



A new species of the *Liolaemus alticolor-bibronii* group (Iguania: Liolaemidae) from East-central Argentina

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Abstract

We describe a new species of *Liolaemus* of the *L. alticolor-bibronii* group of the subgenus *Liolaemus* sensu stricto. We studied meristic, morphometric and qualitative pattern characters. Statistical tests were performed in order to evaluate morphological differences among the candidate species and the most closely geographically distributed species. Molecular analyses of Cyt-b mitochondrial gene were performed in order to estimate the position of the new species in relation to other taxa. We also recorded natural history data such as habitat, behavior, reproductive state, diet, and body temperature. *Liolaemus absconditus* sp. nov. differs from other species of *Liolaemus* in presenting a distinct combination of morphological character states of lepidosis and color pattern, being phylogenetically close to *Liolaemus tandiliensis*, *Liolaemus gracilis* and *Liolaemus saxatilis*. The new species is a saxicolous and endemic lizard of the Tandilia Mountain Range System of Buenos Aires Province.

Key words: Argentinean Pampas, Endemic, Lizard, Rocky habitat, new taxon

Introduction

Liolaemid lizards of the genera *Ctenoblepharys*, *Liolaemus* and *Phymaturus* are typically small diurnal reptiles of southern South America. They are distributed from the Andes of central Peru to the shores of Tierra del Fuego, encompassing elevations from sea level up to more than 5000 m (Ceí 1986, 1993; Etheridge & Espinoza 2000; Lobo & Quinteros 2005; Abdala 2007). Within this family, the *Liolaemus* genus currently has 262 species (Abdala *et al.* 2015) included into different taxonomic groups (Abdala & Quinteros 2014). *Liolaemus alticolor-bibronii* group is one of the 13 groups recognized in the subgenus *Liolaemus sensu stricto* (*chiliensis* group) (Quinteros 2012, 2013), and it has grown quickly since it was proposed (Ortiz 1981; Ceí 1986) currently comprising 30 species (Abdala *et al.* 2015). Recent molecular (Morando *et al.* 2007) and morphological studies (Quinteros 2013) have been published along with the addition of new species (Martínez *et al.* 2011; Quinteros 2012; Quinteros *et al.* 2014; Abdala *et al.* 2015). This group of lizards has the largest latitudinal distribution within the *Liolaemus* genus. They occupy high elevation areas, such as the Peruvian Andes, the Bolivian Plateau, and the Chilean and Argentinian Andean regions (Lobo *et al.* 2007; Díaz Gómez 2007), including the Patagonian forests (Quinteros 2012). As well as lower mountainous places of the Sierras Subandinas, Pampeanas and Septentrionales Bonaerenses (Tandilia), and in lowlands regions of the Atlantic coast of Argentina (Ceí 1993; Avila *et al.* 1992; Vega *et al.* 2008).

During the '90s, a saxicolous lizard morphologically different of *Liolaemus tandiliensis* was discovered in Sierra de Los Padres, part of the Tandilia mountain range of the Buenos Aires province (Argentina). This lizard was

included as *Liolaemus* sp. in the checklist of Tandilia's herpetofauna (Vega & Bellagamba 1990). At that time, two specimens were collected and sent for examination to Dr. Raymond Laurent at the Instituto de Herpetología of the Fundación Miguel Lillo, Argentina, who personally commented us about the likelihood of being a new species of *Liolaemus*. Lately, more individuals of this potential candidate species were detected in different sites of Sierra de Los Padres and also in Sierra La Brava and Sierra de la Vigilancia located 17 and 20 km NW from Sa. Los Padres, respectively. Individuals of this candidate species were found in environments similar to those described for *L. tandiliensis* (Vega *et al.* 2008), moving over horizontal and vertical planes of large blocks of rocks and using the crevices as retreats. New surveys of different geographical sites of the southeastern range of Tandilia's outcrops allowed us to be aware of the secretive habits and/or the seeming low abundance of this lizard.

In this study, we analyzed this candidate species and compared with a number of species of the *L. alticolor-bibronii* group and, in particular, with the most closely geographically distributed species: *Liolaemus tandiliensis*, *Liolaemus gracilis*, and *Liolaemus saxatilis* (Díaz Gómez & Lobo, 2006; Vega *et al.* 2008). A comparative study combining morphological characters and also molecular analyses of Cyt-b of this potential new taxon in order to estimate its position in relation to other taxa of the *L. alticolor-bibronii* group, is presented. The distribution of this potential new taxon could be relevant for conserving the unique habitat of Sierras Septentrionales (36° 30'–38° 10' S; 57° 30'–61° 00' W) in order to preserve this and other local endemisms enclosed within the highly modified pampas' ecosystem of the Buenos Aires province of Argentina.

Material and methods

As even one individual may be a significant loss from small populations whose conservation status is unknown, the individuals of this candidate species were extracted at different times (years) and from five different geographical points (mountain subsystems), taking into account the minimum required sample for a proper description. In order to describe this potential new taxon, we collected twelve specimens with a noose and then sacrificed them with over-anesthesia. Prior to fixation, samples of tail and liver tissues were extracted from two individuals. Fresh lizard bodies were fixed in 10% formalin and then stored in 70% ethanol.

Morphological analysis. To determine the taxonomic status, we studied the morphological characters traditionally used in *Liolaemus* taxonomy describing primarily lepidosis, color patterns, and body proportions used in phylogenetic analyses, including those of Laurent (1985), Cei (1986, 1993), Etheridge (1993, 1995, 2000), Etheridge & Espinoza (2000) Lobo (2001, 2005) and Quinteros (2012, 2013). Descriptions of color in life were based on visual observations of living animals, freshly collected specimens and the inspection of photographs of several individuals taken in the field. We registered visually dorsal and ventral coloration of individuals in the field, and also searched for any evidence of clinal variation or hybridization (i.e. morphologically intermediate individuals). Nomenclature for neck folds follows Frost (1992) and Abdala (2007) and that for color patterns follows Lobo & Espinoza (1999) and Abdala (2007). The observations of lepidosis characters and body measurements were done with the aid of a stereo microscope and a caliper with a precision of 0.01 mm. The following variables of lepidosis (and their abbreviations) were counted: Number of midbody scales (MS); Number of dorsal scales (DS); Number of temporal scales (TS); Number of neck scales (NS); Number of gular scales (GS); Number of lorilabial scales (LS); Number of supralabial scales (SS); Number of infralabial scales (IS); Number of ventral scales (VS); Number of preloacal pores (PP) (Quinteros 2013). When characters were bilateral, data were taken from the right side of the specimen. The following morphometric traits (and their abbreviations) were measured in mm: snout–vent length (SVL), head length (HL, from posterior edge of auricular opening to rostral scale), head width (HW, between corners of the mouth), head height (HH, between chin and frontal skull), body length (BL, from axilla to groin), foot length (FL, including fourth toe claw), and tail length (TL, from cloaca opening to the tip of the tail) (Vega *et al.* 2008).

For the purposes of diagnoses of the candidate new species described here, we examined type series of other species of the genus *Liolaemus* when available, including all currently recognized species of the *L. alticolor-bibronii* group with the exception of *L. cyaneinotatus*, *L. chavin*, *L. pachacutec*, and *L. wari* (the three latter are from Peru, and this material was not available). For species that were not collected, color pattern data were taken from the literature: the four species named above, plus *Liolaemus fuscus* Boulenger, 1885; *L. pseudolemniscatus* Lamborot and Ortiz 1990 and *L. walkeri* Shreve 1838 (Shreve 1938; Cei 1986; Pincheira–Donoso & Núñez 2005;

Scolaro 2005, 2006). We examined a total of 643 specimens from 18 Institutions from Argentina, Bolivia, Chile, and United States (specimens and species are listed in Appendix I). Institutional acronyms follow Leviton *et al.* (1985), with the exception of Colección Boliviana de Fauna (CBF), La Paz, Bolivia; Colección Herpetológica de la Facultad de Ciencias Exactas y Naturales (UNSJ), San Juan, Argentina; Colección Herpetológica del Centro de Biodiversidad y Genética (CBGR), Cochabamba, Bolivia; Museo de Ciencias Naturales de la Universidad Nacional de Salta (MCN), Salta, Argentina; Colección de Reptiles del Instituto de Biología Animal (IBA), Mendoza, Argentina, Colección Herpetológica del Laboratorio Vertebrados de la Facultad de Ciencias Exactas y Naturales de la Universidad Nacional de Mar del Plata (UNMDP), Mar del Plata, Argentina; Colección Zoológica de Zonas Áridas y Andinas, Universidad de Tarapacá (CZZA), Tarapacá, Chile; Colección Herpetológica del Instituto de Bio y Geociencias del NOA (IBIGEO) Salta, Argentina; Museo de Zoología de la Universidad de Concepción, (MZUC), Concepción, Chile; Carnegie Museum of Natural History (CMNH), Pittsburgh, United States; United States National Museum (USNM), Washington, United States; and Gustavo Scrocchi's field numbers collection (GS) to be entered to FML, Tucumán, Argentina. Specimens of the new species were deposited at Colección Herpetológica del Laboratorio Vertebrados de la Facultad de Ciencias Exactas y Naturales de la Universidad Nacional de Mar del Plata (UNMDP), and Colección Herpetológica del Instituto de Bio y Geociencias del NOA (IBIGEO) Salta, Argentina.

Statistical Analysis. We focalized in the comparative examination of the candidate species ($n=12$) and the most closely distributed species of the *L. alticolor-bibronii* group: *L. tandiliensis* ($n=21$), *L. gracilis* ($n=19$) and *L. saxatilis* ($n=22$), using univariate statistics to compare group (species) means of the meristic and morphometric variables separately. Homocedasticity and normality of data were checked with Levene and Shapiro-Wilks Tests, respectively, posteriorly using log 10 transformed data in some cases to fit those assumptions. One-way ANOVA and Tukey post-hoc ($\alpha = 0.05$) or, alternatively, non-parametric Kruskal Wallis with Dunn's post-hoc Test ($\alpha = 0.05$) in those cases that did not fit assumptions of normality and homocedasticity, were used (Zar 1984). When morphometric variables were correlated with overall body size (SVL) (checked by Pearson Correlation Tests, with $r > 0.50$, and $p < 0.05$), size-adjusted morphometric variables were calculated pooling all data and doing a regression of each variable against SVL to obtain the standardized residuals as input data (Shepard *et al.* 2011). Sexual dimorphism in meristic and morphometric characters of the candidate species was tested using Student's t Test or, in those cases where assumptions previously described were not met, Mann-Whitney U Test was implemented. All statistical analyses were carried out using R software, version 3.1.3 (R Core Team 2015).

DNA extraction, PCR amplification, and sequencing. Samples from caudal muscle and liver were obtained from two specimens of the candidate new species and three specimens of *Liolaemus tandiliensis* belonging to Universidad Nacional de Mar del Plata Herpetological Collection (see Appendix II for details). DNA extraction protocol followed Ocampo *et al.* (2013). A fragment of Cytochrome b mitochondrial gene (Cyt-b) was amplified using the light strand primer GluDGL (5'-TGACTTGAARAACCAAYCGTTG-3') and the heavy strand reverse primer C3 (5'-GGCAAATAGGAARTATCATTC-3') (Palumbi 1996). The F1 forward primer (5'-TGAGGACARATATCHTTYTGRGG-3') (Whiting *et al.* 2003) and the heavy strand reverse primer C3 were used to amplify an internal fragment (~400 bp) for sequencing. DNA mitochondrial samples were added to a PCR reaction mixture (20 μ l) containing 1 X PCR buffer, 1.5 mM MgCl₂, 0.2 mM deoxynucleotide triphosphates (dNTPs), 0.5 U DNA Taq enzyme (PBL- Biologics Products), 1 μ M primers mix (1:1), and 10 – 20 ng DNA. The PCR program was followed: 94 °C (4 min); 35 cycles of 94 °C (30 s), 52 °C (45 s), 72 °C (1 min); and 72 °C (5 min). Successful PCR reactions were confirmed with the aid of SYBR Gold (Invitrogen) in an agarose gel, purified using QIAquick Gel Extraction Kit (Quiagen), and then sequenced with the ABI Genetic Analyzer 3130xl y 3500xl (Applied Biosystems) following Applied Biosystems' protocols. For comparative analysis, available Cyt-b sequences of specimens of the *L. alticolor-bibronii* group were retrieved from GenBank (Appendix II). Sequences were aligned using ClustalW (Thompson *et al.* 1994), as implemented in MEGA v.7.0.25 software (Kumar *et al.* 2016).

Phylogenetic analysis. We used three approaches for sequence analysis to estimate the position of the new species in relation to other taxa of the *L. alticolor-bibronii* group. First, the model of evolution that best fit the data (GTR+G) was determined with the software JModelTest 2 based on both the BIC and AICc indices (Guindon & Gascuel 2003, Darriba *et al.* 2012). Phylogenetic analysis was conducted using MrBayes v.3.2.6 (Ronquist *et al.* 2012) for Bayesian inference (BI) and MEGA v.7.0.25 (Kumar *et al.* 2016) for maximum likelihood (ML) and maximum parsimony (MP). BI analysis was conducted by sampling two sets of four chains, for 10 x 10⁶

generations sampled at intervals of 1000 generations using default priors. The trees were retained after a burn-in of 25% to generate a 50% majority rule consensus tree. Posterior probability was reported in each branch. ML and MP analysis were performed with 1000 bootstrap replicates. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test is shown in each node. *Liolaemus punmahuida* was used as out-group for the species' trees estimations (Martinez *et al.* 2011)

Natural history. We registered notes on the habitat and behavior in the field. We also examined the reproductive state and stomach contents of twelve specimens of *Liolaemus sp. nov.* Females were considered adults if they had yolked follicles over 2 mm that were opaque and yellow, or oviductal eggs and/or distended oviducts (Vega *et al.* 2008). For males, sexual maturity was based on the presence of enlarged testes and convoluted epididymes. Stomach contents were examined under a stereomicroscope to identify arthropods items to the level of Order. We also measured lizards' body temperature in the field with an ultra-thin thermocouple connected to a digital thermometer (SC133, Schwyz MR., Buenos Aires, Argentina).

Results

Morphological comparisons. Means and ranks for meristic and morphometric characters registered for the closely distributed species: *L. tandiliensis*, *L. gracilis*, *L. saxatilis*, and *L. sp. nov.*, are summarized in Table 1. Comparisons of these characters through univariate statistics differentiated *Liolaemus sp. nov.* from *L. tandiliensis* by having less number of temporal, neck, gular and ventral scales. Besides, compared to *L. saxatilis*, *Liolaemus sp. nov.* had more number of midbody, dorsal and supralabial scales. On the other hand, *Liolaemus sp. nov.* had less number of neck scales than *L. gracilis* which, in contrast with the other two species, showed differences with *Liolaemus sp. nov.* in some morphometric characters, as snout-vent length was larger and the head length, head width and foot length was shorter in *L. gracilis* than in *Liolaemus sp. nov.* (Table 1). There were found no evidences of sexual dimorphism in meristic and morphometric characters of the new species (Table 2).

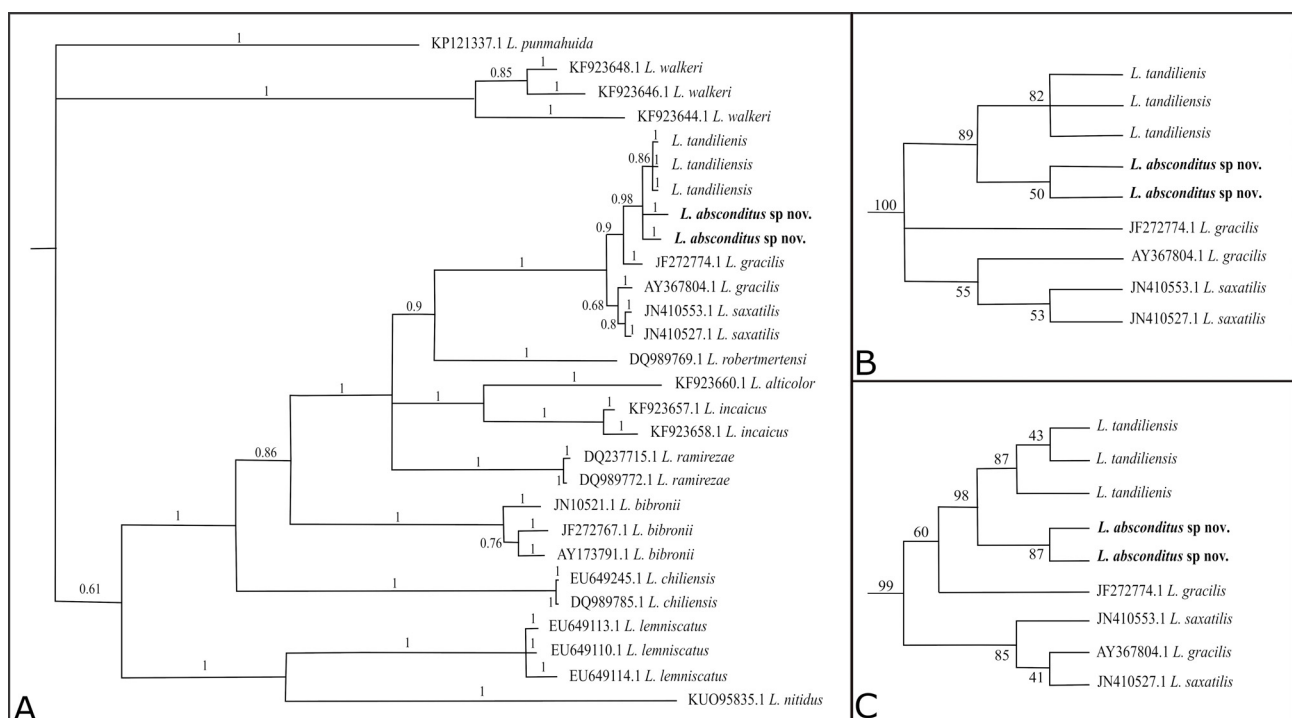


FIGURE 1. Bayesian consensus tree (A) based on Cyt-b showing the position of *Liolaemus sp. nov.* in relation to other taxa of the *L. alticolor-bibronii* group. Posterior probability values are indicated in each branch. Maximum Likelihood (B) and Maximum Parsimony consensus trees (C) inferred from 1000 replicates showing the relationships among *L. sp. nov.*, *L. tandiliensis*, *L. gracilis* and *L. saxatilis*. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown in each node.

TABLE 1. Meristic and morphometric attributes of *Liolaemus sp. nov.*, *L. tandiliensis*, *L. gracilis*, and *L. saxatilis*. Range to the left, and mean in brackets. F: Fisher's statistic. H: Kruskal-Wallis statistic MS: Number of midbody scales. DS: Number of dorsal scales. TS: Number of temporal scales. NS: Number of neck scales. GS: Number of gular scales. LS: Number of lorilabial scales. SS: Number of supralabial scales. IS: Number of infralabial scales. VS: Number of ventral scales. PP: Number of precloacal pores. SVL: Snout-vent length, mm. HL: Head length, mm. HW: Head width, mm. HH: Head height, mm. BL: axilla-groin distance, mm. FL: foot length, mm. TL: Tail length, mm. P: probability value. n: sample size. df: degrees of freedom. (*) Indicates differences whereas (=) indicates no significant differences according to the results of post-hoc tests, where only the contrasts for *L. sp. nov.* are shown. (1) only males were considered. (2) only adult individuals were considered. (3) only individuals with non-injured tails were considered.

Species/ Character	<i>L. absconditus sp. nov.</i>	<i>L. tandiliensis</i>	<i>L. gracilis</i>	<i>L. saxatilis</i>	Statistic	P	Post-hoc test
MERISTIC	n = 12	n = 21	n = 19	n = 22			
MS	39-46 (43.16)	38-48 (42.90)	36-44 (40.15)	31-46 (38.22)	H = 22.52 df: 3	< .001	<i>L</i> α = <i>L</i> <i>t</i> ; <i>L</i> α = <i>L</i> <i>g</i> ; <i>L</i> α ≠ <i>L</i> <i>s</i>
DS	40-49 (42.83)	40-50 (43.33)	37-48 (41.63)	35-46 (39.91)	H = 16.44 df: 3	< .001	<i>L</i> α = <i>L</i> <i>t</i> ; <i>L</i> α = <i>L</i> <i>g</i> ; <i>L</i> α ≠ <i>L</i> <i>s</i>
TS	6-7 (6.83)	6-9 (8.04)	6-8 (6.63)	6-10 (7.63)	$F_{3,70} = 21.01$	< .001	<i>L</i> α ≠ <i>L</i> <i>t</i> ; <i>L</i> α = <i>L</i> <i>g</i> ; <i>L</i> α = <i>L</i> <i>s</i>
NS	19-23 (20.83)	20-27 (23.57)	22-26 (23.94)	18-25 (21.81)	$F_{3,70} = 10.92$	< .001	<i>L</i> α ≠ <i>L</i> <i>t</i> ; <i>L</i> α ≠ <i>L</i> <i>g</i> ; <i>L</i> α = <i>L</i> <i>s</i>
GS	24-30 (27.25)	27-37 (32.38)	25-33 (28.26)	23-35 (28.04)	$F_{3,70} = 15.30$	< .001	<i>L</i> α ≠ <i>L</i> <i>t</i> ; <i>L</i> α = <i>L</i> <i>g</i> ; <i>L</i> α = <i>L</i> <i>s</i>
LS	6-7 (6.16)	5-7 (6)	5-8 (6.10)	1-8 (6.54)	H = 13.64 df: 3	< .05	<i>L</i> α = <i>L</i> <i>t</i> ; <i>L</i> α = <i>L</i> <i>g</i> ; <i>L</i> α = <i>L</i> <i>s</i>
SS	5-6 (5.75)	5-7 (5.95)	5-6 (5.31)	4-7 (5.18)	H = 24.07 df: 3	< .001	<i>L</i> α = <i>L</i> <i>t</i> ; <i>L</i> α = <i>L</i> <i>g</i> ; <i>L</i> α ≠ <i>L</i> <i>s</i>
IS	4-5 (4.16)	4-5 (4.10)	4-5 (4.26)	4-5 (4.18)	H = 1.92 df: 3	0.584	-----
VS	70-80 (73.33)	72-90 (80.71)	68-83 (75.37)	64-83 (74.09)	H = 16.00 df: 3	< .05	<i>L</i> α ≠ <i>L</i> <i>t</i> ; <i>L</i> α = <i>L</i> <i>g</i> ; <i>L</i> α = <i>L</i> <i>s</i>
PP ⁽¹⁾	3-5 (4.50) (n = 5)	3-5 (4.00) (n = 9)	3-4 (4.00) (n = 9)	3-4 (4.00) (n = 12)	H = 6.21 df: 3	0.101	-----
MORPHOMETRIC ⁽²⁾	n = 8	n = 21	n = 19	n = 22			
SVL	26.30-58.31 (44.69)	40.73-57.95 (50.45)	36.31-58.15 (45.61)	40.62-55.77 (48.84)	$F_{3,66} = 4.59$	< .05	<i>L</i> α = <i>L</i> <i>t</i> ; <i>L</i> α ≠ <i>L</i> <i>g</i> ; <i>L</i> α = <i>L</i> <i>s</i>
HL	7.44-14.01 (10.39)	9.62-12.25 (10.98)	8.37-12.59 (9.87)	9.93-12.57 (10.88)	$F_{3,66} = 3.28$	< .05	<i>L</i> α = <i>L</i> <i>t</i> ; <i>L</i> α ≠ <i>L</i> <i>g</i> ; <i>L</i> α = <i>L</i> <i>s</i>
HW	5.06-10.06 (7.57)	6.56-9.20 (8.01)	5.87-9.19 (7.06)	6.84-9.79 (8.06)	$F_{3,66} = 4.67$	< .05	<i>L</i> α = <i>L</i> <i>t</i> ; <i>L</i> α ≠ <i>L</i> <i>g</i> ; <i>L</i> α = <i>L</i> <i>s</i>
HH	3.31-6.81 (5.26)	4.51-7.30 (5.34)	4.37-6.26 (5.20)	4.77-7.63 (6.06)	$F_{3,66} = 10.25$	< .001	<i>L</i> α = <i>L</i> <i>t</i> ; <i>L</i> α = <i>L</i> <i>g</i> ; <i>L</i> α = <i>L</i> <i>s</i>
BL	13.21-29.86 (21.14)	19.24-30.11 (24.86)	17.10-28.29 (21.31)	15.63-30.69 (23.89)	$F_{3,66} = 1.02$	0.389	-----
FL	9.82-17.48 (14.06)	12.92-18.90 (14.98)	11.06-14.68 (12.83)	12.06-16.20 (13.60)	$F_{3,66} = 10.08$	< .001	<i>L</i> α = <i>L</i> <i>t</i> ; <i>L</i> α ≠ <i>L</i> <i>g</i> ; <i>L</i> α = <i>L</i> <i>s</i>
TL ⁽³⁾	51.33-113.03 (79.91) (n = 8)	70.11-76.65 (74.09) (n = 3)	69.63-94.11 (82.10) (n = 11)	74.11-109.23 (89.65) (n = 8)	H = 4.19 df: 3	0.241	-----

TABLE 2. Comparison of meristic and morphometric characters between males and females of *L. absconditus* sp. nov. *t* = Student's statistic ($\alpha = 0.05$), *U* = Mann-Whitney's statistic ($\alpha = 0.05$), *n* = number of samples, *P* = probability value.

Character	Statistic	<i>n</i>	<i>P</i>
Meristic			
MS	<i>t</i> = 0.23	12	0.823
DS	<i>t</i> = 1.72	12	0.115
TS	<i>U</i> = 24.50	12	0.268
NS	<i>t</i> = -0.40	12	0.695
GS	<i>t</i> = 0.92	12	0.377
LS	<i>U</i> = 16.50	12	0.876
SS	<i>U</i> = 10.00	12	0.268
IS	<i>U</i> = 16.50	12	0.876
VS	<i>U</i> = 7.50	12	0.106
Morphometric			
SVL	<i>t</i> = -0.95	8	0.378
HL	<i>U</i> = 14.00	8	0.071
HW	<i>U</i> = 6.00	8	0.786
HH	<i>t</i> = -1.35	8	0.226
AG	<i>t</i> = -0.58	8	0.579
FL	<i>t</i> = -0.43	8	0.680
TL	<i>U</i> = 14.00	8	0.070

Phylogenetic analysis. Segments of ~400 bp in length of mitochondrial gene Cyt-b were obtained from two specimens of *Liolaemus* sp. nov. and three specimens of *Liolaemus tandiliensis*. The three phylogenetic analysis (BAY, ML, and MP) resulted in well-supported and topologically similar trees. These trees depict the position of *L. sp nov.* and the position of *L. tandiliensis* based in comparisons of these Cyt-b sequences with those of other taxa of the *L. alticolor-bibronii* group. In this sense, results showed that *L. sp nov.* and *L. tandiliensis* were clustered together in a monophyletic clade with respect to the rest of the members of the group, and also that *L. gracilis* and *L. saxatilis* were the closest-related taxa to *L. sp nov.* and *L. tandiliensis* (Fig. 1).

Species Account. *Liolaemus absconditus* sp. nov.
(Fig. 2)

1990. *Liolaemus* sp., Vega L. & Bellagamba P., Cuadernos de Herpetología, 5, 10–14.

Holotype. UNMDP 1817. Male. (Fig. 3)

Estancia Paititi. Sierra de la Peregrina. Partido de General Pueyrredón. (37° 55' 40.74'' S; 57° 49' 05.84'' W). Buenos Aires Province. Argentina. 22 May 2013. Stelatelli, O., Block, C. & Isacch, J.P. cols.

Paratypes. UNMDP 0565. Sierra de los Padres (37° 56' 30.74'' S; 57° 48' 05.15'' W), Partido de General Pueyrredón, Buenos Aires Province, Argentina. 01 July 1985; Vega, L. & Bellagamba P. cols. UNMDP 0566. Sierra de los Padres (37° 56' 30.74'' S; 57° 48' 05.15'' W), Partido de General Pueyrredón, Buenos Aires Province, Argentina. 02 November 1986; Vega, L. & Bellagamba, P. cols. UNMDP 1782, IBIGEO-R 5459 (ex UNMDP 1783). Sierra La Brava (37° 53' 53.15'' S; 58° 00' 01.70'' W), Partido de Balcarce, Buenos Aires Province, Argentina. May 2009; Larrubia, L. & Stelatelli, O. cols. UNMDP 1817. Estancia Paititi (37° 55' 40.74'' S; 57° 49' 05.84'' W), Sierra de La Peregrina, Partido de General Pueyrredón. Buenos Aires Province. Argentina. 22 May 2013; Stelatelli, O., Block, C. & Isacch, J.P. cols. UNMDP 1818. Estancia Paititi (37° 55' 04.10'' S; 57° 49' 15.73'' W), Sierra de La Peregrina, Partido de General Pueyrredón, Buenos Aires Province, Argentina. 08 June 2013;

Stellatelli, O. col. UNMdP 1823. Estancia Paititi. (37° 55' 35.40" S; 57° 49' 09.20" W). Sierra de la Peregrina, Partido de General Pueyrredón, Buenos Aires Province, Argentina. 05 May 2013; Stellatelli, O. & Rocca, C. cols. UNMdP 1824. Estancia Paititi. (37° 55' 35.40" S; 57° 49' 09.20" W), Sierra de la Peregrina, Partido de General Pueyrredón, Buenos Aires Province, Argentina. 05 May 2013; Stellatelli, O. col. UNMdP 1825. Sierra La Vigilancia (37° 52' 00.01" S; 58° 01' 24.90" W), Partido de Balcarce, Buenos Aires Province, Argentina. 23 March 2014; Stellatelli, O. & Rocca, C. cols. UNMdP 1826–27. Sierra de los Difuntos (37°53'19.53" S; 57°50'21.23" W), Partido de Gral Pueyrredón, Buenos Aires Province, Argentina. 30 March 2014; Bellagamba, P., Vega, L., Stellatelli, O. & Block, C. cols. IBIGEO-R 5460 (ex UNMdP 1830). Sierra de los Difuntos (37° 53' 21.38" S; 57° 50' 27.64" W). Partido de General Pueyrredón, Buenos Aires Province, Argentina. 05 March 2015; Stellatelli, O. & Villalba, A. cols.

Diagnosis. *Liolaemus absconditus* **sp. nov.** is a small (Max SVL 58.3 mm), slender species member of the *L. alticolor-bibronii* group. It is a member of the *L. alticolor-bibronii* group because exhibits the character states proposed by Quinteros (2012, 2013) for this group. As a member of this group, *L. absconditus* **sp. nov.** differs in color pattern from the species members of *L. belli*, *L. chillanensis*, *L. elongatus*, *L. kriegi*, *L. leopardinus*, *L. monticola*, *L. nigromaculatus*, and *L. pictus* groups. Some of the members of the *L. gravenhorsti* and *L. robertmertensi* groups show a similar color pattern, but those species differ from those of the *L. alticolor-bibronii* group in the maximum SVL (65 mm in those two groups, and, 60 mm in *L. alticolor-bibronii* group). The members of the *L. alticolor-bibronii* group also have well-developed neck folds, which are absent in some species of the *L. robertmertensi* and *L. gravenhorsti* groups. *L. absconditus* **sp. nov.** is phenetically and geographically close to *L. tandiliensis* and *L. gracilis*. But the new species exhibits a combination of character states which distinguish it from these and from all other species of the group.

Specimens of *L. absconditus* **sp. nov.** show dorsal scales with an evident mucron, whereas the mucron is absent in dorsal scales of *L. tandiliensis*. Temporal scales of *L. absconditus* **sp. nov.** are slightly keeled whereas in *L. gracilis* are smooth. Besides, temporal scales in the new species are in less number than in *L. tandiliensis* (Table 1). Neck scales of *L. absconditus* **sp. nov.** are laminar and keeled, distinguishing from laminar and smooth neck scales of *L. gracilis*. Neck scales in a *L. absconditus* **sp. nov.** are in less number than in *L. tandiliensis* and *L. gracilis* as well (Table 1). Subocular scale is whitish (lighter than loreal region) in *L. tandiliensis*, whereas in *L. absconditus* **sp. nov.** and *L. gracilis* the subocular scale shows the same color than loreal region. Paravertebral spots are evident in *L. tandiliensis*, but absent in *L. gracilis* and in the new species. In *L. absconditus* **sp. nov.**, dorsolateral stripes are absent or barely visible without black border, being evident in *L. tandiliensis*, and evident, bordered in black, and wider in *L. gracilis*. Vertebral line is absent in *L. absconditus* **sp. nov.** distinguishing from *L. gracilis* (evident and segmented) and from *L. tandiliensis* (evident in some specimens). Vertebral line in dorsal surface of the tail is evident in *L. gracilis* and *L. tandiliensis*, but absent in *L. absconditus* **sp. nov.** Throats of *L. tandiliensis* and *L. absconditus* **sp. nov.** are immaculate (spotless), differing from males of *L. gracilis* (black lines in throat).

Dorsal scales of *L. absconditus* **sp. nov.** show an evident mucron, differing from *L. alticolor*, *L. chavin*, *L. pachacutec*, *L. paulinae*, and *L. tacnae* (without mucron). Upper temporal scales are slightly keeled in *L. absconditus* **sp. nov.**, being smooth in *L. bibronii*, *L. paulinae*, *L. pachacutec*, *L. puna*, *L. tacnae*, and *L. walkeri*; and markedly keeled in *L. alticolor*, *L. aparicioi*, *L. bitaeniatus*, *L. cyaneinotatus*, *L. lemniscatus*, *L. sanjuanensis*, *L. saxatilis*, and *L. variegatus*. Scales of neck are laminar and keeled in *L. absconditus* **sp. nov.**, distinguishing from *L. bibronii*, *L. exploratorum*, and *L. yalguaraz* (laminar and smooth), from *L. abdalai*, *L. curicensis*, and *L. puna* (some scales are keeled), from *L. alticolor* and *L. yanalco* (laminar and weakly keeled), and from *L. chungara* (which exhibits both granular and laminar scales). Subocular scale is whitish (lighter than loreal region) in *L. alticolor*, *L. bibronii*, *L. bitaeniatus*, *L. pagaburoi*, *L. ramirezae*, *L. variegatus*, and *L. walkeri*, whereas *L. absconditus* **sp. nov.** exhibits the same color than loreal region. Dorsal surface of the head is smooth in *L. absconditus* **sp. nov.**, being slightly rough in *L. exploratorum* and *L. pagaburoi* and markedly rough in *L. bitaeniatus*, *L. lemniscatus*, *L. saxatilis*, *L. tacnae*, and *L. variegatus*. In *L. absconditus* **sp. nov.** there are two scales between canthal and nasal, being one scale in *L. alticolor*, *L. bibronii*, *L. bitaeniatus*, *L. chaltin*, *L. fuscus*, *L. incaicus*, *L. lemniscatus*, *L. pagaburoi*, *L. paulinae*, *L. puna*, *L. pyriphlogos*, *L. ramirezae*, *L. tacnae*, *L. variegatus*, *L. walkeri*, and *L. yalguaraz*. Lack of precloacal pores in females distinguishes the new taxon from *L. aparicioi*, *L. bitaeniatus*, *L. incaicus*, *L. ramirezae*, *L. variegatus*, and *L. yanalco* (females exhibit precloacal pores). The absence of paravertebral markings, distinguishes the new taxon from *L. abdalai*, *L. bibronii*, *L. exploratorum*, *L.*

incaicus, *L. lemniscatus*, *L. pagaburoi*, *L. robertmertensi*, *L. sanjuanensis*, *L. saxatilis*, and *L. variegatus*. Vertebral line is absent in *L. absconditus* **sp. nov.** differing from *L. alticolor*, *L. aparicioi*, *L. bibronii*, *L. chavin*, *L. curicencis*, *L. cyaneinotatus*, *L. gracilis*, males of *L. incaicus*, *L. pachacutec*, females of *L. puna*, *L. pyriphlogos*, *L. sanjuanensis*, *L. tacnae*, *L. variegatus*, *L. walkeri*, and *L. wari*. Throat of the new species is immaculate, differing from *L. alticolor*, *L. chungara*, *L. pagaburoi*, *L. puna*, *L. pyriphlogos*, *L. variegatus*, *L. walkeri*, and *L. yalguaraz*. Males of *L. chavin*, *L. pachacutec*, *L. wari*, and *L. walkeri* exhibit partial or total ventral melanism, which is absent in *L. absconditus* **sp. nov.**

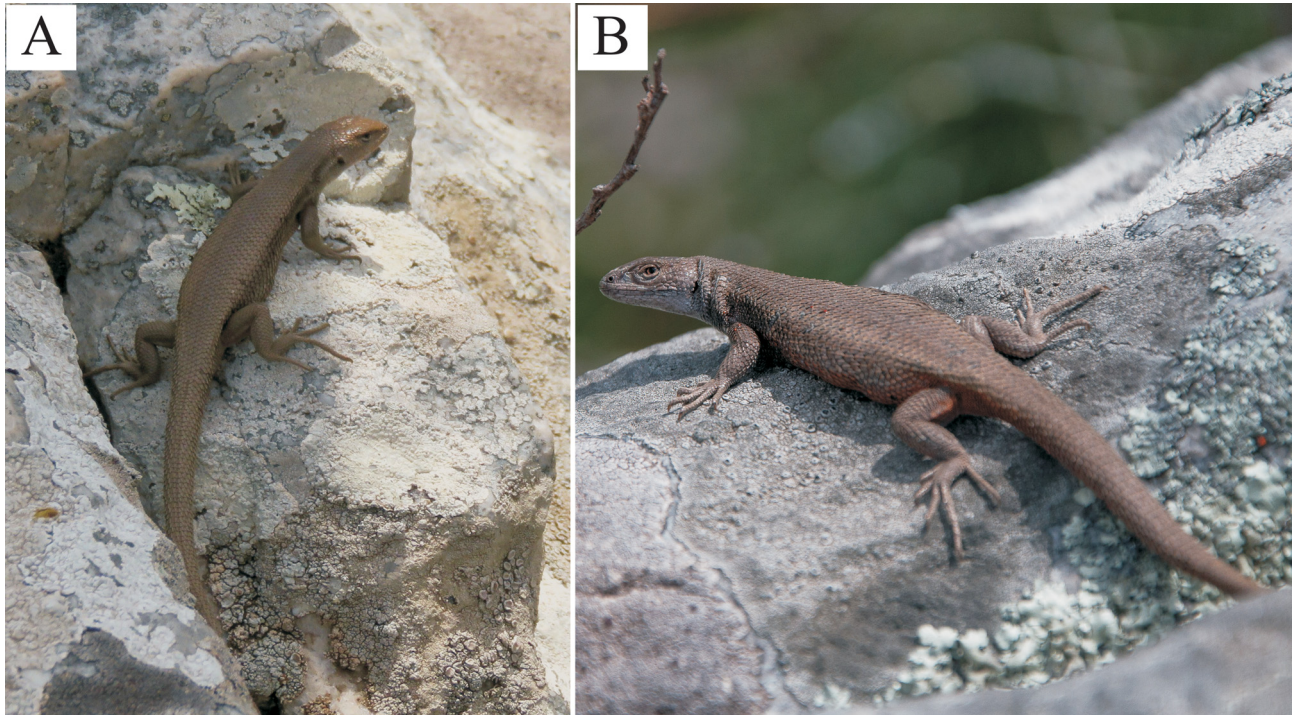


FIGURE 2. Color in life of A- a male of *Liolaemus absconditus* **sp. nov.** (Photo: Oscar Stellatelli) and B- a female of *Liolaemus absconditus* **sp. nov.** (Photo: Carolina Block) in rocky outcrops of Sierra de los Difuntos, Mar del Plata, Buenos Aires, Argentina (37° 53' 19.53" S; 57° 50' 21.23" W).

Description of the holotype. Adult male. Snout-vent length (SVL) 50.1 mm; Axilla-groin distance 20.8 mm. Head 11.5 mm long (from anterior border of auditory meatus to tip of snout), 8.8 mm wide (at anterior border of auditory meatus), 6.1 mm high. Interorbital distance (between postorbital semicircles) 5.9 mm. Eye-nostril distance 4.4 mm. Tibia length 8.3 mm. Foot length 6.4 mm (from ankle to tip of claw on fourth toe). Tail length 96.3 mm. Dorsal head scales smooth between rostral and anterior border of auditory meatus. Seven temporals, uppers slightly keeled. Interparietal subpentagonal, smaller than parietal, surrounded by five scales. Frontal azygous. Six scales between frontal and rostrals, five between frontal and superciliaries. Two postrostrals with seven (left) and five (right) scale organs each. Supraorbital semicircles incomplete. Five supraoculars, three of them enlarged. Six superciliaries flat, elongate, imbricate. Canthal separated from nasal by two scales. Loreal region flat. Six scales, including rostral, surrounding nasals. Nasals in broad contact with rostral. Six lorilabials, lorilabials 4–6 contacting subocular. Six enlarged supralabials; supralabial 4 curved dorsal posteriorly, not contacting subocular. Four infralabials, slightly taller than supralabials. Orbit with 13 upper and 11 lower ciliaries. Subocular scale elongate, 3.6 mm long. Preocular unfragmented, 0.8 mm long. Postocular length 1.6 mm. Longitudinal ridge along upper margin of the three ocular scales. Rostral scale 3.1 times wider (2.8 mm) than high (0.9 mm). Mental 1.8 times wider (2.5 mm) than high (1.4 mm), followed posteriorly by two rows of four chinshields. Two scales in contact with second infralabial ventrally. Scales of throat between chinshields sub-imbricate. Twenty-nine gulars, between both auditory meatuses. Auricular scale evident, four (one enlarged) outward projecting laminar scales along anterior border of auditory meatus. Auditory meatus higher (2.3 mm) than wide (0.6 mm). Scales of neck laminar and keeled. Antehumeral fold distinct. Nineteen scales on neck (between posterior margin of auditory meatus and

shoulder). Forty-one dorsal scales between occiput and anterior surface of thighs. Dorsal body scales lanceolate, imbricate, keeled, and with evident mucron. Forty-four scales around midbody. Seventy-three ventrals between mental and precloacal pores row. Four precloacal pores. Fourth finger with 22 subdigital lamellae. Fourth toe with 24 subdigital lamellae.

Color of the holotype in ethanol. Dorsal background color uniform brown. Paravertebral spots, and vertebral line absent. Dorsolateral stripes faded, barely visible. Lateral field slightly darker than dorsum. Ventrolateral region lighter than dorsum. Ventrolateral line absent. Dorsal and lateral region of head same color as dorsum. Granular scales of eye, light gray. Mental, and first lorilabial scales (left and right) gray (owing to fixation). Temporal and neck region same color as dorsum. Region below auditory meatus gray. Subocular scale same color than loreal region. Fore and hind limbs same color as dorsum. Tail, dorsally same color as dorsum, without vertebral line. Throat, chest, and belly gray. Throat darker than chest and belly. Ventral scales with tiny black spots. Femoral regions cream-colored. Cloacal region gray. Tail ventrally light brown.

Variation. Based on eleven paratypes (six females and five males). Snout-vent length 32.7–58.3 mm ($X = 46.5 \pm 11.1$) in males and 26.3–49.5 ($X = 41.3 \pm 11.4$) in females; Axilla-groin distance 15.4–29.8 mm ($X = 22.0 \pm 6.1$) in males and 13.2–28.6 mm ($X = 20.0 \pm 6.5$) in females; Head length 8.2–14.0 mm ($X = 10.8 \pm 2.5$) in males and 10.2–11.2 mm ($X = 9.6 \pm 1.4$) in females; Head width 5.8–10.0 mm ($X = 7.9 \pm 1.7$) in males and 5.0–8.7 mm ($X = 6.9 \pm 1.4$) in females; Head height 4.1–6.8 mm ($X = 5.5 \pm 1.1$) in males and 3.3–5.9 mm ($X = 4.8 \pm 1.0$) in females; Foot length 10.5–17.4 mm ($X = 14.3 \pm 2.5$) in males and 9.8–14.7 mm ($X = 13.1 \pm 2.9$) in females; Tail length 63.0–113.0 mm ($X = 80.4 \pm 22.3$) in males and 51.3–92.9 mm ($X = 75.2 \pm 19.7$); Midbody scales 39–46 ($X = 43.2 \pm 2.5$); Dorsal scales 40–49 ($X = 42.8 \pm 2.7$) between occiput and anterior surface of thighs; Dorsal head scales 11–14 ($X = 12.6 \pm 0.7$); Ventrals 70–80 ($X = 73.3 \pm 2.8$); Scales around interparietal 5–7 ($X = 5.7 \pm 0.7$); Supraoculars 4–5, three to four of them enlarged; Preocular not divided, not fused to subocular; Temporals 6–7 ($X = 6.8 \pm 0.4$), upper slightly keeled; Neck scales from posterior edge of auricular meatus to shoulder 19–23 ($X = 20.8 \pm 1.5$), keeled; Gulars 24–30 ($X = 27.2 \pm 1.9$); Supralabials 5–6 ($X = 5.7 \pm 0.4$); Infralabials 4–5 ($X = 4.1 \pm 0.4$); Posterior tip of fourth supralabial upturned, contacting subocular in 50% of specimens; Six to seven ($X = 6.7 \pm 0.5$) scales around nasal; Internasals 4; Scales between rostral and frontal 5–7 ($X = 5.7 \pm 0.7$); Postrostrals 2 with 2–9 scale organs on the left one ($X = 6 \pm 2.2$) and 3–8 on the right one ($X = 4.9 \pm 1.4$); Lorilabials 6–7 ($X = 6.2 \pm 0.4$), 3–4 of them contacting subocular scale; Subdigital lamellae on fourth finger 17–18 ($X = 17.2 \pm 0.5$), on fourth toe 21–26 ($X = 23.2 \pm 1.5$); Precloacal pores 3–5 in males ($X = 4.5 \pm 1.2$), absent in females.

Color in life. Dorsal background color brown to gray. Two light brown dorsolateral stripes are evident. Those begin on posterior margin of auditory meatus and extend to hindlimbs. Paravertebral spots and vertebral line absent. Lateral field darker than dorsum. Ventrolateral line absent. Ventrolateral region brownish gray or light brown. Lateroventral region and ventral surface of hindlimbs and tail bright orange during reproductive season. Dorsal head with same background as dorsum. Lateral head same background as dorsum. Neck same color as lateral field. Fore and hind limbs dorsally same color as dorsum. Tail dorsally same background color as dorsum, without vertebral line. In some specimens, tail can be lighter than dorsum. Throat, chest, and belly, gray spotless. Cloacal region and ventral surface of thighs yellow-orange in males, gray in females. Ventral surface of tail, light brown.

Natural history. In general terms, components of habitat structure of *L. absconditus* sp. nov. are similar to those of the sympatric *Liolaemus tandiliensis*, that is, patches of rocks within a mosaic landscape of mountains that rises up at 50–250 m over the plain. The new species is a genuine saxicolous form, whose individuals are moving over nearly flat and also inclined rocky substrates, even though when threatened they may flee to proximal vegetated patches or crevices between rocks. Preferred microhabitats are mainly under the eaves of large quartzite rocks that cover smooth rocky platforms and medium to large rocks at the upper raised area of the range of mountains. Individuals are mainly seen basking in sunny patches of less exposed sites between rocks, rather in the open sunny surfaces of the vertical walls. Two aggressive encounters between adult individuals of *L. absconditus* sp. nov. and *L. tandiliensis* were observed, in both occasions initial attacks corresponded to *L. tandiliensis* obtaining withdrawal of the new species. Individuals of *L. absconditus* sp. nov. are mostly active from late winter (August) through spring and summer, to early autumn (May), although some may be seen in sunny days of winter. Daily activity starts with basking behavior at approximately 9.00–10.00 h and activity continues to the afternoon (approximately 17.00–18.00 h). Field body temperatures were recorded in seven individuals ranging from 34.2 to 38.2°C, being the mean body temperature of 35.92 °C.

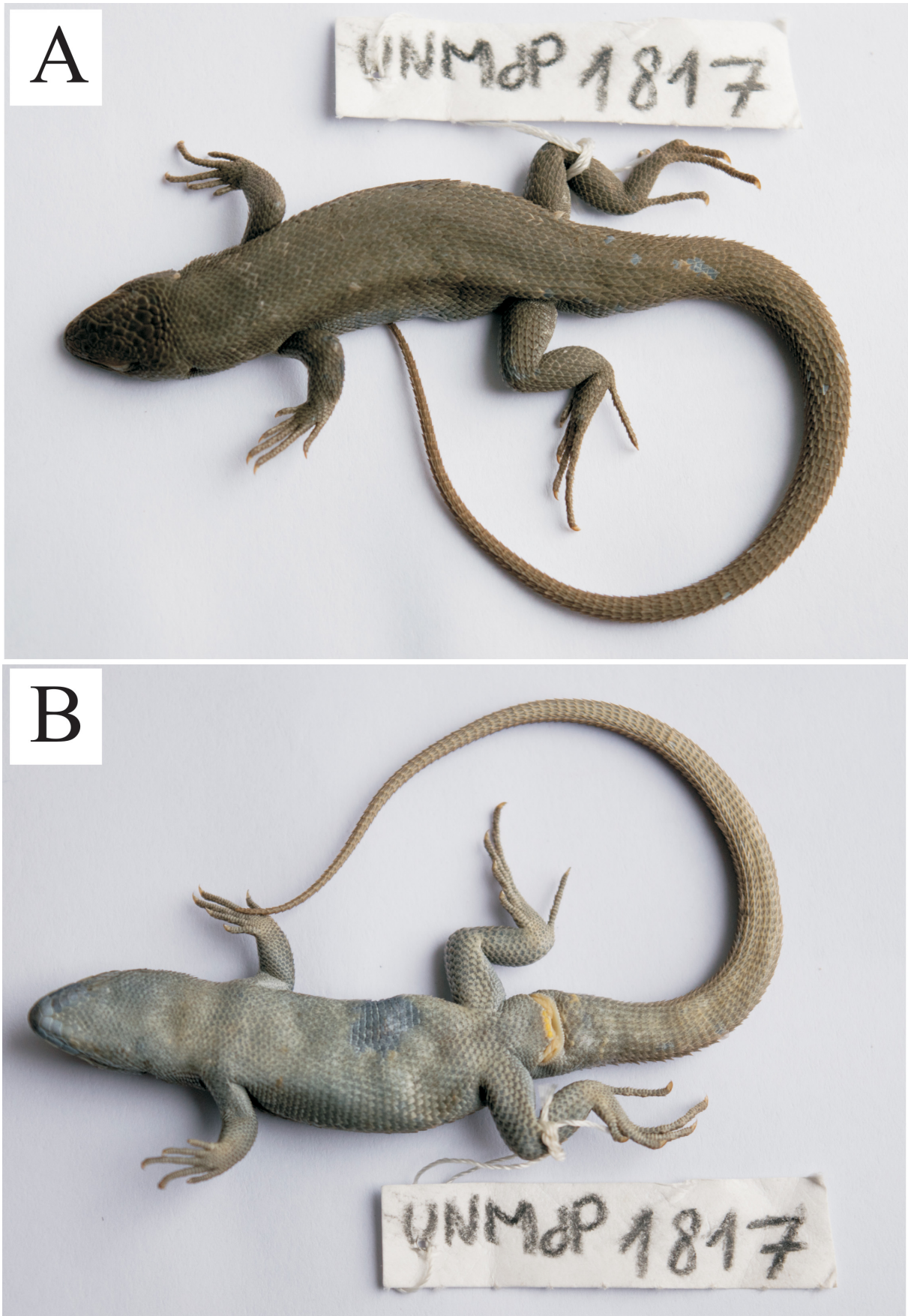


FIGURE 3. Holotype (UNMdp 1817) of *Liolaemus absconditus* sp. nov. Snout-vent length: 50.1 mm. (A) Dorsal view and (B) ventral view. Photos: Carolina Block.

Liolaemus absconditus **sp. nov.** is probably oviparous like *L. tandiliensis*, *L. gracilis*, and *L. saxatilis*. (Avila *et al.* 1992; Vega & Bellagamba 2005, Vega *et al.* 2008), although due to the low sample of females no oviductal eggs were detected, which it might confirm this mode of reproduction. Yolked follicles were registered in a number of 1–2 per ovary, so, based on this number, clutch size might vary between two and four eggs. This species appears to feed on a variety of insects and other small arthropods. Stomach contents ($n = 12$) showed mainly adult individuals of Coleoptera. External parasites (Acarina) were extracted from five of the twelve specimens collected.

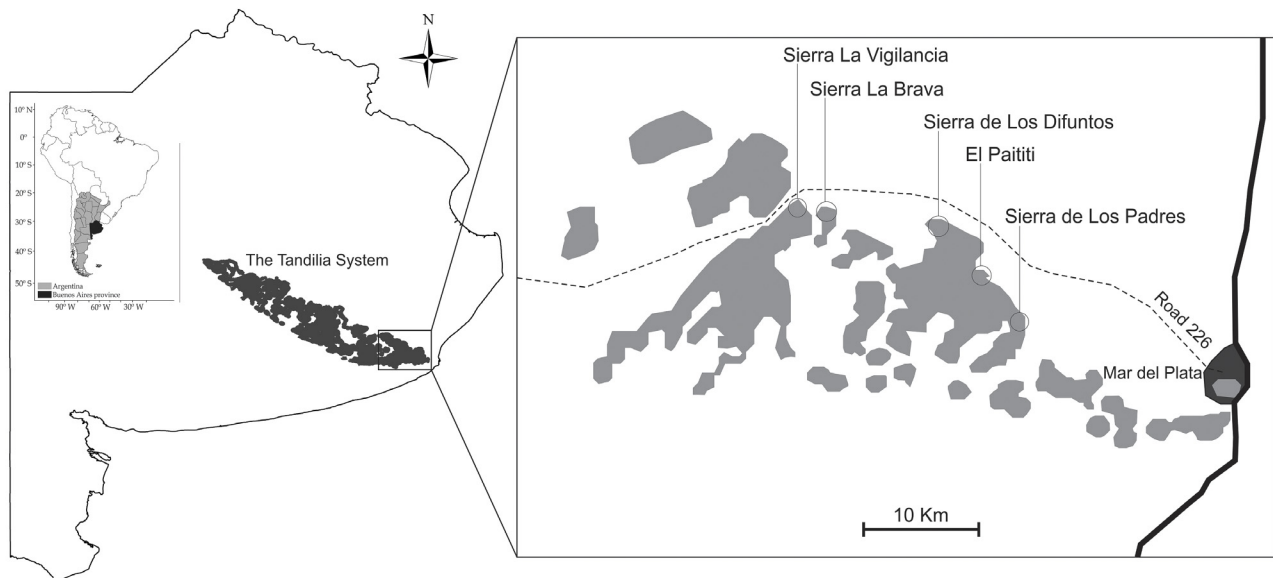


FIGURE 4. Known distribution of *Liolaemus absconditus* **sp. nov.** in Buenos Aires province of Argentina.

Distribution. *L. absconditus* **sp. nov.** is known only from the Tandilia Mountain Range System (Fig. 4). Localities where this species was found included Sierra de los Padres, Sierra de los Difuntos (both in Sierra de la Peregrina of Mar del Plata subsystem), Sierra La Brava and Sierra de la Vigilancia (included in the Balcarce subsystem) The range of the new species could be constant all over the area of Tandilia, but as the extreme NW and the central part of these range was not surveyed yet, we cannot confirm this range.

Etymology. The name *absconditus* comes from Latin and means hidden, concealed, and secret. This name refers to the secretive and underexposed habits of this lizard.

Discussion

The new species has similar phenotypical traits that relate it to other species that belong to the *L. alticolor-bibronii* group, having the same morphometric and lepidosis characters (Quinteros 2013, Abdala & Quinteros 2014). As other members of this group, *L. absconditus* **sp. nov.** has a small body size, slender body, small limbs, long tail and well-developed neck folds, but it has a different combination of morphological character states that distinguish it from the other species. We found primary differences in relation to general patterns of meristic traits, coloration, qualitative characters of lepidosis and some differences in morphometry between the typical form of *Liolaemus absconditus* **sp. nov.** and other species of the *Liolaemus alticolor-bibronii* group. Particularly, there is a striking difference in presenting both, males and females, a uniform brown dorsal coloration without a dorsal pattern, with barely two faded dorsolateral stripes over a slightly darker lateral field. This uniform coloration makes this lizard distinctive from other species of the group, whose members usually show different combinations of vertebral, and paravertebral lines, markings, spots and/or lateral and dorsolateral stripes as a dorsal pattern (Quinteros 2012, 2013). There are also differences in the meristic and morphometric characters, among the new species and the closest distributed, and phylogenetically-related: *Liolaemus tandiliensis*, *Liolaemus gracilis* and *Liolaemus saxatilis*.

Liolaemus absconditus **sp. nov.** is geographically close to *L. tandiliensis* and *L. gracilis*, add to this,

phylogenetic comparison based on the mitochondrial gene Cyt-b recovered *L. absconditus* **sp. nov.** as monophyletic, closely-related to *L. tandiliensis* and close to *L. gracilis* and *L. saxatilis*. However, the new species exhibits a combination of character states which distinguish it from *L. tandiliensis* and from all other species of the group (see Diagnosis). Intensive sampling efforts in different Tandilia's mountain sites, yielded no evidence of being a clinal variation or hybridization (i.e. morphologically intermediate individuals) between *L. absconditus* **sp. nov.** and sympatric *L. tandiliensis*. On the other hand, there are no apparent differences in general features of the habitat structure they occupy and feeding habits of the new species with respect to *L. tandiliensis* and *L. saxatilis*, being a generalist forager and a saxicolous form like these latter species (Avila *et al.* 1992; Vega *et al.* 2008); nevertheless, additional detailed information of the biology and niche characteristics of the new species is needed.

Lizards of the *Liolaemus alticolor-bibronii* group have the largest latitudinal distribution of *Liolaemus*, from central Peru to southern Argentina, most of them inhabiting high altitudes (Díaz Gómez 2007; Martínez *et al.* 2011). *L. absconditus* **sp. nov.** and *L. tandiliensis* populations of Tandilia, together with those of *L. gracilis*, reach the central part of Argentina and are currently the most eastern distributed of the native Andean-Patagonic clade. Of the four closely-related species studied here, three are restricted to mountain-range habitats, i.e. *L. tandiliensis* and *L. absconditus* **sp. nov.** in the Tandilia mountain range of Buenos Aires and *L. saxatilis* in Sierras de Cordoba and San Luis; although Avila (1995) has mentioned some specimens of this species deposited in the FML collection that come from Chacoan areas without rocky substrate. The island effect of the rocky outcrops of Tandilia was probably similar to that of the Sierras Pampeanas and Sierras Subandinas, leading to the origin of morphological similar forms (see Vega *et al.* 2008). These related *Liolaemus* species (with the exception of *L. gracilis*) lives almost exclusively on rocky substrates where they often move up, down and along vertical surfaces using narrow crevices as retreats. Usually, rock-dwelling forms have involved evolutionary change towards a decreased body and head heights and an increased limb length (mainly long hands and feet) in response to functional demands (Revell *et al.* 2007; Edwards 2014). In this sense, saxicolous *L. absconditus* **sp. nov.**, *L. tandiliensis*, and *L. saxatilis* have larger foot length than terrestrial *L. gracilis*. Probably an ancestral lineage state of these species was already adapted to these habitats, however, new studies on the *L. alticolor-bibronii* clade are necessary to test the hypothesis that these mountain species belong to a natural group and share a common evolutionary history.

The Río de la Plata craton is one of the continental blocks at the core of western Gondwana whose southernmost outcrops are exposed in the Tandilia System, covered by modern sediments (Cingolani 2010). This region is one of the most relevant Argentine mining districts since the XIX century, and there is a broad consensus in considering this place as a “geopark” because it preserves the most ancient rocks and fossil structures of Argentina (Cingolani 2008). Additionally, it contains a diversity of taxa and endemism which, according to the Crisci hypothesis (Crisci *et al.* 2001), are the result of arid conditions during the Tertiary and/or Quaternary geological periods in southern South America. This possibly led to an eventual isolation and differentiation of populations in the more elevated areas. Unlike *L. tandiliensis*, which was previously confused with *L. gracilis* (Vega *et al.* 2008), *Liolaemus absconditus* **sp. nov.** has not been mentioned earlier in any other study of the *L. alticolor-bibronii* group. It was only referenced as *Liolaemus* sp. in the herpetofauna record list of Sierras de Mar del Plata and Balcarce (Vega & Bellagamba 1990). Until now, conservation of endemic populations of *L. absconditus* **sp. nov.** and *L. tandiliensis* rely on the Paititi Reserve, a small area (220 hectares) of the Estancia Paititi located in Sierra de Los Padres (system of La Peregrina), which has been recently incorporated on the initiative of their owners to the Argentinian Network of Private Nature Reserves.

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APPENDIX I. Specimens examined.

Voucher numbers for lots are followed by the number of specimens in parentheses.

- Liolaemus alticolor*. BOLIVIA: **La Paz**: Near Tiaguanacu, MCZR 169064 (lectotype), MCZ-R 7287 (paralectotype); Rio Huarcocondo, MCZ 12409; Tiahuanaco, near Lake Titicaca, MCZR 128518–525; Tiahuanaco (16° 33' S; 68° 42' W), CBF 2925, 2893–2896.
- Liolaemus abdalai*. ARGENTINA: **Neuquén**: Provincial Road 23, near Pilolil (39° 22' 29" S; 70° 57' 21" W), MCN 2741 (holotype), MCN 2739–40, 2742–43, FML 7843–44; Provincial Road 11, 0.2 km W from Arroyo Remecó (39° 02' S; 71° 21' W), MCN 2744–50; Arroyo Quilanlahue, Lanin National Park, Lacar, FML 1776.
- Liolaemus bibronii*. ARGENTINA: **Santa Cruz**: Gruta de Lourdes, 2 km E Provincial Road 281, 11.2 km NW Puerto Deseado, FML 10106–107. **Mendoza**: Malargüe, IBA R-0175 (2); 0185.
- Liolaemus bitaeniatus*. ARGENTINA: **Catamarca**: Agua de las Palomas, FML 1932, 3593; Quebrada Peña La Horqueta, Distrito Espinillo, FML 6347; Confluence of the rivers Quebrada and Candado, Andalgalá, FML 7137–38. **Salta**: San Fernando de Escoipe, Chicoana FML 1655 (6). **Tucumán**: Sierra de Medina, FML 2237 (2), 2345 (2); Dique La Angostura, El Mollar, FML 2384 (4), 2499 (2); El Mollar, FML 2462, 2475 (5); Cerro Las Botijas, Sierra de Medina, MCN 900–901.
- Liolaemus chaltin*. ARGENTINA: **Jujuy**: Departamento Cochinoaca: 3 km NW Abrapampa, FML 1461 (5); Abrapampa FML 1871 (4), 2513 (2); Provincial Road 71, 4.2 km W Abrapampa (22° 42' 24.4" S; 65° 43' 12.4" W), FML 9874 (holotype); 2 km N Abrapampa (23° 19' 673" S; 66° 05' 399" W), MCN 235; 2.9 km from the intersection of roads 7 and 71, near Cochinoaca, 6.8 km W Abra Pampa (22° 45' 59.4" S; 65° 44' 54.7" W), MCN 2221–31.
- Liolaemus chungara*. CHILE: **Arica y Parinacota**: Putre (18° 10' 53.4" S; 69° 31' 58.6" W), 3874 m, FML 26505 (holotype), FML 26506 (paratype); southern shore of Lago Chungará (18° 16' 17" S; 69° 09' 37.7" W), 4583 m, FML 26504–508, MCN 4734–35 (paratypes); Parinacota, Andean road A93, km number 12.5, Visviri (18° 8.11' S; 69° 18.00' W), CZZA 346–350 (paratypes); near Putre and Colpita, FML 26509–513 (paratypes).
- Liolaemus exploratorum*. ARGENTINA: **Santa Cruz**: MLP.S 571 (holotype), 567, 570, 573 (paratypes).
- Liolaemus fuscus*. CHILE: MACN 16718–23, 21621. **Coquimbo**: Coquimbo, AMNH 131833–834, MCZ 165146. **Región Metropolitana**: El Cerezo, MCZ 65395; La Calera, Aconcagua, MCZ 165150; road to La Disputada, 1.5 km past turn off Forest Los Farellones (33° 20' S; 70° 22' W), MVZ 187797; on road to La Disputada Mines (33° 22' S; 70° 23' W), MVZ 187804; road to Farellones, (33° 21' S; 70° 21' W), MVZ 196546–548, 196550, 196559, 196562, 196565, 196574–575, 196581. **Región de Valparaíso**: Bahía Oscuro, FML 1592(2); Parque Nacional Campana, SDSU 1866; Valparaíso, MCZ 38621–626, MCZ 165147.
- Liolaemus gracilis*. ARGENTINA: **Buenos Aires**: Mar del Sur, General Alvarado, MCN 2156–58, UNMDP 320, 326, 474. **San Luis**: Estancia el Centenario, MLPR 5306. **Chubut**: 40 km N Trelew, MCN 1345. **La Pampa**: National Road 28, km number 38, Curacó, FML 8371. **Mendoza**: Tupungato, FML 00963 (3); Malargüe, FML 02731; San Rafael, FML 7234–36, 7238. **Río Negro**: Adolfo Alsina, Caleta de Los Loros, FML 2970 (2); El Cuy, FML 8399; Valcheta, MLPR 1692.
- Liolaemus incaicus*. PERU: **Calca**: near Calca, Hacienda Urco FMNH 266542 (holotype), FMNH 34104, FMNH 34127 (14) (paratypes); Sicuani, AMNH 38068–070.
- Liolaemus lemniscatus*. CHILE: **Región de BioBio**: Concepción, CMNH 64727, 64730, MCZ 164037–038; 164041; 164045; 164047; 164049; 164056; 164059–060; 164062–064; FMNH 214220–230; Escuadrón, Concepción, CMNH 64728; Curanilahue, Arauco, CMNH 64729, USNM 58710. **Región de Coquimbo**: Coquimbo, FML 1559 (2). **Región Metropolitana**: Santiago, USNM 165620.
- Liolaemus pagaburoi*. ARGENTINA: **Tucumán**: Trancas FML 16132–33; Huacahuasi, Tafi del Valle, FML 16838; Tafi del Valle, FML 1829 (4); Puesto el Muñoz, Tafi del Valle, FML 2435(9); Hualinchai, Trancas, FML 2722 (4) 2746 (11) FML 2633 (8).
- Liolaemus paulinae*. CHILE: **Región de Antofagasta**: shore of Loa River, Calama, FML 1196 (paratype), 1341 (2); shore of Loa River, SDSU 1909–11, MZUC 19360, 19362–367, 193671, 19370, 19382.
- Liolaemus puna*. ARGENTINA: **Jujuy**: near Laguna Blanca, FML 929; Susques, FML 1265; Laguna larga, Rinconada, FML 1512; Cuesta de Fundiciones, near Mina Piriquitas, Rinconada, FML 1517 (3); Rinconada, FML 1519 (2); Pampa de los

Pozuelos, Abra Pampa, Rinconada, FML 1533 (8); Abdón Castro Tolay, Cochino, FML 1874; Abdón Castro Tolay (23° 19' 67.3" S; 66° 05' 39.9" W), MCN 229–232; Casa Mocha, NW Nevado del Chañi, MCN 698–99; 2.5 km SE Susques, Road 16 to Salinas Grandes, MCN 1718–19. **Salta:** Quebrada Los Berros, 5 km E Olacapato, Los Andes (24° 08' 35" S; 66° 42' 05" W), FML 1364 (holotype), FML 9914–27 (paratypes); Cuesta del Acay, La Poma, FML 1661 (5), 1663 (9); Quebrada de Los Berros, Olacapato, FML 2779 (2); Campo Amarillo, Los Andes, FML 3647; near Sey, La Poma, FML 3348 (2); Cerro Verde, Los Andes, FML 3649; near Abra del Acay, MCN 949–50; km 210, National Road 51. 6.4 km S of entrance road to Olacapato (24° 14' 27.7" S; 66° 40' 37.6" W), MCN 1890–92, 1894–97; 10 km W from Las Arcas School, Cachi Adentro, way to Cerro de la Virgen (25° 02' 40.2" S; 66° 16' 42.0" W), MCN 2177–79; Olacapato, Los Andes (24° 08' 21.3" S; 66° 42' 3.71" W), SDSU 3579–82. **CHILE: Región de Tarapaca:** Chiapa, SDSU 1697–99, MCZ 149852, 149854–56, 149858; Volcán Tatío, USNM 165641, MZUC 19392 (3). **Región de Atacama:** San Pedro de Atacama, MNHN 583, 585, 588.

Liolaemus pyriphlogos. ARGENTINA: **Jujuy:** vicinity of Laguna Leandro, Humahuaca Department, 23° 01' 50" S; 65° 14' 46.8" W, FML 18199 (holotype), FML 18198, 18200–201 (paratypes); 10 km near Aparzo, 23° 09' 50.5" S; 65° 11' 48" W), FML 18208–210; road from Laguna Leandro near Choracán, FML 18236; road from Uquía to Mudana (23° 20' 30" S; 65° 13' 27.5" W), FML 18250–252; between Aparzo and Humahuaca (23° 10' 09.3" S; 65° 11' 01.4" W), FML 18258–259; between Choracán and Laguna Leandro (23° 01' 57.5" S; 65° 14' 14.3" W), FML 18260–262; road from Humahuaca to Choracán (23° 10' 761" S; 65° 11' 70.9" W), MCN 226, 228, 589–98; Laguna Leandro, W of Choracán, Humahuaca, FML 1463 (32); to Laguna Leandro, Humahuaca, FML 3488–89.

Liolaemus ramirezae. ARGENTINA: **Catamarca:** Mina Capillitas, Andalgalá, FML 3612; Morro El Arenal, el Ingenio, Andalgalá, FML 2561 (3). **Salta:** La Poma, FML 1658, MCN 1733–35; 21 km N La Poma, FML 3006; Santa Rosa de Tastil, Rosario de Lerma, FML 3335. **Tucumán:** Provincial Road 307, km 98, Amaicha del Valle, Tafi del Valle FML 2240, 1367, 2275 (4), 2279 (2), 2330 (4), 2383 (2), 2384–86, 2436, 2463, 2481, 2486; Provincial Road 307, O from El Infiernillo, Tafi del Valle, FML 2715; Provincial Road 307, km 98.5. Tafi del Valle, FML 8182; Provincial Road 307, km 95, Tafi del Valle, FML 6012, 17438; Provincial Road 307, km 95 (26° 40.82' S; 65° 48.74' W), MCN 466, 469–70.

Liolaemus sanjuanensis. ARGENTINA: **San Juan:** Sierra de Pie de Palo, FML 1016 (paratype), UNSJ 735–49, 766.

Liolaemus saxatilis. ARGENTINA: **Córdoba:** Achiras, Río Cuarto, AMNH 65193–199, MCN 903–05; Achiras, Departamento Río IV, SDSU 1736–37; Achiras (33° 10' S; 57° 69' W), SDSU 126616, MLPS 1166–167.

Liolaemus tacnae. PERU: **Arequipa:** River crossing the road at 15 meters from Arequipa (road from Arequipa to Puno), Arequipa, FML 1544. **Tacna:** Mina Toquepala, MCZ 45806 (holotype), 45807–08 (paratypes).

Liolaemus tandiliensis. ARGENTINA: **Buenos Aires:** Sierra Los Difuntos (37° 53' 30" S; 57° 50' 30" W), Partido General Pueyrredón, MCN 1606–11, 1616–17, UNMDP 557, UNMDP 559, UNMDP 560, UNMDP 563. Sierra de Los Padres (37° 56' 30" S; 57° 48' 15" W), Partido de General Pueyrredón, UNMDP 0549, 0550, MCN 1605, 1614 (ex UNMDP 0554 and 0552), MCN 1604, 1612 (ex UNMDP 0553, 0555). Sierra del Volcán (37° 51' 30" S; 58° 03' W), Partido de Balcarce, UNMDP 0551. Sierra La Brava (37° 53' 41" S; 57° 59' 50" W), Partido de Balcarce, MCN 1613 (ex UNMDP 0556).

Liolaemus variegatus. BOLIVIA: **Cochabamba:** FML 1210 (2) (paratypes), CBGR S/N (4), CBGR 116, 118, 121, 124, 130, 132–39, 145, 150–53, 90–92, 122, MLPS 841.

Liolaemus walkeri. PERU: AMNH 88324–326. **Ayacucho:** Rapi, Ayacucho (13° 5' 51.0" S; 73° 48' 49.0" W), MCZ 45850; Huancavelica, FMNH 81380–389; 81395–396. **Junín:** 6 km NE Paccha, SDSU 1937; Junín, AMNH 63389–390 (paratypes); Lloclla pampa (11° 49' 12.5" S; 75° 37' 27.7" W), MCZ 43770–775, 43777; Mina Juanchiscochas, 40 km N Jauja (11° 35' 57.3" S; 75° 28' 7.9" W), MCZ 43779–781; Maraynioc, NE Tarma, (11° 22' 0.1" S; 75° 24' 0.0" W), MCZ 45887–888; Casa Pato, MCZ 100111, FML 371 (2). **Apurímac:** Punna near Abancay, FML372; Route near Abancas, FML 1283. **Lima:** Ticlio (11° 34' 42.4" S; 76° 11' 38.0" W), MCZ 45783.

Liolaemus yalguaraz. ARGENTINA: **Mendoza:** Pampa de Yalguaraz, Departamento Las Heras (32° 19' 59.0" S; 69° 22' 54.5" W), FML 27622 (holotype); FML 27623–634 (paratypes); MCN 5068–69 (paratypes). 5 km to Cruz de Paramillo, road to Uspallata, Departamento Las Heras, GS 3479–3480; 3482; 3489.

Liolaemus yanalco. ARGENTINA: **Salta:** road from Estación Muñano to Acay, 6 km near San Antonio de los Cobres, MCN 955–60, 1038, 1635; road from Estación Muñano to Acay, 5–6 km (24° 18' 31.6" S 66° 09' 070" W), MCN 360–61, 535–36, 541; road from Estación Muñano to Acay, 8–9 km, MCN 702, 705–07; road from Estación Muñano to Acay, MCN 725–26; km 148, National Road 51, E of San Antonio de los Cobres, 24° 13' 15.9" S; 66° 15' 46.4" W, MCN 728–29; 5 km S Estación Muñano, road to Acay, MCN 1449; 6.7 km W Estación Muñano, road to Acay (24° 20' 47.5" S; 66° 09' 33.9" W), MCN 1750; 7 km from Estación Muñano to Nevado del Acay, (24° 20' 51.8" S; 66° 09' 27.2" W), MCN 2236–39, 2501, 2613–16.

Liolaemus absconditus sp. nov. ARGENTINA. **Buenos Aires:** Sierra Los Difuntos (37° 53' 30" S; 57° 50' 30" W), Partido General Pueyrredón, UNMDP 1826, 1827, IBIGEO-R 5460 (ex UNMDP 1830). La Brava (37° 53' 41" S; 57° 59' 50" W), Partido de Balcarce, UNMDP 1782, IBIGEO-R 5459 (ex UNMDP 1783). Estancia Paititi (37° 55' 36.84" S; 57° 49' 04.48" W), La Peregrina, Partido de General Pueyrredón, UNMDP 1817, 1818, 1823, 1824. Sierra La Vigilancia (37° 52' 18.74" S; 58° 01' 31.03" W), Partido de Balcarce, UNMDP 1825. Planta Transmisora Sierra de Los Padres (37° 57' 7.92" S; 57° 47' 49.20" W), Partido de General Pueyrredón, UNMDP 565, 566.

APENDIX II. Specimens used for phylogenetic analysis.

Voucher: voucher numbers. GB: accession numbers from GenBank for DNA sequence.

Species	Voucher	GB
<i>L. absconditus</i> sp. nov.	UNMdP-1825; UNMdP-1827	---
<i>L. alticolor</i>	MUSM31393	KF923660
<i>L. bibronii</i>	LJAMM-3667; LJAMM-9897; BYU47183	JN410521; JF272767; AY173791
<i>L. chiliensis</i>	UConfn362; E11CHTR08	DQ989785; EU649245
<i>L. gracilis</i>	LJAMM-10517; JAMM26	JF272774; AY367804
<i>L. incaicus</i>	MUSM31398; BYU50124	KF923657; KF923658
<i>L. lemniscatus</i>	F5LL4; F5LL1; F5LL6	EU649113; EU649110; EU649114
<i>L. nitidus</i>	SSUC-Re-298	KU095835
<i>L. punmahuida</i>	LJAMM-CNP-6165	KP121337
<i>L. ramirezae</i>	BYU47180; LJAMM4416	DQ237715; DQ989772
<i>L. robertmertensi</i>	LJAMM-1961	DQ989769
<i>L. saxatilis</i>	LJAMM-5044; LJAMM-8456	JN410553; JN410527
<i>L. tandiliensis</i>	UNMdP-987; UNMdP-988; UNMdP-989	---
<i>L. walkeri</i>	BYU50342; BYU50340; BYU50118	KF923648; KF923646; KF923644