Trabajo

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Description of a new species of the *Liolaemus elongatus* group (Squamata: Iguania) through integrative taxonomy

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ABSTRACT
Liolaemus is the genus with the highest number of lizard species described in South America up to date, with approximately 290. One of the groups within the genus, the *Liolaemus elongatus* group, is distributed in central-south Argentina and Chile. In this work, we describe a new species belonging to the *L. petrophilus* clade using an integrative approach that includes the analysis of morphological (lepidosis, morphometric, coloration and hemipenis characters) and molecular evidence (genetic distances and phylogeny). We provide information about the geological formation of the study area and the clade distribution, and present an extensive description of its natural history (including diet, habitat, behaviour, phytogeography, mode of life, and sympatric species). Additionally, we present a time divergence analysis of internal branches for all representatives of the *L. elongatus* group. This newly described species shows character states (morphological and molecular) that allow its clear distinction from the other members of the *L. elongatus* group, as well as from the remaining *Liolaemus* species. According to our results, the *L. elongatus* group originated during the Miocene, whereas the new species diverged from its sister taxon during the Pleistocene.

Key words: Divergence times; Lizards; Patagonia; South America; Phylogeny

RESUMEN
Liolaemus es el género con el mayor número de especies de lagartijas descritas en América del Sur hasta la fecha, con aproximadamente 290 especies. Uno de los grupos dentro del género, el grupo de *Liolaemus elongatus*, se distribuye en el centro-sur de Argentina y Chile. En este trabajo, describimos una nueva especie perteneciente al clado de *L. petrophilus* usando un enfoque integrador que incluye el análisis de evidencia morfológica (lepidosis, morfométrica, coloración y caracteres de hemipenes) y evidencia molecular (distancias genéticas y filogenia). Brindamos información sobre la formación geológica del área de estudio y la distribución del clado, y presentamos una descripción extensa de su historia natural (que incluye dieta, hábitat, comportamiento, fitogeografía, modo de vida y especies simpátricas). Además, presentamos un análisis de tiempos de divergencia de las ramas internas y de todos los representantes del grupo de *L. elongatus*. Esta especie recién descrita muestra estados de carácter (morfológicos y moleculares) que permiten su clara distinción de los otros miembros del grupo de *L. elongatus*, así como de las restantes especies de *Liolaemus*. Según nuestros resultados, el grupo de *L. elongatus* se originó durante el Mioceno, mientras que la nueva especie se separó de su taxón hermano durante el Pleistoceno.

Palabra claves: Tiempos de divergencia; Lagartos; Patagonia; Sudamérica; Filogenia

Introduction

The family Liolaemidae (Frost *et al.,* 2001) is the most species-rich family of lizards in South America. One of the genera within this family, *Liolaemus* (Wiegmann, 1834), is the second most diverse genus in the world, with ~290 small and medium-sized species described in South America (Abdala *et al.,*

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2021a; Arapa-Aquino *et al.,* 2021; Avila *et al.,* 2021; Bulacios Arroyo *et al.,* 2021; Quiroz *et al.,* 2021; Ruiz *et al.,* 2021; Troncoso-Palacios and Ramírez-Álvarez, 2021; Valladares-Faúndez *et al.,* 2021). *Liolaemus* has been the subject of numerous studies in various disciplines. The interest in this genus can be explained by its great morphological, functional and ecological diversity. The species that compose this taxon occur in different substrates (there are saxicolous, arboreal, and sand-dwelling species), have two distinct reproductive modes (viviparous and oviparous), and present a wide variety of diets (herbivorous, insectivorous and omnivorous) (Ramírez Pinilla, 1991; Schulte *et al.,* 2000; Martínez Oliver and Lobo, 2002; Espinoza *et al.,* 2004; Halloy *et al.,* 2013; Esquerré *et al.,* 2019). Regarding coloration patterns, in some species there is no sexual dichromatism, whereas in other this phenomenon is conspicuous; there are also varying levels of polymorphism (Abdala and Quinteros, 2014). Geographically, *Liolaemus* is distributed from Tierra del Fuego, in the southernmost point in South America, to the Peruvian Andes in the north. Its range covers regions in Argentina, Uruguay, Bolivia, Chile and Peru, with an altitudinal range from sea level to over 5000 m a.s.l. (Aparicio and Ocampo, 2010). Thus, this group has captured the attention of herpetologists for years, and is still the subject of many ongoing studies, since there are still many interesting questions that remain unanswered.

Regarding the phylogenetic relationships within the genus *Liolaemus*, Laurent (1983, 1985, 1995) and Etheridge (1995) split the *Liolaemus* genus into two main groups, subgenus *Liolaemus* (sensu stricto) (Laurent, 1983) or "Chileno group", and *Eulaemus* (Laurent, 1983) or "Argentino group", distributed mainly to the west and east of the Andes, respectively. This split was supported by many phylogenetic analyses (Schulte, 2000; Espinoza *et al.,* 2004; Pyron *et al.,* 2013; Olave *et al.,* 2014; Zheng and Wiens, 2016). Different phylogenetic hypotheses have been proposed for *Liolaemus* sensu stricto subgenus, and several subgroups have been recognized inside (Lobo *et al.,* 2010; Abdala and Quinteros, 2014; Morando *et al.*, 2020; Abdala *et al.*, 2021b, Esquerré *et al.*, 2022). One of them is the *L. elongatus* group, proposed by Cei (1974) as "*L. elongatus* complex" and later renamed as *L. elongatus* group (Cei, 1986), which is distributed in central-south Argentina and Chile, along the Andean and extra-Andean regions (Abdala *et al.*, 2010; Avila *et al.*, 2015; Troncoso-Palacios *et al.*, 2018).

Morando *et al.* (2003) performed a phylogeographic analysis of the relationships within *Liolaemus elongatus* group, including specimens of all recognized species at that time. Morando *et al.* (2003) and Avila *et al.* (2004) recognized three groups: the *L. elongatus*, the *L. kriegi*, and the *L. petrophilus* groups, and renamed the most inclusive group as the *L. elongatus-kriegi* complex. In addition, Morando *et al.* (2003) mentioned the existence of many candidate species within this complex. Subsequently, Lobo (2005) and Díaz Gómez and Lobo (2006) proposed a new clade within the *L. elongatus* group, named *L. capillitas* group, which included the species of the *L. petrophilus* group by Morando *et al.* (2003), distributed in north-western Argentina. Based on a consensus of previous studies (Etheridge, 1995; Schulte *et al.,* 2000; Lobo, 2001, 2005; Espinoza *et al.,* 2004), Lobo *et al.* (2010) defined the *L. kriegi* group (four species) and the *L. elongatus* group, which includes the *L. capillitas* clade (15 species), grouping the species in the *L. elongatus* and *L. petrophilus* groups by Morando *et al.* (2003). More recently, Avila *et al.* (2010) recovered four clades: the *L. elongatus*, *L. kriegi*, *L. petrophilus* (including the *L. capillitas* subclade), and *L. punmahuida* clades. The relationships among the clades are as follows: the *L. elongatus* clade is sister to the *L. kriegi* clade; in turn, the *L. petrophilus* group is sister to the group formed by the *L. elongatus* and *L. kriegi* clades. Finally, the *L. punmahuida* clade is sister to all of them. Abdala and Quinteros (2014) performed an update of the study of Lobo *et al.* (2010) and proposed the same groups but included all the new species described at that time in their phylogeny. Avila *et al.* (2015) recovered four clades (which are similar to the complexes of Morando *et al.,* 2003): the *L. elongatus*, *L. kriegi*, *L. petrophilus*, and *L. punmahuida* clades. The same groups (except for *L. punmahuida* clade) were recovered by Medina *et al.* (2015), who studied the *L. kriegi* complex in detail. Escobar-Huerta *et al.* (2015) and Troncoso-Palacios *et al.* (2016) recovered the same clades and relationships as Avila *et al.* (2012). Medina *et al.* (2017) conducted a phylogeographic study of the *L. elongatus* group based on mitochondrial and nuclear genes. They did not retrieve the clades proposed for the group so far, since the results contained multiple polytomies among the group's internal clades. Later, Medina *et al.* (2018) added more evidence, both mitochondrial and nuclear, and analysed the *L. elongatus* group including all the representatives described until then. In this case, the four clades proposed before were recovered (Avila *et al.,* 2012) and the relationships between them were in agreement with the results of Avila *et al.* (2015) and in part with the results of Medina *et al.* (2015), who reported that the *L. elongatus* clade is sister to the *L. petrophilus* clade, and the *L. kriegi* clade is sister to the group formed by the two mentioned groups. The most recent contributions to the *L. elongatus* group continue to disagree with respect to the internal relationships of their clades. Troncoso-Palacios *et al.* (2018) and Ruiz *et al.* (2020) recovered the same clades and relationships as those recovered by Avila *et al.* (2012), whereas Escobar-Huerta *et al.* (2015), Troncoso-Palacios *et al.* (2016) and Avila *et al.* (2021) recovered the relationships of Avila *et al.* (2015) and Medina *et al.* (2018). Finally, Esquerré *et al.* (2022) performed a DNA phylogenetic study and proposed that the *L. elongatus-kriegi* complex is formed by six groups: *L. austromendocinus* Cei, 1974, *L. capillitas* Hulse, 1979, *L. elongatus* Koslowsky, 1896, *L. kriegi* Müller and Hellmich, 1939, *L. petrophilus* Donoso-Barros and Cei, 1971 and *L. punmahuida* Avila *et al.* 2003, but with two different arrangements for mitochondrial and nuclear DNA data.

Since, higher taxonomy of these groups is still matter of debate; here we deal with the *Liolaemus elongatus* group in the wide sense (all proposed groups at date excluding the *L. kriegi* group). The distribution of the *L. elongatus* group ranges from the locality of Tafí del Valle in Tucumán province, northern Argentina, along the Andes in Chile and Argentina, to Chubut province in Argentina. The species of the *L. elongatus* group are characterized by their elongated body shape; they are usually saxicolous, viviparous and omnivorous (Cei, 1986; Quatrini *et al*., 2001; Robles and Halloy, 2011). Currently, the group is composed of 34 valid species, many of which have been described in the last 10 years (Abdala *et al*., 2010; Avila *et al*., 2010; Avila *et al*., 2012; Avila *et al*., 2015; Escobar-Huerta *et al*., 2015; Troncoso-Palacios *et al*., 2016; Ruiz *et al*., 2019; Troncoso-Palacios *et al*., 2019; Abdala *et al*., 2021a; Avila *et al*., 2021; Troncoso-Palacios and Ramírez-Álvarez, 2021).

In recent years, several authors analysed representatives of the *Liolaemus elongatus* group to estimate phylogenies (relationships among families, genera or species), divergence times or to study the evolution of certain biological features (Schulte, 2013; Medina *et al.,* 2014; Zheng and Wiens, 2016; Medina *et al.,* 2017; Esquerré *et al.,* 2019; Ruiz *et al.,* 2020; Esquerré *et al.,* 2022). Table 1 summarises the ages of the group and clades estimated by different studies. Very few systematic studies on *Liolaemus* incorporated morphological evidence (Lobo, 2001; Abdala, 2005; Lobo, 2005; Abdala, 2007; Lobo *et al.,* 2010; Quinteros, 2013) and even fewer studies incorporated genital morphology, which proved to be very informative within *Liolaemus* (Quipildor *et al.,* 2018).

Table 1. Divergence times obtained for the clades of the *Liolaemus elongatus* group. (*) Studies based on more inclusive taxonomic groups.

Authors **Clades**	**Schulte (2013)***	**Medina *et al.* (2014)**	**Zheng & Wiens (2016)***	**Medina *et al.* (2017)**	**Esquerré *et al.* (2019)***	**Ruiz *et al.* (2020)**	**Esquerré *et al.* (2022)***
L. elongatus Group	16 Ma	-	12.30 Ma	-	13 Ma	11.50 Ma	15.50 Ma
L. punmahuida Clade	-	-	-	-	2 Ma	4 Ma	4 Ma
L. elongatus-petrophilus Clade	Not recovered	3.75 Ma	10.54 Ma	2.25 Ma	9.50 Ma	10.10 Ma	12.5 Ma
L. petrophilus Clade	Not recovered	-	Not recovered	1.60 Ma	8.20 Ma	7.70 Ma	11 Ma
L. capillitas Clade	Not recovered	Not recovered	6.01 Ma	-	4.50 Ma	4.25 Ma	6 Ma
L. elongatus-kriegi Clade	Not recovered	1.90 Ma	4.74 Ma	1.60 Ma	5.80 Ma	6 Ma	6 Ma
L. kriegi Clade	6 Ma	1.10 Ma	2.93 Ma	1.35 Ma	4 Ma	3 Ma	4 Ma
L. elongatus sensu stricto Clade	Not recovered	-	2.93 Ma	1.30 Ma	4 Ma	4.16 Ma	4.5 Ma

The main aim of this study was to describe a new species of the *Liolaemus elongatus* group, which we recognized as distinct from other members based on morphological characters (scalation, hemipenis, color pattern), and DNA sequences. We inferred a DNA-based phylogeny of the whole group using all available molecular information, including the new taxon described here. Furthermore, we obtained the divergence times of the *L. elongatus* group in a calibrated tree.

Materials and methods

Specimens studied

We studied 84 specimens representing the seven species of the *Liolaemus petrophilus* clade (sensu Avila *et al.,* 2012) and one candidate species. Individuals were collected by hand or noose, euthanized with sodium Pentothal 1%, fixed in 10% formalin, and preserved in 70% ethanol. Field studies did not involve endangered species. We studied the morphological characters commonly included in *Liolaemus* taxonomic studies, such as those described in Laurent (1985), Frost (1992), Etheridge (1993, 1995, 2000), Cei (1986), Lobo and Espinoza (1999), Lobo (2001, 2005), Abdala (2007), Quinteros (2013) and Quipildor *et al.* (2018), which altogether conform a record of more than 200 morphological characters, including scale counts, shape, ornamentation, variation in the disposal of the scales (imbrications), precloacal pores, neck folding, color pattern, life colors, hemipenis, among others. The description of colors in life was made based on photographs taken in the field immediately after capture of individuals. Observations of scalation and body measurements were made using a binocular dissecting microscope (10-40×). All measurements in this study were taken using a digital calliper 0.05 mm (Mitutoyo USA, CD-6"CX, Illinois, USA). The studied specimens are deposited in the Museo Patagónico de Ciencias Naturales "Juan Carlos Salgado" (MPCN), Fundación Miguel Lillo (FML) and the Instituto de Bio y Geociencias del NOA (IBIGEO); they are listed in Appendix S1.

Statistical analyses

To perform our statistical analyses, we considered 91 characters (44 morphometric characters and 47 characters of lepidosis) from 84 adult specimens (see Appendix A) belonging to seven species of *Liolaemus*: *L. austromendocinus* (*n*=17), *L. capillitas* (*n*=15), *L. gununakuna* Avila *et al.* 2004 (*n*=6), *L. parvus* Quinteros *et al.* 2008 (*n*=12), *L. petrophilus* (*n*=7), *L. quinterosi* Ruiz *et al.* 2019 (*n*=5), *L. tulkas* Quinteros *et al.* 2008 (*n*=8) and *Liolaemus* sp. (*n*= 14).

We measured the following morphometric characters: snout-vent length (SVL; from tip of snout to vent), head length (HeL; from tip of snout to posterior edge of auditory meatus), head width (HeW; distance between temporal regions), head height (HeH), distance between orbits (DO), tail length (TL; distance between the cloaca and the tip), base of tail width (TW; at the base of tail in the cloacal region), trunk length (TrL; distance between fore and hind limbs), femur length (FL), tibia length (TiL), foot length (FoL; distance from the tip of fourth toe to ankle), humerus length (HML), humerus width (HMW), radius length (RL), hand length (HdL), auditory meatus height (AMH), auditory meatus width (AMW), neck width (NW), 1st finger length (1stFL), 2nd finger length (2ndFL), 3rd finger length (3rdFL), 4th finger length (4thFL), 5th finger length (5thFL), 1st toe length (1stTL), 2nd tor length (2ndTL), 3rd toe length (3rdTL), 4th toe length (4thTL), 5th toe length (5thTL), eye-tympanum length (ETL; distance between ocular scale and tympanic region), distance between nostrils (DN), subocular scale length (SSL), rostral scale width (RSW), rostral scale height (RSH), mental scale length (MSL), mental scale width (MSW), 4th supralabial scale length (4thSL), 4th lorilabial scale length (4thLL), 5th lorilabial scale length (5thLL), postocular scale length (PoSL), preocular scale length (SPL), auricular scale length (ASL), proportion of scale organs on one side of the body (SOB), relationship between dorsal and lateral body scales (DLB), and relationship between humeral and dorsal body scales (HDS).

We also took classical lepidosis characters using a binocular stereoscope. We counted: supralabial scales (SS), lorilabial scales (LS), infralabial scales (IS), supraocular scales (SOS), frontal scales (FS), scales contact with interparietal (SIn), scales surrounding the nasal (SN), scales between nasal and canthal scale (SNC), scales between rostral and frontal scale (SRF), lorilabials in contact with subocular (LCS), temporal scales (TS), superior ciliary scales (SCS), scale organs in right postrostral (ORP), superciliaries scale (SuS), scales between preocular and lorilabials (SPL), semicircles scale (SeS), postmental scales (PoS), dorsal head scales (DHS), scale organs in left postrostral (OLP), subdigital lamellae on 1st finger (1st FSL), subdigital lamellae on 2nd finger (2nd FSL), subdigital lamellae on 3rd finger (3rd FSL), subdigital lamellae on 4th finger (4th FSL), subdigital lamellae on 5th finger (5th FSL), subdigital lamellae on 1st toe (1st TSL), subdigital lamellae on 2nd toe (2nd TSL), subdigital lamellae on 3rd toe (3rd TSL), subdigital lamellae on 4th toe (4th TSL), subdigital lamellae on 5th toe (5th TSL), scales between 1st postmentals (1st SPo), scales between 2nd postmentals (2nd SPo), scales between 3rd postmentals (3rd SPo), scales between 4th postmentals (4th SPo), scales between subocular and canthal (SSC), scales between subocular and nasal (SSN), scale organs in neck scales (ONS; counted in six scales in the central region of the neck), scale organs on the sides of the body (OTS; counted in six scales on the lateral region of the trunk), scale keels on 4th toe (4th SKT), scales that contact 2nd infralabial (2nd SI), precloacal pores in males (PPM), scales around body (SAB), dorsal scales (DS; between occiput and thighs region), neck scales (NS), gular scales (GS), ventral scales (VS), pygal scales (PS), scales between posterior margin of auditory meatus and antehumeral fold (SNF).

To reduce the number of variables for statistical comparison, a principal component analysis was performed and based on the results, the characters that most contributed to the variability among species were selected. Then, due to the low number of specimens of some species, the statistical analyses were carried out with a non-parametric Kruskal Wallis ANOVA, following procedures described in Conover (1999).

Following previous morphological and taxonomic studies on the sister genus *Phymaturus* (Lobo *et al.,* 2019; Lobo *et al.,* 2021) and recommendations of Chan and Grismer (2021), we performed a regression analysis of each measurement character with body size, and used the residuals of these correlations to remove the possible effect of body size. Moreover, for the analysis of measurements, we only worked with adult specimens; we did not consider juveniles to avoid result biases. Since the number of scales is not influenced by body size, juveniles were included in the analysis of scale count characters. It is worked with the set of individuals without differentiation between sexes due to the small number of samples of some species.

The components of the principal components analysis that explained 75-80% of each subset of characters were retained. Thus, we retained the first four components for scale counts and the first three components for measurement characters. Then, from these components, the characters that most contributed to the variability were chosen for statistical comparisons. The criterion for choosing the variables was a contribution of least 80% to the variability of each component, using as a maximum (100%) the variable with the highest value of each component (Table 2).

Hemipenial morphology

We studied hemipenial morphology of representatives of species of the *Liolaemus petrophilus* clade: *L. austromendocinus, L. parvus*, *L. petrophilus*, *L. quinterosi*, *L. capillitas* (representing the *L. capillitas* subclade) and *Liolaemus* sp. The sample size varied from one to five pairs of hemipenes per species. The specimens studied are listed in Appendix S1. We followed the protocol of Zaher and Prudente (2003) for preparing snake organs, which consisted of removing one of the hemipenes from each fixed specimen through a small incision at the base of the tail. The removed organ was immersed in a 2% KOH solution for 3–5 min or until it became translucent and flexible. The hemipenis was checked and everted manually using forceps to make sure that it was completely everted. Once fully everted, the organ was filled with coloured Vaseline to allow a clear visualisation of ornamentation structures. We obtained digital images of hemipenes in sulcate, asulcate,

Table 2. Components of the PCA that explain between 75–80% of the total variability for morphometric and lepidosis characters.

Lambda	**Value**		**Proportion**		**Cumulative Proportion**	
	Morphometric	Lepidosis	Morphometric	Lepidosis	Morphometric	Lepidosis
1	16.10	16.73	0.40	0.32	0.40	0.32
2	8.90	12.50	0.22	0.24	0.63	0.55
3	7.45	7.53	0.19	0.14	0.81	0.69
4		5.69		0.11		0.80

and lateral views using a camera (Olympus DP25) attached to a stereomicroscope. Terminology of hemipenial character states follows that of Dowling and Savage (1960), Savage (1997), Zaher (1999), Ziegler and Böhme (1999), Zaher and Prudente (2003) and Quipildor *et al.* (2018).

Extraction, amplification and DNA sequencing

DNA extraction from the candidate species was performed using a Qiagen® DNeasy® 96 kit, following the manufacturer's instructions. We sequenced two fragments of mitochondrial genes (12S rRNA [12S ~853bp, 2 individuals] and cytochrome-b [cyt-b, ~800bp, 2 individuals]) and a nuclear gene (a member of the kinesins family 24 [KIF24 ~490 bp, 2 individuals]). The protocols for PCR and DNA sequencing followed Morando *et al.* (2003; 2004) and Portik *et al.* (2010). We used the following primers: 12e (Forward) and tPhe (Reverse) for 12S (Wiens *et al.,* 1999); GLUDGL (Forward) and CB3 3' (Reverse) for Cyt-b (Palumbi, 1996); and KIF24 F1 (Forward) and KIF24 R1 (Reverse) for KIF24.

Both DNA extraction and amplification were performed at the Institute of Diversity and Austral Evolution (IDEAUS-CONICET). All sequences were edited and concatenated using BioEdit v7.2.6 (Hall, 1999). Sequence alignment was performed by running MEGA v7.0.26 and MUSCLE (Kumar *et al.,* 2018) and then checked by eye to maximise identity blocks of sequences. Missing data were coded as "?". Appendix S2 summarises locality data and GenBank accession numbers for the specimens used in this study. In addition, the following sequences obtained from GenBank were included: Avila *et al.* (2004; 2006; 2015), Fontanella *et al.* (2012), Medina *et al.* (2014, 2015, 2017, 2018), Morando *et al.* (2003), and Olave *et al.* (2014).

Divergence time estimates

Tree topology, node ages and substitution rates were simultaneously estimated using Bayesian MCMC (Markov chain Monte Carlo) approach as implemented in BEAST v2.5 (Bouckaert *et al.,* 2019). We used the fossil belonging to the *Eulaemus* clade, which is the earliest record of this subgenus (Albino, 2008) to place a mean prior of 20 Ma on the tree height. A lognormal prior is typically most appropriate for most fossil calibrations (Hedges and Kumar, 2004) because it assumes that the divergence event actually occurred sometime before the appearance of the fossil. In this model, fossils thus represent a hard lower bound and a soft upper bound on a given divergence event. The Yule prior assumes a constant lineage birth rate for each branch in the tree and is considered most suitable for trees describing the relationships between individuals of different species (Ho *et al.,* 2005). An uncorrelated lognormal distributed relaxed clock (UCLD) model was employed, which allows evolutionary rates to vary along branches within lognormal distributions (Drummond *et al.,* 2006). The calibration was conducted for all genes jointly.

Three independent runs of 20 million generations each were performed with sampling every 5000 generations. The three separate runs were then combined (following removal of 10% burn-in) using Log Combiner v2.0 (Drummond and Rambaut, 2007; Rambaut and Drummond, 2008). Adequate sampling and convergence of the chain to stationary distribution were confirmed by inspection of MCMC samples using Tracer v2.0 (Drummond and Rambaut, 2007). The effective sample size (ESS) values of all parameters were greater than 200, which was considered a sufficient level of sampling. The sampled posterior trees were summarised using Tree Annotator v2.0 (Drummond and Rambaut, 2007; Rambaut and Drummond, 2008) to generate a maximum clade credibility tree (maximum posterior probabilities) and calculate the mean ages, 95% highest posterior density (HPD) intervals and posterior probabilities for each node. The recovered topology was visualised with Fig Tree v1.2 (Rambaut and Drummond, 2008). We also calculated the uncorrected average pairwise genetic distances using MEGA 10.2.4 (Kumar *et al.,* 2018).

Results

Statistical analyses

The first three and four principal components explained most of the total variance (Table 2). The analysis of the characters of *Liolaemus* sp. and of the other species that belong to the *L. petrophilus* subclade showed that 59 morphological variables had significant differences ($P < 0.05$). These variables clearly differentiate *Liolaemus* sp. from the rest of the clade, with a total of 21 linear morphometric characters (Table 3) and 38 meristic characters (Table 4).

Phylogeny

We recovered the traditional *Liolaemus elongatus* group composed of five clades; the *L. elongatus kriegi*

Table 3. Summary of statistical values (mean ± standard error) of the of 24 morphometric characters. The ANOVA results obtained from comparisons across species of the Liolaemus petrophilus clade are also indicated. Different capital letters indicate a significant difference between species. Sample size is indicated between parentheses. SVL: snout vent length ; RSW: rostral scale width; PoSL: postocular scale length; TiL: tibia length; TrL: trunk length; HML: humerus length; HMW: humerus width; AMH: auditory meatus height; 4thFL: 4th finger length; 1st toe length; RSH: rostral scale height; MSW: mental scale width; ASL: auricular scale length; 2ndTL: 2nd toe length; 5thTL: 5th toe length; MSL: mental scale length; 4thSL: 4th supralabial scale length; 3rdFL: 3rd finger length; 2ndFL: 2nd finger length; HeH: head height; DO: distance between orbits.

	L. austromendocinus (n=17)		*L. capillitas* (n=11)		*L. gununakuna* (n=6)		*L. parvus* (n=10)		*L. petrophilus* (n=7)		*L. quinterosi* (n=5)		*L. splendidus* sp. nov. (n=11)		*L. tulkas* (n=8)		Test	*p*
SVL	81.14±5.81	BC	74.74±5.65	B	79.16±8.21	BC	59.27±5.43	A	77.64±7.07	B	82.32±5.02	BC	88.18±6.88	C	63.87±5.15	A	H=50.17	<0.0001
RSW	-0.13±0.27	B	-0.09±0.25	BC	0.12±0.34	BCD	-0.04±0.18	BC	-0.13±0.19	AB	-0.60±0.19	A	0.48±0.37	D	0.19±0.23	CD	H=36.03	<0.0001
PoSL	0.08±0.46	ABC	0.14±0.27	BC	0.41±0.35	C	-0.15±0.32	AB	0.13±0.48	ABC	0.16±0.25	BC	-0.41±0.70	A	-0.13±0.10	AB	H=16.00	0.0251
TiL	0.21±1.14	A	-0.13±1.68	A	-1.52±2.08	A	-0.04±1.39	A	-0.60±0.90	A	-0.76±0.47	A	1.83±2.32	B	-0.61±1.49	A	H=18.35	0.0105
TrL	-0.22±2.93	ABC	-2.07±1.66	A	-0.19±2.99	ABCD	0.63±1.88	BCD	-2.30±2.82	AB	-1.32±3.18	ABC	3.03±4.68	D	1.34±5.16	CD	H=16.99	0.0175
HML	-0.76±0.97	A	-0.06±0.92	A	-0.25±0.77	A	0.19±0.87	AB	-0.80±0.64	A	-0.29±1.05	A	1.99±1.56	B	-0.21±0.97	A	H=23.67	0.0013
HMW	-0.55±0.71	A	-0.23±0.41	AB	-0.49±0.76	AB	0.10±0.35	BC	-0.67±0.54	A	-0.36±0.52	AB	1.73±1.16	C	0.16±1.03	AB	H=27.02	0.0003
AMH	-0.11±0.31	A	-0.12±0.33	A	-0.18±0.30	A	-0.10±0.20	A	-0.07±0.20	AB	-0.52±0.41	A	0.44±0.57	BC	0.45±0.40	C	H=24.90	0.0008
4thFL	0.01±0.47	BC	0.25±0.75	BCD	-1.20±3.40	ABC	-0.22±0.56	AB	-0.01±0.97	BCD	-0.98±0.47	A	0.68±0.54	D	0.51±0.33	CD	H=22.07	0.0025
1stTL	0.63±0.48	C	-0.03±0.62	B	0.23±0.56	BC	-0.24±0.48	AB	-0.15±0.59	B	0.46±0.74	BC	-0.91±0.58	A	-0.06±0.40	B	H=33.72	<0.0001
RSH	-0.07±0.14	ABC	0.01±0.11	CD	0.28±0.57	CD	-0.01±0.08	BCD	-0.15±0.17	AB	-0.25±0.10	A	0.16±0.16	D	0.01±0.15	BCD	H=24.42	0.0010
MSW	0.03±0.30	B	-0.21±0.24	AB	0.04±0.73	AB	0.80±0.20	B	-0.25±0.21	A	-0.68±0.31	A	0.47±0.30	C	0.11±0.28	BC	H=33.47	<0.0001
ASL	0.17±0.21	C	0.25±0.17	C	0.00±0.00		-0.05±0.11	AB	0.05±0.37	ABC	0.08±0.35	BC	-0.49±0.27	A	-0.04±0.07	AB	H=33.95	<0.0001
2ndTL	0.08±0.81	BC	-0.08±0.58	ABC	0.48±0.47	C	-0.55±0.47	A	0.17±0.50	BC	-0.10±0.71	ABC	-0.28±0.66	AB	0.57±0.45	C	H=17.85	0.0127
5thTL	0.44±0.76	B	0.54±0.89	B	-0.07±2.51	A	-0.54±0.43	A	-0.13±1.04	AB	-0.80±0.52	A	-0.60±0.72	A	0.49±0.68	B	H=28.81	0.0002
MSL	0.01±0.20	C	0.01±0.16	BC	-0.05±0.47	ABC	-0.09±0.18	AB	-0.06±0.14	BC	-0.01±0.12	BC	0.02±0.20	A	0.13±0.16	C	H=5.83	0.5593
4thSL	0.30±0.45	C	0.24±0.76	BC	-0.19±1.00	ABC	-0.44±0.48	AB	0.25±0.71	BC	0.17±0.87	BC	-0.73±0.77	A	0.39±0.19	C	H=25.10	0.0007
3rdFL	0.09±0.41	C	0.20±0.78	C	-0.08±0.84	ABC	-0.53±0.42	AB	-0.14±0.92	BC	-0.98±0.51	A	0.15±0.52	CD	0.79±0.43	D	H=27.96	0.0002
2ndFL	0.29±0.51	C	0.08±0.68	BC	-0.10±0.52	ABC	-0.37±0.53	AB	-0.48±0.74	AB	-0.73±0.55	A	-0.11±0.33	AB	0.85±0.26	D	H=32.35	<0.0001
HeH	-0.41±0.44	A	0.23±0.71	C	0.34±1.50	ABC	-0.55±0.41	A	0.29±0.49	BC	0.96±0.58	C	-0.33±0.46	AB	0.59±0.59	C	H=31.67	<0.0001
DO	-0.39±0.38	BC	-0.38±0.54	BC	-0.43±0.63	ABC	-0.60±0.37	AB	-1.16±0.39	A	0.39±0.51	CD	1.24±1.40	D	1.49±0.69	D	H=39.65	<0.0001

Table 4. Summary of statistical values (mean ± standard error) of the of 26 lepidosis characters. The non-parametric ANOVA results obtained from comparisons across species of the Liolaemus petrophilus clade are also indicated. Different capital letters indicate a significant difference between species. Sample size is indicated between parentheses. 2nd SI: scales that contact 2nd infralabial; LS: lorilabial scales; LCS: lorilabials in contact with subocular; TS: temporal scales; SCS: superior ciliary scales; OLP: scale organs in left postrostral; ORP: scale organs in right postrostral, ONS: scale organs in neck scales; PPM: precloacal pores in males; SAB: scales around of body; 1st TSL: 1st toe subdigital lamellae; 2nd TSL: 2nd toe subdigital lamellae; 5th TSL: 5th toe subdigital lamellae; 2nd FSL: 2nd finger subdigital lamellae; 3rd FSL: 3rd finger subdigital lamellae; VS: ventral scales; PS: pygal scales; 1st SPo: scales between 1st posmentals; 2nd SPo: scales between 2nd posmentals; 3rd SPo: scales between 3rd postmentals; 4th SPo: scales between 4th postmentals; 5th SPo: scales between 5th postmentals; SNC: scales between nasal and canthal scale; SRF: scales between rostral and frontal scale; SuS: superciliary scales; GS: gular scales; NS: neck scales; SNF: scales between posterior margin of auditory meatus and antehumeral fold; DS: dorsal scales; PoS: postmental scales; SeS: semicircles scales; 4th TSL: toe subdigital lamellae; 4th FSL: finger subdigital lamellae; 1st FSL: 1st finger subdigital lamellae; SS: supralabial scales; SOS: supraocular scales; FS: frontal scales; SN: scales surrounding the nasal.

	L. austromendocinus (n=17)		*L. capillitas* (n=15)		*L. gununakuna* (n=6)		*L. parvus* (n=12)		*L. petrophilus* (n=7)		*L. quinterosi* (n=5)		*L. splendidus* sp. nov. (n=14)		*L. tulkas* (n=8)		Test	*p*
2nd SI	4.18±0.39	B	4.09±0.30	B	4.67±0.82	B	4.00±0.00	B	4.29±0.49	B	4.00±0.00	B	4.00±0.00	B	2.25±0.46	A	H=24.79	<0.0001
LS	7.47±0.87	AB	8.27±2.00	BC	10.50±1.05	D	8.00±0.67	BC	10.00±1.00	D	8.80±0.84	CD	8.73±0.79	CD	6.88±0.35	A	H=37.88	<0.0001
LCS	4.12±0.78	AB	5.27±1.90	BCD	5.67±0.82	D	3.80±0.63	A	5.71±0.49	D	5.40±1.14	CD	4.36±1.03	ABC	3.63±0.52	A	H=28.12	0.0001
TS	10.06±1.09	BC	10.82±0.87	CDE	10.83±1.33	BCDE	10.30±0.95	BCD	11.57±0.53	E	11.40±0.55	DE	9.36±2.01	AB	7.88±0.64	A	H=31.75	<0.0001
SCS	13.88±1.17	B	14.09±1.14	BC	15.33±0.52	CD	16.00±1.05	D	15.00±1.15	BCD	16.20±1.30	D	14.55±1.29	BCD	11.00±0.00	A	H=39.99	<0.0001
OLP	7.53±2.55	AB	6.27±3.13	A	9.83±3.60	BC	7.70±1.34	AB	10.43±3.36	BC	8.80±2.59	ABC	11.55±2.30	C	6.38±1.19	A	H=25.12	0.0006
ORP	6.65±3.39	A	6.45±1.63	A	8.83±3.43	AB	7.60±.2.32	A	10.71±2.87	BC	9.00±1.22	ABC	12.18±1.72	C	7.50±1.20	A	H=31.11	0.0001
ONS	0.87±0.13	AB	0.95±0.11	BC	1.00±0.00	C	1.00±0.00	C	0.93±0.09	BC	0.97±0.08	BC	1.00±0.00	C	0.75±0.09	A	H=25.29	<0.0001
PPM	3.00±0.00	AB	2.71±0.95	AB	3.00±0.00	AB	1.50±0.55	A	4.25±0.96	B	0.00±0.00	A	1.71±0.95	A	0.33±0.58	A	H=26.14	0.0002
SAB	73.41±3.57	C	63.82±5.23	A	76.83±4.79	CD	73.60±3.44	C	80.29±4.31	CD	73.40±3.44	BC	85.27±4.61	D	66.00±1.77	AB	H=55.89	<0.0001
1st TSL	12.41±0.62	BC	11.64±1.03	AB	12.67±0.82	BC	11.60±0.97	AB	12.00±1.53	BC	12.80±0.45	C	12.27±1.42	BC	10.63±0.74	A	H=20.85	0.0018
2nd TLS	17.82±0.88	BC	16.55±0.69	A	17.83±1.33	BC	16.80±0.63	AB	19.14±0.90	C	18.00±1.22	BC	18.45±1.29	C	16.88±1.13	AB	H=30.01	<0.0001
5th TLS	18.94±1.30	B	18.91±1.30	B	18.67±1.37	B	18.70±1.25	B	19.71±0.49	BC	29.20±2.17	C	19.36±1.50	B	12.75±0.89	A	H=36.25	<0.0001
2nd FLS	16.18±0.81	CD	15.45±0.93	ABC	16.50±1.38	CDE	14.80±0.92	AB	16.57±0.53	DE	19.60±0.89	E	15.55±1.04	BCD	14.25±1.04	A	H=36.87	<0.0001
3rd FLS	20.59±1.23	B	20.64±1.36	AB	21.00±2.68	AB	20.20±1.69	AB	21.43±0.79	BC	23.80±1.92	C	21.09±1.14	B	19.00±1.31	A	H=20.74	0.0030
VS	119.00±4.73	B	104.36±7.06	A	121.83±10.53	B	111.60±3.89	A	129.00±7.14	B	108.00±3.81	A	127.82±7.10	B	107.25±5.23	A	H=53.63	<0.0001
PS	16.24±1.35	CD	15.27±1.74	BC	18.33±2.16	DE	15.00±0.94	ABC	19.43±1.40	E	17.20±1.48	CDE	14.27±2.37	AB	12.38±1.85	A	H=42.01	<0.0001
1st SPo	0.00±0.00	A	0.00±0.00	A	0.00±0.00	A	0.00±0.00	A	0.43±0.53	A	0.00±0.00	A	0.00±0.00	A	2.50±0.53	B	H=23.88	<0.0001
2nd SPo	2.12±0.33	A	2.00±0.00	A	1.83±0.41	A	2.00±0.00	A	2.00±0.00	A	2.20±0.45	A	2.09±0.30	A	4.63±0.52	B	H=22.40	<0.0001
3rd SPo	4.47±0.72	AB	4.09±0.94	AB	3.83±0.41	A	4.20±0.42	AB	4.57±0.53	AB	5.00±0.71	BC	4.00±1.00	A	5.88±0.35	C	H=24.62	0.0002
4th Spo	7.00±0.00	C	6.00±0.77	AB	6.50±1.38	BC	6.30±0.67	B	6.14±0.38	AB	6.00±1.22	AB	6.18±1.25	B	5.13±0.83	A	H=24.16	0.0004
5th SPo	8.38±1.04	B	6.50±0.55	A	8.33±0.82	B	7.89±0.93	B	8.71±0.95	B	6.33±0.58	A	7.64±1.03	AB	6.60±0.55	A	H=26.28	0.0002
SNC	2.00±0.00	B	2.00±0.00	B	2.00±0.00	B	2.00±0.00	B	2.00±0.00	B	2.00±0.00	B	1.27±0.65	A	2.00±0.00	B	H=14.70	<0.0001
SRF	5.71±0.59	B	4.91±0.30	A	5.50±0.55	AB	5.50±0.71	AB	6.00±0.00	BC	5.40±0.55	AB	6.82±0.87	C	7.00±0.53	C	H=38.20	<0.0001

SuS	6.82±0.53	B	7.00±0.63	B	7.00±0.63	B	6.90±0.74	B	6.57±0.79	AB	7.00±0.00	B	6.00±1.34	A	6.00±0.00	A	H=18.97	0.0016
GS	43.18±2.90	B	38.36±5.05	A	40.50±4.23	ABC	39.00±1.89	A	43.14±3.76	AB	38.20±2.39	A	54.73±7.75	C	43.13±2.42	B	H=40.74	<0.0001
NS	39.47±2.07	A	37.55±3.27	A	38.50±1.97	A	37.90±2.13	A	36.86±3.53	A	42.00±3.46	AB	55.00±10.17	B	51.88±3.23	B	H=39.81	<0.0001
SNF	29.88±1.65	B	27.27±2.20	A	28.50±2.35	AB	30.10±2.05	B	28.29±1.98	AB	30.80±3.49	BC	41.82±8.47	C	34.25±2.92	C	H=35.88	<0.0001
DS	72.00±3.72	A	74.64±5.33	AB	82.50±6.19	CD	80.10±3.14	C	77.14±3.72	BC	73.00±5.61	AB	89.55±4.82	D	76.25±4.46	ABC	H=43.95	<0.0001
PoS	4.76±0.44	A	4.55±0.52	A	5.00±0.00	A	4.80±0.42	A	5.00±0.00	A	4.60±0.55	A	6.82±0.40	B	4.63±0.52	A	H=31.11	<0.0001
SeS	10.65±1.32	A	10.73±0.90	A	11.17±0.98	AB	11.00±0.47	AB	11.86±0.38	BC	10.80±0.84	AB	13.27±1.19	C	10.13±0.83	A	H=31.75	<0.0001
4th TSL	28.41±2.00	B	27.91±1.45	B	28.33±1.37	B	27.70±1.70	B	31.14±0.90	C	19.00±0.71	A	28.09±2.02	B	26.88±0.64	AB	H=30.54	0.0001
4th FSL	22.71±2.31	B	22.27±1.19	B	24.67±1.21	C	22.20±1.48	B	23.00±0.82	BC	11.20±2.39	A	23.82±2.99	C	22.25±1.04	B	H=30.95	<0.0001
1st FSL	10.65±0.61	CD	10.18±0.40	ABC	10.67±1.21	BCD	9.70±0.82	AB	10.00±0.82	ABC	16.60±2.51	E	11.36±1.21	DE	9.50±0.53	A	H=34.50	<0.0001
SS	7.00±0.87	AB	6.55±0.52	A	7.67±0.82	BC	7.00±0.94	AB	8.43±0.53	C	7.20±0.84	AB	7.73±1.01	BC	7.50±0.53	BC	H=22.16	0.0009
SOS	4.59±0.71	AB	4.18±0.75	A	5.17±0.75	ABCD	5.10±0.74	ABC	5.71±0.49	CD	4.40±0.55	AB	10.82±3.52	D	5.25±0.46	BCD	H=29.23	<0.0001
FS	2.12±0.60	AB	2.82±0.60	BC	2.00±0.63	AB	2.70±0.82	B	2.86±0.69	BC	2.40±0.55	AB	3.73±1.01	C	1.75±0.71	A	H=25.36	<0.0001
SN	6.29±0.59	A	7.18±0.40	BC	6.67±0.82	ABC	7.40±0.52	C	7.29±0.49	BC	6.40±0.89	AB	6.73±0.47	ABC	7.25±0.46	BC	H=22.99	0.0001

clade, formed by the *L. elongatus* sensu stricto clade + *L. kriegi* clade; a clade formed by the *L. petrophilus* clade + *L. capillitas* clade; and the *L. punmahuida* clade (Fig. 1).

Within the *Liolaemus petrophilus* group, we found that the sister clade of *Liolaemus* sp. is the clade formed by (*L. quinterosi L. gununakuna*). At the same time, their sister clade is formed by (*L. austromendocinus* + *L. parvus*). The sister group to all of them is the *L. capillitas* clade together with its eight species (sensu Ruiz *et al*., 2020). Finally, *L. petrophilus* is the sister species to all the remaining species forming the clade.

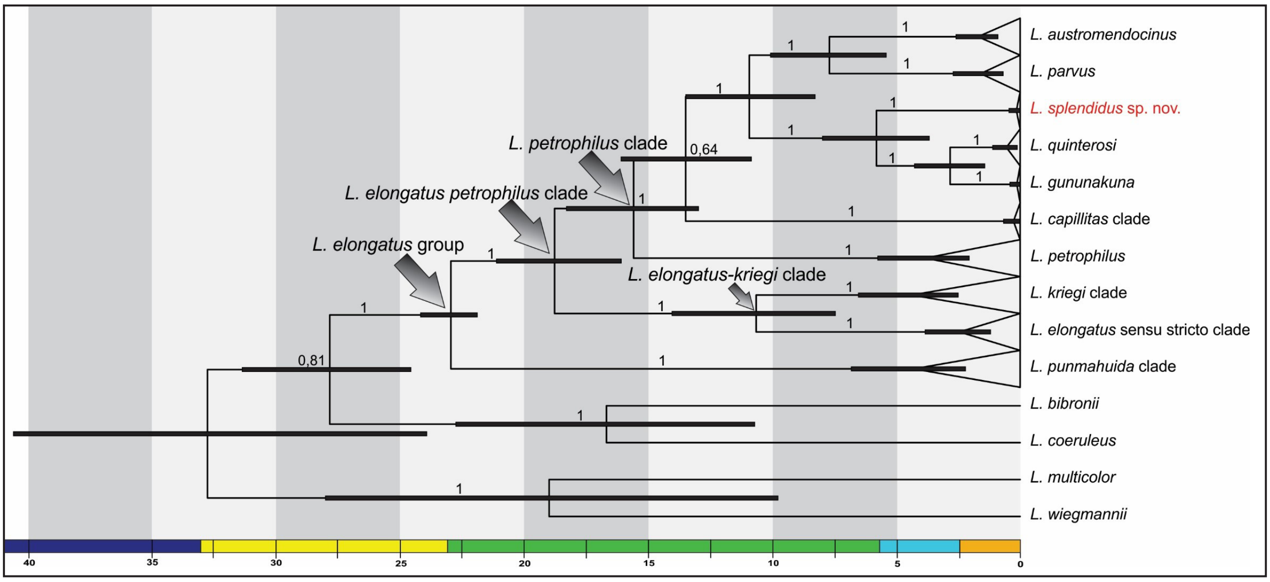

Figure 1. Main clades of the *Liolaemus elongatus* group. Estimates of divergence times for the *L. elongatus* group, under BI topology. Ultrametric tree scaled in Ma. Numbers and horizontal bars on nodes represent posterior probability values and 95% credibility intervals. The different colors of the bar represent the different times. Orange: Pleistocene. Light blue: Pliocene. Green: Miocene. Yellow: Oligocene. Blue: Eocene.

Divergence time estimates

Our results (Fig. 1) show that the *Liolaemus elongatus* group diverged at 23 Ma (95% highest posterior density interval- HPD: 24.5-22) during the Early Miocene. Within this group, the clades originated from the Miocene to the Pleistocene. The *L. punmahuida* clade diverged at 4 Ma (95% HPD: 7-2.3) during the Middle Pliocene. The *L. elongatus-petrophilus* clade would have originated at 19 Ma (95% HPD: 21.5-15.2) during the Early Miocene. The *L. capillitas* clade diverged at 8 Ma (95% HPD: 9.5- 7) during the Late Miocene. The *L. elongatus-kriegi* clade diverged at 11 Ma (95% HPD: 13.5-7.5) during the Middle Miocene. The *L. kriegi* clade originated at 4 Ma (95% HPD: 6.5-2.5) during the Middle Pliocene. The *L. elongatus* sensu stricto clade diverged at 6 Ma (95% HPD: 7.5-5) during the Late Miocene.

Regarding the *Liolaemus petrophilus* clade, our results show that the divergence of the clade occurred during the Middle Miocene around 15 Ma (95% HPD: 18-13). Within the group, the species that belong to the *L. petrophilus* clade originated between the Pliocene and the Pleistocene.

Within the *Liolaemus petrophilus* clade, we found that *L. austromendocinus* and *L. parvus* diverged of their ancestor in common around 1.9 Ma (95%HPD: 2.5-1) and 1.7 Ma (95% HPD: 2.8-0.8) respectively in the Early Pleistocene. *Liolaemus gununakuna* and *L. quinterosi* diverged of their ancestor in common around 0.1 Ma (95%HPD: 0.3-0.01) and 0.5 Ma (95% HPD: 1-0.1) respectively in the Late Pleistocene. *Liolaemus* sp. was separated from the ancestor of *L. gununakuna* and *L. quinterosi* around 0.1 Ma (95% HPD: 0.5-0.01) in the Late Pleistocene. Finally, *L. petrophilus* diverged around 0.5 Ma (95% HPD: 1-0.1) in the Late Pleistocene.

Genetic distances

Genetic distances among cytb sequences within members of the *Liolaemus petrophilus* clade and some species of the *L. elongatus* group are shown in Table 5. *Liolaemus* sp. shows 4.08% distance from

Table 5. Genetic distances of mitochondrial marker (Cyt-b) between the new species (*Liolaemus splendidus* sp. nov.) and related species. The values are expressed as a percentage.

	Liolaemus austromendocinus	*Liolaemus capillitas*	*Liolaemus elongatus*	*Liolaemus gununakuna*	*Liolaemus kriegi*	*Liolaemus parvus*	*Liolaemus petrophilus*	*Liolaemus punmahuida*	*Liolaemus quinterosi*	***Liolaemus splendidus* sp. nov.**
Liolaemus austromendocinus										
Liolaemus capillitas	19.72									
Liolaemus elongatus	18.27	19.27								
Liolaemus gununakuna	10.86	16.07	16.57							
Liolaemus kriegi	17.57	18.24	8.11	13.89						
Liolaemus parvus	9.79	19.53	16.11	10.17	16.39					
Liolaemus petrophilus	18.53	18.77	16.29	16.23	17.98	16.27				
Liolaemus punmahuida	19.87	20.45	15.56	16.77	17.77	18.27	19.70			
Liolaemus quinterosi	10.62	16.66	16.52	1.78	14.76	10.14	16.50	16.72		
***Liolaemus splendidus* sp. nov.**	11.57	16.12	18.56	4.09	15.59	11.23	16.08	17.83	4.08	

L. quinterosi (the shortest distance in the analysis). We found a distance of 4.09% between *Liolaemus* sp. and *L. gununakuna*. The distance between *Liolaemus* sp. and *L. parvus* was 11.23%. The distance obtained between *Liolaemus* sp. and *L. austromendocinus* was 11.57%. *Liolaemus* sp. shows 15.59% distance from *L. kriegi*. We obtained a 16.2% distance between *Liolaemus* sp. and *L. petrophilus*. We found 16.12% distance between *Liolaemus* sp. and *L. capillitas*. The distance obtained between *Liolaemus* sp. and *L. punmahuida* was 17.83%. Finally, we found 18.56% distance between *Liolaemus* sp. and *L. elongatus*.

Hemipenial morphology (Fig. 2)

Hemipenes are cylindrical. The apex is shell-shaped. The asulcate and sulcate faces have calyces. Asulcate face has diffused calyces, homogeneously distributed along the distal region of the organ. On this face it also has a hump-shaped protrusion. Sulcate face has regular calyces and narrow and open sulcus spermaticus, bifurcated at the base of distal lobes of the hemipenes. Apical lobes are conspicuously delimited.

Liolaemus splendidus sp. nov. (Fig. 3)

http://zoobank.org/urn:lsid:zoobank.org:act:76C7B714-FAB3-46DD-8646-05245792202B

Holotype

MPCN-H 503 (Adult male): National Route No. 237, 9 km north of Piedra del Águila, (39º58'54.3''S; 70º02'36''W, 650 m a.s.l.), Collón Curá department, Neuquén province, Argentina. Chafrat P., Flores A., and cols. December 21, 2021.

Paratypes

IBIGEO 5531-5533 (male, female, juvenile respectively): National Route No. 237, 9 km north of Piedra del Águila, (39º58'54.3''S; 70º02'36''W, 638 m), Collón Curá department, Neuquén province, Argentina. Hibbard T., Lobo F., Quipildor M., Slodki D., Valdecantos S. cols. December 8, 2016. MPCN-H-500-502 (female, male, male respectively): National Route No. 237, 9 km north of Piedra del Águila, (39º58'54.3''S; 70º02'36''W, 644 m), Collón Curá department, Neuquén province, Argentina. Chafrat P., Gonzales L., Chafrat H., Medina V., Chafrat C., Chafrat P.J. cols. December 2, 2021. MPCN-H- 504-510 (juvenile, female, male, male, female, male and juvenile respectively): National Route No. 237, 9 km north of Piedra del Águila, (39º58'54.3''S; 70º02'36''W, 650 m), Collón Curá department, Neuquén province, Argentina. Chafrat P., Flores A. cols. December 21, 2021.

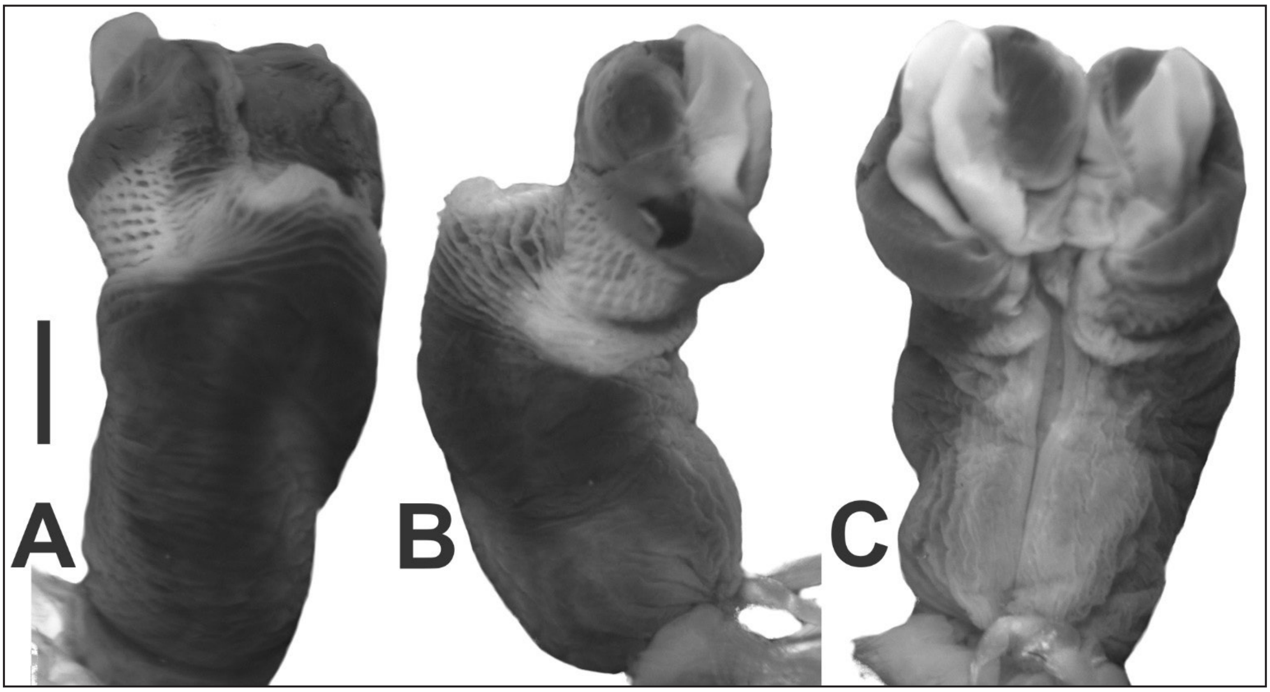

Figure 2. Hemipenial morphology of the *Liolaemus splendidus* sp.nov.(IBIGEO 5531). A: asulcate face, B: lateral face, C: sulcate face. Scale=2mm.

Etymology

The specific epithet "splendidus" is from the Latin 'bright' or 'glittering'. It refers to the predominantly bright green body coloration in this population.

Diagnosis.

Liolaemus splendidus sp. nov. is a large-sized (max. SVL 96.1 mm) member of the *L. elongatus* species group (sensu Avila *et al*., 2021; Troncoso-Palacios *et al*., 2021; this study). *Liolaemus splendidus* sp. nov. is distributed in the proximity of the distribution of *L. ceii*, *L. crandalli*, *L. gununakuna*, *L. kriegi*, *L. quinterosi* and *L. shitan* (Fig. 4). Within the *L. petrophilus* clade, the diagnostic characters that differentiate *L. splendidus* sp. nov. from the phylogenetically closest species are the presence of precloacal pores and sexual dichromatism not evident, which separate it from *L. quinterosi*; the larger number of ventral scales, which distinguishes it from *L. gununakuna*; and the max. SVL, which distinguishes it from *L. petrophilus*.

Liolaemus splendidus sp. nov. differs from other species of the *L. elongatus* group in the number of scales around midbody, which in *L. splendidus* sp. nov. (77–95) is lower than in *L. ceii* (102–115) but higher than in *L. capillitas* (58–67), *L. dicktracyi* (60–73), *L. galactostictos* (64–69), *L. heliodermis* (62–69), *L. talampaya* (58–69), *L. tulkas* (63–68) and *L. umbrifer* (58–76). *Liolaemus splendidus* sp. nov. differs from the following eight species: *L. carlosgarini, L. flavipiceus, L. lonquimayensis, L. punmahuida, L. quinterosi, L. riodamas, L. thermarum,* and *L. tregenzai,* males of these species lack precloacal pores (1-3 in *L. splendidus* sp. nov.). Moreover, specimens of *L. splendidus* sp. nov. (max. SVL recorded=96.1 mm) are smaller than specimens of *L. antumalguen* (max. SVL=107.8 mm), *L. austromendocinus* (max. SVL=98.0 mm), *L. buergeri* (max. SVL=108.0 mm), *L. choique* (max. SVL=116.2 mm), *L. gununakuna* (max SVL=97.5 mm), *L. kriegi* (max. SVL=98.0 mm), *L. petrophilus* (max. SVL=97.7 mm), and *L. shitan* (max. SVL=98.7 mm), but larger than specimens of *L. antonietae* (max. SVL=77.6 mm), *L. burmeisteri* (max. SVL=85.2 mm), *L. carlosgarini* (max. SVL=68.8 mm), *L. crandalli* (max. SVL=93.4 mm), *L. galactostictos* (max SVL=81.3 mm), *L. janequeoae* (max SVL=69.6 mm), *L. lonquimayensis* (max SVL=69.7 mm), *L. pikunche* (max. SVL=91.3 mm),

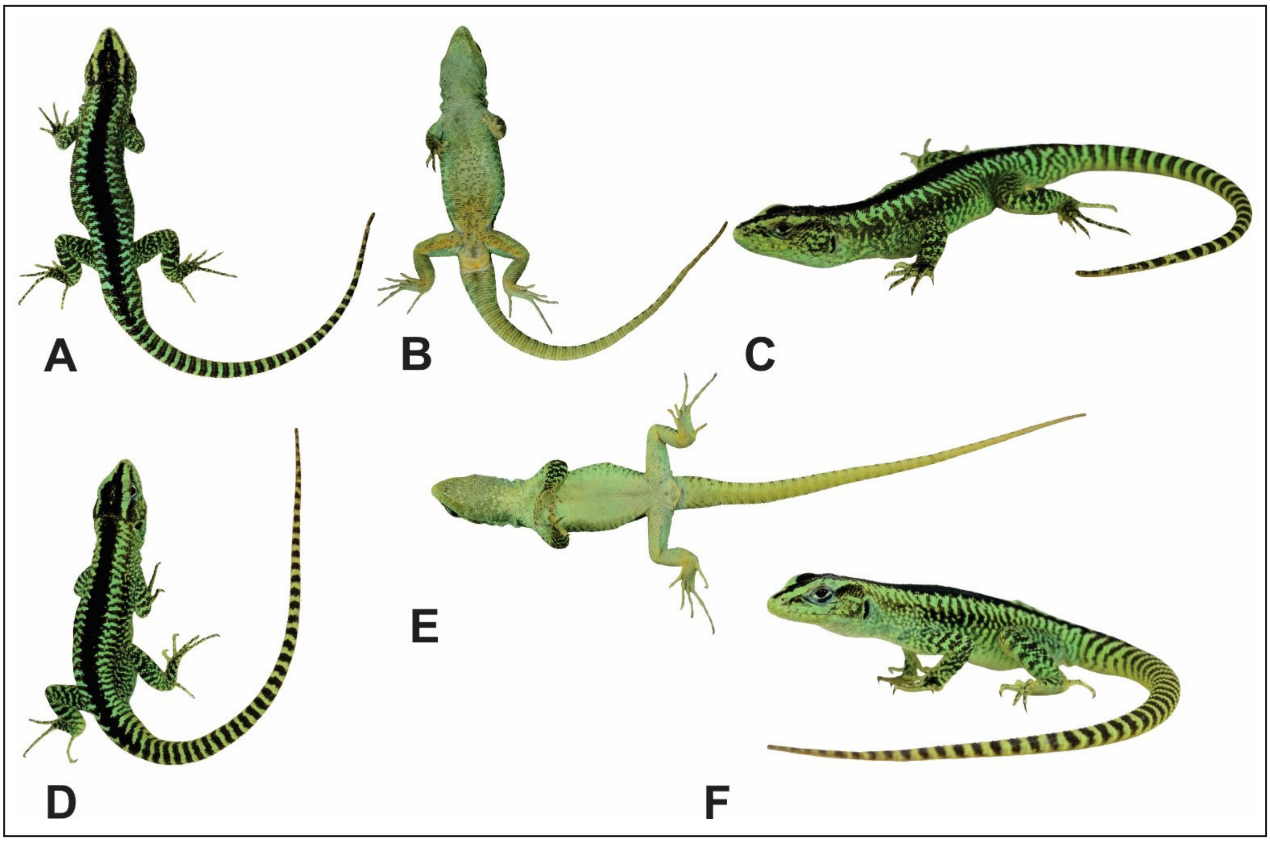

Figure 3. Color in life of *Liolaemus splendidus* sp nov. specimens. A: Male in dorsal view. B: Male in ventral view. C: Male in lateral view. D: Female in dorsal view. E: Female in ventral view. F: Female in lateral view.

L. quinterosi (max. SVL=88.0 mm), *L. scorialis* (max SVL=69.9 mm), *L. smaug* (max. SVL=71.3 mm) *L. tregenzai* (max SVL=90.2 mm), and *L. zabalai* (max SVL=90.3 mm).

The number of dorsal scales in *Liolaemus splendidus* sp. nov. (83–96) is higher than in *L. antumalguen* (70–78), *L. capillitas* (60–73), *L. choique* (65–81), *L. dicktracyi* (64–72), *L. heliodermis* (62–65), *L. galactostictos* (70–79), *L. parvus* (70–81), *L. scorialis* (74–81), *L. talampaya* (64–69), and *L. tulkas* (67–76). The number of scales that contact the second infralabial in *L. splendidus* sp. nov. (4) is higher than in *L. tulkas* (2–3). The number of ventrals in *L. splendidus* sp. nov. (121–145) is higher than in *L. antumalguen* (105–118), *L. burmeisteri* (99–110), *L. capillitas* (96–109), *L. dicktracyi* (98–110), *L. galactostictos* (102–108), *L. gununakuna* (108–112), *L. heliodermis* (109–116), *L. parvus* (96–113), *L. talampaya* (104–108), *L. tulkas* (102–113), and *L. umbrifer* (100–115). Scales of dorsum in *L. splendidus* sp. nov. are lanceolate; this character distinguishes it from *L. buergeri, L. burmeisteri, L. capillitas, L. ceii, L. choique, L. dicktracyi, L. elongatus, L. flavipiceus, L. heliodermis, L. janequeoae, L. kriegi, L. lonquimayensis, L. quinterosi, L. talampaya,* and *L. thermarum*, which have rhomboidal dorsal scales. Sexual dichromatism is absent in *L. splendidus* sp. nov., whereas in *L. heliodermis*, *L. quinterosi*, *L. shitan*, *L. smaug*, *L. tregenzai* and *L. umbrifer* sexual dichromatism is evident. Surface of temporal scales is slightly keeled in *L. splendidus* sp. nov., whereas in *L. tulkas* and *L. carlosgarini,* temporal scales are smooth. Dorsal scales in *L. splendidus* sp. nov. show a strong keel, whereas *L. carlosgarini*, *L. janequeoae*, *L. riodamas*, and *L. tregenzai* exhibit dorsals with only a slight median keel and *L. parvus* has dorsals with only a slight keel or no keel). Dorsal scales in *L. splendidus* sp. nov. present mucron, differing from *L. antonietae*, *L. capillitas*, *L. janequeoae*, *L. scorialis*, *L. tulkas*, *L. umbrifer,* and *L. zabalai* (dorsals without mucron).

Regarding genital morphology, we found subtle differences in the hemipenis length to SVL ratio. The hemipenes of *Liolaemus splendidus* sp nov are proportionally longer (hemipenis length/SVL: 0.12) than in other species of the *L. petrophilus* clade, such as *L. austromendocinus* (0.09), *L. parvus* (0.09), *L. petrophilus* (0.06), and *L. quinterosi* (0.09). Ratios of hemipenes to length and width of proximal, medial and distal regions are higher in *L. splendidus* sp nov. (proximal l/w: 0.32; medial l/w: 0.42, distal l/w: 0.50, respectively) than in *L. austromendocinus* (0.24;0.30;0.42), *L. parvus*, (0.22;0.26;0.40), *L. petrophilus* (0.27;0.31;0.38), and *L. quinterosi* (0.29;0.39;0.43). Larger sample sizes of each species are necessary to confirm these differences.

Several characters regarding color patterns discriminate between species belonging to the *Liolaemus petrophilus* clade (Table 6).

Description of the holotype

Adult male. MPCN-H-503. SVL 96.14 mm. Head length 22.05 mm. Head width 17.30 mm. Head height 9.65 mm. Subocular length 5.34 mm. Auditory meatus taller (4.89 mm) than wide (2.02 mm). Interorbital distance 10.04 mm. Rostral wider (4.32 mm) than tall (1.53 mm). Mental twice wider (5.07 mm) than long (2.14 mm). Trunk length 44.65 mm. Humerus length 12.60 mm, humerus width 6.73 mm, radius length 11.45 mm, manus length 14.24 mm. Femur length 19.78 mm, tibia length 19.60 mm, and foot length 26.71 mm. Tail length 140.19 mm. Base of tail width 13.88 mm.

The dorsal surface of the head is smooth, with 16 scales. Nasal in contact with rostral, surrounded by seven scales, and separated from the canthal by one scale. Six scales between frontal and superciliaries. Five superciliaries. Frontal divided into four scales. Interparietal larger than parietals, in contact with five scales. Semicircles complete. Fifteen supraoculars. Preocular separated from lorilabial row by one scale. Nine slightly keeled temporals. Eight lorilabials, two of them in contact with subocular. Seven supralabials. Six infralabials, the second in contact with four scales. Four scales in contact with mental. Seven posmental scales.

Eighty-seven scales around midbody. Ninety-four scales between occiput and hind limbs. Dorsal scales lanceolate, laminar, imbricate, and keeled. Fifty-seven granular and smooth neck scales. Forty-five scales between posterior margin of auditory meatus and antehumeral fold. Antehumeral, auricular and longitudinal folds evident. Fifty-nine gulars. One hundred thirty ventrals. Thirteen pygal scales. Three precloacal pores. Fourth finger with 24 subdigital lamellae, and fourth toe with 30 subdigital lamellae. Dorsal tail scales laminar with mucron and keel.

Color of the holotype in life (Fig. 3 A-B)

Head yellowish-green with a melanic triangular pattern. Pineal scale yellowish-green with a transversal black line. Lateral region of the head with irregular black spots. Dorsal background light green. Melanic

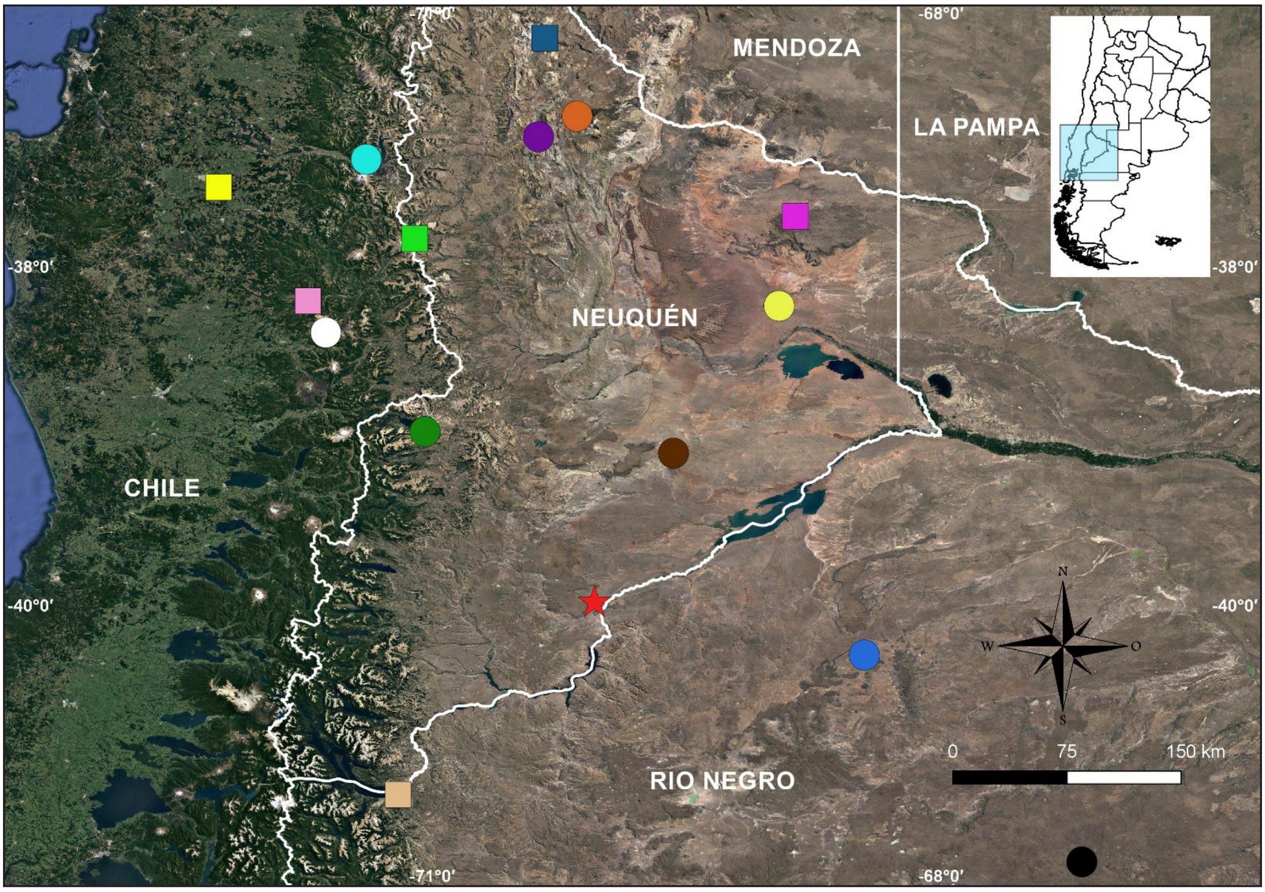

Figure 4. Map of SW Argentina showing the distribution of the *Liolaemus petrophilus* clade. Red star: *L. splendidus* sp. nov. Green circle: *L. ceii*. Fuchsia square: *L. crandalli*. Brown circle: *L. gununakuna*. Pink square: *L. janequeoae*. Beige square: *L. kriegi*. White circle: *L. lonquimayensis*. Black circle: *L. petrophilus*. Orange circle: *L. punmahuida*. Yellow circle: *L. quinterosi*. Turquoise circle: *L. scorialis*. Blue circle: *L. shitan*. Light green square: *L. tregenzai*. Yellow square: *L. zabalai*. Purple circle: *L. burmeisteri*. Petroleum blue square: *L. antumalguen*.

vertebral stripe extends from the head to the base of the tail. The flanks present a pattern of black transversal stripes. The tail presents black rings formed by two rows of scales. The anterior and posterior limbs are light green with black transversal lines. Ventrally, the limbs are light green. The gular region, neck and chest are light green. Abdominal region, including pigal and thighs, up to cloaca is yellowish. Precloacal pores are orange. Ventral region of tail is light green.

Variation

Based on 14 specimens (seven males and seven females, including holotype): SVL of males 84.30 to 96.14 ($\bar{X}$= 90.36; SD = 4.95) and of females 54.12 to 89.64 ($\bar{X}$= 72.60; SD = 16.72). Supralabials 6–9 ($\bar{X}$= 7.50; SD = 1.01). Infralabials 5–8 ($\bar{X}$= 5.88; SD = 0.73). Lorilabials 8–10 ($\bar{X}$ = 8.67; SD = 0.82). Temporals 6–13 ($\bar{X}$= 9.12; SD = 1.81). Number of scales surrounding nasal 6–8 ($\bar{X}$= 6.83; SD = 0.53). Number of scales between canthal and nasal 1–3 ($\bar{X}$ = 1.19; SD = 0.61). Hellmich index or dorsal scales on the head 16 ($\bar{X}$= 16.00; SD = 0.00). Gulars 40–65 ($\bar{X}$= 53.01; SD = 7.88). Scales around midbody 77–95 ($\bar{X}$= 84.73; SD = 4.75). Scales between posterior margin of auditory meatus to antehumeral fold 28–56 ($\bar{X}$= 40.94; SD = 7.97). Neck scales 39–64 ($\bar{X}$= 53.37; SD = 9.88). Dorsal scales 83–96 ($\bar{X}$ = 89.31; SD = 4.76), lanceolate and keeled between occiput and limbs. Ventral scales 121–145 ($\bar{X}$= 126.85; SD = 6.46). Precloacal pores in males 1–3 ($\bar{X}$= 1.51; SD = 0.95). Precloacal pores in females absent. Sexual dichromatism is not evident. Head is yellowish-green with a melanic triangular pattern in the dorsal region. Some specimens present green scales in the melanic region. Side of head with black spots on temporal region and between the nasal and subocular scale. Background color of the dorsal region is light green. The vertical melanic bar extends from the head to the base of the tail. Flank region with transversal melanic stripes. Anterior and posterior limbs are the same color as that of dorsal region, with thin black stripes. Dorsal region of tail is ringed, formed by a complete row of scales and two incomplete rows on the upper and lower parts of the ring. Ventrally, the gular region and chest are green, and some specimens are dark green. The abdominal region ranges from light green to green with some dark scales, forming irregular spots. Pigal region and thighs are yellowish in males and green in females. Cloacal region ranges from pale yellow to light green. Precloacal pores in males are orange. Ventral region of tail ranges from light green to yellowish with faded rings.

Distribution and Natural history

Liolaemus splendidus sp. nov. is an endemic species, whose only known population to date is in its type locality, on the slopes of a basaltic plateau at 650 m a.s.l., located in the south-east of Neuquén Province, Collón Curá department, 8 km north of Piedra del Águila locality, (39º58'54.3''S; 70º02'36''W), on the Argentine Andes foothills (Fig. 4).

The rocky regions of the Olivinic basaltic plateau where this species occurs correspond to the geologic formation known as "Basalto de Santo Tomas", of the lower Pliocene. This formation leans discordantly on the Collon Cura formation, composed of continental sedimentite, which in turn is formed by tuffs, and cinerites from the middle Miocene. These rocks form the piedmont of the plateau (Leanza and Hugo, 1997; Cucchi, 1998).

The vegetation corresponds to an ecotone between the Monte and Patagonian Steppe phytogeographic regions (Fig. 5; Cabrera, 1971). The vegetation associated with the type locality is characteristic of the piedmont of the basaltic plateau due to the presence of typical species of the Patagonian Steppe mixed with Monte species, such as: *Larrea divaricata*, *Larrea nítida, Grindelia chiloensis*, *Senecio filaginoides var. lobulatus, Schinus johnstonii, Ephedra ochreata, Atriplex lampa*, *Maihuenia patagónica*, *Prosopis alpataco, Hyalis argentea* var. *latisquama, Lycium chilense, Chuquiraga erinacea*, *Prosopis denudans var. patagonica*. On the other hand, the vegetation on the slope and upper region of the plateau is typical of the "Western District" of the "Patagonian Phytogeographic region" (León *et al*., 1998): steppe vegetation of shrubs and grasses, with the occurrence of *Azorella prolifera*, *Prosopidastrum globosum*, *Verbena tridens*, *Pappostipa* sp., *Festuca* sp., *Poa* sp., *Adesmia trijuga*, *Colliguaja integerrima*, *Anarthrophyllum strigulipetalum*, and *Calceolaria biflora*. (Burkart, 1964; Cabrera, 1971; Roig, 1987; Arbo, 1999; Gandullo *et al*., 2004; 2016; Riveros *et al*., 2011).

Liolaemus splendidus sp. nov. is a saxicolous and robust species, with remarkable sexual dimorphism: males are larger than females (SVL: Male 96.14 mm - Female 89.03 mm), while the size relationships also change in the head (width, length and height), the torso and the extremities. Weight is up to 19.5 g in adult females and up to 22.0 g. in adult males. We do not have reproduction data.

Based on the observation of faeces, the diet is predominantly insectivorous. We found a great content of ants of the genera *Acromyrmex* (*A. lobicornis* and *A. lundi), Camponotus* sp., *Pogomomyrmex* sp., *Solenopsis* sp., followed, to a lesser degree, by *Hemiptera indet, Diptera* spp., *Colepotera*, Coccinellidae, *Adalia bipunctata*., Hydrophilidae, *Hydrophilus* sp., Tenebrionidae *and Araneae indet*. Among Coleoptera, we identified Buprestidae, mainly *Lasionota (Lasionota bruchi* and *Lasionota alternans)* and *Agrilus* spp. The diet also included large amounts of vegetation, with presence of Molle (*Schinus johnstonii*) seeds as well as other plant remains.

The new species is abundant and easy to observe. They were observed always between 10:30 in the morning and 6:30 in the evening, with an activity peak between 11:30 in the morning and 1:00 in the afternoon, and another from 4 in the afternoon and 6:30 in the evening; between these peaks, little activity was observed, since they avoid extreme solar radiation. We observed an apparent social stratification, with dominant males and adult females being found generally in the upper part of the plateau, and juveniles and subadults inhabiting the lower part. The dominant males and females descended to the lower part of the plateau towards midday, where they intermingled with the juveniles. Then they returned to the upper part after about 5:00 in the afternoon. This behaviour could be related to feeding and social patterns. They are elusive and tend to hide away under a rock when approached at 5 m distance. After a few minutes, they came out again from their hiding place, displaying head bobbing movements that denote communication.

Their coloration is similar to lichens that are present on the rocks where they inhabit, a feature that would reduce the rate of predation by raptor birds.

Liolaemus splendidus sp. nov. is sympatric with *Liolaemus* cf. *bibronii*, *Liolaemus darwinii* (Bell, 1843), *Liolaemus gracilis* (Bell, 1843), *Homonota*

Table 6. Body pattern and coloration of species of the *Liolaemus petrophilus* clade.

	***Liolaemus splendidus* sp. nov.**	***Liolaemus austromendocinus***	***Liolaemus capillitas***	***Liolaemus gununakuna***	***Liolaemus parvus***	***Liolaemus petrophilus***	***Liolaemus quinterosi***
Head color	Green with black lines	Brown/Black	Brown/Black	Iridescent Yellow	Brown	Brown/ Black	Brown/ Black
Body color	Green/Black	Brown	Brown/Black	Iridescent Yellow	Brown/ Dark brown	Brown/ Yellowish	Brown/ White
Dorsal body pattern	Vertebral band and transverse bars	Indistinct	Indistinct	Transverse bars	Dark scales on vertebral region and flanks	Transverse bars	White dots over vertebral region
Tail rings	Present	Slightly marked to present	Absent	Present	Slightly marked to absent	Present	Present
Sexual Dichromatism	Absent	Absent	Absent	Absent	Absent	Absent	Present
Cloacal region color (males)	Yellowish green	Yellowish	Bright red	Yellowish green	Yellowish	Light grey with dark spots	Yellowish

horrida (Burmeister, 1861) and *Homonota darwinii* (Boulenger, 1885).

Discussion

Evidence and phylogeny

Since it was first diagnosed by Cei (1974) until its current redefinition (Medina *et al.,* 2018; Troncoso-Palacios *et al.,* 2018; Avila *et al.,* 2021 and this study), the *Liolaemus elongatus* group has suffered many changes in its taxonomic composition and several phylogenetic hypotheses have been proposed. In fact, the species, which initially belonged to the *L. elongatus* group, were included in at least three monophyletic groups (*L. elongatus*, *L. kriegi*, and *L. petrophilus* clades), and sometimes four (including the *L. punmahuida* clade). The relationship of these three groups varies in the different proposals. Our results are congruent with those of Morando *et al.* (2003), Avila *et al.* (2004), Medina *et al.* (2014), Escobar-Huerta *et. al.* (2015), Troncoso-Palacios *et al.* (2016; 2018) and Ruiz *et al.* (2020); all of these works suggest that the *L. elongatus* clade is sister to the *L. kriegi* clade, and these species form a clade that is sister to the *L. petrophilus* clade (Fig. 1). In all those studies, including the present one, the group that is sister to those clades is the *L. punmahuida* clade (Avila *et al.,* 2015), formed by *L. punmahuida* and *L. flavipiceus*.

In this study, we present morphological (lepidosis, coloration, hemipenis, Table 3, 4 and 6) and molecular evidence (Fig. 1; Table 5) that supports the species status of *Liolaemus splendidus* sp. nov., a species that belongs to the *L. petrophilus* clade within the *L. elongatus* group. According to observations of Quipildor *et al.* (2018), who described hemipenial morphology of several *Liolaemus* species, the morphology of *L. splendidus* sp. nov. is congruent with the patterns observed within the *Liolaemus* sensu stricto subgenus, due to the presence of calyces in the sulcate face, as well as an elongated margin of the distal apex. Furthermore, our observations are consistent with those in the species of the *L. elongatus* group in the presence of a valve-shaped ornamentation, calyces with thin borders, and ornamentation distributed on the upper third of the hemipenis. According to our morphological and molecular evidence of the *L. elongatus* group, *L. splendidus* sp. nov. is phylogenetically close to *L. quinterosi*. This is reflected in the morphology of the copulating organ, since our observations for *L. splendidus* sp. nov. are similar to findings described by Ruiz *et. al.,* (2019) for *L. quinterosi*: a lump-shaped protuberance on the asulcate face, which has a curvature towards the apex region of the hemipenis, and the same number of stems in the sulcate region. On the other hand, the hemipenes of *L. splendidus* sp. nov. can be clearly distinguished from those of the remaining species of the *L. petrophilus* clade in that it is longer and more robust than in the other species (*L. austromendocinus*, *L. parvus*, *L. petrophilus* and *L. quinterosi*). This could be due to the rapid evolu-

Figure 5. Environment where *Liolaemus splendidus* sp.nov. is distributed.

tion of genital characters in relation to non-genital ones. Recent studies suggest that characters related to copulatory organs evolve more rapidly than other morphological characters, possibly due to the pressure of sexual selection acting on them (Klaczko *et al.,* 2015; Klaczko *et al.,* 2017; Klaczko and Stuart, 2015; Quipildor *et al.,* 2021).

We compared the coloration and the patterns within the *Liolaemus elongatus* group (Table 6) and found that, in general, species have earth tones (mostly greys and browns) with some white stripes or scales (Ruiz, 2020). The group members that have more striking coloration are *L. petrophilus* (only some populations), and *L. gununakuna*, with a yellowish coloration on the back. Notably, all species of *L. elongatus* with highly contrasting coloration belong to the *L. petrophilus* group. Furthermore, the peculiar bright green coloration of *L. splendidus* sp. nov. is noticeable

Our results recovered the relationship of *Liolaemus austromendocinus* as sister to *L. parvus*, which is congruent with other works (Avila *et al.,* 2012; Escobar-Huerta *et al.,* 2020). In this work, besides recovering *L. splendidus* sp. nov. within the *L. petrophilus* clade, we incorporated the sequences of *L. quinterosi*, recovering a clade formed by *L. gununakuna*, sister to *L. quinterosi* and *L. splendidus* sp. nov. as sister to the latter two; in turn, this clade is sister to a clade formed by *L. austromendocinus* and *L. parvus*. Furthermore, we recovered the subclade of *L. capillitas* as sister to the previous clades and finally *L. petrophilus* as sister to all the other species in the clade. The latter topology is congruent with the results of Ruiz et *al.* (2020).

Divergence times

In the last decade, few systematic and biogeographic studies have included the *Liolaemus elongatus* group or some of its representatives. Some studies focused on the group (Medina *et al.,* 2014, 2017; Ruiz *et al.,* 2020), whereas others were conducted at large taxonomic scales (Schulte, 2013; Zheng and Wiens, 2016; Esquerré *et al.,* 2019; Esquerré *et al.,* 2022). The results of this work partly agree with the previously mentioned studies. As for those that do agree, the divergence time obtained in the present work for the *L. punmahuida* clade is 4 Ma, an age that exactly coincides with that reported by Ruiz *et al.* (2020) and Esquerré *et al.* (2022). Regarding the divergence time of the *L. kriegi* clade, our 4 Ma result agrees with results reported by Esquerré *et al.* (2019; 2022) and is within the HPD reported by Schulte (2013), Zheng and Wiens (2016) and Ruiz *et al.* (2020), of 6, 2.93, and 3 Ma for the clade, respectively. Regarding the ages that do not agree with any previous study or are outside the HPD, our finding in the *L. elongatus* group (23 Ma) presents a minimum difference of approximately 7 Ma from the work of Schulte (2013). The *L. elongatus petrophilus* clade (19 Ma) and the *L. petrophilus* clade (15 Ma) have a difference of only between 6–4 Ma with respect to the ages obtained by Esquerré *et al.* (2022). The *L. elongatus kriegi* clade (11 Ma) differs from results of Ruiz *et al.* (2020) by 5 Ma. The *L. capillitas* clade (8 Ma) only differs from the results obtained by Zheng and Wiens (2016) and Esquerré *et al.* (2022) by 2 Ma. Finally, the *L. elongatus* sensu stricto clade differs by only 1.5 Ma from the results of Esquerré *et al.* (2022).

These differences in node ages may be due to differences in methodology and in datasets among studies. As for the concordances in divergence time of the *Liolaemus punmahuida* clade, the works of Ruiz *et al.* (2020) and Esquerré *et al.* (2022) reported the same results as those obtained in this study, probably because all works used the same fossil for calibration. This congruence can also be observed in the divergence time of the *L. kriegi* clade and the times obtained by Esquerré *et al.* (2019; 2022), who used the same fossil. The differences found in this work from other works are probably due to different taxonomic scales of analysis (Schulte 2013; Zheng and Wiens, 2016) and/or in the calibration datum employed (Medina *et al.,* 2014; 2017).

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Appendix 1

Specimens studied. MPCN: Museo Patagónico de Ciencias Naturales “Juan Carlos Salgado”. FML: Fundación Miguel Lillo. IBIGEO: Instituto de Bio y Geociencias del NOA. MLP.S: Museo de La Plata.

Species	**Num. Cols**	**Latitude**	**Longitude**	**Statistical analyses**	**Hemipenis**
L. austromendocinus	MCN 2022	34°44´10”S	68°34´53”W	X	
	MCN 2027	34°49´29”S	70°00´32”W	X	
	MCN 2028	34°49´29”S	70°00´32”W	X	
	MCN 2029	34°49´29”S	70°00´32”W	X	
	MCN 2030	34°49´29”S	70°00´32”W	X	
	MCN 3686	35°55´44”S	68°32´36”W		X
	MCN 3691	35°55´44”S	68°32´36”W		X
	MCN 3698	35°55´44”S	68°32´36”W	X	X
	MCN 3702	35°55´44”S	68°32´36”W	X	
	MCN 3703	35°55´44”S	68°32´36”W	X	

	MCN 3704	35°55´44”S	68°32´36”W	X	
	MCN 3705	35°55´44”S	68°32´36”W	X	
	MCN 3706	35°55´44”S	68°32´36”W	X	
	MCN 3707	35°55´44”S	68°32´36”W	X	
	MCN 3708	35°55´44”S	68°32´36”W	X	
	MCN 3709	35°55´44”S	68°32´36”W	X	
	MCN 3710	35°55´44”S	68°32´36”W	X	
	MCN 3711	35°55´44”S	68°32´36”W	X	X
	MCN 3712	35°55´44”S	68°32´36”W	X	
L. capillitas	FML 01229-11	27°20´15”S	66°23´06”W	X	
	FML 01794-2	28°53’38”S	67°14’52”W	X	
	FML 01794-6	28°53’38”S	67°14’52”W	X	
	FML 01229-20	27°20´15”S	66°23´06”W	X	
	FML 01229-16	27°20´15”S	66°23´06”W	X	
	FML 01794-7	28°53’38”S	67°14’52”W	X	
	FML 01794-8	28°53’38”S	67°14’52”W	X	
	FML 01794-19	28°53’38”S	67°14’52”W	X	
	FML 01794-21	28°53’38”S	67°14’52”W	X	
	FML 01914-15	27°21’05”S	67°20’19”W	X	
	FML 01914-15	27°21’05”S	67°20’19”W	X	
	FML 01914-31	27°21’05”S	67°20’19”W	X	
	FML 01794-9	28°53’38”S	67°14’52”W	X	
	IBIGEO 5835	27°20’41”S	66°22´36”W	X	X
	IBIGEO 5836	27°20’41”S	66°22´36”W	X	
	IBIGEO 5837	27°20’41”S	66°22´36”W	X	
	MCN 2135	27°17’00”S	67°26´00”W		X
L. gununakuna	FML 21537	39°02’55”S	70°16´36”W	X	
	FML 22375	39°02’32”S	70°18´27”W	X	
	MACN 37685	38°32’59”S	70°20´27”W	X	
	MACN 37686	38°32’59”S	70°20´27”W	X	
	MLP.S 2352	39°06’00”S	69°34´37”W	X	
	MLP.S 2353	39°06’00”S	69°34´37”W	X	
L. parvus	MCN 2888	31°11’21”S	69°42´15”W	X	
	MCN 2889	31°11’21”S	69°42´15”W	X	
	MCN 2890	31°11’21”S	69°42´15”W	X	
	MCN 3632	31°11’21”S	69°42´15”W		X
	MCN 4006	29°39’34”S	68°51´31”W	X	
	MCN 4007	29°39’34”S	68°51´31”W	X	
	MCN 4008	29°39’34”S	68°51´31”W	X	
	MCN 4009	29°39’34”S	68°51´31”W	X	
	MCN 4049	29°39’34”S	68°51´31”W	X	
	MCN 4050	29°39’34”S	68°51´31”W	X	
	MCN 4070	29°39’34”S	68°51´31”W	X	
	MCN 4074	29°39’34”S	68°51´31”W	X	
	MCN 4081	29°39’34”S	68°51´31”W	X	
	IBIGEO 6085	32°52’36”S	68°33´35”W		X
	IBIGEO 6103	32°52’36”S	68°33´35”W		X
L. petrophilus	MCN 1347	43°50’51”S	69°04´19”W		X

	MACN 11683	40°43’10”S	69°50´05”W	X	
	MACN 11684	40°43’10”S	69°50´05”W	X	
	MACN 11685	40°43’10”S	69°50´05”W	X	
	MACN 11686	40°43’10”S	69°50´05”W	X	
	MLP.R 5400	41°19’47”S	69°33´59”W	X	
	MLP.R 5401	41°19’47”S	69°33´59”W	X	
	MLP.R 5402	41°19’47”S	69°33´59”W	X	
L. quinterosi	FML 30504	38°13´51”S	68°57´13”W	X	
	FML 30505	38°13´51”S	68°57´13”W	X	
	FML 30506	38°13´51”S	68°57´13”W	X	
	FML 30507	38°13´51”S	68°57´13”W	X	X
	FML 30508	38°13´51”S	68°57´13”W	X	
L. splendidus	MPCH-H-500	39°58´54”S	70°02´36”W	X	
	MPCH-H-501	39°58´54”S	70°02´36”W	X	
	MPCH-H-502	39°58´54”S	70°02´36”W	X	
	MPCH-H-503	39°58´54”S	70°02´36”W	X	
	MPCH-H-504	39°58´54”S	70°02´36”W	X	
	MPCH-H-505	39°58´54”S	70°02´36”W	X	
	MPCH-H-506	39°58´54”S	70°02´36”W	X	
	MPCH-H-507	39°58´54”S	70°02´36”W	X	
	MPCH-H-508	39°58´54”S	70°02´36”W	X	
	MPCH-H-509	39°58´54”S	70°02´36”W	X	
	MPCH-H-510	39°58´54”S	70°02´36”W	X	
	IBIGEO 5531	39°58´54”S	70°02´36”W	X	X
	IBIGEO 5532	39°58´54”S	70°02´36”W	X	
	IBIGEO 5533	39°58´54”S	70°02´36”W	X	
L. tulkas	FML 18316	27°43’12”S	66°58’33”W	X	
	FML 18317	27°43’12”S	66°58’33”W	X	
	FML 18318	27°43’12”S	66°58’33”W	X	
	FML 18319	27°43’12”S	66°58’33”W	X	
	FML 18320	27°43’12”S	66°58’33”W	X	
	FML 18321	27°43’12”S	66°58’33”W	X	
	FML 18322	27°43’12”S	66°58’33”W	X	
	FML 18323	27°43’12”S	66°58’33”W	X	
	IBIGEO 5813	27°48’00”S	68°13’00”W		X

Appendix 2

Accession numbers of the specimens used in this study.

Species	Num. Cols	Cyt-b	12s	KIF24	Latitude	Longitude
L. austromendocinus	LJAMM-CNP 2716	AY173838.1	AY173907.1	MG660175	34°59´29”S	68°37´24”W
	LJAMM-CNP 5147	AY367815.1	AY367843.1	MG660176	36°49’05”S	68°59’09”W
	LJAMM-CNP 10574	MG660005	MG660055	MG660177	34°32´20”S	69°15’56”W
	MCN 3698				35°55'44"S	68°32'36"W
L. buergeri	LJAMM-CNP 5294	KJ494165.1	KJ493986.1	KP121232.1	36°43’41”S	70°37’30”W

L. capillitas	LJAMM-CNP 47100	AY173657.1	AY173913.1	-	27°26´00”S	66°20´00”W
	LJAMM-CNP 2788	AY173555.1	MG660051	MG660168	27°25´14”S	66°24´50”W
L. elongatus	LJAMM-CNP 3715	KY127905.1	KP121215.1	KP121231.1	44°31’02”S	69°11’26”W
	LJAMM-CNP 5532	KY127990	KY127492	KY127597	40°19'31"S	69°26'18"W
L. flavipiceus	LJAMM-CNP 7906	KP121330.1	MG660056	KP121241.1	35°58'47"S	70°23'29"W
L. gununakuna	LJAMM-CNP 2690	AY173545.1	AY173903.1	MG660173	39°06'40"S	69°34'29"W
	LJAMM-CNP 4443	MG660004	MG660054	MG660174	39°12'18"S	70°03'56"W
	LJAMM-CNP 10403	MG660003	MG660053	MG660172	39°06'40"S	69°34'29"W
L. kriegi	LJAMM-CNP 2613	KJ494186.1	KP121213.1	KP121227.1	38°53’12”S	70°58’42”W
	LJAMM-CNP 5562	KJ494190.1	KJ493993.1	KP121233.1	40°34’04”S	69°44’59”W
L. parvus	LJAMM-CNP 2704	AY173610.1	AY173905.1	-	29°22´00”S	69°28´00”W
	LJAMM-CNP 2706	AY173611.1	-	MG660170	29°22´00”S	69°28´00”W
	BYU 47106	AY367809.1	AY173906.1	MG660171	32°59´00”S	69°20´00”W
L. petrophilus	LJAMM-CNP 5481	JN846994.1	MG660049	MG660164	42°22’36”S	67°34’00”W
	LJAMM-CNP 6982	KP121326.1	KP121216.1	KP789577.1	39°44’02”S	68°28’44”W
	LJAMM-CNP 11355	KP789552.1	KP121211.1	MG660166	40°33’41”S	67°51’36”W
L. punmahuida	LJAMM-CNP 2626	MG660007	MG660058	MG660179	37°06’16”S	70°08’27”W
L. quinterosi	MPCN 436				38°13’51”S	68°57’13”W
	MPCN 437				38°13’51”S	68°57’13”W
L. splendidus	IBIGEO 5531				39º58'54"S	70º02'36"W
	IBIGEO 5532				39º58'54"S	70º02'36"W
Outgroup						
L. multicolor	LJAMM-CNP 12006	KF968893	KF969085	KF968144	22°41’00”S	65°43’00”W
L. bibronii	LJAMM-CNP 8212	MG660009.1	MG660059.1	MG660180.1	41°17´04”S	66°28´25”W
L. coeruleus	LJAMM-CNP 978	MG660016.1	MG660062.1	MG660186.1	38°54’05”S	70°48’57”W
L. wiegmannii	LJAMM-CNP 4040	DQ237342.1	KF969173.1	KF968228.1	38°38´00”S	62°18´00”W