



<http://dx.doi.org/10.11646/zootaxa.3815.4.3>

<http://zoobank.org/urn:lsid:zoobank.org:pub:5A25260D-34C4-468E-BC65-7A11FDBE23F3>

## The missing leopard lizard: *Liolaemus ubaghsi* sp. nov., a new species of the *leopardinus* clade (Reptilia: Squamata: Liolaemidae) from the Andes of the O'Higgins Region in Chile

DAMIEN ESQUERRÉ<sup>1,5</sup>, JAIME TRONCOSO-PALACIOS<sup>2</sup>, CARLOS F. GARÍN<sup>3</sup> & HERMAN NÚÑEZ<sup>4</sup>

<sup>1</sup>Division of Evolution, Ecology and Genetics, Research School of Biology, The Australian National University, Canberra, ACT 0200, Australia. E-mail: [damien.esquerre@anu.edu.au](mailto:damien.esquerre@anu.edu.au)

<sup>2</sup>Programa de Fisiología y Biofísica, Facultad de Medicina, Universidad de Chile, Casilla 70005, Santiago, Chile. E-mail: [jtrancosopalacios@gmail.com](mailto:jtrancosopalacios@gmail.com)

<sup>3</sup>Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

<sup>4</sup>Museo Nacional de Historia Natural, casilla 787, Santiago de Chile. E-mail: [hmunez@mnhn.cl](mailto:hmunez@mnhn.cl)

<sup>5</sup>Corresponding author. E-mail: [damien.esquerre@anu.edu.au](mailto:damien.esquerre@anu.edu.au)

### Abstract

*Liolaemus* is an extremely species rich genus of iguanid lizards from southern South America. Most of the diversity though is found in the Andes Cordillera, between Argentina and Chile. Here we describe *Liolaemus ubaghsi* sp. nov., from El Teniente Mine, in the Andean mountains of the O'Higgins Region in Chile. This species presents scalation and pattern traits that belong to the *leopardinus* clade, a group of viviparous, high altitude lizards that inhabit the mountain ranges surrounding Santiago City. The species of this clade in turn belong to the Andean and Patagonian *elongatus-kriegi* complex. *Liolaemus ubaghsi* sp. nov. has been previously recognized as *L. leopardinus* and *L. elongatus*, nevertheless we present diagnostic traits that allow us to describe it as a new species. It mainly differs from the rest of the *leopardinus* clade (*L. leopardinus*, *L. ramonensis*, *L. valdesianus* and *L. frassinettii*) by having the following unique combination of traits: ochre background coloration, a wide dark occipital stripe, dark flanks, white dots dispersed on the dorsum, absence of leopard-like spots and enlarged infralabial scales.

**Key words:** *L. elongatus*, *leopardinus* group, Sewell, El Teniente, Andes

### Resumen

*Liolaemus* es un género extremadamente rico de lagartos iguánidos del sur de Sudamérica. La mayor parte de su diversidad sin embargo se encuentra en la Cordillera de los Andes entre Chile y Argentina. Aquí describimos a *Liolaemus ubaghsi* sp. nov., de la Mina El Teniente, en los Andes de la Región de O'Higgins en Chile. Esta especie presenta caracteres de escamación y diseño que pertenecen al clado *leopardinus*, un grupo de lagartos vivíparos de altura que habitan las montañas alrededor de la ciudad de Santiago. Las especies de este clado pertenecen a su vez al grupo andino patagónico conocido como complejo *elongatus-kriegi*. *Liolaemus ubaghsi* sp. nov. ha sido previamente reconocido como *L. leopardinus* y *L. elongatus*, sin embargo presentamos características diagnósticas que nos permiten describirla como una especie nueva. Se diferencia del resto del clado *leopardinus* (*L. leopardinus*, *L. ramonensis*, *L. valdesianus* y *L. frassinettii*) por tener una combinación única de caracteres: coloración de fondo ocre, una banda occipital ancha oscura, flancos oscuros, puntos blancos dispersos en el dorso, ausencia de manchas de tipo leopardo y escamas infralabiales agrandadas.

### Introduction

Any systematic, evolutionary or ecological work on the iguanian lizard genus *Liolaemus* (Wiegmann 1834), highlights its remarkable species richness and the wide diversity of habitats these species use (Donoso-Barros

1966; Cei 1986; Pincheira-Donoso & Núñez 2005; Pincheira-Donoso *et al.* 2008; Lobo *et al.* 2010). The highest species diversity is found in the Andes Cordillera of southern South America, where frequent *Liolaemus* species descriptions are made (e.g. Abdala *et al.* 2010; Avila *et al.* 2012; Esquerré *et al.* 2013).

The prolific German herpetologists, Lorenz Müller and Walter Hellmich (1932), described the Central Chile Andean species *Liolaemus leopardinus* Müller and Hellmich 1932, and included two subspecies: *L. l. leopardinus* from Fierro Carrera, San Francisco River Valley, El Plomo Mountain, and *L. l. ramonensis* from Quebrada de Ramon, San Ramon Mountain. These lizards are commonly known as the leopard and the Ramon leopard lizards respectively. Later, a new subspecies, *L. l. valdesianus* Hellmich 1950, was described from Lo Valdes in the Maipo River Valley. All these localities are found in the Andean vicinities of Santiago, Chile's capital city. A series of studies (Navarro & Díaz 1986; Espejo *et al.* 1987; Espejo 1989) suggested, based on karyotypic, morphologic and biogeographic evidence that these subspecies might be differentiated enough to be considered full species, however this was only formally proposed by Núñez and Jaksic (1992). Several years later, an additional member of the *leopardinus* group was described: *L. frassinettii* Núñez 2007. This is the only species not present in the Andes but in the Cordillera de la Costa, a lower mountain range west of the Andes. Little has been done to establish the phylogenetic relationships of these species, although several studies have found or acknowledge a relation with the *elongatus-kriegi* complex (Schulte *et al.* 2000; Lobo 2001; Espinoza & Lobo 2003; Espinoza *et al.* 2004; Lobo 2005; Pincheira-Donoso & Núñez 2005). Nevertheless, there is no agreement on what those relationships are; for example, Lobo (2005) found the *leopardinus* clade more related to the *kriegi* than to the *elongatus* clade.

Here we describe a new leopard lizard, found in the Chapa Verde Ski Center and El Teniente Mine, in the Andes of the Libertador Bernardo O'Higgins Region in Chile, east from the city of Rancagua. This population was first identified as *L. l. leopardinus* (Núñez 1992), and later as *L. elongatus* (Pincheira-Donoso & Núñez 2005; Núñez & Torres-Mura 2007). Additional comments on this species and the *leopardinus* group can be found in Hamasaki and Troncoso-Palacios (2011). With a molecular phylogeny that will be published elsewhere (Esquerré *et al.* in prep.), we determined that this species in fact belongs to the *leopardinus* clade, and that this clade in turn is sister to the *elongatus* clade (Cei 1974, 1975; Morando *et al.* 2003; Avila *et al.* 2004; Avila *et al.* 2010; Avila *et al.* 2012). Nevertheless, morphological characters distinguish this species from all of the other species of the *leopardinus* clade.

## Material and methods

We examined 45 specimens belonging to the five species of the *leopardinus* clade as determined by Esquerré *et al.* (in prep.): *L. leopardinus*, *L. ramonensis*, *L. valdesianus*, *L. frassinettii* and the new taxon described below. Juveniles and poorly preserved specimens were excluded from the analysis. Measurements were taken with a digital caliper to the nearest 0.1 mm. Close examination was made using a binocular dissection microscope. The specimens used for this study are deposited in three collections, the Museo Nacional de Historia Natural de Chile (MNHNCL), the Colección de Flora y Fauna, Profesor Patricio Sánchez Reyes of the Pontificia Universidad Católica de Chile (SSUC Re) and the Laboratorio de Citogenética, Facultad de Ciencias, Universidad de Chile (LCUC). Another sample of the new species from a nearby locality of the type locality was examined to determine the reproduction mode, however they were poorly preserved and no phenotypic data was extracted from them (MNHNCL-0605-0613). Specimens are listed in Appendix I.

To test for sexual dimorphism in the head, we used three head measurements: head length (from the anterior edge of the ear opening to the tip of the snout), head width (between the anterior edges of the ear openings) and head height (at the level of the anterior edge of the ear openings). Sub-adult specimens (male MNHNCL-3814 and female SSUC-Re 491) were excluded from these analyses. We performed one-way ANOVAs with sex as the factor and the residuals of the head measurements against SVL (snout-vent length) as the response variable. We used the residuals of the measurements against SVL in order to account for size variation. The analyses were performed with JMP 10.0 (SAS Institute Inc., 2012).

DNA from one specimen of each species was extracted from liver and muscle tissue with the protocol and kit of "DNeasy Blood and Tissue Kit" from Qiagen. We amplified the mitochondrial gene *cytb* with a Polymerase Chain Reaction (PCR) following Morando *et al.* (2003) and using the GLUDG and CB3 light and heavy-strand primers respectively (Palumbi, 1996). We checked the PCR products with an electroforesis in a 1% agarose gel,

and sent the samples for sequencing to Macrogen Inc. (Seoul, Korea). Sequences were aligned using ClustalX 2.1 (Larkin *et al.* 2007). The sequences compared had 758 bp. Pairwise genetic distances were calculated with MEGA 5.2 (Tamura *et al.* 2011).

## Results

Genetic distances in *cytb* are quite shallow, suggesting recent divergence (Table 3). The most distant taxon from the rest is *L. frassinettii*. The distances between *L. valdesianus*, *L. ramonensis* and *L. leopardinus* are especially low.

### *Liolaemus ubaghsi* sp. nov.

1992 *Liolaemus leopardinus leopardinus*, Núñez. Smith. Herpet. Info. Serv. 91, 10.

2005 *Liolaemus elongatus*, Pincheira-Donoso and Núñez. Pub. Oc. Mus. Nac. Hist. Nat., Chile, Santiago 59, 260.

**Holotype.** MNHNCL-3813 (Fig. 1). Male, collected by Herman Núñez, Carlos Garín and Daniel Pincheira-Donoso at Chapa Verde, between the ski field and reservoir, Libertador Bernardo O'Higgins Region, Chile. 34°03'S 70°26'W, 2210 masl. On May 22-23, 2003.

**Paratypes.** MNHNCL-3812, 3814 and 3816 males; MNHNCL-3808, 3809, 3810, 3811, and 3815 females (Fig. 2). Same collection data as the holotype. SSUC Re-491 and 492 females, collected by R. Thomson and G. Ugalde. Tranque Barahona, El Teniente Mine, Libertador Bernardo O'Higgins Region, Chile. On April the 15<sup>th</sup>, 2008. Measurements in Table 1.

**Etymology.** This species is named after Prof. Georges Ubaghs (1916-2005), Belgian paleontologist, who made some of the greatest contributions to the knowledge of Palaeozoic echinoderms in the 20<sup>th</sup> century. He is also the great-grandfather of the first author of this paper (DE). We propose the common name “Ubaghs’ leopard lizard” in English and “Lagarto leopardo de Ubaghs” in Spanish.

**Diagnosis.** *Liolaemus ubaghsi* sp. nov. belongs to the *leopardinus* clade. This group is composed by medium to large lizards (maximum SVL greater than 89 mm), with prominent neck folds, 72–93 scales around mid-body, juxtaposed or subimbricated rhomboidal keeled dorsal scales, with interstitial granular scales around them, nasal scales not in contact with the rostral scale (with some exceptions), undifferentiated auricular scale and parietal scales with a similar size as interparietal (with some exceptions, especially in *L. frassinettii*). Even though the pattern of each species is different, it always involves some kind of dark mottled pattern on a lighter (varying from beige, to olive brown and dark brown) background (see Figs 3–6). All species have leopard-like spots on the dorsum or at least on dorsal surface of the tail (with the exception of *Liolaemus ubaghsi* sp. nov.)

*Liolaemus ubaghsi* sp. nov. is a medium to large, sturdy lizard. It has a mean SVL of 83.3 mm, and a maximum of 89.6 mm. The head is longer than it is wide, and the neck is as wide or wider than the head due to prominent transversal neck folds. On average, the tail is 1.46 times the length of the body (SVL). It has 72–87 scales around midbody, 62 to 83 dorsal scales (through the vertebral line, from the occiput to the level of the anterior surface of the femoral region) and 111 to 137 ventral scales (from tip of the snout to the cloaca).

It differs from *L. valdesianus* and *L. frassinettii* by its dorsal pattern. *L. ubaghsi* sp. nov. displays an occipital stripe or sometimes a vertebral line and has white dots dispersed on the dorsum, instead of the light green transversal stripes present in *L. valdesianus* and *L. frassinettii*. Also, the general background coloration in *L. ubaghsi* sp. nov. is ochre, while in *L. valdesianus* and *L. frassinettii* is olive brown and has a more gray or greenish hue. Furthermore, *L. valdesianus* and *L. frassinettii* have leopard-like spots on the dorsal side of the tail, whereas these are absent on *L. ubaghsi* sp. nov. It also differs from *L. valdesianus* by having more lamellae on the fourth toe, although there is a small overlap (28–35 in *L. ubaghsi* sp. nov. vs. 25–28 in *L. valdesianus*), and because the dorsal scales on *L. valdesianus* are juxtaposed or subimbricated, leaving large spaces between them with abundant interstitial granules (more than in any species of the *leopardinus* clade). These scales are subimbricated in *L. ubaghsi* sp. nov., with less interstitial granules (see Fig. 7). Moreover, the infralabial scales in *L. ubaghsi* sp. nov. and *L. frassinettii* are notoriously enlarged in relation to the supralabial scales, while in *L. valdesianus* the infralabials are barely larger than the supralabials (see Fig. 8). The dorsal scales on *L. ubaghsi* and *L. frassinettii*



FIGURE 1. Holotype of *Liolaemus ubaghsi*. MNHNCL 3813.





**FIGURE 3.** *L. leopardinus* from El Colorado, Metropolitan Region. Photo: Damien Esquerré.



**FIGURE 4.** *L. ramonensis* from San Ramon Mountain, Metropolitan Region. Photo: Jaime Troncoso-Palacios.

are notoriously more keeled than on *L. valdesianus* and *L. leopardinus*. It additionally differs from *L. frassinettii* because this species has a black spot that begins at the axilla and continues until about the middle of the flanks, instead of the complete dark flanks in *L. ubaghsi* **sp. nov.** It strongly differs from *L. leopardinus* and *L. ramonensis* by its dorsal pattern. Although these two species may present a vertebral line, they never exhibit the occipital wide stripe often observed in *L. ubaghsi* **sp. nov.**, and their flanks are not as dark as the flanks in *L. ubaghsi* **sp. nov.** Additionally, *L. leopardinus* never has white dots scattered on the dorsal region, and it has big black leopard-like hollow spots on the dorsal region, which are absent in *L. ubaghsi* **sp. nov.** (as well as in the rest of the clade). In the same way, *L. ramonensis* has small black leopard-like spots absent in *L. ubaghsi* **sp. nov.** In addition to all this diagnostic traits, *L. ubaghsi* **sp. nov.** is slightly smaller (maximum SVL=89.6 mm) than *L. valdesianus* (95 mm), *L. ramonensis* (94.9 mm) and *L. leopardinus* (98.2 mm).

**TABLE 1.** Morphological, meristic and coloration characters in the species of the *leopardinus* clade. SAMB: Scales around midbody; 4TL: Fourth toe lamellae. SVL is measured in mm. Examined juveniles are excluded from SVL measurements. *L. valdesianus* from El Yeso Reservoir were not included in these measurements.

Character	<i>L. ubaghsi</i> (n=11)	<i>L. valdesianus</i> (n=6)	<i>L. frassinettii</i> (n=7)	<i>L. ramonensis</i> (n=6)	<i>L. leopardinus</i> (n=12)
Mean SVL	83.3±7.8	87±5	79.8±7.9	90.2±3.3	87.9±7.3
Maximum SVL	89.6	95	91.1	94.9	98.2
SAMB	77.7±4.6 (72–87)	76.6±4 (72–81)	87.7±4.1 (85–93)	81±3.7 (77–85)	82±3.9 (76–89)
Dorsal scales	70.9±6.3 (62–83)	74.2±4 (68–78)	81±4.4 (76–89)	79.7±4.2 (75–84)	76.2±5.2 (68–84)
Ventral scales	121.1±8.1 (111–137)	108.2±6.9 (100–115)	124.1±10.2 (111–140)	120.7±9.7 (109–136)	116.1±5.6 (108–129)
4TL	31.5±2.2 (28–35)	26.5±1.1 (25–28)	29±2.2 (26–32)	28.5±2.4 (25–31)	28.6±2.2 (25–31)
Precloacal pores in males	4	3–4	3	5	0–4
Head color	Ochre, mottled	Light brown or olive brown to black, sometimes mottled	Brown to olive brown, mottled	Light brown to ochre, mottled	Beige, with big black spots
Dorsal color	Ochre	Grey to olive brown	Olive brown	Light brown to ochre	Beige
Dorsal pattern	Black and white one scale sized dots, which may form transversal lines along the dorsum. Sometimes dark occipital stripe or a discontinuous vertebral line	Light transversal stripes with black on anterior edge	Light transversal stripes with black on anterior edge	Black dots uniformly distributed on the dorsum that may form transversal stripes. Sometimes there is a discontinuous vertebral line	Thick, 2–3 scales wide black continuous or discontinuous vertebral line. At the sides of the dorsum, big black hollow leopard-like spot arranged in transversal lines
Flanks	Dark band	Dark band	Posthumeral dark spot or band	Slightly dark band	Slightly dark band

**Description of the holotype.** Male, with an SVL of 88.2 mm. Axilla-groin distance 39.3 mm. Tail complete, not regenerated, length, 113.8 mm. Left forelimb length, 32.1 mm. Left hind limb length, 51.3 mm. Head length, 21 mm. Head width, 17.1 mm. Head height, 11.3 mm. 4 small precloacal pores.

Rostral scale rectangular, 2.7 times wider than high, in contact with six scales, and not with the nasals. Nasal scales hexagonal, anteriorly elongated, with the nostril occupying the posterior half of the scale's surface. Two postrostrals. Four internasal scales, the medial ones larger, and the side ones transversally divided. Two frontal azygous scales on the snout, the anterior one about double the size of the posterior surrounded by six frontonasals. Three prefrontals, half the size of the frontal. Undivided frontal scale. Two small postfrontals. Interparietal scale

pentagonal, with a white “pineal eye” in the middle, in contact with six scales. Parietals hexagonal, about the same size as interparietal. Occipital scales polymorphic, juxtaposed and smooth. Supratemporals larger than occipitals, also polymorphic, juxtaposed and smooth. Four enlarged supraoculars. Eleven/twelve (left/right) scales forming the supraorbital semicircles. Scale organs abundant in all the head, however a much higher concentration on the anterior tip. Loreal length (from anterior tip of the eye to rostral), 6.8 mm. Eye length, 5.6 mm. Five/six loreal scales. Five elongated and overlapping superciliaries. Large subocular, which spans the whole length of the eye. Twelve/thirteen upper and twelve/thirteen lower squared palpebral scales, each one with a scale organ on it. One row of lorilabial scales. Seven/six supralabial scales, on both sides the fifth one posteriorly curved upwards, a diagnostic trait of the *Liolaemus (sensu stricto)* subgenus. Auditory meatus 4.3 mm high and 2.7 mm wide. Auricular scale not enlarged. Temporal scales polygonal, juxtaposed and smooth. Mental scale wider than rostral, in contact with four scales. Four pairs of postmental scales, the first pair in contact with each other, the second one separated by two scales. Four/five enlarged infralabial scales. Gular scales rounded, smooth and imbricate. Two strong transversal neck folds, on top of them a longitudinal fold. Neck scales granular, small, smooth and juxtaposed, with much smaller granular scales in the interstitial space.



**FIGURE 5.** *L. valdesianus* from El Morado National Monument, Cajón del Maipo, Metropolitan Region. Photo: Damien Esquerré.

Dorsal scales rhomboidal, subimbricated and keeled, without mucrons, around the same size as the ventral scales. There are some visible small granular scales in the interstitial space. Lateral scales become more rounded and with less developed keels, also more granular interstitial scales become visible. There is a longitudinal posthumeral fold on the flanks. Scales are granular at limb insertions. Ventral scales are rounded, smooth and imbricate. Scales around midbody: 80. Dorsal scales: 68. Ventral scales: 129. Dorsal scales of the arm vary from rhomboidal to rounded, and are imbricated and slightly keeled. Dorsal scales of the forearm are rounded, imbricate and smooth, with slight keels towards the posterior surface. Dorsal scales of the hand are rounded, imbricate and smooth. Ventral scales of the arm are granular and juxtaposed, with much smaller granular scales on the interstitial space. Ventral scales of the forearm are rounded, imbricate and slightly keeled. Palmar scales are rhomboidal with rounded tips, imbricate and slightly keeled, with jagged edges. The lamellae on the fingers are rectangular and



imbricate, with three keels each. There are 24 lamellae on the third finger and 22 on the fourth finger. Dorsal femoral scales are rhomboidal with rounded tips, imbricate and slightly keeled. Dorsal tibial scales are similar to dorsal femoral ones but have stronger keels. Dorsal scales of the foot are rounded, imbricate and slightly keeled. There is a patch of granular scales on the ankle. Ventral femoral and tibial scales are rounded, imbricate and smooth. Plantar scales vary from rounded to rhomboidal with rounded tips, and are imbricate and keeled, with jagged edges. Lamellae of the toes are rectangular and have three keels each. There are 30 lamellae on the fourth toe. Dorsal caudal scales are rhomboidal, imbricate and slightly keeled. Ventral caudal scales are rhomboidal, imbricate and smooth.



**FIGURE 6.** *L. frassinettii* from Altos de Cantillana, between Metropolitan and Valparaiso Regions. Photo: Bernardo Segura.

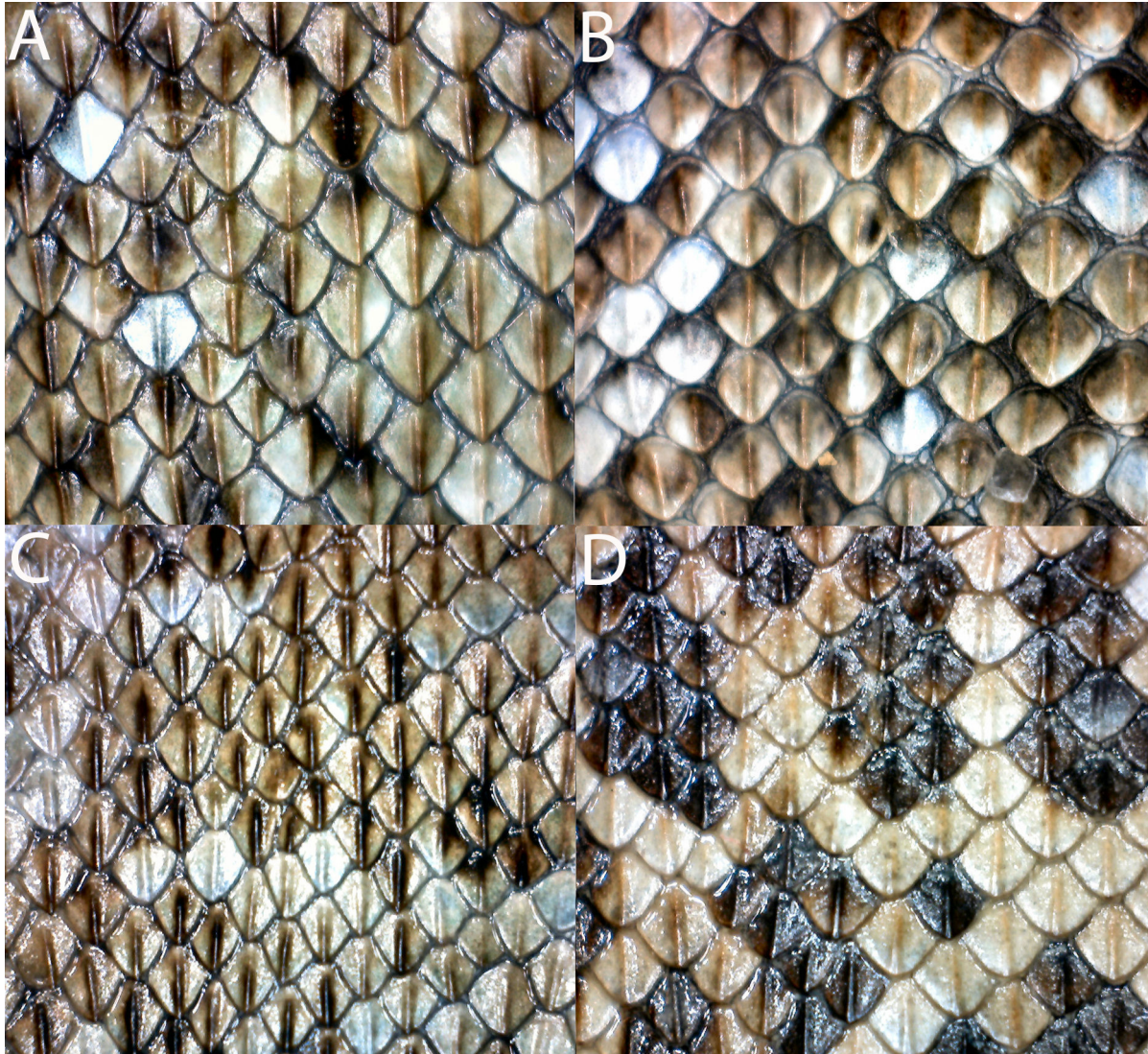
**Color and pattern in preservative.** Background dorsal coloration is ochre with a very slight greenish hue due to loss of pigmentation. Dorsal head color is a bit darker and more brownish than the body. The dorsum has small dots the size of one scale scattered on it. More concentrated on the 10 to 12 mid-dorsal scales, forming some sort of occipital stripe. The white scattered dots observed on live specimens are not seen in preserved ones like the holotype. The flanks are dark brown. The tail is mottled on its dorsal surface. There are few black dots on the dorsal surface of the limbs. The ventral region is gray, with a slightly darker gular region.

**Color in life.** Based on photographs of live individuals. The general coloration of the dorsal surface of the body, head, tail and limbs is brown, with dark brown flanks. Black dots are scattered along the dorsum at regular intervals. The dots may form a wide occipital stripe or a vertebral line as described above. Tiny white dots, made of a single scale are also scattered and may form transversal lines in some specimens. The ventral region is bright lemon yellow or orange. The gular surface is white with dark spots on it (see Fig. 9).

Variation in the paratypes.

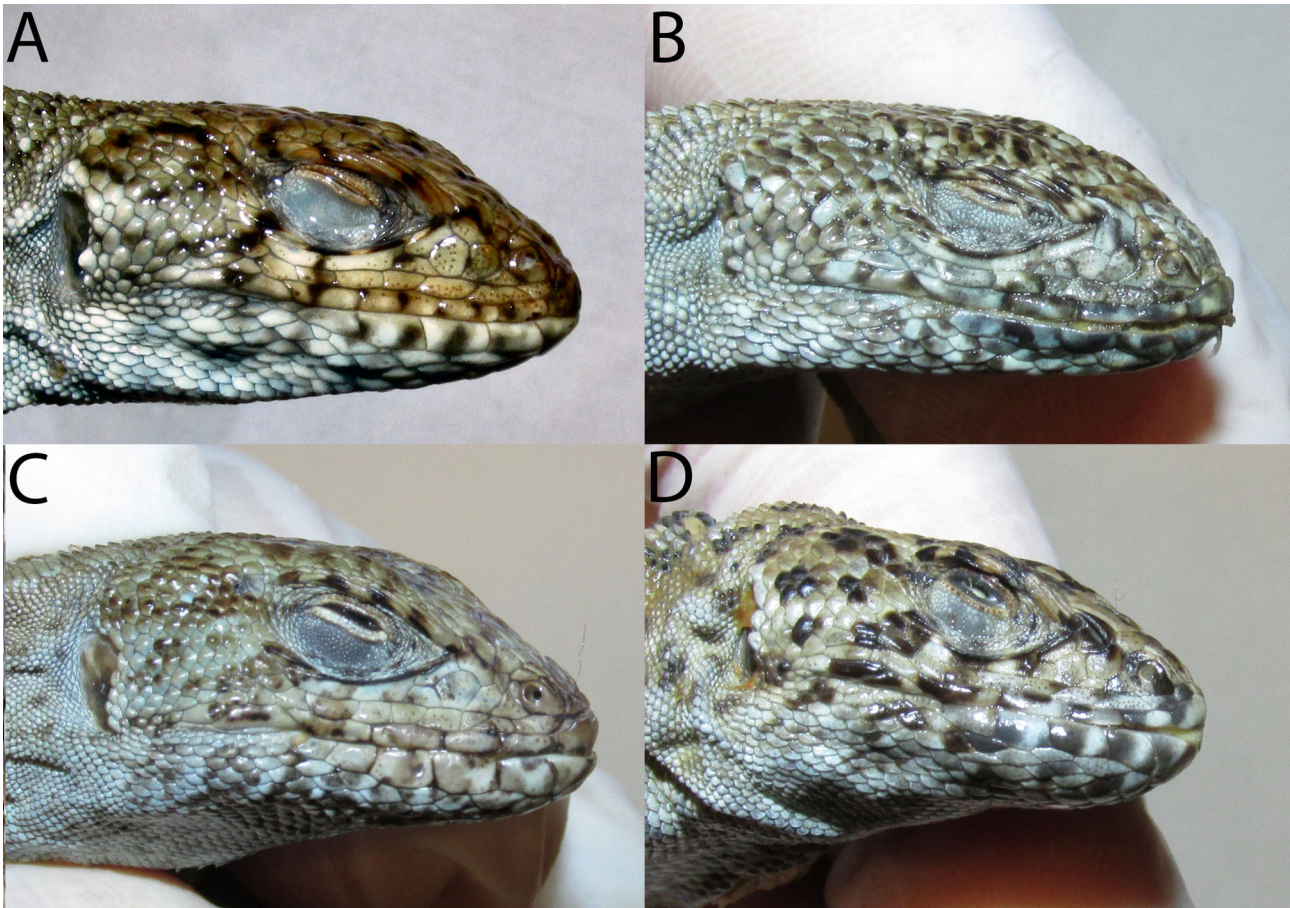
The body measurements for the four males (including the holotype) have the following mean and extreme values (in mm): SVL, 85 (77.5–89.6); axilla-groin distance, 37.4 (35.2–39.3); left forelimb length, 31.7 (30.5–33.1); left hind limb length, 49.8 (46.5–51.8); head length, 19.7 (17.8–21); head width, 15.7 (14–17.1); head height, 10.1 (8.9–11.3); loreal length, 6 (5.1–6.8); eye length, 5.3 (4.5–6.2); auditory meatus height, 4.5 (3.8–5.1); auditory meatus width, 2.7 (2.6–3.1). Tail length was not included because all the male paratypes had the tail cut

off or regenerated. The same measurements for the six adult female paratypes are as follows (juvenile female SSUC Re-491 is excluded from these measurements): SVL, 85.6 (81.2–88.6); axilla-groin distance, 41.2 (37–45.6); tail length, 131.9 (119.4–141.4); left forelimb length, 29.5 (27.2–31.7); left hind limb length, 46.8 (43.1–51.2); head length, 19.3 (18.5–21); head width, 14.2 (13.6–15.1); head height, 9.5 (9.1–9.4) loreal length, 5.9 (5.3–6.9); eye length, 4.8 (4.3–6); auditory meatus height, 4.2 (3.7–5.5); auditory meatus width, 2.3 (1.6–2.8). Based on this measurements and the limited sample size it is difficult to determine whether this species has sexual dimorphism or not. There are no clear differences in body size, however males do have proportionally larger heads than females (head length,  $F=8.03$ ,  $p=0.025$ ; head width,  $F=9.6$ ,  $p=0.017$ ; head height,  $F=6.6$ ,  $p=0.037$ ).



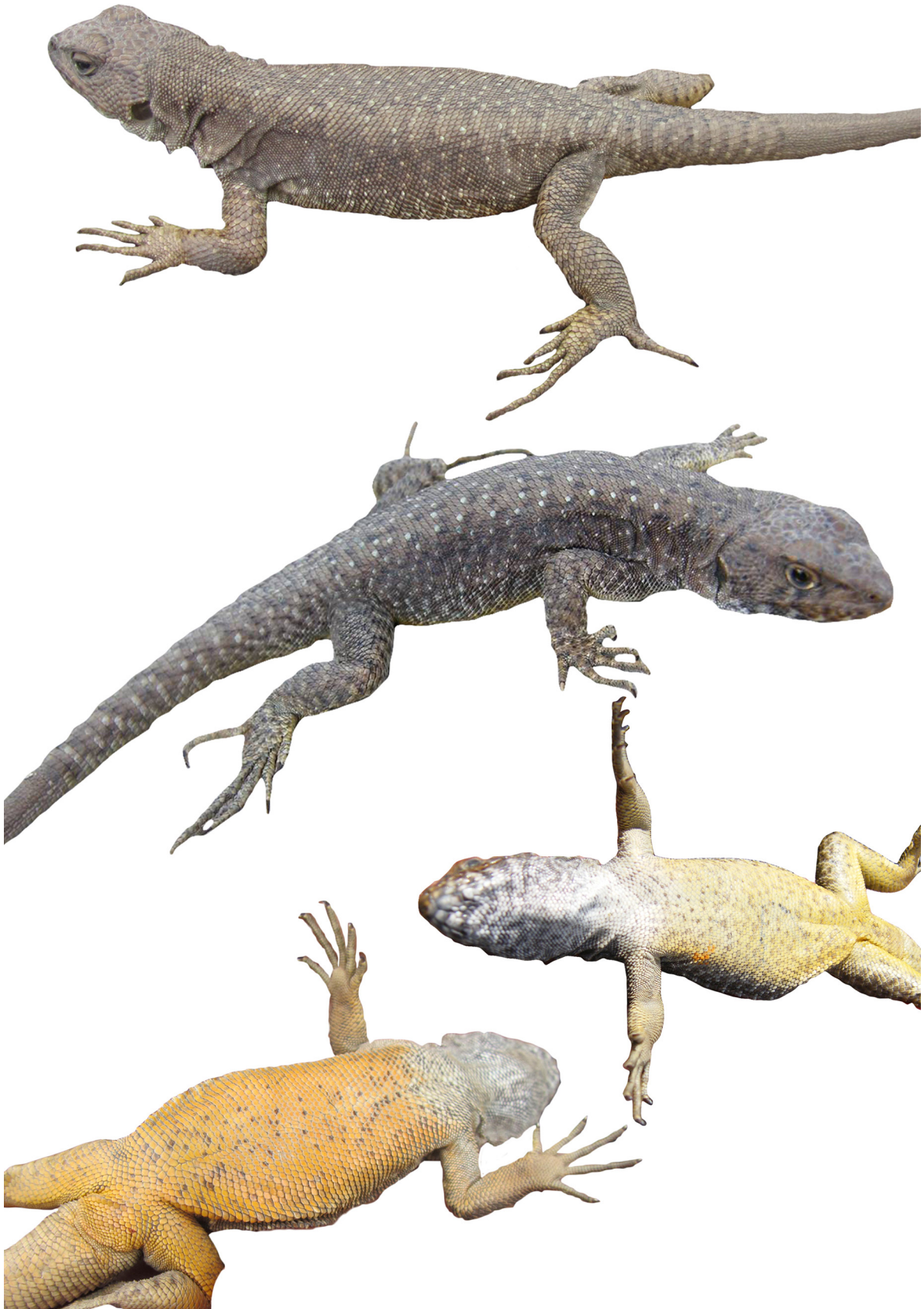
**FIGURE 7.** Comparison of the dorsal scales on some species of the *leopardinus* clade. All figures are 8 mm wide. A: *Liolaemus ubaghsi* sp. nov. (SSUC Re-492). B: *L. valdesianus* (SSUC Re-363). C: *L. frassinettii* (SSUC Re- 80). D: *L. leopardinus* (SSUC Re-364). What this figure illustrates is that the dorsal scales of *L. valdesianus* tend to be much more juxtapsed and with more interstitial space filled with granular scales between them than in the rest of the *leopardinus* clade.

The four males have 73–80 scales around midbody, 64–73 dorsal scales and 111–129 ventral scales. All males have four preloacal pores except for one that has no visible pores, however this one is not an adult and the pores might not have developed yet (MNHCL-3814). The three male paratypes have the following variation in squamation in relation to the holotype: rostral scale 3.8–4.6 mm wide and 1.8–2 mm high. Nasals barely touching the rostral with the anterior tip in one specimen. Anterior frontal azygous scale of the snout smaller than posterior in one specimen, and only one frontal azygous scale in two specimens. Four frontonasals in one specimen. Prefrontals with similar size as the frontal in two specimens. Frontal divided transversally in one specimen. Three

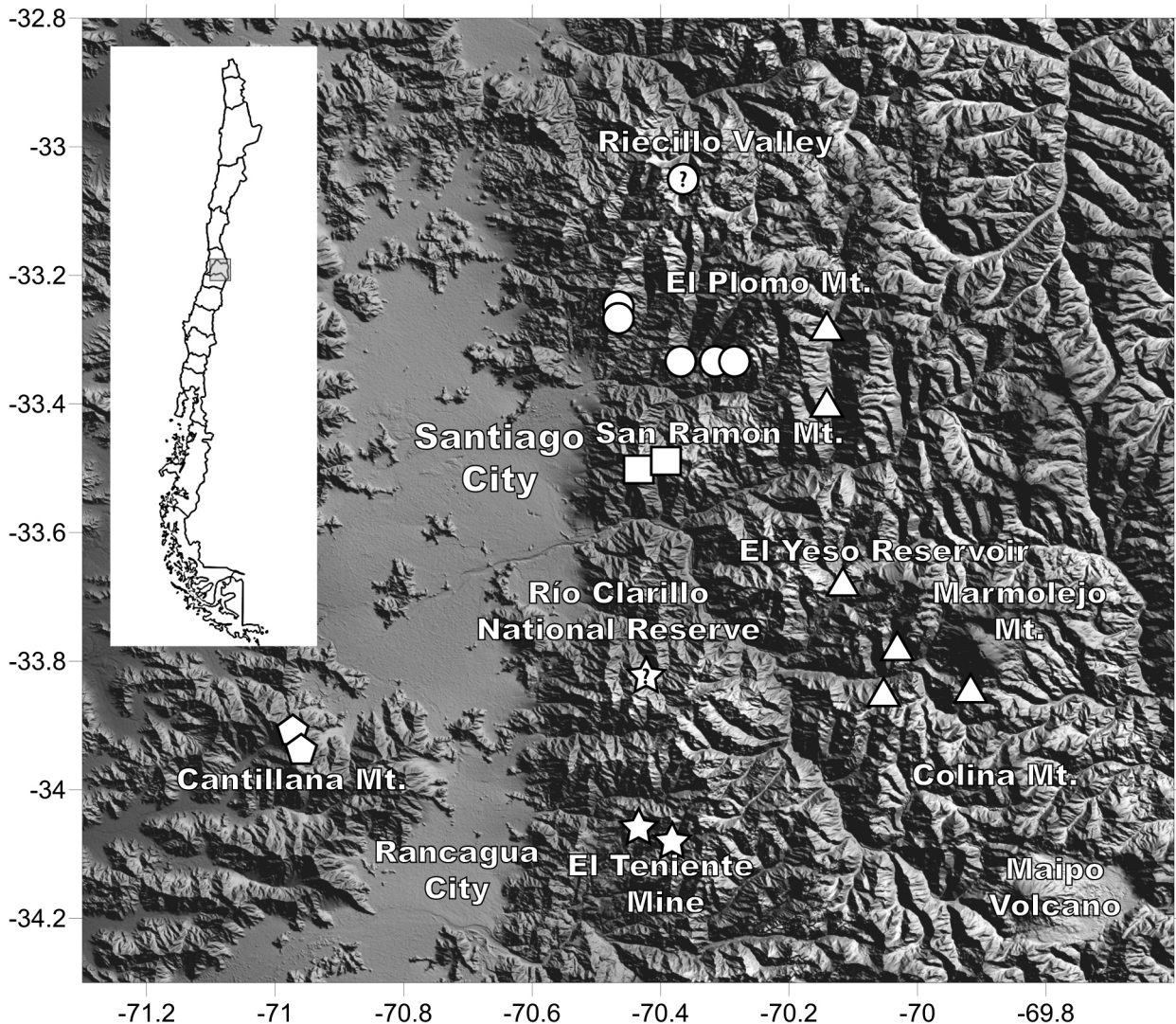


**FIGURE 8.** Comparison of supralabial and infralabial scales on some species of the *leopardinus* clade. A: *Liolaemus ubaghsi* **sp. nov.** (SSUC Re-492). B: *L. valdesianus* (right, SSUC Re-363). C: *L. frassinettii* (SSUC Re-80). D: *L. leopardinus* (SSUC Re-364). What can be seen here is that infralabial scales in *L. ubaghsi* **sp. nov.** and *L. frassinettii* are notoriously enlarged in comparison with *L. valdesianus*. Infralabials can be enlarged in *L. leopardinus* too, as in the specimen shown here.

postfrontals in one and four in another specimen. Interparietal in contact with five scales in one and with seven scales in another specimen. Parietals with irregular shapes instead of hexagonal in all three male paratypes. Four to six supraoculars. Five to six superciliaries. Twelve to fifteen upper and thirteen to fourteen lower palpebrals. Mental as wide as rostral in one specimen. Five pairs of postmentals in two specimens. Smooth scales on the flanks in two specimens. Rhomboidal with rounded tips scales on the dorsal surface of the forearm in one specimen, and slightly keeled in two specimens. Smooth edge on the palmar scales in one specimen. Lamellae on the third finger: 21 to 23. Lamellae on the fourth finger: 22 to 25. A weak mucron on the dorsal femoral scales in one specimen. Rounded dorsal tibial scales in one specimen. Rhomboidal with rounded tips dorsal foot scales in two specimens and smooth in another specimen. Lamellae on the fourth toe: 28 to 34. The seven female paratypes have 72–87 scales around midbody, 62–83 dorsal scales and 114–137 ventral scales. All females lack precloacal pores. The female paratypes have the following variation in squamation in relation to the holotype: rostral scale 3.9–4.3 mm wide and 1.5–1.8 mm high. Nasals barely touching the rostral in three specimens. One frontal azygous scale on the snout in two specimens. Four frontonasals in two specimens. Prefrontals similar size as frontal in four specimens. Frontal divided longitudinally in one and transversally in two other specimens. Three postfrontals in two specimens. Interparietal in contact with five scales in one specimen, with seven scales in three specimens and with eight scales in another specimen. Interparietal smaller than parietals in one specimen. Parietals irregularly shaped in five specimens. Four to seven supraoculars. Four to seven loreal scales. Five to eight superciliaries. Five to eight supralabials. Nine to thirteen upper and ten to eleven lower palpebrals. Mental as wide as rostral in two specimens. Five pairs of postmentals in six specimens. Four to six infralabials. Smooth scales on the flanks in five specimens. Dorsal scales of the arm rounded in one specimen and smooth in three specimens. Ventral scales of the forearm



**FIGURE 9.** Dorsal and ventral views of live adult specimens of *Liolaemus ubaghsi*. Because ventral view specimens were held in hands while being photographed, the complete body is not visible in them. Photos: Alejandra Alzamora.



**FIGURE 10.** Map of the Andes Cordillera surrounding Santiago City. Coordinates are in decimal system. Symbols depict known localities from museum specimens, literature and photographs (in the case for *L. cf. leopardinus*). Stars, *L. ubaghsi*; pentagons, *L. frassinettii*; triangles, *L. valdesianus*; squares, *L. ramonensis*; circles, *L. leopardinus*. Symbols with question marks represent localities for uncertain taxonomic identity, but probably belonging to the species of that symbol (e.g. star with question mark represents *L. cf. ubaghsi*). Names of localities are for reference only.

smooth in four specimens. Palmar scales with smooth edges in one specimen. 20 to 27 lamellae on the third finger. 22 to 27 lamellae on the fourth finger. Dorsal femoral scales rounded in four specimens and smooth in two specimens. Dorsal tibial scales rounded in four specimens. Dorsal scales of the foot rhomboidal with rounded tips in one specimen and smooth in another specimen. 30 to 35 lamellae on the fourth toe.

All preserved specimens have the basic ochre background coloration with black dots scattered along the dorsum and dark flanks. Some specimens, however, have a wide dark occipital stripe along the vertebral region, and others have a thinner black vertebral line instead. The dorsal surface of the head is mottled with black dots in some specimens. There is a high variation in ventral melanism. Some individuals, similar to the holotype, exhibit a low level of melanism, with a gray ventral region, while others exhibit varying degrees of mottled bellies, from separated small black dots scattered all over the ventral surface of the body, head, limbs and tail, to a more intense mottled pattern that appears as white reticulation between the dots. The gular region is always darker than the belly. In some specimens the gular region is only light gray, while in others it is uniformly black.

**Distribution.** Most probably endemic to the Andes East of Rancagua City in Chile (see Fig. 10). From museum collection data we know it is found between the type locality (34°03'32.8"S 70°26'05.3"W, 2210 masl) at the Chapa Verde Ski Center and the Sapos Reservoir (S 34 04' W 70 22' 1870 m 34°04'S 70°22'W, 1870 masl). All

these localities and probably the distribution of *L. ubaghsi* are part of El Teniente copper Mine, property of Codelco (Corporación Nacional del Cobre de Chile), a Chilean state mining company. For this reason public access and therefore the study of this species is very difficult. Another population from the mountains of Río Clarillo National Reserve might also belong to this species (see Discussion).

**Natural history.** Species with viviparous reproduction, determined by examining two pregnant female specimens, not included as paratypes (MNHNCL-605 and 608). A group of nine *Liolaemus ubaghsi* **sp. nov.** was found in brumation underneath a rock in winter along with other five *L. cf. bellii* (Gray 1845). *Liolaemus ubaghsi* **sp. nov.** is found in sympatry with this species and with *L. nigroviridis* (Müller & Hellmich 1932). It lives in a high Andean environment, characterized by short shrubs and a rocky landscape (Fig. 11).

**TABLE 2.** Measurements (in mm) and scale counts of the *L. ubaghsi* **sp. nov.** type series. Captions are: F, female; M, male; SVL, snout vent length; AGD, axilla-groin distance; TL, tail length; FLL, forelimb length; HLL, hindlimb length; HL, head length; HW, head width; HH, head height; SAMB, scales around mid-body; DS, dorsal scales; VS, ventral scales; 4TL, fourth toe lamellae; reg: regenerated.

MNHN/SSUCC	Sex	SVL	AGD	TL	FLL	HLL	HL	HW	HH	SAMB	DS	VS	4TL
3808	F	86.3	41.2	141.4	27.5	46.8	18.7	13.6	9.4	87	74	126	35
3809	F	87.9	40.5	cut	31.7	51.2	19.3	14.4	9.2	81	83	137	30
3810	F	82.4	39.8	reg.	27.2	43.1	18.5	14.1	9.1	75	77	128	32
3811	F	87.0	45.6	134.7	31.3	47.4	18.8	14.5	9.3	78	64	114	31
3812	M	84.5	38.2	cut	33.1	51.8	19.3	14.8	9.8	76	70	111	28
3813	M	88.2	39.3	113.8	31.1	51.3	21.0	17.1	11.3	80	68	129	30
3814	M	77.5	35.2	reg.	32.1	46.5	17.8	14.0	8.9	73	64	117	34
3815	F	88.6	42.9	119.4	28.4	44.7	19.4	13.6	9.1	82	71	123	34
3816	M	89.6	36.8	cut	30.5	49.6	20.6	16.8	10.3	78	73	116	32
491	F	62.7	27.1	111.6	23.9	41.7	18.8	13.2	9.3	72	74	115	30
492	F	81.2	37	reg.	31	47.8	19.6	15.1	10.2	73	62	116	30
Mean		83.3	38.5	124.2	29.8	47.4	19.3	14.7	9.6	77.7	70.9	121.1	31.5
SD		7.8	4.8	13.2	2.7	3.4	1.3	1.3	0.7	4.6	6.3	8.1	2.2
Range		62.7–89.6	27.1–45.6	111.6–141.4	23.9–31	41.7–51.8	17.8–21	13.2–16.8	8.9–11.3	72–87	62–83	111–137	28–35

**TABLE 3.** Estimates of evolutionary divergence for the mtDNA loci *cytb* between species of the *leopardinus* clade. Number of base differences per site are shown.

Species	<i>L. frassinettii</i>	<i>L. ubaghsi</i>	<i>L. valdesianus</i>	<i>L. ramonensis</i>
<i>L. ubaghsi</i>	0.045	-		
<i>L. valdesianus</i>	0.042	0.011	-	
<i>L. ramonensis</i>	0.04	0.08	0.003	-
<i>L. leopardinus</i>	0.04	0.012	0.007	0.004

## Discussion

Organisms adapted to high elevation and that are somewhat unable to live at lower elevations, like the leopard lizards, can be isolated, and thus undergo speciation through “sky islands”, where low elevation valleys serve as geographical barriers (Knowles 2000; Masta 2000; Shepard & Burbrink 2008; Robin *et al.* 2010). Interglacial periods like the present one restrict high elevation species such as the leopard lizards to mountains. Such divergence among mountain-top populations is also observed in another liolaemid taxon, *L. nigroviridis*, with apparently deep divergence (Cianferoni *et al.* 2013), which is mostly co-distributed with the species of the

*leopardinus* group, and may share a similar evolutionary history. On the other hand, *L. nigroviridis* can also be found at lower elevations than the leopard lizards, therefore secondary contact is more likely to have happened in *L. nigroviridis*, which would explain why this species exhibits much less morphological divergence than the species of the *leopardinus* clade. The leopard lizards probably descend from a common ancestor belonging to the *elongatus* clade, a group mainly distributed on the eastern slope of the Andes. It would seem logical that the lineage underwent dispersal to the low elevation valleys of Central Chile during the glacial periods of the Pleistocene (Rabassa & Clapperton 1990), and that different populations retreated to different high elevation locations during interglacial periods where they could diverge without gene flow and therefore undergo speciation (Hellmich 1934; Fuentes & Jaksic 1979).



**FIGURE 11.** Habitat of *L. ubaghsi*. Photo: Alejandra Alzamora.

Pincheira-Donoso and Núñez (2005) mentioned that the population now described as *L. ubaghsi* displayed traits belonging to both *L. valdesianus* and *L. elongatus*. While this species is certainly not *L. elongatus*, mainly because its southern distribution is more than 400 km north of the northern range limits of *L. elongatus*, with its northern boundary at Neuquén and Agrío Rivers in Argentina (Morando *et al.* 2003), it most certainly shares a close common ancestor with *L. valdesianus*. The phylogenetic analysis performed by Esquerre *et al.* (in prep.), which will be published elsewhere, recovers the *leopardinus* group as monophyletic, including *L. ubaghsi*, and this clade is in turn the sister group of the *elongatus* clade. The analysis however does not resolve the relationships within the clade except by locating *L. frassinettii* as the sister taxon of the rest of the group, which makes sense seen from a biogeographic scope. *Liolaemus frassinettii* represents a lineage that colonized the Cordillera de la Costa, a mountain range separate from the Andes by a low elevation valley, where no species of the *elongatus* (thus, also the *leopardinus*) clade live. It would appear, by looking at the morphology, pattern and distribution of the remaining species of the *leopardinus* clade, that there is a morphological gradient from *L. ubaghsi* to *L. leopardinus*. Evidence from their morphology and DNA suggest they are recently diverging lineages, in

comparison to other *Liolaemus* clades. The genetic distances for the mitochondrial marker *cytb* between the Andean *leopardinus* clade (all except for *L. frassinettii*) are quite shallow (Table 3). Despite this, consistent morphological and color pattern differences in addition to great geographic barriers strongly suggest their evolutionary independence as lineages. First, even though the Andean habitat of *L. ubaghsi* is less than 50 km away from the Cordillera de la Costa habitat of *L. frassinettii*, the 15 km-wide valley between the base of both mountain ranges is at an elevation of merely 500 masl. On the other hand there is a mid-elevation connectivity between the two Cordilleras formed by Cuesta de Chada and Challay Hill that goes from 400 and almost 1200 masl. Nevertheless there is no record of any of the leopard lizards living below 1800 masl. Second, *L. valdesianus* or any other leopard lizard have not been found on the eastern side of the mountains west of the Maipo River Canyon, hence the 3500–4000 masl mountain tops and the 1500 masl Maipo River Canyon stand between *L. ubaghsi* and *L. valdesianus*. For these reasons, we think that gene flow has not occurred in recent times, and that these taxa are independently evolving populations, and the phenotypic differences serve as an operational species delimitation criterion (De Queiroz 2007). We think this small species group is an excellent model for studying early speciation and that multiple loci molecular studies will shed more light on their phylogenetic and phylogeographic history.

There still remain a number of problematic populations of the clade that need to be studied, however, these issues are beyond the scope of the current article and should be part of further investigations. A population identified as *L. leopardinus* was found in the high parts of Río Clarillo National Reserve, about 20 km north of the terra typica of *L. ubaghsi* (Díaz & Simonetti 1996; Díaz *et al.* 2002). No specimens of this locality are found in museum collections, and by examining photographs of live specimens it could be determined that this population does not belong to *L. leopardinus* (Hamasaki & Troncoso-Palacios 2011). The true identity of this population remains unresolved until some specimens can be examined, nevertheless judging only by the locality and a poor quality photograph taken by Mr. I. Díaz, it should be expected to be a population of *L. ubaghsi*, and we suggest provisionally naming this population *L. cf. ubaghsi*. There is another population in El Yeso Reservoir (33°41'S 70°07'W) standing between the distributions of *L. valdesianus* and *L. ramonensis*. Núñez (1992), assigned this population to *L. l. leopardinus*, however Núñez & Jaksic (1992) mentioned that this population may represent genetic connectivity between *L. valdesianus* and *L. ramonensis*, additionally noting that the specimens collected at that locality were more similar to the latter. In contrast, Hamasaki & Troncoso-Palacios (2011) found the population not distinct from *L. valdesianus*, proposing that it should be referred as *L. cf. valdesianus* for the moment. We examined specimens from this locality and we think they should be considered as *L. valdesianus*. There is also a population phenotypically similar to *L. ubaghsi* from which there are two specimens in the MNHNCL and photographs (provided by D. Demangel) from Alto Huemul, in the Andes south-east of San Fernando City, and near 100 km south of the type locality of *L. ubaghsi*. With that material it was not possible to determine the exact identity of the population, and it also remains an important aspect of our future research. Based on specimens observed and photographed in the wild, we would also like to extend the northern distributional limit of *L. valdesianus* to the Olivares River (33°24'S 70°08'W and 33°17'S 70°08'W), almost 40 km north of El Yeso Reservoir. Finally, *L. leopardinus* has been mentioned recently for two locations without listing specimens examined and therefore need confirmation: Riecillo Valley, Valparaiso Region (Núñez *et al.* 2010) and Cerro Carpa, Metropolitan Region (Hamasaki & Troncoso-Palacios 2011). We examined photographs from Riecillo Valley, Valparaiso Region (33°03'S 70°22'W) provided by C. Celedón, and have identified it as *L. leopardinus*. Close examination of specimens of that population is necessary, but we provisionally propose extending the northern distribution limit of *L. leopardinus* to that locality.

As an additional remark, close inspection of the *L. frassinettii* type material, revealed that one of the two paratypes was in fact a juvenile female of *L. nigroviridis* (MNHNCL-1598), but poor preservation condition of the specimen made it difficult to identify correctly. This species was described based only in three females (two by correction), even though its species status is supported by genetic evidence (Esquerré *et al.* in prep), geographical isolation and new examined specimens, descriptions of the male and more data about species variation are needed.

To conclude, we think that the biogeographic and phenotypic characteristics of *L. ubaghsi* are enough to determine that it is a divergent and independent evolutionary lineage of the *leopardinus* clade. Nevertheless there seem to be far more populations of the clade in the central Chilean Andes than the ones commonly known and need to be included in our further studies of the group. It also appears to be an excellent model to study several evolutionary processes since speciation is likely to be happening at different levels between the different lineages.



## Acknowledgements

We would like to thank Patricio Zabala (Colección de Flora y Fauna, Profesor Patricio Sánchez Reyes of the Pontificia Universidad Católica de Chile, SSUC Re) and Madeleine Lamborot (Laboratorio de Citogenética, Facultad de Ciencias, Universidad de Chile, LCUC) for allowing us access and facilitating assistance at the specimens under their care. Special thanks to Fernando Torres-Pérez and Romina Yáñez (Pontificia Universidad Católica de Valparaíso) for obtaining the molecular data used on this paper. We would also like to thank Carlos Celedón for providing information on the *L. leopardinus* populations of Riecillo Valley. We thank Alejandra Alzamora and Gabriel Lobos for handing photographs and additional information on *L. ubaghsi*. We thank Bernardo Segura for providing photographs of *L. frassinettii*. We would also like to thank Diego Demangel and Ivan Díaz for showing us pictures of undescribed populations described here. We thank Renee Catullo, Mitzy Pepper and Dan Rosauer (Australian National University) for kindly helping with the elaboration of the distributional map and Lisa Schwanz (University of New South Wales) for kindly checking the manuscript for grammar mistakes. Damien Esquerré is supported by a Becas Chile-CONICYT scholarship. Jaime Troncoso-Palacios thanks Mario Penna for his support. Carlos Garín is supported by a CONICYT-Chile doctoral fellowship.

## References

- Abdala, C.S., Quinteros, A.S., Scrocchi, G.S. & Stazzonelli, J.C. (2010) Three new species of the *Liolaemus elongatus* group (Iguania: Liolaemidae) from Argentina. *Cuadernos de Herpetología*, 24, 93–109.
- 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.  
<http://dx.doi.org/10.1655/03-04>
- Avila, L.J., Morando, M., Perez, D.N. & Sites, J.W. (2010) A new species of the *Liolaemus elongatus* clade (Reptilia: Iguania: Liolaemini) from Cordillera del Viento, northwestern Patagonia, Neuquén, Argentina. *Zootaxa*, 2667, 28–42.
- Avila, L.J., Perez, C.N.F., Medina, C.D., Sites, J.W. & Morando, M. (2012) A new species of lizard of the *Liolaemus elongatus* clade (Reptilia: Iguania: Liolaemini) from Curi Leuvu River Valley, northern Patagonia, Neuquén, Argentina. *Zootaxa*, 3325, 37–52.
- Cei, J.M. (1974) Revision of the Patagonian iguanids of the *Liolaemus elongatus* complex. *Journal of Herpetology*, 8, 219–229.  
<http://dx.doi.org/10.2307/1563167>
- Cei, J.M. (1975) Herpetología patagónica. X. El conjunto evolutivo de *Liolaemus elongatus*: análisis serológico. *Physis*, 34, 203–208.
- 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 di Torino, Monografie 4, 528 pp.
- Cianferoni, F., Yáñez, R.P., Palma, R.E., Garín, C.F. & Torres-Pérez, F. (2013) Deep Divergences within *Liolaemus nigroviridis* (Squamata, Liolaemidae) Lineages Associated with Sky Islands in Central Chile. *Zootaxa*, 3619 (1), 59–69.  
<http://dx.doi.org/10.11646/zootaxa.3619.1.3>
- De Queiroz, K. (2007) Species concepts and species delimitation. *Systematic Biology*, 56, 879–886.  
<http://dx.doi.org/10.1080/10635150701701083>
- Díaz, I.A., Sarmiento, C., Ulloa, L., Moreira, R., Navia, R., Veliz, E. & Peña, C. (2002) Vertebrados terrestres de la Reserva Nacional Río Clarillo, Chile central: representatividad y conservación. *Revista Chilena de Historia Natural*, 75, 433–448.  
<http://dx.doi.org/10.4067/s0716-078x2002000200013>
- Díaz, I. & Simonetti, J.A. (1996) Vertebrados en áreas silvestres protegidas: reptiles de la Reserva Nacional Río Clarillo, Chile Central. *Vida Silvestre Neotropical*, 5, 140–142.
- Donoso-Barros, R. (1966) *Reptiles de Chile*. Ediciones Universidad de Chile, Santiago, 458 pp.
- Espejo, P. (1989) *Estudio de la variabilidad morfológica, cromosómica y bioquímica de dos especies de lagartos del género Liolaemus (Squamata-Iguanidae)*. Bachelor degree thesis, Facultad de Ciencias de la Universidad de Santiago, 103 pp.
- Espejo, P., Navarro, J. & Veloso, A. (1987) Estudio de tres subespecies de *Liolaemus leopardinus* (Squamata: Iguanidae) mediante caracteres cromosómicos y electrofóricos. *I Congreso Argentino y Congreso Sudamericano de Herpetología. Resumen. Tucumán, Argentina.*, 20–21.
- 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.  
[http://dx.doi.org/10.1655/0018-0831\(2003\)059\[0089:tnsoll\]2.0.co;2](http://dx.doi.org/10.1655/0018-0831(2003)059[0089:tnsoll]2.0.co;2)
- 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 of the United States of America*, 101, 16819–16824.

- <http://dx.doi.org/10.1073/pnas.0401226101>
- Esquerré, D., Núñez, H. & Scolaro, J.A. (2013) *Liolaemus carlosgarini* and *Liolaemus riodamas* (Squamata: Liolaemidae), two new species of lizards lacking preloacal pores, from Andean areas of Central Chile. *Zootaxa*, 3619 (4), 428–452.  
<http://dx.doi.org/10.11646/zootaxa.3619.4.2>
- Fuentes, E.R. & Jaksic, F.M. (1979) Lizards and rodents: an explanation for their relative species diversity in Chile. *Archivos de Biología y Medicina Experimentales (Chile)*, 12, 179–190.
- Gray, J.E. (1845) *Catalogue of the specimens of lizards in collection of the British Museum*. Trustees of the British Museum, London, 289 pp.
- Hamasaki, K. & Troncoso-Palacios, J. (2011) Nueva localidad para el Lagarto leopardo (*Liolaemus leopardinus*) y comentarios sobre su distribución. *La Chiricoca*, 12, 13–17.
- Hellmich, W. (1934) *Die Eidechsen Chile, Insbesondere die Gattung Liolaemus. Vol. 24*. Abhandlungen (Bayerische Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse), München, 140 pp.
- Hellmich, W. (1950) Die Eidechsen der Ausbeute Schröder (Gattung *Liolaemus*, Iguan.) Beiträge zur Kenntnis der Herpetofauna Chiles XIII). *Veröffentlichungen Zoologische Staatsammlung (München)*, 1, 129–194.
- Knowles, L.L. (2000) Tests of pleistocene speciation in montane grasshoppers (genus *Melanoplus*) from the sky islands of Western North America. *Evolution*, 54, 1337–1348.  
[http://dx.doi.org/10.1554/0014-3820\(2000\)054\[1337:topsim\]2.0.co;2](http://dx.doi.org/10.1554/0014-3820(2000)054[1337:topsim]2.0.co;2)
- Larkin, M.A., Blackshields, G., Brown, N.P., Chenna, R., McGettigan, P.A., McWilliam, H., Valentin, F., Wallace, I.M., Wilm, A., Lopez, R., Thompson, J.D., Gibson, T.J. & Higgins, D.G. (2007) Clustal W and Clustal X version 2.0. *Bioinformatics*, 23, 2947–2948  
<http://dx.doi.org/10.1093/bioinformatics/btm404>
- Lobo, F. (2001) A phylogenetic analysis of lizards of the *Liolaemus chiliensis* group (Iguania: Tropicuridae). *Herpetological Journal*, 11, 137–150.
- Lobo, F. (2005) Las relaciones filogenéticas dentro del grupo *chiliensis* (Iguania: Liolaemidae: *Liolaemus*): sumando nuevos caracteres y taxones. *Acta Zoologica Lilloana*, 49, 65–87.
- Lobo, F., Espinoza, R.E. & Quinteros, A.S. (2010) A critical review and systematic discussion of recent classification proposals for liolaemid lizards. *Zootaxa*, 2549, 1–30.
- Masta, S.E. (2000) Phylogeography of the jumping spider *Habronattus pugillis* (Araneae: Salticidae): Recent vicariance of sky island populations? *Evolution*, 54, 1699–1711.  
[http://dx.doi.org/10.1554/0014-3820\(2000\)054\[1699:potjsh\]2.0.co;2](http://dx.doi.org/10.1554/0014-3820(2000)054[1699:potjsh]2.0.co;2)
- Morando, M., Avila, L.J. & Sites Jr., J.W. (2003) Sampling Strategies for Delimiting Species; Genes, Individuals, and Populations in the *Liolaemus elongatus-kriegi* Complex (Squamata; Liolaemidae) in Andean-Patagonian South America. *Systematic Biology*, 52, 159–185.  
<http://dx.doi.org/10.1080/10635150309333>
- Müller, L. & Hellmich, W. (1932) Beiträge zur Kenntnis der Herpetofauna Chiles. II. Neue *Liolaemus* Arten und Rassen aus den Hoch-Anden Chiles. *Zoologischer Anzeiger*, 97, 307–329.
- Navarro, J. & Díaz, N. (1986) Comparación de dos subespecies de *Liolaemus leopardinus* mediante caracteres exo y endofenotípicos. *Resúmenes del X Congreso Latinoamericano de Zoología*, 454.
- Núñez, H. (1992) Geographical data of Chilean lizards and snakes in the Museo Nacional de Historia Natural, Santiago, Chile. *Smithsonian Herpetological Information Service*, 91, 1–29.  
<http://dx.doi.org/10.5479/si.23317515.91.1>
- Núñez, H. (2007) *Liolaemus frassinettii*, nueva especie de lagartija para los Altos de Cantillana, Región Metropolitana (Reptilia: Sauria). *Boletín del Museo Nacional de Historia Natural de Chile*, 56, 81–87.
- Núñez, H. & Jaksic, F. (1992) Lista comentada de los reptiles terrestres de Chile continental. *Boletín del Museo Nacional de Historia Natural de Chile*, 43, 63–91.
- Núñez, H. & Torres-Mura, J.C. (2007) Estado de conservación de los anfibios y reptiles de la Región de O'Higgins. In: Serey, I., Ricci, M. & Smith-Ramirez, C. (Eds.), *Libro Rojo de la Región de O'Higgins*. Corporación Nacional Forestal - Universidad de Chile, Rancagua, Chile, pp. 43–52.
- Núñez, H., Veloso, A., Espejo, P., Veloso, C., Cortés, A. & Araya, S. (2010) Nuevas especies de *Phymaturus* (grupo "*Palluma*") para la zona cordillerana central de Chile (Reptilia, Sauria, Liolaemidae). *Boletín del Museo Nacional de Historia Natural de Chile*, 59, 41–74.
- Palumbi, S.R. (1996) Nucleic acids I: the polymerase chain reaction. In: Hillis, D.M., Moritz, C., Mable, B.K. (Eds.), *Molecular Systematics*, second ed. Sinauer Associates, Sunderland, MA, pp. 205–247.
- Pincheira-Donoso, D. & Núñez, H. (2005) *Las especies chilenas del género Liolaemus (Iguanidae Tropicuridae, Liolaeminae). Taxonomía, sistemática y evolución*. . Publicación Ocasional del Museo Nacional de Historia Natural, Santiago, 486 pp.
- Pincheira-Donoso, D., Scolaro, J.A. & Sura, P. (2008) A monographic catalogue on the systematics and phylogeny of the South American iguanian lizard family Liolaemidae (Squamata, Iguania). *Zootaxa*, 1800, 1–85.
- Rabassa, J. & Clapperton, C.M. (1990) Quaternary glaciations of the Southern Andes. *Quaternary Science Reviews*, 9, 153–174.  
[http://dx.doi.org/10.1016/0277-3791\(90\)90016-4](http://dx.doi.org/10.1016/0277-3791(90)90016-4)
- Robin, V.V., Sinha, A. & Ramakrishnan, U. (2010) Ancient Geographical Gaps and Paleo-Climatic Shape the Phylogeography

of an Endemic Bird in the Sky Islands of Southern India. *PLoS ONE*, 5, 1–13.

<http://dx.doi.org/10.1371/journal.pone.0013321>

Schulte, 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.

<http://dx.doi.org/10.1111/j.1095-8312.2000.tb01670.x>

Shepard, D.B. & Burbrink, F.T. (2008) Lineage diversification and historical demography of a sky island salamander, *Plethodon ouachitae*, from the Interior Highlands. *Molecular Ecology*, 17, 5315–5335.

<http://dx.doi.org/10.1111/j.1365-294x.2008.03998.x>

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance and maximum parsimony methods. *Molecular Biology and Evolution*, 28, 2731–2739.

<http://dx.doi.org/10.1093/molbev/msr121>

Wiegmann, A.F.A. (1834) *Herpetologica Mexicana seu descriptio amphibiorum Novae Hispaniae quae itineribus comitis de Sack, Ferdinandi Deppe et Chr. Guil. Schiede in Museum Zoologicum Berolinense pervenerunt. Pars prima, Saurorum species amplectens, adiecto Systematis Saurorum Prodomo, additisque multis in hunc amphibiorum ordinem observationibus*. C. G. Lüderitz, Berlin, 54 pp.

#### APPENDIX I. Specimens examined (specimens additionally used for genetic distance in bold)

*Liolaemus frassinettii*: Altos de Cantillana, Metropolitan Region, Chile: Unknown coordinates: MNHNCL 1035 (Holotype), LCUC 800, 801. 33°56'S 70°57'W, 2109 masl: MNHNCL 4140–4142. 33°54'S; 70°58'W: **SSUC Re 80**.

*Liolaemus leopardinus*: El Colorado, Metropolitan Region, Chile: 33°20'S 70°17'W, 2745 masl: MNHNCL 3437–3439. Farellones, Metropolitan Region, Chile: 33°34'S 70°29'W: MNHNCL 4025, 4027, 4028, **4890**, 4891, SSUC Re 364–367.

*Liolaemus ramonensis*: Quebrada de Macul, Metropolitan Region, Chile: MNHNCL 4007, 4008, 4012, 4015, 4016, 4017. For genetic distance: San Ramon Mountain, Metropolitan Region, Chile: 33°28'S 70°23'W: **SSUC Re 490**.

*Liolaemus ubaghsi*: Chapa Verde, Sewell, between the ski field and reservoir, Libertador Bernardo O'Higgins Region, Chile. 34°03'S 70°26'W, 2210 masl: MNHNCL 3808–3816. Tranque Barahona, O'Higgins Region, Chile: **SSUC Re 491–492**. Sapos Reservoir, El Teniente Mine, O'Higgins Region, Chile. 34°04'S 70°22'W, 1870 masl: MNHNCL 0605–0613.

*Liolaemus valdesianus*: Panimávida area, Morado Mountain, Cajón del Maipo, Metropolitan Region, Chile. 33°47'S 70°02'W, 2800 masl: MNHNCL 0002, 0004, 0005, 0006. Cajón del Maipo, Metropolitan Region, Chile (Exact location unknown): SSUC Re 129. Lo Valdes, Cajón del Maipo, Metropolitan Region, Chile. 33°51'S 70°03'W: **SSUC Re 363**. El Yeso Reservoir, Cajón del Maipo, Metropolitan Region, Chile. 33°39'S 70°03'W: MNHNCL 403–404, SSUC Re 559.

*Liolaemus sp.*: Alto Huemul, Sierras de Bellavista, O'Higgins Region, Chile: MNHNCL 4081–4082.