

Biogeographic history of South American arid lands: A view from its arthropods using TASS analysis

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Abstract

Arid and semi-arid ecosystems in South America include several different habitats, such as the Peruvian and Atacama Deserts of the Pacific Coast, Monte Desert of central Argentina, Patagonian steppes, Chaco xeric woodlands, Andean Puna, and Brazilian Cerrado and Caatinga. All these areas belong to two biotic tracks, one stretching from Patagonia to the Peruvian coastal desert province, at approximately 5° South latitude in the Pacific coast of Peru and the second stretching on the coasts of the Atlantic ocean, from northern Patagonia to Caatinga. Twenty-one natural areas have been recognized and seventeen taxa of Arthropoda were analysed applying paralogy-free subtrees, using the TASS program. The obtained data matrix was analysed using NONA and TNT programs. The strict consensus tree shows that the first areas to become separate from the rest were Caatinga, septentrional deserts of Chile and Peru, the Uspallata-Calingasta Valley, and the natural areas from the western and eastern slopes of the Andes. The vicariant event most clearly correlated with the cladogram is the uplifting of the Andes mountain chain, which attained 3000 m in the Quechua phase, between 14–11 Ma in the middle Miocene. This event split, until present time, the taxa into occidental groups (from the central area of Chile) and oriental groups (from Argentina), and also generated the natural areas of Puna. The general area cladogram shows that Monte and Puna are not areas that were isolated from the rest and evolved separately, because the considered sub-areas are linked to other biogeographical provinces. The five areas that form Patagonia are all related.

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1. Introduction

South America has been subject to many biogeographical studies due to the particular distribution patterns of its flora and fauna, specially the austral region, which has been considered to be different from the rest of South America (Jeannel, 1967; Monrós, 1958; Kuschel, 1964). Several theories have been proposed to explain the origin and relationship of this region's biota with other temperate areas such as Australia, New Zealand, and South Africa. Nonetheless, these studies are centered on taxa shared with the other austral continents (austral component, Kuschel, 1964) and few studies have taken into consideration taxa from austral South America which are restricted to arid lands and have no phylogenetic relationships with other austral taxa (eremic component, Kuschel, 1964; Roig-Juñent and Flores, 2001).

Many authors have considered the biota distributed in the arid regions as of very recent age. According to Raven and Axelrod (1974) aridity was at its maximum between the Middle Pliocene and Quaternary. This idea, the formation of the deserts in the upper Cenozoic, stems from the fact that in the lower Cenozoic the subtropical forests were much widely spread, up to 45° South, and the climate in South America was much more humid. Following this idea Raven and Axelrod (1975) and Lewis (1966) considered: (1) that the eremic biota of America evolved since the Pliocene and speciated quickly and explosively, (2) that the similarity between the deserts of North America and South America are due to long distance dispersal, and (3) that semi-arid conditions were widespread during glacial ages and allowed the existence of a corridor between South America and North America.

Other authors consider that the sub-desertic regions existed during the Cenozoic, but with a restricted distribution: during the Eocene, the central western part of Argentina was a semi-arid zone (Volkheimer, 1971). Another fact that supports the idea that deserts have existed for a long time is that the high diversity of families of American plants that exist only in arid areas could not have evolved solely in the Pliocene, for example the Agavaceae (13 genera and 210 species) and Cactaceae (87 genera and 2000 species). Another point of view is that the desertic flora and deserts have existed before the breaking of Gondwana, an idea supported by Kuschel (1969) who considered that most beetles of South America have existed through the Tertiary and many since Jurassic times. The huge number of genera and species from different taxa are indicators of ancient desert conditions (Shmida, 1985). Some plant groups (e.g., Zygophyllaceae) have evolved since the Mesozoic in arid regions and are found at present time worldwide with a disjunct distribution (Shmida, 1985). As for insects, the same pattern can be found in the Pimeliinae (Coleoptera: Tenebrionidae) with 8000 species distributed in arid areas of the world (Watt, 1974) and adapted to live in conditions of extreme aridity. In this subfamily, there is a monophyletic group of three tribes: Nycteliini, Praocini, and Physogasterini, with 470 species, which are endemics in South America (Roig-Juñent and Flores, 2001) and are widely distributed in arid regions. The old age of the deserts is also pointed out by the existence of paleo-endemic relicts adapted to desertic conditions, as indicated for the Sahara by Shmida (1985). This is also the case of the Cicindisini, a tribe of Pangeic carabid beetles, only represented at present in the Llanos chaqueños of Argentina and in Iran (Kavanaugh and Erwin, 1991).

Based on the above mentioned, the eremic component of South American biota is probably very ancient, and has been isolated during the Cenozoic from other continents, in which it diversified. The objective of this study is to propose a hypothesis concerning the

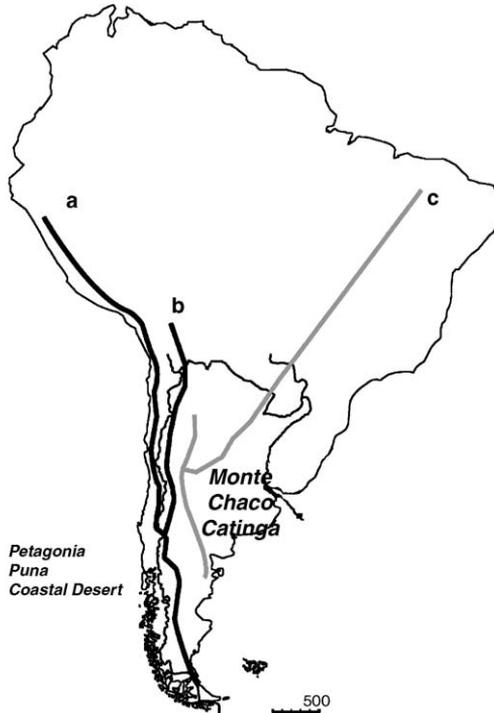


Fig. 1. Tracks that related the xeric natural areas of South America (according to Roig-Juñent et al., 2003).

biogeographical history of the biota of the desert areas south of parallel 5° South (Fig. 1) based on evidence from several taxa of arthropods with endemic representatives in the studied areas and considering paleo-geographical aspects of South America during the Cenozoic.

2. Material and methods

Study area. In this study, desert plains or high altitude areas south of parallel 5° South were considered, with annual rainfalls under 750 mm. The components of these areas point out the existence of a common history and it was possible to distinguish two different biotic tracks (Fig. 1) (Roig-Juñent et al., 2003). The first track is a western track, that begins in Patagonia, and splits into two branches [the first branch reaches the desert areas of the Pacific coast in Peru (Fig. 1a), and the second one reaches the different high altitude habitats of Puna (Fig. 1b)]. The second track starts from northern Patagonia and reaches the Caatinga area in Brazil (Fig. 1c). Small areas of Venezuela and Colombia near the Caribbean coast or in sheltered valleys support desert-like vegetation with arborescent cacti, *Prosopis*, *Capparis*, and other arid elements are not discussed here, because they do not show biotic relationships with southern areas.

Areas of endemism. The contributions of several authors on the fauna of arthropods were consulted to establish the different areas of endemism (Peña, 1966; O'Brien, 1971; Maury, 1979; Roig-Juñent, 1994; Morrone, 1996; Roig-Juñent et al., 2001; Roig-Juñent

and Flores, 2001; Morrone et al., 2002). Twenty-one areas of endemism have been recognized (Fig. 2, Table 1) whose environmental characteristics are listed in Table 1.

Choice of taxa. In this contribution, taxa belonging to the South American eremic component (Kuschel, 1964) were chosen, because they are representatives of desertic areas. This fauna (eremic component) is defined by Kuschel (1964) as the South American taxa restricted to arid lands that have no relation with taxa of Australia or New Zealand. But this is not true for all taxa that inhabit arid lands, because some taxa, such as the Broscini (Carabidae) show close phylogenetic relationships with other austral taxa, or the Plumariidae (Hymenoptera) that show Gondwanic distribution (Roig-Juñent et al., 2001). The area cladograms of the taxa also have to include at least three areas of endemism from the study area and at least one of the terminal taxa of the area has to be endemic to one area.

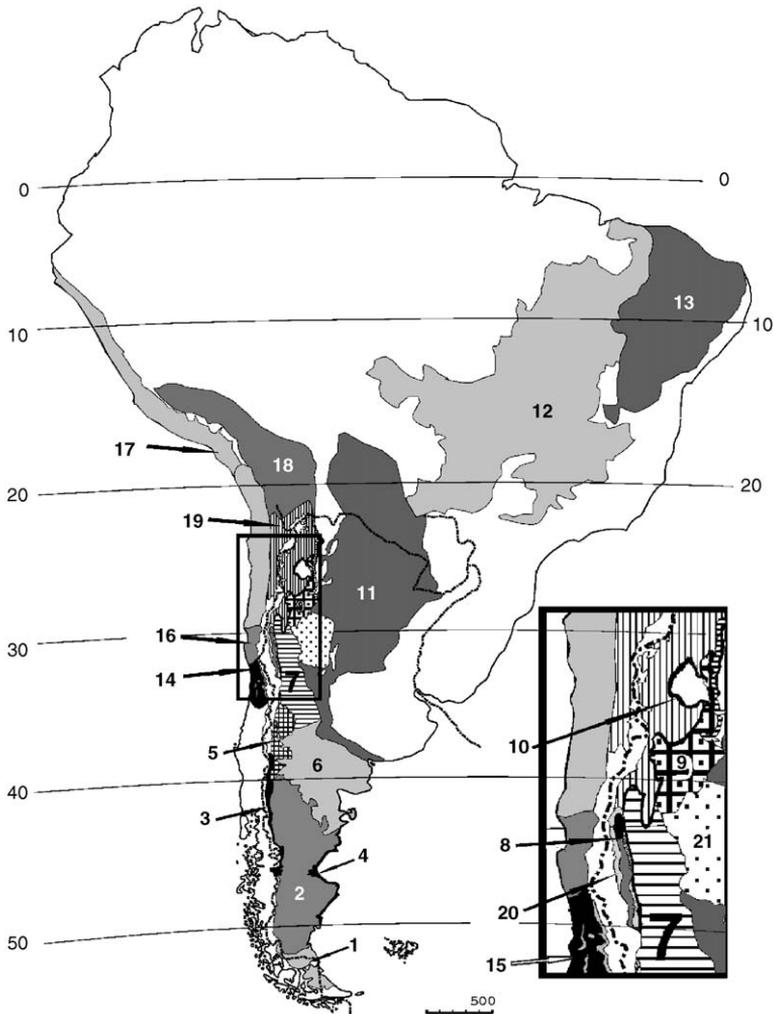


Fig. 2. Natural areas with xeric conditions. Numbers are denoted in Table 1.

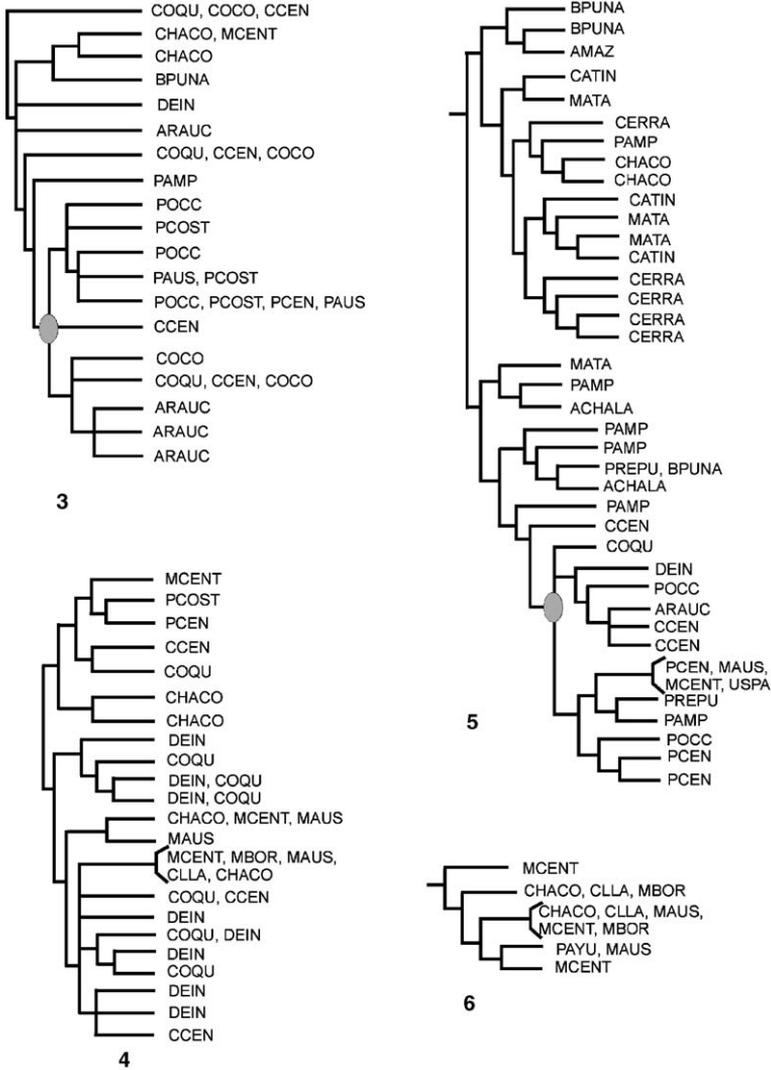
Table 1
Areas of endemisms considered in the analysis

	Area of endemism	Acronimous	Vegetation	Reference
1	Austral Patagonia	PAUS	Steppe of <i>Festuca gracillima</i> . Lowland	Morrone et al., 2002
2	Central Patagonia	PCEN	Shrub steppe of <i>Nassauvia</i> spp. Lowland	Morrone et al., 2002
3	Western Patagonia	POCC	Steppe of <i>Festuca pallescens</i> . Lowland	Morrone et al., 2002
4	Coastal Patagonia	PCOST	Shrub steppe. Lowland	
5	Payunia	PAYU	Steppe of <i>Nassauvia axillaris</i>	Morrone et al., 2002
6	Austral Monte	MAUS	Shrub steppe of <i>Larrea</i>	Roig-Juñent et al., 2001
7	Central Monte	MCENT	Shrub steppe of <i>Larrea</i> . Lowland	Roig-Juñent et al., 2001
8	Uspallata Calingasta	USPA	Shrub steppe of <i>Larrea</i> . 1900-2500 m altitude	Roig-Juñent et al., 2001
9	Northern Monte	MBOR	Shrub steppe of <i>Larrea</i> . 700-2500 m altitude	Roig-Juñent et al., 2001
10	Prepuna	PREPU	Columnar cacti and rock plants. 1500- 2500 m altitude	Roig-Juñent et al., 2003
11	Chaco	CHACO	Xeric woodlands of <i>Schinopsis</i> and <i>Prosopis</i> . Lowland	Roig-Juñent and Flores, 2001
12	Cerrado	CERRA	Savannah and woodlands	Cabrera and Willink, 1980
13	Catinga	CATIN	Xeric woodlands, shrubland and savannahs with cacti	Cabrera and Willink, 1980
14	Central Chile	CCEN	Shrublands and xeric woodlands	Roig-Juñent and Flores, 2001
15	Coastal Mountains	COCO	High altitude thorny bushes and grass steppes	Roig-Juñent and Flores, 2001
16	Coquimbo	COQU	Shrublands and evergreen woodlands	Roig-Juñent and Flores, 2001
17	Desierto intermedio	DEIN	Coastal desert of Peru and Chile	Roig-Juñent and Flores, 2001
18	Bolivian Puna	BPUNA	Highland grassland	Roig-Juñent and Flores, 2001
19	Puna Jujeña	JPUNA	Highland grassland	Roig-Juñent and Flores, 2001
20	Cuyoan Puna	CPUNA	Highland grassland	Roig-Juñent and Flores, 2001
21	Llanos Chaqueños	CLLA	Xeric woodlands of <i>Aspidosperma</i>	Roig-Juñent and Flores, 2001

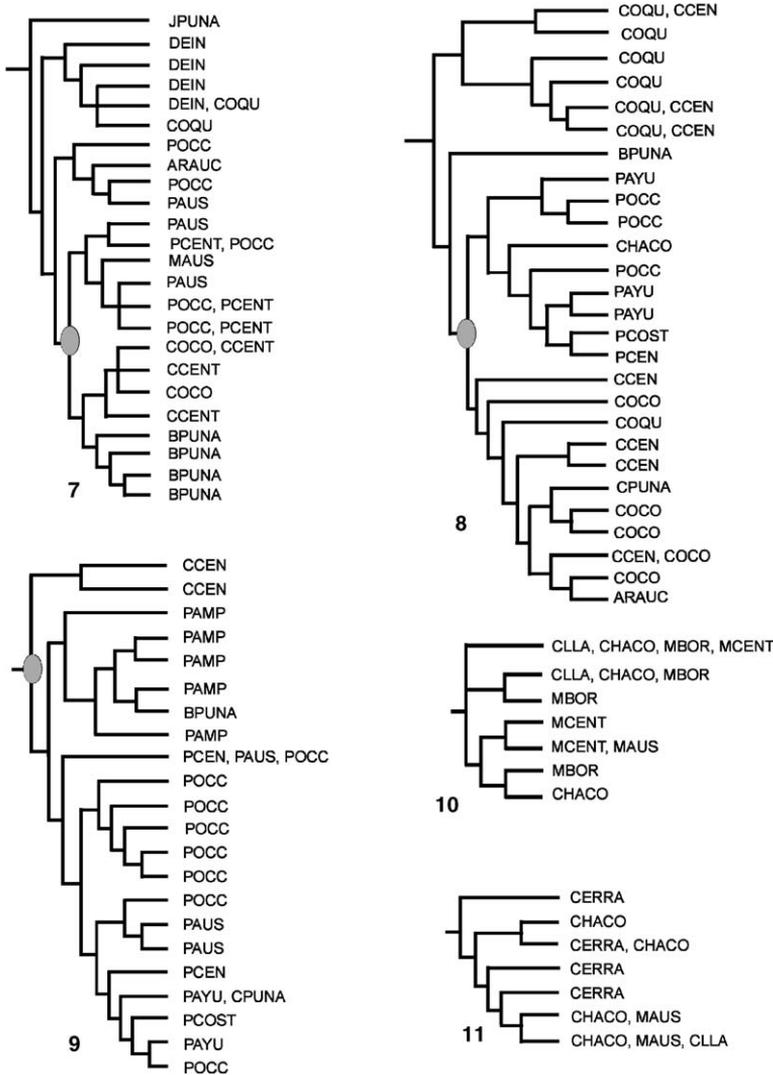
Numbers refers to the Fig. 2.

The taxa used are *Acanthogonatus* Karsch (Araneae, Nemesiidae) (Goloboff, 1995) (Fig. 3); *Diplotheopsini* (Araneae, Nemesiidae) (Goloboff, 1995) (Fig. 4); *Bothriurus* Peters (Scorpiones, Bothriuridae) (Mattoni, 2003) (Fig. 5); *Timogenes* Simon (Scorpiones, Bothriuridae) (Mattoni, unpublished data) (Fig. 6); *Tristiridae* (Orthoptera) (Cigliano, 1989) (Fig. 7); *Cnemalobini* (Coleoptera: Carabidae) (Roig-Juñent, 2002) (Fig. 8); *Barypus* Dejean (Coleoptera: Carabidae) (Roig-Juñent, 1995) (Fig. 9); *Enoplopactus* Heller (Coleoptera: Curculionidae) (Lanteri, 1990) (Fig. 10); *Aramigus* Horn (Coleoptera: Curculionidae) (Lanteri and Díaz, 1994) (Fig. 11); *Listroderes* Schoenherr (Coleoptera, Curculionidae) (Morrone, 1993a) (Fig. 12); *Acrostomus* Kuschel (Coleoptera, Curculionidae)

(Morrone, 1994a) (Fig. 13); *Hyperiodes* Marshall (Coleoptera, Curculionidae) (Morrone, 1993b) (Fig. 14); *Adioristidius* Voss (Coleoptera: Curculionidae) (Fig. 15) (Morrone, 1994b); *Puranius* Germain (Coleoptera: Curculionidae) (Morrone, 1994b) (Fig. 16); *Plathestes* Waterhouse and related genera (Coleoptera: Tenebrionidae) (Flores, 2000b) (Fig. 17); Nycteliini (Coleoptera: Tenebrionidae) which includes the cladogram at generic level (Flores, 2000a) and area cladograms at specific level of some genera of the tribe (Flores and Roig-Juñent, 1997, 2001; Flores, 1999; Flores & Vidal 2000; Flores and Triplehorn, 2002) (Fig. 18); *Fannia* Robineaux Desvoidy (Diptera: Fanniidae) (Domínguez, 2004) (Fig. 19).

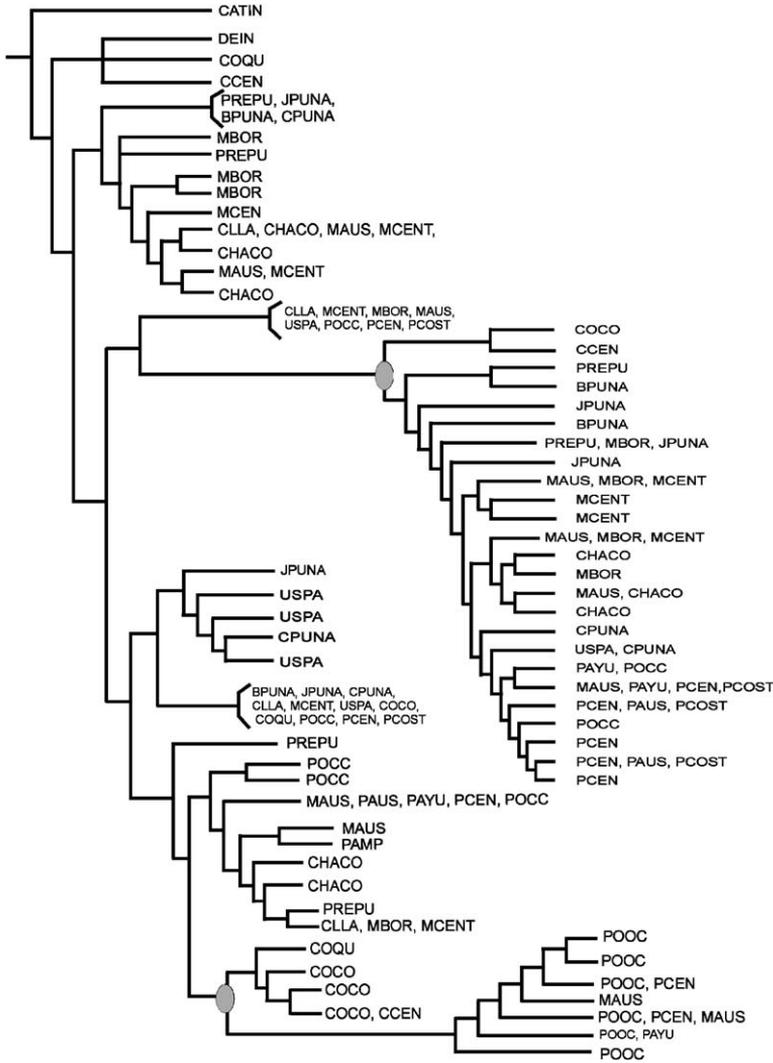


Figs. 3–19. Fundamental cladograms of: 3, *Acanthognatus*; 4, Diplotelopsini; 5, *Bothriurus*; 6, *Timogenes*; 7, Tristiridae; 8, Cnemalobini; 9, *Barypus*; 10, *Enoplopactus*; 11, *Aramigus*; 12, *Listroderes*; 13, *Acrostomus*; 14, *Hyperoides*; 15, *Adioristus*; 16, *Puranius*; 17, *Plathestes* and related genera; 18, Nycteliini; 19, *Fannia*. The oval in the fundamental area cladograms represents the vicariant event produced by the uplift of the Andean Cordillera.



Figs. 3–19. (Continued)

Data analysis. The analysis of paralogy-free subtree (Nelson and Ladiges, 1991a, 1996) was used to eliminate the paralogy of the area cladograms and to obtain a data matrix using assumption 2 (Nelson and Ladiges, 1991b). The matrices were joined in a single matrix (Appendix A), which was analysed using the TASS 2.2 program (Nelson and Ladiges, 1995) with the option maximum (X). In the fundamental cladograms, areas that do not belong to arid environments were considered, such as: Araucania (ARAUC), Pampa (PAMP), Amazonia (AMAZ), Mata Atlantica (MATA), Malvinas Islands (MALV), Pampa de Achala (ACHALA), Neartic, and Neotropical. These areas were not included in the data matrix (Appendix A). The data matrix obtained with TASS (Appendix A) was analysed with NONA version 2.0 (Goloboff, 1993) using a heuristic search, generating 100 Wagner trees with random addition sequences and a rearrangement

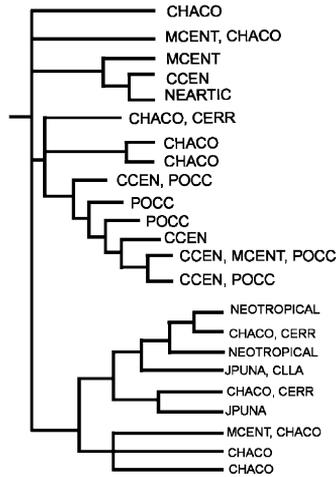


Figs. 3–19. (Continued)

the ‘Jackknife’ option in TNT (probability = 36%, 1000 replicates, each one searching trees using 10 replicates of random addition sequences plus TBR, retaining until 10 trees per replicate), pruning the unstable terminals when consensing each replicate. The support in NONA was calculated doing the same, but without pruning terminals, using the macro file ‘jak.run’ (commands: ‘hold/10; run[; jak 1000 mult*10;’).

3. Results

The analysis of the area cladograms of all the taxa with the TASS program (Figs. 3–19) resulted in a data matrix of 21 terminals and 158 characters (18 uninformative characters



Figs. 3–19. (Continued)

were excluded from the analysis). When analyzing the matrix with NONA, 372 cladograms of 196 steps ($ci = 71$; $ri = 79$) were obtained. The strict consensus of these cladograms did not show any common pattern, and showed very low support values. A second analysis was done using the TNT program, which prunes terminals of the cladograms, and shows the nodes gained on the strict consensus, helping to identify floating terminals. As explained by Goloboff et al. (2003) if a terminal shows a very poorly defined position, it may strongly decrease the support for many groups in the tree. In order to determine if the rest of the tree is well supported, these terminals can be eliminated from the consensus when resampling. Pruning two areas, Cerrado (CERRA) and Llanos Chaqueños (CLLA), the tree gained four nodes (Fig. 20). In this cladogram the first node shows a polytomy between Caatinga (CATIN), Uspallata-Calingasta Valley (USPA), the coastal desert (DEIN) and two monophyletic groups of areas: (1) the areas belonging to the central regions of Chile and (2) all the other areas of the oriental slope of the Andes. The central areas of Chile show that the first Chilean area to become separate is the region of Coquimbo (COQU), Central Chile (CCEN), and the Coastal mountains (COCO) appear as its sister groups. In the group of areas east of the Andes, the first area to become separate is the Bolivian Puna (BPUNA) and only one group can be recognized among the remaining areas, formed by the Central and Boreal regions of the Monte (MCEN, MBOR) and by the Chaco (CHACO). A reanalysis done with NONA, deleting the areas Cerrado (CERRA) and Llanos Chaqueños (CLLA), resulted in five cladograms ($L = 194$, $ci = 72$, $ri = 81$). The strict consensus tree of these five cladograms shows a more resolved tree with high values of support (Fig. 21), and the difference between these five trees is due to the different relationships between the Patagonian areas of endemism.

4. Discussion

Vicariant events of the Cenozoic. One of the goals of historical biogeographic analysis is to correlate the biota fragmentation sequence shown by the general area cladogram with

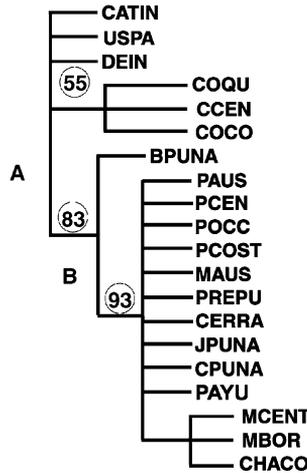


Fig. 20. Strict consensus tree of 371 trees, with the areas CLLA and CERRA pruned.

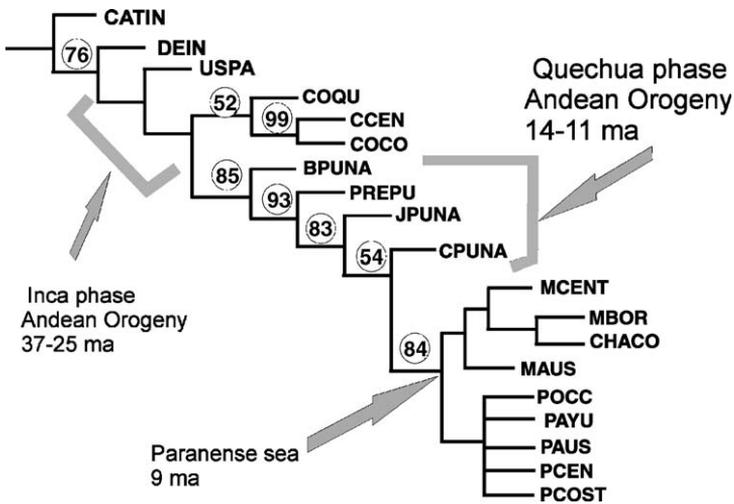


Fig. 21. Strict consensus of the five cladograms obtained by elimination of CLLA and CERRA.

the possible vicariant events. In insular isolation cases (e.g., New Zealand), it is much easier to assign a vicariance event (a division of an ancestral biota), because the possibilities for dispersion are reduced. In continental areas this is more difficult. The effect of a vicariant event in continents can disappear because of the disappearance of the barriers. There may appear cycles, in which first there is a vicariant event that separates two species widely spread, followed by the establishment of new endemic species in more restricted areas, and if the barriers disappear a dispersion of the descendant species will occur, resulting in new widespread taxa, which will be affected by new vicariant events.

The later is what has occurred in southern South America, where the continental area has undergone many important transformations during the Cenozoic (Uliana and Biddle,

1988). In this period, the climate underwent big changes. In the Paleocene, there were subtropical forests in the province of Santa Cruz (Argentina) at 51° South, until the appearance of a cold water current in the circumantarctic sea, that produced the cooling of southern South America and an expansion of open environments like savannas and grasslands. The movements of the continental plates caused the connection of South America with North America and the separation from Antarctica. The uplifting of the Andes caused a decrease in rainfall (Shmida, 1985). Finally, the numerous sea transgressions and regressions were characteristic of this period (Volkheimer, 1971), which in many cases, occupied most of the southern area of South America.

Many cases of redundant distributions can be observed, analyzing the distribution of the species of the groups under study. These may be due to the appearance of barriers that later disappeared allowing new cosmopolitanisms of the new groups formed. This would not be strange for South America, because most of the Cenozoic barriers were continental seas, which underwent great oscillations (ingressions and regressions) (Volkheimer, 1971). If the most important barriers during the early Cenozoic were marine transgressions, these were not stable and allowed new cosmopolitanism of the species as they disappeared. At the present time, there are species that appear at the apex of the cladograms, which display a very wide distribution, e.g., *Entomoderes draco* Waterhouse (Coleoptera: Tenebrionidae) (Flores and Roig-Juñent, 1997), which occupies four of the areas under study: the Central and Austral Monte and the whole of Chaco. This would show that within each group there may exist new cosmopolitanism of some of its members.

Correlation between the general cladograms and vicariant events. The basal vicariant event separated a septentrional area of endemism (Fig. 21), Caatinga. It has not been possible to correlate this separation with any vicariant event. The following three basal nodes of the general area cladogram (Fig. 21) split the Uspallata Valley (USPA), the intermediate desert (DEIN), and the oriental and occidental areas of the Andes. The event that separated these areas must be very old, possibly the beginning of the uplifting of the Andes. The occidental margin of South America was notoriously influenced by the rearrangement of the continental plates during the Eocene, in the period from 48 to 25 Ma. This rearrangement produced the compression of basal strata which led to the Inca Orogeny at the end of the Eocene and beginning of the Oligocene (37 Ma). The progressive uplifting of the Andes Mountains is the only Cenozoic barrier that did not disappear once established. This event is clearly reflected in many of the fundamental area cladograms, which show that the monophyletic groups east and west of the Andes never mixed again (Figs. 7, 8, 9, 18, nodes marked with an oval). This is shown twice in the area cladogram of Nycteliini (Fig. 18) where this event affected this tribe which was widespread at that time, splitting several genera such as: *Epipedonota/Callyntra* and *Auladera/Mitragenius* (Fig. 18, nodes marked with an oval). The uplifting was not even along the Andes mountain range; it was most important in septentrional regions. Today this isolation is only possible in the central Andes, because in certain regions of Patagonia, the low altitude of the mountains allows the continuity of the biotas on both sides. This event, the beginning of the uplift of the Andes, could have isolated the intermediate desert (DEIN) from the remaining areas. Axelrod et al. (1991) postulate that the Atacama Desert was formed during the late Tertiary, nonetheless, all the taxa that occupy this area show a very basal position in the cladograms, which indicates a very old separation. Shmida (1985) proposed that it is an ancient desert, because of the high diversity of unique forms that can be found there. The beginning of the uplift of the Andes may have also caused the isolation of two groups of

areas, those of central Chile (COQU, CCEN and COCO) and the oriental and high altitude areas. Among the areas of Central Chile, the definitive separation of Central Chile and Coquimbo (CCEN and COQU) must have been established in the middle Oligocene, when the Coastal mountains were completely formed.

The separation of the high altitude biotas occurred after the Inca phase and must have been due to the subsequent phases of the uplift of the Andes. Between 14–11 Ma in the middle Miocene, the uplift of the Andes attained the Quechua phase, and the Andes reached altitudes of 2000 to 3000 m which generated the formation of high altitude environments such as the Puna (Fig. 21c). Likewise, it resulted in the development of dry climates along the west coast of South America and on the east side of the Andes the development of xeric scrub steppes such as the Monte in Argentina (Axelrod et al., 1991).

At this time, 9.55–9.11 Ma, one of the greatest marine transgressions occurred (Pascual et al., 1996) that covered a large portion of the northern area of Patagonia and the Chaco plain and Pampean region, reaching the northern portion of the sub-Andean mountains and North western Pampean mountains in Argentina. This probably isolated the Central and Boreal areas of the Monte, together with the Chaco of the Patagonian areas. This marine transition was cyclical (Pascual and Bondesio, 1982); during the Miocene, between 11 and 3 Ma, the “Paranense” sea regression transformed the area occupied by it into the largest continental prairie and plain environment of Argentina. These plains were not separated by orogenic accidents as in present times, but the uplift of the hills that surround the occidental margin of the Chacoan hills, that began at the end the Miocene, created an impassable barrier to the NE winds and caused a drastic desertification of the occidental areas (Pascual and Ortiz-Jaureguizar, 1990). These two biotas, the Patagonian and the Chacoan, evolved under different climatic conditions, in accordance with their latitudinal location (Pascual et al., 1996).

5. Conclusions

Although the major expansion of the deserts occurred during the upper Cenozoic, the diversity of eremic taxa supports the idea of a Gondwanic or Pangeic origin for some of its components. This eremic taxa diversified during the Cenozoic, isolated from other Austral continents. The general area cladogram shows that the first area to become separate was Caatinga. The vicariant event most clearly correlated with the cladogram is the uplift of the Andes, from its beginning in the Inca phase to the Quechua phase, which reached the 3000 m of altitude. This event separated the septentrional deserts of Chile and Peru, which are very old, and the remaining taxa into western groups of the central area of Chile and eastern groups of Argentina, Paraguay, and Brazil, as well as high altitude environments like the Puna.

The general area cladogram shows that the Uspallata Valley, which was considered as part of the Monte, constitutes an area that evolved early from the rest of the areas. Also, the biota of the northern Monte show a closer relationship with the biota of Chaco, than to any other of the Monte. Also, the biota of the different areas of endemism of the Puna show that they were progressively separated from the lowlands during the uplifting of the Andes, and are not a biota that split once and evolved separately. The areas of endemism of Patagonia form a natural group, showing that this biota evolved as a unit, as well the biota that occurs in the areas of Central Chile.

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