Article

Lizards at the end of the world: Two new species of *Phymaturus* of the *patagonicus* clade (Squamata, Liolaemidae) revealed in southern Patagonia of Argentina

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Abstract

The Liolaemidae radiation has resulted in three genera whose patterns of evolutionary diversification exhibit dramatic differences. Two of these lineages, *Ctenoblepharys* and *Liolaemus*, lay at the extremes, being a monotypic genus and one of the most extraordinary adaptive radiations among vertebrates, respectively. In *Phymaturus*, in contrast, 22 species are known, all characterized by similar ecological niches and life-history patterns. The *Phymaturus* genus consists of two major clades, *flagellifer* and *patagonicus*, restricted to Andean-Patagonian environments in Argentina and Chile. While the former lineage occurs primarily at the northern areas of the genus distribution, the latter mostly occupies central and southern Patagonia. In this study, we report evidence to support the existence of two new species of the genus belonging to the austral clade *patagonicus*. These new taxa, *Phymaturus castillensis* and *Phymaturus videlai*, occur close to the southernmost distributional limit known for the entire genus. At these austral latitudes, only two other species of the genus, *P. indistinctus* and *P. patagonicus*, have been found. Therefore, the two new species reported herein reveal a higher species richness at these cold and harsh South American environments, where the predominant lineage is *Liolaemus*. As in the rest of the species of the *Phymaturus* genus, *P. castillensis* and *P. videlai* are saxicolous, herbivorous, and viviparous, as revealed by our field and lab observations. A number of signals support the idea that these two *Phymaturus* populations are the result of speciation events. Essentially, both are strongly isolated by hundreds of kilometers from most species of the *patagonicus* clade, which precludes dynamic gene exchange among them, while substantial divergence in their patterns of coloration differentiate them from the two geographically closest species, *P. indistinctus* and *P. patagonicus*, and from each other. The differences in coloration are not, however, strongly accentuated between the sexes, being monochromatic in *P. castillensis* and moderately dichromatic in *P. videlai*. Interestingly, juveniles *P. videlai* exhibit also these signals of adult sexual dichromatism. Finally, the results reported in this study increase *Phymaturus* species richness up to 24 species.

Key words: *Phymaturus*, Liolaemidae, Patagonia, rock-dwelling lizards, Argentina

Introduction

The evolutionary patterns resulting from the Liolaemidae radiation provide an interesting example of the disparate diversification directions that closely related lineages can follow during the course of their phylogenetic histories. Within this South American lizard family, only three contrastingly different genera have been recognized, one being a monotypic lineage (*Ctenoblepharys*) and another (*Liolaemus*, with >200 species) one of the most extraordinary examples of evolutionary radiation known among living vertebrates (Pincheira-Donoso *et al.* 2008c). The third genus, *Phymaturus*, shows an intermediate species richness of 22 species (Pincheira-Donoso *et al.* 2008c; Corbalan *et al.* 2009). Species numbers are not, however, the only contrasting features found among these lizard lineages. Indeed, while *Liolaemus* has started to be regarded as

an interesting example of adaptive radiation given its dramatic diversity in phylogenetic, ecological and phenotypic features (Schulte *et al.* 2000; Espinoza *et al.* 2004; Pincheira-Donoso *et al.* 2008a, 2008b, 2009), *Phymaturus* has been suggested to be a more consistent candidate example of relatively poor diversification at the ecological and life-history dimensions, mediated by phylogenetic niche conservatism (Scolaro *et al.* 2008). These differences in the species richness between these two clades were even more accentuated until recently, when the diversity of *Phymaturus* (in contrast to *Liolaemus*) remained substantially more underestimated, being known on the basis of a few species (Etheridge 1995). In the recent years, several new *Phymaturus* species have been 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 (Lobo & Quinteros 2005b; Pincheira-Donoso *et al.* 2008c; Figs. 1 and 2).

As a consequence, a much more complete picture of the evolutionary origin and history of the genus *Phymaturus* is currently available (Díaz-Gómez 2009). *Phymaturus* species are primarily characterized by (*i*) stout and flattened body shapes, (*ii*) consistent preference for rocky microhabitats, (*iii*) herbivorous (or almost entirely herbivorous) diets, and (*iv*) viviparous reproductive mode, as well as many other features of their biology (Cei, 1986; Lobo & Quinteros 2005b; Ibargüengoytía *et al.* 2008; Pincheira-Donoso *et al.* 2008c; Boretto & Ibargüengoytía 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.* 2008c), as defined by the major views on this theory (Givnish & Sytsma 1997; Schluter 2000). The genus is widely distributed from the highlands of the Andes in Catamarca (Argentina), to the southern border of Chubut. Most species are endemic to Argentina, although two of them, *P. flagellifer* and *P. vociferator*, extend their distributions to reach Andean and Patagonian areas of the Chilean border (Lobo & Quinteros 2005b; Scolaro 2005, 2006; Pincheira-Donoso *et al.* 2008c; Díaz-Gómez 2009).

A number of recent phylogenetic hypothesis have repeatedly supported the idea that the genus *Phymaturus* consists of two major clades, one primarily distributed at the northern areas of the genus distribution (*flagellifer* group = *palluma* group), and the other one (*patagonicus* group) at central and southern Patagonia of Argentina (Espinoza *et al.* 2004; Lobo & Quinteros 2005b; Pincheira-Donoso *et al.* 2008c; Díaz-Gómez 2009). Interestingly, this phylogenetic evidence has also revealed that several morphological traits previously used to infer evolutionary relationships among *Phymaturus* lineages have the potential to predict the phylogenetic structure of the genus with a considerable extent of accuracy at the higher hierarchical taxonomic levels, as these traits had already suggested that the genus was diversified into these two main clades (Etheridge 1995).

Several of the recently recognized new species of 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 study, we aim to investigate two of such populations from Argentinean Patagonia belonging to the *patagonicus* lineage, close to the southernmost limit of distribution known for *Phymaturus*, one of which has been shown to exhibit patterns of divergence from previously named species (Cei & Castro 1973; Cei 1986; Lobo & Quinteros 2005a), and another one whose geographic isolation and patterns of coloration in adults and juveniles suggest divergence from the rest of *Phymaturus* species. The first of these populations, from Sierra del Castillo (45°08'30"S, 69°10'31"W) in the Chubut Province, has been waiting analyses for a long time, since Cei (1986) concluded that its phenotypic and biogeographic disparity would be the result of broad polymorphism within the species *Phymaturus patagonicus*. More recently, however, Lobo & Quinteros (2005a) suggested that this population should actually be reassessed to establish its position within the genus. In this paper, we carry out these analyses and conclude that both populations represent two distinct *Phymaturus* species, which are formally named.

Material and methods

To investigate the position of the above mentioned populations within the genus *Phymaturus*, we carried out initial exploratory analyses involving specimens from both sexes belonging to all known species of the *patagonicus* group (Appendix; Figs. 1 and 2). However, given that most species of this lineage are

substantially isolated geographically from the two new species here studied, and from *P. indistinctus* and *P. patagonicus*, our quantitative comparative analyses were performed only among these four species. We measured different morphological traits recognized to provide information on species delimitations among Liolaemidae lizards, and within *Phymaturus* (Donoso-Barros 1966; Cei 1986; Etheridge 1995, 2000; Lobo & Quinteros 2005b; Pincheira-Donoso *et al.* 2007; Scolaro *et al.* 2008). All quantitative traits were measured using a precision caliper (0.1 mm), and a dissection stereomicroscope for other observations and scale counts. Data were collected from adult individuals of both sexes, which were categorized as sexually mature after analyzing the presence of mature gonads and the functional development of secondary sex characters.

According to the standard measurement variables proposed for studies in the genus *Phymaturus* (Etheridge 1995, Lobo & Quinteros 2005b) a total of 23 continuous and meristic traits were measured. These variables were employed to run a discriminant analysis (Field 2006; Zar 2009), in order to investigate multivariate patterns of differentiation among the two new species and species of the *patagonicus* clade. As previously mentioned, given that these two new species occur at the southern limits of the distribution of the *patagonicus* clade, and are strongly isolated by hundreds of kilometers from most species of this lineage (see Fig. 3), our multivariate analyses focused on those four species occurring at the same major geographical area (both new species, *P. indistinctus* and *P. patagonicus*). The discriminant factorial analysis was performed, considering 22 variables in the comparison between *Phymaturus* species. The neperian logarithm of the variables was used in order to reduce skewness (Zar 2009). Variables showing significant differences between groups were analyzed for normality by means of Snedecor's *F*-test. 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 or *z*-test was used. For comparative purposes, arithmetic mean and standard deviations (SD) are given (Table 1).

The herpetological collection where the holotype and paratypes are deposited is Museo de La Plata (Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, provincia de Buenos Aires; MLP-R).

Results

Statistical analyses

Quantitative analyses on morphological traits revealed significant differences between the two new *Phymaturus* species and *P. indistinctus* and *P. patagonicus* (Table 1). Three stepwise discriminant analyses were performed separately between *Phymaturus patagonicus versus P. videlai* **sp. nov.** and *P. castillensis* **sp. nov.**; a second between *P. indistinctus* versus *P. videlai* **sp. nov.** and *P. castillensis* **sp. nov.**; and a third between *P. videlai* **sp. nov.** versus *P. castillensis* **sp. nov.**. The variance-covariance equality of matrices showed that morphological traits are normally distributed, and homogeneity of variances among groups and means belonging to the same populations (*P. patagonicus* versus *P. videlai* **sp. nov.** and *P. castillensis* **sp. nov.**, Box's test, $F = 0.35$, $P = 0.91$, Discriminant functions: Wilks' Lambda (λ) = 0.04, Chi-square (χ^2) = 92.6, $P < 0.001$; *P. indistinctus versus P. castillensis* **sp. nov.** and *P. videlai* **sp. nov.**, Box's test, $F = 1.05$, $P = 0.39$, Discriminant functions: Wilks' $\lambda = 0.34$, $\chi^2 = 35.5$, $P < 0.01$; *P. castillensis* **sp. nov.** versus *P. videlai* **sp. nov.**, Box's test, $F = 1.72$, $P = 0.07$, Discriminant functions: Wilks' $\lambda = 0.12$, $\chi^2 = 44.6$, $P < 0.001$). Discriminant analysis of individual specimens resulted in a completely correct classification of cases (100%) in all of the analyses performed.

The discriminant analyses between *Phymaturus castillensis* **sp. nov.** and *P. patagonicus* showed significant divergence in tail length ($t = 3.97$, $P < 0.001$), axilla-groin distance ($t = 4.10$, $P < 0.001$), head length ($t = 2.90$, $P < 0.01$), dorsal head scales ($w = 721$, $P < 0.001$), hindlimb length ($t = 2.20$, $P < 0.05$), fourth finger length ($t = 2.13$, $P < 0.05$), fourth toe lamellae ($t = 2.70$, $P < 0.05$), supralabial scale number ($t = 3.60$, $P < 0.001$), scales around pineal ($w = 652$, $P < 0.01$), and in the number of scales around midbody ($w = 213$, $P < 0.001$). Comparisons between *Phymaturus castillensis* **sp. nov.** and *P. indistinctus* shows significant differences in axilla-groin distance ($t = 2.28$, $P < 0.05$), tail length ($t = 5.11$, $P < 0.001$), forelimb length ($t =$

2.75, $P < 0.01$), hindlimb length ($t = 4.13$, $P < 0.001$), fourth finger length ($t = 3.78$, $P < 0.001$), fourth toe length ($t = 4.41$, $P < 0.001$), ventral scale number ($w = 76$, $P < 0.05$), and in the number of scales around mental ($w = 63$, $P < 0.01$) (see Table 1 for details).

TABLE 1. Patterns of morphological variation in morphometric and meristic traits among four geographically related species of *Phymaturus* of the *patagonicus* clade. For all traits Mean ± Standard Deviations are shown. Significant statistical differences among the two new species (*P. castillensis* and *P. videlai*) and *P. patagonicus* and *P. indistinctus* ($P<0.05*$, $P<0.01**$, $P<0.001***$), and only between both new species ($P<0.05^{[*]}$, $P<0.01^{[**]}$), are indicated with asterisks.

Traits	*P. patagonicus* (N = 21)	*P. indistinctus* (N = 7)	*P. castillensis* (N = 31)	*P. videlai* (N = 10)
Snout-vent length	86.4±3.9	85.6±4.8	88.2±3.7	85.1±8.8
Tail length	113.9±7.0	89.9±3.4	104.8±6.8** [**]	90.4±9.3**
Axilla-groin distance	43.8±2.3	43.9±4.1	47.2±3.3**	47.0±5.6*
Head length	16.0±0.8	16.8±1.3	16.9±1.2**	17.0±1.6*
Head width	15.6±0.9	15.2±0.8	15.6±0.8	15.0±1.6
Eye-nose distance	5.9±0.5	5.9±0.3	6.0±0.4	5.7±0.3
Forelimb length	32.5±1.6	30.7±1.3	32.7±1.7** [*]	30.8±2.4**
Hindlimb length	47.8±2.8	45.6±2.4	49.4±2.2** [**]	42.9±2.7***
Fourth finger length	11.4±0.8	10.6±0.5	11.9±0.9* [**]	10.1±0.6***
Fourth toe length	15.8±0.8	14.4±0.7	16.0±0.9**	14.5±1.6**
Dorsal head scales	21.1±1.3	19.4±1.0	19.7±1.0**	19.4±1.4***
Fourth finger lamellae	23.9±1.3	23.7±0.5	23.3±0.9[**]	24.1±0.9
Fourth toe lamellae	28.2±1.5	27.0±2.2	26.9±1.8* [*]	28.4±0.8
Scales around mental	4.9±0.9	4.0±0.0	5.2±0.9** [**]	6.0±0.0***
Subocular scales	1.0±0.0	1.0±0.0	1.2±0.4[**]	3.1±0.9***
Lorilabial rows	2.0±0.2	2.0±0.0	2.0±0.2[**]	2.7±0.5***
Supralabial scales	8.0±0.2	8.3±0.5	8.4±0.6**	9.0±0.8***
Infralabial scales	7.8±0.7	7.7±0.7	7.8±0.6[**]	8.9±0.4**
Scales around pineal	7.0±0.8	7.3±0.8	7.5±0.8* [**]	8.3±0.5***
Rostral-interparietals	15.7±1.2	14.0±1.2	15.0±1.9	14.3±1.4**
Scales around midbody	180.4±7.9	199.1±10.1	206.9±8.8***	198.9±5.4***
Ventral scales	164.2±8.0	158.1±6.7	166.1±7.6** [**]	159.0±5.4*
Precloacal pores males	9.2±1.2	10.0±2.8	9.7±1.1	10.7±2.2

Contrasts between *Phymaturus videlai* **sp. nov.** and *P. patagonicus*, reveals significant differences in tail length ($t = 5.99$, $P < 0.01$), forelimb length ($t = 2.10$, $P < 0.05$), hindlimb length ($t = 4.11$, $P < 0.001$), fourth finger length ($t = 3.99$, $P < 0.001$), dorsal head scales ($w = 86.5$, $P < 0.01$), the number of scales around mental ($w = 230$, $P < 0.001$), subocular scales ($w = 230$, $P < 0.001$), lorilabial rows ($w = 261$, $P < 0.001$), supralabial scale number ($w = 215$, $P < 0.001$), infralabial scale number ($w = 237$, $P < 0.001$), scales around pineal ($w = 244$, $P < 0.01$), rostral-interparietal scale number ($w = 102$, $P < 0.01$), number of scales around midbody ($w = 263$, $P < 0.001$), and in the number of ventral scales ($w = 109$, $P < 0.05$). On the other hand, comparisons between *Phymaturus videlai* **sp. nov.** and *P. indistinctus* reveals significant differences in hindlimb length ($t = 2.22$, $P < 0.05$), scales around mental ($w = 28$, $P < 0.001$), lorilabial rows ($w = 35$, $P < 0.05$), subocular scales ($w = 28$, $P < 0.001$), scales around pineal ($w = 35.5$, $P < 0.05$), and infralabial scale number ($t = 3.25$, $P < 0.01$) (see Table 1, for details).

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Comparisons performed between the two new species, *Phymaturus videlai* **sp. nov.** and *P. castillensis* **sp. nov.**, reveals that significant differences exist in tail length ($t = 3.97$, $P < 0.001$), forelimb length ($t = 2.40$, $P < 0.05$), hindlimb length ($t = 6.62$, $P < 0.001$), fourth finger length ($t = 5.18$, $P < 0.001$), fourth toe length ($t = 3.38$, $P < 0.01$), the number of fourth finger lamellae ($t = 2.09$, $P < 0.05$), fourth toe lamellae ($t = 2.18$, $P < 0.05$), scales around mental ($w = 295$, $P < 0.001$), subocular scales ($w = 365$, $P < 0.001$), lorilabial rows ($w = 322$, $P < 0.001$), infralabial scale number ($t = 4.84$, $P < 0.001$), scales around pineal ($w = 304$, $P < 0.01$), and the number of ventral scales ($w = 110$, $P < 0.01$) .

Species accounts

Phymaturus castillensis sp. nov.
(Figures 4a, c, e)

Centrura patagonica patagonica Cei (1986: 182–183).

Type material. Holotype: MLP-R. 5441, adult male, collected in rocky outcrops (500 m asl) of Sierra del Castillo in La Juanita farm (45°08'30"S, 69°10'31"W), adjacent to Provincial Road 24, at 58 km north of Sarmiento town, Chubut Province, Argentina. Collected by J.A. Scolaro, O.F. Tappari and A. Marcus, 29 November 2008.

Paratypes: MLP-R 5442, adult male; MLP-R. 5443, adult female; MLP-R 5444 adult female; JAS-DC 1234 adult male; JAS-DC 1219 adult female. The same data as detailed for the holotype.

Etymology. The species name refers to the terra typica where this species is restricted.

Diagnosis. *Phymaturus castillensis* can be distinguished by a peculiar colour pattern similar to the colour patterns observed in females of some species of the *patagonicus* clade (Fig. 4a, c). However, from most species, except *P. videlai*, *P. indistictus* and *P. patagonicus*, *P. castillensis* is considerably isolated geographically by hundreds of kilometers (Fig. 3). From these three geographically closer species, *P. castillensis* can be differentiated by its pattern of coloration (Figs. 1, 2, 4) as well as the morphological differences detailed in the previous paragraph. In this new species there are no dichromatic differences between the sexes. The new species is a member of the *patagonicus* group, distinguished from the *flagellifer* group in having flat imbricate superciliaries rather than being rectangular and non-overlapping; slightly spiny and non-rugose caudal scales in verticilles (as seen among members of the *flagellifer* group). However, it has also the subocular scale not fragmented and separated from supralabials by two rows of lorilabials, as in most species of the *patagonicus* group, but not seen in the majority of members of the *flagellifer* group.

Description of the holotype. A medium-sized lizard; snout-vent length (SVL) 93.0 mm; tail 110.5 mm; head length 19.5 mm; head width 17.3 mm; eye-nose distance 7.0 mm; forelimb length measured from to the insertion of the limb into the body wall to the end of the claw of the fourth finger, 33.3 mm; hind limb length measured from to the insertion of the limb into the body wall to the end of the claw of the fourth toe, 50.8 mm; axilla-groin distance 46.5 mm (50.0 % of SVL); fourth finger length 11.2 mm; fourth toe length 17.0 mm; scales in dorsal head 19; scales around midbody 215; ventral scales between mental and precloacal pores 169; scales between rostral and frontal 14; supralabial scales 9-8; infralabial scales 9-8; subdigital lamellae on fourth finger 23; subdigital lamellae on fourth toe 28; precloacal pores 11; cephalic scales subpentagonals, smooth; supraorbital semicircles with large bulky scales, rounded, without azygous, incomplete posteriorly on both sides; no distinct rounded supraoculars; 7–8 imbricate and enlarged upper ciliaries; subocular scales rectangular, almost irregular but not fragmented, shorter than eye diameter, separated from supralabials by 2-2 irregular rows of lorilabials; preocular in contact with first lorilabial row; canthal separated from nasal by two scales; temporals smooth and rounded irregularly coniform, in 8–9 scales from auditive opening to the subocular; external auditory meatus enlarged, subellipsoidal longitudinally, with 5–6 very protruding or conically enlarged scales on its anterior border; diminute granular scales on posterior border; rostral undivided, wider than higher, separated by one row of medium scales from nasals; nasal large and surrounded by seven small scales; nasals separated by three small irregular scales; nostril rounded and large, over the

centre of nasal scale; parietals irregular and rough with evident interparietal, surrounded by eight scales; nuchals strongly conical organized in 12–14 irregular rows; post-auricular folds very developed with smooth conical scales; mental subpentagonal shorter than width, but higher than rostral, in contact with six irregular rectangular scales; two rows of 5–6 bilateral postmentals decreasing behind; dorsal scales smooth, conics, small and juxtaposed; mid-dorsal scales slightly rounded and smooth, decreasingly smaller and strongly conical toward the flanks; ventro-laterals and ventrals larger than dorsals, almost pentagonal, imbricate and smooth; two gular folds with rounded, small scales; 73 gulars between auditory meatus; caudal scales quadrangular and regularly imbricate in verticiles, proximally large, conical and smooth on dorsum, or slightly keeled, distally more rectangular and strongly keeled; scales on forelimbs subtriangular and smooth in the upper side, granular, rounded and subconical in the under side; scales in hind limbs strongly conical and slightly keeled in the dorsum but larger subpentagonal, imbricate and flat in the under side; in the femoral region, small granular scales in the lower side; infracarpals and infratarsals with round margins, becoming keeled to the base of fingers and toes. Subdigital lamellae of fingers keeled; fourth toe and finger claws very developed, almost 2.5 mm of long. Eleven 11 orange-reddish precloacal glands on the scales of the cloacal region.

Coloration. Colour pattern is similar in both sexes. The general pattern is characterized by two longitudinal series of pale-brown spots on a darker brownish dorsal background. These two parallel series of clear spots are conspicuous between the parietal area of the head and the base of the tail, where disappear gradually on the dorsal tail background. On the neck and fore-back, several black scales result in a partially blackish background. Similarly intense black spots are found on the pre- and post-humeral areas. On the ventral surface, the background colour varies from brick-red to intense orange. Colour pictures of males and females are shown in figures 4a, c, e.

Morphological variation. The sample analyzed comprised 16 adult males and 14 adult females (for means and SD see Table 1). Analyses show slight size differences between the sexes, females being larger (in SVL) than males (mean SVL in females = 89.1 mm, range = 81.1–94.2 mm, SD = 4.0; mean SVL males = 88.0 mm, range = 78.4–93.0, SD = 2.5). Axilla-groin distance in females ranged 42.7–52.5 mm (mean = 48.6 mm, SD = 3.6, representing 50.8–55.7% of SVL); in males ranged = 42.4–49.7 mm (mean = 46.5; SD = 2.1, representing 49.6–56.4% of SVL). In both sexes, head length ranged 15.4–19.7 mm, representing 18.3–21.4% of SVL. Head width ranged 14.2–17.3 mm. Eye-nostril distance ranged 5.2–7.0 mm. Tail length ranged 99.2–113.7 mm, representing 1.18–1.30 times of SVL. Forelimb length ranged 29.7–36.4 mm. Mean of hindlimb length in males was 49.6 mm, but in females ranged 43.6–51.9 mm (mean = 48.4 mm). Scales around midbody ranged 190–225 in both sexes combined. Dorsal head scales ranged 18–21. Ventrals ranged 152–180. Precloacal glands observed only in males, and ranged 8–11. Subocular scales fragmented in 1–2 parts. Two rows of lorilabials between suboculars and supralabials. Scales surrounding interparietal 6–9. Scales contacting mental 4–6. Scales between rostral-interparietal 13–16. Fourth finger subdigital lamellae number 22–25. Fourth toe subdigital lamellae number 23–30.

Geographic distribution. *Phymaturus castillensis* is only known from the type locality (Fig. 3).

Natural history. The biotope of *P. castillensis* is located in the arid Patagonic Phytogeographic Province, Central District, Erial subdistrict, in an ecotonal zone with the district of Subarbustive Steppe of the Argentinean Sierra (León *et al.* 1998). The predominant landscape is characterized by steppes only partially covered (< 50% of the surface) by small bushes and herbaceous coiron vegetation and graminea. In these Patagonian environments, the dominant bush species are *Nassauvia ulicina* and *Chuquiraga aurea*, primarily. In the Sierra del Castillo and in the areas of escorial, the predominant vegetations consists primarily of higher bushes (~1.70m) of the species *Colliguaya integerrima*, and others such as *Schinus polygamus*, *Lycium chilense*, *Berberis heterophylla*, *Nardophhyllum obtusifolium*, *Chuquiraga spp.*, *Verbena ligustrina* and scarce graminea grasses such as *Stipa spp.* and *Poa ligularis.*

Phymaturus castillensis selects rocky microhabitats in areas where other Liolaemidae (*Liolaemus elongatus, L. bibroni, L. kingii, L. fitzingeri*), Leiosauridae (*Diplolaemus bibronii, D. darwinii, Leiosaurus bellii, Pristidactylus nigroiugulus*) and Phyllodactylidae (*Homonota darwinii*) species have been recorded. However, since *P. castillensis* is restricted to the rocky outcrops, few individuals of these other species can be

found in direct coexistence with it. In addition, the colubrid snakes *Philodryas patagoniensis* and *Philodryas trilineata*, and the viperid *Bothrops ammodytoides*, are common elements of the reptile fauna at the same locality, and along with the Leiosaurids, they are likely to predate on the new *Phymaturus* species.

Our field and lab observations reveal that *P. castillensis* is viviparous, as observed in all the other species of the genus. In captivity, two females gave birth to one and two fully developed offspring early on February 2009 (7th–9th), respectively. In the field, this species is often found eating plants, as also observed in most members of the genus.

Phymaturus videlai sp. nov.
(Figures 4b, d, f)

Type material. Holotype: MLP-R.5438, adult male, collected in rocky outcrops (700 masl), near Buen Pasto town, at about 85 km northwest of Sarmiento (45°04'11"S, 69°25'25"W), Chubut Province, Argentina. Collected by J.A. Scolaro and O.F. Tappari, 15 November 2008.
Paratypes: MLP-R. 5439, adult female; MLP-R. 5440, juvenile female; JAS-DC 1149, adult male; JAS-DC 1146 adult male; JAS-DC 1150, adult female and JAS-DC 1199, juvenile female. All specimens have the same data of collection as the holotype.

Etymology. The species is named after Argentinean herpetologist Fernando Videla, who, for many years, accompanied José M. Cei in the field. They both conducted field research in several previously unexplored regions of the Argentinean Andes. As a result, he has made important contributions to the knowledge and diffusion of the herpetofauna of Argentina. We suggest the vernacular English name "Videla rockys' lizard" and the Spanish name "Lagarto de Videla" for this species.

Diagnosis. As in many other species of the *patagonicus* clade, *Phymaturus videlai* can be distinguished from other species of this lineage by features of the colour pattern and the geographical distribution (Figs. 1–4). The coloration of this species is characterized by irregular and small blackish spots spread over the dorsal surface, whose fusion results in a peculiar pattern. This pattern exhibits moderate sexual differences that, remarkably, can also be observed among juveniles, which suggests that sexual dichromatism might not necessarily be a secondary sexual trait in this species. From most species of the *patagonicus* clade, except *P. castillentis*, *P. indistictus* and *P. patagonicus*, *P. videlai* is strongly isolated geographically, as shown in map of figure 3. From these three geographically related species, *P. videlai* can be distinguished by the coloration features described below (Figs. 1, 2, 4), and by divergence in morphological traits detailed in the first part of the results section above. The species is a member of the *patagonicus* group of the genus.

Description of the holotype. A medium-sized lizard; snout-vent length (SVL) 91.4 mm; tail 100.1 mm; head length 18.5 mm; head width 16.4 mm; eye-nose distance 6.1 mm; forelimb length 33.3 mm; hindlimb length 45.7 mm; axilla-groin distance 50.3 mm (55.0% of SVL); fourth finger length 10.1 mm; fourth toe length 13.3 mm; scales in dorsal surface of the head 20; scales around midbody 206; ventral scales between mental and precloacal pores 163; scales between rostral and frontal 15; supralabial scales 9-8; infralabial scales 8-9; subdigital lamellae on fourth finger 24; subdigital lamellae on fourth toe 30; precloacal pores 10; cephalic scales granular and rounded, almost smooth; supraorbital semicircles with large bulky scales, with a small subpentagonal and rounded azygous; no distinct enlarged supraoculars; eight imbricate upper ciliar scales; subocular fragmented in 3-3 almost rectangular scales, slightly shorter than eye diameter, separated from supralabials by 2–3 irregular rows of lorilabials; preocular separated from lorilabial row by two scales; temporals smooth irregularly quadrangular, in 11–12 rows from auditive opening to the subocular; external auditory meatus enlarged, almost ellipsoidal transversally, without enlarged scales on its anterior border and with tiny granular scales on the posterior border; rostral wider than high, separated by one small scales from each nasal; nasal scale with a big central nostril, surrounded by eight small scales; nasals separated by four small irregular scales; parietals irregular and smooth with evident interparietal, surrounded by nine scales; nuchals granular in 5–6 irregular rows; post-auricular folds evident with interposed transversal folds with round, smooth and almost granular scales; mental subpentagonal of almost similar wide, but higher than

rostral, surrounded by six irregular rectangular scales; two rows of 7–8 bilateral postmentals decreasing behind; dorsal scales small, round and juxtaposed; middorsal scales slightly enlarged decreasing smaller and granular toward ventro-laterals; ventrals larger than dorsals, almost pentagonals, imbricate and smooth; two gular folds with rounded, smaller scales; 75 gulars between auditory meatus; caudal scales quadrangular regularly imbricate in verticiles, on dorsum, proximally larger and smooth, centrally keeled or spined, distally more rectangular and completely keeled, but ventrally slightly keeled; scales in forelimbs round and smooth in the upper side, triangular slightly spined in the lateral region, granular and rounded in the lower side; on the hindlimbs scales are dorsally slightly spined, subtriangular, smooth and bifid towards lateral region, larger imbricate and flat in the lower side; infracarpals and infratarsals with round margins, becoming trifid at the base of the fingers and toes. Subdigital lamellae of fingers keeled; strongly curved, long claws (>3 mm). Orange precloacal glands.

Coloration. Coloration in *P. videlai* is characterized by an irregular pattern of black or blackish-brown small spots spread over the dorsal surface, on a pale-brown background. The fusion of many of these spots often creates larger blackish spots with a variety of shapes. Often, these spots fuse to form black asterisks on the back of the neck and head. The patterns of fusion are also highly variable, sometimes forming series of small longitudinal stripes on the middle zone of the back, sometimes forming irregular and slightly transversal stripes, and sometimes appearing more intensely fused on the sides of the body and on the vertebral area, which creates the effect of two poorly delimited longitudinal and parallel pale-brown stripes extended from the head to the base of the tale. Sexual dichromatism is visible, although not remarkable as seen in other species of the group. Interestingly, juveniles can show signals of sexual dichromatism, as seen in adults. On the ventral surface, there is intense orange pigmentation, from the ventral neck to the tail, including hindlimbs as well. Figure 4 (b, d, f) shows colour patterns of both sexes in this species.

Morphological variation. The sample analysed comprises 4 adult males, 4 adult females, and 4 juveniles (1 male, 3 females). Because of the small sample analyzed, we only provide preliminary information on the magnitude of morphological variation observed in this species. There are slight differences in body size between the sexes, females being larger than males in SVL (mean SVL in females = 82.1 mm, range = 75.2–94.9 mm, SD = 11.1; mean SVL males = 91.1 mm, range = 89.5–92.3, SD = 1.43). Axilla-groin distance also differs between sexes, being longer in females, as would be expected. Variation in other traits is as follows: head length = 15.2–19.1 mm, representing 20.2–21% of SVL; head width = 13.1–16.4 mm, representing 17.2–17.9% of SVL; tail length = 79.1–105.2 mm, representing 1.05–1.10 times of SVL; forelimb length = 28.1–33.9 mm, representing 35.7–36.8% of SVL; hindlimb length = 38.7–45.7 mm, representing 50.0–51.5% of SVL; axilla-groin distance in females = 43.2–55.3 mm, representing 54.8–58.3% of SVL; axilla-groin distance in males = 43.4–50.3 mm, 55.0–56.8% of SVL. Variation in meristic traits ranged as follows (means and SD in Table 1): scales around midbody 192–220, dorsal head scales 17–21, ventrals 152–164, precloacal pores 9–14 (restricted to males), subocular scales fragmented in 2–4 units, scales surrounding interparietal 8–10, scales contacting mental 6, scales between rostral-interparietal 13–16 (see Table 1 for additional details on variation).

Geographic distribution. *Phymaturus videlai* is known from the type locality (Fig. 3).

Natural history. *Phymaturus videlai* occurs in isolated rocky outcrops, at elevations over 700 m. The physiognomy of the geographical zone where this species is found shows highlands of basaltic origin with abundant gravel and effusive rocks strongly eroded. The dominant landscape is the barren steppe, with shrubby, low herbaceous coverage, and with high percentage of bare soil. The biotope is similar to that described above in the Natural History of *P. castillensis*. The dominant vegetation is composed by low shrubby, cushion bushes and sparse large clumps, but with more abundant presence of a mean cushion-grass steppe (*Stipa papposa* "coirón", *Poa ligularis* "coirón poa") (León *et al*. 1998).

Even though the ecology of this species remains largely unknown, preliminary field observations revealed that, as recorded in the rest of the species of the genus *Phymaturus*, *P. videlai* is predominantly herbivorous. The reproduction of *P. videlai* is viviparous; we observed two captive females giving birth to two fully developed offspring each, early on February 2009. Other reptile species coexisting with *Phymaturus videlai* are the same mentioned above for the previous species.
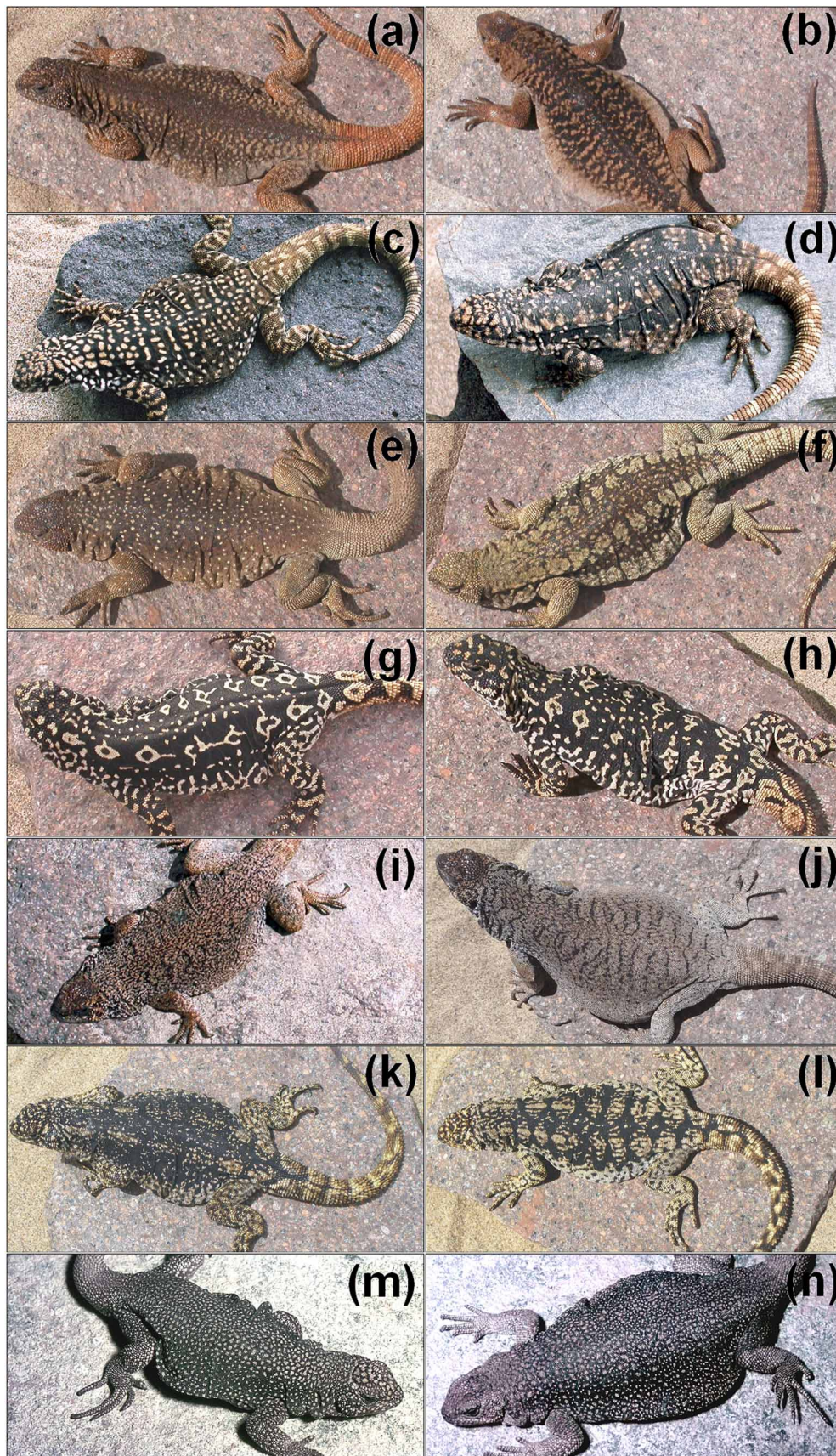
FIGURE 1. *Phymaturus* species of the *patagonicus* clade, showing the remarkable diversity of patterns of coloration known within this lineage. *Phymaturus agilis* (*a*, male; *b*, female), *P. calcogaster* (*c*, male; *d*, female), *P. ceii* (*e*, male; *f*, female), *P. excelsus* (*g*, male; *h*, female), *P. indistinctus* (*i*, male; *j*, female), *P. manuelae* (*k*, male; *l*, female), and *P. nevadoi* (*m*, male; *n*, female). (Photos: all J. A. Scolaro, except *P. nevadoi*, by J. M. Cei).
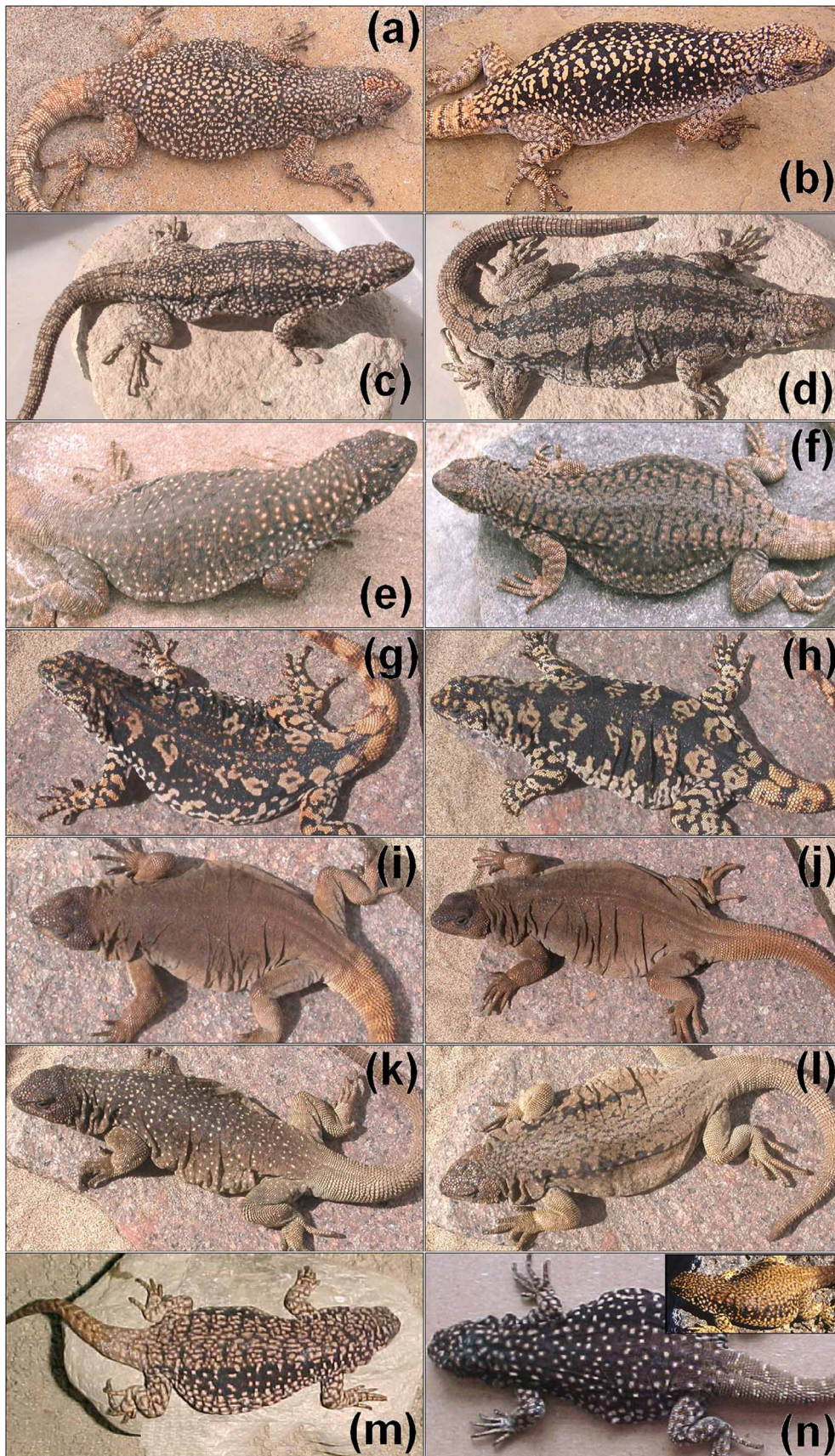
FIGURE 2. *Phymaturus* species of the *patagonicus* clade (continued from figure 1). *Phymaturus patagonicus* (*a*, male; *b*, female), *P. payuniae* (*c*, male; *d*, female), *P. somuncurensis* (*e*, male; *f*, female), *P. spectabilis* (*g*, male; *h*, female), *P. spurcus* (*i*, male; *j*, female), *P. tenebrosus* (*k*, male; *l*, female), and *P. zapalensis* (*m*, male; *n*, female). (Photos: J. A. Scolaro).
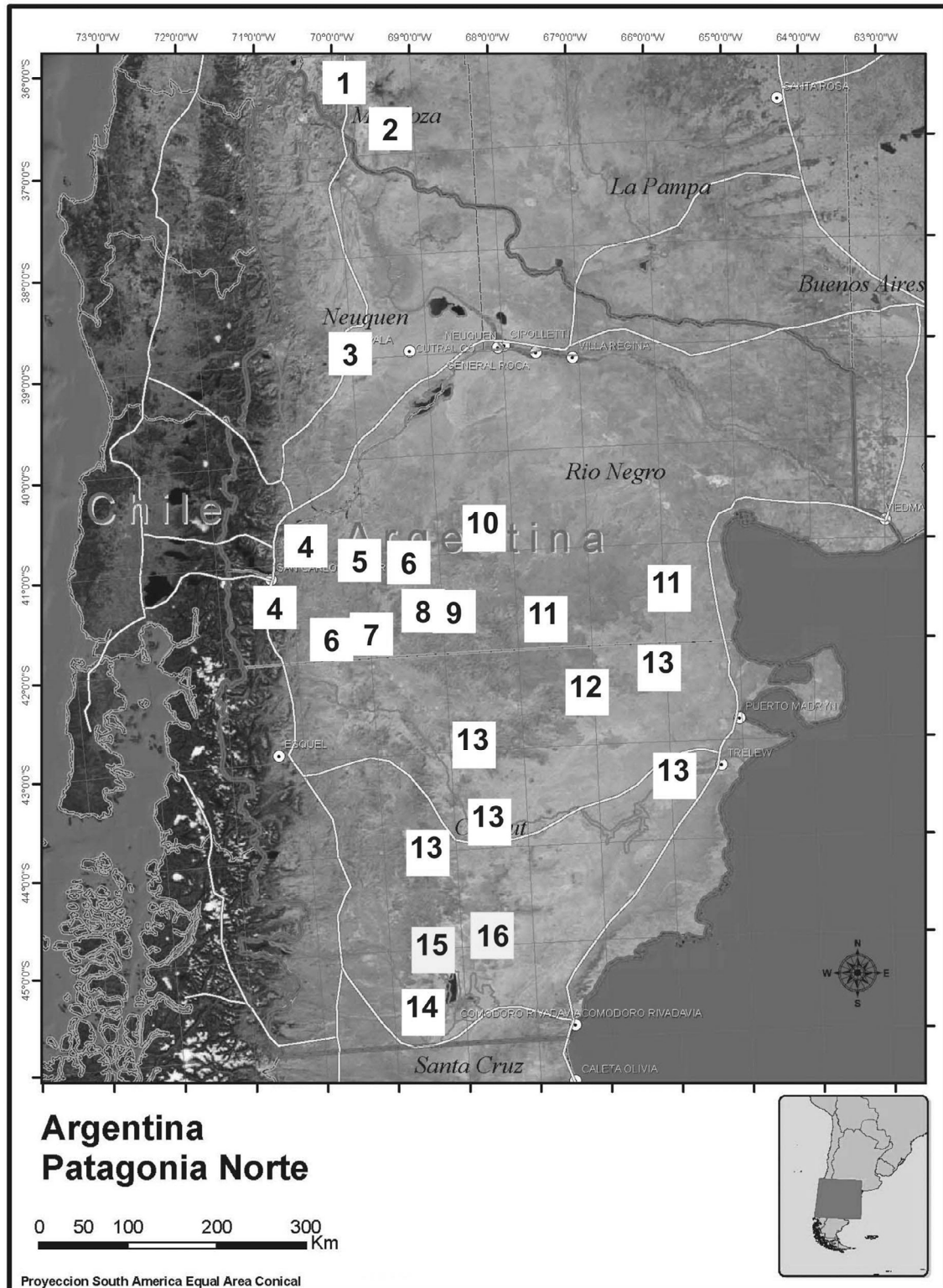
FIGURE 3. Geographic distribution of all known members of the *Phymaturus patagonicus* clade. Note nonoverlapping geographical ranges of most species. Localities are indicated by numbers, and represent *Phymaturus nevadoi* (1), *P. payuniae* (2), *P. zapalensis* (3), *P. tenebrosus* (4), *P. manuelae* (5), *P. spurcus* (6), *P. excelsus* (7), *P. spectabilis* (8), *P. agilis* (9), *P. ceii* (10), *P. somuncurensis* (11), *P. calcogaster* (12), *P. patagonicus* (13), *P. indistinctus* (14), *P. videlai* **sp. nov.** (15), and *P. castillensis* **sp. nov.** (16). The wide and scattered geographical distribution shown for *P. patagonicus* has been considered as the result of several cryptic different species recognized until today as polymorphisms within this species, and many of them are currently under study in order to establish their status within *Phymaturus*.
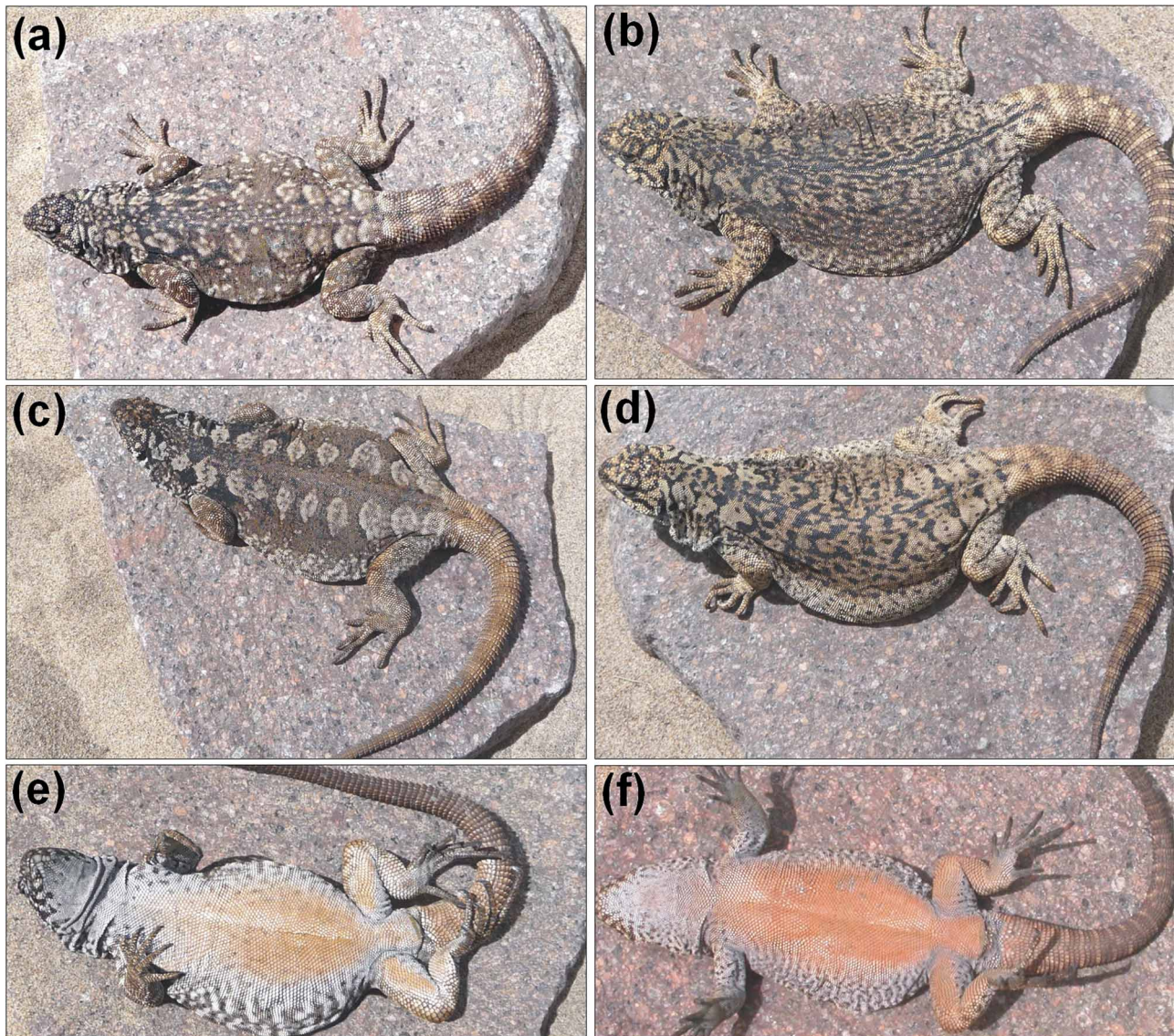
FIGURE 4. Adult males and females of the two new species of *Phymaturus* of the *patagonicus* clade proposed in this study. *Phymaturus castillensis* holotype male (a) and paratype female (c) in dorsal view, and adult paratype male (e) in ventral view. All specimens from the type locality. *Phymaturus videlai* paratype male (b) and paratype female (d) in dorsal view, and female paratype (f) in ventral view. All from the type locality. (Photos: J. A. Scolaro, November 2008).

Discussion

We have presented morphological and biogeographical evidence to support the designation of two new *Phymaturus* species of the *patagonicus* group from Argentina, named herein as *P. castillensis* and *P. videlai*. As a result of our study, the richness of the genus *Phymaturus* reaches a total of 24 species, and a richness of 16 species only for the *patagonicus* lineage, which contrasts with the <10 species known for the sister clade *flagellifer* (Pincheira-Donoso *et al.* 2008c).

A fundamental question behind the study and proposition of candidate new species is whether the integrated biological features of these populations are consistent with the occurrence of speciation events that should have taken place to originate them if they are actually different species. Given that speciation can be driven by different mechanisms that promote a substantial or absolute reduction in gene exchange between diverging populations (Mayr 1963; Schluter 2000; Coyne & Orr 2004; Gavrilets 2004; Ritchie 2007), and given that evolution at the phenotypic dimension is a multivariate process resulting primarily from the impact

of multivariate selection on several traits simultaneously (Lande 1979; Lande & Arnold 1983; Coyne & Orr 2004), it is expected that speciation events will leave signals on different features of the species resulting from this process. Therefore, designations of new species should not be carried out if these signals are entirely hidden. The absence of prominent signals at least at the phenotypic level, however, does not mean that speciation has not occurred, as demonstrated by the existence of groups of cryptic species (e.g. within Liolaemidae, Etheridge 1993; Lobo & Espinoza 1999; Pincheira-Donoso *et al.* 2007). This only means that additional evidence should be accumulated before deciding to add a new additional species to a lineage, as a way to reduce the risk of erroneously inflating clades' diversity, which can have serious and multiple negative consequences (Isaac *et al.* 2004). In general, these signals should be able to suggest that (*i*) the candidate new species and any potentially related species have followed evolutionary histories in different directions, and that (*ii*) gene exchange among these species is likely to be substantially or entirely interrupted, which can occur in sympatry if signals of strong assortative mating resulting from ecological or sexual mechanisms are observed. In the case of the two *Phymaturus* species here proposed, these signals appear to occur. Firstly, geographical signals of spatial isolation are prominent within the genus *Phymaturus*, and particularly within the *patagonicus* clade. The current discontinuous distributions of these lizards are likely to have resulted from phylogenetic constraints affecting traits involved in the evolutionary ability to expand ecologically into a broader diversity of niche conditions (e.g. Scolaro *et al.* 2008). This idea is supported by the fact that *Phymaturus* species occur isolated in areas that show both geographical (e.g. rivers) and ecological barriers (e.g. elevational differentials) separating them (e.g. Cei 1986; Lobo & Quinteros 2005a; Scolaro & Ibargüengoytia 2008; Scolaro *et al.* 2008). Indeed, almost invariably, one species occupying the available rocky microhabitat is found in each area, which is consistent with the idea that diversification in this group is the result of nonadaptive radiation caused by niche conservatism in allopatry (e.g. Wiens 2004). Therefore, isolation among these lizards is unlikely to be a consequence of low field exploration effort.

Specifically, *P. castillensis* occurs in an area with no contact with other species of the genus (reported for decades). As stated in the diagnosis of this species, this isolation is dramatic (the separation range reaches hundreds of kilometers from most species of the *patagonicus* clade) when compared with most species of the same lineage, except *P. indistinctus*, *P. patagonicus* and *P. videlai*. However, the pattern of coloration observed in *P. castillensis* exhibits remarkable overall differences from these species. While *P. videlai* is sexually dichromatic in contrast with the monochromatism found in *P. castillensis*, there is no overlap between the coloration observed in *P. indistinctus*, *P. patagonicus* and *P. castillensis*. This would suggest that patterns of coloration of these species may have been subjected to (and are maintained by) divergent selection regimes (Collette 1961; Losos 2009).

In *P. videlai*, on the other hand, sexual dichromatism has evolved (although not as strongly expressed as in other *Phymaturus* species of the same lineage; see Figs. 1 and 2), which suggests that this species has been subjected to antagonistic selection on sex-specific coloration (Andersson 1994; Fairbairn & Roff 2006). Since different forms of sexual phenotypic divergence can result from both natural and sexual selection (Shine 1989; Andersson 1994; Bolnick & Doebeli 2003; Losos 2009), it is difficult, at this time, to detect the evolutionary mechanism that might have caused and that maintains (although they might not be exclusive) these sexual differences in this lizard. Interestingly, juveniles *P. videlai* exhibit signals of sexual dichromatism as well. Therefore, this would potentially reflect different evolutionary scenarios underlying phenotypic differences between *P. videlai* and the other three species of the genus (*P. castillensis*, *P. indistinctus* and *P. patagonicus*), which lack sexual dichromatism, and hence, are unlikely to be subjected to similar selection pressures on coloration.

Despite the fact that this and several previous studies have contributed to increase the knowledge about *Phymaturus* lizards, which for decades were relegated to a secondary position after the prominent *Liolaemus* genus, several aspects of the biology of these peculiar reptiles remain to be studied. Recent research on phylogeography, reproductive and thermal biology (Piantoni *et al.* 2006; Ibargüengoytía *et al.* 2008; Boretto & Ibargüengoytía 2009; Díaz-Gómez 2009) has appeared to provide valuable new information that will be useful to further investigate the genus *Phymaturus* from a broader perspective.

Acknowledgements

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Appendix. Specimens examined and localities

Specimen numbers preceded by the acronym are housed in the following collections: IADIZA-CH, Colección Herpetológica del Instituto Argentino de Investigaciones de Zonas Áridas, CONICET, Mendoza; IBA, Instituto de Biología Animal, Mendoza, Argentina; MACN, Museo Argentino de Ciencias Naturales "B. Rivadavia", Buenos Aires, Argentina; MLP-R and MLP-S, Colección Herpetológica del Museo de La Plata, Buenos Aires, Argentina; JAS-DC, J.A. Scolaro-Diagnostic Collection, CENPAT-CONICET, Puerto Madryn, Argentina; JMC-DC, J. M. Cei-Diagnostic Collection, Facultad de Ciencias Naturales, Universidad Nacional de San Luis, Argentina; UNCo-PH, Universidad Nacional del Comahue, Colección Herpetológica, Bariloche, Río Negro.

*Phymaturus agilis***:** Provincial road 6 south of Ingeniero Jacobacci, Rio Negro Province, Argentina: MLP-R 5343 (Holotype), MLP-R 5344-5346, and JAS-DC 1644 and 1119 (Paratypes). *Phymaturus ceii***:** Rio Negro, Chasicó, 1150 m asl, south of El Cuy Plateau: MLP-R 5289 (Holotype), MLP-R 5290-93 (Paratypes); JAS-DC 1000, 1002-09, 1018-24, 1026-29, 1031. *Phymaturus calcogaster***:** Laguna de las Vacas, Telsen, Chubut: MACN 38109 (Holotype), MLP-R 5130-5135 (Paratypes); JAS-DC 797-804. *Phymaturus excelsus***:** Ojos de Agua, Río Negro: JAS-DC 1127-1136. *Phymaturus indistinctus***:** Puerta del Diablo, Sarmiento, Chubut: JAS-DC 55, 399; Sierra de San Bernardo, Sarmiento, Chubut: JAS-DC 838, 839; Las Pulgas, Sarmiento, Chubut: IBA 666-1, IBA-2, 3. *Phymaturus manuelae***:** Comallo, Rio Negro: MLP-R. 5370 (Holotype); MLP-R. 5371; UNCo-PH 201, 202 (Paratypes); JAS-DC 1100, 1101. *Phymaturus nevadoi***:** Agua de la India Muerta, Nevado, Mendoza: IBA R-0999 (1-3). *Phymaturus patagonicus***:** 40 km west Dolavon, Chubut: IADIZA-CH 00080; JAS-DC 813-820; IBA-R 0789; JMC-DC 335-336, 760, 842-845, 1300. *Phymaturus payuniae***:** Base del Volcán Payún, Mendoza: IBA 769-2(4-8); Payún plateau, Volcán Payún, Mendoza: IADIZA-CH 00087-8, 00087-9; JMC-DC 99, 807, 808. *Phymaturus somuncurensis***:** Meseta de Somuncurá, Río Negro: MLP-S 908-909, 1645-1651; MACN 37431-37440, 36147-48; Laguna Raimundo, Meseta Somuncurá, Río Negro: JMC-DC 337-338, 832-833; Cerro Corona, Meseta de Somuncurá, Río Negro: IADIZA-CH 00212 and 00254; JAS-DC 154, 211, 217-220, Laguna Blanca, Meseta de Somuncurá, R.Negro: JAS-DC 60, 609-614, 875-879, 883-884. *Phymaturus spectabilis***:** Ruta provincial 6, Km 24, Ing. Jacobacci, Río Negro: JAS-DC 1033-38, 1041-1042, 1047-52, 1054-59, 1061-63, 1066, 1091. *Phymaturus spurcus***:** Estancia Huanuluán, Río Negro: JAS-DC 821-823, 825-831. *Phymaturus tenebrosus***:** Cerro Alto, Ruta 40, Río Negro: MACN 1271; JAS-DC 811, 824, 832-837, 1103. *Phymaturus zapalensis***:** Laguna Teru, Zapala, Neuquén: IBA-R 0590, 0861, 0792; JMC-DC 007, 008; Laguna Blanca, Zapala, Neuquén: MLP-S 1942; south of Piedra del Águila, Neuquén: IBA-R 0866; Laguna del Burro: MLP-S 2273; Laguna Blanca: UNCo-PH 38,104, 109-113.