Historical Biogeography of the Genus *Cyriocosmus* (Araneae: Theraphosidae) in the Neotropics According to an Event-Based Method and Spatial Analysis of Vicariance

Nelson Ferretti[1,*], Alda González[1], and Fernando Pérez-Miles[2]

[1]*Centro de Estudios Parasitológicos y de Vectores CEPAVE (CCT- CONICET- La Plata) (UNLP), Calle 2 N° 584, (1900) La Plata, Argentina. E-mail:asgonzalez@cepave.edu.ar*

[2]*Facultad de Ciencias, Sección Entomología, Montevideo, Uruguay. E-mail:myga@fcien.edu.uy*

Nelson Ferretti, Alda González, and Fernando Pérez-Miles (2012) Historical biogeography of the genus *Cyriocosmus* (Araneae: Theraphosidae) in the Neotropics according to an event-based method and spatial analysis of vicariance. *Zoological Studies* **51**(4): 526-535. The distributional history of the South American endemic genus *Cyriocosmus* (Araneae, Theraphosidae) was reconstructed, and a spatial analysis of vicariance was conducted. Results obtained with the software RASP (Reconstruct Ancestral State in Phylogenies), suggest that *Cyriocosmus* originated within an area currently represented by the biogeographical subregions of the Amazonian and Paramo Punan. We found 3 vicariant nodes: the 1st into the Amazonian-Caribbean, the 2nd into the Caribbean, and the 3rd into the Amazonian-Parana, Amazonian-Chacoan, and Amazonian-Parana and Chacoan. Using the Vicariance Inference Program we found that 1 vicariant node different from that obtained with RASP, and the hypothetical barriers for the clade were represented by the Voronoi lines in South America. In order to interpret biogeographical events that affected the genus *Cyriocosmus*, these results are contrasted with major geological events that occurred in South America, and also with previous biogeographical hypotheses. http://zoolstud.sinica.edu.tw/Journals/51.4/526.pdf

Key words: Neotropical, Mygalomorphae, Theraphosid, Ancestral area, Vicariant barrier.

The genus *Cyriocosmus* Simon 1903 is a monophyletic theraphosid group (Pérez-Miles 1998, Fukushima et al. 2005, Pérez-Miles and Weinmann 2009) endemic to South America. The genus was determined to be monophyletic, which was supported by the presence of a long paraembolic apophysis (with reversion to a short one in some species) on the male palpal organ, a weakly developed prolateral superior keel (with reversion to a short one in some species), spermathecae with a convex basal plate (with some reversions), and a blackish cephalic pattern (with several reversions) (Pérez-Miles and Weinmann 2009). The genus *Cyriocosmus* originally included the type species *C. sellatus* (Simon, 1889) and

C. elegans (Simon, 1889) respectively from the upper Amazonas and Orinoco regions. Mello-Leitão (1939) described 2 species: *C. nigriventris* now transferred to *Hapalopus nigriventris* (Mello-Leitão 1939) by Fukushima et al. (2005), and *C. semifasciatus*. Later the genus was exhaustively revised by Schiapelli and Gerschman (1973) (they synonymized *C. semifasciatus* with *C. elegans*), Pérez-Miles (1998), and Fukushima et al. (2005) (these authors rejected the synonymy of *C. fasciatus* and *C. elegans*). Vol (1999) described *C. leetzi* from Colombia; Kaderka (2007) described *C. perezmilesi* from Bolivia; and Pérez-Miles and Weinmann (2009) described *C. pribiki* and *C. rogerioi* from Peru. One of these specimens

---

*To whom correspondence and reprint requests should be addressed. E-mail:nferretti@conicet.gov.ar

collected at 3000 m represents the highest elevational record of a *Cyricosmus* species (Pérez-Miles and Weinmann 2009). Later, Kaderka (2010) described *C. venezuelensis* from Venezuela, and *C. rogerioi* was considered a junior synonym of *C. pribiki*. To summarize, 14 species belonging to *Cyriocosmus* are known: *C. bertae* Pérez-Miles 1998, *C. blenginii* Pérez-Miles 1998, *C. chicoi* Pérez-Miles 1998, *C. elegans*, *C. fasciatus* (Mello-Leitão 1930), *C. fernandoi* Fukushima, Bertani & da Silva 2005 (Fig. 1), *C. leetzi* Vol 1999, *C. nogueiranetoi* Fukushima, Bertani & da Silva 2005 (Fig. 2), *C. perezmilesi* Kaderka 2007, *C. pribiki* Pérez-Miles & Weinmann, 2009, *C. ritae* Pérez-Miles 1998, *C. sellatus*, *C. venezuelensis* Kaderka 2010, and *C. versicolor* (Simon, 1897). The number of species described in this genus gradually increased during the last decade, and the geographic distribution of the genus now extends to Argentina, Bolivia, Brazil, Colombia, Paraguay, Peru, Trinidad and Tobago, and Venezuela. The geographic distribution of *Cyriocosmus* extends 10°N-28°S, mainly in forested regions, and none of the sites given in Fukushima et al. (2005) occurs in the Andean highlands nor the narrow Pacific lowlands, although some species are present in drier and more-xeric habitats (Fukushima et al. 2005).

Even though the genus *Cyriocosmus* seems to be specious and additional undescribed species may be expected in the future (Pérez-Miles and Weinmann 2009), no hypothesis has been postulated related to the origin and biogeography of this group. The purpose of this paper was to analyze the distributional patterns of *Cyriocosmus* within the framework of a historical biogeographic event-based method. Furthermore, we provide a

spatial analysis of vicariance (using a vicariance inference program, implemented in VIP) as the main goal of detecting disjunct distributions of sister nodes. Finally, our results are discussed within the context of a geobiotic evolutionary and biogeographical hypothesis proposed for southern South America.

MATERIALS AND METHODS

Areas of analysis

Distributional data for the genus *Cyriocosmus* were taken from Fukushima et al. (2005). Five main areas belonging to Neotropical and Andean regions (Fig. 3) defined in previous biogeographic schemes (Cabrera and Willink 1973, Morrone 2001 2006) were considered in the analysis. The following areas were used in this study.

The Amazonian (A), between 5°N and 20°S in central South America, is the largest subregion of the Neotropical region, and includes Brazil, the Guyanas, Venezuela, Colombia, Ecuador, Peru, Bolivia, Paraguay, and Argentina. This territory possesses a warm and extremely humid climate, with a mean annual temperatures of 26°C and a low annual range. The annual precipitation is 2000-2600 ml. The flora of this province is characteristic of the rainforest that extends from the Atlantic to the Andes with trees such as *Aldina*, *Bowdichia*, and *Pithecolobium*.

The Paramo Punan (B), which belongs to the Andean region, extends along the highlands of the Andes between western Venezuela, northern Chile, and west central Argentina. This is considered the South American transition zone and extends

Fig. 1. *Cyriocosmus fernandoi*, male, live habitus. Photo by R. Bertani.

Fig. 2. *Cyriocosmus nogueiranetoi*, female, live habitus. Photo by R. Bertani.

between 8°N and 37°S. The climate is cold, dry, and xeric; shrublands comprise the dominant vegetation. The entomofauna of the South American transition zone contains Neotropical and Andean insect taxa.

The Caribbean (C) is a Neotropical subregion that extends through southern Mexico, Central America, the Antilles, and northwestern South America, in Ecuador, Colombia, Venezuela, and Trinidad and Tobago. It extends between 26°N and 2°S. It has a complex geobiotic history, which is reflected in its multiple relationships with other areas of the Neotropics, the Nearctic, and the Old World tropics. The flora is heterogeneous from cloud forests to desert shrublands.

The Chacoan (D) is a Neotropical subregion which occupies northern and central Argentina, southern Bolivia, western and central Paraguay, Uruguay, and central and northeastern Brazil. It extends between 5° and 42°S. The Chacoan subregion is closely related to the Amazonian. The climate is variable, predominately continental, with low and moderate rainfall, mild winters, and warm summers. The flora consists of xeric deciduous forests and herbaceous steppe. Some characteristics trees are *Prosopis*, *Acacia*, *Caesalpinia*, and *Cercidium*.

The Parana (E) is a Neotropical subregion situated in northeastern Argentina, eastern Paraguay, and southern (west of Serra do Mar and central to Rio Grande do Sul) and eastern Brazil. It extends between 7° and 32°S.

Fig. 3. Areas considered in the biogeographical analysis. White, Neotropical region; gray, Andean region. Modified from Morrone (2001).

Phylogenetic analysis

The historical biogeography was analyzed using the phylogeny of *Cyriocosmus* proposed by Fukusima et al. (2005) and Pérez-Miles and Weinmann (2009). The 1st phylogeny includes 11 *Cyriocosmus* species, and the cladistic analysis resulted in a single totally resolved tree (Fig. 4A) with the same topology in each search. In a more-recent cladistic analysis (Pérez-Miles and Weinmann 2009), relationships of *C. perezmilesi* with *C. versicolor*, *C. pribiki*, and *C. rogeroi* were uncertain, and considering that later Kaderka (2010) proposed *C. rogerioi* as a junior synonym of *C. pribiki*, the position of several newly described species since Fukushima et al. (2005) are still doubtful, so we used a reduced phylogeny, specifically considering the different placements of *C. chicoi* and *C. ritae* (Fig. 4B) obtained from 1 tree with maximum fit by Pérez-Miles and Weinmann (2009). *Cyriocosmus* was proposed as being a sister group to *Hapalopus*, and many species were used as outgroups in previous phylogenetic

analyses (Fukushima et al. 2005, Pérez-Miles and Weinmann 2009). Based on these considerations, we used a hypothetical outgroup of *Hapalopus* species (*H. formosus* and *H. butantan*) as defined in Fukushima et al. (2005) and Pérez-Miles and Weinmann (2009).

Biogeographic analysis

Event-based methods are increasingly being used in historical biogeographic studies during the past few years, due to the exponential increase in phylogenetic studies (Miranda-Esquivel 1999, Voelker 1999, Zink et al. 2000, Sanmartín et al. 2001, Vinnersten and Bremer 2001, Donato et al. 2003, Sanmartín 2003, Near and Keck 2005, Donato 2006, Guo and Wang 2007, Antonelli et al. 2010). 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,
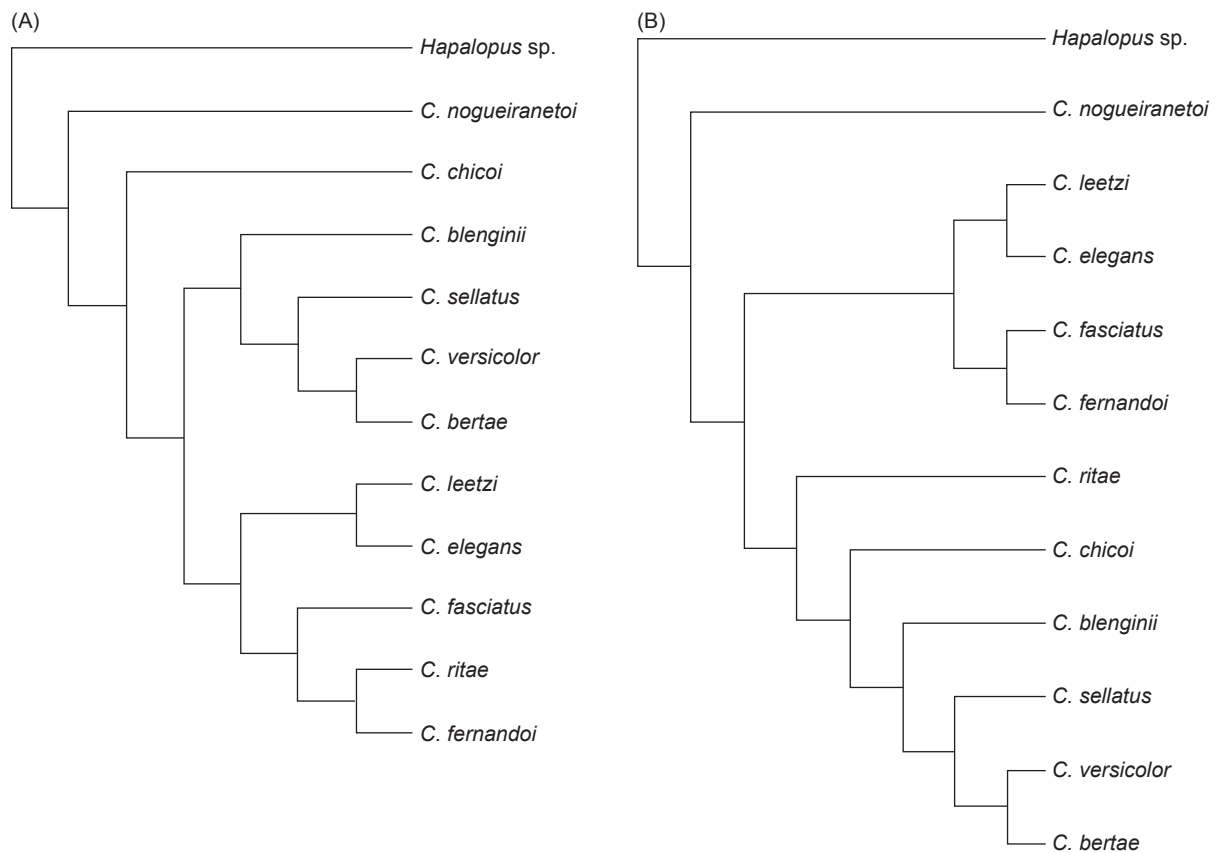

Fig. 4. (A) A single, totally resolved cladogram of *Cyriocosmus* species obtained by Fukushima et al. (2005). (B) A single, totally resolved cladogram of *Cyriocosmus* species adapted from the single cladogram of Pérez-Miles and Weinmann (2009) by pruning several taxa.

and extinction) are identified and assigned values of cost-benefit under an explicit model of natural functioning (Crisci et al. 2003). To reconstruct ancestral distributions of the *Cyriocosmus* genus we used Reconstruct Ancestral State in Phylogenies (RASP) which is in vers. 2.0 of S-DIVA (Nylander et al. 2008, Yu et al. 2010). This program complements DIVA, with the methods of Nylander et al. (2008) and Harris and Xiang (2009); it also determines statistical support for ancestral range reconstructions using a novel method, the S-DIVA or RASP value. In S-DIVA or RASP, frequencies of an ancestral range at a node in the ancestral reconstructions are averaged over all trees, and each alternative ancestral range at a node is weighted by the frequency at which the node occurs or by some other measure of support for the node (Yu et al. 2010).

In order to discover disjunct (allopatric or vicariant) distributions among sister groups in a phylogenetic context, we used the Vicariance Inference Program (VIP) (Arias et al. 2011) as an optimality criterion. The assumption of the VIP is that the only evidence left from a speciation process in a geographic context is an allopatric distribution. Unfortunately, although many clades show allopatric distributions, others do not. There are some overlapping distributions, others with widespread terminals, or clades for which several of the ancestral nodes are uninformative (Arias et al. 2011). The spatial information that VIP requires was obtained by georeferencing the distributional data from Fukushima et al. (2005) (Fig. 5) using international gazetteers in DIVA-GIS 9.0; these datasets consisted of 29 georeferenced records, and the phylogenetic information was taken from Fukushima et al. (2005). The VIP analysis was performed using a grid of 1.5 × 1.5 (Von Neumann neighborhood) and a maximum fill of 1, and the barrier was represented by Voronoi lines (De Berg 2008).

RESULTS

According to the RASP optimization, the 2 trees produced 3 possible ancestral distributions each with a respective RASP value (statistical value of an optimal reconstruction) of 983.3333 and 983.3334. Results of the ancestral distributions of both reconstructions were similar and are summarized in figure 6. The ancestral areas reconstructed at the root of the genera *Cyriocosmus* and *Hapalopus* are most likely to

be either Amazonian or both Amazonian-Paramo Punan. A vicariant event (node 1, Fig. 6) took place resulting in 2 isolated groups: *Hapalopus* (Amazonian-Paramo Punan) and *Cyriocosmus* (Amazonian). Subsequently, a 2nd vicariant event (node 2, Fig. 6) separated the species, *C. leetzi* and *C. elegans*, in the Caribbean from the clade containing *C. fasciatus*, *C. ritae*, and *C. fernandoi* in the Amazonian, with possible ancestral areas of the Amazonian-Caribbean. Then, a new vicariant event (node 3, Fig. 6) split *C. leetzi* in the Paramo Punan-Caribbean from *C. elegans* in the Caribbean, with the possible ancestral area being the Caribbean. Finally, a new vicariant event (node 4, Fig. 6) separated *C. versicolor* in the Chacoan and Parana regions from *C. bertae* in the Amazonian. The possible ancestral areas for this node were the Amazonian-Parana, Amazonian-Chacoan, and Amazonian-Chacoan-Parana.

The VIP analysis produced 3 possible reconstructions, and the consensus resulted in 1 tree with 4 vicariant nodes and 1 node was removed (Fig. 7). The 1st vicariant node (node 1, Fig. 7) corresponded to the split of *Hapalopus* species from *Cyriocosmus* species,

Fig. 5. Map showing distributions of *Cyriocosmus* and *Hapalopus* species in South America considered in this analysis.

and the possible barrier is shown in figure 8. This barrier had a northern limit at the biogeographic province of Imerí in the Amazonian, extended to southeastern South America through the central Amazonian and involved 5 biogeographic

provinces of this area. A 2nd vicariant event (node 2, Fig. 7) resulted in the separation of *C. leetzi* from *C. elegans* with a hypothetical barrier through the Andean region in the north of the South American transition zone in the biogeographic province of Paramo Norandino as shown in figure 9. The next vicariant event (node 3, Fig. 7) took place between *C. fernandoi* and *C. ritae*. The possible vicariant barrier shown in figure 10 comprised 1 in the east at the limit of the Chacoan and Amazonian subregions that involved 4 biogeographic provinces and extended to the limit of the South American transition zone (Paramo Punan) and Chacoan in the west. Finally, a vicariant node (node 4, Fig. 7) between *C. bertae* and *C. versicolor* was obtained with a possible barrier from northeast to southwest through the Amazonian subregion (involving 4 biogeographic provinces) and reaching the South American transition zone at the provinces of Puna and Atacama (Fig. 11).
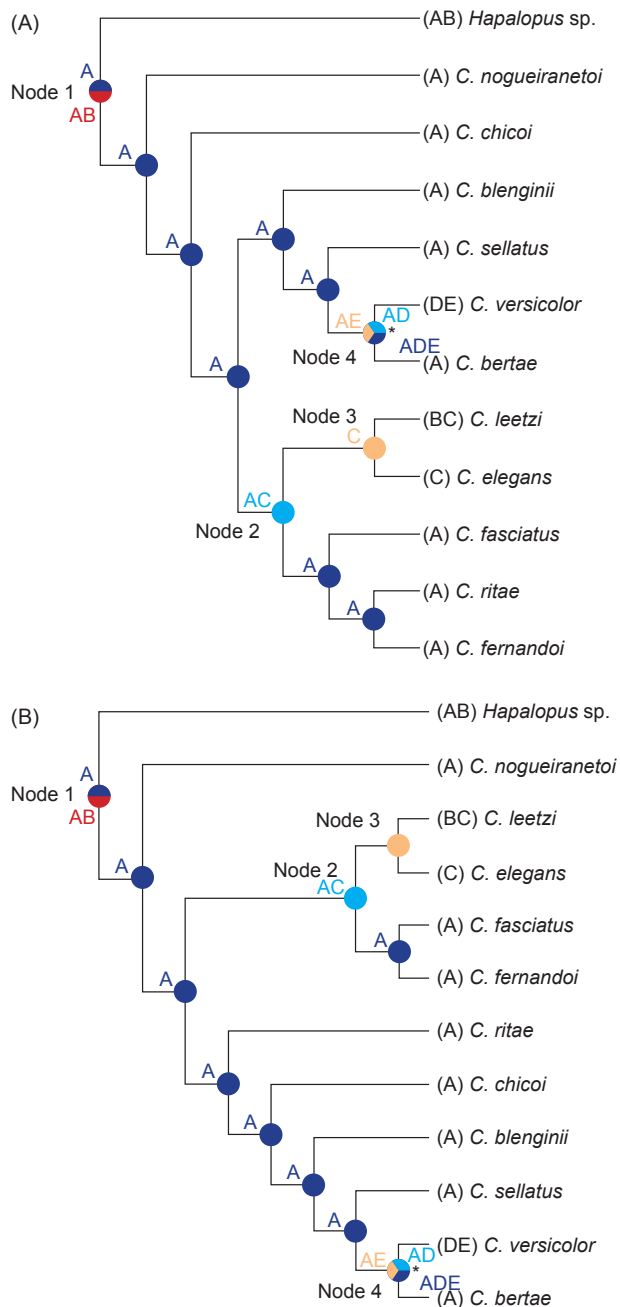

Fig. 6. Ancestral distributions reconstructed by RASP. Pie charts at the nodes give the relative frequencies of the ancestral-area reconstruction. (A) Reconstruction obtained from the phylogeny of Fukushima et al. (2005). (B) Reconstruction obtained from the phylogeny of Pérez-Miles and Weinmann (2009). A, Amazonian; B, Paramo Punan; C, Caribbean; D, Chacoan, E, Parana.
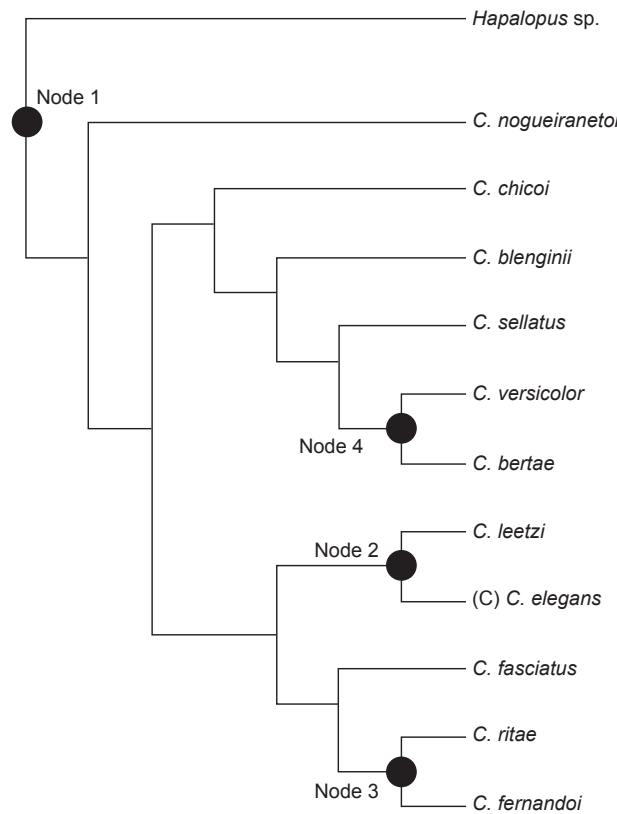

Fig. 7. Vicariant nodes obtained from the VIP analysis using a 1.5 × 1.5 grid.

Fig. 8. Hypothetical barrier generated by the VIP at vicariant node 1, showing the split of *Hapalopus* and *Cyriocosmus*.

Fig. 9. Hypothetical barrier generated by the VIP at vicariant node 2, showing the split of *C. leetzi* from *C. elegans*.

Fig. 10. Hypothetical barrier generated by the VIP at vicariant node 3, showing the split of *C. fernandoi* from *C. ritae*.

Fig. 11. Hypothetical barrier generated by the VIP at vicariant node 4, showing the split of *C. bertae* from *C. versicolor*.

DISCUSSION

The genus *Cyriocosmus* is endemic to South America, and according to the RASP results, there are 2 optimal ancestral distributions of the basal node (node 1) of *Cyriocosmus* species, represented by the Amazonian and Paramo Punan areas. This inferred ancestral distribution is postulated as the possible geographical origin of the genus *Cyriocosmus*. During the late Oligocene early Miocene period, a time in which the family Theraphosidae probably originated (Selden 1993 1996, Dunlop et al. 2009), the Amazonian and Paramo Punan could be considered as a single unit due to the homogeneous climate (Donato 2006, Ortiz-Jaureguizar and Cladera 2006). Also, in the pre-Quaternary, the South American Neotropical biota expanded northward to Central America and Mexico and southward to the South American transition zone (Paramo Punan) and the Andean region (Ringuelet 1961, Morrone and Lopretto 1994, Maury et al. 1996). This node, identified by the VIP analysis, showed a barrier (Fig. 8) northwest to southeast through the Amazonian and Chacoan that splits the Paramo Punan and western Amazonian from the eastern Amazonian and Chacoan. This barrier could have originated during the latest Cretaceous-earliest Paleocene span, when the absence of large continental topographic barriers allowed a widespread Atlantic transgression (called the Salamancan Sea). This transgression covered a major part of southern South America from Patagonia in the south, to Bolivia and Peru in the north (Ortiz-Jaureguizar and Cladera 2006). This seaway divided the entire continent into 2 large northeastern and southwestern regions. Additionally, the southwestern area was also divided into several, relatively extensive island territories (Ortiz-Jaureguizar and Cladera 2006). Conversely, the ancestral distribution obtained by RASP agreed with the Paramo Punan (Andean zone) and Amazonian, reflecting the origin of the group in these areas. Node 2 in RASP indicated the occurrence of a vicariant event that split the Amazonian lineage in 1 branch from the Caribbean lineage in the other. This event could be explained by the Atlantic marine transgression known as the Paranean Sea and a new phase of Andean orogenesis during the middle and late Miocene in southern South America (Ortiz-Jaureguizar and Cladera 2006). An open seaway newly separated terrestrial environments of southern South America from those farther north, spreading over virtually all of eastern Argentina, western Uruguay, southern Paraguay, and southeastern Bolivia (Pascual et al. 1996). The northwestern part of the Paranean Sea was connected with the so-called Tethys Waterspout, which covered widespread areas among the Andean Cordillera and the Guayanian and Brazilian bedrocks (Rässänen et al. 1995, Webb 1995, Ortiz-Jaureguizar and Cladera 2006). This could have acted as a barrier promoting subsequent speciation or otherwise affected or disturbed the landscape. A cold and dry climate was recorded since the middle Miocene, appearing first in southern Patagonia and then extending northwards (Donato 2006). Node 3 obtained by RASP, which split *C. leetzi* from *C. elegans*, was also recovered by the VIP, and the hypothetical barrier was confined to the northern Paramo Punan (South American transition zone). This inference is in agreement with the final phase of the Puna uplift, which occurred during the late Pliocene. Previous to the Puna uplift, the climate was cooler, and seasonality was more marked than in the middle Miocene, with a more-varied environmental subdivision (Alberdi et al. 1997, Donato et al. 2003). The final uplift of the Puna installed the present extreme climatic conditions which characterize this region today. Consequently, the separation observed inside this node could be interpreted as a response of taxa to the Puna uplift and the resulting isolation. Node 4 in RASP, which split *C. bertae* from *C. versicolor*, was also obtained by the VIP analysis. These barriers could have originated during the Middle Miocene when a great increase in the equator-to-pole thermal gradient occurred, and oceanic gradients first attained values exceeding 20°C (Ortiz-Jaureguizar and Cladera 2006). This cold trend was interpreted as the result of the combined action of the Andean uplift and the Western Antarctic glaciation. Both events caused an increase in the thermal gradient from the equator to the poles (Hinojosa and Villagrán 1997, Gregory-Wodzicki 2000, Zachos et al. 2001, Ortiz-Jaureguizar and Cladera 2006). During the Late Miocene-Early Pliocene (ca. 11-3 Ma), the widespread surface flooded by the Paranean Sea was succeeded by similarly spread-out plains, which extended north from northern Patagonia, reaching central and northern Argentina, Uruguay, the eastern slopes of the rising Andes of northern Bolivia, southern Peru, and Venezuela, and also the upper Amazon basin (Marshall et al. 1983, Pascual et al. 1996). These new habitats were so conspicuous that this period is known as the Age of the Southern

Plains (Pascual and Bondesio 1982, Pascual et al. 1996, Ortiz-Jaureguizar 1998). Finally, the barrier obtained with the VIP that split *C. fernandoi* from *C. ritae* was not obtained with RASP and could be explained by the Miocene marine transgression that isolated northern Brazilian, the Guayanian Bedrock, and the southern portion of the Brazilian Bedrock (Donato et al. 2003, Donato 2006).

REFERENCES

Alberdi MT, FP Bonadonna, E Ortiz Jaureguizar. 1997. Chronological correlation, paleoecology, and paleobiogeography of the late Cenozoic South American Rionegran land mammal fauna: a review. Rev. Esp. Paleontol. **12:** 249-255.

Antonelli A, CF Verola, D Parisod, ALF Gustaffson. 2010. Climate cooling promoted the expansion and radiation of a threatened group of South American orchids (Epidendroideae: Laeliinae). Biol. J. Linn. Soc. **100:** 597-607.

Arias JS, C Szumik, P Goloboff. 2011. Spatial analysis of vicariance: a method for using direct geographical information in historical biogeography. Cladistics **27:** 1-12.

Cabrera AL, A Willink. 1973. Biogeografía de América Latina. Washington, DC: OEA, Serie Biología, Monografia no. 13, 122 pp.

Crisci JV, L Katinas, P Posadas. 2003. Historical biogeography: an introduction. Cambridge, MA: Harvard Univ. Press, 250 pp.

De Berg M, O Cheong, M Van Kreveld, M Overmars. 2008. Computational geometry, algorithms and applications. Berlin: Springer-Verlag.

Donato M. 2006. Historical biogeography of the family Tristiridae (Orthoptera: Acridomorpha) applying dispersal-vicariance analysis. J. Arid Environ. **66:** 421-434.

Donato M, P Posadas, DR Miranda-Esquivel, E Ortiz-Jaureguizar, G Cladera. 2003. Historical biogeography of the Andean region: evidence from *Listroderina* (Coleoptera: Curculionidae: Rhytirrhinini) in the context of the South American geobiotic scenario. Biol. J. Linn. Soc. **80:** 339-352.

Dunlop JA, D Penney, D Jekel. 2009. A summary list of fossil spiders. *In* NI Platnick, ed. The world spider catalog, vers. 10.0. New York, NY: American Museum of Natural History. Available at http://research.amnh.org/entomology/spiders/catalog/index.html Accessed 4 Aug. 2011.

Fukushima CS, R Bertani, PI Da Silva. 2005. Revision of *Cyriocosmus* Simon, 1903, with notes on the genus *Hapalopus* Ausserer, 1875 (Araneae, Theraphosidae). Zootaxa **846:** 1-31.

Gregory-Wodzicki KM. 2000. Uplift history of the central and northern Andes: a review. Geol. Soc. Am. Bull. **112:** 1091-1105.

Guo Y, Y Wang. 2007. Partitioned Bayesian analyses, dispersal-vicariance analysis, and the biogeography of Chinese toad-headed lizards (Agamidae: Phrynocephalus): a re-evaluation. Mol. Phylogen. Evol. **45:** 643-662.

Harris AJ, QY Xiang. 2009. Estimating ancestral distributions of lineages with uncertain sister groups: a statistical approach to dispersal-vicariance analysis and a case using *Aesculus* L (Sapindaceae) including fossils. J. Syst. Evol. **47:** 349-368.

Hinojosa LF, C Villagrán. 1997. Historia de los bosques del sur de Sudamérica, 1: antecedentes paleobotánicos, geológicos y climáticos del Terciario del cono sur de América. Rev. Chil. Hist. Nat. **70:** 225-239.

Kaderka R. 2007. *Cyriocosmus perezmilesi* sp. n. from Bolivia (Araneae: Theraphosidae: Theraphosinae). Rev. Iber. Aracnol. **14:** 63-68.

Kaderka R. 2010. *Cyriocosmus venezuelensis* sp. n. from Venezuela (Araneae: Theraphosidae: Theraphosinae). Rev. Iber. Aracnol. **18:** 87-96.

Marshall LG, R Hoffstetter, R Pascual. 1983. Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. Palaeovertebrata **83:** 1-93.

Maury EA, R Pinto da Rocha, JJ Morrone. 1996. Distribution of *Acropsopilio chilensis* Silvestri, 1904, in southern South America (Opiliones, Palpatores, Caddidae). Biogeographica **72:** 127-132

Mello-Leitão C. 1930. Aranhas do Cuminá. Arq. Mus. Nac. Rio J. **32:** 51-75.

Mello-Leitão C. 1939. Araignées américaines du Musée d´histoire naturelle de Bâle. Rev. Suisse Zool. **46:** 43-93.

Miranda-Esquivel DR. 1999. Análisis Filogenético de la Tribu Simuliini (sensu Crosskey, 1987) para las Regiones Zoogeográficas Neotropical, Etiópica y Australiana. PhD dissertation, Univ. Nacional de La Plata, La Plata, Argentina.

Morrone JJ. 2001. Biogeografía de América Latina y el Caribe, Vol. 3. Zaragoza, Spain: Manuales & Tesis.

Morrone JJ. 2006. Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. Annu. Rev. Entomol. **51:** 467-494.

Morrone JJ, EC Lopretto. 1994. Distributional patterns of freshwater Decapoda (Crustacea: Malacostraca) in southern South America: a panbiogeographic approach. J. Biogeogr. **21:** 97-109.

Near TJ, BP Keck. 2005. Dispersal, vicariance, and timing of diversification in Nothonotus darters. Mol. Ecol. **14:** 3485-3496.

Nylander JAA, U Olsson, P Alström, I Sanmartín. 2008. Accounting for phylogenetic uncertainty in biogeography: a Bayesian approach to dispersal vicariance analysis of the thrushes (Aves: *Turdus*). Syst. Biol. **57:** 257-268.

Ortiz-Jaureguizar E. 1998. Paleoecología y evolución de la fauna de mamíferos de América del sur durante la "Edad de las Planicies Australes" (Mioceno Superior-Plioceno Superior). Estud. Geol. **54:** 161-169.

Ortíz-Jaureguizar E, GA Cladera. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. J. Arid Environ. **66:** 498-532

Pascual R, E Ortiz-Jaureguizar, JL Prado. 1996. Land mammals: paradigm of Cenozoic South American

geobiotic evolution. Münchner Geowiss. Abh. **30:** 265-319

Pascual R, P Bondesio. 1982. Un roedor Cardiatheriinae (Hydrochoeridae) de la Edad Huayqueriense (Mioceno tardío) de La Pampa. Sumario de los ambientes terrestres en la Argentina durante el Mioceno. Ameghiniana **19:** 19-36.

Pérez-Miles F. 1998. Revision and phylogenetic analysis of the Neotropical genus *Cyriocosmus* Simon 1903 (Araneae, Theraphosidae). Bull. Br. Arachnol. Soc. **11:** 95-103.

Pérez-Miles F, D Weinmann. 2009. Two new species of *Cyriocosmus* Simon, 1903 from Peru and the highest record for the genus (Araneae: Theraphosidae: Theraphosinae). Rev. Iber. Aracnol. **17:** 29-35.

Rässänen ME, AM Linna, JCR Santos, FR Negri. 1995. Late Miocene tidal deposits in the Amazonian foreland basin. Science **269:** 386-390.

Ringuelet RA. 1961. Rasgos fundamentales de la zoo-geografía de la Argentina. Physis **22:** 151-170.

Sanmartín I. 2003. Dispersal vs. vicariance in the Mediterranean: historical biogeography of the Palearctic Pachydeminae (Coleoptera, Scarabaeoidea). J. Biogeogr. **30:** 1883-1897.

Sanmartín I, H Enghoff, F Ronquist. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. Biol. J. Linn. Soc. **73:** 345-390.

Schiapelli RD, BS Gerschman de Pikelin. 1973. El género *Cyriocosmus* Simon 1901 (Araneae, Theraphosidae). Physis **32:** 61-70.

Selden PA. 1993. Fossil arachnids – recent advances and future prospects. Mem. Queensl. Mus. **33:** 389-400.

Selden PA. 1996. La historia geológica de las arañas (Araneae). Paleoentomología **16:** 105-112.

Simon E. 1889. Voyage de M.E. Simon au Venezuela, Arachnides. Ann. Soc. Entomol. Fr. **6:** 169-220.

Simon E. 1897. Liste des Arachnides recueillis aux îles du Cap Vert, dans la République Argentine et le Paraguay et descriptions d'espèces nouvelles. Boll. Mus. Zool. Anat. Comp. Torino **12:** 12-56.

Vinnersten A, K Bremer. 2001. Age and biogeography of major clades in Liliales. Am. J. Bot. **88:** 1695-1703.

Voelker G. 1999. Dispersal, vicariance, and clocks: historical biogeography and speciation in a cosmopolitan Passerine genus (*Anthus*: Motacillidae). Evolution **53:** 1536-1552.

Vol F. 1999. Description d´une nouvelle espece de *Cyriocosmus* Simon 1903 (Araneae, Theraphosidae), *Cyriocosmus leetzi* sp. n. de Colombie. Arachnides **43:** 2-10.

Webb SD. 1995. Biological implications of the middle Miocene Amazon seaway. Science **269:** 361-362.

Yu Y, AJ Harris, X He. 2010. S-DIVA (Statistical Dispersal-Vicariance Analysis): a tool for inferring biogeographic histories. Mol. Phylogen. Evol. **56:** 848-850.

Zachos J, M Pagani, L Sloan, E Thomas, K Billups. 2001. Trends, rhythms, and aberrations in global climate 65Ma to present. Science **292:** 686-693.

Zink RM, RC Blackwell-Rago, F Ronquist. 2000. The shifting roles of dispersal and vicariance in biogeography. Proc. R. Soc. Lond. **267:** 497-503.