



Liolaemus carlosgarini and *Liolaemus riodamas* (Squamata: Liolaemidae), two new species of lizards lacking precloacal pores, from Andean areas of central Chile

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Abstract

Most of the lizards of the *Liolaemus* genus present precloacal pores in males, with few exceptions in species of the *lineomaculatus* and *neuquensis* groups, and in the *elongatus-kriegi* complex. The *elongatus-kriegi* complex, belonging to the *Liolaemus* (*sensu stricto*) subgenus, is composed of medium sized, saxicolous, viviparous and insectivorous or omnivorous lizards, distributed between the Andean and Patagonian zones of Chile and Argentina. We reviewed the taxonomic history of this group, and we describe two new species, *Liolaemus carlosgarini*, found in the vicinity of the Maule Lagoon, in the Maule Region, Chile, and *Liolaemus riodamas*, described from the population that was originally designated as *Liolaemus cf. ceii*, from Las Damas River, near the Termas del Flaco locality, in the Libertador Bernardo O'Higgins Region, thereby based on this research *L. ceii* is eliminated from the species belonging to Chile.

Both species have as a diagnostic character the absence of precloacal pores, and we suggest here their presumptive systematic relationships in *Liolaemus*. We analyzed ten species of *Liolaemus*, in order to perform a phylogenetic analysis based on external morphology, using mostly squamation and morphometric characters. The analysis was performed using PAUP, with the Maximum Parsimony criterion. In addition, through diaphanisation, we studied and described the osteology of the new species. We conclude that species lacking precloacal pores do not form a monophyletic group, and that constructing a phylogeny using only external morphology, at least for this group of reptiles, is insufficient to establish solid phyletic relationships. Other sort of characters should complement the morphological ones.

Key words: Reptilia, Andes Cordillera, *elongatus-kriegi* complex, osteology, taxonomy

Resumen

La mayoría de las especies de lagartos del género *Liolaemus* presentan poros precloacales en los machos, con excepciones en especies de los grupos *lineomaculatus*, *neuquensis* y el complejo *elongatus-kriegi*; este último, del subgénero *Liolaemus* (*sensu stricto*), se compone de lagartos de tamaño medio, saxícolas, vivíparos e insectívoros u omnívoros, distribuidos entre las zonas andinas y patagónicas de Chile y Argentina. Revisamos la historia taxonómica de este grupo y describimos dos nuevas especies, *Liolaemus carlosgarini*, que se registra en las cercanías de Laguna del Maule, Región del Maule, y *Liolaemus riodamas*, descrita a partir de la población que originalmente había sido designada como *L. cf. ceii*, del Río Las Damas, cerca de la localidad de Termas del Flaco, Región del Libertador Bernardo O'Higgins. Por lo tanto, sobre las bases de las investigaciones efectuadas, se elimina a *L. ceii* de las especies presentes en territorio chileno.

Ambas especies presentan como carácter diagnóstico la ausencia de poros precloacales, y sugerimos aquí sus posibles relaciones sistemáticas en el género *Liolaemus*. Se analizaron especímenes de lagartos pertenecientes a diez especies de *Liolaemus*, con el objetivo de realizar un análisis filogenético basado en morfología externa, usando caracteres en su gran mayoría de lepidosis y morfométricos. El análisis se realizó con PAUP, usando el criterio de Máxima Parsimonia. Además, a través de diafanización, estudiamos y describimos la osteología de las nuevas especies. Concluimos que las especies carentes de poros precloacales no forman un grupo monofilético, y que construir una filogenia usando solo caracteres exomorfológicos, por lo menos para este grupo de reptiles, no basta para establecer relaciones filéticas sólidas. Otro tipo de caracteres debiera complementar a los morfológicos.

Palabras clave: Reptilia, Cordillera de los Andes, complejo *elongatus-kriegi*, osteología, taxonomía

Introduction

The genus *Liolaemus* (Wiegmann 1834), included within the iguanid family Liolaemidae (Frost *et al.* 2001) now approaches more than 230 described species, reaching the status of the second most diversified reptilian genus on the planet after *Anolis* (Pincheira-Donoso & Núñez 2005; Pincheira-Donoso *et al.* 2008; Lobo *et al.* 2010; Breitman *et al.* 2011). *Liolaemus* is distributed in Argentina, Bolivia, Brazil, Chile, Paraguay, Peru and Uruguay, from 0 to 5000 m, and in a wide diversity of environments. Most of the species occur in high Andean environments, possibly due to the formation of the Andes, active during the Miocene, that would have originated multiple vicariant speciation events (Ceï 1986; Pincheira-Donoso & Núñez 2003). Species descriptions of the genus have enormously increased during the last two decades, with several taxa described per year (Etheridge & Espinoza 2000; Lobo *et al.* 2010).

Laurent (1983, 1985, 1995), and supported by Etheridge (1995), split the genus into two groups; the “Chilean” group, or subgenus *Liolaemus (sensu stricto)*, and the “Argentinean” group, or subgenus *Eulaemus*, mostly distributed west and east of the Andes, respectively. *Liolaemus (sensu stricto)* is characterized by four or five flat and anteroposteriorly elongated supralabials, with the fourth or fifth curved upwards in the posterior margin, a reduction in the number of preloacal pores (generally four or less), lateral nostrils and a fused Meckel’s groove. *Eulaemus* is characterized by short and tall supralabials, in general five or more, with the last one lacking a curvature in the posterior margin, five or more preloacal pores, dorsolateral nostrils, a hypertrophied puboischiotibialis muscle and a blade-like tibial process. This proposal has had strong support from subsequent analyses using both molecular and morphological evidence (Young-Downey 1998; Etheridge 2000; Schulte *et al.* 2000; Espinoza *et al.* 2004; Cruz *et al.* 2005; Pincheira-Donoso & Núñez 2005; Abdala 2007).

The vast majority of the *Liolaemus* species have preloacal pores in males, with few exceptions belonging to the *lineomaculatus* and *neuquensis* groups, and within the *elongatus-kriegi* complex. The *elongatus-kriegi* complex, of the subgenus *Liolaemus (sensu stricto)*, consists of medium-sized lizards (up to 112 mm snout-vent length), saxicolous, viviparous and insectivorous or omnivorous, inhabiting between 350 and 3900 m (Morando *et al.* 2003), distributed in the Andean and Patagonian regions of Chile and Argentina. The systematic relationship of this complex with other groups of *Liolaemus* is subject to much debate, thus it appears relevant to make a brief historical review of the taxonomy and systematics of this group and other species lacking preloacal pores.

Ceï (1974) achieved the first formal review and definition of the *elongatus* group, which included *L. elongatus elongatus* {=*L. elongatus* (Koslowky, 1896)}, *L. elongatus petrophilus* {=*L. petrophilus* (Donoso-Barros & Ceï 1971)} and *L. austromendocinus* (Ceï 1974). Later, Ceï (1975) would find the *elongatus* group closely related to the species of the *kriegi* group based on serological evidence. Ceï (1986) included in this last group *L. kriegi* (Müller & Hellmich 1939), *L. ceii* (Donoso-Barros 1971), and *L. buergeri* (Werner 1907). At first, Núñez *et al.* (1991) ascribed the newly described *L. cristiani*, lacking preloacal pores, to the *kriegi* group, for sharing common traits with this group of species, e.g., keeled scales on the dorsal midline, and smooth or scarcely keeled lateral scales. Later, Núñez & Torres-Mura (1992) added *Liolaemus cf. ceii* to the Chilean herpetofauna, based on some specimens collected in Las Damas River, east of Termas del Flaco, in the mountain region of San Fernando, Maule Region. Nevertheless they mentioned existing differences in squamation and pattern with the original description of *L. ceii*, whose type locality is Lonco Luan, Neuquén, Argentina.

When Videla & Ceï (1996) described *L. thermarum* they linked this species to *L. cristiani*, *L. coeruleus* (Ceï & Ortiz, 1983) and *L. neuquensis* (Ceï 1986) because all of them lacked preloacal pores. Espinoza *et al.* (2000) and Espinoza & Lobo (2003) included *L. thermarum* into the *elongatus* group, but they misidentified the sample collected at the Niña Encantada Lagoon, Malargüe, Mendoza, Argentina, which in fact belonged to *L. austromendocinus*, after Ceï & Videla (2003). In addition, these latter authors proposed the *neuquensis* group, which included the newly described *L. flavipiceus*, and *L. coeruleus*, *L. cristiani*, *L. neuquensis* and *L. thermarum*, which shared the absence of preloacal pores, and which were similar in squamation and dorsal coloration pattern. Therefore, it was possible to separate them from the *elongatus* group.

Espinoza *et al.* (2000) and Espinoza & Lobo (2003) included in the *elongatus* group (besides the already mentioned *L. thermarum*), *L. austromendocinus*, *L. capillitas* (Hulse 1979), *L. dicktracyi* (Espinoza & Lobo 2003), *L. elongatus*, *L. heliodermis* (Espinoza *et al.* 2000), *L. petrophilus* and *L. umbrifer* (Espinoza & Lobo 2003). Even with the differences between the *elongatus* and *neuquensis* groups, some authors have mentioned their possible close phyletic relations, especially because of the extreme reduction in the number of preloacal pores, totally

absent in the *neuquensis* group, and with a notable reduction in the *elongatus* group (Espinoza *et al.* 2000; Cei & Videla 2002; Espinoza & Lobo 2003). Schulte *et al.* (2000) recovered as monophyletic the clade formed by *L. buergeri* and *L. ceii*, with *L. leopardinus* (Müller & Hellmich 1932) as a sister clade of them, and as a sister clade to all the species in the clade mentioned above, they present *L. petrophilus*, *L. austromendocinus* and *L. elongatus*. It is also worth noting that *L. coeruleus* is recovered in a separate clade distant to the species just mentioned.

Morando *et al.* (2003) and Avila *et al.* (2004) concluded in their molecular phylogenies that the *elongatus* and *kriegi* groups are more closely related to each other than with the *petrophilus* group, an idea that had been previously suggested by Cei (1979). The sister taxon of the clade formed by the *petrophilus*, *elongatus* and *kriegi* groups is *L. punmahuida* (Avila *et al.* 2003, Avila *et al.* 2010, Avila *et al.* 2012). Finally, Morando, in the mentioned work and in a subsequent one (2004), did not recover the *neuquensis* group as part of the *elongatus* clade.

Pincheira-Donoso & Núñez (2005) added to the *elongatus* group the Chilean species *L. leopardinus*, *L. ramonensis* (Müller & Hellmich 1932) and *L. valdesianus* (Hellmich 1950), pointing out that those species showed evident affinities with *L. elongatus*, being more divergent as they ranged to the north, with *L. leopardinus* being the more distant, and *L. valdesianus* the nearest, to *L. elongatus*. Finally, considering morphological and biogeographical similarities, Pincheira-Donoso & Núñez (2005) added *L. villaricensis* (Müller & Hellmich 1932), *L. chillanensis* (Müller & Hellmich 1932) and *L. curis* (Núñez & Labra 1985) to the *elongatus* group. These authors left *L. cristiani* out of the *kriegi* group, leaving it in the *neuquensis* group, as proposed by Cei & Videla (2002, 2003), along with the other species lacking precloacal pores. In the morphology-based phylogeny done by Lobo (2005), the *kriegi* group appears more closely related to the *leopardinus* group than to the *elongatus* or *petrophilus* groups. In addition, *L. coeruleus* and *L. neuquensis* once again are not recovered as closely related to any species of the *elongatus-kriegi* complex, and *L. cristiani* is shown in the *kriegi* group in one of the cladograms presented in the study, but never related to the *neuquensis* group.

Lobo *et al.* (2010), based on a consensus of several studies (Etheridge 1995; Schulte *et al.* 2000; Lobo 2001, 2005; Espinoza *et al.* 2004; Abdala 2007), proposed the evolutionary groups of Liolaemidae, thus leaving each group of interest in this study as follows: *leopardinus* group: *L. frassinetti* (Núñez 2007), *L. leopardinus*, *L. ramonensis* and *L. valdesianus*; *kriegi* group: *L. buergeri*, *L. ceii*, *L. cristiani* and *L. kriegi*; *chillanensis* group: *L. chillanensis* and *L. villaricensis*; *elongatus* group: *L. austromendocinus*, *L. elongatus*, *L. flavipiceus*, *L. gununakuna*, *L. parvus* (Abdala *et al.* 2010), *L. petrophilus*, *L. punmahuida*, *L. thermarum* and *L. tregenzai* (Pincheira-Donoso & Scolaro, 2007), including inside the latter group the *capillitas* group: *L. capillitas*, *L. dicktracyi*, *L. heliodermis*, *L. talampaya* (Avila *et al.* 2004), *L. tulkas* (Quinteros *et al.* 2008) and *L. umbrifer*. *L. coeruleus* and *L. neuquensis* are included in the *pictus* group. Abdala *et al.* (2010) described three new species that were included in the *elongatus* group (*sensu* Lobo *et al.* 2010): *L. smaug*, *L. choique* and *L. shitan*.

In the current study we describe two new species, *Liolaemus carlosgarini*, occurring in the vicinity of the Maule Lagoon, Maule Region, Chile, a few kilometers away from the border with Argentina, and *Liolaemus riodamas*, described from the population that was originally designated as *L.cf. ceii* from Las Damas River, near Termas del Flaco, Libertador Bernardo O'Higgins Region, Chile. Therefore, based on our conclusions, *L. ceii* is eliminated from the list of species that inhabit the Chilean territory. Both species lack precloacal pores, and we suggest here their possible systematic relations within the *elongatus-kriegi* complex. In addition, we performed osteological descriptions of the new species, because these characters will be useful to compare with other species whose osteology could be described.

Materials and methods

The specimens used in this study are deposited in several collections. The herpetological collection of the National Museum of Natural History of Chile (MNHNCL) has *Liolaemus carlosgarini*; *L. riodamas*; *L. flavipiceus*; the paratypes of *L. buergeri* from El Planchón, mountain region of Curicó; *L. buergeri* from Pichuante, Teno River; *L. cristiani*; *L. leopardinus* and *L. monticola*. The zoological collection of the Universidad de Concepción (MZUC) has *L. kriegi* from the mountain region of Curicó and from Malleco, Antuco Volcano. The Argentinean specimens were obtained from the personal collection of A. Scolaro (JAS-DC) (*L. ceii* from Lonco Luan, Neuquén, the type locality; *L. kriegi* from Primeros Pinos, Neuquén, and from Jacobacci, Rio Negro; *L. buergeri* from Copahue, Neuquén; and *L. elongatus* from the Sierra San Bernardo, Chubut and from Jacobacci, Rio Negro).

An additional sampling of *L. riodamas* was held in Las Damas River, north-east of the origin of the Tinguiririca River, during February of 2011. Seven specimens were captured using a loop of fishing line tied to a fishing rod, or by hand, and then sacrificed with an intraperitoneal injection of dimecaine (2%) and preserved in alcohol (70%).

The data to perform the diagnosis of the new species that was not obtained from our samples was obtained from Cei (1986), Espinoza *et al.* (2000), Cei & Videla (2003), Avila *et al.* (2003), Espinoza & Lobo (2003), Avila *et al.* (2004), Pincheira-Donoso & Núñez (2005), Pincheira-Donoso & Scolaro (2007), Abdala *et al.* (2010) and Avila *et al.* (2010).

One hundred and ten specimens were analyzed (see Appendix), belonging to ten different species of *Liolaemus*, in order to perform a phylogenetic analysis based on external morphology using 141 traits, mostly of squamation and morphometric. The character matrix originally contained 161 traits, then we omitted traits that presented more variability within than between populations, as well as pattern traits, because some samples that were important were too old and badly preserved, and no pattern was left to see. *L. monticola* was used as the outgroup. The analysis was performed using PAUP Version 4.0b10 for Macintosh, using the Maximum Parsimony criterion, with all traits having the same weight assigned, and bootstrap values obtained with 1000 pseudoreplicates.

Specimens of *L. riodamas* and *L. carlosgarini* were diaphonized, after Mahoney (1973), in order to describe their osteology. Measurements were taken with a caliper, precision 0.1 mm, following the criteria of Peters (1964).

Results

Liolaemus carlosgarini sp. nov.

Figures 1 to 4

Holotype. MNHNCL-4563. Male, collected by Carlos Garín at International Road 115, below the Maule Lagoon. 19 H 358560 E-6018117 S. 1915 masl. WGS84. On February 22, 2008.

Paratypes. MNHNCL-4562 and one used for diaphanisation, males; MNHNCL-4561, 4564, 4565, 4566, 4567, 4568 and one used for diaphanisation, females. Same collection data as the holotype. Measurements in Table 1.

TABLE 1.—Measurements (in mm) of the *L. carlosgarini* sample including holotype plus paratypes. Captions are: MNHNCL, Museo Nacional de Historia Natural, Chile; F, female, M, male; SVL, snout vent length; AGD, axilla-groin distance; FLL, forelimb length; HLL, hindlimb length; TL, tail length; MBS, midbody scales; HL, head length; HW, head width; HH, head height; reg, regenerated.

MNHNCL	Sex	SVL	AGD	FLL	HLL	TL	MBS	HL	HW	HH
4561	F	68,8	29,65	25,11	39,16	reg.	94	14,7	11,25	7,27
4562	M	61,25	27,59	21,74	40,6	111	90	14,66	12,3	8,82
4563	M	65,35	29,12	25,07	37,23	89	95	15,59	12,05	9,91
4564	F	54,86	24,62	22,65	32,53	85	95	12,88	9,98	8,52
4565	F	60,31	25,41	22,33	33,36	reg.	93	12,36	10,1	7,54
4566	F	62,26	26,37	23,57	36,41	113	95	13,96	10,17	6,9
4567	F	53,46	22,65	23,57	36,78	102	86	13,17	9,93	6,97
4568	F	59,28	27,95	22,42	38,89	cut	-	12,82	9,95	6,55
Mean		60,7	26,67	23,31	36,87	100	92,57	13,77	10,72	7,81
SD		4,73	2,22	1,18	2,62	11,31	3,16	1,06	0,94	1,09

Etymology. We dedicate this species to Carlos Garín, who besides being a good friend, collected these specimens, and provided great assistance. We propose as a common name "Garín's Lizard", and "Lagartija de Garín" in Spanish.



FIGURE 1.—Holotype of *Liolaemus carlosgarini*. MNHNCL-4563

Diagnosis. Small to medium sized lizard, with a mean SVL (Snout-Vent Length) of 60.7 mm and a maximum of 68.8 mm. Slender body, moderately robust limbs, head longer than wide, tail over 1.5 times body length, and 86-101 scales around midbody. Background dorsal coloration is ochre, with a dark occipital stripe, parietal stripes as the background color, and lateral stripes the same coloration as the occipital stripe. Black spots distributed variably between the dorsal region of the head and limbs. Individual white scales scattered on the dorsal region of the body, and a clear and mottled ventral region. It can be distinguished from almost all of the species of the *elongatus-kriegi* complex by its extreme reduction of precloacal pores. None of the male samples, despite being only three, had these pores, and it seems that a very low frequency of males has them (C. Garín *in litt.* 2011). Because the absence of precloacal pores is not absolute in this species, minimum diagnostic traits to distinguish it from all the species of the *elongatus-kriegi* complex are given.

L. carlosgarini is distinguished from *L. austromendocinus*, *L. elongatus*, *L. gununakuna* (Avila *et al.* 2004), *L. petrophilus*, *L. choique*, *L. shitan*, *L. capillitas*, *L. dicktracyi*, *L. heliodermis*, *L. talampaya*, *L. antumalguen* (Avila *et al.* 2010), *L. umbrifer* and *L. burmeisteri* (Avila *et al.* 2012) because all of these species have a significantly larger SVL (with a maximal SVL ranging from 82 mm in *L. heliodermis* to 107.8 mm in *L. antumalguen*). In addition, all of them exhibit a lower number of scales around midbody. The only species that overlaps that number with *L. carlosgarini* (86–101), is *L. gununakuna* (84–97), but the latter has iridescent yellow body coloration, with dark transversal bars, very distinguishable from the ochre coloration and longitudinal stripes in *L. carlosgarini*. Finally, none of the species mentioned above exhibit the design pattern of *L. carlosgarini*, with longitudinal stripes. It is worth noting the striking exomorphological similarity *L. carlosgarini* has with *L. smaug*, which in addition is found relatively close to the type locality of *L. carlosgarini* (between Las Loicas and Volcán Peteroa provincial road, Malargüe, Mendoza, Argentina: 35°39'51,3"S; 70°12'00,9"W, 1688 m), but it differs from this species because *L. smaug* has a lower number of scales around midbody (73–80), in addition to a constant presence of precloacal pores in males (3–4) (Abdala 2010; Abdala *in litt.* 2011). Sexual dichromatism has not been observed in *L. carlosgarini* as in *L. smaug*, nor have golden yellow specimens of *L. carlosgarini* been observed, but this trait deserves further analysis of live specimens.

From *L. cristiani* it can be differentiated because *L. cristiani* has a very dark and pronounced melanistic stripe on the flanks (quite different from the paler stripe in *L. carlosgarini*), and in the absence of an occipital stripe, present in *L. carlosgarini*. *L. cristiani* is larger (mean SVL of 70.67 vs. 60.7 mm), and has fewer number of scales around midbody (83–89 vs 86–101), although these values overlap.

It is differentiated from *L. ceii*, *L. kriegi*, *L. buergeri*, *L. ramonensis*, *L. valdesianus* and *L. leopardinus* because all of them are larger, the smallest being *L. buergeri* from Pichuante in Teno River, Chile, with a mean SVL of 73.2 mm and a maximum of 87.2 mm. All of these species have precloacal pores and differences in pattern, coloration and squamation. Nevertheless, *L. leopardinus* males lacking pores can be found, although the exomorphological differences, especially in pattern, are very notorious. From *L. coeruleus* and *L. neuquensis* it can be distinguished by the blue or greenish ventral coloration in both species, and in having fewer scales around midbody. From *L. thermarum*, *L. punmahuida*, *L. flavipiceus*, *L. tregenzai* and *L. riordamas* it can be differentiated because all of these have a lower number of scales around midbody, larger size, and a uniform pattern, opposed to the well-defined design in *L. carlosgarini*.

Description of the holotype. Male, with SVL of 65.35 mm. Head slightly longer than wide: 15.59 mm long (from the anterior edge of the ear opening to the point of the snout), 12.05 mm wide (between the anterior edges of the ear openings) and 9.91 mm high (at the level of the anterior edge of the ear openings). Snout length (from the anterior margin of the eye to the rostral scale): 4.02 mm. Neck slightly wider than head, effect of the transversal folds of the neck. Hind limb extended forward barely exceeds the armpit. The tail length is 1.36 times the SVL. It lacks precloacal pores.

Rostral scale rectangular, 2.3 times wider than high and in contact with eight scales, including the nasals, which touch the rostral with only the anterior corner of the scale. Nasals polygonal, the nostril located posteriorly, occupying half of the scale's surface. Two postrostrals elongated laterolaterally, followed by four internasal scales, being the two medial ones about four times larger than the side ones. Two frontal azygos, the anterior two times longer than the posterior. Six frontonasals in contact with the frontal azygos. Two prefrontal scales, and the frontal divided transversely; the anterior larger than the posterior. Four small postfrontals. Interparietal pentagonal, posteriorly elongated, in contact with five scales. A gray pineal eye in the middle of interparietal scale. The two parietal scales are about twice the size of the interparietal. The scales in the nuchal and supratemporal regions are small, polymorphic, juxtaposed and generally smooth, with small ridges on some scales. 7-6 large supraoculars, accompanied by 21-18 small supraoculars. 6-8 very elongated and imbricate superciliary scales, excluding the canthal. Numerous scale organs on all the dorsal region of the head, increasing in numbers towards the anterior part of the head. 7-6 loreal scales, excluding the canthal, and a large and elongated subocular scale that spans the entire length of the eye. 7-7 lorilabial scales, in one row, being the sixth one the most elongated. 7-6 supralabials, fifth-fourth one more elongated and curved upwards posteriorly. It has a slightly elongated snout, with the loreal distance (distance between the anterior margin of the eye and the rostral scale) greater than the ocular diameter. The scales in the anterior border of the eye are elongated and overlapping, each one with a scale organ on it. 16–19 upper and 16–15 lower palpebrals, all squared and each one with a scale organ on it. Temporal scales rounded, smooth and subimbricate. Auricular scale is poorly developed but distinct.

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FIGURES 2 to 4.—Different morphotypes of *Liolaemus carlosgarini*. Pictures: Carlos Garín.

Tympanic scales small and highly convex. Scale organs present in all the lateral region of the head, being especially numerous in the lorilabial and loreal scales. Mental scale barely wider than rostral, but notably higher, and in contact with four scales. Five pairs of postmentals, the second pair separated by two scales. 5-5 infralabials, with scale organs scattered on them. Scales on the gular region rounded, smooth and imbricate. Lateral region of neck with two prominent transversal folds. Neck scales small, convex, granular and with very small granular scales in the interstitial space.

Dorsal scales small, the same size as the ventral scales. They vary from rounded to subtriangular, and from juxtaposed to subimbricate. Moderate keels on the mid-dorsal scales form longitudinal lines along the dorsum, reaching the base of the tail. The keels become less prominent towards the side of the body, having already disappeared on the flanks. The scales on the flanks therefore are smooth, but in form and arrangement very similar to the dorsal scales, only being slightly smaller. Tiny granular scales are scattered in interstitial space in the dorsal region and flanks, where they are more evident. In the lateral region of the body a slight and thin fold extends longitudinally from the armpit to the groin. Ventral scales are rounded, smooth and imbricate. 95 scales around midbody. Dorsal scales of the arm are subtriangular, smooth and imbricate. Dorsal scales of forearm are very similar but more rounded, and then the more triangular shape is observed in the dorsal region of the hand. On the ventral region of the arm the scales are small, granular, juxtaposed, and surrounded by even smaller granular scales in the interstitial space. Then, the scales on the ventral region of the forearm are as large as the dorsal ones, subtriangular, imbricate, with very few granular scales in the interstitial space, and they start showing keels towards the palm, where the scales are completely keeled, triangular, imbricate and with a jagged edge. The third finger of the left hand has 20 rectangular and transversally disposed lamellae, each one provided with three keels. The scales on the dorsal femoral region are subtriangular, smooth and imbricate. In the dorsaltibial region they are more rounded, subimbricate, slightly keeled and with visible tiny granular scales in the interstitial region. In the dorsal region of the foot the scales are subtriangular, smooth and imbricate, more similar to the scales on the femoral region rather than those on the tibial region. The scales on the ventral femoral and tibial regions are rounded, smooth and imbricate. In the plantar region scales are triangular, keeled and imbricate. Some scales in the plantar region are slightly jagged on the edges. The fourth toe has 26 rectangular and transversally disposed lamellae, each one provided with three keels. The dorsal scales on the tail are quadrangular, imbricate and keeled, with a slight mucron. Ventral scales on the tail are triangular, smooth and imbricate.

Color and pattern in preservative. The background dorsal coloration is ochre, with tiny black spots scattered in the dorsal region of the head and limbs. A well-defined black occipital stripe, although with approximately only half of the scales on the stripe being melanistic. This stripe reaches the base of the tail, and from there it continues as a thin line of tiny black spots longitudinally elongated. On the sides of the occipital stripe follows a pair of parietal stripe shaving the background ochre coloration, and then, in the flanks a pair of melanistic temporal stripes, which originate at the posterior edge of the eye, and end at the groin. The back of the body exhibits white scales evenly scattered. Ventral coloration is whitish gray, with dark and inconspicuous dots in the gular region.

Variation in the paratypes. Body measurements were divided into males and females (holotype is included within males since there are only two males in the whole sample): Mean and extreme values, in mm, for the males (two specimens) are: snout-vent length: 63.3 (61.25–65.35); axilla-groin distance: 28.36 (27.59–29.12); left forelimb length: 23.41 (21.74–25.07); left hindlimb length: 38.92 (37.23–40.6); tail length: 100 (89–111); head length: 15.13 (14.66–15.59); head width: 12.18 (12.05–12.3); and head height: 9.37 (8.82–9.91). For the females (six specimens) the measurements are: snout-vent length: 59.83 (53.46–68.8); axilla-groin distance: 26.12 (22.65–29.65); left forelimb length: 23.28 (22.65–25.11); left hindlimb length: 36.19 (32.53–39.16); tail length: 100 (85–113); head length: 13.32 (12.82–14.7); head width: 10.23 (9.93–11.25); and head height: 7.29 (6.55–7.54). Therefore we assume there is no evidence of sexual dimorphism, even though we measured only two males, the ranges of males measurements are within the range of the females. Nevertheless, a slightly larger size in the head measurements in males in relation to measurements in females is seen. Qualitatively the two males have a slightly more robust appearance than the six females.

In the two males, the mean and extreme values of the number of scales around midbody are 92.5 (90–95). None has preloacal pores. The male paratype exhibits the following variation in squamation with respect to the holotype: Three postfrontal scales instead of four, interparietal in contact with six scales instead of five, 5-5 large supraoculars instead of 7-6, 18-16 small supraoculars instead of 21-18. 6-7 lorilabials instead of 7-7. Slightly more rounded dorsal scales. 21 lamellae on the third finger of the left hand instead of 20. Scales in the dorsal femoral

region are rounded and slightly keeled. Plantar scales do not have a jagged edge. 27 lamellae on the fourth toe of the left foot instead of 26. In the females, the mean and extreme values of the number of scales around midbody are 92.6 (86–95). None has precloacal pores. In comparison with the holotype the females exhibit the following variation: longitudinal neck fold instead of two transversal folds in one specimen. Rostral scale in contact with six scales, and without contact with the nasals in two specimens. Undivided frontal scale in one specimen. Three postfrontals in three specimens, and two in three specimens. 4 to 6 large supraocular and 13 to 20 small supraoculars. 6 to 9 lorilabials. 5 to 8 supralabials. 4 to 6 infralabials. Four pairs of postmentals in two specimens. Dorsal scales rounded, imbricate and without visible small granular scales in the interstitial region in two specimens, and triangular, imbricate and without visible small granular scales in the interstitial region in one specimen. Dorsal scales of the forearm very slightly keeled in one specimen. Ventral scales of the forearm rounded and without visible small granular scales in the interstitial region in four specimens, and completely smooth in one specimen. Scales in the palmar region without a jagged edge in two specimens. 20 to 23 lamellae on the third finger of the left hand. Dorsal femoral scales rounded in one specimen, and slightly keeled in another specimen. Dorsal tibial scales triangular in one specimen, and without visible small granular scales in the interstitial region in four specimens. Plantar scales with a strongly jagged edge in one specimen. 27 to 30 lamellae on the fourth toe of the left foot.

There is no evidence of sexual dichromatism in the preserved specimens. This could not be inferred from the pictures because the sex of the specimens photographed is unknown. In some of the specimens the melanistic occipital stripe is weaker, consisting of only a few black scales between the ochre ones. In the specimens with a more pronounced and filled stripe, little black dots are scattered in the background colored parietal stripes. One of the female paratypes exhibits the whole ventral and gular regions mottled with black dots, while in the rest of the sample, this trait is very weak, or simply not present.

Osteological description. Based on specimen MNHNCL-4560, female, double-stained skeleton. (Figure 5)

Cranium features: cranium length 15.26 mm (from occipital condyle to premaxilla); cranium width 9.11 mm (between sutures of jugal and maxilla); cranium height 5.09 mm (the highest part of the calvarium); ocular orbit 5.55 mm (from the lacrimal bone to the postorbital one); rostrum 5.27 mm (from the lacrimal to the premaxilla). Rounded premaxilla with lateral process, maximum width of premaxilla half of its length. Two foramina are evident, these are the passages for the medial ethmoidal nerves (Oelrich 1956). These foramina are limited to the premaxilla and the maxilla. Nasal process of the premaxilla is acutely projected backward, lying beneath the divergence of the nasal bones. Ventrally, the premaxilla bears six acute teeth, chiseled, and caniniform on their free tip. Posterior margins of premaxilla are projected forward, almost horizontally. The premaxilla is strongly sutured to the vomer bones.

Nasal capsules (=fenestra exoanalis) with medial margins limited by the premaxillar spine, the floor is formed by the septomaxilla and the premaxillar process of the maxilla. The roof is formed by a cartilage. The nasal capsule is pierced and communicates with the fenestra exochoanalis. Paired nasal bones, twice as long than wide, medially sutured, anteriorly they cover the caudal tip of the premaxillar spine as described. Laterally the nasals are sutured to the ascendant process of the maxilla, and solidly to the prefrontal bones. Nasals exhibit small foramina, scattered, variable in diameter. Caudally the nasals diverge to embrace the anterior tip of the frontal bone, where they are solidly sutured. The divergence is located at the anterior orbital level. Dorsal surface of nasal bones appear wrinkled, with depressions and scars of the scales on them. Paired and triangular prefrontal bones; medially they are sutured to the nasal bones; their caudal tips are sutured to the single frontal bone. Prefrontals are sutured to the ascendant process of the maxilla and to the tiny lachrymal bone. Prefrontals are abruptly deflected downward forming the descendant process of the prefrontals. This process is strongly sutured to the palatine bones, forming the anterior wall of the ocular capsule. The lachrymal foramen is completely limited by the descendant process of the prefrontals. Its external wall is completely formed by the lachrymal bone.

The frontal bone is an unpaired, flat and tubular bone. The anterior process is sutured to the nasal and prefrontal bones. The frontal is the superior margin of the ocular orbits. Backwards it becomes broadly wider and it sutures to the parietal bone. At least in this specimen, the pineal foramen is completely included in the frontal. At both sides of that foramen there are irregular windows. The external borders of the frontal are sutured to the small postfrontal bones. Ventrally, the frontal has the olfactory channel. The postfrontals are paired bones, bridging the frontal and postorbital bones.

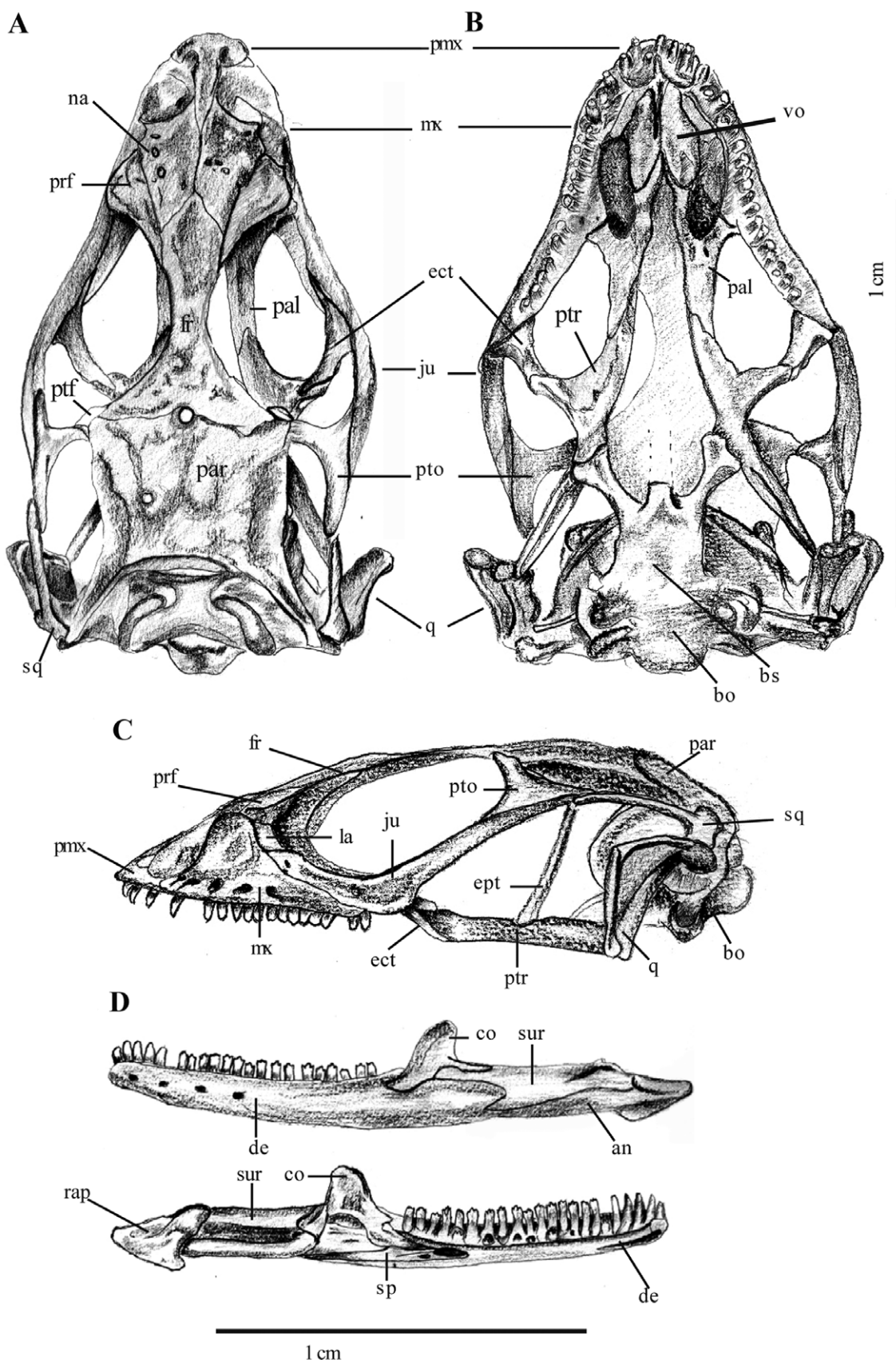


FIGURE 5.—A, dorsal view of *Liolaemus carlosgarini* skull; B, ventral view of the same skull; C, lateral left view; D, labial view of left jaw; below, lingual view. Captions are: an, angular; bo, basioccipital; bs, basisphenoid; co, coronoid; de, dentary; ect, ectopterygoid; ept, epipterygoid; fr, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pal, palatine; par, parietal; pmx, premaxilla; prf, prefrontal; ptf, postfrontal; pto, postorbital; q, quadrate; rap, retroarticular process; sp, splenial; sq, squamosal; sur, suprangular; vo, vomer.

The parietal bone is a single one, broad, and widely sutured to the frontal. By its anterior and external process, the parietal is sutured to the postfrontal and postorbital bones. Laterally, the parietal is deflected downward; the epipterygoid bones reach these deflections. The parietal is projected towards caudal and lateral. Those projections are the supratemporal processes. These processes are sutured to the squamosal bones, to the tail of the supratemporal, and to the paraoccipital and exoccipital bones. The caudal portion of the supratemporal bones is surrounded externally by the squamosal and quadrate bones and medially by the paraoccipital and exoccipital processes. The parietal has a notch beneath the supratemporal processes, in which is housed the anterior portion of the supratemporal bones. Supratemporal fenestra measures 3.83 mm in anteroposterior axis.

Squamosal bones are paired, stick shaped, curved and with an anterior process weakly joined to the postorbital bones. Posteriorly they become broader like an anchor. This caudal portion has a process inserted in a notch of the quadrate. The superior process is sutured to the supratemporal process of the parietal. Quadrates are paired, auricular-shaped bone. Ventrally they have sulcated condyles, supporting the mandibular set of bones. Dorsally they have the cephalic condyles. These condyles have a notch, and in it, is inserted the caudal portion of the squamosal bones, which are joined by cartilaginous fibers. There is a posterior crest rising from the mandibular condyle upwards. On the inferior and internal area there is a union with the posterior valves of the pterygoid bones.

Postorbitals are flattened paired bones, with three processes. The anterior one is sutured to the jugal bone, the posterior process is connected to the anterior process of the squamosal bone and the medial process is projected inward, joining the parietal and postfrontal bones. Jugals are paired bones, long and curved, slanting downward and forming the inferior margin of the ocular orbit. On their lowest part they are deflected forward and then upward riding on the maxilla, to which they are sutured, reaching the lachrymal bone. On their external surface, the jugals are pierced. On their lowest part, they are strongly sutured to the ectopterygoid.

Maxillae are paired bones, with an anterior process sutured to the premaxilla with a medial process. The ascendant process sutures to the nasal, the prefrontal and the lachrymal ones. The posterior process sutures to the jugal as described. The maxillae bear 18 pleurodont teeth, housed in a basin, the crista dentalis. Teeth 1 to 13 have tricuspidated crowns; 14 to 18 are strongly acute and caniniform. Anteriorly, the maxillae are sutured by a little extension to the vomerian bones. Ventrally, the maxilla forms the outer margin of the fenestra exochoanalis, a broad arch. It features a rounded palatal process, which is sutured to the palate. Posteriorly, the maxilla forms the outer margin of the infraorbital fenestra, completed externally by the ectopterygoid; the internal margins of the infraorbital fenestra are formed by the pterygoid and palatine bones. In dorsal view, the ectopterygoid is prolonged via an acute anterior process that reaches the level of tooth 5.

Paired vomers strongly sutured to each other. Anteriorly they are sutured to the premaxilla, and then to the palatine to which they bind obliquely. The vomer bones form the medial margin of the fenestra exochoanalis. Between them there is a shallow recess. The paired palatine bones are elongated, with three processes. The anterior one is sutured to the vomers. An anterior and external process is projected to the maxillae to which it sutures. Its caudal process is sutured to the pterygoid. Sutures are so skewed, that dorsally and forth they are sutured to the descending process of the prefrontal. On the ventral surface of the palate, the roof of the mouth, are presented noticeable longitudinal striations.

Palatine bones are not sutured together, and form the anterior piriform recess. This recess is continued, consisting of pterygoid divergent branches. The pterygoid bones are paired, anteriorly joining the palatines. In the middle of the pterygoid there is an extension that is projected obliquely outwards to join solidly to the pterygoid process of the ectopterygoid bone. Pterygoids are caudally projected in two valves to reach the base of the quadrate. The pterygoids in the middle of their length have two basins that host the basipterygoid processes of the basisphenoid bone. Immediately above them, on the dorsal side of the pterygoid there is a notch from which rises a slender rod that is the epipterygoid. In this individual at least, there are no pterygoid teeth.

The basisphenoid is a single bone, projecting forward it has basipterygoid processes that attach to the pterygoid bones. The basioccipital is fused to the basipterygoid. On the anterior part is the basisphenoid process, projected deep into the piriform recess. The basioccipital is a medial bone carrying the cephalic condyle. There is a pair of lateral eminences projecting to the ventral side, in front and sides of the occipital condyle: the spheno-occipital tubercles. The recesses for the jugular vein open like winged bodies. The otic occipital portion is projected forward as a rounded body.

The mandible: the dentary bears 23 teeth. Teeth 1 to 16 (17 missing) are tricuspid, 18 to 23 are caniniform, housed in a deep basin, typically pleurodont. The dentary at its distal end ventrally presents a discrete Meckel's

groove. Caudally and via lingual view, the dentary diverges to house the splenial bone with a strong suture. Together, both bones form the anterior inferior alveolar foramen (see Oelrich 1956) that extends at the level of teeth 3 and 4. The dentary is deflected upward by the dorsum of the splenial process of the coronoid. The dentary bone, by ventral view, is projected backward, beyond the coronoid bone, to suture with both the angular and suprangular bones.

The dentary via ventral and lingual view is projected backward until the ventral mandibular coronoid, beyond the coronoid it sutures with the angular and suprangular bones.

The coronoid bone rides on both the dentary and splenial bones. Posteriorly it is sutured to the suprangular bone. The latter has a large basin, the mandibular foramen. The articular is the most proximal bone and articulates with the quadrate as described.

The sternal apparatus: paired clavicles, flat and dorsally curved at the tips. They are widened as a spatula, without processes along the bone. The single interclavicular bone is arrow-shaped. Two lateral processes at the anterior end projecting to the side and backward, and a medial process that is projected straight caudally, reaching the middle of the sternal fontanelle; the angle between the two processes is 66°. The medial process is flat with a widening in the middle that ends in a point with the appearance of a necktie.

The epicoracoid is centered, covered by interclavicular bone. With the coracoid they form two fossae: the anterior coracoid fenestra and the smaller posterior coracoid fossa. The coracoids are paired bones that come together with the epicoracoid as described. They bear the glenoid fossa in connection with the humerus. The coracoids exhibit a foramen. The sternum is a triangular-shaped shield featuring a sternal fossa. The outer edges of the sternum have jagged ends to contact with four pairs of ribs. The last two are the xiphisternum.

The tibia of this species lacks the presence of a blade-shaped tibial process, therefore this indicates it belongs to *Liolaemus (Liolaemus) sensu strictu*.

Distribution. The vicinity of the Maule Lagoon, the type locality, is the only place where this species' presence can be assured. Very similar specimens also lacking precloacal pores have been found at the base of the Copahue Volcano, Argentina, at 2000 masl, very close to the Chilean border, and also in Caviahué, Argentina (J.A. Scolaro). It is also possible to find similar specimens at the Puelche River, Chile, slightly north of the type locality, although that must be confirmed with further sampling (C. Garín *in litt.* 2011).

Natural History. Probably a viviparous species, just like similar species that inhabit high altitudes. Saxicolous. Diet unknown. The sympatric herpetofauna consists of *L. buergeri*, *L. flavipiceus*, *Phymaturus maulense* (Núñez *et al.* 2010) and *Pleurodema bufonina*.

Liolaemus riodamas sp. nov.

Figures 6 to 10

Holotype. MNHNCL-4684, male. Collected by Damien Esquerré and Herman Núñez at Las Damas River, Termas del Flaco, Libertador Bernardo O'Higgins Region; S 34°56'714-887'' W 70°23'634-682'' 2012-2057 masl, between February 1 and 2, 2011.

Paratypes. MNHNCL-1962 to 1966 and MNHNCL-4682, 4683, 4685 and 4686. MNHNCL-1962, 4682 and 4686 are males and MNHNCL-1963, 1964, 1965, 1966 and 4685 are females. MNHNCL 4682-4686 same data as holotype. MNHNCL-1962-1966 same locality, collected by Herman Núñez and Antonieta Labra, February 24, 1985. MNHNCL-1964 and 4683 were used for diaphanisation.

Etymology. The name comes from the locality they were found: Las Damas River (In Spanish known as "Río Las Damas"). The common names "Las Damas River Lizard" in English and "Lagarto del Río Las Damas" in Spanish are proposed.

Diagnosis. Medium to large-sized lizard, with a mean SVL of 80.9 mm and a maximum of 85.5 mm. Sturdy aspect, robust limbs and a strongly folded neck. Tail about 1.5 times the length of the body. 83–96 scales around midbody. General background coloration brown to dark gray, with no defined pattern. Dorsal coloration of the head dark brown to black. Some specimens have individual yellow scales scattered on the posterior region of the dorsum. A light-yellow coloration is observed at the ventral region of some live specimens that extends to the sides of the tail. This species presents the characteristic dorsal squamation pattern of the *kriegi* group, with small rounded and juxtaposed scales, and tiny granular scales in the interstitial region. The dorsal scales are weakly

keeled and only around the vertebral line. It completely lacks precloacal pores, which makes it distinct from almost all of the species of the *elongatus-kriegi* complex. It is important, therefore, to differentiate this species from all of the species lacking these glands. First, because of this trait, it can be said that this species is not *L. ceii* as was previously suggested (Núñez & Torres-Mura 1992). Furthermore *L. ceii* has 102–115 scales around midbody, in contrast with the 83–96 scales in *L. riodamas*. From the original description of *L. thermarum* (Videla & Cei 1996), where it is described lacking precloacal pores, it differs in that *L. thermarum* would exhibit a dark bilateral stripe on the flanks, absent in the uniform pattern of *L. riodamas*. According to Avila *et al.* (2010), *L. thermarum* has two to three precloacal pores and a dorsal stripe, both traits absent in *L. riodamas*, however in a recent article (Avila *et al.* 2012) that sample of lizards is assigned to *L. smaug*. *L. riodamas* differs from *L. neuquensis* and *L. coeruleus* because these species have a lower number of scales around midbody (68–74 and 63–69 respectively, after Videla & Cei (1996) and Sclaro *et al.* (2007)), presence of dorsal pattern and a blue/greenish ventral coloration. From *L. cristiani* it differs because this species has a black stripe along the sides of the trunk, and a smaller body size much smaller, body size (mean SVL of 70.7 vs. 80.9 mm in *L. riodamas*). The species differs from *L. flavipiceus* because the latter has a lower number of scales around midbody (73–81). In addition *L. riodamas* lacks the body melanism of *L. flavipiceus*, and the red ventral coloration in some specimens of *L. flavipiceus*. From *L. punmahuida* it differs because this species is larger (maximum SVL of 95 mm in *L. punmahuida* vs. 85 mm in *L. riodamas*); furthermore *L. punmahuida* has an ochre background coloration, and bright red-yellowish coloration in the cloacal region, in contrast to the brown to gray dorsal coloration, and the occasional and slight yellow pigmentation in the cloacal region of *L. riodamas*. *L. riodamas* differs from *L. tregenzai* because this species has a green-bluish ventral coloration, and an evident sexual dichromatism, both traits not observed in *L. riodamas*. Some *L. leopardinus* males lack precloacal pores, but this species is clearly distinct from *L. riodamas* because of the leopard-like dorsal pattern of *L. leopardinus*. *L. capillitas* males also lack precloacal pores sometimes, but this species has only 58–67 scales around midbody, and a red cloacal coloration in females, not observed in *L. riodamas*.

Description of the holotype. Male, with an SVL of 81.83 mm. Head slightly longer than wide: 17.4 mm long (from the anterior edge of the ear opening to the point of the snout), 15.75 mm wide (between the anterior edges of the ear openings) and 10.78 mm high (at the level of the anterior edge of the ear openings). Snout length (from the anterior margin of the eye to the rostral scale): 6.21 mm. Neck wider than head, effect of a prominent longitudinal fold on the neck. Hind limb extended forward barely reaches the armpit. The tail is regenerated. It lacks precloacal pores.

Rostral scale rectangular, 3.2 times wider than high and in contact with eight scales, including the nasals, which touch the rostral with only the anterior corner of the scale. Nasals polygonal, the nostril located posteriorly, occupying half of the scale's surface. Two postrostrals irregularly squared, followed by four internasal scales, the two medial ones about two times larger than the other two. Three frontal azygos, the most anterior the largest, and the most posterior the smallest. Eight frontonasals in contact with the frontal azygos. Two squared prefrontal scales, the frontal undivided. Two longitudinally elongated postfrontals, the left one transversally divided in half. Interparietal irregularly pentagonal, in contact with six scales. A gray pineal eye in the middle of interparietal scale. Four small and squared parietal scales, slightly larger than the interparietal, although they resemble two longitudinally elongated parietal scales transversally divided in half. The scales in the nuchal and supratemporal regions are medium-sized, polymorphic, juxtaposed and smooth. 4-5 large supraoculars, accompanied by 22-20 small supraoculars. 8-8 very elongated and imbricate superciliary scales, excluding the canthal. Numerous scale organs on all the dorsal region of the head, increasing in numbers towards anterior part of the head. Canthal scales sharpened towards the anterior end. 6-6 loreal scales, excluding the canthal. A large and elongated subocular scale, divided at the posterior end, forming a small scale, and both together spanning the entire length of the eye. 8-8 lorilabial scales, in one row. 7-8 supralabials, the fourth-fifth one more elongated and curved upwards posteriorly. It has a slightly elongated snout, with the loreal distance (distance between the anterior margin of the eye and the rostral scale) barely larger than the ocular diameter. The scales in the anterior border of the eye are elongated and overlapping, each one with a scale organ on it. 15-15 upper and 14-14 lower palpebrals, all squared and each one with a scale organ on it. Temporal scales rounded, smooth and juxtaposed. Auricular scale barely distinguishable. Timpanic scales poorly developed, small and convex. Scale organs present in all the lateral region of the head, being especially numerous in the lorilabial and loreal scales. Mental scale barely wider than rostral, although twice its height, and in contact with four scales. Four pairs of postmentals, the second pair separated by two scales. 5-5 infralabials, with scale organs scattered on them. Scales in the gular region rounded, smooth and imbricate. Lateral

region of neck with a pronounced longitudinal fold, ending with an antehumeral fold. Neck scales small, convex, granular and with very small granular scales in the interstitial space.

Dorsal scales small, smaller than the ventral scales, rounded and juxtaposed. Poorly developed keels on the mid-dorsal scales, and disappearing to the sides. The scales on the flanks therefore are smooth, but in form and arrangement very similar to the dorsal scales, being only slightly larger. Tiny granular scales are scattered in interstitial space in the dorsal region and flanks. No folds are observed in the lateral region of the trunk. Ventral scales are rounded, smooth and imbricate. 85 scales around midbody. Dorsal scales of the arm are subtriangular, smooth and imbricate. Dorsal scales of forearm are very similar but more rounded, as they are in the dorsal region of the hand. On the ventral region of the arm the scales are small, granular, juxtaposed, and surrounded by even smaller granular scales in the interstitial space. The scales on the ventral region of the forearm are as large as the dorsal ones, subtriangular, imbricate, and start showing keels towards the palm, where the scales are completely keeled, triangular, imbricate and with a slightly jagged edge. The third finger of the left hand has 16 rectangular and transversally disposed lamellae, each one provided with three keels. The scales in the dorsal femoral region are rounded, smooth, subimbricate and with few small granular scales on the interstitial region. In the dorsal tibial region they are subtriangular, juxtaposed, slightly keeled and with visible tiny granular scales in the interstitial region. In the dorsal region of the foot the scales are rounded, smooth and imbricate. The scales on the ventral femoral and tibial regions are rounded, smooth and imbricate. In the plantar region scales are triangular, slightly keeled and imbricate. Some scales in the plantar region are slightly jagged on the edges. The fourth toe has 25 rectangular and transversally disposed lamellae, each one provided with three keels. The dorsal scales on the tail are quadrangular, imbricate and keeled. Ventral scales on the tail are triangular, smooth and imbricate.

Color and pattern in preservative. It lacks pattern. The dorsal region is uniformly brownish, with the dorsal region of the head darker than the rest of the body. From the groin, towards the posterior dorsal part of the body, a few white scales are scattered, not going further than the middle of the trunk. The ventral coloration is light gray.

Variation in the paratypes. Body measurements were divided into males and females (holotype is included within the males): Mean and extreme values, in mm, for the males (five specimens) are: snout-vent length: 80.17 (72.71–85.5); axilla-groin distance: 38.12 (34.71–41.11); left forelimb length: 31.59 (27.43–33.16); left hindlimb length: 46.18 (42.7–48.85); tail length: 123.5 (112–135); head length: 17.19 (15.42–18.09); head width: 15.21 (13.44–16.24); and head height: 10.26 (9.57–10.78). For the females (six specimens) the measurements are: snout-vent length: 81.61 (78.7–84.8); axilla-groin distance: 38.92 (36.1–41.9); left forelimb length: 31.72 (29.8–34.4); left hindlimb length: 46.1 (42.8–50.2); tail length: 124 (value of only non-regenerated tail); head length: 17.82 (16.18–19.53); head width: 15.34 (14.15–16.64); and head height: 9.95 (9.52–10.3). No evident sexual dimorphism is observed.

In the five males (including the holotype), the mean and extreme values of the number of scales around midbody are 86.4 (83–90). None has precloacal pores. Two transverse gular folds, including the antehumeral fold, instead of a longitudinal neck fold, are observed in two specimens. The male paratypes exhibit the following variation in squamation with respect to the holotype. Two frontal azygos, with the posterior one being larger, in two specimens. Two longitudinally elongated parietal scales in three specimens, 3 to 5 large supraoculars and 13 to 18 small supraoculars, 5 to 7 superciliaries, 4 to 7 loreal scales, 5 to 6 lorilabials, 5 to 6 supralabials and 5 to 6 infralabials. Slight keels in the dorsal region of the forearm in two specimens. Ventral scales of forearm rounded in two specimens. 18 to 19 lamellae on the third finger of the left hand. Scales in the dorsal femoral region are imbricate and with no small granular scales in the interstitial region in one specimen, and imbricate but with granular scales in interstitial region in another specimen. Scales in the dorsal femoral region are slightly keeled in one specimen. Scales in the dorsal tibial region are subimbricate in one specimen and completely imbricate in another. 24 to 27 lamellae on the fourth toe of the left foot. In the females, the mean and extreme values of the number of scales around midbody are 84 (80–93). None has precloacal pores. Two transverse gular folds, including the antehumeral fold, instead of a longitudinal neck fold, are observed in one specimen. In comparison with the holotype the five female paratypes exhibit the following variation. Two frontal azygos, with the posterior one bigger, in three specimens. Six frontonasal scales in one specimen. Longitudinally enlarged frontal scale and short squared postfrontals in two specimens. Squared interparietal scale in one specimen. Two longitudinally elongated parietal scales in four specimens. 4 to 5 large supraocular and 14 to 19 small supraoculars, 6 to 8 superciliaries, 4 to 7 loreals, 6 to 8 lorilabials, 6 to 7 supralabials and 5 to 6 infralabials. Five pairs of postmentals in one specimen. Dorsal scales subimbricate in one specimen. Dorsal scales of the forearm very slightly keeled in three specimens. Ventral scales of the forearm rounded in two specimens. 18 to 21 lamellae in the third finger of the left hand. Dorsal femoral scales imbricate in two specimens, and with poorly developed keels in another specimen. Dorsal tibial

scales subimbricate in two specimens. Dorsal scales of the foot slightly keeled in one specimen. 24 to 29 lamellae in the fourth toe of the left foot.

Color variation is poorly visible within the preserved specimens. No kind of sexual dichromatism is observed. Some specimens are clearer, reaching a whitish gray tone, especially in the specimens of the older sample (1985). Perhaps the most pronounced variability is found in the melanism level of the dorsal region of the head, varying from dark brown to almost black. The clear scales scattered towards the dorsum starting from the groin, visible on the holotype, are visible only on the specimens of the newer sample (2011). The ventral region varies from whitish gray to gray. In some specimens a slight yellowish tone on the sides of the posterior half of the ventral region is observed. In all of specimens the ventral region of the head exhibits a pattern consisting of a gray background, mottled with white spots.

Distribution. It has only been registered at the type locality, in an area of the narrow canyon of Las Damas River, between 2012 and 2057 masl. The river ends at the origin of the Tinguiririca River, near the locality of Termas del Flaco, in the Andean area west of the city of San Fernando, in the Libertador Bernardo O'Higgins Region, Chile.

TABLE 2.—Measurements (in mm) of the *L. riodamas* sample including holotype plus paratypes. Captions are the same as in Table 1.

<i>MNHN</i>	<i>Sex</i>	<i>SVL</i>	<i>AGD</i>	<i>FLL</i>	<i>HLL</i>	<i>TL</i>	<i>MBS</i>	<i>HL</i>	<i>HW</i>	<i>HH</i>
1962	M	85,5	40,2	32,8	45,6	135	83	17,86	16,24	10,6
1963	F	78,7	41,5	30,7	44	reg.	83	16,18	15,57	9,72
1964	F	80	41,9	29,8	42,8	reg.				
1965	F	84,8	36,1	32,9	50,2	reg.	80	19,53	16,64	10,3
1966	F	84,8	39	34,4	45,6	reg.	80	17,28	15,01	9,52
4682	M	78,01	35,32	32,2	46,72	112	88	18,09	15,39	10,1
4683	M	82,82	41,11	32,35	48,85	reg.	90			
4684	M	81,83	39,19	33,16	47,04	reg.	85	17,4	15,75	10,8
4685	F	79,74	36,11	30,73	47,72	124	93	18,3	14,15	10,3
4686	M	72,71	34,71	27,43	42,7	reg.	86	15,42	13,44	9,57
Mean		80,89	38,51	31,65	46,12	123,7	85,33	17,51	15,27	10,1
SD		3,92	2,73	2,01	2,49	11,5	4,42	1,27	1,06	0,47

Natural History. Viviparous species. Saxicolous habits, it is found basking over the large rocks that form its natural habitat, with relatively low vegetation. It can also be seen climbing branches of *Berberis* sp., possibly to eat their flowers (Núñez & Torres-Mura 1992). In the altitudinally lowest part of its distribution it is sympatric with *L. curis*, and with *Phymaturus damasense* (Troncoso-Palacios & Lobo 2012) in all of its distribution.

Osteological description. Based on specimen MNHNCL-1964, female, double-stained skeleton. (Figure 11)

Cranium features: cranium length (from cephalic condyle to premaxilla) 17.1 mm; cranium width (between sutures of maxilla and jugal) 11.88 mm; cranium height 6,95 mm; orbit length (between lacrimal and premaxilla) 6.78 mm. Anteriorly rounded premaxilla. The maxillar process is shorter than the nasal process (spine) of the premaxilla of the premaxilla; the premaxilla is pierced by two foramina, one on each side. The margin of these foramina is made by the premaxilla and the maxilla; those tiny holes are the passage for the medial ethmoidal nerves (Oelrich 1956). The widest part of the premaxilla is slightly shorter than the nasal spine of the premaxilla. The nasal process is projected backward and rests beneath the anterior junction of the nasal bones. Ventrally, the premaxillae bear six caniniform and pleurodont teeth. Also, ventrally is the incisive process, an antero-inferior projection, which is long, conspicuous and swollen.

Nasal capsules relatively enlarged, medially and anteriorly margined by the nasal process of the premaxilla and by the premaxillar process of the nasal bones; the floor of the nasal capsule is the flat premaxillar process of the maxilla. The nasal capsule has a foramina connected with the choanae. Paired nasal bones, twice as long as wide, medially sutured to each other. The anterior portion of both bones covers the spinal process of the premaxilla as described. Laterally and anteriorly, these are sutured to the ascendant process of the maxilla and, caudally at the wide

margin with the prefrontal bones. The nasals, at their posterior margin, broadly diverge to house the anterior tip of the frontal bone. The divergence is located at the level of the anterior margin of the orbit. The dorsal surface of the nasal bone is pierced by five small foramina, which are the passages for the cutaneous branches of the ethmoidal nerve and veins (Oelrich 1956). Also, the surface of the nasal bones is wrinkled, sinuous and carved out by the scales.

Paired prefrontal bones triangular, with an acute projection backwards. The medial margin is broadly sutured to the nasals and anteriorly strongly sutured to the ascendant process of the maxilla and to the tiny lacrimal. Ventrally the prefrontals form the anterior ceiling of the ocular orbit. The prefrontals are deflected downwards, forming the descendant process of the prefrontals, sutured solidly to the palatine bones. This process forms the medial wall of the lacrimal foramen, whose external wall is completely margined by the small lacrimal bone. The descendant process of the prefrontal forms a small part of the orbito-nasal fenestra, which is completely formed by the descendant process of the frontal.

Unpaired flat frontal bone, with a wrinkled surface, product of the overtopping scales. Anteriorly it is sutured to the nasals and prefrontal bones as described. The frontal forms the anterior margin of the ocular orbit. Backwards the frontal diverges widely to join with the parietal. Together, those bones form the epiphyseal foramen. The frontal is weakly sutured to the tiny postfrontal. Ventrally it has a tubular shape housing the olfactory channel. The paired postfrontal bones are laminar, quite small and forming a bridge, connecting the frontal and the postorbital bones.

The parietal is a single bone, sutured anteriorly with the frontal as previously described. It is dorsally flattened with a wrinkled surface. Laterally the parietal is abruptly deflected downwards to form the posterior cranial cage. Anteriorly it has two postorbital processes, sutured to the postorbital bones. Towards the caudal end the parietal is widely spread in the supratemporal processes; these processes are sutured to the respective supratemporal bones and also to the paraoccipital process of the exoccipital. The caudal portion of the supratemporal bones is externally margined by the squamosal bone, medially by the paraoccipital process of the exoccipital, and ventrally by the postero-superior portion of the cephalic condyle of the quadrate bone. The supratemporal bones are projected forward through the inferior margin of the supratemporal process to house the parietal in a groove, as was described by Etheridge (1995). The parietal bone, on its external walls receives the superior tip of the epipterygoid bone, an osseous rod, attached to the pterygoid bone. Length of the temporal fenestra 5.5 mm. Postorbital bones are paired. They are flat bones with three processes, at their anterior margin they form the posterior margin of the orbit, and at their posterior margin, they form the anterior margin of the temporal fenestra. The dorsal (medial) apex of the postorbital joins the postfrontal and parietal as previously described. The anterior process is firmly sutured to the jugal, and at its posterior tip it is weakly sutured to the squamosal bone.

Squamosal bones are paired, and are like curved rods, whose anterior processes are joined to the postorbital, as was described. Their caudal tips are widened, and there is a process projected to a notch on the cephalic condyle of the quadrate, which is pierced by this process. Quadrates are auricular-shaped paired bones. Inferiorly they present a grooved condyle attached to the mandible. Dorsally the quadrate has a cephalic condyle, sutured strongly to the paraoccipital process, to the supratemporal, and to the squamosal, as described. The attachment is weak and made through cartilaginous fibers. Posteriorly and medially there is a column that reaches the very summit of the quadrate: the posterior crista (Oelrich 1956). Close to the lower part of this column the pterygoid valve reaches the quadrate, to which it is attached by cartilaginous fibers. Jugals are two long and curved rods, forming the inferior ridge of the orbit, distally they are strongly sutured to the maxilla and to the tiny lacrimal; the lowest part of the jugal is deflected backwards and upwards and weakly attached to the anterior tip of the postorbital and squamosal by ligaments. Also, in the lowest part, the jugal is strongly attached to the ectopterygoid. On the external surface it exhibits four conspicuous foramina.

Maxillae are paired bones, roughly triangular. The anterior process is sutured to the premaxilla as described. Medially, and as a part of the floor of the nasal concha it is sutured to the septomaxilla. This maxilla has cartilage covering the nasal concha. The ascendant process is strongly sutured to the nasal, to the lacrimal, and to the jugal. The external surface has eight foramina; the four on the lower part arranged in a line, and the most caudal is the biggest. The maxilla bears 16 pleurodont teeth in deep cavities. Teeth 1 y 12 are tricuspidous, 13 to 16 are caniniform, the transition is gradual. Ventrally and anteriorly, the maxilla is strongly attached, with a few extensions, to the vomer bones. Also ventrally, the maxilla forms a wide arc whose apex is strongly sutured to the maxillar process of the palatine bones, and together these bones form the caudal margin of the exochoanal fenestra. The maxilla is slightly deflected outwards, forming the external margin of the infraorbital fenestra. Its caudal portion is solidly sutured to the jugal and to the ectopterygoid. Dorsally the maxilla is projected at the level of the tooth 3. In this specimen, the anterior tip of the ectopterygoid is truncated.



FIGURE 6.—Holotype of *Liolaemus riodamas*. MNHNCL-4684

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FIGURES 7 to 9.—Different morphotypes of *Liolaemus riodamas*. Pictures: Damien Esquerré

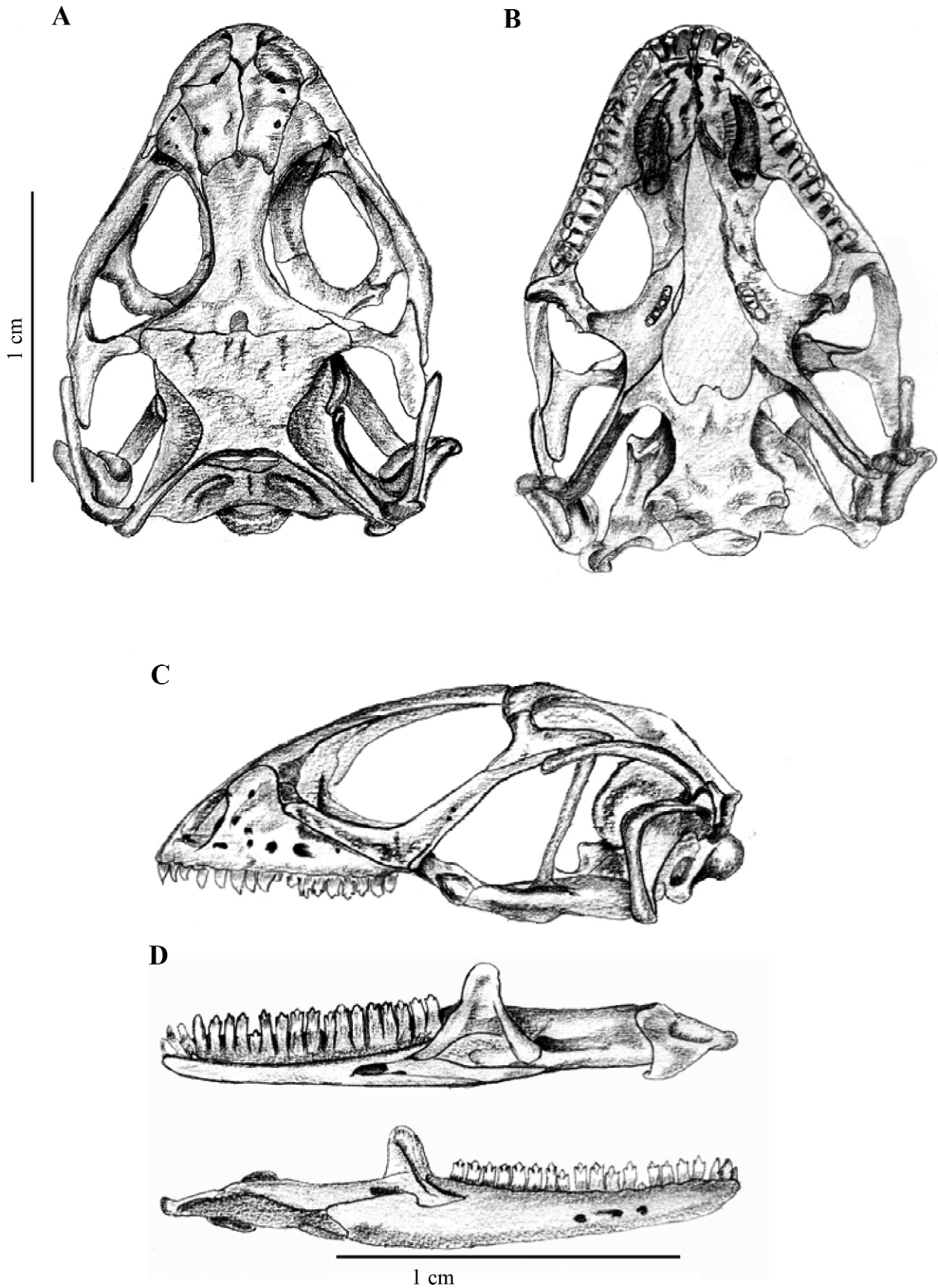


FIGURE 10.—A, dorsal view of *Liolaemus riodamas* skull; B, ventral view of the same skull; C, lateral left view; D, labial view of left jaw; below, lingual view. Bones are nominated in figure 5.

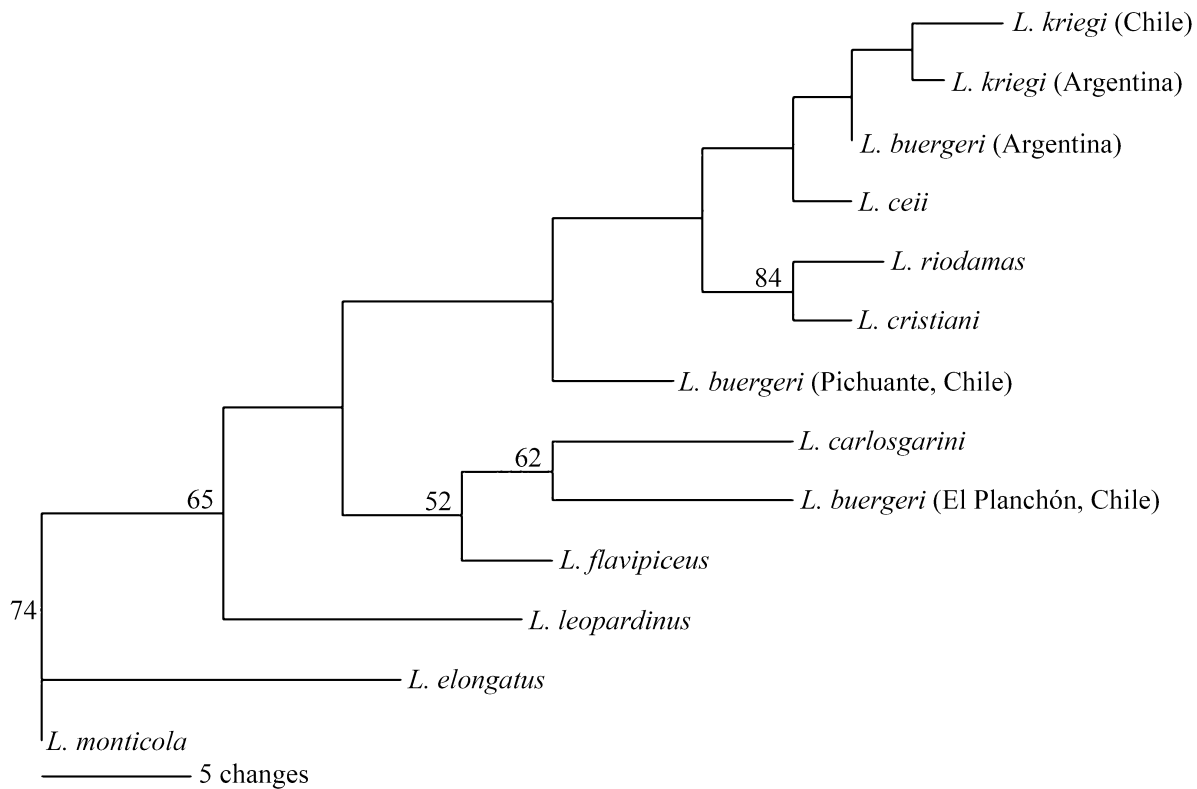


FIGURE 11.—MP Cladogram of the *Liolaemus* species used in this study. The values on the nodes correspond to Bootstrap values. Nodes with no values on them correspond to Bootstrap values below 50. The tree has a Consistency Index of 0.64, and a re-escalated Consistency Index of 0.4213.

Vomer bones are paired and medially sutured. Anteriorly they are sutured to the premaxilla as described. Vomers are sutured to the vomerian processes with a strong attachment, converging forward and medially. Vomers form the medial margin of the exochoanal fenestra, and at the middle and caudally they form a recess. Palatine bones are paired, laminar and with two anterior processes. The medial vomerian processes are sutured to the vomers as described. Palatines are not sutured to each other and they caudally diverge to form the piriform recess. They are projected toward the sides to suture with the pterygoid bones, and together they form the ceiling of the palatal roof. The attachment to the pterygoid is biased. Dorsally the palatine bones are sutured to the descendent process of the prefrontal, see above. The broader area of the piriform is formed by the divergent caudal branches of the pterygoids.

Pterygoid bones are paired, distally they are sutured to the palatines as described. In the external lateral area, the pterygoid has an ectopterygoid process sutured to the ectopterygoid bone, forming a strong bridge. There is a third process projected caudally, making contact with the quadrate just above the basal condyle; this process of the pterygoid is valve-like shaped. The pterygoid bones have, on the ventral face, a cavity with six pterygoid caniniform teeth, slanted downwards and inwards. The pterygoid has a notch on its posterior half, on it is inserted the thin rod-like eipterygoid, and behind this notch there is a small groove that holds the processes of the basisphenoid bone.

The basisphenoid is a single bone, medially located, and is forward projected with the basiptyergoid processes as described above. The basisphenoid is fused with the basioccipital. The basisphenoid is projected into the piriform recess and forward to a thin stalk, called the basisphenoid process. The basioccipital is a single bone, bearing the occipital condyle. A pair of eminences, the sphenoccipital tubercles, are projected downwards, emerging at the front and to the sides of the condyle. The recessus jugularis is a winged body with a cavity projected forward in the oticoccipital part. The bones of the posterior face of the head are fused around the big foramen magnum. The supraoccipital has a slight crest.

The mandible: the dentary bears 20 teeth; teeth 1 to 17 are tricuspid, and 18, 19 and 20 are caniniform, housed in deep cavities in the crista dentalis. Teeth are typically pleurodont. The dentary, on its distal end, ventrally presents a very slight opening of Meckel's groove. Caudally and through a lingual aspect, the dentary diverges to suture with the splenial. Both bones form the antero-inferior alveolar foramen (See Oelrich 1956) at the level of teeth 5 and 6. The dentary is deflected upwards, riding on the splenial process of the coronoid bone. The dentary projects its length, through the ventral region of the mandible, beyond the coronoid bone to suture with the angular and the suprangular bone. The coronoid rides on the dentary and on the splenial, and at its posterior portion it is sutured to the suprangular. The suprangular has a large cavity: the mandibular foramen. The articular is the most proximal bone, and has notches to receive the quadrate as previously described.

The hyoids set: The hyoid is a set of thin rod-like processes. Forward, the body of the hyoid is projected as the hypohial; backwards this body diverges into two branches: the ceratobranchials 2 (see de Queiroz 1987). Fused and towards the sides, on the anterior part of the body, the basihials are projected in a slanted position. From the posterior part of the body two curved branches, the ceratobranchials 1 (*ibid.*), broadly diverge to the sides of the neck, reaching the quadrate. On the external margin of the basihials, the ceratohials are attached, whose anterior and internal margins are expanded inwards with alar processes of cartilaginous nature.

The tibia shows the typical form of the *Liolaemus (Lioaemus) sensu stricto* subgenus, *i.e.*, without a tibial blade, and with a circular section.

Phylogenetic analysis (See Fig. 12). Of the 141 morphological traits used in the tree, 98 are fixed, 21 are parsimoniously uninformative, and only 22 are parsimoniously informative. Most of the nodes have bootstrap values below 50, except the node including the ingroup, with a value of 74; the one including all of the ingroup except for *L. elongatus*, with a value of 65; the one including *L. flavipiceus*, *L. carlosgarini* and *L. buergeri* from the type locality (El Planchón), with a value of 52; the one including *L. carlosgarini* and *L. buergeri* (from El Planchón) with a value of 62; and finally the most supported clade formed by *L. riodamas* and *L. cristiani*, with a value of 84.

Discussion

Several authors have worked on clarifying the evolutionary relationships among the species of the *elongatus-kriegi* complex and those species who lack precloacal pores, however for now we have little certainty of these relationships. Different authors, using diverse techniques and different taxa, have grouped these reptiles in different ways (Videla & Cei 1996; Espinoza *et al.* 2000; Schulte *et al.* 2000; Cei & Videla 2003; Espinoza & Lobo 2003; Morando *et al.* 2003; Avila *et al.* 2004; Pincheira-Donoso & Núñez 2005; Lobo 2005; Torres-Perez *et al.* 2009; Avila *et al.* 2012).

However, it is quite clear that the species lacking precloacal pores do not form a monophyletic group in relation to the rest of the complex (once called *neuquensis* group), like has been proposed by several authors (Espinoza *et al.* 2000; Cei & Videla 2002; Espinoza & Lobo 2003; Pincheira-Donoso & Núñez 2005). Moreover, it seems that *L. flavipiceus* and *L. thermarum* are more closely related to the *elongatus* group (Espinoza *et al.* 2000; Espinoza & Lobo 2003; Avila *et al.* 2010; Lobo *et al.* 2010), *L. cristiani* to the *kriegi* group (Núñez *et al.* 1991; Lobo 2005; Lobo *et al.* 2010), and that *L. coeruleus* and *L. neuquensis* do not share a close ancestral relation with the *elongatus-kriegi* complex (Schulte *et al.* 2000; Morando *et al.* 2003; Morando 2004; Lobo 2005; Pincheira-Donoso *et al.* 2008). Another proposal that has remained solid over time is the close relation existing between the *leopardinus* group and the *elongatus-kriegi* complex (Cei 1975; Shulte *et al.* 2000; Morando *et al.* 2003; Avila *et al.* 2004; Lobo 2005; Pincheira-Donoso *et al.* 2008). Nevertheless, more evidence is needed to determine if the *leopardinus* group is more related to the *elongatus* or to the *kriegi* group.

At first, we thought that the population we now describe as *L. carlosgarini* might belong to the populations of small *L. elongatus* of the Pehuenche Pass, Mendoza, Argentina, described by Cei (1974), and to *Liolaemus* sp. 5 from Morando *et al.* (2003) and Avila *et al.* (2004). However, with the description of *L. smaug* it seems that this species would in fact be *Liolaemus* sp. 5, instead of *L. carlosgarini*. The biogeographic and morphologic similarity between *L. carlosgarini* and *L. smaug* is remarkable, and most likely they share a close common ancestor. In addition the arse strong pattern and squamation similarities between *L. carlosgarini* and *L. elongatus*. Therefore, we suggest including *L. carlosgarini* in the *elongatus* group (were *L. smaug* has been included (Abdala *et al.* 2010)).

Our phylogenetic tree yielded confusing results (i.e. the separation of the different populations of *L. buergeri*). In addition it recovers a low consistency index and low bootstrap values, therefore we have little confidence in its results and we will not propose systematic arrangements based on it. The close relationship between *L. rioldamas* and *L. cristiani* is what appears to be the most robust results of the phylogenetic analysis. Leaving the tree aside, these two species share strong similarities in their squamation and body proportions, in addition to the absence of precloacal pores. Nevertheless, the phylogenetic relationship between these two species and the rest of the group remains unresolved, and is part of another study in progress.

We conclude that a phylogeny using only external morphology and incomplete taxon sampling, at least for this group of reptiles, is not sufficient to establish solid phyletic relations, and that these data should be complemented with more types of evidence, like nuclear or mitochondrial DNA, muscular, osteological or ecological traits. A further study using considerably more of the species now described for the *elongatus-kriegi* complex, with samples from both Chile and Argentina, and more types of evidence is needed to further clarify this problem.

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APPENDIX

Specimens used for the phylogenetic analysis. *Liolaemus carlosgarini*: International Road 115, waters below Maule Lagoon, Maule Region, Chile 19 H 358560 E – 6018117 S. 1915 masl. WGS84: MNHNCL4561-4567. *Liolaemus riodamas*: Las Damas River, Termas del Flaco, Libertador Bernardo O'Higgins Region, Chile S 34°56'714-887'' W 70°23'634-682'' 2012-2057m: MNHNCL 1962-1966, 4682-4686. *Liolaemus ceii*: Lonco Luán, Neuquén, Argentina: JAS-DC 970-973, 1102. *Liolaemus kriegi*: Cordillera of Curicó, mountains descending to Argentina, Maule Region, Chile: MZUC 873-874. Malleco, Antuco Volcano, Araucania Region, Chile: MZUC1091, 1093, 1102, 1190, 1194, 1205, 1207-1209. 1212, 1215, 1217, 1223, 1226, 1229. Primeros Pinos, Provincial Road 13, Neuquén, Argentina: JAS-DC 179, 180, 194, 951. Ingeniero Jacobacci, Rio Negro, Argentina: JAS-DC 1267, 1567, 1807. *Liolaemus buergeri*: El Planchón, Cordillera of Curicó, Maule Region, Chile: MNHNCL 1471-1476. Puesto Militar Pichuante, Rio Teno, Cordillera of Curicó, Maule Region, Chile: MNHNCL 1603-1606. Copahue, Neuquén, Argentina: JAS-DC 890-893, 900-911, 991. *Liolaemus cristiani*: Cerro El Peine, Altos de Vilches, Maule Region: MNHNCL 1957-1961, 4171-4172. *Liolaemus elongatus*: Sierra San Bernardo, Sarmiento, Chubut, Argentina: JAS-DC 402-403. Ingeniero Jacobacci, Rio Negro, Argentina: JAS-DC 1264, 1569, 1777, 1808. *Liolaemus flavipiceus*: Maule Lagoon, Maule Region, Chile: MNHNCL 2166-2171. *Liolaemus leopardinus*: Farellones (2300 m), Cordillera of Santiago, Metropolitan Region, Chile: MNHNCL 1113-1123. *Liolaemus monticola*: San Luis de Macul, Santiago, Metropolitan Region, Chile: MNHNCL 1018-1019. Los Dominicos, Santiago, Metropolitan Region, Chile: MNHNCL 100-105.