

## Multiple lines of evidence show that *Phymaturus agilis* Scolaro, Ibargüengoytía & Pincheira-Donoso, 2008 is a junior synonym of *Phymaturus spectabilis* Lobo & Quinteros, 2005

Fernando Lobo<sup>1</sup>, Félix Benjamín Cruz<sup>2</sup>, Cristian Simón Abdala<sup>3</sup>

<sup>1</sup>IBIGEO (Instituto de Bio y Geociencias del NOA), CONICET-Universidad Nacional de Salta. Avda. Bolivia 5150. 4400-Salta, Argentina.

<sup>2</sup>INIBIOMA (CONICET – UNCOMA) Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Quintral 1250. 8400-Bariloche, Río Negro, Argentina.

<sup>3</sup>Instituto de Herpetología, Fundación Miguel Lillo, CONICET-Universidad Nacional de Tucumán. Miguel Lillo 251. 4000-Tucumán, Argentina.

Recibido: 16 Febrero 2011

Revisado: 09 Mayo 2011

Aceptado: 16 Noviembre 2011

Editor Asociado: R. Espinoza

### ABSTRACT

Lobo and Quinteros (2005) described *Phymaturus spectabilis* from Río Negro Province, Argentina. The species was characterized most notably by having a brown background with a more-or-less bilaterally symmetrical pattern of bold, light tan markings, some enclosing small brown spots, on the head, limbs, body, and tail. In 2008, Scolaro *et al.* described *P. agilis* from a locality 22 km south of the type locality of *P. spectabilis*. It was reported to differ from *P. spectabilis* in its nearly uniform brown color and certain morphometric and meristic characteristics. In 2009 we collected, at the type locality of *P. agilis*, five adults (both sexes) with the bold pattern of *P. spectabilis*, and five adults (both sexes) with the uniform color of *P. agilis*. Subsequently, one of the females with the *P. spectabilis* pattern gave birth to two individuals, one of which had the pattern of *P. agilis*, the other with the pattern of *P. spectabilis*. Our analyses of specimens assignable to *P. agilis* and *P. spectabilis* detected no significant differences between individuals with the two patterns for nine morphological variables (including those used to diagnose *P. agilis*), with overlap in the ranges of the variables for both patterns. We therefore conclude that *P. agilis* is a junior synonym of *P. spectabilis*.

Key words: Liolaemidae; Lizard; *Phymaturus*; Synonymy; Taxonomy.

### RESUMEN

En 2005 Lobo y Quinteros describieron *Phymaturus spectabilis* de la Provincia de Río Negro, Argentina. La especie fue caracterizada, como lo mas notable, por contar con un fondo general castaño de un patrón más oscuro que delimita manchas castañas claras dispuestas simétricamente en la cabeza, cuerpo extremidades y cola. En el 2008, Scolaro *et al.* describieron *Phymaturus agilis* de una localidad 22 km al sur de la localidad tipo de *P. spectabilis*. Se indicó diferir de *P. spectabilis* por su casi uniforme color castaño y por ciertas características merísticas y morfométricas. En 2009 colectamos, en la localidad tipo de *P. agilis*, cinco adultos (ambos sexos) con el patrón manchado oscuro de *P. spectabilis*, y cinco adultos (ambos sexos) con el color uniforme de *P. agilis*. Subsecuentemente una de las hembras con el patrón de *P. spectabilis* dio a luz dos individuos, uno con el patrón de *P. agilis*, el otro con el patrón de *P. spectabilis*. Nosotros no encontramos diferencias significativas entre los individuos con los dos patrones para nueve variables morfológicas, exhibiendo superposición los rangos de las variables morfológicas de los patrones. Nosotros concluimos que *P. agilis* es un sinónimo de *P. spectabilis*.

Palabras clave: Liolaemidae; Lagartijas; *Phymaturus*; Sinonimia; Taxonomía.

## Introduction

*Phymaturus* is a clade of saxicolous and herbivorous lizards with a viviparous mode of reproduction that lives at high elevations in the Andes of Chile and Argentina, as well as volcanic Patagonian basins in Argentina. The number of species of *Phymaturus* has grown rapidly in recent years (37), with several new species described within the last decade (Scolaro and Cei, 2003; Cei and Videla, 2003; Pincheira-Donoso, 2004; Lobo and Quinteros, 2005a, b; Scolaro and Ibarquengoytía, 2007, 2008; Lobo and Abdala, 2007; Scolaro *et al.*, 2008; Corbalán *et al.*, 2009; Lobo *et al.*, 2010; Núñez *et al.*, 2010; Avila *et al.*, 2011). Among these, there are two sympatric species belonging to the *Phymaturus patagonicus* group from Río Negro province, Argentina: *P. spectabilis* Lobo & Quinteros, 2005a and *P. agilis* Scolaro *et al.*, 2008, which are the subjects of this study. The latter was considered to be a distinct species based on a comparison of morphometric characters and the fact that the dorsal color was uniformly brown, whereas in *P. spectabilis* the pattern is one of bold, light tan markings, some enclosing small brown spots on the head, limbs, body, and tail. Scolaro *et al.* (2008) reported statistically significant differences among meristic and morphometric characters for the members of the *P. patagonicus* group included in their study. Ultimately, they concluded, «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*)» (Scolaro *et al.*, 2008:57).

Here we show that there are no statistical differences (based on univariate and multivariate analyses) between these two species for the same meristic and morphometric characters used by Scolaro *et al.* (2008) based on our examination and measurements of the same and additional individuals from both type localities. We also describe and provide photographs of the dorsal color pattern of two neonates—one with the uniform dorsal pattern of *P. agilis*, the other with the bold pattern of *P. spectabilis*—born from a single female assignable to *P. spectabilis*. We therefore conclude that *P. agilis* and *P. spectabilis* are color variants of the same species, and that *P. agilis* is a junior synonym of *P. spectabilis*.

## Material and Methods

In February 2009, during a fieldtrip to Patagonia, CSA and FBC collected specimens with the color pattern of both *Phymaturus agilis* and *P. spectabilis*, both 300 m east of the precise type locality of *P. agilis* and on the same foothills where both species were postulated to live in sympatry (Scolaro *et al.*, 2008). Specifically, five adult *P. spectabilis* (males: FML 23512–13; females: FML 23502, 23510–11) and five adults with the *P. agilis* pattern (males: FML 23505, 23508–09; females: FML 23503–04) were collected on Provincial Road 6, approximately 27 km south of the intersection with Provincial Road 23 (41°25'40.25" S; 69°45'24" W; 924 m on 4 February 2009; C. S. Abdala, F. B. Cruz, L. Moreno, and M. Bonino, collectors). Specimens were housed individually for subsequent examination. Among them, one pregnant female *P. spectabilis* (FML 23502) gave birth to two offsprings that were kept alive for 1 wk (Fig. 1). One of these newborn lizards (FML 23506) has the typical bold pattern of *P. spectabilis*, and looks almost identical to that of its mother, whereas the other (FML 23507) has the uniform brown color typical of *P. agilis*. This fortuitous discovery led us to re-examine interspecific variation in these *Phymaturus* populations (following Lobo and Quinteros, 2005a).

For this study we examined seven *Phymaturus agilis* and 18 *P. spectabilis*, plus 10 *P. excelsus* and 9 *P. spurcus*, all collected from their respective type localities (see Appendix 1). The latter two species were included to replicate the meristic character analysis used by Scolaro *et al.* (2008) to diagnose *P. agilis*. We also conducted multivariate analyses on a set of morphometric data following the methods of Scolaro *et al.* (2008), including analyzing each sex separately via MANOVA and MANCOVA (accounting for body size). For these analyses we used seven *P. agilis*, 18 *P. spectabilis*, 10 *P. excelsus*, 16 *P. spurcus*, 9 *P. ceii*, and 18 *P. tenebrosus*. The morphometric data we included in these analyses were those used by Scolaro *et al.* (2008): snout–vent length (SVL), head length (HL), head width (HW), interlimb length (ILL; left side; = axilla–groin distance), and hind limb length (HLL).

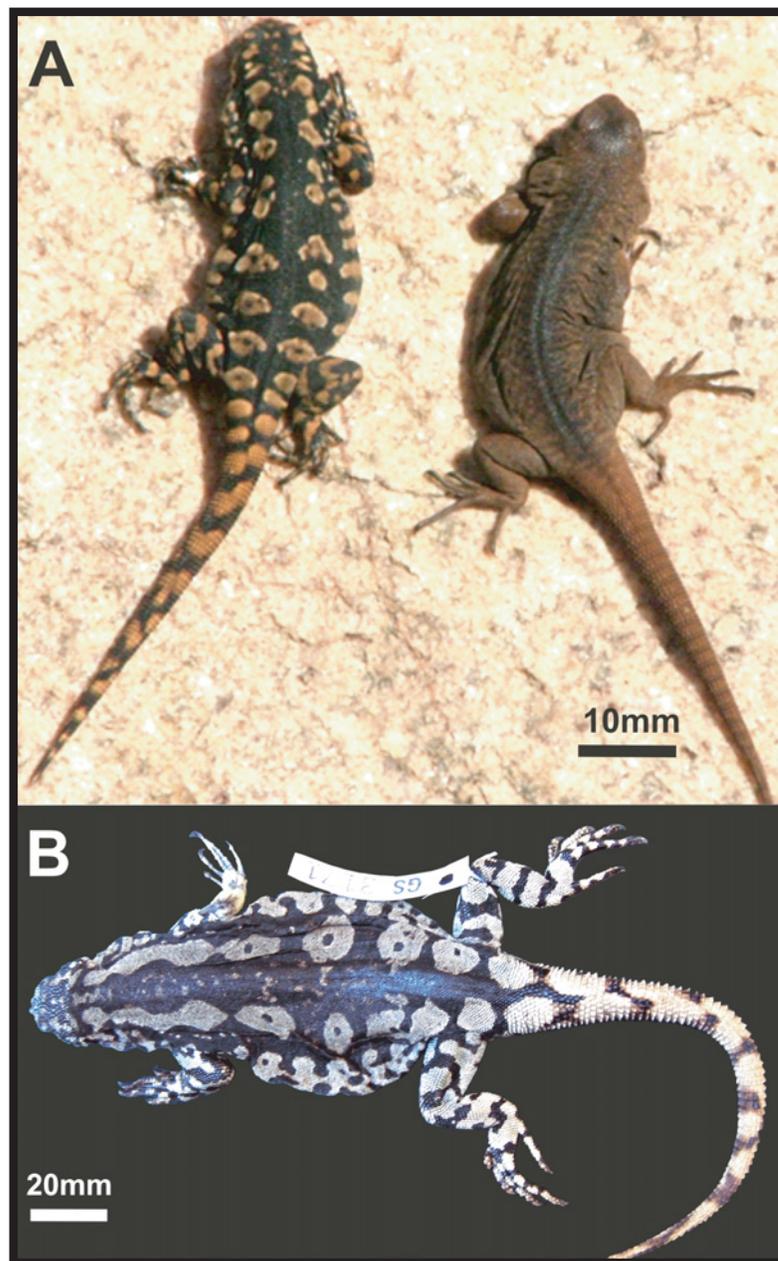
For the meristic data, we performed paired comparison between the *Phymaturus agilis* form and each of the following species: *P. spectabilis*, *P. excelsus*, and *P. spurcus* following the same procedures used by Scolaro *et al.* (2008). For these

analyses we compared the following character states: number of scales around midbody (SAMB), number of ventral scales (VS), number of supralabial scales (SLS), number of infralabial scales (ILS), number of lorilabial scales (LLS), and number of rows of subocular scales (SOS). We used *t*-tests when the assumptions of normality and equal variance were met, or Mann–Whitney *U* tests when the data did not conform to these assumptions. We included the following species (sample sizes) in these analyses: *P. agilis* (7), *P. spectabilis* (18), *P. excelsus* (10), *P. spurcus* (16), *P. ceii* (9), and *P.*

*tenebrosus* (18).

## Results

We show data for nine morphological variables (meristic) of *Phymaturus spectabilis* and *P. agilis* comparing the results of Scolaro *et al.* (2008) with those obtained in our study (two different samples; Table 1). In contrast to Scolaro *et al.* (2008) found no significant differences between *P. agilis* and *P. spectabilis* in scales around midbody (SAMB), lorilabial scale rows (LS), and fragments of



**Figure 1.** (A) Neonate *Phymaturus spectabilis* (FML 23506) with the typical bold pattern (left). Neonate *P. spectabilis* (FML 23507) brown morph (right). (B) Female *P. spectabilis* (FML 23502) with a bold pattern, which gave birth to the two neonates (A).

subocular scales (FSS) (Table 1). When we compared *P. agilis* to *P. excelsus* and *P. spurcus*, we found differences in the number of ventral scales (*P. agilis* vs. both species), the number of subocular scales vs. *P. excelsus*, and for the number of lorilabial scales (Table 2). Our results also show overlap in the ranges of these variables for *P. agilis* and *P. spectabilis*. The range of subocular scales reported by Scolari *et al.* (2008) is different from our data (Table 1). It is possible that we counted different sets of scales (perhaps Scolari *et al.*, 2008 included the preocular and postocular scales?). However, if this were the case, we would also expect a similar difference in subocular scale counts for the other *Phymaturus* species included in Scolari *et al.*'s study, which was not the case.

With regard to the morphometric variables, we found differences among females of *Phymaturus agilis* and *P. spectabilis* forms, *P. excelsus*, *P. spurcus*, *P. ceii*, and *P. tenebrosus* (MANOVA Wilks'  $\lambda = 0.247$ ,  $F_{5, 25} = 1.996$ ,  $P = 0.005$ ), where  $F \geq 2.224$  and  $P \leq 0.048$  for the following morphometric variables: SVL, HW, ILL, and HLL, but HL was not

different among species. In our analyses, *P. agilis* and *P. spectabilis* were always in the same statistical group as defined by a Tukey's post-hoc test. This indicates that the differences detected by the MANOVA resulted from a statistical difference in one or more of the other species (in this case *P. spurcus*). After accounting for body size of females via MANCOVA, we found similar results (Wilks'  $\lambda = 0.346$ ;  $F_{5, 20} = 1.832$ ,  $P = 0.027$ ) and only HLL was significantly different among the six taxa included in the analysis ( $F_5 = 7.274$ ,  $P < 0.001$ ). The same result was found when just considering males (MANOVA Wilks'  $\lambda = 0.139$ ,  $F_{5, 20} = 3.058$ ,  $P = 0.001$ ). Likewise, most of the morphometric variables (except for HL) were significant (lower  $F_5 = 4.411$ ,  $P = 0.003$ ), and after accounting for body size, there were significant differences among the six taxa (MANCOVA Wilks'  $\lambda = 0.253$ ,  $F_{5, 20} = 2.490$ ;  $P = 0.002$ ), with HW, ILL, and HLL different ( $F_5 = 2.213$ ,  $P = 0.049$ ). In the case of males, the Tukey's post hoc test] revealed that *P. ceii* was different from other taxa, yet *P. agilis* and *P. spectabilis* formed a homogeneous group in all analyses.

**Table 1.** Variation in morphological traits between *Phymaturus «agilis»* and *P. spectabilis* in Scolari *et al.* (2008) «SIP» and this study. Listed are those characters for which we were confident that the data were collected in the same way as SIP. Asterisks indicate meristic characters for which SIP detected significant differences between *P. «agilis»* and *P. spectabilis*. Final column is comparisons of our data, which were made by *t*-test (*t*) and Mann-Whitney *U* (*U*) tests depending on whether the assumptions for normality and equal variance were met or not, respectively.

Variables	<i>P. "agilis"</i> SIP			<i>P. "agilis"</i> This study			<i>P. spectabilis</i> SIP			<i>P. spectabilis</i> This study			t-test (t), This study M-W test (U), P-value	
	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD		
Snout-vent length	24	85.8	4.7	7	86.1	6.4	31	83.9	4.4	10	85.8	7.3	$t_{15} = 0.09$ ;	$P = 0.926$
Scales around midbody*	11	227.8	9.1	7	210.6	11.9	7	206.6	10.3	10	212.0	10.2	$t_{15} = 0.26$ ;	$P = 0.794$
Dorsals in head-length	24	21.1	1.1	7	20.8	0.9	31	20.9	0.7	10	22.1	0.9	$t_{15} = 1.71$ ;	$P = 0.108$
Ventrals	11	169.0	6.6	7	156.8	9.7	7	164.8	10.4	10	166.1	9.0	$t_{15} = 2.01$ ;	$P = 0.063$
Suboculars*	24	4.2	0.7	7	2.8	1.1	31	2.5	0.5	10	2.0	0.7	$U_{5,5} = 34.0$ ;	$P = 0.222$
Lorilabial rows *	24	2.5	0.5	7	2.4	0.6	31	2.1	0.4	10	2.6	0.6	$U_{7,10} = 81.0$ ;	$P = 0.073$
Scales contacting mental	24	4.2	0.5	7	4.1	0.4	31	4.3	0.6	10	4.0	0.0	$U_{7,10} = 68.0$ ;	$P = 0.282$
Precloacal pores (males)	11	10.2	1.9	4	9.5	1.7	11	10.3	1.9	3	9.0	0.0	$t_8 = 0.75$ ;	$P = 0.474$

## Discussion

Our statistically rigorous analysis of the same sets of characters used by Scolari *et al.* (2008), together with discovery of siblings with different color patterns, appears to confirm the intraspecific

variability of *P. spectabilis*, as originally described by Lobo and Quinteros (2005a), and rejects the recognition of *P. agilis* as distinct from *P. spectabilis*. More specifically, although Scolari *et al.* (2008)

**Table 2.** Variation in meristic characters between pairs, *Phymaturus «agilis»* vs. *P. spectabilis*; *P. «agilis»* vs. *P. excelsus*, and *P. «agilis»* vs. *P. spurcus*. Comparisons were made by *t*-test (*t*) and Mann–Whitney *U* (*U*) tests depending on whether the assumptions for normality and equal variance were met or not, respectively. See text for definitions of abbreviations. Asterisks denote significant differences.

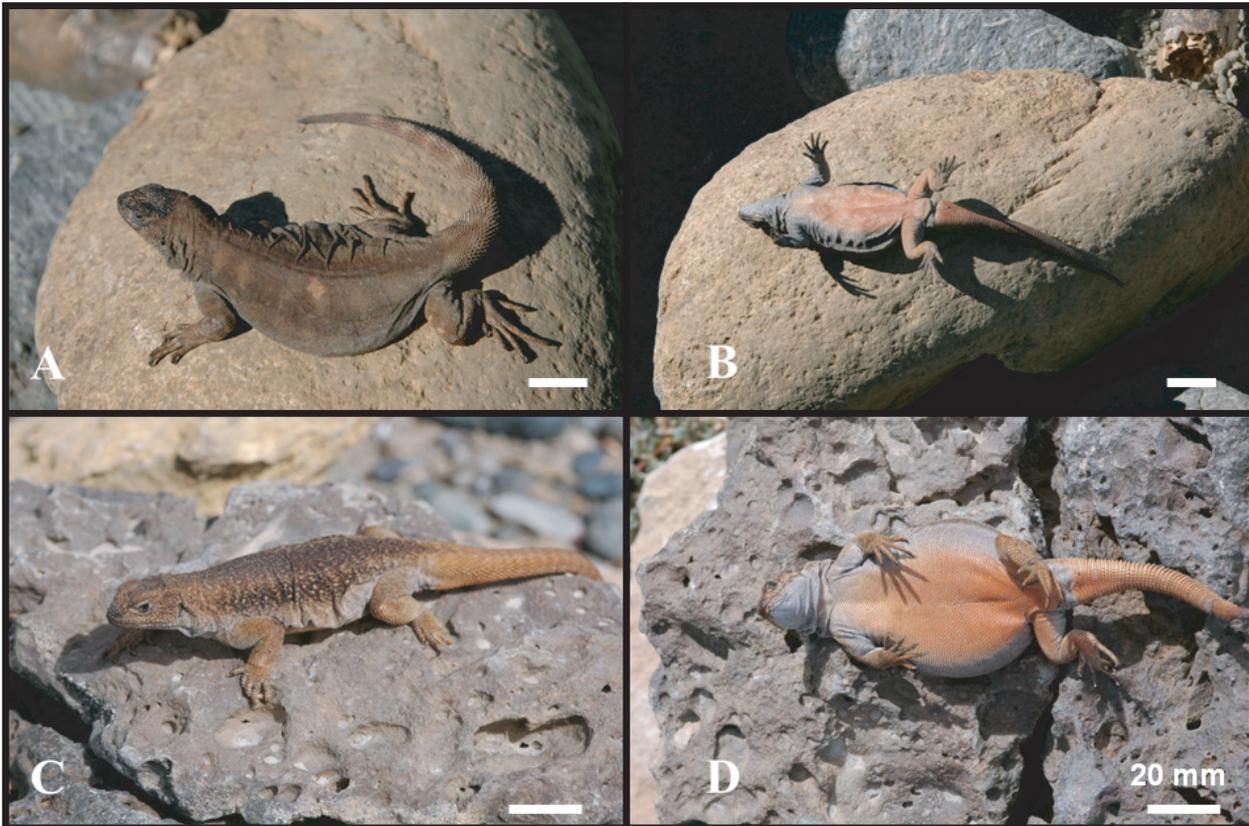
Variable	<i>P. «agilis»</i> vs. <i>P. spectabilis</i>			<i>P. «agilis»</i> vs. <i>P. excelsus</i>			<i>P. «agilis»</i> vs. <i>P. spurcus</i>		
	<i>n</i>	<i>t</i> or <i>U</i>	<i>P</i>	<i>n</i>	<i>t</i> or <i>U</i>	<i>P</i>	<i>n</i>	<i>t</i> or <i>U</i>	<i>P</i>
<b>SAMB</b>	7-10	<i>t</i> = 0.26	0.794	7-10	<i>t</i> = 0.94	0.363	7-9	<i>t</i> = 0.47	0.642
<b>VS</b>	7-10	<i>t</i> = 2.01	0.063	7-10	<i>t</i> = 2.61	0.020*	7-7	<i>t</i> = 2.63	0.022*
<b>SLS</b>	5-5	<i>t</i> = 0.53	0.608	5-6	<i>t</i> = 0.98	0.353	5-5	<i>U</i> = 14.0	0.190
<b>ILS</b>	7-10	<i>U</i> = 71.5	0.413	7-10	<i>U</i> = 70.0	0.504	7-9	<i>t</i> = 0.45	0.614
<b>SOS</b>	5-5	<i>U</i> = 34.0	0.222	5-8	<i>t</i> = 2.55	0.027*	5-5	<i>t</i> = 0.56	0.587
<b>LLS</b>	7-10	<i>U</i> = 81.0	0.073	7-10	<i>U</i> = 72.5	0.347	7-8	<i>U</i> = 78.5	0.006*

recovered statistical differences in their analysis of morphometric characters between *P. «agilis»* and the other species included in their analyses, they did not test whether any of the species formed groups that differed from other individuals or groups of species (i.e., post-hoc tests). We also found differences among species in our multivariate analyses, but our post-hoc tests revealed that *P. «agilis»* and *P. spectabilis* were never different from each other ( $P > 0.999$ ) for any of the morphometric characters. So although, our main results from the multivariate morphometric analysis are in accordance with those of Scolaro *et al.* (2008), our post-hoc analyses of the MANOVA do not support their conclusions that *P. «agilis»* is distinct and diagnosable from *P. spectabilis*.

Although we are confident that the disagreement between our study and that of Scolaro *et al.* (2008) reflects a lack of distinction of *P. «agilis»* with respect to *P. spectabilis*, we consider alternative explanations and the types of additional information that would be needed to conclusively resolve this issue. First, our sample sizes were smaller than those of Scolaro and colleagues (2008) as show in Tables 1 and 2. Another potential discrepancy is that there may have been differences in how we and Scolaro *et al.* (2008) counted scales. Although we acknowledge that the use of different specimens and differences in sample sizes may account for minor differences in our counts, we are confident that differences in counts attributable to human error are likely very small because of the substantial experience of both teams in describing other *Phymaturus* species. There is a chance that

the two offsprings representing both morphs that were born from our female *P. spectabilis* were the product of hybridization between two closely related species. However, when two species are indistinguishable other than their color pattern, and when newborns from a single female express this variation, it is more likely that color variants represent a single species rather than different taxa. This conclusion is further supported by the fact that other members of the *P. patagonicus* group also exhibit intraspecific color-pattern dimorphism. Indeed, the intraspecific dimorphism in color pattern of *Phymaturus spectabilis* (bold vs. brown pattern) has also been reported for *P. excelsus*, and less commonly in *P. tenebrosus* (Lobo and Quinteros, 2005a). In fact, intraspecific variability in dorsal color pattern appears to be fairly common trait of species belonging to the *P. patagonicus* group (see plates in Cei, 1986). In contrast, *P. spurcus* Barbour, 1921 is uniformly brown dorsally, with no individuals exhibiting the bold pattern (Lobo and Quinteros 2005b). These three *Phymaturus* species (*P. excelsus*, *P. spectabilis*, and *P. tenebrosus*) have considerable color-pattern variation both dorsally and ventrally (Fig. 2). Last, we acknowledge that our conclusion is a hypothesis that should be tested by additional studies including analyses of mate selection in nature, natural pattern-class frequencies (to test whether the morphs are in Hardy–Weinberg equilibrium), chromosomes, population genetics, or/and molecular phylogeography.

Researchers have cautioned that it is important to fully characterize intraspecific variation when diagnosing new species based



**Figure 2.** Brown morphs of two *Phymaturus* species of Río Negro province. (A) Dorsal and (B) ventral views of *P. excelsus* (FML 21452); (C) dorsal and (D) ventral views of *P. spectabilis* (FML 23510).

primarily on morphometric data (e.g., Gnaspini, 1999). Fortunately, it is uncommon in herpetology for a species to be diagnosed either solely or primarily on morphometrics and/or meristic characters. Indeed, the diagnoses of new species should include all available information: meristic and morphometric data, scale arrangement, shape, and surface conditions, color pattern, sexual dichromatism, and when possible ontogenetic variance, genetic data, and biogeographic information. Additionally, because *Phymaturus* are viviparous, and most are likely collected during summer months when females are pregnant, newborn lizards may provide a useful tool to insure the identity of a taxon or as an aid in diagnosing new ones. Scolaro *et al.*'s (2008) description of *P. agilis* is based only on meristic and morphometric data. We suggest that if other types of information were included, they might have concluded that the sympatric unpatterned morph is not a distinct species, but a conspecific pattern class of *P. spectabilis*.

In conclusion, the finding of sympatric and apparently interbreeding individuals is evidence of a lack of reproductive isolation between the *P.*

«*agilis*» morph and *P. spectabilis*. Couple this with the lack of significant differences in meristic and morphometric characters between these morphs compels us to conclude that *P. agilis* is a junior synonym of *P. spectabilis*. Finally, the intraspecific dimorphism in *P. excelsus* and *P. spectabilis* offer unique opportunities for researchers who are interested in identifying the factors that select for color-pattern polymorphisms in vertebrate populations (e.g., Sinervo and Lively, 1996; Robertson and Rosenblum, 2009).

#### Acknowledgements

We thank M. Bonino, L. Moreno, R. Semhan, and G. Scrocchi for help in the field. We thank two anonymous reviewers and to J. Schulte who made very important comments to an earlier draft of the manuscript. We also thank the AE for the time he expended in helping us to make the manuscript clearer. We acknowledge the Provincial Department of Fauna of Río Negro, Argentina for providing authorization for collecting *Phymaturus* (permit 127414/08). This study was supported by grants from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina

(PIP 5982, 2841) to FL and PIP6287 to FBC, ANPCyT PICT 2006–01205 to FBC and CSA and Consejo de Investigaciones de la Universidad Nacional de Salta, Argentina (CIUNSA 1663) to FL.

### Literature cited

- Avila, L. J., Pérez, C. H. F., Pérez, D. R. & Morando, M. 2011. Two new mountain lizard species of the *Phymaturus* genus (Squamata: Iguania) from northwestern Patagonia, Argentina. *Zootaxa* 2924: 1–21.
- Barbour, T. 1921. On a small collection of reptiles from Argentina. *Proceedings of the Biological Society of Washington* 34: 139–141.
- Cei, J.M. 1986. Reptiles del centro, centro-oeste y sur de la Argentina. Herpetofauna de las zonas áridas y semiáridas. *Museo Regionale di Scienze Naturali, Torino, Monografie IV*: 1–527
- Cei, J.M. & Videla, F. 2003. A new *Phymaturus* species from volcanic cordilleran mountains of the south-western Mendoza province, Argentina (Liolaemidae, Iguania, Lacertilia, Reptilia). *Bolletino del Museo Regionale di Scienze Naturale, Torino* 20: 291–314.
- Corbalán, V., Scolaro, A. & Debandi, G. 2009. A new species of the genus *Phymaturus* of the *flagellifer* group from Central-Western Mendoza, Argentina (Reptilia: Iguania: Liolaemidae). *Zootaxa* 2021: 42–56.
- Gnaspini, P. 1999. The use of morphometric characteristics for the recognition of species among goniosomatine harvestmen (Arachnida, Opiliones, Gonyleptidae). *Journal of Arachnology* 27: 129–134.
- Lobo, F. & Abdala, C. 2007. Descripción de una nueva especie de *Phymaturus* del grupo de *p. palluma* de la provincia de Mendoza, Argentina. *Cuadernos de Herpetología* 21: 103–113.
- Lobo, F. & Quinteros, S. 2005a. A morphology-based phylogeny of *Phymaturus* (Iguania: Liolaemidae) with the description of four new species from Argentina. *Papeis Avulsos de Zoologia* 45: 143–177.
- Lobo, F. & Quinteros, S. 2005b. Taxonomic studies of the genus *Phymaturus* (Iguania: Liolaemidae): redescription of *Phymaturus patagonicus* Koslowsky 1898, and revalidation and redescription of *Phymaturus spurcus* Barbour 1921. *Journal of Herpetology* 39: 533–540.
- Lobo, F., Espinoza, R.E. & Quinteros, S. 2010. A critical review and systematic discussion of recent classification proposals for liolaemid lizards. *Zootaxa* 2549: 1–30.
- Mayr, E. 1942. Systematics and the origin of species. Columbia University Press, New York, New York.
- Núñez, H., Veloso, A., Espejo, P., Veloso, C., Cortes, A. & Araya, S. 2010. Nuevas especies de *Phymaturus* (Grupo «*palluma*») para la zona cordillerana central de Chile (Reptilia, Sauria, Liolaemidae). *Boletín del Museo Nacional de Historia Natural, Chile* 59: 41–74.
- Robertson, J.M. & Rosenblum, E.B. 2009. Rapid evolution of social signal coloration in White Sands lizards. *Biological Journal of the Linnean Society* 98: 243–255.
- Scolaro, J. & Cei, J.M. (2003). Una excepcional nueva especie de *Phymaturus* de la precordillera de Chubut, Argentina (Liolaemidae, Iguania, Lacertilia, Reptilia). *Facena* 19: 107–112.
- Scolaro, J.A. & Ibarzüengoytia, N.R. 2007. A new species of *Phymaturus* from rocky outcrops in the central steppe of Rio Negro province, Patagonia Argentina (Reptilia: Iguania: Liolaemidae). *Zootaxa* 1524: 47–55.
- Scolaro, J.A. & Ibarzüengoytia, N.R. 2008. A new fragment for the understanding of the puzzling evolutive process of the *Phymaturus* genus: a new species of the *patagonicus* group from Patagonia, Argentina (Reptilia: Iguania: Liolaemidae). *Zootaxa* 1936: 38–50.
- Scolaro, J.A., Ibarzüengoytia, N.R. & Pincheira-Donoso, D. 2008. When starvation challenges the tradition of niche conservatism: on a new species of the saxicolous genus *Phymaturus* from Patagonia Argentina with pseudoarbooreal foraging behaviour (Iguania, Liolaemidae). *Zootaxa* 1786: 48–60.
- Sinervo, B. & Lively, C.M. 1996. The rock-scissors-paper game and the evolution of alternative male strategies. *Nature* 340: 240–246

### Appendix 1

#### List of specimens examined

- Phymaturus «agilis»* (*P. spectabilis*): FML 23503–23505, 23508–09. On Ruta Prov. 6, approximately 27 km S of intersection with Ruta Prov. 23, Río Negro, Argentina (41°25'43.25"S, 69°45'24"W; 924 m). MCN 1212–13. On Ruta Prov. 6, 28 km S of Ingeniero Jacobacci, Río Negro, Argentina.
- Phymaturus ceii*: MCN 910–918. Argentina, Prov. de Río Negro, Dpto. 25 de Mayo, Ruta Prov. 8, 17 km S de San Antonio del Cuy. MCN 908–909. Ruta Provincial 8. A 17 km S de San Antonio del Cuy. Prov. Río Negro, Argentina. 40°17'13"S, 68°27'32"W.
- Phymaturus excelsus*: MCN 1582 (holotype). Ruta Prov. 6, 1 km NW of Ojo de Agua, Dpto. Ñorquinco, Río Negro, Argentina (41°32'30"S, 69°51'33"W; 1141 m). MCN 1386, 1388 (paratypes). Ojo de Agua, Ruta Prov. 6, Dpto. Ñorquinco, Río Negro, Argentina. MCN 1587–88. No data. MCN 1385, 1387. Ojo de Agua, Ruta Prov. 6, Dpto. Ñorquinco, Río Negro, Argentina. MCN 1590. Ruta Prov. 6, 1 km NW de Ojo de Agua, Dpto. Ñorquinco, Río Negro, Argentina (41°32'30"S, 69°51'33"W; 1141 m).
- Phymaturus spectabilis*: MCN 1203 (holotype). On Ruta Prov. 6, 28 km S of Ingeniero Jacobacci, Río Negro, Argentina. MCN 1204–1211, 1214–1215 (paratypes). Same data as holotype. FML 23502, 23510–23513. On Ruta Prov. 6, approximately 27 km S of intersection with Ruta Prov. 23, Río Negro, Argentina (41°25'43.25"S, 69°45'24"W; 924 m).
- Phymaturus spurcus*: MCZ 14791 (holotype). Huanuluan, Depto. Ñorquinco, Río Negro, Argentina. MCZ 14914–15 (paratypes). Same data as holotype. MCN 1238–40, 1244–49. Cerro frente Estancia Huanuluan, Ruta 23, 22 km W Jacobacci, Depto. Ñorquinco, Río Negro, Argentina. MVZ 188904–07. Along Rimrock, 4 km S and 1 km E Alto del Escorial, Depto. Ñorquinco, Río Negro, Argentina (1100 m).
- Phymaturus tenebrosus*: MCN 1271 (holotype). 20 km S of Cerro Alto, Ruta Nacional 40, Dpto. Pilcaniyeu, Río Negro, Argentina. MCN 1264–70, 1272–73 (paratypes). Same data as holotype. MCN 1591–95, 1597–99. Between Bariloche and Pilcaniyeu, Dpto. Pilcaniyeu, Río Negro, Argentina.

