

Research article

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A new species of *Liolaemus* (Iguania: Liolaemidae) from the hot deserts of northern Patagonia, Argentina

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Abstract. A new species of *Liolaemus* is described from southwest of the town of Añelo, Neuquén Province, Argentina. Integrative evidence methodology of external morphological characters and molecular phylogenetic analyses of mitochondrial DNA (*cyt-b*) is used to place the new species to the species group of *Liolaemus boulengeri*. The new species is phenotypically close to *L. mapuche*. The new *Liolaemus* is medium to large in size (males 77.64–83.98 mm, females 72.88–78.58 mm), with evident sexual dichromatism. Genetic distances of the mtDNA (*cyt-b*) between the new species and its closest relative species are greater than 3% (*L. cuyanus* 7.48–12.02%; *L. josei* 7.56–9.60%; *L. puelche* 8.23–9.93%; *L. mapuche* 8.51–9.79%). Molecular and morphological phylogenetic results show *L. mapuche* as the sister species of the new one. The new species is larger than *L. mapuche*. Dorsal and ventral scales are more numerous in the new species than in *L. mapuche*, precloacal pores in females are present in *L. mapuche* and absent in the new species. It has strict psammophilic habits, using sand mounds and sheltering, under Alpataco (*Neltuma alpataco*) bushes. The *L. boulengeri* group now contains 75 species distributed in Argentina, Bolivia, Brazil, Chile, Paraguay, Peru and Uruguay.

Keywords. *Boulengeri* group, *Liolaemus*, Neuquén, Phylogeny, Taxonomy.

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Introduction

The genus *Liolaemus* Wiegmann 1834 is the third most diverse genus of all living tetrapods with 283 valid species (Abdala *et al.* 2021a) and, thus, constitutes a very attractive study group of lizards for different disciplines of biology. Year after year, new species are being described throughout the distributional range of the genus which extends from central Peru, covering a large part of Bolivia, some regions of Paraguay, Uruguay and eastern Brazil, to Tierra del Fuego in Argentina and Chile (Aguilar-Puntriano *et al.* 2019; Quinteros *et al.* 2020; Chaparro *et al.* 2020; Huamani-Valderrama *et al.* 2020; Abdala *et al.* 2020, 2021b; Avila *et al.* 2021; Bulacio Arroyo *et al.* 2021). These advances in the taxonomy of *Liolaemus* have improved our understanding of the ecology, systematics and biogeography, and conservation status of the genus (Abdala *et al.* 2012a, 2020; Semhan 2015; Cruz *et al.* 2010; Portelli & Quinteros 2018; Ruiz-Monachesi *et al.* 2021). Interestingly, environmental impact studies for mining and oil projects in many countries, has led to the discovery of new species of *Liolaemus* such as *Liolaemus graciellae* Abdala, Acosta, Cabrera, Villavicencio & Marinero, 2009 (Martínez Carretero *et al.* 2007; Abdala *et al.* 2009); *L. cuyumhue* Avila, Morando, Perez & Sites, 2009, *L. crandalli* Avila, Medina, Perez, Morando, Sites & Morando, 2015 *L. calliston* Avila, Fulvio-Perez, Minoli, Medina, Sites & Morando, 2017 (Ávila *et al.* 2009, 2015, 2017); *L. cazaniae* Lobo, Slodki & Valdecantos, 2010; *L. halonastes* (Lobo *et al.* 2010); *L. qalaywa* Chaparro, Quiroz, Mamani, Gutiérrez, Condori, De la Riva, Herrera-Juárez, Cerdeña, Arapa & Abdala, 2020 (Chaparro *et al.* 2020); *L. salitrosus* Abdala, Paz, Semhan, García, Aguilar-Kirigin, Farías, Valladares, Poblete, Quipildor, Valdes & Langstroth, 2021; *L. kunza* Abdala, Semhan & Paz, 2021 (Abdala *et al.* 2021b) and *L. yauri* Arapa-Aquino, Abdala, Huamani-Valderrama, Gutiérrez, Sardinia, Quiroz & Chaparro, 2021 (Arapa *et al.* 2021).

For an environmental impact study, to establish an environmental baseline, we studied a herpetological collection from the locality of Aguada Pichana, and a new population of *Liolaemus* lizard with a unique morphological characteristic was discovered. In this work, we test the hypothesis that this population is distinct from other nominal species of *Liolaemus* – combining molecular and morphological data and the integrative evidence methodology (Carrasco *et al.* 2019).

The *Liolaemus boulengeri* group (= section of *L. boulengeri* Koslowsky, 1898 sensu Schulte *et al.* 2000), with 74 currently valid nominal species, is one of the most diverse within the genus. Currently, the *L. boulengeri* group is made up of four main clades: *L. anomalus* Koslowsky, 1896, *L. wiegmanni* (Duméril & Bibron, 1837), *L. darwini* Bell, 1843 and *L. melanops* Burmeister, 1888 clades. Preliminary analyses of molecular and morphological evidence suggest that the putative new species of *Liolaemus* belongs to the *Liolaemus boulengeri* group and is nested within the *L. melanops* clade. Within this clade, the new species was found nested within the *Liolaemus cuyanus* complex. The *L. cuyanus* complex was proposed by Abdala (2007), and is partly equivalent to the *Liolaemus donosobarrosi* group proposed by Ávila *et al.* (2006). The *L. cuyanus* complex is made up of medium – and large – sized *Liolaemus* with sexual dichromatism, a melanic gular ring, scapular spots, and four to six scales in contact with the mental scales. Most of the species are psammophilic, associated with large bushes, and their highest daily activity is generally at midday. Some species of this complex have an antehumeral arch and the presence of six scales surrounding the mental scale (Abdala 2007). This species complex is distributed from Catamarca to the centers of Río Negro and Neuquén provinces, and consists of *Liolaemus calliston*, *L. cuyanus* Cei & Scolaro, 1980, *L. donosobarrosi* (Cei, 1974), *L. goetschi* Müller & Hellmich, 1938, *L. hugoi* Bulacios-Arroyo, Semhan, Paz, Chafrat & Abdala, 2021, *L. mapuche* Abdala, 2002, *L. puelche* Ávila, Morando, Perez & Sites, 2007 and *L. tirantii* Ávila, Perez, Minoli, Medina, Sites & Morando, 2017 (Bulacios Arroyo *et al.* 2021). There are other candidate species, not yet described, that also belong within this complex. Here, we describe a new species from Neuquén Province, in southern Argentina.

Material and methods

Collection of specimens and preparation

Nine individuals of the new species were collected, southwest of Añelo, Neuquén Province. Specimens were captured using a two meter long telescopic ‘herpetological rod’, with a nylon thread loop at its end. The capture was made by slowly approaching the rod to the lizard’s body then the loop is placed around the neck and pulled up and backwards. This technique is effective for capturing lizards of various sizes and elusive behavior, when they are momentarily perched in places within reach of a person, and without causing them any physical harm. Some basic morphological characters were examined from each captured individual, sex was determined and confirmed, and photographs were taken from different angles and perspectives in their natural environment. Most of the captured lizards were georeferenced from a mobile phone GPS waypoints application. Numerous other photographic records of lizards were made without capturing them. The individuals were sacrificed by injecting 1 ml of 1% Pentothal sodium and were fixed with 10% formaldehyde and preserved in 70% alcohol after having collected tissue samples stored in 96% ethanol. Permits for collections were obtained from the Department of Territorial Development and Environment of Neuquén Province (Exp. 8903-3148/21), managed and authorized in the name of Pablo Chafrat. The tissue samples were sent to the molecular genetics’ laboratory of IBONE, Corrientes, Argentina. Genomic DNA was isolated from ethanol-preserved liver samples using the extraction protocol described in Aljanabi & Martinez (1997). We apply polymerase chain reactions (PCR) to amplified target regions of the mtDNA cytochrome b (*cyt-b*) region for 705 bp, under the conditions described in Aguilar-Puntriano *et al.* (2013). The integrity and quality of each amplified DNA were verified by electrophoresis and spectrophotometry, respectively. The samples were sent to Macrogen Inc., Korea, for sequencing.

Institutional abbreviations

FML = Miguel Lillo Foundation of Tucumán, Tucuman, Argentina

MPCN = Patagonian Museum of Natural Sciences “Juan Carlos Salgado” of General Roca, Río Negro, Argentina

Morphological observations

The characters described by Laurent (1985), Etheridge (1995), Abdala (2007), Abdala & Juárez Heredia (2013), and Quinteros *et al.* (2020) that are used in the taxonomy of *Liolaemus* were also used here to carry out the diagnosis and variations of the new species (Appendix 1). Description of the colors in life was made from photographs taken when capturing the lizards. The terminology of the body coloring pattern follows Hellmich (1934), Lobo & Espinoza (1999), and Abdala (2007). Observations of scaling and body measurements were taken using a binocular magnifying glass (10–40 ×) and a precision caliper of 0.01 mm (Mitutoyo®).

Phylogenetic analysis

Phylogenetic analyses based on morphological and molecular characters were carried out separately. For the development of the morphological matrix, we used the one cited by Abdala (2007), later modified by Abdala & Juárez Heredia (2013) that included 90% of all species of the *L. boulengeri* group. The species used as an external group (five species) were the same as those used in the work by Abdala (2007). The classification used for the diagnosis in the non-formal categories of the subgenus *Eulaemus* corresponds to the new proposal by Abdala *et al.* (2021c). This proposal integrates phylogenetic hypotheses from various scientific manuscripts and authors, and suggests the following categories: genus, subgenus, section, group, clade, subclade, complex. The morphological matrix comprises 73 terminal taxa and 155 characters. Of these 155 characters, 32 are continuous and 123 are discrete, which were classified as non-polymorphic binaries, polymorphic binaries, non-polymorphic multistate, and polymorphic multistate. Following Abdala (2007), the multistate characters were divided into additives and non-additives. Polymorphic binary characters (Wiens 1995) were treated as such. The polymorphic multistate was treated as such with the values found for each taxon. In the phylogenetic analysis, the parsimony criterion was used as the optimality criterion. The software used to search for phylogenetic hypotheses was TNT 1.5 (Tree Analysis Using New Technology, ver. 1.5, Goloboff & Catalano 2016), since it is the only program that allows the analysis of continuous characters without converting them, for their treatment, into discrete characters. The continuous characters were treated using the methodology proposed by Goloboff *et al.* (2006), where they are analyzed as such, avoiding their discretization. For each character the range formed by the mean \pm standard deviation was used. As the continuous characters are taken under different scales, a ‘standardization’ or ‘rescaling’ was carried out to avoid using some characters with greater influence over others in the analysis, using a script (mkstandb.run) associated with the TNT software (Goloboff *et al.* 2003). With this script, the maximum transformation costs that can exist between two continuous characters are standardized. In this way, from the smallest state to the largest, in a continuous character, a specific value is taken with respect to what it costs to transform it into a discrete character. For this analysis, 2 was considered as the highest transformation cost. Heuristic tests were carried out to find the most parsimonious trees. For each heuristic search, 1000 replicas were made and 50 trees were saved for each one. The matrix was treated by analyzing the characters with equal weights and low implied weights (Goloboff 1993). For the latter, values of the weighing constant “K” from 1 to 20 were used.

We performed a molecular phylogenetic analysis under Bayesian Inference based on a matrix size of 143 terminals of *cyt-b* sequences of the *Liolaemus boulengeri* group (appendix 2) and two terminal taxa as an external group (*L. vulcanus* Quinteros & Abdala, 2011 and *L. multicolor* Koslowski, 1898). These sequences were obtained from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>), and we also included sequences from the new taxon and other taxa obtained for this study. The sequences were aligned in MEGA X (Kumar *et al.* 2018), using the Muscle algorithm. We used jModel Test ver. 3.0.4 (Posada 2008) to select the best fitting model (GTR + Γ + I). The analysis was carried out in BEAST2 ver. 2.6.6 (Drummond & Rambaut 2007). We ran two runs of 50 million generations each. Adequate mixing and convergence of the chain to the stationary distribution were confirmed by inspection of MCMC samples

using Tracer ver. 1.6 (Rambaut *et al.* 2014). The first 20% of generations were discarded as burn-in, after evaluating the stability and adequate ‘mixing’ of sampled log-likelihood values assessed from the parameter estimates across generations (ESS > 200) of both runs were combined.

We use Tree Annotator ver. 2.0 (Drummond & Rambaut 2007) to generate a tree of maximum credibility and calculate the posterior probabilities and substitution rates for each node. The topology was visualized with Fig Tree ver. 1.2 (Rambaut 2010). We calculated the average of uncorrected genetic distances of the closest species of *L. kulinko* sp. nov., *L. cuyanus*, *L. josei*, *L. mapuche* and *L. puelche* in MEGA X (Kumar *et al.* 2018).

Results

Taxonomy

Class Reptilia Laurenti, 1768
Subclase Lepidosauria Haeckel, 1866
Order Squamata Opperl, 1811
Family Liolaemidae Frost & Etheridge, 1989
Genus *Liolaemus* Wiegmann, 1834

Liolaemus kulinko sp. nov.

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Figs 1–2, 5–7, Table 1–2

Diagnosis

Liolaemus kulinko sp. nov. belongs to the section of *Liolaemus montanus* Koslowsky, 1898 of the *Liolaemus boulengeri* group (Abdala 2007; Abdala *et al.* 2021c) because it has a patch of enlarged scales on the posterior aspect of the thigh (Etheridge 1995; Abdala 2007) (Fig. 1D). Within the group of *L. boulengeri* it belongs to the clade of *L. melanops*, subclade of *L. goetschi*, and *L. cuyanus* complex because it has light blue scales on the flanks of the body and tail, a black margin on the posterior border of the paravertebral spots, four to six scales in contact with mental scale (Fig. 1E), presence of a melanic gular ring, evident scapular spots, and the same body shape and similar lepidosis (Abdala 2007; Abdala *et al.* 2012b, 2021c). It differs from the species of the clades of *L. anomalus* and *L. darwinii* by having posterior teeth with crowns of expanded edges and four to six scales in contact with mental scale. It also differs from the species of the clade *L. anomalus* (Abdala & Juárez Heredia, 2013) (*Liolaemus acostai* Abdala & Juárez-Heredia, 2013, *L. anomalus*, *L. ditatadi* Cei, 1983, *L. lentus* Gallardo, 1966, *L. millcayac* Abdala & Juárez-Heredia, 2013, *L. pipanaco* Abdala & Juárez-Heredia, 2013 and *L. pseudoanomalus* Cei, 1981) by having less developed palpebral strap or ‘comb’, males with a greater number of precloacal pores, a greater relationship between snout–vent length (SVL) and the tail length (TL). *Liolaemus kulinko* sp. nov. also differs from the species of the clade of *L. darwinii* (Abdala, 2007) (*L. abaucan* Etheridge, 1993, *L. calchaqui* Lobo & Kretzschmar, 1996, *L. chacoensis* Shreve, 1948, *L. cinereus* Monguillot, Cabrera, Acosta & Villavicencio, 2006, *L. crepuscularis* Abdala & Diaz Gómez, 2006, *L. darwinii*, *L. diaguita* Abdala, Quinteros, Arias, Portelli & Palavecino, 2011, *L. espinozai* Abdala, 2005, *L. grosseorum* Etheridge, 2001, *L. koslowskyi* Etheridge, 1993, *L. laurenti* Etheridge, 1992, *L. lavillai* Abdala & Lobo, 2006, *L. messi* Ruiz, Quipildor, Ruiz-Monachesi, Escalante, Valdecantos & Lobo, 2021, *L. montanezi* Cabrera & Monguillot, 2006, *L. olongasta* Etheridge, 1993, *L. ornatus* Koslowsky, 1898, *L. pacha* Juárez Heredia, Robles & Halloy, 2013, *L. quilmes* Etheridge, 1993, and *L. uspallatensis* Macola & Castro, 1982) in having less evident sexual dichromatism, fewer precloacal pores in males, and a clearly different dorsal coloration pattern. It differs from the species of the clade *L. wiegmanni* (Etheridge 2000) (*L. arambarensis* Verrastro, Veronese, Bujes & Martins Dias Filho, 2003, *L. azarai* Ávila, 2003, *L. cranwelli* (Donoso-Barros, 1973), *L. cuyumhue*, *L. lutzae*

Mertens, 1938, *L. multimaculatus* (Duméril & Bibron, 1837), *L. occipitalis* Boulenger, 1885, *L. rabinoi* (Cei, 1974), *L. riojanus* (Cei, 1979), *L. salinicola* Laurent, 1986, *L. scapularis* Laurent, 1982, and *L. wiegmanni*) in having one row of loreolabial scales (never two or three). Within the *L. melanops* group, *L. kulinko* sp. nov. differs from *L. dumerili* Abdala, Semhan, Moreno Azocar, Bonino, Paz & Cruz, 2012, *L. josei* Abdala, 2005, *L. martorii* Abdala, 2003 and *L. lobo* Abdala, 2003 by having a longer SVL, the presence of an evident antehumeral arch, and greater number of dorsal scales. It differs from *L. trome* Abdala, Semhan, Moreno Azocar, Bonino, Paz & Cruz, 2012 by having a greater number of scales around the body, greater number of dorsal scales, and less ventral melanism.

It differs from the *Liolaemus telsen* subclade (Abdala 2007; Abdala *et al.* 2021c) (*L. boulengeri*, *L. inacayali* Abdala, 2003, *L. purul* Abdala, Semhan, Moreno Azócar, Bonino, Paz & Cruz, 2012, *L. senguier* Abdala, 2005, *L. tehuelche* Abdala, 2003, and *L. telsen* Cei & Scolaro, 1999) in having a greater SVL, four to six scales in contact with mental scales and a clearly different dorsal coloration pattern.

It differs from the *L. rothi* subclade (Abdala 2007; Abdala *et al.* 2021c) (*L. hermannunezi* Pincheira-Donoso, Scolaro & Schulte, 2007, *L. sagei* Etheridge & Christie, 2003, *L. sitesi* Ávila, Olave, Perez, Perez & Morando, 2013, and *L. rothi* Koslowsky, 1898) by having light blue scales on the flanks of the body and tail, four to six scales in contact with the mental scale, and a clearly different dorsal and ventral coloration pattern.

It differs from the *L. fitzingerii* complex (Abdala 2007; Abdala *et al.* 2021c) (*L. camarones* Abdala, Díaz-Gómez & Juárez-Heredia, 2012, *L. canqueli* Cei, 1975, *L. casamiquelai* Ávila, Perez, Morando & Sites, 2010, *L. chehuachekenk* Ávila, Morando & Sites, 2008, *L. fitzingerii* (Duméril & Bibron, 1873), *L. melanops*, *L. morenoi* Etheridge & Christie, 2003, *L. shehuen* Abdala, Díaz-Gómez & Juárez-Heredia, 2012, and *L. xanthoviridis* Cei & Scolaro, 1980) in having a shorter SVL, less ventral melanism, four to six scales in contact with mental scales, and a clearly different dorsal coloration pattern.

Within the *L. cuyanus* complex, it differs from *L. calliston*, *L. donosobarrosi*, *L. hugoi*, and *L. tirantii* by having a greater SVL, four to six scales in contact with the mental scales, and a clearly different dorsal coloration pattern. It differs from *L. cuyanus*, and *L. puelche* by having a smaller SVL, four to six scales in contact with mental scale, presence of light blue scales in males and evident sexual dichromatism. It differs from *L. goetschi* by having a greater SVL, more evident sexual dichromatism, presence of an antehumeral arch, a greater quantity of light blue scales, greater number of scales around the body, greater number of dorsal scales, and fewer ventral scales. It differs from *L. mapuche* by having a greater number of dorsal scales between the occiput and the level of the anterior aspect of the thigh (90–96 vs 70–86), a greater number of loreolabial scales (8–10 vs 6–7), lower number of gular scales (22–25 vs 25–35), greater number of dorsal scales on the head (16–18 vs 13–16), a smooth head surface in *L. kulinko* sp. nov. but a wrinkled head surface in *L. mapuche*, and the absence of precloacal pores in females and up to six in *L. mapuche*. The color of the head differs in males of *L. kulinko* sp. nov., that varies from light brown to gray, while in *L. mapuche* it is generally blue or light blue (although in some individuals there is the light gray color) and the pattern of body coloration in paravertebral and posterolateral spots of males in *L. mapuche* does not fade as they do in *L. kulinko* sp. nov. (Figs 2–4, see Table 1 for more differences.)

Etymology

The specific epithet ‘kulinko’ means ‘aguada’ in the language of the Mapuche, a group of indigenous inhabitants of south-central Chile and southwestern Argentina, including parts of Patagonia, and refers to the place where the species lives, “Aguada Pichana”.

Table 1. Morphological differences between *L. kulinko* sp. nov. and its closest relative, *L. mapuche* Abdala, 2002. * =Morphological data of number of specimens examined and traits.

species/ characters	<i>L. mapuche</i> Abdala, 2002 (n = 26)	<i>L. kulinko</i> sp. nov. (n = 13)*
min–max SVL (mm)	61.97–82.70	72.88–83.90
scales around body	65–76 (69.7 ± 3.0)	69–82 (75.77 ± 4.6)
dorsal scales	70–86 (76.27 ± 3.8)	87–97 (95.07 ± 3.94)
ventral scales	94–117 (108.87 ± 6.9)	100–104 (102.57 ± 1.51)
gular scales	25–35 (29.57 ± 2.6)	34–38 (35.57 ± 1.76)
precloacal pores in males	6–9 (7.87 ± 1.0)	6–7 (6.57 ± 0.6)
preloacal pores in females	0–6 (1.007 ± 2.2)	0–0
scales in contact with mental scales	4–6 (5.67 ± 1.1)	4–6 (5.87 ± 0.7)
sexual dichromatism	evident	evident
head color in males	blue, light blue, brown or gray	brown, gray
body color in males	yellow, light blue, brown, gray, light green	brown, gray
light blue scales in males	numerous	few or numerous
colored scales on the sides of the body and tail in males	with numerous colored scales, yellow, green and / or blue	absent or some greenish
posterior paravertebral spots in males	evident	blurred or absent
pre scapular and post scapular spots	evident	variable (from evident to absent)

Material examined

Holotype

ARGENTINA • ♂; Neuquén, Añelo, Bajo Añelo from south of Route 7, on the way to Aguada Pichana; 38°14'57.87" S, 68°56'37.38" W; alt. 321 m; 9 Mar. 2021; I. Procheret and P. Chafrat leg.; MPCN-H-469.

Paratypes (12 specimens)

ARGENTINA–**Neuquén** • 2 ♀♀; same collection data as for holotype; 38°14'57.82" S, 68°56'37.55" W; alt. 321 m; 2 Feb. 2021; C. Abdala, P. Chafrat and I. Procheret leg.; MPCN-H-456–457 • 1 ♀; same collection data as for holotype; 37°59'45.32" S, 69° 7'51.53" W; alt. 286 m; 2 Feb. 2021; C. Abdala, P. Chafrat and I. Procheret leg.; MPCN-H-458 • 1 ♂; same collection data as for holotype; 38°20'42.28" S, 69°4'46.55" W; alt. 374 m; 2 Feb. 2021; C. Abdala, P. Chafrat and I. Procheret leg.; MPCN-H-459 • 1 ♀; same collection data as for holotype; 38°14'57.82" S, 68°56'37.55" W; alt. 321 m; 9 Feb. 2021; P. Chafrat and I. Procheret leg.; MPCN-H-468 • 1 ♀, 1 ♂; same collection data as for holotype; 38°14'57.82" S, 68°56'37.55" W; alt. 319 m; 9 Feb. 2021; P. Chafrat and I. Procheret leg.; MPCN-H-470–471 • 1 ♀; same collection data as for holotype; 37°59'45.32" S, 69° 7'51.53" W; alt. 286 m; 9 Feb. 2021; P. Chafrat and I. Procheret leg.; MPCN-H-472 • 2 ♀♀; same collection data as for holotype; 38°25'43.7" S,

69°09'31.3" W; alt. 433 m; 7 February 2021; P. Chafrat, A. Planchart, L. Retamal and D. Ubieta leg.; MPCN-H-473–474 • 1 ♀; same collection data as for holotype; 38°24'33.41" S, 69° 8'15.91" W; alt. 402 m; 2 Feb. 2021; C. Abdala, P. Chafrat and I. Procheret leg.; MPCN-H-476 • 1 ♂; same collection data as for holotype; 38°24'32.79" S, 69° 8'24.96" W; alt. 405 m; 2 Feb. 2021; by C. Abdala, P. Chafrat and I. Procheret leg.; MPCN-H-477.

Description (holotype)

MEASUREMENTS. Weight 15 gm. Snout vent length 79.93 mm. Head 1.31 mm times longer (17.53 mm) than wide (13.31 mm). Head height 9.81 mm. Neck width 14.82 mm. Interorbital distance 8.12 mm. Eye length (horizontal) 3.07 mm. Ear–eye length 7.11 mm. Auditory meatus height 3.06 mm and width 1.6 mm. Distance from eye to upper lip 2.57 mm and distance between nostrils 2.75 mm. Subocular length 4.83 mm. Torso length 39.04 mm. Tail length 112.35 mm. Body width 26.98 mm. Thigh length 14.02 mm. Tibia length 18.41 mm. Foot length 22.47 mm. Humerus length 11.69 mm. Forearm length 9.98 mm. Hand length 13.24 mm. Pygal region length 5.98 mm. Cloaca width 6.26 mm.

MORPHOLOGY. Dorsal surface of head smooth, with sixteen dorsal scales. Rostral wider than height and in contact with six scales. Mental scale same size as rostral scale, trapezoidal in shape, in contact with six scales. No contact between nasal and rostral scales, separated by scale. Two internasal scales higher than wide. Nine scales surrounding nasal that is separated from canthal by two scales. Seven scales between rostral and frontal. Front divided into two scales. Interparietal slightly smaller than parietal scales, in contact with six scales. Preocular separated from lorilabials by one scale. Six superciliaries and 15 superior ciliary scales. Anterior border of ear with two differentiated ear scales; upper border without differentiated scales. Nine temporal scales keeled. Subocular in contact with three lorilabials, without contacting fourth supralabial. Six supraoculars. Ten supralabials. Nine lorilabials. With seven infralabials, second in contact with two ventral scales. Six shield scales. Second shield separated by two scales. Scales around the body 26. With 75 dorsal scales from occiput to hind limb, with rounded posterior end, imbricated and with evident keel, without mucron. Ventral scales 105 (from mental scale to cloaca, following ventral midline of body), larger than dorsals, imbricate and laminar. Gular scales 22, imbricate and keeled. Neck with 51 scales, from posterior border of auditory meatus to shoulder, along longitudinal fold. Seven precloacal pores. Vestigial pores in gulars, pectoral, pygal, and posterior abdominal areas. Antehumeral granular scales, imbricated and well differentiated from rest. Marked atrial and longitudinal fold. Longitudinal fold scales smooth and without keel. Fourth finger with 21 scales and foot with 29 scales. A femoral patch present. Dorsal tail scales without mucron and with keel, ventral smooth. Laminar imbricate and trifid infracarpal. Infratarsals laminar imbricate and trifid. Gular fold developed. No developed postscapular fold. Patch scales rounded, with mucron, without notch. Trifid center palm scales without keel.

COLORATION IN LIFE (Fig. 1). Dorsal and temporal region of head, brown with few whitish scales. Supralabial and infralabial light yellow. Dark spot through the subocular, loreolabial and supralabial scales. Sides of neck with thick white line reaching forelimbs. Brown body slightly darker than head. Undefined vertebral region, with yellowish-white circular or irregular spots. Evident paravertebral spots on neck to middle of body that gradually fade until disappearing when reaching tail. Paravertebral black spots with white posterior border. Antehumeral arch defined, black, wide, short. Faint prescapular spot, and large, evident postscapular spot, of deep black color. Sides of body same color as back, with numerous white circular spots, which disappear before reaching groin. Limbs with same color as body, with irregular black and whitish spots. Tail dorsally reddish brown without spots at its proximal end and with faint black vertebral line at its distal end. Ventral is yellowish white; yellow color is more accentuated in gular region and thighs. Gular band incomplete and two black lines extend from gular band to forelimbs. Numerous black scales distributed irregularly across venter, forming melanic spot in pectoral and anterior abdominal area.

MORPHOLOGICAL VARIATION. Based on nine specimens (4 ♂♂ and 5 ♀♀). Dorsal surface of head smooth with 16–18 (mean = 16.22; SD = 0.67) scales between the rostral and occiput. Nasal surrounded by 8–9 (mean = 8.22; SD = 0.6) scales. Supralabials 8–10 (mean = 9.00; SD = 0.50); 8–10 (mean = 8.89; SD = 0.78). Lorilabials arranged in single row. Supraocular 5–7 (mean = 5.75; SD = 0.4). Parietals larger than or equal in size to interparietal, surrounded by 6–8 scales (mean = 6.89; SD = 0.78). Infralabials 6–11 (mean = 7.78; SD = 1.39). Gulars 22–25 (mean = 23.78; SD = 1.39). Temporals 8–11 (mean = 10.1; SD = 0.46) keeled. Auditory meatus higher (mean = 2.92 mm; SD = 0.33) than wide (mean = 1.63 mm; SD = 0.20). Developed antehumeral fold. Head longer (mean = 16.34 mm; SD = 0.98) than wide (mean = 11.98 mm; SD = 1.18) and high (mean = 8.73 mm; SD = 1.09). Trunk length (mean = 40.19 mm; SD = 3.18). Maximum snout–vent length 83.98 mm. Arm length (mean = 11.45 mm; SD = 1.48). Forearm length (mean = 9.60 mm; SD = 0.95). Hand length (mean = 11.65 mm; SD = 0.93). Thigh length

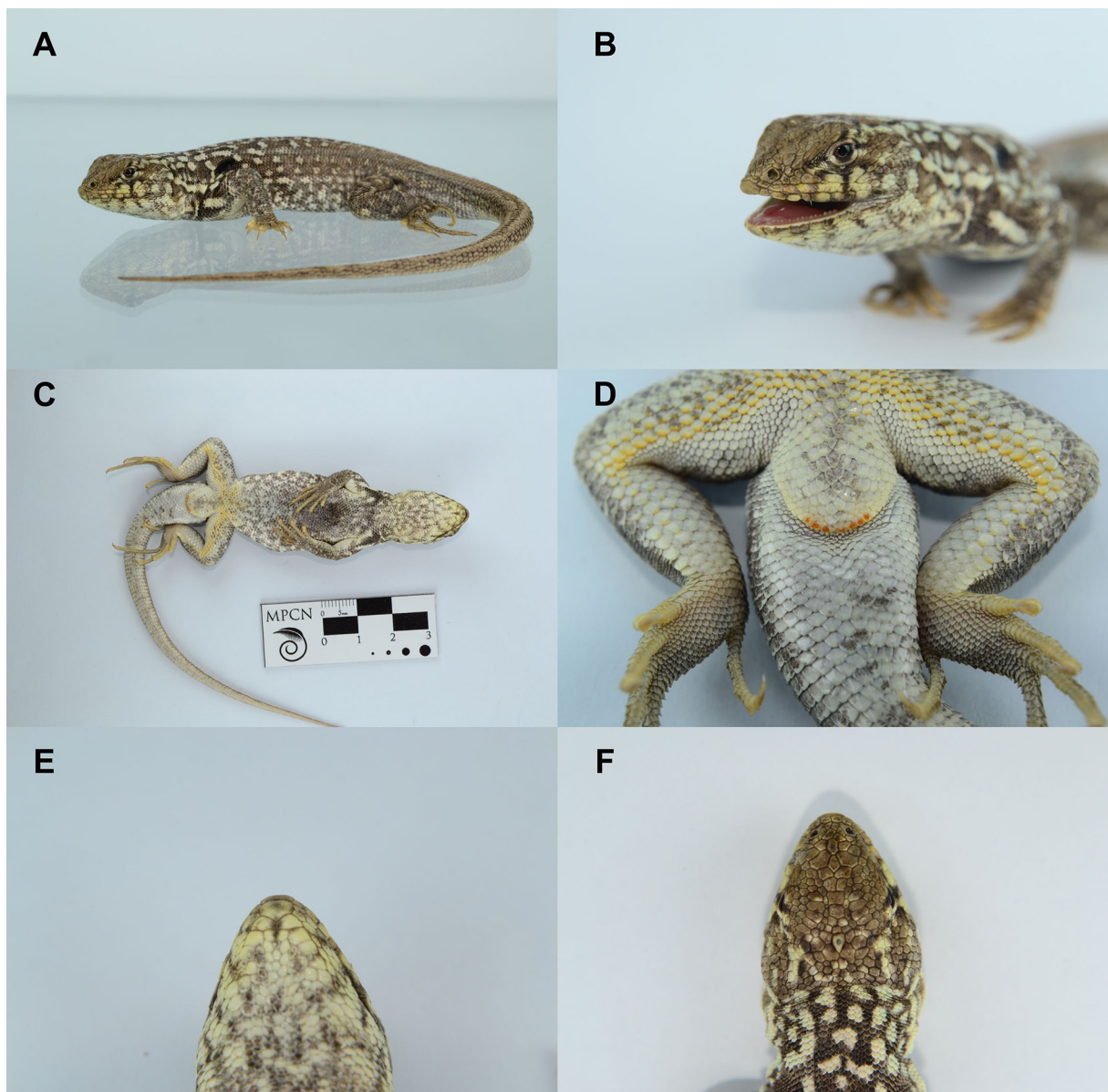


Fig. 1. Details of *Liolaemus kulinko* sp. nov., holotype (MPCN-H-469) (SVL 79.93 mm, tail 112.35 mm). **A, C.** Dorsal and ventral views of the body. **B, E–F.** Lateral, ventral and dorsal views of the head. **D.** Ventral view of preloacal pores. Photographs: P. Chaftrat.

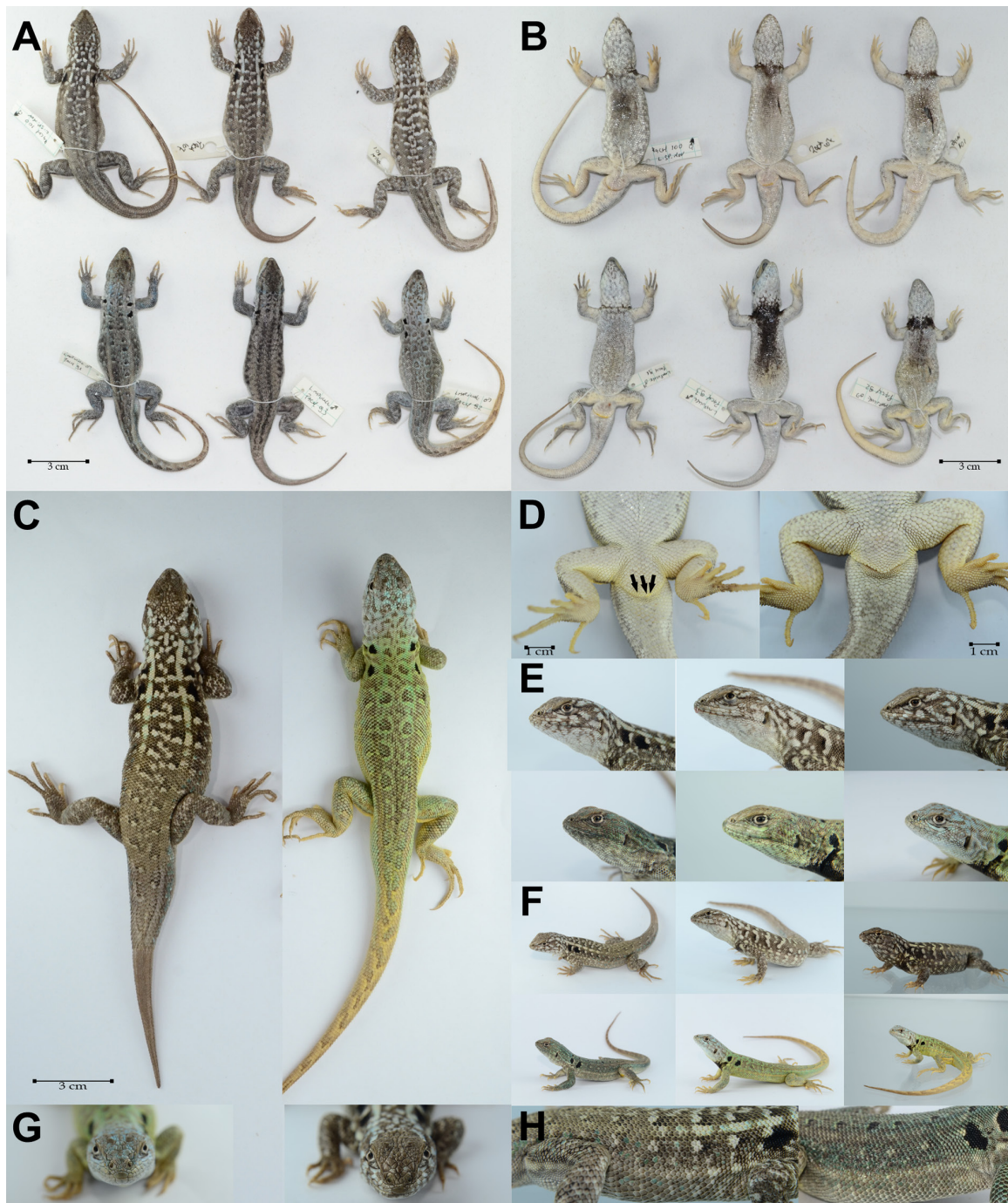


Fig. 2. A. Preserved male specimens of *L. kulinko* sp. nov. (top) and *L. mapuche* Abdala, 2002 (bottom) in dorsal view showing the color pattern. B. Ventral view of *L. kulinko* sp. nov. (top) and *L. mapuche* (bottom). C. Living male specimens of *L. kulinko* sp. nov. (left) and *L. mapuche* (right) in dorsal view showing the color pattern. D. Preserved male specimens of *L. kulinko* sp. nov. (left) and *L. mapuche* (right) showing the cloaca, the arrows indicate the preloacal pores. E. Live male specimens of *L. kulinko* sp. nov. (top line) and *L. mapuche* (bottom line) exhibiting the color pattern of the head and neck with the scapular spots. F. Live male specimens of *L. kulinko* sp. nov. (top line) and *L. mapuche* (bottom line) showing the varieties in color pattern. G. *L. kulinko* sp. nov. (left) and *L. mapuche* (right) showing the front nose. H. *L. kulinko* sp. nov. (left) and *L. mapuche* (right) exhibiting details of the color pattern of the body in lateral view.



Fig. 3. A–B. Adult male specimen of *Liolaemus mapuche* Abdala, 2002 from the type locality. C. Adult male specimen of *L. cayanus* Cei & Scolaro, 1980 from Matagusano, San Juan. D. Adult male specimen of *L. goetschi* Müller & Hellmich, 1938 from the type locality. E. Adult male specimen of *L. puelche* Ávila, Morando, Perez & Sites, 2007 from the type locality. F. Adult male specimen of *L. josei* Abdala, 2005 from the type locality. Photographs: C.S. Abdala.

(mean = 15.02 mm; SD = 1.71). Number of scales around body from 69–82 (mean = 75.67; SD = 4.61). Dorsal scales between occiput and thighs 90–96 (mean = 92.78; SD = 1.86). Dorsal scales with rounded edges, imbricated, with evident keel. Fourth finger of hand with 20–24 (mean = 21.44; SD = 1.42) digital lamellae. Fourth toe with 27–31 (mean = 28.78; SD = 1.48) digital lamellae. Infracarpal with laminar, imbricate, trifold scales. Infratarsal with laminar, imbricate and smooth scales. Ventral thigh with femoral patch. Ventrals larger than dorsals 98–116 (mean = 108.67; SD = 5.53). Tail longer (mean = 82.68 mm; SD = 16.48) than snout–vent length. Males with 6–7 (mean = 6.5 mm; SD = 0.58) precloacal pores, and absent in females. Gular fold developed. With presence of vestigial pores in the gulars, pectoral and abdominal regions. Scales of the patch with rounded edges and mucron, without notch.

COLOR VARIATION IN LIFE (Fig. 4A, C, E, G; based on nine specimens in life and 18 specimens photographed; with moderate sexual dichromatism). Males with highly variable coloration pattern and more showy colors than females; color of head varies from light brown to gray. Subtle dark brown line running from eye to neck, crossing temporal region. This line absent or attenuated in some large adults. Subocular generally white or gray in color, with dark upper border. Supralabials and lorilabials always lighter in color, generally light gray or white. General body color light brown or light gray, some specimens with bluish color. Vertebral region thin and not marked, except in proximal area of neck. A wide, short, antehumeral arch, black or gray in color, not expanded towards forelimbs. In larger males the gular melanism continues. With pre- and post-scapular spots of variable size and intensity, from almost absent to black or dark brown. Post-scapular generally slightly larger than pre-scapular. Several specimens with spots posterior to post-scapular, and these always smaller, black, or dark brown. Paravertebral spots arranged in non-aligned pairs along body, generally sub-quadrangular, dark brown on front and black on back, with white or light blue back edge. In some specimens spots in shape of line or stripe across body, while in others in the shape of point or small circle. In larger males, paravertebral spots in posterior region of body fainter or absent. A few specimens with almost total absence of paravertebral and lateral spots. Lateral spots diffuse or absent, but with same shape and color as paravertebral spots. Numerous scales and white spots on sides of neck and body. Some males with light blue scales forming thin line in lateral–posterior region of body. Same design as on body continues onto tail, but with line of light blue and / or green scales, iridescent on sides of tail. In several individual this line reaches sides of body. Ventrally, males white, with melanism present in gular, pectoral and abdominal region. Females with more uniform and consistent pattern of coloration than males. Head gray, bordered by gray in degrade. Line from eye to neck generally more notable than in males. Body also varies from gray to brown in color. Vertebral region more delimited in males than females, reddish-brown on back of body and tail. Antehumeral arch more diffuse than in males. Pre- and post-scapular spots present. Generally, largest post-scapular always black or dark gray in color. With sub-quadrangular paravertebral spots that are black or brown in color and white or yellow along posterior border and may be pointed in shape. On paravertebral spots, some females have reddish-brown spot or reddish-brown anterior border. Dorsolateral bands yellow, orange or white color, which can be continuous or fragmented and usually join at base of tail. In larger females dorsolateral bands not distinguishable or very faint. With and without lateral spots. When present they have same shape and color as paravertebral spots. Paravertebral spots unite on tail, where they form single stripe that extends longitudinally. White underneath with some irregularly scattered gray spots and scales.

Geographic distribution

The new species is restricted to the type locality and surroundings, in the localities of Aguada Pichana and Bajo de Añelo, Neuquén Province, Añelo Department, Argentina (Fig. 5), at elevations between 286–433 m a.s.l.

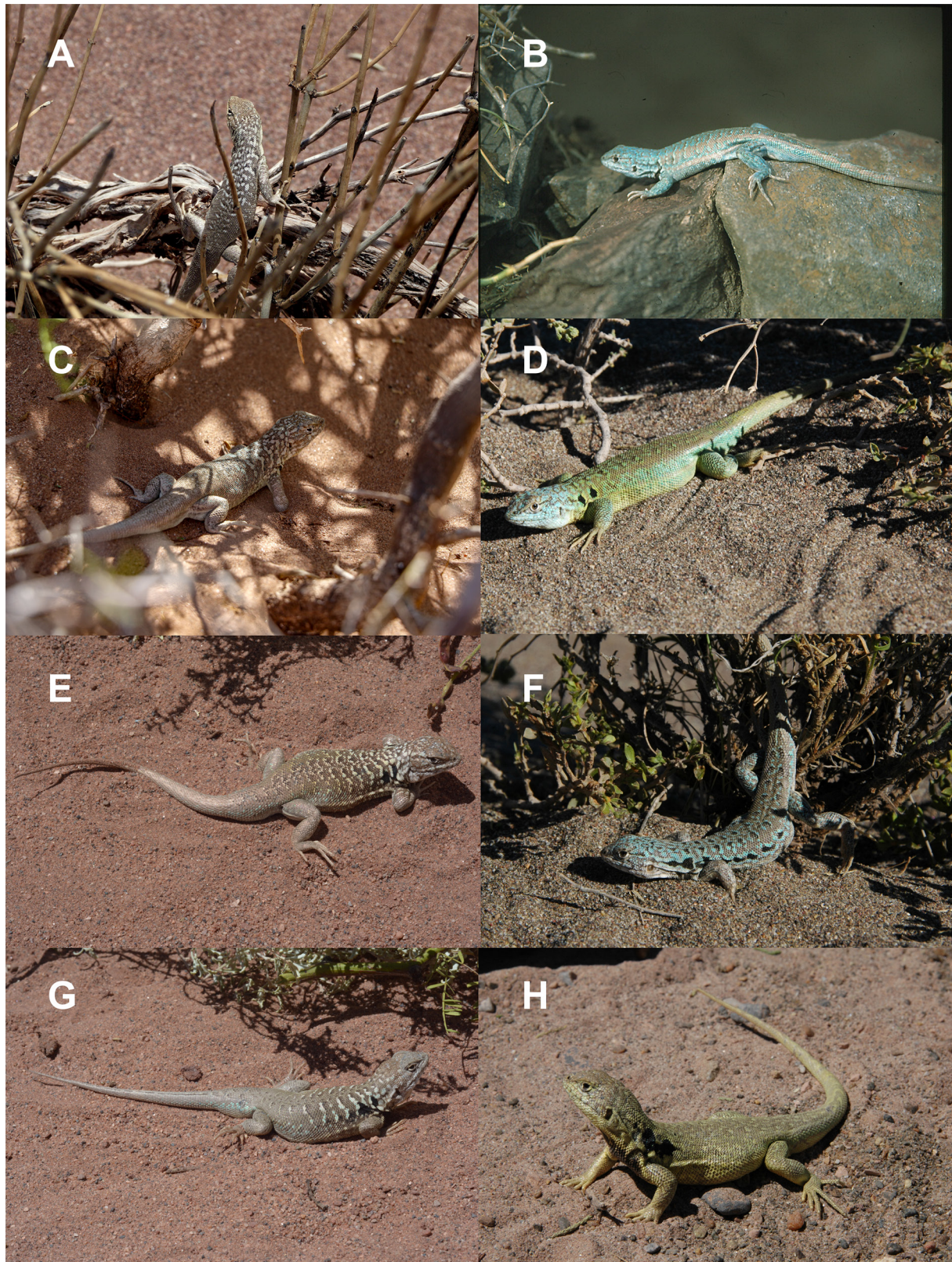


Fig. 4. A, C, E, G. Coloring patterns. Adult males of *Liolaemus kulinko* sp. nov. in dorsal view. B, D, F, H. Adult males of *L. mapuche* Abdala, 2002 in dorsal view. Photographs by I. Procheret (A, C) and C.S. Abdala (B, D–H).

Phylogenetic analysis (Figs 6–7)

Both molecular and morphological analyses indicate that *Liolaemus kulinko* sp. nov. belongs to the *L. boulengeri* group. According to molecular data, *Liolaemus kulinko* is recovered within the subclade of *L. goetschi*, complex of *L. cuyanus*, as a sister species of *L. mapuche*. This relationship is nested within a clade made up of (*L. goetschi* (*L. cuyanus* (*L. josei* + *L. puelche*)) + (*L. mapuche* + *L. kulinko* sp. nov.)) (Fig. 4). This relationship is also reflected in the table of molecular distances (Table 2).

The results of the morphological analysis are partially consistent with the molecular ones. In all the runs carried out, the species under study was recovered as a sister species of *L. mapuche* (Fig. 7). Nevertheless, the *L. cuyanus* complex was not always recovered as monophyletic, since the species related to *L. donosobarrosi* ((*L. tiranti* + *L. calliston*) + (*L. donosobarrosi* + *L. hugoi*)) are recovered basal throughout the clade of *L. melanops*, very distant from the rest of species of *L. cuyanus* complex. In the hypothesis presented in this work, *Liolaemus kulinko* sp. nov. shows 28 autoapomorphies, of which nine correspond to continuous characters and 21 to discrete ones (12 of scaling and nine of coloration). The relationship between *L. kulinko* and *L. mapuche* (Fig. 7), was recovered based on five characters, one continuous and four discrete (one of scales and three of coloring).

Natural history

Liolaemus kulinko sp. nov., is an endemic species of the Añelo Department in the center of Neuquén Province, and whose type locality is located 30 km from the eponymous city, in the area between provincial route number 7 and Neuquén River. We consider that the river is a biogeographical barrier separating it from its sister species *L. mapuche* (Fig. 5). The Bajo de Añelo comprises an area of 280 km² that constitutes an extensive closed basin, displaying a convergent radial network of temporary channels (Pérez *et al.* 2009) and whose lowest elevation is at 223 m a.s.l. Sediments from the Cretaceous Period predominate in the area and correspond to different geological formations. These are mainly from the Neuquén group and modern sedimentary deposits of various origins (fluvial, alluvial and aeolian). The internal dune system is the environment in which most of the endemic species of the area are found.

The vegetation is part of the Monte Phytogeographic Region (Cabrera 1971), which constitutes an arid to semi-arid biome that extends from Salta to Chubut Province (Abraham *et al.* 2009). The appearance of the vegetation is as islands or patches of shrubs that alternate with areas of bare soil (Bulacios Arroyo *et al.* 2021). Each patch constitutes a microenvironment that is used in different ways by the species that inhabit it (Bertiller *et al.* 2009). This ecosystem is characterized by the presence of numerous endemic species of insects, birds and reptiles (Roig-Juñent *et al.* 2001; Roig *et al.* 2009). The characteristic vegetation includes *Larrea divaricata* Cav., *L. cuneifolia* Cav., *L. nitida* Cav., *Cyclolepis genistoides* D. Don, *Suaeda divaricata* Moq., *Atriplex lampa* (Moq.) Gillies ex Small, *Prosopidastrum globosum* Burkart, *Neltuma alpataco* Phil. (C.E. Hughes & G.P. Lewis 2022), *Hyalis argentea* var. *latisquama* Cabrera, *Parkinsonia praecox* (Ruiz & Pav.) Hawkins, *Schinus johnstonii* F.A. Barkley, *Erodium cicutarium* (L.) L'Hér. ex Aiton, *Maihuenia patagonica* Phil. (Britton & Rose), *Grindelia chilensis* (Cornel.) Cabrera, *Senecio filaginoides* var. *lobulatus* (Hook. & Arn.) Cabrera, *Acantholippia seriphioides* (A. Gray) Moldenke, *Ephedra ochreatea* Miers., *Monttea aphylla* (Miers.) Benth. & Hook.f. (Burkart 1964; Cabrera 1971; Roig 1987; Arbo 1999; Gandullo *et al.* 2004, 2016; Riveros *et al.* 2011).

Liolaemus kulinko sp. nov. is sympatric with *L. grosseorum*, *L. calliston*, *L. cuyumhue*, *L. quinterosi* Ruiz, Quipildor, Bulacios-Arroyo, Chafrat & Abdala, 2019, *L. darwinii*, *L. gracilis*, *Aurivela longicauda* Bell, 1843, *Leiosaurus bellii* Duméril & Bibron, 1837, *Homonota darwinii* Boulenger, 1885, *H. horrida* (Burmeister, 1861), and *H. underwoodi* Kluge, 1964. Snakes seen during several visits to the locality were *Bothrops ammodytoides* Leybold, 1873, *B. diporus* Cope, 1862, *Erythrolamprus sagittifer* (Jan, 1863), *Philodryas patagoniensis* Girard, 1858, *Ph. trilineata* (Burmeister, 1861), *Ph. psammophidea*

Table 2. Pairwise uncorrected p-distance for *cyt-b* rRNA between *L. kulinko* sp. nov. and related species in the *L. boulengeri* group. The maximum and minimum values from the terminal taxa are included for each species. * = morphological data of number of specimens examined and traits.

species	<i>L. cuyanus</i> Cei & Scolaro, 1980	<i>L. josei</i> Abdala, 2005	<i>L. puelche</i> Avila, Morando, Fulvio-Pérez & Sites, 2007	<i>L. mapuche</i> Abdala, 2002
<i>L. cuyanus</i>				
<i>L. josei</i>	9.36–10.17			
<i>L. puelche</i>	9.64–10.36	6.24		
<i>L. mapuche</i>	7.04–9.20	8.51–9.58	8.65–8.94	
<i>L. kulinko</i> sp. nov.	7.48–12.02	7.56–9.60	8.23–9.93	8.51–9.79

Günther, 1872, *Micrurus pyrrhocryptus* Wagler, 1824, and *Pseudotomodon trigonatus* (Leybold, 1873), all of which represent potential predators of *Liolaemus kulinko*.

Liolaemus kulinko sp. nov., is a robust, psammophilic species, adult females weigh between 9.5 and 12.5 gm while adult males between 14 and 15 gm showing sexual dimorphism in other measurements. They are oviparous. Two females observed in November were pregnant, while two adult females collected in February had three and four shelled eggs, another female collected in March had one shelled egg, suggesting two clutches per year with one to four eggs per clutch.

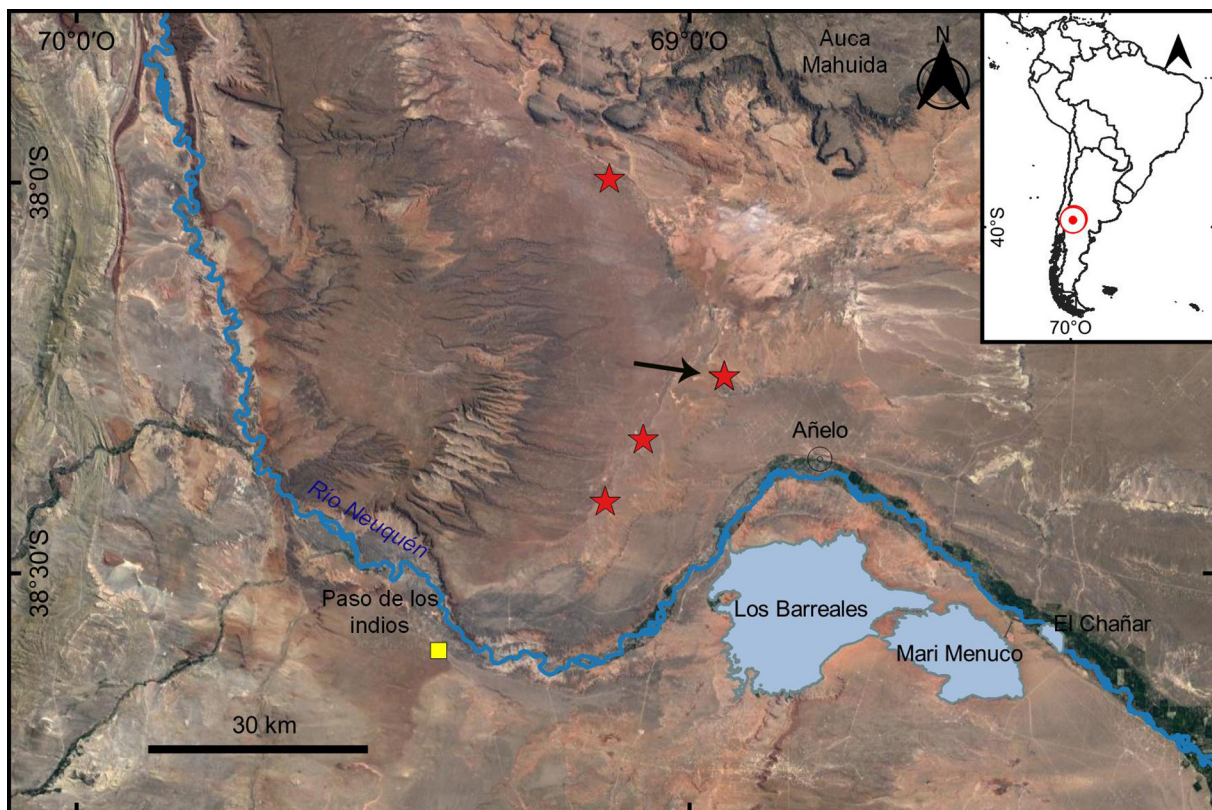


Fig. 5. Map of the distribution area of *Liolaemus kulinko* sp. nov. (red star), type locality of the holotype (black arrow with red star) and type locality of *Liolaemus mapuche* Abdala, 2002 (yellow square).

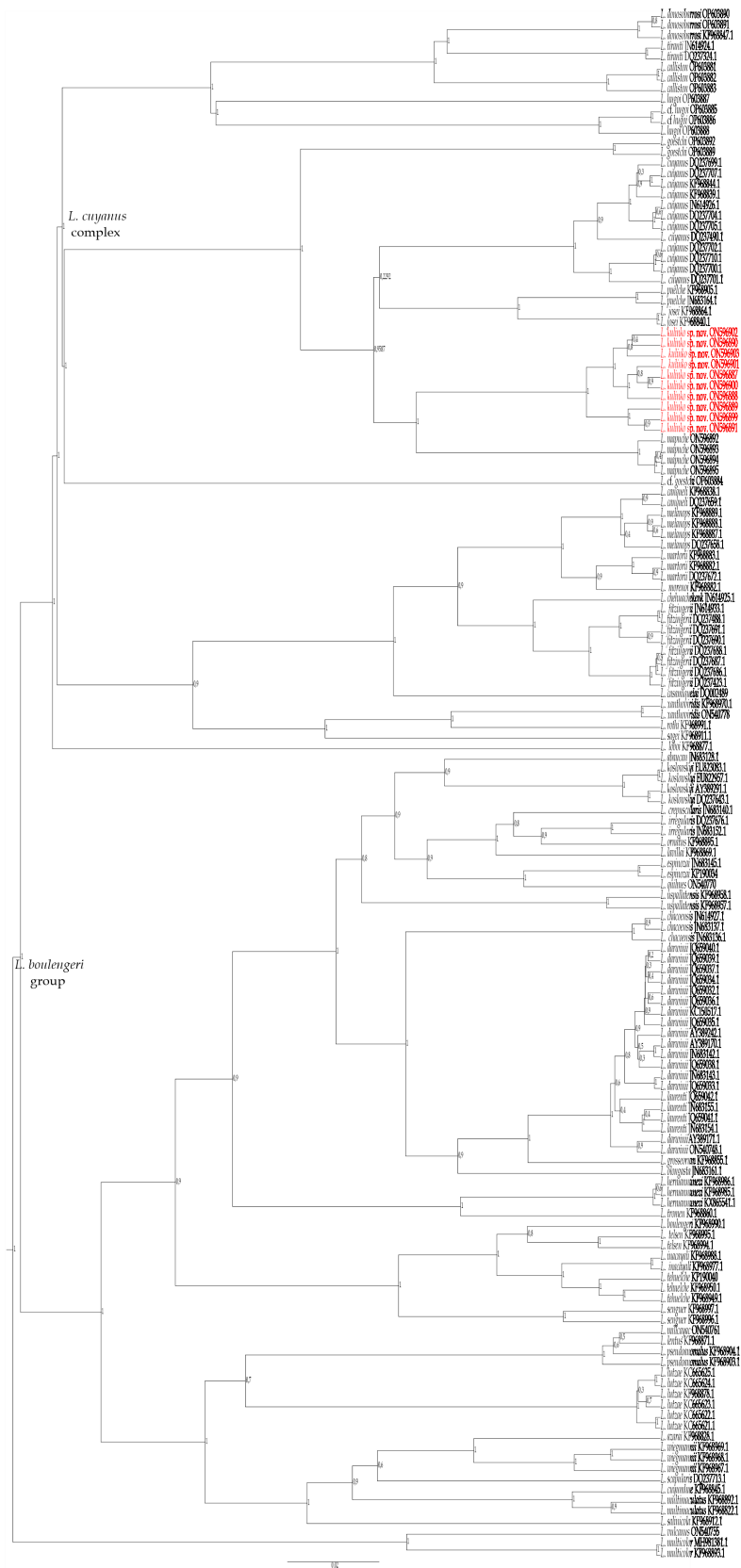


Fig. 6. Molecular phylogenetic tree showing the relationships between the species of the *Liolaemus boulengeri* group, including *L. kulinko* sp. nov.

Based on the analysis of stomach content and feces, its diet consists mainly of insect species, with a high content of ants of the genera *Acromyrmex* Mayr, 1865 (*Acromyrmex lobicornis* Emery, 1888) and *Camponotus* Mayr, 1861 (*Camponotus* sp.), and, to a lesser extent, Hemiptera, Diptera, Coleoptera (Fam. Buprestidae Leach, 1815), and spiders (indeterminate). Seeds and other plant remains were also found. This species is abundant and easy to observe, between 11 and 16 hrs. It takes refuge mainly under large bushes of *Neltuma* Raf. (*Neltuma alpataco*) and *Schinus* L. (*S. johnstonii* F.A. Barkley). It frequents dunes and sandy areas, although it also lives in higher stony areas, on the lower slopes of Añelo.

In March 2021, at twilight time, females were identified in patches of vegetation along with newborn juveniles that may be their progeny; this suggests possible maternal care (Procheret personal observation).

Discussion

The validity of the new species *L. kulinko* sp. nov. is supported by molecular data (monophyly and p-distances > 8% on *cyt-b*) and is characterized by a unique combination of morphological characters. The main different morphological characteristics of *L. kulinko* that differentiate it from its sister species *L. mapuche*, are: The precloacal pores in females which are absent in *L. mapuche*, and present in *L. kulinko*. The new species also has a greater number of dorsal (87–97 vs 70–86 scales), more scales around body (69–82 vs 65–76 scales), and more gulars scales (34–38 vs 25–35 scales). Patterns of coloration differ between the species. For example, head color in males of *L. mapuche*, is blue, light blue, brown or gray, but only brown or gray in *L. kulinko*; and in *L. mapuche* the posterior paravertebral spots in male *L. mapuche* are prominent, but blurred or absent in *L. kulinko*.

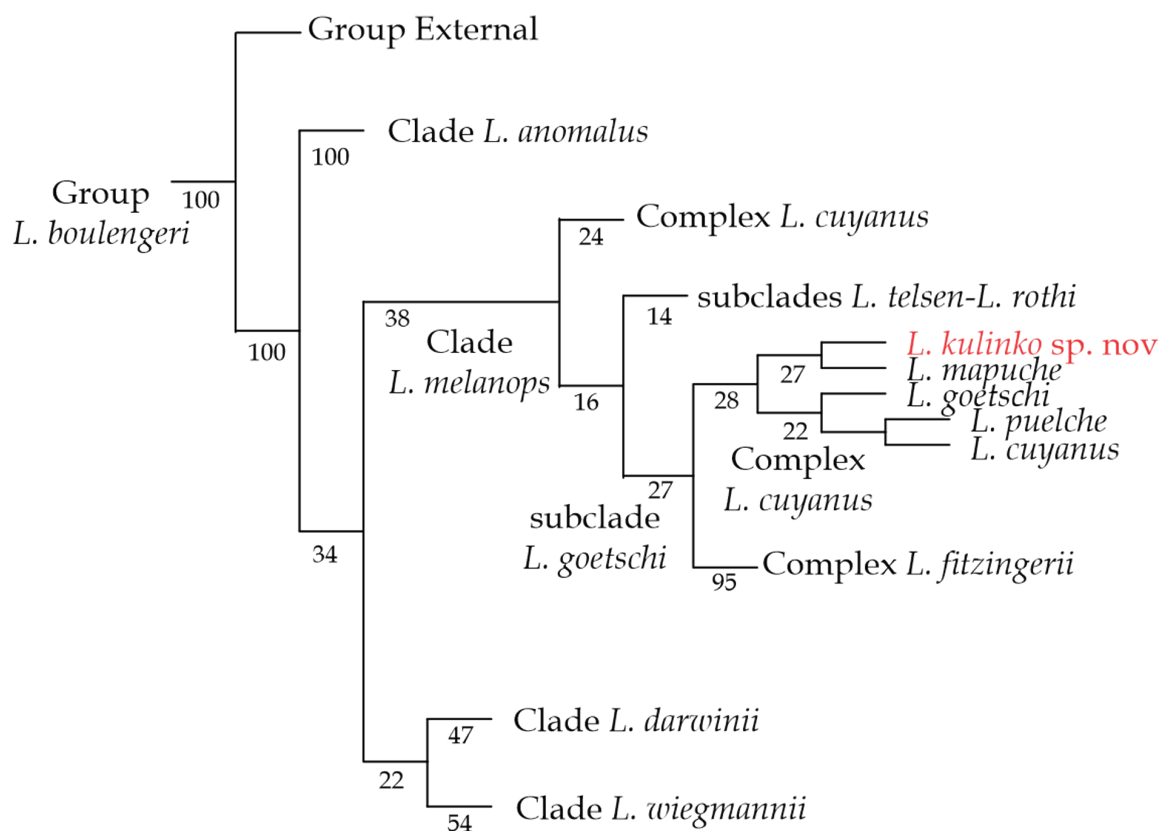


Fig. 7. Morphological phylogenetic tree showing the relationships between the species of *Liolaemus boulengeri* group, including *L. kulinko* sp. nov.

With the description of *Liolaemus kulinko* sp. nov., the *Liolaemus boulengeri* group reaches 75 nominal species. In this work we recover the new species as a member of the *L. melanops* clade, and within the *L. cuyanus* complex (Abdala 2007). This complex is similar to the *L. donosobarrosi* group proposed by Avila *et al.* (2006), with few exceptions. Avila *et al.* (2006) recovered *L. donosobarrosi* as the sister species of *L. cuyanus*, while for Abdala (2007), and in this work, these species are not recovered as sisters, but forming part of a more inclusive group (i.e., the *L. melanops* clade). Within this complex *Liolaemus kulinko* is phenotypically closest to *L. mapuche*. But we find morphological evidence that differentiates these two species. We also found high genetic distance values between *L. kulinko*, and *L. mapuche* (> 8%; Table 2). Genetic distance values greater than 3% are considered sufficient to establish a species limit within *Liolaemus* (Avila *et al.* 2009; Troncoso-Palacios *et al.* 2016; Quinteros *et al.* 2020) following the proposal from Breitmann *et al.* (2012).

The new species inhabits the localities of Aguada Pichana and Bajo de Añelo, Añelo Department, Neuquén Province, Argentina. This area has one of the most diverse species community of lizards in Argentina (n =14 species, in five different genera). There are eight species in the genus *Liolaemus* (*Liolaemus kulinko* sp. nov., *L. calliston*, *L. cuyumhue*, *L. darwinii*, *L. gracilis*, *L. grosseorum*, *L. quinterosi*, *L. calliston*); three species of *Homonota* (*H. darwinii*, *H. horrida*, *H. underwoodi*); two species of the family Leiosauridae Frost, Etheridge, Janies & Titus, 2001 (*Leiosaurus belli* Duméril & Bibron, 1837 and *Pristidactylus fasciatus* (d'Orbigny & Bibron, 1837)) and one species of Teiidae Gray, 1827 (*Aurivela longicauda* (Bell, 1843)). There are only a few similar cases in the country: among these other high-diversity areas are Caviahue-Copahue (Neuquén Province), with an assemblage of ten species of lizards (Abdala personal observation); El Nihuil (Mendoza Province), with eleven species (Semhan 2015; Abdala *et al.* 2016); Los Colorados in the Chaco Salteño with thirteen species (Lavilla *et al.* 1995). Such a rich assemblage of species should be a very important factor to be taken into account in the monitoring and conservation plans for certain areas of Aguada Pichana and Bajo de Añelo. Several of these species of *Liolaemus* show strict endemism for the Bajo de Añelo basin: the new species, *L. cuyumhue*, *L. calliston*, and *L. quinterosi*. This elevated endemism results from the combination of a rich geological history of macro and micro environmental conditions, which have led to speciation in the populations of *Liolaemus* over time.

Conclusions

Morphological and molecular data are concordant in confirming that the focal population of *Liolaemus* correspond to a new species, which we name and describe. Morphological studies indicate that *Liolaemus kulinko* sp. nov. has 28 autoapomorphies (unique characters in the group) and that it belongs to the *L. boulengeri* species group, and is positioned within the clade of *L. melanops*, within the complex of *L. cuyanus* and that its closest relative is *L. mapuche*. The inter-morphological differences with this latter species are important despite their spatial and phylogenetical proximity. The Bajo de Añelo locality represents an area with strikingly rich and high endemism of lizards, such as *L. cuyumhue* and *L. quinterosi* to which *L. kulinko* is added. The new species is considered as a DD IUCN category.

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Appendix

Appendix 1. Specimens examined. Those not cited in this section are added to those previously analyzed in Abdala (2007), and Abdala & Juárez Heredia (2013).

Liolaemus donosobarrosi Cei, 1974 (n =26)

Material examined

Holotype

ARGENTINA – **Mendoza** • Malargüe, Matancilla; IBA-R 824.

Other material

ARGENTINA – **Mendoza** • same collection data as for holotype; FML 027701 to 027703 • same collection data as for preceding; FML 026871 to 026873 • same collection data as for preceding; FML 02871 to 02876 • same collection data as for preceding; FML 17710 to 17720.

L. hugoi Bulacios-Arroyo, Semhan, Paz, Chafrat & Abdala, 2021 (n =6)

Material examined

Holotype

ARGENTINA – **Río Negro** • General Roca, 18 km from General Roca; 38°55'14.41" S, 67°39'39.19" W; FML 17 28711.

Paratypes

ARGENTINA – **Río Negro** • same collection data as for holotype; FML 28709 to 28712 • same collection data as for preceding; MPCN-H-147 to 148.

L. mapuche Abdala, 2002 (n =26)

Material examined

Holotype

ARGENTINA – **Neuquén** • Zapala, 15 km south of Paso de Indios, over provincial route 10; FML 11462.

Other material

ARGENTINA – **Neuquén** • same collection data as for holotype; FML 11463 to 11472 • Zapala, 3 km south west of Ramon Castro, over national route 22; FML 11473 to 11480 • Zapala, 33 km south east of Zapala, over national route 40; FML 11482 to 11487.

L. tirantii Ávila, Perez, Minoli, Medina, Sites & Morando, 2017 (n =23)

Material examined

ARGENTINA – **Neuquén** • Zapala, Cerro Bandera, 22 km west of Cutralcó; FML 27255, 27841 to 27842 • Zapala, La Amarga; 39°06' S, 69°34' W; FML 08320 to 08321 • Zapala, Cerro Banderas Field 40 km east of Zapala; FML 29769–76FML • Zapala; 38°55'23.2" S, 69°41'52.9" W; FML 08323 • Confluence, 41 km west of Cutralcó; 38°55'39.2" S, 69°41'13.2" W; FML 10059 • Confluence; 7.4 km northwest of Cutralcó; FML 22345 to 22352.

Appendix 2 (continued on next four pages). GenBank codes for sequences of *Liolaemus* lizards of *boulengeri* group and the outgroup used in this study.

n	species	cyt-b	museum voucher	source
1	<i>L. abaucan</i> Etheridge, 1993	JN683128.1	LJAMM_2372	Morando <i>et al.</i> 2007
2	<i>L. azarai</i> Avila, 2003	KF968828.1	LJAMMCNP 1095	Olave <i>et al.</i> 2014
3	<i>L. boulengeri</i> Koslowsky, 1898	KF968990.1	LJAMMCNP 3485	Olave <i>et al.</i> 2014
4	<i>L. calliston</i> Lobo & Kretzschmar, 1996	OP603881	MPCN-H-628	this study
5	<i>L. calliston</i> Lobo & Kretzschmar, 1996	OP603882	MPCN-H-629	this study
6	<i>L. calliston</i> Lobo & Kretzschmar, 1996	OP603883	MPCN-H-630	this study
7	<i>L. canqueli</i> Cei, 1975	KF968838.1	LJAMMCNP	Olave <i>et al.</i> 2014
8	<i>L. canqueli</i> Cei, 1975	DQ237659.1	MLPS2470	Avila <i>et al.</i> 2006
9	<i>L. casamiquelai</i> Avila, Fulvio Perez, Morando & Sites, 2010	DQ002489	LJAMMCNP 2947	Olave <i>et al.</i> 2014
10	<i>L. chacoensis</i> Shreve, 1948	JN614927.1	LJAMM-CNP 10854	Camargo <i>et al.</i> 2012
11	<i>L. chacoensis</i> Shreve, 1948	JN683137.1	MLPS_2508	Morando <i>et al.</i> 2007
12	<i>L. chacoensis</i> Shreve, 1948	JN683136.1	LJAMM-CNP 10649	Camargo <i>et al.</i> 2012
13	<i>L. chehuachekenk</i> Avila, Morando & Sites, 2008	JN614925.1	LJAMMCNP 5581	Olave <i>et al.</i> 2014
14	<i>L. crepuscularis</i> Abdala & Diaz Gómez 2006	JN683140.1	LJAMM-CNP 12644	Camargo <i>et al.</i> 2012
15	<i>L. cuyanus</i> Cei & Scolaro, 1980	KF968844.1	LJAMM2388	Avila <i>et al.</i> 2006
16	<i>L. cuyanus</i> Cei & Scolaro, 1980	KF968839.1	LJAMMCNP 4155	Avila <i>et al.</i> 2006
17	<i>L. cuyanus</i> Cei & Scolaro, 1980	JN614926.1	LJAMMCNP 4155	Olave <i>et al.</i> 2014
18	<i>L. cuyanus</i> Cei & Scolaro, 1980	DQ237490.1	BYU47312	Avila <i>et al.</i> 2006
19	<i>L. cuyanus</i> Cei & Scolaro, 1980	DQ237710.1	BYU47314	Avila <i>et al.</i> 2006
20	<i>L. cuyanus</i> Cei & Scolaro, 1980	DQ237707.1	LJAMM4172	Avila <i>et al.</i> 2006
21	<i>L. cuyanus</i> Cei & Scolaro, 1980	DQ237705.1	LJAMMCNP 12565	Olave <i>et al.</i> 2014
22	<i>L. cuyanus</i> Cei & Scolaro, 1980	DQ237704.1	BYU47312	Avila <i>et al.</i> 2006
23	<i>L. cuyanus</i> Cei & Scolaro, 1980	DQ237702.1	LJAMMCNP 4155	Fontanella <i>et al.</i> 2012
24	<i>L. cuyanus</i> Cei & Scolaro, 1980	DQ237701.1	LJAMMCNP 4155	Fontanella <i>et al.</i> 2012
25	<i>L. cuyanus</i> Cei & Scolaro, 1980	DQ237700.1	LJAMMCNP 12565	Olave <i>et al.</i> 2014

Appendix 2 (continued).

n	species	cyt-b	museum voucher	source
26	<i>L. cuyanus</i> Cei & Scolaro, 1980	DQ237699.1	LJAMM4077	Avila <i>et al.</i> 2006
27	<i>L. cuyumhue</i> Avila, Morando, Perez & Sites 2009	KF968845.1	LJAMMCNP 3690	Olave <i>et al.</i> 2014
28	<i>L. darwini</i> Bell, 1843	JQ659040.1	LJAMM 2275	Morando <i>et al.</i> 2007
29	<i>L. darwini</i> Bell, 1843	JQ659039.1	LJAMM-CNP 5104	Camargo <i>et al.</i> 2012
30	<i>L. darwini</i> Bell, 1843	JQ659037.1	FML_13064	Morando <i>et al.</i> 2007
31	<i>L. darwini</i> Bell, 1843	JQ659036.1	LJAMM-CNP 8355	Camargo <i>et al.</i> 2012
32	<i>L. darwini</i> Bell, 1843	JQ659035.1	LJAMM-CNP 14634	Leache <i>et al.</i> 2015
33	<i>L. darwini</i> Bell, 1843	JQ659034.1	LJAMMCNP 10391	Olave <i>et al.</i> 2014
34	<i>L. darwini</i> Bell, 1843	JQ659033.1	LJAMM-CNP 5104	Camargo <i>et al.</i> 2012
35	<i>L. darwini</i> Bell, 1843	JQ659038.1	LJAMM-CNP 12630	Camargo <i>et al.</i> 2012
36	<i>L. darwini</i> Bell, 1843	JQ659032.1	LJAMM-CNP 5104	Camargo <i>et al.</i> 2012
37	<i>L. darwini</i> Bell, 1843	JN683143.1	LJAMM-CNP 4038	Camargo <i>et al.</i> 2012
38	<i>L. darwini</i> Bell, 1843	JN683142.1	LJAMM-CNP 4404	Camargo <i>et al.</i> 2012
39	<i>L. darwini</i> Bell, 1843	KC150252.2	LJAMM-CNP 12775	Camargo <i>et al.</i> 2012
40	<i>L. darwini</i> Bell, 1843	AY389170.1	LJAMM-CNP 1983	Camargo <i>et al.</i> 2012
41	<i>L. darwini</i> Bell, 1843	AY389242.1	FML_13064	Morando <i>et al.</i> 2004
42	<i>L. darwini</i> Bell, 1843	AY389171.1	LJAMM-CNP 5104	Camargo <i>et al.</i> 2012
43	<i>L. darwini</i> Bell, 1843	ON540748.1	FBC78	this study
44	<i>L. donosobarrosi</i> (Cei, 1974)	KF968847.1	LJAMMCNP 5076	Olave <i>et al.</i> 2014
45	<i>L. donosobarrosi</i> (Cei, 1974)	OP603890	FML17712	this study
46	<i>L. donosobarrosi</i> (Cei, 1974)	OP603891	FML17713	this study
47	<i>L. espinozai</i> Abdala, 2005	JN683145.1	LJAMM-CNP 12668	Camargo <i>et al.</i> 2012
48	<i>L. espinozai</i> Abdala, 2005	KP190034	LJAMM-CNP 4338	Camargo <i>et al.</i> 2012
49	<i>L. fitzingerii</i> (Duméril & Bibron, 1873)	JN614933.1	LJAMMCNP 2420	Olave <i>et al.</i> 2014
50	<i>L. fitzingerii</i> (Duméril & Bibron, 1873)	DQ237488.1	LJAMM2427	Avila <i>et al.</i> 2006
51	<i>L. fitzingerii</i> (Duméril & Bibron, 1873)	DQ237691.1	BYU47289	Avila <i>et al.</i> 2006
52	<i>L. fitzingerii</i> (Duméril & Bibron, 1873)	DQ237690.1	BYU47287	Avila <i>et al.</i> 2006
53	<i>L. fitzingerii</i> (Duméril & Bibron, 1873)	DQ237688.1	LJAMMCNP 4891	Olave <i>et al.</i> 2014
54	<i>L. fitzingerii</i> (Duméril & Bibron, 1873)	DQ237687.1	BYU46769	Avila <i>et al.</i> 2006
55	<i>L. fitzingerii</i> (Duméril & Bibron, 1873)	DQ237686.1	LJAMM2889	Avila <i>et al.</i> 2006
56	<i>L. fitzingerii</i> (Duméril & Bibron, 1873)	DQ237423.1	LJAMM2464	Avila <i>et al.</i> 2006
57	<i>L. goetschi</i> Müller & Hellmich, 1938	OP603889	MPCN-H-181	this study
58	<i>L. goetschi</i> Müller & Hellmich, 1938	OP603892	FML21501	this study
59	<i>L. cf goetschi</i> Müller & Hellmich, 1938	OP603884	MPCN-H-47	this study
60	<i>L. grosseorum</i> Etheridge, 2001	KF968855.1	LJAMMCNP 4046	Olave <i>et al.</i> 2014
61	<i>L. hermannunezi</i> Pincheira-Donoso, Scolaro & Schulte, 2007	KF968986.1	LJAMMCNP 14193	Olave <i>et al.</i> 2014
62	<i>L. hermannunezi</i> Pincheira-Donoso, Scolaro & Schulte, 2007	KF968985.1	LJAMMCNP 14193	Olave <i>et al.</i> 2014

Appendix 2 (continued).

n	species	cyt-b	museum voucher	source
63	<i>L. hermannunezi</i> Pincheira-Donoso, Scolaro & Schulte, 2007	KX865541.1	LJAMMCNP 14150	Olave <i>et al.</i> 2014
64	<i>L. hugoi</i> Bulacios-Arroyo, Semhan, Paz, Chafrat & Abdala, 2021	OP603887	MPCN-H-147	this study
65	<i>L. hugoi</i> Bulacios-Arroyo, Semhan, Paz, Chafrat & Abdala, 2021	OP603888	MPCN-H-148	this study
66	<i>L. cf hugoi</i> Bulacios-Arroyo, Semhan, Paz, Chafrat & Abdala, 2021	OP603885	MPCN-H-624	this study
67	<i>L. cf hugoi</i> Bulacios-Arroyo, Semhan, Paz, Chafrat & Abdala, 2021	OP603886	MPCN-H-625	this study
68	<i>L. inacayali</i> Abdala, 2003	KF968988.1	LJAMMCNP 2175	Olave <i>et al.</i> 2014
69	<i>L. inacayali</i> Abdala, 2003	KF968977.1	LJAMMCNP 2175	Olave <i>et al.</i> 2014
70	<i>L. irregulari</i> Laurent, 1986	DQ237676.1	LJAMM2628	Avila <i>et al.</i> 2006
71	<i>L. irregularis</i> Laurent, 1986	JN683152.1	LJAMM-CNP 2629	Camargo <i>et al.</i> 2012
72	<i>L. josei</i> Abdala, 2005	KF968864.1	LJAMMCNP 5761	Olave <i>et al.</i> 2014
73	<i>L. josei</i> Abdala, 2005	KF968840.1	LJAMMCNP 7953	Olave <i>et al.</i> 2014
74	<i>L. koslowskyi</i> Etheridge, 1993	EU823083.1	LJAMM-CNP 5011	Camargo <i>et al.</i> 2012
75	<i>L. koslowskyi</i> Etheridge, 1993	EU822957.1	LJAMM-CNP 4206	Morando <i>et al.</i> 2007
76	<i>L. koslowskyi</i> Etheridge, 1993	AY389291.1	LJAMMCNP 4159	Olave <i>et al.</i> 2014
77	<i>L. koslowskyi</i> Etheridge, 1993	DQ237643.1	LJAMM2330	Avila <i>et al.</i> 2006
78	<i>L. kulinko</i> sp. nov.	ON596887	MPCN-H-456	this study
79	<i>L. kulinko</i> sp. nov.	ON596888	MPCN-H-457	this study
80	<i>L. kulinko</i> sp. nov.	ON596889	MPCN-H-458	this study
81	<i>L. kulinko</i> sp. nov.	ON596890	MPCN-H-468	this study
82	<i>L. kulinko</i> sp. nov. (holotype)	ON596891	MPCN-H-469	this study
83	<i>L. kulinko</i> sp. nov.	ON596899	MPCN-H-470	this study
84	<i>L. kulinko</i> sp. nov.	ON596900	MPCN-H-471	this study
85	<i>L. kulinko</i> sp. nov.	ON596901	MPCN-H-472	this study
86	<i>L. kulinko</i> sp. nov.	ON596902	MPCN-H-473	this study
87	<i>L. kulinko</i> sp. nov.	ON596903	MPCN-H-474	this study
88	<i>L. laurenti</i> Etheridge, 1992	JQ659042.1	LJAMM-CNP 4038	Camargo <i>et al.</i> 2012
89	<i>L. laurenti</i> Etheridge, 1992	JQ659041.1	LJAMM-CNP 2334	Camargo <i>et al.</i> 2012
90	<i>L. laurenti</i> Etheridge, 1992	JN683155.1	LJAMM-CNP 4210	Camargo <i>et al.</i> 2012
91	<i>L. laurenti</i> Etheridge, 1992	JN683154.1	LJAMM-CNP 4210	Camargo <i>et al.</i> 2012
92	<i>L. lavillai</i> Abdala & Lobo, 2006	KF968869.1	LJAMMCNP 4428	Olave <i>et al.</i> 2014
93	<i>L. lentus</i> Gallardo, 1966	KF968871.1	LJAMMCNP 13164	Olave <i>et al.</i> 2014
94	<i>L. lobo</i> Abdala, 2003	KF968877.1	LJAMMCNP 3295	Olave <i>et al.</i> 2014
95	<i>L. lutzae</i> Abdala, 2003	KF968878.1	LJAMMCNP 916862	Olave <i>et al.</i> 2014
96	<i>L. lutzae</i> Abdala, 2003	KC665625.1	LJAMMCNP 916862	Olave <i>et al.</i> 2014
97	<i>L. lutzae</i> Abdala, 2003	KC665624.1	LJAMMCNP 916862	Olave <i>et al.</i> 2014

Appendix 2 (continued).

n	species	cyt-b	museum voucher	source
98	<i>L. lutzae</i> Abdala, 2003	KC665623.1	LJAMMCNP 916862	Olave <i>et al.</i> 2014
99	<i>L. lutzae</i> Abdala, 2003	KC665622.1	S/C	Olave <i>et al.</i> 2014
100	<i>L. lutzae</i> Abdala, 2003	KC665621.1	S/C	Olave <i>et al.</i> 2014
101	<i>L. mapuche</i> Abdala, 2002	ON596892	MPCN-H-227	this study
102	<i>L. mapuche</i> Abdala, 2002	ON596893	MPCN-H-464	this study
103	<i>L. mapuche</i> Abdala, 2002	ON596894	MPCN-H-461	this study
104	<i>L. mapuche</i> Abdala, 2002	ON596895	MPCN-H-462	this study
105	<i>L. martorii</i> Abdala, 2003	KF968883.1	LJAMMCNP 2561	Olave <i>et al.</i> 2014
106	<i>L. martorii</i> Abdala, 2003	KF968882.1	LJAMMCNP 12928	Olave <i>et al.</i> 2014
107	<i>L. martorii</i> Abdala, 2003	DQ237672.1	LJAMM2561	Avila <i>et al.</i> 2006
108	<i>L. melanops</i> Burmeister, 1888	KF968889.1	LJAMMCNP 13553	Olave <i>et al.</i> 2014
109	<i>L. melanops</i> Burmeister, 1888	KF968888.1	LJAMMCNP 6017	Olave <i>et al.</i> 2014
110	<i>L. melanops</i> Burmeister, 1888	KF968887.1	LJAMMCNP 6017	Olave <i>et al.</i> 2014
111	<i>L. melanops</i> Burmeister, 1888	DQ237658.1	LJAMM2431	Avila <i>et al.</i> 2006
112	<i>L. millcayac</i> Abdala & Juárez-Heredia, 2013	ON540761	LJAMMCNP 12851	Olave <i>et al.</i> 2014
113	<i>L. morenoi</i> Etheridge & Christie, 2003	KF968882.1	LJAMMCNP 6477	Olave <i>et al.</i> 2014
114	<i>L. multimaculatus</i> (Duméril & Bibron, 1837)	KF968892.1	LJAMMCNP 15	Olave <i>et al.</i> 2014
115	<i>L. multimaculatus</i> (Duméril & Bibron, 1837)	KF968822.1	LJAMMCNP 15	Olave <i>et al.</i> 2014
116	<i>L. olongasta</i> Etheridge, 1993	JN683161.1	LJAMM-CNP 10821	Camargo <i>et al.</i> 2012
117	<i>L. ornatus</i> Koslowsky, 1898	KF968895.1	LJAMMCNP 12021	Olave <i>et al.</i> 2014
118	<i>L. pseudoanomalous</i> Cei, 1981	KF968903.1	LJAMMCNP 10911	Olave <i>et al.</i> 2014
119	<i>L. pseudoanomalous</i> Cei, 1981	KF968904.1	LJAMMCNP 2300	Olave <i>et al.</i> 2014
120	<i>L. puelche</i> Avila, Morando, Fulvio-Pérez & Sites, 2007	KF968905.1	LJAMMCNP 5759	Olave <i>et al.</i> 2014
121	<i>L. puelche</i> Avila, Morando, Fulvio-Pérez & Sites, 2007	JN683164.1	LJAMM-CNP 4404	Camargo <i>et al.</i> 2012
122	<i>L. quilmes</i> Etheridge, 1993	ON540770	LJAMM-CNP 4404	Camargo <i>et al.</i> 2012
123	<i>L. rothi</i> Koslowsky, 1898	KF968991.1	LJAMMCNP 3065	Olave <i>et al.</i> 2014
124	<i>L. sagei</i> Etheridge & Christie, 2003	KF968911.1	LJAMMCNP 8731	Olave <i>et al.</i> 2014
125	<i>L. salinicola</i> Laurent, 1986	KF968912.1	LJAMMCNP 2375	Olave <i>et al.</i> 2014
126	<i>L. scapularis</i> Laurent, 1982	DQ237713.1	LJAMMCNP 12699	Olave <i>et al.</i> 2014
127	<i>L. senguier</i> Abdala, 2005	KF968997.1	LJAMMCNP 2187	Olave <i>et al.</i> 2014
128	<i>L. senguier</i> Abdala, 2005	KF968996.1	LJAMMCNP 9027	Olave <i>et al.</i> 2014
129	<i>L. tehuelche</i> Abdala, 2003	KP190040	LJAMMCNP 5462	Olave <i>et al.</i> 2014
130	<i>L. tehuelche</i> Abdala, 2003	KF968950.1	LJAMMCNP 5462	Olave <i>et al.</i> 2014
131	<i>L. tehuelche</i> Abdala, 2003	KF968949.1	LJAMMCNP 5461	Olave <i>et al.</i> 2014
132	<i>L. telsen</i> Cei & Scolaro, 1999	KF968995.1	LJAMMCNP 5530	Olave <i>et al.</i> 2014
133	<i>L. telsen</i> Cei & Scolaro, 1999	KF968994.1	LJAMMCNP 8693	Olave <i>et al.</i> 2014
134	<i>L. tiranti</i> Avila, Fulvio-Perez, Minoli, Medina, Sites & Morando, 2017	DQ237324.1	LJAMM2542	Avila <i>et al.</i> 2006

Appendix 2 (continued).

n	species	cyt- <i>b</i>	museum voucher	source
135	<i>L. tiranti</i> Avila, Fulvio-Perez, Minoli, Medina, Sites & Morando, 2017	JN614924.1	BYU47301	Avila <i>et al.</i> 2006
136	<i>L. tromen</i> Abdala, Semhan, Moreno Azocar, Bonino, Paz & Cruz, 2012	KF968860.1	LJAMMCNP 12156	Olave <i>et al.</i> 2014
137	<i>L. uspallatensis</i> Macola & Castro, 1982	KF968958.1	LJAMMCNP 12500	Olave <i>et al.</i> 2014
138	<i>L. uspallatensis</i> Macola & Castro, 1982	KF968957.1	LJAMM-CNP 12506	Camargo <i>et al.</i> 2012
139	<i>L. wiegmannii</i>	KF968969.1	LJAMMCNP 10925	Olave <i>et al.</i> 2014
140	<i>L. wiegmannii</i>	KF968968.1	LJAMMCNP 3099	Olave <i>et al.</i> 2014
141	<i>L. wiegmannii</i>	KF968967.1	LJAMMCNP 12772	Olave <i>et al.</i> 2014
142	<i>L. xanthoviridis</i>	KF968970.1	LJAMMCNP 2420	Olave <i>et al.</i> 2014
143	<i>L. xanthoviridis</i>	ON540778	LJAMMCNP 2420	Olave <i>et al.</i> 2014
144	<i>L. multicolor</i> (outgroup)	MH981381.1	LJAMMCNP 12047	Olave <i>et al.</i> 2014
145	<i>L. multicolor</i> (outgroup)	KF968893.1	LJAMMCNP 4464	Olave <i>et al.</i> 2014
146	<i>L. vulcanus</i> (outgroup)	ON540755	LJAMMCNP 5019	Olave <i>et al.</i> 2014