LIOLAEMUS OMORFI, A NEW LIZARD SPECIES FROM THE ANDES OF NORTHERN CHILE (SAURIA, LIOLAEMIDAE)

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ABSTRACT

The South American lizard genus Liolaemus embodies one of the most exceptional examples of prolific diversification among living vertebrates on the planet. These iguanians have extensively colonized a wide range of environments, including a successful succession of historical invasions of The Andes. Accumulating evidence reveals that Andean ecosystems have operated as engines promoting Liolaemus diversification, where numerous new species are continuously reported. Here, we describe a new species of Liolaemus lizard belonging to the Eulaemus (or montanus) lineage, and distributed in the area of Zorritas ravine, nearby the Llullaillaco volcano. We employ a number of phenotypic and bioclimatic quantitative analyses to test the hypothesis that this Liolaemus has evolutionarily diverged from other species of the same group distributed in the same Andean areas.

Key words: Liolaemus, South America, adaptive radiation, diversification, The Andes, lizards

RESUMEN

El género Liolaemus corresponde a uno de los ejemplos de diversificación más notables de vertebrados en el planeta. Estos iguanidos han colonizado una gran cantidad de hábitats dentro de Sudamérica, incluyendo la sucesión de invasiones históricas de la Cordillera de los Andes. Distintas pruebas revelan que los ecosistemas andinos han operado como motores en la generación de diversidad. Se describe una nueva especie de lagartija Liolaemus, perteneciente al linaje Eulaemus. Esta especie habita en las zonas montañosas de la Región de Antofagasta en Chile, en la aislada quebrada Zorritas, en las cercanías del volcán Llullaillaco. Pusimos a prueba análisis fenotípicos y bioclimáticos cuantitativos para probar la hipótesis de que esta especie ha divergido evolutivamente de otras especies del mismo grupo. Para esto comparamos con otros Liolaemus distribuidos en las mismas zonas andinas.

Palabras clave: Liolaemus, radiación adaptativa, diversificación, Los Andes

INTRODUCTION

The Andes range in Western South America has increasingly been identified as an engine for evolutionary proliferation of biodiversity (Hughes et al. 2006; Antonelli et al. 2009; Elias et al. 2009; Pincheira-Donoso et al. 2013a). The diversification history of the lizard genus Liolaemus has rapidly emerged as one of the potentially major outcomes of the role of the Andes as an agent of lineage radiation (Pincheira-Donoso et al. 2013a, 2015). In only ~20 million years since its origin (Albino 2008; Fontanella et al. 2012), Liolaemus lizards have diversified into 240+ species adapted to one of the widest ranges of ecological and climatic conditions recorded for a single group of living reptiles (Espinoza et al. 2004; Pincheira-Donoso & Núñez 2005; Pincheira-Donoso et al. 2007, 2008a, 2013a, 2015; Labra et al. 2009; Pincheira-Donoso & Tregenza 2011), being currently recognized as the second most species-rich lineage of amniotes on Earth (Pincheira-Donoso et al. 2013b). In recent years, it has been suggested that the Andes have operated as a large-scale source of ecological opportunity that promote radiations of species into multiple available new niches. According to this theory, as the Andes started to uplift ~25 million years ago (Norabuena et al. 1998; Gregory-Wodzicki 2002), new high-elevation ecosystems emerged along the current area of distribution of Liolaemus. These uplifts created new environments with abundant
niche space (i.e., ecological opportunity) that were rapidly exploited via adaptive radiation by ancestral Liolaemus that invaded the Andes (Pincheira-Donoso 2011; Pincheira-Donoso et al., 2013a, 2015). Given the cold temperatures dominating the new Andean ecosystems, natural selection promoted the evolution of viviparous reproduction (live-bearing) from oviparity (egg laying), which operated as a key adaptation that opened these new climates for Liolaemus to proliferate (Pincheira-Donoso 2011; Pincheira-Donoso et al., 2013a; Pincheira-Donoso & Hunt 2015). Subsequently, as the Andes kept uplifting in different historical pulses and across space, Liolaemus experienced episodic explosions of diversification via adaptive radiation, resulting in the extraordinary diversity we observe at present (Pincheira-Donoso et al. 2015). These analyses also revealed high extent of phenotypic diversification among species (Harmon et al. 2003; Pincheira-Donoso et al. 2015), and showed that transitions to smaller body sizes accelerated significantly the rates of Liolaemus diversification (Pincheira-Donoso et al. 2015). Therefore, a major implication of these newly arising evidences is that Andean ecosystems accommodate a large biodiversity of Liolaemus, and that rather small species (e.g., below 75-80 mm snout-vent length) are more likely to be considerably more diverse than larger-bodied groups.

During a fauna prospection around the area of the Llullaillaco volcano, we identified a population of Liolaemus lizards. Following field and laboratory examination of the collected samples (including a range of Liolaemus species belonging to the same lineage), we suggested the hypothesis that these animals belong to an unknown species. In this paper, we test the hypothesis of this new Liolaemus species. We employ a number of qualitative and quantitative approaches involving traditional taxonomic analyses of body conformation and scale anatomy and numbers, as well as multivariate phenotypic analyses and bioclimatic modeling to quantify multivariate niche differentiation between this suggested new taxon and a number of other species of the genus.

Taxonomic background

Laurent (1983) proposed the split of the Liolaemus genus into four main lineages with subgeneric status: Liolaemus (Liolaemus), mostly Chilean and Andean lizards, and Liolaemus (Eulaemus) mostly Argentinean lizards. This author also added the subgenus Rhytidodeira and Austrolaemus. Laurent’s concepts were subsequently and only partially supported by Etheridge (1995). With the emergence of molecular phylogenetic, Schulte et al. (2000) supported the hypothesis of the existence of these two lineages (Liolaemus and Eulaemus), a conclusion that has then been followed by a number of authors (v.g. Pincheira-Donoso y Núñez 2005, Pincheira-Donoso et al. 2008b, and many others; see also Laurent 1983, and Schulte et al. 2000). Furthermore, within these basic proposals of subgeneric lineages, and as a result of the high diversity of species known within Liolaemus, numerous further taxonomic subdivisions have subsequently been suggested. Laurent (1983, 1985, 1992, 1995), in Liolaemus (Eulaemus) proposed two groups: fitzingeri and signifer. Later, Etheridge (1995) proposed two groups: nitidus and signifer, within the latter one, this author identified the montanus group, among many finer-scale subdivisions. Schulte et al. (2000), for the Argentinean clade, stated the section montanus and the serie montanus including the species L. ruibali, L. andinus, L. jamatinus, L. orientalis, L. dorbignyi, L. scrocuti, L. pocciochromus, L. multicolor. To this group of species have been added this set (see Lobo et al. 2010): L. duellmani, L. eleodori, L. erguetae, L. foxi, L. griseus, L. huacahuasicus, L. manueli, L. molinai, L. multicolor, L. nigriceps, L. orko, L. patriciaiutrae, L. pleopholis, L. potonchilensis, L. pulcherrimus, L. robertoi, L. rosenmanni, L. vallecurensis, L. cazianae and L. halonastes, the latter two made up by Lobos et al (ibid. to this subgroup). Other species included within the montanus group are: L. audituvelatus, L. hajeki, L. insolitus, L. isluguenis, L. janesi, L. pantherinus, L. porosus, L. puritamensis, L. schmidtii, L. signifer, L. torresi.

The overwhelming majority of species of the montanus group are concentrated in Andean areas from Perú, Bolivia, North of Argentina and Chile, in geographic areas with extremely limited access. The montanus group has been poorly studied from the molecular phylogenetics point of view. Therefore, we are still lacking a large extent of molecular data to achieve an integral view of the relationships and evolutionary history of these species.
MATERIAL AND METHODS

Specimen collection and measurements

Animals were captured using fishing rods with a nylon noose. Upon capture, specimens were taken to the National Museum of Natural History in Santiago, where they were fixed with 96º Ethanol and preserved in 80º Ethanol. All individuals were measured with a digital caliper (0.01 mm precision) following Peters’s (1964) protocol: Snout-vent length (SVL), from the tip of the snout to the cloaca; axilla-groin length (AGL), from the interior angle of the arm to the interior angle of the hind leg; Forelimb length (FLL), from the anterior angle of the left arm to the tip of the third finger with straight arm; Hindlimb length (HLL), from the anterior angle of the hind leg to the fourth finger with straight leg; Tail length (TL), from the cloaca to the tip of the tail, only complete appendixes were measured; head length (HL), from the anterior angle of the auditory meatus to the tip of the face (rostral scale); width head length (WHL) at the widest part of the head, and height head length (hLL) at the level of eyes, the highest part.

To perform analyses of scale anatomy and counts, we observed individuals under binocular microscope. Our focal *Liolaemus* species was compared with all species belonging to the same clade and distributed in the surrounded areas of the zone where our samples were collected (see Figure 1).

Phenotypic analyses

To address the question whether the focal new species differs from other *Liolaemus* in the same area and clade, we employed the above mentioned body size measures to perform multivariate analyses of variance (MANOVA) and covariance (MANCOVA, body size as a covariate). Prior to all analyses data were ln-transformed to normalize distribution and to equalize variances. We first conducted a MANCOVA comparing six traits (SVL, HL, WHL, FLL, HLL, AGL; see above for details) across 10 species (*L. audituvelatus*, *L. erguetae*, *L. fabiani*, *L. hajeki*, *L. molinai*, *L. multicolor*, *L. nigriceps*, *L. puritamensis*, *L. rosenmannii*, and our focal new species), using body size (SVL) as our covariate, based on the assumption that variation in species body shapes may be linked to variation in body size (e.g., Schulte *et al.* 2004; Pincheira-Donoso *et al.* 2009; Pincheira-Donoso & Tregenza 2011). We subsequently conducted a MANOVA on the first three Principal Components (PCs) calculated from all morphological variables used in the above covariance analysis. With the same PCs (1 to 3) we then created a multivariate phenotypic morphospace to visualize the position of each *Liolaemus* species and their relationships with our focal new species.

Bioclimatic and Niche Modeling analyses

We studied the geographic distribution of *Liolaemus sp.* and its closed related species, *i.e.*, *L. audituvelatus*, *L. chlorostictus*, *L. erguetae*, *L. fabiani*, *L. hajeki*, *L. molinai*, *L. multicolor*, *L. nigriceps*, *L. porosus*, *L. puritamensis* and *L. rosenmannii* (Figure 1). Occurrence data (515 records) have been collected over 15+ years of field work and from museum collections around the world.

To analyze and display the environmental space occupied by these species, we used only non-interactive and non-consumable scenopoetic variables. Environmental dataset consisted of ‘climatic’ variables characterizing climates during the 1950-2000 periods, drawn from the WorldClim data archive (Hijmans *et al.* 2005), available at: http://www.worldclim.org/, with a spatial resolution of 30 sec (1 km at the equator). To prevent the combination of information between precipitation and temperature in the same layer and the spatial anomalies in the study area in the form of odd discontinuities between neighbouring pixels, we excluded the variables: Mean temperature of wettest quarter (bio 8), Mean temperature of the coldest quarter (bio 9), Precipitation of warmest quarter (bio 18) and Precipitation of coldest quarter (bio19).

Based on the occurrences of the species in study, we ran Species Distribution Models (SDM) in order to know the most suitable geographic locations for this species. To avoid the oversampling effects in our model, occurrences were resampled to one point per pixel on our environmental grids. Species distribution models were performed using the algorithm of maximum entropy implemented in Maxent 3.3.3k (Phillips *et al.* 2006). Maxent is a presence-background technique that estimates suitability via an
FIGURE 1. Geographic distribution of the *Liolaemus* species included in this study.
index of similarity that resembles a heterogeneous point process or logistic regression function (Phillips et al. 2006; Phillips & Dudik 2008). Model settings were as follows: evaluation of predictive power with 20% of the occurrences, and 10,000 background points. All other parameters were set to default. In order to facilitate the interpretations, we focused on the raw output (Phillips & Dudik 2008). Suitable area for the species was defined on a Boolean (presence/absence) map that was thresholded based on the minimum training presence. To calibrate the model, we ran models under different values of regularization multiplier (i.e., 0.5, 1, 3, 5, 10, 15 and 20) (Warren 2011). Then, by employing a model selection approach implemented in ENMTools (Warren 2011) and we assessed AIC values to choose the best model (Table 1). Once the models have been selected, we evaluated the models’ predictive performance using Area Under Curve (AUC) values, where values = 0.5 indicate random confidence, while AUC = 1 indicates 100% confidence in the strength of the model.

<table>
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TABLE 1. Model selection using Akaike Information Criterion in ENMTools. Values in bold represent the lowest AIC scores.

We determined the climatic niche breadth of Liolaemus sp. nov., L. multicolour, L. porosus and its closed related species (L. molinai, L. audituvelatus, L. chlorostictus, L. erguetae, L. fabiani, L. hajeki, L. nigriceps, L. puritamensis and L. rosenmannii) based in the method proposed by Quintero & Wiens (2013). We calculated the thermal niche breadth for each locality by subtracting the minimum temperature of the coldest month (Bio6) from the maximum temperature of the warmest month (Bio5). We also conducted similar analyses using precipitation variables based on the difference in precipitation between the wettest (Bio16) and driest quarters of the year (Bio17).

Finally, to identify the extent of niche overlap between Liolaemus sp. nov., L. multicolour, L. porosus and related species distributed in the same area (L. audituvelatus, L. chlorostictus, L. erguetae, L. fabiani, L. hajeki, L. molinai, L. nigriceps, L. puritamensis and L. rosenmannii) in the environmental space, we performed a principal component analysis (PCA) in NicheA software (Qiao 2015). This PCA allowed us to create a multivariate and uncorrelated environmental space scenario in which niche overlap estimations were developed comparing the different niche spaces based on Jaccard’s similarity index.
RESULTS

Our phenotypic analyses suggest that significant differences exist between the multivariate body shape (for the above five traits, controlling for allometric effects of body size by adding SVL as the covariate) among the *Liolaemus* species distributed around our focal new species (MANCOVA, Wilk’s $\lambda = 0.31$, $F = 7.01, P<0.001$). The decomposition of the MANCOVA model into univariate comparisons among individual traits reveals that all five traits significantly differ across species (Wilk’s $\lambda_{\text{range}} = 0.13-0.55$, $F_{\text{range}} = 1.93-16.22$, $P_{\text{range}} = 0.001-0.049$). Body size alone was also found to significantly differ among species (ANOVA$_{\text{SVL}}$, $F_{9,243} = 52.51, P<0.001$). Finally, an integrated analysis of multivariate variation across species based on PCAs (PCs 1-3) reveals that significant differentiation exists across species in their occupation of phenotypic morphospace (MANOVA, Wilk’s $\lambda = 0.24$, $F = 16.49, P<0.001$; Figure 2).

Regarding bioclimatic and niche analyses, the high AUC values obtained in the model performance evaluation of the SDMs (>0.95) show a strong accuracy and reliability of the predictions (Figure 3). Our niche breadth analyses reveal that the species in study exploit similar environmental conditions, which are characterized by a large range (~33.7°C) between the minimum temperature in the coldest month and the maximum temperature in the warmest month. In relation to precipitation, these species live in extremely dry conditions, where the precipitation levels during the wettest month are less than 70 mm (Figure 4).

Finally, the analysis of niche similarity between our focal new species and the other species in our study show a very low relationship between them (*i.e.*, *Liolaemus* sp. nov. vs *L. multicolor* [0.04%], vs *L. porosus* [0.85%], and vs all other species combined [7.18%]). While in the geographical space, the similarity in their spatial distribution shows a higher proportion (*i.e.*, *L. nov. sp.* vs *L. multicolor* [16.76%], vs *L. porosus* [69.32%], and vs all other species combined [27.17%]).

![FIGURE 2. Distribution of a set of *Liolaemus* species of the *montanus* group in a multivariate morphospace based on the first three PCs calculated from the body size and shape traits described in the methods. All these species occur around the distribution of the focal new species described in this paper. In the figure, filled black circles are the new species, white circles are *L. molinai* from Chile, the stars are *L. multicolor* and the smaller grey circles represent all the remaining species presented in the map of Figure 1. These visual analyses show that the focal new species occupies a distinctive region of the morphospace which significantly differs from the regions occupied by closely related species occurring at similar geographic zones (see Results’ text for quantitative details).](http://example.com/figure2.png)
FIGURE 3. Species Distribution Models of *Liolaemus omorfi* (*Liolaemus* sp. nov.) and its closely related species represented in the environmental (centre) and the geographical space (around). The central figure shows the niche relationship between *L. sp. nov.*, *L. multicolor*, *L. porosus* and the other species (*L. audituvelatus*, *L. chlorostictus*, *L. erguetae*, *L. fabiani*, *L. hajeki*, *L. molinai*, *L. nigriceps*, *L. puritamensis* and *L. rosenmanni*). AUC values show the performance of the models.
Liolaemus omorfi sp. nov.

Description of the Holotype. Male Museo Nacional de Historia Natural, Chile (MNHNCL)-4737, preserved in 80º Ethanol. Collected in quebrada Zorritas (24°37′17.75″S, 68°35′12.73″O, 4200 masl) on April 5th, 2012, by Diego Demangel, Cristian Sepúlveda, Denise Donoso and Herman Núñez.

Paratypes, males MNHNCL-4740, 4741, and 4742; females 4736, 4738, and 4739, same data as holotype, plus MNHNCL-4944 male, and 4945 female. Collected in Quebrada Zorritas, on November 12, 2012, by H. Núñez, D. Demangel and Alfredo Ugarte.

Diagnosis. This species is a Liolaemus because it satisfies all diagnostic features given by Cei (1986: 189) and Pincheira-Donoso & Núñez (2005), e.g., flat body, without dorsal crest of scales, gular area without folds, no swelling fold toward sides, sub cylindrical fingers with keeled lamellae, small and smooth cephalic scales, cilindro conical tail; tricuspid lateral teeth, within other characters (our translation from Cei 1986: 189).

This species belongs to the Eulaemus subgenus because has a bladelike process (Figure 5) associated to the enlargement of the tibialis anticus muscle, the Liolaemus montanus section (see Etheridge 1995, Pincheira-Donoso y Núñez 2005, Abdala et al. 2006 and also Lobo et al. 2010, and Schulte et al. 2000). External character is a large number of supralabial scales, all of them straight, short, no one curved upward, and more than five precloacal pores. According to Lobo et al. (2010: 282) the andinus subgroup of Liolaemus montanus sectios is (sic) “characterized by having very small, juxtaposed or subimbricate dorsal round scales. Lateral scales of their neck are granular, the temporal scales are smooth, and they show strong sexual dichromatism”, all these features are present in L. omorfi, therefore, could be assigned to this lineage. The species belonging to the boulengeti group (sensu Etheridge 1995) have a patch of enlarged scales on the posterior side of the thigh, a feature not observed in L. omorfi. Liolaemus omorfi differs from L. cazianiae, because the last one “has 6-10 dorsolateral bright red spots” (sic, see Lobo et al. 2010: 282), also this character is present in L. nigriceps; instead, no such pattern is found in L. omorfi. Furthermore both species are larger, the largest L. nigriceps individual vouched in MNHNCL has 93.5 mm snout-vent length (MNHNCL-2174); Lobo et al. (2010) reported 76 mm for specimens of L. cazianiae. L. nigriceps has the head with a strong melanism, non present in anyone L. omorfi individuals.

Liolaemus omorfi is smaller than L. foxi, (Núñez et al. 2000) and L. patriciaiturrae (Navarro and Núñez 1993); recently Núñez et al. (2012) described a population of small individuals preliminary assigned to L. foxi, nevertheless the dorsal pattern is strikingly different, these new population of L. foxi has huge patches of jet black areas, feature not present in L. omorfi which is multicolored. According to Lobo et al.
The species *L. multicolor*, *L. ruibali*, *L. orko*, and *L. pulcherrimus* have slightly keeled to strongly keeled scales on dorsum, while the scales in *L. omorfi* have a completely flat surface.

*Liolaemus audituvelatus* and *L. manueli* have the auditive meatus covered partially or fully with scales, whereas *L. omorfi* has naked tympanum; *L. stolzmanni* (ex *L. reichei*, see Langsthrot 2011), *L. torresi* and *L. poconchilensis* have short snout, and, the “eyelids” are swelling scales like a comb, whereas these traits are not seen in *L. omorfi*, which shows short palpebrals scales. *L. rosenmanni* has more than 100 scales around midbody (Núñez and Navarro 1992), *L. halonastes* has 80-97, *L. andinus* has 88-99, *L. andinus* has 98-110 (see Lobo et al. 2010: 287; however, see Troncoso-Palacios 2014, who considers “L. andinus” as nomen dubium); *L. duellmani* has 86-90 (Cei 1986: 227); *L. vallecurensis* has 85 to 95 (Pereyra 1992); *L. robertoi* has 85-94 scales (Pincheira-Donoso and Núñez 2004); *L. pleopholis* has 86-93 scales (this paper); *L. omorfi* has 65, and this last feature is enough to differentiate this species from the related species. *L. omorfi* is the species that exhibits the least amount of scales around midbody among the species so far included into this group. *Liolaemus omorfi* has 14-16 scales along the midline over the dorsum of the head; *L. eleodori* has 24-35 (see Lobo et al. 2010: 283). *Liolaemus huacahuasicus* has larger adult size reaching 75 mm, *L. omorfi* is shorter (see Table 1); dorsal scales in *L. huacahuasicus* are imbricate, slightly keeled, according with the Figure 6 (Laurent 1985: 242) those scales are almost triangular, in *L. omorfi* are smooth, juxtaposed, and those from dorsal surface are definitively quiet smaller than the ventral scales, feature non present in *L. huacahuasicus*.

Cei (1986) reported for *L. famatinae*, these features: keeled dorsal scales, imbricate, usually the nasal scale is contacted with the rostral one. *L. omorfi* has smooth scales, juxtaposed, and, least the sample we have do not show any evidence of contacting rostral-nasal scales.

*Liolaemus omorfi* differs from *L. dorbignyi*, *L. jamesi*, *L. pleopholis*, *L. puritamensis*, *L. schroechichi* and *L. signifer*, because all of them have an adult SVL larger than 70 mm. *L. omorfi* has smooth scales, juxtaposed, and, least the sample we have do not show any evidence of contacting rostral-nasal scales.

*Liolaemus omorfi* differs from *L. dorbignyi*, *L. jamesi*, *L. pleopholis*, *L. puritamensis*, *L. schroechichi* and *L. signifer*, because all of them have an adult SVL larger than 70 mm. *L. omorfi* differs from *L. porosus* and *L. islugensis*, because the latter two species are more plump and the adults exceeds 65 mm SVL and sometimes exceed 70 mm. *L. omorfi* is slender and shorter. In addition, those two species have a higher number of midbody scales, as well as a different dorsal pattern.

The only two specimens that can be attributed to *L. schmidti* are the holotype and a paratype, and both have greater number of midbody (70 and 84 respectively), while the holotype of *L. omorfi* has 63. Moreover, the holotype of *L. schmidti* has the tail longer than one and a half body length, in *L. omorfi* the tail is noticeably short, and throughout the type serie is shorter. In *L. omorfi* tail ratio relative to body decreases as the specimens get greater size and with only two known specimens in *L. schmidti* can be seen that this relationship is reversed. In addition, according to on the location provided by Marx (40 miles east of San Pedro de Atacama) both locations are separated by 220 km in a straight line and a fairly rugged terrain.
Description of the Holotype

Head length 13.62 mm, width head length 9.63 mm, height of the head 7.04 mm. Prismatic rostral, 3 to 4 times wider than its height, surrounded by six scales. Rostral separated of the nasal, a lorilabial scales is in between those scales. Two tiny quadrangular postrostral shields. Four internasals, the most external are smaller in comparison with the medial ones. Three small and irregular unpaired scale of the snout, surrounded by eight scales like a rosette, the nasorostral set of scales. Two tiny prefrontals. Two frontal azigous, two postfrontal. Quite small interparietal, irregular in shape, contacted with six scales, the epifisial organ appears quite small. Parietal shields similar size than interparietal, these scales are separated by tiny scales, these parietals are confused with the surrounded ones, very undifferentiated. Irregular supratemporal scales, juxtaposed, smooth and slightly convexed. Smooth temporal scales, irregular shape, juxtaposed, similar to those covering the supratemporal area. Anterior border of auditive meatus with a conspicuous auricular scale, but without tympanic scales on the anterior edge of the meatus. Non deep tympanus, instead it is shallow. 10/10 supralabial scales, almost square shaped. Only one line of lorilabial scales. A subocular shield upcurved on its tips, extended from the 4th to the 7th supralabials. 6/6 loreal scales. Sensorial organs oversparsed on the internasal scales, and concentrated on the lorilabial shields. Thirty supraocular shields on the left ocular fossa, and 28 on the right one. 5/5 superciliars long and narrow, slanted. Twelve inferior palpebral shield on the left eye, also 12 on superior eyelid. On right eye there are 13 superior palpebral and 11 on the inferior one. At the tip of each scales there are sensory organs. Sinfinisial higher than rostral, as wide as the rostral scale. Four postsinfinisial on right hand side and three on the left one. Covering scales of the throat smooth, rounded, juxtaposed, those close to the chest are slightly imbricate. Seven infralabial scales on left, and six in right.

Antehumeral pocket clearly defined; a fold of skin extended toward the head, it reaches, toward anterior, the auditive area, spreading into to two folds like a V, straddling the meatus. These folds are not projected to the gular area. Scales covering the neck, by lateral are granular, smooth, juxtaposed. Without heteronotes.

Dorsal scales are rounded, smooth subimbricated, almost juxtaposed. Scales covering the belly almost quadrangular, smooth, subimbricated, bigger than those of the back. Without heteronotes. In the

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holotype, there are 63 scales around midbody. Scales on the dorsum are smaller than those of the belly. Dorsal scales on the humeral segment are triangular, the free tip is rounded, smooth and imbricate; ventrally the humeral area is covered with granular, smooth and juxtaposed scales. Dorsal radio-ulnar area covered with round, smooth and imbricate scales, by ventral is covered with rounded, smooth and imbricate scales, without heteronotes. Dorsal scales of the hand similar sculation than those of the foreleg. Palm covered with rhomboidal, and slightly keeled scales. Transversal lamellae, with three keels, imbricate; there are 18 lamellae under the third finger of the left hand. Digits sequence 3-4-2-5-1. Femoral area, by dorsal view, covered with rounded, subimbricate and smooth scales. Tibial zone by dorsal view is covered with rounded, smooth and imbricate scales. Femoral scales by ventral view are rounded, smooth and imbricate. Tibial area by ventral view covered with rounded, smooth and imbricate scales. There are not a patch of swelling scales behind the femoral area. The front (outer area) is covered with granular scales; there is no transition of scales size. Plant covered with rounded, smooth subimbricate scales, with free edge non toothed by indentations. Transversal lamellae slightly keeled, imbricate, toothed free edge. There are 23 lamellae under the fourth finger. Dorsum of the tail covered with smooth, rounded and imbricate scales. Those of the ventral surface are rhomboidal, smooth and imbricate. Six precloacal pores arranged in just one line.

Dorsal colours pattern; this description of dorsal pattern follows Hellmich’s (1934) design.
Narrow occipital band, pale grey in color, involving 2 to 4 scales. At the edge of this band there are dark spots, underlined by a clearer spots. The occipital band runs from the pileus and reaches the base of the tail. Parietal bands reddish in color, or brownish, involving 5 to 7 scales, running from the pileus area till the beginning of the tail.
A band starting from the eyes has dark spots, these spots has groups of bluish scales in number of three blue scales and other just one scale, this band runs by the sides of the animal and reaches beyond the end of the tail. Also this animal has a maxillary band, brownish in color. A lines runs from the axilla to the
groin, this character is present either in males as in females. Belly without design. Gular area with small spots, almost arranged suggesting diffuse lines.

Variation. Midbody scales have a range within 60 to 68, media: 64.9. Males do not have heteronotes on the dorsal surface; nevertheless the females have those tiny scales surrounding the bigger ones.

![Figure 7. Female (above) and holotype of *Liolaemus omorfi*. Photographs taken in Quebrada Zorritas, Antofagasta, Chile.](image)

This species shows sexual dimorphism, the pattern of females is different than that of the males. Here we describe the female’s pattern: general color brownish with black dots irregularly over sparse by all the back, even reaching the lateral areas, however these dots, just on the vertebrae, dots do not cross the animal back, forming a tenuous occipital band, brownish in color. Two diffuse band reddish or yellowish in color running from the parietal area to the nearby of the tail (Figure 8). At both sides of the back, there is a clearer line running from the axilla to the groin. These lines are present either in males as in females. Belly of the female does not have pattern and just can be seeing small dots involving a single scale a little bit darker. Slightly marmoreous throat. Yellowish hands and feet, either for male and females.

![Figure 8. Female with yellowish pattern. Photographs taken in Quebrada Zorritas, Antofagasta, Chile.](image)
Etimology

*Liolaemus* means “smooth throat”, the Greek term omorfi (όμορφη) means beautiful, gorgeous. It is pronounced “ómorfi”. Given the intense coloration presented by this species, particularly in the adult males, we propose to give it the common name “Beautiful lizard” and in Spanish “Lagartija hermosa”.

*Liolaemus omorfi* is known from its *terra typica*, ranging between 4170 to 4250 masl, in the nearby area of the Llullaillaco National Park, located in the Andean range of the Antofagasta Region. Some individuals were found 10 kilometers from the border with Argentina, which makes as presume that this species is highly likely to inhabit this country (a speculation quantitatively supported by the reconstructed SDMs presented in Figure 3, which identifies a common area between Chile and Argentina as suitable environments for *L. omorfi*). There are two related populations that can be assigned to this species, one in Los Flamencos National Reserve (Miscanti and Miñique lagoons sector), within 4150 and 4200 masl, and another one in Salar de Aguas Calientes III, close to the Salar de Talar, within 3950 and 4150 masl, also in the Antofagasta Region.

Individuals were found on the ground and on rocks of about one meter in diameter, and at about two meters at the sides of the bottom of the ravine, also in the adjacent slopes reaching 50 m above the bottom.
The bottom of the ravine has permanent surface water and three species of grasses have been recorded: *Deyeuxia* sp., *Festuca* sp. and *Pappostipa* sp.

Slopes have a sandy substrate and, in some areas, there are outcropping rocks of about one meter in diameter. In these microhabitats, a number of herbaceous and bushy vegetation species have been found, such as *Fabiana* bryoides, *Parastrephia* quadrangularis, *Baccharis tola*, *Senecio adenophyllus*, *Pappostipa* sp. and *Maihueniopsis* sp.

A number of mammal species have been observed in the *terra typica* of *L. omorfi*, including *Puma concolor*, *Lycalopex culpaeus*, *Vicugna vicugna*, *Equus asinus*, *Ctenomys* sp., *Phyllotis xanthopygus* and *Abrothrix andinus*. Birds are also found, which include species such as *Bubo magellanicus*, *Buteo polosoma, Gallinago andina*, *Phrygilus atriceps*, *Phrygilus gayi*, *Phrygilus plebejus*, *Phrygilus unicolor*, *Sicalis olivascens*, *Asthene modesta*, *Cinclodes atacamensis*, *Geositta isabellina*, *Geositta punensis*, *Leptasthenura aegithaloides* y *Agriornis montanus*. In terms of lizard biodiversity, two other *Liolaemus* species (*Liolaemus nigriceps* and *Liolaemus porosus*) have been recorded. Interestingly, the latter is recorded for the first time in Chile; it has so far being known exclusively from Argentina.

During our field explorations carried out in 2012, 2013 and 2014, active animals were found between November and early May. In similar abundances either in both sunny and cloudy days. *Liolaemus omorfi* appears to be a rare animal with low population density. The maximal number of individuals were up to seven during one trip. In windy days we were unable to see active animals.

The faeces have vegetal fibers and insects fragments. In the field we saw that *Liolaemus omorfi* predates upon insects. No information is available about the parity mode of this species.

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Tibia figure was drawn from a dental radiograph made by Dr. Juan José Latorre Astaburuaga and Mrs. Patricia Novoa. Many thanks.

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BIBLIOGRAPHIC REFERENCES

ABDALA, V., C.S. ABDALA, and M.J. TULLI  

ABDALA, C.S., M.M. PAZ and R.V. SEMHAN  

ALBINO AM.  

ANTONELLI, A., J.A.A. NYLANDER, C. PERSSON and I. SAN MARTÍN  
2009 Tracing the impact of the Andean uplift on Neotropical plant evolution. Proceedings of the National Academy of Sciences USA, 106:9749-9754.

CEI, J. M.  
1986 Reptiles del Centro, Centro-Oeste y Sur de la Argentina. Museo Regionale di Scienze Naturali, Monografia IV, Torino, Italy.


ESCOBAR HUERTA, G., J. SANTIBÁÑEZ TORO and J.C. ORTIZ  
ESPINOZA, R.E., J.J. WIENS and C.R. TRACY

ETHERIDGE, R.

FONTANELLA, F.M., M. OLA VE, L.J. A VILA, J.W. SITES and M. MORANDO

GREGORY-WODZICKI K.M.

HARMON, L.J., J.A. SCHULTE, A. LARSON and J.B. LOSOS

HELLMICH, W.

HUGHES, C. and R. EASTWOOD
2006 Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. Proceedings of the National Academy of Sciences USA, 103:10334-10339.

LABRA, A., J. PIENAAAR and T.F. HANSEN

LANGSTROTH, R.P.

LAURENT, R.F.

LAURENT, R.F.

LAURENT, R.F.

LAURENT, R.F.

LOBO, F., D. SLODKI and S. VALDECANTO

NAVARRO, J. and H. NÚÑEZ

NORAMBUENA, E., L. LEFFLER-GRiffin, A. MAO, T. DIXON, S. STEIN, I.S. SACKS, L. OCOLA and M. ELLIS

NÚÑEZ H and J. NAVARRO
NÚÑEZ, H., J.YÁÑEZ and J.C. TORRES-MURA

NÚÑEZ H., J.NAVARRO and A. VELOSO
2000 Liolaemus foxi, una nueva especie de lagarto para el norte de chile (Squamata: Reptilia: Sauria Boletín del Museo Nacional de Historia Natural 49: 117-130.

PADIAL, J.M., A. MIRALLES, I. DE LA RIVA and M. VENCES

PEREYRA, E.A.
1992 Nueva especie de lagarto andino: Liolaemus vallecurensis (Tropiduridae, Liolaeminae). Noticiario Mensual del Museo Nacional de Historia Natural, Santiago (Chile) 321: 10-14

PETERS, J.A.

PINCHEIRA-DONOSO, D.

PINCHEIRA-DONOSO, D., A.M. BAUER, S. MEIRI and P. UETZ

PINCHEIRA-DONOSO, D., L.P. HARVEY and M. RUTA

PINCHEIRA-DONOSO, D., D.J. HODGSON, J. STIPALA and T. TREGENZA

PINCHEIRA-DONOSO, D., D.J. HODGSON and T. TREGENZA
2008a The evolution of body size under environmental gradients in ectotherms: why should Bergmann’s rule apply to lizards? BMC Evolutionary Biology, 8: 68.

PINCHEIRA-DONOSO, D. and J. HUNT

PINCHEIRA-DONOSO, D. and H. NÚÑEZ

PINCHEIRA-DONOSO, D. and H. NÚÑEZ

PINCHEIRA-DONOSO, D., J.A. SCOLARO and P. SURA

PINCHEIRA-DONOSO, D. and T. TREGENZA

PINCHEIRA-DONOSO, D., T. TREGENZA and D.J. HODGSON

PINCHEIRA-DONOSO, D., T. TREGENZA, M.J. WITT and D.J. HODGSON
2013a The evolution of viviparity opens opportunities for lizard radiation but drives it into a climatic cul-de-sac. Global Ecology and Biogeography, 22, 857-867.

QIAO, H., J. SOBERÓN, L.E. ESCOBAR, L. CAMPBELL and A.T. PETERSON

QUINTEROS, A.S., C.S. ABDALA and F.J. LOBO
DEMANGEL et al. / Liolaemus omorfi, a New Species of Lizard, from Northern Chile

SCHULTE, J.A., J.B. LOSOS, F.B. CRUZ and H. NÚÑEZ

SCHULTE, J. A., II., J. R. MACEY, R. E. ESPINOZA, and A. LARSON

TORRES-PÉREZ, F., M.A. MÉNDEZ, E. BENAVIDES, R.A. MORENO, M. LAMBOROT, R.E. PALMA and J.C. ORTIZ

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