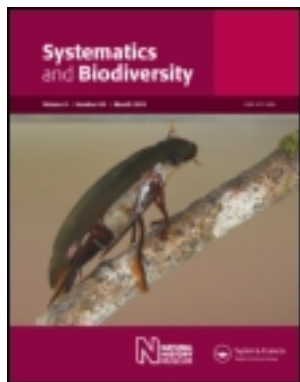


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## Systematics and Biodiversity

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tsab20>

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Version of record first published: 18 Jun 2012

To cite this article: Nelson Ferretti, Alda González & Fernando Pérez-Miles (2012): Historical biogeography of mygalomorph spiders from the peripampasic orogenic arc based on track analysis and PAE as a panbiogeographical tool, *Systematics and Biodiversity*, 10:2, 179-193

To link to this article: <http://dx.doi.org/10.1080/14772000.2012.694375>

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## Research Article

# Historical biogeography of mygalomorph spiders from the peripampasic orogenic arc based on track analysis and PAE as a panbiogeographical tool

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(Received 19 March 2012; revised 10 May 2012; accepted 11 May 2012)

A panbiogeographical analysis of Mygalomorphae spiders was undertaken in order to determine generalized tracks and biogeographical nodes in the peripampasic orogenic arc. This arc comprises mountainous systems that harbour a high number of endemic species, while they exhibit biotic connections that have become fragmented probably during Tertiary tectonics. They are considered relevant areas for biodiversity conservation. A total of 1078 records of 51 Mygalomorphae species were analysed and ten areas were delimited based on geological data. We used track analysis and parsimony analysis of endemism as a panbiogeographical tool. Five generalized tracks and three nodes were recovered. The tracks recovered in Argentina could be explained as a consequence of two events: (i) Atlantic marine transgressions during the Middle and Late Miocene; and (ii) changes in the climate of southern South America from the Miocene to Pliocene, caused by the gradual raising of the Andean chain and also, the additional uplift of Pampean and Subandean ranges. The southeastern Brazil and Uruguayan generalized tracks could be explained by the Rio de La Plata Craton.

**Key words:** generalized tracks, Mygalomorphae, nodes, panbiogeography, South America

## Introduction

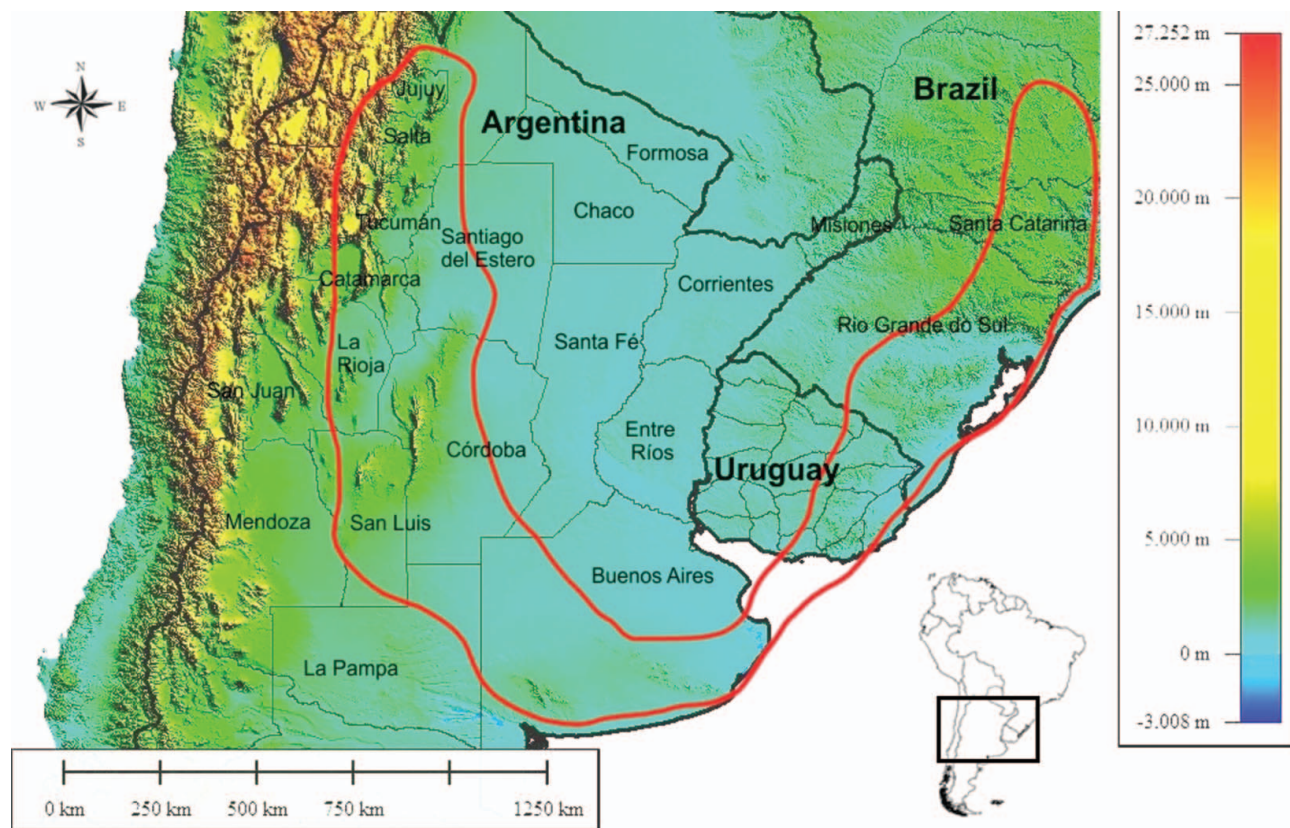
Panbiogeography (Croizat, 1958, 1964) is based on coincident distribution of different taxa (generalized tracks) that reveal the existence of ancestral biotas, with distributions fragmented due to past vicariant events. Panbiogeographical analyses have been undertaken in many different groups of organisms to elucidate the common evolution of areas and biotas. Although in recent years panbiogeography has become one of the main research programmes in historical biogeography (Morrone & Crisci, 1995; Craw *et al.*, 1999; Crisci, 2001; Morrone, 2004; Martínez-Gordillo & Morrone, 2005; Alzate *et al.*, 2008; Cavalcanti & Gallo, 2008; Heads, 2008, 2010; Arzamendia & Giraud, 2009; Moreira Pires *et al.*, 2011), so far the panbiogeographical method has not been applied to the analysis of spider distributions. The panbiogeographical method emphasizes the relevance of the geographical distributions as direct objects of analysis.

Parsimony analysis of endemism (PAE) was proposed by Rosen & Smith (1988) and involves studying the

distributions of taxa in different localities and geological horizons. Recently, Morrone (2005, 2009) considered that the use of PAE is a quantitative method in panbiogeography, allowing the identification of primary biogeographical homology (this is the historical relationships between areas) (Morrone, 2001). Moreover, this method can be used to identify biotic components under a panbiogeographical approach (Morrone, 2005, 2009). It was demonstrated that parsimony analysis of endemism could be a method implementing the panbiogeographical approach (Echeverry & Morrone, 2010). A PAE by individual tracks enables the generation of historical hypothesis of area relationships into an area fragmentation sequence frame (Echeverry & Morrone, 2010).

The ‘peripampasic track’ (Acosta, 1989, 1993; Mattoni & Acosta, 1997) or ‘peripampasic orogenic arc’ comprises a group of mountain ranges from Argentina, Uruguay and southern Brazil (Frenguelli, 1950). It describes an arc extending from southern Brazil, mountain ranges of southeastern Uruguay and mountainous systems from Central and northern Argentina (Fig. 1). Frenguelli (1950) gave the name of peripampasic orogenic arc to the biotic corridor constituted by Pampean ranges, Mahuidas (group of

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**Fig. 1.** Map showing the extension of the peripampasic orogenic arc delimited by the red line.

mountain ranges in La Pampa province, in Central Argentina) and Tandilia. Later, studies based on scorpions and harvestmen (Maury, 1973; Acosta, 1989, 1993; Mattoni & Acosta, 1997) showed a zoogeographical link between Tandilia and Ventania with the Pampean ranges but also an extension of the peripampasic track in northwestern Argentina and southern Brazil was proposed. The peripampasic orogenic arc is interesting from a biogeographical viewpoint. This arc comprises mountainous systems which due to their unique biota have attracted several generations of geologists and biologists (Darwin, 1846; Cabrera, 1938; Teruggi & Kilmurray, 1975; Crisci *et al.*, 2001). Many of the hilly systems harbour a high number of endemic species (Crisci *et al.*, 2001; Grell, 2004; Pinto-da-Rocha *et al.*, 2005; Aagesen *et al.*, 2009) and exhibit biotic connections that have become fragmented probably during the last 65 Ma from the Tertiary tectonics (Ringuet, 1961; Acosta, 1989, 1993; Mattoni & Acosta, 1997; Crisci *et al.*, 2001). These areas are considered relevant for biodiversity conservation (Szumik *et al.*, 2007; Navarro *et al.*, 2009; Nori *et al.*, 2011).

Mygalomorph spiders are well-suited models for biogeographical analysis of the peripampasic orogenic arc. These spiders are distributed worldwide, but they are especially

abundant in tropical regions and temperate austral regions of South America, southern Africa and Australasia (Raven, 1985; Platnick, 2011). They are long-lived and univoltine, and show high local endemism. They are among the first spiders to be listed as threatened, but often their low incidence, cryptic habits and burrowing behaviour severely limit useful knowledge about their biology (Raven, 2010). Moreover, mygalomorphs possess life-history traits that markedly differ from other spiders. For example, some species live for 15–30 years and require 5–6 years to reach reproductive maturity (Main, 1978). They are habitat specialists and females and juveniles are sedentary (Main, 1987; Coyle & Icenogle, 1994). These life-history traits promote geographic isolation through fragmentation over space and time, resulting in a large number of taxa that have small geographical distributions (Bond *et al.*, 2006). Biogeographically, they seem informative because mygalomorphs are animals with poor vagility, limited dispersal mechanisms and sedentary habits. Those characteristics have isolated many groups on continents by continental drift, restricted by glaciations, orogenic activity and habitat fragmentation through progressive drying (Raven, 2010). Moreover, some groups seem to be Gondwanan in distribution and origin (Raven, 1984; Griswold, 1985). These

biological characteristics of the Mygalomorphae make them a promising group of organisms for biogeographical studies. To date, there are few formal contributions to the biogeography of mygalomorph spiders (Bertani, 2001; Bond *et al.*, 2006; Hendrixson & Bond, 2007; Starrett & Hedin, 2007; Guadanucci, 2011).

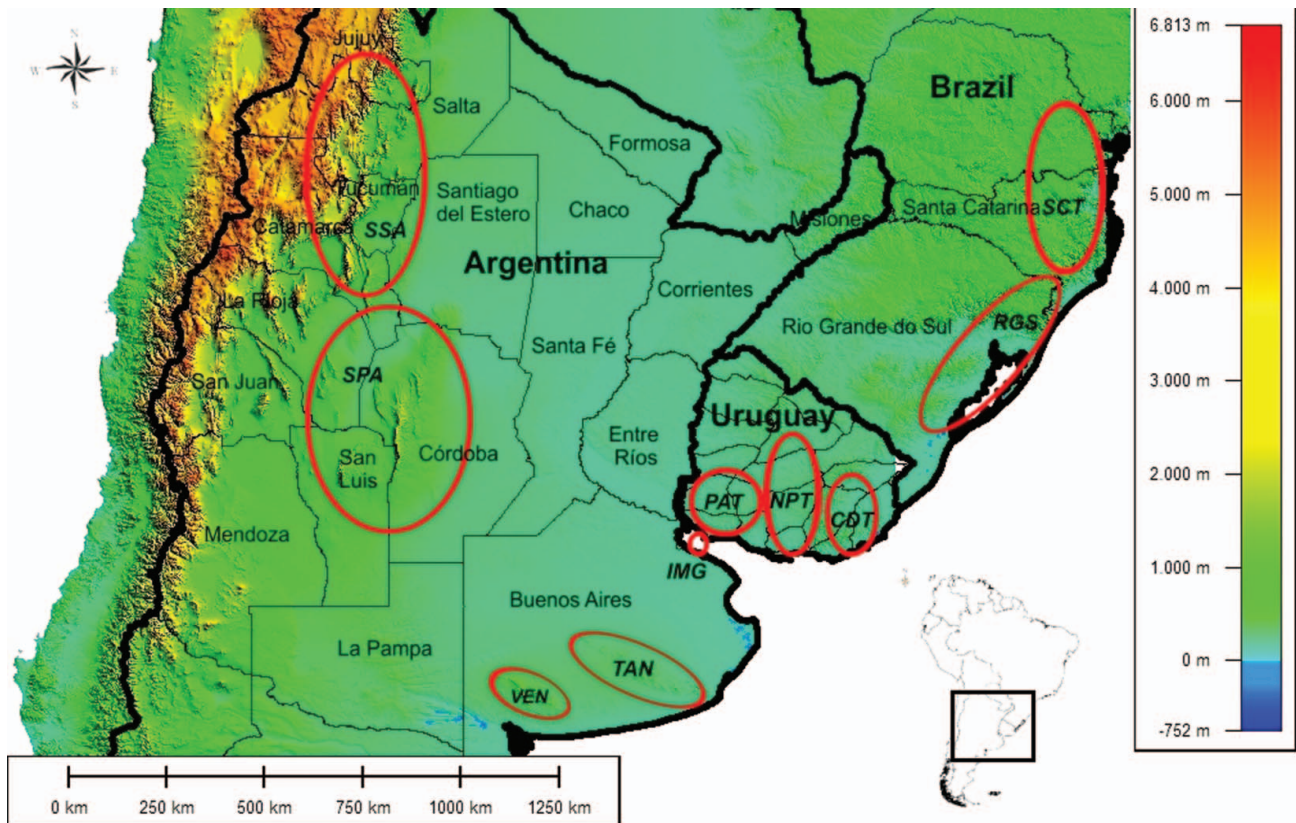
Here, we present the first panbiogeographical analysis of Mygalomorphae spiders in Argentina, Uruguay and southern Brazil seeking to establish distributional patterns for these spiders, allowing us to test the hypothesis proposed by many authors (Ringuelet, 1961; Acosta, 1989, 1993; Mattoni & Acosta, 1997; Crisci *et al.*, 2001) whether some species with disjoint distributions were part of an ancient biota, occupying the mountain ranges currently fragmented within the ‘peripampasic track’. The selected analytical tool was panbiogeography because this technique generates explicit spatial hypotheses on the distributional patterns of taxa rather than comparing simple faunal similarity (Maya-Martínez *et al.*, 2011). This analysis helps to establish spatial homologies, that is, the historical biogeographical coherence of biotic components (Craw, 1988; Morrone & Crisci, 1995; Grehan, 2003). The advantages of well-sampled, fully resolved phylogenies are obvious. For

example, it is possible to construct a biogeographical hypothesis based on the notions of phylogeny and tracks, but results are much more powerful if the method is extended to incorporate orientation of tracks using phylogenetic criteria (Page, 1987; Heads, 2010). However, if phylogenetic information is not available, which is the case of most of genera of Mygalomorphae, panbiogeography might be a useful tool to elucidate the common evolution of areas and biotas (Alzate *et al.*, 2008). Additionally, we interpret our results in the context of the geobiotic evolution of southern South America.

## Materials and methods

### Study area

On the basis of several overlapping in taxa distribution (mainly for Argentinean areas) (Ringuelet, 1961; Acosta, 1993; Mattoni & Acosta, 1997; Crisci *et al.*, 2001), and geological criteria, such as different formation types (Argentina, Uruguay and southern Brazil areas), the areas delimited here are the following (Fig. 2).



**Fig. 2.** Areas considered in the historical biogeographical analysis: VEN = Ventania, TAN = Tandilia, SPA = Pampean ranges, SSA = Subandean ranges, IMG = Martín García Island, PAT = Piedra Alta Terrane, NPT = Nico Pérez Terrane, CDT = Cuchilla Dionisio Terrane, SCT = Santa Catarina, RGS = Rio Grande do Sul.

### Subandean ranges (SSA)

They consist of a group of mountain ranges about 3000–5000 m high (Mingramm *et al.*, 1980), in north-western Argentina, extending from north to south of the provinces of Salta, Jujuy and Tucumán (between 23°22'S–65°19'W and 28°51'S–65°34'W). Large outcrops of the Precambrian and Cambrian rocks predominate in the eastern ranges of the Andes, whereas Palaeozoic, Mesozoic and Cenozoic rocks crop out in the Subandean ranges (occasionally, a large mass of Ordovician rocks, cored by Cambrian and Precambrian rocks, crops out in the Subandean ranges) (Poblet *et al.*, 2008).

### Pampean ranges (SPA)

They are located at northwestern and central Argentina (between 29°41'S – 64°51'W and 33°20'S – 65°33'W), and comprise a group of mountain ranges extending in the provinces of Córdoba, Santiago del Estero, eastern Catamarca and San Luis. They are 3000 m high surrounded by vast plains of 600–900 m (Gordillo & Lencinas, 1980). The Pampean ranges consist of metamorphic and plutonic igneous basement that were uplifted by reverse west faulting during the Andean orogeny (Von Gosen, 1998; Galindo *et al.*, 2004).

### Ventania (VEN)

This area comprises a hilly system located southwest of Buenos Aires province, Argentina (38°07'S – 62°03'W). It shows a 180 km long sigmoidal mountain belt from northwest to southwest and 50 km width, composed of basement and sedimentary cover. The basement consists of Late Precambrian–Early Palaeozoic deformed granites, rhyolites and andesites. Deformational episodes occurred during the Upper Devonian and Permian (Sellés–Martínez, 2001; Gregori da López & Grecco, 2005). The mountains that form the Ventania range culminate at varying altitudes and correspond to differentially uplifted blocks (Demoulin *et al.*, 2005).

### Tandilia (TAN)

Located southeast of Buenos Aires province, Argentina (37°19'S–59°9'W), the 'Sierras de Tandil' (Tandilia) is a northwest trending, 350 km long, subdued mountainous system consisting of ranges and hills that rise 50–250 m above the surrounding Pampean plain (González–Bonorino *et al.*, 1956; Demoulin *et al.*, 2005). The Tandilia range is made up of a Proterozoic crystalline basement that pertains to the Rio de la Plata craton (Dalla Salda, 1999), mainly composed of granitoids, migmatites, amphibolites and hypabyssal igneous rocks overlain by Precambrian and lower

Palaeozoic sedimentary rocks (Teruggi & Kilmurray, 1975; Pankhurst *et al.*, 2003).

### Martín García Island (IMG)

Martín García Island (Buenos Aires province, Argentina) lies at the confluence of the Uruguay and Paraná Rivers (Upper Rio de la Plata River) (34°11'S–58°15'W). This island is 37.5 km from the Argentinean coast and 3.5 km from the Uruguayan coast. It is an outcrop of the crystalline basement, overlain by Pleistocene and Holocene sediments (Ravizza, 1984). Martín García Island consists of a small remnant of rocks of the Precambrian crystalline basement, with the oldest rocks dating from 2085–2050 Ma (Dalla Salda, 1981).

### Uruguayan Shield (PAT, NPT and CDT)

The Uruguayan Shield exposes the Rio de la Plata Craton outlined by Neoproterozoic orogens, and it is composed of three major tectonic units (Hartmann *et al.*, 2001), namely from west to east: Piedra Alta Terrane (PAT), Nico Pérez Terrane (NPT) and Cuchilla Dionisio Terrane (CDT). The PAT is located on the west, the NPT in the centre and the CDT along the Atlantic coast (Hartmann *et al.*, 2001). The PAT and NPT constitute the Rio de la Plata Craton in Uruguay, encompassing essentially Archean to Palaeoproterozoic units (Hartmann *et al.*, 2001). The CDT is considered a Neoproterozoic mobile belt that defines the eastern limits of the craton (Hartmann *et al.*, 2001).

### Southern Brazil

This area extends from the states of Santa Catarina (SCT) (26°55'S – 49°22'W) (which seems to be the northern limit for the Rio de la Plata craton) to Rio Grande do Sul (RGS) (31°42'S – 52°41'W) (Rapela *et al.*, 2007). The most significant evolutionary characteristics of the Rio de la Plata craton are: a lithology dominated by juvenile Palaeoproterozoic rocks of the Transamazonian cycle with an isochron age of 2140 ± 88 Ma (Preciozzi *et al.*, 1999; Pankhurst *et al.*, 2003); and the lack of any major Mesoproterozoic or younger event, except for the tholeiitic dyke swarms. However, it is worth noting that the age patterns of the different terranes and blocks of the Rio de la Plata craton are also present in other Archaean/Palaeoproterozoic blocks and microplates of southern Brazil, such as those in Santa Catarina and Paraná areas (Saalman *et al.*, 2006; Rapela *et al.*, 2007).

### Taxa

The analysis was performed using 1078 distributional records of 51 species of Mygalomorphae (Appendix 1, see supplementary material, which is available on the

Supplementary tab of the article's Informaworld page at <http://www.informaworld.com/mpp/uploads/tsab...>) belonging to the families Actinopodidae, Dipluridae, Idiopidae, Migidae, Mecicobothriidae, Microstigmatidae, Nemesiidae and Theraphosidae, distributed in Argentina, Uruguay and southern Brazil. Data included in the analysis were obtained by examination of two museum collections (MACN: Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; FCIEN: Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay) and from the arachnological literature (Schiapelli & Gerschman de Pikelin, 1945, 1960, 1963, 1964, 1967, 1970, 1975; Gerschman de Pikelin & Schiapelli, 1960, 1963, 1966, 1971, 1973, 1978; Gerstch & Platnick, 1979; Goloboff, 1987, 1995; Goloboff & Platnick, 1992; Bertani, 2001; Guadanucci, 2004; Indicatti *et al.*, 2007, 2008; Miglio, 2009; Bertani *et al.*, 2011; Ferretti *et al.*, 2011; Fukushima *et al.*, 2011). The latitude and longitude of the respective localities were defined according to the following databases: Global Gazetteer (Falling Rains Genomics, [www.fallingrain.com](http://www.fallingrain.com)); a gazetteer extension from Argentina and Uruguay with DIVA-GIS 7.4 (Hijmans *et al.*, 2011); and Geody ([www.geody.com](http://www.geody.com)).

### Track analysis

The panbiogeographical analysis seeks to detect generalized tracks, which indicate the existence of ancestral biotic components inferred to have been fragmented by climatic or tectonic events (Croizat, 1958; Craw, 1988; Craw *et al.*, 1999). Generalized tracks are equated to biogeographical homology or areas of endemism (Page, 1987; Craw, 1988; Morrone & Crisci, 1995; Craw *et al.*, 1999; Luna-Vega *et al.*, 2000; Morrone, 2001, 2004; Corona & Morrone, 2005) and by determining them, we are testing the hypothesis of biogeographical homology and the existence of a biota modelled by barriers or corridors using current tracks (Arzamendia & Giraud, 2009). Individual tracks for each species were constructed by plotting their localities of occurrence on maps with the Global Mapper 9.0 and connecting them by minimum-spanning trees using the Trazos extension (Rojas-Parra, 2007) with the Arcview 3.2 software (ESRI, 1999). To construct generalized tracks, all the individual track maps were printed and then overlapped. Generalized tracks were determined from the areas of overlap of individual tracks. In order to avoid the ambiguity and the subjective factor produced when overcrowded geographical points are evaluated, the dataset was analysed by using the MartiTracks (Echeverría-Londoño & Miranda-Esquível, 2011) software with the following parameters: cut value = 3, lmin = 3, lmax = 2.5, lmax.line = 4, and min-SI = 0.8. MartiTracks is a quantitative alternative to traditional track analysis (e.g. that originally devised by Croizat).

### Parsimony analysis of endemism (PAE) as a panbiogeographical tool

PAE is a method to reconstruct area history based on patterns of shared endemic species (Rosen, 1988), without the need for detailed phylogenetic studies of individual lineages. The original version of PAE was intended to cross temporal samples, detecting appearance of new species in stratified samples through time (Nihei, 2006). This approach bases inferences on a matrix of species  $\times$  sites, and uses maximum parsimony analysis to link area units on the basis of shared endemic species, which are ostensibly analogous to shared derived characters in a phylogenetic analysis (Posadas *et al.*, 2006; Peterson, 2008). Echeverry & Morrone (2010) postulated that when using PAE as a panbiogeographical tool you should take into account the basic panbiogeographical concept of the individual track, allowing the incorporation of the spatial component a priori. In the panbiogeographical implementation of PAE, the spatial or geographical information is highlighted by the use of individual tracks (instead of simple sample localities) as the source from which generalized tracks are recognized (Echeverry & Morrone 2010). Moreover, the algorithm implementing PAE as a panbiogeographical method comprises the construction of individual tracks and then the generation of an  $r \times c$  matrix, where the rows ( $r$ ) represent geographic units and the columns ( $c$ ) represent individual tracks. In order to identify composite areas or nodes and single areas that are involved in different generalized tracks, we used PAE with progressive character elimination (Luna-Vega *et al.*, 2000; García-Barros *et al.*, 2002; Echeverry & Morrone, 2010). We constructed geographic units (defined before)  $\times$  individual tracks matrix. Each matrix entry is '1' when an individual track is present in or crosses a given geographical unit and '0' if it is absent or does not cross it. Also a hypothetical area coded '0' for all columns in the data matrix were included to root the resulting cladogram. The parsimony analysis of the data matrix was performed with TNT 1.1 package (Goloboff *et al.*, 2003). We made a traditional heuristic search using collapsing rule 'tbr' (tree bisection reconnection). Under this algorithm the tree is divided into two parts, and these are reconnected through every possible pair of branches in order to find a shorter tree. This is done after each taxon is added, and for all possible divisions of the tree (Goloboff *et al.*, 2008).

### Results

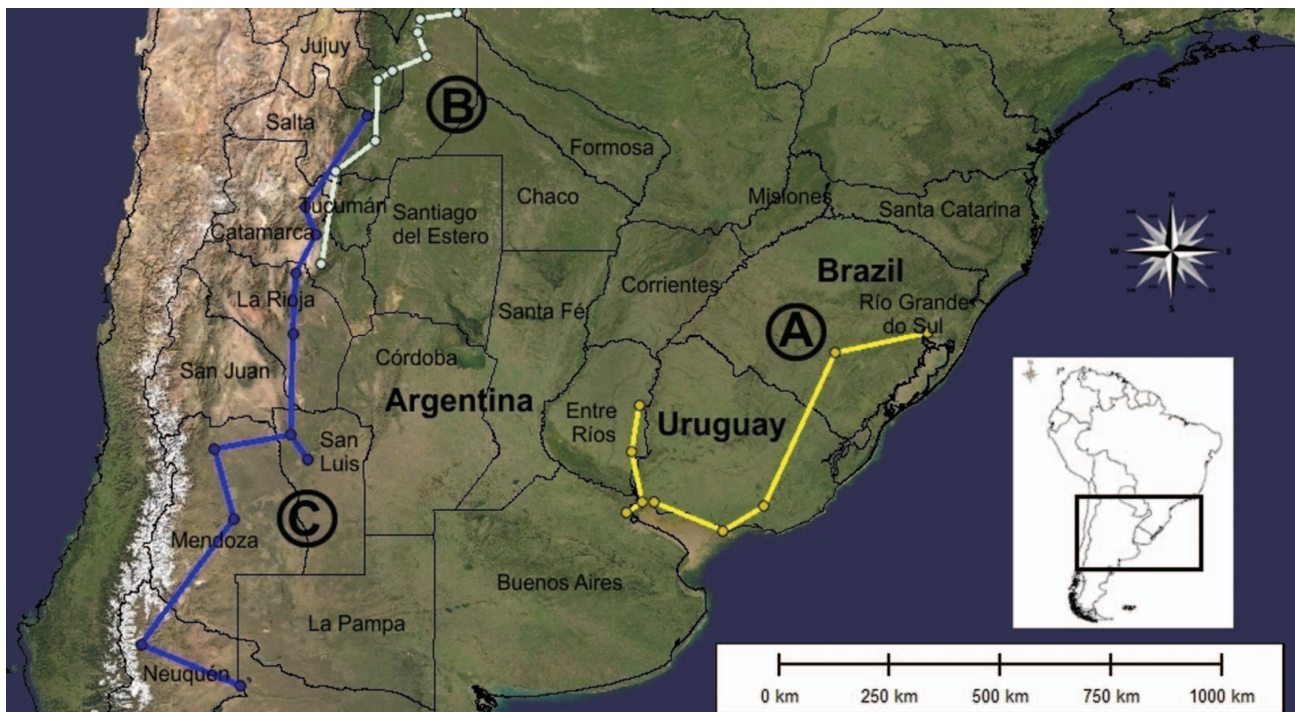
Some of the individual tracks found for some species of Mygalomorphae whose distributions are clearly within the peripampasic arc or with some points outside it, are shown in Figs 3 and 4. Five generalized tracks were identified for Mygalomorphae (Figs 5 and 6) using manual track analysis and MartiTracks (Table 1). The first (T1) supported by 12 species, was located through southern Brazil at the states of



**Fig. 3.** Individual tracks. *Acanthogonatus centralis* (A), *Mecicobothrium thorelli* (B) and *Catumiri parvum* (C).

Santa Catarina and Rio Grande do Sul. This track joins the geographic units of SCT and RGS (Fig. 5). The track T2 (Fig. 5), defined by 9 species, was located in southern Brazil, at the RGS geographic unit, from east to western Uruguay

(including the three geographic units CDT, NPT and PAT). Also, it reached central-eastern Argentina in Entre Rios province and IMG. In PAT (Uruguay), this track extended to the northeast at the Sierra de las Ánimas complex.



**Fig. 4.** *Xenonemesia platensis* (A), *Melloleitaoina crassifemur* (B) and *Grammostola inermis* (C).

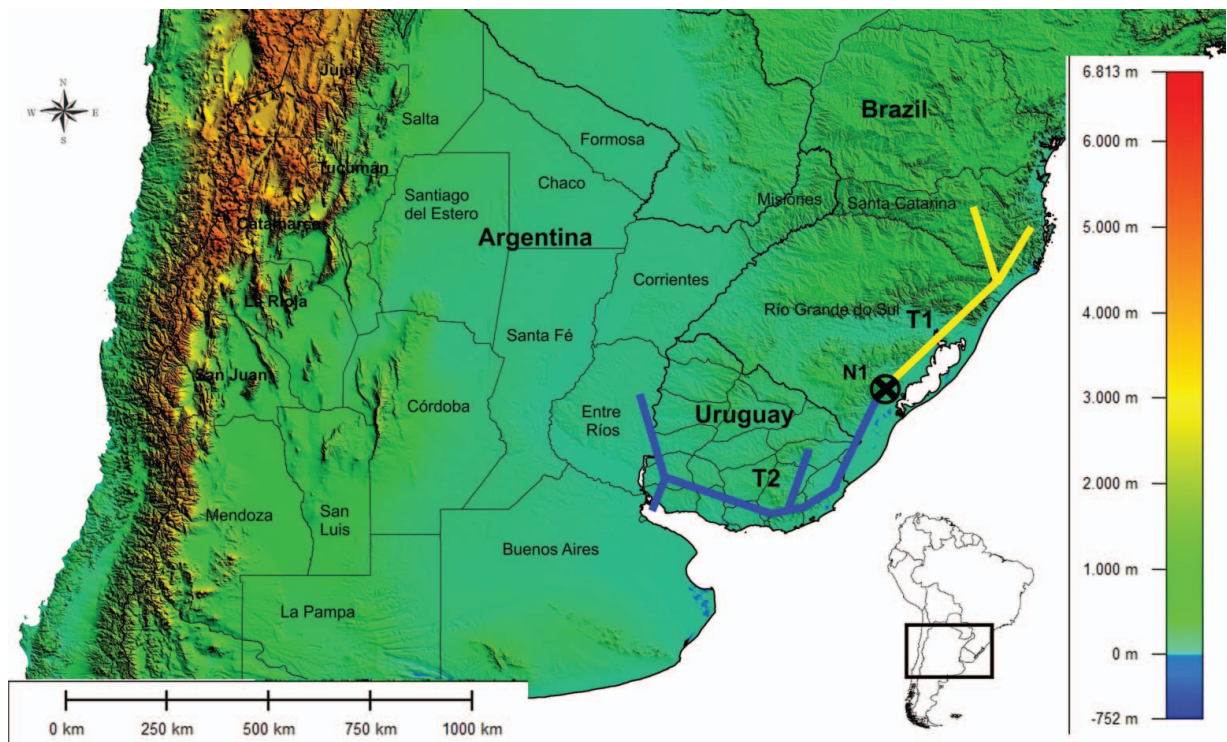
The other three tracks recovered are located in Central and north Argentina. Track T3 (Fig. 6), defined by five species, was situated at the south of Buenos Aires province, at the geographic units of VEN and TAN. Track T4 (Fig. 6), supported by seven species, was located from Central to northwestern Argentina. This track included the areas of VEN, SPA and south of the SSA. The northernmost track T5 (Fig. 6), defined by 15 species, was situated in the SSA and also extended to the eastern Andes.

In addition to the tracks recovered, three biogeographical nodes (Figs 5 and 6) were established in the intersection of tracks T1 and T2 in southern Brazil, T3 and T4 in southwestern Buenos Aires province (Argentina) and T4 and T5 in northwestern Argentina. Node 1 was located at the geographic unit of RGS. Node 2 was located at the geographical unit of VEN and node 3 was located at the SSA and eastern Andes.

The PAE of the geographical units × individual tracks produced one tree, with 62 steps, a consistency index of 0.823 and a retention index of 0.828 (Fig. 7). Five generalized tracks were identified (T1 to T5 in Fig. 8). The first (T1) supported by the species *Actinopus ceciliae* Mello-Leitão, 1931, *Stenoterommata palmar* Goloboff, 1995, *Vitalius roseus* (Mello-Leitão, 1923) and *Xenonemesia platensis* Goloboff, 1989 joins the geographical units of SCT and RGS. The track T2 defined by two species: *Catumiri parvum* (Keyserling, 1878) and *Xenonemesia*

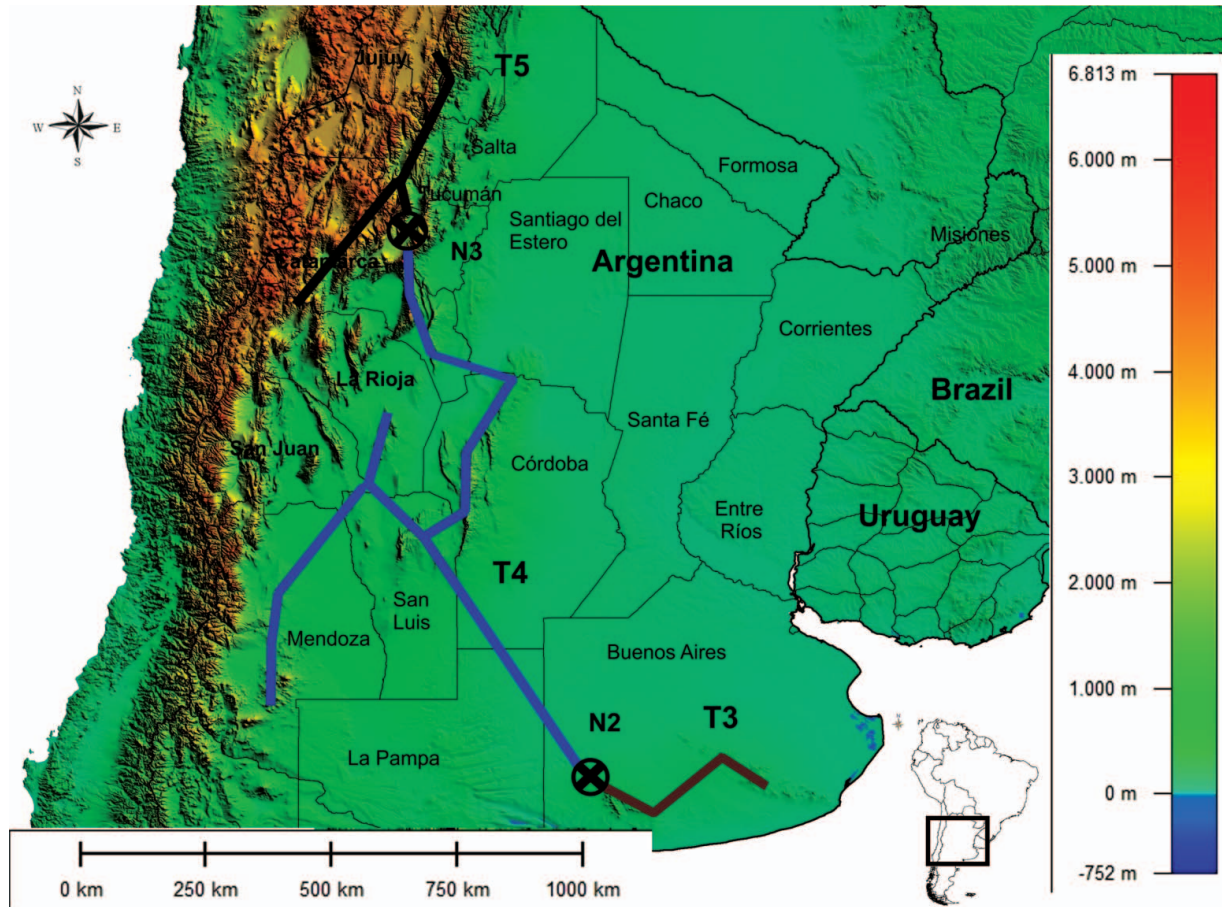
**Table 1.** Generalized tracks recovered in the panbiogeographical analyses of Mygalomorphae, with species supporting each track and geographic units. VEN = Ventania, TAN = Tandilia, SPA = Pampean ranges, SSA = Subandean ranges, IMG = Martín García Island, PAT = Piedra Alta Terrane, NPT = Nico Pérez Terrane, CDT = Cuchilla Dionisio Terrane, SCT = Santa Catarina, RGS = Rio Grande do Sul.

Track	Species	Geographical units
T1	<i>E. campestratus</i> , <i>S. crassistyla</i> , <i>X. platensis</i> , <i>A. ceciliae</i> , <i>A. dubimaculatus</i> , <i>P. vitiosum</i> , <i>S. arnolisei</i> , <i>S. curiy</i> , <i>S. grimpa</i> , <i>V. longisternalis</i> , <i>V. roseus</i> and <i>V. wackei</i>	SCT and RGS (Brazil)
T2	<i>A. longipalpis</i> , <i>C. parvum</i> , <i>G. iheringi</i> , <i>G. mollicoma</i> , <i>H. uruguayense</i> , <i>S. platensis</i> , <i>P. modesta</i> and <i>X. platensis</i>	CDT, NPT and PAT (Uruguay) RGS (Brazil) and IMG (Argentina)
T3	<i>G. vachoni</i> , <i>C. simoni</i> , <i>P. longisternalis</i> , <i>M. thorelli</i> and <i>C. argentinense</i>	VEN and TAN (Argentina)
T4	<i>A. centralis</i> , <i>A. sternalis</i> , <i>C. argentinense</i> , <i>D. bonariensis</i> , <i>G. vachoni</i> , <i>N. chancani</i> and <i>P. modesta</i>	VEN and SPA (Argentina)
T5	<i>A. cordubensis</i> , <i>A. sternalis</i> , <i>C. argentinense</i> , <i>C. obscura</i> , <i>C. tucumana</i> , <i>E. trunculentus</i> , <i>G. inermis</i> , <i>G. vachoni</i> , <i>I. hirsutipedis</i> , <i>I. annulata</i> , <i>L. longipes</i> , <i>M. crassifemur</i> , <i>N. minima</i> , <i>N. toba</i> and <i>P. modesta</i>	SPA and SSA (Argentina)



**Fig. 5.** Generalized tracks and nodes obtained for Mygalomorphae spiders by track analysis. A. Tracks are numbered T1 and T2 and node N1.





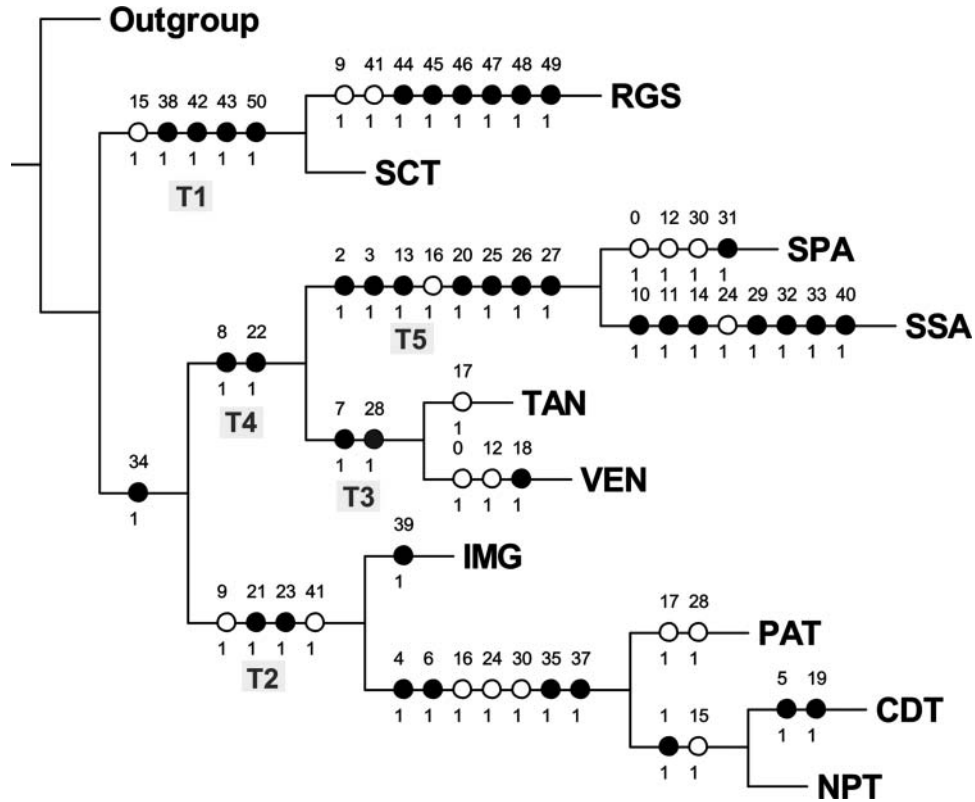
**Fig. 6.** Generalized tracks and nodes obtained for Mygalomorphae spiders by track analysis. Tracks are numbered T3–T5 and nodes N2 and N3.

*platensis* was located from east to western Uruguay (including the three geographic units CDT, NPT and PAT) and also, it reached IMG in Argentina. This generalized track includes the nested generalized track that joins the geographic units of CDT, NPT and PAT). Track T3, supported by the species *Calathotarsus simoni* Schiapelli & Gerschman, 1975 and *Mecicobothrium thorelli* Holmberg, 1882, was situated at the south of Buenos Aires province, at the geographic units of VEN and TAN. Track T4, defined by two species: *Catumiri argentinense* (Mello-Leitão, 1941) and *Grammostola vachoni* Schiapelli & Gerschman, 1961 was located from Central to northwestern Argentina. This track joins the areas of VEN, TAN with SPA and SSA and includes the nested generalized track (T5) that was situated in the SPA and SSA supported by the species *Acanthoscurria cordubensis* Thorell, 1894, *Acanthoscurria sternalis* Pocock, 1903, *Diplotheopsis ornata* Tullgren, 1905, *Grammostola inermis* Mello-Leitão, 1941, *Idiops hirsutipedis* Mello-Leitão, 1941, *Ischnothele annulata* Tullgren, 1905 and *Lycinus longipes* Thorell, 1894. When the synapomorphic individual tracks (supporting the five generalized tracks obtained) were removed from the matrix,

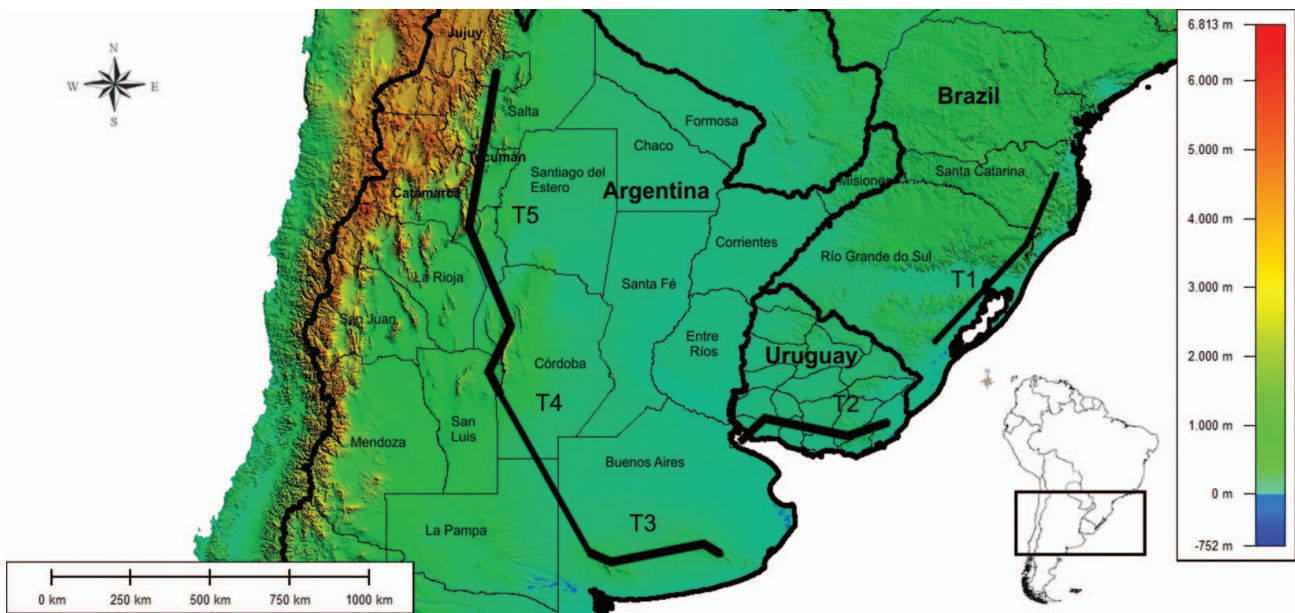
and the reduced matrix was analysed to search for alternative clades supported by other individual tracks, eight most parsimonious trees, with 24 steps, a consistency index of 0.91 and a retention index of 0.71 were produced. The strict consensus tree had 27 steps, a consistency index of 0.81 and a retention index of 0.28 (Fig. 9). For this dataset, one additional generalized track was found (named T4\*) supported by two species: *Acanthogonatus centralis* Goloboff, 1995 and *Diplotheopsis bonariensis* Mello-Leitão, 1938. This track, joining the geographic units of VEN and SPA, was similar to the T4 found analysing the original matrix. No additional generalized tracks were found when the synapomorphic individual tracks were removed from the matrix, and the four most parsimonious trees were found with 21 steps, a consistency index of 0.952 and a retention index of 0.8. The strict consensus tree had 25 steps, a consistency index of 0.8 and a retention index of zero.

## Discussion

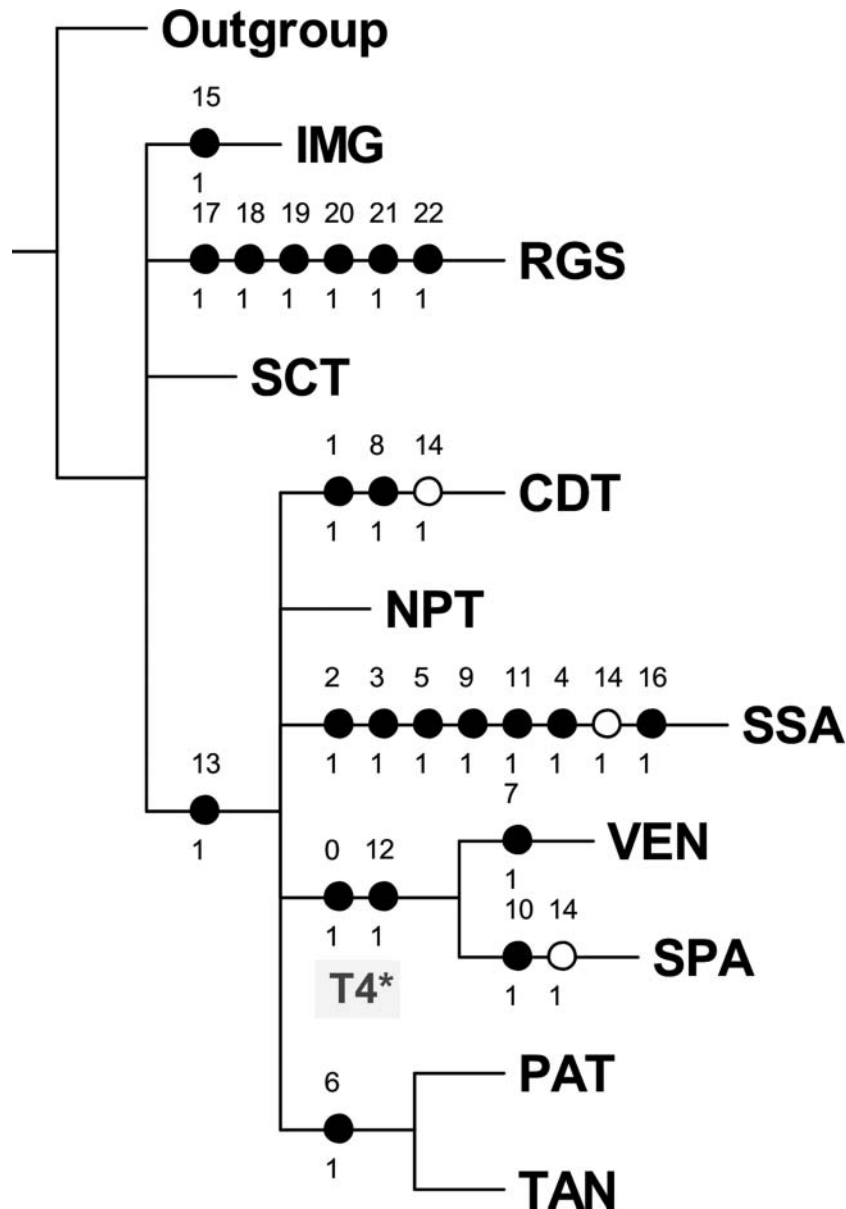
The main distributional pattern of Mygalomorphae connecting Tandilia and Ventania with Pampean and



**Fig. 7.** Tree with 62 steps, a consistency index of 0.823 and a retention index of 0.828. VEN = Ventania, TAN = Tandilia, SPA = Pampean ranges, SSA = Subandean ranges, IMG = Martín García Island, PAT = Piedra Alta Terrane, NPT = Nico Pérez Terrane, CDT = Cuchilla Dionisio Terrane, SCT = Santa Catarina, RGS = Rio Grande do Sul. Generalized tracks are numbered T1–T5.



**Fig. 8.** Generalized tracks (with the relative thickness representing the tracks nested) obtained by PAE with progressive character elimination. Tracks are numbered T1–T5.



**Fig. 9.** Strict consensus tree with 27 steps, a consistency index of 0.81 and a retention index of 0.28 obtained after eliminating synapomorphic individual tracks. VEN = Ventania, TAN = Tandilia, SPA = Pampean ranges, SSA = Subandean ranges, IMG = Martín García Island, PAT = Piedra Alta Terrane, NPT = Nico Pérez Terrane, CDT = Cuchilla Dionisio Terrane, SCT = Santa Catarina, RGS = Rio Grande do Sul. Generalized track is numbered T4\*.

Subandean ranges (T3, T4 and T5), and the closer relationship that links Uruguayan ranges with southern Brazilian ranges (T1 and T2) obtained through track analysis and PAE, partially agree with the previous hypothesis. Hicken (1918) and Brade (1942) postulated a biotic migratory route from the Andes to Brazil, through Pampean ranges, Ventania, Tandilia, and Uruguay and Brazil mountain ranges. Later, Frenguelli (1950) gave the name of peripampasic orogenic arc to the biotic corridor constituted by Pampean ranges, Mahuidas (group of mountain ranges in La Pampa province, in Central Argentina) and Tandilia.

Studies based on scorpions and harvestmen (Maury, 1973; Acosta, 1989, 1993; Mattoni & Acosta, 1997) showed a link between Tandilia and Ventania and the Pampean ranges, but also an extension of the peripampasic track in northwestern Argentina and southern Brazil was proposed. The relationships among the areas of the main distributional patterns of Asteraceae (Crisci *et al.*, 2001) showed a connection among Tandilia and Ventania and southern Brazil, Pampa, Uruguay and Pampean ranges, although the authors proposed that Tandilia is closer to Uruguay and southern Brazil than to Ventania.

In this study, Ventania, Tandilia, Pampean ranges and Subandean ranges are connected by generalized tracks (T3, T4 and T5) obtained in track analysis and PAE yielded similar results through a closer relationship between these areas supported by at least two synapomorphic individual tracks. Also, both methods showed a closer relationship between Ventania and Tandilia (generalized track T3). Although the geological evidence suggests that both mountain ranges resulted from independent geological processes at different geological times, they are geographically close to each other. Ventania was a continuous basin fringing the southwestern margin of Gondwana during Palaeozoic times (Ramos, 1989; Sellés-Martínez, 2001). Moreover, this basin with the South African, Australian and Antarctic counterparts was deformed in the Permo–Triassic to become the Gondwanides. In Ventania area, the basin was tectonically active from Lower to Upper Palaeozoic (Sellés-Martínez, 2001). Tandilia, on the other hand, was part of the Rio de La Plata craton (together with northeastern Argentina, eastern Paraguay, Uruguay and southeastern Brazil) before the end of the Precambrian (570 Ma) (Pankhurst *et al.*, 2003; Rapela *et al.*, 2007). Accordingly, we obtained generalized tracks that connected Ventania and Tandilia mountain ranges with Pampean and Subandean ranges and a closer relationship was found between the hilly system of Ventania and the Pampean ranges through the analysis of PAE after eliminating synapomorphic individual tracks recovered during in the first step.

The main distributional pattern found in this study connecting these mountain ranges could be explained as a consequence of two events: successive marine transgressions and the rise of the Andean chain. During the Middle and Late Miocene three successive Atlantic marine transgressions were recorded in southern South America, known as the ‘Paranean Sea’ (Ortíz-Jaureguizar & Cladera, 2006). Accordingly, during this time an open seaway newly separated terrestrial environments of southern South America from that farther north, spreading over eastern Argentina, western Uruguay, southern Paraguay and southeastern Bolivia (Pascual *et al.*, 1996). The northwestern part of this sea was connected with the so-called ‘Tethys Waterspout’, and included areas among the Andean Cordillera, and the Guayanan and Brazilian Bedrocks (Ramos, 1989; Räsänen *et al.*, 1995; Webb, 1995). During this marine transgression, the lands that emerged corresponded to the mountain ranges of Tandilia, Ventania, Pampean and Subandean ranges (Ortíz-Jaureguizar & Cladera, 2006). The other major event that could affect the distributional patterns of Mygalomorph spiders took place from the Miocene to Pliocene, when the climate changed and became drier in southern South America due to the slow rise of the Andean chain and the cold Humboldt Current that intensified aridity (Hinojosa & Villagrán, 1997; Gregory-Wodzicki, 2000; Zachos *et al.*, 2001). In addition, the last phase of the Andean orogeny in the upper Pliocene

caused an additional uplift of Pampean and Subandean ranges (Pascual *et al.*, 1985; Taylor, 1991). Arguably, all these events may result in an eventual separation of populations to more elevated regions, restricted until then to rocky and loose soils. The nodes found in the connection of these mountain ranges corresponded to Ventania (N2) and Subandean ranges (N3). The two nodes recovered in Central Argentina could be considered as areas with different ancient biotic components, supporting the hypothesis of a hybrid zone where ecological and historical processes have allowed the evolution of mixed biota (Heads, 2004). Moreover, N3 is geographically close to a node found in the Sierras of the Llanos (Catamarca province) for scorpions, with mixing species proceeding from different mountainous systems (Mattoni & Acosta, 1997). Nodes are basically composite areas, resulting from the interconnection and mixing of differently evolved biota in separate coordinates of space–time (Heads, 2004). Although these nodes are clearly related to mountainous systems in Argentina, nodes are not barriers to dispersal and many of them are not correlated with any geographical barrier (Heads, 2004). Nodes can be centres of endemism, high diversity, distribution boundaries, disjunction, specimens that are difficult to identify, or ecological anomalies (Heads, 2004).

Southern Brazil and Uruguayan mountain ranges are connected by generalized tracks (T1 and T2). Also, the Uruguayan tectonic units are connected with Martín García Island. Track analysis and PAE showed a close relation between the three tectonic units of the Uruguayan shield and Martín García Island. The Rio de la Plata craton is the oldest and southernmost core of South America and is a key piece in the cratonic assemblage of southwestern Gondwana (Rapela *et al.*, 2011). It is mostly covered by a thick pile of younger sediments. However, geophysical and deep bore-hole geochronological studies indicate that the western edge of the craton is in sharp contact with the Early Palaeozoic eastern Pampean ranges (Booker *et al.*, 2004; Rapela *et al.*, 2007). Most of the area of Uruguay is included in this craton (Rapela *et al.* 2007) with rocks of Early Proterozoic ages (*c.* 2500–2000 Ma) and with the Uruguayan Shield composed of the tectonic units PAT, NPT and CDT (Mallmann *et al.*, 2007). In Argentina, rocks assigned to this craton are known from Martín García Island in the Rio de la Plata estuary (Dalla Salda, 1981; Pankhurst *et al.*, 2003) and Tandilia (Cingolani & Dalla Salda, 2000; Teixeira *et al.*, 2002; Rapela *et al.*, 2007). Internally, the Rio de La Plata craton includes terranes, blocks and belts covered by modern sediments, except perhaps in southeastern Uruguay (Rapela *et al.*, 2007). The most conspicuous of these continental fragments are in southern Brazil, the Nico Pérez and Piedra Alta terranes in Uruguay, the Tandilia belt in Argentina and the southern sector of the ‘Asunción arch’ in Paraguay (Rapela *et al.*, 2007).

With the two methods applied, southeastern Brazil was recovered by a generalized track (T1) that connected Santa Catarina and Rio Grande do Sul. The Rio de La Plata craton extends from southern Buenos Aires province in Argentina up to Rio Grande do Sul and possibly to Santa Catarina state in southeastern Brazil (Rapela *et al.*, 2007; Rapallini & Bettucci, 2008). Southern Brazil, Santa Catarina and Paraná areas have Archean/Palaeoproterozoic blocks and microplates with age patterns of the Rio de La Plata craton (Rapela *et al.*, 2007). Finally, the node found in southeastern Brazil at Rio Grande do Sul (N1), corresponded to the Atlantic Rain forest and exhibited an enormous diversity, even higher than in most parts of the Amazonian rain forest, with a remarkable endemism (50% on average and as high as 95% in some groups of amphibians) (Morellato & Haddad, 2000; Pinto-da-Rocha *et al.*, 2005). At this area, vicariant events in relation to the biogeographical history of harvestmen have been proposed involving mountain uplift (Serra do Mar) and the appearance of valleys (Pinto-da-Rocha *et al.*, 2005).

The present study not only adds valuable information about the distributional patterns of mygalomorph spiders from Argentina, Uruguay and Brazil, but also discusses possible geological events that could have modelled or fragmented spiders' distributions in the past, leading to the current distributional patterns along the peripampasic orogenic arc. It is to be hoped that this initial analysis, as adopted here, can contribute to strengthen and motivate new research on biogeography of mygalomorph spiders.

## Acknowledgements

Thanks to John Grehan for his critical reading and opinion, and Juan Morrone and an anonymous reviewer for the improvement of the the manuscript. Thanks also to Laura Montes de Oca and Anita Aisenberg who gave valuable comments on the manuscript and improved the English. We are grateful to CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas). We would like to thank C. Scioscia, M. Ramírez and C. Grismado for their help during the scientific stage at the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Argentina.

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Associate Editor: Elliot Shubert