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Historical Biogeography of a Clade of *Liolaemus* (Iguania: Liolaemidae) based on ancestral areas and dispersal-vicariance analysis (DIVA)

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ABSTRACT

Although many phylogenetic studies have been made on the genus Liolaemus, *they are inappropriate for a biogeographic study because of incomplete taxon sampling. Here we develop a biogeographic analysis using a new phylogenetic study of the* chiliensis *group, which differs from the other studies in having his members fully represented. The biogeographic analysis presented here consists in reconstructing the ancestral area of this clade, under three different methods of analysis: Fitch Optimisation, Dispersal Vicariance Analysis and Weighted Ancestral Area Analysis. The analyses were made on phylogenies from parsimony under equally weighted characters, as well as under implied weighting. The equally weighted tree recovers most of the groupings proposed in previous studies. The strict consensus of the implied weighting trees recovers fifteen groups, but there is no agreement of the relationships between those groups. The ancestral area analyses agree in an Andean-Patagonian origin for the* chiliensis *clade, and are congruent with previous hypotheses and paleontological data.*

KEYWORDS: *Liolaemus, chiliensis*-group, biogeography, ancestral area, DIVA, Fitch, Patagonia, Andes.

INTRODUCTION

The genus *Liolaemus* includes about one hundred and sixty species (Espinoza *et al.,* 2004), and is the second most specious genus of Lizards. Its distribution extends from Tierra del Fuego *(Liolaemus magellanicus)* in the southernmost extreme of South America, to the Peruvian Andes *(L. walkeri). Liolaemus* species occupy diverse habitats, including terrestrial and arboreal, some are saxicolous, some arenicolous, others live in very rig-

orous climates, in very high latitudes or at high altitudes (over 4000 m above sea level). This diversity and wide distribution has allowed the development of very diverse biological characteristics, like oviparous and viviparous species (perhaps related to cold conditions, Schulte *et al.* 2000) and a diverse diet, existing omnivorous, herbivorous and insectivorous species.

Some authors included several statements regarding the distributional patterns of this genus in their taxonomic studies. One of them is Hellmich (1951)

who described the distribution of six species groups from Chile, which occupy very different areas. Hellmich explained these current distributions as a consequence of expansions and contractions of the original distributions. According to him, this happened during the interglacial and glacial periods of the Tertiary, and this would have given rise to the 'races' recognized. For Hellmich, the final explanation was dispersal, a statement which was also used by Lamborot *et al.* (1981) to explain the chromosomic variation in the *monticola* species complex.

Laurent (1983, 1985, 1992) also included biogeographic comments when dividing the genus into two major subgroups (subgenus *Eulaemus* or Argentine group and subgenus *Liolaemus* or Chilean group), division attributed to the uplift of the Andes.

Cei (1979) described the composition of the Patagonian and Andean herpetofauna, characterising these regions by their high endemicity, and described centres of speciation and dispersal by using paleontological and paleoclimatic data.

Lobo (2001) described the areas of distribution on the phylogeny of the *chiliensis* group, following the biogeographic characterization of Roig-Juñent (1994) and adding areas not considered previously (i.e: Puna).

There are only two works where the historical biogeography of *Liolaemus* is discussed using some cladistic methodology. Young-Downey (1998) performed a Brooks Parsimony Analysis by using areas defined by Cabrera & Willink (1980) and Brown & Gibson (1983), and compared her results with the hypothesis of Solbrig (1976) on the origin and evolution of those areas. Schulte *et al.* (2000) proposed a hypothesis in which the species inhabiting three general areas, Andes, West of the Andes and East of the Andes were monophyletic. Using a molecular-based phylogeny, they optimized the distributions of the species, and ultimately rejected that hypothesis as the shortest phylogenetic estimate required multiple invasions of each of the areas. The pattern of distribution of *Liolaemus* is explained by recurring vicariance with subsequent dispersal between the areas that allowed further vicariance. Both studies had the problem that the areas of distribution were represented by biogeographic units (provinces) or arbitrarily defined, and in many cases, those units were not fully occupied by the species. Using areas much larger than the ranges of the species used in the analysis, as is the case with biogeographic provinces, will cause a loss of resolution in the analysis, because sometimes species separated by hundreds of kilometres will be included in the same province. Even worse, the sampling of species in the cited studies was not complete, then, the identification

of dispersal events could be just a problem of taxon sampling.

Although in the last years many works have been focused on the phylogeny of *Liolaemus* (Ortiz, 1981; Etheridge, 1995, Halloy *et al.* 1998; Young-Downey, 1998; Etheridge, 2000; Schulte *et al.* 2000), they are not useful for a biogeographic analysis because they are focused on subgroups or the genus is not fully represented. The cladistic analysis on the *chiliensis* group recently performed by Lobo (2001, 2005) differs from the other studies in having the *chiliensis* group, which is half the genus *Liolaemus,* fully represented.

In this paper we present a new cladistic analysis of the *chiliensis* group, based on already published data as well as evidence not previously considered. We include species recently described and ethological characters, and use parsimony to obtain a new hypothesis for the clade, and study its historical biogeography based on the topologies obtained. We apply three different methods of ancestral area analysis: Fitch optimisation (Ronquist, 1994), Weighted Ancestral Area Analysis (WAAA, Hausdorf, 1998) and Dispersal Vicariance Analysis (DIVA, Ronquist, 1997). The results are compared with previous hypothesis, and the methods are discussed.

MATERIALS AND METHODS

Taxa and Characters

The biogeographic analyses are based on a new hypothesis for the *chiliensis* group, and include all the species currently known for this group (83 species). We constructed a matrix using the morphological data from Lobo (2005), which was updated by adding three new species and 35 characters. The new species are *Liolaemus yanalcu,* (Martinez Oliver & Lobo, 2002), *L. puna* and *L. chaltin* (Lobo & Espinoza, 2004). Three new characters are original to this study: gravid coloration, plant-microhabitat preference and lateral black spots; character states are included in appendix 1. We also included in the morphological matrix the allozyme data set of Young-Downey (1998) (32 characters for 26 taxa of the *chiliensis* group); the species *L. alticolor* of Young-Downey (op.cit.) analysis is actually *L. puna* (Lobo & Espinoza, 2004). Sp 1 is a new *Liolaemus* under description (Vega *et al.* pers. comm), Sp 2 is a new species (Lobo *et al.* submitted). Being *Phymaturus* the closest living relative to *Liolaemus* (Espinoza *et al.* 2004), we used *Phymaturus indisctintus* as outgroup. Data matrix is available at www.unsa.edu.ar/acunsa/index02.html.

Cladistic Analysis

Parsimony analysis was made under implied weighting (Goloboff, 1993). This weighting method weights each character according to the number of extra or homoplasious steps in a tree, using a concave function that gives lower weights to the characters with high homoplasy (Kitching *et al.* 1998). For the implied weighting analysis 6 concavity values were used (K, 1 to 6). Also we made a parsimony analysis under equal weights. For both analyses TNT version 1.0b4 (Goloboff *et al.* 2003) was used. We searched for optimal trees using TBR branch swapping, making 500 replications saving up to 10 trees for both the equally weighted and implied weights analysis. A strict consensus tree was generated using the topologies obtained from the implied weights. Continuous characters were coded using the gap weighting method (Thiele, 1993). Characters 0-20, 22-34, 37-82, 115 and 116 were coded as additive.

Biogeographic Analysis

Ancestral Area Analysis was proposed by Bremer (1992) as a way for identifying the area of distribution of the ancestor of a monophyletic taxon, which he named the ancestral area. The analytical methods for ancestral areas are based on the assumption that there is information about the ancestral area of a taxon in the topology of its area cladogram, that is, the probability for an area of being part of the ancestral area increases with its presence in plesiomorphic branches and its general presence in the cladogram (Hausdorf, 1998). We applied three methods proposed in the last years: Fitch optimisation (Ronquist, 1994), Weighted Ancestral Area Analysis (WAAA) (Hausdorf, 1998) and Dispersal Vicariance Analysis (DIVA) (Ronquist, 1997). All these methods use optimisations with reversible parsimony for estimating ancestral areas. Fitch Optimisation was proposed by Ronquist (1994) to avoid the problems of Camin-Sokal (irreversible) parsimony originally proposed by Bremer (1992). WAAA uses Fitch parsimony with a weighting scheme that weights favourably areas located in plesiomorphic branches, and areas more common as terminals. In this method, a Probability Index (PI) is calculated to give a measure of the likelihood of a particular area of being part of the ancestral area. The index is calculated for each area from the ratio of gains (assuming that the area was not part of the ancestral area) over losses (assuming that the area was part of the ancestral area). DIVA searches ancestral areas using a three dimensional cost matrix that gives different costs to events, minimizing the dispersal events needed for explaining the distributions. In this approach, the vicariance events have no cost, while the dispersals and extinctions cost one per area unit added to the distribution.

Ancestral area analysis has been considered by some authors as a reimplementation of the centre of origin concept, and recently criticized on the basis that it utilizes paralogy (widespread taxa and redundant distributions) instead of reducing it, as is the usual procedure for methods of cladistic biogeography (Ebach, 1999). However, ancestral area methods rely on the fact that all taxa have an area where their ancestor was distributed, and the search for that area is a valid procedure. The ancestral area of a taxon needs not to be smaller than the actual distribution of its descendants, it can be larger or equal (Bremer, 1992), and dispersal needs not to be postulated as the only possible explanation. Ancestral area analysis tries to identify areas that may have been part of the ancestral area, and to distinguish vicariance events from possible dispersals (Hausdorf, 1998). As Hovenkamp (1997) pointed out, methods that try to elucidate Earth history search for common patterns in cladograms, discard the incongruences, opposed to methods that try to search for taxon histories (as ancestral area methods), which have different methodologies and does not need to discard paralogies.

Selection of Areas

The areas used were taken from Roig-Juñent (1994). To better represent the distribution of several species, we decided to include some new areas not considered in that study like Puna, Atacama, Cordillera Oriental and Andes. This last area was divided into Andes, Andes Centrales and Andes Meridionales. We also divided the Monte area from Roig-Juñent (1994) into the new areas Sierras Pampeanas and Sierras Subandinas. The areas used are (Fig. 1): Andes, Andes Centrales, Andes Meridionales, Atacama, Coquimbo, Cordillera Oriental, Maulina, Monte, Patagonia, Puna, Selva Valdiviana, Sierras Pampeanas, Sierras Subandinas, and Valle Central.

To make comparisons with a previous biogeographic hypothesis, we also replicated the topology from Schulte *et al.* (2000) for the *chiliensis* group, and applied the three methods replacing the areas used by Schulte *et al.* with the areas used in this study.
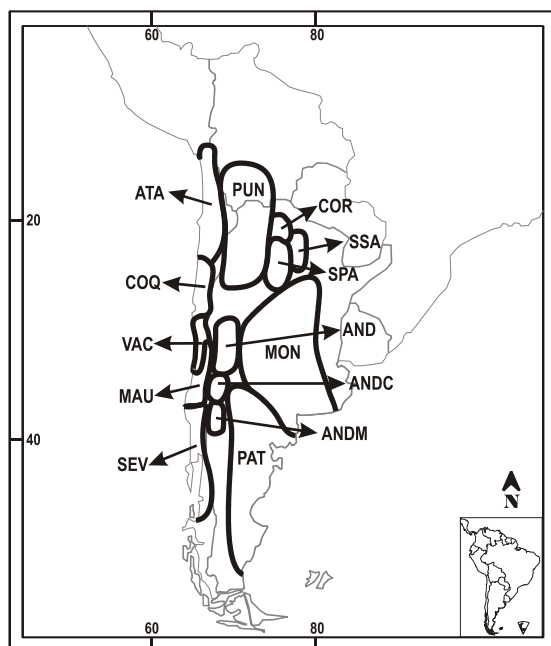
FIGURE 1: Areas used in the Ancestral Area Analysis. AND: Andes; ANDC: Andes Centrales; ANDM: Andes Meridionales; ATA: Atacama; COQ: Coquimbo; COR: Cordillera Oriental; MAU: Maulina; MON: Monte; PAT: Patagonia; PUN: Puna; SEV: Selva Valdiviana; SPA: Sierras Pampeanas; SSA: Sierras Subandinas; VAC: Valle Central

RESULTS

Liolaemus systematics

Four different topologies were obtained using the six concavity values (K). The strict consensus indicates that these four topologies have in common thirteen groups (Fig. 2). The analysis under equal weights yielded one tree (Fig. 3). Eight groups of species are recovered. The list of groups and the species included are in Table 1.

Liolaemus biogeography

The results for the three methods utilized are resumed on Table 2. These assignations refer to the most basal node of the tree.

Fitch Optimisation. The Fitch optimization on the consensus tree (Fig. 2) assigns the most basal node Andes as the ancestral area. The Fitch optimisation on the equally weighted tree (Fig. 3) assigns for the most basal node the areas Patagonia, Andes or Monte as the ancestral area.

TABLE 1: List of groups and species belonging to each group according to the parsimony analysis under equal weights and implied weighting. The species not included were found not belonging to any group.

Group	Equally weighted analysis	Implied weighting analysis
alticolor	*L. chaltin*	*L. alticolor*
	L. alticolor	*L. paulinae*
	L. puna	*L. puna*
	L. walkeri	*L. variegatus*
		L. tacnae
		L. walkeri
bibronii		*L. exploratorum*
		L. hernani
		L. bibronii
		L. yanalcu
		L. ramirezae
		L. bitaeniatus
		L. chaltin
capillitas	*L. capillitas*	*L. buergueri*
	L. heliodermis	*L. heliodermis*
	L. dicktracyi	*L. capillitas*
	L. umbrifer	*L. dicktracyi*
		L. umbrifer
ceii-kriegi	*L. ceii*	*L. ceii*
	L. kriegii	*L. kriegii*
	L. buergueri	
elongatus		*L. petrophilus*
		L. austromendocinus
		L. elongatusRN
gravenhorsti	*L. gravenhorsti*	*L. brattstroemi*
	L. cyanogaster	*L. cyanogaster*
	L. schroederi	*L. gravenhorsti*
		L. schroederi
leopardinus	*L. leopardinus*	*L. leopardinus*
	L. ramonensis	*L. ramonensis*
		L. valdesianus
nigroviridis		*L. maldonadae*
		L. campanae
		L. nigroviridis
nigromaculatus	*L. donosoi*	*L. platei*
	L. monticola	*L. atacamensis*
	L. tacnae	*L. silvai*
	L. platei	*L. sieversi*
	L. velosoi	*L. nigromaculatus*
	L. atacamensis	*L. kuhlmanni*
	L. ater	*L. copiapensis*
	L. bisignatus	*L. bisignatus*
	L. copiapensis	*L. ater*
	L. nigromaculatus	
	L. sieversi	
	L. zapallarensis	
	L. kuhlmanni	
	L. hellmichi	
	L. silvai	
pictus		*L. pictus*
		L. talcanensis
		L. argentinus
		L. chiloensis
robertmertensi	*L. robertmertensi*	*L. curicensis*
	L. chiliensis	*L. chiliensis*
	L. nitidus	*L. nitidus*
		L. robertmertensi
		L. saxatilis
		L. gracilis
		L. sp 2
tenuis	*L. tenuis*	*L. coerulus*
	L. punctatissimus	*L. neuquensis*
	L. argentinus	*L. punctatissimus*
	L. pictus	*L. tenuis*
	L. talcanensis	
	L. brattstroemi	
	L. chiloensis	
	L. coerulus	
	L. neuquensis	

Phymaturus indistinctus PAT

AND AND
L. leopardinus AND
L. ramonensis AND — leopardinus
L. valdesianus AND

AND AND
L. cei AND
L. kriegi AND — cei-kriegi
L. cristiani AND
L. chillanensis ANDC
L. villaricensis ANDM

AND *AND*
L. constanzae PUN
L. velosoi COQ
L. sanjuanensis SPA
L. nigroroseus ATA
L. moradoensis AND
L. monticola AND
L. lorenzmulleri COQ
L. isabelae ATA
L. hellmichi ATA
L. fitzgeraldi AND
L. elongatus ME AND
L. donosoi ATA
L. curis ANDC

AND AND
L. maldonadae AND
L. campanae VAC — nigroviridis
L. nigroviridis AND

SEV SEV
L. pictus MAU, SEV
L. talcanensis SEV
L. argentinus SEV — pictus
L. chiloensis SEV

AND AND
L. altissimus AND
L. coeruleus AND
L. neuquensis AND
L. punctatissimus MAU — tenuis
L. tenuis MAU

AND, VAC
MAU, SPA
VAC, COQ
L. curicensis MAU
L. chiliensis VAC, MAU
L. nitidus VAC, COQ
L. robertmertensi SPA — robertmertensi
L. saxatilis SPA
L. gracilis MON
sp 2 PUN

SPA PAT, AND
L. exploratorum PAT
L. hernani AND, MAU
L. bibroni PAT, MON
L. yanalcu COR — bibronii
L. ramirezae SPA
L. bitaeniatus SPA, SSA
L. chaltin PUN

MON AND
L. petrophilus MON
L. austromendocinus AND — elongatus
L. elongatus RN MON, AND

SPA SPA
L. buergeri AND
L. heliodermis SPA
L. capillitas SPA — capillitas
L. dicktracyi SPA
L. umbrifer PUN

COQ
COQ, ATA
L. platei COQ
L. atacamensis ATA
L. zapallarensis VAC
L. silvai COQ
L. sieversi COQ
L. nigromaculatus COQ — nigromaculatus
L. kuhlmanni VAC
L. copiapensis COQ
L. bisignatus COQ
L. ater COQ

PUN
PUN
L. alticolor PUN
L. paulinae ATA
L. puna PUN
L. variegatus COR — alticolor
L. tacnae PUN
L. walkeri PUN

SEV
MAU
L. brattstroemi SEV
L. cyanogaster VAC
L. gravenhorsti VAC — gravenhorsti
L. schroederi VAC, MAU
sp 2 PUN
L. araucanensis AND M
L. pagaburoi SPA
L. pseudolemniscatus COQ
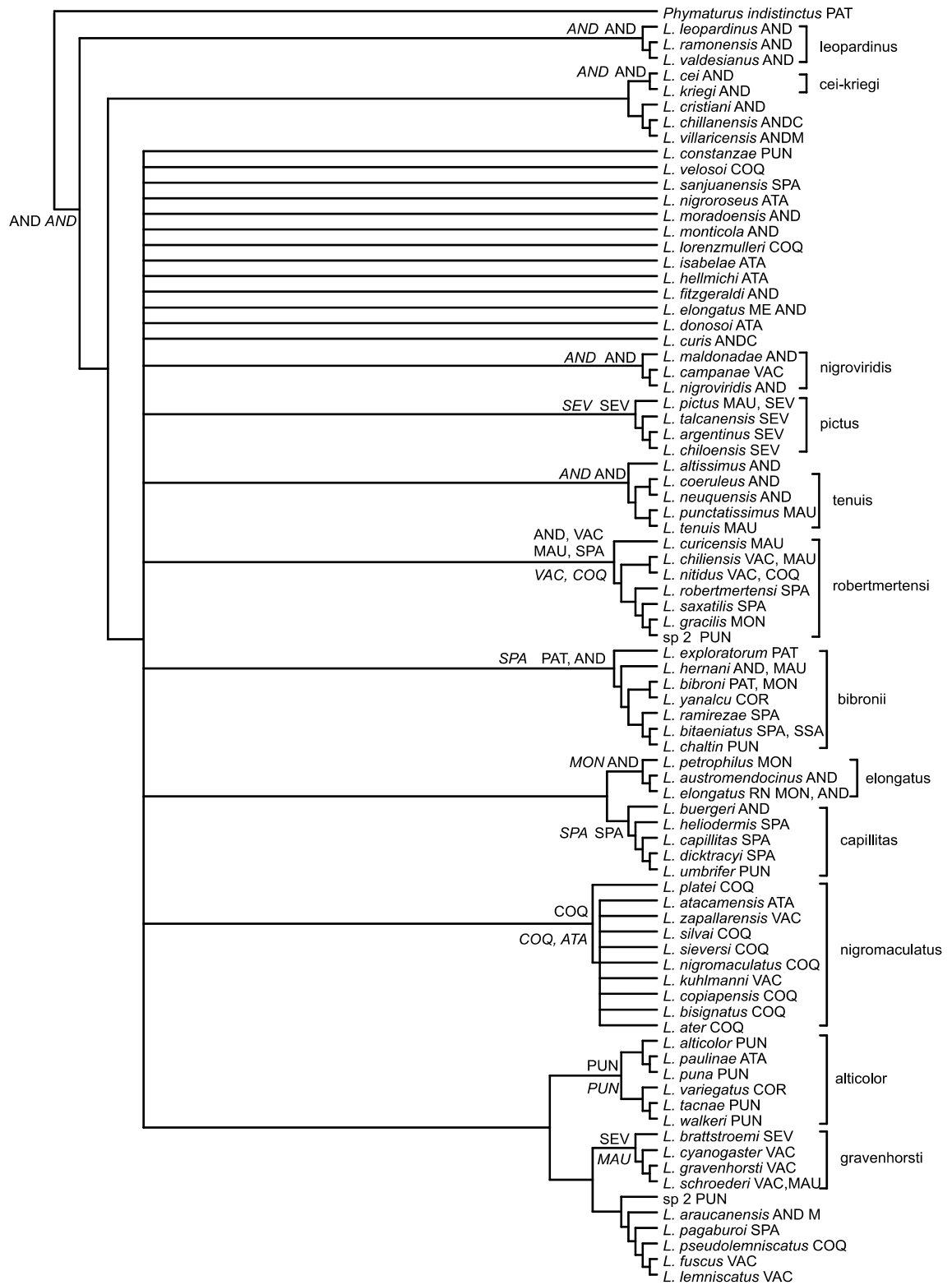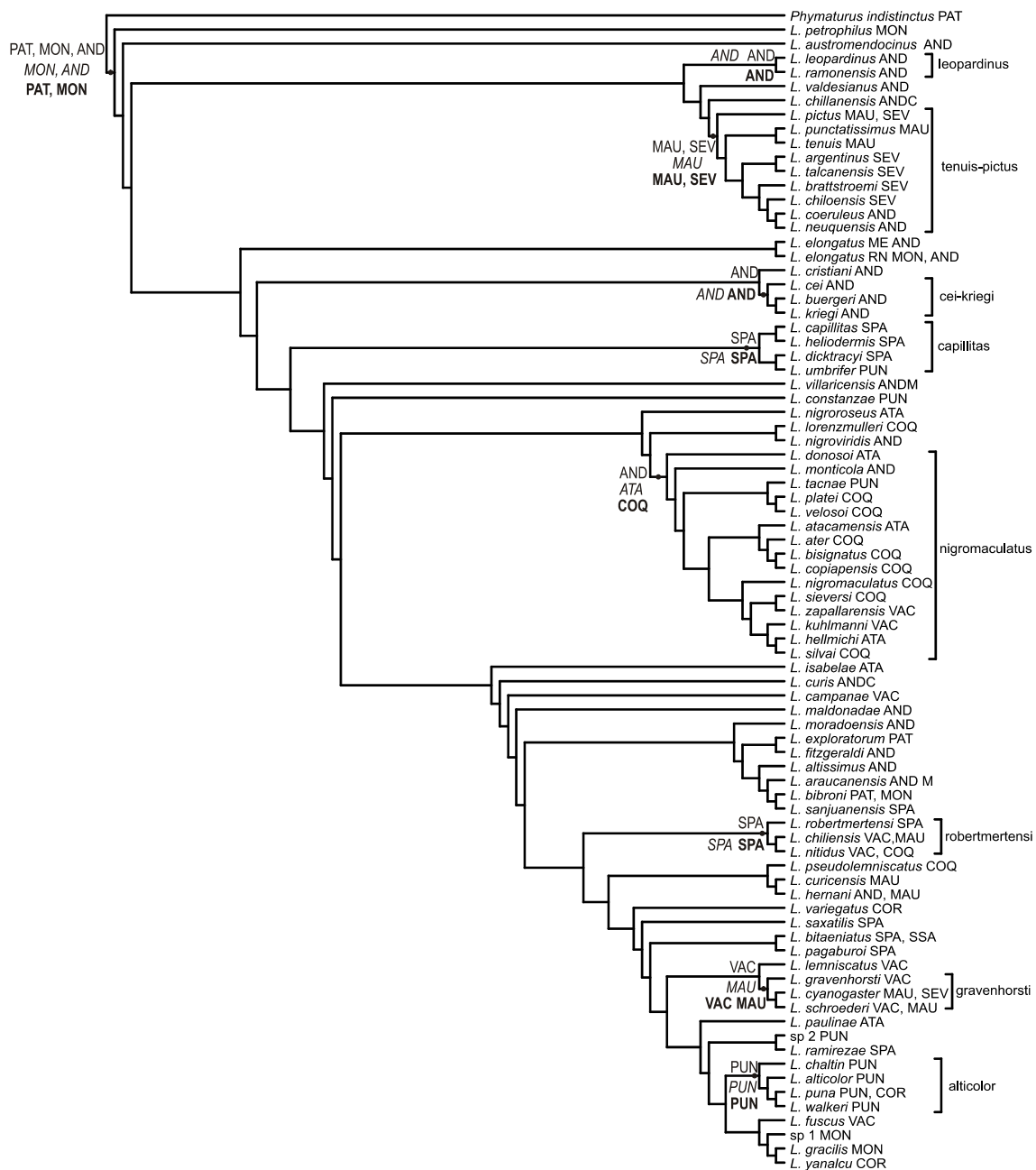*L. fuscus* VAC
L. lemniscatus VAC

FIGURE 2: Strict consensus from the four topologies obtained with the implied weights analysis. The area assignations are as follow: Normal, Fitch optimization; Italics, Weighted Ancestral Area Analysis.

FIGURE 3: Tree from the equally weighted analysis. The area assignations are as follow: Normal, Fitch optimization; Italics, Weighted Ancestral Area Analysis; Bold, DIVA (constrained to 2 maximum areas)

Dispersal Vicariance analysis (DIVA). The DIVA on the equally weighted tree achieved an exact solution, with 6 optimal reconstructions, requiring 45 dispersals each. (Table 2). For the most basal node, the areas Puna, Atacama, Monte, Andes, Valle Central, Coquimbo, Sierras Pampeanas, Andes Meridionales y Andes Centrales are repeated in all reconstructions. Maulina appears in four of six reconstructions, and Selva Valdiviana in three.

The only areas that don't appear in any reconstruction are Sierras Subandinas and Patagonia.

The DIVA could not be done on the consensus tree, as the software cannot handle trees with polytomies. We selected for DIVA the trees corresponding to K = 1 and 2, and K = 5 and 6, because those hypothesis represented two different weighting schemes: a stronger for K = 1,2 and weaker for K = 5, 6. Because of time con-

TABLE 2: Results of the ancestral area analysis. The abbreviations for the areas are from Fig. 1.

	Equally Weighted Analysis		Consensus	K = 1,2	K = 5,6
Fitch	PAT, AND, MON		AND	AND	AND
WAAA	AND, MON		AND	AND, PAT	AND, SPA
Constrained DIVA	Max areas = 2 PAT, MON PAT, AND, MON	Max areas = 3 PAT, AND, MON	—	Max areas = 2,3,4 PAT, AND	Max areas = 2,3,4,5,6 PAT, AND

Unconstrained DIVA

Equally Weighted Analysis	K = 1,2	K = 5,6
PUN ATA MON AND ANDM ANDC VAC COQ SPA	PUN ATA MON AND ANDM ANDC VAC COQ MAU SEV SPA COR	ATA MON AND ANDM VAC COQ MAU SEV SPA COR
PUN ATA MON AND ANDM ANDC VAC COQ MAU SPA	PAT PUN ATA MON AND ANDM ANDC VAC COQ MAU SEV SPA COR	PAT PUN ATA MON AND ANDM VAC COQ MAU SEV SPA COR
PUN ATA MON AND ANDM ANDC VAC COQ SEV SPA	PUN ATA MON AND ANDM ANDC VAC COQ MAU SEV SPA SSA COR	PUN ATA MON AND ANDM VAC COQ MAU SEV SPA SSA COR
PUN ATA MON AND ANDM ANDC VAC COQ MAU SEV SPA	PAT PUN ATA MON AND ANDM ANDC VAC COQ MAU SEV SPA SSA COR	PAT PUN ATA MON AND ANDM VAC COQ MAU SEV SPA SSA COR
PUN ATA MON AND ANDM ANDC VAC COQ MAU SPA COR		PUN ATA MON AND ANDM ANDC VAC COQ MAU SEV SPA COR
PUN ATA MON AND ANDM ANDC VAC COQ MAU SEV SPA COR		PAT PUN ATA MON AND ANDM ANDC VAC COQ MAU SEV SPA COR
		PUN ATA MON AND ANDM ANDC VAC COQ MAU SEV SPA SSA COR
		PAT PUN ATA MON AND ANDM ANDC VAC COQ MAU SEV SPA SSA COR

straints the solution was heuristic, yielding 4 optimal reconstructions that required 41 dispersals each. These reconstructions are both essentially the same, except that Andes and Sierras Subandinas are not present in three of them: in one reconstruction both areas are missing, and one of them is absent from each of the other two. The last reconstruction includes all the areas. The analysis on the tree resulting form K = 5 and 6, also heuristic, produced 8 optimal reconstructions, requiring 42 dispersals. One of the optimal reconstructions involves all the areas, the other seven differ in the presence or absence of Patagonia, Sierras Subandinas, and Andes Centrales. These results are summarized in Table 2. Given the number of possible reconstructions, it's hard to identify unambiguous vicariance events, making difficult to hypothesize a sequence of events for the distribution of *Liolaemus*.

When constraints were used on the maximum number of areas allowed for the ancestral area, on the equally weighted analysis, for a maximum of 2 areas the reconstruction is Patagonia-Monte or Patagonia-Andes; for a maximum of 3 to 6 areas the reconstruction is Patagonia, Andes, Monte (Table 2). For the trees with implied weights, when making DIVA on the topologies corresponding to K = 1 and 2, the reconstruction for a maximum of 2 to 4 areas is Patagonia and Andes; for K = 5 and 6 with a maximum of 2 to 6 areas, the reconstruction is Patagonia and Andes (Table 2). In all cases, the optimizations for a maximum number of areas superior to 6 showed several ambiguous reconstructions (data not shown).

Weighted Ancestral Area Analysis (WAAA). The PI values for the WAAA analysis were calculated for the most basal node of the tree, and for the nodes that give rise to groups of species.

Equally weighted analysis. The areas with higher PI are Andes and Monte (0.67 and 0.44 respectively), and have more probability of being part of the ancestral area (Table 2). This result is congruent with Fitch optimisation, which has Patagonia, Andes or Monte as equally probable reconstructions for the basal node, and Andes as the ancestral reconstruction for the nodes as we go up in the tree. Nevertheless, the area Patagonia has a very low PI (0.04), discarding it as part of the ancestral area. There are other areas that have low values of PI, but slightly higher than the remaining, these areas are Sierras Pampeanas and Selva Valdiviana (0.13 and 0.12 respectively). This may be reflecting the fact that these areas appear in more plesiomorfic branches, and are given more weight accordingly.

Implied weighting analysis. The WAAA analysis was made on the strict consensus tree as well as the topologies corresponding to K = 1, 2 and K = 5, 6 (Table 2). The areas with higher PI in the consensus were Andes (0.48) and Coquimbo (0.23). Monte has a low PI of 0.10. The areas with higher PI for the tree with K 1 and 2 are Andes (0.69) and Patagonia (0.30). Again Monte has a very low PI (0.07). Sierras Pampeanas (0.19) and Coquimbo (0.17) are areas that present higher values of PI than the rest. The tree resulting from K 5 and 6 has only Andes with a high PI of 0.59, the values for other areas are: 0.16 (Atacama), 0.16 (Sierras Pampeanas), 0.16 (Selva Valdiviana) and 0.12 (Coquimbo).

Ancestral Area analysis on the topology of Schulte *et al.* (2000)

The topology of Schulte *et al.* (2000) (Fig. 4) has a polytomy with the taxons *Liolaemus bellii, L. chiliensis* and *L. cyanogaster;* the polytomy was resolved, and the two resolutions used for the DIVA analysis. For the Fitch optimization (11 steps) on the topology of Schulte *et al.* (2000) assigns Andes as the ancestral area. Unconstrained DIVA (8 equally optimal reconstructions) assigns to the basal node all the areas, requiring 15 dispersal events. When using constraints to a maximum of 2 areas, it requires 18 dispersal events, with two equally optimal reconstructions between Andes and Sierras Pampeanas. Weighted Ancestral Area Analysis found Andes with the higher PI (0.44) followed by Sierras Pampeanas and Maulina (0.39), and Valle Central in Chile (0.38).

DISCUSSION

Liolaemus systematics

Lobo (2005) found six different resolutions among subclades of the *chiliensis* group, some of those resolutions are recovered here, i.e. the basal position of *leopardinus* and *kriegi* groups is recovered in every analysis, and the clade formed by the *robertmertensi, gravenhorsti* and *alticolor* groups appears only on the equally weighted tree. The strict consensus of the implied weighting analysis recovered 15 groups, most of them found in previous studies, but the relationships among these groups remain unresolved.

Cei (1986, 1993) and Avila *et al.* (1992) defined the *bibronii* group based on a character combination including as members of this group the following species:
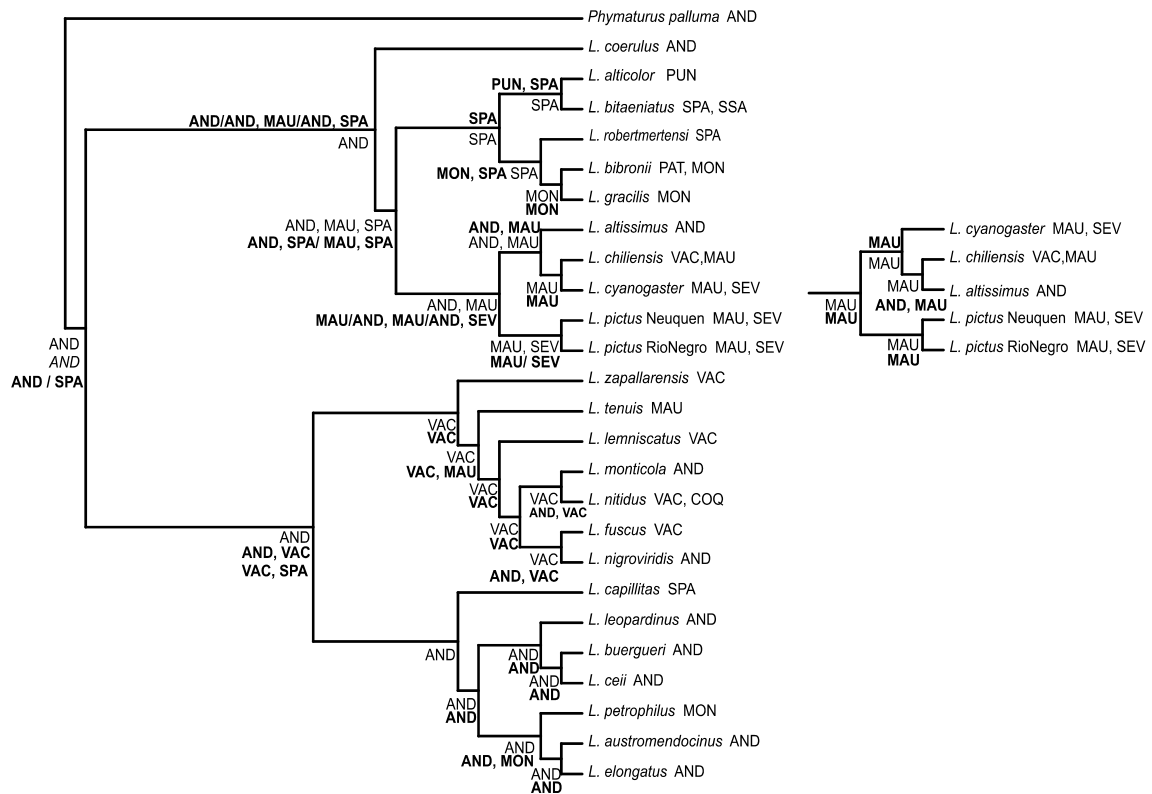
FIGURE 4: Tree from Schulte *et al.* (2000), showing the possible resolutions of the polytomy. The area assignations are as follow: Normal, Fitch optimization; Italics, Weighted Ancestral Area Analysis; Bold, DIVA (constrained to 2 maximum areas). *Liolaemus alticolor* is actually *Liolaemus puna* (Lobo & Espinoza, 2004).

Liolaemus bibronii, L. exploratorum, L. sanjuanensis, L. saxatilis, L. gracilis, L. robertmertensi and *L. fuscus*. In this study this group is paraphyletic. In the equally weighted analysis *L. bibronii* is sister taxon of *L. sanjuanensis* included in a subclade related to the most terminal grouping formed by *robertmertensi, gravenhorsti* and *alticolor* groups; *L. saxatilis, L. bitaeniatus, L. fuscus* and *L. gracilis* are nested within this clade but not forming a monophyletic group. In the Implied weighting analysis species belonging to the traditional *bibronii* group are separated in two groups which here we redefine as *bibronii* (including only *L. exploratorum, L. bibronii, L. hernani* and northern Argentina species: *L. bitaeniatus, L. chaltin, L. yanalcu* and *L. ramirezae*) and *robertmertensi* group including now *L. curicensis, L. chiliensis, L. nitidus, L. robertmertensi, L. saxatilis, L. gracilis* and *L. tandilensis. Liolaemus robertmertensi, L. saxatilis* and *L. tandilensis* are distributed following the mountain arc formed by Sierras Pampeanas, and Sierras de Tandil in eastern Argentina, *L. robertmertensi* in the slopes of Sierras of Catamarca and La Rioja, *L. saxatilis* in Sierras de San Luis and

Córdoba, *L. tandilensis* in Sierra de Tandil. *Liolaemus sanjuanensis* lives in Sierra Pie de Palo (San Juan province, Argentina) a chain of mountains related to the same system of Sierras Pampeanas but in this analysis is not found related to this group of species, perhaps this is due to problems of taxon sampling, because only two paratypes of this species were available for our study.

The *alticolor-bibronii* group of Espinoza *et al.* (2004) includes 10 species in two clades one formed by *Liolaemus bibronii, L. gracilis, L. robertmertensi, L. yanalcu, L. ramirezae,* and other clade with *L. bitaeniatus, L. pagaburoi, L. chaltin, L. puna,* and *L. cf. walkeri,* which is actually *L. puna* according to Lobo & Espinoza (2004). Lobo (2005) also found the *alticolor-bibronii* group, with between 14 and 17 species in different analysis.

In this study the *alticolor-bibronii* is not recovered. In the equally weighted analysis is only formed by 4 species (Fig. 3), and in the consensus the *alticolor* and *bibronii* groups appear separated, with species inhabiting Northern Argentina *(L. puna),* northeastern Chile *(L. paulinae),* Puna and high mountains in Bolivia

(*L. variegatus* and *L. alticolor)* and Perú *(L. tacnae* and *L. walkeri)* forming the *alticolor* group, and the remaining species of *alticolor-bibronii* which are oviparous *(L. ramirezae, L. yanalcu, L. bitaeniatus* and *L. chaltin)* are included in the *bibronii* group. *Liolaemus fuscus* and *L. lemniscatus* form a separated monophyletic group, *lemniscatus* group (congruent with the *fuscus-lemniscatus* group of Ortiz (1981), and *lemniscatus* group of Cei, 1986).

The *petrophilus* group recovered in the analysis with implied weights includes the *capillitas* group; this is congruent with the results of Morando *et al.* (2003). The morphological information does not support the inclusion of the *ceii-kriegi* within the *petrophilus* group as suggested by the mitochondrial DNA analysis.

Liolaemus Biogeography

The results are summarized in Table 2. There is congruence between the three methods because all sustain the hypothesis of an Andean-Patagonian origin for the *chiliensis* group. The common area to all the analyses is Andes, followed by Patagonia, and Monte.

This results show some degree of congruence with previous studies. Cei (1979) sustained that Patagonia was a center of origin for at least four groups of *Liolaemus,* describing two major faunal regions in Patagonia (see Cei 1979, Fig. 13:3): the northern or ancient Patagonian region and the southern or Santa Cruz region, the former includes part of the Patagonia and Andes areas used in this study. The first fossil attributed to *Liolaemus* (Albino, 1998) comes from the Miocene of Patagonia, found in sediments of the Miembro Trelew, Formación Sarmiento, near Gaiman in Chubut Province, this locality is included in the area Patagonia. These studies, although not focused on the *chiliensis* group but on the entire genus, are congruent with the ancestral areas found here. Recently, Albino (2005) found new fossils attributed to *Liolaemus* from the late Quaternary in the Southwest of Buenos Aires Province, included in the Monte Area of this study.

Because the BPA results of Young-Downey (1998) had incongruences with the hypothesis of Solbrig (1976), she evaluated the area cladogram of *Liolaemus* regarding ancestral distributions and evaluating possible dispersals, extinctions, and lack of response to vicariance. Thus, Young-Downey (1998) postulates that the ancestor of *Liolaemus* inhabited areas comprising the Southern *Nothofagus* forest (Subantartic Province), Central Argentina and Central-Northern Chile, and from there, it vicariated by the appearance of the Andes, and by the following climate effects (desertification of the Patagonian steppe). Unfortunately, the areas indicated as occupied by the ancestor of *Liolaemus* are not clearly described by Young-Downey and is difficult to establish direct correspondences with the areas used here. Young-Downey (1998) found Atacama region as more related to Coquimbo and Chilean (Valle Central) in congruence with Solbrig (1976). The current distributions of the species and the phylogenetic analysis used here as well as the cladogram of Lobo (2005) suggest different area relationships. The *nigromaculatus* group from the Northern deserts in Chile (Coquimbo and Atamaca areas) in that analysis is sister taxon of the *alticolor* group (Puna); interestingly Morrone (1996) found Puna and the Northern deserts forming a monophyletic unit.

Comparisons with the distribution of the groups more related with *Liolaemus* may prove useful. The sister clade of *Liolaemus, Phymaturus* (Schulte *et al.* 2003; Espinoza *et al.* 2004), is distributed in Patagonia and in both sides of the Andes, reaching north to the Puna of Catamarca Province in Argentina, distribution that is shared with many species of *Liolaemus* and does not contradict the hypothesis of ancestral areas for the *chiliensis* group. Nevertheless, *Ctenoblepharis,* the basal taxa for Liolaemidae (Schulte *et al.* 2003; Espinoza *et al.* 2004), is found only in coastal deserts of Peru, thus making necessary further studies including these two genera.

Fitch optimisation. The Fitch optimisation on the equally weighted analysis yielded Andes, Patagonia and Monte. This shows the perhaps excessive effect that Fitch optimization places in the more plesiomorfic areas, because, Patagonia only appears again in more terminal branches of the tree.

Effect of constraining the number of areas

Ronquist (1997) noted that when using DIVA for reconstruct the ancestral area of a taxon, the root node will tend to include all the areas occupied by the terminals, making it very uninformative. The solutions to this suggested by Ronquist are two: the inclusion of more outgroups, thus making the root node no longer the root node, and constraining the maximum number of areas that may form part of the ancestral area. The first of this possible solutions is, at least in this case, not useful: for example, the inclusion of other outgroups related to *Liolaemus,* i.e. *Phymaturus* and *Ctenoblepharis,* will not solve the problem, given that *Phymaturus* is distributed in the same areas used for *Liolaemus,* and *Ctenoblepharis,* distributed in coastal Peru,

probably will only add this new area to the ancestral area reconstruction in the root, leaving the ancestral area for *Liolaemus* without major changes. The second alternative presents the problem that there is no criteria for choosing the number of areas for constraining. The sympatry of sister groups is evidence for dispersal (Hausdorf, 1998), so it can be argued that the ancestral distribution may have been larger o smaller than the present area occupied by the taxon. Examples of such sympatry in sister species are *L. chiliensis* and *L. nitidus,* both living in Valle Central (Chile); *L. cyanogaster* and *L. schroederi,* both distributed in Maulina (Chile). On this basis, one may assume that the ancestral area may have been smaller in the past, and this provides a rationale for constraining the maximum number of areas allowed in the ancestral distribution, taking into account that this practice remains *ad hoc.*

When using constrained DIVA (Table 2), constraining the maximum number of areas that may form the ancestral distribution from 3 to 6 areas, yield as optimal reconstruction Andes, Patagonia and Monte, the same areas that yield the Fitch optimization on the equally weighted tree (when constraining to 2 areas, the reconstruction is Andes and Monte). Andes also have the highest PI in the WAAA analysis, being Monte the second. Sadly, there are no criteria for selecting a number of area units by constraining the ancestral distributions, making any further statements speculative.

Commentaries about Schulte *et al.* (2000)

Schulte *et al.* (2000) postulated that the ancestral area for the subgenus *Liolaemus* (equivalent to the *chiliensis* group) in their reconstruction is equivocal between Andes, western lowlands and eastern lowlands, the three areas used for the analysis. With the exception of Andes, the other areas found in the analysis (Sierras Pampeanas, Maulina and Chile Central) are not hypothesized as ancestral in the biogeographic analysis of the more complete phylogeny herein. This shows the effects of a limited taxon sampling for making biogeographic inferences about ancestral areas. There are areas not represented in the analysis, and the species located plesiomorphically on the cladogram have a strong influence in the result of the optimization. There are only three species inhabiting Sierras Pampeanas *(L. bitaeniatus, L. robertmertensi* and *L. capillitas)* but ten in Andes, but both areas appear as equally probable ancestral areas. Also, there is an oversimplification of the distribution of the species used by Schulte *et al.* (2000); any ambiguity at any node will involve at least two of the three

areas, making the results uninformative, given the size of the areas.

A last remark is needed about the areas used for this study. These areas from Roig-Juñent (1994) are based on distributions of arthropods, and despite they are accurate respect to the distribution of *Liolaemus,* some regions are missing (i.e. Puna), and others do not represent very well the distributions of *Liolaemus,* like Monte, and would need a reformulation.

The ancestral area of a taxon, as defined by Bremer (1992), needs not to be limited to a single place, it may be equal or larger than the current area occupied by the taxa. However, as implemented by the methods, the results of the ancestral area analysis will be an ancestral area for a taxon at least equal or smaller than the combined distributions of his descendants. The only possible way to find an ancestral area larger than the sum of the distributions used would be with the inclusion of fossil groups distributed in areas not currently occupied by the taxa in study. For many groups, this is very difficult. For example, the fossil record may be absent, or the fossils may be found only in the areas already present in the analysis, as is the case with the fossils attributed to *Liolaemus* (Albino, 1998, 2005). Even in the case that a fossil distribution could be used, the area occupied by the fossil taxa would have to be present in deep branches of the cladogram or in numerous terminals or it would have no influence in the analysis and could not be hypothesized as being part of the ancestral area. Thus, although the methods contemplate the possibility of identifying an ancestral area larger than the current distribution using data from fossils, is very difficult to this situation to effectively appear in an analysis.

CONCLUSIONS

In recent years several studies have dealt with the phylogenetic relationships of the *chiliensis* group (Schulte *et al.* 2000; Lobo, 2001; Espinoza *et al.* 2004; Lobo, 2005; this study). Some groups are recovered in this analysis, but others do not, as the *alticolor-bibronii,* which appears splitted. The consensus of the implied weighting analysis shows that the relationships between the groups are not yet resolved, and would require further studies to clarify the intern relationships inside the *chiliensis* group. As with any cladistic biogeographic analysis, the results of the ancestral area methods may vary according to the different hypothesis. However, if the degree of variation is only on the terminal groups, the ancestral area assignations will likely not be affected. Nevertheless, some area relationships found in other studies (Morrone, 1996;

Lobo, 2005) are recovered here, like the sister relationship between Puna and the Northern deserts of Chile (Coquimbo and Atacama).

Of the studies that include biogeographic considerations about *Liolaemus,* only Young-Downey (1998) applied an explicit methodology. However, these studies have the problem of limited taxon sampling and area definitions, making difficult to make comparisons between the results. However, the results of the ancestral area analysis of this work are congruent with previous studies and paleontological data, hypothesizing an Andean-Patagonian ancestral area for the *chiliensis* group. A large part of the genus is not included in the *chiliensis* group (the *Eulaemus* subgenus or Argentine group), and its inclusion is necessary for the completion of the ancestral area analysis of the genus. This work is underway and will be published elsewhere.

A last consideration is needed regarding the ancestral area methodologies. Although they erroneously are criticized as an absolute dispersalist approach, they are a valid procedure for studying the historical biogeography of a taxon. These methods, however, present some problems, as the sometimes uninformative multiple reconstructions of DIVA, or the excessive importance of the basal areas for the Fitch optimization.

This work represents the first study of the historical biogeography of the *chiliensis* group, a major part of the genus *Liolaemus* using explicit methodology and with a complete taxon sampling. Further studies need to be carried out, especially concerning the areas used, particularly its unambiguous definition, and using geomorphologic data to contrast the hypothesis produced.

RESUMO

Ainda que tenham sido feito muitos estudos filogenéticos no género Liolaemus, *os mesmos não são apropriados para uma análise biogeográfica, porque não possuem uma amostragem taxonômica adequada. Desenvolve-se neste trabalho, uma análise biogeográfica do grupo de* L. chilensis, *que se diferencia das contribuições prévias por representar a todos os membros do grupo. A análise biogeográfica consiste em reconstruir a área ancestral deste clado, utilizando três métodos diferentes: Otimização de Fitch, Análise de Dispersão-Vicariância e Áreas Ancestrais Pesadas. As análises foram realizadas em filogenias feitas com o critério de parsimônia sob pesos iguais e pesos implicados. A árvore obtida sob pesos iguais, recupera a maioria dos grupos encontrados em análises prévias. O consenso estrito das árvores de pesos implicados, recupera quinze grupos, mas não pode-se estabelecer as relações entre eles. A análise de áreas ancestrais permite postular a região Andino-Patagônica como provável área ancestral, resultado este, congruente com hipóteses prévias e com informação paleontológica.*

PALABRAS-CHAVE: *Liolaemus, chilinesis,* Dispersão-Vicariância, Fitch, Áreas Ancestrais Pesadas, Andes, Patagonia.

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APPENDIX 1

New characters used:

1. Gravid Coloration: (0) Absent; (1) Present

2. Plant-Microhabitat: (0) Bunch grass *(Festuca sp);* (1) Spiny shrub *(Parastrephia);* (2) Both

3. Lateral Black Spots: (0) Absent; (1) Present