

Historical biogeography of the family Tristiridae (Orthoptera: Acridomorpha) applying dispersal–vicariance analysis

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Abstract

Distributional history of the South American endemic group Tristiridae was reconstructed applying DIVA. The results suggest that Tristiridae originated within an area currently represented by Puna and Patagonia. Three lineages split thence: one dispersed into Desert, a second one became restricted to Patagonia and a third persisted in the original areas. The latter lineage underwent a vicariant event that split Puna and Patagonia, and dispersed from Puna to Yungas and Central Chile. A subsequent vicariant event divided Puna and Yungas from Central Chile. Finally, Puna was separated from Yungas, possibly due to a vicariant or dispersal event. In order to interpret biogeographical events that affected the family Tristiridae, these results are contrasted with the major geologic events occurring in South America since early Miocene.

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1. Introduction

The family Tristiridae is a monophyletic group (Cigliano, 1989a, b; Cigliano and Lange, 2000) belonging to Acridoidea, a superfamily with worldwide distribution. Tristiridae is endemic for South America and comprises 24 species distributed in two subfamilies: Atacamacridinae, with one monotypic genus; and Tristirinae, with three tribes and 16

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Table 1
Tribes and genera belonging to Tristiridae with their biogeographic distributions

Family	Subfamily	Tribe	Genus	Distribution	
Tristiridae	Atacamacridinae	Tristirini	<i>Atacamacris</i>	Puna	
			<i>Tristira</i>	Patagonia	
			<i>Circacris</i>	Patagonia	
			<i>Bufanacris</i>	Patagonia	
			<i>Motuchacris</i>	Central Chile	
			<i>Peplacris</i>	Central Chile	
			<i>Punacris</i>	Puna	
	Tristirinae	Tropidostethini	<i>Incacris</i>	Yungas	
			<i>Crites</i>	Yungas	
			<i>Paracrites</i>	Yungas	
			<i>Tropidostethus</i>	Patagonia + Subantarctic	
			<i>Elysiacris</i>	Patagonia + Subantarctic	
			<i>Tebacris</i>	Patagonia	
			<i>Eremopachys</i>	Patagonia	
			Elasmoderini	<i>Elasmoderus</i>	Desert
				<i>Enodisiomacris</i>	Desert
				<i>Uretacris</i>	Desert

genera. Proposals have been advanced for relating the Tristiridae to families Lentulidae and Pyrgomorphidae of the Chasmosacci group based on some characters of male internal genitalia (Eades, 1962; Kevan and Akbar, 1964; Eades and Kevan, 1974), and to the Cryptosacci group based on other characters of male internal genitalia and karyotypic characteristics (Eades, 1962; Eades and Kevan, 1974; Mesa et al., 1982). No fossil record of Tristiridae is known.

Currently, Tristiridae are set apart within the Acridoidea. Due to the peculiarity of the male genitalia, tristirids are regarded as a key group in understanding the phallic “homologies” between Robert’s (1941) Chasmosacci and Cryptosacci groups (Cigliano, 1989a, b; Cigliano and Lange, 2000).

As was mentioned above, tristirids are endemic for South America, and their geographical distribution extends along the Andes mountain range from Tierra del Fuego in Argentina up to parallel 10°S in Peru and from the Patagonian Atlantic coast of Argentina in the east to the Chilean coast in the west. Most genera of this family occur in extremely arid environmental conditions. As is shown in Table 1, 12 of 17 genera included in the family inhabit arid or semi-arid biogeographic provinces (i.e. Puna, Central Chile, Patagonia, and Desert); whereas, three genera inhabit only humid areas (Yungas) and two genera are distributed both in humid and arid environments (Subantarctic and Patagonia). The monotypic subfamily Atacamacridinae is restricted to Punaean province between 3000–3700 m (Andean–Patagonic domain of Cabrera and Willink, 1973). The subfamily Tristirinae is distributed along the Andean–Patagonic domain, in the Yungas province (Amazonic domain of Cabrera and Willink, 1973), and in the Subantarctic province (Subantarctic domain of Cabrera and Willink, 1973). Table 1 summarizes the distribution of tristirid genera. For more details concerning distributional data, ecological features, and taxonomy for the entire family see Cigliano (1989a).

Several hypotheses has been postulated related to the origin and biogeography of the group. Rehn (1942) proposed the Tristiridae as an old group which probably evolved before Andean orogeny. Carbonell (1977) defined tristirids as evidently South American in origin, and he proposed that their geographical origin and dispersion centre was located in southern South America (Patagonia and southern Chile) based on the highest richness of genera and species recorded in those areas. Carbonell (1977) also proposed that the group had its origin in temperate to cold climate and that these insects were able to migrate north only through the Andes highlands, reaching Peru (and possibly Ecuador). Conversely, Amedegnato (1993) has stated that the existence of some winged and apterous geophylic forms, along with forms that inhabit the leaf litter, supports the ancient adaptation of the group to Cenozoic forest undergrowth. She (Amedegnato, 1993) has also proposed that this diversified faunal group, whose weak dispersal capability did not allow it to colonize the rest of South America, seems relatively recent in the South American continent and probably came from Antarctica.

The purpose of this paper is to analyse the distributional patterns of Tristiridae within the framework of historical biogeography event-based methods, by means of dispersal–vicariance analysis (DIVA) (Ronquist, 1997). Additionally, the obtained results are integrated within the context of the geobiotic evolution of the South American continent.

2. Geological setting

Taking into account the extensive studies carried out by paleontologists in South America, I have used the compositional changes of land mammal communities as well as the geographic range and lithofacies of the typical mammal bearing formations to illustrate the climatic–environmental changes occurred in South America during the early Miocene–Recent span (see Donato et al., 2003). I considered this period because of the time of origin of tristirids. In the absence of tristirid fossils, this temporal assignation is based on the first record for the Pyrgomorphidae, the closest related family with known fossil record (Ross and Jarzembowski, 1993). This latter group has been considered by some authors (Eades, 1962; Kevan and Akbar, 1964; Eades and Kevan, 1974) to be closely related to the Tristiridae, thus the origin of the latter can be assumed to go back to approximately the same time.

Late Oligocene–early Miocene span (ca. 26–20 Ma): A Patagonian Atlantic transgression occurred during the latest Oligocene–earliest Miocene span (Fig. 1). This transgression occurred earlier in Patagonia than in eastern and north-western Argentina, and conversely, the marine retreat started earlier near the Andes and in southern Patagonia (Uliana and Biddle, 1988). The waters of this Patagonian Sea were cold, because of the influence of the Antarctic currents. During the last phases of this transgression, a generalized Pacific transgression occurred on the west margin of South America (Malumián, 1999). During this period the climates in southern South America were quite homogeneous (Pascual et al., 1996) and this area was characterized by forest and grasslands landscapes (Pascual and Ortiz Jaureguizar, 1990).

Middle Miocene–late Miocene span (ca. 15–11 Ma): Starting in the middle Miocene (ca. 15 Ma), southern South America landscapes were progressively dominated by the processes that led to the present configuration of the Andean tectonic–magmatic belt. During the middle and late Miocene, three successive Atlantic marine transgressions, known informally by geologists and paleontologists as the “Paranean Sea”, were recorded

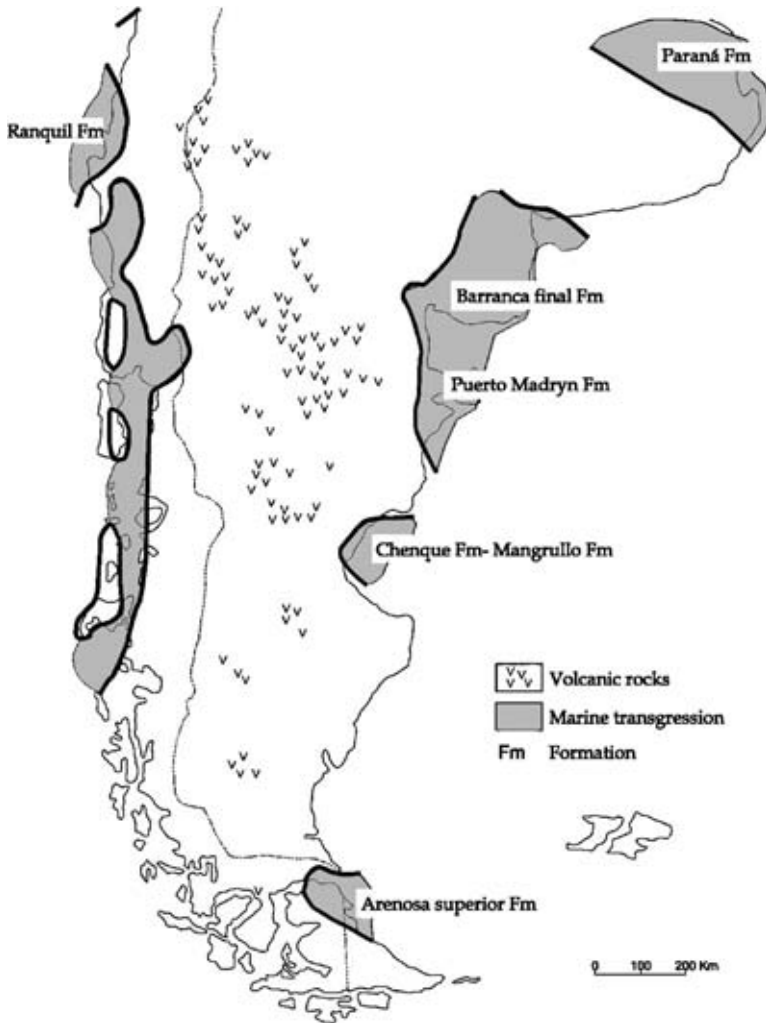


Fig. 1. Main geographical areas affected by the late Oligocene–early Miocene marine transgression and volcanic activity (modified from Donato et al., 2003).

in southern South America. During the middle Miocene, a small Pacific transgression covered Central Chile. Accordingly, during the middle and late Miocene an open seaway newly separated the terrestrial environments of southern South America from those situated farther north, spreading over virtually all of eastern Argentina, 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. 2), that covered large areas between the Andean Cordillera and the Guayanian and Brazilian Bedrocks (see Rässänen et al., 1995; Webb, 1995; Ramos, 1989).

Late Miocene–late Pliocene span (ca. 11–3 Ma): After the disappearance of the Paranean Sea, new and varied land environments arose in the formerly flooded plains and extended northward from northern Patagonia. These new habitats, occurring from late



Fig. 2. Main geographical areas affected by the Miocene–late Miocene marine transgression (modified from Donato et al., 2003).

Miocene to earliest late Pliocene, were so conspicuous that South American paleontologists knew this period as “the Age of the Southern Plains” (see Pascual and Bondesio, 1982; Pascual et al., 1996; Ortiz Jaureguizar, 1998). Land-mammal-bearing sediments containing similar kinds of taxa have been recorded in 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 et al., 1983; Pascual et al., 1996). This fact indicates that similar climate and vegetation prevailed in all of these areas. The emergence of these new habitats is simultaneous with the “Quechua Phase” of Andean diastrophism

(see Yrigoyen, 1979). Under its influence, the Patagonian Andean Cordillera was successively uplifted, progressively forming a major barrier for the moisture-laden South Pacific winds. The rain-shadow effect produced by this mountain barrier on the eastern Patagonia landscapes led to the first stages in the differentiation of both current biogeographic provinces of southern South America (Fig. 3): the Subantarctic province in the west, and the Patagonian province in the centre and south (Pascual et al., 1996).

Additionally, at the beginning of the “Age of the Southern Plains” (ca. 13–11 Ma), the complete separation of South America from the Antarctic Peninsula was established by the

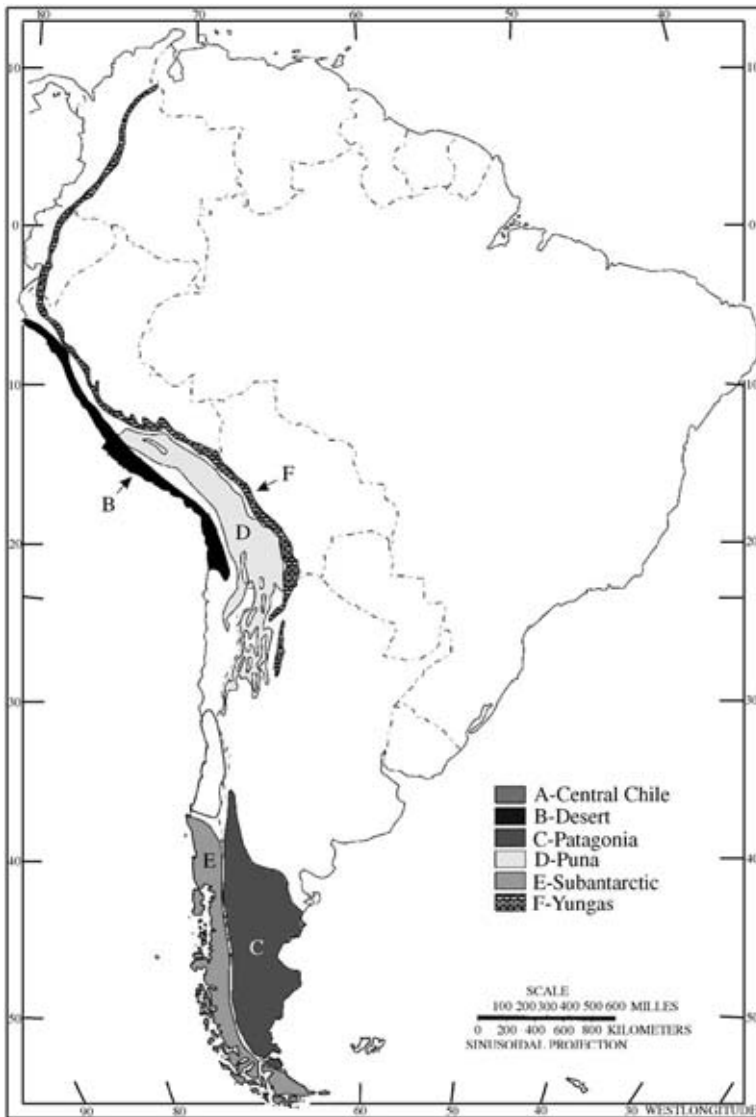


Fig. 3. Biogeographic provinces of the Andean–Patagonic domain, Neotropical region.

final opening of the Drake Passage (Kvasov and Verbitski, 1981). Consequently, the cold Circum–Antarctic Current was finally established and the warm Atlantic waters flowing from the north were pushed aside. Under these conditions, the formation of an ice sheet began in West Antarctica, so that apparently the extent of the glaciation in this continent reached levels similar to the present conditions (Pascual et al., 1996). Thus, during the “Age of the Southern Plains” the climate was cooler and seasonality was more marked than in the middle Miocene, giving rise to a more varied environmental subdivision.

The end of the “Age of the Southern Plains” is concurrent with a new Andean diastrophic phase known as “Diaguita Phase” (see Yrigoyen, 1979; Pascual et al., 1996). This diastrophic event resulted in the elevation of the Central Cordillera of Argentina and Chile, the eastern orographic systems of Argentina (e.g. “Puna”, Pampean Mountain Range, Bonaerian Mountain Range), and the uplift of the Mesopotamian region. The final uplift of the “Pampean Mountain Range” in central Argentina and the “Central Andes” of Chile had evident ecological consequences, as the areas situated between them, which had been well-watered during the “Age of the Southern Plains”, acquired their current extremely xeric nature as a result of the rain shadow effect (Pascual et al., 1996; Alberdi et al., 1997). The final uplift of the “Puna” (according to Ramos and Alonso, 1995, its first stages began during the middle Miocene) also had dramatic effects on the biota, establishing the very arid extreme climatic conditions that are prevalent in this area today.

Early Pleistocene–Holocene span (ca. 2 Ma to Recent): During the Pleistocene, the planet underwent several glacial–interglacial cycles accompanied by the advance and retreat of continental glaciers. During the periods of glacial maxima the climates of many non-glaciated temperate regions were cooler and wetter than those of today. In contrast, tropical regions tended to be drier during glacial maxima. In the Southern Hemisphere, the glaciations were mostly confined to high elevations at high altitudes. The ice coverage of the Andean mountain range reached its maximum in Chile and Argentina (Brown and Lomolino, 1998). Climatic changes associated with the glacial periods caused a general expansion of steppes, savannas, and other open-canopied terrestrial ecosystems instead of closed ecosystems such as tropical rain forests. During the late Pleistocene “Megafaunal extinction” most of the large herbivore mammals became extinct, probably due to climatic changes, hunting by human beings, or temporal coincidence of both (Pascual et al., 1996). At the Pleistocene–Holocene boundary the onset of pluvial conditions allowed the rapid spread of rain forests (Pennington et al., 2000). During the Holocene current conditions were established, with minor but marked fluctuations in rainfall (van der Hammen and Absy, 1994).

3. Methods

3.1. Areas of analysis

The distributional data for the family Tristiridae were taken from Cigliano 1989a. Six main areas of endemism, defined in previous biogeographic schemes (Kuschel, 1969; Cabrera and Willink, 1973), were considered in the analysis. The following areas were used in this study (Fig. 3):

- (1) *Central Chile (A)*: between 32° and 37° South latitude in Chile. This province presents shrubs that form bushes interspersed with small low-height forests.

- (2) *Desert (B)*: This territory is located near the Pacific ocean coast of the north of Chile, Peru, and south of Ecuador, from parallel 5° up to 30° of South latitude. This territory possesses a warm and extremely dry climate due to the Humboldt cold marine current that flows south to north along the Pacific coast. The flora of this province is very peculiar, including both Andean–Patagonic and Chacoan elements. Vegetation is almost completely absent in some areas, whereas succulents or xeric shrublands dominates others.
- (3) *Patagonia (C)*: east of the Southern Andes to the Atlantic coast in Argentina, also extending to Chile in some places. The landscape comprises plateaus, hills and valleys. The climate is dry and cold temperate. Patagonian steppe is the dominant vegetation.
- (4) *Puna (D)*: Highlands extending between the two arms of the Andes mountain range, between parallels 15° and 17° South latitude. The climate is cold and dry. Xeric shrublands make up the dominant vegetation.
- (5) *Subantarctic (E)*: Southern Andes from 37°S to Cape Horn including the archipelago of southern Argentina and Chile. This area comprises valleys and mountains with temperate humid climate. The dominant vegetation is *Nothofagus* forest with small areas of evergreen forest, but also prairies and extensive peat bogs occur.
- (6) *Yungas (F)*: This province extends along the eastern Andes hillsides in a narrow strip from Venezuela to north-western Argentina. The climate is cool and very humid, by reason of the abundant precipitations, and especially because of the almost permanent cloud cover over the mountains. The province extends altitudinally between 500 and 2500–3500 m over sea level, according to latitudes. Cloud forest that extends up to 1800–2500 m over sea level is the dominant vegetation. Above this biome, deciduous forests (*Alnus acuminata*), *Podocarpus* forests, and prairies occur.

3.2. Phylogenetic hypothesis

The historical biogeography of Tristiridae was analysed using the phylogeny of the group proposed by Cigliano and Lange (2000) who used genera as terminals. This phylogeny includes a total of 17 genera (see Table 1). In a previous cladistic analysis of the family performed by Cigliano (1989b) it was not possible to determine its sister group due to the isolated position of the taxon within Acridoidea. As it was mentioned above, the Tristiridae has been related to the families Lentulidae and Pyrgomorphidae of the Chasmosacci group but also to the Cryptosacci group; for these reasons Cigliano (1989b) used a “functional outgroup” to root and polarize the tree. In a second cladistic analysis of the family (Cigliano and Lange, 2000) the authors used *Atacamacris* (Tristiridae) as outgroup, as the goal was to analyse the phylogenetic relationships of genus *Eremopachys*. Based on these considerations I have used a hypothetical outgroup present in all the areas considered in the analysis.

The analysis performed by Cigliano and Lange (2000) resulted in three most parsimonious trees, whose strict consensus tree is shown in Fig. 4. As DIVA only accepts fully resolved cladograms as input, I followed Ronquist’s (1996) suggestion of working with the original trees. The ancestral distributions were inferred from the three trees but the biogeographical conclusions were based only on those biogeographical events supported by the consensus tree.

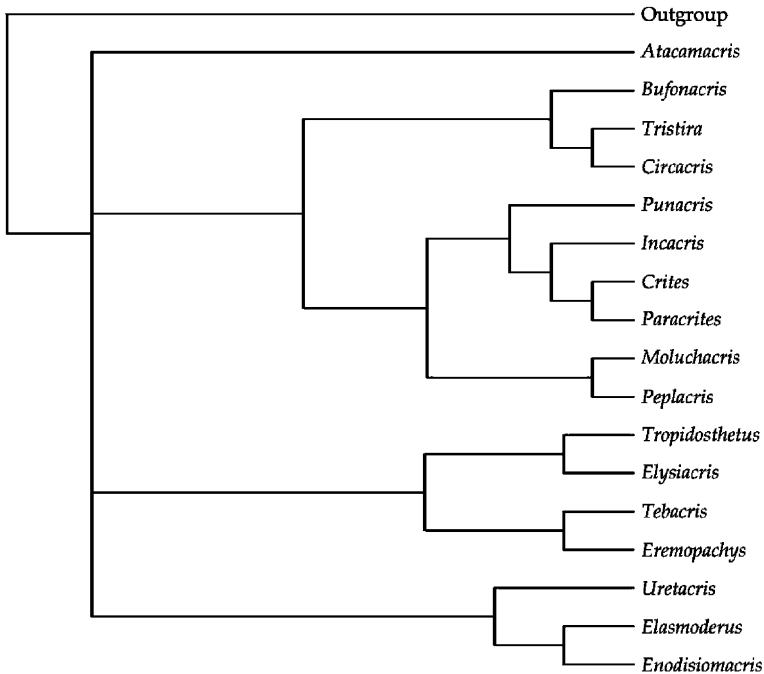


Fig. 4. Strict consensus of the three equally parsimonious cladograms obtained by Cigliano and Lange (2000).

3.3. Biogeographic analysis

The importance of event-based methods has increased in historical biogeographic studies during the last few years (Miranda-Esquivel, 1999; Voelker, 1999; Zink et al., 2000; Sanmartín et al., 2001; Vinnersten and Bremer, 2001; Donato et al., 2003; Sanmartín, 2003). A distinctive characteristic of event-based methods, in contrast to pattern-based methods, is the proposal of explicit models for the processes that affect the geographic distribution of living organisms (Crisci et al., 2003). The different types of processes (e.g. vicariance, dispersal, extinction) are identified and assigned values of cost–benefit under an explicit model of nature functioning (Crisci et al., 2003).

DIVA (Ronquist, 1996) is a method that allows reconstruction of ancestral distributions by maximization of vicariant events and minimization of dispersal and extinction events, but unlike pattern-based methods of cladistic biogeography, it permits non-hierarchical area relationships. For the reconstruction of the ancestral distributions of Tristiridae genera I used DIVA 1.1 (Ronquist, 1996) applying exact search according to the dispersal–vicariance optimization proposed by Ronquist (1997). This software allows to infer the ancestral distribution of a taxon and to calculate the frequencies of vicariance and dispersal events among different areas under consideration. To achieve this, the software constructs a three-dimensional cost matrix derived from a simple biogeographic model and the phylogenetic information encoded in the taxon cladogram (Ronquist, 1997). In DIVA, vicariant and duplication events take a cost of zero, whereas dispersal and extinction events cost one (one per unit area added or deleted from the distribution). A problem of

DIVA is that ancestral area optimizations become less reliable as the analysis approaches the basal node; this becomes apparent as a tendency for the root node to include most of the areas used in the analysis. Sanmartín (2003) proposed the addition of more outgroups into the analysis in order to restrict the ancestral distributions at the basal node. As the phylogenetic relationships of Tristiridae are not yet clear, I chose to include a hypothetical outgroup present in all the areas considered in the analysis to solve this uncertainty.

The results obtained by DIVA were interpreted in the context of the South American geobiotic evolution. As was mentioned above, I have used the compositional changes of land mammal communities as well as the geographic range and lithofacies of the typical mammal bearing formations to illustrate the climatic–environmental changes occurred in South America during the early Miocene–Recent time span.

4. Results and discussion

According to the results obtained by DIVA for the original three cladograms, there are 250 alternative equally optimal reconstructions, each requiring eight dispersal events. Fig. 5 shows the optimal area reconstructions at each node. Although the number of alternative reconstructions is high, they are very similar and only differ in the ancestral distributions at some internal nodes.

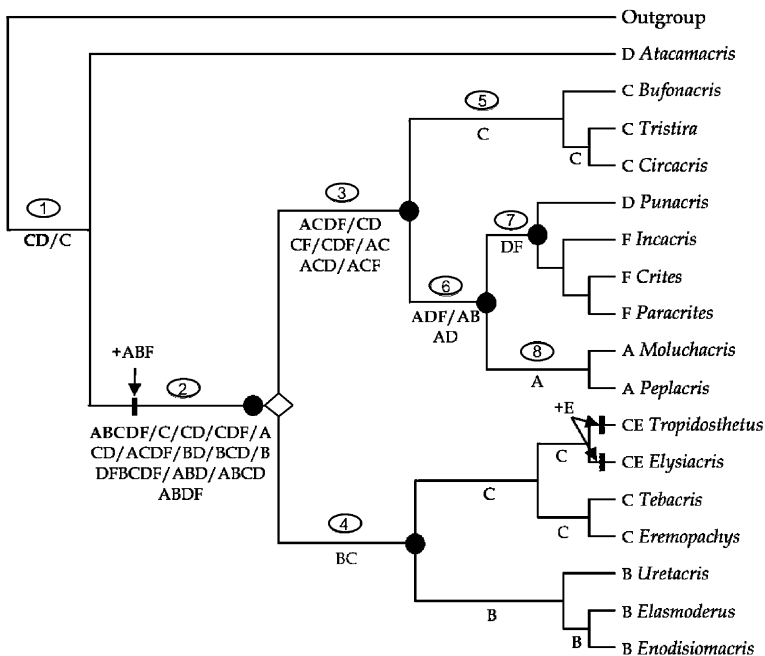


Fig. 5. Cladogram of South American Tristiridae showing the main biogeographic events as result from DIVA. The cladogram is one of the three most parsimonious trees obtained by Cigliano and Lange (2000). All optimal distributions are given at each node; bold type indicates those that were chosen. Symbols: circle = vicariance event; rhomb = duplication event (sympatric speciation); arrow with (+) = dispersal event.

Tristirids are endemic for South America and according to DIVA results, there is only one optimal ancestral distribution for the basal node of the family Tristiridae, represented by the areas Puna and Patagonia (node 1 on Fig. 5). This inferred ancestral distribution is partially congruent with the hypothesis proposed by Carbonell (1977), who postulated Patagonia and Southern Chile as the geographical origin of tristirids. During the late Oligocene–early Miocene span (time in which the tristirids probably originated), Patagonia and Puna could be considered as a whole due to the homogeneous climate. In fact, at this time, both areas were characterized by land-mammal communities dominated by a unique association of frugivorous, browser, and grazer types. This association indicates the existence of a balance between woodlands and grasslands (Pascual et al., 1996). From a climatic point of view, the presence of primates and other climate-sensitive vertebrates in latitudes as high as 53°S indicates the existence of warm-temperate wet climates. Unfortunately, the floristic record for the middle Miocene is deficient, and/or not well dated (Pascual et al., 1996).

The ancestral distribution at node 2 (Fig. 5) is considered as a dispersal event of the ancestral Tristiridae from Puna + Patagonia to Central Chile, Desert, and Yungas. It is worth mentioning that this node differs in each tree. In the chosen cladogram the ancestral distribution at this node hypothesizes a possible vicariant event splitting Central Chile + Patagonia + Puna + Yungas lineage and Desert + Patagonia lineage with duplication and/or extinction events. In the other trees the ancestral distributions hypothesize a vicariant event that split Desert lineage from the rest of the areas (with the final result of the genera *Uretacris*, *Elasmoderus*, and *Enodisiomacris* occurring in this area) or a vicariant event splitting Patagonia lineage from the rest of the areas (with the final result of the genera *Tropidosthetus*, *Elysiacris*, *Tebacris*, and *Eremopachys* present in this area). Any of these cases could be explained by the marine transgression known as the Paranean Sea (middle Miocene). This could have acted as a barrier promoting subsequent speciation or otherwise affected or disturbed the landscapes. Cold and dry climate has been recorded since the middle Miocene, appearing first in southern Patagonia and then extending northwards.

Node 3 (Fig. 5) indicates the occurrence of a vicariant event that split Patagonia lineage in one branch from Central Chile + Puna + Yungas lineage in the other. The events recorded at this node could have taken place during the late Miocene. Grazer and cursorial types (characteristic of the “Age of the Southern Plains”, ca. 13–3 Ma) dominated South American land-mammal communities at this time (Pascual et al., 1996; Ortiz Jaureguizar, 1998). During this period, the climate was cooler and seasonality was more marked than in the middle Miocene, and environmental subdivision was greater. For example, the habitats at the flood plains located in the north-western end of Patagonia and eastern Mesopotamian region were wet and forested. Conversely, the habitats at the higher-plain alluvial deposits of central-western Argentina were relatively more arid and shrubby (Alberdi et al., 1997).

The end of the “Age of the Southern Plains” was marked by the “Diaguita Phase” of Andean diastrophism (see Pascual et al., 1996), when these southern South American landscapes changed dramatically. Thus, the final uplift of the “Pampean Mountain Range” in central Argentina and the “Central Andes” of Chile had pronounced ecological consequences, producing a rain shadow effect that resulted in the extremely xeric conditions currently prevailing on the areas located between these mountain ranges (Pascual et al., 1996; Alberdi et al., 1997). The “Diaguita Phase” could explain the

vicariant event registered in node 6 (Fig. 5) with the consequent separation of Puna and Yungas lineages on one side and Central Chile lineage on the other, with the current occurrence of the genera *Moluchacris* and *Peplacris* on the latter area.

The final uplift of the “Puna” established the very arid and extreme climatic conditions currently found in this area. Consequently, the isolation of genus *Punacris* (node 7) could be a result of the progressively drier and extreme climatic conditions of the Puna plateau, which is at present located at 4000 m over sea level and undergoes striking temperature differences between day and night, as well as between summer and winter. The event at node 6 seems to be vicariant, splitting Puna lineage from Yungas lineage, but Yungas was not the current subtropical semi-evergreen forest (= “rainforest”) at this time. Xeric conditions prevailed during late Pleistocene. DIVA frequencies for dispersal between single areas show high values for Puna to Yungas. The spread of rainforests occurred at the Pleistocene–Holocene boundary due to more marked pluvial conditions. Therefore, the evidence as to which event occurred (vicariance or dispersal) at this node is inconclusive.

Finally, the abovementioned presence of genera *Tropidostethus* and *Elysiacris* in the Subantarctic province plus Patagonia could be explained as recent dispersal events.

5. Summary

Based on the results of dispersal–vicariance analysis (DIVA), I propose a Punaean + Patagonian diversification of the family Tristiridae. The first ancestral distribution resulting from the analysis shows the ancestral tristirid inhabiting the areas Puna and Patagonia considered jointly. This ancestral distribution coincides with the Andean Subregion sensu Crisci et al. (1991) and probably reflects the Andean origin of the group.

The ancestral Tristiridae dispersed from Puna + Patagonia to Central Chile, Desert, and Yungas. As a result of the marine transgression known as the Paranean Sea (middle Miocene) this lineage splits by a vicariant event in Central Chile + Patagonia + Puna + Yungas and Desert + Patagonia with duplication and/or extinction events. The former suffers a vicariant event that split a Patagonian lineage in one branch and Central Chile + Puna + Yungas lineage in the other. The events recorded at this node could have taken place during the late Miocene. The later undergoes a vicariant event that splits a Patagonian lineage with the final result of the genera *Tropidostethus*, *Elysiacris*, *Tebacris*, and *Eremopachys* present in this area, and a Desert lineage with the final result of the genera *Uretacris*, *Elasmoderus*, and *Enodisiomacris* occurring in this area.

The ancestral distribution Central Chile + Patagonia + Puna + Yungas suffered a vicariant event due to drastic environmental changes known as the “Age of the Southern Plains” and could have taken place during the late Miocene. One branch occurred in Patagonia with the final result of the genera *Bufonacris*, *Tristira*, and *Circaecris* occurring in this area.

Another vicariant event, due to the final uplift of the “Pampean Mountain Range” in central Argentina and the “Central Andes” of Chile, divided Puna and Yungas lineages from Central Chile lineage. In the former, possibly due to a vicariant or a dispersal event, Puna lineage (with the final result of *Punacris* living in this area) was separated from Yungas lineage (with the occurrence of *Incacris*, *Crites*, and *Paracrites* living in this area). The later persists in the area with the current occurrence of the genera *Moluchacris* and *Peplacris* in Central Chile.

As a corollary, the progressively arid conditions occurring in this part of South America due to the aforementioned processes that occurred during the early Miocene–Recent time span, had major bearing on the biogeographic ancestral distribution of the Tristiridae.

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