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Discovering the biogeographic history using predefined areas and explicit geographical data in the South American *Liolaemus elongatus* group (Iguania: Liolaemidae)

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The genus *Liolaemus* includes 268 species, classified in two subgenera, *Eulaemus* and *Liolaemus sensu stricto*. The latter is formed by 12 monophyletic groups; one of them being the *Liolaemus elongatus* group, distributed in South America. We studied the biogeographic history of the *L. elongatus* group. We obtained a phylogenetic hypothesis recovering five main clades: the *L. punmahuida*, *L. elongatus sensu stricto*, *L. kriegi*, *L. petrophilus* and *L. capillitas* clades. Based on that hypothesis we obtained a time calibrated tree. The ancestral ranges were estimated applying three methodologies: DEC, DEC+j (using predefined areas) and GEM (using explicit geographical data). Our results show that the ancestral area of the *L. elongatus* group was located in central Argentina, and its divergence began around 11.5 Mya. From here, a combination of events (founder events and/or vicariances) led the species to their current distribution. Despite their differences, DEC+j and GEM show congruent results.

Keywords: biogeography, divergence times, ancestral area, lizards

INTRODUCTION

The *Liolaemus* Wiegman, 1834 genus includes small and medium size lizards and is the second most diverse iguanian group in the world. It comprises ~268 species (Abdala & Quinteros, 2014; Abdala et al., 2016; Verrastro et al., 2017; Gutierrez et al., 2018) and only the genus *Anolis* (Daudin, 1802) is more diverse. Laurent (1983; 1985; 1995) initially, and later Etheridge (1995), split the genus into two main groups, subgenus *Liolaemus sensu stricto* or "Chileno group", and *Eulaemus* or "Argentino group", distributed mainly to the west and east of the Andes, respectively. This proposal has been supported by many phylogenetic analyses based on both molecular and/or morphological evidence (Schulte et al., 2000; Espinoza et al., 2004; Esquerré et al., 2019; Pyron et al., 2013; Zheng & Wiens, 2016).

Liolaemus sensu stricto subgenus has been the object of many phylogenetic studies, which proposed hypotheses recognising several subgroups within. Two independent studies recovered twelve monophyletic groups inside the *L. sensu stricto* subgenus: Lobo (2005) and Díaz Gómez & Lobo (2006), (see also Lobo et al., 2010; Abdala & Quinteros, 2014). One of those groups is the *L. elongatus* group, which is distributed in central-south Argentina and Chile. Specifically, this group ranges from Tafi del Valle in northern Argentina, along the Andes

mountain range in Chile and Argentina until the province of Chubut, in southern Argentina.

Species in the *Liolaemus elongatus* group are characterised by large stout bodies and they are usually saxicolous, viviparous, and omnivorous (Ceí, 1986). The *L. elongatus* group is formed by endemic species like the majority of the lizards of austral distribution (Medina et al., 2017). The *L. elongatus* group was primarily defined by Ceí (1974) including three species: *L. elongatus* (Koslowky, 1986), *L. petrophilus* (Donoso-Barros & Ceí, 1971), and *L. austromendocinus* (Ceí, 1974), using morphological characters. Many posterior analyses confirmed the monophyly of the group, including some recent ones which are based on molecular data (Avila et al., 2004; Lobo et al., 2010; Abdala & Quinteros, 2014). In the last 15 years, many new species belonging to this group have been described (Abdala et al., 2010; Avila et al., 2010; Avila et al., 2012; Avila et al., 2015; Troncoso et al., 2016) increasing the number of species to 23.

Several hypotheses have been proposed on the constitution of the *Liolaemus elongatus* group (Morando et al., 2003; Avila et al., 2004; Lobo, 2005; Díaz Gómez & Lobo, 2006; Lobo et al., 2010). The most recent taxonomic revision of the *Liolaemus* genus is that of Abdala & Quinteros (2014). They perform an update of the study of Lobo et al. (2010), proposing the same groups but including all the new species described at

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that time. Avila et al. (2015) recovered four clades inside the *L. elongatus* group (that resemble the complexes of Morando et al. (2003): the *L. elongatus*, *L. kriegi*, *L. petrophilus*, and *L. punmahuida* clades). The same groups (with the exception of *L. punmahuida* clade) are recovered by Medina et al. (2015), who studied in detail the *L. kriegi* complex. Escobar-Huerta et al. (2015), Troncoso et al. (2016) and Esquerré et al. (2019) recovered the same clades as Avila et al. (2015).

Over the years, many authors have made biogeographic general assertions on the *Liolaemus* genus, generally without formal methodology to support these. Many of these hypotheses will be tested in the present study. For example, Cei (1979) characterised Patagonia as an active center of speciation and dispersion, including *Liolaemus* as an example of recent adaptive radiation. There have also been studies with formal methodology, although these have focused mainly on larger groups, with only a few *L. elongatus* representatives. Since the publication of these studies, many new species of the *L. elongatus* group have been described. Young-Downey (1998) performed a Brooks Parsimony Analysis (BPA; Brooks 1990), over a phylogeny of *Liolaemus*. Later, Schulte et al. (2000) performed a molecular based phylogeny of *Liolaemus*, where they arrive at several general conclusions on the genus, for example that subsequent events of dispersals across the Andes mountain range followed by vicariations have shaped the genus over its history. Lobo (2001), in a phylogeny of the *L. chiliensis* group assigned to the species studied the distribution areas defined by Roig-Juñent (1994), found that major groups correspond to these areas, although in that analysis, the *L. elongatus* group is not recovered as monophyletic. Díaz Gómez & Lobo (2006) were the first to perform formal biogeographical analyses in which an ancestral area is assigned to the *L. elongatus* group, although the focus of this work is more general, that is, the *L. sensu stricto* group. They obtain an ancestral area for the *L. elongatus* group that they call “Andes”, using three different methodologies: Fitch optimisation (Fitch, 1970), DIVA (Ronquist, 1997) and Weighted Ancestral Areas (Hausdorf, 1998). This area corresponds to northern Payunia and southern Central Monte, in the Andes mountain range. The most recent biogeographical analysis where the members of the *L. elongatus* group were included is Esquerré et al. (2019), where they use almost all the species members of the group and predefined larger areas at the South American level, since the objective of their study is a much larger group (Liolaemidae). They obtained “central Andes” as the ancestral area of the *L. elongatus* group. The divergence times obtained by the different authors for the clades of the *L. elongatus* group are detailed in Table 1.

In the present study, we inferred a DNA-based phylogeny and estimated divergence times in a time calibrated tree. We used this time calibrated tree and applied different methodologies to reconstruct the ancestral range of distribution in order to identify the main biogeographic events. We study the biogeographic history of the *L. elongatus* group applying three

methods: DEC (Dispersal-Extinction-Cladogenesis model, (Ree et al., 2005), DEC+j (Matzke, 2014), and GEM (Geographically explicit Event Model; Arias, 2017). Applying those methods, we try to elucidate the factors which promoted the diversification of the species members of the *L. elongatus* group. The comprehension of the diversification can provide valuable information not only about the date of origin of the taxonomic groups, but also the impacts of climatic and geological events in it (Weir, 2006), as well as rates of speciation and extinction (Weir & Schulte, 2007; Mercer & Roth, 2003). Moreover, the time and mode of diversification can be studied in the group of *L. elongatus* to test the biogeographical hypothesis in a more quantitative way. The results obtained here will be compared with previous studies, as the processes driving evolution tend to affect many of the taxa inhabiting the same region. This will allow us to test if taxa with different life histories share a common biogeographical history. It should also be noted that the particular environment of these lizards (saxicolous), and the fact that they inhabit rocky outcrops on both sides of the Andes mountain range, make them a good candidate for understanding the role of geological processes (e.g. the uplift of the Andes) in shaping diversity (Esquerré et al., 2019). Additionally, this group of lizards is biogeographically interesting given the wide range of habitats they use, as well as there being many syntopic species -a phenomenon that must be explained either through sympatric speciation or dispersal. It is to be noted that, in the last categorization (Abdala et al., 2012), five species (included in this work) have been declared vulnerable. Therefore, conclusions reached here may prove to be a valuable contribution to the conservation of these endangered species since information about their distributions is incorporated. Unlike previous biogeographical studies, which have focused on divergences deeper in the tree of Liolaemidae, we will focus on the divergences happening at derived nodes within this group. We include almost all known species and populations, which will result in a more robust phylogeny than previously attained, as well as a more complete sample of the group’s distribution. Since biogeographical methods are dependent on phylogenies and distribution records, the hypothesis we arrive at are likely to be more reliable.

MATERIAL AND METHODS

Phylogenetic Analyses

We included the sequences of nuclear gene KIF24, mitochondrial gene CytB and ribosomal gene of the subunit 12s from Morando et al. (2003), Avila et al. (2004), Fontanella et al. (2012), Medina et al. (2014), Olave et al. (2014), Avila et al. (2015), Medina et al. (2015), Medina et al. (2017) and Medina et al. (2018). Accession numbers of sequences used and specimens studied are listed in Supplementary Material S1. We performed three analyses, one under Parsimony, one under Maximum Likelihood (ML) and the other under Bayesian MCMC. We included all described species members of

Table 1. Previous studies showing the methodology used and divergence times obtained for the clades of the *Liolaemus elongatus* group. (*) Studies based on major scales to genres.

	Schulte (2013)*	Medina et al. (2014)	Zheng & Wiens (2016)*	Medina et al. (2017)	Esquerré et al. (2019)*
Methodology Groups	Relaxed clock	Strict clock	Penalised likelihood	Relaxed clock	Relaxed clock
<i>L. elongatus</i> group	16 Mya	-	12.30 Mya	-	13 Mya
<i>L. punmahuida</i> clade	-	-	-	-	2 Mya
<i>L. elongatus-petrophilus</i> clade	Not recovered	3.75 Mya	10.54 Mya	2.25 Mya	9.50 Mya
<i>L. petrophilus</i> clade	Not recovered	-	Not recovered	1.60 Mya	8.20 Mya
<i>L. capillitas</i> clade	Not recovered	Not recovered	6.01 Mya	-	4.50 Mya
<i>L. elongatus-kriegi</i> clade	Not recovered	1.90 Mya	4.74 Mya	1.60 Mya	5.80 Mya
<i>L. kriegi</i> clade	6 Mya	1.10 Mya	2.93 Mya	1.35 Mya	4 Mya
<i>L. elongatus sensu stricto</i> clade	Not recovered	-	2.93 Mya	1.30 Mya	4 Mya

the group (a total of 23), with the exception of *Liolaemus antonietae*, *L. janequeoae*, and *L. lonquimayensis*, (for which no published sequences were available), plus five populations of uncertain taxonomic status.

Parsimony analysis was performed with TNT 1.5v (Goloboff et al., 2003; Goloboff & Catalano, 2016) using heuristic search using Tree Bisection Reconnection, with 500 addition sequences saving 50 trees in each sequence. Also, we performed an analysis under the New Technology Search (Sectorial search, Ratchet, Tree Drifting, and Tree Fusing) implemented in TNT, with 50 initial add sequences and finding the minimum tree length at least 20 times. The support was measured under Bootstrapping standard, with 500 replicates.

ML analyses were conducted using RAxML v7.0.4 (Stamatakis, 2006) on the platform CIPRES Science Gateway (Miller et al., 2010) based on 1000 rapid bootstrap analyses, and the GTRGAMMA evolution model. We also obtained bootstrap support values with RAxML v7.0.4 (Stamatakis, 2006) based on 1000 quick replicates and a GTRGAMMA model for all genes.

Time of divergence estimates

Tree topology, age of nodes and substitution rates were simultaneously estimated using Bayesian MCMC (Markov chain Monte Carlo) approach as implemented in BEAST v2.5 (Bouckaert et al., 2019). We used the fossil from the *Eulaemus* clade, representing the earliest record of this subgenus (Albino, 2008) to place a mean prior of 20 Mya on the tree height. A lognormal prior is typically most appropriate for the majority of fossil calibrations (Hedges & Kumar, 2004) because it assumes that the divergence event actually occurred sometime before the appearance of the fossil. Under this model, fossils thus represent a hard lower bound and a soft upper bound on a given divergence event. The Yule prior assumes a constant lineage birth rate for each branch in the tree and is considered most suitable for trees describing the relationships between individuals from different species (Ho et al., 2005). An uncorrelated lognormal distributed relaxed clock (UCLD) model was employed, which allow evolutionary rates to vary along branches within lognormal distributions (Drummond et al., 2006). The calibration was conducted for all genes jointly.

Three independent runs of 10 million generations each were performed with sampling every 5000 generations. The three separate runs were then combined (following removal of 10 % burn-in) using Log Combiner v2.0 (Drummond & Rambaut, 2007; Rambaut & Drummond, 2008). Adequate sampling and convergence of the chain to stationary distribution were confirmed by inspection of MCMC samples using Tracer v2.0 (Drummond & Rambaut, 2007). The effective sample size (ESS) values of all parameters were greater than 200, which were considered a sufficient level of sampling. The sampled posterior trees were summarised using Tree Annotator v2.0 (Drummond & Rambaut, 2007; Rambaut & Drummond, 2008) to generate a maximum clade credibility tree (maximum posterior probabilities) and calculate the mean ages, 95 % highest posterior density (HPD) intervals and posterior probabilities for each node. The topology recovered was visualised with Fig Tree v1.2 (Rambaut & Drummond, 2008).

Biogeographical analyses

We applied three different methods to assess the historical distribution processes of the species members of the *Liolaemus elongatus* group. Two use predefined areas (DEC and DEC+j), and the other uses explicit geographical ranges (GEM).

Dispersal-Extinction-Cladogenesis (DEC; Ree et al., 2005) establishes ancestral ranges of the species included in a phylogenetic tree, evaluating different scenarios. DEC is a dispersal-extinction-cladogenesis model for geographic range evolution that specifies instantaneous transition rates between discrete states (ranges) along phylogenetic branches and apply it to estimating likelihoods of ancestral states (range inheritance scenarios) at cladogenesis events (Ree & Smith, 2008). DEC is an attempt to implement DIVA in a maximum likelihood context.

The DEC+j (Matzke, 2014) model is implemented by assigning a parameter, *j*, to specify the weight of each jump dispersal event in the cladogenesis matrix. To calculate the probabilities of a particular range inheritance event at cladogenesis, conditional on a particular ancestral range, the weight of each of the allowed range inheritance events is divided by the sum of the weights.

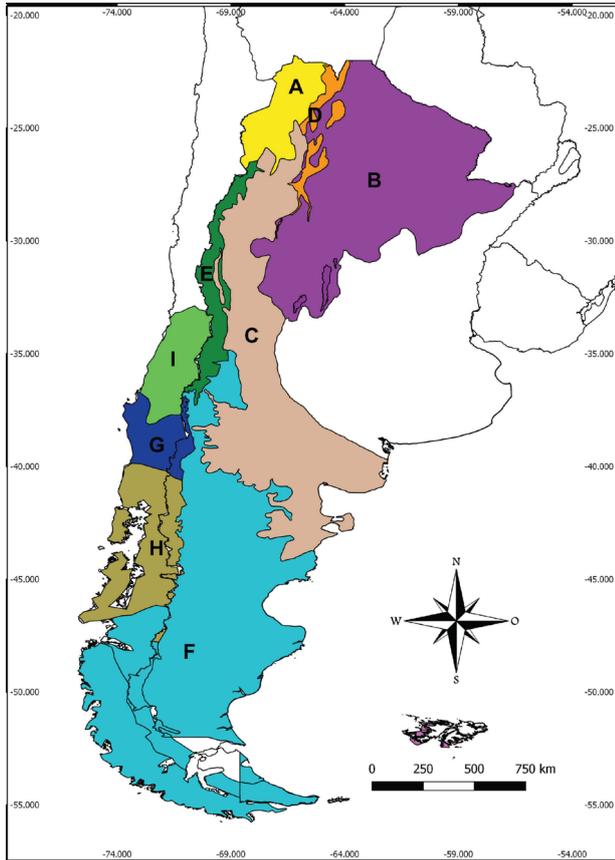


Figure 1. Map of Argentina and Chile showing the biogeographic regions used. Biogeographic regions of Arana et al. (2017) employed in DEC analyses. **A:** Puna Province, **B:** Chaco Province, **C:** Monte Province, **D:** Yungas Province, **E:** Cuyan High Andean Province, **F:** Patagonian Province, **G:** Maule Province, **H:** Valdivian Forest Province, **I:** Principal Cordillera of the Andes.

Conversely, Geographical Explicit Model (GEM, Arias, 2017) uses explicit geographic ranges by drawing actual occurrence data on a grid, instead of using predefined areas. The software then uses these ranges to assign a scenario for every node, choosing between four possibilities: vicariance, founder event, sympatry and point sympatry, and then specifies an ancestral area, accordingly. Each event has a cost which is related to the distribution of the daughter nodes. In order to find the less costly reconstruction, the software performs a heuristic search. GEM can be seen as an attempt to merge the ideas of Hovenkamp (1997; 2001) and Ronquist (1997).

The main difference between DEC, DEC+j and GEM lies in the fact that GEM, which is a novel methodology, does not use predefined areas, but distributions drawn on a grid. Because of the, GEM basically only assumes the presence of a species in the corresponding cell in which the actual coordinate of the species lies. Using grid cells of adequate size, this assumption can be thought of as conservative. When using DEC and DEC+j, on the other hand, one has to assume that a given species is present in the whole area where the coordinate lies, whether this represents an accurate description of the actual

range of the species or not. Of course the danger is overestimating the range of the species. This is a known limitation of these methods, which is why we intend to compare these results with those of GEM.

DEC methodology

Since DEC uses pre-defined areas, in order to optimise the ancestral areas of distribution, we used the Geological Provinces proposed by Arana et al. (2017). In this paper, diverse regions of Argentina were distinguished by combining climatic, geologic, and biotic criteria. The Provinces used in the present study were chosen based on the georeferenced current distribution of the species included, being other areas too extensive for the current distribution. The Provinces used were: **A:** Puna Province, **B:** Chaco Province, **C:** Monte Province, **D:** Yungas Province, **E:** Cuyan High Andean Province, **F:** Patagonian Province, **G:** Maule Province, **H:** Valdivian Forest Province, **I:** Santiago Province. The last three (G, H and I) were taken from Morrone (2006) and combined with those from Arana et al. (2017) to include all the individuals with distribution to the east and west of the Andes (Fig. 1).

To infer the processes that moulded the current distribution of the species of the *Liolaemus elongatus* group, we used a parametric method implemented in Lagrange vC++ (Ree & Smith, 2008). This method is based in Dispersal-Extinction-Cladogenesis models which require information about a single ultrametric dated phylogeny and distributional information of extant species. Based on previous studies (Chacón & Renner, 2014; Portelli & Quinteros, 2018) we used a constrained adjacency matrix (Matrix I. Table 2). This matrix assigns user-defined probability values to dispersal events between areas. Values included were: 0.8 for adjacent areas; 0.6 for areas separated by one intermediate area; 0.4 for areas separated by two intermediate areas; 0.2 for areas separated by three intermediate areas; and 0.08 for areas separated by four intermediate areas. We also used a second matrix (Matrix II. Table 3) to apply dispersal through geographic barriers cost. As such, we consider the probabilities of the first matrix plus a value, assigned to a geographic barrier (the Andes mountain range), close to 0 (0.001).

DEC+J methodology

To obtain the ancestral areas with DEC+J, the BioGeoBears 0.2.1 package (Matzke, 2013) implemented in R 3.0.2 (R Core Team) was used. For this test, the tree generated in Beast was used previously and the values of the following parameters were used, dispersion (d) = 0.8, extinction (e) = 0 and a third parameter whose value is predetermined by the method corresponding to speciation by founder effect (J) = 0.001. Furthermore, we use the same matrices (Tables 2 and 3) used for the DEC dispersion.

Finally, DEC and DEC+J were compared by Likelihood Ratio Test and Akaike Information Criterion (AIC wt), which gave relative probability values of both analyses. This was also obtained from the BioGeoBears package.

Table 2. Probabilities of dispersal cost between the areas (A_I) employed in the DEC analysis. Matrix I. See “Materials and Methods” for area names.

	A	B	C	D	E	F	G	H	I
A	1	0.6	0.8	0.8	0.8	0.6	0.4	0.4	0.6
B	0.6	1	0.8	0.8	0.6	0.6	0.4	0.4	0.4
C	0.8	0.8	1	0.8	0.8	0.8	0.6	0.6	0.6
D	0.8	0.8	0.8	1	0.6	0.6	0.4	0.4	0.4
E	0.8	0.6	0.8	0.6	1	0.8	0.6	0.6	0.8
F	0.6	0.6	0.8	0.6	0.8	1	0.8	0.8	0.8
G	0.4	0.4	0.6	0.4	0.6	0.8	1	0.8	0.8
H	0.4	0.4	0.6	0.4	0.6	0.8	0.8	1	0.6
I	0.6	0.4	0.6	0.4	0.8	0.8	0.8	0.6	1

Table 3. Probabilities of dispersal cost between the areas (A_I) employed in the DEC analysis. Matrix II. See “Materials and Methods” for area names.

	A	B	C	D	E	F	G	H	I
A	1	0.6	0.8	0.8	0.8	0.6	0.001	0.001	0.001
B	0.6	1	0.8	0.8	0.6	0.6	0.001	0.001	0.001
C	0.8	0.8	1	0.8	0.8	0.8	0.001	0.001	0.001
D	0.8	0.8	0.8	1	0.6	0.6	0.001	0.001	0.001
E	0.8	0.6	0.8	0.6	1	0.8	0.001	0.001	0.001
F	0.6	0.6	0.8	0.6	0.8	1	0.001	0.8	0.001
G	0.001	0.001	0.001	0.001	0.001	0.001	1	0.8	0.8
H	0.001	0.001	0.001	0.001	0.001	0.8	0.8	1	0.6
I	0.001	0.001	0.001	0.001	0.001	0.001	0.8	0.6	1

GEM methodology

GEM can assign one of four possible states to each node: vicariance, founder event, sympatry or point sympatry. Each event has a cost depending on the cell distribution of the sister nodes which come from it. According to this, an ancestral range is assigned to each node, as well as an event, which indicates what event happened at that node. The final cost of the reconstruction will be the number of cell changes in range, plus the cost of each event. A heuristic search is performed in order to find the least costly reconstruction. The possibilities for these are: vicariance, founder event, sympatry and point sympatry. Since this is a relatively new methodology, we will attempt to summarise it, although a more in-depth explanation can be found in the original paper (Arias et

al, 2017).

- Vicariance: the ancestral area will be equal to the sum of the ancestral ranges of two sister nodes. The number of overlapping cells of the two nodes will be given as extra cost to the event. This is due to the assumption that, in order to get this overlap, one or both of the sister nodes must have crossed a barrier which caused the allopatry in the first place.

- Founder event: considering two sister nodes, one will inherit the ancestral area, while the other (the one born out of the founder event), occupies new territory. Since founder event is supposed to happen at a given spot, after the crossing of a barrier has occurred, the bigger the area of the node originated by founder event, the less likely it is for the event to have happened. Therefore, the cost of the event is given by the amount of cells occupied by the node which does not inherit the ancestral area, minus one.

- Sympatry: in this case, both sister nodes inherit the ancestral range. The event will be given no extra cost only if both sister nodes share the exact same range. Any cells that are not shared by both nodes will be taken as extra cost.

- Point sympatry: when one of the descendant nodes inherits only a point of the ancestral range, instead of the whole range. In this case, the cost assigned is similar to the founder event, that is, the number of cells occupied by the node that does not inherit the whole range, minus one.

We ran the data with GEM as implemented in *evs* program, using a raster grid with pixels of 0.5° x 0.5° degrees, with a filling of 1. Costs were set as follows: vicariance and founder events to a default cost of 1, while sympatry and point sympatry events were set to a cost of 1.5. This is due to the unique set of factors which must happen for sympatric speciation to take place. If an alternative explanation for current distributions is possible, then this must generally be preferred, although sympatry will be considered in light of very strong evidence. In order to avoid having too large ancestral areas, we penalised them using $Z = 10$. The search was made with the flipping algorithm applying 10 independent runs each with 10,000 flip replicates (for a grand total of 100,000 flips replicates).

RESULTS

Table 4. Divergence times obtained for the *Liolaemus elongatus* group and its internal clades with their corresponding highest posterior density intervals (HPD).

Clades	Times of divergence (Mya)	95 % HPD (Mya)
<i>L. elongatus</i> group	11.5	14.2-5.9
<i>L. punmahuida</i> clade	4	4.47-0.59
<i>L. elongatus-petrophilus</i> clade	10.1	15.6-4.6
<i>L. petrophilus</i> clade	7.7	10.4-5.01
<i>L. capillitas</i> clade	4.25	7.9-0.6
<i>L. elongatus-kriegi</i> clade	6	11.02-1.01
<i>L. kriegi</i> clade	3	3.12-0.95
<i>L. elongatus sensu stricto</i> clade	4.16	7.32-1.01

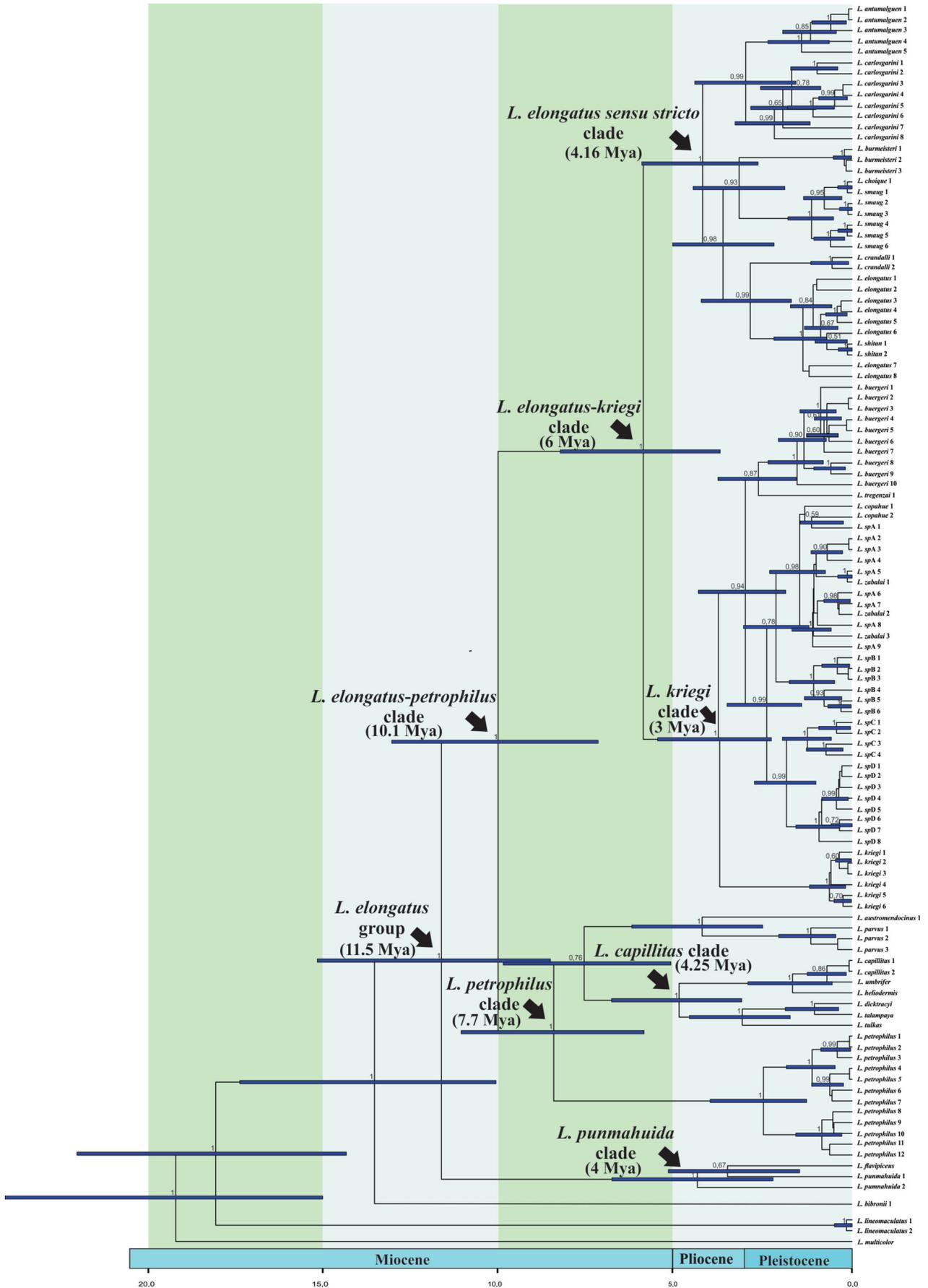


Figure 2. Main clades of the *L. elongatus* group. Times of divergences estimates for the *L. elongatus* group, under BI topology Ultrametric tree scaled in Myr. Numbers and horizontal bars on nodes represent posterior probabilities values and 95 % credibility intervals.

Table 5. Ancestral ranges obtained for DEC, DEC + j and GEM with their corresponding probabilities (P DEC and P DEC + j) of the *L. elongatus* group and their internal clades. Ancestral ranges obtained by DEC and DEC + j: C: Monte Province; F: Patagonian Province; CF: Monte and Patagonian Provinces; FG: Patagonian and Maule Provinces. Ancestral ranges obtained by GEM: CM: Central Monte; NCP: Norther Central Patagonia; Pa: Payunia.

Clades	Ancestral range DEC	P DEC	Ancestral range DEC+j	P DEC+j	Ancestral range GEM
<i>L. elongatus</i> group	CF	0.87	CF	1	NCP
<i>L. punmahuida</i> clade	F	1	F	1	Pa
<i>L. elongatus-petrophilus</i> clade	CF	1	CF	0.89	NCP
<i>L. petrophilus</i> clade	CF	1	CF	1	NCP
<i>L. capillitas</i> clade	C	1	C	0.74	CM
<i>L. elongatus-kriegi</i> clade	F	0.86	F	1	Pa
<i>L. kriegi</i> clade	FG	0.78	FG	0.82	Pa
<i>L. elongatus sensu stricto</i> clade	F	0.86	F	1	Pa

Table 6. Likelihood ratio test and Akaike information criterion (AIC) obtained through an analysis of BioGeoBears in R.

Modelo	lnL	p	d	e	j	AIC
DEC	-10.12		0.034	0.032	0	26.34
DEC+j	-7.23	0.009	0.018	0	0.39	19.76

Phylogeny

We obtained a time calibrated tree with the aim of dating the diversification events of the *Liolaemus elongatus* group. The clade topology recovered with BEAST is the same as those recovered under Parsimony and ML (Fig. 2). The main clades recovered were: 1) the *L. punmahuida* clade is the sister clade of the rest of the *L. elongatus* group; and 2) the *L. elongatus-petrophilus* clade, which includes three clades: the *L. kriegi*, *L. elongatus sensu stricto*, and *L. petrophilus* clades. The *L. kriegi* and *L. elongatus sensu stricto* clades were found to be sister clades (*L. elongatus-kriegi* clade hereafter). Within the *L. petrophilus* clade, we found the previously defined *L. capillitas* clade to be monophyletic group. The list of species belonging to each clade is available in the Supplementary Material S2.

Divergence time estimates

Our results show that the divergence of the *Liolaemus elongatus* (Table 4) group probably began during the Middle Miocene around 11.5 Mya (95 % highest posterior density interval- HPD: 14.2- 5.9). Inside, the clades that belong to the *L. elongatus* group have their origin in the Late Miocene to the Middle-Late Pliocene, with the exception of a few species which have their origin in during the Pleistocene.

The *Liolaemus punmahuida* clade, which includes *L. flavipiceus* and *L. punmahuida* began its diversifications around 4 Mya (95 %HPD: 4.47-0.59). The *L. elongatus-petrophilus* clade, diverged around 10.1 Mya (95 %HPD: 15.6-4.6). The *L. petrophilus* clade diverged around 7.7 Mya (95 % HPD: 10.4- 5.01) in the Lower Miocene, and inside the *L. capillitas* clade around 4.25 Mya (95 % HPD: 7.9- 0.6). The *L. elongatus-kriegi* clade diverged around 6 Mya (95 % HPD: 11.02- 1.01), giving two clades: the *L. elongatus sensu stricto* clade, which diverged at 4.16Mya (95 % HPD 7.32- 1.01) and the *L. kriegi* clade which

diverged around 3 Mya (95 % HPD 3.12- 0.95).

Ancestral distribution reconstruction

When comparing the DEC and DEC+j analyses (Table 5), the latter showed a better fit to the analysis, using values expressed with a likelihood ratio test and the Akaike information criterion (AIC). The likelihood ratio favours DEC+j when compared to DEC ($p = 0.009$), and in that it presents a better fit of AIC (AIC = 19.76) (Table 6).

The preferred biogeographical model was DEC+j; therefore, the results and discussion will be based on this. The results obtained by DEC can be seen in the Supplementary Material section (Fig S1 and S3 File).

The biogeographic reconstructions recovered with DEC+j show that the ancestral range of the *Liolaemus elongatus* group is most likely the combined Monte and Patagonian Provinces (Range CF; P:1). From here, the *L. elongatus* group diversifies into two clades: *L. punmahuida* and the *L. elongatus-petrophilus* clade. The *L. punmahuida* clade originates from the ancestral range Patagonian Province (Area F; P:1). The ancestral range of the *L. elongatus-petrophilus* clade is most likely the combined Monte and Patagonian Provinces (Range CF; P:0.89).

Inside the *Liolaemus elongatus-petrophilus* clade, the ancestral range of the *L. petrophilus* clade is most likely the combined Monte and Patagonian Provinces (Range CF; P:1). Inside the *L. petrophilus* clade, the ancestral range of the *L. capillitas* clade is most likely the Monte Province (Area C; P:0.74).

Conversely, the group sister of the *Liolaemus petrophilus* clade is the *L. elongatus-kriegi* clade, and the ancestral range of it most likely to corresponds the Patagonian Province (Area F; P:1). The ancestral range of the *L. kriegi* clade is most likely the combined Patagonian and Maule Provinces (Range FG; P:0.82). Finally, the ancestral range of the *L. elongatus sensu stricto* clade is most likely the Patagonian Province (Area F; P:1).

GEM results

The search with GEM found 354 different reconstructions with a cost of 67. All the reconstruction yielded 22 founder events and no vicariances. The number of sympatry events varied between 7 and 8, and the number of point sympatry events varied between 2 and 3. In order to process this amount of information, we made a consensus of the main nodes, those being: *Liolaemus elongatus* group, *L. elongatus-petrophilus* clade, the *L. capillitas* clade, *L. elongatus-kriegi* and *L. elongatus sensu stricto* (Fig. 4). All reconstructions assign the same events to the main nodes, although they vary in the direction of one founder event in the *L. capillitas* clade. This indicates that although there are many reconstructions, these are minor variations at very terminal nodes (Fig. 5).

We obtained the ancestral area of *Liolaemus elongatus* group, located in northern Central Patagonia, and from that node, a founder event occurred that originated the *L. punmahuida* clade in the Payunia region. The *L. elongatus-petrophilus* clade inherited the ancestral area of the *L. elongatus* group, and from this node a new founder event towards Payunia happened which originated the *L. elongatus-kriegi* clade. The *L. petrophilus* clade, on the other hand remained in the area of its immediate ancestor. In the *L. elongatus-kriegi* clade, whose ancestral area is in Payunia, a speciation by sympatry occurred, which originated the *L. elongatus sensu stricto* and the *L. kriegi* clades. Finally, within the *L. petrophilus* clade, whose ancestral area is in northern Central Patagonia, there is a founder event which originated a clade formed by *L. austromendocinus* + *L. parvus* and the *L. capillitas* clade in the central Monte region. Within the *L. capillitas* clade, a founder event which split the northern clade in northern Monte region (*L. capillitas*, *L. heliodermis* and *L. umbrifer*) from the southern clade (*L. dicktracyi*, *L. talampaya* and *L. tulkas*), the latter having inherited the area of its immediate ancestor.

DISCUSSION

Phylogeny

Since it was first proposed by Cei (1974), until the actual proposals (Medina et al., 2014, 2015, 2018; Avila et al., 2015; Troncoso et al., 2016; Esquerré et al., 2019, among others), the *Liolaemus elongatus* group has shown many changes in its taxonomic composition and phylogenetic relationships. In fact, since the identification of the *L. elongatus* group, four monophyletic groups have been identified within it (*L. elongatus*, *L. kriegi*, *L. petrophilus*, and *L. punmahuida* clades). The relationship of these three groups varies in the different proposals. Our results are congruent with those of Morando et al. (2003), Avila et al. (2004), Medina et al. (2014), Escobar Huerta et al. (2015), Troncoso et al. (2016), Zheng & Wiens (2016), Medina et al. (2017) and Esquerré et al. (2019) where the *L. elongatus* clade is sister to *L. kriegi* clade, and those are sister to the *L. petrophilus* clade (Fig. 2). Other relationships are found in Schulte (2013), Avila

et al. (2015), Medina et al. (2015), Medina et al. (2018; *L. elongatus* clade, *L. petrophilus* clade, *L. kriegi* clade). In all studies, including the present, the *L. punmahuida* named as such by Avila et al. (2015) clade is recovered as sister to the whole group.

Divergence time estimates

In general, previous biogeography studies that have included representatives of the *Liolaemus elongatus* group were mainly focused on larger groups, such as *L. sensu stricto*, *Liolaemus*, or even Liolaemidae. This work focuses exclusively on the biogeographic history of this unique group of lizards, which is part of an extensive monophyletic group studied both from a phylogenetic perspective (Schulte, 2013; Zheng & Wiens, 2016; Esquerré et al., 2019) and a biogeographical perspective (Díaz Gómez & Lobo, 2006; Esquerré et al., 2019) making it comparable with previous studies. The divergence time was calculated using BEAST and the divergence events were estimated with DEC, DEC+j and GEM.

The correct dating of nodes is important in order to assess possible geological events and paleogeographical changes that might have induced speciation events. Previous works have dated some of the nodes that we have dated here (Table 1), which we must necessarily compare these results in order to evaluate the validity and the confidence of these estimates. Schulte (2013) proposed a phylogeny for Liolaemidae where he dated the main nodes, including *Liolaemus elongatus-petrophilus* clade (although in this work *L. curis* was included in the group, which was recovered as a member of the *L. bellii* group by Abdala & Quinteros, 2014). Schulte (2013) estimated that the age of the *L. elongatus* group is approximately 16 million years, which is just outside our HDP (10.5 million years, 95 % HPD: 15.6-4.6). Schulte (2013) used several mitochondrial genes for this estimate, although only seven taxa of the *L. elongatus* group were used. He did not include *Cytb* genes in his analysis. Nevertheless, it must be noted that Schulte (2013) did not recover the clades that have been recovered consistently by different authors since Avila et al. (2015), as has been mentioned previously, and were also recovered in our own analysis. As he did not recover the same clades as us, we cannot further compare node estimates. Medina et al. (2014) used terminals mainly within the *L. kriegi* clade to date nodes, using *Cytb* sequences. Their results are largely congruent with ours, albeit she obtains slightly younger nodes for the *L. elongatus-petrophilus*, *L. elongatus-kriegi* and *L. kriegi* clades. Our divergence estimates mostly agree with those of Zheng & Wiens (2016) (see supplementary material therein). Although they did not work with the entire group, their representatives are enough to recover the internal clades of the *L. elongatus* group. Our mean estimates and those of Zheng & Wiens (2016) are close (his estimates are within our 95 % HPD), although they obtain slightly older dates. For example, their estimate for the *L. elongatus* group is 12.3 Mya, while we get only 11.5 Mya. They also date the *L. elongatus-petrophilus* clade at 9.9 Mya, while we get 10.1 Mya. Finally, the most recent work where the nodes

of the *L. elongatus* group are estimated is Esquerré et al. (2019) (see supplementary material therein). The estimates of the main group are within the HPD 95 % range of our work. The dates obtained by Esquerré et al. (2019) are the most similar to ours. The estimates of the main group are within the HPD 95 % range of our work. The dates obtained by Esquerré et al. (2019) are the most similar to ours. Their estimate for the *L. elongatus* group is 13 Mya, while we get only 11.5 Mya. They also date the *L. elongatus-petrophilus* clade at 9.5 Mya, while we get 10.1 Mya. For its sister clade, the *L. punmahuida* clade obtained 2 Mya and we date it in 4 Mya. For the *L. elongatus-kriegi* clade they estimate 5.8 Mya and we obtain 6 Mya. The *L. petrophilus* clade is dated at 8.2 Mya while we date 7.7 Mya. For the sister clades *L. elongatus sensu stricto* and *L. kriegi* they obtain 4 Mya for each, while we date 4.16 Mya and 3 Mya, respectively. Continuing with the comparison, in Esquerré et al. (2019), 95 % HPD ranges are slightly higher than ours. For the *L. elongatus-petrophilus* clade they obtain a range of 13.5 Mya to 6.75 Mya, while our range is 13 Mya to 7.5 Mya, and for the clade *L. elongatus-kriegi* they obtain a range of 8 Mya to 4 Mya and our range is 7.5 Mya to 4 Mya, are some examples. Here we can observe that although the of *L. elongatus* group only represents 9 % of the totality of species included by Esquerré et al. (2019), we find more similarities than differences. At the same time, said differences expressed in longer divergence times as HPD ranges may be due to the amount of information analyzed by Esquerré et al. (2019) that increases the variability of the data with which they worked.

Naturally, the differences in node ages found between our own study and any other must come from a difference either in the methodology the datasets (see Table 1). On the other hand, there are in some cases striking similarities despite these differences, which attests to the robustness of these conclusions. We will consider these differences next.

Schulte (2013) uses a relaxed clock to analyse a large number of taxa and genes. Nevertheless, he only included seven species from the *Liolaemus elongatus* group, which could explain the discrepancies with our own study. Medina et al. (2014), on other hand, uses a strict clock to analyse four species within the inner *L. kriegi* clade. Both the lack of representatives from the *L. elongatus sensu stricto* clade, and the low number of overall representatives of the group could explain the differences in our study, although there is some concordance. Later, in their paper, Zheng & Wiens (2016) analyse a large amount of information (studied Squamata and 52 genes) and eleven representatives of the *L. elongatus* group, but unlike Schulte (2013), they chose to use the penalised likelihood method (Sanderson, 2002), which compensates for the large number of taxa and genes. As mentioned in the previous paragraph, their results are much more similar to ours. Medina et al. (2017) analyse eleven species of the *L. elongatus* group through a relaxed clock to analyse their data. Some species fall within the range of our results. Finally, Esquerré et al. (2019) use a relaxed clock to analyse their

data. Given that they included most species of the group, the ages obtained are largely concordant with ours, our within our ranges.

Ancestral distribution reconstruction

Although currently there is not yet a methodology that is fully accepted to reconstruct biogeographical histories, when there is a complete record of the distribution of all or most of the descendants, and when we have estimates of the divergence of nodes, sometimes patterns can be seen that imply a specific history regardless of the methodology used.

Although GEM analyses have not yet been published, there is a recent study of DEC+j within the *Liolaemus elongatus* group, Esquerré et al. (2019). Although they use more extensive areas, we can find concordance with this work. For example, for Esquerré et al. (2019), the most probable ancestral range for the *L. elongatus* group is what they call the Central Andes or a combination of this area next to Patagonia. While the most probable ancestral range for us is the combination of Monte with Patagonia (Areas C and F respectively; Fig. 3). Here we find a correspondence since the combination of Monte with Patagonia (CF) is part of the distribution that Esquerré et al. (2019) called Patagonia and Central Andes. At the same time, these ancestral ranges (either individual areas or combinations of them) are repeated in the work of Esquerré et al. (2019) and ours for the clades of *L. punmahuida*, *L. elongatus-petrophilus*, *L. petrophilus*, *L. elongatus-kriegi*, *L. kriegi* and *L. elongatus sensu stricto* clades. For the *L. capillitas* clade, Esquerré et al. (2019) locates that the most probable ancestral range is the Altiplanic Andes or the combination of them with the Eastern lowlands, while for us it is the Monte (Area C) or a combination of Monte and Chaco (Areas C and B; Fig. 3). In this case, again the results are concordant since Monte (C) has an area of overlap with the southern part of the Altiplanic Andes and Chaco (B) is part of what is called the Eastern lowlands.

When analysing that the DEC+j studies were quite similar, we can compare this with GEM. DEC+j uses predefined areas as a starting point, while GEM uses species records mapped on a grid. The immediate consequence of this, as can be seen by our results, is that the ancestral areas found by GEM, not being constrained to the user-defined areas, are a lot smaller, and only cover a small portion of the DEC+j areas. Despite this difference, it can be said that in general, GEM does not directly contradict DEC+j, and instead can be seen as a more specific result of what DEC+j shows. The ancestral area for the *Liolaemus elongatus* group obtained by GEM, a portion of northern Patagonia, is part of the ancestral area obtained by DEC+j and by Esquerré et al. (2019). The same can be said of the ancestral areas of *L. elongatus-petrophilus*, *L. punmahuida*, *L. elongatus-kriegi* clades, although as mentioned above, they are actually much smaller areas. On the other hand, as we look at these nodes, we note that the ancestral areas obtained by GEM are much better fitted to elucidate events happening at those nodes. For example, GEM

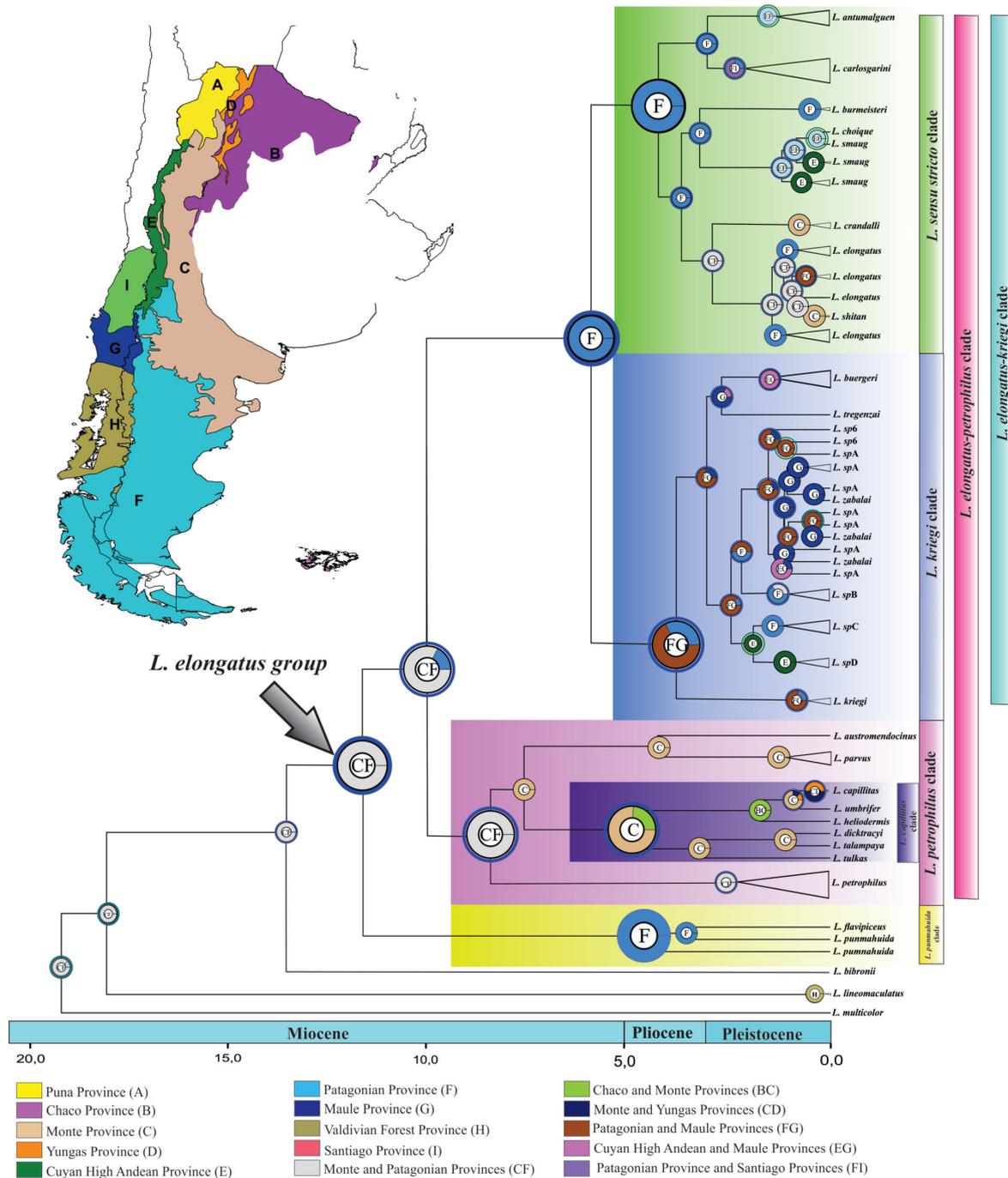


Figure 3. Ancestral area of distribution. Pie charts of each node depict the relative probabilities of ancestral area/ranges and the assigned area (central circle). The colours of the circles correspond to the colours used in the map for each predefined area or the combination of them. Circles around pie charts represent events: blue circle: dispersal event; green circle: vicariance. Time axis (in Myr) is annotated with major geological events.

specifies a founder event which originated the *L. punmahuida* clade. This event cannot be picked up by DEC+j, as both the ancestor and descendant areas of the node are part of the same large area, that is, Patagonian Province. Another important difference between GEM and DEC+j are the possible events which the former can assign to each node. Given the very specific set of conditions which would have to occur for a speciation by sympatry event to occur, we decided to give this event a slightly larger cost than the rest (1.5 vs 1). We considered that GEM's way of assigning cost to events might have

led to assigning this type of event, which we consider improbable, to some nodes where a different explanation (for example vicariance + posterior dispersal) might be preferable (Dieckmann & Doebeli, 1999; Barraclough & Vogler, 2000; Gray & McKinnon, 2007). Given that the assignment of sympatry was punished, we find it very interesting that the program found that both *L. kriegii* and *L. elongatus* clades inherited the exact same area in Payunia from their common ancestor. Even though we find that the evidence for this is still not conclusive, it may be possible that we have underestimated the capacity for

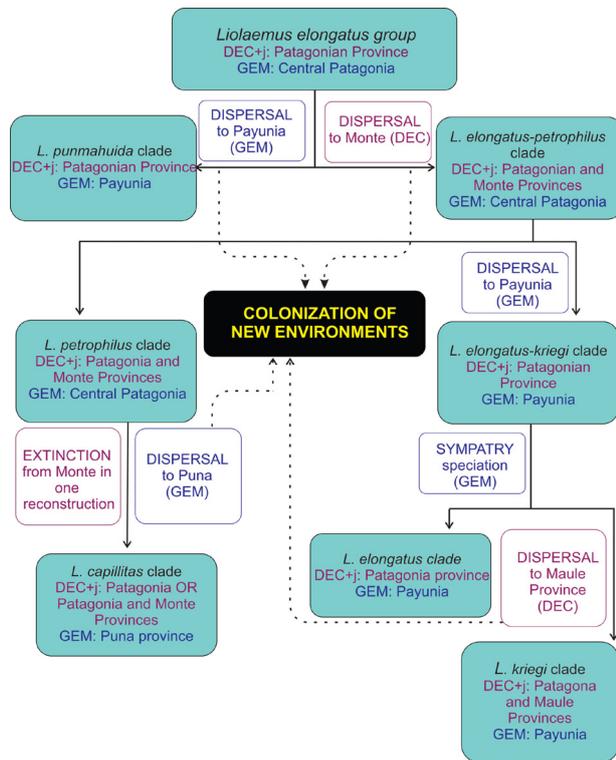


Figure 4. Event flow chart. The main speciation and extinction events, according to our DEC (blue letters) and GEM (red letters) analyses. Solid arrows represent the relationships between clades and dotted arrows indicate the colonisation of new environments.

these lizards to form biological barriers in the absence of geographical ones. There are some studies which show evidence of sympatric speciation (Losos et al., 1998), or sympatric divergence (Huyghe et al., 2010), therefore it would be interesting to see if there are more examples of this kind of speciation in lizards.

Geological and biogeography implications

The historical biogeography of the *Liolaemus elongatus* group provides information about the effect of geological events on its diversification patterns, revealing a complex interaction between dispersion and vicariance. According to our estimates, the *L. elongatus* group began its diversification at a time when the Andes entered its final uplifting phase. During this period (11–3Mya), the Paranaense sea began to retreat, leaving behind plains, which were empty niches ready to be exploited. During this period, the Andes reached its current height and became a barrier to moisture coming from the west, which transformed the areas to the east of the Andes in steppe biome (Donato et al., 2003). Meanwhile, Patagonia is likely to have started experiencing a process of desertification at approximately 16.5 Mya as a result of the Andean uplift (Stern & Blisniuk, 2002), with the severity of this process increasing at approximately 14 Mya (Blisniuk et al., 2005), when a new tectonic pulse increased the efficiency of the orographic effect, limiting the incoming humid winds from the southern Pacific Ocean (Ramos & Ghiglione, 2008). This process generated a marked west–east climatic gradient similar

to the one that characterises present-day Patagonia east of the Andes (Martínez & Kutschker, 2011). This new panorama, in which the cooling and drying of the extra-Andean Patagonia generated the disappearance of the last megathermal taxa and together with an increasing diversity and abundance of xerophytic adapted taxa as pastures (Barreda & Palazzesi, 2007). This set of events facilitated the diversification of the *L. elongatus* group, since when megathermal taxa and potential predators disappeared, small animals such as lizards had greater chances of survival and conquest of new niches. The outcrop of volcanoes east of the Patagonian Andes also facilitated the isolation of populations that at the same time confronted altitudinal changes. All this can explain the unusual number of lizard species in the region (Avila et al., 2013; Corbalán et al., 2011). At least half of the lizard species in the Patagonia area are endemic (Corbalán et al., 2011), and has been proposed as the centre of origin for several lizard genera (Lamborot & Díaz, 1987; Cei & Videla, 2003; Scolaro et al., 2003; Díaz Gómez, 2009). In support of this hypothesis, according to a recent paper by Esquerré et al. (2018) of the Liolaemidae family, the speciation rates have been much higher in the Andes or in adjacent areas. They also found a strong correlation between diversification rates in liolaemids and rising altitudes. They provide a simple explanation for this: the elevation of the Andes provides what they call “sky islands”, that is mountain tops become a novel niche to be inhabited, and at the same time, these become isolated among themselves, as they are surrounded by different environments. The *L. elongatus* group suffered two major speciation peaks during its history (Unpublished data), one corresponds to the Late Miocene and another during the Pleistocene. This corresponds with events described for the Miocene and for a series of events that determined the limits of the distribution of this group of saxicolous lizards. The northern end of the *L. elongatus* group distribution is given by *L. heliodermis* with a possible origin at 1 Mya and whose type locality is found in Tafí del Valle (Tucumán, Argentina). During the Middle and Upper Pleistocene, the Tafí del Valle Formation was formed (Collantes et al., 1993, Sayago et al., 1998). At the same time, in the Quebrada de las Conchas, to the south center of Salta province (located just north of Tafí del Valle), pleistocene formations composed of sand and gravel were defined and no paleontological record is known (Frenguelli, 1936). At an estimated age for the Upper Pleistocene–Lower Holocene, the sedimentary environment of this unit is interpreted as a lake of shallow depth and low salinity, with stages of greater evaporation (Salfity & Monaldi, 2006). The presence of a lake and the rapid formation of Tafí del Valle could explain why *L. heliodermis* has not expanded its distribution range and today is only found in its type locality. On the other hand, there are species which are widely distributed, occupying a range that includes high and low sections of the Andes, such as *L. kriegi* (Patagonia and Maule Province), although they might prove to be in fact a complex of species, including misidentified populations which in fact correspond to

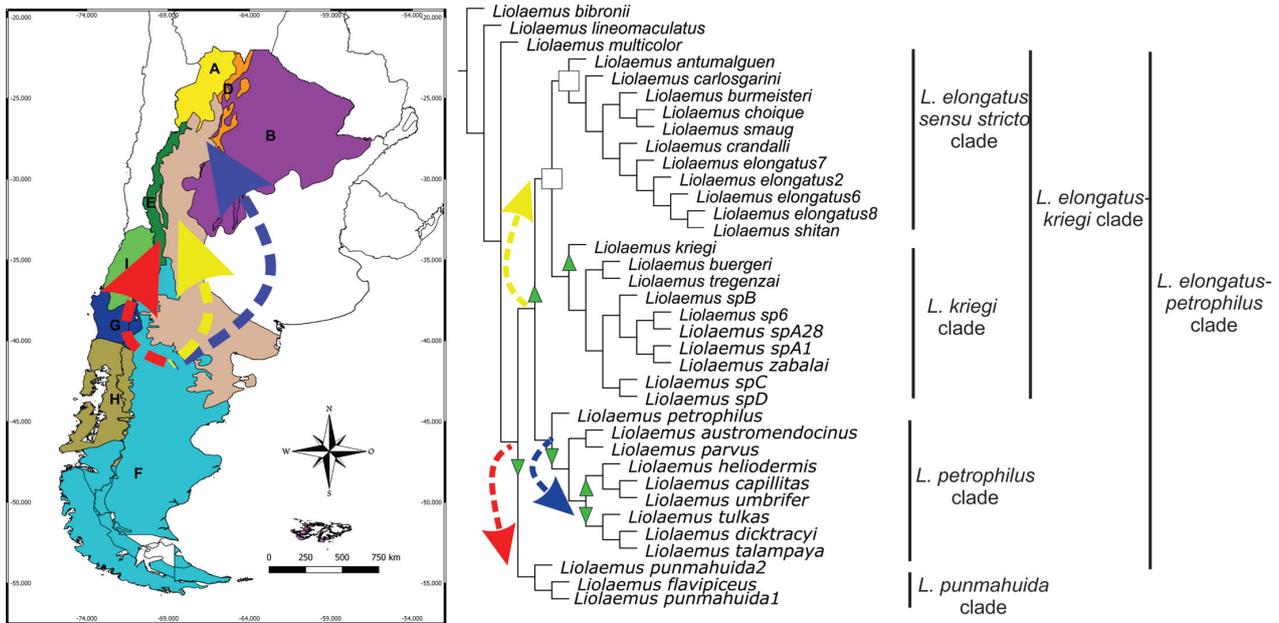


Figure 5. GEM reconstruction. The speciation events in the main clades recovered from GEM are shown here. The green arrow indicates the occurrence of a founder event in the direction of the arrow (i.e. the clade not pointed at inherits the ancestral range). The white square at the node indicates a sympatry event (i.e. both clades inherit the ancestral range). In addition, the events are superimposed on the map of predefined areas used for DEC + j.

novel species or it could be that *L. kriegi* had a recent diversification according to our results and we could be talking about a widely distributed polymorphic species. GEM shows support for this hypothesis in the *L. petrophilus* and the *L. punmahuida* clades, the ancestors of which speciated by founder event from central Andes to Payunia, occupying higher lands.

We find that our results are congruent with many of the previous analyses made on the group. Cei (1979) mentioned in his book the possibility that Patagonia served as a dispersal centre for *Liolaemus* lizards. Therefore, we find it interesting that previous works have found Patagonia as the ancestral area for Liolaemidae, and for groups within Liolaemidae (Díaz Gómez & Lobo, 2006; Portelli & Quinteros, 2018). Similarly, in this study we find that Patagonia, is the ancestral area for the *L. elongatus* group, and for clades within (*L. punmahuida*, *L. elongatus-petrophilus*, *L. petrophilus* and *L. elongatus-kriegi* clades; Fig. 3), which would give further supports to Cei's claims. This can also be seen in Díaz Gómez & Lobo (2006), who obtains similar ancestral areas to ours (northern Patagonia, an area which they call "Andes"). This pattern is also appreciated in a related group of lizards, which share a similar lifestyle: the saxicolous genus *Phymaturus*. In fact, many species of the *L. elongatus* group and *Phymaturus* are found syntopically (for example: *Phymaturus tromen* with *Liolaemus punmahuida*; *Phymaturus verdugo* with *Liolaemus thermaurum*; *Phymaturus sitesi* with *Liolaemus crandalli*; *Phymaturus lobo* with *Liolaemus carlosgarini*; *Phymaturus denotatus* and *Phymaturus tromen* with *Liolaemus umbrifer*, among others). According to Esquerré et al. (2019), these two groups must have shared much of their history, as *Phymaturus*

was calculated to be 16 million years old, while the *L. elongatus* group was 12.3 million years old (11.2 in this work). Although, the divergence time is not exactly the same, a correspondence can be observed between the diversification of the palluma group and patagonicus group (members of the genus *Phymaturus*) with the clades of *L. punmahuida*, *L. capillitas*, *L. kriegi* and *L. elongatus sensu stricto* because their diversification would have begun during the Pliocene. We can even find a correspondence between the possible ancestral ranges of some clades. For example, in Esquerré et al. (2019) found that the most probable ancestral range for the palluma group corresponds to the Central Andes or a combination of these with Patagonia that corresponds to our results that show that the most probable ancestral range for the *L. capillitas* clade would be in Monte (C) or a combination of it with Chaco (CB). In support of this hypothesis, both groups have representatives west of the Andes, distributed mostly in southern areas, between 34°-38° latitude, and they share most of their distribution range in the east of the Andes (between 26°-43° latitude).

In spite of the coincidences, we must take into account that by using smaller predefined areas (DEC) than previous studies, as well as by using explicit occurrence data (GEM), our level of detail for each of the ancestral ranges is greater. Therefore, it is easier to assess possible geological events that might have caused the speciation in said areas. Having greater detail of these ancestral ranges, we were able to integrate the analyses into a geological context, which generated a hypothesis for the diversification of the group. This is the first time that such hypothesis, with these level of detail, were produced for the group.

Finally, we can conclude that, although implementing

two different methodologies, we were able to see a similar sequence of events that explains the current distribution of the *Liolaemus elongatus* group. Furthermore, our results are largely consistent with previous studies (at the level of inner clades), but our results expressed with greater detail for the *L. elongatus* group. We believe our study can be used as a basis for future studies within each clade and/or sister species.

For both methodologies, the ancestral area of the *Liolaemus elongatus* group is located in the center of Argentina, more specifically, in the Patagonia region. The diversification of the *L. elongatus* group would have begun along with the final phase of the Andes uplift, with the founding events prevailing over others such as vicariance. All this set of events determined the current distribution of the group, which is why we currently find representatives of the group in the east and west of the Andes.

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