



## The limits of polymorphism in *Liolaemus rothi*: Molecular and phenotypic evidence for a new species of the *Liolaemus boulengeri* clade (Iguanidae, Liolaemini) from boreal Patagonia of Chile

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### Abstract

Studies conducted over the last few years in Andean boreal Patagonia along the border of Argentina and Chile (36°50'S–37°53'S) have shown that its reptile diversity is comprised of several endemic lizards. Increasing research has led to recognize a number of cryptic iguanian species from previously named taxa. In this area is common the only known Chilean population of the Patagonian *Liolaemus rothi*, considered as a polymorphic species with wide geographical distribution. In this paper, we provide evidence to support the hypothesis that such population represents a new taxon, herein described as *Liolaemus hermannunezi*. This new species occurs in the southeastern areas of Laguna del Laja, in the Los Barros and Río de Los Pinos basins of Antuco Volcano (1428–1521 m) in the Bio Bio Region. *Liolaemus hermannunezi* is closely related to *L. rothi*, from which is significantly differentiated by molecular variables. In addition, this new species appears to be related to *L. lobo*i and *L. sagei*, from which differs in having a smaller body size, a distinctive colour pattern and an isolated geographical distribution. *Liolaemus hermannunezi* is known from the boreal Patagonia of Chile, whereas *L. lobo*i, *L. rothi*, and *L. sagei* are endemic to Argentinean Patagonia. The new species is a member of the *boulengeri* clade, diagnosed by the presence of a patch of abruptly enlarged scales on the posterior medial surface of the thigh, a character that is more conspicuous in adult males. Finally, a phylogenetic hypothesis for 67 Liolaemini taxa based on DNA sequences is presented.

**Key words:** *Liolaemus* phylogeny, *Liolaemus hermannunezi*, *Liolaemus rothi*, *boulengeri* clade, *Liolaemus*, Patagonia, Chile

### Resumen

Diversos estudios desarrollados durante los últimos años en la Patagonia boreal Andina localizada en la frontera común a Argentina y Chile (36°50'S–37°53'S) han demostrado que su diversidad de reptiles está formada por varias lagartijas endémicas. La evidencia acumulada ha llevado a reconocer numerosas especies crípticas de iguanianos a partir de taxa descritos previamente. En esta área es común la única población chilena de la forma patagónica *Liolaemus rothi*, considerada una especie polimórfica con amplia distribución geográfica. En el presente estudio, presentamos evidencia a favor de la hipótesis de que esta población representa un nuevo taxón, descrito acá como *Liolaemus hermannunezi*. Esta nueva especie está distribuida al sureste de la Laguna del Laja, en las áreas de Los Barros y del Río Los Pinos, Volcán Antuco (1428–1521 m), en la región del Bío Bío. *Liolaemus hermannunezi* está filogenéticamente relacionado con *L. rothi*, del cual difiere significativamente en variables moleculares. Adicionalmente, esta nueva especie parece estar relacionada con *L. lobo*i y *L. sagei*, de las cuales difiere debido a un tamaño corporal más pequeño, un patrón de coloración diferente y una distribución geográfica aislada. *Liolaemus hermannunezi* es conocido únicamente de la Patagonia boreal de Chile,

mientras que *L. lobo*, *L. rothi* y *L. sagei* son endémicos de la Patagonia Argentina. La nueva especie pertenece al clado *boulengeri*, identificado por la presencia de un parche de escamas abruptamente agrandadas en la superficie posterior medial del muslo, un carácter más desarrollado en los machos adultos. Finalmente, presentamos una hipótesis filogenética para 67 taxa del clado Liolaemini basada en secuencias de ADN.

**Palabras clave:** Filogenia de *Liolaemus*, *Liolaemus hermannunezi*, *Liolaemus rothi*, clado *boulengeri*, *Liolaemus*, Patagonia, Chile

## Introduction

The South American iguanian genus *Liolaemus* is one of the largest living vertebrate lineages, with more than 180 currently described species (Donoso-Barros 1970; Etheridge & Espinoza 2000; Abdala & Lobo 2006). The extraordinary rates of speciation observed in this group are coupled with notable diversity in phenotypic specializations, ecology, behaviour and geographical distribution (Espinoza *et al.* 2004; Schulte *et al.* 2004; Núñez & Pincheira-Donoso 2006). *Liolaemus* occur in almost all available habitats in central-southern and southern South America. Species inhabit from the Atacama Desert, the driest place on Earth, to Tierra del Fuego, the southernmost place where reptiles have been found (Donoso-Barros 1966; Jaksic & Schwenk 1983; Cei 1986), and from sea level to more than 5000 m in the Andes (Cei 1993; Schulte *et al.* 2004; Pincheira-Donoso & Núñez 2005), an elevational record comparable only to the Asiatic agamid lizards of the genus *Phrynocephalus* (Zhao 1999; Pang *et al.* 2003).

Studies conducted over the last two decades throughout the wide range of the *Liolaemus* genus indicate that many systematic of this lineage remain still unknown, and that several species may be still discovered. Indeed, almost every exploration developed in commonly ignored areas leads to the recognition of new readily diagnosable species (*e.g.* Espinoza *et al.* 2000; Cei & Videla 2003; Pincheira-Donoso & Ramírez 2005). Many of these new discoveries have been essential to increase the knowledge of the biogeography, evolution, and phylogeny of the genus (Pincheira-Donoso & Núñez 2005). For example, studies conducted by Cei and Sclaro (1996) and Sclaro and Cei (1997, 2006) on Patagonian *Liolaemus* communities have revealed that austral groups belonging to the *Donosolaemus* subgenus (see Pincheira-Donoso & Núñez 2005) are much more diverse than previously thought. These new findings have led to an understanding that in austral ecosystems, small geographic areas may consist by several species with limited distributions. Also, the accumulation of ecological and distributional data has fostered the development of surprising evolutionary inferences. A recent study conducted by Espinoza *et al.* (2004) for instance, showed that *Liolaemus* lizards do not follow the so called “rules” of herbivory (see Pough *et al.* 2004; Vitt 2004, for details), because of the existence of herbivory in small cold-climate taxa.

Particularly the study of *Liolaemus* species occurring in Andean and Patagonian habitats has been limited by the rugged topography of these regions (Donoso-Barros 1966). In fact, during the last few years a number of new taxa have been reported from high latitudes and elevations, and many others are under study (*e.g.* Lobo & Espinoza 1999, 2004; Cruz *et al.* 2005; Abdala & Lobo 2006). Some of these recently recognized species are the result of new discoveries, whereas many others are the result of more detailed research conducted on populations previously considered polymorphic and widely distributed taxa (Etheridge 1993; Lobo & Espinoza 1999; Etheridge & Christie 2003; Pincheira-Donoso & Núñez 2003, 2005). For example, several new cryptic species have been described that were previously recognized as *L. alticolor* or *L. walkeri* (Lobo & Espinoza 1999; Martínez-Oliver & Lobo 2002; Lobo & Espinoza 2004; Pincheira-Donoso 2005; Pincheira-Donoso & Núñez 2005), *L. darwini* (Cei 1993; Cei & Sclaro 1999; Etheridge 1992, 1993, 2001), or *L. elongatus* and *L. petrophilus* (Espinoza *et al.* 2000; Espinoza & Lobo 2003; Avila *et al.* 2004). This increasing accumulation of information suggests that Andean and Patagonian regions are likely to produce more undiscovered species, which could broaden the understanding of the evolution of *Liolaemus* lizards.

Along the western edge of the Patagonia, a region with high lizard endemism, which straddle the Argentinean and Chilean border between 36°50'S–37°53'S, and 70°35'–71°30'W has been recognized (Pincheira-Donoso 2004). In this area several new cryptic lizard species have been described on the basis of populations identified as previously named taxa. For instance, the populations identified as *Diplolaemus leopardinus* and *Phymaturus flagellifer* by Donoso-Barros (1974) at Laguna del Laja (Chile), were recently described as the new species *Diplolaemus sexcinctus* (Cei *et al.* 2003) and *Phymaturus vociferator* (Pincheira-Donoso 2004), respectively. In the same zone, it is also common the only known Chilean population of *Liolaemus rothi* (Donoso-Barros 1974; Núñez & Jaksic 1992; Pincheira-Donoso 2003a; Schulte *et al.* 2004; Pincheira-Donoso & Núñez 2005). This species has been recognized as a polymorphic taxon with wide Patagonian distribution (Cei 1986; Pincheira-Donoso & Núñez 2005). However, recent studies conducted on different populations assigned to this taxon have revealed that its boundaries of polymorphism have been overestimated. For example, Etheridge and Christie (2003) concluded that the population from Neuquén Province in Argentina largely identified as *L. rothi* comprises two different species. One of these populations was supported as *L. rothi*, while the other was described as *L. sagei*. Interestingly, detailed analyses conducted on the above mentioned Chilean *L. rothi* population also indicate that it may be a different species (Pincheira-Donoso & Núñez 2005).

In the present paper, this population from Laguna del Laja, Antuco Volcano in Chile (37°31'S; 71°15'W) is studied. We test the hypothesis that this Chilean *Liolaemus* is the result of a diversification event, which has led to the origin of a different species apparently restricted to boreal Patagonia of that country. To address this problem we performed comparative analyses mainly on molecular and phenotypic variables.

## Material and methods

### Field work

Three expeditions were conducted in the Patagonian zone of Los Barros (37°31'S; 71°15'W) located in the south-eastern area of Laguna del Laja, Antuco, Bio Bio Region of Chile over the late summer 2000–2001 and late spring-summer 2001–2002. During the first field trip, specimens of the new *Liolaemus* species were collected and deposited in the MNHNC (see appendix). In the second field trip we collected additional samples used in the description of the new species, and in the third, environmental and ecological data were collected. Specimens were caught by hand or noose. Other lizard species were recorded in the area.

### Specimens examined and data analysis

All type specimens were initially preserved in 10% formalin and later transferred to 70% ethanol. Species within the *boulengeri* clade (see examined material), preserved in 70% ethanol, were studied for comparisons. The studied material is housed in the herpetological collections detailed in the appendix.

Measurements were taken with digital calipers to the nearest 0.01 mm. Snout-vent length (SVL) was measured from the tip of the snout to the anterior margin of the cloaca. Head length from the tip of the snout to the inferior apex of the external auditory meatus, and head width across the widest region of the head in the postocular zone (see Etheridge and Christie 2003; Núñez *et al.* 2003, 2004). Scales around midbody were counted half-way between the axilla and groin regions. Subdigital lamellae were counted from the most proximal scale wider than long, to the most distal scale bordering the claw (see Etheridge & Christie 2003). Scale counts were conducted with the aid of a binocular microscope at different magnifications.

A one-way random effects-model analysis of variance (ANOVA) was used to compare body sizes among *L. loboii*, *L. rothi*, *L. sagei*, and the population from Chile. The first three species were selected for statistical analyses due to their clear phenotypic similitude and geographical proximity in relation to the Chilean population. Tukey-Kramer post-hoc test for multiple comparisons was used to determine significant similitude and differences between the studied species. Prior to analyses, data were tested for normality using a Shapiro-Wilk test ( $W > 0.05$ ).

A single individual of the new species from Chile was included in a dataset comprised of sequences from Schulte *et al.* (2000) and Cruz *et al.* (2005). GenBank accession numbers are listed in the Reference material section (see appendix). Genomic DNA extraction and sequencing protocols, including primers used and alignment procedures were identical to those used in Schulte *et al.* (2000). The DNA sequence representing the specimen from Chile was aligned with 68 *Liolaemini* sequences previously published in Schulte *et al.* (2000, 2003) and Cruz *et al.* (2005) for a total of 1775 aligned positions. Nucleotide site homology was inferred to be ambiguous at 65 positions resulting in a final alignment of 1710 base pairs. The alignment is available from TreeBase (*matrix accession number and study number to be included upon acceptance of manuscript*). Of the 1710 unambiguously aligned DNA sequence positions, 921 were variable and 769 were parsimony informative.

DNA data were examined phylogenetically using PAUP\* v. 4.0b10 (Swofford 2002) and implementation of a heuristic search with TBR branch swapping and 1000 random taxon additions using maximum parsimony (MP). Bootstrap resampling (Felsenstein 1985) assessed the support for individual nodes using 1000 bootstrap replicates with TBR and 100 random taxon additions per replicate. Decay indices (= Bremer's "branch support") were calculated for all internal branches using TreeRot v. 2c (Sorenson 1999) and heuristic searches as conducted above for each node present in the overall MP tree(s). Maximum likelihood (ML) analyses were conducted following Sullivan *et al.* (2005). ML bootstrap analysis was not conducted because the size of the matrix made this analysis computationally intractable.

## Results

### Phenotypic comparisons

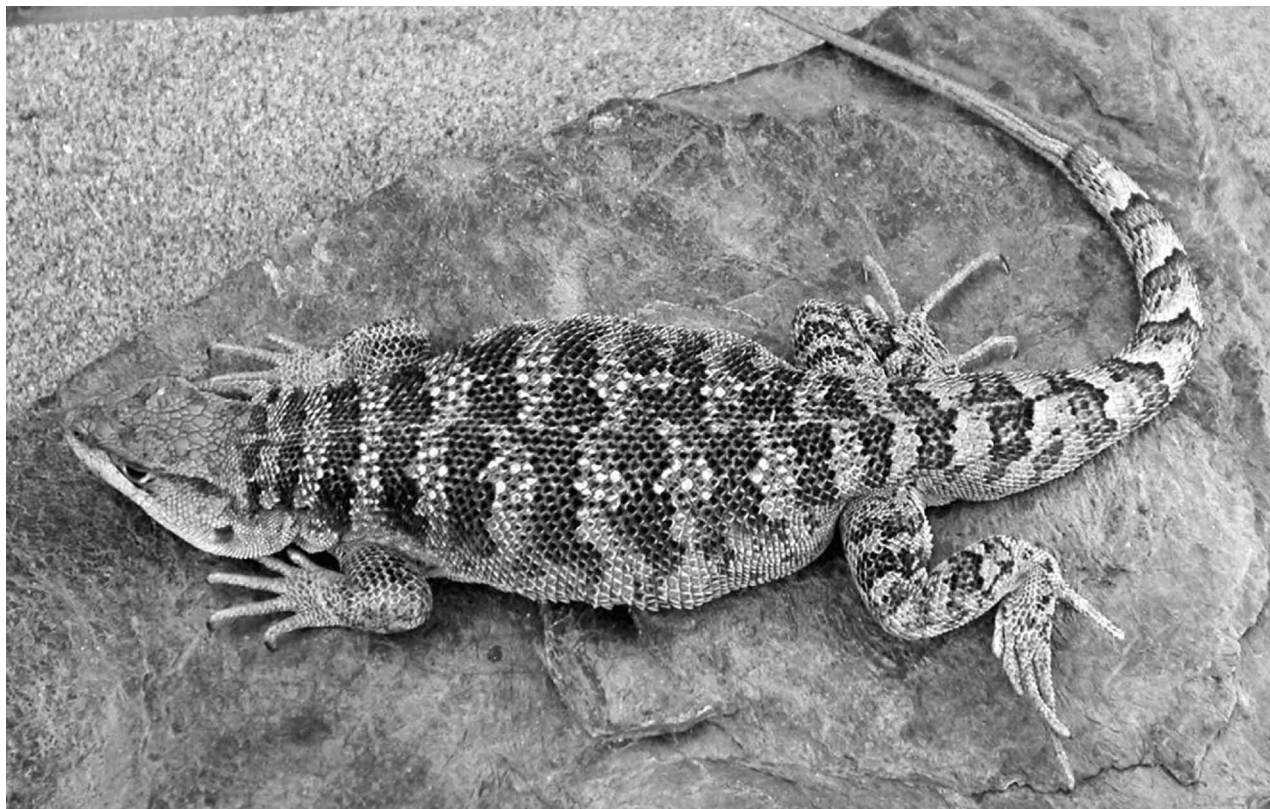
There were significant differences in body size among *L. lobo*, *L. rothi*, *L. sagei* and the Chilean population (ANOVA  $F_{3,34} = 96.49$ ,  $P < 0.0001$ ). The Chilean population was the smallest species, with a maximum SVL of 64.1 mm, compared to 72.7 mm for *L. lobo* (Abdala 2003), 102 mm for *L. rothi*, and 88 mm for *L. sagei* (Etheridge & Christie 2003). Post-hoc analyses revealed that body size of the Chilean population was significantly smaller than all other species ( $P < 0.001$ ), and only *L. rothi* and *L. sagei* were statistically indistinguishable in size ( $P = 0.124$ ).

Comparisons performed specifically between *L. rothi* and the Chilean population also revealed clear phenotypic divergence. *Liolaemus rothi* (Fig. 1) is characterized by a large stout body (SVL =  $91.1 \pm 10.6$  mm; range = 77.3–102.3 mm), with a dorsal pattern of transverse series of black spots on a gray or green background, with a pale gray or white ventral colour irregularly spotted with small and almost indistinct dark marks arranged in the middle of each abdominal scale. In contrast, the Chilean population (Fig. 2) is smaller (SVL =  $53.1 \text{ mm} \pm 5.5$ ; range = 49.1–64.1 mm), and although dorsally similar to *L. rothi*, is melanic ventrally, slightly darker in males. Comparisons on additional traits are detailed in Table 1.

### Evidence of divergence in molecular sequences (DNA)

Maximum parsimony analysis produced five equally parsimonious trees each with a length of 5810 steps (Fig. 3). The overall topology is very similar to Schulte *et al.* (2000) with several minor differences. The sample previously referred to as *L. melanops* in Schulte *et al.* (2000) was misidentified and is now considered more closely related to *L. rothi*. *Liolaemus melanops* from Cruz *et al.* (2005) is correctly identified, although may be a new species closely related to *L. melanops*. We consider the position of *L. melanops* as the sister taxon to the *L. fitzingerii* group as the best hypothesis of phylogenetic relationships between these taxa. Also, the sample representing *L. cyanogaster* in Schulte *et al.* (2000) was misidentified and is more closely related to some populations of *L. pictus* from Chile (JAS II, unpublished data). Other differences are restricted to weakly supported areas of the tree with low bootstrap values and decay indices. Successive approximations

ML analysis of these data (878 unique site patterns) revealed a single highest maximum likelihood tree (-lnL = 26844.57). Model parameters identified using successive approximations were as follows: alpha = 0.669; proportion of invariant sites = 0.389; substitution rates R(a) = 0.400, R(b) = 9.000, R(c) = 0.422, R(d) = 0.316, R(e) = 5.246, and R(f) = 1.000; and estimated base frequencies A = 0.422, C = 0.297, G = 0.051, and T = 0.230.



**FIGURE 1.** Adult male of *L. rothi*. Photo J.A. Scolaro.

**TABLE 1.** Maximum snout-vent length (SVL, mm), and ranges of meristic variables in four *Liolaemus* species of the boreal Patagonia of Chile and Argentina. Black pigment of ventral surfaces (1 = throat, 2 = chest, 3 = belly). Precloacal glands (PG).

Species	Maximum SVL		Midbody Scales	Black Pigment	PG	4th Toe Lamellae
	Males	Females				
<i>L. hermannunezi</i>	64.1	57.0	66-77	1, 2, 3	7-9	24-27
<i>L. loboï</i> <sup>a</sup>	72.7	66.4	59-70	–	8-11	24-27
<i>L. rothi</i>	93.0	102.3	53-71	–	7-12	22-28
<i>L. sagei</i> <sup>b</sup>	88.0	85.0	81-100	–	7-10	24-32

<sup>a</sup>Some of the data ranges taken from Abdala (2003)

<sup>b</sup>Some of the data ranges taken from Etheridge and Christie (2003)

The phylogenetic position of the Chilean population is weakly supported in the MP consensus tree as sister to a clade containing *L. rothi* and *L. cf. rothi*. In the ML analysis, this sequence is the sister taxon to all species of the *darwinii* group and their close relatives, although this branch is likely to be weakly supported due to its very short branch length (not shown). The average uncorrected p-distance between the new species and the two most closely related sequences currently recognized as *L. rothi* was 9.7% (ML-corrected distance =

14.0%). This divergence is as high as or higher than distances between currently recognized species of *Liolaemus* (Schulte *et al.* 2000), providing strong genetic evidence for recognition of this population as a new species.

***Liolaemus hermannunezi* sp. nov.**

Figures 2 and 4

*Liolaemus rothi* Donoso-Barros (1974:287); Núñez and Jaksic (1992:76); Pincheira-Donoso (2003a:18); Schulte *et al.* (2004:410).

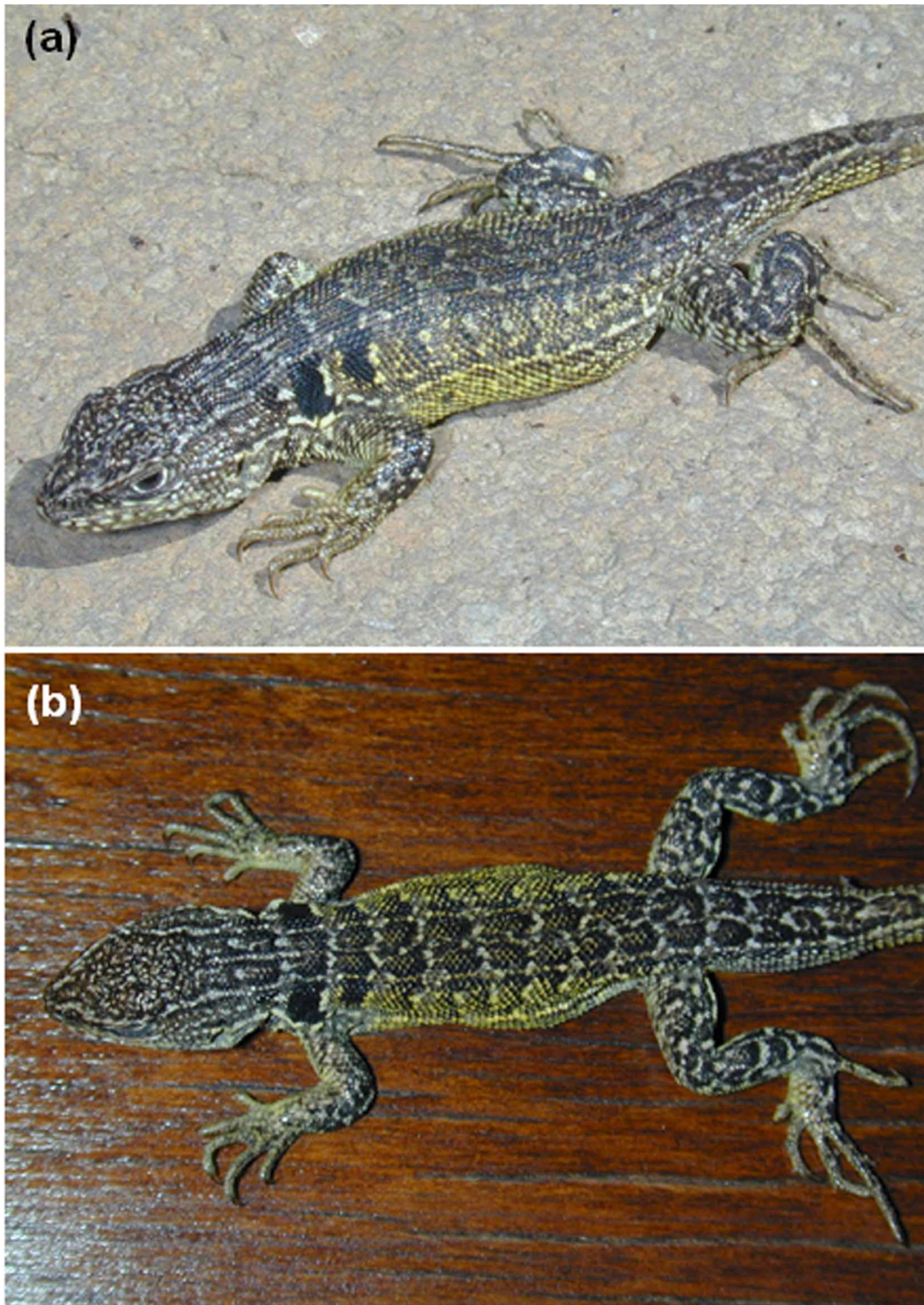
*Liolaemus (Eulaemus) rothi* Pincheira-Donoso and Núñez (2005:99).

**Type material.** *Holotype*. MNHNC-3785, male, collected 10 km E from Los Barros (37°31'S; 71°15'W) on the road to Pichachén Pass, Eighth Administrative Region, Chile, 18 November 2001 by D. Pincheira-Donoso.

*Paratypes*. MNHNC-3501, male, same locality as holotype, collected 10 February 2001 by J. A. Schulte II and J. P. Valladares; MNHNC-3502, 3503, both females, same data as male paratype; JAS-DC-718, female, same data as holotype; CHDPD-995, female, same data as holotype.

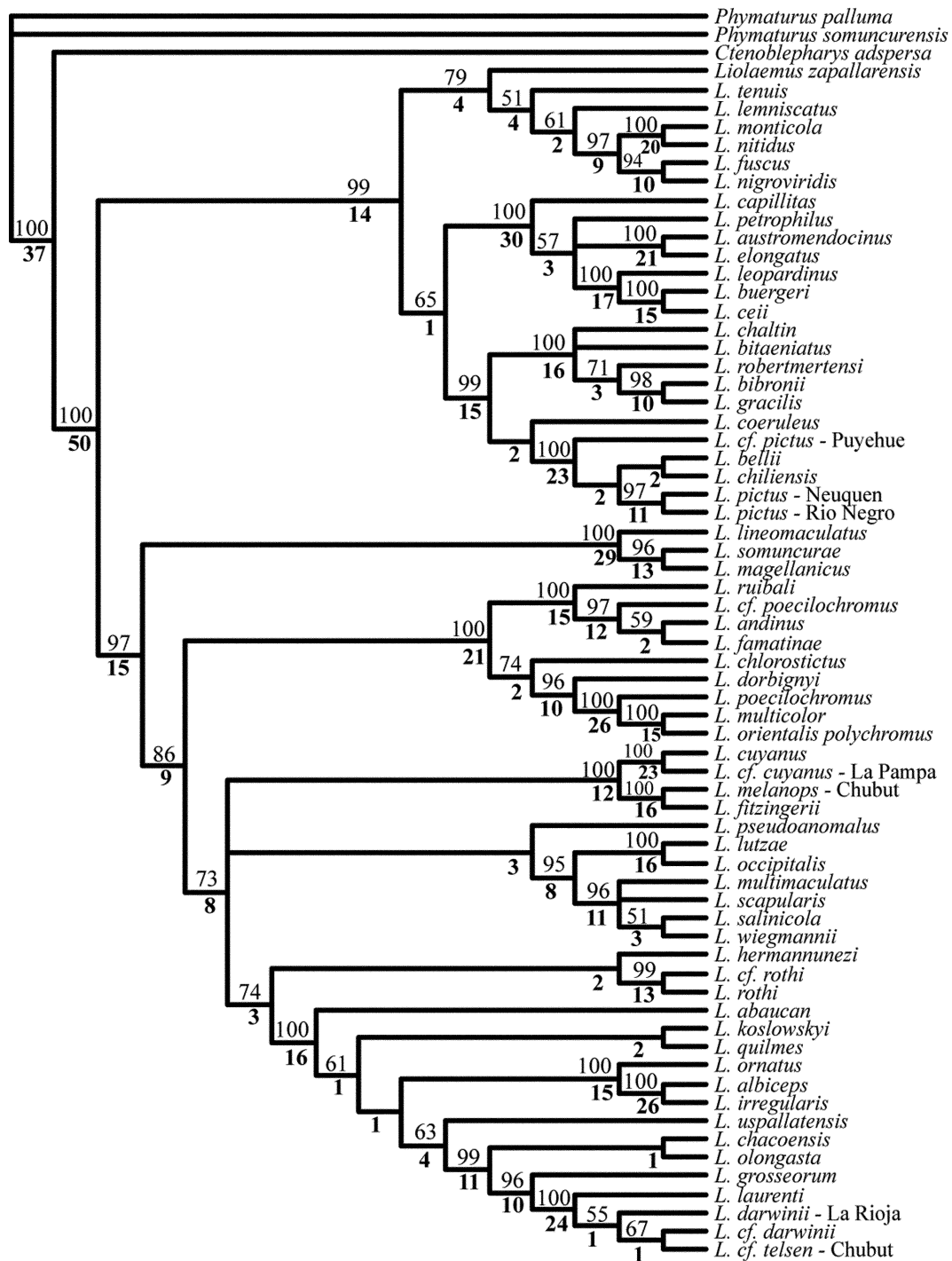
**Etymology.** This species is dedicated to Herman Núñez, from the National Museum of Natural History of Chile, in recognition of his great contribution to the systematics and ecology of Chilean lizards of the genus *Liolaemus*. DP-D particularly thanks his teachings, his intimate friendship and his persistent help and encouragement.

**Diagnosis.** A small bodied *Liolaemus* species belonging to the *boulengeri* clade diagnosed by Etheridge (1995), as having a femoral patch of abruptly enlarged scales on the posterior surface of the thigh, and by the hypertrophied puboischiotibialis muscle (recently recognized as flexor tibialis internus; Abdala *et al.* 2006), a trait well-developed in adult males. Into the *boulengeri* clade, Etheridge (1995, 2000) also recognized the *wiegmannii* species group, which is characterized by lorilabials distinctly smaller than supralabials, usually in two rows between the subocular and supralabials, with the posteriormost not elongate, with sublabials contacting the mental shield, which is widest posteriorly, and infralabials flat to concave. However, traits of the *wiegmannii* group are not observed in *L. hermannunezi*, and morphology and coloration differentiate *L. hermannunezi* from most of the remaining species belonging to the *L. boulengeri* clade, except *L. loboii*, *L. rothi*, *L. sagei* and *L. tehuelche*. *Liolaemus hermannunezi* differs from *L. tehuelche* in having a black belly, a smaller body size (49.1–64.1 mm; mean = 53.1 mm), and a distribution restricted to the Laguna del Laja in Chile (37°31'S; 71°15'W), whereas *L. tehuelche* is only black on the throat, has a larger body size (55.5–74.2 mm; mean = 66.4 mm), and a more austral distribution in Argentina (40°44'S; 70°34'W). *Liolaemus hermannunezi* differs from *L. sagei* in having a smaller body size (see above), larger and fewer body scales (Table 1), and has ventral melanism, mainly in abdominal and gular areas, whereas *L. sagei* is uniformly grey or blue ventrally. From *L. rothi*, *L. hermannunezi* differs in having a smaller body size (SVL over 100 mm in *L. rothi*; see above), smaller and therefore more body scales (Table 1), and a black belly in males, restricted to the gular region in females. This last trait is absent in *L. rothi* (Table 1). Finally, *L. hermannunezi* differs from *L. loboii* in having a smaller body size (see results for statistical comparisons), a higher number of scales around the middle of body (range in *L. hermannunezi* = 66–77, mean = 71.8; versus range in *L. loboii* = 59–70, mean = 63.7), is black ventrally, and has a more boreal distribution in Chile, whereas in *L. loboii* ventral melanism is conspicuous, and occurs in more austral areas in Argentina (see Results for details, also Fig. 5, Table 1).



**FIGURE 2.** (a) Adult male of *L. hermannunezi* in life. Specimen collected approximately 8 km E of Los Barros, Laguna del Laja, Chile; (b) adult female from the same locality. Photos J. A. Schulte.

**Description of the Holotype** – A small lizard with a relatively stout body. Snout-vent length 53.3 mm, axilla-groin distance 24.0 mm. Head slightly longer (12.6 mm) than wide (10.7 mm). Head height 7.8 mm. Snout moderately large. Neck as wide as head, with a shallow lateral fold, extending from posterior edge of external auditory meatus to insertion of the forelimb, forming an antehumeral fold and deep antehumeral pocket. Dorso-cervical and hemigular folds absent. Forelimb length 22.2 mm. Hind limb length 34.9 mm. Toe tips of adpressed hind limb reach posterior edge of external auditory meatus. Tail 88.7 mm long, cylindrical, longer than snout-vent length.



**FIGURE 3.** Phylogenetic relationships among 67 Liolaemini taxa based on maximum parsimony analysis of 1710 aligned positions of DNA sequence data (length = 5810 steps). Strict consensus of five equally most parsimonious trees. Bootstrap values are presented above branches and decay indices are shown in bold below branches on the cladogram.

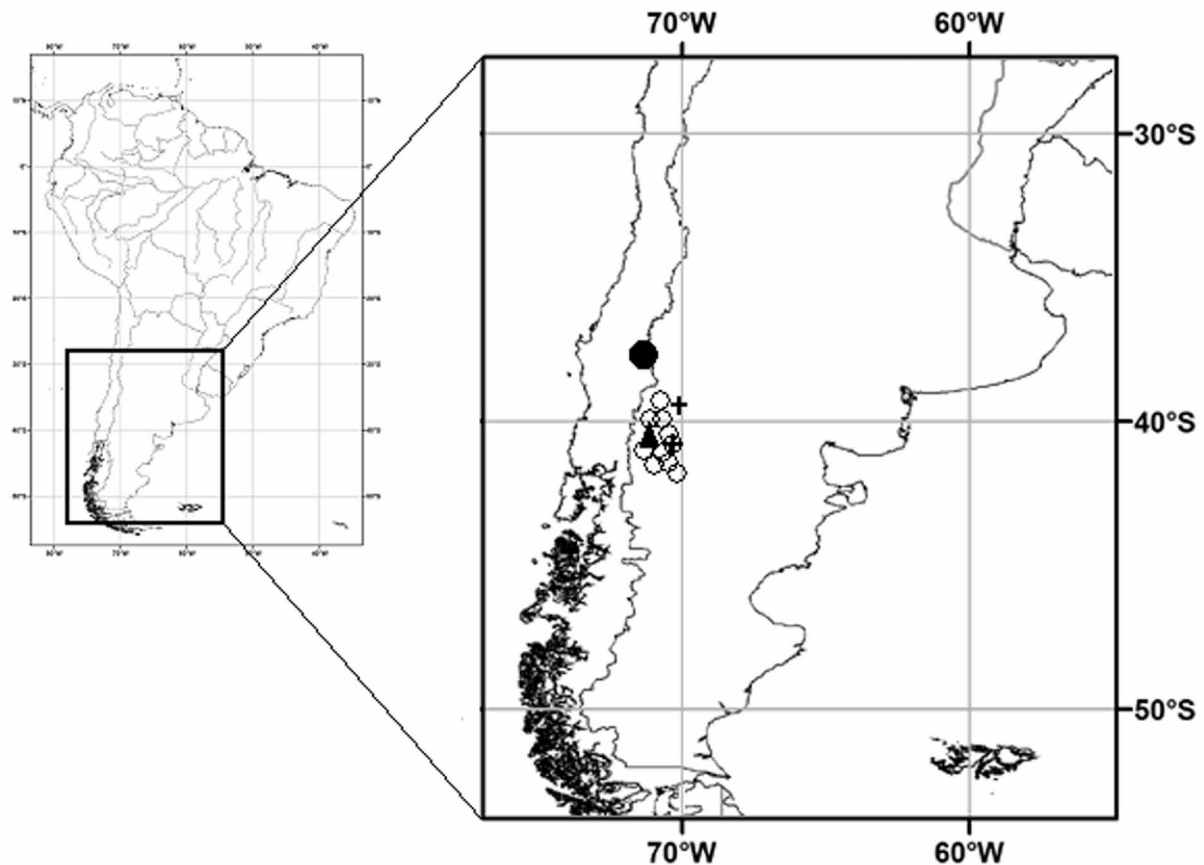
Dorsal head scales slightly convex and smooth. Rostral pentagonal, expanded laterally, contacting six smaller scales. Two tiny pentagonal postrostrals. Nasal contacting seven smaller scales, surface twice as large as interparietal shield. A single row of four azygous scales surrounded by 10 frontonasals. Two prefrontals. Frontal divided transversely and longitudinally into seven small scales of similar size, 3–4 times smaller than prefrontals. Three postfrontals arranged in a transverse row, directly in contact with interparietal, hexagonal, and slightly larger than postfrontals. Parietals irregular, twice as large as interparietal, and with a smaller scale inserted between them. Occipital scales homogeneous, small, irregular, juxtaposed. Supraorbital semicircles



convex. Circum orbitalis consisting of 13–13 small scales. Supraoculars 6–6, hexagonal, and wider than long, larger than other dorsal head scales. Superciliaries imbricate. Two rows of scales between supraoculars and superciliaries. Upper-ciliary scales 15–14, and 12–10 lower-ciliaries. Suboculars and postoculars enlarged, first one contacting an irregular polygonal preocular. Loreal region slightly concave, covered by three small scales, medial larger than other two. Supralabials 7–7, posteriors three times longer than anteriors. A single and irregular row of loreolabial scales between subocular and supralabials. Temporal subcircular, smooth, and subimbricate. Frontonasal, loreals, canthal, supralabials, loreolabials, temporals, and supraorbitals with tiny scale organs.



**FIGURE 4.** Holotype of *Liolaemus hermannunezi*, male, MNHNC 3785, from 10 km E of Los Barros, near Pichachén Pass, Eighth Region, Chile. Photo D. Pincheira-Donoso.



**FIGURE 5.** Map of the North-Western Patagonia of Argentina and Chile, showing the distribution of *Liolaemus hermannunezi* (black circle), *L. rothi* (empty circles), *L. sagei* (cross), and *L. lobo* (black triangle). Details on the wide Patagonian geographical distribution of *L. rothi* can be found in Cei (1986)

Mental subtriangular, slightly wider than rostral, bordered by two lower labials and two postmentals. Two divergent rows of 7–8 postmental scales, posteriors smaller than anteriors. Infralabials 6–7, larger than supralabials, smaller than those in posterior region. Single row of sublabials between postmentals and infralabials, that turn into two rows under second infralabial and in three rows under fifth infralabial. Gulars subcircular, smooth, and imbricate. External auditory meatus higher than wide, smaller than orbit, surrounded by several tiny granular scales, with two large scales along anterior margin, and conspicuous auricular scale in dorsal margin.

Dorsal body scales subtriangular and subimbricate, strongly keeled, never mucronate, lacking interstitial granules. Scales of body flanks similar to dorsals, but become smooth, with tiny interstitial granules. Ventral body scales 1.5 times larger than dorsals, rhomboidal, smooth, and imbricate, subtriangular and smaller in precloacal region. Scales around midbody 66. Lateral neck folds covered by several tiny granular scales. Similar scales on shoulders, axilla, and cloacal regions.

Forelimb scales subtriangular, imbricate, and slightly keeled, becoming smooth on dorsal surface of front feet. Lower humeral region covered by granular, juxtaposed tiny scales, becoming larger and subimbricate on forearm. Hind limbs with rhomboidal, slightly keeled, and subimbricate-imbricate scales, with a few tiny interstitial granules. Ventral scales of hind limbs rhomboidal, smooth, and imbricate. Coxal scales never projected. Posterior surface of thighs with a patch of abruptly enlarged scales. Twenty six strongly keeled subdigital lamellae on the fourth toe of right foot. Dorsal and lateral caudal scales rhomboidal, strongly keeled, becoming distinctly rectangular on distal tail. Ventral scales of the tail subtriangular, smooth, and imbricate, longer and keeled distally. Nine precloacal glands.

**Coloration (on the basis of the entire type series)** – The ground colour in living specimens is grayish or brownish olive on the dorsal head and body surfaces, becoming gray or blue in preserved animals. Head with irregular and small brown, black, and white spots. Suboculars and supralabial scales white, with indistinct gray spots. Two fine (1–2 scales wide) white dorsolateral stripes run from superior margin of nasals, to tail base. Nine subcircular paravertebral black spots, similar or larger in size than orbit (each 19–25 dorsal scales), bordered by gray and white tiny marks, and arranged alternately or in pairs, in two parallel and longitudinal rows, most conspicuous at tail base. Prescapular and postcapular spots black and conspicuous. Fine (1–2 scales wide) white stripe on dorsal neck, normally fragmented on the back. Flanks with white ventrolateral stripe and black spots, slightly smaller than paravertebral ones, and bordered by tiny white and blue irregular spots in upper region. Flanks with distinct yellow scales in life. The same pattern is represented on the dorsal tail surface, being clearly more irregular. Distinct black, grey, and white spots are irregularly distributed on the dorsal surface of limbs.

Pale gray-whitish ground colour ventrally, but black on mid-belly and gular surface. Lower ventrolateral field irregularly scattered with small brown marks. Ground colour of ventral limbs similar to ventral body. Ventral tail unspotted, with small and indistinct gray marks in postcloacal region. Precloacal region pale. Precloacal glands orange. In preserved specimens ventral colour fades pale blue.

**Variation.** No obvious differences were detected between sexes, except in precloacal glands, developed in males and totally absent in females. Also, ventral and gular melanism is slightly more conspicuous in males.

Frontonasal azygous 2–4, frequently with small supernumerary scales. Frontal region transversely and longitudinally divided, resulting 6–8 similarly sized small frontals. Single transverse row of 3–5 postfrontals behind frontal. Parietal scales irregular, smaller, equal, or larger than interparietal shield, frequently separated by tiny supernumerary scales. Supraorbital semicircles surrounded by 13–16 small scales. Supraoculars 4–7 on each supraorbital semicircle. Upper ciliaries 13–15, and 10–13 lower ciliaries. Loreals 3–6, polygonal, variable in size. Anterior supralabials similar or larger than the posterior ones, 7–9 on each side; 2–3 enlarged scales on anterior margin of external auditory meatus. Single auricular shield differentiated. Two divergent rows of 5–8 postmental scales contacting mental. Infralabials 6–7, similar or slightly larger than supralabials.

Dorsal body scales rhomboidal or subtriangular, keeled, subimbricate or juxtaposed, often with interstitial granules. Scales around midbody 66–77. Ventral body scales with negligible variation. Dorsal scales of forelimbs rhomboidal or sublanceolate. On hind limbs, dorsal scales rhomboidal, slightly keeled, imbricate or subimbricate, with interstitial granules. Fourth toes with 24–27 subdigital lamellae. Dorsal tail scales subcircular or subtriangular, keeled and imbricate, becoming more polygonal medially. Ventral scales of tail subcircular or subtriangular, smooth and imbricate, becoming more triangular and keeled medially. Precloacal glands 7–9, restricted to males.

**Geographic distribution.** *Liolaemus hermannunezi* is only known from the type locality (Fig. 5).

**Natural history.** We know little about the biology of *L. hermannunezi*. It is diurnal and inhabits mountainous areas of the Patagonian steppe with short ( $\leq 0.5$  m), bushy vegetation growing on sandy-gravel substrata. This vegetation is used almost exclusively for refuge and on several occasions individuals entering vegetation were found buried in loose sand at the base of the shrub. Nothing is known about its diet or reproductive mode. Individuals were never found under or basking on rocks. The vegetation in the type area is characterized by *Acaena pinnatifida*, *Agrostis serranoi*, *Arenaria serpens*, *Berberis empetrifolia*, *Chaetanthera lycopodioides*, *Cyperus reflexus*, *Epilobium nivale*, *Erigeron andicola*, *Gaultheria pumila*, *Geranium sessiliflorum*, *Haplopappus diplopappus*, *Heliotropium geissei*, *Hypochaeris* spp., *Plagiobothrys myosotoides*, *Plantago lanceolata*, *Poa* sp., *Rumex acetocella*, *Spergularia rubra*, *Trifolium* spp., and *Viola subandina* (M. Molina-Montenegro, pers. comm.).

## Discussion

The limits of polymorphism in the *Liolaemus* genus

*Liolaemus* lizards have radiated in one of the widest environmental ranges known among living reptiles (Ceï 1993). The extraordinary diversity of adaptations acquired by this lineage in response to contrasting habitat conditions has led to the development of high polymorphism at interspecific and intraspecific levels (Donoso-Barros 1966; Ceï 1993; Pincheira-Donoso 2005). Nevertheless, the establishment of lineage boundaries has become in one of the main challenges to understand the evolutionary history of this clade. Indeed, over the last few years, a number of studies (e.g. Etheridge 1993; Scolaro & Ceï 1997; Lobo & Espinoza 1999; Pincheira-Donoso & Núñez 2005) have provided evidence to support the idea that *Liolaemus* polymorphism at intraspecific level has been overestimated in the case of many species. The accumulation of phenotypic and molecular data has convincingly proved that several populations largely considered to be members of a single polymorphic taxa, represent different species often closely related phylogenetically (see Schulte *et al.* 2000; Cruz *et al.* 2005). *Liolaemus darwini* is one of the clearest examples. Over a period of one decade, more than five species were diagnosed from populations assigned to this taxon, on the basis of this kind of evidence (Etheridge 1992, 1993; Ceï & Scolaro 1999; Cruz *et al.* 2005).

In this study, we provided significant support in favour of our prediction that the limits of polymorphism in the Patagonian species *L. rothi* have also been overestimated. Phenotypic and molecular analyses revealed that the only Chilean population assigned to this common Argentinean taxon is a different species, herein recognized as *L. hermannunezi*. Therefore, the clear morphological divergence (in relation to *L. rothi*) reported in recent studies for this new species (Pincheira-Donoso & Núñez 2005), is not the result of significant phenotypic plasticity at interpopulational and intraspecific level, but a consequence of speciation. Recently, Etheridge and Christie (2003) also discussed about the overestimation of polymorphism boundaries in Patagonian *Liolaemus* species. These authors provided a detailed diagnosis to suggest that one of the populations from the Neuquén Province in Argentina commonly identified as *L. rothi* is indeed a different taxon, recognized as *L. sagei* (see above).

It seems to be clear that many other *Liolaemus* species need to be studied in more detail, in order to establish with powerful evidence their limits of polymorphism and their species boundaries. However, this challenge should involve the two sides of the same coin. It means that this kind of research must be focused not only in species with wide geographical ranges and phenotypic variation, but also, in many populations currently recognized as different species on the basis of subjective and meaningless traits suggested as diagnostics. For example, until recently, in the *nigromaculatus* group from Atacama Desert in Chile, several species were identified on phenotypic variables without statistical significance. Even, surprisingly, the explicit comparison of traits suggested as diagnostic for some of these taxa (including geographical distribution) did not revealed any difference. More importantly, several of them exhibited significant overlap in all the studied variables (*i.e.* not only those traits previously considered as diagnostics), being therefore suggested as synonymous of other species (Pincheira-Donoso & Núñez 2005).

Although most *Liolaemus* species have been supported by recent phylogenetic analyses (Schulte *et al.* 2000, 2004; Espinoza *et al.* 2004; Cruz *et al.* 2005; this study), further studies are still necessary to clarify the impact of evolutionary radiation in the cladogenesis of this lineage. In fact, the high diversification rates experienced by *Liolaemus* lizards make this group a valuable model system to address hypotheses concerning evolutionary factors involved in adaptive radiation. But at the same time, it is fundamental to make sure that these analyses are not biased by taxonomic inflation or by polymorphism overestimation, for instance. Misleading estimations of species-richness and polymorphism may affect conclusions when performing evolutionary studies (Isaac *et al.* 2004).

## A potential zone of endemism in boreal Patagonia

Based on our findings and other recent species descriptions, the region between 36°50'S–37°53'S, and 70°35'W–71°30'W, in boreal Patagonia straddling Argentina and Chile, appears to be a zone of lizard endemism (see Pincheira-Donoso 2004). Several iguanian populations occurring in this area that were previously considered widely distributed Patagonian species have recently been identified as distinct endemic taxa, with restricted distributions. For example, during one of the first field trips to Laguna del Laja, Donoso-Barros (1974) reported the presence of boreal populations of *Liolaemus bibronii*, *Diplolaemus leopardinus*, and austral populations of *Phymaturus flagellifer* (= *P. palluma*, see Etheridge & Savage 2003; but also Cei & Scolaro 2006). All these species are widely spread in Andean and Patagonian habitats (Donoso-Barros 1966; Cei 1986). However, recent studies suggested that the population identified as *L. bibronii* represents the northernmost locality of *L. araucaniensis*, a Chilean species with much more restricted range (Pincheira-Donoso 2003b, c; Pincheira-Donoso & Núñez 2005). Whereas, those identified as *D. leopardinus* and *P. flagellifer* (see above) were described as the new taxa *Diplolaemus sexcinctus* (Cei *et al.* 2003, reported as *Diplolaemus* “altopatagonica” by Schulte *et al.* 2003), and *Phymaturus vociferator* (Pincheira-Donoso 2004). The description of *L. hermannunezi* herein represents the fourth case in this northern Patagonian zone of a population identified under the name of a widely distributed Patagonian lizard, later demonstrated to be a different species.

Other lizards reported from the same area remain still poorly known. For example, *L. chillanensis chillanensis*, *L. buergeri* and *L. kriegi* are fairly common in the same area where *L. hermannunezi* inhabits. *Liolaemus c. chillanensis* (see Pincheira-Donoso & Núñez 2005) is endemic to Chile, and occurs from the Andes of Chillan (36°51'S; 71°24'W) to the Lonquimay Valley (38°28'S; 71°34'W) (Pincheira-Donoso 2003c). *Liolaemus buergeri* is widely distributed in Argentina, and was recently reported in Laguna del Laja (Pincheira-Donoso 2001). Last, *L. kriegi* is common in Argentinean Patagonia, and was also recorded in this region by Donoso-Barros (1974; see also Cei 1986). The study of populations currently recognized as *L. buergeri* and *L. kriegi* may be particularly interesting, as they have never been analyzed in detail. Consequently, further research in this area may provide additional insights on the structure of lizard communities, and their relationships with species widespread in Andean and Patagonian habitats.

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## References

- Abdala, C.S. (2003) Cuatro nuevas especies del género *Liolaemus* (Iguania: Liolaemidae), pertenecientes al grupo *boulengeri*, de la Patagonia, Argentina. *Cuadernos de Herpetología*, 17, 3–32.
- Abdala, C.S. & Lobo, F. (2006) Description of a new Patagonian lizard species of the *Liolaemus silvanae* group (Iguania: Liolaemidae). *South American Journal of Herpetology*, 1, 1–8.
- Abdala, V., Abdala, C. & Tulli, M.J. (2006) Muscular characters in the phylogeny of *Liolaemus* (Squamata: Iguania: Liolaemidae): a reappraisal. *Zootaxa*, 1205, 55–68.
- Avila, L.J., Morando, M., Perez, C.H.F. & Sites, J.W. (2004) Phylogenetic relationships of lizards of the *Liolaemus petrophilus* group (Squamata, Liolaemidae), with description of two new species from western Argentina. *Herpetologica*, 60, 187–203.
- Cei, J.M. (1986) *Reptiles del centro, centro-oeste y sur de la Argentina*. *Herpetofauna de las zonas áridas y semiáridas*, Museo Regionale di Scienze Naturali, Torino, 527 pp.
- Cei, J.M. (1993) *Reptiles del noroeste, nordeste y este de la Argentina*. *Herpetofauna de las selvas subtropicales, puna y pampas*. Museo Regionale di Scienze Naturali, Torino, 947 pp.
- Cei, J.M. & Scolaro, J.A. (1996) A new species of *Liolaemus* of the *archeforus* group from the precordilleran valley of the Zeballos river, Santa Cruz Province, Argentina (Reptilia, Tropicuridae). *Bollettino del Museo Regionale di Scienze Naturali di Torino*, 14, 389–401.
- Cei, J.M. & Scolaro, J.A. (1999) Speciation of the “*darwinii* complex” (genus *Liolaemus*, “patch group”) in the southernmost area of its distribution (Reptilia: Tropicuridae). *Revue Française de Aquariologie*, 26, 79–82.
- Cei, J.M. & Scolaro, J.A. (2006) The neotype of the type species of the neotropical iguanian genus *Phymaturus*: A critical commentary on a recent opinion of the International Commission on Zoological Nomenclature. *Zootaxa*, 1297, 17–22.
- Cei, J.M. & Videla, F. (2003). A new species of *Liolaemus* lacking precloacal pores in males from the Andean south-eastern mountains of Mendoza Province, Argentina (Liolaemidae, Iguania, Lacertilia, Reptilia). *Bollettino del Museo Regionale di Scienze Naturali di Torino*, 20, 275–290.
- Cei, J.M., Scolaro, J.A. & Videla, F. (2003) A taxonomic revision of recognized Argentine species of the leiosaurid genus *Diplolaemus* (Reptilia, Squamata, Leiosauridae). *Facena*, 19, 87–106.
- Cruz, F.B., Fitzgerald, L.A., Espinoza, R.E. & Schulte II, J.A. (2005) The importance of phylogenetic scale in tests of Bergmann’s and Rapoport’s rules: lessons from a clade of South American lizards. *Journal of Evolutionary Biology*, 18, 1559–1574.
- Donoso-Barros, R. (1966) *Reptiles de Chile*, Ediciones de la Universidad de Chile, Santiago, 458 pp.
- Donoso-Barros, R. (1970) Catálogo herpetológico chileno. *Boletín del Museo Nacional de Historia Natural de Chile*, 31, 49–124.
- Donoso-Barros, R. (1974) Notas herpetológicas. *Boletín de la Sociedad de Biología de Concepción*, 47, 285–287.
- Espinoza, R.E. & Lobo, F. (2003) Two new species of *Liolaemus* lizards from Northwestern Argentina: speciation within the northern subclade of the *elongatus* group (Iguania: Liolaemidae). *Herpetologica*, 59, 89–105.
- Espinoza, R.E., Lobo, F. & Cruz, F.B. (2000) *Liolaemus heliodermis*, a new lizard from northwestern Argentina with remarks on the content of the *elongatus* group (Iguania: Tropicuridae). *Herpetologica*, 56, 507–516.
- Espinoza, R.E., Wiens, J.J. & Tracy, C.R. (2004) Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. *Proceedings of the National Academy of Sciences, USA*, 101, 16819–16824.
- Etheridge, R. (1992) A new psammophilus lizard of the genus *Liolaemus* (Squamata: Tropicuridae) from northwestern Argentina. *Bollettino del Museo Regionale di Scienze Naturali di Torino*, 10, 1–19.
- Etheridge, R. (1993) Lizards of the *Liolaemus darwinii* Complex (Squamata: Iguania: Tropicuridae) in northern Argentina. *Bollettino del Museo Regionale di Scienze Naturali di Torino*, 11, 137–199.
- Etheridge, R. (1995) Redescription of *Ctenoblepharys adspersa* Tschudi, 1845, and the taxonomy of Liolaeminae (Reptilia: Squamata: Tropicuridae). *American Museum Novitates*, 3142, 1–34.
- Etheridge, R. (2000) A review of lizards of the *Liolaemus wiegmanni* group (Squamata, Iguania, Tropicuridae), and a history of morphological change in the sand-dwelling species. *Herpetological Monographs*, 14, 293–352.
- Etheridge, R. (2001) A new species of *Liolaemus* (Reptilia: Squamata: Tropicuridae) from Mendoza Province, Argentina. *Cuadernos de Herpetología*, 15, 3–15.
- Etheridge, R. & Christie, M.I. (2003) Two new species of the lizard genus *Liolaemus* (Squamata: Liolaemidae) from northern Patagonia, with comments on *Liolaemus rothi*. *Journal of Herpetology*, 37, 325–341.
- Etheridge, R. & Espinoza, R.E. (2000) Taxonomy of the Liolaeminae (Squamata: Iguania: Tropicuridae) and a semi-annotated bibliography. *Smithsonian Herpetological Information Service*, 126, 1–64.
- Etheridge, R. & Savage, J.M. (2003) *Phymaturus* Gravenhorst, 1837 and *Lacerta palluma* Molina, 1782 (currently *Phymaturus palluma*; Reptilia, Sauria): proposed conservation of usage of the names by designation of a neotype for

- Lacerta palluma* Molina, 1782. *Bulletin of Zoological Nomenclature*, 60, 38–41.
- Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39, 783–791.
- Isaac, N.J.B., Mallet, J. & Mace G.M. (2004) Taxonomic inflation: Its influence on macroecology and conservation. *Trends in Ecology and Evolution*, 19, 464–469.
- Jaksic, F. & Schwenk, K. (1983) Natural history observations on *Liolaemus magellanicus*, the southern-most lizard in the world. *Herpetologica*, 39, 457–461.
- Lobo, F. & Espinoza, R.E. (1999) Two new cryptic species of *Liolaemus* (Iguania: Tropiduridae) from northwestern Argentina: resolution of the purported reproductive bimodality of *Liolaemus alticolor*. *Copeia*, 1999, 122–140.
- Lobo, F. & Espinoza, R.E. (2004) Two new *Liolaemus* from the Puna Region of Argentina and Chile: further resolution of purported reproductive bimodality in *Liolaemus alticolor* (Iguania: Liolaeminae). *Copeia*, 2004, 850–867.
- Martínez Oliver, I. & Lobo, F. (2002). Una nueva especie de *Liolaemus* del grupo *alticolor* (Iguania: Liolaemidae) de la Puna Salteña, Argentina. *Cuadernos de Herpetología*, 16, 47–64.
- Núñez, H. & Jaksic, F.M. (1992) Lista comentada de los reptiles terrestres de Chile continental. *Boletín del Museo Nacional de Historia Natural de Chile*, 43, 63–91.
- Núñez, H. & Pincheira-Donoso, D. (2006) *Liolaemus confusus*, una nueva especie de lagartija para la cordillera de la costa central de Chile (Sauria, Liolaeminae): evidencia fenética y citogenética. *Boletín del Museo Nacional de Historia Natural de Chile* (In Press).
- Núñez, H., Navarro, J., Garín, C., Pincheira-Donoso, D. & Meriggio, V. (2003) *Phrynosaura manuelei* y *Phrynosaura torresi*, nuevas especies de lagartijas para el norte de Chile (Squamata: Sauria). *Boletín del Museo Nacional de Historia Natural de Chile*, 52, 67–88.
- Núñez, H., Pincheira-Donoso, D. & Garín, C. (2004) *Liolaemus hajeki*, nueva especie de lagartija de Chile (Squamata, Sauria). *Boletín del Museo Nacional de Historia Natural de Chile*, 53, 85–97.
- Pang, J., Wang, Y., Zhong, Y., Hoelzel, A.R., Papenfuss, T.J., Zeng, X., Ananjeva, N.B. & Zhang, Y. (2003) A phylogeny of Chinese species in the genus *Phrynocephalus* (Agamidae) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 27, 398–409.
- Pincheira-Donoso, D. (2001) Distribución geográfica de *Liolaemus buergeri* Werner, 1907 (Reptilia-Tropiduridae) en Chile y Argentina; nuevos datos y comentarios. *Museo Nacional de Historia Natural de Chile, Noticiero Mensual*, 346, 8–11.
- Pincheira-Donoso, D. (2003a) Primer registro para Chile de *Liolaemus coeruleus* Cei y Ortiz, 1983 (Iguania: Tropiduridae: Liolaeminae), con comentarios adicionales sobre sus relaciones sistemáticas. *Multequina, Latinamerican Journal of Natural Resources*, 12, 17–22.
- Pincheira-Donoso, D. (2003b) *Liolaemus altissimus araucaniensis* en Antuco, Octava Región del Bío Bío, Chile (Sauria: Tropiduridae). *Revista de Biología Tropical*, 51, 284.
- Pincheira-Donoso, D. (2003c) Sobre la sistemática y biogeografía de *Liolaemus altissimus araucaniensis* Müller y Hellmich de Chile, y sus vinculaciones con la taxonomía de *Liolaemus monticola chillanensis* y *Liolaemus monticola villaricensis* (Iguania: Tropiduridae: Liolaeminae). *Museo Nacional de Historia Natural de Chile, Noticiero Mensual*, 352, 1–8.
- Pincheira-Donoso, D. (2004) Una nueva especie del genero *Phymaturus* (Iguania: Tropiduridae: Liolaemini) del centro-sur de Chile. *Multequina, Latinamerican Journal of Natural Resources*, 13, 57–70.
- Pincheira-Donoso, D. (2005) Anfibios y Reptiles de la Provincia de El Loa. In: Ramírez, G.M. & Pincheira-Donoso, D. (Ed.), *Fauna del Altiplano y Desierto de Atacama, Vertebrados de la Provincia de El Loa*. Phrynosaura Ediciones, Calama, 93–150.
- Pincheira-Donoso, D. & Núñez, H. (2003) *Liolaemus robertoi*, una nueva especie de Los Andes del Norte de Chile perteneciente al grupo *ruibali* (Iguania: Tropiduridae: Liolaeminae). *Multequina, Latin American Journal of Natural Resources*, 12, 1–15.
- Pincheira-Donoso, D. & Núñez, H. (2005) *Las especies chilenas del género Liolaemus (Iguania, Tropiduridae, Liolaeminae)*. *Taxonomía, sistemática y evolución*, Museo Nacional de Historia Natural de Chile, Publicación Ocasional, Santiago, 486 pp.
- Pincheira-Donoso, D. & Ramírez, G.M. (2005) Desplazamiento de caracteres como evidencias de un posible caso de especiación simpátrica entre dos *Liolaemus* del grupo *jamesi* en la Provincia de El Loa, con la descripción de una nueva especie. In: Ramírez, G.M. & Pincheira-Donoso, D. (Ed.), *Fauna del Altiplano y Desierto de Atacama, Vertebrados de la Provincia de El Loa*. Phrynosaura Ediciones, Calama, 350–365.
- Pough, F.H., Andrews, R.M., Cadle, J.E., Crump, M.L., Savitzky, A.H. & Wells, K.D. (2004) *Herpetology*, 3<sup>rd</sup> Edition, Pearson, Prentice Hall, New Jersey, 726 pp.
- Schulte II, J.A., Losos, J.B., Cruz, F.B. & Núñez, H. (2004) The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropidurinae: Liolaemini). *Journal of Evolutionary Biology*, 17, 408–420.
- Schulte II, J.A., Macey, J.R., Espinoza, R.E. & Larson, A. (2000) Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal.

- Biological Journal of the Linnean Society*, 69, 75–102.
- Schulte II, J.A., Valladares, J.P. & Larson, A. (2003) Phylogenetic relationships within Iguanidae inferred using molecular and morphological data and a phylogenetic taxonomy of iguanian lizards. *Herpetologica*, 59, 399–419.
- Scolaro, J.A. & Cei, J.M. (1997) Systematic status and relationships of *Liolaemus* species of the *archeforus* and *kingii* groups: a morphological and taxonumerical approach (Reptilia: Tropicuridae). *Bollettino del Museo Regionale di Scienze Naturali di Torino*, 15, 369–406.
- Scolaro, J. A. & Cei, J.M. (2006) A new species of *Liolaemus* from central steppes of Chubut, Patagonia Argentina (Reptilia: Iguania: Iguanidae). *Zootaxa*, 1133, 61–68.
- Sorenson, M.D. (1999) *TreeRot, Version 2*, Boston University, Boston.
- Sullivan, J., Abdo, Z., Joyce, P. & Swofford, D.L. (2005) Evaluating the performance of a successive-approximations approach to parameter optimization in maximum-likelihood phylogeny estimation. *Molecular Biology and Evolution*, 22, 1386–1392.
- Swofford, D.L. (2002) *PAUP\*: Phylogenetic Analysis Using Parsimony (\* and Other Methods), Version 4.0b10*, Sinauer, Sunderland, Massachusetts.
- Vitt, L.J. (2004) Shifting paradigms: Herbivory and body size in lizards. *Proceedings of the National Academy of Sciences, USA*, 101, 16713–16714.
- Zhao, K.T. 1999. *Phrynocephalus* Kaup, 1825. In: Zhao, E.M., Zha, K.T. & Zhou, K.Y. (Ed.), *Fauna Sinica, Reptilia Vol. 2. Squamata. Lacertilia*. Science Press, Beijing, 151–193.



## Appendix.

### Examined material

Museo Nacional de Historia Natural de Santiago, Chile (MNHNC), Zoological Museum, Facultad de Ciencias Naturales y Oceanográficas of the Universidad de Concepcion, Chile (MZUC), Museo de Historia Natural de Concepcion, Chile (MHNC), Departamento de Biología Celular y Genética, Facultad de Medicina Norte, Universidad de Chile (DBCUGH), Instituto de Biología Animal, Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo, Mendoza, Argentina (IBA-UNC), Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina (CH-IADIZA), Natural History Museum of London, United Kingdom (NHML), and in the diagnostic collections of J. M. Cei (JMC-DC), J. A. Scolaro (JAS-DC), and D. Pincheira-Donoso (CHDPD).

*Liolaemus boulengeri*, MNHN-2846, Neuquén Province, Argentina. Six specimens at IBAUNC, no catalog number, all collected in Neuquén Province, Argentina.

*Liolaemus canqueli*, IBAUNC-861-9, Holotype, Callejas, Meseta Canquel, Chubut Province, Argentina, 19-Jan-1973; IBAUNC-861-1–8, 861-10–12, Paratypes, Callejas, Meseta Canquel, Chubut Province, Argentina.

*Liolaemus cuyanus*, IBAUNC-1929-1–5, Paratypes, Baldecitos, Talampaya, La Rioja Province, Argentina; IBAUNC-1269, Paratype, Alpero, Lavalle, Mendoza Province, Argentina; IBAUNC-1271-1–15, Paratypes, Carrizal del Medio, Mendoza Province, Argentina; IBAUNC-1206-1–16, Paratypes, Carrizal del Medio, Mendoza Province, Argentina.

*Liolaemus darwinii*, IADIZACH-119, Ñacuñán, Santa Rosa, Mendoza Province, Argentina; IADIZACH-211, Puesto La Mojada, Camino a Altas Cumbres, Lavalle, Mendoza Province, Argentina; IADIZACH-124-1, Ñacuñán, Santa Rosa, Mendoza Province, Argentina; IADIZACH-202, Puesto Gómez, Meseta de Guachal, San Carlos, Mendoza Province, Argentina; CHDPD-773, Mendoza, Mendoza Province, Argentina.

*Liolaemus fitzingerii*, MNHN-1701–07, 1712–19, Chile Chico, S General Carrera Lake, 22-Oct-1956; CHDPD-00869, 00870, Telsen, Chubut Province, Argentina.

*Liolaemus lobo*, three CHDPD specimens, without collection number, collected NE Lago Nahuel Huapi, Neuquén Province, Argentina.

*Liolaemus rothi*, CHDPD-819, 15 km S Cerro Corona, Meseta Somuncurá, Río Negro Province, Argentina; CHDPD-820, Cerro Corona, Meseta Somuncurá, Río Negro Province, Argentina; CHDPD-821, Cerro Corona, Meseta Somuncurá, Río Negro Province, Argentina; CHDPD-929, 930, Meseta Telsen, Chubut Province, Argentina; CHDPD-931, 932, Meseta Telsen, Chubut Province, Argentina.

*Liolaemus sagei*, four CHDPD specimens without number, recollected at W Laguna Blanca, Neuquén Province, Argentina.

### GenBank accession numbers of DNA sequences

The following specimen identifications from Schulte *et al.* (2000) are corrected: *L. alticolor* is now *L. chaltin*, *L. boulengeri* is now *L. cf. darwinii*, *L. darwinii* from Mendoza is now *L. grosseorum*, *L. melanops* is now *L. cf. rothi*, *L. cyanogaster* is now *L. cf. pictus*.

*Ctenoblepharys adspersa* (SDSU 3781, AF305784); *Phymaturus palluma* (SDSU 3387, AF099216); *Phymaturus somuncurensis* (SDSU 1648, AF049865) *L. abaucan* (SDSU 3532, AF099263); *L. albiceps* (SDSU 3380, AF099267); *L. andinus*-Jujuy (SDSU 3599, AF099251); *L. andinus*-La Rioja (REE 265, AF099245); *L. austromendocinus* (SDSU 3425, AF099239); *L. bellii* (SDSU 3719, AF099223); *L. bibronii* (SDSU 3407, AF099221); *L. bitaeniatus* (SDSU 3568, AF099219); *L. buergeri* (SDSU 3420, AF099236); *L. capillitas* (SDSU 3481, AF099234); *L. ceii* (MIC 1139, AF099237); *L. chacoensis* (FML 3640, AF099270); *L. chaltin* (SDSU 3574, AF099218); *L. chilensis* (MIC 1259, AF099224); *L. coeruleus* (SDSU 3692, AF099217); *L. cuyanus* (SDSU 3541, AF099252); *L. cf. cuyanus* (FML-FBC67, DQ002487); *L. darwinii*-La Rioja (SDSU 3477, AF099274); *L. cf. darwinii* (SDSU 3469, AF099275); *L. dorbignyi* (SDSU 3443, AF099248); *L. elongatus* (SDSU 3459, AF099240); *L. famatinae* (REE 193, AF099246); *L. fitzingerii* (FML not cat., AF099253); *L. fuscus* (MVZ-RDS 12818, AF099232); *L. gracilis* (SDSU 3409, AF099222); *L. grosseorum* (SDSU 3472, AF099272); *L. hermannunezi* (JAS 066 –MNHN 3501, male, Los Barros (37°31'S; 71°15'W) on the road to Pichachén Pass, Eighth Administrative Region, Chile); *L. irregularis* (SDSU 3525, AF099268); *L. koslowskyi* (SDSU 3598, AF099264); *L. laurenti* (SDSU 3530, AF099273); *L. lemmiscatus* (SDSU 3721, AF099229); *L. leopardinus* (SDSU 3717, AF099235); *L. lineomaculatus* (MLP 1670, AF099241); *L. lutzae* (MNRJ 4720, AF099255); *L. magellanicus* (MVZ 180141, AF099243); *L. melanops* (FML-FBC58, DQ002488); *L. monticola* (SDSU 3724, AF099230); *L. multicolor* (SDSU 3591, AF099250); *L. multimaculatus* (UNMdP 407, AF099257); *L. nigroviridis* (SDSU 3715, AF099233); *L. nitidus* (SDSU 3720, AF099231); *L. occipitalis* (UFRGS 2753, AF099256); *L. olongasta* (SDSU 3546, AF099271); *L. orientalis* (SDSU 3517,

AF099247); *L. ornatus* (SDSU 3521, AF099266); *L. petrophilus* (MLP 1671, AF099238); *L. cf. pictus*-Puyehue (MIC 1241, AF099225); *L. pictus* – Neuquén (MIC 1108, AF099226); *L. pictus* – Rio Negro (MVZ 162076, U82684); *L. cf. poecilochromus* (USNM-JAS157, DQ002485); *L. poecilochromus* (SDSU 3593, AF099249); *L. pseudoanomalus* (SDSU 3539, AF099254); *L. quilmes* (SDSU 3558, AF099265); *L. robertmertensi* (SDSU 3498, AF099220); *L. cf. rothi* (SDSU 3704, AF099261); *L. rothi* (MLP 1662, AF099262); *L. ruibali* (SDSU 3455, AF099244); *L. salinicola* (SDSU 3531, AF099259); *L. scapularis* (SDSU 3560, AF099258); *L. somuncurae* (MLP 1661, AF099242); *L. cf. telsen* (FML-FBC62, DQ002491); *L. tenuis* (SDSU 3723, AF099228); *L. uspallatensis* (SDSU 3465, AF099269); *L. wiegmanni* (SDSU 3494, AF099260); *L. zapallarensis* (SDSU 3658, AF099227).