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A NEW LIZARD OF *PHYMATURUS* (IGUANIA: LIOLAEMIDAE) FROM ARGENTINA

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ABSTRACT: In this study, we describe a new taxon for the genus *Phymaturus* from the Sierra Laguna Blanca, Catamarca Province, Argentina. This area is known to be an isolated part of the Puna region where other endemic species of vertebrates occur. This new species of lizard belongs to the *palluma* group because it exhibits juxtaposed superciliary scales, rugose caudal scales, and typically a fragmented subocular scale. Also, this new *Phymaturus* is assignable, within the *palluma* group, to the northern or Puna clade because it presents the typical “spray” pattern and brown tails in males, which are distinct from the dorsal-reticulated pattern and yellow tails in species of the southern *palluma* group. It differs from its relatives in the Puna clade by having the following combination of characters: scapular spot present (more conspicuous in juveniles and females), yellow color in flank of females, males without enlarged scales on ventral surface of the base of tail, males with dark brown throat, enlarged scales on borders of posterior gular fold inconspicuous, ringed tails in both sexes, incomplete pigmentation over dorsum of neck, diffuse white transverse stripes over dorsum of body in females, absence of vertebral stripe, and in some specimens a divided rostral scale. Finally, we present new characters to be considered in future studies of *Phymaturus* systematics.

Key words: Catamarca, Argentina; Liolaemidae; Morphology; New species; *Phymaturus denotatus* sp. nov.; Puna; Taxonomy

THE LIOLAEMID genus *Phymaturus* is a clade of saxicolous and herbivorous iguanian lizards that has been studied extensively over the last decade and now includes 37 species (Lobo and Quinteros 2005a,b; Lobo and Abdala, 2007; Scolaro and Ibargiengoytía, 2007, 2008; Scolaro and Tappari, 2009; Lobo et al. 2010a,b; Núñez et al., 2010; Scolaro and Pincheira-Donoso, 2010; Avila et al., 2011). This is a genus of South American lizards that inhabits the arid western region of Argentina and the adjacent Andean region of Chile, between 26°S and 45°30'S latitude (i.e., between the Patagonian Chubut province and the Catamarca province in northern Argentina). *Phymaturus* is characterized by a wide, flat head and body, prominent fat-filled lateral nuchal skin folds, and a tail that has regular whorls of spinose scales (Etheridge, 1995).

Etheridge (1995) recognized 10 species in two groups, the *patagonicus* and *palluma* groups. The former contained *Phymaturus patagonicus* Koslowsky (1898) and five species originally described as subspecies of *P. patagonicus*: *P. indistinctus* Cei and Castro

(1973), *P. nevadoi* Cei and Roig (1975), *P. payuniae* Cei and Castro (1973), *P. somuncurensis* Cei and Castro (1973), and *P. zapalensis* Cei and Castro (1973). The *palluma* group included *P. mallimacci* Cei (1980), *P. palluma* (Molina, 1782), *P. punae* Cei et al. (1983), and *P. antofagastensis* Pereyra (1985). Subsequently, Scolaro and Cei (2003) described *P. calcogaster* from the precordillera of Chubut (later emended to the eastern region of the Chubut province by Scolaro et al., 2005). Cei and Videla (2003) described *P. verdugo* and Pincheira-Donoso (2004) described *P. vociferator*, both members of the *palluma* group. In a comprehensive taxonomic revision and phylogenetic study, Lobo and Quinteros (2005a) described four new species: *P. dorsimaculatus* in the *palluma* group and *P. excelsus*, *P. spectabilis*, and *P. tenebrosus* all in the *patagonicus* group. After that, Pincheira-Donoso et al. (2008) claimed that *P. dorsimaculatus* is a synonym of *P. vociferator*. Lobo and Quinteros (2005b) redescribed *P. patagonicus* and revalidated *P. spurcus* Barbour (1921), which was synonymized to *P. patagonicus* by Burt and Burt (1931). Recently, Scolaro and Ibarguengoytía (2007, 2008) described

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two new species, *P. ceii* and *P. manuela*e, in the *patagonicus* group from the Rio Negro province in the northern part of Patagonia. Lobo and Abdala (2007) studied populations that inhabit a pair of ancient volcanic tablelands located in the area that biogeographers call “Payunia” (Roig-Juñent et al., 2006) in the southern and central Mendoza province in Argentina, and described *P. roigororum* in the *palluma* group. More recently, Scolaro et al. (2008) described *P. agilis*, which lives syntopically with *P. spectabilis* (Lobo and Quinteros, 2005a). Corbalán et al. (2009) found a population in Laguna Diamante in the Mendoza province that differs from the other species that were known in this region (*P. verdugo*, *P. palluma*, and *P. roigororum*), and named it *P. gynechlonus*. Scolaro and Tappari (2009) described *P. desuetus* in the *patagonicus* group, and Scolaro and Pincheira-Donoso (2010) described two additional species from Chubut, *P. castillensis* and *P. videlai*. Lobo et al. (2010a) described four new species—*P. laurenti*, *P. querque*, *P. etheridgei*, and *P. felixi*—and Núñez et al. (2010) described another four new species from Chile, *P. pahuanense*, *P. alicahuense*, *P. darwini*, and *P. maulense*. Recently, Avila et al. (2011) described two new species of the *patagonicus* group, *P. sitesi* and *P. delheyi*.

In contrast to the exponential growth in the number of described species of *Liolaemus* in recent decades (see Etheridge and Espinoza, 2000), *Phymaturus* had not been exhaustively revisited between the works of Etheridge (1995) and Lobo and Quinteros (2005a). As we noted above, since the study of Lobo and Quinteros (2005a) many isolated populations have been described (Lobo et al., 2010a; Avila et al., 2011). Both the taxonomy and phylogeny of *Phymaturus* still need further study, and more new species are likely to be discovered. The main purpose of this study is to provide a formal description of a new species from a specific area of the Puna region in the Catamarca province of Argentina, as well as new information about several populations of *Phymaturus* in northern Argentina that are currently under study.

MATERIALS AND METHODS

We examined 220 specimens of *Phymaturus* belonging to nine species and nine

populations of the *palluma* group, including 21 specimens of the type series of the new species described herein (see Appendix I). We took digital photographs of live specimens in the field, and measured specimens to the nearest 0.02 mm using digital calipers, and examined most of the characters under a stereo microscope. Most characters described in the diagnoses and descriptions followed standard descriptions published in Smith (1946), Laurent (1984, 1986), Cei (1986, 1993), Etheridge (1995), and Lobo and Quinteros (2005a). We recorded sites of collection using a global positioning system receiver, with coordinates based on the WGS84 datum. All of the specimens that we collected in the summer of 2010 were fixed using 10% formalin and stored in 70% ethanol. We entered all collection data into the databases of the Museo de Ciencias Naturales, Universidad Nacional de Salta, Argentina (MCN) and the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN). We also extracted tissue samples of the new species for karyotype and DNA studies (MCN 3159–61).

SPECIES DESCRIPTION

Phymaturus denotatus sp. nov. (Fig. 1A,B; Table 1)

Holotype.—MACN 40512 (ex-MCN 3184). Adult female from Laguna Blanca, 26°34'09"S 66°56'40"W, 3440 m elevation, Belén, Catamarca Province, Argentina. Collected 13 March 2010 by L. Fernández, F. Lobo, S. Nenda, and D. Slodki (Fig. 1A,B).

Paratypes.—Nine females, three males, and eight juveniles. Same data as for holotype: MACN 40513 (ex-MCN 3175 male); MACN 40514 (ex-MCN 3185 female); MACN 40515 (ex-MCN 3182 female); MACN 40516 (ex-MCN 3180 female); MACN 40517 (ex-MCN 3160 female); MCN 3159, 3176 (males); MCN 3161, 3170, 3181, 3183, 3186 (females); MCN 3177–79, 3187–89, (juveniles); MACN 40373–40374 (two juveniles). Laguna Blanca, 26°34'40"S 66°58'58"W, 3800 m, Belén, Catamarca Province, Argentina. Collected 12 November 2009 by S. Barriosuevo, B. Blotto, and S. Nenda.

Diagnosis.—The genus *Phymaturus* is divided in the *palluma* and *patagonicus* groups

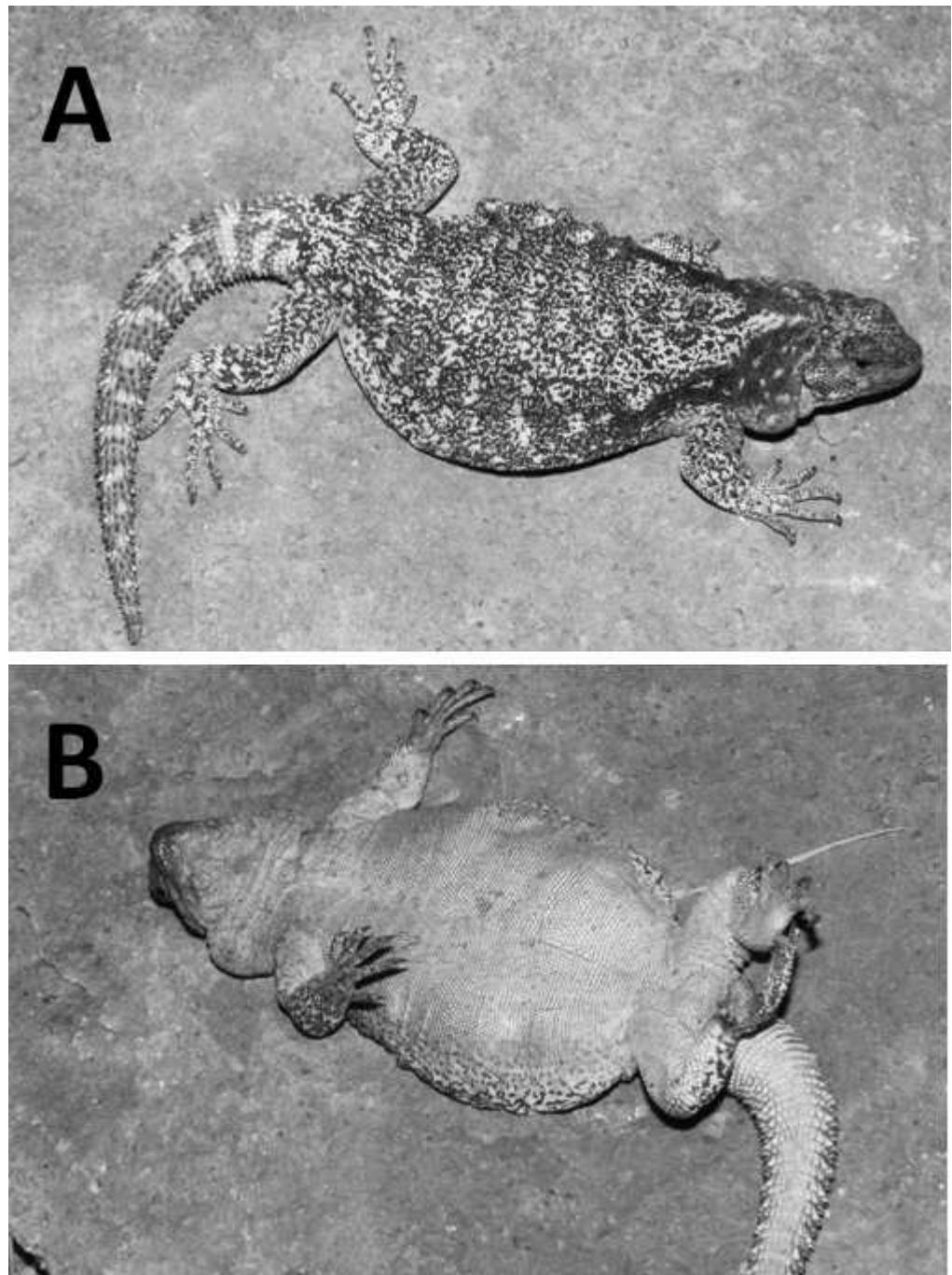


FIG. 1.—(A) Dorsal view of *Phymaturus denotatus* sp. nov. (holotype, MACN-He 40512). (B) Ventral view of the same specimen. Snout–vent length: 94.4 mm. Photo: S. Nenda.

TABLE 1.—Taxonomic distribution of 16 morphological characters among species of the Puna clade of *Phymaturus*. BCF: bronze color in females; DPB: dorsal pattern of body; ESC: enlarged scales in the center of chest; ESF: enlarged scales in the border of antehumeral fold; EST: enlarged scales in ventral surface of the base of tail in males; FCF: flank color in females; MON: melanism over dorsum of neck; PCC: Preocular–canthal scales contact; POC: Preocular same size or larger than canthal; ROS: rostral scale; SCS: scapular spot; TPF: dorsal pattern of tail in females; TPM: dorsal pattern of tail in males; TSC: tarsal scales; TWS: transverse white stripe; VST: Vertebral stripe.

| | MON | EST | TSC | TPM | TPF | DPB | ESF |
|---------------------------|---------------------|---------|-----------------|-------------|-------------|------------|---------|
| <i>P. antofagastensis</i> | incomplete | absent | strongly keeled | none/ringed | ringed | aggregated | present |
| Agua Negra | complete | present | strongly keeled | none | none | spray | absent |
| Caspiso | complete/incomplete | absent | strongly keeled | none/ringed | none/ringed | aggregated | absent |
| S. La Invernada | incomplete | absent | strongly keeled | ringed | ringed | spray | present |
| Fiambalá | ? | absent | strongly keeled | ? | ringed | spray | present |
| Gualcamayo | complete | present | slightly | none | ? | spray | absent |
| <i>P. laurenti</i> | incomplete | present | slightly | none/ringed | ringed | spray | present |
| <i>P. mallimaccii</i> | complete | absent | strongly keeled | ringed | ringed | spray | absent |
| <i>P. punae</i> | incomplete | absent | strongly keeled | ringed | ringed | spray | absent |
| Laguna Brava | incomplete | absent | slightly | none | ringed | spray | present |
| <i>P. denotatus</i> | incomplete | absent | strongly keeled | ringed | ringed | spray | present |

*Part of population exhibiting this character.

**One subadult male with scapular spot.

(Etheridge, 1995). *Phymaturus denotatus* belongs to the *palluma* group because it has short juxtaposed superciliaries, rugose dorsal scales on tail, typically a fragmented subocular scale, and undifferentiated chin shields. Members of the *patagonicus* group have flat and imbricated superciliaries, smooth dorsal scales on the tail, typically an unfragmented subocular scale, and differentiated chin shields. Within the *palluma* group, *P. denotatus* lacks the reticulated dorsal pattern that is typical of species in the southern *palluma* group, instead having a “spray” pattern consisting of dispersed small dark brown spots that are characteristic of the Puna clade (Lobo and Quinteros, 2005a). *Phymaturus denotatus* females have small white spots dispersed over the dorsum and sides of their necks (Fig. 2), a condition unknown in all other species of *Phymaturus*.

The species most similar to *P. denotatus* phenotypically is *P. laurenti*. *Phymaturus denotatus* has a scapular spot (Fig. 2) that is more conspicuous in females and juveniles (absent in *P. laurenti*), and lacks enlarged scales on the posterior margin of the gular fold (present in *P. laurenti*; Fig. 3A,B). Males of *P. denotatus* lack enlarged scales on the ventral surface of the base of the tail (present in *P. laurenti*; Fig. 3C,D), have a dark brown throat (black in *P. laurenti*) and an abdominal region that is homogeneously yellow (being less strongly colored in the posterior half in *P.*

laurenti). In females of *P. denotatus*, the flank color is yellow (orange in *P. laurenti*, with color recorded in the same season).

Phymaturus denotatus differs from *P. antofagastensis* in the following characters: presence of scapular spot (absent in *P. antofagastensis*), spray pattern (thick condensed pattern in *P. antofagastensis*), preocular and canthal scales in contact and of the same size (separated and with preocular larger than canthal in *P. antofagastensis*). *Phymaturus denotatus* differs from *P. punae* in the following characters: more scales around midbody ($\bar{X} = 209.6$, SD = 13.2) ($\bar{X} = 184.5$, SD = 11.8 in *P. punae*) female flank color present (absent in *P. punae*), vertebral gray stripe absent (present in *P. punae*), and scapular spot present (absent in *P. punae*; Fig. 2). *Phymaturus denotatus* differs from *P. mallimaccii* in the following characters: dark pigmentation on dorsum of neck forms incomplete V-shape (complete in *P. mallimaccii*; Fig. 2), more scales around midbody ($\bar{X} = 209.6$, SD = 13.2) ($\bar{X} = 191.4$, SD = 10.7 in *P. mallimaccii*) female flank color yellow (orange in *P. mallimaccii*), vertebral stripe absent (light gray dorsal stripe present in *P. mallimaccii*).

Description of holotype.—Female. Snout–vent length (SVL) 94.4 mm. Head length 15.5 mm. Head width 15.9 mm. Head height (at parietal) 10.1 mm. Axilla–groin distance 51.7 mm (54.8% of SVL). Tail length (complete, not regenerated) 79.6 mm (84% of

TABLE 1.—Extended

| ESC | FCF | VST | TWS | BCF | SCS | POC | PCC | ROS* |
|---------|--------|------------------|----------------|---------|----------------|-----------|----------------------|---------|
| present | yellow | absent | present | absent | absent | larger | separated | divided |
| absent | absent | dark gray/absent | absent | present | absent | larger | separated | unique |
| absent | absent | light gray | absent | present | absent** | larger | contacting | divided |
| absent | absent | absent | absent | absent | present | larger | contacting | divided |
| present | yellow | absent | present | absent | present | same size | contacting | unique |
| absent | ? | light gray | absent | absent | absent | larger | contacting | unique |
| present | orange | absent | present/absent | absent | absent | same size | separated | unique |
| absent | orange | light gray | present | absent | present | ? | ? | unique |
| absent | absent | light gray | absent | absent | absent | larger | separated | divided |
| absent | yellow | absent | absent | absent | absent/present | larger | contacting/separated | divided |
| absent | yellow | absent | present* | absent | present | same size | contacting | divided |

SVL). Body moderately wide; trunk width: 42.1 mm (44.6% of SVL). Twenty-two smooth dorsal head scales counted along the middorsal line of the head between the occiput and the rostral scale. From one to two scale organs in each postrostral. Nasal bordered by nine scales, not in contact with rostral. Canthal separated from nasal by two scales. Flat loreal

region, becoming slightly concave toward the supralabials. Eleven enlarged supralabials. Ten enlarged infralabials. Oval auditory meatus with six pointed, but not enlarged, projecting scales on the anterior margin. Auricular scale absent. Eleven convex, juxtaposed temporals. Lower temporal region with conical scales. Rostral divided into two scales.

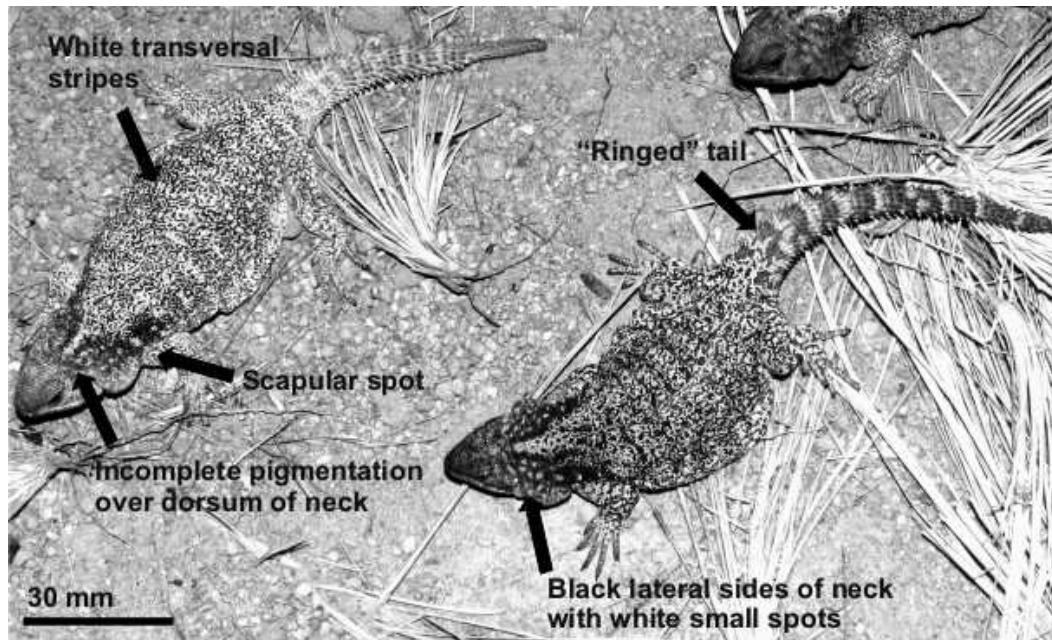


FIG. 2.—Typical dorsal pattern shown in two females of *Phymaturus denotatus* sp. nov. showing a scapular spot, lateral neck pattern with small white dispersed spots, incomplete dorsal neck melanism in the midline, transverse stripes, and ringed tails. Photo: S. Nenda.

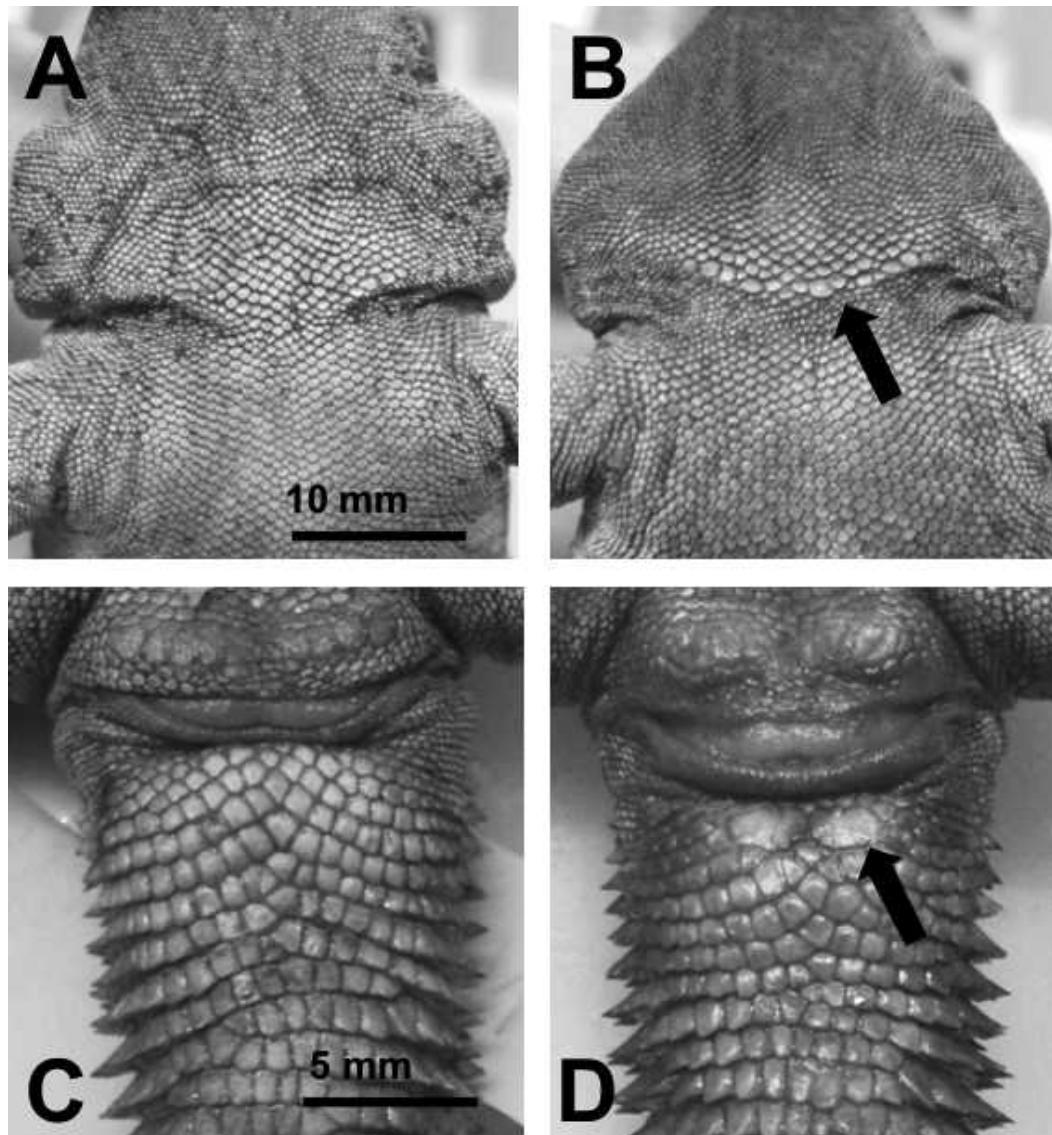


FIG. 3.—(A) Ventral view of throat and chest in *Phymaturus denotatus* sp. nov. (MCN 3176, male). (B) Same view in *Phymaturus laurenti* (MCN 2855-male) showing the enlarged scales on the anterior margin of the gular fold. (C) Ventral view of the cloacal region in *Phymaturus denotatus* sp. nov. (MCN 3176-male). (D) Same view in *Phymaturus laurenti* (MCN 2855-male) showing two enlarged scales posterior to the cloacal opening.

Mental elongated, in contact with six scales. Interparietal bordered by 10 scales. Frontal region without an azygous scale divided into several scales. Inconspicuous supraorbital semi-circles. Slightly enlarged posterior supraoculars. Eleven nonimbricate superciliaries. Subocular fragmented into two scales, separated from supralabials by two rows of lorilabials. Sixteen scales forming the lower row of lorilabials, none

contacting subocular. Preocular separated from lorilabial row by four scales. Throat with round, flat, juxtaposed scales. Eighty gulars between auditory meatus. Well developed lateral nuchal folds, with granular scales over longitudinal fold. Antehumeral pocket well developed. Eighty-three scales between auditory meatus and shoulder. From ventral view, anterior and posterior gular folds present; margin of the

posterior one without enlarged scales. Dorsal scales of trunk round, smooth, juxtaposed: 220 around midbody. Thirty-three dorsal scales along midline of the trunk in a length equivalent to head length. Middorsal scales not enlarged in comparison to those on flanks. Ventral scales slightly larger than dorsals. Ventral scales between mental and cloacal opening: 203. No traces of precloacal pores. Smooth brachial and antebrachial scales with rounded posterior margins. Flat, round, smooth supracarpals. Subdigital lamellae of fingers with three keels. Number of subdigital lamellae of fingers: I, 9; II, 13; III, 17; IV, 22; V, 12. Moderately long, thin, point-ended claws. Convex and imbricate supradigital lamellae. Infracarpals and infratarsals rhomboidal. Posterior infratarsal scales and subdigital lamellae of the fifth toe not strongly keeled. Smooth supracarpals and supratarsals, with round posterior margins. Subdigital lamellae of toes: I, 11; II, 15; III, 21; IV, 25; V, 19.

Color of holotype in life.—Light brown dorsal background speckled with small, dark brown markings, dispersed irregularly all over dorsum of trunk. Six diffuse, white, transverse stripes on both sides of the trunk. Darkened supravittal region with black and dark brown scales. A conspicuous scapular spot with a few yellow scales in the center. This dark area is continuous over dorsum of neck, which shows from five to six small white spots. Incomplete V-shaped dorsal pigmentation over neck with black margins. Brown spotted dorsum of head with dispersed darker scales. Flanks with same pattern as dorsum, almost reaching ventral surfaces of body. A bright yellow color covers flanks, axilla, and chest. Dominant light gray color on ventral surfaces, slightly darker in the throat without forming any kind of pattern. Dorsum of tail with a ringed pattern, ventral surface without pattern. Forelimbs and hindlimbs have color similar to dorsum of body, with dark brown color forming a thin reticulation over dorsum of thighs.

Variation.—Squamation and measurements based in 14 individuals, 3 adult males and 11 adult females (including the holotype). SVL 68.6–112.1 mm ($\bar{X} = 99.2$, SD = 10.6). Head length 15.1–19.4% of SVL ($\bar{X} = 16.9\%$, SD =

1.1). Tail length 0.81–1.05 times SVL ($\bar{X} = 0.89$, SD = 0.08). Scales around midbody 183–230 ($\bar{X} = 209.6$, SD = 13.2). Dorsal head scales 19–26 ($\bar{X} = 22.6$, SD = 1.9). Ventrals 169–210 ($\bar{X} = 191$, SD = 10.4). Scales in contact with interparietal 7–10 ($\bar{X} = 8.6$, SD = 1.0). Scales of neck along longitudinal fold from posterior border of auditory meatus to shoulder 53–79 ($\bar{X} = 70.1$, SD = 7.8). Gulars 65–98 ($\bar{X} = 80.1$, SD = 10.1). Scales between rostral and frontal 8–12 ($\bar{X} = 10.1$, SD = 1.0). Most females are light brown, with their “spray” pattern formed by very thin, irregularly distributed dark brown to black spots. This dark spotting forms irregularly shaped paravertebral spots in two individuals, and slender, dark, transverse stripes in two other individuals. Scapular region darkened or completely black, with one or two conspicuous white scapular spots; sides of neck black with a few thin white spots (Fig. 2). Dorsum of neck always without dark background pigmentation, in most individuals marked with two dark parallel lines. There is no melanism over dorsum or sides of head. Chest and belly light gray to white, almost immaculate, but with small, inconspicuous, spread-out light brown spots. Sides of belly and chest with a bright yellow color that extends into the axillary area. Tails ringed (with alternating bands of lighter and darker scales; Fig. 2).

Males with extensive yellow color over dorsal surfaces of trunk, neck, arms, and proximal halves of thighs. Light brown head, sides of neck, and scapular region; scapular spots almost inconspicuous or absent. One unique male had dorsal medial area of neck marked by two dark lines, as in females. Uniformly brown throat, chest, belly, flanks, cloacal region; ventral surfaces of forelimbs and hind limbs bright yellow. Tails ringed or without a specific pattern, light brown. Juveniles show same pattern as adult females. The holotype (female) and one juvenile have white transverse stripes, as commonly found in females of *P. antofagastensis*, a few *P. laurenti*, and an unnamed population in the Sierra de Fiambalá.

Etymology.—The specific epithet *denotatus* means “marked out,” alluding to a scapular spot (conspicuous particularly in newborns, juveniles, and females; less noticeable in males).

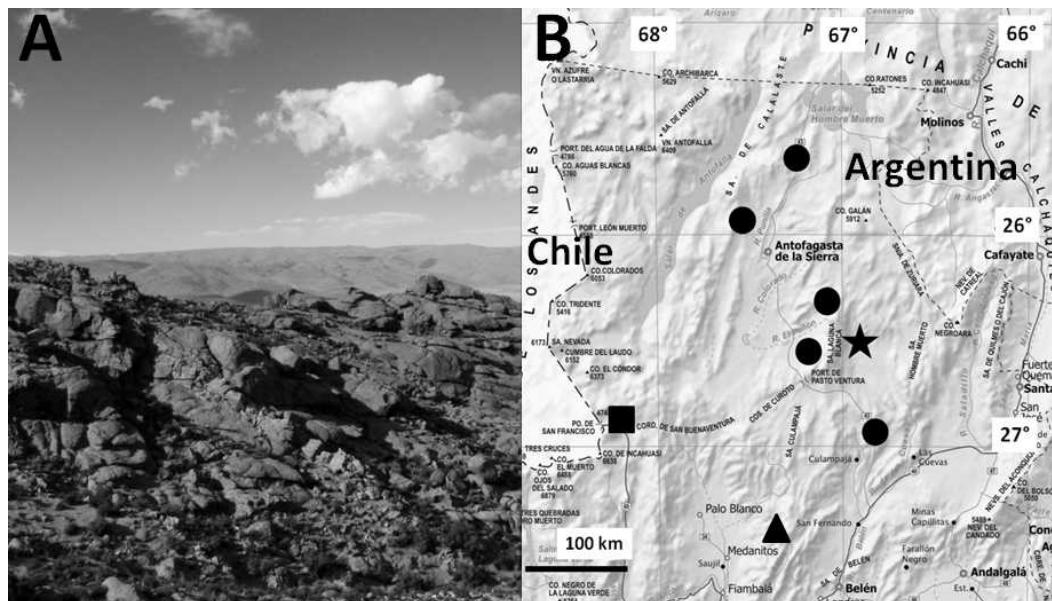


FIG. 4.—(A) Habitat of *Phymaturus denotatus* sp. nov. on the eastern side of Sierra Laguna Blanca. (B) Map with the distribution of the four *Phymaturus* species in the Catamarca province, Puna region of Argentina. Black circles: *Phymaturus laurenti* from Randolfo, El Peñón, and Calalaste; black square: *Phymaturus antofagastensis*; black star: *Phymaturus denotatus*; black triangle: *Phymaturus* sp. from Sierra de Fiambalá.

Habitat and distribution.—Only known from the type locality (Fig. 4A,B). Individuals of this new species inhabit rock outcrops on the eastern slopes of the Sierra Laguna Blanca, above elevations of 3400 m. This population was discovered on the slopes of canyons that cut through granitic rock a few kilometers (4–5 km) west of the village of Laguna Blanca. Vegetation in the area where the new species was found is characterized by a typical combination of plants of prepuna and steppe (Martínez Carretero, 1995). This area is known to be an isolated part of the vast highland known as the Puna. Other species of *Liolaemus* that inhabit the area are *L. umbrifer* (Espinoza and Lobo, 2003) and an unnamed population of the *Liolaemus ornatus* group (Abdala, 2007). Other endemic species of vertebrates have been described from this area (e.g., three species of the catfish genus *Trichomycterus*; Fernández and Vari, 2000, 2002) or are suspected to be endemic (e.g., an unstudied population of the aquatic frog *Telmatobius*). *Phymaturus denotatus* is isolated from populations of *P. laurenti*, the geographically most proximate congener, by the

Sierra de Laguna Blanca range, which reaches elevations of almost 6000 m (Fig. 4B).

DISCUSSION

Lizards of the northern or Puna clade within the *palluma* group (Lobo and Quinteros, 2005a) have at least two characters that differentiate them from the southern species of the group (Neuquén and Mendoza provinces of Argentina, and Regiones Metropolitana, VI, and VII of Chile): a spotted pattern formed by thin and dispersed brown spots (“spray pattern”) that never form a reticulated pattern, and males without yellow or orange tails. Females of several species in this group exhibit a flank color of yellow or orange. Females of all species in this clade show ringed tails, with the exception of Agua Negra population. This fact can be considered an additional apomorphy, although it is important to note that this character is also found in at least three southern species of the *palluma* group (*P. dorsimaculatus*, *P. roigorum*, and *P. querque*). The absence of ringed tails in both sexes of Agua Negra and Gualcamayo populations (but only one male known) may be the result of a secondary loss.



FIG. 5.—Female of *Phymaturus laurenti* from El Peñón exhibiting salt around its nasal area. This nasal salt excretion was found also in specimens of other two species of the Puna clade. Photo: S. Valdecantos.

A character that may be unique among the Liolaemidae is the excretion of salt through the nares in individuals of *P. laurenti* (Fig. 5); *Phymaturus* sp. from the Sierra La Invernada, San Juan; and *P. denotatus*. A nasal gland for salt secretion is common in herbivorous desert lizards, in particular those whose only water sources are the plants that they eat (Gabe and Saint Girons, 1971, 1976). The regulation of plasma electrolyte concentration in iguanid lizards of North America has been shown in *Sauromalus obesus* (Norris and Dawson, 1964; Templeton, 1964; Shuttleworth et al., 1987) and *Dipsosaurus dorsalis* (Templeton, 1966; Shoemaker et al., 1972; Hazard, 2001). Although the literature on salt excretion in reptiles is quite extensive and beyond the scope of this study, we report here the potential existence of a nasal salt gland in *Phymaturus*, and note the need for future studies on its structure, function, and significance in the life history of these lizards.

The species described here exhibits variation in the same set of characters that vary in other members of the group. In Table 1, we

summarize the main characters in this group of species that were used to develop a key to the species by Lobo et al. (2010a). Until a formal cladistic analysis of all these taxa is performed, we are not able to propose a reliable hypothesis of relationships. However, a few observations can be made: within the Puna clade, species inhabiting the Puna of the Catamarca province (*P. antofagastensis*, *P. denotatus*, and *P. sp* of Fiambalá) and *P. mallimaccii* (Sierra de Famatina, La Rioja Province) are the northernmost species and seem to be more closely related to one another; they exhibit flank color in females, the absence of a vertebral stripe, and the presence of white transverse slender stripes over the trunk, as well as the presence of enlarged scales in the anterior margin of antehumeral fold (absent in *P. mallimaccii* and present in the Sierra La Invernada population). Another hypothesis that should be also tested by a cladistic analysis is the potential relationship among species of the marginal eastern Puna sierras (Sierra de la Invernada, San Juan Province; Sierra de

Famatina, La Rioja Province; Sierra de Fiambalá, Catamarca Province; Sierra de Laguna Blanca, Catamarca Province: *P. denotatus*), but its support currently seems to be weak; all of these species show a scapular spot, and no other feature appears to be unique for these species. The scapular spot is also present in other non-Puna *Phymaturus*, which suggests that it represents a plesiomorphy. All of the populations mentioned above are currently being described in separate studies.

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APPENDIX I

Justification for considering *P. gynecholomus* as a synonym of *P. palluma* was given in Lobo et al. (2010a); use of the name “*adrianae*” was considered in Lobo and Abdala (2007) and Lobo et al. (2010a).

Phymaturus antofagastensis.—SDSU 1991. Argentina: Catamarca Prov.: Dpto Antofagasta: Road from Agua de los Pocitos to Paso San Francisco. Collected by E. Terán and O. Pagaburo. MCN 309–310. Collected by C. Abdala, R. Espinoza, F. Lobo, and M. I. Martínez Oliver. MCN 1429–1436. Argentina: Catamarca Prov.: Dpto. Antofagasta: 130 km from Fiambalá on route to Paso San Francisco. Collected by J. C. Acosta.

Phymaturus dorsimaculatus.—Holotype: MCN 1573. Argentina: Neuquén Prov.: Dpto. Norquin: Copahue. 37°49' S 71°06' W. Collected by C. Abdala, L. Avila, F. Lobo, and M. Morando. Paratypes: MCN 1571–72, 1574–75. Same data as for holotype. MCN 1568–69. Argentina: Neuquén Prov.: Dpto. Norquin: Termas de Copahue. 37°49'14"S 71°05'12"W; elevation 2050 m. MCN 1566–67. Argentina: Neuquén Prov.: Dpto. Norquin: Copahue. MVZ 232503. Argentina: Neuquén Prov.: Dpto. Norquin: Termas de Copahue; elevation 2050 m. Collected by M. I. Christie. MCN 1566–67. Argentina: Neuquén Prov.: Dpto. Norquin: Copahue. Collected by D. Pérez.

Phymaturus laurenti.—Holotype: MCN 2855. Argentina: Catamarca Prov.: Dpto. Antofagasta de la Sierra: Approximately 10 km S of El Peñón. 26°39'40.6"S

67°13'26.3"W; elevation 3815 m; rock outcrops 300 m east of provincial road 43. Collected by F. Lobo and S. Valdecantos. Paratypes: MCN 2838–2854, 2856–2862. Same data as for holotype. MCN 313–317, 320, 322. Argentina: Catamarca Prov.: Dpto. Antofagasta de la Sierra: Cuesta de Randolph. Collected by C. Abdala, R. Espinoza, F. Lobo, and I. Martínez Oliver. MCN 306–307, 323–327. Argentina: Catamarca Prov.: Dpto. Antofagasta de la Sierra: Cuesta de Calalaste. Collected by C. Abdala, R. Espinoza, F. Lobo, and I. Martínez Oliver. MCN 1919–21. Argentina: Catamarca Prov.: Dpto. Antofagasta de la Sierra: North Antofagasta de la Sierra. 25°38'06.00"S 67°13'53.65"W. Collected by B. Casimiro, R. Espinoza, F. Lobo, and S. Quinteros. MCN 3133. Argentina: Catamarca Prov.: Dpto. Antofagasta de la Sierra: East El Peñon, road to Cerro Galán. 26°20'28.88"S 67°08'01.51"W. Collected by R. Chocobar.

Phymaturus mallimaccii.—REE CSUN 183, 489–491. Argentina: La Rioja Prov.: Dpto. Famatina: Sierra de Famatina: Cueva de Pérez. Collected by R. Espinoza and F. Cruz. MCN 920 and MCN 1483–84 (CS). Argentina: La Rioja Prov.: Dpto. Famatina: Road to La Mejicana. 28°54'43"S 67°42'47"W; elevation 3430 m. Collected by M. Morando, L. Avila, and L. Belver.

Phymaturus palluma (=*Phymaturus gynechlonus* according to Lobo et al. 2010a).—MCN 3130–31. Argentina: Mendoza Prov.: Dpto. Tunuyán: Road to Portillo Argentino (Cordón del Portillo) 33°36'53.8"S 69°29'16.7"W. Collected by C. Abdala and V. Juárez. MVZ 126991. Argentina: Mendoza Prov.: Dpto. Malargüe: Valle Hermoso. Collected by R. Sage. 35°20'S 70°15'W. MVZ 126992–94. Argentina: Mendoza Prov.: Dpto. Malargüe: Lago de la Niña Encantada. 6 km E from Llos Molles. 33°18'S 69°83"W; elevation 2000 m. Collected by R. Sage. MVZ 126995. Argentina: Mendoza Prov.: Dpto. Malargüe: northern extreme of Valle Hermoso. 35°11'S 70°10'W. Collected by R. Sage. MVZ 126996–126999. Argentina: Mendoza Prov.: Dpto. Tupungato: Quebrada de Chupasangral, 4 km NW of Cerro Chupasangral. 33°21'S 69°51'W; elevation 2800 m. Collected by R. Sage. MVZ 127023. Argentina: Mendoza Prov.: Dpto. Las Heras: 2 km E of Los Hornillos. 32°51'S 68°99'W. Collected by R. Sage. MVZ 127025–27. Argentina: Mendoza Prov.: Dpto. Malargüe: 2 km E of Agua Botada. 35°62'S 69°95'W. Collected by R. Sage.

Phymaturus punae.—Holotype: MCZ 19217. Argentina: San Juan Prov.: Dpto. Iglesia: 7 km SE of refuge from the Reserva Provincial San Guillermo, near the river San Guillermo; elevation 3500 m. Collected by R. E. Etheridge, J. M. Cei, and F. Videla. Paratypes: MCZ 163982, 163984, 163986–88. Same data as holotype. SDSU 1978–79. Argentina: San Juan Prov.: Dpto. Iglesia: Llano de los Hoyos: Reserva Provincial San Guillermo. Collected by R. E. Etheridge. MCN 3114–3126. Argentina: San Juan Prov.: Dpto. Iglesia: Reserva San Guillermo. Collected by J. C. Acosta.

Phymaturus querque.—Holotype: FML 21556. Argentina: Neuquén Prov.: Dpto. Zapala: Laguna Blanca: Parque Nacional Laguna Blanca. Collected by C. Abdala, S. Quinteros, G. Scrocchi, and J. C. Stazzonelli. Paratypes: FML 21211. Same data as for holotype. IBA 793. Four specimens. Argentina: Neuquén Prov.: Dpto. Zapala: Laguna Blanca. Collected by J. M. Cei, L. Cei, and R. Ferreira. MACN 34514 (five specimens). Argentina:

Neuquén Prov.: Dpto. Zapala: Laguna Blanca. Collected by G. Gnida. MVZ 232504–05. Neuquén Prov.: Dpto. Zapala: Laguna Blanca: Parque Nacional Laguna Blanca: Puesto Control, 3.5 km N of the hill. 23°80'S 56°83'W; elevation 1800 m. Collected by M. I. Christie. SDSU 1971. Argentina: Neuquén Prov.: Dpto. Zapala: Laguna Blanca: south shore of Laguna Blanca. Collected by R. E. Etheridge.

Phymaturus roigorum.—Holotype: MCN 1963. Argentina: Mendoza Prov. Dpto. San Rafael: El Nevado: Puesto Rojas, 16 km from Route Provincial 180. Collected by C. Abdala, R. Juárez, and C. Robles. MCN 1962. Same data as for holotype. Paratypes: FML 17705–708. Same data as for holotype. Paratypes: MCN 2096–2103. Argentina: Mendoza Prov.: Dpto. Malargüe: 6 km S of Real del Molle, at the base of Volcán Payún Liso. 36°28'51.1"S 69°22'27.9"W; elevation 2128 m. Collected by C. S. Abdala, R. Juárez, J. P. Juliá, and A. Brunetti. SDSU 1948–51, 1948–56, 1948–62, 1948–64–65. Argentina: Mendoza Prov: Dpto Malargüe: 3 km NW at the base of Volcán Payún Liso. Collected by R. E. Etheridge. SDSU 1972, 1974–75. Argentina: Mendoza Prov.: Dpto. Malargüe: 10 km S at the base of Volcán Payún Liso. Collected by R. E. Etheridge. IADIZA-CH 00091. Argentina: Mendoza Prov: Dpto. Malargüe: at the base of Volcán Payún Liso. Elevation 1800–2000 m. Collected by J. M. Cei and F. Videla. IBA 733 (five specimens). Argentina: Mendoza Prov: Dpto. Malargüe: southwest Volcán Payún Liso. Collected by L. P. Castro.

Phymaturus sp. (*Phymaturus "adrianae*" in Lobo et al., 2010b).—SDSU 1969–1970. Argentina: Mendoza Prov.: Dpto. Las Heras: 20 km NE of Uspallata. Elevation 2500 m. Collected by R. E. Etheridge. SDSU 3387. Argentina: Mendoza Prov.: Dpto. La Heras: 27 km NE of Uspallata. 32°28'52.2"S 69°09'59.2"W; elevation 2768 m. Collected by R. E. Etheridge, R. Espinoza, S. Torres, and E. Pereyra. SDSU 3388. Argentina: Mendoza Prov.: Dpto. La Heras: 27 km NE Uspallata. 32°28'52.2"S 69°09'59.2"W; elevation 2768 m. Collected by R. E. Etheridge, R. Espinoza, and S. Torres. MVZ 145146. Argentina: Mendoza Prov.: Dpto. La Heras: Pampa de Canota, 20 km E and 8 km S of Estancia Uspallata. 32°65'S 69°27'W; elevation 3000 m. Collected by R. Sage. MVZ 180771–74. Argentina: Mendoza Prov.: Dpto. San Carlos: Quebrada Cruz de Piedra. 34°26'S 68°90'W. Collected by R. Sage. MVZ 92902, 92904, 92908. (DS). Argentina: Mendoza Prov.: Dpto. La Heras: Collected by R. Sage. IADI ZA-CH. S/N (two specimens). Argentina: Mendoza Prov. Dpto. San Rafael: Paramillos. IBA 760 (four specimens). Argentina: Mendoza Prov. Dpto. San Rafael: Paramillos. Elevation 2000 m. Collected by L. G. Castro. MCN 2650–53, 2659–62, 2696–2708. Argentina: San Juan Province: Dpto. Sarmiento: El Portezuelo. Collected by R. E. Espinoza, F. Lobo, E. Sanabria, and L. Quiroga.

Phymaturus sp. *Phymaturus cf. palluma* (CH) in Lobo and Quinteros (2005a).—MVZ 199435–38, 230992. Chile: Región VIII (=Región del Biobío): Termas de Chillán Hotel. Collected by J. H. Carothers. MCZ 165456. Chile: Región VIII (=Región del Biobío): Cordillera de Chillán. Collected by G. Moreno. MCZ 169935. Chile. Collected by R. A. Philippi.

Phymaturus sp. *Phymaturus cf. palluma* (EP) in Lobo and Quinteros (2005a).—MNHN 2352, 2460–61. Chile:

Region VII (=Region del Maule): San Clemente: Talca: Baños del Campanario. Elevation 1500 m. Collected by J. C. Torres-Mura. MNHN 3505–09. Chile: Region VII

(=Region del Maule): Curicó: Puesto Militar San Pedro, Pichuante, Cuesta Vergara. 35°10'S 70°36'W. Collected by H. Núñez, and A. Labra. MNHN 1632–33, 1638, 1643. Chile: Region VII (=Region del Maule): Curicó: El Planchón. Collected by M. A. Labra, and H. Núñez.

Phymaturus sp. (Fiambalá of Table 1).—MCN 2122–23, 2125. Argentina: Catamarca Prov.: Dpto. Tinogasta: Puesto la Lagunita. 35–38 km NE of Medanitos. Collected by S. Barriónuevo, J. M. Díaz Gómez, and S. Quinteros.

Phymaturus sp. (Laguna Brava of Table 1).—REE-CSUN 270–271, 504–508. Argentina: La Rioja Prov.: Dpto. Vinchina: Reserva Laguna Brava, Agua Quemada, Puesto Leoncito. Collected by R. Espinoza, and F. Cruz. FML 2925–2, 2925–4, 2925–8 through 2925–11, 2925–13. Argentina: La Rioja Prov.: Dpto. Sarmiento: Puerta Quebrada del Leoncito, road to Laguna Brava, 57 km from Alto Jagüel. Collected by O. Pagaburo and Bracamonte. FML 2926 (three specimens). Argentina: La Rioja Prov.: Dpto. Sarmiento: Alto Jagüel Agua Quemada, road to Laguna Brava. Collected by O. Pagaburo and C. Bracamonte.

Phymaturus sp. (Gualcamayo of Table 1).—MCN 1641–43. Argentina: San Juan Prov.: Dpto. Jáchal: El Peñón, west of Gualcamayo. 29°41'28.9"S 68°48'39.3"W; elevation 2820 m. Collected by C. Abdala, S. Barriónuevo, and M. J. Tulli.

Phymaturus sp. (Casposo of Table 1).—MCN 2808–10, 2812–17, 2820–21. Argentina: San Juan Prov.: Dpto.

Calingasta: 40 km W of Calingasta town. 31°11'21"S 69°42'15.1"W; elevation 3000 m. Collected by A. Laspur and J. C. Acosta.

Phymaturus sp. (Agua Negra of Table 1).—MCN 975. Argentina: San Juan Prov.: Dpto. Iglesia: Paso Agua Negra. 30°23'S 69°34'W; elevation 2900 m. Collected by A. Laspur, E. Sanabria, and L. Quiroga. MCN 969, 973–975, 977, 979, 982, 984, 988, 990–991, 995 and 971–972, 976, 978, 980, 981, 983, 986–987, 989, 992–993. Same data as for MCN 975.

Phymaturus sp. (S. La Invernada of Table 1).—MCN 2657. Argentina: San Juan Prov.: Dpto. Ullum: Sierra La Invernada, behind the field station, Reserva Natural de Uso Múltiple Don Carmelo. 30°55'91"S 69°04'98"W; elevation 3133 m. Collected by R. E. Espinoza, F. Lobo, L. Quiroga, and E. Sanabria. MCN 2655–56, 2665–66, 2669–71, 2673, 2721–35, 2737 (MCN 2656, 2665–66 are skeletons). Same data as for MCN 2657. MCN 2709–20 (MCN 2713 is a skeleton). San Juan Prov.: Dpto. Ullum: Aguada de Pinchagua, Reserva Natural de Uso Múltiple Don Carmelo. 30°58'66"S 69°05'21"W; elevation 3122 m. Collected by R. E. Espinoza, F. Lobo, L. Quiroga, and E. Sanabria.

Phymaturus verdugo.—MCN 1958, 1960–61. Argentina: Mendoza Prov.: Dpto. Malargüe: El Gancho river, 4 km from Las Loicas. Collected by C. Abdala, C. R. Juárez, and C. Robles. MCN 1973–77. Argentina: Mendoza Prov.: Dpto. Malargüe: 12.5 km from Las Loicas to Bardas Blancas, road to El Pehuenche. Collected by C. Abdala, C. R. Juárez, and C. Robles.