

## ENDEMISM IN *LIOLAEMUS* (IGUANIA: LIOLAEMIDAE) FROM THE ARGENTINIAN PUNA

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**ABSTRACT:** Areas of endemism are considered the fundamental unit in historical biogeography because they are the entities to be compared in biogeographic analysis. However, until recently, there were no formal methods for its identification. In this paper, I applied two different methods for the identification of areas of endemism of the genus *Liolaemus*, the parsimony analysis of endemicity (PAE), and a recently proposed method based on an optimality criterion implemented in the computer program NDM. I analyzed the distributions of 29 species of *Liolaemus* inhabiting the Puna region in Northwestern Argentina. The analysis with NDM found four areas of endemism that show a repeated pattern of species groups, with the same groups in each area. On the other hand, results generated through PAE were not congruent with those of NDM and sometimes violated the definition of endemism. The patterns found suggest that these groups of species could have been affected by the same historical events.

**KEYWORDS:** Historical biogeography; Endemism; Argentina; Puna; *Liolaemus*.

### INTRODUCTION

The genus *Liolaemus* is the second most speciose genus of lizards, including more than 170 species (Etheridge y Espinoza, 2000; Abdala, 2005). Its distribution extends from Tierra del Fuego in the southernmost extreme of South America, to the Andes of Peru. Although there are many works dealing with the systematics, ecology and ethology of *Liolaemus*, very little is known of its biogeography. Some previous contributions were made by Hellmich (1951), Laurent (1983, 1985, 1992), Cei (1979) and Duellman (1979), regarding the distribution, probable centers of origin, and routes of dispersion of the genus. Recently, several authors used cladistic methodologies to analyze the biogeography of *Liolaemus*. Young-Downey (1998) did a Brooks Parsimony Analysis (BPA – Brooks, 1990) using the areas defined by Cabrera and Willink (1980). Schulte et al (2000) optimized on a molecular phylogeny the distributions of species assigned to three Andean areas. Finally, Lobo (2001) computed in the phylogeny of the *chiliensis* group the areas of distribution defined by Roig-Juñent (1994). In addition to these contributions, Cruz et al. (2005) provided information on the increase in body size with latitude in *Liolaemus*, and Morando et al. (2004) performed a phylogeographic study of the *darwinii* complex.

According to Platnick (1991): “In systematics, we have no way of knowing, in advance, what character system will be most likely to resolve a particular set of relationships. In biogeography, however, we can always prefer to initiate our studies with those taxa

that are maximally endemic – those which include the largest number of species, with the smallest ranges, in the area of interest.” *Liolaemus* meets these requirements: in addition to several phylogenies that encompass most species, the genus has a great diversity and the areas of distribution are small compared to the area of study (Schulte et al., 2000; Etheridge, 2000; Lobo, 2001; Morando et al., 2004; Abdala, 2005). However, it is difficult to analyze the historical biogeography of *Liolaemus* because the units of study, the areas of endemism, are not known. The areas used in previous studies are based on distributions of other organisms that have no affinities to *Liolaemus*.

Areas of endemism are central to studies of historical biogeography because they are the entities to be compared (Linder, 2001). Additionally, areas of endemism are crucial for determining conservation priorities (Peterson and Watson, 1998; Linder, 1995; Vane-Wright et al., 1991). Axelius (1991) warned that the failure to use areas of endemism in a biogeographic analysis may lead to meaningless results. Hovenkamp (1997) questioned the uncritical use of areas of endemism, and stated that its existence should not be assumed *a priori*, but be a subject of investigation. Hausdorf (2002) and Hausdorf and Hennig (2003) proposed to restrict the concept of areas of endemism to ideal situations, and replaced it with a new entity called “biotic element.” An area of endemism could be defined by the congruent distribution of at least two species of restricted range (Platnick, 1991). Exact congruence of the distributions is not required by the definitions, but a relative sympatry (Morrone and

Crisci, 1995) or at least relative congruence (Wiley, 1981) is expected. This vagueness in the definition for congruence was criticized by Henderson (1991), who indicated the need for a more formal method of quantifying biogeographic congruence.

Traditionally, areas of endemism were recognized intuitively, examining the individual distribution of taxa and simply superimposing its areas of distribution (Müller, 1973). The first explicit method designed for the identification of areas of endemism was the Parsimony Analysis of Endemicity (PAE – Morrone, 1994), based on the method proposed by Rosen (1988). Harold and Mooi (1994) did not consider sympatry as a prerequisite for the recognition of areas of endemism, and stated that non-overlapping areas could be considered as historical associations if there is available additional evidence supporting separate areas as forming one. Harold and Mooi, however, did not propose a method (Szumik *et al.*, 2002). Linder (1998, 2001) proposed four criteria that any protocol searching for areas of endemism should meet, and proposed the use of clustering methods (UPGMA using Jaccard similarities) or parsimony with different weighting schemes. Szumik *et al.* (2002) and Szumik and Goloboff (2004) proposed an optimality criterion that allows a way to assign a score of endemicity to an area, and for the first time, included a spatial component. The criterion is implemented in the computer program NDM (Goloboff, 2004). Hausdorf and Hennig (2003) restricted the term “area of endemism” to ideal situations where there is perfect congruence on the distributions, and proposed a new entity called “biotic elements” to replace the concept of area of endemism. Hausdorf and Hennig used a distance method to evaluate the distributions and applied a Maximum Likelihood criterion for the search procedure.

In this paper I analyze the distributional data corresponding to 29 species of *Liolaemus* of the Argentinian Puna, applying two methods: the commonly used Parsimony Analysis of Endemicity (PAE; Morrone, 1994), and the more recent analysis of endemism implemented in the computer program NDM. The proposal of Hausdorf and Hennig was not applied here because I disagree with their concept of biotic elements.

#### MATERIALS AND METHODS

**Study area** – The region chosen for the study (Fig. 1) corresponds to the Puna and Cordillera Oriental geological provinces in Argentina (Turner and Mendez, 1979b). The Puna is a plateau ranging from 4200-3500

meters above sea level in the northern border to 3100-2700 meters above sea level in the south. Its climate is arid and cold, with frosts on summer and win-

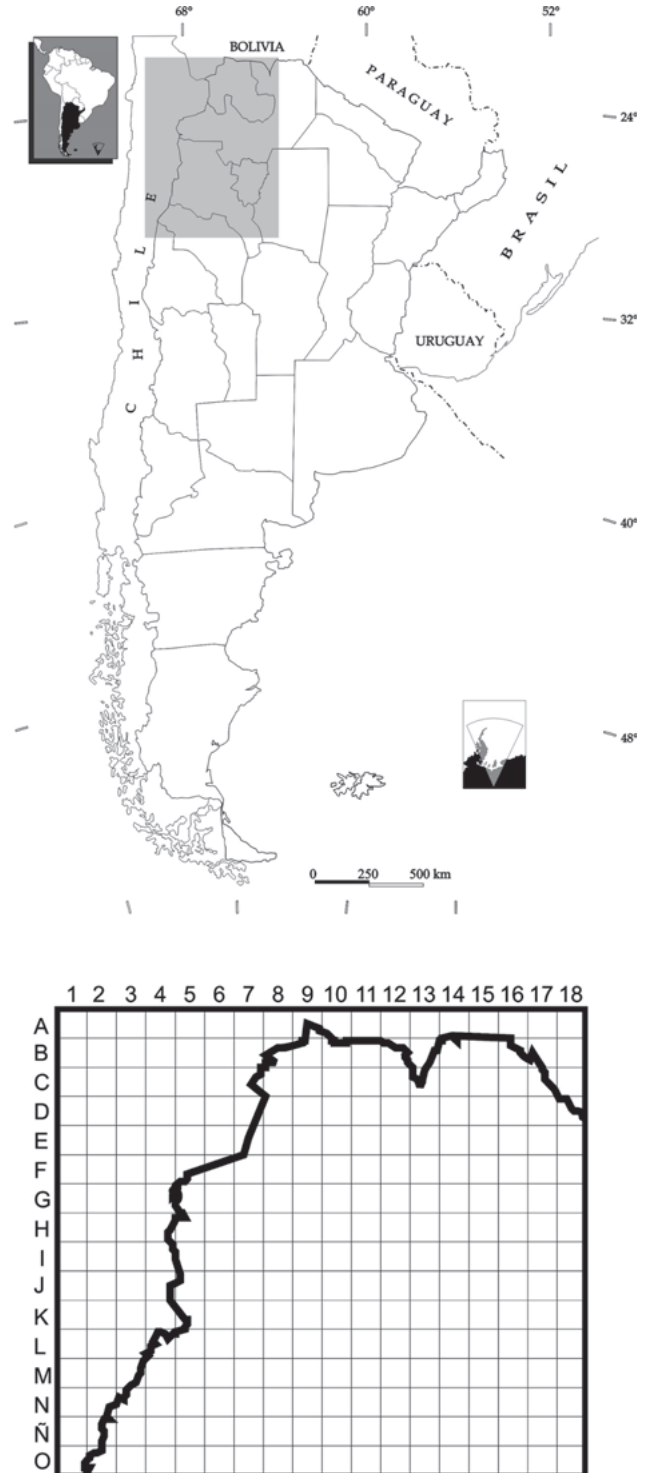


FIGURE 1: Study area. Upper figure: Map showing the study area, with the shaded rectangle representing approximately the area studied, including the Puna and Cordillera Oriental in Argentina. Lower figure: Study area divided in a grid consisting of 288 cells of  $0.5^\circ \times 0.5$  sexagesimal degrees each. This grid was used to construct the data matrix for the analysis with PAE and NDM.

ter (Martínez Carretero, 1995). Its limits are: in the North, the Argentinian-Bolivian border (21°45'S); in the South the Cordillera de San Buenaventura (26°45'S) in Catamarca province; in the West the limit corresponds with the political limit between Argentina and Chile; the Western limit extends from the Argentinian-Bolivian border South, through the Sierra de Cochinoca, Salinas Grandes, San Antonio de los Cobres and the Valles Calchaquies, to Santa Maria in Catamarca. The distinction between the Argentinian and the Chilean Puna (or Puna de Atacama) is based on the climatic divisor of the main cordillera volcanoes (Keidel 1927; 1937). The Cordillera Oriental extends from the Argentinian-Bolivian border towards south, passing by the west of San Salvador de Jujuy in Jujuy province, Metán, and the Sierra de la Candelaria in Salta province, to the south of San Miguel de Tucumán in Tucumán province. The western limit of the province of Cordillera Oriental coincides with the Eastern border of the Puna (Turner and Méndez, 1979a). Because the distribution of some species fell outside those two areas, I included in the region of study The Cumbres Calchaquies in Tucumán province, and part of Catamarca and La Rioja provinces. That area is congruent with the Distrito Central of Martínez Carretero (1995) between 25°30' and 29°S.

*Species analyzed* – For this study, I collected distributional data of 260 individuals belonging to 29 species of the genus *Liolaemus*, from the Colección Herpetológica de la Fundación Miguel Lillo (FML), the Colección Herpetológica of the Museo de Ciencias Naturales de la Universidad Nacional de Salta (MCN) and from relevant literature. In several cases, the geographic coordinates were not available in the original descriptions, and they were obtained by using cartography and satellite images. In several cases, there were multiple records for the same species at the same locality; in those cases I listed only one or two records. The type locality for almost every species was included in the analysis. The list of specimens used is on Appendix. The species and groups to which they belong are as follow:

*alticolor* group (sensu Lobo y Espinoza, 2004): *Liolaemus chaltin* Lobo and Espinoza, *L. puna* Lobo and Espinoza, *L. ramirezae* Lobo and Espinoza, *L. yanalcu* Martínez Oliver and Lobo, *L. pagaburoi* Lobo and Espinoza, *L. bitaeniatus* Laurent.

*darwinii* group (Etheridge, 1993): *Liolaemus abaucan* Etheridge, *L. quilmes* Etheridge, *L. olongasta*

Etheridge, *L. koslowsky* Etheridge, *L. ornatus* Koslowsky, *L. albiceps* Lobo and Laurent, *L. irregularis* Laurent, *L. calchaqui* Lobo and Kretzschmar, *L. cuyanus* Laurent.

*capillitas* group (Lobo 2004): *Liolaemus heliodermis* Espinoza, Lobo and Cruz, *L. capillitas* Hulse, *L. umbrifer* Espinoza and Lobo, *L. dicktracyi* Espinoza and Lobo.

*andinus* group (following in part Ceï, 1993): *L. cf multicolor*, *L. multicolor* Laurent, *L. pulcherrimus* Laurent, *L. huacahuasicus* Laurent, *L. poecilochromus* Laurent, *L. famatinae* Ceï, *L. nigriceps* (Philippi).

*dorbignyi* group (Díaz Gómez, 2007): *L. chlorostictus* Laurent, *L. orientalis* Müller, *L. montanus* Koslowsky, *L. dorbignyi* Koslowsky (four populations).

The *andinus* group includes species with well marked sexual dichromatism, with small, granular scales. The *dorbignyi* group (Díaz Gómez, 2007) corresponds partially to the *montanus* and *signifer* groups of Ceï (1993), and includes species larger in size, with bigger, laminar scales. Both *andinus* and *dorbignyi* groups have not been corroborated through a formal phylogenetic analysis, and were included within the *montanus* group by Etheridge (1995), a group characterized by the presence of a hypertrophied M. tibialis anterior in association with the presence of a sharp, blade-like process of the tibia (Etheridge, 1995). Schulte et al (2000) included species from the *andinus* and *dorbignyi* groups in their *montanus* section, within the subgenus *Eulaemus*.

I divided the distribution of *Liolaemus dorbignyi* into four taxonomically distinct populations (Abdala and Quinteros, pers. comm) that are geographically distributed in the following regions: 1) Cachi in Salta province, 2) Volcán Pichao in Tucumán province, 3) Antofagasta de la Sierra in Catamarca province, and 4) Susques, in Jujuy province.

*Analysis* – The distributional data of the *Liolaemus* species were analyzed using two distinct methods. The first one is the Parsimony Analysis of Endemicity (Morrone, 1994), that consists on scoring on a grid presences/absences of a set of species in a matrix, and then analyzing it under parsimony using the grids as terminals and the species as characters. Clades supported by two or more taxa are considered to represent areas of endemism. The second method for identifying areas of endemism used in this study

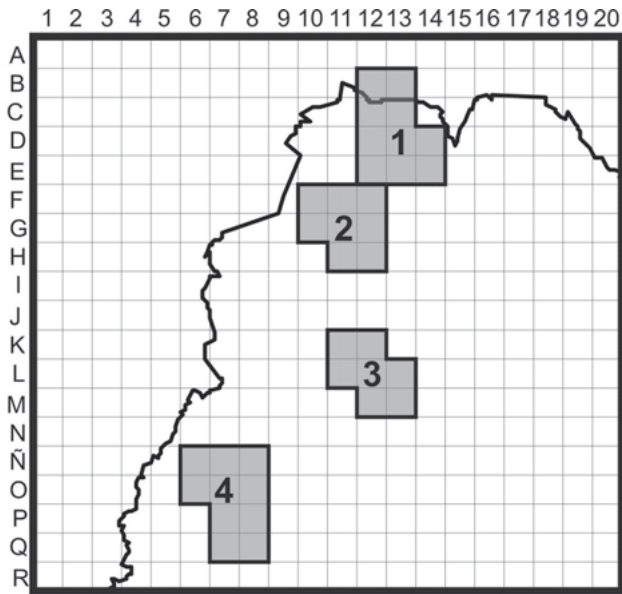


FIGURE 2: Sets of cells found by the endemism analysis with NDM. The list of species of each set is on Table 2.

was the one described in Szumik *et al.* (2002), and uses an optimality criterion that assign an endemism value to an area or to a set of grid cells, according to the number of endemic species present in that area. A posterior modification of the method (Szumik and Goloboff, 2004) weights the species of a given set of cells according to the “fit” of distribution of each species to the set of cells. Species with data outside of the set are weighted negatively, but favourably for the records inside the set. The original criterion and its modifications are implemented in the computer program NDM (Goloboff, 2004). The analysis was performed using grids of  $0.5^\circ \times 0.5^\circ$  (Fig. 1B), performing a heuristic search, with the following options: radius size to fill,  $x = 30$ ,  $y = 30$ ; radius size to assume,  $x = 50$ ,  $y = 50$ . The grid origin was  $x = 23.00$ ,  $y = 18.00$ . Sets with score above 1.00 were saved, and the analysis was made swapping

one cell at a time. In a preliminary analysis, larger or smaller cells caused a loss of resolution making the results uninformative. Obviously, the size and position of the grid will affect the results. The NDM program allows evaluating if small grid movements can produce better endemism scores, using the option ‘optimize grid position’. Each of the sets of grids found was evaluated under this option. The analysis was made with version 1.6 of the program, and the program VNDM (Goloboff, 2004) used to visualize the results.

For the Parsimony analysis of endemism, a presence/absence matrix was generated from VNDM, with the option “assumed = 1.” The matrix was analyzed under parsimony assuming equal weights, using the program TNT (Tree analysis using New Technology; Goloboff, 2003) with fifteen random addition sequences, followed by Tree bisection-reconnection (TBR) branch swapping, saving up to 5 trees for replication. The resulting trees were swapped by TBR until 1000 most parsimonious trees were found. Then, the common synapomorphies were mapped on the strict consensus of those trees.

## RESULTS

*NDM Analysis* – The analysis found four sets of cells (Fig. 2). Set 1 is located in the Quebrada de Humahuaca, Abrapampa and La Quiaca in Jujuy province; set 2 is located in San Antonio de los Cobres, Nevado del Acay, Abra del Acay and Los Patos, in Salta province; set 3 is located in the Cumbres Calchaquies and Nevados del Aconquija in Tucumán province and set 4 is on the Sierra de Famatina, in Catamarca and La Rioja provinces. The endemism score and the species endemics to each set are given in Table 1. When the grid optimization was applied to each set, sets 1 and 3 increased its endemism score, and 2 species were added as endemic to this set. Set 2 increased its

TABLE 1: Set of cells found by NDM. Numbers in bold correspond to the endemism index after the grid optimization. Names of species in bold means that these species are added to the sets after optimizing the grid

Set	Number of cells	Endemism score	Number of endemic species	Endemic species
1	10	1,42 <b>2,10</b>	2 <b>4</b>	<i>L. chaltin</i> , <i>L. orientalis</i> , <b><i>L. ornatus</i>, <i>L. multicolor</i></b>
2	8	3,38 <b>3,62</b>	5	<i>L. yanalcu</i> , <i>L. albiceps</i> , <i>L. irregularis</i> , <i>L. cf multicolor</i> , <i>L. dorbignyi</i> (Susques)
3	7	2,76 <b>3,03</b>	4 <b>6</b>	<i>L. pagaburoi</i> , <i>L. calchaqui</i> , <i>L. heliodermis</i> , <i>L. dorbigny</i> (Pichao), <b><i>L. huacahuasicus</i>, <i>L. ramirezae</i></b>
4	10	1,52	2	<i>L. olongasta</i> , <i>L. famatinae</i>

TABLE 2: Groups of species in the sets found by NDM. In set 4 there is a species from the *capillitas* group (*L. dicktracyi*) that is not recovered by the analysis, and a new species of a group related to the *alticolor* group.

GROUP	SET 1	SET 2	SET 3	SET 4
ALTICOLOR	X	X	X	?
DARWINI	X	X	X	X
ANDINUS	X	X	X	X
CAPILLITAS	—	—	X	—
DORBIGNYI	X	X	X	?

endemism score, but no new endemic species. Set 4 did not increase its score.

More than half of the 29 species utilized in the analysis were considered endemic (17 species – 58 percent) by the NDM analysis. Examination of the endemic species showed a pattern consisting in the repetition of groups in the sets (Table 2). Sets 1, 2 and 3 have each a different species from the *alticolor*, *darwinii*, and *andinus* groups, and one from the *dorbignyi* group. Set 3 also retain a species from the *capillitas* group. Set 4 only have represented the *darwinii* and *andinus* groups.

*Parsimony Analysis of Endemicity* – The analysis found seven sets of cells (Fig. 3), none of which is totally congruent with the sets found by NDM. A list with cells of each set and their endemic species is given on Table 3. Set 1 from PAE shares a cell with set 1 of NDM (cell F10) and a species, *Liolaemus irregularis*. The cells included in the PAE sets 2 and 3 are not represented in any of the sets found by NDM. PAE set 4 shares 2 cells (L9, L10) with set 3 of NDM and one species, *L. pagaburoi*. PAE set 5, included within set 4, shares one cell (L10) with set 3 of NDM and one species, *L. dorbignyi* from Pichao in Tucumán. Set 6 shares four cells (F8, F9, G9, G10) with set 1 from NDM, and one species, *L. cf. multicolor*. Set 7, included within set 6, shares 2 cells (G9, G10) but no species with set 1.

## DISCUSSION

The main hypothesis of Vicariance Biogeography postulates that the emergence of barriers fragment distributions of taxa simultaneously, producing patterns of distributions that are explained as a result from common history, rather than by *ad hoc* hypotheses like the ones used by the dispersalist approach. Congruent distributions of several taxa, or areas of endemism, are examples of those patterns that are of main interest to historical biogeography.

The endemism analysis with NDM identified four areas with congruent distributions of *Liolaemus* species, these areas could be hypothesized as areas of endemism. Besides, there is a pattern on the composition of the species inhabiting those areas, with each area including four groups of species, but with different species (Table 2). The NDM analysis does not take into account any information regarding taxonomic groupings nor make any assumption on the causes underlying recovered patterns. It only tries to establish an explicit link between evidence (distributions) and conclusions (areas) (Szumik *et al.*, 2002). Nevertheless, a pattern could be identified in the present work, with the same groups of species repeated, but with different species, in each area. Among the species on set number 1, *Liolaemus orientalis* does not have a defined taxonomic position. However, a known suite of morphological data (Lobo and Quinteros, pers. comm.) seems to support the placement of *L. orientalis* in the *dorbignyi* group. Set number 4 have only 2 groups of species represented in the analysis. However, in the area included in Set number 4 there is a species from the *capillitas* group, *Liolaemus dicktracyi*, which is not recovered by the endemism analysis. This could be caused by its very restricted distribution, *L. dicktracyi* is only known for a few individuals from the Sierra de Famatina and has records only for two cells out of ten that form the area. *Liolaemus dicktracyi* could be present in other cells, but has not

TABLE 3: Sets of cells found by the Parsimony Analysis of Endemicity (PAE). N: number of cells, Nsp: number of endemic species. Cell designation is from Fig. 3

SET	N	Cells	n. sp	Endemic species
1	2	F10, F11	2	<i>L. calchaqui</i> , <i>L. bitaeniatus</i>
2	2	I9, I10	3	<i>L. yanalco</i> , <i>L. albiceps</i> , <i>L. cf. multicolor</i>
3	2	N8, N9	2	<i>L. quilmes</i> , <i>L. umbrifer</i>
4	7	L9, L10, L11, M9, M10, M11, N10	3	<i>L. pagaburoi</i> , <i>L. huacahuasicus</i>
5	4	L9, L10, M9, M10	3	<i>L. ramirezae</i> , <i>L. dorbignyi</i> (Pichao)
6	8	F8, F9, G8, G9, G10, H8, H9, H10	4	<i>L. yanalco</i> , <i>L. cf. multicolor</i> , <i>L. multicolor</i>
7	6	G8, G9, G10, H8, H9, H10	3	<i>L. ornatus</i> , <i>L. nigriceps</i>

been found yet, making necessary an increase in sampling efforts in the cells that are part of set number 4 and where *L. dicktracyi* was not recovered. A possible solution for this problem, namely an endemic species that is not recovered by the analysis, could be the ad-

dition of cells with assumed presences in order to increase the endemism score for the species. Recently, a new species of *Liolaemus* has been found (Quinteros and Abdala, pers. comm.) on the slopes of the Sierra de la Famatina, which could be morphologically

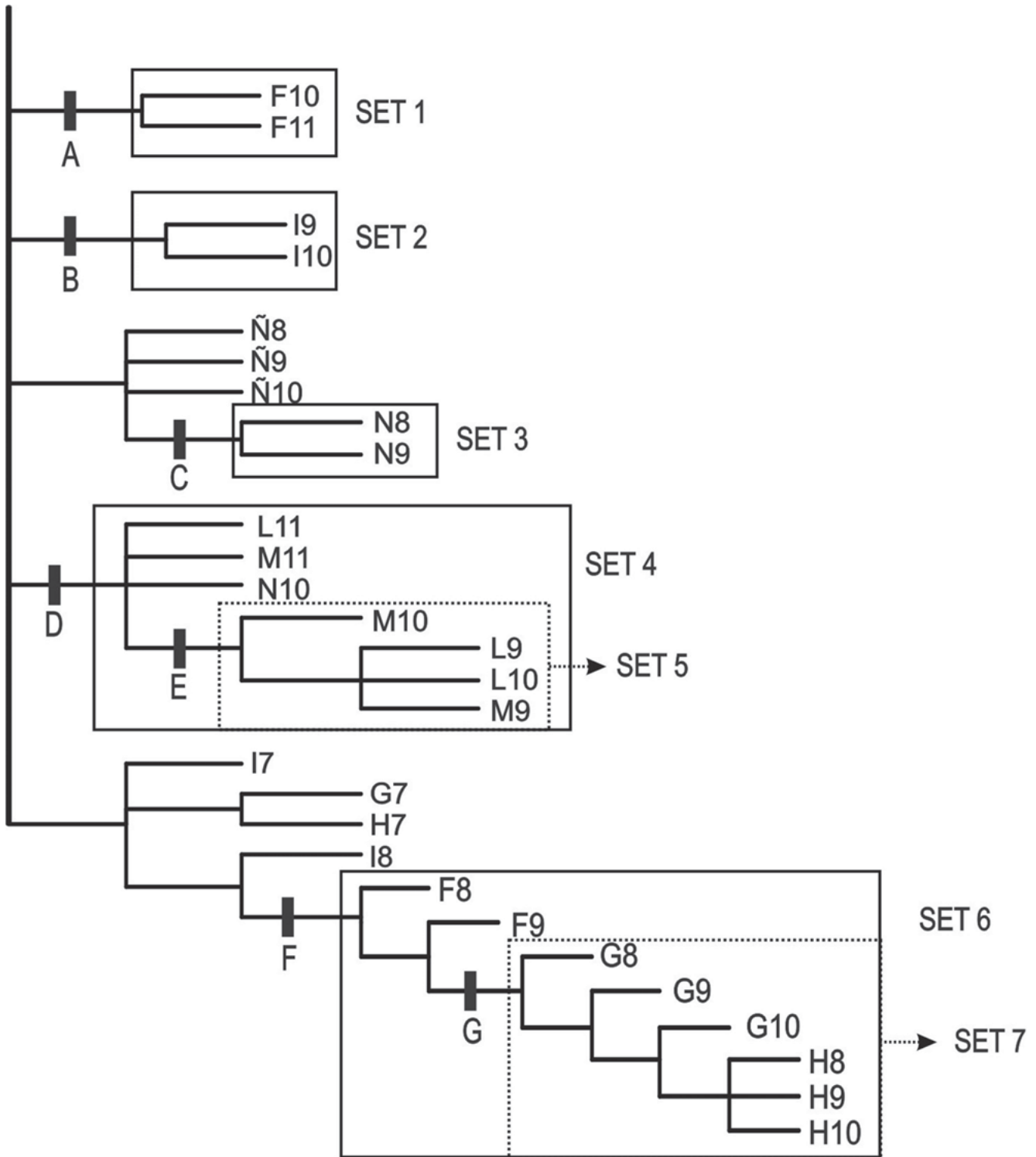


FIGURE 3: Strict Consensus of 1000 most parsimonious trees. The numbers on the nodes are the species that support the areas found by PAE. A: *Liolaemus calchaqui*, *L. bitaeniatus*; B: *L. yanalco*, *L. albiceps*, *L. cf multicolor*; C: *L. quilmes*, *L. umbrifer*; D: *L. pagaburoi*, *L. huacahuasicus*; E: *L. ramirezae*, *L. dorbignyi* (Pichao); F: *L. yanalco*, *L. cf multicolor*, *L. multicolor*; G: *L. ornatus*, *L. nigriceps*.

assigned to the *robertmertensi* group, related to the *alticolor* group (Lobo and Espinoza, 2004). With this two species, set 4 would have a species of the *capillitas* group, and another of a group related to *alticolor*, thus ending up with all the groups represented.

#### Parsimony analysis of endemism (PAE)

Some of the results reached with PAE are peculiar. For example, set number 1 is defined by two species, *Liolaemus calchaqui* and *L. bitaeniatus*. However, the latter has most of its distribution records outside the area found by PAE. *Liolaemus yanalco* and *L. cf multicolor* are synapomorphies of sets number 2 and 6, both sets are adjacent but do not share any cell. Thus, both species violate the requirement of endemism that is being restricted to an area and not found in other place. This is the result of the use of the parsimony criterion for biogeographic analysis. Parsimony means that, from several hypotheses, the one to prefer is the one that implies the smallest number of ad hoc assumptions, or homoplasies. The parsimony criterion minimizes but does not prohibit homoplasy. As a result, any analysis may present distinct degrees of homoplasy, which is not a problem per se for a phylogenetic analysis, but is a drawback for an endemism analysis because it allows the identification of areas of endemism defined by species that are not endemic (Szumik *et al.*, 2002).

This study is the first formal analysis of endemism for species of the genus *Liolaemus* in the Argentinian Puna. It has allowed the identification of four areas of endemism, with a clear pattern of distribution for several species of *Liolaemus*. This information could be useful as additional evidence for studies dealing with species of uncertain taxonomic status. For example, in the case of *Liolaemus orientalis*, the biogeographic information from this study could be considered as another source of evidence for placing *L. orientalis* in the *dorbignyi* group. Another use of this information could be for the prediction of the occurrence of species in areas where there are no records of its presence. The recent discovery of a species for the slopes of the Sierra de Famatina that is congruent with the pattern found in this study supports this hypothesis.

#### RESUMEN

Las áreas de endemismo son consideradas la unidad fundamental en biogeografía histórica, dado que son las entidades utilizadas en los análisis biogeográficos. De todas maneras, hasta hace poco tiempo no

había métodos formales para su identificación. En este trabajo, apliqué dos métodos diferentes para identificar áreas de endemismo en el género *Liolaemus*, el Análisis de Parsimonia de Endemicidad (PAE) y un método propuesto recientemente que está basado en un criterio de optimalidad y ha sido implementado en el programa NDM. Analicé las distribuciones de 29 especies de *Liolaemus* que habitan la Puna en el Noroeste de Argentina. El análisis con NDM encontró cuatro áreas de endemismo con un patrón repetido de grupos de especies, con los mismos grupos en cada área. Por otro lado, los resultados encontrados con PAE no fueron congruentes con los de NDM y en ocasiones incluso violaron la definición de áreas de endemismo. Los patrones hallados sugieren que estos grupos de especies podrían haber sido afectados por los mismos eventos históricos.

#### ACKNOWLEDGMENTS

Thanks are due to Fernando Lobo, Sebastián Quinteros, Cristian Abdala, Federico Arias and Soledad Valdecantos, for advice and valuable discussions. Two anonymous reviewers and Husam Zaher made several suggestions that improved the manuscript. Claudia Szumik and Félix Cruz read earlier versions of the manuscript and made valuable suggestions. Claudia Szumik and Dolores Casagrande provided advice and help with NDM. I am indebted to the members of the Abdala family, for their friendship and hospitality, and to Elisa Núñez for her patience and help in various stages of the work. This investigation was supported by the Consejo de Investigación de la Universidad Nacional de Salta (CIUNSA), Trabajo N° 1271, and the Consejo Nacional de Ciencia y Técnica (CONICET).

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Submitted 11 January 2007

Accepted 09 April 2007

## APPENDIX

List of specimens utilized in the study. Acronyms: FML: Fundación Miguel Lillo, Tucumán, Argentina; MCN: Museo de Ciencias Naturales, Salta, Argentina; MACN: Museo Argentino de Ciencias Naturales; CM: Carnegie Museum of Natural History; MF: Museo Zoologico, Firenze, Italy; MLP: Museo de Ciencias Naturales de La Plata; MNHNC: Museo Nacional de Historia Natural de Chile.

*L. abaucan*: FML 2638 (Holotype) – FML 2640, – FML 2641 – FML 2642 – FML 2643 – FML 3426 – FML 1814;  
*L. albiceps*: MCN 328 – MCN 343 – MCN 1058 – MCN 1061 – MCN 1440 – MCN 1441 – MCN 423 – MCN 640 – FML 3370 (Holotype); *L. andinus*: MCN 340 – MCN 375 – FML 1853, – FML 1911 – FML 3068 – FML 3074 – FML 8808 – FML 1764 – FML 1768 – FML 6337 – MCN 376 – MCN 448; *L. bitaeniatus*: FML 2993 – FML 742 – FML 846 – FML 811 – FML 921 – FML 1554 – FML 2280 – FML 1655 – FML 6789 – FML 7705 – MCN 1656 – MCN 1655; *L. calchaqui*: MCN 617 – FML 3082 (Holotype) – FML 2750 – FML 2425 – FML 890;  
*L. capillitas*: FML 852 – FML 1229 – FML 1914 – FML 6402 – FML 834 – FML 1794 – FML 1110 – FML 1316 – FML 7136 – FML 1225 – CM 70114 (Holotype); *L. cf. multicolor*: MCN 657 – MCN 758 – MCN 927 – MCN 1001 – MCN 1014 – MCN 1062 – MCN 1470 – FML 839; *L. chaltin*: FML 1459 – FML 1460 – FML 1524 – FML 1531 – FML 1461 – FML 1528 – FML 1538 – FML 1871 – FML 1878 – FML 3428 – FML 973 – FML 9874 (Holotype) – MCN 234 – MCN 236 – MCN 791; *L. chlorostictus*: FML 2284 – FML 1510 – MACN 2253 – FML 2706 – FML 1515; *L. dicktracyi*: FML 9928 (Holotype) – CM 147716 – CM 147717 – FML 9929 – MCN 461;  
*L. dorbigny*: FML 1669 – FML 952 – FML 1219 – FML 1167 – FML 802 – FML 1763 – FML 1762 – FML 1766 – FML 482 – FML 751 – FML 976 – FML 978; *L. famatinae*: MF 23821 (Holotype) – FML 1720; *L. heliodermis*: FML 6006 – FML 7196 (Holotype) – FML 8974 – FML 6007; *L. huacahuasicus*: FML 677 – FML 1232 – FML 1583 – FML 7124 – FML 7140 – FML 00535/2 (Holotype); *L. irregularis*: MCN 1065 – MCN 243 – MCN 245 – MCN 246 – MCN 332 – MCN 336 – MCN 338 – MCN 380 – MCN 740 – FML 1360 (Holotype); *L. koslowky*: FML 1309 – FML 1476 – FML 1484 – FML 1486 – FML – FML 2665 – FML 2659 (Holotype) – MCN 1394 – MCN 1395 – MCN 1413 – MCN 573; *L. montanus*: FML 279 – FML 289 – FML 908 – FML 909 – FML 910 – FML 2141; *L. multicolor*: MCN 602 – MCN 727 – FML 1464 – FML 1539 – FML 2992 – FML 3347 – FML 259 – FML 1507 – MLP 56 (Holotype); *L. nigriceps*: FML 923 – FML 1636 – FML 924 – FML 696 – FML 1632 – FML 1633 – FML 1634 – FML 1786; *L. olongasta*: FML 2667 (Holotype) – FML 2668 – FML 2974 – FML 3454 – FML 7351; *L. orientalis*: FML 2044 – FML 928 – FML 930 – FML 938 – FML 939 – FML 944 – FML 949 – FML 1456 – FML 1457 – FML 1537 – FML 2035 – FML 2036 – FML 2064; *L. ornatus*: FML 975 – FML 1470 – FML 1514 – MCN 220 – MCN 222 – MCN 241 – MCN 247 – MCN 742 – MCN 745 – MCN 748 – MCN 750 – MCN 752 – MCN 773 – MLP-S (Neotype); *L. pagaburoi*: MCN 625 – MCN 619 – MCN 621 – MCN 482 – MCN 478 – MCN 472 – FML 648 – FML 6069 (Holotype); *L. poecilochromus*: FML 1413 – FML 1415 – FML 01176/5 (Holotype) – FML 01176/1 – FML 1171; *L. pulcherrimus*: MCN 223 – MCN 224 – MCN 238 – MCN 239 – MCN 240 – FML 2202 (Holotype); *L. puna*: FML 1265 – FML 1364 (Holotype) – FML 1512 – FML 1533 – FML 1761 – FML 1852 – FML 1871 – FML 1915 – MNHNC 583 – MZUC 19392; *L. quilmes*: FML 2644 (Holotype) – FML 2657 – FML 2655 – FML 2656 – FML 2658 – FML 2919 – FML 766 – FML 1664 – FML 1665 – FML 1667 – FML 1675 – FML 101 – FML 288 – FML 1217 – FML 1905; *L. ramirezae*: MCN 465 – FML 3339 – FML 3006 – FML 2275 – FML 2498 – FML 3506 – FML 3500 – FML 3431 – FML 1228 – FML 6071 (Holotype); *L. umbrifer*: MCN 488 – MCN 489 – MCN 463 – MCN 464 – FML 9934 (Holotype) – CM 147714; *L. yanalcu*: MCN 680 – MCN 688 – MCN 725 – MCN 728 – MCN 729 – MCN 939 – MCN 541 (Holotype)