

**LIZARDS AT THE END OF THE WORLD: A NEW MELANIC SPECIES OF
PHYMATURUS OF THE *PATAGONICUS* CLADE FROM ROCKY OUTCROPS IN THE
NORTHWESTERN STEPPE OF CHUBUT PROVINCE, PATAGONIA ARGENTINA
(REPTILIA: IGUANIA: LIOLAEMIDAE)**

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ABSTRACT

A new *Phymaturus* species is described as a new member of the “*patagonicus*” group of the genus. The Patagonian lizard genus *Phymaturus* is regarded as a candidate for non-adaptive radiation given the tendency toward non-overlapping distributions among its phenotypically and ecologically similar species (*i.e.*, niche conservatism). In this paper, we provide the description of a sexually monomorphic species new to this clade. It is distinguished from other members of the *patagonicus* group by having metric and meristic differences, as well as by a peculiar, almost homogeneous, black colour pattern over the whole body. It lives at about 1000 m of altitude in very dark basalt rocky outcrops, in northwestern Chubut Province, Argentina. The new species is morphologically compared with the closely related species of the *patagonicus* group, and its distribution and natural history are highlighted.

Key Words: *Phymaturus*, Liolaemidae, Patagonian Reptiles, Rocky Lizard, taxonomy.

RESUMEN

Lagartijas del fin del mundo: una nueva especie melánica de *Phymaturus* del clado *patagonicus* de roquedales en la estepa noroeste de la provincia de Chubut, Patagonia Argentina (Reptilia: Iguania: Liolaemidae). Se describe una nueva especie perteneciente al grupo “*patagonicus*” del género *Phymaturus*. Las lagartijas de este género patagónico son consideradas como candidatos de una radiación no adaptativa dada la tendencia a no tener sobreposición de su distribución entre especies fenotípica y ecológicamente similares (ejemplo de conservación del nicho). En este trabajo, se provee la descripción de una nueva especie sexualmente monomórfica de este clado. Ella puede ser distinguida de otros miembros del grupo *patagonicus* por tener diferencias métricas y merísticas, además de un peculiar color negro casi homogéneo en todo su cuerpo. Ellos viven a una altitud alrededor de 1000 msnm en roquedales basálticos muy oscuros, en el noroeste de la provincia de Chubut, Argentina. La nueva especie se compara morfológicamente con las especies cercanamente relacionadas del grupo *patagonicus*, y se destaca su distribución e historia natural.

Palabras claves: *Phymaturus*, Liolaemidae, Reptiles Patagónicos, Lagarto de Rocas, taxonomía.

INTRODUCTION

Phymaturus comprises Andean and Patagonian lizards of Argentina and Chile. Within the genus, two clades are clearly differentiated by morphological characteristics (Cei 1986, Etheridge 1995): the *palluma* (previously *flagellifer*) group in the north (from 25° to 39° S) and the *patagonicus* group in the south (between 36° and 46°S). The nomenclature of this genus has been the focus of debate by several authors over decades (see Cei and Scolaro 2006 for details) and its taxonomy still remains controversial. The genus has quickly increased in number of species, since Donoso Barros (1966) and Peters and Donoso Barros (1970) to this day, from only one species with two forms to about 50 species at present.

Etheridge (1995) elevated several subspecies to species and formally described the two groups proposed by Cei (1993) based on squamation and skeletal morphology: the *P. palluma* group and the *P. patagonicus* group. As Etheridge (1995) pointed out, *Phymaturus* species are primarily characterized by a stout and flattened body shape, tail with regular whorls of spinous scales and lateral nuchal skin folds with fat-filled pouches. Moreover, all species of the genus have a viviparous reproductive mode, consistent preference for rocky microhabitats, and herbivorous (or almost entirely herbivorous) diets, among other exclusive characters of their biology (Cei 1993, Etheridge 1995, Lobo and Quinteros 2005, Ibarquengoytía *et al.* 2008, Pincheira-Donoso *et al.* 2008a, Boretto and Ibarquengoytía 2009, Lobo *et al.* 2010).

For the *patagonicus* group, characters defining the clade are the presence of elongate overlapping superciliary scales, a single elongate subocular usually not fragmented, caudal scales smooth rather than keeled. Characters defining the *palluma* group are non-imbricate superciliary scales, five or more suboculars, three to four rows of lorilabials, symphyisial narrower than rostral and usually in contact with infralabials, well developed caudal spines, and two annuli per segment (Lobo *et al.* 2010).

Currently, 50 species have been described, 24 belong to the *palluma* group and 26 to the *patagonicus* group. However, the identity of several species is under debate, and there is no consensus among authors about the number of valid species (see Cei and Scolaro 2006, Etheridge and Savage 2006, Scolaro 2010, and Lobo and Etheridge 2013). According to Cei (1986, 1993) and Avila *et al.* (2014), the genus shows very polymorphic populations generally in geographically isolated or endemic areas, which has induced confusion in some authors respecting an incomplete or speculative species description (see Pincheira-Donoso *et al.* 2008b, Lobo *et al.* 2010, Lobo *et al.* 2012, Abdala and Quinteros 2014, Corbalán *et al.* in press.). A summary of current species can be found in Avila *et al.* (2014).

Regardless, until a more detailed study is available, we provisionally accept the validity of all described species. Almost all this species diversity was described based on descriptive external morphology and coloration, in some cases coupled with assumed geographical isolation.

Besides, Morando *et al.* (2013) defined some molecular-based groups within this clade, and proposed some species trees with moderate support and geographically interesting relations and some unassigned species/populations inhabiting the basaltic plateaus and rocky hills throughout north and central Patagonia. However, as Lobo *et al.* (2012), Morando *et al.* (2013) and Avila *et al.* (2014) have pointed out, this hypothesis diversity is controversial and more detailed surveys are needed.

Phymaturus has been suggested to be a good, consistent candidate example of a relatively poor diversification in the ecological and life-history dimensions, mediated by phylogenetic niche conservatism (Scolaro *et al.* 2008). The difference in species richness between the two clades (*Phymaturus* vs *Liolaemus*) of the family Liolaemidae was always very conspicuous.

However, the full diversity of *Phymaturus* species had remained underestimated until recently. In the recent years, several new *Phymaturus* species have begun to be proposed from different areas of the Andes and Patagonia, which has resulted in the discovery of a fascinating diversity, especially at the level of patterns of coloration (Pincheira-Donoso *et al.* 2008b).

As a consequence, a much more complete picture of the evolutionary origin and history of the genus *Phymaturus* is currently available (Lobo and Quinteros 2005; Díaz-Gómez 2009). Overall, these constant ecological and life-history patterns reported among species suggest that these lizards have not undergone their diversification following an adaptive radiation (Pincheira-Donoso *et al.* 2008a), as defined by the major views about this theory (Schluter 2000). Most species are endemic to Argentina and Chile (Pincheira-Donoso *et al.* 2008a, Díaz-Gómez 2009).

Several of the recently recognized new species for the genus *Phymaturus* are the result of intense field exploration in unknown areas or in zones where enigmatic populations had been found in the past. In this paper, we investigate a population of *Phymaturus* from the *patagonicus* clade which is characterized by sexual dimorphism and dichromatism. However, as it has recently been proposed by the members of this group, a subclade (the *calcogaster* group) is conformed by species in which these intersexual asymmetries are slight or entirely absent (Morando *et al.* 2013). Based on a combination of morphological and morphometric evidence we suggest this population as a new species of the genus which is formally named.

MATERIAL AND METHODS

The new specimens (N = 15) were carefully examined, accurately measured, and compared with other *Phymaturus* species. To perform these morphological comparisons, we used both categorical (for meristic analyses) and continuous (for morphometric analyses) variables. Twelve meristic variables were obtained: (1) scales around midbody (SSM, counted half-way between the axilla and groin region), (2) dorsal head scales (counted between the tip of the snout to the top of the neck), (3) number of fourth finger subdigital lamellae on the right hand, (4) number of fourth toe subdigital lamellae on the right foot, (5) number of scales surrounding symphyseal scale, (6) number of fragments or subocular scales (SSO), (7) number of rows of lorilabial scales between suboculars and supralabial scales, (8) number of supralabial scales on the half right of the mouth (SBL), (9) number of infralabial scales on the half right of the mouth, (10) number of scales surrounding interparietal (pineal) scale, (11) number of scales between the rostral scale and the interparietal scale (SRI), (12) number of ventral scales between mental scale to the anterior edge of the cloacae (Etheridge and Christie 2003; Pincheira-Donoso *et al.* 2007).

For morphometric analyses, we measured ten variables using calliper to the nearest 0.1 mm: (1) snout-vent length (SVL, from the tip of the snout to the anterior edge of the cloacae), (2) head length (HEL, lateral measurement from the anterior edge of the ear opening to the tip of the snout), (3) head width (HEW, the widest zone of the head immediately anterior to the ear), (4) forelimb length (FLL, distance from insertion of the limb into the body wall to the end of the third toe), (5) hind limb length (HLL, distance from the insertion of the limb into the body wall to the end of the fourth toe), (6) axilla-groin distance (AGL, from the axilla to the anterior insertion of hind limb on the body wall), (7) eye-nose distance (from the tip of the snout to the anterior edge of the right eye), (8) fourth finger length on the right hand, (9) fourth toe length of the right foot, (10) tail length (from the posterior edge of the cloaca to the tip of the tail, excluding individuals with broken, missing or regenerated tails).

Measurements of standardized morphological characters, used in taxonomic studies, were performed with a precision calliper (0.1 mm), and a dissection stereomicroscope was used for other observations and scale counts. Data were obtained on adult individuals, recognized by the presence of mature gonads and the functional development of secondary sexual characters.

Meristic variables were analyzed using univariate non-parametric Mann-Whitney rank sum test or z-test. Since previous evidence suggests that the numbers of male precloacal glands in lineages of the family Liolaemidae show a strong phylogenetic conservatism (Pincheira-Donoso *et al.* 2008b), we did not include this variable in the meristic analyses.

Morphometric variables showing significant differences between groups were analyzed for normality by means of Snedecor's F-test (Sokal and Rohlf 1969). When normal Gaussian distributions were observed, the comparison between means was made employing general linear models. When character distributions were not normal, the Mann-Whitney U-test, Kruskal Wallis test or z-test was used. The neperian logarithm of the variables was used in order to reduce skewness (Zar 2009). For comparative purposes, arithmetic mean and standard deviations (SD) are given (Tables 1 and 2).

The type series of the new species is housed in the Museum of La Plata, Facultad de Ciencias Naturales y Museo de la Universidad Nacional de La Plata, Provincia de Buenos Aires (MLP.R). Details on the studied material are provided in the Appendix.

RESULTS

***Phymaturus curivilcun* n. sp.**

(Figures 1 and 2)

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Type Material—Holotype: MLP.R. 6339, adult male, collected from open rocky outcrops in Paraje El Mirador (42° 27' S; 70° 03' W; 1100 m asl, datum = WGS84), Provincial road N° 4, approximately 80 km NW of Gastre, Cushamen Department, Chubut Province, Argentina. Collected by J.A. Scolaro and O.F. Tappari, 16 December 2014.



FIGURE 1. Adult male holotype of *Phymaturus curivilcun* in life from Cushamen, Chubut, dorsal view (right). Photo: J.A. Scolaro, 20-12-2014. Adult male holotype of *Phymaturus curivilcun* in life from Cushamen, Chubut, ventral view (left). Photo: J.A. Scolaro, 20-12-2014.



FIGURE 2. Adult female paratype of *Phymaturus curivilcun* in life from Cushamen, Chubut, dorsal view (right). Photo: J.A. Scolaro, 20-12-2014. Adult female paratype of *Phymaturus curivilcun* in life from Cushamen, Chubut, ventral view (left). Photo: J.A. Scolaro, 20-12-2014.

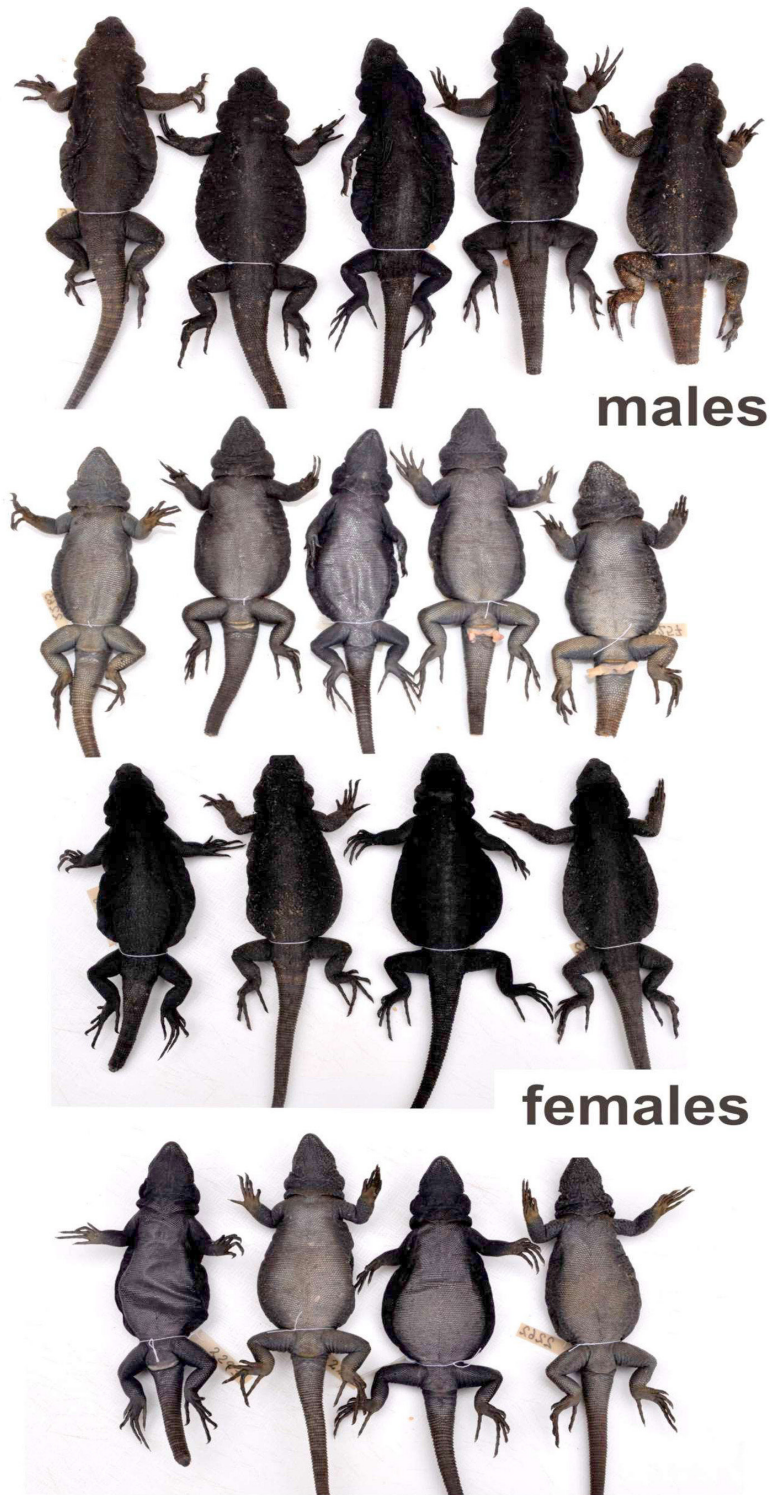


FIGURE 3. *Phymaturus curivilcum* variations in ventral view of males (upper) and females (below).
Photos: J.F. Escobar, 24-11-2015

Paratypes: MLP.R. 6340, adult male; MLP.R. 6341, adult female; MLP.R. 6342, adult female; MLP.R. 6343 adult male; JAS-DC 2258 adult male; JAS-DC 2260 adult male; JAS-DC 1210 adult male; JAS-DC 2293 adult female and JAS-DC 2237 adult female. All specimens have the same data of collection as the holotype.

Etymology—The specific name, “*curivilcun*” refers to the dorsal dark colour of the species, (as *curi* = black colour and *vilcún* = lizard) that comes from the *mapudungún* language of Mapuche natives that inhabited Argentina and Chile in the past. In Spanish, it refers to “Lagarto negro” or Black lizard.

Diagnosis—*Phymaturus curivilcun* shows neither sexual dichromatism nor dimorphism (except for head width, which is larger in males) (Table 1). Adult males show a uniform dorsal body pattern, entirely black, including head, dorsal body, limbs and tail; some specimens show a homogeneous dorsal pattern with lead-black background, sometimes irregularly and sparsely scattered with a few small dark grey spots. Females show a similar dorsal pattern. Ventrally, the black pattern includes throat, neck, abdomen, thighs and tail. But, during reproductive months, some specimens show the abdomen, ventral surface of tail and thighs with a pale copper colour over the dark background. Juveniles sometimes show ventrally a uniformly dark grey colour, occasionally soft light grey. On the caudal whorls there appear light grey rings alternating with pale copper coloured rings. *Phymaturus curivilcun* differs from the rest of species of the *patagonicus* clade by its darker coloration.

Furthermore, it can also be distinguished from *P. etheridgei* and *P. camilae* by a major expression of head width, hindlimb length and a significantly lower number of ventral scales and number of scales around midbody (Table 2). Besides, *P. curivilcun* has the subocular fragmented into 2-3 parts, a characteristic

TABLE 1. *Phymaturus curivilcun*: means and ranges of the main morphometric characters. Measurements in mm and scale numbers; ratios as proportions. Comparisons ** P<0.01.

Variable	Males (N = 8) Mean (Range)	Females (N = 7) Mean (Range)
Snout-vent length (SVL)	91.2 (78.9 – 97.7)	91.6 (87.2 – 93.8)
Tail length (TL)	111.2 (102.7 – 120.8)	102.8 (90.0 – 117.5)
Axilla-groin distance (AGD)	44.7 (51.9 – 36.4)	44.5 (47.5 – 41.6)
Head length (HL)	17.6 (15.9 – 20.2)	17.5 (15.7 – 20.4)
Head width (HW)	17.0 (16.3 – 17.4) **	15.4 (14.6 – 16.2)
Eye-nose distance (ED)	5.7 (5.0 – 6.7)	6.0 (5.1 – 6.8)
Forelimb length (FLL)	32.7 (30.0 – 33.9)	32.0 (30.5 – 33.8)
Hindlimb length (HLL)	48.8 (45.9 – 51.0)	47.8 (46.8 – 48.7)
Fourth finger length (FFL)	11.6 (9.3 – 14.2)	11.4 (8.9 – 13.2)
Fourth toe length (FTL)	16.4 (15.2 – 17.6)	16.3 (14.9 – 18.1)
Head dorsal scales (HDS)	20.5 (19.0 – 22.0)	20.3 (19.0 – 21.0)
Scales surrounding interparietal	7.4 (6.0 – 8.0)	7.6 (7.0 – 9.0)
Fourth toe subdigital lamellae	22.6 (21.0 – 25.0)	22.9 (22.0 – 25.0)
Fourth finger subdigital lamellae	28.5 (25.0 – 30.0)	28.1 (25.0 – 30.0)
Supralabial scale number	8.0 (8.0 – 8.0)	8.1 (9.0 – 8.0)
Infralabial scale number	7.3 (7.0 – 8.0)	7.3 (7.0 – 8.0)
Scales contacting mental	4.1 (4.0 – 5.0)	4.0 (4.0 – 4.0)
Precloacal pore number	9.9 (8.0 – 12.0)	0.0
AGD/SVL ratio	0.49 (0.46 – 0.50)	0.47 (0.43 – 0.51)
HLL/SVL ratio	0.54 (0.50 – 0.60)	0.52 (0.50 – 0.55)

normally not shared by the other species. It also presents thin and imbricate superciliary scales and smooth dorsal scales on the tail. It shows two rows of lorilabial scales between subocular and supralabials.

Absence of sexual dichromatism differentiated *Phymaturus curivilcun* from *P. camilae*, *P. excelsus*, *P. somuncurensis*, *P. manuelae*, *P. spectabilis*, *P. yachanana*, *P. ceii* and *P. tenebrosus*. However, the dorsal pattern uniformly dark colour appears similar to can be observed in the nearest geographically species *P. sinervoi* and *P. spurcus*. Besides, scarce small and irregular different speckled spots or stripes have never observed in *P. curivilcun*.

TABLE 2. Patterns of morphological variation in morphometric and meristic traits among three geographically related species of *Phymaturus* of the *patagonicus* clade. For all traits Mean \pm Standard Deviations are shown. Significant statistical differences among the new species (*P. curivilcun*) and *P. etheridgei* and *P. camilae* ($P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$), are indicated with asterisks.

Traits	<i>P. etheridgei</i> (N = 14)	<i>P. camilae</i> (N = 30)	<i>P. curivilcun</i> (N = 15)
Snout-vent length	85.9 \pm 4.0	90.3 \pm 5.0	91.4 \pm 4.6
Axilla-groin distance	45.6 \pm 2.8	45.0 \pm 3.5	44.6 \pm 3.6
Head length	15.3 \pm 0.6	16.2 \pm 0.6	17.6 \pm 1.4
Head width	15.1 \pm 0.7	16.4 \pm 0.7	16.2 \pm 0.9 ***
Eye-nose distance	6.2 \pm 0.6	6.4 \pm 0.3	5.8 \pm 0.7
Forelimb length	31.1 \pm 1.9	32.4 \pm 2.1	32.4 \pm 1.4
Hindlimb length	43.2 \pm 3.0	45.9 \pm 2.3	48.3 \pm 1.5 ***
Fourth finger length	9.5 \pm 0.7	9.8 \pm 0.7	11.5 \pm 1.5
Fourth toe length	13.0 \pm 1.3	13.2 \pm 0.7	16.4 \pm 1.0
Dorsal head scales	21.4 \pm 0.8	22.2 \pm 1.2	20.4 \pm 0.8
Fourth finger lamellae	24.2 \pm 1.1	23.3 \pm 1.5	22.7 \pm 1.2
Fourth toe lamellae	28.6 \pm 1.1	28.6 \pm 1.8	28.3 \pm 1.6
Scales around mental	5.4 \pm 0.7	4.8 \pm 0.9	4.1 \pm 0.3
Subocular scales	1.5 \pm 0.6	1.1 \pm 0.2	2.5 \pm 0.6 ***
Lorilabial rows	2.0 \pm 0.0	2.2 \pm 0.4	2.0 \pm 0.0
Supralabial scales	7.3 \pm 0.7	8.5 \pm 0.4 **	8.1 \pm 0.3 ***
Infralabial scales	7.6 \pm 0.5	8.3 \pm 0.6	7.3 \pm 0.5
Scales around pineal	6.5 \pm 0.8	7.2 \pm 0.8	7.5 \pm 0.7
Rostral-interparietals	15.7 \pm 1.2 **	12.3 \pm 1.0	15.1 \pm 0.7 ***
Ventral scales	183.4 \pm 7.5 ***	167.9 \pm 8.6 ***	155.8 \pm 8.3
Scales around midbody	226.3 \pm 4.7 ***	217.8 \pm 8.4 ***	185.5 \pm 4.6
Precloacal pores males	8.1 \pm 1.8	9.5 \pm 1.2	9.9 \pm 1.1

Ventral scale count in *Phymaturus curivilcun* is lower than in *P. ceii*, *P. etheridgei*, *P. camilae*, *P. tenebrosus*, *P. somuncurensis* and *P. calcogaster* and shows some overlap with *P. yachanana*, *P. agilis*, *P. excelsus*, *P. manuelae*, *P. patagonicus*, *P. desuetus*, *P. sinervoi*, *P. spurcus* and *P. spectabilis* but with different average. Besides, with respect the number of scales around midbody *P. curivilcun* shows overlapping with *P. yachanana*, *P. spectabilis*, *P. excelsus*, *P. agilis*, *P. patagonicus* and *P. calcogaster* but minor number than in *P. somuncurensis*, *P. spurcus*, *P. tenebrosus*, *P. ceii*, *P. etheridgei*, *P. camilae*, *P. manuelae*, *P. desuetus* and *P. sinervoi*.

Description of the holotype—A medium-sized lizard; snout-vent length SVL 97.7 mm; tail length 120.8 mm (complete, not regenerated, 1.2 times the SVL); head length 20.2 mm; head width 17.3 mm; eye-nose distance 5.9 mm; forelimb length 33.5 mm; hindlimb length 49.2 mm; axilla-groin distance 49.1 mm (50.3% of SVL); fourth finger length 12.1 mm; fourth toe length 16.2; scales in dorsal head 21; scales around midbody 189; ventral scales between mental and precloacal pores 160; supralabial scales 8-8; infralabial scales 7 (right) and 8 (left) decreasing posteriorly; twenty-four subdigital lamellae on the fourth

finger of the right hand; subdigital lamellae on fourth toe 30; precloacal pores 9; cephalic scales granular, almost smooth; supraorbital semicircles with large bulky scales in two of five irregular rows, rounded, incomplete posteriorly on both sides; no distinct enlarged supraoculars; nine elongate and overlapped upper ciliary scales; subocular elongate almost concave, fragmented into two different scales, slightly shorter than eye diameter, separated from supralabials by two rows of lorilabials; preocular contacting lorilabial row; temporals smooth, irregularly quadrangular, in 7-8 rows from auditory opening to subocular; external auditory meatus enlarged, transverse, without notorious or enlarged scales on its anterior border and with minute granular scales on posterior border; rostral wider than high, separated by one small scale from nasals; nasals large, central, surrounded by 7 small scales; parietals irregular and rough with evident interparietal scale, surrounded by 6 scales; nuchals granular in few irregular rows; post-auricular folds large, very distinct, with interposed transverse folds with round, almost granular, scales; mental pentagonal, smaller than rostral, surrounded by four irregular rectangular scales; two rows of 8-9 bilateral postmentals decreasing posteriorly; dorsal scales small, round and juxtaposed; middorsal scales slightly enlarged, growing smaller and granular toward ventro-lateral areas; ventrals larger than dorsals, pentagonal scales almost square and smooth; gulars rounded and smaller; 57-60 gulars between auditory meatus; caudal scales quadrangular, regularly imbricate on verticils, proximally larger and smooth on dorsum, or softly keeled, distally more rectangular and keeled; scales on limbs round and slightly keeled on upper side, granular and rounded in lateral region, larger and flat on lower side, infracarpals and infratarsals almost pentagonal, with round margins, becoming trifid at the base of fingers and toes. Subdigital lamellae of fingers keeled; claws robust, moderately long.

Coloration— In life, the new species shows a noticeable black colour. More details have been described in diagnosis (see Figures 1 to 3). Adult males and females have indistinguishable coloration. Ventrally, neither sex shows the peculiar reticulated dark grey on the throat over a light grey background observed in the majority of the species of the *patagonicus* clade. In the preservative, no variations were observed.

Morphological variation—The sample comprised eight adult males and seven adult females. Preliminary analyses allowed us to establish no sexual differences morphometrically between the sexes. Only one morphometric measurement, head width, was significantly larger in males than in females (head width 16.3-17.4 mm representing 0.18-0.19% of SVL, $P < 0.01$). Other measurements showed no statistical differences: SVL ranged 78.9-97.7 mm in males (mean = 91.2 mm) and 87.2-93.8 mm in females (mean = 91.6 mm); average tail length 90.0-120.8 mm (0.98-1.32 times the SVL). Scales around midbody 178-191 (mean = 185.5; SD = 4.6). Dorsal head scales 19-22. Ventrals 142-178 (mean = 155.8; SD = 8.3). Precloacal pores only in males 8-12 (mean = 9.9; SD = 1.1); in females ($n = 7$) not observed. Scales surrounding interparietal scale 6-9 (mean = 7.5; SD = 0.7). Scales contacting mental 4-5 (mean = 4.1; SD = 0.3) (Table 1). No variation in colour pattern was observed (Figure 3). In some specimens the ventral is pale copper, suggesting that this coloration may be related to season or physiological conditions (breeding cycle). Other morphological measurements, means and ranges are shown in Table 1.

Geographic distribution—*Phymaturus curivilcun* was found on isolated volcanic outcrops of the type locality. More explorations in neighbouring areas are necessary in order to determine the whole species' range (Figure 4).

Natural history—The Cushamen locality in Chubut has the physiognomy of a volcanic-pyroclastic complex with outcrops at the western edge of the North-Patagonian Massif, (which has been estimated to date back to the Early Eocene by paleomagnetic means, Zachos *et al.* 2001), and irregularly mixed with a landscape of mountain formations, basalt plateaus and eroded slopes. The area shows altitudes around 1000-1200 m above sea level. Volcanic effusions and strong wind erosion have sculptured the present relief of this vast area. The region's climate is predominantly cold and arid, with 150-250 mm of annual rainfall, 8-10°C of mean temperature, a strongly marked seasonal lack of humidity (in spring and summer), and intense winds from the west. Morello *et al.* (2012) include the area in the Patagonian Steppe Eco-region, a complex ecosystem of central flat areas and highlands (*Complejos ecosistémicos de Planicies y serranías centrales*). The arid Patagonian phytogeographic province lies within this ecosystem.

This area consists predominantly of shrub-steppe, where shrub cover is scattered (~50% of the surface area), with dwarf cushion shrubs and a few grassy patches. Shrubs are primarily represented by *Nassauvia glomerulosa*, *Senecio filaginoides*, *Ephedra frustillata*, *Adesmia volkmanii*, *Mulinum spinosum*, *Lycium chilense* and *Lycium gillesianum*. This steppe landscape can occasionally be altered by volcanic scoria resulting from the intense volcanic activities of the past. Interestingly, these deposits of volcanic scoria constitute the exclusive biotope of *Phymaturus curivilcun* (Figure 5).

In its area of distribution, the new species coexists (sometimes on the same rocky systems) with some other lizard species, mainly members of the *Liolaemus* genus (*Liolaemus bibroni* Bell, 1843, *L. ceii* Donoso Barros, 1971, *L. elongatus* Koslowsky, 1896, *L. inacayali* Abdala, 2003, *L. uptoni* Scolaro and Ceï, 2006), some Leiosaurids (*Diplolaemus darwini* Bell, 1843, *Diplolaemus sexcinctus* Ceï, Scolaro and Videla, 2003, and *Pristidactylus nigroiugulus* Ceï, Scolaro and Videla 2001) and *Homonota darwini* Boulenger, 1885 (Phyllodactylidae). Given that *Phymaturus curivilcun* tends to exclusively occupy rocky outcrops, only a few individuals of these other species can be found in actual syntopy with the new species. After multiple field trips to the area, no species of snakes were found.

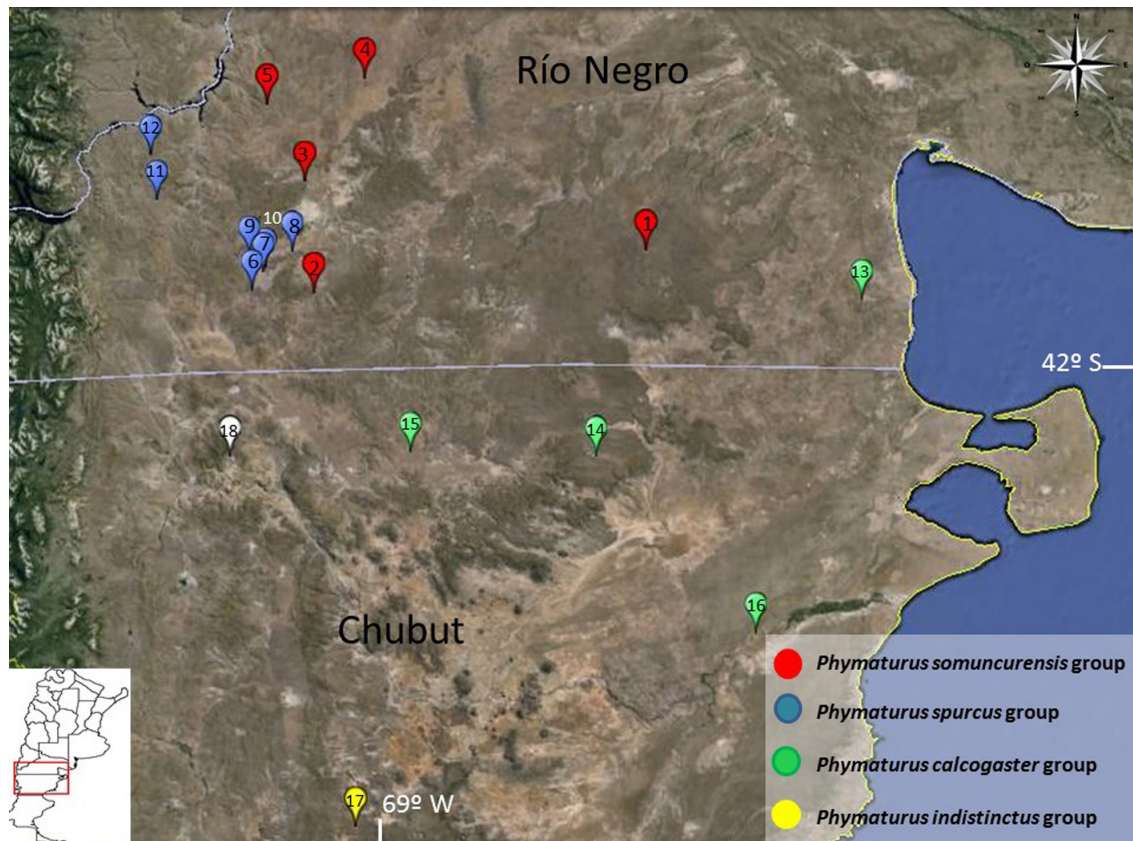


FIGURE 4. Geographic distribution of all known neighbouring members of the *Phymaturus patagonicus* clade of northwestern Chubut and southwestern Río Negro provinces (Argentina). Colour marks represent species groups following Avila *et al* (2014). Localities are indicated by numbers and represent: *P. somuncurensis* (1), *P. etheridgei* (2), *P. sinervoii* (3), *P. ceii* (4), *P. cacivioi* (5), *P. excelsus* (6), *P. spectabilis* (7), *P. desuetus* (8), *P. spurcus* (9), *P. agilis* (10), *P. manuelae* (11), *P. tenebrosus* (12), *P. yachanana* (13), *P. calcogaster* (14), *P. camilae* (15), *P. patagonicus* (16), *P. felixi* (17) and *P. curivilcun sp.nov.* (18).

Phymaturus curivilcun, consistently with all other known species of the genus, has viviparous reproduction. Based on data from the studied specimens, we observed three females giving birth in captivity late (13th-24th) in February 2015. Two females gave birth to two offspring and one female to three offspring.

Finally, the new *Phymaturus* species was observed in the field feeding on different genera of plants (*Lycium* spp. and *Adesmia boronioides*), which suggests an essentially herbivorous diet. Regarding experimental diet, *Phymaturus curivilcun* accepts *Tenebrio molitor* (mealworms) when kept in captivity, as previously observed in other *Phymaturus* spp. Although consumption of animal prey cannot be ruled out at present, we argue that (at least predominantly) herbivory is the most parsimonious assumption given that the rest of the species in the genus are consistently herbivorous.



FIGURE 5. Female *Phymaturus curivilcun* with its newborns in captivity (upper). General view of the biotope where the species lives (below).

Statistical analyses

According to the standard measurement variables proposed for studies of the genus *Phymaturus* (Etheridge 1995, Lobo and Quinteros 2005, Lobo *et al.* 2012), a total of 21 continuous and meristic traits were measured. These variables were employed firstly to run a principal component analysis (PCA), and then, based on six selected significant morphometric traits (SSM, SRI, SBL, SSO, HLL and HEW, see Table 2 for details), several discriminant analyses (SPSS v. 15.0; 2006; Zar 2009) were performed in order to investigate multivariate patterns of differentiation between the new species and the closest geographically neighbouring species of the *patagonicus* clade (*P. etheridgei* Lobo, Abdala and Valdecantos 2010 and *P. camilae* Scolaro, Jara and Pincheira-Donoso 2013).

All the variables were ln-transformed to reduce skewness and make variances homogeneous (Zar 2009). After ln transformation, all the studied variables met the statistical assumptions required for parametric analyses. We aim to test whether (1) the overall morphological characteristics of the studied *Phymaturus* species differ significantly, and (2) the body proportions of these species differ significantly. The variables SVL, HEL, HEW, AGL and FLL were included in multivariate analyses, whereas HLL were compared using univariate analyses, as they were not available for all the studied specimens. To compare the overall morphology of our samples, we used simple multivariate (MANOVA) and univariate (ANOVA) analyses of variance. For body shape comparisons, on the other hand, we used a different statistical approach. Since quantitative variation in body size between species may lead to allometric bias in the morphometric variables, we removed this allometric effect of snout-vent length, in order to obtain size-independent body shape variables. Least square linear regressions of body size, such as SVL, against linear measures of shape have often been used to produce size-effect-free residual indices (Scolaro *et al.* 2013). To circumvent this problem, analyses of covariance offer a more powerful statistical alternative. Therefore, we controlled the allometric effect of body size using multivariate (MANCOVA) and univariate (ANCOVA) analyses of covariance, with body size (SVL) as covariate, and the remaining quantitative traits as dependent variables. All these analyses were conducted separately for both males and females.

Quantitative analyses of morphological traits revealed significant differences between the new *Phymaturus* species and *P. etheridgei* (N = 14) and *P. camilae* (N = 30), the two geographically nearest species (Table 2).

Two stepwise discriminant analyses were performed separately between *Phymaturus etheridgei* and *P. camilae* versus *Phymaturus curivilcun*, including treatment of 21 morphometric and meristic variables, and of the six significant variables. The variance-covariance equality of matrices showed that the data are normally distributed, and variances are homogeneous within each group (*P. etheridgei*, *P. camilae* and *Phymaturus curivilcun*). The results for the 21 or six variables treated showed: Box's test, $F = 2.21$, $N = 59$, $P < 0.001$, Discriminant functions: Wilks' $\lambda = 0.10$, $\chi^2 = 122.3$, $N = 59$, $P < 0.001$. Discriminant analysis of individual specimens resulted in a completely correct classification of cases (100%) in all of the analyses performed.

Comparisons between *Phymaturus curivilcun* and *P. etheridgei* showed a significant divergence in head width (*P. curivilcun*, N = 15, mean = 16.2, SD = 0.9; *P. etheridgei*, N = 14, mean = 15.1; SD = 0.7; Student $t = 3.60$, $N = 29$, $P < 0.001$), hindlimb length (*P. curivilcun*, N = 15, mean = 48.3; SD = 1.5; *P. etheridgei*, N = 14, mean = 43.2; SD = 3.0; Student $t = 5.72$, $N = 29$, $P < 0.001$), number of supralabial scales (*P. curivilcun*, N = 15, mean = 8.1; SD = 0.3; *P. etheridgei*, N = 14, mean = 7.3; SD = 0.7; z test = 3.38, $N = 29$, $P < 0.01$), and number of subocular scales (*P. curivilcun*, N = 15, mean = 2.5; SD = 0.6; *P. etheridgei*, N = 14, mean = 1.5; SD = 0.6; z test = 3.50, $N = 29$, $P < 0.01$), all variables with major expression in *Phymaturus curivilcun*. Instead, the number of scales around midbody (Mann-Whitney $w = 120$, $N = 29$, $P < 0.001$) showed major expression in *Phymaturus etheridgei* (*P. curivilcun*, N = 15, mean = 185.5; SD = 4.6; *P. etheridgei*, N = 14, mean = 226.3; SD = 4.7).

Comparisons between *Phymaturus curivilcun* and *P. camilae* revealed significant differences in hindlimb length (*P. curivilcun*, N = 15, mean = 48.3; SD = 1.5; *P. camilae*, N = 30, mean = 45.9; SD = 2.3; Student $t = 4.13$, $N = 45$, $P < 0.001$), number of scales around pineal scale (*P. curivilcun*, N = 15, mean = 7.5; SD = 0.7; *P. camilae*, N = 30, mean = 7.2; SD = 0.8; Mann-Whitney $w = 491$, $N = 45$, $P < 0.001$)

and number of subocular scales (*P. curivilcun*, N = 15, mean = 2.5 ; SD = 0.6 ; *P. camilae*, N = 30, mean = 1.1 ; SD = 0.2 ; Mann-Whitney $w = 465$, N = 45, $P < 0.001$), all traits with major expression in *Phymaturus curivilcun*. Instead, the number of scales around midbody (*P. curivilcun*, N = 15, mean = 185.5 ; SD = 4.6 ; *P. camilae*, N = 30, mean = 217.8 ; SD = 8.4 ; Mann-Whitney $w = 129$, N = 45, $P < 0.001$) and the number of supralabial scales (*P. curivilcun*, N = 15, mean = 8.1 ; SD = 0.3 ; *P. camilae*, N = 30, mean = 8.5 ; SD = 0.4 ; Mann-Whitney z test = 3.76, N = 45, $P < 0.001$) showed major expression in *P. camilae* (see Table 2 for details).

To visualize the position of each individual species in a multivariate morphospace (as a complement to the abovementioned quantitative analyses), we conducted a principal component analysis (PCA) based on the same six significant morphometric traits. Based on eigenvalues, we retained the first two principal components, given that PC1 and PC2 scored eigenvalues of 11.16 (explained variance: 55.8%) and 8.84 (explained variance: 44.2%), respectively. We then used these two PCs to plot each individual in our dataset and build the ellipses of equiprobability ($P < 0.05$) following Sokal and Rolf (1969) (Figure 6).

DISCUSSION AND CONCLUSIONS

The new species, *Phymaturus curivilcun*, is a member of the *patagonicus* group of *Phymaturus*. It presents the characteristics defined by Etheridge (1995) and Lobo and Quinteros (2005) for the “*patagonicus*” group, like thin and imbricate superciliary scales and smooth dorsal scales on the tail. Nevertheless, it distinguishes itself from the other *Phymaturus* species by its subocular scale fragmented into 2-3 parts, lepidosis, length of hindlimbs and coloration.

The two latter characteristics may have ecological implications. On the one hand, hindlimb length is known to be positively related to locomotor performance across a wide diversity of lizard taxa (Tulli *et al.* 2012). Lizards that use rocky habitats must climb vertical surfaces, jump over gaps between adjacent rocks, and look for refuge in narrow crevices (Goodman *et al.* 2008). In these habitats, stretching out their limbs laterally allows them to maintain the centre of their body mass (and balance) close to the substrate (Goodman *et al.* 2008). Although the species dwelling on vertical surfaces are expected to run faster on an inclined surface than those using horizontal microhabitats, *Phymaturus* species show slow performance (sprint speed) compared to other lizard species (Tulli *et al.* 2012). However, Tulli *et al.* (2012) compared performance among different ecological groups of lizards (terrestrial, saxicolous, arenicolous and arboreal), not among species within an ecological group. These authors propose that the inclination of the substrate has a greater influence than substrate *per se* on the performance of saxicolous lizards. So, differences may arise if different species inhabiting rocky outcrops with different slope are compared. The habitat of *P. curivilcun* has a very pronounced slope, and long hindlimbs may have evolved in this species to improve its locomotor performance.

On the other hand, the ventral pigmentation and the almost homogeneous dorsal dark black coloration are unique to *P. curivilcun* (Figures 1 to 3). Melanism was reported for individuals of some species of *Phymaturus* of the *patagonicus* clade, such as *P. cacivioi*, *P. ceii*, *P. tenebrosus* and *P. sitesi* (Lobo and Nenda 2015), but all individuals in the population of *P. curivilcun* share this characteristic. The most similar species is *P. tenebrosus*, but it is characterized by a black dorsum scattered with small white spots. The thermal melanism hypothesis states that dark ectothermic individuals are at an advantage in cold climates since the low reflectance (or high absorbance) allows them to heat up faster than light individuals (Clusella Trullas *et al.* 2007). Debandi *et al.* (2012) made environmental niche models for the *Phymaturus* genus based on climatic and non-climatic variables. Interestingly, in the predictive maps for the *patagonicus* group, the area that *P. curivilcun* inhabits appears as an area of low probability of occurrence (around 30-40%) for species of this clade. Variables related to temperature (such as mean annual temperature, mean temperature of driest quarter and temperature seasonality) were positively associated with the distribution of the clade (Debandi *et al.* 2012). Then, the area of distribution of *P. curivilcun* could be sub-optimal (i.e. colder than areas occupied by the rest of species), and melanism could have arisen as an adaptive advantage for coping with these harsh conditions. Moreover, this coloration may play a role in the

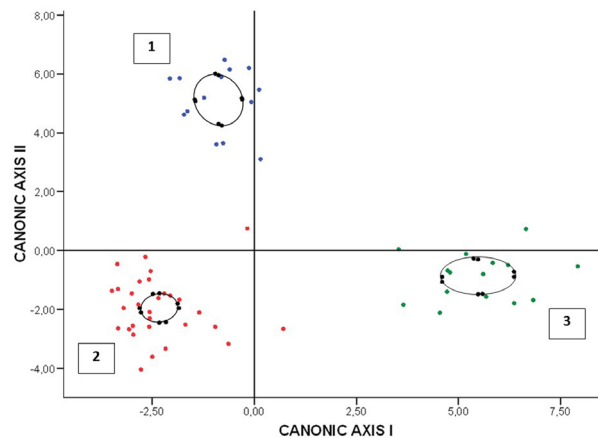


FIGURE 6. Ellipses of equiprobability for all cases ($P < 0.05$): **1.** *Phymaturus etheridgei*, **2.** *Phymaturus camilae* and **3.** *Phymaturus curivilcun*.

cripticity of individuals. However, predators like birds (hawks) have a visual system that includes visible and UV spectra (Stuart-Fox *et al.* 2003). So, conclusions about predation avoidance are premature. Studies using spectrometry in the entire wavelength range could solve questions about the role of melanism in the thermoregulation and cripticity of this new species.

As occurs in several species of the “*patagonicus* group” of the genus (such as *P. sinervoi*, *P. etheridgei*, and their more geographically distant species of this clade like *P. patagonicus*, *P. sitesi*, *P. nevadoi* or *P. indistinctus*) *P. curivilcun* lacks sexual dichromatism. This is also true for the species that make up the group *P. spectabilis*, *P. excelsus*, *P. agilis*, *P. spurcus*, although it is possible that this group is composed of a single species with high polymorphism (Corbalán *et al. in press*). The lack of sexual dichromatism is expected for species that have undergone non-adaptive radiation (i.e. lineage diversification with minimal ecological diversification linked to allopatric or parapatric species distributions). Moreover, *P. curivilcun* is substantially spatially isolated from other species. Both characteristics (sexual monochromatism and allopatric distribution) are in agreement with previous contributions that propose the genus *Phymaturus* as a candidate for non-adaptive radiation (Scolaro *et al.* 2013).

The species here described has singularities from the evolutionary point of view. Its natural history is consistent with the conservative character of the genus (herbivorous diet, viviparous mode of reproduction, rock-dwelling). However, published predictive models for the clade did not show the area that *P. curivilcun* inhabits as an area of high probability of occurrence. The distinctive morphology of this species (especially their homogeneous melanism in both males and females) has probably evolved to compensate for the adverse conditions it has to face.

According to Avila *et al.* (2014) and Morando *et al.* (2013), based mainly on molecular studies, the know location of *P. curivilcun* appears outside the edges of the species distribution of both subclades, *P. calcogaster* clade and *P. somuncurensis* clade. To correct allocate *P. curivilcun* species, more molecular analysis will be needed.

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Appendix

Specimens examined and localities

Specimen numbers preceded by the acronym are housed in the following collections: IBA, Instituto de Biología Animal, Mendoza, Argentina; MLP-R and MLP-S, Herpetological Collection Museo de La Plata, Buenos Aires, Argentina; JAS-DC, J.A. Scolaro-Diagnostic Collection, CENPAT-CONICET, Puerto Madryn, Argentina; UNCo-PH, Universidad Nacional del Comahue, Centro Universitario Bariloche Colección Herpetológica, Bariloche, Río Negro.

Phymaturus camilae. Sacanana stream bridge, adjacent to Provincial Road 4, Chubut: MLP-R 5586 (Holotype), MLP-R 5587-89 (Paratypes), UNCo-PH 1614, 1308 (Paratypes); JAS-DC 1316, 1318, 1320, 1609 (Paratypes), 1306, 1307, 1309-1317, 1319, 1321, 1477, 1479, 1581, 1587, 1959, 1604-1606, 1613, 1614.

Phymaturus curivilcun. Cushamen, Chubut: MLP.R. 6339 (Holotype), MLP.R. 6340-43 (Paratypes); JAS-DC 2258, 2260, 1210, 2293, 2237 (Paratypes), JAS-DC 1211, 2259, 2261-63.

Phymaturus etheridgei. Pje. Quetrequile, Provincial Road 76, Km 39 SE of Jacobacci, Río Negro JAS-DC 1907-1916; 2093, 2094, 2115, 2150.

Phymaturus patagonicus: 40 km west of Dolavon, Chubut: IADIZA-CH 00080; JAS-DC 813-820; IBA-R 0789; JMC-DC 335-336, 760, 842-845, 1300, 2003-2009.