

Historical biogeography of the Andean region: evidence from *Listroderina* (Coleoptera: Curculionidae: Rhytirrhinini) in the context of the South American geobiotic scenario

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The weevil subtribe *Listroderina* belongs in the tribe Rhytirrhinini (subfamily Cyclominae), and has 25 genera and 300 species in the Americas. The distributional history of this subtribe was reconstructed applying dispersal-vicariance analysis (DIVA) using its genera as terminals. The results suggest that *Listroderina* originated within an area presently represented by the Central Chile, Paramo, Puna, Patagonia and Subantarctic subregions of the Andean region. Posteriorly, the subtribe was affected by extinctions and was confined to Central Chile, Paramo and Subantarctic subregions. Later, extinctions and dispersals took place and the subtribe was restricted to the Paramo and Puna subregions. From there, a dispersal event to the Subantarctic subregion occurred, enlarging again the geographical range of the subtribe. Subsequently, a vicariant event separated the Puna and Paramo subregions from the Subantarctic one. While the *Macrostyphlus* generic group was confined to the Paramo and Puna subregions and from there dispersed to other areas, the *Antarctobius*, *Falklandius*, *Listronotus*, and *Listroderes* generic groups diversified in the Subantarctic subregion. The results obtained by DIVA may be linked to major geological events of South America. Thus, the geobiotic scenarios recorded in this subcontinent since the late Cretaceous could be used to interpret the biogeographical events which drove *Listroderina* evolution. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, 80, 339–352.

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INTRODUCTION

Weevils (Coleoptera: Curculionidae) comprise more than 57 000 described species belonging to 6000 genera distributed around the world (Morrone & Posadas,

1998). The first fossil records of this family come from late Cretaceous beds of the United States of America (Crowson, 1981) and southern Chile (Kuschel, 1959). The subtribe *Listroderina* is a monophyletic group (Morrone, 1997) belonging to the tribe Rhytirrhinini, which is widely distributed in the temperate-cold areas of South America, North America, Africa, Europe, Australia and New Zealand. In South Amer-

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ica, *Listroderina* includes 25 genera and 300 species, and is extraordinarily diversified in the Andean region, especially in the Subantarctic subregion of southern Chile and Argentina, and in the Paramo subregion of the northern Andes (Morrone & Roig-Juñent, 1995; Anderson & Morrone, 1996). Some species extend to the Chacoan dominion of the Neotropical region and to the Nearctic region.

Morrone (1994a) analysed the distributional patterns of 21 extant genera of *Listroderina* using track compatibility analysis (Craw, 1988) and parsimony analysis of endemism based on areas of endemism (Craw, 1988). Morrone (1994a) postulated that an ancient Austral biota was originally restricted to the southern portion of the Andean region (Subantarctic and Central Chilean subregions); then this biota spread to occupy the entire region and finally it was affected by the uplift of the Andes, with the development of open country communities.

The purpose of this paper was to analyse the distributional patterns of the subtribe *Listroderina*, applying dispersal-vicariance analysis (DIVA) (Ronquist, 1997). Additionally, we have attempted to interpret the biogeographical evolution of *Listroderina* in the context of the geobiotic evolution of the South American continent.

THE GEOLOGICAL SCENARIO: PALAEOGEOGRAPHICAL EVOLUTION OF SOUTH AMERICA DURING THE LATE CRETACEOUS–RECENT SPAN

In this paper only the last 83 Myr (i.e. the latest Cretaceous–Cenozoic span) of the 3800 Myr of South American geological history will be considered (see Yrigoyen, 1999). Likewise, the geobiotic history of the southern part of the continent will be principally considered. These spatial and temporal restrictions have been made due to the aforementioned geographical distribution and the probable time of origin of *Listroderina*.

According to Uliana & Biddle (1988), during the Mesozoic and Cenozoic the tectonic development of southern South America was controlled by a complex subduction regime along its western margin, and the evolving spreading centre of the Mid-Atlantic Ridge along its eastern margin. Sea-level variations were the other major geological forces that modified the palaeogeography of the southern part of the continent. These factors drove the landscape and climatic evolution of South America and, consequently, the compositional changes of its biota (see Pascual, Ortiz Jaureguizar & Prado, 1996).

Late Cretaceous–early Palaeocene span (c. 70–64 Mya)

The late Cretaceous was a time of general tectonic quiescence, during which the epeiric flooding reached its

apogee. During the latest Cretaceous–earliest Palaeocene span the absence of large continental topographic barriers allowed a widespread Atlantic transgression that covered the major part of southern South America, from Patagonia to Bolivia and Peru, from south to north (Fig. 1). This shallow and warm-temperate sea ('Salamancan Sea') divided the whole continent into two large regions, the north-eastern and the south-western regions. Additionally, the south-western area was further divided into several relatively extensive island territories (Pascual *et al.*, 1996).

Late Palaeocene–Oligocene span (c. 64–24 Mya)

During the Palaeogene (Palaeocene–Oligocene), there was a pause in the Andean magmatism and a marine retreat. The sequences of the Andean dominion show considerable variation in depositional regimes from north to south (e.g. volcanic and volcanoclastic from south-western Peru to Puna latitudes; volcanic rocks associated with lacustrine deposits between 30°S and 39°S, and few indications of volcanic activity on the southernmost Andes; see Uliana & Biddle, 1988; Pascual *et al.*, 1996).

During the late Palaeocene, the Salamancan Sea (Fig. 1) was transformed into a series of broad alluvial plains and large lake basins. During the late Palaeocene–Eocene (c. 64–36 Mya), while the southern tip of Patagonia was still covered by the sea, central and northern Patagonian territories turned into vast loess plains, whose sediments were pyroclastic in origin. Suggestively, most of the correlated extra-Patagonian land-mammal bearing beds were deposited within broad alluvial sedimentary basins, filled with epiclastic sediments. This sedimentological characteristic could be due to the aforementioned period of relative magmatic quiescence. Conversely, the pyroclastic sediments of the Patagonian land-mammal bearing beds could be related to the swing of the volcanic belt to the North Patagonian Andes and the Somuncurá Massif (Pascual *et al.*, 1996).

Most of the Oligocene (36.6–23.7 Mya) was again a time of relative tectonic quiescence (Malvicini & Llambías, 1982). But during the latest Oligocene (c. 25 Mya) the modification of the convergence direction between the Nazca and the South American plates induced important modifications in the Andean arc, reactivating the main magmatic belt. Igneous activity expanded over large areas and invaded the foreland in west-central Argentina, Bolivia, and Peru, while in southern Argentina and Chile the magmatic activity was modest (Uliana & Biddle, 1988).

Late Oligocene–early Miocene span (c. 26–20 Mya)

During late Oligocene–early Miocene, the present morphostructural configuration of the Andes of Central Chile began to develop. Also during this span a



Figure 1. Main geographical areas affected by the late Cretaceous–early Palaeocene marine transgression (modified from Pascual *et al.*, 1996).

new Patagonian Atlantic transgression ('Patagonian Sea') occurred in the same general areas as had occurred in the late Cretaceous–early Palaeocene (Fig. 2). During the last phases of this transgression, a generalized Pacific transgression occurred on the west margin of South America (Malumian, 1999). As in the Palaeogene, thin pyroclastic loess with palaeosols con-

tinued to dominate the subaerial setting of Patagonia (Uliana & Biddle, 1988; Pascual *et al.*, 1996).

Middle Miocene–late Miocene span (c. 15–11 Mya)

Beginning with the middle Miocene (c. 15 Mya), southern South American landscapes began to be dominated by the processes that led to the present

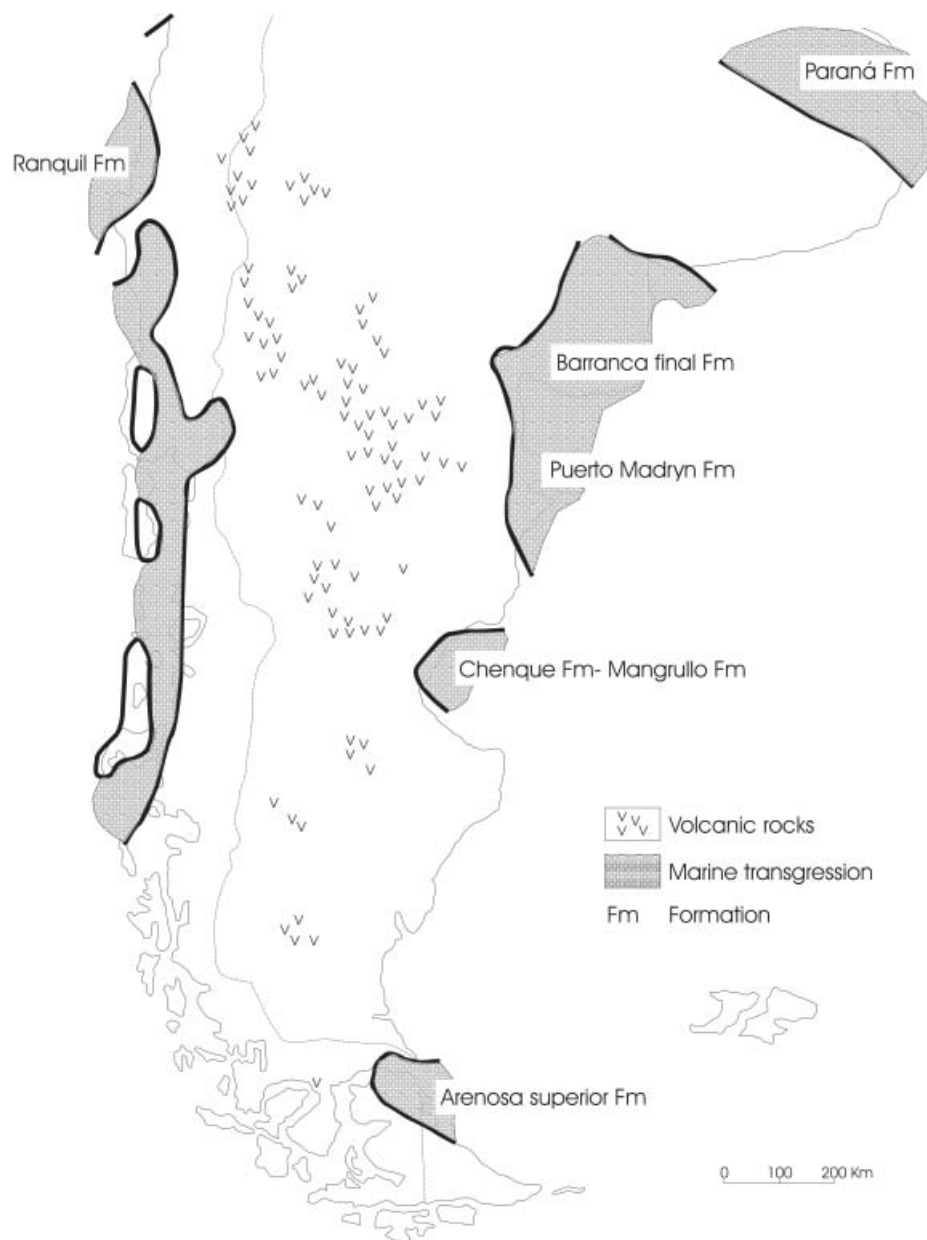


Figure 2. Main geographical areas affected by the late Oligocene–early Miocene marine transgression and volcanic activity.

configuration of the Andean tectonic-magmatic belt (Uliana & Biddle, 1988).

During the middle Miocene, a small Pacific transgression covered Central Chile. Also, during the middle and late Miocene, three successive Atlantic marine transgressions were recorded in southern South America, informally known as the 'Paranean Sea'. Accordingly, during the middle and late Miocene an open seaway again separated the terrestrial environments of southern South America from those farther north, spreading over virtually all of eastern Argen-

tina, western Uruguay, southern Paraguay and south-eastern Bolivia (Pascual *et al.*, 1996). The north-western part of this Paranean Sea was connected with the so called 'Tethys Waterspout' (Fig. 3), that covered widespread areas of the Andean Cordillera and the Guayanan and Brazilian Bedrocks (see Ramos, 1989; Rässänen *et al.*, 1995; Webb, 1995).

Late Miocene–Late Pliocene span (c. 11–3 Mya)

The widespread surface flooded by the Paranean Sea was succeeded by likewise widespread and varied

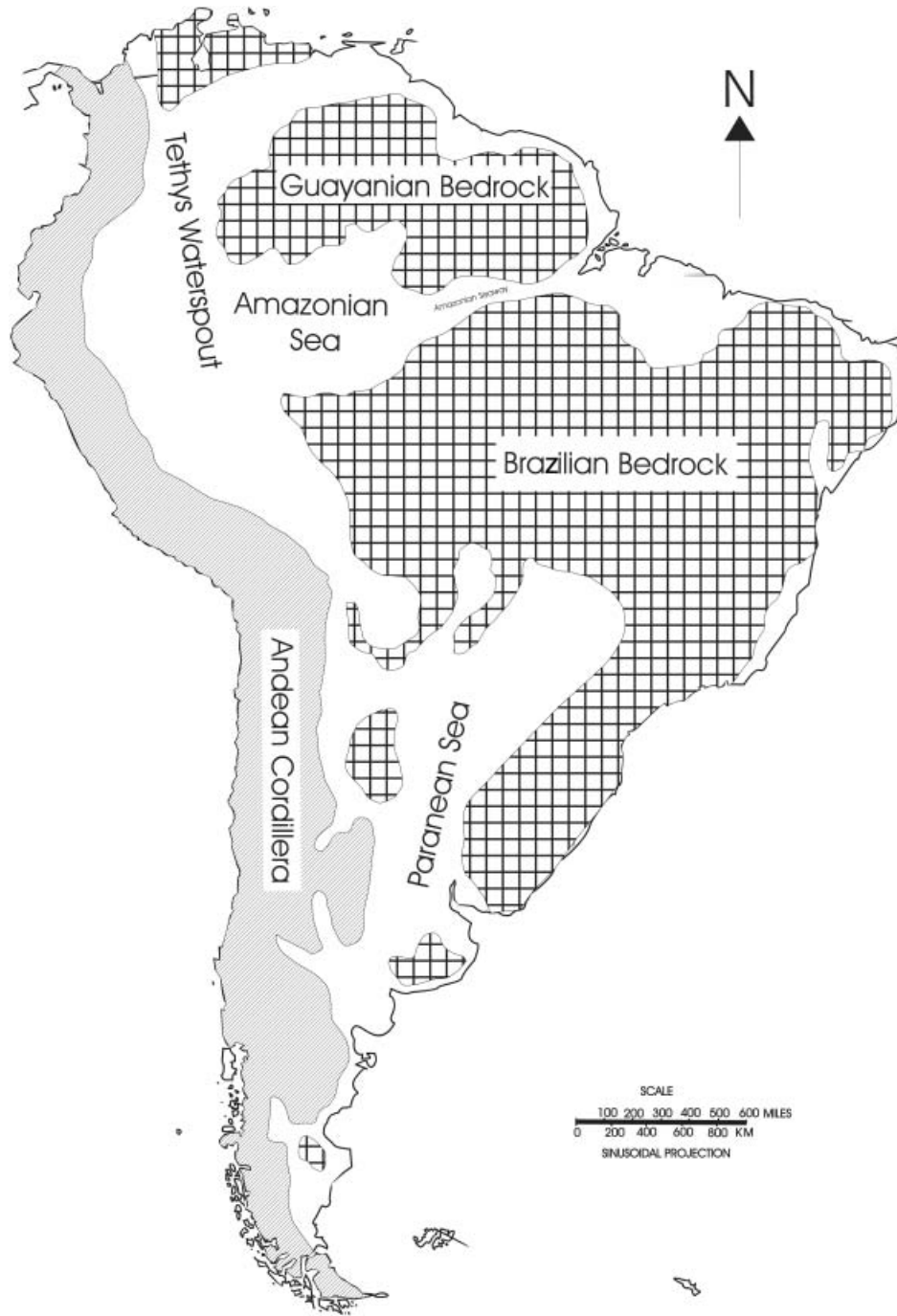


Figure 3. Main geographical areas affected by the middle Miocene–late Miocene marine transgression.

plains, extending from northern Patagonia northward, reaching central and northern Argentina, Uruguay, along the eastern slopes of the rising Andes of northern Bolivia, southern Peru and Venezuela, and also in the upper Amazon basin (Marshall, Hoffstetter & Pascual, 1983; Pascual *et al.*, 1996). These new habitats were so conspicuous that this period is known as ‘the Age of the Southern Plains’ (see Pascual & Bondesio,

1982; Pascual *et al.*, 1996; Ortiz Jaureguizar, 1998). The beginning of these new habitats is correlated to the ‘Quechua Phase’ of the Andean diastrophism (see Yrigoyen, 1979). Under its influence, the Patagonian Andean Cordillera was successively uplifted, progressively forming a major barrier to moisture-laden South Pacific winds. The resulting rain-shadow effect on the eastern Patagonian landscapes led to the first

stages on the differentiation of both of the present biogeographical subregions of southern South America (Fig. 4): the Subantarctic and Patagonia (Pascual *et al.*, 1996).

Additionally, at the beginning of the Age of the Southern Plains (c. 13–11 Mya) the final opening of

the Drake Passage occurred (Kvasov & Verbitski, 1981), separating South America from the Antarctic Peninsula. Consequently, the cool Circum-Antarctic Current was finally established, and an ice sheet formation was initiated in West Antarctica. Thus, during the Age of the Southern Plains the climate was cooler

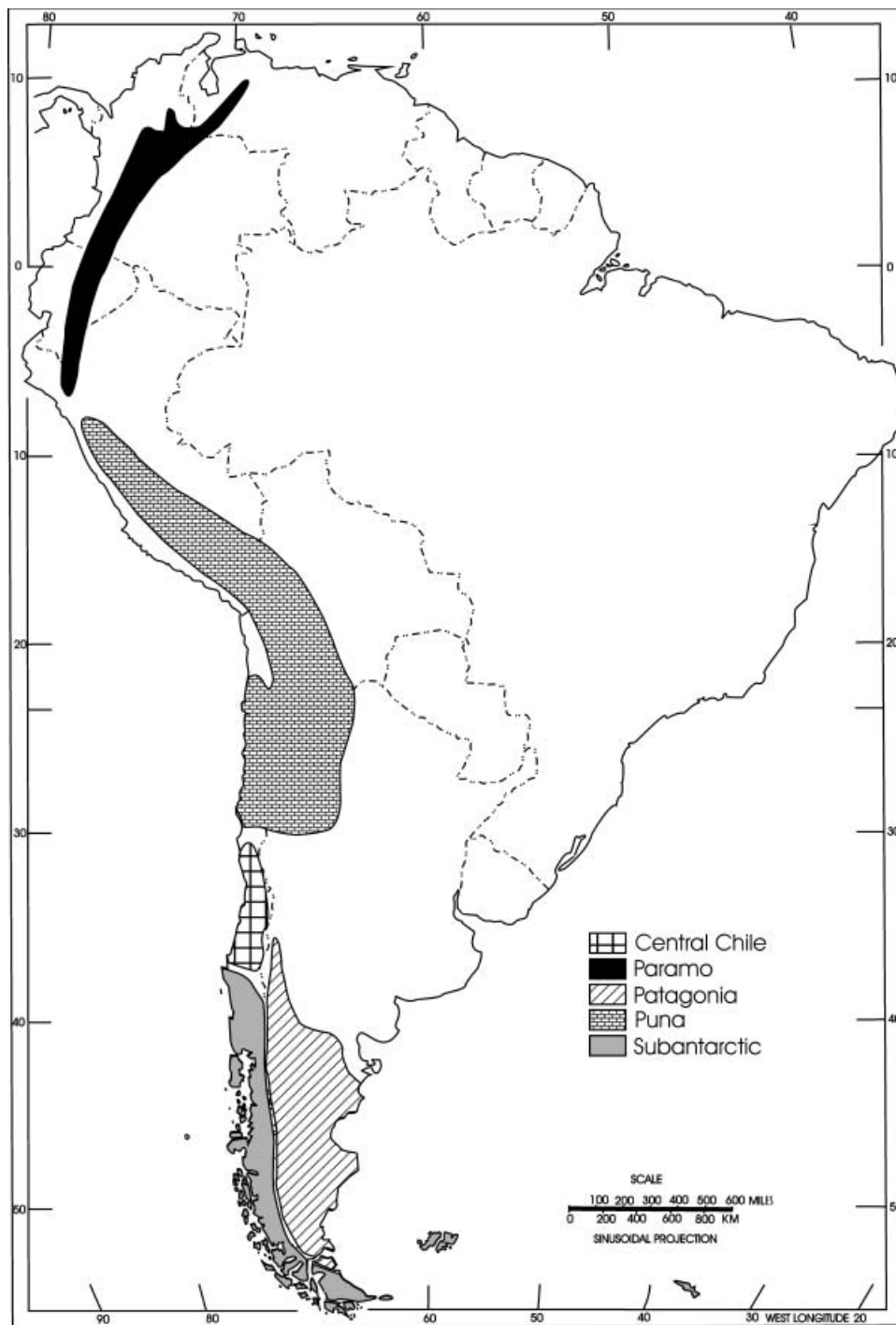


Figure 4. Biogeographical subregions of the Andean region.

and seasonally it was more marked than it was in the middle Miocene, with more varied environmental subdivision (Pascual *et al.*, 1996).

The end of the Age of the Southern Plains is correlated to a new Andean diastrophic phase, named 'Diaguaita Phase' (see Yrigoyen, 1979; Pascual *et al.*, 1996). It resulted in the elevation of the Central Cordillera of Argentina and Chile, the eastern orographic systems of Argentina (e.g. Puna, Pampean Mountain Range), and the uplift of the Mesopotamian region. The final uplift of the Pampean Mountain Range and the Central Andes had marked ecological consequences, producing a rain-shadow effect that resulted in the extremely xeric conditions presently existing in the areas located between them (Pascual *et al.*, 1996; Alberdi, Bonadonna & Ortiz Jaureguizar, 1997). The final uplift of the Puna also had dramatic effects on the biota, installing the very arid and extreme climatic conditions prevalent in this area today.

METHOD

In the last few years, event-based methods have increased in importance in historical biogeographical studies (Miranda-Esquivel, 1999; Voelker, 1999; Zink, Blackwell-Rago & Ronquist, 2000; Sanmartín, Enghoff & Ronquist, 2001; Vinnersten & Bremer, 2001). Unlike pattern-based methods, the event-based ones postulate explicit models of the processes that have an effect on the geographical distribution of living organisms (Crisci, Katinas & Posadas, 2000). The different types of processes (e.g. vicariance, dispersal, extinction) are identified and values of benefit–cost under an explicit model of the functioning of nature are assigned (Crisci *et al.*, 2000).

Dispersal–vicariance analysis (Ronquist, 1996) is a method that allows reconstruction of ancestral distributions, maximizing vicariant events and minimizing dispersal and extinction events, but unlike pattern-based methods of cladistic biogeography, it allows non-hierarchical area relationships.

To reconstruct the genera of *Listroderina* ancestral distributions we used DIVA 1.1 (Ronquist, 1996), applying an exact search according to the dispersal–vicariance optimization proposed by Ronquist (1997). This software allows inference of the ancestral distribution of a taxon and calculates the frequencies of vicariance and dispersal events among different areas under consideration. To do so, the software constructs a three-dimensional cost matrix derived from a simple biogeographical mode (Ronquist, 1997). The input information is the phylogenetic and distributional information encoded on the taxon–area cladogram.

The historical biogeography of *Listroderina* was analysed in terms of the phylogeny of the group proposed by Morrone (1997), who used genera as terminals. This cladogram presents three trichotomies (Fig. 5). As DIVA only accepts as input fully resolved cladograms, we performed all possible resolved cladograms in a single analysis and summarized the results using the option 'sumareas'. Seven main areas of endemism, defined in previous biogeographical schemes (Kuschel, 1969; Cabrera & Willink, 1973; Morrone, 1999, 2000a,b), were considered in the analysis. Since the focus of this study was the Andean taxa of *Listroderina*, we used areas that exhibit different hierarchies in these biogeographical schemes. The areas not belonging to the Andean region were considered at the broadest level (region level for Nearctic and Neotropics), while the areas belonging to the Andean region were considered at the lowest level of biogeographical subregions. The areas used in this study were as follows (Fig. 4).

1 Central Chile: between 32° and 37° south in Chile. This subregion presents bushland which alternates with small forests of less than 10 m in height.

2 Neotropics: Central America south of Sierra Occidental, Oriental and del Sur (Mexico) and all the South American subcontinent except for those areas belonging to the Andean region.

3 Nearctic: the remaining area of the American continent, north of Sierra Occidental, Oriental and del Sur (Mexico).

4 Paramo: Northern Andes of Ecuador, Colombia and Venezuela, over 3000 m in altitude. It is an area without trees, with abundant precipitation and frequent snow. The dominant vegetation community is moorland.

5 Patagonia: to the east of the Southern Andes to the Atlantic coast in Argentina, also extending in some places to Chile. The landscape is formed by plateaus, hills and valleys. The climate is dry and cold-temperate. The dominant vegetation is the Patagonian steppe.

6 Puna: highland plateau located 4000 m above sea level that extends between the two arms into which the Andes opens up among the parallels 15° and 17° south. The climate is cold and dry, with dramatic thermic amplitude recorded between day and night, and between summer and winter. The dominant vegetation is xeric shrubland.

7 Subantarctic: Southern Andes from 37° south to Cape Horn including the archipelago of southern Argentina and Chile. This area consists of valleys and mountains with a temperate and humid climate. The dominant vegetation is the *Nothofagus* forest, with small areas of evergreen forest, but there are also prairies and extensive peat-bogs regions.

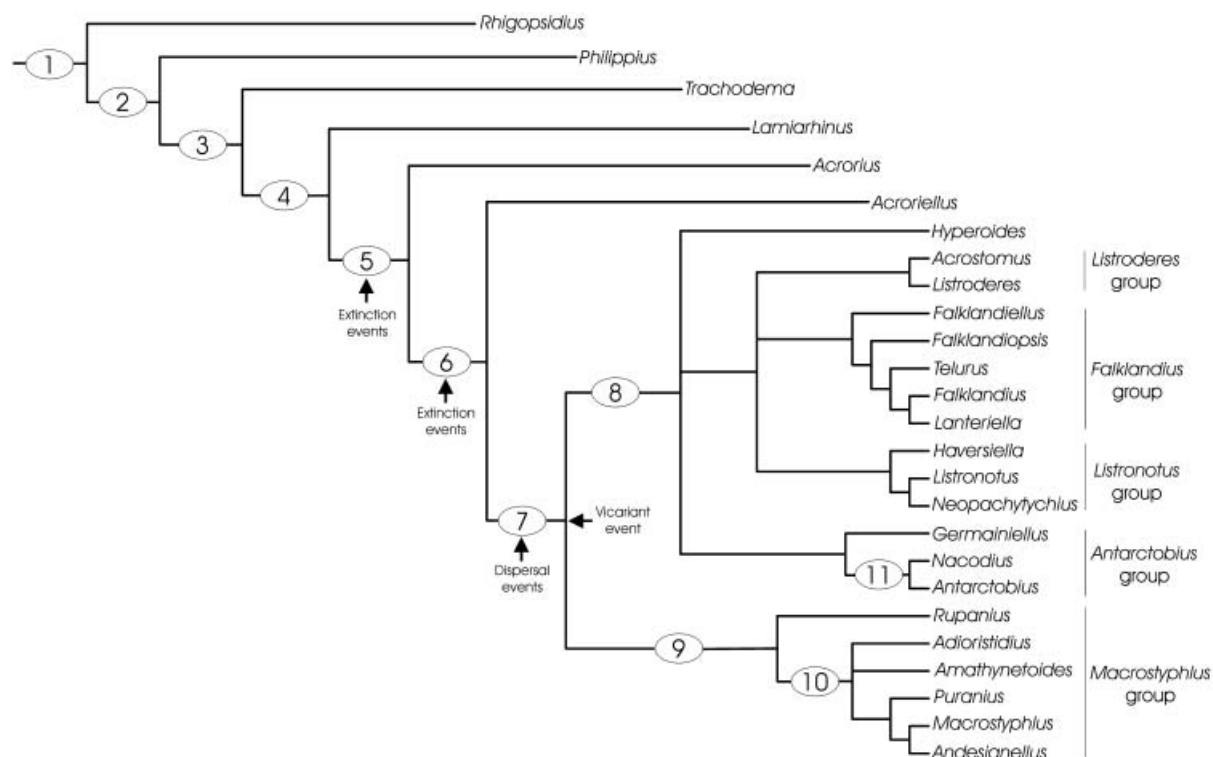


Figure 5. Cladogram of South American Listroderina showing the main biogeographical events according to dispersal–vicariance analysis.

The phylogeny proposed by Morrone (1997) includes a total of 25 genera (see Table 1). To define the distribution area for each genus we used the following criteria:

1 If the genus was monotypic, then the distribution area of the genus was defined as that of the single species included in it.

2 If the genus comprised two species, then the distribution area of the genus was defined as the sum of the single distribution areas of both species included in it.

3 If the genus comprised more than two species and there was no phylogenetic hypothesis available, then we considered as the distribution area of the genus the sum of the areas that each species of the genus inhabits. For example, the genus *Listronotus* has no cladistic analysis; therefore we considered all the areas that its 117 species inhabit (Central Chile, Nearctic, Neotropics and Subantarctic).

4 If the genus comprised more than two species and a phylogenetic hypothesis was available, we used DIVA and the distribution area of the genus was defined as its resulting ancestral area. For example, for the genus *Listroderes* there has been a cladistic analysis (Morrone, 1993b), so we performed DIVA and obtained the probable ancestral areas (Central Chile,

Neotropics, Patagonia, Puna and Subantarctic) for this genus. These areas were considered as the distribution area corresponding to *Listroderes* in the DIVA of the subtribe Listroderina.

The results obtained by DIVA were included in the context of the South American geobiotic evolution. Additionally, we used the compositional changes on the land-mammal communities, and the geographical range and lithofacies of the typical mammal-bearing formations to illustrate the climatic–environmental changes that occurred in South America during the late Cretaceous–Cenozoic span. These changes drove the biogeographical history of Listroderina. The use of mammals allowed us to infer with confidence the habits and the kind of environments in which the fossilized mammals dwelt. This was possible because mammals are the most successful of the Cenozoic land vertebrates, and their distinctive morphofunctional features enable them to inhabit almost any kind of land environment, from the Equator to the Poles. Most mammal adaptations are impressed on their skeleton and teeth, the most commonly preserved elements of fossil mammals. The record of the late Cretaceous–Cenozoic South American land mammals is, geographically and chronologically, one of the most com-

Table 1. Genera and number of species of the subtribe Listroderina with indications of cladistic analysis

Genus	Number of species	Cladistic analysis
<i>Acroriellus</i> Morrone & Ocampo	6	Morrone & Ocampo, 1995
<i>Acrorius</i> Kirsch	10	Ocampo & Morrone, 1996
<i>Acrostomus</i> Kuschel	7	Morrone, 1994b
<i>Adioristidius</i> Morrone	24	Morrone, 1994c
<i>Amathynetoides</i> Morrone	10	Morrone, 1994c
<i>Andesianellus</i> Anderson & Morrone	9	Anderson & Morrone, 1996
<i>Antarctobius</i> Fairmaire	8	Morrone, 1992
<i>Falklandiellus</i> Kuschel	1	No*
<i>Falklandiopsis</i> Morrone & Anderson	1	No*
<i>Falklandius</i> Enderlein	6	No*
<i>Germainiellus</i> Morrone	12	Morrone, 1993a
<i>Haversiella</i> Schweiger	1	No
<i>Hyperoides</i> Marshal	7	Morrone, 1993c
<i>Lamiarhinus</i> Morrone	2	No
<i>Lanteriella</i> Morrone	1	No*
<i>Listroderes</i> Schoenherr	40	Morrone, 1993b
<i>Listronotus</i> Jekel	117	No
<i>Macrostyphlus</i> Kirsch	14	Morrone, 1994c
<i>Nacodius</i> Morrone	4	Morrone, 1994d
<i>Neopachytychius</i> Hustache	1	No
<i>Philippius</i> Germain	1	No
<i>Puranius</i> Germain	20	Morrone, 1994c
<i>Rupanius</i> Morrone	1	No
<i>Telurus</i> Kuschel	2	No*
<i>Thracodema</i> Blanchard	2	No

*These genera belong to the *Falklandius* generic group; for this group there has been a cladistic analysis (Morrone & Anderson, 1995).

plete of the world. Consequently, it has permitted palaeontologists to establish a very detailed biostratigraphical and biochronological chart of the late Cretaceous–Cenozoic span of this area (see Pascual, 1984a, 1984b; Pascual *et al.*, 1996).

RESULTS

The DIVA produced 84 alternative, equally optimal reconstructions requiring 30 dispersal events. All possible ancestral distributions at each node are summarized in Table 2.

VICARIANT EVENTS

The highest frequencies for vicariant events were assigned to Paramo + Puna related to Subantarctic (28.69%), followed by Central Chile + Paramo related to Subantarctic (16.80%), Neotropics + Puna related to Central Chile + Paramo + Subantarctic (14.75%), and

Paramo related to Central Chile + Subantarctic (13.11%).

DISPERSAL EVENTS

Most of the dispersal events observed occurred between contiguous areas. Two dispersal events had the highest scores; both of them implied bidirectional dispersal. The first of these two events occurred between Puna and Paramo with a score representing 45.69% of the total dispersal events between single areas; in this case the main dispersal direction was from Puna to Paramo. The second event was between Subantarctic and Central Chile with a score of 21.89%, and a main direction from Subantarctic to Central Chile. The third and fourth scores of dispersal were assigned to Subantarctic to Patagonia and Puna to Neotropics; in both cases the dispersal events were unidirectional and had a score of 8.84%. The remaining 14.47% implied uni- and bidirectional dispersal events.

Table 2. Ancestral distribution of the subtribe *Listroderina* at each node obtained applying DIVA

Node	Areas present at each node
1	(Neotropics + Puna + Subantarctic)–(Central Chile + Neotropics + Puna + Subantarctic)–(Central Chile + Neotropics + Paramo + Puna + Subantarctic)
2	Subantarctic–(Central Chile + Subantarctic)–(Central Chile + Paramo + Subantarctic)
3	Central Chile–(Central Chile + Paramo)–Subantarctic–(Central Chile + Paramo + Subantarctic)
4	(Central Chile + Paramo)–(Central Chile + Puna)–(Paramo + Subantarctic)–(Central Chile + Paramo + Subantarctic)–(Puna + Subantarctic)–(Central Chile + Puna)
5	Paramo–Puna
6	Paramo–Puna
7	(Paramo + Subantarctic)–(Puna + Subantarctic)–(Paramo + Puna + Subantarctic)
8	Subantarctic
9	(Paramo + Puna)
10	Puna
11	(Paramo + Subantarctic)–(Puna + Subantarctic)–(Paramo + Puna + Subantarctic)

DISCUSSION

The first fossil records of *Listroderina* come from the Oligocene in North America (Alonso-Zarazaga & Lyal, 1999). But taking into account the lowest diversity reached by this subtribe in North America, the highest diversity reached in South America, and the fact that the first South American Curculionidae comes, suggestively, from late Cretaceous beds of southern Chile (Kuschel, 1959), it is highly probably that the *Listroderina* were differentiated in South America during the late Cretaceous–Palaeocene span. During this span, and more precisely between the latest Cretaceous and the lowest Palaeocene, the fossil records of North and South America show an interchange of vertebrates, including dinosaurs and mammals (see Pascual *et al.*, 1996, 2000; Pascual, 1998). After this connection, South America was again isolated from North America. This isolation ended when the Panamanian land bridge connected both continents beginning in the Pliocene (see Stehli & Webb, 1985; Pascual *et al.*, 1996, 2000; Pascual, 1998). Thus, the North American Oligocene record of a *Listroderina* can be considered to be more probably a relict of an older *Listroderina* lineage that immigrated to North America from South America during the geologically brief late Cretaceous–early Palaeocene biotic interchange.

As Ronquist (1996: 12) pointed out: ‘optimizations become less reliable as you approach the root node . . . In DIVA this uncertainty will be manifested as a tendency for the root node distribution to be large and include most or all the areas occupied by the terminals’. Our results reflect this problem at the basal node, numbered as 1 in Figure 5, in which the ancestral distribution includes all but one of the areas inhabited by the terminals.

The cladogram nodes 2, 3, and 4 (Fig. 5) show an ancestral distribution of *Listroderina* confined to Central Chile, Paramo, Puna and Subantarctic subregions. This result rejects the hypothesis of Morrone (1994a) who postulated the existence of an ancient Austral biota restricted to Central Chile and Subantarctic subregions. Conversely, the ancestral distribution obtained by DIVA agreed with the Andean region reflecting the Andean origin of the group during the late Cretaceous–earliest Palaeocene. At this time (*c.* 70–64 Mya), the widespread Salamanca Sea divided South America into north-eastern and south-western regions (Fig. 1). Thus it was in this last region where the *Listroderina* were probably differentiated. From this region they probably reached the Caribbean area, immigrating to North America during the aforementioned late Cretaceous–early Palaeocene biotic interchange (see Pascual *et al.*, 1996, 2000; Pascual, 1998).

Subsequently, according to DIVA (Fig. 5), the subtribe was restricted to the areas presently occupied by the Paramo and Puna subregions (nodes 5 and 6), probably as a consequence of local extinction events. The climatic–environmental changes recorded during the Eocene (*c.* 58–37 Mya) could explain the Patagonian extinction of *Listroderina*, and its persistence in the more propitious extra-Patagonian areas.

Mammals and other vertebrates attest the trend followed by climatic changes after the Salamanca transgression: the rupture of climatic homogeneity, a progressive increase of seasonality at higher latitudes, and an increase of latitudinal gradient. Thus, the close biogeographical similarity showed by mammal communities from Itaboraí (Brazil) and central Patagonia during early–late Palaeocene was replaced by a latitudinal biogeographical differentiation during the latest Palaeocene–Eocene. In Patagonia, several lineages

of herbivorous mammals show a progressive increase of molar-crown height, associated with the pyroclastic nature of the sediments and an increase of grasslands. Conversely, those extra-Patagonian land-mammal communities (found in epiclastic sediments) were clearly dominated by low-crowned, browser mammals, more adapted to forested habitats (Pascual *et al.*, 1996). At the same time, a mixed flora composed of cold-temperate species together with subtropical ones ('Mixed Palaeoflora') was present in the Antarctic peninsula and southern South America, while the most typical subtropical and tropical plant communities occupied the central and northern regions of the continent (Romero, 1978, 1986). This latitudinal biogeographical differentiation, which is shown by mammals and flora, could be considered as the cause of *Listroderina* southern extinction events. These events restricted *Listroderina* distribution to the Paramo and Puna subregions.

A new dispersal event occurred after the Patagonian Eocene local extinction, resulting in a return of *Listroderina* to the area presently occupied by the Subantarctic subregion (node 7, Fig. 5). This increase of the geographical distribution of the subtribe could be explained by the relative tectonic quiescence that characterized most of the Oligocene and, particularly, the aforementioned modest magmatic activity recorded in southern Argentina and Chile (Malvicini & Llambías, 1982; Uliana & Biddle, 1988).

Flora and fauna suggest that the climate was relatively warm and wet during the Oligocene, but with spatial variation (Barreda, 1997). Thus, the Mixed Palaeoflora woodlands were still dominant in Patagonia, while in the east more open habitats began to develop (Barreda, 1997). Here the land-mammal bearing sediments contain abundant phytoliths, indicating extensive grasslands. In agreement with the floristic evidence, land-mammal communities show a remarkable radiation of the high-crowned grazer types in many families of notoungulates (Pascual *et al.*, 1996).

Later, a vicariant event separated the Subantarctic subregion (node 8) from the Puna + Paramo subregion (node 9, Fig. 5). The marine transgression represented by the Paranean Sea (Fig. 3) and a new phase of the Andean uplift that began during the middle Miocene could have generated a biogeographical barrier which split the *Listroderina* distribution through the aforementioned vicariant event. Middle Miocene mammal-bearing deposits were stratigraphically related to and succeeded by the marine deposits of the Paranean Sea. Land-mammal communities were dominated by a unique association of frugivorous, browser and grazer types. This association indicates the existence of a balance between woodlands and grasslands, probably provided by a savannah (Pascual *et al.*, 1996). From a climatic point of view, the presence of primates and

other climate-sensitive vertebrates at latitudes as high as 53°S, indicates the existence of warm-temperate and wet climates. This implication agrees with those provided by marine palaeotemperatures (see Haq, Hardenbol & Vail, 1987; Pascual *et al.*, 1996).

The ancestral distribution at node 10 (Fig. 5), and subsequent ones, shows that a group of *Listroderina* were confined to the Puna. This fact is in agreement with the final phase of the Puna uplift, which occurred during the late Pliocene. Previous to the Puna uplift, South American land-mammal communities were dominated by the grazer and cursorial types that characterized the Age of the Southern Plains (*c.* 13–3 Mya; see Pascual *et al.*, 1996; Ortiz Jaureguizar, 1998). During this lapse, the climate was cooler and the seasonality was more marked than in the middle Miocene, with a more varied environmental subdivision (e.g. wet and forested habitats in the north-western end of Patagonia and the eastern Mesopotamian region, and more arid and shrubby habitats in central-western Argentina; see Alberdi *et al.*, 1997).

The Andean diastrophic Diaguita Phase resulted in the final uplift of the Pampean Mountain Range in central Argentina and the Central Andes of Chile. The subsequent rain-shadow effect resulted in the extremely xeric conditions presently existing in the areas located between them (Pascual *et al.*, 1996; Alberdi *et al.*, 1997). Also, the final uplift of the Puna installed the present extreme climatic conditions which characterize this region. Consequently, the high endemism and local diversification observed inside node 10 and the subsequent ones could be interpreted as the response of the taxa to the Puna uplift and the resulting isolation.

In the Subantarctic subregion *Antarctobius*, *Falklandius*, *Listronotus* and *Listroderes* generic groups diversified widely. All but one of the internal nodes of this clade at node 8 show the Subantarctic as the ancestral distribution; the exception is node 11, for which the ancestral distribution of at least some of the reconstructions comprises Puna, Paramo and Subantarctic. All the remaining widespread distributions of terminal genera in this clade could be due to recent dispersal events. As a result of the aforementioned vicariant event, which split Subantarctic from Paramo + Puna (the barrier constituted by the Paranean Sea), the *Macrostyphlus* generic group was confined to Paramo and Puna subregions, and from there dispersed to other areas.

Morrone (1994a) analysed the distributional patterns of *Rhythirrinini* (Coleoptera: Curculionidae), applying two pattern-based methods (track compatibility analysis and parsimony analysis of endemism). This author postulated the existence of an 'ancient austral biota [which] was originally restricted to the southern portion of the Andean region (Subantarctic

and Central Chilean subregions' (Morrone, 1994a: 192). Our results do not confirm this hypothesis because the ancestral area resulting from DIVA suggests a broad area for such ancestral biota, which probably occupied the entire Andean region. Also, he proposed that this ancient biota then spread to occupy the entire Andean region. According to our results, the present distribution of *Listroderina* is the result of many changes in its geographical range. These changes imply that not just dispersal events increased *Listroderina* distribution. Instead, the present distribution of this taxa implies a complex history of extinction, dispersal, and vicariant events, all of which could be linked to major events in the geobiotic evolution of South America. Finally, Morrone (1994a) proposed that the Central Chile area could be considered as a panbiogeographical node. This proposal is sustained by this paper, because after the vicariant event had occurred during the middle Miocene, Central Chile could have acted as a contact point of the two isolated clades which evolved independently in the Subantarctic and Paramo + Puna areas.

CONCLUSIONS

According to the fossil record, we infer a possible *Listroderina* time of origin in the Late Cretaceous. From DIVA, we have postulated a South American diversification of the subtribe *Listroderina*. The first ancestral distribution resulting from the analysis showed *Listroderina* inhabiting the areas today occupied by the Central Chile, Paramo, Puna and Subantarctic subregions. This ancestral distribution is in agreement with the Andean region and probably reflects the Andean origin of the group during the late Cretaceous–earliest Palaeocene. The *Listroderina* were probably differentiated in this last region, and from this area they probably emigrated to the Caribbean region. Also, during the geologically brief late Cretaceous–early Palaeocene biotic interchange, *Listroderina* immigrated to North America from South America (see Pascual *et al.*, 1996, 2000; Pascual, 1998). This event is evidenced by a *Listroderina* fossil record from the Oligocene of North America (Alonso-Zarazaga & Lyal, 1999). This record is here interpreted to be a relict of an older *Listroderina* lineage. This interpretation is sustained by the lower diversity reached by this subtribe in North America, and the isolation of South America after the South and North American connection, which ended in the Pliocene when the Panamanian bridge connected both continents (Stehli & Webb, 1985; Pascual *et al.*, 1996, 2000; Pascual, 1998).

Later the subtribe was restricted to the areas presently occupied by the Paramo and Puna subregions, probably due to local extinction events. This restricted distribution could be linked to the climatic and

geological events which occurred during the Eocene (c. 58–37 Mya).

The return of the subtribe to the area presently occupied by the Subantarctic subregion could be explained by the relative tectonic quiescence that characterized most of the Oligocene and the modest magmatic activity recorded in southern Argentina and Chile at this time (Uliana & Biddle, 1988). After that, the Subantarctic subregion was separated from Puna and Paramo subregions by a vicariant event. The development of a sea barrier represented by the Paranayan Sea and a new phase of the Andean uplift, beginning in the middle Miocene, could be the cause of this vicariant event.

As a result of the aforementioned vicariant event, which split Subantarctic from Paramo + Puna, the *Macrostyphlus* generic group was confined in Paramo and Puna subregions, and from there it dispersed to other areas. The *Antarctobius*, *Falklandius*, *Listronotus* and *Listroderes* generic groups were restricted to the Subantarctic subregions. The widespread distributions of terminal taxa could be interpreted as being the result of recent dispersal events.

Finally, in the Diagueta Phase Puna was uplifted, creating an isolated and climatic extreme habitat and resulting in the local diversification and high endemism exhibited by the *Listroderinae* which today inhabit this area.

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