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A new species of the *Liolaemus nigroviridis* group from the Andes of Central Chile (Iguania: Liolaemidae)

Una nueva especie del grupo de *Liolaemus nigroviridis* de los Andes de Chile central (Iguania: Liolaemidae)

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ABSTRACT

Species of the *Liolaemus nigroviridis* group are robust lizards with a medium body size, whose males usually exhibit striking coloration patterns in green, yellow, orange or blue colors, accompanied by black stripes. All species of this group are endemic to central Chile, distributed along the Andean and Coastal mountain ranges. Several DNA phylogenetic studies have pointed out that the nominal species of this group, *L. nigroviridis*, is indeed a species complex, formed by *L. nigroviridis* and other lineages that could constitute candidate species. Here we review the taxonomic status of one of these lineages, whose previous record was based mainly on juvenile specimens. However, the examination of adult specimens allows us to conclude that this lineage should be described as a new species, in which males have a very remarkable dorsal color pattern. We also propose the revalidation of the taxon formerly known as *L. nigroviridis campanae* to full species status.

Keywords — Endemism, Valparaíso Region, Principal component analysis, Cyt-b, mtDNA, Coloration pattern.

RESUMEN

Las especies del grupo de *Liolaemus nigroviridis* son lagartijas robustas y de tamaño mediano, cuyos machos usualmente presentan llamativos patrones de coloración,

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con colores verdes, amarillos, anaranjados o azules, acompañadas por líneas negras. Todas las especies de este grupo son endémicas de Chile central, distribuidas en las montañas de la costa y de los Andes. Varios estudios filogenéticos basados en ADN han señalado que la especie nominal de este grupo, *L. nigroviridis*, es en realidad un complejo de especies, conformado por *L. nigroviridis* y otros linajes que constituyen especies candidatas. Nosotros revisamos el estatus taxonómico de uno de estos linajes, cuyos registros previos estaban basados principalmente en juveniles. Sin embargo, la revisión de especímenes adultos nos permitió concluir que este linaje debería ser descrito como una especie nueva, cuyos machos presentan un diseño de coloración dorsal muy llamativo. También proponemos la revalidación como especie del taxón anteriormente conocido como *L. nigroviridis campanae*.

Palabras clave — Endemismo, Región de Valparaíso, Análisis de Componentes Principales, Cyt-b, mtADN; Patrón de coloración.

INTRODUCTION

Within Iguania, *Liolaemus* is the second higher lizards rich-species genus (more than 270 spp) after *Anolis* (Abdala, Laspiur, Langstroth 2021; Esquerré et al., 2022). *Liolaemus* lizards are distributed widely in southern South America from Tierra del Fuego (Argentina and Chile) to the Ancash Region of Peru, including some coastal areas of Brazil and Uruguay (Abdala and Quinteros, 2014; Pincheira-Donoso et al., 2015; Abdala et al., 2019; Abdala et al., 2021a, b). Diversity within this genus includes two subgenera, *Liolaemus* (*sensu stricto*) and *Eulaemus*, each one splits into several sections and groups (Schulte, Macey, Espinoza, Larson, 2000; Abdala et al., 2020; Quinteros, Ruiz-Monachesi, Abdala, 2020; Abdala et al., 2021b, c). Pincheira-Donoso and Núñez (2005) based on a phenetic study, proposed a new arrangement of the *Liolaemus* genus, which they split in several subgenera. Among them, the *Liolaemus* subgenus (*sensu stricto*) was split in two clades: *L. chiliensis* complex and *L. nigromaculatus* complex. However, this proposal was rejected and criticized by Lobo, Espinoza, Quinteros (2010), arguing that Pincheira-Donoso and Núñez (2005) used an outdated methods (phenetic analysis), without provide a data matrix and which results are taxonomically untenable (subgenera split in other subgenera), thus at current only two subgenera are accepted in *Liolaemus* (Abdala et al., 2021b). However, Troncoso-Palacios, Schulte, Marambio-Alfaro, Hiriart (2015), based on DNA data, found that in fact the subgenus *Liolaemus* (*sensu stricto*) should be split in two main clades, which they proposal as *L. chiliensis* section and *L. nigromaculatus* section. Later this proposal was also supported by other molecular phylogenies: Panzera, Leaché, D'Elía, Victoriano (2017) and Esquerré et al. (2019a, 2022) and is also included in the recent two volumes book Liolaemidae (Abdala et al. 2021b). In the most recent phylogenetic proposal, the *L. nigromaculatus* section includes seven species groups (Esquerré et al., 2022), almost all of them endemic to Chile (Troncoso-Palacios et al., 2015; Panzera et al., 2017; Esquerré et al., 2019a, 2022; Abdala et al. 2021b). Among these groups, the *L. nigroviridis* group (*L. fuscus* group in Esquerré et al., 2022, see our Discussion) is a clade of lizards endemic to central Chile, inhabiting mainly in mountains from Coastal and Andes, but one species is found also in valleys and even shoreline. Almost all species are robust and medium size lizards, have black dorsal stripes/spots and blue, yellow or green dorsal scales; have 54–64 scales around midbody; males always have precloacal pores, and almost all species have allopatric distribution (Pincheira-Donoso and Núñez, 2005; Troncoso-Palacios, Elorza, Puas, Alfaro-Pardo, 2016).

Troncoso-Palacios et al. (2016), lists the following eight species within the *L. nigroviridis* group, updating the previous studies (Pincheira-Donoso and Núñez, 2005; Lobo et al., 2010; Troncoso-Palacios, 2013; Abdala and Quinteros, 2014): *L. constanzae* Donoso-Barros, 1961, *L. isabelae* Navarro and Núñez, 1993, *L. juanortizi* Young-Downey and Moreno, 1992, *L. lorenzmuelleri* Hellmich, 1950, *L. maldonadae* Navarro and Núñez, 1991, *L. melanopleurus* (Philippi, 1860), *L. nigroviridis* Müller and Hellmich, 1932, and *L. uniformis* Troncoso-Palacios, Elorza, Puas and Alfaro-Pardo, 2016. However, *L. melanopleurus* was included in this group as "*incertae sedis*" by Pincheira-Donoso and Núñez (2005), but although it is an available name in regard to the nomenclature, the three type specimens are deteriorated and although these can be assigned to the subgenus *Liolaemus*, they cannot be assigned to any known *Liolaemus* population or species group (Troncoso-Palacios and Marambio-Alfaro, 2021); thus, it should be excluded of the *L. nigroviridis* group.

Moreover, the recently publication of some DNA phylogenetic studies, both mitochondrial and nuclear, has significantly changed the composition of the *L. nigroviridis* group. *Liolaemus fuscus* (Boulenger, 1985) has been added as basal species, to the *L. nigroviridis* group (Schulte and Moreno-Roark, 2010; Troncoso-Palacios et al., 2015; Esquerré et al., 2022), but an alternative hypothesis for this species can be read in Quinteros et al. (2020). *Liolaemus isabelae* has been excluded of the *L. nigroviridis* group (Schulte and Moreno-Roark, 2010; Troncoso-Palacios et al., 2015; Esquerré et al., 2022). Besides, Esquerré et al. (2022) based on nuclear and mitochondrial DNA loci, place *L. constanzae*, *L. maldonadae* and *L. lorenzmuelleri* outside of the *L. nigroviridis* group. We remark that *L. juanortizi* was suggested as probably junior synonym of *L. lorenzmuelleri* by Pincheria-Donoso and Núñez (2005). Thus, *L. juanortizi* also should be excluded of the *L. nigroviridis* group until a further study that can solve its relationship with *L. lorenzmuelleri*. Then, the current composition of the *L. nigroviridis* group is restricted to: *L. fuscus*, *L. nigroviridis* and *L. uniformis*.

In regard to *L. nigroviridis*, this species was formerly composed of three subspecies: *L. nigroviridis nigroviridis*, *L. nigroviridis minor* Müller and Hellmich, 1932, and *L. nigroviridis campanae* Hellmich, 1950. However, Valencia et al. (1979) found few differences in the biometrics and karyotype between these subspecies. Thus, Núñez and Jaksic (1992) following Valencia, Veloso, Sallaberry (1979) decided that only the nominal *L. nigroviridis* should be considered as valid. Modern DNA phylogenetic studies (Cianferoni et al., 2013; Torres-Pérez et al., 2017) partially support Valencia et al. (1979), pointing out that *L. nigroviridis minor* is not a valid subspecies, but they strongly suggest that "*L. nigroviridis*" is a species complex (without shared haplotypes between the terminal lineages) formed by the nominal *L. nigroviridis*, the formerly "*L. nigroviridis campanae*", and other lineages that could represent candidate species.

In fact, one lineage within the "*L. nigroviridis*" complex was recently described as *L. uniformis* (Troncoso-Palacios et al., 2016). Moreover, Esquerré et al. (2022) proposed that "*L. nigroviridis campanae*" could be a full species and also proposed the candidate species *L.* sp. Cantillana. Besides, there is a population from El Arpa, Valparaíso Region (Torres-Pérez et al., 2005, 2017), whose record is mainly based on juvenile specimens (JTP, personal data of specimens SSUC Re 001–006) and to date it has not aroused taxonomic interest, being for example excluded of the GenBank sampling of some phylogenetic studies (eg. Troncoso-Palacios et al., 2016; Esquerré et al., 2022). However, based on the examination of adult specimens, we hypothesized that this population could be assigned to a new species of *Liolaemus*. This taxon can be differentiated from the rest of the species of the genus by a combination of morphological and genetic characters and a description for it is provided. Additionally, we provide morphological evidence to support *L. campanae* as full species.

MATERIALS AND METHODS

Morphological data and analyses

Specimens of *Liolaemus* sp. nov., were collected in the field by hand, o using a lasso. We examined the previously collected specimens of all species of the *Liolaemus nigroviridis* group. All the specimens directly examined (n = 86) are listed in Appendix I. Morphological characters commonly used in *Liolaemus*, described and cited mainly by Etheridge (1995) and Lobo (2005) were studied. In the case of *L. fuscus*, which inhabits in a very wide geographical range, from coastal localities near the Pacific Ocean to 2100 m above sea level (Troncoso and Ortiz, 1987; Pincheira-Donoso, Scolaro, Sura, 2008), distributional data was taken from Núñez and Gálvez (2015) and Esquerré et al. (2022). Body measurements were taken with a ± 0.02 mm precision caliper. Scales were observed with different magnifying lenses. Only adult males were used in the multivariate analysis to avoid confounding effects of intraspecific allometric variation (Losos, 1990; Abdala et al., 2021b). All bilateral characters were recorded on the right side of the specimen. The measured morphometric traits were: snout-vent length (SVL), head length, head height, head width, axilla-groin distance, foot length, and arm length. The following meristic characters were counted: number of scales around midbody, number of dorsal scales between the occiput and the level of the anterior edge of the thigh, number of ventral scales, number of supralabials, number of infralabials, and lamellae of the fourth toe of the hind limb.

As a visualization and exploratory analysis, a principal component analysis (PCA) was employed to analyze the morphometric variation with the R package FactoMineR (Lê, Josse, Husson, 2008) to compare all the species of the *Liolaemus nigroviridis* group, including "*L. nigroviridis campanae*" and the candidate species *Liolaemus* sp. Arpa. We did not include the candidate species *L.* sp. Cantillana, due to the lack of published morphological data, because we did not collect specimens and because the specimens in the SSUC Re collection (053–58, 060–68, 070–71, 81, 83, 085–86 and 093–94) are in loan at least since 2011 to a researcher not related to us (JTP, personal notes on the SSUC Re, entry book). This analysis was performed in the R statistical environment version 3.2.3 (RDCT, 2016). To assess the importance of shape, the effect of size on all morphological characters was removed by using the residuals of each of these characters regressed on snout-vent length, in a correlation matrix. However, for a better visualization of the size effect, we also perform an analysis with the snout-vent length. Missing data from some measurements of some individuals were imputed using the imputePCA function from the MissMDA R package (Josse and Husson, 2012).

We performed a normality test (Shapiro-Wilk) and an homoscedasticy test (Levene) for the meristic variables (on square root), but we include also the continuous character SVL to determine if there are size differences between the adult males of these species. We used a One Way ANOVA followed by a Holm-Sidak *post hoc* to compare among species, but we used the Kruskal-Wallis One Way Analysis of Variance on Ranks, followed by a Dunn Test if the data does not archive normality or if the homoscedasticy test failed (dorsal, infralabial and supralabial scales). Only significant results are shown (Zar, 2010).

We also used qualitative features, such as the color pattern and the shape of the dorsal scales, to compare among species, by following the recently published descriptions of *Liolaemus* (e.g. Abdala et al., 2019; Aguilar-Puntriano et al., 2019; Esquerré et al., 2019b; Quinteros et al., 2020; Avila et al., 2021) and the recently published pattern color proposal of Abdala et al. (2021b).

Cytochrome-b pairwise differences

We follow the most updated study of the relationships between the lineages of *Liolaemus nigroviridis* group (Torres-Pérez et al., 2017), but we use the name *L. nigroviridis* only in regard to the clade that includes the sequences from the surroundings of the type locality (Fig. 1). We compare the genetic pairwise differences using the cyt-b marker because it is the locus with largely more available data in GenBank and has been used to calculate the pairwise differences in several clades of *Liolaemus* (Morando et al., 2007, 2021; Avila et al., 2009, 2010; Esquerré et al., 2014; Medina, Avila, Sites, Morando, 2014). We were able to collect data for almost all species or candidate species of the *L. nigroviridis* group. Then, our analysis includes: the former taxon "*L. nigroviridis campanae*" (from La Campana, 32° 57'S - 71° 07'W; El Roble, 32°58'S - 71°00'W; and Chicauma, 33°17'S - 70°58'W), *L. nigroviridis* (Farellones valley, near type locality 33°21'S - 70°17'W; El Yeso, near the type locality of the former *L. nigroviridis minor* 33°43'S - 70°37'W), *L. uniformis* (Chepical Lagoon, 32°15'S – 70°30'W), *L.* sp. Arpa (32°39'S, 70°28'W) and *L.* sp. Cantillana (33°58'S, 70°58'W). All sequences were collected from GenBank (Appendix II). We did not include *L. fuscus* in our analysis, because there is only one cyt-b sequence available in GenBank (MK472105) and we were unable to check the voucher identity and to our knowledge, this sequence has not been used in a publication. Besides, DNA sequences of *L. fuscus* generated by Esquerré et al. (2022) were not published, thus, these are not included in our study. Cytochrome-b haplotypes were identified using DnaSP v5.10 (Librado and Rozas, 2009) and aligned with MUSCLE (Edgar, 2004).

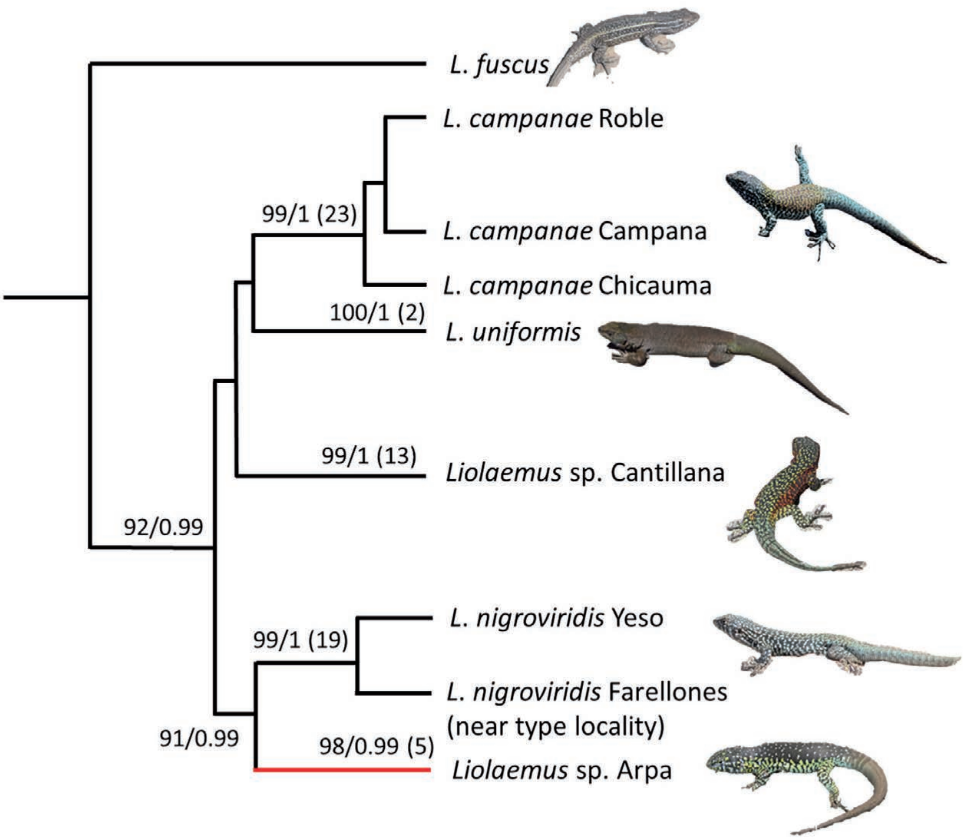

Figure 1. Phylogenetic relationships of the species of the *L. nigroviridis* complex group, modified from Torres-Pérez et al. (2017), based on the mitochondrial gene cytochrome b, including the bootstrap values for maximum likelihood, the posterior probabilities for Bayesian inference and the number of haplotypes used for each terminal taxon. *Liolaemus fuscus* is added as the basal species of the group, following Schulte and Moreno-Roark (2010), Troncoso-Palacios et al. (2015) and Esquerré et al. (2022). Specific name *L. nigroviridis* is used only for the clade that contains the samples from near the type locality. The candidate species *Liolaemus* sp. Arpa is in red. Male dorsal pattern is compared.

Figura 1. Relaciones filogenéticas de las especies del grupo complejo *L. nigroviridis*, modificado de Torres-Pérez et al. (2017), con base en el gen mitocondrial citocromo b, incluidos los valores de bootstrap para la máxima verosimilitud, las probabilidades posteriores para la inferencia bayesiana y el número de haplotipos utilizados para cada taxón terminal. Se añade *Liolaemus fuscus* como especie basal del grupo, siguiendo a Schulte y Moreno-Roark (2010), Troncoso-Palacios et al. (2015) y Esquerré et al. (2022). El nombre específico *L. nigroviridis* se usa solo para el clado que contiene las muestras cercanas a la localidad tipo. La especie candidata *Liolaemus* sp. Arpa está en rojo. Se compara el patrón dorsal del macho.

Uncorrected average pairwise differences were calculated using MEGA v6.06 (Tamura et al., 2013) and standard errors were estimated using the Bootstrap method with 1000 replications. Since Breitman, Avila, Sites, Morando (2012) found that in several clades of *Liolaemus* the uncorrected pairwise difference between species is around 3%, we considered all populations with less than 3% of uncorrected pairwise difference as conspecific.

Table 1. Principal component (PC) axes loadings of continuous characters (only males) for *L.* sp. Arpa (n = 6), *L. campanae* (n = 5), *L. fuscus* (n = 7), *L. nigroviridis* (n = 9) and *L. uniformis* (n = 2). Eigenvectors, eigenvalues, and percentage of variance explained for the first three principal components from data in the putative species of *L. nigroviridis* group.

Tabla 1. Cargas de ejes de componente principal (PC) de caracteres continuos (solo machos) para *L.* sp. Arpa (n = 6), *L. campnae* (n = 5), *L. fuscus* (n = 7), *L. nigroviridis* (n = 9) y *L. uniformis* (n = 2). Eigenvectores propios, eigenvalores propios y porcentaje de varianza explicados para los tres primeros componentes principales a partir de datos en las especies putativas del grupo *L. nigroviridis.*

Axes	PC1	PC2	PC3
PCA of the residuals of each character in a regression with the snout-vent length			
Percentage variation accounted for	57.9	18.7	10.1
Eigenvalue	3.47	1.12	0.61
Head length	0.88	0.10	-0.19
Head height	0.71	0.43	-0.44
Head width	0.81	0.02	-0.54
Axilla-groin distance	0.60	0.61	0.03
Foot length	0.74	-0.57	0.08
Arm length	0.77	-0.46	0.27
PCA including the snout-vent length			
Percentage variation accounted for	89.9	5.3	2.9
Eigenvalue	6.29	0.37	0.20
Snout-vent length	0.96	-0.16	-0.17
Head length	0.98	0.01	-0.04
Head height	0.82	0.56	0.01
Head width	0.98	-0.10	-0.07
Axilla-groin distance	0.96	-0.02	-0.18
Foot length	0.93	-0.11	0.33
Arm length	0.97	-0.07	0.14

RESULTS

In regard to the PCA analysis performed with the residuals of each character regressed on snout-vent length, the first three components cumulatively account for 86.8% of the variation (Table 1), and a screen plot of the PCs indicated that only those components contain relevant information. The first axis (PC1, 57.9 %, Table 1) is mainly explained by variation in head length, head width and arm length. PC2 (18.7 %, Table 1) mostly represents variation in axilla-groin distance, foot length and arm length. PC3 (10.1 %, Table 1) mostly represents variation in head width, head height and arm length. The PCA plots (Fig. 2) have 95.0% confidence ellipses around the centroid of the species and illustrate the morphometric differences between the species included in the analysis. In both, the PC1 vs PC2 and PC1 vs PC3 graphs, *Liolaemus* sp. Arpa partially overlaps with "*L. nigroviridis campanae*" and *L. nigroviridis*; whereas there is no overlap with *L. fuscus*. However, in both graphs, the orientation of the central axis of the ellipse for the *Liolaemus* sp. Arpa and *L. nigroviridis* are opposed. Remarkably, "*L. nigroviridis campanae*" and *L. nigroviridis* do not show a complete overlap in none of these PCA graphs.

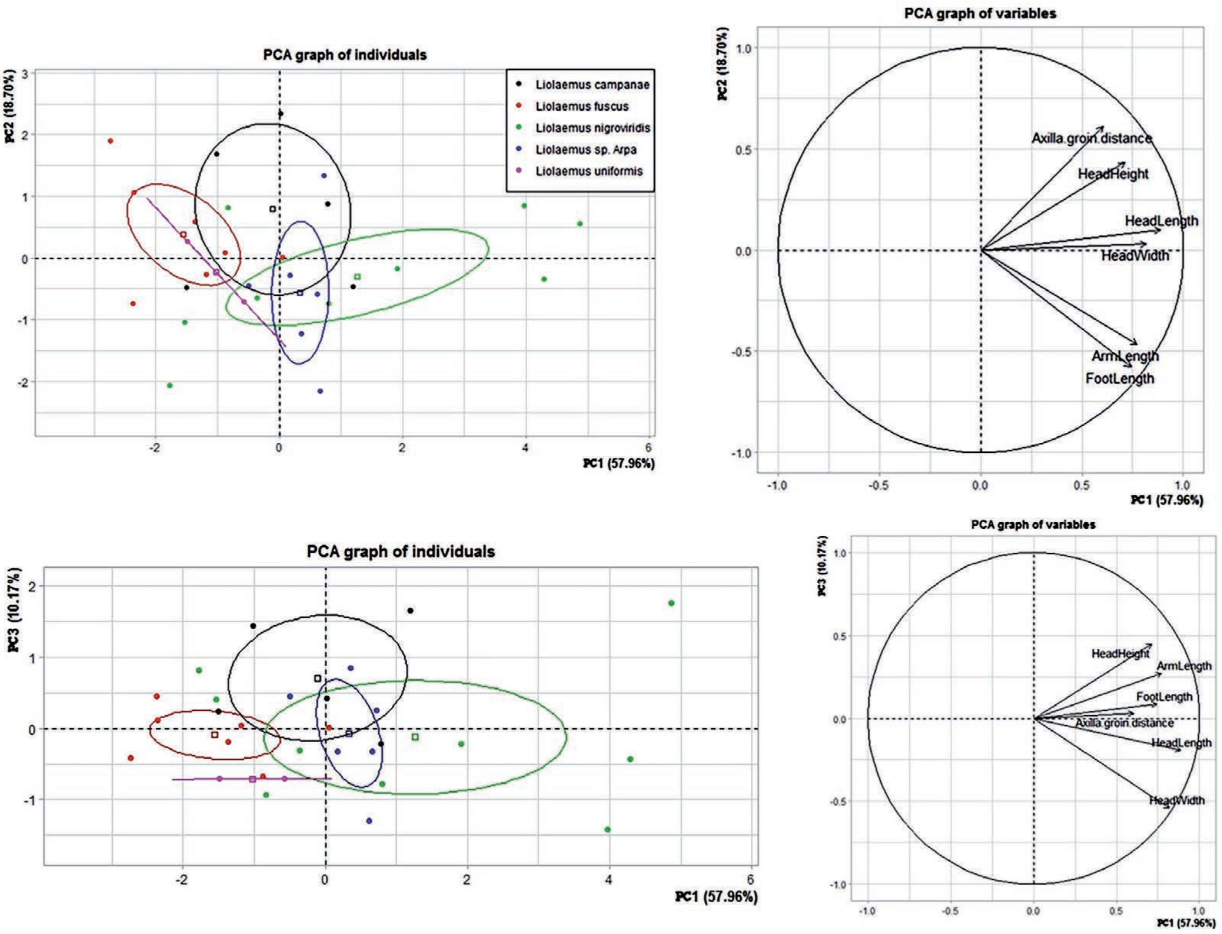

Figure 2. Principal Component Analysis (PCA) plots of the species of the *L. nigroviridis* group, performed with the residuals of each character regressed on snout-vent length. On the left panels, the individuals are colored according to their species as shown on the legend on the top right corner. Ellipses represent the 95% confidence interval around the centroid for each species. On each axis, the PC is labeled according to its number and the percentage of the total variance that PC explains. On the right, the variable graphs, which illustrate the contribution of each variable to the construction of the axes.

Figura 2. Gráficas de Análisis de Componentes Principales (ACP) de las especies del grupo *L. nigroviridis*, realizadas con los residuos de cada carácter en regresión sobre la longitud hocico-cloaca. En los paneles de la izquierda, los individuos están coloreados según su especie, como se muestra en la leyenda en la esquina superior derecha. Las elipses representan el intervalo de confianza del 95 % alrededor del centroide para cada especie. En cada eje, el CP está etiquetado según su número y el porcentaje de la varianza total que explica el CP. A la derecha, los gráficos de variables, que ilustran la contribución de cada variable a la construcción de los ejes.

In the PCA analysis performed with the snout-vent length as a variable (Fig. 3), the first three components cumulatively account for 98.2% of the variation (Table 1), and a screen plot of the PCs indicated that only those components contain relevant information. PC1 (89.9 %, Table 1) is mainly explained by variation in head length, head width and arm length. PC2 (5.3 %, Table 1) mostly represents variation in head height, snout-vent length and foot length. PC3 (2.9 %, Table 1) mostly represents variation in foot length, axilla-groin distance and snout-vent length. In both, the PC1 vs PC2 and PC1 vs PC3 graphs, *Liolaemus* sp. Arpa marginally overlaps with "*L. nigroviridis campanae*", whereas there is no overlap with *L. fuscus* and *L. nigrovir-*

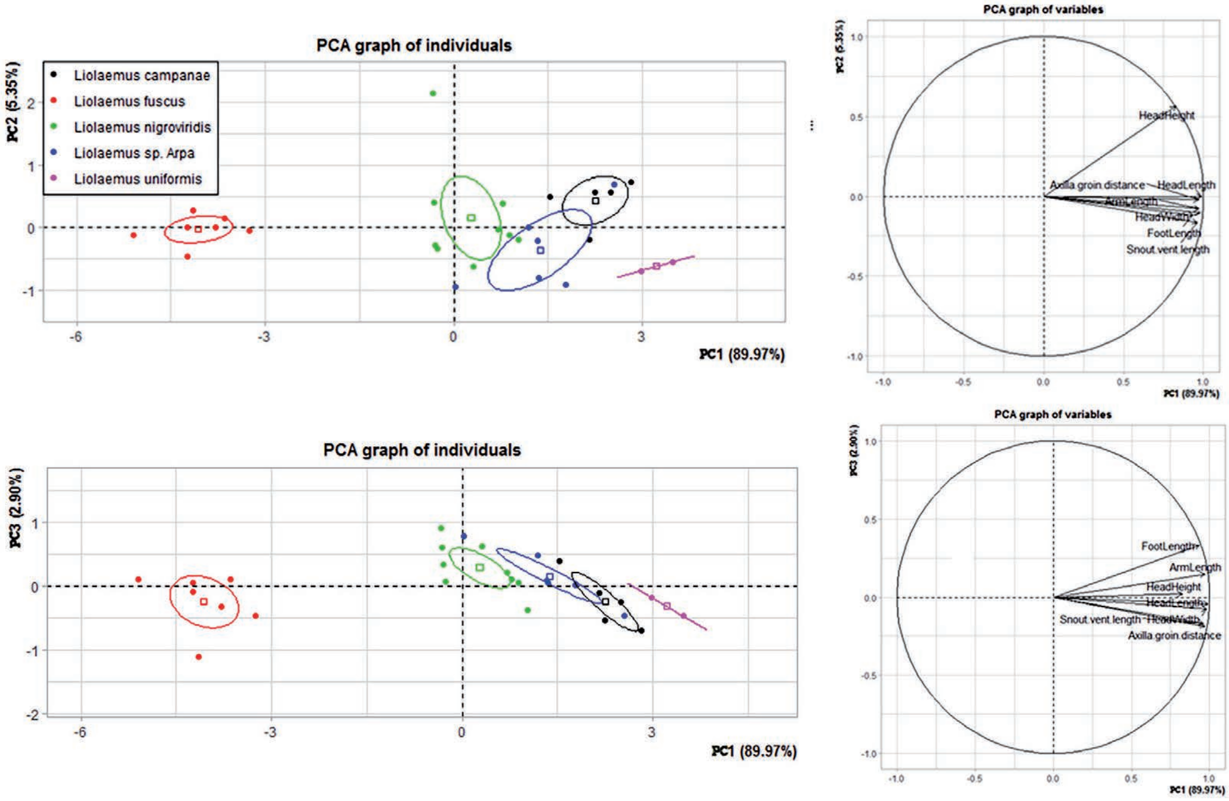

Figure 3. Principal Component Analysis (PCA) plots of the species of the *L. nigroviridis* group, performed with the snout-vent length as a variable. On the left panels, the individuals are colored according to their species as shown on the legend on the top left corner. Ellipses represent the 95% confidence interval around the centroid for each species. On each axis, the PC is labeled according to its number and the percentage of the total variance that PC explains. On the right, the variable graphs, which illustrate the contribution of each variable to the construction of the axes.

Figura 3. Gráficos de Análisis de Componentes Principales (ACP) de las especies del grupo *L. nigroviridis*, realizados con la longitud hocico-cloaca como variable. En los paneles de la izquierda, los individuos están coloreados según su especie, como se muestra en la leyenda en la esquina superior izquierda. Las elipses representan el intervalo de confianza del 95 % alrededor del centroide para cada especie. En cada eje, el CP está etiquetado según su número y el porcentaje de la varianza total que explica el CP. A la derecha, los gráficos de variables, que ilustran la contribución de cada variable a la construcción de los ejes.

idis. Also, "*L. nigroviridis campanae*" and *L. nigroviridis* do not show overlap in these graphs.

In general, both results, the PCA with the snout-vent length and the PCA with the residuals of each character regressed on snout-vent length, are similar, because *Liolaemus* sp. Arpa shows a partial or marginal overlap with "*L. nigroviridis campanae*"; a partial overlap with different axis orientation or not overlap with *L. nigroviridis*, and no overlap with *L. fuscus*.

Statistical analyses on the meristic characters revealed significant differences in five of the six variables analyzed (Table 2). There are statistical differences in some meristic character between *Liolaemus* sp. Arpa and *L. nigroviridis*, which is the species that show the major overlap with it in the PCA graphs.

In regard to cytochrome-b analysis, there are not shared haplotypes between the species or candidate species analyzed. The uncorrected average pairwise difference between the populations of *L. nigroviridis* from Farellones valley (near type locality) and *L. nigroviridis* population from El Yeso (formerly known as *L. nigroviridis minor*), is 0.9% (se = ± 0.4), thus, we considered both as conspecific in agreement with the previous studies (Cianferoni et al., 2013; Torres-Pérez et al., 2017). In regards to *Liolaemus* sp. Arpa, the uncorrected average pairwise difference between it and any

Table 2. Statistical results for the characters among the species of the *Liolaemus nigroviridis* group.

Tabla 2. Resultados estadísticos para los caracteres entre las especies del grupo *Liolaemus nigroviridis.*

	One Way ANOVA			**Holm-Sidak method**
	F	*P*	*df*	
Fourth toe lamellae	5.4	< 0.01	4	*L. campanae* > *L. nigroviridis, L. fuscus.*
Midbody scales	33.6	< 0.01	4	*Liolaemus* sp. Arpa > *L. fuscus;* *L. campanae* > *L. fuscus;* *L. nigroviridis* > *L. fuscus;* *L. uniformis* > *L. fuscus.*
SVL	66.6	< 0.01	4	*Liolaemus* sp. Arpa > *L. fuscus;* *L. campanae* > *L. fuscus, L. nigroviridis; L. nigroviridis* > *L. fuscus; L. uniformis* > *Liolaemus* sp. Arpa, *L. fuscus, L. nigroviridis.*
Ventral scales	5.9	< 0.01	4	*L. campanae* > *L. fuscus, L. nigroviridis.*
	Kruskal-Wallis test			**Dunn Test**
	H	*P*	*df*	
Dorsal scales	22.7	< 0.01	4	*Liolaemus* sp. Arpa > *L. fuscus;* *L. campanae* > *L. fuscus;* *L. uniformis* > *L. fuscus.*
Infralabial scales	11.8	> 0.05	4	No significant results.
Supralabial scales	12.9	< 0.05	4	*Liolaemus* sp. Arpa > *L. nigroviridis.*

Table 3. Average percentages of cyt-b pairwise differences and standard error estimated with bootstrap (above diagonal) between *Liolaemus* sp. Arpa and the species of the *L. nigroviridis* group with available data.

Tabla 3. Porcentajes promedio de diferencias por pares para cyt-b y error estándar estimado con bootstrap (arriba de la diagonal) entre *Liolaemus* sp. Arpa y las especies del grupo de *L. nigroviridis* con datos disponibles.

	L. campanae	*L. nigroviridis*	*L. uniformis*	*L.* sp. Arpa	*L.* sp. Cantillana
L. campanae	—	1.1	1.2	1.1	1.1
L. nigroviridis	8.6	—	1.2	0.9	1.0
L. uniformis	8.8	8.5	—	1.1	1.2
L. sp. Arpa	8.7	4.6	7.3	—	1.1
L. sp. Cantillana	8.1	6.7	8.0	7.3	—

other lineage is more than 3% (Table 3) which adds support to its recognition as a full species.

Taxonomic status of *Liolaemus campanae*

The uncorrected average pairwise difference between the populations from La Campana and El Roble is 1.2% (se = ± 0.4), between La Campana and Chicauma is 2.6% (se = ± 0.6); and between El Roble and Chicauma is 2.7% (se = ± 0.6), thus, following the proposal of Breitman et al. (2012) in regards to the pairwise difference in the *Liolaemus* genus, we considered all these populations as conspecific. Besides, the uncorrected average pairwise difference between this taxon and *L. nigroviridis* is 8.6% (se = ± 1.1, Table 3) and both are not sister lineages neither in the MtDNA phylogeny nor in the nDNA phylogeny of Esquerré et al. (2022). Then, in agreement with the proposal of Esquerré et al. (2022), we recognized *L. campanae* as full species a not as subspecies or synonymy of *L. nigroviridis*, being this taxon composed by the populations from La Campana, El Roble and Chicauma. The holotype (ZSM 195/1947) and paratypes (ZSM 194/1947a–c, ZSM 196/1947a–k) of *L. campanae* are currently placed in the Zoologische Staatssammlung München and is out of our reach to provide a re-description. However, we provide the following diagnosis based on our morphologic data. *Liolaemus campanae* differs from *L. fuscus*, because it has more four toe lamellae (27.6 ± 0.9 vs 24.0 ± 1.4, Tables 2 and 4), more midbody scales (60.8 ± 3.0 vs 45.4 ± 2.5, Tables 2 and 4), more ventral scales (102.2 ± 8.4 vs 85.6 ± 5.0, Tables 2, 4), more dorsal scales (53.0 ± 1.8 vs 35.6 ± 3.9, Tables 2, 4) and is bigger (maximum SVL = 81.7 mm vs 52.3 mm, Tables 2 and 4). Both species are easily distinguishable because males the *L. fuscus* never have green or intense yellow color, and never have black dorsal reticulation. *Liolaemus campanae* differs from *L. nigroviridis* because it has more four toe lamellae (27.6 ± 0.9 vs 25.0 ± 1.0, Tables 2 and 4), more ventral scales (102.2 ± 8.4 vs 90.5 ± 4.0, Tables 2, 4) and is bigger (maximum SVL = 81.7 mm vs 73.8 mm, Tables 2 and 4). Females of *L. campanae* frequently have reddish coloration on the dorsolateral bands and on the lateral fields (not observed in our sample of *L. nigroviridis*). Color pattern of the males in *L. campanae* is green on the dorsal field of the head, lateral fields, limbs and tail, and intense yellow on the occipital band (wide and extended between the lateral fields, without other discernable bands or lines), with dorsal black thin reticulation. Although the dorsal color in the males of *L. nigroviridis* is very variable, the yellow color (when present) on the occipital band always invades the lateral fields. Finally, *L. campanae* is easily distinguishable from *L. uniformis* because this last species totally lack dorsal color pattern, besides few light scales dispersed in some individuals. However, *L. campanae* always have dorsal color pattern in both sexes, being the most distinctive characters the black thin reticulation in males. On the other hand, females of *L. campanae* have brown color on the head with dispersed black lines or spots, brown color between the dorsolateral bands, with dark brown fragmented vertebral line and inconspicuous fragmented superciliary band, also with dark brown spots in the paravertebral fields, dorsolateral black band with reddish shades and reddish lateral fields with transversal black fragmented stripes.

Table 4 (part 1 of 2). Morphological characteristics of some species of the *Liolaemus nigroviridis* group. Males in the first row and females in the second. Since few females were examined for some species and characters, statistical and PC analyses were performed only on males. Juvenile data is not show. Mean ± standard deviation.

Tabla 4 (parte 1 de 2). Características morfológicas de algunas especies del grupo *Liolaemus nigroviridis*. Machos en la primera fila y hembras en la segunda. Dado que se examinaron pocas hembras para algunas especies y caracteres, los análisis estadísticos y de CP se realizaron solo en los machos. Los datos juveniles no se muestran. Media ± desviación estándar.

	L. campanae M = 5, F = 12	*L. fuscus* M = 9, F = 4	*L. nigroviridis* M = 8, F = 4	*L. uniformis* M = 2, F = 3	*L.* sp. Arpa nov. M = 6, F = 3
Meristic characters					
Dorsal scales	50–55 (53.0 ± 1.8)	31–41 (35.6 ± 3.9)	45–52 (48.5 ± 2.4)	56–58 (57.0 ± 1.4)	54–57 (54.8 ± 1.1)
	48–58 (53.1 ± 3.0)	-	48–53 (51.0 ± 2.4)	61–63 (62.0 ± 1.0)	52–59 (55.3 ± 3.5)
Fourth toe lamellae	27–29 (27.6 ± 0.9)	22–25 (24.0 ± 1.4)	23–27 (25.0 ± 1.0)	27	24–29 (26.5 ± 1.8)
	25–28 (27.0 ± 1.0)	-	24–26 (25.0 ± 1.0)	26–27 (26.0 ± 1.0)	24–28 (26.7 ± 2.3)
Infralabial scales	5	4–5 (4.4 ± 0.5)	4–5 (4.8 ± 0.3)	4–5 (4.5 ± 0.7)	5–6 (5.5 ± 0.5)
	5	-	4–5 (4.5 ± 0.7)	4–5 (4.3 ± 0.6)	5
Midbody scales	54–64 (60.8 ± 3.0)	42–48 (45.4 ± 2.5)	54–64 (59.7 ± 2.9)	60	56–64 (60.3 ± 2.9)
	54–67 (58.9 ± 3.7)	43–48 (45.0 ± 2.6)	58–64 (60.3 ± 20.6)	58–62 (60.7 ± 2.3)	54–60 (57.3 ± 3.1)
Supralabial scales	6–7 (6.2 ± 0.5)	6–7 (6.8 ± 0.8)	5–7 (5.8 ± 0.6)	6	7
	6–7 (6.3 ± 0.5)	-	6	6	6
Vental scales	94–114 (102.2 ± 8.4)	81–92 (85.6 ± 5.0)	85–97 (90.5 ± 4.0)	91–92 (91.5 ± 0.7)	86–101 (92.1 ± 5.9)
	95–112 (102.3 ± 6.8)	-	88–94 (90.8 ± 3.2)	96–102 (99.3 ± 3.1)	97–109 (102.7 ± 6.0)
Preclocal pores (males)	3	2–3 (2.4 ± 0.5)	2–3 (2.8 ± 0.3)	3	2–3 (2.1 ± 0.4)
Continuous characters					
Arm length	23.2–24.6 (23.6 ± 0.6)	13.5–14.4 (14.5 ± 0.7)	20.2–22.1 (21.4 ± 0.5)	24.9–25.7 (25.3 ± 0.5)	21.9–24.3 (23.4 ± 0.9)
	16.5–21.2 (18.5 ± 1.2)	-	17.5–19.4 (18.3 ± 1.0)	19.2–21.2 (20.4 ± 1.0)	18.4–19.7 (19.3 ± 0.8)
Axilla-groin distance	31.1–38.0 (34.4 ± 2.8)	15.5–22.4 (18.6 ± 2.4)	26.3–31.6 (28.1 ± 1.7)	34.9–37.7 (36.6 ± 2.0)	26.4–35.2 (31.5 ± 3.3)
	21.8–28.9 (24.7 ± 2.3)	-	24.4–26.1 (25.4 ± 0.9)	33.1–35.7 (34.6 ± 1.3)	24.7–28.4 (27.1 ± 2.0)

Table 4 (part 2 of 2).

Tabla 4 (parte 2 de 2).

	L. campanae M = 5, F = 12	*L. fuscus* M = 9, F = 4	*L. nigroviridis* M = 8, F = 4	*L. uniformis* M = 2, F = 3	*L.* sp. Arpa nov. M = 6, F = 3
Foot length	20.5–21.6 (21.1 ± 0.4)	10.6–14.6 (13.3 ± 1.5)	18.7–21.8 (20.3 ± 0.8)	22.4–22.9 (22.6 ± 0.3)	20.3–22.0 (21.4 ± 0.6)
	14.3–19.3 (17.1 ± 1.5)	-	15.6–16.9 (16.4 ± 0.7)	17.9–18.6 (18.3 ± 0.5)	16.7–17.0 (17.0 ± 0.2)
Head height	11.0–13.5 (12.4 ± 1.0)	5.0–6.7 (5.9 ± 0.7)	8.5–10.9 (9.5 ± 0.8)	10.3–11.1 (10.7 ± 0.5)	7.4–13.2 (9.8 ± 2.0)
	7.0–9.6 (8.2 ± 0.8)	-	6.4–8.3 (7.2 ± 1.1)	7.5–8.2 (7.9 ± 0.4)	6.1–7.6 (7.0 ± 0.8)
Head length	16.4–18.4 (17.7 ± 0.8)	9.3–11.4 (10.7 ± 0.8)	14.7–17.0 (16.0 ± 0.9)	19.0–19.3 (19.1 ± 0.2)	15.3–17.8 (16.4 ± 0.8)
	11.3–13.8 (12.7 ± 0.8)	-	11.0–12.8 (12.1 ± 0.9)	14.5–15.1 (14.7 ± 0.3)	12.4–12.9 (12.8 ± 0.3)
Head width	12.7–14.8 (14.0 ± 0.9)	7.1–8.9 (8.2 ± 0.6)	11.8–13.6 (12.9 ± 0.7)	15.7–16.3 (16.0 ± 0.3)	12.2–14.9 (13.7 ± 1.0)
	8.8–10.9 (9.8 ± 0.8)	-	8.8–9.8 (9.3 ± 0.5)	11.8–13.2 (12.6 ± 0.7)	10.3–10.8 (10.6 ± 0.3)
SVL (mm)	71.5–81.7 (78.5 ± 4.1)	39.5–52.3 (44.4 ± 5.6)	60.6–73.8 (68.1 ± 4.1)	84.6–89.1 (86.8 ± 3.1)	65.1–78.8 (73.2 ± 4.6)
	50.1–65.6 (55.6 ± 4.5)	36.8–42.3 (39.8 ± 2.8)	53.4–59.0 (58.0 ± 3.7)	67.7–73.0 (70.1 ± 2.7)	59.1–62.5 (61.1 ± 1.8)
Dorsal pattern (males)	Thin black dorsal reticulation	Vertebral line, superciliary band, subocular band	Thin black dorsal reticulation	Absent	Thick black dorsal reticulation/partial melanims
Green dorsal color (males)	Present	Absent	Present	Absent	Absent/ Inconspicuous
Sexual dichromatism	Present	Absent	Present	Absent	Present

***Liolaemus nigrodorsum* sp. nov.**

Fig. 4

2005 *Liolaemus nigroviridis*, Torres-Pérez, Gómez-Lobo, Garín. Herpetological Review 36, p. 80.

2013 *Liolaemus nigroviridis*, Garín and Hussein. Guía de Reconocimiento de Anfibios y Reptiles, p. 48.

2013 *Liolaemus nigroviridis*, Cianferoni, Yáñez, Palma, Garín, Torres-Pérez. Zootaxa 3619, p. 60.

2016 *Liolaemus nigroviridis* (?), Troncoso-Palacios, Elorza, Puas, Alfaro-Pardo. Zookeys 555, p. 91.

2017 *Liolaemus nigroviridis* (in map), Torres-Pérez, Boric-Bargetto, Rodríguez-Valenzuela, Escobar, Palma. Revista Chilena de Historia Natural 90, p. 3.

Holotype.— SSUC Re 787. Adult male (Fig. 4A, B). Collected in the ski center El Arpa (32º39'31"S – 70º28'46"W, 2604 m above sea level), approximately 21 km NE Los Andes city, Valparaíso Region, Chile. Collectors: J. Troncoso-Palacios and F. Contreras. January 11, 2021.

Paratypes (Fig. 4C, D, E, F).— SSUC Re 788–90, three males. SSUC Re 791–93, three females. SSUC Re 794, juvenile. Same data as the holotype. SSUC Re 005–06. Two males. SSUC Re 001–04. Four juveniles. Ski center El Arpa (32°39'S – 70°28'W) Collectors: F. Torres-Pérez and G. Lobos. September 10, 2003.

Etymology.— The name of this species is a composition of "*nigro*", from the Latin word "*niger*" (black) and the Latin word "*dorsum*" (back). The species epithet made reference to the color pattern of the males.

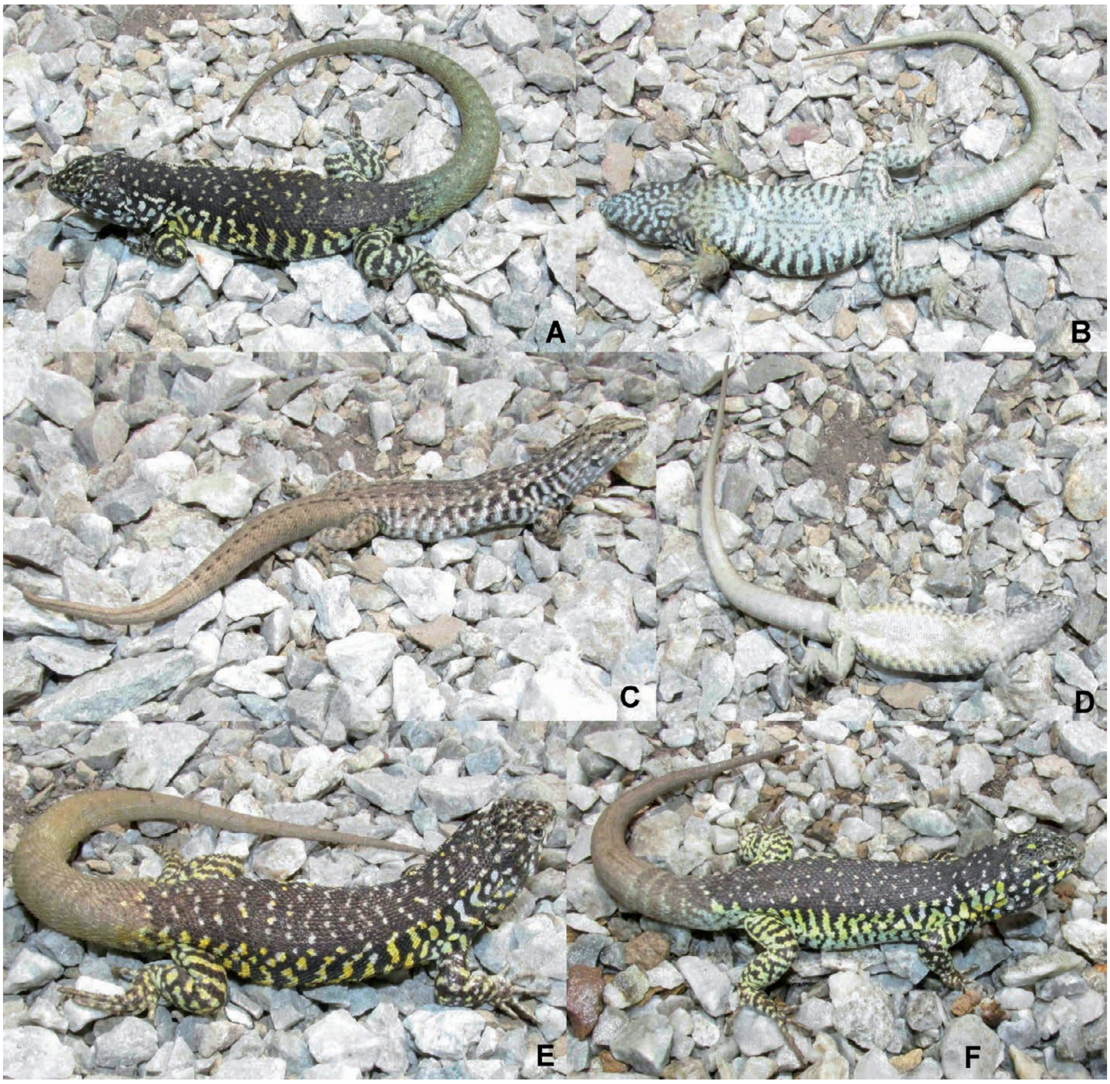

Figure 4. *Liolaemus nigrodorsum* sp. nov. A) and B) Holotype, male SSUC Re 787. C) and D) Paratype, female SSUC Re 792. E) SSUC Re 789 and F) SSUC Re 788, paratypes, males.

Figura 4. *Liolaemus nigrodorsum* sp. nov. A) y B) Holotipo, macho SSUC Re 787. C) y D) Paratipo, hembra SSUC Re 792. E) SSUC Re 789 y F) SSUC Re 788, paratipos, macho.

Diagnosis.— DNA phylogenetic evidence shows that *Liolaemus nigrodorsum* sp. nov. is a member of the *L. nigroviridis* group (Cianferoni et al., 2013; Torres-Pérez et al., 2017), being the sister species of *L. nigroviridis* (Fig. 1, Table 3). It shows the morphological features of this group (Pincheira-Donoso and Núñez, 2005; Troncoso-Palacios et al., 2016), which are robust lizards with black dorsal stripes and yellow dorsal scales, males have precloacal pores and are bigger than females. Almost all species have approximately 54–64 scales around midbody.

Liolaemus nigrodorsum sp. nov. strongly differs from *L. campanae* in color pattern, especially among males (Fig. 5). The males of *L. campanae* have orange or yellow background color on the occipital band (wide and extended between the lateral fields) and light green on the lateral fields, with thin black stripes forming a reticulation; whereas the males of *L. nigrodorsum* sp. nov. have yellow or white background color on the occipital band (wide and extended between the lateral fields) and yellow on the lateral fields (light green color is absent or is inconspicuous, restricted to the sides of the neck and the dorsal base of the tail), with thick black stripes forming a reticulation or almost complete melanism on the occipital band area. Females of *L. campanae* have brown background color between the dorsolateral bands with reddish shades on the dorsolateral bands and the lateral fields in several individuals, whereas the females of *L. nigrodorsum* sp. nov. completely lack the reddish color.

Liolaemus nigrodorsum sp. nov. is bigger than *L. fuscus* (maximum SVL = 78.8 mm vs 52.3 mm, Tables 2 and 4), has more midbody scales (60.3 ± 2.9 vs 45.4 ± 2.5, Table 2, 4) and more dorsal scales (54.8 ± 1.1 vs 35.6 ± 3.9, Tables 2 and 4). Moreover, *L. fuscus* lack sexual dichromatism and although its dorsal color pattern loosely resembles the color pattern in the juveniles and females of *L. nigrodorsum* sp. nov., the males never have black thick dorsal reticulation or partial melanism as the males of *L. nigrodorsum* sp. nov. (Fig. 5). We remark that *L. nigrodorsum* sp. nov. and *L. fuscus* do not overlap in the PC1 vs PC2 and PC2 vs PC3 graphs, in both, the PCA with the snout-vent length and the PCA with the residuals of each character regressed on snout-vent length (Figs. 2 and 3), explained by the small size and the slender body shape of *L. fuscus*.

Liolaemus nigrodorsum sp. nov. has more supralabial scales than *L. nigroviridis* (7 vs 5.8 ± 0.6, Table 2, 4). The dorsal color pattern of the males of *L. nigroviridis* is more variable than in the other species analyzed, but never has a pattern similar to *Liolaemus nigrodorsum* sp. nov. (Fig. 5). In fact, *L. nigroviridis* males have the following color combinations of background color on the occipital band (wide and extended between the lateral fields) and the lateral fields, respectively: light green-light green, light green-yellow and yellow-yellow, always with thin black stripes forming a reticulation, whereas the males of *L. nigrodorsum* sp. nov. have only yellow-yellow or white-yellow color combinations, with thick black stripes forming a reticulation or almost complete dorsal melanism and the light green color is absent or is inconspicuous (restricted to the sides of the neck and/or on the dorsal base of the tail). We point out that *L. nigrodorsum* sp. nov. and *L. nigroviridis* overlap, but always with different orientation axis, in the PCAs graphs constructed with the residuals of each character regressed on snout-vent length (Fig. 2). Remarkably, both species do not overlap in in the PCAs graphs constructed with the snout-vent length (Fig.

Figure 5. Species of the *Liolaemus nigroviridis* group. A) Male of *L. campanae* (photograph by S. Berhó Fuenzalida). B) Female of *L. campanae* (photograph by R. Arroyo Castro). C) and D) Males of *L. fuscus* (photographs by JTP). E) and F) Males of *L. nigroviridis* (photographs by JTP). G) Female of *L. nigroviridis* (photograph by JTP). H) and I) Male and female, respectively, of of *L. uniformis* (photographs by JTP).

Figura 5. Especies del grupo de *Liolaemus nigroviridis*. A) Macho de *L. campanae* (fotografía de S. Berhó Fuenzalida). B) Hembra de *L. campanae* (fotografía de R. Arroyo Castro). C) y D) Machos de *L. fuscus* (fotografías de JTP). E) y F) Machos de *L. nigroviridis* (fotografías de JTP). G) Hembra de *L. nigroviridis* (fotografía de FCP). H) e I) Macho y hembra, respectivamente, de *L. uniformis* (fotografías de JTP).

3), probably explained by the bigger size of *L. nigrodorsum* sp. nov. (maximum SVL = 78.8 mm vs 73.8 mm, Table 4).

Liolaemus nigrodorsum sp. nov. is smaller than *L. uniformis* (SVL = 78.8 mm vs 89.1 mm, Tables 2 and 4). Both species are easily distinguishable, because *L. uniformis* lacks sexual dichromatism and has no noticeable dorsal color pattern (Fig. 5). In fact, it has brown dorsal color, with few whitish or dark scales dispersed, whereas *L. nigrodorsum* sp. nov. has marked sexual dichromatism and males and females have dorsal pattern with think black stripes forming a reticulation or partial melanism on males, and dorsolateral dark bands with fragmented vertebral line in females.

A summary of these features is provided in Table 4.

Description of holotype.— Adult male. SVL = 76.2 mm. Horizontal diameter of the eye: 3.5 mm. Subocular length: 4.2 mm. Length of the fourth supralabial: 3.4 mm. Head length (from the anterior border of the auditory meatus to the tip of the snout): 16.5 mm. Head height (at the level of ear openings): 8.9 mm. Head width (distance between the two ear openings): 14.3 mm. Neck width: 15.1 mm. Interorbital distance: 5.4 mm. Ear-eye distance: 6.8 mm. Internasal scales distance: 2.4 mm. Ear width: 1.7 mm. Ear height: 3.0 mm. Axilla-groin distance: 35.0 mm. Body width: 21.7 mm. Forelimb length: 24.2 mm. Hindlimb length: 42.4 mm. Tail length (not autotomized): 126.0 mm, relation tail length/SVL = 1.7. Rostral scale, wider (3.1 mm) than high (1.4 mm).

Two postrostrals. Four internasals. The Interparietal is hexagonal, with a small central spot marking the position of the parietal eye. The interparietal is smaller than the parietals and is surrounded by ten scales. The parietal scales are in contact. Seven scales between the interparietal and rostral. Thirteen scales between the occiput and the rostral. Orbital semicircles are complete and formed by 11 (left) and 12 (right) scales. Four supraoculars on both sides. Seven superciliary scales. The frontal area is divided into three scales, from anterior to posterior: 1 and 2. Preocular separated from the lorilabials by one loreal scale. Two scales between nasal and canthal. The nasal is in contact with the rostral and surrounded by seven scales (including the rostral). One row of lorilabials is between the supralabials and the subocular. Seven supralabials, the fourth is curved upward without contacting the subocular. Six infralabials scales. The Pentagonal mental scale, in contact with four scales. Four pairs of post-mental shields, the second is separated by two scales. The temporal scales are of variable shape, but mainly hexagonal, slightly keeled or smooth, juxtaposed or subimbricated. Eight temporal scales are between the level of superciliary scales and the rictal level. There are five projected scales on the anterior edge of the ear, which do not cover the auditory meatus. Differentiated auricular scale, wide, placed on the upper section of the auditory meatus. There are thirty-four gular scales between the auditory meatuses. The lateral neck fold is "Y" shaped. There is an antehumeral transversal neck fold. There is a slightly developed dorso-lateral fold running from the neck to the half the groin. Midbody scales: 64. Dorsal scales are lanceolate, imbricate and keeled with mucron, almost without interstitial granules. Dorsal scales and ventral scales have similar size. Dorsal scales: 54. Ventral scales are rounded, smooth, imbricated and without interstitial granules. Ventral scales: 101. Two dark brown precloacal pores. Supra-femoral scales are lanceolate, imbricate and keeled, some have a mucron. Infra-femoral scales are rounded, smooth and imbricated. Supra-antebrachial scales are lanceolate, imbricate and keeled, some have a mucron. The Infra-antebrachials are rounded or rhomboidal, imbricated and smooth or slightly keeled, imbricated or juxtaposed, with interstitial granules. Dorsal scales of the first third of the tail are rhomboidal, imbricate, keeled and mucronate. Ventral scales: in the first third of the tail are rounded, smooth and imbricate. Lamellae of the fingers: I: 8, II: 13, III: 17, IV: 19 and V: 11. Lamellae of the toes: I: 10, II: 15, III: 19, IV: 25 and V: 16.

Color of holotype in life.— The dorsal pattern is as follows: Dorsal field of the head and temporal area are black, with abundant white and light brown dispersed dots. Wide occipital band (there are no other discernible bands between the lateral fields), covering both, dorsal and dorsolateral fields, running from the neck to the base of the tail. It is black, with several yellow dots on the dorsum forming inconspicuous fragmented transversal lines. The subocular field of the head and the sides of the neck are whitish with thick black lines that from a reticulation. The lateral fields are yellow with ten transversal black thick stripes, between the axilla and the groin, some of these are partially fused. "H" shaped black spot over the shoulder, on the pre and post scapular area. The ventral field (side view) is whitish, with the same transversal black thick stripes of the lateral field running through it. The Forelimbs and hind limbs are light yellow with transversal black thick stripes. The tail is light brown, with yellowish shades. There are few black dots on the vertebral zone, without forming an inconspicuous fragmented vertebral line. Ventrally, the gular area and the chest are whitish with black transversal thick stripes, forming a reticulation. The sides of the abdominal area are whitish with transversal thick black stripes. The middle of the abdominal area and the area between the groins and the cloaca are whitish with transversal thin black fragmented stripes and a ventral black line running from the chest to the cloaca. There are yellowish shades on the chest and cloacal area. Ventrally, the limbs are white with black stripes, but the palms are white. The base of the tail is white with a few black dots, but the rest of the tail is white.

Variation.— Based on six adult males: SVL: 65.1–78.8 mm (73.2 ± 4.6). Axilla-groin distance: 26.4–35.2 mm (31.5 ± 3.3). Head length: 15.3–17.8 mm (16.4 ± 0.8). Head width: 12.2–14.9 mm (13.7 ± 1.0). Head height: 7.4–13.2 mm (9.8 ± 2.0). Leg length: 38.5–42.4 mm (40.0 ± 1.7). Arm length: 21.9–24.3 mm (23.4 ± 0.9). Foot length: 20.3–22.0 mm (21.4 ± 0.6). Tail length: 126.0 mm (only one specimen, autotomized in the rest). Tail length/SVL = 1.7 (n = 1). In three adult females: SVL: 59.1–62.5 mm (61.1 ± 1.8). Axilla-groin distance: 24.7–28.4 mm (27.1 ± 2.0). Head length: 12.4–12.9 mm (12.8 ± 0.3). Head width: 10.3–10.8 mm (10.6 ± 0.3). Head height: 6.1–7.6 mm (7.0 ± 0.8). Leg length: 29.8–30.9 mm (30.3 ± 0.6). Arm length: 18.4–19.7 mm (19.3 ± 0.8). Foot length: 16.7–17.0 mm (17.0 ± 0.2). Tail length: 91.0–111.0 mm (101.0 ± 14.1, two specimens, autotomized on another), with relation tail length/SVL = 1.5–1.9 (1.7 ± 0.3, n = 2).

The variation in the scalation on the male adult specimens is as follows. Midbody scales: 56–64 (60.3 ± 2.9). Dorsal scales: 54–57 (54.8 ± 1.1). Ventral scales: 86–101 (92.1 ± 5.9). Fourth finger lamellae: 18–20 (19.2 ± 0.9). Fourth toe lamellae: 24–29 (26.5 ± 1.8). Supralabial scales: 7, the fourth curved upward. Infralabial scales: 5–6 (5.5 ± 0.5). The variation in the scalation on the female adult specimens is as follows. Midbody scales: 54–60 (57.3 ± 3.1). Dorsal scales: 52–59 (55.3 ± 3.5). Ventral scales: 97–109 (102.7 ± 6.0). Fourth finger lamellae: 19–20 (19.3 ± 0.6). Fourth toe lamellae: 24–28 (26.7 ± 2.3). Supralabial scales: 6, the fourth curved upward. Infralabial scales: 5. On the adult specimens of both sexes, the interparietal scale is pentagonal, hexagonal or heptagonal bordered by 6–10 scales (7.5 ± 2.0). Interparietals are smaller than the parietal scales or have similar size. Interparietals are in contact or separated. Nasal and rostral are in contact or separated by one scale. Precloacal pores in males: 2–3 (2.1 ± 0.4). Precloacal pores are absent in females.

Adult male paratypes have a similar color pattern compared with the holotype. Some males have white dots between the lateral fields (on the black area formed by the wide occipital band), forming fragmented transversal stripes instead of yellow dorsal dots between the lateral fields, forming fragmented transversal stripes as on the holotype. Some males have thick black reticulation and yellow or whitish background color between the lateral fields (on the black area formed by the wide occipital band) instead of black dorsal color as on the holotype. There are males with an inconspicuous light green shade restricted to the sides of the neck and/or on the dorsal base of the tail. The black transversal stripes on the lateral fields are continued on the ventrolateral fields and vary from nine to 11. Male juveniles have dark brown dorsal color between the lateral fields, instead of black dorsal color as in the adult male holotype, and have a dark brown fragmented vertebral line running from the occiput to almost the tip of the tail. In the adult females the dorsal surface of the head is light brown with some dispersed dark brown spots. The temporal area and the sides on the neck are brown with few light yellow or white fragmented transversal stripes. There is a dark brown fragmented vertebral line running from the occiput to almost the tip of the tail and some white dots dispersed on the vertebral field. There are approximately 10 series of paravertebral spots composed of a dark brown anterior area and white posterior area (few and inconspicuous in some females). The lateral field is yellow or white with light brown or dark brown transversal stripes which continue to the whitish ventrolateral filed. The dorsal surface of the limbs is brown with few and inconspicuous light or dark brown sports dispersed. The dorsal surface of the tail is light brown with a dark brown fragmented vertebral line accompanied by dark brown dots (almost immaculate tail in some females). Ventrally, the gular area is white with black reticulation. The chest is white with dark spots dispersed. The belly and the tail are white. The sides of the belly have yellow in almost all females. The ventral surface of the limbs is white with dark brown dots dispersed.

Distribution and natural history.— This species is currently known only from the type locality in El Arpa ski center, approximately 21 km NE of Los Andes, Valparaíso Region, Chile (Fig. 6). It was found between 2604 (32°39’31”S – 70°28’46”W) and

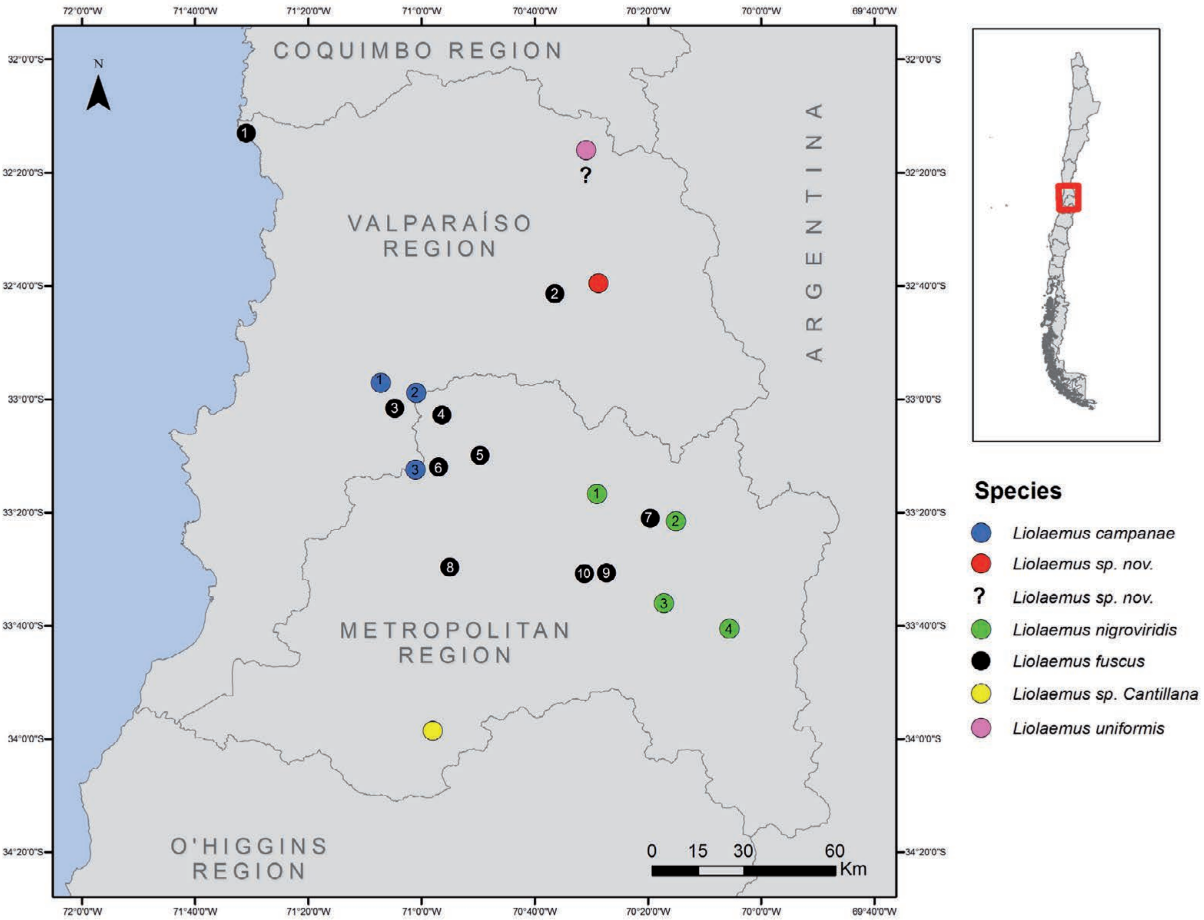

Figure 6. Distributional map for *Liolaemus nigrodorsum* sp. nov. along with the species of the *L. nigroviridis* group following the most recent phylogenetic studies (Torres–Pérez et al., 2017; Esquerré et al., 2022). *Liolaemus campanae*: Blue circles (1 = La Campana, 2 = El Roble, 3 = Chicauma). *Liolaemus fuscus*: Black circles (1 = Los Molles, 2 = Altos de Jahuel, 3 = La Campana, 4 = El Roble, 5 = Cerro Blanco, 6 = Chicauma, 7 = Farellones, 8 = Quebra de la Plata, 9 = Quebrade de Macul, 10 = San Luis de Macul). *Liolaemus nigrodorsum* sp. nov: Red circle (El Arpa, type locality) and question mark (Laguna Chepical, possible record). *Liolaemus nigroviridis*: Green circles (1 = Cerro Conchali, 2 = Farellones, 3 = Lagunillas, 4 = El Yeso). *Liolaemus uniformis*: pink circle (Laguna Chepical). *Liolaemus* sp. Cantillana: Yellow circle (Altos de Cantillana).

Figura 6. Mapa de distribución de *Liolaemus nigrodorsum* sp. nov. junto con las especies del grupo *L. nigroviridis* siguiendo los estudios filogenéticos más recientes (Torres–Pérez et al., 2017; Esquerré et al., 2022). *Liolaemus campanae*: Círculos azules (1 = La Campana, 2 = El Roble, 3 = Chicauma). *Liolaemus fuscus*: Círculos negros (1 = Los Molles, 2 = Altos de Jahuel, 3 = La Campana, 4 = El Roble, 5 = Cerro Blanco, 6 = Chicauma, 7 = Farellones, 8 = Quebra de la Plata, 9 = Quebrade de Macul, 10 = San Luis de Macul). *Liolaemus nigrodorsum* sp. nov: Círculo rojo (El Arpa, localidad tipo) y signo de interrogación (Laguna Chepical, posible registro). *Liolaemus nigroviridis*: Círculos verdes (1 = Cerro Conchali, 2 = Farellones, 3 = Lagunillas, 4 = El Yeso). *Liolaemus uniformis*: círculo rosado (Laguna Chepical). *Liolaemus* sp. Cantillana: círculo amarillo (Altos de Cantillana).

3059 masl (32º39'24"S – 70º28'01"W) inhabiting rocky areas with shrubby vegetation composed mainly of high-Andean bushes such as *Tetraglochin alatum*, *Mulinum spinosum* and *Chuquiraga oppositifolia*. This lizard species was found in abundance and was observed to have saxicolous habits. We found individuals in syntopy with *Liolaemus monticola* Müller and Hellmich 1932, whereas *L. nitidus* (Wiegmann, 1834) was found near at lower altitudes. Besides, Troncoso-Palacios et al. (2016), based on field observations, recorded "*L. nigroviridis*" from the surroundings of the Chepical Lagoon, Valparaíso Region, Chile (32º16'S – 70º30'W). Although no specimens were collected, most likely, this record is assignable to *L. nigrodorsum* sp. nov. since the color pattern matches this species (JTP, personal observations).

Several males were observed near a female (less than five meters). While the reproductive mode is yet unknown, at the time of sampling (January) no evidence of embryos was found, all females have several small oocytes.

DISCUSSION AND CONCLUSIONS

In our work, we used the restricted composition of the *L. nigroviridis* group, supported by several molecular phylogenetic studies based on different markers and methodologies (Schulte and Moreno-Roark, 2010; Troncoso-Palacios et al., 2015; Esquerré et al., 2022). In this hypothesis, *L. fuscus* is included in the *L. nigroviridis* group. In fact, Esquerré et al. (2022) rename the *L. nigroviridis* group as "*L. fuscus*" group, because *L. fuscus* is the first described species of this group. However, we suggest keeping "*L. nigroviridis* group" denomination to maintain the taxonomic consistency with the majority of the *Liolaemus* studies published at date that deal with these species (e.g. Abdala et al., 2021b, book of Liolaemidae mention it as *L. nigroviridis* group), and because there is not a strictly rule to name the species groups. For example, Esquerré et al. (2022) use "*L. kriegi* group" instead rename it as "*L. buergeri* group" (the older described species of this group), thus, they not follow the same criterion for all clades. We remark that adult specimens of *L. fuscus* resembles the color pattern of the juveniles of *L. campanae*, *L. nigrodorsum* sp. nov. and *L. nigroviridis* (JTP, personal obs.). Besides, *L. fuscus* also resembles the color pattern of the adult specimens of the *L. alticolor-bibronii* group, in which is placed according to other phylogenetic hypothesis (Quinteros et al., 2020).

The new species, *Liolaemus nigrodorsum* sp. nov. was previously recorded by Torres-Pérez et al. (2005) based on four juveniles and two adult males (SSUC Re 001–06), but we think that the lack of more adult specimens did not allow to notice the differences in regard to *L. nigroviridis*, especially in the color pattern. Then, probably the specimens from El Arpa were not hypothesized as a new species.

Although *L. campanae* has been considered a subspecies of *L. nigroviridis*, based on morphological evidence and the cyt-b uncorrected average pairwise difference, we propose to resurrect *L. campanae*, as was previously suggested by Esquerré et al. (2022) In fact, the haplotypes of both lineages do not form sister clades (Cianferoni et al., 2013; Torres-Pérez et al., 2017). Hellmich (1950) proposed a brief diagnosis for *L. campanae*: smaller, more midbody scales and less developed keels on the temporal scales compared to *L. nigroviridis*. We did not find these differences between both species, but noted that the body scales of *L. campanae* are smaller and it has more ventral scales than *L. nigroviridis*. Donoso-Barros (1966) also proposed a diagnosis based on the midbody scale counts, but adding as diagnostic characters the differences in the color pattern. However, both taxa were considered conspecific by Núñez and Jaksic (1992), following the few biometric and karyotype differences found by Valencia et al. (1979). In our PCA analysis, both taxa do not show a complete overlap in none of the three graphs and we also found statistical differences for the scale counts, but since Valencia et al. (1979) used a phenetic analysis of similar, but not the same characters that we used (measures and scales counts), these differences in the conclusions are expected.

We call attention to the lineage named by Esquerré et al. (2022) as *Liolaemus* sp. Cantillana, which we also considered a candidate species. The haplotypes of *Liolaemus* sp. Cantillana form a clade, sister to the clade composed of *L. campanae* + *L. uniformis* (Torres-Pérez et al., 2017), thus, *Liolaemus* sp. Cantillana is not the sister lineage of *L. nigroviridis*. In addition, we found that the cyt-b uncorrected average pairwise difference between *Liolaemus* sp. Cantillana and any other lineage included in our analysis is more than 6.0%, the double of the value proposed by Breitman et al. (2012) to identify candidate species. This evidence strongly suggests that *Liolaemus* sp. Cantillana is not conspecific with *L. nigroviridis* as is currently thought (e.g. Núñez and Gálvez, 2015). Moreover, Altos the Cantillana highlands are a relatively isolated mountain coastal range in Central Chile, from which some vertebrate species are endemic, like *L. frassinettii* Núñez, 2007, the lizard *Pristidactylus valeriae* (Donoso-Barros, 1966) and the frog *Alsodes cantillanensis* Charrier, Correa, Castro and Méndez, 2015 (Donoso-Barros, 1966; Núñez, 2007; Charrier et al., 2015), which points out that these mountains constitute a good locality for the study of allopatric speciation (see Esquerré et al., 2019a). We recommend a further investigation on this issue to clarify the taxonomic status of *Liolaemus* sp. Cantillana.

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Appendix I

Specimens examined. Acronyms are: Museo de Historia Natural de Concepción (MRC) and Colección de Flora y Fauna, Profesor Patricio Sánchez Reyes de la Pontificia Universidad Católica de Chile (SSUC).

Liolaemus campanae (n = 36). SSUC Re 405–09. El Roble, Valparaíso Region, Chile. F. Torres and E. Palma colls. December, 2010. SSUC Re 497–525, 556–57. El Roble, Valparaíso Region, Chile. F. Torres coll. January 23, 2003.

Liolaemus fuscus (n = 15). SSUC Re 255–57. Curva Nº20, Road to Farellones, Metropolitan Region, Chile. F. Ferri coll. December 8, 2010. SSUC Re 258–59. Altos de Jahuel, Valparaíso Region, Chile. F. Ferri and J. Troncoso-Palacios colls. December 19, 2010. SSUC Re 260. Near Las Chinchillas Reservoir, road to Ovalle, Coquimbo Region. F. Ferri coll. Marsh 17, 2012. SSUC Re 579. Huasco, Atacama Region, Chile. J. Troncoso-Palacios coll. November, 2011. MRC 229. Vallenar, Atacama Region, Chile. Unknown collector. May 9, 1983. MRC 230–34, 236. Huasco bajo, Atacama Region, Chile. Unknown collector. May 9, 1983. SSUC Re 762. Maitenes, Machali, O`Higgins Region, Chile. D. Ramirez and E. Acevedo colls. May 15, 2017.

Liolaemus nigroviridis (n = 15). SSUC Re 016. El Yeso, Metropolitan Region, Chile. C. Garín coll. April 1, 2004. SSUC Re 190–200. Farellones, Casa de Piedra, road to Valle Nevado, Metropolitan Region, Chile. F. Ferri coll. October 12, 2010.

Liolaemus uniformis (n = 6). SSUC Re 674–79. West shore of the Chepical Lagoon, approximately 30 km NE Alicahue, San Felipe de Aconcagua Province, Valparaíso Region, Chile. J. Troncoso-Palacios and E. Alfaro. December 15–16, 2012.

Liolaemus nigrodorsum sp. nov. (n = 14). SSUC Re 787–794. Ski center El Arpa, approximately 21 km NE Los Andes city, Valparaíso Region, Chile. J. Troncoso-Palacios and F. Contreras colls. January 11, 2021. SSUC Re 001–06. Ski center El Arpa, Valparaíso Region, Chile. F. Torres-Pérez and G. Lobos colls. September 10, 2003.

Appendix II

Sequences used for the cyt-b uncorrected average pairwise difference analysis.

Liolaemus campanae. El Roble, Valparaíso Region, Chile: AY850633, KC313212–22. Altos de Chicauma, Metropolitan Region, Chile: KC313253–61. La Campana, Valparaíso Region, Chile: KY575291–304. *Liolaemus nigroviridis*. Farellones, Metropolitan Region, Chile: KC313199–211. El Yeso, Metropolitan Region, Chile: KC313223–33. *Liolaemus uniformis*. Laguna Chepical, Valparaíso Region, Chile: KU095836–37. *Liolaemus nigrodorsum*. El Arpa, Valparaíso Region, Chile: KC313234–39. *Liolaemus* sp. Cantillana. Altos de Cantillana, Metropolitan Region, Chile: KC313240–52.