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# Molecular phylogenetic relationships of the *Liolaemus rothi* complex and a new species of lizard from Auca Mahuida Volcano (Squamata: Liolaemini)

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## Abstract

A new species of lizard of the genus *Liolaemus* from Neuquén Province, western Argentina, is described. The new species is a member of the *Liolaemus rothi* species complex, and mitochondrial and nuclear molecular data show it as sister taxon of the clade composed of (*L. hermannunezi* (*L. tromen* + *L. loboi*)), differing in size, squamation, coloration, and sexual dimorphism from the other species of this group. *Liolaemus sitesi* sp. nov. has a dark body coloration with series of notched blotches on the dorsum, with bright spots, and a very iridescent yellow-green coloration in natural light. *Liolaemus sitesi* sp. nov. is found only in the Auca Mahuida volcano and is terrestrial, dwelling on the stony slopes with sandy soil between 1300 m and the volcano summit.

**Key words:** Patagonia, *Liolaemus sitesi* sp. nov., *rothi* complex phylogeny, Argentina

## Resúmen

Se describe una nueva especie de lagartija del genero *Liolaemus* del norte de la Provincia de Neuquén, oeste de Argentina. La nueva especie es un miembro del complejo de especies *Liolaemus rothi*, y datos moleculares mitocondriales y nucleares la muestran como el taxón hermano del clado (*L. hermannunezi* (*L. tromen* + *L. loboi*)), diferenciándose en tamaño, escamación, coloración y en dimorfismo sexual de las otras especies del grupo. *Liolaemus sitesi* sp. nov. tiene una coloración corporal oscura con series de manchas con muescas en el dorso, puntos brillantes y una coloración amarilla-verdosa iridiscente al sol. *Liolaemus sitesi* sp. nov. solo se encuentra en el volcán Auca Mahuida y es terrestre, viviendo en las pendientes rocosas con suelo arenoso encontradas entre los 1300 m y la cumbre del volcán.

**Palabras claves:** Patagonia, *Liolaemus sitesi* sp. nov., filogenia complejo *rothi*, Argentina

## Introduction

Northwestern Patagonia and adjacent southern Andes, including the regions of northern Neuquén and southern Mendoza provinces in Argentina and neighboring areas of Chile are geographically very complex, with high mountains and steep volcanic peaks, deep valleys, and isolated high plateaus, products of Andean orogeny, and a subsequent history of volcanism and glaciations that produced pronounced climatic changes in the last million years (MY) (e.g. Rabassa & Clapperton 1990; Ramos & Kay 2006; Ramos & Folguera 2010). These events produced an intricate physiographic landscape that probably fostered multiple population divergence processes across different geographic and temporal scales, shaping a rich biodiversity of lizards. Today this

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region can be considered as a "hotspot" for *Liolaemus* lizards. In the last decades field surveys in this region have revealed new species of *Liolaemus* that were previously either unknown or confused with other species (*Liolaemus duellmani* Cei 1980; *L. thermarum* Videla & Cei 1996; *L. punmahuida* Avila *et al*. 2003; *L. morenoi* Etheridge and Christie 2003, *L. sagei* Etheridge and Christie 2003, *L. flavipiceus* Cei & Videla 2003; *L. gununakuna* Avila *et al*. 2004; *L. josei* Abdala 2005; *L. tregenzai* Pincheira-Donoso & Scolaro 2007; *L. hermannunezi* Pincheira *et al.* 2007; *L. puelche* Avila *et al*. 2007; *L. cuyumhue* Avila *et al*. 2008; *L. antumalguen* Avila *et al*. 2010; *L. choique, L. smaug* Abdala *et al*. 2010; *L. cyaneinotatus* Martinez *et al*. 2011; *L. purul* and *L. tromen* Abdala *et al*. 2012; *Liolaemus abdalai* Quinteros 2012; *L. burmeisteri* Avila *et al*. 2012). New surveys in poorly known areas, coupled with the application of molecular techniques, have revealed at least 16 additional "candidate" species of *Liolaemus* that previously were confused with *L. elongatus* Koslowsky 1896, *L. rothi* Koslowsky 1898, *L. boulengeri* Koslowsky 1898, *L. petrophilus* Donoso-Barros & Cei 1971and *L. bibronii* (Bell 1843), in this area and that require detailed morphological study (Morando *et al.* 2003, 2004, 2007; Martinez *et al*. 2011; Avila *et al.* 2004, 2006; Morando *et al*. unpublished data). The *Eulaemus* clade of *Liolaemus* includes several subclades (Morando 2004; Avila *et al*. 2006; Abdala 2007), including five groups of species distributed along a north-south axis in western Argentina between southern Mendoza and southern Santa Cruz; these are the *fitzingerii*, *melanops*, *donosobarrosi*, *boulengeri* and *rothi* clades (*sensu* Morando 2004; Avila *et al*. 2006; Fontanella *et al*. 2012). Species of the *rothi* and *boulengeri* complexes were recognized as the *telsen* group by Abdala (2007), but more recently Abdala *et al.* (2012) presented morphologically-based phylogenetic hypothesis in which neither the monophyly of the *telsen* group nor the monophyly of the species included in the *rothi* complex were recovered. The *rothi* and *boulengeri* complexes are widely distributed in Neuquén, but the majority of the populations are not well defined and they harbor several potential new species (Morando 2004; Avila *et al*. 2006; Olave *et al*. unpublished data). These species are mainly distributed along the eastern slope of the Andes, where they are restricted to areas with Andean and Patagonian steppe environments of western Neuquén, southern Río Negro, and northern Chubut, in Argentina, and in a small high mountain valley of Administrative Region VIII (Bio Bio) in Chile.

In this work we present mitochondrial and nuclear molecular evidence that strongly supports monophyly of the *rothi* complex, including *Liolaemus rothi*, *L. hermannunezi*, *L. loboi*, *L. sagei* and *L. tromen*, and the new species described here.

## Material and methods

We examined sample series of related species of the *rothi* clade (Table 1, Appendix I) from the herpetological collections of Monte L. Bean Life Science Museum, Brigham Young University (BYU); Museo de La Plata, Universidad Nacional de La Plata (MLP.S/R); Museum of Vertebrate Zoology, University of California – Berkeley (MVZ); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (MACN), and the herpetological collection LJAMM-CNP of the Centro Nacional Patagónico, Puerto Madryn, Argentina (CENPAT–CONICET). All tissue vouchers are deposited in the last collection. Reference specimens were collected by hand, fork or noose, sacrificed by a pericardiac injection of sodium tiopental Pentovet®, dissected slightly to extract a sample of liver/muscle for molecular study, fixed in 10-20% formalin and later transferred to 70% ethanol. Morphological characters used were those commonly used for *Liolaemus* (e.g. Etheridge & Christie 2003) or previous works from authors. Where numbers of paired scales are provided they are given as left-right. Squamation terminology follows Smith (1946) and lateral neck-fold terminology follows Frost (1992). Measurements were taken with a digital caliper to the nearest 0.1 mm. Some character states were observed with the aid of a binocular stereomicroscope. Descriptions of color in life are based on notes taken in the field and color photographs of recently captured animals. Data for Table 1 comparisons for the species *Liolaemus loboi*, *L. rothi*, *L. sagei* and *L. hermannunezi* were taken from the original descriptions, or a redescription in the case of *L. rothi* (Abdala 2003, Etheridge & Christie 2003, Pincheira-Donoso *et al*. 2007).
*Molecular analysis*: Genomic DNA was extracted using the Qiagen ® DNeasy ® 96 Tissue Kit following the protocol provided by the manufacturer. PCR and sequencing protocols follow Morando *et al.* (2003, 2004) for

the mitochondrial genes (cyt b and 12S), for the Anonymous Nuclear Loci (ANL): 1D, 12D, 4B and 9C, we follow Camargo *et al*. (2012). We also included four Nuclear Protein Coding Loci (NPCL): EXPH5, KIF24 (Portik *et al*. 2011) and PRLR, SNCAIP (Townsend *et al*. 2008). PCRs for EXPH5 and KIF24 loci were performed with the temperature profile of Noonan and Yoder (2009), with standard reaction conditions (per sample: 2 µl dNTPs (1.25 mM), 2 µl 5x Taq buffer, 1 µl each primer (10 µM), 1 µl MgCl (25 mM), and 0.1 µl Taq DNA polymerase (5 U/µl; Promega Corp., Madison, WI); 14 ml total reaction volume). For PRLR and SNCAIP, we used the touch-down cycling protocol for nuclear genes described in Reyes-Velasco and Mulcahy (2010). All sequences were edited using the program Sequencher v4.8. (™Gene Codes Corporation Inc. 2007), and aligned with MAFFT (Katoh *et al*. 2002) performing 100 tree rebuilding iterations and a maxirate of 100; alignments were checked by eye and manually adjusted if necessary to maximize blocks of sequence identity. Missing data in all cases were coded as "?". For each gene we selected the best-fitting model using JModelTest v0.1.1 (Guindon & Gascuel 2003; Posada 2008) using the corrected Akaike Information Criterion (AICc) (Table 1). In all nuclear genes, recombination was tested using RDP: Recombination Detection Program v3.44 (Heath *et al*. 2006; Martin & Rybicki 2000). *Phylogenetic analysis*: A concatenated matrix of ten loci (n = 30; 6,386 bp) was run twice for a Bayesian analysis, as implemented in MrBayes 3.2.1 (Ronquist & Huelsenbeck, 2003). From a random starting tree, 10 x $10^6$ generations were run, and the Markov chains were sampled at intervals of 1,000 generations. Stationarity was estimated (to discard the 'burn-in' samples), and ESS values were observed using Tracer v1.5. The equilibrium samples were used to generate a 50% majority rule consensus tree.

**TABLE 1.** Molecular markers used for phylogenetic reconstruction with details on length, substitution model and original primer references.

| Loci | Type of marker | Length (bp) | Substitution model | Reference |
|---|---|---|---|---|
| 12S | Mitochondrial | 804 | GTR+G | Morando et al. (2004) |
| cyt-b | Mitochondrial | 807 | HKY+I+G | Morando et al. (2004) |
| A1D | ANL | 770 | HKY+G | Camargo et al. (2012) |
| A12D | ANL | 635 | GTR+G | Camargo et al. (2012) |
| A4B | ANL | 416 | HKY+I | Camargo et al. (2012) |
| A9C | ANL | 741 | K80 | Camargo et al. (2012) |
| EXPH5 | NPCL | 849 | HKY+G | Portik et al. (2011) |
| KIF24 | NPCL | 495 | HKY+G | Portik et al. (2011) |
| PRLR | NPCL | 442 | HKY | Townsend et al. (2008) |
| SNCAIP | NPCL | 420 | HKY+I | Townsend et al. (2008) |

## Results

Comparisons between morphological trait values show that the proposed new species can be easily differentiated from other species of the *rothi* complex by a combination of coloration and scale count characters (Table 2). *Liolaemus sitesi* **sp. nov.** shows distinguishable chromatic patterns and a general body color not found in other species of the *rothi* complex. A combined analyses of ten genes (two mitochondrial and eight nuclear) shows that this species is highly supported as a member of the *rothi* complex (posterior probability = 1). The *rothi* complex includes two clades, one represented by *L. rothi* + *L. sagei*, and the other recovers *L. sitesi* as the sister taxon of a clade formed by ((*L. tromen* + *L. loboi*) + *L. hermannunezi*)). All of these relationships are strongly supported by posterior probabilities of 1 (Fig. 1).

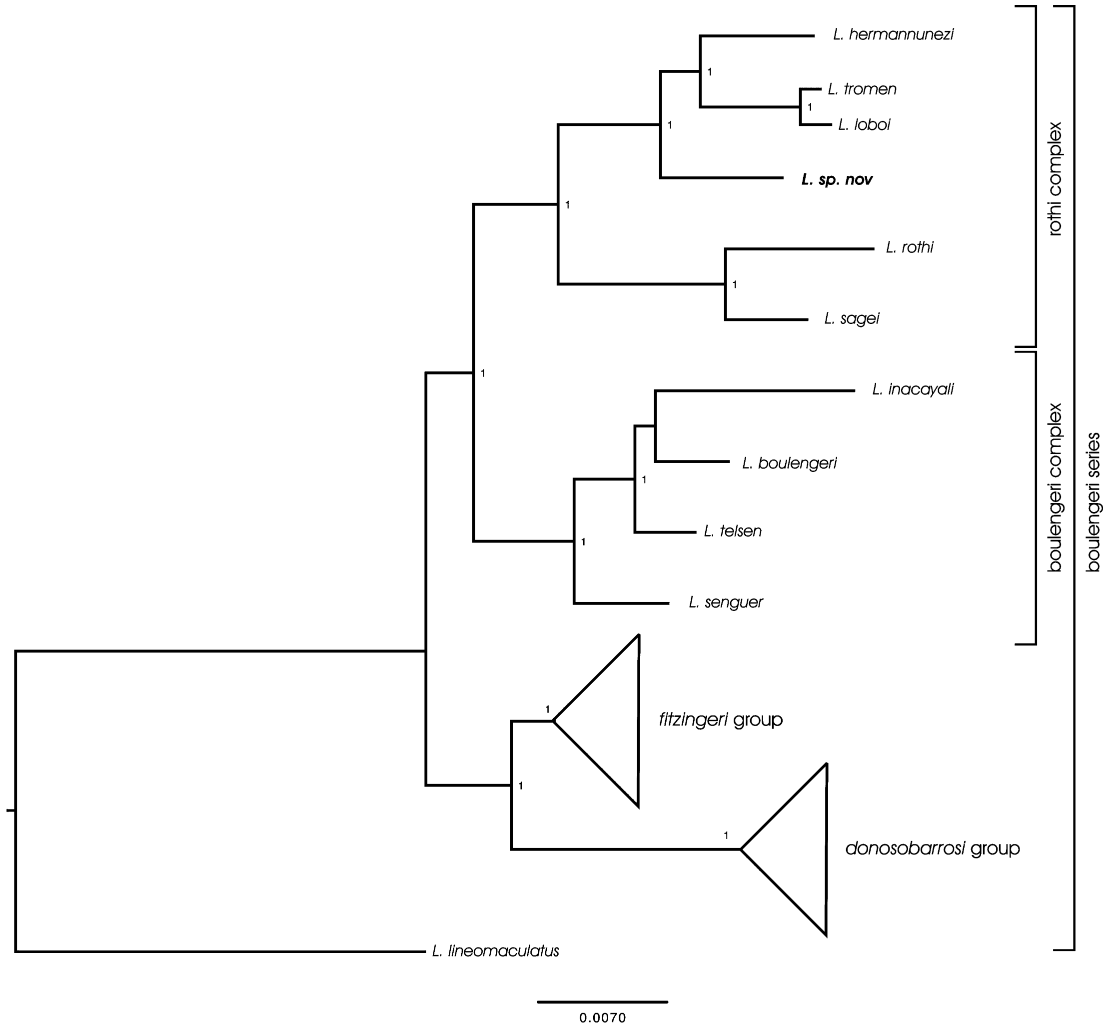


**FIGURE 1.** Phylogenetic relationships of described species of the *Liolaemus rothi* complex and other related species of the *boulengeri* complex and representatives of the *fitzingerii* and *donosobarrosi* groups. Numbers on nodes correspond to posterior probabilities.

**TABLE 2.** Selected morphometric, meristic, and chromatic characteristics in species of the *Liolaemus rothi* complex. Range, means and standard deviations (SD) of the main morphometric and meristic characters. Measures in mm and scale counts in numbers. Data for *Liolaemus sagei* and *L. rothi* were taken from Etheridge and Christie (2003), for *Liolaemus loboi* from Abdala (2003) and for *L. tromen* from Abdala (2012). NA = data no available.

| Characters | *sitesi* sp. nov. (N=22) | *hermannunezi* (N=6) | *rothi* | *sagei* | *tromen* | *loboi* |
|---|---|---|---|---|---|---|
| Snouth–Vent Length | 56.4–79.8 (68.9±6.9) | 46.7–71.4 (59.6±10.1) | 91–97 | 85–88 | 61.6–82.5 (73.9±8.5) | 48.1–72.7 (58.3) |
| Midbody scales | 67–78 (72.0±2.9) | 68–75 (70.5±2.3) | 54–70 (64.7±4.27) | 82–100 (90.3±4.68) | 59–70 (65.1±3.8) | 59–70 (63.7) |
| Dorsal scales | 78–87 (82.0±2.5) | 71–74 (71.8±1.1) | 59–85 (72.9±6.53) | 91–117 (101.2±6.59) | 67–75 (70.1±2.7) | 63–73 (67.1) |
| Ventral scales | 96–112 (101.4±4.2) | 86–89 (87.3±1.0) | NA | NA | 96–109 (102.4) | NA |
| Precloacal pores | 7–10 (8.3±1.1) | 8–10 (9.0±1.4) | 7–12 (9.0±1.63) | 7–10 (8.3±1.00) | 7–9 | 8–11 (9.6) |

...... *continued on the next page*

**TABLE 2.** (Continued)

| Characters | *sitesi* sp. nov. (N=22) | *hermannunezi* (N=6) | *rothi* | *sagei* | *tromen* | *loboi* |
|---|---|---|---|---|---|---|
| Supralabials | 7–10 (8.0±0.9) | 6–8 (7.1±0.7) | 5–7 (5.49±0.56) | 4–7 (5.25±0.60) | 6–7 (6.5±0.5) | 7–9 (8.4) |
| Infralabials | 5–6 (5.6±0.4) | 5–6 (5.6±0.5) | 5–7 (6.26±0.50) | 6–7 (6.22±0.42) | 4–7 (5.6±1.0) | 6–8 (6.4) |
| Finger lamellae | 18–23 (20.0±1.1) | 17–20 (18.5±1.3) | NA | NA | 18–22 (20.3±1.4 | 17–20 |
| Toe lamellae | 25–30 (27.2±1.4) | 25–28 (26.8±1.1) | 22–28 (24.7±1.95) | 24–32 (27.2±2.14) | 25–31 (26.8; ±2.6)- | 24–27 |
| Dorsal background | dark brown | light gray and yellowish in dorsal region | light gray | brown, gray, and sometimes with yellowish | light brownish with yellowish | opaque yellow |
| Dorsal pattern | blotches series with dots in the margins | conspicuous dark blotches series | conspicuou s dark band or blotches series | conspicuous dark blotches series scattered with white dots | series of subsquare paravertebral spots | conspicuous black blotches series scattered with cyan, yellow, green or blue dots |
| Sexual dichromatism evident | Yes | Yes | No | No | No | Yes |

## Species accounts

### *Liolaemus sitesi* sp. nov.

(Figure 2)

**Holotype**.—MLP.S 2637, an adult male from Park Ranger Post, 25.9 km S junction Provincial Road 6, road to Auca Mahuida volcano, Auca Mahuida Natural Protected Area (37º 42’ S, 68º 51’ W, 1560 m), Pehuenches Department, Neuquén Province, Argentina. L.J. Avila, M.L. Kozykariski, and M.F. Breitman, collectors.

**Paratypes**.—LJAMM-CNP 11021, 12300, 12243, 12328-30, males, LJAMM-CNP 12301, 12331-4, females, LJAMM-CNP 12335-7, 12212-3, juveniles, same data as the holotype. LJAMM-CNP 12305-6, males, Cerro del Este (37º 46’ S, 68º 53’ W, 1935 m), L.J. Avila, M.L. Kozykariski, and M.F. Breitman collectors. LJAMM-CNP 10566, juvenile, eastern slope of Auca Mahuida volcano (37º 41’ S, 68º 49’ W, 1332 m), C.H.F. Pérez and D.R. Pérez, collectors. LJAMM-CNP 10558, male, northeastern slope of Auca Mahuida volcano (37º 43’ S, 68º 53’ W, 1757 m), C.H.F. Pérez and D.R. Pérez, collectors. All of these localities are located in Auca Mahuida Natural Protected Area, Pehuenches Department, Neuquén Province, Argentina. LJAMM-CNP 13382, female, northern slope of Auca Mahuida volcano (37º 47’ S, 68º 53’ W, 1486 m), LJAMM-CNP 14234, female, 14236, male, track to Punta de Castillo (37º 49’ S, 68º 54’ W, 1366 m), L.J. Avila and I. Minoli, collectors. LJAMM-CNP 14241, female, 0.5 km W La Aguada (37º 45’ S, 68º 54’ W, 1843 m), L.J. Avila, I. Minoli, M. Kozykariski, D. Janish Alvarez and S. Quiroga, collectors. All of these localities are also located in Auca Mahuida Natural Protected Area, Añelo and Pehuenches Departments, Neuquén Province, Argentina.

**Diagnosis.**—*Liolaemus sitesi* is a member of the *rothi* complex, that includes *L. hermannunezi*, *L. loboi*, *L. sagei*, *L. rothi*, and *L. tromen* and several other potential species that require further study (Avila *et al*. 2006; Morando *et al*. 2004; Olave unpublished data). *Liolaemus sitesi* can be easily distinguished from all other members of its clade by its black/dark brown background body coloration with small bright yellow, green or white spots distributed along its dorsal and lateral trunk areas; in full sun males take on a yellow-green iridescent coloration on neck, body, limbs and tail; colors not observed in any other species of the group. *Liolaemus sitesi* differs from *L. rothi*, *L. sagei* and *L. tromen* by its marked sexual dichromatism. *Liolaemus sitesi* is smaller than *L. rothi* (maximum SVL: 79.8 vs. 97.00 mm), has more scales around midbody (72.0 ± 2.9 vs. 64.7 ± 4.27) and more supralabial scales (8.0 ± 0.9 vs. 5.49 ± 0.56). *Liolaemus sitesi* lacks of the conspicuous yellow spots irregularly distributed along the body of *L. rothi*. *Liolaemus sitesi* is larger than *L. hermannunezi* (maximum SVL: 79.8 vs. 71.4 mm), has more dorsal (82.0 ± 2.5 vs. 71.8 ± 1.1), ventral (101.4 ± 4.2 vs. 87.3 ± 1.0), and supralabial scales (8.0 ± 0.9 vs. 7.1 ± 0.7). *Liolaemus sitesi* is smaller than *L. sagei* (maximum SVL: 79.8 vs. 88.00 mm), has fewer scales around midbody (72.0 ± 2.9 vs. 90.3 ± 4.68), fewer dorsal scales (82.0 ± 2.5 vs. 101.2 ± 6.59), more supralabials (8.0 ± 0.9 vs. 5.25 ± 0.60), and fewer infralabial scales (5.6 ± 0.4 vs. 6.22 ± 0.42). *Liolaemus sitesi* is larger than *L. loboi* (maximum SVL: 79.8 vs. 72.7 mm), has more scales around midbody (72.0 ± 2.9 vs. 63.7), more dorsal scales (82.0 ± 2.5 vs. 67.1), and fewer infralabials (5.6 ± 0.4 vs. 6.4). *Liolaemus sitesi* differs from *L. tromen* by having a slender body, a higher number of scales around midbody (72.0 ± 2.9 vs. 65.8 ± 2.2), more dorsal (82.0 ± 2.5 vs. 72.2 ± 3.1) and supralabial scales (8.0 ± 0.9 vs. 7.0 ± 0.6), and a coloration pattern without suprascapular marks or series of subsquare paravertebral spots fused forming transversal bands.

**Description of holotype**.—Adult male (Figs. 2, 3), 76.1 mm snout-vent length (SVL); tail length 114.2 mm. Axilla-groin distance 34.9 mm. Head length 16.3 mm (from anterior border of tympanum to tip of snout), 16.3 mm wide (at anterior border of tympanum), 9.1 mm high (at anterior border of tympanum). Snout length 6.4 mm (orbit-tip of snout distance). Interorbital distance 6.4 mm. Eye-nostril distance 5.1 mm. Orbit-auditory meatus distance 6.4 mm. Forelimb length 22.3 mm. Tibial length 14.9 mm. Foot length 23.6 mm (ankle to tip of claw on fourth toe). Dorsal head scales bulged, smooth, 19 between occiput at level of anterior border of tympanum to rostral, pitted with numerous scale organs in the anterior region, reduced to a single organ, or without organ in the posterior half of the head. Rostral scale wider (2.8 mm) than high (1.4 mm). Two postrostrals, together with anterior lorilabial, separate nasal scales from rostral. Nasal scales longer than wide, rhombic; nostril one-half length of nasal, posterior in position. Scales surrounding nasals 8–6 (on the left and right side respectively). Five internasals. Three frontonasal scales, two on the sides approximately squared, and one central rectangular and twice as large. Five prefrontals, a small pentagonal scale in the center (1.3 mm), and two pairs on the sides: a pair of larger dorso-lateral scales, irregularly hexagonal (1.9 mm), and a pair of medium-sized lateral scales (1.7 mm), almost pentagonal. Six frontal scales, fragmented. Six frontoparietal scales in two longitudinal rows. Interparietal hexagonal (1.9 mm), surrounded by seven scales; five smaller and irregular in front and sides (0.88 mm), and two larger posteriorly (1.6 mm). Parietal eye evident. Parietals irregularly shaped, some bulged. Circumorbitals 9–13 (damaged on the left side). Transversally expanded supraoculars 7–8; lateral supraoculars smaller: 19–18. Anterior canthal approximately square, separated from nasal by one postnasal. Posterior canthal longer than wide, subtriangular. Loreal scales, something bulged, five on each side. Lorilabials longer than wide (8–7), larger than labials. Seven superciliaries on each side, flattened and elongated, anterior four broadly overlapping dorsally. Orbit with 16–14 upper and 14–13 lower ciliaries. Orbit diameter 6.1 x 2.4 mm. Preocular small, unfragmented, longer than wide. Subocular scale elongated, five times longer than wide (4.3 x 0.8 mm). A well marked longitudinal ridge along upper margin of preocular and subocular scales. Postocular small, slightly bulged, very inconspicuous. Palpebral scales small granular and bulged. Supralabials 9–7, quadrangular, convex. Temporals smooth, convex, imbricate with one scale organ in the tip. Anterior auriculars smaller than adjacent posterior temporals, granular. Posterior auriculars small and granular. Smaller than the anterior auriculars. External auditory meatus conspicuous, higher (3.0 mm) than wide (1.1 mm). Lateral scales of neck granular with inflated skin. Mental scale wider (3.0 mm) than high (1.4 mm), in contact with four scales. Mental followed posteriorly by two postmentals, and two rows of three chinshields on each side. Six infralabials on each side, first scale twice as high as posterior infralabials, posterior slightly larger than supralabials. Gular scales smooth, flat, imbricated, with rounded posterior margins, with melanophores. Scales of throat between chinshields slightly juxtaposed, becoming slightly imbricated toward auditory meatus. Thirty-two gulars between tympanum openings. Infralabials separated from chinshields by one to three rows of scales. Antehumeral and longitudinal neck folds well developed; postauricular very distinctive; gular, rictal, dorsolateral, oblique inconspicuous.

Scales of dorsal neck region rhomboidal, imbricate, slightly keeled. Seventy-eight dorsal scales between occiput and anterior surface of thighs. Dorsal body scales rhomboidal, imbricated, slightly keeled to moderately keeled towards the posterior half of body. Dorsal scales grading laterally into slightly smaller, smooth scales at midbody. Scales, immediately anterior and posterior to forelimb and hindlimb insertion, small, smooth, granular, and non-overlapping. Body lateral scales grading from slightly smaller to larger towards the ventral region, at midbody. Ventral body scales rhomboidal, smooth, flat, imbricate, and larger than dorsal scales. Seventy-six around midbody; scales between mental and precloacal pores 99. Scales of cloacal region about equal in size to ventral body scales. Nine conspicuous precloacal pores.

**FIGURE 2.** *Liolaemus sitesi* sp. nov. Above: holotype MLP.S 2637, adult male from Park Ranger Post, 25.9 km S junction Provincial Road 6, Auca Mahuida Natural Protected Area, Pehuenches Department, Neuquén Province, Argentina. Below: unidentified paratype, adult male with typical dorsal coloration at full sun.


**FIGURE 3.** *Liolaemus sitesi* sp. nov., holotype adult male in dorsal and ventral view (MLP.S 2637); type locality details given in Fig. 2 caption.

Anterior suprabrachials rhomboidal, imbricated, smooth, slightly larger in size to dorsal body scales. Infrabrachials smaller, granular. Postbrachials smaller, smooth, becoming granular near axilla. Supra-antebrachials similar to suprabrachial. Infra-antebrachials rhomboidal, imbricate, smooth. Supracarpals imbricated, rhomboidal, smooth. Infracarpals strongly imbricated, rhomboidal, smooth, with few scales moderately keeled towards the anterior area. Subdigital lamellae with 3 keels, numbering: I: 11, II: 15, III: 21, IV: 23, V: 14. Claws robust, curved and sharp, opaque light brown.

Suprafemorals as large as dorsal body scales, rhomboidal, imbricated, smooth, some very slightly keeled. Infrafemorals scale small, granular and smooth. Femoral patch with enlarged and bulged scales, with forty-one scales, ending in a blunt margin. Supratibial rhomboidal, imbricated, slightly keeled. Infratibials rhomboidal, imbricated, smooth. Supratarsals rhomboidal, imbricated and smooth. Infratarsal small, rhomboidal, imbricated, smooth. Subdigital scales 1–2 keeled, numbering: I: 10, II: 17, III: 24, IV: 28, V: 18. Claws robust, curved and sharp, opaque light brown. Tail complete, non-regenerated. Dorsal caudal scales quadrangular and moderately keeled. Dorsal-lateral caudal scales quadrangular and slightly keeled. Ventral subtriangular and smooth, toward posterior half slightly keeled.

**Color in life**.—Dorsal background coloration black/dark brown with nine black transversal series of four blotches with posterior notches occupied by white spots from the occiput to the rump. First three series fused and irregular; fourth and fifth shaped as half-moon, almost in contact; all others becoming well-separated, rounded and uneven to rump. Paravertebral blotches with 3–5 white dots on its posterior margins, each dot composed by 1–2 scales. Five dorsolateral black blotches from the neck to the groin, rounded, with 2–5 white dots on its margins, each dot composed of 1–2 scales. Six dorsolateral, transversals and elongated black blotches from the axilla to the groin, with 4–11 white dots on its margins, each dot composed of 1–2 scales. Lateral neck region, from the postauricular area to the shoulder, black with scattered white spots of 1–8 scales (small and granular). Axilla dark brown with white dots formed by 1–6 scales (small and granular). Body lateral region dark brown with some scattered white dots of one scale. Head dark brown with maxillary region and half temporal area melanic with a white dot on each scale. Limbs light brown with inconspicuous dark reticulations. Tail beige with three inconspicuous black blotch series to level of the postcloacal region, to join in only one blotch becoming less marked toward the tip. Throat and gular region fully melanic. Chest, belly, ventral region of the limbs and tail melanic. In preservative the general color pattern is conserved but the dorsal background and ventral coloration become darker. All yellow or green colors disappear. On the dorsal surface of the head darker blotches become more evident, one longitudinal blotch on the prefrontals and postnasals scales, two subtriangular blotches on anterior region in the orbits, two small blotches at the back of the orbits, and several smaller irregularly arranged blotches in the temporal, parietal and occipital regions.

**Variation**.—*Liolaemus sitesi* shows a remarkable sexual dichromatism (Figs. 2, 4 & 5). In eleven males (Table 3): SVL: 60.8–79.8 mm. Axilla–groin distance: 27.5–38.7 mm. Head length: 13.6–16.9 mm. Head width: 10.9–13.6 mm. Head height: 7.5–9.6 mm. Foot length: 20.2–23.6 mm. Tibial length: 12.4–15.8 mm. Arm length: 19.2–22.5 mm. Midbody scales: 67–78. Dorsal scales (between occiput at the anterior margin of auditory meatus and anterior surface of thighs): 78–86. Ventral scales: 95–104. Third finger lamellae: 18–23. Fourth toe lamellae: 25–29. Supralabial scales: 7–10. Infralabial scales: 5–6. Cloacal pores: 7–10. In eleven females (Table 3): SVL: 56.4–73.9 mm. Axilla–groin distance: 25.7–38.7 mm. Head length: 12.2–14.6 mm. Head width: 9.9–11.9 mm. Head height: 6.7–8.2 mm. Foot length: 18.3–22.0 mm. Tibial length: 11.6–13.8 mm. Arm length: 18.0–20.9 mm. Midbody scales: 67–76. Dorsal scales: 80–87. Ventral scales: 98–112. Third finger lamellae: 19–22. Fourth toe lamellae: 25–30. Supralabial scales: 7–9. Infralabial scales: 5–6. *Liolaemus sitesi* exhibits strong sexual dichromatism. The female LJAMM-CNP 13382 (Fig. 3) exhibits grayish-brown dorsal background coloration with a series of eleven vertebral dark brown blotches. The three first series formed by three round blotches with a white dot on the back, covering 1–2 scales; the following six series shaped an hourglass with a white dot on the posterior concavity, composed of 1–3 scales; and the last two series, round, with one white dot of one scale. Nine dorsolateral series of dark brown blotches. The first three series round with a white dot on the posterior margin, composed of five scales; the following four series elongated and transversal with a white dot on the posterior concavity, composed of 2–3 scales; the last two that are above the groin, round with a white dot composed of four scales. The lateral region of the body with a yellowish color and five brown lateral blotches, elongated, inconspicuous, with a white dot composed of 2–3 scales. The anterior area of tail, at the level of the postcloacal area, presents three dark brown blotches series, rounded, with a lighter band in the posterior margin. This series then becomes one central blotch from postcloacal area to the tip of the tail. These blotches are brown with a dark brown posterior margin. Limbs lighter brown than the dorsal area with a dark reticulate. Head gray with a blotch in the anterior area of the head fork shaped, and small irregular blotches in posterior area. Lateral head gray with postciliar brown and elongated blotch. Gular region, chest, belly and ventral region of the limbs and tail, gray. In all females dorsal background color is the same, only varying in intensity, just like the series of dorsal blotches. The white dots in the posterior area of the brown blotches vary only in size and scale number. Only one female has white scattered dots as males but in lower density. A single specimen has white blotches of 2–12 scales between vertebral and paravertebral series. All specimens have the brown blotches in the head, but one specimen shows some small white blotches between the brown blotches. Four specimens have two dorsolateral dashed white lines from the occiput to the postcloacal area. In three juveniles, the dorsolateral lines are inconspicuous, but these are more evident in one adult female with a yellowish color from the middle of the body toward the rear. Three specimens also exhibit lateral white lines between axilla and groin but usually this characteristic is not found in mature females of larger size. One specimen shows light gray coloration on the throat and gular region, another black reticulation, and the remaining females an inconspicuous dark reticulate. Ventral coloration of the chest, belly, limbs and tail vary between white and dark gray.

**FIGURE 4.** *Liolaemus sitesi* sp. nov., paratype LJAMM-CNP 13382, adult female in dorsal view; type locality details given in Fig. 2 caption.

Basking adult males exhibit a brightly yellow or yellow/green emerald iridescent general coloration that disappears almost immediately after capture, this coloration is only evident after a few minutes of basking but not in individuals just emerged from bush or rock shadows, or burrows. Dorsal background of the males only varies in intensity, but in four specimens, blotch series vary between black and brown, slightly darker than the background. The white dots vary in size and a single specimen varied in color. On three males, dots are formed by 1-8 scales. In only two males did the back margin of the brown blotches give the appearance of bands. In one male of the type series, but in several males observed alive but not collected, dots were bright yellow (see figure 2), this coloration was lost in preservative. On the dorsal surface of head, some observed individuals have darker blotches, one longitudinal blotch on the prefrontals and postnasals scales, two subtriangular or quadrangular blotches in the anterior region in the orbits, two small at the back of the orbits and several smaller irregularly arranged upon the temporal, parietal and occipital region. These blotches became evident on the holotype after some time on preservative. In the tail, both the background and the blotches vary in some specimens only in intensity (Fig. 5).

**TABLE 3.** Morphometric and meristic variation in *Liolaemus sitesi* sp. nov. type series. Means and standard deviations (SD) of the main morphometric and meristic characters. Measures in mm.

| | Males (N= 11) | | Females (N= 11) | |
|---|---|---|---|---|
| | Mean | SD | Mean | SD |
| Snouth-Vent Length | 71.57 | 7.63 | 66.36 | 5.25 |
| Axilla-groin distance | 33.75 | 3.70 | 32.47 | 4.04 |
| Head length | 15.26 | 1.23 | 13.70 | 0.81 |
| Head width | 12.36 | 1.03 | 11.20 | 0.72 |
| Head height | 8.67 | 0.78 | 7.54 | 0.51 |
| Foot length | 21.64 | 1.17 | 20.05 | 1.05 |
| Tibial length | 14.40 | 1.19 | 12.70 | 0.61 |
| Arm length | 21.37 | 1.19 | 19.63 | 1.02 |
| Midbody scales | 71.63 | 3.41 | 72.45 | 2.46 |
| Dorsal scales | 81.27 | 2.64 | 82.81 | 2.31 |
| Ventral scales | 99.27 | 2.93 | 103.63 | 4.34 |
| Fourth toe lamellae | 27.09 | 1.30 | 27.45 | 1.69 |
| Third finger lamellae | 20.18 | 1.25 | 20.00 | 1.09 |
| Supralabial scales | 8.54 | 0.93 | 7.63 | 0.67 |
| Infralabial scales | 5.72 | 0.46 | 5.63 | 0.50 |
| Cloacal pores | 8.22 | 1.16 | - | - |

All adult males have ventral melanism with variable degree of development, but in all individuals the gular and throat regions are always black. In three individuals the melanism in the mental region or the tail disappears. In immature males melanism is incipient with less extension and intensity, but one individual has a dark reticulate pattern on the throat and gular region. Juveniles have a color pattern similar to females but with the dorsolateral and lateral light lines always present. The throat and gular region white with a dark gray reticulate, the chest and belly white, and tail gray (Fig. 5).

**Etymology**.—The specific name is to honor our friend and colleague Jack Walter Sites, Jr. from Brigham Young University, Provo, Utah, USA, who strongly supported and collaborated with us on studies of Patagonian herpetofauna for the last 12 years. Dr. Sites is a herpetologist and evolutionary biologist and devoted the last 30+ years to collaborate with herpetologists from many Central and South American countries, including Argentina, Bolivia, Brazil, Colombia, Chile, Mexico, Peru, Uruguay and Venezuela.

**Geographic distribution**.—*Liolaemus sitesi* is known only from Patagonian Steppe vegetation environments found above 1300–1500 m elevation in Auca Mahuida Volcanic Field, Añelo and Pehuenches Departments, in Neuquén Province (Fig. 6). The main physiographic element in the Auca Mahuida Volcanic Field is the volcano of the same name that occupies the majority of the volcanic field and harbors all the Patagonian Steppe environments. This environment is isolated from other similar Patagonian Steppe environments, and surrounded by dune fields or sandy/rocky flatlands with extremely arid characteristics and vegetation typical of the Monte phytogeographic region. *Liolaemus sitesi* is not in contact with the geographic distribution range of other members of the *rothi* group; the geographically closest related species is *Liolaemus tromen* found in the Tromen volcanic field, near 130 km NW of Auca Mahuida volcanic field.


**FIGURE 5.** *Liolaemus sitesi* sp. nov., variation in color pattern of individuals of the type series. Dorsal and ventral view of males (upper) and females (below).

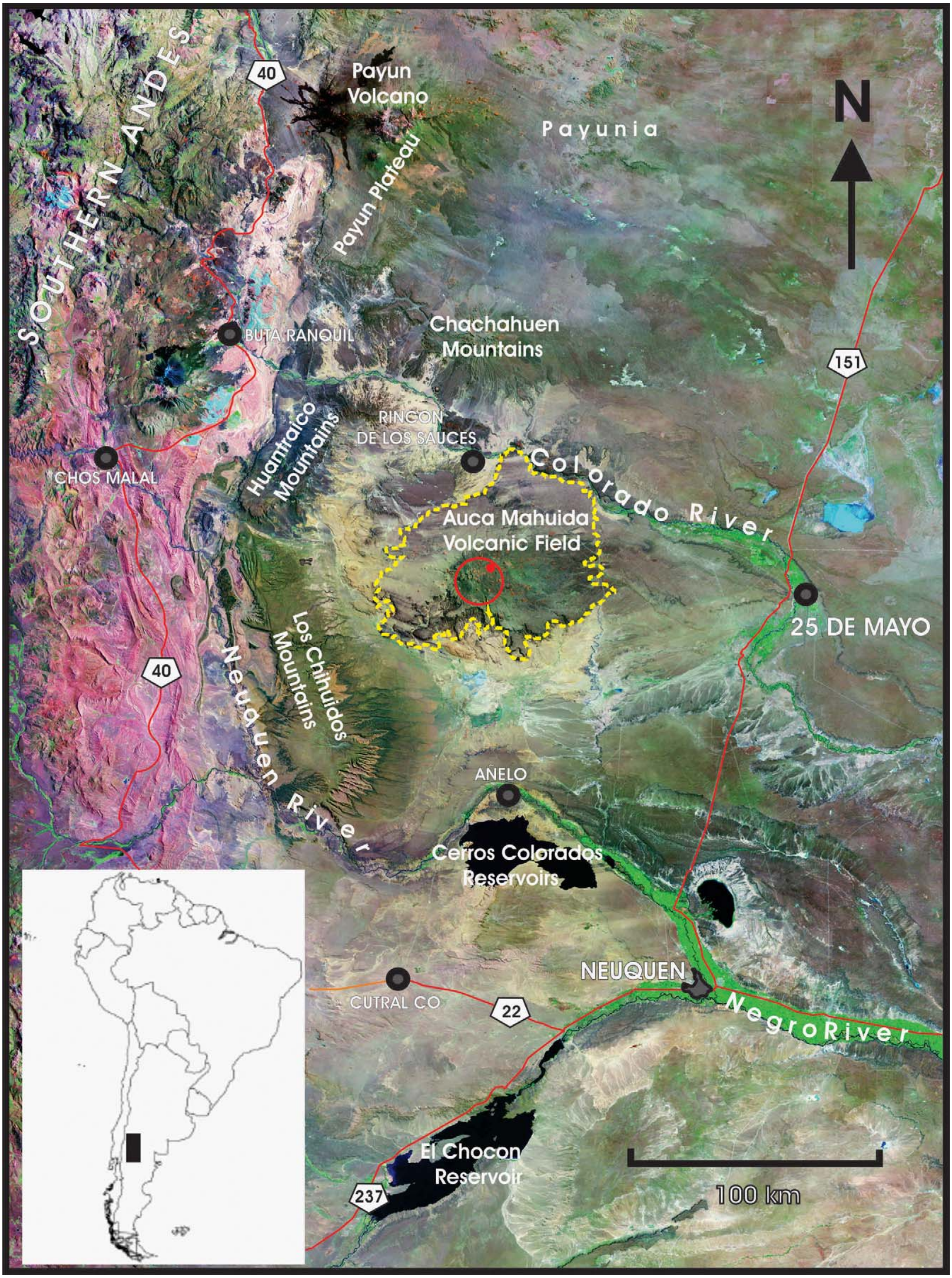


**FIGURE 6.** Map of northwestern Neuquén province showing the complex landscape of northern Patagonian Andes. Red dot marks the *Liolaemus sitesi* type locality. Red circle mark approximate distribution of *Liolaemus sitesi* on the slopes of Auca Mahuida Volcano; main mountain ranges, cities, and roads are also marked. Yellow outline: approximate boundaries of the Auca Mahuida Volcanic Field. Inset: Region in South América.

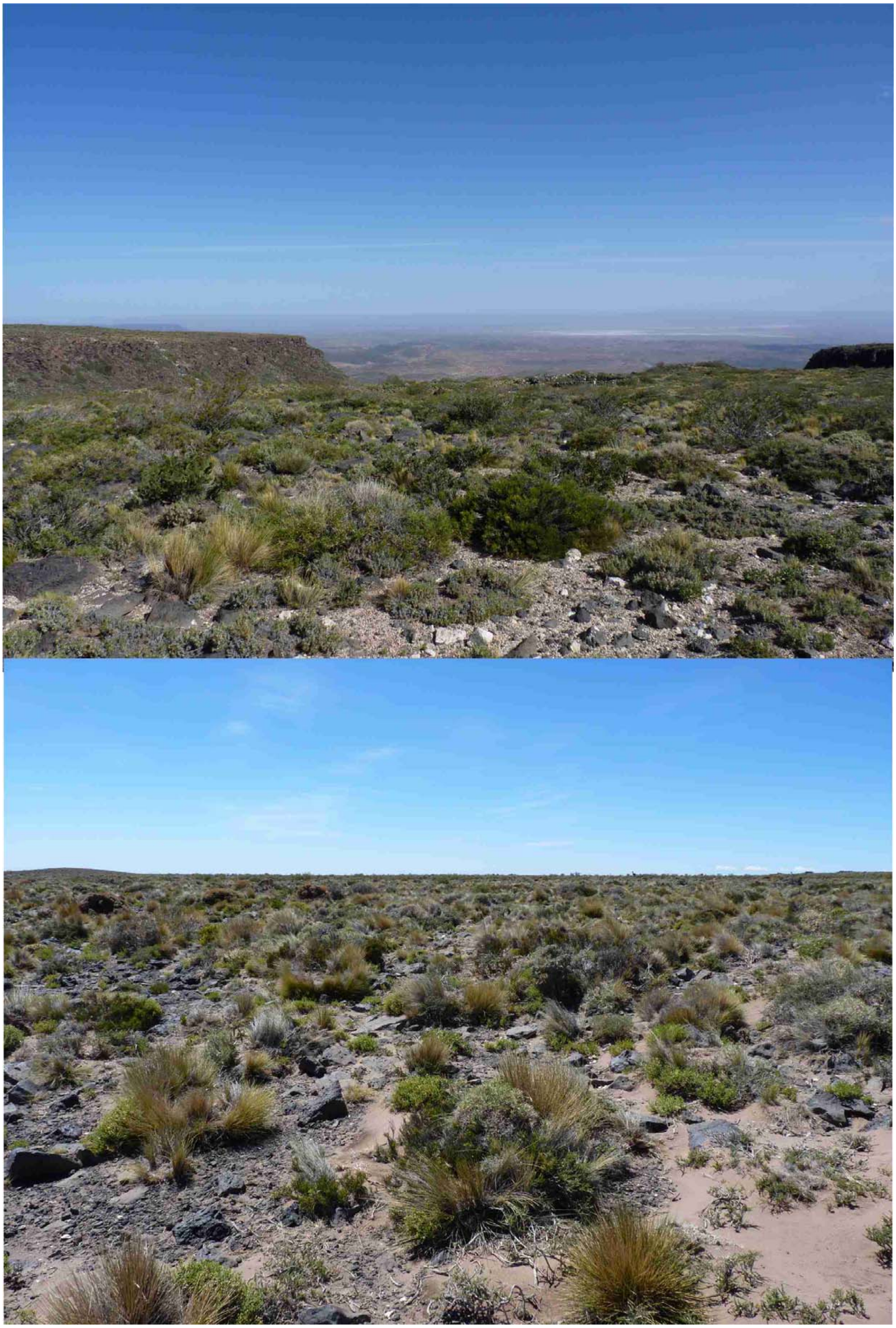

**FIGURE 7.** Type locality of *Liolaemus sitesi*. Upper: general view of the area. Below: close view of the common outcrops where lizards were collected.

**Natural history**.— Lizards were found by active search along transects established along the main roads, trails or open field on the slopes of the Auca Mahuida volcano. They were most frequently found basking on rocks and when approached would drop off the rock directly into a burrow, or flee to hide under another rock or burrow under roots. They were often found by turning over rocks. They have never been seen to climb the low vegetation or bury in the sand, but early in the morning juveniles were commonly observed in the sand accumulations found in the edges of shrubby vegetation (*Prosopis denudans, Senna kurtzii*, *S. arnottiana*). Adults were wary and dropped off into burrows below the stones when the intruder is still at a considerable distance. If pursued, they would run from rock to rock across patches of bare soil, usually seeking cover in vegetation.

Individuals were observed active between 09:00 to 19:00 on sunny days of austral summer, but showed a bimodal activity pattern on the hottest days and a unimodal pattern on cloudy or cold days. Several individuals were observed sharing basking areas, and usually juveniles and adults were found under small bushes, sharing refuge or foraging areas. Juvenile activity was more frequent in early hours of the morning or late hours of the afternoon. They seem to be territorial at some point because aggressive encounters between males or females were observed. This species shares its habitat with other *Liolaemus* species (*Liolaemus cyaneinotatus*, *Liolaemus austromendocinus*, *Liolaemus* aff. *elongatus*), as well as *Diplolaemus leopardinus*, *Leiosaurus belli*, *Phymaturus sitesi* and *P. roigorum*. *Liolaemus sitesi* usually occupies the microhabitat around scattered shrubs separated by an open, loose sand substrate (Fig. 7). No data about reproduction are available, but *L. sitesi* is probably oviparous like others members of its clade (Cei 1986). Our analysis of two guts revealed a few ant heads and beetle legs, mixed with partially digested small leaves and vegetable remains. Several snakes were observed in the area, including *Bothrops ammodytoides*, *Philodryas trilineata*, *Pseudotomodon trigonatus* and *Micrurus pyrrhocryptus*, all potential predators of this species.

**Remarks**.—In 1898, Julio Koslowsky described *Liolaemus rothi* from the ‘‘territorio del Neuquén’’. Since then, numerous similar populations from central and northwestern Patagonia have been referred to this species. Based on his wide-ranging collecting efforts, Cei (1986) extended the range of *L. rothi* from southwestern Neuquén Province southward through southwestern Rio Negro Province to the east, including the Somuncurá plateau, and northern Chubut Province. He was the first to propose a “*rothi* group” composed at that time of *L. rothi* and *L. ruizleali*. In 2003, Etheridge and Christie redescribed *Liolaemus rothi*, and described *L. sagei* but they placed both in the more inclusive *boulengeri* group, which at that time was considered a subgroup of the *montanus* group, and included 26 species. Morando (2004) and Avila *et al*. (2006) were the first to propose a *rothi* complex that included several populations recognized as *Liolaemus rothi* and *Liolaemus* spp. Pincheira-Donoso *et al*. (2007), in the description of *L. hermannunezi*, were the first to compare morphologically four of the species here included as members of the *rothi* complex, but they did not include *L. loboi*, described earlier by Abdala (2003). In a recent paper, Abdala *et al*. (2012) described a new species of the complex, but on the basis of morphological characters, they were unable to resolve the internal relationships of their “*telsen* group”. This species complex still includes additional candidate species in Neuquén and Rio Negro provinces (Olave *et al*., in prep.), and based on all the available information published in the last few years, there is no doubt that lizard diversity in Neuquén province remains substantially underestimated. Based on current studies in progress, we expect that the number of lizard’s taxa will increase by 15–20 % in the near future, and we hope that an improved understanding of the evolutionary diversity of this conspicuous group of Patagonian vertebrates, will contribute to conservation efforts aimed at preserving the natural regions of the province.

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## APPENDIX I

Specimens Examined (morphology): *Liolaemus sitesi* (22).—ARGENTINA: NEUQUEN: Pehuenches Department: Park Ranger Post, 25.9 km S junction Provincial Road 6, Auca Mahuida Natural Protected Area (37º 42' S, 68º 51' W, 1560 m): MLP.S 2637 (Holotype), LJAMM-CNP 12212/3, 12243, 12328/7 (Paratypes). Communication Station Site, South Slope, Auca Mahuida Natural Protected Area, (37º 46' S, 68º 53' W, 1935 m): LJAMM-CNP 12305/6 (Paratypes). Park Ranger Post, Auca Mahuida Natural Protected Area (37º 43' S, 68º 54' W, 1873 m): LJAMM-CNP 11021, 12300/1 (Paratypes). Auca Mahuida Natural Protected Area (37º 41' S, 68º 49' W, 1332 m): LJAMM-CNP 10566 (Paratypes). Auca Mahuida Natural Protected Area (37º 43' S, 68º 53' W, 1757 m): LJAMM-CNP 10558 (Paratypes). Añelo Department: Auca Mahuida Natural Protected Area, (37º 47' S, 68º 53' W, 1486 m): LJAMM-CNP 13382 (Paratypes). Auca Mahuida Natural Protected Area, way Punta del Castillo, transition environment (37º 49' S, 68º 54' W, 1366 m): LJAMM-CNP 14234, 14236 (Paratypes). Auca Mahuida Natural Protected Area, 500 m W La Aguada (37º 45' S, 68º 54' W, 1843 m): LJAMM-CNP 14241 (Paratypes). *Liolaemus hermannunezi* (6).—CHILE: VIII Region: Bio-Bío Province: Paso Pichachen, Ruta Antuco-Los Barros-Moncol, 10 km E de Los Barros (37º31'S, 71º14'W, 1489 m): LJAMM-CNP 14149-14151, 14192-14194. *Liolaemus rothi* (33): CHUBUT: Telsen Department: Ruta Provincial 67, 17.7 km N Gan Gan (2 km junction to Cañada Leona): LJAMM-CNP 11526/32. RIO NEGRO: 9 de Julio Department: Ruta Provincial 8, 2.9 km S junction Ruta Provincial 5, 14.9 km S El Cain: LJAMM-CNP 10961/4; Meseta de Somuncurá: LJAMM-CNP 4457/8/61; Pilcaniyeu Department: Ruta Provincial 80, road to Cerro Bernal: LJAMM-CNP 12939/2; Ruta Provincial 80, 28,1 km SE junction Ruta Nacional 237, Camino a Las Bayas: LJAMM-CNP 14280/3. Ñorquinco Department: Ruta Provincial 6, 1 Km Nw Ojo de Agua: LJAMM-CNP 2134/5, 2152/53, 2236/7. 25 de Mayo Department: Ruta Provincial 67, 17.7 km N Gan Gan (2 km road to Cañada Leona): LJAMM-CNP 3554/58. *Liolaemus sagei* (8): NEUQUEN: Zapala Department: Ruta Provincial 46, 17.8 km SW junction Ruta Nacional 40, entrada NE Parque Nacional Laguna Blanca: LJAMM-CNP 8730/2. Collon Cura Deparment: northeastern shore of Laguna del Toro (= Laguna Barra Tom Cura´), 7 km south, 3.5 km east Cerro Mesa MLP.S 2227. Pampa de La Horqueta, just east of Estancia La Rinconada, 5 km west and 2.5 km north Cerro Horqueta MVZ 188706, intersection, 1 km south, 1 km east Laguna Jabon, Parque Nacional Laguna Blanca MLP.S 2228–9, MVZ 232162.

Specimens Examined (molecular): boulengeri complex: Liolaemus boulengeri: LJAMM-CNP 3610/12, Chubut Province, Cushamen Department, Ruta Provincial 12 y Embarcadero La Cancha (42°47' S; 70°57' W). Liolaemus inacayali: LJAMM-CNP 2818, Río Negro Province, 25 de Mayo Department, Ruta Nacional 23, 22.3 km E Ingeniero Jacobacci (41°18' S; 69°17' W), LJAMM-CNP 11103, Laguna Cari Lafquen Chica, 7 Km N Ingeniero Jacobacci (41°13' S; 69°24' W). Liolaemus senguer: LJAMM-CNP 2187, Chubut Province, Río Senguer Department, Ruta Provincial 20, 23 Km W Los Manantiales (45°27' S; 69°45' W); LJAMM-CNP 9180, Ruta Nacional 26, 22.3 km NW junction Ruta Provincial 18 (45°57' S; 69°52' W). LJAMM-CNP 5530: Liolaemus telsen, Chubut Province, Telsen Department, Ruta Provincial 4, 65,5 Km W Telsen (42°22' S; 67°39' W);

LJAMM-CNP 8693; Ruta Provincial 67, 10 km N Gan Gan (42°25' S; 68°16' W). donosobarrosi complex: Liolaemus donosobarrosi, LJAMM-CNP 5051, 5076, Mendoza Province, Malargüe Department, Ruta Provincial 180, 15 km S La Cortadera (36°39' S; 68°40' W). fitzingeri complex: Liolaemus canqueli: LJAMM-CNP 2200, Chubut Province, Paso de Indios Department, Ruta Provincial 53, between 7-20 Km SE Paso de Indios (43°56' S; 68°50' W). LJAMM-CNP 4665, Ruta Nacional 25, 5 km W Pampa de Agnia (43°44' S; 69°42' W). Liolaemus fitzingerii: LJAMM-CNP 4891, Santa Cruz Province, Deseado Department, 1 km W Tellier (47°39' S; 66°03' W). Liolaemus melanops: LJAMM-CNP 6007, Río Negro Province, Valcheta Department, Ruta Provincial 8 (41°58' S, 66°38' W); LJAMM-CNP 6017, 24 km W Cona Niyeu, road to El Cain (41°49' S; 67°10' W). Liolaemus morenoi: LJAMM-CNP 6477, 11246, Neuquén Province, Collon Curá Department, Ruta Nacional 40, 2 km S Cerrito Piñon, 19.1 km N junction Ruta Nacional 237 (40°17'S; 70°38' W). Liolaemus xanthoviridis: LJAMM-CNP 2284, Chubut Province, Ameghino Department, Ruta Provincial 1, 1 Km S Dos Pozos (43°54' S; 65°24' W). LJAMM-CNP 2420, Rawson Department, 12 km S Estancia Dos Naciones (43°32' S; 65°20 W). rothi complex: Liolaemus hermannunezi: LJAMM-CNP 14192/4, Chile, VIII Región, BioBío, Paso Pichachen, Ruta Antuco-Los Barros-Moncol, 10 km E de Los Barros, 37°31' S; 71°14'W. Liolaemus loboi:LJAMM-CNP 1217, Neuquén Province, Los Lagos Department, Ruta Nacional 231, 1 Km W junction Ruta Nacional 237 (41°01' S; 71°09' W). LJAMM-CNP 3091/2. Río Negro Province, Bariloche Department, Bariloche (41°09' S, 71°18' W). Liolaemus sagei: LJAMM-CNP 8730/1, Neuquén Province, Zapala Department, Ruta Provincial 46, 17.8 km SW junction Ruta Nacional 40, gate NE Parque Nacional Laguna Blanca (39°02'S; 70°16'W). Liolaemus tromen: LJAMM-CNP 12154/5, Neuquén Province, Chos Malal Department, Ruta Provincial 37, 29.2 km N junction Ruta Nacional 40, gate Area Natural Protegida Tromen, Laguna Los Barros (37°07' S; 70°08' W). LJAMM-CNP 11341, Neuquén Department, Ñorquin Province, Ruta Provincial 4, 14.4 km SE El Huecu (37°43' S; 70°29' W). Outgroup: Liolaemus lineomaculatus: LJAMM-CNP 7471, Santa Cruz Province, Deseado Department, 5.5 km N Puerto Deseado by coastal road (47°43' S; 65°50' W).