

HISTORICAL BIOGEOGRAPHY OF SOUTHERN SOUTH AMERICA

JORGE V. CRISCI,^{1,2} MARÍA MARTA CIGLIANO,^{1,3} JUAN J. MORRONE,^{1,3}
AND SERGIO ROIG-JUÑENT^{1,3}

¹Laboratorio de Sistemática y Biología Evolutiva (LASBE),

²División Plantas Vasculares,

³División Entomología,

Museo de La Plata, Paseo del Bosque, 1900 La Plata, Argentina

Abstract.—Historical biogeographic patterns of relationships among southern and northern South America, North America, and southern temperate areas were investigated by a cladistic biogeographic analysis of 17 taxon cladograms. Three techniques were applied: Wiley's biogeographic parsimony analysis, Nelson and Platnick's component analysis, and Humphries, Ladiges, Roos, and Zandee's quantification of component analysis. Biogeographic parsimony analysis yielded two general area cladograms (CI = 0.74). Under component analysis, six general area cladograms (two under Nelson and Platnick's assumption 1 and four under their assumption 2) were obtained through the intersection of a maximum of 10 sets of area cladograms. Quantification of component analysis produced nine cladograms (CI = 0.50) under assumption 1 and one (CI = 0.45) under assumption 2. The results support a hybrid origin of the South American biota. The northern South American biota is most closely related to that of North America, and southern South America constitutes a monophyletic group together with Australia, Tasmania, New Guinea, New Caledonia, and New Zealand, reflecting the existence of an ancient austral biota. Four conflicting hypotheses of area relationships concerning southern South America and the other austral areas are proposed, suggesting that southern South America may be a composite area in itself. [South America; cladistics; biogeography; parsimony analysis; component analysis.]

The biota of southern South America has always captivated the minds of those interested in biogeography, due to the interesting distributional patterns exhibited by representatives of its flora and fauna. For more than a century, biologists have proposed numerous theories to account for the origin and close relationships of biotas found in southern South America and other southern temperate regions, such as Australia, New Zealand, and South Africa. Many biogeographic schemes place southern South America in a different region from the rest of the South American continent (Jeannel, 1942, 1967; Monrós, 1958; Croizat, 1960; Skottsberg, 1960; Kuschel, 1964b; Rapoport, 1968; Fittkau, 1969; Takh-tajan, 1969; Cabrera and Willink, 1973; Müller, 1979). Recently, authors have postulated that South America is a continent of hybrid origin and should be divided for biogeographic studies in two areas, namely southern temperate and northern tropical areas (Humphries, 1981b; Parenti, 1981; Patterson, 1981; Humphries and Parenti, 1986).

Many contributions on southern South American biogeography focused on overall biotic similarity with other regions of the world. Most frequently, hypotheses of biotic dispersal have been proposed to account for the observed similarity (Fleming, 1964; Preest, 1964; Simpson, 1964; Darlington, 1965; Kuschel, 1969; Raven and Axelrod, 1975). The use of cladistic methodology in systematics (Hennig, 1966) and the subsequent development of cladistic or vicariance biogeography (Platnick and Nelson, 1978; Rosen, 1978; Nelson and Platnick, 1981; Humphries and Parenti, 1986) have provided an operational tool for analyzing relationships of areas. Cladistic biogeography assumes a correspondence between taxon relationships and area relationships. Comparisons between phylogenies of unrelated groups of organisms occurring in the same areas might elucidate general patterns that can be used to propose hypotheses of the historical relationships of those areas. Some controversy over the most appropriate technique for elucidating these general patterns has arisen

recently. Few attempts have been made to use cladistic biogeography to formulate hypotheses about the relationships of South America and its related areas (Humphries, 1981a, 1981b; Parenti, 1981; Patterson, 1981; Humphries and Parenti, 1986), and none of these attempts has treated southern South America as an independent unit of analysis.

The objectives of this paper are twofold: (1) to postulate hypotheses on the relationships between southern South America and its related areas and (2) to explore and compare different cladistic biogeographic methodologies. Although it may be questionable to treat large areas, such as southern South America, as a single area of endemism, biogeographic analyses at this level have proved useful in other studies (Humphries, 1981a, 1981b; Parenti, 1981; Patterson, 1981; Humphries and Parenti, 1986; Seberg, 1988; Craw, 1989).

MATERIAL AND METHODS

Choice of Areas

An approximation of a definition of southern South America may be obtained by looking at the distribution of many individual taxa, such as *Azara* (Flacourtiaceae); *Escallonia* (Escalloniaceae); *Lucilia*, *Perezia*, *Nassauvia*, and *Leucheria* (Asteraceae); Mummucidae and Daesiidae (Solifugae); Tristiridae (Orthoptera); Aucacrinae (Orthoptera: Ommexechidae); *Pompilocalus* (Hymenoptera: Pompilidae); Migadopini, Homaloderina, *Metius*, *Mimodromius*, *Feroniola*, and *Barypus* (Coleoptera: Carabidae); Faroninae (Coleoptera: Pselaphidae); Liparetrini (Coleoptera: Scarabeidae); Nyciteliini, Scotobiini, and Praocini (Coleoptera: Tenebrionidae); and Nemonychidae, Oxycorynidae, *Aegorhinus*, *Listroderes*, and *Cylydrorhinus* (Coleoptera: Curculionidae). Based on these distributions, southern South America is defined here as the area south of 30° south latitude. The Andean highlands north of 30° south latitude are also included in the area. This definition is congruent with the biogeographic schemes of Kuschel (1969) and Takhtajan (1986) and with Humphries and Parenti's

(1986) definition of southern South America.

In order to determine the geographic regions exhibiting affinities to southern South America, a nonexhaustive search of distributional patterns of several groups of plants and animals was conducted. Table 1 shows the taxa (including taxonomic placement, geographic distribution, and recent references) that suggest the selection of the areas to be included in the analysis. The selected areas were (1) southern South America (SSA), (2) northern South America (NSA), (3) Australia (AUS), (4) New Guinea (NG), (5) New Caledonia (NC), (6) Tasmania (TAS), (7) New Zealand (NZ), (8) South Africa (AF), and (9) North America (NA).

Choice of Taxa

From the taxa included in Table 1 we chose those 17, listed below, for which phylogenetic analyses were available. Their original area cladograms are presented in Figure 1. Taxa included in our study were (a) *Oxelytrum* plus *Ptomaphila* (Coleoptera: Silphidae); (b) Diamesinae (Diptera: Chironomidae); (c) Podonominae (Diptera: Chironomidae); (d) Pseudopsinae (Coleoptera: Staphylinidae); (e) *Crinodendron*, *Dubouzetia*, and *Peripentadenia* (Elaeocarpaceae); (f) Embothriinae (Proteaceae); (g) Metallicina (Coleoptera: Carabidae); (h) Siphonuridae (Ephemeroptera); (i) *Nothofagus* plus *Fagus* (Fagaceae); (j) *Cyttaria* (Cyttariaceae); (k) *Eriococcus* plus *Madarococcus* (Hemiptera: Eriococcidae); (l) *Negria* plus *Drepanthus* (Gesneriaceae); (m) *Oreomyrrhis* (Apiaceae); (n) *Drapetes* (Thymelaeaceae); (o) Nannochoristinae (Mecoptera); (p) *Drimys* (Winteraceae); and (q) *Aristotelia* (Elaeocarpaceae).

Data Analysis

Cladistic biogeographic analysis comprises two main steps: (1) constructing a fundamental area cladogram for each taxon cladogram by replacing the name of each terminal taxon with the name of the area(s) in which it occurs and (2) generating a general area cladogram based on

TABLE 1. Continued.

Taxa	Geographic distribution											Main reference	
	SSA	NSA	AUS	NG	NC	TAS	NZ	AF	NA				
Apiaceae	+		+				+						Constance, 1988
	+												Constance, 1988
	+												Constance, 1988
	+												Melville, 1981
Araliaceae	+		+				+						Rosow, 1988b
Gesneriaceae	+		+		+		+						Humphries, 1981b
Scrophulariaceae	+		+		+		+						Van Steenis, 1972
	+						+						Knox, 1964
Donatiaceae	+						+						Correa, 1984
Asteraceae	+		+			+	+						Cabrera, 1971
	+	+											Cabrera, 1971
	+												Cabrera, 1971
Juncaginaceae	+		+			+	+						Heywood, 1978
Restionaceae	+		+			+	+						Cutler, 1972
Juncaceae	+		+				+						Barros, 1969b
	+						+						Barros, 1969b
Poaceae	+		+			+	+						Nicora, 1978
	+						+						Nicora, 1978
Cyperaceae	+		+			+	+						Barros, 1969a
Iridaceae	+		+			+	+						Ravenna, 1969b
Liliaceae	+						+						Ravenna, 1969a
Corsiaceae	+						+						Correa, 1969
Annelida													
Megascotlecidae	+		+				+						Ringuelet, 1955
Araneae	+		+										Ringuelet, 1955
Agelenidae													
Archaetidae	+		+			+	+						Forster, 1964
Opiliones	+		+				+						Ringuelet, 1955
Acropsopilionidae	+						+						Ringuelet, 1961
Isopoda													
Diplopoda	+		+			+	+						Ringuelet, 1961
Sphaerotracheidae	+		+			+	+						Ringuelet, 1961

TABLE 1. Continued.

Taxa	Geographic distribution										Main reference	
	SSA	NSA	AUS	NG	NC	TAS	NZ	AF	NA			
Collembola												
<i>Delamarellina</i>	+						+					Rapoport, 1971
<i>Zealandella</i>	+						+					Rapoport, 1971
<i>Cryptopygus</i>	+		+			+		+				Rapoport, 1971
<i>Sorensia</i>	+						+					Rapoport, 1971
<i>Tomocerura</i>	+		+				+					Wise, 1964
<i>Lepidophorella</i>	+		+				+					Wise, 1964
Ephemeroptera												
*Siphonuridae	+		+				+				+	Edmunds, 1981
Isonychiidae	+		+				+					Knox, 1964
Orthoptera												
Mimnermidae	+		+		+		+					Kevan, 1982
Macropathidae	+		+			+				+		Kevan, 1982
Cylindrachetidae	+		+	+								Kevan, 1982
Hemiptera												
Aphidae	+		+				+					Schlinger, 1974
Peloriidae	+		+				+					Darlington, 1965
Eriococcidae	+		+				+					Humphries et al., 1986
Mecoptera												
*Nannochoristinae	+		+				+					Edmunds, 1981
Coleoptera												
Carabidae												
<i>Bembidion</i>	+		+				+					Darlington, 1965
<i>Broschini</i>	+		+				+					Darlington, 1965
<i>Merizodini</i>	+		+				+					Darlington, 1964
<i>Migadopini</i>	+		+				+					Darlington, 1965
* <i>Metallicina</i>	+		+				+				+	Shpeley, 1986
<i>Trechimi</i>	+		+		+		+					Darlington, 1965
<i>Plagiotelum</i>	+		+		+		+					Darlington, 1964

TABLE 1. Continued.

Taxa	Geographic distribution											Main reference		
	SSA	NSA	AUS	NG	NC	TAS	NZ	AF	NA					
Staphylinidae	+										+			Steel, 1964
*Pseudopsinae	+	+												Herman, 1975
*Oxelytrum-Ptomaphila	+	+	+											Peck and Anderson, 1985
Nemonychidae	+													Kuschel, 1959
Oxycorinidae	+													Kuschel, 1959
Belidae	+	+	+	+							+			Vanin, 1976
Belinae	+	+												Vanin, 1976
Pachyurinae	+													Kuschel, 1950
Polydrusus	+													Kuschel, 1987
Phrynixini	+				+									Kuschel, 1962
Listroderini	+													Kuschel, 1966
Araucarini	+	+			+									Kuschel, 1966
Pentarthrum	+				+									Kuschel, 1964a
Rhopalomerus	+													Kuschel, 1952
Hymenoptera														
Proctotrupidae														
Diapriidae	+													Masner, 1969
Austroserphus	+													Masner, 1969
Austropria-Coecopria	+		+											Loiácono, 1988
Gladicauda	+													Naumann, 1982
Parabetyla	+													Loiácono and Diaz, 1977
Archaeoteleia	+													Roig-Alsina, 1987
Sphictostethus	+													
Diptera														
Empididae	+													Smith, 1964
Empididae	+													Brundin, 1966
*Diamesinae	+													Brundin, 1966
*Podonominae	+													
Siphonaptera														
Rhopalopsyllidae	+													Smit, 1964
<i>Parapsyllus longicornis</i> species group														
Osteichthyes														
Galaxiidae	+													Darlington, 1965

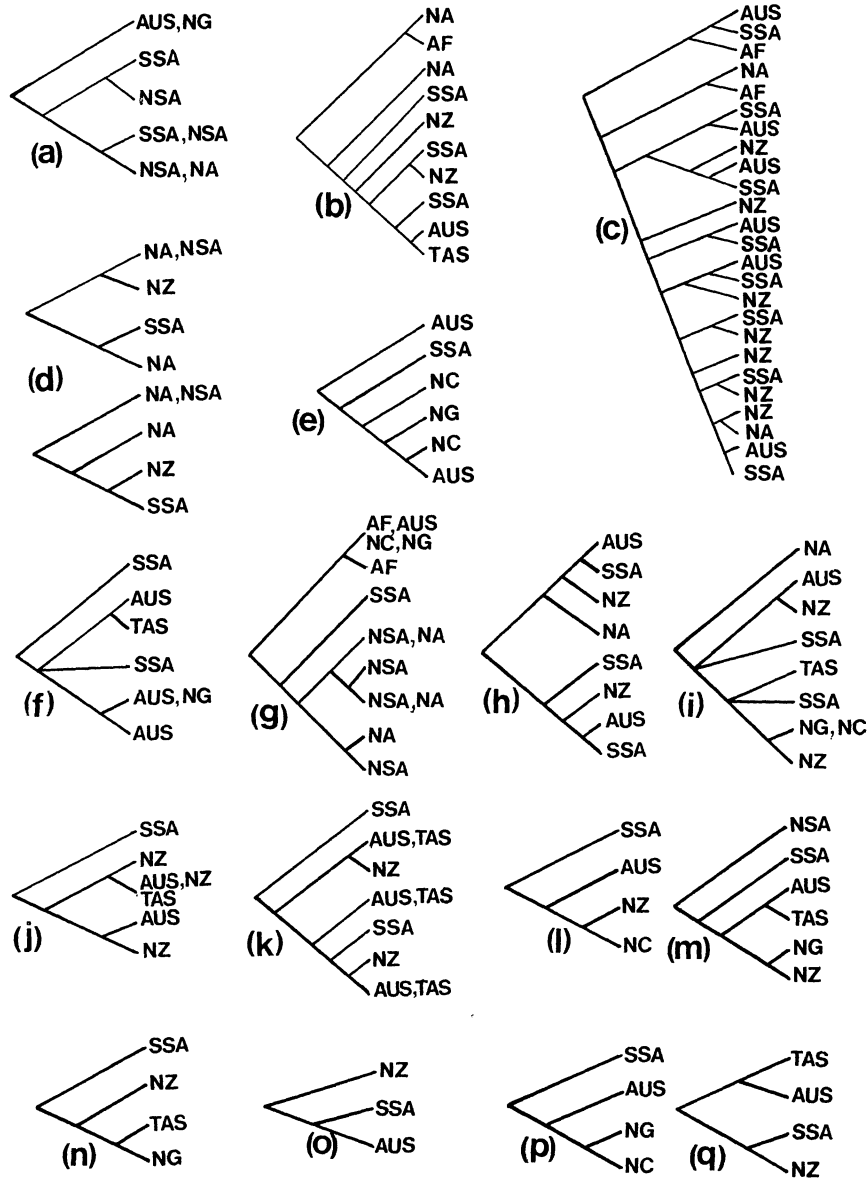


FIGURE 1. Original area cladograms derived from the 17 taxa used as input in the study. (a) *Oxelytrum-Ptomaphila* (Coleoptera: Silphidae), after Peck and Anderson (1985). (b) *Diamesinae* (Diptera: Chironomidae), after Brundin (1966). (c) *Podonominae* (Diptera: Chironomidae), after Brundin (1966). (d) *Pseudopsinae* (Coleoptera: Staphylinidae), after Herman (1975). (e) *Crinodendron-Dubouzetia-Peripentadenia* (Elaeocarpaceae), after Coode (1987). (f) *Embothriinae* (Proteaceae), after Weston and Crisp (1987). (g) *Metallicina* (Coleoptera: Carabidae), after Shpeley (1986). (h) *Siphonuridae* (Ephemeroptera), after Edmunds (1981). (i) *Nothofagus-Fagus* (Fagaceae), after Humphries et al. (1986). (j) *Cyttaria* (Cyttariaceae), after Crisci et al. (1988). (k) *Eriococcus-Madarococcus* (Hemiptera: Eriococcidae), after Humphries et al. (1986). (l) *Negria-Drepanthus* (Gesneriaceae), after Humphries (1981b). (m) *Oreomyrrhis* (Apiaceae), after Melville (1981). (n) *Drapetes* (Thymelaeaceae), after Humphries (1981b). (o) *Nannochoristinae* (Mecoptera), after Edmunds (1981). (p) *Drimys* (Winteraceae), after Humphries (1981b). (q) *Aristotelia* (Elaeocarpaceae), after Coode (1985).

the information contained in the area cladograms.

Area cladograms.—The first step of analysis is trivial if every taxon is endemic to a unique area: it consists of substituting areas for taxa. This procedure is complicated when the data have missing areas, widespread taxa, and redundant distributions (Nelson, 1984; Page, 1988, 1990). In such cases, procedures for converting taxon cladograms into area cladograms have been proposed, namely assumptions 1 and 2 (Nelson and Platnick, 1981) and assumption 0 (Wiley, 1987, 1988; Zandee and Roos, 1987).

Missing areas are treated as uninformative under the three assumptions, except under Zandee and Roos's (1987) interpretation of assumption 0, in which missing areas are treated as absent.

Areas inhabited by one widespread taxon are considered to be monophyletic (sister areas) under assumption 0. Assumption 1 treats them as mono- or paraphyletic; assumption 2 considers them as mono-, para-, or polyphyletic.

Regarding redundant distributions (areas harboring more than one taxon), assumption 0 considers that if two taxa are present in the same area, their occurrences are both valid (Wiley, 1988). Very little attention has been directed toward how assumptions 1 and 2 deal with redundant distributions. In this paper we apply the procedure implemented by Page (1989b) in his program COMPONENT, where all the occurrences of a redundant distribution are considered simultaneously valid under assumption 1, and each occurrence of a redundant distribution is considered separately under assumption 2 (Page, 1990).

General area cladograms.—The procedures designed to obtain general area cladograms are still being developed and their advantages and limitations are poorly known. Based on these reasons, three different techniques were employed herein: biogeographic parsimony analysis, based on assumption 0 (Wiley, 1987, 1988), and component analysis (Nelson and Platnick, 1981; Nelson, 1984; Humphries and Parenti, 1986) and quantification of component

analysis (Humphries et al., 1988), both based on assumptions 1 and 2.

Biogeographic parsimony analysis: Biogeographic parsimony analysis builds a data matrix (areas \times components) based on all the fundamental area cladograms. The matrix is then analyzed under a Wagner parsimony algorithm (Kluge and Farris, 1969) to obtain a general area cladogram. In this study, missing areas were coded in a neutral manner (missing state option in the HENNIG86 program). Zandee and Roos (1987) and Wiley (1988) coded terminal taxa as autapomorphies of areas; these apomorphies are uninformative with regard to area relationships, so they were not included in our data matrix. The basal component was not considered in the data matrix when it replicated an already coded component of the cladogram.

Component analysis: For each of the two groups of area cladograms independently derived under assumptions 1 and 2, the general area cladograms were obtained by intersection (Nelson, 1984; Page, 1988), which consists of finding the tree(s), if any, that is (are) shared by the sets of area cladograms obtained from each taxon cladogram. The computational problem created by the high number of cladograms generated by missing areas was handled by not including the resulting missing areas in each particular case. When more than one cladogram was obtained from a taxon cladogram (and in order to avoid a high number of illustrations in the paper), a strict consensus tree was constructed.

Quantification of component analysis: Humphries et al.'s (1988) quantification of component analysis codes the components from each area cladogram derived under assumption 1, then constructs a data matrix (areas \times components), which is analyzed under the Wagner parsimony algorithm. The same procedure is used for the area cladograms derived under assumption 2. In contrast to the method of Humphries et al. (1988), and following Page's (1989a) suggestion, we permitted only one entry of each different component for every set of area cladograms derived from the same taxon cladogram.

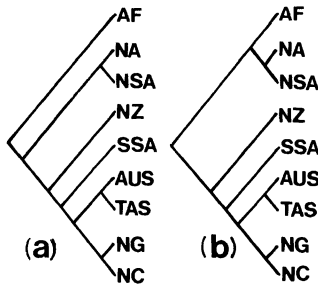


FIGURE 2. Two general area cladograms produced by biogeographic parsimony analysis.

The calculations regarding assumptions 1 and 2, intersections, and strict consensus analyses were performed using COMPONENT version 1.5 (Page, 1989b). It must be pointed out that assumption 1 as implemented in Page's program COMPONENT has differences from the approach of Nelson and Platnick (1981) to the same assumption (N. I. Platnick, pers. comm.).

Wagner parsimony analyses were performed using HENNIG86 version 1.5 (Farris, 1988), applying the implicit enumeration option for calculating trees. Every time a Wagner parsimony analysis was performed, the consistency (Kluge and Farris, 1969) and retention indices (Farris, 1989) were calculated. When the Wagner parsimony analysis yielded more than two trees, the Nelson consensus tree (Nelson, 1979) of HENNIG86 was calculated to be used as illustration.

RESULTS

Biogeographic Parsimony Analysis

Analysis of the data matrix (10 areas \times 88 components; Appendix 1) yielded two general area cladograms with a consistency index of 0.74 and a retention index of 0.62 (Fig. 2). These cladograms show North America and northern South America as sister areas; southern South America is included in a monophyletic group with Australia, Tasmania, New Guinea, and New Caledonia, with New Zealand as the sister area. North America plus northern South America either is the sister area of South Africa or is the sister area of the rest of the areas, exclusive of South Africa.

Component Analysis

Eleven out of the 17 original area cladograms showed widespread taxa and/or redundant distributions. Consequently, assumptions 1 and 2 were applied to them, producing a variable number of resolved area cladograms. Generally, more than one resolved area cladogram was obtained from each fundamental taxon cladogram, so strict consensus trees were then constructed to be used as illustrations (Fig. 3).

No general area cladogram common to the 17 sets of area cladograms derived under assumption 1 or 2 could be found by intersection. Even though not supported by the 17 sets of area cladograms, searches for a tree shared by a smaller number of sets of area cladograms were performed. As a result of this procedure, the largest number of sets able to share one or more cladograms was 10.

Under assumption 1, two general area cladograms were obtained through the intersection of the sets of area cladograms derived from the following 10 taxa: *Oreomyrrhis*, *Drimys*, *Negria-Drepanthus*, *Cyttaria*, *Nothofagus-Fagus*, *Diamesinae*, *Pseudopsinae*, *Crinodendron-Dubouzetia-Peripentadenia*, *Embothriinae*, and *Eriococcus-Madarococcus*. Both general area cladograms (Figs. 4a, b) show almost the same relationships, except for the basal branch, which may be either the pair North America-northern South America (Fig. 4a) or South Africa (Fig. 4b). In the two cladograms, northern South America is the sister area of North America, and the southern temperate areas (southern South America, Australia, Tasmania, New Zealand, New Guinea, and New Caledonia) constitute a monophyletic group where southern South America is the sister area of the remaining units.

Under assumption 2, four general area cladograms were found through the intersection of two groups of trees derived from 10 taxa each. Based on *Eriococcus-Madarococcus*, *Embothriinae*, *Diamesinae*, *Podonominae*, *Drimys*, *Oreomyrrhis*, *Pseudopsinae*, *Siphonuridae*, *Crinodendron-Dubouzetia-Peripentadenia*, and *Negria-Dre-*

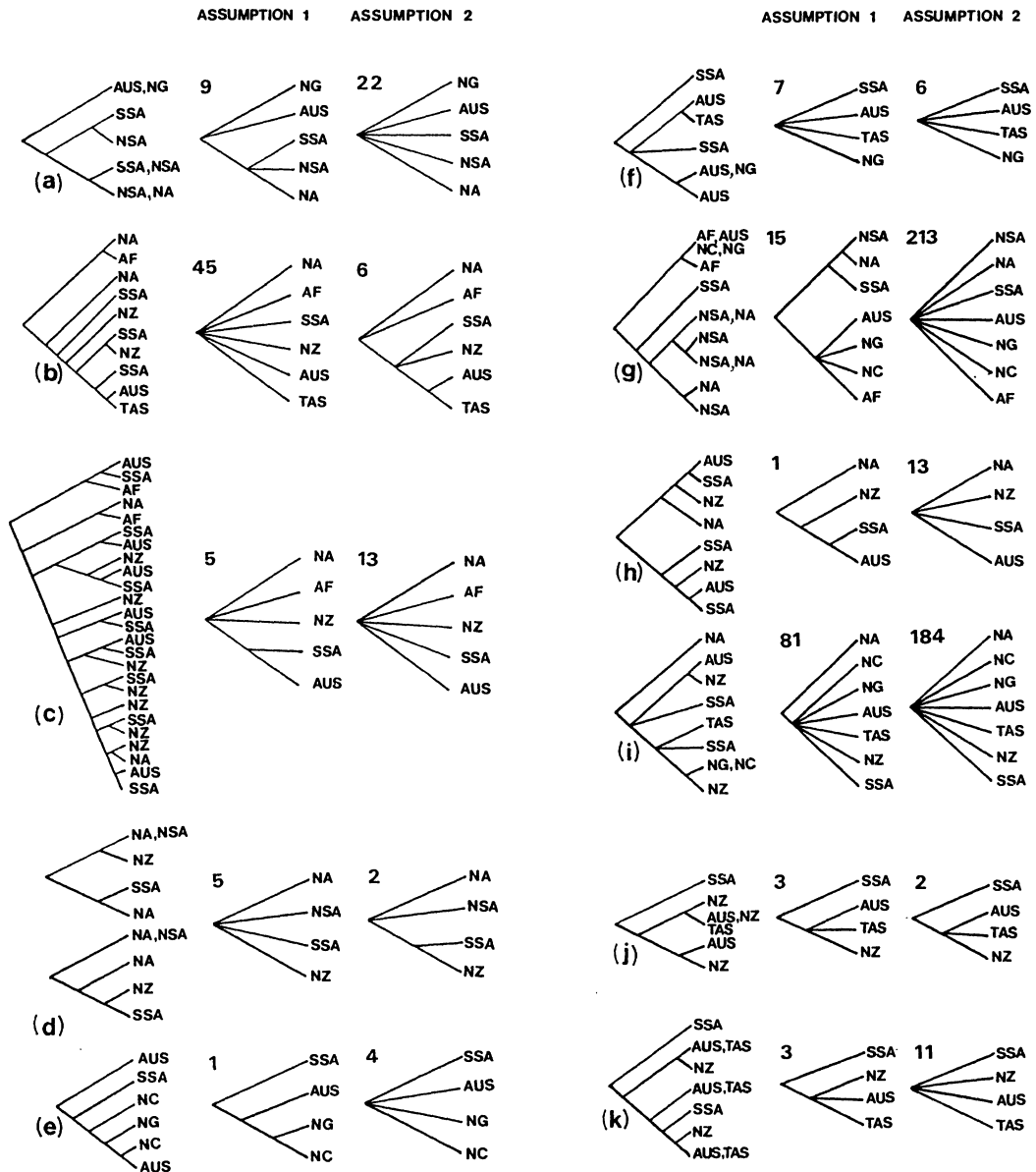


FIGURE 3. Eleven taxa (out of the 17) that presented widespread taxa and/or redundant distributions, and their resolution under assumptions 1 and 2. When more than one cladogram was produced, strict consensus trees are presented; the numbers of cladograms generated are stated to the left of them. (a) *Oxelytrum-Ptomaphila* (Coleoptera: Silphidae). (b) Diamesinae (Diptera: Chironomidae). (c) Podonominae (Diptera: Chironomidae). (d) Pseudopsinae (Coleoptera: Staphylinidae). (e) *Crinodendron-Dubouzetia-Peripentadenia* (Elaeocarpaceae). (f) Embothriinae (Proteaceae). (g) Metallicina (Coleoptera: Carabidae). (h) Siphonuridae (Ephemeroptera). (i) *Nothofagus-Fagus* (Fagaceae). (j) *Cyttaria* (Cyttariaceae). (k) *Eriococcus-Madarococcus* (Hemiptera: Eriococcidae).

panthus, two general area cladograms were obtained. One of these replicates the second general area cladogram obtained under assumption 1 (Fig. 4b); the other is con-

sistent with both general area cladograms obtained under assumption 1 (Fig. 4c). The remaining two general area cladograms (which resulted from the intersection of

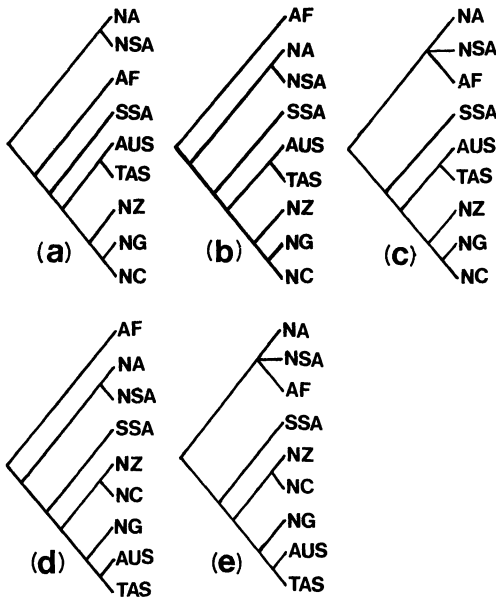


FIGURE 4. Five general area cladograms produced by component analysis. Each of them is the result of the intersection of 10 sets of area cladograms. (a) Under assumption 1. (b) Under assumptions 1 and 2. (c-e) Under assumption 2.

cladograms derived from *Eriococcus-Madarococcus*, *Embothriinae*, *Diamesinae*, *Podonominae*, *Drimys*, *Pseudopsinae*, *Siphonuridae*, *Crinodendron-Dubouzetia-Peripentadenia*, *Drapetes*, and *Nannochoristinae*) are consistent with the others obtained under assumption 2, with the exception of the placement of New Guinea (Figs. 4d, e). Both of these general area cladograms differ from the others obtained under component analysis in the interrelationships of New Zealand, New Caledonia, New Guinea, Australia, and Tasmania.

Quantification of Component Analysis

Two data matrices of areas versus components were built with the components extracted from the sets of resolved area cladograms obtained under assumption 1 or 2 (Figs. 3a-k) and from the original area cladograms that showed neither widespread taxa nor redundant distributions (Figs. 11-q).

Under assumption 1, a data matrix of 10

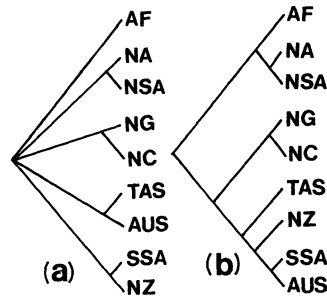


FIGURE 5. General area cladograms produced by quantification of component analysis. (a) Nelson consensus tree of the nine general cladograms obtained under assumption 1. (b) General area cladogram obtained under assumption 2.

areas \times 104 components (Appendix 2) was constructed. Parsimony analysis of this data matrix produced nine general area cladograms with a consistency index of 0.50 and a retention index of 0.39. The Nelson consensus tree (Fig. 5a) for these nine general area cladograms shows only the following pairs of sister areas: Australia-Tasmania, New Guinea-New Caledonia, southern South America-New Zealand, and northern South America-North America.

Under assumption 2, analysis of the data matrix (10 areas \times 182 components; Appendix 3) led to only one general area cladogram (Fig. 5b) with a consistency index of 0.45 and a retention index of 0.36. This cladogram shows northern South America, North America, and South Africa as a monophyletic group where the first two are sister areas. The southern temperate areas constitute a monophyletic group where southern South America is the sister area of Australia.

DISCUSSION

Although no single hypothesis of area relationships is postulated, some repeated patterns were observed, and the following conclusions can be drawn from the analysis. Southern South America and northern South America never constituted a monophyletic group; southern South America was related to the other southern temperate areas (except South Africa), whereas northern South America was al-

ways the sister area of North America or they both constituted a trichotomy with South Africa. This pattern corroborates the idea that South America is a continent of hybrid biotic origin, reflecting a separate history of southern South America from northern South America. Southern South America shares a basic component of its history with the austral regions, thus expressing the existence of an austral biota, while northern South America shows a common biotic history with North America.

Southern South America is related to the other austral areas according to four conflicting patterns: (1) southern South America is the sister area of the remaining austral areas; (2) southern South America is the sister area of the group constituted by Australia, Tasmania, New Guinea, and New Caledonia; (3) southern South America is the sister area of New Zealand; and (4) southern South America is the sister area of Australia. These incongruences in the relationships of southern South America invite an explanation.

Some biological causes—such as randomization effects of population dispersion, extinction, or phylogenetic groups representing different time frames—can be offered to explain the incongruences.

To see if past land connections can explain the conflicting patterns, we review two current theories of Earth history concerning southern South America. The Pangaea theory (Cox and Hart, 1986) considers the existence of a supercontinent (comprising all known landmasses) that split and drifted to form the current configuration of the continents. Many different explanations of the timing of the subdivision of Pangaea have been proposed. Regarding the southern continents, it was suggested that southern South America has been related to New Zealand across West Antarctica and later to Australia across East Antarctica (Tarling, 1980; Archer and Clayton, 1984). A second theory suggests the existence of a southern supercontinent, Pacifica, that split into several subcontinents that subsequently drifted in various directions across the Pacific Ocean and collided

with South America and other continental landmasses distributed around the Pacific Ocean (Nur and Ben-Avraham, 1981). Under this theory, Patagonia and part of Peru were part of Pacifica. Some biogeographers (Jeannel, 1967; Brundin, 1988) have claimed that the relationships in various groups of organisms support the Pangaea hypothesis, whereas others (Edmunds, 1981; Melville, 1981; Humphries and Parenti, 1986) have made alternative claims that relationships represented in other groups support the existence of a Pacifica continent. The multiple patterns of relationships of southern South America with the other austral areas shown in our results are consistent with both theories in a broad sense.

Congruent results are found in the literature if we compare our analysis with those where similar approaches were used, although not always including the same whole areas. Parenti (1981), commenting on the area cladograms presented by Patterson (1981), suggested that southern South America is closely related to Australia and New Guinea, whereas northern South America shows closer relationships to North America and Europe. Humphries (1981a, 1981b) presented a general area cladogram in which South America had two alternative positions, suggesting a composite origin for this continent; the relationships proposed for southern South America and the remaining austral areas are not congruent with our results. The general area cladogram presented by Schuh and Stonedahl (1986) also supports the hypothesis of a hybrid origin of South America. Craw (1989) presented three general area cladograms in which South America was always the sister area of Australia and Tasmania, and Africa was the sister area of the remaining austral areas.

Besides biological and geological causes, differences in the methodologies and assumptions applied can be invoked to explain the conflicting hypotheses postulated in our results. Biogeographic parsimony analysis (Wiley, 1987, 1988) and quantification of component analysis (Humphries et al., 1988) assume that there is a single set of interrelationships among the areas

being analyzed. Thus, the results produced by these methods are always based on the information contained in all the fundamental area cladograms. In contrast, component analysis (Nelson and Platnick, 1981) does not presuppose that the areas being analyzed will conform to a single pattern. It seeks the most parsimonious area relationships for each taxon under study, and then asks whether there are patterns of interrelationships that are repeated in many or all the taxa. In other words, component analysis investigates (rather than assumes) whether there is a single set of area interrelationships that can explain all the data (Platnick and Nelson, 1988), so the yielded results may not necessarily be based on the whole pool of data.

Moreover, the techniques differ in the application of the parsimony criterion. According to Wiley (1988), assumption 0 is the most economical explanation for the data when obtaining the fundamental area cladograms. In contrast, and according to Page (1988), application of assumptions 1 and 2 in component analysis leads to extra solutions in the construction of fundamental area cladograms that eventually allow a more parsimonious result when constructing a general area cladogram.

It must be pointed out that the application of component analysis to our data did not lead to a unified result; no common pattern of interrelationships recurs in the area cladograms derived from all the taxa. Following Platnick and Nelson's (1988) definition of component analysis, our approach to this problem was to search for patterns of interrelationships that are repeated in many of the taxa involved. The intersection of the 17 sets of area cladograms did not lead to a unified hypothesis, thus we can infer that the areas analyzed are related in more than one way. The hypotheses obtained from the 10 taxa may be telling us some of those ways.

Finally, we can conclude that southern South America shares a common history with the other austral areas, reflecting the existence of an ancient austral biota. The conflicting hypotheses of area relationships concerning southern South America

are probably due to the fact that southern South America has more than one history of area relationships.

ACKNOWLEDGMENTS

We thank Paul Berry, James Carpenter, Joel Craft, Chris Humphries, Analía Lanteri, Roderic Page, Marino Zandee, and three anonymous reviewers for comments and/or discussion on the manuscript. Steve Farris and Roderic Page generously made available copies of their software, HENNIG86 and COMPONENT, respectively. Nelly E. Vittet and Piero Marchionni assisted with the typing of the manuscript. This research was supported by grant 3966-88 from the National Geographic Society. The continued support of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina, to which the authors belong, is gratefully acknowledged.

REFERENCES

- ARCHER, M., AND G. CLAYTON (eds.). 1984. Vertebrate zoogeography and evolution in Australasia. Hesperian Press, Marrickville, Australia. 1203 pp.
- BARROS, M. 1969a. Cyperaceae. Pages 38-92 in *Flora Patagónica*, 8 part 2 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- BARROS, M. 1969b. Juncaceae. Pages 109-137 in *Flora Patagónica*, 8 part 2 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- BRUNDIN, L. Z. 1966. Transantarctic relationships and their significance as evidenced by chironomid midges. *K. Sven. Vetenskapskad. Handl.* 11:1-472.
- BRUNDIN, L. Z. 1988. Phylogenetic biogeography. Pages 343-369 in *Analytical biogeography* (A. A. Myers and P. S. Giller, eds.). Chapman and Hall, London, New York.
- CABRERA, A. L. 1971. Compositae. Pages 1-451 in *Flora Patagónica*, 8 part 8 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- CABRERA, A. L., AND A. WILLINK. 1973. *Biogeografía de América Latina*. Monografías de la O.E.A., Serie de Biología, 13. Washington, D.C. 117 pp.
- CONSTANCE, L. 1988. Umbelliferae. Pages 310-379 in *Flora Patagónica*, 8 part 5 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- COODE, M. J. E. 1985. *Aristotelia* and *Vallea*, closely related in Elaeocarpaceae. *Kew Bull.* 40:479-507.
- COODE, M. J. E. 1987. *Crinodendron*, *Dubouzetia* and *Peripentadenia*, closely related in Elaeocarpaceae. *Kew Bull.* 42:777-814.
- CORREA, M. N. 1969. Corsiaceae. Page 187 in *Flora Patagónica*, 8 part 2 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- CORREA, M. N. 1984. Donatiaceae. Pages 46-47 in *Flora Patagónica*, 8 part 4b (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- COX, A., AND R. B. HART. 1986. Plate tectonics. How it works. Blackwell, London. 392 pp.
- CRAW, R. 1989. New Zealand biogeography: A pan-biogeographic approach. *N.Z. J. Zool.* 16:527-547.
- CRESPO, S., AND R. L. PÉREZ-MOREAU. 1984. Polygo-

- naecae. Pages 60–98 in *Flora Patagónica*, 8 part 4a (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- CRISCI, J. V., I. J. GAMUNDÍ, AND M. N. CABELLO. 1988. A cladistic analysis of the genus *Cyttaria* (Fungi—Ascomycotina). *Cladistics* 4:279–290.
- CROIZAT, L. 1960. *Principia botanica*. Published by the author, Caracas. 1821 pp.
- CUTLER, D. F. 1972. Vicarious species of Restionaceae in Africa, Australia and South America. Pages 73–83 in *Taxonomy, phytogeography and evolution* (D. H. Valentine, ed.). Academic Press, London, New York.
- DARLINGTON, P. J., JR. 1964. Insects of Campbell Island. Coleoptera: Carabidae. *Pac. Insects Monogr.* 7:335–339.
- DARLINGTON, P. J., JR. 1965. Biogeography of the southern end of the world. Harvard Univ. Press, Cambridge, Massachusetts. 235 pp.
- EDMUNDS, G. F., JR. 1981. Discussion. Pages 287–297 in *Vicariance biogeography: A critique* (G. Nelson and D. E. Rosen, eds.). Columbia Univ. Press, New York.
- FARRIS, J. S. 1988. HENNIG86 reference. Version 1.5. Published by the author, Port Jefferson, New York. 18 pp.
- FARRIS, J. S. 1989. The retention index and the rescaled consistency index. *Cladistics* 5:417–419.
- FITTKAU, E. J. 1969. The fauna of South America. Pages 624–650 in *Biogeography and ecology in South America*, 2 (E. J. Fittkau, J. Illies, H. Klinge, G. H. Schwabe, and H. Sioli, eds.). Junk, The Hague. 946 pp.
- FLEMING, C. A. 1964. Paleontology and southern biogeography. Pages 369–385 in *Pacific Basin biogeography: A symposium, 1963 [1964]* (J. L. Gressitt, C. H. Lindroth, F. R. Fosberg, C. A. Fleming, and E. G. Turbott, eds.). Bishop Museum Press, Honolulu, Hawaii.
- FORSTER, R. R. 1964. The Araneae and Opiliones of the subantarctic islands of New Zealand. *Pac. Insects Monogr.* 7:58–115.
- GIUSTI, L. 1984. Chenopodiaceae. Pages 99–137 in *Flora Patagónica*, 8 part 4a (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- HAIR, J. B. 1964. Cytogeographical relationships of the southern podocarps. Pages 401–414 in *Pacific Basin biogeography: A symposium, 1963 [1964]* (J. L. Gressitt, C. H. Lindroth, F. R. Fosberg, C. A. Fleming, and E. G. Turbott, eds.). Bishop Museum Press, Honolulu, Hawaii.
- HENNIG, W. 1966. *Phylogenetic systematics*. Univ. Illinois Press, Urbana. 263 pp.
- HERMAN, L. H., JR. 1975. Revision and phylogeny of the monogeneric subfamily Pseudopsinae for the world (Staphylinidae, Coleoptera). *Bull. Am. Mus. Nat. Hist.* 155:241–318.
- HEYWOOD, V. H. (ed.). 1978. *Flowering plants of the world*. Mayflower Books, New York. 335 pp.
- HOCH, P. C. 1988. Onagraceae. Pages 267–298 in *Flora Patagónica*, 8 part 5 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- HUMPHRIES, C. J. 1981a. Biogeographical methods and the southern beeches. Pages 283–297 in *Chance, change and challenge, 2. The evolving biosphere* (P. L. Forey, ed.). British Museum (Natural History) and Cambridge Univ. Press, London.
- HUMPHRIES, C. J. 1981b. Biogeographical methods and the southern beeches (Fagaceae: *Nothofagus*). Pages 177–207 in *Advances in cladistics: Proceedings of the first meeting of the Willi Hennig Society* (V. A. Funk and D. R. Brooks, eds.). New York Botanical Garden, Bronx, New York.
- HUMPHRIES, C. J., J. M. COX, AND E. S. NIELSEN. 1986. *Nothofagus* and its parasites: A cladistic approach to coevolution. Pages 55–76 in *Coevolution and systematics* (A. R. Stone and D. L. Hawksworth, eds.). Clarendon Press, Oxford, England.
- HUMPHRIES, C. J., P. Y. LADIGES, M. ROOS, AND M. ZANDEE. 1988. Cladistic biogeography. Pages 371–404 in *Analytical biogeography: An integrated approach to the study of animal and plant distributions* (A. A. Myers and P. S. Giller, eds.). Chapman and Hall, London, New York.
- HUMPHRIES, C. J., AND L. R. PARENTI. 1986. *Cladistic biogeography*. Clarendon Press, Oxford, England. 98 pp.
- JEANNEL, R. 1942. *La genèse des faunes terrestres. Eléments de biogéographie*. Presses Universitaires de France, Paris. 513 pp.
- JEANNEL, R. 1967. *Biogéographie de l'Amérique Australe*. Pages 401–460 in *Biologie de l'Amérique Australe*, 3 (C. D. Deboutteville and E. H. Rapoport, eds.). CNRS and CONICET, Paris.
- KALKMAN, F. L. S. 1988. The phylogeny of the Rosaceae. *Bot. J. Linn. Soc.* 98:37–59.
- KEVAN, K. MCE. 1982. Orthoptera. Pages 352–383 in *Synopsis and classification of living organisms* (S. P. Parker, ed.). McGraw-Hill, New York.
- KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 18:1–32.
- KNOX, G. A. 1964. Antarctic relationships in Pacific biogeography. Pages 465–474 in *Pacific Basin biogeography: A symposium, 1963 [1964]* (J. L. Gressitt, C. H. Lindroth, F. R. Fosberg, C. A. Fleming, and E. G. Turbott, eds.). Bishop Museum Press, Honolulu, Hawaii.
- KUSCHEL, G. 1950. Nuevos Brachyderinae y Magdalininae chilenos (Coleoptera Curculionidae). *Arthropoda* 1:181–195.
- KUSCHEL, G. 1952. Los Curculionidae de la cordillera chileno-argentina (1.a parte) (aporte 13 de Coleoptera Curculionidae). *Rev. Chil. Entomol.* 2:229–279.
- KUSCHEL, G. 1959. Nemonychidae, Belidae y Oxycorinidae de la fauna chilena, con algunas consideraciones biogeográficas (Coleoptera Curculionidae, aporte 28). *Invest. Zool. Chil.* 5:229–271.
- KUSCHEL, G. 1962. The Curculionidae of Gough Island and the relationships of the weevil fauna of the Tristan da Cunha group. *Proc. Linn. Soc. Lond.*, 1960–1961 (1962) 173:69–78.
- KUSCHEL, G. 1964a. Insects of Campbell Island. Coleoptera: Curculionidae of the subantarctic islands of New Zealand. *Pac. Insects Monogr.* 7:416–493.

- KUSCHEL, G. 1964b. Problems concerning an austral region. Pages 443-449 in *Pacific Basin biogeography: A symposium, 1963 [1964]* (J. L. Gressitt, C. H. Lindroth, F. R. Fosberg, C. A. Fleming, and E. G. Turbott, eds.). Bishop Museum Press, Honolulu, Hawaii.
- KUSCHEL, G. 1966. A cossonine genus with bark-beetle habits, with remarks on relationships and biogeography (Coleoptera Curculionidae). *N.Z. J. Sci.* 9:3-29.
- KUSCHEL, G. 1969. Biogeography and ecology of South American Coleoptera. Pages 709-722 in *Biogeography and ecology in South America*, 2 (E. J. Fittkau, J. Illies, H. Klinge, G. H. Schwabe, and H. Sioli, eds.). Junk, The Hague.
- KUSCHEL, G. 1987. The subfamily Molytinae (Coleoptera: Curculionidae): General notes and descriptions of new taxa from New Zealand and Chile. *N.Z. Entomol.* 9:11-29.
- LOIÁCONO, M. S. 1988. Estudio preliminar del género *Gladicauda* Early en la República Argentina y Chile (Hymenoptera—Diapriidae). *Rev. Asoc. Cienc. Nat. Litoral* 19:39-47.
- LOIÁCONO, M. S., AND N. B. DÍAZ. 1977. Anotaciones sobre himenópteros proctotrupeoides y cinipoideos argentinos (Hymenoptera: Proctotrupeoidea, Cynipoidea). *Neotropica* 23:95-102.
- LOURTEIG, A. 1988. Zygophyllaceae. Pages 50-56 in *Flora Patagónica*, 8 part 5 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- MASNER, L. 1969. Two new genera of Diapriinae (Diapriidae, Hymenoptera) with transantarctic relationships. *Psyche* 76:311-325.
- MELVILLE, R. 1981. Vicarious plant distributions and paleogeography of the Pacific region. Pages 238-274 in *Vicariance biogeography: A critique* (G. Nelson and D. E. Rosen, eds.). Columbia Univ. Press, New York.
- MOLINA, A. M. 1988. Gunneraceae. Pages 301-304 in *Flora Patagónica*, 8 part 5 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- MONRÓS, F. 1958. Consideraciones sobre la fauna del Sur de Chile y revisión de la tribus Stenomelini (Coleoptera, Chrysomelidae). *Acta Zool. Lilloana* 15:143-153.
- MOORE, D. M. 1972. Connections between cool temperate floras, with particular references to southern South America. Pages 115-138 in *Taxonomy, phylogeography and evolution* (D. H. Valentine, ed.). Academic Press, London, New York.
- MÜLLER, P. 1979. Introducción a la zoogeografía. Blume, Barcelona. 232 pp.
- NAUMANN, I. D. 1982. Systematics of the Australian Ambositriinae (Hymenoptera: Diapriidae), with a synopsis on non-Australian genera of the subfamily. *Aust. J. Zool., Suppl. Ser.* 85:1-239.
- NELSON, G. 1979. Cladistic analysis and synthesis: Principles and definitions, with a historical note on Adanson's Familles des Plantes (1763-64). *Syst. Zool.* 28:1-21.
- NELSON, G. 1984. Cladistics and biogeography. Pages 273-293 in *Cladistics: Perspectives on the reconstruction of evolutionary history* (T. Duncan and T. F. Stuessy, eds.). Columbia Univ. Press, New York.
- NELSON, G., AND N. I. PLATNICK. 1981. Systematics and biogeography: Cladistics and vicariance. Columbia Univ. Press, New York. 567 pp.
- NICORA, E. G. 1978. Gramineae. Pages 1-563 in *Flora Patagónica*, 8 part 3 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- NUR, A., AND Z. BEN-AVRAHAM. 1981. Lost Pacifica continent: A mobilistic speculation. Pages 341-358 in *Vicariance biogeography: A critique* (G. Nelson and D. E. Rosen, eds.). Columbia Univ. Press, New York.
- PAGE, R. D. M. 1988. Quantitative cladistic biogeography: Constructing and comparing area cladograms. *Syst. Zool.* 37:254-270.
- PAGE, R. D. M. 1989a. Comments on component-compatibility in historical biogeography. *Cladistics* 5:167-182.
- PAGE, R. D. M. 1989b. COMPONENT user's manual. Release 1.5. Published by the author, Auckland, New Zealand. 106 pp.
- PAGE, R. D. M. 1990. Component analysis: A valiant failure? *Cladistics* 6:119-136.
- PARENTI, L. R. 1981. Discussion. Pages 490-497 in *Vicariance biogeography: A critique* (G. Nelson and D. E. Rosen, eds.). Columbia Univ. Press, New York.
- PATTERSON, C. 1981. Methods of paleobiogeography. Pages 446-489 in *Vicariance biogeography: A critique* (G. Nelson and D. E. Rosen, eds.). Columbia Univ. Press, New York.
- PECK, S. B., AND R. S. ANDERSON. 1985. Taxonomy, phylogeny and biogeography of the carrion beetles of Latin America (Coleoptera: Silphidae). *Quaest. Entomol.* 21:247-317.
- PLATNICK, N. I., AND G. NELSON. 1978. A method of analysis for historical biogeography. *Syst. Zool.* 27:1-16.
- PLATNICK, N. I., AND G. NELSON. 1988. Spanning-tree biogeography: Short cut, detour, or dead-end? *Syst. Zool.* 37:410-419.
- PREEST, D. S. 1964. A note on the dispersal characteristics of the seed of the New Zealand podocarps and beeches and their biogeographical significance. Pages 415-424 in *Pacific Basin biogeography: A symposium, 1963 [1964]* (J. L. Gressitt, C. H. Lindroth, F. R. Fosberg, C. A. Fleming, and E. G. Turbott, eds.). Bishop Museum Press, Honolulu, Hawaii.
- RAPOPORT, E. H. 1968. Algunos problemas biogeográficos del Nuevo Mundo con especial referencia a la Región Neotropical. Pages 54-110 in *Biologie de l'Amérique Australe*, 4 (C. D. Deboutteville and E. H. Rapoport, eds.). CNRS and CONICET, Paris.
- RAPOPORT, E. H. 1971. The geographical distribution of Neotropical and Antarctic Collembola. *Pac. Insects Monogr.* 25:99-118.
- RAVEN, P. H., AND D. I. AXELROD. 1975. History of the flora and fauna of Latin America. *Am. Sci.* 63:420-429.
- RAVENNA, P. F. 1969a. Liliaceae. Pages 138-151 in *Flora Patagónica*, 8 part 2 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.

- RAVENNA, P. F. 1969b. Iridaceae. Pages 167–186 in *Flora Patagónica*, 8 part 2 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- RINGUELET, R. A. 1955. Vinculaciones faunísticas de la zona boscosa del Nahuel Huapi y el dominio zoogeográfico Australcordillerano. *Notas Mus. La Plata*, 18, Zool. 160:81–121.
- RINGUELET, R. A. 1961. Rasgos fundamentales de la zoogeografía de la Argentina. *Physis* 63:151–170.
- ROIG-ALSINA, A. 1987. Contribución al conocimiento de los Pepsinae sudamericanos. IV. El género *Sphictostethus* Kohl (Hymen., Pompilidae). *Rev. Soc. Entomol. Argent.* 44:277–315.
- ROSEN, D. E. 1978. Vicariant patterns and historical explanation in biogeography. *Syst. Zool.* 27:159–188.
- ROSSOW, R. A. 1988a. Coriariaceae. Pages 92–95 in *Flora Patagónica*, 8 part 5 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- ROSSOW, R. A. 1988b. Araliaceae. Pages 307–309 in *Flora Patagónica*, 8 part 5 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- ROSSOW, R. A. 1988c. Cornaceae. Pages 380–381 in *Flora Patagónica*, 8 part 5 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- SÁNCHEZ, M. I. 1988. Eucryphiaceae. Pages 154–155 in *Flora Patagónica*, 8 part 5 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- SCHLINGER, E. I. 1974. Continental drift, *Nothofagus*, and some ecologically associated insects. *Annu. Rev. Entomol.* 19:323–343.
- SCHUH, R. T., AND G. M. STONEDAHL. 1986. Historical biogeography in the Indo-Pacific: A cladistic approach. *Cladistics* 2:337–355.
- SEBERG, O. 1988. Taxonomy, phylogeny, and biogeography of the genus *Oreobolus* R. Br. (Cyperaceae), with comments on the biogeography of the South Pacific continents. *Bot. J. Linn. Soc.* 96:119–195.
- SHEPELEY, D. 1986. Genera of the subtribe Metallicina and classification, reconstructed phylogeny and geographical history of the species of *Euproctinus* Leng and Mutchler (Coleoptera: Carabidae: Lebiini). *Quaest. Entomol.* 22:261–349.
- SIMPSON, G. G. 1964. Evolución y geografía: Historia de la fauna de América Latina. EUDEBA, Buenos Aires. 87 pp.
- SKOTTSBERG, C. 1960. Remarks on the plant geography of the southern cold temperate zone. *Proc. R. Soc., Ser. B, Biol. Sci.* 152:447–457.
- SLEUMER, H. 1984. Proteaceae. Pages 20–27 in *Flora Patagónica*, 8 part 4a (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- SMIT, F. G. A. M. 1964. Insects of Campbell Island. Siphonaptera. *Pac. Insects Monogr.* 7:330–334.
- SMITH, K. G. V. 1964. Insects of Campbell Island. Diptera: Empididae. *Pac. Insects Monogr.* 7:325–328.
- STEEL, W. O. 1964. Insects of Campbell Island. Coleoptera: Staphylinidae. *Pac. Insects Monogr.* 7:340–375.
- TAKHTAJAN, A. 1969. Flowering plants: Origin and dispersal. Oliver and Boyd, Edinburgh. 310 pp.
- TAKHTAJAN, A. 1986. Floristic regions of the world. Univ. California Press, Berkeley. 522 pp.
- TARLING, D. H. 1980. The geologic evolution of South America with special reference to the last 200 million years. Pages 1–41 in *Evolutionary biology of the New World monkeys and continental drift* (R. L. Ciochon and A. B. Chiarelli, eds.). Plenum Press, New York, London.
- TORTOSA, R. D. 1988. Rhamnaceae. Pages 111–122 in *Flora Patagónica*, 8 part 5 (M. N. Correa, ed.). Colección Científica del INTA, Buenos Aires.
- VANIN, S. A. 1976. Taxonomic revision of the South American Belidae (Coleoptera). *Arq. Zool. (São Paulo)* 28:1–75.
- VAN STEENIS, C. G. G. J. 1972. *Nothofagus*, key genus to plant geography. Pages 275–288 in *Taxonomy, phytogeography and evolution* (D. H. Valentine, ed.). Academic Press, London, New York.
- WESTON, P., AND M. D. CRISP. 1987. Evolution and biogeography of the waratahs. Pages 17–34 in *Waratahs: Their biology, cultivation and conservation* (J. A. Armstrong, ed.). *Austr. Nat. Bot. Gard. Occas. Publ.* 9.
- WILEY, E. O. 1987. Methods in vicariance biogeography. Pages 238–306 in *Systematics and evolution: A matter of diversity* (P. Hovenkamp, E. Gittenberger, E. Hennipman, R. De Jong, M. C. Roos, R. Sluys, and M. Zandee, eds.). Utrecht Univ., Utrecht.
- WILEY, E. O. 1988. Parsimony analysis and vicariance biogeography. *Syst. Zool.* 37:271–290.
- WISE, K. A. J. 1964. Insects of Campbell Island. Colembola. *Pac. Insects Monogr.* 7:178–207.
- ZANDEE, M., AND M. C. ROOS. 1987. Component-compatibility in historical biogeography. *Cladistics* 3:305–332.

Received 9 April 1990; accepted 28 October 1990

APPENDIX 3. Data matrix for quantification of component analysis under assumption 2 using the 17 selected taxa.

a													b				
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1
NSA	0	0	1	0	1	0	0	1	0	1	1	0	1	1	0	0	0
AUS	1	1	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1
TAS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
NG	0	0	0	0	0	1	1	1	0	0	1	1	1	0	1	0	0
NC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NZ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
AF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NA	0	1	1	1	1	0	1	1	1	1	0	1	1	1	0	0	0

c													d				e
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	0	1	1	1	1	1	0	0	1	0	1	0	0	1	1	0	0
NSA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
AUS	0	0	1	1	1	1	1	1	0	0	1	0	1	0	0	0	1
TAS	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
NC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NZ	0	1	0	0	0	1	0	1	1	1	0	0	1	1	1	0	0
AF	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
NA	1	0	0	0	1	1	1	0	0	1	0	1	1	0	1	1	0

f																	
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
NSA	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
AUS	1	0	1	0	1	1	1	1	0	0	1	1	1	1	0	0	0
TAS	0	0	0	0	1	1	1	0	1	0	1	1	0	0	1	0	1
NG	1	1	0	1	0	1	1	1	1	0	1	0	1	0	0	1	1
NC	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
NZ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

g																		
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	0	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1
NSA	1	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	0	0
AUS	0	0	1	1	1	0	0	1	0	0	0	1	1	0	1	0	0	1
TAS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NG	0	0	0	0	0	1	1	1	0	0	1	0	0	1	1	1	0	0
NC	0	0	0	0	1	0	0	0	1	1	1	0	1	0	0	1	1	0
NZ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AF	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
NA	1	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0

ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NSA	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	0	0
AUS	1	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	1	1
TAS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NG	0	1	1	0	0	0	1	1	0	0	1	0	1	1	1	0	1	0
NC	1	0	1	1	0	0	0	0	1	0	0	1	0	1	0	1	1	0
NZ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AF	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
NA	0	0	0	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0

h																		
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
NSA	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
AUS	1	1	1	1	0	0	0	1	1	1	1	0	1	1	1	0	0	0
TAS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NG	1	1	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0
NC	0	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
NZ	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
AF	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
NA	0	1	0	1	0	1	1	1	1	0	0	0	0	1	1	1	1	1

