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Biogeographic Areas and Transition Zones of Latin America and the Caribbean Islands Based on Panbiogeographic and Cladistic Analyses of the Entomofauna

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■ **Abstract** Track and cladistic biogeographic analyses based on insect taxa are used as a framework to interpret patterns of the Latin American and Caribbean entomofauna by identifying biogeographic areas on the basis of endemicity and arranging them hierarchically in a system of regions, subregions, dominions, and provinces. The Nearctic region, inhabited by Holarctic insect taxa, comprises five provinces: California, Baja California, Sonora, Mexican Plateau, and Tamaulipas. The Mexican transition zone comprises five provinces: Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Balsas Basin, and Sierra Madre del Sur. The Neotropical region, which harbors many insect taxa with close relatives in the tropical areas of the Old World, comprises four subregions: Caribbean, Amazonian, Chacoan, and Parana. The South American transition zone comprises five provinces: North Andean Paramo, Coastal Peruvian Desert, Puna, Atacama, Prepuna, and Monte. The Andean region, which harbors insect taxa with close relatives in the Austral continents, comprises three subregions: Central Chilean, Subantarctic, and Patagonian.

INTRODUCTION

Biogeography is the discipline that describes distributional patterns of specific and supraspecific groups and attempts to explain how they have come about by hypothesizing historical and ecological processes (95). In spite of the existence of two distinct subdisciplines, historical and ecological biogeography, it is evident that both historical and ecological processes should be taken into account (72, 125, 144). Reig (125) used the term coenogenesis to indicate that all evolutionary biogeographic inquiry is historical and should be understood as the development of ecological communities, not of isolated taxa.

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Insects are especially important for researchers who attempt to answer biogeographic questions and to understand properly global distributional patterns. Inadequate knowledge of their distribution, phylogeny, and high diversity, however, has impeded greatly the progress of insect biogeography (35). Researchers have made generalizations about the distribution of insect and other taxa from Latin America and the Caribbean as data have accumulated over the twentieth century (8, 31, 40, 43, 53, 89, 108, 124, 131–134, 152).

Many modern biogeographers reject dispersal as an a priori explanation, prompted by panbiogeographic theory, cladistics, and modern theory of continental drift (109). Croizat (21, 22) developed panbiogeography, a method that consists of plotting distributions of organisms on maps and connecting the localities together with lines called individual tracks (18, 98). Individual tracks for unrelated taxa are highly repetitive, and the resulting summary lines are generalized tracks, which indicate the previous existence of ancestral biotic components, subsequently fragmented by tectonic and/or climatic changes. Parsimony analysis of endemicity (PAE) (76, 140), a method that joins areas by their shared taxa and arranges them in a cladogram, is considered a quantitative implementation of panbiogeography (18, 103). Cladistic biogeography assumes that the congruence between taxon-area cladograms from different taxa inhabiting the areas under study indicates the sequence of vicariant events that fragmented them (47, 109). A cladistic biogeographic analysis comprises three basic steps: (*a*) construction of taxon-area cladograms from taxon cladograms by replacing the terminal taxa with the area(s) where they are found; (*b*) conversion of taxon-area cladograms into resolved area cladograms by resolving problems due to widespread taxa, redundant distributions, and missing areas; and (*c*) derivation of general-area cladogram(s), which represents the most logical solution for all the taxa analyzed (81, 96, 98).

Panbiogeography and cladistic biogeography have challenged traditional biogeographic systems by showing that some of the areas recognized do not represent natural units because parts of them show relationships with different areas. On the basis of a review of several panbiogeographic and cladistic biogeographic studies, a general biogeographic system was presented (94). In addition, a biogeographic scheme for Latin America and the islands of the Caribbean Basin (89), based on previous biogeographic analyses, is integrated herein into a single model of hierarchically arranged biogeographical areas, and transition zones are defined. Although the entomofauna is the basic target of this review, some key biogeographic papers dealing with other taxa are also considered.

Biotic components (90, 95) are sets of spatiotemporally integrated taxa that characterize a biogeographic area. They are historical individuals, so their unity is due to common history, and their recognition is a key element for understanding evolution. Given that they are parts of more inclusive biotic components, which in turn are parts of even more inclusive biotic components, they may be arranged into a hierarchical system of kingdoms, regions, subregions, dominions, provinces, and districts (90). They represent primary statements of biogeographic homology

(90), whose validity may be tested by cladistic biogeographic analyses or secondary statements of biogeographic homology (90), by well-corroborated geological area cladograms (96), or by correlating dates of vicariance events with molecular clocks of particular taxa (70).

Transition zones (95, 144) are located at the boundaries between biogeographic regions (Figure 1) and represent areas of biotic overlap, which are promoted by historical and ecological changes that allow the mixture of different biotic elements. In panbiogeographic analyses, transition zones are detected by the presence of nodes or areas where different generalized tracks coincide, whereas in cladistic biogeographic analyses, putative transition zones should give conflicting results because they result in sister areas with different biogeographic areas. Although transition zones may harbor a depauperate biota (24), sometimes they exhibit unusually high diversity. The Mexican transition zone (43, 64) provides such an example. From an evolutionary viewpoint, transition zones deserve special attention, because they represent areas of biotic interaction, whereas static lines do not (144).

Following is an outline of the biogeographical areas and transition zones of Latin America and the Caribbean islands, in which each area is ranked (Table 1), its boundaries specified (Figure 2), and relationships noted.

NEARCTIC REGION

The Nearctic region basically comprises the cold temperate areas of North America, i.e., Canada, the United States (excluding southern Florida), and northern Mexico (8, 24, 89, 100, 124). It belongs to the Holarctic kingdom, which corresponds to the paleocontinent of Laurasia and also includes the Palaearctic region (Europe; Asia, north of the Himalayan mountains; Africa, north of the Sahara; and Greenland) (80, 82). The entomofauna of the Nearctic region is basically Holarctic. In a cladistic biogeographic analysis of the Holarctic kingdom, including 41 insect genera or species groups (150), a basic separation between the Nearctic and Palaearctic regions due to vicariance was hypothesized. In addition, within each region, an eastern/western vicariant event occurred more recently. Continental dispersals (western Nearctic/eastern Nearctic and western Palaearctic/eastern Palaearctic) were significantly more frequent than paleocontinental (western Nearctic/eastern Palaearctic and western Palaearctic/eastern Nearctic) and disjunct (eastern Nearctic/eastern Palaearctic and western Palaearctic/western Nearctic) dispersal events.

The five Latin American provinces of the Nearctic region are in Mexico, and with the exception of the Baja California province, they extend northward into the United States (100). They have been assigned to the North American Pacific subregion (99) and have been arranged into two dominions: Californian and Continental Nearctic (104).

The Californian dominion comprises two provinces (104). The California province represents the northern portion of the Baja California peninsula, in the

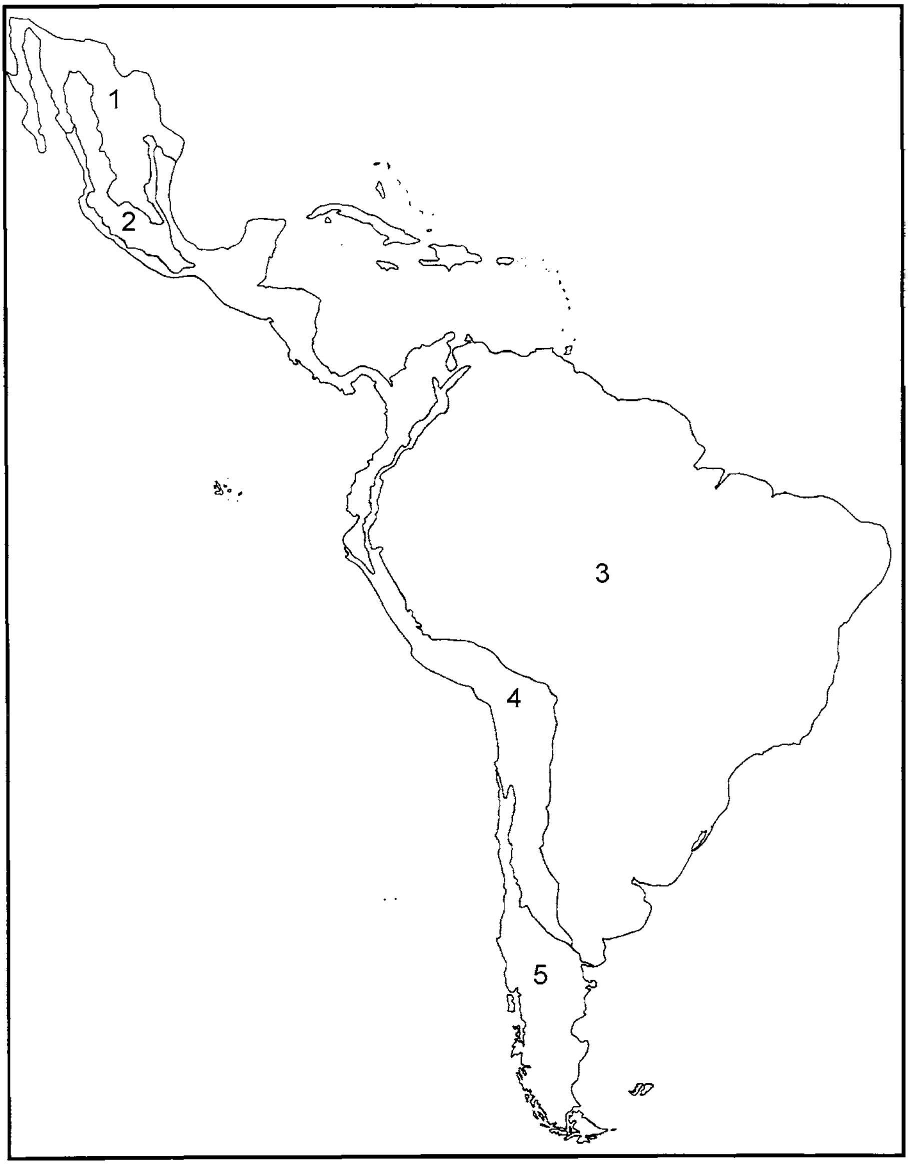

Figure 1 Biogeographic regions and transition zones of Latin America and the Caribbean islands. 1, Nearctic region; 2, Mexican transition zone; 3, Neotropical region; 4, South American transition zone; 5, Andean region.

TABLE 1 Biogeographic classification of Latin America and the Caribbean islands

Regions/transition zones	Subregions	Dominions	Provinces[a]	Selected references
Nearctic region	North American Pacific	Californian	California (1)	28, 89, 99, 100, 104
			Baja California (2)	28, 89, 99, 100, 104, 138
		Continental Nearctic	Sonora (3)	28, 89, 99, 100, 104
			Mexican Plateau (4)	28, 89, 99, 100, 104
			Tamaulipas (5)	28, 89, 99, 100, 104
Mexican transition zone			Sierra Madre Occidental (6)	28, 92, 89, 99, 100, 104
			Sierra Madre Oriental (7)	28, 92, 89, 99, 100, 104
			Transmexican Volcanic Belt (8)	28, 92, 89, 99, 100, 104
			Balsas Basin (9)	28, 89, 99, 100, 104
			Sierra Madre del Sur (10)	28, 92, 89, 99, 100, 104
Neotropical region	Caribbean	Mesoamerican	Mexican Pacific Coast (11)	28, 92, 89, 99, 100, 104
			Mexican Gulf (12)	28, 92, 89, 99, 100, 104
			Chiapas (14)	28, 92, 89, 99, 100, 104
			Eastern Central America (15)	92, 89, 100
			Western Panamanian Isthmus (16)	92, 89
		Antillean	Yucatan Peninsula (13)	6, 28, 92, 89, 99, 100, 104
			Bahama (17)	92, 89
			Cuba (18)	55, 92, 89, 143
			Cayman Islands (19)	92, 89
			Jamaica (20)	92, 89
			Hispaniola (21)	92, 89
			Puerto Rico (22)	92, 89
			Lesser Antilles (23)	92, 89

(*Continued*)

TABLE 1 (*Continued*)

Regions/transition zones	Subregions	Dominions	Provinces[a]	Selected references
		Northwestern South American	Choco (24)	92, 89
			Maracaibo (25)	92, 89
			Venezuelan Coast (26)	92, 89
			Trinidad and Tobago (27)	92, 89
			Magdalena (28)	92, 89
			Venezuelan Llanos (29)	92, 89
			Cauca (30)	92, 89
			Galapagos Islands (31)	5, 50, 58, 59, 92, 89, 115
			Western Ecuador (32)	92, 89
			Arid Ecuador (33)	92, 89
			Tumbes-Piura (34)	92, 89
	Amazonian		Napo (35)	83, 89
			Imeri (36)	83, 89
			Guyana (37)	83, 89
			Humid Guyana (38)	83, 89
			Roraima (39)	83, 89
			Amapa (40)	83, 89
			Varzea (41)	83, 89
			Ucayali (42)	83, 89
			Madeira (43)	83, 89
			Tapajos-Xingu (44)	83, 89
			Para (45)	83, 89
			Pantanal (46)	83, 89
			Yungas (47)	27, 83, 89

	Chacoan	Caatinga (48)	8, 87, 89
		Cerrado (49)	8, 83, 87, 89
		Chaco (50)	8, 83, 87, 89, 137
		Pampa (51)	8, 27, 83, 87, 89, 137
	Parana	Brazilian Atlantic Forest (53)	1, 8, 91, 89
		Parana Forest (54)	8, 91, 89
		Araucaria angustifolia Forest (55)	8, 91, 89
South American transition zone		North Andean Paramo (56)	8, 93, 89
		Coastal Peruvian Desert (57)	8, 93, 89
		Puna (58)	8, 48, 93, 89, 137
		Atacama (59)	93, 89
		Prepuna (60)	93, 89, 137
		Monte (52)	8, 83, 87, 89, 157, 163
Andean region	Central Chilean	Coquimbo (61)	87, 85, 89, 101
		Santiago (62)	85, 89, 101
	Subantarctic	Juan Fernandez Islands (63)	50, 84, 89
		Maule (64)	49, 84, 89, 137
		Valdivian Forest (65)	49, 84, 89
		Magellanic Forest (66)	49, 84, 89
		Magellanic Paramo (67)	49, 84, 89
		Malvinas Islands (68)	84, 89, 120
	Patagonian	Central Patagonia (69)	86, 89
		Subandean Patagonia (70)	86, 89

[a] Numbers in parentheses refer to provinces in Figure 2.

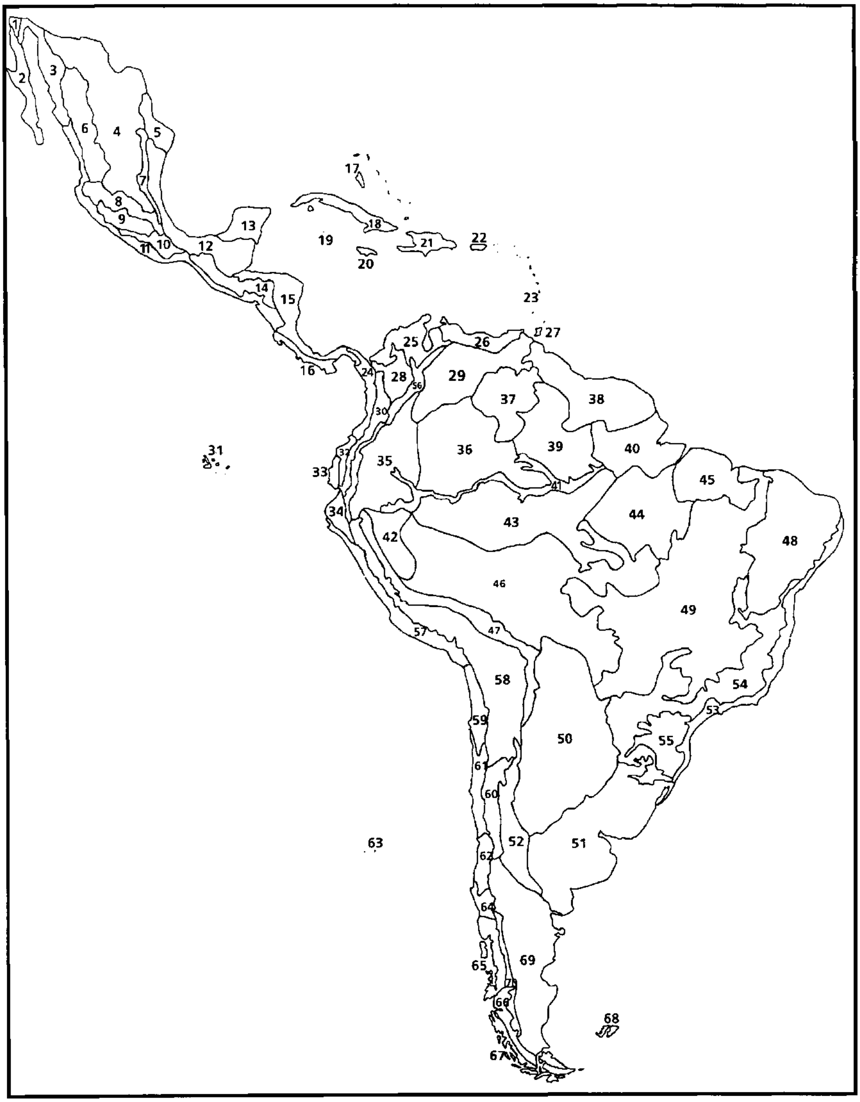

Figure 2 Biogeographic provinces of Latin America and the Caribbean islands. Numbers refer to the provinces listed in Table 1.

state of California, from the mountains of San Pedro Mártir and Juárez, extending to the north, along the Sierra Nevada, to southwestern United States (8, 10, 29, 30, 89, 99, 100, 123, 146, 147). The Baja California province represents the Baja California peninsula (29, 30, 89, 99, 100, 146, 147). Several authors have distinguished a distinct province in the southern portion of the Baja California peninsula, named the Cabo province (10, 29, 30, 99, 123), which has been combined with the Baja California province (89, 100); although it constitutes a well-defined clade, it is nested within the other areas in the Baja California peninsula (138). A PAE based on plant, insect (Coleoptera, Ephemeroptera, Hemiptera, and Lepidoptera), and bird taxa showed the close relationship between the California and Baja California provinces (99).

The Continental Nearctic dominion comprises three provinces (104). The Sonora province consists of coastal areas from northwestern Mexico, from the northeastern portion of the Baja California peninsula to the Piaxtla river in the south; it is relatively low, with plains interrupted by small mountains and dunes (29, 30, 68, 89, 99, 100, 123). The Mexican Plateau province consists of the extensive plateau in central Mexico situated between the Sierra Madre Occidental and the Sierra Madre Oriental (10, 30, 89, 100, 146, 147). Many insect species of Neotropical ancient origin, which dispersed from South America, survived and diversified on the Mexican plateau during the Eocene-Pliocene, although they disappeared from other areas (38, 57). Marshall & Liebherr (68) combine the Mexican Plateau province with most of the Sierra Madre Occidental in a single biogeographic unit. The Tamaulipas province comprises coastal areas in the northern portion of the Mexican Gulf, north of the Pánuco river in Mexico, and the adjacent portion of Texas in the United States (10, 29, 30, 89, 99, 100, 123, 146, 147). A PAE based on plant, insect (Coleoptera, Ephemeroptera, Hemiptera, and Lepidoptera), and bird taxa (99) showed the close relationship between the Sonora, Tamaulipas, and Mexican Plateau provinces.

MEXICAN TRANSITION ZONE

Halffter (37–44) defined the Mexican transition zone as a complex and varied area where Neotropical and Nearctic biotic elements overlap, which includes southwestern United States, Mexico, and a large part of Central America, extending into the Nicaraguan lowlands. The isthmus south of Lake Nicaragua, with stronger Neotropical affinities, was not included in the Mexican transition zone. Halffter (43) analyzed distributional patterns of montane scarabaeid (Coleoptera) taxa in the Mexican transition zone and categorized them as three distributional patterns, taking into consideration the distribution of their closest relatives, their species richness, the degree of species sympatry, the geological history, and the diversity of habitats occupied by the species (61, 62, 64, 126).

The Mesoamerican distributional pattern includes Neotropical taxa that evolved in situ in humid montane habitats. They have their highest species diversity in Central America, with species in the tropical and cloud forests in the mountains of Oaxaca and further north and west along the Atlantic and Pacific watersheds. They have South American affinities and are hypothesized (43) to have diversified in the Mexican transition zone earlier in the Oligocene than the taxa assigned to the other patterns.

The Paleoamerican distributional pattern includes Neotropical taxa that underwent diversification prior to the Pliocene closure of the isthmus of Tehuantepec. They are restricted to Mexican mountain areas, with ecological preferences for deserts, grasslands, and rain forests; they may also have some species in Central America. Their closest relatives are Old World temperate and tropical taxa.

The Nearctic distributional pattern includes taxa that diversified in the mountains of Mexico during the Pliocene and Pleistocene. The isthmus of Tehuantepec basically constitutes their southern limit, but these taxa may have a few species in Central America. Taxa belonging to this pattern occupy usually temperate conifer forests and grasslands found at an altitude above 1700 m. Their closest relatives are found further north, along the Rocky Mountain Cordillera and areas across the United States and Canada.

Morrone & Márquez (103) undertook a panbiogeographic analysis based on beetle (Coleoptera) taxa from the Mexican transition zone, which included representatives of Attelabidae, Carabidae, Cerambycidae, Chrysomelidae, Cleridae, Curculionidae, Elateridae, Sphindidae, Scarabaeidae, Staphylinidae, and Passalidae. They found a northern generalized track, basically comprising mountain areas (Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Balsas Basin, and Sierra Madre del Sur), and a southern generalized track (Sierra Madre de Chiapas and lowland areas in Chiapas, the Mexican Gulf, and the Mexican Pacific Coast, reaching south to the Panamanian Isthmus). The northern generalized track is the place with the highest mixture of Nearctic and Neotropical elements, which is not only latitudinal but also altitudinal, with a major Nearctic influence at higher altitudes and a higher Neotropical influence at lower altitudes. Its entomofauna is basically Neotropical, whereas vertebrates are mostly Nearctic (38). Most of the insect taxa have been assigned to the Nearctic and Paleoamerican patterns (43, 148). Owing to its mixed biota and its placement between the other regions, it represents the Mexican transition zone sensu stricto (29, 95). A study based on mammals (112) arrived at a similar transition zone. Submontane areas of this transition zone were connected by a generalized track based on species of Pieridae and Nymphalidae (Lepidoptera) (111). A cladistic biogeographic analysis based on the carabid (Coleoptera) genera *Elliptoleus* and *Calathus* (61) showed two basic clades: one comprising the Sierra Madre Occidental and the northern part of the Sierra Madre Oriental, and the other comprising the Transmexican Volcanic Belt, Sierra Madre del Sur, and the southern part of the Sierra Madre Oriental.

The Mexican transition zone comprises five provinces (95). The Sierra Madre Occidental province comprises western Mexico (the states of Chihuahua, Durango, Zacatecas, Sonora, Sinaloa, Nayarit, and Jalisco) and is at an altitude above 1000 m (10, 25, 29, 30, 43, 89, 92, 99, 100, 123, 146, 147). Marshall & Liebherr (68) combine most of this province with the Mexican plateau in a single biogeographic unit. The Sierra Madre Oriental province represents eastern Mexico (the states of San Luis Potosí, Coahuila, Hidalgo, Nuevo León, Veracruz, Puebla, and Querétaro) and is at an altitude above 1500 m (10, 25, 29, 30, 68, 89, 92, 99, 100, 123, 146, 147). A cladistic biogeographic analysis based on the carabid genera *Elliptoleus* and *Calathus* (61) showed that this province may be a composite of two portions: the northern portion related to the Sierra Madre Occidental and the southern portion related to the Sierra Madre del Sur and the Transmexican Volcanic Belt. The Transmexican Volcanic Belt province represents central Mexico (the states of Guanajuato, Mexico, Distrito Federal, Jalisco, Michoacán, Puebla, Oaxaca, Tlaxcala, and Veracruz) (10, 29, 43, 68, 89, 92, 99, 100, 123). The Balsas Basin province comprises central Mexico (the states of Guerrero, Mexico, Jalisco, Michoacán, Morelos, Oaxaca, and Puebla), is at an altitude below 2000 m, and is situated between the Transmexican Volcanic Belt and Sierra Madre del Sur provinces (25, 29, 89, 92, 99, 100, 123, 146, 147). The Sierra Madre del Sur province comprises southcentral Mexico, from southern Michoacán to Guerrero, Oaxaca, and part of Puebla, and is at an altitude above 1000 m (10, 29, 43, 68, 89, 92, 99, 100, 123). A PAE based on plant, insect, and bird taxa (99) and a panbiogeographic analysis based on species of Coleoptera (103) showed the close relationship between the Sierra Madre Occidental, Sierra Madre del Sur, Sierra Madre Oriental, Transmexican Volcanic Belt, Balsas Basin, Sonora, and Tamaulipas provinces, as well as the northern portion of the Mexican Plateau province. A cladistic biogeographic analysis based on insect, fish, reptile, and plant taxa (68) showed that the Sierra Madre del Sur, Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Balsas Basin, and Mexican Pacific Coast provinces are closely related.

NEOTROPICAL REGION

The Neotropical region comprises the tropics of the New World, i.e., most of South America, Central America, southern Mexico, the West Indies, and southern Florida (3, 8, 24, 31, 38, 82, 88, 89, 94, 124, 163). It does not include the Andean portion of South America (53, 88, 89). In the pre-Quaternary, the South American Neotropical biota expanded northward to Central America and Mexico (38, 43) and southward to the South American transition zone and the Andean region (69, 102, 131). The Neotropical region is assigned to the Holotropical kingdom, which corresponds to eastern Gondwanaland (20) and includes the tropical areas of the world between latitude 30° south and latitude 30° north, and comprises three other regions: Ethiopian or Afrotropical (central Africa, the Arabian peninsula, Madagascar, and the West Indian Ocean islands), Oriental (India, Burma, Malaysia, Indonesia, the Philippines, and the Pacific islands), and Tropical Australian (northwestern Australia) (80, 94, 124). The Neotropical entomofauna comprises several insect taxa with close relatives in the Old World tropics.

Schuh & Stonedahl (153) carried out a cladistic biogeographic analysis of some insect taxa belonging to the plant bug family Miridae (Hemiptera) to analyze the interrelationships of several areas of the Holotropical kingdom. Their general-area cladogram shows two major biotic components, Laurasia and Gondwanaland. Within the latter, a trichotomy involves the Indo-Pacific (tropical Africa plus the Oriental region), tropical America, and the southern temperate areas (South

Africa, temperate South America, and Australia). Although these authors placed the Neotropical region in an equivocal position in their general-area cladogram, they discussed its close relationship with tropical Africa. Another cladistic biogeographic analysis (4) based on several plant and animal taxa, including the dipteran families Olbiogasteridae, Anisopodidae, and Mycetobiidae, presented a general-area cladogram supporting the separation of Laurasia from Gondwanaland, with a distinction within the latter of a circumtropical and a circumantarctic component—the Holotropical and Austral kingdoms, respectively—and demonstrated the composite nature of the Neotropical region in the traditional sense. The Neotropical region comprises four subregions: Caribbean, Amazonian, Chacoan, and Parana (88, 89).

Caribbean Subregion

The Caribbean subregion extends through southern Mexico, Central America, the Antilles, and northwestern South America (8, 25, 31, 82, 89, 92, 124, 133, 146, 149). It has a complex geobiotic history (54, 68, 141, 142), which is reflected in its multiple relationships with other areas of the Neotropics, the Nearctic, and the tropics of the Old World (8, 63, 64, 141, 152). A South American–Caribbean generalized track (Greater Antilles, Lesser Antilles, and South America) and a North American–Caribbean generalized track (Greater Antilles and Central America) have been postulated (141). According to cladistic biogeographic analyses based on animal taxa, including genera and species groups of the dipteran families Ditomyiidae, Scatopsidae, and Sciaridae and of the hemipteran family Pentatomidae (2, 3), and a PAE based on anurans (139), the Caribbean subregion is hypothesized to be the sister area of the remaining Neotropical subregions. The Caribbean subregion comprises 24 provinces, which are arranged in three dominions (95): Mesoamerican, Antillean, and Northwestern South American.

The Mesoamerican dominion, in addition to Central America and the Sierra Madre de Chiapas, extends to the lowlands of the Mexican Gulf and the coast of the Pacific Ocean (95). Generalized tracks connecting the areas of this dominion have been postulated for species of Lepidoptera (111), Coleoptera (67, 103), and other plant and animal taxa (13, 99). Five provinces are assigned to this dominion (95). The Mexican Pacific Coast province comprises a narrow strip in the Pacific coast of Mexico (the states of Sinaloa, Nayarit, Colima, Jalisco, Michoacán, Guerrero, Oaxaca, and Chiapas), El Salvador, Honduras, Nicaragua, Costa Rica, and Guatemala (10, 29, 89, 92, 99, 100, 146, 147), including also the archipelago of the Revillagigedo Islands, situated 350 km from the continent (89, 92). The Mexican Gulf province comprises the coast of the Gulf of Mexico, in eastern Mexico, Belize, and northern Guatemala (6, 10, 29, 30, 92, 89, 99, 100, 146, 147). The Chiapas province comprises southern Mexico, Guatemala, Honduras, El Salvador, and Nicaragua and also the Sierra Madre de Chiapas, which range in altitude from 500 to 2000 m (6, 10, 29, 68, 89, 92, 100, 108, 123, 145). Marshall & Liebherr (68) combine the Chiapas and Yucatan Peninsula provinces in a single province.

The Eastern Central America province corresponds to eastern Central America, from Guatemala to Panama (89, 92). The Western Panamanian Isthmus province corresponds to western Central America, from Costa Rica to western Panama (25, 68, 89, 92, 108, 145). A panbiogeographic analysis of the species of *Bombus* (Hymenoptera: Apidae) (1) has shown two smaller generalized tracks, one in the Mexican coast of the Pacific Ocean and the other in Central America, that overlap in a node in the Isthmus of Tehuantepec.

The Antillean dominion extends to areas of the Caribbean Basin and comprises eight provinces (95). The Yucatan Peninsula province consists of the Yucatan peninsula (the states of Campeche, Yucatan, and Quintana Roo) and is at an altitude below 200 m (6, 89, 92, 100, 108, 145–147). The Bahama province corresponds to the archipelago of the Bahamas (25, 89, 92). The Cuba province consists of the island of Cuba (25, 89, 92). The Cayman Islands province comprises the archipelago of the Grand Cayman, Little Cayman, and Cayman Brac islands (25, 89, 92). The Jamaica province consists of the island of Jamaica (25, 89, 92). The Hispaniola province consists of the island of Hispaniola (Dominican Republic and Haiti) (25, 89, 92). The Puerto Rico province consists of the island of Puerto Rico (25, 89, 92). The genus *Barylaus* (Coleoptera: Carabidae), with one species from Hispaniola and another from Puerto Rico, is cladistically more closely related to Old World taxa rather than to Central American taxa, emphasizing the isolation of these provinces, especially when upland taxa are considered (60). The Lesser Antilles province comprises the archipelagos of the Lesser Antilles and Virgin Islands (25, 89, 92). A cladistic biogeographic analysis based on vertebrate, crustacean, insect (Coleoptera and Trichoptera), and arachnid taxa (23) showed the close relationship between the Cuba, Hispaniola, and Puerto Rico provinces.

The Northwestern South American dominion comprises 11 provinces (95). The Choco province comprises the Pacific coast of northern Ecuador, Colombia, and Panama (16, 25, 89, 92, 108, 132, 133). The Maracaibo province comprises northern Colombia and northwestern Venezuela (82, 89, 92, 132). The Venezuelan Coast province comprises northern Venezuela and Colombia (25, 89, 92, 108, 132). The Trinidad and Tobago province comprises the islands of Trinidad and Tobago (25, 89, 92, 132). The Magdalena province comprises western Venezuela and northwestern Colombia (25, 89, 92, 108, 132). The Venezuelan Llanos province comprises the plains of a great part of Venezuela and northwestern Colombia (8, 25, 31, 89, 92, 133). The Cauca province comprises western Colombia and Ecuador (25, 89, 92, 108). The Western Ecuador province comprises western Ecuador and southwestern Colombia (25, 89, 92). The Arid Ecuador province comprises western Ecuador (25, 89, 92, 133). The Tumbes-Piura province comprises southern Ecuador and northern Peru (25, 89, 92, 108, 132). The Galapagos Islands province comprises the archipelago of Colón, in the Pacific Ocean, 950 km west of the coast of Ecuador (8, 25, 50, 82, 89, 92, 108, 133). Several authors have suggested that the Galapagos biota is basically Neotropical (50), with Caribbean and Central and South American biotic elements (8, 115); for example, from the cladogram of *Galapaganus*, a weevil genus from the Galapagos Islands and coastal Peru and

Ecuador, Lanteri (58, 59) inferred two or three dispersal events from the South American continent to the islands. Panbiogeographic analyses (18, 34) have shown that the Galapagos archipelago constitutes a panbiogeographic node, where three generalized tracks intersect, connecting these islands with the Pacific coast of North America, with the Antilles, and with the Pacific coast of Ecuador. This node is associated with the tectonic placement of the islands near the union of the Nazca, Cocos, and Pacific plates and the Panama fracture zone, raising the possibility that the original Galapagos biota inhabited an island arc in the eastern Pacific. Other evidence corroborating this hypothesis is that iguanas (162) and weevils (154) from the islands seem much older than the oldest island, which is four million years old.

Amazonian Subregion

The Amazonian is the largest subregion of the Neotropical region, extending to Brazil, the Guyanas, Venezuela, Colombia, Ecuador, Peru, Bolivia, Paraguay, and Argentina (8, 31, 83, 89, 97, 124, 133, 132, 163). The first explanation for Amazonian distributional patterns was provided by Wallace (161), who considered the rivers from the Amazonian basin to act as barriers to dispersal. An alternative explanation, the refuge theory, postulated that the forest was fragmented through Pleistocene climatic changes, which resulted in an archipelago of patches or refuges (36). Colinvaux (12), however, postulated that these climatic changes were not arid enough to fragment the forest and that vicariance was caused by the formation of islands in elevated areas. Other authors (17, 21, 22, 114) postulated more ancient, pre-Quaternary changes to explain patterns of distribution of several Amazonian taxa. Another explanation is the "Amazonian lake" hypothesis (33), which postulates that during the Pleistocene/early Holocene a lake existed that fragmented the Amazonian forest.

Thirteen provinces are assigned to the Amazonian subregion (83, 89). The Napo province comprises northern Peru, southwestern Colombia, and eastern Ecuador (16, 25, 83, 89, 108). The Imeri province comprises southern Venezuela, southwestern Colombia, northeastern Peru, and northern Brazil (16, 25, 83, 89, 133, 139, 155). The Guyana province comprises northwestern South America, in the Guyanan Shield, between Venezuela, Colombia, Guyana, Surinam, and northern Brazil, where there are sandy plateaus known as tepuis that are at an altitude of higher than 2000 m (8, 25, 82, 83, 89, 108); it has been separated from the remaining Amazonian provinces in a distinct dominion (8), but its relationships with them are strong (14, 108). The Humid Guyana province comprises southwestern Venezuela, northern Brazil, Surinam, and Guyana (82, 83, 89, 108, 132, 133). The Roraima province comprises northern Brazil, southeastern Venezuela, Surinam, and Guyana (25, 82, 83, 89, 108). The Amapa province comprises Surinam and northeastern Brazil (25, 82, 83, 89). The Varzea province comprises northwestern Brazil and northwestern Peru (25, 82, 83, 89). The Ucayali province comprises eastern Peru, northern Bolivia, and western Brazil (25, 82, 83, 89).

The Madeira province comprises northwestern Brazil, bordered to the north by the Amazon river, to the west by the Madeira and Beni rivers, to the east by the Xingu river, and to the west by the Oriental Cordillera of Bolivia (25, 82, 83, 89, 108, 133, 139, 155). The Tapajos-Xingu province comprises northwestern Brazil (25, 83, 89, 133). The Para province comprises northwestern Brazil, bordered to the north and west by the Tocantins and Araguaia rivers, to the south by the Serra do Gurupi and the Grajau river, and to the east by the Guana river (25, 82, 83, 89, 108, 133, 139, 155). The Pantanal province comprises southern and central Brazil, northwestern Bolivia, and northern Paraguay (25, 82, 83, 89, 132, 133, 139, 155). The Yungas province consists of the western slopes of the Andes, from northern Peru to northwestern Argentina, at an altitude ranging from 300 to 3500 m (8, 25, 82, 83, 89, 108, 133, 163). Several PAE and cladistic biogeographic analyses have reconstructed the relationships among Amazonian provinces (2, 17, 45, 114, 122, 139, 155), but there is little agreement among the alternative hypotheses.

Chacoan Subregion

The Chacoan subregion occupies northern and central Argentina, southern Bolivia, western and central Paraguay, Uruguay, and central and northeastern Brazil (8, 31, 82, 87, 97, 134, 163). Evidence of a "savanna corridor" or "diagonal of open formations" (121) led to the hypothesis that the Cerrado province, formerly assigned to the Amazonian domain, connected the Caatinga with the other Chacoan provinces (82, 87, 89). The Chacoan subregion is closely related to the Amazonian and Parana subregions. The development of the Chacoan subregion during the Tertiary split the formerly continuous Amazonian-Parana forest, representing an example of dynamic vicariance (164). Certain insect taxa show the Amazonian-Parana disjunction (2), whereas others, which probably evolved later, are found in both the Chacoan and Parana subregions, namely the weevil genus *Cyrtomon* (56). A phylogeographic analysis of small mammal species (15) showed that the central Brazil gallery and dry forests play an important role as present and past habitats for forest species from the Amazonian and Parana subregions. Populations of Chacoan mammals have their closest relatives in either the Amazonian subregion or in the Parana subregion, or they are basal to both subregions.

Four provinces are assigned to the Chacoan subregion (87, 89). The Caatinga province comprises northeastern Brazil (the states of Bahia, Sergipe, Alagoas, Pernambuco, Paraiba, Rio Grande do Norte, Ceara, Piaui, and Minas Gerais) (8, 25, 87, 89, 97, 108, 133, 134). The Cerrado province comprises southcentral Brazil (the states of Minas Gerais, Mato Grosso, Goias, São Paulo, Parana, Maranhao, and Piaui), northeastern Paraguay, and Bolivia (8, 25, 82, 87, 89, 97, 108, 133). The Chaco province comprises southern Bolivia, western Paraguay, southern Brazil, and northcentral Argentina (8, 25, 87, 89, 108, 121, 133, 163); a cladistic biogeographic analysis based on beetle (Curculionidae) and plant taxa (73) showed that it is related to the Monte province. The Pampa province comprises central western

Argentina between latitudes 30 and 39° south, Uruguay, and south of the Brazilian state of Rio Grande do Sul (8, 25, 82, 87, 89, 131, 133, 163). It is related to the Chaco and Monte provinces, comprising a biotic impoverishment from the Chaco to the Pampa, although Amazonian, Patagonian, and Subantarctic biotic elements have also been postulated (127, 128).

Parana Subregion

The Parana subregion is situated in northeastern Argentina, eastern Paraguay, and southern and eastern Brazil (8, 82, 89, 91, 133, 163). In addition to its relationships with the other Neotropical subregions, several authors have discussed its relationships with the Subantarctic subregion (49, 69, 102, 160). Paleontological, paleoclimatological, and geological evidence indicates that a temperate climate prevailed in southern South America during the Tertiary, allowing the existence of a continuous cloud forest that extended further south than today. Cooling and aridification began in the Oligocene and Miocene, and later the forest fragmented simultaneously with the climatic changes induced by the uplift of the Andes and the expansion of the Chacoan biota (53). The disjunct distributions of the weevil families Belidae (160) and Nemonychidae (54) in the Subantarctic and Parana subregions support this relationship. A PAE based on species of anurans (139) showed the close relationship between the Parana and Amazonian subregions.

The Parana subregion comprises three provinces (89, 91). The Brazilian Atlantic Forest province consists of a narrow strip along the Brazilian Atlantic coast east of the coastal cordillera, between latitudes 7 and 32° south (8, 25, 82, 89, 91, 97, 108, 133). The Parana Forest province comprises southeastern Brazil, northeastern Argentina, and eastern Paraguay (8, 25, 91). The *Araucaria angustifolia* Forest province comprises southern Brazil and northeastern Argentina and is at an altitude between 600 and 1800 m (8, 25, 82, 91, 97, 108). Using a PAE based on the family Reduviidae, Morrone & Coscarón (97) showed the close relationship between the Brazilian Atlantic Forest and Parana provinces.

SOUTH AMERICAN TRANSITION ZONE

The South American transition zone, formerly treated as the Paramo Punan subregion of the Andean region (75, 80, 89, 93), extends along the highlands of the Andes between western Venezuela, northern Chile, and westcentral Argentina (95). A similar transition zone was postulated for mammal species (144). The Prepuna, Coastal Peruvian Desert, and Monte provinces, previously assigned to the Neotropical region, are assigned to this transition zone because of their close biotic links with the Puna and North Andean Paramo (32, 95, 107, 117, 157). Owing to the preeminence given to some tropical elements, Cabrera & Willink (8) assigned the North Andean Paramo to the Neotropical region; its close relationships with other Paramo Punan provinces (32, 134) led other authors (75, 77, 80, 117) to place it in the Andean region. The entomofauna of the South American transition zone shows an overlap of Neotropical and Andean insect taxa.

Six provinces are assigned to the South American transition zone (89, 93). The North Andean Paramo province comprises the high cordilleras of Venezuela, Colombia, Ecuador, and Peru, and is at an altitude above 3000 m (8, 25, 31, 75, 80, 89, 93, 108, 117, 132–134). A characteristic entomofauna, known as frailejones (158), is found on the giant rosette Espeletiinae (Asteraceae). The Puna province comprises eastern Bolivia, northern Argentina and Chile, and southern Peru (8, 25, 75, 82, 89, 93, 108, 116, 117, 133, 163). Panbiogeographic, PAE, and cladistic biogeographic analyses based on insect and plant taxa (75, 77, 117) showed that the North Andean Paramo province is closely related to the Puna province. The Coastal Peruvian Desert province consists of a narrow strip along the Pacific Ocean coast, from northern Peru to northern Chile (8, 25, 82, 89, 93, 108, 133, 134). The Atacama province comprises northern Chile, between latitudes 18 and 28° south (8, 25, 82, 89, 93, 108, 110, 116, 133); its entomofauna is related to the entomofauna of the Coquimbo province of the Central Chilean subregion (110). The Prepuna province comprises central and northwestern Argentina (8, 25, 82, 89, 93). The Monte province comprises central Argentina, between latitudes 24 and 43° south (8, 87, 89, 108, 133, 135, 136, 157, 163); its entomofauna is basically of Chacoan origin, although some elements are Patagonian, Prepunan, and Subantarctic (27, 66, 136, 137, 163). It has been suggested that the Monte represents an "impoverished" Chaco (163); a cladistic biogeographic analysis based on beetle and plant taxa (73) showed that these provinces are related. In addition, the Monte province shows biotic similarities to the Sonora province of the Nearctic region (11, 163). Several hypotheses postulated to explain these similarities have been reviewed by Solbrig et al. (156), who concluded that they originated by parallel evolution, owing to adaptations to arid environments from common or closely related mesic ancestors. For example, bruchids (Coleoptera) associated with fabaceous shrubs in both areas belong to different genera, with the exception of three that are widely distributed in the Americas (157), and the same occurs with the weevil *Sibinia sulcifer* (Curculionidae) (11).

ANDEAN REGION

The Andean region extends to central Chile and Patagonia (66, 95). Many species of Orthoptera, Coleoptera, Diptera, Hymenoptera, and Lepidoptera are common to this region and the South American transition zone (88, 89). Most of the Andean biota originally evolved in Patagonia and then gradually spread northward into the South American transition zone during the Tertiary and Pleistocene, with the conversion of the tropical forests in temperate and arid communities (53, 75, 124). The Andean region is included in the Austral kingdom, which corresponds to western Gondwanaland (20) and comprises five other regions: Antarctic (Antarctica), Cape or Afrotemperate (South Africa), Neoguinean (New Guinea and New Caledonia), Temperate Australian (southeastern Australia), and Neozelandic (New Zealand) (80, 94). Several insect taxa are distributed in the Austral kingdom (7, 124). The weevil tribe Araucariini illustrates an Austral distributional pattern (52).

Brundin (7) documented the relationships among the Austral continents in his phylogenetic analysis of some Chironomidae (Diptera) from New Zealand, Australia, Patagonia, and South Africa. Edmunds (26) corroborated these connections on the basis of phylogenetic evidence from mayflies (Ephemeroptera). More recent biogeographic studies searched for congruence between distributional patterns of insects and other animal and plant taxa. Two cladistic biogeographic analyses based on plant, fungal, and animal taxa, including Coleoptera, Diptera, Ephemeroptera, Hemiptera, and Mecoptera (19, 151), showed that South America is a composite area because southern South America is more closely related to the southern temperate areas that correspond to the Austral kingdom, whereas tropical South America is more closely related to Africa and North America. Other cladistic and panbiogeographic studies (18, 48, 65, 78, 113) also support the hypothesis that South America is a composite area, with the Andean region closely related to the southern temperate areas and the Neotropical region closely related to the Old World tropics. Other authors have addressed the dual nature of South America (20, 51, 53). The Andean region comprises the Central Chilean, Subantarctic, and Patagonian subregions (95).

Central Chilean Subregion

The Central Chilean subregion extends to central Chile, between latitudes 30 and 34° south (8, 25, 31, 75, 80, 82, 85, 89, 101, 117, 132–134, 163). PAE and cladistic biogeographic analyses based on extant arthropod and plant taxa (9, 66, 75, 77, 101, 118, 119), as well as fossil evidence (159), showed that this subregion is closely related to the Subantarctic subregion. The close relationship between the Central Chilean subregion and the northern part of the Subantarctic subregion (Maule and Valdivian Forest provinces) may have resulted from dispersal rather than vicariance, according to a cladistic biogeographic analysis based on weevil taxa (119).

Two provinces are assigned to the Central Chilean subregion (85, 89). The Coquimbo province represents northcentral Chile, between latitudes 28 and 32° south (82, 85, 86, 108, 110, 116, 133, 135); its entomofauna is related to the entomofauna of the Atacama province (110). The Santiago province represents southcentral Chile, between latitudes 32 and 36° south (25, 82, 85, 89, 110, 116, 133, 135).

Subantarctic Subregion

The Subantarctic subregion comprises the austral Andes, from latitude 36° south to Cape Horn, including the archipelago of southern Chile and Argentina (8, 75, 80, 82, 84, 89, 108, 117, 124, 130–134, 163). Several authors (8, 19, 49, 80) have emphasized the distinctive character of the Subantarctic biota and its links with the biota of the Austral continents, especially Australia and New Zealand. A cladistic biogeographic analysis of *Nothofagus* (Nothofagaceae) and some insects, such as the genus *Heterobathmia* (Lepidoptera) and the family Eriococcidae (Hemiptera), that feed on species of this genus has shown that coevolution only partially accounts for the patterns of biotic relationships and that Subantarctic-coevolved insect herbivores may be as old as or older than their host plants (46). Within the Andean region, the Subantarctic subregion is more closely related to the Central Chilean subregion (9, 66, 75, 79, 101, 118, 119, 159), although it has some Patagonian elements (27). In addition, the Subantarctic subregion shows relationships with the Parana subregion that indicate a former connection (see above).

Six provinces are assigned to the Subantarctic subregion (82, 84, 89). The Juan Fernandez Islands province comprises the Chilean islands of Masatierra (or Robinson Crusoe), Masafuera (or Alejandro Selkirk), and Santa Clara situated in the Pacific Ocean 600 km west of Valparaiso at latitude 33° south (8, 50, 82, 84, 89, 133). The Maule province comprises southern Chile and Argentina between latitudes 36 and 39° south (8, 49, 82, 84, 89, 110, 116, 133, 135). The Valdivian Forest province comprises southern Chile and Argentina, south of the Maule province, reaching latitude 47° south (8, 25, 49, 82, 84, 89, 110, 116, 133, 135); typical insects of this province have been listed by Kuschel (49). The Magellanic Forest province comprises southern Chile, from latitude 47° south to Cape Horn, and southern Argentina in small parts of western Santa Cruz and Tierra del Fuego (8, 25, 49, 82, 84, 110, 116, 135); the entomofauna is similar to that of the Valdivian forest, although biotically impoverished (49). The Magellanic Paramo province comprises southern Chile and Argentina, from the Golfo de Penas (latitude 48° south) to Cape Horn, bordered to the west by the Magellanic Forest province (25, 49, 82, 84, 89, 110, 116, 133). The Malvinas Islands province comprises the Argentinean archipelago of Malvinas (or Falklands) and South Georgia Islands situated in the South Atlantic Ocean 550 km from Tierra del Fuego (8, 25, 82, 84, 89). Their inclusion in the Subantarctic subregion was postulated by Ringuelet (129) and corroborated by panbiogeographic and cladistic biogeographic analyses (74, 105).

A panbiogeographic analysis based on insect (Coleoptera, Diptera, Hemiptera, and Phthiraptera), plant, crustacean, and other animal taxa (71) showed that the southern portion of Tierra del Fuego (which corresponds to both the Magellanic Forest and Magellanic provinces) is a node, showing biotic links with Malvinas and Campbell (New Zealand) Islands, and that the Malvinas Islands are another node, showing biotic links with South Georgia, Tristan da Cunha-Gough, Crozet, and Tierra del Fuego. A PAE based on Ceratopogonidae (Diptera) (66) and cladistic biogeographic analyses based on beetle taxa (74, 105, 118, 119) showed that the Magellanic Paramo province either is closely related to the Magellanic Forest, Maule, Valdivian Forest, and Malvinas Islands provinces or is the sister area of the Magellanic Paramo province. The biota of the Juan Fernandez Islands shows a close relationship with the remaining Subantarctic provinces (50), which has been corroborated by a panbiogeographic analysis (71) in which these islands were connected by a generalized track with the Magellanic Forest and Malvinas Islands. Cladistic biogeographic analyses based on beetles (74, 105, 118, 119) showed that this province is closely related to the Magellanic Forest, Valdivian Forest, and Magellanic Paramo provinces.

Patagonian Subregion

The Patagonian subregion extends to southern Argentina, from central Mendoza, widening through Neuquen, Rio Negro, Chubut, and Santa Cruz, to northern Tierra del Fuego, and reaches Chile in Aisen and Magallanes (8, 25, 31, 49, 80, 82, 86, 89, 108, 116, 117, 131–134, 163). The Patagonian subregion comprises two provinces (86, 89). The Subandean Patagonia province extends to southwestern Argentina, constituting a narrow strip along the austral Andes, south of latitude 51° south, widening southward to Santa Cruz (8, 82, 86, 89, 116, 133). The Central Patagonia province comprises southwestern Argentina, from central Mendoza to southern Santa Cruz, and reaches Chile in Aisen and Magallanes (8, 25, 82, 86, 89, 133, 135). A panbiogeographic analysis based on beetle taxa belonging to families Carabidae and Tenebrionidae (106) allowed researchers to recognize three districts within the latter province: Payunia, Central, and Fuegian.

DISCUSSION

Biogeographic systems are not definitive; they change as our view of geobiotic patterns changes. Under an evolutionary perspective, a biogeographic system represents a set of hypotheses concerning delimitation of biotic components and their historical interrelationships. The biogeographic system presented herein should be considered under this perspective. Delimitation of regions, subregions, dominions, and provinces based on the identified biotic components may change with future analyses based on other taxa. In addition, when more phylogenetic analyses of insect taxa become available, more rigorous hypotheses of secondary biogeographic homology may be postulated.

The transition zones recognized in Mexico and South America represent outstanding areas because the interaction of different biotic components within them has provided the conditions for evolutionary diversification and interesting ecological interactions. In addition to testing their existence and extension, future analyses should detect whether secondary transition zones exist within the regions and dominions. The Isthmus of Tehuantepec, within the Mesoamerican dominion of the Caribbean subregion, may be a good example. Although interaction between historical and ecological biogeographers has not been easy, efforts to cooperate should be initiated. Transition zones are well suited for this interaction because in addition to historical processes they are modeled by ecological conditions.

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