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## Lizards from the end of the world: Phylogenetic relationships of the *Liolaemus lineomaculatus* section (Squamata: Iguania: Liolaemini)

M. Florencia Breitman<sup>a</sup>, Luciano J. Avila<sup>a</sup>, Jack W. Sites Jr.<sup>b</sup>, Mariana Morando<sup>a,\*</sup>

<sup>a</sup>Centro Nacional Patagónico – Consejo Nacional de Investigaciones Científicas y Técnicas, Boulevard Almirante Brown 2915, ZC: U9120ACF, Puerto Madryn, Chubut, Argentina

<sup>b</sup>Department of Biology and M.L. Bean Life Science Museum, 401 WIDB, Brigham Young University, ZC: 84602, Provo, UT, USA

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## ABSTRACT

The *Liolaemus lineomaculatus* section is a geographically widely distributed group of lizards from the Patagonian region of southern South America, and includes 18 described species representing the most southerly distributed *Liolaemus* taxa (the genus includes 228 species and extends from Tierra del Fuego north to south-central Peru). Despite high species diversity, the phylogenetic relationships of this section are unknown. In the present work we sampled all described species in the *L. lineomaculatus* section as well as currently undescribed candidate species to reconstruct the first complete phylogenetic hypothesis for the clade. Our data set included four anonymous nuclear loci, three nuclear protein-coding loci, and two mitochondrial genes. We compared results obtained with three different phylogenetic methods for the concatenated data set (Maximum Parsimony, Maximum Likelihood and Bayesian Inference) with a coalescent-based species tree approach (BEST), and recovered congruent, strongly-supported topological arrangements across all methods. We identified four main clades within the *L. lineomaculatus* section: the *lineomaculatus*, *magellanicus*, *somuncurae*, and *kingii* + *archeforus* groups, for which we estimated divergence times. We discuss the taxonomic implications of these results and how the future integration of phylogeographic, niche modeling and morphological approaches will allow testing biogeographical hypotheses in this clade.

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### 1. Introduction

Lizards have been used as model organisms for testing many ecological and evolutionary hypotheses at different levels (populations, communities) and at multiple spatial and temporal scales (reviewed in Camargo et al., 2010). In some regions, chiefly Australia, Europe, and North America, baseline taxonomic and phylogenetic knowledge is sufficient to support detailed hypothesis-driven studies that have provided important insights into general ecological and evolutionary processes (reviewed in Camargo et al., 2010). However, in other areas of the world, alpha diversity, basic taxonomic knowledge, and distributions of regional lizard faunas are insufficient to support more synthetic studies. Thus lizards provide an excellent example of “Linnean” and “Wallacean” shortfalls, which means respectively incomplete knowledge of species and their distributions (Lomolino, 2004). These can be rectified only by intensive and careful field work, followed by morphological, molecular, and ecological studies. In the Patagonian region of southern South America, the *Liolaemus lineomaculatus* section is characterized by these Linnean and Wallacean shortfalls.

\* Corresponding author.

E-mail addresses: [breitman@cenpat.edu.ar](mailto:breitman@cenpat.edu.ar) (M.F. Breitman), [avila@cenpat.edu.ar](mailto:avila@cenpat.edu.ar) (L.J. Avila), [jack\\_sites@byu.edu](mailto:jack_sites@byu.edu) (J.W. Sites), [morando@cenpat.edu.ar](mailto:morando@cenpat.edu.ar) (M. Morando).

The genus *Liolaemus* is one of the most ecologically diverse and species-rich genera of lizards on earth, with 228 recognized species (Lobo et al., 2010a; and the recently described *Liolaemus chacabuense*, Núñez and Sclaro, 2009, *Liolaemus casamiquelai*, Avila et al., 2010a, *Liolaemus antumalguen*, Avila et al., 2010b, *Liolaemus cazianiae* and *Liolaemus halonastes*, Lobo et al., 2010b). Moreover, the true diversity of the genus may be as much as twice this number or more by some estimates (Morando et al., 2003). *Liolaemus* is distributed over a wide geographic area spanning a large range of latitudinal ( $14^{\circ} \pm 30' - 52^{\circ} \pm 30'S$ ), altitudinal (0–4,500 m) and climatic regimes, from the extremely arid Atacama Desert to temperate *Nothofagus* rainforest (Cei, 1986, 1993; Donoso-Barros, 1966; Etheridge and de Queiroz, 1988; Etheridge and Espinoza, 2000; Frost and Etheridge, 1989; Hellmich, 1951; Lobo, 2001). Two main groups were proposed by Laurent in 1983 within *Liolaemus*, based on a set of morphological characters (number of preclacal pores, tail length, and position of the nasal scales): *Liolaemus sensu stricto* (or the “Chileno group”, mainly distributed in Chile) with 91 described species, and *Eulaemus* (or the “Argentino group” largely confined to Argentina) with 137 described species (Lobo et al., 2010a). Laurent’s hypothesis has been supported by several recent molecular and morphological studies (Abdala, 2007; Cruz et al., 2005; Espinoza et al., 2004; Morando, 2004; Schulte et al., 2000).

The *L. lineomaculatus* section includes 18 described species. Based on morphological characters, it is commonly divided in three groups: (1) the *archeforus* group (Ceï, 1986) with eight described species: *Liolaemus archeforus*, *Liolaemus sarmientoi*, *Liolaemus gallardoi*, *Liolaemus zullyae*, *Liolaemus tari*, *Liolaemus scolaroï*, *Liolaemus escarchadosi* and *L. chacabucoense*; (2) the *kingii* group (Ceï, 1986) with five described species: *Liolaemus kingii*, *Liolaemus sumuncurae*, *Liolaemus baguali*, *Liolaemus tristis* and *Liolaemus uptoni*; and (3) the *lineomaculatus* group (Etheridge, 1995) with four described species: *L. lineomaculatus*, *Liolaemus hatcheri*, *Liolaemus silvanae* and *Liolaemus kolengh*. One other species, *Liolaemus magellanicus*, is recognized as a member of the *L. lineomaculatus* section, but it is not clearly assigned to any of these groups.

Etheridge (1995) assigned species from the *L. lineomaculatus* section to the *Liolaemus sensu stricto* group on the basis of morphological evidence, but later several authors found evidence for placing the *L. lineomaculatus* section into the *Eulaemus* group. In the first quantitative phylogenetic analysis of the genus, Young Downey (1998) recovered four species of the *L. lineomaculatus* section (*L. lineomaculatus*, *L. kingii*, *L. archeforus* and *L. silvanae*) as forming the sister clade to the *montanus* section (both members of the *Eulaemus* group), based on allozyme data. Schulte et al. (2000) found similar results based on mitochondrial DNA (mtDNA) sequences of three species (*L. lineomaculatus*, *L. somuncurae* and *L. magellanicus*), and used the name "*L. lineomaculatus* section" to identify this clade. A similar clade (*L. kingii*, *L. magellanicus* and *L. lineomaculatus*), was also recovered by Morando (2004) based on mtDNA and nuclear DNA (nucDNA).

The *L. lineomaculatus* section is among the least studied of all *Liolaemus* groups, with a majority of species known only from type localities and described from limited material, with poor diagnoses and limited justification (see Lobo et al., 2010a, e.g.: Núñez and Sclaro, 2009; Pincheira-Donoso and Núñez, 2005; Pincheira-Donoso et al., 2008a,b). Further, the group has the most southerly distribution of the genus, ranging from northern Patagonia south to the tip of the continent, and across the Strait of Magellan to Tierra del Fuego (Abdala and Lobo, 2006). This region has been subjected to a complex geological history including the uplift of the Andes, volcanism, marine introgressions, and extreme climatic oscillations driven by cyclic glaciations–deglaciations (Rabassa et al., 2005; Rabassa, 2008). Furthermore, species from the *L. lineomaculatus* section are distributed across extremely heterogeneous landscapes (annual temperatures vary from  $-20^{\circ}\text{C}$  to more than  $40^{\circ}\text{C}$ ); thus, its phylogenetic/phylogeographic history has also likely been complex and interesting. A well-resolved and well-supported phylogenetic hypothesis for this group can contribute to studies of its evolutionary history and how this compares with the histories of other co-distributed taxa (Azpilicueta et al., 2009; Coronato et al., 1999; Cosacov et al., 2010; Lessa et al., 2010; Marchelli et al., 1998; Marchelli and Gallo, 2004, 2006; Markgraf, 1983; Markgraf et al., 1995; Morando et al., 2007; Muellner et al., 2005; Villagran, 1991). Further, ecological, physiological, and behavioral studies, some focused on adaptations to cold climates for some *Eulaemus* species (Ibargüengoytía et al., 2002, 2010; Jacksic and Schwenk, 1983; Kozykariski et al., 2008; Medina and Ibargüengoytía, 2010; Pincheira-Donoso et al., 2008a, 2009a,b), can in the future be evaluated within a more inclusive evolutionary context for the *L. lineomaculatus* section.

No phylogenetic hypothesis exists for most species of the *L. lineomaculatus* section; thus, our main objective is to provide a well-supported phylogeny for the entire clade. We use a multi-locus molecular data set, and compare the inferred topologies across multiple phylogenetic reconstruction methods. Our sampling includes all 18 described species represented by specimens from their type localities in most cases, and eight distinct molecular lineages that may represent undescribed species ("candidate species"; Morando

et al., 2003) included in the *L. lineomaculatus* section. We sequenced two mitochondrial gene regions, three nuclear protein-coding genes, and four anonymous nuclear loci for all named and candidate species. We then performed phylogenetic analyses based on different partitions of the concatenated sequences (all genes separately, all nuclear genes, all mitochondrial genes, and all genes combined), using Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian Inference (BI) methods. We also used a coalescent-based species tree approach (Liu and Pearl, 2007), because several studies have demonstrated that concatenation methods can recover inaccurate topologies under some conditions (incomplete lineage sorting, hybridization/introgression, gene duplication, horizontal gene transfer, and gene tree error estimation) (Degnan and Rosenberg, 2009; Heled and Drummon, 2009; Kubatko and Degnan, 2007; Liu and Pearl, 2007; Maddison, 1997; Pamilo and Nei, 1988). Coalescent-based species tree methods can accommodate gene tree heterogeneity caused by incomplete lineage sorting into species tree estimation (Degnan and Rosenberg, 2009; Edwards, 2009; Liu and Pearl, 2007; Rannala and Yang, 2003), and BEST is among the few methods that directly infer the evolutionary history of the species rather than gene trees (Liu et al., 2009). Few studies have used this combination of methods in lizards (Fujita et al., 2010; Leaché, 2009, 2010; Wiens et al., 2009).

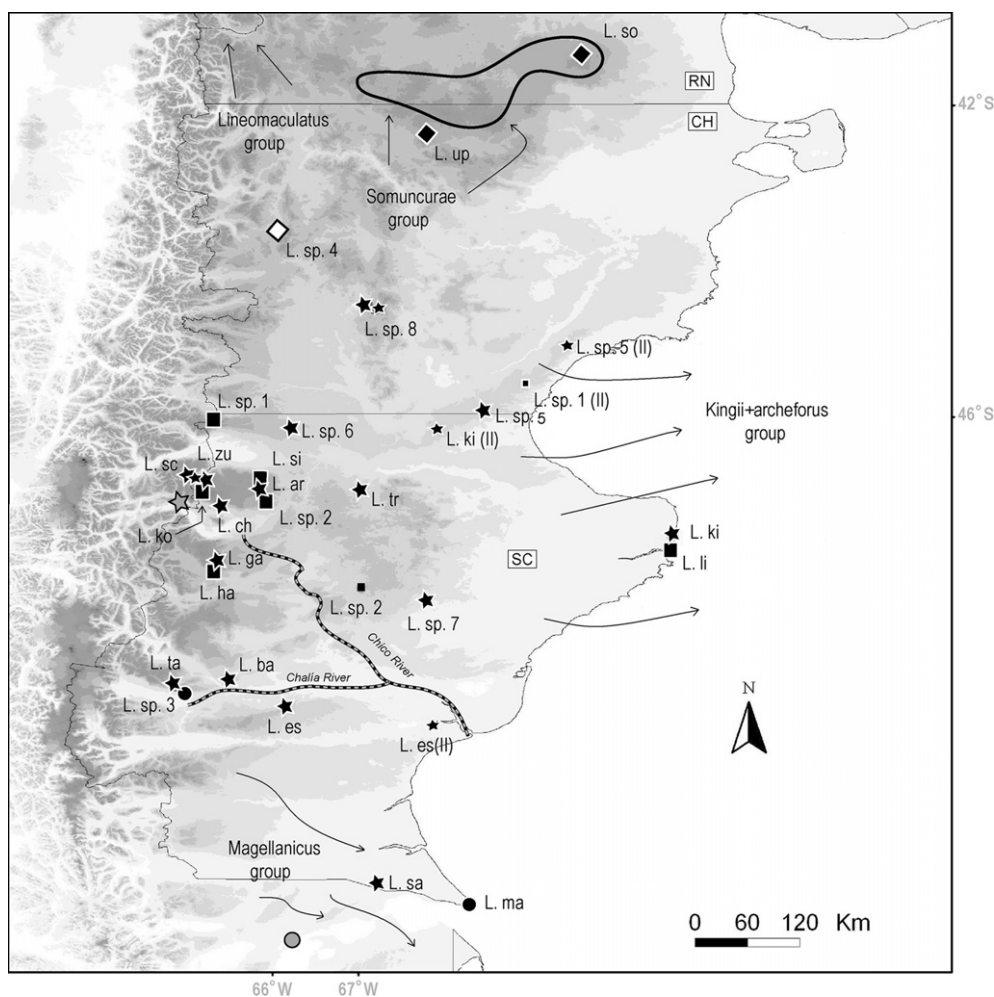
## 2. Materials and methods

### 2.1. Taxon sampling

The *L. lineomaculatus* section includes 18 recognized species; 16 of the type localities are located in Argentina and two in Chile. Samples were collected from 15 of the Argentina type localities and one in Chile (*L. scolaroï*; Fig. 1). We could not collect samples from the type localities of *L. magellanicus* and *L. chacabucoense*, but we included samples collected 50 km and 200 km east of their type localities, respectively. In both cases, the morphological characters of our specimens matched those of the vouchers described from their respective type localities. We also included individuals from eight candidate species (they represent different lineages with more than three percent of molecular distance with other described species, and morphological differences) that are currently being studied by our research group. We also included a sample of *L. zullyae* from Chile, as it was found in sympatry with *L. scolaroï*, and although males from both species are considerably different, the uncorrected pairwise cyt-b distance between them is zero.

To test monophyly of the *L. lineomaculatus* section and its phylogenetic position within *Liolaemus*, we selected five other species of the genus as outgroups, including *Liolaemus boulengeri* and *Liolaemus darwini* from the *montanus* section (member of *Eulaemus* clade), and *Liolaemus bibronii*, *Liolaemus gracilis* and *Liolaemus petrophilus* from *L. sensu stricto* clade. We rooted all trees using two species of *Phymaturus*, the sister genus to *Liolaemus* (Etheridge, 1995; Lobo et al., 2010a). This rooting scheme permitted us to test both monophyly of the *L. lineomaculatus* section and its affinity with either the *Eulaemus* clade or the *L. sensu stricto*. We used a total of 65 lizards from a wide geographic area (Fig. 1); details of the specimens and localities are summarized in Appendix A.

Two individuals collected in the same locality were chosen as representatives of each terminal taxon to check for mistakes. We constructed NJ trees on cyt-b sequences to confirm that in all cases individuals from the same locality were conspecific, and then we usually selected one specimen for further amplification of all markers. In a few cases some genes did not amplify for one individual, so we included the conspecific from the same locality to complete the data set, and in three cases where this second animal (and others from that locality) did not yield a PCR product, we used another



**Fig. 1.** Distribution map for species of the *Liolaemus lineomaculatus* section sampled for this study. Squares: *lineomaculatus* group (L. li: *L. lineomaculatus*, L. ha: *L. hatcheri*, L. si: *L. silvanae*, L. ko: *L. kolenghi*, L. sp.1 and L. sp. 2); circles: *magellanicus* group (L. ma: *L. magellanicus*, L. sp. 3); black diamonds: *somuncurae* group (L. so: *L. somuncurae*, L. up: *L. uptoni*), and white diamond: L. sp. 4 (partial support for its inclusion on this group); stars: *kingii* + *archeforus* group (L. ki: *L. kingii*; L. sa: *L. sarmientoi*, L. es: *L. escarchadosi*, L. ba: *L. baguali*, L. ta: *L. tari*, L. ga: *L. gallardoi*, L. ch: *L. chacabuense*, L. sc: *L. scolaroi*, L. zu: *L. zullyae*, L. ar: *L. archeforus*, L. tr: *L. tristis*, L. sp. 5, L. sp. 6, L. sp. 7, L. sp. 8). Gray symbols indicate non-sampled type localities; larger size symbols identify sampled type localities, while small symbols and (II) show additional sampled localities. Chalia and Chico Rivers are indicated with gray and black lines. Arrows indicate the proposed refugia for the *lineomaculatus*, *magellanicus* and *kingii* + *archeforus* groups; in the *somuncurae* group arrows and the circled area indicate the Somuncura Plateau, a possible refugium for this group. RN: Río Negro Province, CH: Chubut Province, SC: Santa Cruz Province.

individual from a nearby locality (and identified as a conspecific in the cyt-b NJ tree; see [Appendices A and B](#) for details on voucher specimens amplified for each species and gene).

## 2.2. Gene sampling

We collected new sequence data for seven nuclear genes (three protein-coding loci [NPCL], and four anonymous loci [ANL]) and two mitochondrial genes (cytochrome *b* and 12S). Our gene sampling was based on a screening of published sets of nuclear primers ([Gamble et al., 2008](#); [Kocher et al., 1989](#); [Saint et al., 1998](#); [Townsend et al., 2008](#); [Wiens et al., 1999](#)), and on a non-published set of ANL primers developed by A. Camargo (Personal Communication) for lizards of the *L. darwini* complex (members of the *montanus* section of *Eulaemus*). We screened primers for 36 genes and selected the most informative for different hierarchical levels of divergence in the focal group of this study. These genes include the NPCL Cmos, ACM4tg, and PRLR ([Gamble et al., 2008](#); [Saint et al., 1998](#); [Townsend et al., 2008](#)); and the anonymous fragments LDA8F, LDA1D, LDA9C, LDA9E (Camargo, Personal Communication).

## 2.3. Molecular data

Genomic DNA was extracted using the Quiagen® DNeasy® 96 Tissue Kit for animal tissues following the protocol provided by the manufacturer. Protocols for PCR and sequencing procedures follow [Morando et al. \(2003, 2004\)](#) for 12S and cyt-b, [Avila et al. \(2004\)](#) for the NPCL, and the touchdown cycle described by [Noonan and Yoder \(2009\)](#), with standard reaction conditions (per sample: 2 µl dNTPs (1.25 mM), 2 µl 5× Taq buffer, 1 µl each primer (10 µM), 1 µl MgCl (25 mM), and 0.1 µl Taq DNA polymerase (5 U/µl; Promega Corp., Madison, WI); 14 µl total reaction volume) for the ANL genes. All sequences (ANL, NPCL and mitochondrial) were edited and aligned using the program Sequencher v4.8. (™Gene Codes Corporation Inc., 2007) and checked by eye to maximize blocks of sequence identity, except for the mitochondrial fragment 12S, for which we used Clustal X ([Higgins and Sharp, 1988, 1989](#); [Thompson et al., 1997](#)) for alignment. We identified some indels in the following loci: LDA1D: three indels (three, four and five bp); LDA8F: six indels (three, four, five, eight, 13, and 51 bp); LDA9C: three indels (12, 14, and 16 bp); and LDA9E: three indels of one bp plus two larger indels (two and 80 bp). The 12S

fragment included only small indels; nine single and one two bp in length. We confirmed open reading frame in all protein-coding genes by translation into amino acids. Missing data in all cases were coded as "?", and sequences are deposited in GenBank (Accession Nos. JF272765–JF273049). For each gene we selected the best-fitting model using JModelTest v0.1.1 (Guindon and Gascuel, 2003; Posada, 2008) using the corrected Akaike information criterion (Table 1). In all nuclear genes, recombination was tested and excluded using RDP: Recombination Detection Program v3.44 (Heath et al., 2006; Martin and Rybicki, 2000).

#### 2.4. Gene partitions and data congruence

To accommodate the possibility of third-base saturation, we split the cyt-b data into two partitions; the (a) 1st + 2nd positions and (b) the 3rd position, and then used JModeltest v0.1.1 (Guindon and Gascuel, 2003; Posada, 2008) to select the appropriate model of evolution for each partition. Similar models were selected for both partitions (TPM2uf + G and TIM2 + I + G for a and b, respectively), and we estimated Bayesian trees for both using the same search parameters as used for mtDNA analyses (below). Topologies were concordant, but with different levels of resolution, suggesting that the third base does not present a saturation problem. We therefore considered the addition of more parameters unnecessary and did not further partition the cyt-b data set. When deciding whether combining gene partitions prior to phylogenetic analyses is valid, it is important for investigators to use an objective test. Several studies have shown that the incongruence length difference test (ILD; also the partition homogeneity test in PAUP\*) may be biased as a test of congruence between gene partitions (Barker and Lutzoni, 2002; Cunningham, 1997; Yoder et al., 2001). Therefore, we assessed levels of incongruence among gene partitions using a method similar to Westneat and Alfaro (2005). We calculated MP jackknife, ML bootstrap, and BI posterior probability trees for each gene partition, then compared congruence and incongruence of strongly supported clades across trees. Although some partitions showed only weak resolving power, there was no conflict among partitions; all well-supported clades were similar across all trees, so we combined all data partitions in subsequent analyses.

#### 2.5. Phylogenetic analyses

Phylogenetic relationships were inferred from concatenated sequences using MP, ML, and BI methods. Parsimony analyses were

conducted using TNT (Goloboff et al., 2003), based on a traditional search re-sampling the matrix with jackknife (36 removal probability) and with 1000 replicates for single-genes, and with 10,000 replicates for the concatenated matrixes. Likelihood analyses for individual loci were conducted using RAxML v7.0.4 (Stamatakis, 2006), based on 1000 rapid bootstrap analyses for the best ML tree. For concatenated analyses we used PAUP v4.0b4b (Swofford, 2001) to run 10,000 bootstrap pseudoreplicates (Felsenstein, 1985), with strong nodal support being inferred for bootstrap values  $\geq 70$  (Hillis and Bull, 1993; with caveats).

Separate Bayesian analyses were conducted for each gene and for the partitioned concatenated matrix (using partitions previously identified for each gene) using MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003). Each analysis used four heated Markov chains (using default heating values) run for 5 million generations for individual genes, and 50 million generations for the partitioned concatenated analyses, with Markov chains sampled at intervals of 1000 generations. The equilibrium samples (after 25% of burn-in) were used to generate a 50% majority-rule consensus tree, and posterior probabilities ( $Pp$ ) were considered significant when  $\geq 0.95$  (Huelsenbeck and Ronquist, 2001).

To reconstruct a species tree incorporating the multispecies coalescent approach, we used the hierarchical Bayesian model implemented in BEST v2.2 (Edwards et al., 2007; Liu and Pearl, 2007; Liu et al., 2008). Two separate analyses were run for 70 million generations (sampling every 1000 generations). The gene mutation prior was set to 0.2 and 1.8 (Castillo-Ramírez et al., 2010). The prior distribution for the effective population size was modeled using an inverse gamma distribution over a broad range of  $\Theta$  priors, with mean values of  $\Theta = 0.015$ ,  $\Theta = 0.0105$ ,  $\Theta = 0.105$ , and  $\Theta = 0.6$  ( $\beta = 0.03$ ,  $\beta = 0.021$ ,  $\beta = 0.21$ , and  $\beta = 0.12$ , respectively, while holding  $\alpha$  constant at  $\alpha = 3$ ). We excluded the first 50% of trees as burn-in, even though likelihood values appeared to reach stationarity much earlier ( $\sim 5\%$ ). Posterior probability values for species relationships were obtained by summarizing the post-burn-in posterior distribution of species trees with a 50% majority-rule consensus tree. As above, we considered clades with  $Pp > 0.95$  to be strongly supported; however, we are aware that the relationship between  $Pp$  from BEST and the probability of a species tree clade being correctly reconstructed remains under-explored (Wiens et al., 2009).

To ensure that convergence was reached before default program burn-in values, we evaluated convergence of Bayesian MCMC phylogenetic analyses (MrBayes and BEST) by examining likelihood and parameter estimates over time in Tracer v1.5.0 (Rambaut

**Table 1**

Nucleotide substitution models selected (out of 88 candidate models) for all the genes/partitions with the corrected Akaike information criterion. Parsimony-informative-characters (P-I-C) and Parsimony-non-informative-characters (P-N-I-C) for ingroup species are shown, with outgroups used for the phylogenetic inference of each gene/partition.

Gene/partition	Length (bp)	Evolution model	Nst-rates	P-I-C	P-N-I-C	Nature	Outgroup
LDA8F	673	TPM1uf + G	6 – Gamma	26	31	Nuclear non-coding	<i>L. boulengeri</i>
LDA1D	749	HKY + G	2 – Gamma	16	22	Nuclear non-coding	<i>L. boulengeri</i>
LDA9C	706	TPM3uf + G	6 – Gamma	30	26	Nuclear non-coding	<i>L. petrophilus</i>
LDA9E	676	TPM2uf + G	6 – Gamma	27	14	Nuclear non-coding	<i>L. petrophilus</i>
ACM4tg	431	TIM2 + G	6 – Gamma	8	5	Nuclear	<i>Phymaturus</i>
Cmos	480	TPM2 + I	6 – Equal	8	2	Nuclear	<i>Phymaturus</i>
PRLR	465	HKY + I	2 – Equal	7	8	Nuclear	<i>Phymaturus</i>
Cyt-B	804	TrN + I + G	6 – Gamma	191	56	Mitochondrial	<i>Phymaturus</i>
1 + 2 Position	536	TPM2uf + G	6 – Gamma	32	15	Mitochondrial	<i>Phymaturus</i>
3 Position	268	TIM2 + I + G	6 – Gamma	159	41	Mitochondrial	<i>Phymaturus</i>
12S	881	TIM3 + I + G	6 – Gamma	100	32	Mitochondrial	<i>Phymaturus</i>
Mitochondrials	1685	GTR + I + G	6 – Gamma	291	88	Cyt-B + 12S	<i>Phymaturus</i>
Nuclear non-coding	2804	TPM3uf + G	6 – Gamma	99	93	LDA8F + LDA1D + LDA9C + LDA9E	<i>L. petrophilus</i>
Nuclear coding	1376	TrN + I + G	6 – Gamma	31	15	ACM4tg + Cmos + PRLR	<i>Phymaturus</i>
Nuclears	4180	TIM3 + I + G	6 – Gamma	130	108	Nuclear coding + non-coding	<i>Phymaturus</i>
All	5865	GTR + I + G	6 – Gamma	421	196	Nuclear + mitochondrial + coding	<i>Phymaturus</i>

and Drummond, 2009). All parameters had effective sample sizes (ESS) greater than 200, and most were greater than 300 upwards to over 15,000; thus, most runs had at least several hundred independent samples from the MCMC chains, a good indication that the analyses adequately sampled the posterior distributions.

## 2.6. Comparisons

To evaluate between-method differences in our results, we compared gene trees recovered by the three concatenation approaches (MP, BI, ML) and did the same for topologies for the mtDNA locus, combined nuclear loci, and the combined mtDNA plus nucDNA data sets. We compared topologies recovered from analyses based on the concatenated matrix for all genes with those recovered with BEST. Lastly, we discuss our results in the context of earlier non-phylogenetic morphological hypotheses and the limited molecular phylogenetic hypotheses available for the *L. lineomaculatus* section.

## 2.7. Divergence time analysis

We provide a “first pass” temporal calibration by estimating divergence times between the main clades of *L. lineomaculatus* section and between *Liolaemus* (*sensu stricto*) and *Eulaemus*. We performed a Likelihood ratio test (LRT) using jModeltest v0.1.1 (Guindon and Gascuel, 2003; Posada, 2008) to test for deviation from a strict molecular clock, and then applied a “standard” 2% sequence divergence per million years with a standard deviation of 0.14 to our cyt-b matrix. Because the cyt-b data do not conform to the strict molecular clock (LRT = 1335.463051,  $P < 0.01$ ), we used BEAST v1.6.1 with a relaxed uncorrelated lognormal clock model (Drummond and Rambaut, 2007). Two independent analyses were performed for 75 million generations and sampled every 1000 generations, with a GTR model of nucleotide substitution with gamma distributed rate variation among sites (determined from jModeltest, Posada, 2008), and assuming a Yule tree prior. The ESS for parameter estimates and convergence were checked using Tracer v1.5 (Rambaut and Drummond, 2009). We excluded the first 10% of trees as burn-in and almost all parameters had ESS greater than 500 (except for “prior” that was 198.828). The value of dating the splits in main clades of this complex allows us to hypothesize possible scenarios under which lineages have diverged; however, we do recognize the limitations of our approach (Graur and Martin, 2004), and interpret our results cautiously (Hillis et al., 1996).

## 3. Results

### 3.1. Lineages recovered

We recovered phylogenetic hypotheses that were highly concordant across methods implemented in this study. In all single-gene and concatenated analyses, results obtained with different methods (MP, ML, BI) were topologically very similar, and none recovered any strongly supported conflicting nodes. In almost all cases MP topologies were less resolved than model-based methods (BI and ML), while the performance between the last two was similar.

Concatenation algorithms provide a generally well-resolved picture of higher-level relationships in the *L. lineomaculatus* section (Fig. 2). Four main clades are recovered in a pectinate topology with strong support in almost all cases ( $Pp = 1$ , MP jackknife and ML bootstrap >95%): (1) the *lineomaculatus* group, including four described species plus two candidate species, recovered as the sister clade of the rest of the species; (2) the *magellanicus* group (*L. magellanicus* + *L. sp. 3*); (3) the *somuncurae* group, defined here

as (*L. somuncurae* + *L. uptoni*); and (4) the *kingii* + *archeforus* group, including all remaining species plus five candidate species. No support was found for the hypothesized (from morphological data) *kingii* and *archeforus* groups as two different clades (Fig. 2).

Based on combined nuclear and mitochondrial markers, we recovered the *lineomaculatus* group as sister clade of ((*magellanicus*) (*somuncurae* (*kingii* + *archeforus*))) (Fig. 2). The trees recovered with mtDNA vs. nuDNA were congruent (not shown) with three exceptions: (1) within the *lineomaculatus* group the mtDNA tree recovered a clade ((*L. lineomaculatus* + *L. sp. 1*) + *L. sp. 2*) which was contradicted in the nuDNA tree (the topology is the same as in Fig. 2b); (2) *L. sarmientoi*, in the mtDNA tree is recovered within the (*L. kingii* + *L. sp. 7* + *L. sp. 6*) clade, while in the nuDNA tree it is recovered in the (*L. escarchadosi* + *L. tari*) clade; and (3) *L. sp. 4*, in the mtDNA tree the species is recovered within the *somuncurae* group, while in the nuDNA tree it is recovered in the *kingii* + *archeforus* clade.

### 3.2. Comparisons

At a more inclusive level, the *L. lineomaculatus* section was recovered with strong support for monophyly, and strongly supported as the sister clade to the *montanus* section, corroborating earlier hypotheses that they are part of the *Eulaemus* group.

Trees recovered with different priors using BEST were always congruent. The combined BEST analysis (allDNA\_BEST) was in general concordant with the allDNA\_con topology, but support values were considerably lower (Fig. 2). The only statistically supported incongruence between these analyses was the relationship of *L. sp. 4* which was recovered as the sister group to the (*L. somuncurae* + *L. uptoni*) clade in all concatenated analyses, but was nested in the (*kingii* + *archeforus*) clade in the BEST analyses. We are not confident in resolving this relationship in favor of the coalescent vs. concatenated analyses, so we consider the phylogenetic position of this species in need of further study.

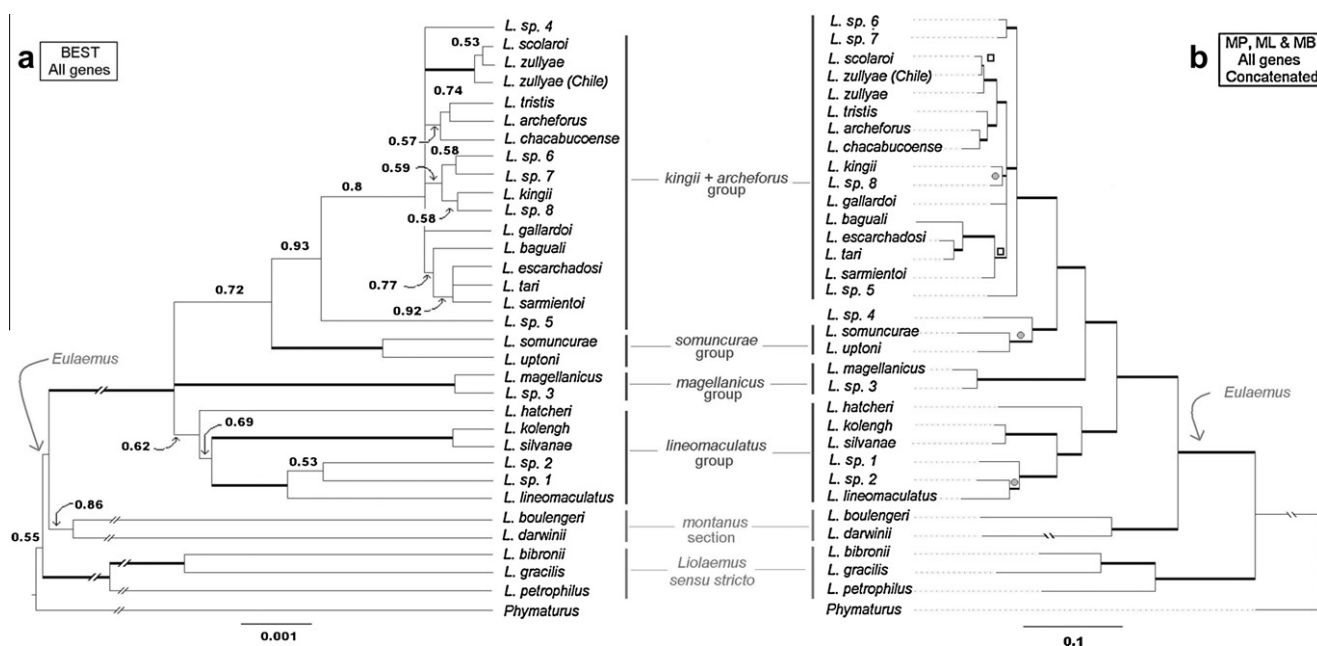
### 3.3. Divergence time estimation

The divergence time estimation between *Liolaemus* (*sensu stricto*) and *Eulaemus* was 18.50 million years ago (Mya) (95% HPD = 13.50 – 23.82) during the Early Miocene, right after the uplift of the southern Andes (~23 Mya; Ramos, 1989) started. Estimated divergence between the *lineomaculatus* and *montanus* sections puts this split in the Middle Miocene (~14.36 Mya; 95% HPD = 10.25 – 18.64), and the split between *lineomaculatus* group and the (*magellanicus* (*somuncurae* (*kingii* – *archeforus*))) clade at the Late Miocene (~8.46 Mya; 95% HPD = 6.26 – 10.84). Divergence between the *magellanicus* and (*somuncurae* (*kingii* + *archeforus*)) clades is estimated at Late Miocene/Early Pliocene (~5.87 Mya; 95% HPD = 4.26 – 7.62); while divergence between *somuncurae* and (*kingii* + *archeforus*) groups is estimated at the Early Pliocene (~4.25 Mya; 95% HPD = 3.17 – 5.48). Divergence times between taxa from the *kingii* + *archeforus* group are estimated for Late Pliocene and during the Pleistocene between 2.2 and 0.0199 Mya with a 95% HPD of (1.57 – 2.85) and (0.00 – 0.056), respectively.

## 4. Discussion

### 4.1. Relationships of the *L. lineomaculatus* section

Based on analyses of representatives from described and candidate species of the *L. lineomaculatus* section sequenced for nine loci, and tested with several other congeneric species representing a diversity of other clades of *Liolaemus*, we found strong support for



**Fig. 2.** On the left (a) consensus tree from BEST, all genes analyses. Posterior probability values higher than 0.5 are shown, bold branches show clades with  $Pp > 0.95$ . On the right (b) Bayesian tree, representing concatenated analyses and summarizing information from MP and ML methods. Nodes with high support from three methods (MP jackknife and ML bootstrap  $> 0.70$ ;  $Pp > 0.95$ ) are identified by bold branches; open squares show nodes with weak MP support, and open circles nodes with weak MP and ML support.

monophyly of the group (Fig. 2). We recovered the *L. lineomaculatus* section as the sister clade to the *montanus* section, with an estimated Middle Miocene divergence, and included within the *Eulaemus* clade, a relationship congruent with previous molecular phylogenetic studies. For example, the mtDNA study of Schulte et al. (2000), based on 57 *Liolaemus* species including three representatives of the *L. lineomaculatus* section, also recovered the *L. lineomaculatus* section as part of the *Eulaemus* clade. Moreover, this same sister-group relationship between the *L. lineomaculatus* section and the *montanus* section has been recovered by many recent studies (Avila et al., 2004; Cruz et al., 2005; Espinoza et al., 2004; Morando, 2004; Morando et al., 2003; Schulte et al., 2004). Interestingly, the cold-adapted lizards of the *L. lineomaculatus* section are the southernmost-distributed of the diverse *Eulaemus* clade, which extends north to southern Peru and east to coastal habitats in Brazil. In this context, our study provides a critical first step towards a well-supported multi-locus phylogeny of the more inclusive clade *Eulaemus*, which will provide opportunities to test several thermal-adaptation hypotheses in the future.

Historically, the *L. lineomaculatus* section has been in taxonomic flux. Laurent (1985, and see also Laurent, 1995) proposed the subgenus *Rhytidodeira* Girard (1858; including *L. archeforus*, *L. gallardoii*, *L. kingii*, *L. sarmientoi*, and *L. somuncurae*), and designated *Proctotretus kingii* Bell as the type species of the group despite the fact that Donoso-Barros (1970) had previously designated *L. bibronii* as the type species for *Rhytidodeira*. This taxonomic disagreement led Pincheira-Donoso and Núñez (2005) to consider the use of *Rhytidodeira* inappropriate and to propose a new subgeneric name: *Donosolaemus*, for the same species group (excluding *L. bibronii*). Pincheira-Donoso and Núñez (2005; p. 32) listed six characters to justify recognition of this new subgenus, three of which are based on the absence of characters that are widespread in other *Liolaemus* groups (see Cei, 1993; Etheridge, 1995; Etheridge and Espinoza, 2000), and three others that are present in different *Liolaemus* groups (see Etheridge, 1995; Laurent, 1983). However, we agree with Lobo et al. (2010a) that this

argument is invalid and we discourage the use of this name. Schulte et al. (2000) used the name “*L. lineomaculatus* section,” and Espinoza et al. (2004) referred to the group as the “*lineomaculatus* clade.” Since there is no clear justification for its status as a separate subgenus (Lobo et al., 2010a), we follow Schulte’s nomenclature and call this clade the *L. lineomaculatus* section.

As noted above, very few studies have included even a modest number of species from this section; thus, it is not surprising that relationships within the *L. lineomaculatus* section are poorly known. The first molecular study was based on allozymes and included four species of this section (Young Downey, 1998), and the first DNA-sequence study of Schulte et al. (2000) included only three species. Espinoza et al. (2004) published an ecological study on the origins of herbivory, based on a *Liolaemus* phylogeny generated from a combination of morphological and molecular characters (some characters taken from the literature and new data presented by those authors). Espinoza et al. (2004) included 12 species of the *L. lineomaculatus* section (*L. archeforus*, *L. zullyae*, *L. gallardoii*, *L. sarmientoi*, *L. baguali*, *L. tari*, *L. escarchadosi*, *L. kingii*, *L. magellanicus*, *L. lineomaculatus*, *L. silvanae*, and *L. hatcheri*), which were recovered as the sister clade to the *L. montanus* section. Although there are no support values associated with their tree, the recovered relationships are congruent with those recovered in this work, with the exception of the position of *L. kingii*; Espinoza et al. (2004) recovered this species outside the clade comprising the rest of the (*kingii* + *archeforus*) clade, while we found strong support for its position nested within this clade. We could not find locality data for the *L. kingii* samples used by Espinoza et al. (2004), and given the wide distribution of this taxon and the fact that it is likely a species complex (Breitman et al., unpublished data), it is possible that their sample represents a different species.

We found support with BEST and concatenated analyses for recognition of four major groups within the *L. lineomaculatus* section: (1) the *lineomaculatus* group, including *L. lineomaculatus*, *L. hatcheri*, *L. silvanae* and *L. kolengh*, plus candidate species *L. sp.*

1 and *L. sp. 2* (with a Late Miocene divergence from the rest of the section); (2) the *magellanicus* group including *L. magellanicus* and *L. sp. 3* (Late Miocene/Early Pliocene divergence from the (*somuncurae*, *kingii* + *archeforus*) clade); (3) the *somuncurae* group including *L. somuncurae* and *L. uptoni* (Early Pliocene divergence from *kingii* + *archeforus* group); and (4) the *kingii* + *archeforus* group including *L. baguali*, *L. escarchadosi*, *L. tari*, *L. sarmientoi*, *L. scolaroi*, *L. zullyae*, *L. tristis*, *L. archeforus*, *L. chacabucoense*, *L. kingii*, *L. gallardoii*, plus four candidate species (*L. sp. 5*, *L. sp. 6*, *L. sp. 7* and *L. sp. 8*; divergence times between these species are Late Pliocene and during Pleistocene). Relationships between the *lineomaculatus*, *magellanicus*, and *somuncurae* + (*kingii* + *archeforus*) groups are not resolved by BEST analyses, but with all concatenated analyses we recover a pectinated topology with strong support for the following structure: (*lineomaculatus* group (*magellanicus* group (*somuncurae* group (*kingii* + *archeforus* group)))) (Fig. 2b).

#### 4.2. Discordances between BEST and concatenated trees

The BEST species tree recovers a deep trichotomy between the *lineomaculatus*, *magellanicus* and (*somuncurae* + *kingii* + *archeforus*) clades, which might reflect geographic fragmentation in which three or more lineages differentiated more or less simultaneously from a common ancestor. If this was the most plausible hypothesis, then we should have recovered the same history with the concatenation analyses, but they all recover strongly supported and well-resolved topologies. Moreover, separate mtDNA and nuDNA concatenated analyses recover this same topology; thus, we suggest that our dataset is insufficient for BEST to resolve this trichotomy. Absence of resolution by BEST might be due to an insufficient number of individuals, loci, alleles, base pairs (Brito and Edwards, 2009), and/or locus quality (Knowles, 2009). These limitations may be further compounded by unknown demographic issues including past and/or present gene flow, ancestral population sizes, and branch lengths between nodes (time between speciation events) (Carling and Brumfield, 2007; Castillo-Ramírez et al., 2010; Eckert and Carstens, 2008; Maddison and Knowles, 2006; Camargo et al., 2011).

*Liolaemus sp. 4* was recovered as the sister group to the (*L. somuncurae* + *L. uptoni*) clade in all concatenated analyses, but was nested in the (*kingii* + *archeforus*) clade in the BEST analyses. This incongruence could be an example of fully resolved branching order due to the mtDNA locus over-riding the nuclear signal in the all genes concatenated analyses (because mitochondrial genes should sort to monophyly four times faster than any single nuclear locus, Ballard and Whitlock, 2004). With concatenated nuclear genes only, we recovered with strong support the same results as with all genes with BEST (*L. sp. 4* nested into the *kingii* + *archeforus* clade), while with mitochondrial genes we recovered this species nested into the *somuncurae* group. This observation is consistent with a past hybridization hypothesis with asymmetrical mtDNA gene flow from one of these clades into another (common in animals; Funk and Omland, 2003), but further study is needed to rule out other alternatives, and establish directionality of introgression if this hypothesis is supported. The lower level of resolution in the shallower parts of the phylogenetic trees, particularly with BEST approach, could also simply reflect a lack of information from more recent divergence events without sufficient time for differentiation. Avila et al. (2006) suggested that for the *fitzingerii* clade (included in *Eulaemus*), which has a partially overlapping distribution with the *kingii* + *archeforus* group, glacial advances most probably pushed populations to the east (when the sea level was lower), fostering fragmentation and recent divergence events. A similar history could have affected lineages from this group, with “incipient” species dispersing back to the west during interglacials, and possibly contacting and hybridizing with other “incipient” species.

#### 4.3. The morphological hypothesis

There are three frequently referenced morphological groups within the *L. lineomaculatus* section, including the *lineomaculatus*, *kingii* and *archeforus* groups (Ceí, 1986; Etheridge, 1995); all are recognized on the basis of meristic characters (scale counts) and disjunct geographic distributions. Our study recovered the *lineomaculatus* group, but we do not have support for the “traditional” *kingii* and *archeforus* groups recognized in these earlier studies. Moreover, our evidence places the species distributed on and adjacent to the Somuncurá Plateau into a different lineage (*somuncurae* group) external to the clade comprising the rest of the species of the *kingii* + *archeforus* group. The incorrect assumption of the monophyly of a group will mislead other researchers (behaviorists, ecologists, etc.), but so far only one ecological study has been based on most of the species from the *L. lineomaculatus* section (Espinoza et al., 2004), and it was not based on the “traditional” morphological hypothesis. On the basis of support for the clades recovered in this study, from multiple unlinked gene regions and across different methods and optimality criteria, we suggest that researchers interested in comparative ecological/evolutionary studies in *Eulaemus* adopt the topology presented here as the best-supported working hypothesis.

#### 4.4. Post-hoc biogeographical hypotheses

Although we only used individuals collected from (or near) type localities, our findings indicate that some distributional remarks and post-hoc biogeographical hypotheses are warranted. The *lineomaculatus* group is widely distributed over a large area in Santa Cruz and Chubut Provinces, ranging from the coast west to the Andes and north to central Neuquén Province (Ceí, 1986; Christie, 2002; Ilbargüengoytia et al., 2001; Williams, 1997; Fig. 1). The *lineomaculatus* group was recovered as the sister taxon to a clade comprising the rest of the section, while the next clade (*magellanicus* group) is restricted to the southernmost area of Santa Cruz Province (south of the Rio Chico) and in Tierra del Fuego (Fig. 1). The *somuncurae* group is restricted to the northernmost part of the distribution of this section (mainly on the Somuncurá Plateau; Ceí, 1986), while the sister clade to the *somuncurae* group (the *archeforus* + *kingii* group) is distributed in southern Chubut and Santa Cruz Provinces. The concatenated analyses also provide strong support for one clade (*L. scolaroi*, *L. zullyae*, *L. tristis*, *L. archeforus* and *L. chacabucoense*) confined to a relatively small area between the Buenos Aires–General Carrera and Cochrane–Posada–Pueyrredón Lakes of northwestern Santa Cruz Province (around 46°S). A second clade (*L. tari*, *L. escarchadosi* and *L. baguali*) inhabits plateaus of the upper Santa Cruz River basin, in southwestern Santa Cruz Province (around 50°S; Fig. 1).

Our phylogenetic hypotheses, taken in combination with these distributional patterns and previous hypotheses of ancestral refugia for other Patagonian taxa (see below), allow us to hypothesize that during glacial advances, ancestral populations of the four main clades (*lineomaculatus*, *magellanicus*, *somuncurae* and *kingii* + *archeforus* groups) likely persisted in the north (Somuncurá Plateau) (42°S), south (55°S), east (46–50°S) and west (40°S) of their current distributions. Specifically, we suggest that the *lineomaculatus* clade (*L. sp. 1*, see above) persisted in southwestern Neuquén Province (around 40°S, arrows in Fig. 1), a refugial region proposed for other taxa (Azpilicueta et al., 2009; Cosacov et al., 2010; Marchelli et al., 1998; Marchelli and Gallo, 2004, 2006; Morando et al., 2007; Muellner et al., 2005; Villagran, 1991). For the *magellanicus* clade, we hypothesize a refugium south of the Chafía and Chico Rivers and/or in the southeastern Tierra del Fuego (55°S, arrows in Fig. 1). This is also coincident with a recent study that



identified a phylogeographic break in populations of the plant *Calceolaria polyrhiza* at the Chico River, and the authors hypothesized the presence of a refugium south of this River (Cosacov et al., 2010). Other authors have hypothesized a refugium in south-eastern Tierra del Fuego (55°S) (Coronato et al., 1999; Markgraf, 1983; Markgraf et al., 1995), or a break in populations of rodents at the Strait of Magellan (Lessa et al., 2010). Given these findings, the hypotheses of such a refugium for the *magellanicus* group could be tested by sampling these lizards from Tierra del Fuego.

We suggest that ancestral lineages of the *kingii* + *archeforus* clade could have persisted in refugial areas now under sea level along the eastern margin of Patagonia (arrows in Fig. 1). These refugia have been suggested previously for others organisms (Avila et al., 2006; Cosacov et al., 2010; Huck et al., 2009; Mráz et al., 2007; Pinceel et al., 2005; Ronikier et al., 2008), as reduced ocean volumes during glacial advances (Hulton et al., 2002) shifted the Atlantic Patagonian coastline four degrees to the east (Auer, 1956). This new land may have offered suitable habitats to escape permafrost conditions during glacial times in what is now southern Patagonia (Jakob et al., 2009), especially for species that are today restricted to low-elevation areas on the eastern margin of Patagonia. One paleo-modeling study of niche in *L. petrophilus* identified a Last Glacial Maximum (LGM) refugium on the shallow continental shelf E of Patagonia at latitude 41–43°S (Fontanella et al., 2011). Lastly, for the *somuncurae* clade we hypothesize a refugium on the Somuncurá Plateau (42°S), based on a phylogeographic analysis that found evidence for a North-to-South colonization pattern (Breitman, unpublished data).

Our divergence estimates suggest that speciation events within the *kingii* + *archeforus* clade occurred during the Late Pliocene and during Pleistocene, perhaps during the glacial advances of the Great Patagonian Glaciation (GPG; 1.2–1.0 Mya; Rabassa, 2008). During this largest Patagonian glaciation, ice tongues extended to the Atlantic Ocean in the continental area south of the Gallegos River (southern Santa Cruz Province), for the first time in the Cenozoic (Clapperton, 1993; Rabassa et al., 2000). This event would have had a massive impact on the abundance and distribution of lizards and other terrestrial taxa. However, the divergence events that gave origin to the *lineomaculatus*, *magellanicus*, *somuncurae* and *kingii* + *archeforus* clades, were deeper in the past (Miocene), and we cannot yet compare our divergence estimation times with other studies (see above) because most of these have been focused on Quaternary events and very few have presented molecular-divergence estimates (e.g. Cosacov et al., 2010).

## 5. Future directions

The chronology of southern South American glaciations is one of the best known in the world, due in part to precision dating ( $^{40}\text{Ar}/^{39}\text{Ar}$ ) of volcanic rocks associated with glacial deposits (Rabassa et al., 2005). This record shows that some glacial events were

synchronized with those in the Northern Hemisphere (Heusser and Heusser, 2006), while others were not (Schaefer et al., 2006). The earliest glaciations occurred in the late Miocene/early Pliocene (~7.0–5.0 Mya), followed by at least eight glaciations from Middle- to Late-Pliocene, and then 14–16 further glaciations after the GPG (Rabassa et al., 2005). In the context of this complex but fascinating geological history, lizards of the *L. lineomaculatus* section can provide one model system for testing a number of evolutionary hypotheses. For example, what might have been the locations of glacial refugia for these lizards, and did the multiple post-glacial re-colonizations occur from one or several refugia via one or multiple dispersal events? How well do lizard phylogeographic histories match those of co-distributed populations of small mammals, flowering plants, or other taxa currently under study? Has this clade experienced different speciation rates relative to other co-distributed clades, and how do patterns of species diversification relate to their current distributions and ecology? Molecular, morphological and ecological/geographical data are being used to conduct integrative phylogeographic analyses to delimit species boundaries within this clade (in addition to alpha taxonomic studies and new species descriptions), and to reconstruct a temporal sequence of demographic histories. We present here the first step for this work by delimiting well-supported clades within the *L. lineomaculatus* section and suggesting some possible biogeographic scenarios for future hypothesis testing.

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**Appendix A. Species and individuals used in this study with information on author and year of description. Sampling localities with geographic coordinates are provided; all samples were collected in Argentina except for *L. scolaroi* and *L. zullyae* (both collected in Chile).**

Species	Descriptor (year)	LJAMM – CNP	Locality	South	West
<i>L. archeforus</i>	Donoso-Barros and Cei (1971)	9238, 9240, 9242	Santa Cruz. Dto. Lago Buenos Aires. Puesto Lebrun (ahora Puesto Viejo) 27.3 km W casco Estancia La Vizcaina. Meseta del Lago Buenos Aires	–46.96438	–71.10755
<i>L. baguali</i>	Cei and Scolaro (1983)	9394, 9395	Santa Cruz. Dto. Lago Buenos Aires. Sierra del Bagual, camino 1 km E de Ruta Nacional 40	–49.41025	–71.49952
<i>L. chacabucoense</i>	Núñez and Scolaro (2009)	13,049, 13,048, 13,050	Santa Cruz. Dto. Lago Buenos Aires. Ruta Provincial 41, 35.3 km E Paso Roballos, cerca Rio Correntoso	–47.19705	–71.58583
<i>L. escarchadosi</i>	Scolaro and Cei, 1997	7163	Santa Cruz. Dto. Corpen Aike. Ruta Nacional 288, 1 km E empalme Ruta Nacional 3, 24 km W Puerto Santa Cruz	–50.05427	–68.88588
		9340	Santa Cruz. Dto. Lago Argentino. Ruta Provincial 65, 43.5 km W empalme Ruta Provincial 17, 1 km S Cerro Mank Aike	–49.77133	–70.72997
<i>L. gallardoi</i>	Cei and Scolaro (1982)	9446, 9454	Santa Cruz. Dto. Rio Chico. Estancia Cerro Beltza, 12 km N Ruta Provincial 37	–47.99372	–71.68041
<i>L. hatcheri</i>	Stejneger (1909)	9485, 9489, 9491	Santa Cruz. Dto. Rio Chico. Estancia Cerro Beltza, 12 km N Ruta Provincial 37	–47.99372	–71.68041
<i>L. kingii</i>	Bell (1843)	9776, 10,157	Santa Cruz. Dto. Deseado. 5.5 km N Puerto Deseado Santa Cruz. Dto. Deseado. Ruta Provincial 16, 42.1 km N Las Heras, 2 km W Estancia Sarai	–47.71497 –46.20961	–65.83919 –68.78733
<i>L. kolengh</i>	Abdala and Lobo (2006)	7300	Santa Cruz. Dto. Lago Argentino. Camino a Los Antiguos, 15.6 a 21 km N paso Roballos	–47.02105	–71.80883
<i>L. lineomaculatus</i>	Boulenger (1885)	7470, 7471	Santa Cruz. Dto. Deseado. 5.5 km N Puerto Deseado por camino costero	–47.71697	–65.84108
<i>L. magellanicus</i>	Hombron and Jacquinot (1847)	6722	Santa Cruz. Dto. Guer Aike. Reserva Provincial Cabo Vírgenes, 3 km S Faro.	–52.35258	–68.38808
<i>L. sarmientoi</i>	Donoso-Barros (1973)	7204, 7206	Santa Cruz. Dto. Guer Aike. Laguna Azul, Reserva Geológica Provincial Laguna Azul, cerca de estancia Monte Aymond	–52.07472	–69.58127
<i>L. scolaroi</i>	Pincheira-Donoso and Núñez (2005)	13,033, 13,034	XI Region de Aysen, Chile Chico. Camino a Reserva Jeinimeni, 49 km SW empalme camino Los Antiguos – Chile Chico, 4 km NE entrada a Reserva Jeinimeni, 1 km NE Rio Jeinimeni	–46.81286	–71.97822
<i>L. silvanae</i>	Donoso-Barros and Cei (1971)	9221	Santa Cruz. Dto. Lago Argentino. Puesto Lebrun (ahora Puesto Viejo) 27.3 km W casco Estancia La Vizcaina. Meseta del Lago Buenos Aires	–46.96438	–71.10755
<i>L. somuncurae</i>	Cei and Scolaro (1981)	6911, 6914	Río Negro. Dto. 9 de Julio. 65.6 km destacamento policial El Rincon, cerca de cerro Corona, entre cerro Corona Grande y cerro Corona Chico	–41.39466	–66.95925
<i>L. tari</i>	Scolaro and Cei (1997)	9407	Santa Cruz. Dto. Lago Argentino. Meseta basáltica Punta del Lago, camino a Meseta Campo las Piedras, 7 km N Estancia Punta del Lago	–49.56972	–72.04775
<i>L. tristis</i>	Scolaro and Cei (1997)	9618, 9619	Santa Cruz. Dto. Lago Buenos Aires. Ruta Provincial 39, 7.5 km N Estancia La Maria, 16 km S Arroyo Piramides	–46.98261	–69.79991
<i>L. uptoni</i>	Scolaro and Cei (2006)	8426	Chubut. Dto. Gastre. Ruta provincial 4, 58, 3 km W Gan Gan	–42.39180	–68.93331
<i>L. zullyae</i> (LT)	Cei and Scolaro (1996)	7391	Santa Cruz. Dto. Lago Buenos Aires. Camino paso Roballos – Los Antiguos, 49.1 km N puente metálico sobre el Río Ghio	–46.84627	–71.87125
		8894	Chubut. Dto. Senguer. Ruta Nacional 40, 26 km N Alto Río Senguer	–44.80608	–70.70691
<i>L. zullyae</i> (Chile)		13,039, 13,040	XI Region de Aysen, Chile Chico. Camino a Reserva Jeinimeni, 17 km NE entrada a Reserva Jeinimeni	–46.77986	–71.80261

## Appendix A (continued)

Species	Descriptor (year)	LJAMM – CNP	Locality	South	West
<i>L. sp. 1</i>		9258	Santa Cruz. Dto. Lago Buenos Aires. Laguna de los Gendarmes, Ruta Provincial 45, camino a El Portezuelo, 87.6 km NW Perito Moreno	–46.09952	–71.68269
		9678	Chubut. Dto. Escalante. Ruta Provincial 37, 2.5 km W empalme Ruta Nacional 3	–45.62872	–67.68433
<i>L. sp. 2</i>		9275, 9277	Santa Cruz. Dto. Lago Buenos Aires. Meseta Lago Buenos Aires, 18.7 SW Puesto Lebrun	–47.09138	–71.02025
		9542	Santa Cruz. Dto. Lago Buenos Aires. Camino vecinal a Estancia La Morocha, 5.1 km NW ex Hotel Dos Manantiales, NW Ruta Provincial 12	–48.25236	–69.78072
<i>L. sp. 3</i>		9388	Santa Cruz. Dto. Lago Argentino. Meseta basáltica Punta del Lago, camino a Meseta Campo las Piedras, 7 km N Estancia Punta del Lago	–49.56972	–72.04775
<i>L. sp. 4</i>		9183	Chubut. Dto. Languineo. Ruta Nacional 40, 16.1 km S Tecka	–43.62991	–70.84088
<i>L. sp. 5</i>		9202	Chubut. Dto. Escalante. Ruta Nacional 3, 70.2 km SW Garayalde	–43.62991	–70.84088
		9205	Chubut. Dto. Escalante. Estación Holdich (abandonada)	–45.96663	–68.19958
<i>L. sp. 6</i>		13,053, 13,055	Santa Cruz. Dto. Lago Buenos Aires. Ruta Nacional 40, 39.7 km N empalme Ruta Provincial 43, Cordon El Pluma	–46.18225	–70.66791
<i>L. sp. 7</i>		9814, 9815, 9999	Santa Cruz. Dto. Magallanes. Ruta Provincial 77, 77.7 km NW empalme Ruta Provincial 25, 2 km N Estancia Vega Grande	–48.40952	–68.93452
<i>L. sp. 8</i>		8898	Chubut. Dto. Paso de Indios. Ruta Provincial 23, 65.1 km E empalme Ruta Provincial 20, camino a Estancia Los Flamencos	–44.59741	–69.69058
		9190	Chubut. Dto. Paso de Indios. Ruta Provincial 23, 77.6 km E empalme Ruta Provincial 20, 1 km SE Estancia Los Flamencos	–44.66616	–69.6062
<i>L. boulengeri</i>		10,177, 10,178	Santa Cruz. Dto. Deseado. Ruta Provincial 16, 42.1 km N Las Heras, 2 km W Estancia Sarai	–46.20961	–68.78733
		3610	Santa Cruz. Dto. Cushamen. Ruta Provincial 12 y embarcadero La Cancha	–42.79661	–70.95838
<i>L. darwinii</i>		10,392, 10,391	Río Negro. Dto. San Antonio. Gran Bajo del Gualicho. 42, 4 km NW San Antonio Oeste, por Ruta Provincial 2	–40.34883	–65.04983
<i>L. bibronii</i>		9896	Santa Cruz. Dto. Deseado. 5.5 km N Puerto Deseado	–47.71497	–65.83919
		9897, 9898	Santa Cruz. Dto. Deseado. Ruta Provincial 47, 55.4 km SW Tellier, 3 km S puente sobre Río Deseado, en empalme Ruta Provincial 89	–47.85033	–66.62216
<i>L. gracilis</i>		10,517	La Pampa. Dto. Puelén. Ruta Provincial 16, 23, 6 km W empalme Ruta Nacional 151	–37.07494	–67.78544
<i>L. petrophilus</i>		11,121	Río Negro. Dto. 9 de Julio. Ruta Provincial 8, 34, 8 km S Los Menucos (camino a Prahuaníyeyu)	–41.08775	–67.89072
<i>P. dorsimaculatus</i>		983, 982	Neuquén. Dto. Ñorquín. Copahue	–37.82055	–71.0866
<i>P. patagonicus</i>		3205	Chubut. Dto. Gaiman. Ruta Nacional 25, 40 km WSW Dolavon	–43.45438	–66.12119

**Appendix B. Voucher individuals from LJAMM – CNP collection used for sequencing each gene. Missing data is shown with boldface questions marks.**

Species	12S	LDA8F	ACM4tg	Cmos	Cyt-b	LDA1D	LDA9C	LDA9E	PRLR
<i>L. archeforus</i>	9240	9240	9240	9240	9240	9238	9240	9242	9240
<i>L. baguali</i>	9395	9395	9395	9395	9394	9395	9395	9395	9395
<i>L. chacabucoense</i>	13,049	13,049	13,048	13,050	13,049	13,049	13,049	13,049	13,049
<i>L. escarchadosi</i>	9340	9340	9340	9340	9340	9340	9340	7163	9340
<i>L. gallardoi</i>	9446	9446	9446	9454	9446	9446	9446	9454	9446
<i>L. hatcheri</i>	9491	9491	9491	9489	9491	9491	9491	9485	9491
<i>L. kingii</i>	9776	9776	9776	9776	9776	9776	9776	10,157	9776
<i>L. kolengh</i>	7300	7300	7300	7300	7300	7300	7300	7300	7300
<i>L. lineomaculatus</i>	7470	7471	7470	7470	7470	7470	7470	7470	7470
<i>L. magellanicus</i>	6722	6722	6722	6722	6722	6722	6722	6722	6722
<i>L. sarmientoi</i>	7206	7206	7204	7206	7206	7206	7204	7206	7206
<i>L. scolaroi</i>	13,034	13,034	13,034	13,034	13,033	13,033	13,033	13,034	13,033
<i>L. silvanae</i>	9221	9221	9221	9221	9221	9221	9221	9221	9221
<i>L. somuncurae</i>	6914	6914	6914	6914	6914	6914	6911	6911	6914
<i>L. tari</i>	9407	9407	9407	9407	9407	9407	9407	9407	9407
<i>L. tristis</i>	9618	9618	9618	9619	9618	9618	9618	9618	9618
<i>L. uptoni</i>	8426	8426	8426	8426	8426	8426	8426	8426	8426
<i>L. zullyae</i>	7391	7391	8894	7391	7391	7391	7391	7391	7391
<i>L. zullyae</i> (Chile)	13,039	13,039	13,039	13,039	13,039	13,040	13,039	13,039	13,039
<i>L. sp. 1</i>	9678	9678	9678	9678	9678	9678	9678	9258	9678
<i>L. sp. 2</i>	9277	9277	9277	9277	9277	9277	9275	9542	9277
<i>L. sp. 3</i>	9388	9388	9388	9388	9388	9388	9388	9388	9388
<i>L. sp. 4</i>	9183	9183	9183	9183	9183	9183	9183	9183	9183
<i>L. sp. 5</i>	9202	9202	9202	9205	9202	9202	9202	9202	9202
<i>L. sp. 6</i>	13,053	13,053	13,053	13,055	13,053	13,053	13,053	13,053	13,053
<i>L. sp. 7</i>	9814	9814	9814	9815	9814	9999	9814	9814	9814
<i>L. sp. 8</i>	9190	9190	9190	8898	9190	9190	9190	9190	9190
<i>L. darwinii</i>	10,392	10,391	10,391	10,392	10,391	10,391	10,392	10,391	10,391
<i>L. boulengeri</i>	10,177	10,178	10,177	10,177	3610	10,177	10,177	10,177	3610
<i>L. bibronii</i>	9897	????	9896	9896	9897	????	9896	9898	9896
<i>L. gracilis</i>	10,517	????	10,517	10,517	10,517	????	????	10,517	10,517
<i>L. petrophilus</i>	11,121	????	11,121	11,121	11,121	????	11,121	11,121	????
<i>P. patagonicus</i> (3205) and <i>P. dorsimaculatus</i> (982/3).	983	????	982	3205	983	????	????	????	983

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## New species of lizard from the *magellanicus* clade of the *Liolaemus lineomaculatus* section (Squamata: Iguania: Liolaemidae) from southern Patagonia

MARIA FLORENCIA BREITMAN<sup>1</sup>, CRISTIAN HERNÁN FULVIO PÉREZ<sup>1</sup>, MICAELA PARRA<sup>2</sup>,  
MARIANA MORANDO<sup>1</sup>, JACK WALTER SITES, JR.<sup>3</sup> & LUCIANO JAVIER AVILA<sup>1</sup>

<sup>1</sup>Centro Nacional Patagónico – Consejo Nacional de Investigaciones Científicas y Técnicas, Boulevard Almirante Brown 2915, ZC: U9120ACD, Puerto Madryn, Chubut, Argentina. Tel: 0054 – 02965 – 451024.

E-mail: liolaemu@criba.edu.ar; morando@cenpat.edu.ar; avila@cenpat.edu.ar

<sup>2</sup>Universidad Nacional de la Patagonia San Juan Bosco, Boulevard Almirante Brown 3150, ZC: U9120ACX, Puerto Madryn, Chubut, Argentina. Tel: 0054 – 02965 – 472885. E-mail: mica\_fop@hotmail.com

<sup>3</sup>Department of Biology and Monte L. Bean Life Science Museum, Brigham Young University, 401 WIDB, Provo, UT 84602, USA. E-mail: jack\_sites@byu.edu

<sup>4</sup>Corresponding author. E-mail: breitman@cenpat.edu.ar

### Abstract

A new species of the *Liolaemus lineomaculatus* section is described from southwestern Santa Cruz Province, Argentina. The new species is a member of the monotypic *magellanicus* clade; morphological, molecular and geographical data are sufficient to diagnose this new species as distinct form from *L. magellanicus*. The new species differs from *L. magellanicus* in having higher number of midbody, dorsal and ventral scales, and higher number of infradigital third finger and fourth toe lamellae. The new species also differs in having smaller dorsal blotches on the hindlimbs and a more clearly defined vertebral line, fewer preloacal pores and reduced dorsal scale mucronation, compared to *L. magellanicus*. *Liolaemus caparensis* **sp. nov.** is the second species described for the *magellanicus* group, and is geographically isolated from *L. magellanicus* on the Campo Las Piedras Plateau, where it is sympatric with other endemic species of the *L. lineomaculatus* section.

**Key words:** Iguania, Liolaemidae, *Liolaemus lineomaculatus* section, *L. caparensis* **sp. nov.**, Patagonia, new species

### Resumen

Se describe una nueva especie de la sección *Liolaemus lineomaculatus* del suroeste de la provincia de Santa Cruz. La nueva especie pertenece al clado monotípico *magellanicus*. Datos morfológicos, moleculares y geográficos ofrecen evidencia para considerar esta nueva especie diferente a *L. magellanicus*. La nueva especie se diferencia de *L. magellanicus* por tener un mayor número de escamas: alrededor del cuerpo, dorsales y ventrales, así también por poseer un mayor número de lamelas subdigitales en el tercer dedo de la pata delantera y en el cuarto dedo de la pata trasera. La nueva especie también se diferencia de *L. magellanicus* por tener manchas más pequeñas en las patas delanteras y una línea vertebral mejor definida. La nueva especie posee un menor número de poros prelocales respecto de *L. magellanicus*. Las escamas dorsales de la nueva especie son menos mucronadas que las de *L. magellanicus*. *Liolaemus caparensis* **sp. nov.**, es la segunda especie descrita del grupo *magellanicus*, viviendo aislada de *L. magellanicus* en la Meseta Campo Las Piedras, lugar habitado por otra especie endémica de la sección *L. lineomaculatus*.

**Key words:** Iguania, Liolaemidae, Sección *Liolaemus lineomaculatus*, *L. caparensis* **sp. nov.**, Patagonia, nueva especie

### Introduction

*Liolaemus* is one of the most ecologically diverse and species-rich genera of lizards on earth, with more than 230 recognized species (Núñez & Scolaro 2009; Abdala *et al.* 2010; Avila *et al.* 2010a, 2010b; Lobo *et al.* 2010a,

2010b; Martinez *et al.* 2011; Quinteros & Abdala 2011; Breitman *et al. in press*). *Liolaemus* extends from Perú to Tierra del Fuego ( $14^{\circ} \pm 30'$  –  $52^{\circ} \pm 30'S$ ) and ranges in altitude from sea level to almost 5,000 m, thereby inhabiting many climatic regimes (Hellmich 1951; Donoso-Barros 1966; Cei 1986, 1993; Etheridge & de Queiroz 1988; Frost & Etheridge 1989; Etheridge & Espinoza 2000).

The *Liolaemus lineomaculatus* section is part of the subgenus *Eulaemus* and includes 20 formally described species (Breitman *et al.* 2011; Breitman *et al. in press*). This group of species has the most southerly distribution of the genus, which extends from the Andean mountains of central Neuquén to coastal areas of Tierra del Fuego (Bottari 1975; Cei 1986; Christie 2002). Historically the *L. lineomaculatus* section was divided morphologically into three main groups: *lineomaculatus* (Etheridge 1995), *kingii* (Cei 1986) and *archeforus* (Cei 1986); plus the species *L. magellanicus* that was always recognized as part of the section, but not clearly assigned to any of these three main groups.

*Liolaemus magellanicus* was described by Hombron and Jacquinot in 1847 as *Proctotretus magellanicus* (type locality: Havre Pecquet, in the Strait of Magellan, Chile), and is the most southerly distributed species of lizard of the world. In 1858 Girard placed *P. magellanicus* in the new genus *Rhytidodeira* (Girard 1858) and since then, multiple taxonomic changes have been made. In 1979, Cei proposed the “*L. magellanicus-lineomaculatus* complex”, and later morphological characters supported placement of the species in an ancestral line of *Liolaemus* called “fueguiano (*magellanicus-lineomaculatus*)” (Laurent 1983). Two years later Laurent (1985) formally proposed the *magellanicus* group, but with species relationships that today are not considered valid (Etheridge 1995, Schulte *et al.* 2000). Cei (1986) proposed the morphological “*kingii*”, “*archeforus*” and “*magellanicus*” groups; the *magellanicus* group included the species *L. magellanicus*, *L. lineomaculatus* and the genus *Vilcunia* (Donoso-Barros & Cei 1971, which included *L. silvanae* and *L. hatcheri*). Cei (1986) did suggest that *L. lineomaculatus* probably comprised a different group and later Laurent (1995) formally removed *L. lineomaculatus* from the genus *Vilcunia* on the basis of its geographical distribution and several morphological characters. Laurent (1995) erected the monotypic subgenus *Austrolaemus* for *L. magellanicus*, but later studies considered *Austrolaemus* as a synonym of *Liolaemus* (e.g., Etheridge & Espinoza 2000; Pincheira-Donoso & Nuñez 2005; Pincheira-Donoso *et al.* 2008a) and returned to the idea of the “*magellanicus* group” as a separate lineage from the “*lineomaculatus* group”. However, all these authors recognized the need for further study of relationships among these groups.

The first phylogenetic study of the *Liolaemus lineomaculatus* section, employing morphological and genetic markers, showed that *L. magellanicus* was the sister species of the *kingii* and *archeforus* groups and a different lineage from the *lineomaculatus* group; although, they did not show nodal-support values (Espinoza *et al.* 2004). New evidence based on nine molecular markers (mitochondrial: *cyt-b* and 12S; and nuclear: *Cmos*, *ACM4tg*, *PRLR*, *LDA8F*, *LDA1D*, *LDA9C* and *LDA9D*; 5865 bp of total alignment length) and phylogenetic inference from concatenation and species-tree methods (Breitman *et al.* 2011) identified four main clades within the *L. lineomaculatus* section: (1) the *lineomaculatus* group (*L. hatcheri*, *L. kolengh*, *L. silvanae*, *L. lineomaculatus*); (2) the monotypic *magellanicus* group; (3) the *somuncurae* group (*L. somuncurae* and *L. uptoni*); and (4) the *kingii+archeforus* group (*L. baguali*, *L. escarchadosi*, *L. tari*, *L. sarmientoi*, *L. scolaroi*, *L. zullyae*, *L. tristis*, *L. archeforus*, *L. chacabucoense*, *L. kingii* and *L. gallardoi*); (Figure 1). The four clades recovered from the molecular work support the “traditional morphological” *lineomaculatus* group, but do not support the *kingii* and *archeforus* groups as separate clades; moreover the authors proposed two different clades: the *L. somuncurae* and the *L. magellanicus* groups. Breitman *et al.* (2011) also identified eight candidate species spread through the four main clades including the *magellanicus* group (*L. magellanicus* and another terminal identified as *Liolaemus sp.* 3) and particularly from the *lineomaculatus* group the species referred as *L. sp. 1* and *L. sp. 2* are under description (Breitman *et al. in press*).

The *magellanicus* group presents the southernmost distribution of *Liolaemus*, extending across the Strait of Magellan to Tierra del Fuego island. This group has attracted scientific attention due to its ability to live in extremely harsh environments (Jacksic & Schwenk 1983; Pincheira-Donoso *et al.* 2008b; Ibarguengoytía *et al.* 2010; Fernández *et al.* 2011). Here, we use an integrative approach based on color pattern, morphometric, meristic, molecular and qualitative characters to describe a new species belonging to the *magellanicus* group (the *Liolaemus sp.* 3 terminal in Breitman *et al.* 2011).



## Material and methods

We examined series of specimens from the type localities of the following species; *lineomaculatus* group: *L. kolengh* (n = 42), *L. hatcheri* (n = 20), *L. silvanae* (n = 21) and *L. lineomaculatus* (n = 17); *magellanicus* group (n = 29): eleven specimens of the new species and eighteen specimens from *L. magellanicus* (Appendix I); all of these specimens were previously used in Breitman *et al.* (2011). Specimens were collected by hand and sacrificed by pericardial injection of sodium pentothal Abbot®. After a liver sample was extracted for molecular analyses, specimens were fixed in 20% formalin and later transferred to 70% ethanol. Voucher specimens were placed in La Plata Museum, Argentina (MLPS) and in the Herpetological collection LJAMM-CNP of Centro Nacional Patagónico in Puerto Madryn, Argentina, <http://www.cenpat.edu.ar/nuevo/colecciones03.html>. Other material examined (but not included in the analysis) is placed in the following herpetological collections: Jose Miguel Cei - Diagnostic Collection (JMC-DC), University of San Luis, Argentina (JMCDC); Field Museum of Natural History, Chicago, USA (FMNH); University of La Plata, Argentina (MLPS/R); Museum of Vertebrate Zoology, University of California, Berkeley, USA (MVZ); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (MACN) (Appendix I). The general geographic distribution of *L. magellanicus* was obtained from the collections listed above and bibliographic references (Cei 1971; Bottari 1975; Jaksic & Schwenk 1983; Scolaro 1992; Schulte *et al.* 2000).

Because there is strong morphological and molecular evidence (see introduction) to consider the *magellanicus* group as a separate clade, for this description we only performed detailed comparisons among the new species and *Liolaemus magellanicus*. We used 18 morphometric characters and 12 meristic characters (commonly used and defined elsewhere, e.g. Vega *et al.* 2008; Avila *et al.* 2010a, 2010b; Martinez *et al.* 2011; see Appendix II for names and definitions of characters), as well as 94 qualitative characters: 84 on squamation and 10 on body patterns. Measurements were taken only on adults (seventeen of *L. magellanicus* and eight of the new species) with a Schwyz® electronic digital caliper to the nearest 0.1 mm; scale counts were made on juveniles and adults with a stereoscopic microscope from fixed specimens; and qualitative characters were observed and registered only on adults. Scale terminology, measurements, and chromatic states follow Smith (1946), nomenclature for neck folds follows Frost (1992), and coloration in life was observed from pictures taken at the time of capture. Sex was determined by the thickness of the base of the tail and presence of precloacal pores. Where numbers of paired scales are provided, they are given as left-right.

Univariate tests were performed in INFOSTAT® 2009 (Di Rienzo *et al.* 2010). We implemented statistical tests for both morphometric and meristic characters, and compared frequencies of qualitative characters. A Student's T test was used to evaluate the significance of differences of variable means between the new species and *Liolaemus magellanicus*, and assumptions (normality and variance homogeneity) were checked with the Levene and Shapiro-Wilks tests (Montgomery 1991). When the assumptions of Student's T test were not met, we performed a nonparametric Kruskal-Wallis test (Kruskal & Wallis 1952). Sexual dimorphism was tested in for all variables with either Student's T or Kruskal-Wallis test (when same assumptions previously described were not met).

Phylogenetics relationships between all the species plus eight candidate species of the *L. lineomaculatus* section were recovered by Breitman *et al.* (2011) and our methods are briefly described here as follows. Sequence data for seven nuclear genes (Cmos, ACM4tg, PRLR, LDA8F, LDA1D, LDA9C and LDA9E) and two mitochondrial genes (12S and *cyt-b*) were amplified (Saint *et al.* 1998; Wiens *et al.* 1999; Gamble *et al.* 2008; Townsend *et al.* 2008), and then edited and aligned using the programs Sequencher v4.8 (™ Gene Codes Corporation Inc. 2007) and Clustal X (Higgins & Sharp 1988, 1989; Thompson *et al.* 1997). The total length of the nuclear alignment was 4180 bp, while the total length of the nuclear plus the mitochondrial alignment was 5865 bp; sequences are deposited in GenBank (Accession Nos. JF272765 - JF273049). The best-fitting evolutionary model for each gene was selected using JModelTest v0.1.1 (Guindon & Gascuel 2003; Posada 2008); recombination was tested and excluded using RDP: Recombination Detection Program v3.44 (Martin & Rybicki 2000; Heat *et al.* 2006). Bayesian analyses were conducted for the concatenated matrix using MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003) with four chains and run for 50 million generations sampled at intervals of 1,000 generations. The equilibrium samples were used to generate a 50% majority-rule consensus tree (after a 25% burn-in), and posterior probabilities (*Pp*) were considered significant when  $\geq 0.95$  (Huelsenbeck & Ronquist 2001). We assumed convergence because all parameters had effective sample sizes greater than 200, as determined from Tracer v1.5.0 (Rambaut & Drummond 2009).

We used the *cyt-b* fragment from individuals of the new species and *L. magellanicus* collected near the type

locality, to calculate genetic distance between species. Genetic distances between species (corrected pairwise differences = intergroup distance – intragroup distance) was calculated using Arlequin v3.11 (Excoffier *et al.* 2005).

## Results

Morphological tests showed significant differences between the new species and *Liolaemus magellanicus*, which are described in the *Diagnosis* section of the new species. The means, standard deviations and ranks for meristic and qualitative characters are summarized in Tables 1 and 2, and the *p* values of Levene, Shapiro-Wilks and Kruskal-Wallis tests are summarized in Tables 3 and 4. Sexual dimorphism was not found in any of the meristic variables, although some statistical differences in the morphometric variables were found. Variables that present sexual dimorphism are mainly related to head size, for which females were smaller than males (head height: 5.65-6.07, X = 6.16 vs. 6.72-7.77, X = 7.05; *p* = 0.0390, head width: 8.4-9.33, X = 8.8 vs. 9.37-11.07, X = 10.41; *p* = 0.013, head length: 10.43-11.4, X = 10.95 vs. 11.69-13.41, X=12.38; *p* = 0.018, rostral length: 2.26-2.66, X = 2.41 vs. 2.71-2.93, X = 2.83; *p* = 0.088, distance from rostral to eye: 4.38-4.99, X = 4.65 vs. 5.09-5.49, X = 5.23; *p* = 0.016, auditory meatus high: 1.65-2.09, X = 1.82 vs. 1.94-2.24, X = 2.13; *p* = 0.047) and the variable foot length (11.37-13.19, X = 12.52 vs. 14.68-15.3, X = 14.99; *p* = 0.0068) (Table 5). Since these variables did not show statistical differences for discriminating the new species from *L. magellanicus*, and the meristic data set showed strong evidence for discriminating species, we did not perform comparisons between species by separating sexes for these analyses.

The uncorrected genetic distance between the new species and *L. magellanicus* was 2.99%, while the corrected distance was > 2.6%. Figure 1 summarizes phylogenetic relationships among species and distinct lineages within the *L. lineomaculatus* section, using all of the data and the nuclear-only data set, and shows the position of the new species.

**TABLE 1.** Values (in millimeters) of morphometric characters from species of the *magellanicus* group; sample sizes are shown in parentheses, as well as mean ± SD (min–max); abbreviations for characters are defined in Appendix II.

Var	<i>L. caparensis</i> sp. nov. (n=8)	<i>L. magellanicus</i> (n=17)
SVL	51.75±3.92 (47–59)	55.41±5 (49–68)
TL	67.71±8.01 (60–84)	63.58±7.28 (51–77)
DFH	24.23±1.43 (21.2–25.9)	25.96±3.52 (22.1–36.2)
FOL	13.23±1.35 (11.37–15.3)	13.91±0.72 (12.85–15.1)
TFL	7.24±0.77 (6.19–8.62)	9.09±0.91 (6.91–10.76)
EWL	5.24±0.4 (4.58–5.66)	5.98±0.52 (5.22–6.88)
HAL	7.92±0.72 (7.08–8.91)	8.24±0.57 (7.25–9.19)
HH	6.5±0.63 (5.65–7.7)	6.92±0.65 (5.53–7.89)
HW	9.41±1.02 (8.4–11.07)	9.76±0.75 (8.50–11.22)
HL	11.49±0.93 (10.43–13.41)	11.78±0.89 (10.33–13.47)
EH	1.86±0.21 (1.58–2.29)	1.98±0.31 (1.47–2.87)
EL	3.06±0.17 (2.85–3.38)	2.95±0.21 (2.6–3.28)
RND	1.95±0.25 (1.58–2.26)	2.03±0.17 (1.77–2.29)
RH	0.98±0.07 (0.9–1.12)	0.92±0.10 (0.74–1.10)
RL	2.57±0.26 (2.26–2.93)	2.75±0.26 (2.37–3.29)
DRE	4.87±0.38 (4.38–5.49)	4.72±0.32 (4.16–5.3)
AH	1.93±0.23 (1.65–2.24)	1.92±0.18 (1.53–2.3)
AL	1.6±0.19 (1.33–1.88)	1.57±0.20 (1.15–1.91)

**TABLE 2.** Values of meristic variables from species of the *magellanicus* group; sample sizes are shown in parentheses, as well as mean  $\pm$  SD (min–max); abbreviations for characters are defined in Appendix II.

Var	<i>L. caparensis</i> sp. nov. (n=11)	<i>L. magellanicus</i> (n=18)
SCI	6.55 $\pm$ 1.04 (5–8)	6.89 $\pm$ 0.90 (6–9)
LS	4.82 $\pm$ 0.75 (3–6)	4.28 $\pm$ 0.67 (3–5)
SS	6.73 $\pm$ 0.79 (6–8)	6.56 $\pm$ 0.51 (6–7)
IS	4.73 $\pm$ 0.65 (3–5)	4.61 $\pm$ 0.61 (4–6)
MS	43.82 $\pm$ 4.33 (39–55)	40.44 $\pm$ 3.45 (34–48)
DS	41.45 $\pm$ 2.5 (39–47)	37.50 $\pm$ 2.62 (34–45)
VS	68.36 $\pm$ 2.98 (64–73)	59.17 $\pm$ 5.91 (49–77)
IL3	15 $\pm$ 1.18 (14–18)	13.33 $\pm$ 1.08 (11–15)
IL4	20.3 $\pm$ 1.49 (18–23)	18.24 $\pm$ 1.35 (15–20)
Pores	3.67 $\pm$ 0.58 (3–4)	3.91 $\pm$ 0.94 (3–5)

**TABLE 3.** Student's T tests and related tests for means of characters showing significant differences between the two species compared in Table 1; the Shapiro-Wilks and Levene *p*-values are shown when Student's T tests were significant, as described in the text. To assume normality and variance homogeneity Shapiro-Wilks and Levene test should not be rejected ( $p > 0.05$ ).

Var	Student's T test	<i>p</i>	Shapiro-Wilks	Levene
SVL	1.79	0.0866*	0.1869	0.5091
TL	37.37	< 0.0001***	0.4642	0.8976
TFL	4.98	< 0.0001***	0.9724	0.6559
RUL	3.55	0.0017**	0.2495	0.4699

**TABLE 4.** Student's T tests and related tests for means of characters showing significant differences between the two species compared in Table 2; the Shapiro-Wilks and Levene *p*-values are shown when Student's T tests were significant, as described in the text. To assume normality and variance homogeneity Shapiro-Wilks and Levene test should not be rejected ( $p > 0.05$ ). Kruskal Wallis *p* is shown for DS (dorsal scales) variable (assumptions for Student's T test were not met).

Var	Student's T test	<i>p</i>	Shapiro-Wilks	Levene
LS	-2.02	0.0539*	0.1394	0.8026
MS	-2.32	0.0282**	0.0536	0.4175
DS	Kruskal Wallis	0.0003 ***	non-parametric	
VS	-5.55	< 0.0001***	0.5038	0.4339
IL3	-3.88	0.0006***	0.2754	0.7425
IL4	-3.69	0.0011**	0.5513	0.088

***Liolaemus caparensis* sp. nov.**

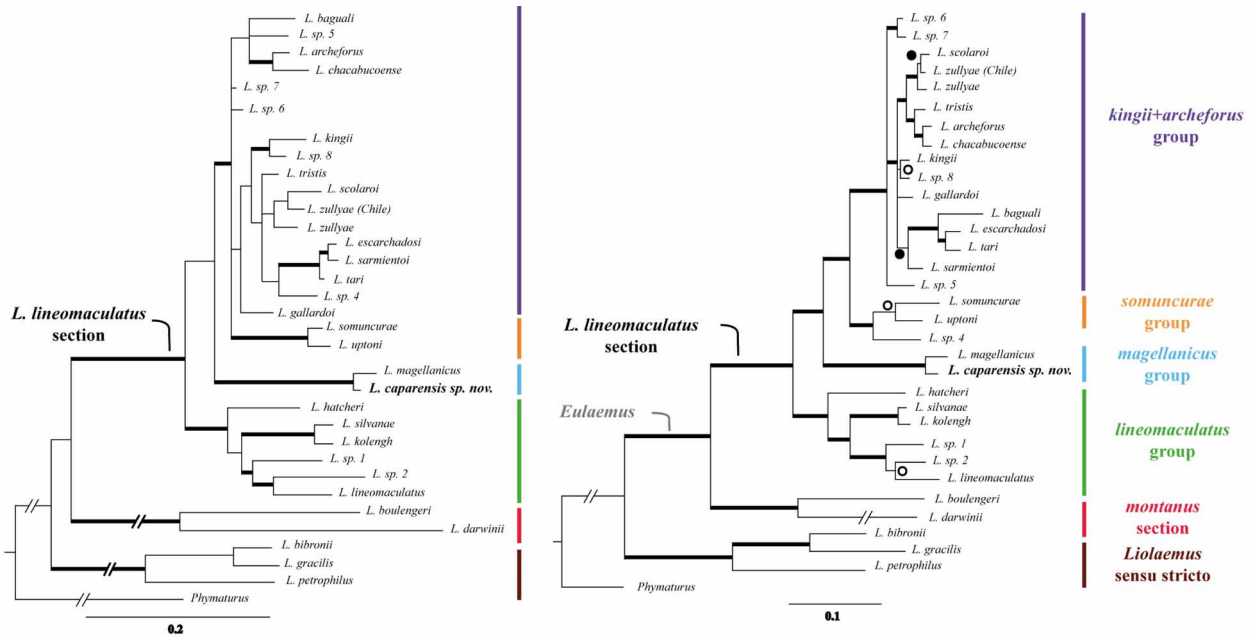
(Figure 2)

**Holotype.** MLPS 2628 (Figure 2), an adult male from Campo Las Piedras plateau, 7 km N Punta del Lago ranch, Lago Argentino department, Santa Cruz province, Argentina (49° 34' 11.0" S, 72° 02' 51.9" W, 868 m; Figures 3, 4), L.J. Avila, C.H.F. Pérez, M.F. Breitman and N. Feltrin collectors, 16<sup>th</sup> January 2008.

**Paratypes.** LJAMM–CNP 9379–9380 adult males, LJAMM–CNP 9383–9387 females and LJAMM–CNP 9382, 9388, 9389 juveniles; from the same locality of holotype, L.J. Avila, C.H.F. Pérez, M.F. Breitman and N. Feltrin collectors, 16<sup>th</sup> January 2008.

**Diagnosis.** *Liolaemus caparensis* sp. nov. is a member of the *magellanicus* group, in the *L. lineomaculatus* section, based on molecular evidence (Figure 1). *Liolaemus caparensis* sp. nov. differs from *L. magellanicus* in the following traits: shorter tibia-fibula length (6.19–8.62, X = 7.24 vs. 6.91–10.76, X = 9.09;  $p < 0.0001$ ), shorter

radius-ulna length (5.24-5.66,  $X = 5.24$  vs. 5.22-6.88,  $X = 5.98$ ;  $p = 0.0017$ ), larger number of midbody scales (39-55,  $X = 43.82$  vs. 34-48,  $X = 40.44$ ;  $p = 0.0282$ ), larger number of dorsal scales (39-47,  $X = 41.45$  vs. 34-45,  $X = 37.5$ ;  $p = 0.0003$ ), more ventral scales (64-73,  $X = 68.36$  vs. 49-77,  $X = 59.17$ ;  $p < 0.0001$ ), more infradigital lamellae of the third finger (14-18,  $X = 15$  vs. 11-15,  $X = 13.33$ ;  $p = 0.0006$ ), and more infradigital lamellae of the fourth toe (18-23,  $X = 20.3$  vs. 15-20,  $X = 18.24$ ;  $p = 0.0011$ ) (for details see Tables 1 to 4). *Liolaemus caparensis* **sp. nov.** has smaller dorsal blotches on the hindlimbs and a more defined vertebral line in comparison with *L. magellanicus* (Figure 5), as well as fewer precloacal pores than *L. magellanicus* (3-4 vs. 3-5). Dorsal scales of *Liolaemus caparensis* **sp. nov.** have a shorter mucron than those of *L. magellanicus*. The dorsal surface of limb scales is more carinated and less mucronated in *L. caparensis* **sp. nov.** than in *L. magellanicus* (Figure 5).



**FIGURE 1.** Relationships between *Liolaemus caparensis* **sp. nov.** and species of the *L. lineomaculatus* section and selected species of the subgenus *Eulaemus* and *Liolaemus* sensu stricto. On the left, phylogenetic relationships recovered using seven nuclear genes (Cmos, ACM4tg, PRLR, LDA8F, LDA1D, LDA9C and LDA9E, 4180 bp total alignment length) with Bayesian species-tree inference; bold branches represent well supported nodes ( $Pp > 0.95$ ). On the right, the Bayesian tree (modified from Breitman *et al.* 2011), represents a concatenated analyses (5865 bp) including the seven nuclear genes plus two mitochondrial genes (12S and *cyt-b*), and summarizes information from MP and ML methods. Nodes with high support from three methods (MP, jackknife and ML bootstrap  $> 0.70$ ; Bayesian  $Pp > 0.95$ ) are identified by bold branches; solid circles show nodes with weak MP support, and open circles nodes with weak MP and ML support.

**Description of holotype.** Adult male. Snout-vent length 59.0 mm. Tail length (complete, not regenerated) 84.0 mm. Radius-ulna length 25.9 mm. Head length 13.4 mm (from anterior border of tympanum to tip of snout), 11.0 mm wide (at anterior border of tympanum), 7.7 mm long (at anterior border of tympanum). Snout length 4.9 mm (orbit-tip of snout distance). Auditory meatus-eye distance 4.7 mm. Interorbital distance 4.2 mm. Eye-nostril distance 3.1 mm. Forelimb length 17.5 mm. Tibial length 8.6 mm. Foot length 14.6 mm (ankle to tip of claw on fourth toe).

Dorsal head scales slightly bulged, smooth, 14 between occiput, at level of anterior border of tympanum, to rostral, pitted with numerous scale organs in the anterior region, and reducing to no organ in the posterior half of the head. Rostral scale wider (2.8 mm) than long (0.9 mm). Two postrostrals that together with anterior lorilabial separate nasal scales from rostral, surrounded by six scales. Nasal scales longer than wide, irregularly hexagonal; nostril one-half length of nasal, posterior in position. Scales surrounding nasals 7 on each side. Four internasals. Frontonasals and prefrontals 14, irregular in shape, size and position. Two frontal scales. Frontoparietals in two rows, two anterior and one posterior scale. Interparietal pentagonal (1.3 mm), surrounded by five scales; three smaller and irregular in front and sides, two larger in back. Parietal eye evident. Parietals slightly bulged, irregularly shaped, equal in size to interparietal. Circumorbitals: 9 on the left side, incomplete; 10 on the right side, incomplete. Transversally expanded supraoculars 4–3. Smaller lateral supraoculars: 16–19. Three canthals on the left side, one posterior large, higher than wide, in contact with postnasal, two inferior, small; four canthal on the

right side, one posterior with similar characteristics that the left side, and three inferior, small. Loreal scales slightly bulged, 4–5 on each side. Lorilabials longer than wide (7–8), slightly smaller than labials. Superciliaries 7 on each side, flattened and elongated, anterior four broadly overlapping dorsally. Orbit with 13–12 upper and 11–10 lower ciliaries on each side. Orbit diameter 4.7 x 2.3 mm. Preocular small, unfragmented, longer than wide. Subocular scale elongated, approximately nine times longer than wide (4.0 x 0.5 mm). A well marked longitudinal ridge along upper margin of preocular and subocular scales. Postocular small, slightly bulged, quarter superimposed to subocular, with a marked longitudinal ridge. Palpebral scales, small granular and bulged. Supralabials 6 on each side, convex. Temporals smooth, convex, juxtaposed with one scale organ in the tip. Anterior auriculars smaller than adjacent posterior temporals, slightly projecting outward (1 on each side). Posterior auriculars small and granular. External auditory meatus conspicuous, rounded (1.8 x 1.5 mm). Lateral scales of neck granular with inflated skin. Mental scale wider (3.0 mm) than high (1.3 mm), in contact with four scales. Mental followed posteriorly by two postmentals, and two rows of 2–1 chinshields. Five infralabials on each side, first on each side quadrangular two times wider than supralabials, all others elongated, slightly smaller than supralabials. Gular scales smooth, flat, imbricate, with rounded posterior margins, with melanophores. Scales of throat between chinshields slightly imbricate. Twenty-six gular scales between tympanum openings. Infralabials separated from chinshields by one to two rows of scales. Antehumeral and longitudinal neck folds well developed; gular fold incomplete; postauricular, rictal, dorsolateral and oblique folds un conspicuous.

Scales of dorsal neck region rhomboidal, imbricate, strongly keeled, mucronate. Thirty-nine scales between occiput and anterior surface of thighs. Dorsal body scales rhomboidal, imbricate, strongly keeled and mucronate. Dorsal scales grade laterally into slightly smaller, slightly keeled scales at midbody. Scales immediately anterior and posterior to forelimb and hindlimb insertion small, smooth, granular, and non-overlapping. Body lateral scales grading smaller to larger at midbody. Ventral body scales rhomboidal, smooth, flat, imbricate, and bigger than dorsal scales. Forty-four midbody scales; scales between mental and precloacal pores 71. Scales of cloacal region about equal in size to ventral body scales. Four precloacal pores.

Anterior suprabrachials rhomboidal, imbricate, smooth, slightly larger in size to dorsal body scales. Postbrachials smaller, smooth, becoming granular near axilla. Supra-antibrachials rhomboidal, imbricate, smooth, some of the external lateral slightly keeled. Infra-antibrachials rhomboidals, imbricate, smooth, toward the hand slightly keeled. Supracarpals imbricated, rhomboidal, smooth. Infracarpals strongly imbricate, rhomboidal, slightly keeled and mucronate. Infradigital lamellae with 3-keels, each terminating in a short mucron, 3-mucronate, numbering: I: 8, II: 12, III: 16, IV: 19, V: 11. Claws robust, curved and sharp, opaque brown.

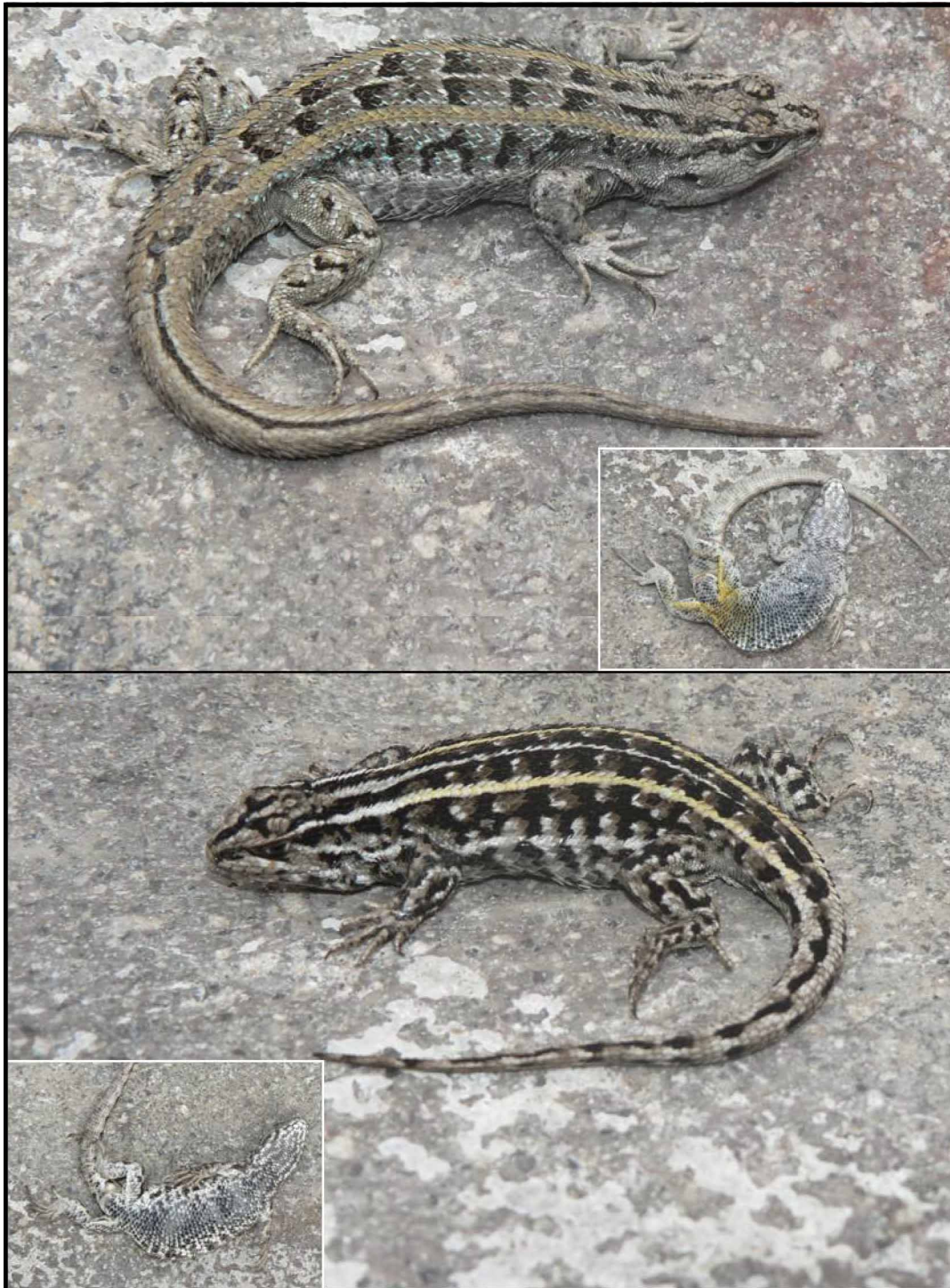
Suprafemorals as large as dorsal body scales, rhomboidal, imbricated, strongly keeled and mucronate. Postfemorals small, granular shape. Supratibial rhomboidal, imbricated, strongly keeled and mucronate. Infracremoral scales small, granular and smooth. Supratarsals rhomboidals, imbricated and smooth, some lateral scales slightly keeled. Infracremoral scales small, rhomboidal, imbricate, smooth, mucronate, some slightly keeled and mucronate near the digit. Subdigital scales 3-keeled, 3-mucronate, numbering: I: 9, II: 13, III: 19, IV: 21, V: 14. Claws robust, curved and sharp, opaque brown. Tail complete, non-regenerated. Dorsal and lateral caudal scales, rhomboidal in the first half of the tail, becoming quadrangular toward the tip, strongly keeled and mucronate. Ventrals subtriangular and smooth, toward posterior half moderately keeled.

**Color of holotype in life.** Grey dorsal background (Figure 2). The posterior borders of the dorsal scales, between neck and pelvic region, present one or two contrasting light colors (white or light blue). Dorsal pattern with eight series of paravertebral and quadrangular black (with a white end) blotches, appearing from the nuchal region to about the first autotomy line, those series fuse into a dark line that is present to the tip of the tail. Dorsolateral region, between the occipital and the pelvic regions, has eight irregular black and white-bordered blotches. Between the series of blotches there are three longitudinal lines, a white vertebral and two light brownish paravertebral lines, the last ones are wider than the vertebral (one and half scale vs. a quarter of scale). The coloration in the vertebral and lateral area is light brown.

Anterior region of the head shows a dark gray background with a central black blotch from the internasals to the frontal scales. Orbitals, postfrontals and parietals are light brown, the black circumorbital scales continue in a line of the same color until the nuchal region. Gray temporal and lateral head regions. Limbs dorsal region are gray with a scarce black reticulation with some lighter color scales.

Ventral scales with melanophores. Black color is present throughout all the ventral body until the postcloacal region. Dark reticulate area is present in the throat and extends to the adjacent malar and maxilla region. Cloacal

and postcloacal regions are black. Ventral area of lower belly and femoral region present a bright yellow color. Tail is light gray (Figure 2).



**FIGURE 2.** Upper, dorsal and ventral views of male holotype in life of *Liolaemus caparensis* **sp. nov.** MLPS 2628; below, dorsal and ventral views of female (LJAMM-CNP 9387).

**Color of holotype in preservative.** After three years in preservative, the dorsal coloration of the head, dorsum, body flanks and tail becomes darker while maintaining the contrast, but the two light brownish paravertebral lines turned gray. Ventral scales of throat, neck, chest, belly and forelimbs maintain the same dark coloration as in life, and the distinctive yellow ventral coloration of the femoral and belly regions turns gray (Figure 5).

**Variation.** Morphological and meristic characters variation, between males and females of *Liolaemus caparensis* **sp. nov.** are shown in Table 5. Females in life present basically the same dorsal and lateral pattern as present in

males, but the coloration has a light brown background; vertebral and paravertebral lines are wider and much more notorious than the ones in males, the lines are white; although, one of the lizards presents yellowish dorsolateral lines. Only the females present a white lateral line from the axilla to the groin. Ventral coloration shows a dark reticulate pattern in throat, melanic chest and belly, but two specimens present a yellowish coloration in the ventrolateral, femoral, cloacal and postcloacal regions. All distinctive dorsal lines, and ventral coloration, femoral and lower belly areas turns in preservative from yellowish or bright yellow to gray.

**TABLE 5.** Variation between females and males of *Liolaemus caparensis* **sp. nov.** summarized as mean  $\pm$  SD (min–max) values for all meristic and morphometric (in millimeters) variables.

Var	Females (n=5)	Males (n=3)
SCI	6.75 $\pm$ 1.04 (5–8)	6 $\pm$ 1 (5–7)
LS	5 $\pm$ 0.53 (4–6)	4.33 $\pm$ 1.15 (3–5)
SS	6.88 $\pm$ 0.83 (6–8)	6.33 $\pm$ 0.58 (6–7)
IS	4.75 $\pm$ 0.71 (3–5)	4.67 $\pm$ 0.58 (4–5)
MS	44.25 $\pm$ 4.95 (39–55)	42.67 $\pm$ 2.31 (40–44)
DS	42.13 $\pm$ 2.59 (39–47)	39.67 $\pm$ 1.15 (39–41)
VS	68.75 $\pm$ 3.01 (64–73)	67.33 $\pm$ 3.21 (65–71)
IL3	14.88 $\pm$ 1.36 (14–18)	15.33 $\pm$ 0.58 (15–16)
IL4	20.25 $\pm$ 1.67 (18–23)	20.5 $\pm$ 0.71 (20–21)
Pores	0	3.67 $\pm$ 0.58 (3–4)
SVL	49.8 $\pm$ 2.77 (47–54)	55 $\pm$ 3.61 (52–59)
TL	63 $\pm$ 2.94 (60–67)	74 $\pm$ 8.72 (68–84)
DFH	23.84 $\pm$ 1.62 (21.2–25.2)	24.87 $\pm$ 0.93 (24.1–25.9)
FOL	12.52 $\pm$ 0.71 (11.37–13.19)	14.99 $\pm$ 0.44 (14.68–15.3)
TFL	6.86 $\pm$ 0.55 (6.19–7.55)	7.86 $\pm$ 0.72 (7.19–8.62)
RUL	5.08 $\pm$ 0.44 (4.58–5.66)	5.51 $\pm$ 0.12 (5.38–5.61)
HAL	7.55 $\pm$ 0.53 (7.08–8.36)	8.53 $\pm$ 0.59 (7.85–8.91)
HH	6.16 $\pm$ 0.41 (5.65–6.7)	7.05 $\pm$ 0.56 (6.72–7.7)
HW	8.8 $\pm$ 0.43 (8.4–9.33)	10.41 $\pm$ 0.91 (9.37–11.07)
HL	10.95 $\pm$ 0.37 (10.43–11.4)	12.38 $\pm$ 0.91 (11.69–13.41)
EH	1.79 $\pm$ 0.14 (1.58–1.89)	1.98 $\pm$ 0.27 (1.77–2.29)
EL	2.99 $\pm$ 0.1 (2.85–3.07)	3.16 $\pm$ 0.24 (2.91–3.38)
RND	1.83 $\pm$ 0.22 (1.58–2.15)	2.16 $\pm$ 0.13 (2.01–2.26)
RH	0.97 $\pm$ 0.05 (0.9–1.01)	1 $\pm$ 0.1 (0.94–1.12)
RL	2.41 $\pm$ 0.16 (2.26–2.66)	2.83 $\pm$ 0.11 (2.71–2.93)
DRE	4.65 $\pm$ 0.25 (4.38–4.99)	5.23 $\pm$ 0.22 (5.09–5.49)
AH	1.82 $\pm$ 0.18 (1.65–2.09)	2.13 $\pm$ 0.17 (1.94–2.24)
AL	1.58 $\pm$ 0.25 (1.33–1.88)	1.62 $\pm$ 0.03 (1.59–1.64)

**Etymology.** The specific epithet of this species “caparensis” refers to the name “Capar” given to the actual Viedma lake by the Aónikenk aborigines that inhabited this area. The Campo Las Piedras plateau is located on the northwestern edge of Viedma Lake.

**Distribution.** *Liolaemus caparensis* **sp. nov.** is known only from the type locality, from Campo Las Piedras plateau, 7 km N Punta del Lago ranch, Lago Argentino department, Santa Cruz province, Argentina. 868 m (Figures 3 and 4).

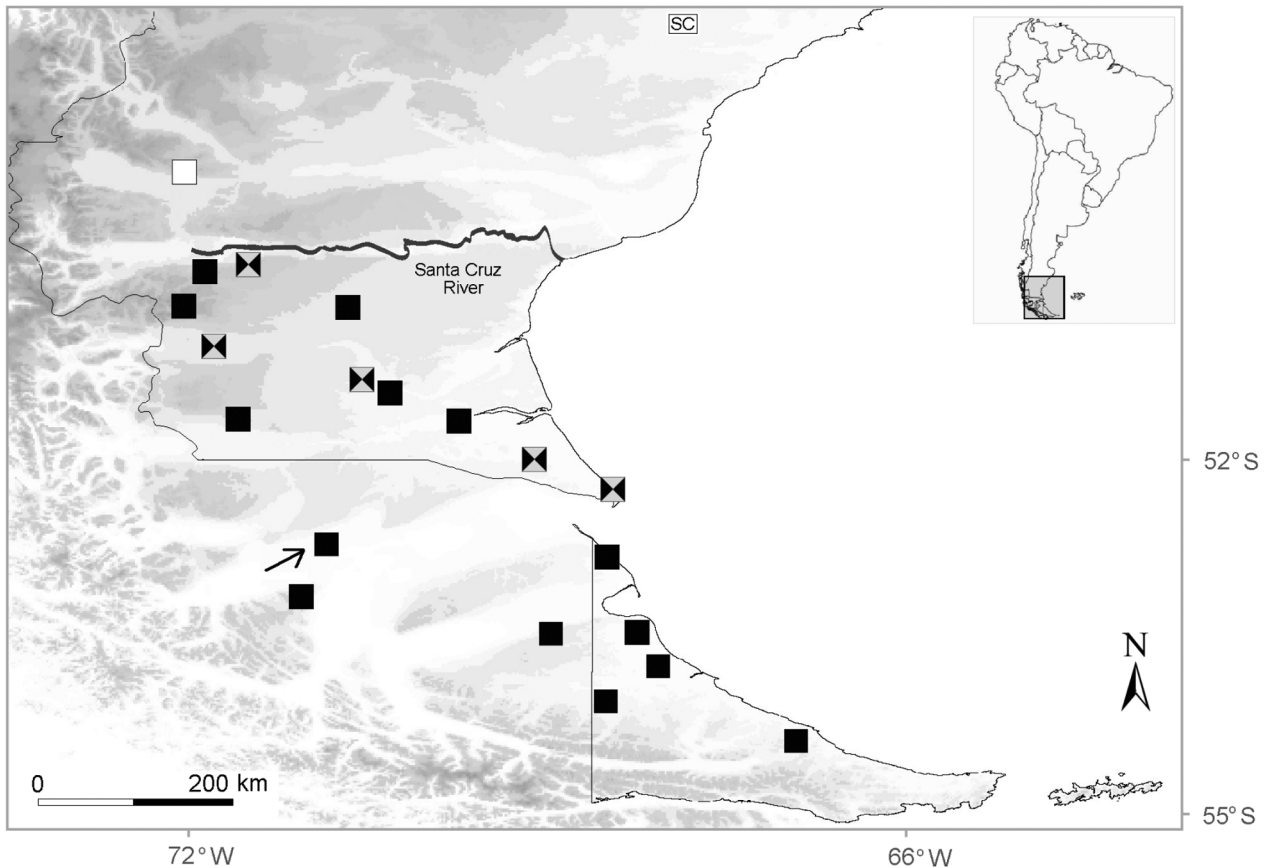
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**FIGURE 3.** Type locality of *Liolaemus caparensis* sp. nov., Subantarctic Phytogeographic province, Estepa de *Festuca pallens* District (49° 34' 11.0" S, 72° 02' 51.9" W).





**FIGURE 4.** Distribution map for species of the *magellanicus* group, with localities sampled superimposed on regional elevation (shading). White square: *Liolaemus caparensis* sp. nov.; black squares: distribution of *L. magellanicus*; black and gray squares: *L. magellanicus* localities used in this study from LJAMM-CNP collection. Arrow indicates type locality of *L. magellanicus* (in Chile). SC: Santa Cruz province. Notice *L. caparensis* sp. nov. distribution does not overlap with the distribution of *L. magellanicus* (south of the Santa Cruz river).

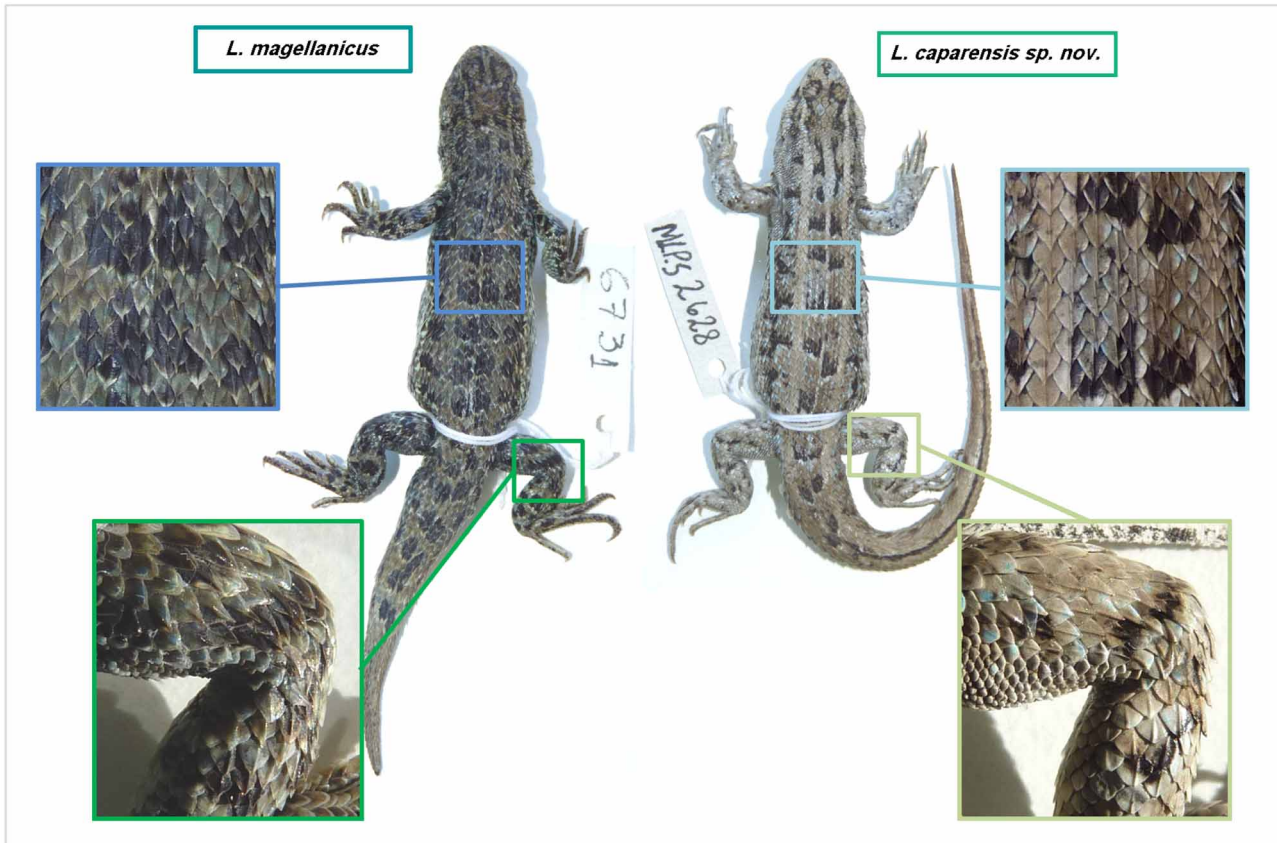
**Natural history.** The new species is viviparous and probably insectivorous (inferred from the biology of its sister species *Liolaemus magellanicus*; Iburgüengoytía *et al.* 2010). Out of five females, only two presented a ventral yellowish coloration and one of those was gravid, thus we inferred that the yellowish coloration in females is not directly related with the reproductive state. The specimens were found in the Subantarctic Phytogeographic province, Estepa de *Festuca pallescens* district, in an environment mainly characterized as *Festuca* grasslands (Roig 1998). Other dominant vegetation included short bushes (*Anartrophyllum desideratum*, *Senecio* spp.) and grasses (*Stipa* spp.) (Figure 3). This species was found in open substrates between rocks, sharing the habitat with *Liolaemus tari*.

**Concluding remarks.** Lizards from the *magellanicus* group have a general phenotype (general body form, coloration, and color pattern) similar to lizards of the *lineomaculatus* group, but they have precloacal pores, a synapomorphy shared with all other species of the *Liolaemus lineomaculatus* section (*kingii+archeforus* and *somuncurae* groups) but not with species from the *lineomaculatus* group.

Fouquet *et al.* (2007), proposed for Neotropical frogs a mtDNA approach to species delimitation based on isolation-by-distance population structure. The method tests for correlation of geographic distance with genetic distance, which characterized most samples up to uncorrelated values of 3%. At this value the isolation-by-distance correlation was not significant and Fouquet *et al.* (2007) interpreted this break as the limit to intra-specific gene flow.

Martinez (*personal communication*) found that within *Liolaemus* the mean genetic distance value of cytochrome *b* between sister species was ~ 4%; moreover, she found that different groups of *Liolaemus* had values ranging from 1 to 6%. In the *L. lineomaculatus* section, average genetic distance between described species is 1.6% (based on the sister species *L. kolengh* vs. *L. hatcheri*), and 2.25% between species of the *kingii+archeforus* group

(based on sister species *L. archeforus* vs. *L. chacabucoense* and *L. escarchadosi* vs. *L. tari*). Even though the genetic distance values calculated for *L. caparensis* sp. nov. relative to *L. magellanicus* are slightly higher than values of other species from the *L. lineomaculatus* section, we want to highlight that the discovery of the new species started with the genetics analyses presented by Breitman *et al.* (2011), in which several clades were recognized as candidate species, continued with the nuclear data here presented and concluded with the morphological differentiation and characterization of *L. caparensis* sp. nov. presented here.



**FIGURE 5.** Morphological comparison between *Liolaemus magellanicus* (left) and *L. caparensis* sp. nov. (right). Differences in dorsal scales are shown in blue/light blue, in *L. magellanicus* scales are more mucronated than in *L. caparensis* sp. nov.; differences in dorsal scales of hindlimbs are shown in green/light green, in *L. magellanicus* scales are more mucronated and less carinated than in *L. caparensis* sp. nov. Notice differences in color pattern on the tails, size of blotches on the limbs, and the differences in vertebral lines.

Even though there is not a formal description of the morphological characteristics that define the *magellanicus* group, the features that defined the species *Liolaemus magellanicus* do differentiate it from the other groups of the *L. lineomaculatus* section (scale counts and shape, coloration patterns, presence of precloacal pores and size, among others: Scolari 1992; Laurent 1995; Etheridge & Espinoza 2000; Pincheira-Donoso & Núñez 2005). The divergence of the *magellanicus* group from the rest of the section was inferred to have occurred during the Late Miocene (~8.46 million years ago, Breitman *et al.* 2011).

Morphological, molecular, and geographic distributional data provide evidence to consider *Liolaemus caparensis* sp. nov. a distinct species most closely related to *L. magellanicus*, forming the *magellanicus* group. Because the aim of this work was to describe the new species and not to propose new taxonomical arrangements, we avoid hypothesizing new taxonomies or presenting morphological features that might characterize new classifications. Including the species described here and two more species described in another manuscript (Breitman *et al. in press*), the number of species included in the *L. lineomaculatus* section increases to 21.

Our research group is studying the *Liolaemus lineomaculatus* section to delimit species boundaries and reconstruct relationships from multiple sources of evidence. Our goal is to present monographic revisions of poorly known groups on the basis of an “integrative taxonomy” approach (Padial *et al.* 2010), based on independent lines of evidence to propose taxonomic re-arrangements and support hypotheses of species limits. In parallel, we are

using integrative phylogeographic analyses based on molecular, morphological, ecological, and geographical data, to reconstruct a temporal sequence of demographic histories, and to eventually test for shared patterns of divergence with other Patagonian clades (Sérsic *et al.* 2011).

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**APPENDIX I.** Individuals examined by species, sample sizes, museum collection, collection numbers and locality. RP: Provincial Road, RN: National Road, prov: province, dep: department, Ea: ranch. Where possible: F: females; M: males and J: juveniles are indicated. LJAMM-CNP (Herpetological collection of Centro Nacional Patagónico in Puerto Madryn, Argentina), JMC-DC (JMC diagnostic collection in University of San Luis, Argentina), FMNH (Field Museum of Natural History), MLP.S (University of La Plata), MACN (Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires) and MVZ (Museum of vertebrate zoology, USA)

Species	n	Coleccion	Number	Locality
<i>L. caparensis</i> sp. nov.	10	LJAMM-CNP	H: 9383-9387 M: 9379-9380 J:9382, 9388; 9389	Santa Cruz prov. Lago Argentino dep. Campo las Piedras plateau. 7 km N Ea. punta del Lago.
	1	MLP.S	M: 2628	Santa Cruz prov. Lago Argentino dep. Campo las Piedras plateau, 7 km N Ea. punta del Lago.
<i>L. magellanicus</i>	10	LJAMM-CNP	H: 6725; 6729-6730 M: 6723-6724; 6726-6728; 6731 J: 6732	Santa Cruz prov. Guer Aike dep. Cañadon Lueacho, 8 km N light house.
	2	LJAMM-CNP	M: 11471; 11472	Santa Cruz prov. Guer Aike dep. RP 1 between RN 3 and Cabo Virgenes, 20 km N Ea El Condor.
	3	LJAMM-CNP	M: 7247-7249	Santa Cruz prov. Lago Argentina dep. RN 40, 29.4 km SE joint RP 11 to El Calafate.
	1	LJAMM-CNP	M: 11493	Santa Cruz prov. Guer Aike dep. 14.6 km W RP 5. Near Ea Corpie Aike.
	2	LJAMM-CNP	F: 11495; 11496	Santa Cruz prov. Guer Aike dep. RN 40, 1.7 km N Tapi Aike, joint RP 7.
<i>L. magellanicus</i>	1	DMG-DC	M: 84	Santa Cruz prov. 40 km S of Argentino lake, S of Santa Cruz river.
	8	DMG-DC	M: 929, 931, 933, 935 F: 932, 934 J: 930, 936	Santa Cruz prov. Vizcachas plateau.
	1	DMG-DC	F: 937	Santa Cruz prov. 15 km. NW Ea Guarumba.
	1	DMG-DC	M: 321	Santa Cruz prov. Ea Vizcachas.
	2	DMG-DC	M: 614 F: 615	Santa Cruz prov. Punta Dúngenes.
<i>L. magellanicus</i>	7	FMNH	M: 132838, 132859 F: 133103, 132847, 132845, 132857, 133521	Santa Cruz prov. Monte Aymond.
	2	FMNH	M: 132824, 132826	Santa Cruz prov. 20 km NE Monte Aymond.
<i>L. magellanicus</i>	1	MLP.S	00012	Santa Cruz prov.
<i>L. magellanicus</i>	1	MACN	31731	Santa Cruz prov. 10 km. E Fuentes del Coyle.
	1	MACN	31714	Santa Cruz prov. Esperanza lake.
	1	MACN	31718	Santa Cruz prov. Penitentes River.
	3	MACN	31429-31431	Santa Cruz prov. Los escaichados.
	1	MACN	31436	Santa Cruz prov. Del blanquillo lake.
	1	MACN	31437	Santa Cruz prov. Escondida lake.
<i>L. magellanicus</i>	1	MVZ	180818	Chile, Onaisin
<i>L. hatcheri</i>	20	LJAMM-CNP	9485-9492, 9498-9506, 10321-10323	Santa Cruz prov. Río Chico dep. Ea Cerro Beltza, 12 km N RP 37.
<i>L. kolengh</i>	42	LJAMM-CNP	7276-7291, 7293-7317, 10590	Santa Cruz prov. Lago Buenos Aires dep. Near Los Antiguos, 15.6 to 21 km N paso Roballos.
<i>L. lineomaculatus</i>	17	LJAMM-CNP	9971-9972, 9731, 9953, 9847, 7470-7472, 10054-10055, 9750-9756	Santa Cruz prov. Deseado dep. Puerto Deseado and surroundings
<i>L. silvanae</i>	21	LJAMM-CNP	9218-9237, 10320	Santa Cruz prov. Lago Buenos Aires dep. Puesto Lebrun 27.3 km W Ea La Vizcaina.

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**APPENDIX II.** Acronyms used for characters examined in this study; for definitions see Avila *et al.* (2010a, 2010b), Vega *et al.* (2008), and Martinez *et al.* (2011).

### Morphometric characters

**SVL:** Snout-vent length

**TL:** Tail length

**DFH:** Distance between fore and hind limbs

**FOL:** Foot length

**TFL:** Tibia-fibula length

**RUL:** Radius-ulna length

**HAL:** Hand length

**HH:** Head height

**HW:** Head wide

**HL:** Head length

**EH:** Eye height

**EL:** Eye length

**RND:** Rostral-nasal distance

**RH:** Rostral height

**RL:** Rostral length

**DRE:** Distance from rostral to the eye

**AH:** Auditory meatus height

**AL:** Auditory meatus length

### Meristic characters

**SCI:** Scales in contact with interparietals

**LS:** Lorilabial scales

**SS:** Supralabial scales

**IS:** Infralabial scales

**MS:** Midbody scales

**DS:** Dorsal scales

**VS:** Ventral scales

**IL3:** Infradigital lamellae (3<sup>rd</sup> on left hand)

**IL4:** Infradigital lamellae (4<sup>th</sup> on left foot)



## Two new species of lizards from the *Liolaemus lineomaculatus* section (Squamata: Iguania: Liolaemidae) from southern Patagonia

MARIA FLORENCIA BREITMAN<sup>1,4</sup>, MICAELA PARRA<sup>2</sup>, CRISTIAN HERNÁN FULVIO PÉREZ<sup>1</sup>  
& JACK WALTER SITES, JR<sup>3</sup>

<sup>1</sup>Centro Nacional Patagónico – Consejo Nacional de Investigaciones Científicas y Técnicas, Boulevard Almirante Brown 2915, ZC: U9120ACD, Puerto Madryn, Chubut, Argentina. Tel: 0054 – 02965 – 451024. E-mail: chfperez@cenpat.edu.ar

<sup>2</sup>Universidad Nacional de la Patagonia San Juan Bosco, Boulevard Almirante Brown 3150, ZC: U9120ACX, Puerto Madryn, Chubut, Argentina. Tel: 0054 – 02965 – 472885. E-mail: mica\_fop@hotmail.com

<sup>3</sup>Department of Biology and Monte L. Bean Life Science Museum, Brigham Young University, 401 WIDB, Provo, UT 84602, USA. E-mail: jack\_sites@byu.edu

<sup>4</sup>Corresponding author. E-mail: breitman@cenpat.edu.ar

### Abstract

Two new species of the *lineomaculatus* clade of the *Liolaemus lineomaculatus* section are described from southern Patagonia in Argentina. *Liolaemus morandae* **sp. nov.** is found in S Chubut province and *Liolaemus avilae* **sp. nov.** inhabits NW Santa Cruz province. Several tests were performed to diagnose these new species as distinct lineages. Univariate analysis of variance (ANOVA), principal component analysis (PCA), discriminant function analysis (DFA), non-parametric multivariate analysis of variance (NPMANOVA), as well as a genetic characterization through molecular analysis of variance (AMOVA) were performed; genetic distances between described and these new species are reported. The new *Liolaemus* species differ from other members of the *lineomaculatus* group in morphometric, meristic, qualitative and genetic characters; moreover they inhabit different phylogeographical provinces and districts. With these descriptions, the number of species now recognized in the *lineomaculatus* section is twenty one (including one more description that is in press).

**Key words:** Iguania, Liolaemidae, *Liolaemus lineomaculatus* section, *Liolaemus morandae* **sp. nov.**, *Liolaemus avilae* **sp. nov.**, Patagonia, new species

### Resumen

Se describen dos nuevas especies pertenecientes al clado *lineomaculatus* de la sección *Liolaemus lineomaculatus* de la región sur de la Patagonia Argentina. *Liolaemus morandae* **sp. nov.** se distribuye en el sur de la provincia del Chubut, mientras que *Liolaemus avilae* **sp. nov.** se encuentra circunscrita al Noroeste de la provincia de Santa Cruz. En este trabajo se utilizan diferentes análisis estadísticos y moleculares para caracterizar y diferenciar las nuevas especies de las actualmente descritas en el grupo *lineomaculatus*: análisis univariados de la varianza (ANOVA), análisis de componentes principales (PCA), análisis de funciones discriminantes (DFA), análisis multivariados no paramétricos de la varianza (NPMANOVA); también se realiza una caracterización genética a través de un análisis molecular de la varianza (AMOVA) y se reportan las distancias genéticas entre especies. Las nuevas especies de *Liolaemus* se diferencian de los otros miembros del grupo *lineomaculatus* en base a caracteres morfológicos, cualitativos y genéticos; además de habitar diferentes provincias fitogeográficas y distritos. El número actual de especies de la sección *lineomaculatus* asciende a veintiuno, incluyendo la presente descripción y otra que se encuentra en prensa.

**Palabras clave:** Iguania, Liolaemidae, sección *Liolaemus lineomaculatus*, *Liolaemus morandae* **sp. nov.**, *Liolaemus avilae* **sp. nov.**, Patagonia, nueva especie



## Introduction

One of the most ecologically diverse and species-rich genera of iguanian lizards on earth is *Liolaemus*, with more than 230 recognized species distributed from Perú to Tierra del Fuego (Núñez & Scolaro 2009; Abdala *et al.* 2010; Avila *et al.* 2010a, 2010b; Lobo *et al.* 2010a, 2010b; Martínez *et al.* 2011; Quinteros & Abdala 2011; Breitman *et al. in press*). These lizards extend across a wide range of latitudinal ( $14^{\circ} \pm 30'$  –  $52^{\circ} \pm 30'$  S), altitudinal (0 – 4,500 m), and climatic regimes (Hellmich 1951; Donoso-Barros 1966; Etheridge & de Queiroz 1988; Frost & Etheridge 1989; Cei 1986, 1993; Etheridge & Espinoza 2000). Two main species groups have been recognized within *Liolaemus* since the first comprehensive study of the genus (Laurent 1983): *Liolaemus* *sensu stricto* (the Chilean group) and the *Eulaemus* (the Argentinean group). The *Liolaemus lineomaculatus* section is part of the subgenus *Eulaemus* and includes 19 formally described species (Breitman *et al.* 2011; Breitman *et al. in press*). The distribution of the *L. lineomaculatus* section extends from central Neuquén province in northwest Argentinean Patagonia, and south to Tierra del Fuego Island (Donoso-Barros & Codoceo 1962; Donoso-Barros 1966; Bottari 1975; Cei 1986). Extremely heterogeneous landscapes are occupied by lizards from the *L. lineomaculatus* section; thus, its phylogenetic/phylogeographic history has also likely been complex (Breitman *et al.* 2011).

Species of the *L. lineomaculatus* section were historically classified into three main morphological groups: *lineomaculatus* (Etheridge 1995), *kingii* (Cei 1986) and *archeforus* (Cei 1986); plus the species *L. magellanicus* that has been recognized as part of the section, but was not clearly assigned to any of these three main groups. Breitman *et al.* (2011), based on nine molecular markers (mitochondrial and nuclear) and two phylogenetic approaches (concatenation and species tree), identified four main lineages within the *L. lineomaculatus* section: (1) the *lineomaculatus* group including: *L. hatcheri*, *L. kolengh*, *L. silvanae* and *L. lineomaculatus*; (2) the *magellanicus* group including *L. magellanicus* and one more species under description (Breitman *et al. in press*); (3) the *somuncurae* group including *L. somuncurae* and *L. uptoni*; and (4) the *kingii*+*archeforus* group including: *L. baguali*, *L. escarchadosi*, *L. tari*, *L. sarmiento*, *L. scolaroi*, *L. zullyae*, *L. tristis*, *L. archeforus*, *L. chacabucoense*, *L. kingii* and *L. gallardo* (Figure 1). The four clades recovered from the molecular approach support the “traditional morphological” *lineomaculatus* group, but do not support the *kingii* and *archeforus* groups; moreover they included eight potentially new undescribed species spread through the four main clades.

*Liolaemus lineomaculatus* was described by Boulenger in 1885, with “Patagonia” as the type locality; later Donoso-Barros (1966) restricted the type locality to “Puerto Deseado, Patagonia, Argentina”. Since then, specimens possessing morphological features of *L. lineomaculatus* and collected between central Neuquén and southern Santa Cruz were assigned to this species (e.g. Cei 1986; Williams 1997; Ibarguengoytía *et al.* 2001; Christie 2002). However, recent evidence suggests that this species is a species complex comprised of at least five lineages (Breitman *et al.* 2011; Breitman *unpublished data*).

Here we used an integrative approach to distinguish and describe two new species from the *lineomaculatus* group of the *L. lineomaculatus* section. Morphometric, meristic, qualitative and genetic characters, were used to analyze this group of species through a battery of statistical tests. The two new species described here belong to the *lineomaculatus* group identified as *L. sp. 1* and *L. sp. 2* by Breitman *et al.* (2011).

## Material and methods

We examined series of specimens from the *L. lineomaculatus* clade, particularly those of the *lineomaculatus* group (specimens that were used in Breitman *et al.* 2011). *Liolaemus kolengh* (n = 42), *L. hatcheri* (n = 20), *L. silvanae* (n = 21), and *L. lineomaculatus* (n = 17), including specimens collected from their type localities, were compared with nine specimens of the first new species, and ten specimens of the second new species (Appendix I). Specimens were collected by hand and sacrificed by a pericardial injection of sodium pentothal Abbot®, slightly dissected to extract a sample of liver for molecular study, fixed in 20% formalin and later transferred to 70% ethanol. Voucher specimens were placed in the La Plata Museum (MLPS) and in the Herpetological Collection LJAMM-CNP of Centro Nacional Patagónico in Puerto Madryn, Argentina.

The *lineomaculatus* and *magellanicus* groups are morphologically different (scale counts and shape, coloration patterns, presence/absence of preloacal pores, among others; Scolaro 1992; Laurent 1995; Etheridge & Espinoza 2000; Pincheira-Donoso & Núñez 2005), and divergence of these groups is inferred to be Late Miocene (~8.46 mil-

lion years ago, Breitman *et al.* 2011). Because they are considered as two different morphological and molecular clades, for the present descriptions we only performed comparisons among the species of the *lineomaculatus* group. We used 18 morphometric characters and 12 meristic characters (scale counts) commonly used (defined elsewhere, e.g. Vega *et al.* 2008; Avila *et al.* 2010a, 2010b; Martinez *et al.* 2011; see Appendix II for names and definitions of characters), as well as 94 qualitative characters, 84 on squamation and 10 on body patterns. Measurements were taken only on adults, with a Schwyz® electronic digital caliper to the nearest 0.1 mm; scale counts were made on juveniles and adults with a stereoscopic microscope from fixed specimens, and qualitative characters were observed and registered only on adults. Scale terminology, measurements, and chromatic states follow Smith (1946), nomenclature for neck folds follows Frost (1992). Coloration in life was recorded from pictures taken at the time of capture. Sex was determined by the thickness of the base of the tail. Where numbers of paired scales are provided they are given as left-right.

**Morphological statistical tests.** We implemented statistical tests for both morphometric and meristic characters, and compared frequencies of qualitative characters. ANOVA was implemented to evaluate the significance of differences of variable means between new and described species, DGC comparisons (Di Rienzo, Guzmán and Casanoves test; Di Rienzo *et al.* 2002) were performed, and assumptions of variance equality and normality were checked with Levene and Shapiro-Wilks tests, respectively (Montgomery 1991). When ANOVA *p* values were significant but assumptions of the statistical tests were not met (*p* values of Levene and Shapiro-Wilks tests < 0.05), we performed nonparametric Kruskal-Wallis tests (Kruskal & Wallis 1952) using INFOS-TAT® 2009 program (Di Rienzo *et al.* 2010). Sexual dimorphism was tested for all variables with either Student's T or Kruskal-Wallis tests (when same assumptions previously described were not met).

We performed principal component analyses (PCA) separately on the morphometric and meristic data sets; the first six principal components (PC) were saved to perform a discriminant-function analysis (DFA) using INFOS-TAT® 2009. The objective of this analysis was to present a visualization of differences and similarities among species. The discriminant functions computed by this method are linear combinations of the original variables that maximize differences between given groups (Crochet *et al.* 2003). Given all of the analyses performed in the present manuscript (see below, cross-validation with morphology, genetics, and distribution), an exhaustive analysis of PCA was considered redundant (Crochet *et al.* 2003).

The overall differences between the new and the described species were statistically compared using the software PAST v2.02 (Hammer *et al.* 2001) for only the meristic dataset, because the scales counts are independent of body size. One-way non-parametric MANOVA with 100,000 permutations (NPMANOVA, also known as PERMANOVA) was implemented, this test provides a non-parametric approximation to test for significant differences between two or more groups based on (in our case) a Gower distance measure (Anderson 2001).

**Genetic characterization.** Phylogenetics relationships among all the species plus eight candidate species of the *L. lineomaculatus* section were recovered by Breitman *et al.* (2011), and our methods are briefly described here as follows. Sequence data for seven nuclear genes (Cmos, ACM4tg, PRLR, LDA8F, LDA1D, LDA9C and LDA9E) and two mitochondrial genes (12S and cyt-*b*) were amplified (Saint *et al.* 1998; Wiens *et al.* 1999; Gamble *et al.* 2008; Townsend *et al.* 2008) edited and aligned using the program Sequencher v4.8. (™Gene Codes Corporation Inc. 2007) and Clustal X (Higgins & Sharp 1988, 1989; Thompson *et al.* 1997). The combined nuclear alignment was 4180 bp in length, while the nuclear plus the mitochondrial alignment was 5865 bp. All sequences are deposited in GenBank (Accession Nos. JF272765 - JF273049). The best-fitting evolutionary model for each gene was selected using JModelTest v0.1.1 (Guindon & Gascuel 2003; Posada 2008); recombination was tested and excluded using RDP v3.44 (recombination detection program; Martin & Rybicki 2000; Heat *et al.* 2006). Bayesian analyses were conducted for the concatenated matrix (nuclear and nuclear + mitochondrial) using MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003) with four chains, run for 50 million generations and sampled at intervals of 1,000 generations. The equilibrium samples were used to generate a 50% majority-rule consensus tree (after a 25% burn-in), and posterior probabilities (*Pp*) were considered significant when  $\geq 0.95$  (Huelsenbeck & Ronquist 2001). We assume convergence because all parameters had effective sample sizes greater than 200 (using Tracer v1.5.0; Rambaut & Drummond 2009).

Genetic structure within and among the species of the *lineomaculatus* group was characterized using a sub-set of our recently published molecular data set (Breitman *et al.* 2011); specifically the mitochondrial cytochrome *b* fragment from individuals collected in the type localities of *L. lineomaculatus*, *L. hatcheri*, *L. kolengh*, *L. silvanae*, and the new species identified as *L. sp. 1* and *L. sp. 2* in Breitman *et al.* (2011). Genetic distances between species

(corrected pairwise differences = intergroup distance – intragroup distance) and analyses of molecular variance (AMOVA), between described species and *L. sp. 1* and *L. sp. 2*, were calculated using Arlequin v3.11 (Excoffier *et al.* 2005). AMOVA analysis estimates genetic structure indices using the information on the allelic content of haplotypes as well as their frequencies (Excoffier *et al.* 1992). The information on the differences in allelic content between haplotypes is entered as a matrix of Euclidean squared distances. The significance of the covariance components associated with the different possible levels of genetic structure (within species, within groups of species, among species) is tested using non-parametric permutation procedures (Excoffier *et al.* 1992).

## Results

### Morphological statistical tests

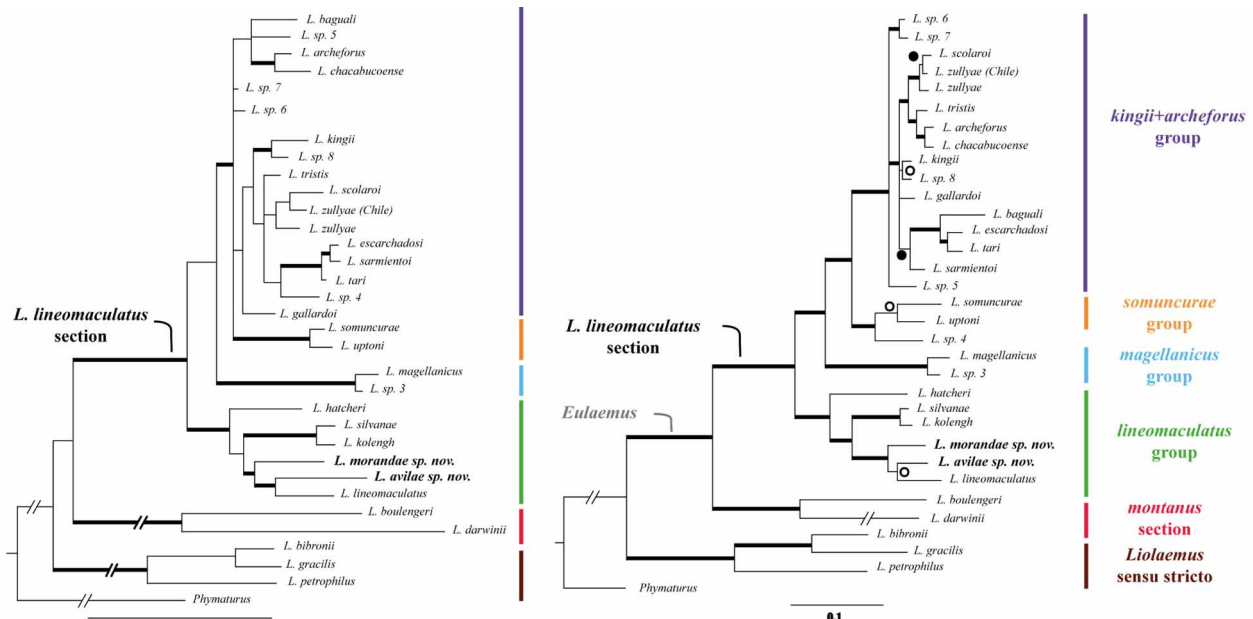
Morphological tests showed significant differences between the new species and the other taxa of the *lineomaculatus* group. Univariate tests showed that several variables differed significantly between the new species and the named taxa, which are described in the *Diagnosis* section of each new species. The means, standard deviations, and ranks for meristic and qualitative characters are summarized in Tables 1 and 2, and Levene and Shapiro-Wilks or Kruskal-Wallis *p* values are summarized in Tables 3 and 4. Sexual dimorphism was not detected in most of the twenty seven studied variables. In the first new species, similarities between males and females were rejected in only two variables (rostral height: females 0.84–1.06,  $X = 0.97$  vs. males 1.18–1.18,  $X = 1.18$ ;  $p = 0.037$ ; dorsal scales: females 47–67,  $X = 52.5$  vs. males 50–50,  $X = 50$ ;  $p = 0.033$ ), while for the second new species similarities between males and females were rejected in only three variables (distance between fore and hind limbs: females 28.4–29.5,  $X = 28.4$  vs. males 19.4–26.9,  $X = 23.44$ ;  $p = 0.043$ ; foot length: females 13.82–14.57,  $X = 14.08$  vs. males 15.19–5.98,  $X = 15.54$ ;  $p = 0.0036$ ; auditory meatus length: females 1.11–1.33,  $X = 1.22$  vs. males 1.44–2.1,  $X = 1.68$ ;  $p = 0.03$ ).

Principal component analyses (PCA, see Appendixes III to VI) recovered the first six axes with almost 80% of the accumulated explained variance. The first axis was mainly explained by differences in size (snout-vent, foot, tibia-fibula, radius-ulna, hand, head, eye and auditory meatus lengths; head width, eye height, rostral nasal distance, rostral height and distance from rostral to the eye), variables that explained axis number two were differences in scale numbers (scales in contact with the interparietal, scales around midbody, dorsal scales, ventral scales and infradigital lamellae of third finger and fourth toe); the third axis was mostly explained by the number of lorilabial, supralabial and infralabial scales. Axes 4, 5, and 6 were explained by: rostral height and number of supralabial scales; rostral-nasal distance, auditory meatus length and lorilabial scales; and scales in contact with interparietal, respectively. Discriminant-function analysis was performed with the first six principal components recovered with the PCA (Figure 2), and revealed that size is the principal difference that separates *L. sp. 1* and *L. sp. 2* from *L. silvanae*. Number of scales (variables that describe differences in axis number two for the PCA, explained above) is the main variable that differentiated *L. sp. 1* and *L. sp. 2* from *L. hatcheri* and *L. kolengh*. We found that the CP4 (mainly described by supralabial scales) differentiated *L. sp. 1* from *L. sp. 2*, and *L. lineomaculatus*. *Liolaemus sp. 1* differed from *L. lineomaculatus* based on the variables that were described by axes one and two (number of scales and size), although some overlap was evident.

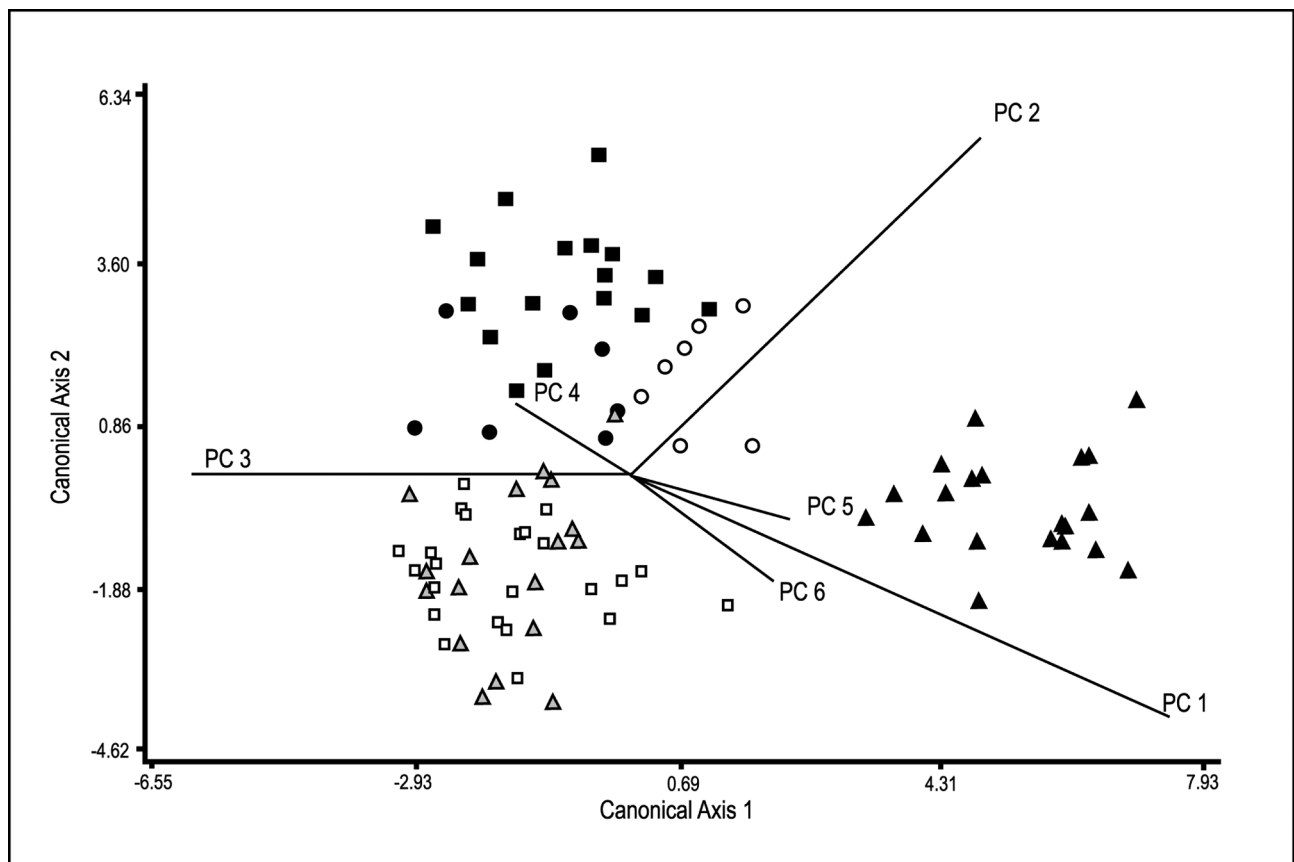
The multivariate analyses (MPMANOVA) conducted on the meristic data set revealed statistically significant differences among all the species of the *lineomaculatus* group (MPMANOVA,  $F = 13.51$ ,  $p < 0.00001$ ; Bonferroni corrected pairwise comparisons between species were significant at  $\alpha = 0.05$ , with two exceptions at  $\alpha = 0.1$ : *L. sp. 1* vs. *L. lineomaculatus*,  $p = 0.083$  and *L. sp. 1* vs. *L. silvanae*,  $p = 0.051$ ).

**Genetic characterization.** The AMOVA revealed that 89.48% of the variation was explained by among-species differences, whereas intrapopulation differences explained 10.52% of the variation,  $p < 0.0001$ . The  $F_{st}$  value for each species was greater than 0.893, and *p* values were significant ( $p < 0.0001$ ) in all cases, showing that differences between species were high and the intra-species variance (between population samples within a species) was low. The uncorrected genetic distance between the new species and the others of the *lineomaculatus* group, calculated using cytochrome *b*, was higher than 4.6% (Table 5).

Figure 1 summarizes phylogenetic relationships inferred, using the complete and nuclear-only data sets, among species and distinct lineages within the *L. lineomaculatus* section, and shows the position of the new species.



**FIGURE 1.** Relationships between *Liolaemus morandae* sp. nov. and *L. avilae* sp. nov. within the *L. lineomaculatus* section, and selected species of the subgenus *Eulaemus* and *Liolaemus sensu stricto*. On the left, phylogenetic relationships recovered with Bayesian inference using seven nuclear genes (Cmos, ACM4tg, PRLR, LDA8F, LDA1D, LDA9C and LDA9E, 4180 bp total alignment length), bold branches represent well supported nodes ( $Pp > 0.95$ ). On the right, the Bayesian tree (modified from Breitman *et al.* 2011) represents a concatenated analyses including the seven nuclear genes plus two mitochondrial genes (12S and *cyt-b*; 5865 bp) and summarizes information from MP and ML methods. Nodes with high support from three methods (MP, jackknife and ML bootstrap  $> 0.70$ ; Bayesian  $Pp > 0.95$ ) are identified by bold branches; solid circles show nodes with weak MP support and open circles nodes with weak MP and ML support.



**FIGURE 2.** Discriminant-function analysis summarizing principal components 1 – 6, for all six species of the *L. lineomaculatus* group. Black circles: *L. morandae* sp. nov.; white circles: *L. avilae* sp. nov.; black squares: *L. lineomaculatus*; white squares: *L. kolengah*; gray triangles: *L. hatcheri*; black triangles: *L. silvanae*.

**Table 1:** Values (in millimeters) of morphometric characters from species of the *lineomaculatus* group, samples sizes are shown in parenthesis, as well as mean  $\pm$  SD (min – max); abbreviations of characters are defined in Appendix II.

Var	<i>L. morandae</i> sp. nov. (n=6)	<i>L. avilae</i> sp. nov. (n=8)	<i>L. lineomaculatus</i> (n=17)	<i>L. hatcheri</i> (n=18)	<i>L. kolengh</i> (n=25)	<i>L. sibvanae</i> (n=17)
SVL	55.67 $\pm$ 4.32 (50 - 61)	55.38 $\pm$ 3.66 (48 - 59)	54.94 $\pm$ 3.82 (46 - 60)	61.89 $\pm$ 4.27 (55 - 69)	57.48 $\pm$ 2.86 (52 - 62)	73 $\pm$ 3.64 (65 - 78)
TL	70.33 $\pm$ 9.02 (61 - 79)	68.88 $\pm$ 4.79 (64 - 77)	70.46 $\pm$ 6.69 (60 - 82)	63.3 $\pm$ 9.63 (49 - 78)	60.52 $\pm$ 5.97 (47 - 70)	76.13 $\pm$ 3.72 (72 - 84)
DFH	25.9 $\pm$ 4.33 (19.7 - 30.8)	25.3 $\pm$ 3.56 (19.4 - 29.5)	25.07 $\pm$ 2.73 (20.9 - 29.8)	28.95 $\pm$ 3.92 (19.5 - 35.3)	25.65 $\pm$ 2.49 (20.7 - 31.1)	32.38 $\pm$ 3.94 (25.1 - 39.7)
FOL	14.9 $\pm$ 1.16 (13.42 - 16.8)	14.91 $\pm$ 0.85 (13.82 - 15.98)	14.09 $\pm$ 0.87 (12.58 - 16.1)	15.02 $\pm$ 0.89 (13.5 - 16.3)	15.05 $\pm$ 0.86 (13.55 - 16.3)	18.46 $\pm$ 0.93 (16.5 - 20.1)
TFL	9.1 $\pm$ 1.26 (7.57 - 10.56)	10.16 $\pm$ 0.45 (9.72 - 11.08)	9.2 $\pm$ 1.47 (6.78 - 11.24)	8.68 $\pm$ 1.4 (5.06 - 10.47)	9.85 $\pm$ 0.71 (8.67 - 10.92)	13.37 $\pm$ 0.76 (11.77 - 14.48)
RUL	5.32 $\pm$ 0.36 (4.69 - 5.56)	5.76 $\pm$ 0.66 (4.89 - 6.81)	5.87 $\pm$ 0.54 (4.83 - 6.7)	6.44 $\pm$ 0.5 (5.67 - 7.33)	6.16 $\pm$ 0.58 (4.6 - 7.03)	7.71 $\pm$ 0.6 (6.83 - 8.82)
HAL	7.83 $\pm$ 0.79 (6.69 - 9.14)	8.02 $\pm$ 0.7 (7.27 - 9.52)	8.01 $\pm$ 0.58 (6.9 - 8.89)	9.15 $\pm$ 0.56 (8.5 - 10.57)	9.65 $\pm$ 0.63 (8.31 - 11.12)	12.23 $\pm$ 0.92 (10.65 - 13.76)
HH	7.23 $\pm$ 0.67 (6.52 - 8.21)	7.07 $\pm$ 0.51 (6.43 - 7.67)	6.99 $\pm$ 0.62 (5.77 - 8.09)	7.45 $\pm$ 0.61 (6.31 - 8.42)	6.82 $\pm$ 0.47 (6.04 - 7.5)	8.18 $\pm$ 0.58 (6.84 - 9.06)
HW	9.84 $\pm$ 0.61 (9.08 - 10.58)	9.59 $\pm$ 0.45 (9.02 - 10.19)	9.56 $\pm$ 0.71 (8.03 - 10.55)	11.22 $\pm$ 0.94 (9.7 - 13.05)	10.73 $\pm$ 0.85 (8.95 - 11.71)	13.14 $\pm$ 1.05 (11.31 - 14.71)
HL	11.96 $\pm$ 0.72 (10.96 - 13.06)	11.78 $\pm$ 0.83 (10.94 - 12.9)	11.76 $\pm$ 0.63 (10.43 - 12.71)	12.97 $\pm$ 0.92 (11.43 - 14.65)	12.04 $\pm$ 0.77 (10.58 - 13.17)	14.42 $\pm$ 1.04 (12.47 - 15.9)
EH	1.99 $\pm$ 0.23 (1.7 - 2.27)	2.2 $\pm$ 0.26 (2 - 2.62)	1.84 $\pm$ 0.22 (1.5 - 2.21)	2.05 $\pm$ 0.19 (1.72 - 2.55)	2.07 $\pm$ 0.17 (1.77 - 2.37)	2.46 $\pm$ 0.24 (2.09 - 2.9)
EL	3.15 $\pm$ 0.19 (2.91 - 3.42)	3.07 $\pm$ 0.21 (2.63 - 3.32)	2.83 $\pm$ 0.26 (2.35 - 3.3)	3.29 $\pm$ 0.3 (2.84 - 4.01)	3.37 $\pm$ 0.23 (2.85 - 3.81)	3.86 $\pm$ 0.19 (3.59 - 4.18)
RND	2.15 $\pm$ 0.14 (2.02 - 2.42)	1.95 $\pm$ 0.2 (1.69 - 2.25)	2.05 $\pm$ 0.2 (1.72 - 2.5)	2.27 $\pm$ 0.13 (1.97 - 2.48)	2.15 $\pm$ 0.16 (1.83 - 2.41)	2.38 $\pm$ 0.19 (2.08 - 2.73)
RH	1.04 $\pm$ 0.13 (0.84 - 1.18)	0.85 $\pm$ 0.2 (0.55 - 1.09)	0.93 $\pm$ 0.11 (0.76 - 1.11)	0.99 $\pm$ 0.11 (0.79 - 1.19)	1.03 $\pm$ 0.09 (0.87 - 1.2)	1.19 $\pm$ 0.1 (1.01 - 1.35)
RL	2.64 $\pm$ 0.15 (2.4 - 2.78)	2.51 $\pm$ 0.13 (2.31 - 2.69)	2.37 $\pm$ 0.18 (2.08 - 2.79)	2.7 $\pm$ 0.25 (2.14 - 3.02)	2.77 $\pm$ 0.18 (2.46 - 3.12)	3.13 $\pm$ 0.21 (2.61 - 3.47)
DRE	5.08 $\pm$ 0.26 (4.78 - 5.45)	4.9 $\pm$ 0.26 (4.53 - 5.31)	4.95 $\pm$ 0.31 (4.43 - 5.52)	5.59 $\pm$ 0.4 (4.78 - 6.41)	5.36 $\pm$ 0.35 (4.56 - 5.89)	6.18 $\pm$ 0.4 (5.47 - 6.88)
AH	1.95 $\pm$ 0.32 (1.6 - 2.44)	1.95 $\pm$ 0.3 (1.6 - 2.56)	1.83 $\pm$ 0.21 (1.5 - 2.23)	2.15 $\pm$ 0.22 (1.85 - 2.61)	2.22 $\pm$ 0.3 (1.63 - 2.95)	2.54 $\pm$ 0.26 (1.95 - 2.95)
AL	1.27 $\pm$ 0.4 (0.86 - 1.81)	1.51 $\pm$ 0.31 (1.11 - 2.1)	1.15 $\pm$ 0.14 (0.87 - 1.39)	1.77 $\pm$ 0.19 (1.38 - 2.16)	1.67 $\pm$ 0.24 (1.22 - 2.24)	2.04 $\pm$ 0.31 (1.49 - 2.57)

All of these analyses reveal significant meristic, morphometric, nuclear and mitochondrial DNA differences among all six species in this group, the two new species are formally named and described below.

**TABLE 2.** Values of meristic variables from species of the *lineomaculatus* group, sample sizes are shown in parentheses, as well as mean  $\pm$  SD (min – max); abbreviations for characters are defined in Appendix II.

Var	<i>L. morandae</i> sp. nov. (n=6)	<i>L. avilae</i> sp. nov. (n=8)	<i>L. lineomaculatus</i> (n=17)
SCI	6.33 $\pm$ 0.52 (6–7)	8.13 $\pm$ 1.25 (7–10)	7.18 $\pm$ 1.07 (6–10)
LS	4 $\pm$ 0.89 (3–5)	4.38 $\pm$ 0.52 (4–5)	4.41 $\pm$ 0.71 (4–6)
SS	7.17 $\pm$ 1.94 (5–10)	5.25 $\pm$ 0.46 (5–6)	6.71 $\pm$ 0.92 (5–8)
IS	5.33 $\pm$ 0.52 (5–6)	4.63 $\pm$ 0.74 (4–6)	4.76 $\pm$ 0.56 (4–6)
MS	59.83 $\pm$ 2.71 (55–63)	55.5 $\pm$ 2.67 (53–59)	60 $\pm$ 3.39 (54–65)
DS	51.67 $\pm$ 3.5 (47–57)	53.75 $\pm$ 2.12 (51–58)	58.41 $\pm$ 3.84 (52–68)
VS	81.33 $\pm$ 2.94 (79–85)	83 $\pm$ 6.32 (72–91)	85.29 $\pm$ 4.48 (80–95)
IL3	15.33 $\pm$ 1.21 (13–16)	16.25 $\pm$ 0.89 (15–18)	16.18 $\pm$ 1.29 (14–19)
IL4	21.17 $\pm$ 1.72 (18–23)	21.29 $\pm$ 0.95 (20–23)	21.41 $\pm$ 1.58 (19–25)

continued.

Var	<i>L. hatcheri</i> (n=20)	<i>L. kolengh</i> (n=31)	<i>L. silvanae</i> (n=17)
SCI	6.85 $\pm$ 1.39 (5–10)	6.26 $\pm$ 0.89 (4–8)	6.94 $\pm$ 1.03 (5–8)
LS	4.5 $\pm$ 0.69 (4–6)	4.29 $\pm$ 0.59 (3–5)	4.18 $\pm$ 0.64 (3–5)
SS	6.85 $\pm$ 0.75 (6–8)	6.65 $\pm$ 0.8 (5–8)	6.18 $\pm$ 0.73 (5–7)
IS	5.25 $\pm$ 0.79 (4–7)	5.29 $\pm$ 0.53 (5–7)	4.88 $\pm$ 0.7 (4–6)
MS	48.65 $\pm$ 3.33 (43–57)	50.55 $\pm$ 2.55 (44–55)	59.65 $\pm$ 2.89 (55–65)
DS	48.75 $\pm$ 3.49 (43–55)	49.35 $\pm$ 2.78 (44–54)	56 $\pm$ 3.12 (52–64)
VS	67.8 $\pm$ 3.37 (62–74)	68.58 $\pm$ 3.89 (61–76)	74.59 $\pm$ 2.74 (70–80)
IL3	14.85 $\pm$ 1.39 (13–18)	14.6 $\pm$ 0.93 (13–16)	16.24 $\pm$ 1.15 (14–18)
IL4	19.45 $\pm$ 1.28 (18–22)	18.74 $\pm$ 1.46 (16–22)	20.24 $\pm$ 1.39 (18–23)

### *Liolaemus morandae* sp. nov.

(Figure 3–6)

**2001.** *Liolaemus lineomaculatus*, Ibarguengoytía, N., Casalins, L., Schulte II, J.A., Amico, G.A. and Sympson, L., *Herpetological Review*, 32, 120.

**Holotype.** MLP.S 2626 (Figure 3), an adult male from Provincial Road 37, 22.8 km SW junction National Road 3, Escalante department, Chubut province, Argentina (45°41'10.6" S; 67°53'49.9" W, 693 m) (Figures 4, 5); L.J. Avila, M. Kozykariski, M.F. Breitman and R. Martinez collectors, 12<sup>th</sup> March 2010.

**Paratypes.** LJAMM-CNP 13020, adult female and LJAMM-CNP 13021, juvenile; same locality as holotype. LJAM-CNP 9677-9679, adult females and LJAMM-CNP 9680, juvenile; from Holdich station, Escalante department, Chubut province, Argentina (45°58'00.1" S; 68°11'58.8" W, 761 m); L.J. Avila, C.H.F. Pérez, M.F. Breitman and N. Feltrin collectors, 2<sup>nd</sup> February 2008. LJAMM-CNP 10201, adult male and LJAM-CNP 10202, juvenile; from Provincial Road 37, 2.5 km W junction National Road 3, Escalante department, Chubut province, Argentina (45°37'43.4" S; 67°41'03.6" W, 637 m); L.J. Avila, C.H.F. Pérez, M.F. Breitman and N. Feltrin collectors, 2<sup>nd</sup> February 2008.

**Diagnosis.** *Liolaemus morandae* sp. nov. is a member of the *L. lineomaculatus* section, included in the *lineomaculatus* group, and is characterized by the absence of precloacal pores in both sexes, and presence of dorsal trifold scales (Etheridge 1995). Molecular evidence includes this species in the *lineomaculatus* group, closely related to the clade (*L. sp. 2* + *L. lineomaculatus*) Figure 1. All the following differences are summarized in Tables 1 to 4 and in Figure 6.



**FIGURE 3.** Upper, dorsal and ventral views of male holotype in life of *Liolaemus morandae* **sp. nov.** MLPS 2626; lower, dorsal and ventral views of female (LJAMM-CNP 13020).

Relative to *L. lineomaculatus*, *L. morandae* **sp. nov.** has fewer dorsal scales (47–57,  $X = 51.67$  vs. 52–68,  $X = 58.41$ ;  $p < 0.0001$ ), fewer third finger lamellae (13–16,  $X = 15.33$  vs. 14–19,  $X = 16.18$ ;  $p < 0.0001$ ), shorter fourth toe length (13.4–16.8,  $X = 14.9$  vs. 12.6–16.1,  $X = 14.09$ ;  $p < 0.0001$ ) and a larger eye (eye height: 1.7–2.27,  $X = 1.99$  vs. 1.5–2.21,  $X = 1.84$ , eye length: 2.91–3.42,  $X = 3.15$  vs. 2.35–3.3,  $X = 2.83$ ;  $p < 0.0001$  in both cases). *Liolaemus morandae* **sp. nov.** has more dorsal blotches than *L. lineomaculatus*, and the blotches in *L. morandae* **sp. nov.** have (in 50% of the cases) a yellow-orange coloration while *L. lineomaculatus* blotches have dark gray color.

In general, dorsal scales of *L. morandae* **sp. nov.** are more mucronated than those of *L. lineomaculatus*, and dorsal leg scales of *L. morandae* **sp. nov.** are less carinated with respect to *L. lineomaculatus*.

Compared to *L. hatcheri*, *L. morandae* **sp. nov.** has higher number of midbody scales (55–63,  $X = 59.83$  vs. 43–57,  $X = 48.65$   $p < 0.0001$ ), larger number of scales from occiput to rump (47–57,  $X = 51.67$  vs. 43–55,  $X = 48.75$ ;  $p < 0.0001$ ), more ventral scales (79–85,  $X = 81.33$  vs. 62–74,  $X = 67.8$ ;  $p < 0.0001$ ), more fourth toe lamellae (18–23,  $X = 21.17$  vs. 18–22,  $X = 19.45$ ;  $p < 0.0001$ ), smaller body size (snout-vent length: 50–61,  $X = 55.67$  vs. 55–69,  $X = 61.89$ , axilla-groin distance: 19.7–30.8,  $X = 25.9$  vs. 19.5–35.5,  $X = 28.95$ ;  $p < 0.0001$  in both cases), shorter forelimbs (elbow-wrist length: 4.69–5.56,  $X = 5.32$  vs. 5.67–7.33,  $X = 6.44$ , third finger length: 6.69–9.14,  $X = 7.83$  vs. 8.5–10.57,  $X = 9.15$ ;  $p < 0.0001$  in both cases), smaller head (head width: 9.08–10.58,  $X = 9.84$  vs. 9.7–13.05,  $X = 11.22$ , head length: 10.96–13.06,  $X = 11.96$  vs. 11.43–14.65,  $X = 12.97$ ;  $p < 0.0001$  in both cases), and smaller auditory meatus (auditory meatus height: 1.6–2.44,  $X = 1.95$  vs. 1.85–2.61,  $X = 2.15$ ; auditory meatus length: 0.86–1.81,  $X = 1.27$  vs. 1.38–2.16,  $X = 1.77$ ;  $p < 0.0001$  in both cases). *Liolaemus morandae* **sp. nov.** has more dorsal blotches and better defined vertebral and paravertebral lines than *L. hatcheri*; ventral melanism is more pronounced in *L. hatcheri*, while *L. morandae* **sp. nov.** has fewer melanophores. Dorsal scales of *L. morandae* **sp. nov.** are less “bristly” than those of *L. hatcheri*. Dorsal and ventral limb scales are non-mucronate and carinate in *L. morandae* **sp. nov.** while in *L. hatcheri* they are mucronate and non-carinate. Belly scales are round-shaped in *L. morandae* **sp. nov.** and rhomboidal in *L. hatcheri*.

*Liolaemus morandae* **sp. nov.** differs from *L. kolengh* in the following traits: larger number of midbody scales (55–63,  $X = 59.83$  vs. 44–55,  $X = 50.55$ ;  $p < 0.0001$ ), larger number of scales from occiput to rump (47–57,  $X = 51.67$  vs. 44–54,  $X = 49.35$ ;  $p < 0.0001$ ), more ventral scales (79–85,  $X = 81.33$  vs. 61–76,  $X = 68.58$ ;  $p < 0.0001$ ), larger number of fourth toe lamellae (18–23,  $X = 21.17$  vs. 16–22,  $X = 18.74$ ;  $p < 0.0001$ ), shorter forelimbs (elbow-wrist length: 4.69–5.56,  $X = 5.32$  vs. 4.6–7.03,  $X = 6.16$ , third finger length: 6.69–9.14,  $X = 7.83$  vs. 8.31–11.12,  $X = 9.65$ ;  $p < 0.0001$  in both cases), smaller auditory meatus (auditory meatus height: 1.6–2.44,  $X = 1.95$  vs. 1.63–2.95,  $X = 2.22$ , auditory meatus length: 0.86–1.81,  $X = 1.27$  vs. 1.22–2.24,  $X = 1.67$ ;  $p < 0.0001$  in both cases) and longer tail (61–79,  $X = 70.33$  vs. 47–70,  $X = 60.52$ ;  $p = 0.0019$ ). *Liolaemus morandae* **sp. nov.** has more dorsal blotches and better defined vertebral and paravertebral lines than *L. kolengh*; ventral melanism is stronger in *L. kolengh* than in *L. morandae* **sp. nov.**; the general background coloration of *L. kolengh* is dark gray or black, though in almost 50% of our samples the dorsal pattern cannot be recognized. In general, the dorsal scales of *L. morandae* **sp. nov.** are less “bristly” than those of *L. kolengh*. Dorsal and ventral limb scales are non-mucronate and non-bristly in *L. morandae* **sp. nov.**, but mucronate and “bristly” in *L. kolengh*.

*Liolaemus morandae* **sp. nov.** differs from *L. silvanae* in several characters, including: a smaller number of scales from occiput to rump (47–57,  $X = 51.67$  vs. 52–64,  $X = 56$ ;  $p < 0.0001$ ), higher number of ventral scales (79–85,  $X = 81.33$  vs. 70–85,  $X = 74.59$ ;  $p < 0.0001$ ), fewer third finger lamellae (13–16,  $X = 15.33$  vs. 14–18,  $X = 16.24$ ;  $p < 0.0001$ ), smaller body size (snout-vent length: 50–61,  $X = 55.67$  vs. 65–78,  $X = 73$ , axilla-groin distance: 19.7–30.8,  $X = 25.9$  vs. 25.1–39.7,  $X = 32.38$ ;  $p < 0.0001$  in both cases), shorter forelimbs (elbow-wrist length: 4.69–5.56,  $X = 5.32$  vs. 6.83–8.82,  $X = 7.71$ , third finger length: 6.69–9.14,  $X = 7.83$  vs. 10.65–13.76,  $X = 12.23$ ;  $p < 0.0001$  in both cases), smaller head (head height: 6.52–8.21,  $X = 7.23$  vs. 6.84–9.06,  $X = 8.18$ , head width: 9.08–10.58,  $X = 9.84$  vs. 11.31–14.71,  $X = 13.14$ , head length: 10.96–13.06,  $X = 11.96$  vs. 12.47–15.9,  $X = 14.42$ ;  $p < 0.0001$  in all cases), smaller eye (eye height: 1.7–2.27,  $X = 1.99$  vs. 2.09–2.9,  $X = 2.46$ , eye length: 2.91–3.42,  $X = 3.15$  vs. 3.59–4.18,  $X = 3.86$ ;  $p < 0.0001$  in both cases), and smaller auditory meatus (auditory meatus height: 1.6–2.44,  $X = 1.95$  vs. 1.95–2.95,  $X = 2.54$ ; auditory meatus length: 0.86–1.81,  $X = 1.27$  vs. 1.49–2.57,  $X = 2.04$ ;  $p < 0.0001$  in both cases). The general background coloration of *L. silvanae* is black; there is no recognizable dorsal pattern, and the venter is also strongly melanistic, whereas the venter is weakly melanistic in *L. morandae* **sp. nov.** *Liolaemus morandae* **sp. nov.** possesses well-defined vertebral and paravertebral lines that are not present in *L. silvanae*. In general, *L. silvanae* possesses a “bristly” appearance that is not present in *L. morandae* **sp. nov.** Limb scales are less mucronated in *L. morandae* **sp. nov.** than in *L. silvanae*.

**Description of holotype.** Adult male. Snout-vent length 56.0 mm. Tail length (complete, not regenerated) 79.0 mm. Axilla-groin distance 22.8 mm. Auditory meatus-eye distance 4.8 mm. External auditory meatus conspicuous, higher (2.1 mm) than wide (1.2 mm). Head length 13.0 mm (from anterior border of tympanum to tip of snout), 10.5 mm wide (at anterior border of tympanum), 7.8 mm high (at anterior border of tympanum). Snout length 4.0 mm (orbit-tip of snout distance). Interorbital distance 4.2 mm. Eye-nostril distance 3.1 mm. Forelimb length 16.7 mm. Tibial length 10.3 mm. Foot length 16.8 mm (ankle to tip of claw on fourth toe).

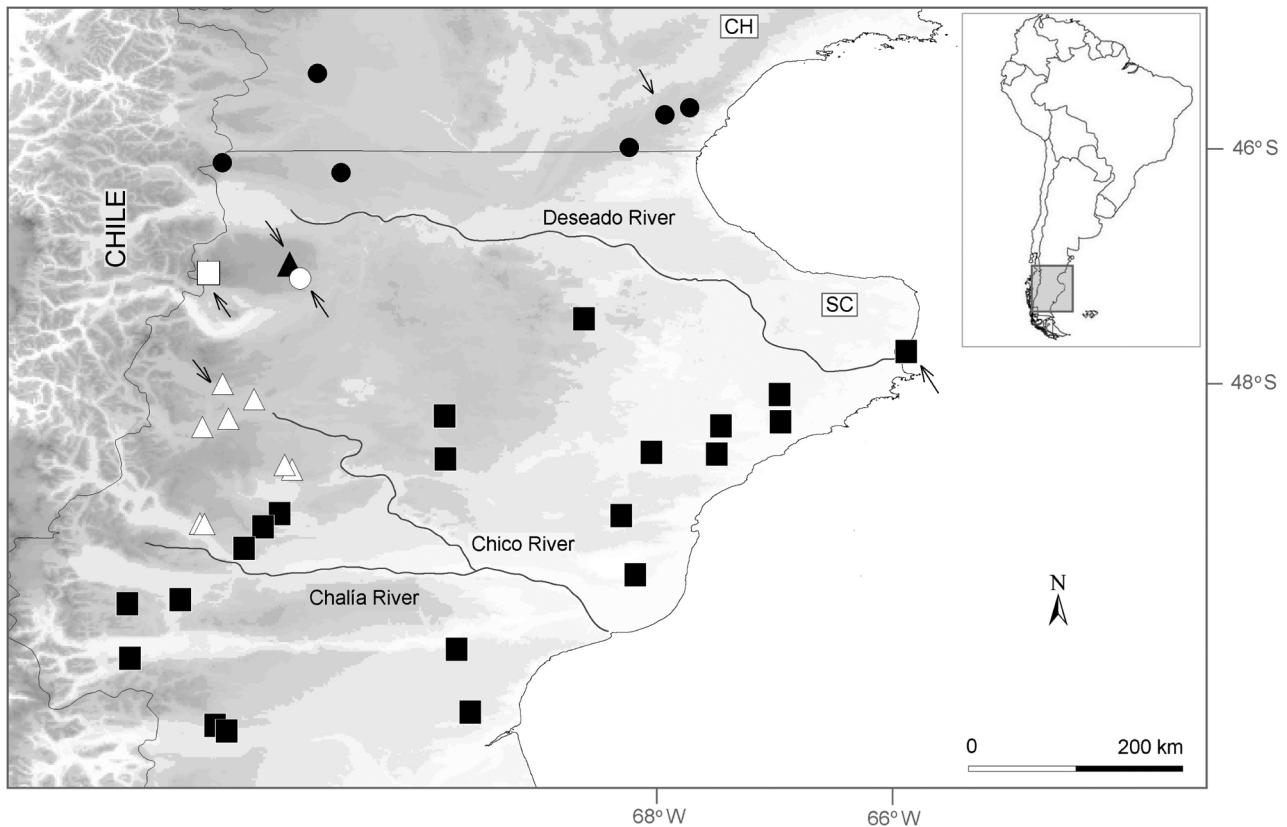


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**FIGURE 4.** Type locality of *Liolaemus morandae* sp. nov., Patagonic phytogeographic province, del Golfo de San Jorge District (45°41'10,6" S; 67°53'49,9" W, 693 m).



**FIGURE 5.** Distribution map for species of the *lineomaculatus* group, with geographical localities sampled in this study superimposed on regional elevation (shading). Black circles: *L. morandae* sp. nov.; white circle: *L. avilae* sp. nov.; black squares: *L. lineomaculatus*; white square: *L. kolengh*; white triangles: *L. hatcheri*; black triangle: *L. silvanae*. Arrows indicate type localities. CH: Chubut province; SC: Santa Cruz province.

Dorsal head scales bulged, smooth, 15 between occiput, at the level of anterior border of tympanum, to rostral, pitted with numerous scale organs in the anterior region, and reducing to a single organ, or lack, in the posterior half of the head. Rostral scale wider (2.4 mm) than high (0.9 mm). Two postrostrals, together with anterior lorilabial, separate nasal scales from rostral, surrounded by six scales. Nasal scales longer than wide, irregularly hexagonal; nostril one-half length of nasal, posterior in position. Scales surrounding nasals 7 on the left side and 8 on the right side. Four internasals. Frontonasals six, irregular in size and position. Prefrontals 6, a small rhomboidal scale in the center (0.9 mm). Three dorso-lateral larger scales, one for the fragmentation of the right scale, and a pair lateral medium-sized scales (1.3 mm), approximately quadrangular. Two frontal scales. Frontoparietals in two rows, one anterior and one posterior scale, unfragmented. Interparietal pentagonal, surrounded by six scales; four smaller and irregular in front and sides, two larger in back. Parietal eye evident. Parietals slightly bulged, irregularly shaped, equal in size to interparietal (1.5 vs. 1.5 mm). Circumorbitals: 13–10. Transversally expanded supraoculars 4–3. Smaller lateral supraoculars: 16–17. One canthal higher than wide, separated from nasal by one postnasal. Loreal scales bulged, two on the left side (by fusion of the posterior loreal scale with preocular scale) and three on the right side. Lorilabials longer than wide (8–6), approximately equal to labials. Superciliaries 7–7, flattened and elongated, anterior five broadly overlapping dorsally. Orbit with 15–17 upper and 12–13 lower ciliaries on each side. Orbit diameter 4.5 x 1.9 mm. Preocular small, unfragmented, longer than wide. Subocular scale elongated, approximately nine times longer than wide (3.7 x 0.6 mm). A well marked longitudinal ridge along upper margin of preocular and subocular scales. Postocular small, slightly bulged, quarter superimposed to subocular, with a marked longitudinal ridge. Palpebral scales small granular and bulged. Supralabials 9–10, convex. Temporals smooth, convex, juxtaposed with one scale organ in the tip. Anterior auriculars smaller than adjacent posterior temporals, slightly projecting outward (3–2). Posterior auriculars small and granular. External auditory meatus conspicuous, higher (2.1 mm) than wide (1.2 mm). Lateral scales of neck granular with inflated skin. Mental scale wider (2.9 mm) than high (1.4 mm), in contact with four scales. Mental posterior followed by two postmentals, and

two rows of three chinshields on each side. Six infralabials on each side, first on each side quadrangular two times wider than supralabials, all others elongated, slightly smaller than supralabials. Gular scales smooth, flat, imbricate, with rounded posterior margins, with melanophores. Scales of throat between chinshields slightly juxtaposed, becoming slightly imbricate toward auditory meatus. Thirty gulars between tympanum openings. Infralabials separated from chinshields by one to two rows of scales.

Antehumeral, longitudinal and postauricular neck folds well developed; gular, rictal, dorsolateral and oblique not conspicuous.

Scales of dorsal neck region rhomboidal, imbricate and strongly keeled. Fifty dorsal scales between occiput and anterior surface of thighs. Dorsal body scales rhomboidal, imbricate, strongly keeled, mucronate, very few trifid scales. Dorsal scales grade laterally into slightly smaller, slightly keeled scales at midbody. Scales immediately anterior and posterior to forelimb and hindlimb insertion small, smooth, granular, and non-overlapping. Body lateral scales grading smaller to larger at midbody. Ventral body scales rhomboidal, smooth, flat, imbricate, larger than dorsal scales. Sixty-one midbody scales; scales between mental and precloacal pores 85. Scales of cloacal region about equal in size to ventral body scales; without precloacal pores.

Anterior suprabrachials rhomboidal, imbricate, smooth, slightly larger in size to dorsal body scales. Postbrachials smaller, smooth, becoming granular near axilla. Supra-antibrachials similar to suprabrachial. Infra-antibrachials rhomboidal, imbricate, smooth, toward the hand slightly mucronate. Supracarpals imbricated, rhomboidal, smooth. Infracarpals strongly imbricate, rhomboidal, slightly keeled, 3-mucronate. Subdigital lamellae with 2–5 keels, each terminating in a short mucron, 2–5 mucronate, numbering: I: 8, II: 12, III: 16, IV: 17, V: 11. Claws robust, curved and sharp, opaque brown.

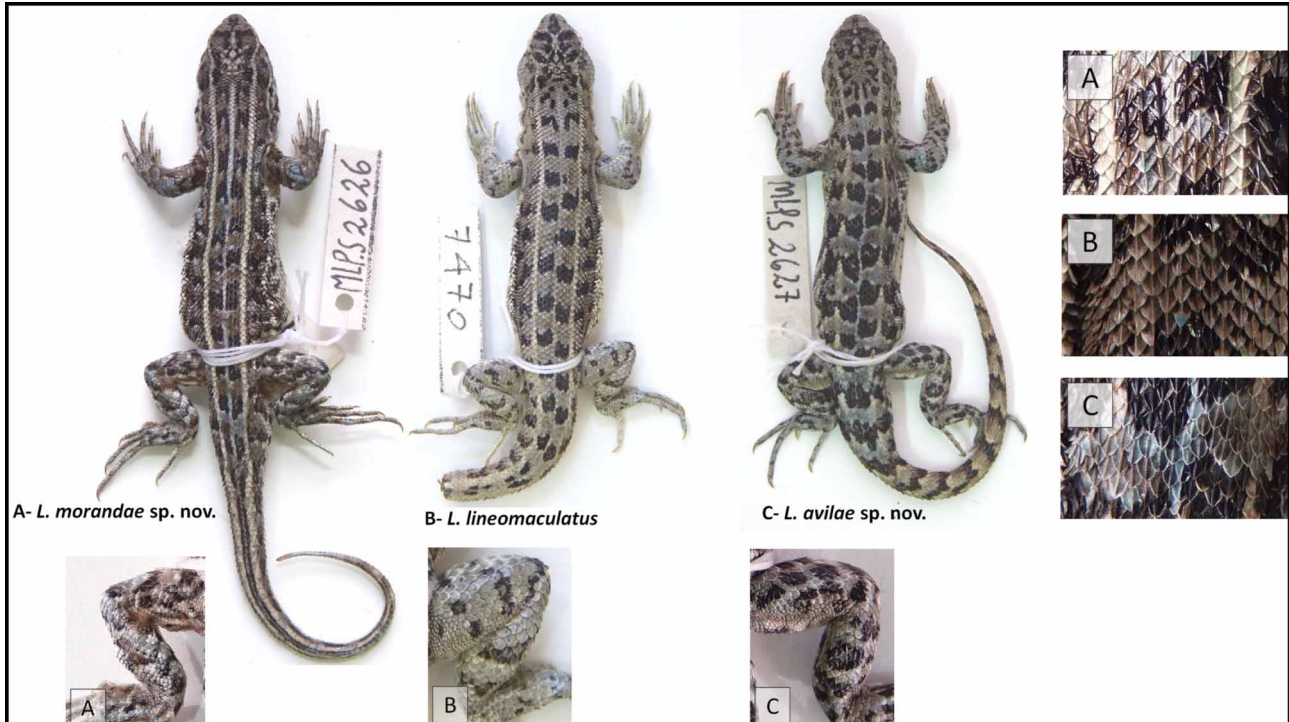
Suprafemorals as large as dorsal body scales, rhomboidal, imbricated, smooth near the body, toward to the knee slightly keeled. Postfemorals small, granular shape. Supratibials rhomboidal, imbricated, keeled, some mucronate, smaller and smooth toward to the foot. Infracarpals small, granular and smooth. Supratarsals rhomboidal, imbricated and smooth. Infracarpals small, rhomboidal, imbricate, smooth, mucronate, slightly keeled near the digit. Subdigital scales 1–3 keeled, 1–5 mucronate, numbering: I: 9, II: 14, III: 20, IV: 21, V: 14. Claws robust, curved and sharp, opaque brown. Tail complete, non-regenerated. Dorsal and lateral caudal scales, rhomboidal in the first half of the tail, becoming quadrangular toward the tip, strongly keeled. Ventrals subtriangular and smooth, toward posterior half moderate keeled.

**Color of holotype in life.** Dark grey dorsal background (Figure 3) that becomes lighter on the lateral region, between axilla and groin. Dorsal pattern presents twelve paravertebral, quadrangular, black blotches, extending from the nuchal to the postcloacal region, those series fuse into a dark line that is present to the tip of the tail. Dorsolateral region, in between the occipital and the tip of the tail, formed by black and white-bordered blotches. Lateral region, between axilla and groin, is characterized by a black and white reticulate pattern. In between the series of blotches, one white vertebral line and two light orange paravertebral longitudinal lines appear, one and one and a half scale wide, respectively. Vertebral line extends from the nuchal region, while the paravertebral lines extend from the temporal region; all of them continue to the tip of the tail. Dorsal region of the limbs are dark gray with a black reticulation.

Dark gray head background. Lateral white line along the longitudinal folds is present from the top of the auditory meatus to the antehumeral fold. White subocular scale with black longitudinal ridge. Dorsal surface with black blotches, one longitudinal blotch is present in the anterior part of the head, crossing through internasals, postnasals and prefrontals; two transverse blotches are crossing through postfrontals and first circumorbitals, and extend back to the last circumorbitals, forming a cross with the longitudinal blotch. The interparietal scale is surrounded by three small dark-brown blotches and the occipitals show a white longitudinal band of the same color.

White ventral color with a black reticulate pattern over the entire body, most strongly marked in the pectoral region and throat, and extending to the adjacent malar and maxilla region. Ventral scales with melanophores. Ventral area of chest, belly, cloacal region and limbs tinged with a light yellowish color. Cloacal and postcloacal region with few black blotches. Gray tail.

**Color of holotype in preservative.** After one year in preservative, the dorsal coloration of the head, dorsum, body flanks and tail becomes darker while maintaining the contrast, but the two yellowish paravertebral lines turned gray. Ventral scales of throat, neck, chest, belly and forelimbs retain the same coloration as in life, and the distinctive light ventral yellowish tinge of chest, belly, cloacal region and limbs turns gray (Figure 6).



**FIGURE 6.** Morphological comparison between *Liolaemus morandae* **sp. nov.** (A), *L. lineomaculatus* (B) and *L. avilae* **sp. nov.** (C). Notice differences in color pattern on the tails, size of blotches on the limbs and differences in vertebral and paravertebral lines. Dorsal scales (shown on the right) are less mucronated in *L. lineomaculatus*. Dorsal scales of hindlimbs are less carinated in *L. morandae* **sp. nov.** than in the other species, while they are more mucronated in *L. avilae* **sp. nov.**

**Variation.** Morphological and meristic character variation between males and females of *Liolaemus morandae* **sp. nov.**, are shown in Table 6. Females in life present basically the same dorsal and lateral pattern as present in males, but females generally have a lighter brown background coloration; vertebral and paravertebral lines are strongly defined, and in both sexes paravertebral lines vary from white to yellow. Ventrally, one male shows a light orange color on the belly, while in other males and all females the ventral region ranged from white to gray due to different degrees of melanism. All distinctive ventral light orange coloration changed to gray in preservative.

**Etymology.** The specific epithet of this species “*morandae*” refers to our colleague and the first author’s PhD advisor Dr. Mariana Morando, to honor her after more than ten years of research and teaching on the Patagonian herpetofauna.

**Distribution.** *Liolaemus morandae* **sp. nov.** is known only from the type locality and a few localities on the Pampa del Castillo Plateau; and from three localities from southern Chubut and northern Santa Cruz provinces. The holotype and some paratypes are from Provincial Road 37, 22.8 km SW junction National Road 3, Escalante department, Chubut province, Argentina (Figures 4, 5). The other paratypes are from Provincial Road 37, 2.5 km W junction National Road 3 in Holdich Station, Escalante department, Chubut province, Argentina (Figures 4, 5). The distance from the type locality to the first locality is more than 17.8 km airline, and more than 38.8 km airline to the second locality.

**Natural history.** *Liolaemus morandae* **sp. nov.** occurs in Patagónica province, Golfo de San Jorge District, in environments characterized as grasslands and steppe highlands (Roig 1998), with vegetation dominated by the shrubs *Stipa* spp., *Senecio filaginoides*, *Mulinum spinosum*, *Nassauvia* spp., among others. This species was found in open substrates, sharing the habitat with *Liolaemus kingii*, *L. bibronii*, *Diplolaemus bibronii* and *D. darwini* (Figure 4). Based on the natural history of its close relative *L. lineomaculatus*, we hypothesize that *L. morandae* **sp. nov.** is herbivorous and likely to also be viviparous, perhaps giving birth to between three and six neonates per clutch (Ceï 1986; Espinoza *et al.* 2004).

**TABLE 3.** Statistical tests of values presented in Table 1. Letters correspond to groups found by the Di Rienzo, Guzmán and Casanoves comparisons (DGC). ANOVA or Kruskal Wallis (KW), Shapiro-Wilks and Levene *p*-values are shown. To assume normality and variance homogeneity Shapiro-Wilks and Levene test should not be rejected (*p*>0.05). In six cases (identified as “non-parametric”) either normality or variance homogeneity was rejected, and for those comparisons a Kruskal Wallis test (non-parametric ANOVA test) was performed and *p*-values are shown.

Var	<i>L. morandae</i> sp. nov.	<i>L. avilae</i> sp. nov.	<i>L. lineomaculatus</i>	<i>L. hatcheri</i>	<i>L. kolengh</i>	<i>L. silvanae</i>	ANOVA or KW	Shapiro-Wilks	Levene
SVL	A	A	A	B	A	C	<0.0001 ***	0.2184	0.5449
TL	A-B (n=3)	B (n=8)	B (n=13)	A (n=9)	A (n=19)	A-B (n=9)	0.0019 **	non-parametric	
DFH	A	A	A	B	A	C	<0.0001 ***	0.697	0.2135
FOL	B	B	A	B	B	C	<0.0001 ***	0.1457	0.9732
TFL	A-B	B	A-B	A	B	C	<0.0001 ***	non-parametric	
RUL	A	B	B	C	C	D	<0.0001 ***	0.4858	0.7104
HAL	A	A	A	B	B	C	<0.0001 ***	0.384	0.3608
HH	A	A	A	A	A	B	<0.0001 ***	0.1767	0.8703
HW	A-B	A	A	C	B-C	D	<0.0001 ***	non-parametric	
HL	A	A	A	B	A	C	<0.0001 ***	0.2542	0.324
EH	B	B	A	B	B	C	<0.0001 ***	non-parametric	
EL	B	B	A	C	C	D	<0.0001 ***	0.8917	0.4724
RND	B	A	B	C	B	C	<0.0001 ***	0.4459	0.2274
RH	A-B	A	A	A-B	B	C	<0.0001 ***	non-parametric	
RL	B	A	A	B	B	C	<0.0001 ***	0.7419	0.3528
DRE	A	A	A	B	B	C	<0.0001 ***	0.4063	0.2821
AH	A	A	A	B	B	C	<0.0001 ***	0.7545	0.7538
AL	A-B	B-C	A	C-D	C	D	<0.0001 ***	non-parametric	

**TABLE 4.** Statistical tests of values presented in Table 2. Letters correspond to groups found by the DGC comparisons. ANOVA or Kruskal Wallis (KW), Shapiro-Wilks and Levene *p*-values are shown. To assume normality and variance homogeneity Shapiro-Wilks and Levene test should not be rejected (*p*>0.05). In two cases identified as “non-parametric”, either normality or variance homogeneity was rejected, for those ones KW test (non-parametric ANOVA test) was performed and *p*-values are shown. LS and IS variables are not shown because ANOVA or KW test was not significant.

Var	<i>L. morandae</i> sp. nov.	<i>L. avilae</i> sp. nov.	<i>L. lineomaculatus</i>	<i>L. hatcheri</i>	<i>L. kolengh</i>	<i>L. silvanae</i>	ANOVA or KW	Shapiro-Wilks	Levene
SCI	A	B	C	A	A	C	0.0027 **	non-parametric	
SS	B	A	B	B	B	B	0.0008***	non-parametric	
MS	C	B	C	A	A	C	<0.0001***	0.6695	0.8527
DS	B	B	C	A	A	C	<0.0001***	0.3285	0.4944
VS	C	C	D	A	A	B	<0.0001***	0.709	0.0987
IL3	A	B	B	A	A	B	<0.0001***	0.3209	0.2703
IL4	B	B	B	A	A	B	<0.0001***	0.2463	0.809

**TABLE 5.** Average pairwise genetic distances (expressed in percentage) calculated for cytochrome *b* (659 bp). Intragroup distances are presented in the first column, while uncorrected and corrected distances (in parentheses) are present in the second and third columns. These are comparisons among *L. morandae* **sp. nov.**, *L. avilae* **sp. nov.** and all other members of the *lineomaculatus* clade.

	Intragroup distance	<i>L. morandae</i> <b>sp. nov.</b>	<i>L. avilae</i> <b>sp. nov.</b>
<i>L. hatcheri</i>	1.26	12.4 (11.3)	11.5 (10.6)
<i>L. silvanae</i>	1.36	9.88 (8.78)	9.29 (8.3)
<i>L. kolengh</i>	0.12	9.61 (9.13)	8.99 (8.65)
<i>L. lineomaculatus</i>	1.35	7.64 (6.54)	5.86 (4.92)
<i>L. avilae</i> <b>sp. nov.</b>	0.83	4.61 (3.91)	
<i>L. morandae</i> <b>sp. nov.</b>	0.55		

**TABLE 6.** Variation between females and males of *L. morandae* **sp. nov.** and *L. avilae* **sp. nov.** Summarized as mean  $\pm$  SD (min – max) values for all meristic and morphometric (in millimeters) variables.

VAR	<i>L. morandae</i> <b>sp. nov.</b>		<i>L. avilae</i> <b>sp. nov.</b>	
	Females	Males	Females	Males
SCI	6.25 $\pm$ 0.5 (6–7)	6.5 $\pm$ 0.71 (6–7)	9 $\pm$ 1.73 (7–10)	7.6 $\pm$ 0.55 (7–8)
LS	4 $\pm$ 0.82 (3–5)	4 $\pm$ 1.41 (3–5)	4.33 $\pm$ 0.58 (4–5)	4.4 $\pm$ 0.55 (4–5)
SS	6.75 $\pm$ 1.71 (5–9)	8 $\pm$ 2.83 (6–10)	5.33 $\pm$ 0.58 (5–6)	5.2 $\pm$ 0.45 (5–6)
IS	5 $\pm$ 0 (5–5)	6 $\pm$ 0 (6–6)	4 $\pm$ 0 (4–4)	5 $\pm$ 0.71 (4–6)
MS	60.75 $\pm$ 1.71 (59–63)	58 $\pm$ 4.24 (55–61)	55.33 $\pm$ 3.21 (53–59)	55.6 $\pm$ 2.7 (53–59)
DS	52.5 $\pm$ 4.2 (47–57)	50 $\pm$ 0 (50–50)	54.33 $\pm$ 3.51 (51–58)	53.4 $\pm$ 1.14 (52–55)
VS	81 $\pm$ 2.83 (79–85)	82 $\pm$ 4.24 (79–85)	86.33 $\pm$ 4.04 (84–91)	81 $\pm$ 6.96 (72–90)
IL3	15.25 $\pm$ 1.5 (13–16)	15.5 $\pm$ 0.71 (15–16)	16 $\pm$ 0 (16–16)	16.4 $\pm$ 1.14 (15–18)
IL4	21.25 $\pm$ 2.22 (18–23)	21 $\pm$ 0 (21–21)	20.67 $\pm$ 0.58 (20–21)	21.75 $\pm$ 0.96 (21–23)
SVL	57 $\pm$ 4.24 (52–61)	53 $\pm$ 4.24 (50–56)	56.67 $\pm$ 2.08 (55–59)	54.6 $\pm$ 4.39 (48–59)
DFH	23.73 $\pm$ 3.49 (19.7–28.1)	30.25 $\pm$ 0.78 (29.7–30.8)	28.4 $\pm$ 1.05 (27.4–29.5)	23.44 $\pm$ 3.18 (19.4–26.9)
FOL	15.19 $\pm$ 1.17 (14.09–16.8)	14.31 $\pm$ 1.26 (13.42–15.2)	14.08 $\pm$ 0.43 (13.82–14.57)	15.54 $\pm$ 0.33 (15.19–15.98)
TFL	9.23 $\pm$ 1.47 (7.57–10.56)	8.84 $\pm$ 1.1 (8.06–9.62)	9.86 $\pm$ 0.18 (9.72–10.06)	10.34 $\pm$ 0.48 (9.79–11.08)
RUL	5.33 $\pm$ 0.43 (4.69–5.56)	5.29 $\pm$ 0.32 (5.06–5.51)	5.34 $\pm$ 0.37 (4.91–5.58)	6 $\pm$ 0.7 (4.89–6.81)
HAL	7.78 $\pm$ 1.02 (6.69–9.14)	7.94 $\pm$ 0.18 (7.81–8.06)	7.91 $\pm$ 0.34 (7.67–8.3)	8.09 $\pm$ 0.89 (7.27–9.52)
HH	7.09 $\pm$ 0.58 (6.52–7.89)	7.51 $\pm$ 1 (6.8–8.21)	6.66 $\pm$ 0.32 (6.43–7.03)	7.31 $\pm$ 0.45 (6.54–7.67)
HW	9.64 $\pm$ 0.62 (9.08–10.52)	10.26 $\pm$ 0.45 (9.94–10.58)	9.25 $\pm$ 0.07 (9.2–9.33)	9.79 $\pm$ 0.47 (9.02–10.19)
HL	11.88 $\pm$ 0.87 (10.96–13.06)	12.12 $\pm$ 0.52 (11.75–12.49)	11.07 $\pm$ 0.12 (10.94–11.16)	12.2 $\pm$ 0.78 (11.01–12.9)
EH	1.93 $\pm$ 0.26 (1.7–2.27)	2.1 $\pm$ 0.19 (1.96–2.23)	2.29 $\pm$ 0.28 (2.07–2.6)	2.14 $\pm$ 0.27 (2–2.62)
EL	3.14 $\pm$ 0.21 (2.91–3.42)	3.17 $\pm$ 0.2 (3.03–3.31)	3.13 $\pm$ 0.13 (3.02–3.27)	3.03 $\pm$ 0.25 (2.63–3.32)
RND	2.19 $\pm$ 0.17 (2.02–2.42)	2.09 $\pm$ 0.07 (2.04–2.14)	1.98 $\pm$ 0.26 (1.74–2.25)	1.93 $\pm$ 0.19 (1.69–2.16)
RH	0.97 $\pm$ 0.09 (0.84–1.06)	1.18 $\pm$ 0 (1.18–1.18)	0.86 $\pm$ 0.18 (0.73–1.06)	0.84 $\pm$ 0.24 (0.55–1.09)
RL	2.61 $\pm$ 0.18 (2.4–2.76)	2.69 $\pm$ 0.13 (2.6–2.78)	2.51 $\pm$ 0.18 (2.31–2.67)	2.51 $\pm$ 0.12 (2.36–2.69)
DRE	5.06 $\pm$ 0.31 (4.78–5.45)	5.13 $\pm$ 0.2 (4.99–5.27)	4.73 $\pm$ 0.18 (4.53–4.89)	5.01 $\pm$ 0.26 (4.64–5.31)
AH	2.03 $\pm$ 0.39 (1.6–2.44)	1.8 $\pm$ 0.08 (1.74–1.86)	1.8 $\pm$ 0.15 (1.68–1.96)	2.05 $\pm$ 0.34 (1.6–2.56)
AL	1.19 $\pm$ 0.43 (0.86–1.81)	1.42 $\pm$ 0.39 (1.14–1.69)	1.22 $\pm$ 0.11 (1.11–1.33)	1.68 $\pm$ 0.26 (1.44–2.1)
TL	66 $\pm$ 7.07 (61–71)	79 $\pm$ 0 (79–79)	67.33 $\pm$ 4.93 (64–73)	69.8 $\pm$ 5.02 (65–77)

***Liolaemus avilae* sp. nov.**

(Figures 6, 7)

**1971**, *Liolaemus lineomaculatus*, Donoso-Barros, R. and Cei, J.M., *Journal of Herpetology*, 5, 89–95.**1975**, *Liolaemus lineomaculatus*, Cei, J.M., *Herpetologica*, 31, 109–116.**1982**, *Liolaemus lineomaculatus*, Cei, J.M. and Scolaro, J.A., *Journal of Herpetology*, 16, 354–363.**1992**, *Liolaemus lineomaculatus*, Scolaro, J.A., *Acta zoologica lilloana*, 41, 287–293.

**Holotype.** MLPS 2627 (Figure 7), an adult male from Lago Buenos Aires plateau, 18.7 SW Puesto Lebrun, Lago Buenos Aires department, Santa Cruz province, Argentina (47°05'29.0" S, 71°01'12.9" W, 1154 m) (Figures 5, 8), L.J. Avila, C.H.F. Pérez, M.F. Breitman and N. Feltrin collectors, 9<sup>th</sup> January 2008.

**Paratypes.** LJAMM-CNP 9250, 9253, 9274, adult males, LJAMM-CNP 9276-9277, 9399, adult females and LJAMM-CNP 9251, 9252, juveniles; from same locality as holotype, L.J. Avila, C.H.F. Pérez, M.F. Breitman and N. Feltrin collectors, 9 January 2008. LJAMM-CNP 9243, an adult male from Puesto Lebrun, 27.3 km W Estancia La Vizcaina, Lago Buenos Aires Plateau, Lago Buenos Aires department, Santa Cruz province, Argentina (46°57'51.8" S, 71°06'27.2" W, 1353 m), L.J. Avila, C.H.F. Pérez, M.F. Breitman and N. Feltrin collectors, 8<sup>th</sup> January 2008.

**Diagnosis.** *Liolaemus avilae* sp. nov., a member of the *L. lineomaculatus* section and specifically the *lineomaculatus* group, has dorsal trifold scales but lacks of precloacal pores in either sex (Etheridge 1995); molecular evidence places this species in the *lineomaculatus* group, as the sister species to *L. lineomaculatus* (Breitman *et al.* 2011; see Tables 1 to 4 and Figure 6).

Relative to *L. morandae* sp. nov., *L. avilae* sp. nov. has more scales in contact with the interparietal scale (7–10, X = 8,13 vs. 6–7, X = 6.33;  $p = 0.0027$ ), fewer supralabial scales (5–6, X = 5.25 vs. 5–10, X = 7.17;  $p = 0.0008$ ), fewer midbody scales (53–59, X = 55.5 vs. 55–63, X = 59.83;  $p < 0.0001$ ), more third finger lamellae (15–18, X = 16.25 vs. 13–16, X = 15.33;  $p < 0.0001$ ), a longer elbow-wrist distance (4.89–6.81, X = 5.76 vs. 4.69–5.56, X = 5.32;  $p < 0.0001$ ), and a shorter rostral-nasal distance (1.69–2.25, X = 1.95 vs. 2.02–2.42, X = 2.15;  $p < 0.0001$ ). *Liolaemus avilae* sp. nov. has fewer dorsal blotches than *L. morandae* sp. nov., and the blotches in *L. morandae* sp. nov. have (50% of cases) brownish coloration, while *L. avilae* sp. nov. blotches have dark gray color. Ventral hand and foot surfaces of *L. morandae* sp. nov. present mucronated and “bristly” scales that are less obvious in *L. avilae* sp. nov.

*Liolaemus avilae* sp. nov. differs from *L. lineomaculatus* in the following traits: more scales in contact with the interparietal (7–10, X = 8,13 vs. 6–10, X = 7.18;  $p = 0.0027$ ), fewer supralabial scales (5–6, X = 5.25 vs. 5–8, X = 6.71;  $p = 0.0008$ ), fewer midbody scales (53–59, X = 55.5 vs. 54–65, X = 60;  $p < 0.0001$ ), fewer scales from occiput to rump (51–58, X = 53.75 vs. 52–68, X = 58.41;  $p < 0.0001$ ), fewer ventral scales (72–91, X = 83 vs. 80–95, X = 85.29;  $p < 0.0001$ ), larger eyes (eye height: 2–2.62, X = 2.2 vs. 1.5–2.21, X = 1.84, eye length: 2.63–3.32, X = 3.07 vs. 2.35–3.3, X = 2.83;  $p < 0.0001$  in both cases), and longer auditory meatus lengths (1.11–2.1, X = 1.51 vs. 0.87–1.39, X = 1.15;  $p < 0.0001$ ). *Liolaemus avilae* sp. nov. has fewer dorsal blotches than *L. lineomaculatus*. The vertebral line is less well defined in *L. avilae* sp. nov. than in *L. lineomaculatus*. In general, dorsal scales of *L. avilae* sp. nov. are more mucronated than in *L. lineomaculatus*. *Liolaemus avilae* sp. nov. possesses scales in the dorsal surface of the forelimbs that are less carinated than those of *L. lineomaculatus*.

Compared with *L. hatcheri*, *L. avilae* sp. nov. has more scales in contact with the interparietal (7–10, X = 8,13 vs. 5–10, X = 6.85;  $p = 0.0027$ ), fewer supralabial scales (5–6, X = 5.25 vs. 6–8, X = 6.85;  $p = 0.0008$ ), more midbody scales (53–59, X = 55.5 vs. 43–57, X = 48.65;  $p < 0.0001$ ), more scales from occiput to rump (51–58, X = 53.75 vs. 43–55, X = 48.75;  $p < 0.0001$ ), more ventral scales (72–91, X = 83 vs. 62–74, X = 67.8;  $p < 0.0001$ ), more third finger lamellae (15–18, X = 16.25 vs. 13–18, X = 14.85;  $p < 0.0001$ ), more fourth toe lamellae (20–23, X = 21.29 vs. 18–22, X = 19.45;  $p < 0.0001$ ), smaller body size (snout-vent length: 48–59, X = 55.38 vs. 55–69, X = 61.89, axilla-groin distance: 19.4–29.5, X = 25.5 vs. 19.5–35.5, X = 28.95;  $p < 0.0001$  in both cases), shorter forelimbs (elbow-wrist length: 4.89–6.81, X = 5.76 vs. 5.67–7.33, X = 6.44, third finger length: 7.27–9.52, X = 8.02 vs. 8.5–10.57, X = 9.15;  $p < 0.0001$  in both cases), and smaller head width (9.02–10.19, X = 9.59 vs. 9.7–13.05, X = 11.22;  $p < 0.0001$ ). *Liolaemus avilae* sp. nov. possesses fewer dorsal blotches and a more defined vertebral line relative to *L. hatcheri*. Ventral melanism is more pronounced in *L. hatcheri* than in *L. avilae* sp. nov. (fewer melanophores). Dorsal scales of *L. avilae* sp. nov. are less “bristly” than those of *L. hatcheri*. In the new species, limb surface scales (fore-hind and dorsal-ventral) are non-mucronate and carinated (in *L. hatcheri* the

majority are mucronated and non-carinate). Ventral scales are round-shaped in *L. avilae* **sp. nov.** and rhomboidal in *L. hatcheri*.

Compared with *L. kolengh*, *L. avilae* **sp. nov.** has fewer scales in contact with the interparietal (7–10,  $X = 8.13$  vs. 4–8,  $X = 6.26$ ;  $p = 0.0027$ ), fewer supralabial scales (5–6,  $X = 5.25$  vs. 5–8,  $X = 6.65$ ;  $p = 0.0008$ ), more midbody scales (53–59,  $X = 55.5$  vs. 44–55,  $X = 50.55$ ;  $p < 0.0001$ ), more scales from occiput to rump (51–58,  $X = 53.75$  vs. 44–54,  $X = 49.35$ ;  $p < 0.0001$ ), more ventral scales (72–91,  $X = 83$  vs. 61–76,  $X = 68.58$ ;  $p < 0.0001$ ), more third finger lamellae (15–18,  $X = 16.25$  vs. 13–16,  $X = 14.6$ ;  $p < 0.0001$ ), more fourth toe lamellae (20–23,  $X = 21.29$  vs. 16–22,  $X = 18.74$ ;  $p < 0.0001$ ), longer tails (64–77,  $X = 68.88$  vs. 47–70,  $X = 60.52$ ,  $p = 0.0019$ ), shorter forelimbs (elbow-wrist length: 4.89–6.81,  $X = 5.76$  vs. 4.6–7.03,  $X = 6.16$ , third finger length: 7.27–9.52,  $X = 8.02$  vs. 8.31–11.12,  $X = 9.65$ ;  $p < 0.0001$  in both cases), smaller head width (9.02–10.19,  $X = 9.59$  vs. 8.95–11.71,  $X = 10.73$ ;  $p < 0.0001$ ), and smaller rostral scale (rostral height: 0.55–1.09,  $X = 0.85$  vs. 0.87–1.2,  $X = 1.03$ , rostral length 2.31–2.69,  $X = 2.51$  vs. 2.46–3.12,  $X = 2.77$ ;  $p < 0.0001$  in both cases). *Liolaemus avilae* **sp. nov.** exhibits a light background coloration, while the general background coloration of *L. kolengh* is dark gray or black; however, the dorsal pattern could not be recognized in around 50% of our samples. *Liolaemus kolengh* exhibits more dorsal blotches than *L. avilae* **sp. nov.** Ventral melanism is stronger in *L. kolengh* than in *L. avilae* **sp. nov.** In general, the dorsal scales of *L. avilae* **sp. nov.** are less “bristly” than scales of *L. kolengh*. Limb scales (fore-hind and dorsal-ventral) are non-mucronate and non-“bristly” in *L. avilae* **sp. nov.** (mucronated and “bristly” in *L. kolengh*).

*Liolaemus avilae* **sp. nov.** differs from *L. silvanae* in several characters, including: a smaller number of scales in contact with the interparietal (7–10,  $X = 8.13$  vs. 5–8,  $X = 6.94$ ;  $p = 0.0027$ ), fewer supralabial scales (5–6,  $X = 5.25$  vs. 5–7,  $X = 6.18$ ;  $p = 0.0008$ ), fewer midbody scales (53–59,  $X = 55.5$  vs. 55–65,  $X = 59.65$ ;  $p < 0.0001$ ), fewer scales from occiput to rump (51–58,  $X = 53.75$  vs. 52–64,  $X = 56$ ;  $p < 0.0001$ ), more ventral scales (72–91,  $X = 83$  vs. 70–80,  $X = 74.59$ ;  $p < 0.0001$ ), smaller body size (snout-vent length: 48–59,  $X = 55.38$  vs. 65–78,  $X = 73$ , axilla-groin distance: 19.4–29.5,  $X = 25.3$  vs. 25.1–39.7,  $X = 32.38$ ;  $p < 0.0001$  in both cases), shorter fourth toe length (13.82–15.98,  $X = 14.91$  vs. 16.5–20.1,  $X = 18.46$ ), shorter forelimbs (elbow-wrist length: 4.89–6.81,  $X = 5.76$  vs. 6.83–8.82,  $X = 7.71$ , third finger length: 7.27–9.52,  $X = 8.02$  vs. 10.65–13.76,  $X = 12.23$ ;  $p < 0.0001$  in both cases), smaller head (head height: 6.43–7.67,  $X = 7.07$  vs. 6.84–9.06,  $X = 8.18$ , head width: 9.02–10.19,  $X = 9.59$  vs. 11.31–14.71,  $X = 13.14$ , head length: 10.94–12.9,  $X = 11.78$  vs. 12.47–15.9,  $X = 14.42$ ;  $p < 0.0001$  in all cases), smaller eyes (eye height: 2–2.62,  $X = 2.2$  vs. 2.09–2.9,  $X = 2.46$ , eye length: 2.63–3.32,  $X = 3.07$  vs. 3.59–4.18,  $X = 3.86$ ;  $p < 0.0001$  in both cases), smaller rostral scale (rostral height: 0.55–1.09,  $X = 0.85$  vs. 1.01–1.35,  $X = 1.19$ , rostral length: 2.31–2.69,  $X = 2.51$  vs. 2.61–3.47,  $X = 3.13$ ;  $p < 0.0001$  in both cases), and smaller auditory meatus (auditory meatus height: 1.95–2.56,  $X = 1.95$  vs. 1.95–2.95,  $X = 2.54$ , auditory meatus length: 1.11–2.01,  $X = 1.51$  vs. 1.49–2.57,  $X = 2.04$ ;  $p < 0.0001$  in both cases). Background coloration in *L. silvanae* is black, there is a no recognizable dorsal pattern, and ventral area is strongly melanistic, whereas the ventral area is weakly melanistic in *L. avilae* **sp. nov.** *Liolaemus avilae* **sp. nov.** has a defined vertebral and paravertebral lines that are not present in *L. silvanae*. In general, *L. silvanae* possesses a “bristly” appearance that is absent in *L. avilae* **sp. nov.** Scales of limbs (fore-hind and dorsal-ventral) are less mucronated in *L. avilae* **sp. nov.** than in *L. silvanae*.

**Description of holotype.** Adult male. Snout-vent length 59.0 mm. Tail length (complete, not regenerated) 77.0 mm. Axilla-groin distance 26.9 mm. Head length 12.3 mm (from anterior border of tympanum to tip of snout), 10.1 mm wide (at anterior border of tympanum), 7.6 mm high (at anterior border of tympanum). Snout length 4.2 mm (orbit-tip of snout distance). Interorbital distance 4.5 mm. Eye-nostril distance 3.5 mm. Auditory meatus-eye distance 4.9 mm. Forelimb length 16.3 mm. Tibial length 11.0 mm. Foot length 15.9 mm (ankle to tip of claw on fourth toe).

Dorsal head scales bulged, smooth, 15 between occiput at level of anterior border of tympanum to rostral, pitted with numerous scale organs in the anterior region, and reducing to a single organ, or absence at the posterior half of the head. Rostral scale wider (2.8 mm) than high (0.8 mm). Two postrostrals, together with anterior lorilabial, separate nasal scales from rostral, surrounded by six scales. Nasal scales longer than wide, irregularly hexagonal, nostril one-half length of nasal, in a posterior position. Scales surrounding nasals 7 on the left side and 6 on the right side. Four internasals. Frontonasals four, irregular in size and position. Prefrontals 5, a small quadrangular scale in the center (1.1 mm), two dorso-lateral larger scales roughly hexagonal (1.7 mm), and a pair of lateral medium-sized scales (1.2 mm), approximately triangular. Three frontal scales. Frontoparietals in two rows, one anterior and two posterior scales. Interparietal pentagonal (1.3 mm), surrounded by seven scales; five in front and



sides, irregular in shape and size, and two larger posterior scales. Parietal eye evident. Parietals slightly bulged, irregularly shaped, similar in size to interparietal. Circumorbitals: 12–10. Transversally expanded supraoculars 5–4. Smaller lateral supraoculars: 16–19. One canthal higher than wide, separate from nasal by one postnasals. Loreal scales bulged, four on each side. Lorilabials longer than wide (7–6), approximately equal to labials. Superciliaries 7–8, flattened and elongated, anterior four broadly overlapping dorsally. Orbit with 12–15 upper and 13–11 lower ciliaries on each side. Orbit diameter 4.3 x 2.0 mm. Preocular small, unfragmented, square. Subocular scale elongated, approximately nine times longer than wide (3.8 x 0.6 mm). A well marked longitudinal ridge along upper margin of preocular and subocular scales. Postocular small, slightly bulged, ~ 25% superimposed onto subocular, with a marked longitudinal ridge. Palpebral scales small granular and bulged. Supralabials 6–5, convex. Temporals smooth, convex, juxtaposed with one scale organ in the tip. Anterior auriculars smaller than adjacent posterior temporals, projecting slightly outward (3–2). Posterior auricular scales small and granular. External auditory meatus conspicuous, higher (1.7 mm) than wide (1.2 mm). Lateral scales of neck granular with inflated skin. Mental scale wider (3.0 mm) than high (1.0 mm), in contact with four scales. Mental followed posteriorly by two postmentals, and two rows of three chinshields on each side. Infralabials 5-4 on each side, first on each side quadrangular two times wider than supralabials, all others elongated, slightly smaller than supralabials. Gular scales smooth, flat, imbricate, with rounded posterior margins, with melanophores. Scales of throat between chinshields slightly juxtaposed, becoming slightly imbricate toward auditory meatus. Thirty-seven gulars between tympanum openings. Infralabials separated from chinshields by one to two rows of scales. Antehumeral and longitudinal neck folds well developed; postauricular, rictal, dorsolateral, oblique and gular not conspicuous.

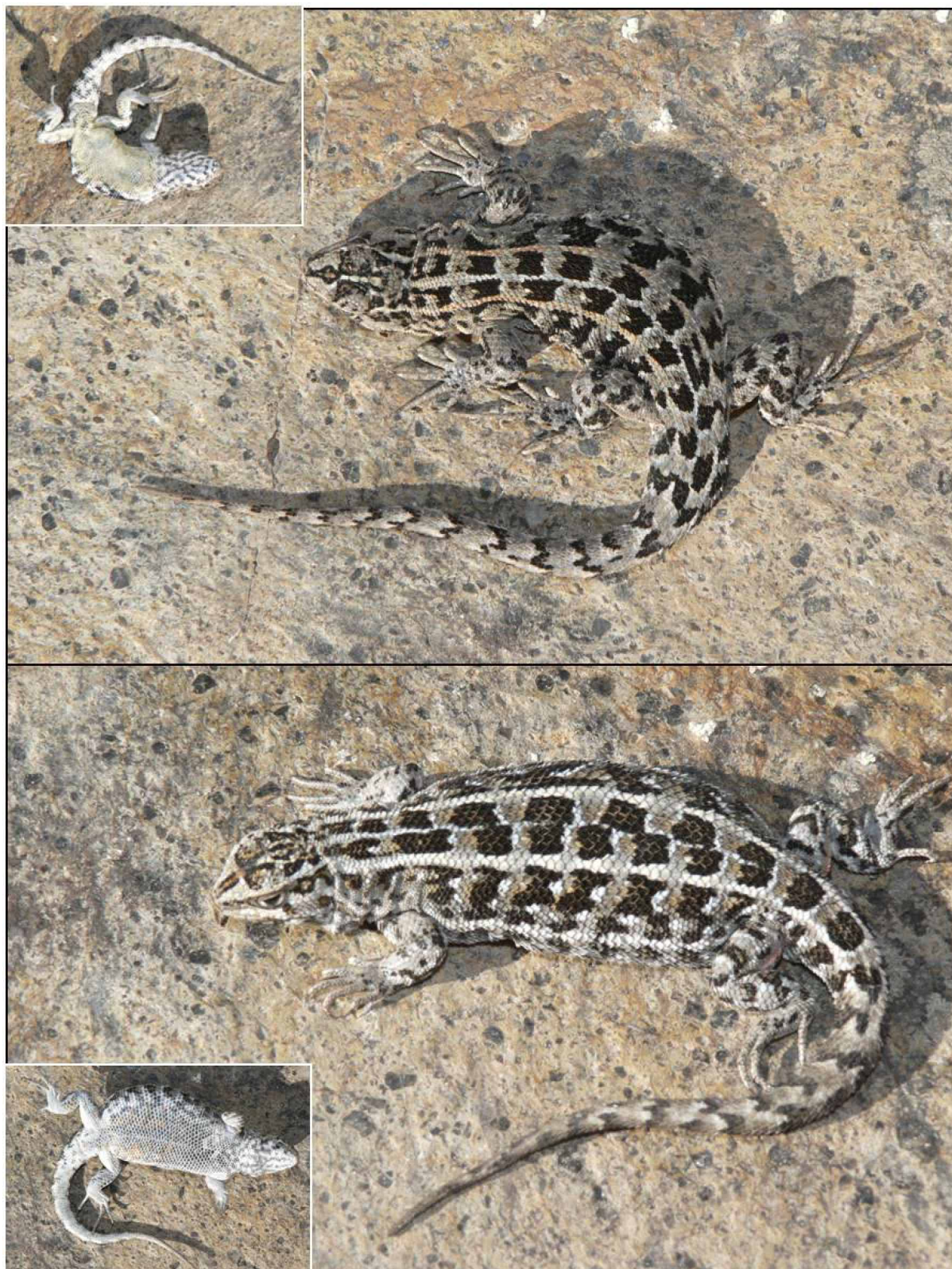
Scales of dorsal neck region rhomboidal, imbricate, strongly keeled. Very few trifids scales. Fifty-five dorsal scales between occiput and anterior surface of thighs. Dorsal body scales rhomboidal, imbricate, strongly keeled. Dorsal scales grade laterally into slightly smaller and keeled scales at midbody. Scales immediately anterior and posterior to forelimb and hindlimb insertion small, smooth, granular, and non-overlapping. Body lateral scales grading smaller to larger at midbody. Ventral body scales rhomboidals, smooth, flat, imbricate, larger than dorsal scales. Fifty-eight midbody scales; scales between mental and precloacal pores 90. Scales of cloacal region similar in size to ventral body scales; without precloacal pores.

Anterior suprabrachials rhomboidal, imbricate, smooth, slightly larger in size to dorsal body scales. Postbrachials smaller, smooth, becoming granular near axilla. Supra-antebrachials similar to suprabrachial. Infra-antebrachials rhomboidal, imbricate, smooth. Supracarpals imbricated, rhomboidal, smooth. Infracarpals imbricate, rhomboidal, very slightly keeled. Subdigital lamellae with 2–3 keels, each terminating in a short mucron, 2–3 mucronate, numbering: I: 8, II: 14, III: 17, IV: 19, V: 12. Claws robust, curved and sharp, opaque brown. Suprafemorals larger as dorsal body scales, rhomboidal, imbricated, smooth upper thigh, toward to the lateral thigh keeled. Postfemorals small, granular shape. Supratibials rhomboidal, imbricated, moderately keeled, smaller and smooth toward to the foot. Infracarpals small, granular and smooth. Supratarsals rhomboidal, imbricated and smooth. Infratarsals small, rhomboidal, imbricate, smooth, some keeled and mucronate near the digit. Subdigital scales have 3 keels, 3–4 mucronate, numbering: I: 9, II: 14, III: 19, IV: 22, V: 16. Claws robust, curved and sharp, opaque brown. Tail complete, non-regenerated. Dorsal and lateral caudal scales, rhombic in the first half of the tail, quadrangulars toward the tip, strongly keeled. Ventral subtriangular and smooth, toward posterior half moderately keeled.

**Color of holotype in life.** Dark gray dorsal background (Figure 7) that becomes lighter on the lateral region between axilla and groin. Dorsal pattern presents nine paravertebral, quadrangulars, dark brown blotches, extending from the nuchal to the pelvic region, these series or blotches are combined at the beginning of the pelvic region into a pattern of transversal bands, which is present to the tip of the tail. Dorsolateral region between the occipital and the pelvic region is characterized by eight irregular, black and white-bordered blotches that are combined with the transversal bands of the tail. Lateral region, between axilla and groin, is characterized by a black and white reticulate pattern. In between the series of blotches a white vertebral and two yellowish paravertebral lines, one-scale wide, are present. Vertebral line extends from the nuchal region, while the paravertebral lines extend from the temporal region; all are present to the pelvic region.

Dark gray head background. Two lateral white lines along the longitudinal fold are present from the top of the auditory meatus to the antehumeral fold. White subocular scale with a black longitudinal ridge. One longitudinal band is present in the anterior part of the head, crossing through internasals, postnasals, prefrontals, frontals, postfrontals and interparietal scales, ending in the interparietal scale that is surrounded by small brown spots; however,

a lighter central region is observable in the frontal, postfrontal and interparietal scales. Anterior circumorbitals present a transverse dark brown band. Nasals scales dark brown. Small dark brown blotches on postocular, temporal and occipital region. Dorsal region of the limbs are dark gray with a dark brown reticulation.



**FIGURE 7.** Upper, dorsal and ventral views of holotype in life of *L. avilae* sp. nov. MLP.S 2627; below, dorsal and ventral views of female (LJAMM-CNP 9399).

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**FIGURE 8.** Type locality of *Liolaemus avilae* **sp. nov.** Altoandina phytogeographic province, Altoandino Austral District (47°05'29.0" S, 71°01'12.9" W, 1154 m).

Gray ventral color with a dark reticulate pattern over the entire body, it is strongly marked in throat, chest, tail and body laterals, and extend to the adjacent malar and maxilla region. Ventral scales with melanophores. Ventral area of chest, belly, cloacal region and limbs tinged with a light orange color. Gray tail.

**Color of holotype in preservative.** After three years in preservative, the dorsal coloration of the head, dorsum, body flanks and tail become darker while maintaining the contrast, but the two yellowish paravertebral lines turned gray. Ventral scales of throat, neck, chest, belly and forelimbs retain the same coloration as in life, and the distinctive light ventral orange color of the chest, belly, cloacal region and limbs turns gray (Figure 6).

**Variation.** Morphological and meristic character variation between male and female *Liolaemus avilae* **sp. nov.**, is shown in Table 6. Females in life present basically the same dorsal and lateral patterns as present in males, but females generally have a lighter brown background coloration; vertebral and paravertebral lines are variable, in some individuals they are strongly defined while in others they are less conspicuous; lines vary from white to yellow in females and from light orange to pink in males. Ventrally dark reticulate pattern in the entire body is present and is strongly marked in the throat, tail and lateral body scales. Ventral, ventro-lateral, limb, cloacal and postcloacal regions vary from males to females, in the former a ventral light orange coloration is present, while in one female (out of three) a light pink ventral coloration is present. All distinctive ventral and dorsal coloration changed from yellow, orange or pink to gray or white in preservative.

**Etymology.** The specific epithet of this species “*avilae*” refers to our colleague and the first author’s PhD advisor Dr. Luciano Javier Avila, to honor him after more than fifteen years of research and teaching on the Patagonian herpetofauna.

**Distribution.** *Liolaemus avilae* **sp. nov.** is known only from the type locality and surroundings, from Lago Buenos Aires Plateau in Puesto Lebrun and 18.7 SW from there, Santa Cruz province, Lago Buenos Aires department, Argentina (Figures 5, 8).

**Natural history.** Out of three females, only one presents a ventral pinkish coloration and a different one was pregnant; thus we infer that the pinkish coloration in females is not related to pregnancy. The species occurs in the Altoandina Phytogeographic province, Altoandino Austral district, in environments characterized as sparse grasslands and chamaephytes such as *Empetrum rubrum*, *Nassauvia pygmaea* and *Azorrella ameghinoi*, among others (Roig 1998); some *Festuca* spp. and *Senecio* spp. were also observed. This new species was found in open volcanic-sand substrates between patches of basaltic rocks, sharing the habitat with *Liolaemus archeforus* and *Liolaemus silvanae* (Figure 8). Based on the natural history of its sister species *L. lineomaculatus*, we hypothesize that *L. avilae* **sp. nov.** is herbivorous and likely to also be viviparous, perhaps giving birth to between three and six individuals per clutch (Cei 1986; Espinoza *et al.* 2004).

## Discussion

Lizards of the *L. lineomaculatus* section inhabit a large, heterogeneous area in Patagonia. This area possesses an interesting geological history, including several glacial cycles and sea level shifts, making the phylogenetic and phylogeographic history of this section complex and interesting. The *L. lineomaculatus* section includes 21 nominal species and several “candidate species” that remain unstudied (Breitman *et al.* 2011; Breitman *et al. in press*). Morando *et al.* (2003) have shown that, by some estimates, that the diversity of *Liolaemus* may be as high as twice the number of species described in the genus, and a recent study has shown that in the past decade the rate of species description in *Liolaemus* has been growing exponentially (Martinez *et al. in review*).

Fouquet *et al.* (2007), proposed for Neotropical frogs a mtDNA approach to species delimitation based on isolation-by-distance population structure. The method tests for correlation of geographic distance with genetic distance, which characterized most samples up to uncorrelated values of 3%. At this value the isolation-by-distance correlation was not significant and Fouquet *et al.* (2007) interpreted this break as the limit to intra-specific gene flow.

Martinez (*personal communication*) found that within *Liolaemus* the mean genetic distance value of cytochrome *b* between sister species was ~ 4%; moreover, she found that different groups of *Liolaemus* had values ranging from 1 to 6%. In the *L. lineomaculatus* section, average genetic distance between described species is 1.6% (based on the sister species *L. kolengh* vs. *L. hatcheri*), and 2.25% between species of the *kingii*+*archeforus* group (based on sister species *L. archeforus* vs. *L. chacabucoense* and *L. escarchadosi* vs. *L. tari*). In this context we want

to highlight that the discovery of the new species described here started with the molecular analyses presented by Breitman *et al.* (2011), in which several clades were recognized as candidate species, continued with the nuclear data here presented, and concluded with the morphological differentiation and characterization documented here for each new species.

Even though the first attempt of classification of the *L. lineomaculatus* section placed these species in the *Liolaemus* sensu stricto group (Etheridge 1995), recent studies support the placement of the *L. lineomaculatus* section within the *Eulaemus* group, sister to the *montanus* section within the broader *Liolaemus* phylogeny (Young Downey 1998; Schulte *et al.* 2000; Morando 2004; Breitman *et al.* 2011).

In contrast to this well-supported position of the *L. lineomaculatus* section in the generic phylogeny, this clade has until recently been in a state of taxonomic flux, with several authors interpreting this section nested within the subgenus of *Liolaemus*. Laurent (1985, 1995) proposed the subgenus *Rhytidodeira* Girard (1858) for the *L. lineomaculatus* section, whereas Pincheira-Donoso and Núñez (2005) considered the use of *Rhytidodeira* inappropriate.

The *lineomaculatus*, *kingii* and *archeforus* groups have all been subject to several taxonomic rearrangements. Before the description of these new species (*L. morandae* sp. nov. and *L. avilae* sp. nov.) the *lineomaculatus* group included: *L. lineomaculatus*, *L. hatcheri*, *L. kolengh* and *L. silvanae*, and depending on the author, also *L. magellanicus*. Some authors have considered the species *L. silvanae*, *L. hatcheri* and *L. kolengh* as members of a different genus: *Vilcunia* (Donoso-Barros & Cei 1971) or later as a subgenus (Pincheira-Donoso *et al.* 2008) including *L. lineomaculatus*, although this classification has been discouraged (Lobo *et al.* 2010a). Etheridge (1995) recognized the *lineomaculatus* group (characterized morphologically by the absence of precloacal pores in males and the presence of some dorsal trifold scales) formed by the *silvanae* group (*L. silvanae*, *L. hatcheri* and *L. kolengh*) and the species *L. lineomaculatus*. The *silvanae* group is characterized by the presence of keeled and imbricated nuchal scales and post-femoral sub-imbricated scales (Abdala & Lobo 2006), but the use of “sub-imbricated” as a character for classification seems ambiguous and in practice is not useful. The species *L. magellanicus* has been considered by Pincheira-Donoso and Núñez (2005) and Breitman *et al.* (2011) a separate evolutionary lineage, since the latter hypothesis was proposed based on molecular data, morphological work is needed to test it.

Analyses of all species of the *L. lineomaculatus* section using molecular sequence data from nine genes, defined four well-supported clades: *lineomaculatus*, *magellanicus*, *somuncurae* and *kingii+archeforus* (Breitman *et al.* 2011). Based on the previous morphology-based proposals and molecular data, the *lineomaculatus* group is the only group that is clearly distinct from all other members of the section. Genetically, two hypotheses have been proposed for species relationships within the *lineomaculatus* group: (1) a species tree approach (((*L. lineomaculatus* + *L. morandae* sp. nov. + *L. avilae* sp. nov.) (*L. silvanae* + *L. kolengh*)) *L. hatcheri*); versus (2) a concatenation approach (*L. hatcheri* (((*L. kolengh* + *L. silvanae*) (*L. morandae* sp. nov. (*L. avilae* sp. nov. + *L. lineomaculatus*)))) (Breitman *et al.* 2011). Neither of these topologies support the previously defined *silvanae* group (*L. silvanae* + *L. kolengh* + *L. hatcheri*) within the *lineomaculatus* group (Breitman *et al.* 2011) because it recovers *L. hatcheri* as the sister taxa of all the other species of the *lineomaculatus* group. Based on these conflicts between the morphologically proposed group and the molecular hypotheses, the need of a taxonomic revision of the *lineomaculatus* group based on additional lines of evidence is now necessary.

At a more inclusive level, the entire *L. lineomaculatus* section is in need of a more detailed study to evaluate each of its groups and taxonomic affinities. Our longer term goal is to prepare monographic revisions of poorly known groups using an “integrative taxonomy” approach (Padial *et al.* 2010). We are currently using molecular, morphological, ecological and geographical data, to reconstruct a temporal sequence of demographic histories, species limits and relationships, and to eventually test for shared patterns of divergence with other Patagonian clades (Sérsic *et al.* 2011).

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**APPENDIX I.** Individuals examined by species, sample sizes, museum collection, collection numbers and locality. RP: Provincial Road, RN: National Road, prov: province, F: females, M: males and J: juveniles are indicated. All individuals are located in LIAMM-CNP (Herpetological collection of Centro Nacional Patagónico in Puerto Madryn, Argentina) except for the ones indicated with asterisk that are placed in MLP.S (University of La Plata)

Species	n	LJAMM-CNP number	Locality
<i>L. hatcheri</i>	20	F: 9490; 9491; 9504-9506; 10321-10323 M: 9485-9489; 9492; 9498-9503	Santa Cruz province. Río Chico department. Estancia Cerro Beltza, 12 km N RP 37.
<i>L. kollegh</i>	31	F: 7276-7278; 7280; 7284; 7294; 7304; 7306; 7307; 7309-7315 M: 7279; 7281; 7282; 7289; 7290; 7295-7303; 10590	Santa Cruz province. Lago Buenos Aires department. Near Los Antiguos, 15.6 to 21 km N paso Roballos.
<i>L. lineomaculatus</i>	10	F: 7471; 9752; 9753; 9756 M: 7470; 7472; 9750; 9751; 9754; 9755	Santa Cruz province. Deseado department. 5.5 km N Puerto Deseado.
	2	F: 9971-9972	Santa Cruz province. Magallanes department. RP 47, 19.5 km S RP 87 (near Tres Cerros)
	1	F: 9731	Santa Cruz province. Magallanes department. RP 47, 47.9 km S RP 83.
	1	F: 9953	Santa Cruz province. Deseado department. RP 47, 93.3 km S RP 62, Estancia La Chaira, 37.4 km NE RP 87.
	1	M: 9847	Santa Cruz province. Deseado department. RP 62, 37.1 km S RP 47, 28.1 km S Estancia La Chaira.
	2	M: 10054; 10055	Santa Cruz province. Magallanes department. RP 75, 28.8 km NW RN 3, near Río Seco in Estancia Loma Alta.
<i>L. silvanae</i>	17	F: 9220; 9228-9233; 10320 M: 9218; 9219; 9221-9227	Santa Cruz province. Lago Buenos Aires department. Puesto Lebrun 27.3 km W Estancia La Vizcaina.
<i>L. morandae</i> sp. nov.	4	F: 9677-9679 J: 9680	Chubut province. Escalante department. RP 37, 2.5 km W RN 3.
	2	F: 13020 J: 13021	Chubut province. Escalante department. RP 37, 22.8km SW RN 3.
	2	M: 10201 J: 10202	Chubut province. Escalante department. Holdich station.
<i>L. morandae</i> sp. nov.*	1	M: 2626	Chubut province. Escalante department. RP 37, 22.8km SW RN 3
<i>L. avilae</i> sp. nov.	8	F: 9276; 9277; 9399 M: 9250; 9253; 9274 J: 9251; 9252	Santa Cruz province. Lago Buenos Aires department. Lago Buenos Aires plateau, 18.7 SW Puesto Lebrun.
	1	M: 9243	Santa Cruz province. Lago Buenos Aires department. Puesto Lebrun 27.3 km W Estancia La Vizcaina.
<i>L. avilae</i> sp. nov.*	1	M: 2627	Santa Cruz province. Lago Buenos Aires department. Lago Buenos Aires plateau, 18.7 SW Puesto Lebrun.

**TERMS OF USE**

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**APPENDIX II.** Acronyms used for characters examined in this study; for definitions see Avila *et al.* (2010a, 2010b), Vega *et al.* (2008), Martinez *et al.* (2011) and Abdala and Lobo (2006)

Morphometric characters	Meristic characters
<b>SVL:</b> Snout-vent length	<b>SCI:</b> Scales in contact with the interparietal
<b>TL:</b> Tail length	<b>LS:</b> Lorilabial scales
<b>DFH:</b> Distance between fore and hind limbs	<b>SS:</b> Supralabial scales
<b>FOL:</b> Foot length	<b>IS:</b> Infralabial scales
<b>TFL:</b> Tibia-fibula length	<b>MS:</b> Scales around midbody
<b>RUL:</b> Radius-ulna length	<b>DS:</b> Dorsal scales
<b>HAL:</b> Hand length	<b>VS:</b> Ventral scales
<b>HH:</b> Head height	<b>IL3:</b> Infradigital lamellae (3 <sup>rd</sup> on left hand)
<b>HW:</b> Head wide	<b>IL4:</b> Infradigital lamellae (4 <sup>rd</sup> on left foot)
<b>HL:</b> Head length	
<b>EH:</b> Eye height	
<b>EL:</b> Eye length	
<b>RND:</b> Rostral-nasal distance	
<b>RH:</b> Rostral height	
<b>RL:</b> Rostral length	
<b>DRE:</b> Distance from rostral to the eye	
<b>AH:</b> Auditory meatus height	
<b>AL:</b> Auditory meatus length	

**APPENDIX III.** Eigenvalues, percent of explained variance, cumulated percent of explained variance for the first six principal components (PC) and the contribution of each variable to the PCs (see Appendix I for names definitions)

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	11.76	3.79	1.71	1.19	1.08	0.89
Percent of explained variance	45	15	7	5	4	3
Cumulated percent of explained variance	45	60	66	71	75	78
Contributions of the variables to the factors:						
SVL	0.27	0.07	-0.10	0.10	-0.13	0.06
DFH	0.15	0.10	-0.21	0.23	-0.29	0.27
FOL	0.26	0.09	-0.07	-0.07	0.13	-0.07
TFL	0.22	0.18	-0.14	-0.06	0.22	-0.10
RUL	0.26	0.03	0.04	-0.15	0.01	-0.05
HAL	0.26	0.00	-0.08	-0.01	0.19	0.03
HH	0.23	0.13	0.11	0.04	-0.22	-0.08
HW	0.28	-0.01	0.06	0.01	-0.08	-0.03
HL	0.27	0.05	0.10	0.01	-0.12	-0.04
EH	0.21	0.03	-0.09	-0.16	0.15	0.20
EL	0.25	-0.06	0.02	-0.02	0.07	0.20
RND	0.22	-0.04	0.15	0.02	-0.31	-0.25
RH	0.19	-0.03	-0.09	0.36	0.06	-0.07
RL	0.25	-0.08	-0.05	0.05	-0.08	-0.05
DRE	0.27	-0.03	0.09	0.00	-0.15	-0.07
AH	0.24	-0.08	0.04	-0.04	0.12	0.00
AL	0.22	-0.11	0.06	-0.14	0.29	0.18
SCI	-0.01	0.21	0.24	-0.18	-0.25	0.74
LS	0.00	0.03	0.43	-0.36	-0.30	-0.33
SS	0.00	-0.07	0.43	0.62	-0.04	0.06
IS	0.03	-0.15	0.49	0.21	0.45	0.06
MS	0.01	0.44	-0.13	0.16	0.06	-0.21
DS	-0.02	0.42	-0.08	0.21	0.07	0.00
VS	-0.10	0.42	-0.03	0.11	-0.04	0.00
IL3	0.02	0.35	0.21	-0.20	0.33	-0.05
IL4	-0.04	0.39	0.32	-0.05	0.02	-0.02

**APPENDIX IV.** Discriminant-function analysis. Contribution of the principal components to the Canonical Axis, standardized by the variance.

	CA1	CA2
PC 1	1.03	-0.58
PC 2	0.69	0.83
PC 3	-0.83	0.00
PC 4	-0.2	0.16
PC 5	0.33	-0.12
PC 6	0.29	-0.26

**APPENDIX V.** Position of the centroids in the discriminant space. Notice that the centroid of *L. avilae* **sp. nov.** is the only one present in the (+ ; +); while the centroid of *L. morandae* **sp. nov.** is in the same discriminant quadrant (- ; +) than *L. lineomaculatus*, but its position is considerably lower respect to the axis 2.

Species	Axis 1	Axis 2
<i>L. hatcheri</i>	-1.63	-1.51
<i>L. kolengh</i>	-1.63	-1.66
<i>L. lineomaculatus</i>	-0.93	3.28
<i>L. silvanae</i>	5.11	-0.61
<i>L. morandae</i> <b>sp. nov.</b>	-1.5	1.63
<i>L. avilae</i> <b>sp. nov.</b>	0.91	1.68

**APPENDIX VI.** Cross-validation obtained from the discriminant-function analysis.

Species	<i>L. hatcheri</i>	<i>L. kolengh</i>	<i>L. lineomaculatus</i>	<i>L. silvanae</i>	<i>L. morandae</i> <b>sp. nov.</b>	<i>L. avilae</i> <b>sp. nov.</b>	Error (%)
<i>L. hatcheri</i>	10	7	0	0	1	0	44
<i>L. kolengh</i>	4	20	0	0	0	0	17
<i>L. lineomaculatus</i>	0	0	13	0	3	1	24
<i>L. silvanae</i>	0	0	0	17	0	0	0
<i>L. morandae</i> <b>sp. nov.</b>	0	0	2	0	4	0	33
<i>L. avilae</i> <b>sp. nov.</b>	0	0	0	0	0	7	0

## Categorización del estado de conservación de las lagartijas y anfisbenas de la República Argentina

**Cristian Simón Abdala<sup>1</sup>, José Luís Acosta<sup>2</sup>, Juan Carlos Acosta<sup>3</sup>, Blanca Beatriz Álvarez<sup>2</sup>, Federico Arias<sup>4</sup>, Luciano Javier Avila<sup>5</sup>, Graciela Mirta Blanco<sup>3</sup>, Marcelo Bonino<sup>6</sup>, Jorgelina Mariela Boretto<sup>7</sup>, Gabriela Brancatelli<sup>8</sup>, María Florencia Breitman<sup>5</sup>, Mario Roberto Cabrera<sup>9</sup>, Samanta Cairo<sup>8</sup>, Valeria Corbalán<sup>10</sup>, Alejandra Hernando<sup>2</sup>, Nora Ruth Ibargüengoytía<sup>7</sup>, Federico Kacolis<sup>11</sup>, Alejandro Laspiur<sup>3</sup>, Ricardo Montero<sup>1</sup>, Mariana Morando<sup>5</sup>, Nicolás Pelegrin<sup>12</sup>, Cristian Hernán Fulvio Pérez<sup>5</sup>, Andrés Sebastián Quinteros<sup>4</sup>, Romina Valeria Semhan<sup>1</sup>, María Esther Tedesco<sup>2</sup>, Laura Vega<sup>13</sup>, Sergio Martín Zalba<sup>8</sup>**

<sup>1</sup> Instituto de Herpetología, Fundación Miguel Lillo- CONICET -Facultad de Ciencias Naturales e IML. Universidad Nacional de Tucumán. Miguel Lillo 205, (4000) Tucumán, Argentina.

<sup>2</sup> Laboratorio de Herpetología. Facultad de Ciencias Exactas y Naturales y Agrimensura. Universidad Nacional del Nordeste. Av. Libertad 5470. (3400) Corrientes, Argentina.

<sup>3</sup> Departamento de Biología, Facultad de Ciencias Exactas y Naturales. Universidad Nacional de San Juan. (5400), San Juan, Argentina.

<sup>4</sup> IBIGEO-CONICET, Facultad de Ciencias Naturales, Universidad Nacional de Salta, Avenida Bolivia 5150. (4400), Salta, Argentina.

<sup>5</sup> CENPAT-CONICET, Boulevard Almirante Brown 2915, (U9120ACD), Puerto Madryn, Chubut, Argentina.

<sup>6</sup> Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA) CONICET-UNCOMA, (8400), Bariloche, Argentina.

<sup>7</sup> Departamento de Zoología, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue - (INIBIOMA-CONICET), Quintral 1250. (8400), San Carlos de Bariloche, Río Negro, Argentina.

<sup>8</sup> GEKKO – Grupo de Estudios en Conservación y Manejo, Universidad Nacional del Sur, San Juan 670 (8000), Bahía Blanca, Argentina.

<sup>9</sup> CONICET- Departamento de Diversidad Biológica y Ecología, Universidad Nacional de Córdoba, Avenida Vélez Sarsfield 299 (5000), Córdoba, Argentina

<sup>10</sup> Instituto Argentino de Investigaciones de las Zonas Áridas - IADIZA - CCT - Mendoza - CONICET. Av. Ruiz Leal s/n, Parque Gral. San Martín, Mendoza, Argentina.

<sup>11</sup> Sección Herpetología, División Zoología Vertebrados, Museo de La Plata. Paseo del Bosque, s/n (1900), Buenos Aires, Argentina.

<sup>12</sup> Centro de Zoología Aplicada FCEfYn - Universidad Nacional de Córdoba - Instituto de Diversidad y Ecología Animal (IDEA) - CONICET. Av. Vélez Sarsfield 299 (5000) Córdoba, Argentina.

<sup>13</sup> Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3350, Mar del Plata, Buenos Aires, Argentina.

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### RESUMEN

Luego de la elaboración de la primera lista roja de la herpetofauna de la República Argentina, realizada en el año 2000, son numerosos los cambios y estudios efectuados en los diferentes grupos de saurios de la Argentina. Si bien hay avances realizados en todas las ramas de la biología relacionadas a las lagartijas, los progresos taxonómicos y ecológicos son los más evidentes. Debido a estos progresos, y a la implementación de sustanciales modificaciones con respecto a la metodología que se utilizara en el año 2000, un grupo de veintisiete especialistas de diferentes instituciones académicas de la Argentina aportaron información biológica, ecológica, geográfica y taxonómica en un taller que permitió reevaluar el estado de conservación de las 256 especies de lagartijas y anfisbenas de la Argentina. Los resultados obtenidos indican que setenta y ocho especies se encuentran incluidas en la lista roja (una En Peligro, nueve Amenazadas y 68 Vulnerables), 31 Insuficientemente Conocidas y 147 No Amenazadas. Con respecto a la categorización anterior de la AHA, se agregaron 94 especies, de las cuales 87 son nuevos taxa, cuatro revalidadas, y otras tres especies fueron incorporadas a la fauna argentina. Asimismo cinco especies fueron extraídas del listado de la fauna de la República Argentina. En comparación con los resultados obtenidos en la categorización del año 2000, observamos que el número de especies Amenazadas se incrementó de cinco a nueve especies y de siete a 68 especies como Vulnerable, incluyendo a los géneros *Phymaturus* y *Anisolepis*. Asimismo, se

categorizó como Insuficientemente Conocida a 31 especies contra 108 del año 2000. Estos resultados son en parte debido al incremento en el conocimiento sistemático, biológico, ecológico y biogeográficos de las lagartijas y anfisbenas de la Argentina, por el cambio radical de la metodología utilizada y también por los efectos de la presión antrópica sobre las especies y/o sus habitats.

Palabras clave: Lagartijas; Anfisbenas, Conservación; Listas rojas; Evaluación; Argentina.

#### ABSTRACT

After the first herpetofaunal red list for Argentina, which was published in the year 2000, there had been numerous changes and studies made on different groups of lizards from Argentina. Although there had been contributions in all areas of lizard biology, those made in taxonomy and ecology are the most evident. Due to these and the implementation of substantial modifications with respect to the methodology used in the year 2000, a group of twenty-seven specialists from different Argentinian institutions contributed biological, ecological, geographic and taxonomic information to a workshop that allowed re-evaluation of the conservation status of the 256 lizard and amphisbaenian species from Argentina. Results indicate that 78 species are included in the red list (one Endangered, nine Threatened, and 68 Vulnerable), 31 are insufficiently known and 147 Non-threatened. Compared with the previous AHA categorization, 94 new species have been added, of which 87 are new taxa, four re-validations, and three species were incorporated to the Argentina fauna; five species were deleted from the Argentina list. Compared with the 2000 yr results, threatened species increased from five to nine species, and vulnerable species increased from seven to 68, including all species of the genera *Phymaturus* and *Anisolepis*. There are 31 species considered as insufficiently known against 108 listed in this category in 2000. These results are partially based on the increase in systematic, biological, ecological and biogeographical knowledge of lizards and amphisbaenians, and by the radical change in methodology and by effects of anthropogenic pressure on species and/or their habitats.

Key words: Lizards; Anphisbaenians; Conservation; Red lists; Assessment; Argentina.

## Introducción

Las lagartijas y anfisbenas están presentes en los más diversos ambientes de la Argentina, ocupando todas las regiones fitogeográficas conocidas (Cabrera y Willink, 1980). Dentro del gran conjunto de saurios del país, varias especies tienen una distribución muy restringida, revelando microendemismos significativos, mientras que otras especies presentan especializaciones ecológicas (Ceï, 1986, 1993; Avila *et al.*, 2000; Morando, 2004; Abdala, 2005; Lobo *et al.*, 2010a; Scrocchi *et al.*, 2010). Las especies que son endémicas o que presentan especializaciones ecológicas se encuentran en un delicado balance con su hábitat, por lo tanto la alteración de sus ambientes expone a estas lagartijas a un alto grado de vulnerabilidad (Abdala *et al.*, 2012). Debido al crecimiento humano y sus actividades, la destrucción y la degradación del hábitat son la principal causa de pérdida de biodiversidad (Turner, 1996; Primack *et al.*, 2001). Este factor afecta tanto a los saurios como a los demás animales terrestres de la Argentina y del mundo (Sodhi y Ehrlich, 2010). Es evidente que el avance de la frontera agropecuaria (principalmente por la plantación de soja) es el factor que causa

mayores efectos negativos en las poblaciones de saurios (Bennet, 2004; Rudd, 2011). Los continuos y extensivos desmontes en áreas tan sensibles y diversas, como en las regiones fitogeográficas del Chaco, Yungas, Monte y Espinal, han traído como consecuencias la disminución de varias poblaciones de especies de saurios, las cuales se ven reflejadas en la categorización actual.

Otros factores derivados de la actividad humana que actúan negativamente en las poblaciones de lagartijas de Argentina son el sobrepastoreo, la minería, la extracción petrolera, y las actividades turísticas (Pelegrin *et al.*, 2009; Pelegrin y Bucher, 2010, 2012; Abdala *et al.*, 2012). El sobrepastoreo es producido por la excesiva carga de animales domésticos por encima de la capacidad de la vegetación y el suelo; este fenómeno produce una disminución drástica de la vegetación y compactación del suelo modificando el hábitat del área. Este fenómeno se acentúa en la estepa patagónica, así como en zonas de Chaco, Puna, Prepuna y Altoandina. La minería a cielo abierto y extracción petrolera producen grandes modificaciones en el ambiente, que afectan

directamente a las poblaciones de saurios debido a la importante remoción de las capas de suelo. Asimismo, los desechos, deposición y tránsito de material producidos por la actividad minera, y la fragmentación del área mediante caminos y rutas, también afectan las poblaciones de lagartijas. Las actividades recreativas y turísticas presentan, en casos puntuales, efectos nocivos para las poblaciones de lagartijas, principalmente cuando los ambientes son frágiles o las especies que habitan en los mismos tienen requerimientos de hábitat muy complejos. Los casos más representativos se dan en lugares de grandes médanos, donde habitan lagartijas muy especializadas a dichos ambientes, en los cuales se desarrollan travesías con vehículos todo terreno (Kacoliris *et al.*, 2009; Abdala *et al.*, 2012).

El cambio climático global es otro factor que afecta a las poblaciones de saurios. Cerca del 45% de las especies de saurios de la Argentina tienen modo reproductivo vivíparo. Estas especies, que habitan a elevada altitud (o latitud), serían las más afectadas por el cambio climático global, según el estudio de Sinervo *et al.* (2010). Dicho estudio, también expresa que el 6% de las especies y el 16% de las poblaciones estarán extintas para el año 2050, y entre el 20% y el 30% de las poblaciones para el 2080. Es fundamental seguir realizando estudios que permitan evaluar el verdadero efecto del cambio climático global en las poblaciones de saurios de la Argentina.

Otro factor que afecta en menor medida a las poblaciones de saurios locales es la introducción de especies exóticas, las cuales compiten con éstas por los refugios, nichos tróficos, reproductivos, etc. (Álvarez *et al.*, 2002; Baldo *et al.*, 2008; Rödder *et al.*, 2008).

Es indudable que es necesario emplear estrategias de conservación a diferentes escalas regionales para aminorar los efectos producidos por la actividad humana (Primack *et al.*, 2001). Una acción directa y efectiva para priorizar las medidas de conservación a emplear, es la categorización de especies amenazadas (EA), cuyo objetivo es proporcionar listados de especies que presentan altos riesgos de extinguirse (Primack *et al.*, 2001). Estas listas son mundialmente conocidas como Listas Rojas y es la IUCN ([www.iucnredlist.org](http://www.iucnredlist.org)), quien lidera la elaboración de las mismas a nivel global. Sin embargo, es imprescindible que se confeccionen listas rojas a nivel regional (Gärdenfors *et al.*, 2001), y de esa manera desarrollar acciones concretas de conservación.

Varios trabajos relacionados al estado de con-

servación de las lagartijas de diferentes áreas o provincias de la Argentina se han publicado en los últimos 20 años, destacándose los de Úbeda *et al.* (1994), Bertoni (1994), Úbeda y Grigera (1995), Avila y Acosta (1996), Grigera y Úbeda (1997), Acosta y Murúa (1998), Cei *et al.* (2003), Abdala *et al.* (2004), Chébez *et al.* (2005), Scolaro (2005, 2006), Chébez (2008), Scrocchi *et al.* (2010). Corbalán *et al.*, (2011) y Abdala *et al.* (2012). Sin embargo, en el año 2000 se concretó, de manera práctica y legal, la evaluación y categorización de las lagartijas y anfisbenas de Argentina (Avila *et al.*, 2000). Desde entonces, el incremento del grupo de especialistas que ha volcado sus investigaciones en el estudio de los saurios es realmente sorprendente. Este aumento de investigadores se ve reflejado en los diversos trabajos relacionados a las lagartijas en las más diversas áreas de la biología. Sin lugar a dudas, los estudios taxonómicos han experimentado un incremento sustancial, permitiendo que el número de especies de lagartijas de la Argentina se eleve de 167 en el año 2000 a 256 en el 2012. Asimismo, los trabajos ecológicos, etológicos, biogeográficos, filogenéticos, morfológicos y fitogeográficos han aportado un conjunto de información crucial y fundamental para llevar a cabo esta nueva categorización de los saurios de la república Argentina.

En la primera categorización de la herpetofauna Argentina (Lavilla *et al.*, 2000) se utilizó la metodología de Reca *et al.* (1994) modificada; en este trabajo se implementó el mismo método pero con cambios sustanciales (Giraud *et al.*, 2012).

Es evidente que el crecimiento en el número de investigadores e información aportada en el estudio de los saurios, sumado a los cambios metodológicos propuestos por Giraud *et al.* (2012), han posibilitado categorizar sólo un porcentaje bajo de especies como Insuficientemente Conocida (IC), a diferencia de la categorización anterior (Avila *et al.*, 2000).

## Materiales y Métodos

Para confeccionar el listado total de especies de lagartijas y anfisbenas de la Argentina, se tomó como base el esquema propuesto en la categorización del año 2000 (Avila *et al.*, 2000). El listado de especies categorizadas en el presente trabajo incluye novedades taxonómicas desde el año 2000 hasta el 30 de marzo de 2012. Dichas novedades taxonómicas incluyen cambios nomenclatoriales, nuevos taxa descritos,

así como especies incorporadas y otras eliminadas del listado de la fauna Argentina. La nueva lista registra un total de 246 taxa de lagartijas y 10 de anfibenas reconocidos para Argentina. Asimismo, esta categorización ha incorporado las novedades en la distribución (datos publicados e inéditos) y en aspectos ecológicos de gran cantidad de especies. La nomenclatura y ordenamiento taxonómico sigue básicamente a Conrad (2008), con modificaciones de Frost *et al.*, (2001) para las familias Leiosauridae, Liolaemidae, Tropicuridae y Polychrotidae; a Montero y Autino (2009) para Amphisbaenia; a Gamble *et al.* (2008) para la familia Phyllodactylidae; a Doan (2003) para la familia Gymnophthalmidae y a Giugliano *et al.* (2007) para la familia Teiidae.

La categoría de los taxones se basó en la revisión metodológica y recomendaciones publicadas en este volumen (Giraudó *et al.*, 2012), utilizada por los evaluadores para asignar valores a seis variables analizadas incluyendo: Distribución nacional y grado de endemismo (DINAC), Rareza ecológica (RARECOL), Efectos humanos (EFHU), Potencial reproductivo (POTRE), Tamaño (TAM) y Abundancia (ABUND). Se asignaron valores a dichas variables indicándose para cada especie los evaluadores responsables de la información utilizada, proveniente de datos propios y/o de la literatura científica. Una vez obtenidos los valores de cada especie se realizó una reunión plenaria entre los evaluadores en donde se discutieron las categorías asignadas a las especies. Las categorías asignadas se basaron tanto en los valores umbrales teóricos sugeridos en la propuesta metodológica (Vulnerable entre 18 y 19, Amenazada entre 20 y 23, En Peligro entre 24 y 30, No Amenazados entre 0 y 12), recomendándose revisar caso por caso a los taxones con valores entre 13 y 17, como en el análisis de las incertidumbres que fueron consensuadas entre los evaluadores (ver Giraudó *et al.*, 2012 para mayores detalles).

## Resultados y Discusión

### Comentarios taxonómicos

Los cambios nomenclaturales y taxonómicos desde la última categorización (Avila *et al.*, 2000) hasta la actual se detallan a continuación.

### Cambios nomenclaturales en lagartijas y anfibenas propuestos desde la primera categorización

1. Representantes de los géneros *Anisolepis*, *Diplolaemus*, *Leiosaurus*, *Pristidactylus* y *Urostrophus*

listados dentro de la familia Polychrotidae en la categorización anterior (Avila *et al.*, 2000), se incluyen en la familia Leiosauridae de acuerdo con Frost *et al.* (2001).

2. Representantes de los géneros *Liolaemus* y *Phymaturus* listados dentro de la familia Tropicuridae en la categorización anterior (Avila *et al.*, 2000), se incluyen en la familia Liolaemidae de acuerdo con Frost *et al.* (2001).

3. En acuerdo con la hipótesis filogenética de Frost *et al.* (2001), la familia Polychrotidae está representada en Argentina solamente por el género *Polychrus*.

4. En acuerdo con la hipótesis filogenética de Frost *et al.* (2001), la familia Tropicuridae está representada en Argentina por los géneros *Stenocercus* y *Tropicurus*.

5. Representantes de los géneros *Homonota* y *Phyllolopezus* listados dentro de la familia Gekkonidae en la categorización anterior (Avila *et al.*, 2000), se incluyen en la familia Phyllodactylidae de acuerdo con Gamble *et al.* (2008).

6. Representantes del género *Pantodactylus* de la categorización anterior (Avila *et al.*, 2000) ahora son considerados dentro del género *Cercosaura* de acuerdo con Doan (2003).

7. ***Amphisbaena heterozonata***: Esta especie era considerada en la última categorización (Avila *et al.*, 2000) una subespecie de *Amphisbaena darwini*. Fue elevada a nivel específico por Gans (2005).

8. ***Amphisbaena plumbea***: Esta especie era considerada en la última categorización (Avila *et al.*, 2000) una subespecie de *Amphisbaena angustifrons*. Fue elevada a nivel específico por Gans (2005).

9. ***Amphisbaena prunicolor***: Esta especie era considerada en la última categorización (Avila *et al.*, 2000) como *Amphisbaena prunicolor prunicolor*. Fue elevada a nivel específico por Gans (2005).

10. ***Liolaemus abdalai***: Incluye las poblaciones argentinas que fueron consideradas en la última categorización (Avila *et al.*, 2000) como *Liolaemus lemniscatus* (especie que queda restringida a Chile) de acuerdo con Quinteros (2012).

11. ***Liolaemus boulengeri***: Parte de sus poblaciones, que fueron incluidas en la categorización del año 2000 (Avila *et al.*, 2000), ahora son consideradas como *Liolaemus inacayali*, *Liolaemus josei*, *Liolaemus lobo*, *Liolaemus senguer* y *Liolaemus tehuelche* de acuerdo con Abdala (2003, 2005)

12. ***Liolaemus chlorostictus***: Elevada a nivel específico por Díaz Gómez (2007). Considerada subespecie de *Liolaemus orientalis*, en la categorización anterior

(Avila *et al.*, 2000).

**13. *Liolaemus ditadai*:** Elevada a nivel específico por Abdala (2007). Considerada subespecie de *Liolaemus anomalus*, en la categorización anterior (Avila *et al.*, 2000).

**14. *Liolaemus dorbignyi*:** Parte de sus poblaciones, que fueran incluidas en la categorización del año 2000, ahora son consideradas como *Liolaemus huayra*, *Liolaemus inti*, *Liolaemus scrocchii* y *Liolaemus vulcanus* de acuerdo con Abdala *et al.* (2008); Quinteros *et al.* (2008a) y Quinteros y Abdala (2011).

**15. *Liolaemus darwini*:** Parte de sus poblaciones, que fueran incluidas en la categorización del año 2000 (Avila *et al.*, 2000), ahora son consideradas como *Liolaemus grosseorum* de acuerdo con Etheridge (2001).

**16. *Liolaemus elongatus*:** Parte de las poblaciones que fueran incluidas en la categorización del año 2000 (Avila *et al.*, 2000), ahora son consideradas como especies diferentes: *Liolaemus choique*, *Liolaemus smaug* y *Liolaemus parvus*, de acuerdo con Abdala *et al.* (2010) y Quinteros *et al.* (2008b).

**17. *Liolaemus goetschi*:** Considerada en la última categorización (Avila *et al.*, 2000) sinónimo junior de *Liolaemus melanops*. Revalidada por Cei y Scolaro (2003).

**18. *Liolaemus lentus*:** Considerada en la última categorización (Avila *et al.*, 2000) sinónimo junior de *Liolaemus anomalus*. Revalidada por Abdala (2005).

**19. *Liolaemus lineomaculatus*:** Parte de sus poblaciones que, fueran incluidas en la categorización del año 2000 (Avila *et al.*, 2000), ahora son consideradas como especies diferentes: *Liolaemus avilae* y *Liolaemus morandae* de acuerdo con Breitman *et al.* (2011a).

**20. *Liolaemus magellanicus*:** Parte de sus poblaciones, que fueran incluidas en la categorización del año 2000 (Avila *et al.*, 2000), ahora son consideradas como *Liolaemus caparensis* de acuerdo con Breitman *et al.* (2011b).

**21. *Liolaemus ornatus*:** Parte de sus poblaciones, que fueran incluidas en la categorización del año 2000 (Avila *et al.*, 2000), ahora son consideradas como *Liolaemus crepuscularis* y *Liolaemus lavillai* de acuerdo con Abdala y Díaz Gómez (2006) y Abdala y Lobo (2006).

**22. *Liolaemus quilmes*:** Parte de sus poblaciones, que fueran incluidas en la categorización del año 2000 (Avila *et al.*, 2000), ahora son consideradas como *Liolaemus espinozai* de acuerdo con Abdala (2005).

**23. *Phymaturus antofagastensis*:** Parte de sus pobla-

ciones, que fueran incluidas en la categorización del año 2000 (Avila *et al.*, 2000), ahora son consideradas como *Phymaturus laurenti* de acuerdo con Lobo *et al.* (2010).

**24. *Phymaturus palluma*:** Considerada en la primera categorización (Ávila *et al.*, 2000) como *Phymaturus flagellifer*. Parte de sus poblaciones, que fueran incluidas en la categorización del año 2000, ahora son consideradas como especies diferentes: *Phymaturus dorsimaculatus*, *Phymaturus gynechlomus*, *Phymaturus roigorum* y *Phymaturus querque*, de acuerdo con Corbalán *et al.* (2009); Lobo y Quinteros (2005); Lobo y Abdala (2007) y Lobo *et al.* (2010b).

**25. *Phymaturus patagonicus*:** Parte de sus poblaciones, que fueran incluidas en la categorización del año 2000 (Avila *et al.*, 2000), ahora son consideradas como especies diferentes: *Phymaturus spurcus*, *Phymaturus calcogaster*, *Phymaturus spectabilis* y *Phymaturus tenebrosus* de acuerdo con Scolaro y Cei (2003) y Lobo y Quinteros (2005).

**26. *Phymaturus spurcus*:** Considerada en la última categorización (Avila *et al.*, 2000) sinónimo junior de *Phymaturus patagonicus*. Revalidada por Lobo y Quinteros (2005).

**27. *Pristidactylus araucanus*:** Considerada en la última categorización (Avila *et al.*, 2000) sinónimo junior de *Pristidactylus fasciatus*. Fue revalidada por Cei *et al.* (2001).

#### Especies de lagartijas incorporadas a la fauna Argentina

***Liolaemus araucanensis*** Descripta para Chile (Müller y Hellmich, 1932) y citada para Argentina por Scolaro (2006).

***Liolaemus puritamensis*** Descripta para Chile por Núñez y Fox (1989) y citada para Argentina por Quinteros y Abdala (2007).

***Liolaemus scolaroi*:** Descripta para Chile por Pincheira-Donoso y Núñez (2005) y citada para la Argentina por Scolaro (2006).

#### Especies de lagartijas que fueron excluidas de la fauna Argentina

***Liolaemus alticolor*:** Parte de sus poblaciones, que fueran incluidas en la primera categorización (Avila *et al.*, 2000), ahora son consideradas como especies diferentes: *Liolaemus chaltin* y *Liolaemus puna*. La distribución de *Liolaemus alticolor* queda restringida para Bolivia y Chile.

***Liolaemus constanzae*:** Fue considerada en la prime-



ra categorización (Avila *et al.*, 2000), sin embargo no hay ninguna publicación que evidencie su presencia en la Argentina.

***Liolaemus lemniscatus***: Actualmente esta especie está restringida a Chile y las poblaciones consideradas en Argentina corresponden a *Liolaemus abdalai*.

***Liolaemus monticola***: Fue considerada en la primera categorización (Avila *et al.*, 2000), sin embargo no hay ninguna publicación que evidencie su presencia en la Argentina.

***Liolaemus pictus pictus***: Actualmente está especie está restringida a Chile según Avila *et al.* (2006)

### Especies descritas con posterioridad a la primera categorización e incluidas en el nuevo listado de especies de lagartijas y anfisbenas de la República Argentina

Leiosauridae

***Diplolaemus sexcinctus*** Cei, Scolaro y Videla, 2003

***Leiosaurus jaguaris*** Laspiur, Abdala y Acosta, 2007

***Pristidactylus nigroiugulus*** Cei, Scolaro y Videla, 2001

Liolaemidae

***Liolaemus abdalai*** Quinteros, 2012

***Liolaemus antumalguen*** Avila, Morando, Pérez y Sites, 2010

***Liolaemus avilae*** Breitman, Parra, Pérez y Sites, 2011

***Liolaemus azarai*** Ávila 2003

***Liolaemus camarones*** Abdala, Díaz Gómez y Juárez Heredia, 2012

***Liolaemus caparensis*** Breitman, Pérez, Parra, Morando, Sites y Avila, 2011

***Liolaemus casamiquelai*** Avila, Pérez, Morando y Sites, 2010

***Liolaemus cazaniae*** Lobo, Slodki y Valdecantos, 2010

***Liolaemus chacabucoense*** Núñez y Scolaro, 2009

***Liolaemus chaltin*** Lobo y Espinoza, 2004

***Liolaemus chehuachekenk*** Ávila, Morando y Sites, 2008

***Liolaemus choique*** Abdala, Quinteros, Scrocchi y Stazonelli, 2010

***Liolaemus cinereus*** Monguillot, Cabrera, Acosta y Villavicencio, 2006

***Liolaemus crepuscularis*** Abdala y Díaz Gómez, 2006

***Liolaemus cuyumhue*** Ávila, Morando, Pérez y Sites, 2009

***Liolaemus cyaneinotatus*** Martínez, Avila, Pérez, Pérez, Sites y Morando, 2011

***Liolaemus diaguita*** Abdala, Quinteros, Arias, Portelli y Palavechino, 2011

***Liolaemus dicktracyi*** Espinoza y Lobo, 2003

***Liolaemus dumerilli*** Abdala, Semhan, Moreno Azocar, Bonino, Paz y Cruz, 2012

***Liolaemus espinozai*** Abdala, 2005

***Liolaemus flavipiceus*** Cei y Videla, 2003

***Liolaemus graciela*** Abdala, Acosta, Cabrera, Villavicencio y Marinero, 2009

***Liolaemus grosseorum*** Etheridge, 2001

***Liolaemus gununakuna*** Ávila, Morando, Pérez y Sites, 2004

***Liolaemus halonastes*** Lobo, Slodki y Valdecantos, 2010

***Liolaemus heliodermis*** Espinoza, Lobo y Cruz, 2000

***Liolaemus huayra*** Abdala, Quinteros y Espinoza, 2008

***Liolaemus inacayali*** Abdala, 2003

***Liolaemus inti*** Abdala, Quinteros y Espinoza, 2008

***Liolaemus josei*** Abdala, 2005

***Liolaemus kolengh*** Abdala y Lobo, 2006

***Liolaemus lavillai*** Abdala y Lobo, 2006

***Liolaemus lobo*** Abdala, 2003

***Liolaemus mapuche*** Abdala, 2002

***Liolaemus martorii*** Abdala, 2003

***Liolaemus montanezi*** Cabrera y Monguillot, 2006

***Liolaemus morandae*** Breitman, Parra, Pérez y Sites, 2011

***Liolaemus morenoi*** Etheridge y Christie, 2003

***Liolaemus orko*** Abdala y Quinteros, 2008

***Liolaemus parvus*** Quinteros, Abdala, Díaz Gómez y Scrocchi, 2008

***Liolaemus piriphlogos*** Quinteros, 2012

***Liolaemus puelche*** Ávila, Morando, Pérez y Sites, 2007

***Liolaemus puna*** Lobo y Espinoza, 2004

***Liolaemus punmahuida*** Ávila, Pérez y Morando, 2003

***Liolaemus purul*** Abdala, Semhan, Moreno Azocar, Bonino, Paz y Cruz, 2012

***Liolaemus sagei*** Etheridge y Christie, 2003

***Liolaemus scrocchii*** Quinteros, Abdala y Lobo, 2008

***Liolaemus senguier*** Abdala, 2005

***Liolaemus shehuen*** Abdala, Díaz Gómez y Juárez Heredia, 2012

***Liolaemus shitan*** Abdala, Quinteros, Scrocchi y Stazonelli, 2010

***Liolaemus smaug*** Abdala, Quinteros, Scrocchi y Stazonelli, 2010

***Liolaemus talampaya*** Ávila, Morando, Pérez y Sites, 2004

- Liolaemus tandiliensis* Vega, Vellagamba y Lobo, 2008  
*Liolaemus tehuelche* Abdala, 2003  
*Liolaemus tregenzai* Pincheira-Donoso y Scolaro, 2007  
*Liolaemus tromen* Abdala, Semhan, Moreno Azocar, Bonino, Paz y Cruz, 2012  
*Liolaemus tulkas* Quinteros, Abdala, Gómez y Scrocchi, 2008  
*Liolaemus umbrifer* Espinoza y Lobo, 2003  
*Liolaemus uptoni* Scolaro y Cei, 2006  
*Liolaemus vulcanus* Quinteros y Abdala, 2011  
*Liolaemus yanalcu* Martínez Oliver y Lobo, 2002  
*Phymaturus calcogaster* Cei y Scolaro, 2003  
*Phymaturus castillensis* Scolaro y Pincheira-Donoso, 2010  
*Phymaturus ceii* Scolaro e Ibargüengoytía, 2007  
*Phymaturus delyhei* Avila, Perez, Perez y Morando, 2011  
*Phymaturus denotatus* Lobo, Nenda y Slodki, 2012  
*Phymaturus desuetus* Scolaro y Tappari, 2009  
*Phymaturus dorsimaculatus* Lobo y Quinteros, 2005  
*Phymaturus etheridgei* Lobo, Abdala y Valdecantos, 2010  
*Phymaturus excelsus* Lobo y Quinteros, 2005  
*Phymaturus extrilidus* Lobo, Espinoza, Sanabria y Quiroga, 2012  
*Phymaturus felixi* Lobo, Abdala y Valdecantos, 2010  
*Phymaturus gynechlomus* Corbalán, Scolaro y Debandi, 2009  
*Phymaturus laurenti* Lobo, Abdala y Valdecantos, 2010  
*Phymaturus manuelae* Scolaro e Ibargüengoytía, 2008  
*Phymaturus querque* Lobo, Abdala y Valdecantos, 2010  
*Phymaturus roigorom* Lobo y Abdala, 2007  
*Phymaturus sitesi* Avila, Pérez, Pérez y Morando, 2011  
*Phymaturus spectabilis* Lobo y Quinteros, 2005  
*Phymaturus tenebrosus* Lobo y Quinteros, 2005  
*Phymaturus verdugo* Cei y Videla, 2003  
*Phymaturus videlai* Scolaro y Pincheira-Donoso, 2010

Teiidae

- Cnemidophorus tergoaevigatus* Cabrera, 2004

Amphisbaenidae

- Amphisbaena hiata* Montero y Céspedes, 2002

**Lista actualizada de categorías de conservación de las lagartijas y anfisbenas de la República Argentina**

Los resultados de este trabajo se exhiben en las Tablas 1 a 4, las cuales presentan la información disponible sobre las lagartijas y anfisbenas de Argentina a nivel genérico y específico. La nueva lista registra un total de 256 taxa reconocidos para la Argentina, incluyendo 10 especies de anfisbenas y 246 de lagartijas (Tabla 1). Los resultados obtenidos indican que del total de lagartijas y anfisbenas, 78 especies enfrentan algún grado de riesgo para su conservación (una En Peligro, nueve Amenazadas y 68 Vulnerables); las restantes se consideran No Amenazadas (147 taxa) o Insuficientemente Conocidas (31 taxa) (Tabla 2).

**Comparaciones con listados anteriores, categorización del 2000 y las listas rojas de la UICN**

La primera categorización de lagartijas y anfisbenas (Avila *et al.* 2000) incluía 167 especies de saurios, mientras que la actual abarca 256, evidenciando un crecimiento importante en el número de taxa en la última década (Tabla 1). El promedio de nuevos taxa de lagartijas para la Argentina se va acrecentando año a año, dato que queda evidenciado al comparar el número actual de especies (260 según Avila *et al.*, 2012), con el trabajo de Avila *et al.* (2010), el cual incluye un listado de lagartijas y anfisbenas para la Argentina hasta diciembre de 2010 y contiene 242 especies (14 especies menos que en este trabajo). Este crecimiento se debe principalmente a la descripción de más de 60 especies de *Liolaemus* y 20 de *Phymaturus* en la última década. En el listado actual de saurios no se ha suprimido ninguna especie por considerarla extinta a escala local o global o por retracción de sus rangos de distribución en la región.

En comparación con la categorización anterior (Avila *et al.*, 2000) (Fig. 1), cabe resaltar que a pesar de haberse incrementado considerablemente el número de lagartijas para la Argentina, se pudo categorizar más del 87% de las especies quedando sólo el 12.1 % (31 especies) como Insuficientemente Conocida (IC). En la categorización anterior el porcentaje de especies Insuficientemente Conocida (IC) era del 64.6 % (108 especies). Otro dato importante, es que el número de especies con la categoría Vulnerable (VU) ascendió del 4.2 % (siete especies) en el año 2000 al 26.5 % (68 especies), incluyendo a todo el género *Phymaturus* bajo esa categoría. El número de especies En Peligro (EP) disminuyó a la mitad con respecto a la categorización del 2000

**Tabla 1.** Familias y géneros de lagartijas y anfisbenas de la República Argentina. Se indica entre paréntesis, el número de taxones reconocidos.

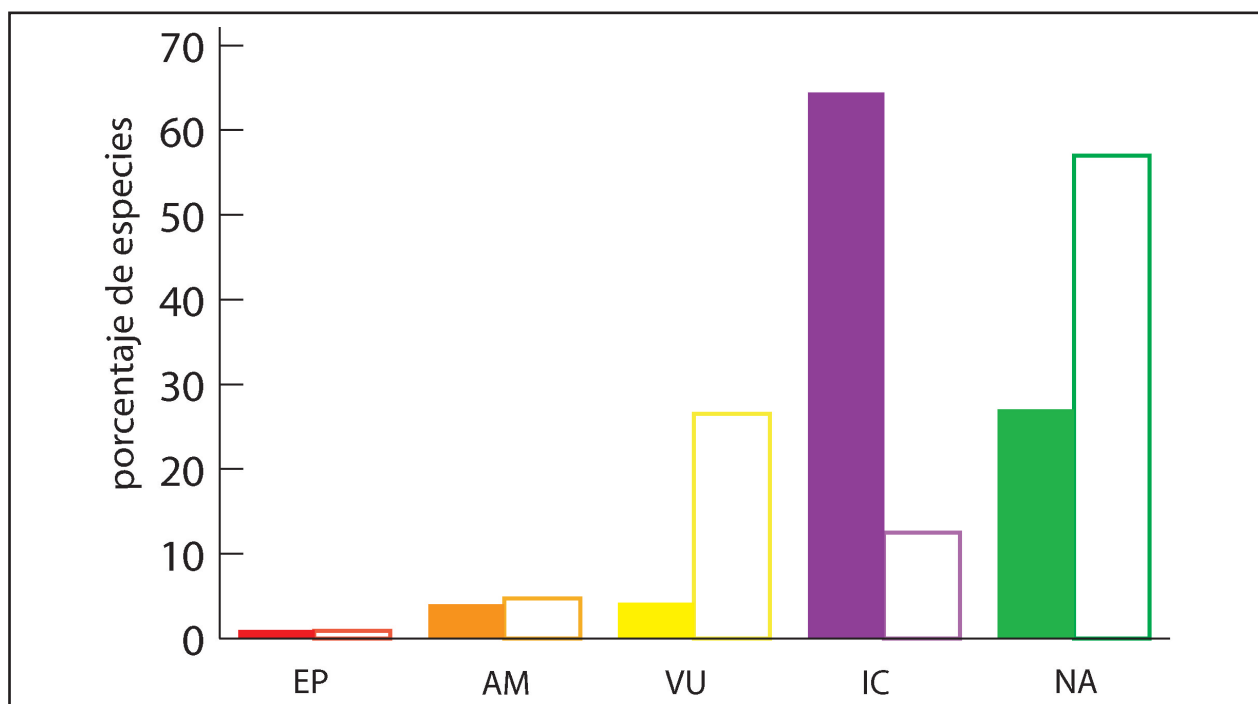
<b>Iguania</b>
<b>Leiosauridae (18)</b>
<i>Anisolepis</i> (3); <i>Diplolaemus</i> (4); <i>Leiosaurus</i> (4); <i>Pristidactylus</i> (6); <i>Urostrophus</i> (1)
<b>Liolaemidae (184)</b>
<i>Liolaemus</i> (152); <i>Phymaturus</i> (32)
<b>Polychrotidae (1)</b>
<i>Polychrus</i> (1)
<b>Tropiduridae (10)</b>
<i>Stenocercus</i> (6); <i>Tropidurus</i> (4)
<b>Gekkota</b>
<b>Phyllodactylidae (8)</b>
<i>Homonota</i> (7); <i>Phyllopezus</i> (1)
<b>Anguinomorpha</b>
<b>Anguidae (3)</b>
<i>Ophiodes</i> (3)
<b>Scincomorpha</b>
<b>Gymnophthalmidae (6)</b>
<i>Cercosaura</i> (4); <i>Opieuter</i> (1); <i>Vanzosaura</i> (1)
<b>Scincidae (2)</b>
<i>Mabuya</i> (2)
<b>Teiidae (14)</b>
<i>Ameiva</i> (1); <i>Cnemidophorus</i> (6); <i>Kentropyx</i> (2); <i>Teius</i> (3); <i>Tupinambis</i> (2)
<b>Amphisbaenia</b>
<b>Amphisbaenidae (9)</b>
<i>Amphisbaena</i> (8); <i>Anops</i> (1)
<b>Leposternidae (1)</b>
<i>Leposternon</i> (1)

(sólo *Liolaemus rabinoi* ha sido asignada con esta categoría, mientras que *Pristidactylus casuhatiensis* cambió de En Peligro a Amenazada), mientras que el número de especies Amenazadas (AM) creció de cinco a nueve especies. El número de especies No Amenazadas (NA) ascendió del 27 % (45 especies) al 57.4 % (147 especies). El aumento de especies categorizadas como Amenazadas (AM) y Vulnerables (VU) manifiesta el incremento de los factores que actúan negativamente en el estado de conservación de los saurios de la Argentina.

La información reunida nos permite evaluar la riqueza y estado de conservación de lagartijas y anfisbenas en una escala provincial de la República Argentina (Tabla 3). Los resultados indican que, en general, las provincias del centro-oeste y Patagonia son las que poseen los mayores valores de riqueza de lagartijas y anfisbenas: Mendoza (54 especies), Salta (53 especies), Neuquén (50 especies), Catamarca (48 especies), Río Negro (46 especies), Chubut (39 especies) y San Juan (38 especies). Tierra del Fuego posee sólo una especie, siendo *Liolaemus magellanicus* la lagartija con distribución más austral del planeta.

Los resultados obtenidos indican que Mendoza es la provincia con mayor número de especies con algún grado de amenaza (15 especies), seguido por Río Negro (11 especies), Catamarca, Neuquén y Salta (con 10 especies).

En relación al número de especies de cada provincia, Buenos Aires, Mendoza y Córdoba tienen el mayor porcentaje de especies amenazadas con poco más del 27%, Chaco (24.1%), Río Negro (23.9%), Santiago del Estero (23.33%) y Catamarca y Formosa (20.8%) (Fig. 2). En el caso particular de la provincia de Buenos Aires el elevado porcentaje de especies amenazadas se debe tanto al alto grado de transformación ambiental por desarrollo urbano y agrícola, como a características propias de la historia y bio-ecología de las especies. Las cinco especies de lagartijas amenazadas en esta provincia poseen un rango de distribución limitado y entre ellas cuatro ocurren solamente en esta provincia. Estas cuatro especies muestran además un alto grado de adaptación a la vida en hábitats particulares dentro del territorio nacional, como son la selva en galería en el caso de *Anisolepis undulatus*, las dunas costeras



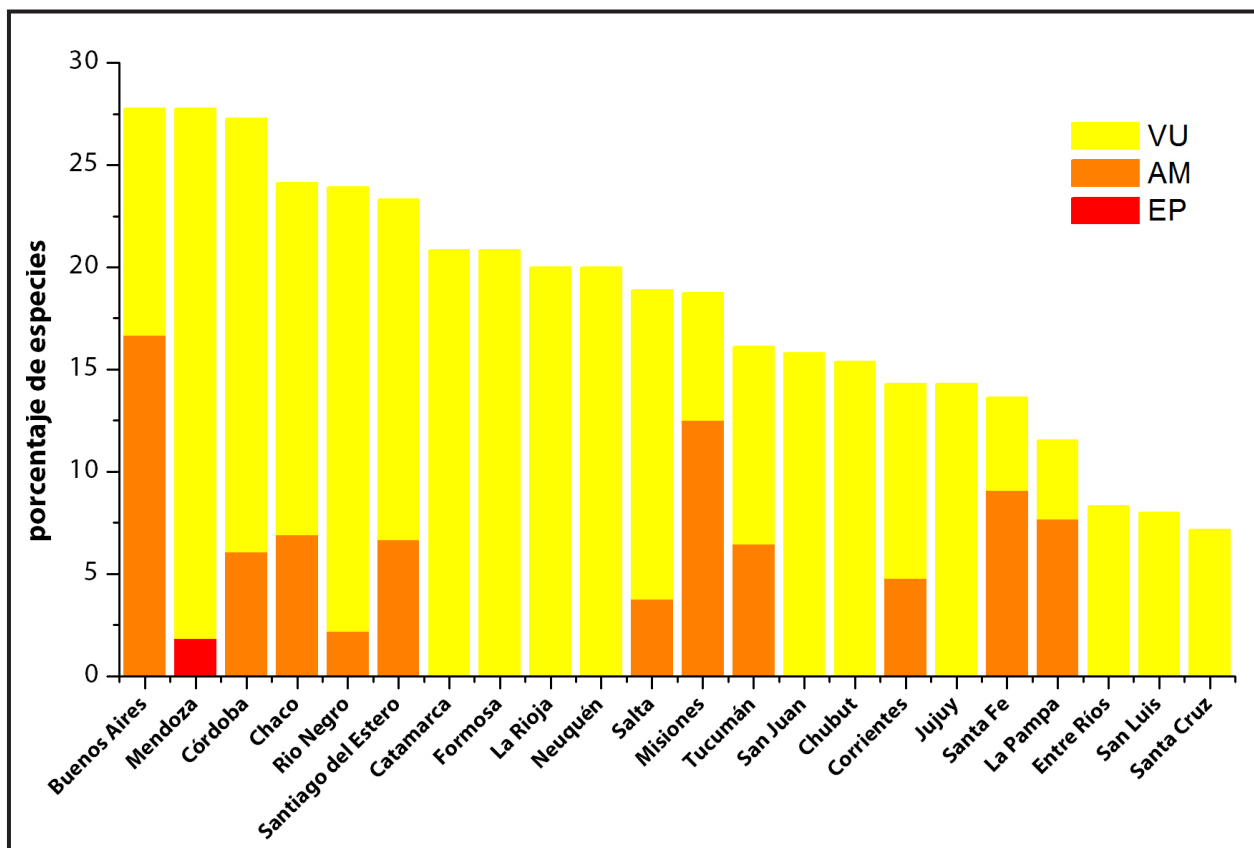
**Figura 1.** Porcentaje de especies de lagartijas y anfibios de la República Argentina en cada categoría de conservación en la categorización 2000 (barras llenas) y en la categorización actual (barras vacías). EP: En Peligro; AM: Amenazadas; VU: Vulnerables; IC: Insuficientemente Conocidas; NA: No Amenazadas.

en el caso de *Liolaemus multimaculatus* y los pastizales serranos de Tandilia y Ventania en el caso de *Liolaemus tandiliensis* y *Pristidactylus cashuatiensis* respectivamente.

Estos hábitats ocupan un área muy restringida de la provincia y actualmente se encuentran altamente disturbados por diversos tipos de actividades antrópicas. En la provincia de Mendoza, el mayor porcentaje de especies amenazadas tiene relación con dos factores primordiales: (1) la elevada riqueza de especies y, especialmente de endemismos, registradas mayormente en los ecosistemas Andino y Patagónico (Payunia); (2) las actividades humanas. La región de la Payunia (al sur de la provincia) posee una elevada heterogeneidad ambiental, con intrusiones de vegetación del Monte, estepa patagónica y pastizales pampeanos, permitiendo tanto la existencia de elementos propios de estas regiones así como de endemismos (Corbalán y Debandi, 2008). Teniendo en cuenta que el grado de endemismo (DINAC) es una variable que contribuye al índice de amenaza, muchas especies fueron asignadas a la categoría Vulnerable. Las actividades humanas también juegan un papel importante de amenaza en esta provincia. El caso más problemático lo constituye el uso intensivo de vehículos de doble tracción en los médanos del Nihuil, incluyendo las competencias internacionales como el Rally Dakar, poniendo en

peligro la única población conocida de *Liolaemus rabinoi* (única especie de lagartija categorizada En Peligro). Otras actividades como la construcción de diques y rutas también constituyen una amenaza para especies de distribución restringida. Un caso puntual es la pavimentación de la ruta internacional N° 145, que provocó la desaparición de varias poblaciones de *Phymaturus verdugo* por destrucción del hábitat y podría afectar las poblaciones de la especie endémica *Liolaemus flavipiceus*. Las actividades mineras y petroleras también son un factor de amenaza, ya que están ubicadas en áreas de alta riqueza de especies y/o endemismos, debiendo intensificar los controles y monitoreos estrictos por parte del gobierno provincial.

Las provincias chaqueñas tuvieron en general altos porcentajes de especies en algún grado de amenaza (Fig. 2). A pesar que Chaco y Formosa albergan una moderada cantidad de especies de lagartos, en comparación con las provincias del oeste argentino, alrededor de un cuarto de las especies registradas para sus territorios presentan cierto grado de amenaza, esto se debe a que las mismas son de hábitos arborícolas o están asociadas al bosque chaqueño. El que se encuentra actualmente con severas modificaciones por el avance de las fronteras agropecuarias, siendo el desmonte el principal factor que amenaza a las poblaciones de estos saurios. La pérdida de há-



**Figura 2.** Porcentaje de taxones de lagartos y anfibenas en cada categoría de amenaza (AM: Amenazada, EP: EN Peligro, VU: Vulnerable) en las provincias argentinas.

bitat por deforestación en las provincias chaqueñas ocurre a altas tasas anuales (período 1998-2006, tasa media de deforestación: 1.18 %)(Unidad de Manejo del Sistema de Evaluación Forestal, 2007), siendo Córdoba la provincia con la mayor tasa anual de pérdida de bosque nativo en toda la región chaqueña (período 2002-2006: 2.52%) seguida por Santiago del Estero (2.17%) y Salta (1.54%). Asimismo, si bien la tasa de deforestación en las provincias de Formosa y Chaco se encuentra entre las más bajas de la región, se observó una tendencia creciente entre el período 1998-2002 (Formosa: 0.16%, Chaco: 0.57%) y 2002-2006 (Formosa: 0.25%, Chaco: 0.65%) (Unidad de Manejo del Sistema de Evaluación Forestal, 2007). La pérdida de bosques nativos se relaciona principalmente con la conversión a cultivos, principalmente soja (Paruelo *et al.*, 2005). En algunas provincias los incendios forestales constituyen un importante factor de pérdida de hábitat. En la provincia de Córdoba, por ejemplo, se quemaron en promedio aproximadamente 38365 ha por año entre 2007 y 2010, de los cuales aproximadamente 5557 ha eran de bosque nativo (Programa Nacional de Estadísticas Forestales, 2011). La degradación del bosque

chaqueño debido a fuego, tala y sobrepastoreo afecta a la fauna de lagartos del Chaco Árido de diversas formas, incluyendo la disminución de sus abundancias poblacionales y modificaciones en la selección de microhabitats (Pelegrin *et al.*, 2009; Pelegrin y Bucher, 2010; 2012).

La comparación de la actual categorización y la lista roja de la IUCN (2012) (Tabla 4) es disímil debido a que la IUCN sólo ha evaluado el 11.7 % (30 especies) de las lagartijas y anfibenas de la Argentina. De las 30 especies evaluadas solo tres están categorizadas como Vulnerables, 19 como No Amenazadas y ocho como Insuficientemente Conocida (Tabla 5).

### Consideraciones finales

El presente trabajo constituye un importante esfuerzo a favor de la conservación de las lagartijas y anfibenas de Argentina, representando la información incorporada en los últimos años un importante salto cuantitativo y cualitativo. Sin embargo, es necesario aumentar el conocimiento sobre la biología de nuestras lagartijas y anfibenas, en especial de aquellas especies insuficientemente conocidas. Asimismo

los resultados indican que hay varias consideraciones que deberán tenerse en cuenta con el fin de desarrollar estrategias particulares de conservación. Los principales aspectos a considerar se refieren a las especies que tienen algún grado de amenaza (EP, AM, VU), así como las especies Insuficientemente conocidas (IC).

A nivel taxonómico de familia, Leiosauridae contiene la mayor cantidad de especies con alguna categoría de riesgo o amenaza (50 %). De las 18 especies que componen la familia, cinco tienen la categoría de Amenazada (AM) y cuatro Vulnerable (VU). Dentro de Leiosauridae se deberá tener consideración especial para el género *Urostrophus*, representado en la Argentina por una especie, a la cual se le ha asignado la categoría de Amenazada (AM). *Anisolepis* es el género no monotípico del país más comprometido en cuanto a su estado de conservación, ya que es el único género que tiene todas las especies que habitan en la Argentina con la categoría Amenazada (AM). Otro género de la familia Leiosauridae que presenta un alto porcentaje de especies con algún grado de amenaza (50 %) es el género *Pristidactylus*, que contiene una especie con la categoría Amenazada (AM) y dos como Vulnerable (VU).

La familia Liolaemidae está presente en Argentina con los géneros *Liolaemus* y *Phymaturus*. El género *Liolaemus* es el más diverso del país (el segundo en el mundo) y está representado por 152 especies, de las cuales una tiene la categoría En Peligro (EP), tres Amenazada (AM) y 24 Vulnerable (VU). Estos datos indican que el 17.7 % de las especies de los *Liolaemus* de Argentina tiene algún grado de amenaza. Sin embargo, el género *Phymaturus* muestra otra realidad, tornándose un caso único dentro de la herpetofauna Argentina, ya que la totalidad de las especies (32) tienen la categoría de Vulnerable (VU). El consenso entre los especialistas que decidieron incluir a todo el género *Phymaturus* como Vulnerable (VU) radicó en los aspectos biológicos esenciales muy especializados, como su modo de vida (saxícola), su tipo de reproducción (vivíparo) y su dieta (herbívoros). Igualmente se consideró el estado de las poblaciones, que en la mayoría de las especies son poco abundantes, así como el marcado endemismo presente en numerosos taxa integrantes del género.

Dentro de la familia Tropiduridae se destaca el vacío de información para el género *Stenocercus*, representado en Argentina por seis especies, de las

cuales cuatro están categorizadas como Insuficientemente Conocida. Asimismo, de las cuatro especies que tiene el género *Tropidurus* en la Argentina, dos están con la categoría Vulnerable (VU), dato que deberá ser tomado en cuenta debido a que en la categoría anterior (Avila *et al.*, 2000) ninguna especie del género presentó alguna categoría de amenaza.

En las familias Phyllodactylidae, Anguidae y Scincidae ninguna especie tiene asignada alguna categoría de amenaza. La situación en los Gymnophthalmidae de la Argentina es similar al de las familias nombradas anteriormente, ya que de las seis especies (tres géneros) que conforman la familia sólo *Vanzosaura rubricauda* tiene la categoría de Vulnerable (VU).

Dentro de los cinco géneros (14 especies) que integran la familia Teiidae, sólo tres tienen la categoría de Vulnerable (VU), dos especies (33 %) del género *Cnemidophorus* y una (50 %) de *Kentropyx*.

Finalmente en la familia Amphisbaenidae, de las 10 especies que están presentes en Argentina, sólo una (*Amphisbaena borelli*) tiene la categoría de Amenazada (AM), sugiriendo que las anfisbenas no presentan mayores riesgos de conservación.

La información obtenida no debe tratarse como meros datos estadísticos, sino que debe ser el detonante para desarrollar nuevos y efectivos planes de conservación que permitan detener los procesos que están influyendo en el deterioro de las poblaciones amenazadas. Asimismo, los planes de conservación deben incluir estudios y análisis más detallados de las causas y procesos que actualmente están afectando a dichas especies, así como también estudios relacionados a la biología de las especies. El desarrollo de nuevos planes de conservación por parte de diferentes entidades gubernamentales y no gubernamentales no debe encasillarse en la prohibición de la intervención del hombre, sino que debe contemplar la manera de aminorar sus acciones. Asimismo, es imprescindible el trabajo mancomunado entre los diferentes entes de gobiernos y los investigadores-especialistas, para desarrollar y ejecutar los planes de conservación que permitan un mayor conocimiento y preservación de las especies de lagartijas y anfisbenas de la Argentina. La prohibición o impedimento, por parte de las autoridades de gobierno, para desarrollar estudios científicos con las especies amenazadas, marcaría una involución al evidente crecimiento en el conocimiento de la herpetofauna argentina experimentado en los últimos 10 años.

**Tabla 2.** Valores asignados a los taxones de lagartijas y anfibenas de la República Argentina para cada variable descripta en Giraudó *et al.*, (2012) y categoría de conservación asociada. La abreviaturas de las variables indican: DINAC: Distribución Nacional y grado de endemismo; RARECOL: Rareza ecológica; EFHU: Efectos Humanos; POTRE: Potencial Reproductivo; TAM: Tamaño; ABUND: Abundancia. Las abreviaturas de las categorías de conservación son: NA: No Amenazada; EP: En Peligro; A: Amenazada; VU: Vulnerable; IC: Insuficientemente Conocida.

	DINAC	RARECOL	EFHU	POTRE	TAM	ABUND	VALOR	CATEGORÍA	Evaluadores*
<b>Leiosauridae</b>									
<i>Anisolepis grillii</i>	4	4	4	3	2	3	20	AM	CAT ANT
<i>Anisolepis longicauda</i>	4	4	4	0	2	3	17	AM	JLA, BBA, AH, MET
<i>Anisolepis undulatus</i>	4	4	4	3	2	4	21	AM	CAT ANT
<i>Diplolaemus bibronii</i>	2	3	0	3	2	2	12	NA	CSA, LJA, MM
<i>Diplolaemus darwinii</i>	2	3	0	3	2	2	12	NA	CSA, LJA, MM
<i>Diplolaemus leopardinus</i>	5	2	0	3	2	3	15	VU	CSA, LJA, MM
<i>Diplolaemus sexcinctus</i>	2	5	0	3	2	1	13	NA	CSA, LJA, JMB, NRI, MM
<i>Leiosaurus bellii</i>	2	3	0	3	2	2	12	NA	CSA, AL, LJA, MM
<i>Leiosaurus catamarcensis</i>	4	3	0	3	2	1	13	NA	CSA, JCA, AL
<i>Leiosaurus jaguaris</i>	4	3	0	3	2	2	14	NA	CSA, JCA, AL
<i>Leiosaurus paronae</i>	1	2	2	3	2	2	12	VU	CSA, JCA, MRC, AL, MM, NP
<i>Pristidactylus achalensis</i>	5	4	5	0	2	2	18	VU	MRC, LJA, MB
<i>Pristidactylus araucanus</i>	5	4	0	3	2	3	17	VU	CSA, LJA
<i>Pristidactylus casuhatiensis</i>	5	5	5	3	2	3	23	AM	GB, SC, SMZ
<i>Pristidactylus fasciatus</i>	3	3	?	3	2	3	14+?	IC	CSA, LJA, MM
<i>Pristidactylus nigroiugulus</i>	5	3	0	3	2	1	14	NA	CSA, LJA, MM
<i>Pristidactylus scapulatus</i>	3	3	0	3	2	1	12	NA	CSA, JCA, AL
<i>Urostrophus gallardoii</i>	3	4	3	0	1	3	14	AM	JLA, BBA, AH, MET
<b>Liolaemidae</b>									
<i>Liolaemus abaucan</i>	5	4	0	3	1	1	14	NA	CSA
<i>Liolaemus abdalai</i>	4	?	?	5	1	1	14+??	IC	ASQ
<i>Liolaemus albiceps</i>	5	5	1	4	2	0	17	NA	CSA
<i>Liolaemus andinus</i>	5	5	0	5	1	2	18	VU	CSA
<i>Liolaemus anomalus</i>	5	4	0	3	1	3	16	VU	CSA
<i>Liolaemus antumalguen</i>	5	4	0	5	2	3	19	VU	LJA, MM
<i>Liolaemus araucanensis</i>	4	2	0	3	1	1	11	NA	CSA
<i>Liolaemus archeforus</i>	5	3	0	5	2	1	16	NA	CSA
<i>Liolaemus austromendocinus</i>	4	4	0	4	2	0	14	NA	CSA, LJA, MM
<i>Liolaemus avilae</i>	5	4	0	4	1	2	16	NA	MFB
<i>Liolaemus azarai</i>	5	4	3	5	1	1	19	VU	JLA, BBA, AH, RVS, MET
<i>Liolaemus baguali</i>	5	4	0	5	1	1	16	NA	CSA, MB, LJA, MM
<i>Liolaemus bibronii</i>	2	0	0	5	0	1	8	NA	CSA, JCA, LJA, GMB, JMB, NRI, AL, MM
<i>Liolaemus bitaeniatus</i>	3	3	0	5	1	0	12	NA	CSA
<i>Liolaemus boulengeri</i>	4	4	0	5	1	0	14	NA	CSA, LJA, JMB, NRI
<i>Liolaemus buergeri</i>	5	3	0	5	2	1	16	NA	CSA, LJA, VC, MM

	DINAC	RARECOL	EFHU	POTRE	TAM	ABUND	VALOR	CATEGORÍA	Evaluadores*
<i>Liolaemus calchaqui</i>	5	4	0	5	1	1	16	NA	CSA
<i>Liolaemus camarones</i>	5	4	1	3	1	1	15	NA	CSA
<i>Liolaemus canqueli</i>	4	4	2	5	2	0	17	NA	CSA
<i>Liolaemus caparensis</i>	5	4	0	4	1	2	16	NA	MFB
<i>Liolaemus capillitas</i>	5	4	0	5	2	1	17	NA	CSA
<i>Liolaemus casamiquelai</i>	5	4	0	3	2	1	15	NA	LJA, MM
<i>Liolaemus cazianiae</i>	5	5	0	5	1	2	18	VU	CSA
<i>Liolaemus ceii</i>	4	5	0	5	1	1	16	NA	CSA, LJA, MM
<i>Liolaemus chacabucoense</i>	5	4	0	4	1	2	16	NA	MFB
<i>Liolaemus chacoensis</i>	3	3	4	3	1	0	14	NA	CSA, JLA, BBA, LJA, MRC, AH, NP, MET
<i>Liolaemus chaltin</i>	4	3	0	3	1	1	12	NA	CSA
<i>Liolaemus chehuachekenk</i>	5	4	0	4	2	1	16	NA	LJA, MM
<i>Liolaemus chiliensis</i>	3	0	0	3	1	1	8	NA	CSA
<i>Liolaemus chillanensis</i>	3	?	?	3	1	1	8+??	IC	LJA
<i>Liolaemus chlorostictus</i>	5	3	1	5	2	2	18	VU	CSA
<i>Liolaemus choique</i>	5	3	0	3	2	1	14	NA	CSA
<i>Liolaemus cinereus</i>	5	1	?	5	?	2	13+??	IC	JCA, MRC, AL
<i>Liolaemus coeruleus</i>	5	4	0	5	1	1	16	NA	CSA, MB
<i>Liolaemus crepuscularis</i>	5	4	0	5	1	1	16	NA	CSA, RVS
<i>Liolaemus cuyanus</i>	2	4	3	3	1	1	14	NA	CSA, JCA, LJA, AL, MM
<i>Liolaemus cuyumhue</i>	5	4	2	5	1	2	19	VU	LJA, MM
<i>Liolaemus cyanogaster</i>	3	?	?	3	1	1	8+??	IC	LJA
<i>Liolaemus cyaneinotatus</i>	4	?	?	?	1	?	5+????	IC	ASQ
<i>Liolaemus darwinii</i>	1	1	0	3	1	0	6	NA	CSA, JCA, LJA, AL, MM
<i>Liolaemus diaguita</i>	5	2	1	3	1	1	13	NA	CSA
<i>Liolaemus dicktracyi</i>	5	4	0	5	1	2	17	NA	CSA
<i>Liolaemus ditadai</i>	5	5	3	3	1	3	20	AM	CSA, MRC
<i>Liolaemus donosobarrosi</i>	5	4	0	3	1	2	15	NA	CSA
<i>Liolaemus dorbignyi</i>	5	5	0	5	1	2	18	VU	CSA
<i>Liolaemus duellmani</i>	5	3	0	5	1	4	18	VU	CSA
<i>Liolaemus dumerili</i>	5	3	1	3	1	1	13	NA	CSA
<i>Liolaemus eleodori</i>	5	5	0	5	1	1	17	NA	JCA, MRC, AL
<i>Liolaemus elongatus</i>	3	3	0	5	1	0	12	NA	CSA, LJA, MB, JMB, NRI, MM
<i>Liolaemus escarchadosi</i>	4	3	0	5	1	1	14	NA	CSA
<i>Liolaemus espinozai</i>	5	4	0	3	1	1	14	NA	CSA
<i>Liolaemus exploratorum</i>	5	?	?	5	1	5	16+??	IC	CSA
<i>Liolaemus famatinae</i>	5	4	0	5	1	1	16	NA	CSA
<i>Liolaemus fitzgeraldi</i>	5	4	?	?	?	1	10+???	IC	CSA, VC
<i>Liolaemus fitzingerii</i>	4	4	2	3	1	1	15	NA	CSA, LJA, MM



	DINAC	RARECOL	EFHU	POTRE	TAM	ABUND	VALOR	CATEGORÍA	Evaluadores*
<i>Liolaemus flavipiceus</i>	5	3	4	3	1	1	17	VU	CSA, VC
<i>Liolaemus gallardoii</i>	5	3	0	5	1	2	16	NA	CSA, LJA
<i>Liolaemus goetschi</i>	5	4	0	3	1	2	15	NA	CSA, LJA
<i>Liolaemus graciellae</i>	5	5	0	5	1	1	17	NA	CSA, JCA, MRC, AL
<i>Liolaemus gracilis</i>	3	3	0	4	1	0	11	NA	CSA, LJA, MM, RVS, LV
<i>Liolaemus gravenhorstii</i>	5	?	?	?	?	2	7+????	IC	MM
<i>Liolaemus griseus</i>	5	?	?	5	1	?	11+??	IC	CSA
<i>Liolaemus grosseorum</i>	4	2	0	5	1	0	12	NA	CSA, LJA, MM, RVS
<i>Liolaemus gununakuna</i>	5	4	0	?	1	1	11+?	IC	LJA, MM
<i>Liolaemus halonastes</i>	5	5	0	5	1	3	19	VU	CSA
<i>Liolaemus hatcheri</i>	4	4	0	5	1	1	15	NA	CSA, LJA
<i>Liolaemus heliodermis</i>	5	4	0	5	1	2	17	NA	CSA
<i>Liolaemus huacahuasicus</i>	5	5	0	5	1	2	18	VU	CSA
<i>Liolaemus huayra</i>	5	4	0	5	1	3	18	VU	CSA
<i>Liolaemus inacayali</i>	4	3	0	3	1	1	12	NA	CSA, JCA, LJA, GMB
<i>Liolaemus inti</i>	5	5	0	5	1	3	19	VU	CSA
<i>Liolaemus irregularis</i>	5	5	1	5	1	0	17	NA	CSA
<i>Liolaemus josei</i>	4	3	2	5	1	1	16	NA	CSA, LJA
<i>Liolaemus kingii</i>	3	4	0	4	1	0	12	NA	CSA, LJA, MB, MM
<i>Liolaemus kolengh</i>	5	5	0	5	1	1	18	VU	CSA
<i>Liolaemus koslowskyi</i>	4	3	0	3	1	0	11	NA	CSA, JCA, LJA, MM, AL, RVS
<i>Liolaemus kriegi</i>	4	5	0	5	1	1	16	NA	CSA, LJA, MM
<i>Liolaemus laurenti</i>	3	3	0	3	1	1	11	NA	CSA, JCA, AL
<i>Liolaemus lavillai</i>	5	4	0	5	1	1	16	NA	CSA
<i>Liolaemus lentus</i>	5	4	3	3	1	4	20	A	CSA, LJA, CHFP
<i>Liolaemus lineomaculatus</i>	4	3	0	5	1	1	14	NA	CSA, LJA, JMB, NRI, MM
<i>Liolaemus loboii</i>	5	4	0	4	1	2	16	NA	CSA
<i>Liolaemus magellanicus</i>	5	5	0	5	1	1	17	NA	CSA, LJA, JMB, NRI
<i>Liolaemus mapuche</i>	5	4	0	3	1	1	14	NA	CSA
<i>Liolaemus martori</i>	5	4	2	3	1	1	16	NA	CSA
<i>Liolaemus melanops</i>	5	4	0	3	1	0	13	NA	CSA
<i>Liolaemus montanezi</i>	5	5	4	?	1	2	17+?	IC	MRC
<i>Liolaemus montanus</i>	5	0	0	0	1	2	8+????	IC	CSA
<i>Liolaemus morandae</i>	4	4	0	4	1	2	15	NA	MFB
<i>Liolaemus morenoi</i>	5	4	0	3	1	1	14	NA	CSA
<i>Liolaemus multicolor</i>	4	5	1	5	1	1	17	NA	CSA
<i>Liolaemus multimaculatus</i>	5	4	5	3	1	1	19	VU	FK, LV
<i>Liolaemus neuquensis</i>	5	4	0	5	1	1	16	NA	CSA
<i>Liolaemus nigriceps</i>	5	5	0	?	1	1	12+?	IC	CSA

	DINAC	RARECOL	EFHU	POTRE	TAM	ABUND	VALOR	CATEGORÍA	Evaluadores*
<i>Liolaemus olongasta</i>	4	2	0	5	1	0	12	NA	CSA, JCA, AL
<i>Liolaemus orientalis</i>	4	5	1	5	1	2	18	VU	CSA
<i>Liolaemus orko</i>	5	5	0	5	1	1	17	VU	CSA
<i>Liolaemus ornatus</i>	3	3	0	5	1	0	12	NA	CSA
<i>Liolaemus pagaburoi</i>	4	4	0	5	1	0	14	NA	CSA, JCA, AL
<i>Liolaemus parvus</i>	4	2	0	5	1	0	12	NA	CSA
<i>Liolaemus petrophilus</i>	2	2	0	3	1	1	9	NA	CSA, LJA, MM
<i>Liolaemus pictus argentinus</i>	3	2	0	5	1	0	11	NA	CSA, LJA, JMB, NRI
<i>Liolaemus piriphlogos</i>	5	3	0	3	0	1	12	NA	ASQ
<i>Liolaemus poecilochromus</i>	5	5	0	5	1	1	17	NA	CSA
<i>Liolaemus pseudoanomalus</i>	4	2	0	3	1	2	12	NA	CSA, JCA, LJA, AL, MM
<i>Liolaemus puelche</i>	5	?	0	?	1	?	6+?	IC	LJA, MM
<i>Liolaemus pulcherrimus</i>	5	5	0	5	1	2	18	VU	CSA
<i>Liolaemus puna</i>	2	3	0	5	1	0	11	NA	CSA
<i>Liolaemus punmahuida</i>	5	4	0	4	1	1	15	NA	LJA, MM
<i>Liolaemus puritamensis</i>	5	3	0	5	1	2	16	NA	CSA
<i>Liolaemus purul</i>	4	3	1	4	1	1	14	NA	CSA
<i>Liolaemus quilmes</i>	4	3	0	3	1	0	11	NA	CSA
<i>Liolaemus rabinoi</i>	5	4	5	5	1	4	24	EP	CSA, JLA, AL, RVS
<i>Liolaemus ramirezae</i>	3	3	0	3	1	0	10	NA	CSA, RVS
<i>Liolaemus riojanus</i>	2	5	3	5	1	2	18	VU	CSA, JCA, GMB, AL
<i>Liolaemus robertmertensi</i>	4	3	0	3	1	1	12	NA	CSA
<i>Liolaemus rothi</i>	2	2	0	3	1	1	9	NA	CSA, LJA, MM
<i>Liolaemus ruibali</i>	5	4	0	5	1	0	15	NA	CSA, JCA, AL
<i>Liolaemus sagei</i>	5	2	0	3	1	1	12	NA	CSA
<i>Liolaemus salinicola</i>	4	4	0	3	1	0	12	NA	CSA
<i>Liolaemus sanjuanensis</i>	5	4	0	5	1	1	16	NA	JCA, GMB, AL
<i>Liolaemus sarmientoi</i>	5	4	0	5	1	1	16	NA	CSA, LJA, JMB, NRI, MM
<i>Liolaemus saxatilis</i>	4	3	0	5	1	1	14	NA	MRC
<i>Liolaemus scapularis</i>	4	4	3	3	1	1	16	NA	CSA
<i>Liolaemus scolaroi</i>	5	4	?	5	1	1	16+?	IC	LJA, MM
<i>Liolaemus scrocchii</i>	4	4	0	5	1	1	15	NA	CSA
<i>Liolaemus senguier</i>	5	4	0	5	1	2	17	NA	CSA
<i>Liolaemus shehuen</i>	5	4	1	4	1	1	16	NA	CSA
<i>Liolaemus shitan</i>	5	3	0	3	1	1	13	NA	CSA
<i>Liolaemus smaug</i>	5	3	0	3	1	0	12	NA	CSA
<i>Liolaemus silvanae</i>	5	5	0	5	1	3	19	VU	CSA, LJA
<i>Liolaemus somuncurae</i>	5	?	?	?	1	?	6+????	IC	CSA, LJA
<i>Liolaemus talampaya</i>	5	4	0	3	1	1	14	NA	CSA

	DINAC	RARECOL	EFHU	POTRE	TAM	ABUND	VALOR	CATEGORÍA	Evaluadores*
<i>Liolaemus tandiliensis</i>	5	4	3	5	1	2	20	AM	LV
<i>Liolaemus tari</i>	5	4	?	5	1	1	16+?	IC	LJA
<i>Liolaemus tehuelche</i>	5	4	0	5	1	2	17	NA	CSA
<i>Liolaemus telsen</i>	5	4	0	5	1	2	17	NA	CSA
<i>Liolaemus tenuis tenuis</i>	4	4	0	3	1	1	13	NA	CSA
<i>Liolaemus thermanum</i>	5	3	3	4	1	2	18	VU	CSA
<i>Liolaemus tregenzai</i>	5	4	4	5	1	1	20	VU	LJA
<i>Liolaemus tristis</i>	5	4	0	5	1	1	16	IC	LJA
<i>Liolaemus tromen</i>	5	4	1	4	1	2	17	NA	CSA
<i>Liolaemus tulkas</i>	5	4	0	5	1	1	16	NA	CSA
<i>Liolaemus umbrifer</i>	5	4	0	5	1	1	16	NA	CSA
<i>Liolaemus uptoni</i>	5	4	?	5	1	1	16+?	IC	LJA
<i>Liolaemus uspallatensis</i>	4	2	0	5	1	1	13	NA	CSA, JCA, AL
<i>Liolaemus vallecurensis</i>	5	5	0	5	1	2	18	VU	JCA, AL
<i>Liolaemus vulcanus</i>	5	4	0	4	1	1	15	NA	CSA
<i>Liolaemus wiegmanni</i>	1	2	2	3	1	1	10	NA	CSA, MRC, LV
<i>Liolaemus xanthoviridis</i>	5	4	0	3	1	1	14	NA	CSA, LJA, MM
<i>Liolaemus yanalco</i>	5	2	0	3	1	1	12	NA	CSA
<i>Liolaemus zullyi</i>	5	4	0	5	1	1	16	NA	CSA, LJA
<i>Phymaturus antofagastensis</i>	5	5	0	5	2	1	18	VU	CSA, JCA JMB, NRI, AL
<i>Phymaturus calcogaster</i>	5	5	0	5	2	1	18	VU	LJA, LJ, JMB, NRI, MM
<i>Phymaturus castillensis</i>	5	5	0	5	2	1	18	VU	CSA, JCA LJA, LJ, JMB, NRI, MM
<i>Phymaturus ceii</i>	5	5	0	5	1	2	18	VU	CSA, LJA, MM
<i>Phymaturus delheyi</i>	5	5	0	5	1	2	18	VU	CSA, LJA, MM
<i>Phymaturus denotatus</i>	5	5	?	5	1	2	18	VU	CSA
<i>Phymaturus desuetus</i>	5	5	?	5	1	3	18	VU	CSA
<i>Phymaturus dorsimaculatus</i>	5	5	0	5	1	1	17	VU	CSA, LJA, MM
<i>Phymaturus etheridgei</i>	5	5	0	5	1	1	17	VU	CSA, LJA, MM
<i>Phymaturus excelsus</i>	5	5	0	5	1	1	17	VU	CSA, LJA, JMB, NRI, MM
<i>Phymaturus extrilidus</i>								VU	AL, JCA
<i>Phymaturus felixi</i>	5	5	0	5	1	1	17	VU	CSA, LJA, MM
<i>Phymaturus gynechloinus</i>	5	5	0	5	1	1	17	VU	VC
<i>Phymaturus indistinctus</i>	5	5	0	5	1	1	17	VU	CSA, LJA, JMB, NRI, MM
<i>Phymaturus laurenti</i>	5	5	0	5	1	1	17	VU	CSA
<i>Phymaturus mallimaccii</i>	5	5	0	5	1	2	18	VU	CSA, LJA, MM
<i>Phymaturus manuelae</i>	5	5	0	5	1	2	18	VU	LJA, JMB, NRI, MM
<i>Phymaturus nevadoi</i>	5	5	0	5	2	2	19	VU	VC
<i>Phymaturus palluma</i>	4	5	0	5	2	1	17	VU	CSA, VC
<i>Phymaturus patagonicus</i>	5	5	0	5	2	1	18	VU	CSA, LJA, MM

	DINAC	RARECOL	EFHU	POTRE	TAM	ABUND	VALOR	CATEGORÍA	Evaluadores*
<i>Phymaturus payuniaie</i>	5	5	0	5	2	1	18	VU	VC
<i>Phymaturus punae</i>	5	5	0	5	1	2	18	VU	CSA, JCA JMB, NRI, AL
<i>Phymaturus querque</i>	5	5	0	5	1	1	17	VU	CSA, LJA, MM
<i>Phymaturus roigorum</i>	5	5	0	5	1	0	16	VU	CSA, VC
<i>Phymaturus sitesi</i>	5	5	0	5	1	1	17	VU	LJA, MM
<i>Phymaturus somuncurensis</i>	5	5	0	5	1	2	16	VU	CSA, LJA, MM
<i>Phymaturus spectabilis</i>	5	5	0	5	1	1	17	VU	CSA, LJA, MM
<i>Phymaturus spurcus</i>	5	5	0	5	1	1	17	VU	CSA
<i>Phymaturus tenebrosus</i>	5	5	0	5	1	1	17	VU	CSA, JMB, NRI
<i>Phymaturus verdugo</i>	5	5	0	5	1	1	17	VU	CSA, VC
<i>Phymaturus videlai</i>	5	5	0	5	1	1	17	VU	CSA
<i>Phymaturus zapalensis</i>	5	5	0	5	1	1	17	VU	CSA, JMB, NRI
<b>Polychrotidae</b>									
<i>Polychrus acutirostris</i>	3	4	5	0	2	3	17	VU	JLA, BBA, AH, MET
<b>Tropiduridae</b>									
<i>Stenocercus azureus</i>	3	?	?	?	1	?	4+????	IC	ASQ
<i>Stenocercus caducus</i>	3	?	?	?	1	?	4+????	IC	ASQ
<i>Stenocercus doellojuradoi</i>	4	3	5	3	1	2	18	VU	JLA, BBA, MRC, AH, NP, MET
<i>Stenocercus marmoratus</i>	3	?	?	?	1	?	4+????	IC	ASQ
<i>Stenocercus pectinatus</i>	1	2	2	3	1	2	11	NA	MRC, LV
<i>Stenocercus roseiventris</i>	3	?	?	?	1	?	4+????	IC	ASQ
<i>Tropidurus etheridgei</i>	4	3	3	3	1	1	15	NA	CSA, JLA, BBA, MRC, AH, NP, MET
<i>Tropidurus melanopleurus</i>	5	4	0	3	2	2	16	VU	CSA, MRC
<i>Tropidurus spinulosus</i>	3	3	3	3	2	1	15	VU	CSA, JLA, BBA, MRC, AH, MET
<i>Tropidurus torquatus</i>	4	1	1	3	2	1	12	NA	JLA, BBA, AH, MET
<b>Phyllodactylidae</b>									
<i>Homonota andicola</i>	2	3	0	5	0	2	12	NA	JCA, AL
<i>Homonota borelli</i>	2	3	0	5	0	1	11	NA	JCA, MRC, AL
<i>Homonota darwini darwini</i>	4	5	0	5	1	1	16	NA	LJA, JMB, NRI, MM
<i>Homonota d. macrocephala</i>	5	?	?	?	0	4	9+???	IC	CSA, FA
<i>Homonota fasciata</i>	1	2	3	5	0	1	12	NA	JCA, JLA, BBA, MRC, AH, AL, NP, MET
<i>Homonota underwoodi</i>	1	0	0	5	0	0	6	NA	JCA, AL
<i>Homonota whitii</i>	4	2	0	5	0	1	12	NA	MRC
<i>Phyllopezus pollicaris przewalskyi</i>	4	1	2	5	1	1	14	NA	JLA, BBA, AH, MET
<b>Anguidae</b>									
<i>Ophiodes vertebralis</i>	1	2	1	3	2	1	10	NA	MRC, LV
<i>Ophiodes intermedius</i>	1	3	1	5	1	1	12	NA	JLA, MRC, BBA, AH, MET
<i>Ophiodes yacupoi</i>	4	?	?	?	2	2	8+???	IC	FA
<b>Gymnophthalmidae</b>									

	DINAC	RARECOL	EFHU	POTRE	TAM	ABUND	VALOR	CATEGORÍA	Evaluadores*
<i>Cercosaura ocellata petersi</i>	?	?	0	?	0	?	0+???	IC	JLA, BBA, AH, MET
<i>Cercosaura parkeri</i>	2	0	0	5	0	1	8	NA	JLA, BBA, AH, MET
<i>Cercosaura schreibersii</i>	1	3	0	0	0	0	4	NA	JLA, BBA, MRC, AH, MET
<i>Cercosaura steyeri</i>	5	?	?	5	1	?	11+???	IC	JLA, BBA, AH, MET
<i>Opieuteer xestus</i>	4	?	?	?	1	1	6+???	IC	FA
<i>Vanzosaura rubricauda</i>	4	4	3	5	0	2	18	VU	JLA, BBA, MRC, AH, NP, MET
<b>Scincidae</b>									
<i>Mabuya dorsivittata</i>	1	1	0	4	1	1	8	NA	JLA, BBA, MRC, AH, NP, MET
<i>Mabuya frenata</i>	1	1	0	4	1	1	8	NA	JLA, BBA, MRC, AH, MET
<b>Teiidae</b>									
<i>Ameiva ameiva</i>	3	4	3	3	2	1	16	NA	JLA, BBA, FA, MRC, AH, MET
<i>Cnemidophorus lacertoides</i>	2	2	4	5	1	2	16	VU	FA, MRC
<i>Cnemidophorus leachi</i>	5	?	?	5	1	2	13+??	IC	
<i>Cnemidophorus longicauda</i>	1	0	4	5	1	0	11	NA	FA, JCA MRC, AL
<i>Cnemidophorus ocellifer</i>	1	2	1	3	1	1	9	NA	JLA, BBA, FA, MRC, AH, MET
<i>Cnemidophorus serranus</i>	5	2	3	3	1	2	16	VU	MRC
<i>Cnemidophorus tergoaevigatus</i>	1	2	4	5	1	1	14	NA	FA, MRC
<i>Kentropyx lagartija</i>	3	4	?	5	1	2	15?	IC	FA
<i>Kentropyx viridistriga</i>	3	4	2	5	1	2	17	VU	JLA, BBA, AH, MET
<i>Teius oculatus</i>	1	1	1	3	2	1	9	NA	JLA, BBA, MRC, AH, MET
<i>Teius suquiensis</i>	2	2	0	3	2	2	8	NA	MRC
<i>Teius teyou</i>	3	1	2	3	2	1	12	NA	JLA, BBA, MRC, AH, NP, MET
<i>Tupinambis merianae</i>	0	0	2	1	3	1	7	NA	JLA, BBA, MRC, AH, MET, MB
<i>Tupinambis rufescens</i>	1	3	2	1	3	1	11	NA	JLA, BBA, MRC, AH, MET
<b>Amphisbaenidae</b>									
<i>Amphisbaena angustifrons</i>	1	2	1	4	2	1	11	NA	MRC, RM
<i>Amphisbaena bolivica</i>	3	2	1	3	2	1	12	NA	MRC, RM
<i>Amphisbaena heterozonata</i>	1	2	1	3	2	2	11	NA	MRC, RM
<i>Amphisbaena hiata</i>	4	2	1	0	2	2	11	NA	RM
<i>Amphisbaena mertensii</i>	2	2	1	3	2	2	12	NA	RM
<i>Amphisbaena plumbea</i>	3	2	1	3	2	2	13	NA	RM
<i>Amphisbaena prunicolor</i>	2	2	1	3	2	2	12	NA	RM
<i>Amphisbaena borellii</i>	4	2	1	5	2	5	19	AM	RM
<i>Anops kingi</i>	0	3	1	5	2	1	12	NA	MRC, RM, LV
<b>Leposternidae</b>									
<i>Leposternon microcephalum</i>	3	2	1	4	2	1	13	NA	RM

\* **Siglas Evaluadores:** AH: Alejandra Hernando; AL: Alejandro Laspiur; ASQ: Andrés Sebastián Quinteros; BBA: Blanca Beatriz Álvarez; CHFP: Cristian Hernán Fulvio Pérez; CSA: Cristian Simón Abdala; FA: Federico Arias; FK: Federico Kacolis; GB: Gabriela Brancatelli; GMB: Graciela Mirta Blanco; JCA: Juan Carlos Acosta; JMB: Jorgelina Mariela Boretto; JLA: José Luis Acosta; LJA: Luciano Javier Ávila; LV: Laura Vega; MB: Marcelo Bonino; MET: María Esther Tedesco; MFB: María Florencia Breitman; MM: Mariana Morando; MRC: Mario Roberto Cabrera; NP: Nicolás Pelegrin; NRI: Nora Ruth Ibarguengoytia; RM: Ricardo Montero; RVS: Romina Valeria Semhan; SC: Samanta Cairo; SMZ: Sergio Martín Zalva; VC: Valeria Corbalán. El orden de los autores en la Tabla 2, presentan disposición alfabética según el apellido.

**Tabla 3.** Distribución por provincias de las lagartijas y anfisbenas de la República Argentina, indicando su categoría de conservación actual y el número de especies por provincia. IC: Insuficientemente Conocida; EP: En Peligro; AM: Amenazada; VU: Vulnerable; NA: No Amenazada.

	Buenos Aires	Catamarca	Chaco	Chubut	Córdoba	Corrientes	Entre Ríos	Formosa	Jujuy	La Pampa	La Rioja	Mendoza	Misiones	Neuquén	Río Negro	Salta	San Juan	San Luis	Santa Fe	Santa Cruz	Santiago del Estero	Tierra del Fuego	Tucumán	Nº de provin- cias presente	
<i>Anisolepis grillii</i>												AM												1	
<i>Anisolepis longicauda</i>		AM				AM							AM						AM						4
<i>Anisolepis undulatus</i>	AM																								1
<i>Diplolaemus bibronii</i>			NA												NA					NA					3
<i>Diplolaemus darwini</i>			NA												NA					NA					3
<i>Diplolaemus leopardinus</i>												VU													1
<i>Diplolaemus sexcinctus</i>				NA								NA		NA	NA										4
<i>Leiosaurus bellii</i>				NA						NA		NA		NA	NA										6
<i>Leiosaurus catamarcensis</i>		NA								NA	NA	NA					NA								6
<i>Leiosaurus jaguaris</i>											NA						NA								2
<i>Leiosaurus paronae</i>		VU								VU	VU	VU						VU				VU			7
<i>Pristidactylus achalensis</i>										VU	VU							VU							2
<i>Pristidactylus araucanus</i>												VU													2
<i>Pristidactylus casuhatiensis</i>																									1
<i>Pristidactylus fasciatus</i>												IC													4
<i>Pristidactylus nigroiugulus</i>				NA											NA										2
<i>Pristidactylus scapulatus</i>												NA													3
<i>Urostrophus gallardoi</i>										AM													AM		7
<i>Liolaemus abaucan</i>		NA																							1
<i>Liolaemus abdalai</i>														IC											1
<i>Liolaemus albiceps</i>																									1
<i>Liolaemus andinus</i>																									1

	Buenos Aires	Catamarca	Chaco	Chubut	Córdoba	Corrientes	Entre Ríos	Formosa	Jujuy	La Pampa	La Rioja	Mendoza	Misiones	Neuquén	Río Negro	Salta	San Juan	San Luis	Santa Fe	Santa Cruz	Santiago del Estero	Tierra del Fuego	Tucumán	Nº de provincias presente	
<i>Liolaemus anomalus</i>											VU	VU												3	
<i>Liolaemus antumalguen</i>													VU												1
<i>Liolaemus araucanensis</i>													NA												1
<i>Liolaemus archeforus</i>																				NA					1
<i>Liolaemus austromendocinus</i>										NA		NA													3
<i>Liolaemus avilae</i>																				NA					1
<i>Liolaemus azarai</i>																									1
<i>Liolaemus baguali</i>																				NA					1
<i>Liolaemus bibronii</i>												NA	NA	NA	NA					NA					6
<i>Liolaemus bitaeniatus</i>		NA														NA							NA		3
<i>Liolaemus boulengeri</i>				NA																					1
<i>Liolaemus buergeri</i>												NA	NA												2
<i>Liolaemus calchaqui</i>																							NA		2
<i>Liolaemus camarones</i>				NA																					1
<i>Liolaemus canqueli</i>				NA																					1
<i>Liolaemus caparensis</i>																					NA				1
<i>Liolaemus capillitas</i>																									1
<i>Liolaemus casamiquelai</i>															NA										1
<i>Liolaemus cazianiae</i>																									1
<i>Liolaemus ceii</i>																									1
<i>Liolaemus cyaneinotatus</i>														IC											1
<i>Liolaemus chacabucoense</i>																									1
<i>Liolaemus chacoensis</i>		NA	NA		NA			NA			NA					NA	NA	NA			NA		NA		10
<i>Liolaemus chaltin</i>																									1

	Buenos Aires	Catamarca	Chaco	Chubut	Córdoba	Corrientes	Entre Ríos	Formosa	Jujuy	La Pampa	La Rioja	Mendoza	Misiones	Neuquén	Río Negro	Salta	San Juan	San Luis	Santa Fe	Santa Cruz	Santiago del Estero	Tierra del Fuego	Tucumán	Nº de provincias presente
<i>Liolaemus chehuacheken</i>				NA																				1
<i>Liolaemus chilensis</i>													NA	NA	NA									2
<i>Liolaemus chillanensis</i>													IC											1
<i>Liolaemus chlorostictus</i>							VU																	1
<i>Liolaemus choique</i>										NA														1
<i>Liolaemus cinereus</i>																	IC							1
<i>Liolaemus coeruleus</i>													NA											1
<i>Liolaemus crepuscularis</i>		NA																						1
<i>Liolaemus cuyanus</i>		NA							NA	NA	NA	NA	NA	NA	NA	NA	NA							6
<i>Liolaemus cuyumhue</i>													VU											1
<i>Liolaemus cyanogaster</i>													IC											1
<i>Liolaemus darwini</i>	NA	NA							NA	NA	NA	NA	NA	NA	NA	NA	NA	NA						11
<i>Liolaemus diaguaita</i>																NA								1
<i>Liolaemus dicktracyi</i>											NA													1
<i>Liolaemus ditadai</i>																					AM			2
<i>Liolaemus donosobarrosi</i>												NA		NA										2
<i>Liolaemus dorbignyi</i>																								1
<i>Liolaemus duellmani</i>												VU												1
<i>Liolaemus dumerili</i>																								1
<i>Liolaemus eleodori</i>																								1
<i>Liolaemus elongatus</i>												NA		NA	NA									4
<i>Liolaemus escarchadosi</i>																								1
<i>Liolaemus espinozai</i>		NA																						1
<i>Liolaemus exploratorum</i>																								1



	Buenos Aires	Catamarca	Chaco	Chubut	Córdoba	Corrientes	Entre Ríos	Formosa	Jujuy	La Pampa	La Rioja	Mendoza	Misiones	Neuquén	Río Negro	Salta	San Juan	San Luis	Santa Fe	Santa Cruz	Santiago del Estero	Tierra del Fuego	Tucumán	No de provin- cias presente
<i>Liolaemus famatinae</i>									NA															1
<i>Liolaemus fitzgeraldi</i>												IC					IC							2
<i>Liolaemus fitzingerii</i>				NA																NA				2
<i>Liolaemus flavipiceus</i>												VU												1
<i>Liolaemus gallardoi</i>																				NA				1
<i>Liolaemus goetschi</i>															NA									1
<i>Liolaemus graciellae</i>									NA		NA						NA							2
<i>Liolaemus gracilis</i>									NA	NA		NA	NA	NA			NA	NA						7
<i>Liolaemus gravenhorstii</i>												IC												1
<i>Liolaemus griseus</i>																							IC	1
<i>Liolaemus grosseorum</i>									NA	NA		NA	NA											3
<i>Liolaemus gununakuna</i>													IC	IC										2
<i>Liolaemus halonastes</i>															VU									1
<i>Liolaemus hatcheri</i>																				NA				1
<i>Liolaemus heliodermis</i>																						NA		1
<i>Liolaemus huacahuasicus</i>																						VU		1
<i>Liolaemus huayra</i>																						VU		1
<i>Liolaemus inacayali</i>														NA										1
<i>Liolaemus inti</i>																							VU	1
<i>Liolaemus irregularis</i>																							NA	1
<i>Liolaemus josei</i>									NA	NA		NA												2
<i>Liolaemus kingii</i>																							NA	2
<i>Liolaemus kolengh</i>																							VU	1
<i>Liolaemus koslowskyi</i>											NA													2

	Buenos Aires	Catamarca	Chaco	Chubut	Córdoba	Corrientes	Entre Ríos	Formosa	Jujuy	La Pampa	La Rioja	Mendoza	Misiones	Nequén	Río Negro	Salta	San Juan	San Luis	Santa Fe	Santa Cruz	Santiago del Estero	Tierra del Fuego	Tucumán	Nº de provincias presente
<i>Liolaemus kriegi</i>			NA										NA	NA										3
<i>Liolaemus laurenti</i>		NA									NA	NA					NA							4
<i>Liolaemus lavillai</i>																NA								1
<i>Liolaemus lentus</i>										AM					AM									2
<i>Liolaemus lineomaculatus</i>				NA									NA	NA	NA					NA				4
<i>Liolaemus loboii</i>													NA									NA		1
<i>Liolaemus magellanicus</i>													NA							NA		NA		2
<i>Liolaemus mapuche</i>													NA											1
<i>Liolaemus martori</i>															NA									1
<i>Liolaemus melanops</i>				NA									NA		NA									2
<i>Liolaemus montanezi</i>																	IC							1
<i>Liolaemus montanus</i>		IC																						1
<i>Liolaemus morandae</i>				NA																NA				2
<i>Liolaemus morenoi</i>														NA	NA									2
<i>Liolaemus multicolor</i>									NA							NA								2
<i>Liolaemus multimaculatus</i>	VU														VU									2
<i>Liolaemus neuquensis</i>														NA										1
<i>Liolaemus nigriceps</i>																								1
<i>Liolaemus olongasta</i>											NA	NA												3
<i>Liolaemus orientalis</i>																								1
<i>Liolaemus orko</i>		VU																						1
<i>Liolaemus ornatus</i>									NA							NA								2
<i>Liolaemus pagaburoi</i>		NA																					NA	2
<i>Liolaemus parvus</i>											NA	NA												3

	Buenos Aires	Catamarca	Chaco	Chubut	Córdoba	Corrientes	Entre Ríos	Formosa	Jujuy	La Pampa	La Rioja	Mendoza	Misiones	Neuquén	Río Negro	Salta	San Juan	San Luis	Santa Fe	Santa Cruz	Santiago del Estero	Tierra del Fuego	Tucumán	Nº de provin- cias presente	
<i>Liolaemus petrophilus</i>			NA										NA	NA											3
<i>Liolaemus pictus argentinus</i>			NA											NA	NA					NA					4
<i>Liolaemus piriphlogos</i>								NA																	1
<i>Liolaemus poecilochromus</i>		NA														NA									2
<i>Liolaemus pseudoanomalus</i>		NA									NA					NA									3
<i>Liolaemus puelche</i>												IC													1
<i>Liolaemus pulcherrimus</i>								VU																	1
<i>Liolaemus puna</i>		NA						NA								NA									3
<i>Liolaemus punmahuida</i>																									1
<i>Liolaemus puritamensis</i>									NA																1
<i>Liolaemus purul</i>																									1
<i>Liolaemus quilmes</i>		NA														NA							NA		3
<i>Liolaemus rabinoi</i>												EP													1
<i>Liolaemus ramirezae</i>		NA							NA							NA									3
<i>Liolaemus riojanus</i>											VU	VU					VU								3
<i>Liolaemus robertmertensi</i>		NA									NA														2
<i>Liolaemus rothi</i>																									3
<i>Liolaemus ruibali</i>																									2
<i>Liolaemus sagei</i>												NA													1
<i>Liolaemus salinicola</i>																									1
<i>Liolaemus sanjuanensis</i>		NA																							1
<i>Liolaemus sarmientoi</i>																								NA	1
<i>Liolaemus saxatilis</i>																								NA	3
<i>Liolaemus scapularis</i>		NA																						NA	2

	Buenos Aires	Catamarca	Chaco	Chubut	Córdoba	Corrientes	Entre Ríos	Formosa	Jujuy	La Pampa	La Rioja	Mendoza	Misiones	Nequén	Río Negro	Salta	San Juan	San Luis	Santa Fe	Santa Cruz	Santiago del Estero	Tierra del Fuego	Tucumán	Nº de provincias presente
<i>Liolaemus scolaroii</i>																				IC				1
<i>Liolaemus scrocchii</i>								NA												NA				2
<i>Liolaemus sengeri</i>				NA																NA				2
<i>Liolaemus shehueni</i>				NA																				1
<i>Liolaemus shitan</i>												NA			NA									1
<i>Liolaemus smaui</i>												NA												1
<i>Liolaemus silvanae</i>																				VU				1
<i>Liolaemus somuncurae</i>				IC											IC									2
<i>Liolaemus talampaya</i>										NA														1
<i>Liolaemus tandiliensis</i>	AM																							1
<i>Liolaemus tari</i>																				IC				1
<i>Liolaemus tehuelche</i>															NA									1
<i>Liolaemus telsen</i>				NA											NA									2
<i>Liolaemus tenuis tenuis</i>														NA										1
<i>Liolaemus thermanum</i>												VU												1
<i>Liolaemus tregenzai</i>													VU											1
<i>Liolaemus tristis</i>														VU						IC				1
<i>Liolaemus tromeni</i>														NA										1
<i>Liolaemus tulkas</i>		NA																						1
<i>Liolaemus umbrifer</i>		NA																						1
<i>Liolaemus uptoni</i>				IC																				1
<i>Liolaemus usspallatensis</i>												NA												2
<i>Liolaemus vallecurensis</i>																								1
<i>Liolaemus vulcanus</i>		NA														NA								2

	Buenos Aires	Catamarca	Chaco	Chubut	Córdoba	Corrientes	Entre Ríos	Formosa	Jujuy	La Pampa	La Rioja	Mendoza	Misiones	Neuquén	Río Negro	Salta	San Juan	San Luis	Santa Fe	Santa Cruz	Santiago del Estero	Tierra del Fuego	Tucumán	Nº de provincias presente
<i>Liolaemus wiegmannii</i>	NA	NA		NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	13
<i>Liolaemus xanthoviridis</i>				NA																				1
<i>Liolaemus yanalco</i>								NA																2
<i>Liolaemus zullyi</i>																				NA				1
<i>Phymaturus antofagastensis</i>		VU																						1
<i>Phymaturus calcogaster</i>			VU																					1
<i>Phymaturus castillensis</i>			VU																					1
<i>Phymaturus ceii</i>															VU									1
<i>Phymaturus delheyi</i>														VU										1
<i>Phymaturus denotatus</i>		VU																						1
<i>Phymaturus desuetus</i>															VU									1
<i>Phymaturus dorsimaculatus</i>														VU										1
<i>Phymaturus etheridgei</i>															VU									1
<i>Phymaturus excelsus</i>															VU									1
<i>Phymaturus extrilidus</i>																	VU							1
<i>Phymaturus felixi</i>																								1
<i>Phymaturus gynochlomus</i>												VU												1
<i>Phymaturus indistinctus</i>																								1
<i>Phymaturus laurenti</i>																								1
<i>Phymaturus mallimaccii</i>											VU													1
<i>Phymaturus manuelae</i>																								1
<i>Phymaturus nevadoi</i>																								1
<i>Phymaturus palluma</i>																								2
<i>Phymaturus patagonicus</i>																								1

	Buenos Aires	Catamarca	Chaco	Chubut	Córdoba	Corrientes	Entre Ríos	Formosa	Jujuy	La Pampa	La Rioja	Mendoza	Misiones	Neuquén	Río Negro	Salta	San Juan	San Luis	Santa Fe	Santa Cruz	Santiago del Estero	Tierra del Fuego	Tucumán	Nº de provincias presente
<i>Phymaturus payuniae</i>												VU												1
<i>Phymaturus punae</i>																	VU							1
<i>Phymaturus querque</i>														VU										1
<i>Phymaturus roigorum</i>												VU												1
<i>Phymaturus sitesi</i>														VU										1
<i>Phymaturus somuncurensis</i>															VU									1
<i>Phymaturus spectabilis</i>														VU										1
<i>Phymaturus spurcus</i>														VU										1
<i>Phymaturus tenebrosus</i>														VU										1
<i>Phymaturus verdugo</i>												VU												2
<i>Phymaturus videlai</i>																								1
<i>Phymaturus zapalensis</i>														VU										1
<i>Polychrus acutirostris</i>																VU								4
<i>Stenocercus azureus</i>																								1
<i>Stenocercus caducus</i>																								2
<i>Stenocercus doellojuradoi</i>																								8
<i>Stenocercus marmoratus</i>																								1
<i>Stenocercus pectinatus</i>																								7
<i>Stenocercus roseiventris</i>																								2
<i>Tropidurus etheridgei</i>																								9
<i>Tropidurus melanopleurus</i>																								1
<i>Tropidurus spinulosus</i>																								6
<i>Tropidurus torquatus</i>																								5
<i>Homonota andicola</i>																								4

	Buenos Aires	Catamarca	Chaco	Chubut	Córdoba	Corrientes	Entre Ríos	Formosa	Jujuy	La Pampa	La Rioja	Mendoza	Misiones	Neuquén	Río Negro	Salta	San Juan	San Luis	Santa Fe	Santa Cruz	Santiago del Estero	Tierra del Fuego	Tucumán	No de provincias presente
<i>Homonota borelli</i>	NA	NA			NA					NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	10
<i>Homonota darwini darwini</i>				NA					NA			NA	NA	NA	NA					NA				6
<i>Homonota d. macrocephala</i>																IC								1
<i>Homonota fasciata</i>	NA	NA	NA		NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	17
<i>Homonota underwoodi</i>	NA								NA	NA	NA	NA			NA									7
<i>Homonota whitii</i>					NA												NA				NA			3
<i>Phyllopezus pollicaris przewalskyi</i>			NA					NA								NA					NA			5
<i>Ophiodes vertebralis</i>	NA				NA														NA		NA			4
<i>Ophiodes intermedius</i>			NA	NA?	NA	NA	NA	NA	NA	NA?	NA?					NA	NA	NA	NA	NA	NA	NA	NA	11
<i>Ophiodes yacupoi</i>						IC	IC					IC												3
<i>Cercosaura ocellata petersi</i>						IC																		1
<i>Cercosaura parkeri</i>		NA						NA								NA								3
<i>Cercosaura schreibersii</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA							NA		NA			10
<i>Cercosaura steyeri</i>						IC																		1
<i>Opipeuter xestus</i>								IC								IC								2
<i>Vanzosaura rubricauda</i>	VU	VU	VU		VU		VU	VU		VU						VU					VU		VU	8
<i>Mabuya dorsivittata</i>	NA	NA	NA		NA	NA	NA	NA		NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	14
<i>Mabuya frenata</i>		NA	NA			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	12
<i>Ameiva ameiva</i>		NA	NA				NA	NA								NA					NA			4
<i>Cnemidophorus lacertoides</i>	VU				VU		VU																	3
<i>Cnemidophorus leachi</i>								IC								IC								2
<i>Cnemidophorus longicauda</i>	NA			NA	NA				NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	10
<i>Cnemidophorus ocellifer</i>		NA	NA			NA	NA	NA		NA	NA					NA					NA	NA	NA	8
<i>Cnemidophorus serranus</i>					VU																VU			2

	Buenos Aires	Catamarca	Chaco	Chubut	Córdoba	Corrientes	Entre Ríos	Formosa	Jujuy	La Pampa	La Rioja	Mendoza	Misiones	Neuquén	Río Negro	Salta	San Juan	San Luis	Santa Fe	Santa Cruz	Santiago del Estero	Tierra del Fuego	Tucumán	Nº de provincias presente
<i>Cnemidophorus tergo-laevigatus</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4
<i>Kentropyx lagartija</i>	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	IC	3
<i>Kentropyx viridistriga</i>	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	5
<i>Teius oculatus</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	11
<i>Teius suquiensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3
<i>Teius teyou</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	12
<i>Tupinambis merianae</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	10
<i>Tupinambis rufescens</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15
<i>Amphisbaena angustifrons</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	13
<i>Amphisbaena bolivica</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	10
<i>Amphisbaena borellii</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2
<i>Amphisbaena heterozonata</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	14
<i>Amphisbaena hiata</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2
<i>Amphisbaena mertensii</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4
<i>Amphisbaena plumbea</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	10
<i>Amphisbaena prunicolor</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2
<i>Anops kingi</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15
<i>Leposternon microcephalum</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	8
<b>Nº de Especies en la Provincia</b>	<b>18</b>	<b>48</b>	<b>29</b>	<b>39</b>	<b>33</b>	<b>21</b>	<b>12</b>	<b>24</b>	<b>28</b>	<b>26</b>	<b>35</b>	<b>54</b>	<b>16</b>	<b>50</b>	<b>46</b>	<b>53</b>	<b>38</b>	<b>25</b>	<b>22</b>	<b>28</b>	<b>30</b>	<b>1</b>	<b>31</b>	
<b>Especies En Peligro</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	
<b>Especies Amenazadas</b>	<b>2</b>	<b>0</b>	<b>2</b>	<b>0</b>	<b>2</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>2</b>	<b>0</b>	<b>0</b>	<b>2</b>	<b>0</b>	<b>1</b>	<b>2</b>	<b>0</b>	<b>0</b>	<b>2</b>	<b>0</b>	<b>2</b>	<b>0</b>	<b>2</b>	
<b>Especies Vulnerables</b>	<b>2</b>	<b>10</b>	<b>5</b>	<b>6</b>	<b>7</b>	<b>2</b>	<b>1</b>	<b>5</b>	<b>4</b>	<b>1</b>	<b>7</b>	<b>14</b>	<b>1</b>	<b>10</b>	<b>10</b>	<b>8</b>	<b>6</b>	<b>2</b>	<b>1</b>	<b>2</b>	<b>5</b>	<b>0</b>	<b>3</b>	
<b>Especies No Amenazadas</b>	<b>13</b>	<b>38</b>	<b>21</b>	<b>31</b>	<b>24</b>	<b>15</b>	<b>10</b>	<b>19</b>	<b>20</b>	<b>22</b>	<b>28</b>	<b>34</b>	<b>11</b>	<b>35</b>	<b>32</b>	<b>36</b>	<b>27</b>	<b>23</b>	<b>19</b>	<b>22</b>	<b>23</b>	<b>1</b>	<b>23</b>	
<b>Especies Insuficientemente Conocidas</b>	<b>0</b>	<b>1</b>	<b>1</b>	<b>2</b>	<b>0</b>	<b>3</b>	<b>1</b>	<b>0</b>	<b>4</b>	<b>1</b>	<b>0</b>	<b>4</b>	<b>2</b>	<b>5</b>	<b>3</b>	<b>7</b>	<b>4</b>	<b>0</b>	<b>0</b>	<b>4</b>	<b>0</b>	<b>0</b>	<b>3</b>	



**Tabla 4.** Comparaciones entre el número de especies categorizadas a nivel familia entre las categorías de conservación establecidas a nivel global en las Listas Rojas de la IUCN (2012) y las establecidas en la República Argentina. Se comparan categorías homologadas entre ambas listas (ver Giraud *et al.*, 2012): CR: En Peligro Crítico (Critically Endangered) / EP: En Peligro; EN: En Peligro (Endangered) / AM: Amenazada; VU: Vulnerable / VU: Vulnerable; DD: Data Deficient / IC: Insuficientemente Conocida; LC: Preocupación Menor (Least Concern) / NA: No Amenazada. NE: No evaluadas. No existen lagartijas ni anfisbenas Extinguidas (EX), Extinguidas en la Naturaleza (EW) o Cercanas a la Amenaza (NT, Near Threatened) en la Argentina.

Infraorden/Familia	CR/EP	EN/AM	VU/VU	LC/NA	DD/IC	ne
<b>Iguania</b>						
Leiosauridae	-/-	-/5	1/4	3/8	-/1	14
Liolaemidae	-/1	-/3	2/56	10/105	7/20	166
Polychrotidae	-/0	-/0	-/1	-/-	-/0	1
Tropiduridae	-/0	-/0	-/3	2/3	-/4	8
<b>Total Iguania</b>	-/1	-/8	3/64	15/116	7/25	189
<b>Gekkota</b>						
Phyllodactylidae	-/0	-/0	-/0	1/7	-/1	7
<b>Total Gekkota</b>	-/0	-/0	-/0	1/7	-/1	7
<b>Anguinomorpha</b>						
Anguidae	-/0	-/0	-/0	-/2	-/1	3
<b>Total Anguinomorpha</b>	-/0	-/0	-/0	-/2	-/1	3
<b>Scincomorpha</b>						
Gymnophthalmidae	-/0	-/0	-/1	1/2	-/3	5
Scincidae	-/0	-/0	-/0	-/2	-/0	2
Teiidae	-/0-	-/0	-/3	1/9	-/2	13
<b>Total Scincomorpha</b>	-/0	-/0	-/4	2/13	-/5	20
<b>Amphisbaenia</b>						
Amphisbaenidae	-/-	-/1	-/0	-/7	-/0	8
Leposternidae	-/-	-/0	-/0	-/1	-/0	1
<b>Total Amphisbaenia</b>	-/-	-/1	-/0	-/8	-/0	9
<b>TOTAL</b>	-/2	-/8	3/68	18/146	7/32	228

**Tabla 5.** Comparación entre las categorías de conservación establecidas en las Listas Rojas de la República Argentina y a nivel global (IUCN, 2012). En el caso que existan diferencias se indica las posibles causas. EP: En Peligro; AM: Amenazada; VU: Vulnerable; IC: Insuficientemente Conocida; NA: No Amenazada; LC: Preocupación Menor (Least Concern).

	Categoría en Argentina	Categoría IUCN (2012)	Comparación y posibles causas de diferencias
<b>Leiosauridae</b>			
<i>Anisolepis grillii</i>	AM	LC	Escala geográfica de la evaluación
<i>Anisolepis undulatus</i>	AM	VU	Escala geográfica de la evaluación
<b>Liolaemidae</b>			
<i>Liolaemus chaltin</i>	NA	DD	Nueva evidencia aportada
<i>Liolaemus duellmani</i>	VU	DD	Nueva evidencia aportada
<i>Liolaemus fitzgeraldi</i>	IC	LC	Escala geográfica de la evaluación
<i>Liolaemus flavipiceus</i>	VU	DD	Nueva evidencia aportada

	Categoría en Argentina	Categoría IUCN (2012)	Comparación y posibles causas de diferencias
<i>Liolaemus mapuche</i>	NA	DD	Nueva evidencia aportada
<i>Liolaemus rabinoi</i>	EP	VU	Nueva evidencia aportada
<i>Liolaemus vallecurensis</i>	VU	LC	Nueva evidencia aportada
<i>Liolaemus xanthoviridis</i>	NA	DD	Nueva evidencia aportada
<i>Phymaturus calcogaster</i>	VU	DD	Nueva evidencia aportada
<i>Phymaturus palluma</i>	VU	LC	Nueva evidencia aportada
<b>Teiidae</b>			
<i>Kentropyx viridistriga</i>	VU	LC	Nueva evidencia aportada

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## Fichas de los taxones

# LAGARTIJAS y ANFISBENAS

### **Formato de Cita sugerida para las Fichas individuales:**

Autor/es. Año. Nombre del taxón (incluir el nombre común). En: Categorización del Estado de Conservación de la Herpetofauna de la República Argentina. Ficha de los Taxones. Lagartijas y Anfisbenas. *Cuadernos de Herpetología* 26 (supl. 1): pp.

### **Ejemplo:**

Brancatelli, G. I; Cairo, S. L. & Zalba, S. M. 2012. *Pristidactylus casuhatiensis* (Gallardo, 1964). Iguana de cobre. En: Categorización del Estado de Conservación de la Herpetofauna de la República Argentina. Ficha de los Taxones. Lagartijas y Anfisbenas. *Cuadernos de Herpetología* 26 (supl. 1): 254.



## Orden Squamata

### Familia Leiosauridae

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#### ***Anisolepis grilli* Boulenger, 1891**

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Acosta, J. L.

**Categoría 2012**

AMENAZADA

**Categoría anterior en Argentina**

Amenazada (Avila *et al.*, 2000)

**Categoría UICN**

Preocupación Menor (UICN, 2010)

**Justificación**

Especie arborícola y de movimientos lentos, habita

ambientes de selva atlántica primaria y bosques de araucaria, los cuales han sufrido una gran disminución en décadas pasadas. Se distribuye ampliamente en Brasil (Morato, 2010); sin embargo, en Argentina únicamente fue registrada para la provincia de Misiones.

**Sugerencias y acciones de conservación**

El conocimiento de los aspectos biológicos y ecológicos de esta especie es muy escaso, por lo que se sugiere intensificar los estudios sobre ambos aspectos.

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#### ***Anisolepis longicauda* (Boulenger, 1891)**

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Acosta, J.; Álvarez, B.; Hernando, A.; Tedesco, M. E.

**Categoría 2012**

AMENAZADA

**Categoría anterior en Argentina**

Amenazada (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación**

Tiene una distribución restringida a la zona septentrional de la ecoregión Esteros del Iberá, con escasos registros avalados por material de referencia

en la provincia de Corrientes, y registros antiguos de cuatro localidades del triángulo noreste de la provincia del Chaco perteneciente a la ecoregión Chaco Húmedo. Hábitat circunscrito a pastizales inundables, ambientes con alto impacto antrópico en la actualidad.

**Sugerencias y acciones de conservación**

Si bien se encuentra protegida por la Reserva Provincial del Iberá y Apipé, el conocimiento de los aspectos biológicos y ecológicos de esta especie son muy escasos, por lo que se sugiere intensificar los estudios sobre ambos aspectos.

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#### ***Anisolepis undulatus* (Wiegmann, 1834)**

---

Acosta, J. L.

**Categoría 2012**

AMENAZADA

**Categoría anterior en Argentina**

Amenazada (Avila *et al.*, 2000)

**Categoría UICN**

Vulnerable

**Justificación**

De escaso registro y biología prácticamente desco-



nocida. Se distribuye en Brasil (Río Grande do Sul), Uruguay y Argentina (Di Bernardo y Martins, 2000); sin embargo, en nuestro país sólo ha sido registrada para la localidad de Punta Lara en la provincia de Buenos Aires, donde aparentemente habría desaparecido. No obstante la escasa representación en colecciones herpetológicas podría responder a factores

como abundancia o dificultad de hallazgo y colecta.

#### **Sugerencias y acciones de conservación**

El escaso conocimiento de la especie justifica su categorización y se considera necesario ampliar los relevamientos y estudios de aspectos básicos sobre su historia natural.

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## ***Diplolaemus leopardinus* (Werner, 1898)**

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Abdala, C. S.

**Categoría 2012**  
VULNERABLE

**Categoría anterior en Argentina**  
Vulnerable (Avila *et al.*, 2000)

**Categoría UICN**  
No Evaluada

#### **Justificación**

Estudios taxonómicos recientes indican que esta especie se distribuye sólo en el sur de la provincia de Mendoza, con un endemismo menor a 20.000 km<sup>2</sup> (Victoriano *et al.*, 2010). Es una especie escasa y difícil de observar, que sufre el ataque por parte del

hombre por considerarla erróneamente una especie “venenosa” y “mortal”.

#### **Sugerencias y acciones de conservación**

Sería conveniente incorporar la zona de El Nevado, Mendoza (parte del hábitat de *D. leopardinus*) al sistema de áreas naturales provinciales protegidas, debido entre otros factores, a los importantes endemismos que alberga dicha zona. Asimismo se debería realizar una campaña de educación ambiental en las áreas donde habita *D. leopardinus* a fin de desmitificar aspectos de su biología, enseñar las verdaderas cualidades y el peligro de extinción que posiblemente enfrenta esta especie.

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## ***Leiosaurus paronae* Peracca, 1897**

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Laspiur, A.

**Categoría 2012**  
VULNERABLE

**Categoría anterior en Argentina**  
Vulnerable (Avila *et al.*, 2000)

**Categoría UICN**  
No Evaluada

#### **Justificación**

Esta especie, como resultado de registros históricos de avistaje y captura ha sido asociada a ambientes chaqueños de bosque nativo. Los criterios de vulnerabilidad utilizados en la categorización anterior se refieren a destrucción de hábitat por tala de bos-

ques y construcciones de obras de ingeniería, como factores causantes de la declinación de las poblaciones. Desde el año 2000 al presente, no ha habido contribuciones al conocimiento sobre la biología de la especie, y tampoco han sido documentados nuevos registros. Esto último permite inferir, con incertidumbre, que posiblemente las poblaciones de la especie pueden presentar bajas densidades o se trata de un caso de especie altamente críptica. Sin embargo, ante las evidentes acciones destructivas del hábitat natural, es probable que la vulnerabilidad de las poblaciones sea una condición probable.

#### **Sugerencias y acciones de conservación**

Teniendo en cuenta sus afinidades con microam-

bientes de bosque nativo, es probable que con la ejecución de la propuesta de la ley de emergencia forestal (Ley de Bosques) las poblaciones se vean beneficiadas indirectamente. Es prioridad contribuir al conocimiento general de la especie, en este caso, al ser una especie de relativa amplitud en su distribución, es necesario recopilar información bibliográfica y de material depositado en museos para poder conocer su distribución y posibles poblaciones donde será posible realizar futuros estudios. En un

estado posterior, evaluar el estado de las poblaciones a nivel ecológico y estructural (grupos de edad y asociación a diferentes microambientes). La realización de estudios autoecológicos permitirá conocer con certeza si la especie tiene relación estricta con ciertos tipos de microambientes y si ésta se encuentra sometida a impacto. Lo anteriormente mencionado es necesario antes de evaluar posibilidades y alternativas de conservación y manejo.

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## ***Pristidactylus achalensis* Gallardo, 1964**

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Avila, L. J.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Vulnerable (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie de distribución restringida y con poblacio-

nes en áreas de desarrollo turístico y con cada vez más desarrollo de infraestructura (caminos) que posibilitan el acceso a sectores antes poco perturbados. Probable uso como mascota.

### **Sugerencias y acciones de conservación**

Extender el área de protección establecida con el Parque Nacional El Condorito, además del grado de efectividad de la protección. Concientizar a los visitantes y usuarios de la tierra de la importancia de la especie.

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## ***Pristidactylus araucanus* Gallardo, 1964**

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Avila, L. J.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie poco conocida, con pocos registros de presencia y probablemente estatus taxonómico poco claro. Poblaciones aparentemente aisladas y de baja densidad poblacional. Algunas zonas con incremento de actividad petrolera y minera, otras con probable desarrollo de grandes emprendimientos hidroeléctricos. Algunas zonas de distribución con

alto grado de desertificación por sobrepastoreo.

### **Sugerencias y acciones de conservación**

Incrementar el relevamiento para evaluar adecuadamente su distribución geográfica y su densidad poblacional. Incremento del área protegida por el Parque Nacional Laguna Blanca y aplicación efectiva de control en Reserva Provincial La Payunia.

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## ***Pristidactylus casuhatiensis* (Gallardo, 1964). Iguana de cobre**

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Brancatelli, G. I; Cairo, S. L.; Zalba, S. M.

### **Categoría 2012**

AMENAZADA

### **Categoría anterior en Argentina**

En Peligro (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie endémica del sistema de Ventania (Buenos Aires). Restringida a pastizales de altura, en ambientes de roquedal, por encima de los 700 m s.n.m. (Brancatelli *et al.*, 2010). Parte de su distribución (Cerro Ventana) se encuentra dentro de un área protegida, el Parque Provincial Ernesto Tornquist (PPET) donde coincide con el área de uso turístico más intenso de las sierras australes bonaerenses. Se alimenta principalmente de una especie de caracol endémico (*Plagiodontes patagonicus*) (Cei *et al.*, 2004). Su hábitat está amenazado por el avance de especies invasoras como el pino tosquero (*Pinus halepensis*) y la zarzamora (*Rubus* sp.) (Zalba y Villamil,

2002). Las poblaciones están expuestas además al impacto directo e indirecto del turismo (Brancatelli, obs. pers.), habiéndose reportado el decomiso de individuos capturados ilegalmente (Guarapardarques PPET, com. pers.).

El cambio respecto de la categorización anterior de especie En peligro obedece al uso de una metodología distinta.

### **Sugerencias y acciones de conservación**

Se recomienda evitar el avance y promover la erradicación de especies leñosas invasoras, especialmente por encima de los 700 m s.n.m. Deben implementarse y reforzarse las acciones de educación dirigidas a la población local y a los turistas que transitan senderos dentro y fuera del PPET con el objetivo de evitar modificaciones del ambiente y la colecta de individuos, adecuadamente complementadas con tareas de fiscalización. Se requiere investigación orientada a conocer la distribución de la especie y la relación entre las poblaciones de los distintos cerros, así como a identificar factores de su biología que resulten clave para su conservación.

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## ***Pristidactylus fasciatus* (D'Orbigny & Bibron, 1837)**

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Abdala, C. S.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Es una especie muy poco conocida, con muy pocos registros en las colecciones herpetológicas. Se distribuye desde el centro sur de la provincia de La Rioja, hasta el este de la provincia de Río Negro en las cercanías de Viedma, con poblaciones que se encuentran bastante separadas (disyuntas) dentro de esta gran área. Se desconoce la tendencia poblacional

y aspectos biológicos.

Es imprescindible realizar estudios taxonómicos sobre las poblaciones conocidas a fin de determinar su verdadera identidad y distribución real, así como estudios relacionados a la biología de la misma.

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## ***Urostrophus gallardoi* Etheridge & Williams, 1991**

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Acosta, J.; Álvarez, B. B.; Hernando, A.; Tedesco, M. E.

### **Categoría 2012**

AMENAZADA

### **Categoría anterior en Argentina**

Amenazada (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie netamente chaqueña que habita en la ecoregión del Chaco Seco con muy escasos registros

documentados en los últimos diez años, con biología y ecología poco conocida, altamente mimética, habita preferentemente troncos recubiertos por abundantes líquenes a escasa altura del suelo.

### **Sugerencias y acciones de conservación**

No se encuentra protegida en el sistema de reservas naturales, y su hábitat natural, el bosque chaqueño, está altamente modificado por un alto nivel de deforestación. Se recomienda intensificar los estudios sobre aspectos biológicos y ecológicos.

## Familia Liolaemidae

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### ***Liolaemus abdalai* Quinteros, 2012**

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Quinteros, S.

#### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

#### **Categoría anterior en Argentina**

Insuficientemente Conocida como *L. lemniscatus* (Avila *et al.*, 2000)

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Estudios taxonómicos recientes indican que esta especie se distribuye sólo en la provincia de Neuquén. Existe un registro para el Parque Nacional Lanin en

la misma provincia (Quinteros, 2012). Las poblaciones de *Liolaemus abdalai* estuvieron confundidas con *L. lemniscatus* (Cei, 1986; Donoso Barros, 1966; Lobo y Abdala, 2001; 2002; Lobo y Espinoza, 1999).

A pesar de la población correspondiente a la localidad tipo esta en muy buen estado de conservación y que existe un registro para el Parque Nacional Lanin, es conveniente incorporar regiones aledañas al parque al sistema de áreas protegidas, con el fin de preservar las poblaciones de *Liolaemus abdalai* que no se encuentran dentro del parque. Asimismo se recomienda incentivar los estudios relacionados a la historia natural de esta especie a fin de ampliar los conocimientos de la misma.

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### ***Liolaemus andinus* Koslowsky, 1895**

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Abdala, C. S.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Durante muchos años hubo una gran confusión sobre las poblaciones que integraban esta especie, sin embargo estudios taxonómicos recientes (Abdala,

datos no publicados) indican que es una especie, con una distribución altitudinal y latitudinal muy restringida en el suroeste de la cordillera de la provincia de Catamarca. Asimismo es una especie vivípara, especialista en hábitat (altiplano con poca vegetación), uso del substrato (se moviliza en suelo pedregoso utilizando las cuevas para refugiarse) y en su alimentación (fuerte tendencia a la herbivoría).

#### **Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presentan los ambientes que habita.

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### ***Liolaemus anomalus* Koslowsky, 1896**

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Abdala, C. S.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación**

Estudios taxonómicos recientes (Juárez y Abdala, 2010; Juárez, 2011) indican que esta especie se distribuye en un área restringida en el centro sur de la provincia de la Rioja y centro norte de la provincia de San Juan. Las poblaciones del Sur de San Juan y Mendoza corresponderían a nuevos taxa en descripción (Abdala y Juárez, datos no publicados). Es una especie con poblaciones muy escasas, sus avistajes son ocasionales y fortuitos. Hay hipótesis muy

contradictorias en cuanto a sus hábitos y actividad diaria. Se conoce muy poco sobre su biología, pero es una especie especialista en el tipo de hábitat y sustrato que necesita para vivir (se la encuentra en lugares muy áridos y salitrosos, con escasa vegetación).

**Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presentan el ambiente que habita. Si bien está protegida en los Parques Nacionales Talampaya e Ischigualasto, es necesario detectar las causas de la baja densidad poblacional.

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## ***Liolaemus antumalguen* Avila, Morando, Perez & Sites, 2010**

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Avila, L. J.; Morando, M.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Habita exclusivamente los bordes rocosos del piedemonte del este del Volcán Domuyo, en la Quebrada de Chadileu (36° 39' S, 70° 20' W), en el departamento Chos Malal, provincia de Neuquén. Las áreas circundantes han sido muestreadas y no se ha

encontrado evidencia de esta especie, pero sí de otras cercanamente relacionadas. La evidencia indica que su distribución es restringida y puede ser afectada por actividad minera o por eventos naturales como una erupción del Volcán Domuyo. Eventualmente la extensión de la actividad turística y el desarrollo asociado podría afectar su población.

**Sugerencias y acciones de conservación**

Relevamientos en los alrededores de su área de distribución para determinar la extensión de su distribución geográfica, que probablemente se extienda hacia el sur de la Cordillera del Viento. Eventualmente, se podría extender el Área Natural Protegida Domuyo para incluir poblaciones más australes.

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## ***Liolaemus azarai* Avila, 2003**

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Acosta, J.; Álvarez, B.; Hernando, A.; Tedesco, M. E.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Distribución restringida a la Isla Apipé y a escasas localidades de la costa occidental del Sistema del Iberá, ecorregión Esteros del Iberá, con poblaciones limitadas a parches en hábitats de dunas y suelos arenosos con alto impacto antrópico debido a la forestación y actividades pecuarias.

**Sugerencias y acciones de conservación**

Se recomienda control del impacto de las actividades antrópicas sobre los ambientes típicos de la especie.

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## ***Liolaemus cazaniae* Lobo, Slodki & Valdecantos, 2010**

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Abdala, C. S.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Es una especie con un endemismo marcado, se encuentra en grandes elevaciones, entre los 3.500 y 4.300 m s.n.m., de la región de la puna al oeste del Salar de Arizaro (provincia de Salta). Es especialista

en el hábitat, uso del estrato – substrato (habita en un antiguo lago hipersalino desecado) y alimentación (fuerte tendencia a la herbivoría). Además es una especie vivípara y relativamente escasa.

### **Sugerencias y acciones de conservación**

Debido a que es una especie recientemente descrita, se conoce muy poco sobre su biología y distribución, por lo tanto se recomienda realizar mayores estudios sobre el estado de sus poblaciones, biología, distribución y grado de amenaza que presentan el ambiente que habita, principalmente con algunas mineras instaladas en la zona.

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## ***Liolaemus chillanensis* Müller y Hellmich, 1932**

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Avila, L. J.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie citada en base a fotografías para Argentina y de estatus taxonómico muy confuso.

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## ***Liolaemus chlorostictus* Laurent, 1991**

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Abdala, C. S.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Es una especie con un microendemismo marcado, menos de 20.000 km<sup>2</sup> (noroeste de la puna de la pro-

vincia de Jujuy, Argentina y en el suroeste de la provincia de Potosí, Bolivia), siempre a más de 3500 m s.n.m. Es saxícola estricto, con fuerte tendencia a la herbivoría. Es una especie vivípara y las poblaciones conocidas presentan una abundancia relativamente normal comparada con los *Liolaemus* del mismo grupo. En algunos pueblos de la puna, durante la Pascua se suele salir a “cazar” estas lagartijas como costumbre de antaño. Esta práctica puede traer consecuencias para la conservación de esta especie.

**Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presentan el ambiente que habita. Asimismo se de-

bería realizar una campaña de educación ambiental en las áreas donde habita esta especie, a fin de desmitificar mitos, enseñar las verdaderas cualidades y peligro que corre esta especie.

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***Liolaemus cinereus* Monguillot, Cabrera, Acosta & Villavicencio, 2006**

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Acosta, J. C.

**Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Especie recientemente descrita. Su distribución es

desconocida sólo se ha encontrado en el sector sur del Parque Nacional San Guillermo, provincia de San Juan, (Junta de Palca y margen norte del cauce del río Blanco, salida de la quebrada Alcaparrosa). Sólo se han encontrado 3 individuos en ambientes típicos de Monte, por encima de los 2000 m s.n.m. Lagarto de pequeño tamaño (60 a 65 mm, LHC), microhábitat con grava y suelo arenoso, con escasa vegetación. Su biología es completamente desconocida (Acosta *et al.*, 2007).

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***Liolaemus cuyumhue* Avila, Morando, Perez & Sites, 2009**

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Avila, L. J.; Morando, M.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Especie endémica de distribución muy restringida, habita exclusivamente dunas vivas encontradas en algunas áreas del denominado Bajo de Añelo, en el Departamento Añelo, provincia de Neuquén, (aprox. 38° 11' S, 69° 01' W, 259 m s.n.m.). Su densidad es baja y con requerimientos ecológicos muy específicos. La región donde se distribuye se encuentra en una zona de cada vez mayor actividad humana por el desarrollo de la industria petrolera y el desarrollo de obras que pueden destruir el hábitat de la especie.

hacia el sur de sus actuales límites para incluir áreas de distribución de la especie. Informar a los actores principales de los cambios ambientales, empresas petroleras y gobierno, de la existencia de este endemismo y sugerir acciones de conservación.

**Sugerencias y acciones de conservación**

Extender el Área Natural Protegida Auca Mahuida



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## ***Liolaemus cyaneinotatus* Martínez, Avila, Perez, Perez, Sites & Morando, 2011**

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Quinteros, S.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie conocida sólo para su localidad tipo, en el

Volcán Auca Mahuida, ubicado en el departamento Añelo de la provincia de Neuquén. No se conocen más datos sobre su distribución.

En las regiones donde se encuentra el Volcán Auca Mahuida, conviven con *L. cyaneinotatus* diversas especies del género *Liolaemus* (*L. austromendocinus*, *L. cf. elongatus*, *L. cf. boulengeri*), así como de su género hermano *Phymaturus* (*P. sitesi* y *P. roigorum*), por lo que sería interesante proponer como área prioritaria de conservación a las regiones donde se encuentra el volcán.

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## ***Liolaemus cyanogaster* Duméril & Bibron, 1837**

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Avila, L. J.; Morando, M.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie con distribución muy restringida, su presencia en Argentina sólo está confirmada por unos pocos ejemplares de referencia.

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## ***Liolaemus ditadai* Cei, 1983**

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Abdala, C. S.

### **Categoría 2012**

AMENAZADA

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Esta especie habita en las Salinas Grandes de la provincia de Córdoba límite con Catamarca. Presenta una biología muy particular relacionada con

el ambiente halófilo. Desde su descripción hasta la actualidad se han recolectado no más de 15 ejemplares a pesar de haber sido buscada intensamente en distintas estaciones, años y en diferentes horarios del día. Sumado a que presenta una densidad poblacional muy baja presenta un microendemismo evidente de unos pocos km<sup>2</sup>. Abdala (2007) amplió su rango de distribución 270 km al este en la provincia de Santiago del Estero, al hallar un ejemplar de *L. ditadai* en la colección Herpetológica del Museo Argentino de Ciencias Naturales (MACN), sin embargo esta población no ha podido ser encontrada hasta el día de hoy. Otro factor que seguramente ha diezmando

sus poblaciones es el anegamiento del área donde habita en innumerables ocasiones en estos últimos años (Abdala, 2007).

#### **Sugerencias y acciones de conservación**

Es necesario emprender estudios profundos y completos acerca de la biología y la dinámica poblacional

de esta especie, así como también evaluar los factores que están actuando en la baja densidad de la población conocida. Al mismo tiempo se deberán realizar exhaustivas campañas para corroborar la existencia de la población a la cual perteneció el ejemplar hallado en la colección Herpetológica del MACN.

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## ***Liolaemus dorbignyi* Koslowsky, 1998**

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Abdala, C.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Es una especie con un microendemismo marcado, confinada a la Sierra de Fiambalá, provincia de

Catamarca, por encima de los 3500 m s.n.m. Es estrictamente saxícola, herbívoro y vivípara. Presenta poblaciones relativamente escasas comparadas con otros *Liolaemus* de su grupo.

#### **Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presenta el ambiente que habita. Si bien en la Sierra donde habita la acción del hombre es casi nula, se deberán detectar por qué las poblaciones conocidas presentan baja densidad.

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## ***Liolaemus duellmani* Cei, 1978**

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Abdala, C. S.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

#### **Categoría UICN**

Insuficientemente Conocida (UICN, 2010)

#### **Justificación**

Es una especie con un microendemismo muy marcado, restringida a la localidad tipo (Paso El Choique, Malargüe, provincia de Mendoza). No ha sido registrada en los últimos 25 años a pesar de realizarse varias búsquedas en la localidad tipo.

realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presentan el ambiente que habita.

#### **Sugerencias y acciones de conservación**

Se conoce muy poco sobre esta especie, se deberían

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## ***Liolaemus exploratorum* Cei & Williams, 1984**

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Abdala, C. S.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Es una especie muy poco conocida, que fue descrita en base a material coleccionado por Koslowsky en 1896 en los alrededores del Lago Buenos Aires, en su

orilla norte. A pesar de que se han realizado varias campañas para hallar ejemplares de esta especie, no se ha podido encontrar un solo espécimen de *L. exploratorum*. La categoría propuesta se basa en que no se conoce con exactitud la localidad tipo, o que podría tener un dato de colección incorrecto. Por estos motivos, se prefiere asumir que no se ha encontrado debido a que se lo buscó en lugares donde no se encuentra, y no presuponer que está extinta.

Es imprescindible realizar intensivas y numerosas campañas, siguiendo los recorridos que realiza Koslowsky en la Patagonia Argentina a fin de evaluar su verdadera existencia.

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## ***Liolaemus fitzgeraldi* Boulenger, 1899**

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Corbalán, V.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

Preocupación Menor (UICN, 2010)

### **Justificación**

Especie endémica del norte de Mendoza y sur de

San Juan (Cei, 1986). Está presente también en Chile (Donoso-Barros, 1966). Se desconoce la tendencia poblacional.

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## ***Liolaemus flavipiceus* Cei & Videla, 2003**

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Corbalán, V.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

Insuficientemente Conocida (UICN, 2010)

### **Justificación**

Especie micro-endémica de Paso Pehuenche (Mendoza), zona altoandina casi límite con Chile. Las obras viales desarrolladas en el área de distribución podrían afectar las poblaciones de esta especie por destrucción del hábitat y atropellamiento.

### **Sugerencias y acciones de conservación**

No se encuentra protegida en el sistema de reservas naturales. Se sugiere realizar mayores controles a las obras de infraestructura y proteger su hábitat.

También son necesarios estudios para mejorar el conocimiento de aspectos biológicos de la especie.

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## ***Liolaemus gravenhorsti* (Gray, 1845)**

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Avila, L. J.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

sólo dos localidades mencionadas y pocos individuos coleccionados. Sólo unos pocos ejemplares en colecciones. Probable confusión taxonómica.

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie prácticamente desconocida para Argentina,

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## ***Liolaemus griseus* Laurent, 1984**

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Abdala, C. S.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

plares colectados que corresponden a los ejemplares tipo y paratipos, de la falda este del Cerro Isabel, por arriba de los 4500 m s.n.m, en los Valles Calchaquíes, departamento de Tafi del Valle, Tucumán. Es una especie vivípara, pero se desconocen la mayoría de los aspectos biológicos de esta especie.

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Es una especie muy poco conocida. Hay pocos ejem-

Es indispensable realizar nuevas búsquedas de esta especie a fin de determinar su verdadera distribución, su posible sinonimia con *L. huacahuasicus*, así como los principales aspectos biológicos y el estado de sus poblaciones.

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## ***Liolaemus gununakuna* Avila, Morando, Perez & Sites, 2004**

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Avila, L. J.; Morando, M.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría UICN**

No Evaluada

### **Categoría anterior en Argentina**

No Evaluada

### **Justificación**

Especie de distribución restringida, densidad pobla-

cional no muy alta y en ambientes muy característicos. Distribución geográfica poco conocida. Actividad petrolera muy intensa en todas las zonas conocidas de distribución, ambiente con alto grado

de degradación por sobrepastoreo, varias localidades probablemente afectadas por emprendimientos hidroeléctricos.

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## ***Liolaemus halonastes* Lobo, Slodki & Valdecantos, 2010**

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Abdala, C. S.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Es una especie con un microendemismo muy marcado, conocida solamente para un área restringida en los márgenes hipersalinos del Salar de Arizaro (provincia de Salta), sobre los 3000 m s.n.m. Habita

un área donde la cobertura de las pequeñas plantas es muy escasa y donde el suelo es extremadamente salino, debiendo considerarse como especialista en el hábitat, uso del estrato – substrato. Además es una especie cuya población conocida es muy escasa.

### **Sugerencias y acciones de conservación**

Debido a que es una especie recientemente descrita, se conoce muy poco sobre su biología y distribución, por lo tanto se recomienda realizar mayores estudios sobre el estado de sus poblaciones, biología, distribución y grado de amenaza que presentan el ambiente que habita, principalmente con algunas mineras instaladas en la zona.

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## ***Liolaemus huacahuasicus* Laurent, 1985**

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Abdala, C. S.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

Vulnerable (World Conservation Monitoring Centre, 1996)

### **Justificación**

Es una especie con un microendemismo muy marcado, restringida a las lagunas de Huaca Huasi, y algunas cerranías aledañas, todas localidades en las Cumbres Calchaquíes siempre a más de 3700 m s.n.m., provincia de Tucumán. Es especialista en su alimentación con una fuerte tendencia a la herbivoría. Las poblaciones conocidas presentan una densidad relativamente alta comparada con

otros *Liolaemus* del mismo grupo, a excepción de la población del Abra de Lara, donde es muy difícil observar ejemplares de *L. huacahuasicus*.

### **Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado de sus poblaciones y biología, asimismo se debería controlar y evitar las travesías con vehículos doble tracción en el área donde esta habita, las cuales afectan considerablemente la vegetación y el suelo de esta área tan frágil.

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## ***Liolaemus huayra* Abdala, Quinteros & Espinoza, 2008**

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Abdala, C. S.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Es una especie con un microendemismo muy marcado, sólo se conoce para su localidad tipo (Cerro el Pichao, Sierra de Quilmes, Tafi del Valle, pro-

vincia de Tucumán). Es saxícola estricto, vivípara y con tendencia a la herbivoría. Es una especie muy escasa, pobremente representada en las colecciones herpetológicas (sólo se conocen nueve ejemplares coleccionados).

**Sugerencias y acciones de conservación**

Debido a que es una especie recientemente descrita, se conoce muy poco sobre su biología y distribución, por lo tanto se recomienda realizar mayores estudios sobre el estado de sus poblaciones, biología, distribución y grado de amenaza que presentan el ambiente que habita.

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## ***Liolaemus inti* Abdala, Quinteros & Espinoza, 2008**

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Abdala, C. S.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Es una especie con un microendemismo muy marcado, sólo se conoce para su localidad tipo y cerros cercanos (Cerro de la Virgen, Cachi, provincia de Salta). Es saxícola estricto, vivípara y con tendencia a la herbivoría. Es una especie relativamente escasa,

comparado con otras especies del mismo grupo de *Liolaemus*.

**Sugerencias y acciones de conservación**

Debido a que es una especie recientemente descrita, se conoce muy poco sobre su biología y distribución, por lo tanto se recomienda realizar mayores estudios sobre el estado de sus poblaciones, biología, distribución y grado de amenaza que presentan el ambiente que habita. La localidad tipo de esta especie (Cerro de la Virgen) es un lugar concurrido por cientos de personas año a año para realizar el Vía Crucis en la Pascua Cristiana, por lo tanto habría que estudiar los efectos de la misma sobre *L. inti*.

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## ***Liolaemus kolengh* Abdala & Lobo, 2006**

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Abdala, C. S.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Es una especie con un microendemismo muy mar-

cado, sólo se conoce para su localidad tipo (Cerro Ceballos, cerca del río Ceballos, Lago Buenos Aires, provincia de Santa Cruz), y además se la encuentra a una altitud elevada para la latitud que habita a más de 1400 m s.n.m. Es una especie que habita un área muy árida y fría con poca vegetación y está altamente especializada en el sustrato que utiliza para refugiarse (siempre bajo piedras lajas). Es insectívora y vivípara con hasta cinco crías y presenta una abundancia relativamente baja comparada con

otras especies del mismo grupo de *Liolaemus*.

#### **Sugerencias y acciones de conservación**

Debido a que es una especie recientemente descrita, se conoce muy poco sobre su biología y distribución, por lo tanto se recomienda realizar mayores estudios sobre el estado de sus poblaciones, biología, distribución y grado de amenaza que presenta el ambiente que habita.

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## ***Liolaemus lentus* Gallardo, 1966**

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Abdala, C. S.

#### **Categoría 2012**

AMENAZADA

#### **Categoría anterior en Argentina**

No Evaluada

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Es una especie de la cual se conoce muy poco. Gallardo (1966), al describirla brinda una completa reseña sobre su biología y distribución. En los últimos años a pesar de haberse realizado numerosas prospecciones en la localidad tipo (Altos de Cochicó, Cochicó, Departamento Puelén, La Pampa, Argentina) no se pudo hallar ni observar un solo ejemplar de *L. lentus*. Recientemente, Perez y Avila (2011), encontraron un ejemplar macho a 18.3 km al norte de la locali-

dad de Ingeniero Huergo, provincia de Río Negro, ampliando su distribución. Este ejemplar es el único hallado desde su descripción original hace 46 años. En la zona comprendida por la localidad tipo y áreas aledañas, se pudo observar un sobrepastoreo bovino y caprino considerable, efecto que seguramente está actuando o ha actuado negativamente en las poblaciones de *L. lentus*. Estos elementos, sumado a la particular biología de esta especie, la cual está relacionada a ambientes áridos y halófilos, determinan que sea una especie amenazada y posiblemente extinta en su localidad tipo.

#### **Sugerencias y acciones de conservación**

Comprobar si en la localidad tipo hay ejemplares de *L. lentus* es imprescindible para determinar acciones de conservación de esta especie. Asimismo se deberá evaluar la población encontrada en Río Negro y determinar su estado de conservación.

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## ***Liolaemus montanezi* Cabrera & Monguillot, 2006**

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Abdala, C. S.

#### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

#### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Es una especie muy poco conocida, restringida a un sector del Parque Nacional San Guillermo, en la provincia de San Juan. Sólo se conocen dos ejemplares, un macho y una hembra, correspondiente a la serie tipo. Se desconocen la mayoría de los aspectos biológicos de esta especie.

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## ***Liolaemus montanus* Koslowsky, 1898**

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Abdala, C. S.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Es una especie muy poco conocida, se conocen muy

pocos ejemplares en las colecciones herpetológicas. Está restringida a la Sierra del Manchao, provincia de Catamarca por arriba de los 3800 m s.n.m. Se desconocen la mayoría de los aspectos biológicos necesarios para categorizarla así como el estado de sus poblaciones.

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## ***Liolaemus multimaculatus* (Duméril & Bibron, 1837). Lagartija de las dunas**

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Vega, L.; Kacolis, F.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Vulnerable (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Es un endemismo del ecosistema de médanos costeros de Argentina, presente sólo en las provincias de Buenos Aires y Río Negro. Especialista de sustrato

arenícola y de la vegetación psamófila pionera. Ha demostrado ser vulnerable a la modificación de su hábitat, el cual actualmente se encuentra amenazado. Alimentación insectívora. Su distribución a lo largo de la costa bonaerense es disyunta y en algunos lugares es muy poco abundante.

### **Sugerencias y acciones de conservación**

Creación de reservas para conservar sus poblaciones. Control del impacto que producen actividades de urbanización, minería, recreación y forestación, sobre el ecosistema de médanos costeros argentinos.

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## ***Liolaemus nigriceps* (Philippi, 1860)**

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Abdala, C. S.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Es una especie muy poco conocida, si bien en algunos museos hay numerosos ejemplares de esta especie, las colectas fueron realizadas hace más de 25 años y no hay estudios realizados sobre la biología de esta especie. Se distribuye en una zona de puna entre Atacama, Chile y la provincia de Salta, Argentina. Se desconocen la mayoría de los aspectos biológicos



necesarios para categorizarla, así como el estado real de sus poblaciones.

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## ***Liolaemus orientalis* Müller, 1924**

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Abdala, C. S.

**Categoría 2012**  
VULNERABLE

**Categoría anterior en Argentina**  
Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**  
No Evaluada

**Justificación**  
Es una especie endémica de la puna de Argentina y Bolivia, con una distribución menor a 20.000 km<sup>2</sup>

(noroeste de la puna de la provincia de Jujuy, Argentina y en el sur de la puna de Bolivia), siempre a más de 3500 m s.n.m. Es saxícola estricto, con fuerte tendencia a la herbivoría. Es una especie vivípara y la densidad de las poblaciones conocidas para Argentina es normal comparada con otros *Liolaemus* del mismo grupo.

**Sugerencias y acciones de conservación**  
Se deberían realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presentan el ambiente que habita.

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## ***Liolaemus orko* Abdala & Quinteros, 2008**

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Abdala, C. S.

**Categoría 2012**  
VULNERABLE

**Categoría anterior en Argentina**  
No Evaluada

**Categoría UICN**  
No Evaluada

**Justificación**  
Es una especie con un microendemismo muy marcado, confinada a la Sierra de Fiambalá, provincia de Catamarca, por encima de los 4000 m s.n.m. Está

asociado a ambientes muy frágiles de altura donde abundan las gramíneas, es una especie vivípara. Presenta poblaciones con una densidad normal a alta comparada con otros *Liolaemus* de su grupo, sin embargo solo se conocen 10 ejemplares de esta especie.

**Sugerencias y acciones de conservación**  
Se deberían realizar mayores estudios sobre el estado de sus poblaciones, distribución y biología. Si bien en la Sierra donde habita está aislada y la acción del hombre es de bajo impacto, los ambientes donde habita son muy frágiles ante la intervención antrópica.

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## ***Liolaemus puelche* Avila, Morando, Perez & Sites, 2007**

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Avila, L. J.; Morando, M.

**Categoría 2012**  
INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**  
No Evaluada

**Categoría UICN**  
No Evaluada

**Justificación**  
Especie de distribución geográfica muy restringida,

prácticamente a su localidad tipo y alrededores. Densidad poblacional baja. Especie poco conocida. Emprendimientos hidroeléctricos y mineros además

de actividad petrolera intensa en áreas de su probable distribución geográfica.

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## ***Liolaemus pulcherrimus* Laurent, 1992**

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Abdala, C. S.

**Categoría 2012**  
VULNERABLE

**Categoría anterior en Argentina**  
Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**  
No Evaluada

**Justificación**  
Es una especie con un microendemismo muy marcado, conocida sólo para su localidad tipo, Mudana, Humahuaca, provincia de Jujuy, por arriba de los 4000 m s.n.m. Es una especie asociada a las rocas sin

ser saxícola estricta, pero está asociada a un frágil ambiente de altura donde abundan las gramíneas y se realiza pastoreo de ganado caprino de manera constante. Es una especie vivípara, con tendencia a la herbivoría y presenta poblaciones con una densidad normal comparada con otros *Liolaemus* de su grupo. Sin embargo, sólo se conocen muy pocos ejemplares de esta especie.

**Sugerencias y acciones de conservación**  
Se deberían realizar mayores estudios sobre el estado de sus poblaciones, distribución y biología. Asimismo se deberá estudiar el efecto del pastoreo caprino sobre el hábitat de esta especie.

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## ***Liolaemus pyriphlogos* Quinteros, 2012**

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Quinteros, S.

**Categoría 2012**  
INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**  
No Evaluada

**Categoría UICN**  
No Evaluada

**Justificación**  
Esta especie se encuentra distribuída en diversas localidades en la provincia de Jujuy. Es una especie abundante en todas las regiones en las que se encuentra (Laguna Leandro, Sierra de Aparzo y Mudana), hacia el oeste de la Quebrada de Humahuaca.

Las regiones en las que habita esta especie, son zonas donde la urbanización no ha llegado. Son pueblos originarios con pocos habitantes cuyo impacto sobre la fauna de reptiles que habitan en esas regiones es escaso o nulo. Pero siempre es interesante

poder realizar alguna política de conservación para evitar que esas zonas se vean afectadas negativamente en el futuro.

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## ***Liolaemus rabinoi* (Ceï, 1974). Lagartija de El Nihuil**

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Abdala, C. S.

### **Categoría 2012**

EN PELIGRO

### **Categoría anterior en Argentina**

En Peligro (Avila *et al.*, 2000)

### **Categoría UICN**

Vulnerable (Baillie y Groombridge, 1996)

### **Justificación**

Es una especie que fue reencontrada luego de 35 años (Abdala *et al.*, 2011) y se conoce sólo una población microendémica para esta especie, en cercanías al embalse El Nihuil, San Rafael, provincia de Mendoza. Es estrictamente arenícola, que habita en las cúspides de los médanos y es muy vulnerable a la modificación de su hábitat. Las poblaciones halladas por Ceï (1974) para describir esta especie

se han extinguido, muy probablemente debido a la fuerte acción antrópica. El hábitat donde fue hallada la población existente está fuertemente amenazado, sobre todo por el uso intensivo de vehículos doble tracción. Incluso los médanos donde habita *Liolaemus rabinoi* son utilizados para realizar competencias provinciales, nacionales e internacionales como el Rally Dakar.

### **Sugerencias y acciones de conservación**

Como medida inmediata, detener la circulación de vehículos doble tracción en los médanos donde se localiza la población existente de *L. rabinoi*. Además, incorporar dicha zona como área natural protegida por parte del gobierno de Mendoza. Realizar campañas de educación ambiental en la zona, utilizando como eje a *L. rabinoi*.

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## ***Liolaemus riojanus* Ceï, 1979**

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Laspiur, A.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Respecto a la categorización anterior, nueva información ecológica ha sido sumada, más algunos factores que han sido reconocidos como perniciosos, han permitido el cambio de Insuficientemente Conocida a Vulnerable. Factores de amenaza en torno a poblaciones reconocidas de esta especie han sido evidentes. Debido a la particularidad de ser una especie estrictamente psamófila, han sido claras algunas restricciones. La expansión de la frontera agrícola debido a nuevas tecnologías ha llevado a la instalación de cultivos, donde antes las condiciones

no lo permitían. La expansión agrícola, en sí misma, tiene como consecuencia la pérdida de hábitat en la mayoría de los sitios de distribución reconocidos en la provincia de San Juan.

Por otra parte, este factor antrópico puede alterar la dinámica de los procesos de formación de médanos en áreas aledañas. Debido a la discontinuidad local generada a nivel paisaje, los mecanismos de depósito y arrastre de materiales se ven alterados, pudiendo ser evidentes en zonas próximas a los cultivos. Modificaciones en el volumen de arena en médanos inalterados por el hombre. Estos fenómenos naturales pueden originar cambios en el hábitat estructural de la especie y por consiguiente, cambios en la dinámica poblacional.

A la pérdida de hábitat en estos ambientes subyace la fragmentación de poblaciones y el posterior empobrecimiento de la diversidad genética, por constituir este tipo de amenazas indirectas, una barrera al flujo de genes.

### **Sugerencias y acciones de conservación**

Identificar poblaciones en terreno a fin de determinar las áreas efectivas de distribución y sus límites. Evaluar el estado de las poblaciones a nivel ecológico y estructural (grupos de edad y asociación a diferentes microambientes) en poblaciones sujetas a perturbación, respecto de aquellas halladas en

hábitats naturales. Este tipo de estudios, además de ser una contribución al conocimiento general de la biología de esta especie poco conocida, permitirá evaluar el impacto de la expansión agrícola sobre la especie, como primer objetivo antes de evaluar y proponer alternativas de manejo y conservación.

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## ***Liolaemus scolaroi* Pincheira-Donoso & Núñez, 2005**

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Avila, L. J.; Morando, M.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

En Argentina sólo está sugerida sin ejemplares de referencia.

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie con distribución muy restringida, su presen-

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## ***Liolaemus silvanae* (Donoso-Barros & Cei, 1971)**

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Abdala, S. C.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie que presenta un alto grado de endemismo, relativo a la Meseta del Lago Buenos Aires, provincia de Santa Cruz, por arriba de los 1400 m s.n.m. Asimismo es una especie con especializaciones en su hábitat, su sustrato (saxícola), su alimentación (fuerte tendencia a la herbivoría) y modo reproductivo (vivípara). Sus poblaciones son muy escasas y hay un fuerte efecto antrópico en la meseta debido a la actividad ganadera ovina.

### **Sugerencias y acciones de conservación**

Se recomienda realizar intensos estudios referidos a la dinámica poblacional, especialmente evaluar la situación real de las poblaciones de *L. silvanae*. También se deberá inspeccionar áreas aledañas a fin de determinar la existencia de poblaciones adyacentes. Por último es imprescindible evaluar el efecto concreto que produce la intensa actividad ovina sobre las poblaciones de *L. silvanae*.

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## ***Liolaemus somuncurae* Cei & Scolaro, 1981**

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Abdala, C. S.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

Datos Insuficientes (UICN, 2009)

### **Justificación**

Es una especie muy poco conocida, poco represen-

tada en las colecciones herpetológicas. Se distribuye sobre la meseta de Somuncurá, en las provincias de Río Negro y Chubut. Es una especie vivípara, pero se desconocen la mayoría de los aspectos biológicos necesarios para categorizarla, así como el estado real de sus poblaciones.

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## ***Liolaemus tandiliensis* Vega, Bellagamba & Lobo, 2008**

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Vega, L.

### **Categoría 2012**

AMENAZADA

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Microendemismo. Su distribución conocida está restringida al sistema serrano de Tandilia de la

provincia de Buenos Aires, a una superficie menor a los 20.000 km<sup>2</sup>. Especialista de hábitats rocosos y de alimentación insectívora. Su puesta es inferior a los cinco huevos por año. Es una lagartija muy poco abundante.

### **Sugerencias y acciones de conservación**

Sus poblaciones no están protegidas. Debería garantizarse la creación de reservas en el Sistema Serrano de Tandilia. Controlar la explotación de canteras en campos privados y el origen de incendios.

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## ***Liolaemus tari* Scolaro & Cei, 1997**

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Avila, L. J.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

nocida.

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie de distribución muy restringida, poco co-

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## ***Liolaemus thermarum* Videla & Cei, 1996**

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Abdala, C. S.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación**

Es una especie con un microendemismo marcado, restringida a las cercanías del Volcán Peteroa, Malar-güe, provincia de Mendoza. Es una especie saxícola,

vivípara y con fuerte tendencia a la herbivoría. Presenta una densidad muy baja comparada con otras especies de *Liolaemus* del mismo grupo.

**Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado de sus poblaciones, distribución y biología. Además se deberá realizar un estudio en el cual se analice el estado de sus poblaciones en relación a la actividad del Volcán Peteroa, el cual afecta la región desde hace varios años con una gran emisión de cenizas desde 2010.

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## ***Liolaemus tregenzai* Pincheira-Donoso & Scolaro, 2007**

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Avila, L. J.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Especie de distribución geográfica muy restringida, sólo conocida para su localidad tipo, en un área de

incremento del desarrollo turístico y con planes de avance de la industria geotérmica. Población única con una aparente baja densidad poblacional.

**Sugerencias y acciones de conservación**

Aumentar los estudios en la región para conocer los límites de distribución de la especie, aumentar las medidas de protección en el área natural protegida donde se encuentra la especie y concientizar a las autoridades de la importancia de la herpetofauna protegida en el lugar.

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## ***Liolaemus tristis* Scolaro & Cei, 1997**

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Avila, L. J.

**Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación**

Especie de distribución muy restringida, poco conocida.

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## ***Liolaemus uptoni* Scolaro & Cei, 2006**

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Avila, L. J.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie de distribución muy restringida, poco conocida.

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## ***Liolaemus vallecurensis* Pereyra, 1992**

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Acosta, J. C.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie endémica de Valle del Cura, Cordillera de Colangüil, norte de la provincia de San Juan. Habita bajadas pedemontanas con matorrales de *Adesmia aegiceras* y *A. crassiculis*, a 3700 m s.n.m. Estudios realizados sugieren que es bimodal, de fisiología térmica conservativa con marcada reducción del horario de actividad comparada con otras especies del género, debido quizás a restricciones ambientales (Villavicencio *et al.*, 2007).

El cambio de categorización anterior de especie Insuficientemente Conocida se debe a que habita una región de clima riguroso que restringe el desempeño de los organismos. Es probablemente vivípara, al igual que otras especies del género que habitan ambientes similares. Se desconoce completamente su biología reproductiva.

En el área se desarrollan actualmente varios proyectos mineros, ha sido concesionada por 20 años a sus propietarios, dificultando el acceso a la misma, con el consiguiente riesgo para la conservación de la especie.

### **Sugerencias y acciones de conservación**

Para esta especie endémica el conocimiento de su biología es insuficiente. Es necesario realizar estudios que permitan monitorear el estado actual de las poblaciones. Explorar el área que habita es dificultoso, puesto que los proyectos mineros impiden el libre acceso, aún si se llevaran a cabo gestiones ante autoridades provinciales para el desarrollo de campañas de investigación. Se sugiere gestionar ante funcionarios de ambiente el estudio del impacto que la actividad minera ejercerá sobre ésta y otras especies afectadas.

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## ***Phymaturus antofagastensis* Pereyra, 1985**

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Blanco, G. M.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Es una especie endémica del sector noroeste de la puna de la provincia de Catamarca. Varios aspectos de la biología de esta especie incluyendo su dieta herbívora, el uso de microhábitat especializado, el modo reproductivo vivíparo, y su ciclo reproductivo bienal (Boretto e Iburgüengoytía, 2006; Iburgüengoytía *et al.*, 2008), están fuertemente conservados. Habita por encima de los 3700 m.s.n.m. en formaciones rocosas.

El cambio respecto de la categorización anterior (Insuficientemente Conocida) se debe a la riguro-

sidad climática del área que habita la especie (clima frío, semiárido, de amplio rango térmico diario), a su bajo tamaño de camada de dos crías por hembra, cada dos años, resultando en un bajo potencial reproductivo (Boretto e Iburgüengoytía, 2006), y su ecología trófica (Acosta *et al.*, 2008), constituyendo probablemente un potencial dispersor de las plantas de las que se alimenta (frutos), cumpliendo quizás un rol fundamental en la fenología de la escasa flora existente en su área de distribución.

### **Sugerencias y acciones de conservación**

Es evidente la necesidad de contar con más estudios que permitan conocer el estado de las poblaciones. Se sugiere la realización de investigaciones que permitan confirmar el rol de esta especie endémica de la Puna, específicamente completar estudios biológicos y su interacción con el medio físico evaluando a largo plazo la dinámica poblacional como herramienta para fijar pautas de conservación

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## ***Phymaturus calcogaster* Scolaro & Cei, 2003. Lagarto de rocas de vientre cobrizo**

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Boretto, J. M.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie microendémica de roquedales ubicados en la localidad tipo, ubicada en el ecotono subarbustivo xerófilo Monte-Patagonia de alrededores de Laguna de las Vacas, en el departamento Telsen, Chubut (Scolaro *et al.*, 2005). En este sitio y alrededores se realizaron extensos muestreos a fin de encontrar ejemplares, debido a su reducida distribución (Scola-

ro *et al.*, 2005). Es especialista en ambientes rocosos, escoriales con derrumbes y avalanchas de la ladera de la meseta hacia el valle de la cuenca del arroyo y la Laguna Las Vacas, Chubut (Scolaro *et al.*, 2005). Al igual que el resto de las especies de *Phymaturus*, es especialista tanto en su hábitat como en sus hábitos, es saxícola, herbívora y su modo reproductivo es vivíparo (Scolaro *et al.*, 2005). Vive agrupada en familias (Scolaro, 2005) y presenta un bajo tamaño de camada de dos individuos por hembra (Boretto *et al.*, 2006).

### **Sugerencias y acciones de conservación**

Sus poblaciones no están protegidas. Se debería realizar estudios sobre la bio-ecología de la especie, en especial acerca de su biología reproductiva. Además se sugiere explorar la región en busca de otras po-



blaciones y monitorear el impacto de la explotación ovina y del cambio climático global.

Es necesario proteger la localidad tipo, prohibiendo la extracción de individuos y la modificación del

hábitat, promoviendo que al menos las localidades tipo se conserven en forma prístina el mayor tiempo posible.

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## ***Phymaturus castillensis* Scolaro & Pincheira-Donoso, 2010**

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Boretto, J. M.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie microendémica de roquedales ubicados en la zona patagónica de Sierra del Castillo, en la provincia de Chubut (Scolaro y Pincheira-Donoso, 2010). Asimismo se trata de una especie especialista

en su hábitat y en sus hábitos saxícolas y herbívoros, además de ser vivípara y presentar un bajo tamaño de camada de uno a dos individuos por hembra (Scolaro y Pincheira-Donoso, 2010).

### **Sugerencias y acciones de conservación**

Sus poblaciones no están protegidas. Podría explorarse la región en busca de otras poblaciones, monitorearse el impacto de la explotación ovina y aumentar los estudios relacionados con su historia de vida aún poco conocida. Es necesario proteger la localidad tipo, prohibiendo la extracción de individuos y la modificación del hábitat, promoviendo que al menos las localidades tipo se conserven en forma prístina el mayor tiempo posible.

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## ***Phymaturus ceii* Scolaro & Ibarzüengoytía, 2008**

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Avila, L. J.; Morando, M.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Distribución geográfica muy restringida. La evidencia indica que la mayoría de las especies de *Phymaturus* presentan este patrón de distribución puntual y extremadamente limitada. Las especies de este género tardan entre siete y nueve años en alcanzar la madurez reproductiva (Piantoni *et al.*, 2006) y sólo tienen dos crías cada dos años en la mayoría de los casos (Habit y Ortiz, 1996; Ibarzüengoytía, 2004; Boretto e Ibarzüengoytía, 2006; 2009; Boretto *et al.*, 2007; Cabezas-Cartes *et al.*, 2010). Zona muy afecta-

da por fenómenos naturales recientes (vulcanismo) y consiguiente depósito de gran cantidad de ceniza volcánica, a lo que se suma alto grado de deterioro ambiental por sobrepastoreo y actividad minera creciente en algunas regiones cercanas.

### **Sugerencias y acciones de conservación**

No realizar ningún tipo de emprendimiento que pueda afectar el hábitat de los mismos. Limitar los permisos de colecta científica a trabajos que de manera imprescindible y justificada lo requieran.

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## ***Phymaturus delheyi* Avila, Perez, Perez & Morando, 2011**

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Avila, L. J.; Morando, M.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No evaluada

### **Categoría UICN**

No evaluada

### **Justificación**

Distribución geográfica muy restringida. La evidencia indica que la mayoría de las especies de *Phymaturus* presentan este patrón de distribución puntual

y extremadamente limitada. Las especies de este género tardan entre siete y nueve años en alcanzar la madurez reproductiva y sólo tienen dos crías cada dos años en la mayoría de los casos (Habit y Ortiz, 1996; Ibargüengoytía, 2004; Boretto e Ibargüengoytía, 2006; 2009; Piantoni *et al.*, 2006; Boretto *et al.*, 2007; Cabezas-Cartes *et al.*, 2010).

### **Sugerencias y acciones de conservación**

No realizar ningún tipo de emprendimiento que pueda afectar el hábitat de los mismos. Limitar los permisos de colecta científica a trabajos que de manera imprescindible y justificada lo requieran.

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## ***Phymaturus denotatus* Lobo, Nenda & Slodki, 2012**

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Abdala, C. S.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Es una especie microendémica de la Sierra Laguna Blanca en la provincia de Catamarca. Habita por

encima de los 3400 m s.n.m. Al igual que los demás *Phymaturus* del grupo de *P. palluma*, es una especie asociada a las rocas, vivípara, con fuerte tendencia a la herbivoría.

### **Sugerencias y acciones de conservación**

Se deberán realizar mayores estudios sobre la dinámica poblacional de esta especie, así como el estado de conservación de sus poblaciones. Es necesario conocer mayores datos de la biología de este taxón.

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## ***Phymaturus desuetus* Scolaro & Tappari, 2009**

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Abdala, C. S.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Es una especie microendémica en las proximidades de Ingeniero Jacobacci, provincia de Río Negro. Sólo se conoce un ejemplar (holotipo), por lo que su biología se extrapola en base a la de sus congéneres.

### **Sugerencias y acciones de conservación**

Debido a que sólo se conoce un ejemplar de esta especie, se deberían realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presentan el ambiente que habita.

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## ***Phymaturus dorsimaculatus* Lobo & Quinteros, 2005**

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Avila, L. J.; Morando, M.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Distribución geográfica muy restringida. La evidencia indica que la mayoría de las especies de *Phymaturus* presentan este patrón de distribución puntual y extremadamente limitada. Las especies

de este género tardan entre siete y nueve años en alcanzar la madurez reproductiva y sólo tienen dos crías cada dos años en la mayoría de los casos (Habit y Ortiz, 1996; Ibargüengoytía, 2004; Boretto e Ibargüengoytía, 2006; 2009; Piantoni *et al.*, 2006; Boretto *et al.*, 2007; Cabezas-Cartes *et al.*, 2010). Estatus taxonómico no bien determinado.

### **Sugerencias y acciones de conservación**

No realizar ningún tipo de emprendimiento que pueda afectar el hábitat de los mismos. Limitar los permisos de colecta científica a trabajos que de manera imprescindible y justificada lo requieran.

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## ***Phymaturus etheridgei* Lobo, Abdala & Valdecantos, 2010**

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Avila, L. J.; Morando, M.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Distribución geográfica muy restringida. La evidencia indica que la mayoría de las especies de *Phymaturus* presentan este patrón de distribución puntual

y extremadamente limitada. Las especies de este género tardan entre siete y nueve años en alcanzar la madurez reproductiva y sólo tienen dos crías cada dos años en la mayoría de los casos (Habit y Ortiz, 1996; Ibargüengoytía, 2004; Boretto e Ibargüengoytía, 2006; 2009; Piantoni *et al.*, 2006; Boretto *et al.*, 2007; Cabezas-Cartes *et al.*, 2010).

### **Sugerencias y acciones de conservación**

No realizar ningún tipo de emprendimiento que pueda afectar el hábitat de los mismos. Limitar los permisos de colecta científica a trabajos que de manera imprescindible y justificada lo requieran.

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## ***Phymaturus excelsus* Lobo & Quinteros, 2005**

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Avila, L. J.; Morando, M.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

No Evaluada

### **Categoría UICN**

No Evaluada

### **Justificación**

Distribución geográfica muy restringida. La evidencia indica que la mayoría de las especies de *Phymaturus* presentan este patrón de distribución puntual y extremadamente limitada. Las especies de este género tardan entre siete y nueve años en alcanzar

la madurez reproductiva y sólo tienen dos crías cada dos años en la mayoría de los casos (Habit y Ortiz, 1996; Ibagüengoytía, 2004; Boretto e Ibagüengoytía, 2006; 2009; Piantoni *et al.*, 2006; Boretto *et al.*, 2007; Cabezas-Cartes *et al.*, 2010).

#### **Sugerencias y acciones de conservación**

No realizar ningún tipo de emprendimiento que pueda afectar el hábitat de los mismos. Limitar los permisos de colecta científica a trabajos que de manera imprescindible y justificada lo requieran.

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## ***Phymaturus extrilidus* Lobo, Espinoza, Sanabria & Quiroga, 2012**

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Laspiur, A.; Acosta, J. C.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

No Evaluada

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Distribución geográfica muy restringida, con evidencias de distribución poco más amplia a lo largo del cordón montañoso donde se emplaza la población. Esta especie, al igual que los otros miembros del género, son especialistas en el uso de hábitat,

ocupando únicamente diaclasas y rocas basálticas de buena exposición solar y presencia de vegetación típica de la que basa su dieta herbívora. Es una especie vivípara con ciclo reproductivo caracterizado por una gestación prolongada y producción de tamaños de camada por hembra de dos crías cada dos años.

#### **Sugerencias y acciones de conservación**

Actualmente la localidad tipo está incluida en la Reserva Natural de Usos Múltiples Don Carmelo, departamento de Ullum. Es prioritario realizar exploraciones en inmediaciones a la reserva para determinar efectivamente su rango de distribución y evaluar la posibilidad de realizar estudios biológicos en la especie.

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## ***Phymaturus felixi* Lobo, Abdala & Valdecantos, 2010**

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Avila, L. J.; Morando, M.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

No Evaluada

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Distribución geográfica muy restringida. La evidencia indica que la mayoría de las especies de *Phymaturus* presentan este patrón de distribución puntual y extremadamente limitada. Las especies de este género tardan entre siete y nueve años en alcanzar la madurez reproductiva y sólo tienen dos crías cada dos años en la mayoría de los casos (Habit y Ortiz, 1996; Ibagüengoytía, 2004; Boretto e Ibagüengoytía, 2006; 2009; Piantoni *et al.*, 2006; Boretto *et al.*, 2007; Cabezas-Cartes *et al.*, 2010).

ytía, 2006; 2009; Piantoni *et al.*, 2006; Boretto *et al.*, 2007; Cabezas-Cartes *et al.*, 2010).

#### **Sugerencias y acciones de conservación**

No realizar ningún tipo de emprendimiento que pueda afectar el hábitat de los mismos. Limitar los permisos de colecta científica a trabajos que de manera imprescindible y justificada lo requieran.

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## ***Phymaturus gynechlomus* Corbalán, Scolaro & Debandi, 2009**

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Corbalán, V.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Especie de distribución restringida, endémica de la

provincia de Mendoza. Al igual que otras especies del género es vivípara y especialista de hábitat, ocupando áreas rocosas de montaña.

**Sugerencias y acciones de conservación**

Está protegida en la Reserva Hídrica y Paisaje Protegido Laguna del Diamante (departamento San Carlos, Mendoza). Se sugiere explorar nuevas áreas para determinar su rango de distribución y mejorar el conocimiento de su biología.

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## ***Phymaturus indistinctus* Cei & Castro, 1973**

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Boretto, J. M.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Es microendémica de roquedales ubicados en escoriales, bordes y acantilados de la meseta basáltica en la estepa xerófila de altura, y subarbustiva abierta de la Sierra de San Bernardo y de alrededores del Lago Musters en la provincia de Chubut (Cei y Castro, 1973; Scolaro, 2005). Al igual que el resto de las especies del género, *P. indistinctus* es especialista en su

hábitat y en sus hábitos, es saxícola, principalmente herbívora, aunque se la ha observado alimentarse de insectos, y su modo reproductivo es vivíparo (Cei y Castro, 1973; Scolaro, 2005).

**Sugerencias y acciones de conservación**

Sus poblaciones no están protegidas. Se deberían realizar estudios sobre la bio-ecología de la especie, en especial acerca de su biología reproductiva. Se debe explorar la región en busca de otras poblaciones y monitorear el impacto de la explotación ovina y del cambio climático global. Es necesario proteger la localidad tipo, prohibiendo la extracción de individuos y la modificación del hábitat, promoviendo que al menos las localidades tipo se conserven en forma prístina el mayor tiempo posible.

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## ***Phymaturus laurenti* Lobo, Abdala & Valdecantos, 2010**

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Abdala, C. S.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Es una especie endémica de zonas de altura del cen-

tro de la provincia de Catamarca. Sólo conocida para cinco localidades siempre por encima de los 3500 m s.n.m. Presenta una biología muy particular, con varias especializaciones, principalmente en el uso del sustrato ya que es saxícola estricto y en la dieta debido a que es una especie totalmente herbívora. Asimismo es una especie vivípara y presenta pobla-

ciones con una densidad normal a alta comparada con otras especies de *Phymaturus*.

#### **Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presentan el ambiente que habita.

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## ***Phymaturus mallimaccii* Cei, 1980**

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Abdala, C. S.

**Categoría 2012**  
VULNERABLE

**Categoría anterior en Argentina**  
Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**  
No Evaluada

#### **Justificación**

Es una especie con un microendemismo muy marcado, restringida a la Sierra de Famatina, provincia de La Rioja, siempre por encima de los 3800 m s.n.m. Al igual que los demás *Phymaturus* presenta una biología muy particular, es saxícola estricto y está especializada en la dieta debido a que es totalmente herbívora.

Es una especie vivípara y presenta poblaciones con una densidad no muy elevada comparada con otras especies de *Phymaturus*.

#### **Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presenta el ambiente que habita. Además se deberá determinar los motivos por los cuales las poblaciones presentan una densidad baja. En el área se desarrollan proyectos turísticos y posiblemente efectúen impacto sobre el ambiente de *P. mallimacci*. Otro punto importante a tener en cuenta es la actividad minera que se pretende reactivar en el futuro y que se desarrollara en el área hace varias décadas a gran escala y el impacto que puede ocasionar en las poblaciones.

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## ***Phymaturus manuelae* Scolaro & Ibarquengoytía, 2008**

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Boretto, J. M.

**Categoría 2012**  
VULNERABLE

**Categoría anterior en Argentina**  
No Evaluada

**Categoría UICN**  
No Evaluada

#### **Justificación**

Es microendémica de roquedales ubicados sólo en inmediaciones de la localidad tipo, situada en mesetas basálticas en la estepa patagónica adyacente a la Ruta Nacional 23, al Oeste de Comallo, en la provincia de Río Negro (Scolaro e Ibarquengoytía,

2008). Estudios recientes muestran que esta especie se ha extinguido del roquedal en el que fuera colectada para su determinación (localidad tipo) poniendo de manifiesto la gran vulnerabilidad de esta especie y la imperante necesidad de proteger las localidades tipo, prohibiendo la extracción de individuos y la modificación del hábitat, promoviendo que al menos las localidades tipo se conserven en forma prístina el mayor tiempo posible. Actualmente, el resto de las poblaciones se encuentran afectadas por la gran acumulación de cenizas volcánicas como consecuencia de la reciente erupción del Volcán Puyehue, alterando el hábitat y la disponibilidad de recursos y refugios. Al igual que el resto de las especies del género, *P. manuelae* es especialista en su hábitat y en

sus hábitos, es saxícola, herbívora y su modo reproductivo es vivíparo (Scolaro e Ibargüengoytía, 2008).

#### **Sugerencias y acciones de conservación**

Sus poblaciones no están protegidas. Se deberían realizar estudios sobre la bio-ecología de la especie, en especial acerca de su biología reproductiva. Se debería monitorear el impacto de la acumulación de

cenizas volcánicas producto de la reciente erupción de Volcán Puyehue, así como el posible impacto de las obras viales proyectadas sobre la ruta 23, la explotación ovina y los efectos del cambio climático global. Se debe explorar la región en busca de otras poblaciones y proteger la localidad tipo, prohibiendo la extracción de individuos y la modificación del hábitat.

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## ***Phymaturus nevadoi* Cei & Roig 1975**

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Corbalán, V.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Especie de distribución restringida, endémica de la provincia de Mendoza. Al igual que otras especies del

género es vivípara y especialista al hábitat, ocupando áreas rocosas de la Sierra del Nevado.

El cambio respecto de la categorización anterior de especie Insuficientemente Conocida a Vulnerable se debe a su endemidad, su especialización al hábitat y su rareza.

#### **Sugerencias y acciones de conservación**

No se encuentra protegida en la red de reservas naturales. Se sugiere explorar nuevas áreas para determinar su rango de distribución y mejorar el conocimiento de su biología.

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## ***Phymaturus palluma* Bell, 1843**

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Corbalán, V.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

#### **Categoría UICN**

Preocupación Menor (UICN, 2010)

#### **Justificación**

Especie de distribución restringida. Al igual que otras especies del género es vivípara y especialista al hábitat, ocupando áreas rocosas de montaña.

El cambio respecto de la categorización anterior de especie Insuficientemente Conocida a Vulnerable se debe a su endemidad y su especialización al hábitat.

#### **Sugerencias y acciones de conservación**

Se sugiere realizar estudios para mejorar el conoci-

miento de aspectos biológicos de la especie.

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## ***Phymaturus patagonicus* Koslowsky, 1898**

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Avila, L. J.; Morando, M.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Distribución geográfica muy restringida. La evidencia indica que la mayoría de las especies de *Phymaturus* presentan este patrón de distribución puntual

y extremadamente limitada. Las especies de este género tardan entre siete y nueve años en alcanzar la madurez reproductiva y sólo tienen dos crías cada dos años en la mayoría de los casos (Habit y Ortiz, 1996; Ibagüengoytía, 2004; Boretto e Ibagüengoytía, 2006; 2009; Piantoni *et al.*, 2006; Boretto *et al.*, 2007; Cabezas-Cartes *et al.*, 2010).

### **Sugerencias y acciones de conservación**

No realizar ningún tipo de emprendimiento que pueda afectar el hábitat de los mismos. Limitar los permisos de colecta científica a trabajos que de manera imprescindible y justificada lo requieran.

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## ***Phymaturus payuniae* Cei & Castro, 1973. Lagarto de Payunia**

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Corbalán, V.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie de distribución restringida, endémica de la provincia de Mendoza. Al igual que otras especies del género es vivípara y especialista al hábitat, ocupando

áreas rocosas de la Payunia. La creciente actividad petrolera en el área de distribución podría afectar las poblaciones de esta especie.

El cambio respecto de la categorización anterior de especie Insuficientemente conocida a Vulnerable se debe a su endemidad y su especialización al hábitat.

### **Sugerencias y acciones de conservación**

Se encuentra protegida en la Reserva de la Payunia. Se sugiere realizar estudios para mejorar el conocimiento de aspectos biológicos de la especie.

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## ***Phymaturus punae* Cei, Etheridge & Videla, 1983**

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Blanco, G. M.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Especie endémica, distribuida en la Reserva de la Biósfera San Guillermo (Parque Nacional y Reserva Provincial), en el extremo noroeste de la provincia de San Juan. No obstante su distribución restringida ocupa todos los roquedales, ya sean cordones continuos o agrupamientos rocosos de llanos y bolsones. Ser endémica es razón suficiente para ser protegida.



El cambio de categorización anterior de especie (Insuficientemente Conocida) se debe a que habita una región de clima riguroso, en la cota de los 4000 m s.n.m., con veranos frío-templados e inviernos nevados que disminuyen el crecimiento, la fecundidad y la duración de la reproducción. Las hembras se reproducen una vez cada dos años, y presentan un tamaño de camada de una a dos crías por hembra, dando como resultado una baja fecundidad media anual de 0,75 cría (hembra . año)<sup>-1</sup> (Boretto *et al.*, 2007;). Es vivípara, herbívora y saxícola (Acosta *et al.*, 2007; Iburgüengoytía *et al.*, 2008). El área es de difícil acceso restringiendo el alcance a las poblaciones para evaluar si existe algún riesgo de impacto sobre ellas, sobre todo por el inminente desarrollo minero.

#### Sugerencias y acciones de conservación

Para esta especie vivípara de la Puna, la probabilidad de que un descendiente sobreviva está bajo fuerte selección. Se conocen datos térmicos y reproductivos, por lo que es clara la necesidad de contar con más estudios que permitan monitorear y conocer el estado actual de sus poblaciones. Explorar el área donde habita es de difícil logística requiriendo coordinar acciones entre las autoridades provinciales y nacionales para realizar campañas en colaboración. Se sugiere gestionar ante funcionarios de ambiente provinciales y nacionales planes de investigación que permitan el estudio exhaustivo de la especie.

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## ***Phymaturus querque* Lobo, Abdala & Valdecantos, 2010**

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Avila, L. J.; Morando, M.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

No Evaluada

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Distribución geográfica muy restringida. La evidencia indica que la mayoría de las especies de *Phymaturus* presentan este patrón de distribución puntual y extremadamente limitada. Las especies

de este género tardan entre siete y nueve años en alcanzar la madurez reproductiva y sólo tienen dos crías cada dos años en la mayoría de los casos (Habit y Ortiz, 1996; Iburgüengoytía, 2004; Boretto e Iburgüengoytía, 2006; 2009; Piantoni *et al.*, 2006; Boretto *et al.*, 2007; Cabezas-Cartes *et al.*, 2010). Alteración del hábitat por sobrepastoreo.

#### **Sugerencias y acciones de conservación**

No realizar ningún tipo de emprendimiento que pueda afectar el hábitat de los mismos. Limitar los permisos de colecta científica a trabajos que de manera imprescindible y justificada lo requieran.

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## ***Phymaturus roigorum* Lobo & Abdala 2007. Lagarto cola de piche de Payunia**

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Corbalán, V.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

No Evaluada

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Especie de distribución restringida, endémica de la provincia de Mendoza. Al igual que otras especies del género es vivípara y especialista al hábitat, ocupando áreas rocosas del Payún Matrú, Sierras del Nevado y Sierras de Palauco.

La creciente actividad petrolera en el área de distribución podría afectar las poblaciones de esta

especie, principalmente por la fragmentación y pérdida del hábitat.

Se sugiere realizar estudios para mejorar el conocimiento de aspectos biológicos de la especie.

#### **Sugerencias y acciones de conservación**

Se encuentra protegida en la Reserva de la Payunia.

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## ***Phymaturus sitesi* Avila, Perez, Perez & Morando, 2011**

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Avila, L. J.; Morando, M.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

No Evaluada

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Distribución geográfica muy restringida. La evidencia indica que la mayoría de las especies de *Phymaturus* presentan este patrón de distribución puntual

y extremadamente limitada. Las especies de este género tardan entre siete y nueve años en alcanzar la madurez reproductiva y sólo tienen dos crías cada dos años en la mayoría de los casos (Habit y Ortiz, 1996; Ibagüengoytía, 2004; Boretto e Ibagüengoytía, 2006; 2009; Piantoni *et al.*, 2006; Boretto *et al.*, 2007; Cabezas-Cartes *et al.*, 2010).

#### **Sugerencias y acciones de conservación**

No realizar ningún tipo de emprendimiento que pueda afectar el hábitat de los mismos. Limitar los permisos de colecta científica a trabajos que de manera imprescindible y justificada lo requieran.

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## ***Phymaturus somuncurensis* Cei & Castro, 1973**

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Abdala, C. S.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Es una especie con un microendemismo muy marcado, restringida a la Meseta de Somuncurá, provincia de Río Negro, siempre por encima de los 1200 m s.n.m. Su biología es similar a la de las demás taxa del género, es un especie saxícola, vivípara y herbívora. Presenta poblaciones con una densidad no muy elevada comparada con otras especies de *Phymaturus*.

de sus poblaciones, biología y grado de amenaza que presenta el ambiente que habita. Además se deberá determinar los motivos por los cuales las poblaciones presentan una densidad baja. En el área se desarrollan proyectos de ganadería ovina a gran escala y probablemente efectúen impacto sobre el ambiente de *P. somuncurensis*.

#### **Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado

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## ***Phymaturus spectabilis* Lobo & Quinteros, 2005**

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Abdala, C. S.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Es una especie con un microendemismo muy marcado, restringida a una zona de roquedales ubicados al sur de Ingeniero Jacobacci. Al igual que las demás especies del género es una especie saxícola, vivípara y herbívora. Las hembras se reproducen cada uno

o dos años, y tienen un tamaño de camada fijo de dos crías, resultando en una baja fecundidad media anual de  $1,33 \text{ cría (hembra} \cdot \text{año)}^{-1}$  (Boretto *et al.*, 2011). Sus poblaciones conocidas presentan una densidad normal comparada con otras especies de *Phymaturus*.

**Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presenta el ambiente que habita. Se debería monitorear el impacto de la acumulación de cenizas volcánicas producto de la reciente erupción de Volcán Puyehue, así como el impacto de la explotación ovina y los efectos del cambio climático global.

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## ***Phymaturus spurcus* Barbour, 1921**

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Abdala, C. S.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Es una especie con un microendemismo muy marcado, conocida sólo para su localidad tipo (Estancia

Huanuluan, provincia de Río Negro). Es una especie altamente especializada, es saxícola, vivípara y herbívora. Sus poblaciones conocidas presentan una densidad normal a baja comparada con otras especies de *Phymaturus*.

**Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presenta el ambiente que habita. Además se deberá determinar los motivos por los cuales las poblaciones presentan una densidad baja.

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## ***Phymaturus tenebrosus* Lobo & Quinteros, 2005. Lagarto tenebroso de las rocas**

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Boretto, J. M.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

En Peligro (Ibargüengoytía y Boretto, 2005)

**Justificación**

El hábitat de *P. tenebrosus* es restringido y muy

fragmentado, se encuentra ubicado en zonas de la espeta patagónica que están atravesando un proceso de desertificación, sumado a los significativos impactos antrópicos causadas por la sobre-explotación de la tierra, especialmente por la ganadería de ovejas y los incendios que ocurren a menudo en verano. Adicionalmente, las hembras se reproducen cada dos años y presentan un tamaño de camada de dos crías por hembra (Ibargüengoytía, 2004).

El cambio respecto de la categorización anterior (En Peligro), se debe al estudio detallado de la especie en cuanto a su biología reproductiva (Ibargüengoytía, 2004), biología térmica (Ibargüengoytía, 2005), a los estudios de edad y crecimiento (Piantoni *et al.*, 2006), y la baja densidad poblacional, constatándose la presencia de la especie sólo en roquedales aislados en un rango geográfico limitado (aproximadamente 700 km<sup>2</sup>). En sucesivos muestreos se ha observado una disminución en las poblaciones, la cual continúa siendo amenazada por la explotación ovina de las tierras, recientes eventos eruptivos del Volcán Puyehue que han afectado notablemente el hábitat y la disponibilidad de recursos y refugios,

sumado a los efectos del cambio climático global. Todos estos eventos podrían afectar severamente la supervivencia de la especie, especialmente si se tiene en cuenta su especialización en cuanto a la alimentación herbívora, su modo reproductivo vivíparo, su baja fecundidad media anual (Ibargüengoytía, 2004), y la adquisición de la madurez sexual a los 7 - 9 años de vida, con una longevidad máxima de 16 años (Piantoni *et al.*, 2006).

#### **Sugerencias y acciones de conservación**

Sus poblaciones no están protegidas. Se debería monitorear el impacto de la acumulación de cenizas volcánicas producto de la reciente erupción de Volcán Puyehue, así como el posible impacto de las obras viales proyectadas sobre la ruta 23, la explotación ovina y los efectos del cambio climático global. Se debe explorar la región en busca de otras poblaciones y es necesario proteger la localidad tipo, prohibiendo la extracción de individuos y la modificación del hábitat, promoviendo que al menos las localidades tipo se conserven en forma prístina el mayor tiempo posible.

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## ***Phymaturus verdugo* Cei & Videla 2003. Dragoncito de tres colores**

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Corbalán, V.

#### **Categoría 2012**

VULNERABLE

#### **Categoría anterior en Argentina**

No Evaluada

#### **Categoría UICN**

No Evaluada

#### **Justificación**

Especie de distribución restringida, endémica de las provincias de Mendoza y Neuquén (Ávila *et al.*, 2007). Al igual que otras especies del género es vivípara y especialista al hábitat, ocupando áreas rocosas de la cordillera de los Andes. Se ha observado que las hembras paren dos crías. Las obras viales desarrolladas en el área de distribución afectan las poblaciones de esta especie por destrucción del hábitat, habiéndose observado la desaparición de varias poblaciones.

#### **Sugerencias y acciones de conservación**

No se encuentra protegida en el sistema de reservas naturales. Se sugiere realizar mayores controles a las obras de infraestructura y proteger su hábitat. También son necesarios estudios para mejorar el conocimiento de aspectos biológicos de la especie.

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## ***Phymaturus videlai* Scolaro & Pincheira-Donoso, 2010**

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Abdala, C. S.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Evaluada

**Categoría UICN**

No Evaluada

**Justificación**

Es una especie con un microendemismo marcado, restringida a las cercanías de Buen Paso, provincia

de Chubut. Como los demás *Phymaturus* es saxícola, vivípara y herbívora. Sus poblaciones conocidas presentan una densidad baja comparada con otras especies del género.

**Sugerencias y acciones de conservación**

Se deberían realizar mayores estudios sobre el estado de sus poblaciones, biología y grado de amenaza que presenta el ambiente que habita. Además se deberá determinar los motivos por los cuales las poblaciones presentan una densidad baja.

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## ***Phymaturus zapalensis* Cei & Castro, 1973**

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Abdala, C. S.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación**

Es una especie endémica de los alrededores de la Laguna Blanca, provincia de Neuquén, encontrándose protegida en el Parque Nacional Laguna Blanca. Su biología al igual que los demás *Phymaturus* presenta

varias especializaciones, es una lagartija saxícola y vivípara. Las hembras se reproducen cada uno o dos años, el tamaño de camada es de uno a dos individuos, dando como resultado una baja fecundidad media anual de una cría (hembra . año)<sup>-1</sup> (Boretto e Ibarzüengoytía, 2009).

**Sugerencias y acciones de conservación**

A pesar de que es una de las pocas especies de *Phymaturus* que está protegida, se deberán realizar estudios relacionados al estado de las poblaciones y determinar su verdadera distribución haciendo hincapié en estudios taxonómicos en las poblaciones por fuera de la localidad tipo.

## Familia Polychrotidae

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### ***Polychrus acutirostris* Spix, 1825**

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Acosta, J.; Alvarez, B.; Hernando, A.; Tedesco, M. E.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

Vulnerable (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación**

Lagarto característico de la región chaqueña, de

hallazgo poco frecuente en algunos lugares de su distribución geográfica. Especializado para la vida arborícola, por lo que es vulnerable a la tala del bosque chaqueño que está alterando seriamente su hábitat natural.

**Sugerencias y acciones de conservación**

Se recomienda el control del impacto de la deforestación en la región chaqueña y su protección en áreas de reservas.

## Familia Tropiduridae

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### ***Stenocercus azureus* (Müller, 1882)**

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Quinteros, S.

**Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación**

Esta especie fue citada para la provincia de Misiones, pero no se ha podido reconfirmar su presencia en Argentina. Esta distribuída en Brasil y Uruguay.

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### ***Stenocercus caducus* (Cope, 1862)**

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Quinteros, S.

**Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación**

Especie que habita en zonas selváticas de Bolivia, Brasil y Paraguay. En Argentina se encuentra en las zonas de Yungas (selva de transición) de las provincias de Jujuy y de Salta.

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## ***Stenocercus doellojuradoi* (Freiberg, 1944)**

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Acosta, J., Álvarez, B., Hernando, A., Tedesco, M. E.

**Categoría 2012**  
VULNERABLE

**Categoría anterior en Argentina**  
Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**  
No Evaluada

**Justificación**  
Especie típica del bosque chaqueño que habita am-

bientes xerófilos de la ecoregión del Chaco Seco, vive bajo matas arbustivas en suelos limo-arenosos. De biología poco conocida y escaso hallazgo. Está severamente afectada por las modificaciones de su hábitat.

**Sugerencias y acciones de conservación**  
Se recomienda el control del impacto de las actividades antrópicas que están alterando severamente los ambientes naturales de esta especie.

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## ***Stenocercus marmoratus* (Duméril & Bibron, 1837)**

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Quinteros, S.

**Categoría 2012**  
INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**  
Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**  
No Evaluada

**Justificación**  
Especie poco conocida. Habita en el norte de Argen-

tina (en la provincia de Salta). Distribuída también en el Sur de Bolivia. Se conoce muy poco sobre su distribución, biología y dinámica poblacional.

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## ***Stenocercus roseiventris* D'Orbigny, 1837**

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Quinteros, S.

**Categoría 2012**  
INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**  
Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**  
No Evaluada

**Justificación**

Especie de amplia distribución, encontrándose en Bolivia, Brasil y Perú. En Argentina se distribuye en las provincias de Jujuy y Salta. Al igual que *S. marmoratus* se conoce muy poco sobre la biología y distribución de esta especie.

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## ***Tropidurus melanopleurus* (Müller, 1902)**

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Quinteros, S.

**Categoría 2012**  
VULNERABLE

quizás a que es muy escasa, está muy restringida y que no habita un área protegida.

**Categoría anterior en Argentina**  
Insuficientemente Conocida (Avila *et al.*, 2000)

**Sugerencias y acciones de conservación**  
Ceí (1993) cita esta especie para la quebrada de Acambuco, en la provincia de Salta. Esta región a sido determinada Reserva Provincial en 1979, por lo que se debería tener en cuenta de integrar a esta reserva, una región mayor en la cual se distribuya esta especie, con el fin de intensificar estudios sobre su biología, para poder plantear con exactitud otras acciones para su conservación

**Categoría UICN**  
No Evaluada

**Justificación**  
Especie poco conocida, se distribuye en Bolivia y en la provincia de Salta, en Argentina. Esta especie fue previamente categorizada como Vulnerable, debido

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## ***Tropidurus spinulosus* (Cope, 1862)**

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Acosta, J., Álvarez, B., Hernando, A., Tedesco, M. E.

**Categoría 2012**  
VULNERABLE

ser rupícola o arborícola. Críptica con la corteza de los quebrachos del bosque chaqueño donde es común hallarla, se refugia en grietas de rocas o en hoquedades de los árboles. En el bosque chaqueño, hábitat que se encuentra actualmente con severas modificaciones por el avance de la frontera agropecuaria, sus poblaciones han experimentado una notable reducción.

**Categoría anterior en Argentina**  
No Amenazada (Avila *et al.*, 2000)

**Categoría UICN**  
No Evaluada

**Justificación**  
Es una especie típica de la ecorregión Chaco Seco que muestra plasticidad en su hábitat pudiendo

**Sugerencias y acciones de conservación**  
Se recomienda un control del impacto de las actividades antrópicas sobre la ecorregión del Chaco Seco.



## Familia Phyllodactylidae

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### ***Homonota darwinii macrocephala* Cei, 1978**

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Arias, F.

**Categoría 2012**  
INSUFICIENTEMENTE CONOCIDA

el Quebrachal, al sur de la provincia de Salta (Cei, 1993).

**Categoría anterior en Argentina**  
Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**  
No Evaluada

**Justificación:**  
El único registro que existe para esta especie es en

## Familia Anguidae

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### ***Ophiodes yacupoi* Gallardo, 1966**

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Arias, F.

**Categoría 2012**  
INSUFICIENTEMENTE CONOCIDA

hallado en Entre Ríos, en los pantanales orientales, extendiéndose desde el norte a lo largo de la selva (Gallardo, 1983). Se citó en Mato Grosso, Brasil.

**Categoría anterior en Argentina**  
Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**  
No Evaluada

**Justificación:**  
Esta especie se encuentra en Misiones y también fue

## Familia Gymnophthalmidae

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### ***Cercosaura ocellata petersi* Ruibal, 1952**

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Acosta, J.; Álvarez, B.; Hernando, A.; Tedesco, M. E.

**Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**

No evaluada

**Justificación**

El único registro para Argentina es un ejemplar macho, hallado en una localidad del extremo norte de la ecorregión Esteros del Iberá, en un ambiente de pastizal. Su distribución geográfica y biología deberá ser estudiada y analizada en detalle.

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### ***Cercosaura steyeri* (Tedesco 1998)**

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Acosta, J.; Álvarez, B.; Hernando, A.; Tedesco, M. E.

**Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

original de la especie, basada en un ejemplar hembra, grávida con tres huevos, hallada en el extremo suroriental de la ecorregión Esteros del Iberá, en un ambiente pastizales bajos.

Por haberse hallado en una localidad del borde de la reserva natural provincial se considera que está protegida. Se considera necesario ampliar los relevamientos y los estudios biológicos básicos.

**Justificación**

Conocida únicamente a partir de la descripción

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### ***Opipeuter xestuz* (Uzzell, 1969)**

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Arias, F.

**Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

tros para las yungas de orientales de Bolivia (Tarija y Cochabamba).

**Justificación**

Esta especie se encuentra en áreas de la selva subtropical de la provincia de Jujuy y de Salta (Parque Nacional Baritú y Calilegua). Además existen regis-

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## ***Vanzosaura rubricauda* (Boulenger, 1902)**

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Acosta, J.; Álvarez, B.; Hernando, A.; Tedesco, M. E.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

No Amenazada (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación**

Pequeño lagarto típicamente chaqueño, que busca

refugio debajo de restos vegetales. Bajo potencial reproductivo, con tamaño fijo de la puesta limitado a dos huevos. De escaso hallazgo y biología poco conocida. Es una especie afectada por las modificaciones de la ecorregión del Chaco Seco.

**Sugerencias y acciones de conservación**

Como para otras especies características de la ecorregión Chaco Seco, se recomienda un control del impacto de las actividades antrópicas sobre este ecosistema.

## Familia Teiidae

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### ***Cnemidophorus lacertoides* Duméril & Bibron, 1839**

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Arias, F.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

Vulnerable (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación:**

Estudios taxonómicos de *Cnemidophorus lacertoides* indican que esta especie se distribuye desde el

sur de Brasil, atravesando Uruguay, hasta el centro de Argentina. Es una especie abundante en zonas rocosas, en la Sierra de la Ventana, extendiéndose hasta Achiras, en Córdoba (Ceí, 1993). Los efectos humanos están afectando considerablemente las poblaciones de esta especie.

**Sugerencias y acciones de conservación**

Sería conveniente proteger áreas donde se encuentra esta especie, como las Sierras de la Ventana en la provincia de Buenos Aires.

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### ***Cnemidophorus leachei* (Peracca, 1879)**

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Arias, F.

**Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

**Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación**

Trabajos taxonómicos (Scrocchi y Ceí, 1991; Ceí,

1993) indican que esta especie se distribuye en la región de las yungas en el norte del país, en diferentes localidades la provincia de Jujuy y Salta. Debido a que se trata de una especie poco abundante y muy escurridiza, hay pocos ejemplares de esta especie depositados en colecciones herpetológicas.

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### ***Cnemidophorus serranus* Ceí & Martori, 1991**

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Arias, F.

**Categoría 2012**

VULNERABLE

**Categoría anterior en Argentina**

Vulnerable (Avila *et al.*, 2000)

**Categoría UICN**

No Evaluada

**Justificación**

Esta especie se ubica se encuentra a lo largo de las Sierras de Córdoba y al norte en la Sierra de Tulumba (Ceí, 1991). En el Parque Nacional Copo, Santiago del Estero, se encontró una población de *Cnemidophorus serranus* (Arias y Lobo, 2005).

**Sugerencias y acciones de conservación**

En las Sierras de Córdoba, *Cnemidophorus serranus* es una especie representativa, pero la zona donde

se encuentra no es área protegida por lo que sería conveniente preservar esa área.

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## ***Kentropyx lagartija* (Gallardo, 1962)**

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Arias, F.

### **Categoría 2012**

INSUFICIENTEMENTE CONOCIDA

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

No Evaluada

### **Justificación**

Estudios taxonómicos indican que esta especie

se distribuye en el noroeste de Argentina, desde la provincia de Tucumán, hasta el norte de Salta. Antiguamente era considerada una subespecie de *Kentropyx viridistriga*, pero en un estudio comparativo de distintas poblaciones de la Argentina se elevó a categoría de especie (Tedesco *et al.*, 1994; Tedesco y Cei, 1997).

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## ***Kentropyx viridistriga* Boulenger, 1894**

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Acosta, J., Alvarez, B., Hernando, A., Tedesco, M. E.

### **Categoría 2012**

VULNERABLE

### **Categoría anterior en Argentina**

Insuficientemente Conocida (Avila *et al.*, 2000)

### **Categoría UICN**

Preocupación Menor (UICN, 2010)

### **Justificación**

Habita pastizales de ambientes abiertos mesófilos del norte del país con escasos registros en la última década producto de la alteración de su ambiente

natural por la expansión humana. Vive en suelos preferentemente arenosos. Ecología y actividad reproductiva poco conocidas con una postura limitada a cuatro o cinco huevos.

### **Sugerencias y acciones de conservación**

Si bien está protegida en el Parque Nacional Mburucuyá sus poblaciones son escasas. Se recomienda encarar estudios biológicos y ecológicos de la especie, cuya distribución y abundancia se encuentran muy afectadas por la alteración de sus ambientes naturales.

## Familia Amphisbaenidae

### ***Amphisbaena borellii* Peracca, 1897 (= *Cercolophia borellii*)**

Montero, R.

#### **Categoría 2012**

AMENAZADA

#### **Categoría anterior en Argentina**

Amenazada (Avila *et al.*, 2000)

#### **Categoría UICN**

No Evaluada

#### **Justificación:**

Es una especie aparentemente no amenazada en Bolivia, sobre todo en la zona del chaco boliviano, alrededores de Santa Cruz (Montero *et al.*, 1995; Cortez, 2009). Sin embargo, en Argentina sólo se conocen dos ejemplares colectados hace más de 50 años (Montero, 1996): uno de Lules, Tucumán (FML 00317, Golbach-Viera cols., 07/09/1958) y otro de Hickman, Salta (FML 00252; S. A. Pierotti col., 03/02/1945). Los colectores de los dos registros son conocidos, por lo que pueden considerarse registros confiables; por otra parte, la identidad de los ejemplares fue confirmada por dos especialistas

en el tema (P. A. Vanzolini y R. Montero). Desde ese entonces, la especie no ha sido formalmente colectada en nuestro país, aunque no se hicieron esfuerzos específicos en su búsqueda. La captura de anfisbénidos es bastante azarosa, pero a las colecciones herpetológicas llegan con cierta regularidad por ser colectadas por personas que las confunden con ofidios peligrosos.

Según el puntaje asignado en el método utilizado, esta especie debería ser considerada como Vulnerable; sin embargo dada su distribución restringida en Argentina y su escasa abundancia, se considera que debe ser elevada su categorización a Amenazada. Aunque por el momento no se pueda aseverar, es probable que *A. borellii* esté extinta en Argentina.

#### **Sugerencias y acciones de conservación**

Confirmar en primer lugar si esta especie se encuentra en Argentina en la actualidad, con búsquedas específicas e intensivas en los lugares donde fue colectada históricamente, para luego, en función de estos resultados, decidir acciones de conservación.

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# How lizards survived blizzards: phylogeography of the *Liolaemus lineomaculatus* group (Liolaemidae) reveals multiple breaks and refugia in southern Patagonia and their concordance with other codistributed taxa

M. FLORENCIA BREITMAN,\* LUCIANO J. AVILA,\* JACK W. SITES JR† and MARIANA MORANDO\*

\*Grupo de Herpetología Patagónica, Centro Nacional Patagónico, Boulevard Almirante Brown 2915, (U9120ACD), Puerto

Madryn, Chubut, Argentina, †Biology Department and Monte L. Bean Life Science Museum, Brigham Young University, 401 WIDB, Provo, UT 84602, USA

## Abstract

Patagonia was shaped by a complex geological history, including the Miocene uplift of the Andes, followed by volcanism, marine incursions, and extreme climatic oscillations during Pliocene–Pleistocene glaciation–deglaciation cycles. The distributional patterns and phylogenetic relationships of southern patagonian animals and plants were affected in different ways, and those imprints are reflected in the seven phylogeographic breaks and eight refugia that have been previously proposed. In this study, we estimated time-calibrated phylogenetic/phylogeographic patterns in lizards of the *Liolaemus lineomaculatus* group and relate them to historical Miocene-to-Pleistocene events of Patagonia and the previously proposed phylogeographic patterns. Individuals from 51 localities were sequenced for the mitochondrial marker (*cyt-b*) and a subsample of individuals from each mitochondrial lineage was sequenced for one nuclear (LDA12D) and one slow evolving mitochondrial gene (12S). Our analyses revealed strong phylogeographic structure among lineages and, in most cases, no signal of demographic changes through time. The *lineomaculatus* group is composed of three strongly supported clades (*lineomaculatus*, *hatcheri* and *kolengh* + *silvanae*), and divergence estimates suggested their origins associated with the oldest known Patagonian glaciation (7–5 Ma); subsequent diversification within the *lineomaculatus* clade coincided with the large Pliocene glaciations (~3.5 Ma). The *lineomaculatus* clade includes nine strongly genetically and geographically structured lineages, five of which are interpreted as candidate species. Our findings suggest that some *Liolaemus* lineages have persisted *in situ*, each of them in a different refugium, through several glaciation–deglaciation cycles without demographic fluctuations. We also summarize and update qualitative evidence of some shared phylogeographic breaks and refugia among plants, rodents and lizards.

**Keywords:** biogeography, Liolaemidae, nuclear and mitochondrial genes, Patagonia, refugia

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## Introduction

The Patagonian region of southern South America became a large arid landscape during the Miocene (23.8

–5.3 Ma), after the elevation of the Andes blocked moisture-bearing air masses coming from the Pacific (Compagnucci 2011). Miocene subtropical savannas were replaced by today's arid steppes, and ancient forests retreated to the Andean slopes before and during the aridification (Rabassa 2008; Tambussi 2011). The oldest known Patagonian glaciation took place ~7–5 million

Correspondence: Mariana Morando, Fax: +(54) (280) 4451543; E-mail: morando@cenpat.edu.ar

years ago (Ma) during the Middle Pliocene and was followed by large Late Pliocene glaciations ~3.5 Ma (Rabassa *et al.* 2005). The Pleistocene (1.8–0.01 Ma) was characterized by a temperature decrease of 6–7 degrees relative to the present (Markgraf *et al.* 1995; Moreno 1997; Hulton *et al.* 2002), during which several glaciation–deglaciation cycles are identified. These include the Great Patagonian Glaciation (~1.68–1.016 Ma), the Coldest Pleistocene Glaciation (~0.7 Ma), the Last Southern Patagonian Glaciation (~0.180–0.140 Ma) and the Last Glacial Maximum (LGM, ~0.025–0.016 Ma) (Rabassa *et al.* 2005). During glacial advances, the Patagonian coastline shifted east about four degrees, and much of the original extra-Andean landscape cooled to form permafrost (frozen soil for most of the year, except for short periods when surface ice may be absent; Trombotto 2000). These sea level shifts and the *in situ* formation of periglacial refugia (first proposed by Premoli 1998; and summarized in S ersic *et al.* 2011) exposed suitable habitats for organisms to shift distributions to more equitable climates (Hulton *et al.* 2002; Jakob *et al.* 2009; Fontanella *et al.* 2012a).

Past environmental changes in Patagonia have modified ecosystems (Rabassa *et al.* 2005) and species distributions, while population contractions–recovery dynamics, with concordant range contractions and expansions, and the formation of secondary contact areas, have shaped today's phylogeographic patterns (S ersic *et al.* 2011). Potential refugia can be identified by a genetic signature of allopatric fragmentation, high species and genetic diversity and distinct genetic structure, while recently colonized areas show a signature of range expansion and sometimes secondary contact and hybridization (e.g. Zemlak *et al.* 2008; Tremetsberger *et al.* 2009; Cosacov *et al.* 2010; Nicolas *et al.* 2011; Olave *et al.* 2011).

S ersic *et al.* (2011) summarized the literature on phylogeographic patterns of terrestrial vertebrates and plants from Patagonia (Argentina and Chile) and synthesized available information on glacial refugia, phylogeographic breaks, range expansions and colonization routes. In southern Patagonia (mainly Santa Cruz province), eight refugia and seven phylogeographic breaks have been proposed based on plant studies (e.g. Premoli 1998; Muellner *et al.* 2005; Jakob *et al.* 2009; Tremetsberger *et al.* 2009; Cosacov *et al.* 2010; Mathiasen & Premoli 2010), whereas only two phylogeographic breaks were proposed for terrestrial vertebrates. The small number of published terrestrial vertebrate studies have been based exclusively on rodents (summarized in Pardi nas *et al.* 2011), but population sampling has been sparse and restricted mainly to mountain habitats. Several lizard phylogenetic/phylogeographic studies (all based on various clades of *Liolaemus*) have been

conducted in northern Patagonia and Chile (e.g. Morando *et al.* 2003, 2004, 2007; Avila *et al.* 2006; Victoriano *et al.* 2008), and these studies have recovered signals of both demographic expansion and stability.

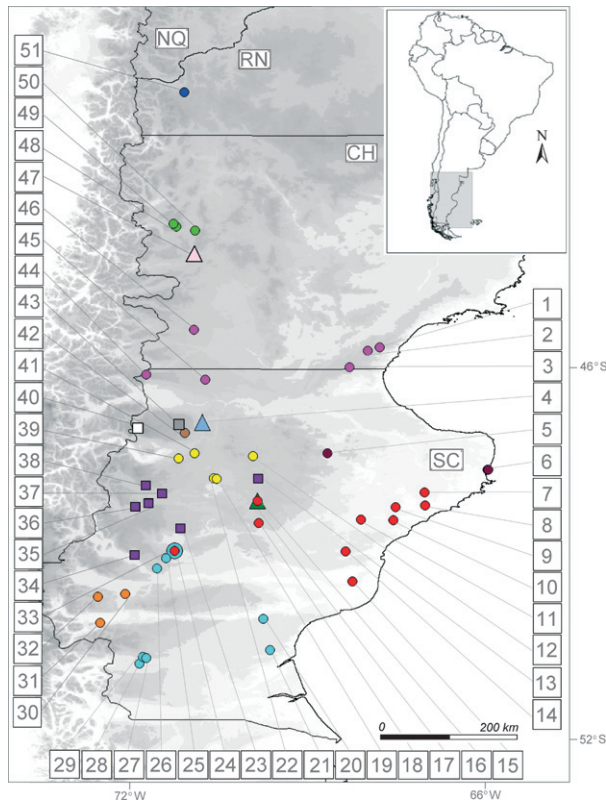
Lizards from the *Liolaemus lineomaculatus* group (Etheridge 1995; Squamata: Liolaemidae) provide an excellent model to test the phylogeographic hypotheses proposed for plants and rodents because of its widespread distribution throughout southern Patagonia. The *lineomaculatus* group was thought to include four species (*L. lineomaculatus*, *L. silvanae*, *L. hatcheri* and *L. kolengh*), but a recent molecular phylogenetic study (Breitman *et al.* 2011a) resolved three genetically distinct lineages within the species *L. lineomaculatus*, two of which were recently described as new species (*L. avilae* and *L. morandae*; Breitman *et al.* 2011b). While *L. lineomaculatus*, *L. avilae* and *L. morandae* are distributed throughout most of southern Patagonia, *L. kolengh* and *L. silvanae* are endemic to Lago Buenos Aires Plateau, and *L. hatcheri* is confined to high elevation areas of Asador Plateau in northwestern Santa Cruz (Cei 1986; Etheridge 1998; Christie 2002; Abdala & Lobo 2006).

Our specific goals here are to: (i) provide a well-resolved, time-calibrated phylogenetic/phylogeographic hypothesis for the *lineomaculatus* group and to assess clade and lineage origins within the historical Miocene–Pleistocene events of southern Patagonia; and (ii) qualitatively evaluate geographic concordance of refugia and phylogeographic breaks inferred from these lizards, with those proposed for plants and rodents in the same region. Because both phylogeography and species delimitation are integrative and iterative fields of study (Buckley 2009; Padi al *et al.* 2010), this research will contribute to a foundation upon which future studies, based on additional data for these lizards and studies of codistributed species, will further clarify phylogenetic and speciation histories in this region.

## Materials and methods

### Sampling design

A total of 278 specimens of the *lineomaculatus* group were collected (*Liolaemus lineomaculatus*  $n = 109$ , *L. kolengh*  $n = 51$ , *L. hatcheri*  $n = 73$ , *L. avilae*  $n = 9$ , *L. morandae*  $n = 15$  and *L. silvanae*  $n = 21$ ) from 51 localities. Samples were collected across most of the distribution area of the group, from the R o Negro, Chubut and Santa Cruz Provinces (Fig. 1; Table 1). *Liolaemus kingii*, *L. boulengeri*, *L. darwinii*, *L. bibronii*, *L. gracilis*, *L. petrophilus* and *Phymaturus dorsimaculatus* were used as outgroups (Table 1). Voucher specimens were catalogued in the herpetological collections of La Plata Museum, Argentina (MLP.S) and Centro Nacional Patag nico in



**Fig. 1** Map of southern Patagonia showing sampled localities. Each colour represents a lineage recovered in the Bayesian tree. Circles and triangles represent the distribution of the *lineomaculatus* clade; squares represent the distribution of the *hatcheri* and *kolenghi + silvanae* clades. Circles (red: lineage 1; dark red: lineage 2 [*Liolaemus lineomaculatus* type locality]; light blue: lineage 3; orange: lineage 4; brown: lineage 5 [*L. avilae*]; yellow: lineage 6; pink: lineage 7 [*L. morandae*]; light green: lineage 8; blue: lineage 9); triangles (blue: singleton 6514; light pink: singleton 9093; green: singleton 9545); squares (grey: *L. silvanae*; white: *L. kolenghi*; dark purple: *L. hatcheri*). Province names: Neuquén (NQ), Río Negro (RN), Chubut (CH) and Santa Cruz (SC).

Puerto Madryn, Argentina (LJAMM-CNP). From this total sample, 196 individuals were used for molecular analyses.

#### DNA extraction, amplification and sequencing

Genomic DNA was extracted using the Qiagen<sup>®</sup> DNeasy<sup>®</sup> 96 Tissue Kit, following the protocol provided by the manufacturer. Two mitochondrial (12S and *cyt-b*; Kocher *et al.* 1989; Wiens *et al.* 2010; respectively) and one nuclear fragment (LDA12D, Camargo *et al.* 2012; the most informative selected from a screening of 36 genes; Appendix S1, Supporting information) were amplified following the PCR and sequencing protocols for mitochondrial and nuclear fragments described by Morando *et al.* (2003, 2004) and Noonan & Yoder (2009),

respectively. The cytochrome *b* fragment was sequenced for 196 samples of the *lineomaculatus* group (3.76 per locality and 16 per lineage, on average) and several outgroups, the sequences were used to construct Bayesian and maximum-likelihood (ML) trees (Appendix S2, Supporting information; see 'Phylogenetic relationships and clade/lineage identity' below). To represent most of the *cyt-b* variation, and following the sampling design proposed by Morando *et al.* (2003), two to four individuals from each lineage recovered in the Bayesian *cyt-b* tree were selected for further amplification of 12S ( $n = 45$ ) and LDA12D ( $n = 39$ ) fragments.

Sequences were edited using SEQUENCHER v4.8. (™Gene Codes Corporation Inc. 2007) and checked by eye to maximize blocks of sequence identity. Alignments were performed with MAFFT (Kato *et al.* 2002). Seven indels were identified in the 12S data set (five of one bp and two of two bp in length), and eight indels were identified in the LDA12D data set (three of one bp, three of two bp, one of three to five bp, and one of 18 bp in length). The *cyt-b* open reading frame was confirmed by translation into amino acids; all sequences and alignments are deposited in GenBank and in Dryad, respectively (GenBank accession nos. JX522219–JX522456; Dryad doi:10.5061/dryad.n5d5t). Nuclear gene recombination was tested using RDP v3.44 (Martin & Rybicki 2000; Heath *et al.* 2006). Cytochrome *b* was used in all the analyses described later, while LDA12D and 12S fragments were used to generate a concatenated alignment for Bayesian and Likelihood analyses, to compare tree topologies across genes and to estimate divergence time with a fossil calibration; the nuclear gene was also used to construct a haplotype network.

#### Phylogenetic relationships and clade/lineage identity

We used the word 'lineage' to identify species or candidate species (see Discussion) that are well-supported clades that include several 'haplogroups'; haplogroups are composed of one or several individuals from one or more localities. To identify clades/lineages and relationships within the focal group, we first identified *cyt-b* haplotypes with COLLAPSE v1.2 (Posada 2004) and performed separate Bayesian and ML analyses for each gene (12S, LDA12D and *cyt-b* haplotypes), for the mitochondrial gene data set (*cyt-b*+12S) and for the nuclear and mitochondrial genes. The best-fit evolutionary model for each gene (*cyt-b*: TrN+I+G; 12S: TiM3+G; LDA12D: HKY) was selected using the corrected Akaike information criterion in JMODELTEST v0.1.1 (Posada 2008). We are aware that gene trees may not recover the same topology as species tree (Maddison & Knowles 2006), but we do not evaluate species trees here due to our limited nuclear data (one locus). Bayesian analyses were

**Table 1** Species with locality numbers and sample sizes used for this study, all the individuals are catalogued in the Centro Nacional Patagónico collection (LJAMM-CNP), except for 2626 and 2627 that are catalogued in the La Plata National Museum (MLP.S)

Species	N <sub>Loc</sub>	Network	Mr Bayes	SAMOYA	Final name	No. of LJAMM-CNP/MLP.S	South	West	N <sub>Ind</sub>	N <sub>seq</sub>	N <sub>hap</sub>
<i>Liolaemus lineomaculatus</i>	7	-	-	-	Lineage 1	9953	-48.10261	-66.92003	1	0	-
	8	1	1	G1	Lineage 1	9847	-48.32656	-66.91108	1	1	1
	9	-	-	-	Lineage 1	9971, 9972	-48.36169	-67.42189	2	0	-
	10	1	1	G1	Lineage 1	9731, 9732	-48.58522	-67.45922	2	2	1
	11	1	1	G1	Lineage 1	10054-10055	-48.57561	-68.01233	2	2	2
	14	1	1	G1	Lineage 1	11435-11436	-49.11914	-68.27594	2	2	2
	15	1	1	G1	Lineage 1	11453-11455	-49.63214	-68.15253	3	2	2
	16	1	1	G1	Lineage 1	9537-9544, 9546-9555	-48.25236	-69.78072	18	13	4
	18	1	1	G1	Lineage 1	9521-9523	-48.62914	-69.7615	3	3	1
	33	1	1	G1	Lineage 1	9438	-49.104	-71.1985	1	1	1
	5	2	1	G2	Lineage 2 (lineo LT)	10122	-47.43475	-68.58308	1	1	1
	6	2	1	G2	Lineage 2 (lineo LT)	7470-7473, 9750-9756	-47.71697	-65.84108	11	9	6
	20	3	1	G3	Lineage 3	9321-9325	-50.26806	-69.68003	5	3	1
	21	3	1	G3	Lineage 3	11469	-50.80383	-69.56344	1	1	1
	24	3	1	G3	Lineage 3	9318	-49.104	-71.1985	1	1	1
	25	3	1	G3	Lineage 3	7337	-49.23042	-71.34203	1	1	1
	26	3	1	G3	Lineage 3	9398, 9412-9417	-49.41025	-71.49953	7	6	5
	27	3	1	G3	Lineage 3	7227-7228	-50.93989	-71.68433	2	2	2
	28	3	1	G3	Lineage 3	11497	-51.04297	-71.79789	1	1	1
	29	3	1	G3	Lineage 3	7223-7225	-50.92219	-71.73725	3	3	2
	30	4	1	G4	Lineage 4	7254-7256	-49.84778	-72.04083	3	2	2
	31	4	1	G4	Lineage 4	11542	-50.33983	-72.46919	1	1	1
	32	4	1	G4	Lineage 4	11549-11553	-49.89014	-72.50461	5	5	4
	42	5	3	G5	Lineage 5 ( <i>L. avilae</i> )	9250-9253, 9274, 9276, 9277, 9399, 2627	-47.09139	-71.02025	9	9	7
	12	5	5	G6	Lineage 6	9626	-47.48736	-69.85058	1	1	1
	19	5	5	G6	Lineage 6	11607	-47.87206	-70.47814	1	1	1
	22	5	5	G6	Lineage 6	11600-11604	-47.86492	-70.52508	4	4	4
	39	5	5	G6	Lineage 6	7335, 7360, 7361	-47.52586	-71.12503	3	3	3
	41	5	5	G6	Lineage 6	7416, 7496	-47.43355	-70.85297	2	2	2
	1	6	6	G7	Lin. 7 ( <i>L. morandae</i> )	9677-9680	-45.62872	-67.68433	4	4	3
	2	6	6	G7	Lin. 7 ( <i>L. morandae</i> )	2626, 13020	-45.68628	-67.89719	2	1	1
	3	6	6	G7	Lin. 7 ( <i>L. morandae</i> )	10201-10202	-45.96669	-68.19967	2	2	1
	44	6	6	G7	Lin. 7 ( <i>L. morandae</i> )	9258-9261	-46.09953	-71.68269	4	4	3
	45	6	6	G7	Lin. 7 ( <i>L. morandae</i> )	13060, 13061	-46.18225	-70.66792	2	2	2
	46	6	6	G7	Lin. 7 ( <i>L. morandae</i> )	3998	-45.33375	-70.86828	1	1	1
	48	10	10	G9	Lineage 8	3685, 3687	-43.56217	-71.16703	2	2	2
	49	10	10	G9	Lineage 8	3664	-43.51567	-71.21803	1	1	1
	50	10	10	G9	Lineage 8	9182	-43.62992	-70.84089	1	1	1
	51	9	9	G8	Lineage 9	12934-12938, 14284-14292	-41.26408	-71.02906	14	5	4
	4	Singleton	Singleton	G5	Singleton	6514	-46.91256	-70.72208	1	1	1

Table 1 continued

Species	$N_{Loc}$	Network	Mr Bayes	SAMOVA	Final name	No. of LJAMM-CNP/MLPS	South	West	$N_{ind}$	$N_{seq}$	$N_{hap}$
<i>L. hatcheri</i>	47	Singleton	Singleton	G9	Singleton 9093	9093	-44.03144	-70.85286	1	1	1
	17	5	Singleton	G5	Singleton 9545	9545	-48.25236	-69.78072	1	1	1
	35	7	7	G I	<i>Hatcheri</i> pop. a	11587–11590, 11592–11594	-48.28875	-71.62992	7	5	2
<i>L. kolengk</i>	38	7	7	G I	<i>Hatcheri</i> pop. a	9485–9492, 9498–9506, 10321–10323	-47.99372	-71.68042	20	11	4
	37	7	7	G I	<i>Hatcheri</i> pop. a,b,c	9493–9497	-48.12256	-71.41236	5	5	2
	23	7	7	G II	<i>Hatcheri</i> pop. b	11554–11563	-48.68556	-71.15017	10	10	6
	36	7	7	G II	<i>Hatcheri</i> pop. b	11583–11585	-48.36017	-71.85264	3	3	2
	13	7	7	G III	<i>Hatcheri</i> pop. c	9562–9565	-47.87317	-69.76083	4	4	3
	34	7	7	G IV	<i>Hatcheri</i> pop. d	7263, 7264, 7331, 7497, 9359–9378	-49.18714	-71.8755	24	21	9
	40	8	8		<i>L. kolengk</i>	7276–7291, 7293–7317, 7600–7606, 7836, 7837, 10590	-47.02106	-71.80883	51	13	2
<i>L. silvanae</i>	43	8	8		<i>L. silvanae</i>	9219–9237, 10320	-46.96439	-71.10756	21	16	7
					<i>Kingii + archetoforus</i>	9776	-47.71497	-65.83919	1	1	–
					<i>Montanus</i>	10177, 3610	-46.20961	-68.78733	2	2	–
					<i>Montanus</i>	10392, 10391	-40.34883	-65.04983	2	2	–
					<i>Liolaemus</i>	9897	-47.85033	-66.62216	1	1	–
					<i>Liolaemus</i>	10517	-37.07494	-67.78544	1	1	–
					<i>Liolaemus</i>	11121	-41.08775	-67.89072	1	1	–
					<i>Phymaturus</i>	983	-37.82055	-71.0866	1	1	–
					<i>dorsinaculatus</i>						

$N_{Loc}$  number of locality;  $N_{ind}$  number of individuals collected by site;  $N_{seq}$  number of individuals sequenced for Cyt-*b*;  $N_{hap}$  number of haplotypes per locality. Names in parenthesis represent individuals from type localities (Lineo LT) and the new species described by Breitman *et al.* 2011b (*L. morandae* and *L. avillae*). "Lin." and "pop" mean Lineage and population, respectively. Results of phylogenetic network, SAMOVA analyses and clade identities are shown.



performed in MRBAYES v3.1.2 (Ronquist & Huelsenbeck 2003) using four heated Markov chains (default heating values) sampled at intervals of 1000 generations and run for 50 million generations. The equilibrium samples (after 25% 'burn-in') were used to generate a 50% majority-rule consensus tree, and posterior probabilities ( $Pp$ )  $\geq 0.95$  were considered significant (Huelsenbeck & Ronquist 2001). Likelihood analyses were conducted using RAXML v7.0.4 (Stamatakis 2006), based on 1000 rapid bootstrap analyses for the best ML tree; strong nodal support was inferred for bootstrap values  $\geq 70$  (Hillis & Bull 1993; with caveats).

We used statistical parsimony to construct networks of the *cyt-b* and LDA12D sequences (Templeton *et al.* 1992) using TCS v1.21 (Clement *et al.* 2000) with the default connection significance (95%), and we qualitatively compared haplotype distributions between markers.

Lastly, using the *cyt-b* data set, we searched for genetically homogenous groups of populations (K) that were maximally differentiated from other groups using SAMOVA v1.0 (Dupanloup *et al.* 2002). Two independent runs were performed for the *lineomaculatus* and *hatcheri* clades, analyses were performed with 'K' values ranging from 2 to 20 and 2 to 8, respectively; the *kolengh + silvanae* clade was not analysed because samples were collected from only two localities. Analyses were conducted using 5000 independent annealing processes, and the best grouping option was identified based on the highest  $F_{CT}$  score (Dupanloup *et al.* 2002).

#### Genetic differentiation and divergence time analysis

Cytochrome *b* genetic distances between the main lineages were estimated using the Arlequin program (Excoffier *et al.* 2005). Divergence times among main clades and lineages were calculated using BEAST v1.6.1 (Drummond & Rambaut 2007) and likelihood ratio tests (LRT) were performed using JModeltest to assess deviation from a strict molecular clock. The importance of calibrations in molecular dating is considered essential (Inoue *et al.* 2010; Parham *et al.* 2012), and calibration points are very informative when fossil data are placed close to the root of the focal taxa (Drummond *et al.* 2006). For *Liolaemus*, there is one recently available fossil [lizard dentary bones; MPEF 1442 and MLP 90-II-13-47, Museo Paleontológico Egidio Feruglio (MPEF), Museo de La Plata (MLP), both in Argentina], the taxonomic status of the fossil was identified as a *Liolaemus* on the basis of the following characters: open Meckel channel, extended splenial, the absence of posterior extension of dentary and tricuspid teeth (Albino 2008). The presence of remains of the genus *Liolaemus* from the Early Miocene of Gaiman (Sarmiento Formation, Chubut,

Argentina) suggests a minimum age of ~20 to 18.5 Ma (Albino 2008) for the genus, according to the calibration of the Colhuehuapian Age proposed by Madden (2004). We therefore performed divergence dating analyses using this fossil calibration point and all gene sequences (Appendix S3, Supporting information).

A data set, including the three gene sequences for one to four individuals from each mitochondrial lineage and the above-mentioned outgroups, was utilized to perform the divergence time analyses (Appendix S3, Supporting information). This analysis was run using a relaxed uncorrelated lognormal clock model (*cyt-b* data do not conform to the strict molecular clock, LRT = 66.780625,  $P < 0.015$ ), implemented in BEAST v1.6.2 (Drummond & Rambaut 2007; Ho & Phillips 2009). The fossil information was placed on the node representing the most recent common ancestor of the two *Liolaemus* subgenera ('Tmrca *Liolaemus*') with the prior set to a lognormal distribution (mean: 1, standard deviation: 1.5, offset 18.5; Ho 2007). Two independent analyses were performed for 200 million generations and sampled every 1000 generations, with a GTR+G evolutionary model for the mitochondrial genes and a HKY model for the nuclear gene (selected by jModeltest), and assuming a Yule tree prior. Trees were summarized (discarding 10% as burn-in) using TREEANNOTATOR v1.6.1 (Drummond & Rambaut 2007). Convergence of estimated parameters was verified when effective sample sizes (ESS) were  $>150$ , using TRACER v1.5.0 (Rambaut & Drummond 2009).

Dating the divergence times for the clades and lineages allowed us to hypothesize past phylogeographic histories in a temporal context (McCormack *et al.* 2010), and while these types of inferences are important, we recognize the limitations of our approach (e.g. Graur & Martin 2004) and interpret our results cautiously as specific hypotheses for further testing.

#### Genetic signature of past demographic histories

To characterize past demographic events for the clades and lineages recovered in our analyses, summary statistics were calculated as follows using the *cyt-b* data set. We calculated standard molecular diversity indices (number of haplotypes:  $h$ ; number of segregating sites:  $S$ ; average number of differences between two random sequences:  $k$ ; haplotype diversity:  $Hd$ ; and nucleotide diversity:  $\pi$ ) using DNASP v5.0 (Librado & Rozas 2009). Tajima's  $D$  and Fu's  $F_s$  (Tajima 1989; Fu 1997) are classical neutrality tests used to assess population demographic history, and both assume that populations have been in mutation-drift balance for a long period of time (Nei & Kumar 2000); when this is not the case due to sudden expansion, these indices usually have negative

values (although they do not provide information about the shape of the change). The  $R_2$  test is considered a sensitive indicator for detecting demographic growth using small sample sizes (Ramos-Onsins & Rozas 2002). Tajima's  $D$ , Fu's  $F_s$  and  $R_2$  were calculated and the significance of these values was examined using 5000 samples simulated under a coalescent algorithm in DnaSP.

Date and shape of past lineage dynamics were estimated using Bayesian Skyline Plots (BSLP) (Drummond *et al.* 2005). Separate analyses were run using the HKY model (selected with JModeltest), with an uncorrelated relaxed clock (Drummond *et al.* 2006), and a mutation rate of 0.0223 substitutions per lineage per site per million years (Fontanella *et al.* 2012b), using BEAST. The number of groups ( $k$ ) that the program required to run was chosen based on the number of samples ( $n$ ) and taking into account that ' $k$ ' could not be higher than  $n$  (thus when  $n = 4-5$ ,  $k = 2-3$ ;  $n = 8-29$ ,  $k = 5$ ;  $n = 59$ ,  $k = 10$ ; Heled & Drummond 2008); Metropolis Coupling of Markov chains simulations were run with 30 million iterations twice for each lineage. Genealogies and model parameters were sampled every 1000 iterations, and after 10% burn-in, results were combined in LogCombiner and summarized results as BSLP after verifying convergence in Tracer, where all parameters had ESS values  $>200$ . Even though BSLP are widely used and seem to perform accurately (Minin *et al.* 2008; Ho & Shapiro 2011), choosing an excessive number of groups ( $k$ ) can increase the error estimation (Heled & Drummond 2008). Bayesian skyride methods (Minin *et al.* 2008) were developed to provide an alternative model of demographic history with fewer parameters assuming that demographic sizes changed gradually over time (Ho & Shapiro 2011). Few empirical studies have used both methods together, and we generated Bayesian skyride plots (BSRP) using the same data and settings described previously. Our use of both methods permits assessment of the influence of different assumptions on the results of these analyses.

## Results

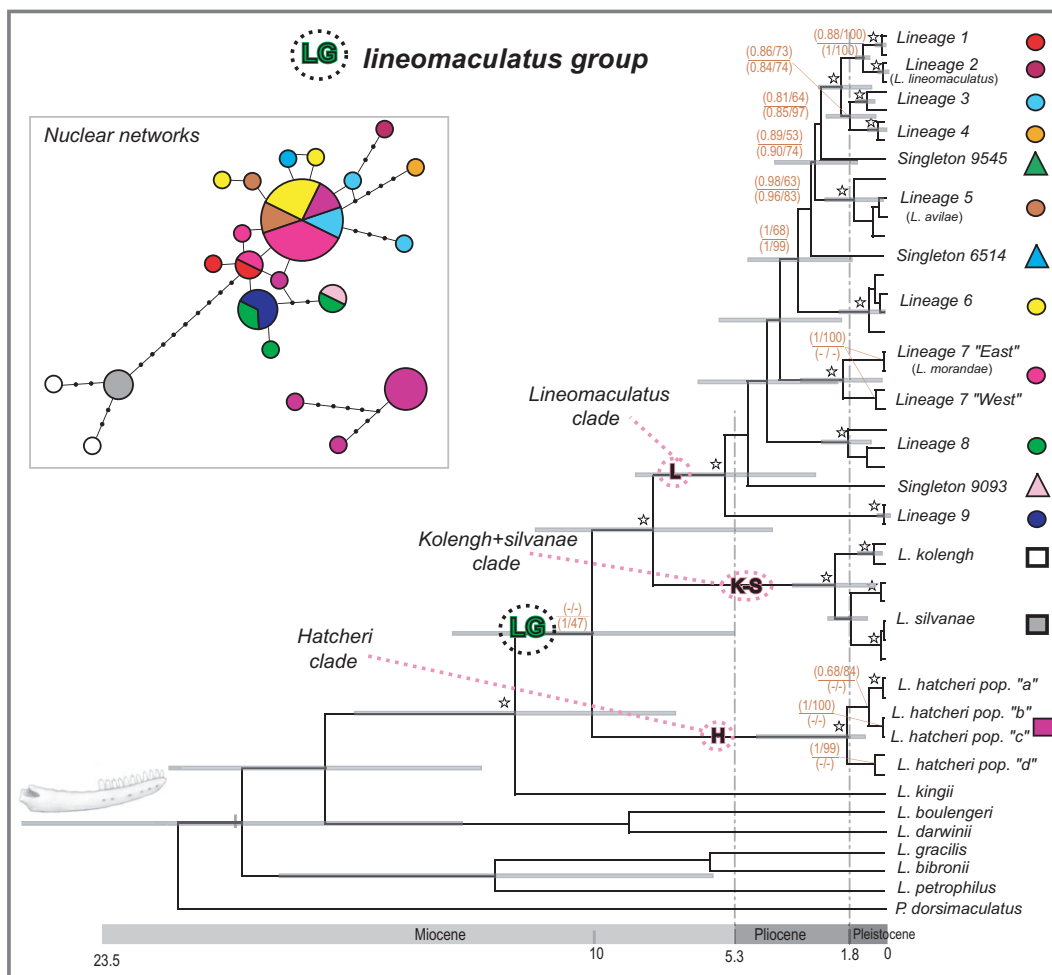
### *Phylogenetic relationships and clade/lineage identity*

Three genes were amplified for this study: *cyt-b* (length: 659 bp; 180 informative sites), 12S (length: 771 bp; 91 informative sites) and LDA12D (length: 627 bp; 40 informative sites). A total of 112 haplotypes were recovered from our original *cyt-b* matrix ( $n = 196$ ). Gene trees recovered from both mitochondrial gene regions separately and combined were topologically concordant across phylogenetic analyses with no well-supported conflict, except for the position of two samples in the

nuclear tree when compared with the mitochondrial tree (see following paragraph). Relationships recovered using the concatenated matrix of the nuclear plus mitochondrial markers were similar to those recovered in the mitochondrial gene tree (see support values in Fig. 2). Three clades were recovered within the *lineomaculatus* group (Fig. 2): *lineomaculatus*, *kolengh + silvanae* and *hatcheri*, all with high support ( $P_p > 0.95$ ; ML bootstrap  $\geq 70$ ), but with poor resolution for the phylogenetic position of *L. hatcheri* (only Bayesian posterior probability for the nuclear plus mitochondrial genes was significant). The *lineomaculatus* clade includes nine lineages: one lineage represents the type locality of the species [lineage 2], two are referred to *L. avilae* [lineage 5] and *L. morandae* [lineage 7] in the study described by Breitman *et al.* (2011b), and three lineages are each comprised of singletons (Fig. 2, Table 1). The lineages divergence order within the *lineomaculatus* clade is recovered in a pectinate topology with the northernmost (lineage 9) sister to all others, which form successively more southern-derived lineages. Lineages 3 and 4 were the most southerly distributed ones and were recovered in a sister relationship to clade (lineage 1 + lineage 2), which are the most easterly distributed in Santa Cruz province.

Recombination was excluded for the nuclear gene (LDA12D), whose tree (not shown) recovered some concordant patterns relative to the mitochondrial tree (similar results between Bayesian and ML analysis): three well-supported clades were recovered in a tricotomy representing the *kolengh + silvanae* clade, the *lineomaculatus* clade and the *hatcheri* clade; although two individuals of *L. hatcheri* (9562 from locality 13 and 7264 from locality 34) were recovered interdigitated in the *lineomaculatus* clade, this could be caused by incomplete lineage sorting or introgression. Nested in the *lineomaculatus* clade we also recovered a monophyletic group formed by the individuals with the northernmost distribution (lineage 9 + lineage 8 + singleton 9093).

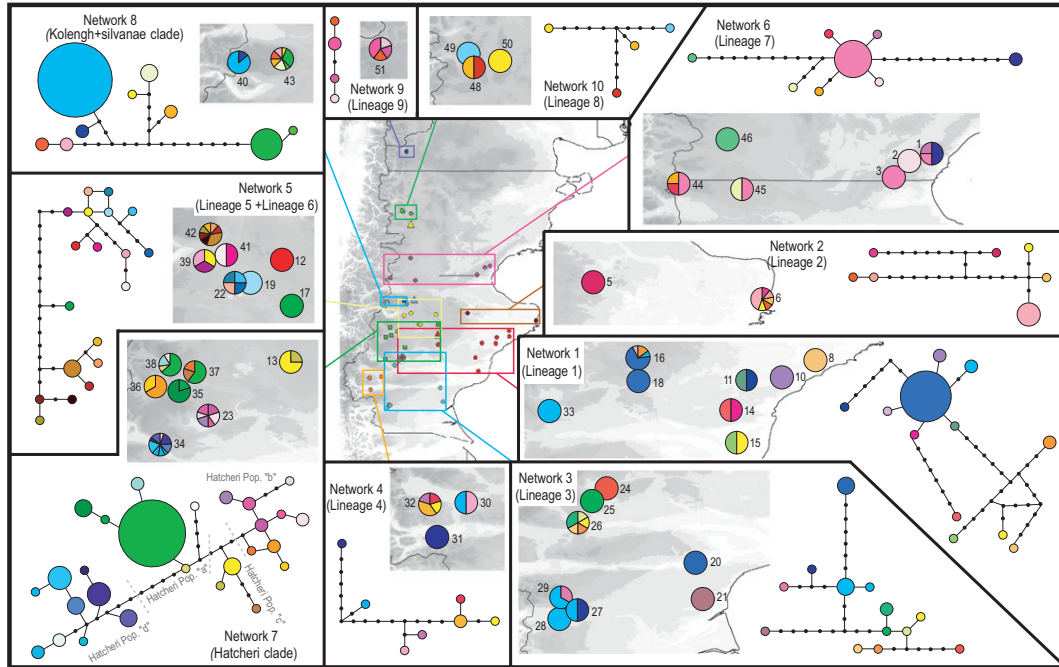
Network analysis performed on the *cyt-b* data set recovered ten different networks and two singletons (Fig. 3; Table 1) within the *lineomaculatus* group. Networks were concordant with the lineages recovered in the mitochondrial tree, with the exception of network 5 in which lineages 3 and 5 were connected by singleton 9545. Networks showed evidence of strong genetic structure, including no star-like connections, several haplotypes connected by more than 1–2 steps, high number of different haplotypes per locality; six localities (6, 23, 26, 34, 42 and 43) were characterized by more than five haplotypes. tcs analysis performed on the nuclear gene recovered two networks (Fig. 2); a small one composed of almost all the individuals from



**Fig. 2** Mitochondrial gene tree and nuclear allele network for the *Liolaemus lineomaculatus* group (colour codes as in Fig. 1). Support values calculated from Bayesian and Maximum Likelihood methods for the mitochondrial genes (above line), and nuclear plus mitochondrial genes (below line) are presented when significant; stars represent nodes with significant posterior probabilities and ML bootstrap values for all mitochondrial genes, and nuclear plus mitochondrial genes. Diversification times are shown in the bottom of the figure based on fossil calibration; grey bars on the nodes represent 95% highest prior density estimates for the divergence dates. Nuclear allele network for individuals of main clades and lineages for the LDA12D gene, haplotypes are colour coded as in Fig. 1.

the *hatcheri* clade, and a bigger network composed of all the individuals from the *lineomaculatus* group, the *kolengh + silvanae* clade and two individuals from the *hatcheri* clade. In the big network, individuals from the *kolengh + silvanae* clade were recovered in a group highly differentiated from the rest of the individuals; a close relationship among individuals of the northernmost clade of the *lineomaculatus* clade (lineage 8, 9 and singleton 9093) was recovered, as was a close relationship among individuals from lineages 2, 3 and 4. Finally, a highly differentiated haplotype was identified from the southernmost lineage of the *lineomaculatus* clade (individual 7223, from locality 29). Two haplotypes (individual 7264 'locality 34' and individual 9562 'locality 13') belonging to the *hatcheri* clade were recovered mixed among haplotypes of the *lineomaculatus* clade.

Results for the SAMOVA analyses recovered nine lineages within the *lineomaculatus* clade and four haplogroups within the *hatcheri* clade (Appendix S4, Supporting information, Table 1). Genetic structure was high among these clades (AMOVA, permutation test  $P < 0.00001$ ), most of the variation was partitioned among groups (78.27% and 69.51% in the *lineomaculatus* and *hatcheri* groups, respectively), and a small portion of variance was contained among-populations within groups (10.55%, 7.61%) or within populations (11.18%, 22.89%; Appendix S4, Supporting information). Using SAMOVA, four haplogroups were identified in the *hatcheri* clade (I, II, III and IV) and all the samples belonging to locality 37 were recovered in *hatcheri* 'I' haplogroup. In contrast, *cyt-b* phylogenetic tree reconstruction did not recover members of this locality in a clade; in other



**Fig. 3** Geographical distribution and network relationships for the 112 *cyt-b* haplotypes. Singletons are not shown. Haplotypes are shown in circles in which sizes correspond to their frequencies in the total sample. Colours in the pie charts correspond to frequencies of different haplotypes in population samples identified by number.

words, except for individuals of locality 37, similar grouping patterns were found between *SAMOVA* and the *cyt-b* phylogenetic reconstruction. This was not surprising because *SAMOVA* groups populations (defined as group of individuals from one locality) and not individuals as phylogeny and network reconstructions do (Dupanloup *et al.* 2002). Thus, following the phylogenetic results, we assigned individuals of locality 37 to each *hatcheri* population according to the mitochondrial tree (individual 9493 belonging to *hatcheri* population 'b', 9494 to *hatcheri* population 'c' and 9495–97 to *hatcheri* population 'a'; Appendix S2, Supporting information, Table 1, Fig. 3).

For the *lineomaculatus* clade, *SAMOVA* grouping was concordant with network analysis for all lineages except for lineages 5 and 6, which were recovered in one network (Figs. 2 and 3, Table 1); two singletons were recovered within Group 5, and singleton 9093 was recovered within Group 9 (Appendix S4, Supporting information, Table 1).

#### Genetic differentiation and divergence time analyses

Most of the pairwise genetic distances within each lineage were small. Distances among main lineages of the *lineomaculatus* clade were much higher than 3%, except for distances between lineages 1 vs. 2 (2.28%) and 5 vs. 6 (2.88%). Distances within *hatcheri* and *kolengh + silvanae* clades were  $\sim$ 2% (mean = 1.47,

min = 1.05, max = 2.01) (Appendix S5, Supporting information).

Divergence times estimated from the fossil calibration between main clades were inferred to be in the Miocene, the divergence between *hatcheri* and (*kolengh + silvanae*) clade was  $\sim$ 9.98 Ma [95% HPD = 5.78–14.49], while divergence between the *kolengh + silvanae* clade and *lineomaculatus* clade occurred  $\sim$ 8.13 Ma [95% HPD = 4.64–12.25]. Splits among most of the lineages of the *lineomaculatus* clade and within *hatcheri* and *kolengh + silvanae* clades occurred during the Late Pliocene; lineages 1 and 2 (within the *lineomaculatus* clade) diverged during the Pleistocene  $\sim$ 1.33 Ma [95% HPD = 0.43–2.47] (Fig. 2; Appendix S3, Supporting information).

#### Genetic signature of past demographic histories

We found high haplotype diversity (except for the *kolengh* clade, Table 2) and intermediate to low nucleotide diversity in all lineages. The lowest values of nucleotide diversity were found in lineage 5 and 6 (0.005, 0.007, respectively), *L. kolengh* (0.0001), and *hatcheri* populations a, b, c and d (0.002, 0.001, 0.002 and 0.005, respectively). Neutrality tests were significant only for lineage 1 ( $n = 26$ ;  $R_2 = 0.07$ ,  $P = 0.02$ ), lineage 6 ( $n = 11$ ;  $R_2 = 0.10$ ,  $P = 0.03$ ;  $Fu's F_s = -7.40$ ,  $P = 0.0004$ ), lineage 7 ( $n = 14$ ;  $R_2 = 0.09$ ,  $P = 0.03$ ) and lineage 8 ( $n = 4$ ;  $R_2 = 0.07$ ,  $P = 0.01$ ; although sample size was low).

Table 2 Standard molecular diversity indices values

	N	S	h <sub>t</sub>	k	Hd	$\pi \pm$ SD of $\pi$	D (95% C.I.)	P D coal	R <sub>2</sub> (95% C.I.)	P R <sub>2</sub> coal	Fu's F <sub>s</sub> (95% C.I.)	P Fu's F <sub>s</sub> coal
Lineage 1	26	33	12	5.3	0.78	0.008 ± 0.0017	-1.43 (-1.72 to 1.81)	0.057	<b>0.07 (0.07-0.19)</b>	<b>0.02</b>	-1.21 (-4.80 to 5.67)	0.31
Lineage 2	10	27	7	8.9	0.86	0.013 ± 0.0026	-0.29 (-1.73 to 1.67)	0.4	0.14 (-1.70 to 1.64)	0.4	0.61 (-3.80 to 4.71)	0.59
Lineage 3	18	33	13	8.4	0.95	0.012 ± 0.0012	-0.49 (-1.66 to 1.66)	0.33	0.11 (0.08-0.19)	0.25	-2.24 (-4.88 to 5.41)	0.15
Lineage 4	8	22	7	7.8	0.96	0.011 ± 0.0025	-0.40 (-1.62 to 1.61)	0.36	0.13 (0.10-0.26)	0.12	-0.93 (-3.02 to 4.54)	0.24
Lineage 5	9	10	7	3.6	0.91	0.005 ± 0.0010	-0.05 (-1.84 to 1.74)	0.5	0.13 (0.10-0.25)	0.12	-2.02 (-3.97 to 4.26)	0.09
Lineage 6	11	17	11	4.6	1	0.007 ± 0.0011	-0.91 (-1.75 to 1.69)	0.19	<b>0.10 (0.09-0.233)</b>	<b>0.03</b>	<b>-7.40 (-4.23 to 4.69)</b>	<b>0.0004</b>
Lineage 7	14	25	8	5.5	0.82	0.008 ± 0.0023	-1.26 (-1.77 to 1.65)	0.09	<b>0.09 (0.09-0.21)</b>	<b>0.03</b>	-0.15 (-4.44 to 4.73)	0.46
Lineage 8	4	16	4	8	1	0.012 ± 0.0024	-0.84 (-0.84 to 2.07)	0.07	<b>0.07 (0.09-0.43)</b>	<b>0.01</b>	0.06 (0.06-5.09)	0.13
Lineage 9	5	4	4	2	0.9	0.003 ± 0.0007	0.27 (-1.09 to 1.64)	0.68	0.19 (0.14-0.4)	0.12	-1.01 (-3.30 to 3.022)	0.33
kol + silv clade	29	27	9	8.2	0.82	0.012 ± 0.0010	0.73 (-1.75 to 1.79)	0.8	0.15 (0.06-1.18)	0.84	3.36 (-5.78 to 6.0)	0.9
<i>L. kolentgh</i>	13	3	2	0.7	0.26	0.001 ± 0.0006	-0.49 (-1.67 to 1.96)	0.32	0.13 (0.12-0.25)	0.13	2.03 (-2.28 to 3.64)	0.81
<i>L. silvanuae</i>	16	23	7	8.9	0.86	0.013 ± 0.0008	1.19 (-1.77 to 1.73)	0.91	0.19 (0.08-0.20)	0.92	2.98 (-4.59 to 4.91)	0.9
<i>Hatcheri</i>	59	40	27	8.2	0.95	0.012 ± 0.0004	-0.14 (-1.64 to 1.85)	0.5	0.09 (0.05-0.16)	0.49	-5.59 (-8.19 to 7.27)	0.07
clade												
<i>Hatcheri</i> pop. a	19	9	6	1.6	0.69	0.002 ± 0.0008	-1.20 (-1.74 to 1.91)	0.1	1.13 (0.08-0.23)	0.48	-0.83 (-2.89 to 4.31)	0.29
<i>Hatcheri</i> pop. b	14	10	9	2.5	0.94	0.001 ± 0.0006	-0.75 (-1.79 to 1.85)	0.25	0.12 (0.09-0.22)	0.22	-3.80 (-3.96 to 4.05)	0.029
<i>Hatcheri</i> pop. c	5	4	3	1.6	0.7	0.002 ± 0.0010	-1.09 (-1.09 to 1.64)	0.3	0.29 (0.14-0.4)	0.73	0.27 (-3.30 to 3.02)	0.47
<i>Hatcheri</i> pop. d	21	12	9	3.3	0.9	0.005 ± 0.0004	0.04 (-1.76 to 1.81)	0.57	0.13 (0.07-0.20)	0.54	-1.19 (-4.61 to 4.67)	0.3
<i>lineomaculatus</i>	193	206	112	53	0.98	0.081 ± 0.0007	1.66 (-1.5 to 1.88)	0.96	0.12 (0.04-0.13)	0.96	-12.1 (-19.30 to 18.45)	0.08

N, number of samples; S, number of segregating sites; h<sub>t</sub>, number of haplotypes; k, average number of differences between two random sequences; Hd, haplotype diversity;  $\pi$ , nucleotide diversity and standard deviation.

Tajima's D, R<sub>2</sub> and Fu's F<sub>s</sub> values, confidence intervals and P values are shown. Enlarged and bolded fonts identify the statistically significant results.

Similar results were recovered using BSLP or BSRP, with relatively constant or only slightly different demographic size changes through time (Appendix S6, Supporting information). No strong signals of demographic expansions or declines were recovered; weak signals of demographic expansion were recovered for lineage 6 (0.07 Ma), and expansion (0.15 Ma) followed by a slight demographic decline (0.0125 Ma) was inferred for the *hatcheri* clade (Appendix S6, Supporting information). We are aware that sample size could be an issue here and that more sampling is needed for some lineages, but, our results seem to be robust to sample size differences across lineages. Moreover, despite variable sample sizes among lineages (mean = 16, min = 4, max = 59), no differences were found between BSLP vs BSRP results (when 95% HPD was taken into account), suggesting that both tests perform similarly although, as expected, the BSRP showed smoother curves (Minin *et al.* 2008; Ho & Shapiro 2011).

Because results varied among neutrality tests and Bayesian demographic plots, we conservatively inferred that only lineages 6 and 7 have experienced past demographic changes, because both analyses detected signals of the same directional changes. The *hatcheri* populations presented low nucleotide diversity, little within population pairwise divergence, and BSLP/BSRP showed signals of demographic changes through time (for the *hatcheri* clade). All of these analyses indicated that these populations had experienced past demographic expansions, but as neutrality tests did not show significant signals of demographic changes, we hypothesize past demographic expansions in these populations but with caveats.

## Discussion

### General patterns within the *Liolaemus lineomaculatus* group

Three main clades, whose divergence was inferred to occur during the Miocene, are recovered within the *lineomaculatus* group: *hatcheri*, *kolengh* + *silvanae* and *lineomaculatus* (Fig. 2). The *hatcheri* clade is restricted to the Asador Plateau (Fig. 1, dark purple squares) and is genetically structured into four haplogroups (East, Central, South and West) with low to moderate genetic distances between them (Fig. 3, Appendix S5, Supporting information), these populations may have experienced recent demographic expansions. The *kolengh* + *silvanae* clade includes two nominal species (Fig. 2), both known only from type localities (Fig. 1; localities 40 and 43, respectively) northwest and northeast of the Lago Buenos Aires Plateau. Several morphological differences are diagnostic of both species (Abdala & Lobo 2006), and

our time-calibrations suggest a late Pliocene (~2.26 Ma [95% HPD = 0.61–4.67]) divergence. Moreover, *Liolaemus kolengh* has very low haplotype and nucleotide diversity values, suggesting a very recent speciation event in a lineage that has remained relatively small, possibly under a selective regime that fostered morphological divergence in both species. Lizards of the *lineomaculatus* clade are present throughout the study area except in localities where *L. hatcheri* and *L. kolengh* occur. The *lineomaculatus* clade includes nine lineages with high genetic distances among them (except for lineages 1 and 2), and three of them have been described as different species (*L. lineomaculatus*, *L. avilae* and *L. morandae*). All of these lineages are allopatric except at one locality where individuals from lineages 1 and 3 were collected together (Fig. 1, locs. 24 and 33, respectively; different locality numbers were given to the same area for different lineages).

Most of our analyses were performed using the *cyt-b* gene, and we are aware that the nature of this marker (rapid saturation, matrilineal history) could mislead interpretations. However, a well-resolved mtDNA gene tree is an excellent starting point for phylogeographic investigations, and mtDNA data can be taken as reliable indicators of female geographic population structure and 'first pass' identification of 'candidate' species (Morando *et al.* 2003). The incorporation of multiple unlinked nuclear loci will increase the strength of phylogeographical inferences, but nuclear loci may or may not be concordant with mtDNA patterns, suggesting different evolutionary processes (Zink & Barrowclough 2008). Here, we incorporated one nuclear gene and found that the geographic patterns of variation in LDA12D were largely concordant with the mtDNA results.

### 'Candidate species' within the *lineomaculatus* clade

*Liolaemus* species have been recognized on the basis of morphological differences, but several recent publications have first identified 'candidate species' on the basis of mtDNA divergence (well-sampled and well-supported haploclades that show geographic concordance; Morando *et al.* 2003), which have then been described based on morphological discontinuities (for example see Breitman *et al.* 2011a,b,c). Those studies have used an 'arbitrary' percentage of >3% uncorrected mtDNA divergence to identify 'candidate species' that merit detailed taxonomic study. The use of an 'arbitrary' 3% mtDNA is justified by two features: morphological diagnosability and geographic isolation. From a morphological perspective, the mean sequence divergence between morphologically described sister species within *Liolaemus* is ~3.1% [based on recalculations of

data from Martínez (2012)]. Martínez estimated a mean of 4% *cyt-b* divergence using several sister species pairs of *Liolaemus*, and here, we recalculated this mean excluding the pair *L. somuncurae*–*L. uptoni* because they are not sister species (Breitman *et al.* 2011a), and specifically, within the *L. lineomaculatus* section, the threshold of mtDNA differentiation is 2.23% (recalculated from Martínez 2012). Our adjustments suggest that sister species of *Liolaemus* are in general morphologically diagnosed with an average of ~3% mtDNA divergence. Based on our divergence estimates, 3% mtDNA differentiation requires ~1.5 million years to accumulate.

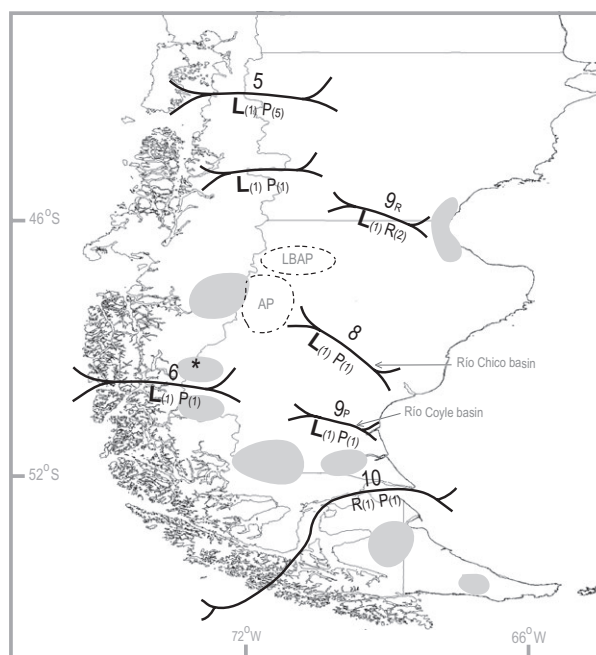
In this study, we find *cyt-b* distances >3% between geographically isolated lineages of the *lineomaculatus* group and hypothesize that these are ‘candidate species’ based on the arguments described in the above paragraph. Specifically, we find the highest values of mtDNA differentiation in lineage 9 (estimated to be the oldest ~6 Ma); this is the northernmost lineage and the most morphologically differentiated (M. F. Breitman, personal observation) from the others, suggesting that it is a well-corroborated candidate species. Lineages 5 and 7 were recently described as new species (*L. avilae* and *L. morandae*, respectively; Breitman *et al.* 2011b), and our evidence suggests that lineages 3, 4, 6 and 8 should be also considered as candidate species for which more integrative studies are needed.

#### *The role of Miocene-to-Pleistocene glaciations in diversification*

The oldest known Patagonian glaciation took place ~7–5 Ma in the late Miocene (Rabassa *et al.* 2005); this event may have promoted the origin of the three main clades of the *lineomaculatus* group. This period was followed by a warming phase, in the Pliocene, during which geodynamic events and climatic fluctuations probably favoured the diversification of many groups (Cosacov *et al.* 2010; Cione *et al.* 2011; Compagnucci 2011), especially *Liolaemus* (Albino 2008, 2011). The Pliocene was a warm period characterized by multiple large glaciations (~3.5 Ma; Rabassa *et al.* 2005), and this timing is correlated with our estimate of the divergence times of lineages 3–9 and within the *kolengh + silvoane* and *hatcheri* clades. Our divergence estimates also suggest a Pleistocene role for the separation of sister lineages (1 + 2). At this time, the Patagonian climate shifted to cooler conditions (Lisiecki & Raymo 2007; Compagnucci 2011), with latitudinal and altitudinal vegetation shifts in response to recurrent glacial oscillations (Quatrocchio *et al.* 2011).

During the full glacial expansions of the Pliocene and Pleistocene, water flows were significantly higher than at the present, and they endured for several thousands

of years. The capacity for erosion and the magnitude of water transported were also increased by lowered sea level; followed by shorter periods called ‘terminations’ representing the abrupt ending of the main glacial events. During these ‘terminations’, large volumes of water were released as a result of the intensive melting of the Cordilleran ice sheets (Martínez & Kutschker 2011). These past events are inferred from depositions of rocks called ‘Rodados Patagónicos’, for which there is extensive evidence along the Río Chico and Río Coig (Río Coyle on some maps) basins in central-south Santa Cruz (Martínez & Coronato 2008; Martínez & Kutschker



**Fig. 4** Phylogeographic breaks and refugia from southern Patagonia, modified and updated from Sérsic *et al.* (2011; Fig. 2), with the addition of lizard data from this study. Phylogeographic breaks (lines), hypothesized refugia (grey areas) and Lago Buenos Aires and Asador plateaus (LBAP and AP dotted lines, respectively) are shown. Breaks and refugia areas inferred for species of the *Liolaemus lineomaculatus* group are shown with ‘L’. Breaks with ‘R’ and ‘P’ correspond to those proposed for rodents and for plants, respectively. The unnumbered break was not proposed in Sérsic *et al.* (2011), and the number of taxa for each break is given in parentheses (names are preserved from Sérsic *et al.* 2011). All refugia shown here were proposed based on plants, one of which is also supported by the lizards studied here (marked with the asterisk). Breaks that are concordant with water courses are: Break 10 following the Magellan strait, Break 9p following the Río Coig Basin and Break 8 following the Río Chico basin; these water courses were strong glaciofluvial rivers during the Pliocene and Pleistocene and have almost certainly been major causes of fragmented habitats and influenced diversification in some animals and plants from Patagonia. Lago Buenos Aires and Asador plateaus are both proposed as refugia based on this study.

2011). The volume and velocity of water in these two basins (breaks 8 and 9<sub>P</sub> in Fig. 4) during the sea level draw down followed by termination events, would provide long periods of time during which both rivers were much larger than today. We hypothesize that fragmented habitats influenced relatively recent patterns of diversification in several groups of southern Patagonia; these include lizards (this study), plants (Mathiasen & Premoli 2010; Sede *et al.* 2012), rodents (Pardiñas *et al.* 2011) and freshwater fishes (Ruzzante *et al.* 2011); see also Sérsic *et al.* (2011) for a summary of patterns.

#### *Shared phylogeographic patterns among codistributed taxa in southern Patagonia*

Relative to northern Patagonia, few phylogeographic studies have focused on southern Patagonian clades. Sérsic *et al.* (2011) summarized all phylogeographic studies of Patagonian plants and terrestrial vertebrates and mapped all proposed phylogeographic breaks and refugia (their Fig. 2). Figure 4 presents an update of a section of the Sérsic *et al.* (2011) map with our results for the *lineomaculatus* group. In Fig. 4, we number these breaks following Sérsic *et al.* (2011) and identify each by taxon: lizards ('L'), rodents ('R') and plants ('P'). In southern Patagonia, two breaks for terrestrial vertebrates (rodents, breaks 9, 10) and five breaks for plants (5, 6, 8, 9, 10) were previously proposed; here, we show that five of these also represent phylogeographic breaks for lizards (5, 6, 8, 9<sub>P</sub>, 9<sub>R</sub>). The number of taxa for which each break is resolved is shown in subscripted parentheses: (1) 9/L<sub>(1)</sub>R<sub>(2)</sub>, at latitude 45°S; (2) 5/L<sub>(1)</sub>P<sub>(5)</sub>, 43°S; (3) 6/L<sub>(1)</sub>P<sub>(1)</sub>, 50°S; (4) 8/L<sub>(1)</sub>P<sub>(1)</sub>, following the Río Chico basin; and (5) 9/L<sub>(1)</sub>P<sub>(1)</sub>, following the Río Coig basin. In this study, we present evidence of a new phylogeographic break at ~47°S (break with no number in Fig. 4) recently proposed for the tree *Nothofagus pumilio* (Mathiasen & Premoli 2010). There is one other proposed phylogeographic break for the Strait of Magellan, 10/R<sub>(1)</sub>P<sub>(1)</sub>, which is not included in the distribution of our focal group (Fig. 4).

Within the *lineomaculatus* clade a north-to-south diversification pattern was recovered, which is concordant with other *Liolaemus* clades, rodents and plants (Morando *et al.* 2003, 2004; Cosacov *et al.* 2010; Lessa *et al.* 2010; reviewed in Sérsic *et al.* 2011). Moreover, only two studies (to our knowledge) have presented divergence estimates for the phylogeographic breaks of southern Patagonian taxa included here, those estimations were made for breaks 8 and 5, by Cosacov *et al.* (2010), for the annual herb *Calceolaria polyrhiza*, and Premoli *et al.* (2012), for trees of the genus *Nothofagus*, respectively. For break 8, Cosacov *et al.* (2010) inferred a divergence time of ~1.16–1.45 Ma; this is slightly

younger than our estimate (~2.48 Ma [95% HPD = 1.1–4.2]) between the lineages (1 + 2) and (3 + 4), which are separated by this same break. Across break 5, our estimates of divergence between lineages 9 and 8 (5.97 Ma [95% HPD = 3.2–9.36]) were again slightly older than the 2.96–4.6 Ma estimates for *Calceolaria* from northern and southern Patagonia (Cosacov *et al.* 2010). However, both of these estimates for break 5 are much younger than the 32 Ma estimated for *Nothofagus* by Premoli *et al.* (2012). This older estimate is in the line with the 'pre-Quaternary' fragmentation and isolation estimated for trees of this region by other authors (Mathiasen & Premoli 2010; Soliani *et al.* 2011). These results suggest that differentiation in *Liolaemus* may have predated differentiation in *Calceolaria*, while differentiation in *Nothofagus* is much older than both.

Despite these differences in timing of divergence, the shared patterns of divergence between the annual plants and lizards suggest the possible presence of 'suture zones' (Remington 1968) in some regions (breaks 5, 6, 8, 9<sub>P</sub>, 9<sub>R</sub>). A suture zone is defined as a cluster of hybrid zones, contact zones or phylogeographic breaks (as extended by Swenson & Howard 2005), which may be associated with present-day physiographic features. Such regions are natural laboratories for the studies of adaptation, divergence and speciation (Moritz *et al.* 2009), and future phylogeographic studies can now focus on dense sampling of multiple taxa in these regions. Future studies, when coupled with GIS tools (either for spatial analyses of genotypes to resolve the 'fine structure' of contact zones, or the inclusion of niche models), and molecular analyses can provide deeper resolution of the spatial components of evolutionary processes (Swenson 2008; Moritz *et al.* 2009).

#### *How lizards survived blizzards? Refugia hypotheses*

New studies have clarified some of the geological and climatic events that have shaped Patagonia and since then several phylogeographic refugia (i.e. *in situ* persistence during Pleistocene glaciations) have been proposed based mainly on plants (Sérsic *et al.* 2011). Studies of several species complexes of *Liolaemus* inhabiting northern Patagonia have revealed signals of demographic expansion and recent colonization (Morando *et al.* 2003, 2004, 2007; Avila *et al.* 2006), particularly in central Chubut and northern Santa Cruz. In contrast, our study recovers signals of genetically structured lineages that have persisted *in situ* in the absence of expansions. Interestingly, Fontanella *et al.* (2012a) working on the northern species *L. petrophilus*, found that the species was structured in two haploclades, one of which had a signature of LGM stability and its sister haploclade showed a signal of demographic expansion.



The Asador Plateau [Fig. 1 (dark purple squares), Fig. 4] has been proposed as a refugium for *in situ* survival of plants and rodents (Cosacov *et al.* 2010; Lessa *et al.* 2010; Mathiasen & Premoli 2010; Sede *et al.* 2012; Villa-Martínez *et al.* 2012); our evidence of the *hatcheri* clade age (3.44 Ma [95% HPD = 1.2–6.5]), combined with a demographically stable genetic signature (high genetic structure, high haplotype diversity) suggests that the survival of a common ancestor may have been possible there. In contrast, a demographic expansion signature within each one of the *hatcheri* populations suggests that population increases may have occurred after diversification (~1.8–2 Ma [95% HPD = 0.52–3.67]). Sampling of additional populations and genes and further studies are needed to understand the evolutionary history of these lizards that inhabit a hypothesized glacial refugium.

The Lago Buenos Aires Plateau (Fig. 4) is inhabited by the *kolengh* + *silvanae* clade, available geological data on this Plateau suggest that it was partially affected by several glacial advances, with the first being dated ~1.3 Ma and followed by at least six glacial advances between 0.0227 and 0.0144 Ma (Rabassa *et al.* 2011). Glaciations were present in this area surrounding the Plateau, the Buenos Aires and the Pueyrredón lakes and their valleys were covered by glaciers and permafrost was present on the plateau; moreover, because the mean annual air temperature of the plateau is below 0 °C, permafrost is nowadays present on several places of the Lago Buenos Aires Plateau (Hubbard *et al.* 2005; Trombotto 2008). The age of this clade and its geographical restriction to this plateau suggest that it may have survived *in situ* through multiple glaciation–deglaciation cycles.

The north–south zone along the eastern flank of the Andes (between 47°S and 51°S) has been identified as a refugial area for plants of the genera *Calceolaria*, *Fitzroya*, *Hypochaeris* and *Nothofagus* (Sérsic *et al.* 2011), but not for terrestrial vertebrates. Our findings (marked with asterisk in Fig. 4) suggest that this area (between Argentino and Viedma lakes) was also a refugium for *in situ* persistence of some populations of the *lineomaculatus* clade. Several terminal moraines were mapped in the valley of the Argentino Lake indicating the occurrence of at least nine glacial advances from the Pliocene to the LGM (Rabassa 2008). Glaciations occurred in the period 2.1–1.0 Ma, in the valleys surrounding the lakes Viedma and Argentino (Rabassa *et al.* 2011).

Finally, we found weak signals of demographic expansion only for lineages 6 and 7 dating to about 0.07 and 0.05 Ma, respectively, between the last southern Patagonian glaciation (0.140–0.180 Ma) and the LGM (~0.025–0.016 Ma; Rabassa *et al.* 2005).

More detailed comparative studies are needed to test these hypotheses, to assess how geological and climatic

events have influenced patterns of diversification observed in other co-distributed taxa, to find the locations of proposed refugia and to estimate the genetic structure and divergence time of each lineage that may have persisted through multiple glacial cycles. In southern Patagonia, several organisms appear to have survived *in situ* through glacial advances; thus, it will not be surprising if future studies find further evidence for shared refugia and phylogeographic breaks.

## Conclusions

This is the first phylogeographic study of lizards from southern Patagonia using nuclear and mitochondrial data in a multispecies framework. We found that geological and climatic conditions affecting Patagonia since the Miocene seems to have strongly influenced the diversification of the *lineomaculatus* group. In contrast with other species of lizards from northern Patagonia, most of the lineages included in this study are genetically and geographically structured and do not show evidence of demographic expansions, suggesting *in situ* survival for several lineages throughout glaciation–deglaciation cycles. If true, these patterns suggest considerable thermoregulatory plasticity in these lizards, because regional environments were dominated mainly by permafrost and arid conditions (Trombotto 2000). Within the *lineomaculatus* clade, some candidate species were identified. We present the first evidence that many of the phylogeographic breaks and refugia previously proposed for plants and rodents in southern Patagonia are also present in lizards, and we predict that wider taxonomic sampling of other terrestrial groups will reinforce these patterns.

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Argentinean M.F.B. holds a CONICET fellowship and is a PhD candidate at Universidad Nacional de Córdoba. This study is part of her dissertation 'Phylogeny, phylogeography and diversification patterns in the *Liolaemus lineomaculatus* section (Iguania: Liolaemini) from austral South America (Patagonia)'. Her research interests include conservation, evolution and characterization of species diversity. The authors of this manuscript are interested in evolution, systematics and conservation of lizard species with special interest in species from Patagonia. (<http://www.cenpat.edu.ar/unidades06.html>) (<http://patagonia.byu.edu/Research/TaxonomicGroups/Lizards.aspx>).

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### Data accessibility

DNA sequences: GenBank accessions numbers (JX522219–JX522456).

DNA alignments and gene trees are on DRYAD (doi:10.5061/dryad.n5d5t).

**Supporting information**

Additional supporting information may be found in the online version of this article.

**Appendix S1** Screened genes.

**Appendix S2** Bayesian *cyt-b* tree for all samples.

**Appendix S3** Divergence time analysis.

**Appendix S4** SAMOVA.

**Appendix S5** Genetic distances.

**Appendix S6** Bayesian Skyline and skyride plots.

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# MOLECULAR ECOLOGY



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**Past and present taxonomy of the *Liolaemus lineomaculatus* section (*Liolaemidae*): is the morphological arrangement hypothesis valid?**

Journal:	<i>Zoological Journal of the Linnean Society</i>
Manuscript ID:	ZOJ-12-2012-1416
Manuscript Type:	Original Article
Keywords:	archeforus, kingii, lineomaculatus and magellanicus groups, Liolaemidae, <i>Liolaemus lineomaculatus</i> section, lizards < Taxa, morphology < Anatomy, Patagonia < Geography, Review, Sexual dimorphism

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3                   1                   **ABSTRACT**  
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6                   2                   Twenty one species of lizards are included in the southernmost clade of South America, the  
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8                   3                   *Liolaemus lineomaculatus* section. There are two hypotheses of species-grouping within this  
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10                  4                  section, one based on morphological similarities and other based on molecular phylogenetic  
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12                  5                  relationships; although discordant, both are in use. The ‘morphological arrangement hypothesis’,  
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14                  6                  which sorts the species of the section in three groups, was proposed ~30 years ago, however, despite  
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16                  7                  taxonomic changes and almost doubling the species diversity of this section since then, the  
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18                  8                  hypothesis has never been tested. Here, we (i) present an updated chronological review of  
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20                  9                  taxonomic changes, species descriptions, morphological groups and genetic clades proposed for the  
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22                  10                 *L. lineomaculatus* section, and (ii) evaluate the accuracy of the ‘morphological arrangement  
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24                  11                 hypothesis’. We show that the traditional practice of classifying eleven of these species in two of  
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26                  12                 the three traditional morphological groups of the section (*kingii* and *archeforus*), which is not  
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28                  13                 supported by molecular data, is also not supported by morphological data, and therefore should be  
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30                  14                 abandoned; we suggest referring to this clade as the *kingii* group. We characterized the  
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32                  15                 *magellanicus* group based on morphology, and extend the previously published morphological  
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34                  16                 characteristics of the *lineomaculatus* group. Finally, we comment on future prospects for studies of  
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36                  17                 sexual dimorphism and its possible ecological implications. This manuscript provides a critical  
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38                  18                 synthesis of our understanding of the morphological and phylogenetic patterns within the *L.*  
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40                  19                 *lineomaculatus* section and presents a useful framework for future tests of taxonomic hypotheses,  
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42                  20                 physiological, behavioral and evolutionary questions within this section.

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50                  22                 **Keywords:** *archeforus*, *kingii*, *lineomaculatus* and *magellanicus* groups; Liolaemidae; *Liolaemus*  
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52                  23                 *lineomaculatus* section; Lizards; Morphology; Patagonia; Review; Sexual dimorphism.  
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## INTRODUCTION

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6 26 Lizards in general are considered model systems for the study of phylogeography and  
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8 27 speciation processes (Camargo, Sinervo & Sites, 2010), and in particular, the genus *Liolaemus* is  
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10 28 emerging as a model system itself. *Liolaemus* has been considered an interesting genus for studies  
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12 29 of conservation (Corbalán *et al.*, 2011), physiology (e.g., Labra, 1998, 2012; Labra & Leonard,  
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14 30 1999; Labra, Pienaar & Hansen, 2009; Ibagüengoytía *et al.*, 2010; Cruz *et al.*, 2011), behavioral  
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16 31 ecology (e.g., Halloy & Laurent, 1988; Labra & Leonard, 1999; Kacoliris, Williams & Molinari,  
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18 32 2010; Kacoliris *et al.*, 2011), comparative anatomy (e.g., Pincheira-Donoso, Tregenza & Hodgson,  
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20 33 2007; Tulli *et al.*, 2007; Tulli, Abdala & Cruz, 2011) and herbivory (e.g., Espinoza, Wiens & Tracy,  
21  
22 34 2004). The genus *Liolaemus*, one of the world's most ecologically diverse and speciose genera of  
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24 35 lizards (Lobo, Espinoza & Quinteros, 2010; Breitman *et al.*, 2011a), is distributed from Perú to  
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26 36 Tierra del Fuego ( $14^{\circ}\pm 30'$  –  $52^{\circ}\pm 30'$ S) and ranges in altitude from sea level to almost 5000 m,  
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28 37 thereby inhabiting many climatic regimes (Etheridge & Espinoza, 2000). The great diversity of  
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30 38 biological traits observed in these lizards is related to the many different habitats that *Liolaemus*  
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32 39 occupy, their reproductive mode (oviparous or ovoviviparous), and diet variation (insectivorous,  
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34 40 herbivorous or omnivorous) (Cei, 1986). Moreover, color patterns are highly variable and colors  
35  
36 41 such as blue, green, red, orange, and yellow are found in multiple species; this color variability  
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38 42 combined with variation in other characters (e.g., body size), makes this genus attractive for  
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40 43 morphological studies (e.g., Abdala, 2007). Sexual dimorphism is present in several species in a  
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42 44 variety of traits, including body size, shape, size of the home range, and/or coloration (Valdecantos  
43  
44 45 & Lobo, 2007; Vanhooydonck *et al.*, 2010; Medina, Avila & Morando, in press); although sexual  
45  
46 46 dimorphism have been reported in *Liolaemus* (Villavicencio *et al.*, 2003; Verrastro, 2004; Vidal *et*  
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48 47 *al.* 2005; Cánovas *et al.*, 2006), it has not been deeply studied yet. The variation in biological  
49  
50 48 attributes present in these lizards has led to many taxonomic rearrangements since *Liolaemus* was  
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52 49 originally described by Wiegmann (1834; see Lobo *et al.*, 2010 for a recent general overview).  
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3 50 In the last decade, the studies of *Liolaemus* have increased dramatically, and the rate of  
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5 51 species descriptions has grown exponentially (Avila *et al.*, 2010; Lobo *et al.*, 2010; Martinez,  
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7 52 2012). To date, the number of *Liolaemus* species exceeds 235 and several new species are described  
8  
9 53 every year. The genus was included in the group Liolaemini under the free rank taxonomy (*sensu*  
10  
11 54 Schulte, Valladares & Larson, 2003), and also included in the family Liolaemidae (*sensu* Frost *et*  
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13 55 *al.*, 2001; reinforced in Townsend *et al.*, 2011) using the traditional rank-based classification. There  
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15 56 is no consensus among researchers about which classification scheme should be the standard, and  
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17 57 both remain in use (Knapp & Gomez-Zlatar, 2006; Lobo *et al.*, 2010); in the present manuscript we  
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19 58 have followed the free rank taxonomy proposed by Schulte and collaborators (Schulte *et al.* 2000,  
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21 59 2003). Two main clades of *Liolaemus* are recognized based on molecular and morphological  
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23 60 evidence: *Liolaemus sensu stricto* or the Chilean group, and *Eulaemus* or the Argentinean group  
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25 61 (Laurent, 1983; Schulte *et al.*, 2000). Genetic analyses suggest that these groups diverged ~19 Mya  
26  
27 62 (million years ago; 95% HPD = 13.5 – 23.82) after the onset of the Andean orogenies (Breitman *et*  
28  
29 63 *al.*, 2011a). Within *Eulaemus*, the well-supported *Liolaemus lineomaculatus* section (Schulte *et al.*,  
30  
31 64 2000) includes 21 species (Breitman *et al.*, 2011a, b, c) and its divergence from the *montanus*  
32  
33 65 section (its sister clade) has been inferred to be ~14.5 Mya (Breitman *et al.*, 2011a; 95% HPD =  
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35 66 10.25 – 18.64).

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40 67 The *Liolaemus lineomaculatus* section (Schulte *et al.*, 2000) is distributed throughout  
41  
42 68 Patagonia and ranges from central Neuquén province south to Tierra del Fuego Island, and includes  
43  
44 69 the southernmost distributed species of the genus (Donoso-Barros & Codoceo, 1962; Donoso-  
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46 70 Barros, 1966; Bottari, 1975; Cei, 1986). As a result, lizards from this section inhabit extremely  
47  
48 71 heterogeneous landscapes that have been directly affected by several glacial cycles since the  
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50 72 Miocene (see Breitman *et al.*, 2011a). Several refugia and phylogeographic breaks in Patagonia are  
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52 73 hypothesized for this group of lizards, and interestingly several of these breaks are shared with other  
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54 74 species of plants and rodents (Breitman *et al.*, 2012). Lizards of the *L. lineomaculatus* section are  
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3 75 able to survive extreme thermal environments, condition that has captured the attention of  
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5 76 physiologists and behavioral scientists, and they include both omnivorous and herbivorous species  
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7 77 of small body size (Jacksic & Schwenk, 1983; Ibarzüengoytía, Halloy & Crocco, 2002; Espinoza *et*  
8  
9 78 *al.*, 2004; Pincheira-Donoso, Hodgson & Tregenza, 2008; Ibarzüengoytía *et al.*, 2010; Medina &  
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11 79 Ibarzüengoytía, 2010; Bonino *et al.*, 2011; Fernández *et al.*, 2011).

14  
15 80 A recent molecular phylogeny of the *Liolaemus lineomaculatus* section (Breitman *et al.*,  
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17 81 2011a), based on nine genetic markers (nuclear and mitochondrial) and two phylogenetic  
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19 82 approaches (species tree, and concatenation based on Bayesian, Likelihood and Parsimony  
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21 83 methods), identified four main lineages: (1) the *lineomaculatus* group, including *L. avilae*, *L.*  
22  
23 84 *hatcheri*, *L. kolengh*, *L. lineomaculatus*, *L. morandae* and *L. silvanae*; (2) the *magellanicus* group,  
24  
25 85 including *L. caparensis* and *L. magellanicus*; (3) the *somuncurae* group, including *L. somuncurae*  
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27 86 and *L. uptoni*; and (4) the *kingii+archeforus* group, including *L. archeforus*, *L. chacabucoense*, *L.*  
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29 87 *baguali*, *L. escarchadosi*, *L. gallardoi*, *L. kingii*, *L. sarmientoi*, *L. scolaroi*, *L. tari*, *L. tristis* and *L.*  
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31 88 *zullyae*.

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35 89 Traditionally, species of the *Liolaemus lineomaculatus* section have been morphologically  
36  
37 90 classified in three groups: (1) *lineomaculatus* (Etheridge, 1995), including the same species listed  
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39 91 above; (2) *kingii* (Cei & Scolaro, 1982a), including *L. baguali*, *L. kingii*, *L. somuncurae*, *L. tristis*,  
40  
41 92 and *L. uptoni*; and (3) *archeforus* (Cei & Scolaro, 1982a), including *L. archeforus*, *L.*  
42  
43 93 *chacabucoense*, *L. escarchadosi*, *L. gallardoi*, *L. sarmientoi*, *L. scolaroi*, *L. tari* and *L. zullyae*.  
44  
45 94 However, the species *L. magellanicus* could not been unambiguously assigned to any of these  
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47 95 groups. These species groups were originally recognized on the basis of scale counts and disjunct  
48  
49 96 geographical distributions (Cei & Scolaro, 1982a), and later work extended distinguishing  
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51 97 characteristics among species groups to include variation in scale shape, color patterns, and size-  
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53 98 based characters (Scolaro & Cei, 1997). It has been 30 years since this ‘morphological arrangement  
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55 99 hypothesis’ was proposed and, although the number of species belonging to the section has almost  
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3 100 doubled since then, this ‘morphological arrangement hypothesis’ (our terminology) has never been  
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5 101 revised or tested, thus the importance of testing the validity of this currently accepted hypothesis  
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7 102 within the larger context of *Liolaemus* systematics (Lobo *et al.*, 2010; Breitman *et al.*, 2011a).  
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10 103 Our broader goal is to evaluate the accuracy of the current ‘morphological arrangement  
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12 104 hypothesis’ of this section, and hence to recommend whether this classification should be followed  
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14 105 by future researchers. To accomplish this goal, we (i) perform an updated chronological review of  
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16 106 the taxonomic changes, species descriptions, morphological groups and genetic clades proposed for  
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18 107 the *L. lineomaculatus* section, summarizing characters that have been proposed to diagnose the  
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20 108 morphological groups (key characters); (ii) evaluate the accuracy of key characters for  
21  
22 109 discrimination among morphological groups using analyses of our measurements of lizards  
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24 110 collected in type localities (and surrounding areas); and (iii) incorporate more characters (broadly  
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26 111 used for characterization of species in *Liolaemus*, and in this section) to test if discrimination among  
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28 112 morphological groups is possible based on a larger number of characters. We used a novel  
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30 113 morphological dataset generated from 345 lizards representing all the species of the section,  
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32 114 collected from (or nearby) their type localities. In total, we qualitatively and quantitatively analyzed  
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34 115 35 morphological variables (including meristic, morphometric, squamation and coloration patterns),  
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36 116 using univariate and multivariate statistical techniques, and we discuss our results and their  
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38 117 taxonomic implications. We also briefly discuss novel patterns of sexual dimorphism discovered in  
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40 118 some groups. We show how extensive morphological analysis improves our understanding of the  
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42 119 species of the *L. lineomaculatus* section, and how our findings and recommendations should aid  
43  
44 120 future alpha taxonomic work, and should be of particular use to researchers interested in testing  
45  
46 121 physiological, behavioral or evolutionary hypotheses within the *L. lineomaculatus* section.  
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4 123 MATERIALS AND METHODS5  
6 124 HISTORICAL REVIEW

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9 125 We conducted a bibliographic search and collated a total of 46 publications that met the  
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11 126 goals of this review. This literature database included all publications in which species of the  
12  
13 127 *Liolaemus lineomaculatus* section were described or where morphological or molecular  
14  
15 128 arrangements were proposed or mentioned. Additionally, other papers where more than four species  
16  
17 129 of the group were studied systematically were also selected. We carefully read each paper and  
18  
19  
20 130 extracted information concerning species descriptions, morphological differences among described  
21  
22 131 species, diagnostic characters used to define each of the three traditional morphological groups  
23  
24 132 (*lineomaculatus*, *kingii* and *archeforus*), phylogenetic relationships among species of the section,  
25  
26 133 and the phylogenetic method used to perform the reconstruction. We summarized this information  
27  
28 134 chronologically, and tabulated morphological and distributional characteristics of these three groups  
29  
30 135 that are in current use. *Liolaemus magellanicus* and *L. caparensis* are not formally included in any  
31  
32 136 of the traditional morphology-defined groups (*kingii*, *archeforus* and *lineomaculatus*), but have  
33  
34 137 been recovered as a distinct genetic lineage (Breitman *et al.*, 2011a) within the *L. lineomaculatus*  
35  
36 138 section. As a result, we follow Breitman *et al.*'s (2011a) recommendations and consider both  
37  
38 139 species part of the *magellanicus* group. Thus the validity of the *archeforus*, *kingii*, *lineomaculatus*  
39  
40 140 and *magellanicus* groups was morphologically evaluated throughout the present study.  
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## 44 141 MATERIAL EXAMINED

45  
46 142 A total of 345 lizards, representing all the species included in the *Liolaemus lineomaculatus*  
47  
48 143 section, were collected from type localities (or within 50 km when sample size was extremely low):  
49  
50 144 *L. archeforus* (n = 12), *L. avilae* (n = 9), *L. baguali* (n = 21), *L. caparensis* (n = 10), *L.*  
51  
52 145 *chacabucoense* (n = 21), *L. escarchadosi* (n = 13), *L. gallardoi* (n = 41), *L. hatcheri* (n = 20), *L.*  
53  
54 146 *kingii* (n = 29), *L. kolengh* (n = 31), *L. lineomaculatus* (n = 11), *L. magellanicus* (n = 10), *L.*  
55  
56 147 *morandae* (n = 7), *L. sarmientoi* (n = 11), *L. scolaroi* (n = 6), *L. silvanae* (n = 17), *L. somuncurae* (n  
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3 148 = 16), *L. tari* (n = 12), *L. tristis* (n = 29), *L. uptoni* (n = 11) and *L. zullyae* (n = 8) (Figure 1,  
4  
5 149 Appendix 1). About 35% of the individuals used in the present study were employed in our  
6  
7 150 previous studies to infer phylogenetic and phylogeographic relationships, to describe new species  
8  
9 151 and to propose genetic breaks and refugia in southern Patagonia (Breitman *et al.*, 2011a, b, c, 2012).  
10  
11 152 All specimens are deposited in the herpetological collections of La Plata Museum (MLP.S) and  
12  
13 153 Centro Nacional Patagónico in Puerto Madryn (LJAMM-CNP), Argentina.

#### 14 15 16 17 154 CHARACTERS STUDIED

18  
19 155 From fixed specimens, we evaluated variation at 14 morphometric and 10 meristic (scale  
20  
21 156 count) characters, as well as 10 qualitative characters representing squamation and patterns of body  
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23 157 coloration (e.g., Vega, Bellagamba & Lobo, 2008; Table 1). The 34 characters we examined  
24  
25 158 included all those that have been used in previous literature to describe and/or compare species of  
26  
27 159 the *Liolaemus lineomaculatus* section, as well as several additional characters that have been shown  
28  
29 160 to be informative in other groups of *Liolaemus* (e.g., Abdala, 2007). Measurements were taken to  
30  
31 161 the nearest 0.1 mm from adult specimens using a Schwyz® electronic digital caliper. Scale counts  
32  
33 162 were made on juveniles and adults with a stereoscopic microscope, and qualitative characters were  
34  
35 163 observed and recorded only from adults. Scale terminology, measurements, and chromatic states  
36  
37 164 follow Smith (1946). Measurements and scale counts were principally made on the right side of  
38  
39 165 each specimen, but when this was impossible (e.g., lack of a leg) they were taken on the left side.  
40  
41 166 Coloration in life was observed from digital photographs taken at the time of capture. Sex was  
42  
43 167 determined by the thickness of the base of the tail and the presence of precloacal pores (where  
44  
45 168 present) and adults were identified by size and coloration patterns (Cei, 1986).

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48  
49 169 Morphometric characters used in this study were: (1) **SVL**, snout–vent length, measured  
50  
51 170 from the tip of the snout to the posterior margin of the precloacal scales; (2) **TL**, tail length, from  
52  
53 171 the cloaca to the tip of the tail, measured only on individuals with intact tails; (3) **DFH**, distance  
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55 172 between fore and hind limbs, taken from the armpit of the front leg to the anterior insertion of the  
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3 173 hind limb; (4) **FOL**, foot length, measured ventrally along the fourth toe, from the base of the heel  
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5 174 to the base of the claw; (5) **TFL**, tibia-fibula length, the distance from the knee to the ankle; (6)  
6  
7 175 **RUL**, radius-ulna length, measured from the elbow to the wrist; (7) **HAL**, hand length, the ventral  
8  
9 176 length of the third finger from the base of the wrist to the base of the claw; (8) **HH**, head height, the  
10  
11 177 distance of the head measured perpendicularly to the auditory meatus; (9) **HW**, head width, taken  
12  
13 178 between corners of the mouth; (10) **HL**, head length, length taken from the posterior edge of the  
14  
15 179 auricular opening to the rostral scale; (11) **RND**, rostral–nasal distance, measured between rostral  
16  
17 180 and nasal scales; (12) **RH**, rostral height, the longest vertical measure of the rostral scale; (13)  
18  
19 181 **DRE**, rostral–eye distance, measured from the rostral scale to the posterior edge of the eye; and (14)  
20  
21 182 **AH**, auditory meatus height, the longest vertical diameter of the auditory meatus.  
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25 183 Meristic characters used in this study were: (1) **SCI**, scales in contact with the interparietal;  
26  
27 184 (2) **LS**, lorilabial scales, number of scales above the supralabial scales; (3) **SS**, supralabial scales,  
28  
29 185 number of scales on the upper edge of the mouth, from the rostral scale (but without including it) to  
30  
31 186 the corner of the mouth; (4) **IS**, infralabial scales, number of scales on the lower edge of the mouth,  
32  
33 187 from the mental scale (but without including it) to the corner of the mouth; (5) **MS**, midbody scales,  
34  
35 188 number of scales around the body at the trunk; (6) **DS**, dorsal scales, number of scales from the first  
36  
37 189 nuchal scale to the line of scales between the hindlimbs; (7) **VS**, ventral scales, counted after the  
38  
39 190 mental scale (without including it) to the precloacal scales; (8) **IL3**, infradigital lamellae of the third  
40  
41 191 finger; (9) **IL4**, infradigital lamellae of the fourth toe; and (10) **PP**, number of precloacal pores.  
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45 192 The qualitative characters used in this study were taken from fixed specimens and from  
46  
47 193 digital photographs of specimens taken at the time of capture. Variables taken from fixed  
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49 194 specimens: (1) dorsal stripe pattern, referring to the shape and size of white or yellow dorsal bands  
50  
51 195 (perpendicular to the body axe), four categories were recorded (1a) complete or slightly broken  
52  
53 196 bands, (1b) dotted bands, (1c) irregular bands, (1d) indistinct or almost indistinct bands; all these  
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55 197 variables were illustrated and respectively described as 0–20, 40, 60 and 80–100 in Scolaro (1987);  
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3 198 (2) presence/absence of vertebral line; (3) presence/absence of paravertebral line; (4)  
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5 199 presence/absence of dorsolateral lines, between the insertions of fore and hind limbs; (5)  
6  
7 200 presence/absence of any degree of variegation on the belly, measured from the mental scale to the  
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9 201 tip of the tail; (6) ventral melanism from the mental scale to the cloacal region, five categories were  
10  
11 202 recorded (m0) no melanism, (m1) melanism only present on the gular zone, (m2) melanism only  
12  
13 203 present on the belly, (m3) melanism present on all body regions except the cloacal region and limbs,  
14  
15 204 (m4) melanism present on all body except the limbs, (m5) melanism present on all the body.  
16  
17 205 Variables taken from pictures: (1) presence of red or orange scales on any part of the body; (2) color  
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19 206 of dorsal background; (3) colors present on dorsal side; and (4) colors present on ventral side.  
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## 23 STATISTICAL ANALYSIS

### 24 *Testing the 'morphological arrangement hypothesis' among groups*

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28 209 To test the 'morphological arrangement hypothesis' among groups, we qualitatively and  
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30 210 quantitatively evaluated whether morphological characters listed as diagnostic among groups in the  
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32 211 literature validly discriminated the 21 described species in the *kingii*, *archeforus*, *lineomaculatus*  
33  
34 212 and *magellanicus* groups. Shape and disposition of dorsal scales were qualitatively compared  
35  
36 213 among species groups by comparing variation captured in digital photos; dorsal background color,  
37  
38 214 presence of red/orange scales and belly color were scored and compared among species of each  
39  
40 215 group. Dorsal pattern (including dorsal stripe pattern and vertebral, paravertebral and dorsolateral  
41  
42 216 line pattern), variegation and melanism were converted to percentages reflecting their prevalence  
43  
44 217 among members of each species and groups before being qualitatively compared. Midbody scales,  
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46 218 snout–vent length, forelimb length (calculated as radius-ulna length + hand length) and number of  
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48 219 precloacal pores were statistically compared through univariate tests (see below “morphological  
49  
50 220 comparisons among species within groups”). Although the species and groups considered in this  
51  
52 221 study have mainly been distinguished based on morphological characteristics, geographic  
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54 222 distributions have also prominently figured in the current taxonomic arrangement within the *L.*  
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3 223 *lineomaculatus* section. Therefore, we also tested the hypothesis that the (morphologically distinct)  
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5 224 species and groups in the section correspond to distinct geographical groupings, by comparing  
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7 225 distributional maps that we constructed for each species using the geographical coordinates from  
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9  
10 226 our collections.

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12 227 We tested whether there were generalized morphological differences (extending those  
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14 228 proposed in the literature) among the four morphological groups using Discriminant Function  
15  
16 229 Analyses (DFA) performed on 13 meristic and 9 morphometric variables (tail length and precloacal  
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18 230 pores were excluded from the analysis because several individuals had no intact tail and precloacal  
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21 231 pores were present only on males of some species) (Shepard, Irwin & Burbrink, 2011).  
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23 232 Discriminant Function Analyses are linear combinations of the original variables that maximize  
24  
25 233 differences between given groups (e.g., Crochet, Geniez & Ineich, 2003). For our purposes, if DFA  
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27 234 differences between groups were not clear (> 50% group overlap in morphospace plus a large  
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29 235 classification error) then we interpreted this as indicative of no evidence for considering those  
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32 236 groups valid. Discriminant Function Analyses provided allows a graphic visualization of group  
33  
34 237 differences and yielded axes standardized by the common variance. Three DFAs were performed,  
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36 238 one on the meristic data set, another on the morphometric data set, and a third one on the  
37  
38 239 morphometric data set standardized by the SVL (though division; Das & Grismer, 2003; Vukov *et*  
39  
40 240 *al.*, 2006; Shepard *et al.*, 2011). Prior to the DFA, a Multivariate Analyses of Variance (MANOVA)  
41  
42 241 was used to test whether there were differences between sexes within each morphological group (in  
43  
44 242 both meristic and morphometric data sets). In cases where sexual differences were present, groups  
45  
46 243 were divided by sex (Medina *et al.*, *in press*; Vukov *et al.*, 2006). The general trends in sexual  
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48 244 dimorphism recovered from DFA graphics are discussed in a comparative and evolutionary  
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51 245 framework in order to provide a starting point for future research.

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54 246 *Morphological comparisons among species within groups*  
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3 247 Based on the results of the previous section, species were placed in three morphological  
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5 248 groups: *lineomaculatus*, *magellanicus* and *kingii-archeforus*. We did not find evidence for  
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7 249 differentiation among the *kingii* and *archeforus* groups, but all these species were recovered in one  
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9 250 group morphologically differentiated from the *lineomaculatus* and *magellanicus* groups. Thus  
10  
11 251 through the *Materials and Methods* and *Results* sections of this paper, we refer to these 11 species,  
12  
13 252 as the *kingii-archeforus* group, to discriminate it from the traditional five-species *kingii* group. In  
14  
15 253 the *Discussion* section, based on the results presented here, we call these 11 species 'the *kingii*  
16  
17 254 group', since *L. kingii* was the first described species of this group and a single-word clade name is  
18  
19 255 appropriate. In order to provide an updated analysis of the morphological differences between  
20  
21 256 genders of each species and among species of each group, univariate tests were performed as  
22  
23 257 described in the next paragraph on the morphometric and meristic data sets.  
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27 258 One-way Analysis of Variance (ANOVA) was implemented to evaluate the significance of  
28  
29 259 differences in variable means among species, DGC comparisons (Di Rienzo, Guzmán and  
30  
31 260 Casanoves test; Di Rienzo, Guzmán & Casanoves, 2002) were performed, and assumptions of equal  
32  
33 261 variance and normality were checked using Levene and Shapiro-Wilks tests, respectively  
34  
35 262 (Montgomery, 1991). When assumptions of the statistical tests were not met (*p* values of Levene  
36  
37 263 and Shapiro-Wilks tests < 0.05), nonparametric Kruskal-Wallis tests (Kruskal & Wallis, 1952) were  
38  
39 264 used. All the analyses were performed using INFOSTAT® 2011 (Di Rienzo *et al.*, 2011). All  
40  
41 265 variables were tested for sexual dimorphism with either Student's *t* or Kruskal-Wallis tests (if the  
42  
43 266 above assumptions were not met). In cases where SVL was significantly different between sexes  
44  
45 267 within species, all other morphometric variables were standardized by SVL, and univariate tests  
46  
47 268 were performed on these new variables (Das & Grismer, 2003; Vukov *et al.*, 2006; Shepard *et al.*,  
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49 269 2011).  
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## 53 270 RESULTS

### 54 271 HISTORICAL REVIEW

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3 272 Species belonging to the *Liolaemus lineomaculatus* section possess a long taxonomic  
4  
5 273 history accompanied by many of the nomenclatural changes proposed for *Liolaemus*. The discovery  
6  
7 274 of the first species of this section began with the arrival of the H.M.S. Beagle to the Santa Cruz  
8  
9 275 River in Patagonia (17 of April of 1834), when Charles Darwin collected, drew and “described” in  
10  
11 276 his notes two species of lizards (that were later formally described) from the *L. lineomaculatus*  
12  
13 277 section, both from Puerto Deseado. The rate of species descriptions in the *L. lineomaculatus* section  
14  
15 278 can be divided in three periods. The first period including the years 1850–1900 and was followed  
16  
17 279 by 70 years of stasis where no descriptions were published. A second period with a high rate of  
18  
19 280 species descriptions occurred from 1971 to 1997, and then low-cost DNA sequencing techniques  
20  
21 281 coupled with increased accessibility to remote places characterizes the last (present) period of  
22  
23 282 species description, which spans 2005 to the present.  
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26  
27 283 The first species described in the *Liolaemus lineomaculatus* section was discovered by  
28  
29 284 Charles Darwin in 1834, but wasn't formally described until almost ten years later as *Liolaemus*  
30  
31 285 *kingii* (originally as *Proctotretus kingii*), with Puerto Deseado (Argentina) as its type locality (Bell,  
32  
33 286 1843). The description of this species was based on head form, coloration, shape of the auditory  
34  
35 287 meatus, and number and shape of scales. The second species described from the *L. lineomaculatus*  
36  
37 288 section was *L. magellanicus* (originally *Proctotretus magellanicus*) whose type locality is Havre  
38  
39 289 Pecquet, Chile, in the Strait of Magellan (Hombron & Jacquinot, 1847). The third species belonging  
40  
41 290 to the section was *L. lineomaculatus* (Boulenger, 1885), and has the same type locality as *L. kingii*,  
42  
43 291 Puerto Deseado (restricted by Donoso-Barros, 1966) and was also collected by C. Darwin. An early  
44  
45 292 revision of the genus *Liolaemus* by Koslowsky (1896, 1898) considered *L. lineomaculatus* as a  
46  
47 293 subspecies, or a variety, of *L. magellanicus*; however, his proposal has not prospered. Anderson  
48  
49 294 (1898) resumed the species of amphibian and reptiles of Tierra del Fuego and listed *L. magellanicus*  
50  
51 295 and *L. lineomaculatus* as different species. The last species described in this first period was *L.*  
52  
53 296 *hatcheri*, with the type locality restricted to the area between Pueyrredón and Buenos Aires Lakes  
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55 297 (Stejneger, 1909); this new species was not considered in several publications in which different  
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3 298 collections were revised (Burt & Burt, 1935; Hellmich, 1934, 1952; Donoso-Barros & Codoceo,  
4  
5 299 1962), until 1970 when the species was considered a synonym of *L. magellanicus* (Peters &  
6  
7 300 Donoso-Barros, 1970).

8  
9  
10 301 The second period of progress in taxonomy of this section, characterized by a high rate of  
11  
12 302 species descriptions, started with the proposal of the genus *Vilcunia* in 1971; the new species  
13  
14 303 *Liolaemus silvanae* (originally *Vilcunia silvanae*) was described as the type species of this new  
15  
16 304 genus with Puesto Lebrum, Lago Buenos Aires Plateau (Argentina) as the type locality (Donoso-  
17  
18 305 Barros & Cei, 1971). This new genus was characterized by the absence of precloacal pores in both  
19  
20 306 sexes and presence of trifold scales. *Liolaemus archeforus* was described in the same publication,  
21  
22 307 based on material from the same type locality (Donoso-Barros & Cei, 1971). Additionally in the  
23  
24 308 same year, Gallardo (1971) published a paper identifying a parallelism between lizard and plant  
25  
26 309 distributions, in which he proposed that lizards could be grouped by size and aspect. Gallardo  
27  
28 310 classified *L. lineomaculatus*, *L. magellanicus* and *L. hatcheri* in a different group relative to *L.*  
29  
30 311 *kingii*, and also mentioned that *L. hatcheri* was similar to *L. magellanicus*. Again, in the same year,  
31  
32 312 *L. magellanicus* and *L. lineomaculatus* were compared and proposed to belong to a group called  
33  
34 313 “*magellanicus* group” because of their morphological resemblance and their shared southern  
35  
36 314 distribution (Cei, 1971). Donoso-Barros (1973) described *Liolaemus sarmientoi* from lizards taken  
37  
38 315 at Monte Aymond (in southern Santa Cruz province, Argentina), the type locality, and included the  
39  
40 316 new species in the “*kingii* group” without further explanation.  
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45 317 Since 1975, several proposals to group all of the aforementioned species (*L. archeforus*, *L.*  
46  
47 318 *hatcheri*, *Liolaemus kingii*, *L. lineomaculatus*, *L. magellanicus*, *L. sarmientoi* and *L. silvanae*) have  
48  
49 319 been published. The first of these was made by Cei (1975) using serological and morphological  
50  
51 320 data; Cei proposed the “*Liolaemus kingii* complex”, composed of *L. archeforus*, *L. kingii* and *L.*  
52  
53 321 *sarmientoi*. In the same publication Cei (1975) proposed subspecific status for *L. archeforus* and *L.*  
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3 322 *sarmientoi* and considered *L. archeforus* as an ancient stock of a primitive *L. kingii* line, although  
4  
5 323 morphological features that defined the complex were not given.  
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7

8 324 Cei (1979) recognized two complexes that have not undergone recent (post-Pleistocene)  
9  
10 325 speciation. The first group, the “*Liolaemus kingii-archeforus* complex,” included *L. archeforus*, *L.*  
11 326 *kingii* and *L. sarmientoi*, was characterized by no femoral patch; “moderately high” number of  
12  
13 327 keeled scales around midbody (58–84); high number of precloacal pores (6–10); short legs and tail  
14  
15 328 (slightly longer than body); variegated ventral color pattern; absence of dark coloration in nuchal  
16  
17 329 region; and a dark dorsal coloration with series of yellowish or whitish transversal bars. The second  
18  
19 330 group, the “*Liolaemus magellanicus-lineomaculatus* complex,” was composed of *L. magellanicus*  
20  
21 331 and *L. lineomaculatus* and characterized by no femoral patch; low number of large mucronated  
22  
23 332 dorsally acuminate scales around midbody (40–70); moderate number of precloacal pores (3–8);  
24  
25 333 very short limbs and tail; absence of dark coloration in nuchal or ventral melanism; and dorsal  
26  
27 334 coloration being “irregularly spotted” with black and white longitudinal lines (Cei, 1979).  
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32 335 *Liolaemus somuncurae* (*L. kingii somuncurae*) was described as a subspecies whose type  
33  
34 336 locality was the Somuncurá Plateau (Río Negro, Argentina) near Lago Raimundo (Cei & Scolaro,  
35  
36 337 1981). A close morphological similarity between this new ‘subspecies’ and *L. kingii* was found, and  
37  
38 338 the authors suggested that this pattern could be explained by incipient speciation initiated during a  
39  
40 339 dry glacial phase of the Pleistocene (Cei & Scolaro, 1981). Interestingly, Cei and Scolaro (1981)  
41  
42 340 placed those species plus *L. archeforus* and *L. sarmientoi* within the “*kingii* group” (Donoso-Barros,  
43  
44 341 1973) but they did not use the name “*kingii-archeforus* complex” proposed in Cei’s previous  
45  
46 342 publication (Cei, 1979).  
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50 343 A new subspecies called *Liolaemus gallardoi* (*L. archeforus gallardoi*) was described by  
51  
52 344 Cei and Scolaro (1982a) with the type locality identified as the “Aguila-Asador Plateau” in Santa  
53  
54 345 Cruz province (Argentina). This was the first paper in which the “*kingii-archeforus* complex” was  
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56 346 formally divided in two groups and diagnostic characters were provided to identify each. The first  
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3 347 group was the “*kingii* group” formed by *L. kingii* and *L. somuncurae* and characterized by a high  
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5 348 number of small scales around midbody (75–94). The second group was deemed the “*archeforus*  
6  
7 349 group” formed by *L. archeforus*, *L. gallardoi* and *L. sarmientoi*, and was characterized by a low  
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9  
10 350 number of big mucronated scales around the midbody (58–78), which suggested that the latter two  
11  
12 351 species in the group had a close relationship (inferred from size and shape of dorsal scales). Cei and  
13  
14 352 Scolaro (1982a) hypothesized that the “*archeforus* group” was evolutionarily derived from the  
15  
16 353 “*kingii* group”. The same year, *Liolaemus periglacialis* (as *Vilcunia periglacialis*) was described  
17  
18 354 from the surroundings of Belgrano Lake (Santa Cruz, Argentina), the type locality (Cei & Scolaro,  
19  
20 355 1982b). However, the species was later considered to be a junior synonym of *L. hatcheri*  
21  
22 356 (Etheridge, 1998). Cei and Scolaro (1982b) made an important comparison between *Vilcunia* and  
23  
24 357 *Liolaemus* in which they provided diagnostic characters to differentiate them. The main characters  
25  
26 358 separating *Vilcunia* from *Liolaemus* were the presence of dorsal trifid scales, acuminate femoral  
27  
28 359 scales, and absence of precloacal pores in *Vilcunia*.

30  
31  
32 360 In 1983, the new subspecies *Liolaemus baguali* (*L. kingii baguali*) was described from the  
33  
34 361 “*kingii* group” (Cei & Scolaro, 1983) with western Santa Cruz province, the Sierra del Bagual  
35  
36 362 (Argentina) indicated as the type locality. In this publication the idea of two groups (*archeforus* and  
37  
38 363 *kingii*) was reinforced and the groups were geographically restricted. The “*archeforus* group” was  
39  
40 364 composed of isolated populations distributed in volcanic mountains along the western area of  
41  
42 365 Patagonia, while the “*kingii* group” was described with a more widespread distribution,  
43  
44 366 encompassing lowlands from the coast to the subandean region of the Santa Cruz province.

46  
47 367 Laurent (1983) performed an early taxonomic and evolutionary study using morphological  
48  
49 368 variables of several species of *Liolaemus*, and described a “primitive line”, sister to an “ancestral  
50  
51 369 line” that gave rise to two main groups in *Liolaemus*. This “primitive line” was formed by  
52  
53 370 *Liolaemus kingii* and *L. archeforus*, which were deemed primitive because both had characters that  
54  
55 371 were present in the two main groups, while the “ancestral line” was formed by *L. magellanicus* and  
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3 372 *L. lineomaculatus* in a sister relationship with *Vilcunia* (*L. hatcheri* and *L. silvanae* based on the  
4  
5 373 absence of preloacal pores).

6  
7  
8 374 Two years later, based on morphological characters from a larger number of species, the  
9  
10 375 relationships proposed by Laurent (1983) were reinforced by additional studies, the generic name  
11  
12 376 *Rhytidodeira* (Girard, 1857) was assigned to the primitive group formed by the species of the *kingii*-  
13  
14 377 *archeforus* group plus the species *Liolaemus ruizleali* (although this species was later synonymized  
15  
16 378 with *L. rothi* and removed from the group; Cei & Scolaro, 1987; Cei, 1990), and *L. kingii* was  
17  
18 379 designated as the type species of this new genus (Laurent, 1985). *Liolaemus lineomaculatus* was  
19  
20 380 included in *Vilcunia* (a genus characterized by absence of preloacal pores, small scale size, short  
21  
22 381 tail, small auditory meatus and big mental scale), and a monotypic group formed by *L. magellanicus*  
23  
24 382 (based on a small auditory meatus and big mental scale) was proposed (Laurent, 1985). In this  
25  
26 383 publication, the first phylogenetic hypothesis for the group (*Liolaemus sensu stricto*, ((*L.*  
27  
28 384 *magellanicus*, *Vilcunia*), (*kingii-archeforus* group, *Eulaemus*))) was proposed; but, Laurent (1985)  
29  
30 385 also suggested the alternative hypothesis that the “*kingii-archeforus* group” belonged to the  
31  
32 386 *Vilcunia-L. magellanicus* branch forming a “basal” or ancestral stock. We want to emphasize here  
33  
34 387 that from this interpretation, the name “basal” was used for about 25 years to recognize the group of  
35  
36 388 species belonging to the *L. lineomaculatus* group.

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39  
40  
41 389 In 1986, Cei wrote the first monograph about reptiles of southern Argentina in which the  
42  
43 390 “*kingii* group”, “*archeforus* group” and “*magellanicus* group” were included within the genus  
44  
45 391 *Liolaemus*. Moreover, he recognized the “*magellanicus* group” to include the southern species *L.*  
46  
47 392 *magellanicus* and *L. lineomaculatus*, and described them as being characterized by short tails,  
48  
49 393 bristly and mucronated scales, and light dorsolateral bands and asymmetric blotches along the  
50  
51 394 vertebral line. He also recognized *Vilcunia* as a genus (Cei, 1986).

52  
53  
54 395 In 1995, Laurent attempted to reinforce the subgeneric status of *Vilcunia* and proposed the  
55  
56 396 monotypic subgenus *Austrolaemus*, in which he designated *Liolaemus magellanicus* as the type  
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3 397 species, but his ideas did not gain acceptance since other systematic changes were proposed the  
4  
5 398 same year (Laurent, 1995). Etheridge (1995) used data on squamation, neck folds, skull and  
6  
7 399 skeleton measurements to revise the taxonomic arrangement of *Liolaeminae*, and identified several  
8  
9 400 synapomorphies supporting the monophyletic status of *Liolaemus*. Etheridge argued that all the  
10  
11 401 species included in *Vilcunia*, *Rhytidodeira* and *Eulaemus* (among other genera) should be included  
12  
13 402 in *Liolaemus*, and that while *Vilcunia* and *Eulaemus* might represent monophyletic subsets of  
14  
15 403 *Liolaemus*, he argued that they should not be used as formal names for taxa until their monophyletic  
16  
17 404 status were verified by cladistic analysis (Etheridge, 1995). In the same publication, Etheridge  
18  
19 405 proposed the “*lineomaculatus*” group including the species *L. lineomaculatus*, *L. silvanae* and *L.*  
20  
21 406 *hatcheri* (the last two forming a subgroup called *silvanae*). Characteristics cited as unifying the  
22  
23 407 *lineomaculatus* group included absence of precloacal pores and the presence of dorsal tridentate  
24  
25 408 scales, whereas the *silvanae* group (*L. silvanae* and *L. hatcheri*) was distinguished by keeled and  
26  
27 409 imbricate lateral nuchal scales and subimbricated postfemoral scales (Etheridge, 1995).  
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31

32 410 *Liolaemus zullyae* (*L. zullyi*) was described by Ceï and Scolaro (1996), with type locality  
33  
34 411 designated from Rio Zeballos valley (Santa Cruz, Argentina). Interestingly, although the mean scale  
35  
36 412 count around the midbody presented in the description was 86.6, the species was included in the  
37  
38 413 “*archeforus* group” (scales around midbody 58–78). Ceï and Scolaro (1996) stated that the new  
39  
40 414 species differed from the other *Liolaemus* species but not from the ones included in the *kingii* and  
41  
42 415 *archeforus* groups, by having the characteristics listed in Etheridge (1995: Appendix 2, Part A).  
43  
44 416 Moreover, they claimed “*L. zullyi* along with other species of the *archeforus* group, may be  
45  
46 417 distinguished from members of the *kingii* group by its larger forelimbs, the more strongly keeled  
47  
48 418 dorsal or lateral scales, the prevailing presence of red and orange-red scales in dorsal and lateral  
49  
50 419 patterns, and a generally stronger ventral pigmentation leading to a true condition of melanism”  
51  
52 420 (Ceï & Scolaro, 1996: 393). We believe that a chronological problem existed with the publication of  
53  
54 421 this article relative to another article published the next year by the same authors, because  
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3 422 differences among species of the *archeforus* and *kingii* groups were listed in 1997, yet the species *L.*  
4  
5 423 *zullyae* was not mentioned in the publication. We also note that the authors recognized that the  
6  
7 424 elevated number of midbody scales indicated that *L. zullyae* should belong to the *kingii* group;  
8  
9 425 however, the authors justified the inclusion of *L. zullyae* in the *archeforus* group based on the  
10  
11 426 characteristics discussed above, and claiming that the species shows an “exceptionally high”  
12  
13 427 number of scales around midbody and this is the “most striking condition” of *L. zullyae* lepidosis  
14  
15 428 (Cei & Scolaro, 1996) caused by genetic drift. Several years later, the species name was corrected to  
16  
17 429 *L. zullyae* by Michels and Bauer (2004).

20  
21 430 In 1997, three more species were described and the morphological criterion for grouping  
22  
23 431 species in the *kingii* or *archeforus* group was extended as follows (Scolaro & Cei, 1997). The  
24  
25 432 distribution of the species of the *kingii* group was defined to encompass much of Río Negro, Chubut  
26  
27 433 and Santa Cruz provinces (Argentina), and the group was distinguished based on the following  
28  
29 434 characteristics: (1) dorsal body scales not “strongly” keeled but “distinctly” imbricated; (2) number  
30  
31 435 of midbody scales: 72–97 (mean: 79.15); (3) SVL: 62–100 mm; (4) “relatively” short forelimbs; (5)  
32  
33 436 reddish or yellowish-brown dorsal pattern, with “prevailing distinct” white or yellowish, black  
34  
35 437 bordered bands mainly with conspicuous central spot; (6) “unusual” dorsolateral stripes; (7) a low  
36  
37 438 percentage of red-orange dorsolateral scales; (8) light gray or yellowish ventral color, more or less  
38  
39 439 mottled with black in most of the specimens, seldom melanistic; and (9) number of precloacal  
40  
41 440 pores: 5–10 (Scolaro & Cei, 1997). The distribution of the species of the *archeforus* group was  
42  
43 441 considered subandean and austral, inhabiting only Santa Cruz province, and the defining  
44  
45 442 characteristics of the group were shown to include: (1) “more strongly” keeled and “sharply”  
46  
47 443 imbricated dorsal body scales; (2) number of midbody scales: 58–78 (mean: 68.94); (3) SVL: 64–  
48  
49 444 102 mm (not diagnostic but suggesting a stouter body); (4) larger forelimbs; (5) dark gray or  
50  
51 445 brownish dorsal pattern, with white or yellow transverse broken lines that are irregular and almost  
52  
53 446 indistinct in many specimens; (6) broken dorsolateral stripes; (7) “noticeable” percentage of red-  
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3 447 orange dorsolateral scales; (8) strongly black-mottled ventral zone, strong melanism in most of the  
4  
5 448 forms; and (9) number of precloacal pores: 6–8 (Scolaro & Cei, 1997). In the same publication,  
6  
7 449 three species were described. Belonging to the *kingii* group, *Liolaemus tristis* was described with  
8  
9 450 type locality at Lagunas sin Fondo Plateau (Santa Cruz, Argentina); and within the “*archeforus*  
10  
11 451 group,” *L. tari* was described from a type locality of del Viento Plateau, and *L. escarchadosi* was  
12  
13 452 described from Cordón de los Escarchados (both places in Santa Cruz, Argentina). Differences  
14  
15 453 among these species and other members of the *kingii* and *archeforus* groups were evaluated and a  
16  
17 454 dichotomous key was presented. We should mention here that the species *L. zullyae* was not  
18  
19 455 included in the analysis due to a lag in publication (see above), and although the authors recognized  
20  
21 456 that most of the morphometric and meristic characters of *L. escarchadosi* were statistically too  
22  
23 457 weak to be used for diagnostic proposes, they presented several differences in coloration patterns  
24  
25 458 among species. Finally, the authors quoted an Etheridge personal communication highlighting that  
26  
27 459 all the characters shared by species belonging to both groups were plesiomorphic, e.g., high number  
28  
29 460 of precloacal pores, granular lateral nuchal scales, keeled and imbricated dorsal scales, and the  
30  
31 461 absence of a hypertrophied puboischiotibialis muscle, among others (Scolaro & Cei, 1997).  
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36 462 The final and most recent period of species descriptions and nomenclatural changes to the  
37  
38 463 *Liolaemus lineomaculatus* section began with the first quantitative evolutionary analysis of several  
39  
40 464 species of *Liolaemus* using allozyme data. Based on these data, Young Downey (1998) supported  
41  
42 465 the monophyly of *Liolaemus* and its two major groups: *Eulaemus* and *Liolaemus sensu stricto*.  
43  
44 466 Moreover, a clade formed by *L. kingii*, *L. lineomaculatus*, *L. archeforus* and *L. silvanae* was  
45  
46 467 recovered, and hypothesized to be the sister group of the *montanus* section, both belonging to the  
47  
48 468 *Eulaemus* group (Young Downey, 1998). Two years later, the same relationships were corroborated  
49  
50 469 by analyses of mitochondrial DNA sequence, from which divergence among *Liolaemus sensu*  
51  
52 470 *stricto* and *Eulaemus* was inferred to have been ~12.6 Mya or earlier (the authors did not provide  
53  
54 471 confidence intervals or error terms in their estimates); where the group formed by *L.*  
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3 472 *lineomaculatus*, *L. magellanicus* and *L. somuncurae* was named “*L. lineomaculatus* section”  
4  
5 473 (Schulte *et al.*, 2000); name that is currently used to recognize this group of southernmost species.  
6  
7 474 Morando (2004) obtained similar results using analyses of both nuclear and mitochondrial genes.  
8  
9 475 To our knowledge, the only paper that has not recovered the monophyly of the *L. lineomaculatus*  
10  
11 476 section was published by Lobo (2001) based on several morphological traits, where the species *L.*  
12  
13 477 *lineomaculatus* was recovered within “*Liolaemus sensu stricto* or Chilean group”; however, the  
14  
15 478 author recognized the necessity of further studies to confirm or reject this hypothesis (Lobo, 2001).

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19 479 Espinoza *et al.* (2004) using morphology and mitochondrial genes published a phylogeny of  
20  
21 480 *Liolaemus* that included several species of the *L. lineomaculatus* section, but they did not present  
22  
23 481 support values for any of the relationships. However, the relationships recovered among species of  
24  
25 482 this section were as follows: ((*L. hatcheri*, (*L. lineomaculatus*, *L. silvanae*)), (*L. magellanicus*, (*L.*  
26  
27 483 *kingii*, ((*L. escarchadosi*, (*L. tari*, *L. baguali*)), (*L. sarmientoi*, *L. gallardoii*)), (*L. zullyae*, *L.*  
28  
29 484 *archeforus*)))))).

30  
31  
32 485 In 2005, the new species *Liolaemus scolaroi* (*L. donosolaemus scolaroi*) was described with  
33  
34 486 a designated type locality in Jeimini, XI administrative region of Chile, and this new species was  
35  
36 487 included in the *archeforus* group (Pincheira-Donoso & Núñez, 2005). Since no clear  
37  
38 488 synapomorphic characters that could be used to support the monophyly of a group formed by the  
39  
40 489 *kingii* and *archeforus* groups was available, Pincheira-Donoso & Núñez (2005) grouped all of these  
41  
42 490 species in a new subgenus named *Donosolaemus*, characterized by (1) nasal and rostral scales  
43  
44 491 separated by anterior lorilabials; (2) absence of curved supralabial scales; (3) absence of point and  
45  
46 492 projecting outer ciliaries; (4) absence of femoral patch; (5) high number >5 of precloacal pores; and  
47  
48 493 (6) straight tibia, lacking hypertrophied puboischiotibialis and anterior tibialis muscles (Pincheira-  
49  
50 494 Donoso & Núñez, 2005: 32). Three of these are based on the absence of widespread characters of  
51  
52 495 *Liolaemus* and the other three characters are also present in other *Liolaemus* groups, thus the use of  
53  
54 496 the name “*Donosolaemus*” has been discouraged (see Lobo *et al.*, 2010; Breitman *et al.*, 2011a).

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3 497 *Liolaemus uptoni*, another species of the *L. lineomaculatus* section related to *L.*  
4  
5 498 *somuncurae*, was described in 2006 with type locality Bajada del Buey (Chubut, Argentina). For its  
6  
7 499 description, the species was mainly compared with *L. somuncurae*, but comparisons among the new  
8  
9 500 species and other species of the *kingii* group are also mentioned (Scolaro & Cei, 2006). The same  
10  
11 501 year *Liolaemus kolengh* was described with type locality Zeballos Hill (Santa Cruz, Argentina),  
12  
13 502 included in the “*silvanae* group”; *L. kolengh* was compared with the previously described species of  
14  
15 503 the *lineomaculatus* group and a key for identification of males was proposed (Abdala & Lobo,  
16  
17 504 2006). In 2009, *Liolaemus chacabucoense* was described with type locality Chacabuco River valley  
18  
19 505 (Aisén, Chile), the new species was proposed to belong to the *archeforus* group, differing from the  
20  
21 506 other species mainly in body size (Núñez & Scolaro, 2009).

22  
23  
24  
25 507 Schulte & Moreno-Roark (2010), extended the results and the data set of Espinoza *et al.*  
26  
27 508 (2004) and published a phylogeny (using mitochondrial markers and a Likelihood approximation)  
28  
29 509 in which species of the *Liolaemus lineomaculatus* section were recovered in the following topology:  
30  
31 510 ((*L. hatcheri*, (*L. silvanae*, *L. lineomaculatus*)), (*L. magellanicus*, ((*L. kingii*, *L. somuncurae*), (*L.*  
32  
33 511 *escarchadosi*, (*L. baguali*, *L. tari*)), (*L. archeforus*, *L. zullyae*), (*L. gallardoi*, *L. sarmientoi*))))). The  
34  
35 512 next year Breitman *et al.* (2011a), based on nine markers (nuclear and mitochondrial) and two  
36  
37 513 phylogenetic approaches (species tree and concatenation approaches with Bayesian, Likelihood and  
38  
39 514 Parsimony analyses), presented another phylogeny including all recognized species of the *L.*  
40  
41 515 *lineomaculatus* section, and four main clades were recovered (see Introduction). These three papers  
42  
43 516 (Breitman *et al.* 2011a; Espinoza *et al.* 2004; Schulte & Moreno-Roark, 2010) were based on  
44  
45 517 molecular markers and recovered concordant topologies except for the position of *L. kingii*; but they  
46  
47 518 did not recover two of the groups previously described in the ‘morphological arrangement  
48  
49 519 hypothesis’ as clades (the *kingii* and the *archeforus* groups). Moreover, Breitman *et al.* (2011a)  
50  
51 520 recovered a *somuncurae* group (*L. somuncurae* + *L. uptoni*) in a sister relationship with a clade  
52  
53 521 formed by the remaining species of the morphological *kingii* and *archeforus* groups. Breitman *et al.*  
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3 522 (2011a) used the name ‘*kingii+archeforus* group’ to refer to this latter clade, and estimated that it  
4  
5 523 had diverged from the *somuncurae* group ~ 4.25 Mya (95% HPD = 3.17 – 5.48). Incongruence  
6  
7 524 among the concatenation vs. the species tree approaches were found with respect to the placement  
8  
9 525 of the candidate species *Liolaemus sp. 4* (belonging to the *somuncurae* group or not included in it),  
10  
11 526 and Breitman *et al.* (2011a) offered several hypotheses for these patterns. These included a possible  
12  
13 527 hybrid origin of the species *Liolaemus sp. 4*, although the authors recognize the need for further  
14  
15 528 study to clarify the status and species composition of the *somuncurae* group (Breitman *et al.*,  
16  
17 529 2011a).

20  
21 530 The last two species recently described for the *lineomaculatus* group were *Liolaemus*  
22  
23 531 *morandae* from south of Chubut province (Argentina) and *L. avilae* from Puesto Lebrum (Santa  
24  
25 532 Cruz, Argentina; Breitman *et al.*, 2011b); both species were compared with the remaining species of  
26  
27 533 the group. The last recently described species of the section is *L. caparensis* from Campo Las  
28  
29 534 Piedras Plateau (Santa Cruz, Argentina); this new species was compared with *L. magellanicus*  
30  
31 535 (Breitman *et al.*, 2011c) and both are proposed to comprise the *magellanicus* group (Breitman *et al.*,  
32  
33 536 2011a, c). Including this last described three species, the number of species now included in the *L.*  
34  
35 537 *lineomaculatus* section reaches 21; but Breitman *et al.* (2012; MF Breitman, unpubl. data) found at  
36  
37 538 least ten more candidate species are present in the *L. lineomaculatus* section, several of which are  
38  
39 539 under formal description.

40  
41  
42 540 Table 2 summarizes the details of this review and includes characters that have been  
43  
44 541 proposed to be diagnostic among groups. We did not include the *magellanicus* group (*sensu* Cei,  
45  
46 542 1986) in this table because when it was morphologically diagnosed, the species *Liolaemus*  
47  
48 543 *lineomaculatus* was included, and (since then) sufficient evidence has been presented to consider *L.*  
49  
50 544 *lineomaculatus* more closely related to other species of the *lineomaculatus* group (*sensu* Etheridge,  
51  
52 545 1995). Figure 2 shows the phylogenetic relationships proposed for most of the species of the section  
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3 546 by Schulte & Moreno-Roark (2011; which includes data from Espinoza *et al.*, 2004) and Breitman  
4  
5 547 *et al.*, 2011a.  
6  
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8 548 MORPHOLOGICAL ANALYSES  
9

10 549 *Evaluating the morphological hypothesis among groups*  
11

12  
13 550 Differences among morphological groups recognized in the literature (Table 2) were  
14  
15 551 evaluated qualitatively. Figure 3 depicts shape, disposition and size of dorsal scales of one adult  
16  
17 552 male from each species collected from its type locality or nearby. Among species in the *kingii* and  
18  
19 553 *archeforus* groups scales exhibited variation in keel expression, imbrication, size and mucronation;  
20  
21 554 no differentiation in the characters among groups could be found to match what has previously been  
22  
23 555 described in the literature. All species of the *lineomaculatus* group possess keeled tridentate scales,  
24  
25 556 although these scale types were scarce in individuals of *Liolaemus avilae*, *L. lineomaculatus* and *L.*  
26  
27 557 *morandae*.  
28  
29  
30

31 558 Table 3 summarizes results of qualitative comparisons among species of each group based  
32  
33 559 on dorsal background color, presence of red/orange scales and belly color. In contrast to  
34  
35 560 descriptions in the literature, we found that reddish/yellowish-brown and gray dorsal background  
36  
37 561 colors were present in all groups; and none were diagnosed by unique dorsal background colors.  
38  
39 562 Red or orange scales occurred in nearly all species of the *kingii* and the *archeforus* groups, one  
40  
41 563 species of the *lineomaculatus* group, and neither species of the *magellanicus* group. A higher  
42  
43 564 percentage of red scales was not observed among species of the *archeforus* group compared with  
44  
45 565 those of the *kingii* group, and we found no evidence that gray or yellowish colors were exclusive to  
46  
47 566 the *kingii* group, as suggested in the literature.  
48  
49  
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51 567 Although 30% of the *kingii* group's individuals were striped dorsally with complete or  
52  
53 568 broken bands and no *archeforus* group's individuals showed this pattern, this character was far from  
54  
55 569 exclusive or "prevailing" in the *kingii* group. Fully 75% of *archeforus* group males had indistinct or  
56  
57 570 almost indistinct dorsal bands, but this percentage was not observed in females (Tables 2, 4,  
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3 571 Appendix 2). Small differences in vertebral and paravertebral lines were observed among females  
4  
5 572 of the *kingii* and *archeforus* groups, but no differences were observed when males were compared.  
6  
7 573 Moreover, no differences in dorsolateral patterns or ventral variegation were found between the  
8  
9 574 *kingii* and *archeforus* groups, as proposed in the literature (Tables 2, 4, Appendix 2). Once again, in  
10  
11 575 contradiction to what has previously been reported in the literature, we observed whole ventral  
12  
13 576 melanism in only 12.5% of *kingii* and *archeforus* group males, and we found no differences in the  
14  
15 577 percentage of whole ventral melanism among groups (Table 2, 4, Appendix 2).  
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18  
19 578 Because sexual dimorphism in the variable midbody scales was not observed within each  
20  
21 579 group (Appendix 3), we performed a non-parametric Kruskal-Wallis test among groups (without  
22  
23 580 sex discrimination). Statistical differences in midbody scales were observed among all groups ( $H =$   
24  
25 581  $243.89$ ,  $p = 0.0001$ ). However, we recovered highly overlapped ranges (*kingii* group: mean = 75.72,  
26  
27 582 min = 64, max = 93; *archeforus* group: mean = 69.97, min = 55, max = 84) that were rather  
28  
29 583 different than those proposed in the literature (*kingii* group: mean = 79.15, min = 72, max = 97;  
30  
31 584 *archeforus* group: mean = 68.94, min = 58, max = 78) (Figure 4).  
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34  
35 585 We compared SVL among groups using ANOVA (since assumptions were met) and found  
36  
37 586 differences among groups partitioned by sex (females:  $F = 36.67$ ,  $p = 0.0001$ ; males:  $F = 57.42$ ,  $p =$   
38  
39 587  $0.0001$ ). Although DGC comparisons did not show differences among *kingii* and *archeforus* groups,  
40  
41 588 we found statistically significant differences among *lineomaculatus*, *magellanicus* and *kingii*-  
42  
43 589 *archeforus* groups (Figure 5). Moreover, only *Liolaemus tari* reached the SVL reported in the  
44  
45 590 literature (101 mm) while most of the other species did not reach 90 mm (Figure 6).  
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48  
49 591 We did not find that forelimb length was shorter in specimens of the *kingii* group relative to  
50  
51 592 the *archeforus* group, as reported in the literature. Forelimb length was calculated as radius-ulna  
52  
53 593 length + hand length distance, females and males were analyzed separately since there were  
54  
55 594 statistical differences among them within each species, with males having longer forelimbs than  
56  
57 595 females (Appendix 4). Differences in forelimb length among groups without SVL standardization  
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3 596 calculated using ANOVA were significant (females:  $F = 21.49$ ,  $p = 0.0001$ ; males:  $F = 34.65$ ,  $p =$   
4  
5 597  $0.0001$ ) among the *lineomaculatus*, *magellanicus* and *kingii-archeforus* groups, but not different  
6  
7 598 between the *kingii* and *archeforus* groups. When differences in forelimb length were evaluated  
8  
9 599 using the standardized (by SVL) data set, no statistical significance was found across the four  
10  
11 600 morphological groups (females:  $F = 3.07$ ,  $p = 0.38$ ; for males, although ANOVA's  $p$ -value was  
12  
13 601 significant, no differences were found using DGC comparisons, meaning that no differences were  
14  
15 602 recovered:  $H = 30.37$ ,  $p = 0.0001$ ). While *lineomaculatus* group males did not have precloacal pores,  
16  
17 603 the number of precloacal pores did not differ among males of the *kingii* and *archeforus* groups  
18  
19 604 (*kingii* group: mean = 7.21, min:5, max:10; *archeforus* group: mean = 7.39, min:4, max:11),  
20  
21 605 although those values were higher than those for the *magellanicus* group (mean = 3.67, min:3,  
22  
23 606 max:5).  
24  
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26

27 607 Multivariate analysis showed sexual dimorphism in the *kingii* and *archeforus* groups for the  
28  
29 608 meristic, morphometric and standardized (by SVL) morphometric data sets, and in the  
30  
31 609 *lineomaculatus* group for the morphometric and standardized morphometric data set (Table 5). No  
32  
33 610 evidence of differentiation among the *kingii* and *archeforus* groups was observed in any of the  
34  
35 611 DFA, while differentiation among *magellanicus*, *lineomaculatus* and *kingii-archeforus* groups was  
36  
37 612 observed.  
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41 613 The DFA of the meristic data set recovered the first two axes with 97.99% of the explained  
42  
43 614 variance. The first axis was mainly explained by ventral (0.69), supralabial (0.39) and midbody  
44  
45 615 (0.34) scales; while the second axis was mainly explained by dorsal (-0.62), lorilabial (0.64),  
46  
47 616 supralabial (0.4) and ventral scales (0.34). Figure 7-a shows the bivariate plot for axes 1 and 2.  
48  
49 617 Total classification error of this analysis was 36.36%, and it was particularly high for *kingii* and  
50  
51 618 *archeforus* groups separated by sex (*archeforus* females: 59.26%; *archeforus* males: 47.14%; *kingii*  
52  
53 619 females: 51.85%; *kingii* males: 45.1%). This error was low for the *lineomaculatus* group (8.51%),  
54  
55 620 and zero for the *magellanicus* group. From this analysis we find support for recognizing the  
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3 621 *lineomaculatus* and *magellanicus* groups as morphologically distinct groups of species, and  
4  
5 622 although there is a tendency of separation among the *kingii* and *archeforus* groups, statistically this  
6  
7 623 is insufficient to discriminate these last two groups.  
8  
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10 624 The DFA on the morphometric data set recovered the first two axes with 91.58% of the  
11  
12 625 explained variance. The first axis was mainly explained by head width (-0.75), distance between  
13  
14 626 fore and hind limbs (0.67), auditory meatus height (0.58), tibia-fibula length (0.55), hand length (-  
15  
16 627 0.54), foot length (0.49) and rostral-eye distance (-0.83), while the second axis was mainly  
17  
18 628 explained by head length (1.3), distance between fore and hind limbs (-1.04), rostral-eye distance (-  
19  
20 629 0.83) and head height (0.52). Figure 7-b shows the bivariate plot, with a total classification error of  
21  
22 630 29.82%; similar values were obtained for all the groups (*archeforus* females: 41.03%; *archeforus*  
23  
24 631 males: 32.26%; *kingii* females: 22.86%; *kingii* males: 29.79%; *lineomaculatus* females: 28.95%;  
25  
26 632 *lineomaculatus* males: 25%; *magellanicus*: 25%). Overall, a slight differentiation in size among the  
27  
28 633 *kingii-archeforus* and the *lineomaculatus-magellanicus* groups is evident, with males being bigger  
29  
30 634 in head size (HL) while females show higher values of SVL, distance between fore and hind limbs  
31  
32 635 and rostral-eye distance (Figure 7-b). Similar results were observed in the DFA of the standardized  
33  
34 636 morphometric (by SVL) data set, with the first two axes explaining 91.1% of the variance. The first  
35  
36 637 axis was mainly explained by rostral-eye distance/SVL (-0.85), distance between fore and hind  
37  
38 638 limbs/SVL (-0.57), hand length/SVL (0.48) and tibia-fibula length/SVL (-0.43), while the second  
39  
40 639 axis was mainly explained by auditory meatus height/SVL (0.53), head length/SVL (0.48) and  
41  
42 640 distance between fore and hind limbs/SVL (-0.44). Figure 7-c shows the bivariate plot for axes 1  
43  
44 641 and 2; the total classification error of this analysis was 30.77%, and similar values were obtained for  
45  
46 642 all the groups (*archeforus* females: 38.46%; *archeforus* males: 35.48%; *kingii* females: 31.43%;  
47  
48 643 *kingii* males: 25.53%; *lineomaculatus* females: 21.05%; *lineomaculatus* males: 27.08%;  
49  
50 644 *magellanicus*: 41.18%). As in the previous analysis, the plot shows size differentiation between the  
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3 645 *kingii-archeforus* and *lineomaculatus-magellanicus* groups, and some minor differences between  
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5 646 the sexes within them.  
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8 647 *Morphological comparisons among species within groups*  
9

10 648 Mean, standard deviation and range of variables from each species discriminated by sex is  
11  
12 649 presented in Appendices 5 to 7. Sexual dimorphism for the meristic data set was observed only for  
13  
14 650 the characters supralabial scales in *Liolaemus baguali* and *L. tristis*, infralabial scales in *L.*  
15  
16 651 *sarmientoi* and dorsal scales in *L. silvanae* and *L. tari* (Appendix 5). Sexual dimorphism for the  
17  
18 652 morphological data set was observed in several variables of most of the species, but results ranged  
19  
20 653 from no differences in any studied variables in *L. magellanicus*, to sexual dimorphism in almost all  
21  
22 654 the variables in *L. gallardoi* and *L. tristis* (Appendix 6). Sexual dimorphism in SVL was found in *L.*  
23  
24 655 *chacabucoense*, *L. kolengh* and *L. tristis*, and for those species data was standardized by the SVL  
25  
26 656 (Appendix 7).  
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29

30 657 Morphometric and meristic differences among all species within each group were found  
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32 658 (Table 6, 7, 8 and 9; Appendices 8 and 9); between-sex tests were performed according to the  
33  
34 659 MANOVA results (see materials and methods; Table 5). A higher number of between-species  
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36 660 differences in the morphometric variables were found among females of the *kingii-archeforus* group  
37  
38 661 relative to males, much less differences were found in the meristic data set. Although we found  
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40 662 morphometric and/or meristic differences among all species within all groups, there were two pairs  
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42 663 of species in which no differences were found: between female *Liolaemus kingii* and *L. tristis*, and  
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44 664 between male *L. chacabucoense* and *L. archeforus*, but in both cases differences were found in  
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46 665 coloration patterns (Table 3).  
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60**DISCUSSION**

667  
668           The morphological classification of the species included in the *Liolaemus lineomaculatus*  
669 section was proposed several decades ago, and while it is currently in use (Cei & Scolaro, 1982a,  
670 1983; Scolaro & Cei, 1997; Núñez & Scolaro, 2009; Minoli, Kozykarisky & Avila, 2010;  
671 Fontanella *et al.*, 2012) it has never been properly revised until now. In this manuscript we have  
672 summarized the characters that were proposed to diagnose three morphological groups within the *L.*  
673 *lineomaculatus* section (*kingii*, *archeforus* and *lineomaculatus*), and we evaluated the  
674 morphological variation in two species (*L. magellanicus* and *L. caparensis*) that were not clearly  
675 assigned to any of these three morphological groups, but were included in an independent clade  
676 with molecular data called *magellanicus* group (Etheridge, 1995; Breitman *et al.*, 2011a). We show  
677 that the traditional practice of classifying eleven species in two (*kingii* and *archeforus*) of the tree  
678 traditional morphological groups of the section, which is not supported by molecular data, also is  
679 not supported by morphological data and therefore should be abandoned. We also documented  
680 some interesting patterns of sexual dimorphism within each group, and discuss these in an  
681 ecological and evolutionary context.

***LIOLAEMUS LINEOMACULATUS* SECTION: PAST**

682  
683           Lizards from the *Liolaemus lineomaculatus* section have been used for testing evolutionary  
684 hypotheses about past demographic changes and speciation patterns (Breitman *et al.*, 2011a, 2012),  
685 ecological and physiological questions have been also addressed for some species of this section  
686 (Ibargüengoytía *et al.*, 2010; Bonino *et al.*, 2011; Fernández *et al.*, 2011). Refugia and  
687 phylogeographic breaks have been proposed for Patagonia based on the molecular study of these  
688 lizards (Breitman *et al.*, 2012), some of which are geographically concordant with those identified  
689 in other lizards clades, rodents, flowering plants and trees (Sérsic *et al.*, 2011).

690           Two lines of evidence have been used to evaluate the species arrangement within the  
691 *Liolaemus lineomaculatus* section, a traditional one based on general morphological similarities

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3 692 (Ceï & Scolaro, 1982b, 1983), and another one based on molecular markers analyzed using  
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5 693 phylogenetic methods (Espinoza *et al.*, 2004; Schulte & Moreno-Roark, 2010; Breitman *et al.*,  
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7 694 2011a). Both sources of evidence have shown congruence as well as incongruence, and since the  
8  
9 695 last extension of the ‘morphological arrangement hypothesis’ eight new species have been  
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11 696 described (Ceï & Scolaro, 1996; Pincheira-Donoso & Nuñez, 2005; Abdala & Lobo, 2006; Scolaro  
12  
13 697 & Ceï, 2006; Nuñez & Scolaro, 2009; Breitman *et al.*, 2011b, c), but there has been no revision of  
14  
15 698 the morphological hypothesis nor a comparison with the molecular one. Morphological as well as  
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17 699 molecular evidence supported the *lineomaculatus* group (Etheridge, 1995; Espinoza *et al.*, 2004;  
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19 700 Schulte & Moreno-Roark, 2010; Breitman *et al.*, 2011a), and the ‘morphological arrangement  
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21 701 hypothesis’ (but not the molecular hypothesis) supported the recognition of the *kingii* and  
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23 702 *archeforus* groups as distinct sister groups (Ceï, 1979; Ceï & Scolaro, 1982a, 1983; Laurent, 1983,  
24  
25 703 1895; Scolaro & Ceï, 1997; Pincheira-Donoso & Nuñez, 2005). The species *L. magellanicus* was  
26  
27 704 hypothesized as closely related to *L. lineomaculatus* on the basis of morphological similarities, but  
28  
29 705 based on the first molecular phylogenetic study of this section (Breitman *et al.*, 2011a, c), *L.*  
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31 706 *magellanicus* and *L. caparensis* are recovered in a strongly supported clade identified as  
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33 707 *magellanicus* group.

#### 38 708 *LIOLAEMUS LINEOMACULATUS* SECTION: PRESENT

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41 709 The *Liolaemus lineomaculatus* section is composed of 21 species distributed over a large  
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43 710 area in Patagonia. In this paper, we present several classes of statistical analyses of morphological  
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45 711 data and our results are concordant with the molecular evidence in recognizing three groups within  
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47 712 *L. lineomaculatus* section: *lineomaculatus*, *magellanicus* and *kingii* groups. The *kingii* group  
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49 713 (referred as *kingii-archeforus* group in the *Materials and Methods* and *Results* sections of this  
50  
51 714 paper) includes all the species that were previously recognized as two separate groups (*kingii* and  
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53 715 *archeforus*); since all the characters that had been previously considered diagnostic under the  
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55 716 ‘morphological arrangement hypothesis’ for each group failed to clearly distinguish between them,  
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3 717 we discourage the recognition of the *kingii* and *archeforus* groups as two differentiated entities and  
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5 718 we consider all their 11 species included in one group called the *kingii* group (since this was the  
6  
7 719 first described species from the group). Morphological characters do support differentiation of the  
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9  
10 720 *magellanicus* group, recently proposed on the basis of molecular data.

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12 721 Molecular data suggested that the divergence time between the *L. lineomaculatus* section  
13  
14 722 and its sister clade (*montanus* section) occurred at Middle Miocene (14.36 Mya; 95% HPD =  
15  
16 723 10.25–18.64); the *lineomaculatus* group got differentiated from the (*magellanicus*, *kingii*) clade  
17  
18 724 around the Late Miocene (8.46 Mya; 95% HPD = 6.26–10.84); and the *kingii* group diverged from  
19  
20 725 the *magellanicus* group around Late Miocene/Early Pliocene (5.87 Mya; 95% HPD = 4.26–7.62)  
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22 726 (Breitman *et al.*, 2011a).

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26 727 *The lineomaculatus* group

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28 728 The *lineomaculatus* group includes six species: *Liolaemus avilae*, *L. hatcheri*, *L. kolengh*, *L.*  
29  
30 729 *lineomaculatus*, *L. morandae* and *L. silvanae*. The distribution of these species extends from central  
31  
32 730 Neuquén (Christie, 2002) to south of Santa Cruz province, with some species widespread and others  
33  
34 731 geographically restricted. The group and the morphological characters that define it were  
35  
36 732 established by Etheridge (1995): absence of preloacal pores and presence of dorsal tridentate (or  
37  
38 733 trifold) scales. Molecular support for this group is based on mitochondrial (Espinoza *et al.*, 2004;  
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40 734 Schulte & Moreno-Roark, 2010) and nuclear genes, both analyzed using standard concatenation as  
41  
42 735 well as a species tree approach (Breitman *et al.*, 2011a).

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45  
46 736 This group differs from the *magellanicus* and the *kingii* groups by the absence of preloacal  
47  
48 737 pores and the presence of trifold scales (individuals of *Liolaemus avilae*, *L. morandae* and *L.*  
49  
50 738 *lineomaculatus* present a lower percentage of trifold scales relative to *L. hatcheri*, *L. kolengh* and *L.*  
51  
52 739 *silvanae*), a characteristic that was previously described in the literature (Etheridge, 1995). Also, the  
53  
54 740 number of ventral scales (61–94 *lineomaculatus*, 49–72 *magellanicus*, 78–113 *kingii*) and midbody  
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56 741 scales (43–65 *lineomaculatus*, 36–46 *magellanicus*, 55–93 *kingii*) is intermediate for the

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3 742 *lineomaculatus* group compared to the *magellanicus* and *kingii* groups (with some degree of  
4  
5 743 overlapping); and also, they have an intermediate body size in agreement with the meristic  
6  
7 744 variables. A disparate coloration pattern relative to the *kingii* group was also observed, while  
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9  
10 745 species of the *lineomaculatus* group are characterized by two paravertebral and quadrangular black  
11  
12 746 or brown series of blotches surrounded by two well-defined whitish lines (in general, to the tip of  
13  
14 747 the tail); species of the *kingii* group do not show this pattern and present transversal lines or a wide  
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16 748 vertebral line (Fig. 1). Sexual dimorphism is not evident in the meristic characters, but it is in the  
17  
18 749 morphometric characters within the species included in the *lineomaculatus* group, with males  
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20 750 having bigger heads and females having longer bodies.

#### 21 22 23 751 *The magellanicus group*

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25  
26 752 The *magellanicus* group includes *Liolaemus magellanicus* and *L. caparensis*, which have  
27  
28 753 the southernmost distributions of the *L. lineomaculatus* section; with *L. caparensis* only known  
29  
30 754 from its type locality (Breitman *et al.*, 2011c), while *L. magellanicus* is widespread south of the  
31  
32 755 Santa Cruz river and is the only species of *Liolaemus* inhabiting Tierra del Fuego Island (Bottari,  
33  
34 756 1975).

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36  
37 757 The *magellanicus* group is a well-differentiated clade in both molecular and morphological  
38  
39 758 characters. This two-species group have the lowest number of ventral and midbody scales of the  
40  
41 759 *Liolaemus lineomaculatus* section, both possess precloacal pores but these are fewer in number  
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43 760 relative to the *kingii* group, and are strongly differentiated from the *kingii* group in both the dorsal  
44  
45 761 and ventral patterns. Sexual dimorphism is not present in either meristic or morphometric characters  
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47 762 within this group.

#### 48 49 50 51 763 *The kingii group*

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53 764 With this morphological review, we set up a “new” starting point for the species of this  
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55 765 group because the traditional differentiation in two groups (*kingii* and *archeforus*), that was not  
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57 766 supported by molecular data (Espinoza *et al.*, 2004; Schulte & Moreno-Roark, 2010; Breitman *et*

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2  
3 767 *al.*, 2011a, c), is neither supported by the extensive morphological data presented here. Thus, we  
4  
5 768 strongly recommend using the name *kingii* to refer to the group formed by: *Liolaemus archeforus*,  
6  
7 769 *L. baguali*, *L. chacabucoense*, *L. escarchadosi*, *L. gallardoi*, *L. kingii*, *L. sarmientoi*, *L. scolaroi*, *L.*  
8  
9 770 *somuncurae*, *L. tari*, *L. tristis*, *L. uptoni* and *L. zullyae*. Some of these species present relative large  
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11 771 distributions (e.g., *L. escarchadosi*, *L. gallardoi*, *L. kingii* and *L. sarmientoi*) while others have  
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13 772 more restricted ones (e.g., *L. somuncurae*, *L. tari*, *L. tristis* and *L. uptoni*).  
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16  
17 773 The *kingii* group is differentiated from the *lineomaculatus* and *magellanicus* groups based  
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19 774 on molecular and morphological evidence, as described above. Species within the *kingii* group are  
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21 775 the largest and present the highest number of scale counts among the groups of the *Liolaemus*  
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23 776 *lineomaculatus* section. They also present a different coloration pattern characterized by the  
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25 777 presence of transversal bands (complete, broken or indistinct), but never showing the characteristic  
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27 778 dorsal pattern of the *lineomaculatus* or *magellanicus* groups (two paravertebral and quadrangular  
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29 779 series of black or brown blotches surrounded by two well-defined whitish lines). Sexual  
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31 780 dimorphism is evident in the meristic as well as in the morphometric characters in the species  
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33 781 included in this group.  
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#### 36 782 SEXUAL DIMORPHISM

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39 783 Beyond the immediate implications of this study, we found some interesting patterns of  
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41 784 sexual dimorphism within each group. In the *magellanicus* group sexual dimorphism is not found in  
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43 785 either meristic or morphometric variables, while in the *lineomaculatus* group it is present only in the  
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45 786 morphometric data set, and in the *kingii* group it is present in both meristic and morphometric data  
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47 787 sets.  
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51 788 In the *kingii* and *lineomaculatus* groups the same characters explained the morphometric  
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53 789 differences between males and females; we found that males possess longer and wider heads than  
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55 790 females, and females show thinner snouts (measured as the distance from the eye to rostral scale).  
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57 791 Sexual differences in shape and size have been widely studied in animals and in lizards specifically  
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3 792 (Selander, 1966; Schoener, 1967; Anderson & Vitt, 1990), and two principal causes are mentioned  
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5 793 in the literature to explain them. The first one is sexual selection, where a trait is selected because it  
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7 794 confers an advantage in intrasexual competition or mate choice. The other explanation is ecological  
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9 795 niche divergence, when resources are scarce species may partition the niche in order to avoid  
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11 796 competition, thus natural selection promotes phenotypic divergence (Selander, 1966; Schoener,  
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13 797 1967; Anderson & Vitt, 1990). The different causes of sexual dimorphism in head size were  
14  
15 798 recently studied in 19 species of *Liolaemus* (including two from the *lineomaculatus* group and five  
16  
17 799 from the *kingii* group), different sex-dependent mechanisms promoting the divergence in head size  
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19 800 were reported, suggesting that male and female *Liolaemus* are subject to different selective  
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21 801 pressures (Vanhooydonck *et al.*, 2010). For males, sexual selection seems to be operating on bite-  
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23 802 force performance, which favors increased head size; while for females differentiation in head size  
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25 803 is being promoted by natural selection for prey capture (Vanhooydonck *et al.*, 2010). We did not  
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27 804 find head-size sexual dimorphism in the *magellanicus* group, suggesting that either sexual or natural  
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29 805 selection mechanisms are not acting on these traits. One possible explanation is that since the  
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31 806 species *L. magellanicus* inhabits suboptimal thermal environments (Bonino *et al.*, 2011; Fernández  
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33 807 *et al.*, 2011), selection pressures may operate more strongly on traits related to surviving in cold  
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35 808 environments. Interestingly, in northern hemisphere lizards all lineages that occur in seasonal areas  
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37 809 with colder temperature are reported to be monomorphic (Anguilletta, Oufiero & Leaché, 2006;  
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39 810 Corl *et al.*, 2009).

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45 811 Females from the *lineomaculatus* and *kingii* groups have larger body sizes than males, this  
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47 812 characteristic was also observed in other *Liolaemus* species (e.g., Verrastro, 2002) as well as in  
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49 813 other lizard genera (e.g., Butler, 2007). Larger female body sizes are generally associated with  
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51 814 larger clutch sizes or individual egg/embryo sizes (Vitt & Cooper, 1985; Olsson *et al.*, 2002),  
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53 815 thereby providing higher reproductive success.  
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3 816 Sexual dimorphism was also observed in the meristic data but only for the *kingii* group, in  
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5 817 which males are characterized by a higher number of lorilabial and supralabial scales and a lower  
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7 818 number of dorsal scales relative to females; these results are concordant with the morphometric data  
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9 819 showing males with bigger heads and females with larger body sizes. Abundant evidence have been  
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11 820 presented for the invariance of scale number with respect to the age (thus, size) in lizards; thus,  
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13 821 these meristic results may be suggesting that further study needs to be conducted within the *kingii*  
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15 822 group to understand the differential selective pressures on body size.  
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19 823 The topic of sexual dimorphism is complex and interesting, and traditional as well as new-  
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21 824 available methods offer a wide set of tools for testing these first round of hypotheses. We included  
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23 825 this section on *Sexual Dimorphism* in our manuscript to highlight some interesting observations  
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25 826 with the aim of encourage more detailed studies on these emerging patterns within the *Liolaemus*  
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27 827 *lineomaculatus* section. We foresee many future and interesting studies in behavioral, evolutionary  
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29 828 and physiological ecology.  
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## 32 829 CONCLUSION

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35 830 In this study, we have not found evidence to support the formerly recognized *kingii* and  
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37 831 *archeforus* species groups within the *Liolaemus lineomaculatus* section. Our review and analyses  
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39 832 provide evidence that species within both of these groups should be considered as a single group  
40  
41 833 called the *kingii* group, which is clearly differentiated from the *lineomaculatus* and *magellanicus*  
42  
43 834 groups. We are tentatively more confident in this conclusion because the morphological  
44  
45 835 differentiation of this *kingii* group is also supported by the current molecular phylogenetic  
46  
47 836 hypothesis for the section. Finally, we have briefly discussed the sexual dimorphism present in  
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49 837 these lizards in order to provide a starting point for future research. We hope that, through this  
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51 838 contribution, we have provided a strong foundation for future research in *Liolaemus*.  
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3 1132 **FIGURE 1:** Map of southern Patagonia showing distribution sites for species formerly included in  
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5 1133 the *archeforus* (blue), *kingii* (green), *lineomaculatus* and *magellanicus* (pink) groups. Numbers  
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7 1134 represent localities used in this study, type localities are shown in bold (black or white). Picture-size  
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9 1135 differences represent differences in body size among species.

10 1136 **FIGURE 2:** Phylogenetic relationships hypothesized for the *L. lineomaculatus* section using  
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12 1137 nuclear (nu) and/or mitochondrial (mt) genes; (A) Species tree inferred using mt and nu genes by  
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14 1138 Breitman *et al.* 2011a; posterior probability (*Pp*) values higher than 0.5 are shown, bold branches  
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16 1139 show clades with *Pp* > 0.95; (B) Bayesian tree, representing concatenated analyses and  
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18 1140 summarizing information from Maximum Parsimony (MP) and Maximum Likelihood (ML)  
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20 1141 methods from Breitman *et al.* 2011a; nodes with high support from three methods (MP jackknife  
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22 1142 and ML bootstrap >0.70; *Pp* > 0.95) are identified by bold branches; open squares show nodes with  
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24 1143 weak MP support, and circles nodes with weak MP and ML support; (C) Maximum Likelihood tree  
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26 1144 recovered using mt genes by Schulte and Moreno-Roark 2010.

27 1145 **FIGURE 3:** Pictures of dorsal scales of all the species belonging to the *archeforus*, *kingii*,  
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29 1146 *lineomaculatus* and *magellanicus* groups. Squares are 1 cm<sup>2</sup>. No differences or trends can be  
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31 1147 observed among scales of the species included in the *kingii* and *archeforus* groups.

32 1148 **FIGURE 4:** Number of midbody scales among individuals of the *archeforus*, *kingii*, *lineomaculatus*  
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34 1149 and *magellanicus* groups. No statistically significant differences are found between the *kingii* and  
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36 1150 *archeforus* groups. Females are shown in white and males are shown in gray.

37 1151 **FIGURE 5:** Snout–vent length (SVL, expressed in millimeters) among individuals of the  
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39 1152 *archeforus*, *kingii*, *lineomaculatus* and *magellanicus* groups. No statistically significant differences  
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41 1153 are found between the *kingii* and *archeforus* groups. Females are shown in white and males are  
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43 1154 shown in gray.

44 1155 **FIGURE 6:** Snout–vent length (SVL, expressed in millimeters) among individuals of all the species  
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46 1156 of the *archeforus*, *kingii*, *lineomaculatus* and *magellanicus* groups. Females are shown in white and  
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48 1157 males are shown in gray.

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3 1158 **FIGURE 7:** Graphics of the Discriminant Function Analysis performed on the: (A) meristic; (B)  
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5 1159 morphometric; and (C) morphometric standardized by SVL data sets. In orange *magellanicus*  
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7 1160 group, in purple *lineomaculatus* group (fuchsia: males, pink: females), in blue *archeforus* group  
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9 1161 (dark blue: males, light blue: females) and in green *kingii* group (dark green: males, light green:  
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11 1162 females). No statistically significant differences were found between the *kingii* and *archeforus*  
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13 1163 groups. There are significant differences between the *magellanicus* and *lineomaculatus* groups, and  
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15 1164 between these and all the species of the *kingii* and *archeforus* groups.  
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**TABLE 1:** Sample size of individuals used in morphometric and meristic analyses; sample size of individuals having intact tail is also provided. Values are given for Females (F), Males (M) and total.

	Morphometric			Meristic			Intact tail		
	F	M	Total	F	M	Total	F	M	Total
<i>L. archeforus</i>	3	8	11	4	8	12	1	2	3
<i>L. avilae</i>	4	5	9	4	5	9	4	5	9
<i>L. baguali</i>	6	6	12	13	8	21	3	4	7
<i>L. caparensis</i>	5	3	8	7	3	10	4	3	7
<i>L. chacabucoense</i>	6	9	15	9	12	21	4	6	10
<i>L. escarchadosi</i>	4	5	9	5	8	13	2	3	5
<i>L. gallardoi</i>	15	17	32	23	18	41	14	14	28
<i>L. hatcheri</i>	6	12	18	8	12	20	3	6	9
<i>L. kingii</i>	10	14	24	14	15	29	6	10	16
<i>L. kolengh</i>	12	15	27	16	15	31	9	12	21
<i>L. lineomaculatus</i>	4	6	10	5	6	11	4	4	8
<i>L. magellanicus</i>	4	6	10	4	6	10	4	4	8
<i>L. morandae</i>	4	2	6	5	2	7	2	1	3
<i>L. sarmientoi</i>	4	7	11	4	7	11	4	6	10
<i>L. scolaroi</i>	1	4	5	1	5	6	1	4	5
<i>L. silvanae</i>	8	9	17	8	9	17	5	3	8
<i>L. somuncurae</i>	6	10	16	6	10	16	3	6	9
<i>L. tari</i>	5	5	10	7	5	12	4	4	8
<i>L. tristis</i>	9	11	20	17	12	29	6	9	15
<i>L. uptoni</i>	4	6	10	5	6	11	4	5	9
<i>L. zullyae</i>	1	7	8	1	7	8	1	6	7
<b>Total</b>	121	167	288	167	179	345	88	117	205

**TABLE 2:** Species included in each traditional morphological group of the *L. lineomaculatus* section (*kingii*, *archeforus* and *lineomaculatus* groups), distribution and morphological differences are taken from bibliographic references. Quoted sentences were textually extracted from the source. SVL: snout–vent length. Blank cells indicate no available data in the literature. The species *L. magellanicus* and *L. caparensis* were not formally included in any of the traditional morphological groups, thus they are not included in this table. Results from this study are presented in the last column. “Rejected” means that alluded morphological differences among groups are not recovered with our data.

	<i>kingii</i> group	<i>archeforus</i> group	<i>lineomaculatus</i> group	This study
<b>Species</b>	<i>L. baguali</i> , <i>L. kingii</i> , <i>L. somuncurae</i> , <i>L. tristis</i> , <i>L. uptoni</i>	<i>L. archeforus</i> , <i>L. chacabucoense</i> , <i>L. escarchadosi</i> , <i>L. gallardoi</i> , <i>L. sarmientoi</i> , <i>L. scolaroi</i> , <i>L. tari</i> , <i>L. zullyae</i>	<i>L. avilae</i> , <i>L. hatcheri</i> , <i>L. kolengh</i> , <i>L. lineomaculatus</i> , <i>L. morandae</i> , <i>L. silvanae</i>	No evidence for separation of these species in the <i>kingii</i> and <i>archeforus</i> groups
<b>Distribution</b>	“Widespread, from the coast to the sub-andean region of the Santa Cruz”. In Chubut and on the Somuncurae Plateau (Río Negro)	“Isolated populations in volcanic mountains along the western area of Santa Cruz”	Some widespread from Neuquén to Santa Cruz, others endemic to Andean plateaus of Santa Cruz	Not all the species of the <i>archeforus</i> groups are isolated. Some species of the <i>kingii</i> group are isolated
<b>Dorsal scales</b>	“Not strongly keeled, distinctly imbricated”; small scales	“More strongly keeled and sharply imbricated”; big and mucronated	Presence of keeled tridentate scales	Partially Rejected. No differentiation among scales of <i>kingii</i> and <i>archeforus</i> clades. Tridentate scales were observed only in the <i>lineomaculatus</i> group
<b>Midbody scales</b>	72–97 (Mean: 79.15)	58–78 (Mean: 68.94)	-	Partially observed. Differences in mean but not in ranges (Figure 4)
<b>SVL</b>	62–100 mm	64–102 mm	-	Not diagnostic
<b>Forelimbs</b>	“Relatively short”	“Larger than in <i>kingii</i> group”	-	Rejected. No differences in forelimb length between <i>kingii</i> and <i>archeforus</i> groups (Appendix 4)
<b>Dorsal background</b>	“Reddish/yellowish-brown”	“Dark gray or brownish”	-	Rejected. No differences in coloration among groups (Table 3)
<b>Dorsal pattern</b>	“Prevailing white or yellowish black bordered bands mainly with conspicuous central spot”	“White or yellowish transverse streaks or broken irregular and almost indistinct lines”	-	Not exclusive. Tendency of absence of bands was observed in males of the <i>archeforus</i> group. Only 30% of individuals of the <i>kingii</i> group showed bands (Table 4)
<b>Dorsolateral lines</b>	Unusually	Broken lines	-	Rejected. Same percentage of DL lines in both groups (Table 4)
<b>% Red/Orange</b>	Very low	Noticeable percentage	-	Rejected. Almost all the species of both groups presented red or orange scales (Table 3)

## scales

<b>Belly color</b>	Whitish gray or yellowish	-	-	Rejected. Several colors were observed including: Black, white, orange and yellow (Table 3)
<b>Variiegation</b>	More or less variegated	Strongly variegated	-	Rejected. 90% of males and females of both groups present ventral variegation (Table 4)
<b>Melanism</b>	-	Usually whole ventral melanism	-	Rejected. No differences in ventral melanism were observed (Table 4)
<b># precloacal pores</b>	5–10	6–8	Absent	Rejected (similar values between <i>kingii</i> and <i>archeforus</i> groups)
<b>Source</b>	Cei & Scolaro, 1982, 1983; Scolaro & Cei, 1997	Cei & Scolaro, 1982, 1983; Scolaro & Cei, 1997	Etheridge, 1995	

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**TABLE 3:** Qualitative characters of coloration of specimens discriminated by sex, observed from pictures taken at the time of capture. F: females; M: males; in three cases pictures were not available (No pict). Colors are expressed as: B-black, W-white, Br-Brown, G-gray, R-red, Y-yellow, O-orange, Gr-green, LB-light blue and Bl-blue.

	% Red/orange scales		Dorsal background		Dorsal colors		Belly colors	
	F	M	F	M	F	M	F	M
<i>L. baguali</i>	No	No	Br	B	B-W	B-W	B-W	B-W-Y
<i>L. kingii</i>	Yes	Yes	Br	B	B-W-Br	B-W-Y	B-W-O-Y	B-O-Y
<i>L. somuncurae</i>	No pict	Yes	No pict	R-Br	No pict	W-R-Br	No pict	O-Y
<i>L. tristis</i>	No	Yes	G	B	B-W-Br	B-W-O	B-Y	B-W-O
<i>L. uptoni</i>	Yes	Yes	R	R	B-R-O-G	R-O-Y	No pict	B-O-Y
<i>L. archeforus</i>	No	No	B	B	B-W-Y	B-W-Y	B-W-Y	B-W-Y
<i>L. chacabucoense</i>	No	Yes	B-Br	B	B-W-Br	B-W-Y	B-W-Y	B-W-Y-O
<i>L. escarchadosi</i>	Yes	Yes	B	B	B-W-Y-R	B-W-Y-R	B-W-Y-O	B-W-Y-O
<i>L. gallardoi</i>	Yes	Yes	Br-G	B	B-W-Y-O-Gr-Br	B-Y-O-R-Gr-Br	B-W-G-Bl	B-W-Y-G
<i>L. sarmientoi</i>	Yes	Yes	B	B-Y	B-Y	B-W-Y-R	B-Y-R	B-Y-R
<i>L. scolaroi</i>	Yes	Yes	G	G	B-R-Br	B-W-R-Br	B-Y-R	B-W-Y
<i>L. tari</i>	Yes	Yes	G	B	B-G	B-Y-R-G	B-W	B-W-Y-R
<i>L. zullyae</i>	Yes	Yes	Br-R	B-G	B-R-Y-Br	B-R-Y-LB	B-W	B-W-Y-O
<i>L. avilae</i>	No	No	Br-G	Br-G	B-W-Br	B-W-Br	B-W-P	B-W-Y
<i>L. hatcheri</i>	No	No	Br-G	Br-G	B-Br-G	B-W-Y	B-W	B-W
<i>L. kolengh</i>	No	Yes	Br	Y-O	B-Br	B-O-Y-Br	B-W-Y	B-W
<i>L. lineomaculatus</i>	No	No	Br	Br	B-Br-G	B-Br-G	B-W-Y-P	B-W-Y
<i>L. morandae</i>	No	No	G	G	B-W-Br-G	B-W-Y-Br-G	B-W	B-W-Y
<i>L. silvanae</i>	No	No	B	B	B-Bl	B-O-Bl	B-Bl	B-Bl
<i>L. caparensis</i>	No	No	Br	Br	B-W-Y-Br	B-O-Br-LB	B-W	B-W-Y
<i>L. magellanicus</i>	No pict	No	No pict	Br	No pict	B-W-Y-Br-LB	No pict	B-W-Y

**TABLE 4:** Dorsal pattern (including vertebral, paravertebral and dorsal strip pattern), variegation and melanism present in the morphological groups (converted to percentage whiting each group). Dorsal stripe pattern: (A) complete or slightly broken bands, (B) dotted bands, (C) irregular bands, (D) indistinct or almost indistinct bands; all these variables were illustrated and respectively described as 0–20, 40, 60 and 80–100 by Sclaro (1987). Ventral melanism: (m0) no melanism, (m1) melanism only present in gular zone, (m2) melanism only present in belly, (m3) melanism present on all body regions except the cloacal region and limbs, (m4) melanism present on all body except in limbs, (m5) melanism present in all body. F: females; M: males. N: no pattern/coloración; Y: pattern/coloration presented.

Group	Dorsal stripe pattern		Vertebral		Paravertebral		Dorsolateral		Variegation		Ventral melanism	
	F	M	F	M	F	M	F	M	F	M	F	M
<i>magellanicus</i>	-	-	40% N; 60% Y	60% N; 40% Y	40% N; 60% Y	60% N; 40% Y	100% Y	100% Y	75%	75%	50% m0; 25% m2; 12.5% m3; 12.5% m4	50% m0; 50% m2
<i>lineomaculatus</i>	-	-	85% N; 15% Y	90% N; 10% Y	85% N; 15% Y	90% N; 10% Y	40% N; 60% Y	40% N; 60% Y	80%	80%	50% m0; 50% m2	50% m0; 12.5% m2; 25% m4; 12.5% m5
<i>kingii</i>	30% A; 40% B; 15% C; 15% D	30% A; 25% B; 10% C; 35% D	50% N; 50% Y	95% N; 5% Y	50% N; 50% Y	75% N; 25% Y	95% N; 5% Y	100% N	90%	90%	50% m0; 20 m2; 20 m3; 10 m5	50% m0; 25% m2; 12.5% m3; 12.5% m5
<i>archeforus</i>	20% B; 40% C; 40% D	15% B; 10% C; 75% D	75% N; 25% Y	95% N; 5% Y	75% N; 25% Y	75% N; 25% Y	95% N; 5% Y	100% N	90%	90%	50% m0; 30 m2; 15 m3; 5 m4	50% m0; 12.5% m1; 12.5% m3; 12.5% m4; 12.5% m5

**TABLE 5:** Sexual dimorphism (Sex dim) in each group evaluated in the different data sets (morphometric, standardized morphometric and meristic) using MANOVAs.  $\neq$ : presence of sexual dimorphism;  $=$ : absence of sexual dimorphism.

Group	Morphometric			Morphometric/SVL			Meristic		
	Stadistic	<i>p</i>	Sex dim.	Stadistic	<i>p</i>	Sex dim	Stadistic	<i>p</i>	Sex Dim
<i>archeforus</i>	17.24	0.0001	$\neq$	18.06	0.0001	$\neq$	2.06	0.0384	$\neq$
<i>kingii</i>	16.26	0.0001	$\neq$	13.5	0.0001	$\neq$	2.66	0.0085	$\neq$
<i>lineomaculatus</i>	12.94	0.0001	$\neq$	19.41	0.0001	$\neq$	1.49	0.1658	$=$
<i>magellanicus</i>	4.21	0.1392	$=$	6.63	0.1383	$=$	0.51	0.832	$=$

**TABLE 6:** Meristic (below diagonal) and morphometric standardized by SVL (above diagonal) characters with statistically significant differences for **females** of the *kingii-archeforus* group are shown (taken for comparisons of significant ANOVA or Kruskal-Wallis tests). Morphometric variable names: **SVL:** snout–vent length; **TL:** tail length; **DFH:** distance between fore and hind limbs; **FOL:** foot length; **TFL,** tibia-fibula length; **RUL:** radius-ulna length; **HAL:** hand length; **HH:** head height; **HW:** head width; **HL:** head length; **RND:** rostral–nasal distance; **RH:** rostral height; **DRE:** distance from rostral to the eye; **AH:** auditory meatus height. Meristic variable names: **SCI:** scales in contact with the interparietal; **LS:** lorilabial scales; **SS:** supralabial scales; **IS:** infralabial scales; **MS:** midbody scales; **DS:** dorsal scales; **VS:** ventral scales; **IL3:** infradigital lamellae of the third finger; **IL4:** infradigital lamellae of the fourth toe.

Females	<i>L. archeforus</i>	<i>L. chacabucoense</i>	<i>L. escarchadosi</i>	<i>L. gallardoi</i>	<i>L. sarmientoi</i>	<i>L. scolaroi</i>	<i>L. tari</i>	<i>L. zullyae</i>	<i>L. baguali</i>	<i>L. kingii</i>	<i>L. somuncurae</i>	<i>L. tristis</i>	<i>L. uptoni</i>
<i>L. archeforus</i>		DFH, HAL	TFL, RUL, HW, HL, RND, DRE	RUL, HAL	RUL, HAL	RUL, HAL	RUL, HAL, HL, RND, DRE	DFH, RUL, HAL, RND	TFL, RUL, HW	DFH, RUL, HAL, AH	RUL, HAL, HL, RND, DRE	DFH, RUL, HAL	TFL, RUL, HW, HL, RND, DRE
<i>L. chacabucoense</i>	-		DFH, TFL, RUL, HAL, HW, HL, RND, DRE	DFH, RUL	DFH, RUL	DFH, RUL	DFH, RUL, HL, RND, DRE	RUL, RND	DFH, TFL, RUL, HW	RUL, AH	DFH, RUL, HL, RND, DRE	RUL	DFH, TFL, RUL, HW, HL, RND, DRE
<i>L. escarchadosi</i>	SS, DS	SS, DS		TFL, HAL, HW, HL, RND, DRE	TFL, HAL, HW, HL, RND, DRE	TFL, HAL, HW, HL, RND	TFL, HAL, HW	DFH, TFL, HAL, HW	HAL, RND	DFH, TFL, HAL, HW, RND, DRE	TFL, HAL, HW	DFH, TFL, HAL, HW, HL, RND, DRE	RUL, HAL
<i>L. gallardoi</i>	SS	SS	DS		AH	-	HL, RND, DRE	DFH, RND	TFL, HAL, HW	DFH, AH	HL, RND, DRE	DFH	TFL, RUL, HAL, HW, HL, RND, DRE, AH
<i>L. sarmientoi</i>	SS, DS, VS	SS, DS, VS	VS	DS, VS		-	HL, RND, DRE	DFH, RND	TFL, HAL, HW	DFH	HL, RND, DRE	DFH	TFL, RUL, HAL, HW, HL, RND, DRE
<i>L. scolaroi</i>	-	-	SS, MS, DS	SS	SS, MS, DS		HL, RND	DFH, RND	TFL, HAL, HW	DFH	HL, RND	DFH	TFL, RUL, HAL, HW, HL, RND
<i>L. tari</i>	SS, DS	SS, DS	-	DS	VS	SS, MS, DS		DFH	TFL, HAL, HW, RND	DFH, RND, DRE, AH	-	DFH, HL, RND, DRE	TFL, RUL, HAL, HW
<i>L. zullyae</i>	SS	SS	DS	-	DS, VS	SS	DS		DFH, TFL, HAL, HW, RND	RND	DFH	RND	DFH, TFL, RUL, HAL
<i>L. baguali</i>	SS	SS	MS, DS	-	MS, DS, VS	SS	MS, DS	-		DFH, TFL, HAL, HW	TFL, HAL, HW, RND	DFH, TFL, HAL, HW	RUL, RND
<i>L. kingii</i>	SS	SS	DS	-	DS, VS	SS	DS	-	-		DFH, RND, DRE	-	DFH, TFL, RUL, HAL, HW, RND, DRE
<i>L. somuncurae</i>	SS, IL4	SS, IL4	MS, DS, IL4	IL4	MS, DS, VS, IL4	SS, IL4	MS, DS, IL4	IL4	IL4	IL4		DFH, HL, RND, DRE	TFL, RUL, HAL, HW
<i>L. tristis</i>	SS	SS	MS, DS	-	MS, DS, VS	SS	MS, DS	-	-	-	IL4		DFH, TFL, RUL, HAL, HW, HL, RND, DRE
<i>L. uptoni</i>	SS, IL4	SS, IL4	DS, IL4	IL4	DS, VS, IL4	SS, IL4	DS, IL4	IL4	IL4	IL4	-	IL4	

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**TABLE 7:** Meristic (below diagonal) and morphometric standardized by SVL (above diagonal) characters with statistically significant differences for **males** of the *kingii*-*archeforus* group are shown (taken for comparisons of significant ANOVA or Kruskal-Wallis tests). Morphometric and Meristic variable names as in Table 6.

Males	<i>L. archeforus</i>	<i>L. chacabucoense</i>	<i>L. escarchadosi</i>	<i>L. gallardoi</i>	<i>L. sarmientoi</i>	<i>L. scolaroi</i>	<i>L. tari</i>	<i>L. zullyae</i>	<i>L. baguali</i>	<i>L. kingii</i>	<i>L. somuncurae</i>	<i>L. tristis</i>	<i>L. uptoni</i>
<i>L. archeforus</i>		-	RUL, HL, DRE, AH	RH	FOL, AH	HH	HW, HL, DRE	HL, RND	HH, HL, AH	DFH, FOL, HL, AH	FOL, HL, DRE	-	FOL, RUL, HH, HL, RND, DRE, AH
<i>L. chacabucoense</i>	-		RUL, HL, DRE	FOL, RUL, RH	AH	HH	RUL, HW, HL, DRE	DFH, RUL, HW, HL, RND, DRE	HH, HL	RUL, HL, AH	DFH, RUL, HL, DRE	-	RUL, HH, HL, RND, DRE, AH
<i>L. escarchadosi</i>	MS, DS, IL3	MS, DS, IL3		HW, HL, RH, DRE, AH	RUL, HL, DRE	RUL, HH	-	RUL, RND	RUL, HH	RUL, DRE	RUL	HL, DRE	HH
<i>L. gallardoi</i>	SS	SS	SS, MS, DS, IL3, IL4		TL, FOL, RH, DRE, AH	TL, HH, RH	FOL, HW, HL, RH, DRE	HL, RND, RH	HH, HL, RH	FOL, HL, RH, AH	TL, FOL, HL, RH, DRE	RH	FOL, HH, HL, RND, RH, DRE, AH
<i>L. sarmientoi</i>	SS, MS, DS	SS, MS, DS	SS	MS, DS		HH, RND, DRE	HW, HL, RND, DRE	TL, HL, RND, DRE	HH, HL, DRE	HL	HL, RND, DRE, AH	-	RUL, HH, HL, RND, DRE
<i>L. scolaroi</i>	-	-	MS, DS	SS	SS, DS		HH, HW, HL	HH, HW	-	HH	HH	HH, RND	RUL, HH, HL, DRE
<i>L. tari</i>	DS	MS, DS	LS	SS, MS, DS, IL4	LS, SS	DS		-	HH, HW	HW, DRE, AH	TL, HW	HW, RND, DRE	HH
<i>L. zullyae</i>	-	MS	MS, DS, IL3	SS	SS, MS, DS	IL3	MS, DS, IL3		HH, RND	DFH, HW, RND, DRE, AH	TL, FOL	RND, DRE	DFH, FOL, HH
<i>L. baguali</i>	SS, MS, VS, IL3	SS, MS, VS, IL3	LS, SS, MS, DS, VS, IL3, IL4	VS, IL3	LS, MS, DS, VS, IL3, IL4	SS, MS, VS, IL3	SS, MS, DS, VS, IL3, IL4	SS, VS		DFH, HH, DRE	HH	HH	HH
<i>L. kingii</i>	LS, SS, VS	SS, VS	LS, SS, MS, DS, VS, IL3	VS	LS, MS, DS, VS	SS, VS	SS, MS, DS, VS, IL3	SS, VS	IL3		DFH, DRE, AH	AH	HH, HL, RND, DRE
<i>L. somuncurae</i>	LS, SS, MS, VS, IL4	SS, MS, VS, IL4	LS, SS, MS, DS, VS, IL3, IL4	MS, VS	LS, MS, DS, VS, IL3, IL4	SS, MS, VS, IL3, IL4	SS, MS, DS, VS, IL3, IL4	SS, MS, VS, IL4	VS	MS, VS, IL4		HL, RND, DRE	DFH, HH
<i>L. tristis</i>	SS, VS	SS, VS	SS, MS, DS, VS, IL3, IL4	VS	MS, DS, VS, IL4	SS, VS, IL3, IL4	SS, MS, DS, VS, IL3, IL4	SS, VS	-	-	MS, VS		HH, HL, RND, DRE
<i>L. uptoni</i>	IS, VS	IS, VS	IS, MS, DS, VS, IL3, IL4	SS, IS, VS	SS, IS, DS, VS, IL4	IS, VS, IL3, IL4	IS, DS, VS, IL3, IL4	IS, VS	SS, IS, MS	SS, IS	SS, IS, MS, VS	SS, IS	



**TABLE 8:** Meristic (below diagonal) and morphometric standardized by SVL (above diagonal) characters with statistically significant differences for the females and males of the *lineomaculatus* group are shown (taken for comparisons of significant ANOVA or Kruskal-Wallis tests). Differences in morphometric characters when exclusive for females are underlined and when exclusive for *males* are in bold and italics. Morphometric and Meristic variable names as in Table 6.

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<u>Females &amp; Males</u>	<i>L. avilae</i>	<i>L. hatcheri</i>	<i>L. kolengh</i>	<i>L. lineomaculatus</i>	<i>L. morandae</i>	<i>L. silvanae</i>
<i>L. avilae</i>		TL, FOL, TFL, HH, <b>HL</b>	TL, HAL, HW, <u>RH</u> , <u>DRE</u> , <u>AH</u> , <b>HH</b> , <b>HL</b>	<u>HH</u> , <b>FOL</b> , <b>HL</b>	HH, <u>TFL</u> , <u>RH</u> , <b>HL</b> , <b>RH</b>	TL, HAL, HH, <u>RND</u> , <b>FOL</b> , <b>HL</b> , <b>DRE</b>
<i>L. hatcheri</i>	SCI, SS, IS, DS, VS, IL3, IL4		TFL, HAL, RH, <u>TL</u> , <u>FOL</u> , <u>HH</u> , <u>HW</u> , <u>HL</u> , <u>DRE</u> , <u>AH</u>	TL, TFL, HH, <u>FOL</u> , <u>HL</u>	TL, FOL, HH, HL, <u>RH</u> , <b>TFL</b> , <b>AH</b>	TFL, HAL, RND, <u>FOL</u> , <b>HH</b> , <b>HL</b> , <b>DRE</b>
<i>L. kolengh</i>	SCI, SS, IS, DS, VS, IL3, IL4	-		TL, HAL, HH, HW, AH, <u>RH</u> , <u>DRE</u>	TL, HAL, HH, <u>TFL</u> , <u>HW</u> , <u>DRE</u> , <u>AH</u> , <b>FOL</b> , <b>HL</b> , <b>RH</b>	HH, HW, HL, RND, RH, DRE, <u>AH</u>
<i>L. lineomaculatus</i>	SS, MS, DS, VS	IS, MS, DS, VS, IL3, IL4	IS, MS, DS, VS, IL3, IL4		<u>TFL</u> , <u>RH</u> , <b>FOL</b> , <b>HH</b> , <b>HL</b> , <b>DRE</b> , <b>AH</b>	TL, HAL, HH, HL, RND, <b>HW</b>
<i>L. morandae</i>	SCI, SS, IS, MS, IL3	MS, DS, VS, IL4	MS, DS, VS, IL4	IS, DS, VS, IL3		TL, HAL, HH, HL, RND, RH, <u>TFL</u> , <b>FOL</b> , <b>DRE</b> , <b>AH</b>
<i>L. silvanae</i>	SS, MS, DS, VS	MS, DS, VS, IL3, IL4	MS, DS, VS, IL3, IL4	VS	IL3	

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**TABLE 9:** Meristic (below diagonal) and morphological (above diagonal) characters with statistically significant differences for females and males of the *magellanicus* group are shown (taken for comparisons of significant ANOVA or Kruskal-Wallis tests). Morphometric and Meristic variable names as in Table 6.

Females & Males	<i>L. caparensis</i>	<i>L. magellanicus</i>
<i>L. caparensis</i>		TFL, RUL
<i>L. magellanicus</i>	DS, VS, IL3, IL4	

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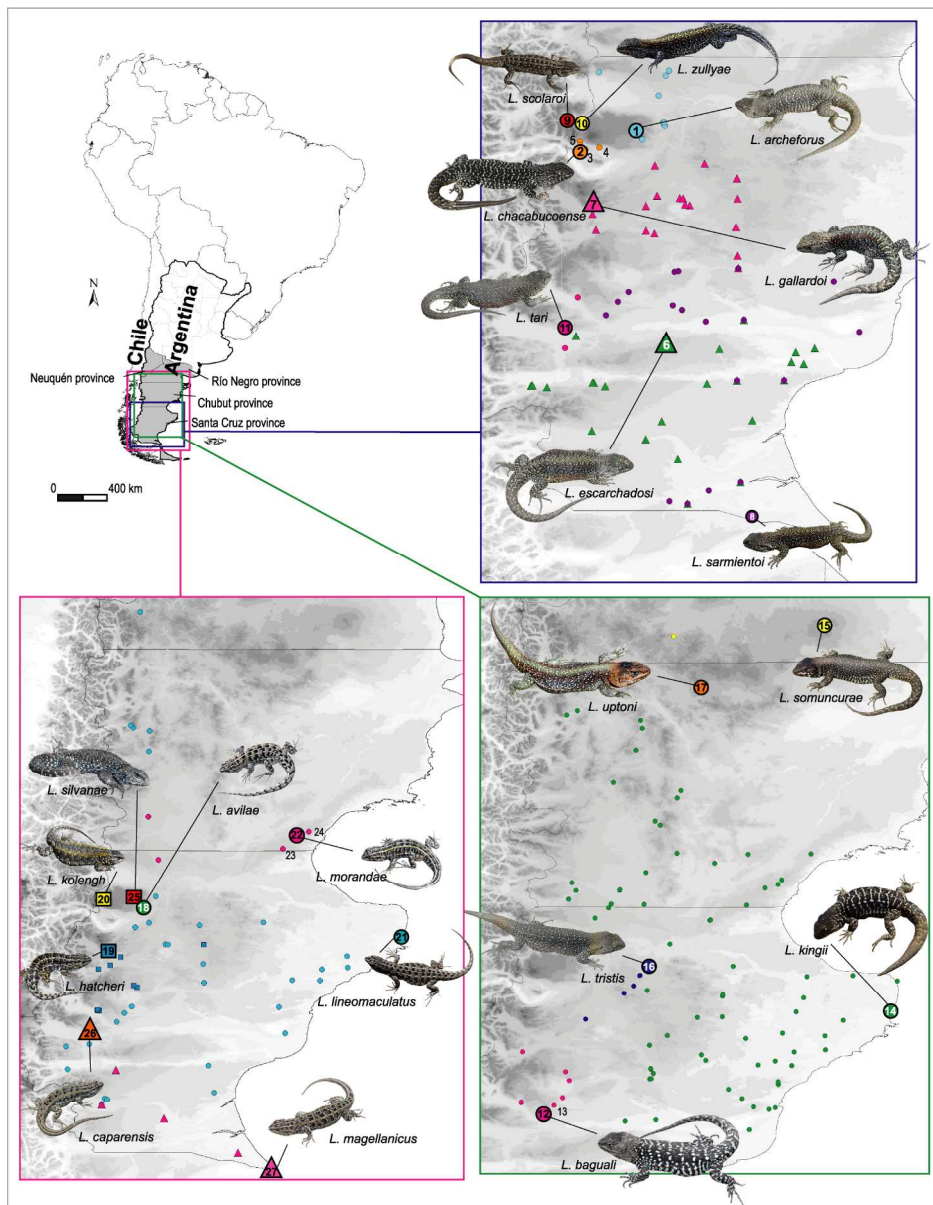


Figure 1: Map of southern Patagonia showing distribution sites for species formerly included in the archeforus (blue), kingii (green), lineomaculatus and magellanicus (pink) groups. Numbers represent localities used in this study, type localities are shown in bold (black or white). Picture-size differences represent differences in body size among species.

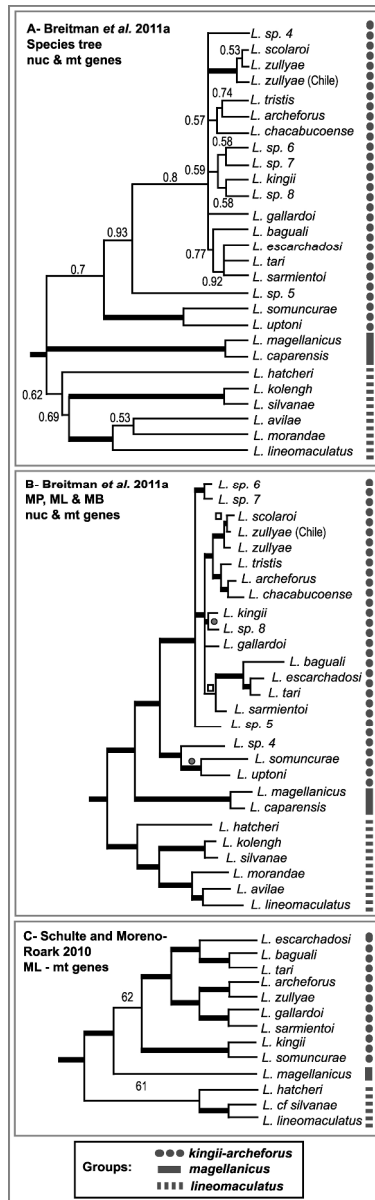


Figure 2: Phylogenetic relationships hypothesized for the *L. lineomaculatus* section using nuclear (nu) and/or mitochondrial (mt) genes; (A) Species tree inferred using mt and nu genes by Breitman et al. 2011a; posterior probability (Pp) values higher than 0.5 are shown, bold branches show clades with Pp > 0.95; (B) Bayesian tree, representing concatenated analyses and summarizing information from Maximum Parsimony (MP) and Maximum Likelihood (ML) methods from Breitman et al. 2011a; nodes with high support from three methods (MP jackknife and ML bootstrap >0.70; Pp > 0.95) are identified by bold branches; open squares show nodes with weak MP support, and circles nodes with weak MP and ML support; (C) Maximum Likelihood tree recovered using mt genes by Schulte and Moreno-Roark 2010.

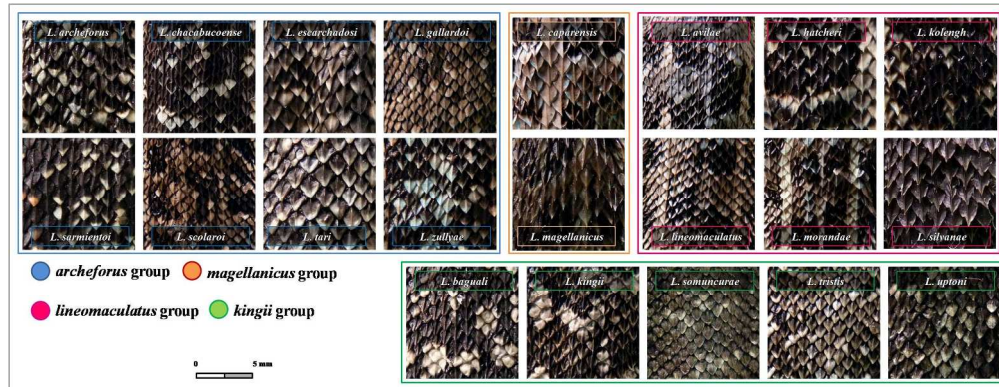


Figure 3: Pictures of dorsal scales of all the species belonging to the archeforus, kingii, lineomaculatus and magellanicus groups. Squares are 1 cm<sup>2</sup>. No differences or trends can be observed among scales of the species included in the kingii and archeforus groups.  
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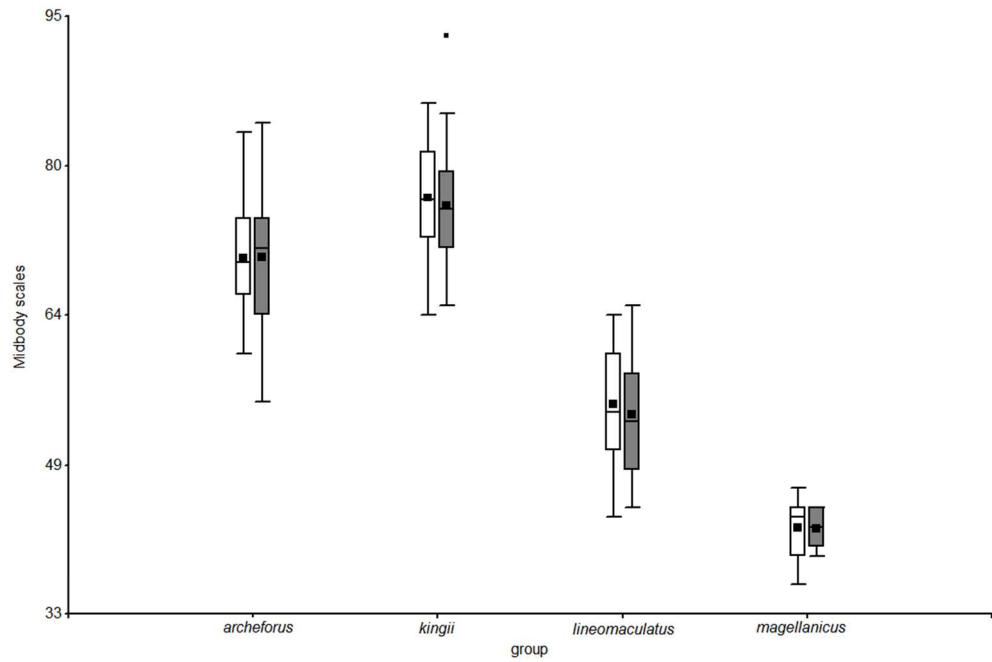


Figure 4: Number of midbody scales among individuals of the archeforus, kingii, lineomaculatus and magellanicus groups. No statistically significant differences are found between the kingii and archeforus groups. Females are shown in white and males are shown in gray.

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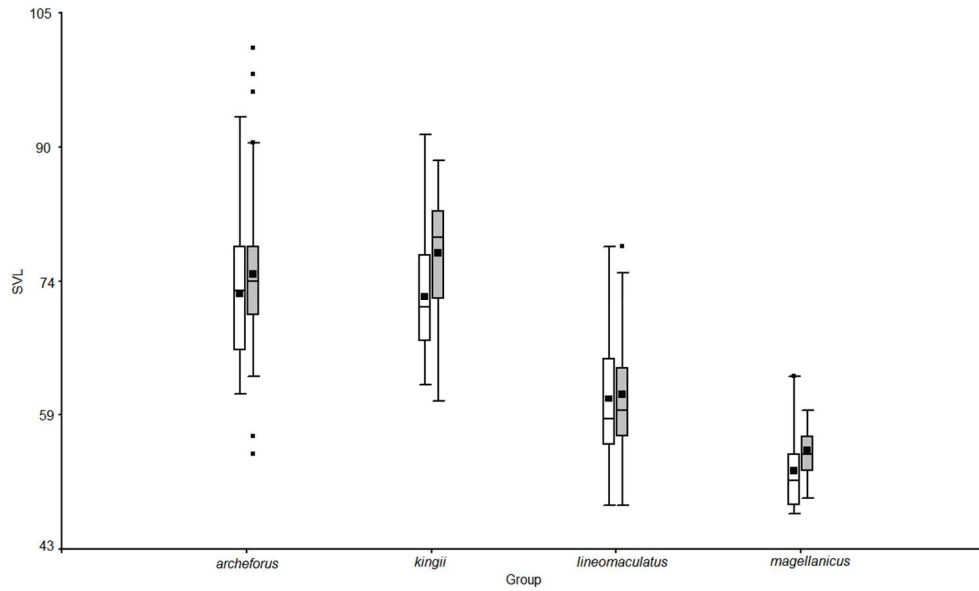


Figure 5: Snout-vent length (SVL, expressed in millimeters) among individuals of the archeforus, kingii, lineomaculatus and magellanicus groups. No statistically significant differences are found between the kingii and archeforus groups. Females are shown in white and males are shown in gray.

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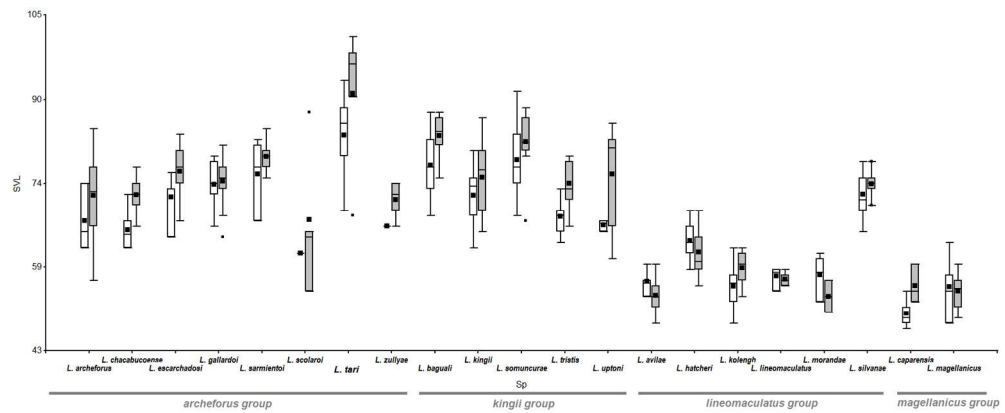


Figure 6: Snout-vent length (SVL, expressed in millimeters) among individuals of all the species of the archeforus, kingii, lineomaculatus and magellanicus groups. Females are shown in white and males are shown in gray.

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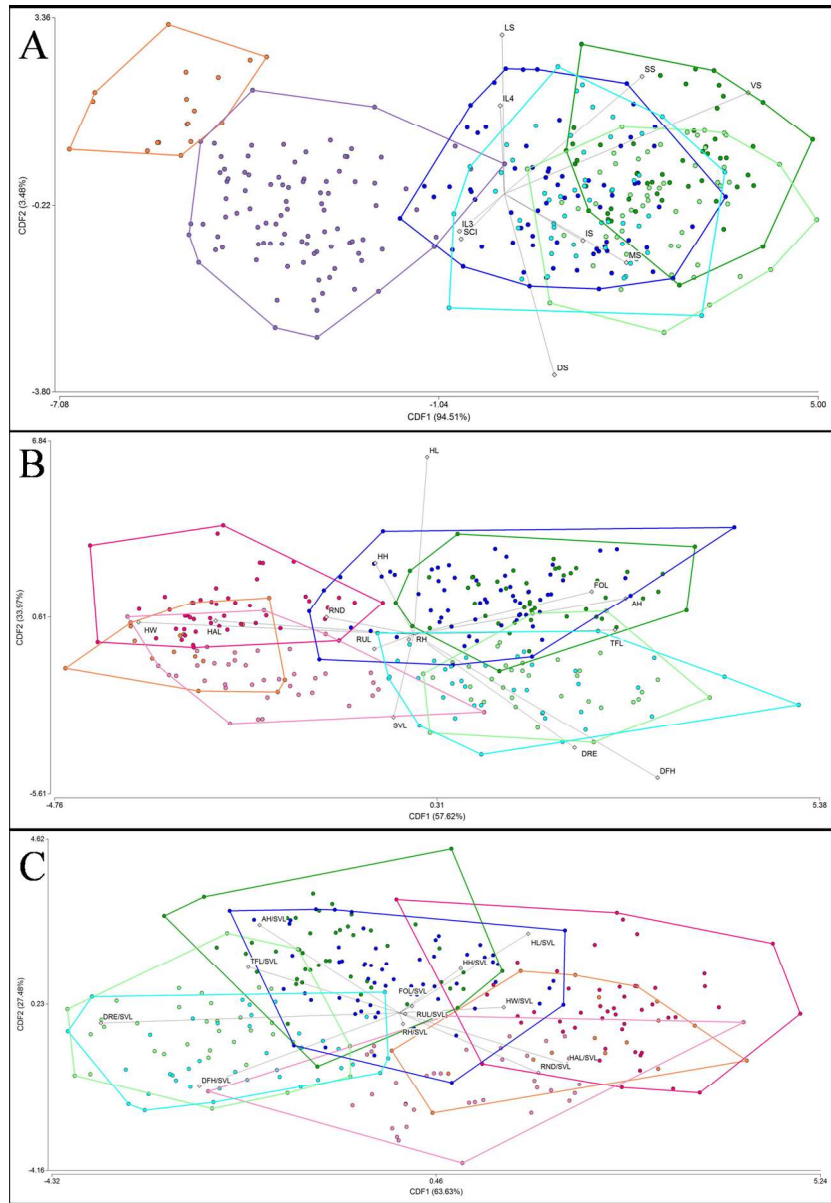


Figure 7: Graphics of the Discriminant Function Analysis performed on the: (A) meristic; (B) morphometric; and (C) morphometric standardized by SVL data sets. In orange magellanicus group, in purple lineomaculatus group (fuchsia: males, pink: females), in blue archeforus group (dark blue: males, light blue: females) and in green kingii group (dark green: males, light green: females). No statistically significant differences were found between the kingii and archeforus groups. There are significant differences between the magellanicus and lineomaculatus groups, and between these and all the species of the kingii and archeforus groups.  
254x370mm (150 x 150 DPI)

**APPENDIX 1:** Species with locality numbers, geographic coordinates, and voucher numbers used in this study. All individuals are catalogued in the Centro Nacional Patagónico Herpetological collection (LJAMM-CNP), Puerto Madryn, Chubut, Argentina; except for 2626-2628 that are catalogued in the La Plata National Museum (MLP.S), Buenos Aires, Argentina.

Locality	Species	Voucher number	Latitude	Longitude
1	<i>L. archeforus</i>	9238-9240; 9270-9271; 9320; 9244-9249	-46.96439	-71.10756
2	<i>L. chacabucoense</i>	7375-7384	-47.16475	-71.83925
3	<i>L. chacabucoense</i>	7364-7369	-47.22497	-71.76978
4	<i>L. chacabucoense</i>	13048-13050	-47.19706	-71.58583
5	<i>L. chacabucoense</i>	7371-7372	-47.11822	-71.84314
6	<i>L. escarchadosi</i>	9286; 9335-9346	-49.77133	-70.72997
7	<i>L. gallardoi</i>	9315; 9440-9467; 9469-9476; 9478-9479; 9481-9482	-47.99372	-71.68042
8	<i>L. sarmientoi</i>	7197-7200; 7204-7208; 7211-7212	-52.07472	-69.58128
9	<i>L. scolaroi</i>	13033-13034	-46.81286	-71.97822
10	<i>L. scolaroi</i>	7392-7395	-46.84628	-71.87125
11	<i>L. tari</i>	9317; 9400-9410	-49.56972	-72.04775
10	<i>L. zullyae</i>	7385-7391; 7371-7372	-46.84628	-71.87125
9	<i>L. zullyae</i>	13032	-46.81286	-71.97822
12	<i>L. baguali</i>	7231-7233; 7258-7259; 9394-9397	-49.41025	-71.49953
13	<i>L. baguali</i>	7266-7275; 7338-7339	-49.23042	-71.34203
14	<i>L. kingii</i>	7457-7467; 9713-9717; 9721-9725; 9766-9770; 9774-9776	-47.71697	-65.84108
15	<i>L. somuncurae</i>	6571; 6764-6767; 6769-6770; 6835-6868; 6908-6914	-41.39467	-66.95925
16	<i>L. tristis</i>	9618-9623; 9439; 9593-9611; 9613, 9615-9616	-46.98261	-69.79992
17	<i>L. uptoni</i>	8426; 10943-10952	-42.39181	-68.93336
18	<i>L. avilae</i>	<b>2627</b> ; 9250-9253; 9274-9276; 9399	-47.09139	-71.02025
19	<i>L. hatcheri</i>	9485-9492; 9498-9506; 10321-10323	-47.99372	-71.68042
20	<i>L. kolengh</i>	7276-7282; 7284; 7289-7290; 7294-7304; 7306-7307; 7309-7315; 10590	-47.02106	-71.80883
21	<i>L. lineomaculatus</i>	7470-7473; 9750-9756	-47.71697	-65.84108
22	<i>L. morandae</i>	<b>2626</b> ; 13020	-45.68628	-67.89719
23	<i>L. morandae</i>	10201-10202	-45.96669	-68.19967
24	<i>L. morandae</i>	9677-9679	-45.62872	-67.68433
25	<i>L. silvanae</i>	9218-9233; 10320	-46.96439	-71.10756
26	<i>L. caparensis</i>	<b>2628</b> ; 9379-9380; 9382-9388	-49.56972	-72.04775
27	<i>L. magellanicus</i>	6722-6731	-52.25143	-68.43116

**APPENDIX 2:** Dorsal pattern (including vertebral, paravertebral and dorsal strip pattern), variegation and melanism (converted to percentage whitening each species). Dorsal stripe pattern: (A) complete or slightly broken bands, (B) dotted bands, (C) irregular bands, (D) indistinct or almost indistinct bands; all these variables were described, illustrated and respectively described as 0–20, 40, 60 and 80–100 by Scolaro (1987). Ventral melanism: (m0) no melanism, (m1) melanism only present in gular zone, (m2) melanism only present in belly, (m3) melanism present on all body regions except the cloacal region and limbs, (m4) melanism present on all body except in limbs, (m5) melanism present in all body. F: females; M: males. N: no pattern/coloración; Y: pattern/coloration presented.

	Dorsal stripe pattern		Vertebral		Paravertebral		Dorsolateral		Variegation		Melanism	
	F	M	F	M	F	M	F	M	F	M	F	M
<i>L. baguali</i>	75% A; 25% B	50% A; 50% B	100% N	60% N; 40% Y	80% N; 20% Y	100% N	100% N	100% N	75%	75%	25% m0; 25% m3; 50% m5	25% m3; 25% m5; 50% m4
<i>L. kingii</i>	100% B	50% A; 50% B	25% N; 75% Y	50% N; 50% Y	100% N	100% N	100% N	100% N	100%	100%	100% m0	75 m0; 25% m2
<i>L. somuncurae</i>	75% A; 25% D	50% A; 50% D	60% N; 40% Y	100% N	100% N	100% N	100% N	100% N	75%	100%	25% m2; 75 m3	50% m2; 50% m3
<i>L. tristis</i>	50% B; 50% D	25% B; 25% C; 50% D	60% N; 40% Y	100% N	60% N; 40% Y	100% N	75% N; 25% Y	100% N	100%	100%	50% m0; 50% m2	50% m0; 50% m2
<i>L. uptoni</i>	100% A	50% A; 50% D	100% Y	50% N; 50% Y	75% N; 25% Y	100% N	100% N	100% N	50%	50%	100% m0	75 m0; 25% m3
<i>L. archeforus</i>	33% B; 33% C; 33% D	12.5% A; 12.5% B; 75% D	100% N	100% N	100% N	100% N	100% N	100% N	100%	50%	75 m0; 25% m1	25% m0; 25% m3; 25% m4; 25% m5
<i>L. chacabucoense</i>	50% C; 50% D	10% A; 50% B; 40% C	40% N; 60% Y	50% N; 50% Y	20% N; 80% Y	100% N	75% N; 25% Y	100% N	25%	50%	25% m0; 50% m3; 25% m5	25% m0; 25% m2; 25% m4; 25% m5
<i>L. escarchadosi</i>	25% A; 75% B	25% A; 25% B; 25% C; 25% D	25% N; 75% Y	75% N; 25% Y	25% N; 75% Y	25% N; 75% Y	100% N	100% N	100%	100%	75 m2; 25% m0	25% m3; 75 m4
<i>L. gallardoi</i>	25% B; 50% C; 25% D	25% C; 75% D	75% N; 25% Y	100% N	100% N	100% N	100% N	100% N	100%	100%	50% m0; 50% m2	25% m0; 75 m2
<i>L. sarmientoi</i>	100% D	100% D	75% N; 25% Y	50% N; 50% Y	100% N	100% N	100% N	100% N	100%	100%	50% m2; 25% m3; 25% m4	25% m2; 75 m4
<i>L. scolaroii</i>	100% C	25% B; 50% C; 25% D	100% Y	100% Y	100% Y	100% Y	100% N	100% N	100%	100%	100% m0	100% m0
<i>L. tari</i>	25% A; 25% B; 25% C; 25% D	12.5% A; 12.5% C; 75% D	75% N; 25% Y	100% N	100% Y	40% N; 60% Y	100% N	100% N	100%	100%	25% m0; 75m2	100% m0
<i>L. zullyae</i>	100% C	100% D	100% N	75% N; 25% Y	25% N; 75% Y	100% N	100% N	50% N; 50% Y	100%	100%	100% m0	75 m0; 25% m3
<i>L. avilae</i>	-	-	100% N	100% N	100% Y	100% Y	25% N; 75% Y	25% N; 75% Y	100%	100%	100% m0	75 m0; 25% m3

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<i>L. hatcheri</i>	-	-	100% N	100% N	100% Y	100% Y	25% N; 75% Y	50% N; 50% Y	100%	100%	25% m0; 75 m2	50% m2; 25% m4; 25% m5
<i>L. kolengh</i>	-	-	100% N	100% N	100% Y	100% Y	50% N; 50% Y	25% N; 75% Y	100%	100%	75 m2; 25% m4	25% m4; 75 m5
<i>L. lineomaculatus</i>	-	-	25% N; 75% Y	50% N; 50% Y	100% Y	100% Y	100% Y	100% Y	100%	100%	75 m0; 25% m1	100% m0
<i>L. morandae</i>	-	-	75% N; 25% Y	100% N	100% Y	100% Y	100% Y	100% Y	100%	100%	75 m0; 25% m2	100% m0
<i>L. silvanae</i>	-	-	100% N	100% N	80% N; 20% Y	100% N	100% N	100% N	0%	0%	100% m5	100% m5
<i>L. caparensis</i>	-	-	60% N, 50% Y	100% N	100% Y	100% Y	100% Y	100% Y	75%	75%	25% m0; 25% m2; 25% m3; 25% m4	25% m0; 75 m2
<i>L. magellanicus</i>	-	-	50% N; 50% Y	40% N; 60% Y	100% Y	100% Y	100% Y	25% N; 75% Y	75%	75%	50% m0; 50% m2	50% m0; 50% m2

For Review Only

**APPENDIX 3:** Number of midbody scales for each morphological group. n: sample size; mean  $\pm$  SD (min–max) are shown for females and males and all the sample; Student's *t* test or Kruskal Wallis (when assumptions were rejected: *non-parametric*) *p*-values and statistics are shown. Assumptions to perform a parametric test (Student's *t*) are normality (*p*-Hom-Var: Levene test) and variance homogeneity (*p*-SW: Shapiro-Wilks test); when those tests were rejected ( $p > 0.05$ ) then a non-parametric test was performed.

Group	n	Females	Males	All	Statistic	<i>p</i> - <i>t</i> -test/KW	<i>p</i> -HomVar	<i>p</i> -SW
<i>archeforus</i>	124	69.89 $\pm$ 5.52 (60-83)	70.03 $\pm$ 6.73 (55-84)	69.97 $\pm$ 6.21 (55-84)	-0.12	0.90	0.13	0.90
<i>kingii</i>	97	76.13 $\pm$ 5.49 (64-86)	75.27 $\pm$ 5.39 (65-93)	75.72 $\pm$ 5.43 (64-93)	0.81	0.42	0.89	0.44
<i>lineomaculatus</i>	105	54.70 $\pm$ 5.48 (43-64)	53.67 $\pm$ 5.86 (44-65)	54.17 $\pm$ 5.67 (43-65)	1.03	0.31	<i>non-parametric</i>	
<i>magellanicus</i>	11	44.91 $\pm$ 3.05 (36-46)	41.78 $\pm$ 1.92 (39-44)	41.85 $\pm$ 2.54 (36-46)	0.11	0.91	0.15	0.51

**APPENDIX 4:** Forelimb length (calculated as RUL+HAL, in millimeters) for each species and morphological group. Mean  $\pm$  SD (min–max) for females, males and all the sample are shown; Student's *t* test or Kruskal-Wallis (when assumptions were rejected; *non-parametric*) *p*-values and statistics are shown. Assumptions to perform a parametric test (Student's *t*) are normality (*p*-Hom-Var: Levene test) and variance homogeneity (*p*-SW: Shapiro-Wilks test); when those tests were rejected ( $p > 0.05$ ) a non-parametric test was performed. Significant values are in italics and boldface. *Not eval.*, *nF=1* denotes that females sample size was one thus the test was not performed.

<i>Species</i>	Females	Males	All	Statistic	<i>p</i> - <i>t</i> -test/KW	<i>p</i> -HomVar	<i>p</i> -SW
<i>L. archeforus</i>	17 $\pm$ 1.77 (15.41-18.91)	17.89 $\pm$ 1.88 (14.8-21.41)	17.65 $\pm$ 1.81 (14.8-21.41)	-0.71	0.50	0.90	0.9538
<i>L. chacabucoense</i>	14.85 $\pm$ 0.7 (14.06-15.66)	17.6 $\pm$ 1.26 (15.89-19.63)	16.5 $\pm$ 1.74 (14.06-19.63)	-4.83	<b>0.00</b>	0.21	0.8131
<i>L. escarchadosi</i>	18.8 $\pm$ 0.48 (18.2-19.34)	20.13 $\pm$ 0.68 (19.24-20.85)	19.54 $\pm$ 0.9 (18.2-20.85)	-3.29	<b>0.01</b>	0.58	0.537
<i>L. gallardoii</i>	17.86 $\pm$ 0.57 (17-19.05)	19.69 $\pm$ 1.19 (16.67-22.06)	18.83 $\pm$ 1.32 (16.67-22.06)	17.17	<b>&lt;0.0001</b>	<i>non-parametric</i>	
<i>L. sarmientoi</i>	17.72 $\pm$ 0.43 (17.3-18.21)	19.92 $\pm$ 0.43 (19.16-20.42)	19.12 $\pm$ 1.18 (17.3-20.42)	-8.16	<b>&lt;0.0001</b>	0.89	0.4935
<i>L. scolarioi</i>	14.72 $\pm$ 0 (14.72-14.72)	16.1 $\pm$ 1.19 (14.88-17.34)	15.82 $\pm$ 1.2 (14.72-17.34)		<i>Not eval., n F =1</i>		0.6729
<i>L. tari</i>	20.27 $\pm$ 1.73 (17.6-21.83)	23.09 $\pm$ 2.09 (19.55-24.65)	21.68 $\pm$ 2.34 (17.6-24.65)	3.94	0.06	<i>non-parametric</i>	
<i>L. zullyae</i>	15.58 $\pm$ 0 (15.58-15.58)	18.29 $\pm$ 1.12 (16.48-19.65)	17.95 $\pm$ 1.41 (15.58-19.65)		<i>Not eval., n F =1</i>		0.24
<i>L. baguali</i>	19.46 $\pm$ 1.32 (17.46-21.16)	21.51 $\pm$ 1.04 (20.53-23.3)	20.48 $\pm$ 1.56 (17.46-23.3)	-2.99	<b>0.01</b>	0.62	0.6967
<i>L. kingii</i>	16.93 $\pm$ 1.02 (15.04-18.24)	18.83 $\pm$ 1.11 (16.83-20.23)	18.04 $\pm$ 1.42 (15.04-20.23)	9.81	<b>0.00</b>	<i>non-parametric</i>	
<i>L. somuncurae</i>	18.86 $\pm$ 1.57 (16.28-20.76)	21.1 $\pm$ 0.98 (19.01-22.15)	20.26 $\pm$ 1.63 (16.28-22.15)	-3.56	<b>0.00</b>	0.21	0.56
<i>L. tristis</i>	16.05 $\pm$ 0.66 (14.79-17.23)	18.98 $\pm$ 1.4 (16.6-21.29)	17.66 $\pm$ 1.86 (14.79-21.29)	13.58	<b>0.00</b>	<i>non-parametric</i>	
<i>L. uptoni</i>	17.99 $\pm$ 0.72 (17.03-18.79)	19.59 $\pm$ 1.8 (16.76-21.43)	18.95 $\pm$ 1.63 (16.76-21.43)	-1.67	0.13	0.17	0.6549
<i>L. avilae</i>	12.99 $\pm$ 0.7 (12.22-13.83)	13.77 $\pm$ 0.91 (12.16-14.29)	13.42 $\pm$ 0.87 (12.16-14.29)	-1.40	0.20	0.78	0.1962
<i>L. hatcheri</i>	14.85 $\pm$ 0.33 (14.41-15.26)	15.96 $\pm$ 0.87 (14.7-17.01)	15.59 $\pm$ 0.91 (14.41-17.01)	5.93	<b>0.01</b>	<i>non-parametric</i>	
<i>L. kolengh</i>	14.67 $\pm$ 0.89 (12.91-15.8)	16.51 $\pm$ 0.55 (15.75-17.7)	15.66 $\pm$ 1.17 (12.91-17.7)	-6.42	<b>&lt;0.0001</b>	0.11	0.71
<i>L. lineomaculatus</i>	13.26 $\pm$ 0.44 (12.89-13.88)	14.97 $\pm$ 0.45 (14.31-15.51)	14.29 $\pm$ 0.98 (12.89-15.51)	-5.94	<b>0.00</b>	0.96	0.5408
<i>L. morandae</i>	12.73 $\pm$ 0.95 (11.38-13.57)	13.98 $\pm$ 0.97 (13.29-14.66)	13.15 $\pm$ 1.07 (11.38-14.66)	-1.51	<b>0.21</b>	0.76	0.392
<i>L. silvanae</i>	19.37 $\pm$ 1.31 (17.64-21.88)	20.44 $\pm$ 1.15 (18.78-21.98)	19.94 $\pm$ 1.31 (17.64-21.98)	-1.79	0.09	0.71	0.63
<i>L. caparensis</i>	12.63 $\pm$ 0.75 (11.83-13.73)	14.04 $\pm$ 0.5 (13.46-14.36)	13.16 $\pm$ 0.96 (11.83-14.36)	-2.85	<b>0.03</b>	0.67	0.5933
<i>L. magellanicus</i>	13.4 $\pm$ 1.36 (11.4-14.31)	14.68 $\pm$ 0.7 (13.89-15.63)	14.17 $\pm$ 1.15 (11.4-15.63)	-1.99	<b>0.08</b>	0.19	0.2346
<i>archeforus</i> group	17.58 $\pm$ 1.83 (14.06-21.83)	19.10 $\pm$ 2.07 (14.80-24.65)	18.51 $\pm$ 2.11 (14.06-24.65)	-3.75	<b>0.00</b>	0.43	0.21
<i>kingii</i> group	17.59 $\pm$ 1.65 (14.79-21.16)	19.79 $\pm$ 1.62 (16.6-23.3)	18.85 $\pm$ 1.96 (14.79-23.3)	-6.03	<b>&lt;0.0001</b>	0.91	0.16
<i>lineomaculatus</i> group	14.99 $\pm$ 2.44 (11.38-21.88)	16.32 $\pm$ 2.2 (12.16-21.98)	15.74 $\pm$ 2.39 (11.38-21.98)	12.67	<b>0.00</b>	<i>non-parametric</i>	
<i>magellanicus</i> group	12.63 $\pm$ 0.75 (11.83-13.73)	14.04 $\pm$ 0.5 (13.46-14.36)	13.16 $\pm$ 0.96 (11.83-14.36)	-2.85	<b>0.03</b>	0.67	0.44

**APPENDIX 5:** Meristic variables for each species discriminated by sex. Mean  $\pm$  SD (min–max) are shown; Student's *t* test or Kruskal-Wallis (when assumptions were rejected; *non-parametric*) *p*-values and statistics are shown. Assumptions to perform a parametric test (Student's *t*) are normality (*p*-Hom-Var: Levene test) and variance homogeneity (*p*-SW: Shapiro-Wilks test); when those tests were rejected ( $p > 0.05$ ) then a non-parametric test was performed. For *L. scolaroi* and *L. zullyae* sexual dimorphism was not evaluated due to small female sample sizes (Not eval). Significant values are shown in italics and boldface. *Not eval.*, *nF=1* denotes that females sample size was one thus the test was not performed. **PP:** number of precloacal pores; **SCI:** scales in contact with the interparietal; **LS:** lorilabial scales; **SS:** supralabial scales; **IS:** infralabial scales; **MS:** midbody scales; **DS:** dorsal scales; **VS:** ventral scales; **IL3:** infradigital lamellae of the third finger; **IL4:** infradigital lamellae of the fourth toe.

Species	Var	Females	Males	All	Statistic	<i>p</i> - <i>t</i> -test/KW	<i>p</i> -HomVar	<i>p</i> -SW
<i>L. archeforus</i>	PP	-	7.38 $\pm$ 1.06 (6-9)	-	-	-	-	0.48
<i>L. archeforus</i>	SCI	6 $\pm$ 0 (6-6)	6.5 $\pm$ 0.76 (6-8)	6.33 $\pm$ 0.65 (6-8)	1.04	0.42	<i>non-parametric</i>	
<i>L. archeforus</i>	LS	5 $\pm$ 0.82 (4-6)	4.63 $\pm$ 0.52 (4-5)	4.75 $\pm$ 0.62 (4-6)	0.98	0.35	0.29	0.22
<i>L. archeforus</i>	SS	6.75 $\pm$ 0.5 (6-7)	7.13 $\pm$ 0.83 (6-8)	7 $\pm$ 0.74 (6-8)	-0.82	0.43	0.43	0.09
<i>L. archeforus</i>	IS	5.75 $\pm$ 0.5 (5-6)	5.88 $\pm$ 0.35 (5-6)	5.83 $\pm$ 0.39 (5-6)	0.12	>0.99	<i>non-parametric</i>	
<i>L. archeforus</i>	MS	71.25 $\pm$ 2.22 (69-74)	72.5 $\pm$ 6.26 (64-84)	72.08 $\pm$ 5.16 (64-84)	-0.38	0.71	0.12	0.58
<i>L. archeforus</i>	DS	64.5 $\pm$ 1.73 (63-67)	64.25 $\pm$ 2.12 (62-68)	64.33 $\pm$ 1.92 (62-68)	0.2	0.84	0.80	0.31
<i>L. archeforus</i>	VS	101.25 $\pm$ 4.65 (97-107)	98.63 $\pm$ 2.83 (94-102)	99.5 $\pm$ 3.55 (94-107)	1.23	0.25	0.25	0.55
<i>L. archeforus</i>	IL3	16 $\pm$ 1.63 (14-18)	17 $\pm$ 1.31 (15-19)	16.67 $\pm$ 1.44 (14-19)	-1.15	0.28	0.57	0.26
<i>L. archeforus</i>	IL4	21 $\pm$ 1.41 (20-23)	22.25 $\pm$ 0.71 (21-23)	21.83 $\pm$ 1.11 (20-23)	-2.09	0.06	0.12	0.38
<i>L. chacabucoense</i>	PP	-	7.25 $\pm$ 1.22 (5-9)	-	-	-	-	<b>0.08</b>
<i>L. chacabucoense</i>	SCI	6.78 $\pm$ 1.3 (5-9)	7.17 $\pm$ 0.83 (6-9)	7 $\pm$ 1.05 (5-9)	-0.83	0.41	0.17	0.30
<i>L. chacabucoense</i>	LS	4.67 $\pm$ 0.5 (4-5)	4.92 $\pm$ 0.67 (4-6)	4.81 $\pm$ 0.6 (4-6)	0.56	0.38	<i>non-parametric</i>	
<i>L. chacabucoense</i>	SS	6.89 $\pm$ 1.27 (5-9)	7.08 $\pm$ 1 (5-8)	7 $\pm$ 1.1 (5-9)	-0.39	0.70	0.45	0.3768
<i>L. chacabucoense</i>	IS	5.67 $\pm$ 0.5 (5-6)	5.92 $\pm$ 0.51 (5-7)	5.81 $\pm$ 0.51 (5-7)	0.73	0.28	<i>non-parametric</i>	
<i>L. chacabucoense</i>	MS	74.22 $\pm$ 5.91 (61-83)	72.58 $\pm$ 2.91 (68-78)	73.29 $\pm$ 4.39 (61-83)	2.02	0.15	<i>non-parametric</i>	
<i>L. chacabucoense</i>	DS	68.44 $\pm$ 5.22 (62-80)	66.5 $\pm$ 4.17 (60-72)	67.33 $\pm$ 4.63 (60-80)	0.95	0.35	0.48	0.3901
<i>L. chacabucoense</i>	VS	98 $\pm$ 7.91 (84-110)	94.92 $\pm$ 3.32 (90-101)	96.24 $\pm$ 5.79 (84-110)	1.38	0.23	<i>non-parametric</i>	
<i>L. chacabucoense</i>	IL3	16.67 $\pm$ 1.22 (15-18)	17.08 $\pm$ 1.31 (16-20)	16.9 $\pm$ 1.26 (15-20)	-0.74	0.47	0.87	0.1731
<i>L. chacabucoense</i>	IL4	22.67 $\pm$ 1.5 (21-26)	22.33 $\pm$ 1.07 (21-25)	22.48 $\pm$ 1.25 (21-26)	0.32	0.55	<i>non-parametric</i>	
<i>L. escarchadosi</i>	PP	-	6.88 $\pm$ 0.83 (6-8)	-	-	-	-	<b>0.01</b>
<i>L. escarchadosi</i>	SCI	6.6 $\pm$ 0.55 (6-7)	6.75 $\pm$ 0.71 (6-8)	6.69 $\pm$ 0.63 (6-8)	0.09	>0.99	<i>non-parametric</i>	
<i>L. escarchadosi</i>	LS	5.2 $\pm$ 0.45 (5-6)	4.5 $\pm$ 0.76 (4-6)	4.77 $\pm$ 0.73 (4-6)	2.83	0.06	<i>non-parametric</i>	
<i>L. escarchadosi</i>	SS	8.4 $\pm$ 1.14 (7-10)	7.75 $\pm$ 1.04 (6-9)	8 $\pm$ 1.08 (6-10)	1.06	0.31	0.77	0.62
<i>L. escarchadosi</i>	IS	5.6 $\pm$ 0.89 (5-7)	5.5 $\pm$ 0.53 (5-6)	5.54 $\pm$ 0.66 (5-7)	0	>0.99	<i>non-parametric</i>	
<i>L. escarchadosi</i>	MS	64 $\pm$ 0 (64-64)	60.63 $\pm$ 2.88 (55-65)	61.92 $\pm$ 2.78 (55-65)	4.02	<b>0.01</b>	<i>non-parametric</i>	
<i>L. escarchadosi</i>	DS	55.2 $\pm$ 3.83 (49-58)	53 $\pm$ 1.77 (51-56)	53.85 $\pm$ 2.82 (49-58)	1.42	0.18	0.07	0.12
<i>L. escarchadosi</i>	VS	98.2 $\pm$ 6.38 (91-107)	91.5 $\pm$ 8.52 (83-111)	94.08 $\pm$ 8.21 (83-111)	1.5	0.16	0.60	0.09
<i>L. escarchadosi</i>	IL3	16 $\pm$ 0.71 (15-17)	15.38 $\pm$ 1.19 (14-17)	15.62 $\pm$ 1.04 (14-17)	1.06	0.31	0.33	0.23
<i>L. escarchadosi</i>	IL4	21 $\pm$ 0.71 (20-22)	20.88 $\pm$ 1.13 (19-22)	20.92 $\pm$ 0.95 (19-22)	0.22	0.83	0.39	0.14
<i>L. gallardoi</i>	PP	-	8.28 $\pm$ 1.13 (7-11)	-	-	-	-	<b>0.00</b>
<i>L. gallardoi</i>	SCI	7.26 $\pm$ 0.92 (6-9)	6.89 $\pm$ 0.96 (6-9)	7.1 $\pm$ 0.94 (6-9)	1.56	0.19	<i>non-parametric</i>	
<i>L. gallardoi</i>	LS	4.78 $\pm$ 0.52 (4-6)	5 $\pm$ 0.49 (4-6)	4.88 $\pm$ 0.51 (4-6)	1.1	0.18	<i>non-parametric</i>	
<i>L. gallardoi</i>	SS	7.96 $\pm$ 1.02 (5-9)	8.5 $\pm$ 0.79 (7-10)	8.2 $\pm$ 0.95 (5-10)	2.01	0.12	<i>non-parametric</i>	
<i>L. gallardoi</i>	IS	6.13 $\pm$ 0.55 (5-7)	6.39 $\pm$ 0.7 (5-8)	6.24 $\pm$ 0.62 (5-8)	1.1	0.22	<i>non-parametric</i>	
<i>L. gallardoi</i>	MS	71.39 $\pm$ 3.71 (65-79)	74.83 $\pm$ 5 (66-84)	72.9 $\pm$ 4.6 (65-84)	-2.53	<b>0.02</b>	0.19	0.61
<i>L. gallardoi</i>	DS	64 $\pm$ 3.66 (59-71)	63.5 $\pm$ 3.63 (57-71)	63.78 $\pm$ 3.61 (57-71)	0.44	0.67	1.00	0.21
<i>L. gallardoi</i>	VS	99.52 $\pm$ 3.99 (92-106)	99.67 $\pm$ 5.13 (90-109)	99.59 $\pm$ 4.47 (90-109)	-0.1	0.92	0.26	0.74
<i>L. gallardoi</i>	IL3	16.7 $\pm$ 1.36 (14-18)	17.06 $\pm$ 1.3 (15-19)	16.85 $\pm$ 1.33 (14-19)	0.4	0.52	<i>non-parametric</i>	

1	<i>L. gallardoi</i>	IL4	22.17 ± 1.67 (19-26)	22.94 ± 2.07 (19-27)	22.51 ± 1.87 (19-27)	-1.32	0.19	0.34	0.19
2	<i>L. sarmientoi</i>	PP	-	6 ± 1.41 (4-8)	-	-	-	-	0.71
3	<i>L. sarmientoi</i>	SCI	6.75 ± 0.5 (6-7)	7.29 ± 1.5 (6-10)	7.09 ± 1.22 (6-10)	-0.68	0.51	0.10	0.17
4	<i>L. sarmientoi</i>	LS	4.25 ± 0.5 (4-5)	4.43 ± 0.79 (4-6)	4.36 ± 0.67 (4-6)	0.04	0.83	<i>non-parametric</i>	
5	<i>L. sarmientoi</i>	SS	8 ± 0 (8-8)	8.43 ± 0.79 (8-10)	8.27 ± 0.65 (8-10)	0.57	0.49	<i>non-parametric</i>	
6	<i>L. sarmientoi</i>	IS	6.75 ± 0.96 (6-8)	5.43 ± 0.53 (5-6)	5.91 ± 0.94 (5-8)	2.99	<b>0.02</b>	0.21	0.08
7	<i>L. sarmientoi</i>	MS	61 ± 1.15 (60-62)	61.71 ± 2.36 (58-64)	61.45 ± 1.97 (58-64)	-0.56	0.59	0.27	0.31
8	<i>L. sarmientoi</i>	DS	56.25 ± 2.06 (54-58)	55 ± 2.58 (52-60)	55.45 ± 2.38 (52-60)	0.82	0.43	0.76	0.65
9	<i>L. sarmientoi</i>	VS	90.5 ± 4.43 (85-95)	89.86 ± 6.2 (78-96)	90.09 ± 5.39 (78-96)	0.18	0.86	0.62	0.26
10	<i>L. sarmientoi</i>	IL3	15.75 ± 0.5 (15-16)	16.14 ± 1.21 (15-18)	16 ± 1 (15-18)	-0.61	0.56	0.17	0.26
11	<i>L. sarmientoi</i>	IL4	21.25 ± 2.22 (18-23)	21.29 ± 1.8 (19-24)	21.27 ± 1.85 (18-24)	-0.03	0.98	0.61	0.66
12	<i>L. scolaroi</i>	PP	-	6.8 ± 1.3 (6-9)	-	-	-	-	<b>0.03</b>
13	<i>L. scolaroi</i>	SCI	6 ± 0 (6-6)	6.2 ± 0.45 (6-7)	6.17 ± 0.41 (6-7)	<i>Not eval, n F = I</i>		<b>0.00</b>	
14	<i>L. scolaroi</i>	LS	4 ± 0 (4-4)	4.8 ± 0.84 (4-6)	4.67 ± 0.82 (4-6)	<i>Not eval, n F = I</i>		0.38	
15	<i>L. scolaroi</i>	SS	7 ± 0 (7-7)	7.2 ± 0.45 (7-8)	7.17 ± 0.41 (7-8)	<i>Not eval, n F = I</i>		<b>0.00</b>	
16	<i>L. scolaroi</i>	IS	5 ± 0 (5-5)	6 ± 0.71 (5-7)	5.83 ± 0.75 (5-7)	<i>Not eval, n F = I</i>		0.25	
17	<i>L. scolaroi</i>	MS	80 ± 0 (80-80)	69.8 ± 5.72 (63-78)	71.5 ± 6.6 (63-80)	<i>Not eval, n F = I</i>		0.83	
18	<i>L. scolaroi</i>	DS	63 ± 0 (63-63)	63.4 ± 3.05 (60-67)	63.33 ± 2.73 (60-67)	<i>Not eval, n F = I</i>		0.64	
19	<i>L. scolaroi</i>	VS	101 ± 0 (101-101)	93 ± 6.82 (87-104)	94.33 ± 6.92 (87-104)	<i>Not eval, n F = I</i>		0.40	
20	<i>L. scolaroi</i>	IL3	16 ± 0 (16-16)	15.8 ± 0.84 (15-17)	15.83 ± 0.75 (15-17)	<i>Not eval, n F = I</i>		0.38	
21	<i>L. scolaroi</i>	IL4	22 ± 0 (22-22)	21.2 ± 2.05 (19-23)	21.33 ± 1.86 (19-23)	<i>Not eval, n F = I</i>		0.09	
22	<i>L. tari</i>	PP	-	8.6 ± 0.89 (8-10)	-	-	-	-	<b>0.01</b>
23	<i>L. tari</i>	SCI	6.43 ± 0.79 (6-8)	7 ± 1 (6-8)	6.67 ± 0.89 (6-8)	0.95	0.35	<i>non-parametric</i>	
24	<i>L. tari</i>	LS	4.86 ± 0.69 (4-6)	5.4 ± 0.55 (5-6)	5.08 ± 0.67 (4-6)	-1.46	0.18	0.68	0.46
25	<i>L. tari</i>	SS	8.43 ± 0.98 (7-10)	7.6 ± 0.89 (6-8)	8.08 ± 1 (6-10)	1.5	0.16	0.91	0.32
26	<i>L. tari</i>	IS	5.86 ± 0.38 (5-6)	5.6 ± 0.55 (5-6)	5.75 ± 0.45 (5-6)	0.53	0.52	<i>non-parametric</i>	
27	<i>L. tari</i>	MS	65.71 ± 2.69 (61-68)	64.8 ± 2.59 (62-69)	65.33 ± 2.57 (61-69)	0.59	0.57	0.99	0.90
28	<i>L. tari</i>	DS	56.43 ± 3.82 (52-61)	51.8 ± 2.68 (50-56)	54.5 ± 4.03 (50-61)	2.32	<b>0.04</b>	0.51	0.06
29	<i>L. tari</i>	VS	100.57 ± 6.5 (94-113)	96.6 ± 7.09 (88-104)	98.92 ± 6.75 (88-113)	1.01	0.34	0.81	0.57
30	<i>L. tari</i>	IL3	15.29 ± 1.38 (13-17)	15.6 ± 1.14 (14-17)	15.42 ± 1.24 (13-17)	-0.42	0.69	0.74	0.49
31	<i>L. tari</i>	IL4	20.57 ± 1.81 (17-22)	20.8 ± 1.1 (19-22)	20.67 ± 1.5 (17-22)	-0.25	0.81	0.35	0.06
32	<i>L. zullyae</i>	PP	-	6.86 ± 1.07 (5-8)	-	-	-	-	0.33
33	<i>L. zullyae</i>	SCI	7 ± 0 (7-7)	6.86 ± 0.9 (6-8)	6.88 ± 0.83 (6-8)	<i>Not eval, n F = I</i>		0.05	
34	<i>L. zullyae</i>	LS	5 ± 0 (5-5)	4.86 ± 0.38 (4-5)	4.88 ± 0.35 (4-5)	<i>Not eval, n F = I</i>		<b>&lt;0.0001</b>	
35	<i>L. zullyae</i>	SS	8 ± 0 (8-8)	7.86 ± 0.69 (7-9)	7.88 ± 0.64 (7-9)	<i>Not eval, n F = I</i>		0.14	
36	<i>L. zullyae</i>	IS	6 ± 0 (6-6)	6.14 ± 0.69 (5-7)	6.13 ± 0.64 (5-7)	<i>Not eval, n F = I</i>		0.14	
37	<i>L. zullyae</i>	MS	75 ± 0 (75-75)	73.43 ± 4.72 (69-83)	73.63 ± 4.41 (69-83)	<i>Not eval, n F = I</i>		0.18	
38	<i>L. zullyae</i>	DS	70 ± 0 (70-70)	63.57 ± 4.76 (57-70)	64.38 ± 4.96 (57-70)	<i>Not eval, n F = I</i>		0.80	
39	<i>L. zullyae</i>	VS	100 ± 0 (100-100)	95.43 ± 3.41 (91-102)	96 ± 3.55 (91-102)	<i>Not eval, n F = I</i>		0.47	
40	<i>L. zullyae</i>	IL3	17 ± 0 (17-17)	17.43 ± 1.62 (15-20)	17.38 ± 1.51 (15-20)	<i>Not eval, n F = I</i>		0.86	
41	<i>L. zullyae</i>	IL4	22 ± 0 (22-22)	22 ± 2 (20-25)	22 ± 1.85 (20-25)	<i>Not eval, n F = I</i>		0.35	
42	<i>L. baguali</i>	PP	-	8.25 ± 1.39 (6-10)	-	-	-	-	<b>&lt;0.0001</b>
43	<i>L. baguali</i>	SCI	7 ± 0.91 (5-8)	7.13 ± 1.13 (6-9)	7.05 ± 0.97 (5-9)	-0.28	0.78	0.50	0.29
44	<i>L. baguali</i>	LS	5.15 ± 0.55 (4-6)	5.5 ± 1.2 (4-7)	5.29 ± 0.85 (4-7)	0.42	0.47	<i>non-parametric</i>	
45	<i>L. baguali</i>	SS	8.69 ± 0.75 (8-10)	9.38 ± 0.52 (9-10)	8.95 ± 0.74 (8-10)	3.68	<b>0.04</b>	<i>non-parametric</i>	
46	<i>L. baguali</i>	IS	5.77 ± 0.73 (5-7)	6.25 ± 0.71 (5-7)	5.95 ± 0.74 (5-7)	-1.49	0.15	0.99	0.18
47	<i>L. baguali</i>	MS	76.85 ± 4.65 (69-84)	77.5 ± 3.25 (71-80)	77.1 ± 4.1 (69-84)	-0.35	0.73	0.35	0.51
48	<i>L. baguali</i>	DS	63.62 ± 3.31 (58-69)	64 ± 3.38 (58-68)	63.76 ± 3.25 (58-69)	-0.26	0.80	0.90	0.49
49	<i>L. baguali</i>	VS	106.38 ± 4.37 (96-112)	106 ± 4.28 (99-111)	106.24 ± 4.23 (96-112)	0.2	0.85	1.00	0.12
50	<i>L. baguali</i>	IL3	17.54 ± 1.94 (14-20)	18.5 ± 0.53 (18-19)	17.9 ± 1.61 (14-20)	0.76	0.37	<i>non-parametric</i>	
51	<i>L. baguali</i>	IL4	22.62 ± 2.53 (16-26)	23.25 ± 1.28 (21-25)	22.86 ± 2.13 (16-26)	-0.65	0.52	0.08	0.12
52	<i>L. kingii</i>	PP	-	7.73 ± 1.03 (6-10)	-	-	-	-	<b>0.00</b>
53	<i>L. kingii</i>	SCI	6.79 ± 1.05 (6-9)	6.4 ± 0.51 (6-7)	6.59 ± 0.82 (6-9)	0.52	0.41	<i>non-parametric</i>	
54	<i>L. kingii</i>	LS	4.79 ± 0.58 (4-6)	5.47 ± 0.74 (4-7)	5.14 ± 0.74 (4-7)	-2.74	<b>0.01</b>	0.38	0.22
55	<i>L. kingii</i>	SS	8.64 ± 0.84 (7-10)	9.13 ± 0.92 (8-11)	8.9 ± 0.9 (7-11)	-1.5	0.15	0.77	0.47
56	<i>L. kingii</i>	IS	6.5 ± 0.85 (5-8)	6.13 ± 0.99 (4-8)	6.31 ± 0.93 (4-8)	1.06	0.30	0.60	0.58
57	<i>L. kingii</i>	MS	75 ± 5.42 (67-85)	73.2 ± 4.68 (67-85)	74.07 ± 5.04 (67-85)	0.96	0.34	0.59	0.09
58	<i>L. kingii</i>	DS	66.79 ± 4.71 (58-73)	63.53 ± 6.01 (51-74)	65.1 ± 5.58 (51-74)	1.61	0.12	0.39	0.68
59	<i>L. kingii</i>	VS	102.07 ± 8.3 (84-123)	102.87 ± 7.53 (90-115)	102.48 ± 7.78 (84-123)	-0.27	0.79	0.72	0.79



1	<i>L. kingii</i>	IL3	16.86 ± 1.96 (13-21)	17.13 ± 1.13 (15-20)	17 ± 1.56 (13-21)	0.21	0.63	<i>non-parametric</i>	
2	<i>L. kingii</i>	IL4	22.36 ± 2.5 (19-27)	22.33 ± 2.32 (19-28)	22.34 ± 2.36 (19-28)	0.04	0.98	<i>non-parametric</i>	
3	<i>L. somuncurae</i>	PP	-	5.6 ± 0.7 (5-7)	-	-	-	<i>non-parametric</i>	
4	<i>L. somuncurae</i>	SCI	6.67 ± 1.63 (6-10)	6.1 ± 0.32 (6-7)	6.31 ± 1.01 (6-10)	0.07	0.75	<i>non-parametric</i>	
5	<i>L. somuncurae</i>	LS	5 ± 0.89 (4-6)	5.6 ± 0.97 (4-7)	5.38 ± 0.96 (4-7)	-1.23	0.24	0.91	0.33
6	<i>L. somuncurae</i>	SS	8.33 ± 0.82 (7-9)	8.6 ± 0.7 (8-10)	8.5 ± 0.73 (7-10)	-0.69	0.50	0.65	0.29
7	<i>L. somuncurae</i>	IS	6.17 ± 1.17 (5-8)	5.6 ± 0.52 (5-6)	5.81 ± 0.83 (5-8)	0.75	0.45	<i>non-parametric</i>	
8	<i>L. somuncurae</i>	MS	79.17 ± 4.17 (73-83)	80.50 ± 5.21 (75-93)	80.00 ± 4.75 (73-93)	-0.53	0.60	0.64	0.30
9	<i>L. somuncurae</i>	DS	69.83 ± 1.47 (68-72)	69.3 ± 2.79 (65-74)	69.5 ± 2.34 (65-74)	0.43	0.67	0.17	0.86
10	<i>L. somuncurae</i>	VS	110 ± 8.85 (98-118)	113.3 ± 3.62 (108-118)	112.06 ± 6.06 (98-118)	0.07	0.80	<i>non-parametric</i>	
11	<i>L. somuncurae</i>	IL3	17.17 ± 0.98 (16-19)	18 ± 0.94 (17-19)	17.69 ± 1.01 (16-19)	2.31	0.11	<i>non-parametric</i>	
12	<i>L. somuncurae</i>	IL4	23.83 ± 1.47 (22-26)	24.1 ± 1.37 (22-26)	24 ± 1.37 (22-26)	-0.37	0.72	0.80	0.22
13	<i>L. tristis</i>	PP	-	7.75 ± 0.97 (6-9)	-	-	-	-	<b>0.01</b>
14	<i>L. tristis</i>	SCI	6.59 ± 1 (6-9)	7 ± 1.41 (6-10)	6.76 ± 1.18 (6-10)	0.31	0.52	<i>non-parametric</i>	
15	<i>L. tristis</i>	LS	4.59 ± 0.51 (4-5)	4.92 ± 0.67 (4-6)	4.72 ± 0.59 (4-6)	1.38	0.17	<i>non-parametric</i>	
16	<i>L. tristis</i>	SS	8 ± 0.61 (7-9)	8.58 ± 0.67 (8-10)	8.24 ± 0.69 (7-10)	-2.43	<b>0.02</b>	0.73	0.05
17	<i>L. tristis</i>	IS	6.29 ± 0.85 (5-8)	6.42 ± 0.67 (5-7)	6.34 ± 0.77 (5-8)	0.44	0.47	<i>non-parametric</i>	
18	<i>L. tristis</i>	MS	77.35 ± 5.74 (67-86)	74.25 ± 5.14 (65-84)	76.07 ± 5.62 (65-86)	1.5	0.15	0.72	0.39
19	<i>L. tristis</i>	DS	68.47 ± 4.32 (62-75)	67.17 ± 3.9 (60-73)	67.93 ± 4.13 (60-75)	0.83	0.41	0.75	0.10
20	<i>L. tristis</i>	VS	103.12 ± 5.91 (94-118)	103.5 ± 5.92 (95-114)	103.28 ± 5.81 (94-118)	-0.17	0.87	0.97	0.44
21	<i>L. tristis</i>	IL3	17.35 ± 1.27 (15-20)	17.58 ± 1.51 (16-20)	17.45 ± 1.35 (15-20)	-0.45	0.66	0.52	0.09
22	<i>L. tristis</i>	IL4	23 ± 1.77 (18-25)	23.75 ± 1.76 (20-26)	23.31 ± 1.77 (18-26)	5.33	0.06	<i>non-parametric</i>	
23	<i>L. uptoni</i>	PP	-	6.67 ± 0.52 (6-7)	-	-	-	-	<b>0.00</b>
24	<i>L. uptoni</i>	SCI	6.25 ± 0.5 (6-7)	7.5 ± 1.05 (6-9)	7 ± 1.05 (6-9)	-2.19	0.06	0.25	0.85
25	<i>L. uptoni</i>	LS	4.4 ± 0.55 (4-5)	4.83 ± 0.41 (4-5)	4.64 ± 0.5 (4-5)	-1.51	0.17	0.53	0.16
26	<i>L. uptoni</i>	SS	8.4 ± 0.89 (7-9)	7.5 ± 1.05 (6-9)	7.91 ± 1.04 (6-9)	1.51	0.16	0.78	0.27
27	<i>L. uptoni</i>	IS	5.2 ± 0.45 (5-6)	4.67 ± 1.03 (3-6)	4.91 ± 0.83 (3-6)	1.07	0.31	0.13	0.81
28	<i>L. uptoni</i>	MS	69.6 ± 3.71 (64-73)	70.83 ± 2.4 (68-75)	70.27 ± 2.97 (64-75)	-0.67	0.52	0.36	0.41
29	<i>L. uptoni</i>	DS	65.4 ± 2.79 (62-68)	65.5 ± 3.27 (60-68)	65.45 ± 2.91 (60-68)	0.01	0.95	<i>non-parametric</i>	
30	<i>L. uptoni</i>	VS	106.2 ± 9.52 (95-118)	108.33 ± 5.99 (99-114)	107.36 ± 7.45 (95-118)	-0.45	0.66	0.34	0.68
31	<i>L. uptoni</i>	IL3	16.6 ± 0.55 (16-17)	17.67 ± 1.51 (16-20)	17.18 ± 1.25 (16-20)	-1.49	0.17	0.07	0.16
32	<i>L. uptoni</i>	IL4	24.8 ± 1.1 (23-26)	24 ± 1.67 (21-26)	24.36 ± 1.43 (21-26)	0.91	0.38	0.43	0.24
33	<i>L. avilae</i>	PP	-	-	-	-	-	-	-
34	<i>L. avilae</i>	SCI	8.5 ± 1.73 (7-10)	7.2 ± 0.84 (6-8)	7.78 ± 1.39 (6-10)	1.49	0.18	0.19	0.10
35	<i>L. avilae</i>	LS	4 ± 0.82 (3-5)	4.4 ± 0.55 (4-5)	4.22 ± 0.67 (3-5)	-0.88	0.41	0.46	0.65
36	<i>L. avilae</i>	SS	5 ± 0.82 (4-6)	5 ± 0 (5-5)	5 ± 0.5 (4-6)	0	>0.99	<i>non-parametric</i>	
37	<i>L. avilae</i>	IS	4.25 ± 0.5 (4-5)	4.8 ± 0.45 (4-5)	4.56 ± 0.53 (4-5)	-1.74	0.13	0.81	0.59
38	<i>L. avilae</i>	MS	56.75 ± 3.86 (53-61)	56.6 ± 2.88 (53-59)	56.67 ± 3.12 (53-61)	0.06	0.95	<i>non-parametric</i>	
39	<i>L. avilae</i>	DS	55.75 ± 4.03 (51-60)	53.6 ± 1.34 (52-55)	54.56 ± 2.88 (51-60)	1.13	0.29	0.06	0.95
40	<i>L. avilae</i>	VS	84.75 ± 4.57 (80-91)	81.2 ± 6.83 (72-90)	82.78 ± 5.89 (72-91)	0.89	0.40	0.54	0.90
41	<i>L. avilae</i>	IL3	15.75 ± 0.5 (15-16)	16.2 ± 0.84 (15-17)	16 ± 0.71 (15-17)	-0.94	0.38	0.42	0.44
42	<i>L. avilae</i>	IL4	21.5 ± 1.73 (20-24)	22.8 ± 1.48 (21-25)	22.22 ± 1.64 (20-25)	-1.22	0.26	0.75	0.23
43	<i>L. hatcheri</i>	PP	-	-	-	-	-	-	-
44	<i>L. hatcheri</i>	SCI	6.75 ± 1.04 (6-9)	6.92 ± 1.62 (5-10)	6.85 ± 1.39 (5-10)	0.01	0.90	<i>non-parametric</i>	
45	<i>L. hatcheri</i>	LS	4.25 ± 0.46 (4-5)	4.67 ± 0.78 (4-6)	4.5 ± 0.69 (4-6)	100017	0.21	<i>non-parametric</i>	
46	<i>L. hatcheri</i>	SS	7 ± 0.76 (6-8)	6.75 ± 0.75 (6-8)	6.85 ± 0.75 (6-8)	0.48	0.45	<i>non-parametric</i>	
47	<i>L. hatcheri</i>	IS	5.25 ± 0.46 (5-6)	5.25 ± 0.97 (4-7)	5.25 ± 0.79 (4-7)	0	>0.99	<i>non-parametric</i>	
48	<i>L. hatcheri</i>	MS	48.75 ± 3.41 (43-54)	48.58 ± 3.42 (44-57)	48.65 ± 3.33 (43-57)	0.11	0.92	0.97	0.76
49	<i>L. hatcheri</i>	DS	50.5 ± 2.67 (47-55)	47.58 ± 3.58 (43-54)	48.75 ± 3.49 (43-55)	1.96	0.07	0.45	0.14
50	<i>L. hatcheri</i>	VS	68.25 ± 4.03 (62-73)	67.5 ± 3 (63-74)	67.8 ± 3.37 (62-74)	0.48	0.64	0.37	0.78
51	<i>L. hatcheri</i>	IL3	14.75 ± 1.39 (13-17)	14.92 ± 1.44 (13-18)	14.85 ± 1.39 (13-18)	-0.26	0.80	0.95	0.17
52	<i>L. hatcheri</i>	IL4	19.63 ± 1.3 (18-22)	19.33 ± 1.3 (18-22)	19.45 ± 1.28 (18-22)	0.25	0.60	<i>non-parametric</i>	
53	<i>L. kolengh</i>	PP	-	-	-	-	-	-	-
54	<i>L. kolengh</i>	SCI	6.25 ± 0.86 (4-7)	6.27 ± 0.96 (5-8)	6.26 ± 0.89 (4-8)	0.09	0.75	<i>non-parametric</i>	
55	<i>L. kolengh</i>	LS	4.31 ± 0.48 (4-5)	4.27 ± 0.7 (3-5)	4.29 ± 0.59 (3-5)	0.03	0.98	<i>non-parametric</i>	
56	<i>L. kolengh</i>	SS	6.56 ± 0.89 (5-8)	6.73 ± 0.7 (6-8)	6.65 ± 0.8 (5-8)	0.17	0.65	<i>non-parametric</i>	
57	<i>L. kolengh</i>	IS	5.25 ± 0.45 (5-6)	5.33 ± 0.62 (5-7)	5.29 ± 0.53 (5-7)	0.02	0.84	<i>non-parametric</i>	
58	<i>L. kolengh</i>	MS	51.13 ± 2.22 (48-55)	49.93 ± 2.81 (44-54)	50.55 ± 2.55 (44-55)	1.31	0.20	0.37	0.38
59	<i>L. kolengh</i>	DS	50.31 ± 2.18 (46-54)	48.33 ± 3.04 (44-54)	49.35 ± 2.78 (44-54)	2.09	<b>0.05</b>	0.22	0.26

1	<i>L. kolengh</i>	VS	70.13 ± 3.83 (63-76)	66.93 ± 3.33 (61-73)	68.58 ± 3.89 (61-76)	2.47	<b>0.02</b>	0.61	0.24
2	<i>L. kolengh</i>	IL3	14.25 ± 0.86 (13-16)	15 ± 0.88 (13-16)	14.6 ± 0.93 (13-16)	-2.37	<b>0.03</b>	0.92	0.26
3	<i>L. kolengh</i>	IL4	18.88 ± 1.36 (17-22)	18.6 ± 1.59 (16-21)	18.74 ± 1.46 (16-22)	0.52	0.61	0.55	0.18
4	<i>L. lineomaculatus</i>	PP	-	-	-	-	-	-	-
5	<i>L. lineomaculatus</i>	SCI	6.8 ± 0.84 (6-8)	7 ± 0.89 (6-8)	6.91 ± 0.83 (6-8)	-0.38	0.71	0.92	0.08
6	<i>L. lineomaculatus</i>	LS	4.2 ± 0.45 (4-5)	4.5 ± 0.84 (4-6)	4.36 ± 0.67 (4-6)	0.21	0.85	<i>non-parametric</i>	
7	<i>L. lineomaculatus</i>	SS	6.8 ± 0.84 (6-8)	6.33 ± 0.82 (5-7)	6.55 ± 0.82 (5-8)	0.93	0.37	0.93	0.62
8	<i>L. lineomaculatus</i>	IS	4.4 ± 0.55 (4-5)	4.67 ± 0.52 (4-5)	4.55 ± 0.52 (4-5)	0.53	0.57	<i>non-parametric</i>	
9	<i>L. lineomaculatus</i>	MS	59.8 ± 4.15 (53-63)	60.83 ± 3.87 (55-65)	60.36 ± 3.83 (53-65)	-0.43	0.68	0.86	0.10
10	<i>L. lineomaculatus</i>	DS	59 ± 3.94 (55-64)	57.83 ± 1.6 (56-60)	58.36 ± 2.8 (55-64)	0.67	0.52	0.07	0.65
11	<i>L. lineomaculatus</i>	VS	85.2 ± 5.45 (81-94)	85.33 ± 2.25 (83-89)	85.27 ± 3.8 (81-94)	-0.06	0.96	0.08	0.24
12	<i>L. lineomaculatus</i>	IL3	16 ± 1.41 (15-18)	16 ± 1.55 (15-19)	16 ± 1.41 (15-19)	0.01	>0.99	<i>non-parametric</i>	
13	<i>L. lineomaculatus</i>	IL4	21.6 ± 1.52 (20-24)	22 ± 1.67 (20-25)	21.82 ± 1.54 (20-25)	-0.41	0.69	0.87	0.25
14	<i>L. morandae</i>	PP	-	-	-	-	-	-	-
15	<i>L. morandae</i>	SCI	6.2 ± 0.45 (6-7)	6.5 ± 0.71 (6-7)	6.29 ± 0.49 (6-7)	-0.7	0.51	0.38	0.06
16	<i>L. morandae</i>	LS	4 ± 0.71 (3-5)	4 ± 1.41 (3-5)	4 ± 0.82 (3-5)	0	>0.99	0.23	0.11
17	<i>L. morandae</i>	SS	6.6 ± 1.52 (5-9)	8 ± 2.83 (6-10)	7 ± 1.83 (5-10)	-0.9	0.41	0.27	0.38
18	<i>L. morandae</i>	IS	5.2 ± 0.45 (5-6)	6 ± 0 (6-6)	5.43 ± 0.53 (5-6)	2.4	0.14	<i>non-parametric</i>	
19	<i>L. morandae</i>	MS	60.4 ± 1.67 (59-63)	58 ± 4.24 (55-61)	59.71 ± 2.5 (55-63)	1.19	0.29	0.13	0.55
20	<i>L. morandae</i>	DS	52 ± 3.81 (47-57)	50 ± 0 (50-50)	51.43 ± 3.26 (47-57)	2.4	0.62	<i>non-parametric</i>	
21	<i>L. morandae</i>	VS	81.4 ± 2.61 (79-85)	82 ± 4.24 (79-85)	81.57 ± 2.76 (79-85)	-0.24	0.82	0.36	0.16
22	<i>L. morandae</i>	IL3	15.6 ± 1.52 (13-17)	15.5 ± 0.71 (15-16)	15.57 ± 1.27 (13-17)	0.09	0.93	0.67	0.10
23	<i>L. morandae</i>	IL4	21.4 ± 1.95 (18-23)	21 ± 0 (21-21)	21.29 ± 1.6 (18-23)	3.04	0.29	<i>non-parametric</i>	
24	<i>L. silvanae</i>	PP	-	-	-	-	-	-	-
25	<i>L. silvanae</i>	SCI	6.88 ± 0.99 (6-8)	7 ± 1.12 (5-8)	6.94 ± 1.03 (5-8)	0.08	0.78	<i>non-parametric</i>	
26	<i>L. silvanae</i>	LS	4 ± 0.53 (3-5)	4.33 ± 0.71 (3-5)	4.18 ± 0.64 (3-5)	-1.08	0.30	0.48	0.24
27	<i>L. silvanae</i>	SS	6 ± 0.53 (5-7)	6.33 ± 0.87 (5-7)	6.18 ± 0.73 (5-7)	1.02	0.31	<i>non-parametric</i>	
28	<i>L. silvanae</i>	IS	4.88 ± 0.83 (4-6)	4.89 ± 0.6 (4-6)	4.88 ± 0.7 (4-6)	0.01	0.84	<i>non-parametric</i>	
29	<i>L. silvanae</i>	MS	60 ± 2.62 (56-64)	59.33 ± 3.24 (55-65)	59.65 ± 2.89 (55-65)	0.46	0.65	0.59	0.60
30	<i>L. silvanae</i>	DS	57.25 ± 1.91 (54-60)	54.89 ± 3.66 (52-64)	56 ± 3.12 (52-64)	5.11	<b>0.02</b>	<i>non-parametric</i>	
31	<i>L. silvanae</i>	VS	73.5 ± 2.27 (70-76)	75.56 ± 2.88 (71-80)	74.59 ± 2.74 (70-80)	-1.62	0.13	0.54	0.66
32	<i>L. silvanae</i>	IL3	16.25 ± 1.04 (14-17)	16.22 ± 1.3 (15-18)	16.24 ± 1.15 (14-18)	0.05	0.96	0.56	0.18
33	<i>L. silvanae</i>	IL4	19.75 ± 1.39 (18-22)	20.67 ± 1.32 (19-23)	20.24 ± 1.39 (18-23)	-1.39	0.18	0.88	0.09
34	<i>L. caparensis</i>	PP	-	3.67 ± 0.58 (3-4)	-	-	-	<i>non-parametric</i>	
35	<i>L. caparensis</i>	SCI	6.71 ± 1.11 (5-8)	6 ± 1 (5-7)	6.50 ± 1.08 (5-8)	0.95	0.37	0.77	0.42
36	<i>L. caparensis</i>	LS	5 ± 0.58 (4-6)	4.33 ± 1.15 (3-5)	4.80 ± 0.79 (3-6)	1.26	0.25	0.09	0.21
37	<i>L. caparensis</i>	SS	6.71 ± 0.76 (6-8)	6.33 ± 0.58 (6-7)	6.60 ± 0.79 (6-8)	0.77	0.46	0.83	0.20
38	<i>L. caparensis</i>	IS	4.71 ± 0.76 (3-5)	4.67 ± 0.58 (4-5)	4.79 ± 0.67 (3-5)	0.12	>0.99	<i>non-parametric</i>	
39	<i>L. caparensis</i>	MS	42.71 ± 2.56 (39-46)	42.67 ± 2.31 (40-44)	42.70 ± 2.36 (39-46)	0.03	0.98	0.97	0.35
40	<i>L. caparensis</i>	DS	41.43 ± 1.81 (39-45)	39.67 ± 1.15 (39-41)	40.90 ± 1.79 (39-45)	1.53	0.16	0.63	0.21
41	<i>L. caparensis</i>	VS	68.14 ± 2.67 (64-72)	67.33 ± 3.21 (65-71)	67.90 ± 2.69 (64-72)	0.42	0.69	0.61	0.56
42	<i>L. caparensis</i>	IL3	14.43 ± 0.53 (14-15)	15.33 ± 0.58 (15-16)	14.70 ± 0.67 (14-16)	2.92	0.11	<i>non-parametric</i>	
43	<i>L. caparensis</i>	IL4	19.86 ± 1.35 (18-22)	20.5 ± 0.71 (20-21)	20.00 ± 1.22 (18-22)	-0.63	0.55	0.76	0.96
44	<i>L. magellanicus</i>	PP	-	3.67 ± 0.82 (3-5)	-	-	-	-	0.12
45	<i>L. magellanicus</i>	SCI	6.5 ± 1 (6-8)	7.17 ± 0.98 (6-9)	6.9 ± 0.99 (6-9)	1.38	0.24	<i>non-parametric</i>	
46	<i>L. magellanicus</i>	LS	4.25 ± 0.5 (4-5)	4.67 ± 0.52 (4-5)	4.5 ± 0.53 (4-5)	-1.26	0.24	0.98	0.16
47	<i>L. magellanicus</i>	SS	6.75 ± 0.5 (6-7)	6.5 ± 0.55 (6-7)	6.6 ± 0.52 (6-7)	0.41	0.57	<i>non-parametric</i>	
48	<i>L. magellanicus</i>	IS	5 ± 0.82 (4-6)	4.67 ± 0.52 (4-5)	4.8 ± 0.63 (4-6)	0.8	0.45	0.35	0.40
49	<i>L. magellanicus</i>	MS	40.5 ± 3.7 (36-44)	41.33 ± 1.75 (39-44)	41 ± 2.54 (36-44)	-0.49	0.64	0.14	0.78
50	<i>L. magellanicus</i>	DS	37 ± 1.83 (35-39)	36.83 ± 2.48 (34-41)	36.9 ± 2.13 (34-41)	0.11	0.91	0.65	0.77
51	<i>L. magellanicus</i>	VS	58.25 ± 3.2 (55-61)	57.5 ± 5.09 (49-63)	57.8 ± 4.24 (49-63)	0.26	0.80	0.48	0.65
52	<i>L. magellanicus</i>	IL3	12.25 ± 0.96 (11-13)	13.67 ± 1.03 (12-15)	13.1 ± 1.2 (11-15)	-2.18	0.06	0.96	0.53
53	<i>L. magellanicus</i>	IL4	17.25 ± 0.96 (16-18)	18.2 ± 1.1 (17-20)	17.78 ± 1.09 (16-20)	-1.36	0.21	0.86	0.41

**APPENDIX 6:** Morphometric variables from each species discriminated by sex. Mean  $\pm$  SD (min–max) are shown; Student's *t* test or Kruskal Wallis (when assumptions were rejected; *non-parametric*) *p*-values and statistics are shown. Assumptions to perform a parametric test (Student's *t*) are normality (*p*-Hom-Var: Levene test) and variance homogeneity (*p*-SW: Shapiro-Wilks test); when those tests were rejected ( $p > 0.05$ ) a non-parametric test was performed. For *L. scolaroi* and *L. zullyae* sexual dimorphism was not evaluated due to small female sample sizes (Not eval). Significant values are in italics and boldface. *Not eval.*,  $nF=1$  denotes that females sample size was one thus the test was not performed. **SVL**: snout–vent length; **DFH**: distance between fore and hind limbs; **FOL**: foot length; **TFL**, tibia–fibula length; **RUL**: radius–ulna length; **HAL**: hand length; **HH**: head height; **HW**: head width; **HL**: head length; **RND**: rostral–nasal distance; **RH**: rostral height; **DRE**: distance from rostral to the eye; **AH**: auditory meatus height.

<i>Sp</i>	Var	Females	Males	All	Statistic	<i>p</i> - <i>t</i> -test/KW	<i>p</i> -HomVar	<i>p</i> -SW
<i>L. archeforus</i>	SVL	67 $\pm$ 6.24 (62-74)	71.75 $\pm$ 8.51 (56-84)	70.45 $\pm$ 7.97 (56-84)	-0.87	0.41	0.79	0.90
<i>L. archeforus</i>	DFH	33.49 $\pm$ 1.45 (32.1-35)	32.98 $\pm$ 4.62 (23.57-37.6)	33.12 $\pm$ 3.93 (23.57-37.6)	0.18	0.86	0.18	0.32
<i>L. archeforus</i>	FOL	17.28 $\pm$ 2.09 (15.9-19)	18.98 $\pm$ 2.07 (15.-22.33)	18.52 $\pm$ 2.12 (15.03-22.33)	-1.21	0.26	0.81	0.95
<i>L. archeforus</i>	TFL	11.45 $\pm$ 1.17 (10.6-12.8)	13.59 $\pm$ 1.77 (10.46-15.9)	13 $\pm$ 1.86 (10.46-15.85)	-1.9	0.09	0.67	0.86
<i>L. archeforus</i>	RUL	6.33 $\pm$ 1.19 (5.1-7.48)	7.13 $\pm$ 1.18 (5.79-8.7)	6.91 $\pm$ 1.18 (5.1-8.68)	-1.01	0.34	0.81	0.06
<i>L. archeforus</i>	HAL	10.67 $\pm$ 1.68 (9.2-12.5)	10.76 $\pm$ 1.89 (8.11-14.51)	10.73 $\pm$ 1.75 (8.11-14.51)	-0.07	0.95	0.98	0.89
<i>L. archeforus</i>	HH	7.67 $\pm$ 0.61 (7.31-8.38)	8.98 $\pm$ 1.21 (7.09-10.77)	8.62 $\pm$ 1.21 (7.09-10.77)	-1.75	0.11	0.44	0.92
<i>L. archeforus</i>	HW	10.72 $\pm$ 0.79 (10-11.58)	12.94 $\pm$ 1.8 (9.74-15.51)	12.34 $\pm$ 1.86 (9.74-15.51)	-2.01	0.08	0.34	0.89
<i>L. archeforus</i>	HL	12.85 $\pm$ 0.61 (12.2-13.4)	15.11 $\pm$ 1.67 (12.4-17.97)	14.49 $\pm$ 1.77 (12.21-17.97)	-2.22	0.05	0.25	0.98
<i>L. archeforus</i>	RND	1.88 $\pm$ 0.16 (1.78-2.07)	2.41 $\pm$ 0.27 (2-2.89)	2.26 $\pm$ 0.34 (1.78-2.89)	-3.08	<b>0.01</b>	0.59	0.99
<i>L. archeforus</i>	RH	0.98 $\pm$ 0.04 (0.94-1.02)	1.18 $\pm$ 0.15 (0.9-1.34)	1.12 $\pm$ 0.16 (0.9-1.34)	-2.27	<b>0.05</b>	0.15	0.50
<i>L. archeforus</i>	DRE	5.48 $\pm$ 0.43 (4.99-5.78)	6.49 $\pm$ 0.59 (5.59-7.19)	6.21 $\pm$ 0.71 (4.99-7.19)	-2.66	<b>0.03</b>	0.78	0.17
<i>L. archeforus</i>	AH	2.47 $\pm$ 0.04 (2.42-2.5)	2.75 $\pm$ 0.47 (2.21-3.47)	2.67 $\pm$ 0.41 (2.21-3.47)	0.67	0.49	<i>non-parametric</i>	
<i>L. archeforus</i>	TL	79 $\pm$ 0 (79-79)	90 $\pm$ 7.07 (85-95)	86.33 $\pm$ 8.08 (79-95)		<i>Not eval</i> , $n F=1$		>0.99
<i>L. chacabucoense</i>	SVL	65.33 $\pm$ 3.88 (62-72)	71.89 $\pm$ 3.3 (66-77)	69.27 $\pm$ 4.76 (62-77)	-3.52	<b>&lt;0.001</b>	0.65	0.80
<i>L. chacabucoense</i>	DFH	36.14 $\pm$ 2.85 (33.1-41.2)	34.49 $\pm$ 2.7 (30.7-38.1)	35.15 $\pm$ 2.79 (30.7-41.23)	1.14	0.28	0.85	0.56
<i>L. chacabucoense</i>	FOL	15.34 $\pm$ 1.03 (13.6-16.9)	18.25 $\pm$ 0.9 (16.29-19.4)	17.08 $\pm$ 1.74 (13.63-19.4)	-5.81	<b>&lt;0.001</b>	0.71	0.21
<i>L. chacabucoense</i>	TFL	11.02 $\pm$ 0.41 (10.5-11.6)	13.41 $\pm$ 0.48 (12.41-14)	12.45 $\pm$ 1.28 (10.47-13.99)	10.13	<b>&lt;0.001</b>	0.79	0.45
<i>L. chacabucoense</i>	RUL	5.78 $\pm$ 0.6 (5.13-6.79)	6.91 $\pm$ 0.87 (5.5-8.26)	6.46 $\pm$ 0.94 (5.13-8.26)	-2.76	<b>0.02</b>	0.43	0.88
<i>L. chacabucoense</i>	HAL	9.07 $\pm$ 0.74 (7.97-9.92)	10.69 $\pm$ 1.02 (9.21-11.97)	10.04 $\pm$ 1.21 (7.97-11.97)	-3.34	<b>0.01</b>	0.49	0.32
<i>L. chacabucoense</i>	HH	7.25 $\pm$ 0.45 (6.75-7.75)	9.18 $\pm$ 0.81 (8.13-10.93)	8.41 $\pm$ 1.19 (6.75-10.93)	-5.29	<b>&lt;0.001</b>	0.22	0.56
<i>L. chacabucoense</i>	HW	10.56 $\pm$ 0.52 (9.8-11.14)	12.72 $\pm$ 0.77 (11.34-13.7)	11.86 $\pm$ 1.28 (9.79-13.72)	-5.99	<b>&lt;0.001</b>	0.39	0.66
<i>L. chacabucoense</i>	HL	12.66 $\pm$ 0.68 (11.9-13.4)	14.87 $\pm$ 0.99 (13.1-16.29)	13.98 $\pm$ 1.41 (11.85-16.29)	-4.72	<b>&lt;0.001</b>	0.43	0.81
<i>L. chacabucoense</i>	RND	2 $\pm$ 0.23 (1.75-2.32)	2.35 $\pm$ 0.26 (2.05-2.81)	2.21 $\pm$ 0.3 (1.75-2.81)	-2.65	<b>0.02</b>	0.78	0.28
<i>L. chacabucoense</i>	RH	0.91 $\pm$ 0.12 (0.8-1.06)	1.12 $\pm$ 0.14 (0.97-1.36)	1.04 $\pm$ 0.17 (0.8-1.36)	5.01	<b>0.02</b>	<i>non-parametric</i>	
<i>L. chacabucoense</i>	DRE	5.83 $\pm$ 0.52 (5.27-6.56)	6.47 $\pm$ 0.34 (6.14-7.16)	6.22 $\pm$ 0.52 (5.27-7.16)	-2.91	<b>0.01</b>	0.28	0.15
<i>L. chacabucoense</i>	AH	2.48 $\pm$ 0.18 (2.22-2.69)	2.95 $\pm$ 0.19 (2.67-3.23)	2.76 $\pm$ 0.3 (2.22-3.23)	-4.74	<b>&lt;0.001</b>	0.92	0.35
<i>L. chacabucoense</i>	TL	72.75 $\pm$ 13.18 (55-85)	85.67 $\pm$ 7.28 (73-92)	80.5 $\pm$ 11.48 (55-92)	-2.02	0.08	0.23	0.48
<i>L. escarchadosi</i>	SVL	71.5 $\pm$ 5.2 (64-76)	76.2 $\pm$ 6.14 (67-83)	74.11 $\pm$ 5.93 (64-83)	-1.22	0.26	0.82	0.36
<i>L. escarchadosi</i>	DFH	35.31 $\pm$ 4.56 (28.7-38.4)	35.43 $\pm$ 2.85 (31.14-38.7)	35.37 $\pm$ 3.45 (28.7-38.7)	-0.05	0.96	0.39	0.13
<i>L. escarchadosi</i>	FOL	17.93 $\pm$ 0.61 (17.4-18.8)	19.59 $\pm$ 1.03 (18.45-21.1)	18.85 $\pm$ 1.2 (17.43-21.12)	-2.82	<b>0.03</b>	0.41	0.75
<i>L. escarchadosi</i>	TFL	13.26 $\pm$ 0.59 (12.8-14.1)	14.5 $\pm$ 0.33 (14.2-14.99)	13.95 $\pm$ 0.78 (12.8-14.99)	-4.03	<b>0.01</b>	0.29	0.22
<i>L. escarchadosi</i>	RUL	8.15 $\pm$ 0.45 (7.61-8.69)	9.25 $\pm$ 0.48 (8.52-9.81)	8.76 $\pm$ 0.73 (7.61-9.81)	-3.53	<b>0.01</b>	0.97	0.49
<i>L. escarchadosi</i>	HAL	10.66 $\pm$ 0.05 (10.6-10.7)	10.88 $\pm$ 0.35 (10.6-11.46)	10.78 $\pm$ 0.28 (10.59-11.46)	1.5	0.28	<i>non-parametric</i>	
<i>L. escarchadosi</i>	HH	8.64 $\pm$ 0.65 (8.03-9.53)	10.02 $\pm$ 1.26 (8.45-11.64)	9.41 $\pm$ 1.21 (8.03-11.64)	-1.97	0.09	0.31	0.93
<i>L. escarchadosi</i>	HW	12.4 $\pm$ 0.48 (11.7-12.79)	14.1 $\pm$ 1.17 (12.35-15.5)	13.35 $\pm$ 1.26 (11.71-15.5)	-2.7	<b>0.03</b>	0.18	0.81
<i>L. escarchadosi</i>	HL	15.5 $\pm$ 0.62 (14.75-16.2)	17.47 $\pm$ 1.58 (15.03-19.2)	16.59 $\pm$ 1.58 (14.75-19.2)	-2.34	0.05	0.16	0.86

1	<i>L. escarchadosi</i>	RND	2.5 ± 0.2 (2.29-2.76)	2.71 ± 0.31 (2.37-2.99)	2.62 ± 0.27 (2.29-2.99)	-1.16	0.29	0.49	0.12
2	<i>L. escarchadosi</i>	RH	2.57 ± 5.13 (1.06-1.3)	1.21 ± 0.15 (1.04-1.37)	2.11 ± 3.42 (1.04-1.37)	0	>0.99	non-parametric	
3	<i>L. escarchadosi</i>	DRE	9.34 ± 0.33 (9.01-9.66)	10.14 ± 0.82 (9.16-11.32)	9.78 ± 0.75 (9.01-11.32)	-1.82	0.11	0.17	0.92
4	<i>L. escarchadosi</i>	AH	2.84 ± 0.45 (2.25-3.29)	3.37 ± 0.4 (2.73-3.76)	3.13 ± 0.48 (2.25-3.76)	-1.89	0.10	0.78	0.20
5	<i>L. escarchadosi</i>	TL	83 ± 5.66 (79-87)	95.67 ± 4.04 (92-100)	90.6 ± 8.02 (79-100)	-2.99	0.06	0.59	0.12
6	<i>L. gallardoi</i>	SVL	73.8 ± 3.69 (66-79)	74.41 ± 4.15 (64-81)	74.13 ± 3.89 (64-81)	-0.44	0.66	0.66	0.44
7	<i>L. gallardoi</i>	DFH	37.69 ± 3.17 (33.1-43.4)	35.21 ± 2.04 (30.16-39.8)	36.37 ± 2.88 (30.16-43.44)	2.66	<b>0.01</b>	0.10	0.80
8	<i>L. gallardoi</i>	FOL	18.74 ± 1.09 (17-20.96)	20.33 ± 1.03 (18.2-22.26)	19.58 ± 1.32 (17.01-22.26)	-4.24	<b>&lt;0.001</b>	0.81	0.87
9	<i>L. gallardoi</i>	TFL	12.69 ± 0.43 (12-13.61)	14.23 ± 0.91 (11.79-15.4)	13.51 ± 1.06 (11.79-15.38)	16.79	<b>&lt;0.001</b>	non-parametric	
10	<i>L. gallardoi</i>	RUL	7.84 ± 0.4 (7-8.42)	8.66 ± 0.8 (6.6-9.64)	8.28 ± 0.76 (6.6-9.64)	11.68	<b>&lt;0.001</b>	non-parametric	
11	<i>L. gallardoi</i>	HAL	10.02 ± 0.46 (9.4-10.68)	11.03 ± 0.55 (10.-12.42)	10.56 ± 0.72 (9.39-12.42)	-5.63	<b>&lt;0.001</b>	0.47	0.65
12	<i>L. gallardoi</i>	HH	8.43 ± 0.55 (7.49-9.51)	9.49 ± 0.81 (7.54-10.87)	8.99 ± 0.87 (7.49-10.87)	-4.25	<b>&lt;0.001</b>	0.15	0.95
13	<i>L. gallardoi</i>	HW	11.82 ± 0.74 (10.5-13.2)	13.64 ± 1.19 (11.1-16.3)	12.79 ± 1.35 (10.54-16.3)	-5.11	<b>&lt;0.001</b>	0.08	0.98
14	<i>L. gallardoi</i>	HL	13.81 ± 0.62 (13-15.16)	15.63 ± 1.01 (13.25-17.9)	14.78 ± 1.25 (12.99-17.93)	-6.01	<b>&lt;0.001</b>	0.08	0.70
15	<i>L. gallardoi</i>	RND	2.19 ± 0.19 (1.93-2.58)	2.48 ± 0.25 (2.1-2.9)	2.34 ± 0.27 (1.93-2.9)	-3.7	<b>&lt;0.001</b>	0.30	0.22
16	<i>L. gallardoi</i>	RH	1.2 ± 0.15 (0.97-1.42)	1.4 ± 0.16 (0.98-1.6)	1.3 ± 0.19 (0.97-1.6)	-3.58	<b>&lt;0.001</b>	0.78	0.20
17	<i>L. gallardoi</i>	DRE	6.33 ± 0.28 (5.92-6.84)	6.82 ± 0.39 (6.1-7.57)	6.59 ± 0.42 (5.92-7.57)	-4.01	<b>&lt;0.001</b>	0.24	0.58
18	<i>L. gallardoi</i>	AH	2.58 ± 0.23 (2.16-3)	3 ± 0.26 (2.39-3.47)	2.8 ± 0.32 (2.16-3.47)	-4.86	<b>&lt;0.001</b>	0.69	0.90
19	<i>L. gallardoi</i>	TL	87.71 ± 5.33 (78-96)	96.21 ± 5.48 (88-107)	91.96 ± 6.84 (78-107)	-4.16	<b>&lt;0.001</b>	0.92	0.62
20	<i>L. sarmientoi</i>	SVL	75.75 ± 7.09 (67-82)	78.86 ± 2.79 (75-84)	77.73 ± 4.71 (67-84)	-1.06	0.32	0.05	0.68
21	<i>L. sarmientoi</i>	DFH	39.45 ± 6.34 (31.8-46.6)	36.83 ± 2.23 (34.38-41.3)	37.78 ± 4.1 (31.8-46.6)	1.08	0.34	non-parametric	
22	<i>L. sarmientoi</i>	FOL	17.43 ± 0.78 (16.7-18.5)	19.23 ± 1.19 (17.88-21)	18.57 ± 1.36 (16.66-20.99)	-2.68	<b>0.03</b>	0.53	0.40
23	<i>L. sarmientoi</i>	TFL	12.92 ± 1.08 (11.9-13.9)	14.41 ± 0.54 (13.8-15.26)	13.87 ± 1.05 (11.86-15.26)	-3.1	<b>0.01</b>	0.14	0.29
24	<i>L. sarmientoi</i>	RUL	7.7 ± 0.67 (7.02-8.62)	8.63 ± 0.54 (8.17-9.75)	8.29 ± 0.73 (7.02-9.75)	-2.52	<b>0.03</b>	0.59	0.11
25	<i>L. sarmientoi</i>	HAL	10.02 ± 0.62 (9.6-10.92)	11.29 ± 0.58 (10.4-12.25)	10.83 ± 0.85 (9.59-12.25)	-3.43	<b>0.01</b>	0.79	0.48
26	<i>L. sarmientoi</i>	HH	8.88 ± 0.5 (8.33-9.31)	9.85 ± 0.44 (8.94-10.3)	9.49 ± 0.66 (8.33-10.3)	-3.33	<b>0.01</b>	0.72	0.20
27	<i>L. sarmientoi</i>	HW	11.98 ± 0.72 (11.4-12.9)	14.04 ± 0.74 (13-14.95)	13.29 ± 1.25 (11.38-14.95)	-4.5	<b>&lt;0.001</b>	0.94	0.13
28	<i>L. sarmientoi</i>	HL	14.17 ± 1.07 (12.9-15.2)	16.27 ± 0.55 (15.38-17)	15.5 ± 1.28 (12.91-16.97)	-4.36	<b>&lt;0.001</b>	0.16	0.70
29	<i>L. sarmientoi</i>	RND	2.44 ± 0.16 (2.31-2.67)	2.53 ± 0.19 (2.22-2.78)	2.5 ± 0.18 (2.22-2.78)	-0.82	0.44	0.85	0.79
30	<i>L. sarmientoi</i>	RH	1.07 ± 0.23 (0.82-1.3)	1.26 ± 0.18 (0.89-1.41)	1.19 ± 0.21 (0.82-1.41)	0.57	0.14	0.54	0.36
31	<i>L. sarmientoi</i>	DRE	6.03 ± 0.4 (5.62-6.5)	6.51 ± 0.29 (6.12-6.97)	6.33 ± 0.4 (5.62-6.97)	-2.3	<b>0.05</b>	0.44	0.28
32	<i>L. sarmientoi</i>	AH	3.27 ± 0.55 (2.78-3.96)	3.62 ± 0.21 (3.4-3.96)	3.5 ± 0.38 (2.78-3.96)	1.08	0.34	non-parametric	
33	<i>L. sarmientoi</i>	TL	77 ± 8.29 (70-89)	89.17 ± 4.4 (83-95)	84.3 ± 8.55 (70-95)	-3.06	<b>0.02</b>	0.21	0.51
34	<i>L. scolaroi</i>	SVL	61 ± 0 (61-61)	67.25 ± 14.01 (54-87)	66 ± 12.45 (54-87)	Not eval., n F = 1		0.52	
35	<i>L. scolaroi</i>	DFH	29.87 ± 0 (29.87-29.87)	29.58 ± 2.52 (27.23-33.1)	29.64 ± 2.19 (27.23-33.13)	Not eval., n F = 1		0.55	
36	<i>L. scolaroi</i>	FOL	16.05 ± 0 (16.05-16.05)	16.43 ± 1.23 (14.66-17.5)	16.35 ± 1.07 (14.66-17.49)	Not eval., n F = 1		0.39	
37	<i>L. scolaroi</i>	TFL	10.73 ± 0 (10.73-10.73)	11.09 ± 0.95 (9.67-11.71)	11.01 ± 0.84 (9.67-11.71)	Not eval., n F = 1		0.10	
38	<i>L. scolaroi</i>	RUL	6.65 ± 0 (6.65-6.65)	6.68 ± 0.27 (6.45-6.97)	6.68 ± 0.24 (6.45-6.97)	Not eval., n F = 1		0.28	
39	<i>L. scolaroi</i>	HAL	8.07 ± 0 (8.07-8.07)	9.42 ± 0.92 (8.43-10.37)	9.15 ± 1 (8.07-10.37)	Not eval., n F = 1		0.75	
40	<i>L. scolaroi</i>	HH	7.49 ± 0 (7.49-7.49)	7.81 ± 0.56 (6.98-8.11)	7.75 ± 0.5 (6.98-8.11)	Not eval., n F = 1		<b>0.02</b>	
41	<i>L. scolaroi</i>	HW	9.91 ± 0 (9.91-9.91)	10.67 ± 1.05 (9.45-11.9)	10.52 ± 0.97 (9.45-11.9)	Not eval., n F = 1		>0.99	
42	<i>L. scolaroi</i>	HL	11.98 ± 0 (11.98-11.98)	13.62 ± 0.87 (12.46-14.4)	13.29 ± 1.05 (11.98-14.43)	Not eval., n F = 1		0.73	
43	<i>L. scolaroi</i>	RND	1.89 ± 0 (1.89-1.89)	2.5 ± 0.07 (2.41-2.56)	2.38 ± 0.28 (1.89-2.56)	Not eval., n F = 1		0.60	
44	<i>L. scolaroi</i>	RH	0.92 ± 0 (0.92-0.92)	1.03 ± 0.08 (0.95-1.11)	1.01 ± 0.09 (0.92-1.11)	Not eval., n F = 1		0.28	
45	<i>L. scolaroi</i>	DRE	5.64 ± 0 (5.64-5.64)	6.04 ± 0.35 (5.54-6.33)	5.96 ± 0.35 (5.54-6.33)	Not eval., n F = 1		0.38	
46	<i>L. scolaroi</i>	AH	2.52 ± 0 (2.52-2.52)	2.75 ± 0.32 (2.53-3.22)	2.71 ± 0.29 (2.52-3.22)	Not eval., n F = 1		0.14	
47	<i>L. scolaroi</i>	TL	79 ± 0 (79-79)	71 ± 9.56 (63-82)	72.6 ± 9.02 (63-82)	Not eval., n F = 1		0.39	
48	<i>L. tari</i>	SVL	82.8 ± 9.23 (69-93)	90.6 ± 13.26 (68-101)	86.7 ± 11.53 (68-101)	-1.08	0.31	0.50	0.11
49	<i>L. tari</i>	DFH	41.37 ± 5.5 (33.4-48.49)	42.73 ± 6.61 (31.3-47.25)	42.05 ± 5.78 (31.3-48.49)	-0.35	0.73	0.73	0.28
50	<i>L. tari</i>	FOL	19.86 ± 1.5 (17.57-21.5)	22.39 ± 1.89 (19.13-23.7)	21.12 ± 2.09 (17.57-23.74)	-2.34	<b>0.05</b>	0.67	0.09
51	<i>L. tari</i>	TFL	14.49 ± 1.25 (12.7-15.7)	17.22 ± 1.62 (14.6-18.69)	15.86 ± 1.98 (12.7-18.69)	-2.99	<b>0.02</b>	0.63	0.25
52	<i>L. tari</i>	RUL	9.47 ± 1.01 (8.06-10.44)	10.6 ± 1.03 (8.84-11.45)	10.03 ± 1.13 (8.06-11.45)	-1.75	0.12	0.98	0.05
53	<i>L. tari</i>	HAL	10.8 ± 0.83 (9.54-11.82)	12.5 ± 1.13 (10.71-13.45)	11.65 ± 1.29 (9.54-13.45)	-2.71	<b>0.03</b>	0.56	0.29
54	<i>L. tari</i>	HH	9.69 ± 1.34 (8.03-11.5)	12.34 ± 2.28 (8.46-14.44)	11.01 ± 2.25 (8.03-14.44)	-2.24	0.06	0.33	0.36
55	<i>L. tari</i>	HW	13.69 ± 1.33 (12.5-15.4)	18.57 ± 3.07 (13.4-21.46)	16.13 ± 3.41 (12.45-21.46)	-3.26	<b>0.01</b>	0.14	0.48
56	<i>L. tari</i>	HL	17.76 ± 1.81 (14.9-19.6)	21.53 ± 3.05 (16.6-24.25)	19.64 ± 3.09 (14.86-24.25)	-2.38	<b>0.04</b>	0.34	0.27
57	<i>L. tari</i>	RND	2.85 ± 0.3 (2.62-3.36)	3.41 ± 0.76 (2.16-4.02)	3.13 ± 0.62 (2.16-4.02)	-1.51	0.17	0.10	0.18
58	<i>L. tari</i>	RH	1.36 ± 0.32 (1.09-1.9)	1.46 ± 0.2 (1.13-1.63)	1.41 ± 0.26 (1.09-1.9)	-0.63	0.55	0.41	0.71
59	<i>L. tari</i>	DRE	10.59 ± 0.99 (9.1-11.87)	12.49 ± 1.45 (10.39-13.8)	11.54 ± 1.54 (9.11-13.8)	-2.41	<b>0.04</b>	0.48	0.26

1	<i>L. tari</i>	AH	3.16 ± 0.24 (2.83-3.39)	3.71 ± 0.59 (2.83-4.34)	3.44 ± 0.51 (2.83-4.34)	-1.9	0.09	0.10	0.93
2	<i>L. tari</i>	TL	93 ± 18.94 (68-112)	112.5 ± 16.58 (90-130)	102.75 ± 19.5 (68-130)	-1.55	0.17	0.83	0.25
3	<i>L. zullyae</i>	SVL	66 ± 0 (66-66)	71 ± 2.89 (66-74)	70.38 ± 3.2 (66-74)		<i>Not eval., n F = 1</i>		0.57
4	<i>L. zullyae</i>	DFH	35.54 ± 0 (35.54-35.54)	31.46 ± 1.16 (30.1-33.45)	31.97 ± 1.8 (30.09-35.54)		<i>Not eval., n F = 1</i>		0.64
5	<i>L. zullyae</i>	FOL	15.61 ± 0 (15.61-15.61)	18.57 ± 1.15 (17.37-20.2)	18.2 ± 1.49 (15.61-20.2)		<i>Not eval., n F = 1</i>		0.34
6	<i>L. zullyae</i>	TFL	11.56 ± 0 (11.56-11.56)	13.36 ± 0.78 (12.26-14.2)	13.13 ± 0.96 (11.56-14.2)		<i>Not eval., n F = 1</i>		0.38
7	<i>L. zullyae</i>	RUL	6.77 ± 0 (6.77-6.77)	7.89 ± 0.43 (7.27-8.42)	7.75 ± 0.56 (6.77-8.42)		<i>Not eval., n F = 1</i>		0.47
8	<i>L. zullyae</i>	HAL	8.81 ± 0 (8.81-8.81)	10.4 ± 0.85 (9.1-11.82)	10.2 ± 0.97 (8.81-11.82)		<i>Not eval., n F = 1</i>		0.83
9	<i>L. zullyae</i>	HH	8.1 ± 0 (8.1-8.1)	9.47 ± 0.75 (8.22-10.73)	9.3 ± 0.85 (8.1-10.73)		<i>Not eval., n F = 1</i>		0.76
10	<i>L. zullyae</i>	HW	10.82 ± 0 (10.82-10.82)	13.13 ± 0.8 (11.48-14)	12.84 ± 1.1 (10.82-14)		<i>Not eval., n F = 1</i>		0.11
11	<i>L. zullyae</i>	HL	13.46 ± 0 (13.46-13.46)	15.81 ± 0.81 (14.6-16.84)	15.52 ± 1.12 (13.46-16.84)		<i>Not eval., n F = 1</i>		0.62
12	<i>L. zullyae</i>	RND	2.37 ± 0 (2.37-2.37)	2.83 ± 0.22 (2.53-3.27)	2.77 ± 0.26 (2.37-3.27)		<i>Not eval., n F = 1</i>		0.22
13	<i>L. zullyae</i>	RH	1.03 ± 0 (1.03-1.03)	1.19 ± 0.13 (1.03-1.46)	1.17 ± 0.14 (1.03-1.46)		<i>Not eval., n F = 1</i>		0.30
14	<i>L. zullyae</i>	DRE	6.1 ± 0 (6.1-6.1)	6.99 ± 0.42 (6.47-7.6)	6.88 ± 0.5 (6.1-7.6)		<i>Not eval., n F = 1</i>		0.41
15	<i>L. zullyae</i>	AH	2.53 ± 0 (2.53-2.53)	3.02 ± 0.2 (2.75-3.2)	2.96 ± 0.25 (2.53-3.2)		<i>Not eval., n F = 1</i>		0.08
16	<i>L. zullyae</i>	TL	74 ± 0 (74-74)	90.33 ± 7.2 (82-101)	88 ± 9.02 (74-101)		<i>Not eval., n F = 1</i>		0.67
17	<i>L. baguali</i>	SVL	77.33 ± 6.92 (68-87)	82.67 ± 4.41 (75-87)	80 ± 6.19 (68-87)	-1.59	0.14	0.35	0.84
18	<i>L. baguali</i>	DFH	37.92 ± 4.45 (32.1-42.4)	37.49 ± 3.54 (31.83-42)	37.7 ± 3.84 (31.83-42.43)	0.18	0.86	0.62	0.11
19	<i>L. baguali</i>	FOL	18.95 ± 1.26 (17.8-21.3)	21.37 ± 0.65 (20.27-22.3)	20.16 ± 1.59 (17.75-22.3)	-4.2	<b>&lt;0.001</b>	0.17	0.21
20	<i>L. baguali</i>	TFL	13.94 ± 0.81 (12.8-14.8)	15.28 ± 0.77 (14.33-16.1)	14.61 ± 1.03 (12.84-16.12)	-2.96	<b>0.01</b>	0.91	0.04
21	<i>L. baguali</i>	RUL	8.3 ± 0.89 (6.98-9.04)	9.08 ± 0.81 (8.13-10.38)	8.69 ± 0.9 (6.98-10.38)	-1.59	0.14	0.85	0.61
22	<i>L. baguali</i>	HAL	11.15 ± 0.74 (10.4-12.4)	12.43 ± 0.27 (12.18-12.9)	11.79 ± 0.85 (10.36-12.92)	5.39	<b>0.02</b>	<i>non-parametric</i>	
23	<i>L. baguali</i>	HH	8.56 ± 0.75 (7.31-9.62)	9.79 ± 1.01 (8.17-10.72)	9.17 ± 1.06 (7.31-10.72)	-2.38	<b>0.04</b>	0.54	0.31
24	<i>L. baguali</i>	HW	13.42 ± 1.6 (11.1-15.98)	15.39 ± 1.49 (12.96-17.3)	14.4 ± 1.79 (11.1-17.3)	-2.21	0.06	0.88	0.70
25	<i>L. baguali</i>	HL	15.68 ± 1.37 (13.5-17.7)	18.43 ± 0.93 (17.17-19.6)	17.06 ± 1.82 (13.52-19.63)	-4.07	<b>&lt;0.001</b>	0.41	1.00
26	<i>L. baguali</i>	RND	2.39 ± 0.25 (2.07-2.68)	2.67 ± 0.78 (1.13-3.32)	2.53 ± 0.57 (1.13-3.32)	3.69	0.07	<i>non-parametric</i>	
27	<i>L. baguali</i>	RH	1.18 ± 0.16 (1.04-1.46)	1.29 ± 0.17 (1.09-1.53)	1.23 ± 0.17 (1.04-1.53)	-1.16	0.27	0.89	0.23
28	<i>L. baguali</i>	DRE	8.27 ± 2.11 (5.89-10.8)	9.41 ± 2.09 (7.24-11.71)	8.84 ± 2.09 (5.89-11.71)	2.08	0.18	<i>non-parametric</i>	
29	<i>L. baguali</i>	AH	3.1 ± 0.53 (2.13-3.66)	3.55 ± 0.45 (2.9-4)	3.32 ± 0.53 (2.13-4)	-1.61	0.14	0.72	0.31
30	<i>L. baguali</i>	TL	87 ± 14 (71-97)	98.75 ± 13.5 (80-112)	93.71 ± 14 (71-112)	-1.12	0.31	0.89	0.15
31	<i>L. kingii</i>	SVL	71.8 ± 5.67 (62-80)	75.07 ± 6.18 (65-86)	73.71 ± 6.08 (62-86)	-1.32	0.20	0.81	0.23
32	<i>L. kingii</i>	DFH	39.04 ± 3.1 (34.39-44.1)	36.43 ± 3.75 (30.9-43.63)	37.52 ± 3.67 (30.9-44.1)	1.8	0.09	0.57	0.53
33	<i>L. kingii</i>	FOL	16.82 ± 1.03 (15.1-18)	18.32 ± 0.72 (17.1-19.59)	17.69 ± 1.13 (15.1-19.59)	-4.2	<b>&lt;0.001</b>	0.25	0.14
34	<i>L. kingii</i>	TFL	11.89 ± 0.81 (10.6-13.4)	13.76 ± 1.25 (11.35-15.6)	12.98 ± 1.43 (10.61-15.61)	-4.16	<b>&lt;0.001</b>	0.20	0.79
35	<i>L. kingii</i>	RUL	7.49 ± 0.82 (6.28-8.58)	8.46 ± 0.86 (6.74-10.29)	8.06 ± 0.96 (6.28-10.29)	-2.78	<b>0.01</b>	0.89	0.84
36	<i>L. kingii</i>	HAL	9.45 ± 0.49 (8.62-10)	10.37 ± 0.54 (9.52-11.23)	9.98 ± 0.69 (8.62-11.23)	-4.28	<b>&lt;0.001</b>	0.79	0.21
37	<i>L. kingii</i>	HH	8.3 ± 0.52 (7.81-9.52)	9.74 ± 0.89 (8.25-11.56)	9.14 ± 1.04 (7.81-11.56)	-4.57	<b>&lt;0.001</b>	0.12	0.58
38	<i>L. kingii</i>	HW	11.33 ± 0.85 (10.4-12.7)	13.11 ± 1.68 (9.11-14.97)	12.37 ± 1.63 (9.11-14.97)	8.57	<b>&lt;0.001</b>	<i>non-parametric</i>	
39	<i>L. kingii</i>	HL	14.39 ± 1.33 (12.5-16.6)	16.52 ± 1.15 (14.57-18.3)	15.63 ± 1.61 (12.47-18.31)	-4.19	<b>&lt;0.001</b>	0.62	0.16
40	<i>L. kingii</i>	RND	2.09 ± 0.21 (1.65-2.46)	2.51 ± 0.25 (2.13-2.94)	2.34 ± 0.31 (1.65-2.94)	-4.29	<b>&lt;0.001</b>	0.63	0.65
41	<i>L. kingii</i>	RH	0.99 ± 0.18 (0.72-1.3)	1.2 ± 0.25 (0.87-1.87)	1.11 ± 0.25 (0.72-1.87)	-2.23	<b>0.04</b>	0.34	0.29
42	<i>L. kingii</i>	DRE	5.76 ± 0.4 (5.21-6.33)	6.66 ± 0.47 (5.87-7.36)	6.28 ± 0.62 (5.21-7.36)	-4.9	<b>&lt;0.001</b>	0.62	0.20
43	<i>L. kingii</i>	AH	3.21 ± 0.42 (2.41-3.88)	3.54 ± 0.27 (3.08-4.02)	3.4 ± 0.37 (2.41-4.02)	-2.37	<b>0.03</b>	0.12	0.95
44	<i>L. kingii</i>	TL	83.5 ± 7.4 (72-91)	84 ± 11.01 (69-102)	83.81 ± 9.54 (69-102)	-0.1	0.92	0.40	0.49
45	<i>L. somuncurae</i>	SVL	78.33 ± 7.89 (68-91)	81.6 ± 6.1 (67-88)	80.38 ± 6.76 (67-91)	-0.93	0.37	0.47	0.78
46	<i>L. somuncurae</i>	DFH	38.26 ± 3.49 (34.7-42.9)	37.15 ± 2.44 (31.67-40)	37.56 ± 2.82 (31.67-42.87)	0.76	0.46	0.33	0.78
47	<i>L. somuncurae</i>	FOL	17.85 ± 0.55 (17-18.6)	19.81 ± 1.04 (17.85-21.5)	19.08 ± 1.31 (16.97-21.49)	-4.24	<b>&lt;0.001</b>	0.17	0.95
48	<i>L. somuncurae</i>	TFL	13.39 ± 0.38 (12.93-14)	14.93 ± 0.89 (12.9-16.12)	14.35 ± 1.05 (12.92-16.12)	-3.98	<b>&lt;0.001</b>	0.08	0.39
49	<i>L. somuncurae</i>	RUL	8.46 ± 1.09 (6.83-9.91)	9.18 ± 0.73 (7.96-10.4)	8.91 ± 0.92 (6.83-10.4)	-1.6	0.13	0.29	0.79
50	<i>L. somuncurae</i>	HAL	10.4 ± 0.55 (9.45-10.85)	11.92 ± 0.63 (11.05-13.1)	11.35 ± 0.96 (9.45-13.14)	-4.9	<b>&lt;0.001</b>	0.79	0.61
51	<i>L. somuncurae</i>	HH	9.43 ± 0.45 (8.73-10.1)	10.17 ± 0.83 (8.93-11.98)	9.89 ± 0.79 (8.73-11.98)	-1.99	0.07	0.20	0.82
52	<i>L. somuncurae</i>	HW	13.12 ± 1 (11.6-14.5)	14.64 ± 1.12 (12.1-15.85)	14.07 ± 1.29 (11.6-15.85)	-2.73	<b>0.02</b>	0.85	0.34
53	<i>L. somuncurae</i>	HL	16.67 ± 1.48 (14.74-19)	18.32 ± 1.18 (15.5-19.74)	17.7 ± 1.5 (14.74-19.74)	-2.47	<b>0.03</b>	0.52	0.93
54	<i>L. somuncurae</i>	RND	2.73 ± 0.13 (2.48-2.85)	2.99 ± 0.22 (2.6-3.29)	2.89 ± 0.23 (2.48-3.29)	-2.63	<b>0.02</b>	0.23	0.66
55	<i>L. somuncurae</i>	RH	1.19 ± 0.15 (0.98-1.38)	1.41 ± 0.17 (1.2-1.73)	1.33 ± 0.19 (0.98-1.73)	-2.62	<b>0.02</b>	0.81	0.38
56	<i>L. somuncurae</i>	DRE	10.02 ± 0.43 (9.3-10.65)	11.2 ± 0.6 (9.82-11.8)	10.76 ± 0.79 (9.31-11.8)	-4.22	<b>&lt;0.001</b>	0.49	0.14
57	<i>L. somuncurae</i>	AH	2.98 ± 0.2 (2.75-3.28)	3.29 ± 0.42 (2.57-3.95)	3.17 ± 0.38 (2.57-3.95)	-1.65	0.12	0.12	0.81
58	<i>L. somuncurae</i>	TL	85.67 ± 3.51 (82-89)	86.33 ± 11.36 (71-102)	86.11 ± 9.16 (71-102)	-0.1	0.93	0.18	0.96
59	<i>L. somuncurae</i>								
60	<i>L. tristis</i>	SVL	67.78 ± 3.15 (63-73)	74 ± 4.05 (66-79)	71.2 ± 4.79 (63-79)	-3.76	<b>&lt;0.001</b>	0.49	0.47

1	<i>L. tristis</i>	DFH	37.34 ± 1.84 (34.4-40.9)	34.83 ± 2.29 (31.85-38.1)	35.96 ± 2.41 (31.85-40.92)	2.66	<b>0.02</b>	0.55	0.23
2	<i>L. tristis</i>	FOL	16.56 ± 1.12 (14.7-17.9)	19.14 ± 1.33 (17-21.22)	17.98 ± 1.79 (14.71-21.22)	-4.62	<b>&lt;0.001</b>	0.64	0.50
3	<i>L. tristis</i>	TFL	11.62 ± 0.37 (11.1-12.1)	14.07 ± 0.73 (12.79-15.2)	12.96 ± 1.38 (11.13-15.24)	14.14	<b>&lt;0.001</b>	0.06	0.97
4	<i>L. tristis</i>	RUL	7.07 ± 0.47 (6.38-7.65)	8.39 ± 0.68 (7.4-9.18)	7.8 ± 0.89 (6.38-9.18)	-4.91	<b>&lt;0.001</b>	0.31	0.08
5	<i>L. tristis</i>	HAL	8.98 ± 0.49 (8.4-9.95)	10.59 ± 0.81 (9.12-12.11)	9.86 ± 1.06 (8.4-12.11)	-5.21	<b>&lt;0.001</b>	0.16	0.93
6	<i>L. tristis</i>	HH	7.51 ± 0.74 (6.26-8.7)	9.53 ± 0.88 (7.94-10.58)	8.62 ± 1.31 (6.26-10.58)	-5.48	<b>&lt;0.001</b>	0.63	0.33
7	<i>L. tristis</i>	HW	10.86 ± 0.72 (9.38-11.9)	13.32 ± 1.37 (10.43-14.8)	12.21 ± 1.67 (9.38-14.84)	-4.85	<b>&lt;0.001</b>	0.08	0.23
8	<i>L. tristis</i>	HL	13.15 ± 0.47 (12.2-13.8)	15.81 ± 1.07 (14.1-17.25)	14.61 ± 1.59 (12.2-17.25)	14.14	<b>&lt;0.001</b>	non-parametric	
9	<i>L. tristis</i>	RND	1.98 ± 0.13 (1.72-2.16)	2.38 ± 0.25 (2.09-2.91)	2.2 ± 0.28 (1.72-2.91)	-4.27	<b>&lt;0.001</b>	0.09	0.35
10	<i>L. tristis</i>	RH	1.08 ± 0.11 (0.96-1.28)	1.24 ± 0.19 (0.88-1.53)	1.16 ± 0.18 (0.88-1.53)	-2.2	<b>0.04</b>	0.14	0.96
11	<i>L. tristis</i>	DRE	5.74 ± 0.51 (4.99-6.75)	6.67 ± 0.4 (5.91-7.17)	6.25 ± 0.65 (4.99-7.17)	-4.57	<b>&lt;0.001</b>	0.46	0.76
12	<i>L. tristis</i>	AH	2.73 ± 0.25 (2.45-3.31)	3.11 ± 0.31 (2.6-3.51)	2.94 ± 0.34 (2.45-3.51)	-2.98	<b>0.01</b>	0.57	0.90
13	<i>L. tristis</i>	TL	79 ± 11.01 (59-91)	83.67 ± 11.96 (66-96)	81.8 ± 11.43 (59-96)	1	0.34	non-parametric	
14	<i>L. uptoni</i>	SVL	66.25 ± 0.96 (65-67)	75.67 ± 10.17 (60-85)	71.9 ± 9.02 (60-85)	1.38	0.29	non-parametric	
15	<i>L. uptoni</i>	DFH	34.28 ± 1.55 (32-35.37)	36.55 ± 5.38 (28.56-42.4)	35.64 ± 4.27 (28.56-42.4)	-0.81	0.44	0.07	0.68
16	<i>L. uptoni</i>	FOL	16.69 ± 0.84 (15.7-17.8)	18.02 ± 1.7 (15.35-19.98)	17.49 ± 1.52 (15.35-19.98)	-1.42	0.19	0.27	0.91
17	<i>L. uptoni</i>	TFL	11.92 ± 0.57 (11.4-12.7)	13.78 ± 1.55 (11.7-15.16)	13.04 ± 1.54 (11.37-15.16)	2.91	0.05	0.13	0.23
18	<i>L. uptoni</i>	RUL	8.28 ± 0.28 (7.88-8.55)	8.96 ± 1 (7.67-10.14)	8.69 ± 0.84 (7.67-10.14)	-1.31	0.23	0.06	0.57
19	<i>L. uptoni</i>	HAL	9.71 ± 0.45 (9.15-10.24)	10.63 ± 1.06 (8.85-11.84)	10.26 ± 0.96 (8.85-11.84)	-1.61	0.15	0.18	0.80
20	<i>L. uptoni</i>	HH	8.04 ± 0.17 (7.8-8.18)	10.92 ± 2.58 (7.98-14.7)	9.77 ± 2.44 (7.8-14.7)	1.64	<b>0.25</b>	non-parametric	
21	<i>L. uptoni</i>	HW	11.68 ± 0.28 (11.35-12)	13.27 ± 2.34 (10.4-15.79)	12.63 ± 1.94 (10.39-15.79)	0.73	0.47	non-parametric	
22	<i>L. uptoni</i>	HL	15.11 ± 0.39 (14.8-15.7)	18.16 ± 2.18 (15.14-19.7)	16.94 ± 2.27 (14.8-19.73)	4.55	<b>0.04</b>	non-parametric	
23	<i>L. uptoni</i>	RND	2.61 ± 0.13 (2.5-2.77)	2.83 ± 0.47 (2.2-3.39)	2.74 ± 0.38 (2.2-3.39)	-0.89	0.40	0.05	0.67
24	<i>L. uptoni</i>	RH	1.05 ± 0.11 (0.95-1.18)	1.21 ± 0.23 (0.85-1.45)	1.14 ± 0.2 (0.85-1.45)	-1.25	0.25	0.28	0.64
25	<i>L. uptoni</i>	DRE	9.1 ± 0.23 (8.85-9.4)	10.65 ± 1.29 (8.94-11.79)	10.03 ± 1.26 (8.85-11.79)	2.33	0.17	non-parametric	
26	<i>L. uptoni</i>	AH	2.82 ± 0.11 (2.68-2.94)	3.49 ± 0.56 (2.65-4.14)	3.22 ± 0.55 (2.65-4.14)	2.91	0.11	non-parametric	
27	<i>L. uptoni</i>	TL	79.5 ± 16.74 (55-92)	88.4 ± 15.63 (65-105)	84.44 ± 15.79 (55-105)	-0.82	0.44	0.86	0.11
28	<i>L. avilae</i>	SVL	55.75 ± 2.5 (53-59)	53.2 ± 4.15 (48-59)	54.33 ± 3.57 (48-59)	1.07	0.32	0.43	0.99
29	<i>L. avilae</i>	DFH	27.08 ± 2.79 (23.1-29.5)	22.92 ± 3.01 (19.4-26.9)	24.77 ± 3.5 (19.4-29.5)	2.12	0.07	0.94	0.61
30	<i>L. avilae</i>	FOL	13.88 ± 0.53 (13.3-14.6)	14.88 ± 1.12 (13.1-15.98)	14.44 ± 1.01 (13.08-15.98)	-1.65	0.14	0.26	0.66
31	<i>L. avilae</i>	TFL	9.58 ± 0.58 (8.73-10.06)	10.29 ± 0.5 (9.79-11.08)	9.97 ± 0.63 (8.73-11.08)	-1.95	0.09	0.76	0.97
32	<i>L. avilae</i>	RUL	5.24 ± 0.36 (4.91-5.58)	5.89 ± 0.73 (4.89-6.81)	5.6 ± 0.66 (4.89-6.81)	-1.59	0.15	0.28	0.89
33	<i>L. avilae</i>	HAL	7.75 ± 0.42 (7.27-8.3)	7.88 ± 0.51 (7.27-8.48)	7.82 ± 0.45 (7.27-8.48)	-0.41	0.69	0.79	0.38
34	<i>L. avilae</i>	HH	6.54 ± 0.36 (6.18-7.03)	7.08 ± 0.67 (6.2-7.67)	6.84 ± 0.59 (6.18-7.67)	-1.44	0.19	0.33	0.38
35	<i>L. avilae</i>	HW	9.2 ± 0.12 (9.04-9.33)	9.6 ± 0.62 (8.89-10.19)	9.42 ± 0.49 (8.89-10.19)	0.24	0.73	non-parametric	
36	<i>L. avilae</i>	HL	10.91 ± 0.33 (10.4-11.2)	11.98 ± 0.71 (11.01-12.9)	11.5 ± 0.78 (10.43-12.9)	-2.76	<b>0.03</b>	0.25	>0.99
37	<i>L. avilae</i>	RND	1.97 ± 0.21 (1.74-2.25)	1.93 ± 0.19 (1.69-2.16)	1.95 ± 0.19 (1.69-2.25)	0.33	0.75	0.84	0.34
38	<i>L. avilae</i>	RH	0.77 ± 0.23 (0.51-1.06)	0.76 ± 0.25 (0.55-1.09)	0.76 ± 0.22 (0.51-1.09)	0.06	0.95	0.92	0.18
39	<i>L. avilae</i>	DRE	4.65 ± 0.21 (4.42-4.89)	4.95 ± 0.2 (4.64-5.2)	4.82 ± 0.25 (4.42-5.2)	-2.14	0.07	0.88	0.61
40	<i>L. avilae</i>	AH	1.8 ± 0.12 (1.68-1.96)	1.99 ± 0.36 (1.6-2.56)	1.9 ± 0.28 (1.6-2.56)	-1	0.35	0.10	0.60
41	<i>L. avilae</i>	TL	65.75 ± 5.12 (61-73)	70.6 ± 4.34 (67-77)	68.44 ± 5.08 (61-77)	-1.54	0.17	0.73	0.11
42	<i>L. hatcheri</i>	SVL	63.33 ± 3.83 (58-69)	61.17 ± 4.45 (55-69)	61.89 ± 4.27 (55-69)	1.02	0.32	0.78	0.31
43	<i>L. hatcheri</i>	DFH	33.02 ± 1.82 (30.1-35.3)	26.92 ± 2.95 (19.5-31.6)	28.95 ± 3.92 (19.5-35.3)	4.61	<b>&lt;0.001</b>	0.30	0.43
44	<i>L. hatcheri</i>	FOL	14.38 ± 0.96 (13.5-15.9)	15.35 ± 0.68 (14.01-16.3)	15.02 ± 0.89 (13.5-16.3)	-2.49	<b>0.02</b>	0.31	0.85
45	<i>L. hatcheri</i>	TFL	8.8 ± 1.15 (6.73-9.71)	8.62 ± 1.55 (5.06-10.47)	8.68 ± 1.4 (5.06-10.47)	0.25	0.80	0.53	0.32
46	<i>L. hatcheri</i>	RUL	6.02 ± 0.29 (5.67-6.49)	6.66 ± 0.44 (6.15-7.33)	6.44 ± 0.5 (5.67-7.33)	-3.24	<b>0.01</b>	0.38	0.05
47	<i>L. hatcheri</i>	HAL	8.83 ± 0.3 (8.52-9.24)	9.31 ± 0.59 (8.5-10.57)	9.15 ± 0.56 (8.5-10.57)	-1.83	0.09	0.14	0.44
48	<i>L. hatcheri</i>	HH	7.04 ± 0.45 (6.31-7.56)	7.65 ± 0.59 (6.41-8.42)	7.45 ± 0.61 (6.31-8.42)	-2.23	<b>0.04</b>	0.56	0.37
49	<i>L. hatcheri</i>	HW	10.77 ± 0.78 (9.7-11.94)	11.44 ± 0.96 (9.95-13.05)	11.22 ± 0.94 (9.7-13.05)	-1.5	0.15	0.69	0.66
50	<i>L. hatcheri</i>	HL	12.33 ± 0.56 (11.4-13)	13.29 ± 0.91 (12.1-14.65)	12.97 ± 0.92 (11.43-14.65)	-2.34	<b>0.03</b>	0.29	0.19
51	<i>L. hatcheri</i>	RND	2.21 ± 0.17 (1.97-2.48)	2.3 ± 0.1 (2.11-2.48)	2.27 ± 0.13 (1.97-2.48)	-1.35	0.20	0.17	0.92
52	<i>L. hatcheri</i>	RH	0.97 ± 0.15 (0.79-1.19)	1 ± 0.09 (0.85-1.13)	0.99 ± 0.11 (0.79-1.19)	-0.51	0.62	0.18	0.85
53	<i>L. hatcheri</i>	DRE	5.32 ± 0.36 (4.78-5.84)	5.73 ± 0.36 (5.24-6.41)	5.59 ± 0.4 (4.78-6.41)	-2.3	<b>0.04</b>	0.88	0.54
54	<i>L. hatcheri</i>	AH	2.02 ± 0.21 (1.85-2.33)	2.22 ± 0.21 (1.91-2.61)	2.15 ± 0.22 (1.85-2.61)	-1.89	0.08	0.95	0.49
55	<i>L. hatcheri</i>	TL	57.33 ± 4.73 (52-61)	68.67 ± 7.81 (55-78)	64.89 ± 8.71 (52-78)	-2.27	0.06	0.58	0.77
56	<i>L. kolengh</i>	SVL	54.92 ± 4.21 (48-62)	58.27 ± 2.58 (53-62)	56.78 ± 3.73 (48-62)	-2.55	<b>0.02</b>	0.09	0.62
57	<i>L. kolengh</i>	DFH	26.16 ± 3.11 (20.7-31.1)	24.83 ± 1.99 (20.7-28.4)	25.42 ± 2.58 (20.7-31.1)	1.35	0.19	0.12	0.95
58	<i>L. kolengh</i>	FOL	14.21 ± 0.61 (13.5-15.3)	15.54 ± 0.66 (14.31-16.3)	14.94 ± 0.92 (13.48-16.3)	13.39	<b>&lt;0.001</b>	0.78	0.40
59	<i>L. kolengh</i>	TFL	9.1 ± 0.71 (7.55-10.28)	10.25 ± 0.47 (9.3-10.92)	9.74 ± 0.82 (7.55-10.92)	-5.11	<b>&lt;0.001</b>	0.15	0.92

1	<i>L. kolengh</i>	RUL	5.6 ± 0.61 (4.6-6.56)	6.45 ± 0.39 (5.84-7.03)	6.07 ± 0.65 (4.6-7.03)	-4.37	<0.001	0.11	0.63
2	<i>L. kolengh</i>	HAL	9.07 ± 0.36 (8.31-9.6)	10.03 ± 0.46 (9.46-11.12)	9.59 ± 0.64 (8.31-11.12)	-5.81	<0.001	0.43	0.83
3	<i>L. kolengh</i>	HH	6.35 ± 0.45 (5.71-7.31)	7.05 ± 0.37 (6.11-7.5)	6.74 ± 0.53 (5.71-7.5)	-4.42	<0.001	0.52	0.91
4	<i>L. kolengh</i>	HW	9.93 ± 0.78 (8.95-11.28)	11.17 ± 0.58 (9.76-11.71)	10.62 ± 0.91 (8.95-11.71)	12.17	<0.001	0.29	0.64
5	<i>L. kolengh</i>	HL	11.22 ± 0.59 (10.2-12.2)	12.52 ± 0.43 (11.7-13.17)	11.94 ± 0.83 (10.18-13.17)	-6.61	<0.001	0.28	0.82
6	<i>L. kolengh</i>	RND	2.02 ± 0.17 (1.74-2.3)	2.23 ± 0.13 (1.99-2.41)	2.14 ± 0.18 (1.74-2.41)	-3.62	<0.001	0.32	0.72
7	<i>L. kolengh</i>	RH	0.99 ± 0.09 (0.84-1.11)	1.05 ± 0.08 (0.91-1.2)	1.02 ± 0.09 (0.84-1.2)	-2	0.06	0.78	0.17
8	<i>L. kolengh</i>	DRE	4.98 ± 0.3 (4.56-5.58)	5.56 ± 0.21 (5.13-5.89)	5.31 ± 0.39 (4.56-5.89)	-5.91	<0.001	0.17	0.50
9	<i>L. kolengh</i>	AH	2 ± 0.24 (1.69-2.43)	2.33 ± 0.3 (1.63-2.95)	2.18 ± 0.32 (1.63-2.95)	-3.09	<0.001	0.42	1.00
10	<i>L. kolengh</i>	TL	57.89 ± 3.1 (53-62)	65.17 ± 3.79 (60-70)	62.05 ± 5.03 (53-70)	11.16	<0.001	non-parametric	
11	<i>L. lineomaculatus</i>	SVL	56.75 ± 1.89 (54-58)	56.17 ± 1.17 (55-58)	56.4 ± 1.43 (54-58)	0.61	0.56	0.33	0.67
12	<i>L. lineomaculatus</i>	DFH	27.35 ± 1.65 (25.6-28.9)	24.1 ± 0.72 (23.1-24.9)	25.4 ± 2 (23.1-28.9)	4.36	<0.001	0.10	0.66
13	<i>L. lineomaculatus</i>	FOL	13.71 ± 0.59 (13. -14.46)	14.83 ± 0.75 (13.99-16.1)	14.38 ± 0.87 (13.05-16.1)	-2.5	0.04	0.74	0.65
14	<i>L. lineomaculatus</i>	TFL	9.46 ± 0.59 (8.65-10.06)	10.69 ± 0.58 (9.79-11.24)	10.2 ± 0.84 (8.65-11.24)	-3.24	0.01	0.91	0.06
15	<i>L. lineomaculatus</i>	RUL	5.63 ± 0.21 (5.4-5.91)	6.49 ± 0.22 (6.08-6.7)	6.14 ± 0.49 (5.4-6.7)	-6.15	<0.001	0.99	0.82
16	<i>L. lineomaculatus</i>	HAL	7.63 ± 0.5 (7.1-8.3)	8.49 ± 0.32 (8.17-8.89)	8.14 ± 0.58 (7.1-8.89)	-3.32	0.01	0.36	0.73
17	<i>L. lineomaculatus</i>	HH	6.95 ± 0.17 (6.79-7.17)	7.44 ± 0.28 (7.15-7.87)	7.24 ± 0.34 (6.79-7.87)	-3.09	0.01	0.42	0.56
18	<i>L. lineomaculatus</i>	HW	9.63 ± 0.42 (9.1-10.13)	10.11 ± 0.29 (9.83-10.55)	9.92 ± 0.41 (9.1-10.55)	-2.13	0.07	0.45	0.63
19	<i>L. lineomaculatus</i>	HL	11.65 ± 0.31 (11.35-12)	12.08 ± 0.45 (11.26-12.5)	11.91 ± 0.44 (11.26-12.5)	-1.66	0.14	0.59	0.42
20	<i>L. lineomaculatus</i>	RND	2 ± 0.07 (1.89-2.04)	2.22 ± 0.21 (1.98-2.5)	2.13 ± 0.2 (1.89-2.5)	-2.05	0.07	0.11	0.78
21	<i>L. lineomaculatus</i>	RH	0.89 ± 0.09 (0.77-0.99)	1 ± 0.07 (0.93-1.1)	0.95 ± 0.09 (0.77-1.1)	-2.19	0.06	0.49	0.66
22	<i>L. lineomaculatus</i>	DRE	4.86 ± 0.21 (4.64-5.14)	5.16 ± 0.24 (4.91-5.52)	5.04 ± 0.27 (4.64-5.52)	-2.03	0.08	0.91	0.20
23	<i>L. lineomaculatus</i>	AH	1.85 ± 0.21 (1.56-2.05)	1.86 ± 0.23 (1.63-2.23)	1.86 ± 0.21 (1.56-2.23)	-0.1	0.93	0.93	0.65
24	<i>L. lineomaculatus</i>	TL	71 ± 2 (70-74)	77.5 ± 4.2 (73-82)	74.25 ± 4.62 (70-82)	-2.79	0.03	0.25	0.57
25	<i>L. morandae</i>	SVL	57 ± 4.24 (52-61)	53 ± 4.24 (50-56)	55.67 ± 4.32 (50-61)	1.09	0.34	0.78	0.19
26	<i>L. morandae</i>	DFH	28.23 ± 2.84 (24.3-30.8)	21.25 ± 2.19 (19.7-22.8)	25.9 ± 4.33 (19.7-30.8)	2.99	0.04	0.99	0.58
27	<i>L. morandae</i>	FOL	14.48 ± 0.88 (13.4-15.2)	15.73 ± 1.52 (14.65-16.8)	14.9 ± 1.16 (13.42-16.8)	-1.34	0.25	0.37	0.10
28	<i>L. morandae</i>	TFL	8.41 ± 0.87 (7.57-9.62)	10.47 ± 0.13 (10.4-10.56)	9.1 ± 1.26 (7.57-10.56)	-3.12	0.04	0.22	0.64
29	<i>L. morandae</i>	RUL	5.21 ± 0.41 (4.69-5.56)	5.54 ± 0.03 (5.52-5.56)	5.32 ± 0.36 (4.69-5.56)	1.34	0.34	0.10	0.66
30	<i>L. morandae</i>	HAL	7.53 ± 0.6 (6.69-8.06)	8.44 ± 1 (7.73-9.14)	7.83 ± 0.79 (6.69-9.14)	-1.46	0.22	0.39	0.31
31	<i>L. morandae</i>	HH	7.13 ± 0.74 (6.52-8.21)	7.41 ± 0.68 (6.93-7.89)	7.23 ± 0.67 (6.52-8.21)	-0.44	0.68	0.86	0.31
32	<i>L. morandae</i>	HW	9.78 ± 0.64 (9.08-10.58)	9.97 ± 0.78 (9.41-10.52)	9.84 ± 0.61 (9.08-10.58)	-0.31	0.77	0.61	0.53
33	<i>L. morandae</i>	HL	11.75 ± 0.63 (11-12.49)	12.4 ± 0.94 (11.73-13.06)	11.96 ± 0.72 (10.96-13.06)	-1.05	0.35	0.46	0.29
34	<i>L. morandae</i>	RND	2.12 ± 0.06 (2.04-2.17)	2.22 ± 0.28 (2.02-2.42)	2.15 ± 0.14 (2.02-2.42)	0	>0.99	non-parametric	
35	<i>L. morandae</i>	RH	1.05 ± 0.16 (0.84-1.18)	1.01 ± 0.07 (0.96-1.06)	1.04 ± 0.13 (0.84-1.18)	0.32	0.77	0.61	0.39
36	<i>L. morandae</i>	DRE	4.97 ± 0.22 (4.78-5.27)	5.31 ± 0.21 (5.16-5.45)	5.08 ± 0.26 (4.78-5.45)	-1.8	0.15	0.83	0.42
37	<i>L. morandae</i>	AH	1.76 ± 0.11 (1.6-1.86)	2.35 ± 0.13 (2.26-2.44)	1.95 ± 0.32 (1.6-2.44)	-5.82	<0.001	0.70	0.35
38	<i>L. morandae</i>	TL	66 ± 7.07 (61-71)	79 ± 0 (79-79)	70.33 ± 9.02 (61-79)	Not evaluated, nF=1		>0.99	
39	<i>L. silvanae</i>	SVL	72 ± 4.66 (65-78)	73.89 ± 2.37 (70-78)	73 ± 3.64 (65-78)	-1.07	0.30	0.08	0.71
40	<i>L. silvanae</i>	DFH	34.25 ± 4.06 (28.1-39.7)	30.71 ± 3.16 (25.1-35.1)	32.38 ± 3.94 (25.1-39.7)	2.02	0.06	0.50	0.49
41	<i>L. silvanae</i>	FOL	17.75 ± 0.71 (16.5-18.6)	19.1 ± 0.57 (18.1-20.1)	18.46 ± 0.93 (16.5-20.1)	-4.33	<0.001	0.56	0.80
42	<i>L. silvanae</i>	TFL	13.23 ± 1.5 (11.8-16.68)	13.94 ± 0.34 (13.47-14.5)	13.6 ± 1.09 (11.77-16.68)	6.75	0.01	non-parametric	
43	<i>L. silvanae</i>	RUL	7.36 ± 0.49 (6.83-8.12)	8.02 ± 0.54 (7.04-8.82)	7.71 ± 0.6 (6.83-8.82)	-2.62	0.02	0.84	0.58
44	<i>L. silvanae</i>	HAL	12.01 ± 0.93 (10.8-13.8)	12.42 ± 0.93 (10.65-13.)	12.23 ± 0.92 (10.65-13.76)	-0.92	0.37	0.98	0.99
45	<i>L. silvanae</i>	HH	7.73 ± 0.52 (6.74-8.41)	8.57 ± 0.32 (8.16-9.06)	8.17 ± 0.6 (6.74-9.06)	-4.09	<0.001	0.21	0.48
46	<i>L. silvanae</i>	HW	12.3 ± 0.86 (11.3-13.69)	13.88 ± 0.49 (13.02-14.7)	13.14 ± 1.05 (11.31-14.71)	-4.72	<0.001	0.14	0.71
47	<i>L. silvanae</i>	HL	13.59 ± 0.85 (12.5-15)	15.16 ± 0.49 (14.63-15.9)	14.42 ± 1.04 (12.47-15.9)	-4.77	<0.001	0.14	0.67
48	<i>L. silvanae</i>	RND	2.24 ± 0.16 (2.08-2.54)	2.5 ± 0.13 (2.26-2.73)	2.38 ± 0.19 (2.08-2.73)	-3.56	<0.001	0.58	0.64
49	<i>L. silvanae</i>	RH	1.21 ± 0.1 (1.09-1.35)	1.18 ± 0.1 (1.01-1.33)	1.19 ± 0.1 (1.01-1.35)	0.6	0.56	1.00	0.30
50	<i>L. silvanae</i>	DRE	5.9 ± 0.33 (5.47-6.43)	5.79 ± 1.95 (0.64-6.88)	5.84 ± 1.4 (0.64-6.88)	4.69	0.03	non-parametric	
51	<i>L. silvanae</i>	AH	2.37 ± 0.23 (1.95-2.66)	2.7 ± 0.18 (2.49-2.95)	2.54 ± 0.26 (1.95-2.95)	-3.26	0.01	0.45	0.40
52	<i>L. silvanae</i>	TL	74.6 ± 2.41 (72-78)	78.67 ± 4.62 (76-84)	76.13 ± 3.72 (72-84)	-1.68	0.14	0.25	0.10
53	<i>L. caparensis</i>	SVL	49.8 ± 2.77 (47-54)	55 ± 3.61 (52-59)	51.75 ± 3.92 (47-59)	-2.31	0.06	0.59	0.12
54	<i>L. caparensis</i>	DFH	23.84 ± 1.62 (21.2-25.2)	24.87 ± 0.93 (24.1-25.9)	24.23 ± 1.43 (21.2-25.9)	-0.98	0.36	0.52	0.28
55	<i>L. caparensis</i>	FOL	12.52 ± 0.71 (11.4-13.2)	14.99 ± 0.44 (14.68-15.3)	13.23 ± 1.35 (11.37-15.3)	-4.44	0.01	0.86	0.42
56	<i>L. caparensis</i>	TFL	6.86 ± 0.55 (6.19-7.55)	7.86 ± 0.72 (7.19-8.62)	7.24 ± 0.77 (6.19-8.62)	-2.23	0.07	0.59	0.20
57	<i>L. caparensis</i>	RUL	5.08 ± 0.44 (4.58-5.66)	5.51 ± 0.12 (5.38-5.61)	5.24 ± 0.4 (4.58-5.66)	-1.62	0.16	0.14	0.99
58	<i>L. caparensis</i>	HAL	7.55 ± 0.53 (7.08-8.36)	8.53 ± 0.59 (7.85-8.91)	7.92 ± 0.72 (7.08-8.91)	-2.44	0.06	0.76	0.60
59	<i>L. caparensis</i>	HH	6.16 ± 0.41 (5.65-6.7)	7.05 ± 0.56 (6.72-7.7)	6.5 ± 0.63 (5.65-7.7)	-2.63	0.04	0.53	0.30

1	<i>L. caparensis</i>	HW	8.8 ± 0.43 (8.4-9.33)	10.41 ± 0.91 (9.37-11.07)	9.41 ± 1.02 (8.4-11.07)	-3.49	<b>0.01</b>	0.19	0.39
2	<i>L. caparensis</i>	HL	10.95 ± 0.37 (10.4-11.4)	12.38 ± 0.91 (11.7-13.41)	11.49 ± 0.93 (10.43-13.41)	-3.21	<b>0.02</b>	0.13	0.80
3	<i>L. caparensis</i>	RND	1.83 ± 0.22 (1.58-2.15)	2.16 ± 0.13 (2.01-2.26)	1.95 ± 0.25 (1.58-2.26)	-2.4	0.05	0.60	0.79
4	<i>L. caparensis</i>	RH	0.97 ± 0.05 (0.9-1.01)	1 ± 0.1 (0.94-1.12)	0.98 ± 0.07 (0.9-1.12)	-0.74	0.49	0.17	0.36
5	<i>L. caparensis</i>	DRE	4.65 ± 0.25 (4.38-4.99)	5.23 ± 0.22 (5.09-5.49)	4.87 ± 0.38 (4.38-5.49)	-3.29	<b>0.02</b>	0.96	0.18
6	<i>L. caparensis</i>	AH	1.82 ± 0.18 (1.65-2.09)	2.13 ± 0.17 (1.94-2.24)	1.93 ± 0.23 (1.65-2.24)	-2.49	<b>0.05</b>	0.97	0.48
7	<i>L. caparensis</i>	TL	63 ± 2.94 (60-67)	74 ± 8.72 (68-84)	67.71 ± 8.01 (60-84)	4.5	<b>0.06</b>	0.11	0.57
8	<i>L. magellanicus</i>	SVL	54.75 ± 6.65 (48-63)	54 ± 3.69 (49-59)	54.3 ± 4.74 (48-63)	0.23	0.82	0.24	0.76
9	<i>L. magellanicus</i>	DFH	24.95 ± 6.01 (16.5-30.6)	23.88 ± 1.67 (22.1-26)	24.31 ± 3.73 (16.5-30.6)	1.14	0.35	<i>non-parametric</i>	
10	<i>L. magellanicus</i>	FOL	13.19 ± 1.25 (11.4-14.2)	14 ± 0.98 (12.85-15.1)	13.64 ± 1.12 (11.4-15.1)	-1.09	0.31	0.64	0.32
11	<i>L. magellanicus</i>	TFL	8.29 ± 1.31 (6.44-9.51)	9.61 ± 0.69 (8.84-10.76)	9.08 ± 1.14 (6.44-10.76)	-2.11	0.07	0.20	0.76
12	<i>L. magellanicus</i>	RUL	5.55 ± 0.82 (4.47-6.28)	6.3 ± 0.48 (5.63-6.88)	6 ± 0.71 (4.47-6.88)	-1.83	0.10	0.28	0.43
13	<i>L. magellanicus</i>	HAL	7.85 ± 0.79 (6.93-8.83)	8.39 ± 0.73 (7.25-9.19)	8.17 ± 0.77 (6.93-9.19)	-1.1	0.30	0.81	0.65
14	<i>L. magellanicus</i>	HH	6.3 ± 1.02 (4.96-7.14)	7.25 ± 0.7 (6.27-7.89)	6.87 ± 0.93 (4.96-7.89)	-1.76	0.12	0.43	0.13
15	<i>L. magellanicus</i>	HW	8.78 ± 1.13 (7.28-9.7)	10 ± 0.74 (8.81-10.53)	9.51 ± 1.06 (7.28-10.53)	-2.1	0.07	0.38	0.12
16	<i>L. magellanicus</i>	HL	10.84 ± 1.37 (9.1-11.95)	11.89 ± 1.06 (10.5-13.37)	11.47 ± 1.24 (9.13-13.37)	-1.38	0.20	0.58	0.39
17	<i>L. magellanicus</i>	RND	1.86 ± 0.3 (1.47-2.15)	2.07 ± 0.19 (1.77-2.29)	1.98 ± 0.25 (1.47-2.29)	-1.36	0.21	0.34	0.44
18	<i>L. magellanicus</i>	RH	0.91 ± 0.12 (0.76-1.03)	0.89 ± 0.12 (0.74-1.08)	0.9 ± 0.12 (0.74-1.08)	0.31	0.76	0.94	0.51
19	<i>L. magellanicus</i>	DRE	4.49 ± 0.51 (3.82-4.92)	4.75 ± 0.42 (4.16-5.3)	4.65 ± 0.45 (3.82-5.3)	-0.88	0.41	0.65	0.28
20	<i>L. magellanicus</i>	AH	1.74 ± 0.32 (1.27-1.95)	1.99 ± 0.21 (1.69-2.3)	1.89 ± 0.27 (1.27-2.3)	-1.48	0.18	0.39	0.55
21	<i>L. magellanicus</i>	TL	55.25 ± 9.54 (44-65)	63.5 ± 6.45 (59-73)	59.38 ± 8.73 (44-73)	-1.43	0.20	0.54	0.31

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**APPENDIX 7:** Statistical tests performed on the morphometric variables standardized by SVL for species with sexual dimorphism for SVL. Student's *t* test or Kruskal-Wallis (when assumptions were rejected; *non-parametric*) *p*-values and statistics are shown. Assumptions to perform a parametric test (Student's *t*) are normality (*p*-Hom-Var: Levene test) and variance homogeneity (*p*-SW: Shapiro-Wilks test); when those tests were rejected ( $p > 0.05$ ) a non-parametric test was performed). Significant values are in italics and boldface. Variable names are explained in Appendix 6.

<i>Sp</i>	<i>Var</i>	Statistic	<i>p</i> - <i>t</i> -test/KW	<i>p</i> -HomVar	<i>p</i> -SW
<i>L. chacabucoense</i>	DFH/SVL	6.01	< <b>0.0001</b>	0.299	0.924
<i>L. chacabucoense</i>	FOL/SVL	5.01	<b>0.0256</b>	<i>non-parametric</i>	
<i>L. chacabucoense</i>	TFL/SVL	-5.83	<b>0.0001</b>	0.0884	0.972
<i>L. chacabucoense</i>	RUL/SVL	-1.23	0.242	0.705	0.62
<i>L. chacabucoense</i>	HAL/SVL	-2	0.0668	0.8125	0.135
<i>L. chacabucoense</i>	HH/SVL	-5.27	<b>0.0002</b>	0.0788	0.555
<i>L. chacabucoense</i>	HW/SVL	-5.57	<b>0.0001</b>	0.7904	0.781
<i>L. chacabucoense</i>	HL/SVL	-2.53	<b>0.025</b>	0.642	0.038
<i>L. chacabucoense</i>	RND/SVL	-1.02	0.3271	0.4587	0.717
<i>L. chacabucoense</i>	RH/SVL	-1.87	0.0842	0.6989	0.489
<i>L. chacabucoense</i>	DRE/SVL	-0.15	0.881	0.0666	0.73
<i>L. chacabucoense</i>	AH/SVL	-2.68	<b>0.0189</b>	0.8233	0.437
<i>L. chacabucoense</i>	TL/SVL	0.06	0.84	<i>non-parametric</i>	
<i>L. kolengh</i>	DFH/SVL	4.61	<b>0.0001</b>	0.3847	0.067
<i>L. kolengh</i>	FOL/SVL	-1.8	0.0848	0.1023	0.282
<i>L. kolengh</i>	TFL/SVL	8.57	<b>0.0034</b>	<i>non-parametric</i>	
<i>L. kolengh</i>	RUL/SVL	-2.52	<b>0.0187</b>	0.6932	0.418
<i>L. kolengh</i>	HAL/SVL	-1.83	0.0799	0.0653	0.858
<i>L. kolengh</i>	HH/SVL	-2.98	<b>0.0063</b>	0.4002	0.829
<i>L. kolengh</i>	HW/SVL	-3.4	<b>0.0023</b>	0.5619	0.114
<i>L. kolengh</i>	HL/SVL	11.01	<b>0.0009</b>	<i>non-parametric</i>	
<i>L. kolengh</i>	RND/SVL	-1.57	0.1288	0.3831	0.153
<i>L. kolengh</i>	RH/SVL	-0.15	0.8799	0.806	0.408
<i>L. kolengh</i>	DRE/SVL	-3.41	<b>0.0022</b>	0.6804	0.81
<i>L. kolengh</i>	AH/SVL	-2.03	0.0533	0.1288	0.465
<i>L. kolengh</i>	TL/SVL	0.04	0.85	<i>non-parametric</i>	
<i>L. tristis</i>	DFH/SVL	14.14	<b>0.0002</b>	<i>non-parametric</i>	
<i>L. tristis</i>	FOL/SVL	-2.16	<b>0.0445</b>	0.9674	0.851
<i>L. tristis</i>	TFL/SVL	14.14	<b>0.0002</b>	<i>non-parametric</i>	
<i>L. tristis</i>	RUL/SVL	-3.08	<b>0.0065</b>	0.6677	0.465
<i>L. tristis</i>	HAL/SVL	-2.22	<b>0.0393</b>	0.5496	0.634
<i>L. tristis</i>	HH/SVL	-4.76	<b>0.0002</b>	0.4016	0.164
<i>L. tristis</i>	HW/SVL	-3.93	<b>0.001</b>	0.1731	0.069
<i>L. tristis</i>	HL/SVL	13.02	<b>0.0003</b>	<i>non-parametric</i>	
<i>L. tristis</i>	RND/SVL	-2.13	<b>0.0473</b>	0.667	0.697
<i>L. tristis</i>	RH/SVL	-0.84	0.4111	0.1559	0.601
<i>L. tristis</i>	DRE/SVL	-1.92	0.0707	0.0874	0.06
<i>L. tristis</i>	AH/SVL	-0.97	0.3447	0.4722	0.327
<i>L. tristis</i>	TL/SVL	0.04	0.85	<i>non-parametric</i>	

**APPENDIX 8:** Statistical tests for meristic values. A- females of the *kingii-archeforus* group; B- males of the *kingii-archeforus* group; C- *lineomaculatus* group; D- *magellanicus* group. Letters correspond to groups found by the Di Rienzo, Guzmán and Casanoves comparisons (DGC). ANOVA or Kruskal-Wallis (KW), Shapiro-Wilks and Levene *p*-values are shown. To assume normality and variance homogeneity Shapiro-Wilks and Levene test should not be rejected ( $p > 0.05$ ). In cases (*non-par*) whether either normality or variance homogeneity was rejected, for those ones Kruskal-Wallis tests (non-parametric ANOVA test) were performed and *p*-values are shown. Z indicates that there were no statistical differences in the comparisons. Significant values are shown in italics and boldface. **SCI:** scales in contact with interparietal; **LS:** lorilabial scales; **SS:** supralabial scales; **IS:** infralabial scales; **MS:** midbody scales; **DS:** dorsal scales; **VS:** ventral scales; **IL3:** infradigital lamellae of the third finger; **IL4:** infradigital lamellae of the fourth toe.

A-

Females	SCI	LS	SS	IS	MS	DS	VS	IL3	IL4
<i>L. archeforus</i>	-	-	A	Z	A-B	B	B	-	A
<i>L. chacabucoense</i>	-	-	A	Z	A-B	B	B	-	A
<i>L. escarchadosi</i>	-	-	B	Z	A	A	B	-	A
<i>L. gallardoi</i>	-	-	B	Z	A-B	B	B	-	A
<i>L. sarmientoi</i>	-	-	B	Z	A	A	A	-	A
<i>L. scolaroi</i>	-	-	A	Z	B	B	B	-	A
<i>L. tari</i>	-	-	B	Z	A	A	B	-	A
<i>L. zullyae</i>	-	-	B	Z	A-B	B	B	-	A
<i>L. baguali</i>	-	-	B	Z	B	B	B	-	A
<i>L. kingii</i>	-	-	B	Z	A-B	B	B	-	A
<i>L. somuncurae</i>	-	-	B	Z	B	B	B	-	B
<i>L. tristis</i>	-	-	B	Z	B	B	B	-	A
<i>L. uptoni</i>	-	-	B	Z	A-B	B	B	-	B
Statistic	16.08	13.49	3.48	20.13	57.37	10.35	3.44	17.63	2.23
<i>p</i> - ANOVA or KW	0.1	0.12	<b>0.0003</b>	<b>0.02</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0003</b>	0.1	<b>0.0158</b>
<i>p</i> - Shapiro-Wilks	<i>non-par</i>	<i>non-par</i>	0.37	<i>non-par</i>	<i>non-par</i>	0.93	0.91	<i>non-par</i>	0.61
<i>p</i> - Levene	-	-	0.09	-	-	0.16	0.18	-	0.24

B-

Males	SCI	LS	SS	IS	MS	DS	VS	IL3	IL4
<i>L. archeforus</i>	-	A-B	A	B	C-D	B	A	B-C-D-E	A-B-C-D
<i>L. chacabucoense</i>	-	A-B-C	A	B	D	B	A	B-C-D-E	A-B-C-D
<i>L. escarchadosi</i>	-	A	A	B	A	A	A	A	A
<i>L. gallardoi</i>	-	A-B-C	B	B	D-E	B	A	B-C-D-E	B-C-D-E
<i>L. sarmientoi</i>	-	A	B	B	A-B	A	A	A-B-C-D	A-B
<i>L. scolaroi</i>	-	A-B-C	A	B	B-C-D	B	A	A-B-C	A-B-C
<i>L. tari</i>	-	B-C	A	B	A-B-C	A	A	A-B	A
<i>L. zullyae</i>	-	A-B-C	A	B	D-E	B	A	D-E-F	A-B-C-D
<i>L. baguali</i>	-	B-C	B	B	E-F	B	B	F	C-D-E
<i>L. kingii</i>	-	C	B	B	D-E	B	B	C-D-E	A-B-C-D
<i>L. somuncurae</i>	-	C	B	B	F	B	C	E-F	E
<i>L. tristis</i>	-	A-B-C	B	B	D-E	B	B	D-E-F	D-E
<i>L. uptoni</i>	-	A-B-C	A	A	B-C-D	B	B	D-E-F	D-E

Statistic	17.1	20.82	8.14	3.98	67.27	15.27	12.66	36.87	35.04
<i>p</i> - ANOVA or KW	0.07	<b>0.01</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0003</b>
<i>p</i> - Shapiro-Wilks	<i>non-par</i>	<i>non-par</i>	0.2	0.58	<i>non-par</i>	0.99	0.79	<i>non-par</i>	<i>non-par</i>
<i>p</i> - Levene	-	-	0.72	0.2	-	0.08	0.23	-	-

C-

Males and Females	SCI	LS	SS	IS	MS	DS	VS	IL3	IL4
<i>L. morandae</i>	A	-	B	B	C	B	C	A	B
<i>L. avilae</i>	B	-	A	A	B	B	C	B	B
<i>L. lineomaculatus</i>	A-B	-	B	A	C	C	D	B	B
<i>L. hatcheri</i>	A	-	B	B	A	A	A	A	A
<i>L. kolengh</i>	A	-	B	B	A	A	A	A	A
<i>L. silvanae</i>	A-B	-	B	A-B	C	C	B	B	B
Statistic	12.1	1.81	23.05	14.2	47.56	21.7	50.97	5.97	11.51
<i>p</i> - ANOVA or KW	<b>0.02</b>	0.8	<b>0.0008</b>	<b>0.002</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>
<i>p</i> - Shapiro-Wilks	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	0.6695	0.3285	0.709	0.3209	0.2463
<i>p</i> - Levene	-	-	-	-	0.8527	0.4944	0.0987	0.2703	0.809

D-

Males and females	SCI	LS	SS	IS	MS	DS	VS	IL3	IL4
<i>L. caparensis</i>	-	A	A	A	-	B	B	B	B
<i>L. magellanicus</i>	-	A	A	A	-	A	A	A	A
Statistic	0.6	0.05	0.2	0.87	2.03	19.3	30.72	14.2	13.92
<i>p</i> - ANOVA or KW	0.45	0.52	0.99	0.82	0.17	<b>0.0005</b>	<b>0.0001</b>	<b>0.001</b>	<b>0.0022</b>
<i>p</i> - Shapiro-Wilks	0.27	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	0.0536	0.23	0.5038	0.2754	0.5513
<i>p</i> - Levene	0.34	-	-	-	0.4175	0.41	0.4339	0.7425	0.088

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**APPENDIX 9:** Statistical tests for morphometric values. A- females of the *kingii-archeforus* group; B- males of the *kingii-archeforus* group; C- females of the *kingii-archeforus* group standardized by SVL; D- males of the *kingii-archeforus* group standardized by SVL; E- females of the *lineomaculatus* group; F- males of the *lineomaculatus* group G- females of the *lineomaculatus* group standardized by SVL; H- males of the *lineomaculatus* group standardized by SVL I- *magellanicus* group. Letters correspond to groups found by the Di Rienzo, Guzmán and Casanoves comparisons (DGC). ANOVA or Kruskal-Wallis (KW), Shapiro-Wilks and Levene *p*-values are shown. To assume normality and variance homogeneity Shapiro-Wilks and Levene test should not be rejected ( $p > 0.05$ ). In several cases (*non-par*) either normality or variance homogeneity was rejected, for those ones Kruskal-Wallis test (non-parametric ANOVA test) was performed and *p*-values are shown. Significant values are in italics and boldface. **SVL:** snout–vent length; **TL:** tail length; **DFH:** distance between fore and hind limbs; **FOL:** foot length; **TFL,** tibia-fibula length; **RUL:** radius-ulna length; **HAL:** hand length; **HH:** head height; **HW:** head width; **HL:** head length; **RND:** rostral–nasal distance; **RH:** rostral height; **DRE:** distance from rostral to the eye; **AH:** auditory meatus height.

A-

Females	SVL	TL	DFH	FOL	TFL	RUL	HAL	HH	HW	HL	RND	RH	DRE	AH
<i>L. archeforus</i>	A-B	A-B-C	-	A	A-B	A-B	A-B-C-D	A-B	A	A	A	A	A	A
<i>L. chacabucoense</i>	A	A-B	-	A	A	A	A-B	A	A	A	A	A	A-B	A
<i>L. escarchadosi</i>	A-B	B-C	-	A	B-C-D	B-C	C-D	B-C	A	B	B	A-B	B-C	A-B
<i>L. gallardoi</i>	B	B-C	-	B	A-B-C	B	A-B-C	B-C	A	A-B	A	A-B	A-B-C	A-B
<i>L. sarmientoi</i>	B	A-B	-	A	A-B-C-D	B	A-B-C-D	B-C	A	A-B	B	A-B	A-B	B
<i>L. scolaroi</i>	A	A	-	A	A	A-B	A	A-B	A	A	A	A	A-B	A-B
<i>L. tari</i>	B	C	-	B	D	C	C-D	C	B	B	C	B	C	B
<i>L. zullyae</i>	A-B	B-C	-	A	A-B	A-B	A-B	A-B-C	A	A-B	B	A-B	A-B-C	A-B
<i>L. baguali</i>	B	B-C	-	B	C-D	B-C	D	B-C	B	B	B	A-B	B-C	B
<i>L. kingii</i>	A-B	A-B	-	A	A-B	B	A-B	B-C	A	A-B	A	A	A-B	B
<i>L. somuncurae</i>	B	A-B	-	A	B-C-D	B-C	B-C-D	C	B	B	C	A-B	C	B

<i>L. tristis</i>	A-B	A-B	-	A	A-B	A-B	A-B	A-B	A	A	A	A-B	A-B	A-B
<i>L. uptoni</i>	A-B	A-B-C	-	A	A-B	B-C	A-B-C	A-B	A	A-B	C	A-B	B-C	A-B
Statistic	36.68	28.9	18.45	7.81	53.77	43.85	44.62	41.35	7.67	49.73	12.85	28.21	53.88	37.31
<i>p</i> - ANOVA or KW	<b>0.0002</b>	<b>0.004</b>	0.1026	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0051</b>	<b>0.0001</b>	<b>0.0002</b>
<i>p</i> - Shapiro-Wilks	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	0.47	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	0.96	<i>non-par</i>	0.89	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>
<i>p</i> - Levene	-	-	-	0.3	-	-	-	-	0.12	-	0.34	-	-	-

B-

Males	SVL	TL	DFH	FOL	TFL	RUL	HAL	HH	HW	HL	RND	RH	DRE	AH
<i>L. archeforus</i>	A-B	B	A-B	B	B-C	A	A-B	A-B	A-B	A-B-C	A-B	A	A-B	A
<i>L. chacabucoense</i>	A	B	A-B-C	B	A-B	A	A-B	A-B	A-B	A-B	A	A	A-B	A-B
<i>L. escarchadosi</i>	A-B-C	B	B-C-D	B	C-D-E	C	A-B	B-C-D	B-C-D-E	D-E-F	B-C-D-E-F	A	C-D	C-D-E-F
<i>L. gallardoi</i>	A-B	B	B-C	B	C-D	C	B	B-C	B-C-D	A-B-C	A-B-C	B	B	A-B-C
<i>L. sarmientoi</i>	B-C	B	B-C-D	B	C-D	C	B-C	B-C-D	B-C-D-E	C-D-E	A-B-C-D-E	A	A-B	F
<i>L. scolaroi</i>	A	A	A	A	A	A	A	A	A	A	A-B-C-D-E	A	A	A
<i>L. tari</i>	C	C	D	C	E	D	C	D	E	F	E-F	B	D	F
<i>L. zullyae</i>	A	B	A	B	A-B-C	B	A-B	B-C	A-B	A-B-C-D	D-E-F	A	B-C	A-B-C-D
<i>L. baguali</i>	C	B	B-C-D	C	D-E	C	C	B-C-D	D-E	E-F	D-E-F	A	C-D	E-F
<i>L. kingii</i>	A-B	B	B-C-D	B	B-C	C	A	B-C-D	B	C-D-E	A-B-C-D	A	A-B	F
<i>L. somuncurae</i>	C	B	C-D	B	D-E	C	C	C-D	C-D-E	E-F	F	B	D	B-C-D-E-F
<i>L. tristis</i>	A-B	B	B-C	B	B-C	C	A-B	B-C	B-C	B-C-D	A-B	A	A-B	A-B-C-D-E
<i>L. uptoni</i>	A-B-C	B	B-C-D	B	B-C-D	C	A-B	B-C-D	B-C-D	D-E-F	C-D-E-F	A	D	D-E-F
Statistic	37.23	4.45	34.43	9.24	46.07	11.22	49.24	25.56	37.09	58.93	39.55	3.32	75.32	50.62
<i>p</i> - ANOVA or KW	<b>0.0002</b>	<b>0.0001</b>	<b>0.0006</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0124</b>	<b>0.0002</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0005</b>	<b>0.0001</b>	<b>0.0001</b>
<i>p</i> - Shapiro-Wilks	<i>non-par</i>	0.21	<i>non-par</i>	0.83	<i>non-par</i>	0.87	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	0.59	<i>non-par</i>	<i>non-par</i>
<i>p</i> - Levene	-	0.08	-	0.23	-	0.16	-	-	-	-	-	0.78	-	-

C-

Females	TL/SVL	DFH/SVL	FOL/SVL	TFL/SVL	RUL/SVL	HAL/SVL	HH/SVL	HW/SVL	HL/SVL	RND/SVL	RH/SVL	DRE/SVL	AH/SVL
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1														
2														
3	<i>L. archeforus</i>	-	A	-	A	A	B	-	A	A	A	-	A	A-B
4	<i>L. chacabucoense</i>	-	B	-	A	A	A	-	A	A	A	-	A	A-B
5	<i>L. escarchadosi</i>	-	A	-	B	B	B	-	B	B	B	-	B	A-B-C
6	<i>L. gallardoi</i>	-	A	-	A	B	A	-	A	A	A	-	A	A
7	<i>L. sarmientoi</i>	-	A	-	A	B	A	-	A	A	A	-	A	B-C
8	<i>L. scolaroi</i>	-	A	-	A	B	A	-	A	A-B	A	-	A-B	A-B-C
9	<i>L. tari</i>	-	A	-	A	B	A	-	A	B	B	-	B	A-B
10	<i>L. zullyae</i>	-	B	-	A	B	A	-	A	A-B	B	-	A-B	A-B-C
11	<i>L. baguali</i>	-	A	-	B	B	B	-	B	A-B	A	-	A-B	A-B-C
12	<i>L. kingii</i>	-	B	-	A	B	A	-	A	A-B	A	-	A	C
13	<i>L. somuncurae</i>	-	A	-	A	B	A	-	A	B	B	-	B	A-B
14	<i>L. tristis</i>	-	B	-	A	B	A	-	A	A	A	-	A	A-B-C
15	<i>L. uptoni</i>	-	A	-	B	C	B	-	B	B	B	-	B	B-C
16	Statistic	9.98	5.03	1.63	2.15	5.37	3.19	20.89	2.61	45.36	5.92	14.53	51.12	29.97
17	<i>p</i> - ANOVA or KW	0.62	<b>0.0001</b>	0.11	<b>0.03</b>	<b>0.0001</b>	<b>0.0014</b>	0.052	<b>0.007</b>	<b>0.0001</b>	<b>0.0001</b>	0.27	<b>0.0001</b>	<b>0.003</b>
18	<i>p</i> - Shapiro-Wilks	<i>non-par</i>	0.37	0.88	0.36	0.46	0.21	<i>non-par</i>	0.99	<i>non-par</i>	0.48	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>
19	<i>p</i> - Levene	-	0.11	0.22	0.14	0.11	0.84	-	0.11		0.13	-	-	-

## D-

Males	TL/SVL	DFH/SVL	FOL/SVL	TFL/SVL	RUL/SVL	HAL/SVL	HH/SVL	HW/SVL	HL/SVL	RND/SVL	RH/SVL	DRE/SVL	AH/SVL	
30	<i>L. archeforus</i>	A-B-C-D	A-B	C-D	-	A-B	-	B	A-B-C	A	A-B	A	A-B-C-D	A
31	<i>L. chacabucoense</i>	A-B-C-D	B-C	A-B-C	-	A	-	B	A-B	A	A-B	A	A-B-C	A-B-C
32	<i>L. escarchadosi</i>	A-B-C-D	A-B-C	A-B-C-D	-	D	-	B	B-C-D	C-D	A-B-C	A	E-F	C-D-E
33	<i>L. gallardoi</i>	D	A-B-C	D	-	B-C-D	-	B	A-B-C	A	A-B	B	B-C-D	A-B
34	<i>L. sarmientoi</i>	A-B	A-B-C	A-B	-	A-B	-	B	A-B-C	A	A	A	A	D-E
35	<i>L. scolaroi</i>	A-B-C	A-B-C	A-B-C-D	-	A-B	-	A	A	A-B-C	B-C-D	A	B-C-D-E	A-B-C-D-E
36	<i>L. tari</i>	B-C-D	A-B-C	A-B-C	-	B-C-D	-	B	D	D	B-C-D	A	E-F	A-B-C-D
37	<i>L. zullyae</i>	C-D	A	B-C-D	-	B-C	-	B	C-D	B-C-D	D	A	D-E-F	A-B-C-D
38	<i>L. baguali</i>	A-B-C-D	A-B	A-B-C-D	-	A-B-C	-	A	A-B-C	B-C-D	A-B-C	A	C-D-E-F	B-C-D-E
39	<i>L. kingii</i>	A-B-C	C	A-B	-	B-C	-	B	A-B	B-C	A-B	A	A-B	E



Statistic	32.01	6.5	10.81	39.29	32.47	22.13	39.23	26.82	38.9	29.19	10.2	18.73	26.24	9.48
<i>p</i> - ANOVA or KW	<b>0.0001</b>	<b>0.0005</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0021</b>	<b>0.0001</b>	<b>0.0001</b>
<i>p</i> - Shapiro-Wilks	<i>non-par</i>	0.63	0.37	0.29	<i>non-par</i>	0.62	<i>non-par</i>	<i>non-par</i>	0.83	<i>non-par</i>	0.1	<i>non-par</i>	<i>non-par</i>	0.94
<i>p</i> - Levene	-	0.45	0.38	0.35	-	0.06	-	-	0.06	-	0.15	-	-	0.87

## G-

Females	TL/SVL	DFH/SVL	FOL/SVL	TFL/SVL	RUL/SVL	HAL/SVL	HH/SVL	HW/SVL	HL/SVL	RND/SVL	RH/SVL	DRE/SVL	AH/SVL
<i>L. avilae</i>	C	-	B	B	-	A	B	A	A-B	B	A	A	A
<i>L. hatcheri</i>	A	-	A	A	-	A	A	A	A	B	A	A	A
<i>L. kolengh</i>	B	-	B	B	-	B	B	B	B	B	B	B	B
<i>L. lineomaculatus</i>	C	-	B	B	-	A	C	A	B	B	A	A	A
<i>L. morandae</i>	C	-	B	A	-	A	C	A	B	B	B	A	A
<i>L. silvanae</i>	B	-	B	B	-	B	A	A	A	A	A	A	A
Statistic	17.3	1.88	3.82	5.79	2.11	16.99	7.74	4.4	18.44	6.27	4.44	9.06	3.44
<i>p</i> - ANOVA or KW	<b>0.0001</b>	0.13	<b>0.0081</b>	<b>0.0006</b>	0.09	<b>0.0001</b>	<b>0.0001</b>	<b>0.0036</b>	<b>0.002</b>	<b>0.0004</b>	<b>0.0035</b>	<b>0.0001</b>	<b>0.01</b>
<i>p</i> - Shapiro-Wilks	0.79	<i>non-par</i>	0.94	0.2	0.92	0.98	0.56	0.61	<i>non parametric</i>	0.55	0.9	0.5	0.82
<i>p</i> - Levene	0.46	-	0.54	0.63	0.59	0.21	0.26	0.06	-	0.58	0.56	0.69	0.6

## H-

Males	TL/SVL	DFH/SVL	FOL/SVL	TFL/SVL	RUL/SVL	HAL/SVL	HH/SVL	HW/SVL	HL/SVL	RND/SVL	RH/SVL	DRE/SVL	AH/SVL
<i>L. avilae</i>	B	-	B-C	B	-	A	C	A-B	C	A-B	A-B	B-C	A-B
<i>L. hatcheri</i>	A	-	A	A	-	A	B	A-B-C	B	B	A	B-C	A
<i>L. kolengh</i>	A	-	A-B	B	-	B	B	C	B	B	B	B-C	B-C
<i>L. lineomaculatus</i>	B	-	A	B	-	A	C	A	B	B	A-B	A-B	A
<i>L. morandae</i>	B	-	C	B	-	A	D	A-B-C	D	B	B	C	C
<i>L. silvanae</i>	A	-	A	B	-	B	A	B-C	A	A	A	A	A-B
Statistic	16.16	10.06	17.47	37.39	5.61	9.34	17.53	15.43	13.54	17.56	14.05	20.81	16.32
<i>p</i> - ANOVA or KW	<b>0.0001</b>	0.07	<b>0.0037</b>	<b>0.0001</b>	0.35	<b>0.0001</b>	<b>0.0001</b>	<b>0.0087</b>	<b>0.0001</b>	<b>0.0035</b>	<b>0.015</b>	<b>0.0009</b>	<b>0.006</b>
<i>p</i> - Shapiro-Wilks	0.71	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	0.63	0.46	<i>non-par</i>	0.7	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>	<i>non-par</i>



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<i>p</i> - Levene	0.38	-	-	-	-	0.35	0.23	-	0.76	-	-	-	-
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Males and Females	SVL	TL	DFH	FOL	TFL	RUL	HAL	HH	HW	HL	RND	RH	DRE	AH
<i>L. caparensis</i>	-	-	-	-	A	A	-	-	-	-	-	-	-	-
<i>L. magellanicus</i>	-	-	-	-	B	B	-	-	-	-	-	-	-	-
Statistic	1.49	13.29	0.00	0.45	15.22	7.13	0.53	0.95	0.05	0.00	0.07	3.28	1.24	0.14
<i>p</i> - ANOVA or KW	0.24	0.08	0.95	0.51	<b>0.00</b>	<b>0.02</b>	0.47	0.34	0.83	0.97	0.80	0.09	0.28	13.28
<i>p</i> - Shapiro-Wilks	0.46	0.79	0.66	0.71	0.77	0.58	0.18	0.71	0.69	0.90	0.27	0.53	0.26	0.87
<i>p</i> - Levene	0.42	0.83	0.08	0.61	0.54	0.34	0.80	0.22	0.87	0.33	0.77	0.06	0.44	0.92

## NOTA

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 ALGUNAS OBSERVACIONES  
 ETOLÓGICAS SOBRE EL PARTO  
 DE *LIOLAEMUS LINEOMACULATUS*  
 (SAURIA: LIOLAEMINI)
 

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M. L. KOZYKARISKI

C. H. F. PÉREZ

M. F. BREITMAN

L. J. ÁVILA

Grupo de Herpetología Patagónica. CENPAT-CONICET: Boulevard Almirante Brown 2825, (U9120ACF) Puerto Madryn, Chubut, Argentina

*Liolaemus lineomaculatus* forma parte de un grupo de lagartos denominados basales para el clado *Eulaemus* (Laurent, 1983; Laurent, 1985; Etheridge, 1995; Schulte *et al.*, 2000; Morando *et al.*, 2003; Morando, 2004), dentro del cual se encuentran al menos tres grupos de especies: *kingii*, *archeforus* y *lineomaculatus* (Lobo, 2001; Abdala y Lobo, 2006).

*Liolaemus lineomaculatus* es un lagarto pequeño y esbelto de unos 60 mm de longitud hocico-cloaca, de amplia distribución en la Patagonia, desde el centro-oeste de la provincia de Neuquén y oeste de Río Negro y Chubut hasta casi la totalidad de la provincia de Santa Cruz (Ceí, 1986; Williams, 1997; Ibargüengoytía *et al.*, 2001; Christie, 2002). Habita ambientes arenosos, rocosos o pedregosos de la estepa patagónica, tanto arbustivos como de pastizal. Es un lagarto omnívoro y vivíparo y puede dar a luz entre tres y seis crías (Ceí, 1986).

Observaciones etológicas relacionadas a la reproducción en *Liolaemus* han sido realizadas por Halloy y Halloy (1997) en *L. huacahuasicus*, Ibargüengoytía *et al.* (2002) en *L. kingii* y Cabrera y Monguillot (2007) en *L. eleodori*. En este trabajo se presentan observaciones del parto de una hembra de *Liolaemus lineomacu-*

*latus* mantenida en cautiverio y se las comparan con observaciones realizadas para otras especies del género.

El ejemplar estudiado fue capturado el 21 de enero de 2007, en la ruta Provincial 39, a 7,2 km E de Bajo Caracoles, Departamento Río Chico, provincia de Santa Cruz (47°26'S, 70°51' W, 880 m snm). El individuo fue trasladado y mantenido en cautiverio en el Centro Nacional Patagónico (CENPAT-CONICET) hasta el momento de la parición, ocurrida el 30 de enero de 2007. Con el fin de poder observar en detalle el parto, el individuo fue colocado en un terrario circular y fue filmado con una videocámara Sony Digital HI8 y una cámara Panasonic Lumix FZ5. Se registró el largo hocico-cloaca, con calibre tipo Vernier ( $\pm 0,02$  mm), y el peso, utilizando balanzas tipo Pesola® de 10 g y de 20 g, tanto de las crías como de la madre inmediatamente después del parto. Luego de éste, el ejemplar y las crías fueron sacrificadas con inyección pericárdica de Pentotal Sódico Abbot®, fijados en formol 20% y luego de dos días transferidos a etanol 70%.

Tanto la hembra como el lote de crías se encuentran depositados en la colección LJAMM (Luciano Javier Avila Mariana Morando), Centro Nacional Patagónico, Puerto Madryn, Argentina (CENPAT-CONICET), con los números LJAMM 7497 y LJAMM 7498 (lote), respectivamente.

Se observó la parición de tres de las cinco crías. La duración total de los tres partos observados fue de sesenta minutos aproximadamente, mientras que los intervalos entre pariciones fueron variables, entre 8 a 17 minutos.

En ninguno de los casos se observó que la hembra levantara la cola, al inicio de la fase de contracción, pudiéndose observar que siempre la mantuvo en línea recta y elevó levemente las patas traseras. En todos los casos se observó

que la fase de contracción comenzó con movimientos laterales y una vez que la cabeza del neonato comenzó a salir, la hembra ayudó a la expulsión total de la cría mediante movimientos espasmódicos de las patas traseras. Todos los individuos nacieron de cabeza y todos los individuos observados salieron por el lado derecho de la cloaca. Las cinco crías se mostraron activas luego de su respectiva parición y se observó un desplazamiento normal de la hembra por el terrario después de cada parición. Para cada uno de los individuos se obtuvieron los siguientes resultados: Cría 1: largo hocico-cloaca (LHC) (en cm): 3,0; largo total (LT) (en cm): 5,8; peso (en g): 0,7; Cría 2: LHC: 2,5.; LT: 6,1.; peso: 0,6; Cría 3: LHC: 2,5; LT: 6,0.; peso: 0,6; Cría 4: LHC: 2,6; LT: 5,7; peso: 0,5; y Hembra: LHC: 5,5.; LT: 8,5; peso (después de la parición): 4,0.

Las escasas observaciones realizadas sobre pariciones en especies vivíparas de *Liolaemus*, confirman similitudes con las realizadas en el presente trabajo. Halloy y Halloy (1997) observaron en *Liolaemus huacahuasicus*, que los tamaños de las camadas fueron de cuatro a seis crías, que todos los individuos nacieron de cabeza y no hubo ayuda por parte de la madre. Por otra parte, Ibargüengoytía *et al.* (2002) trabajando con *Liolaemus kingii*, especie cercanamente relacionada a *L. lineomaculatus*, informaron que el tamaño de camada fue entre dos y cinco crías y la fecha de parto a finales de enero, mientras que Cabrera y Monguillot (2007) observaron en tres hembras de *L. eleodori* que los tamaños de las camadas fueron de dos a cuatro crías, que los individuos nacieron de cabeza y que los nacimientos ocurrieron en diciembre y enero.

Nuestros resultados indican que el período de parición de *Liolaemus lineomaculatus* es a fines de enero. La fecha de parición y el tamaño de la camada son similares a otras especies pertenecientes al género (Ibargüengoytía *et al.*, 2002). Resultados similares fueron

observados en las especies *L. hatcheri*, *L. silvanae* y *L. kingii* en condiciones de cautiverio. Tres hembras de *L. hatcheri*, tuvieron partos entre los días 30 y 31 de enero, con un tamaño de camada de tres a cinco crías las cuales conservaron el vitelo después del parto, mientras que para dos hembras de *L. silvanae*, el tamaño de camada fue de tres a cuatro crías. También se observaron que los nacimientos en *L. kingii* se produjeron a principios de febrero y el tamaño de la camada fue de cinco crías, lo que concuerda con Ibargüengoytía *et al.* (2002), quienes también observaron que la madre realizó movimientos de lengüeteo hacia las crías. En el presente trabajo no se pudo determinar este comportamiento.

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