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Discovering hidden diversity: A new species of *Liolaemus* (Squamata: Liolaemidae) from the Peruvian highlands

Descubriendo la diversidad oculta: Una nueva especie de *Liolaemus* (Squamata: Liolaemidae) de las tierras altas del Perú

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Abstract

The diversity of *Liolaemus* is astonishing, and new species are continuously being described throughout the southern part of South America. In Peru, twelve species of *Liolaemus* have been described in the last seven years, almost all belonging to the *Liolaemus montanus* group. Several of these species inhabit the southern Pacific coast, while others are found in mountain ranges extending across the central and southern regions of the country. In this study, we describe a new species of lizard from the *L. montanus* group, previously referred to as *L.* aff. *forsteri*, based on molecular and morphological evidence. The new species is unique and can be distinguished from its congeners by a combination of morphological traits, particularly its color pattern and scalation. It inhabits mountainous areas of the Puno Department and is molecularly related to Peruvian species within the *L. forsteri* and *L. huacahuasicus* clades.

Keywords: Puno Department, dry Puna, High Plateau, *Liolaemus montanus* group.

Resumen

La diversidad de *Liolaemus* es asombrosa, y continuamente se describen nuevas especies en la región austral de Sudamérica. En Perú, durante los últimos siete años se han descrito doce especies de *Liolaemus*, casi todas pertenecientes al grupo de *Liolaemus montanus*. Varias de estas especies habitan la costa sur del Pacífico, mientras que otras se encuentran en sistemas montañosos que se extienden por las regiones central y meridional del país. En este estudio describimos una nueva especie de lagartija del grupo de *L. montanus*, previamente referida como *L.* aff. *forsteri*, sobre la base de evidencia molecular y morfológica. La nueva especie es única y puede distinguirse de sus congéneres mediante una combinación de caracteres morfológicos, particularmente por su patrón de coloración y escamación.

Habita zonas montañosas del Departamento de Puno y está molecularmente relacionada con especies peruanas pertenecientes a los clados de *L. forsteri* y *L. huacahuasicus*.

Palabras clave: Departamento de Puno, Puna árida, Altiplano, grupo *Liolaemus montanus*.

INTRODUCTION

At the southern end of the southern hemisphere, lizards of the genus *Liolaemus* have undergone extraordinary diversification (Pincheira-Donoso et al., 2015; Esquerré et al., 2019, 2022). This genus comprises more than 290 valid species (Abdala et al., 2021a, 2023, 2025; Campos-Soto et al., 2023; Ruiz et al., 2023, 2025; Troncoso-Palacios & Contreras-Piderit, 2023; San Millán & Abdala, 2024; Santa Cruz et al., 2025), making it the fourth most diverse genus among living tetrapods (Padial et al., 2014; Poe et al., 2017; Abdala et al., 2021b, 2021c; Grismer et al., 2021; Frost, 2024). Remarkably, members of this genus inhabit climatically extreme environments, ranging from the Atlantic coastal zones to the high Andes (Abdala & Quinteros, 2014; Abdala et al., 2021c). Their geographic distribution is highly variable, extending across salt flats at both high and low elevations, continental and coastal dunes, Patagonian and Chacoan montane forests, Patagonian steppes, isolated plateaus in the far south of Patagonia, and even the Atacama Desert, considered the most arid region on Earth. This environmental diversity reflects the remarkable morphological and ecological variation within the genus, including the only known unisexual species among all members of the Iguanidae Pleurodonta, *Liolaemus parthenos* (Abdala et al., 2016); the southernmost distributed lizard species in the world, *Liolaemus magellanicus*, which inhabits Tierra del Fuego in Argentina and Chile (Breitman et al., 2011; Jaksic, 2022); *Liolaemus misti*, which occurs at high elevations reaching up to 5400 m above sea level (Cerdeña et al., 2021), and *Liolaemus crepuscularis*, considered the smallest herbivorous lizard in the world, with a mean snout-vent length of just 54 mm (Abdala & Díaz Gómez, 2006; Semhan et al., 2013).

The taxonomic and phylogenetic complexity of the genus *Liolaemus* reflects its extensive variation in shape, coloration, and other morphological characters. The taxonomy of this group of lizards remains far from resolved and has undergone a series of intricate and sometimes conflicting revisions since its original description (Wiegmann, 1834; Etheridge, 1995, 2000; Abdala, 2005; Lobo et al., 2010; Langstroth, 2011; Valladares-Faúndez et al., 2018; Quinteros et al., 2020; Troncoso-Palacios & Escobar-Gimpel, 2020). The phylogeny of *Liolaemus* continues to be the subject of ongoing

research, with various hypotheses being explored using different lines of evidence, including morphological traits (Etheridge, 1995; Lobo, 2001, 2005; Abdala & Juárez Heredia, 2013; Gutiérrez et al., 2018; Abdala et al., 2019), molecular data (Morando et al., 2003; Espinoza et al., 2004; Avila et al., 2006; Breitman et al., 2011; Aguilar-Puntriano et al., 2018; Schulte et al., 2000; Troncoso-Palacios et al., 2018; Esquerré et al., 2019; Chaparro et al., 2020; Ruiz et al., 2020; Villegas Paredes et al., 2020), behavioral characters (Halloy et al., 1998), and total evidence approaches (Abdala, 2007; Portelli & Quinteros, 2018; Abdala et al., 2020; Huamaní-Valderrama et al., 2020). Most phylogenetic hypotheses support a division of *Liolaemus* into two subgenera: *Liolaemus* sensu stricto or the "Chilean group", and *Eulaemus* or the "Argentine group" (Laurent, 1984; Schulte et al., 2000). Each subgenus encompasses major groups, which are further subdivided into sections, groups, clades, subclades, and species complexes (Abdala et al., 2021c).

The *Liolaemus montanus* group, which includes more than 65 species (Abdala et al., 2020, 2021b, 2025), constitutes a clade that has experienced a notable increase in recognized species diversity in recent years (Abdala et al., 2019, 2021a, 2021d; Aguilar-Puntriano et al., 2019; Gutiérrez et al., 2018; Chaparro et al., 2020; Villegas Paredes et al., 2020). This trend is primarily attributed to the growing number of phylogenetic studies (Aguilar-Puntriano et al., 2018; Abdala et al., 2020; Chaparro et al., 2020), which until recently were absent for this group, leaving their kinship relationships to be inferred without robust phylogenetic frameworks. Nonetheless, early formal phylogenies based on a limited set of morphological characters were proposed by Cei (1993), Laurent (1992), Etheridge (1995) and Lobo et al. (2010). Traditionally, species recognition within the *L. montanus* group relied on morphological analyses and geographic distribution to infer species boundaries or reproductive isolation (Koslowsky, 1898; Cei, 1978; Laurent, 1982, 1992, 1998; Núñez & Yáñez, 1983-1984). Subsequent studies adopted a morphological phylogenetic approach (Lobo et al., 2010; Gutiérrez et al., 2018), while others integrated molecular phylogenies to define species boundaries and taxonomic status (Aguilar-Puntriano et al., 2019; Chaparro et al., 2020; Villegas Paredes et al., 2020). More recently, some researchers have addressed the general, or unified, concept of species proposed by de Queiroz (1998, 2007), using an integrative taxonomy framework that incorporates multiple lines of evidence for species delimitation (Aguilar et al., 2017; Abdala et al., 2019, 2021a, 2021d).

In this study, we test the taxonomic hypothesis that a population of lizards within the *L. montanus* group, previously identified as *Liolaemus* aff. *forsteri* from southeastern Puno, Peru, occurring at elevations between 4000 and 5000 m a.s.l., represents an independent evolutionary lineage and may constitute a new species to science. This population appears as a distinct terminal in the Total Evidence phylogeny of the *L. montanus* group proposed by Abdala et al. (2020). The taxonomic hypothesis follows the

unified concept of species (de Queiroz, 1998, 2007), which defines species as independent evolving metapopulation lineages, typically exhibiting unique morphological characters that distinguish them from sympatric or phylogenetically related taxa. To test the independence of this lineage, we integrate molecular phylogenetic analyses, comparative morphology, and the identification of diagnostic characters.

MATERIAL AND METHODS

Lizard sampling and material examined

On 17 October 2013, we visited the District of Putina, Province of San Antonio de Putina, Puno Department, Peru, at 4000 to 5000 m asl elevation to conduct a survey of lizards. Sampling was carried out by lassoing or hand capture in all available microhabitats (e.g. boulders, vegetation patches, bare soil). We collected a total of 12 individuals (5 males, 4 females, and 3 juveniles) assignable to *Liolaemus* aff. *forsteri.* All specimens were photographed in life using a Nikon ® DSLR camera, euthanized with an overdose of 1% Halatal KT solution, fixed with 10% formaldehyde, and stored in 70% ethanol. Before fixation, we collected muscle tissue samples for DNA extraction and preserved them in 96% ethanol. The collected specimens were deposited in the Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa, Peru (MUSA), and the Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina (FML).

Additionally, we examined 309 specimens belonging to the *Liolaemus montanus* group housed in the herpetological collections of the following institutions: Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa, Peru (MUSA); Museo de Biodiversidad del Perú, Cusco, Peru (MUBI); Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina (FML), Museo de Historia Natural de la Universidad Nacional de San Marcos, Lima, Peru (MUSM), Universidad Nacional Jorge Basadre Grohmann de Tacna, Tacna, Peru (HP-CBP), and the Colección Boliviana de Fauna, La Paz, Bolivia (CBF). A complete list of examined specimens and their associated collection data is provided in Appendix I.

MORPHOLOGY

The examined body folds, color patterns, meristic, and morphometric characters correspond to those commonly used in taxonomic studies in *Liolaemus* (Laurent, 1985; Etheridge, 1995, 2000; Abdala, 2007; Abdala & Juárez-Heredia, 2013), particularly within the *L. montanus* group (Abdala et al., 2019, 2020, 2021a, 2021d). Nomenclature of body folds follows Frost (1992). Description of color pattern characters follow Abdala and Quinteros

(2008), Abdala et al. (2008, 2009, 2013, 2019, 2020, 2021c), Quinteros et al. (2008), Quinteros and Abdala (2011), Gutiérrez et al. (2018), Chaparro et al. (2020), Huamaní-Valderrama et al. (2020), Arapa-Aquino et al. (2021), Quiroz et al. (2021), Ubalde-Mamani et al. (2021), and Valladares-Faúndez et al. (2021). Color definitions follow Köhler (2012). Color pattern description were based exclusively on high-quality digital photographs of live specimens taken in the field.

Definitions and descriptions of scalation followed Smith (1946). We recorded eight meristic characters, following the protocol outlined by Abdala et al. (2020) and Laspiur et al. (2024), abbreviated as follows: supralabials (SL), dorsal head scales (DH), subdigital lamellae of the fourth toe (LT-iv), dorsal body scales (DS), scales around midbody (SAM), ventrals (V), scales on the neck fold (NF), and temporals (T). Scale counts were performed under a binocular stereoscope (10–40 ×) on the right side of the body of each specimen.

We measured 17 morphometric characters following the descriptions provided by Abdala et al. (2019, 2020), abbreviated as follows: snout-vent length (SVL), head width (HW), head length (HL), head height (HH), auditory meatus height (HaM), auditory meatus width (WaM), neck width (NW), forearm length (FAL), hand length (HDL), arm length (AL), thigh length (THL), shank length (SHL), length of the fourth toe excluding the claws (FT-iv), foot length (FOL), trunk length (TL), trunk width (TW), tail-base width (WTB). Measurements were taken using a Mitutoyo Corp. digital caliper (0.01 mm precision) on the right side of the lizards, except when the limbs were partially or completely damaged.

STATISTICAL ANALYSIS

Principal Components Analyses (PCA) were performed in PAST version 3.25 (Hammer et al., 2019) to identify the main axes of variation in morphometric and meristic traits among the closely related phylogenetic species and the newly described taxon. Because scale counts are not influenced by body size, PCAs were carried out separately for meristic and morphometric datasets.

Prior to the analyses, variables were centered by subtracting the mean of each variable from individual morphometric measurements or scale counts (Legendre & Legendre, 1998; Quinn & Keough, 2002). Mean-centering shifts the origin of the multivariate space to the overall mean, allowing principal components to describe variation around the average phenotype rather than around an arbitrary zero point. This procedure ensures that PCA characterizes the covariance structure among variables and that the resulting axes represent directions of maximal variance relative to the dataset mean, thereby facilitating the biological interpretation of component scores and loadings (McGarigal et al., 2000; Palacio et al., 2020).

The mean of each variable was calculated across all species pooled together, but separately for males and females. Only adult individuals (> 57 mm SVL) were included in all analyses in order to minimize the potential influence of intraspecific allometric variation (Losos, 1990; Abdala et al., 2019, 2021d; Huamaní-Valderrama et al., 2020).

PCAs were performed on covariance matrices, and scree plots were analyzed to determine the optimal number of principal components that can be retained using the "broken-stick" criterion (Peres-Neto et al., 2003). Component loadings were considered significant when their absolute values exceeded 0.5 (McGarigal et al., 2000). The resulting principal component (PC) scores were saved and subsequently used as input for a multivariate analysis of variance (MANOVA) with 'species' as the fixed factor to identify which retained PC axes differed significantly among species. Finally, in order to detect potential diagnostic characters between species, we tested morphological variation within each original dataset using permutational ANOVA (PERMANOVA). When significant differences were detected, pairwise comparisons were performed using the Bonferroni *p*-correction method. All analyses were conducted in Statistica version 12.0 (StatSoft, Inc., 2014) and in PAST version 3.25 (Hammer et al., 2019).

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

We extracted genomic DNA from muscle samples using the GenElute Mammalian Genomic DNA Miniprep Kit (Sigma-Aldrich) following the manufacturer's protocol. The mitochondrial cytochrome *b* gene (cyt-*b*) was amplified by polymerase chain reaction (PCR) using the primers IguaCytob_F2 (5'-CCACCGTTGTTATTCAACTAC-3') and IguaCytob_R2 (5'-GGTTTACAAGACCAATGCTTT-3'). The PCR cycle consisted of an initial denaturation at 94 ºC for 5 minutes, followed by 35 cycles of 30 seconds at 94 ºC, 30 seconds at 55 ºC, 60 seconds at 72 ºC, and 2 minutes at 72 ºC for amplification. The PCR product was visualized on a 1.5% agarose gel stained with Gel-Red (Biotium, Inc.). Finally, the samples were sent to Macrogen, Inc. (Seoul, Republic of Korea) for purification and sequencing. The nucleotide sequences were visualized and edited using the 4 Peaks software (https://nucleobytes.com/4peaks/). The sequences obtained in this study will be available in GenBank (accession numbers will be provided upon acceptance). A full list of sequences comprising our molecular data set, including GenBank accession number, vouchers, localities, and original sources is provided in Table S1.

PHYLOGENETIC ANALYSIS

We constructed a matrix based on molecular characters (cyt-*b* marker) with 139 terminal taxa (corresponding to 51 species) and 1161 characters. Sequences of the new species, and those previously described by some coauthors, were obtained in this study. Sequences for other species were obtained from GenBank (https://www.ncbi.nlm.nih.gov/genbank/). The sequences were aligned in MEGA X (Kumar et al., 2018) using the MUSCLE algorithm. The phylogenetic analysis was conducted using Bayesian Inference (BI), with the best-fitting model selected via jModelTest 3.0.4 (Posada, 2008). The best-fitting model identified was GTR + G + I, according to the Akaike Information Criterion (AIC). The analysis was performed in BEAST2 v2.6.6 (Drummond & Rambaut, 2007) with two independent runs of 50 million generations each. Convergence of the chain to the stationary distribution was assessed using Tracer v1.6 (Rambaut et al., 2014). The first 20% of generations were discarded as burn-in, and the stability and adequate mixing of the log-likelihood values were evaluated. The effective sample size (ESS) values for all parameters exceeded 200, indicating sufficient sampling (Lanfear et al., 2016). The posterior distribution of trees was summarized using TreeAnnotator v2.0 (Drummond & Rambaut, 2007) to generate a maximum clade credibility tree (maximum posterior probabilities). The final topology was visualized in FigTree v1.2 (Rambaut et al., 2014). Additionally, we calculated average uncorrected genetic distances between the new species and its closest related species using MEGA X (Kumar et al., 2018).

RESULTS

Molecular Phylogenetic analyses and sequence divergence

The BI analyses recovered *Liolaemus* aff. *forsteri* as a member of a clade that includes species from the *L. huacahuasicus* and *L. forsteri* clades (sensu Abdala et al., 2020). *Liolaemus* aff. *forsteri* was inferred as sister taxon to the clade composed of (*L. annectens* + *L. etheridgei*). This group, in turn, forms the sister clade to ((*L. forsteri* + *L. multiformis*) *L. tacora*)) (Fig. 1). This phylogenetic analysis does not attempt to resolve the relationships within the *L. montanus* group sensu lato, as such resolution is beyond the scope of this study. Rather, it provides a preliminary approximation of the phylogenetic placement of *L.* aff. *forsteri* within the *L. montanus* group sensu Abdala et al. (2020).

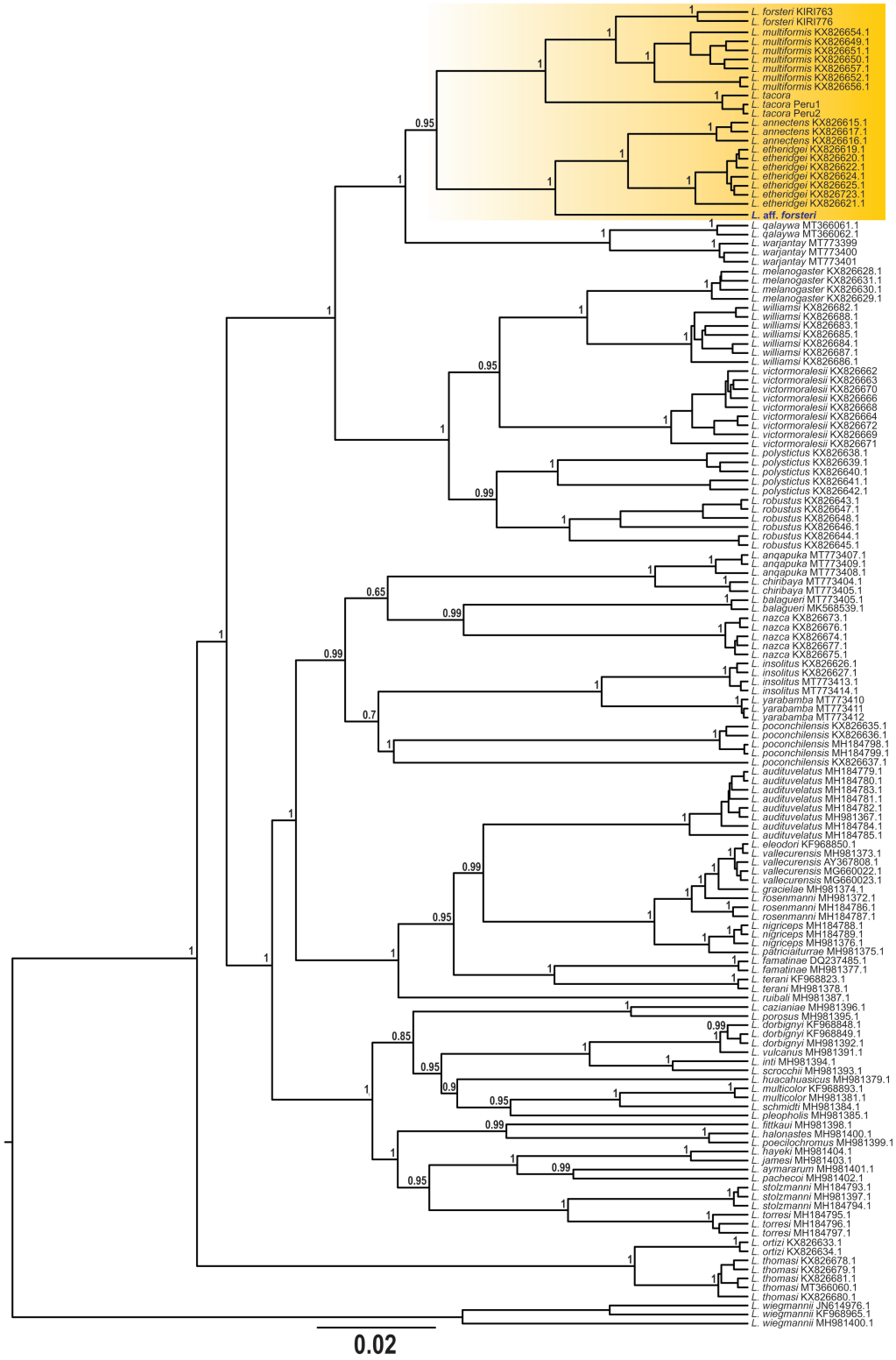

Figure 1. Bayesian inference (BI) tree based on cytochrome *b* (cyt-*b*) sequences of taxa belonging to the *Liolaemus montanus* group. Numbers above branches correspond to Bayesian posterior probabilities (PP).

Figura 1. Árbol de inferencia bayesiana (BI) basado en secuencias de citocromo *b* (cyt-*b*) de taxones pertenecientes al grupo de *Liolaemus montanus*. Los números sobre las ramas corresponden a las probabilidades posteriores bayesianas (PP).

Table 1. Uncorrected pairwise genetic distances (*p*-distances) based on cytochrome *b* (cyt-*b*) between *Liolaemus* aff. *forsteri* and related species.

Tabla 1. Distancias genéticas pareadas no corregidas (distancias *p*) basadas en el citocromo *b* (cyt-*b*) entre *Liolaemus* aff. *forsteri* y especies relacionadas.

	L. annectens	*L. etheridgei*	*L. forsteri*	*L. multiformis*	*L. aff. forsteri*	*L. tacora*
L. annectens	–					
L. etheridgei	6.3665	–				
L. forsteri	9.4868	9.7978	–			
L. multiformis	9.4868	9.1757	4.0435	–		
L. aff. forsteri	5.4432	5.7543	8.4287	8.8647	–	
L. tacora	8.7092	9.1757	6.3011	5.9098	9.0705	–

Uncorrected pairwise genetic *p*-distances based on cyt-*b* sequences among species phylogenetically related to *L.* aff. *forsteri* are presented in Table 1. Genetic differentiation between *L.* aff. *forsteri* and related taxa ranges from 4.04% to 9.79%. The lowest cyt-*b* divergence was observed between *L. forsteri* – *L. multiformis* (4.04%), while the highest between *L. forsteri* – *L. etheridgei* (9.79%). *Liolaemus* aff. *forsteri* shows a 5.44% genetic distance from *L. annectens*, 5.75% from *L. etheridgei*, 8.42% from *L. forsteri*, 8.86% from *L. multiformis*, and 9.07% from *L. tacora*.

Morphology

The morphometric and meristic profiles of species phylogenetically related to *L.* aff. *forsteri* are summarized in Tables 2 and 3. In females, the PCA based on centered morphometric variables showed that *L.* aff. *forsteri* overlapped with *L. tacora* and *L. annectens*, but was clearly separated from the remaining species along the PC1 and PC2 axes, which together explained 88.06% of the total variance, with PC1 primarily influenced by SVL (Fig. 2A, Table S2). The MANOVA performed on the scores of the retained axes revealed significant differences among species only along PC1, but not along PC2 (PC1: $P = 0.004$, PC2: $P = 0.229$; Table S2). Furthermore, although PERMANOVA detected significant interspecific differences for all morphometric variables except SHL and TBW, none of the pairwise comparisons were significant (Table S3). In males, the PCA showed that *L.* aff. *forsteri* was clearly separated from all other species along the PC1 and PC2 axes, which accounted for 84.25% of the total variance and were mainly influenced by SVL, NW, and AL (Fig. 2B, Table S4). The MANOVA performed on the scores of the retained PC axes revealed significant differences among species along both PC1 and PC2 axes (PC1: $P = 0.02$, PC2: $P < 0.001$; Table S4). The PERMANOVA revealed significant interspecific differences in almost all morphometric variables except FOL and TBW.

Table 2 (1 of 2). Descriptive statistics for morphometric characters of *Liolaemus* aff. *forsteri* and phylogenetically related species. Measurements are presented separately for females, males, and the pooled sample (overall) as mean ± SD, and ranges in parentheses (see Materials and methods for abbreviations).

Tabla 2 (1 de 2). Estadística descriptiva de los caracteres morfométricos de *Liolaemus* aff. *forsteri* y especies filogenéticamente relacionadas. Las mediciones se presentan por separado para hembras, machos y la muestra combinada (total) como media ± DE y los rangos entre paréntesis (véase Materiales y Métodos para las abreviaturas).

Characters	Sexes	*L. annectens* n = 14	*L. etheridgei* n = 3	*L. forsteri* n = 11	*L. multiformis* n = 3	*L. tacora* n = 10	*L.* aff. *forsteri* n = 9
SVL	Males	85.2 ± 8.80 (74.9 - 98.4)	–	86.5 ± 6.48 (78.5 - 96.1)	66.8 ± 0.00 (66.8 - 66.8)	88.0 ± 7.53 (79.5 - 97.9)	87.9 ± 4.05 (82.1 - 91.6)
	Females	76.3 ± 4.71 (68.1 – 82.1)	60.2 ± 2.68 (57.8 – 63.1)	82.0 ± 4.14 (78.3 – 86.5)	68.8 ± 16.51 (57.2 – 80.5)	83.5 ± 9.51 (69.6 – 93.2)	79.4 ± 5.15 (73.7 – 84.9)
	Overall	81.4 ± 8.42 (68.1 – 98.4)	60.1 ± 2.68 (57.8 – 63.1)	85.2 ± 6.09 (78.2 – 96.0)	68.1 ± 11.73 (57.1 – 80.5)	85.7 ± 8.43 (69.6 – 97.9)	84.1 ± 6.16 (73.6 – 91.5)
HW	Males	19.0 ± 2.93 (15.8 - 23.3)	–	17.8 ± 1.84 (15.4 - 20.4)	13.8 ± 0.00 (13.8 - 13.8)	18.8 ± 1.65 (17.2 - 20.7)	20.3 ± 1.56 (18.7 - 22.3)
	Females	15.1 ± 1.50 (13.2 – 17.6)	10.9 ± 1.28 (10.1 – 12.4)	16.0 ± 1.95 (13.9 – 17.8)	12.3 ± 3.49 (9.8 – 14.7)	15.9 ± 2.50 (13.8 – 19.9)	16.9 ± 0.56 (16.3 – 17.5)
	Overall	17.3 ± 3.06 (13.1 – 23.3)	10.9 ± 1.28 (10.0 – 12.3)	17.3 ± 1.95 (13.9 – 20.3)	12.7 ± 2.61 (9.7 – 14.7)	17.3 ± 2.50 (13.8 – 20.7)	18.7 ± 2.13 (16.2 – 22.2)
HL	Males	20.0 ± 1.62 (18.0 - 22.9)	–	20.3 ± 1.72 (17.8 - 23.3)	15.5 ± 0.00 (15.5 - 15.5)	20.6 ± 1.82 (18.6 - 23.4)	21.1 ± 1.32 (19.6 - 22.2)
	Females	16.1 ± 1.08 (14.7 – 17.8)	13.4 ± 0.92 (12.8 – 14.5)	17.8 ± 1.25 (16.7 – 19.2)	15.1 ± 3.12 (12.9 – 17.3)	17.8 ± 1.92 (16.1 – 20.9)	17.3 ± 1.23 (15.8 – 18.7)
	Overall	18.3 ± 2.42 (14.7 – 22.8)	13.4 ± 0.91 (12.8 – 14.4)	19.6 ± 1.92 (16.6 – 23.3)	15.2 ± 2.21 (12.8 – 17.3)	19.1 ± 2.30 (16.0 – 23.3)	19.3 ± 2.34 (15.7 – 22.2)
HH	Males	10.7 ± 0.70 (9.4 - 11.5)	–	10.9 ± 1.05 (9.6 - 12.9)	10.4 ± 0.00 (10.4 - 10.4)	12.2 ± 1.44 (10.7 - 14.4)	13.1 ± 1.02 (12.2 - 14.5)
	Females	9.4 ± 1.27 (7.8 – 11.5)	8.3 ± 0.84 (7.7 – 9.2)	10.3 ± 0.94 (9.3 – 11.2)	8.9 ± 1.32 (8.0 – 9.8)	11.0 ± 1.41 (9.8 – 13.5)	11.1 ± 0.65 (10.5 – 12.0)
	Overall	10.1 ± 1.13 (7.7 – 11.5)	8.2 ± 0.83 (7.7 – 9.2)	10.7 ± 1.01 (9.3 – 12.8)	9.3 ± 1.25 (7.9 – 10.3)	11.6 ± 1.47 (9.7 – 14.3)	12.1 ± 1.35 (10.4 – 14.5)
HaM	Males	2.9 ± 0.33 (2.6 - 3.6)	–	3.8 ± 0.31 (3.5 - 4.4)	3.4 ± 0.00 (3.4 - 3.4)	3.5 ± 0.40 (3.0 - 4.1)	4.0 ± 0.39 (3.5 - 4.3)
	Females	2.7 ± 0.30 (2.3 – 3.1)	2.4 ± 0.23 (2.1 – 2.6)	3.4 ± 0.43 (3.1 – 3.9)	2.9 ± 0.24 (2.7 – 3.1)	3.3 ± 0.51 (2.5 – 4.0)	3.1 ± 0.38 (2.6 – 3.5)
	Overall	2.8 ± 0.32 (2.3 – 3.6)	2.3 ± 0.23 (2.1 – 2.5)	3.6 ± 0.38 (3.1 – 4.3)	3.0 ± 0.34 (2.7 – 3.4)	3.4 ± 0.44 (2.5 – 4.0)	3.5 ± 0.59 (2.6 – 4.3)
WaM	Males	1.6 ± 0.35 (1.1 - 2.3)	–	2.1 ± 0.48 (1.6 - 3.2)	2.4 ± 0.00 (2.4 - 2.4)	1.4 ± 0.22 (1.2 - 1.7)	1.9 ± 0.64 (1.4 - 2.9)
	Females	1.7 ± 0.12 (1.5 – 1.8)	1.0 ± 0.04 (0.9 – 1.0)	1.8 ± 0.14 (1.6 – 1.9)	1.5 ± 0.33 (1.3 – 1.8)	1.4 ± 0.11 (1.3 – 1.6)	1.7 ± 0.18 (1.4 – 1.9)
	Overall	1.6 ± 0.27 (1.1 – 2.3)	0.9 ± 0.04 (0.9 – 1.0)	2.0 ± 0.44 (1.5 – 3.1)	1.8 ± 0.56 (1.3 – 2.4)	1.4 ± 0.17 (1.2 – 1.7)	1.7 ± 0.48 (1.3 – 2.8)
NW	Males	19.1 ± 3.87 (14.5 - 24.6)	–	14.1 ± 1.24 (11.9 - 15.8)	12.6 ± 0.00 (12.6 - 12.6)	19.3 ± 1.61 (17.5 - 21.8)	21.8 ± 2.84 (17.7 - 25.4)
	Females	15.9 ± 2.74 (13.5 – 20.4)	13.9 ± 2.26 (12.4 – 16.5)	12.9 ± 1.30 (11.6 – 14.2)	13.3 ± 2.38 (11.6 – 15.0)	17.8 ± 2.20 (15.8 – 20.3)	18.9 ± 1.61 (17.8 – 21.3)
	Overall	17.7 ± 3.70 (13.4 – 24.5)	13.8 ± 2.26 (12.3 – 16.4)	13.7 ± 1.31 (11.6 – 15.8)	13.05 ± 1.72 (11.6 – 14.9)	18.5 ± 1.98 (15.8 – 21.8)	20.5 ± 2.70 (17.7 – 25.4)
FAL	Males	9.9 ± 0.63 (8.6 - 10.5)	–	10.3 ± 0.82 (9.5 - 12.0)	8.6 ± 0.00 (8.6 - 8.6)	10.7 ± 0.66 (9.9 - 11.8)	11.8 ± 0.51 (11.1 - 12.3)
	Females	9.0 ± 0.55 (8.1 – 9.5)	7.7 ± 0.57 (7.3 – 8.3)	9.8 ± 0.69 (9.1 – 10.4)	8.9 ± 0.47 (8.6 – 9.2)	8.6 ± 1.24 (7.1 – 10.3)	10.4 ± 0.92 (9.1 – 11.1)
	Overall	9.4 ± 0.73 (8.05 – 10.5)	7.6 ± 0.57 (7.3 – 8.3)	10.1 ± 0.78 (9.0 – 12.0)	8.7 ± 0.38 (8.5 – 9.2)	9.6 ± 1.47 (7.1 – 11.7)	11.1 ± 0.98 (9.1 – 12.3)
AL	Males	12.5 ± 1.24 (11.1 - 14.8)	–	10.2 ± 0.50 (9.5 - 10.9)	9.9 ± 0.00 (9.9 - 9.9)	12.5 ± 0.35 (12.1 - 13.0)	17.8 ± 1.18 (15.8 - 18.8)
	Females	11.6 ± 1.13 (10.2 – 13.0)	8.5 ± 1.10 (7.2 – 9.2)	9.8 ± 0.78 (9.1 – 10.7)	9.4 ± 1.68 (8.2 – 10.6)	9.6 ± 2.46 (7.1 – 13.6)	15.2 ± 1.38 (13.7 – 17.0)
	Overall	12.1 ± 1.23 (10.1 – 14.7)	8.5 ± 1.09 (7.2 – 9.1)	10.0 ± 0.56 (9.1 – 10.9)	9.5 ± 1.21 (8.2 – 10.6)	11.06 ± 2.22 (7.1 – 13.5)	16.6 ± 1.79 (13.7 – 18.8)

Table 2 (2 of 2). Descriptive statistics for morphometric characters of *Liolaemus* aff. *forsteri* and phylogenetically related species. Measurements are presented separately for females, males, and the pooled sample (overall) as mean ± SD, and ranges in parentheses (see Materials and methods for abbreviations).

Tabla 2 (2 de 2). Estadística descriptiva de los caracteres morfométricos de *Liolaemus* aff. *forsteri* y especies filogenéticamente relacionadas. Las mediciones se presentan por separado para hembras, machos y la muestra combinada (total) como media ± DE y los rangos entre paréntesis (véase Materiales y Métodos para las abreviaturas).

Characters	Sexes	*L. annectens* n = 14	*L. etheridgei* n = 3	*L. forsteri* n = 11	*L. multiformis* n = 3	*L. tacora* n = 10	*L.* aff. *forsteri* n = 9
HDL	Males	13.2 ± 1.47 (10.7 - 14.8)	–	14.0 ± 0.78 (12.7 - 15.3)	10.5 ± 0.00 (10.5 - 10.5)	13.8 ± 1.07 (12.5 - 14.8)	10.8 ± 0.92 (10.0 - 12.4)
	Females	11.6 ± 1.44 (9.6 – 12.9)	10.2 ± 0.64 (9.5 – 10.8)	13.0 ± 1.59 (11.3 – 14.4)	10.8 ± 0.88 (10.2 – 11.4)	12.8 ± 1.14 (11.4 – 14.3)	10.3 ± 0.33 (10.0 – 10.8)
	Overall	12.5 ± 1.63 (9.5 – 14.7)	10.1 ± 0.64 (9.4 – 10.7)	13.7 ± 1.05 (11.2 – 15.2)	10.7 ± 0.65 (10.2 – 11.4)	13.3 ± 1.16 (11.4 – 14.8)	10.5 ± 0.73 (10.0 – 12.4)
THL	Males	15.6 ± 1.48 (14.0 - 18.2)	–	15.2 ± 0.72 (14.0 - 16.1)	11.7 ± 0.00 (11.7 - 11.7)	16.3 ± 0.57 (15.6 - 17.0)	16.1 ± 1.03 (14.9 - 17.2)
	Females	14.0 ± 1.25 (12.3 – 15.7)	12.1 ± 0.63 (11.4 – 12.7)	13.9 ± 1.17 (13.1 – 15.3)	11.7 ± 1.55 (10.6 – 12.8)	14.5 ± 1.89 (13.1 – 17.6)	14.4 ± 0.39 (13.9 – 14.8)
	Overall	14.8 ± 1.56 (12.3 – 18.2)	12.1 ± 0.63 (11.4 – 12.6)	14.8 ± 0.99 (13.1 – 16.1)	11.7 ± 1.09 (10.6 – 12.8)	15.3 ± 1.62 (13.0 – 17.5)	15.3 ± 1.19 (13.8 – 17.1)
SHL	Males	15.1 ± 0.88 (13.7 - 16.7)	–	15.7 ± 0.62 (14.9 - 16.7)	12.9 ± 0.00 (12.9 - 12.9)	16.4 ± 0.42 (15.9 - 17.0)	16.9 ± 0.71 (16.2 - 17.9)
	Females	13.4 ± 0.93 (12.3 – 15.0)	11.2 ± 1.12 (10.4 – 12.5)	14.7 ± 1.05 (13.8 – 15.8)	12.2 ± 1.99 (10.8 – 13.6)	12.4 ± 2.88 (10.1 – 17.0)	14.4 ± 0.90 (13.1 – 15.0)
	Overall	14.3 ± 1.25 (12.2 – 16.7)	11.2 ± 1.12 (10.3 – 12.5)	15.4 ± 0.85 (13.7 – 16.7)	12.4 ± 1.45 (10.7 – 13.5)	14.4 ± 2.87 (10.1 – 17.0)	15.7 ± 1.54 (13.0 – 17.9)
FT–iv	Males	14.3 ± 0.70 (13.5 - 15.6)	–	11.6 ± 0.91 (10.5 - 12.8)	10.8 ± 0.00 (10.8 - 10.8)	14.4 ± 0.76 (13.2 - 15.3)	14.4 ± 0.71 (13.3 - 15.2)
	Females	12.4 ± 1.30 (11.0 – 14.7)	10.5 ± 1.28 (9.2 – 11.8)	11.5 ± 0.55 (10.9 – 12.0)	10.8 ± 0.91 (10.2 – 11.4)	14.8 ± 0.35 (14.5 – 15.4)	11.5 ± 1.66 (9.7 – 13.0)
	Overall	13.4 ± 1.36 (10.9 – 15.5)	10.4 ± 1.28 (9.2 – 11.7)	11.5 ± 0.80 (10.4 – 12.8)	10.8 ± 0.64 (10.1 – 11.4)	14.6 ± 0.58 (13.2 – 15.3)	13.1 ± 1.93 (9.7 – 15.1)
FOL	Males	22.6 ± 2.90 (18.2 - 25.9)	–	20.0 ± 0.98 (18.8 - 21.4)	18.3 ± 0.00 (18.3 - 18.3)	21.7 ± 4.87 (13.3 - 25.8)	23.9 ± 0.44 (23.2 - 24.3)
	Females	19.7 ± 3.30 (14.3 – 23.7)	16.1 ± 1.75 (14.9 – 18.1)	19.1 ± 1.43 (18.1 – 20.8)	16.4 ± 0.93 (15.7 – 17.0)	22.0 ± 1.82 (20.4 – 25.1)	19.6 ± 1.60 (18.1 – 21.7)
	Overall	21.3 ± 3.30 (14.3 – 25.8)	16.1 ± 1.75 (14.9 – 18.1)	19.7 ± 1.12 (18.1 – 21.3)	17.0 ± 1.27 (15.7 – 18.2)	21.8 ± 3.47 (13.3 – 25.7)	21.9 ± 2.51 (18.0 – 24.3)
TL	Males	36.7 ± 3.58 (31.4 - 41.6)	–	37.3 ± 2.52 (34.0 - 40.6)	27.7 ± 0.00 (27.7 - 27.7)	41.9 ± 3.60 (38.5 - 46.7)	40.4 ± 2.58 (37.6 - 43.4)
	Females	36.3 ± 2.44 (32.5 – 38.6)	30.3 ± 1.21 (29.6 – 31.7)	41.1 ± 2.40 (38.6 – 43.4)	31.2 ± 9.14 (24.7 – 37.6)	40.1 ± 4.84 (31.7 – 43.2)	40.1 ± 1.86 (37.4 – 41.3)
	Overall	36.4 ± 3.03 (31.3 – 41.5)	30.3 ± 1.20 (29.5 – 31.7)	38.3 ± 2.95 (34.0 – 43.3)	30.0 ± 6.76 (24.7 – 37.6)	40.9 ± 4.13 (31.6 – 46.6)	40.2 ± 2.15 (37.3 – 43.4)
TW	Males	27.0 ± 2.20 (24.0 - 30.5)	–	25.3 ± 4.20 (19.6 - 32.6)	14.1 ± 0.00 (14.1 - 14.1)	29.3 ± 2.99 (24.7 - 32.6)	30.0 ± 1.04 (28.4 - 31.3)
	Females	26.4 ± 3.02 (22.5 – 30.5)	18.4 ± 3.11 (16.2 – 22.0)	26.2 ± 1.70 (24.5 – 27.9)	18.8 ± 4.36 (15.7 – 21.9)	25.9 ± 5.28 (21.6 – 34.2)	27.4 ± 2.73 (23.3 – 29.0)
	Overall	26.7 ± 2.49 (22.5 – 30.5)	18.3 ± 3.11 (16.2 – 21.9)	25.5 ± 3.62 (19.6 – 32.5)	17.2 ± 4.11 (14.0 – 21.8)	27.5 ± 4.41 (21.5 – 34.1)	28.8 ± 2.30 (23.2 – 31.2)
TBW	Males	12.0 ± 1.64 (10.0 - 14.3)	–	11.3 ± 1.48 (8.4 - 12.7)	10.0 ± 0.00 (10.0 - 10.0)	11.8 ± 1.62 (10.1 - 13.8)	12.5 ± 1.37 (10.7 - 13.8)
	Females	10.4 ± 0.95 (9.5 – 12.1)	8.3 ± 0.84 (7.7 – 9.3)	10.0 ± 0.85 (9.0 – 10.6)	8.4 ± 0.93 (7.7 – 9.1)	11.4 ± 5.51 (7.7 – 21.1)	10.8 ± 1.05 (9.2 – 11.6)
	Overall	11.2 ± 1.57 (9.5 – 14.3)	8.3 ± 0.84 (7.7 – 9.28)	10.9 ± 1.44 (8.4 – 12.7)	8.9 ± 1.13 (7.7 – 9.9)	11.6 ± 3.84 (7.7 – 21.0)	11.7 ± 1.46 (9.2 – 13.8)

Table 3. Descriptive statistics for meristic characters of *Liolaemus* aff. *forsteri* and phylogenetically related species. Measurements are presented separately for females, males, and the pooled sample (overall) as mean ± SD, and ranges in parentheses (see Materials and methods for abbreviations).

Tabla 3. Estadística descriptiva de los caracteres merísticos de *Liolaemus* aff. *forsteri* y especies filogenéticamente relacionadas. Las mediciones se presentan por separado para hembras, machos y la muestra combinada (total) como media ± DE y los rangos entre paréntesis (véase Materiales y Métodos para las abreviaturas).

Characters	Sexes	*L. annectens* n = 14	*L. etheridgei* n = 3	*L. forsteri* n = 11	*L. multiformis* n = 3	*L. tacora* n = 10	*L.* aff. *forsteri* n = 9
SL	Males	7.4 ± 0.92 (6 – 9)	–	8.5 ± 0.93 (7 – 10)	7.0 ± 0.00 (7 – 7)	9.6 ± 0.55 (9 – 10)	7.2 ± 0.45 (7 – 8)
	Females	7.7 ± 1.37 (6 – 10)	6.3 ± 0.58 (6 – 7)	8.7 ± 1.53 (7 – 10)	8.5 ± 0.71 (8 – 9)	9.2 ± 1.30 (7 – 10)	7.0 ± 0.82 (6 – 8)
	Overall	7.5 ± 1.09 (6 – 10)	6.3 ± 0.58 (6 – 7)	8.5 ± 1.04 (7 – 10)	8.0 ± 1.00 (7 – 9)	9.4 ± 0.97 (7 – 10)	7.1 ± 0.60 (6 – 8)
DH	Males	16.6 ± 2.39 (15 – 22)	–	23.9 ± 1.89 (21 – 27)	20.0 ± 0.00 (20 – 20)	16.2 ± 0.84 (15 – 17)	16.6 ± 2.97 (14 – 21)
	Females	17.8 ± 1.33 (16 – 19)	15.7 ± 0.58 (15 – 16)	21.0 ± 1.00 (20 – 22)	14.5 ± 3.54 (12 – 17)	15.4 ± 1.82 (13 – 18)	16.2 ± 1.50 (15 – 18)
	Overall	17.1 ± 2.03 (15 – 22)	15.6 ± 0.58 (15 – 16)	23.0 ± 2.12 (20 – 27)	16.3 ± 4.04 (12 – 20)	15.8 ± 1.40 (13 – 18)	16.4 ± 2.30 (14 – 21)
LT–iv	Males	23.9 ± 0.83 (23 – 25)	–	21.6 ± 1.77 (20 – 25)	19.0 ± 0.00 (19 – 19)	23.2 ± 0.45 (23 – 24)	20.4 ± 0.89 (19 – 21)
	Females	23.5 ± 0.84 (23 – 25)	21.3 ± 0.58 (21 – 22)	23.0 ± 1.73 (21 – 24)	20.5 ± 0.71 (20 – 21)	23.0 ± 1.58 (21 – 25)	21.2 ± 1.26 (20 – 23)
	Overall	23.7 ± 0.82 (23 – 25)	21.3 ± 0.57 (21 – 22)	22.0 ± 1.78 (20 – 25)	20.0 ± 1.00 (19 – 21)	23.1 ± 1.10 (21 – 25)	20.7 ± 1.09 (19 – 23)
DS	Males	59.6 ± 5.34 (51 – 65)	–	90.4 ± 4.90 (85 – 99)	84.0 ± 0.00 (84 – 84)	69.6 ± 4.04 (66 – 76)	77.4 ± 3.21 (74 – 82)
	Females	64.5 ± 7.15 (57 – 73)	65.7 ± 5.69 (61 – 72)	93.3 ± 2.52 (91 – 96)	80.5 ± 2.12 (79 – 82)	78.0 ± 10.93 (64 – 89)	80.2 ± 2.63 (78 – 84)
	Overall	61.7 ± 6.42 (51 – 73)	65.6 ± 5.68 (61 – 72)	91.1 ± 4.46 (85 – 99)	81.6 ± 2.51 (79 – 84)	73.8 ± 8.94 (64 – 89)	78.6 ± 3.16 (74 – 84)
SAM	Males	65.1 ± 6.45 (57 – 73)	–	83.4 ± 3.89 (78 – 90)	73.0 ± 0.00 (73 – 73)	65.0 ± 1.22 (63 – 66)	75.4 ± 7.27 (70 – 87)
	Females	68.3 ± 6.28 (62 – 78)	60.3 ± 5.13 (56 – 66)	84.3 ± 53 (79 – 89)	69.0 ± 1.41 (68 – 70)	64.2 ± 1.79 (62 – 66)	72.8 ± 4.11 (69 – 78)
	Overall	66.5 ± 6.34 (57 – 78)	60.3 ± 5.13 (56 – 66)	83.6 ± 3.98 (78 – 90)	70.3 ± 2.51 (68 – 73)	64.6 ± 1.50 (62 – 66)	74.2 ± 5.89 (69 – 87)
V	Males	83.1 ± 2.03 (80 – 85)	–	85.0 ± 3.16 (82 – 90)	78.0 ± 0.00 (78 – 78)	81.2 ± 2.59 (77 – 84)	75.6 ± 1.95 (73 – 77)
	Females	90.0 ± 3.29 (85 – 94)	82.3 ± 5.51 (77 – 88)	87.3 ± 97 (77 – 94)	92.5 ± 4.95 (89 – 96)	84.4 ± 35 (82 – 89)	74.0 ± 4.24 (70 – 80)
	Overall	86.0 ± 4.34 (80 – 94)	82.3 ± 5.51 (77 – 88)	85.6 ± 4.97 (77 – 94)	87.6 ± 9.07 (78 – 96)	82.8 ± 3.15 (77 – 89)	74.8 ± 3.06 (70 – 80)
NF	Males	44.9 ± 4.22 (38 – 50)	–	36.1 ± 8.76 (28 – 57)	36.0 ± 0.00 (36 – 36)	44.8 ± 1.64 (43 – 47)	46.0 ± 1.41 (44 – 48)
	Females	45.5 ± 4.72 (40 – 52)	43.0 ± 2.65 (41 – 46)	36.0 ± 7.81 (31 – 45)	33.0 ± 4.24 (30 – 36)	34.2 ± 8.14 (27 – 44)	43.5 ± 30 (40 – 46)
	Overall	45.1 ± 4.28 (38 – 52)	43.0 ± 2.65 (41 – 46)	36.0 ± 8.12 (28 – 57)	34.0 ± 3.46 (30 – 36)	39.5 ± 7.86 (27 – 47)	44.8 ± 2.47 (40 – 48)
T	Males	10.6 ± 0.92 (9 – 12)	–	12.9 ± 1.46 (11 – 15)	14.0 ± 0.00 (14 – 14)	9.8 ± 0.84 (9 – 11)	9.4 ± 0.55 (9 – 10)
	Females	10.0 ± 1.10 (8 – 11)	9.7 ± 1.53 (8 – 11)	13.0 ± 1.73 (12 – 15)	11.0 ± 1.41 (10 – 12)	7.2 ± 1.79 (6 – 10)	9.2 ± 0.50 (9 – 10)
	Overall	10.3 ± 1.01 (8 – 12)	9.6 ± 1.52 (8 – 11)	12.9 ± 1.44 (11 – 15)	12.0 ± 2.00 (10 – 14)	8.5 ± 1.90 (6 – 11)	9.3 ± 0.50 (9 – 10)

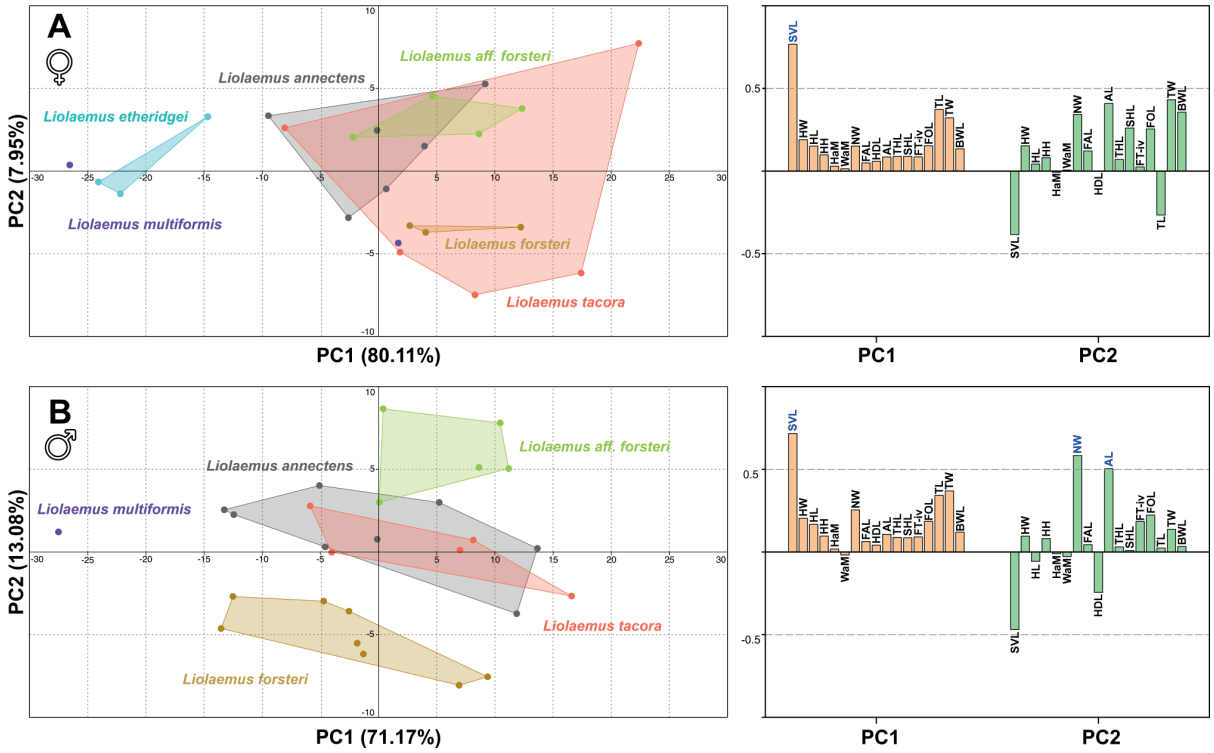

Figure 2. Principal Component Analysis (PCA) of centered morphometric variables for phylogenetically related *Liolaemus* species. **A.** Females. **B.** Males. The left panels show the distribution of individuals in the morphospace defined by the first two principal components, with convex hulls enclosing specimens of each species. The right panels show the loadings of the morphometric variables on PC1 and PC2. Percentages on the axes indicate the proportion of total variance explained by each principal component.

Figura 2. Análisis de componentes principales (PCA) de las variables morfométricas centradas para especies de *Liolaemus* filogenéticamente relacionadas. **A.** Hembras. **B.** Machos. Los paneles izquierdos muestran la distribución de los individuos en el morfoespacio definido por los dos primeros componentes principales, con envolventes convexas que delimitan los ejemplares de cada especie. Los paneles derechos muestran las cargas de las variables morfométricas sobre PC1 y PC2. Los porcentajes en los ejes indican la proporción de la varianza total explicada por cada componente principal.

However, pairwise comparisons detected significant differences in HaM, NW, AL and FT-iv between *L. annectens* and *L. forsteri*; in HH, HaM, FAL, and AL between *L. annectens* and *L.* aff. *forsteri*; in NW, AL, and FT-iv between *L. forsteri* and *L. tacora*; and in HH, NW, HDL, AL, FT-iv, and FOL between *L. forsteri* and *L.* aff. *forsteri* (Table S5).

In females, the PCA based on centered meristic variables showed that *L.* aff. *forsteri* was notably separated from all other species along the PC1, PC2, and PC3 axes, which accounted for 93.53% of the total variation and were largely influenced by DS, V, SAM, and NF (Fig. 3A, Table S6). The MANOVA performed on the scores of the three retained PC axes revealed significant differences among species along PC1, PC2, and PC3 (PC1: $P < 0.001$, PC2: $P < 0.001$, PC3: $P < 0.001$; Table S6). The PERMANOVA detected significant interspecific differences for all meristic variables;

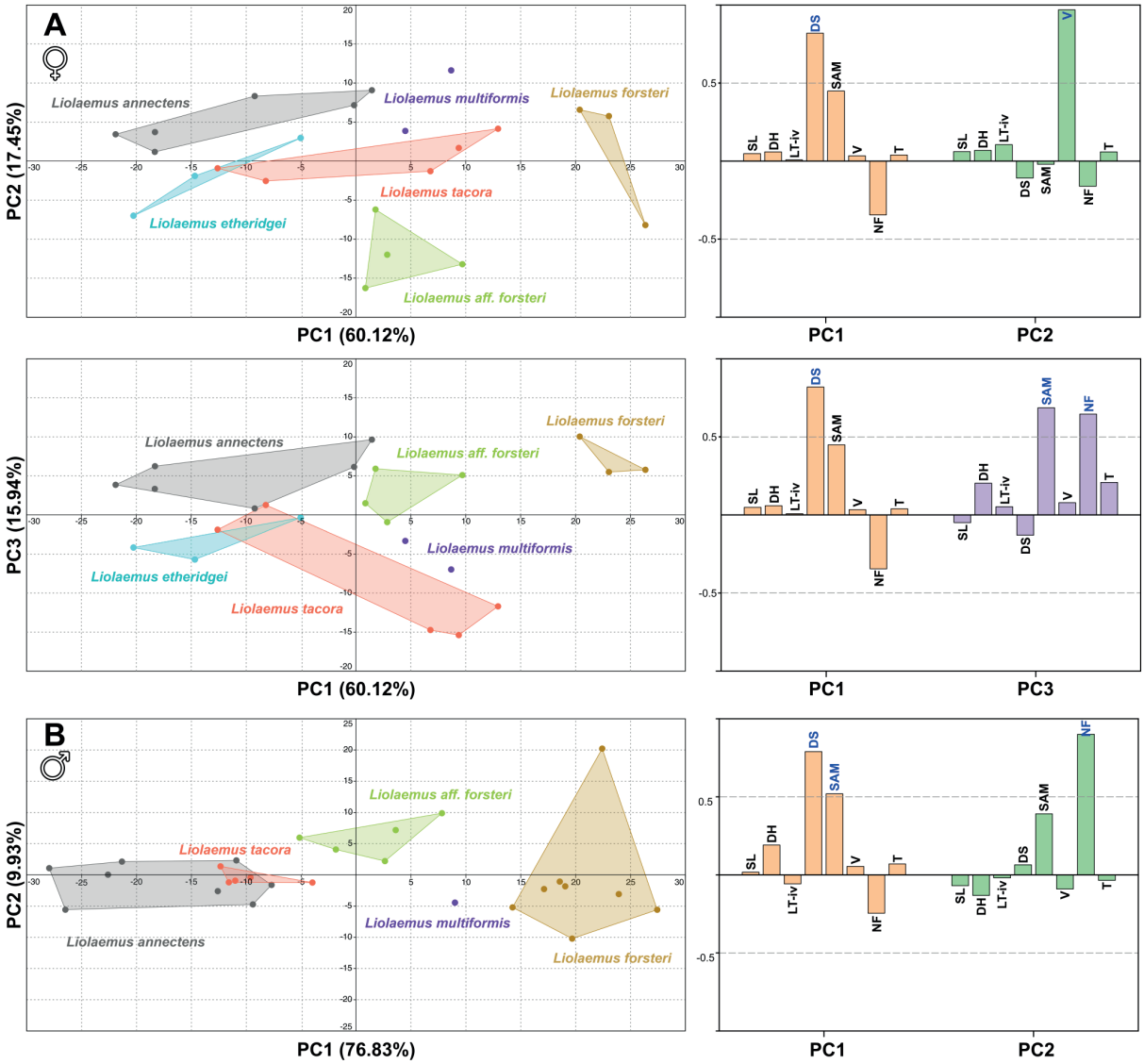

Figure 3. Principal Component Analysis (PCA) of centered meristic variables for phylogenetically related *Liolaemus* species. **A.** Females. Scatterplots of PC1 versus PC2 (top) and PC1 versus PC3 (center), with convex hulls enclosing specimens of each species. The right panels show the loadings of the meristic variables on the first three principal components. **B.** Males. Scatterplot of PC1 versus PC2, with convex hulls enclosing specimens of each species. The right panel shows the loadings of the meristic variables on PC1 and PC2. Percentages on the axes indicate the proportion of total variance explained by each principal component.

Figura 3. Análisis de componentes principales (PCA) de las variables merísticas centradas para especies de *Liolaemus* filogenéticamente relacionadas. **A.** Hembras. Diagramas de dispersión de PC1 frente a PC2 (arriba) y de PC1 frente a PC3 (centro), con envolventes convexas que delimitan los ejemplares de cada especie. Los paneles derechos muestran las cargas de las variables merísticas sobre los tres primeros componentes principales. **B.** Machos. Diagrama de dispersión de PC1 frente a PC2, con envolventes convexas que delimitan los ejemplares de cada especie. El panel derecho muestra las cargas de las variables merísticas sobre PC1 y PC2. Los porcentajes en los ejes indican la proporción de la varianza total explicada por cada componente principal.

however, none of the pairwise comparisons were significant (Table S7). In addition, in males, the PCA showed that *L.* aff. *forsteri* was clearly separated from all other species along the PC1 and PC2 axes, which accounted for 86.77% of the total variance and were mainly influenced by DS, SAM, and NF (Fig. 3B; Table S8). The MANOVA performed on the scores of the retained PC axes revealed significant differences among species along PC1, but not along PC2 (PC1: P = 0.001, PC2: P = 0.13; Table S8). The PERMANOVA revealed significant interspecific differences in all meristic traits, and pairwise comparisons detected significant differences in DH, DS, SAM, and T between *L. annectens* and *L. forsteri*; in SL and DS between *L. annectens* and *L. tacora*; in LT-iv, DS, and V between *L. annectens* and *L.* aff. *forsteri*; in DH, DS, SAM, and T between *L. forsteri* and *L. tacora*; and in DH, DS, V, and T between *L. forsteri* and *L.* aff. *forsteri* (Table S9).

Taxonomic highlights

The combination of phylogenetic, molecular, and morphological evidence supports the conclusion that *Liolaemus* aff. *forsteri* represents an independent evolutionary lineage. To formally delimit this taxon, we provide a morphological diagnosis relative to other members of the *L. montanus* species group, along with a comprehensive morphological description of this new species.

Nomenclatural acts

This contribution follows the requirements of the International Code of Zoological Nomenclature, and the new names contained herein are available from the electronic publication of this article. All the nomenclatural acts it contains have been registered in Zoobank. The ZooBank LSIDs (Life Science Identifiers) can be resolved, and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub:0F0DE7B1-E2BA-4270-97F5-944C56658D2F

Species description

***Liolaemus yawar,* new species**
urn:lsid:zoobank.org:pub:0F0DE7B1-E2BA-4270-97F5-944C56658D2F
Liolaemus aff. forsteri (Abdala et al., 2020)

Holotype.— MUSA 5603 (CSA 1516), an adult male from between Putina and Mina Rinconada, on National Road 34H, 9 km after Señor de la Exaltación de Chipalca, District of Putina, Province of San Antonio de Putina, Puno Department, Peru (14º48'34.60" S, 69º39'0.00" W – WGS84

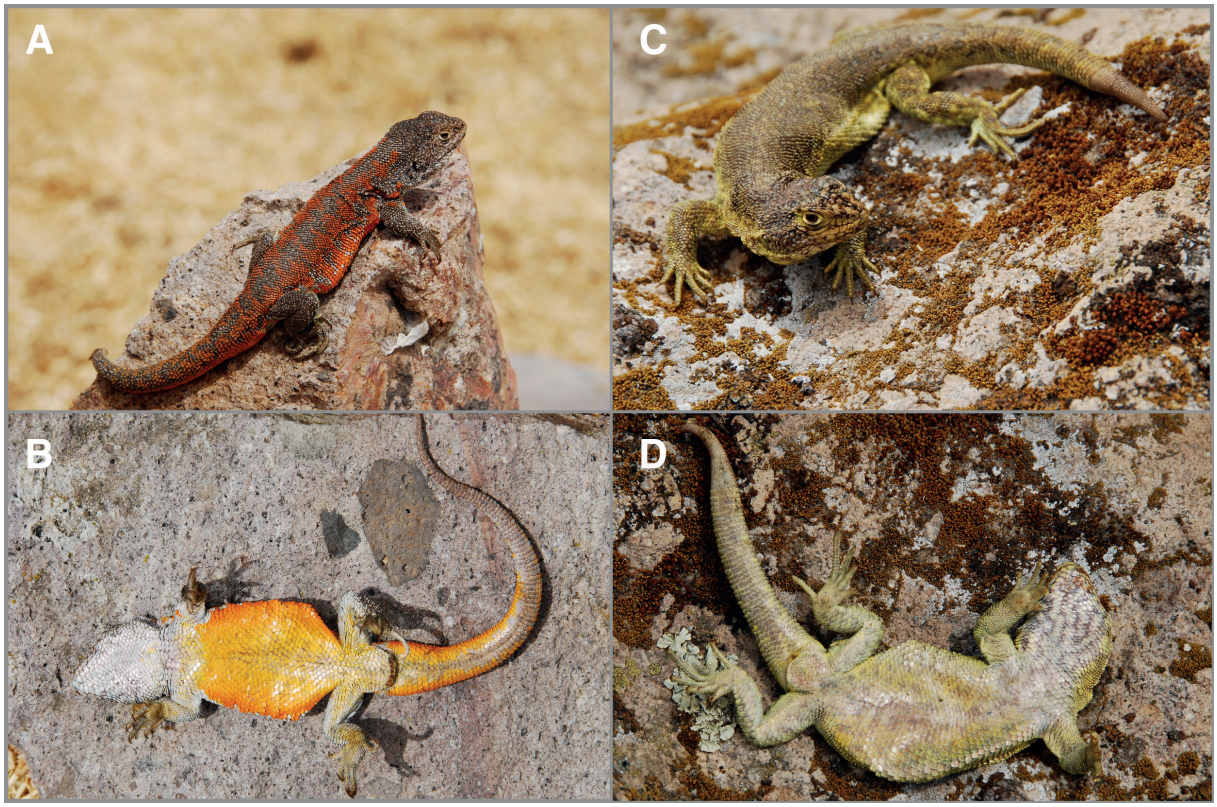

Figure 4. Holotype of *Liolaemus yawar* **sp. nov.** [MUSA 5603 (CSA 1516); adult male, SVL = 90.09 mm]: dorsal view **(A)** and ventral view **(B)**. Paratype [FML (CSA 1519); adult female, SVL = 82.3 mm]: dorsal view **(C)** and ventral view **(D)**. Photos by C. S. Abdala.

Figura 4. Holotipo de *Liolaemus yawar* **sp. nov.** [MUSA 5603 (CSA 1516); macho adulto, SVL = 90.09 mm]: vista dorsal **(A)** y vista ventral **(B)**. Paratipo [FML (CSA 1519); hembra adulta, SVL = 82.3 mm]: vista dorsal **(C)** y vista ventral **(D)**. Fotografías de C. S. Abdala.

system; 4132 m a.s.l. Fig. 4); Collected by Cristian S. Abdala, Romina V. Semhan, José L. Acosta, Roberto C. Gutiérrez, and Sebastián Barrionuevo, on 17 november 2013.

Paratypes.— MUSA 5602, MUBI 2501, FML (CSA 1522–23) adult males, MUSA 5604–05, FML (CSA 1519–20) adult females, FML (CSA 1524), FML (CSA 1527), MUBI 2502 juveniles, same data as holotype.

⋆ FML specimens with field collection number pending assignment.

Diagnosis.— *Liolaemus yawar* **sp. nov.** belongs to the subgenus *Eulaemus*, and within it, to the *L. montanus* group, based on the presence of a blade-like distal posterior process on the tibia associated with hypertrophy of the *tibialis anticus* muscle (Etheridge, 1995; Abdala et al., 2006). It differs from the species of the *L. boulengeri* group (Abdala, 2007; Schulte et al., 2000) by having posterior thigh scales of uniform size. Within the *L. montanus* group, *L. yawar* **sp. nov.** is a robust lizard (maximum snout vent-length [SVL_{max}] = 91.6 mm), differing in size from *L. andinus*, *L. anqapuka*, *L. audituvelatus*, *L. balagueri*, *L. cazianiae*, *L. chiribaya*, *L. duellmani*, *L. eleodori*, *L. erroneus*, *L.*

etheridgei, *L. evaristoi*, *L. fabiani*, *L. famatinae*, *L. fittkaui*, *L. foxi*, *L. gracielae*, *L. griseus*, *L. hajeki*, *L. halonastes*, *L. huacahuasicus*, *L. insolitus*, *L. kunza*, *L. lilloi*, *L. montanus*, *L. multicolor*, *L. nazca*, *L. orko*, *L. omorfi*, *L. ortizi*, *L. pantherinus*, *L. poconchilensis*, *L. poecilochromus*, *L. porosus*, *L. pulcherrimus*, *L. reichei*, *L. robertoi*, *L. rosenmanni*, *L. ruibali*, *L. salitrosus*, *L. schmidti*, *L. stolzmanni*, *L. tajzara*, *L. thomasi*, *L. terani*, *L. torresi*, *L. vallecurensis*, *L. williamsi*, and *L. yarabamba*, all of which are smaller (SVL = 50–80 mm).

The presence strongly keeled dorsal body scales distinguishes *L. yawar* **sp. nov.** from species with smooth scales, including *L. andinus*, *L. anqapuka*, *L. audituvelatus*, *L. balagueri*, *L. cazianiae*, *L. chiribaya*, *L. eleodori*, *L. fabiani*, *L. foxi*, *L. gracielae*, *L. halonastes*, *L. insolitus*, *L. jamesi*, *L. kunza*, *L. nigriceps*, *L. omorfi*, *L. patriciaiturrae*, *L. pleopholis*, *L. poconchilensis*, *L. poecilochromus*, *L. porosus*, *L. reichei*, *L. robertoi*, *L. robustus*, *L. rosenmanni*, *L. ruibali*, *L. salitrosus*, *L. schmidti*, *L. scrocchii*, *L. terani*, *L. torresi*, *L. vallecurensis*, and *L. vulcanus*. *Liolaemus yawar* **sp. nov.** lacks sky-blue scales on the lateral and dorsal surfaces of the body and tail, distinguishing it from *L. basadrei*, *L. chiribaya*, *L. evaristoi*, *L. etheridgei*, *L. insolitus*, *L. multicolor*, *L. omorfi*, *L. poconchilensis*, *L. pulcherrimus*, *L. robertoi*, *L. ruibali*, *L. schmidti*, and *L. yarabamba*.

The number of midbody scales (69–78; mean = 73.2) separates *L. yawar* **sp. nov.** from species with consistently higher counts (means > 85), such as *L. andinus*, *L. eleodori*, *L. gracielae*, *L. halonastes*, *L. nigriceps*, *L. patriciaiturrae*, *L. porosus*, *L. robertoi*, *L. rosenmanni*, *L. vallecurensis* , and those with lower means (< 68), such as *L. annectens*, *L. aymararum*, *L. chlorostictus*, *L. dorbignyi*, *L. etheridgei*, *L. fabiani*, *L. famatinae*, *L. fittkaui*, *L. griseus*, *L. hajeki*, *L. huayra*, *L. huacahuasicus*, *L. igneus*, *L. inti*, *L. jamesi*, *L. lilloi*, *L. melanogaster*, *L. montanus*, *L. orko*, *L. ortizi*, *L. pachecoi*, *L. pantherinus*, *L. poconchilensis*, *L. polystictus*, *L. puritamensis*, *L. qalaywa*, *L. robustus*, *L. scrocchii*, *L. tacora*, *L. thomasi*, *L. victormoralesii*, *L. vulcanus*, *L. warjantay*, and *L. williamsi*.

The number of ventrals from the mental and the cloaca (70–80; mean = 74.8) in *L. yawar* **sp. nov.** is lower than in species with higher counts (means > 85), including *L. andinus*, *L. annectens*, *L. audituvelatus*, *L. cazianiae*, *L. chlorostictus*, *L. eleodori*, *L. erroneus*, *L. foxi*, *L. gracielae*, *L. hajeki*, *L. halonastes*, *L. hauthali*, *L. huayra*, *L. inti*, *L. kunza*, *L. multicolor*, *L. multiformis*, *L. nigriceps*, *L. pachecoi*, *L. patriciaiturrae*, *L. pleopholis*, *L. poecilochromus*, *L. porosus*, *L. robertoi*, *L. rosenmanni*, *L. salitrosus*, *L. torresi*, *L. vallecurensis*; and higher than species with mean counts below 70, such as *L. ortizi* and *L. thomasi.*

The dorsal scale counts (74–84; mean = 78.7) further separates *L. yawar* **sp. nov.** from species with higher mean values (> 85), such as *L. andinus*, *L. cazianiae*, *L. eleodori*, *L. erroneus*, *L. forsteri*, *L. gracielae*, *L. halonastes*, *L. nigriceps*, *L. patriciaiturrae*, *L. pleopholis*, *L. poecilochromus*, *L. porosus*, *L. pulcherrimus*, *L. robertoi*, *L. rosenmanni*, *L. schmidti*, *L. torresi*, *L. vallecurensis,* and lower values (< 70) found in *L. aymararum*, *L. chiribaya*, *L. chlorostictus*, *L. dorbignyi*, *L. etheridgei*, *L. fittkaui*, *L. griseus*, *L. hajeki*, *L.*

huayra, *L. huacahuasicus*, *L. igneus*, *L. inti*, *L. jamesi*, *L. lilloi*, *L. melanogaster*, *L. montanus*, *L. nazca*, *L. ortizi*, *L. pachecoi*, *L. poconchilensis*, *L. polystictus*, *L. puritamensis*, *L. qalaywa*, *L. robustus*, *L. scrocchii*, *L. tacora*, *L. thomasi*, *L. victormoralesii*, *L. vulcanus*, *L. warjantay*, *L. williamsi*, and *L. yauri*.

Among four examined females of *L. yawar* **sp. nov.**, only one exhibited a precloacal pore (range = 0–1). This contrasts with species where females consistently show numerous precloacal pores, such as *L. aymararum*, *L. cazianiae*, *L. chiribaya*, *L. chlorostictus*, *L. dorbignyi*, *L. eleodori*, *L. erroneus*, *L. etheridgei*, *L. fabiani*, *L. famatinae*, *L. griseus*, *L. hajeki*, *L. hauthali*, *L. huayra*, *L. huacahuasicus*, *L. inti*, *L. jamesi*, *L. lenzi*, *L. montanus*, *L. multiformis*, *L. nazca*, *L. nigriceps*, *L. orko*, *L. pachecoi*, *L. pantherinus*, *L. patriciaiturrae*, *L. porosus*, *L. pulcherrimus*, *L. qalaywa*, *L. scrocchii*, and *L. vulcanus*.

Phenotypically, the new species is similar to *L. forsteri*; however, it can be distinguished because its males have greater NW, AL, FT-iv, and FOL but a shorter HDL than *L. forsteri* (Table 2, Table S5). Furthermore, it differs by having lower scale counts in DH, DS, V, and T compared to *L. forsteri* (Table 3, Table S9). The distinct combination of coloration pattern traits observed in both males and females of *Liolaemus yawar* **sp. nov.** clearly distinguishes it from all other known species of the genus.

Description of the holotype.— Adult male, MUSA 5603 (CSA 1516). Snout-vent length 90.09 mm. Head 1.03 times longer (21.77 mm) than wide (21.06 mm); head height 12.21 mm. Neck width 21.02 mm. Eye diameter 3.99 mm. Interorbital distance 10.01 mm. Orbit-auditory meatus distance 8.96 mm. Auditory meatus 4.30 mm height, 2.86 mm width. Orbit-commissure of mouth distance 7.92 mm. Internasal distance 2.81 mm. Subocular length 5.19 mm. Trunk length 40.72 mm, trunk width 31.26 mm. Tail length 103.9 mm. Thigh length 15.18 mm, shank length 17.37 mm, and foot length 24.34 mm. Arm length 18.37 mm, forearm length 12.19 mm, and hand length 10.79 mm. Pygal region length 8.72 mm; cloacal flap width 8.47 mm. Dorsal surface of head rugose, with 18 scales. Rostral scale 3.06 times longer (4.01 mm) than wide (1.31 mm). Mental scale triangular, slightly longer (4.06 mm) than rostral, in contact with four adjacent scales. A single scale separates rostral from the nasal. Two internasals, slightly longer than wide. Nasal surrounded by six scales and separated from the canthals by two scales. Seven scales between the frontal and rostral. Frontal divided into five scales. Interparietal slightly longer than the parietals, in contact with seven scales. One lorilabial row separates preoculars from supralabials. Five superciliaries, and 15 upper ciliaries. Anterior margin of auditory meatus with five differentiated scales. Ten temporals. Five lorilabials in contact with the subocular. Seven supralabials, not in contact with the subocular. Five supraoculars. Nine lorilabials. Six infralabials. Five pairs of chinshields; the fourth pair separated by six scales. Seventy-two scales around midbody. Dorsal scales between occiput and hind limb insertion 65, triangular, subjuxtaposed, leaf-shaped, and strongly keeled. Anterior scales

of forelimbs and hind limbs laminar, imbricate and keeled. Dorsal tail scales triangular, imbricated, and keeled. Seventy-seven ventral scales from mental to cloaca opening, laminar and imbricated. Forty-two gulars, imbricate, and smooth. Neck fold composed of 46 conical, non-keeled scales. Auricular and antehumeral folds present; gular fold incomplete. Ventral surface of forelimbs with laminar, subjuxtaposed to imbricate, smooth scales; hind limbs ventral scales laminar, imbricate, and unkeeled. Fourteen subdigital lamellae on the fourth finger. Twenty subdigital lamellae of the fourth toe, each with three keels. Tarsal scales keeled. Ventral caudal scales laminar and imbricate; smooth on the proximal third, slightly keeled on distal two-thirds. Seven precloacal pores. Supernumerary pores present.

Color of holotype in life.— Head background ranging from brownish olive to blackish, distinctly darker than the rest of the body. Subocular scale whitish, lighter than the loreolabials, supralabials, and infralabials, which display a pale buff tone. Temporal region similar in color to the dorsal head background. Neck cinnamon-drab, with lighter lateral surfaces. Dorsal body background is also cinnamon-drab, bearing large, bright to burnt orange paravertebral blotches. These paravertebral blotches merge laterally with blotches of the same color, giving the individual an overall intensely reddish appearance. Paravertebral blotches not fused within the vertebral field, which is dark and irregular, forming a middorsal series of continuous rhomboid-like shapes sparsely speckled with white. Forelimbs and hind limbs are similar in color to the vertebral field but lack contrasting speckles. Tail is similar in pattern and coloration to the body dorsum. Ventral surfaces of chin, gular region, and chest white; belly, pygal region, limbs, cloaca flap and proximal tail orange-yellowish, with coloration becoming more intense along the margins. Ventral surface of the distal end of tail dirty dark gray (Fig. 4A and B).

Color of holotype in preservative.— Overall coloration of the holotype is largely retained after fixation and preservation in ethanol. Dark gray to brownish coloration of the head, neck and vertebral field mostly conserved. Whitish subocular remains distinguishable, slightly darkened. Paravertebral and lateral blotches washed off; bright orange tones replaced by dull brownish-pink, reducing contrast with dark dorsal background. Whitish scales in vertebral field are still visible but less conspicuous. Dorsal surfaces of the limbs retain general dark coloration. Belly, limbs, pygal region, and cloacal flap have lost original intense orange, now appearing pale bluish-gray (Fig. 5A and B, see asterisk symbols).

Variation in morphology.— Based on nine adult specimens (5 males and 4 females). Variation in morphometric and meristic characters for males and females is summarized in Table 2 and 3.

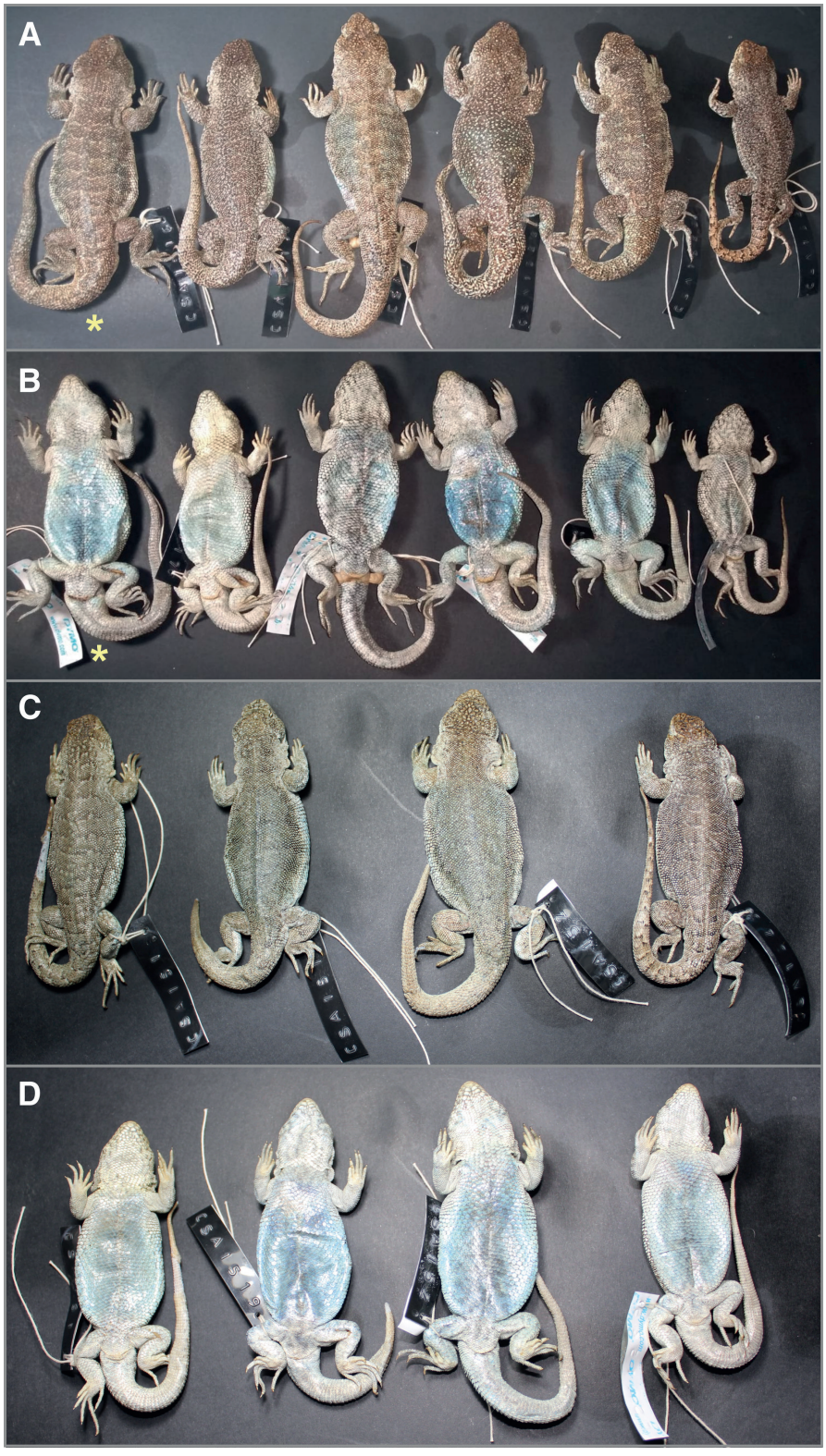

Figure 5. Type series of *Liolaemus yawar* **sp. nov.** Adult males in dorsal view **(A)** and ventral view **(B)**; adult females in dorsal view **(C)** and ventral view **(D)**. The holotype is indicated by an asterisk.

Figura 5. Serie tipo de *Liolaemus yawar* **sp. nov.** Machos adultos en vista dorsal **(A)** y vista ventral **(B)**; hembras adultas en vista dorsal **(C)** y vista ventral **(D)**. El holotipo está indicado con un asterisco.

Variation in color pattern.— Sexual dichromatism is evident. Adult males: Head background and temporal region ranging from gray to dark brown, always darker than the body color. In most individuals, the lorilabials, supralabials, and infralabials are lighter than the rest of the head. Subocular whitish, irregularly scattered with dark gray. Neck coloration resembles the body dorsum; neck sides and scapular region gray or light brown. Body dorsum dark gray, occasionally turning brownish or displaying yellowish hues. Distinct paravertebral blotches of intense orange or bright yellow, forming transverse bars or thick lines merged to lateral blotches of same coloration, often more rounded. Background coloration of the dorsum restricted to the vertebral region and narrow interspaces between paravertebral spots, with dark gray. Vertebral region irregular, decorated with small, randomly distributed whitish-yellow spots. The vertebral line, dorsolateral bands, antehumeral arch, scapular spots, and light-blue speckles are absent. The forelimb and hind-limb patterns are similar to the body dorsum. The tail pattern is similar to the dorsum, but the paravertebral blotches merge into a single mid-dorsal stripe. Ventral ground coloration whitish on chinshields, gular and upper chest region; bright yellow on lower chest, belly, pygal region, cloacal flap and limbs (Fig. 4A and B, Fig. 5A and B). Adult Females: Head background ranging from gray to dark brown, irregularly scattered with black. Supralabials, infralabials and lorilabials lighter than head background, predominantly yellowish or greenish-gray. Body dorsum ranging from gray to brown, decorated with small, inconspicuous subquadrangular or rounded paravertebral spots, often scattered with pale whitish speckles. The body flanks are striking, displaying varying hues of yellow. Some individuals exhibit lateral blotches similar in shape and color pattern to paravertebrals. The vertebral line and dorsolateral bands are absent. The forelimb, hind-limb, and tail patterns are similar to the body dorsum. Ventral ground color white, with light sulphur yellow to light greenish yellow along the margins (Fig. 4C and D, Fig. 5C and D). Juveniles: Body dorsum decorated with randomly distributed yellow speckles. Ventrolateral margin with an orangey longitudinal stripe extending from axilla to groin.

Etymology.— The specific epithet *'yawar'* comes from the Quechua word for 'blood', referring primarily to the striking blood-red coloration exhibited by adult males, arguably the most distinctive diagnostic trait of this new species. Beyond its descriptive value, the name carries deep cultural resonance in the Andean world, where yawar appears in the name of the Inca ruler Yawar Huaca ("He Who Weeps Blood"), a figure whose story was recorded by the chronicler Inca Garcilaso de la Vega in *Comentarios Reales de los Incas* (Ardito & Castro, 2024). Tradition holds that the young prince was given this name after shedding tears of blood as a child, an event regarded at the time as a powerful omen. Thus, the epithet not only emphasizes one of the species' most striking diagnostic characters but also

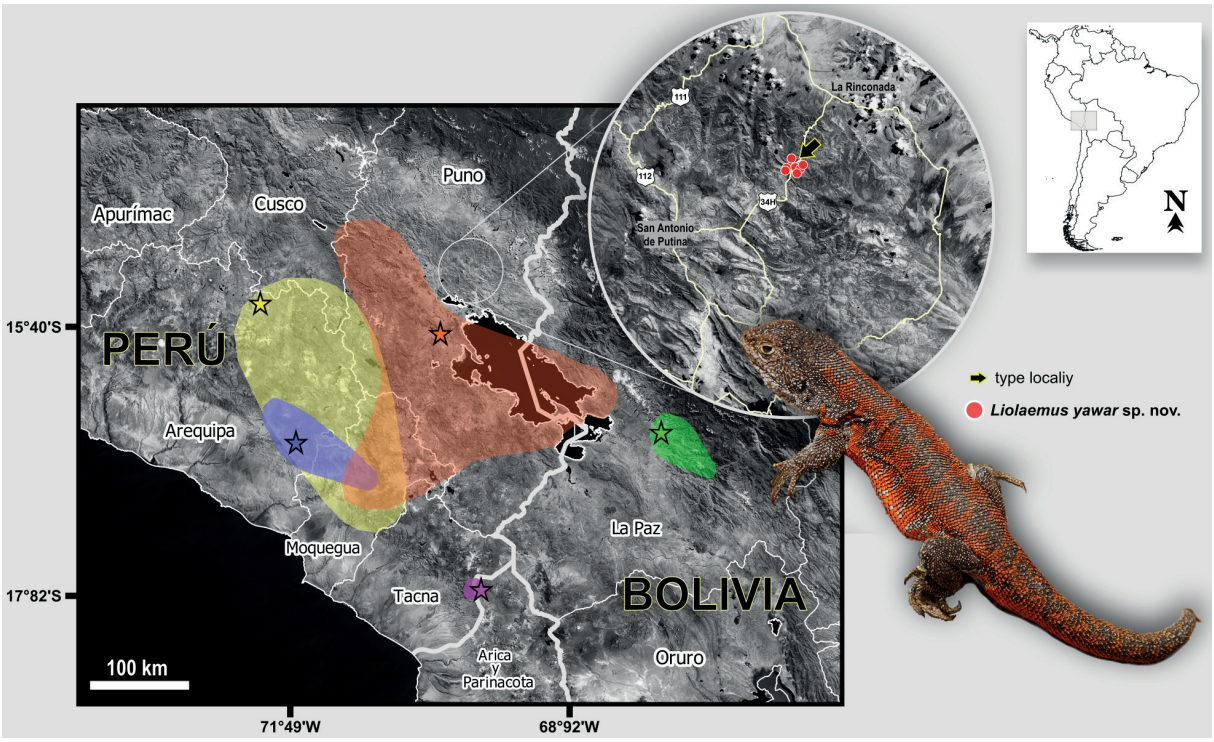

Figure 6. Geographic distribution of *Liolaemus yawar* **sp. nov.** (red dots) and ranges of phylogenetically related species: *L. annectens* (yellow), *L. etheridgei* (electric blue), *L. forsteri* (green); *L. multiformis* (orange) and *L. tacora* (magenta). Colored stars indicate type localities of the respective species. The black arrow outlined in yellow indicates the type locality of the new taxon (14º48'34.60" S, 69º39'0.00" W).

Figura 6. Distribución geográfica de *Liolaemus yawar* **sp. nov.** (puntos rojos) y áreas de distribución de especies filogenéticamente relacionadas: *L. annectens* (amarillo), *L. etheridgei* (azul eléctrico), *L. forsteri* (verde); *L. multiformis* (naranja) y *L. tacora* (magenta). Las estrellas de colores indican las localidades tipo de las especies respectivas. La flecha negra contorneada en amarillo indica la localidad tipo del nuevo taxón (14º48'34.60" S, 69º39'0.00" W).

honors the linguistic and cultural heritage of the Quechua language, spoken throughout much of the central Andes, including the region where this species occurs.

Distribution and natural history.— *Liolaemus yawar* **sp. nov.** is known only from its type locality, along the road between San Antonio de Putina and Mina Rinconada, Department of Puno, Peru, at elevation of 4132 m a.s.l. (Fig. 6). Based on its phylogenetic placement within the *L. montanus* group, the species is presumed to be viviparous. It inhabits Andean grassland environments along the western Andean and inter-Andean slopes and Puna (MINAM, 2015). It is a terrestrial species and moves among medium size rocks; several individuals were observed sheltered in burrows at the base of stones (Fig. 7). Other aspects of its natural history remain unknown.

Figure 7. Overview of the habitat (type locality) of *Liolaemus yawar* **sp. nov.**, photographed on 17 November 2013 along National Road 34H, approximately 9 km past Señor de la Exaltación de Chipalca, District of Putina, Puno Department, Peru, at 4132 m a.s.l. Photo by C. S. Abdala.

Figura 7. Vista general del hábitat (localidad tipo) de *Liolaemus yawar* **sp. nov.**, fotografiada el 17 de noviembre de 2013 a lo largo de la Ruta Nacional 34H, aproximadamente 9 km después de Señor de la Exaltación de Chipalca, distrito de Putina, departamento de Puno, Perú, a 4132 m s. n. m. Fotografía de C. S. Abdala.

DISCUSSION

Liolaemus, after *Pristimantis*, *Anolis*, and *Cyrtodactylus*, ranks among the most species-rich living tetrapod genera (Padial et al., 2014; Poe et al., 2017; Abdala et al., 2021c; Grismer et al., 2021; Frost, 2024). Although the greatest known richness occurs in Argentina and Chile, the diversity of *Liolaemus* in Peru has historically been understudied and poorly documented. In recent years, however, focused research has led to a remarkable increase in the number of recognized species along both the Peruvian coast and in the high Andes (Chaparro et al., 2020; Huamani-Valderrama et al., 2020; Villegas Paredes et al., 2020; Abdala et al., 2021b; Arapa-Aquino et al., 2021; Quiroz et al., 2021; Ubalde-Mamaní, 2021; Valladares et al., 2021; Santa Cruz et al., 2025). As a result, the description of twelve new species has raised the currently recognized *Liolaemus* species count in Peru to 25, significantly altering our understanding of the genus in the country.

The phylogenetic diversity of *Liolaemus*, as reflected in several hypotheses, has prompted the division of the genus into subgenera, sections, groups, clades, subclades, and species complexes (Abdala et al., 2021b, 2021c). These frameworks have proven largely congruent, resulting in the recognition and consistent implementation of natural species groups (Schulte et al., 2000; Lobo, 2001, 2005; Morando et al., 2003, 2004; Avila et al., 2006; Abdala, 2007; Quinteros et al., 2008; Abdala et al., 2020, 2021a, 2021d). Among these, the *Liolaemus montanus* group stands out for its rapid increase in recognized taxonomic diversity. In the recent years, taxonomic efforts have resulted in the description of 22 new species within this group, including *L. anqapuka* (Huamaní-Valderrama et al., 2020), *L. balagueri* (Villegas Paredes et al., 2020), *L. basadrei* (Valladares-Faúndez et al., 2021), *L. cazianiae* and *L. halonastes* (Lobo et al., 2010), *L. chiribaya*, *L. nazca,* and *L. victormoralesii* (Aguilar-Puntriano et al., 2019), *L. evaristoi* (Gutiérrez et al., 2018), *L. hauthali* and *L. terani* (Abdala et al., 2021a), *L. kunza* and *L. salitrosus* (Abdala et al., 2021d), *L. lilloi* (Abdala et al., 2025), *L. omorfi* (Demangel et al., 2015), *L. porosus* (Abdala et al., 2013), *L. qalaywa* (Chaparro et al., 2020), *L. tajzara* (Abdala et al., 2019), *L. vulcanus* (Quinteros & Abdala, 2011), *L. warjantay* (Ubalde-Mamani et al., 2021), *L. yarabamba* (Quiroz et al., 2021) and *L. yauri* (Arapa-Aquino et al., 2021). These new taxa represent approximately one-third of the total known diversity of the *L. montanus* group.

In the department of Puno, southern Peru, current records indicate the presence of 38 squamate species, of which 19 are lizards. Among these, three are assigned to the genus *Liolaemus*, and only one belongs to the *L. montanus* group. The recent revision by Langstroth Plotkin (2021), has profoundly reshaped the taxonomy of the *L. montanus* group, with far-reaching implications for understanding species diversity and distributions in Peru. Prior to this work, *L. signifer* was considered the dominant species across Puno department; however, it was later deemed a *nomen nudum*;

L. tropidonotus was synonymized with *L. multiformis*, and *L. lenzi* was revalidated. This new taxonomic arrangement compels a reanalysis of populations previously assigned to these names, and subsequent systematic studies are likely to reveal previously unrecognized diversity hidden within the *L. montanus* group.

The new species described herein, *Liolaemus yawar* **sp. nov.**, exhibits a unique combination of morphological characters. Its large body size, high number of midbody scales, small dorsal body scales, and striking coloration pattern suggests a similarity with *L. forsteri* and other populations of uncertain taxonomic status that exhibit similar traits. This observation is consistent with the Total Evidence phylogenetic hypothesis proposed by Abdala et al. (2020), in which *L. yawar* **sp. nov.** was recovered within the *L. forsteri* clade, likely reflecting the phenotypic similarity among the representatives of that group. In addition to the disjunct distribution of more than ~200 km between *L. yawar* **sp. nov.** and *L. forsteri* (See Fig. 6), the presence of numerous autapomorphies strongly supports the recognition of *L. yawar* **sp. nov.** as an independent evolutionary lineage. Although it shares phenotypic similarities with *L. forsteri* and morphologically similar populations of uncertain taxonomic status, our molecular phylogenetic analysis places *L. yawar* **sp. nov.** not only as closely related to species within the *L. forsteri* clade, but also as allied with species belonging to the *L. huacahuasicus* clade (*L. annectens* + *L. tacora*). In addition, the genetic distances observed among these phylogenetically related species are greater than those reported in other studies involving species of the *L. montanus* group (e.g., cyt $b < 2\%$; see Olave et al., 2014; Ruiz De Gamboa et al., 2018). These findings highlight the complexity of morphological convergence within the *L. montanus* group and underscore the importance of integrating molecular data to resolve species boundaries and elucidate evolutionary relationships.

The phylogenetic analyses of Abdala et al. (2020, 2021a, 2021d) also identified several unnamed populations in the intervening region, whose taxonomic status remains unresolved. Detailed morphological studies of these populations are needed to clarify their identity. Further fieldwork north of the type locality of *L. yawar* **sp. nov.** is essential to determine the full extent of the species' distribution and to assess the taxonomic status of morphologically similar populations (Langstroth, pers. comm.). These poorly known populations, which includes additional undescribed species, appear to extend into northern Bolivia and southeastern Peru, consistently occupying high Andean environments above 3500 m a.s.l.

CONCLUSION

The recognition of *Liolaemus yawar* **sp. nov.** provides further evidence that the diversity of the *Liolaemus montanus* group remains incompletely understood, particularly in the high Andes of southern Peru and neighboring Bolivia. By integrating molecular, phylogenetic, and morphological evidence, this study demonstrates that *L. yawar* sp. nov. represents a distinct evolutionary lineage and reinforces the importance of an integrative taxonomic framework for resolving species limits in morphologically similar groups. Rather than relying on a single source of evidence, the congruence among independent datasets provides a robust foundation for the taxonomic hypothesis proposed here.

Our results also highlight that the current knowledge of Andean *Liolaemus* diversity is still far from complete. The existence of several geographically intermediate populations whose taxonomic status remains unresolved strongly suggests that additional undescribed species are likely to occur throughout the central Andes. Continued field surveys, broader geographic sampling, and the integration of molecular and phenotypic datasets will be essential for refining our understanding of the evolutionary history, diversification, and biogeographic patterns of one of the most remarkable reptile radiations in South America.

Beyond its systematic contribution, this study emphasizes the urgency of documenting Andean biodiversity while there is still time to do so. High-elevation ecosystems are increasingly affected by mining expansion, road construction, overgrazing, and the growing impacts of climate change, all of which are transforming landscapes that harbor highly specialized and geographically restricted species. These pressures are already causing habitat degradation, population declines, and, in some cases, local extirpations. In this context, taxonomy becomes much more than the formal description of species; it provides the fundamental knowledge upon which ecological research, conservation planning, and biodiversity management depend. As human activities continue to reshape the Andes, the opportunity to discover and understand their unique evolutionary heritage is rapidly diminishing. Recognizing and documenting this diversity before it is irreversibly lost represents one of the most important challenges facing contemporary herpetology.

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CREDIT AUTHORSHIP CONTRIBUTION STATEMENT

Cristian S. Abdala designed the study, participated in the sampling and analysis of samples, wrote the original draft of the manuscript, methodology, results analysis, visualization, validation, and funding acquisition. **Alejandro Laspiur** participated in the study design, wrote the original draft and final version of the manuscript, methodology, data curation, designed statistic framework for morphological analysis, visualization, designed and constructed the tables and figures, and validation. **Álvaro Aguilar-Kirigin** participated in the study design, wrote the original draft of the manuscript, methodology, data curation, morphological analysis, investigation, and validation. **Ling Huamaní-Valderrama** participated in the study design, contributed to methodology, data curation, investigation, and validation. **Sebastián A. Quinteros** participated in the study design, wrote the original draft of the manuscript, participated in methodology, molecular phylogenetic analysis, data curation, investigation, and validation. **Romina V. Semhan** participated in the study design, sampling, methodology, investigation, and validation. **Roberto C. Gutiérrez Poblete** participated in

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DECLARATION OF COMPETING INTEREST

The authors report no competing interests to declare.

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APPENDIX I

List of specimens examined

Liolaemus annectens (n = 15). **PERU: Arequipa:** Sumbay: MUSA 4114, 4265–66; Caylloma: MUSA 1591–97, 4344–48.

Liolaemus anqapuka (n = 21). **PERU: Arequipa:** Uchumayo: MUBI 13521–22, MUSA 4131, 4133–34; Arequipa: Uchumayo: Quebrada Tinajones, LSF 001–2, MUBI 14680, MUSA 1766–67, MUSA 4545, MUSA 5207–12, MUSA 5214; Uchumayo: between Quebrada Tinajones and Quebrada San José: MUSA 5573–75.

Liolaemus balagueri (n = 18). **PERU: Arequipa:** Camaná: Quilca: Lomas de Quilca: MUBI 13206–09, 16483–84, MUSA 1772–74, 5575–78, MUSM 39193–95; Camaná: Lomas de La Chira: MUSM 5579, MUSM 39192.

Liolaemus basadrei (n = 4). **PERU: Tacna:** Jorge Basadre: Locumba valley: HP-CBT 20-23.

Liolaemus chiribaya (n = 11). **PERU: Moquegua:** Mariscal Nieto: Torata: Jaguay Chico: MUSA 31548–50, MUSA 31553; Mariscal Nieto: Torata: Cerro los Calatos: MUSM 31386, MUSM 31388–91, MUSM 31547; Mariscal Nieto: between Moquegua and Torata: MUSM 31387.

Liolaemus etheridgei (n = 17). **PERU: Arequipa:** Cabrerías: Cayma: MUSA 501; Cayma: Cerro Uyupampa: Sabandia: MUSA 549–54; Pocsi: Monte Ribereño de la Quebrada de Tilumpaya-Chiguata: MUSA 1113–14, MUSA 1116, MUSA 1264–68, MUSA 1353; Yura: Anexo de Yura Viejo: MUSA 1229.

Liolaemus evaristoi (n = 16). **PERU: Huancavelica:** Huaytara: Pilpichaca: Los Libertadores: MUSA 2841, 2781–85, 2840, 2842–45; MUBI 10474–78.

Liolaemus forsteri (n = 31). **BOLIVIA: La Paz:** Murillo: Chacaltaya: CBF 1056, CBF 3126–27; Murillo: Alto Milluni: CBF 2482–84, CBF 3064–65, CBF 3070, CBF 3106, CBF 3108–10, CBF 3114; CBF 2485, CBF 2703, CBF 2708, CBF 3052–55, CBF 3057–58, CBF 3061, CBF 3117, CBF 3123–24, CBF 3149, CBF 3154, CBF 3158, CBF 3163.

Liolaemus insolitus (n = 19). **PERU: Arequipa:** Dean Valdivia Islay: Mejía: Lomas de Mejía: MUSA 346, MUSA 1741, MUSA 2187–90; Mejía: Lomas de Challascapa: Quebrada Quialaque: MUSA 313–15, MUSA 320–24, MUSA 448; Mollendo: Alto Inclan: MUSA 4787–88, MUSA 4812, MUSA 4815.

Liolaemus melanogaster (n = 12). **PERU: Arequipa:** Laguna de Corococha, Orcopampa, MUSA 372–76; **Ayacucho:** 45 Km east E Puquio: FML 2491; **Huancavelica:** Huancavelica: 1 Km. SW Betania: MUSA 2762–67.

Liolaemus multiformis (n = 11). **PERU: Puno:** Titicaca Lake: FML 1434; Titicaca Lake, road to Puno: FML 1557; near Tirapata: MUSA 1415; Huancané: Taurahuta community: MUSA 1441–43; Huerta Huayara community: 3 Km before Puno: MUSA 1483–87.

Liolaemus nazca (n = 7). **PERU: Ica:** Nazca: MUSM 16100, MUSM 31520–21, MUSM 31523, MUSM 31525–26, MUSM 31541.

Liolaemus qalaywa (n = 28). **PERU: Apurimac:** Choaquere: MUBI 13286, MUBI 12096–99, MUBI 12100–12104; Ñahuinlla: MUBI 13260, MUBI 13264–65; Progreso: MUBI 12981–83: Punchayoc Ccasa: MUBI 17621; Ccosana: MUBI 17622–23; Pumamarca: MUBI 13287, MUSA 5600; Chila: MUBI 12081, MUBI 12084, MUSA 5601; Ccomerococha: MUBI 15900–03.

Liolaemus ortizi (n = 3). **PERU: Cusco:** Huacoto: MUSA 1432; Santa Barbara: MUSA 1443, MUSA 1511.

Liolaemus poconchilensis (n = 4). **PERU: Tacna:** Morro Sama: Las Yaras: MUSA 1428–29, MUSA 1638–39.

Liolaemus polystictus (n = 13). **PERU: Huancavelica:** Pilpichaca: mountain near Rumichaca: MUSA 1337–38; Santa Inés: FML 1683; Santa Inés: Castrovirreyna: MUSA 2448–57.

Liolaemus robustus (n = 11). **PERU: Lima:** Surroundings of Huancaya: Reserva Paisajística Nor Yauyos Cochas: MUSA 1693–1702; **Junín:** Junín: FML 1682.

Liolaemus tacora (n = 10). **CHILE: Arica y Parinacota:** Volcán Tacora, CSA 11340-42; **PERÚ: Tacna:** Nevado Chipiquiña: RGP 6199-203, RGP 6341, RGP 6346.

Liolaemus thomasi (n = 16). **PERU: Cusco:** after Mahuayani pass: MUSA 1398–412; Pampacancha Quispicanchi: MUBI 5925.

Liolaemus warjantay (n = 11). **PERU: Arequipa:** La Unión: Pampamarca: MUBI 17683–84, MUSA 5691–94, MUSA 5696, MUSA 5698, MUSA 5700–02.

Liolaemus williamsi (n = 15). **PERU: Ayacucho:** Lucanas: Pampa Galeras: MUSA 1519–31, FML 1701, FML 13403.

Liolaemus yarabamba (n = 5). **PERU: Arequipa:** Yarabamba: MUSA 5570, MUSA 501, MUSA 178–79, MUBI 17663.

Liolaemus yauri (n = 11). **PERU: Cusco:** Vizcachane: MUSA 5672, MUSA 5670–71, 5673–74; Huano Huano: MUBI 2500, MUBI 15899, MUSA 5675–78.

SUPPLEMENTARY MATERIAL

Tables S1, S2, S3, S4, S5, S6, S7, S8, and S9: https://www.lillo.org.ar/journals/index.php/acta-zoologica-lilloana/article/view/2503/2213