



When starvation challenges the tradition of niche conservatism: On a new species of the saxicolous genus *Phymaturus* from Patagonia Argentina with pseudoarborescent foraging behaviour (Iguania, Liolaemidae)

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Abstract

The genus *Phymaturus* is known on the basis of almost twenty species with clear tendency to conserve saxicolous or terrestrial, and herbivorous niche. In this work, we present the description of a remarkable new *Phymaturus* species, *Phymaturus agilis*, with the peculiar ability to climb on large shrubs to feed on fresh flowers and fruits. This new species is a member of the *Phymaturus patagonicus* clade, restricted to Patagonia Argentina. *Phymaturus agilis* occurs at about 1100 m of elevation in a volcanic rocky plateau close to Ingeniero Jacobacci, in the south western area of Río Negro Province, Argentina. Comparative analyses conducted on morphological and coloration traits revealed substantial differences from *Phymaturus spectabilis*, the only *Phymaturus* species living in sympatry with *P. agilis*. Individuals of both species had recently been recognized as members of a single taxon with broad phenotypic variation.

Key words: *Phymaturus agilis*, Liolaemidae, Patagonian Reptiles, Rocky Lizard

Resumen

Cuando el hambre desafía la tradición del conservacionismo de nicho: Sobre una nueva especie del género saxícola *Phymaturus* de la Patagonia Argentina con conductas pseudoarborescentes de forrajeo (Iguania, Liolaemidae).

El género *Phymaturus* es conocido sobre la base de casi veinte especies con clara tendencia a conservar el nicho saxícola o terrestre, y herbívoro. En este trabajo, presentamos la descripción de una notable nueva especie de *Phymaturus*, *Phymaturus agilis*, con la peculiar habilidad de trepar sobre grandes arbustos para alimentarse de flores y frutas frescas. Esta nueva especie pertenece al clado *Phymaturus patagonicus*, restringido a la Patagonia argentina. *Phymaturus agilis* se distribuye a unos 1100 m de altura en una meseta volcánica rocosa localizada cerca de Ingeniero Jacobacci, en el área sur-oeste de la Provincia de Río Negro, en Argentina. Análisis comparativos desarrollados sobre caracteres morfológicos y de coloración revelaron sustanciales diferencias con *Phymaturus spectabilis*, la única especie de *Phymaturus* que vive en simpatria con *P. agilis*. Individuos de ambas especies habían sido recientemente reconocidos como miembros de un mismo taxón con amplia variabilidad fenotípica.

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

Introduction

The evolutionary history of South American Liolaemidae lizards has produced strikingly asymmetrical patterns of diversification and radiation across its only three known genera, *Ctenoblepharys*, *Liolaemus* and *Phymaturus* (Pincheira-Donoso *et al.* 2008c). This asymmetry is better appreciated when comparing *Ctenoblepharys* and *Liolaemus*. While the first lineage is known on the basis of a single species (*Ctenoblepharys adspersa*) restricted to the deserts of central and southern Peru (Etheridge 1995), *Liolaemus* has achieved one of the highest taxonomic richness reported among living vertebrates, with around 200 named species (Etheridge & Espinoza 2000; Pincheira-Donoso *et al.* 2008c). In the middle of these extremes lays the genus *Phymaturus*, a group of Andean and Patagonian lizards whose diversity was underestimated until recently. However, increasing studies have revealed that this clade represents an interesting case of phylogenetic diversification across a wide geographical range of relatively similar environments (Cei 1986; Lobo & Quinteros 2005b; Scolaro 2006). Indeed, over the last few years, seven valid species have been discovered and named (Cei & Videla 2003; Scolaro & Cei 2003; Pincheira-Donoso 2004; Lobo & Quinteros 2005b; Scolaro & Ibarquengoytía 2007) and one has been revalidated (Lobo & Quinteros 2005a).

Currently, the genus *Phymaturus* comprises 19 species (*P. dorsimaculatus* was recently placed into the synonymy of *P. vociferator*, see Pincheira-Donoso *et al.* 2008c) primarily distributed in Argentina, but also reaching marginal Andean areas of central Chile (Cei & Videla 2003; Pincheira-Donoso 2004). The Argentinean species range from Catamarca to the southern border of Chubut, in the highlands of the Andes and in the volcanic plateaus of Patagonia (Chebez *et al.* 2005; Scolaro 2005, 2006; Scolaro & Ibarquengoytía, 2007).

Even though the genus *Phymaturus* is poorly known ecologically, most evidence suggests that these lizards exhibit a clear trend to conserve major aspects of the ancestral niche. In fact, all the extant reported populations are primarily saxicolous, herbivorous and viviparous (Cei 1986; Lobo & Quinteros 2005b; Boretto *et al.* 2007; Pincheira-Donoso *et al.* 2008c). This ecological similarity appears to have also a strong impact on the morphological variation of these lizards, invariably characterized by robust and flattened bodies that allow them to get hidden into small rock crevices (Cei 1986; Scolaro 2005, 2006).

Recent phylogenetic research (Espinoza *et al.* 2004; Lobo & Quinteros 2005b) has allowed to understand the evolutionary relationships between the main clades and species of this genus. At the present, *Phymaturus* contains two groups of species, readily recognizable on the basis of morphological traits, the *flagellifer* (= *palluma*, Cei & Scolaro 2006) and the *patagonicus* groups (Cei 1986; 1993; Etheridge 1995). Species belonging to the *flagellifer* (= *palluma*) group show non-imbricate superciliar scales, five or more suboculars, three to four rows of lorilabials, mental narrower than rostral and usually in contact with infralabials, well developed caudal spines, and two annuli per segment. Seven species are recognized as members of this group: *P. flagellifer* (= *palluma*) (Molina 1782), *P. mallimacci* Cei 1980, *P. punae* Cei, Etheridge & Videla 1983, *P. antofagastensis* Pereyra 1985, *P. verdugo* Cei & Videla 2003, *P. vociferator* Pincheira-Donoso 2004, and *P. roigorom* Lobo & Abdala 2007. On the other hand, the *patagonicus* group exhibits elongate and overlapping superciliar scales, a single elongate subocular, usually unfragmented, smooth caudal scales, and Meckel's groove fused and closed (Cei 1986; Etheridge 1995). This clade, restricted to the Patagonian steppe, comprises twelve species: the nominal *P. patagonicus* Koslowsky 1898, *P. calcogaster* Scolaro & Cei 2003, *P. ceii* Scolaro & Ibarquengoytía 2007, *P. excelsus* Lobo & Quinteros 2005, *P. indistinctus* Cei & Castro 1973; *P. nevadoi* Cei & Castro 1973, *P. payuniaie* Cei & Castro 1973, *P. somuncurensis* Cei & Castro 1973, *P. spectabilis* Lobo & Quinteros 2005, *P. spurcus* Barbour 1921, *P. tenebrosus* Lobo & Quinteros 2005, and *P. zapalensis* Cei & Castro 1973.

In this paper, we present the description of a new *Phymaturus* species from Rio Negro, in Patagonia Argentina. This new taxon exhibits the peculiar ability to climb on large shrubs (~2–3 m) to feed on fresh fruits and flowers. This species was recently considered as part of the population variance of *Phymaturus spectabilis* by Lobo & Quinteros (2005b). Nevertheless, phenotypic analyses reveal that these two taxa exhibit substantial differences, both in morphology and coloration.

Material and methods

Specimens and variables examined. We performed a general comparison of the new *Phymaturus* species ($n = 24$, see details below) with 11 out of the 12 species currently reported for the *patagonicus* group (see section on examined species, below). More detailed comparative meristic and morphometric analyses were conducted between the new taxon and some of the most phenotypically and geographically related *Phymaturus* species. For meristic analyses, we compared the new taxon with *P. excelsus*, *P. spectabilis* and *P. spurcus*, and for morphometric tests, with *P. ceii*, *P. excelsus*, *P. spectabilis*, *P. spurcus* and *P. tenebrosus*. Only adults of both sexes were studied. Sexual maturity was determined by the presence of mature gonads and the development of secondary sexual traits.

To perform these morphological comparisons, we used both categorical (for meristic analyses) and continuous (for morphometric analyses) variables. Six categorical variables were obtained: (1) scales around mid-body (SAMB, counted half-way between the axilla and groin region), (2) dorsal scales (DS, counted between the tip of the snout to the base of the tail), (3) rows of lorilabial scales (LS), (4) fragments of subocular scales (FSS), (5) number of supralabial scales (SLS), and (6) number of infralabial scales (ILS) (Etheridge & Christie 2003; Pincheira-Donoso *et al.* 2007a). 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.* 2008a), we did not include this variable in the meristic analyses. For morphometric analyses, we measured seven 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, selecting the largest two-thirds of the adult samples; e.g. Losos *et al.* 2003; Pincheira-Donoso *et al.* 2007b, 2008b), (2) head length (HDL, lateral measurement from the anterior edge of the ear opening to the tip of the snout), (3) head width (HDW, 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 length (AXGL, from the axilla to the anterior insertion of hind limb on the body wall), and (7) tail length (TL, from the anterior edge of the cloaca to the tip of the tail, excluding individuals with broken, missing or regenerated tails).

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 (MLPR). Details on the studied material are provided in the Appendix.

Statistical Analyses. Meristic analyses were conducted on raw data, using univariate Mann-Whitney tests to compare pairs of species. The non-normality of the data was observed using Snedecor *F* tests (Sokal & Rohlf 1969).

For morphometric analyses, all variables were ln-transformed to reduce skewness and make variances homogeneous (Miles & Ricklefs 1984; Zar 1999). 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, HDL, HDW, AXGL and FLL were included in multivariate analyses, whereas HLL and TL 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 (Green 2001). Nevertheless, it has been claimed in recent studies that a number of important assumptions might not hold for residuals, and that residual index is an ad-hoc sequential procedure with no demonstrated statistical

justification (Hayes & Shonkwiler 1996; Smith 1999; Garcia-Berthou 2001; Green 2001). 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 (Zelditch *et al.* 2004). All these analyses were conducted separately for both males and females.

Results

Morphological tests conducted on both meristic and morphometric variables revealed significant differences between the new *Phymaturus* species and a set of other congeneric taxa belonging to the clade *patagonicus* (Etheridge 1995).

Analyses on meristic traits showed that most variables differ between the four species included in these tests (*Phymaturus* **sp. nov.**, *P. excelsus*, *P. spectabilis*, *P. spurcus*). *Phymaturus* **sp. nov.** differed significantly from *P. excelsus* (Mann-Whitney test, SAMB $z = 3.26$, $P < 0.01$, LS $z = 2.41$, $P < 0.01$) and *P. spectabilis* (SAMB $z = 3.13$, $P < 0.01$, LS $z = 2.67$, $P < 0.01$), but not from *P. spurcus* (SAMB $z = 0.56$, $P = 0.58$, LS $z = 0.93$, $P = 0.35$) in the variables SAMB and LS, from *P. excelsus* ($z = 3.19$, $P < 0.001$), but not from *P. spectabilis* ($z = 1.13$, $P = 0.26$) and *P. spurcus* ($z = 0.63$, $P = 0.53$) in DS, and from *P. excelsus* ($z = 2.06$, $P < 0.03$), *P. spectabilis* ($z = 5.9$, $P < 0.001$) and *P. spurcus* ($z = 2.14$, $P < 0.03$) in FSS, and from *P. spurcus* ($z = 3.52$, $P < 0.001$) but not from *P. excelsus* ($z = 1.14$, $P = 0.25$) and *P. spectabilis* ($z = 0.66$, $P = 0.51$) in ILS. In contrast, the variable SLS did not show significant qualitative differences between these four species.

The multivariate and univariate analyses conducted on quantitative traits also revealed substantial morphological differences between the studied *Phymaturus* species (*Phymaturus* **sp. nov.**, *P. ceii*, *P. excelsus*, *P. spectabilis*, *P. spurcus* and *P. tenebrosus*). Male analyses on overall morphology (including SVL as a dependent variable) showed significant differences between the species (MANOVA, Wilks' $\lambda = 0.14$, $F = 3.49$, $P < 0.001$). Only HDL did not differ (ANOVA, $F = 2.19$, $P = 0.07$). Univariate analyses of variance conducted on HLL and TL (*P. excelsus* and *P. spurcus* removed, respectively, see above) revealed that the former trait differs significantly between the species (HLL, ANOVA $F = 6.39$, $P < 0.01$), in contrast to the latter, which did not show qualitative differences (TL, $F = 1.24$, $P = 0.32$). Multivariate and univariate analyses of covariance (SVL as covariate) also revealed that these species differ significantly in body shape (MANCOVA, Wilks' $\lambda = 0.22$, $F = 3.15$, $P < 0.001$). Only HDL did not differ between the studied taxa (ANOVA, $F = 2.12$, $P = 0.08$), as observed in the above multivariate analysis. Univariate covariance analyses showed that HLL differs significantly between the species (ANCOVA, $F = 4.11$, $P < 0.01$; *P. excelsus* removed), while TL did not show statistical differences ($F = 1.37$, $P = 0.27$; *P. spurcus* removed).

The same tests conducted on females showed that the studied *Phymaturus* species differ significantly in overall morphology (MANOVA, Wilks' $\lambda = 0.29$, $F = 3.35$, $P < 0.001$). Univariate analysis performed on HLL (*P. excelsus* removed) revealed significant differences between the species (ANOVA, $F = 4.14$, $P < 0.01$), in contrast to TL (*P. spurcus* removed), which was qualitatively identical across these taxa ($F = 1.67$, $P = 0.17$). Body shape tests based on covariance analyses (SVL as covariate) showed significant multivariate differences between the species (MANCOVA, Wilks' $\lambda = 0.37$, $F = 3.35$, $P < 0.001$). Only AXGL did not differ significantly (ANOVA, $F = 0.57$, $P = 0.73$). Univariate covariance analyses showed significant differences in HLL (ANCOVA, $F = 4.32$, $P < 0.01$; *P. excelsus* removed), but not in TL ($F = 0.69$, $P = 0.61$; *P. spurcus* removed).

These analyses support the idea that the species recognized as new in this study is an unknown *Phymaturus* taxon, which is formally named and described above.

***Phymaturus agilis* sp. nov.**

(Figures 1 and 2)

Type material. Holotype: MLP.R. 5343, adult male, collected in rocky tableland (41° 25' 40" S; 69° 45' 07" W; 1030 m asl), neighbour Provincial road 6 south of Ingeniero Jacobacci, Rio Negro Province, Argentina. Collected by J.A. Scolaro and O.F. Tappari, 10 March 2006.

Paratypes: MLP.R. 5344, adult male; MLP.R.5345, adult female; MLP.R. 5346, adult female; JAS-DC 1644, adult male and JAS-DC 1119, adult female. All specimens have the same data of collection as the holotype.

Etymology. The specific name *agilis* refers to the ability of this lizard to climb and forage on large *Lycium* spp. (~ 2–3 m) shrubs, an unusual behaviour in the genus *Phymaturus*. We suggest the vernacular English name “Climber lizard” and the Spanish name “Lagarto trepador” for this species.

Diagnosis. *Phymaturus agilis* exhibits slight sexual differences in body size, being females larger than males. However, sexual dichromatism is not observed. The species is a member of the *patagonicus* group of the genus, distinguished from the *flagellifer* (= *palluma*) group in having flat imbricate superciliar scales rather than rectangular and non-overlapping, slightly spiny and non-rugose caudal scales in verticilles (as seen among members of the *flagellifer* group). Additionally, it presents the Meckel’s groove fused. It has also the subocular scale fragmented (in 4–5 scales) and separated from supralabials by 2–3 rows of lorilabials, as in most species of the *flagellifer* group, but not seen in the majority of members of the *patagonicus* group. *Phymaturus agilis* can be distinguished from other members of the *patagonicus* group in having a unique and homogeneous colour pattern with only slight intersexual differences, by showing an attenuate incomplete ringed tail of 2x1 scales of red brick-like dark and light respectively, and a ventrally intense orange-red brick-like colour.

Phymaturus agilis differs from the sympatric *P. spectabilis* in having more fragmented the subocular scale, being fragmented in only two scales in *P. spectabilis*; in addition, in *P. agilis* the subocular scale is separated from supralabials by 2–3 rows of lorilabials, while in *P. spectabilis* is separated by only one row of lorilabials (see more details in the results paragraph). *Phymaturus spurcus* (Lobo & Quinteros 2005a) exhibits 3–4 fragmented suboculars and two rows of lorilabials separating suboculars and supralabials (our own data), resulting significantly different from *P. agilis* (Student’s *t*-test = 4.4; *df* = 41; *P* < 0.01). *Phymaturus agilis* differs from *P. calcogaster*, because this last species shows the subocular fragmented in four scales, separated from the supralabials by two rows of lorilabials, and similar wide of rostral and mental scales (Scolaro & Cei 2003; Scolaro *et al.* 2005), and from *P. indistinctus*, because it shows the subocular frequently fragmented in two scales and two rows of lorilabials between suboculars and supralabials. *Phymaturus agilis* differs from *P. patagonicus*, *P. excelsus*, *P. tenebrosus*, *P. ceii*, *P. somuncurensis*, because these species exhibit non divided subocular scale, and separated from the supralabials by a single row of lorilabials. From *P. zapalensis*, *P. payuniaie* and *P. nevadoi* differs because in these species there is strong sexual dichromatism, absent from *P. agilis*. In addition, the high number of scales around midbody and on the ventral surface differentiates *P. agilis* from *P. patagonicus*, *P. spurcus*, *P. excelsus*, *P. spectabilis*, and *P. tenebrosus*.

Description of the holotype. A medium-sized lizard; snout-vent length (SVL) 88.3 mm; tail regenerated; head length 16.4 mm; head width 15.0 mm; eye-nose distance 5.7 mm; forelimb length 29.7 mm; hindlimb length 46.3 mm; axilla-groin distance 46.3 mm (52.4 % of SVL); fourth finger length 10.1 mm; fourth toe length 14.7 mm; scales in dorsal surface of the head 19; scales around midbody 225; ventral scales between mental and precloacal pores 165; scales between rostral and frontal 11; supralabial scales 9-9; infralabial scales 9-9; subdigital lamellae on fourth finger 23; subdigital lamellae on fourth toe 27; precloacal pores 13; cephalic scales granular, almost smooth; supraorbital semicircles with large bulky scales, rounded, with an small azygous anteriorly, incomplete posteriorly on both sides; no distinct enlarged supraoculars; eight imbricate upper ciliaries; subocular fragmented in 4-4 almost rectangular scales, slightly shorter than eye diameter, separated from supralabials by 3-3 irregular rows of lorilabials; preocular separated from lorilabial row by

two scales; temporals smooth irregularly quadrangular, in 8–9 rows from auditory opening to the subocular; external auditory meatus enlarged, subtriangular transversally, with few notably enlarged (3–4) scales on its anterior border and diminute granular scales on posterior border; rostral more wide than high, separated by two small scales from nasals; nasal moderate, lateral, surrounded by nine small scales; nasals separated by five small irregular scales; parietals irregular and rough with evident interparietal, surrounded by nine scales; nuchals granular in 4–5 irregular rows; post-auricular folds evident with interposed transversal folds with round, almost granular, scales; mental subpentagonal less wide but higher than rostral, surrounded by four irregular rectangular scales; two rows of 6–5 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; 67 gulars between auditory meatus; caudal scales quadrangular regularly imbricate in verticils, proximally larger and smooth on dorsum, or softly keeled, distally more rectangular and keeled; scales in limbs round and slightly keeled in the upper side, granular and rounded in the lateral region, larger imbricate and flat in the lower side, infracarpals and infratarsals with round margins, becoming trifid to the base of fingers and toes. Subdigital lamellae of fingers keeled; claws moderately long.

Coloration. Males and females do not show clear differences in coloration. There is an irregular and discontinuous pattern of speckled black spots, more dispersed and attenuated in two dorso-lateral stripes, on a greyish and light brown background. The black spots pattern finish in the base of the tail in males, while in females it extends until the first third of the tail. The head is dark brown in males and females. The middle vertebral line is conspicuous. Ventrally, the males show a yellow and brick-like coloration from the throat zone to the tail, being darker in the tail. Orange anal pores. In females the throat zone, and the upper part of the chest is grey, but then turns reddish in the middle chest extending, like in males, along the tail. In both sexes the throat, the ventral side of the hands and legs are light grey, but the ventral zone of the legs are brick-like coloration. In the dorsal side of the tail there are 23/24 incomplete rings of two verticils of orange/dark-brown scales, separated by one verticil conformed by one pale-orange or yellowish scale. These rings cannot be distinguished ventrally, where ground colour is dark red. Dorsal side of legs and throat folds are light grey irregularly spread with small black spots. Body flanks are light grey without black spots, but with some small orange scales. The abdominal orange-red coloration disappears in the individuals kept in alcohol; the rings still in the fixed exemplars, but the orange coloration diminish, as well as the one of the thighs (Fig. 1a, b; Fig. 2a).

Morphological variation. The sample analysed comprises 7 adult males and 17 adult females. Preliminary observations allow us to establish minor morphological sex differences, being females slightly larger in body size than males. However, as expected, axilla-groin distance differs significantly between sexes, being greater in females ($t = 2.6$, $P < 0.01$; range in females = 38.7–51.6 mm, mean = 47.8 mm, SD = 3.8, representing 47.1–58.7% of SVL; range in males = 36.9–46.5 mm, mean = 42.2 mm, SD = 3.0, representing 46.7–53.9 % of SVL). Other morphometric variables include head length = 14.6–18.8 mm representing 18.0–21% of SVL, head width = 13.6–15.8 mm, tail length = 81.0–105.9 mm, representing 1.08–1.23 times of SVL. Variation in meristic traits is as follows: scales around midbody 220–240 (mean = 227.8; SD = 9.1), dorsal head scales 19–22, ventrals 158–176 (mean = 169.0; SD = 8.6), precloacal pores 7–13 (mean = 10; SD = 1.9) restricted to males, fragmented subocular scales in 3–5 (mean = 4.2; SD = 0.7), scales surrounding interparietal 6–9 (mean = 7.1; SD = 0.9), scales contacting mental 4–6 (mean = 4.2; SD = 0.5), scales between rostral-interparietal 14–17 (mean = 15.6; SD = 0.8). Further traits (means and ranges) are shown in Tables 1 and 2. All specimens show strong ventral coloration (brick-like red).

Geographic distribution. *Phymaturus agilis* was found on isolated volcanic outcrops on the tableland of the type locality. More explorations in neighbouring areas are necessary in order to determine the whole species range.



FIGURE 1. (a) Adult male holotype of *Phymaturus agilis* in life from Terra Typica, Río Negro, dorsal view. Photo: J.A. Scolaro, 10-03-2006. (b) Adult female paratype of *Phymaturus agilis* in life from Terra Typica, Río Negro, dorsal view. Photo: J.A. Scolaro, 10-03-2006.

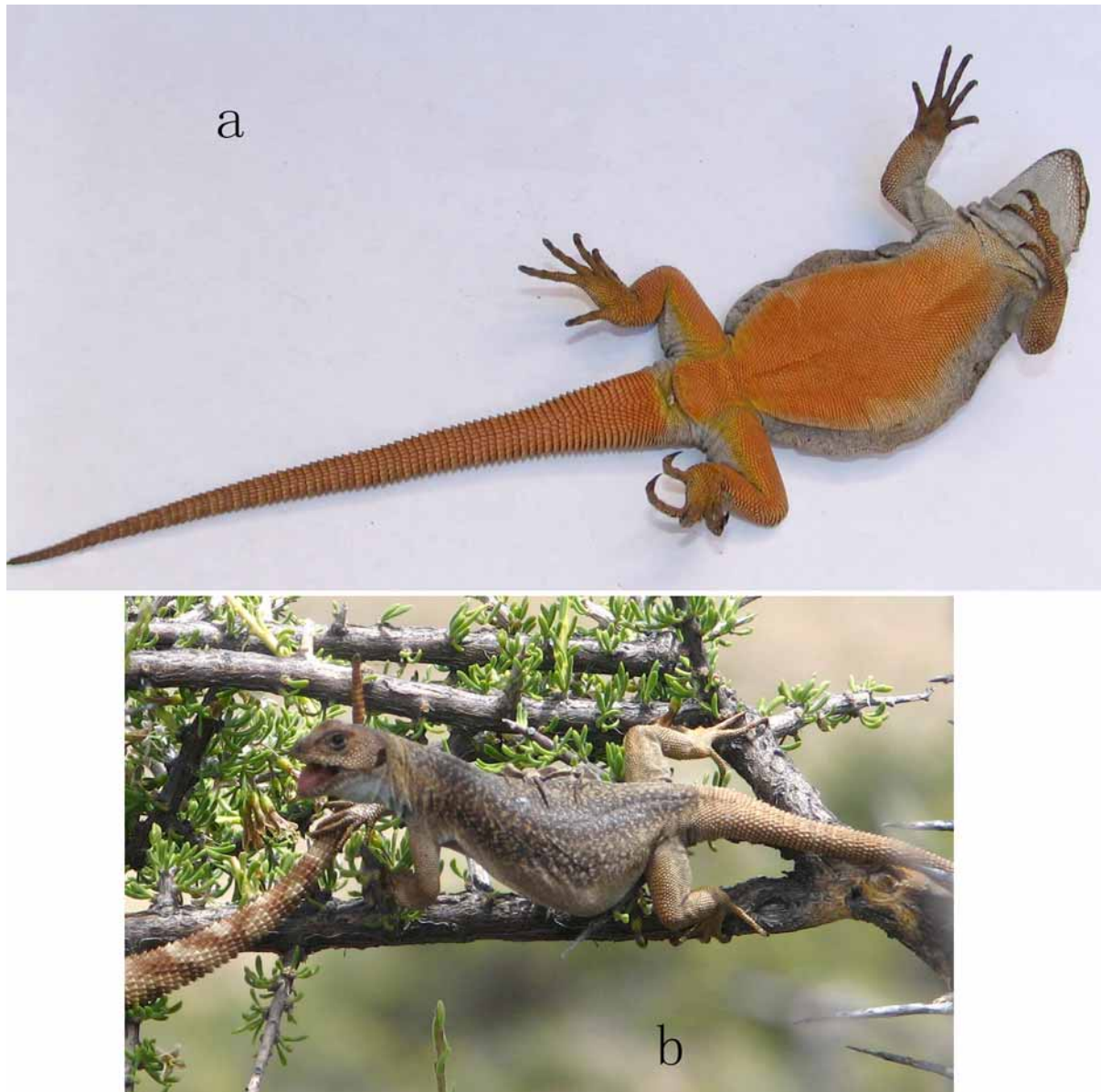


FIGURE 2. (a) Adult female paratype of *Phymaturus agilis* in life from Terra Typica, Río Negro, ventral view. Photo: F.O. Tappari, 11-10-2007. (b) Adult of *Phymaturus agilis* foraging and feeding on a *Lycium gillesianum* shrub. Photo: Cynthia González, 26-11-2006.

Natural history. *Phymaturus agilis* occurs in an isolated basaltic plateau, at elevations over 1000 m. The geological history of this geographical zone has originated several similar altitudinal plateaus, where this and other lizard species tend to live relatively isolated (Scolaro 2006).

Even though the ecology of *Phymaturus agilis* remains largely unknown, preliminary field observations revealed remarkable information. In contrast to other *Phymaturus*, this lizard exhibits the ability to climb and forage on large shrubs (up to 3 m) of the species *Lycium chilense* and *Lycium gillesianum*, to feed on fresh fruits and flowers. Specimens have also been observed foraging on the herbaceous species *Amsinkia calycima*. This pseudoarboreal foraging behaviour has never been reported for other *Phymaturus* species. However, since the ecology of most of these lizards is still poorly known (almost entirely unknown in the case of some species), it remains possible that other species of this genus also climb on shrubs to forage. Regarding experimental diet, *Phymaturus agilis* accepts *Tenebrio molitor* (mealworms) when kept in captivity, as previously

observed in *Phymaturus zapalensis* (Boretto & Ibarquengoytía 2005). This last observation might also suggest the incomplete available information on the ecology of *Phymaturus* lizards, whose diets have largely been considered almost exclusively herbivorous (Ceí 1986; Lobo & Quinteros 2005b; Scolaro 2006; Pincheira-Donoso *et al.* 2007). The reproduction of *P. agilis* is probably viviparous, as observed in all the remaining species belonging to this clade (Lobo & Quinteros 2005b; Pincheira-Donoso *et al.* 2007).

TABLE 1. Means, standard deviations (SD) and ranges of some morphological traits measured in *Phymaturus agilis*. Measurements in mm and scale numbers; ratios as proportions.

Variable	Males (N = 7)		Females (N = 17)		Both	
	Mean	Range	Mean	Range	Mean	SD
Snout-vent length (SVL)	83.8	74.7–90.1	86.6	79.4–93.0	85.8	4.69
Tail length (TL)	92.2	81.0–105.9	93.7	85.6–103	94.6	5.23
Axilla-groin distance (AXGD)	42.2	36.9–46.5	47.8	38.7–51.6	44.9	3.75
Head length (HDL)	16.1	14.6–18.8	16.4	15.5–17.9	16.3	0.86
Head width (HDW)	14.7	13.6–15.8	14.4	13.0–15.8	14.7	0.85
Eye-nose distance (ED)	5.9	5.5–6.5	5.8	5.3–6.6	5.8	0.42
Forelimb length (FLL)	28.9	27.1–30.5	29.9	29.5–32.3	29.6	1.62
Hindlimb length (HLL)	44.6	39.6–47.1	43.9	37.9–46.8	44.1	2.7
Fourth finger length (FFL)	10.2	8.8–11.1	9.8	8.1–11.1	9.9	0.83
Fourth toe length (FTL)	13.7	11.1–14.7	13.6	11.9–14.8	13.6	0.96
Dorsals in Head-Length (DS)	20.8	19–22	21.2	19–22	21.1	1.07
Scales surrounding interparietal	7.6	6–9	6.9	6–9	7.1	0.89
Fourth toe subdigital lamellae	22.1	20–24	22.0	18–24	22.0	1.50
Fourth finger subdigital lamellae	27.4	25–29	26.7	24–29	26.9	1.63
Supralabial scale number (SLS)	9.0	9–10	8.2	6–10	8.4	0.92
Infralabial scale number (ILS)	8.3	7–9	8.2	7–9	8.2	0.58
Scales contacting mental	4.3	4–6	4.2	4–5	4.2	0.51
Subocular scales (FSS)	3.8	3–5	4.2	4–5	4.2	0.73
Lorilabial rows (LS)	2.9	2–3	2.4	2–3	2.5	0.51

TABLE 2. Variation in some morphological traits between *Phymaturus agilis* and *P. spectabilis* and *P. spurcus*.

Variables	<i>P. agilis</i>			<i>P. excelsus</i>			<i>P. spectabilis</i>			<i>P. spurcus</i>		
	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
Snout-vent length	24	85.8	4.7	12	79.4	8.4	31	83.9	4.4	12	81.4	9.1
Scales around midbody	11	227.8	9.1	8	201.7	13.8	7	206.6	10.3	11	224.4	14.6
Dorsals in head-length	24	21.1	1.1	12	19.9	0.8	31	20.9	0.7	12	20.9	1.1
Ventral scales	11	169.0	6.6	8	168.8	8.4	7	164.8	10.4	11	174.2	9.7
Subocular scales	24	4.2	0.7	12	3.1	1.3	31	2.5	0.5	12	4.5	0.5
Lorilabial rows	24	2.5	0.5	12	2.1	0.3	31	2.1	0.4	12	2.3	0.5
Scales contacting mental	24	4.2	0.5	12	4.1	0.3	31	4.3	0.6	12	4.5	0.5
Axilla-groin distance	24	44.9	3.8	11	41.9	3.4	31	43.9	4.6	10	46.1	3.8
Precloacal pores in males	11	10.2	1.9	4	9.7	0.5	11	10.3	1.9	7	9.7	2.4

This biotope is found inside the arid district of the Monte Austral, a steppe showing open ground, with gravel and effusive rocks. The dominant landscape is the barren steppe, with shrubby, low herbaceous coverage, with bare soil percentages above 50%. The dominant vegetation is composed by cushion bushes and sparse large clumps, the Floristic Physiognomy Dominion are low shrubby steppes (with *Nassauvia glomerulosa* “colapiche”, *Chuquiraga opositifolia* “quilimbay”, *Mulinum spinosum* “neneo”, *Senecio filaginoides* “charcao”, *Stillingia patagonica* “Mata loca”, *Junellia* spp., *Amsinkia calycina* “Ortiga”, *Acaena splendens* “Abrojo”, *Perezia* spp., *Ephedra* spp. “Solupe”, *Fabiana patagonica*, *Grindelia coronensis* “melosa”, *Austrocactus patagonicus* “cactus”), and mean shrubby-grass steppes (with *Prosopis denudans* “algarrobillo patagónico”, *Lycium chilense* “yaoyín”, *Lycium gillesianum*, *Adesmia patagonica*, *A. volckmanni* “Mamuel choique”, *Schinus johnstonii* “Molle”, and bund grasses (*Stipa papposa* “coirón”, *Poa ligularis* “coirón poa”, *Bromus catharticus*) (Cabrera 1971).

Other reptile species coexisting with *Phymaturus agilis* are the iguanids *Liolaemus elongatus*, *L. bibronii*, *L. rothi*, *Diplolaemus sexcinctus* and the gekkonid *Homonota darwini*. The colubrid snakes *Philodryas patagoniensis* and *Philodryas trilineata*, and the viperid *Bothrops ammodytoides* are also common in the same locality, representing potential predators.

Discussion

In this study we present multidimensional phenotypic evidence to support the hypothesis that *Phymaturus agilis* represents a different species from *P. spectabilis* (and from all the remaining taxa of *Phymaturus*). In a recent study, Lobo & Quinteros (2005b) considered specimens from both species as part of the population variation exhibited by *P. spectabilis*. Our findings allow adding a further species to this still poorly known genus of iguanian lizards, whose study has increased substantially over the last few years (Lobo & Quinteros 2005b; Scolaro 2006; Pincheira-Donoso *et al.* 2008c). With the present work, *Phymaturus* reaches a known diversity of 20 species.

Several aspects of the biology of *Phymaturus agilis* contrast with the general patterns observed in the remaining species of this genus, apparently dominated by a strong influence of phylogenetic niche conservatism. This means that most of the known *Phymaturus* species tend to inhabit relatively or entirely isolated areas characterized by relatively similar environmental conditions (e.g. Cei 1986). In general, as mentioned above, these lizards occur in Andean or Patagonian ecosystems, selecting boulders as primary microhabitats. Since these environments tend to be poor in the abundance of potential invertebrate prey (Pough 1973; Pianka & Vitt 2003; Espinoza *et al.* 2004), *Phymaturus* taxa retain a herbivorous or omnivorous diet. Therefore, the idea of dominant niche conservatism within this genus is plausible. In spite of these largely observed distributional and ecological patterns, *P. agilis* lives in close sympatry with *P. spectabilis* (see above), in a zone of Patagonian plateaus. So far, similar reports of coexisting *Phymaturus* species of the *patagonicus* group are rare. Some of the unusual examples are certain areas where populations of *P. excelsus* and *P. spurcus* have been found living together (Lobo & Quinteros 2005b). This suggests that *Phymaturus* lizards may represent an interesting model organism to explore the ecological impact that small areas of sympatry produce on primarily allopatric species. For example, in areas of contact between interspecific populations, secondary sexual traits involved in mate recognition might be enhanced (Coyne & Orr 2004). On the other hand, although *Phymaturus* lizards are largely rock and ground dwellers (e.g. Cei 1986), *P. agilis* exhibits the peculiar ability to climb and actively forage on large shrubs (2–3 m), to reach plant matter otherwise difficult to get from the ground, such as flowers and fruits. This might suggest that this species has acquired a novel or at least unusual pseudoarboreal behaviour, which may contribute substantially to increase ecological success. However, as stated above, pseudoarboreal foraging behaviours might not be restricted exclusively to *P. agilis*. Indeed, since these lizards remain poorly studied ecologically, it is possible that other species of the genus also forage on high perches, in order to supply energy to their robust bodies.

Even though our conclusions are still largely unsupported by proper ecological and biogeographical evidence, and our own ecological observations might be enhanced in interest by the still limited available information on some aspects of *Phymaturus* biology (albeit increasingly studied in relation to their reproductive cycles and thermal biology; e.g. Ibagüengoytía 2005; Boretto *et al.* 2007), we believe that our findings represent an interesting contribution to the current understanding of this group of cold climate reptiles. We hope that these observations stimulate the arising of new ecological studies directed to elucidate with stronger evidence the historical factors responsible for the evolution of this peculiar clade of Liolaemidae lizards.

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Appendix

Specimens examined and localities. Specimen numbers preceded by the acronym are in collections as follows: 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, MLP-S, Colección Herpetológica del Museo de La Plata, Buenos Aires, Argentina; MCN-UNS, Museo de Ciencias Naturales, Universidad Nacional de Salta; 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 ceii. Río Negro, Chasicó, 1150 m, 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 797-800; JAS-DC 801-804.

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 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; MCN-UNS 1284-87.

Phymaturus payuniaie. Base del Volcán Payún, Mendoza: IBA 769-2(4-8); Meseta del Payún, 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 y 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.

Phymaturus agilis. Ruta Provincial 6, Km 24, Ingeniero Jacobacci, Río Negro: MLP.R. 5343-46; JAS-DC 1039-40, 1043-46, 1053, 1064-65, 1067-71, 1073, 1078, 1081, 1084-85, 1087-90, 1119; JAS-DC PH 212, PH 202-08.

Phymaturus spurcus. Estancia Huanuluán, Río Negro: MCN-UNS 1237-49, 1262; JAS-DC 821-823, 825-831.

Phymaturus tenebrosus. Cerro Alto, Ruta 40, Río Negro: MACN 1271; MCN-UNS 1263-73; JAS-DC 811, 824, 832-837.

Phymaturus zapalensis. Laguna Teru, Zapala, Neuquén: IBA-R 0590, 0861, 0792; JMC-DC 007, 008; Laguna Blanca, Zapala, Neuquén: MLP-S 1942; sur de Piedra del Águila, Neuquén: IBA-R 0866; laguna del Burro: MLP-S 2273; Laguna Blanca: UNCo-PH 38,104, 109-113.