Distributional patterns of the American Peiratinae (Heteroptera: Reduviidae)

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Key words: Heteroptera; Reduviidae; Peiratinae; distribution; patterns; parsimony analysis; endemicity.
Based on distributional data of 40 species of Peiratinae, historical relationships of five Amazonian areas (Paranaense, Atlantic, Pacific, Amazonian, and Cerrado) and two Chacoan areas (Chaco and Caatinga), were investigated through a parsimony analysis of endemicity (PAE). The resulting area cladogram indicates the following sequence of area fragmentation: (Cerrado (Caatinga (Chaco, ((Pacific, Amazonian), (Atlantic, Paranaense))))). It is proposed that these results reflect the gradual development of a diagonal of open formations (Chaco-Cerrado-Caatinga), which separated the former continuous tropical forest into two parts, namely, northwestern (Pacific plus Amazonian) and southeastern (Paranaense plus Atlantic).

Introduction

The Peiratinae (Heteroptera: Reduviidae) are worldwide in distribution, although mainly concentrated in the tropical areas (Willemse, 1985). They are represented in the Americas by 63 species and eight genera: *Froeschneriella* Coscarón (1 species), *Phorastes* Kirkaldy (2), *Rasahus* Amyot & Serville (26), *Sirthenea* Spinola (12), *Thymbreus* Stål (3), *Tydides* Stål (4), *Eidmannia* Taeuber (6), and *Melanolestes* Stål (9). *Sirthenea* is the only genus also distributed in the Old World. The American Peiratinae are mainly Neotropical, with a few species extending their range to the Nearctic (Coscarón, 1983b, 1984).

Within the Neotropical subregion, Peiratinae are basically associated to the forested areas of the Amazonian dominion, but they are also found in the so-called "diagonal of open formations" (Vanzolini, 1963; Vanin, 1976) or "savanna corridor" (Schmidt & Inger, 1951). This area extends across South America, from northeastern Brazil to the Chacoan dominion in Argentina, basically comprising the Caatinga, Cerrado, and Chaco of Cabrera & Willink (1973). Prado & Gibbs (1993), however, found different patterns of geographic distribution for several woody plant species from the dry seasonal forests of South America, which challenge the biogeographic importance of this diagonal.

Our objectives are twofold:

(1) to analyze the patterns of geographic distribution of the genera of American Peiratinae;

(2) to investigate the relationship of the areas of the diagonal of open formations with the rest of the Neotropics, based on a parsimony analysis of endemicity or PAE (Rosen, 1988).

Methods and data

The analysis was based on the distributional patterns of the species of American Peiratinae. Data were taken from the most recent revisions and from material provided by the following collections: American Museum of Natural History, New York (USA); British Museum (Natural History), London (United Kingdom); California Academy of Sciences, California (USA); Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa (Canada); Fundación e Instituto Miguel Lillo, San Miguel de Tucumán (Argentina); Instituto Oswaldo Cruz, Rio de Janeiro (Brazil); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (Argentina); Museo de La Plata, La Plata (Argentina); Museu Paranaense Emílio Goeldi, Belém (Brazil); Museum National d'Histoire Naturelle, Paris (France); Museu de Zoologia de Sâo Paulo, Sâo Paulo (Brazil); Naturhistoriska Riksmuseet, Stockholm (Sweden); Nationaal Natuurhistorisch Museum, Leiden (The Netherlands); Snow Entomological Museum, Kansas (USA); United States National Museum, Washington, D.C. (USA); Universidad Central de Venezuela, Maracay (Venezuela); Universitetets Zoologiske Museum, Copenhagen (Denmark); Zoological Museum, University of Helsinki, Helsinki (Finland); Zoologisches Museum der Humboldt Universität zu Berlin, Berlin (Germany); and private collection of Mr. A. Martínez, Salta (Argentina).

Areas of endemism

The units of the analysis (fig. 19) broadly coincide with some areas of Cabrera & Willink's (1973) scheme (approximate correspondence between brackets):

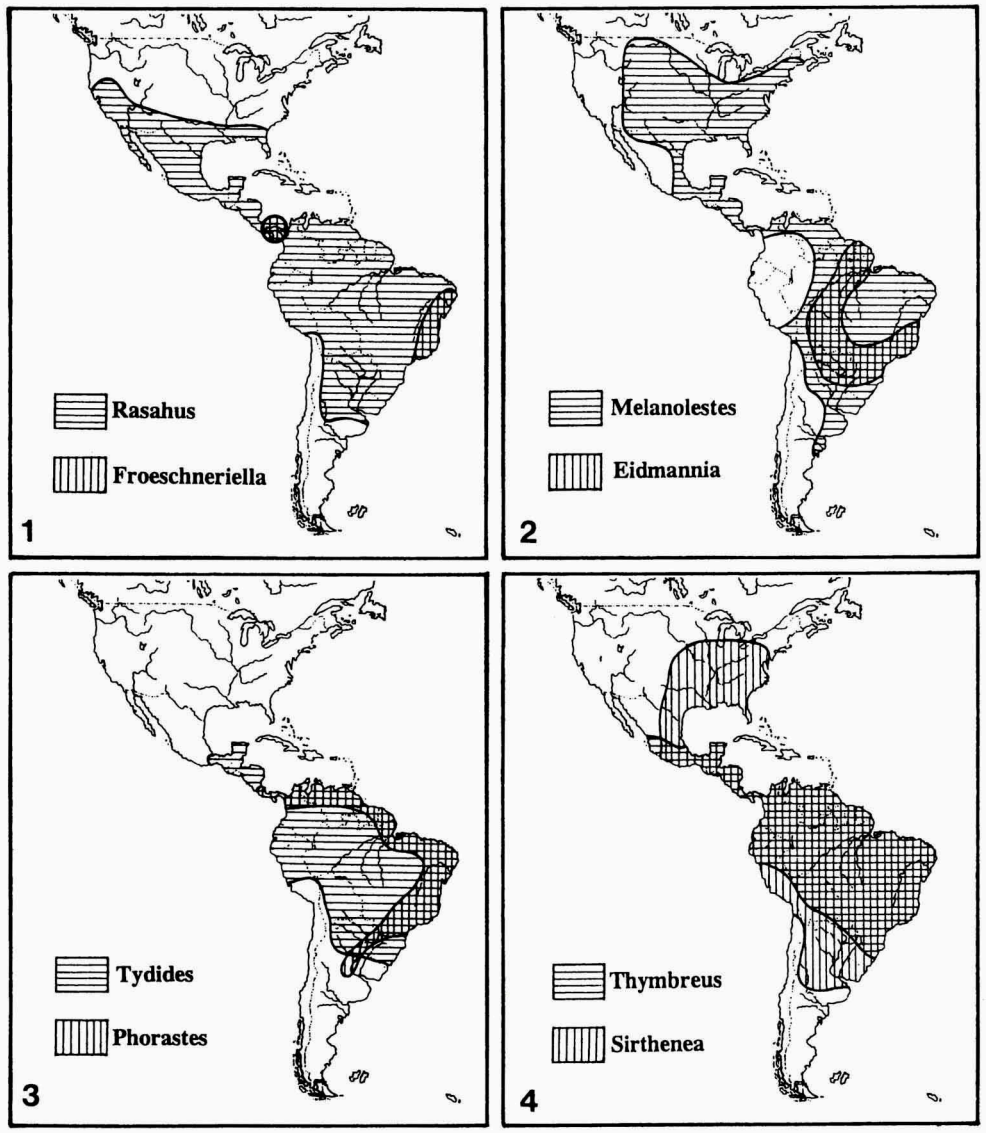
(1) Chaco (Chacoan dominion, with the exception of the Caatinga province).
(2) Cerrado (Cerrado province, Amazonian dominion).
(3) Caatinga (Caatinga province, Chacoan dominion).
(4) Pacific (basically the Pacific province, Amazonian dominion).
(5) Atlantic (Atlantic province, Amazonian dominion).
(6) Paranaense (Paranaense province, Amazonian dominion).
(7) Amazonian (remaining provinces of the Amazonian dominion).

Data analysis

Taxa were coded for their absence (0) or presence (1) in each area of endemism in a data matrix (Table I). Different taxonomic levels were coded hierarchically: species, subspecies, and genera. Parsimony analysis of endemicity or PAE (Rosen, 1988; for applications see Cracraft, 1991, and Myers, 1991) was carried out with Hennig86 (Farris, 1988), applying the implicit enumeration option. The cladogram was rooted with an hypothetical area coded all zeros.

Taxa analyzed

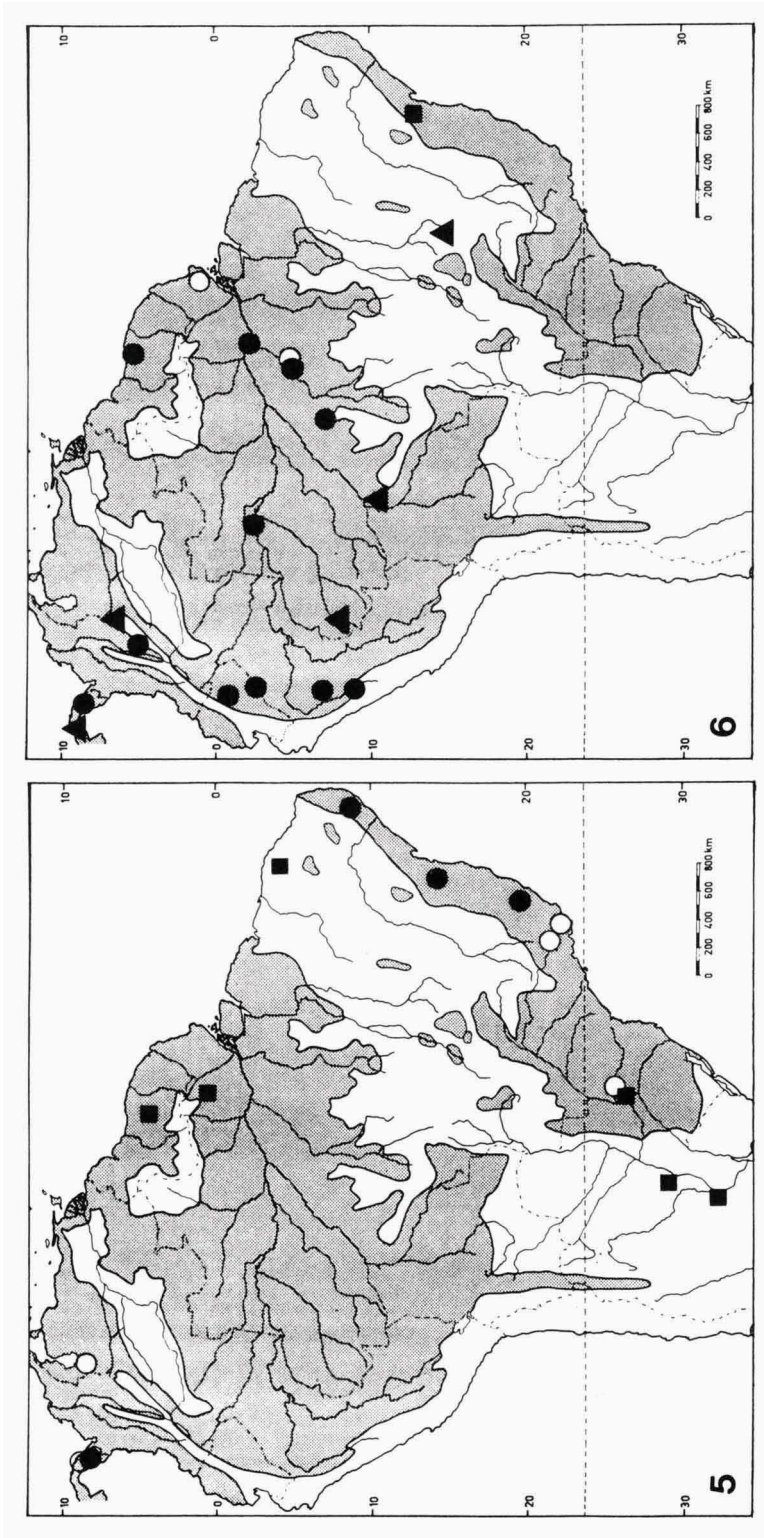
Froeschneriella Coscarón (Coscarón, in press). The only species of this genus, *F. vittata* (Coscarón) has a disjunct distribution in the Pacific and Atlantic biogeographic provinces (figs. 1, 5).



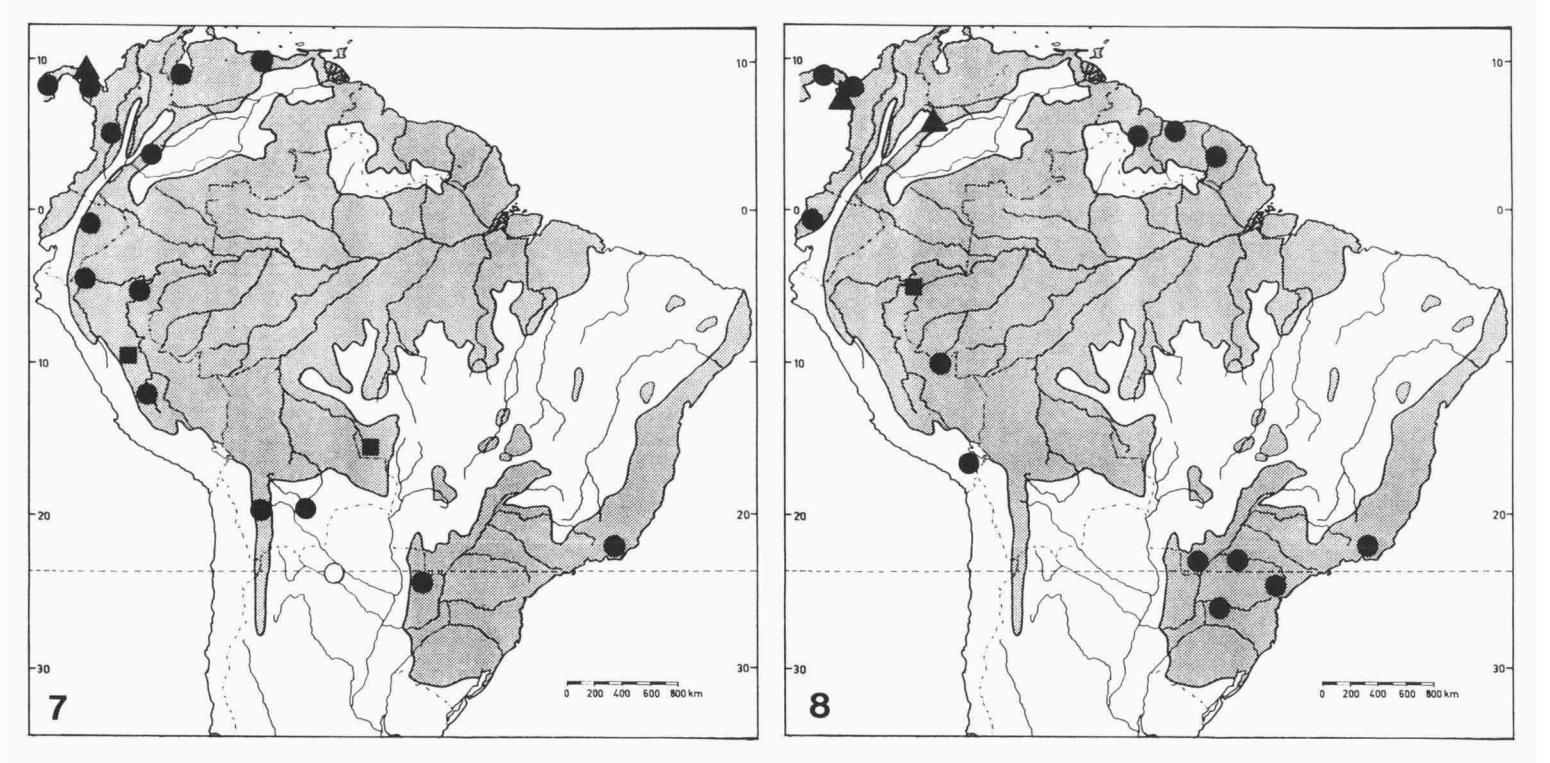
Figs. 1-4. Geographical distribution of the genera *Rasahus*, *Froeschneriella*, *Melanolestes*, *Eidmannia*, *Tydides*, *Phorastes*, *Thymbreus*, and *Sirthenea*.

Phorastes Kirkaldy (Lent & Jurberg, 1966; Doesburg, 1981). It has two species, distributed in the Neotropical subregion (fig. 3). *Phorastes femoratus* (De Geer) (fig. 5) is scattered in the Amazonian, Caatinga, and Chaco provinces. *Phorastes incognitus* (Doesburg) (fig. 5) is scattered in the Pacific, Paranaense, and Atlantic provinces.

Rasahus Amyot and Serville (Coscarón, 1983a, 1986a; Coscarón & Maldonado-Capriles, 1988). This genus, with 26 described species, is widely distributed from southern United States to central Argentina (fig. 1). Its range basically lies in the Neotropical subregion, but in its northern portion it extends partially to the Nearctic.



Figs. 5-6. Geographical distribution of species of Peiratinae. 5: *Froeschneriella vittata* (black circles); *Phorastes incognitus* (open circles); *P. femoratus* (black squares). 6: *Rasahus albomaculatus* (black circles); *R. amapaensis* (open circles); *R. angulatus* (black square); *R. arcitenens* (black triangles).



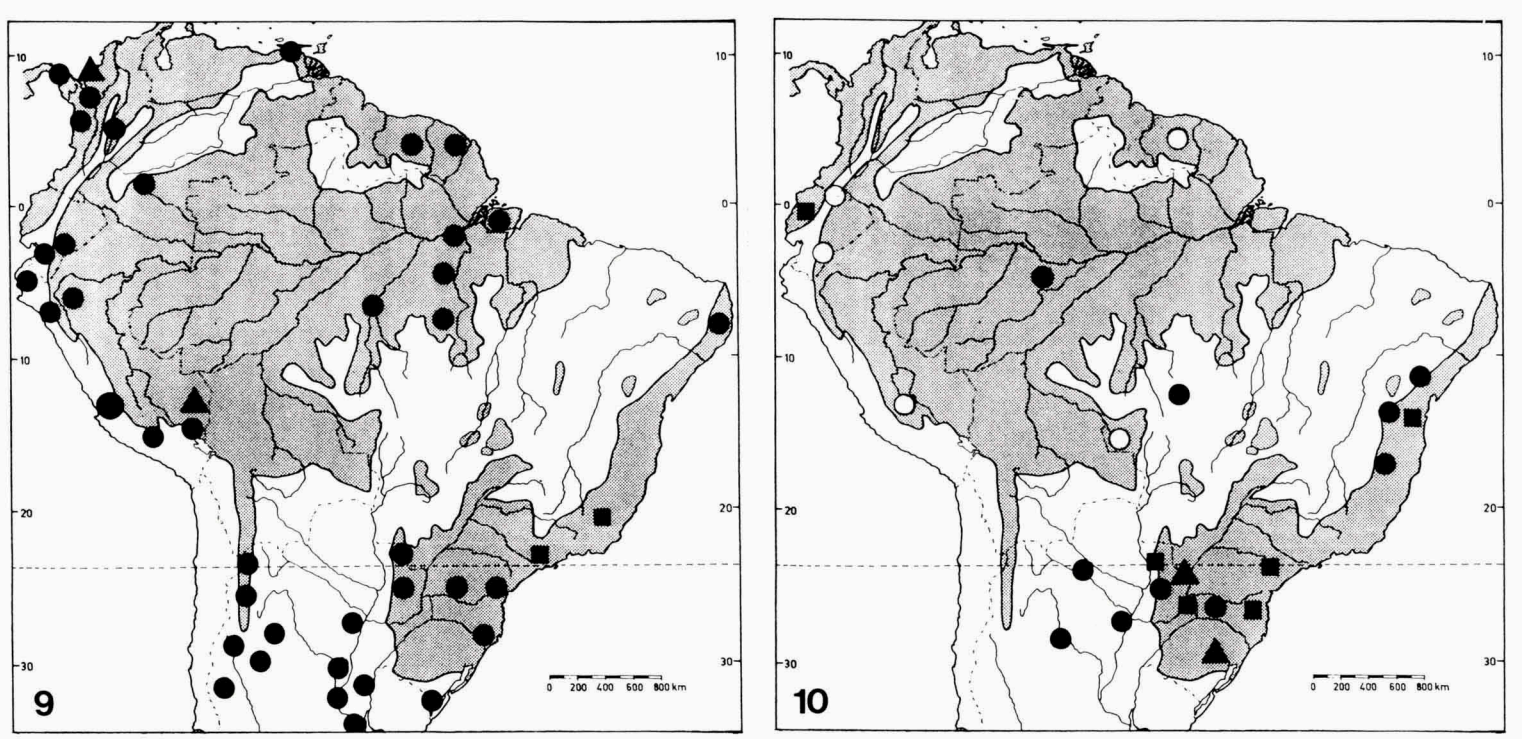
Figs. 7-8. Geographical distribution of species of Peiratinae. 7: *R. arcuiger* (black circles); *R. argentinensis* (open circle); *R. atratus* (black squares); *R. bifurcatus* (black triangle). 8: *R. brasiliensis* (black circles); *R. castaneus* (black square); *R. flavovittatus* (black triangles).

Rasahus albomaculatus (Mayr) and *R. arcitenens* Stål (fig. 6) are widely distributed in the Pacific and Amazonian provinces, extending the latter also to the Cerrado province. *Rasahus amapaensis* Coscarón (fig. 6) and *R. atratus* Coscarón (fig. 7) are endemic to the Amazonian province. *Rasahus arcuiger* (Stål) (fig. 7) is widespread in the Pacific, Amazonian, Chaco, Paranaense, and Atlantic provinces, whereas *R. bifurcatus* Champion, *R. angulatus* Coscarón, and *R. argentinensis* Coscarón (fig. 7) are endemic, respectively, to the Pacific, Amazonian, and Chaco provinces. *Rasahus brasiliensis* Coscarón (fig. 8) is widespread in the Pacific, Amazonian, Paranaense, and Atlantic provinces. *Rasahus flavovittatus* (Stål) (fig. 8) is found in the Pacific province and the north of the Amazonian province, whereas the only known locality for *R. castaneus* Coscarón (fig. 8) is from the latter area. *Rasahus guttatipennis* (Stål) (fig. 9) is found in the Pacific and Amazonian provinces. *Rasahus grandis* Fallou (fig. 9) is endemic to the Atlantic province. *Rasahus limai* Pinto (fig. 10) is widespread in the Amazonian, Chaco, Paranaense, and Atlantic provinces. *Rasahus maculipennis* (Lepelletier & Serville) (fig. 10) is widespread in the Pacific, Paranaense, and Atlantic provinces; *R. paraguayensis* Coscarón and *R. peruensis* Coscarón (fig. 10) are endemic, respectively, to the Paranaense and Amazonian provinces. *Rasahus hamatus* (Fabricius) (fig. 9), *R. rufiventris* Walker, *R. sulcicollis* (Serville), and *R. scutellaris* (Fabricius) (fig. 11) are widespread in many of the studied areas. *Rasahus surinamensis* Coscarón (fig. 11) has been found in the Amazonian and Paranaense provinces. The geographical distribution of the four remaining species of the genus lies in Central and North America.

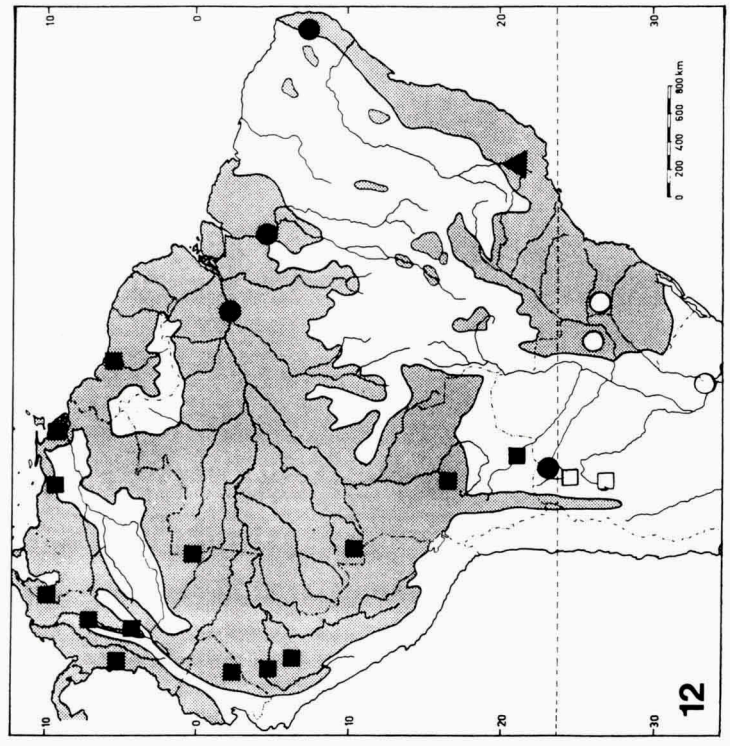
Sirthenea Spinola (Willemse, 1985). It is the only genus of Peiratinae from the Americas also distributed in the Old World. In the New World 12 species are distributed from eastern United States to central Argentina (fig. 4). *Sirthenea amazona* (fig. 12) has two subspecies: *S. amazona amazona* Spinola is distributed in the Amazonian, Chaco, and Atlantic provinces, whereas *S. amazona anduzei* Drake & Harris is widespread in the Pacific, Amazonian, and Chaco province. *Sirthenea atra* Willemse and *S. ferdinandi* Willemse (fig. 12) are endemic, respectively, to the Atlantic and Chaco provinces. *Sirthenea dubia* Willemse (fig. 12) is found in the Paranaense and Chaco provinces. *Sirthenea peruviana* Drake & Harris (fig. 13) has three subspecies: *S. peruviana peruviana* Drake & Harris is widespread in the Pacific and Amazonian provinces; and *S. peruviana gracilis* Willemse and *S. peruviana orientalis* Willemse are endemic, respectively, to the Cerrado and Amazonian provinces. *Sirthenea pedestris* Horváth (fig. 13) is widespread in the Pacific, Amazonian, Paranaense, and Atlantic provinces, and *S. ocularis* Horváth (fig. 13) is endemic to the Atlantic province. *Sirthenea stria carinata* (Fabricius) (fig. 14) is widespread in many of the studied areas, whereas *S. vittata* Distant (fig. 14) is distributed in the Pacific and northwest Amazonian province, and *S. plagiata* Horváth (fig. 14) is found in the Amazonian, Paranaense, and Atlantic provinces. The remaining species and subspecies of *Sirthenea* are distributed outside South America.

Thymbreus Stål (Coscarón, 1994). This genus has three species, all Neotropical (fig. 4). *Thymbreus crocinopterus* Stål (fig. 15) is ranged from Mexico to the northern portion of the Amazonian province, whereas *T. ocellatus* (Signoret) (fig. 15) is endemic to the Amazonian province, and *T. pyrrhopterus* (Stål) (fig. 15) occurs in the Paranaense and Atlantic provinces.

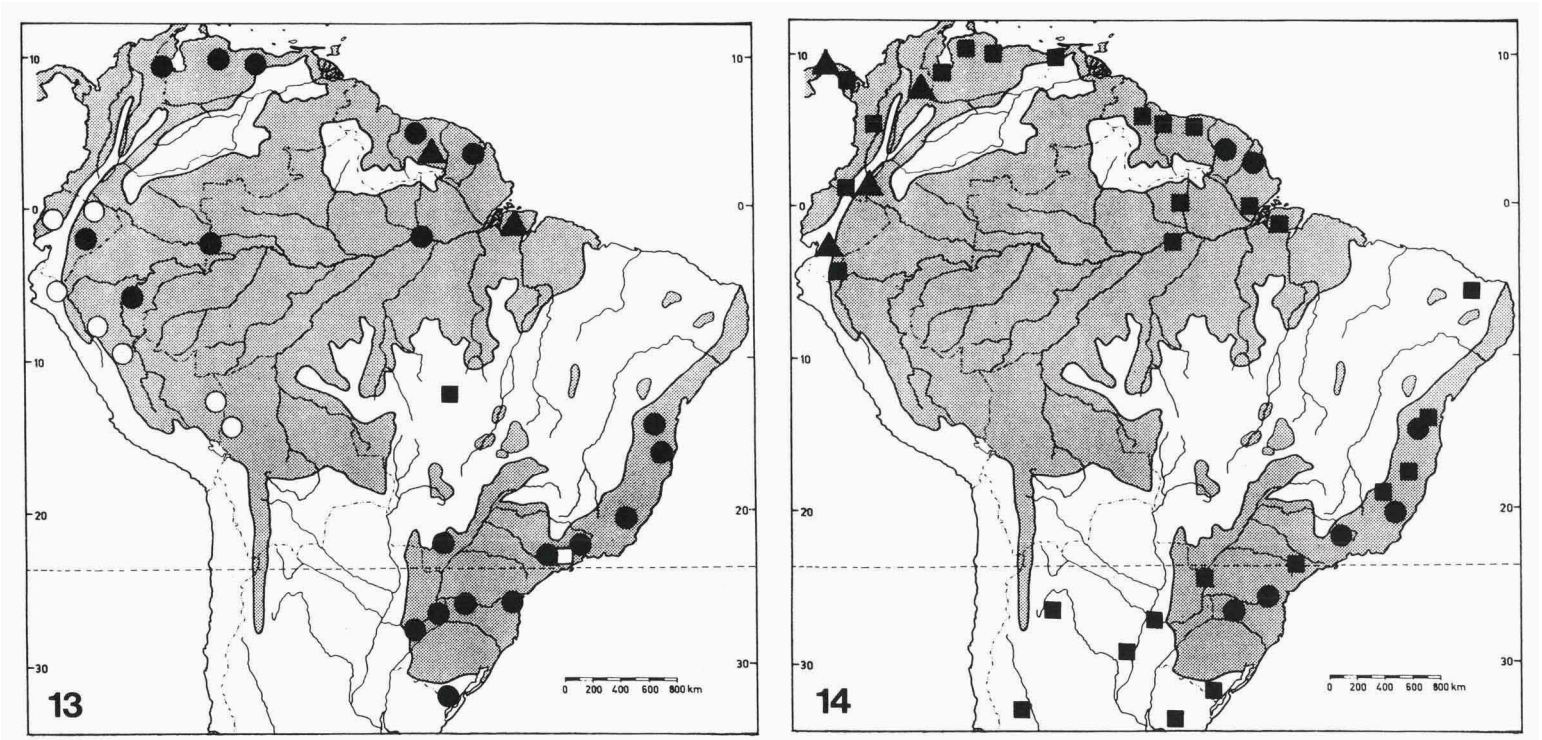
Tydides Stål (Lent, 1955; Lent & Jurberg, 1967). This Neotropical genus (fig. 3) has four species. *Tydides rufus* (Serville) (fig. 16) is widespread in many of the studied areas. *Tydides imitator* Lent (fig. 16) is distributed in the Paranaense and Atlantic



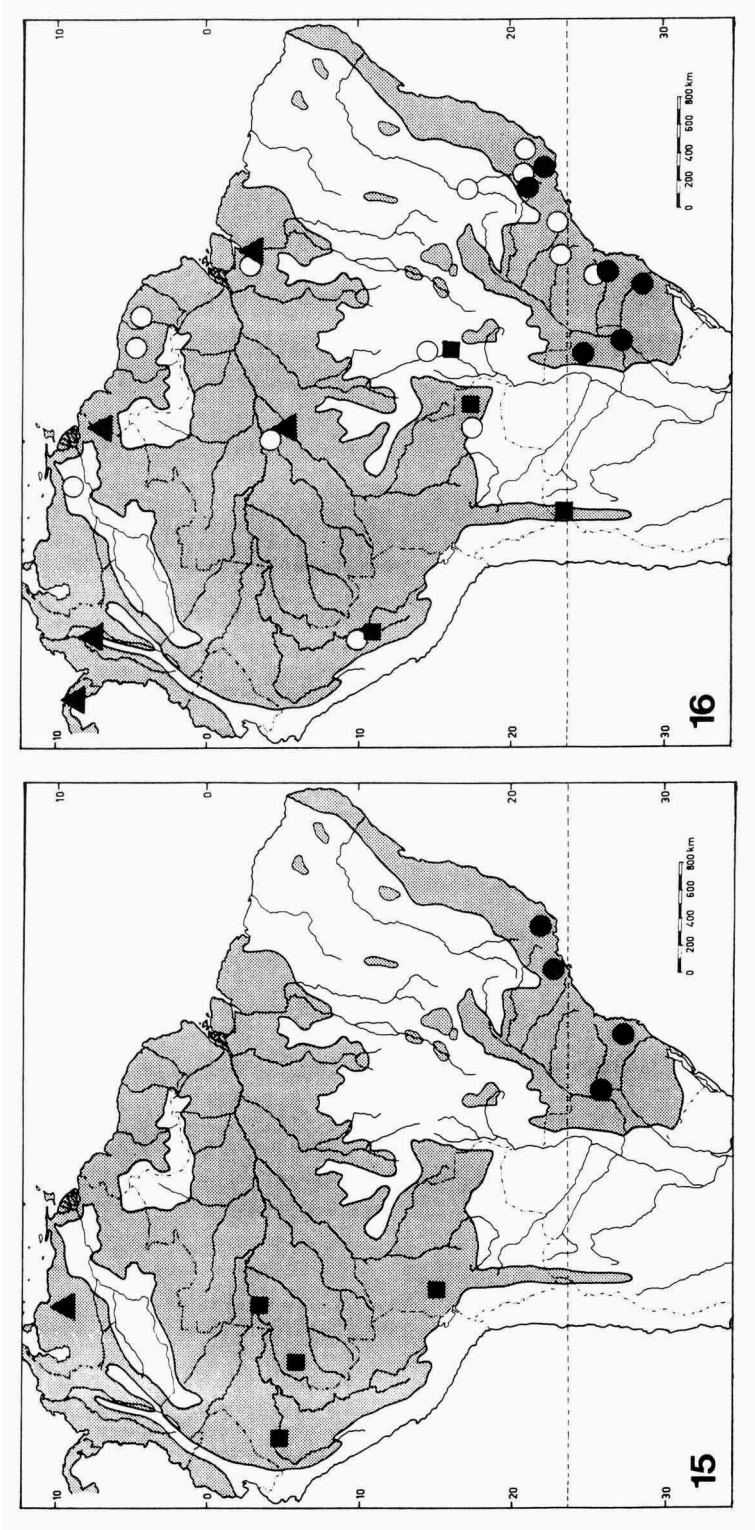
Figs. 9-10. Geographical distribution of species of Peiratinae. 9: *Rasahus hamatus* (black circles); *R. grandis* (black squares); *R. guttatipennis* (black triangles). 10: *R. limai* (black circles); *R. maculipennis* (black squares); *R. paraguayensis* (black triangles); *R. peruensis* (open circles).



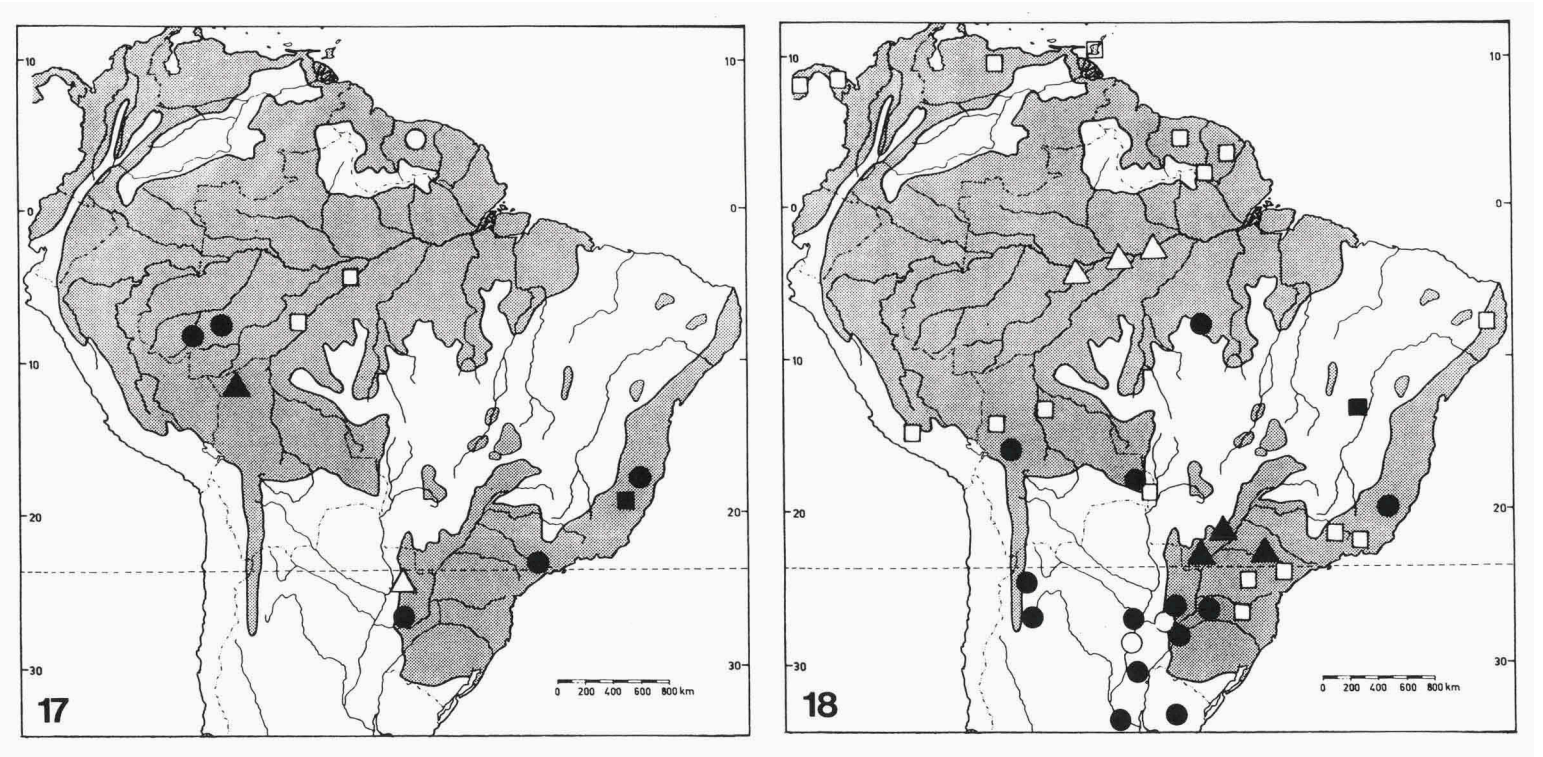
Figs. 11-12. Geographical distribution of species of Peiratinae. 11: *R. rufiventris* (black circles); *R. scutellaris* (black squares); *R. sulcicollis* (black triangles); *R. surinamensis* (open circles). 12: *Sirthenea amazona amazona* (black circles); *S. amazona anduzei* (black squares); *S. atra* (black triangle); *S. dubia* (open circles); *S. ferdinandi* (open squares).



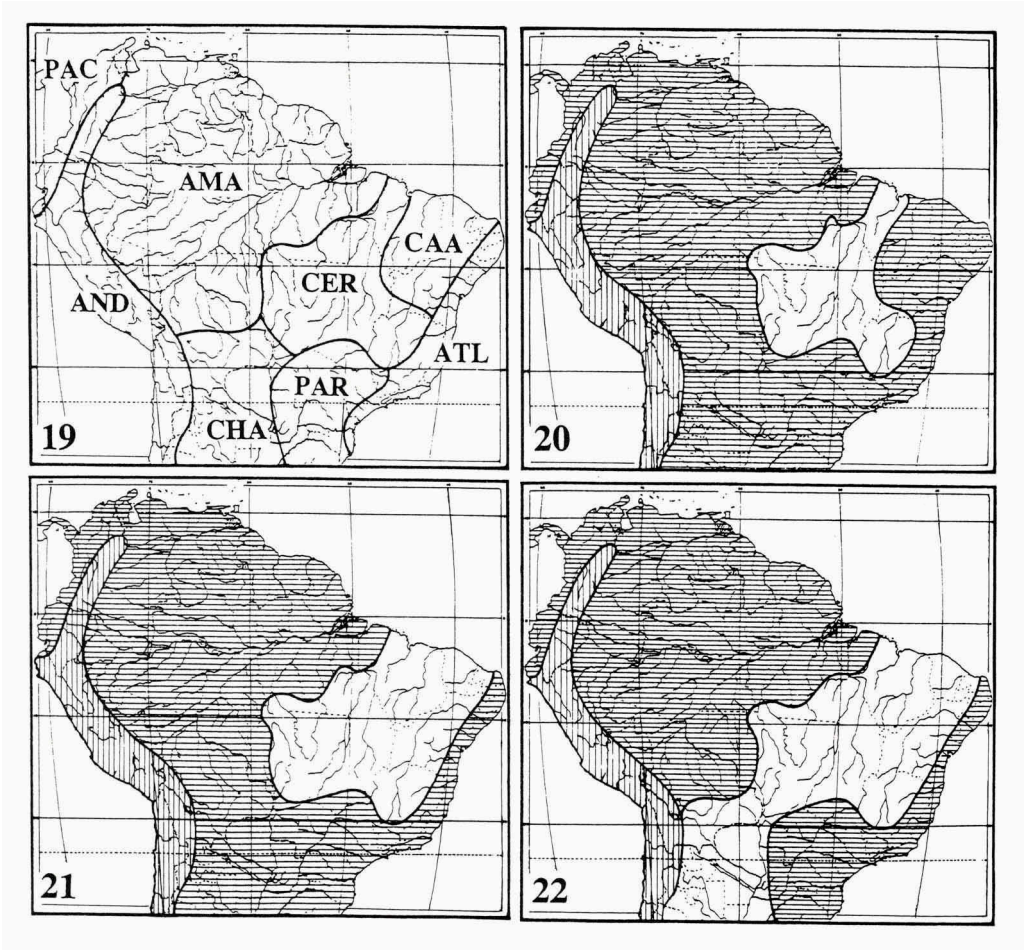
Figs. 13-14. Geographical distribution of species of Peiratinae. 13: *Sirthenea pedestris* (black circles); *S. peruviana gracilis* (black square); *S. peruviana orientalis* (black triangles); *S. peruviana peruviana* (open circles); *S. ocularis* (open square). 14: *S. plagiata* (black circles); *S. stria carinata* (black squares); *S. vittata* (black triangles).



Figs. 15-16. Geographical distribution of species of Peiratinae. 15: *Thymbreus pyrrhopterus* (black circles); *T. ocellatus* (black squares); *T. crocinopterus* (black triangle). 16: *Tydides imitator* (black circles); *T. obscurus* (black squares); *T. quator* (black triangles); *T. rufus* (open circles).



Figs. 17, 18. Geographical distribution of species of Peiratinae. 17: *Eidmannia attaphila* (black circles); *E. bahiensis* (black square); *E. beniensis* (black triangle); *E. guyanensis* (open circle); *E. matogrossensis* (open squares); *E. obscura* (open triangle). 18: *Melanolestes argentinus* (black circles); *M. goiasensis* (black square); *M. lugens* (black triangles); *M. minutus* (open circles); *M. morio* (open squares); *M. picinus* (open triangles).



Figs. 19-22. 19: Areas of the analysis. 20-22: Sequence of area-fragmentation.

provinces; *T. quator* Lent & Jurberg (fig. 16) occurs in the Pacific and Amazonian provinces; and *T. obscurus* Lent (fig. 16) occurs in the Amazonian and Cerrado.

Eidmannia Taeuber (Coscarón, 1986b). It has six species, all distributed in South America (fig. 2). *Eidmannia matogrossensis* Coscarón, *E. guyanensis* Coscarón, and *E. beniensis* Coscarón (fig. 17) are endemic to the Amazonian province, whereas *E. bahiensis* Coscarón and *E. obscura* Coscarón (fig. 17) are endemic, respectively, to the Atlantic and Paranaense provinces. *Eidmannia attaphila* Taeuber (fig. 17) is scattered in the Amazonian, Paranaense, and Atlantic provinces.

Melanolestes Stål (Coscarón & Carpintero, 1993). This Nearctic and Neotropical genus (fig. 2) has nine species. *Melanolestes morio* (Erichson) and *M. argentinus* Berg (fig. 18) are widespread in many of the studied areas. *Melanolestes picinus* Stål, *M. lugens* Coscarón & Carpintero, *M. minutus* Coscarón & Carpintero, and *M. goiasensis* Coscarón & Carpintero (fig. 18) are endemic, respectively, to the Amazonian, Paranaense, Chaco, and Caatinga provinces. The remaining three species of *Melanolestes* are Nearctic.

Parsimony analysis of endemicity

From the species distributed in the Neotropical subregion in South America, we compiled a data matrix (Table I) with those 40 species present in at least two of the areas analyzed (fig. 19). Analysis of this data matrix produced one area cladogram of 167 steps, consistency index of 0.59, and retention index of 0.57 (fig. 23). The area cladogram shows the following cladistic sequence of area fragmentation: (Cerrado, (Caatinga, (Chaco, ((Pacific, Amazonian), (Paranaense, Atlantic))))). When this sequence is superimposed to the study areas (Figs. 20-22), it shows the gradual development of the open vegetated diagonal (Chaco-Cerrado-Caatinga), which separated the former Amazonian forest in a northwestern part (Pacific plus Amazonian provinces) and a southeastern part (Paranaense plus Atlantic provinces).

Discussion

A basic distributional pattern involving two disjunct parts in the Amazonian forest, separated by a diagonal of open formations, results from the parsimony analysis of endemicity of the South American Peiratinae. This pattern is exhibited by other Neotropical taxa, namely, some genera of Bromeliaceae (Smith & Downs, 1977; Forero & Gentry, 1988); the genera *Lithacne*, *Cryptochloa*, and *Olyra* (Poaceae; Soderstrom *et al.*, 1988); *Hillia* (Rubiaceae; Taylor, 1994); the weevil genera *Airosimus* Howden (Howden, 1966) and *Entimus* Germar (Vaurie, 1952; Viana, 1958); and *Pionopsitta* (Aves: Psittacidae; Cracraft, 1988). On the other hand, Prado & Gibbs (1993) have recently emphasized the connections among the areas of the diagonal of open formations. The existence of two separate forest "blocks" have been also postulated by Fernandes & Bezerra (1990).

A number of hypotheses could be advanced to explain Neotropical patterns of distribution. From a historical perspective, an origin posterior to the break up of Gondwanaland into South America and Africa (Upper Jurassic-Lower Cretaceous)

Table I. Data matrix (taxa x areas) for the parsimony analysis. Areas: CAA= Caatinga; CER= Cerrado; CHA= Chaco; ATL= Atlantic; PAR= Paranaense; PAC= Pacific; AMA= Amazonian. Taxa: 1, *Froeschneriella vittata*; 2, *Phorastes incognitus*; 3, *P. femoratus*; 4, *Rasahus albomaculatus*; 5, *R. arcitenens*; 6, *R. arcuiger*; 7, *R. atratus*; 8, *R. brasiliensis*; 9, *R. flavovittatus*; 10, *R. hamatus*; 11, *R. guttatipennis*; 12, *R. limai*; 13, *R. maculipennis*; 14, *R. peruensis*; 15, *R. rufiventris*; 16, *R. scutellaris*; 17, *R. sulcicollis*; 18, *R. surinamensis*; 19, *Sirthenea amazona amazona*; 20, *S. amazona anduzei*; 21, *S. dubia*; 22, *S. pedestris*; 23, *S. peruviana*; 24, *S. plagiata*; 25, *S. stria carinata*; 26, *S. vittata*; 27, *Thymbreus crocinopterus*; 28, *Tydides imitator*; 29, *T. obscurus*; 30, *T. quatuor*; 31, *T. rufus*; 32, *Eidmannia attaphila*; 33, *Melanolestes argentinus*; 34, *M. morio*; 35, *Phorastes*; 36, *Rasahus*; 37, *Tydides*; 38, *Eidmannia*; 39, *Melanolestes*. 0= absent; 1= present.

	1	2	3
Taxa / Area	1234567890123456789012345678901234567890123456789		
CAA	00100000000000000000000010000000010001		
CER	00001000000100100000001000001010000110 0		
CHA	00100100010100101011110010000000111101 1		
ATL	11000101010110101010010110110011111111 1		
PAR	01100101010110001100110110010011111111 1		
PAC	11011101111010011001011011000100011111 1		
AMA	00111111111101111111011111101111111111 1		

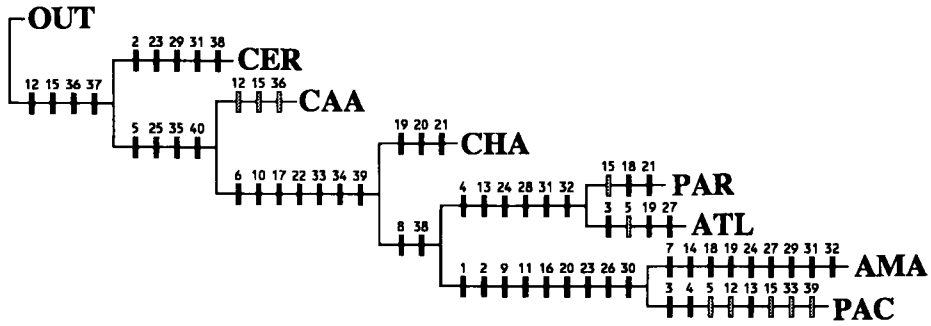


Fig. 23. Area cladogram that resulted from the parsimony analysis of endemicity.

has been hypothesized for the Amazonian forest. From Cretaceous to Eocene, this forest was widespread throughout most of northern South America, and then it began to be shrinked during Oligocene, originating the disjunction between its northwestern and southeastern parts (Vanin, 1976). A pre-Quaternary age for most Amazonian distributional patterns was postulated by Cracraft & Prum (1988) and Bush (1994), with speciation processes taking place over at least the last 25 million years. Basic disjunctions, e.g., the Amazonian-Atlantic, seem to be rather ancient and due to vicariance, mainly caused by the Andean orogeny and the formation of great rivers.

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