
Historical biogeography of *Phymaturus* (Iguania: Liolaemidae) from Andean and patagonian South America

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Establishing the ancestral area of a group of organisms is one of the central objectives of historical biogeography. I applied three methods of ancestral area analysis, Fitch optimization, weighted ancestral area analysis and dispersal-vicariance analysis (DIVA) to establish the ancestral area of the iguanian lizard genus *Phymaturus*. I then extended the analysis to hypothesize the ancestral area for Liolaemidae (*Ctenoblepharys*, *Liolaemus* and *Phymaturus*). The ancestral area for *Phymaturus* is Patagonia Central or Patagonia Central-Cordillera Andina and Valle Central. For Liolaemidae, the ancestral area is Patagonia Central-Coastal Perú, or Patagonia Central-Patagonia Occidental-Cordillera Andina and Valle Central-Coastal Perú. The ancestral area of *Phymaturus* is congruent with previous studies, but the inclusion of *Ctenoblepharys* poses some questions regarding the distribution of the ancestor of the family.

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Inferring the ancestral area of distribution for a clade of organisms is one of the main goals of historical biogeography (Brown & Lomolino 1998), and is part of the natural history of the organisms. In studies that try to assess the relative importance of vicariance and dispersal in the distribution of a group of organisms and its speciation, an important subject is the reconstruction of the ancestral ranges of distribution for the taxa analysed (Drovetski 2003).

Historical biogeography deals with two kind of problems, as pointed by Hovenkamp (1997): Earth history and taxon history. The first approach attempts to establish area relationships based on the phylogenies of at least two taxa inhabiting the areas of interest. The taxon-history approach seeks to elucidate the biogeographical history of particular taxa. The utility of the latter approach has been criticized (Nelson & Platnick 1981; Humphries & Parenti 1986) because inferences are restricted to general patterns. However, as noted by Bremer (1992), the search for the historical biogeography of individual groups is a valid procedure, and it is part of the study of the natural history of the organisms. In many cases, the main assumption of vicariance biogeography, namely that the ancestral area of a taxon is identical to the present distribution, may not apply. For example, let us consider a widespread (cosmopolitan) group consisting of many taxa of very limited distributions (As Asteraceae; Bremer 1992), where it does not seem probable that its common ancestor was cosmopolitan. Another example is when all

relatives of a widespread taxon have all limited distributions, as is the case of the humans and the great apes (Ronquist 1994). In these cases, it is logical to search for an ancestral area different than the sum of the individual areas of the species. As such, ancestral area analysis is not *ad hoc* or unscientific (Hovenkamp 1997), but another way to formulate a hypothesis to explain the distribution of a taxon.

The main procedure to study the biogeography of individual groups is the ancestral area method. Ancestral area analysis was proposed by Bremer (1992) as a way to identify the area of distribution of the ancestor of a monophyletic group, which he termed ancestral area.

The main assumption of the ancestral area approach is that the ancestral area of a taxon can be inferred from the topological information in their area cladogram (Hausdorf 1998), assuming that (i) positionally plesiomorphic areas in a cladogram are more likely part of the ancestral area than apomorphic areas; and (ii) areas represented on more than one branch have a higher probability of being part of the ancestral area than areas less-represented. For ancestral area analysis, I applied three methods: Fitch optimization method (Ronquist 1994), weighted ancestral area Analysis (Hausdorf 1998), and dispersal-vicariance analysis (DIVA; Ronquist 1997). These methods use optimizations with reversible parsimony for estimating ancestral areas. Fitch optimization method was proposed by Ronquist (1994) to avoid the problems of Camin-Sokal (irreversible) parsimony originally proposed by Bremer (1992).

Weighted ancestral area analysis uses Fitch parsimony with a weighting scheme that weights favourably areas that are located in plesiomorphic branches, and areas more common as terminals. With this method, a probability index (PI) is calculated to give a measure of the likelihood of a particular area being 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. Using this approach, vicariance events have no cost, whereas dispersals and extinctions have a cost of one per area unit added to the distribution. The preferred ancestral area assignments are those requiring the minimal number of dispersal events.

Phymaturus is a genus of iguanian lizards that currently includes more than 25 species of herbivorous and viviparous lizards that inhabit rocky places (Espinoza *et al.* 2004; Lobo & Quinteros 2005). *Phymaturus* is an excellent group for biogeographical analysis, because it is monophyletic, the species have very restricted distributions, and there are recent phylogenies available. The genus is distributed from the Puna of Catamarca in north-western Argentina south to the Patagonian steppe and along the Andean Cordillera on both the eastern and western mid- to high elevation slopes of Argentina and Chile (Lobo & Quinteros 2005). *Phymaturus* is one of the three genera belonging to the family Liolaemidae (Frost *et al.* 2001; but see Schulte *et al.* 2003 for an alternative classification). Recent analyses support a *Phymaturus*–*Liolaemus* sister-taxon relationship with *Ctenoblepharys adspersa* as the basal member of the family (Schulte *et al.* 2003; Espinoza *et al.* 2004).

Although there are several studies of the systematics of *Phymaturus* (Ceï & Lescure 1985; Lescure & Ceï 1991; Pereyra 1992), until recently there were no reliable phylogenetic hypothesis for the genus. Based on a morphological analysis, Etheridge (1995) recognized two species groups of *Phymaturus*: *palluma* and *patagonicus*, but noted that these might not be monophyletic. Recently, Lobo & Quinteros (2005) reconstructed a phylogeny for *Phymaturus* that included almost all the described species based on morphology, allozymes and chromosomes (data set of Pereyra 1992). In some of the trees obtained by Lobo & Quinteros (2005), Etheridge's (1995) groups were recovered as monophyletic, but in others the *patagonicus* group was paraphyletic. In recent years, many new species of *Phymaturus* have been described (e.g. Ceï & Videla 2003; Scolaro & Ceï 2003; Lobo & Quinteros 2005; Lobo & Abdala 2007; Scolaro & Ibargiuengoytia 2007) doubling the size of the genus. Still, many others await description (Lobo, personal communication).

Phymaturus biogeography

The historical biogeography of *Phymaturus* is poorly understood and a quantitative study has never been undertaken.

Ceï (1979) described the composition of the Patagonian and Andean herpetofauna, characterizing these regions by their high endemicity, and inferring centres of speciation and dispersal from palaeontological and palaeoclimatic data. Later, Ceï (1986) proposed an Andean-Patagonian origin for *Phymaturus*, based on the 'refuge' theory for geographical speciation, where the patagonic tablelands would have acted as refuges and neo-dispersal centres (Scolaro *et al.* 2003).

Pereyra (1992), based on a phenetic analysis, proposed a dispersal scenario that placed Patagonia as the centre of origin for *Phymaturus* with the northern range of *Phymaturus* in Catamarca province, Argentina, where it is ecologically replaced by a species of *Liolaemus* (possibly *L. dorbignyi* and related species — *L. scrocchi* for example), which inhabits similar rocky habitat as *Phymaturus*. This scenario assumes that the southern populations of *Phymaturus* would have experienced more drastic climatic and vegetation changes than the northern populations, which would have caused extinctions of several of the original southern populations (Ceï 1975). Accordingly, Pereyra (1992) proposed a scenario in which the northern populations would have later repopulated the southern habitats.

Lobo & Quinteros (2005) studied the historical biogeography of *Phymaturus*, assigning to their terminal taxa the areas proposed by Flores & Roig-Juñent (2001), Roig-Juñent & Flores (2001), and Roig-Juñent *et al.* (2002). They discussed the congruence of the various phylogenies that they obtained with the area cladograms of the aforementioned authors. They also compared the area relationships inferred from the *Phymaturus* phylogenies with a biogeographical analysis of the relationships between provinces of the Andean subregion made by Morrone (1994, 1996). However, they did not perform any formal biogeographical analysis.

The purpose of this paper is to evaluate three different approaches for inferring ancestral areas using the lizard genus *Phymaturus*, and make the first attempt to hypothesize the ancestral area of distribution for the family Liolaemidae. This is the first study of the historical biogeography of *Phymaturus* using quantitative methods. Moreover, with the inclusion of *Ctenoblepharys* and a terminal representing the genus *Liolaemus*, this study is the first analysis of the historical biogeography of Liolaemidae using explicit methods.

Materials and methods

I reconstructed a cladogram representing the relationships of the three genera (Fig. 1). For *Phymaturus*, of the various analyses from Lobo & Quinteros (2005), I selected one of the two topologies corresponding to the 'missing' analysis (Wiens 2000), because this is the most conservative way to treat binary polymorphic characters, and this tree had more nodes with jackknife support > 50 (6 nodes, see Lobo & Quinteros 2005; their fig. 7). I also used the areas proposed in that study, which had been previously defined (Flores & Roig-Juñent

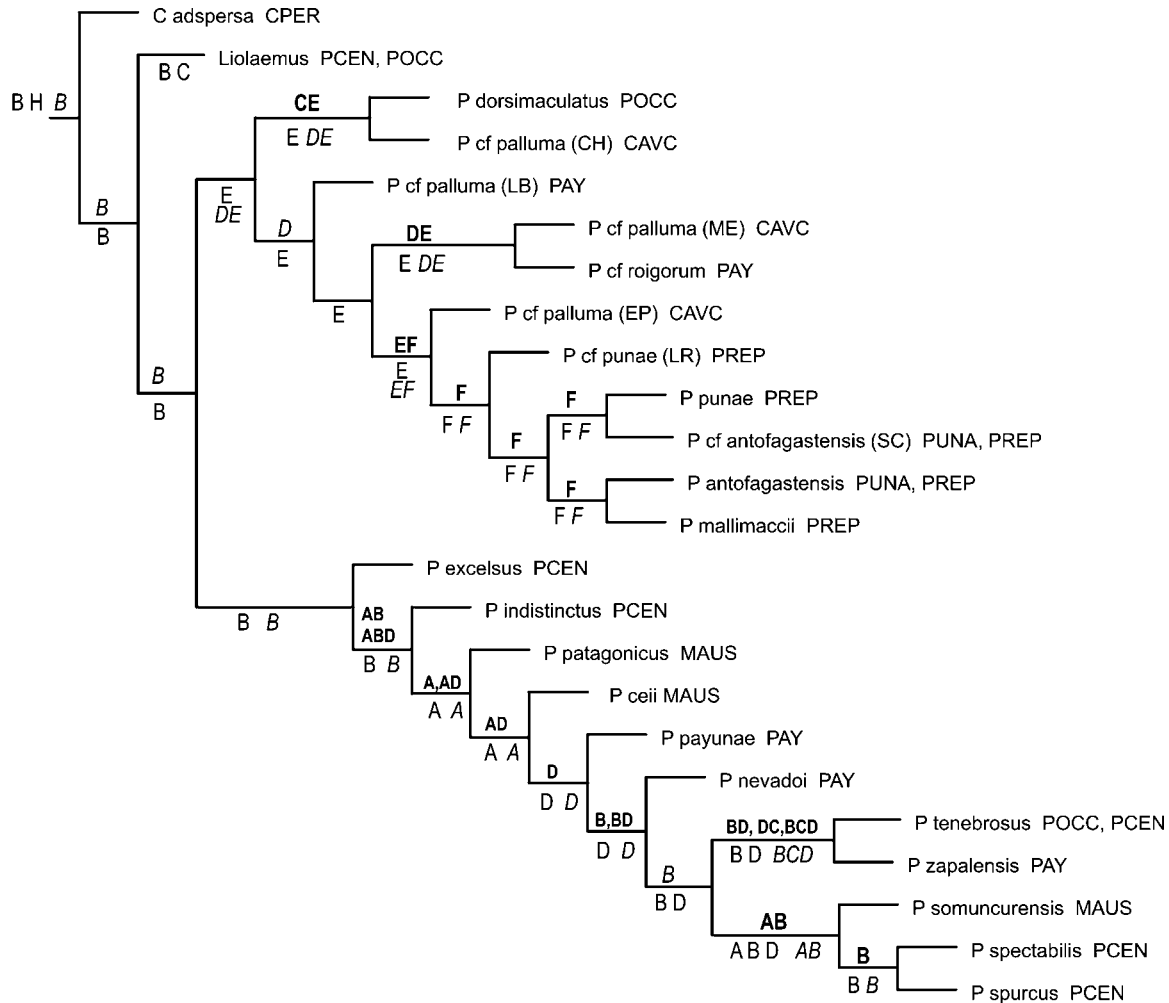


Fig. 1 Cladogram depicting the phylogenetic relationships of *Ctenoblepharys*, *Liolaemus* and *Phymaturus*. The letters on the nodes correspond to the ancestral area assignments for each of the methods used: Bold, Dispersal-vicariance analysis (DIVA); Normal, Fitch optimization; Italics, Weighted ancestral area analysis. A: Monte Austral, B: Patagonia Central, C: Patagonia Occidental, D: Payunia, E: Cordillera Andina y Valle Central, F: Prepuna, H: Coastal Perú.

2001; Roig-Juñent & Flores 2001; Roig-Juñent *et al.* 2002) (Fig. 2). The areas include Cordillera Andina and Valle Central (CAVC), Monte Austral (MAUS), Monte Central (MCEN), Patagonia Central (PCEN), Payunia (PAY), Patagonia Occidental (POCC), Prepuna (PREP), and Puna (PUNA). I included in the present study most of the recognized species of *Phymaturus* (Etheridge & Espinoza 2000; Lobo & Quinteros 2005) except the recently described *P. verdugo* (Cei & Videla 2003), *P. calcogaster* (Scolaro & Cei 2003) and *P. vociferator* (Pincheira-Donoso 2004). The reason for excluding these species is that they are not included in any phylogenetic analysis, and all the methodologies used require a cladogram to optimize the distributions. Nevertheless, their probable placement in the tree (given their similarity to certain other species or groups of species) will not change the overall

results (Lobo, pers. commun.). *Phymaturus cf. patagonicus* (EC) of Lobo & Quinteros (2005) is actually *P. ceii* (Scolaro & Ibagüengoytia 2007), and *P. cf. palluma* (PA) of Lobo & Quinteros (2005) is actually *P. roigorum* (Lobo & Abdala 2007).

I assigned Coastal Perú (CPER) as the distribution area of *Ctenoblepharys*. This area corresponds approximately to the area Desierto Intermedio of Roig-Juñent & Flores (2001). For *Liolaemus*, the areas Patagonia Central (PCEN) and Patagonia Occidental (POCC) were used as the ancestral areas following Díaz Gómez & Lobo (2006), who made an ancestral area analysis for the *chiliensis* group of *Liolaemus* (including 82 species of the approximately 160 of the genus), and identified the Andes and Patagonia as ancestral ones for the *chiliensis* group. Cei (1979) postulated Patagonia as a centre of origin and diversification for *Liolaemus*. Also,

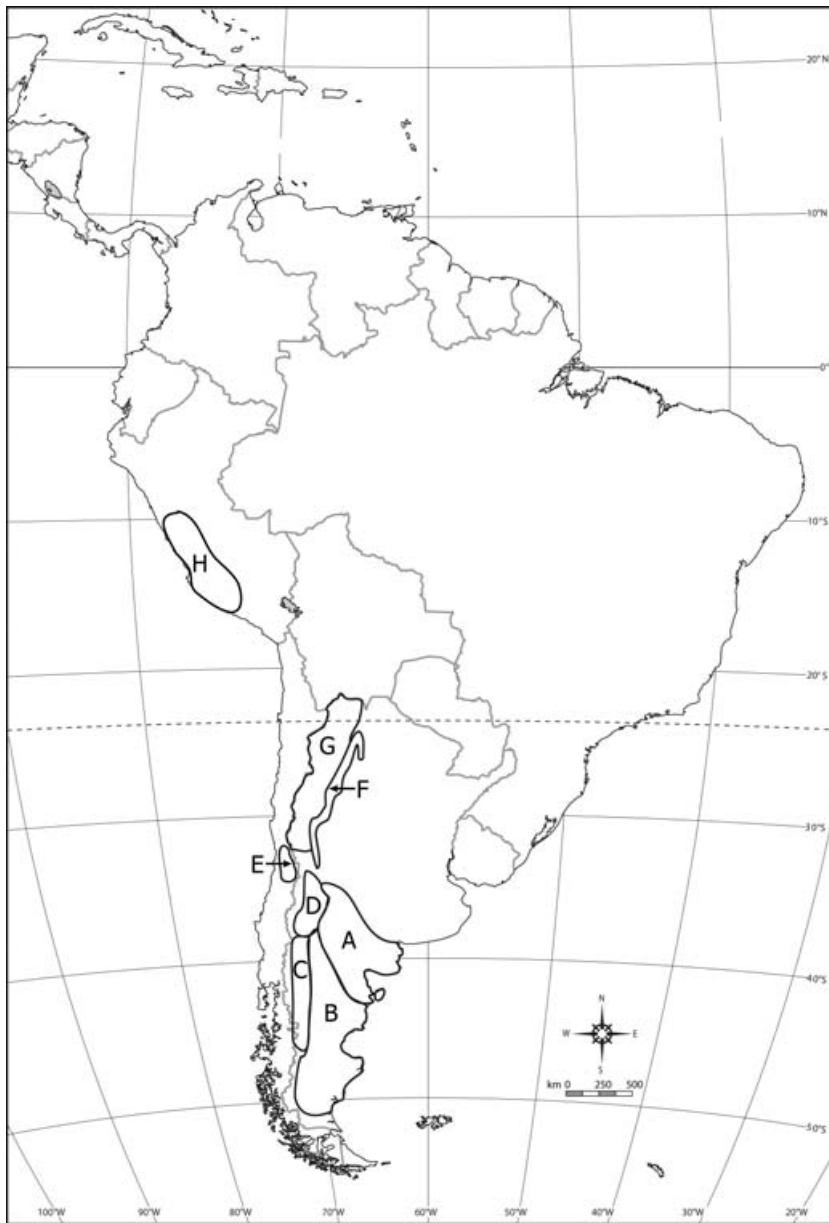


Fig. 2 Map showing the areas used for the analysis. A: Monte Austral, B: Patagonia Central, C: Patagonia Occidental, D: Payunia, E: Cordillera Andina y Valle Central, F: Prepuna, G: Puna, H: Coastal Perú.

Albino (1998) identified the first fossil attributed to *Liolaemus* from the Miocene of Patagonia.

Fitch optimization was made with TNT (Goloboff *et al.* 2003; for reviews see Hovenkamp 2004; Giribet 2005; Meier & Ali 2005), a program for parsimony analysis. DIVA was made with DIVA, version 1.2 (Ronquist 1997). The number of maximum areas allowed at the nodes was restricted to four, and results without restricting the maximum number of areas were also recorded. The following options were used: settings: maxareas = 4, hold = 32 767, weight = 1.000, age = 1.000. Weighted ancestral area analysis was performed in an Excel spreadsheet, weighing the nodes using a simple concave function

($1/x$; where x corresponds to the number of internodes counted from the basal node).

Results

Ancestral area assignments for the cladogram are listed in Fig. 2 and Table 1. The ancestral area assignments for DIVA correspond to the analysis constraining the maximum number of areas allowed as ancestral to four.

For *Phymaturus*, Fitch optimization assigns PCEN as the ancestral area, PCEN for (*Phymaturus*, *Liolaemus*), and PCEN — CPER for the most basal node (*Ctenoblepharys* (*Liolaemus*, *Phymaturus*)).

Table 1 Ancestral Area assignments for the member of the family Liolaemidae.

	Fitch Optimization	Weighted Ancestral Areas	DIVA
<i>Phymaturus</i>	PCEN	PCEN	PCEN + CAVC
<i>Phymaturus</i> + <i>Liolaemus</i>	PCEN	PCEN	PCEN + POCC + CAVC
<i>Phymaturus</i> + <i>Liolaemus</i> + <i>Ctenoblepharys</i>	PCEN + CPER	PCEN	PCEN + POCC + CAVC + CPER

The assignments for the DIVA analysis correspond to the analysis restricting the maximum number of areas allowed as ancestral to four. PCEN: Patagonia Central, POCC: Patagonia Occidental, CAVC: Cordillera Andina y Valle Central, CPER: Coastal Perú.

Table 2 Ancestral Area assignments for the members of the family Liolaemidae.

	DIVA
<i>Phymaturus</i>	BCEH, ABCEH, BCDEH, ABCDEH, BCDEFH, ABCDEFH
<i>Phymaturus</i> + <i>Liolaemus</i>	BCE, ABCE, BCDE, ABCDE, BCDEF, ABCDEF
<i>Phymaturus</i> + <i>Liolaemus</i> + <i>Ctenoblepharys</i>	AE, BE, ABE, ADE, BDE, ABDE, ACDE, BCDE, ABCDE, ADEF, BDEF, ABDEF, ACDEF, BCDEF, ABCDEF

The assignments for the DIVA analysis correspond to the analysis without restricting the maximum number of areas allowed as ancestral. A: Monte Austral, B: Patagonia Central, C: Patagonia Occidental, D: Payunia, E: Cordillera Andina y Valle Central, F: Prepuna, H: Coastal Perú.

Weighted ancestral area analysis assigned PCEN as the ancestral area for the node corresponding to *Phymaturus*, and the most basal node.

DIVA, after constraining the maximum number of areas to four, resulted in an exact solution requiring 13 dispersal events. The results of DIVA without constraining the maximum number of areas also reached an exact solution, with 13 dispersal events postulated. However, there were several different, but equally optimal reconstructions that are listed on Table 2.

The three methods agree on a Patagonian origin for *Phymaturus*, with Patagonia Central as the most probable ancestral area, only the DIVA analysis adds Cordillera Andina and Valle Central as part of the ancestral area. The clade (*Liolaemus*, *Phymaturus*) also has a Patagonian origin (Patagonia Central is the most probable ancestral area), adding Patagonia Occidental and Cordillera Andina and Valle Central as part of the ancestral area.

The three methods postulate a Patagonian origin for Liolaemidae, but Fitch optimization adds Coastal Perú, and DIVA postulates four areas as the most probable as ancestral area for Liolaemidae: Patagonia Central, Cordillera Andina, and Valle Central, Patagonia Occidental, and Coastal Perú.

Discussion

This study is the first attempt to estimate the ancestral area of *Phymaturus* using explicit, quantitative methodology. It supports the hypothesis of a Patagonian origin for *Phymaturus* (Ceï 1986; Pereyra 1992) and provides a preliminary hypothesis of ancestral areas for Liolaemidae.

Each one of the methods used here was proposed as improvements over the previous proposals, but the results obtained by the methods are very similar. The main reason is that the methods are based on reversible optimizations,

namely Fitch optimization. For *Phymaturus* only DIVA adds Cordillera Andina and Valle Central. The same happens for (*Phymaturus* + *Liolaemus*), DIVA shows Patagonia Central, Patagonia Occidental and Cordillera Andina y Valle Central, and the same areas plus Coastal Perú for the node of the family Liolaemidae. The reason for this is that DIVA assigns costs to events, and in that cost scheme, dispersal and extinctions have an associated cost of one, whereas vicariance events have none. As a result, DIVA reconstructions will tend to include many areas at the basal nodes (Ronquist 1997). A clear example is the reconstructions obtained without constraining the maximum number of areas allowed at the nodes, which show multiple equally optimal reconstructions. Fitch optimization also adds Coastal Perú as the ancestral area for the family Liolaemidae, mainly because of the basal position of *Ctenoblepharys*, producing a disjunct ancestral area. These results show some of the differences between the methods: The cost scheme of DIVA will tend to favour an all-vicariance explanation, including all (or most) of the distribution areas of the taxa in study. The problem is that in many cases it will produce uninformative results. On the other hand, Fitch optimization will usually show one area as ancestral, forcing a dispersalist explanation, and because of the nature of the optimization, the areas closer to the base will be more likely included as ancestral. Weighted ancestral area analysis weights the areas according to their position on the tree and the number of times it is present on the terminals. The results of the weighted ancestral area analysis not necessarily would favour a dispersalist explanation over a vicariant one, but in practice, the areas located more plesiomorphically are weighted much more than terminal areas (even though they may be more common), making difficult, as shown by these results, for more than one or two areas to appear as ancestral.

The Patagonian origin for *Phymaturus* is congruent with previous studies, although none of them were based on explicit quantitative methods. Cei (1986) and Pereyra (1992) both postulated Patagonia as a centre of origin for *Phymaturus*. Recently Scolaro *et al.* (2003) proposed a geographical speciation model for the lizards of the genus *Liolaemus* and *Phymaturus*. They posited that the basaltic plateaus of Patagonia (Somuncurá Plateau, Lago Buenos Aires, del Asador, and Laguna Blanca) were 'refuges' and speciation centres. The results of this study support this hypothesis, as these plateaus are located in the Patagonia Central area, and another study of the ancestral area of a major subclade of *Liolaemus* (Díaz Gómez & Lobo 2006) also recovered an Andean-Patagonian origin for this clade.

The DIVA analysis assigned Patagonia Central and Cordillera Andina and Valle Central as ancestral areas for *Phymaturus*. A vicariant event between these two areas would explain the divergence between the two currently recognized groups: *palluma* and *patagonicus*. Following their separation, the *palluma* group would have later dispersed south to the Payunia, and north to the Puna and Prepuna. The species of the *patagonicus* group dispersed to the Payunia, Monte Austral and only one species, *P. tenebrosus*, dispersed to Patagonia Occidental. These results do not support the hypothesis of Pereyra (1992) of northern populations of *Phymaturus* reinvading the southern habitats. Only *P. dorsimaculatus* of the *palluma* group is distributed in Patagonia Occidental, but this species is topologically basal in the *palluma* clade and probably the ancestors of *P. dorsimaculatus* dispersed to their actual distribution from the Cordillera Andina and Valle Central.

The identification of an ancestral area for Liolaemidae should provide the basis for assessing macro-evolutionary questions (Brown & Lomolino 1998). The ancestral area found for the clade (*Liolaemus*, *Phymaturus*) is congruent with previous proposals (Cei 1979, 1986; Díaz Gómez & Lobo 2006), and with palaeontological evidence (Albino 1998). However, the inclusion of *Ctenoblepharys* in the analysis raises some important questions: the ancestral area of Liolaemidae includes the area of distribution of *Ctenoblepharys*, resulting in a disjunct ancestral area for the family. The possible explanations for this are (i) the ancestor of Liolaemidae was widespread in southern South America from Perú to Patagonia, and successive vicariant events resulted in the present distributions; (ii) the ancestor of Liolaemidae had a restricted ancestral distribution, either in Patagonia or similar to the actual distribution of *Ctenoblepharys*, and expanded its distribution via dispersal. Palaeontological information would be useful to elucidate some of these questions, but there are no known fossils of *Phymaturus* or *Ctenoblepharys*; for *Liolaemus* the earliest palaeontological evidence is from the Miocene of Patagonia. The fossil record for Iguanidae is fragmentary in South America (Báez & Gasparini 1979), but the earliest iguanians known

are from the Late Cretaceous of Brazil, and there are records for Cenozoic iguanians from Bolivia (De Muizon *et al.* 1983) and Patagonia in Argentina (Donadío 1983). This evidence, if later found to be related to Liolaemids, would suggest a widespread ancestor for Liolaemidae, which would account for the vicariant events that would lead to the actual distribution of members of this family.

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