three subgenera in Amazonia is restricted to the old Brazilian shield areas.

**RESUMEN. Análisis cladístico de los subgéneros *Inaequalium, Psaroniocompsa* y *Chirostilbia* del género *Simulium*, con comentarios sobre su distribución (Diptera: Simuliidae).** *Inaequalium, Psaroniocompsa* y *Chirostilbia* son subgéneros de *Simulium* característicos del área tropical del sureste del Brasil. Ellos constituyen grupos monofiléticos, compuestos por 12, 15 y 13 especies, respectivamente. Para llevar a cabo su análisis cladístico se usaron los caracteres de la morfología de la larva, pupa e imagos. La polaridad de los caracteres se estableció comparándolo con el grupo externo, utilizando el subgénero *Notolepria* para el primer subgénero e *Inaequalium* para los otros dos. Utilizando la opción ie* del programa Hennig86 se obtuvieron para *Inaequalium* 12 árboles más simples, cada uno con 28 pasos y CI y RI de 1. Con el objeto de reducir el número de árboles se utilizó el programa Pee-wee / Nona, obteniéndose tres árboles, con una longitud de 28 y CI y RI de 1. Cada árbol presenta solamente dos clados bien definidos, que corresponden a los grupos de especies *S. botulibranchium* y *S. inaequale*. El cladograma de consenso estricto define bien al grupo *S. botulibranchium*, en cambio el grupo *S. inaequale* no pudo ser totalmente resuelto. En *Psaroniocompsa*, aplicando la opción ie* se obtuvo un árbol más simple, con una longitud de 42 y CI y RI de 0,92. En *Chirostilbia* con la

opción ie* se obtuvieron 24 árboles de 38 pasos y CI y RI de 0,89. Con el programa Pee-wee / Nona se obtuvieron dos árboles, con una longitud de 33, y CI y RI de 1. El árbol de consenso estricto presentó dos clados monofiléticos, que coinciden con los grupos de especies *S. subpallidum* y *S. pertinax* de acuerdo con Coscarón (1987). Se incluyen mapas de distribución de las especies mostrando que estos subgéneros ocupan la región tropical de América del Sur, a excepción de la zona baja de la Amazonía y el oeste de los Andes al sur de Ecuador. La barrera Amazónica fue sobrepasada por los tres subgéneros, que se encuentran en Guayanas; hacia el sur llegan hasta la Pampa. *Inaequalium* y *Psaroniocompsa* alcanzan hasta las áreas Pacífica, Norandina y Yungas. La presencia en la Amazonia está restringida en los tres subgéneros a las áreas del viejo escudo brasílico. □

## INTRODUCTION

*Simulium* is a cosmopolitan blackfly genus, well represented in the Neotropical realm. It has about 250 species and at least 15 subgenera (Coscarón, 1987), distributed from northern Mexico to Tierra del Fuego. These species show different patterns of distribution and determine areas of endemism (Coscarón & Coscarón-Arias,1995), with high similarity to Cabrera & Willink's (1973) realms. These three subgenera are characteristic of the mountains of southeastern Brazil, together with *S. (Thyrsopelma),* another blackfly subgenus with a similar distribution. The range of the these taxa is extended from north to southern South America. They breed through the north in the Cerrado and northern Brazilian shield, but are absent in the Amazonian Valley hiatus, occurying again in the Guianas up to the Caribbean area, through which they appear in the Pacific area surpassing the northern Andean barrier. The Austral limit is the Pampas, although *Psaroniocompsa* reaches central Patagonia.

Diversification of these three subgenera is very similar, with 12, 13 and 15 species, respectively. They show similar distributions, so we will try to determine if there are some connection among the area cladograms obtained and the possible vicariant events shared by the three subgenera, that induced their diversification.

The objetive of this paper is to undertake a cladistic analysis of the subgenera *Inaequalium* Coscarón & Wygodzinsky, *Psaroniocompsa* Enderlein, and *Chirostilbia* Enderlein, comparing them with their actual systematic arrangement. We also provide the original distribution maps of each subgenus with species distributions, in order to give further evidence that could help understand the systematic position of these taxa.

## MATERIAL AND METHODS

We used the method of phylogenetic systematics developed by Hennig (1966). Characters were derived from the morphology of females, males, pupae, and larvae. Character polarity was determined by the outgroup comparison method (Watrous & Wheeler, 1981).

Data were analyzed using Hennig86 version 1.5 (Farris, 1988). We used the ie* option for calculating trees. The successive weighting procedure was also used, repeated on successively produced trees, until the number of trees no longer changed. In the analysis of *S. (Inaequalium)* and *S. (Chirostilbia),* we also used the programs Pee-wee / Nona, with the amb-option (Goloboff, 1994), in order to reduce the number of trees. When the analysis yielded several trees, the strict consensus tree was calculated using the "nelsen" option of Hennig86. Clados version I.2 (Nixon I992) was used to analyze character distributions in the cladograms.

*Simulium* (*Inaequalium*) was considered in accordance with Coscarón & Wygodzinsky (1984). More information was obtained from Wygodzinsky (1973), Coscarón (1980, 1991), Py-Daniel & Coscarón (1982), Coscarón & Wygodzinsky (1984), Py-Daniel (1984) and Py-Daniel & Moreira (1988). Thirteen species were considered terminal taxa. *Simulium nogueirai* d'Andretta & González, *S. beaupertuyi* Ramírez Pérez, Rassi & Ramírez, *S. clarki* Fairchild, and *S. lurybayae* Smart were not considered because of the absence of material. Taking into account previous descriptions of d'Andretta & González (1964), Ramírez Pérez *et al.* (1977), Fairchild (1940), and Smart (1944), respectively, it can be assumed that the first two species are associated with *S. subnigrum* and the following two with *S. inaequale*. Table I contains the data matrix used for the analysis, and the characters employed are in Table II; 21 characters were used, numbers 2, 3, 4, 11, 18, and 21 were treated as nonadditive. *Simulium* (*Nottolepria*) was used as the outgroup of *Simulium* (*Inaequalium*).

*Simulium* (*Psaroniocompsa*) is considered here "sensu stricto", following Coscarón & Wygodzin-

**Table I.** Data matrix for the species of *S. (Inaequalium)* using *S. (Notolepria)* as outgroup.

| Species | Characters | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
| *Notolepria* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *inaequale* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 |
| *subnigrum* | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *nahimi* | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *subclavibranchium* | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *clavibranchium* | 1 | 1 | 1 | 2 | 0 | ? | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? |
| *mariavulcanoae* | 1 | 1 | 1 | 2 | 0 | ? | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ? | ? |
| *diversibranchium* | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 |
| *rappae* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *travassosi* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *botulibranchium* | 1 | 2 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| *souzalopesi* | 1 | 2 | 2 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *petropoliense* | 1 | 2 | ? | ? | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | ? | ? |
| *parimaensis* | 1 | 1 | ? | ? | ? | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? |

**Table II.** Characters and character states of *S. (Inaequalium)*. 0 plesiomorphic; 1-3 apomorphic.

**Female**

1. Shape of the basal portion of cibarium. (0) Not elevated medially and without teeth. (1) With small teeth arranged over median height.
2. Paraproct size. (0) Shorter than wide basally, truncate distally, sometimes with thin terminal process. (1) Short or as long as wide, rounded distally, without terminal process. (2) Longer than wide basally, acuminate on distal half.

**Male**

3. Distimere shape: proportion length/width at base. (0) 1.0. (1) 1.3-2.0. (2) 2.3-3.0.
4. Distimere shape and position of hook. (0) Subtriangular without hook. (1) Subtriangular with apical hook. (2) Subquadrate with subapical hook. (3) Subcylindrical with apical hook.
5. Distimere hooks number. (0) 0-1, small size. (1) From 1 with big size, plus one or several hooks to 7 smaller than first.

**Pupa**

6. Anterior border of cocoon. (0) Straight. (1) With dorsal projection.
7. Texture of the anterior border of cocoon. (0) With compacted weave. (1) Weave not compacted, with irregular curls.
8. Proportion of cocoon and gill branches length. (0) Longer than gill branches. (1) Shorter than gill branches.
9. Number of gill branches. (0) Below 8. (1) 18-20.
10. Proportion of secondary and tertiary gill branches length. (0) Secondary shorter than tertiary. (1) Secondary and tertiary with similar length and tertiary thicker than secondary branches.
11. Gill branches thickness and shape of ventral branch. (0) Thin, with straight ventral branch. (1) Thick, with straight ventral branch. (2) Thick, with curved ventral branch.
12. Relation mean body length/ gill branches length. (0) 0.70-2.2. (1) 0.57.
13. Filiform gill branches distal portion. (0) Not inflated. (1) Inflated.
14. Primary and secondary dorsal gill branches enlarged( about two times in relation to ventral primary and secondary gill branches diameter). (0) Absent. (1) Present.
15. Presence of appendages in gill branches. (0) Without appendages. (1) With appendages.
16. Gill with 6 filiform branches, branching off from short stalk with very short primary branches. (0) Absent. (1) Present.
17. Position of gill branches. (0) All branches directed forward. (1) Secondary ventral gill branches directed backwards.
18. Types of gill branches cuticular process. (0) Gill branches without cuticular process. (1) Gill branches with tubercle-like cuticular process, showing wide base generally apically accuminated, dorsal branch with relatively stout diverticles apically blunt. (2) Gill branches with hair-like cuticular process, dorsal branch with minute diverticles apically accuminated.
19. Number of branches of thoracic trichomes. (0) Over 3 branches. (1) 1-2 branches.

**Larva**

20. Ornamentation of cephalic apotome. (0) Difuse pigmentation without special ornamentation. (1) Darkened basally and middle longitudinally, including one or two elongated light window medially.
21. Length of gular cleft. (0) Gular cleft absent or very reduced, with relation hypostomium/hypostomial bridge below 0.5. (1) Gular cleft moderately developed, relation hypostomium/hypostomial bridge below 0.6-1.0. (2) Gular cleft well developed, relation hypostomium/hypostomial bridge between 1.2-2.4.

sky (1984) and Coscarón (1987, 1991), i.e., not including *S.* (*Cerqueirellum*) species sensu Py-Daniel (1983) as Crosskey did (1987). Information is based on Coscarón & Wygodzinsky (1984), Field (1969), and Py-Daniel (1988, 1989). *Simulium limbatum* Knab, *S. catarinense* Pinto, and *S. guttatum* (Enderlein) are not included in *Psaroniocompsa* based on the absence of topotypical breeded material. *Simulium limbatum* is not included because with the available information it can be associated with *S. aequifurcatum* Lutz. Fifteen species are the terminal taxa and 24 characters were derived from morphology. Characters 1, 3, 4, 16, 17, 19, and 22 were treated as nonadditive. *Simulium* (*Inaequalium*) was chosen as the outgroup. Table III contains the data matrix used in this analysis and the characters used are detailed in Table IV.

Information on *Simulium (Chirostilbia)* was obtained from Coscarón (1981, 1987, 1991), Py-Daniel (1987), and Py-Daniel & Moreira (1988). Twelve species were considered as terminal taxa and 18 characters were employed for the analysis; *S. (Inaequalium)* was used as outgroup. Characters 2, 3, 7, 9, 11, 12, 13, and 17 were treated as nonadditive. Table V contains the data matrix and the list of characters used are in Table VI.

For the discussion on distributional patterns, a map of areas of simuliid species (Coscarón & Coscarón-Arias, 1995) was used, based on a comparison with Cabrera and Willink's (1973) scheme. Acronyms used to refer to these areas on the strict consensus cladogram correspond to the following areas: AM= Amazonia, CA= Caribbean, CE= Cerrado, GU= Guianas, MO= Monte, NA= northern Andes, PA= Patagonia, PC= Pacific, PM= Pampas, SE= mountains of southeastern Brazil, and YU= Yungas.

## RESULTS AND DISCUSSION

The three subgenera are monophyletic, supported by several synapomorphies. In *S. (Inaequalium)*, the analysis with Hennig86 generated 12 trees, each with 28 steps, and CI and RI of 1; the synapomorphies that define it are 1(1), 3(1), 4(1), and 21(1). Using Pee-wee / Nona, we obtained three trees with similar number of steps and indexes. Cladogram number 1 was chosen in order to show the characters (Fig. 1). The biggest difference among the trees correspond to the S. *parimaense* position.Tree number 2 ((*S. botulibranchium* species group and *S. parimaense), (S. travassossi* and *S. inaequale* species group)) has the clade *(S. botulibranchium* species group, *S. parimaense*)) supported by 3(1) and 4(3), unknown for *S. parimaense*; in tree number 3 *(S. botulibranchium* species group *(S. parimaense, (S. travassosi, S. inaequale* species groups)) the clade *(S. parimaense, (S. travassosi* and *S. inaequale species groups)* supported by 21(2) is unknown also for *S. parimaense*. The dubious position of *S. parimaense* is due to the unknown male and larval characters which include five synapomorphies. All trees obtained in *S. (Inaequalium)* have two clades similar to those of Coscarón (1987, 1991). The strict consensus tree shows a basal trichotomy including the *S. botulibranchium* species group, the independent *S. parimaense*, a couple composed of *S. rappae* + *S. travassosi*, and the last branch showing seven spe-

**Table III.** Data matrix for the species of *S. (Psaroniocompsa)* using *S. (Inaequalium)* as outgroup.

| Species | Characters | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |
| *Inaequalium* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *angrense* | 1 | 0 | ? | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *auripellitum* | 1 | 0 | ? | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *bonaerense* | 1 | 0 | ? | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *jujuyense* | 1 | 0 | ? | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *incrustatum* | 1 | 1 | ? | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *aequifurcatum* | 2 | 1 | 1 | ? | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *schmidtmummi* | 1 | 1 | 3 | ? | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *fuliginis* | 0 | 1 | 0 | ? | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *brevifurcatum* | 0 | 1 | 4 | ? | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *anamariae* | 0 | 1 | 0 | ? | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *auristriatum* | 0 | 1 | 2 | ? | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 7 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *guaporense* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 1 | 0 | 0 | 4 | 0 | 3 | 1 | 1 | 1 | 1 | 0 |
| *siolii* | 2 | ? | ? | ? | ? | ? | ? | 1 | 0 | ? | ? | 0 | 0 | 1 | 1 | 0 | 6 | 0 | 3 | 1 | 1 | 0 | 1 | 1 |
| *lourencoi* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 1 | 1 | 0 | 6 | 0 | 3 | 1 | 1 | 0 | 1 | 0 |
| *damascenoi* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 2 | 6 | 0 | 3 | 1 | 1 | 2 | 0 | 0 |

Table IV. Characters and character states of *Simulium* (*Psaroniocompsa*). 0 plesiomorphic; 1-7 apomorphic.

**Female**

1. Scutum ornamentation. (0) Homogeneously pigmented, without 1+1 longitudinal bands. (1) With 1+1 anterior submedian short cuneiform silvery spots. (2) With 1+1 long submedian silvery stripe crossing from frontal border to or near posterior silver band.
2. Disposition of scutum decumbent hairs. (0) Homogeneously dispossed. (1) Arranged in small groups with scale aspect.
3. Coloration of scutum "scales". (0) Yellow whitish to golden or without "scales". (1) Greenish gray pale. (2) Greenish violaceuos. (3) Golden greenish. (4) Violet golden reddish.
4. Coloration of scutum pilosity homogeneously distributed. (0) Silvery to yellowish gray or pilosity not homogeneously distributed. (1) Tin to pale greenish yellow. (2) Tin to silvery gray.
5. Abundance of scutum pilosity. (0) Moderate pilosity (allowing to see the tegument ornamentation). (1) Abundant pilosity (not allowing to see the 1+1 submedian anterior silvery spot).
6. Species size. (0) Medium to large species (wing length overpassing 1.8 mm in females, 1.6 in males). (1) Small species (wing length not over 1.8 mm in females and 1.6 mm in males).
7. Cibarium basal portion shape. (0) Flat and without teeth. (1) Depressed medially, with small teeth.
8. Front aspect. (0) Gray pollinose, opaque. (1) Iridiscent with nacarous greenish to violet blue bright.
9. Abdomen ornamentation. (0) Blackish, without white spots. (1) Black, with 1+1 submedian whitish spots on tergites II-V.

**Male**

10. Distimere shape. (0) Subtriangular with apical hook. (1) Subquadrate, with submedian hook.
11. Sizes of distimere external angle and position of apical hook. (0) Obtuse angle over 90° and hook near middle. (1) Right angle approximately of 90° and hook near internal angle.

**Pupa**

12. Cocoon anterior border shape. (0) Approximately straight. (1) With dorsal projection.
13. Length of cocoon dorsal anterior projection. (0) Absent or single and below 1/5 of gill length. (1) Bifurcated and about 4/5 of gill length.
14. Cocoon ventral anterior projection. (0) Absent. (1) Present.
15. Number of branches in thoracic trichomes. (0) 3 or more. (1) 1 or 2.
16. Distribution of platelets in frontoclypeus and thorax. (0) Distributed homogeneously and in a moderate number. (1) Very abundant in exposed portion of thorax, frontoclypeus without platelets in a medium longitudinal and 1+1 sublateral areas. (2) Exposed portion of thorax and frontoclypeus without platelets.
17. Number and disposition of gill branches. (0) 6 branches approximately parallel dispossed with primary and secondary branches well developed but not more than 1/3 of gill length. (1) 6 filiform branches curved ventrally with the flexion are in about a half of length gill. (2) 6 filiform branches rising together very close to the base. (3) 6 filiform branches relatively open and dispossed in several planes. (4) 6 filiform branches with secondary branches elongated, about as long as the half of total branches length and all bifurcated at same length. (5) 4 filiform branches branch off at same high near the base and about 4.3 mm length. (6) 4 filiform branches, branch off far away to the base with about 1.14-2.56 mm length. (7) 2 thick branches with a short stem.

**Larva**

18. Hairs of head dorsal sclerite. (0) Well developed and bifids. (1) Very short single and bifids.
19. Type of trichomes on abdominal tegument. (0) Without trichomes. (1) With short single hairs. (2) With 3-6 small branches hairs. (3) With scale shape dorsally.
20. Subtriangular protuberances on abdomen dorsum. (0) Absent. (1) Present.
21. Proportion of hypostomium bridge. (0) About 1/2 o more than hypostomium height. (1) Shorter than 1/5 of hypostomium height.
22. Tubercles on tergites I and VIII. (0) Absent. (1) With 1+1 tubercles on tergite I. (2) With only one tubercle on tergite I and 1+1 tergite VIII.
23. 1+1 big ventral subtriangle shape tubercles on abdomen. (0) Absent. (1) Present.
24. Sclerotized areas on abdominal membranes of abdomen. (0) Absent. (1) Present.

cies with a basal trichotomy (Fig. 2).

The analysis of *Simulium (Psaroniocompsa)* gave only one tree, with a length of 42, and a CI and RI of 0.92. The cladogram shows that *Psaroniocompsa* is a monophyletic taxon sustained by 4 synapomorphies: 1(1), 7(1), 10(1), 15(1); it has two clades: one with four terminal taxa, including the more austral and generalized species, and the opposite including the remaining species. The last clade shows also two trees (Fig. 3).

*Simulium (Chirostilbia)* analysis gave 24 cladograms with 38 steps, and CI and RI of 0.89. No changes were produced after applying succesive weighting. This subgenus is defined by the following synapomorphies: 6(1), 8(1), and 9(1). Using Pee-wee/Nona two trees were obtained, with 33 steps, and CI and RI of 1. Tree number 1 is shown in figure 4; tree number 2 is very similar, showing in the last clade (*S. empascae* (S. *friedlanderi (S. distinctum* species group, *S. prumirimense, S.*

**Table V.** Data matrix for the species of *S. (Chirostilbia)* using *S. (Inaequalium)* as outgroup.

| Species | Characters | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
| *Inaequalium* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *pertinax* | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 1 |
| *laneportoi* | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 |
| *serranum* | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *spinibranchium* | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 0 |
| *empascae* | 0 | 0 | ? | 0 | 0 | 1 | ? | 1 | 1 | 1 | 0 | 4 | 1 | 0 | 0 | 1 | 2 | 0 |
| *distinctum* | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 5 | 2 | 0 | 0 | 1 | 1 | 0 |
| *prumirimense* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 5 | 0 | 1 | 0 | 1 | 1 | 0 |
| *friedlanderi* | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | 1 | 1 | 6 | 0 | 0 | 0 | 1 | 0 | ? |
| *obesum* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 7 | 0 | 0 | 1 | ? | ? | 0 |
| *acarayense* | 1 | 1 | 3 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *subpallidum* | 1 | 2 | 2 | 0 | 1 | 1 | 3 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *papaveroi* | 1 | 0 | 3 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |

**Table VI.** Characters and character states of *Simulium (Chirostilbia)*. 0 plesiomorphic; 1-6 apomorphic.

**Female**

1. General coloration. (0) Blackish to reddish brown. (1) Grayish brown to green yellowish brown.
2. Abdomen coloration. (0) Blackish to brownish dark. (1) Greenish gray, with brown to blackish subquadrate spots. (2) Yellowish tergites III-V grayish, with spots brownish gray and tergites VI-IX brownish.
3. Scutum coloration. (0) Homogeneously blackish, without stripes. (1) Black, with a special illumination it shows gray pollinose ornamented by 1 median and 1+1 blackish lateral stripes; and with another light change the black tonality to led gray and vice versa. (2) Gray yellowish brown. (3) Brown to dark grayish led and scutellum light brown.
4. Hairs on basal portion of R. (0) Present. (1) Absent.
5. Subbasal claw tooth. (0) Present. (1) Absent.
6. Paraproct proportions of length and wide. (0) Shorter or about as long as wide. (1) About twice long of base wide.

**Male**

7. Coloration of scutum. (0) Blackish homogeneously. (1) Black showing with special ilumination silvery on the 1/4 frontal.
8. Apical hook on distimere. (0) Present. (1) Absent.
9. Shape of distimere. (0) Subquadrate and about as longer than wide at base. (1) Subtrapezoidal shape, a little longer than wide at base and without latero-longitudinal crest. (2) Subtriangle to subtrapezoidal shape, about twice longer than wide at base and with latero-longitudinal crest.

**Pupa**

10. Gills enclosed by the cocoon. (0) Covering only the gill base. (1) Covering totally.
11. Cocoon texture. (0) Homogeneous. (1) Open tissue compossed by wide threads on anterior area and covering the gills.
12. Shape of gill branches. (0) 6-8 filiform branches with primary and secondary branches of same diameter and about a half of body pupa length. (1) 8 filiform branches overpassing 2/3 of cocoon length at base. (2) 8 filiform branches relatively bunched with primary and secondary dorsal branches wider than remaining. (3) 8 thick branches on the base and branching off very open with primary and secondary branches very long. (4) 8 branches relatively thick basally, branching off near the short stem with very short primary branches and without tertiary branches. (5) Gill with 10 branches. (6) Gill with 11 branches. (7) Gill with 120 branches.
13. Disposition of frontoclypeus platelets. (0) Platelets always present homogeneously dispossed in variable number and not very abundant. (1) Frontoclypeus without platelets. (2) Frontoclypeus platelets reduced to 1+1 supralaterally group near to facial trichomes. (3) Platelets of frontoclypeus very abundant leaving free only reduced area on the median and sublateral spots area.
14. Disposition of thorax platelets. (0) Homogeneously. (1) On all disc area, but some of them ordered conspicuously on a line on both sides along of median line.
15. Number of thorax disc trichomes. (0) About 5+5. (1) Over 100+100.
16. Cephalic apotome darkened medium basally as triangle shape. (0) Absent. (1) Present.
17. Number of hook on the anal ring. (0) About 70-120. (1) About 150-190. (2) About 201-204.
18. Host preference and inmunological reaction to bites. (0) Zoophilic, producing scarce reaction to bites on men. (1) Antropophilic, producing hard reaction to bites.

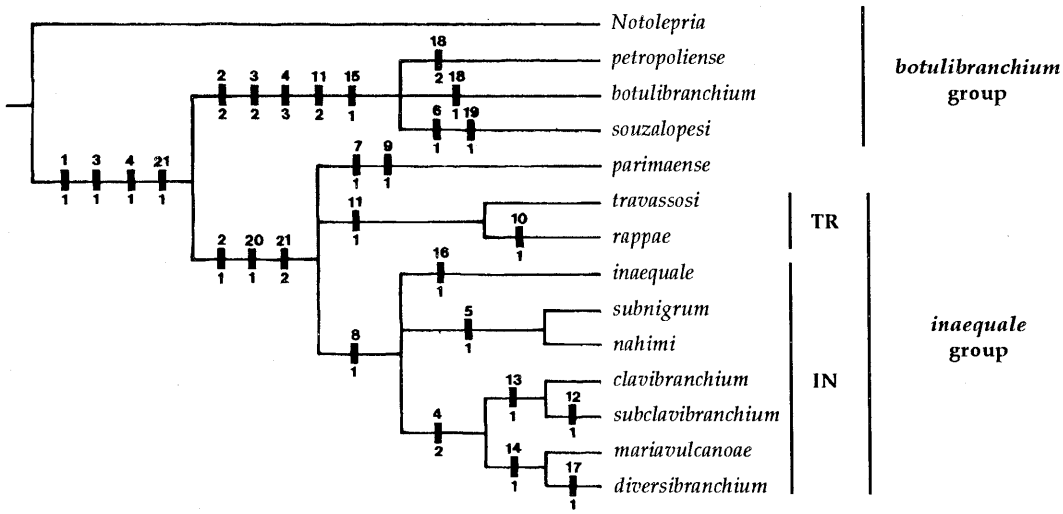


**Fig. 1.** Cladogram number 1 of *S. (Inaequalium)*, selected among the three obtained. Character states superimposed on the cladogram.

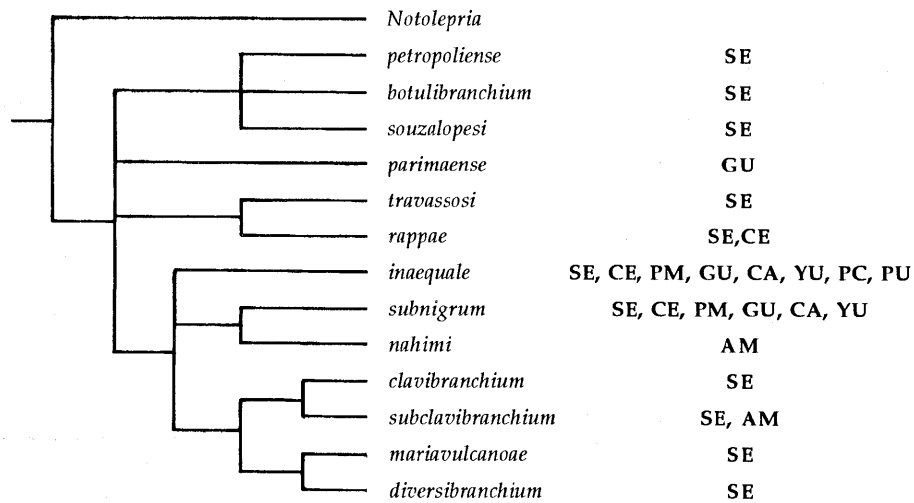


**Fig. 2.** Strict consensus cladogram of *S. (Inaequalium)*.

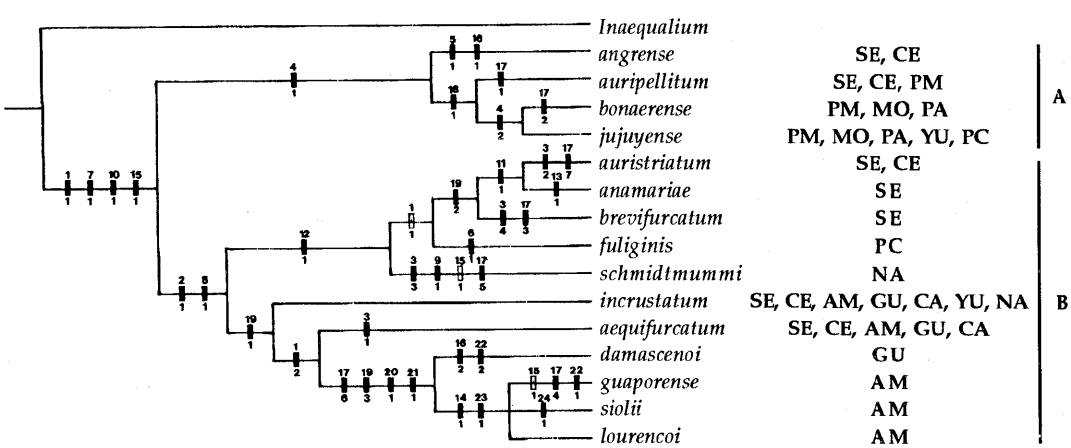


**Fig. 3.** Cladogram of *S. (Psaroniocompsa)*. A = *jujuyense* species group; B = *incrustatum* species group.

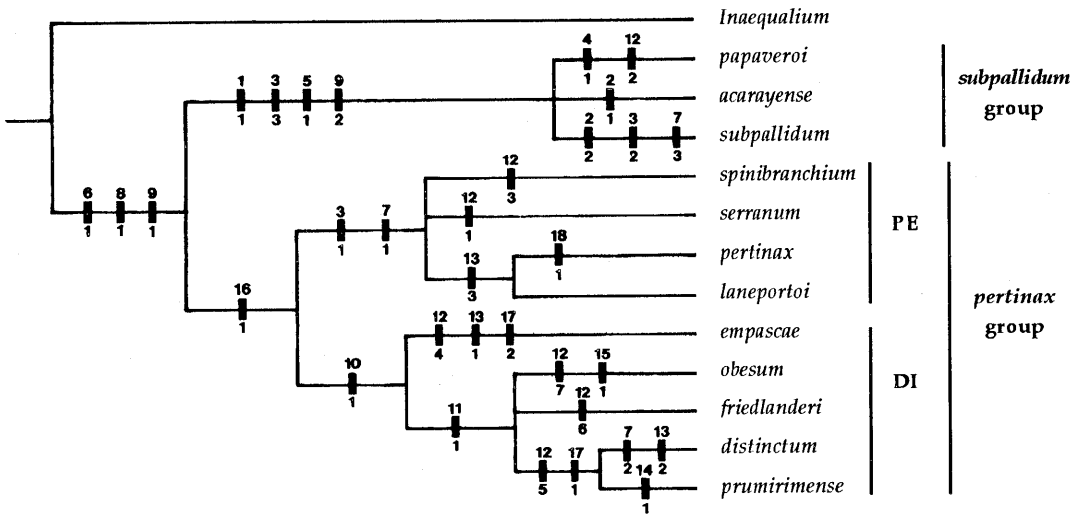


Fig. 4. Cladogram number 1 of *S. (Chirostilbia)*.

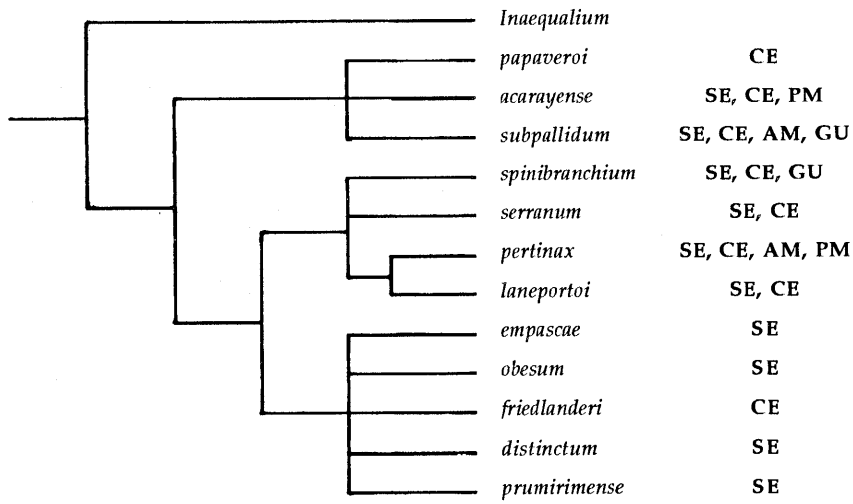


Fig. 5. Strict consensus cladogram of *S. (Chirostilbia)*.

*obesum*))) supported by 17(1) and *S. obesum* lacks that character. Strict consensus tree obtained from the two trees (Fig. 5) is very similar to tree number 1, differing in the presence of a tetratomy in the last clade. The two clades show two species groups: S. *subpallidum* and *S. pertinax,* which agree with Coscarón (1987, 1991).

## DISTRIBUTION

In *Simulium (Inaequalium)* the clade including the *S. botulibranchium* species group corresponds to three species restricted to the mountains of southeastern Brazil. In the no grouped species shows *S. parimaense* for one side, that occurs in Guianas and is the only species of *S. (Inaequalium)* outside the mountains of southeastern Brazil. *Simulium travassosi* and *S. rappae* are inhabitants of the last area, although *S. rappae* lives also in the Cerrado. The *S. inaequale* s. str. branch, has *S. inaequale* in the first place of the trichotomy. This species has a large range, occurrying from the Caribbean in the north, to the Pampas in the south, and from the Pacific crossing the Andes, Yungas and Puna on the west, to Guianas, Cerrado and SE Brazil, in the east, covering most of the tropical area of South America. Only Amazonia was not colonized by this species (Fig. 2). The *S. subnigrum* and *S. nahimi* branches show the first species also with a wide range, covering similar areas as *S. inaequale* at south of the Ecuador line, except the Pacific and

Puna, but surpassing NW Amazonia and Caribbean area in the north. *Simulium nahimi,* the only species living exclusively in Amazonia, is restricted to the Mato Grosso in the old western Brazilian shield. The last branch has four species *(S. clavibranchium, S. subclavibranchium, S. mariavulcanoae,* and *S. diversibranchium)* living only in the mountain area of SE Brazil, except for *S. subclavibranchium* that extends to the Amazonian boundaries. With the available information we can consider that *S. (Inaequalium)* is a South American tropical lowland taxon, whose distribution is only interrupted by the xerophytic area of Monte and Patagonia in the south, the Andes in the west, and leaving the pluvial forest of the Amazonian Valley as a big transversal hiatus (Fig.6).

*Simulium (Psaroniocompsa)* shows sympatrid distribution with *S. (Inaequalium),* and as shown before, SE Brazil is inhabited by the first clade. The cladogram shows in the first clade, the species with

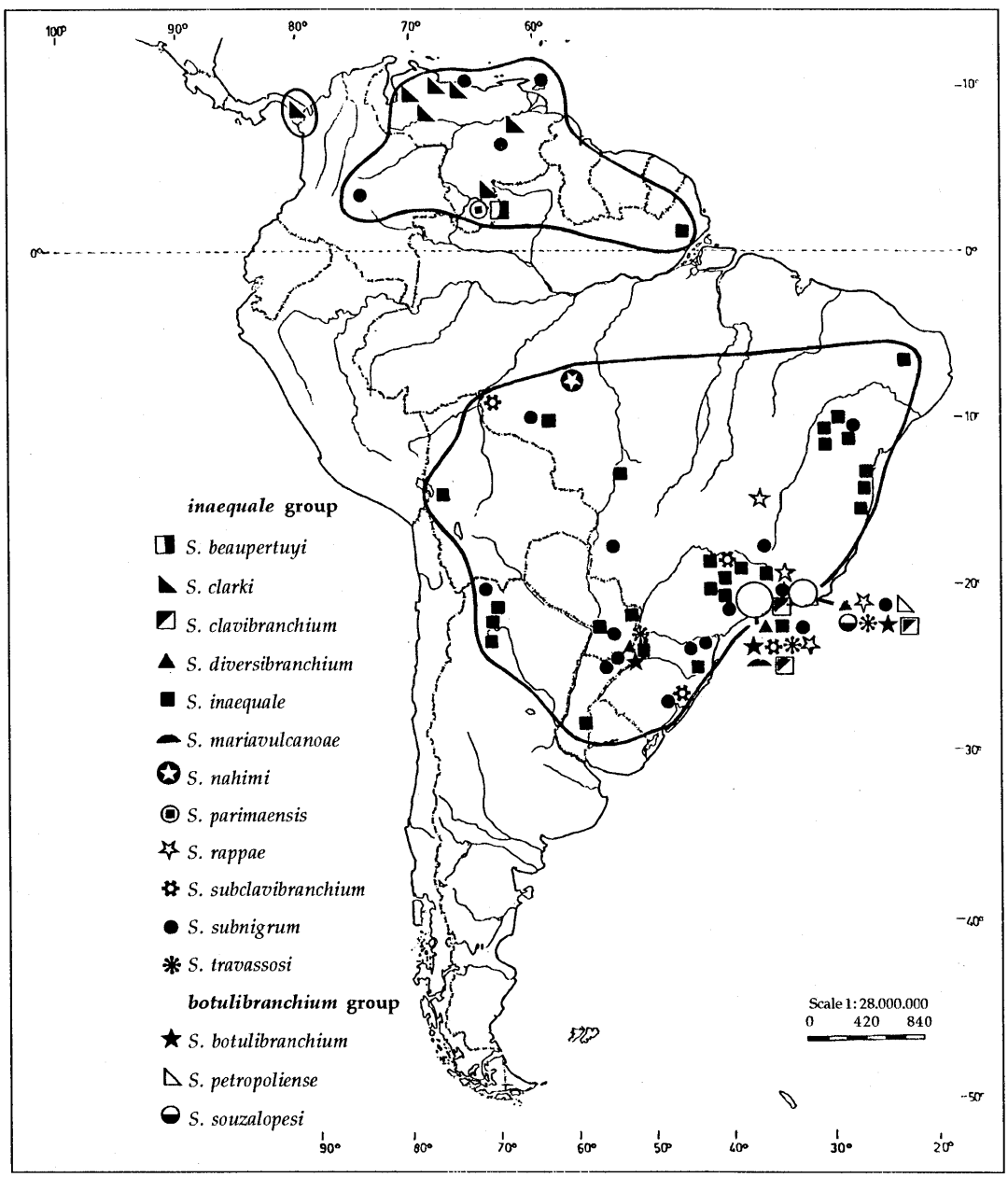


**Fig. 6.** *S. Inaequalium* species distribution map.

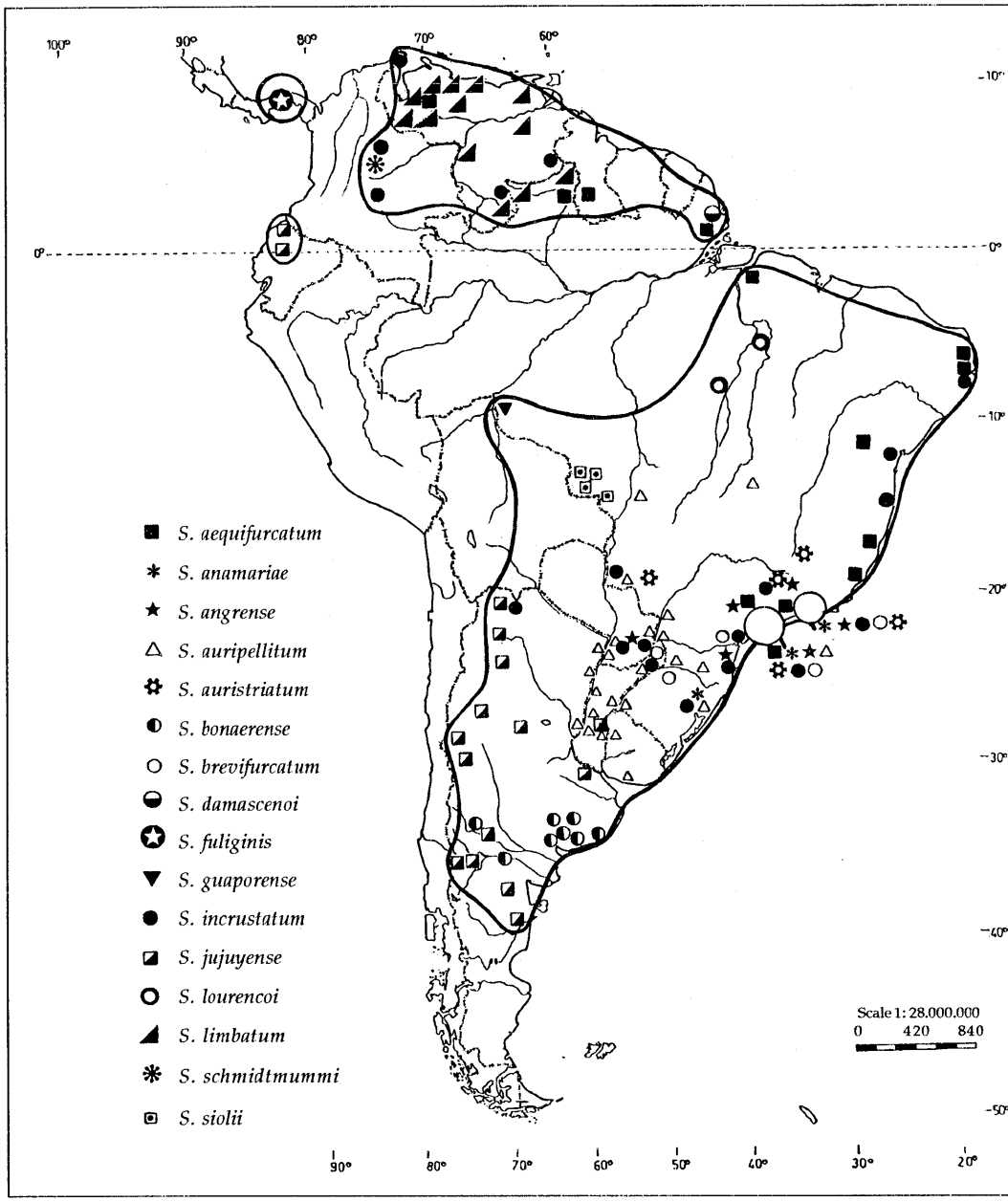


**Fig. 7.** *S. Psaroniocompsa* species distribution map.

the most southern distribution: *S. angrense* and *S. auripellitum* breed from the mountains of SE Brazil to the Cerrado areas, but the last reaches the Pampas. *Simulium bonaerense* and S. *jujuyense* are from Pampas, Monte and Patagonia, but the last one has a broader distribution reaching the west in the Yungas, in the southern tropics, and Pacific areas. The opposite clade has in the upper branch four species; three (*S. auristriatum, S. anamariae,* and *S. brevifurcatum)* are present in SE Brazil; the first reaches the Cerrado realm, *S. fuliginis* is restricted to the Pacific area, and *S. schmidtmummi* to the northern Andes. On the other side (Fig.3), the tree shows six species: *S. incrustatum* with a high range distribution that includes SE Brazil, Cerrado, Amazonia, Guianas, Caribbean, Yungas, and northern Andes areas; *S. aequifurcatum* has a very close distribution with preference for NE South America and absence in the west, northern Andes, and Yungas. In the next branch we find *S. damascenoi* from Guianas, and at the end there is a trichotomy with *S. guaporense, S. siolii* and *S. lourencoi,* that are exclusive from Amazonia.

Within *S. (Chirostilbia),* the *S. subpallidum*

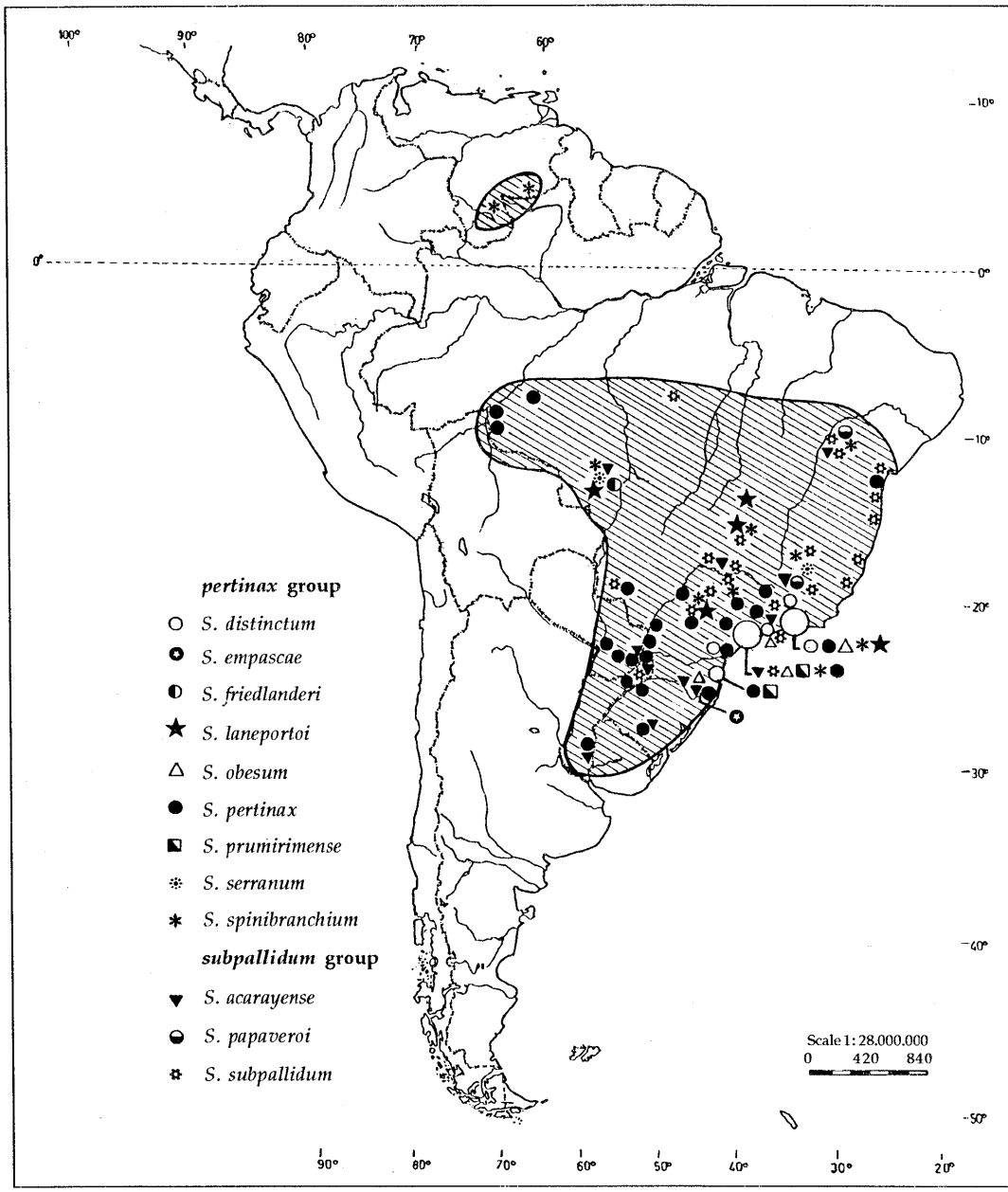


**Fig. 8.** *S. Chirostilbia* species distribution map.

group has three species common to the Cerrado area, but *S. subpallidum* and S. *acarayense* are also distributed in SE Brazil and extend to Amazonia and Guianas in the case of the first, and to the Pampas in the second species. The opposite clade, shows one branch (S. *pertinax* species subgroup) with four species inhabitating the mountains of southeastern Brazil and Cerrado with *S. pertinax* reaching to Amazonia and Pampas and *S. spinibranchium* to Guianas. In the other branch (S. *distinctum* subgroup) four out of five species live in SE Brazil and the remaining one, *S. friedlanderi,* breeds in the Cerrado.

*Simulium (Chirostilbia)* has a distribution restricted to the eastern tropical realm of South America, with special development in the SE Brazil and Cerrado areas. It was able to colonize Amazonia and Guianas, but it could not reach Bolivia and the northwest of Argentina, where only one species arrived to the north of the Pampas area.

## CONCLUSIONS

Cladistic studies support the *S. botulibranchium*

and *S. inaequale* species groups in *Inaequalium*, as well as the *S. subpallidum* and *S. pertinax* species groups in *Chirostilbia* (Coscarón, 1987, 1991). In *Psaroniocompsa*, the *S. jujuyense* and *S. incrustatum* species groups are established as monophyletic groups. In *Chirostilbia* it is also possible to differentiate the *S. pertinax* and *S. distinctum* subgroups in *the S. pertinax* species group (Fig. 4).

It is not easy to ellucidate how the blackfly evolution was like, considering that the actual distribution is a result of different factors, e.g., global climate changes and orogenesis. Some areas nowadays united could have been isolated in the past, and the frequent sympatry of taxa in the Cerrado and mountains of southeastern Brazil can be the result of climatological changes posterior to the cladogenesis, that enabled them to disperse in these realms. Based on the three cladograms, we can infer that a vicariant event acted splitting populations from Cerrado and the mountains of southeastern Brazil. Such event could have been produced by changes in the sea level during the Tertiary as a consequence of temperature oscillation as those of late Oligocene, in which the sea surpassed about 200 m over the actual level, during middle Miocene (near 100 m), or in the Pliocene with several glacial periods. These changes associated with the hard diastrofism not only produced physical barriers that isolated the populations, but also performed climate changes that helped diversification (Pascual, 1984). The lowlands of the Amazonian Valley with the sea invasion in warm periods, associated with rain forests, could be an important barrier among the Guianan and Brazilian fauna. Maybe in *Psaroniocompsa* the segregation of *S. damascenoi* in the north from *S. guaporense*, *S. siolii* and *S. laurencoi* result from this separation, as also could be *S. parimaense* from the big branch of the *S. inaequale* species group, most of which species live in southeastern Brazil. Another marine transgression, known as Entrerriense or Paranense sea, covering east of Argentina from Paraguay to north of Patagonia at late Miocene, could have caused the S. *jujuyense-S. bonaerense* and *S. auripellitum* diversification.

The uplift of the Andean cordillera surely enabled the speciation of *Psaroniocompsa* species, with *S. schmidtmummi* in the northern Andes and *S. fuliginis* in the Pacific realms. The Andes acted not only as barrier, but it also helped dispersion and diversification as occurred with *S. jujuyense*, a species that probably colonized the Pacific realm from southern areas through Yungas, and also influenced on the climate, provoking xerofitic area specially on Monte, Western Cerrado and Patagonia. On the other hand, the Amazonian barrier was not an obstacle for some species with high dispersion range that populate both sides, such as *S. inaequale* and *S. subnigrum* in *Inaequalium*, *S. incrustatum* and *S. aequifurcatum* in *Psaroniocompsa* or *S. subpallidum* and *S. pertinax* in *Chirostilbia*. The Amazonian species correspond to the old Brazilian shield realm in the three subgenera.

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